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# Phytopathogenic *Dothideomycetes*

Pedro W. Crous, Gerard J.M. Verkley and Johannes Z. Groenewald, editors

CBS-KNAW Fungal Biodiversity Centre,
Utrecht, The Netherlands
An institute of the Royal Netherlands Academy of Arts and Sciences

# Studies in Mycology

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Cover: Top from left to right: Conidia of *Alternaria septospora*, leaf symptoms induced by *Pseudocercospora fijiensis*, and conidia of *Stagonospora paludosa*. Bottom from left to right: Asci of *Stagonospora perfecta*, leaf symptoms induced by *Cercospora coniogrammes*, and conidiophores of a *Cercospora* sp.

# Phytopathogenic *Dothideomycetes*

edited by

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## INTRODUCTION

The present issue of *Studies in Mycology* focuses on plant pathogenic *Dothideomycetes*. The *Dothideomycetes* represents the largest class of *Ascomycota*, with more than 100 families and 19 000 species. Of interest, however, is the fact that this class also contains the most genera of plant pathogenic fungi, many of which are frequently encountered by plant health officers at various ports of entry around the world. These officers are subsequently confronted by the fact that the fungus may be expressing its sexual or asexual morph, or worse, maybe sterile mycelium. Traditionally these mycologists have had a range of books with which they could try to identify these organisms based on the phenotype. In recent years however, most of these taxa have been shown to represent species complexes, with some specific to certain regions or hosts. Integrating asexual and sexual names, dealing with species that are cryptic, and genera that are poly- and paraphyletic, and a general lack of DNA data authentic for these species, is a constant stress to which these mycologists are exposed. Identifications made by these mycologists could result in losses of millions of "dollars" to farmers and producers, while wrongful introductions could again destroy local industries and markets.

The present issue focuses on five main groups of fungi that plant health officers deal with on a weekly, or daily basis, namely *Alternaria, Cercospora*, *Phoma*, *Pseudocercospora*, and *Septoria*.

## DEDICATION: To the plant health officers of the world

This special issue is dedicated to three exceptional colleagues, who dedicated their lives and careers to be plant health officers, striving to enhance trade, but also to protect borders from wrongful incursions. To these colleagues we owe a great deal of thanks for their unselfish dedication and commitment. Without their published works, databases, specimens and cultures, we would not have been able to produce the papers reported in this special issue.

## Gerhard H. Boerema (1925–2008)

Gerhard Boerema accepted a position as mycologist at the Dutch Plant Protection Service (Plantenziektenkundige Dienst, PD) in 1956. Gerhard became head of the Mycology Department in 1959 and fulfilled this position until his early retirement in 1988. The main tasks of the Mycology Department at that time was the diagnosis on symptomatic plant material submitted by inspectors, advisory services, companies, research stations, etc. It covered all fields such as agriculture, horticulture, greenhouse products as well as natural environment. Interesting findings were published annually in the Dutch Tijdschrift over Plantenziekten, continued later as Mededelingen van de Plantenziektenkundige Dienst in Wageningen (Yearbook PD). The diversity of topics is demonstrated in his first reports that included bark canker of apple and pear, caused by *Pezicula corticola* (1959), a new species of *Sclerotinia* as the cause of black leg in tulip (1960), and *Chalaropsis thielavioides* on carrots pre-packed in perforated polythene bags (1960). Another important task was to give internal advice concerning quarantine issues.

Shortly after he became head of the Mycology department, a new disease was found on potatoes, caused by *Phoma foveata*, a quarantine organism at that time in Europe. The taxonomy of phoma-like species on potatoes was confusing, and he started his fundamental study on *Phoma*. A second important problem, *Phoma lingam* on seeds of *Brassicaceae* arose, and studies on many other *Phoma* species associated with plant material followed.

Gerhard described many synonyms of the *Phoma* species after detailed studies of herbarium material. He recognised sections in *Phoma* and published his findings in numerous papers in the period 1960–1988. He became the expert on *Phoma* worldwide. Isolates and herbarium material were weekly received for identification and the extensive correspondence in English, French and German language is still preserved at the Dutch Plant Protection Service.

Gerhard established with his team a culture collection and herbarium at PD, and most of the strains were also deposited at the culture collection of CBS. During his career, *Phoma* was his main topic, but he worked on the nomenclature of many important plant pathogens, published as "Check-list for scientific names of common parasitic fungi" in 12 supplement series in the Netherlands Journal of Plant Pathology.

Gerhard collaborated in a new *Phoma* project started at the PD to provide standardised *in vitro* descriptions of *Phoma* species. He established the morphological genus concept with a classification of *Phoma* in nine sections. In collaboration with his successor Chiel Noordeloos, Hans de Gruyter and Marielle Hamers, "*Contributions towards a monograph of* Phoma" were published in *Persoonia* during the period 1992–2003. These papers formed the base for the "Phoma *Identification Manual*" published in 2004 (CABI Publishing, Wallingford, UK). The cultures deposited at the PD and the CBS, however, laid the foundation for the next phase, which was a phylogenetic study of the sections and species in the *Phoma* complex by two PhD students, Aveskamp and de Gruyter, of which one final paper is published in this issue.

## C.F. (Frank) Hill (1941–2009)

Caleb Francis (Frank) Hill was a mycologist at the Ministry of Agriculture and Forestry (MAF) in Auckland, New Zealand. Frank always had a strong focus on diagnostics, and in the process isolated numerous interesting plant pathogenic fungi. For instance, *Calonectria pseudonaviculata* (= *Cylindrocladium buxicola*), which is now a major quarantine problem on *Buxus* in Europe and the USA, was originally described from material Frank collected in New Zealand in 1998, and sent to CBS for a collaborative publication on *Calonectria*, a pathogen that he frequently intercepted at ports of entry into New Zealand. During his career Frank published descriptions of more than 70 novel taxa, contributed to more than 3 000 pest records in the Ministry of Agriculture and Forestry Plant Pest database, and deposited more than 1 500 specimens and cultures. To address the severe shortage of cultures and lack of DNA data in the cercosporoid complex, the CBS started to purposefully cultivate all cercosporoid fungi encountered. One of the best collectors was Frank Hill, who in his function as plant health diagnostician, encountered many pathogens both indigenous and exotic to New Zealand. Frank collected a great many of the specimens treated in the papers published in this issue (ranging from *Alternaria* to *Phoma*, and cercosporoid). It is interesting to note that the collection dates largely correspond with weekends, which gave us the impression that Frank was always roaming the countryside, botanical gardens and arboretums, looking for interesting diseases. Without Frank's

Gerhard H. Boerema

C.F. (Frank) Hill

Flora G. Pollack

collections, these studies would not have been possible. It is only fitting then, that we also dedicate this work to him for his keen eye, and never ending enthusiasm for the subject. Frank may have passed on, but his collection of plant pathogenic fungal cultures will forever remain a living legacy for future generations to study.

## Flora G. Pollack (1919–1997)

As the United States' only plant quarantine mycologist for 12 years, Flora Pollack had the privilege of examining specimens of interesting and unusual fungi from around the world that had been intercepted at various ports of entry. Flora began working for the Bureau of Plant Quarantine in the early 1940's when it was located in the U.S. Department of Agriculture building in downtown Washington. She resigned from her job to raise her children, and 15 years later went to work again as a mycologist at the American Type Culture Collection (ATCC), then in Rockville, MD. During her six and one-half years of employment there, she improved a technique for the preservation of cultures in their original condition as received by ATCC that is still widely used for this purpose. When the opportunity arose, she returned to the U.S. Department of Agriculture in 1967. During her professional years she published many scientific articles in *Mycologia* and other journals often authored in collaboration with others. She described numerous new species in a wide range of fungal groups but had a particular fondness for coelomycetous fungi, a group that still evades accurate classification. At least one unusual species, aptly named *Monosporascus cannonballus* was described by Pollack with F.A. Uecker. Originally encountered as a harmless oddity associated with the roots of cantaloupes, many years later this fungus gained prominence as a virulent pathogen limiting the production of melons in dry areas of the world.

While working for APHIS, Flora was associated with the Mycology Laboratory, now Systematic Mycology & Microbiology Laboratory. As the plant quarantine mycologist she encountered on a daily basis fungi from around the world, many of which she deposited in the U.S. National Fungus Collections. A search of herbarium database yields over 5 000 specimens identified by Flora that remain an important resource for the identification of plant quarantine fungi as well as fodder for taxonomists tackling these difficult species. Following the tradition established by her predecessor, Alice Watson, she maintained a card file of important literature for the identification of plant-associated fungi. This file became the basis for a publication (Rossman AY, Palm ME, Spielman LJ. 1987. *A Literature Guide for the Identification of Plant Pathogenic Fungi*. St. Paul, Minnesota: American Phytopathological Society), and later the database of literature available on the Internet <http://nt.ars-grin.gov/fungaldatabases/literature/litframe.cfm>. After retiring in 1979, Flora was asked to publish a project she had started in her spare time while working in Beltsville. She spent many hours pulling together her "*Annotated Compilation of* Cercospora *Names".* Published in 1987, it served as the most comprehensive reference on this genus, and provided the basis for a later update by Crous & Braun (2003) on "Mycosphaerella *and its anamorphs: 1. Names published in* Cercospora *and* Passalora" (CBS Biodiversity Series 1, CBS-KNAW Fungal Biodiversity Centre, Utrecht, Netherlands), which in turn set the stage for the molecular phylogenetic papers published on this complex in this issue of *Studies in Mycology*.

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# Redisposition of phoma-like anamorphs in *Pleosporales*

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**Abstract:** The anamorphic genus *Phoma* was subdivided into nine sections based on morphological characters, and included teleomorphs in *Didymella*, *Leptosphaeria*, *Pleospora* and *Mycosphaerella,* suggesting the polyphyly of the genus. Recent molecular, phylogenetic studies led to the conclusion that *Phoma* should be restricted to *Didymellaceae*. The present study focuses on the taxonomy of excluded *Phoma* species, currently classified in *Phoma* sections *Plenodomus*, *Heterospora* and *Pilosa*. Species of *Leptosphaeria* and *Phoma* section *Plenodomus* are reclassified in *Plenodomus*, *Subplenodomus* gen. nov., *Leptosphaeria* and *Paraleptosphaeria* gen. nov., based on the phylogeny determined by analysis of sequence data of the large subunit 28S nrDNA (LSU) and Internal Transcribed Spacer regions 1 & 2 and 5.8S nrDNA (ITS). *Phoma heteromorphospora*, type species of *Phoma* section *Heterospora*, and its allied species *Phoma dimorphospora,* are transferred to the genus *Heterospora* stat. nov. The *Phoma acuta* complex (teleomorph *Leptosphaeria doliolum*), is revised based on a multilocus sequence analysis of the LSU, ITS, small subunit 18S nrDNA (SSU), β-tubulin (TUB), and chitin synthase 1 (CHS-1) regions. Species of *Phoma* section *Pilosa* and allied *Ascochyta* species were determined to belong to *Pleosporaceae* based on analysis of actin (ACT) sequence data. Anamorphs that are similar morphologically to *Phoma* and described in *Ascochyta, Asteromella, Coniothyrium, Plectophomella*, *Pleurophoma* and *Pyrenochaeta* are included in this study. Phoma-like species, which grouped outside the *Pleosporineae* based on a LSU sequence analysis, are transferred to the genera *Aposphaeria*, *Paraconiothyrium* and *Westerdykella*. The genera *Medicopsis* gen. nov. and *Nigrograna* gen. nov. are introduced to accommodate the medically important species formerly known as *Pyrenochaeta romeroi* and *Pyrenochaeta mackinnonii*, respectively.

**Key words:** coelomycetes, *Coniothyriaceae, Cucurbitariaceae, Leptosphaeriaceae, Melanommataceae,* molecular phylogeny, *Montagnulaceae, Phaeosphaeriaceae, Pleosporaceae, Sporormiaceae,* taxonomy, *Trematosphaeriaceae*.

**Taxonomic novelties: New genera:** ***Medicopsis*** Gruyter, Verkley & Crous, ***Nigrograna*** Gruyter, Verkley & Crous, ***Paraleptosphaeria*** Gruyter, Verkley & Crous, ***Subplenodomus*** Gruyter, Verkley & Crous. **New species:** ***Aposphaeria*** *corallinolutea* Gruyter, Aveskamp & Verkley, ***Paraconiothyrium*** *maculicutis* Verkley & Gruyter. **New combinations:** ***Coniothyrium*** *carteri* (Gruyter & Boerema) Verkley & Gruyter, *C. dolichi* (Mohanty) Verkley & Gruyter, *C. glycines* (R.B. Stewart) Verkley & Gruyter, *C. multiporum* (V.H. Pawar, P.N. Mathur & Thirum.) Verkley & Gruyter, *C. telephii* (Allesch.) Verkley & Gruyter, ***Heterospora*** (Boerema, Gruyter & Noordel.) Gruyter, Verkley & Crous, *H. chenopodii* (Westend.) Gruyter, Aveskamp & Verkley, *H. dimorphospora* (Speg.) Gruyter, Aveskamp & Verkley, ***Leptosphaeria*** *errabunda* (Desm.) Gruyter, Aveskamp & Verkley, *L. etheridgei* (L.J. Hutchison & Y. Hirats.) Gruyter, Aveskamp & Verkley, *L. macrocapsa* (Trail) Gruyter, Aveskamp & Verkley, *L. pedicularis* (Fuckel) Gruyter, Aveskamp & Verkley, *L. rubefaciens* (Togliani) Gruyter, Aveskamp & Verkley, *L. sclerotioides* (Sacc.) Gruyter, Aveskamp & Verkley, *L. sydowii* (Boerema, Kesteren & Loer.) Gruyter, Aveskamp & Verkley, *L. veronicae* (Hollós) Gruyter, Aveskamp & Verkley, ***Medicopsis*** *romeroi* (Borelli) Gruyter, Verkley & Crous, ***Nigrograna*** *mackinnonii* (Borelli) Gruyter, Verkley & Crous, ***Paraconiothyrium*** *flavescens* (Gruyter, Noordel. & Boerema) Verkley & Gruyter, *Paracon. fuckelii* (Sacc.) Verkley & Gruyter, *Paracon. fusco-maculans* (Sacc.) Verkley & Gruyter, *Paracon. lini* (Pass.) Verkley & Gruyter, *Paracon. tiliae* (F. Rudolphi) Verkley & Gruyter, ***Paraleptosphaeria*** *dryadis* (Johanson) Gruyter, Aveskamp & Verkley, *Paralept. macrospora* (Thüm.) Gruyter, Aveskamp & Verkley, *Paralept. nitschkei* (Rehm ex G. Winter) Gruyter, Aveskamp & Verkley, *Paralept. orobanches* (Schweinitz : Fr.) Gruyter, Aveskamp & Verkley, *Paralept. praetermissa* (P. Karst.) Gruyter, Aveskamp & Verkley, ***Plenodomus*** *agnitus* (Desm.) Gruyter, Aveskamp & Verkley, *Plen. biglobosus* (Shoemaker & H. Brun) Gruyter, Aveskamp & Verkley, *Plen. chrysanthemi* (Zachos, Constantinou & Panag.) Gruyter, Aveskamp & Verkley, *Plen. collinsoniae* (Dearn. & House) Gruyter, Aveskamp & Verkley, *Plen. confertus* (Niessl ex Sacc.) Gruyter, Aveskamp & Verkley, *Plen. congestus* (M.T. Lucas) Gruyter, Aveskamp & Verkley, *Plen. enteroleucus* (Sacc.) Gruyter, Aveskamp & Verkley, *Plen. fallaciosus* (Berl.) Gruyter, Aveskamp & Verkley, *Plen. hendersoniae* (Fuckel) Gruyter, Aveskamp & Verkley, *Plen. influorescens* (Boerema & Loer.) Gruyter, Aveskamp & Verkley, *Plen. libanotidis* (Fuckel) Gruyter, Aveskamp & Verkley, *Plen. lindquistii* (Frezzi) Gruyter, Aveskamp & Verkley, *Plen. lupini* (Ellis & Everh.) Gruyter, Aveskamp & Verkley, *Plen. pimpinellae* (Lowen & Sivan.) Gruyter, Aveskamp & Verkley, *Plen. tracheiphilus* (Petri) Gruyter, Aveskamp & Verkley, *Plen. visci* (Moesz) Gruyter, Aveskamp & Verkley, ***Pleospora*** *fallens* (Sacc.) Gruyter & Verkley, *Pleo. flavigena* (Constantinou & Aa) Gruyter & Verkley, *Pleo. incompta* (Sacc. & Martelli) Gruyter & Verkley, ***Pyrenochaetopsis pratorum*** (P.R. Johnst. & Boerema) Gruyter, Aveskamp & Verkley, ***Subplenodomus*** *apiicola* (Kleb.) Gruyter, Aveskamp & Verkley, *Subplen. drobnjacensis* (Bubák) Gruyter, Aveskamp & Verkley, *Subplen. valerianae* (Henn.) Gruyter, Aveskamp & Verkley, *Subplen. violicola* (P. Syd.) Gruyter, Aveskamp & Verkley, ***Westerdykella*** *capitulum* (V.H. Pawar, P.N. Mathur & Thirum.) de Gruyter, Aveskamp & Verkley, *W. minutispora* (P.N. Mathur ex Gruyter & Noordel.) Gruyter, Aveskamp & Verkley. **New names**: ***Pleospora*** *angustis* Gruyter & Verkley, *Pleospora halimiones* Gruyter & Verkley.

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## INTRODUCTION

The anamorphic genus *Phoma* includes many important plant pathogens. The taxonomy of *Phoma* has been studied intensively in the Netherlands for more than 40 years resulting in the development of a generic concept as an outline for identification of *Phoma* species (Boerema 1997). In this concept species of the genus *Phoma* are classified based on their morphological characters into nine sections: *Phoma, Heterospora, Macrospora, Paraphoma, Peyronellaea, Phyllostictoides, Pilosa, Plenodomus* and *Sclerophomella* (Boerema 1997). The species placed in each of the sections were systematically described culminating in the publication of the "*Phoma* Identification Manual" (Boerema *et al.* 2004), which contained the descriptions of 223 specific and infra-specific taxa of *Phoma*, and more than 1000 synonyms in other coelomycetous genera. The classification of the *Phoma* species in



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sections based on morphology is artificial (Boerema *et al.* 2004), and several species can be classified in more than one section as they reveal multiple "section-specific" characters.

A large, well-studied *Phoma* culture collection that includes more than 1100 strains of *Phoma* resulted from the extensive morphological studies conducted on *Phoma* in The Netherlands. That culture collection is the basis of an intensive molecular phylogenetic study of the genus *Phoma*, which commenced in 2006. Molecular studies of species of *Phoma* prior to the onset of this project concentrated on the development of molecular detection methods for specific, important plant pathogenic *Phoma* species, such as *Ph. macdonaldii, Ph. tracheiphila, Stagonosporopsis cucurbitacearum* (as *Ph. cucurbitacearum*) and *Boeremia foveata* (as *Ph. foveata*) (Aveskamp *et al.* 2008). The phylogeny of the type species of the nine *Phoma* sections and morphologically similar coelomycetes was determined utilising the sequence data of the large subunit 28S nrDNA (LSU) and the small subunit 18S nrDNA (SSU) regions (de Gruyter *et al*. 2009). Results of that study demonstrated that the type species of the nine *Phoma* sections all grouped in *Pleosporales*. The type species of five *Phoma* sections, *Phoma, Phyllostictoides, Sclerophomella, Macrospora* and *Peyronellaea* and similar genera, grouped in a distinct clade in *Didymellaceae.* The type species of the remaining four *Phoma* sections, *Heterospora*, *Paraphoma*, *Pilosa* and *Plenodomus,* clustered in several clades outside *Didymellaceae* based on the LSU and SSU sequence analysis leading to the conclusion that these species should be excluded from *Phoma* (de Gruyter *et al.* 2009, Aveskamp *et al.* 2010).

The molecular phylogeny of the *Phoma* species in *Didymellaceae* was determined in a subsequent study (Aveskamp *et al.* 2010) and, as the phylogenetic placement of the sectional type species already suggested, included species mainly from sections *Phoma, Phyllostictoides, Sclerophomella, Macrospora* and *Peyronellaea*. The molecular phylogeny of 11 *Phoma* species classified in *Phoma* section *Paraphoma* based on their setose pycnidia was investigated using LSU and SSU sequences (de Gruyter *et al.* 2010) and this section was highly polyphyletic, with species clustering mainly in *Phaeosphaeriaceae* and *Cucurbitariaceae*.

The purpose of the present study was to clarify the molecular phylogeny of the *Phoma* species currently classified in sections *Plenodomus* and *Pilosa,* along with *Phoma* species which were determined to be distantly related to the generic type species *Ph. herbarum* in previous molecular studies. Additionally, phoma-like isolates of coelomycetes currently classified in *Ascochyta* and *Coniothyrium* and clustering outside the *Didymellaceae* (de Gruyter *et al.* 2009, Aveskamp *et al.* 2010) are included in this study along with a number of phoma-like species that do not belong to *Pleosporineae*.

In the present study, the initial focus was to determine the molecular phylogeny of *Phoma betae* (teleom. *Pleospora betae*) and *Ph. lingam* (teleom. *Leptosphaeria maculans*), type species of the *Phoma* sections *Pilosa* and *Plenodomus*, respectively, at the generic rank based on the sequence data of the LSU and the SSU regions. In a subsequent study, the sequence data of both the LSU and the ITS regions were used for a revised classification of the *Phoma* species currently classified in *Phoma* section *Plenodomus*. Only a limited number of the species currently classified in this section have a confirmed *Leptosphaeria* teleomorph.

The *Phoma acuta* species complex was subject of a more detailed study. The teleomorph of *Ph. acuta* is *Leptosphaeria doliolum*, type species of the genus *Leptosphaeria*. A multilocus analysis of sequence data of the SSU, LSU, ITS, β-tubulin (TUB), and chitin synthase 1 (CHS-1) regions was performed. The phylogeny of *Phoma* species of section *Pilosa*, with a *Pleospora* teleomorph (*Pleosporaceae*) was studied utilising actin (ACT) sequence data.

Phoma-like species currently attributed to the genera *Aposphaeria*, *Asteromella, Coniothyrium, Phoma*, *Plenodomus, Pleurophoma* and *Pyrenochaeta,* which could not be classified in the *Pleosporineae* based on their molecular phylogeny, were included in a LSU sequence analysis. All *Phoma* taxa that are unrelated to *Didymellaceae* and treated in this paper are redisposed to other genera.

A further aim of this study was to establish a single nomenclature for well-resolved anamorph–teleomorph relationships as discussed by Hawksworth *et al*. (2011). In cases where one anamorph-teleomorph generic relation is involved in a monophyletic lineage, one generic name was chosen based on priority and the other named teleomorph or anamorph state is treated as a synonym. Similar approaches towards single nomenclature have been employed in *Botryosphaeriales* (Crous *et al*. 2006, 2009a, b, Phillips *et al.* 2008), *Pleosporales* (Aveskamp *et al.* 2010), and *Hypocreales* (Lombard *et al*. 2010a–c, Chaverri *et al*. 2011, Gräfenhan *et al*. 2011, Schroers *et al*. 2011).

## MATERIALS AND METHODS

### Isolate selection, culture studies and DNA extraction

The generic abbreviations used in this study are: *Ascochyta* (*A.*), *Coniothyrium* (*C.*), *Heterospora* (*H.*), *Leptosphaeria* (*L.*), *Paraconiothyrium* (*Paracon.*), *Paraleptosphaeria* (*Paralep.*), *Phoma* (*Ph.*), *Plenodomus* (*Plen.*), *Pleospora* (*Pleo.*), *Pyrenochaeta* (*Py.*), *Subplenodomus* (*Subplen.*) and *Westerdykella* (*W.*). The isolates included in this study were obtained from the culture collections of the Centraalbureau voor Schimmelcultures, Utrecht, The Netherlands (CBS-KNAW) and the Dutch National Plant Protection Organization, Wageningen, The Netherlands (PD) (Table 1). The freeze-dried isolates were revived overnight in 2 mL malt/peptone (50 % / 50 %) liquid medium and subsequently transferred and maintained on oatmeal agar (OA) (Crous *et al*. 2009c). The isolates, which were stored at -196 °C, were directly transferred to OA. Cultures growing on OA and malt extract agar (MEA) (Crous *et al*. 2009c) were studied morphologically as described in detail by Boerema *et al.* (2004). The genomic DNA isolation was performed using the Ultraclean Microbial DNA isolation kit (Mo Bio Laboratories, Carlsbad, California) according to the instructions of the manufacturer. All DNA extracts were diluted 10 × in milliQ water and stored at 4 °C before use.

### PCR and sequencing

For nucleotide sequence comparisons, partial regions of SSU, LSU and ITS, as well as part of the ACT, TUB and CHS-1 genes were amplified. The SSU region was amplified with the primers NS1 and NS4 (White *et al*. 1990) and the LSU region was amplified with the primers LR0R (Rehner & Samuels 1994) and LR7 (Vilgalys & Hester 1990). The ITS and TUB regions were amplified as described by Aveskamp *et al*. (2009) using the primer pair V9G (de Hoog & Gerrits van den Ende 1998) and ITS4 (White *et al*. 1990) for the ITS and the BT2Fw and BT4Rd primer pair (Woudenberg *et al.* 2009) for the TUB locus. The ACT and CHS-1 regions were amplified using the primer pairs ACT-512F / ACT-783R and CHS-354R / CHS-79F (Carbone & Kohn 1999). The amplification reactions were performed and analysed as described by de Gruyter *et al*. (2009).

Sequencing of the PCR amplicons was conducted using the same primer combinations, although the primer LR5 (Vilgalys & Hester 1990) was used as an additional internal sequencing primer for LSU. The sequence products were purified using Sephadex columns (Sephadex G-50 Superfine, Amersham Biosciences, Roosendaal, Netherlands) and analysed with an ABI Prism 3730XL Sequencer (Applied Biosystems) according to the manufacturer's instructions. Consensus sequences were computed from both forward and reverse sequences using the Bionumerics v. 4.61 software package (Applied Maths, Sint-Martens-Latem, Belgium) and were lodged with GenBank. All sequences of reference isolates included in this study were obtained from GenBank (Table 1).

## Phylogenetic analyses

To determine the phylogeny of *Phoma betae* and *Ph. lingam* at rank, the SSU and LSU sequence data of two isolates were aligned with the sequences of 46 reference isolates in the *Pleosporales* that were obtained from GenBank (Table 1), 14 of which were classified in the *Pleosporaceae* or *Leptosphaeriaceae*. The phylogeny of *Phoma* section *Plenodomus* was determined with the combined data set of LSU and ITS sequences of 87 isolates, including 53 isolates currently classified in *Leptosphaeria* and *Phoma* section *Plenodomus*. *Phoma apiicola*, *Ph. dimorphospora, Ph. heteromorphospora*, *Ph. lupini*, *Ph. valerianae, Ph. vasinfecta* and *Ph. violicola* classified in *Phoma* sections *Phoma* or *Heterospora* (Boerema *et al.* 2004) grouped in previous molecular phylogenetic studies outside *Didymellaceae* (de Gruyter *et al.* 2009, Aveskamp *et al*. 2010), and are therefore treated here.

In the study of the *Leptosphaeria doliolum* complex, that includes the subspecies of *Ph. acuta*, *viz.* subsp. *acuta*, *errabunda* and also *Ph. acuta* subsp. *acuta* f. sp. *phlogis*, a phylogenetic analysis was performed utilising the ITS, ACT, TUB, CHS-1 sequences of 18 isolates. *Phoma macrocapsa*, *Ph. sydowii* and *Ph. veronicicola* being closely related to this species complex were included.

The species concept of phoma-like anamorphs in *Pleosporaceae* was determined by alignments of the ACT sequences of 15 isolates and five reference isolates. *Phoma fallens*, *Ph. glaucispora* and *Ph. flavigena* were also included. These species were originally classified in *Phoma* sect. *Phoma* (de Gruyter & Noordeloos 1992, de Gruyter *et al.* 1998). However, a molecular phylogenetic study demonstrated that these species grouped in a clade representing *Leptosphaeriaceae* and *Pleosporaceae* (Aveskamp *et al.* 2010). Sequence data were compared with those of isolates currently classified in the genera *Phoma*, *Ascochyta* and *Coniothyrium*, as well as isolates of *Leptosphaeria clavata* and the generic type species *Pleospora herbarum*. *Phoma incompta* is the only species classified in *Phoma* section *Sclerophomella,* which proved to be unrelated to *Didymellaceae* (Aveskamp *et al.* 2010).

The phoma-like species that could not be attributed to *Pleosporineae* (Zhang *et al*. 2009) were studied with the LSU sequences of 40 isolates, including 20 reference isolates representing the anamorph genera *Beverwykella, Neottiosporina, Paraconiothyrium,* as well as the teleomorph genera *Byssothecium, Falciformispora, Herpotrichia, Melanomma, Paraphaeosphaeria, Pleomassaria, Preussia, Roussoella, Splanchnonema*, *Sporormiella, Thyridaria, Trematosphaeria* and *Westerdykella.* Four *Phoma* species were included which are currently described in *Phoma* section *Phoma, viz. Ph. capitulum*, *Ph. flavescens*, *Ph. lini*, and *Ph. minutispora* (de Gruyter & Noordeloos 1992, de Gruyter *et al.* 1993). In addition, the human pathogens *Pyrenochaeta romeroi and Py. mackinnonii*, which could not be classified in a recent study dealing with phoma-like species with setose pycnidia (de Gruyter *et al.* 2010), were included.

The multiple alignments were automatically calculated by the BioNumerics software package, but manual adjustments for improvement were made by eye where necessary. For multilocus alignments, the phylogenetic analyses were done for each dataset individually, and where similar tree topologies were obtained, an analysis was performed on the combined alignment of all the gene regions in the multilocus alignment. Neighbour-Joining (NJ) distance analyses were conducted using PAUP (Phylogenetic Analysis Using Parsimony) v. 4.0b10 (Swofford 2003) with the uncorrected "p", Jukes-Cantor and Kimura 2-parameter substitution models. The robustness of the trees obtained was evaluated by 1000 bootstrap replications. A Bayesian analysis was conducted with MrBayes v. 3.1.2 (Huelsenbeck & Ronqvist 2001) in two parallel runs, using the default settings but with the following adjustments: the GTR model (trees 1–3, 5) with gamma-distributed rate and the HKY+ γ-model (tree 4) were selected for the partitions using the Findmodel freeware (http://hcv.lanl.gov/content/hcv-db/findmodel/findmodel.html), and a MCMC heated chain was set with a "temperature" value of 0.05. The number of generations and sample frequencies were set at 5 million and 10 (trees 3–5) or 100 (trees 1, 2) respectively and the run was automatically stopped as soon as the average standard deviation of split frequencies reached below 0.01. The resulting trees were printed with TreeView v. 1.6.6 (Page 1996) and alignments and trees were deposited into TreeBASE (www.treebase.org).

# RESULTS

The data for the aligned sequence matrices for the trees obtained in the different studies are provided below. In the case that alignments of multiple loci are involved, the topologies of the obtained trees for each locus were compared by eye to confirm that the overall tree topology of the individual datasets were similar to each other and to that of the tree obtained from the combined alignment. The NJ analyses with the three substitution models showed similar tree topologies and were congruent to those obtained in the Bayesian analyses. The results of the molecular phylogenetic analyses are supplied below; the summarised additional ecology and distribution data of the taxa involved were adopted from Boerema *et al.* (2004), where the references to original literature are provided.

## Phylogeny of *Phoma lingam* and *Ph. betae*, the type species of *Phoma* sections *Plenodomus* and *Pilosa* (*Pleosporineae*)

The aligned sequence matrix obtained for the SSU and LSU regions had a total length of 2 671 nucleotide characters, 1 367 and 1 304 respectively. In the alignment, an insertion in the SSU at the positions 478–832 was observed for the cultures CBS 216.75, CBS 165.78, CBS 138.96, CBS 331.37 and CBS 674.75. This insertion was excluded from further phylogenetic analyses. The combined dataset used in the analyses included 48 taxa and contained 2 316 characters with 101 and 213 unique site patterns for SSU and LSU,

**Table 1.** Isolates used in this study and their GenBank accession numbers. Name changes and newly generated sequences are indicated in bold.

| Species name, final identification | Former identification | CBS no. | Other no. | ITS | SSU | LSU | ACT | TUB | CHS-1 | Host, substrate | Country |
|---|---|---|---|---|---|---|---|---|---|---|---|
| ***Aposphaeria corallinolutea* sp. nov.** | *Pleurophoma* sp. | CBS 131286 | PD 83/367 | | | **JF740329** | | | | *Kerria japonica* (*Rosaceae*) | Netherlands |
| | *Pleurophoma* sp. | CBS 131287 | PD 83/831 | | | **JF740330** | | | | *Fraxinus excelsior* (*Oleaceae*) | Netherlands |
| *Aposphaeria populina* | | CBS 543.70 | | | | EU754130 | | | | *Populus canadensis* (*Salicaceae*) | Netherlands |
| | *Pyrenochaeta* sp. | CBS 350.82 | | | | **JF740265** | | | | *Picea abies* (*Pinaceae*) | Germany |
| | *Pleurophoma* sp. | CBS 130330 | PD 84/221 | | | **JF740328** | | | | *Cornus mas* (*Cornaceae*) | Netherlands |
| *Beverwykella pulmonaria* | | CBS 283.53 | ATCC 32983, IFO 6800 | | | GU301804 | | | | *Fagus sylvatica* (*Fagaceae*) | Netherlands |
| *Byssothecium circinans* | | CBS 675.92 | ATCC 52767, ATCC 52678, IMI 266220 | | | AY016357 | | | | *Medicago sativa* (*Fabaceae*) | USA |
| *Chaetodiplodia* sp. | *Chaetodiplodia* sp. | CBS 453.68 | | | | | **JF740115** | | | *Halimione portulacoides* (*Chenopodiaceae*) | Netherlands |
| *Chaetosphaeronema hispidulum* | | CBS 216.75 | | | EU754045 | EU754144 | | | | *Anthyllis vulneraria* (*Fabaceae*) | Germany |
| *Cochliobolus sativus* | | | DAOM 226212 | | DQ677995 | DQ678045 | | | | (*Poaceae*) | Unknown |
| ***Coniothyrium carteri* comb. nov.** | *Phoma carteri* | CBS 101633 | PD 84/74 | **JF740180** | | GQ387593 | | | | *Quercus* sp. *Fagaceae*) | Netherlands |
| | *Phoma carteri* | CBS 105.91 | | **JF740181** | GQ387533 | GQ387594 | | | | *Quercus robur* (*Fagaceae*) | Germany |
| ***Coniothyrium dolichi* comb. nov.** | *Pyrenochaeta dolichi* | CBS 124143 | IMI 217261 | **JF740182** | | GQ387610 | | | | *Dolichos biforus* (*Fabaceae*) | India |
| | *Pyrenochaeta dolichi* | CBS 124140 | IMI 217262 | **JF740183** | GQ387550 | GQ387611 | | | | *Dolichos biforus* (*Fabaceae*) | India |
| ***Coniothyrium glycines* comb. nov.** | *Phoma glycinicola* | CBS 124455 | IMI 294986 | **JF740184** | GQ387536 | GQ387597 | | | | *Glycine max* (*Fabaceae*) | Zambia |
| | *Phoma glycinicola* | CBS 124141 | PG-1 | **JF740185** | | GQ387598 | | | | *Glycine max* (*Fabaceae*) | Zimbabwe |
| ***Coniothyrium multiporum* comb. nov.** | *Phoma multipora* | CBS 501.91 | PD 83/888 | **JF740186** | | GU238109 | | | | Unknown | Egypt |
| | *Phoma multipora* | CBS 353.65 | IMI 113689, ATCC 16207, HACC 164 | **JF740187** | | **JF740268** | | | | Saline soil | India |
| *Coniothyrium palmarum* | | CBS 400.71 | | AY720708 | EU754054 | EU754153 | | | | *Chamaerops humilis* (*Arecaceae*) | Italy |
| ***Coniothyrium telephii* comb. nov.** | *Phoma septicidalis* | CBS 188.71 | | **JF740188** | GQ387538 | GQ387599 | | | | Air | Finland |
| | *Phoma septicidalis* | CBS 856.97 | | **JF740189** | GQ387539 | GQ387600 | | | | Mineral wool | Finland |
| | *Phoma septicidalis* | CBS 101636 | PD 86/1186 | **JF740190** | GQ387540 | GQ387601 | | | | *Glycine max* (*Fabaceae*) | Zimbabwe |
| *Cucurbitaria berberidis*, anam. *Pyrenochaeta berberidis* | | CBS 363.93 | | **JF740191** | GQ387545 | GQ387606 | | | | *Berberis vulgaris* (*Berberidaceae*) | Netherlands |
| *Didymella exigua* | | CBS 183.55 | | | EU754056 | EU754155 | | | | *Rumex arifolius* (*Polygonaceae*) | France |

**Table 1.** (Continued).

| Species name, final identification | Former identification | CBS no. | Other no. | ITS | SSU | LSU | ACT | TUB | CHS-1 | Host, substrate | Country |
|---|---|---|---|---|---|---|---|---|---|---|---|
| *Didymella lycopersici*, anam. *Boeremia lycopersici* | | CBS 378.67 | | | **JF740097** | GU237950 | | | | *Lycopersicon esculentum* (*Solanaceae*) | Netherlands |
| *Falcisormispora lignatilis* | | | BCC 21118 | | | GU371827 | | | | *Elaeis guineensis* (*Arecaceae*) | Thailand |
| *Herpotrichia juniperi* | | CBS 200.31 | | | | DQ678080 | | | | *Juniperus nana* (*Cupressaceae*) | Switzerland |
| ***Heterospora chenopodii* comb. nov.** | *Phoma heteromorphospora* | CBS 448.68 | | FJ427023 | EU754088 | EU754187 | | | | *Chenopodium album* (*Chenopodiaceae*) | Netherlands |
| | *Phoma heteromorphospora* | CBS 115.96 | PD 94/1576 | **JF740227** | | EU754188 | | | | *Chenopodium album* (*Chenopodiaceae*) | Netherlands |
| ***Heterospora dimorphospora* comb. nov.** | *Phoma dimorphospora* | CBS 345.78 | PD 76/1015 | **JF740203** | | GU238069 | | | | *Chenopodium quinoa* (*Chenopodiaceae*) | Peru |
| | *Phoma dimorphospora* | CBS 165.78 | PD 77/884 | **JF740204** | **JF740098** | **JF740281** | | | | *Chenopodium quinoa* (*Chenopodiaceae*) | Peru |
| *Leptosphaeria conoidea* | *Leptosphaeria conoidea*, anam. *Phoma doliolum* | CBS 616.75 | ATCC 32813, IMI 199777, PD 74/56 | **JF740201** | **JF740099** | **JF740279** | | | | *Lunaria annua* (*Brassicaceae*) | Netherlands |
| | *Leptosphaeria conoidea*, anam. *Phoma doliolum* | CBS 125977 | PD 82/888 | **JF740202** | | **JF740280** | | | | *Senecio* sp. (*Asteraceae*) | Netherlands |
| *Leptosphaeria doliolum* | *Leptosphaeria doliolum* subsp. *doliolum* var. *doliolum*, anam. *Phoma acuta* subsp. *acuta* | CBS 505.75 | PD 75/141 | **JF740205** | GQ387515 | GQ387576 | **JF740126** | **JF740144** | **JF740162** | *Urtica dioica* (*Urticaceae*) | Netherlands |
| | *Leptosphaeria doliolum* subsp. *errabunda*, anam. *Phoma acuta* subsp. *errabunda* | CBS 541.66 | PD 66/221 | **JF740206** | | **JF740284** | **JF740127** | **JF740145** | **JF740163** | *Rudbeckia* sp. (*Asteraceae*) | Netherlands |
| | *Phoma acuta* subsp. *acuta* f.sp. *phloxis* | CBS 155.94 | PD 77/80 | **JF740207** | | **JF740282** | **JF740128** | **JF740146** | **JF740164** | *Phlox paniculata* (*Polemoniaceae*) | Netherlands |
| | *Phoma acuta* subsp. *acuta* f.sp. *phloxis* | CBS 125979 | PD 78/37 | **JF740208** | | **JF740283** | **JF740129** | **JF740147** | **JF740165** | *Phlox paniculata* (*Polemoniaceae*) | Netherlands |
| | *Leptosphaeria doliolum* subsp. *doliolum* var. *doliolum*, anam. *Phoma acuta* subsp. *acuta* | CBS 504.75 | PD 74/55 | **JF740209** | | | **JF740130** | **JF740148** | **JF740166** | *Urtica dioica* (*Urticaceae*) | Netherlands |
| | *Leptosphaeria doliolum* subsp. *doliolum* var. *doliolum*, anam. *Phoma acuta* subsp. *acuta* | CBS 130000 | PD 82/701 | **JF740210** | | | **JF740131** | **JF740149** | **JF740167** | *Urtica dioica* (*Urticaceae*) | Netherlands |
| ***Leptosphaeria errabunda* comb. nov.** | *Leptosphaeria doliolum* subsp. *errabunda*, anam. *Phoma acuta* subsp. *errabunda* | CBS 617.75 | ATCC 32814, IMI 199775, PD 74/201 | **JF740216** | | **JF740289** | **JF740132** | **JF740150** | **JF740168** | *Solidago* sp. (hybrid) (*Asteraceae*) | Netherlands |

**Table 1.** (Continued).

| Species name, final identification | Former identification | CBS no. | Other no. | ITS | SSU | LSU | ACT | TUB | CHS-1 | Host, substrate | Country |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | *Leptosphaeria doliolum* subsp. *errabunda*, anam. *Phoma acuta* subsp. *errabunda* | CBS 125978 | PD 74/61 | **JF740217** | | **JF740290** | **JF740133** | **JF740151** | **JF740169** | *Delphinium* sp. (*Ranunculaceae*) | Netherlands |
| | *Leptosphaeria doliolum* subsp. *errabunda*, anam. *Phoma acuta* subsp. *errabunda* | CBS 129999 | PD 78/569 | **JF740218** | | | **JF740134** | **JF740152** | **JF740170** | *Aconitum* sp. (*Ranunculaceae*) | Netherlands |
| | *Leptosphaeria doliolum* subsp. *errabunda*, anam. *Phoma acuta* subsp. *errabunda* | CBS 129998 | PD 84/462 | **JF740219** | | | **JF740135** | **JF740153** | **JF740171** | *Gailardia* (*Asteraceae*) | Netherlands |
| | *Leptosphaeria doliolum* subsp. *errabunda*, anam. *Phoma acuta* subsp. *errabunda* | CBS 129997 | PD 78/631 | **JF740220** | | | **JF740136** | **JF740154** | **JF740172** | *Achillea millefolium* (*Apiaceae*) | Netherlands |
| ***Leptosphaeria etheridgei* comb. nov.** | *Phoma etheridgei* | CBS 125980 | DAOM 216539, PD 95/1483 | **JF740221** | | **JF740291** | | | | *Populus tremuloides* (*Salicaceae*) | Canada |
| ***Leptosphaeria macrocapsa* comb. nov.** | *Phoma macrocapsa* | CBS 640.93 | PD 78/139 | **JF740237** | | **JF740304** | **JF740138** | **JF740156** | **JF740174** | *Mercurialis perennis* (*Euphorbiaceae*) | Netherlands |
| ***Leptosphaeria pedicularis* comb. nov.** | *Phoma pedicularis* | CBS 126582 | PD 77/710 | **JF740223** | | **JF740293** | | | | *Gentiana punctata* (*Gentianaceae*) | Switzerland |
| | *Phoma pedicularis* | CBS 390.80 | PD 77/711 | **JF740224** | | **JF740294** | **JF740137** | **JF740155** | **JF740173** | *Pedicularis* sp. (*Scrophulariaceae*) | Switzerland |
| ***Leptosphaeria rubefaciens* comb. nov.** | *Phoma rubefaciens* | CBS 387.80 | IMI 248432, ATCC 42533, PD 78/809 | **JF740242** | | **JF740311** | | | | *Tilia* (x) *europea* (*Malvaceae*) | Netherlands |
| | *Phoma rubefaciens* | CBS 223.77 | | **JF740243** | | **JF740312** | | | | *Quercus* sp. (*Fagaceae*) | Switzerland |
| ***Leptosphaeria sclerotioides* comb. nov.** | *Phoma sclerotioides* | CBS 144.84 | CECT 20025, PD 82/1061 | **JF740192** | | **JF740269** | | | | *Medicago sativa* (*Fabaceae*) | Canada |
| | *Phoma sclerotioides* | CBS 148.84 | PD 80/1242 | **JF740193** | | **JF740270** | | | | *Medicago sativa* (*Fabaceae*) | Canada |
| *Leptosphaeria slovacica* | *Leptosphaeria slovacica*, anam. *Phoma leonuri* | CBS 389.80 | PD 79/171 | **JF740247** | **JF740101** | **JF740315** | | | | *Balota nigra* (*Lamiaceae*) | Netherlands |
| | *Leptosphaeria slovacica*, anam. *Phoma leonuri* | CBS 125975 | PD 77/1161 | **JF740248** | | **JF740316** | | | | *Balota nigra* (*Lamiaceae*) | Netherlands |
| ***Leptosphaeria sydowii* comb. nov.** | *Phoma sydowii* | CBS 385.80 | PD 74/477 | **JF740244** | | **JF740313** | **JF740139** | **JF740157** | **JF740175** | *Senecio jacobaea* (*Asteraceae*) | UK |
| | *Phoma sydowii* | CBS 125976 | PD 84/472 | **JF740245** | | **JF740314** | **JF740140** | **JF740158** | **JF740176** | *Senecio jacobaea* (*Asteraceae*) | Netherlands |

**Table 1.** (Continued).

| Species name, final identification | Former identification | CBS no. | Other no. | ITS | SSU | LSU | ACT | TUB | CHS-1 | Host, substrate | Country |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | *Phoma sydowii* | CBS 297.51 | | **JF740246** | | | **JF740141** | **JF740159** | **JF740177** | *Papaver rhoeas* (*Papaveraceae*) | Switzerland |
| ***Leptosphaeria veronicae* comb. nov.** | *Phoma veronicicola* | CBS 145.84 | CECT 20059, PD 78/273 | **JF740254** | | **JF740320** | **JF740142** | **JF740160** | **JF740178** | *Veronica chamaedryoides* (*Scrophulariaceae*) | Netherlands |
| | *Phoma veronicicola* | CBS 126583 | PD 74/227 | **JF740255** | | **JF740321** | **JF740143** | **JF740161** | **JF740179** | *Veronica* 'Shirley Blue' (*Scrophulariaceae*) | Netherlands |
| *Massarina eburnea* | | | H 3953, HHUF 26621, JCM 14422 | | AB521718 | AB521735 | | | | *Fagus sylvatica* (*Fagaceae*) | UK |
| *Massarina eburnea* | | CBS 473.64 | ETH 2945 | | GU296170 | GU301840 | | | | *Fagus sylvatica* (*Fagaceae*) | Switzerland |
| ***Medicopsis romeroi* comb. nov.** | *Pyrenochaeta romeroi* | CBS 252.60 | ATCC 13735, FMC 151, UAMH 10841 | | EU754108 | EU754207 | | | | Human, maduromycosis | Venezuela |
| | *Pyrenochaeta romeroi* | CBS 122784 | PD 84/1022 | | | EU754208 | | | | *Hordeum vulgare* (*Gramineae*) | Unknown |
| *Melanomma pulvis-pyrius* | | CBS 371.75 | | | | GU301845 | | | | Wood | France |
| | | CBS 400.97 | | | DQ678020 | DQ678072 | | | | *Fagus* sp. (Fagaceae) | Belgium |
| *Neophaeosphaeria filamentosa* | | CBS 102202 | BPI 802755 | **JF740259** | GQ387516 | GQ387577 | | | | *Yucca rostrata* (*Agavaceae*) | Mexico |
| *Neosetophoma samarorum* | | CBS 138.96 | PD 82/653 | | GQ387517 | GQ387578 | | | | *Phlox paniculata* (*Polemoniaceae*) | Netherlands |
| *Neottiosporina paspali* | | CBS 331.37 | | | EU754073 | EU754172 | | | | *Paspalum notatum* (*Poaceae*) | USA |
| ***Nigrogana mackinnonii* comb. nov.** | *Pyrenochaeta mackinnonii* | CBS 674.75 | FMC 270 | | GQ387552 | GQ387613 | | | | Human, black grain mycetoma | Venezuela |
| | *Pyrenochaeta mackinnonii* | CBS 110022 | | | | GQ387614 | | | | Human, mycetoma | Mexico |
| ***Paraconiothyrium flavescens* comb. nov.** | *Phoma flavescens* | CBS 178.93 | PD 82/1062 | | | GU238075 | | | | Soil | Netherlands |
| ***Paraconiothyrium fuckelii* comb. nov.** | *Coniothyrium fuckelii* | CBS 797.95 | | | GU238204 | GU237960 | | | | *Rubus* sp. (*Rosaceae*) | Denmark |
| ***Paraconiothyrium fusco-maculans* comb. nov.** | *Plenodomus fusco-maculans* | CBS 116.16 | | | | EU754197 | | | | *Malus* sp. (*Rosaceae*) | USA |
| ***Paraconiothyrium lini* comb. nov.** | *Phoma lini* | CBS 253.92 | PD 70/998 | | | EU238093 | | | | Wisconsin tank | Netherlands |
| ***Paraconiothyrium maculicutis* sp. nov.** | *Pleurophoma pleurospora* | CBS 101461 | IMI 320754, UTHSC 87-144 | | | EU754200 | | | | Human, cutaneous lesions | USA |
| *Paraconiothyrium minitans* | | CBS 122788 | PD 07/03486739 | | EU754074 | EU754173 | | | | Unknown | UK |
| | | CBS 122786 | PD 99/1064-1 | | | EU754174 | | | | *Clematis* sp. (*Ranunculaceae*) | Netherlands |
| ***Paraconiothyrium tiliae* comb. nov.** | *Asteromella tiliae* | CBS 265.94 | | | | EU754139 | | | | *Tilia platyphyllos* (*Tiliaceae*) | Austria |
| ***Paraleptosphaeria dryadis* comb. nov.** | *Leptosphaeria dryadis* | CBS 643.86 | | **JF740213** | | GU301828 | | | | *Dryas octopetala* (*Rosaceae*) | Switzerland |

**Table 1.** (Continued).

| Species name, final identification | Former identification | CBS no. | Other no. | ITS | SSU | LSU | ACT | TUB | CHS-1 | Host, substrate | Country |
|---|---|---|---|---|---|---|---|---|---|---|---|
| ***Paraleptosphaeria macrospora* comb. nov.** | *Phoma macrospora* | CBS 114198 | UPSC 2686 | **JF740238** | | **JF740305** | | | | *Rumex domesticus* (*Chenopodiaceae*) | Norway |
| ***Paraleptosphaeria nitschkei* comb. nov.** | *Leptosphaeria nitschkei* | CBS 306.51 | | **JF740239** | | **JF740308** | | | | *Cirsium spinosissimum* (*Asteraceae*) | Switzerland |
| ***Paraleptosphaeria orobanches* comb. nov.** | *Phoma korfii* | CBS 101638 | PD 97/12070 | **JF400230** | | **JF740299** | | | | *Epifagus virginiana* (*Orobanchaceae*) | USA |
| ***Paraleptosphaeria praetermissa* comb. nov.** | *Leptosphaeria praetermissa* | CBS 114591 | | **JF740241** | | **JF740310** | | | | *Rubus idaeus* (*Rosaceae*) | Sweden |
| *Paraphaeosphaeria michoti* | | CBS 652.86 | ETH 9483 | | GQ387520 | GQ387581 | | | | *Typha latifolia* (*Typhaceae*) | Switzerland |
| *Paraphoma radicina* | | CBS 111.79 | IMI 386094, PD 76/437 | | EU754092 | EU754191 | | | | *Malus sylvestris* (*Rosaceae*) | Netherlands |
| *Phaeosphaeria nodorum* | | CBS 110109 | | | EU754076 | EU754175 | | | | *Lolium perenne* (*Gramineae*) | Denmark |
| *Phoma herbarum* | | CBS 615.75 | | FJ427022 | EU754087 | EU754186 | | | | *Rosa multiflora* (*Rosaceae*) | Netherlands |
| *Phoma paspali* | | CBS 560.81 | PD 92/1569 | | GU238227 | G238124 | | | | *Paspalum dilatum* (*Poaceae*) | New Zealand |
| ***Plenodomus agnitus* comb. nov.** | *Leptosphaeria agnita*, anam. *Phoma agnita* | CBS 121.89 | PD 82/903 | **JF740194** | | **JF740271** | | | | *Eupatorium cannabinum* (*Asteraceae*) | Netherlands |
| | *Leptosphaeria agnita*, anam. *Phoma agnita* | CBS 126584 | PD 82/561 | **JF740195** | | **JF740272** | | | | *Eupatorium cannabinum* (*Asteraceae*) | Netherlands |
| ***Plenodomus biglobosus* comb. nov.** | *Leptosphaeria biglobosa* | CBS 119951 | | **JF740198** | **JF740102** | **JF740274** | | | | *Brassica rapa* (*Brassicaceae*) | Netherlands |
| | | CBS 127249 | DAOM 229269 | **JF740199** | | **JF740275** | | | | *Brassica juncea* (*Brassicaceae*) | France |
| ***Plenodomus chrysanthemi* comb. nov.** | *Phoma vasinfecta*, synanam. *Phialophora chrysanthemi* | CBS 539.63 | | **JF740253** | GU238230 | GU238151 | | | | *Chrysanthemum* sp. (*Asteraceae*) | Greece |
| ***Plenodomus collinsoniae* comb. nov.** | *Leptosphaeria collinsoniae* | CBS 120227 | JCM 13073, MAFF 239583 | **JF740200** | | **JF740276** | | | | *Vitis coignetiae* (*Vitaceae*) | Japan |
| ***Plenodomus confertus* comb. nov.** | *Leptosphaeria conferta*, anam. *Phoma conferta* | CBS 375.64 | | AF439459 | | **JF740277** | | | | *Anacyclus radiatus* (*Asteraceae*) | Spain |
| ***Plenodomus congestus* comb. nov.** | *Leptosphaeria congesta*, anam. *Phoma congesta* | CBS 244.64 | | AF439460 | | **JF740278** | | | | *Erigeron canadensis* (*Asteraceae*) | Spain |
| ***Plenodomus enteroleucus* comb. nov.** | *Phoma enteroleuca* var. *enteroleuca* | CBS 142.84 | PD 81/654, CECT20063 | **JF740214** | | **JF740287** | | | | *Catalpa bignonioides* (*Bignoniaceae*) | Netherlands |
| | *Phoma enteroleuca* var. *enteroleuca* | CBS 831.84 | | **JF740215** | | **JF740288** | | | | *Triticum aestivum* (*Poaceae*) | Germany |
| ***Plenodomus fallaciosus* comb. nov.** | *Leptosphaeria fallaciosa* | CBS 414.62 | ETH 2961 | **JF740222** | | **JF740292** | | | | *Satureia montana* (*Lamiaceae*) | France |

**Table 1.** (Continued).

| Species name, final identification | Former identification | CBS no. | Other no. | ITS | SSU | LSU | ACT | TUB | CHS-1 | Host, substrate | Country |
|---|---|---|---|---|---|---|---|---|---|---|---|
| ***Plenodomus hendersoniae* comb. nov.** | *Phoma intricans* | CBS 113702 | UPSC 1843 | **JF740225** | | **JF740295** | | | | *Salix cinerea* (*Salicaceae*) | Sweden |
| | *Phoma intricans* | CBS 139.78 | | **JF740226** | | **JF740296** | | | | *Pyrus malus* (*Rosaceae*) | Netherlands |
| ***Plenodomus influorescens* comb. nov.** | *Phoma enteroleuca* var. *influorescens* | CBS 143.84 | PD 78/883, CECT 20064 | **JF400228** | | **JF740297** | | | | *Fraxinus excelsior* (*Oleaceae*) | Netherlands |
| | *Phoma enteroleuca* var. *influorescens* | | PD 73/1382 | **JF400229** | | **JF740298** | | | | *Lilium* sp. (*Liliaceae*) | Netherlands |
| ***Plenodomus libanotidis* comb. nov.** | *Leptosphaeria libanotis* | CBS 113795 | UPSC 2219 | **JF400231** | | **JF740300** | | | | *Seseli libanotis* (*Apiaceae*) | Sweden |
| ***Plenodomus lindquistii* comb. nov.** | *Leptosphaeria lindquistii*, anam. *Phoma macdonaldii* | CBS 386.80 | PD 77/336 | **JF400232** | | **JF740301** | | | | *Helianthus annuus* (*Asteraceae*) | former Yugoslavia |
| | *Leptosphaeria lindquistii*, anam. *Phoma macdonaldii* | CBS 381.67 | | **JF400233** | | **JF740302** | | | | *Helianthus annuus* (*Asteraceae*) | Canada |
| *Plenodomus lingam* | *Leptosphaeria maculans*, anam. *Phoma lingam* | CBS 275.63 | MUCL 9901, UPSC 1025 | **JF400234** | **JF740103** | **JF740306** | | | | *Brassica* sp. (*Brassicaceae*) | UK |
| | *Leptosphaeria maculans*, anam. *Phoma lingam* | CBS 260.94 | PD 78/989 | **JF400235** | | **JF740307** | **JF740116** | | | *Brassica oleracea* (*Brassicaceae*) | Netherlands |
| | *Leptosphaeria maculans*, anam. *Phoma lingam* | CBS 147.24 | | | | | **JF740117** | | | Unknown | Unknown |
| ***Plenodomus lupini* comb. nov.** | *Phoma lupini* | CBS 248.92 | PD 79/141 | **JF740236** | | **JF740303** | | | | *Lupinus mutabilis* (*Fabaceae*) | Peru |
| ***Plenodomus pimpinellae* comb. nov.** | *Leptosphaeria pimpinellae*, anam. *Phoma pimpinellae* | CBS 101637 | PD 92/41 | **JF740240** | | **JF740309** | | | | *Pimpinella anisum* (*Apiaceae*) | Israel |
| ***Plenodomus tracheiphilus* comb. nov.** | *Phoma tracheiphila* | CBS 551.93 | PD 81/782 | **JF740249** | **JF740104** | **JF740317** | | | | *Citrus limonium* (*Rutaceae*) | Israel |
| | *Phoma tracheiphila* | CBS 127250 | PD 09/04597141 | **JF740250** | | **JF740318** | | | | *Citrus* sp. (*Rutaceae*) | Italy |
| ***Plenodomus visci* comb. nov.** | *Plectophomella visci* | CBS 122783 | PD 74/1021 | **JF740256** | EU754096 | EU754195 | | | | *Viscum album* (*Viscaceae*) | France |
| *Plenodomus wasabiae* | *Phoma wasabiae* | CBS 120119 | FAU 559 | **JF740257** | | **JF740323** | | | | *Wasabia japonica* (*Brassicaceae*) | Taiwan |
| | *Phoma wasabiae* | CBS 120120 | FAU 561 | **JF740258** | | **JF740324** | | | | *Wasabia japonica* (*Brassicaceae*) | Taiwan |
| *Pleomassaria siparia* | | CBS 279.74 | | | | AY004341 | | | | *Betula verrucosa* (*Betulaceae*) | Netherlands |
| ***Pleospora angustis* nom. nov.** | *Leptosphaeria clavata* | CBS 296.51 | | | | | **JF740122** | | | Unknown | Switzerland |
| *Pleospora betae* | *Pleospora betae*, anam. *Phoma betae* | CBS 523.66 | PD 66/270, IHEM 3915 | | EU754080 | EU754179 | **JF740118** | | | *Beta vulgaris* (*Chenopodiaceae*) | Netherlands |
| | *Pleospora betae*, anam. *Phoma betae* | CBS 109410 | PD 77/113 | | | EU754178 | **JF740119** | | | *Beta vulgaris* (*Chenopodiaceae*) | Netherlands |
| *Pleospora calvescens* | *Pleospora calvescens*, anam. *Ascochyta caulina* | CBS 246.79 | PD 77/655 | | EU754032 | EU754131 | **JF740120** | | | *Atriplex hastata* (*Chenopodiaceae*) | Germany |

**Table 1.** (Continued).

| Species name, final identification | Former identification | CBS no. | Other no. | ITS | SSU | LSU | ACT | TUB | CHS-1 | Host, substrate | Country |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | *Pleospora calvescens*, anam. *Ascochyta caulina* | CBS 343.78 | | | | | **JF740121** | | | *Atriplex hastata* (*Chenopodiaceae*) | Netherlands |
| *Pleospora chenopodii* | *Ascochyta hyalospora* | CBS 206.80 | PD 74/1022 | | **JF740095** | **JF740266** | **JF740109** | | | *Chenopodium quinoa* (*Chenopodiaceae*) | Bolivia |
| | *Pleospora calvescens*, anam. *Ascochyta caulina* | CBS 344.78 | PD 68/682 | | | | **JF740110** | | | *Atriplex hastata* (*Chenopodiaceae*) | Netherlands |
| ***Pleospora fallens*** **comb. nov.** | *Phoma fallens* | CBS 161.78 | LEV 1131 | | | | **JF740106** | | | *Olea europaea* (*Oleaeceae*) | New Zealand |
| | *Phoma glaucispora* | CBS 284.70 | PD 97/2400 | | | | **JF740107** | | | *Nerium oleander* (*Apocynaceae*) | Italy |
| ***Pleospora flavigena*** **comb. nov.** | *Phoma flavigena* | CBS 314.80 | PD 91/1613 | | | | **JF740108** | | | Water | Romania |
| ***Pleospora halimiones*** **nom. nov.** | *Ascochyta obiones* | CBS 432.77 | IMI 282137 | | **JF740096** | **JF740267** | **JF740113** | | | *Halimione portulacoides* (*Chenopodiaceae*) | Netherlands |
| | *Ascochyta obiones* | CBS 786.68 | | | | | **JF740114** | | | *Halimione portulacoides* (*Chenopodiaceae*) | Netherlands |
| *Pleospora herbarum* | | CBS 191.86 | IMI 276975 | | GU238232 | GU238160 | **JF740123** | | | *Medicago sativa* (*Fabaceae*) | India |
| ***Pleospora incompta*** **comb. nov.** | *Phoma incompta* | CBS 467.76 | | | | | **JF740111** | | | *Olea europaea* (*Oleaeceae*) | Greece |
| | *Phoma incompta* | CBS 526.82 | | | | | **JF740112** | | | *Olea europaea* (*Oleaeceae*) | Italy |
| *Pleospora typhicola* | *Pleospora typhicola*, anam. *Phoma typharum* | CBS 132.69 | | | **JF740105** | **JF740325** | **JF740124** | | | *Typha angustifolia* (*Typhaceae*) | Netherlands |
| | *Pleospora typhicola*, anam. *Phoma typharum* | CBS 602.72 | | | | | **JF740125** | | | *Typha* sp. (*Typhaceae*) | Netherlands |
| *Pleurophoma pleurospora* | *Pleurophoma* sp. | CBS 116668 | | | | **JF740326** | | | | *Citysus scoparius* (*Fabaceae*) | Netherlands |
| | *Pleurophoma* sp. | CBS 130329 | PD 82/371 | | | **JF740327** | | | | *Lonicera* sp. (*Caprifoliaceae*) | Netherlands |
| *Preussia funiculata* | | CBS 659.74 | | | GU296187 | GU301864 | | | | Soil | Senegal |
| *Pseudorobillarda phragmitis* | | CBS 398.61 | IMI 070678 | | | EU754203 | | | | *Phragmitis australis* (*Poaceae*) | UK |
| *Pyrenochaeta cava* | | CBS 257.68 | IMI 331911 | **JF740260** | EU754100 | EU754199 | | | | Wheat field soil | Germany |
| *Pyrenochaeta lycopersici* | | CBS 267.59 | | **JF740261** | GQ387551 | GQ387612 | | | | *Lycopersicon esculentum* (*Solanaceae*) | Netherlands |
| *Pyrenochaeta nobilis* | | CBS 407.76 | | EU930011 | EU754107/ DQ898287 | EU754206 | | | | *Laurus nobilis* (*Lauraceae*) | Italy |
| *Pyrenochaetopsis leptospora* | | CBS 101635 | PD 71/1027 | **JF740262** | GQ387566 | GQ387627 | | | | *Secale cereale* (*Poaceae*) | Europe |

**Table 1.** (Continued).

| Species name, final identification | Former identification | CBS no. | Other no. | ITS | SSU | LSU | ACT | TUB | CHS-1 | Host, substrate | Country |
|---|---|---|---|---|---|---|---|---|---|---|---|
| ***Pyrenochaetopsis pratorum* comb. nov.** | *Phoma pratorum* | CBS 445.81 | PDDCC 7049, PD 80/1254 | **JF740263** | | GU238136 | | | | *Lolium perenne, leaf* (*Poaceae*) | New Zealand |
| | | CBS 286.93 | PD 80/1252 | **JF740264** | | **JF740331** | | | | *Dactylis glomerata* (*Poaceae*) | New Zealand |
| *Pyrenophora tritici-repentis* | | | OSC 100066 | | AY544716 | AY544672 | | | | (*Poaceae*) | Italy |
| *Roussoella hysterioides* | | CBS 125434 | HH 26988 | | | AB524622 | | | | *Sasa kurilensis* (*Poaceae*) | Japan |
| *Setomelanomma holmii* | | CBS 110217 | | | GQ387572 | GQ387633 | | | | *Picea pungens* (*Pinaceae*) | USA |
| *Setophoma terrestris* | | CBS 335.29 | | | GQ387526 | GQ387587 | | | | *Allium sativum* (*Alliaceae*) | USA |
| *Splanchnonema platani* | | CBS 221.37 | | | DQ678013 | DQ678065 | | | | *Platanus occidentalis* (*Platanaceae*) | USA |
| *Sporormiella minima* | | CBS 524.50 | | | DQ678003 | DQ678056 | | | | Dung of goat | Panama |
| *Stagonosporopsis cucurbitacearum* | | CBS 133.96 | | | GU238234 | GU238181 | | | | *Cucurbita* sp. (*Cucurbitaceae*) | New Zealand |
| ***Subplenodomus apiicola* comb. nov.** | *Phoma apiicola* | CBS 285.72 | | **JF740196** | | GU238040 | | | | *Apium graveolens* var. *rapaceum* (*Umbelliferae*) | Germany |
| | *Phoma apiicola* | CBS 504.91 | PD 78/1073 | **JF740197** | | **JF740273** | | | | *Apium graveolens* (*Umbelliferae*) | Netherlands |
| ***Subplenodomus drobnjacensis* comb. nov.** | *Phoma drobnjacensis* | CBS 269.92 | PD 88/896 | **JF740211** | **JF740100** | **JF740285** | | | | *Eustoma exaltatum* (*Gentianaceae*) | Netherlands |
| | *Phoma drobnjacensis* | CBS 270.92 | PD 83/650 | **JF740212** | | **JF740286** | | | | *Gentiana makinoi* 'Royal Blue' (*Gentianaceae*) | Netherlands |
| ***Subplenodomus valerianae* comb. nov.** | *Phoma valerianae* | CBS 630.68 | PD 68/141 | **JF740251** | | GU238150 | | | | *Valeriana phu* (*Valerianaceae*) | Netherlands |
| | *Phoma valerianae* | CBS 499.91 | PD 73/672 | **JF740252** | | **JF740319** | | | | *Valeriana officinalis* (*Valerianaceae*) | Netherlands |
| ***Subplenodomus violicola* comb. nov.** | *Phoma violicola* | CBS 306.68 | | FJ427054 | GU238231 | GU238156 | | | | *Viola tricolor* (*Violaceae*) | Netherlands |
| | *Phoma violicola* | CBS 100272 | | FJ427055 | | **JF740322** | | | | *Viola tricolor* (*Violaceae*) | New Zealand |
| *Thyridaria rubronotata* | | CBS 419.85 | | | | GU301875 | | | | *Acer pseudoplatanus* (*Aceraceae*) | Netherlands |
| *Trematosphaeria pertusa* | | CBS 122368 | | | | FJ201990 | | | | *Fraxinus excelsior* (*Oleaceae*) | France |
| ***Westerdykella capitulum* comb. nov.** | *Phoma capitulum* | CBS 337.65 | PD 91/1614, ATCC 16195, HACC 167, IMI 113693 | | | GU238054 | | | | Saline soil | India |
| ***Westerdykella minutispora* comb. nov.** | *Phoma minutispora* | CBS 509.91 | PD 77/920 | | | GU238108 | | | | Saline soil | India |
| *Westerdykella ornata* | | CBS 379.55 | | | | GU301880 | | | | Mangrove mud | Mozambique |

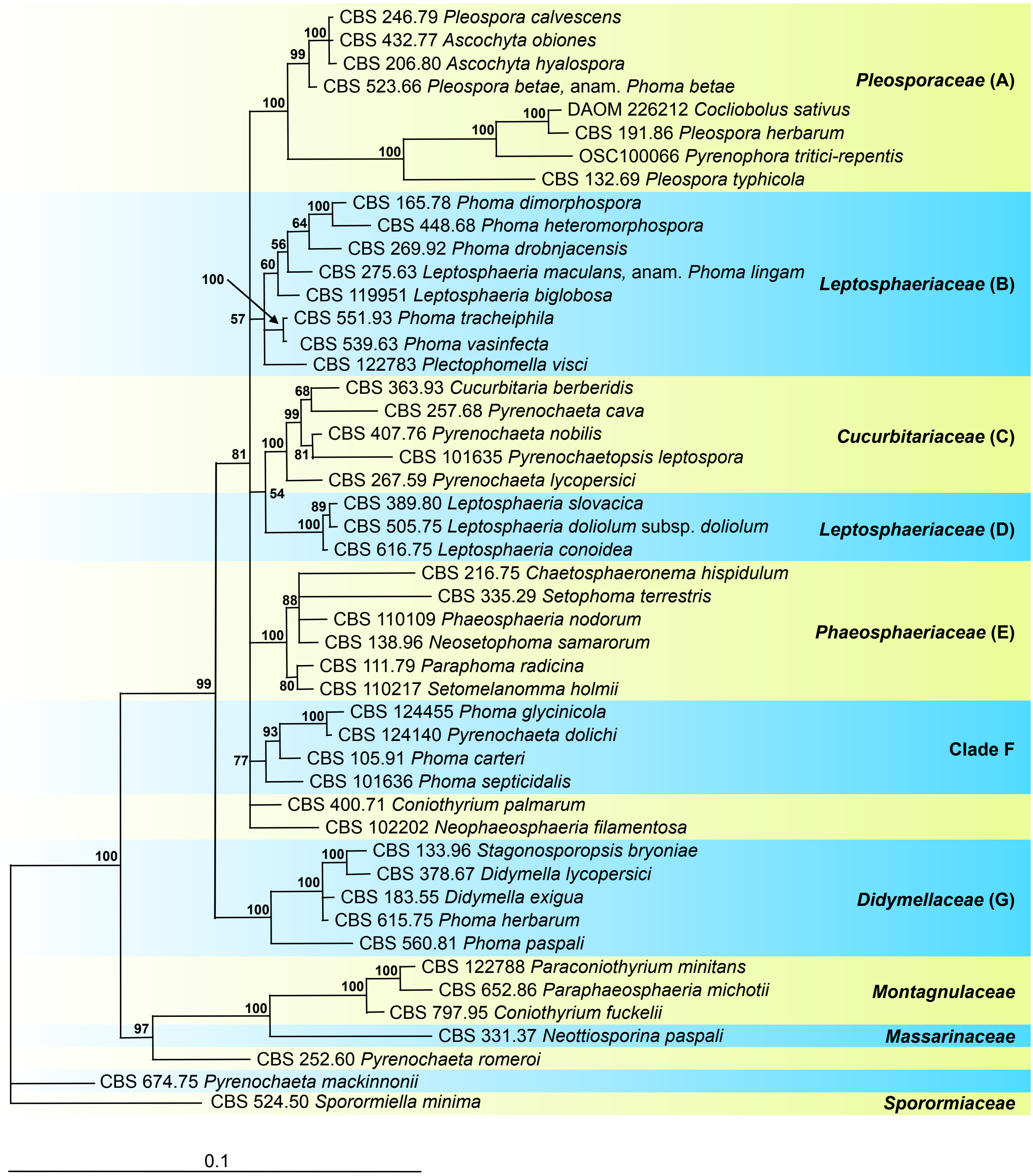


**Fig. 1.** The phylogeny of *Phoma lingam* and *Phoma betae*, the type species of *Phoma* sections *Plenodomus* and *Pilosa*, based on the strict consensus tree from a Bayesian analysis of 48 LSU/SSU sequences. The Bayesian posterior probabilities are given at the nodes. The tree was rooted to *Sporormiella minima* (CBS 524.50).

respectively. The tree (Fig. 1) was rooted to *Sporormiella minima* (CBS 524.50). The Bayesian analysis resulted in 6 5442 trees after 3 272 000 generations, from which the burn-in was discarded and the consensus tree and posterior probabilities were calculated based on 56 028 trees (Fig. 1).

The families that belong to *Pleosporineae*, represented by the species grouping in clades A–G, clustered in a strongly supported clade (99 % posterior probability). Clade A, representing those species classified in *Pleosporaceae*, was strongly supported (100 %) and included two subclades. *Pleospora betae* (anam. *Ph. betae*), clustered with *Pleospora calvescens* (anam. *Ascochyta caulina*), *A. obiones* and *A. hyalospora*; all recorded as pathogens on *Chenopodiaceae*. The generic type species *Pleospora herbarum*, a plurivorous species, grouped with *Cochliobolus sativus*, *Pyrenophora tritici-repentis* and *Pleospora typhicola* (anam. *Ph. typhina*), all recorded from *Poaceae*. Clade B includes *Leptosphaeria maculans* (anam. *Ph. lingam*) and clustered with *Leptosphaeria biglobosa.* In clade B also other important plant pathogens of *Phoma* section *Plenodomus* can be found, such as *Ph. tracheiphila*, *Ph. vasinfecta*, *Ph. drobnjacensis,* and *Plectophomella* *visci. Phoma heteromorphospora*, type species of *Phoma* section *Heterospora* (Boerema *et al.* 1997) and *Ph. dimorphospora* also grouped in this *Leptosphaeria* clade, in congruence with previous findings (de Gruyter *et al.* 2009*,* Aveskamp *et al.* 2010).

*Leptosphaeria doliolum* (anam. *Ph. acuta*), type species of the genus *Leptosphaeria*, is found in Clade D, clustering with *L. conoidea* and *L. slovacica. Leptosphaeria doliolum* and its relatives comprise a sister clade C with species classified in *Cucurbitariaceae*, including *Cucurbitaria berberidis*, the three *Pyrenochaeta* species, *Py. cava*, *Py. lycopersici* and *Py. nobilis*, and *Pyrenochaetopsis leptospora.*

*Phaeosphaeria nodorum* and its relatives *Neosetophoma samarorum*, *Setophoma terrestris*, *Chaetosphaeronema hispidulum*, *Paraphoma radicina* and *Setomelanomma holmii*, represent *Phaeosphaeriaceae* in clade E as has previously been found (de Gruyter *et al.* 2009, 2010).

A distinct clade F includes *Ph. glycinicola*, *Ph. carteri*, *Ph. septicidalis*, and the taxonomic confusing species *Pyrenochaeta dolichi* (Grondona *et al.* 1997). The position of *Coniothyrium palmarum* and *Neophaeosphaeria filamentosa* could not be clarified, but both species are also treated below in a phylogeny including close relatives based on ITS and LSU regions (Fig. 2). *Didymella exigua*, type species of the genus *Didymella*, and *Ph. herbarum* represent *Didymellaceae,* and clustered in a well-supported clade (G) in congruence with previous studies (de Gruyter *et al.* 2009, 2010, Aveskamp *et al.* 2010). The molecular phylogeny of species which group in this analysis outside of Pleosporineae in *Montagnulaceae, Massarinaceae* and *Sporormiaceae* were further analysed utilising LSU sequence data of a broader range of taxa (Fig. 5).

## *Phoma* section *Plenodomus* and close allies

The aligned sequence matrix obtained for the LSU and ITS regions had a total length of 1 921 nucleotide characters, 1 332 and 589 respectively. The combined dataset used in the analyses included 87 taxa and contained 1921 characters with 298 and 118 unique site patterns for LSU and ITS respectively. The tree (Fig. 2) was rooted to *Ph. herbarum* (CBS 615.75), the representative isolate of the type species of *Phoma* (Boerema *et al.* 2004). The Bayesian analysis resulted in 100 002 trees after 5 000 000 generations, from which the burn-in was discarded and the consensus tree and posterior probabilities were calculated based on 90 930 trees (Fig. 2).

The species currently classified in *Leptosphaeria* and *Phoma* section *Plenodomus* grouped in clades A and B representing *Leptosphaeriaceae*, including the type species *Ph. lingam* and *Leptosphaeria doliolum*, respectively. Isolates of the taxa that represent *Cucurbitariaceae*, *Cucurbitaria berberidis* and its related species *Pyrenochaeta cava*, *Py. nobilis*, *Py. lycopersici* and *Pyrenochaetopsis leptospora*, clustered in a distinct clade D only distantly related to *Leptosphaeriaceae*. This finding agrees with a recent study (de Gruyter *et al.* 2010). *Phoma pratorum* clustered with *Pyrenochaetopsis leptospora.*

*Leptosphaeria biglobosa* grouped in a subclade A1 with *Ph. wasabiae*, the cause of black rot disease on *Wasabia japonica* (*Brassicaceae*) and *Ph. pimpinellae*, a necrotroph on *Pimpinella anisum* (*Apiaceae*). *Leptosphaeria maculans*, considered as closely related to the *L. biglobosa* complex, proved to be more distantly related in clade A1. In this subclade, other important pathogens can be found, such as *Ph. tracheiphila*, a quarantine organism on *Citrus* spp. (*Rutaceae)*, *Ph. vasinfecta,* a pathogen on *Chrysanthemum* spp. (*Asteraceae*), *L. lindquistii* (anam. *Ph. macdonaldii*), a worldwide pathogen on *Helianthus annuus* (*Asteraceae*) and *Ph. lupini*, a seed borne pathogen known from *Lupinus* spp. (*Fabaceae*). Subclade A1 also comprises both varieties of *Ph. enteroleuca*, opportunistic pathogens on deciduous trees and shrubs, and the necrotrophic species *L. agnita* (anam. *Ph. agnita*), *Ph. congesta* (both recorded on *Asteraceae*), *Ph. conferta* (mainly on *Brassicaceae*), *L. hendersoniae* (on *Salicaceae*), *L. fallaciosa*, *L. collinsoniae* (mainly on *Lamiaceae)* and *L. libanotis* (on *Apiaceae*). *Plectophomella visci*, recorded from leaves of *Viscum album* (*Viscaceae*), also clustered in the *Leptosphaeriaceae*. The genus *Plenodomus* is re-introduced here to accommodate the species in subclade A1, which are allied to *Ph. lingam*.

Subclade A2 comprises pathogenic species often causing leaf spots such as *Ph. apiicola* on *Apium graveolens* (*Apiaceae*), *Ph. drobnjacensis* (on *Gentianaceae)*, *Ph. violicola* (on *Violaceae*) as well as the necrotrophic species *Ph. valerianae*, on *Valeriana* spp. (*Valerianaceae*). *Phoma apiicola* and *Ph. valerianae* were classified in *Phoma* section *Phoma*, and *Ph. violicola* was classified in *Phoma* sect. *Peyronellaea*; however, the relationship of these species in *Leptosphaeriaceae* is clearly demonstrated (Fig. 2), and therefore the species are transferred to the new genus *Subplenodomus*. These results are in congruence with a recent study where *Ph. violicola*, *Ph. apiicola* and *Ph. valerianae* clustered in a clade representing both *Leptosphaeriaceae* and *Pleosporaceae* (Aveskamp *et al.* 2010).

Four *Leptosphaeria* species, *L. macrospora* (soil) and the necrotrophic species *L. nitschkei* (on *Asteraceae*), *L. praetermissa*, on *Rubus idaeus* (*Rosaceae*) and *L. dryadis*, on *Dryas* spp. (*Rosaceae*) grouped in a subclade A3 and are transferred here to a new genus *Paraleptosphaeria*. *Phoma korfii* also clustered in this subclade. The European species *Ph. heteromorphospora*, type species of *Phoma* section *Heterospora*, and the American counterpart *Ph. dimorphospora*, both pathogens on *Chenopodiaceae*, grouped in a distinct subclade A4. *Phoma* sect. *Heterospora* is raised to generic rank to accommodate both species in *Leptosphaeriaceae.*

Clade B comprises necrotrophic species related to the type species *L. doliolum* (anam. *Ph. acuta*). The phylogeny of this species complex, and the closely related species *Ph. veronicicola*, *Ph. macrocapsa* and *Ph. sydowii*, is treated below. The necrotrophic species *Ph. sclerotioides*, *L. conoidea* (anam. *Ph. doliolum*), *L. slovacica* (anam. *Ph. leonuri*) and *Ph. pedicularis* also proved to be related. The species *Ph. rubefaciens* and *Ph. etheridgei* also belong to clade B, but these species, both recorded on trees, are more distantly related.

The *Phoma* species in clades A and B are in majority currently described as anamorphs of the genus *Leptosphaeria*, or belong to *Phoma* section *Plenodomus*. These *Phoma* anamorphs are only distantly related to the type species *Ph. herbarum* and its relatives in *Didymellaceae*, and therefore these species described in section *Plenodomus* are excluded from the genus *Phoma*. Clade C is more distantly related to *Leptosphaeriaceae* and comprises species that are related to *Coniothyrium palmarum* in *Coniothyriaceae.* Two subclades are recognised in clade C: *Ph. glycinicola, Py. dolichi* and *Ph. carteri* group with the generic type species *C. palmarum,* whereas two isolates of *Ph. septicidalis* group with *Ph. multipora*. The teleomorph *Neophaeosphaeria filamentosa* clustered basal to this clade. Clade D includes the genera *Cucurbitaria*, *Pyrenochaetopsis* and *Pyrenochaeta*, which represent *Cucurbitariaceae*. This finding is in congruence with previous studies (de Gruyter *et al.* 2010).

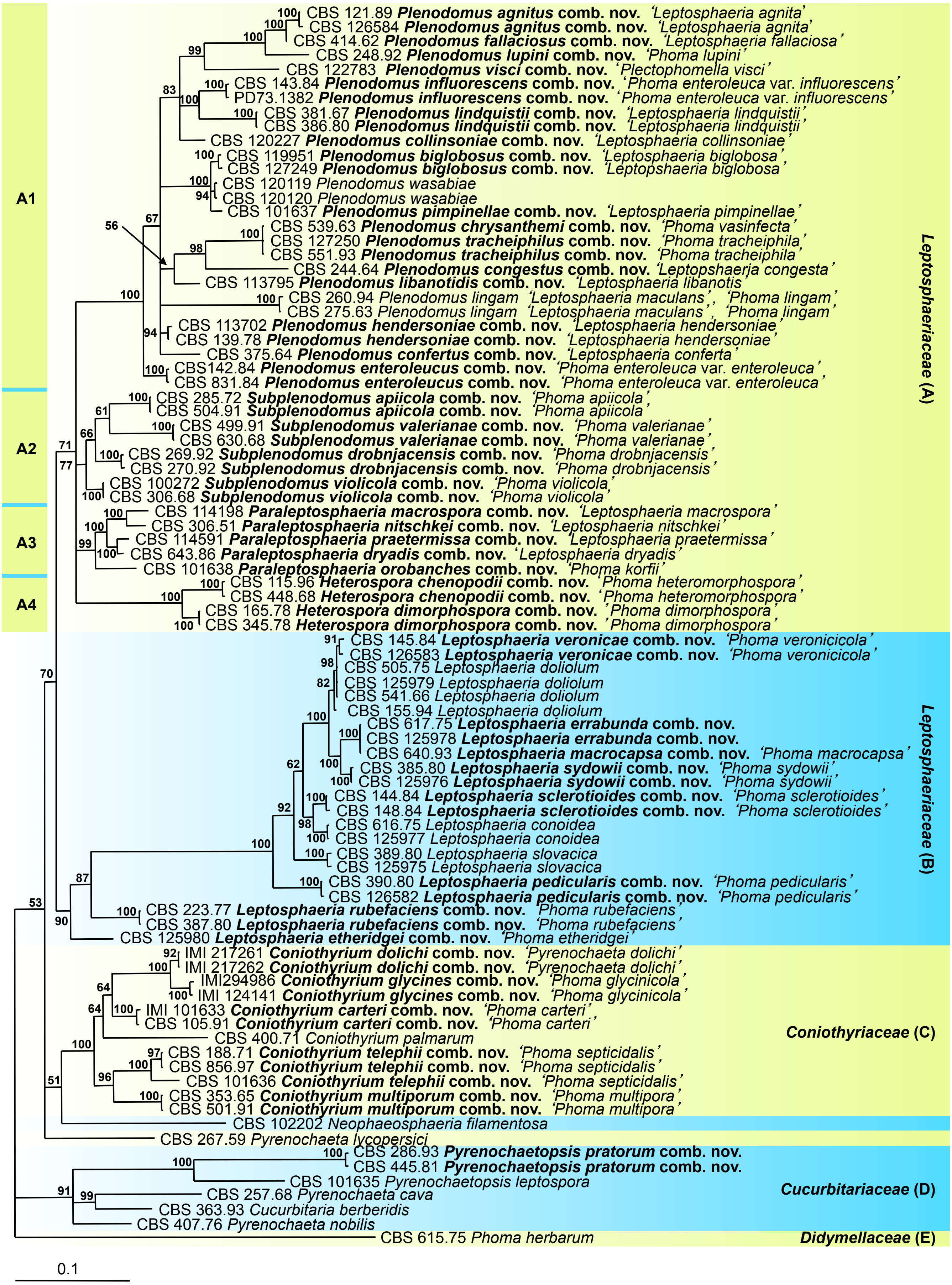


**Fig. 2.** The phylogeny of *Phoma* section *Plenodomus* and *Leptosphaeria,* based on the strict consensus tree from a Bayesian analysis of 87 LSU/ITS sequences. The Bayesian posterior probabilities are given at the nodes. The tree was rooted to *Phoma herbarum* (CBS 615.75).

## Phylogeny of the *Leptosphaeria doliolum* complex

The aligned sequence matrix obtained for the ITS, ACT, TUB and CHS-1 regions had a total length of 1 345 nucleotide characters; ITS 522, ACT 240, TUB 332 and CHS-1 251, respectively. The combined dataset used in the analyses included 18 taxa and contained 1 345 characters with 98 unique site patterns. The tree (Fig. 3) was rooted to "*Ph. pedicularis*" (CBS 390.80). The Bayesian analysis resulted in 6 002 trees after 30 000 generations, from which the burn-in was discarded and the consensus tree and posterior probabilities were calculated based on 3 341 trees.

The phylogenetic tree revealed two clades with high posterior probabilities, 98 and 99 % respectively, clade A with *Ph. acuta* subsp. *errabunda* and *Ph. macrocapsa*, and clade B with *Ph. acuta* subsp. *acuta* (anamorph of *Leptosphaeria doliolum*) and *Ph. acuta* subsp. *acuta* f. sp. *phlogis*. *Phoma sydowii*, a necrotroph on *Asteraceae*, *Senecio* spp. in particular, proved to be closely related to *Ph. acuta* subsp. *errabunda*. The isolate CBS 297.51 preserved as *Ph. acuta* is similar to *Ph. sydowii*, a synonym of *L. sydowii*, see below. *Phoma veronicicola*, as a necrotroph specifically occurring on *Veronica* spp. (*Scrophulariaceae*), also proved to be related to *Leptosphaeria doliolum*.

## Phylogeny of *Phoma* section *Pilosa*

The aligned sequence matrix obtained for the ACT region had a total length of 252 nucleotide characters (20 taxa), and contained 165 unique sites. The tree was rooted to *Ph. lingam* (CBS 147.24 and CBS 260.94). The Bayesian analysis resulted in 34 802 trees after 174 000 generations, from which the burn-in was discarded, and the consensus tree and posterior probabilities were calculated based on 11 728 trees (Fig. 4).

The phylogenetic tree representing the *Pleosporaceae* includes *Ph. betae*, type species of *Phoma* section *Pilosa*. This section is characterised by producing pycnidia that are covered by mycelial hairs. *Phoma betae* clearly groups with other pycnidial fungi pathogenic on *Chenopodiaceae*, including *Ascochyta obiones, A. hyalospora* and *A. caulina* and *Chaetodiplodia* sp. All species produce similar hairy pycnidia, but are classified in *Ascochyta* or *Coniothyrium* due to conidial septation, or brown pigmentation of conidia, respectively.

A subclade comprises the cosmopolitan *Pleospora herbarum* and related species. The species involved are associated with various hosts or substrates. The most closely related *Ph. incompta* is a specific pathogen on *Olea europea* (*Oleaceae*). *Phoma incompta* was classified in *Phoma* section *Sclerophomella* because of its thick-walled pycnidia (de Gruyter & Noordeloos 1992, Boerema & de Gruyter 1998). The pycnidial characters of *Ph. incompta*, pycnidia covered with mycelial hairs and with an indistinct ostiole visible as a pallid spot (de Gruyter & Noordeloos 1992) however, agrees with those of *Ph. betae* and *Ph. typhina*.

*Phoma fallens* proved to be closely related to *Ph. glaucispora* in keeping with the similar *in vitro* characters, especially the low growth-rate and the size and shape of its conidia (Boerema *et al*. 2004). Both species originate from southern Europe, and have been associated with spots on fruits and leaves of *Olea europea,* or leaf spots on *Nerium oleander,* respectively. An isolate preserved as *Leptosphaeria clavata*, CBS 259.51, proved to be closely related. The origin of the isolate, deposited by E. Müller, is unknown; however, it is likely that the isolate was obtained from *Poaceae*, *Triticum vulgare* or *Dactylis glomerata* (Müller 1950). *Phoma flavigena*, once isolated from water and also recorded from southern Europe, proved to be more distantly related in *Pleosporaceae.*

## Phylogeny of phoma-like anamorphs excluded from the suborder *Pleosporineae*

The aligned sequence matrix obtained for the LSU regions had a total length of 808 nucleotide characters, with 208 unique site patterns. The phylogenetic tree (Fig. 5) was rooted to *Pseudorobillarda phragmitis* (CBS 398.61). The Bayesian analysis resulted in 48 402 trees after 242 000 generations, from which the burn-in was discarded and the consensus tree and posterior probabilities were calculated based on 24 876 trees.

Clade A includes the reference isolates of the teleomorph *Paraphaeosphaeria* and the anamorph *Paraconiothyrium* classified in *Montagnulaceae*. This teleomorph/anamorph relation agrees with previous molecular phylogenetic studies (Verkley *et al.* 2004, Damm *et al.* 2008, de Gruyter *et al.* 2009). Other phoma-like species in this clade are *Ph. lini*, *Plenodomus fusco-maculans*, *Pleurophoma pleurospora* (CBS 101461) and *Asteromella tilliae*. *Phoma lini*, a saprobe frequently recorded on dead stems of *Linum* spp., was described in *Phoma* section *Phoma* (de Gruyter *et al*. 1993). Re-examination of the conidia revealed that they are hyaline and thin-walled; however, also darker, greenish to yellowish coniothyrium-like conidia were observed. The conidiogenous cells are phoma-like, doliiform to ampulliform.

The isolate *Asteromella tiliae* (CBS 265.94) clearly represents a species of *Paraconiothyrium*, and therefore, the teleomorph name *Didymosphaeria petrakiana*, *Didymosphaeriaceae*, is probably incorrect. It was already mentioned by Butin & Kehr (1995) that "considering the taxonomical placement of the teleomorph, the authors were informed about forthcoming taxonomic changes".

The morphological characters of the isolate CBS 101461, considered as representing the generic type species *Pleurophoma pleurospora*, resembles *Paraconiothyrium* as was previously discussed (de Gruyter *et al.* 2009). The sterile ex-type strain of *Plenodomus fusco-maculans*, CBS 116.16, recorded from *Malus* sp., also grouped with the *Paraconiothyrium* isolates.

*Coniothyrium fuckelii* clustered in the *Paraphaeosphaeria*/*Paraconiothyrium* clade, in agreement with previous studies (Damm *et al*. 2008, Aveskamp *et al.* 2010), and therefore, the species is transferred to the genus *Paraconiothyrium*. Two phoma-like species obtained from *Citysus scoparius* and *Lonicera* sp. respectively (CBS 116668 and CBS 130329), cluster near *Montagnulaceae* and *Massarinaceae*. The morphological characters of the species are typical for *Pleurophoma pleurospora*. The taxonomic position of both isolates at familial rank could not be determined. The morphology of *Phoma flavescens* proved to be most similar to that of *Paraconiothyrium*, it definitely does not belong to *Phoma*, and therefore the species is transferred to *Paraconiothyrium*. Sequence data of additional species clustering nearby are required to resolve the current classification of *Ph. flavescens*. None of the phoma-like anamorphs included in this study grouped in clade B, which represents *Massarinaceae*.

Clade C includes the recently assigned ex-epitype strain of *Trematosphaeria pertusa*, isolate CBS 122368 (Zhang *et al.* 2008) and *Falcisformispora lignatilis*. Both *T. perusa* and *F. lignatilis* represent *Trematosphaeriaceae* (Suetrong *et al.* 2009). A second isolate preserved as *Trematosphaeria pertusa*, CBS 400.97, proved to be only distantly related, and clustered in clade D with *Aposphaeria populina* and *Melanomma pulvis-pyrius* in

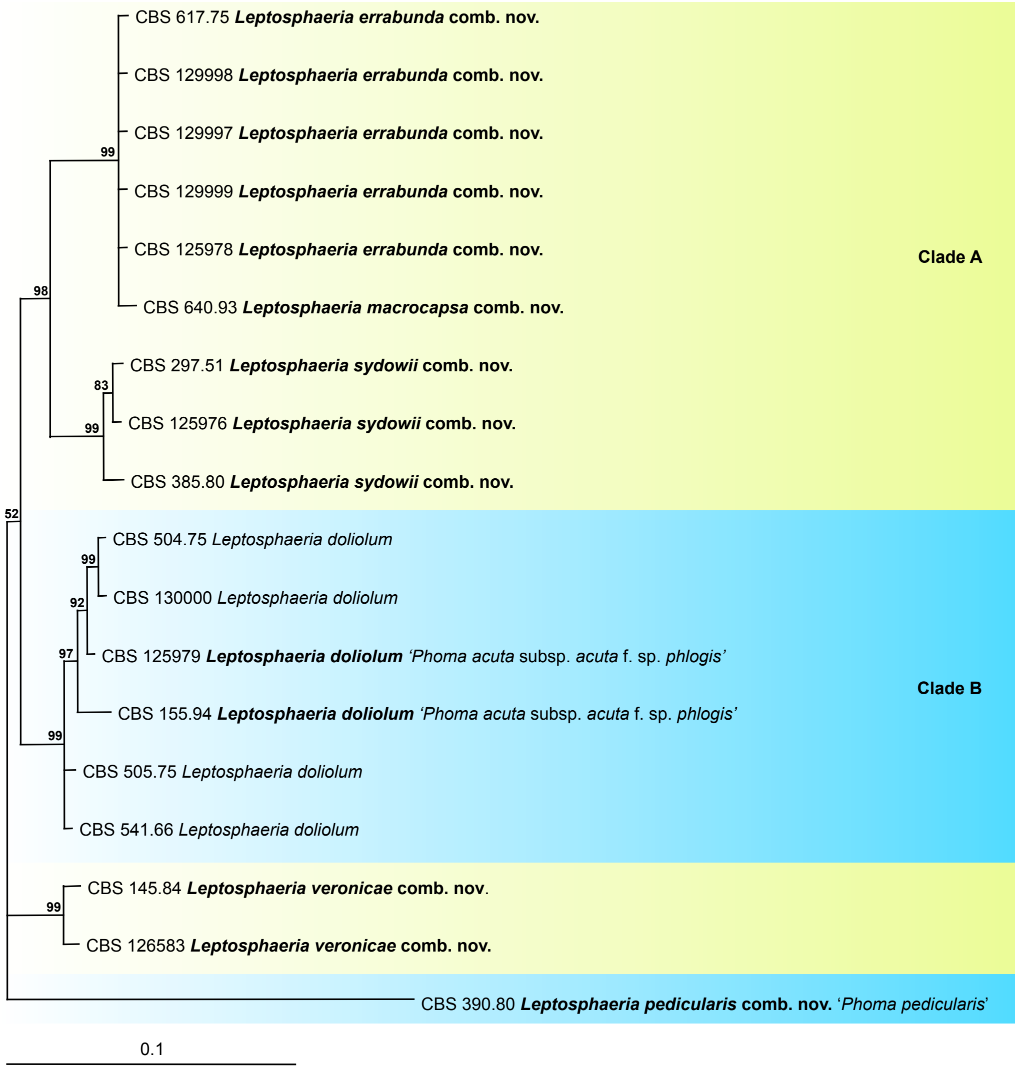


**Fig. 3.** The phylogeny of the *Leptosphaeria doliolum* complex, based on the strict consensus tree from a Bayesian analysis of 18 ITS/ACT/TUB/CHS-1 sequences. The Bayesian posterior probabilities are given at the nodes. The tree was rooted to *Leptosphaeria pedicularis* comb. nov. (CBS 390.80).

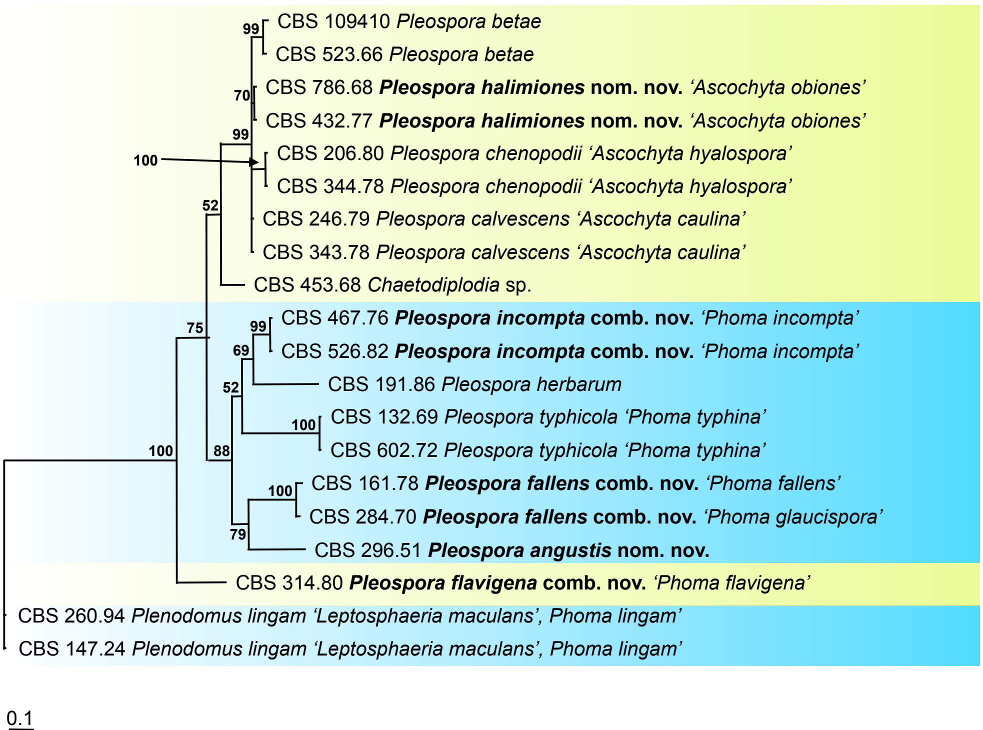


**Fig. 4.** The phylogeny of phoma-like anamorphs in the *Pleosporaceae* based on the strict consensus tree from a Bayesian analysis of 20 ACT sequences. The Bayesian posterior probabilities are given at the nodes. The tree was rooted to *Plenodomus lingam* (CBS 147.24, CBS 260.94).

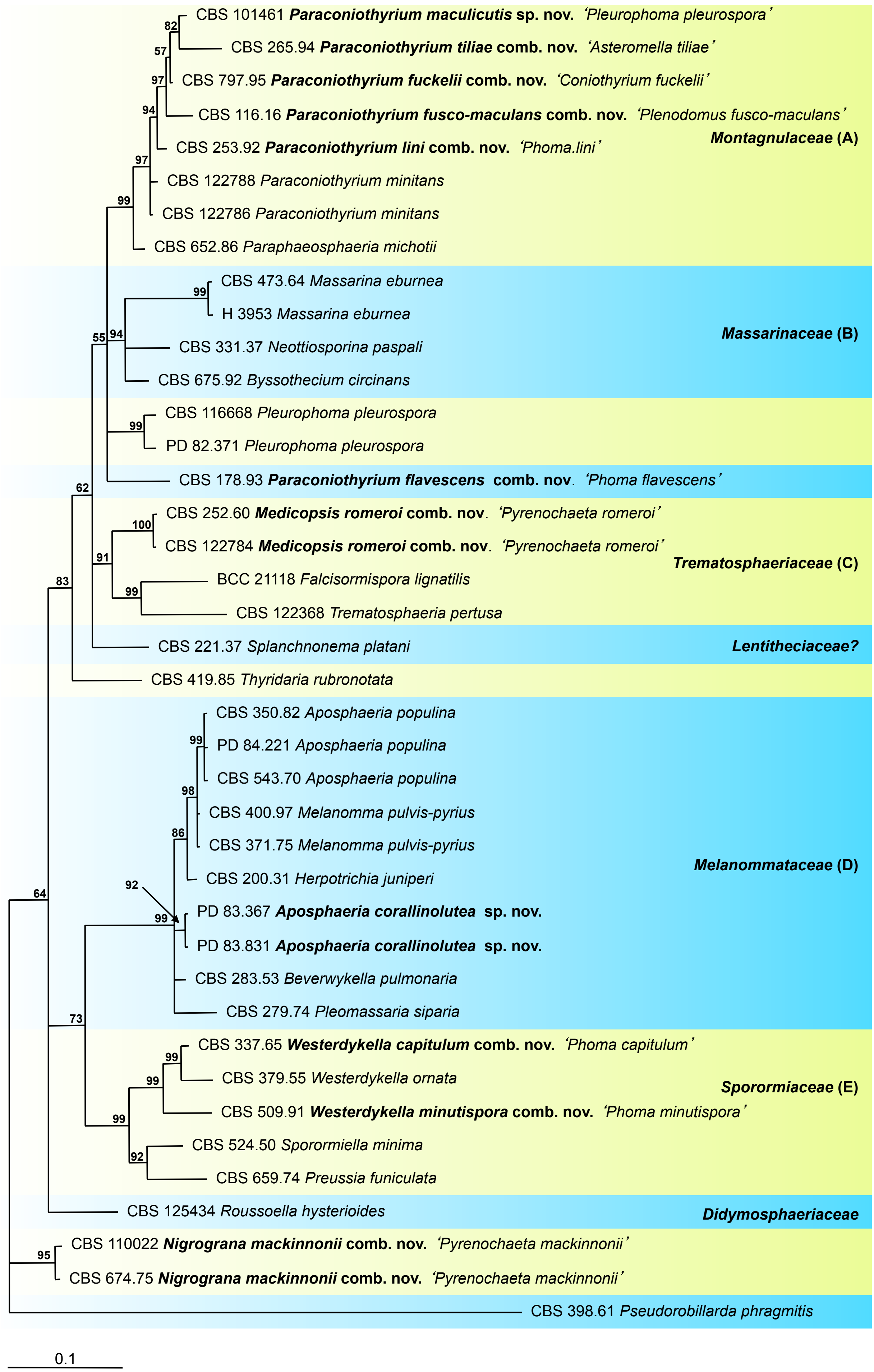


**Fig. 5.** LSU The phylogeny of phoma-like isolates excluded from the *Pleosporineae*, based on the strict consensus tree from a Bayesian analysis of 40 LSU sequences. The Bayesian posterior probabilities are given at the nodes. The tree was rooted to *Pseudorobillarda phragmitis* (CBS 398.61).

*Melanommataceae*. This isolate is considered as an incorrect identification (Mugambi & Huhndorf 2009), and we consider this sterile isolate as representative of *Melanomma pulvis-pyrius*. Clade C also comprises the human pathogen *Pyrenochaeta romeroi.* This species certainly does not belong to *Pyrenochaeta* (de Gruyter *et al.* 2010) and therefore, we describe the new genus *Medicopsis* in *Trematosphaeriaceae* to accommodate this species.

A well-supported clade D represents the *Melanommataceae* and includes *Melanomma pulvis-pyrius, Herpotrichia juniperi* and *Beverwijkella pulmonaria*, in congruence with Zhang *et al.* (2009). There were four phoma-like isolates present in the collections of CBS and PD, *i.e.* CBS 350.82, PD 83/367, PD 83/831 and PD 84/221, which could not be identified according to their morphological characters. The isolates were preserved as *Pleurophoma* spp. This study demonstrates that two strains represent *Aposphaeria populina*, whereas the other two strains represent the new species described here as *Aposphaeria corallinolutea*. Further studies in *Melanommataceae* are needed to clarify the phylogeny of *Aposphaeria* in *Melanommataceae*.

*Sporormiaceae* (clade E) is represented by *Sporormiella minima* and *Preussia funiculata*. *Phoma capitulum* and *Ph. minutispora*, well-defined soil-borne fungi from Asia, group in this clade. Both species are related with the anamorph *Westerdykella ornata*, and therefore the species are transferred to *Westerdykella* in *Sporormiaceae*.

*Pyrenochaeta mackinnonii* could not be assigned to familial rank. A blast search in GenBank with its LSU sequence suggested a relation with *Versicolorisporum triseptum*. However, the typical 3-septate conidia of this anamorph are different. Neither could *V. triseptum* be assigned at familial rank in *Pleosporales* (Tanaka *et al.* 2009). We therefore introduce the new genus *Nigrograna* to accommodate *Py. mackinnonii*.

## TAXONOMY

***Leptosphaeriaceae*** M.E. Barr, Mycotaxon 29: 503. 1987.

***Heterospora*** (Boerema, Gruyter & Noordel.) Gruyter, Verkley & Crous, **stat. nov.** MycoBank MB564701.
*Basionym*: *Phoma* sect. *Heterospora* Boerema, Gruyter & Noordel., Persoonia 16: 336. 1997.

*Type species*: *Heterospora chenopodii* (Westend.) Gruyter, Aveskamp & Verkley, see below (= *Phoma heteromorphospora* Aa & Kesteren).

***Heterospora chenopodii* (**Westend.) Gruyter, Aveskamp & Verkley, **comb. nov.** MycoBank MB564702.
*Basionym*: *Phyllosticta chenopodii* Westend., Bull. Acad. Roy. Sci. Belgique Ser. 2, 2: 567. 1857; not *Phyllosticta chenopodii* Sacc., Syll. Fung. 3: 55. 1884 = *Phoma exigua* Desm. var. *exigua*; not *Plenodomus chenopodii* (P. Karst. & Har.) Arx, Verh. Kon. Ned. Akad. Wetensch., Afd. Natuurk., Sect. 2. 51: 72. 1957 ≡ *Phoma chenopodiicola* Gruyter, Noordel. & Boerema, Persoonia 15: 395. 1993; not *Phoma chenopodii* Pavgi & U.P. Singh, Mycopathol. Mycol. Appl. 30: 265. 1966. nom. illeg. = *Phoma chenopodii* S. Ahmad, Sydowia 2: 79. 1948.

≡ *Septoria westendorpii* G. Winter, Hedwigia 26: 26. 1887. nom. nov.; not *Phoma westendorpii* Tosquinet, Westend., Bull. Acad. Roy. Sci. Belgique Ser. 2, 2: 564. 1857.

≡ *Phoma variospora* Aa & Kesteren, Persoonia 10: 268. 1979, nom. nov., nom. illeg. [not *Phoma variospora* Shreem., Indian J. Mycol. Pl. Pathol. 8: 221. 1979 ("1978")].

≡ *Phoma heteromorphospora* Aa & Kesteren, Persoonia 10: 542. 1980, nom. nov.

*Specimens examined*: **Belgium,** Beverloo, from leaves of *Chenopodium suecicum* (*album*) and *Chenopodium urbicum* (*Chenopodiaceae*), no date, G.D. Westendorp, Herb. Crypt. (Ed. Beyaert-Feys), No. 959. BR, **holotype** of *Phyllosticta chenopodii* Westend. ex herb. G.D. Westendorp. **Netherlands**, Baarn, from leaf spots in *Chenopodium album*, 3 Jul. 1968, H.A. van der Aa, **epitype designated here** CBS H-16386, culture ex-epitype CBS 448.68; Heelsum, from leaf spots in *Chenopodium album*, Sep. 1994, J. de Gruyter, CBS 115.96 = PD 94/1576.

*Notes*: Van der Aa & van Kesteren (1979) provided a nom. nov. since the epithet "*chenopodii*" was occupied in *Phoma*. For more details of the taxonomy of the species see van der Aa & van Kesteren (1979). Although *Leptosphaeria chenopodii-albi* was described from leaves of *Chenopodium album* (Crane & Shearer 1991) no cultures are available for comparison.

***Heterospora dimorphospora*** (Speg.) Gruyter, Aveskamp & Verkley, **comb. nov.** MycoBank MB564703.
*Basionym*: *Phyllosticta dimorphospora* Speg., Anales Mus. Nac. Buenos Aires 13: 334. 1910.

≡ *Phoma dimorphospora* (Speg.) Aa & Kesteren, Persoonia 10: 269. 1979.

= *Stagonospora chenopodii* Peck, Rep. (Annual) New York State Mus. Nat. Hist. 40: 60. 1887 (sometimes erroneously listed as *Stag. chenopodii* "House").

*Specimens examined*: **Argentina**, La Plata, from leaves of *Chenopodium hircinum* (*Chenopodiaceae*), 13 Oct. 1906, C. Spegazzini, Colect. micol. Museo Inst. Spegazzini, No. 11.353, LPS, **holotype** of *Phyllosticta dimorphospora* Speg. **Lima**, from stem of *Chenopodium quinoa*, 1977, L.J. Turkensteen, CBS 165.78 = PD 77/884. **Peru**, from lesions in stems of *Chenopodium quinoa*, 1976, V. Otazu, **epitype designated here** CBS H-16203, culture ex-epitype CBS 345.78 = PD 76/1015.

*Note*: For more details of the taxonomy of the species see van der Aa & van Kesteren (1979).

***Leptosphaeria*** Ces. & De Not., Comment. Soc. Crittog. Ital. 1: 234. 1863.

= *Leptophoma* Höhn., Sitzungsber. Kaiserl. Akad. Wiss., Math.-Naturwiss. Cl., Abt. 1. 124: 73. 1915.

*Type species*: *Leptosphaeria doliolum* (Pers. : Fr.) Ces. & De Not., see below.

*Note*: For full synonymy, including the species listed below, see Crane & Shearer (1991) and Boerema *et al.* (2004).

***Leptosphaeria conoidea*** (De Not.) Sacc., Fungi Venet. Nov. Vel. Crit. Ser. 2: 314. 1875.
*Basionym*: *Leptosphaeria doliolum* var. *conoidea* De Not., Mycoth. Veneti, No. 76. 1873.

= *Leptosphaeria doliolum* subsp. *pinguicula* Sacc., Michelia 2: 598. 1882.

= *Phoma acuta* subsp. *amplior* Sacc. & Roum., Rev. Mycol. 6: 30. 1884.

≡ *Phoma hoehnelii* subsp. *amplior* (Sacc. & Roum.) Boerema & Kesteren, Trans. Brit. Mycol. Soc. 67: 299. 1976.

= *Phoma doliolum* P. Karst., Meddel. Soc. Fauna Fl. Fenn. 16: 9. 1888.

= *Plenodomus microsporus* Berl., Bull. Soc. Mycol. France 5: 55. 1889.

*Specimens examined*: **Netherlands**, Zaltbommel, from dead stem of *Lunaria annua* (*Brassicaceae*), Jan. 1974, G.H. Boerema, CBS 616.75 = ATCC 32813 = IMI 199777 = PD 74/56; Montfoort, *Senecio* sp. (*Asteraceae*), 1982, CBS 125977 = PD 82/888.

***Leptosphaeria doliolum*** (Pers. : Fr.) Ces. & de Not., Comment. Soc. Crittog. Ital. 1: 234. 1863.

*Basionym*: *Sphaeria doliolum* Pers. : Fr., Icon. Desc. Fung. Min. Cognit. (Leipzig) 2: 39. 1800.

= *Sphaeria acuta* Hoffm. : Fr, Veg. cryptog. 1: 22. 1787. Syst. Mycol. 2: 507. 1823.

≡ *Phoma acuta* (Hoffm. : Fr.) Fuckel, Jahrb. Nassauischen Vereins Naturk. 23–24: 125. 1870 (as "*acutum*").

≡ *Leptophoma acuta* (Hoffm. : Fr.) Höhn., Sitzungsber. Kaiserl. Akad. Wiss., Math.-Naturwiss. Cl., Abt. 1. 124: 73. 1915.

≡ *Plenodomus acutus* (Hoffm. : Fr.) Bubák, Ann. Mycol. 13: 29. 1915 [as "(Fuckel)"].

= *Phoma phlogis* Roum., Rev. Mycol. 6: 160. 1884.

= *Phoma hoehnelii* var. *urticae* Boerema & Kesteren, Trans. Brit. Mycol. Soc. 67: 299. 1976.

*Specimens examined*: **Netherlands**, from stem of *Rudbeckia* sp. (*Asteraceae*), Sep. 1966, M.M.J. Dorenbosch, CBS 541.66 = PD 66/221; from stem of *Urtica dioica* (*Urticaceae*), 1974, G.H. Boerema, CBS 504.75 = PD 74/55; Rhenen, from *Urtica dioica*, Feb. 1975, G.H. Boerema, CBS 505.75 = PD 75/141; Wageningen, from stem of *Phlox paniculata* (*Polemoniaceae*), 1977, G.H. Boerema, CBS 155.94 = PD 77/80; from stem of *Phlox paniculata*, 1978, G.H. Boerema, CBS 125979 = PD 78/37; from stem of *Urtica dioica*, 1982, G.H. Boerema, CBS 130000 = PD 82/701.

*Notes*: Isolate CBS 541.66 was preserved as *Phoma acuta* subsp. *errabunda* (teleom. *Leptosphaeria errabunda*, see below); however, the isolate clustered with *L. doliolum*. Both isolates CBS 155.94 and CBS 125979 were considered as *forma specialis* "*phlogis"* (Boerema *et al.* 1994) of the anamorph *Ph. acuta* subsp. *acuta.* The subspecies *acuta* was created by the differentiation of *Phoma acuta* subsp *amplior* Sacc. & Roum., but the latter is a synonym of *Ph. doliolum*, reclassified here as *L. conoidea*, see above. *Sphaeria acuta* Hoffm. was applied as basionym for different anamorphs an a teleomorph of various species of *Leptosphaeria* leading to a confusing nomenclature. The epitet has been unambiguously tied to *Ph. acuta* by Boerema & Gams (1995).

***Leptosphaeria errabunda*** (Desm.) Gruyter, Aveskamp & Verkley, **comb. nov.** MycoBank MB564704.

*Basionym*: *Phoma errabunda* Desm., Ann. Sci. Nat., Bot. Ser. 3, 11: 282. 1849.

≡ *Phoma acuta* subsp. *errabunda* (Desm.) Boerema, Gruyter & Kesteren, Persoonia 15: 465. 1994.

= *Leptophoma doliolum* Höhn., Sitzungsber. Kaiserl. Akad. Wiss., Math.-Naturwiss. Cl., Abt. 1. 124: 75. 1915 [not *Phoma doliolum* P. Karst. = *Leptosphaeria conoidea* (De Not.) Sacc., see above].

≡ *Plenodomus doliolum* (Höhn.) Höhn., Ber. Deutsch. Bot. Ges. 36: 139. 1918.

≡ *Phoma hoehnelii* Kesteren, Netherlands J. Pl. Pathol. 78: 116. 1972, nom. nov.

= *Leptosphaeria doliolum* subsp. *errabunda* Boerema, Gruyter & Kesteren, Persoonia 15: 466. 1994.

*Specimens examined*: **Netherlands**, Leeuwarden, from stem of *Delphinium* sp. (*Ranunculaceae*), 1974, CBS 125978 = PD 74/61; Ferwerderadeel, from *Solidago* sp., hybrid (*Asteraceae*), Mar. 1974, G.H. Boerema, CBS 617.75 = ATCC 32814 = IMI 199775 = PD 74/201; from stem of *Aconitum* sp. (*Ranunculaceae*), CBS 129999 = PD 78/569; from stem of *Achillea millefolium* (*Asteraceae*), CBS 129997 = PD 78/631; from *Gailardia* sp. (*Asteraceae*), 1984, G.H. Boerema, CBS 129998 = PD 84/462.

*Notes*: The isolate CBS 617.75 = ATTC 32814 was deposited as the anamorph *Ph. hoehnelii* var. *hoehnelii*, but interpreted as *L. doliolum* subsp. *conoidea* (Dong *et al*. 1998). The isolate clustered with *L. errabunda* in this study.

***Leptosphaeria etheridgei*** (L.J. Hutchison & Y. Hirats.) Gruyter, Aveskamp & Verkley, **comb. nov.** MycoBank MB564712.

*Basionym*: *Phoma etheridgei* L.J. Hutchison & Y. Hirats., Canad. J. Bot. 72: 1425. 1994.

*Specimen examined*: **Canada**, Alberta, from bark of gall, on trunck of *Populus tremuloides* (*Salicaceae*), Jul. 1989, P. Crane, **holotype** DAOM 216539, culture ex-holotype DAOM 216539 = CBS 125980 = PD 95/1483.

***Leptosphaeria macrocapsa*** (Trail) Gruyter, Aveskamp & Verkley, **comb. nov.** MycoBank MB564713.

*Basionym*: *Phoma macrocapsa* Trail, Scott. Naturalist (Perth) 8: 327. 1886.

≡ *Plenodomus macrocapsa* (Trail) H. Ruppr., Sydowia 13: 20. 1959.

*Specimen examined*: **Netherlands**, from stem of *Mercurialis perennis* (*Euphorbiaceae*), 1978, G.H. Boerema, CBS 640.93 = PD 78/139.

***Leptosphaeria pedicularis*** (Fuckel) Gruyter, Aveskamp & Verkley, **comb. nov.** MycoBank MB564714.

*Basionym*: *Phoma pedicularis* Fuckel, Reisen Nordpolarmeer 3: 318. 1874 (as "*pedicularidis*"); not *Phoma pedicularis* Wehm., Mycologia 38: 319. 1946 (= *Phoma herbicola* Wehm).

= *Sphaeronaema gentianae* Moesz, Bot Közlem. 14: 152. 1915 (as "*Sphaeronema*").

≡ *Plenodomus gentianae* (Moesz) Petr., Ann. Mycol. 23: 54. 1925.

*Specimens examined:* **Switzerland**, Kanton Graubünden, Albulapass, from dead stem of *Pedicularis* sp. (*Scrophulariaceae*), 1977, CBS 390.80 = PD 77/711 = ATCC 42535 = IMI 248430; Zürich, from *Gentiana punctata* (*Gentianaceae*), 1977, CBS 126582 = PD 77/710.

***Leptosphaeria rubefaciens*** (Togliani) Gruyter, Aveskamp & Verkley, **comb. nov.** MycoBank MB564715.

*Basionym*: *Phoma rubefaciens* Togliani, Ann. Sper. Agr. II, 7: 1626. 1953.

*Specimens examined*: **Switzerland**, Zürich, Albis, from twig of *Quercus* sp. (*Fagaceae*), Aug. 1976, W. Gams, CBS 223.77. **Netherlands**, Oploo, from wood of *Tilia* (×) *europaea* (*Tiliaceae*), 1978, G.H. Boerema, CBS 387.80 = ATCC 42533 = IMI 248432 = PD 78/809.

***Leptosphaeria sclerotioides*** (Sacc.) Gruyter, Aveskamp & Verkley, **comb. nov.** MycoBank MB564716.

*Basionym*: *Phoma sclerotioides* Sacc., Fungi Herb. Bruxelles 21. 1892; Syll. Fung. 11: 492. 1895.

= *Plenodomus sclerotioides* Preuss, Klotzsch. Herb. Vivum Mycol. Sistems Fungorum German., No. 1281. 1849, nom. nud. (no description).

= *Plenodomus meliloti* Mark.-Let., Bolezni Rast. 16: 195. 1927.

*Specimens examined*: **Canada**, British Columbia, from *Medicago sativa* (*Fabaceae*), 1980, J. Drew Smith, CBS 148.84 = PD 80/1242; Alberta, from root of *Medicago sativa*, Mar. 1984, G.H. Boerema, CBS 144.84 = CECT 20025 = PD 82/1061.

*Note*: Seven varieties of this species have been recognised (Wunsch *et al.* 2011) in a phylogenetic analysis using 10 loci.

***Leptosphaeria slovacica*** Picb., Sborn. Vysoké Skoly. Zemed. v Brno 7: 7. 1927.

= *Phoma leonuri* Letendre, Revue Mycol. 6: 229. 1884.

≡ *Plenodomus leonuri* (Letendre) Moesz & Smarods in Moesz, Magyar Bot. Lapok 31: 38. 1932.

*Specimens examined*: **Netherlands**, from dead stem of *Ballota nigra* (*Lamiaceae*), 1977, CBS 125975 = PD 77/1161; Arnhem, from dead stem of *Ballota nigra*, 1979, G.H. Boerema, CBS 389.80 = PD 79/171.

***Leptosphaeria sydowii*** (Boerema, Kesteren & Loer.) Gruyter, Aveskamp & Verkley, **comb. nov.** MycoBank MB564717.

*Basionym*: *Phoma sydowii* Boerema, Kesteren & Loer., Trans. Brit. Mycol. Soc. 77: 71. 1981, nom. nov.

= *Sphaeronaema senecionis* Syd. & P. Syd., Ann. Mycol. 3: 185. 1905; not *Phoma senecionis* P. Syd., Beibl. Hedwigia 38: 136. 1899.

≡ *Plenodomus senecionis* (Syd. & P. Syd.) Bubák, Ann. Mycol. 13: 29. 1915.

≡ *Plenodomus senecionis* (Syd. & P. Syd.) Petr., Ann. Mycol. 19: 192. 1921, isonym.

= *Plenodomus rostratus* Petr., Ann. Mycol. 21: 199. 1923; not *Phoma rostrata* O'Gara, Mycologia 7: 41. 1915 (not *Leptosphaeria rostrata* M.L. Far & H.T. Horner, Nova Hedwidgia 15: 250. 1968).

*Specimens examined*: **Switzerland**, Kt. Zürich, Zollikon, from *Papaver rhoeas* (*Papaveraceae*), Oct. 1949, E. Müller, CBS 297.51. **Netherlands**, from *Senecio jacobaea* (*Asteraceae*), G.H. Boerema, 1984, CBS 125976 = PD 84/472. **UK**, Scotland, Isle of Lewis, Hebrides, from dead stem of *Senecio jacobaea*, 1974, R.W.G. Dennis, CBS 385.80 = PD 74/477.

*Notes*: *Leptosphaeria senecionis* (Fuckel) G. Winter was suggested as the possible teleomorph (Boerema *et al.* 2004). Because the teleomorph connection has not been proven, however, we did not include it as a synonym that would have priority as the correct name. The isolate CBS 297.51 was originally identified as *L. doliolum* var. *doliolum*.

***Leptosphaeria veronicae*** (Hollós) Gruyter, Aveskamp & Verkley, **comb. nov.** MycoBank MB564718.

*Basionym*: *Sphaeronaema veronicae* Hollós, Ann. Hist.-Nat. Mus. Natl. Hung. 4: 341. 1906.

≡ *Phoma veronicicola* Boerema & Loer., Trans. Brit. Mycol. Soc. 84: 297. 1985, nom. nov. (not *Phoma veronicae* Roum., Revue Mycol. 6: 160. 1884).

*Specimens examined*: **Netherlands**, from stem of *Veronica* "Shirley Blue" (*Scrophulariaceae*), 1974, CBS 126583 = PD 74/227; Huis ter Heide, from dead stem of *Veronica chamaedryoides*, Mar. 1978, H.A. van Kesteren, **neotype** CBS H-7632, culture ex-neotype CBS 145.84 = CECT 20059 = PD 78/273.

***Paraleptosphaeria*** Gruyter, Verkley & Crous, **gen. nov.** MycoBank MB564720.

*Pseudothecia* immersed, subglobose, solitary or aggregated, thick-walled, pseudoparenchymatous to scleroplectenchymatous, ostiolate, unilocular. *Asci* bitunicate, broadly ellipsoidal, 8-spored, interascal filaments pseudoparaphyses, *Ascospores* biseriate, broadly fusiform, transversally 3–5-septate, hyaline to yellow-brownish. *Conidiomata* pycnidial, globose to subglobose, scleroplectenchymatous, with papillate pore, unilocular. *Conidiogenous cells* phialidic, ampulliform to doliiform. *Conidia* hyaline, aseptate, oblong to ellipsoidal. Sclerotia sometimes produced.

*Type species*: *Paraleptosphaeria nitschkei* (Rehm ex G. Winter) Gruyter, Aveskamp & Verkley (see below).

*Notes*: Munk (1957) recognised *Leptosphaeria* section *Para-Leptosphaeria*, an invalid taxon, as a heterogenous group. The section was differentiated from *Eu-Leptosphaeria*, which included the generic type species *L. doliolum. Leptosphaeria nitschkei* was considered a typical representative of section *Eu-Leptosphaeria* (Müller & von Arx 1950). However, this molecular phylogeny demonstrates that *L. nitschkei* is only distantly related to *L. doliolum.* We introduce *Paraleptosphaeria* to accomodate *L. nitschkei* and its relatives. These necrotrophic species are morphologically closely allied to *Leptosphaeria*. The former classification of *Leptosphaeria* in sections *Eu-Leptosphaeria* and *Para-Leptosphaeria* cannot be upheld from a evolutionary point of view, as two other species attributed to section *Eu-Leptosphaeria,* namely *L. agnita* and *L. maculans* (Munk 1957), were found to group in *Plenodomus*.

***Paraleptosphaeria dryadis*** (Johanson) Gruyter, Aveskamp & Verkley, **comb. nov.** MycoBank MB564721.

*Basionym*: *Melanomma dryadis* Johanson, Hedwigia 29: 160. 1890.

≡ *Leptosphaeria dryadophila* Huhndorf, Bull. Illinois Nat. Hist. Surv. 34: 484 (1992), nom. illeg. via nom. superfl.

= *Leptosphaeria dryadis* Rostr., Bot. Tidsskr. 25: 305. 1903.

*Specimen examined*: **Switzerland**, Kt. Ticino, Leventina, Alpe Campolungo, from *Dryas octopetala* (*Rosaceae*), 24 July 1980, A. Leuchtmann, CBS 643.86.

*Note*: An explanation of the nomenclature of *Leptosphaeria dryadis* has been provided by Chen *et al*. (2002).

***Paraleptosphaeria macrospora*** (Thüm.) Gruyter, Aveskamp & Verkley, **comb. nov.** MycoBank MB564722.

*Basionym*: *Leptosphaeria macrospora* Thüm. Mycotheca Univ. 1359. 1879, nom. nov.

≡ *Metasphaeria macrospora* (Fuckel) Sacc., Syll. Fung. 2: 158. 1883.

*Replaced synonym*: *Pleospora macrospora* Fuckel, Jahrb. Nassauischen Vereins Naturk. 23–24: 138. 1870, nom. illeg., Art. 53.1. [not *Pleospora macrospora* (De Not.) Ces. & De Not., Comment. Soc. Crittog. Ital. 1: 218. 1863].

*Specimen examined*: **Norway**, Troms, Tromsöya, from *Rumex domesticus* (*Polygonaceae*), 20 Aug. 1988, K. & L. Holm, CBS 114198 = UPSC 2686.

***Paraleptosphaeria nitschkei*** (Rehm ex G. Winter) Gruyter, Aveskamp & Verkley, **comb. nov.** MycoBank MB564723.

*Basionym*: *Leptosphaeria nitschkei* Rehm ex G. Winter, Ascomyceten, Fascicle 1, No. 15. 1870, nom. nud. (Flora, Jena und Regensburg 55: 510. 1872).

*Specimens examined*: **Austria**, Ötscher in Niederösterreich, c. 4500', from *Cacalia* sp. (= *Adenostyles* sp, *Asteraceae*), June 1869, Lojka, **holotype** of *Leptosphaeria nitschkei* Rehm Ascomyceten 15b, S. **Switzerland**, Kt. Graubünden, Lü, from *Cirsium spinosissimum* (*Asteraceae*), 16 July 1948, E. Müller, **epitype designated here** CBS H-20822, culture ex-epitype CBS 306.51.

*Note*: The name *Leptosphaeria nitschkei* was considered a nom. nud. by Crane and Shearer (1991) who cited Art. 32.1 but gave no further explanation. In Flora, Jena und Regensburg 55: 510. 1872 Rehm refers to additional notes by G. Winter that include a Latin description. Therefore, we consider this name as valid, following Müller (1950) who provided a detailed description *in vivo*.

***Paraleptosphaeria orobanches*** (Schweinitz : Fr.) Gruyter, Aveskamp & Verkley, **comb. nov.** MycoBank MB564724.

*Basionym*: *Sclerotium orobanches* Schweinitz, Schriften Naturf. Ges. Leipzig 1: 57. 1822 : Fr., Syst. Mycol. 2: 257. 1822.

= *Phoma korfii* Boerema & Gruyter, Persoonia 17: 275. 1999.

*Specimen examined*: **USA**, Ringwood Swamp, Lloyd-Cornell, from stem of *Epifagus virginiana* (*Orobanchaceae*), 13 Sep. 1995, T. Uturriaga, R.P. Korf, P. Mullin, **holotype** of *Sclerotium orobanches* Schweinitz, CUP 63537, culture ex-holotype CBS 101638 = PD 97/12070.

*Note*: A *Phoma* synanamorph of *Sclerotium orobanches* was reported by Yáñez-Morales *et al.* (1998) and described as *Phoma korfii* (Boerema & Gruyter 1999).

***Paraleptosphaeria praetermissa*** (P. Karst.) Gruyter, Aveskamp & Verkley, **comb. nov.** MycoBank MB564725.
*Basionym*: *Sphaeria praetermissa* P. Karst., Bidrag Kannedom Finlands Natur Folk 23: 89. 1873.
≡ *Leptosphaeria praetermissa* (P. Karst.) Sacc., Syll. Fung. 2: 26. 1883.

*Specimen examined*: **Sweden**, Dalarna, Folkärna, from *Rubus idaeus* (*Rosaceae*), 21 Mar. 1993, K. & L. Holm, CBS 114591.

***Plenodomus*** Preuss, Linnaea 24: 145. 1851.
≡ *Phoma* sect. *Plenodomus* (Preuss) Boerema, Kesteren & Loer., Trans. Brit. Mycol. Soc. 77: 61. 1981.
= *Diploplenodomus* Diedicke, Ann. Mycol. 10: 140. 1912.
= *Plectophomella* Moesz, Magyar Bot. Lapok 21: 13. 1922.
= *Apocytospora* Höhn., Mitt. Bot. Lab. TH Wien 1: 43. 1924.
= *Deuterophoma* Petri, Boll. R. Staz. Patalog. Veget. Roma 9: 396. 1929.

*Type species*: *Plenodomus rabenhorstii* Preuss, Linnaea 24: 145. 1851 (dubious synonym, see below) = *Plenodomus lingam* (Tode : Fr.) Höhn., see below.

*Note*: For full synonymy of the anamorph names of the species listed below, see Boerema *et al.* (1994). For additional synonyms of the teleomorph names of the species below that have been recorded on Asteraceous hosts, see Khashnobish *et al.* (1995).

***Plenodomus agnitus*** (Desm.) Gruyter, Aveskamp & Verkley, **comb. nov.** MycoBank MB564726.
*Basionym*: *Sphaeria agnita* Desm., Ann. Sci. Nat., Bot. Ser. 3, 16: 313. 1851.
≡ *Leptosphaeria agnita* (Desm.) Ces. & De Not., Comm. Soc. Crittog. Ital. 1: 236. 1863.
= *Plenodomus chondrillae* Died, Ann. Mycol.. 9: 140. 1911; Krypt.-fl. Brandenburg 9: 236. 1912.
= *Phoma agnita* Gonz. Frag., Mem. Real Acad. Ci. Barcelona 15: 6. 1920.

*Specimens examined*: **Netherlands**, from stem of *Eupatorium cannabinum* (*Asteraceae*), 1982, W.M. Loerakker, CBS 126584 = PD 82/561; from stem of *Eupatorium cannabinum*, 1982, W.M. Loerakker, CBS 121.89 = PD 82/903.

***Plenodomus biglobosus*** (Shoemaker & H. Brun) Gruyter, Aveskamp & Verkley, **comb. nov.** MycoBank MB564727.
*Basionym*: *Leptosphaeria biglobosa* Shoemaker & H. Brun, Canad. J. Bot. 79: 413. 2001.

*Specimens examined*: **France**, Le Rheu, from stem of *Brassica juncea* (*Brassicaceae*), CBS 127249 = DAOM 229269. **Netherlands**, from *Brassica rapa* (*Brassicaceae*), 2006, R. Veenstra, CBS 119951.

*Notes*: *Leptosphaeria biglobosa* was originally described as a less virulent segregate of *L. maculans* (Shoemaker & Brun 2001). The species, also indicated as Tox$^0$ isolates, has been described from cultivated *Brassica* species as the cause of upper stem lesions and considered as less damaging than *L. maculans* (West *et al.* 2002). However, in Poland *L. biglobosa* is the predominant cause of these symptoms (Jedryczka *et al*. 1999, Huang *et al.* 2005). The current species concept of *L. biglobosa* is broadly defined with six distinct subclades recognised by multilocus phylogenetic analyses of ITS, β-tubulin and actin sequences (Mendes-Pereira *et al.* 2003, Vincenot *et al.* 2008). These subclades are named after the host or geographic origin of the isolates involved. It has been suggested that the clades represent distinct subspecies formed over time by reproductive isolation (Mendes-Pereira *et al.* 2003). Alignments of the ITS sequences of *Ph. wasbiae*, *Ph. pimpinellae* and *L. biglobosa* isolates were compared with those of the representative strains of the *L. biglobosa* subclades obtained from GenBank, and both *Ph. wasbiae* and *Ph. pimpinellae* grouped in this species complex (unpubl. data). Both species are maintained here, awaiting a redescription of the taxa representing all clades in the *L. biglobosa* complex.

***Plenodomus chrysanthemi*** (Zachos, Constantinou & Panag.) Gruyter, Aveskamp & Verkley, **comb. nov.** MycoBank MB564728.
*Basionym*: *Cephalosporium chrysanthemi* Zachos, Constantinou & Panag., Ann. Inst. Phytopath. Benaki, N.S. 55. 1960.
≡ *Phialophora chrysanthemi* (Zachos, Constantinou & Panag.) W. Gams, Cephalosporium-artige Schimmelpilze (Stuttgart): 207. 1971.
= *Phoma vasinfecta* Boerema, Gruyter & Kesteren, Persoonia 15: 484. 1994.

*Specimen examined*: **Greece**, from *Chrysanthemum* sp. (*Asteraceae*), Apr. 1963, D.G. Zachos, **holotype** CBS H-7576, culture ex-holotype CBS 539.63.

*Note*: The species was also described as *Phoma tracheiphila* f. sp. *chrysanthemi* (Baker *et al*. 1985).

***Plenodomus collinsoniae*** (Dearn. & House) Gruyter, Aveskamp & Verkley, **comb. nov.** MycoBank MB564729.
*Basionym*: *Leptosphaeria collinsoniae* Dearn. & House, Bull. New York State Mus. Nat. Hist. 233–234: 36. 1921.

*Specimen examined*: **Japan**, Osawa river, Komukai, Miyagi, from *Vitis coignetiae* (*Vitaceae*), 27 Sep. 2003, Y. Takahashi, CBS 120227 = JCM 13073 = MAFF 239583.

***Plenodomus confertus*** (Niessl ex Sacc.) Gruyter, Aveskamp & Verkley, **comb. nov.** MycoBank MB564730.
*Basionym*: *Leptosphaeria conferta* Niessl ex Sacc., Syll. Fung. 2: 20. 1883.
= *Phoma conferta* P. Syd. ex Died., Krypt.-fl. Brandenburg 9: 142. 1912.

*Specimen examined*: **Spain**, Cais do Tejo, from dead stem of *Anacyclus radiatus* (*Asteraceae*), Mar. 1961, M.T. Lucas, CBS 375.64.

***Plenodomus congestus*** (M.T. Lucas) Gruyter, Aveskamp & Verkley, **comb. nov.** MycoBank MB564731.
*Basionym*: *Leptosphaeria congesta* M.T. Lucas, Trans. Brit. Mycol. Soc. 46: 362. 1963.
= *Phoma congesta* Boerema, Gruyter & Kesteren, Persoonia 15: 461. 1994.

*Specimen examined*: **Spain**, Póvoa de Santa Iria, Estremadura, from stem of *Erigeron canadensis* (*Asteraceae*), Mar. 1961, M.T. Lucas, **holotype** of *Leptosphaeria congesta* M.T. Lucas, dried culture LISE 1638, culture ex-holotype CBS 244.64.

***Plenodomus enteroleucus*** (Sacc.) Gruyter, Aveskamp & Verkley, **comb. nov.** MycoBank MB564753.
*Basionym*: *Phoma enteroleuca* Sacc. var. *enteroleuca*, Michelia 1: 358. 1878.

*Specimens examined*: **France**, Alencon, from *Pyrus communis* (*Rosaceae*), 1878, C. C. Gillet, **holotype** of *Phoma enteroleuca* var. *enteroleuca*, Herb. Sacc. '19', PAD. **Germany**, Monheim, from leaf spots of *Triticum aestivum* (*Poaceae*), 15 Aug. 1984, M. Hossfeld, CBS H-3684, culture CBS 831.84. **Netherlands**, Bennekom, from discoloured wood of *Catalpa bignonioides* (*Bignoniaceae*), 1981, G.H. Boerema, **epitype designated here** CBS H-16209, culture ex-epitype CBS 142.84 = PD 81/654 = CECT 20063.

***Plenodomus fallaciosus*** **(**Berl.) Gruyter, Aveskamp & Verkley, **comb. nov.** MycoBank MB564732.
*Basionym*: *Leptosphaeria fallaciosa* Berl., Bull. Soc. Mycol. France. 5: 43. 1889.

*Specimen examined*: **France**, Var, Ste. Baume, from *Satureia montana* (*Lamiaceae*), July 1951, E. Müller, CBS 414.62 = ETH 2961.

***Plenodomus hendersoniae*** (Fuckel) Gruyter, Aveskamp & Verkley, **comb. nov.** MycoBank MB564754.
*Basionym*: *Cucurbitaria hendersoniae* Fuckel, Symb. Myc. p. 172. 1870.
≡ *Melanomma hendersoniae* (Fuckel) Sacc., Syll. Fung. 2: 109. 1883.
≡ *Chiajaea hendersoniae* (Fuckel) Höhn., Sitzungsber. Kaiserl. Akad. Wiss., Math.-Naturwiss. Cl., Abt. 1. 129: 152. 1920.
≡ *Leptosphaeria hendersoniae* (Fuckel) L. Holm, Symb. Bot. Upsal. 14: 26. 1957.
= *Phoma intricans* M.B. Schwarz, Meded. Phytopath. Lab. Willie Commelin Scholten 8: 44. 1922.

*Specimens examined*: **Sweden**, Uppland, Jerusalem, from *Salix cinerea* (*Salicaceae*), 10 Apr. 1986, K. & L. Holm, CBS 113702 = UPSC 1843. **Netherlands**, Wilhelminadorp, from bark of *Pyrus malus* (*Rosaceae*), June 1977, H.A.Th. van der Scheer, CBS 139.78.

***Plenodomus influorescens*** (Boerema & Loer.) Gruyter, Aveskamp & Verkley, **comb. nov.** MycoBank MB564755.
*Basionym*: *Phoma enteroleuca* var. *influorescens* Boerema & Loer., Trans. Brit. Mycol. Soc. 84: 290. 1985.

*Specimens examined*: **Netherlands**, from *Lilium* sp. (*Liliaceae*), 1973, G.H. Boerema, PD 73/1382; Emmeloord, from *Fraxinus excelsior* (*Oleaceae*), 1978, J.D. Janse, **holotype** of *Phoma enteroleuca* var. *influorescens*, CBS H-16208, culture ex holotype CBS 143.84 = PD 78/883 = CECT 20064.

*Note*: The isolate PD 73/1382 is no longer available for study.

***Plenodomus libanotidis*** (Fuckel) Gruyter, Aveskamp & Verkley, **comb. nov.** MycoBank MB564756.
*Basionym*: *Pleospora libanotidis* Fuckel, Jahrb. Nassauischen Vereins Naturk. 27–28: 24. 1873 (as "*libanotis*").
≡ *Leptosphaeria libanotidis* **(**Fuckel) Sacc., Syll. Fung. 2: 16. 1883 (as "*libanotis*").
= *Phoma sanguinolenta* Rostr., Tidsskr. Landokon. 5(7): 384. 1888 (not *Phoma sanguinolenta* Grove, J. Bot. 23: 164. 1885).
≡ *Phoma rostrupii* Sacc., Syll. Fung. 11: 490. 1895, nom. nov.

*Specimen examined*: **Sweden**, Uppland, Gröna strand, from *Seseli libanotis* (*Apiaceae*), 19 May 1987, K. & L. Holm, CBS 113795 = UPSC 2219.

***Plenodomus lindquistii*** (Frezzi) Gruyter, Aveskamp & Verkley, **comb. nov.** MycoBank MB564757.
*Basionym*: *Leptosphaeria lindquistii* Frezzi, Revista Invest. Agropec., Sér. 5, 5: 79. 1968.
= *Phoma macdonaldii* Boerema, Persoonia 6: 20. 1970.

*Specimens examined*: **Canada**, from *Helianthus annuus* (*Asteraceae*), 1967, W.C. McDonald, CBS 381.67. Former **Yugoslavia**, from stem of *Helianthus annuus*, 1977, A. Maric, CBS 386.80 = PD 77/336.

*Note*: Strain CBS 381.67 is ex-holotype of *Phoma macdonaldii* Boerema, pycnidial state of *Leptosphaeria lindquistii* Frezzi (Boerema 1970).

***Plenodomus lingam*** (Tode : Fr.) Höhn., Sitzungsber. Kaiserl. Akad. Wiss., Math.-Naturwiss. Cl., Abt. 1. 120: 463. 1911.
*Basionym*: *Sphaeria lingam* Tode : Fr., Fungi mecklenb. 2: 51. 1791. : Fr., Syst. Mycol. 2: 507. 1823.
≡ *Phoma lingam* (Tode : Fr.) Desm., Ann. Sci. Nat., Bot. Ser. 3, 11: 281. 1849.
= *Sphaeria maculans* Desm., Ann. Sci. Nat., Bot. Ser. 3, 6: 77. 1846, nom. illeg.
≡ *Leptosphaeria maculans* (Desm.) Ces. & De Not., Comment. Soc. Crittog. Ital. 1: 235. 1863.
= *Plenodomus rabenhorstii* Preuss, Linnaea 24: 145. 1851, nom. dub.

*Specimens examined*: **Netherlands**, near Goes, from *Brassica oleracea* (*Brassicaceae*), 1978, M.M.J. Dorenbosch, CBS 260.94 = PD 78/989. Origin unknown, Mar. 1924, A. Weber, CBS 147.24. **UK**, from *Brassica* sp. (*Brassicaceae*), 1963, B.C. Sutton, CBS 275.63 = MUCL 9901= UPSC 1025.

*Notes*: The combination *Plen. lingam* as published by van Höhnel (1911) was preferred over *Plen. rabenhorstii* Preuss (1851) by Boerema & van Kesteren (1964) because the type material of *Plen. rabenhorstii* had been lost during the Second World War. Therefore, *Plen. rabenhorstii* is indicated here as a *nomen dubium*. *Leptosphaeria maculans* causes a serious stem base canker (blackleg) on cultivated *Brassica* spp. (*Brassicaceae*) in Europe, Australia and North America (West *et al.* 2001, Fitt *et al.* 2006).

***Plenodomus lupini*** (Ellis & Everh.) Gruyter, Aveskamp & Verkley, **comb. nov.** MycoBank MB564758.
Basionym: *Phoma lupini* Ellis & Everh., Bull. Washburn Lab. Nat. Hist. 1: 6. 1884.
≡ *Asteromella lupini* (Ellis & Everh.) Petr., Sydowia 9: 495. 1955 (not *Phoma lupini* N.F. Buchw., Møller, Fungi Faeröes 2: 153. 1958, nom. illeg).

*Specimen examined*: **Peru**, Andes region, from stem lesion of *Lupinus mutabilis* (*Fabaceae*), May 1992, J. de Gruyter, CBS 248.92 = PD 79/141.

***Plenodomus pimpinellae*** (Lowen & Sivan.) Gruyter, Aveskamp & Verkley, **comb. nov.** MycoBank MB564759.
*Basionym*: *Leptosphaeria pimpinellae* Lowen & Sivan., Mycotaxon 35: 205. 1989.
= *Phoma pimpinellae* Boerema & Gruyter, Persoonia 17: 278. 1999.

*Specimen examined*: **Israel**, Mt Carmel near Kibbutz Oren, from dead stems of *Pimpinella anisum* (*Apiaceae*), 9 Dec. 1987, R. Rowen, 523-88 NY, **holotype** of *Leptosphaeria pimpinellae* Lowen & Sivan, culture ex-holotype CBS 101637 = PD 92/41.

***Plenodomus tracheiphilus*** (Petri) Gruyter, Aveskamp & Verkley, **comb. nov.** MycoBank MB564760.
*Basionym*: *Deuterophoma tracheiphila* Petri, Boll. Staz. Patol. Veg. Roma 9: 396. 1929.
≡ *Bakerophoma tracheiphila* (Petri) Cif., Ist. Bot. Reale Univ. Reale Lab. Crittog. Pavia Atti Ser. 5, 5: 307. 1946.
≡ *Phoma tracheiphila* (Petri) L.A. Kantsch. & Gikaschvili, Trudy Inst. Zasch. Rast. Tibilisi 5: 20. 1948.

*Specimens examined*: **Israel**, from *Citrus limonium* (*Rutaceae*), Oct. 1993, J. de Gruyter, CBS 551.93 = PD 81/782. **Italy**, from *Citrus* sp. (*Rutaceae*), CBS 127250 = PD 09/04597141.

*Note*: The species produces a phialophora-like synanamorph.

***Plenodomus visci*** (Moesz) Gruyter, Aveskamp & Verkley, **comb. nov.** MycoBank MB564761.
*Basionym*: *Plectophomella visci* Moesz, Magyar Bot. Lapok 21: 13. 1922.
= *Apocytospora visci* Höhn., Mitt. Bot. Lab. TH Wien 1: 43. 1924.

*Specimen examined*: **Hungary**, Tata-Tóváros, from leaves of *Viscum album* (*Viscaceae*), 22 Oct. 1911, G. von Moesz, BP, **holotype** of *Plectophomella visci* Moesz. **France**, from *Viscum album*, 1974, **epitype designated here** CBS H-20823, culture ex-epitype CBS 122783 = PD 74/1021.

*Notes*: *Plectophomella visci* is the type species of the genus *Plectophomella.* This genus was accepted by Sutton (1980) based on the eustromatic conidiomata; branched, septate conidiophores, phialidic conidiogenesis and small, hyaline conidia. However, the phylogenetic analyses clearly demonstrated the placement of *Plectophomella* grouping in the *Plenodomus* clade and therefore it is treated as a synonym.

***Plenodomus wasabiae*** (Yokogi) J.F. White & P.V. Reddy, Canad. J. Bot. 76: 1920. 1999 (1998).
*Basionym*: *Phoma wasabiae* Yokogi, Ann. Phytopathol. Soc. Japan 2: 549. 1933.

*Specimens examined*: **Taiwan**, from *Wasabia japonica* (syn. *Eutrema wasabi*) (*Brassicaceae*), A. Rossman, CBS 120119 = FAU 559; from *Wasabia japonica*, A. Rossman, CBS 120120 = FAU 561.

***Subplenodomus*** Gruyter, Verkley & Crous, **gen. nov.** MycoBank MB564769.

*Etymology*: Although the genus resembles *Plenodomus* in the production of thick-walled pycnidia, the pycnidial cell wall of *Subplenodomus* often remains pseudoparenchymatous, similar to the pycnidial wall of species of *Phoma*.

*Conidiomata* pycnidial, globose to papillate, or with an elongated neck, solitary or aggregated, thin-walled pseudoparenchymatous, or thick-walled scleroplectenchymatous, ostiolate, unilocular. *Conidiogenous cells* phialidic, ampulliform to doliiform. *Conidia* hyaline, aseptate, ellipsoid to cylindrical. *Chlamydospores* sometimes produced, olivaceous, unicellular in chains, or multicellular, dictyosporous-botryoid or forming pseudosclerotioid structures.

*Type species*: *Subplenodomus violicola* (P. Syd.) Gruyter, Aveskamp & Verkley (see below)

***Subplenodomus apiicola*** (Kleb.) Gruyter, Aveskamp & Verkley, **comb. nov.** MycoBank MB564770.
*Basionym*: *Phoma apiicola* Kleb., Z. Pflanzenkrankh. 20: 22. 1910.

*Specimens examined*: **Germany**, from tuber of *Apium graveolens* var. *rapaceum* (*Apiaceae*), Feb. 1972, Diercks, culture CBS 285.72. **Netherlands**, from stem base of *Apium graveolens*, 1978, J. de Gruyter, CBS 504.91 = PD 78/1073.

***Subplenodomus drobnjacensis*** (Bubák) Gruyter, Aveskamp & Verkley, **comb. nov.** MycoBank MB564771.
*Basionym*: *Phoma drobnjacensis* Bubák, Bot. Közlem. 14: 63. 1915
= *Pyrenochaeta gentianae* Chevassut, Bull. Soc. Mycol. France. 81: 36. 1965.

*Specimens examined*: **Netherlands**, from stem base of *Gentiana makinoi* “Royal Blue” (*Gentianaceae*), 1983, M.M.J. Dorenbosch, CBS 270.92 = PD 83/650; Naaldwijk, from red-brown root of *Eustoma exaltatum* (*Gentianaceae*), 1988, M.M.J. Dorenbosch, CBS 269.92 = PD 88/896.

***Subplenodomus valerianae*** (Henn.) Gruyter, Aveskamp & Verkley, **comb. nov.** MycoBank MB564772.
*Basionym*: *Phoma valerianae* Henn., Nyt Mag. Naturvidensk. 42: 29. 1904.
= *Phyllosticta valerianae-tripteris* f. *minor* Unamuno, Mem. Real Soc. Esp. Hist. Nat. 15: 348. 1929.

*Specimens examined*: **Netherlands**, Arnhem, from dead stem of *Valeriana phu* (*Valerianaceae*), Sep. 1968, G.H. Boerema, CBS 630.68 = PD 68/141; Elburg, from stem base of *Valeriana officinalis*, 1973, M.M.J. Dorenbosch, culture CBS 499.91 = PD 73/672.

***Subplenodomus violicola*** (P. Syd.) Gruyter, Aveskamp & Verkley, **comb. nov.** MycoBank MB564774.
*Basionym*: *Phoma violicola* P. Syd., Beibl. Hedwigia 38: 137. 1899.
= *Phyllosticta violae* f. *violae-hirtae* Allesch. Rabenh.-Fl., Ed. 2, Pilze 6: 156. 1898.
= *Phoma violae-tricoloris* Died., Ann. Mycol. 2: 179. 1904.
= *Phyllosticta violae* f. *violae-sylvaticae* Gonz. Frag., Trab. Mus. Nac. Ci. Nat., Ser. Bot. 7: 35. 1914.

*Specimens examined*: **Netherlands**, Baarn, from leaf spot in *Viola tricolor*, 10 Mar. 1968, H.A. van der Aa, CBS 306.68. **New Zealand**, Auckland, Henderson, from leaf spot in *Viola tricolor* (*Violaceae*), 1997, J. Jury, CBS 100272.

***Coniothyriaceae*** W.B. Cooke. Revista Biol. (Lisbon) 12: 289. 1983.

***Coniothyrium carteri*** (Gruyter & Boerema) Verkley & Gruyter, **comb. nov.** MycoBank MB564775.
*Basionym*: *Phoma carteri* Gruyter & Boerema, Persoonia 17(4): 547. 2002 (“2001”), nom. nov.
*Replaced synonym*: *Pyrenochaeta minuta* J.C. Carter, Bull. Illinois Nat. Hist. Surv. 21: 214. 1941 [not *Phoma minuta* Wehm., Mycologia 38: 318. 1946, nor *Phoma minuta* Alcalde, Anales Inst. Bot. Cavanilles 10: 235. 1952; not *Coniothyrium minutum* (Berl.) O. Kuntze, Revis. Gen. Pl. 3: 459. 1898 = *Phoma cava*, syn. of *Pyrenochaeta cava*; not *Coniothyrium minutum* (Died) Petr. & Syd., Feddes Repert. Spec. Nov. Regni Veg. Beih. 42: 349. 1927].

*Specimens examined*: **Germany,** isolated from *Quercus robur* (*Fagaceae*), 1991, CBS 105.91. **Netherlands**, from shoot of *Quercus* sp. (*Fagaceae*), 1984, M.M.J. Dorenbosch, CBS 101633 = PD 84/74.

***Coniothyrium dolichi*** (Mohanty) Verkley & Gruyter, **comb. nov.** MycoBank MB564776.
*Basionym*: *Pyrenochaeta dolichi* Mohanty, Indian Phytopathol. 11: 85. 1958.

*Specimen examined*: **India**, Nani Tal, Sarichuan, from leafspot of *Dolichos biflorus* (*Fabaceae*), 20 Oct. 1955, N.N. Mohandy, CBS 124140 = IMI 217262, CBS 124143 = IMI 217261.

*Notes*: A synanamorph was noted and described as a *Coniosporium* state based on the dark brown to black, dictyosporous conidia (Mohanty 1958). This synanamorph was considered later as monodictys-like (Grodona *et al.* 1997).

***Coniothyrium glycines*** (R.B. Stewart) Verkley & Gruyter, **comb. nov.** MycoBank MB564777.
*Basionym*: *Pyrenochaeta glycines* R.B. Stewart, Mycologia 49: 115. 1957.
≡ *Phoma glycinicola* Gruyter & Boerema, Persoonia 17: 554. 2002 (“2001”), nom. nov., nom. inval. (not *Phoma glycines* Sawada, Special. Publ. Coll. Agric., Natl. Taiwan Univ. 8: 129. 1959, nom. inval). ≡ *Phoma glycines* Sawada ex J.K. Bai & G.Z. Lu, Fl. Fungorum Sin. 15: 33. 2003.

*Specimens examined*: **Zambia**, on Mt. Makulu, from leaf of *Glycine max* (*Fabaceae*), Mar. 1985, J.M. Waller, CBS 124455 = IMI 294986. **Zimbabwe,** from a leaf of *Glycine max* (*Fabaceae*), 2001, C. Lavy, CBS 124141 = PG1.

***Coniothyrium multiporum*** (V.H. Pawar, P.N. Mathur & Thirum.) Verkley & Gruyter, **comb. nov.** MycoBank MB564778.
*Basionym*: *Phoma multipora* V.H. Pawar, P.N. Mathur & Thirum., Trans. Brit. Mycol. Soc. 50: 260. 1967.
≡ *Phoma multipora* V.H. Pawar & Thirum., Nova Hedwigia 12: 501. 1966, nom. nud.

*Specimens examined*: **Egypt**, CBS 501.91 = PD 83/888. **India,** Bombay, Bandra, from saline soil, 15 Jan. 1958, M.J. Thirumalachar, **Isotype** CBS H-16492, culture ex-isotype CBS 353.65 = ATCC 16207 = HACC 164 = IMI 113689.

***Coniothyrium palmarum*** Corda, Icon. Fungorum. (Corda) 4: 38. 1840.
≡ *Clisosporium palmarum* (Corda) Kuntze, Revis. Gen. Pl. 3: 458. 1898.
≡ *Microdiplodia palmarum* (Corda) Died., Ann. Mycol. 11: 47. 1913.

*Specimens examined*: **Italy**, Sardegna, near Dorgali, from a dead petiole of *Chamaerops humilis* (*Arecaceae*), Aug. 1970, W. Gams, CBS H-10891–10893, culture CBS 400.71.

***Coniothyrium telephii*** (Allesch.) Verkley & Gruyter, **comb. nov.** MycoBank MB564779.
*Basionym*: *Pyrenochaeta telephii* Allesch., Ber. bayer. bot. Ges. 4: 33. 1896.
≡ *Phoma septicidalis* Boerema, Versl. Meded. Plantenziektenk. Dienst Wageningen 153 (Jaarb. 1978): 20. 1979, nom. nov. [not *Phoma telephii* (Vestergr.) Kesteren, Netherlands J. Pl. Pathol. 78: 117. 1972].

*Specimens examined*: **Finland**, Helsinki, Asko Kahanpää, obtained from air, Jan. 1971, CBS H-16567, culture CBS 188.71; Oulu, from mineral wool between walls, Dec. 1996, K. Poldmaa, CBS 856.97. **Zimbabwe**, from leaf of *Glycine max* (*Fabaceae*), CBS 101636 = PD 86/1186.

***Cucurbitariaceae*** G. Winter, Rabenh, Krypt.-Fl., Ed 2, 308. 1885.

***Neophaeosphaeria filamentosa*** **(**Ellis & Everh.) Câmara, M.E. Palm & A.W. Ramaley, Mycol. Res. 107: 519. 2003.
*Basionym*: *Leptosphaeria filamentosa* Ellis & Everh., J. Mycol. 4: 76. 1888.
≡ *Paraphaeosphaeria filamentosa* **(**Ellis & Everh.) M.E. Barr, Mycotaxon 43: 392. 1992.

*Specimen examined*: **Mexico**, from *Yucca rostrata* (*Asparagaceae*), Stevens, CBS 102202 = BPI 802755.

***Pyrenochaetopsis pratorum*** **(**P.R. Johnst. & Boerema) Gruyter, Aveskamp & Verkley, **comb. nov.** MycoBank MB564780.
*Basionym*: *Phoma pratorum* P.R. Johnst. & Boerema, New Zealand J. Bot. 19: 395. 1981.

*Specimens examined*: **New Zealand,** Rakura, near Hamilton, from a leaf of *Lolium perenne* (*Poaceae*), 1980, P.R. Johnston, isotype CBS H-7625, CBS H-7626, culture CBS 445.81 = PDDCC 7049 = PD 80/1254; *Dactylis glomerata* (*Poaceae*), 1980, CBS 286.93 = PD 80/1252.

***Pleosporaceae*** Nitschke, Verh. Naturhist. Vereines Preuss. Rheinl. 26: 74. 1869.

***Pleospora angustis*** Gruyter & Verkley, **nom. nov.** MycoBank MB564781.
≡ *Leptosphaeria clavata* A.L. Guyot, Revue Mycol. (Paris) 11: 62. 1946.
≡ *Massariosphaeria clavata* (A.L. Guyot) Shoemaker & C.E. Babc., Canad. J. Bot. 67: 1582.1989; not *Pleospora clavata* Gucevič ("as *clavatis*"), Novosti Sist. Nizsh. Rast. 7: 168. 1970.

*Specimen examined*: **Switzerland**, 1951, E. Müller, CBS 296.51.

*Notes*: The origin of the isolate deposited by E. Müller is unknown; however, it is likely that the isolate was obtained from *Poaceae*, *Triticum vulgare* or *Dactylis glomerata* (Müller 1950). *Pleospora clavata* Gucevič was obtained from *Lonicera alseuosmoides* and refers to a different species.

***Pleospora betae*** (Berl.) Nevod., Grib. ross. Exs., No. 247. 1915.
*Basionym*: *Pyrenophora echinella* var. *betae* Berl. Nuovo Giorn. Bot. Ital. 20: 208. 1888.
= *Pleospora betae* Björl., Bot. Not. 1944: 218. 1944. (later homonym), nom. illeg.
≡ *Pleospora bjoerlingii* Byford, Trans. Brit. Mycol. Soc. 46: 614. 1963, nom. nov.
= *Phoma betae* A.B. Frank, Z. Rúbenzucker-Ind. 42: 904, tab. 20. 1892.
= *Phyllosticta betae* Oudem., Ned. Kruidk. Arch. Ser. 2, 2: 181. 1877.
= *Gloeosporium betae* Dearn. & E.T. Barthol., Mycologia 9: 356. 1917.

*Specimens examined*: **Netherlands**, Wageningen, from *Beta vulgaris* (*Chenopodiaceae*), Sep. 1966, M.M.J. Dorenbosch, CBS H-16156, culture CBS 523.66 = IHEM 3915 = PD 66/270; from *Beta vulgaris*, 1977, G.H. Boerema, CBS 109410 = PD 77/113.

*Note*: The name *Phoma betae* A.B. Frank has been conserved against *Phyllosticta tabifica* and any combination based on that name (Shoemaker & Redhead 1999).

***Pleospora calvescens*** (Fr.) Tul. & C. Tul., Selecta Fung. Carpol. (Paris) 2: 266. 1863.
*Basionym*: *Sphaeria calvescens* Fr., Ann. Sci. Nat., Bot. Ser. 2, 19: 353. 1843.
≡ *Leptosphaeria calvescens* (Fr.) Sacc., Syll. fung. 2: 24. 1883.
≡ *Pyrenophora calvescens* (Fr.) Sacc., Syll. fung. 2: 279. 1883.
= *Chaetodiplodia caulina* P. Karst., Hedwigia 23: 62. 1884.
≡ *Ascochyta caulina* (P. Karst.) v.d. Aa & Kesteren, Persoonia 10: 271. 1979.
= *Microdiplodia henningsii* Staritz, Hedwigia 53: 163. 1913.

*Specimens examined*: **Germany**, Munkmarsch, from leaf spots in *Atriplex hastata* (*Chenopodiaceae*), 20 July 1977, G.H. Boerema, CBS H-8980, culture CBS 246.79 = PD 77/655. **Netherlands**, Texel, from dead stem of *Atriplex hastata,* June 1978, H.A. van der Aa, CBS H-8976, culture CBS 343.78.

*Note:* For additional synonyms see Boerema *et al.* (1993).

***Pleospora chenopodii*** Ellis & Kellerman, J. Mycol. 4: 26. 1888.
= *Diplodia hyalospora* Cooke & Ellis, Grevillea 7: 5. 1878 (not *Pleospora hyalospora* Ellis & Everh., Proc. Acad. Nat. Sci. Philadelphia. 42: 238. 1890).
≡ *Ascochyta hyalospora* (Cooke & Ellis) Boerema, S.B. Mathur & Neerg., Netherlands J. Pl. Pathol. 83: 156. 1977.
= *Diplodina ellisii* Sacc., Syll Fung. 3: 417. 1884

*Specimens examined*: **Bolivia**, isolated from *Chenopodium quinoa* (*Chenopodiaceae*), 1974, S.B. Mathur, CBS H-9051, CBS H-9052, culture CBS 206.80 = PD 74/1022. **Netherlands**, Zoutelande, from *Atriplex hastata* (*Chenopodiaceae*), Aug. 1968, H.A. van Kesteren, CBS 344.78 = PD 68/682.

*Note*: Isolate CBS 344.78 was originally identified as *Ascochyta caulina* but was identical to *Pleospora chenopodii* in the present study.

***Pleospora fallens*** (Sacc.) Gruyter & Verkley, **comb. nov.** MycoBank MB564782.
*Basionym*: *Phoma fallens* Sacc., Syll. Fung. 10: 146. 1892.

= *Phyllosticta glaucispora* Delacr., Bull. Soc. Mycol. France 9: 266. 1893.
≡ *Phoma glaucispora* (Delacr.) Noordel. & Boerema, Versl. Meded. Plantenziektenk. Dienst Wageningen 166 (Jaarb. 1987): 108. 1989 ("1988").
= *Phyllosticta oleandri* Gutner, Trudy Bot. Inst. Akad. Nauk S.S.S.R., Ser. 2, Sporov. Rast. 1: 306. 1933.

*Specimens examined*: **Italy**, Capri, Villa Jovis, from a leaf spot of *Nerium oleander* (*Apogynaceae*), CBS H-16639, culture CBS 284.70 = PD 97/2400. **New Zealand**, Levin, from leaf spot of *Olea europaea* (*Oleaceae*), 1978, G.F. Laundon, CBS 161.78 = LEV 1131.

***Pleospora flavigena*** (Constantinou & Aa) Gruyter & Verkley, **comb. nov.** MycoBank MB564783.
*Basionym*: *Phoma flavigena* Constantinou & Aa, Trans. Brit. Mycol. Soc. 79: 343. 1982.

*Specimen examined*: **Romania**, Bucuresti, isolated from water, 1980, K. Fodor, CBS H-1418, **holotype** of *Phoma flavigena* Constantinou & Aa, culture ex-holotype CBS 314.80 = PD 91/1613.

***Pleospora halimiones*** Gruyter & Verkley, **nom. nov.** MycoBank MB564784.

≡ *Diplodina obiones* Jaap (as "*obionis*"), Verh. Bot. Vereins Prov. Brandenburg 47: 96. 1905 (not *Pleopora obiones* P. Crouan & H. Crouan, Fl. Finistère: 22. 1867).
≡ *Ascochytula obiones* (Jaap) Died., Ann. Mycol. 10: 141. 1912.
≡ *Ascochyta obiones* (Jaap) P.K. Buchanan, Mycol. Pap. 156: 28 1987.
= *Coniothyrium obiones* Jaap (as "*obionis*"), Schriften Naturwiss. Vereins Schleswig-Holstein 14: 29. 1907.

*Specimens examined*: **Netherlands**, Texel, from leaf spots in *Halimione portulacoides* (*Chenopodiaceae*), 27 Oct. 1968, H.A. van der Aa, CBS H-9127, CBS H-9129, culture CBS 786.68; Texel, De Cocksdorp, from dead stems of *Halimione portulacoides*, 6 July 1977, H.A. van der Aa, CBS H-9126, CBS H-9125, culture CBS 432.77 = IMI 282137.

*Notes*: Isolate CBS 453.68 preserved as *Chaetodiplodia* sp. and also isolated from dying stems and leaf sheaths of *Halimione portulacoides* on Texel, is not the same as *Pleo. halimiones* and is probably a different species.

***Pleospora herbarum*** (Pers.) Rabenh., Bot. Zeitung (Berlin) 15: 428. 1857; Klotzschii Herb. Viv. Mycol. 2: no. 547 (1854.)
*Basionym*: *Sphaeria herbarum* Pers., Syn. Meth. Fung. 1: 78. 1801.

= *Stemphylium herbarum* E.G. Simmons, Sydowia 38: 291. 1986 (1985).

*Specimen examined*: **India**, Uttar Pradesh, from a leaf of *Medicago sativa* (*Fabaceae*), 1986 (isolated in 1983), E.G. Simmons, CBS 191.86 = IMI 276975.

*Note*: This isolate is the ex-type culture of *Stemphylium herbarum*.

***Pleospora incompta*** (Sacc. & Martelli) Gruyter & Verkley, **comb. nov.** MycoBank MB564785.
*Basionym*: *Phoma incompta* Sacc. & Martelli, Syll. Fung. 10: 146. 1892.

*Specimens examined*: **Greece**, Crete, from branch of *Olea europaea* (*Oleaceae*), 1976, N. Malathrakis, CBS H-16394, culture CBS 467.76. **Italy**, from branch of *Olea europaea*, Mar. 1982, CBS H-16392, culture CBS 526.82.

***Pleospora typhicola*** (Cooke) Sacc., Syll. Fung. 2: 264. 1883.
*Basionym*: *Sphaeria typhicola* Cooke, Grevillea 5: 121. 1877.

≡ *Clathrospora typhicola* (Cooke) Höhn., Ann. Mycol. 16: 88. 1918.
≡ *Pyrenophora typhicola* (Cooke) E. Müll., Sydowia 5: 256. 1951.
≡ *Macrospora typhicola* (Cooke) Shoemaker & C.E. Babc., Canad. J. Bot. 70: 1644. 1992.
= *Phyllosticta typhina* Sacc. & Malbr., Sacc., Michelia 2: 88. 1880.
≡ *Phoma typhina* (Sacc. & Malbr.) van der Aa & Vanev, A revision of the species described in *Phyllosticta*: 468. 2002.
= *Phoma typharum* Sacc., Syll. Fung. 3: 163. 1884.

*Specimens examined*: **Netherlands,** Texel, from dead leaves of *Typha angustifolia* (*Typhaceae*), 1969, W. Gams, CBS H-16597, culture CBS 132.69; Staverden, from leaf spots of *Typha* sp., 24 June 1972, G.S. de Hoog, CBS H-16598, culture CBS 602.72.

## Phoma-like anamorphs excluded from the suborder *Pleosporineae*

***Montagnulaceae*** M.E. Barr, Mycotaxon 77: 194. 2001.

***Paraconiothyrium*** Verkley, Stud. Mycol. 50: 327. 2004.

*Type species*: *Paraconiothyrium estuarinum* Verkley & M. da Silva, Stud. Mycol. 50: 327. 2004.

***Paraconiothyrium flavescens*** (Gruyter, Noordel. & Boerema) Verkley & Gruyter, **comb. nov.** MycoBank MB564786.
*Basionym*: *Phoma flavescens* Gruyter, Noordel. & Boerema, Persoonia 15(3): 375. 1993.

*Specimen examined*: **Netherlands**, Nagele, from soil, rhizosphere of *Solanum tuberosum* (*Solanaceae*), CBS 178.93 = PD 82/1062.

***Paraconiothyrium fuckelii*** (Sacc.) Verkley & Gruyter, **comb. nov.** MycoBank MB564787.
*Basionym*: *Coniothyrium fuckelii* Sacc., Nuovo Giorn. Bot. Ital. 8: 200. 1876; Michelia 1: 207. 1878

≡ *Clisosporium fuckelii* (Sacc.) Kuntze, Revis. Gen. Pl. 3: 458. 1898.
≡ *Microsphaeropsis fuckelii* (Sacc.) Boerema, 2003, Persoonia 18: 160. 2003.

*Specimen examined*: **Denmark**, Geelskov, from a dead stem of *Rubus* sp. (*Rosaceae*), 1995, A.M. Dahl-Jensen, CBS 797.95.

*Notes*: *Coniothyrium fuckelii* var. *sporulosum* has been redisposed as *Paraconiothyrium sporulosum* (Verkley *et al.* 2004) and it is clearly different from *Paraconiothyrium fuckelii* (Damm *et al*. 2008).

***Paraconiothyrium fusco-maculans*** (Sacc.) Verkley & Gruyter, **comb. nov.** MycoBank MB564788.
*Basionym*: *Phoma fusco-maculans* Sacc., Michelia 2: 275. 1881

≡ *Plenodomus fusco-maculans* (Sacc.) Coons, J. Agric. Res. 5: 714. 1916.

*Specimens examined*: **Italy**, Selva, from decorticated wood of *Malus pumila* (*Rosaceae*), Oct. 1880, PAD, **holotype** of *Phoma fusco-maculans* Sacc. **USA**, from wood of *Malus* sp. (*Rosaceae*), July 1916, G.H. Coons, **epitype designated here** CBS H-20825, culture ex-epitype CBS 116.16.

*Notes*: *Plenodomus fusco-maculans* was discussed by Boerema & Loerakker (1985) and de Gruyter *et al*. (2010). The holotype of the basionym *Aposphaeria fusco-maculans* was studied and considered to be *Aposphaeria pulviscula* (Boerema *et al*. 1996). However, the description of *A. fusco-maculans* given by Boerema *et al*. (1996) fits the generic concept of *Paraconiothyrium,* in congruence with the molecular phylogeny of the culture CBS 116.16.

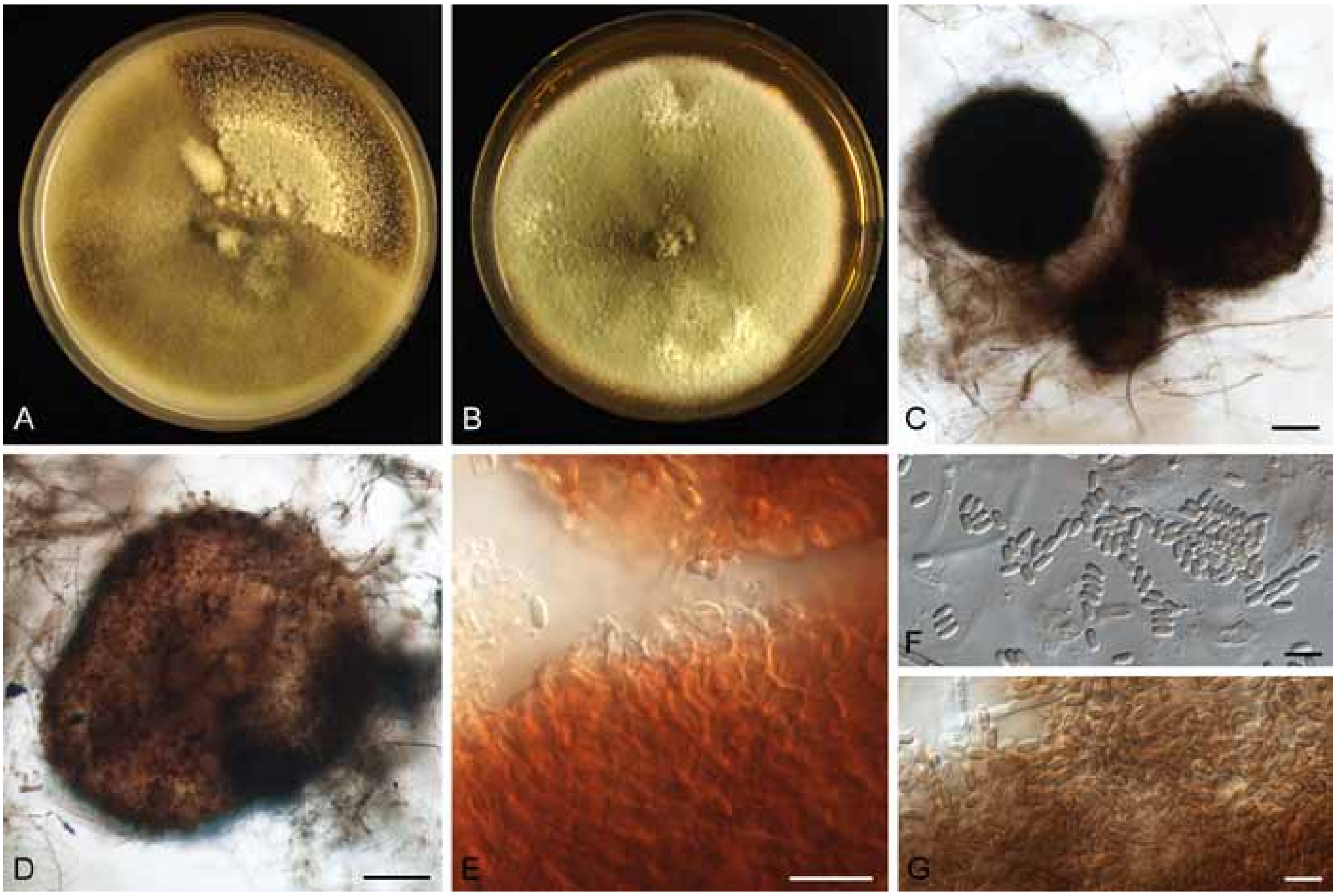


**Fig. 6.** *Paraconiothyrium maculicutis* sp. nov. CBS 101461. A–B. Fourteen day old cultures on OA (A) and MA (B). C–D. Pycnidia. E. Phoma-like conidiogenous cells. F–G. Conidia, initially hyaline to pale olivaceous (F), then becoming olivaceous (G). Scale bars: C–D = 20 µm; E = 10 µm; F–G = 5 µm.

***Paraconiothyrium lini*** (Pass.) Verkley & Gruyter, **comb. nov.** MycoBank MB564789.
*Basionym*: *Phoma lini* Pass., Diagn. Funghi Nuovi 4, No. 81. 1890.

*Specimen examined*: **Netherlands**, from Wisconsin tank, 1970, CBS 253.92 = PD 70/998.

***Paraconiothyrium maculicutis*** Verkley & Gruyter, **sp. nov.** MycoBank MB564796. Fig. 6.

*Etymology*: Latin, cutis = skin; maculae = spots.

*Pycnidia in vitro* 50–125 µm diam, globose to subglobose, glabrous or with mycelial outgrowth, scattered, non-ostiolate or ostiolate, pycnidial wall made up of 5–7 layers of cells. *Conidiogenous cells* 1.5–3 × 0.5–2.5 µm, indeterminate or ampulliform to filiform in a later state, up to 10 µm in length. *Conidia* 1.5–2.5 × 0.5–1.5 µm, ellipsoidal, initially hyaline, then discolouring to olivaceous.

*Description in vitro*: *Colonies* on OA 50–52 mm diam after 7 d, margin entire; colony olivaceous buff to greenish olivaceous/grey olivaceous, with greenish olivaceous to pale olivaceous grey, finely floccose to woolly aerial mycelium; reverse smoke-grey to greenish olivaceous, with olivaceous patches. Colonies on MEA 43–44 mm diam after 7 d, margin entire; colony pale olivaceous grey to greenish olivaceous, with isabelline to cinnamon at centre, with compact pale olivaceous grey, finely floccose to woolly aerial mycelium; reverse buff to honey, isabelline to olivaceous near margin. *Pycnidia* globose to subglobose, olivaceous to brick, finally olivaceous black, scattered, mainly on the agar, 50–125 µm diam, glabrous or with mycelial outgrowth, non-ostiolate or ostiolate, pycnidial wall made up of 5–7 layers of cells. *Conidiogenous cells* 1.5–3 × 0.5–2.5 µm, ampulliform to filiform in a later state, up to 10 µm in length. *Conidia* 1.5–2.5 × 0.5–1.5 µm, av. 1 × 2 µm, length/width ratio = 1.5–3.2, av. 2.2, ellipsoidal, initially hyaline, then discolouring to olivaceous. *Chlamydospores* absent. NaOH spot test: negative. *Crystals* absent.

*Specimen examined*: **USA**, Texas; San Antonio**,** Fort Sam Houston, from human, cutaneous lesions, 1989, D.P. Dooley, **holotype** CBS H-20824, culture ex-holotype CBS 101461 = IMI 320754 = UTHSC 87-144.

*Notes*: Isolate CBS 101461 was identified as *Pleurophoma pleurospora* (Dooly *et al*. 1989). However, *in vitro* data and the molecular phylogeny demonstrate that this isolate does not belong to *Pleurophoma pleurospora*, see below, and therefore is described as a new species in the genus *Paraconiothyrium*.

***Paraconiothyrium minitans*** (W.A. Campb.) Verkley, Stud. Mycol. 50: 332. 2004.
*Basionym*: *Coniothyrium minitans* W.A. Campb., Mycologia 39: 191. 1947.

*Specimens examined*: **Netherlands**, Boskoop, from stem of *Clematis* sp. (*Ranunculaceae*), 1999, J. de Gruyter, CBS 122786 = PD 99/1064-1. **UK**, CBS 122788 = PD 07/03486739.

***Paraconiothyrium tiliae*** (F. Rudolphi) Verkley & Gruyter, **comb. nov.** MycoBank MB564790.
*Basionym*: *Asteroma tiliae* F. Rudolphi, Linnaea 4: 514. 1829.

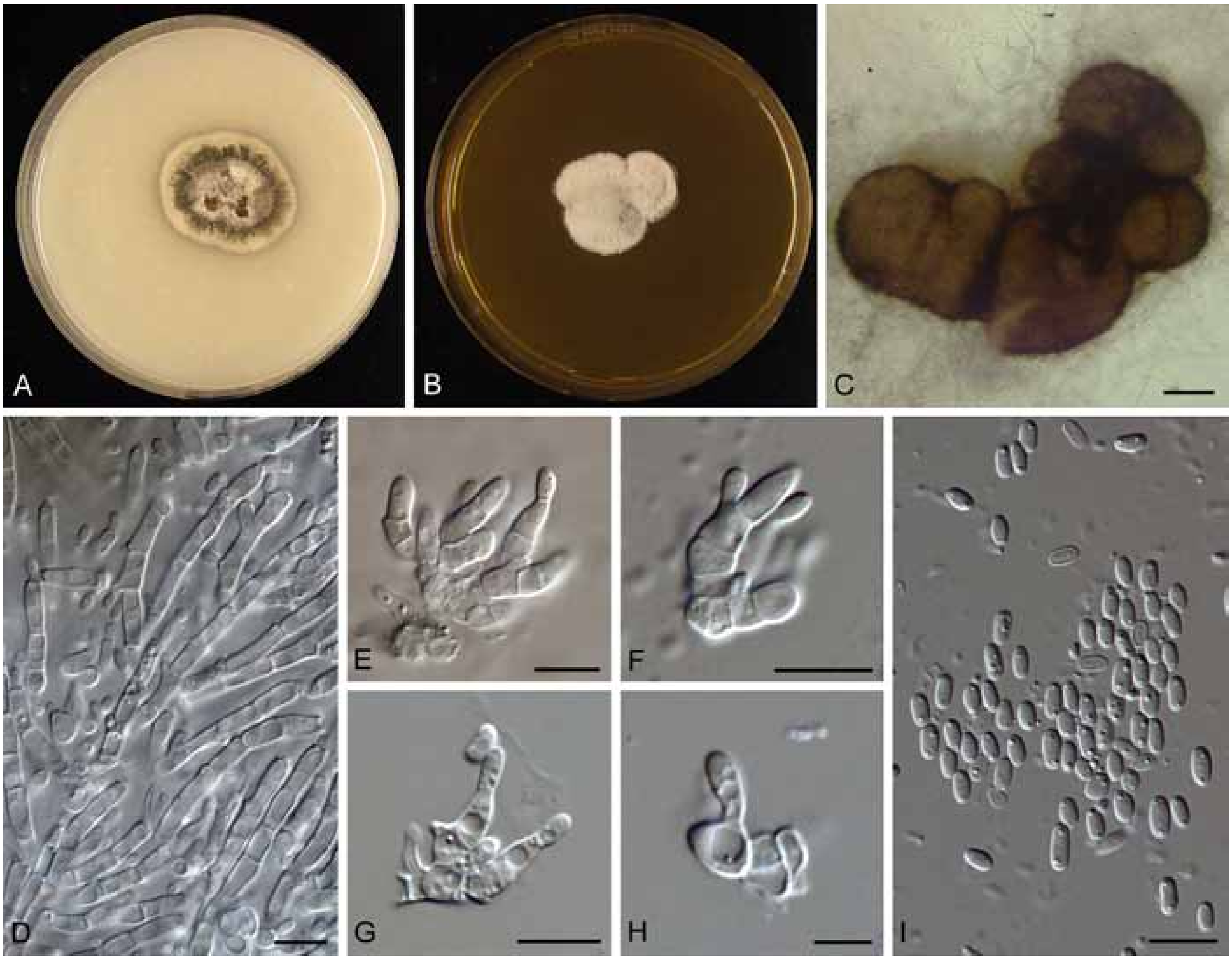


**Fig. 7.** *Pleurophoma pleurospora*. CBS 130329. A–B. Fourteen day old cultures on OA (A) and MA (B). C. Pycnidia. D–H. Conidiogenous cells, septate conidiophores with acropleurogenous conidiogenesis (D–G) or phoma-like (H). I. Conidia. Scale bars: C = 50 µm; D–G, I = 10 µm; H = 5 µm.

≡ *Asteromella tiliae* (F. Rudolphi) Butin & Kehr, Mycol. Res. 99: 1193. 1995, nom. inval., Art. 33.4.

*Specimen examined*: **Austria**, Amlach, from a leaf of *Tilia platyphyllos* (*Tiliaceae*), 10 Sep. 1993, H. Butin, **neotype** IMI 362854, **lectotype designated here** CBS H-20826, culture ex-lectotype CBS 265.94.

***Pleurophoma pleurospora*** (Sacc.) Höhn., Sitzungsber. Kaiserl. Akad. Wiss., Math.-Naturwiss. Cl., Abt. 1. 123: 117. 1914. Fig. 7.
*Basionym*: *Dendrophoma pleurospora* Sacc., Michelia 2: 97. 1880.

*Description in vitro*: *Colonies* on OA 14–18 mm diam after 7 d (18–28 mm after 14 d), margin entire to undulate; colony greenish olivaceous/olivaceous to rosy-buff and sepia, with white, felty aerial mycelium; reverse olivaceous grey to greenish olivaceous/ olivaceous. Colonies on MEA 11–16 mm diam after 7 d (19–29 mm after 14 d), colony margin undulate; colony pale olivaceous grey/ olivaceous grey to dark mouse-grey with rosy-buff tinges, with white, floccose, compact aerial mycelium, reverse umber/ brown olivaceous to olivaceous/olivaceous black. *Pycnidia* globose to subglobose,olivaceous to olivaceous black, abundant, scattered, mainly on the agar, 30–120 µm diam, solitary or aggregated, covered by mycelial outgrowths or setae-like hyphae, up to 50 µm, non-papillated, without or with ostiole, walls made up of 2–5 layers of cells, outer layer(s) pigmented; conidial exudate not observed. *Conidiogenous cells* of two types; ampulliform to doliiform, 4–6.5 × 2–5.5 µm, or filiform, septate, branched, acropleurogenous, up to 60 µm long. *Conidia* 3.5–5.5 × 1.5–2.5 µm, av. 4.5 × 2 µm, length/ width ratio = 1.5–3, av. 2.1, cylindrical to oblong, without or with some minute, polar orientated guttules. *Chlamydospores* absent. NaOH spot test: a weak reddish discolouring may occur on MA, not specific. *Crystals* absent.

*Specimens examined*: **France**, Perpignan, from leaf of *Laurus nobilis* (*Lauraceae*), PAD, **holotype** of *Dendrophoma pleurospora* Sacc. **Netherlands**, from wood of *Lonicera* sp. (*Caprifoliaceae*), **lectotype designated here** CBS H-20626, culture ex-lectotype CBS 130329 = PD 82/371; Molenhoek, Heumense Schans, from twig lesions of *Cytisus scoparius* (*Fabaceae*), 23 Aug. 2004, G. Verkley & M. Starink, CBS 116668.

*Notes*: A specimen derived from isolate CBS 130329 is assigned here as lectotype of *Pleurophoma pleurospora,* the type species of the genus (von Höhnel 1914). The species is known from branches and bare wood of trees and shrubs (Sutton 1980, Boerema *et al.* 1996) and the isolate from *Cytisus scoparius* demonstrates that the species also may occur on green twigs. The isolates showed two types of conidiogenesis characteristic for the genus *Pleurophoma*; phoma-like, ampulliform to doliiform conidiogenous cells, as well as pyrenochaeta-like branched, filiform, septate, acropleurogenous. As a result, species of the genus *Pleurophoma* can easily be confused with taxa classified in the genera *Phoma, Paraphoma, Pyrenochaeta* and *Pyrenochaetopsis*.

***Paraphaeosphaeria michotii*** **(**Westend.) O.E. Erikss., Arkiv før Botanik 6: 406. 1967.
*Basionym*: *Sphaeria michotii* Westend., Bull. Acad. Roy. Sci. Belgique Ser. 2, 7: 87. 1859.

*Specimen examined*: **Switzerland**, Kt. Obwalden, from *Typha latifolia* (*Typhaceae*), 18 May 1980, A. Leuchtmann, CBS 652.86 = ETH 9483.

***Massarinaceae*** Munk, Friesia 5: 305. 1956.

***Byssothecium circinans*** Fuckel, Bot. Zeitung (Berlin) 19: 251. 1861.

≡ *Leptosphaeria circinans* (Fuckel) Sacc., Syll. Fung. 2: 88. 1883.
≡ *Passeriniella circinans* (Fuckel) Sacc., Syll. Fung. 11: 326. 1895.
≡ *Trematosphaeria circinans* (Fuckel) G. Winter, Rabenh. Krypt.-Fl., ed 1(2): 277. 1887.
≡ *Heptameria circinans* (Fuckel) Cooke, Grevillea 18: 30. 1889.
= *Melanomma vindelicorum* Rehm, Ber. Nat. Ver. Augsburg: 116. 1881.
≡ *Trematosphaeria vindelicorum* (Rehm) Sacc., Syll. Fung. 2: 122. 1883.

*Specimen examined*: **USA**, South Dakota, from rotten crown of *Medicago sativa* (*Fabaceae*), G. Semeniuk, CBS 675.92 = ATCC 52767 = ATCC 52678 = IMI 266220.

***Massarina eburnea*** (Tul. & C. Tul.) Sacc., Syll. Fung. 2: 153. 1883.
*Basionym*: *Massaria eburnea* Tul. & C. Tul., Select. Fung. Carpol. (Paris) 2: 239. 1863.

*Specimens examined*: **Switzerland**, Zürich, from *Fagus sylvatica* (*Fagaceae*), S.K. Bose, CBS 473.64 = ETH 2945. **UK**, Wales, isolated from dead branch of *Fagus sylvatica*, HHUF 26621, JCM 14422 = H3953.

***Neottiosporina paspali*** (G.F. Atk.) B. Sutton & Alcorn, Austral. J. Bot. 22: 519. 1974.
*Basionym*: *Stagonospora paspali* G.F. Atk., Bull. Cornell Univ. (Science) 3: 33. 1897.

*Specimen examined*: **USA**, Florida, from *Paspalum notatum* (*Poaceae*), Oct. 1937, R.K. Voorhees, CBS 331.37.

***Trematosphaeriaceae*** Suetrong *et al*. Cryptogamie Mycol. 32: 347. 2011.

***Falciformispora lignatilis*** K.D. Hyde, Mycol. Res. 96: 27. 1992.

*Specimen examined*: **Thailand**, Pinruan Ban Bang, from *Elaeis guineensis* (*Arecaceae*), BCC 21118.

***Medicopsis*** Gruyter, Verkley & Crous, **gen. nov.** MycoBank MB564791.

*Etymology*: refers to Medi- medica, Latin, -opsis, refers to, Greek. The description of the type species as the cause of a mycetoma suggest this is a human pathogen. However, the mycetoma described was secondary to a wound produced by a thorn of Palito blanco tree, and the species was found later on *Hordeum vulgare*.

*Pycnidia* solitary or confluent, on upper surface of the agar, globose to pyriform with elongated neck, setose, ostiolate, olivaceous to olivaceous-black, the wall with pseudoparenchymatal cells. *Conidiogenous cells* hyaline, phialidic, ampulliform to doliiform, to elongated. *Conidia* sub-hyaline to yellowish, ellipsoid, aseptate, catenulate.

*Type species*: *Medicopsis romeroi* (Borelli) Gruyter, Verkley & Crous (see below).

***Medicopsis romeroi*** (Borelli) Gruyter, Verkley & Crous, **comb. nov.** MycoBank MB564792.
*Basionym*: *Pyrenochaeta romeroi* Borelli, Dermatol. Venez. 1: 326. 1959.

*Specimens examined*: **Venezuela**, from human, maduromycosis, no date, D. Borelli, UAMH 2892, **holotype** of *Pyrenochaeta romeroi* Borelli, culture ex-holotype CBS 252.60 = ATCC 13735 = FMC 151 = UAMH 10841. Country unknown, from *Hordeum vulgare* (*Poaceae*), 1984, M.M.J. Dorenbosch, CBS 122784 = PD 84/1022.

*Notes*: The species was described as a human pathogen of tropical origin, and it may cause suppurative subcutaneous or deep nonmycetomatous infections, or a subcutaneous phaeohyphomycotic cyst (Badali *et al.* 2010). However, the species also occurs in plant material.

***Trematosphaeria pertusa*** (Pers.) Fuckel, Jahrb. Nassauischen Vereins Naturk 23–24: 161. 1870.
*Basionym: Sphaeria pertusa* Pers., Syn. Meth. Fung. 1: 83. 1801.

*Specimen examined*: **France**, Deux Sèvres, from bark of a dead stump of *Fraxinus excelsior* (*Oleaceae*), 25 Apr. 2004, Jacques Fournier, **epitype** IFRD 2002, culture ex-epitype CBS 122368.

*Note*: The epitype IFRD 2002 was designated by Zhang *et al.* (2008).

***Lentitheciaceae*** Yin. Zhang, C.L. Schoch, J. Fourn., Crous & K.D. Hyde, Stud. Mycol. 64: 93. 2009.

***Splanchnonema platani*** (Ces.) M.E. Barr, Mycotaxon 15: 364. 1982.
*Basionym*: *Sphaeria* (*Massaria*) *platani* Ces., in Rabenhorst, Klotzschii Herb. Viv. Mycol.: no. 1842. 1854.

*Specimen examined*: **USA**, from *Platanus occidentalis* (*Platanaceae*), Jan. 1937, C.L. Shear, CBS 221.37.

*Note*: This taxon was shown by Zhang *et al*. (2012) to cluster basal to the *Lentitheciaceae*.

***Melanommataceae*** G. Winter, Rabenh. Krypt.-Fl., ed 1(2): 220 (1885) [as "*Melanommeae*"]

***Aposphaeria corallinolutea*** Gruyter, Aveskamp & Verkley, **sp. nov.** MycoBank MB564798. Fig. 8.

*Etymology*: The name refers to the coral coloured colony on OA, and the luteous exudate diffusing into the agar medium.

*Pycnidia* in vitro 65–215 µm diam, solitary or aggregated to confluent, globose to subglobose, ostiolate or non-ostiolate. *Conidiogenous cells* 7–9 × 2–4 µm, ampuliform to filiform. *Conidia* 3–5 × 1–2 µm, ellipsoidal to allantoid, eguttulate or with some small, polar guttules.

*Description in vitro*: *Colonies* on OA 13–15 mm diam after 14 d, margin entire to somewhat lobated; colony vinaceous to brick, with white at centre, ochraceous near margin due to a diffusible pigment, with

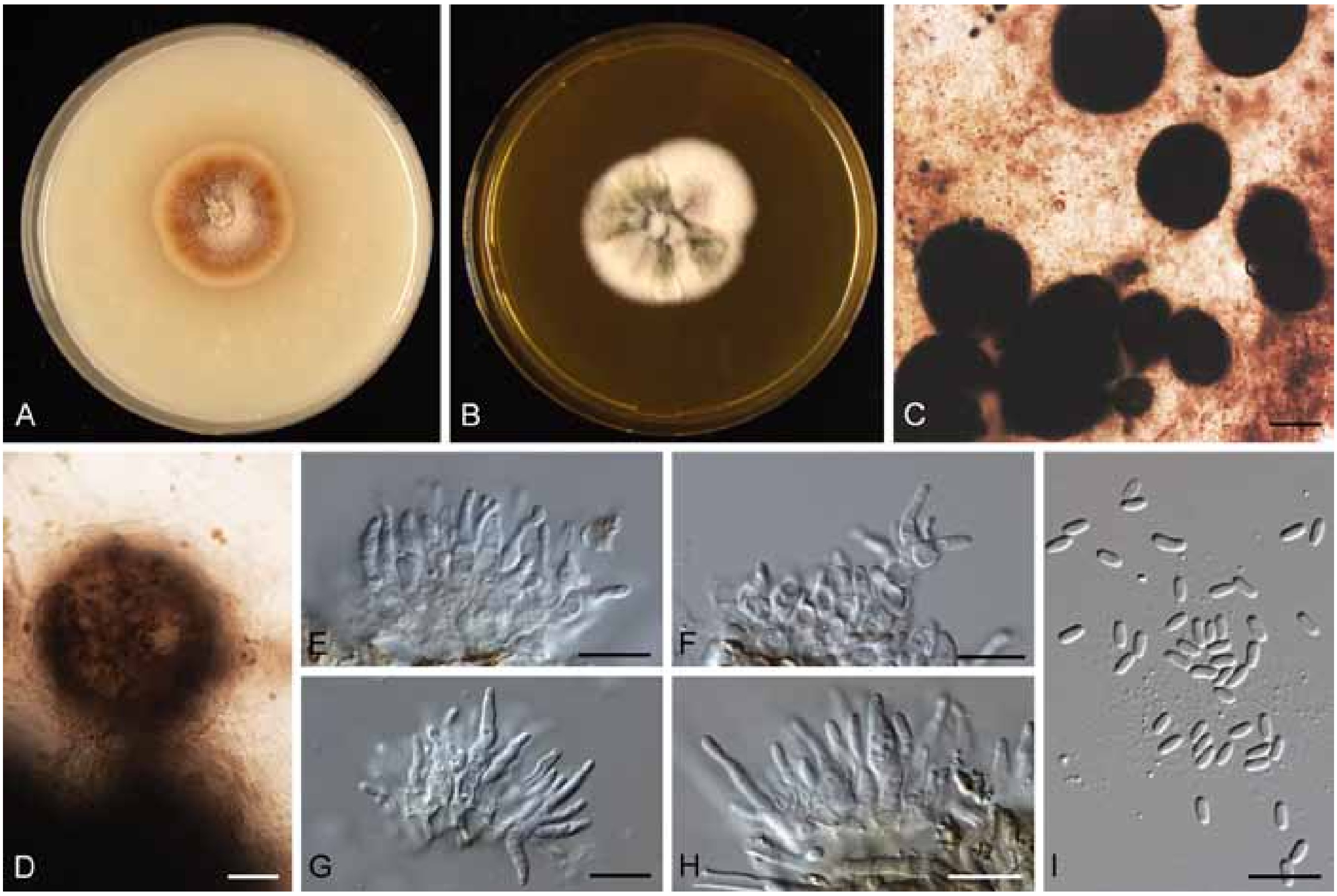


**Fig. 8.** *Aposphaeria corallinolutea* sp. nov. CBS 131287. A–B. Fourteen day old cultures on OA (A) and MA (B). C–D. Pycnidia. E–H. Conidiogenous cells. I. Conidia. Scale bars: C = 50 µm; D = 20 µm; E–I = 10 µm.

white, felty or poorly developed aerial mycelium; reverse cinnamon to brick. Colonies on MEA 15–20 mm diam after 14 d, margin entire to somewhat lobated; colony white with dull green and grey olivaceous sectors and primrose tinges, with white, felty aerial mycelium; reverse sepia to brown olivaceous, greenish grey at centre, white near margin. *Pycnidia* globose to subglobose, olivaceous to brick, then olivaceous black, solitary or aggregated, 65–215 µm diam, non-setose or with short setae-like outgrowths up to 25 µm long, with or without distinct ostiole, pycnidial wall consisting of 3–5 layers of cells. *Conidiogenous cells* 7–9 × 2–4 µm, ampulliform to filiform. *Conidia* 3–5 × 1–2 µm, av. 4 × 1.5 µm, length/width ratio is 1.7–3.3, av. = 2.5, ellipsoidal to allantoid, eguttulate or with some small, polar guttules. *Chlamydospores* absent, NaOH test negative. *Crystals* produced in the agar, small, orange coloured.

*Specimens examined*: Net**herlands**, from wood of *Fraxinus excelsior* (*Oleaceae*), 1983, M.M.J. Dorenbosch, **holotype** CBS H-20625, culture ex-holotype CBS 131287 = PD 83/831; from wood of *Kerria japonica* (*Rosaceae*), 1983, M.M.J. Dorenbosch, CBS 131286 = PD 83/367.

***Aposphaeria populina*** Died., Krypt.-Fl. Brandenburg 9: 206. 1912 (vol. dated "1915"). Fig. 9.

*Description in vitro*: *Colonies* on OA 21–24 mm diam after 7 d (32–37 mm diam after 14 d), margin entire to undulate; colony grey olivaceous/olivaceous to pale luteous/luteous, with white to pale olivaceous grey, finely felty to woolly aerial mycelium; reverse luteous to orange, greenish olivaceous to olivaceous or grey olivaceous/olivaceous grey to iron-grey, a rosy-buff discolouring near margin may occur. Colonies on MEA 16–20 mm diam after 7 d (30–37 mm diam after 14 d), margin entire to undulate; colony pale olivaceous grey with rosy-vinaceous tinges to peach or olivaceous grey, with white, woolly aerial mycelium; reverse saffron to pale olivaceous/olivaceous grey, sometimes with dark vinaceous tinges, rosy-buff near margin. *Pycnidia* globose to subglobose, olivaceous to olivaceous black, scattered, 55–305 µm diam, glabrous or with mycelial outgrowths, non-ostiolate or ostiolate, pycnidial wall composed of up to 10 layers of cells. *Conidiogenous cells* 5–11.5 × 1.5–3 µm, ampulliform to filiform. *Conidia* hyaline, subglobose to ellipsoidal, with 1–3 minute guttules, 1–2 × 1–1.5 µm, av. 1.5 × 1 µm, length/width ratio is 1.0–2.0, av. = 1.4. *Chlamydospores* and crystals absent, NaOH test negative.

*Specimens examined*: **Germany**, Triglitz, from twigs of *Populus canadensis* (*Salicaceae*), Mar. 1904. O. Jaap, B, **holotype**; from branch scars of *Picea abies*, (*Pinaceae*), Feb. 1982, H. von Aufess, CBS 350.82. **Netherlands**, Valkenswaard, from fallen twig of *Populus canadensis* (*Salicaceae*), 23 Mar. 1970, H.A. van der Aa**, epitype designated here** CBS H-9336, culture ex lectotype CBS 543.70; from wood of *Cornus mas* (*Cornaceae*), 1984, M.M.J. Dorenbosch, CBS 130330 = PD 84/221.

***Beverwykella pulmonaria*** (Beverw.) Tubaki, Trans. Mycol. Soc. Japan 16: 139. 1975.

*Basionym*: *Papulaspora pulmonaria* Beverw., Antonie van Leeuwenhoek 20: 11. 1954.

*Specimen examined*: **Netherlands**, Baarn, from submerged leaf in rain water barrel of *Fagus sylvatica* (*Fagaceae*), Apr. 1953, A.L. van Beverwijk, culture CBS 283.53 = ATCC 32983 = IFO 6800.

***Herpotrichia juniperi*** (Duby) Petr., Ann. Mycol. 23: 43. 1925.

*Basionym*: *Sphaeria juniperi* Duby, Klotzsch. Herb. Vivum Mycol. Sistems Fungorum German., no. 1833. 1854.

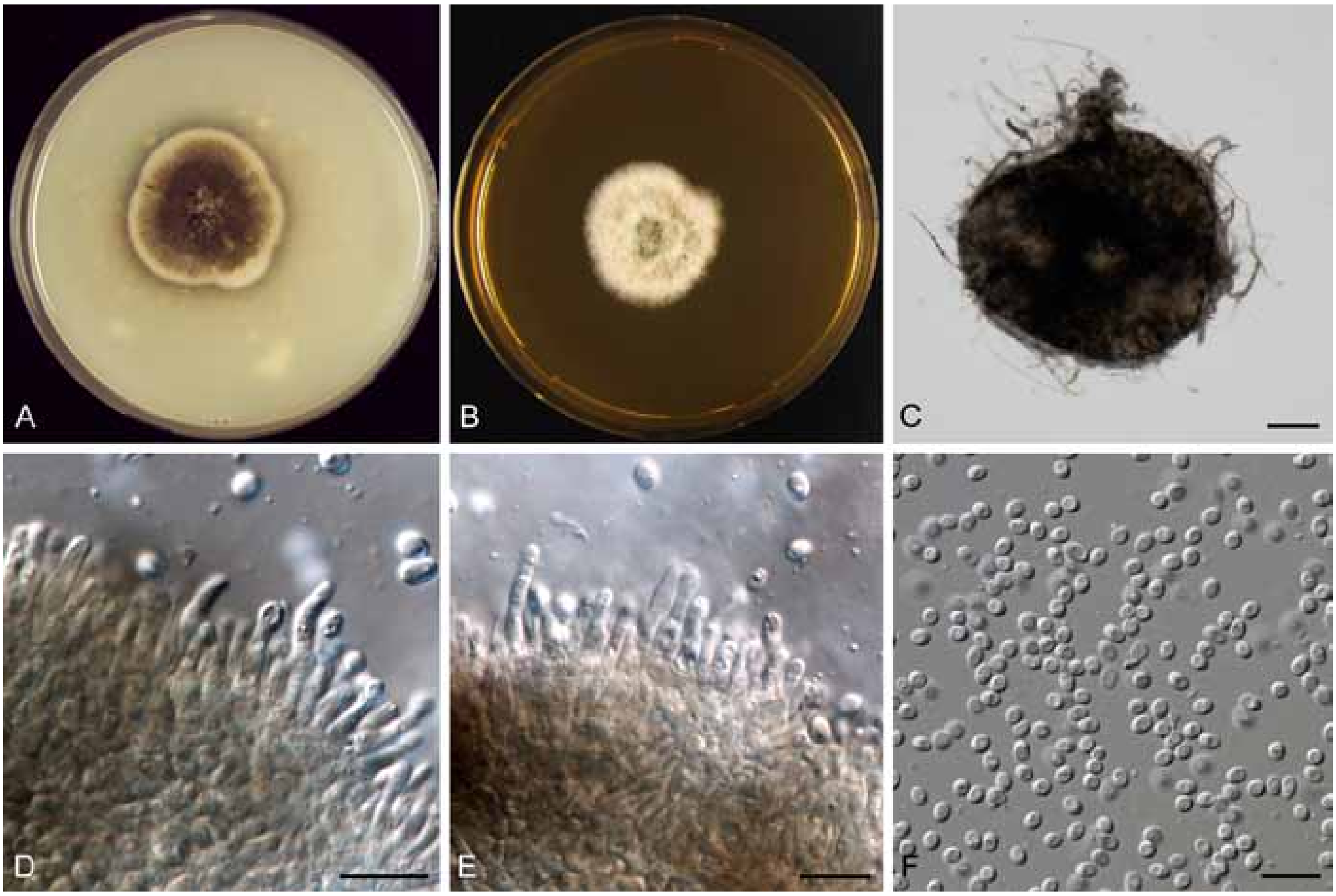


**Fig. 9.** *Aposphaeria populina*. CBS 543.70. A–B. Fourteen day old cultures on OA (A) and MA (B). C. Pycnidium with mycelial outgrowths (CBS 130330). D–E. Conidiogenous cells. F. Conidia. Scale bars: C = 20 µm; D–E = 10 µm; F = 5 µm.

*Specimen examined*: **Switzerland**, Andermatt, from *Juniperus nana* (*Cupressaceae*), Nov. 1931, E. Gäumann, CBS 200.31.

***Melanomma pulvis-pyrius*** (Pers.) Fuckel, Jahrb. Nassauischen Vereins Naturk. 23–24: 160. 1870.
*Basionym*: *Sphaeria pulvis-pyrius* Pers., Syn. Meth. Fung. 1: 86. 1801.

*Specimens examined*: **Belgium**, from wood of *Fagus* sp. (*Fagaceae*), CBS 400.97. **France,** Vosges, Bot. Garden Le Chitelet, from unidentified decaying wood, CBS 371.75.

*Notes*: Phoma-like anamorphs have been reported by Chesters (1938) and Sivanesan (1984), but no anamorphic stage was observed in IFRDCC 2044, CBS 109.77 or CBS 371.75 after culturing 3 mo on PDA (Zhang *et al.* 2008). CBS 400.97 was preserved as *Trematosphaeria pertusa*.

***Pleomassaria siparia*** (Berk. & Broome) Sacc., Syll. Fung. 2: 239. 1883.
*Basionym*: *Sphaeria siparia* Berk. & Broome, Ann. Mag. Nat. Hist. Ser. 2(9): 321. 1852.

*Specimen examined*: **Netherlands**, Uden, from dead branch of *Betula verrucosa* (*Betulaceae*), 8 Dec. 1973, W.M. Loerakker, CBS H-258, CBS H-260, culture CBS 279.74.

***Sporormiaceae*** Munk, Dansk Bot. Ark. 17(1): 450. 1957, nom. inval., Art. 36.1.

***Preussia funiculata*** (Preuss) Fuckel, Jahrb. Nassauischen Vereins Naturk. 23–24: 91. 1870 (1869–70).
*Basionym*: *Perisporium funiculatum* Preuss, Linnaea 24(1): 143. 1851.

*Specimen examined*: **Senegal**, from soil, CBS 659.74.

***Sporormiella minima*** (Auersw.) S.I. Ahmed & Cain, Canad. J. Bot. 50: 449. 1972.
*Basionym*: *Sporormia minima* Auersw., Hedwigia 7: 66. 1868.

*Specimen examined*: **Panama**, from dung of goat, CBS 524.50.

***Westerdykella*** Stolk, Trans. Brit. Mycol. Soc. 38: 422. 1955.

*Type species*: *Westerdykella ornata* Stolk, see below.

***Westerdykella capitulum*** (V.H. Pawar, P.N. Mathur & Thirum) Gruyter, Aveskamp & Verkley, **comb. nov.** MycoBank MB564801.
*Basionym*: *Phoma capitulum* V.H. Pawar, P.N. Mathur & Thirum., Trans. Brit. Mycol. Soc. 50: 261. 1967.

≡ *Phoma capitulum* V.H. Pawar & Thirum., Nova Hedwigia 12: 502. 1966 (as "*capitula*"), nom. nud., nom. inval.

= *Phoma ostiolata* V.H. Pawar, P.N. Mathur & Thirum., Trans. Brit. Mycol. Soc. 50: 262. 1967, var. *ostiolata*.

≡ *Phoma ostiolata* V.H. Pawar & Thirum., Nova Hedwigia 12: 502. 1966, nom. nud., nom. inval.

= *Phoma ostiolata* var. *brunnea* V.H. Pawar, P.N. Mathur & Thirum., Trans. Brit. Mycol. Soc. 50: 263. 1967.

≡ *Phoma ostiolata* var. *brunnea* V.H. Pawar & Thirum., Nova Hedwigia 12: 502. 1966, nom. nud., nom. inval.

*Specimen examined*: **India**, Bandra, Bombay, from saline soil, 15 Jan. 1958, M.J. Thirumalachar, **Isotype** CBS H-7602, culture ex-isotype CBS 337.65 = ATCC 16195 = HACC 167 = IMI 113693 = PD 91/1614.

***Westerdykella minutispora*** (P.N. Mathur ex Gruyter & Noordel.) Gruyter, Aveskamp & Verkley, **comb. nov.** MycoBank MB564793.
*Basionym*: *Phoma minutispora* P.N. Mathur ex Gruyter & Noordel., Persoonia 15: 75. 1992 (as "collection name" originally also referred to Thirumalachar; = depositor).
*Replaced synonym*: *Phoma oryzae* Cooke & Massee, Grevillea 16: 15. 1887 (not *Phoma oryzae* Catt., Arch. Triennale Bot. Crittog. Pavia 2–3: 118. 1879, nom. illeg).
≡ *Phyllosticta oryzae* (Cooke & Massee) I. Miyake. J. Coll. Agric. Imp. Univ. Tokyo 2: 252. 1910, nom. illeg.

*Specimen examined*: **India**, from saline soil, 1977, M.J. Thirumalachar, CBS H-5941, culture CBS 509.91 = PD 77/920.

***Westerdykella ornata*** Stolk, Trans. Brit. Mycol. Soc. 38: 422. 1955.

*Specimen examined*: **Mozambique**, from mangrove mud, CBS 379.55.

***Didymosphaeriaceae*** Munk, Dansk Bot. Ark. 15(2): 128. 1953.

***Roussoella hysterioides*** (Ces.) Höhn., Sitzungsber. Kaiserl. Akad. Wiss., Math.-Naturwiss. Cl., Abt. 1. 128: 563. 1919.
*Basionym*: *Dothidea hysterioides* Ces., Atti Accad. Sci. Fis. 8: 24. 1879.

*Specimen examined*: **Japan**, Aomori, Shimokita Yagen, from culms of *Sasa kurilensis* (*Poaceae*), Y. Ooki, culture CBS 125434 = HH 26988.

## Family *incertae sedis*

***Nigrograna*** Gruyter, Verkley & Crous, **gen. nov.** MycoBank MB564794.

*Etymology*: refers to Nigro-, black, Latin, -grana, grains, Latin. The description refers to the black grains produced by the type species.

*Pycnidia* solitary or rarely confluent, on upper surface or submerged in agar, globose to subglobose or pyriform, with dark brown, septate mycelial outgrowths, with papillate ostioles, olivaceous to olivaceous-black, the wall with pseudoparenchymatous cells. *Conidiogenous cells* hyaline, phialidic, discrete. *Conidia* subhyaline, brown in mass, aseptate, ellipsoidal.

*Type species*: *Nigrograna mackinnonii* **(**Borelli) Gruyter, Verkley & Crous (see below).

***Nigrograna mackinnonii*** (Borelli) Gruyter, Verkley & Crous, **comb. nov.** MycoBank MB564795.

*Basionym*: *Pyrenochaeta mackinnonii* Borelli, Castellania 4: 230. 1976.

*Specimens examined*: **Mexico**, from a mycetoma of a human, Feb. 2002, R. Arenas, CBS 110022; **Venezuela**, from a black grain mycetoma of human, Aug. 1975, D. Borelli, **holotype** FMC 270, culture ex-holotype CBS 674.75.

***Thyridaria rubronotata*** (Berk. & Broome) Sacc., Syll. Fung. 2: 141. 1883.
*Basionym*: *Melogramma rubronotatum* Berk. & Broome, Ann. Mag. Nat. Hist. Ser. 3(3): 20. 1859.

*Specimen examined*: **Netherlands**, Zuidelijk Flevoland, from a dead branch of *Acer pseudoplatanus* (*Aceraceae*), 13 Apr. 1985, N. Ernste, CBS H-18824, culture CBS 419.85.

## DISCUSSION

The genus *Phoma* has been shown to be highly polyphyletic and *Phoma* is now restricted to taxa in the *Didymellaceae* (de Gruyter *et al.* 2009, Aveskamp *et al.* 2010). *Phoma* anamorphs and phoma-like species in *Coniothyriaceae*, *Leptosphaeriaceae*, *Melanommataceae, Montagnulaceae, Pleosporaceae*, *Sporormiaceae* and *Trematosphaeriaceae* are redisposed here as a result of this and previous studies.

The delimitation of *Leptosphaeriaceae* in *Pleosporineae* from *Cucurbitariaceae*, *Didymellaceae*, *Phaeosphaeriaceae* and *Pleosporaceae* agrees with recent studies of phoma-like species in *Pleosporales* (de Gruyter *et al.* 2009, Aveskamp *et al.* 2010, de Gruyter *et al.* 2010). *Cucurbitariaceae* is recognised as the fifth family in *Pleosporineae* in addition to the four families accepted by Zhang *et al.* (2009), which are *Didymellaceae*, *Leptosphaeriaceae Phaeosphaeriaceae and Pleosporaceae*.

### The genera *Leptosphaeria*, *Paraleptosphaeria*, *Plenodomus*, *Subplenodomus* and *Heterospora*

*Plenodomus lingam* and *L. doliolum*, the type species of *Plenodomus* and *Leptosphaeria* respectively, were found to be distant genetically, which agrees with findings of previous molecular phylogenetic studies (Jasalavic *et al.* 1995, Morales *et al.* 1995, Dong *et al.* 1998, Câmara *et al.* 2002, Eriksson & Hawksworth 2003, Wunsch & Bergstrom 2011). In our study the generic type species grouped in sister clades, which represent *Leptosphaeria* and *Plenodomus*. Species of *Leptosphaeria* produce dark brown, 3-septate ascospores, which have been considered the primitive state with more recently evolved species producing ascospores that are paler in colour, longer and narrower, and more than 3-septate (Wehmeyer 1946). This hypothesis is supported by the results obtained in our study. *Paraleptosphaeria* is distinct but seems to be most closely related to *Leptosphaeria* producing 3(–5)-septate, yellow/brown or hyaline ascospores. Both genera include only necrotrophic species. *Plenodomus* and *Subplenodomus* include necrotrophs and plant pathogens. Ascospores in *Plenodomus* are 3–7-septate, whereas in *Subplenodomus* no sexual state has thus far been recorded. The scleroplectenchymatous pycnidial cell wall is typical for *Plenodomus*, whereas in *Subplenodomus* the pycnidial cell wall is pseudoparenchymatous. *Heterospora* is closely allied to *Subplenodomus* and no sexual state has been recorded for this genus either. The distinctive characterisitics of the genera *Heterospora*, *Leptosphaeria*, *Paraleptosphaeria*, *Plenodomus* and *Subplenodomus* are summerised in Table 2. A blast search in GenBank using ITS sequences of five selected species of the *Leptosphaeriaceae*, namely *L. doliolum*, *L. etheridgei*, *Plen. lingam, H. dimorphospora* and *Subplen. drobnjacensis*, did not reveal close matches to other

**Table 2.** Characteristics of ascospores, mitosporic state and pathogenicity of *Leptosphaeria*, *Paraleptosphaeria*, *Plenodomus* and *Subplenodomus in vivo.*

| Genus | Ascospores | Mitosporic state | Pathogenicity |
|---|---|---|---|
| *Leptosphaeria* | Ascospores 3-septate, (dark) brown | Mitosporic state common, pycnidial cell wall usually directly scleroplectenchymatous, conidia mostly aseptate | Necrotrophic |
| *Paraleptosphaeria* | Ascospores 3–5-septate, hyaline to yellow/brown | Mitosporic state rare, pycnidial cell wall directly scleroplectenchymatous, conidia aseptate | Necrotrophic |
| *Plenodomus* | Ascospores 3–7-septate, pale yellow to brown | Mitosporic state common, pycnidial cell wall initially pseudoparenchymatous, later scleroplectenchymatous, conidia aseptate | Necrotrophic or plant pathogenic |
| *Subplenodomus* | No known sexual state | Mitosporic state common, pycnidial cell wall mainly pseudoparenchymatous, conidia aseptate | Necrotrophic or plant pathogenic |
| *Heterospora* | No known sexual state | Mitosporic state common, pycnidial cell wall pseudoparenchymatous, conidia of two types: small aseptate and large septate | Plant pathogenic |

teleomorphic or anamorphic genera.

*Plectophomella visci* grouped in *Plenodomus* in this study and in the *Leptosphaeriaceae* in a previous molecular phylogeny of *Phoma* and allied anamorph genera (de Gruyter *et al.* 2009). *Plectophomella visci* is the type species of *Plectophomella* (Moesz 1922) and three additional species have been described in the genus. Two species were described from the bark of *Ulmus* spp., *viz. Plectophomella ulmi* (basionym *Dothiorella ulmi*) and *Plectophomella concentrica* (Redfern & Sutton 1981). *Dothiorella ulmi* is considered the appropriate name for *Plectophomella ulmi* (Crous *et al.* 2004). A third species, *Plectophomella nypae*, was described from *Nypa fruticans* (*Arecaceae*) (Hyde & Sutton 1992). As a result of the transfer of the type species *Plectophomella visci* to *Plenodomus*, the taxonomy of both *Plectophomella concentrica* and *P. nypae* needs to be reconsidered based on the outcome of a molecular study.

*Plenodomus chrysanthemi* could not be differentiated from *Plen. tracheiphilus* based on comparison of their LSU and ITS sequences. *Plenodomus vasinfecta* was proposed by Boerema *et al.* (1994) for the species originally described as *Phoma tracheiphila* f. sp. *chrysanthemi* (Baker *et al*. 1985). Because these are part of the *Plenodomus* clade the name *Plenodomus chrysanthemi* is proposed with *P. tracheiphila* f. sp. *chrysanthemi* and *P. vasinfecta* as synonyms. *Plenodomus chrysanthemi* and *Plen. tracheiphilus* are host specific (*Chrysanthemum* and *Citrus*, respectively) and the scleroplectenchymatous conidiomatal wall of *Plen. tracheiphilus* differentiates this species from *Plen. chrysanthemi*, where only a parenchymatous wall has been observed (Boerema *et al.* 1994). The results of this molecular study and the production of a *Phialophora* synanamorph by both species demonstrate the close relationship of both taxa.

*Plenodomus enteroleucus* and *Plen. influorescens* have a similar ecological niche as opportunistic pathogens on woody plants in Europe. Both taxa were formerly described as varieties of *Ph. enteroleuca*, vars. *enteroleuca* and *influorescens,* and could be differentiated only by the fluorescence of var. *enteroleuca* under black light. However, the molecular phylogeny demonstrates the two varieties are only distantly related and they are raised from varietal status to species rank. The close relation of *Plen. wasabiae* with *Plen. biglobosus* agrees with the results of a previous study on the production of Phomalignin A and other yellow pigments, as well as ITS sequence analyses (Pedras *et al.* 1995).

*Subplenodomus apiicola, Subplen. drobnjacensis, Subplen. valerianae* and *Subplen. violicola* all produce pycnidia with an elongated neck, resembling *Plenodomus*. The pycnidial wall remains usually pseudoparenchymatous. Pycnidia with a scleroplectenchymatous wall are only observed in *Subplen. drobnjacensis*. *Subplenodomus apicolus, Subplen. drobnjacensis* and *Subplen. valerianae* produce relatively small conidia, up to 4.5 × 2 µm (de Gruyter & Noordeloos 1992) in congruence with many of the *Plenodomus* species described; however, in contrast *Subplen. violicola* produces relatively large conidia, up to 11 × 3 µm (Boerema 1993).

The grouping of species of *Phoma* section *Plenodomus* based on the host being either herbaceous plants or wood of trees and shrubs (Boerema 1982, Boerema *et al.* 1994) is not supported by the molecular phylogeny. The grouping of the species into two categories based on the production of pseudoparenchymatous pycnidia that become scleroplectenchymatous pycnidia (type I), versus always scleroplectenchymatous pycnidia (type 2) (Boerema *et al.* 1981), is partly supported by the molecular phylogeny. In the *Leptosphaeria* clade most species directly develop scleroplectenchymatous pycnidia, whereas in the *Plenodomus* clade the pycnidia generally are pseudoparenchymatous and become scleroplectenchymatous.

*Heterospora* is established for two species of *Phoma* sect. *Heterospora* that cluster in the *Leptosphaeriaceae, viz H. chenopodii* and *H. dimorphospora.* All other species of *Phoma* sect. *Heterospora* are in the *Didymellaceae* (Aveskamp *et al*. 2010).

## The *Leptosphaeria doliolum* species complex

The taxonomy of the generic type species *Leptosphaeria doliolum* and *Phoma* anamorphs is complex with a number of subspecies and varieties described in literature. *Leptosphaeria doliolum* subsp. *doliolum* and *L. doliolum* subsp. *errabunda* are morphologically very similar, as well as the anamorphs *Ph. acuta* subsp. *errabunda* and *Ph. acuta* subsp. *acuta*. It has been suggested that both taxa represent originally American and European counterparts (Boerema *et al.* 1994). Both subspecies of *L. doliolum* proved to be closely related in a phylogenetic analysis utilising LSU and ITS. A detailed multilocus phylogenetic study including the ITS, ACT, TUB and CHS genes, however, demonstrated that both subspecies could be clearly differentiated, and represent two subclades in the *L. doliolum* complex. All species allied with *L. doliolum* and *L. errabunda* are necrotrophic species. Surprisingly, *L. macrocapsa* grouped with the *L. errabunda* isolates. *Leptosphaeria macrocapsa* is described as a host-specialised necrotroph on *Mercurialis perennis* (*Euphorbiaceae*) in Europe (Boerema *et al.* 1994). The species is characterised by large pycnidia (Grove, 1935), with a conspicuously broad, long cylindrical neck (Boerema *et al*. 1994). This is different to the sharply delimited papilla or neck of variable length of the pycnidia of *L. errabunda*. *Leptosphaeria sydowii*, a necrotroph on *Senecio* spp. in particular (*Asteraceae*), proved to be closely related to *L. errabunda*. It can be concluded that the *Leptosphaeria doliolum* complex includes several necrotrophic species, with adapted host specificity.

## The genus *Coniothyrium*

*Coniothyrium palmarum* is the type species of the genus *Coniothyrium*. *Coniothyrium* is characterised by ostiolate pycnidial conidiomata, annellidic conidiogenous cells, the absence of conidiophores, and brown, thick-walled, 0- or 1-septate, verrucose conidia. *Coniothyrium* is similar morphologically to some species in the genus *Microsphaeropsis*. However, *Microsphaeropsis* is characterised by the production of phialidic conidiogenous cells with periclinal thickening, and thin-walled, pale greenish brown conidia.

*Coniothyrium*, *Microsphaeropsis* and *Paraconiothyrium* clearly grouped in different clades in a study of the partial SSU nrDNA (Verkley *et al.* 2004). In a subsequent study utilising SSU and LSU sequences, the generic type species *Microsphaeropsis olivacea* grouped in *Didymellaceae*, whereas *Coniothyrium palmarum* clustered with the genus *Leptosphaeria* in *Leptosphaeriaceae* (de Gruyter *et al.* 2009). In the present study *C. palmarum* and its relatives grouped in a distinct clade, which represents *Coniothyriaceae*. *Phoma carteri*, *Ph. glycinicola*, *Ph. septicidalis* and *Pyrenochaeta dolichi* grouped in this clade and are transferred to the genus *Coniothyrium*. The inclusion of these species with setose pycnidia and conidiogenesis with elongated conidiophores expands the morphological circumscription of *Coniothyrium*. Species with those characters are also found in other genera treated in this paper in the *Cucurbitariaceae*, *Didymellaceae*, *Phaeosphaeriaceae, Leptosphaeriaceae*, *Montagnulaceae* and *Sporormiaceae*, indicating convergent evolution.

The *Coniothyrium* species included here are plurivorous or soil-borne, such as *C. palmarum*, *C. septicidalis* and *C. multiporum*, or are associated with a specific host such as *C. carteri* on *Quercus* spp. (*Fagaceae*), *C. glycinicola* on *Glycine max* (*Fabaceae*) and *C. dolichii* on *Dolichos biflorus* (*Fabaceae*). The species also are diverse geographically.

*Coniothyrium palmarum* was frequently found associated with leaf spots on *Phoenix dactylifera* (*Arecaceae*) in India and Cyprus (Sutton 1980). The *C. palmarum* isolates regularly used in phylogenetic studies are CBS 758.73, from leaf spots on *Phoenix dactylifera* in Israel, and CBS 400.71, from a dead petiole of *Chaemeropsis humulis* (*Arecaceae*) in Italy. The subtropical distribution of these species is similar to that of the most closely allied *C. dolichi* and *C. glycinicola*. *Coniothyrium multiporum*, recorded from marine soil, also is found in warm regions. *Coniothyium carteri,* in contrast, is reported from North America and Europe.

*Coniothyrium dolichi* produces setose pycnidia with hyaline conidia (Mohanty 1958). The conidiogenesis was studied in detail later. phoma-like ampulliform conidiogenous cells as well as conidiogenous cells on filiform, septate conidiophores were found in the same pycnidia leading to confusion regarding the classification of this species in *Phoma* or *Pyrenochaeta* (Grodona *et al*. 1997). This study clearly supports the classification in *Coniothyrium*. *Coniothyrium glycinicola* was originally placed in the genus *Pyrenochaeta* as *Py. glycines* due to its setose pycnidia (Stewart 1957). The conidiogenesis and hyaline conidia are phoma-like and therefore, it was reclassified as *Ph. glycinicola* in *Phoma* sect. *Paraphoma* (de Gruyter & Boerema 2002). However, in the original description it was noted that the conidia were greenish-yellow in mass (Stewart 1957), resembling *Microsphaeropsis* or coniothyrium-like conidia. This study clearly supports the classification in *Coniothyrium*. *Coniothyrium carteri* produces setose pycnidia with hyaline conidia and therefore, the species was classified in *Phoma* section *Paraphoma* (de Gruyter & Boerema 2002). In spite of this similarity, *C. carteri* was determined to be only distantly related to the generic type species *Paraphoma radicina* (de Gruyter *et al.* 2010). *Coniothyrium multiporum* was described in *Phoma* section *Phoma*; however, it proved to be unrelated to *Phoma* in *Didymellaceae* (Aveskamp *et al.* 2010). The conidiogenesis may comprise elongated conidiophores (Pawar *et al*. 1967). Two isolates originally described as *Ph. septicidalis* are placed here in *Coniothyrium telephii.* Other strains deposited as *Ph. septicidalis* proved to be *Pyrenochaeta unguis-hominis* (de Gruyter *et al.* 2010).

The anamorph of the genus *Neophaeosphaeria* was described as coniothyrium-like, producing pigmented, aseptate conidia from holoblastic, percurrently proliferating conidiogenous cells with conspicuous annellations (Câmara *et al.* 2003). Although *Neophaeosphaeria* is related to *Coniothyrium* based on the molecular data, *Neophaeosphaeria* probably belongs to a separate phylogenetic clade. The grouping of *N. filamentosa* with the *Coniothyrium* species included in this study was poorly supported and *N. filamentosa* proved to be more distantly related in previous molecular phylogenetic studies (Verkley *et al.* 2004, Damm *et al.* 2008, de Gruyter *et al.* 2010).

Both anamorph genera *Cyclothyrium* and *Cytoplea* were considered to be related to *Coniothyrium* and *Microsphaeropsis* (Sutton 1980) based on morphological similarities. *Cyclothyrium* also resembles *Paraconiothyrium* but produces conidiogenous cells that are more elongated than in most species of *Paraconiothyrium* and the conidia are almost truncate at the base, or at least they are much less rounded at the base than the conidia of *Paraconiothyrium* (Verkley *et al.* 2004). The generic type species *Cyclothyrium juglandis,* the anamorph of *Thyridaria rubronotata*, proved to be related to *Roussoella hysterioides*, teleomorph of *Cytoplea* (Verkley *et al*. 2004). Based on present results *R. hysterioides* could not be assigned to familial rank. The clustering of this species in *Massariaceae* (Zhang *et al*. 2009) could not be confirmed. Moreover, *Roussoella* probably is not a monophyletic genus (Tanaka *et al.* 2009). *Thyridaria rubronotata*, the teleomorph of *Cyclothyrium juglandis*, proved to be related to *Massariosphaeria phaeospora* but was not assigned to familial rank (Schoch *et al.* 2009).

Coniothyrium-like anamorphs also have been linked to *Mycosphaerella* in the past. However, these species were subsequently accommodated in *Colletogloeopsis* (Cortinas *et al*. 2006), *Readeriella/Kirramyces* (Crous *et al.* 2007) and are now known to be species of *Teratosphaeria* (Crous *et al*. 2009b).

## The genus *Pleospora*

*Pleospora* is a large genus in *Pleosporaceae*, *Pleosporales*, and includes important pathogens that occur on both monocotyledons and dicotyledons. Anamorphs of *Pleospora s. lat.* have been described in various genera of coelomycetes and hyphomycetes as summarised by Zhang *et al.* (2009, 2012). A delimitation of *Pleospora* into two sections, *Pyrenophora* and *Eu-Pleospora* was made based on the size of fruiting bodies and ascospore septation and colour (Munk 1957). The genus *Pyrenophora* (*Drechslera* anamorphs) is recognised at the generic rank. However, *Pleospora* remains heterogenous (Wehmeyer 1961, Berbee 1996) and molecular phylogenetic studies demonstrated that *Pleospora* is polyphyletic in *Pleosporaceae* (Kodsueb *et al.* 2006, Wang *et al.* 2007, Inderbitzin *et al.* 2009). Taxa with a *Stemphylium* anamorph such as *Pleospora sedicola* and *Pleo. tomatonis*, as well as *Pleo. halophola* with no known anamorph, are closely related to *Cochliobolus*, whereas *Pleo. herbarum* and *Pleo. ambigua* were more distantly related in the *Pleosporaceae* (Kodsueb *et al.* 2006, Wang *et al.* 2007). A phylogenetic study of the genus *Massariosphaeria* demonstrated the polyphyly in the genera *Pleospora, Kirschsteiniothelia, Massarina, Melanomma, Trematosphaeria and Massariosphaeria* in the *Loculoascomycetes* (Wang *et al.* 2007) and the paraphyletic character of the genus *Cochliobolus* was demonstrated (Kodsueb *et al.* 2006, Mugambi & Huhndorf 2009). These findings support the previous speculation by several authors that ascomatal and ascospore morphologies have undergone convergent evolution among *Pleosporales* (Wang *et al*. 2007).

*Pleospora betae* groups ambiguously in *Pleosporaceae* (Dong *et al.* 1998). SSU nrDNA sequence data supported the affinity of *P. betae* to *Leptosphaeriaceae.* Partial LSU nrDNA data supported the affinity of *P. betae* to *Pleosporaceae* (Dong *et al.* 1998), but bootstrap support values in that study were low. In a multigene phylogenetic study *Pleo. betae* was found as being basal to *Pleosporaceae* (Zhang *et al*. 2009). Our results demonstrate the sister group relationship of *Pleo. betae* and its relatives to the generic type species *Pleo. herbarum*.

*Pleospora betae* has been often confused with *Pleo. calvescens* as was discussed by Boerema *et al.* (1987). Both species are pathogens of *Chenopodiaceae* and are morphologically rather similar and therefore, a phylogenetic relation of both species was inferred (Boerema 1984). In addition *Ascochyta hyalospora*, originally found on the American continent on *Chenopodiaceae*, also was supposed to be closely related. Our results demonstrate that *Pleo. betae* and *Pleo. calvescens* could be recognised at species rank and confirmed that *A. hyalospora* is related supporting our transfer to *Pleospora* as *Pleo. chenopodii*. The delimitation of both halophytic species *Pleo. chenopodii* and *Pleo. calvescens* needs further study; both species could not be clearly differentiated based on the ACT sequences alone. Additional studies are underway to elucidate these species boundaries, in which also the recently described halophyte, *Ascochyta manawaorae* (Verkley *et al.* 2010), will be included. *Pleospora fallens* and *Pleo. incompta*, formerly described in *Phoma* sect. *Phoma* and producing mainly glabrous pycnidia, grouped in the *Pleo. herbarum* clade. *Pleospora typhicola,* producing pilose pycnidia, also grouped in this clade.

## Phoma-like species excluded from the *Pleosporineae*

The genus *Paraconiothyrium* was introduced by Verkley *et al.* (2004) as the anamorph of *Paraphaeosphaeria*. The morphological characters of *Paraconiothyrium* are variable. The conidiomata can be eustromatic to pycnidial, the phialidic conidiogenous cells are discrete or integrated, and the thin-walled conidia are aseptate or septate, smooth-walled or minutely warted, and hyaline to brown in a later stage (Verkley *et al.* 2004). The morphological characters of *Ph. lini* and *Asteromella tilliae*, redisposed here in *Paraconiothyrium*, fit this description.

*Paraconiothyrium fuckelii* is a serious plant pathogen of *Rosaceae* (Horst & Cloyd 2007), but it also is recorded as an opportunistic human pathogen as summarised by de Hoog *et al*. (2000). The teleomorph is currently known as *Leptosphaeria coniothyrium*, but this is not likely considering the phylogeny of *Leptosphaeriaceae* in *Pleosporales* (Fig 1). The species was also described as *Melanomma coniothyrium* (Holm 1957); however, *Melanomma* is more distantly related in *Melanommataceae*.

*Neottiosporina paspali* proved to be related to *Paraconiothyrium.* However, this species is characterised by conidia with an apical appendage (Sutton 1980) and resembles members of *Massarinaceae. Pyrenochaeta romeroi* is redescribed in the new genus *Medicopsis,* and its taxonomic position is most close to *Trematosphaeriaceae.*

*Aposphaeria corallinolutea* could be recognised as a new species in *Melanommataceae. Phoma capitulum* and *Ph. minutispora* (*Phoma* section *Phoma*) clustered in the *Sporormiaceae*, most closely related to the holotype isolate of *Westerdykella ornata.* Other phoma-like anamorphs have been recorded in *Sporormiaceae*, such as anamorphs of *Sporormia aemulans* (≡ *Preussia aemulans*) and *Westerdykella dispersa* (≡ *Pycnidiophora dispersa*) (von Arx & Storm 1967). The *in vitro* characters of *W. capitulum* and *W. oryzae* agree with the *in vitro* characters of phoma-like anamorphs in the *Sporormiaceae* summarised by Boerema *et al.* (2004). The conidia produced are small, mostly 2–3 × 1–2 µm, arising from undifferentiated cells, but sometimes also elongated conidiogenous cells are observed. The colonies, often with a pink-yellow-red discolouration on OA, usually produce little aerial mycelium, whereas pycnidia are often produced in abundance. No matching sequences were found in a blast search in GenBank using the partial LSU sequences of *W. capitulum* and *W. minutispora. Westerdykella minutispora* from India was most similar to a sequence of *Westerdykella nigra*, isolate CBS 416.72, obtained from soil in Pakistan, and *W. capitulum* was most similar to a sequence of *W. dispersa*, isolate CBS 297.56, obtained from a seedling of *Phlox drummondii*, USA. These blast results support the redisposition of both species in the genus *Westerdykella.*

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# Phylogenetic lineages in *Pseudocercospora*

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**Abstract:** *Pseudocercospora* is a large cosmopolitan genus of plant pathogenic fungi that are commonly associated with leaf and fruit spots as well as blights on a wide range of plant hosts. They occur in arid as well as wet environments and in a wide range of climates including cool temperate, sub-tropical and tropical regions. *Pseudocercospora* is now treated as a genus in its own right, although formerly recognised as either an anamorphic state of *Mycosphaerella* or having mycosphaerella-like teleomorphs. The aim of this study was to sequence the partial 28S nuclear ribosomal RNA gene of a selected set of isolates to resolve phylogenetic generic limits within the *Pseudocercospora* complex. From these data, 14 clades are recognised, six of which cluster in *Mycosphaerellaceae*. *Pseudocercospora s. str.* represents a distinct clade, sister to *Passalora eucalypti*, and a clade representing the genera *Scolecostigmina, Trochophora* and *Pallidocercospora* gen. nov., taxa formerly accommodated in the *Mycosphaerella heimii* complex and characterised by smooth, pale brown conidia, as well as the formation of red crystals in agar media. Other clades in *Mycosphaerellaceae* include *Sonderhenia*, *Microcyclosporella*, and *Paracercospora*. *Pseudocercosporella* resides in a large clade along with *Phloeospora*, *Miuraea*, *Cercospora* and *Septoria*. Additional clades represent *Dissoconiaceae*, *Teratosphaeriaceae*, *Cladosporiaceae*, and the genera *Xenostigmina*, *Strelitziana*, *Cyphellophora* and *Thedgonia*. The genus *Phaeomycocentrospora* is introduced to accommodate *Mycocentrospora cantuariensis*, primarily distinguished from *Pseudocercospora* based on its hyaline hyphae, broad conidiogenous loci and hila. Host specificity was considered for 146 species of *Pseudocercospora* occurring on 115 host genera from 33 countries. Partial nucleotide sequence data for three gene loci, ITS, EF-1α, and ACT suggest that the majority of these species are host specific. Species identified on the basis of host, symptomatology and general morphology, within the same geographic region, frequently differed phylogenetically, indicating that the application of European and American names to Asian taxa, and *vice versa*, was often not warranted.

**Key words:** *Capnodiales*, *Cercospora*, cercosporoid, *Mycosphaerella*, *Mycosphaerellaceae, Paracercospora, Pseudocercosporella,* Multi-Locus Sequence Typing (MLST), systematics.
**Taxonomic novelties: New genera -** *Pallidocercospora* Crous, *Phaeomycocentrospora* Crous, H.D. Shin & U. Braun; **New species -** *Cercospora eucommiae* Crous, U. Braun & H.D. Shin, *Microcyclospora quercina* Crous & Verkley, *Pseudocercospora ampelopsis* Crous, U. Braun & H.D. Shin, *Pseudocercospora cercidicola* Crous, U. Braun & C. Nakash., *Pseudocercospora crispans* G.C. Hunter & Crous, *Pseudocercospora crocea* Crous, U. Braun, G.C. Hunter & H.D. Shin, *Pseudocercospora haiweiensis* Crous & X. Zhou, *Pseudocercospora humulicola* Crous, U. Braun & H.D. Shin, *Pseudocercospora marginalis* G.C. Hunter, Crous, U. Braun & H.D. Shin, *Pseudocercospora ocimi-basilici* Crous, M.E. Palm & U. Braun, *Pseudocercospora plectranthi* G.C. Hunter, Crous, U. Braun & H.D. Shin, *Pseudocercospora proteae* Crous, *Pseudocercospora pseudostigmina-platani* Crous, U. Braun & H.D. Shin, *Pseudocercospora pyracanthigena* Crous, U. Braun & H.D. Shin, *Pseudocercospora ravenalicola* G.C. Hunter & Crous, *Pseudocercospora rhamnellae* G.C. Hunter, H.D. Shin, U. Braun & Crous, *Pseudocercospora rhododendri-indici* Crous, U. Braun & H.D. Shin, *Pseudocercospora tibouchinigena* Crous & U. Braun, *Pseudocercospora xanthocercidis* Crous, U. Braun & A. Wood, *Pseudocercosporella koreana* Crous, U. Braun & H.D. Shin; **New combinations -** *Pallidocercospora acaciigena* (Crous & M.J. Wingf.) Crous & M.J. Wingf., *Pallidocercospora crystallina* (Crous & M.J. Wingf.) Crous & M.J. Wingf., *Pallidocercospora heimii* (Crous) Crous, *Pallidocercospora heimioides* (Crous & M.J. Wingf.) Crous & M.J. Wingf., *Pallidocercospora holualoana* (Crous, Joanne E. Taylor & M.E. Palm) Crous, *Pallidocercospora konae* (Crous, Joanne E. Taylor & M.E. Palm) Crous, *Pallidoocercospora irregulariramosa* (Crous & M.J. Wingf.) Crous & M.J. Wingf., *Phaeomycocentrospora cantuariensis* (E.S. Salmon & Wormald) Crous, H.D. Shin & U. Braun, *Pseudocercospora hakeae* (U. Braun & Crous) U. Braun & Crous, *Pseudocercospora leucadendri* (Cooke) U. Braun & Crous, *Pseudocercospora snelliana* (Reichert) U. Braun, H.D. Shin, C. Nakash. & Crous, *Pseudocercosporella chaenomelis* (Y. Suto) C. Nakash., Crous, U. Braun & H.D. Shin; **Typifications: Epitypifications -** *Pseudocercospora angolensis* (T. Carvalho & O. Mendes) Crous & U. Braun, *Pseudocercospora araliae* (Henn.) Deighton, *Pseudocercospora cercidis-chinensis* H.D. Shin & U. Braun, *Pseudocercospora corylopsidis* (Togashi & Katsuki) C. Nakash. & Tak. Kobay., *Pseudocercospora dovyalidis* (Chupp & Doidge) Deighton, *Pseudocercospora fukuokaensis* (Chupp) X.J. Liu & Y.L. Guo, *Pseudocercospora humuli* (Hori) Y.L. Guo & X.J. Liu, *Pseudocercospora kiggelariae* (Syd.) Crous & U. Braun, *Pseudocercospora lyoniae* (Katsuki & Tak. Kobay.) Deighton, *Pseudocercospora lythri* H.D. Shin & U. Braun, *Pseudocercospora sambucigena* U. Braun, Crous & K. Schub., *Pseudocercospora stephanandrae* (Tak. Kobay. & H. Horie) C. Nakash. & Tak. Kobay., *Pseudocercospora viburnigena* U. Braun & Crous, *Pseudocercosporella chaenomelis* (Y. Suto) C. Nakash., Crous, U. Braun & H.D. Shin, *Xenostigmina zilleri* (A. Funk) Crous; **Lectotypification** - *Pseudocercospora ocimicola* (Petr. & Cif.) Deighton; **Neotypifications** - *Pseudocercospora kiggelariae* (Syd.) Crous & U. Braun*, Pseudocercospora lonicericola* (W. Yamam.) Deighton, *Pseudocercospora zelkovae* (Hori) X.J. Liu & Y.L. Guo.

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## INTRODUCTION

Until recently, *Pseudocercospora* was treated as an anamorphic genus linked to *Mycosphaerella* (*Mycosphaerellaceae, Capnodiales*), along with approximately 30 other anamorphic genera (Crous 2009). The separation of the *Mycosphaerella* complex into families (Crous *et al*. 2007a, 2009b) and genera (Crous *et al*. 2009c) based on DNA sequence data and morphology had substantial implications for *Pseudocercospora*. *Pseudocercospora* is now recognised as a holomorphic genus in its own right, several species of which have mycosphaerella-like teleomorphs, for example, *Pseudocercospora fijiensis* and its mycosphaerella-like teleomorph that cause black leaf streak of banana (Arzanlou *et al*. 2008). The name *Mycosphaerella* is restricted to species with *Ramularia* anamorphs (Verkley *et al*. 2004, Crous *et al*. 2009c, Koike *et al.* 2011), with *Ramularia* being an older name than *Mycosphaerella.* A single generic name is now used for species of *Pseudocercospora* (Hawksworth *et al*. 2011, Wingfield *et al.* 2011)*,* in compliance with the recently accepted changes to the International Code of Nomenclature for algae, fungi and plants (ICN) adoped during the Botanical Congress in Sydney in 2011, in particular, the abolishment of Article 59 dealing with pleomorphic fungi.

Species of *Pseudocercospora* are well recognised as plant pathogens, endophytes or saprobes, with some used as biological control agents of weeds (Den Breeÿen *et al*. 2006). They occur on a large number of plants, many of which are important ornamentals or food crops including fruits, cereals and commercially propagated forest trees (Fig. 1). An early hypothesis was that the majority of *Pseudocercospora* species were strictly host specific. Later studies have reported that a few species occur on different hosts belonging to a single plant family (Deighton 1976, 1979), although DNA data or inoculation studies to support wider host ranges has often been lacking.

The classic monograph of the hyphomycete genus *Cercospora* (Chupp 1954) considered morphological features, including the structure of conidiomata as well as conidial pigmentation, septation, wall thickness, length, width, and shape as valuable features to define species within the genus. Chupp's circumscription of *Cercospora* was rather broadly defined, and the genus was later shown to be extremely heterogenous (Deighton 1976). Deighton (1976) distinguished different groups within *Cercospora* based on characters such as superficial mycelium (and the texture thereof), conidial scar type, conidiophore and conidium pigmentation, septation, and conidial catenulation. These additional features resulted in many *Cercospora* species being transferred to several alternative genera such as *Cercosporella*, *Mycocentrospora*, *Mycovellosiella*, *Phaeoramularia*, *Paracercospora*, *Passalora*, *Pseudocercospora, Ramularia*, *Stenella* and *Stigmina* (Deighton 1971, 1976, 1979, 1987, Braun 1995, 1998). A subsequent morphological treatment of names published in *Cercospora* (Crous & Braun 2003) provided some rationalisation, with the following concepts proposed for the taxonomic treatment of cercosporoid fungi: structure of conidiogenous loci (scars) and hila, as either unthickened (or almost so, but slightly darkened or refractive) or unthickened; presence or absence of pigmentation in conidiophores and conidia.

*Pseudocercospora* was originally introduced by Spegazzini (1910) based on the type species *Pseudocercospora vitis*, a foliar pathogen of grapevines. The majority of *Pseudocercospora* species known to date are regarded as pathogens on a wide variety of plants, predominantly in tropical and sub-tropical environments where they cause leaf spots, blights, fruit spot and fruit rot (Chupp 1954, Deighton 1976, von Arx 1983, Pons & Sutton 1988). Some important plant pathogens include the species associated with Sigatoka disease on banana (Arzanlou *et al.* 2007, 2008, 2010, Churchill 2010), angular leaf spot of bean (Crous *et al.* 2006), husk spot of macadamia (Beilharz *et al.* 2003), Cercospora leaf spot of olive (Ávila *et al.* 2005), cactus (Ayala-Escobar *et al.* 2005), avocado (Deighton 1976), and eucalypts (Braun & Dick 2002). The importance of these diseases is also reflected in quarantine regulations, *e.g.* for *Pseudocercospora angolensis* the cause of fruit and leaf spot disease on citrus (Pretorius *et al*. 2003) (Fig. 2), and *P. pini-densiflorae* the cause of brown needle blight of pine (Evans 1984, Crous *et al.* 1990).

*Pseudocercospora* was established to accommodate synnematal analogues of *Cercospora,* as well as species that produce pigmented conidiogenous structures and conidia with neither thickened nor darkened conidial hila (Deighton 1976, Braun 1995) (Fig. 3). It was proposed that *Pseudocercospora* be divided into several genera (Deighton 1976) based on morphological differences, a view later supported by several authors (Pons & Sutton 1988, Braun 1995, Crous & Braun 1996). Since the first study applied DNA phylogenetic analiysis to species in the *Mycosphaerella* complex (Stewart *et al.* 1999), *Pseudocercospora* has been shown to be heterogenous, accommodating hundreds of species (Crous *et al*. 2000, 2001, Crous & Braun 2003).

There are very few morphological features that are informative at the generic level within the *Pseudocercospora* complex. Deighton (1983) found it difficult to distinguish *Cercoseptoria* from *Pseudocercospora* on the basis of conidial shape, with conidia in the former genus acicular and those in the latter obclavate to cylindrical. In delimiting *Pseudocercospora* as an anamorph of *Mycosphaerella*, von Arx (1983) considered *Pseudocercospora* together in a group of related genera characterised by hyaline or subhyaline conidiogenous structures and unthickened, truncate, flat and broad conidiogenous loci. Later, Braun (1992) and Crous *et al*. (2000) argued that the arrangement of the conidiophores did not distinguish between sections within *Pseudocercospora* due to transitions from solitary to fasciculate to subsynnematal conidiophores. Crous *et al*. (2001) also regarded the slight thickening of conidial scars as a taxonomically uninformative generic character.

DNA sequence data for various gene regions have in recent years provided substantial information to support the generic circumscription of *Pseudocercospora*. Several studies have employed DNA sequence data from the Internal Transcribed Spacer (ITS) region of the rDNA operon for *Pseudocercospora* species from various hosts. Crous *et al*. (2000) examined isolates of *Pseudocercospora* from *Eucalyptus* and found that they could be separated into two clades within *Mycosphaerella.* Another clade of *Pseudocercospora* species occurred on banana, indicating that *Pseudocercospora* could be polyphyletic within the *Mycosphaerella* complex. Further evidence supporting this view emerged in subsequent studies that included many *Pseudocercospora* isolates (Crous *et al*. 2001). These phylogenetic studies have shown that several other genera are congeneric with *Pseudocercospora* and thus *Cercostigmina*, *Paracercospora*, *Phaeoisariopsis* and *Pseudophaeoramularia* were reduced to synonymy with *Pseudocercospora* (Stewart *et al*. 1999, Crous *et al*. 2001, Braun & Hill 2002, Crous *et al.* 2006). Based on these studies, the necessity arose to conserve *Pseudocercospora* over *Stigmina*, which represented an older generic name (Braun & Crous 2006).

Extensive DNA-based phylogenetic research has in recent years been conducted on *Mycosphaerella* and many of its anamorphic genera. These studies have not provided substantial resolution of *Pseudocercospora*. The aims of this study were to define phylogenetic lineages (reflecting genera) within what is perceived to be *Pseudocercospora.* An additional aim was to use the molecular data to infer host range and thus to consider the importance of host specificity in this important genus.

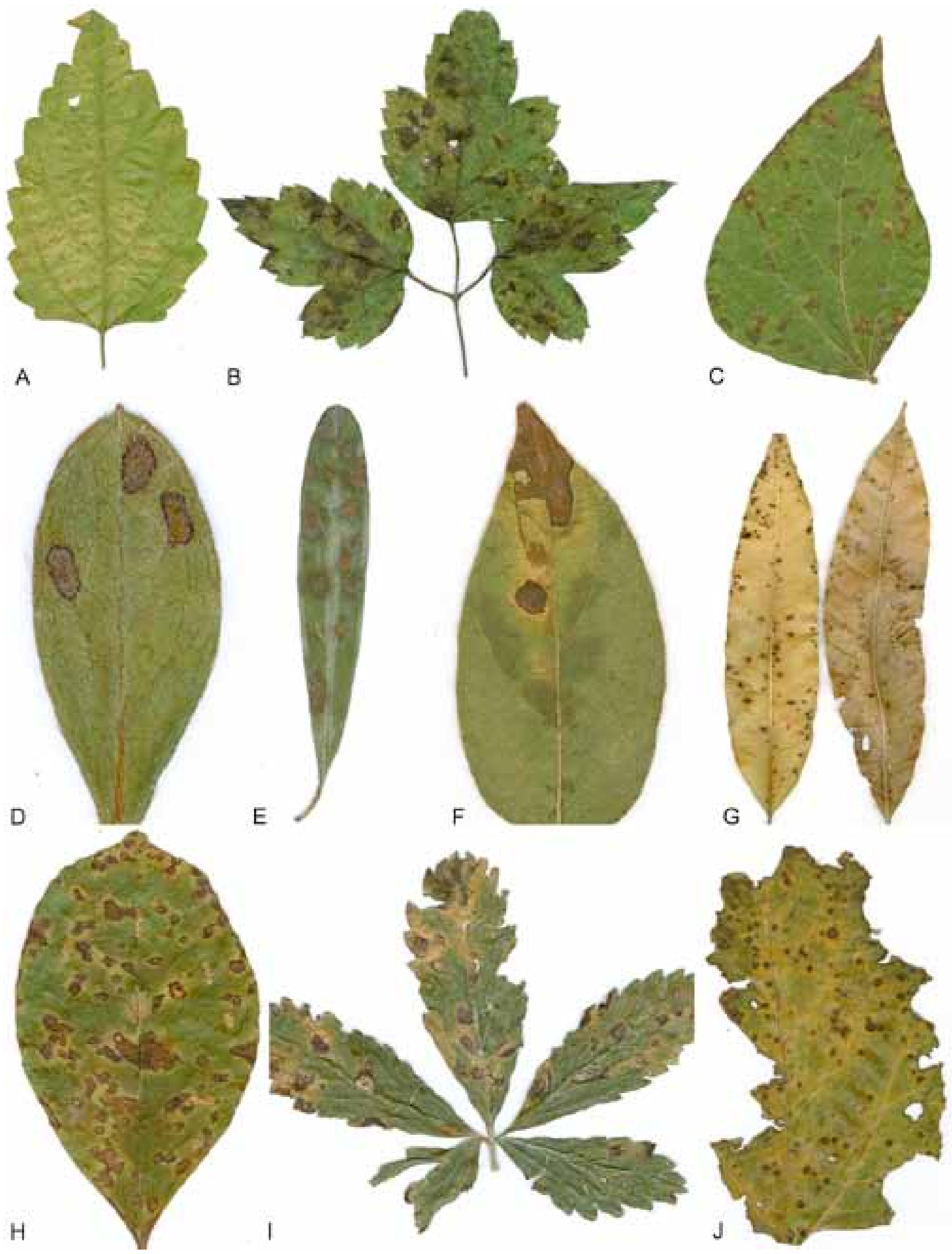

**Fig. 1.** Leaf spot symptoms associated with various species from the *Pseudocercospora* complex. A. *P. fatouae* on *Fatoua villosa*. B. *P. clematidis* on *Clematis apiicola*. C. *P. griseola* on *Phaseolus vulgaris*. D. *P. rhododendron-indici* on *Rhododendron indicum.* E. *P. pyracanthae* on *Pyracantha angustifolia*. F. *P. lonicericola* on *Lonicera japonica*. G. *Scolecostigmina mangiferae* on *Mangifera indica*. H. *P. fraxinites* on *Fraxinus rhynchophylla*. I. *Pseudocercosporella potentillae* on *Potentilla kleiniana*. J. *Pseudocercospora udagawana* on *Hovenia dulcis*.

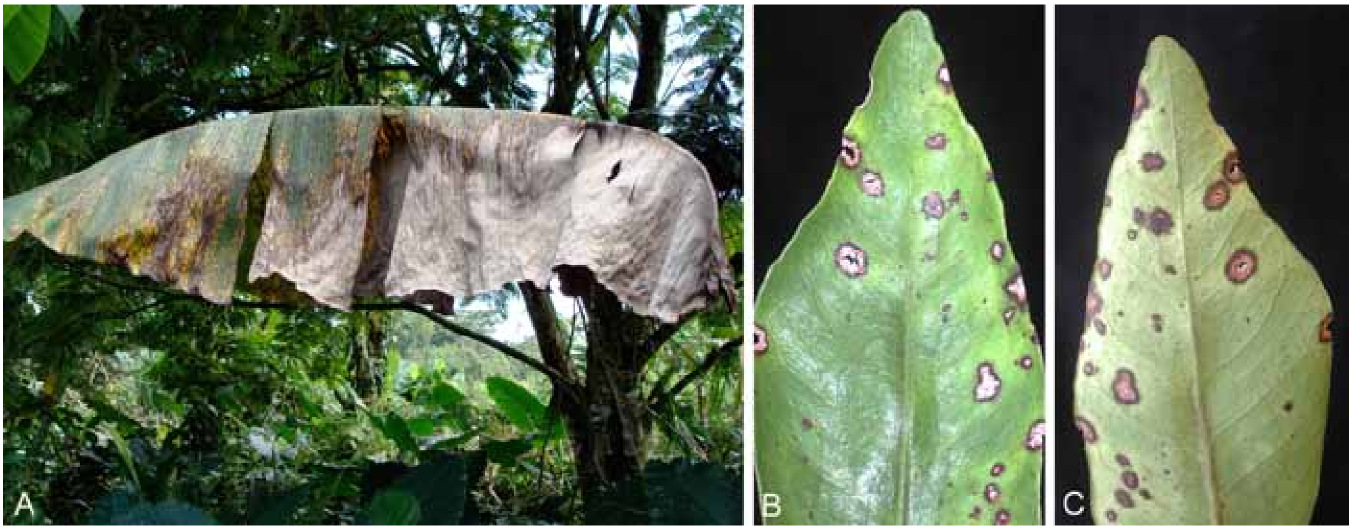

**Fig. 2.** *Pseudocercospora* species of quarantine importance. A. *P. fijiensis* on *Musa* (Black Leaf Streak or Black Sigatoka) (Photo G.H.J. Kema). B, C. *P. angolensis* on *Citrus* (Phaeoramularia Fruit and Leaf Spot).

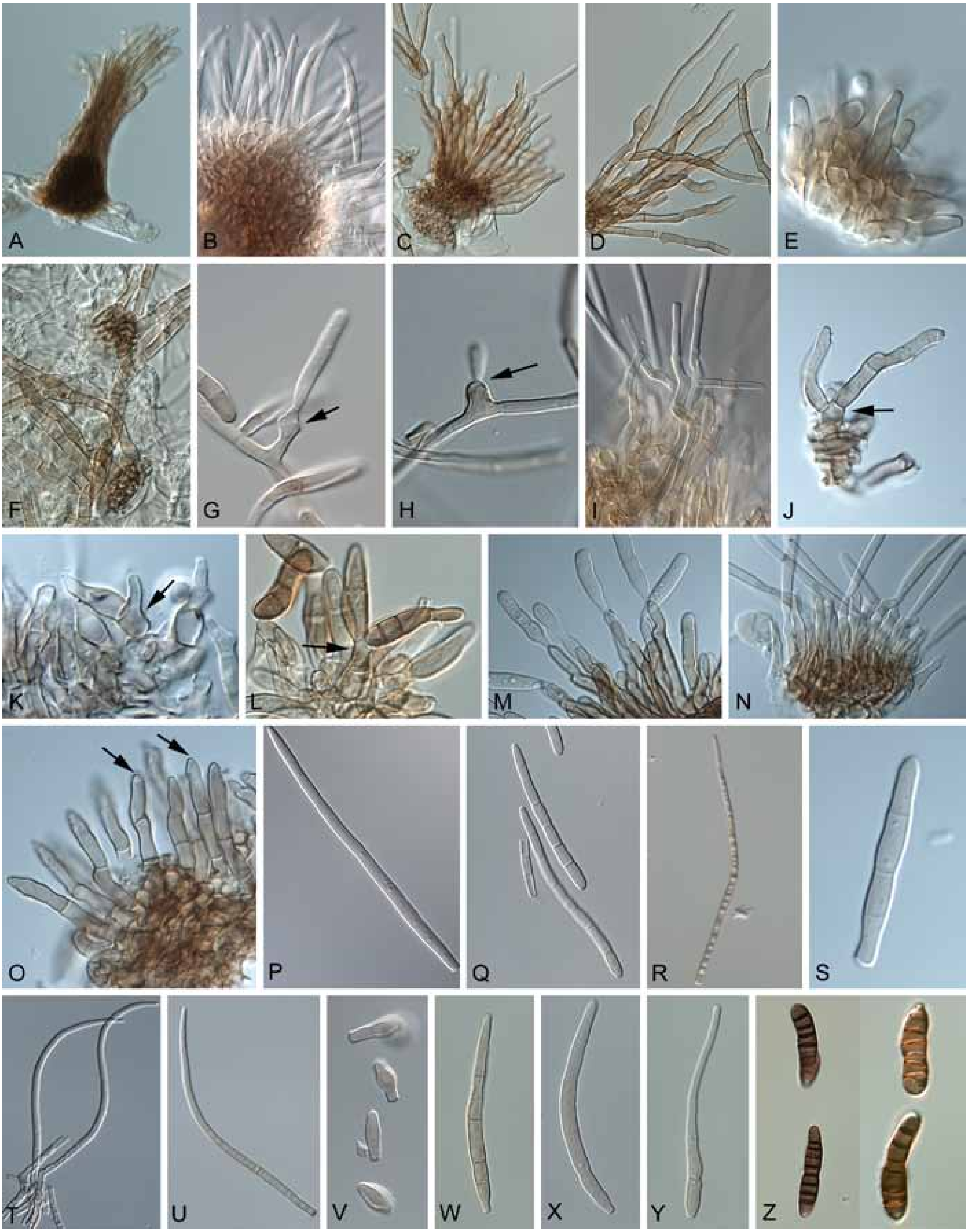


**Fig. 3.** Morphological structures of *Pseudocercospora* spp. A. Synnematous conidiophore. B. Densely aggregated fascicle of conidiophores with well-developed brown stroma. C, D. Loosely branched fascicles of conidiophores with moderate (C) and poorly (D) developed brown stroma. E. Fascicle reduced to conidiogenous cells. F. Conidiophore fascicles arising from stomata. G, H. Solitary conidiogenous cells on superficial hyphae. I. Geniculate conidiophore (arrow) with truncate apical locus. J, K. Conidiophores branched below (arrows). L. Conidiogenous cells with percurrent proliferations (arrows). M, N. Conidiophores with sympodial proliferation. O. Conidiophores with conidiogenous cells (note minutely thickened scars, arrows). P. Subcylindrical conidium with subacute apex and truncate base. Q. Conidia with constrictions at septa. R. Conidium with guttules. S. Cylindrical conidium with obtuse apex, and truncate base. T. Undulate conidia. U. Curved conidium. Aseptate to 1-septate conidia. V. 1-septate conidia. W, X. Obclavate conidia with obconical base. Y. Obclavate conidium with short obconical base. Z. Dark brown, muriformly euseptate conidia (thick-walled, not distoseptate).

## MATERIALS AND METHODS

### Isolates

Direct isolations were made from fascicles of conidiophores on leaves. Some leaves were incubated in moist chambers for up to 1 wk to enhance sporulation before single conidial colonies were established on 2 % malt extract agar (MEA) (Crous 2002). Leaf spots bearing ascomata were soaked in water for approximately 2 h, after which they were attached to the inner surface of Petri dish lids over plates containing MEA. Ascospore germination patterns were examined after 24 h, and single ascospore and conidial cultures established as described previously (Crous *et al*. 1991, Crous 1998). Colonies were sub-cultured onto synthetic nutrient-poor agar (SNA), potato-dextrose agar (PDA), oatmeal agar (OA), and MEA (Crous *et al.* 2009d), and incubated at 25 °C under continuous near-ultraviolet light to promote sporulation. Isolates were also sourced from the culture collections of the CBS-KNAW Fungal Biodiversity Centre (CBS), the working collection of Pedro Crous (CPC), Chiharu Nakashima (CNS) and the culture collection of the laboratory of plant pathology, Mie University, Japan (MUCC), and the mycological herbarium of Mie University (MUMH). Furthermore, isolates representing fungal species from genera allied to *Pseudocercospora, e.g. Cercospora*, *Cercostigmina*, *Cyphellophora*, *Davidiella*, *Dissoconium*, *Miuraea*, *Mycocentrospora*, *Passalora*, *Phaeoisariopsis*, *Phleospora*, *Septoria*, *Strelitziana*, *Stigmina, Teratosphaeria*, *Thedgonia*, *Trochophora,* and *Xenostigmina*, were included in this study (Table 1).

### DNA isolation

Mycelium from actively growing fungal cultures was scraped from the surface of MEA or PDA plates using a sterile scalpel blade. Harvested mycelium was ground to a fine powder using liquid nitrogen and DNA was isolated using the CTAB extraction protocol as outlined by Crous *et al*. (2009d) or the UltraClean™ Microbial DNA Isolation Kit (MoBio Laboratories, Inc., Solana Beach, CA, USA) following the manufacturers' protocols. Isolated DNA was visualised by electrophoresis in 1 % agarose gels (w/v) stained with ethidium bromide and viewed under near ultra-violet light. DNA concentrations were determined by measuring electrophoresed DNA samples against a HyperLadder™ I molecular marker (BIOLINE) or alternatively by a NanoDrop quantification as outlined by the manufacturer.

### PCR amplification

DNA isolated from fungal isolates was used as template for further Polymerase Chain Reaction (PCR) amplifications. Four nuclear gene regions were targeted for PCR amplification and subsequent sequencing. These regions included the Internal Transcribed Spacer regions ITS-1, ITS-2 and the 5.8S nrRNA gene regions (ITS), the first 900 bp of the Large Subunit (28S, LSU) (domains D1–D3) of the rDNA operon and partial gene regions of the translation elongation factor 1-alpha (EF-1α) and the actin (ACT) genes.

The ITS region was amplified using primers ITS-1 or ITS-5 and ITS-4 (White *et al*. 1990) while primers used for amplification of the LSU region were LR0R (Rehner & Samuels 1994) or LSU1Fd (Crous *et al*. 2009b) and LR5 or LR7 (Vilgalys & Hester 1990). Primers employed for the amplification of EF-1α included EF1-728F and EF1-986R (Carbone & Kohn 1999) or EF-2 (O'Donnell *et al*. 1998) while ACT-512F and ACT-783R (Carbone & Kohn 1999) were used to amplify a portion of the ACT gene. All PCR reaction mixtures and conditions followed those outlined by Hunter *et al*. (2006b). Following PCR amplification, amplicons were visualized on 1.5 % agarose gels stained with ethidium bromide and viewed under ultra-violet light and sizes of amplicons were determined against a HyperLadder™ I molecular marker (BIOLINE). The PCR amplicons for the four loci were subsequently diluted 1 to 10 times in preparation for further DNA sequencing reactions.

### DNA sequencing and phylogenetic inference

PCR amplicons of the four gene regions targeted in this study served as templates for DNA sequencing reactions with the BigDye® Terminator Cycle Sequencing Kit v. 3.1 (Applied Biosystems Life Technologies, Carlsbad, CA, USA) following the protocol of the manufacturer. DNA sequencing reactions used the same primers as those for the PCR reactions. However, additional internal primers LR3R (http://www.biology.duke.edu/fungi/mycolab/primers.htm), LR16 (Moncalvo *et al*. 1993) and LR5 were used to sequence the LSU in order to obtain reliable sequences spanning the entire D1-D3 region. DNA sequencing amplicons were purified through Sephadex® G-50 Superfine columns (Sigma Aldrich, St. Louis, MO) in MultiScreen HV plates (Millipore, Billerica, MA). Purified sequence reactions were run on an ABI Prism 3730xl DNA Sequencer (Life Technologies, Carlsbad, CA, USA).

Generated DNA sequence electropherograms were analysed using MEGA (Molecular Evolutionary Genetics Analysis) v. 4.0 (Tamura *et al*. 2007), 4Peaks v. 1.7.2 (http://www.mekentosj.com/) and SeqMan v. 8.0.2. from the DNASTAR Lasergene® software package. Consensus sequences were generated and imported into MEGA for initial alignment and the construction of sequence datasets. DNA sequences representing isolates of closely allied genera, for which material could not be obtained were downloaded from the NCBI GenBank nucleotide database (www.ncbi.nlm.nih.gov) and added to the DNA sequence datasets generated in this study. Sequence datasets for the four genomic loci were aligned in MAFFT ("Multiple alignment program for amino acids or nucleotide sequences") v. 6.0 (Katoh & Toh 2006, Katoh *et al*. 2005; http://mafft.cbrc.jp/alignment/server/index.html) using the Auto alignment strategy with the 200PAM/ K=2 scoring matrix and a gap opening penalty of 1.53 with an offset value of 0.0. Resulting sequence alignments were manually evaluated and adjusted in MEGA, MacClade v.4.08 (Maddison & Maddison 2000) or Sequence Alignment Editor v. 2.0a11 (Rambaut 2002).

A phylogenetic re-construction was conducted for the aligned LSU data set to determine generic relationships using MrBayes v. 3.1.2 (Ronquist & Huelsenbeck 2003). Subsequently, a species level phylogeny was derived from the combined ITS, ACT and EF-1α alignment of *Pseudocercospora* s. str. sequences using PAUP v. 4.0b10 (Swofford 2003). For the LSU alignment, MrModeltest v. 2.2 (Nylander 2004) was used to determine the best nucleotide substitution model settings for MrBayes. Based on the results of the MrModeltest, a phylogenetic analysis was performed with MrBayes v. 3.1.2 applying a general time-reversible (GTR) substitution model with inverse gamma rates and dirichlet base frequencies and a heating parameter set at 0.3. The Markov Chain Monte Carlo (MCMC) analysis of 4 chains started in parallel from a random tree topology and had 8 000 000 generations. Trees were saved each

**Table 1.** *Pseudocercospora* and pseudocercospora-like isolates included in the morphological and/or phylogenetic analyses.

| Species | Culture accession numbers[1] | Collector | Host | Family | Country | GenBank accession numbers[2] | | | |
|---|---|---|---|---|---|---|---|---|---|
| | | | | | | LSU | ITS | EF-1α | ACT |
| *Cercospora eucommiae* | CPC 10047 | H.D. Shin | *Eucommia ulmoides* | *Eucommiaceae* | South Korea | GU253741 | GU269702 | GU384418 | GU320406 |
| | CPC 10802; CBS 131932 | H.D. Shin | *Eucommia ulmoides* | *Eucommiaceae* | South Korea | GU214674 | GU269851/ GU214674 | GU384563 | GU320555 |
| | CPC 11508; CBS 132026 | H.D. Shin | *Eucommia ulmoides* | *Eucommiaceae* | South Korea | GU253742 | GU269703 | GU384419 | GU320407 |
| *Cercospora sojina* | CPC 12322; CBS 132018 | H.D. Shin | *Glycine soja* | *Fabaceae* | South Korea | GU253861 | GU214655 | JQ324984 | JQ325008 |
| *Cyphellophora eucalypti* | CBS 124764; CPC 13412 | P.W. Crous | *Eucalyptus* sp. | *Myrtaceae* | Australia | GQ303305 | GQ303274 | GU384510 | JQ325009 |
| *Dissoconium dekkeri* | CBS 110748; CPC 825; CMW 14906 | G. Kemp | *Eucalyptus grandis* | *Myrtaceae* | South Africa | GU214422 | AF173315 | JQ324985 | DQ147651 |
| *Microcyclospora quercina* | CPC 10712; CBS 130827 | G. Verkley | *Quercus* sp. | *Fagaceae* | Netherlands | GU214681 | GU269789 | GU384499 | GU320490 |
| *Miuraea persicae* | CPC 10069; CBS 132307 | H.D. Shin | *Prunus persica* | *Rosaceae* | South Korea | GU253859 | GU269843 | GU384556 | GU320546 |
| | CPC 10828; CBS 131935 | H.D. Shin | *Prunus armeniaca* | *Rosaceae* | South Korea | JQ324939 | GU269844 | GU384557 | GU320547 |
| *"Mycosphaerella" laricina* | CBS 326.52 | E. Müller | *Larix decidua* | *Pinaceae* | Switzerland | GU253693 | GU269643 | GU384361 | GU320353 |
| *"Mycosphaerella" madeirae* | CBS 112895; CPC 3745 | S. Denman | *Eucalyptus globulus* | *Myrtaceae* | Portugal | DQ204756 | AY725553 | DQ211672 | DQ147641 |
| *"Mycosphaerella" marksii* | CBS 110920; CPC 935; CMW 5150 | A.J. Carnegie | *Eucalyptus botryoides* | *Myrtaceae* | Australia | DQ246250/ GU253694 | AF309588/ GU269644 | DQ235134 | DQ147625 |
| *Pallidocercospora acaciigena* | CBS 112516; CPC 3838 | M.J. Wingfield | *Acacia mangium* | *Fabaceae* | Venezuela | GU214661/ GU253697 | GU269648 | GU384366 | GU320356 |
| | CBS 120740; CPC 13290 | B. Summerell | *Eucalyptus* sp. | *Myrtaceae* | Australia | GU253698 | EF394822/ GU269649 | GU384367 | GU320357 |
| *Pallidocercospora crystallina* | CBS 681.95; CBS 116158; CPC 802; CMW 3033 | M.J. Wingfield | *Eucalyptus bicostata* | *Myrtaceae* | South Africa | DQ204747 | AY490757 | DQ147636/ DQ211662 | DQ147636 |
| *Pallidocercospora heimii* | CBS 110682; CPC 760; CMW 4942 | P.W. Crous | *Eucalyptus* sp. | *Myrtaceae* | Madagascar | DQ204751 | AF309606 | DQ211667 | DQ147638 |
| *Pallidocercospora heimioides* | CBS 111190; CPC 1312; CMW 3046 | M.J. Wingfield | *Eucalyptus* sp. | *Myrtaceae* | Indonesia | DQ204753 | AF309609 | DQ211669 | DQ147633 |
| *Pallidocercospora irregulariramosa* | CBS 114774; CBS 114777; CPC 1360; CMW 4943 | M.J. Wingfield | *Eucalyptus saligna* | *Myrtaceae* | South Africa | DQ204754 | AF309607 | DQ211670 | DQ147634 |
| *Pallidocercospora konae* | CBS 120748; CPC 13469 | W. Himaman | *Eucalyptus camaldulensis* | *Myrtaceae* | Thailand | GU253852 | EF394842 | GU384549 | GU320538 |
| *Paracercospora egenula* | CBS 485.81 | N. Ponnapa | *Solanum melongena* | *Solanaceae* | India | JQ324940 | GU269699 | GU384415 | GU320403 |
| | CPC 12537; CBS 132030 | H.D. Shin | *Solanum melongena* | *Solanaceae* | South Korea | GU253738 | GU269698 | GU384414 | GU320402 |
| | MUCC 883 | T. Mikami | *Solanum melongena* | *Solanaceae* | Japan | GU253739 | GU269700 | GU384416 | GU320404 |
| *Passalora eucalypti* | CBS 111318; CPC 1457 | P.W. Crous | *Eucalyptus saligna* | *Myrtaceae* | Brazil | GU253860 | GU269845 | GU384558 | GU320548 |
| *Phaeomycocentrospora cantuariensis* | CPC 10157 | H.D. Shin | *Humulus scandens* | *Cannabaceae* | South Korea | GU253712 | GU269664 | GU384381 | GU320370 |
| | CPC 10762; CBS 131928 | H.D. Shin | *Luffa cylindrica* | *Cucurbitaceae* | South Korea | GU253713 | GU269665 | GU384382 | GU320371 |

**Table 1.** (Continued).

| Species | Culture accession numbers[1] | Collector | Host | Family | Country | GenBank accession numbers[2] | | | |
|---|---|---|---|---|---|---|---|---|---|
| | | | | | | LSU | ITS | EF-1α | ACT |
| | CPC 11646; CBS 132013 | H.D. Shin | *Acalypha australis* | *Euphorbiaceae* | South Korea | GU253715 | GU269667 | GU384384 | GU320373 |
| | CPC 11694; CBS 132014 | H.D. Shin | *Humulus scandens* | *Cannabaceae* | South Korea | GU253716 | GU269668 | GU384385 | GU320374 |
| *Phloeospora ulmi* | CBS 344.97 | W. Gams | *Ulmus glabra* | *Ulmaceae* | Austria | GU253841 | JQ324974 | JQ324986 | GU320528 |
| | CBS 613.81 | H.A. Van der Aa | *Ulmus* sp. | *Ulmaceae* | Austria | GU253842 | GU269825 | JQ324987 | GU320529 |
| *Pseudocercospora abelmoschi* | CPC 14478; CBS 132103 | H.D. Shin | *Hibiscus syriacus* | *Malvaceae* | South Korea | GU253696 | GU269647 | GU384365 | GU320355 |
| *Pseudocercospora acericola* | CBS 122279 | R. Kirschner | *Acer albopurpurascens* | *Aceraceae* | Taiwan | GU253699 | GU269650 | GU384368 | GU320358 |
| *Pseudocercospora ampelopsis* | CPC 11680; CBS 131583 | H.D. Shin | *Ampelopsis brevipenduncula* var. *heterophylla* | *Vitaceae* | South Korea | GU253846 | GU269830 | GU384542 | GU320534 |
| *Pseudocercospora angolensis* | CBS 112933; CPC 4118 | M.C. Pretorius | *Citrus* sp. | *Rutaceae* | Zimbabwe | GU214470 | AY260063/ GU269836 | GU384548 | JQ325010 |
| | CBS 149.53 | T. de Carvalho & O. Mendes | *Citrus sinensis* | *Rutaceae* | Angola | JQ324941 | JQ324975 | JQ324988 | JQ325011 |
| *Pseudocercospora araliae* | CPC 10154 | H.D. Shin | *Aralia elata* | *Araliaceae* | South Korea | GU253701 | GU269652 | GU384370 | GU320360 |
| | MUCC 873 | T. Kobayashi & C. Nakashima | *Aralia elata* | *Araliaceae* | Japan | GU253702 | GU269653 | GU384371 | GU320361 |
| *Pseudocercospora arecacearum* | CBS 118406 | C.F. Hill | *Rhopalostylis sapidis* | *Arecaceae* | New Zealand | GU253704 | GU269655 | GU384373 | GU320363 |
| | CBS 118792 | C.F. Hill | *Howea forsteriana* | *Arecaceae* | New Zealand | GU253703 | GU269654 | GU384372 | GU320362 |
| *Pseudocercospora assamensis* | CBS 122467 | I. Buddenhagen | *Musa cultivar* | *Musaceae* | India | GU253705 | GU269656 | GU384374 | GU320364 |
| *Pseudocercospora atromarginalis* | CBS 114640 | C.F. Hill | *Solanum* sp. | *Solanaceae* | New Zealand | GU253706 | GU269658 | GU384376 | GU320365 |
| | CPC 11372; CBS 132010 | H.D. Shin | *Solanum nigrum* | *Solanaceae* | South Korea | GU214671 | GU269657 | GU384375 | — |
| *Pseudocercospora balsaminae* | CPC 10044; CBS 131882 | H.D. Shin | *Impatiens textori* | *Balsaminaceae* | South Korea | GU253708 | GU269660 | GU384379 | GU320367 |
| *Pseudocercospora basiramifera* | CBS 111072; CPC 1266 | M.J. Wingfield | *Eucalyptus pellita* | *Myrtaceae* | Thailand | GU253709 | GU269661 | DQ211677 | GU320368 |
| | CBS 114757; CPC 1267 | M.J. Wingfield | *Eucalyptus pellita* | *Myrtaceae* | Thailand | GU253802 | GU269781 | GU384492 | GU320484 |
| *Pseudocercospora basitruncata* | CBS 114664; CPC 1202 | M.J. Wingfield | *Eucalyptus grandis* | *Myrtaceae* | Colombia | GU253710/ DQ204759 | DQ267600/ GU269662 | DQ211675 | DQ147622 |
| *Pseudocercospora callicarpae* | MUCC 888 | T. Kobayashi | *Callicarpa japonica* | *Verbenaceae* | Japan | GU253711 | GU269663 | GU384380 | GU320369 |
| *Pseudocercospora catalpigena* | MUCC 743 | C. Nakashima & I. Araki | *Catalpa ovata* | *Bignoniaceae* | Japan | GU253731 | GU269690 | GU384406 | GU320395 |
| *Pseudocercospora catappae* | MUCC 809 | C. Nakashima & T. Akashi | *Terminalia catappa* | *Combretaceae* | Japan | GU253717 | GU269669 | GU384386 | GU320375 |
| *Pseudocercospora cercidicola* | MUCC 896 | T. Kobayashi & Y. Kobayashi | *Cercis chinensis* | *Fabaceae* | Japan | GU253719 | GU269671 | GU384388 | GU320377 |
| *Pseudocercospora cercidis-chinensis* | CPC 14481; CBS 132109 | H.D. Shin | *Cercis chinensis* | *Fabaceae* | South Korea | GU253718 | GU269670 | GU384387 | GU320376 |
| *Pseudocercospora* cf. *cruenta* | CBS 117232 | R. Kirschner | *Phaseolus vulgaris* | *Fabaceae* | Taiwan | GU253730 | GU269689 | GU384405 | GU320394 |
| *Pseudocercospora* cf. *kaki* | CPC 10636; CBS 131921 | H.D. Shin | *Diospyros lotus* | *Ebenaceae* | South Korea | GU214677 | GU269728 | GU384441 | GU320430 |

**Table 1.** (Continued).

| Species | Culture accession numbers[1] | Collector | Host | Family | Country | GenBank accession numbers[2] | | | |
|---|---|---|---|---|---|---|---|---|---|
| | | | | | | LSU | ITS | EF-1α | ACT |
| *Pseudocercospora chengtuensis* | CPC 10696; CBS 131924 | H.D. Shin | *Lycium chinense* | *Solanaceae* | South Korea | JQ324942 | GU269673 | GU384390 | GU320379 |
| | MUCC 828 | I. Araki & M. Harada | *Lycium chinense* | *Solanaceae* | Japan | JQ324943 | — | — | — |
| *Pseudocercospora chionanthi-retusi* | CPC 14683; CBS 132110 | H.D. Shin | *Chionanthus retusus* | *Oleaceae* | South Korea | GU253721 | GU269674 | GU384391 | GU320380 |
| *Pseudocercospora chrysanthemicola* | CPC 10633; CBS 131888 | H.D. Shin | *Chrysanthemum* sp. | *Asteraceae* | South Korea | GU253722 | GU269675 | GU384392 | GU320381 |
| *Pseudocercospora cladosporioides* | CBS 117482; CPC 10913 | P.W. Crous | *Olea europaea* | *Oleaceae* | Tunisia | JQ324944 | GU269678 | GU384395 | GU320383 |
| *"Pseudocercospora" colombiensis* | CBS 110969; CPC 1106; CMW 4944 | M.J. Wingfield | *Eucalyptus urophylla* | *Myrtaceae* | Colombia | DQ204744 | AY752149 | DQ211660 | DQ147639 |
| *Pseudocercospora contraria* | CPC 14714; CBS 132108 | H.D. Shin | *Dioscorea quinqueloba* | *Dioscoreaceae* | South Korea | JQ324945 | GU269677 | GU384394 | GU320385 |
| *Pseudocercospora coprosmae* | CBS 114639 | C. F. Hill | *Coprosma robusta* | *Rubiaceae* | New Zealand | JQ324946 | GU269680 | GU384397 | GU320386 |
| *Pseudocercospora cordiana* | CBS 114685; CPC 2552 | P.W. Crous & R.L. Benchimol | *Cordia goeldiana* | *Boraginaceae* | Brazil | GU214472 | AF362054/ GU269681 | GU384398 | GU320387 |
| *Pseudocercospora coriariae* | MUCC 840 | I. Araki & M. Harada | *Coriaria japonica* | *Coriariaceae* | Japan | GU253725 | GU269682 | GU384399 | GU320388 |
| *Pseudocercospora cornicola* | MUCC 909 | C. Nakashima & E. Imaizumi | *Cornus alba* var. *sibirica* | *Cornaceae* | Japan | GU253726 | GU269683 | GU384400 | GU320389 |
| *Pseudocercospora corylopsidis* | MUCC 874 | T. Kobayashi & C. Nakashima | *Hamamelis japonica* | *Hamamelidaceae* | Japan | GU253757 | GU269721 | GU384437 | GU320425 |
| | MUCC 908 | C. Nakashima & E. Imaizumi | *Corylopsis spicata* | *Hamamelidaceae* | Japan | GU253727 | GU269684 | GU384401 | GU320390 |
| *Pseudocercospora cotoneastri* | MUCC 876 | T. Kobayashi & C. Nakashima | *Cotoneaster salicifolius* | *Rosaceae* | Japan | GU253728 | GU269685 | GU384402 | GU320391 |
| *Pseudocercospora crispans* | CPC 14883; CBS 125999 | P.W.Crous | *Eucalyptus* sp. | *Myrtaceae* | South Africa | GU253825 | GU269807 | GU384518 | GU320510 |
| *Pseudocercospora crocea* | CPC 11668; CBS 126004 | H.D. Shin | *Pilea hamaoi* | *Urticaceae* | South Korea | JQ324947 | GU269792 | GU384502 | GU320493 |
| *Pseudocercospora crousii* | CBS 119487 | C.F. Hill | *Eucalyptus* sp. | *Myrtaceae* | New Zealand | GU253729 | GU269686 | GU384403 | GU320392 |
| *Pseudocercospora cruenta* | CPC 10846; CBS 132021 | H. Booker | *Vigna* sp. | *Fabaceae* | Trinidad | GU214673 | GU269688 | GU384404 | JQ325012 |
| *Pseudocercospora cydoniae* | CPC 10678; CBS 131923 | H.D. Shin | *Chaenomeles speciosa* | *Rosaceae* | South Korea | GU253732 | GU269691 | GU384407 | GU320396 |
| *Pseudocercospora cymbidiicola* | CBS 115132 | C.F. Hill | *Cymbidium* sp. | *Orchidaceae* | New Zealand | GU253733 | GU269692 | GU384408 | GU320397 |
| *Pseudocercospora davidiicola* | MUCC 296 | C. Nakashima & I. Araki | *Davidia involucrata* | *Nyssaceae* | Japan | GU253734 | GU269693 | GU384409 | GU320398 |
| *Pseudocercospora dendrobii* | MUCC 596 | C. Nakashima & K. Motohashi | *Dendrobium* sp. | *Orchidaceae* | Japan | GU253737 | GU269696 | GU384412 | GU320401 |
| *Pseudocercospora destructiva* | MUCC 870 | S. Uematsu & C. Nakashima | *Euonymus japonicus* | *Celastraceae* | Japan | GU253735 | GU269694 | GU384410 | GU320399 |
| *Pseudocercospora dianellae* | CBS 117746 | C.F. Hill | *Dianella caerulae* | *Liliaceae* | New Zealand | GU253736 | GU269695 | GU384411 | GU320400 |
| *Pseudocercospora dodonaeae* | CBS 114647 | C.F. Hill | *Dodonaea viscosa* | *Sapindaceae* | New Zealand | JQ324948 | GU269697 | GU384413 | JQ325013 |
| *Pseudocercospora dovyalidis* | CPC 13771; CBS 126002 | P.W. Crous | *Dovyalis zeyheri* | *Flacourtiaceae* | South Africa | GU253818 | GU269800 | GU384513 | GU320503 |
| *Pseudocercospora elaeocarpi* | MUCC 925 | C. Nakashima | *Elaeocarpus* sp. | *Elaeocarpaceae* | Japan | GU253740 | GU269701 | GU384417 | GU320405 |
| *"Pseudocercospora" epispermogonia* | CBS 110750; CPC 822 | G. Kemp | *Eucalyptus grandis* | *Myrtaceae* | South Africa | DQ204757 | DQ267596 | DQ211673 | DQ147629 |

**Table 1.** (Continued).

| Species | Culture accession numbers[1] | Collector | Host | Family | Country | GenBank accession numbers[2] | | | |
|---|---|---|---|---|---|---|---|---|---|
| | | | | | | LSU | ITS | EF-1α | ACT |
| *Pseudocercospora eucalyptorum* | CBS 110777; CPC 16; CMW 5228 | P.W. Crous | *Eucalyptus nitens* | *Myrtaceae* | South Africa | DQ204762 | AF309598 | DQ211678 | DQ147614 |
| | CBS 114242; CPC 10390; CMW 14908 | J.P. Mansilla | *Eucalyptus globulus* | *Myrtaceae* | Spain | GU214481 | AY725526 | DQ211681 | DQ147613/ GU320465 |
| | CBS 116359; CPC 3751 | P.W. Crous | *Eucalyptus* sp. | *Myrtaceae* | Madeira | GU253829 | GU269812 | GU384524 | GU320514 |
| | CPC 10500; CBS 114243 | P.W. Crous | *Eucalyptus nitens* | *Myrtaceae* | New Zealand | JQ324949 | AY725527 | GU384474 | JQ325014 |
| | CPC 10507; CBS 116371 | P.W.Crous | *Eucalyptus nitens* | *Myrtaceae* | New Zealand | JQ324950 | GU269687 | JQ324989 | GU320393 |
| | CPC 10916 | P.W. Crous | *Eucalyptus* sp. | *Myrtaceae* | South Africa | GU253788 | GU269763 | GU384475 | GU320464 |
| | CPC 11713; CBS 132015 | P. Mansilla | *Eucalyptus globulus* | *Myrtaceae* | Spain | JQ324951 | GU269811 | GU384523 | JQ325015 |
| | CPC 12406; CBS 132029 | I. Smith | *Eucalyptus globulus* | *Myrtaceae* | Australia | GU253811 | GU269793 | GU384503 | GU320494 |
| | CPC 12568; CBS 132309 | C. Mohammed | *Eucalyptus nitens* | *Myrtaceae* | Australia | GU253814 | GU269796 | GU384506 | GU320497 |
| | CPC 12802; CBS 132032 | A. Phillips | *Eucalyptus globulus* | *Myrtaceae* | Portugal | GU253789 | JQ324976 | JQ324990 | GU320466 |
| | CPC 12957; CBS 132033 | B. Summerell | *Eucalyptus deanei* | *Myrtaceae* | Australia | GU253815 | GU269797 | JQ324991 | JQ325016 |
| | CPC 13455; CBS 132034 | P.W. Crous | *Eucalyptus* sp. | *Myrtaceae* | Portugal | GU253816 | GU269798 | GU384511 | GU320501 |
| | CPC 13769; CBS 132035 | P.W. Crous | *Eucalyptus punctata* | *Myrtaceae* | South Africa | GU253707 | GU269659 | GU384378 | GU320366 |
| | CPC 13816; CBS 132114 | S. Denman | *Eucalyptus glaucescens* | *Myrtaceae* | UK | GU253819 | GU269801 | JQ324992 | GU320504 |
| | CPC 13926; CBS 132105 | S. Denman | *Eucalyptus* sp. | *Myrtaceae* | USA | GU253820 | GU269802 | JQ324993 | GU320505 |
| *Pseudocercospora eupatoriella* | CBS 113372 | M.J. Morris | *Chromolaena odorata* | *Asteraceae* | Jamaica | GU253743 | GU269704 | GU384420 | GU320408 |
| *Pseudocercospora eustomatis* | CBS 110822 | G. Dal Bello | *Eustroma grandiflorum* | *Gentianaceae* | Argentina | GU253744 | GU269705 | GU384421 | GU320409 |
| *Pseudocercospora exosporioides* | MUCC 893 | T. Kobayashi | *Sequoia sempervirens* | *Taxodiaceae* | Japan | GU253746 | GU269707 | GU384423 | GU320411 |
| *Pseudocercospora fijiensis* | CBS 120258; CIRAD 86 | J. Carlier | *Musa* sp. | *Musaceae* | Cameroon | JQ324952 | EU514248 | Genome[3] | Genome[3] |
| | MUCC 792 | T. Kobayashi & C. Nakashima | *Musa* sp. | *Musaceae* | Japan | GU253776 | GU269748 | JQ324994 | GU320450 |
| *Pseudocercospora flavomarginata* | CBS 118841; CMW 13586 | M.J. Wingfield | *Eucalyptus camaldulensis* | *Myrtaceae* | Thailand | DQ153306 | DQ155657 | DQ156548 | DQ166513 |
| | CBS 124990; CPC 13492 | W. Himaman | *Eucalyptus camaldulensis* | *Myrtaceae* | Thailand | GU253817 | GU269799 | GU384512 | GU320502 |
| | CPC 14142; CBS 126001 | X. Zhou | *Eucalyptus* sp. | *Myrtaceae* | China | GU253822 | GU269804 | GU384515 | GU320507 |
| *Pseudocercospora fori* | CBS 113285; CMW 9095 | G.C. Hunter | *Eucalyptus grandis* | *Myrtaceae* | South Africa | DQ204748 | AF468869 | DQ211664 | DQ147618 |
| | CPC 14880; CBS 132113 | P.W. Crous | *Eucalyptus* sp. | *Myrtaceae* | South Africa | GU253824 | GU269806 | GU384517 | GU320509 |
| *Pseudocercospora fraxinites* | CPC 10743; CBS 131927 | H.D. Shin | *Fontanesia phillyraeoides* | *Oleaceae* | South Korea | GU253720 | GU269672 | GU384389 | GU320378 |
| | MUCC 891 | T. Kobayashi | *Fraxinus excelsior* | *Oleaceae* | Japan | GU253748 | GU269710 | GU384426 | GU320414 |
| *Pseudocercospora fukuokaensis* | CPC 14689; CBS 132111 | H.D. Shin | *Styrax japonicus* | *Styracaceae* | South Korea | GU253750 | GU269713 | GU384429 | GU320417 |
| | MUCC 887 | T. Kobayashi | *Styrax japonicus* | *Styracaceae* | Japan | GU253751 | GU269714 | GU384430 | GU320418 |

**Table 1.** (Continued).

| Species | Culture accession numbers[1] | Collector | Host | Family | Country | GenBank accession numbers[2] | | | |
|---|---|---|---|---|---|---|---|---|---|
| | | | | | | LSU | ITS | EF-1α | ACT |
| *Pseudocercospora fuligena* | CPC 12296; CBS 132017 | Z. Mersha | *Lycopersicon* sp. | *Solanaceae* | Thailand | JQ324953 | GU269711 | GU384427 | GU320415 |
| | MUCC 533 | C. Nakashima | *Lycopersicon esculentum* | *Solanaceae* | Japan | GU253749 | GU269712 | GU384428 | GU320416 |
| *Pseudocercospora glauca* | CPC 10062; CBS 131884 | H.D. Shin | *Albizzia julibrissin* | *Fabaceae* | South Korea | GU253752 | GU269715 | GU384431 | GU320419 |
| *Pseudocercospora gracilis* | CBS 243.94; CPC 730 | P.W. Crous | *Eucalyptus urophylla* | *Myrtaceae* | Indonesia | DQ204750 | DQ267582 | DQ211666 | DQ147616 |
| *Pseudocercospora griseola* f. *griseola* | CBS 119112; CPC 10460 | F.S. Ngulu & C. Mushi | *Phaseolus vulgaris* | *Fabaceae* | Tanzania | GU253753 | GU269717 | GU384433 | GU320421 |
| | CBS 194.47 | — | *Phaseolus vulgaris* | *Fabaceae* | Portugal | JQ324954 | DQ289801 | JQ324995 | DQ289868 |
| | CBS 880.72 | H.A. van Kesteren | *Phaseolus vulgaris* | *Fabaceae* | Netherlands | GU214476 | GU269716 | GU384432 | GU320420 |
| | CPC 10462 | M.M. Liebenberg | *Phaseolus vulgaris* | *Fabaceae* | South Africa | GU253865 | GU269849 | GU384562 | GU320553 |
| | CPC 10480; CBS 131887 | M.M. Liebenberg | *Phaseolus vulgaris* | *Fabaceae* | South Africa | GU253864 | GU269848 | GU384561 | DQ289882 |
| | CPC 10779; CBS 131929 | H.D. Shin | *Phaseolus vulgaris* | *Fabaceae* | South Korea | GU253862 | GU269846 | GU384559 | DQ289885 |
| | CPC 12239 | G. Mahuku | *Phaseolus vulgaris* | *Fabaceae* | Colombia | GU253863 | GU269847 | GU384560 | DQ289887 |
| *Pseudocercospora guianensis* | MUCC 855 | C. Nakashima & T. Akashi | *Lantana camara* | *Verbenaceae* | Japan | GU253755 | GU269719 | GU384435 | GU320423 |
| | MUCC 879 | C. Nakashima | *Lantana camara* | *Verbenaceae* | Japan | GU253756 | GU269720 | GU384436 | GU320424 |
| *Pseudocercospora haiweiensis* | CPC 14084; CBS 131584 | X. Zhou | *Eucalyptus* sp. | *Myrtaceae* | China | GU253821 | GU269803 | GU384514 | GU320506 |
| *Pseudocercospora hakeae* | CBS 112226; CPC 3145 | P.W. Crous & B. Summerell | *Grevillea* sp. | *Proteaceae* | Australia | GU253805 | GU269784 | GU384495 | JQ325017 |
| *Pseudocercospora humuli* | MUCC 742 | C. Nakashima & I. Araki | *Humulus lupulus* var. *lupulus* | *Cannabaceae* | Japan | GU253758 | GU269725 | GU384439 | GU320428 |
| *Pseudocercospora humulicola* | CPC 10049; CBS 131883 | H.D. Shin | *Humulus scandens* | *Cannabaceae* | South Korea | JQ324955 | GU269724 | JQ324996 | JQ325018 |
| | CPC 11358; CBS 131585 | H.D. Shin | *Humulus scandens* | *Cannabaceae* | South Korea | JQ324956 | GU269723 | GU384438 | GU320427 |
| *Pseudocercospora indonesiana* | CBS 122473 | I.W. Buddenhagen | *Musa* sp. | *Musaceae* | Sumatra | GU253765 | GU269735 | GU384448 | GU320437/ EU514340 |
| | CBS 122474 | I.W. Buddenhagen | *Musa* sp. | *Musaceae* | Indonesia | JQ324957 | EU514283 | JQ324997 | JQ325019 |
| *Pseudocercospora ixorae* | CBS 118760 | R. Kirschner | *Ixora* sp. | *Rubiaceae* | Taiwan | GU253759 | GU269726 | GU384440 | GU320429 |
| *Pseudocercospora jussiaeae* | CPC 14625; CBS 132117 | H.D. Shin | *Ludwigia prostrata* | *Onagraceae* | South Korea | JQ324958 | JQ324977 | JQ324998 | JQ325020 |
| *Pseudocercospora kaki* | MUCC 900 | S. Uematsu & C. Nakashima | *Diospyros kaki* | *Ebenaceae* | Japan | GU253761 | GU269729 | GU384442 | GU320431 |
| *Pseudocercospora kiggelariae* | CPC 11853; CBS 132016 | W. Gams | *Kiggelaria africana* | *Flacourtiaceae* | South Africa | GU253762 | GU269730 | GU384443 | GU320432 |
| *Pseudocercospora latens* | MUCC 763 | C. Nakashima & T. Akashi | *Lespedeza wilfordii* | *Fabaceae* | Japan | GU253763 | GU269732 | GU384445 | GU320434 |
| *Pseudocercospora leucadendri* | CPC 1869 | S. Denman & P.W. Crous | *Leucadendron* sp. | *Proteaceae* | South Africa | GU214480 | GU269842 | GU384555 | GU320545 |
| *Pseudocercospora libertiae* | CBS 114643 | C.F. Hill | *Libertia ixioides* | *Iridaceae* | New Zealand | JQ324959 | GU269733 | GU384446 | GU320435 |
| *Pseudocercospora lilacis* | CPC 12767; CBS 132031 | C. Hodges | *Ligustrum japonicum* | *Oleaceae* | USA | GU253767 | GU269737 | GU384449 | GU320439 |

**Table 1.** (Continued).

| Species | Culture accession numbers[1] | Collector | Host | Family | Country | GenBank accession numbers[2] | | | |
|---|---|---|---|---|---|---|---|---|---|
| | | | | | | LSU | ITS | EF-1α | ACT |
| *Pseudocercospora longispora* | CBS 122470 | D.R. Jones | *Musa* sp. | *Musaceae* | Malaysia | GU253764 | GU269734 | GU384447 | GU320436/ EU514342 |
| *Pseudocercospora lonicericola* | MUCC 889 | T. Kobayashi | *Lonicera gracilipes* var. *glabra* | *Caprifoliaceae* | Japan | GU253766 | GU269736 | JQ324999 | GU320438 |
| *Pseudocercospora luzardii* | CPC 2556 | A.C. Alfenas | *Hancornia speciosa* | *Apocynaceae* | Brazil | GU214477 | AF362057/ GU269738 | GU384450 | GU320440 |
| *Pseudocercospora lyoniae* | MUCC 910 | C. Nakashima & E. Imaizumi | *Lyonia ovalifolia* var. *elliptica* | *Ericaceae* | Japan | GU253768 | GU269739 | GU384451 | GU320441 |
| *Pseudocercospora lythracearum* | CPC 10707; CBS 131925 | H.D. Shin | *Lagerstroemia indica* | *Lythraceae* | South Korea | GU253769 | GU269740 | GU384452 | GU320442 |
| | MUCC 890 | T. Kobayashi | *Lagerstroemia indica* | *Lythraceae* | Japan | GU253770 | GU269741 | GU384453 | GU320443 |
| *Pseudocercospora lythri* | CPC 14588; CBS 132115 | H.D. Shin | *Lythrum salicaria* | *Lythraceae* | South Korea | GU253771 | GU269742 | GU384454 | GU320444 |
| | MUCC 865 | I. Araki & M. Harada | *Lythrum salicaria* | *Lythraceae* | Japan | GU253772 | GU269743 | GU384455 | GU320445 |
| *Pseudocercospora macrospora* | CBS 114696; CPC 2553 | P.W. Crous & R.L. Benchimol | *Bertholletia excelsa* | *Lecythidaceae* | Brazil | GU214478 | AF362055/ GU269745 | GU384457 | GU320447 |
| *Pseudocercospora mali* | MUCC 886 | T. Kobayashi | *Malus sieboldii* | *Rosaceae* | Japan | GU253773 | GU269744 | GU384456 | GU320446 |
| *Pseudocercospora marginalis* | CPC 12497; CBS 131582 | H.D. Shin | *Fraxinus rhynchophylla* | *Oleaceae* | South Korea | GU253812 | GU269794 | GU384504 | GU320495 |
| *Pseudocercospora melicyti* | CBS 115023 | M. Fletcher | *Melicytus macrophyllus* | *Violaceae* | New Zealand | JQ324968 | GU269769 | GU384481 | GU320472 |
| *Pseudocercospora metrosideri* | CBS 118795 | C.F. Hill | *Metrosideros collina* | *Myrtaceae* | New Zealand | GU253774 | GU269746 | GU384458 | GU320448 |
| *Pseudocercospora musae* | CBS 116634 | J. Carlier | *Musa* sp. | *Musaceae* | Cuba | GU253775 | GU269747 | GU384459 | GU320449 |
| *Pseudocercospora myrticola* | MUCC 632 | C. Nakashima & K. Motohashi | *Myrtus communis* | *Myrtaceae* | Japan | GU253777 | GU269749 | GU384460 | GU320451 |
| *Pseudocercospora nandinae* | CBS 117745 | C.F. Hill | *Nandina domestica* | *Berberidaceae* | New Zealand | GU253778 | GU269750 | GU384461 | GU320452 |
| *Pseudocercospora natalensis* | CBS 111069; CPC 1263 | T. Coutinho | *Eucalyptus nitens* | *Myrtaceae* | South Africa | DQ267576 | DQ303077 | JQ325000 | DQ147620 |
| | CBS 111071; CPC 1265 | T. Coutinho | *Eucalyptus nitens* | *Myrtaceae* | South Africa | GU253801 | GU269780 | GU384491 | GU320483 |
| *Pseudocercospora nephrolepidis* | CBS 119121 | R. Kirschner | *Nephrolepis auriculata* | *Oleandraceae* | Taiwan | GU253779 | GU269751 | GU384462 | GU320453 |
| *Pseudocercospora nogalesii* | CBS 115022 | C.F. Hill | *Chamaecytisus proliferus* | *Fabaceae* | New Zealand | JQ324960 | GU269752 | GU384463 | GU320454 |
| *Pseudocercospora norchiensis* | CBS 114641 | C.F. Hill | *Rubus* sp. | *Rosaceae* | New Zealand | GU253794 | GU269772 | GU384484 | GU320475 |
| | CBS 120738; CPC 13049 | W. Gams | *Eucalyptus* sp. | *Myrtaceae* | Italy | GU253780 | EF394859/ GU269753 | GU384464 | GU320455 |
| *Pseudocercospora ocimi-basilici* | CPC 10283 | M.E. Palm | *Ocimum basilicum* | *Lamiaceae* | Mexico | GU214678 | GU269754 | GU384465 | GU320456 |
| *Pseudocercospora oenotherae* | CPC 10290; CBS 131885 | H.D. Shin | *Oenothera odorata* | *Onagraceae* | South Korea | JQ324961 | GU269856 | GU384567 | GU320559 |
| | CPC 10630; CBS 131920 | H.D. Shin | *Oenothera odorata* | *Onagraceae* | South Korea | GU253781 | GU269755 | GU384466 | GU320457 |
| *Pseudocercospora paederiae* | CPC 10007 | H.D. Shin | *Paederia foetida* | *Rubiaceae* | South Korea | GU253783 | GU269757 | GU384468 | — |
| *Pseudocercospora palleobrunnea* | CBS 124771; CPC 13387 | P.W. Crous | *Syzygium* sp. | *Myrtaceae* | Australia | GQ303319 | GQ303288 | GU384509 | GU320500 |

**Table 1.** (Continued).

| Species | Culture accession numbers[1] | Collector | Host | Family | Country | GenBank accession numbers[2] | | | |
|---|---|---|---|---|---|---|---|---|---|
| | | | | | | LSU | ITS | EF-1α | ACT |
| *Pseudocercospora pallida* | CPC 10776; CBS 131889 | H.D. Shin | *Campsis grandiflora* | *Bignoniaceae* | South Korea | GU214680 | GU269758 | GU384469 | GU320459 |
| *Pseudocercospora pancratii* | CBS 137.94 | R.F. Castaneda | — | — | Cuba | GU253784 | GU269759 | GU384470 | GU320460 |
| *Pseudocercospora paraguayensis* | CBS 111286; CPC 1459 | P.W. Crous | *Eucalyptus nitens* | *Myrtaceae* | Brazil | GU214479/ DQ204764 | DQ267602 | DQ211680 | DQ147606 |
| | CBS 111317; CPC 1458 | P.W. Crous | *Eucalyptus nitens* | *Myrtaceae* | Brazil | GQ852634 | JQ324978 | GU384522 | JQ325021 |
| *Pseudocercospora pini-densiflorae* | MUCC 534 | Y. Tokushige | *Pinus thunbergii* | *Pinaceae* | Japan | GU253785 | GU269760 | GU384471 | GU320461 |
| *Pseudocercospora plecthranthi* | CPC 11462; CBS 131586 | H.D. Shin | *Plectranthus* sp. | *Lamiaceae* | South Korea | JQ324962 | GU269791 | GU384501 | GU320492 |
| *Pseudocercospora pouzolziae* | CBS 122280 | R. Kirschner | *Gonostegia hirta* | *Urticaceae* | Taiwan | GU253786 | GU269761 | GU384472 | GU320462 |
| *Pseudocercospora profusa* | CPC 10042 | H.D. Shin | *Acalypha australis* | *Euphorbiaceae* | South Korea | GU253808 | GU269787 | GU384497 | GU320488 |
| | CPC 10055; CBS 132306 | H.D. Shin | *Acalypha australis* | *Euphorbiaceae* | South Korea | GU253787 | GU269762 | GU384473 | GU320463 |
| *Pseudocercospora proteae* | CPC 15217; CBS 131587 | F. Roets | *Protea mundii* | *Proteaceae* | South Africa | GU253826 | GU269808 | GU384519 | GU320511 |
| *Pseudocercospora prunicula* | CPC 14511; CBS 132107 | H.D. Shin | *Prunus x yedoensis* | *Rosaceae* | South Korea | GU253723 | GU269676 | GU384393 | GU320382 |
| *Pseudocercospora pseudostigmina-platani* | CPC 11726; CBS 131588 | H.D. Shin | *Platanus occidentalis* | *Platanaceae* | South Korea | JQ324963 | GU269857 | GU384568 | GU320560 |
| *Pseudocercospora puderi* | MUCC 906 | S. Maruyama | *Rosa* sp. | *Rosaceae* | Japan | GU253790 | GU269764 | GU384476 | GU320467 |
| *Pseudocercospora punctata* | CPC 14734; CBS 132116 | P.W. Crous | *Syzygium* sp. | *Myrtaceae* | Madagascar | GU253791 | GU269765 | GU384477 | GU320468 |
| *Pseudocercospora purpurea* | CBS 114163; CPC 1664 | P.W. Crous | *Persea americana* | *Lauraceae* | Mexico | GU253804 | GU269783 | GU384494 | GU320486 |
| *Pseudocercospora pyracanthae* | MUCC 892 | T. Kobayashi & C. Nakashima | *Pyracantha angustifolia* | *Rosaceae* | Japan | GU253792 | GU269767 | GU384479 | GU320470 |
| *Pseudocercospora pyracanthigena* | CPC 10808; CBS 131589 | H.D. Shin | *Pyracantha angustifolia* | *Rosaceae* | South Korea | — | GU269766 | GU384478 | GU320469 |
| *Pseudocercospora ranjita* | CPC 11141; CBS 126005 | M.J. Wingfield | *Gmelina* sp. | *Verbenaceae* | Indonesia | GU253810 | GU269790 | GU384500 | GU320491 |
| *Pseudocercospora ravenalicola* | CBS 122468 | M. Arzanlou & W. Gams | *Ravenala madagascariensis* | *Strelitziaceae* | India | GU253828 | GU269810 | GU384521 | GU320513 |
| *Pseudocercospora rhabdothamni* | CBS 114872 | M. Fletcher | *Rhabdothamnus solandri* | *Gesneriaceae* | New Zealand | JQ324964 | GU269768 | GU384480 | GU320471 |
| *Pseudocercospora rhamnellae* | CPC 12500; CBS 131590 | H.D. Shin | *Rhamnella franguloides* | *Rhamnaceae* | South Korea | GU253813 | GU269795 | GU384505 | GU320496 |
| *Pseudocercospora rhapisicola* | CBS 282.66 | K. Tubaki | *Rhapis flabelliformis* | *Arecaceae* | Japan | GU253793 | GU269770 | GU384482 | GU320473 |
| *Pseudocercospora rhododendri-indici* | CPC 10822; CBS 131591 | H.D. Shin | *Rhododendron indicum* | *Ericaceae* | South Korea | JQ324965 | GU269722 | — | GU320426 |
| *Pseudocercospora rhoina* | CPC 11464; CBS 131891 | H.D. Shin | *Rhus chinensis* | *Anacardiaceae* | South Korea | JQ324966 | GU269771 | GU384483 | GU320474 |
| *Pseudocercospora robusta* | CBS 111175; CPC 1269; CMW 5151 | M.J. Wingfield | *Eucalyptus robur* | *Myrtaceae* | Malaysia | DQ204767 | AY309597 | DQ211683 | DQ147617 |
| *Pseudocercospora rubi* | MUCC 875 | T. Kobayashi & C. Nakashima | *Rubus allegheniensis* | *Rosaceae* | Japan | GU253795 | GU269773 | GU384485 | GU320476 |
| *Pseudocercospora rumohrae* | CBS 117747 | C.F. Hill | *Marattia salicina* | *Marattiaceae* | New Zealand | GU253796 | GU269774 | GU384486 | GU320477 |
| *Pseudocercospora sambucigena* | CPC 10292; CBS 131886 | H.D. Shin | *Sambucus williamsii* | *Caprifoliaceae* | South Korea | GU253809 | GU269788 | GU384498 | GU320489 |

**Table 1.** (Continued).

| Species | Culture accession numbers[1] | Collector | Host | Family | Country | GenBank accession numbers[2] | | | |
|---|---|---|---|---|---|---|---|---|---|
| | | | | | | LSU | ITS | EF-1α | ACT |
| | CPC 14397; CBS 126000 | P.W. Crous | *Sambucus nigra* | *Caprifoliaceae* | Netherlands | GU253823 | GU269805 | GU384516 | GU320508 |
| *Pseudocercospora sawadae* | CBS 115024 | C.F. Hill | *Psidium guajava* | *Myrtaceae* | New Zealand | JQ324967 | GU269775 | — | GU320478 |
| *Pseudocercospora securinegae* | CPC 10793; CBS 131930 | H.D. Shin | *Flueggea suffruticosa* | *Euphorbiaceae* | South Korea | GU253797 | GU269776 | GU384487 | GU320479 |
| *Pseudocercospora snelliana* | CPC 11654; CBS 131592 | H.D. Shin | *Morus bombycis* | *Moraceae* | South Korea | — | GU269731 | GU384444 | GU320433 |
| *Pseudocercospora sordida* | MUCC 913 | C. Nakashima & E. Imaizumi | *Campsis radicans* | *Bignoniaceae* | Japan | GU253798 | GU269777 | GU384488 | GU320480 |
| *Pseudocercospora* sp. | CBS 110993; CPC 1057 | M.J. Wingfield | *Populus* sp. | *Salicaceae* | South Africa | GU253800 | GU269779 | GU384490 | GU320482 |
| | CBS 110998; CPC 1054 | M.J. Wingfield | *Eucalyptus grandis* | *Myrtaceae* | South Africa | GU253799 | GU269778 | GU384489 | GU320481 |
| | CBS 111373; CPC 1493 | M.J. Wingfield | *Eucalyptus globulus* | *Myrtaceae* | Uruguay | GU253803 | GU269782 | GU384493 | GU320485 |
| | CBS 112725; CPC 3961 | K.A. Seifert | *Melilotus alba* | *Fabaceae* | Canada | GU253806 | GU269785 | — | — |
| | CBS 113387 | A. den Breeyen | *Lantana camara* | *Verbenaceae* | Jamaica | GU253754 | GU269718 | GU384434 | GU320422 |
| | CPC 10058 | H.D. Shin | *Potentilla kleiniana* | *Rosaceae* | South Korea | — | JQ324979 | JQ325001 | JQ325022 |
| | CPC 10645; CBS 131922 | P.W. Crous | — | — | Brazil | GU253700 | GU269651 | GU384369 | GU320359 |
| | CPC 14711; CBS 132102 | H.D. Shin | *Pyracantha angustifolia* | *Rosaceae* | South Korea | — | JQ324980 | JQ325002 | JQ325023 |
| | CPC 15116; NC1 37A1a | J. Batzer | *Malus* sp. cv. *Golden Delicious* | *Rosaceae* | USA: North Carolina | JQ324969 | JQ324981 | JQ325003 | JQ325024 |
| *Pseudocercospora stahlii* | CBS 117549 | R. Kirschner | *Passiflora foetida* | *Passifloraceae* | Taiwan | GU253830 | GU269813 | GU384525 | GU320515 |
| *Pseudocercospora stephanandrae* | MUCC 914 | C. Nakashima & E. Imaizumi | *Stephanandra incisa* | *Rosaceae* | Japan | GU253831 | GU269814 | GU384526 | GU320516 |
| *Pseudocercospora subsessilis* | CBS 136.94 | R.F. Castaneda | — | — | Cuba | GU253832 | GU269815 | GU384527 | GU320517 |
| *Pseudocercospora subtorulosa* | CBS 117230 | R. Kirschner | *Melicope* sp. | *Rutaceae* | Taiwan | GU253833 | GU269816 | GU384528 | GU320518 |
| *Pseudocercospora subulata* | CBS 118489; CPC 10849 | M. Dick | *Eucalyptus botryoides* | *Myrtaceae* | New Zealand | JQ324970 | DQ303090 | JQ325004 | GU320519 |
| *Pseudocercospora tereticornis* | CBS 124996; CPC 12960 | A.J. Carnegie | *Eucalyptus nitens* | *Myrtaceae* | Australia | GQ852647 | JQ324982 | GU384377 | JQ325025 |
| | CPC 13299; CBS 125214 | P.W. Crous | *Eucalyptus tereticornis* | *Myrtaceae* | Australia | GQ852649 | GQ852770 | GU384508 | GU320499 |
| *“Pseudocercospora” thailandica* | CBS 116367; CPC 10547 | K. Pongpanich | *Acacia mangium* | *Fabaceae* | Thailand | GU253837 | — | DQ835102/ GU384533 | GU320523/ AY752217 |
| | CPC 10548; CBS 116367 | K. Pongpanich | *Acacia mangium* | *Fabaceae* | Thailand | GU253853 | AY752157 | AY840477 | GU320539 |
| *Pseudocercospora theae* | CBS 128.30 | M. Curzi | *Camelia sinensis* | *Theaceae* | Italy | GU253838 | GU269821 | GU384534 | GU320524 |
| *“Pseudocercospora” tibouchinigena* | CBS 116462 | C.F. Hill | *Tibouchina* sp. | *Melastomataceae* | New Zealand | GU253839 | GU269822 | GU384535 | GU320525 |
| *Pseudocercospora timorensis* | MUCC 819 | C. Nakashima & T. Akashi | *Ipomoea indica* | *Convolvulaceae* | Japan | GU253840 | GU269823 | GU384536 | GU320526 |
| *Pseudocercospora udagawana* | CPC 10799; CBS 131931 | H.D. Shin | *Hovenia dulcis* | *Rhamnaceae* | South Korea | — | GU269824 | GU384537 | GU320527 |

**Table 1.** (Continued).

| Species | Culture accession numbers[1] | Collector | Host | Family | Country | GenBank accession numbers[2] | | | |
|---|---|---|---|---|---|---|---|---|---|
| | | | | | | LSU | ITS | EF-1α | ACT |
| *Pseudocercospora variicolor* | MUCC 746 | C. Nakashima & I. Araki | *Paeonia lactiflora* var. *trichocarpa* | *Paeoniaceae* | Japan | GU253843 | GU269826 | GU384538 | GU320530 |
| *Pseudocercospora viburnigena* | CPC 15249; CBS 125998 | M.L. Crous | *Viburnum davidii* | *Caprifoliaceae* | Netherlands | GU253827 | GU269809 | GU384520 | GU320512 |
| *Pseudocercospora viticicola* | MUCC 777 | C. Nakashima | *Vitex trifolia* | *Verbenaceae* | Japan | GU253845 | GU269828 | GU384540 | GU320532 |
| *Pseudocercospora vitis* | CPC 11595; CBS 132012 | H.D. Shin | *Vitis vinifera* | *Vitaceae* | South Korea | GU214483 | DQ289829/ GU269829 | GU384541 | GU320533 |
| | CPC 14661; CBS 132112 | H.D. Shin | *Vitis vinifera* | *Vitaceae* | South Korea | GU253844 | GU269827 | GU384539 | GU320531 |
| *Pseudocercospora weigelae* | MUCC 899 | T. Kobayashi & Y. Kobayashi | *Weigela coraeensis* | *Caprifoliaceae* | Japan | GU253847 | GU269831 | GU384543 | GU320535 |
| *Pseudocercospora xanthocercidis* | CPC 11665; CBS 131593 | A.R. Wood | *Xanthocercis zambesiaca* | *Fabaceae* | South Africa | JQ324971 | JQ324983 | JQ325005 | JQ325026 |
| *Pseudocercospora xanthoxyli* | CPC 10065 | H.D. Shin | *Xanthoxylum ailanthoides* | *Rutaceae* | South Korea | GU253848 | GU269832 | GU384544 | GU320536 |
| *Pseudocercospora zelkovae* | CPC 14484; CBS 132106 | H.D. Shin | *Zelkova serrata* | *Ulmaceae* | South Korea | GU253849 | GU269833 | GU384545 | JQ325027 |
| | CPC 14717; CBS 132118 | H.D. Shin | *Zelkova serrata* | *Ulmaceae* | South Korea | GU253850 | GU269834 | GU384546 | JQ325028 |
| | MUCC 872 | T. Kobayashi & C. Nakashima | *Zelkova serrata* | *Ulmaceae* | Japan | GU253851 | GU269835 | GU384547 | GU320537 |
| *Pseudocercosporella arcuata* | CPC 10050 | H.D. Shin | *Rubus oldhamii* | *Rosaceae* | South Korea | GU214685 | GU269850 | JQ325006 | GU320554 |
| *Pseudocercosporella capsellae* | CPC 14773; CBS 131896 | H.D. Shin | *Raphanus sativus* | *Brassicaceae* | South Korea | GU253714 | GU269666 | GU384383 | GU320372 |
| *Pseudocercosporella chaenomelis* | CPC 14795; CBS 131897 | H.D. Shin | *Chaenomeles speciosa* | *Rosaceae* | South Korea | GU253834 | GU269817 | GU384530 | GU320520 |
| | MUCC 1510; CBS 132131 | C. Nakashima | *Chaenomeles sinensis* | *Rosaceae* | Japan | — | JQ793663 | — | JQ793664 |
| *Pseudocercosporella fraxini* | CPC 11509 | H.D. Shin | *Fraxinus rhynchophylla* | *Oleaceae* | South Korea | GU214682 | GU269709 | GU384425 | GU320413 |
| *Pseudocercosporella koreana* | CPC 11414 | H.D. Shin | *Vicia amurensis* | *Fabaceae* | South Korea | GU214683 | GU269852 | GU384564 | GU320556 |
| *Pseudocercosporella oxalidis* | CBS 118758 | R. Kirschner | *Oxalis debilis* | *Oxalidaceae* | Taiwan | GU253782 | GU269756 | GU384467 | GU320458 |
| *Pseudocercosporella* sp. | CPC 10864; CBS 131890 | H.D. Shin | *Trigonotis peduncularis* | *Boraginaceae* | South Korea | JQ324972 | GU269858 | GU384569 | JQ325029 |
| *Pseudocercosporella zelkovae* | CPC 11592; CBS 132011 | H.D. Shin | *Zelkova serrata* | *Ulmaceae* | South Korea | GU214482 | GU269853 | — | GU320557 |
| *Scolecostigmina mangiferae* | CBS 125467; CPC 17351 | P.W. Crous | *Mangifera indica* | *Anacardiaceae* | Australia | GU253877 | GU269870 | GU384578 | GU320566 |
| | CPC 17352; CBS 125467 | P.W. Crous | *Mangifera indica* | *Anacardiaceae* | Australia | GU253878 | GU269871 | GU384579 | GU320567 |
| *Septoria cerastii* | CPC 12343; CBS 132028 | H.D. Shin | *Cerastium holosteoides* var. *hallasanense* | *Caryophyllaceae* | South Korea | GU253869 | GU269859 | GU384570 | JQ325030 |
| *Septoria chelidonii* | CPC 12337; CBS 132027 | H.D. Shin | *Chelidonium majus* var. *asiaticum* | *Papaveraceae* | South Korea | GU253870 | GU269860 | GU384571 | GU320561 |
| *Septoria crepidis* | CPC 12539; CBS 131895 | H.D. Shin | *Crepis japonica* | *Asteraceae* | South Korea | GU253871 | GU269861 | GU384572 | GU320562 |
| *Septoria dysentericae* | CPC 12328; CBS 131892 | H.D. Shin | *Inula britannica* var. *chinensis* | *Asteraceae* | South Korea | GU253866 | GU269854 | GU384565 | GU320558 |
| *Septoria erigerontis* | CPC 12340; CBS 131893 | H.D. Shin | *Erigeron annuus* | *Asteraceae* | South Korea | GU253872 | GU269862 | GU384573 | JQ325031 |

**Table 1.** (Continued).

| Species | Culture accession numbers[1] | Collector | Host | Family | Country | GenBank accession numbers[2] | | | |
|---|---|---|---|---|---|---|---|---|---|
| | | | | | | LSU | ITS | EF-1α | ACT |
| *Septoria eucalyptorum* | CPC 11282; CBS 118505 | W. Gams | *Eucalyptus* sp. | *Myrtaceae* | India | GU253873 | GU269863 | GU384574 | GU320563 |
| *Septoria justiciae* | CPC 12509; CBS 131894 | H.D. Shin | *Justicia procumbens* | *Acanthaceae* | South Korea | GU253874 | GU269864 | GU384575 | GU320564 |
| *Septoria quercicola* | CBS 663.94 | H.A. van der Aa | *Quercus robur* | *Fagaceae* | Netherlands | GU253867 | GU269855 | GU384566 | JQ325032 |
| *Septoria rubi* | CPC 12331; CBS 132022 | H.D. Shin | *Rubus crataegifolius* | *Rosaceae* | South Korea | GU253875 | GU269865 | GU384576 | — |
| *Stigmina platani* | CBS 336.33 | R.M. Nattrass | *Platanus orientalis* | *Platanaceae* | India | GU253868 | — | JQ325007 | — |
| *Strelitziana australiensis* | CBS 124778; CPC 13421 | P.W. Crous | *Eucalyptus* sp. | *Myrtaceae* | Australia | GQ303326 | GQ303295 | GU384362 | — |
| | CPC 13556; CBS 132310 | P.W. Crous | *Eucalyptus* sp. | *Myrtaceae* | Australia | GU253695 | GU269645 | GU384363 | GU320354 |
| *Teratosphaeria alcornii* | CBS 313.76; CPC 3632 | J.L. Alcorn | *Eucalyptus tessellaris* | *Myrtaceae* | Australia | GU253876 | GU269866 | GU384577 | GU320565 |
| *Teratosphaeria dimorpha* | CPC 14132; CBS 124051 | B.A. Summerell | *Eucalyptus caesia* | *Myrtaceae* | Australia | FJ493215 | FJ023537 | — | — |
| *Teratosphaeria stellenboschiana* | CBS 124989; CPC 13767 | P.W. Crous | *Eucalyptus punctata* | *Myrtaceae* | South Africa | GQ852715 | GQ852823 | — | — |
| *Thedgonia ligustrina* | CPC 10019 | H.D. Shin | *Ligustrum ovalifolium* | *Oleaceae* | South Korea | GU253854 | GU269837 | GU384550 | GU320540 |
| | CPC 10530; CBS 132130 | P.W.Crous | *Ligustrum* sp. | *Oleaceae* | Netherlands | GU253855 | GU269838 | GU384551 | GU320541 |
| | CPC 10861; CBS 132025 | H.D. Shin | *Ligustrum ovalifolium* | *Oleaceae* | South Korea | GU253856 | GU269839 | GU384552 | GU320542 |
| *Trochophora fasciculata* | CPC 10282 | H.D. Shin | *Daphniphyllum macropodum* | *Daphniphyllaceae* | South Korea | FJ839668 | FJ839632 | — | — |
| *Trochophora simplex* | CBS 124744 | H.D. Shin | *Daphniphyllum macropodum* | *Daphniphyllaceae* | South Korea | GU253880 | GU269872 | GU384580 | GU320568 |
| | MUCC 952 | C. Nakashima & I. Araki | *Daphniphyllum teijsmannii* | *Daphniphyllaceae* | Japan | GU253879 | — | — | — |
| *Xenostigmina zilleri* | CBS 115685 | K.A. Seifert | *Acer* sp. | *Aceraceae* | Canada | GU253857 | GU269840 | GU384553 | GU320543 |
| | CBS 115686 | K.A. Seifert | *Acer* sp. | *Aceraceae* | Canada | FJ839676/ GU253858 | GU269841 | GU384554 | GU320544 |
| *Zasmidium nabiacense* | CBS 125010; CPC 12748 | A.J. Carnegie | *Eucalyptus* sp. | *Myrtaceae* | Australia | GQ852734 | GQ852841 | GU384507 | GU320498 |

[1]CBS: CBS-KNAW Fungal Biodiversity Centre, Utrecht, The Netherlands; CIRAD: Centre de Coopération Internationale en Recherche Agronomique pour le Développement, UMR-BGPI, Montpellier, France; CMW: Culture Collection of the Forestry and Agricultural Biotechnology Institute (FABI) of the University of Pretoria, Pretoria, South Africa; CPC: Culture collection of Pedro Crous, housed at CBS; MUCC: Culture Collection, Laboratory of Plant Pathology, Mie University, Tsu, Mie Prefecture, Japan.

[2]LSU: partial 28S nrRNA gene; ITS: internal transcribed spacer regions 1 & 2 including 5.8S nrRNA gene; EF-1α: partial translation elongation factor 1-alpha gene; ACT: partial actin gene.

[3]Sequence for this locus obtained from: http://genome.jgi-psf.org/Mycfi1/Mycfi1.home.html

1 000 generations, resulting in 8 001 saved trees in each of the two tree files. Burn-in was set at 2 000 000 generations after which the likelihood values were stationary. For parsimony analysis of the combined ITS, ACT and EF-1α alignment, alignment gaps were treated as a fifth character state and all characters were unordered and of equal weight. Maximum parsimony analysis was performed in PAUP using the heuristic search option with 100 random taxon additions and tree bisection and reconnection (TBR) as the branch-swapping algorithm. Branches of zero length were collapsed and all multiple, equally most parsimonious trees were saved. The robustness of the trees was evaluated by 1 000 bootstrap replicates (Hillis & Bull 1993). Tree length (TL), consistency index (CI), retention index (RI) and rescaled consistency index (RC) were calculated and the resulting trees were printed with Geneious v. 5.5.4 (Drummond *et al*. 2011). Sequences derived in this study were deposited in GenBank (Table 1), the alignments in TreeBASE (www.treebase.org/treebase/index.html), and taxonomic novelties in MycoBank (www.MycoBank.org; Crous *et al*. 2004b).

## Taxonomy

All taxonomic descriptions were based on structures on herbarium material. Diseased leaf tissue was viewed under a Nikon® SMZ1500 stereoscopic zoom microscope and relevant morphological structures were lifted from lesions with a sterile dissecting needle and mounted on glass slides in clear lactic acid. For measurements, 30–50 replicates of all relevant morphological features were made at ×1 000 magnification using a Carl Zeiss® Axioskop 2 plus light microscope. High-resolution photographic images of diseased material, leaf lesions and microscopic fungal structures were captured with a Nikon® digital sight DS-fi1 high definition colour camera mounted on the light microscope or a Nikon® digital sight DS-5M camera mounted on a stereoscopic zoom microscope. Images of morphological structures were captured, and measurements taken, using the Nikon® software NIS-Elements v. 2.34 while Adobe Photoshop was used for the final editing of acquired images and photographic preparations. Novel *Pseudocercospora* taxa were plated onto MEA and incubated at 24 °C for 2–4 wk in the dark in duplicate. The mycological colour charts of Rayner (1970) were used to define colours of the fungal colonies.

# RESULTS

## DNA sequencing and phylogenetic analyses

*Large Subunit (LSU) phylogeny*: The final aligned LSU dataset contained 316 ingroup taxa with a total of 1305 characters and *Saccharomyces cerevisiae* (GenBank Accession: Z73326) served as the outgroup taxon. From this alignment 827 characters were used for the Bayesian analysis; the consensus trees and posterior probabilities were calculated (Fig. 4) from the 12 002 trees left after discarding those used for burn-in. The resulting LSU phylogeny resolved several clades (Clades 1–14) grouping species of *Pseudocercospora* and allied genera (Fig. 4). Clade 1 (Posterior Probability (PP) value of 1.0) including *Cyphellophora* and *Strelitziana* represented by one of the two basal lineages. *Thedgonia ligustrina* (100 %) represented the second basal clade (PP = 1.0). In the Pleosporales, Clade 3 included *Xenostigmina zilleri* (PP = 1.0) and Clade 4 *Pseudocercospora cantuariensis* (PP = 1.0), the latter being described below as *Phaeomycocentrospora cantuariensis*. Clade 5 contained *Cladosporium* species belonging to the teleomorph genus *Davidiella* (PP = 1.0). Clade 6 (PP = 1.0) represented species belonging to *Teratosphaeria* and including the recently established genus *Microcyclospora*. Clade 7 (PP = 1.0) accommodated species of *Dissoconium*. Clade 8 (PP = 1.0) including species representing *Mycosphaerella*, *Pseudocercospora* and *Zasmidium*, as well as the recently established genus *Microcyclosporella*. Clade 9 (PP = 1.0) included *Pseudocercospora tibouchinigena*, *Pseudocercospora egenula* described below as *Paracercospora egenula* and the *Mycosphaerella ellipsoidea* complex. Clade 10 (PP = 1.0) accommodated species of other genera namely *Pseudocercosporella*, *Mycosphaerella ulmi* (*Phleospora*), *Muiraea*, *Cercospora* and *Septoria*. Clade 11 (PP = 1.0) included *Mycosphaerella* species with *Sonderhenia* anamorphs. Clade 12 (PP = 1.0) is sister to Clade 11 and included species representing taxa of *Mycosphaerella* and their associated pseudocercospora-like anamorphs, appeared to represent a novel genus. Other genera in this clade included *Scolecostigmina* and *Trochophora*. The isolates representing *Trochophora* are accommodated at a basal position in this clade with no PP support. The three isolates of *Scolecostigmina mangiferae* resided in a well-supported sub-clade (PP = 1.0) close to isolates regarded as part of the *Mycosphaerella heimii* complex (*P. acaciigena*, *M. irregulariramosa*, *M. colombiensis*, *P. thailandica*, *M. heimii*, *M. heimioides*, *M. konae*), described below in *Pallidocercospora*. Clade 13 (PP = 1.0) accommodated *Passalora eucalypti*. The remainder of the phylogeny encompassed Clade 14 (PP = 1.0), representing *Pseudocercospora s. str.*, and accommodated the majority of *Pseudocercospora* species from many different hosts. The type species of *Pseudocercospora*, *P. vitis* was included in this clade. Interestingly, *P. vitis* was basal in this clade with the majority of *Pseudocercospora* species radiating out from the basal *Pseudocercospora* isolates. The LSU phylogeny provided a well-supported sub-clade (PP = 1.0) representing the second half of the *sensu stricto* clade (Clade 14). Several isolates representing species from genera morphologically allied to *Pseudocercospora* were also grouped in Clade 14. These included *Stigmina platani*, *Cercostigmina protearum* var. *leucadendri* (as *Pseudocercospora leucadendri*, see below), *Cercostigmina protearum* var. *hakeae* (as *Pseudocercospora hakea*, see below), *Phaeoisariopsis griseola* f. *griseola* (as *Pseudocercospora griseola* f. *griseola*, see Crous *et al.* 2006) and *Pseudophaeoramularia angolensis* (as *Pseudocercospora angolensis*, see below), which supports previous proposals to include these genera in *Pseudocercospora s. str*.

*Pseudocercospora s. str. phylogeny*: A further analysis was conducted on Clade 14 (Fig. 4), representing *Pseudocercospora s. str.* For this analysis, DNA sequence data from the ITS, ACT and EF-1α gene regions were combined in the parsimony analysis. For this dataset, there was a total of 194 taxa, each representing 1 029 characters. *Passalora eucalypti* (CBS 111318) served as the outgroup taxon for this analysis. From the combined alignment of 1 029 characters, 414 were constant, 124 were variable and 491 characters were parsimony uninformative. Only the first 1 000 equally most parsimonious trees were saved, the first of which is shown (Fig. 5) (TL = 4315, CI = 0.312, RI = 0.819, RC = 0.256).

The phylogeny resulting from the combined sequence data was more structured towards the terminal nodes than the LSU phylogeny. Similar to the LSU phylogeny, a split was observed within *Pseudocercospora s. str.*, with at least two main clades being evident. Although present in the strict consensus tree, this

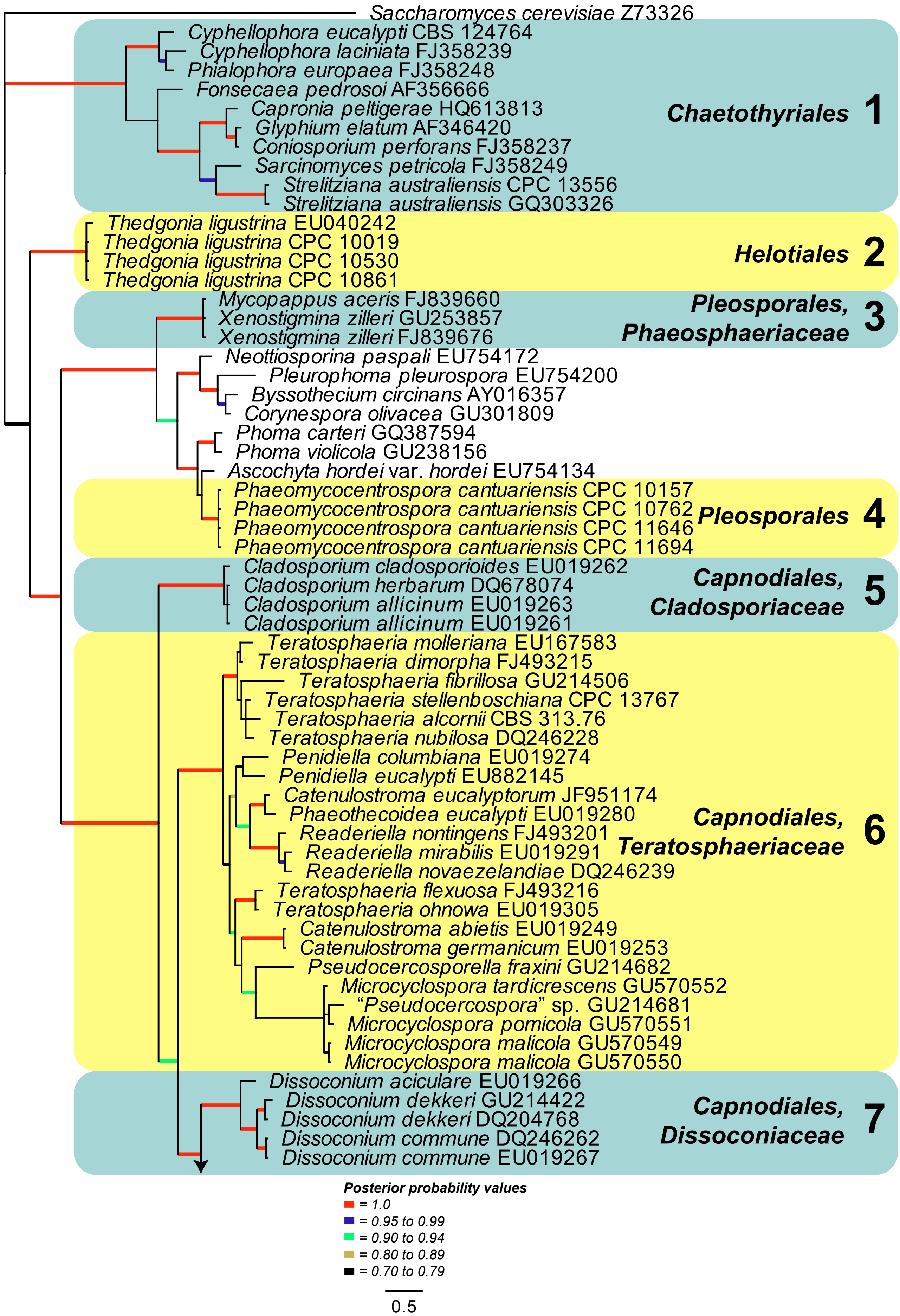


**Fig. 4.** Consensus phylogram (50 % majority rule) of 12 002 trees resulting from a Bayesian analysis of the LSU sequence alignment using MrBayes v. 3.1.2. Bayesian posterior probabilities are indicated with colour-coded branches (see legend) and the scale bar represents the expected changes per site. Important clades are indicated in coloured blocks and numbered. The tree was rooted to *Saccharomyces cerevisiae* (GenBank Z73326).

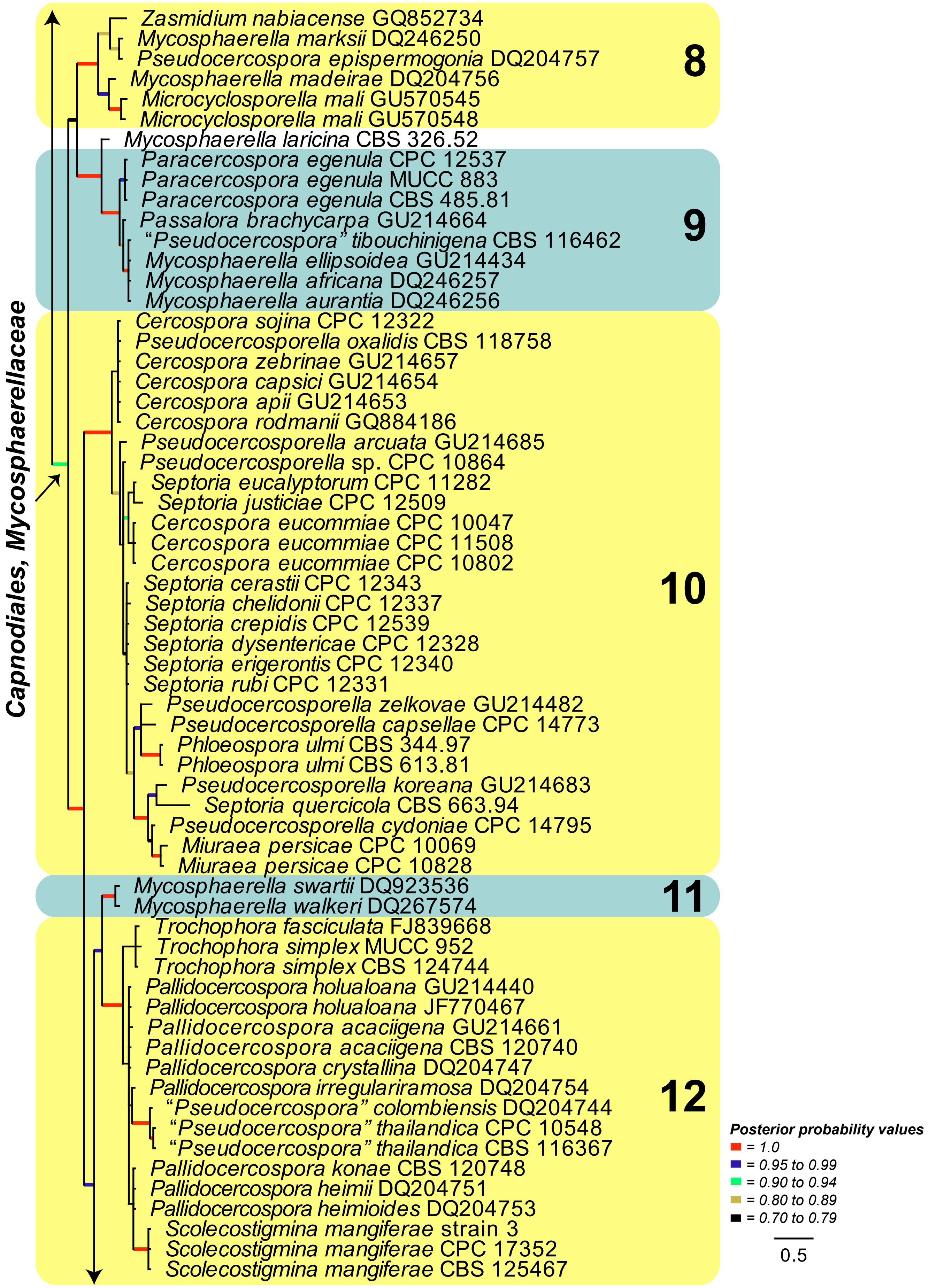


**Fig. 4.** (Continued).

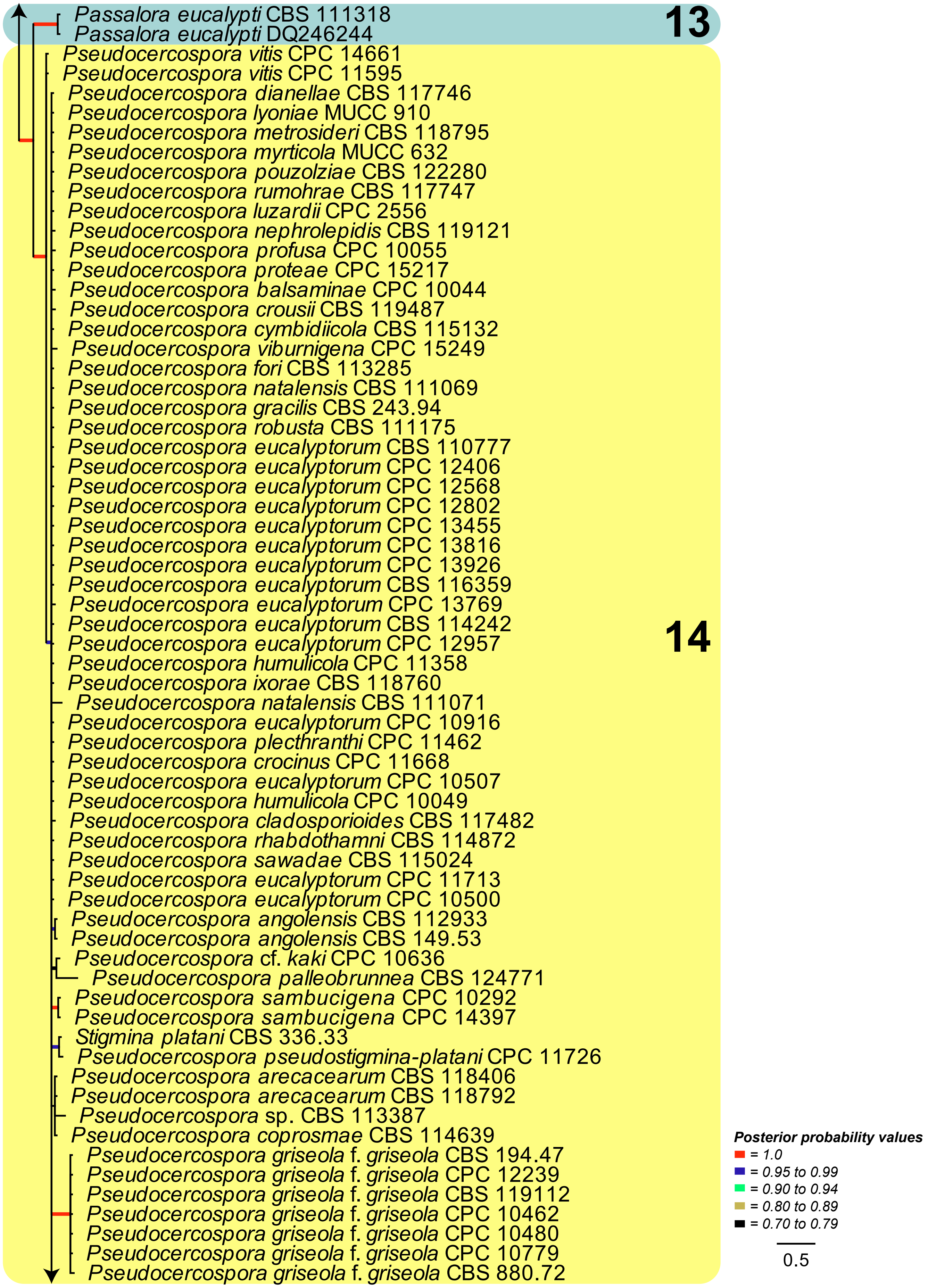


**Fig. 4.** (Continued).

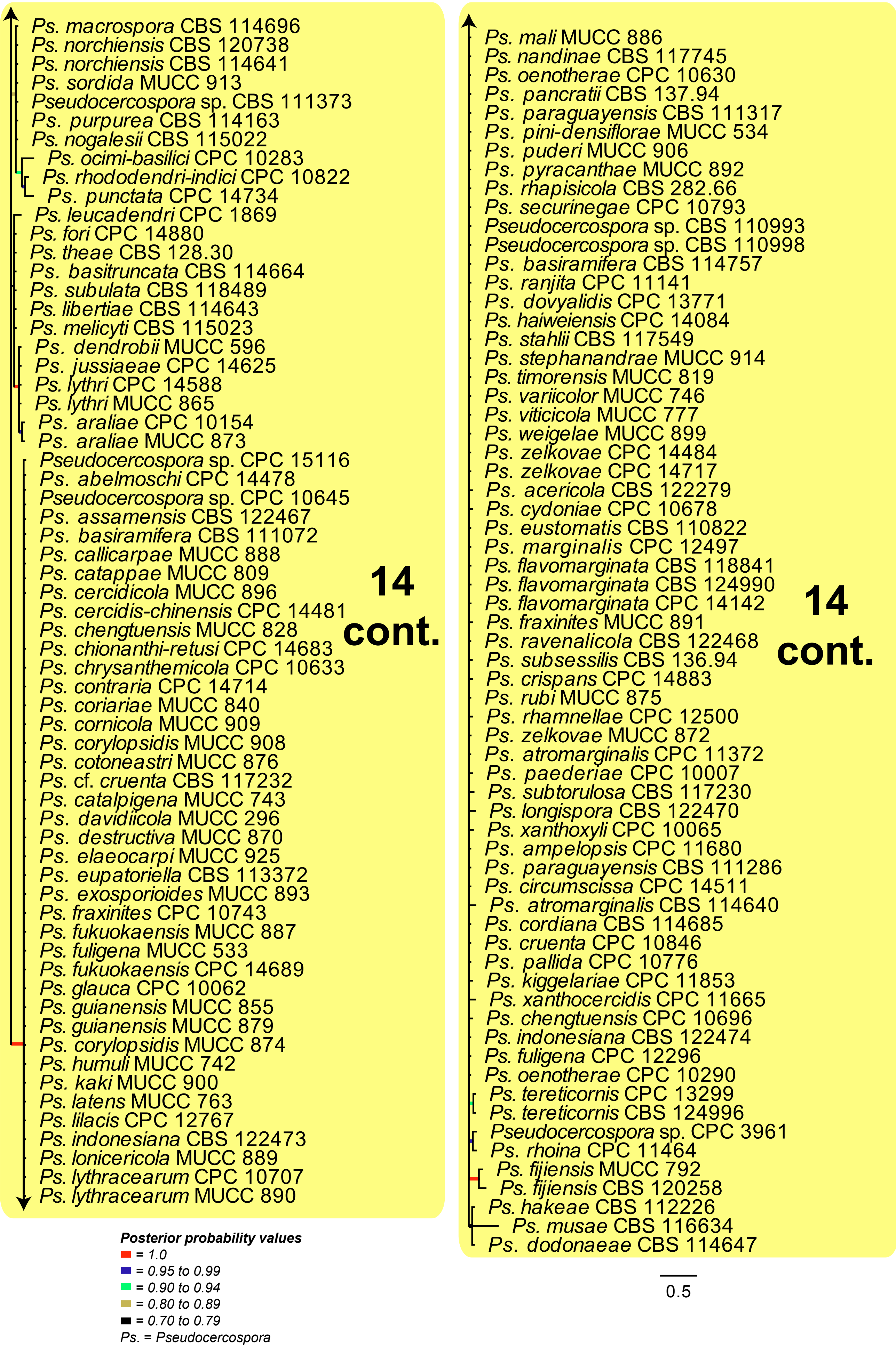


**Fig. 4.** (Continued).

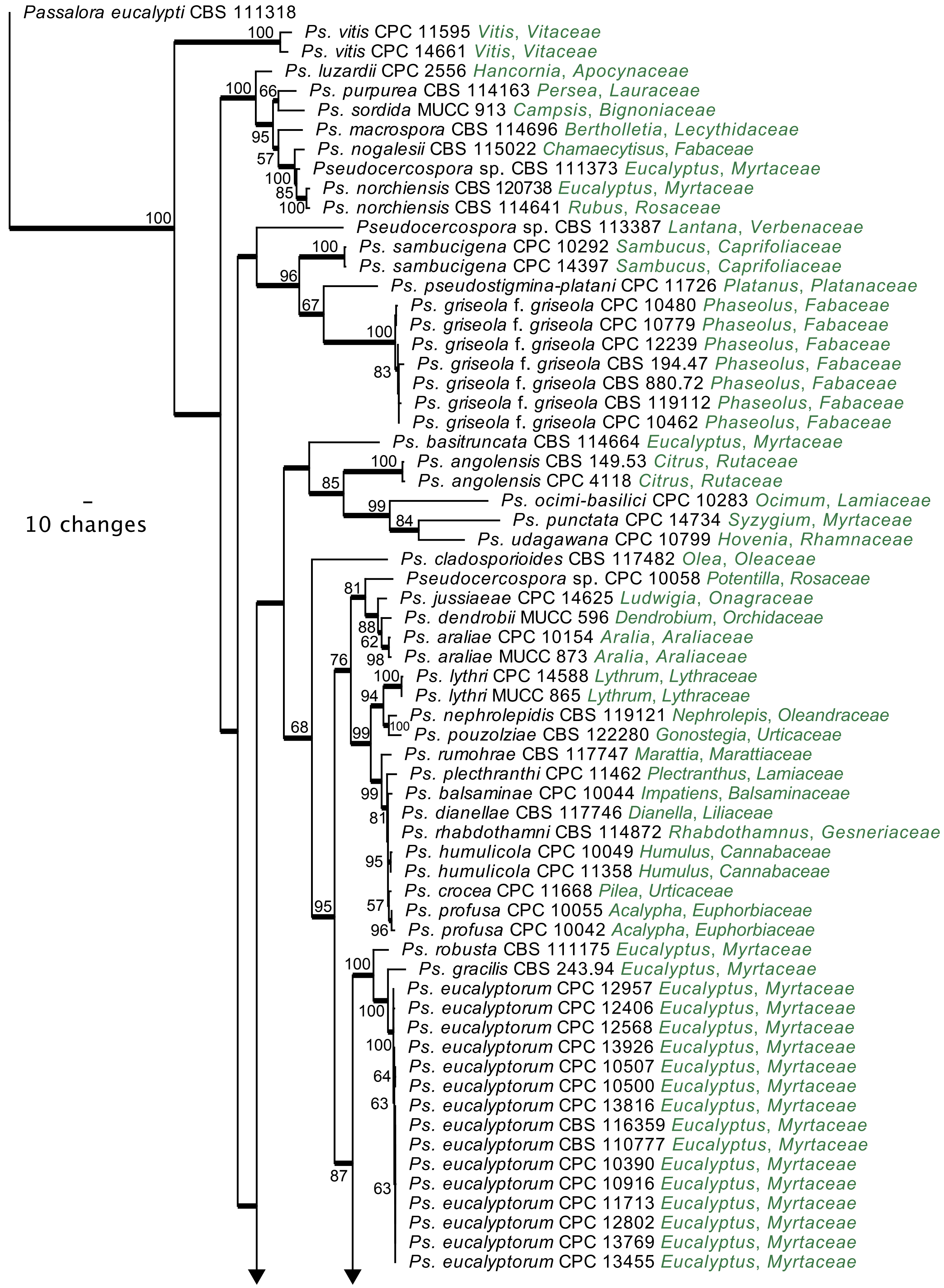


**Fig. 5.** The first of 1 000 equally most parsimonious trees obtained from a heuristic search with 100 random taxon additions of the combined ITS, ACT and EF-1α sequence alignment using PAUP v. 4.0b10. The scale bar shows 10 changes, and bootstrap support values from 1 000 replicates are shown at the nodes. Thickened lines indicate those branches present in the strict consensus tree and the tree was rooted to *Passalora eucalypti* strain CBS 111318 (GenBank GU269845, GU320548 and GU384558, respectively).

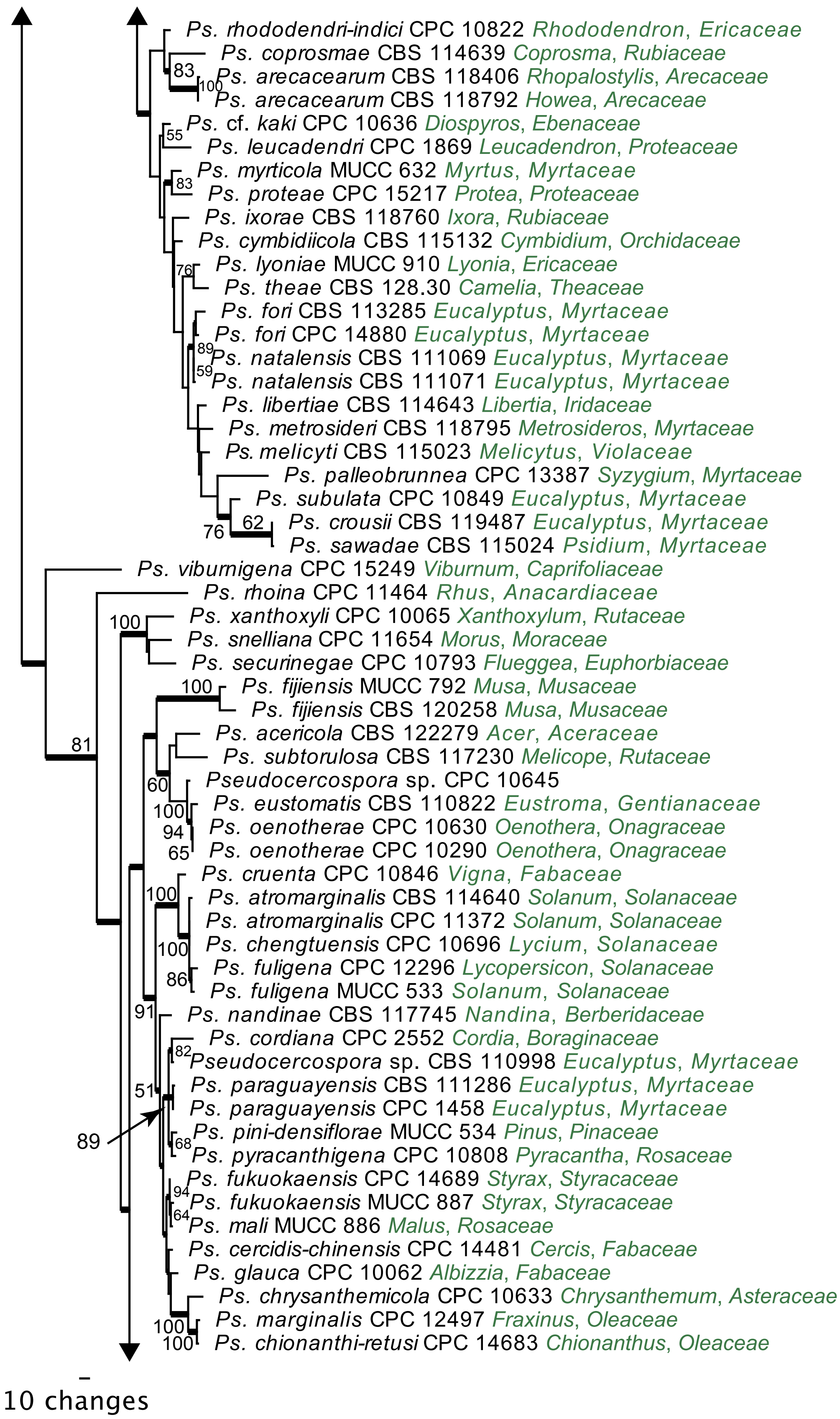


**Fig. 5.** (Continued).

split was not well-supported in the phylogeny. Deeper nodes of the backbone were poorly supported. There were high levels of support for several of the smaller sub-clades in this tree, which are discussed in the Taxonomy section below.

## Taxonomy

Isolates representing 146 species of *Pseudocercospora* were subjected to DNA analysis and morphological comparison. Phylogenetic analyses based on the LSU gene resolved a total of 14 clades in the *Pseudocercospora* complex.

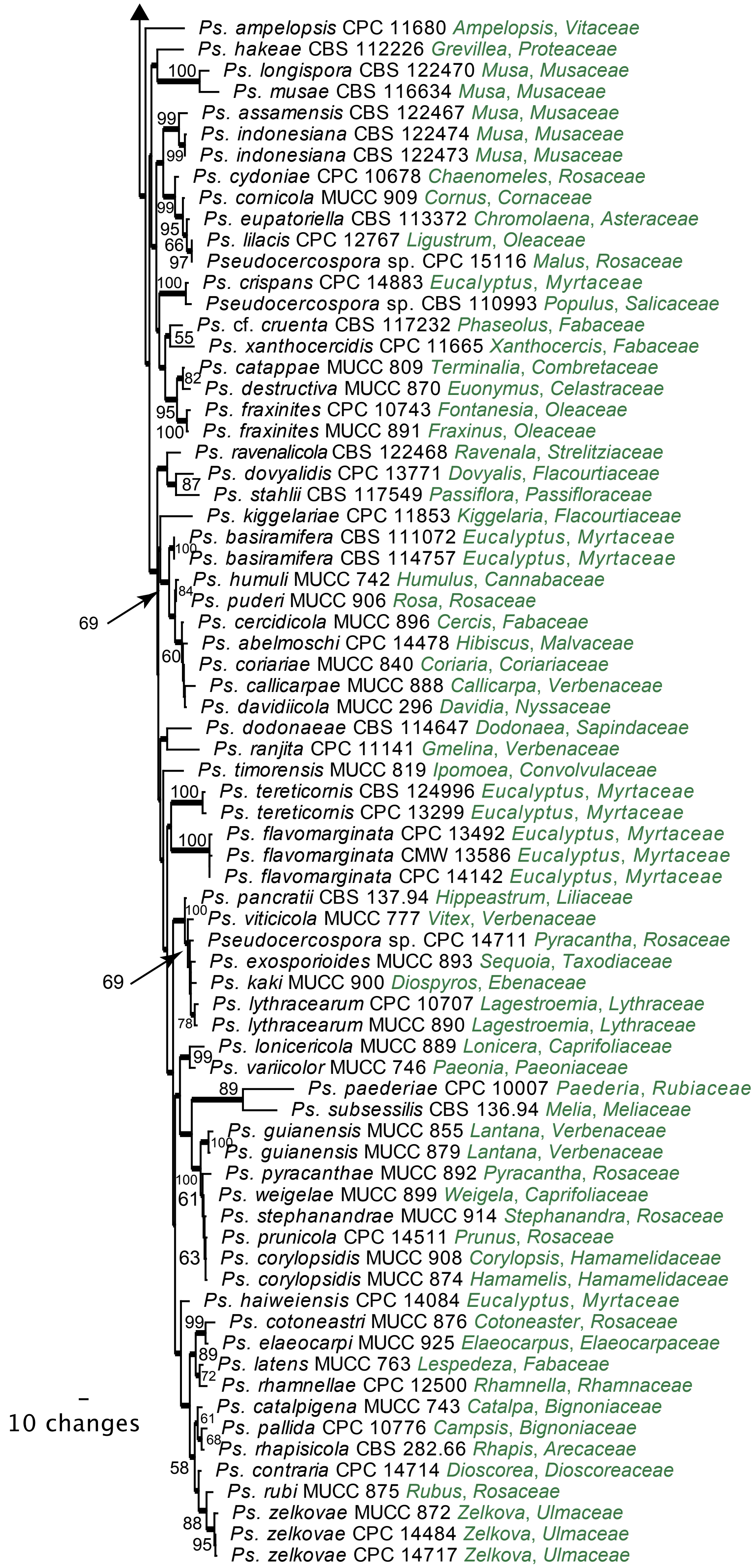


**Fig. 5.** (Continued).

Clade 1 represented *Strelitziana* (pseudocercospora-like but with a separating cell between conidia and conidiogenous cells) and *Cyphellophora* (pseudocercospora-like but phialides with flaring collarettes, situated directly on hyphae). *Thedgonia ligustrina* (pseudocercosporella-like, but conidia in chains) represented Clade 2. Clade 3 included several isolates of *Pseudocercospora cantuariensis*, which represents a novel genus, distinguished from *Pseudocercospora* based on its broad conidial hila and scars, as well hyaline mycelium, and the presence of hyphopodia-like structures. *Xenostigmina zilleri*, characterised as being stigmina-like, but also having sympodial proliferation of the conidiogenous cells, clustered in Clade 4, which was basal to *Cladosporium* (*Cladosporiaceae*; Clade 5). Clade 6 represented several members of *Teratosphaeriaceae*, known to have a wide range of anamorphs, including *Microcyclospora*. Clade 7 represented species of *Dissoconium* (*Dissoconiaceae*), distinct due to their dimorphic conidia that are actively discharged. Clade 8 remains unresolved, and was represented by disjunct elements appearing *Zasmidium*- and pseudocercospora-like in morphology, including *Microcyclosporella*. Clade 9 was represented by several *Mycosphaerella* species such as *M. laricina* (anamorph *Pseudocercospora* sp.), and *Paracercospora egenula*. *Paracercospora* was separated from *Pseudocercospora* based on a combination of characters, including pale olivaceous conidia, and a minute thickening along the rim of its conidial hila and scars. Clade 10 included a diverse assemblage of genera. Two genera that differ mainly based on their conidiomatal structure, *Pseudocercosporella* and *Septoria*, clustered in this clade. *Miuraea*, a genus intermediate between *Cercospora* and *Pseudocercospora*, also resided within this clade. Clade 11 was represented by two coelomycetous species of *Sonderhenia* that clustered basal to Clade 12. The latter included a new genus with pseudocercospora-like anamorphs, mostly distinguished from *Pseudocercospora s. str*. by having species with smooth, pale brown conidia, and the frequent production of red crystals in agar (previously referred to in literature as the *Mycosphaerella heimii* complex). *Scolecostigmina* (based on *S. mangiferae*), which is characterised by verruculose conidia and percurrently proliferating conidiogenous cells, clustered alongside to *Trochophora*, characterised by brown sickle-shaped conidia with three thick, dark septa. *Passalora eucalypti* formed a separate lineage in Clade 13 that was adjacent to *Pseudocercospora s. str*. in Clade 14. This clade included the type species, *P. vitis* that is basal in this cluster. Although there was structure within the clade, we regard it as representing a single genus, including *Stigmina platani*, the type of *Stigmina*, *Phaeoisariopsis* (*P. griseola*), and *Pseudophaeoramularia* (*P. angolensis*). Several isolates identified from different countries as representing the same species based on host, disease symptoms and general morphology, clustered apart from one another. These collections were found to represent novel cryptic species.

## Treatment of species

Several novel taxa were identified in this study on the basis of phylogenetic analyses of the various gene regions together with morphological examination of the specimens and isolates. Recognised clades, as well as novel species and genera, are described and discussed below. Where descriptions of known taxa are freely available online in MycoBank or journals, they are not repeated here, other than their generic circumscriptions.

## Clade 1: *Strelitziana* and *Cyphellophora*

***Strelitziana*** M. Arzanlou & Crous, Fungal Planet No. 8: 2006.

*Conidiophores* erect, solitary, arising from aerial and submerged mycelium, subcylindrical, straight to geniculate-sinuous, pale brown. *Conidiogenous cells* terminal, integrated, rejuvenating percurrently, proliferating apically via several short, conspicuous denticles; *conidiogenesis* holoblastic with rhexolytic conidial secession. *Conidia* solitary, pale brown, smooth, long obclavate, multi-euseptate; microcyclic conidiation present in culture.

*Type species*: *Strelitziana africana* M. Arzanlou & Crous, Fungal Planet No. 8. 2006.

*Notes*: The genus *Strelitziana* presently accommodates four species that are primarily distinguished based on their conidial dimensions. These include *S. africana*, *S. australiensis, S. eucalypti* and *S. mali* (Arzanlou & Crous 2006, Cheewangkoon *et al*. 2009, Zhang *et al.* 2009, Crous *et al.* 2010).

***Cyphellophora*** G.A. de Vries, Mycopathol. Mycol. Appl. 16: 47. 1962.

*Colonies* (on OA) with moderate to rapid growth, velvety to lanose, in various shades of grey; reverse black. *Fertile hyphae* pale brown, sometimes with constrictions at the septa. *Conidiogenous cells* phialidic, intercalary, sometimes on short side branches, each with a short, lateral or terminal collarette. *Conidia* sickle-shaped, brown, smooth-walled, transversely septate, adhering in small bundles (from de Vries 1962).

*Type species*: *Cyphellophora laciniata* G.A. de Vries, Mycopathol. Mycol. Appl. 16: 47. 1962.

*Notes*: The genus *Cyphellophora*, which is based on *C. laciniata* (isolated from human skin; De Vries *et al.* 1986)*,* appears to be heterogeneous (Decock *et al*. 2003, Crous *et al*. 2007a, 2009a, Cheewangkoon *et al*. 2009) and requires further study.

## Clade 2: *Thedgonia*

***Thedgonia*** B. Sutton, Trans. Brit. Mycol. Soc. 61: 426. 1973.

*Foliicolous*, phytopathogenic, causing discrete leaf spots. *Conidiomata* fasciculate, punctiform. *Mycelium* internal, hyphae subhyaline, septate, branched, forming substomatal stromata, hyaline to pale brown. *Conidiophores* fasciculate, arising from stromata, simple, rarely branched, subcylindrical, straight to geniculate-sinuous, continuous to septate, smooth, hyaline to pale yellowish green. *Conidiogenous cells* integrated, terminal, occasionally conidiophores reduced to conidiogenous cells, holoblastic-thalloblastic, sympodial, conidiogenous loci more or less planate, unthickened, non-pigmented. *Conidia* in disarticulating chains, rarely in branched chains, subcylindrical to obclavate, with one to several transverse eusepta, hyaline or almost so, apex rounded to truncate, base truncate, hila flat, unthickened, hyaline (Crous *et al*. 2009a).

*Type species*: *Thedgonia ligustrina* B. Sutton, Trans. Brit. Mycol. Soc. 61: 426. 1973.

***Thedgonia ligustrina*** (Boerema) B. Sutton, Trans. Brit. Mycol. Soc. 61: 428. 1973.
*Basionym*: *Cercospora ligustrina* Boerema, Tijdschr. Plantenziekten 68: 117. 1962.
≡ *Cercoseptoria ligustrina* (Boerema) Arx, Genera of Fungi Sporulating in Pure Culture, ed. 3: 306, Lehre 1981.

*Specimens examined*: **Asia**, on *Ligustrum* sp., H. Evans, CPC 4296 = W2072, CPC 4297 = W 2073, CPC 4298 = W 1877. **Netherlands**, Eefde, on *Ligustrum ovalifolium*, 23 Mar. 1959, G.H. Boerema, **holotype** L, ex-type culture CBS 148.59; Bilthoven, on *L. ovalifolium*, 2003, P.W. Crous, CPC 10530 = CBS 124332, CPC 10532, 10533. **South Korea**, Namyangju, on *L. ovalifolium*, 9 Oct. 2002, leg. H.D. Shin, isol. P.W. Crous, CBS H-20204, CPC 10019, 10861–10863; Suwon, on *L. obtusifolium*, 2 Oct. 2007, leg. H.D. Shin, isol. P.W. Crous, CBS H-20207, CPC 14754–14756.

*Notes*: Contrary to the earlier hypothesis that *Thedgonia* belonged to the *Mycosphaerellaceae* (Kaiser & Crous 1998), Crous *et al*. (2009a) showed that it resides in *Helotiales*. Consequently, thedgonia-like anamorphs that occur in the *Mycosphaerellaceae* must be accommodated elsewhere.

## Clade 3: *Xenostigmina*

***Xenostigmina*** Crous, Mycol. Mem. 21: 154. 1998.

*Foliicolous*, phytopathogenic, causing discrete leaf spots. *Mycelium* internal, consisting of hyaline to pale brown, septate, branched, smooth hyphae. *Conidiomata* sporodochial, brown to black. *Conidiophores* densely aggregated, arising from the upper cells of a pale brown stroma, finely verruculose, hyaline to pale brown, multiseptate, subcylindrical, straight to variously curved, branched. *Conidiogenous cells* terminal and intercalary, hyaline to pale brown, finely verruculose, doliiform to subcylindrical, tapering to flat tipped loci, mono- to polyblastic, proliferating sympodially and percurrent; loci not thickened or conspicuous. *Conidia* solitary, pale to medium brown, with pale brown apical and basal regions, finely verruculose, mostly straight, ellipsoidal, apex subobtuse, frequently extending into a beak; base truncate at dehiscence, inner part extending later to form a short, subobtuse basal appendage; septation muriform; basal marginal frill present (Crous *et al*. 2009a).

*Type species*: *Xenostigmina zilleri* (A. Funk) Crous, Mycol. Mem. 21: 155. 1998.

*Specimens examined*: **Canada**, British Columbia, 15 km east of Sardis, on living leaves of *Acer macrophyllum*, 22 Oct. 1985, A. Funk & C.E. Dorworth, **holotype** DAVFP 23272; British Columbia, on living leaves of *Acer* sp., 2002, leg. K.A. Seifert, isol. P.W. Crous, CBS 115686 = CPC 4010, CBS 115685 = CPC 4011; Victoria BC, 48°30'25.63"N, 123°30'46.99"W, 115 m, fallen leaves of *A. macrophyllum*, 6 Sep. 2007, leg. B. Callan, isol. P.W. Crous, **epitype designated here** CBS H-20208, cultures ex-epitype CPC 14376 = CBS 124108, CPC 14377, 14378 (*Xenostigmina zilleri*), CPC 14379 = CBS 124109, CPC 14380, 14381 (*Mycopappus aceris*).

*Notes*: *Xenostigmina* with its *Mycopappus* synanamorph is distinct from *Stigmina s. str*., which is a synonym of *Pseudocercospora s. str.* (Crous *et al*. 2006, Braun & Crous 2006, 2007). The genus *Xenostigmina* (Crous 1998) appears related to *Seifertia* (Seifert *et al*. 2007) in the *Dothideomycetes* (Crous *et al*. 2009b).

## Clade 4: *Phaeomycocentrospora*

***Phaeomycocentrospora*** Crous, H.D. Shin & U. Braun, **gen. nov.** MycoBank MB564813.

*Etymology*: Name reflects the pale brown appearance of conidia and the superficial similarity to *Mycocentrospora.*

*Foliicolous*, phytopathogenic, causing discrete leaf spots. *Mycelium* internal and external, consisting of hyaline, septate, branched, smooth, 3–5 µm diam hyphae; hyphopodium-like structures present. *Caespituli* amphigenous. *Conidiophores* in loose fascicles, arising from a poorly developed stroma, or from superficial hyphae emerging from stomata, or erumpent through the cuticle; erect on superficial hyphae, olivaceous-brown, straight to slightly curved, unbranched, not geniculate, obconically truncate at the apex; *conidiogenous cells* integrated, terminal or conidiophores reduced to conidiogenous cells, mono- to polyblastic, proliferating sympodially, transversely septate; conidiogenous loci broad, more or less planate, neither thickened nor darkened. *Conidia* solitary, filiform to cylindrical, straight to moderately curved, subhyaline to pale olivaceous, transversely euseptate, usually not constricted at septa, tapering somewhat towards an obtuse apex, truncate at the base; hilum unthickened, not darkened, broad.

*Type species*: *Phaeomycocentrospora cantuariensis* (E.S. Salmon & Wormald) Crous, H.D. Shin & U. Braun, comb. nov.

*Notes*: *Phaeomycocentrospora* is similar to *Pseudocercospora* in that its conidia and conidiophores appear to be pigmented and its conidiogenous loci are unthickened and not darkened. It is distinct from *Pseudocercospora* in that its mycelium is hyaline, hyphopodia-like structures are present, and conidia are hyaline with a pale brown inner wall layer, giving the impression of pigmented conidia. This fungus also has extremely broad conidial loci and scars that are untypical of *Pseudocercospora*. Chupp (1954) commented that *Cercospora cantuariensis* represented an unusual species that should be transferred to a genus of its own. Based on its unique phylogenetic placement (Fig. 4) and morphology, *Phaeomycocentrospora* gen. nov. is established for this taxon. Deighton (1971, 1972) assigned this species to *Mycocentrospora*, but the type species *M. acerina* is phylogenetically distinct from other genera morphologically similar to it and differs in having conidia with filiform appendages and often with strongly swollen intercalary cells.

***Phaeomycocentrospora cantuariensis*** (E.S. Salmon & Wormald) Crous, H.D. Shin & U. Braun, **comb. nov.** MycoBank MB564814. Fig. 6.
*Basionym*: *Cercospora cantuariensis* E.S. Salmon & Wormald, J. Bot. (London) 61: 134. 1923.
≡ *Centrospora cantuariensis* (E.S. Salmon & Wormald) Deighton, Mycol. Pap. 124: 8. 1971.
≡ *Mycocentrospora cantuariensis* (E.S. Salmon & Wormald) Deighton, Taxon 21: 716. 1972.
≡ *Pseudocercospora cantuariensis* (E.S. Salmon & Wormald) U. Braun, Mycotaxon 48: 281. 1993.

**Fig. 6.** *Phaeomycocentrospora cantuariensis* (CPC 11691–11693). A. Leaf spots on upper and lower leaf surface. B, C. Sporulation of leaf surface. D–I. Conidiophores and conidiogenous cells. J–M. Conidia. Scale bars = 10 µm.

*Leaf spots* amphigenous, scattered, often confluent, subcircular to irregular, 1–5 mm diam, becoming up to 10 mm diam when confluent, greyish to white, centre reddish brown with yellowish brown zone on upper surface; greyish brown to grey on lower surface. *Caespituli* amphigenous, but predominantly hypophyllous. *Mycelium* internal and external; internal hyphae hyaline, septate, branched, smooth, 3–4 µm diam; external hyphae plagiotropous, branched, septate, smooth, hyaline, 3–5 µm diam. *Conidiophores* in loose fascicles, arising from a poorly developed stroma, or from superficial hyphae emerging from stomata, or erumpent through the cuticle; erect on superficial hyphae, olivaceous-brown, straight to slightly curved, unbranched, not geniculate, obconically truncate at the apex, proliferating sympodially, 0–3-septate, 30–140 × 7–20 µm. *Conidiogenous cells* terminal, unbranched, pale brown, smooth, tapering to flat-tipped apical loci, with scars neither thickened nor darkened, 4–7 µm diam; at times proliferating percurrently, with 1–3 percurrent proliferations at the apex, 12–45 × 5–8 µm. *Conidia* solitary, filiform to cylindrical, straight to moderately curved, subhyaline to pale olivaceous, smooth, 3–15(–21)-septate, usually not constricted at septa, tapering somewhat towards obtuse apex, truncate at the base, or long obconically subtruncate, (100–)140–200(–500) × (5–)7–12(–20) µm; hilum unthickened, not darkened, 4–7 µm diam; conidia appear to have an inner wall layer that is pale brown when studied in culture (adapted from Shin & Kim 2001).

*Specimens examined*: **South Korea**, Hoengseong, on *Humulus scandens* (= *H. japonicus*), 4 Sep. 2005, H.D. Shin, CBS H-20830; Suwon, *Acalypha australis*, 5 Nov. 2004, H.D. Shin, cultures CPC 11691–11693; Suwon, *H. scandens* , 5 Nov. 2004, H.D. Shin, CBS H-20831, cultures CPC 11694–11696; Hoengseong, on *H.*

*scandens*, 11 Oct. 2004, H.D. Shin, CBS H-20832, cultures CPC 11646, 11647; Wonju, on *H. scandens*, 18 Oct. 2002, H.D. Shin, CBS H-20833, cultures 10157, 10158; Namyangju, on *Luffa aegyptica* (= *L. cylindrica*), 22 Oct. 2003, H.D. Shin, CBS H-20834, cultures CPC 10762–10766.

## Clade 5: *Cladosporium* (*Cladosporiaceae*)

***Cladosporium*** Link, Ges. Naturf. Freunde Berlin Mag. Neuesten Entdeck. Gesammten Naturk. 7: 37. 1816.
*Teleomorph*: *Davidiella* Crous & U. Braun, Mycol. Progr. 2: 8. 2003.

Saprobic or phytopathogenic. *Ascomata* pseudothecial, black to red-brown, globose, inconspicuous and immersed beneath stomata to superficial, situated on a reduced stroma, with 1(–3) short, periphysate ostiolar necks; periphysoids frequently growing down into cavity; wall consisting of 3–6 layers of *textura angularis*. *Asci* fasciculate, short-stalked or not, bitunicate, subsessile, obovoid to broadly ellipsoid or subcylindrical, straight to slightly curved, 8-spored. *Pseudoparaphyses* frequently present in mature ascomata, hyaline, septate, subcylindrical. *Ascospores* bi- to multiseriate, hyaline, obovoid to ellipsoid-fusiform, with irregular luminar inclusions, mostly thick-walled, straight to slightly curved; frequently becoming brown and verruculose in asci; at times covered in mucoid sheath (from Schubert *et al.* 2007). *Mycelium* superficial, loosely branched, septate, sometimes constricted at septa, hyaline, subhyaline to pale brown, smooth or almost so to verruculose or irregularly rough-walled, sometimes appearing irregular in outline due to small swellings and constrictions, walls unthickened to somewhat thickened. *Conidiophores* both macro- and micronematous, arising laterally from plagiotropous hyphae or terminally from ascending hyphae. *Macronematous conidiophores* erect, straight to flexuous, somewhat geniculate-sinuous, nodulose or not, unbranched or occasionally branched, pluriseptate, pale to medium brown, older ones almost dark brown, walls thickened, sometimes even two-layered. *Conidiogenous cells* integrated, terminal or intercalary, mono- to usually polyblastic, nodulose to nodose or not, proliferation sympodial, with several conidiogenous loci, mostly situated on small lateral shoulders, more or less protuberant, characteristically coronate (SEM), *i.e.* with a convex central dome surrounded by a low to distinctly raised rim, appearing to be thickened and somewhat darkened-refractive. *Micronematous conidiophores* hardly distinguishable from hyphae, sometimes only as short lateral outgrowth with a single apical scar, short, conical to almost filiform or narrowly cylindrical, pluriseptate, usually short, subhyaline to pale brown, almost smooth to minutely verruculose or irregularly rough-walled, 0–3-septate. *Conidiogenous cells* integrated, terminal or conidiophores reduced to conidiogenous cells, narrowly cylindrical or filiform, with a single or two loci. *Conidia* solitary (in heterosporium-like species) to usually catenate, in unbranched or loosely branched chains, straight to slightly curved; small terminal conidia without distal hilum, obovoid to ellipsoid to subcylindrical, aseptate, subhyaline to pale brown; intercalary conidia with a single or sometimes up to three distal hila, limoniform, ellipsoid to subcylindrical, 0–1-septate; *secondary ramoconidia* with up to four distal hila, ellipsoid to cylindrical-oblong, 0–1(–2)-septate, pale greyish brown or brown to medium brown, smooth to minutely verruculose to verrucose, walls slightly to distinctly thickened, apex obtuse or slightly truncate, towards the base sometimes distinctly attenuated with hila situated on short stalk-like prolongations, hila slightly to distinctly protuberant, coronate structure as in conidiogenous loci, somewhat thickened and darkened-refractive; microcyclic conidiogenesis occurring; *primary ramoconidia* similar to secondary ramoconidia, except base truncate, uniform with conidiogenous cell, and more subcylindrical in shape (adapted from Schubert *et al.* 2007).

*Type species*: *Cladosporium herbarum* (Pers. : Fr.) Link, Ges. Naturf. Freunde Berlin Mag. Neuesten Entdeck. Gesammten Naturk. 7: 37. 1816.

*Notes*: *Cladosporium* is well-defined by having *Davidiella* teleomorphs and conidiophores that give rise to conidial chains with unique coronate scars (David 1997, Braun *et al*. 2003a, Schubert *et al.* 2007, Bensch *et al.* 2010, 2012), which easily distinguish it from a range of other morphologically similar genera (Crous *et al*. 2007a, b; Braun & Crous, in Seifert *et al*. 2011).

## Clade 6: *Teratosphaeriaceae*

***Teratosphaeria*** Syd. & P. Syd., Ann. Mycol. 10: 39. 1912.

Phytopathogenic, commonly associated with leaf spots, but also on fruit, or causing cankers on stems. *Ascomata* pseudothecial, superficial to immersed, frequently situated in a stroma of brown pseudoparenchymatal cells, globose, unilocular, papillate, ostiolate, canal periphysate, with periphysoids frequently present; wall consisting of several layers of brown *textura angularis*; inner layer of flattened, hyaline cells. *Pseudoparaphyses* frequently present, subcylindrical, branched, septate, anastomosing. *Asci* fasciculate, 8-spored, bitunicate, frequently with multi-layered endotunica. *Ascospores* ellipsoid-fusoid to obovoid, 1-septate, hyaline, but becoming pale brown and verruculose, frequently covered in mucoid sheath (from Crous *et al*. 2007a).

*Type species*: *Teratosphaeria fibrillosa* Syd. & P. Syd., Ann. Mycol. 10: 40. 1912.

*Notes*: *Teratosphaeria* accommodates a group of plant pathogenic fungi that can cause serious leaf spot, blotch and canker diseases of a range of hosts (Crous 2009, Crous *et al*. 2007a, 2009b, Hunter *et al*. 2009, 2011). The *Teratosphaeriaceae* remains to be clearly resolved, and several different genera are presently recognised in the family. Some are plant-associated such as *Batcheloromyces*, *Baudoinea, Capnobotryella, Catenulostroma, Davisoniella, Devriesia, Hortea*, *Penidiella, Phaeothecoidea, Pseudotaeniolina*, *Readeriella, Staninwardia,* and *Stenella s. str.* (Crous *et al*. 2007a, 2009a, 2011b), and others including *Cystocoleus, Racodium, Friedmanniomyces, Elasticomyces*, *Recurvomyces* (Selbmann *et al*. 2008) and *Xanthoriicola* (Ruibal *et al*. 2011) are lichenicolous or rock inhabiting.

***Microcyclospora*** Jana Frank, Schroers & Crous, Persoonia 24: 99. 2010.

Epiphytic and endophytic, occurring on leaves and fruit. *Mycelium* consisting of branched, septate, pale brown, smooth, 2–3 µm wide hyphae. *Conidiophores* reduced to conidiogenous cells, integrated in hyphae, giving rise to peg-like lateral protuberances, 1 µm wide, 1–2 µm tall, mono- to polyblastic. *Conidia* scolecosporous, cylindrical, straight to variously curved, flexuous, apex obtuse, base truncate, 1–multi-septate, somewhat constricted at septa, smooth, pale brown, guttulate, aggregated in mucoid masses; hila not thickened or darkened; microcyclic conidiation observed in culture.

*Type species*: *Microcyclospora pomicola* Jana Frank, B. Oertel, Schroers & Crous, Persoonia 24: 100. 2010.

*Notes*: *Microcyclospora* was recently introduced in *Teratosphaeriaceae* for three taxa associated with sooty blotch of apple (Frank *et al*. 2010). The species described here resembles others presently known in *Microcyclospora* by having pigmented structures and undergoing microcyclic condiation. Other than having distinct conidial dimensions, it differs from other genera in that its conidiogenous cells are annellidic (not mono- to polyblastic), and its conidia are darker brown and verruculose to warty, not pale brown and smooth.

***Microcyclospora quercina*** Crous & Verkley, **sp. nov.** MycoBank MB564815. Figs 7, 8.

*Etymology*: Name reflects its host, *Quercus.*

Foliicolous, endophytic. *Mycelium* consisting of branched, septate, brown, 1.5–3 µm diam hyphae, guttulate, smooth to verruculose or warty, with or without mucoid sheath. *Conidiophores* reduced to conidiogenous cells. *Conidiogenous cells* lateral on hyphae, brown, solitary, not aggregated, 1.5–2 µm diam, with 1–4 percurrent proliferations and flaring collarettes. *Conidia* solitary, subcylindrical (rarely obclavate), gently curved, apex obtuse (rarely subobtuse), base truncate or long obconically truncate, with slight basal taper to hilum that is 2 µm diam, unthickened, nor darkened, frequently with small marginal frill, brown, guttulate to granular, smooth, appearing warty or roughened due to external mucoid layer which is sometimes present, transversely (1–)3–4(–11)-euseptate, becoming constricted at septa with age, (12–)30–45(–70) × (2–)2.5–3 µm; microcyclic conidiation commonly observed.

*Culture characteristics*: Colonies after 2 wk in the dark up to 15 mm diam, with sparse aerial mycelium, folded surface and uneven to somewhat feathery, lobate margins, exuding copious amounts of slime on PDA, but less so on MEA and OA; colonies olivaceous-black on all media.

*Specimen examined*: **Netherlands**, endophytic in leaves of *Quercus robur*, Sep. 2003, G.J.M. Verkley, **holotype** CBS H-20835, culture ex-type CPC 10712 = CBS 130827.

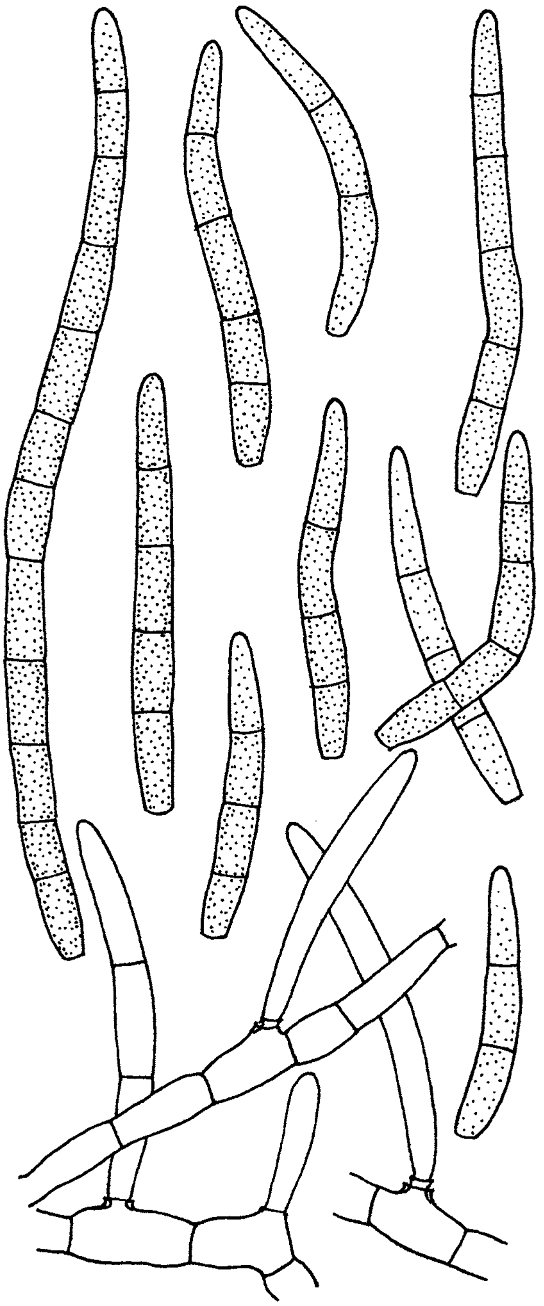

**Fig. 7.** *Microcyclospora quercina* (CPC 10712). Line drawing showing conidiogenous cells and conidia formed in culture. Scale bar = 10 µm.

## Clade 7: *Dissoconium* (*Dissoconiaceae*)

***Dissoconium*** de Hoog, Oorschot & Hijwegen, Proc. K. Ned. Akad. Wet., Ser. C, Biol. Med. Sci. 86(2): 198. 1983.

Hyperparasitic, but also reported to be phytopathogenic. *Ascomata* pseudothecial, immersed, globose, unilocular, papillate, ostiolate, canal periphysate; wall consisting of 3–4 layers of brown *textura angularis*; inner layer of flattened, hyaline cells. *Pseudoparaphyses* absent. *Asci* fasciculate, 8-spored, bitunicate. *Ascospores* ellipsoid-fusoid, 1-septate, hyaline, with or without mucoid sheath. *Mycelium* internal and external, consisting of branched, septate, smooth, hyaline to pale brown hyphae. *Conidiophores* separate, arising from hyphae, subcylindrical, subulate or lageniform to cylindrical, tapering to a bluntly rounded or truncate apex, straight to once geniculate, smooth, medium brown, 0–multi-septate; *conidiogenous cells* polyblastic, with terminal and lateral conidiogenous loci, visible as slightly thickened, darkened scars on a rachis. *Conidia* solitary, pale olivaceous-brown, smooth, ellipsoid to obclavate or globose, 0–1-septate; hila somewhat darkened. *Secondary conidia* present or absent; developing adjacent to primary conidia, pale olivaceous to subhyaline, aseptate, pyriform; conidium discharge active or passive (from Crous *et al.* 2009b).

*Type species*: *Dissoconium aciculare* de Hoog, Oorschot & Hijwegen, Proc. K. Ned. Akad. Wet., Ser. C, Biol. Med. Sci. 86(2): 198. 1983.

*Notes*: *Dissoconium* has mycosphaerella-like teleomorphs (Crous 1998, Crous *et al.* 2004c) and was recently shown to represent a distinct family, *Dissoconiaceae* (Crous *et al.* 2009b). Species are different from other taxa in *Capnodiales* in that they form primary and secondary conidia that are actively discharged and anastomose on the agar surface shortly after germination (De Hoog *et al.* 1991).

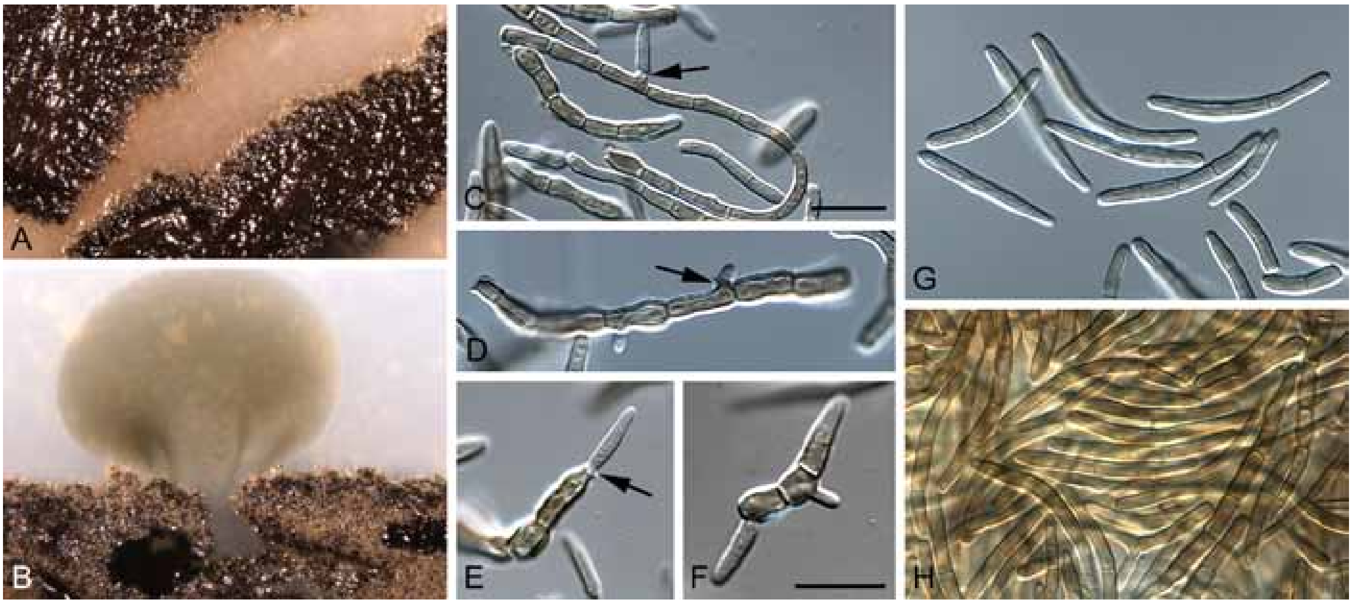


**Fig. 8.** *Microcyclospora quercina* (CPC 10712). A, B. Colony on oatmeal and potato-dextrose agar, respectively. C–E. Conidiogenous cells giving rise to conidia (arrows). F. Microcyclic conidiation. G, H. Conidia. Scale bars = 10 µm.

## Clade 8: *Microcyclosporella* and zasmidium-like

***Microcyclosporella*** Jana Frank, Schroers & Crous, Persoonia 24: 101. 2010.

Epiphytic on leaves and fruit. *Mycelium* consisting of pale brown, smooth to finely verruculose, branched, septate, 2–3.5 µm wide hyphae, at times covered in a mucoid layer, with integrated, lateral, truncate conidiogenous loci. *Conidiophores* mostly reduced to conidiogenous cells. *Conidiogenous cells* integrated, intercalary on hyphae, rarely terminal, cylindrical to doliiform, pale brown, but hyaline if occurring in yeast-like sectors of colonies, smooth, mono- or polyblastic, proliferating sympodially; loci inconspicuous, truncate, unthickened, not darkened, pale brown to hyaline. *Conidia* hyaline, smooth, subcylindrical to narrowly obclavate or narrowly fusoid with acutely rounded apex and obconically truncate base, guttulate, transversely 0–6-septate; microcyclic conidiation common.

*Type species*: *Microcyclosporella mali* Jana Frank, Schroers & Crous, Persoonia 24: 101. 2010.

*Notes*: *Microcyclosporella* was treated as part of the *Pseudocercosporella* generic complex (Batzer *et al.* 2005), but has since been shown to be polyphyletic within *Mycosphaerellaceae* (Crous 2009, Crous *et al*. 2003, 2009b, c, Frank *et al.* 2010). The clade accommodating *Microcyclosporella* contains many disjunct elements that vary in morphology from *Microcyclosporella s. str.* (hyaline structures) to pigmented structures, namely zasmidium-like (verrucuclose conidia) to pseudocercospora-like (smooth conidia) (see Crous *et al.* 2009b). We suspect that these groups may eventually be recognised as distinct genera, but more taxa need to be examined to resolve this issue.

## Clade 9: *Paracercospora* and pseudocercospora-like

***Paracercospora*** Deighton, Mycol. Pap. 144: 47. 1979.

Foliicolous, phytopathogenic, causing leaf spots. *Mycelium* internal, hyaline to pale olivaceous. Stromata absent to poorly developed. *Conidiophores* fasciculate, smooth, subhyaline to pale olivaceous. *Conidiogenous cells* integrated, terminal, mono- to usually polyblastic, proliferating sympodially; conidiogenous loci moderately conspicuous, with narrow thickening along the rim. *Conidia* solitary, subcylindrical to obclavate-cylindrical, smooth, subhyaline to pale olivaceous, with a narrow thickening along the rim of the hilum.

*Type species*: *Paracercospora egenula* (Syd.) Deighton, Mycol. Pap. 144: 48. 1979.

*Specimens examined*: **Japan**, Shimane, on leaves of *Solanum melongena*, 5 Aug. 1998, T. Mikami, CNS-415, cultures MUCC 883, MAFF 237766. **South Korea**, Hongcheon, on leaves of *S. melongena*, 26 Oct. 2005, H.D. Shin, CBS H-20836, culture CPC 12537.

*Notes*: Stewart *et al.* (1999) conducted the first phylogenetic analysis of the *Mycosphaerellaceae* and concluded that the marginal thickening that occurs along the rims of conidial scars and hila, originally thought to be the main character to distinguish *Paracercospora* from *Pseudocercospora*, was not taxonomically significant and suggested that *Paracercospora* be reduced to synonymy with *Pseudocercospora*. The current study provides new evidence that *Paracercospora* is not a synonym of *Pseudocercospora*, but no consistent morphological characters that distinguish it from *Pseudocercospora s. str*. have been identified. Conidia of *Paracercospora egenula* are subhyaline to pale olivaceous with minimal marginal thickening of the conidiogenous loci (Fig. 9). Conidial scars and hila of *Ps. fijiensis* (Arzanlou *et al*. 2008) and *Ps. basiramifera* (Crous 1998) are marginally thickened. Both of the latter species, which belong to *Pseudocercospora s. str*., have pale to medium brown conidia. At present *Paracercospora* may be defined by a combination of the minimal marginal thickening of the conidiogenous loci and its subhyaline conidia.

The taxonomic placement of *Paracercospora* is complicated by two other taxa that resolve in the clade together with it. These are *Passalora brachycarpa* (pale olivaceous, catenate conidia, and

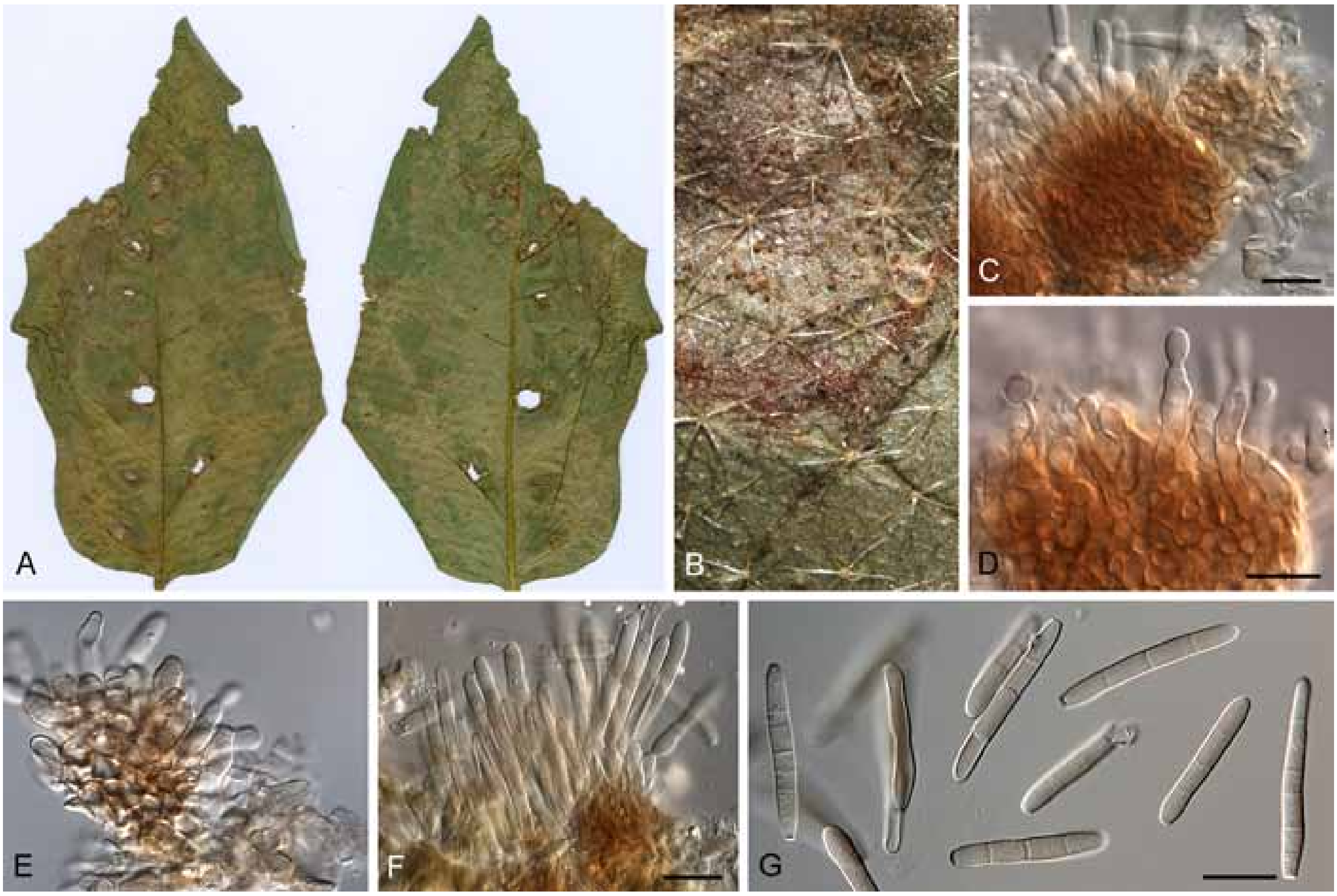


**Fig. 9.** *Paracercospora egenula* (CPC 12537). A. Leaf spots on upper and lower leaf surface. B. Close-up of lesion. C–F. Fascicles with conidiogenous cells. G. Conidia. Scale bars = 10 µm.

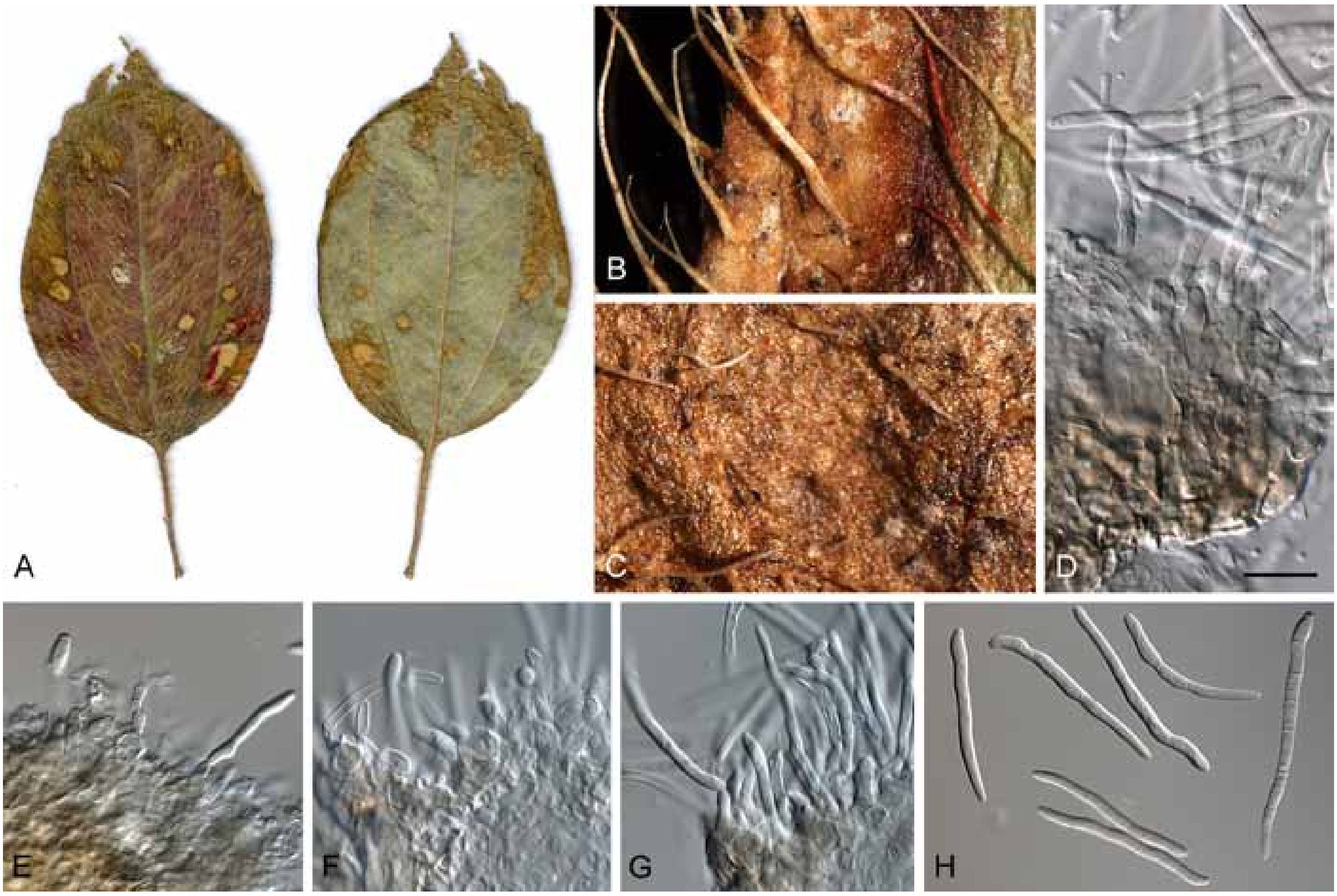


**Fig. 10.** *Pseudocercospora tibouchinigena* (CBS 116462). A. Leaf spots on upper and lower leaf surface. B, C. Close-up of lesions. D–G. Fascicles with conidiogenous cells. H. Conidia. Scale bar = 10 µm.

prominent, thickened, darkened scars; also visible when sporulating in culture), and *Pseudocercospora tibouchinigena* described below, which has subhyaline conidia, and unthickened hila and scars. This indicates that it is neither a species of *Pseudocercospora s. str.* (subhyaline conidia), nor *Paracercospora* (lacking any form of scar thickening). As a temporary solution, the species on *Tibouchina* is described in *Pseudocercospora*, although taxa in this subclade may eventually be shown to represent a distinct genus.

***Pseudocercospora tibouchinigena*** Crous & U. Braun, **sp. nov.** MycoBank MB564816. Fig. 10.

*Etymology*: Name is derived from *Tibouchina,* the host on which it was collected.

*Leaf spots* amphigenous, angular to irregular, 1–3 mm diam, up to 10 mm long, medium brown, with raised, dark brown border. *Mycelium* internal, hyaline, smooth, consisting of septate, branched, smooth, 1.5–2 µm diam hyphae. *Caespituli* fasciculate, predominantly hypophyllous, hyaline to pale olivaceous on leaves, up to 60 µm wide and 40 µm high. *Conidiophores* aggregated in dense fascicles, arising from the upper cells of a hyaline to subhyaline stroma, up to 50 µm wide and 20 µm high; conidiophores subcylindrical to ampulliform, 0–3-septate, straight to variously curved or geniculate-sinuous, unbranched, 15–25 × 3–5 µm. *Conidiogenous cells* terminal, unbranched, hyaline, smooth, tapering to flat-tipped apical loci, proliferating sympodially, 5–10 × 2.5–3.5 µm. *Conidia* solitary, subhyaline, smooth, guttulate or not, subcylindrical or narrowly obclavate, apex subobtuse, base obconically truncate, straight to variously curved, 3–10-septate, (15–)30–40(–60) × (1.5–)2–2.5(–3) µm; hila unthickened, not darkened nor refractive, 1–1.5 µm diam; prominent microcyclic conidiation observed *in vivo*.

*Culture characteristics*: Colonies after 1 mo at 24 ºC in the dark on MEA; erumpent, spreading, with moderate aerial mycelium, and smooth, lobate margins. Surface pale olivaceous-grey; reverse olivaceous-grey. Colonies reaching 30 mm diam.

*Specimen examined*: **New Zealand**, Auckland, Princes Street, Auckland University Campus, on leaves of *Tibouchina* sp. (*Melastomataceae*), 9 Aug. 2004, C.F. Hill 1061, **holotype** HAL 2359F, culture ex-type CBS 116462.

*Notes*: *Pseudocercospora tibouchinigena* was initially reported from New Zealand as *P. tibouchina* (Braun *et al*. 2006), which is hitherto known only from Brazil. It differs from *P. tibouchinae* in that the latter species has narrowly subcylindrical conidia that are larger, 40–120 × 2–3 µm (Viégas 1945), than those of *P. tibouchinigena.* The subhyaline conidia of *P. tibouchinigena* are not typical of *Pseudocercospora s. str*., but for the present, we choose to name it in *Pseudocercospora* until the clade in which it resides has been more fully resolved (Fig. 5).

## Clade 10: *Cercospora*, *Miuraea, Phloeospora, Pseudocercosporella, Septoria, Xenocercospora*

***Cercospora*** Fresen., in Fuckel, Hedwigia 1(15): 133. 1863 and in Fuckel, Fungi Rhen. Exs., Fasc. II, No. 117. 1863.

Mostly phytopathogenic producing conspicuous lesions, but also including saprobes. *Mycelium* internal, rarely also external; hyphae colourless or almost so to pigmented, branched, septate, smooth to faintly rough-walled. *Stromata* lacking to well-developed, subhyaline to usually pigmented, substomatal to intraepidermal. *Conidiophores* mononematous, macronematous, solitary to fasciculate, arising from internal hyphae or stromata, emerging through stomata or erumpent, very rarely arising from superficial hyphae, erect, continuous to pluriseptate, subhyaline to pigmented, smooth to faintly rough-walled, thin- to moderately thick-walled. *Conidiogenous cells* integrated, terminal or intercalary or conidiophores reduced to conidiogenous cells, monoblastic, determinate to usually polyblastic, sympodial, rarely with a few enteroblastically percurrent rejuvenations which are not connected with conidiogenesis; conidiogenous loci (scars) conspicuous, thickened and darkened, planate. *Conidia* solitary, very rarely catenate, scolecosporous, obclavate, cylindrical-filiform, acicular, hyaline or subhyaline (with a pale greenish tinge), mostly pluriseptate, euseptate, rarely with 0–1 or few septa, smooth or almost so, hila thickened and darkened, planate (from Crous & Braun 2003).

*Type species*: *Cercospora penicillata* (Ces.) Fresen., Beiträge zur Mykologie 3: 93. 1863. [= *C. depazeoides* (Desm.) Sacc.].

***Cercospora sojina*** Hara, Nogyo Sekai, Tokyo 9: 28. 1915. Fig. 11.

≡ *Passalora sojina* (Hara) H.D. Shin & U. Braun, Mycotaxon 58: 163. 1996.

*Specimen examined*: **South Korea**, Hongcheon, on *Glycine soja* (= *G. max* subsp. *soja*), 20 Jul. 2004, H.D. Shin, CBS H-20837, culture CPC 12322.

*Notes*: Despite sparingly septate and broadly obclavate-cylindrical conidia that tend to be subhyaline, this species is better accommodated in *Cercospora* than *Passalora* (Shin & Braun 1996) based on phylogenetic analysis.

***Cercospora eucommiae*** Crous, U. Braun & H.D. Shin, **sp. nov.** MycoBank MB564817. Fig. 12.

*Etymology*: Name derived from *Eucommia*, the host on which it occurs.

*Leaf spots* amphigenous, irregular to subcircular, 2–5 mm diam; surface grey-brown to brown with diffuse border; reverse olivaceous-brown with diffuse border. *Mycelium* internal, hyaline, consisting of septate, branched, smooth, 2–3 µm diam hyphae. *Caespituli* fasciculate, pale brown, amphigenous, up to 40 µm diam and 50 µm high (conidial mass white on leaf surface). *Conidiophores* aggregated in loose fascicles arising from the upper cells of a weakly developed brown stroma, up to 30 µm diam and 20 µm high, conidiophores pale brown, smooth, 1–3-septate, subcylindrical, straight to variously curved, unbranched, 20–50 × 4–5 µm. *Conidiogenous cells* terminal, unbranched, pale brown, smooth, tapering to flat-tipped apical loci that are thickened, somewhat darkened, slightly refractive, 2 µm diam, 15–25 × 4–5 µm, proliferating sympodially at the apex. *Conidia* solitary, or in unbranched short chains, hyaline to pale olivaceous (with age), smooth, guttulate, obclavate, apex obtuse to subobtuse or clavate, base obconically subtruncate, straight to mildly curved, 3–8-septate, (35–)60–75(–80) × (4–)5–6(–8) µm; hila thickened along the rim, but not darkened or planate, 1.5–2 µm diam.

*Culture characteristics*: Colonies after 2 wk at 24 ºC in the dark on MEA; erumpent, spreading, with sparse aerial mycelium, and

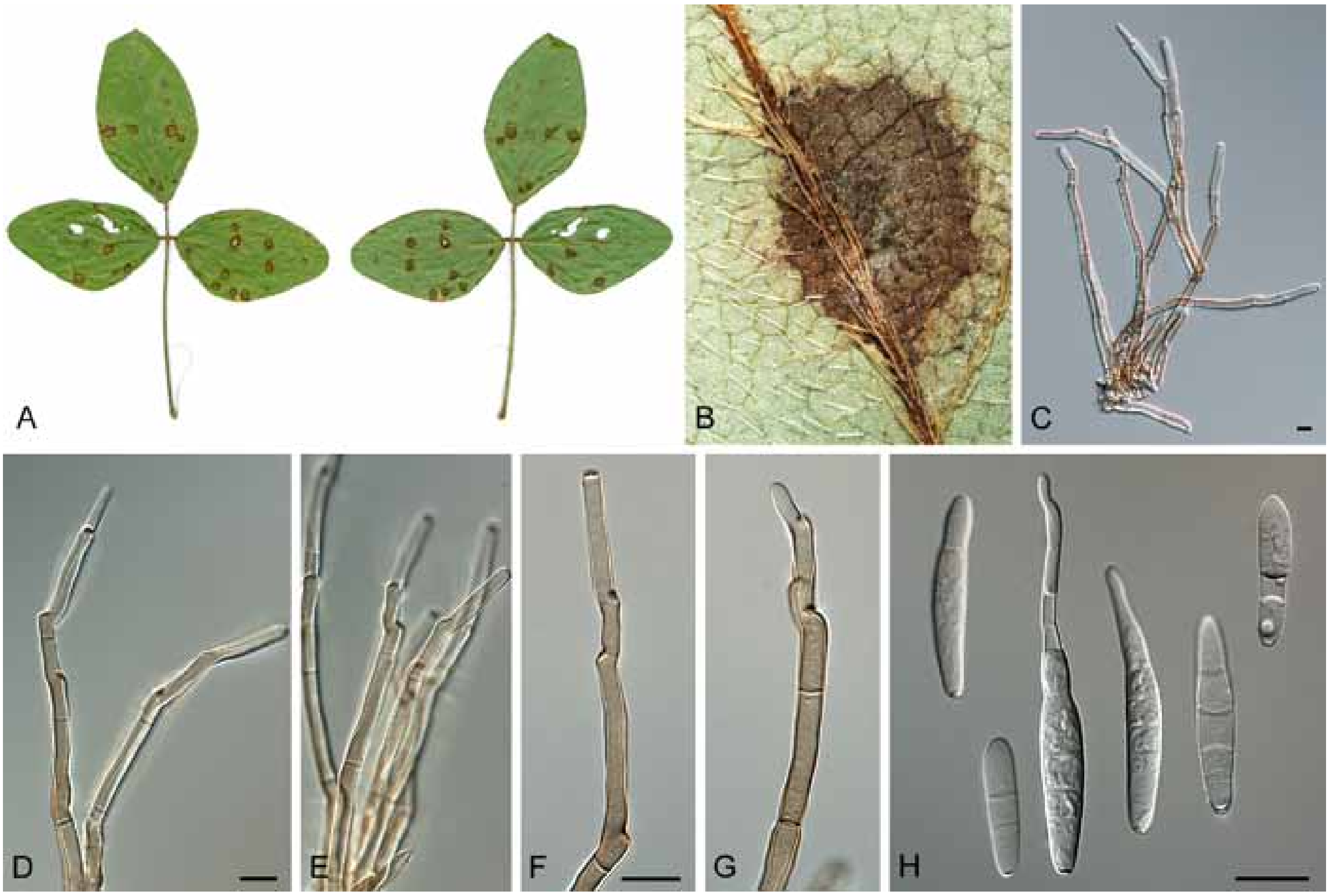


**Fig. 11.** *Cercospora sojina* (CPC 12322). A. Leaf spots on upper and lower leaf surface. B. Close-up of lesion. C–G. Fascicles with conidiophores and conidiogenous cells. H. Conidia. Scale bars = 10 µm.

smooth, lobate margins. Surface folded, dark mouse-grey with patches of dirty white; reverse fuscous black becoming greyish sepia at margin. Colonies reaching 12 mm diam.

*Specimens examined*: **South Korea**, Chuncheon, on *Eucommia ulmoides,* 7 Oct. 2003, H.D. Shin, **holotype** CBS H-20839, cultures ex-type CPC 10802 = CBS 131932, CPC 10803, 10804; Chuncheon, on *E. ulmoides,* 11 Oct. 2002, H.D. Shin, CBS H-20838, culture CPC 10047.

*Notes*: In the Korean material *C. eucommiae* occurred in mixed infections with a *Pseudocercospora* species (conidia 22–160 × 4–7 µm) that resembles *P. eucommiae* (conidia 15–75 × 2–4 um), which is known from this host in China (Guo & Hsieh 1995). The description of *C. eucommiae* reveals the genus *Cercospora* to be paraphyletic. Morphologically *C. eucommiae* is distinct from other species in *Cercospora* in that the conidial hila and conidiogenous scars are different (thickened along the rim, not darkened and planate), and conidia also tend to occur in unbranched chains, which is not typical of *Cercospora*. Interestingly, it does not cluster with *C. eremochloae*, which also forms conidia in chains (Crous *et al*. 2011a). Although this species is not part of *Cercospora s. str*., we name it in this genus until further taxa are collected and studied to resolve the status of this subclade in relation to *Cercospora s. str.*

***Miuraea*** Hara, Byochugai-Hoten (Manual of Pests and Diseases): 779. 1948.
*Synonyms*: See Braun (1995).

Foliicolous, phytopathogenic, causing leaf spots. *Mycelium* internal and external, consisting of septate, branched, hyaline to subhyaline hyphae. *Conidiophores* semi-macronematous, mononematous, reduced to a single conidiogenous cell, integrated on hyphae, with small lateral peg-like protuberances; conidiogenesis holoblastic, monoblastic, determinate, occasionally polyblastic, proliferation sympodial or percurrent; conidiogenous loci more or less truncate, inconspicuous, unthickened, not darkened. *Conidia* solitary, ellipsoid-ovoid, subcylindrical-vermiform, obclavate, subclavate, somewhat asymmetrical, euseptate, transversely pluriseptate to muriformly septate, hyaline to faintly pigmented, thin-walled; hila truncate to somewhat convex, unthickened, not darkened (adapted from Braun 1995).

*Type species*: *Miuraea degenerans* (Syd. & P. Syd.) Hara, Byochugai-Hoten (Manual of Pests and Diseases): 260. 1948.

*Notes*: Morphologically *Miuraea* is intermediate between *Pseudocercospora* and *Pseudocercosporella*, which explains its phylogenetic position in this clade (Fig. 4). It differs from *Pseudocercosporella* in having superficial mycelium, and very broad, muriformly septate conidia.

***Miuraea persicae*** (Sacc.) Hara, Byochugai-Hoten (Manual of pests and diseases): 224. 1948. Fig. 13.
*Basionym*: *Cercospora persicae* Sacc., Hedwigia 15: 119. 1876.
*Teleomorph*: "*Mycosphaerella" pruni-persicae* Deighton, Trans. Brit. Mycol. Soc. 50: 328. 1967.

*Specimens examined*: **South Korea**, Chuncheon, *Prunus persica,* 11 Oct. 2002, H.D. Shin, CBS H-20841, culture CPC 10069; Chuncheon, 7 Oct. 2003, *P. armeniaca,* H.D. Shin, CBS H-20840, CPC 10828–10830.

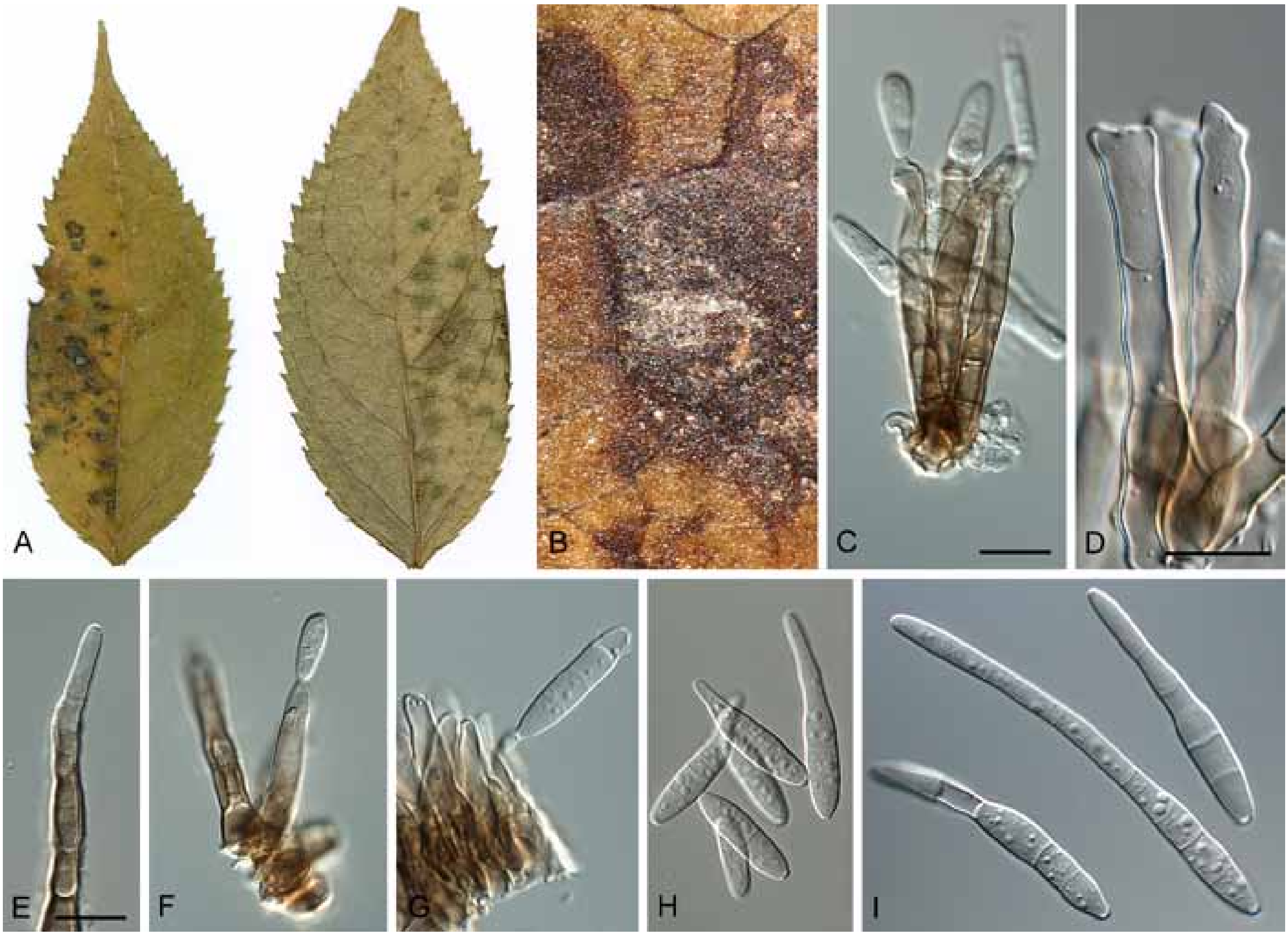


**Fig. 12.** *Cercospora eucommiae* (CPC 10047). A. Leaf spots on upper and lower leaf surface. B. Close-up of lesion. C–G. Fascicles with conidiophores and conidiogenous cells. H, I. Conidia. Scale bars = 10 µm.

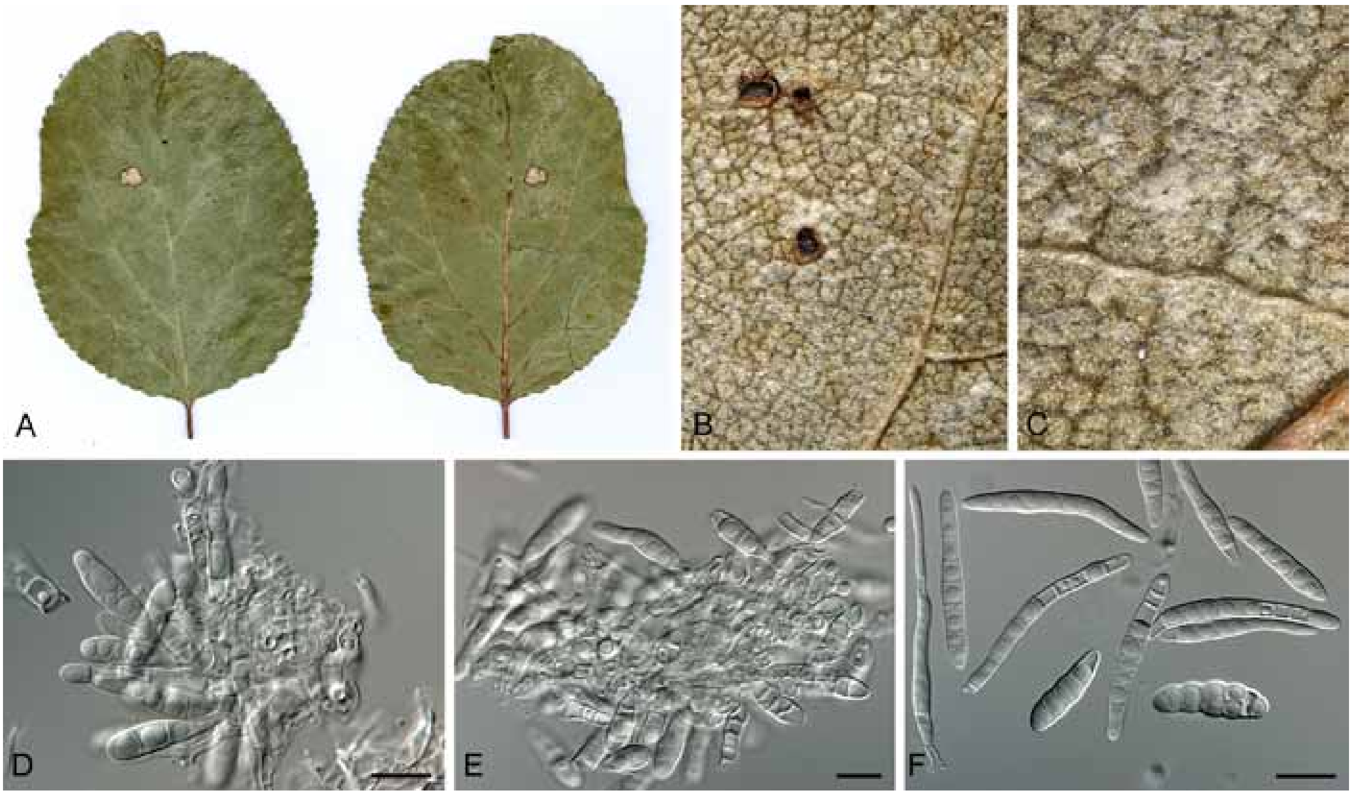


**Fig. 13.** *Miuraea persicae* (CPC 10069). A. Leaf spots on upper and lower leaf surface. B, C. Close-up of fruiting (rather inconspicuous). D, E. Fascicles with conidiophores and conidiogenous cells. F. Conidia (note septation). Scale bars = 10 µm.

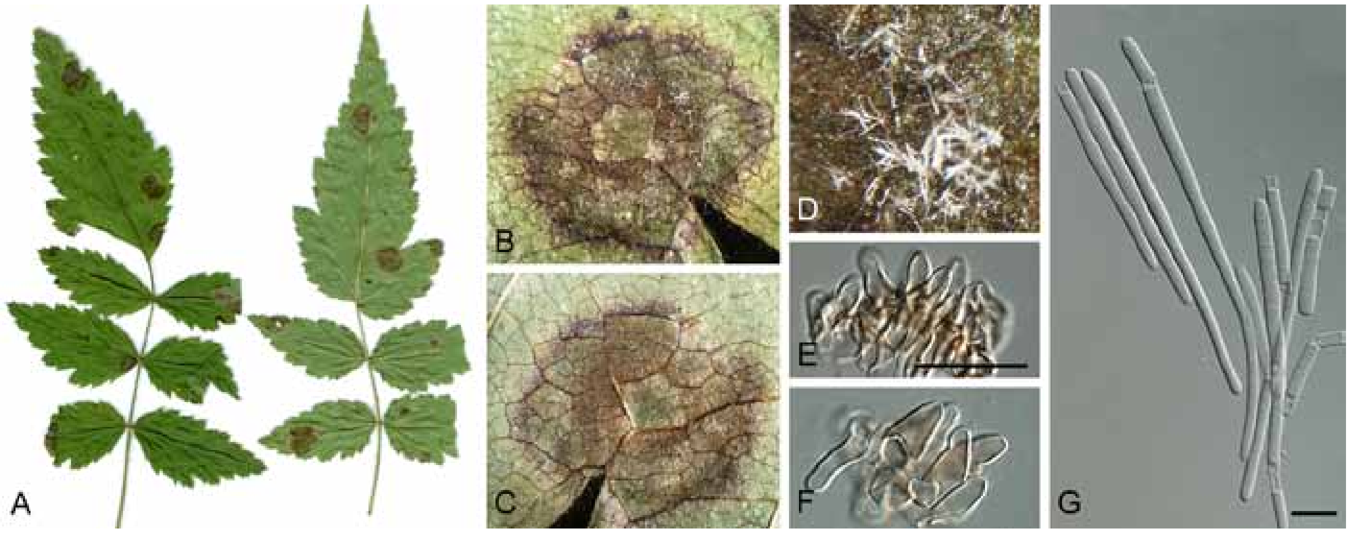


**Fig. 14.** *Pseudocercosporella arcuata* (CPC 10050). A. Leaf spots on upper and lower leaf surface. B–D. Close-up of lesions. E, F. Fascicles with conidiophores and conidiogenous cells. G. Conidia. Scale bars = 10 µm.

***Phloeospora*** Wallr., Flora Cryptogamica Germaniae 2: 176. 1833.

Phytopathogenic, commonly associated with leaf spots, occurring on leaves and fruit. *Mycelium* immersed, consisting of hyaline, septate, branched hyphae. *Conidiomata* acervular, subepidermal, erumpent; wall of thin-walled *textura angularis*, opening by means of an irregular split. *Conidiophores* reduced to conidiogenous cells. *Conidiogenous cells* hyaline, smooth, cylindrical, discrete, indeterminate, proliferating via percurrent proliferations, or sympodially, formed from the upper cells of the acervulus. *Conidia* solitary, hyaline, smooth, septate, cylindrical, apex subobtuse to obtuse, base truncate, straight to curved.

*Type species*: *Phloeospora ulmi* (Fr.) Wallr., Flora Cryptogamica Germaniae 2: 177. 1833.

*Specimens examined*: **Austria**, *Ulmus* sp., H.A. van der Aa, CBS 613.81; *Ulmus glabra,* G. Verkley, CBS 344.97. **Netherlands**, *Ulmus* sp., H.A. van der Aa, CBS 101564.

*Notes*: *Phloeospora* is distinguished from *Septoria* by the production of conidia in acervuli, whereas conidiomata in the latter genus are pycnidial. Both genera are known to be polyphyletic (Verkley & Priest 2000, Quaedvlieg *et al.* 2011) and require further revision.

***Pseudocercosporella*** Deighton, Mycol. Pap. 133: 38. 1973.

Foliicolous, phytopathogenic, causing discrete leaf spots. *Mycelium* mostly consistently internal, in some species with internal as well as external hyphae, hyaline to pale brown, septate, branched, smooth or almost so; *stromata* lacking or weakly to well-developed, substomatal to intraepidermal, usually colourless. *Conidiophores* solitary to fasciculate, emerging through stomata or erumpent through the cuticle, arising from inner hyphae or from stromata, sometimes formed as lateral branches of superficial hyphae, or aggregated in crustose to subglobose sporodochia; conidiophores simple, rarely branched, straight and subcylindrical to geniculate-sinuous, hyaline, occasionally faintly pigmented at the base, rarely throughout, one-celled or septate. *Conidiogenous cells* integrated, terminal, or reduced to conidiogenous cells, mono- to polyblastic, sympodial; conidiogenous loci inconspicuous, unthickened, neither darkened nor conspicuously refractive. *Conidia* formed singly, rarely in simple or branched chains, subcylindrical, filiform, somewhat obclavate, 1–multi-euseptate, hyaline, thin-walled, mostly smooth, apex obtuse to subacute, base subtruncate, hilum unthickened, neither darkened, nor refractive (adapted from Braun 1995).

*Type species*: *Pseudocercosporella ipomoeae* Deighton, Mycol. Pap. 133: 39. 1973. [= *P. bakeri* (Syd. & P. Syd.) Deighton, Mycol. Pap. 133: 41. 1973].

*Note*: *Pseudocercosporella* is polyphyletic (see Frank *et al.* 2010, Crous *et al.* 2011b) and new taxonomically useful morphological features will need to be determined to delineate all the genera presently accommodated in this clade.

***Pseudocercosporella arcuata*** S.K. Singh, P.N. Singh & Bhalla, Mycol. Res. 101: 542. 1997. Fig. 14.

*Specimen examined*: **South Korea**, Chuncheon, on *Rubus oldhamii* (≡ *R. pungens* var. *oldhamii*), 11 Oct. 2002, H.D. Shin, CBS H-20842, culture CPC 10050.

***Pseudocercosporella capsellae*** (Ellis & Everh.) Deighton, Mycol. Pap. 133: 42. 1973.
*Basionym*: *Cylindrosporium capsellae* Ellis & Everh., J. Mycol. 3(11): 130. 1887.
Additional synonyms in Braun (1995).
*Teleomorph*: "*Mycosphaerella" capsellae* A.J. Ingman & Sivan., Mycol. Res. 95: 1339. 1991.

*Specimen examined*: **South Korea**, Namyangju, *Raphanus sativus,* 22 Oct. 2007, H.D. Shin, CBS H-20843, cultures CPC 14773 = CBS 131896.

***Pseudocercosporella chaenomelis*** (Y. Suto) C. Nakash., Crous, U. Braun & H.D. Shin, **comb. nov.** MycoBank MB564818. Fig. 15.
*Basionym*: *Cercosporella chaenomelis* Y. Suto, Mycoscience 40: 513. 1999.
= *Mycosphaerella chaenomelis* Y. Suto, Mycoscience 40: 513. 1999.

*Leaf spots* amphigenous, irregular to angular, 5–20 mm diam, brown, delimited by leaf veins. *Mycelium* internal, hyaline, consisting of septate, branched, smooth, 1.5–2 µm diam hyphae. *Caespituli*

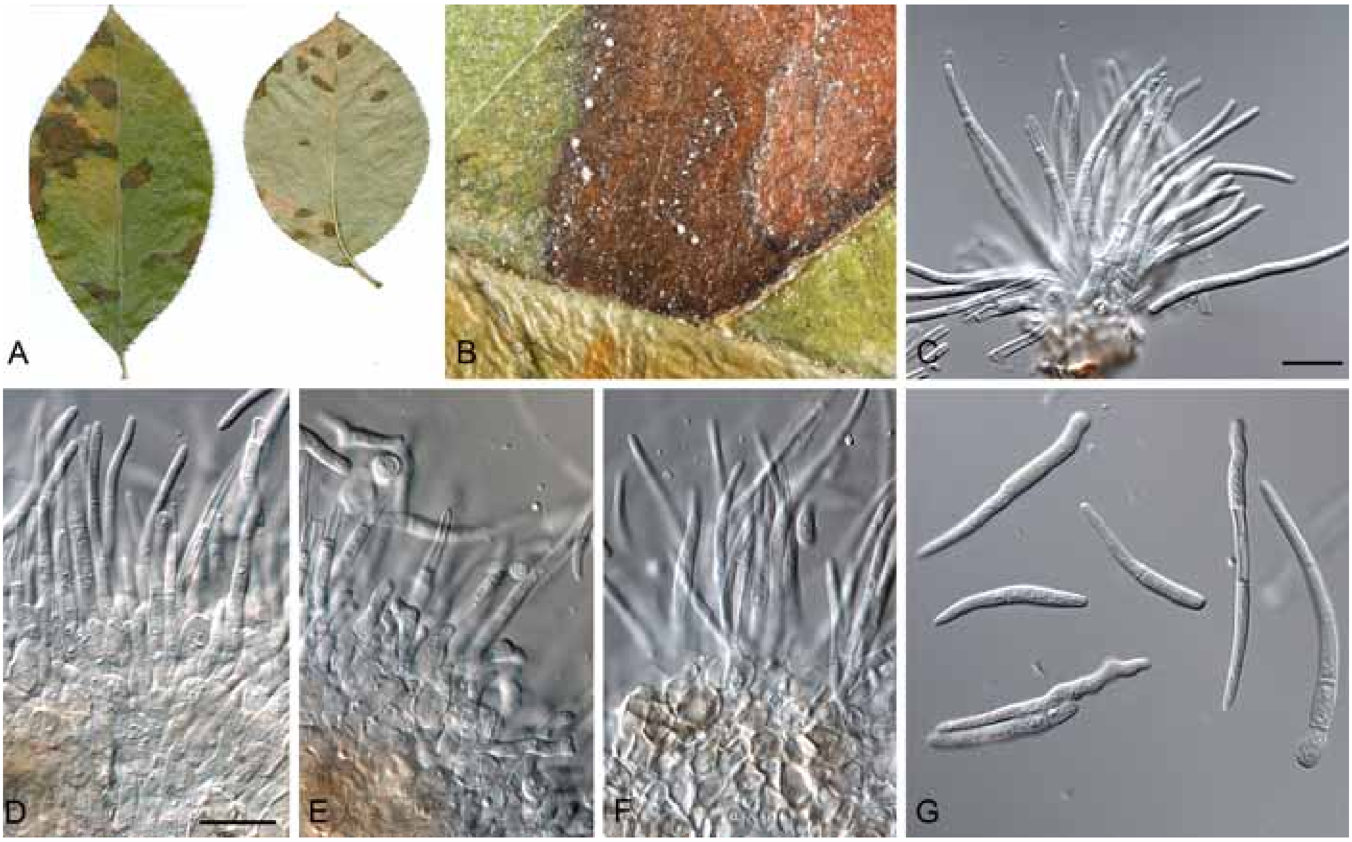


**Fig. 15.** *Pseudocercosporella chaenomelis* (CPC 14795). A. Leaf spots on upper and lower leaf surface. B. Close-up of leaf spot with white fruiting (rather inconspicuous). C–F. Fascicles with conidiophores and conidiogenous cells. G. Conidia. Scale bars = 10 µm.

fasciculate to sporodochial, white, predominantly epiphyllous, up to 200 µm diam and 120 µm high. *Conidiophores* aggregated in dense fascicles, arising from the upper cells of a hyaline stroma, up to 180 µm diam and 100 µm high; conidiophores hyaline, smooth, subcylindrical to ampulliform, straight to variously curved, unbranched, reduced to conidiogenous cells, 5–12 × 3–4 µm, proliferating sympodially at the apex. *Conidia* solitary, hyaline, smooth, guttulate to granular, subcylindrical to obclavate, apex subobtuse, base obconically truncate, straight to variously curved, 1–4-septate, (10–)30–38(–50) × (2–)2.5–3(–4) µm; hila unthickened, not darkened nor refractive, 1.5–2 µm diam; undergoing microcyclic conidiation on the host. Description based on CPC 14795.

*Culture characteristics*: Colonies after 1 mo at 24 ºC in the dark on MEA; Colonies erumpent, spreading, with aerial mycelium sparse to absent, margins smooth, lobate. Surface irregularly folded, with a prominent network of ridges; folds appearing cinnamon, with surrounding areas and border brown-vinaceous; reverse sepia to chestnut, reaching up to 35 mm diam.

*Specimens examined*: **Japan**, Shimane Pref., Matsue, on leaves of *Chaenomeles sinensis,* Y. Suto, 6 Nov. 1983, **holotype** SFH-917, in Herbarium of SPFRC; Mie Pref., Tsu, on leaves of *C. sinensis*, C. Nakashima, 29 Oct. 2011, **epitype designated here** TFM: FPH-8101, culture ex-epitype MUCC 1510 = CBS 132131. **South Korea**, Kimhae, *C. speciosa* (= *C. lagenaria*), 14 Nov. 2007, H.D. Shin, CBS H-20844, culture CPC 14795 = CBS 131897.

*Notes*: Suto (1999) established the connection between *Pseudocercosporella chaenomelis* (as *Cercosporella*) and *Mycosphaerella chaenomelis*, which is the cause of a serious leaf spot disease referred to as frosty mildew on *Chaenomeles sinensis* in Japan. The fungus was found to overwinter by means of ascomata on fallen leaves, which provided the primary inoculum for new infections (April to June). Since the disease was previously known in Japan to be caused by a species of *Cercosporella*, Suto (1999) chose the latter genus to accommodate the anamorph. The hyaline conidia with unthickened conidial hila indicate that the fungus is better placed in *Pseudocercosporella*, and hence a new combination is proposed. Based on DNA sequence data from the ITS and ACT gene regions, strains from Japan and Korea appear identical (unpubl. data).

*Pseudocercosporella chaenomelis* occurs in mixed infections with *Pseudocercospora cydoniae*. *Pseudocercosporella chaenomelis* is morphologically comparable only with *Ps. gei*, known on *Geum* spp. in North America and the Far East of Russia (Braun 1995). The latter species differs in having smaller stromata (20–45 µm diam) and much longer filiform-acicular conidia, 20–120 × 1–3(–4) µm (Braun 1995). *Pseudocercosporella crataegi* on *Crataegus* spp. in North America is distinct, forming superficial hyphae with solitary conidiophores, and its much smaller stromata and much longer conidia, and *Ps. potentillae* on *Potentilla* sp. in Russia also differs by having very long conidia (Braun 1995).

***Pseudocercosporella koreana*** Crous, U. Braun & H.D. Shin, **sp. nov.** MycoBank MB564819. Fig. 16.

*Etymology*: Name derived from the country where it was collected.

*Leaf spots* amphigenous, indistinct, irregular, chlorotic, up to 6 mm diam. *Mycelium* internal, hyaline, consisting of septate, branched, smooth, 1.5–2.5 µm diam hyphae. *Caespituli* fasciculate, white, amphigenous, up to 60 µm diam and 90 µm high. *Conidiophores* aggregated in dense fascicles, on the upper cells of a pale brown to hyaline, usually substomatal stroma, up to 45 µm diam and

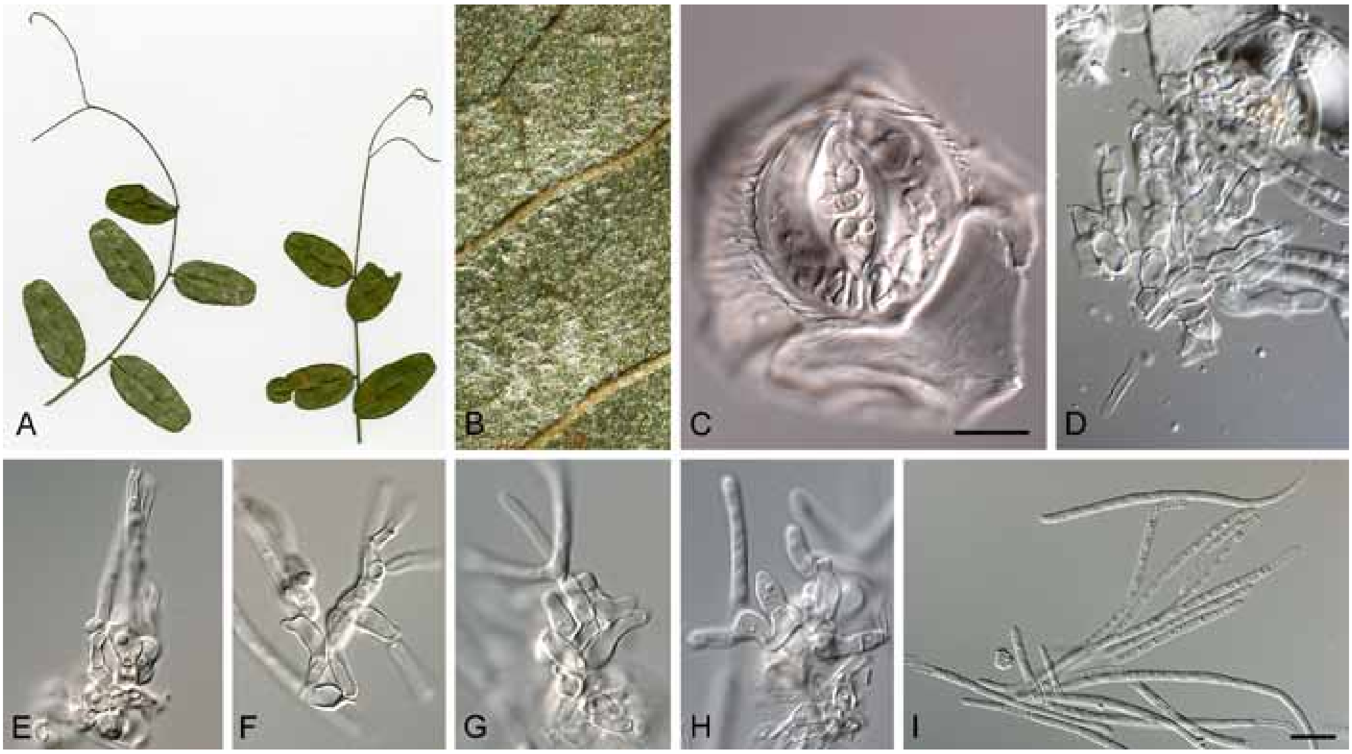


**Fig. 16.** *Pseudocercosporella koreana* (CPC 11414). A. Leaf spots on upper and lower leaf surface. B. Close-up of leaf spot with white fruiting. C. Substomatal stroma. D–H. Fascicles with conidiophores and conidiogenous cells. I. Conidia. Scale bars = 10 µm.

20 µm high; conidiophores hyaline or pale brown at the base, smooth, 0–2-septate, but frequently reduced to conidiogenous cells, subcylindrical, straight to variously curved or geniculate-sinuous, unbranched or branched below, 15–25 × 4–5 µm, proliferating sympodially at the apex. *Conidia* solitary, hyaline, smooth, prominently guttulate, narrowly obclavate, apex obtuse to subobtuse, base obconically subtruncate, straight to variously curved, 3–13-septate, (40–)60–80(–130) × (2.5–)3(–4) µm; hila unthickened, neither darkened nor refractive, 2 µm diam.

*Culture characteristics*: Colonies after 2 wk at 24 ºC in the dark on MEA; surface folded with a prominent network of ridges, erumpent, spreading, with sparse aerial mycelium, and smooth, lobate margins. Surface olivaceous-grey to iron-grey; reverse iron-grey to greenish black. Colonies reaching 6 mm diam.

*Specimen examined*: **South Korea**, Hoengseong, on *Vicia amurensis,* 4 Aug. 2004, H.D. Shin, **holotype** CBS H-20845, **isotype** HAL 1850 F, culture ex-holotype CPC 11414.

*Notes*: Braun (1995) listed several species of *Pseudocercosporella* on *Fabaceae*. None of these occur on *Vicia*, and only one, *Ps. tephrosiae* (on *Tephrosia*, Africa), has conidia of similar length (40–110 × 3–4.5 µm), although they are wider, subcylindrical-acicular, and have 3–6 septa.

***Pseudocercosporella oxalidis*** (Goh & W.H. Hsieh) U. Braun, Nova Hedwigia 55: 218. 1992.
*Basionym*: *Pseudocercospora oxalidis* Goh & W.H. Hsieh, Bot. Bull. Acad. Sinica 30: 127. 1989.

*Specimen examined*: **Taiwan**, Taipei, Wulai, on living leaves of *Oxalis debilis* (= *O. corymbosa*), R. Kirschner, 2258, 22 Feb. 2005, culture CBS 118758.

***Septoria*** Sacc., Syll. Fung. 3: 474. 1884.
*Synonyms*: See Sutton (1980).

Phytopathogenic and endophytic, occurring on leaves, fruit and stems, causing discrete lesions. *Conidiomata* pycnidial, immersed, separate or aggregated, globose, papillate or not, brown, with a thin wall of brown *textura angularis*. *Ostiole* single, circular, central, sometimes papillate. *Conidiophores* reduced to conidiogenous cells. *Conidiogenous cells* hyaline, smooth, ampulliform, doliiform or lageniform to short cylindrical, holoblastic, determinate or indeterminate, proliferating sympodially and/or percurrently; conidiogenous loci unthickened. *Conidia* solitary, hyaline, multiseptate, guttulate or not, thin-walled, filiform, smooth, continuous or constricted at the septa; hila unthickened.

*Type species*: *Septoria cytisi* Desm. Ann. Sci. Nat., Bot., Sér. 3, 8: 24. 1847.

*Note*: *Septoria* is polyphyletic (Quaedvlieg *et al*. 2011).

## Clade 11: *Sonderhenia*

***Sonderhenia*** H.J. Swart & J. Walker, Trans. Brit. Mycol. Soc. 90: 640. 1988.

Foliicolous, phytopathogenic, causing discrete leaf spots. *Leaf spots* amphigenous, round to confluent and irregular, surrounded by a purple border when young, which becomes dark red to brown and raised with age. *Ascomata* pseudothecial, amphigenous, on one side of each lesion, often 1–3, intermingled with conidiomata, immersed, black, punctiform, globose to subglobose; apical ostiole substomatal; wall olive-brown, of 3–4 layers of *textura angularis*, subhymenium of 1–2 layers of colorless cells. *Asci*

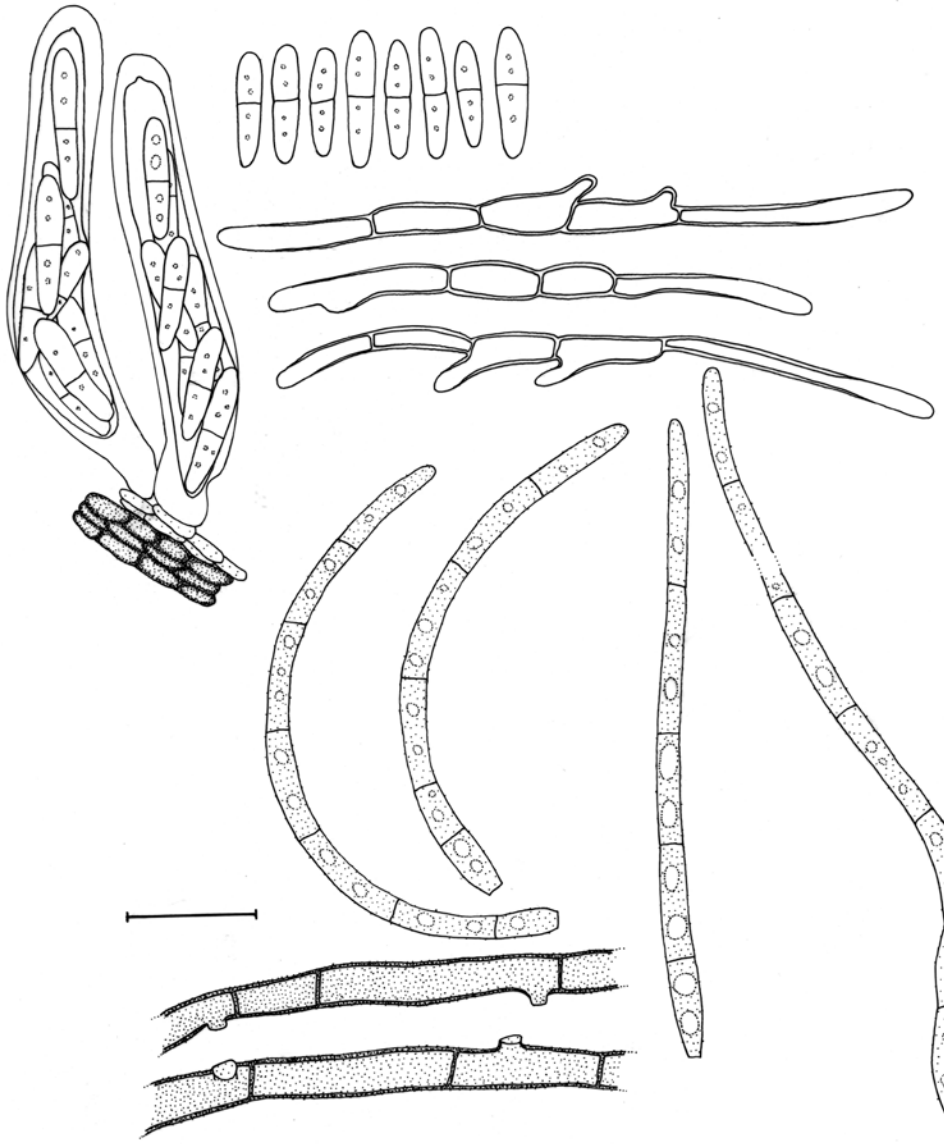

**Fig. 17.** *Pallidocercospora heimii* (CPC 1395). Asci, ascospores, germinating ascospores (after 24 h on malt extract agar), hyphae with conidiogenous loci, and conidia. Scale bar = 10 µm.

fasciculate, bitunicate, subsessile, 8-spored, ovoid to obclavate, straight to incurved. *Ascospores* 2–3-seriate, hyaline, guttulate, straight or slightly curved, fusiform, 1-septate, widest just above median septum, slightly constricted at septum. *Conidiomata* pycnidial, amphigenous, subepidermal with central non-projecting ostiole, scattered, black, globose; wall of 2–3 layers of brown cells. *Conidiogenous cells* minute, olivaceous, proliferating enteroblastically and percurrently, lining the inner pycnidial wall layer. *Conidia* ellipsoid to cylindrical or ovoid, straight or bent, brown, 3-distoseptate, not constricted, verruculose, apex obtuse, base truncate with marginal frill (adapted from Crous 1998).

*Type species*: *Sonderhenia eucalyptorum* H.J. Swart & J. Walker, Trans. Brit. Mycol. Soc. 90: 640. 1988.

*Notes*: *Sonderhenia* includes taxa with mycosphaerella-like teleomorphs and pycnidial anamorphs that form brown, transversely distoseptate conidia on brown, percurrently proliferating conidiogenous cells. Only two species, *S. eucalypticola* and *S. eucalyptorum* are known.

## Clade 12: *Pallidocercospora*, *Scolecostigmina, Trochophora* and pseudocercospora-like

***Pallidocercospora*** Crous, **gen. nov.** MycoBank MB564820. Fig. 17.

*Etymology*: The name reflects the pale brown cercospora-like conidia in this genus.

Foliicolous, phytopathogenic, causing discrete leaf spots. *Ascomata* single, black, immersed, globose, glabrous; wall of 3–4 layers of medium brown *textura angularis*. *Asci* fasciculate, bitunicate, aparaphysate, subsessile, 8-spored, ellipsoid to obclavate or cylindrical, straight or curved, numerous. *Ascospores* 2–multi-seriate, oblique, overlapping, straight ellipsoidal to obovoid, colourless, smooth, 1-septate. *Mycelium* predominantly immersed, consisting of olivaceous-brown hyphae, smooth, branched, septate, 2–4 µm diam. *Conidiophores in vivo* fasciculate, or occurring singly on superficial mycelium as lateral projections, unbranched or branched, septate, cylindrical, straight to geniculate–sinuous, olivaceous-brown. *Conidiogenous cells* integrated, terminal, cylindrical, straight to geniculate-sinuous, olivaceous-brown, proliferating sympodially or percurrently; conidiogenous loci unthickened, not darker than the surrounding conidiogenous cell. *Conidia* solitary, straight to irregularly curved, guttulate, pale olivaceous to olivaceous-brown, subcylindrical to narrowly obclavate, multiseptate; hila neither thickened nor darkened.

*Type species*: *Pallidocercospora heimii* (Crous) Crous, comb. nov.

*Notes*: Species of *Pallidocercospora* have pale olivaceous, smooth conidia (generally referred to as the *Mycosphaerella heimii* complex; Crous *et al.* 2004c), and form red crystals when cultivated in agar (on WA, SNA, PDA, MEA), which distinguishes them from *Pseudocercospora*. *Pseudocercospora* has several synonyms (see Seifert *et al*. 2011). *Cercoseptoria* with its mostly acicular conidia, was correctly treated as synonym of *Pseudocercospora* by Deighton (1976). Other synonyms include *Ancylospora* Sawada (based on *A. costi*), now treated as *P. costina*; *Cercocladospora* G.P. Agarwal & S.M. Singh (based on *C. adinae*, *nom. non rite publ.*), now treated as *P. adinicola*; and *Helicominia* L.S. Olive (based on *H. caperonia*), now *P. caperoniae*, and *Pantospora* Cif. (based on *P. guazumae*) (see Ellis 1971, Deighton 1976), the muriformly septate conidia of the latter are similar to those of *Pseudocercospora pseudostigmina-platani*, though *Pantospora* has been shown to be a genus in its own right (Minnis *et al.* 2011).

***Pallidocercospora acaciigena*** (Crous & M.J. Wingf.) Crous & M.J. Wingf., **comb. nov.** MycoBank MB564821.
*Basionym*: *Pseudocercospora acaciigena* Crous & M.J. Wingf., Stud. Mycol. 50: 464. 2004.
*Teleomorph*: "*Mycosphaerella" acaciigena* Crous & M.J. Wingf., Stud. Mycol. 50: 463. 2004.

*Specimen examined*: **Venezuela**, Acarigua, on leaves of *Acacia mangium*, May 2000, M.J. Wingfield, CBS H-9873, **holotype** of *M. acaciigena* and *P. acaciigena*; cultures ex-type CBS 115432, 112515, 112516 = CPC 3836–3838.

***Pallidocercospora crystallina*** (Crous & M.J. Wingf.) Crous & M.J. Wingf., **comb. nov.** MycoBank MB564822.
*Basionym*: *Pseudocercospora crystallina* Crous & M.J. Wingf., Mycologia 88: 451. 1996.
*Teleomorph*: "*Mycosphaerella" crystallina* Crous & M.J. Wingf., Mycologia 88: 451. 1996.

*Specimens examined*: **South Africa**, Kwazula-Natal Province,Umvoti, on leaves of *Eucalyptus bicostata*, Oct. 1994, M.J. Wingfield (**holotypes** PREM 51922, teleomorph; PREM 51923, anamorph, cultures ex-type CPC 800–802); Kwazula-Natal Province, leaf litter of *E. grandis* × *camaldulensis*, Jun. 1995, M.J. Wingfield (PREM 51937, cultures CPC 1178–1180).

***Pallidocercospora heimii*** (Crous) Crous, **comb. nov.** MycoBank MB564823. Fig. 17.
*Basionym*: *Pseudocercospora heimii* Crous, S. African For. J. 172: 4. 1995.
*Teleomorph*: "*Mycosphaerella" heimii* Crous, S. African For. J. 172: 2. 1995.
≡ "*Mycosphaerella" heimii* Bouriquet, Encycl. Mycol. 12: 418. 1946, nom. nud.

*Specimens examined*: **Madagascar**, Moramanga, on leaves of *Eucalyptus* sp., Apr. 1994, P.W. Crous, PREM 51749, **holotype** of teleomorph; PREM 51748, **holotype** of anamorph, cultures ex-type CPC 760–761 = CBS 110682.

***Pallidocercospora heimioides*** (Crous & M.J. Wingf.) Crous & M.J. Wingf., **comb. nov.** MycoBank MB564824.
*Basionym*: *Pseudocercospora heimioides* Crous & M.J. Wingf., Can. J. Bot. 75: 787. 1997.
*Teleomorph*: "*Mycosphaerella" heimioides* Crous & M.J. Wingf., Can. J. Bot. 75: 787. 1997.

*Specimens examined*: **Indonesia**, N. Sumatra, Lake Toba area, leaves of *Eucalyptus* sp., Mar. 1996, M.J. Wingfield, **holotype** of teleomorph PREM 54966; **holotype** of anamorph PREM 54967; cultures ex-type CPC 1311, 1312 = CBS 111190).

***Pallidocercospora holualoana*** (Crous, Joanne E. Taylor & M.E. Palm) Crous, **comb. nov.** MycoBank MB564825.
*Basionym*: "*Mycosphaerella" holualoana* Crous, Joanne E. Taylor & M.E. Palm, Mycotaxon 78: 458. 2001.

*Specimen examined*: **USA**, Hawaii, Kona district, Holualoa, on a living leaf of *Leucospermum* sp., P.W. Crous & M.E. Palm, 17 Nov. 1998, **holotype** PREM 56926, cultures ex-type CPC 2126–2128).

***Pallidocercospora irregulariramosa*** (Crous & M.J. Wingf.) Crous & M.J. Wingf., **comb. nov.** MycoBank MB564826.
*Basionym*: *Pseudocercospora irregulariramosa* Crous & M.J. Wingf., Can. J. Bot. 75: 785. 1997.
*Teleomorph*: "*Mycosphaerella" irregulariramosa* Crous & M.J. Wingf., Can. J. Bot. 75: 785. 1997.

*Specimens examined*: **South Africa**, Northern Province, Tzaneen, on leaves of *Eucalyptus saligna*, Mar. 1996, M.J. Wingfield, **holotype** of teleomorph PREM 54964; **holotype** of anamorph PREM 54965; cultures ex-type CPC 1360 = CBS 114777).

***Pallidocercospora konae*** (Crous, Joanne E. Taylor & M.E. Palm) Crous, **comb. nov.** MycoBank MB564827.
*Basionym*: "*Mycosphaerella" konae* Crous, Joanne E. Taylor & M.E. Palm, Mycotaxon 78: 459. 2001.

*Specimen examined*: **USA**, Hawaii, Kona district, Holualoa, on a living leaf on *Leucadendron* cv. Safari Sunset, 17 Nov. 1998, P.W. Crous & M.E. Palm, **holotype** PREM 56921; ex-type cultures CPC 2123–2125.

***Scolecostigmina*** U. Braun, N. Z. J. Bot. 37: 323. 1999. Fig. 18.

Foliicolous, phytopathogenic, associated with leaf spots. *Mycelium* immersed, consisting of septate, branched, pigmented hyphae. *Sporodochia* immersed to erumpent; stromata subglobose to applanate, composed of brown, angular to subglobose cells. *Conidiophores* numerous, densely aggregated, arising from stroma, subcylindrical or somewhat tapered towards the apex, occasionally ampulliform, continuous or septate, pigmented, wall somewhat thickened, usually verruculose; conidiogenous cells integrated, terminal or at times conidiophores reduced to conidiogenous cells, holoblastic, proliferating percurrently via conspicuous annellations. *Conidia* solitary, scolecosporous, usually subcylindrical-obclavate, transversely pluriseptate, occasionally with few longitudinal or oblique septa, euseptate, rarely with few intermixed distosepta, thick-walled, pigmented, dark, smooth to verrucose, apex obtuse to subacute, base truncate or obconically truncate; secession schizolytic (adapted from Braun *et al.* 1999).

*Type species*: *Scolecostigmina mangiferae* (Koord.) U. Braun & Mouch., N. Z. J. Bot. 37: 323. 1999.

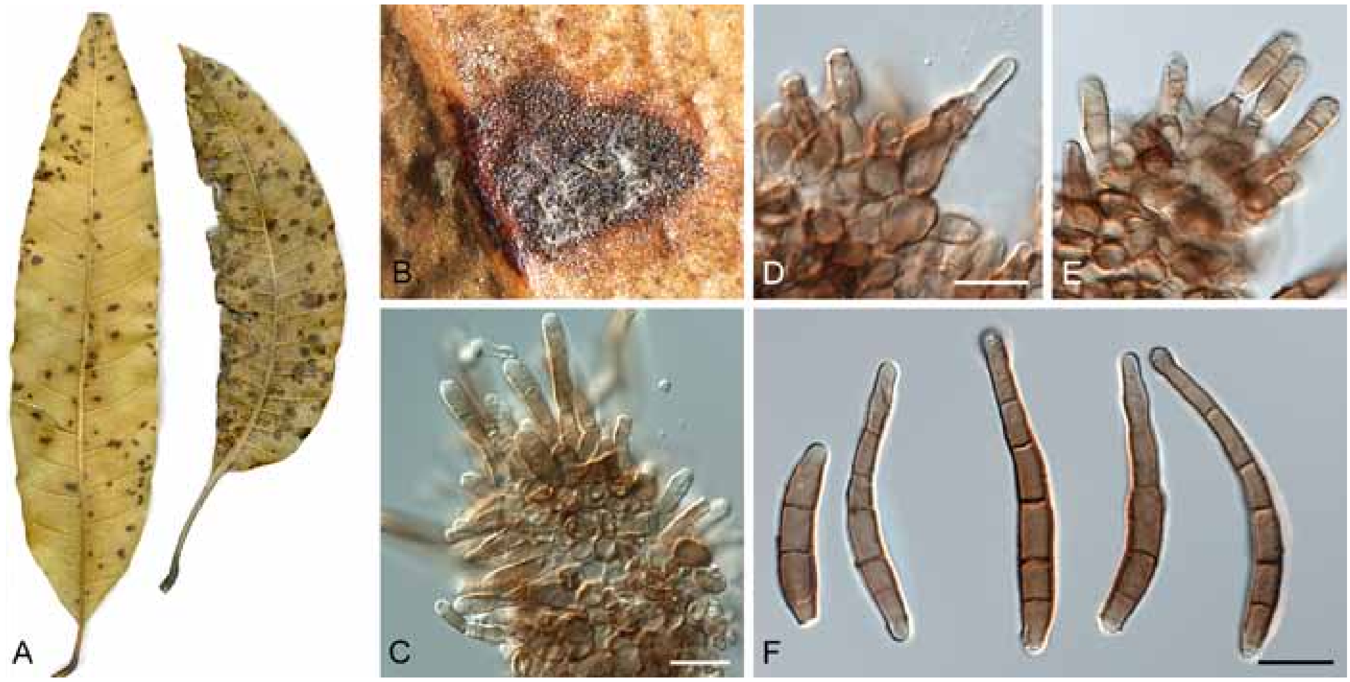


**Fig. 18.** *Scolecostigmina mangiferae* (CBS 125467). A. Leaf spots on upper and lower leaf surface. B. Close-up of leaf spot with fruiting. C–E. Fascicles with conidiophores and conidiogenous cells (note rough percurrent proliferations). F. Conidia. Scale bars = 10 µm.


**Fig. 19.** *Trochophora simplex* (CBS 124744). A. Leaf spots on upper and lower leaf surface. B, C. Close-up of leaf spot with fruiting. D–G. Fascicles with conidiophores and conidiogenous cells. H, I. Conidia. Scale bars = 10 µm.

*Specimen examined*: **Australia**, Queensland, Mareeba, S16º58'75.5" E145º20'60.8", leaves of *Mangifera indica*, 10 Aug. 2009, P.W. Crous & R.G. Shivas, CBS H-20846, culture CPC 17352, 17351 = CBS 125467.

## ***Trochophora*** R.T. Moore, Mycologia 47: 90. 1955. Fig. 19.

Foliicolous, but pathogenicity unproven. *Colonies* hypophyllous, medium to dark brown, consisting of numerous synnemata. *Stroma* absent, but with a superficial network of hyphae linking the various synnemata. *Conidiophores* synnematous, mostly unbranched and straight, or with 1–2 short branches, straight or curved, cylindrical, individual conidiophores tightly aggregated, but separating near the apex, pale to medium brown, smooth. *Conidiogenous cells* polyblastic, integrated, terminal, determinate to sympodial, with visible unthickened scar, clavate. *Conidia* solitary, terminal or lateral on conidiogenous cells, prominently curved to helicoid, pale to medium brown, smooth, transversely euseptate with a darkened, thickened band at the septa (adapted from Crous *et al*. 2009a).

*Type species*: *Trochophora simplex* (Petch) R.T. Moore, Mycologia, 47: 90. 1955.

*Specimens examined*: **Japan**, Shimane, on *Daphniphyllum teijsmannii,* 26 April 2008, C. Nakashima & I. Araki, MUMH 11134, culture MUCC 952. **South Korea**, Jeju, Halla arboretum, on *D. macropodum,* 29 Oct. 2005, H.D. Shin, CBS H-20847, culture CBS 124744.

*Notes*: Other pseudocercospora-like species found in this clade are *P. colombiensis* (foliar pathogen of *Eucalyptus*; Crous 1998), and *P. thailandica* (foliar pathogen of *Acacia*; Crous *et al.* 2004d), both also having mycosphaerella-like teleomorphs. Morphologically, these taxa appear typical members of *Pseudocercospora s. str.* so it would be difficult to identify these as different from *Pseudocercospora* without the aid of DNA sequence comparisons.

## Clade 13: Passalora-like

*Notes*: This clade is represented by *Passalora eucalypti*, which was originally described as a leaf spot pathogen of *Eucalyptus saligna* in Brazil (Crous 1998, Crous & Braun 2003). Recently, a second species was found to belong to this clade, namely *Passalora leptophlebiae,* which was described from *Eucalyptus leptophlebia* leaves collected in Brazil (Crous *et al.* 2011a). Both species are charaterised by fasciculate conidiophores and catenate, pale brown conidia, with thickened, darkened and refractive scars and hila.

## Clade 14: *Pseudocercospora s. str.*

***Pseudocercospora*** Speg., Anales Mus. Nac. Hist. Nat. Buenos Aires, Ser. 3, 20: 437. 1910.

Foliicolous, chiefly phytopathogenic, but also endophytic; commonly associated with leaf spots, but also occurring on fruit. *Mycelium* internal and external, consisting of smooth, septate, subhyaline to brown, branched hyphae. *Stroma* absent to well-developed. *Conidiophores in vivo* arranged in loose to dense fascicles, sometimes forming distinct synnemata or sporodochia, emerging through stomata or erumpent through the cuticle, often arising from substomatal or subcuticular to intraepidermal stromata, or occurring singly on superficial hyphae, short to long, septate or continuous, *i.e.* conidiophores may be reduced to conidiogenous cells, simple to branched and straight to geniculate-sinuous, pale to dark brown, smooth to finely verruculose. *Conidiogenous cells* integrated, terminal, occasionally intercalary, polyblastic, sympodial, or monoblastic, proliferating percurrently via inconspicuous or darkened, irregular annellations, at times denticulate, pale to dark brown; scars inconspicous, or only thickened along the rim, or flat, and slightly thickened and darkened, but never pronounced. *Conidia* solitary, rarely in simple chains, subhyaline, olivaceous, pale to dark brown, usually scolecosporous, *i.e.* obclavate–cylindrical, filiform, acicular, and transversely plurieuseptate, occasionally also with oblique to longitudinal septa, conidia rarely amero- to phragmosporous, short subcylindrical or ellipsoidal-ovoid, aseptate or only with few septa, apex subacute to obtuse, base obconically truncate to truncate, or bluntly rounded, with or without a minute marginal frill, straight to curved, rarely sigmoid, smooth to finely verruculose; hila usually unthickened, not darkened, at most somewhat refractive, occasionally slightly thickened along the rim, or rarely flat, and slightly thickened and darkened, but never pronounced.

*Type species*: *P. vitis* (Lév.) Speg., Anales Mus. Nac. Hist. Nat. Buenos Aires, Ser. 3, 20: 438. 1910.

*Specimens examined*: **South Korea**, Namyangju, on *Vitis vinifera*, 30 Sep. 2004, H.D. Shin, CBS H-20848, CPC 11595 = CBS 132012; *V. vinifera*, 1 Oct. 2007, H.D. Shin, CPC 14661 = CBS 132112.

***Pseudocercospora abelmoschi*** (Ellis & Everh.) Deighton, Mycol. Pap. 140: 138. 1976. Fig. 20.
*Basionym*: *Cercospora abelmoschi* Ellis & Everh., J. Inst. Jamaica 1: 347. 1893.

= *Cercospora hibisci* Tracy & Earle, Bull. Torrey Bot. Club 22: 179. 1895.
= *Cercospora hibisci-manihotis* Henn., Hedwigia 43: 146. 1904.

*Specimen examined*: **South Korea**, Suwon, on *Hibiscus syriacus*, 2 Oct. 2007, H.D. Shin, CBS H-20849, CPC 14478 = CBS 132103.

***Pseudocercospora ampelopsis*** Crous, U. Braun & H.D. Shin, **sp. nov.** MycoBank MB564828. Fig. 21.

*Etymology*: Name derived from the host *Ampelopsis,* from which it was collected.

*Leaf spots* amphigenous, irregular to subcircular, 2–8 mm diam, dark brown on upper surface, dull brownish green on lower surface. *Mycelium* internal and external, pale brown to brown, consisting of septate, branched, smooth, 1.5–4 µm diam hyphae, anastomosing on surface. *Caespituli* fasciculate, brown, amphigenous, emerging through stomata (but stromata lacking). *Conidiophores* aggregated in loose fascicles, or solitary, arising from superficial mycelium, medium to dark brown, smooth to finely verruculose, 3–6-septate, subcylindrical, straight to variously curved, unbranched, 20–80 × (2.5–)3–5(–6) µm. *Conidiogenous cells* terminal, unbranched, brown, finely verruculose, tapering to flat-tipped apical loci, proliferating sympodially, 10–15 × 4–5 µm. *Conidia* solitary, dark brown, finely verruculose, guttulate, obclavate-cylindrical, apex obtuse, base obconically subtruncate, straight to gently curved, 3–12-septate, (35–)40–90(–110) × 3–5(–6) µm; hila unthickened, neither darkened nor refractive, 2 µm diam.

*Culture characteristics*: Colonies after 2 wk at 24 ºC in the dark on MEA; surface folded, erumpent, spreading, with sparse aerial mycelium, and smooth, lobate margins. Surface olivaceous-grey; reverse iron-grey. Colonies reaching 7 mm diam.

*Specimen examined*: **South Korea**, Hongcheon, on *Ampelopsis glandulosa* var. *heterophylla,* 24 Oct. 2004, H.D. Shin, **holotype** CBS H-20850, **isotype** HAL 1866 F, culture ex-type CPC 11680 = CBS 131583.

*Notes*: *Pseudocercospora brachypus*, which also occurs on *Ampelopsis*, has much shorter and narrower conidia, 25–60 × 2–3.5 µm (Guo & Hsieh 1995). *Pseudocercospora ampelopsis* is morphologically close to *P. riachuelii* var. *horiana* on *Ampelocissus*,

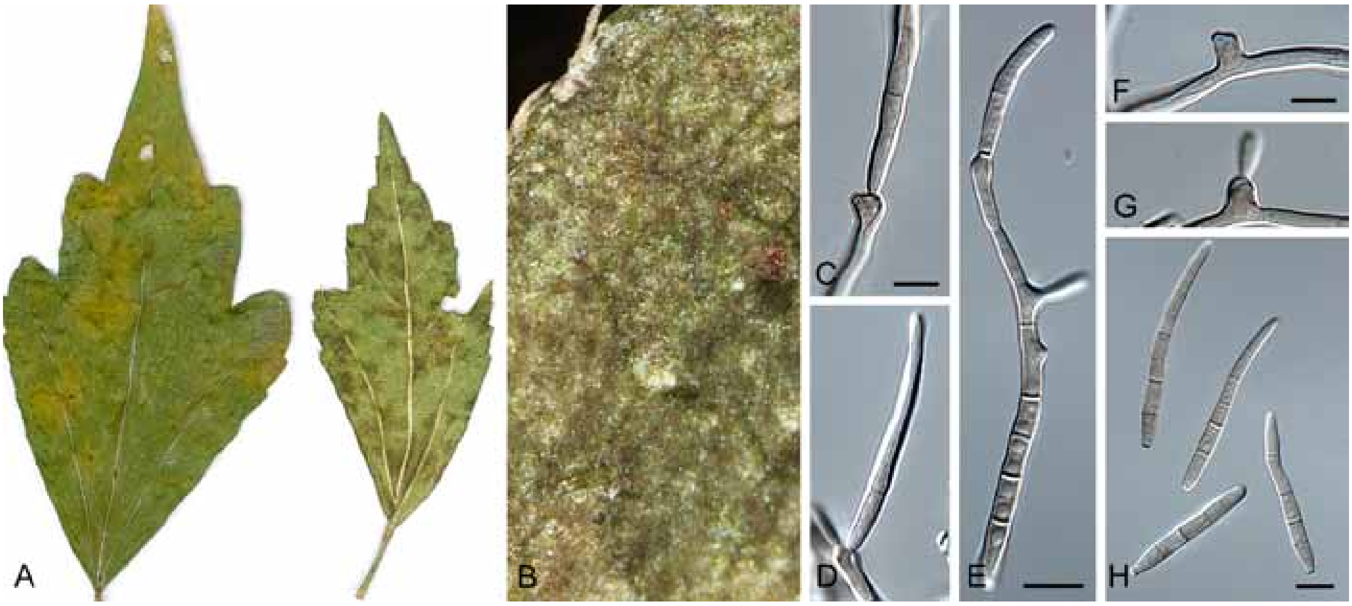


**Fig. 20.** *Pseudocercospora abelmoschi* (CPC 14478). A. Leaf spots on upper and lower leaf surface. B. Close-up of leaf spot with fruiting. C–G. Hyphae giving rise to conidiogenous cells and conidia. H. Conidia. Scale bars = 10 µm.

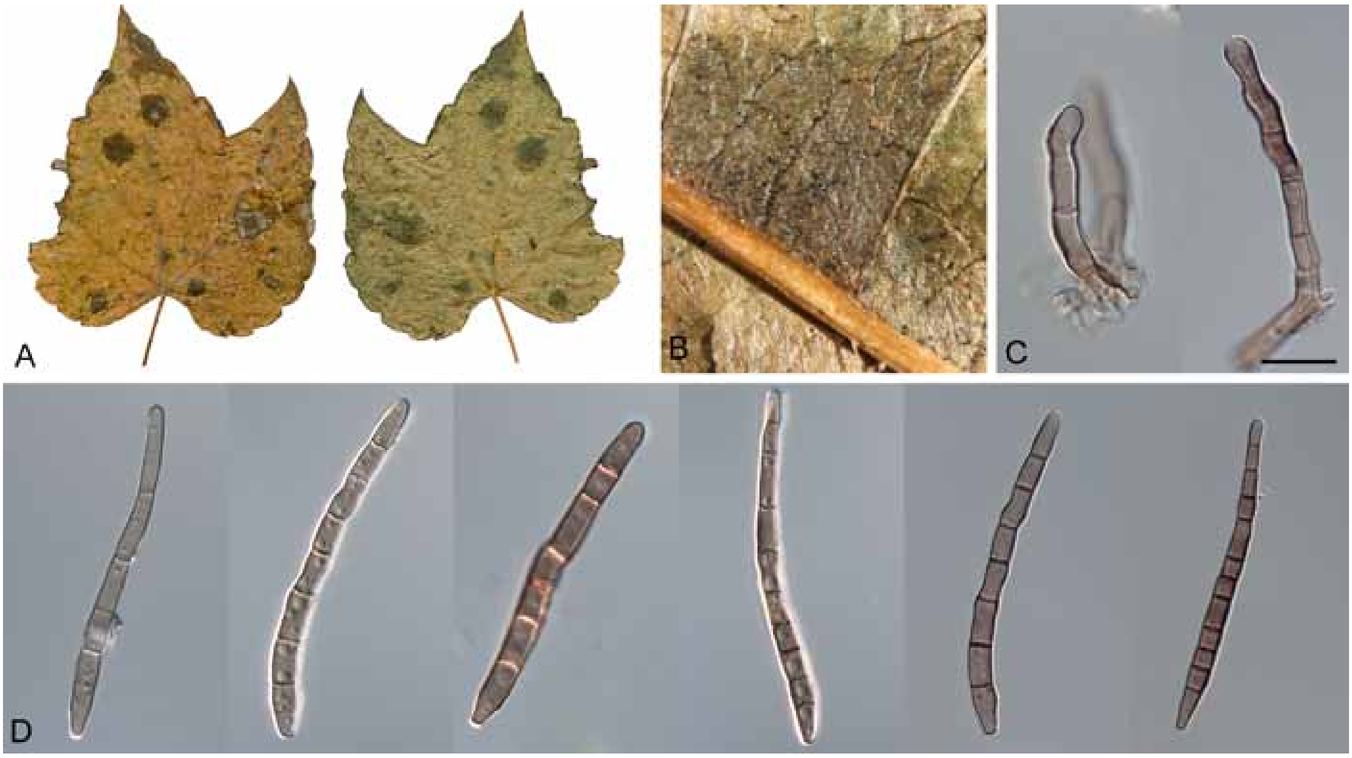


**Fig. 21.** *Pseudocercospora ampelopsis* (CPC 11680). A. Leaf spots on upper and lower leaf surface. B. Close-up of leaf spot with fruiting. C. Conidiophores and conidiogenous cells. D. Conidia. Scale bar = 10 µm.

*Cissus* and *Parthenocissus* species (Crous & Braun 2003). The two are similar in that conidiophores are solitary and form in fascicles and arise from superficial hyphae, and conidia of the two taxa are similar in size. *Pseudocercospora ampelopsis* differs in having much longer pluriseptate conidiophores whereas those of *P. riachuelii* var. *horiana* are much shorter and 0–1-septate.

***Pseudocercospora angolensis*** (T. Carvalho & O. Mendes) Crous & U. Braun, Sydowia 55: 301. 2003.

*Basionym*: *Cercospora angolensis* T. Carvalho & O. Mendes, Bol. Soc. Brot. 27: 201. 1953.

≡ *Phaeoramularia angolensis* (T. Carvalho & O. Mendes) P.M. Kirk, Mycopathologia 94: 177. 1986.

≡ *Pseudophaeoramularia angolensis* (T. Carvalho & O. Mendes) U. Braun, Cryptog. Mycol. 20: 171. 1999.

*Specimens examined*: **Angola**, Mozambique Province, on leaves of *Citrus* × *aurantium* (= × *sinensis*), Dec. 1951, Carvalho & O. Mendes, BPI 432660, BPI 442839 (**paratypes**), BPI 442837 (**holotype**), IMI 56597 (**isotype**). **Camaroon**, Yaoundé, on leaves of *C.* × *aurantium*, 17 Mar. 1978, E. Milla, IMI 252792. **Ethiopia**, on leaves of *Citrus* sp., IMI 361170. **Kenya**, on leaves of *C.* × *aurantium*, 15 Nov. 1991, A. Seif W3753, IMI 351626. **Uganda**, on leaves of *C.* × *aurantium*, 14 Jun. 1991, W.T.H. Peregrine, IMI 384297. **West Africa**, intercepted at San Pedro, California, USA, on leaves of *Citrus* sp., 2 Oct. 1953, L.A. Hart, BPI 432661, BPI 432659. **Zambia**, on leaves of *Citrus* sp., 18 Jun. 1973, R.H. Raemakers 7837, IMI 176562; Chilanga, on leaves of *C.* × *aurantium*, 28 Sep. 1983, D.M. Naik, IMI 280618; Chilanga, on leaves of *Citrus* sp., 18 Jul. 1975, B.K. Patel, IMI 196889; Lusaka, on leaves of *Citrus* sp., 17 June 1977, I. Javaid, IMI 214501. **Zimbabwe**,

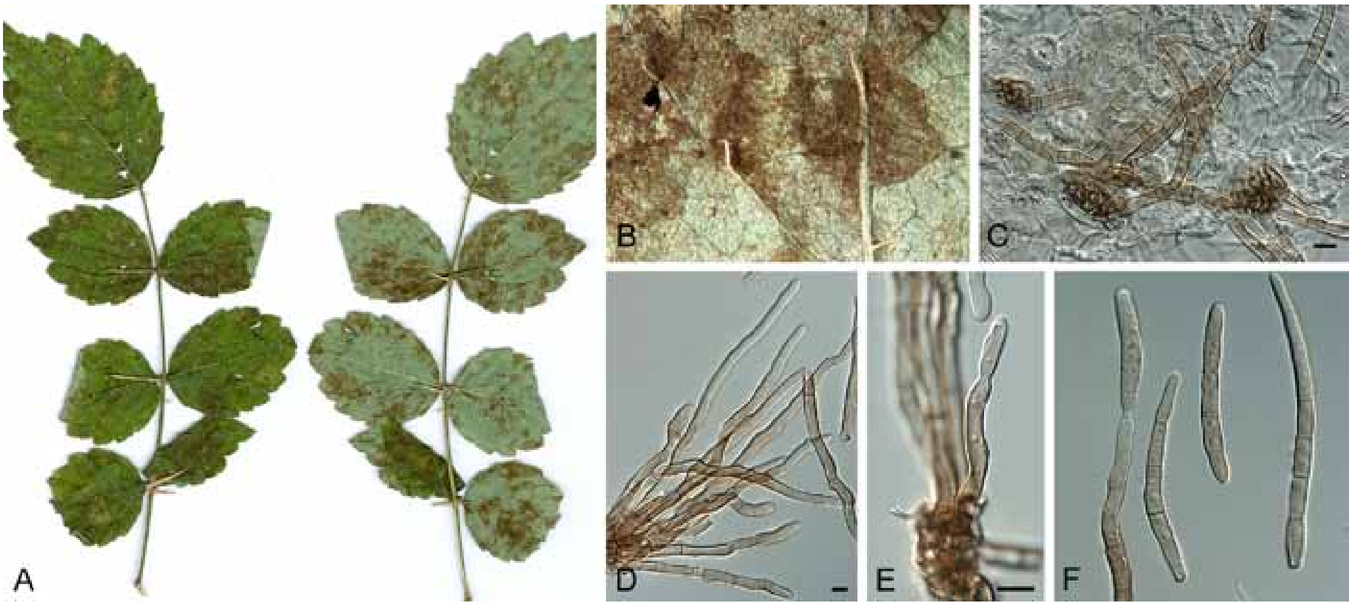


**Fig. 22.** *Pseudocercospora araliae* (CPC 10154). A. Leaf spots on upper and lower leaf surface. B. Close-up of leaf spot with fruiting. C–E. Fascicles with conidiophores and conidiogenous cells. F. Conidia. Scale bars = 10 µm.

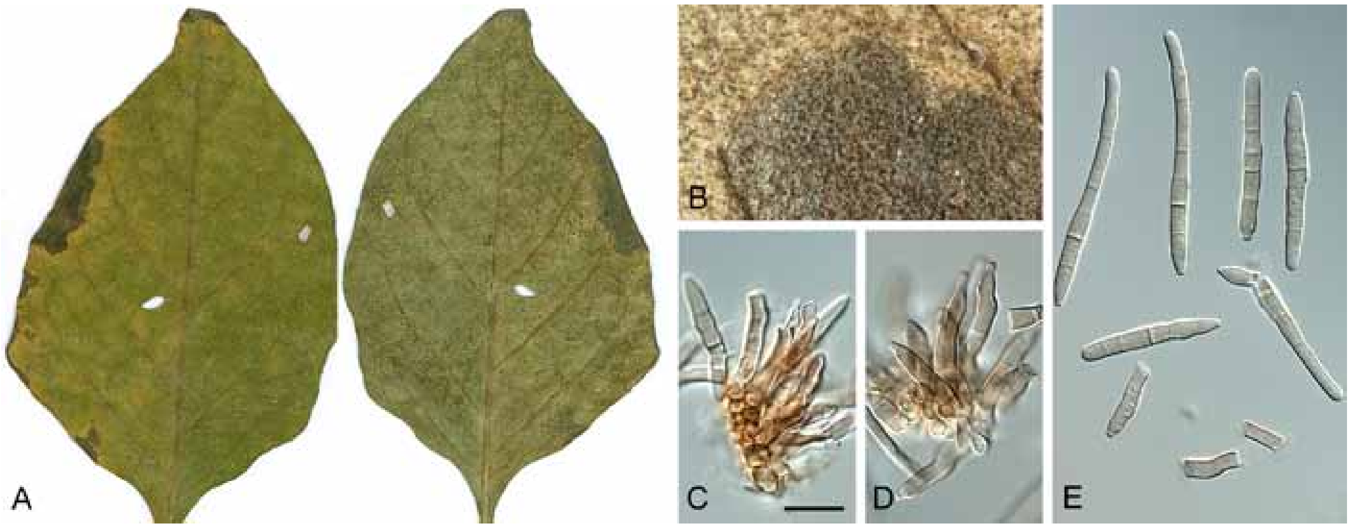


**Fig. 23.** *Pseudocercospora atromarginalis* (CPC 11372–11374). A. Leaf spots on upper and lower leaf surface. B. Close-up of leaf spot with fruiting. C, D. Fascicles with conidiophores and conidiogenous cells. E. Conidia. Scale bar = 10 µm.

Bindura, on leaves of *Citrus* sp., 13 Aug. 1979, A. Rothwell, IMI 240682; on leaves of *Citrus* sp., Sep. 2000, M.C. Pretorius, **epitype designated here** CBS H-20851, culture ex-epitype CPC 4112–4118, 4111 = CBS 112933.

***Pseudocercospora araliae*** (Henn.) Deighton, Mycol. Pap. 140: 19. 1976. Fig. 22.

*Basionym*: *Cercospora araliae* Henn., Bot. Jahrb. Syst. 31: 742. 1902; also 37: 165. 1906.

≡ *Cercosporiopsis araliae* (Henn.) Miura, Fl. Manchuria & E. Mongolia, 27, 3: 533. 1928.

= *Cercospora atromaculans* auct., non Ellis & Everh.

*Specimens examined*: **Japan**, Tosa, Ushioe-yama, on *Aralia elata* var. *glabrescens,* Aug. 1901, T. Yoshinaga, **holotype** B 700015014; *A. elata,* T. Kobayashi & C. Nakashima, **epitype designated here** TFM: FPH-8094, ex-epitype cultures MUCC 873, MAFF 238192. **South Korea**, Jeju, Halla Arboretum, on *A. elata,* 14 Sep. 2002, H.D. Shin, CBS H-20852, culture CPC 10154; Wonju, on *A. elata,* 21 Sep. 2003, H.D. Shin, CBS H-20853, cultures CPC 10782–10784.

***Pseudocercospora atromarginalis*** (G.F. Atk.) Deighton, Mycol. Pap. 140: 139. 1976. Fig. 23.

*Basionym*: *Cercospora atromarginalis* G.F. Atk. (*atramarginalis*), J. Elisha Mitchell Sci. Soc. 8: 59. 1892.

= *Cercospora rigospora* G.F. Atk., J. Elisha Michell Sci. Soc. 8: 65. 1892.

= *Cercospora tosensis* Henn., Bot. Jahrb. Syst. 34: 605. 1905.

= *Cercospora nigri* Tharp, Mycologia 9: 112. 1917.

= *Cercospora solani-biflori* Sawada, Formosan Agric. Rev. 39: 701. 1942, nom. inval.

*Specimens examined*: **Japan**, Prov. Tosa, Aki-machi, on *Solanum nigrum*, Oct. 1903, Yoshinaga No. 43, (**holotype** of *C. tosensis*, B 700015016). **South Korea**, Namyangju, on *S. nigrum*, 27 Jul. 2004, H.D. Shin, CBS H-20854, CPC 11372–11374. **New Zealand**, Auckland, Jan. 2004, C.F. Hill 970, CBS 114640.

*Notes*: *Pseudocercospora atromarginalis* was described from *Solanum* collected in Auburn Alabama, USA. Material studied here from New Zealand and Korea represents the same species, which might be authentic for the name. Fresh material from *Solanum* in the USA, and a detailed study of the synonyms listed by Chupp (1954) would resolve this issue. An isolate identified as *P. chengtuensis* (on *Lycium*, *Solanaceae*) appears identical to *Pseudocercospora atromarginalis*.

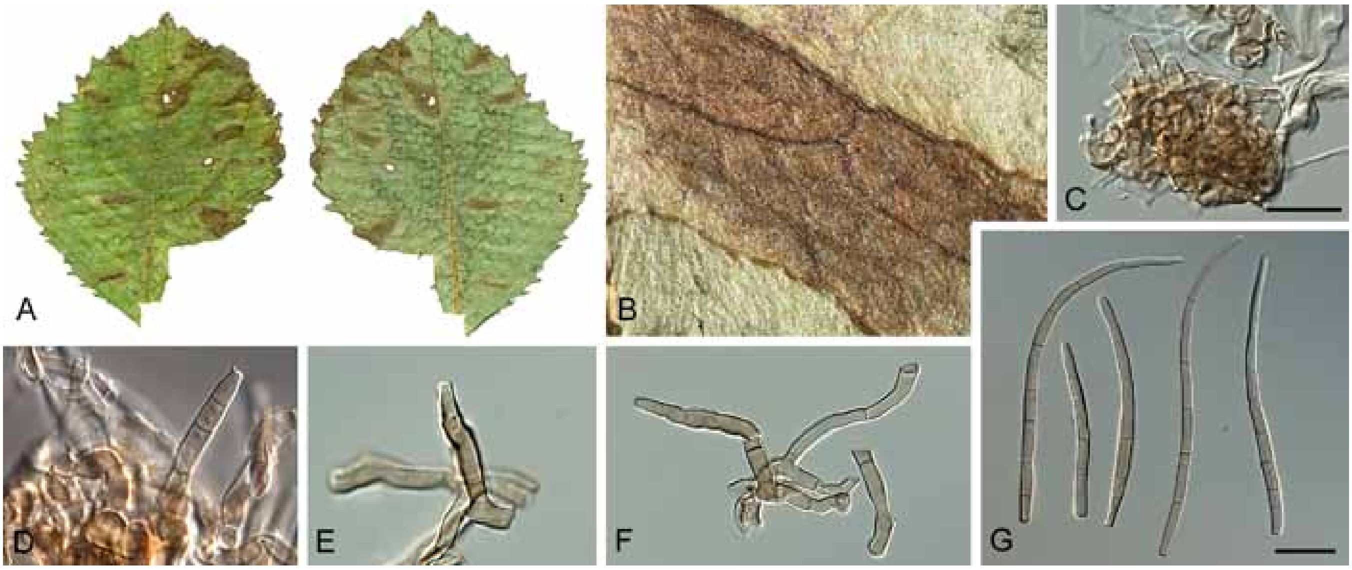


**Fig. 24.** *Pseudocercospora balsaminae* (CPC 10044). A. Leaf spots on upper and lower leaf surface. B. Close-up of leaf spot with fruiting. C–F. Fascicles and solitary conidiophores with conidiogenous cells. G. Conidia. Scale bars = 10 µm.

***Pseudocercospora balsaminae*** (Syd.) Deighton, Mycol. Pap. 140: 139. 1976. Fig. 24.
*Basionym*: *Cercoseptoria balsaminae* Syd., Ann. Mycol. 33: 69. 1935.

*Specimens examined*: **South Korea**, Chuncheon, on *Impatiens textorii*, 11 Oct. 2002, H.D. Shin, CBS H-20856, CPC 10044 = CBS 131882; Dongducheon, on *I. textorii*, 11 Oct. 2004, H.D. Shin, CBS H-20855, CPC 10699–10701.

***Pseudocercospora callicarpae*** (Cooke) Y.L. Guo & W.X. Zhao, Acta Mycol. Sin. 8: 118. 1989.
*Basionym*: *Cercospora callicarpae* Cooke, Grevillea 6: 140. 1878.
= ? *Cercospora callicarpicola* Naito, Mem. Coll. Agric. Kyoto Imp. Univ. 47: 49. 1940.

*Specimen examined*: **Japan**, Ibaraki, on *Callicarpa japonica*, 11 Sep. 1998, T. Kobayashi, MUCC 888, MAFF 237784, CNS-442.

***Pseudocercospora catalpigena*** U. Braun & Crous, Mycol. Progr. 2: 198. 2003.

*Specimen examined*: **Japan**, Wakayama, on *Catalpa ovata*, 30 Oct. 2007, C. Nakashima & I. Araki, MUMH 10868, culture MUCC 743.

***Pseudocercospora catappae*** (Henn.) X.J. Liu & Y.L. Guo, Mycosystema 2: 230. 1989.
*Basionym*: *Cercospora catappae* Henn., Bot. Jahrb. Syst. 34: 56. 1905.
= *Pseudocercospora catappae* Goh & W.H. Hsieh, in Hsieh & Goh, *Cercospora* and similar fungi from Taiwan: 57. 1990, homonym of *P. catappae* (Henn.) X.J. Liu & Y.L. Guo, 1989.
= *Ramularia catappae* Racib., Paras. Algen u. Pilze Javas II, Batavia: 41. 1900.
= *Cercospora terminaliae* Sawada (*terminariae*), Taiwan Agric. Rev. 38: 701. 1942, nom. illeg., homonym of *C. terminaliae* Syd. 1929.

*Specimens examined*: **Tanzania**, Zanzibar, Dar-es-Salam, on *Terminalia catappa*, 26 Oct. 1901, Stuhlmann **holotype** B 700015015. **Japan**, Okinawa, on *T. catappa*, 17 Nov. 2007, C. Nakashima & T. Akashi, MUMH 10913, culture MUCC 809.

***Pseudocercospora cercidicola*** Crous, U. Braun & C. Nakash., **sp. nov**. MycoBank MB564829. Fig. 25.

*Etymology*: Name reflects the host *Cercis,* from which it was collected.

*Leaf spots* amphigenous, irregular to angular, 1–5 mm diam, confined by leaf veins, brown on upper surface, with raised, dark brown border, on lower surface medium brown, with indistinct borders. *Mycelium* internal, consisting of pale brown, smooth, septate, branched, 2–3 µm diam hyphae. *Caespituli* fasciculate to sporodochial, amphigenous, but predominantly epiphyllous, grey-brown on leaves, up to 130 µm wide and 150 µm high. *Conidiophores* aggregated in dense fascicles arising from the upper cells of a brown stroma up to 80 µm wide and 60 µm high; conidiophores brown, finely verruculose, 2–6-septate, subcylindrical, straight to variously curved, unbranched or branched above, 20–50 × 3–5 µm. *Conidiogenous cells* terminal or lateral, unbranched, medium brown, finely verruculose, tapering to flat-tipped apical loci, proliferating sympodially, 10–20 × 2–3 µm. *Conidia* solitary, medium brown, smooth, guttulate, subcylindrical to narrowly obclavate, apex subobtuse, base long obconically subtruncate, straight to variously curved, (0–)3–6-septate, (27–)30–50(–60) × (2.5–)3(–3.5) µm; hila neither thickened, nor darkened-refractive, 1.5–2 µm diam.

*Culture characteristics*: Colonies on MEA 10–15 mm after 2 wk at 20 °C in the dark, restricted, with margin mildly lobed, felty, pale olivaceous or greyish olivaceous, surrounded by greyish margin; reverse olivaceous.

*Specimens examined*: **Japan**, Ibaraki, on *Cercis chinensis*, 10 Sep. 1998, T. & Y. Kobayashi, **holotype** CBS H-20895, culture ex-type MUCC 896, MAFF 237791 = CBS 132041; Tokyo, Koishikawa Botanical Garden, on *Cercis chinensis*, 10 Nov. 2007, I. Araki & M. Harada, MUMH 11108, culture MUCC 937; Japan, Kanagawa, on *Cercis chinensis*, May 1992, K.Kishi, culture MAFF 237128.

*Notes*: Asian collections of cercosporoid fungi on *Cercis chinensis* were considered as representative of *Cercospora chionea* by Chupp (1954). The latter species was shown to be a member of *Passalora* by Braun (1993). Shin & Braun (2000) introduced a new species of *Pseudocercospora* for the taxon occurring on *Cercis* in Asia, namely *P. cercidis-chinensis*, based on material collected in Korea. Phylogenetic data obtained in the present study (Fig. 5) show that the Japanese collections are distinct. As the

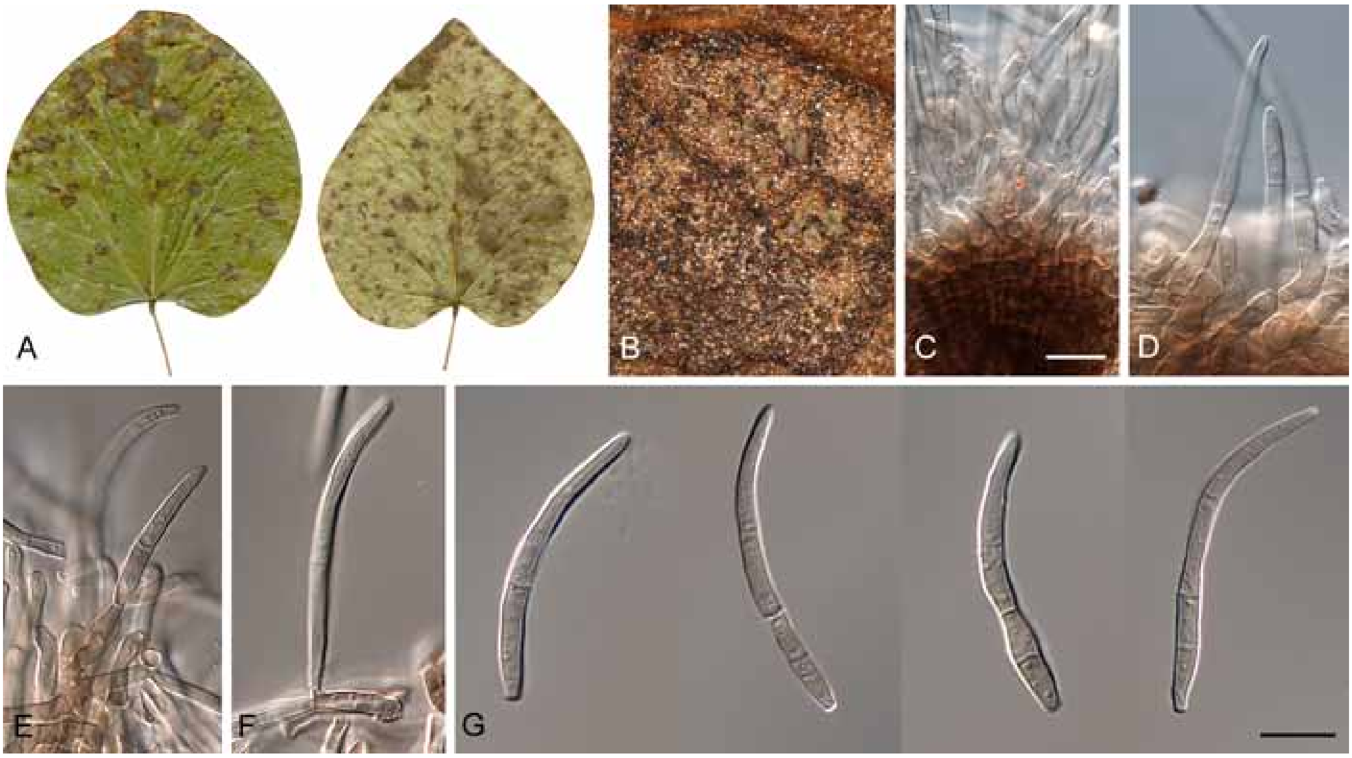


**Fig. 25.** *Pseudocercospora cercidicola* (CBS H-20895). A. Leaf spots on upper and lower leaf surface. B. Close-up of leaf spot with fruiting. C, D. Fascicles with conidiophores and conidiogenous cells. E, F. Conidiophores on superficial hyphae. G. Conidia. Scale bars = 10 µm.

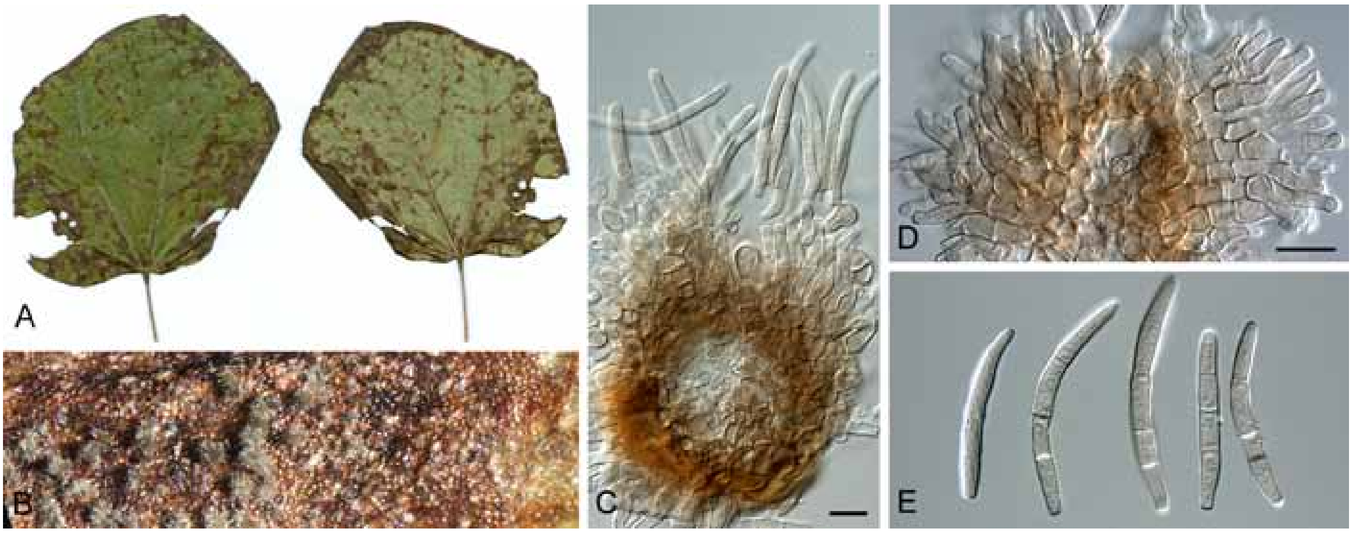


**Fig. 26.** *Pseudocercospora cercidis-chinensis* (CPC 14481). A. Leaf spots on upper and lower leaf surface. B. Close-up of leaf spot with fruiting. C, D. Fascicles with conidiophores and conidiogenous cells. E. Conidia. Scale bars = 10 µm.

name *Cercospora cercidis* Nishikado is illegitimate, a new name, *P. cercidicola* is introduced for the species occurring on *Cercis* in Japan. *Pseudocercospora cercidicola* is morphologically very close to *P. cercidis-chinensis* but superficial hyphae with solitary conidiophores are not formed and the conidia are shorter.

***Pseudocercospora cercidis-chinensis*** H.D. Shin & U. Braun, Mycotaxon 74: 109. 2000. Fig. 26.

*Specimens examined*: **South Korea**, Kyeongju, on *Cercis chinensis*, 26 Aug. 1998, H.D. Shin, **holotype** KUS-F 14914, **isotype** HAL; Suwon, *C. chinensis*, 2 Oct. 2007, H.D. Shin, **epitype designated here** CBS H-20857, culture ex-epitype CPC 14481 = CBS 132109.

*Note*: See *P. cercidicola.*

***Pseudocercospora chengtuensis*** (F.L. Tai) Deighton, Mycol. Pap. 140: 141. 1976. Fig. 27.
*Basionym*: *Cercospora chengtuensis* F.L. Tai, Lloydia 11: 40. 1948.

*Specimens examined*: **China**, Szechuan, Chengtu, *Lycium chinense*, Lee Ling No. 126, 1943, **holotype** (not seen). **South Korea**, Dongducheon, *Lycium chinense,* 28 Sep. 2003, H.D. Shin, CBS H-20858, culture CPC 10696–10698.

*Notes*: The isolate identified here as *P. chengtuensis* appears to be identical to *P. atromarginalis* (also on *Solanaceae*) based on phylogenetic analysis and the two are morphologically similar. Study of of additional collections of both are needed to determine whether they are synonymous or distinct species.

***Pseudocercospora chionanthi-retusi*** Goh & W.H. Hsieh, in Hsieh & Goh, *Cercospora* and similar fungi from Taiwan: 249. 1990. Fig. 28.

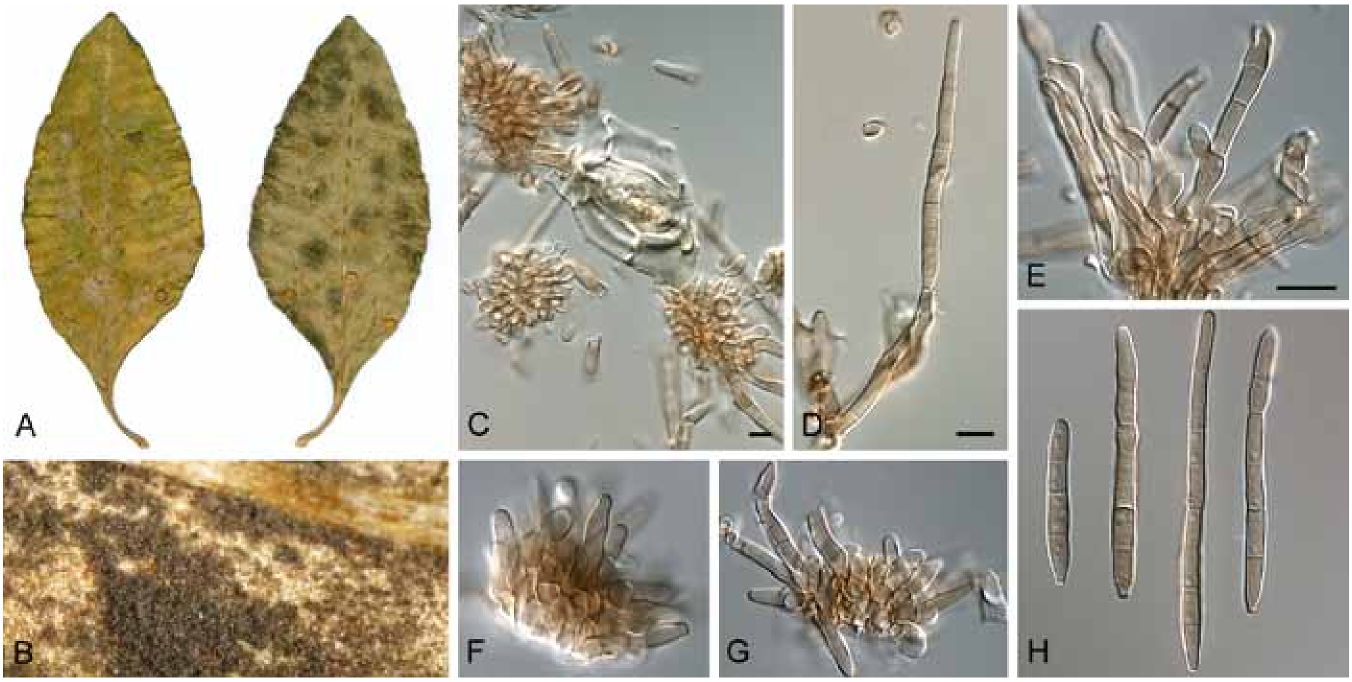

**Fig. 27.** *Pseudocercospora chengtuensis* (CPC 10696–10698). A. Leaf spots on upper and lower leaf surface. B. Close-up of leaf spot with fruiting. C–G. Fascicles with conidiophores and conidiogenous cells. H. Conidia. Scale bars = 10 µm.

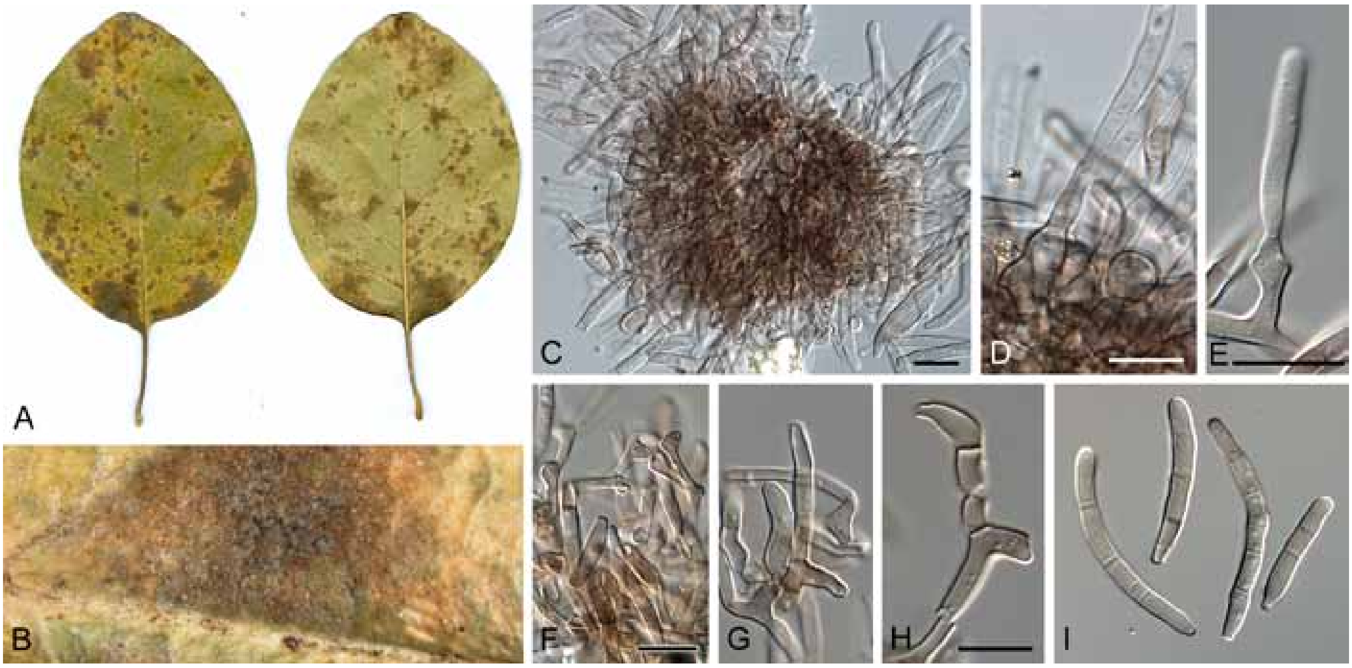

**Fig. 28.** *Pseudocercospora chionanthi-retusi* (CPC 14683). A. Leaf spots on upper and lower leaf surface. B. Close-up of leaf spot with fruiting. C–H. Fascicles and solitary conidiophores with conidiogenous cells. I. Conidia. Scale bars = 10 µm.

= *Cercospora chionanthi-retusi* Togashi & Katsuki, Sci. Rep. Yokohama Nat. Univ. Sect. II, 1: 1. 1952.

≡ *Pseudocercospora chionanthi-retusi* (Togashi & Katsuki) Nishijima, C. Nakash. & Tak. Kobay., Mycoscience 40: 270. 1999, nom. illeg., homonym of *P. chionanthi-retusi* Goh & Hsieh, 1990.

= *Pseudocercospora chionanthicola* C. Nakash. & Tak. Kobay., Mycoscience 43: 98. 2002.

*Specimen examined*: **South Korea**, Osan, on *Chionanthus retusus*, 30 Oct. 2007, H.D. Shin, CBS H-20859, culture CPC 14683 = CBS 132110.

### ***Pseudocercospora chrysanthemicola*** (J.M. Yen) Deighton, Mycol. Pap. 140: 141. 1976.

*Basionym*: *Cercospora chrysanthemicola* J.M. Yen, Rev. Mycol. 29: 216. 1964.

*Specimen examined*: **South Korea**, Seoul, on *Chrysanthemum* sp., 6 Sep. 2003, H.D. Shin, CPC 10633.

### ***Pseudocercospora contraria*** (Syd. & P. Syd.) Deighton, Mycol. Pap. 140: 30. 1976. Fig. 29.

*Basionym*: *Cercospora contraria* Syd. & P. Syd., Ann. Mus. Congo, Bot., Ser. V, 3: 21. 1909.

= *Cercospora wildemanii* Syd. & P. Syd., Ann. Mus. Congo, Bot., Ser. V, 3: 21. 1909.

= *Mycosphaerella contraria* Hansf., Proc. Linn. Soc. London 153: 22. 1941.

*Specimen examined*: **South Korea**, Bukjeju, Jeolmul recreation forest, on *Dioscorea quinqueloba,* 2. Nov. 2007, H.D. Shin, CBS H-20861, CPC 14714 = CBS 132108.

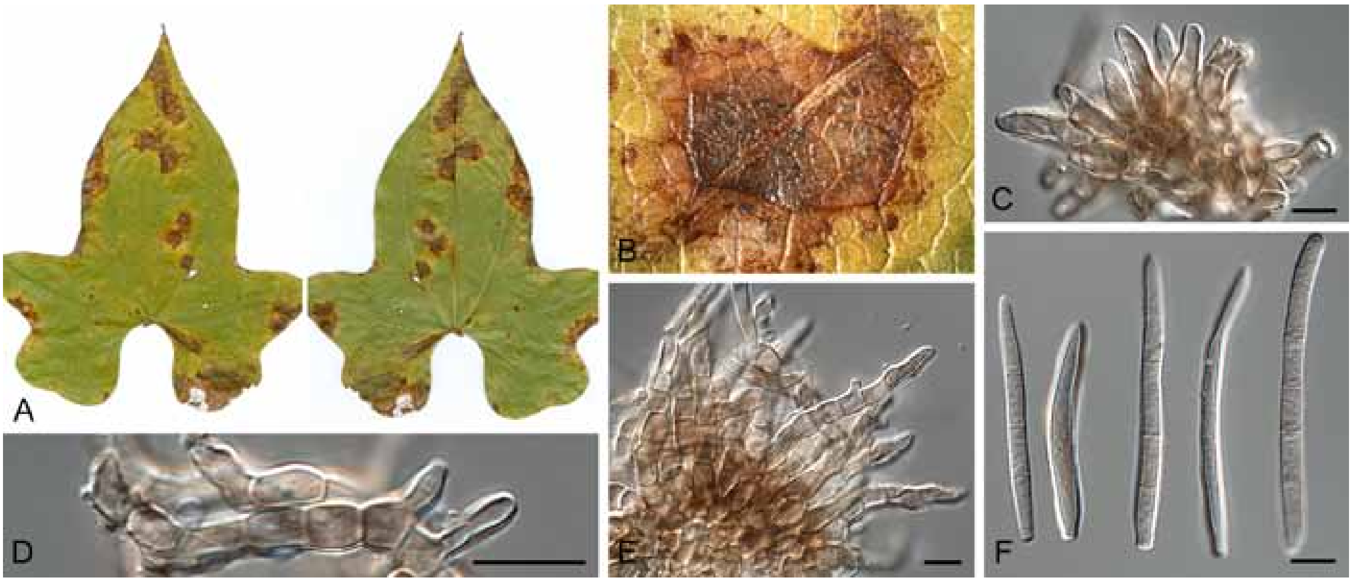


**Fig. 29.** *Pseudocercospora contraria* (CPC 14714). A. Leaf spots on upper and lower leaf surface. B. Close-up of leaf spot with fruiting. C–E. Fascicles with conidiophores, and solitary loci on hyphae. F. Conidia. Scale bars = 10 µm.

*Notes*: This fungus was first reported from Korea by Shin & Kim (2001). Conidial measurements (16–75 × 2.5–4.5 µm) are smaller than those of the type collected in the Democratic Republic of the Congo (20–120 × 5–8 µm, Chupp 1954), and the Korean material may eventually be shown to represent a distinct species.

***Pseudocercospora coriariae*** (Chupp) X.J. Liu & Y.L. Guo, Mycosystema 2: 232. 1989.
*Basionym*: *Cercospora coriariae* Chupp, J. Dept. Agric. Puerto Rico 14: 285. 1930.
= *Cercospora coriariae* F.L. Tai, Lloydia 11: 43. 1948, nom. illeg., homonym of *C. coriariae* Chupp, 1930.

*Specimen examined*: **Japan**, Tokyo, on *Coriaria japonica*, 10 Nov. 2007, I. Araki & M. Harada, MUMH 10942, culture MUCC 840.

***Pseudocercospora cornicola*** (Tracy & Earle) Y.L. Guo & X.J. Liu, Mycosystema 2: 232. 1989.
*Basionym*: *Cercospora cornicola* Tracy & Earle, Bull. Torrey Bot. Club 23: 205. 1896.

*Specimen examined*: **Japan**, Tokyo*, Cornus alba* var. *sibirica*, 7 Nov. 1998*,* C. Nakashima & E. Imaizumi, CNS-494, culture MUCC 909, MAFF 237773.

***Pseudocercospora corylopsidis*** (Togashi & Katsuki) C. Nakash. & Tak. Kobay., Mycoscience 40: 270. 1999.
≡ *Cercospora corylopsidis* Togashi & Katsuki, Bot. Mag. (Tokyo) 65: 20. 1952.
= *Cercospora hamamelidis auct*.; *sensu* Togashi & Katsuki, Bot Mag. (Tokyo) 65: 21. 1952, non (Peck) Ellis & Everh.

*Specimens examined*: **Japan**, Kagoshima, on *Corylopsis pauciflora*, 26 Oct. 1949, S. Katsuki, **holotype** YNU, **Isotype** TNS-F-243824; Ibaraki, Tsukuba Botanical Garden, on *C. pauciflora*, Oct. 1996, T. Kobayashi; Ibaraki, on *C. pauciflora*, 9 Nov. 1998, T. Kobayashi; Tokyo, Todori, on *C. pauciflora*, 12 Oct. 1979, M. Kusunoki, TFM:FPH-6152; Tokyo, Jindai Bot. Park, on *C. spicata*, 7 Nov. 1998, C. Nakashima & E. Imaizumi, **epitype designated here** TFM: FPH-8095, ex-epitype cultures MUCC 908, MAFF 237795; Saitama, isolated from *C. pauciflora*, Nov. 1995, MUCC1249, MAFF 237302; Kagoshima, 26 Oct. 1949, on *Hamamelis japonica*, S. Katsuki, SK2077; Shizuoka, 2 Nov. 1996, on *H. japonica*, T. Koboyashi & C. Nakashima, CNS-114, cultures MAFF 237632, MUCC 874.

*Notes*: Isolate MUCC 874, which was isolated from *Hamamelis japonica* (*Hamamelidaceae*), appears to be phylogenetically identical to *P. corylopsidis*. Based on morphology, there is little difference between these specimens other than the presence or absence of external mycelium.

Togashi & Katsuki (1952) reported a fungus on *Hamamelis japonica* as *Cercospora hamamelidis* (Peck) Ellis & Everh. based on a specimen collected in Kagoshima (SK2077). Recently, *C. hamamelidis* was transferred to the genus *Passalora* (Crous & Braun 2003). The Japanese specimens of *C. hamamelidis* are morphologically and phylogenetically identical to *Pseudocercospora corylopsidis*. We conclude that the fungus on *Corylopsis* and *Hamamelis* in Japan represents *P. corylopsidis*. In addition, a species of *Pseudocercospora* collected in Tokyo (TFM:FPH-4348, isolate MAFF 410032) was recognised as a distinct taxon on *Corylopsis* plants, based on its longer and narrower conidia, and DNA phylogeny.

***Pseudocercospora cotoneastri*** (Katsuki & Tak. Kobay.) Deighton, Trans. Brit. Mycol. Soc. 88: 389. 1987.
*Basionym*: *Cercospora cotoneastri* Katsuki & Tak. Kobay. (as "*cotoneasteris*"), Trans. Mycol. Soc. Japan 17: 276. 1976.

*Specimens examined*: **Japan**, Tokyo, Asakawa Experimental Forest Station, on *Cotoneaster dammeri*, 13 Aug. 1974, T. Kobayashi, **holotype** TFM:FPH-4185, ex-holotype culture MAFF 410089; Tokyo, Tokyo Agric. Exp. Stn., on *C. franchetii*, 27 Sep. 1978, T. Kobayashi, TFM:FPH-4924; Tokyo, Jindai Bot. Park, on *C. horizontalis*, 4 Sep. 1975, H. Horie, TFM: FPH-4417; Tokyo, on *C. horizontalis*, 23 Oct. 1975, K. Sasaki, TFM:FPH-4798; Tokyo, culture isolated from *Cotoneater* sp., 1977, H. Horie, culture MAFF 305633; Fukuoka, Kitakyushu, on *C. horizontalis*,4 Oct. 1975, S. Ogawa (TFM:FPH-4401); Shizuoka, Hamamatsu, on *C. salicifolius*, 1 Nov. 1996, T. Kobayashi & C. Nakashima, CNS-126, culture MUCC 876, MAFF 237629.

*Note*: Three isolates including the ex-holotype, MAFF 410089, 305633 and 237629, were identical based on ACT gene sequence data (data not shown).

***Pseudocercospora crispans*** G.C. Hunter & Crous, **sp. nov.** MycoBank MB564830. Fig. 30.

*Etymology*: Name reflects the characteristic curling or undulate nature of the conidia produced by this fungus.

*Leaf spots* amphigenous, angular to irregular, predominantly occurring next to or close to the mid-rib, 2–15 mm diam, pale

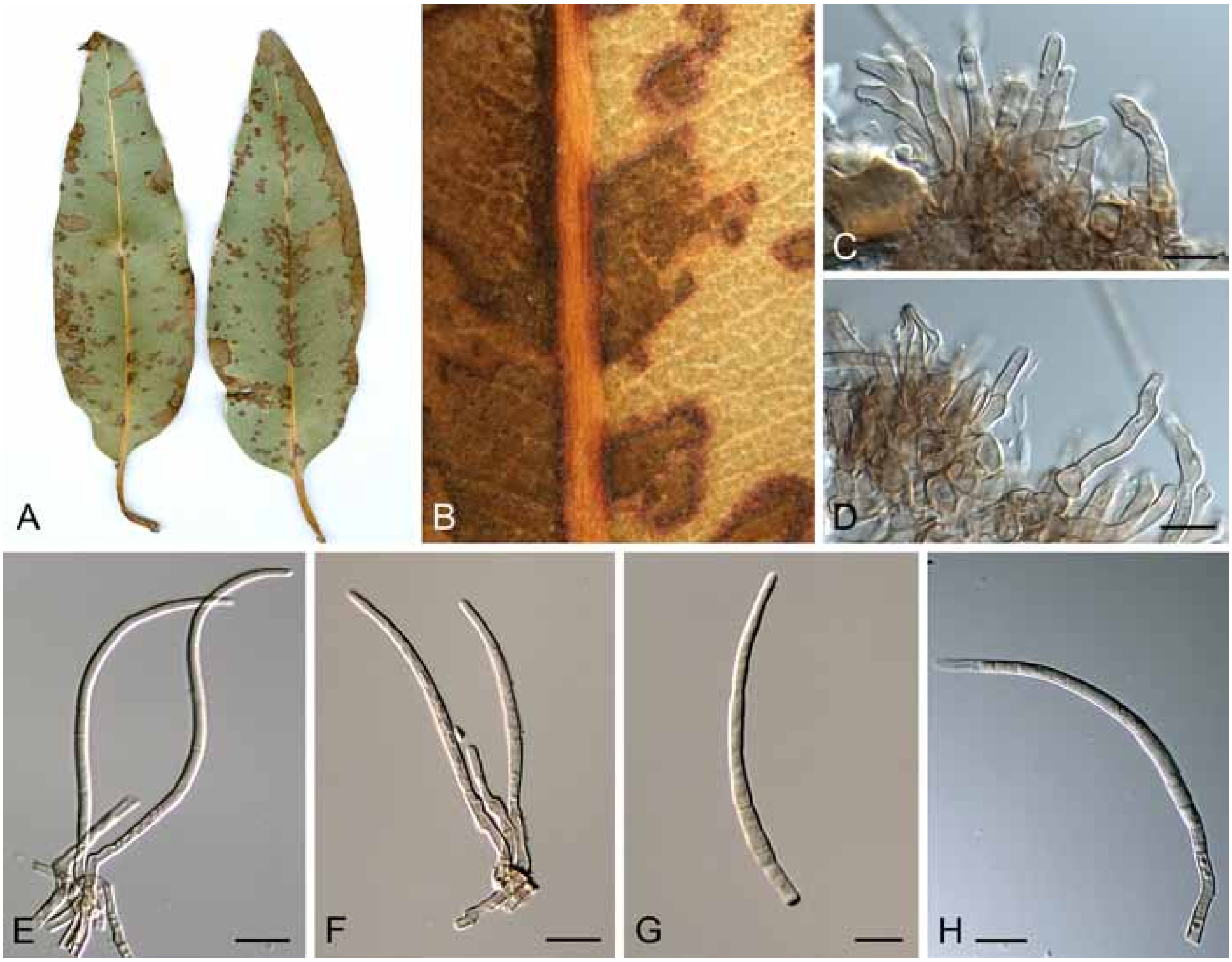


**Fig. 30.** *Pseudocercospora crispans* (CPC 14883). A. Leaf spots on upper and lower leaf surface. B. Close-up of leaf spot with fruiting. C–F. Fascicles with conidiophores and conidiogenous cells. G, H. Conidia. Scale bars = 10 µm.

brown on the upper side of the leaf, and pale to darker brown on the bottom side of the lesion, surrounded by a raised, dark brown border with a diffuse red pigment emanating away from the border; single, discrete lesions may coalesce to form larger lesions. *Mycelium* smooth, septate, guttulate, thick-walled, branched, internal and external, pale brown, 2–4 mm wide. *Caespituli* amphigenous, sparsely scattered over lesion, floccose, whitish. *Stromata* hypophyllous, brown, well-developed, immersed, globular to irregular, 40–120 mm diam. *Conidiophores* brown at the base, becoming paler toward apex, arising from cells of brown stroma; arranged in loose fascicles, smooth, thick-walled, guttulate, unbranched, straight to curved, 0–4-septate, straight to geniculate–sinuous, (14–)17–31(–42) × (2–)3–4(–5) µm. *Conidiogenous cells* terminal, unbranched, smooth, guttulate, pale brown, straight to geniculate to geniculate–sinuous, proliferating sympodially and percurrently, tapering toward apex; apex obtuse to truncate, (8–)9–15(–19) × (2–)3(–4) µm. *Conidia* solitary, smooth, guttulate, curved to undulate, pale brown, 3–9-septate, apex acute to subacute, base truncate, (40–)65–96(–102) × (2–)3(–4) µm; hila unthickened, not darkened.

*Culture characteristics*: Colonies on MEA reaching 54 mm diam after 30 d at 24 °C. Colonies circular, flat to slightly convex, with a feathery margin and profuse aerial mycelium; lavender-grey to glaucous-grey (surface) and olivaceous-grey (reverse).

*Specimen examined*: **South Africa**, Western Cape Province, Knysna, on leaves of *Eucalyptus* sp., Jan. 2008, P.W. Crous, **holotype** CBS H-20392, culture ex-type CPC 14883 = CBS 125999.

Notes: *Pseudocercospora crispans* is phylogenetically distinct from other taxa described from *Eucalyptus* (Crous *et al*. 1989, Crous & Alfenas 1995, Crous & Wingfield 1997, Crous 1998, Braun & Dick 2002, Hunter *et al*. 2006a), and can be distinguished morphologically by its prominently curled conidia.

## ***Pseudocercospora crocea*** Crous, U. Braun, G.C. Hunter & H.D. Shin, **sp. nov.** MycoBank MB564831. Fig. 31.

*Etymology*: Name reflects the typical diffuse yellow border surrounding leaf lesions caused by this fungus.

*Leaf spots* distinct, scattered and at the leaf margin, pale brown to brown, circular to irregular, 2–5 mm diam, indefinite border, with a pale yellow diffuse halo. *Mycelium*, internal and external, subhyaline, septate, branched, smooth, 2–5 mm wide. *Caespituli* amphigenous, grey, scattered over the lesion surface, arachnoid. *Stromata* well-developed, 40–100 mm diam, subimmersed, globular, dark brown. *Conidiophores* fasciculate, brown, becoming paler toward the apex, 0–1-septate, smooth, unbranched, straight to curved, apex truncate to subtruncate, 0–1-septate, (14–)17–24(–32) × (3–)4(–5) µm. *Conidiogenous cells* terminal, unbranched, pale

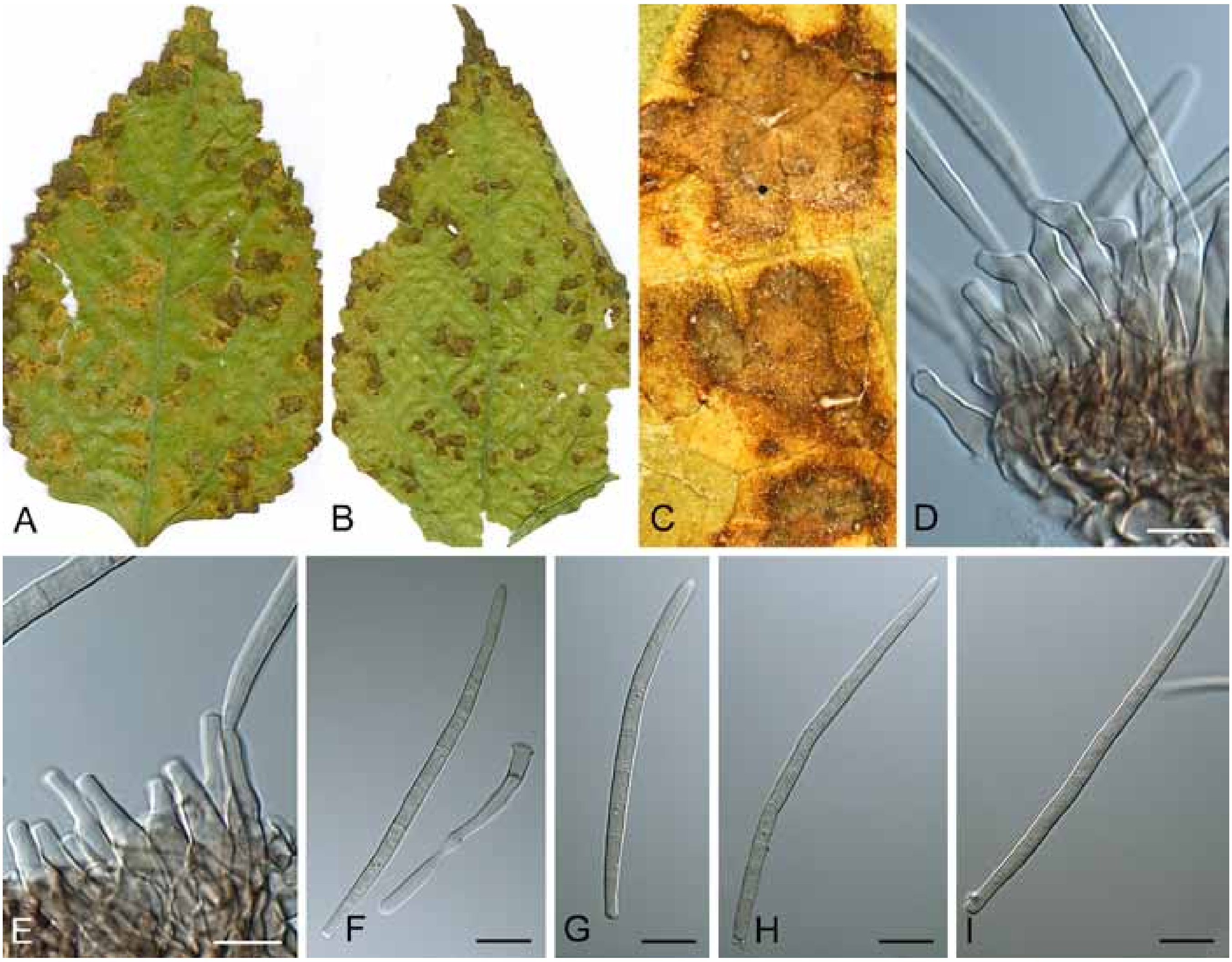


**Fig. 31.** *Pseudocercospora crocea* (CPC 11668). A, B. Leaf spots on upper and lower leaf surface. C. Close-up of leaf spot with fruiting. D, E. Fascicles with conidiophores and conidiogenous cells. F–I. Conidia. Scale bars = 10 µm.

brown, smooth to slightly verruculose, proliferating percurrently, (9–) 13–18(–21) × (3–)4(–5) µm. *Conidia* solitary, 4–10-septate, straight to curved, sparsely guttulate, narrowly obclavate, apex subobtuse, base obconically truncate to long obconically truncate, smooth, subhyaline, (67–)79–94(–104) × (3–)4(–5)µm, hila unthickened not darkened.

*Culture characteristics*: Colonies on MEA reaching 53 mm diam after 30 d at 24 °C. Colonies circular with feathery margin, flat to slightly convex, some folding occurs, with a darker radial ring toward the colony margin, aerial mycelium medium; iron-grey to olivaceous-grey (surface) and iron-grey (reverse).

*Specimen examined*: **South Korea**, Suwon, on leaves of *Pilea hamaoi* (≡ *P. pumila* var. *hamaoi*), 5 Nov. 2004, H.D. Shin, **holotype** CBS H-20387, isotype HAL 1860 F, cultures ex-type CPC 11668 = CBS 126004.

Notes: Singh *et al*. (1996) provide an account of the *Pseudocercospora* spp. present on members of *Urticaceae*. Of these, *P. crocea* is most similar to *P. pileae* as it also has a well-developed stroma. *Pseudocercospora pileae* is distinct from *P. crocea*, which lacks stromata and has conidiophores that are consistently solitary, arising from superficial hyphae.

***Pseudocercospora cydoniae*** (Ellis & Everh.) Y.L. Guo & X.J. Liu, Mycosystema 5: 103. 1992. Fig. 32.

*Basionym*: *Cercospora cydoniae* Ellis & Everh., J. Mycol. 8: 72. 1902.

≡ *Cercosporina cydoniae* (Ellis & Everh.) Sacc., Syll. Fung. 25: 915. 1931.
≡ *Pseudocercospora cydoniae* (Ellis & Everh.) U. Braun & H.D. Shin, Mycotaxon 49: 356. 1993.

*Specimens examined*: **South Korea**, Seoul, on *Chaenomeles speciosa* (= *C. lagenaria*), 17 Sep. 2003, H.D. Shin, cultures CPC 10678 = CBS 131923; Jeonju, *C. sinensis,* 15 Oct. 2003, H.D. Shin, CBS H-20863.

***Pseudocercospora dovyalidis*** (Chupp & Doidge) Deighton, Mycol. Pap. 140: 143. 1976. Fig. 33.

*Basionym*: *Cercospora dovyalidis* Chupp & Doidge, Bothalia 4: 885. 1948.

≡ *Pseudocercosporella dovyalidis* (Chupp & Doidge) B. Sutton, Mycol. Pap. 138: 99. 1975.

*Leaf spots* amphigenous, distinct, 1–3 lesions per leaf, scattered over the leaf, 3–10 mm diam, pale brown surrounded by a dark brown to black border. *Mycelium* internal, consisting of pale brown, septate, smooth, 2–6 µm diam hyphae. *Caespituli* hypophyllous, evenly distributed over the leaf spot, floccose to punctiform, olivaceous to black. *Stromata* well-developed, subimmersed to erumpent, globular, dark brown, 40–100 mm diam. *Conidiophores* fasciculate, emerging from the upper cells of stromata, brown, becoming paler toward the apex, smooth, 0–2-septate, straight to variously curved, guttulate, apex

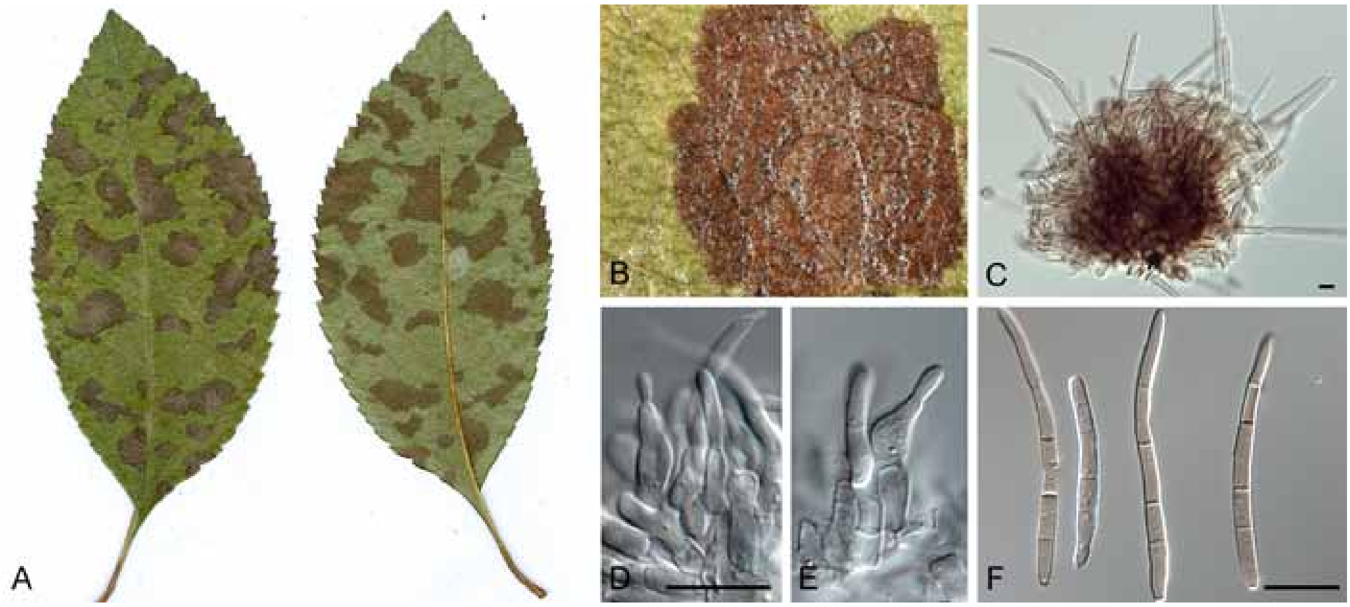


**Fig. 32.** *Pseudocercospora cydoniae* (CPC 10678). A. Leaf spots on upper and lower leaf surface. B. Close-up of leaf spot with fruiting. C. Fascicle with conidiophores and conidiogenous cells. D, E. Conidiogenous cells. F. Conidia. Scale bars = 10 µm.

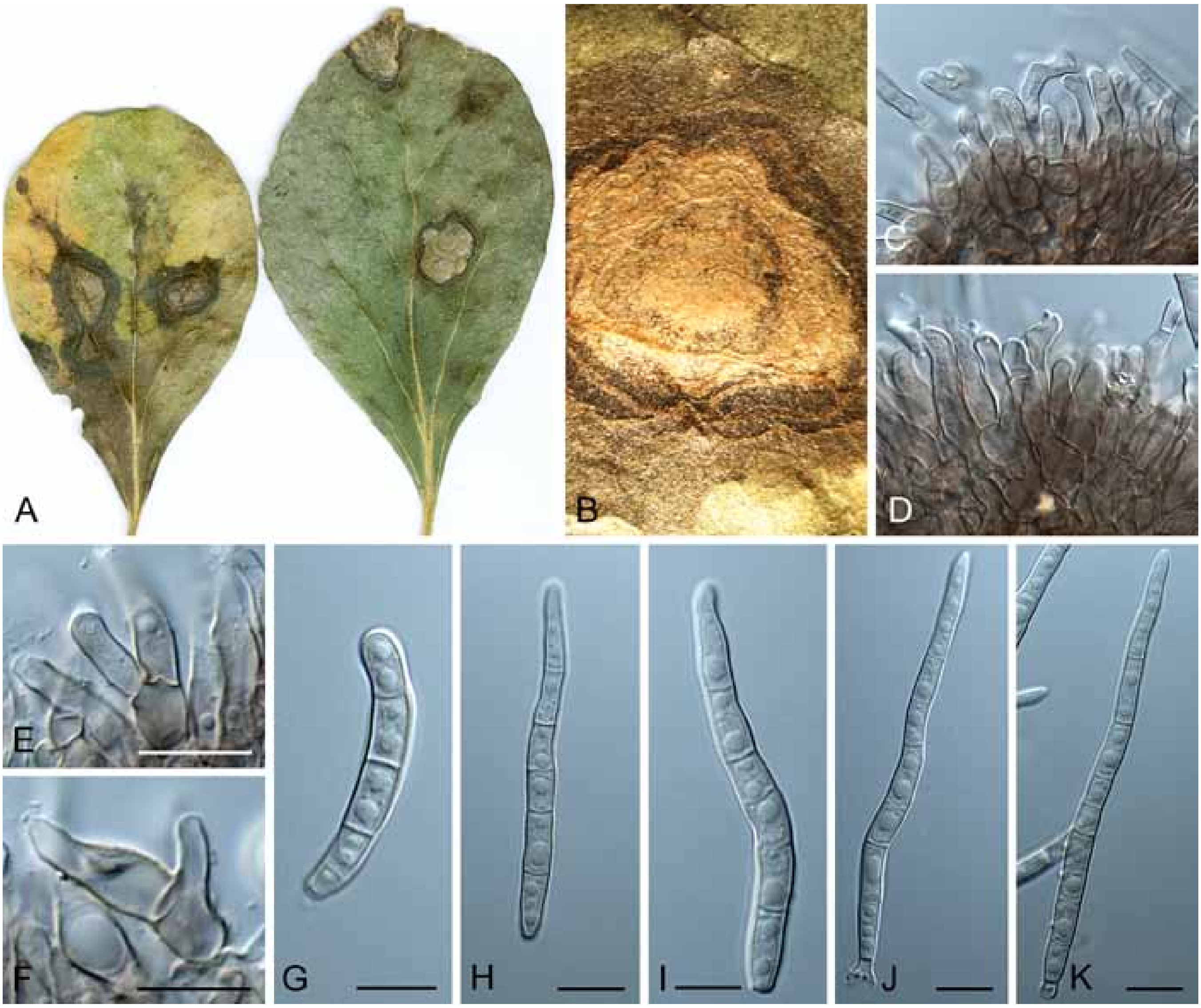


**Fig. 33.** *Pseudocercospora dovyalidis* (CPC 13771–13773). A. Leaf spots on upper and lower leaf surface. B. Close-up of leaf spot with fruiting. C, D. Fascicles with conidiophores and conidiogenous cells. E, F. Conidiogenous cells. G–K. Conidia. Scale bars = 10 µm.

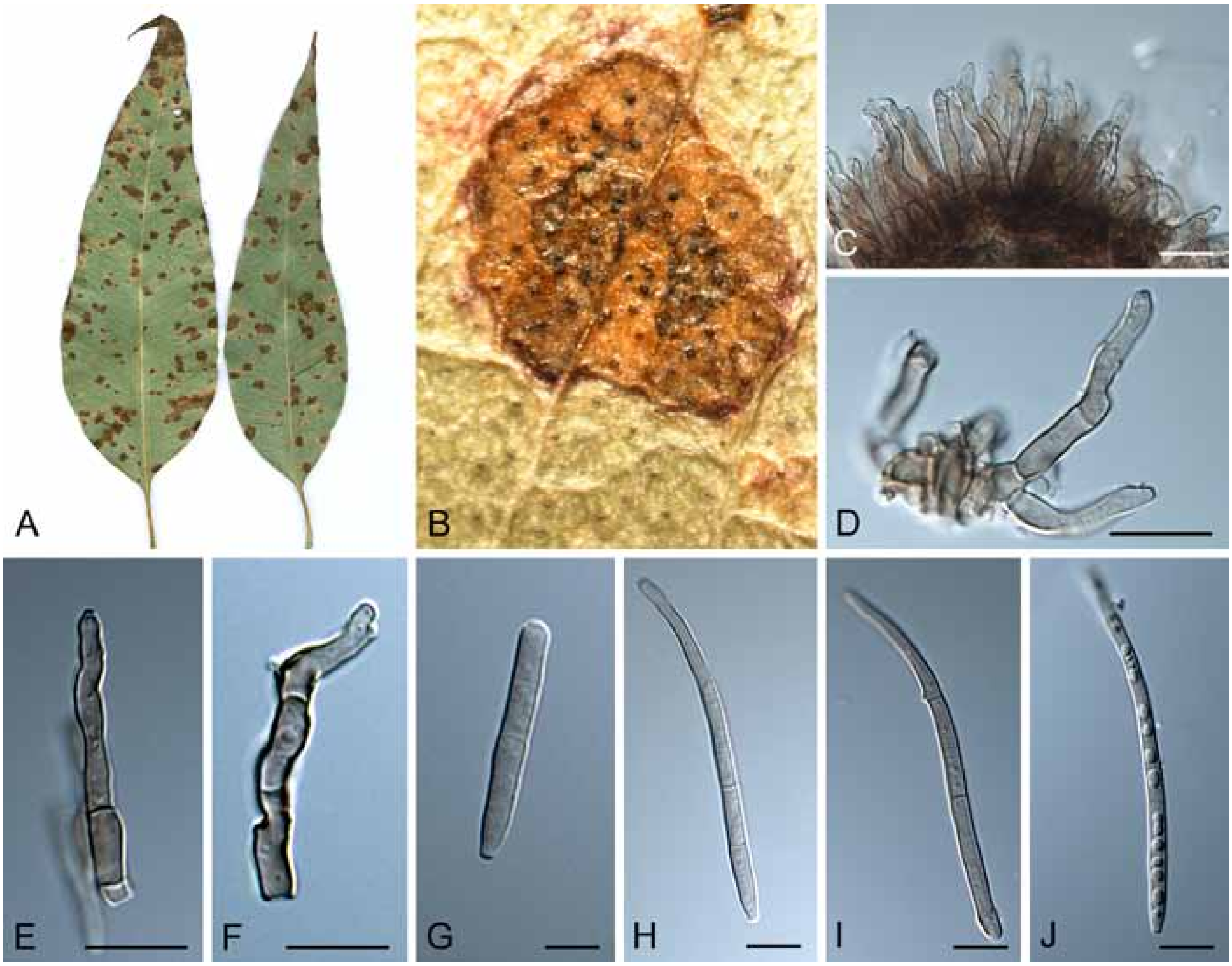


**Fig. 34.** *Pseudocercospora flavomarginata* (CPC 14142). A. Leaf spots on upper and lower leaf surface. B. Close-up of leaf spot with fruiting. C. Fascicle with conidiophores and conidiogenous cells. D–F. Conidiogenous cells. G–J. Conidia. Scale bars = 10 µm.

rounded, conidiophores rarely branched below, (12–)13–22(–34) × (3–)3–5(–6) µm. *Conidiogenous* cells terminal, pale brown, smooth, guttulate, proliferating percurrently, (4–)6–12(–15) × (2–)3–4(–5) µm. *Conidia* solitary, pale brown or subhyaline, smooth, distinctively guttulate, 1–10-septate, thick-walled, straight to curved, broadly filliform to cylindrical, apex rounded to subacute, base long obconically truncate, (20–)30–70(–84) × (3–)3–5(–6) µm; hila neither thickened nor darkened.

*Culture characteristics*: Colonies on MEA reaching 32 mm diam after 30 d at 24 °C. Colonies circular with a smooth margin, either flat with excessive folding into the media or convex, aerial mycelium moderate, margin of colony darker than colony interior; greenish glaucous to olivaceous-grey (surface) and olivaceous-grey (reverse).

*Specimens examined*: **South Africa**, Gauteng, Pretoria, Groenkloof, on *Dovyalis zeyheri*, 18 Feb. 1914, E.M. Doidge, **holotype** PREM 7398; Gauteng, Walter Susulu Botanical Garden, on leaves of *D. zeyheri*, 2 Mar. 2007, P.W. Crous, **epitype designated here** CBS H-20389, culture ex-type CPC 13771 = CBS 126002.

***Pseudocercospora eucalyptorum*** Crous, M.J. Wingf., Marasas & B. Sutton, Mycol. Res. 93: 394. 1989.

= *Pseudocercospora pseudoeucalyptorum* Crous, Stud. Mycol. 50: 210. 2004.

*Specimens examined*: **South Africa**, Western Cape Province, Stellenbosch, Stellenbosch Mountain, on leaves of *E. nitens*, 21 Dec. 1987, P.W. Crous, **holotype** of *P. eucalyptorum* PREM 49112, cultures ex type CPC16 = CBS 110777. **Spain**, Pontevedra, Lourizán, Areeiro, on leaves of *E. globulus*, 2003, J.P. Mansilla, **holotype** of *P. pseudoeucalyptorum* CBS H-9893, culture ex-type CPC 10390 = CBS 114242.

*Note*: *Pseudocercospora pseudoeucalyptorum* is reduced to synonymy with *P. eucalyptorum* on the basis of the phylogeny obtained here and similarity in pigmentation (Crous *et al.* 2004c).

***Pseudocercospora exosporioides*** (Bubák) B. Sutton & Hodges, Mycologia 82: 320. 1990.

*Basionym*: *Cercospora exosporioides* Bubák, Ann. Mycol. 13: 33. 1915.

*Specimen examined*: **Japan**, Ibaraki, on *Sequoia sempervirens*, 11 Sep. 1998, T. Kobayashi, CNS-448, cultures MUCC 893, MAFF 237788.

***Pseudocercospora flavomarginata*** G.C. Hunter, Crous & M.J. Wingf., Fungal Diversity 22: 80. 2006. Fig. 34.

*Specimens examined*: **Thailand**, Chang Gao Province near Pratchinburi, on leaves of *Eucalyptus camaldulensis,* 2004, M.J. Wingfield, **holotype** PREM 58952, cultures ex-type CBS 118841, 118823, 118824; Chachoengsao Province, on leaves of *E. camaldulensis*, 2001, W. Himaman, CBS H-20388, culture CPC 13492–13494.

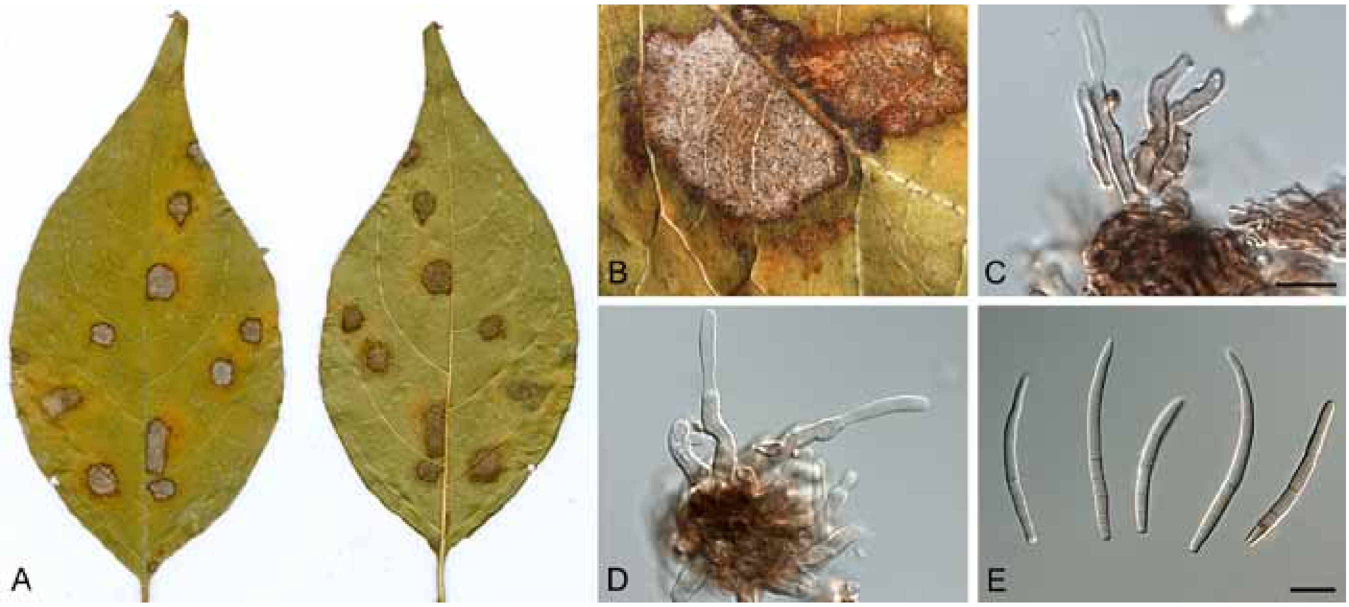


**Fig. 35.** *Pseudocercospora fukuokaensis* (CPC 14689). A. Leaf spots on upper and lower leaf surface. B. Close-up of leaf spot with fruiting. C, D. Fascicles with conidiophores and conidiogenous cells. E. Conidia. Scale bars = 10 µm.

**China**, on leaves of *Eucalyptus* sp., 2003, X. Zhou, CBS H-20390, culture ex-type CPC 14142 = CBS 126001.

*Notes*: *Pseudocercospora flavomarginata* was described as the causal agent of a prominent leaf spot disease of *E. camaldulensis* in Thailand (Hunter *et al*. 2006a). Based on this study it appears that it is present also on this host in China.

***Pseudocercospora fukuokaensis*** (Chupp) X.J. Liu & Y.L. Guo, Mycosystema 5: 103. 1992. Fig. 35.
*Basionym*: *Cercospora fukuokaensis* Chupp, Sci. Rep. Yokahama Natl. Univ., Sect. II, Biol. Sci. 1: 2. 1952.

*Specimens examined*: **Japan**, Fukuoka, Futsukaichi-machi, on *Styrax japonicus*, 5 Sep. 1951, S. Katsuki, **holotype** TNS-F243813; Ibaraki, on *S. japonicus,* 11 Sep. 1998, T. Kobayashi & C. Nakashima, **epitype designated here** TFM: FPH-8096, ex-epitype cultures MUCC 887, MAFF 237768; Ibaraki, Ibaraki Nat. Mus., on *S. japonicus,* 10 Sep. 1998, T. & Y. Kobayashi; Fukuoka, Fukuoka For. Exp. Stn., on *S. japonicus,* 30 Jul. 1975, S. Ogawa (TFM: FPH-4356); Kaogshima, Tanegashima Is., on *S. japonicus,* 18 Oct. 1997, T. Kobayashi & C. Nakashima (culture: MAFF238203); Kagoshima, Tokunoshima Is., on *S. japonicus*, 8 Nov. 1993, T. Kobayashi & T. Hosoya (Culture: MAFF236995); Okinawa, Kunigami, on *S. japonicus*, 18 Nov. 1999, T. Kobayashi & C. Nakashima; Fukuoka, Fukuoka For. Exp. Stn., on *S. obassia*, 14 Sep. 1978, S. Ogawa (TFM: FPH -4941); Fukuoka, on *S. grandiflora* (= *S. japonicus* var. *kotoensis*), Oct. 2001, T. Kobayashi (MAFF 238480); Yamaguchi, on *S. japonicus*, Dec. 1996, T. Kobayashi (MAFF 237634); Saitama, on *S. japonicus*, Sep. 2002, T. Kobayashi & Y.Ono (MAFF 239411). **South Korea**, Osan, *S. japonicus,* 30 Oct. 2007, H.D. Shin, culture CPC 14689 = CBS 132111.

*Notes*: DNA sequence data for different isolates from *Styrax japonica* collected in Japan are identical, and distinct from the strain collected in Korea, suggesting that the Korean material represents a different taxon.

***Pseudocercospora fuligena*** (Roldan) Deighton, Mycol. Pap. 140: 144. 1976.
*Basionym*: *Cercospora fuligena* Roldan, Philipp. J. Sci. 66: 8. 1938.

*Holotype*: **Philippines**, Luzon, Laguna, College of Agriculture Campus, on *Solanum lycopersicum* (≡ *Lycopersicon esculentum*), E.F. Roldan No 32, holotype (not seen).

*Specimens examined*: **Thailand**, on *Solanum lycopersicum* (variety FMMT260), 28 Aug. 2005, Z. Mersha, CBS H-20864, culture CPC 12296 = CBS 132017. **Japan**, Mie, on *Lycopersicon esculentum,* 6 Feb. 2007, C. Nakashima, MUCC 533.

*Notes*: DNA sequence data (ITS and EF-1α) for 40 Japanese isolates revealed variation in only one position (data not shown) and the culture from Thailand is very similar genetically. The collections of *P. fuligena* treated in this study are also morphologically similar to the description of the holotype specimen, which was collected in the Philippines. Chupp (1954) did not see the holotype, nor did Deighton (1976) refer to it. Fresh collections from the type location are needed to resolve this apparent species complex.

***Pseudocercospora glauca*** (Syd.) Y.L. Guo & X.J. Liu, Acta Mycol. Sin. 11: 132. 1992. Fig. 36.
*Basionym*: *Cercospora glauca* Syd., Ann. Mycol. 27: 432. 1929.

*Specimen examined*: **South Korea**, Wando, Wando arboretum, on *Albizzia julibrissin,* 9 Nov. 2002, H.D. Shin, CBS H-20865, culture CPC 10062 = CBS 131884.

***Pseudocercospora guianensis*** (F. Stevens & Solheim) Deighton, Mycol. Pap. 140: 145. 1976.
*Basionym*: *Cercospora guianensis* F. Stevens & Solheim, Mycologia 23: 375. 1931.

*Specimen examined*: **Japan**, Tateyama, Chiba, on *Lantana camara*, 4 June 1997, C. Nakashima CNS-162, cultures MUCC 879, MAFF 238239.

***Pseudocercospora haiweiensis*** Crous & X. Zhou, **sp. nov.** MycoBank MB564832. Fig. 37.

*Etymology*: Name is derived from Hai Wei, China, where this fungus was collected.

*Leaf spots* amphigenous, irregular to subcircular or angular, 2–4 mm diam, brown, with raised border, and at times with a red-purple margin. *Mycelium* internal, subhyaline, consisting of septate, branched, smooth, 2–3 µm diam hyphae. *Caespituli* fasciculate to sporodochial, amphigenous, breaking through epidermis, appearing

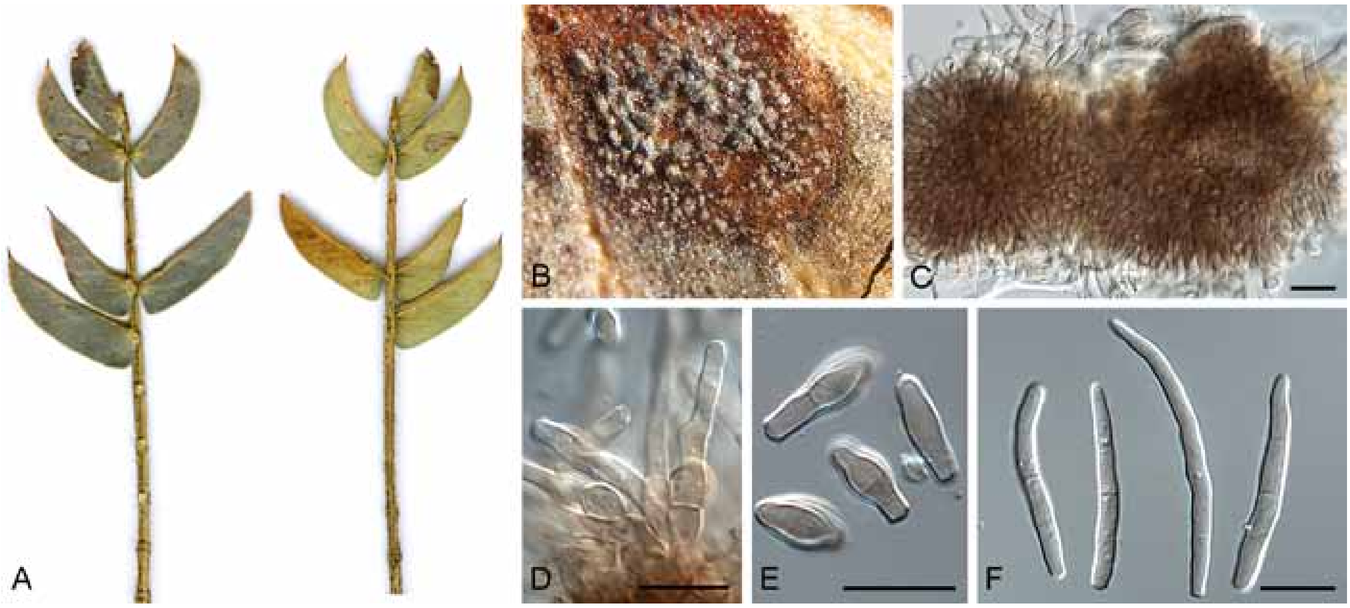

**Fig. 36.** *Pseudocercospora glauca* (CPC 10062). A. Leaf spots on upper and lower leaf surface. B. Close-up of leaf spot with fruiting. C. Fascicle with conidiophores and conidiogenous cells. D. Conidiophores. E, F. Conidia. Scale bars = 10 µm.

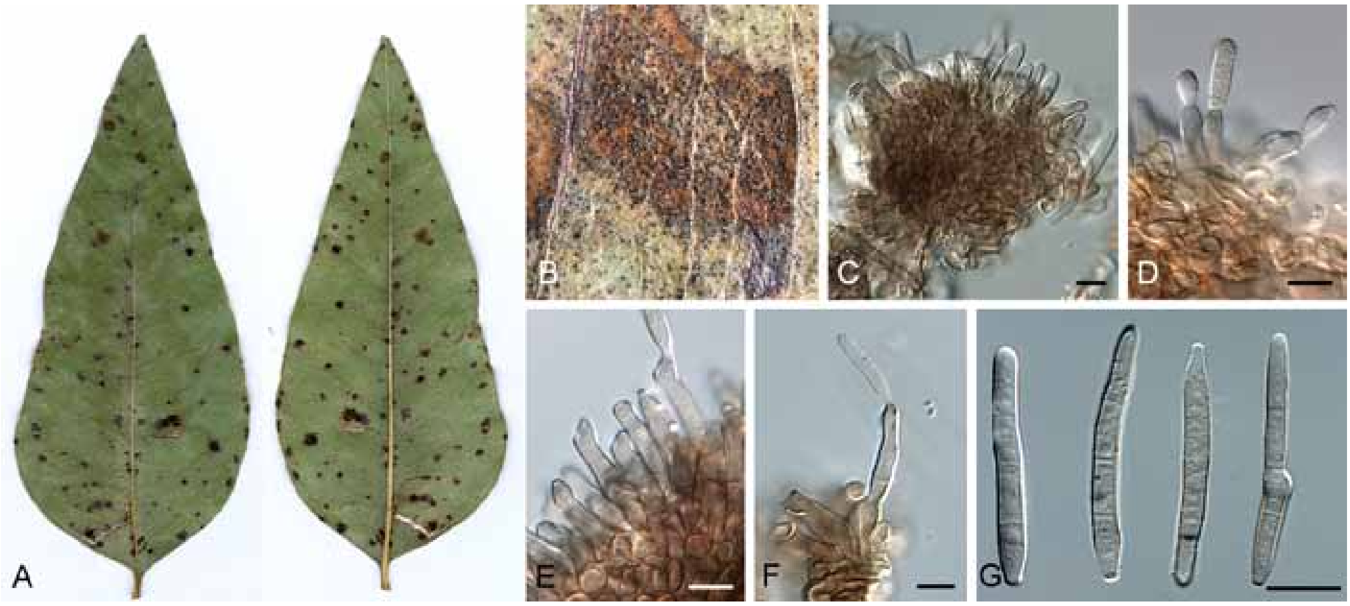

**Fig. 37.** *Pseudocercospora haiweiensis* (CPC 14084). A. Leaf spots on upper and lower leaf surface. B. Close-up of leaf spot with fruiting. C. Fascicle with conidiophores and conidiogenous cells. D–F. Conidiophores. G. Conidia. Scale bars = 10 µm.

almost acervular, grey-brown on leaves, up to 90 µm wide and 50 µm high. *Conidiophores* aggregated in dense fascicles arising from the upper cells of a brown stroma up to 60 µm wide and 30 µm high; conidiophores brown, smooth to finely verruculose, 0–2-septate, subcylindrical, straight to variously curved or geniculate-sinuous, unbranched, 10–25 × 3–4 µm. *Conidiogenous cells* terminal, unbranched, brown, subcylindrical, smooth to finely verruculose, tapering to flat-tipped apical loci, proliferating sympodially, rarely percurrently near apex, 10–15 × 2.5–3.5 µm. *Conidia* solitary, brown, finely verruculose, guttulate, subcylindrical, apex obtuse, base obconically subtruncate to truncate, straight to gently curved, 3(–5)-septate, (25–)30–40(–45) × 3(–4) µm; hila unthickened, neither darkened nor refractive, 1.5 µm wide.

*Culture characteristics*: Colonies after 2 wk at 24 ºC in the dark on MEA; surface folded, erumpent, spreading, with moderate aerial mycelium, and smooth, lobate margins. Surface olivaceous-grey with patches of pale olivaceous-grey; reverse olivaceous-grey. Colonies reaching 12 mm diam.

*Specimen examined*: **China**, Hai Wei, on leaves of *Eucalyptus* sp. (APP 21), 3 June 2007, X. Zhou, **holotype** CBS H-20866, culture ex-type CPC 14084 = CBS 131584.

*Notes*: A combination of relatively short conidia (1–3-septate, 25–45 × 3–4 µm) that are subcylindrical in shape, the absence of superficial mycelium, and dense fascicles with well-developed stromata, distinguish this new species on *Eucalyptus* from other taxa known from this host (Crous 1998, Braun & Dick 2002).

***Pseudocercospora hakeae*** (U. Braun & Crous) U. Braun & Crous, **comb. et stat. nov.** MycoBank MB564833.

*Basionym*: *Cercostigmina protearum* var. *hakeae* U. Braun & Crous, Sydowia 46: 206. 1994.

≡ *Pseudocercospora protearum* var. *hakeae* (U. Braun & Crous) U. Braun & Crous, Mycol. Progr. 1: 22. 2002.

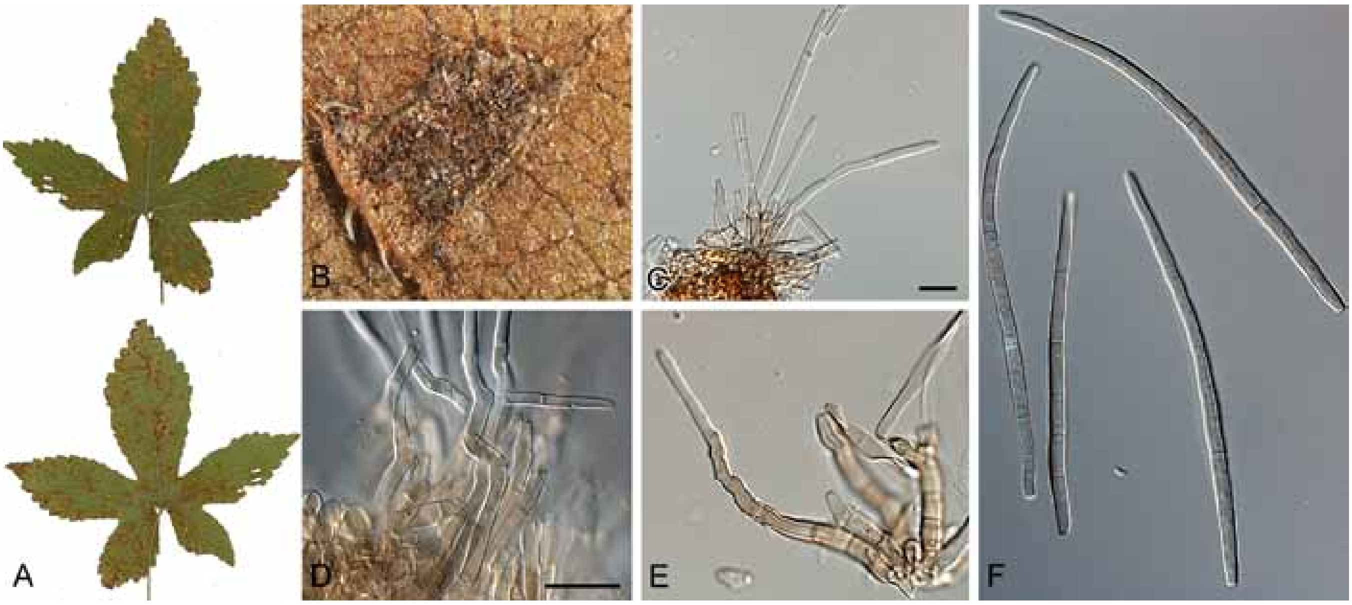


**Fig. 38.** *Pseudocercospora humulicola* (CPC 11358). A. Leaf spots on upper and lower leaf surface. B. Close-up of leaf spot with fruiting. C–E. Fascicles with conidiophores and conidiogenous cells. F. Conidia. Scale bars = 10 µm.

*Specimens examined*: **South Africa**, Northern Province, Louis Trichardt, Hangklip Forest Station, on leaves of *Hakea salicifolia* (= *H. saligna*), Apr. 1988, C. Roux, **holotype** PREM 51117. **Australia**, New South Wales, Mount Annan Botanic Gardens, on leaves of *Grevillea* sp., Aug. 1999, P.W. Crous & B. Summerell, JT 926, DAR 74861, CPC 2968; Mount Tomah Botanic Gardens, on leaves of *Grevillea* sp., Aug. 1999, P.W. Crous & B. Summerell, JT 873, DAR 74862, CPC 3145 = CBS 112226.

*Note:* No culture from *Hakea* is presently available, and thus the position of this taxon on *Hakea* and *Grevillea* has yet to be confirmed based on DNA sequence comparisons.

***Pseudocercospora humuli*** (Hori) Y.L. Guo & X.J. Liu, Acta Mycol. Sin., Suppl. 1: 345. (1986) 1987.
*Basionym*: *Cercospora humuli* Hori, in S. Takimoto, Trans. Agric. Assoc. Chosen 13(12): 34. 1918.
≡ *Cercospora humuli* Hori, in Salmon & Wormald. J. Bot. (London) 61: 135. 1923.
= *Cercospora humuli-japonici* Sawada, Taiwan Agric. Rev. 38: 697. 1942, nom. inval.
≡ *Pseudocercospora humuli-japonici* Sawada ex Goh & W.H. Hsieh, in Hsieh & Goh, *Cercospora* and similar fungi from Taiwan: 239. 1990.

*Specimens examined*: **Japan**, Tokyo, Nishigahara, on *Humulus scandens*, 28 Sep. 1915, S. Hori, **holotype** NIAES herbarium C-487; Wakayama, on *H. lupulus* var. *lupulus*, 30 Oct. 2007, C. Nakashima & I. Araki, **epitype designated here** TFM: FPH-8097, ex-epitype culture MUCC 742.

***Pseudocercospora humulicola*** Crous, U. Braun & H.D. Shin, **sp. nov.** MycoBank MB564834. Fig. 38.

*Etymology*: Name derived from *Humulus*, the plant on which it was collected.

*Leaf spots* amphigenous, irregular to angular, 0.5–1.5 mm diam, brown, with raised border and wide chlorotic halo. *Mycelium* internal, subhyaline, consisting of septate, branched, smooth, 2–3 µm diam hyphae. *Caespituli* fasciculate to sporodochial, amphigenous, predominantly epiphyllous, pale brown on leaves, up to 90 µm wide and 200 µm high. *Conidiophores* aggregated in dense fascicles arising from the upper cells of a brown stroma up to 80 µm wide and 30 µm high; conidiophores pale brown, smooth, 2–5-septate, subcylindrical, straight to variously curved or geniculate-sinuous, unbranched, 40–90 × 3–4 µm. *Conidiogenous cells* terminal, unbranched, subhyaline to pale brown, subcylindrical, smooth, tapering to flat-tipped apical conidiogenous loci, 2 µm diam, proliferating sympodially, 10–30 × 3–4 µm. *Conidia* solitary, subhyaline, smooth, finely granular, subcylindrical, apex obtuse, base truncate, straight to gently curved, 3–12-septate, (70–)80–95(–120) × 2.5(–3) µm; hila unthickened, neither darkened nor refractive, 2–3 µm wide.

*Culture characteristics*: Colonies after 2 wk at 24 ºC in the dark on MEA; surface folded, erumpent, spreading, with sparse aerial mycelium, and smooth, lobate margins. Surface pale olivaceous-grey; reverse olivaceous-grey. Colonies reaching 10 mm diam.

*Specimens examined*: **South Korea**, Hongchon, on leaves of *Humulus scandens,* 9 Jul. 2004, H.D. Shin, **holotype** CBS H-20867, culture ex-type CPC 11358 = CBS 131585; Chuncheon, on *H. scandens,* 11 Oct. 2002, H.D. Shin, CBS H-20868, culture CPC 10049 = CBS 131883; Cheongju, on *H. scandens,* 4 June 2004, H.D. Shin, CBS H-20869, culture CPC 10002.

*Notes*: *Pseudocercospora humulicola* is very similar to *P. humuli*, originally described from Japan, but it is distinct based on DNA sequence comparisons. In *P. humuli* conidia are obclavate-cylindrical, 35–120 × 2.5–4 µm (Chupp 1954), while conidia of *P. humulicola* are subcylindrical, and on average longer than 80 µm. Furthermore, *P. humuli* has shorter conidiophores (10–55 µm long, 0–2-septate) than those of *P. humulicola*, which are 2–5-septate, and 40–90 µm long.

***Pseudocercospora jussiaeae*** (G.F. Atk.) Deighton, Mycol. Pap. 140: 146. 1976. Fig. 39.
*Basionym*: *Cercospora jussiaeae* G.F. Atk., J. Elisha Mitchell Sci. Soc. 8: 50. 1892.
= *Cercospora ludwigiae* G.F Atk., J. Elisha Mitchell Sci. Soc. 8: 58. 1892.

*Specimen examined*: **South Korea**, Hongcheon, on *Ludwigia prostrata*, 9 Oct. 2007, H.D. Shin, KUS-F22981, CBS H-20870, culture CPC 14625 = CBS 132117.


**Fig. 39.** *Pseudocercospora jussiaeae* (CPC 14625). A. Leaf spots on upper and lower leaf surface. B. Close-up of leaf spot with fruiting. C, D. Fascicles with conidiophores and conidiogenous cells. E. Conidia. Scale bars = 10 µm.

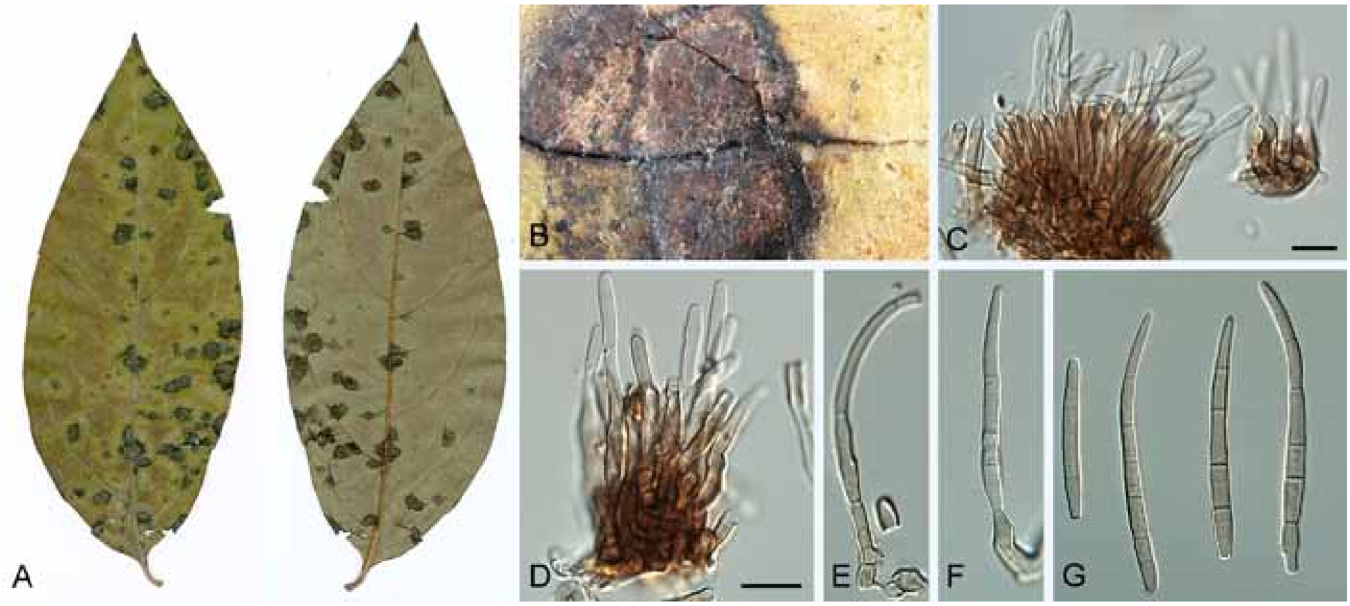


**Fig. 40.** *Pseudocercospora kaki* (CPC 10837–10839). A. Leaf spots on upper and lower leaf surface. B. Close-up of leaf spot with fruiting. C, D. Fascicles with conidiophores and conidiogenous cells. E, F. Conidiogenous cells. G. Conidia. Scale bars = 10 µm.

***Pseudocercospora kaki*** Goh & W.H. Hsieh, in Hsieh & Goh, *Cercospora* and similar fungi from Taiwan: 109. 1990. Fig. 40.

*Specimens examined*: **Japan,** Toyama, Kureha, on *Diospyros kaki*, 25 Sep. 1998, T. Kobayashi & E. Imaizumi, CNS-472, culture MAFF 238214; Chiba, on *D. kaki*, 18 Sep. 1998, S. Uematsu & C. Nakashima, CNS-464, cultures MUCC 900, MAFF 238238; Chiba, on *D. kaki*, Nov. 1993, T. Kobayashi, cultures MAFF 237013. **South Korea**, Gongju, on *D. lotus*, 28 Oct. 2003, H.D. Shin, CBS H-20871, cultures CPC 10837–10839.

*Additional isolates examined (representing a different lineage)*: **Japan,** Kagoshima, Oshima Is., on *D. kaki*, 11 Nov. 1993, T. Kobayashi, CNS-993, culture MAFF 236999; Chiba, on *D. kaki*, Oct. 1991, T. Kobayashi, culture MAFF 235880.

*Notes*: The type specimen of this species is from Taiwan but the type was not cultured or sequenced. It may be synonymous with *Cercospora kaki*, which is based on material from the USA. The Japanese material studied here is different from the Korean material based on DNA sequence data. Actin sequences generated for additional Japanese isolates resolved two different lineages, one of which may be attributed to *Cercospora kakivora*, but this can only be resolved once fresh collections from Taiwan and the USA have been obtained.

***Pseudocercospora kiggelariae*** (Syd.) Crous & U. Braun, Sydowia 46: 215. 1994.
*Basionym*: *Cercospora kiggelariae* Syd., Ann. Mycol. 22: 434. 1924.

*Holotype*: **South Africa**, Western Cape Province, Stellenbosch, on leaves of *Kiggelaria africana*, May 1924, C.K. Brain No 1449 (not preserved).

*Specimens examined*: **South Africa**, Gauteng, Walter Susulu Botanical Garden, on leaves of *K. africana*, Jan. 2005, W. Gams, **neotype designated here** CBS H-20872, cultures ex-neotype CPC 11853 = CBS 132016; Western Cape Province, Hermanus, Fernkloof Botanical Garden, S34º23'52.1" E19º15'58.5", *K. africana*, 2 May 2010, P.W. Crous, CBS H-20873, CPC 18286, 18287.

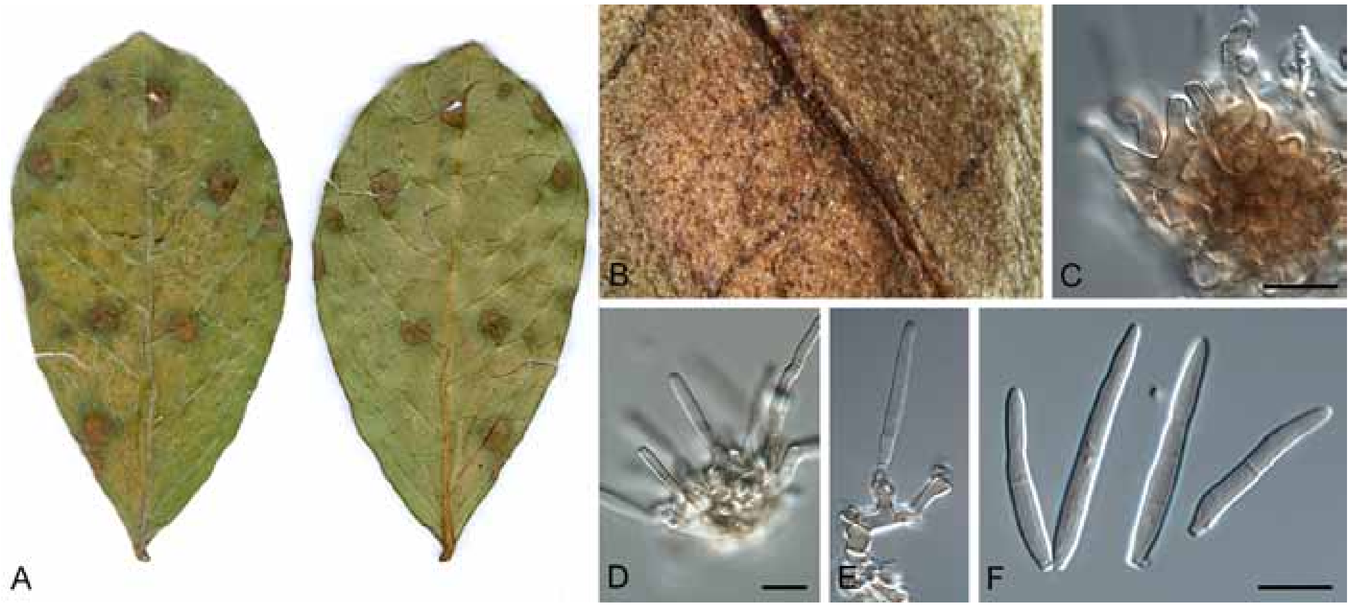


**Fig. 41.** *Pseudocercospora lythracearum* (CPC 10707). A. Leaf spots on upper and lower leaf surface. B. Close-up of leaf spot with fruiting. C, D. Fascicles with conidiophores and conidiogenous cells. E. Conidiophore with conidiogenous cells. F. Conidia. Scale bars = 10 µm.

***Pseudocercospora latens*** (Ellis & Everh.) Y.L. Guo & X.J. Liu, Mycosystema 2: 236. 1989.
*Basionym*: *Cercospora latens* Ellis & Everh., J. Mycol. 4: 3. 1888.
≡ *Pseudocercospora latens* (Ellis & Everh.) U. Braun, Trudy Bot. Inst. im. V.L. Komarova 20: 67. 1997, comb. superfl.

*Specimen examined*: **Japan**, Okinawa, on *Lespedeza wilfordii* (= *L. thunbergii* subsp. *formosa*), 18 Nov. 2007, C. Nakashima & T. Akashi, MUMH 10815, culture MUCC 763.

***Pseudocercospora leucadendri*** (Cooke) U. Braun & Crous, **comb. et stat. nov.** MycoBank MB564835.
*Basionym*: *Cercospora protearum* var. *leucadendri* Cooke, Grevillea 12: 39. 1883.
≡ *Stigmina protearum* var. *leucadendri* (Cooke) M.B. Ellis, Mycol. Pap. 131: 7. 1972.
≡ *Cercostigmina protearum* var. *leucadendri* (Cooke) U. Braun & Crous, in Crous & Braun, Sydowia 46: 206. 1994.
≡ *Pseudocercospora protearum* var. *leucadendri* (Cooke) U. Braun & Crous, Mycol. Progr. 1: 22. 2002.
= *Passalora protearum* Kalchbr. & Cooke, Grevillea 19: 6. 1890.

*Specimen examined*: **South Africa**, Western Cape Province, Stellenbosch, Devon Valley, Protea Heights, on *Leucadendron* sp., 3 Apr. 1998, S. Denman & P.W. Crous, specimen JT-178, culture CPC 1869 (no longer viable).

*Note*: *Pseudocercospora protearum* has three varieties on *Proteaceae*, *viz*. *protearum, leucadendri* and *hakeae* (Braun & Hill 2002), that should be recognised as distinct species (Crous *et al*. 2004a) as shown here (Fig. 5).

***Pseudocercospora lonicericola*** (W. Yamam.) Deighton, Mycol. Pap. 140: 146. 1976.
*Basionym*: *Cercospora lonicericola* W. Yamam. J. Soc. Trop. Agric. 6: 604. 1934.

*Holotype*: **Taiwan**, Taihoku, on *Lonicera japonica* var. *sempervillosa*, 3 Nov. 1933, W. Yamamoto (holotype could not be located, and is probably lost).

*Specimens examined*: **Japan,** Tokyo, Jindai Bot. Park, on *L. japonica*, 21 Oct. 1976, T. Kobayashi, TFM: FPH-4479; Chiba, Matsudo, on *L. japonica*, 14 Sep. 1951, E. Kurosawa, SK -2207; Fukuoka, Yame, on *L. japonica*, 29 Nov. 1949, S. Katsuki, SK -2206; Kagoshima, Yaku Is., on *L. japonica*, 29 Dec. 1952, S. Katsuki, SK -392; Ibaraki, *L. gracilipes* var. *glabra*, 11 Sep. 1998, T. Kobayashi, **neotype designated here** TFM: FPH-8098, ex-neotype cultures MUCC 889, MAFF 237785.

***Pseudocercospora lyoniae*** (Katsuki & Tak. Kobay.) Deighton, Trans. Brit. Mycol. Soc. 88: 389. 1987.
*Basionym*: *Cercospora lyoniae* Katsuki & Tak. Kobay., Trans. Mycol. Soc. Japan 16: 3. 1975.

*Specimens examined*: **Japan**, Tokyo, Asakawa Experimental Forest, Government Forest Experimental Station, on *Lyonia ovalifolia* var. *elliptica,* 21 Sep. 1973, H. Horie, **holotype** TFM: FPH-3999; Tokyo, Jindai Bot. Garden, on *L. ovalifolia* var. *elliptical,* 25 Sep. 1974, T. Kobayashi, TFM: FPH -4202; Tokyo, Jindai Bot. Garden, on *L. ovalifolia* var. *elliptica,* 7 Nov. 1998, C. Nakashima & E. Imaizumi, **epitype designated here** TFM: FPH-8100, ex-epitype cultures MUCC 910, MAFF 237775.

***Pseudocercospora lythracearum*** (Heald & F.A. Wolf) X.J. Liu & Y.L. Guo, Acta Mycol. Sin. 11: 294. 1992. Fig. 41.
*Basionym*: *Cercospora lythracearum* Heald & F.A. Wolf, Mycologia 3: 18. 1911.
≡ *Cercosporina lythracearum* (Heald & F.A. Wolf) Sacc., Syll. Fung. 25: 909. 1931.
= *Cercospora lagerstroemiae* Syd. & P. Syd., Ann. Mycol. 12: 203. 1914.
= *Cercospora lagerstroemiae-subcostatae* Sawada, Taiwan Agric. Res. Inst. Rept. 51: 129. 1931.
≡ *Pseudocercospora lagerstroemiae-subcostatae* (Sawada) Goh & W.H. Hsieh, in Hsieh & Goh, *Cercospora* and similar fungi from Taiwan: 212. 1990.
= *Cercospora lagerstroemiicola* Sawada, Taiwan Agric. Res. Inst. Rept. 85: 112. 1943, nom. inval.

*Specimens examined*: **Japan**, Ibaraki, on *Lagerstroemia indica*, 11 Sep. 1998, T. Kobayashi, CNS-444, cultures MUCC 890, MAFF 237786; Kanagawa, isolated from *L. subcostata*, collection date unknown, T. Kobayashi, MAFF 410017; Ibaraki, isolated from *L. subcostata*, Oct. 1994, T. Nishijima, MAFF 237185; Chiba, isolated from *L. subcostata*, Oct. 1993, T. Kobayashi, MAFF 236964. **South Korea**, Jinju, *L. indica*, 15 Oct. 2003, H.D. Shin, CBS H-20874, KUS-F 19899, culture CPC 10707 = CBS 131925.

*Notes*: The material collected from Korea is genetically similar to that from Japan (Fig. 5). However, fresh collections from the USA are required to determine if the Asian material is the same as that from the USA. The synonyms cited by Chupp (1954) could represent different species.

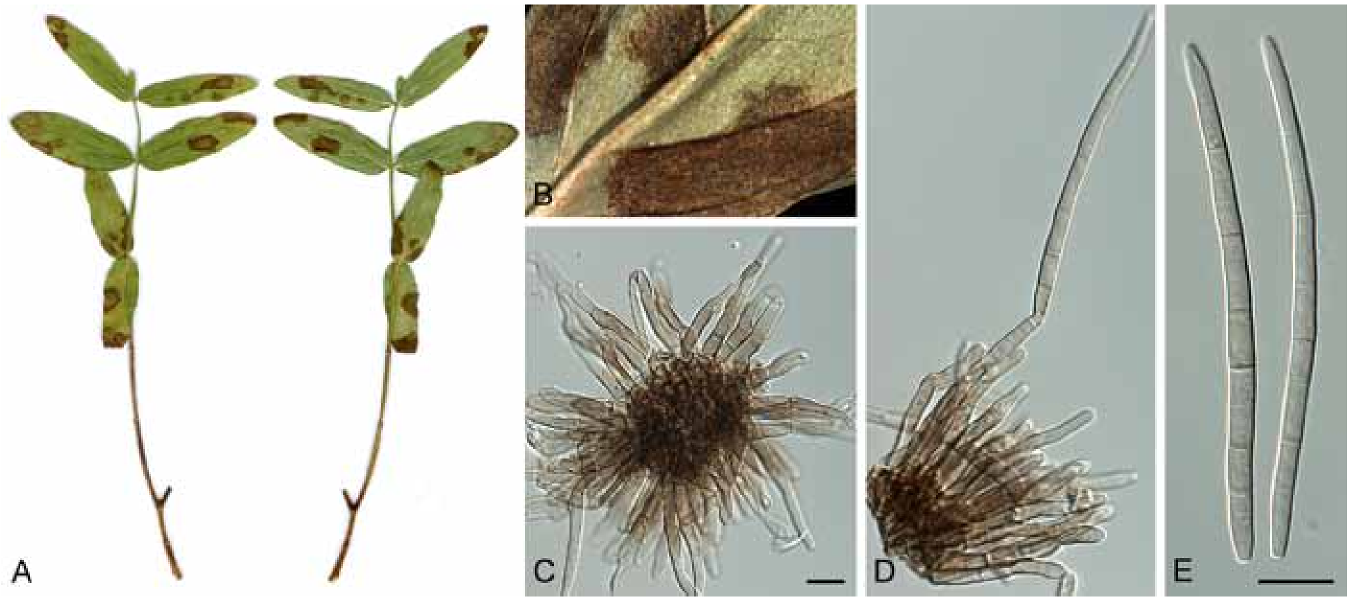


**Fig. 42.** *Pseudocercospora lythri* (CPC 14588). A. Leaf spots on upper and lower leaf surface. B. Close-up of leaf spot with fruiting. C, D. Fascicles with conidiophores and conidiogenous cells. E. Conidia. Scale bars = 10 µm.

***Pseudocercospora lythri*** H.D. Shin & U. Braun, Mycotaxon 74: 111. 2000. Fig. 42.

*Specimens examined*: **Japan**, Tokyo, on *Lythrum salicaria* (incl. *L. anceps*) 10 Nov. 2007, I. Araki & M. Harada, MUMH 11104, culture MUCC865. **South Korea**, Chuncheon, on *L. salicaria*, 21 Sep. 1991, H.D. Shin, **holotype** KUS-F 11109; Yangku, on *L. salicaria,* 28 Sep. 2007, H.D. Shin, **epitype designated here** CBS H-20875, culture ex-epitype CPC 14588 = CBS 132115.

***Pseudocercospora marginalis*** G.C. Hunter, Crous, U. Braun & H.D. Shin, **sp. nov.** MycoBank MB564836. Fig. 43.

*Etymology*: *Margo*, *marginalis*, referring to border or margin; indicating leaf spots that extend along the leaf margin.

*Leaf spots* distinct, 2–5 mm diam, also predominantly forming larger blotches extending along the length of the leaf margin, brown, irregular; border indefinite. *Mycelium* internal and external, septate, smooth, subhyaline, branched, 2–4 µm wide. *Caespituli* epiphyllous, aggregated along leaf veins, floccose, olivaceous, emerging from stomata. *Stromata* well-developed, subimmersed to erumpent, globular to elongated, brown, 20–75 µm diam. *Conidiophores* fasciculate, pale brown to brown, straight to curved to undulate, cylindrical, unbranched, apex rounded to subtruncate, smooth, finely guttulate, 0–4-septate, (15–)18–31(–41) × (3–)4(–5) µm. *Conidiogenous cells* terminal, unbranched, smooth, finely guttulate, pale brown, straight to curved, cylindrical, apex rounded to subtruncate, proliferating sympodially or percurrently, (5–)8–11(–14) × 3(–4) µm. *Conidia* solitary, smooth, cylindrical to narrowly obclavate, guttulate, thick-walled, straight to curved, pale brown to pale olivaceous, apex rounded to obtuse, base obconic to long obconically truncate, 1–7-septate, (19–)30–48(–58) × (3–)4(–5) µm; hila neither thickened nor darkened.

*Culture characteristics*: Colonies after 2 wk at 24 ºC in the dark on MEA; erumpent, spreading, with moderate aerial mycelium, and smooth, even margins. Surface pale olivaceous-grey; reverse olivaceous-grey. Colonies reaching 10 mm diam.

*Specimen examined*: **South Korea**, Jeju, Halla arboretum, on leaves of *Fraxinus rhynchophylla* (≡ *F. chinensis* subsp. *rhynchophylla*), 29 Oct. 2005, H.D. Shin, **holotype** CBS H-20397, culture ex-type CPC 12497 = CBS 131582, CPC 12498, 12499.

*Specimens examined of P. fraxinites*: **South Korea**, Jinju, on *Fontanesia phillyreoides*, 15 Oct. 2003, H.D. Shin, CBS H-20876, cultures CPC 10743–10745. **Japan**, Ibaraki, on *Fraxinus excelsior*, 11 Sep. 1998, T. Kobayashi, CNS-445, cultures MUCC 891, MAFF 237787.

*Notes*: Although similar to *P. fraxinites* (conidia 20–60 × 1.5–3 µm; Chupp 1954) (Fig. 44), conidia of *P. marginalis* are wider and cluster apart from isolates of *P. fraxinites* on *Fontanesia* from Korea (CPC 10743–10745) and *Fraxinus* from Japan (MUCC 891). *Pseudocercospora fraxinites* was originally described from *Fraxinus* in the USA. Morphological and molecular characterisation of new collections and cultures from this host in the USA are needed to clarify the limits of *P. fraxinites* and *P. marginalis*.

***Pseudocercospora melicyti*** U. Braun & C.F. Hill, Australas. Pl. Pathol. 33: 489. 2004.

*Specimen examined*: **New Zealand**, Auckland, Waiatarua, on *Melicytus macrophyllus*, 13 Mar. 2003, C.F. Hill, **holotype** HAL 1787 F (isotype PDD 77567), culture ex-type ICMP 14984 = CBS 115023.

***Pseudocercospora myrticola*** (Speg.) Deighton, Mycol. Pap. 140: 148. 1976.
*Basionym*: *Cercospora myrticola* Speg., Anales Soc. Ci. Argent. 16: 167. 1883.

= *Cercospora myrti* Erikss., Bidrag Känn. om vara odlade Vaxters s jukdomar, Stockholm 8: 79. 1885 and Rev. Mycol. 8: 60. 1886.
= *Cercospora saccardoana* Scalia, Atti Accad. Gioenia Sci. Nat. Catania, Ser. 4, 14: 35. 1901.
= *Cercospora amadelpha* Syd., Ann. Mycol. 30: 89. 1932.
= *Fusariella cladosporioides* P. Karst., Hedwigia 30: 248. 1891.

*Specimen examined*: **Japan**, Kagoshima, on *Myrtus communis*, 29 May 2007, C. Nakashima & K. Motohashi, MUMH 10572, culture MUCC 632.

***Pseudocercospora ocimi-basilici*** Crous, M.E. Palm & U. Braun, **sp. nov.** MycoBank MB564837. Fig. 45.

*Etymology*: Name derived from *Ocimum basilicum*, the host from which it was collected.

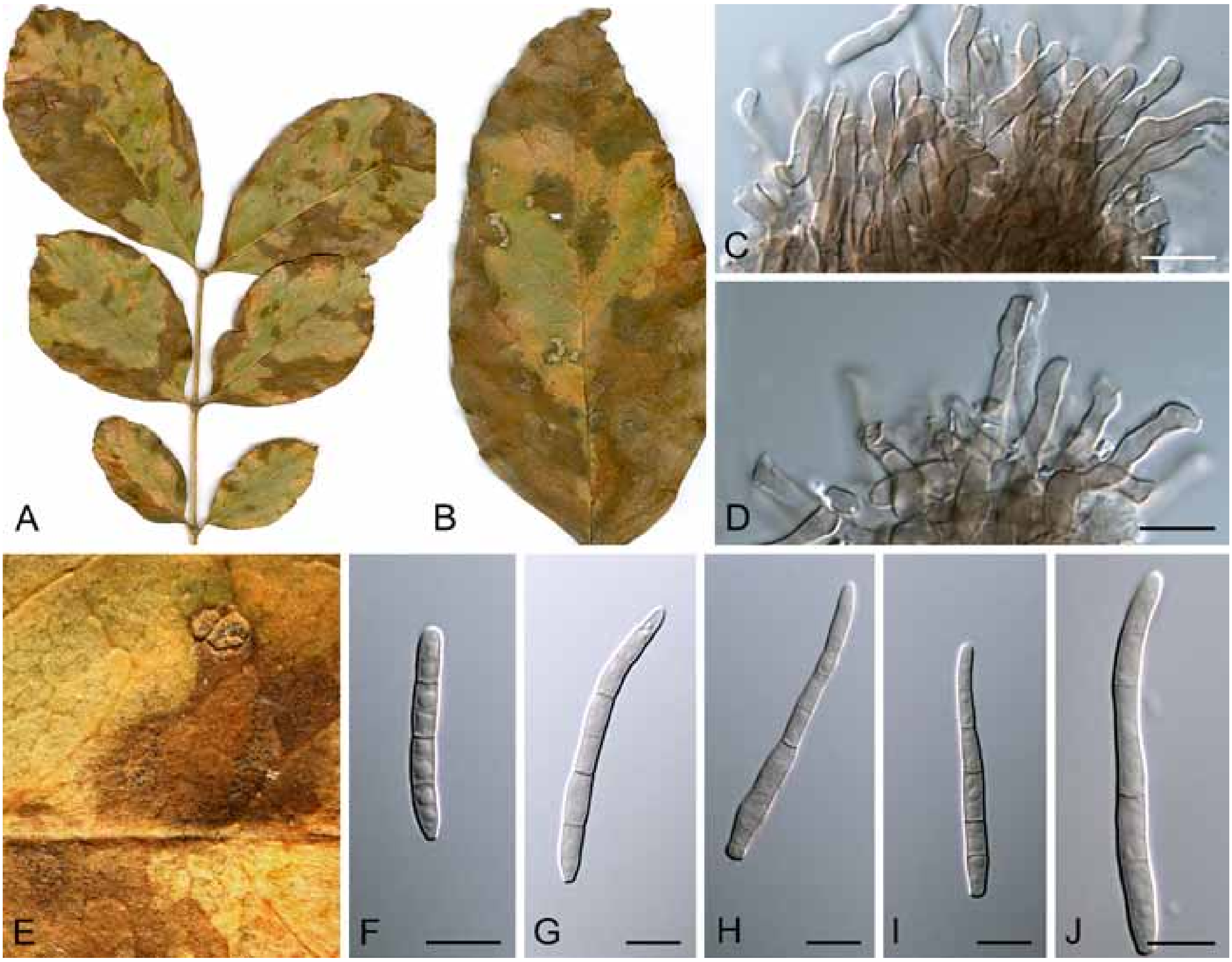

**Fig. 43.** *Pseudocercospora marginalis* (CPC 12497). A, B. Leaf spots on upper and lower leaf surface. C, D. Fascicles with conidiophores and conidiogenous cells. E. Close-up of leaf spot with fruiting. F–J. Conidia. Scale bars = 10 µm.

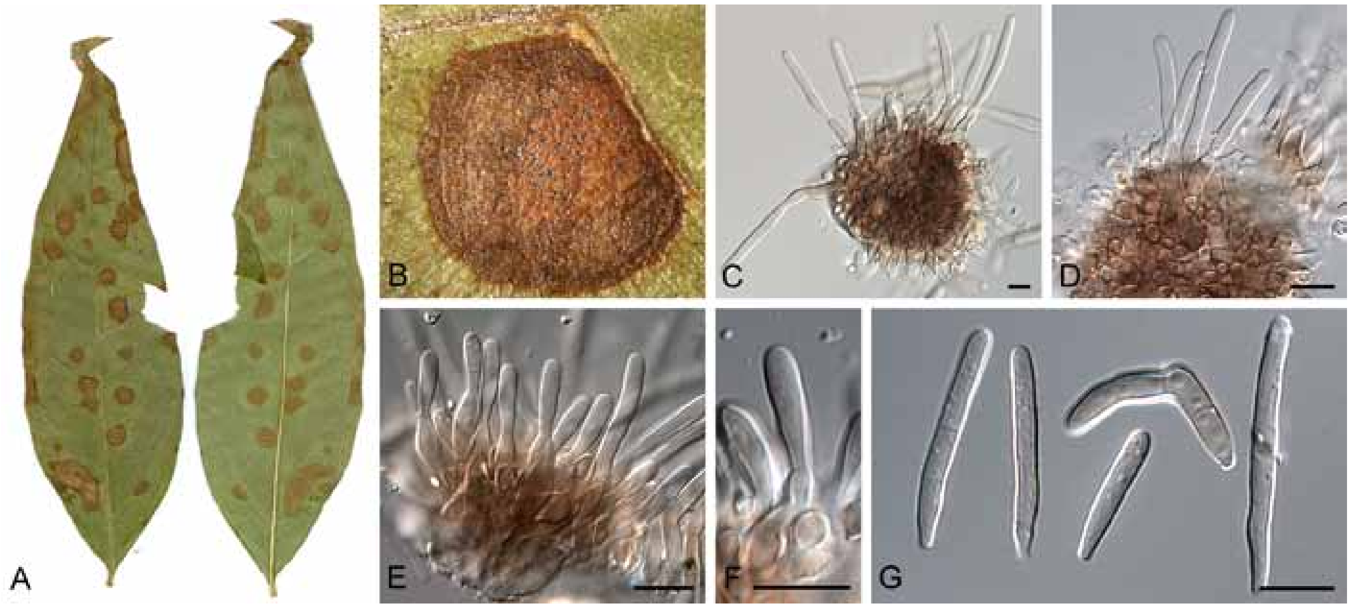

**Fig. 44.** *Pseudocercospora fraxinites* (CPC 10743–10745). A. Leaf spots on upper and lower leaf surface. B. Close-up of leaf spot with fruiting. C–E. Fascicles with conidiophores and conidiogenous cells. F. Conidiogenous cells. G. Conidia. Scale bars = 10 µm.

*Leaf spots* amphigenous, subcircular, circular or somewhat irregular, 2–10 mm diam, greyish green, dull grey to dark brown, border indistinct, at times raised. *Mycelium* internal, pale brown, consisting of septate, branched, smooth, 2–3 µm diam hyphae. *Caespituli* fasciculate to sporodochial, brown, predominantly hypophyllous, up to 90 µm diam and 70 µm high. *Conidiophores* aggregated in mostly

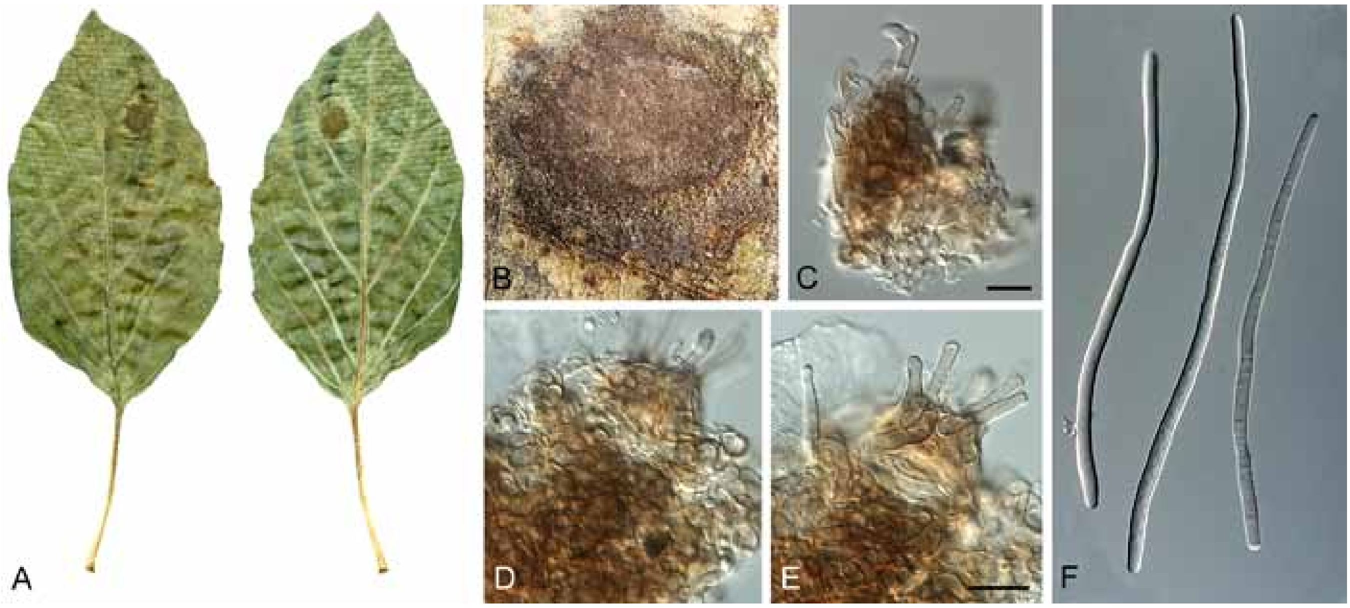


**Fig. 45.** *Pseudocercospora ocimi-basilici* (CPC 10283–10285). A. Leaf spots on upper and lower leaf surface. B. Close-up of leaf spot with fruiting. C–E. Fascicles with conidiophores and conidiogenous cells. F. Conidia. Scale bars = 10 µm.

dense, small to large, sometimes almost sporodochial fascicles, emerging through stomata or erumpent through the cuticle, arising from the upper cells of a brown, substomatal to mostly intraepidermal stroma, 10–80 µm; conidiophores pale to medium brown or olivaceous-brown, smooth, thin-walled, 0–2-septate, subcylindrical or attenuated towards the tip, straight to moderately geniculate-sinuous, unbranched or branched above, 5–35 × 2–5 µm. *Conidiogenous cells* integrated, terminal or conidiophores reduced to conidiogenous cells, pale olivaceous-brown, smooth, tapering to flat-tipped apical loci, 1–2 µm wide, proliferating sympodially, 5–20 × 2–4 µm. *Conidia* solitary, subhyaline to pale olivaceous-brown, smooth, guttulate, shape and size variable, small conidia short obclavate-cylindrical to fusiform, longer conidia narrowly obclavate-filiform, sometimes acicular, apex subacute to subobtuse, base short to long obconically truncate to truncate in acicular conidia, straight to curved, 3–12-septate, (25–)30–120 (–130) × (2–)2.5–5(–5.5) µm; hila unthickened, neither darkened nor refractive, 1.5–2.5 µm diam.

*Specimens examined*: **Fiji** (intercepted at the Auckland International Airport, on basil foliage imported from Fiji), on *Ocimum basilicum,* 24 Feb. 2002, C.F. Hill 529, HAL. **Mexico**, on *O. basilicum,* Dec. 2001, without collector (cultured as MEP 1515), BPI 841445; (intercepted at Los Angeles), 2 Nov. 2002, L.C. Lastra 1395 A, BPI 747831; 6 Dec. 2002, M.E. Palm, **holotype** CBS H-20877, culture ex-type CPC 10283–10285 (unfortunately no longer viable). **New Zealand**, Auckland, Botanical Garden, on *O. basilicum,* 9 Mar. 2002, C.F. Hill 546, HAL. **Vanuatu**, Efate, Vanuatu Tropical Products, on *O. basilicum,* 25 Oct. 1996, E. McKenzie, PDD 66438; Rainbow Garden, on *O. basilicum,* 22 Oct. 1996, E. McKenzie, PDD 66537.

*Notes*: Braun *et al*. (2003b) examined *Pseudocercospora* collections on *Ocimum basilicum* from Fiji, New Zealand, and Vanuatu and identified those collections as *P. ocimicola*, in spite of some morphological differences observed. *Pseudocercospora ocimicola* differs from collections on *Ocimum basilicum,* herein described as *P. ocimi-basilici*, in having shorter conidia (about 25–80 µm long), conidiophores in small, loose fascicles as well as solitary conidiophores arising from superficial hyphae, and lacking or almost lacking stromata.

The description of *Cercospora ocimicola* provided by Chupp (1954) covers type material of this species as well as material on *O. basilicum*. Based on type material and additional collections, *C. ocimicola* is redescribed as *P. ocimicola* in the current study (see below).

## ***Pseudocercospora ocimicola*** (Petr. & Cif.) Deighton, Mycol. Pap. 140: 149. 1976.

*Basionym*: *Cercospora ocimicola* Petr. & Cif., Ann. Mycol. 30: 324. 1932.

= *C. hyptidicola* (as "*hypticola*") Chupp & A.S. Mull., Bol. Soc. Venez. Ci. Nat. 8: 47. 1942, nom. inval.

*Leaf spots* lacking or almost so to indistinct or angular-irregular, yellowish ochraceous, olivaceous to brownish, centre finally sometimes paler, dingy greyish brown to grey, 1–10 mm diam., margin indefinite. *Mycelium* internal and external, superficial, hyphae emerging through stomata, sparingly branched, septate, subhyaline to olivaceous-brown, 1–3 µm wide, thin-walled, smooth. *Stromata* lacking or small, mostly substomatal, occasionally intraepidermal, 10–30 µm diam. *Caespituli* amphigenous, usually not very conspicuous, olivaceous-brown, finely punctiform to subeffuse. *Conidiophores* in small, loose to moderately large and denser fascicles, arising from stromata or internal hyphae, through stomata or erumpent through the cuticle, or conidiophores solitary, arising from superficial hyphae, lateral or occasionally terminal, straight and subcylindrical to conical or usually geniculate-sinuous, unbranched or occasionally branched, pale olivaceous to olivaceous-brown, 0–3-septate, thin-walled, smooth, 5–50 × (2–)3–5 µm. *Conidiogenous cells* integrated, terminal or conidiophores reduced to conidiogenous cells, 5–20 × 2–4 µm, proliferating sympodially, with a single or several inconspicus to flat-tipped conidiogenous loci, 1–2 µm wide. *Conidia* solitary, subhyaline to pale olivaceous or olivaceous-brown, thin-walled, smooth, obclavate-subcylindrical, apex obtuse to subacute, base truncate to obconically truncate, 1–8-septate, (15–)25–75(–85) × 2–4 µm, hila unthickened, neither darkened nor refractive, 1–2 µm diam.

*Specimens examined*: **Brazil**, State of Ceará, Pentecoste County, on *Ocimum* sp., 2 Mar. 2001, F. Freire, HAL; State of Ceará, Cascavel County, Preaoca, on *Marsypianthes chamaedrys*; 12 June 1999, F. Freire, HAL. **Cuba**, Habana, Santiago de las Vegas, on *Ocimum gratissimum*, 6 Sep. 1988, R.F. Castañeda [C88/316], HAL; Habana, Santiago de las Vegas, on *O. sanctum*, 28 Dec. 1987, R.F. Castañeda [C87/382], HAL. **Dominican Republic**, Santiago, Valle del Cibao, Prov. Santiago, Hato

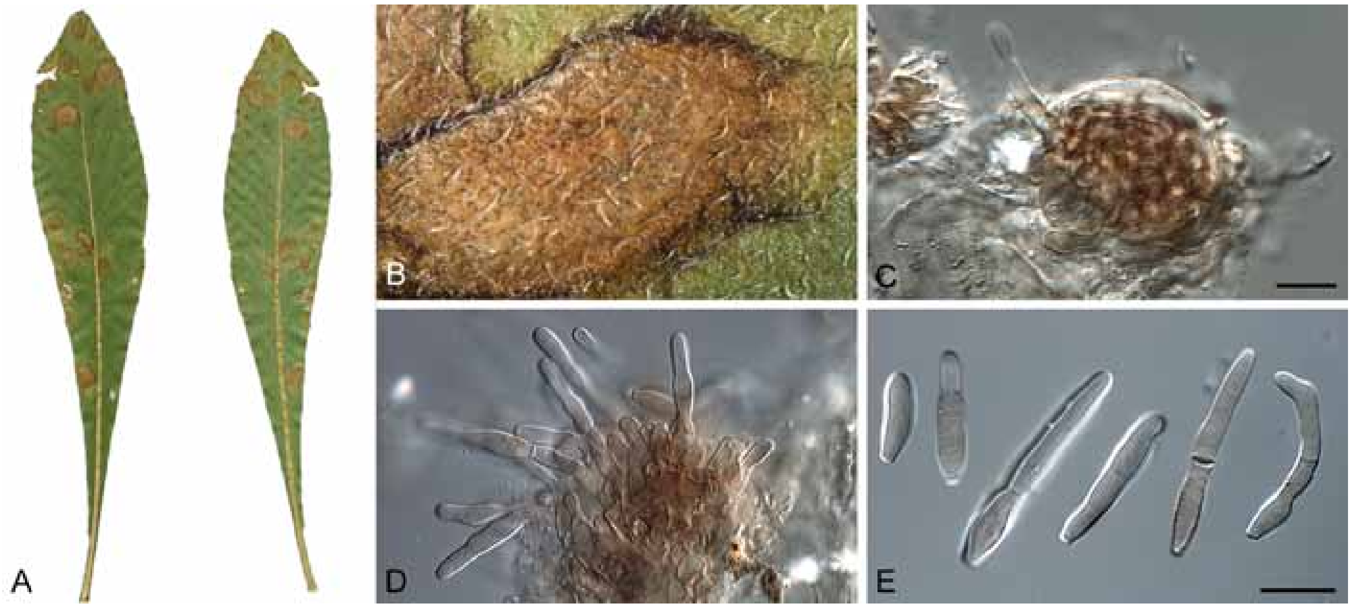


**Fig. 46.** *Pseudocercospora oenotherae* (CPC 10290, 10041). A. Leaf spots on upper and lower leaf surface. B. Close-up of leaf spot with fruiting. C, D. Fascicles with conidiophores and conidiogenous cells. E. Conidia. Scale bars = 10 µm.

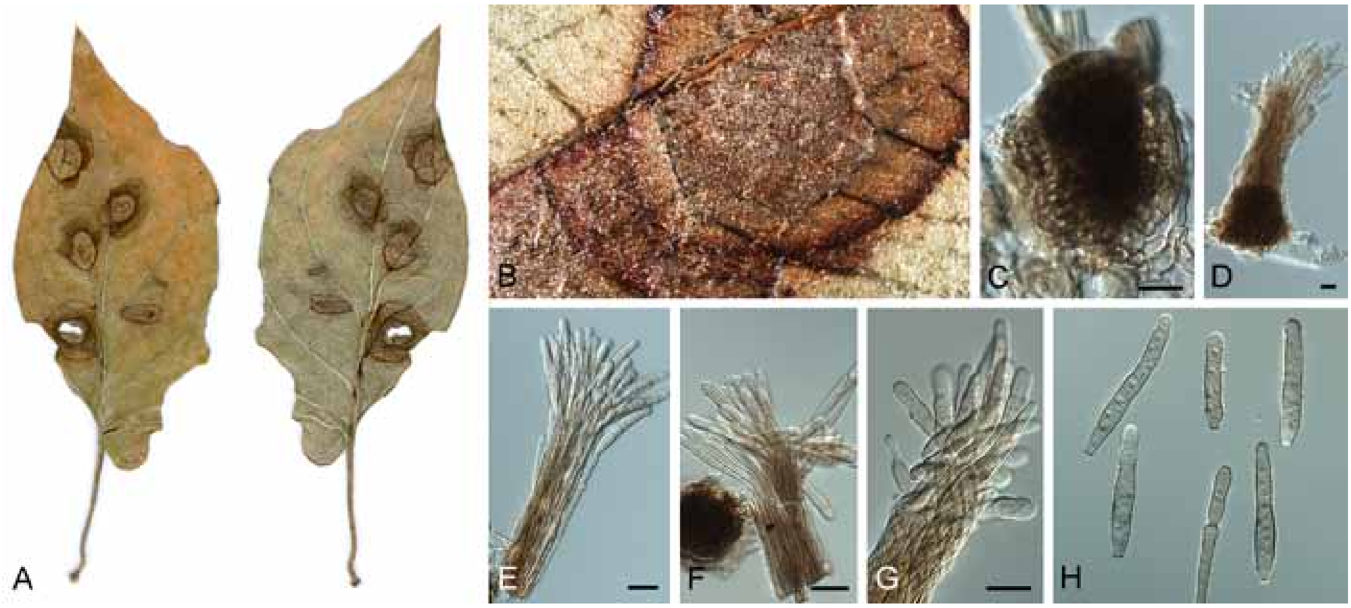


**Fig. 47.** *Pseudocercospora paederiae* (CPC 10007). A. Leaf spots on upper and lower leaf surface. B. Close-up of leaf spot with fruiting. C. Broken base of detached fascicle. D–G. Synnematal fascicles with conidiophores and conidiogenous cells. H. Conidia. Scale bars = 10 µm.

del Yonque, on *O. campechianum* (= *O. micranthum*), 26 Nov. 1930, E.L. Ekman, Cif., Mycofl. Doming. Exs. 359, **lectotype designated here** BPI 845245 and isolectotype BPI 438987. **India**, Midnapur, Daspur, on *O. sanctum*, 3 Dec. 1967, M. Mandal, BPI 438988. **Venezuela**, Les Tincheras, Edo Carabobo, on *Hyptis* sp., 24 Feb. 1940, M.F. Barrus & A.S. Muller, type of *Cercospora hyptidicola*, CUP-VZ 3863; La Cuchilla, Río Claro, Lara, on *Hyptis suaveolens*, June 2007, R. Urtiaga, HAL.

*Notes*: Chupp (1954) reduced *C. hyptidicola*, described from Venezuela on *Hyptis* sp., to synonymy with *C. lycopodis*, and Crous & Braun (2003) followed this treatment. Braun & Urtiaga (2008) examined type material of this species and an additional new collection from Venezuela and considered *C. hyptidicola* a synonym of *C. ocimicola* since the two species are morphologically indistinguishable. Both also occur on two closely related plants, *Hyptis* and *Ocimum*, in the *Lamiaceae* subfam. *Ocimoideae*. *Pseudocercospora* collections on *Marsypianthes* (subfam. *Ocimoideae*) in Brazil, is morphologically also indistinguishable from collections on *Ocimum* spp. and was assigned to *P. ocimicola* by Braun & Freire (2002).

***Pseudocercospora oenotherae*** (Ellis & Everh.) Y.L. Guo & X.J. Liu, Acta Mycol. Sin. 11: 297. 1992. Fig. 46.
*Basionym*: *Cercospora oenotherae* Ellis & Everh., Proc. Acad. Nat. Sci. Philadelphia 46: 380. 1894.

*Specimens examined*: **South Korea**, Seoul, *Oenothera odorata*, 6 Sep. 2003, H.D. Shin, KUS-F 19606, CPC 10630 = CBS 131920; *O. odorata*, 2 Oct. 2002, H.D. Shin, CBS H-20878, cultures CPC 10290 = CBS 131885, CPC 10041.

***Pseudocercospora paederiae*** Goh & W.H. Hsieh, *Cercospora* and similar fungi from Taiwan: 291. 1990. Fig. 47.

*Leaf spots* amphigenous, irregular to subcircular, 3–7 mm diam, pale brown in centre, with raised, dark brown border, at times with concentric zones delimited by dark borders. *Mycelium* internal, occasionally in addition with a few external hyphae

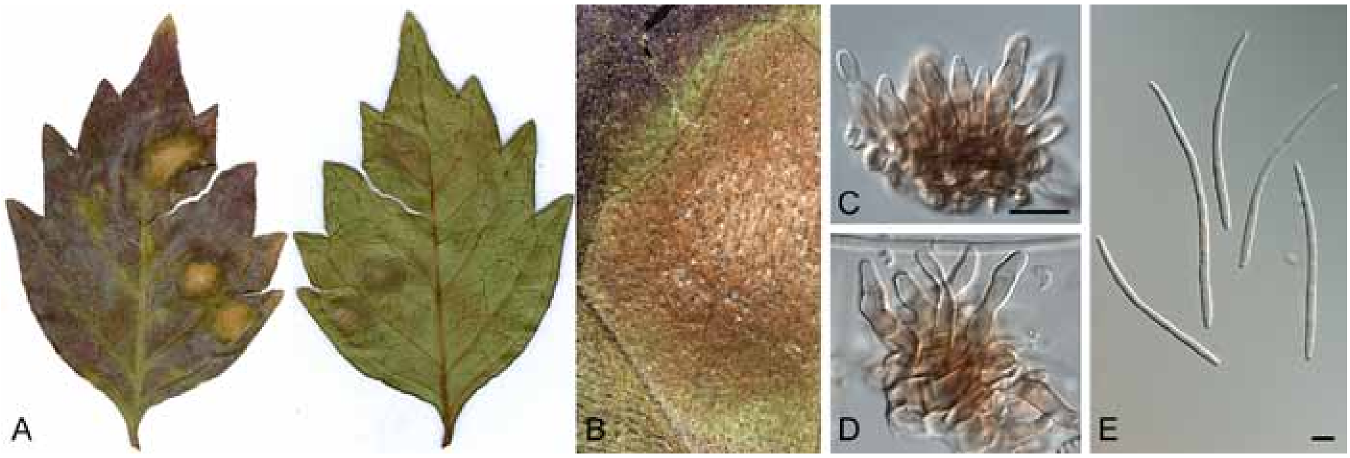


**Fig. 48.** *Pseudocercospora pallida* (CPC 10776–10778). A. Leaf spots on upper and lower leaf surface. B. Close-up of leaf spot with fruiting. C, D. Fascicles with conidiophores and conidiogenous cells. E. Conidia. Scale bars = 10 µm.

emerging through stomata, pale to medium brown, consisting of septate, branched, smooth to finely verruculose, 3–4 µm diam hyphae. *Caespituli* predominantly hypophyllous, synnematous, dark brown on leaves, 25–50 µm wide and 100–200 µm high. *Conidiophores* aggregated in dense synnemata arising from the upper cells of a brown substomatal stroma 20–40 µm diam; individual conidiophores subhyaline to olivaceous-brown, smooth, multiseptate, subcylindrical-filiform, straight to gently curved, unbranched, 80–200 × 3–5 µm. *Conidiogenous cells* terminal, unbranched, brown, subcylindrical to clavate, smooth, tapering to flat-tipped apical loci, neither thickened nor darkened, proliferating sympodially, or rarely percurrently near apex, 20–35 × 2–5 µm. *Conidia* solitary, subhyaline, greenish yellow to pale brown, smooth to finely verruculose, guttulate, obclavate, short conidia sometimes cylindrical or fusiform, apex obtuse to subobtuse, base obconically truncate, straight to curved, 1–10-septate, (20–)40–60(–70) × 3–7 µm; hila not thickened nor darkened or refractive, 1–2 µm diam.

*Specimen examined*: **South Korea**, Pocheon, National Arboretum, *Paederia foetida* (= *P. scandens*), 23 Oct. 2002, H.D. Shin, CBS H-20879, culture CPC 10007 (unfortunately no longer viable).

*Notes*: A brown leaf spot on *P. scandens* was reported from the Keryong Mountain in Chungnam district, South Korea, including the southern districts, Chonnam, Kyeongnam, and Jeju Island by Lee *et al.* (2001). The associated fungus was identified as *Pseudocercospora paederiae*. Characteristics of the Korean material are consistent with the original description of *P. paederiae* (from Taiwan), except for longer conidiophores and shorter conidia that are up to 10-septate. All characterstics overlap, and the Korean collections are tentatively assigned to *P. paederiae*. New collections from Taiwan, together with cultures and sequence data are necessary to reassess *Pseudocercospora* on *Paederia scandens* in Asia.

***Pseudocercospora pallida*** (Ellis & Everh.) H.D. Shin & U. Braun, Mycotaxon 74: 114. 2000. Fig. 48.
*Basionym*: *Cercospora pallida* Ellis & Everh., J. Mycol. 3: 21. 1887.
≡ *Cercospora langloisii* Sacc., Syll. Fung. 10: 647. 1892, nom. superfl.
= *Cercospora duplicata* Ellis & Everh., J. Mycol. 5: 70. 1889.
= *Cercospora capreolata* Ellis & Everh., J. Mycol. 8: 70. 1902.

*Specimen examined*: **South Korea**, Suwon, on *Campsis grandiflora,* 14 Oct. 2003, H.D. Shin, KUS-F 19888, CBS H-20880, CPC 10776 = CBS 131889.

***Pseudocercospora paraguayensis*** (Kobayashi) Crous, Mycotaxon 57: 270. 1996.
*Basionym*: *Cercospora paraguayensis* Kobayashi, Trans. Mycol. Soc. Japan 25: 263. 1984.

*Specimen examined*: **Brazil**, São Paulo, Susano clonal orchard, leaves of *Eucalyptus nitens*, Jun. 1996, P.W. Crous, CPC 1458 = CBS 111317.

***Pseudocercospora pini-densiflorae*** (Hori & Nambu) Deighton, Trans. Brit. Mycol. Soc. 88: 390. 1987.
*Basionym*: *Cercospora pini-densiflorae* Hori & Nambu, J. Pl. Protect. (Tokyo) 4: 353. 1917.
≡ *Cercoseptoria pini-densiflorae* (Hori & Nambu) Deighton, Mycol. Pap. 140: 167. 1976.
*Teleomorph*: "*Mycosphaerella" gibsonii* H.C. Evans, Mycol. Pap. 153: 61. 1984.

*Specimens examined*: **Japan**, C-511, NIAES herbarium; Shizuoka, Kanaya, on *P. densiflora*, 6 Mar. 1976, K. Kasai, TFM: FPH-4544; Kumamoto, isolated from *P. thunbergii,* 24 April 1964, Y. Tokushige, MUCC 534.

***Pseudocercospora plectranthi*** G.C. Hunter, Crous, U. Braun & H.D. Shin, **sp. nov.** MycoBank MB564839. Fig. 49.

*Etymology*: Name derived from the host genus *Plectranthus,* from which it was collected.

*Leaf spots* distinct, scattered over leaf surface and along leaf border, amphigenous, subcircular to irregular, 2–12 mm diam, brown to pale brown. *Mycelium* internal and external, pale brown to hyaline, branched, smooth, 1.5–4 mm diam. *Caespituli* amphigenous, predominantly epiphyllous, black, distributed evenly over the leaf spot, punctiform. *Stromata* almost absent, weakly developed, subimmersed, globular, olivaceous-brown, 20–70 µm diam. *Conidiophores* fasciculate, brown to pale brown, straight to curved, smooth, unbranched, apex rounded to truncate, 0–2-septate, (18–)22–35(–45) × (3–)4(–5) µm. *Conidiogenous cells* integrated, terminal, unbranched, brown to pale brown, smooth, proliferating sympodially, (9–)14–21(–25) × (2–)3–4(–5) µm. *Conidia* solitary, pale brown to subhyaline, guttulate, 2–10-septate, slightly constricted at septa, filiform, apex obtuse to subobtuse, base obconic to long obconic, (41–)62–98(–112) × (3–)4(–5) µm, hila unthickened, not darkened.

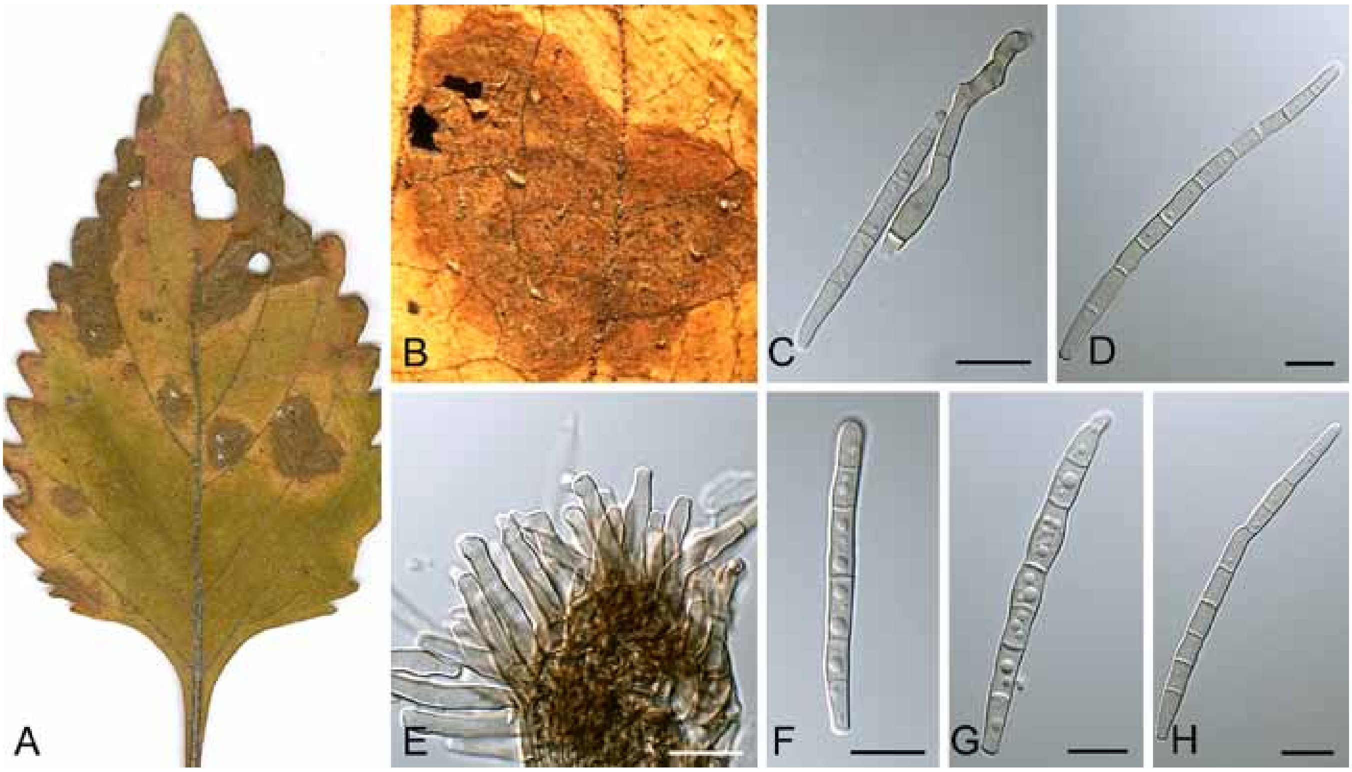


**Fig. 49.** *Pseudocercospora plectranthi* (CPC 11462). A. Leaf spots on lower leaf surface. B. Close-up of leaf spot with fruiting. E. Fascicle with conidiophores and conidiogenous cells. C, D, F–H. Conidia. Scale bars = 10 µm.

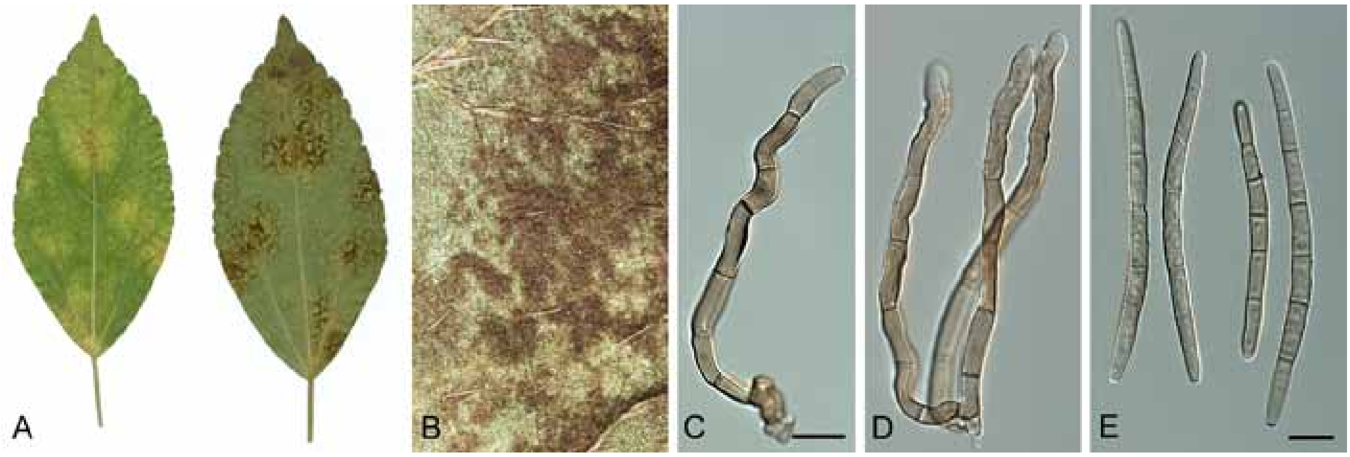


**Fig. 50.** *Pseudocercospora profusa* (CPC 10055). A. Leaf spots on upper and lower leaf surface. B. Close-up of leaf spot with fruiting. C, D. Conidiophores and conidiogenous cells. E. Conidia. Scale bars = 10 µm.

*Culture characteristics*: Colonies after 2 wk at 24 ºC in the dark on MEA; erumpent, spreading, with moderate aerial mycelium, and smooth, lobate margins. Surface pale olivaceous-grey; reverse iron-grey. Colonies reaching 8 mm diam.

*Specimen examined*: **South Korea**, Jeonju, on leaves of *Plectranthus* sp., 1 July 2004, H.D. Shin, **holotype** CBS H-20396, cultures ex-type CPC 11462 = CBS 131586, CPC 11463.

*Notes*: No species of *Pseudocercospora* are presently known from *Plectranthus* and allied genera*,* and as *P. plectranthi* does not correspond to any sequences available in GenBank at present, it is described as a new species. Numerous *Pseudocercospora* species have been described from hosts in the *Lamiaceae*, *e.g. P. anisomelicola*, *P. colebrookiae*, *P. colebrookiicola*, *P. lamiacearum*, *P. leucadis*, *P. lycopodis*, *P. ocimicola*, *P. perillulae*, *P. pogostemonis*, *P. salvia*, and *P. scutellariae*, but all of them are morphologically easily distinguishable from *P. plectranthi* by having different conidial shapes (mostly obclavate-cylindrical), smaller or no stromata or abundant superficial mycelium with solitary conidiophores. *Pseudocercospora salvia* has filiform conidia similar to those of *P. plectranthi* but in the former they are narrower (Hsieh & Goh 1990) and conidiophores are not fasciculate.

***Pseudocercospora profusa*** (Syd. & P. Syd.) Deighton, Trans. Brit. Mycol. Soc. 88: 388. 1987. Fig. 50.

*Basionym*: *Cercospora profusa* Syd. & P. Syd., Ann. Mycol. 7(2): 175. 1909.

≡ *Cercosporiopsis profusa* (Syd. & P. Syd.) Miura, in: M. Miura, Flora of Manchuria and East Mongolia. Part III. Cryptogams, fungi 3: 530. 1928.

*Specimens examined*: **South Korea**, Seoul, *Acalypha australis,* 17 Sep. 2003, H.D. Shin, CBS H-20882, culture CPC 10713–10715; Wonju, *A. australis,* 18 Oct. 2002, H.D. Shin, CBS H-20881, culture CPC 10055.

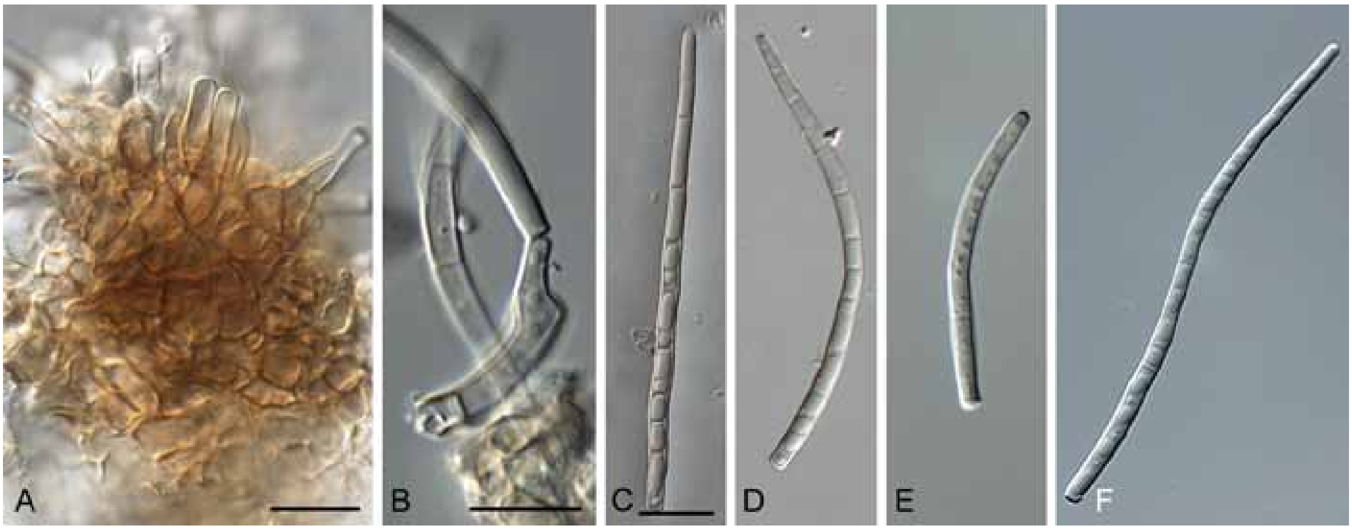


**Fig. 51.** *Pseudocercospora proteae* (CPC 15217). A. Fascicle with conidiophores and conidiogenous cells. B. Conidiogenous cell giving rise to a conidium. C–F. Conidia. Scale bars = 10 µm.

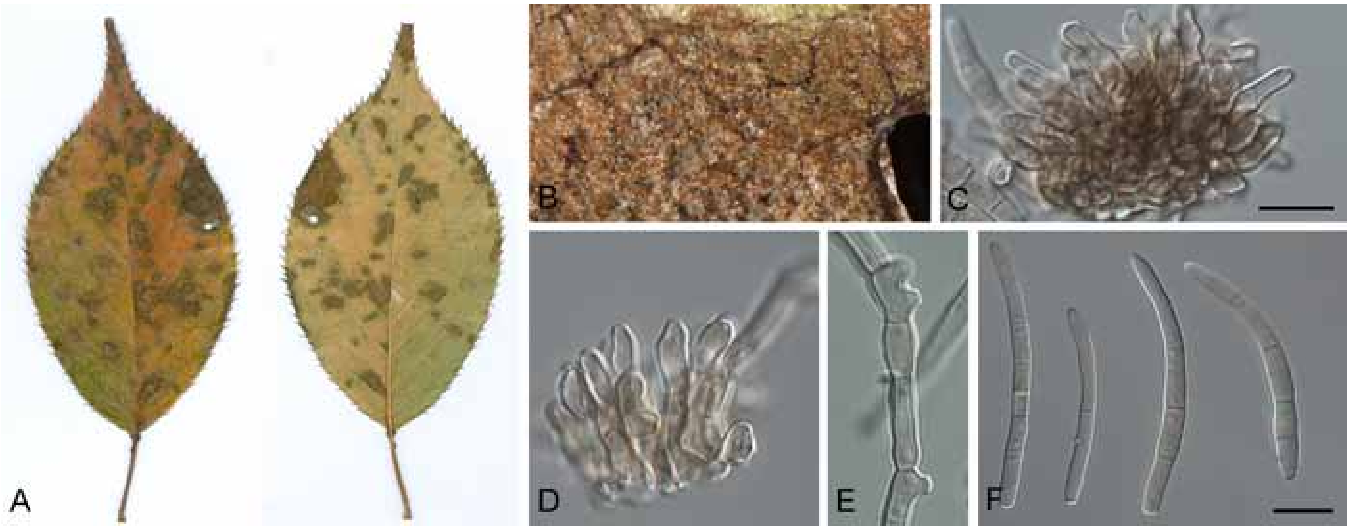


**Fig. 52.** *Pseudocercospora prunicola* (CPC 14511). A. Leaf spots on upper and lower leaf surface. B. Close-up of leaf spot with fruiting. C, D. Fascicles with conidiophores with conidiogenous cells. E. Hypha with conidiogenous loci. F. Conidia. Scale bars = 10 µm.

***Pseudocercospora proteae*** Crous, **sp. nov.** MycoBank MB564840. Fig. 51.

*Etymology*: Name derived from *Protea*, the host genus from which it was collected.

*Leaf spots* absent, with sporulation on adaxial leaf surface, prominent among leaf hairs. *Mycelium* internal and external, pale brown, consisting of septate, branched, smooth, 1.5–2 µm diam hyphae. *Caespituli* fasciculate, brown, hypophyllous, up to 120 µm diam and 40 µm high. *Conidiophores* aggregated in dense fascicles, arising from the upper cells of a brown stroma, up to 100 µm diam and 20 µm high; conidiophores pale brown to brown, smooth, 0–2-septate, subcylindrical to somewhat doliiform at the base, straight to geniculate-sinuous, unbranched or branched above, 15–40 × 3–6 µm. *Conidiogenous cells* terminal, unbranched, pale brown to brown, smooth, proliferating sympodially near apex, with flat-tipped loci, 10–15 × 2.5–5 µm. *Conidia* solitary, pale brown, smooth, guttulate, subcylindrical, straight to curved, apex obtuse, base truncate, (3–)8–12-septate, (35–)70–85(–100) × 3(–3.5) µm; hila unthickened, neither darkened nor refractive, 2.5–3 µm diam.

*Culture characteristics*: Colonies after 2 wk at 24 ºC in the dark on MEA; erumpent, spreading, with sparse aerial mycelium, and smooth, even margins. Surface olivaceous-grey; reverse iron-grey. Colonies reaching 10 mm diam.

*Specimen examined*: **South Africa**, Western Cape Province, Stellenbosch, Assegaaibos, on leaves of *Protea mundii,* 16 Apr. 2008, F. Roets, **holotype** CBS H-20883, culture ex-type CPC 15216 = CBS 131587, CPC 15218, 15217.

Notes: The long, multi-septate, subcylindrical conidia of *P. proteae* are distinct from those of *P. stromatosa* (25–40 × 2.5–3 µm), and from the shorter, verruculose conidia of *P. protearum* (Taylor & Crous 2000, Crous *et al*. 2004a).

***Pseudocercospora prunicola*** (Ellis & Everh.) U. Braun, in: Braun & Mel'nik, Trudy Bot. Inst. Im. V.L. Komarova 20: 82. 1997. Fig. 52.
*Basionym*: *Cercospora prunicola* Ellis & Everh., J. Mycol. 3: 17. 1887.

≡ *Cercoseptoria prunicola* (Ellis & Everh.) J.M. Yen, Bull. Trimest. Soc. Mycol. France 97: 92. 1981.

= *Cercospora pruni-yedoensis* Sawada, Rep. Gov. Agric. Res. Inst. Taiwan 85: 120. 1943, nom. inval.

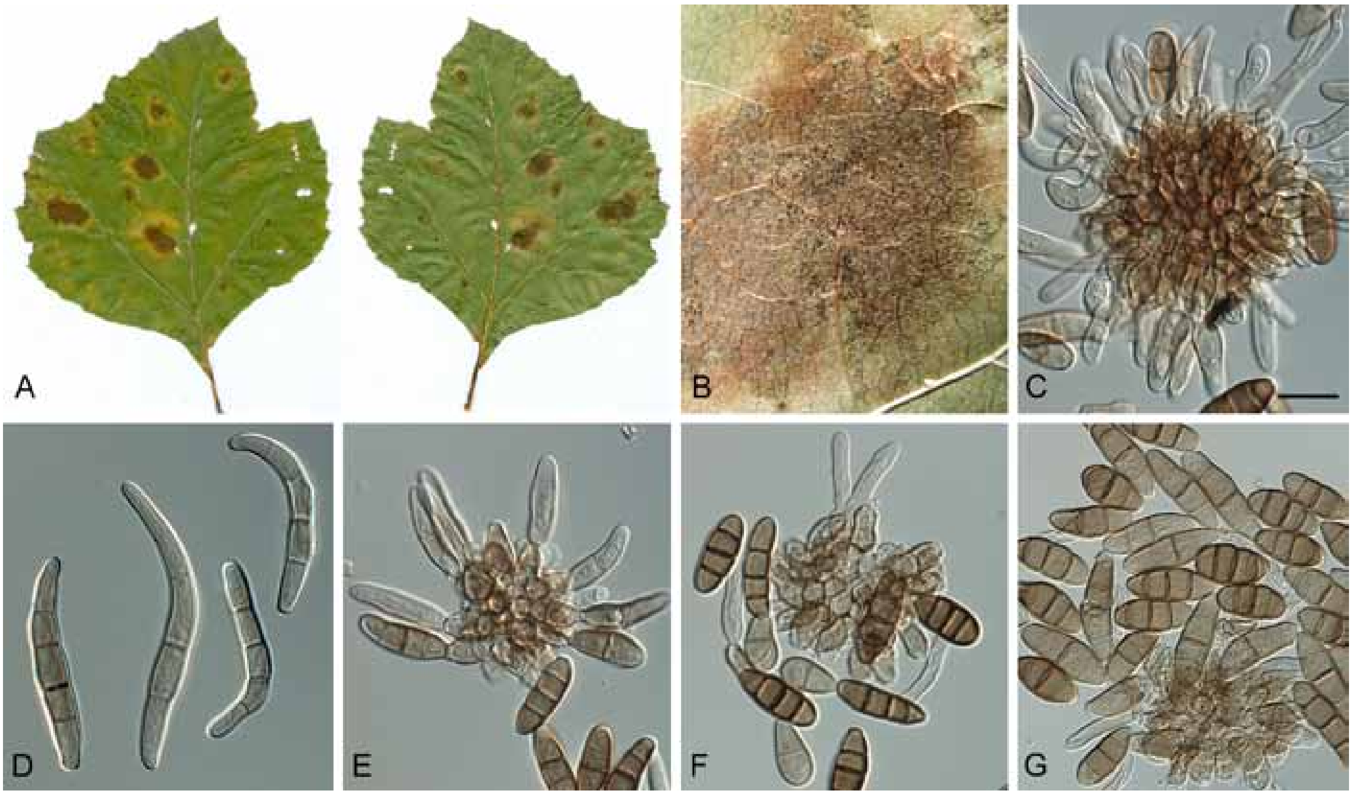


**Fig. 53.** *Pseudocercospora pseudostigmina-platani* (CPC 11726). A. Leaf spots on upper and lower leaf surface. B. Close-up of leaf spot with fruiting. C, E, F. Fascicles with conidiophores and conidiogenous cells, giving rise to dimorphic conidia. D. *Pseudocercospora* conidia. G. Conidia of stigmina-like synanamorph. Scale bars = 10 µm.

≡ *Pseudocercospora pruni-yedoensis* Goh & W.H. Hsieh, in Hsieh & Goh, *Cercospora* and similar genera from Taiwan: 282. 1990.

= *Cercospora pruni-persicae* J.M. Yen, Bull. Trimest. Soc. Mycol. France 94: 61. 1978 and Rev. Mycol. 42: 59. 1978.

≡ *Cercoseptoria pruni-persicae* (J.M. Yen) J. M. Yen, Bull. Trimest. Soc. Mycol. France 97: 92. 1981.

*Misapplied name*: *Pseudocercospora circumscissa* (Sacc.) Y.L. Guo & X.J. Liu, Mycosystema 2: 231. 1989.

*Descriptions*: Hsieh & Goh (1990: 282–283, as *Pseudocercospora pruni-yedoensis*), Braun & Mel'nik (1997: 82–83).

*Illustrations*: Hsieh & Goh (1990: 283, fig. 216, as *Pseudocercospora pruni-yedoensis*), Braun & Mel'nik (1997: 121, fig. 48).

*Specimens examined*: **South Korea**, Suwon, on *Prunus yedoensis* (≡ *Cerasus yedoensis*), 2 Oct. 2007, H.D. Shin, CBS H-20860, CPC 14511 = CBS 132107. **Taiwan**, Taipei, on *Prunus yedoensis*, 30 Nov. 1930, K. Sawada, holotype of *Pseudocercospora pruni-yedoensis*, NTU-PPE. **USA**, Louisiana, Point a la Hache, Langlois 542, holotype of *Cercospora prunicola*, NY (also Ellis & Everh., North American Fungi 1771, NY, isotype).

*Notes*: Braun & Mel'nik (1997) discussed the intricate taxonomy of *Passalora* and *Pseudocercospora* on species of *Prunus s. lat*. in detail and demonstrated, based on type material and other collections, that two distinct species are involved. *Cercospora circumscissa* is a true *Passalora* with somewhat thickened and darkened conidiogenous loci and hila. Its placement in *Passalora s. str.* has recently been confirmed based on molecular data (unpubl.). Superficial mycelium with solitary conidiophores is lacking, and the conidia are mostly somewhat rough-walled. *Passalora circumscissa* is also known from Asia, *e.g.* China, Iran and Japan. Some Chinese collections deposited at HMAS have been examined and proved to be true *Passalora circumscissa* (*e.g.* on *Prunus mandshurica* × *Armeniaca mandshurica*, Yanji, Jilin, HMAS 55845). Other collections belong to *Pseudocercospora prunicola* (*e.g.* on *Prunus yedoensis*, Nanjing, Jiangsu, HMAS 06632, and Changshan, Hunan, HMAS 55847). The Chinese authors misapplied the name *Pseudocercospora circumscissa*. The published descriptions of "*Pseudocercospora circumscissa*" in Guo & Hsieh (1995) and Guo & Liu (1998) cover both species, namely *Passalora circumscissa* as well as *Pseudocercospora prunicola*, but the illustrations seem to be based on material of the true *Pseudocercospora* on *Prunus*. *Pseudocercospora prunicola* is morphologically easily distinguishable from *Passalora circumscissa* by its inconspicuous, unthickened, not darkened conidiogenous loci and hila, well-developed superficial hyphae with solitary conidiophores and smooth conidia. The position of *P. prunicola* within the *Pseudocercospora* clade has been confirmed on the basis of sequence data retrieved from the present Korean culture.

***Pseudocercospora pseudostigmina-platani*** Crous, U. Braun & H.D. Shin, **sp. nov.** MycoBank MB564841. Fig. 53.

*Etymology*: Name reflects its morphological similarity to the *Pseudocercospora* anamorph of *Mycosphaerella stigmina-platani*.

*Leaf spots* amphigenous, irregular to subcircular, 5–10 mm diam, medium brown with a wide chlorotic margin. *Mycelium* predominantly internal, pale brown, consisting of septate, branched, smooth, 2–3 µm diam hyphae. *Caespituli* fasciculate to sporodochial, brown, predominantly hypophyllous, up to 60 µm diam and 30 µm high. *Conidiophores* aggregated in loose to dense fascicles, arising from the upper cells of a brown stroma, up to 50 µm diam and 20 µm high; conidiophores brown, verruculose, 0–1-septate, subcylindrical to somewhat doliiform, straight to slightly curved, unbranched, 10–20 × 7–10 µm. *Conidiogenous cells* terminal, unbranched, brown, verruculose, proliferating percurrently near apex, with 1–4 irregular

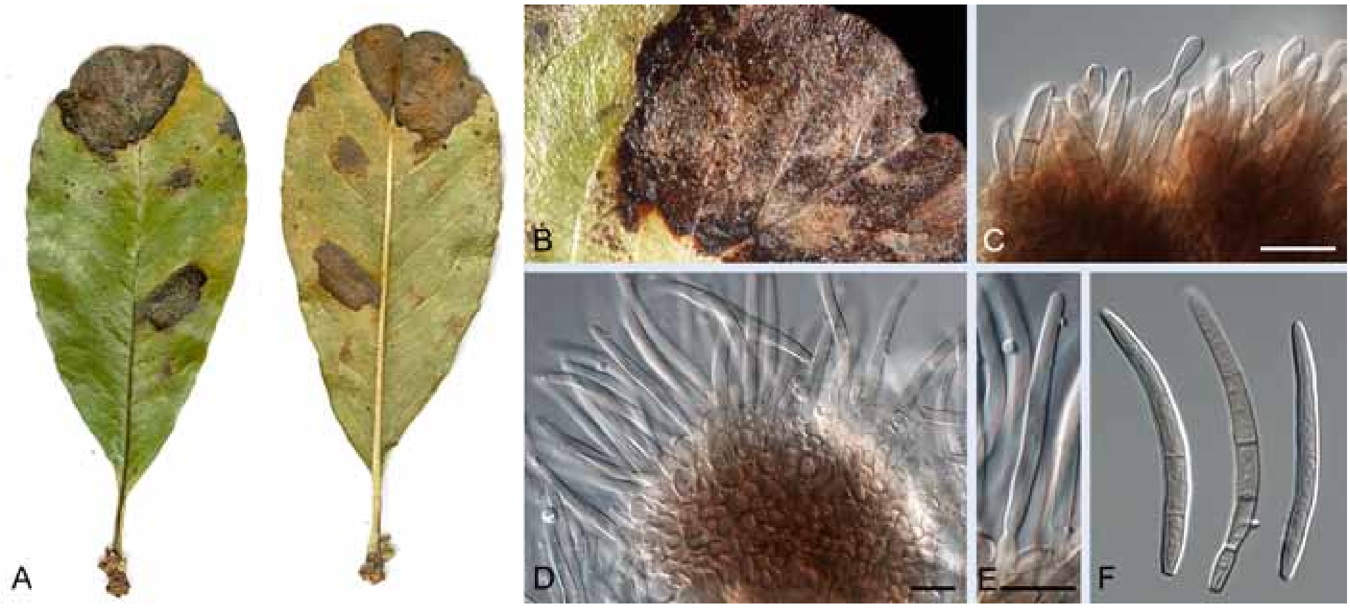


**Fig. 54.** *Pseudocercospora pyracanthigena* (CPC 10808). A. Leaf spots on upper and lower leaf surface. B. Close-up of leaf spot with fruiting. C, D. Fascicles with conidiophores and conidiogenous cells. E. Conidiogenous cell giving rise to a conidium. F. Conidia. Scale bars = 10 µm.

proliferations, 8–20 × 5–8 µm. *Conidia* dimorphic: cercostigmina-like conidia fusoid-ellipsoidal to obclavate, straight to curved, apex obtuse, base obconically subtruncate, brown, verruculose, 3–5-septate, at times constricted at septa, (28–)30–35(–38) × (5–)7–8(–9) µm; stigmina-like conidia broadly ellipsoid, straight to curved, apex obtuse, base obconically subtruncate, brown, verruculose, 3-septate, at times constricted at septa, which can also be darkened, and wall can appear thick though not distoseptate *sensu stricto*, (17–)21–25(–28) × (9–)10–12 µm; hila unthickened, neither darkened nor refractive, 3–3.5 µm diam.

*Culture characteristics*: Colonies after 2 wk at 24 ºC in the dark on MEA; surface folded, erumpent, spreading, with sparse aerial mycelium, and smooth, lobate margins. Surface pale olivaceous-grey, with thin, olivaceous-grey margin; reverse iron-grey. Colonies reaching 7 mm diam.

*Specimen examined*: **South Korea**, Suwon, on leaves of *Platanus occidentalis,* 7 Nov. 2007, H.D. Shin, **holotype** CBS H-20884, culture ex-type CPC 11726 = CBS 131588.

*Notes*: *Pseudocercospora pseudostigmina-platani* resembles the *Pseudocercospora/Stigmina* synanamorphs of *Mycosphaerella stigmina-platani* on *Platanus* in the USA, although its conidia are larger in size. The stigmina-like anamorph has conidia that are 3–6-septate, (15–)23–30(–45) × (6–)8–9(–10) µm, and the *Pseudocercospora* conidia are 3–7-septate, (35–)45–60(–100) × (4–)4.5–6(–6.5) µm (Crous & Corlett 1998). Based on DNA sequence comparisons, the genus *Stigmina* was treated as synonym of *Pseudocercospora* (Crous *et al.* 2006). The two species occurring on *Platanus* both with *Pseudocercospora/Stigmina* synanamorphs treated here, further support this synonymy.

***Pseudocercospora pyracanthae*** (Katsuki) C. Nakash. & Tak. Kobay., Ann. Phytopathol. Soc. Japan 63: 313. 1997.
*Basionym*: *Cercospora pyracanthae* Katsuki, Bull. Agric. Improv. Sect. Econ. Dept. Fukuoka Pref. 1: 19. 1949.

*Specimens examined*: **Japan**, Fukuoka, Kurume, on *Pyracantha angustifolia*, 6 Nov. 1947, S Katsuki, **holotype** TNS-F-243829; Chiba, Sanbu, October 1976, E. Ishizawa, TFM: FPH-4432; Okayama, Okayama, on *P. angustifolia*, 20 Nov. 1960, H. Tanaka, TFM: FPH-3247; *P. angustifolia,* T. Koboyashi & C. Nakashima, CNS-446, culture MUCC892; Ibaraki, on *P. angusti*, Nov. 1994, T. Nishijima, culture MAFF 237140; Kumamoto, on *P. crenulata*, 1973, T. Kobayashi, culture MAFF 410022.

*Notes*: DNA sequence data obtained for Japanese isolates of this species indicate at least two different taxa. Further research is required to select a specimen and isolate that is authentic for the name, while other collections probably represent a novel species.

***Pseudocercospora pyracanthigena*** Crous, U. Braun & H.D. Shin, **sp. nov.** MycoBank MB564842. Fig. 54.

*Etymology*: Name derived from the host plant *Pyracantha*, from which it was collected.

*Leaf spots* amphigenous, irregular to angular, up to 7 mm diam, brown, with inconspicuous border. *Mycelium* internal, hyaline to pale brown, consisting of septate, branched, smooth, 2–3 µm diam hyphae. *Caespituli* fasciculate to sporodochial, amphigenous, but predominantly epiphyllous, olivaceous on leaves, up to 150 µm wide and 60 µm high. *Conidiophores* aggregated in dense fascicles arising from the upper cells of a brown stroma up to 120 µm wide and 35 µm high; conidiophores medium brown, smooth, 0–1-septate, subcylindrical to ampulliform, straight, unbranched, mostly reduced to conidiogenous cells, tapering to flat-tipped apical loci, proliferating sympodially or percurrently near apex, 7–15 × 2–3 µm. *Conidia* solitary, brown, smooth, guttulate, subcylindrical to narrowly obclavate, apex subobtuse, base obconically subtruncate to truncate, straight to gently curved, 1–4-septate, (30–)35–40(–45) × (2.5–)3(–3.5) µm; hila unthickened, neither darkened nor refractive, 1.5 µm wide.

*Culture characteristics*: Colonies after 2 wk at 24 ºC in the dark on MEA; surface folded, erumpent, spreading, with sparse aerial mycelium, and smooth, lobate margins. Surface smoke-grey; reverse olivaceous-grey. Colonies reaching 15 mm diam.

*Specimen examined*: **South Korea**, Jeju, Halla arboretum, on leaves of *Pyracantha angustifolia,* 1 Nov. 2007, M.J. Park, **holotype** CBS H-20885, culture ex-type CPC 10808 = CBS 131589.

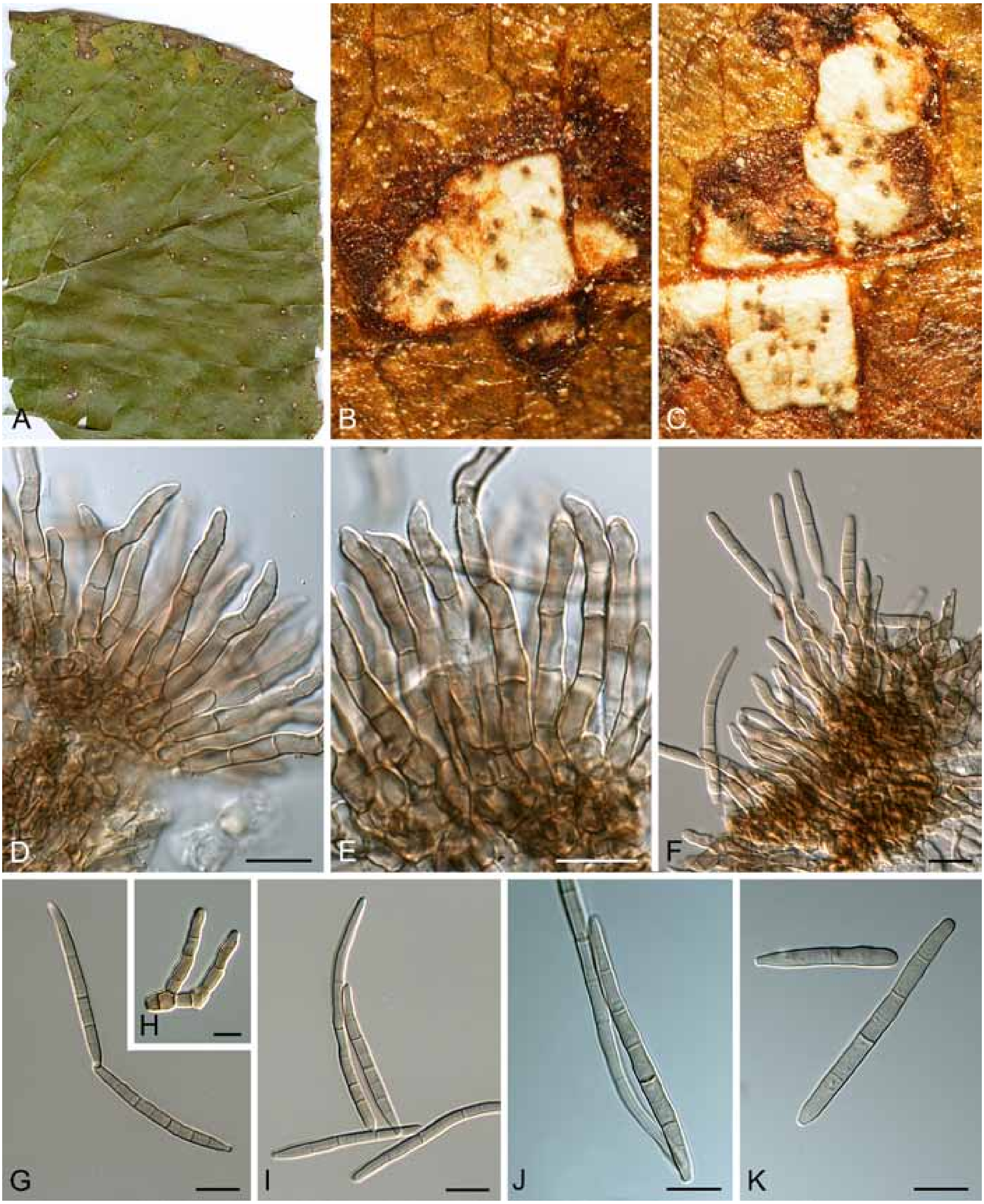


**Fig. 55.** *Pseudocercospora ranjita* (CPC 11141). A. Leaf spots on upper leaf surface. B, C. Close-up of leaf spots with fruiting. D–F. Fascicles with conidiophores and conidiogenous cells. H. Branched conidiophore. G, I–K. Conidia. Scale bars = 10 µm.

*Notes*: *Pseudocercospora pyracanthigena* is distinct from *P. pyracanthae* (conidia 25–65 × 2.4–4 µm, conidiophores 15–40 × 2.5–3 µm; Chupp 1954) in having shorter conidia and conidiophores. A second species has been recorded on *Pyracantha angustifolia* in Korea (CPC 14711–14713), for which a new name is required.

***Pseudocercospora ranjita*** (S. Chowdhury) Deighton, Mycol. Pap. 140: 151. 1976. Fig. 55.

*Basionym*: *Cercospora ranjita* S. Chowdhury, Lloydia 21: 155. 1958.

*Leaf spots* epiphyllous, distinct, scattered, white to pale brown, irregular, 1–4 mm diam, definite raised brown border, surrounded


**Fig. 56.** *Pseudocercospora ravenalicola* (CBS 122468). A. Leaf spots on upper leaf surface. B, C. Close-up of leaf spots. D–G. Fascicles with conidiophores and conidiogenous cells. H–L. Conidia. Scale bars = 10 µm.

entirely or partly by brown to dark brown irregular halo. *Mycelium* internal and external, 2–5 mm wide, branched, smooth, septate, subhyaline to pale brown. *Caespituli* epiphyllous, few in number, distributed over the leaf spot, dark brown to black. *Stromata* well-developed, intraepidermal to subimmersed, brown, globular to irregular, 40–90 µm diam. *Conidiophores* fasciculate, arising from the upper cells of stromata, pale brown, straight to curved, unbranched and branched, 1–4-septate, irregular in width, apex truncate, (20–)27–38(–42) × (3–)3.5–4.5(–5) µm. *Conidiogenous* cells terminal, unbranched, pale brown, smooth to finely verrucose, proliferating percurrently, (8–)9–15(–19) × 3(–4) µm. *Conidia* solitary, cylindrical to obclavate, 2–9-septate, subhyaline to pale brown, smooth, apex rounded to subobtuse, base obconically to long obconically truncate, (26–)44–67(–84) × (3–)4–5(–6) µm; hila unthickened nor darkened.

*Culture characteristics*: Colonies on MEA reaching 27 mm diam after 30 d at 24 °C on MEA. Colonies circular with a smooth margin, that is darker than the colony centre, slight folding; aerial mycelium moderate; greyish blue to olivaceous-grey (surface) and iron-grey (reverse).

*Specimen examined*: **Indonesia**, Northern Sumatra, on leaves of *Gmelina* sp., Mar. 2004, M.J. Wingfield, CBS H-20386, culture CPC 11141 = CBS 126005.

*Note*: The present collection closely matches the morphological description of the type specimen, which was collected from India (Chowdhury 1958).

***Pseudocercospora ravenalicola*** G.C. Hunter & Crous, **sp. nov.** MycoBank MB564843. Fig. 56.

*Etymology*: Name derived from the plant host *Ravenala*, from which this fungus was isolated.

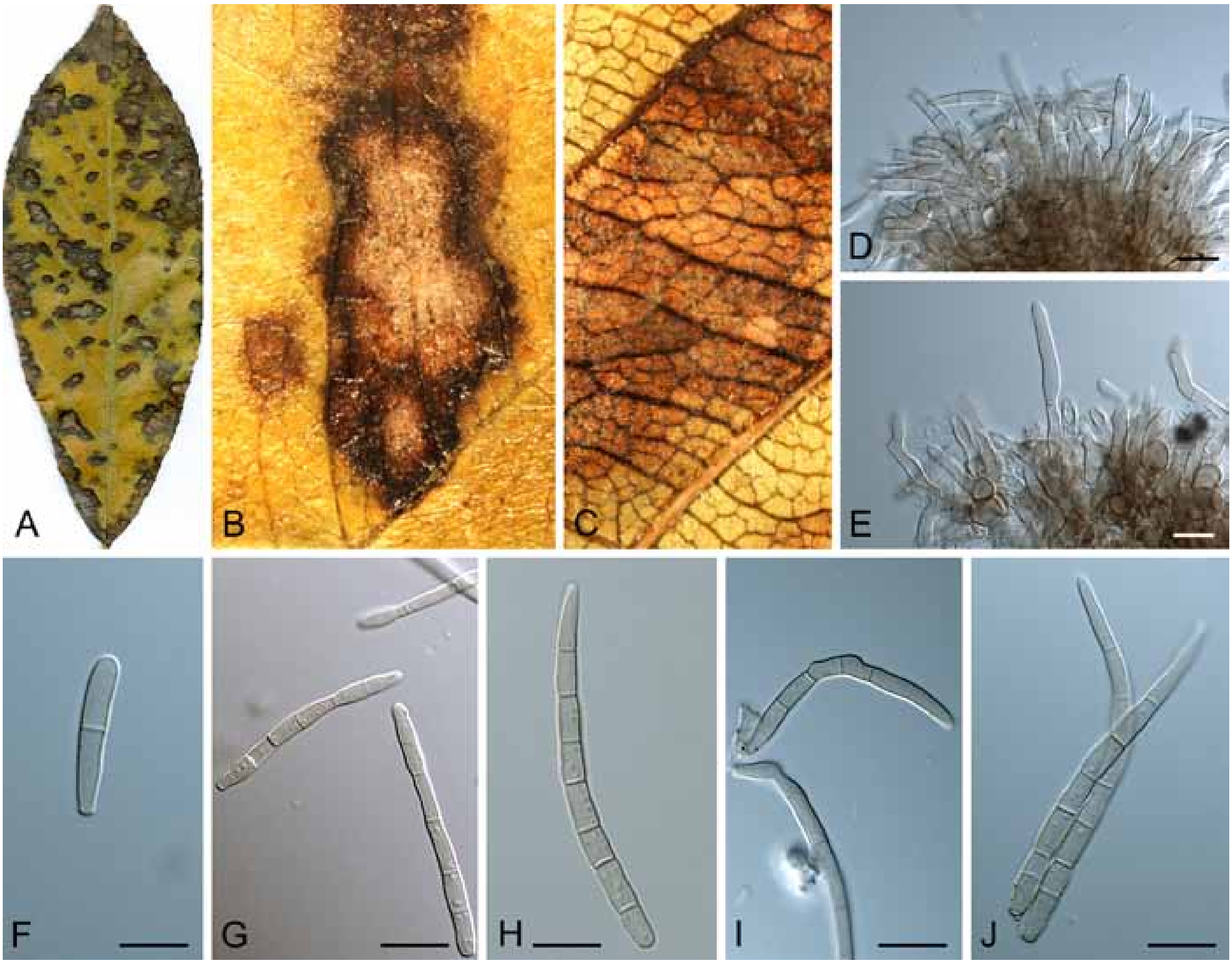


**Fig. 57.** *Pseudocercospora rhamnellae* (CPC 12500–12502). A. Leaf spots on upper leaf surface. B, C. Close-up of leaf spots with fruiting. D, E. Fascicles with conidiophores and conidiogenous cells. F–J. Conidia. Scale bars = 10 µm.

*Leaf spots* amphigenous, distinct, brown to pale, predominantly at leaf margin, but smaller spots are scattered over the whole leaf, elongated to irregular; border definite, raised, with dark brown to black border. *Caespituli* amphigenous, sparsely scattered over the leaf spot and aggregated toward the lesion margin, flocculose, pale to pale olivaceous. *Stromata* erumpent to superficial, globular, pale to dark brown, 30–80 µm diam. *Conidiophores* fasciculate, arising from the stromata, brown, becoming paler toward the apex, smooth, 0–3-septate, straight to curved, apex subtruncate to rounded, predominantly unbranched, sometimes branched below, (14–)17–25(–32) × (3–)4–5(–6) µm. *Conidiogenous cells* terminal, pale brown, smooth, straight to geniculate, tapering to a truncate to blunt apex, proliferating sympodially and percurrently, (7–)13(–15) × (3–)3.5(–4) µm. *Conidia* solitary, cylindrical, straight to curved, smooth, subhyaline to pale brown, 1–6-septate, infrequently constricted at the septa, apex obtuse to narrowly rounded, base obconically truncate to long obconically truncate, (16–)25–47(–60) × (3–)4(–5) µm; hila unthickened, nor darkened.

*Culture characteristics*: Colonies after 1 mo at 24 ºC in the dark on MEA; erumpent, spreading, with moderate aerial mycelium, and smooth, lobate margins. Surface smoke-grey in centre, pale olivaceous-grey in outer region; reverse olivaceous-grey. Colonies reaching 35 mm diam.

*Specimen examined*: **India**, Chandigarh, on leaves of *Ravenala madagascariensis*, 2 Mar. 2004, W. Gams, **holotype** CBS H-20394, culture ex-type CBS 122468.

*Note*: *Pseudocercospora ravenalicola* represents the first species of *Pseudocercospora* known from this host and the *Strelitziaceae*.

***Pseudocercospora rhabdothamni*** U. Braun & C.F. Hill, Australas. Plant Pathol. 33: 489. 2004.

*Specimen examined*: **New Zealand**, Auckland, University Campus, Princes Street, on *Rhabdothamnus solanderi*, 9 Nov. 2003, C.F. Hill, **holotype** HAL 1790 F, isotype PDD 80279, culture ex-isotype CBS 114872, ICMP 15289.

*Note*: Two strains have been deposited in CBS under the name *Ps. rhabdothamni*.

***Pseudocercospora rhamnellae*** G.C. Hunter, H.D. Shin, U. Braun & Crous, **sp. nov.** MycoBank MB564844. Fig. 57.

*Etymology*: Name derived from the plant host *Rhamnella*, from which this fungus was isolated.

*Leaf spots* distinct, amphigenous, subcircular to irregular, pale to dark brown, dark brown to black raised border with effuse spreading pale to dark brown halo, solitary or sometimes coalescing, 2–11

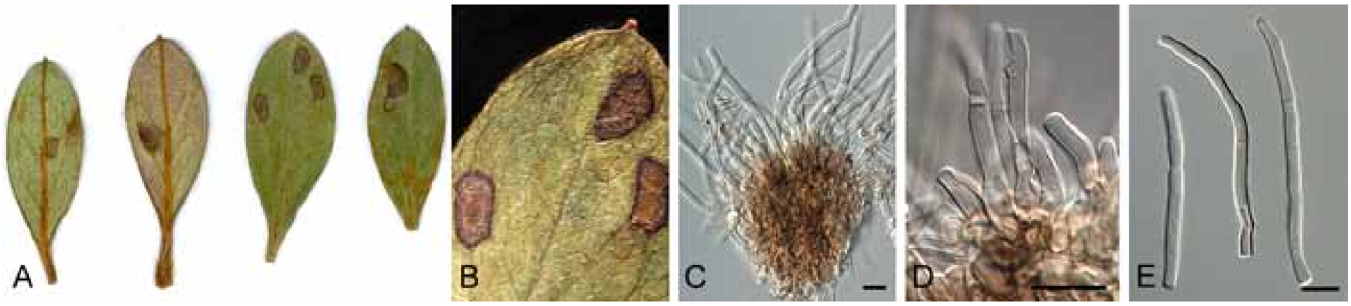


**Fig. 58.** *Pseudocercospora rhododendri-indici* (CPC 10822–10824). A. Leaf spots on upper and lower leaf surface. B. Close-up of leaf spot with fruiting. C, D. Fascicles with conidiophores and conidiogenous cells. E. Conidia. Scale bars = 10 µm.

mm diam. *Mycelium* smooth, branched, internal and external, pale brown, septate 2–4 µm diam. *Caespituli* amphigenous, on adaxial surface single, scattered to slightly aggregated, pale to light brown, on abaxial surface significantly more dense, mostly aggregated over the lesions surface, light brown to light olive-green. *Stromata* medium to large, well-developed, superficial to intraepidermal, pale to dark brown, 30–85 µm diam. *Conidiophores* fasciculate, straight to curved, brown, becoming paler to the apex, unbranched, smooth to finely verruculose, subcylindrical, 0–1-septate, (10–)13–19(–23) × (2–)3–4(–5) µm. *Conidiogenous cells* terminal, unbranched, pale brown, smooth to slightly verruculose, proliferating sympodially or percurrently near apex, (3–)5–10(–15) × (2–)3–4(–5) µm. *Conidia* solitary, guttulate, straight to curved, apex obtusely rounded, base truncate, solitary, pale brown, thin-walled, smooth, subcylindrical to narrowly obclavate, 1–12-septate, (17–)33–57(–80) × (2–)3(–4) µm, hila neither thickened, nor darkened or refractive, 2–3 µm diam.

*Culture characteristics*: Colonies after 2 wk at 24 ºC in the dark on MEA; surface folded, erumpent, spreading, with sparse aerial mycelium, and smooth, lobate margins. Surface olivaceous-grey with patches of pale olivaceous-grey; reverse iron-grey. Colonies reaching 10 mm diam.

*Specimen examined*: **South Korea**, Jeju, Halla arboretum, on leaves of *Rhamnella franguloides*, 29 Oct. 2005, H.D. Shin, **holotype** CBS H-20395, culture ex-type CPC 12500 = CBS 131590, CPC 12501, 12502.

*Notes*: No species of *Pseudocercospora* are presently known to occur on *Rhamnella* (*Rhamnaceae*). *Pseudocercospora rhamnellae* is distinct from *P. rhamnaceicola* (on *Paliurus*, *Rhamnus* and *Zizyphus*; conidia 18–85 × 1.5–2.5 µm, apex pointed, base obconically truncate, Hsieh & Goh 1990) by having wider conidia, which are subcylindrical-obclavate with an obtusely rounded apex and truncate base. The conidiophores are also shorter and wider. Further collections are needed to determine whether isolates from other hosts in the *Rhamnaceae* all represent *P. rhamnaceicola.*

***Pseudocercospora rhododendri-indici*** Crous, U. Braun & H.D. Shin, **sp. nov.** MycoBank MB564845. Fig. 58.

*Etymology*: Name derived from the plant host *Rhododendron indicum*, from which it was collected.

*Leaf spots* amphigenous, subcircular to circular, 2–3 mm diam, medium brown with a raised, dark brown border. *Mycelium* internal, pale brown, consisting of septate, branched, smooth, 2–3 µm diam hyphae. *Caespituli* fasciculate to sporodochial, olivaceous-brown, predominantly epiphyllous, up to 100 µm diam and 80 µm high. *Conidiophores* aggregated in dense fascicles, arising from the upper cells of a brown stroma, up to 80 µm diam and 40 µm high; conidiophores pale brown, smooth, 0–2-septate, subcylindrical, straight to geniculate-sinuous, unbranched, 10–30 × 3–4 µm. *Conidiogenous cells* terminal, pale brown, smooth, tapering to flat-tipped apical loci, proliferating sympodially, 10–15 × 3–3.5 µm. *Conidia* solitary, pale brown, smooth, guttulate, subcylindrical, apex subobtuse, base truncate, straight to variously curved, 1–4-septate, (35–)40–55(–65) × (2–)3 µm; hila unthickened, neither darkened nor refractive, 2–3 µm diam.

*Culture characteristics*: Colonies after 2 wk at 24 ºC in the dark on MEA; erumpent, spreading, with moderate aerial mycelium, and smooth, lobate margins. Surface olivaceous-grey in centre, pale olivaceous-grey in outer region; reverse iron-grey. Colonies reaching 14 mm diam.

*Specimen examined*: **South Korea**, Seoul, on *Rhododendron indicum,* 27 Oct. 2003, H.D. Shin, **holotype** CBS H-20886, cultures ex-type CPC 10822 = CBS 131591, CPC 10823, 10824.

*Notes*: Of the species occurring on *Rhododendron*, *P. rhododendri-indici* differs from *P. handelii* (conidia narrowly linear to obclavate, indistinctly multiseptate, 12–140 × 1.5–3 µm; Chupp 1954) by its subcylindrical, 1–4-septate conidia with truncate base and obtuse apex, and phylogentic position (Fig. 5). The description and illustration of *P. handelii* based on Chinese material (Guo & Hsieh 1995) agrees well with Chupp's (1954) description. The identity of Korean collections on *Rhododendron indicum* described in Shin & Kim (2001), characterised by much longer acicular-filiform conidia with truncate base, is unclear. *Pseudocercospora rhododendri-indici* differs from *P. rhododendricola* (conidia 54–96 × 2–2.5 µm; Yen 1966) by its shorter conidia. Beside epiphyllous colonies, *P. rhododendricola* forms hypophyllous colonies composed of small, loose fascicles of conidiophores that emerge through stomata, together with superficial hyphae that give rise to solitary conidiophores. The hypophyllous fruiting was neither mentioned in the original description nor in Yen & Lim (1980). It was observed during the re-examination of type material (**Singapore**, Botanic Gardens, on *Rhododendron* sp., 13 Apr. 1965, S.H. Yen No. 112, **holotype** PC).

***Pseudocercospora rhoina*** (Cooke & Ellis) Deighton, Mycol. Pap. 140: 152. 1976. Fig. 59.

*Basionym*: *Cercospora rhoina* Cooke & Ellis, Grevillea 6: 89. 1878.

= *Cercospora copallina* Cooke, Grevillea 12: 31. 1883.

= *Cercospora rhoina* var. *nigromaculans* Peck, Rep. (Annual) New York State Mus. Nat. Hist. 42: 129. 1889.

*Specimen examined*: **South Korea**, Namhae, on *Rhus chinensis,* 30 Jun. 2004, H.D. Shin, CBS H-20887, KUS-F 20367, CPC 11464 = CBS 131891.

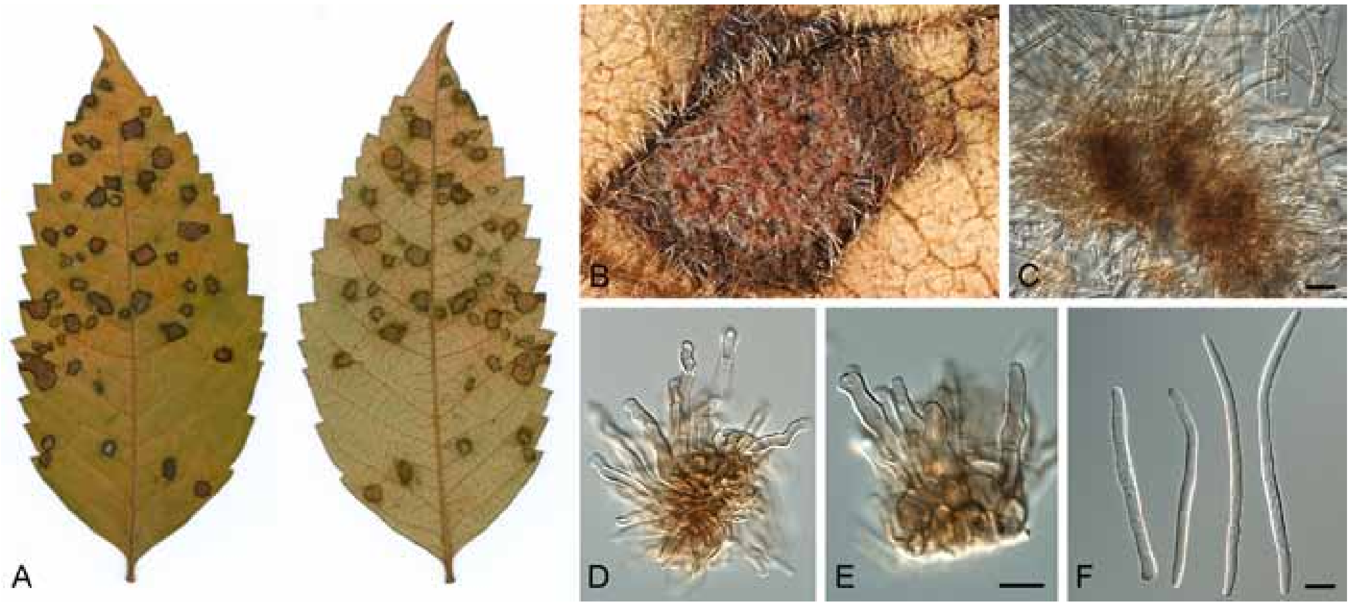


**Fig. 59.** *Pseudocercospora rhoina* (CPC 11464–11465). A. Leaf spots on upper and lower leaf surface. B. Close-up of leaf spot with fruiting. C–E. Fascicles with conidiophores and conidiogenous cells. F. Conidia. Scale bars = 10 µm.

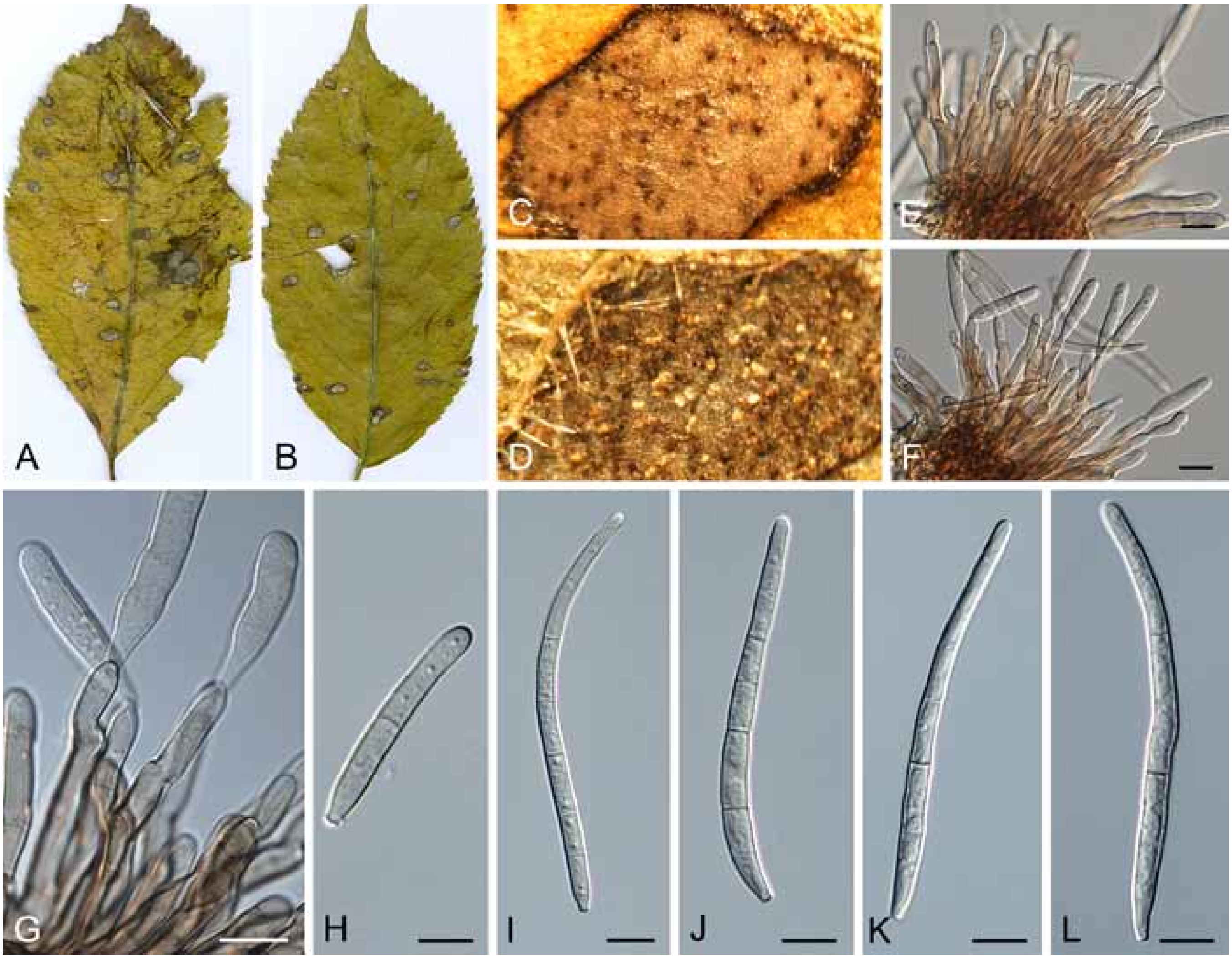


**Fig. 60.** *Pseudocercospora sambucigena* (CPC 14397–14399). A, B. Leaf spots on upper and lower leaf surface. C, D. Close-up of leaf spots with fruiting. E, F. Fascicles with conidiophores and conidiogenous cells. G. Conidiogenous cells. H–L. Conidia. Scale bars = 10 µm.

***Pseudocercospora sambucigena*** U. Braun, Crous & K. Schub., Mycotaxon 92: 400. 2005. Fig. 60.

*Leaf spots* distinct, scattered over leaf surface, amphigenous, upper surface pale brown to grey, with definite border that is raised and dark brown in colour; lower surface pale grey to pale brown,

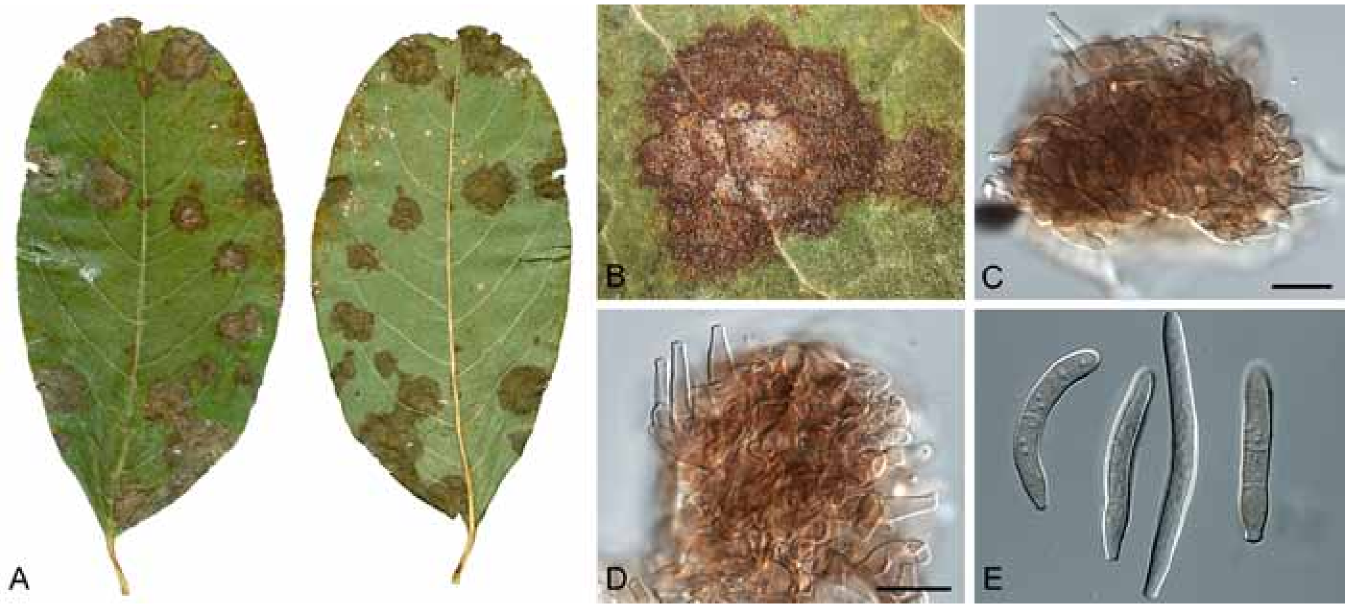


**Fig. 61.** *Pseudocercospora securinegae* (CPC 10793). A. Leaf spots on upper and lower leaf surface. B. Close-up of leaf spot with fruiting. C, D. Fascicles with conidiophores and conidiogenous cells. E. Conidia. Scale bars = 10 µm.

with distinctly raised, brown border, 2–10 mm diam. *Mycelium* smooth, internal and external, consisting of branched, subhyaline, 2–4 µm diam hyphae. *Caespituli* amphigenous, predominantly occurring on the abaxial lesion surface, evenly distributed over the lesion, punctiform, grey to dark brown. *Stromata* well-developed, subimmersed becoming erumpent, globular, dark brown, 45–100 mm diam. *Conidiophores* fasciculate, emerging from stomata, brown, becoming paler toward the apex, unbranched, straight to curved, cylindrical, uniform or irregular in width, rounded apex, indistinctly 0–3-septate, (25–)35–51(–60) × (4–)5(–7) µm. *Conidiogenous cells* terminal, unbranched, smooth, pale brown, proliferating sympodially and percurrently, conidiogenous loci (scars) unthickened to slightly thickened, but not darkened, (10–)19–34(–46) × (3–)5 µm. *Conidia* solitary, pale olivaceous to pale brown, smooth, guttulate, apex obtuse, base long obconically truncate, shape variable from cylindrical to obclavate, 1–7-septate, (40–)68–117(–156) × (4–)5–6(–7) µm; hila unthickened to slightly thickened, but not darkened.

*Culture characteristics*: Colonies on MEA reaching 16 mm diam after 30 d in the dark at 24 °C. Colonies circular to subcircular, smooth to slightly irregular margin, prominently convex, moderate aerial mycelium; pale greenish grey to pale olivaceous-grey (surface) and olivaceous-black (reverse).

*Specimens examined*: **Italy**, Parma, on leaves of *Sambucus nigra*, G. Passerini, **paratype** B 70-6710. **Netherlands**, Milingerwaard on leaves of *Sambucus nigra*, 2007, P.W. Crous, **epitype designated here** CBS H-20391, cultures ex-epitype CPC 14397 = CBS 126000. **USA**, Pennsylvania, Dauphin Co., on leaves of *Sambucus pubens*, 21 Aug. 1921, O.E. Jennings, Acc. 6736, **holotype** NY.

***Pseudocercospora securinegae*** (Togashi & Katsuki) Deighton, Mycol. Pap. 140: 152. 1976. Fig. 61.

*Basionym*: *Cercospora securinegae* Togashi & Katsuki, Ann. Phytopathol. Soc. Japan 17: 7. 1952.

*Specimen examined*: **South Korea**, Yangpyong, on *Flueggea suffruticosa* (≡ *Securinega suffruticosa*), 30 Sep. 2003, H.D. Shin, CBS H-20888, culture CPC 10793 = CBS 131930.

***Pseudocercospora snelliana*** (Reichert) U. Braun, H.D. Shin, C. Nakash. & Crous, **comb. nov.** MycoBank MB564846. Figs 62, 63.

*Basionym*: *Cercospora snelliana* Reichert, Bot. Jahrb. Syst. 56: 724. 1921.

= *Clasterosporium mori* Syd. & P. Syd., Mem. Herb. Boiss. 4: 6. 1900.
≡ *Sirosporium mori* (Syd. & P. Syd.) M.B. Ellis, Mycol. Pap. 87: 7. 1963.
≡ *Cercospora kusanoi* Sawada, Rep. Dept. Agric. Gov. Res. Inst. Formosa 35: 109. 1928, nom. nov., non *Cercospora mori* Hara, 1918.
= *Cercospora bremeri* Petr., Sydowia 2: 312. 1948.
= *Cercospora flexuosa* Tanaka, unknown, nom. nud., non Tracy & Earle, 1895.

*Leaf spots* lacking or amphigenous, but inconspicuous on upper leaf surface, chlorotic, irregular, as small speckles, up to 8 mm diam, or effuse and much larger, forming large blotches or covering large portions of the hypophyllous surface with blackish colonies. *Mycelium* internal and external; internal hyphae pale olivaceous to pale brown, smooth, 3–4 µm diam, arising through stomata, giving rise to external mycelium that is pale yellowish green, olivaceous to brown, smooth, thin-walled, 1.5–5 µm diam. *Conidiophores* arising singly from superficial mycelium and in small, divergent fascicles from a few substomatal swollen hyphal cells, 2–8 µm diam., emerging through stomata, brown, smooth, becoming roughened towards apex, wall up to 1 µm thick, 1–12-septate, subcylindrical to often subclavate, *i.e.* width somewhat increasing towards the apex, straight to variously curved or geniculate-sinuous, unbranched or branched above, 15–100 × 3–6 µm. *Conidiogenous cells* terminal or lateral, unbranched, brown, becoming paler towards the tip, roughened, tapering towards flat-tipped loci, 2–3 µm diam, proliferating sympodially (lateral scars as illustrated by Ellis 1971 observed), or percurrently near apex, 10–30 × 4–7 µm. *Conidia* solitary, medium to dark olivaceous-brown or brown, small young conidia sometimes subhyaline to pale olivaceous, wall up to 1 µm thick, smooth or almost so to verruculose, guttulate, smaller conidia ellipsoid-ovoid, subcylindrical, larger conidia usually distinctly obclavate, apex obtuse, base obconically truncate, subtruncate or sometimes rounded, straight to gently curved, 1–10-septate (septa somewhat refractive, at times also 1(–2) oblique or vertical septa present), (15–)30–70(–80) × (3–)4–6(–7) µm;

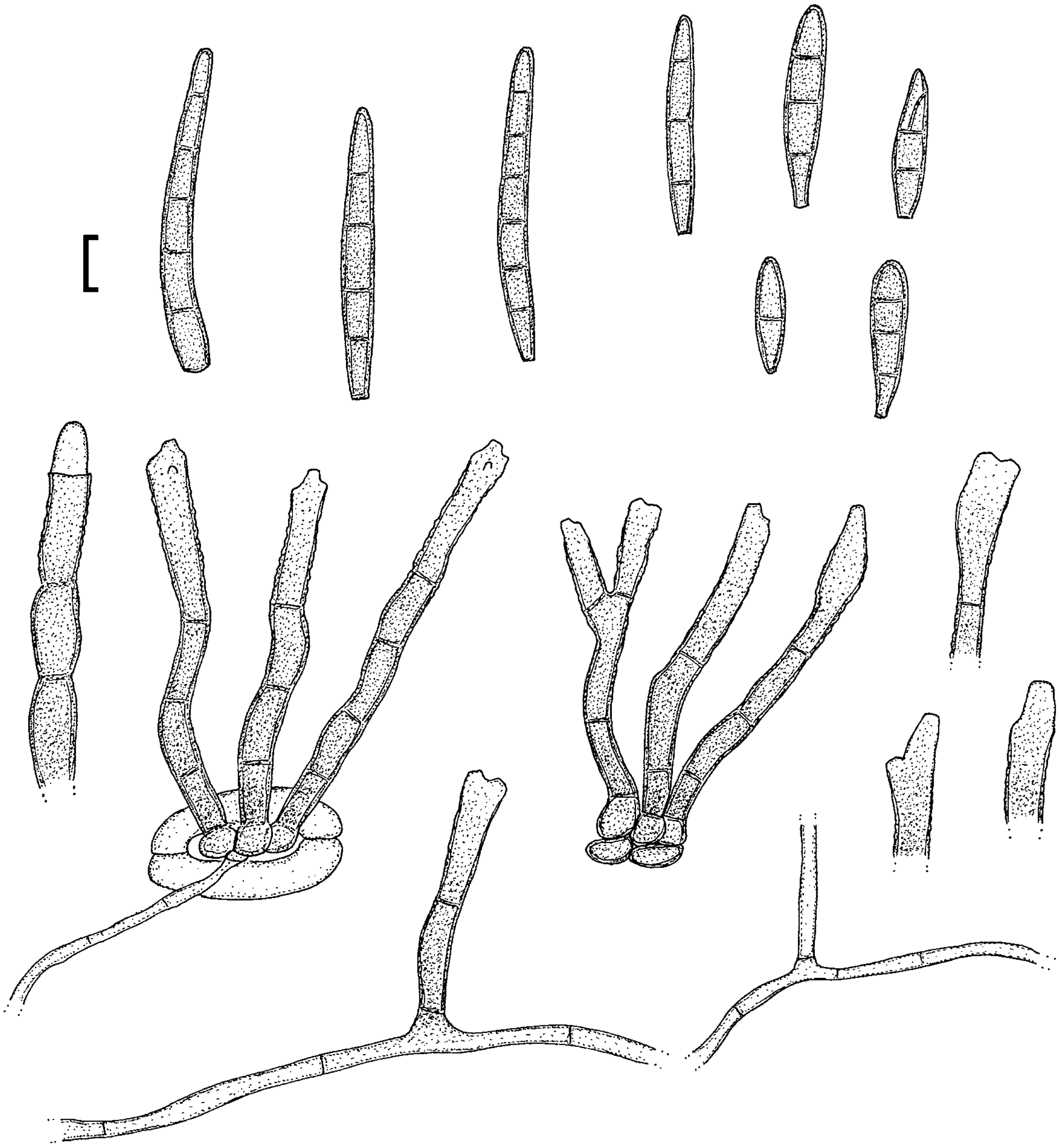

**Fig. 62.** *Pseudocercospora snelliana* (B 700014740, holotype). Sparse fascicles, and solitary conidiophores on superficial mycelium giving rise to muriformly septate, thick-walled conidia. Scale bar = 10 µm.

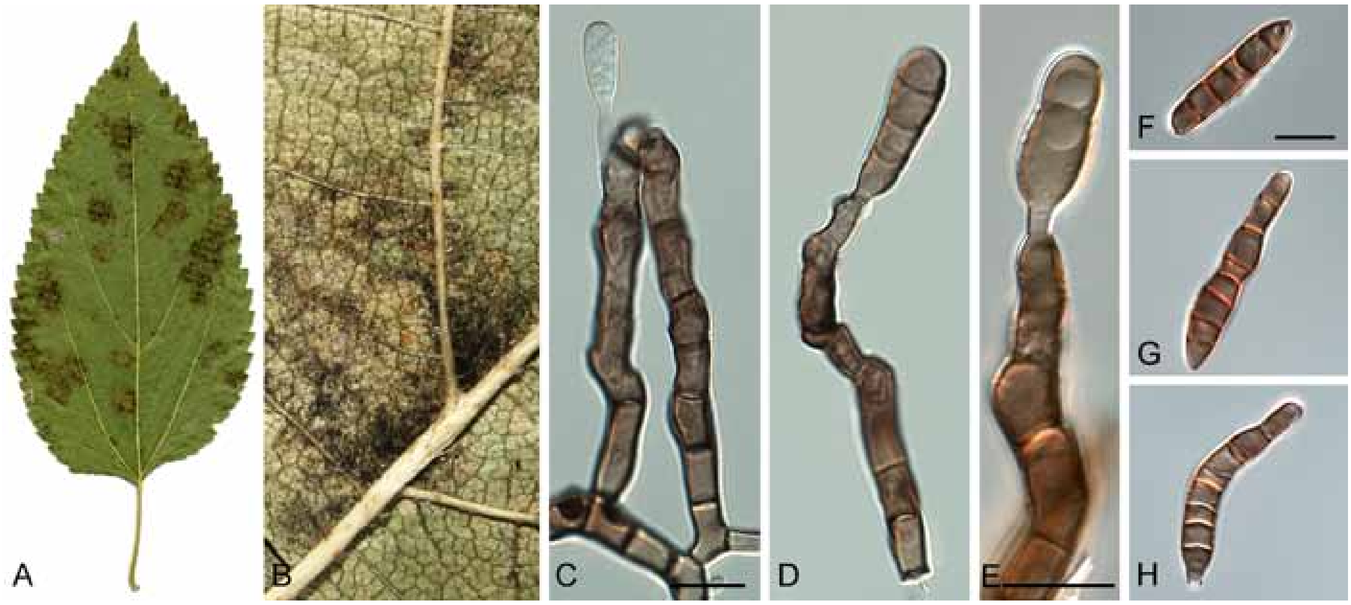


**Fig. 63.** *Pseudocercospora snelliana* (CPC 11654–11656). A. Leaf spots on the lower leaf surface. B. Close-up of leaf spot with fruiting. C–E. Solitary conidiophores and conidiogenous cells. F–H. Conidia. Scale bars = 10 µm.

hila neither thickened, nor darkened or refractive, 1–1.5(–2) µm diam.

*Culture characteristics*: Colonies after 2 wk at 24 ºC in the dark on MEA; erumpent, spreading, with sparse aerial mycelium, and smooth, lobate margins. Surface pale olivaceous-grey; reverse olivaceous-grey. Colonies reaching 7 mm diam.

*Specimens examined*: **Egypt**, Kahirahm, near Bahtim, on *Morus alba*, Nov. 1913, Snell, **holotype** B 700014740. **South Korea**, Hoengseong, on *Morus bombycis,* 11 Oct. 2004, H.D. Shin, CBS H-20889, HAL 1867 F, culture CPC 11654 = CBS 131592, CPC 11655, 11656.

*Notes*: *Cercospora kusanoi* is based on the same type specimen used by Sydow to describe *Clasterosporium mori*. Sawada (1928) considered this fungus a species of *Cercospora*. He introduced the name *Cercospora kusanoi* because the species epithet *mori* was occupied in *Cercospora*. The Korean material we studied closely resembles the description of the type, which was originally described on *Morus alba* from Japan (Sawada 1928). *Pseudocercospora mori* is also already occupied so type material of *P. snelliana*, the next available epithet, was re-examined. We determined it to be conspecific with *C. kusanoi,* so *P. snelliana* is introduced as a new combination.

***Pseudocercospora stephanandrae*** (Tak. Kobay. & H. Horie) C. Nakash. & Tak. Kobay., Mycoscience 41: 27. 2000.
*Basionym*: *Cercospora stephanandrae* Tak. Kobay. & H. Horie, Trans. Mycol. Soc. Japan 20: 331. 1979.

*Specimens examined*: **Japan,** Tokyo, Jindai Bot. Park, on *Stephanandra incisa,* 21 Oct. 1976, T. Kobayashi & H. Horie TFM: FPH-4712; Tokyo, Jindai Botanical Park, Chofu-City, on *S. incisa*, 26 Oct. 1974, H. Horie, **holotype** TFM: FPH 4411; Tokyo, Jindai Bot. Park, on *S. incisa*, 7 Nov. 1998, C. Nakashima & E. Imaizumi, **epitype designated here** TFM: FPH-8099, ex-epitype cultures MUCC 914, MAFF 237799.

***Pseudocercospora timorensis*** (Cooke) Deighton, Mycol. Pap. 140: 154. 1976.
*Basionym*: *Cercospora timorensis* Cooke, Grevillea 12: 38. 1883.
= *Ramularia batatae* Racib., Paras. Algen Pilze Javas, Batavia 1: 35. 1900.
= *Cercospora batatae* A. Zimmerm., Ber. Land.-Forstw. Deutsch Ostafrikas 2: 28. 1904.
= *Cercospora batatae* Henn., Bot. Jahrb. Syst. 38: 118. 1907, nom. illeg., homonym of *C. batatae* A. Zimmerm., 1904.
= *Cercospora ipomoeae-purpureae* J.M. Yen, Rev. Mycol. 30: 173. 1965.
≡ *Pseudocercospora ipomoea-purpureae* (J.M. Yen) J.M. Yen, in Yen & Lim, Gard. Bull., Singapore 33: 177. 1980.

*Specimen examined*: **Japan**, Okinawa, *Ipomoea indica*, 19 Nov. 2007, C. Nakashima & T. Akashi, MUMH 10923, culture MUCC 819.

***Pseudocercospora udagawana*** (Katsuki) X.J. Liu & Y.L. Guo, Mycosystema 2: 238. 1989. Fig. 64.
*Basionym*: *Cercospora udagawana* Katsuki, Ann. Phytopathol. Soc. Japan 20(2–3): 72. 1955.

*Specimen examined*: **South Korea**, Dongducheon, on *Hovenia dulcis,* 28 Sep. 2003, H.D. Shin, CBS H-20890, CPC 10799 = CBS 131931.

***Pseudocercospora viburnigena*** U. Braun & Crous, Mycol. Progr. 1: 23. 2002. Fig. 65.
*Basionym*: *Cercospora tinea* Sacc., Michelia 1(2): 268. 1878 (non *P. tinea* Y.L. Guo & W.H. Hsieh, 1994).
≡ *Cercoseptoria tinea* (Sacc.) Deighton, Mycol. Pap. 140: 167. 1976.
≡ *Cercostigmina tinea* (Sacc.) U. Braun, Cryptog. Bot. 4: 108. 1993.

*Leaf spots* distinct, scattered, amphigenous, 4–15 mm diam, lesions on abaxial surface dark to pale brown, subcircular to irregular, surrounded by a slightly raised dark brown border, lesions on adaxial surface dark to pale brown, surrounded by a dark brown border with a light red diffuse pigment extending outward from the border in older lesions. *Mycelium* internal and external, smooth, subhyaline, branched, 1.5–4 µm wide. *Caespituli* amphigenous, but predominantly hypophyllous, evenly distributed over the leaf spot, velvety, olivaceous. *Stromata* well-developed, subimmersed, globular, dark brown, 30–80 µm diam. *Conidiophores* fasciculate, smooth, 0–2-septate, emerging from the upper cells of the stroma, pale brown, straight to curved, irregular in width, apex subtruncate to rounded, (14–)17–24(–30) × (3–)4–5(–6) µm. *Conidiogenous cells* integrated, terminal, inconspicuously proliferating percurrently, cylindrical, straight, pale brown, at times slightly verruculose, (5–)9–15(–19) × (2–) 3(–4) µm. *Conidia* solitary, pale brown, smooth, guttulate, apex obtusely rounded, base narrowly truncate, narrowly ellipsoidal to acicular, curved or sigmoid, 5–11-septate, (68–)87–110(–120) × (2–)3–4(–5) µm, hila unthickened.

*Culture characteristics*: Colonies on MEA reaching 23 mm diam after 30 d at 24 °C in the dark. Colonies circular, convex, smooth margin that is distinctly darker than the rest of the colony, slight folding occurs toward the edge of the colony, moderate to profuse aerial mycelium; olivaceous-grey (surface) and greenish black (reverse).

*Specimens examined*: **Italy**, Padova, *Viburnum tinus*, Oct. 1877, Bizzozera, Sacc., Mycoth. Venet. 1252, **syntype** HAL. **Netherlands**, Bilthoven, Sweelincklaan 87, on leaves of *Viburnum davidii*, 26 May 2008, M.K. Crous, **epitype designated here** CBS H-20393, culture ex-epitype CPC 15249 = CBS 125998.

*Note*: The epitype closely matches the morphology of the holotype (Braun & Hill 2002), representing a species that is common on *Viburnum* in Europe.

***Pseudocercospora viticicola*** (J.M. Yen & Lim) J.M. Yen, Gardens Bulletin, Singapore 33: 190. 1980.
*Basionym*: *Cercospora viticicola* J.M. Yen & Lim, Cah. Pacifique 17: 104. 1973.
= *Cercospora viticis* Ellis & Everh. (as "*viteae*"), J. Mycol. 3: 18. 1887, non *Pseudocercospora viticis* Goh & W.H. Hsieh, 1989.
≡ *Pseudocercosporella viticis* (Ellis & Everh.) B.K. Gupta & Kamal, Indian Phytopathol. 42: 388. 1989, nom. inval.
≡ *Pseudocercospora viticicola* U. Braun, Mycotaxon 48: 296. 1993, nom. illeg., homonym of *P. viticicola* (J.M. Yen & Lim) J.M. Yen, 1980.
= *Cercospora viticis* Sawada, Rep. Gov. Agric. Res. Inst. Taiwan 87: 90. 1944, nom. illeg., homonym of *C. viticis* Ellis & Everh., 1887.
≡ *Pseudocercospora viticis* Goh & W.H. Hsieh, Trans. Mycol. Soc. Republ. China 4: 11. 1989.
= *Cercospora viticis-quinatae* J.M. Yen, Bull. Trimestriel Soc. Mycol. France 93: 158. 1977.
≡ *Pseudocercospora viticis-quinatae* (J.M. Yen) J.M. Yen, Bull. Trimestriel Soc. Mycol. France 94: 388. (1978) 1979.
= *Pseudocercospora viticigena* J.M. Yen, A.K. Kar & B.K. Das, Mycotaxon 16: 68. 1982.

*Specimens examined*: **Japan**, Okinawa, Okinawa Is, on *Vitex trifolia*, 19 Nov. 2007, C. Nakashima, MUMH 10828, culture MUCC 777; Chiba, Matsudo, on *V. agnus-castus*, 7 Nov. 1987, M. Nagashima & T. Kobayashi, TFM: FPH-6912; Shizuoka, Kanzanji, on *V. agnus-castus*, 1 Nov. 1996, T. Kobayashi & C. Nakashima, CNS-101, culture MUCC 1069, MAFF 237866; Kuroki, Fukuoka, on *V. cannabifolia* (≡ *V. negundo* var. *cannabifolia*), 25 Sep. 1974, S. Ogawa, TFM: FPH-4193.

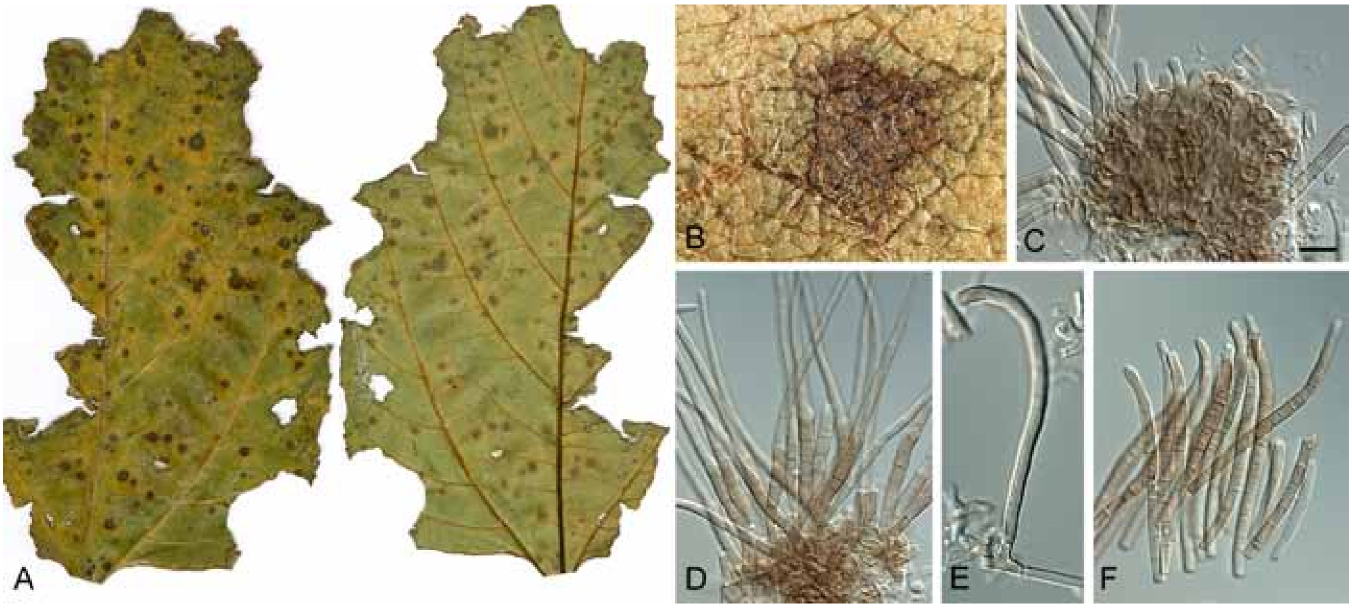


**Fig. 64.** *Pseudocercospora udagawana* (CPC 10799–10801). A. Leaf spots on upper and lower leaf surface. B. Close-up of leaf spot with fruiting. C, D. Fascicles with conidiophores and conidiogenous cells. E. Solitary conidiogenous cell on superficial hypha. F. Conidia. Scale bar = 10 µm.

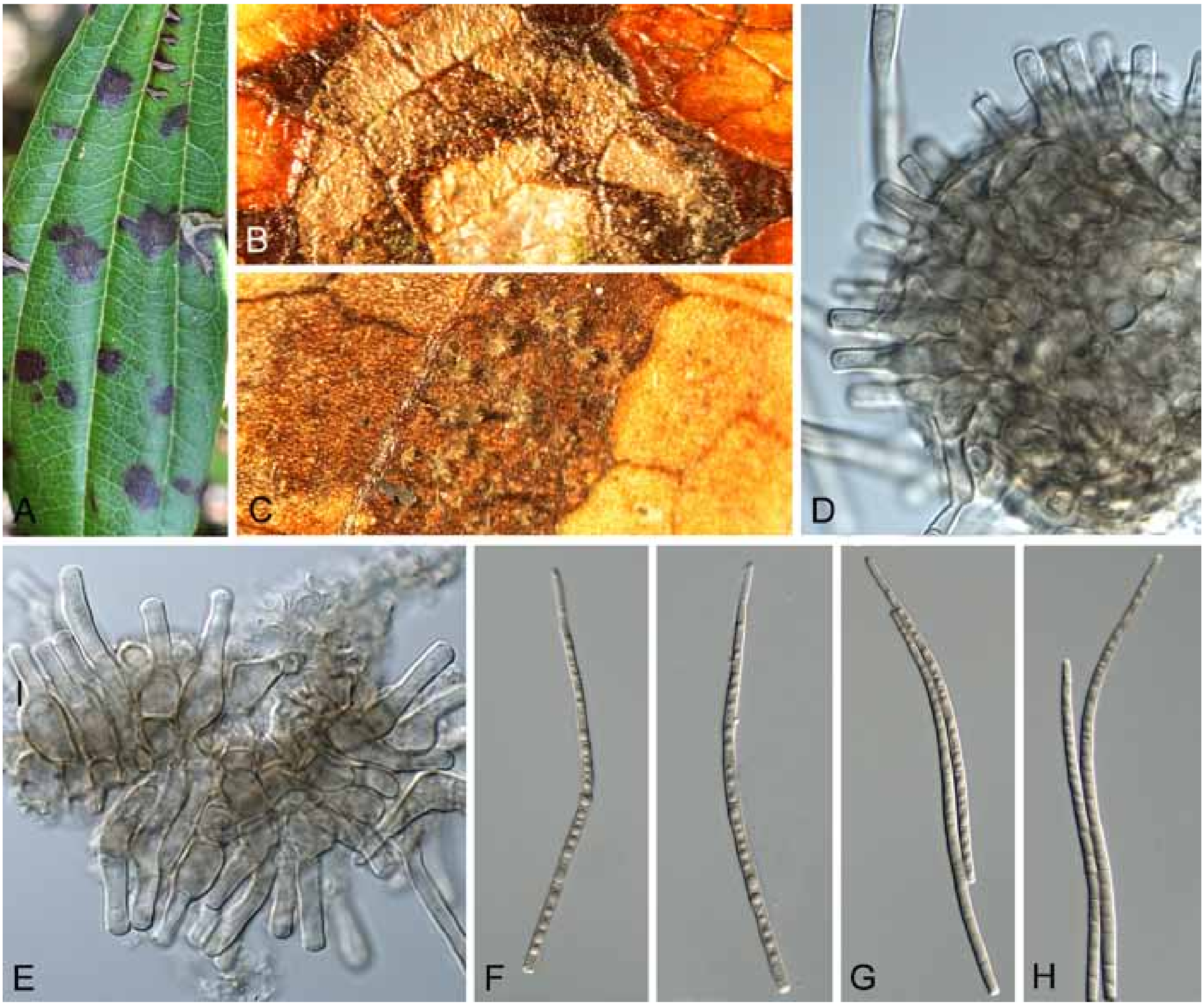


**Fig. 65.** *Pseudocercospora viburnigena* (CPC 15249). A. Leaf spots on upper leaf surface. B, C. Close-up of leaf spots with fruiting. D, E. Fascicles with conidiophores and conidiogenous cells. F–H. Conidia. Scale bars = 10 µm.

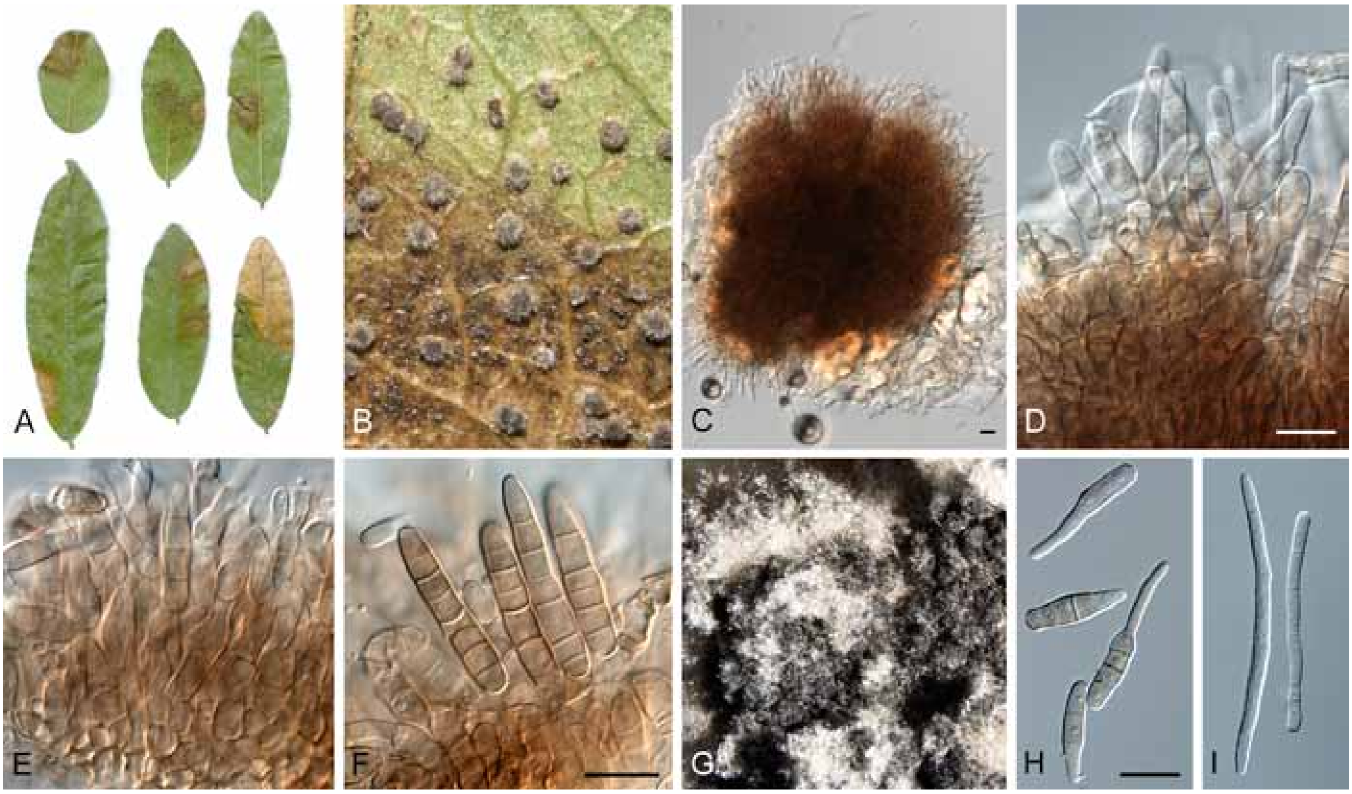


**Fig. 66.** *Pseudocercospora xanthocercidis* (CPC 11665–11667). A. Leaf spots on upper and lower leaf surface. B. Close-up of leaf spot with fruiting. C–E. Fascicles with conidiophores and conidiogenous cells. F. Conidia. G. Colony on malt extract agar. H, I. Conidia formed in culture. Scale bars = 10 µm.

***Pseudocercospora weigelae*** (Ellis & Everh.) Deighton, Trans. Brit. Mycol. Soc. 88: 389. 1987.
*Basionym*: *Cercospora weigelae* Ellis & Everh., Proc. Acad. Nat. Sci. Philadelphia 45: 170. 1893.

*Specimen examined*: **Japan**, Ibaraki, on *Weigela coraeensis*, 10 Sep. 1998, T. & Y. Kobayashi, CNS-455, culture MUCC 899, MAFF 237794.

***Pseudocercospora xanthocercidis*** Crous, U. Braun & A. Wood, **sp. nov.** MycoBank MB564847. Fig. 66.

*Etymology*: Name derived from the plant host *Xanthocercis*, from which it was collected.

*Leaf spots* amphigenous, irregular to subcircular, 3–8 mm diam, pale to medium brown, with indistinct border. *Mycelium* internal, pale brown, consisting of septate, branched, smooth, 2–3 µm diam hyphae. *Caespituli* sporodochial, hypophyllous, also occurring on green leaf tissue, prominent, appearing like insect galls, olivaceous-brown on leaves, up to 400 µm wide and 300 µm high. *Conidiophores* aggregated in dense sporodochial fascicles arising from the upper cells of a brown stroma up to 300 µm wide and 250 µm high; conidiophores brown, finely verruculose, 1–2-septate, subcylindrical, straight to slightly curved, 20–30 × 5–7 µm. *Conidiogenous cells* terminal, unbranched, brown, subcylindrical, finely verruculose, proliferating percurrently near apex, with several irregular, rough proliferations, 7–12 × 5–6 µm. *Conidia* solitary, brown, finely verruculose, guttulate, narrowly obclavate, apex obtuse, base obconically subtruncate to truncate, straight to gently curved, 5–8-septate, (25–)28–36(–40) × (5–)6–7 µm; hila unthickened, neither darkened nor refractive, 3–4 µm diam, with minute marginal frill visible.

*Culture characteristics*: Colonies after 2 wk at 24 ºC in the dark on MEA; surface irregular, folded, erumpent, spreading, with sparse aerial mycelium, and smooth, irregularly lobate margins. Surface olivaceous-grey, with patches of iron-grey; reverse iron-grey. Colonies reaching 5 mm diam.

*Specimen examined*: **South Africa**, Mpumalanga, Nelspruit, Lowveld National Botanical Garden, on *Xanthocercis zambesiaca,* 14 Sep. 2004, A. Wood, **holotype** HAL 1859 F, **isotype** CBS H-20891, culture ex-type CPC 11665 = CBS 131593, CPC 11666, 11667.

*Notes*: No other species of *Pseudocercospora* are known from this host. *Pseudocercospora xanthocercidis* differs from other *Pseudocercospora* species on legumes by its very large sporodochial conidiomata with percurrently proliferating conidiogenous cells and verruculose conidia with visible marginal frill at the base. There is no comparable species on legumes.

***Pseudocercospora xanthoxyli*** (Cooke) Y.L. Guo & X.J. Liu, Mycosystema 4: 115. 1991. Fig. 67.
*Basionym*: *Cercospora xanthoxyli* Cooke, Grevillea 12: 30. 1883.
= *Cercospora fagaricola* Sawada (*fagariae*), Rep. Gov. Agric. Res. Inst. Taiwan 85: 105. 1943, nom. inval.
≡ *Pseudocercospora fagaricola* Goh & W.H. Hsieh, in Hsieh & Goh, *Cercospora* and similar species from Taiwan: 294. 1990.

*Specimen examined*: **South Korea**, Wando, Wando Arboretum, on *Xanthoxylum ailanthoides*, 9 Nov. 2002, H.D. Shin, CBS H-20892, CPC 10009, 10064–10065.

***Pseudocercospora zelkovae*** (Hori) X.J. Liu & Y.L. Guo, Acta Mycol. Sin. 12: 33. 1993. Fig. 68.
*Basionym*: *Cercospora zelkowae* Hori, Nambu N. Jour. Plant Protection 8: 492. 1921.

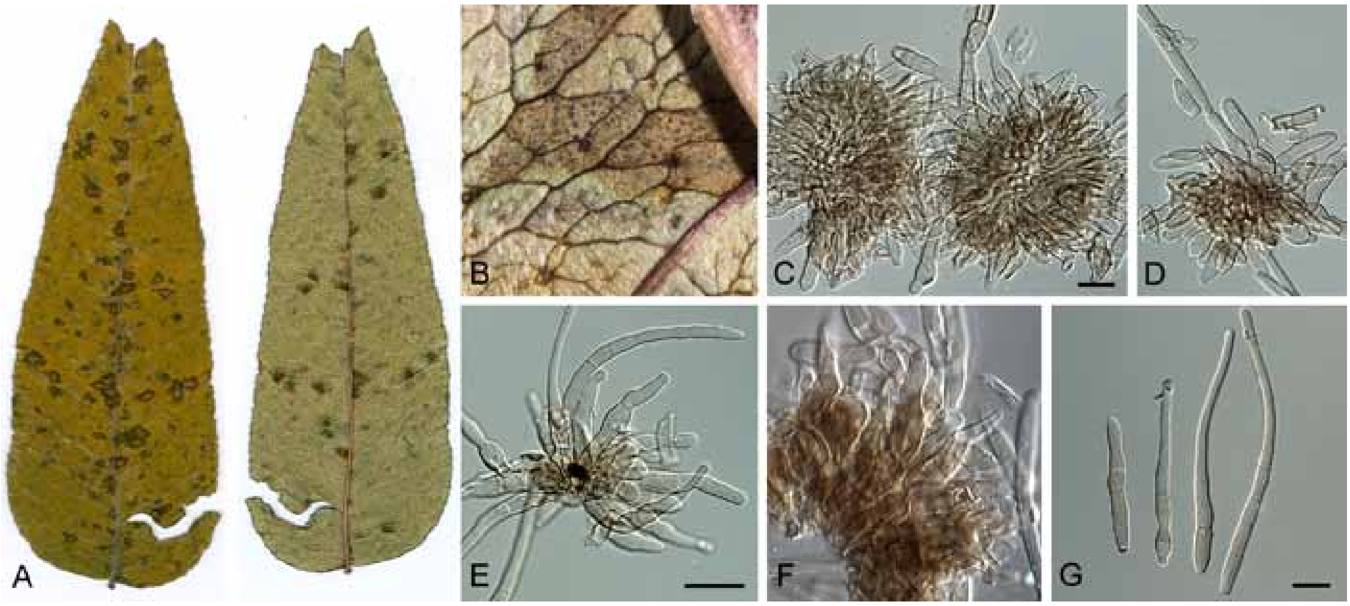


**Fig. 67.** *Pseudocercospora xanthoxyli* (CPC 10009, 10064–10065). A. Leaf spots on upper and lower leaf surface. B. Close-up of leaf spot with fruiting. C–E. Fascicles with conidiophores and conidiogenous cells. F. Close-up of conidiogenous cells. G. Conidia. Scale bars = 10 µm.

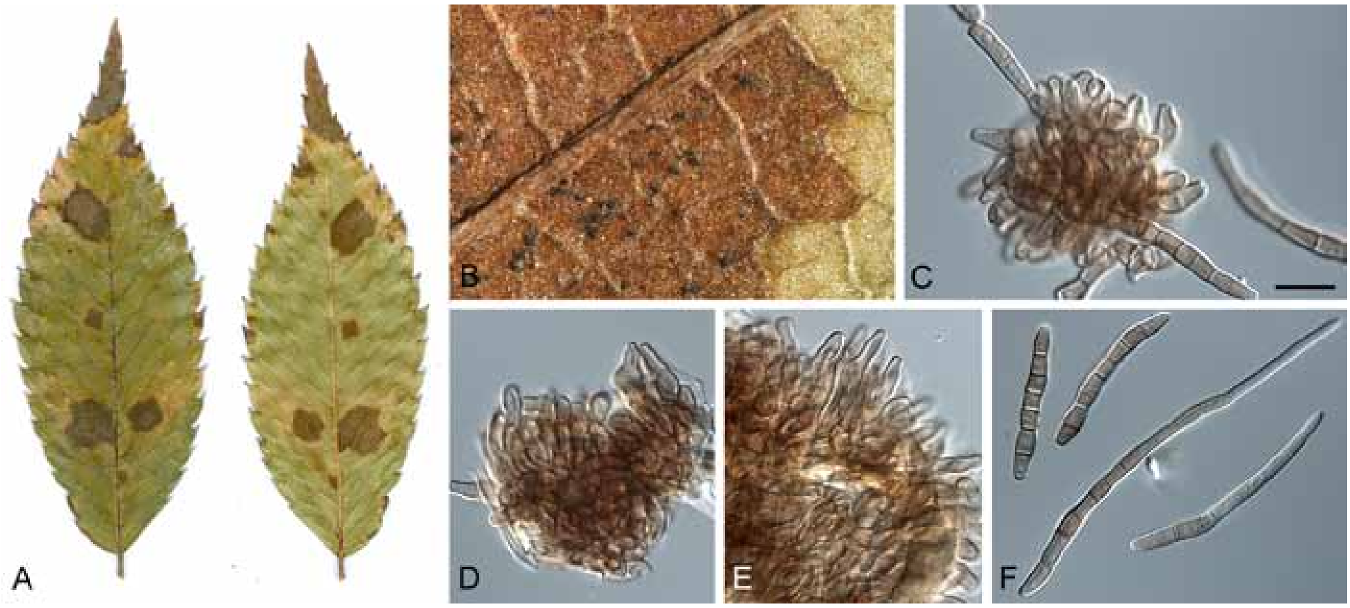


**Fig. 68.** *Pseudocercospora zelkovae* (CPC 14484). A. Leaf spots on upper and lower leaf surface. B. Close-up of leaf spot with fruiting. C–E. Fascicles with conidiophores and conidiogenous cells. F. Conidia. Scale bar = 10 µm.

*Holotype*: **Japan**, Tokyo, Forest Experimental Station, on *Zelkova serrata*, Jun. 1920 (not preserved).

*Specimens examined*: **Japan**, Yamagata, Kamabuchi, on *Z. serrata*, 5 July 1956, K. Ito, **neotype designated here** TFM:FPH169, cultures ex-neotype MAFF 410008, MUCC 1398. **South Korea**, Suwon, on *Z. serrata*, 2 Oct. 2007, H.D. Shin, CBS H-20893, culture CPC 14484 = CBS 132106; Osan, on *Z. serrata*, 30 Oct. 2007, H.D. Shin, CBS H-20894, CPC 14717 = CBS 132118.

## DISCUSSION

This study provides a broad framework and phylogeny for the genus *Pseudocercospora*. These fungi are very common and the foundation that has been set will form the basis for additional species to be described and for specific groups to be more thoroughly investigated. Although the results clarify several issues relating to the taxonomy of *Pseudocercospora s. str*., the study also highlights many remaining taxonomic questions relating to this complex. To resolve these issues many species will need to be recollected, cultured, and sequenced so that they can be placed into this phylogenetic backbone. This is especially true for species described in some of the obscure genera treated by Braun (1995) and Crous & Braun (2003), many of which (or their type species) are not currently known from culture, and thus DNA sequence comparisons and phylogenetic inference has not been possible.

Amongst the cercosporoid fungi, it appears possible and even probable that the approximately 1 500 names in *Pseudocercospora* represent the tip of the iceberg in terms of biodiversity. Indeed it seems likely that this could emerge as the largest genus of cercosporoid fungi known. A significant result of this study was the determination that names based on American or European type specimens could in most cases not be used when identifying identical diseases on the same hosts in Asia, Africa or South America. In this regard, it was surprising to find diversity even within a region such as Asia, where isolates from the same host and disease symptoms from Korea frequently differed from similar collections made in Japan. These important issues, which have significant ramifications pertaining to plant health and quarantine, will only be resolved when fresh collections from the American and European type locations have been made, thus allowing DNA sequence based comparisons. Furthermore, it emphasises the need to ensure that a DNA sequence has been provided for all novel taxa in this complex and that an authentic DNA barcode (Schoch *et al*. 2012) is available. The ITS gene region was found to be capable of differentiating only 25 of the 146 *Pseudocercospora* taxa (17 %) to species level in the present study. Where the ITS locus fails to provide acceptable resolution, it can be supplemented with sequences from the ACT or EF-1α gene regions (Fig. 5), though these loci still proved relatively conserved, and 57 taxa had less than 1% variation from their closest neighbours, suggesting that additional loci still have to be found to provide a more robust identification of *Pseudocercospora* species.

Focused studies on specific crops such as those on *Eucalyptus* (Crous 1998, Hunter *et al*. 2006b), *Musa* (Arzanlou *et al*. 2007, 2008, 2010), *Chromolaena* (Den Breeÿen *et al*. 2006) and *Citrus* (Pretorius *et al*. 2003) will undoubtedly confirm the already emerging view that many plant species are infected by a complex of *Pseudocercospora* spp. Some of these will clearly be specific to the host from which they were isolated, while others reflect chance occurrences or infections or broader host ranges (Crous & Groenewald 2005). In some instances, these chance infections may be caused by fungi that are major pathogens of other, completely unrelated hosts (Crous & Groenewald 2005, Arzanlou *et al*. 2008). Although the present study has succeeded in delineating *Pseudocercospora* within the *Mycosphaerellaceae*, and in the process has also delineated several other pseudocercospora-like genera, the question relating to host specificity still remains largely unanswered.

The taxa investigated during this study represent the largest collection of *Pseudocercospora* and pseudocercospora-like taxa ever subjected to DNA sequence analysis. Of these, the vast majority appear to be host-specific. Of the 146 taxa subjected to multi-gene analysis, only four were found to occur on more than one host. These include *P. norchiensis* (*Myrtaceae* and *Rosaceae*), *P. fraxinites* (*Oleaceae*), *P. atromarginalis* (*Solanaceae*) and *P. corylopsidis* (*Hamamelidaceae*). In the latter three examples, the same species was found on different host genera within the same plant family, but never on unrelated hosts. This result was somewhat surprising as we initially expected to find at least some examples where species are generalists and occur on many hosts which are unrelated such as those in the *Cercospora apii* complex (Groenewald *et al.* 2006, 2007). The occurrence of *P. norchiensis* (a foliar pathogen of *Eucalyptus* in Italy; Crous *et al*. 2007c) on *Rubus* in New Zealand (CBS 114641), was highly unexpected, and further collections on *Rubus* from New Zealand will have to be made to resolve if this was a mere chance occurrence (Crous & Groenewald 2005), or true indication of its host range.

In future studies of *Pseudocercospora*, additional taxa should be included in the analyses, and further loci screened to obtain a better separation of species. There is an urgent need to conduct inoculation tests to confirm inferences from taxonomic studies about host specificity in this important group of predominantly plant pathogenic fungi. For example, it remains to be shown whether isolates from different hosts with identical DNA barcodes and similar morphology have the ability to cross-infect hosts under natural conditions in the field. It appears that for the most part, F.C. Deighton was correct in his statement “If a sparrow flies to a cherry tree, it’s a cherry tree sparrow. If the same sparrow sits in an apple tree, it is an apple tree sparrow”.

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# Species concepts in *Cercospora*: spotting the weeds among the roses

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**Abstract:** The genus *Cercospora* contains numerous important plant pathogenic fungi from a diverse range of hosts. Most species of *Cercospora* are known only from their morphological characters *in vivo*. Although the genus contains more than 5 000 names, very few cultures and associated DNA sequence data are available. In this study, 360 *Cercospora* isolates, obtained from 161 host species, 49 host families and 39 countries, were used to compile a molecular phylogeny. Partial sequences were derived from the internal transcribed spacer regions and intervening 5.8S nrRNA, actin, calmodulin, histone H3 and translation elongation factor 1-alpha genes. The resulting phylogenetic clades were evaluated for application of existing species names and five novel species are introduced. Eleven species are epi-, lecto- or neotypified in this study. Although existing species names were available for several clades, it was not always possible to apply North American or European names to African or Asian strains and *vice versa*. Some species were found to be limited to a specific host genus, whereas others were isolated from a wide host range. No single locus was found to be the ideal DNA barcode gene for the genus, and species identification needs to be based on a combination of gene loci and morphological characters. Additional primers were developed to supplement those previously published for amplification of the loci used in this study.

**Key words:** *Cercospora apii* complex, co-evolution, host jumping, host specificity, speciation.
**Taxonomic novelties: New species -** *Cercospora coniogrammes* Crous & R.G. Shivas, *Cercospora delaireae* C. Nakash., Crous, U. Braun & H.D. Shin, *Cercospora euphorbiae-sieboldianae* C. Nakash., Crous, U. Braun & H.D. Shin, *Cercospora pileicola* C. Nakash., Crous, U. Braun & H.D. Shin, *Cercospora vignigena* C. Nakash., Crous, U. Braun & H.D. Shin. **Typifications: epitypifications -** *Cercospora alchemillicola* U. Braun & C.F. Hill, *Cercospora althaeina* Sacc., *Cercospora armoraciae* Sacc., *Cercospora corchori* Sawada, *Cercospora mercurialis* Pass., *Cercospora olivascens* Sacc., *Cercospora violae* Sacc.; **neotypifications -** *Cercospora fagopyri* N. Nakata & S. Takim., *Cercospora sojina* Hara.

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## INTRODUCTION

Species of the genus *Cercospora* belong to one of the largest genera of hyphomycetes and were often linked to the teleomorph genus *Mycosphaerella* (*Capnodiales*, *Mycosphaerellaceae*; Stewart *et al*. 1999, Crous *et al*. 2000). The genus *Mycosphaerella* was shown to be polyphyletic (Crous *et al.* 2007), and subsequently split into numerous genera, correlating with its different anamorph states (Crous *et al.* 2009a, b). The genus *Cercospora* is now considered a holomorphic genus in its own right, with some species exhibiting the ability to form mycosphaerella-like teleomorphs (Corlett 1991, Crous *et al*. 2004b). *Mycosphaerella s. str*. on the other hand, is restricted to taxa that form *Ramularia* anamorphs (Verkley *et al*. 2004). As *Mycosphaerella* has been widely applied to more than 40 different genera, Crous *et al*. (2009b) expressed their preference to use the older, recently monographed (Braun 1998) anamorph-typified name *Ramularia* (1833) for this holomorphic clade, instead of the younger, confused teleomorph-typified generic name *Mycosphaerella* (1884). This is allowed under the new, changed Article 59 of the International Code for Nomenclature of algae, fungi, and plants (ICN) (Hawksworth 2011, Norvell 2011).

Species of *Cercospora* are commonly associated with leaf spots (Fig. 1), and have also been isolated from necrotic lesions of flowers, fruits and seeds or were associated with postharvest fruit rot disease (Silva & Pereira 2008) of hosts from across the world (Agrios 2005, To-Anun *et al*. 2011). The cercosporoid fungi have also been used as biocontrol agents (Morris & Crous 1994, Inglis *et al*. 2001, Tessman *et al*. 2001). Species of *Cercospora* were traditionally named after the host from which they were isolated, even to the extent that a species of *Cercospora* was described as new when found on a different host plant (Chupp 1954, Ellis 1971). The genus *Cercospora* was first erected by Fresenius for passalora-like fungi with pluriseptate conidia (in Fuckel 1863). Chupp's (1954) monograph accepted 1 419 *Cercospora* species and proposed a broad concept for this genus based on whether hila were thickened or not, and whether conidia were pigmented, single or in chains. The number of *Cercospora* species doubled to more than 3 000 when Pollack (1987) published her annotated list of *Cercospora* names. Since then a combination of characters such as conidiomatal structure, mycelium, conidiophores, conidiogenous cells and conidia has been used to divide the genus into morphologically similar units. Crous & Braun (2003) used the structure of conidiogenous loci and hila as well as the absence or presence of pigmentation in conidiophores and conidia in their revision of names published in *Cercospora* and *Passalora*. They recognised 659 names in the genus *Cercospora,* with a further 281 names referred to as *C. apii s. lat*. The *C. apii* complex represented

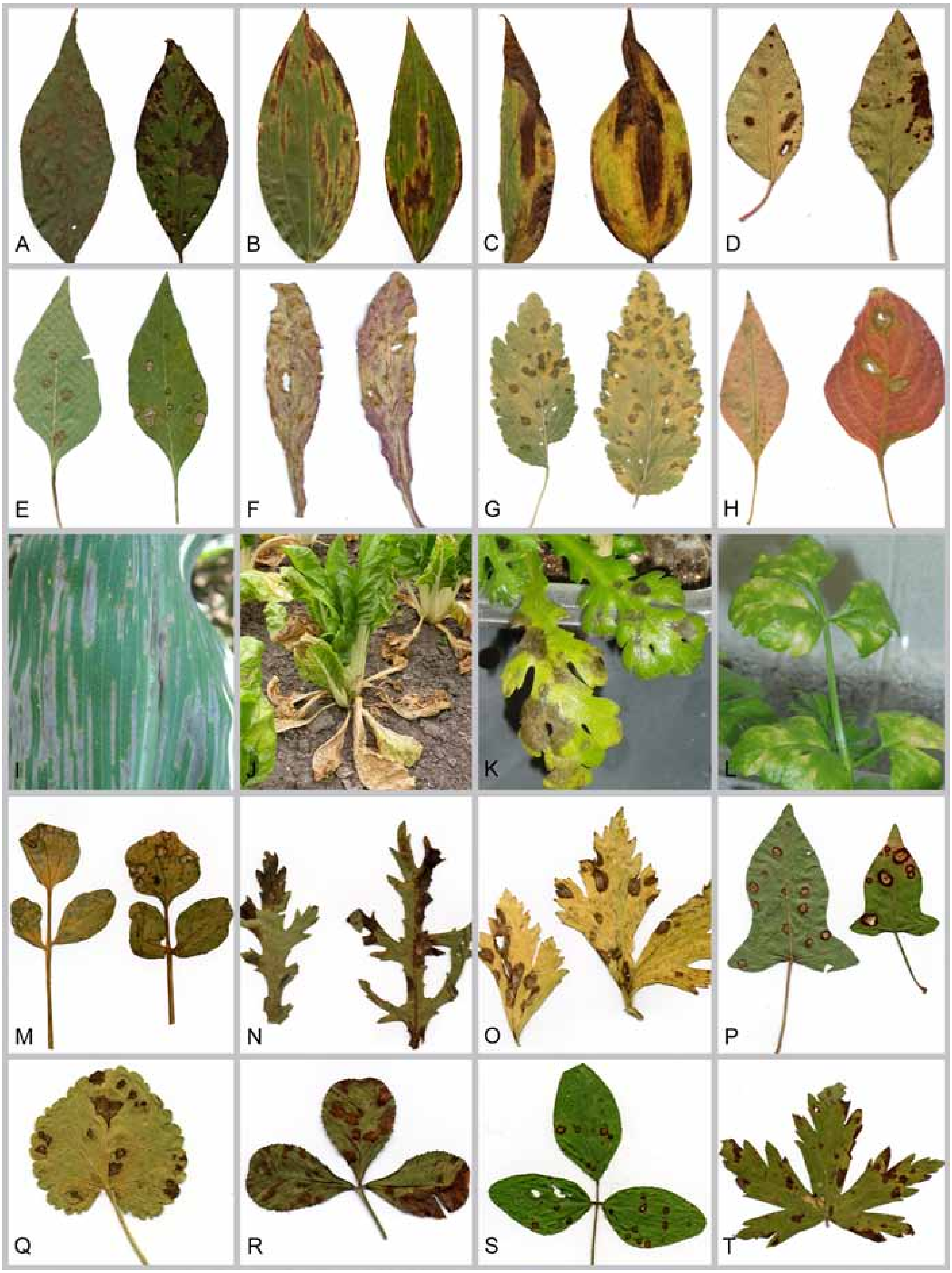



**Fig. 1.** Foliar disease symptoms associated with *Cercospora* spp. A. *C. achyranthis* on *Achyranthes japonica*. B. *C. dispori* on *Disporum viridescens*. C. *C. chinensis* on *Polygonatum humile*. D. *C.* cf. *flagellaris* on *Amaranthus patulus*. E. *C. capsici* on *Capsicum annuum*. F. *Cercospora* sp. on *Ajuga multiflora*. G. *Cercospora* sp. on *Cardamine leucanthe*. H. *C.* cf. *flagellaris* on *Celosia argentea* var. *cristata*. I. *C. zeina* on *Zea mays*. J. *C. beticola* on *Beta vulgaris*. K. *C. chrysanthemi* on *Chrysanthemum*. L. *C. apii* on *Apium*. M. *C. amoraciae* on *Rorippa indica*. N. *C. beticola* on *Chrysanthemum segetum*. O. *C. apiicola* on *Apium*. P. *C. ipomoeae* on *Persicaria thunbergii*. Q. *C. althaeina* on *Althaea rosea*. R. *C. zebrina* on *Trifolium repens*. S. *C. sojina* on *Glycine max*. T. *C. brunkii* on *Geranium nepalense*.

*Cercospora* species that were morphologically indistinguishable from *C. apii* (Ellis 1971, Crous & Braun 2003). In addition, Crous & Braun (2003) introduced the concept of "compound species" which consisted of morphologically indistinguishable species with different races (host range), genetically uniform or heterogeneous, with different degrees of biological specialisation. They also proposed that genetically and morphologically clearly distinguishable taxa should be treated as separate species, although the study was confounded by the general unavailability of *Cercospora* cultures for DNA analyses. Ex-type strains mostly do not exist as such isolates were neither designated nor preserved, for the majority of *Cercospora* species (Groenewald *et al*. 2010a). For most *Cercospora* species, a sexual stage (a mycosphaerella-like state) is not known; or has been reported, but not confirmed (Goodwin *et al*. 2001). The mating type genes of some apparently asexual *Cercospora* species were recently characterised, with the discovery that *C. beticola*, *C. zeae-maydis* and *C. zeina* were heterothallic, although only one mating type was present in populations of *C. apii* and *C. apiicola* (Groenewald *et al*. 2006b, 2010b). The two mating types of *C. beticola* were distributed approximately equally in the tested populations, indicating that these genes might indeed be active, indicative of cryptic sex. More recently a skewed distribution of mating types across sugar beet fields from different localities was report from Iran, with some fields having both mating types and others only the one or the other (Bakhshi *et al.* 2011). A further study conducted over a 3-yr period in the USA, also led to the conclusion that *C. beticola* has potential for sexual reproduction (Bolton *et al*. 2012).

Host specificity and speciation in *Cercospora* has not been studied extensively, but it is known that some species induce leaf spot symptoms when inoculated on other hosts, for example, *C. beticola* on all members of *Beta* (*Chenopodiaceae*) and other plant species (Weiland & Koch 2004) or *C. apii* and *C. beticola* isolated from disease symptoms on other hosts (Groenewald *et al.* 2006a). *Cercospora caricis* is used as a biological control agent of *Cyperus rotundus* (*Cyperaceae*)*,* and Inglis *et al*. (2001) compared Brazilian isolates with an isolate from Florida, USA. The authors used RAPDs (Randomly Amplified Polymorphic DNA), RFLPs (Restriction Fragment Length Polymorphisms) with a telomeric probe and ITS sequencing and found that a cluster of isolates from the Brazilian cerrado region showed high genetic similarity, whereas similarity between this region and others in Brazil was less that 50 %. They also found that the ITS sequence analysis did not support a division in the Brazilian isolates (99 % similar sequences) but that it did separate the Florida isolate from the Brazilian isolates (96 % similar when included with the Brazilian isolates). They concluded that the isolate from Florida probably represented cryptic speciation but that larger sampling of isolates was required from different geographical areas to address this question. Host specificity for some species appears to operate at the strain level, as for *C. rodmanii*, in which the original strains of Conway (1976) were shown to be specific to water hyacinth, whereas strains identified by morphology and multi-locus sequence data as the same species, were able to infect beet and sugar beet (Montenegro-Calderón *et al.* 2011).

A number of molecular studies using ITS phylogenies confirmed that *Cercospora* taxa cluster in a well-supported monophyletic clade in *Mycosphaerella* (Stewart *et al*. 1999, Crous *et al*. 2000, 2009a, b, Goodwin *et al*. 2001, Pretorius *et al*. 2003), in contrast to other polyphyletic genera such as *Septoria* (Verkley *et al*. 2004; compared to the monophyletic *Zymoseptoria*, Quaedvlieg *et al*. 2011), *Pseudocercospora, Passalora* and *Zasmidium* (Crous *et al*. 2009b), to name but a few. The ITS region (ITS1, 5.8S rDNA and ITS2) lacks the resolution to distinguish between most *Cercospora* species (Groenewald *et al*. 2010a). For example, Goodwin *et al*. (2001) found a mean of 1.27 sequence changes over 18 taxa from 11 *Cercospora* species, and Pretorius *et al*. (2003) found a mean of 1.64 changes when they tested 25 taxa representing 11 *Cercospora* species. Both Goodwin *et al*. (2001) and Pretorius *et al*. (2003) observed more transitions than transversions. Only a limited number of studies utilising gene sequences other than ITS have been published thus far (for example Tessmann *et al*. 2001, Crous *et al*. 2004b, Groenewald *et al*. 2005, 2006a, 2010a, Montenegro-Calderón *et al.* 2011). Tessmann *et al*. (2001) found that 14 of the 431 aligned translation elongation factor 1-alpha characters were parsimony-informative, with only six of the 380 characters for beta-tubulin and 17 of the 309 histone H3 characters being parsimony-informative. The ITS region did not contain any differences when compared with the outgroup *C. beticola*. Crous *et al*. (2004b) used fixed nucleotide changes in aligned nucleotide characters (including alignment gaps) to discriminate *C. acaciae-mangii* from *C. apii* and *C. beticola,* and listed changes at none of 521 ITS characters (0 %), nine of 300 translation elongation factor 1-alpha characters (3 %), three of 209 actin characters (1.4 %), 10 of 312 calmodulin characters (3.2 %), and seven of 388 histone H3 characters (1.8 %). A total of 1 730 aligned characters were examined, of which 29 (1.68 %) were observed as fixed nucleotide changes. Using the same five loci, Groenewald *et al*. (2005) found 96 % similarity between *C. apii* and *C. beticola* for the calmodulin gene, with all other loci having identical sequences. Based on the differences in the calmodulin gene, distinctive AFLP banding patterns and different growth rates, the authors recognised *C. apii s. str.* and *C. beticola s. str.* as distinct species. Continuing with the same approach, Groenewald *et al*. (2006a) then proceeded to describe *C. apiicola*, a further distinct species thus far only isolated from *Apium* (*Apiaceae*). Both Groenewald *et al*. (2010a) and Montenegro-Calderón *et al.* (2011) used phylogenetic analyses of combined ITS, translation elongation factor 1-alpha, actin, calmodulin and histone H3 sequence alignments to study species boundaries and diversity in *Cercospora*. Groenewald *et al*. (2010a) concluded that although most loci tested could resolve a large number of species, the sum of the whole provided a better resolution compared to a subset of loci. In that study, the loci differed in their ability to resolve clades, with ITS and translation elongation factor 1-alpha performing worst (distinguishing three and 10 clades, respectively), while actin could distinguish 14 clades, calmodulin 13 clades and histone H3 12 clades compared to the 16 species clades recognised in the combined tree. Montenegro-Calderón *et al.* (2011) concluded that *C. rodmanii* could be distinguished from *C. piaropi* based on actin, calmodulin and histone H3, but that only calmodulin could clearly separate *C. rodmanii* from the other *Cercospora* species included in their study. These results illustrated that the phylogenetic approach using multi-locus sequences was one of the most effective ways to recognise different species of *Cercospora*. Although this approach is not suitable to recognise the true host range of a species without pathogenicity tests, it does provide a handle on the true identity of the strain being used.

Goodwin *et al*. (2001) attributed the short branch lengths observed for their ITS phylogeny to a relatively recent common ancestor that was able to, or acquired the ability to, produce cercosporin, a phytotoxic metabolite of polyketide origin (Daub & Ehrenshaft 2000). The ability to produce cercosporin probably allowed the *Cercospora* ancestor to rapidly expand its host range in a recent adaptive radiation (Goodwin *et al*. 2001). It has been suggested that this compound may enhance virulence (Upchurch *et al*. 1991), but it is not a universal pathogenicity factor as

**Table 1.** Collection details and GenBank accession numbers of isolates included in this study.

| Species | Culture accession number(s)[1] | Host name or isolation source | Host Family | Country | Collector | GenBank accession numbers[2] | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | | | | | | ITS | TEF | ACT | CAL | HIS |
| *Cercospora achyranthis* | CBS 132613; CPC 10879 | *Achyranthes japonica* | *Amaranthaceae* | South Korea: Jeju | H.D. Shin | JX143523 | JX143277 | JX143031 | JX142785 | JX142539 |
| | CPC 10091 | *Achyranthes japonica* | *Amaranthaceae* | South Korea: Jeju | H.D. Shin | JX143524 | JX143278 | JX143032 | JX142786 | JX142540 |
| *Cercospora agavicola* | CBS 117292; CPC 11774 (TYPE) | *Agave tequilana* var. *azul* | *Agavaceae* | Mexico: Penjamo | V. Ayala-Escobar & Ma. de Jesús Yáñez-Morales | AY647237 | AY966897 | AY966898 | AY966899 | AY966900 |
| *Cercospora alchemillicola* | CPC 5259 (TYPE) | *Alchemilla mollis* | *Rosaceae* | New Zealand: Auckland | C.F. Hill | JX143525 | JX143279 | JX143033 | JX142787 | JX142541 |
| *Cercospora* cf. *alchemillicola* | CPC 5126 | *Oenothera fruticosa* | *Onagraceae* | New Zealand: Auckland | C.F. Hill | JX143526 | JX143280 | JX143034 | JX142788 | JX142542 |
| | CPC 5127 | *Gaura lindheimeri* | *Onagraceae* | New Zealand: Auckland | C.F. Hill | JX143527 | JX143281 | JX143035 | JX142789 | JX142543 |
| *Cercospora althaeina* | CBS 126.26; CPC 5066 | *Malva* sp. | *Malvaceae* | — | C. Killian | JX143528 | JX143282 | JX143036 | JX142790 | JX142544 |
| | CBS 132609; CPC 10790 | *Althaea rosea* | *Malvaceae* | South Korea: Suwon | H.D. Shin | JX143529 | JX143283 | JX143037 | JX142791 | JX142545 |
| | CBS 248.67; CPC 5117 (TYPE) | *Althaea rosea* | *Malvaceae* | Romania: Fundulea | O. Constantinescu | JX143530 | JX143284 | JX143038 | JX142792 | JX142546 |
| *Cercospora apii* | CBS 110813; CPC 5110; 01-3 | *Moluccella laevis* | *Lamiaceae* | USA: California | S.T. Koike | AY156918 | DQ233345 | DQ233371 | DQ233397 | DQ233423 |
| | CBS 110816; CPC 5111; 01-4 | *Moluccella laevis* | *Lamiaceae* | USA: California | S.T. Koike | AY156919 | DQ233346 | DQ233372 | DQ233398 | DQ233424 |
| | CBS 114416; CPC 10925 | *Apium* sp. | *Apiaceae* | Austria | Institut fur Pflanzengesundheit | AY840516 | AY840483 | AY840447 | AY840414 | AY840381 |
| | CBS 114418; CPC 10924 | *Apium graveolens* | *Apiaceae* | Italy | M. Meutri | AY840517 | AY840484 | AY840448 | AY840415 | AY840382 |
| | CBS 114485; CPC 10923 | *Apium graveolens* | *Apiaceae* | Italy | M. Meutri | AY840518 | AY840485 | AY840449 | AY840416 | AY840383 |
| | CBS 116455; CPC 11556 (TYPE) | *Apium graveolens* | *Apiaceae* | Germany: Heilbron | K. Schrameyer | AY840519 | AY840486 | AY840450 | AY840417 | AY840384 |
| | CBS 116504; CPC 11579 | *Apium graveolens* | *Apiaceae* | Germany: Heilbron | K. Schrameyer | AY840520 | AY840487 | AY840451 | AY840418 | AY840385 |
| | CBS 116507; CPC 11582 | *Apium graveolens* | *Apiaceae* | Germany: Heilbron | K. Schrameyer | AY840521 | AY840488 | AY840452 | AY840419 | AY840386 |
| | CBS 119.25; B 42463; IHEM 3822; CPC 5086 | *Apium graveolens* | *Apiaceae* | — | L. J. Klotz | AY179949 | AY179915 | AY840443 | AY840410 | AY840377 |
| | CBS 121.31; CPC 5073 | *Beta vulgaris* | *Chenopodiaceae* | Austria: Wien | E.W. Schmidt | AY343371 | AY343334 | AY840444 | AY840411 | AY840378 |
| | CBS 127.31; CPC 5119 | *Beta vulgaris* | *Chenopodiaceae* | Hungary | E.W. Schmidt | AY840514 | AY840481 | AY840445 | AY840412 | AY840379 |
| | CBS 132683; CPC 16663 | *Moluccella laevis* | *Lamiaceae* | Zimbabwe | S. Dimbi | JX143531 | JX143285 | JX143039 | JX142793 | JX142547 |
| | CBS 152.52; IMI 077043; MUCL 16495; CPC 5063 | *Beta vulgaris* | *Chenopodiaceae* | Netherlands: Bergen op Zoom | G. van den Ende | AY840515 | AY840482 | AY840446 | AY840413 | AY840380 |
| | CBS 252.67; CPC 5084 | *Plantago lanceolata* | *Plantaginaceae* | Romania: Domnesti | O. Constantinescu | DQ233318 | DQ233342 | DQ233368 | DQ233394 | DQ233420 |
| | CBS 536.71; CPC 5087 | *Apium graveolens* | *Apiaceae* | Romania: Bucuresti | O. Constantinescu | AY752133 | AY752166 | AY752194 | AY752225 | AY752256 |
| | CBS 553.71; IMI 161116; CPC 5083 | *Plumbago europaea* | *Plumbaginaceae* | Romania: Hagieni | O. Constantinescu | DQ233320 | DQ233344 | DQ233370 | DQ233396 | DQ233422 |
| | CPC 18601 | *Apium graveolens* | *Apiaceae* | USA: California | S.T. Koike | JX143532 | JX143286 | JX143040 | JX142794 | JX142548 |
| | CPC 5112 | *Moluccella laevis* | *Lamiaceae* | New Zealand: Auckland | C.F. Hill | DQ233321 | DQ233347 | DQ233373 | DQ233399 | DQ233425 |
| | CPC 5260 | *Glebionis coronaria* (≡ *Chrysanthemum coronarium*) | *Asteraceae* | New Zealand: Auckland | C.F. Hill | JX143533 | JX143287 | JX143041 | JX142795 | JX142549 |
| | MUCC 567; MUCNS 30; MAFF 238072 | *Apium graveolens* | *Apiaceae* | Japan: Aichi | T. Kobayashi | JX143534 | JX143288 | JX143042 | JX142796 | JX142550 |

**Table 1.** (Continued).

| Species | Culture accession number(s)[1] | Host name or isolation source | Host Family | Country | Collector | GenBank accession numbers[2] | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | | | | | | ITS | TEF | ACT | CAL | HIS |
| | MUCC 573; MAFF 235978 | *Glebionis coronaria* (≡ *Chrysanthemum coronarium*) | *Asteraceae* | Japan: Hokkaido | — | JX143535 | JX143289 | JX143043 | JX142797 | JX142551 |
| | MUCC 593 | *Apium graveolens* | *Apiaceae* | Japan: Shizuoka | M. Togawa | JX143536 | JX143290 | JX143044 | JX142798 | JX142552 |
| | MUCC 923; MAFF 238299 | *Asparagus officinalis* | *Asparagaceae* | Japan: Saga | J. Yamaguchi | JX143537 | JX143291 | JX143045 | JX142799 | JX142553 |
| *Cercospora apiicola* | CBS 116457; CPC 10267 (TYPE) | *Apium* sp. | *Apiaceae* | Venezuela: Caripe | N. Pons | AY840536 | AY840503 | AY840467 | AY840434 | AY840401 |
| | CBS 116458; CPC 10657 | *Apium graveolens* | *Apiaceae* | South Korea: Kangnung | H.D. Shin | AY840537 | AY840504 | AY840468 | AY840435 | AY840402 |
| | CBS 132644; CPC 10248 | *Apium* sp. | *Apiaceae* | Venezuela: Caripe | N. Pons | AY840539 | AY840506 | AY840470 | AY840437 | AY840404 |
| | CBS 132651; CPC 10759 | *Apium graveolens* | *Apiaceae* | South Korea: Namyangju | H.D. Shin | AY840544 | AY840511 | AY840475 | AY840442 | AY840409 |
| | CBS 132666; CPC 11642; GRE-4-2 | *Apium* sp. | *Apiaceae* | Greece | I. Vloutoglou | DQ233341 | DQ233367 | DQ233393 | DQ233419 | DQ233441 |
| | CPC 10220 | *Apium* sp. | *Apiaceae* | Venezuela: Caripe | N. Pons | AY840538 | AY840505 | AY840469 | AY840436 | AY840403 |
| | CPC 10265 | *Apium* sp. | *Apiaceae* | Venezuela: Caripe | N. Pons | AY840540 | AY840507 | AY840471 | AY840438 | AY840405 |
| | CPC 10266 | *Apium* sp. | *Apiaceae* | Venezuela: Caripe | N. Pons | AY840541 | AY840508 | AY840472 | AY840439 | AY840406 |
| | CPC 10279 | *Apium* sp. | *Apiaceae* | Venezuela: Caripe | N. Pons | AY840542 | AY840509 | AY840473 | AY840440 | AY840407 |
| | CPC 10666 | *Apium* sp. | *Apiaceae* | South Korea: Kangnung | H.D. Shin | AY840543 | AY840510 | AY840474 | AY840441 | AY840408 |
| | CPC 11641; GRE-3-2 | *Apium* sp. | *Apiaceae* | Greece | I. Vloutoglou | DQ233340 | DQ233366 | DQ233392 | DQ233418 | DQ233440 |
| *Cercospora armoraciae* | CBS 115060; CPC 5366 | *Gaura* sp. | *Onagraceae* | New Zealand | C.F. Hill | JX143538 | JX143292 | JX143046 | JX142800 | JX142554 |
| | CBS 115394; CPC 5261 | *Nasturtium officinale* (= *Rorippa nasturtium-aquaticum*) | *Brassicaceae* | New Zealand: Auckland | C.F. Hill | JX143539 | JX143293 | JX143047 | JX142801 | JX142555 |
| | CBS 115409; CPC 5359 | *Armoracia rusticana* (= *A. lapathifolia*) | *Brassicaceae* | New Zealand: Manurewa | C.F. Hill | JX143540 | JX143294 | JX143048 | JX142802 | JX142556 |
| | CBS 132610; CPC 10811 | *Armoracia rusticana* (= *A. lapathifolia*) | *Brassicaceae* | South Korea: Suwon | H.D. Shin | JX143541 | JX143295 | JX143049 | JX142803 | JX142557 |
| | CBS 132638; CPC 10100 | *Barbarea orthoceras* | *Brassicaceae* | South Korea: Pocheon | H.D. Shin | JX143542 | JX143296 | JX143050 | JX142804 | JX142558 |
| | CBS 132654; CPC 11338 | *Turritis glabra* (≡ *Arabis glabra*) | *Brassicaceae* | South Korea: Hoengseong | H.D. Shin | JX143543 | JX143297 | JX143051 | JX142805 | JX142559 |
| | CBS 132672; CPC 14612 | *Rorippa indica* | *Brassicaceae* | South Korea: Jecheon | H.D. Shin | JX143544 | JX143298 | JX143052 | JX142806 | JX142560 |
| | CBS 250.67; CPC 5088 (TYPE) | *Armoracia rusticana* (= *A. lapathifolia*) | *Brassicaceae* | Romania: Fundulea | O. Constantinescu | JX143545 | JX143299 | JX143053 | JX142807 | JX142561 |
| | CBS 258.67; CPC 5061 | *Cardaria draba* | *Brassicaceae* | Romania: Fundulea | O. Constantinescu | JX143546 | JX143300 | JX143054 | JX142808 | JX142562 |
| | CBS 538.71; IMI 161109; CPC 5090 | *Berteroa incana* | *Brassicaceae* | Romania: Hagieni | O. Constantinescu | JX143547 | JX143301 | JX143055 | JX142809 | JX142563 |
| | CBS 540.71; IMI 161110; CPC 5060 | *Cardaria draba* | *Brassicaceae* | Romania: Hagieni | O. Constantinescu | JX143548 | JX143302 | JX143056 | JX142810 | JX142564 |
| | CBS 545.71; CPC 5056 | *Erysimum cuspidatum* | *Brassicaceae* | Romania: Valea Mraconiei | O. Constantinescu | JX143549 | JX143303 | JX143057 | JX142811 | JX142565 |
| | CBS 555.71; IMI 161117; CPC 5082 | *Coronilla varia* | *Fabaceae* | Romania: Hagieni | O. Constantinescu | JX143550 | JX143304 | JX143058 | JX142812 | JX142566 |
| | CPC 10133 | *Rorippa indica* | *Brassicaceae* | South Korea: Wonju | H.D. Shin | JX143551 | JX143305 | JX143059 | JX142813 | JX142567 |
| | CPC 11364 | *Turritis glabra* (≡ *Arabis glabra*) | *Brassicaceae* | South Korea: Hoengseong | H.D. Shin | JX143552 | JX143306 | JX143060 | JX142814 | JX142568 |
| | CPC 11530 | *Acacia mangium* | *Fabaceae* | Thailand | W. Himaman | JX143553 | JX143307 | JX143061 | JX142815 | JX142569 |
| | MUCC 768 | *Armoracia rusticana* (= *A. lapathifolia*) | *Brassicaceae* | Japan: Okinawa | C. Nakashima | JX143554 | JX143308 | JX143062 | JX142816 | JX142570 |

**Table 1.** (Continued).

| Species | Culture accession number(s)[1] | Host name or isolation source | Host Family | Country | Collector | GenBank accession numbers[2] | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | | | | | | ITS | TEF | ACT | CAL | HIS |
| *Cercospora beticola* | CBS 113069; CPC 5369 | *Spinacia* sp. | *Chenopodiaceae* | Botswana: Gaborone | L. Lebogang | DQ233325 | DQ233351 | DQ233377 | DQ233403 | DQ233429 |
| | CBS 115478; CPC 5113 | *Limonium sinuatum* | *Plumbaginaceae* | New Zealand: Auckland | C.F. Hill | DQ233326 | DQ233352 | DQ233378 | DQ233404 | DQ233430 |
| | CBS 116.47; CPC 5074 | *Beta vulgaris* | *Chenopodiaceae* | Netherlands: Northwest Brabant | G.E. Bunschoten | AY752135 | AY752168 | AY752196 | AY752227 | AY752258 |
| | CBS 116454; CPC 11558 | *Beta vulgaris* | *Chenopodiaceae* | Germany | S. Mittler | AY840526 | AY840493 | AY840457 | AY840424 | AY840391 |
| | CBS 116456; CPC 11557 (TYPE) | *Beta vulgaris* | *Chenopodiaceae* | Italy: Ravenna | V. Rossi | AY840527 | AY840494 | AY840458 | AY840425 | AY840392 |
| | CBS 116501; CPC 11576 | *Beta vulgaris* | *Chenopodiaceae* | Iran: Pakajik | A.A. Ravanlou | AY840528 | AY840495 | AY840459 | AY840426 | AY840393 |
| | CBS 116502; CPC 11577 | *Beta vulgaris* | *Chenopodiaceae* | Germany | S. Mittler | AY840529 | AY840496 | AY840460 | AY840427 | AY840394 |
| | CBS 116503; CPC 11578 | *Beta vulgaris* | *Chenopodiaceae* | Italy: Ravenna | V. Rossi | AY840530 | AY840497 | AY840461 | AY840428 | AY840395 |
| | CBS 116505; CPC 11580 | *Beta vulgaris* | *Chenopodiaceae* | France: Longvic | S. Garressus | AY840531 | AY840498 | AY840462 | AY840429 | AY840396 |
| | CBS 116506; CPC 11581 | *Beta vulgaris* | *Chenopodiaceae* | Netherlands | M. Groenewald | AY840532 | AY840499 | AY840463 | AY840430 | AY840397 |
| | CBS 117.47 | *Beta vulgaris* | *Chenopodiaceae* | Czech Republic | G.E. Bunschoten | DQ233322 | DQ233348 | DQ233374 | DQ233400 | DQ233426 |
| | CBS 117556; CPC 10171 | *Beta vulgaris* | *Chenopodiaceae* | New Zealand: Auckland | C.F. Hill | AY840534 | AY840501 | AY840465 | AY840432 | AY840399 |
| | CBS 122.31; CPC 5072 | *Beta vulgaris* | *Chenopodiaceae* | Germany: Gmain | E.W. Schmidt | AY752136 | AY752169 | AY752197 | AY752228 | AY752259 |
| | CBS 123.31; CPC 5071 | *Beta vulgaris* | *Chenopodiaceae* | Spain | E.W. Schmidt | AY840522 | AY840489 | AY840453 | AY840420 | AY840387 |
| | CBS 123907; CPC 14616 | *Goniolimon tataricum* | *Plumbaginaceae* | Bulgaria | S.G. Bobev | FJ473422 | FJ473427 | FJ473432 | FJ473437 | FJ473442 |
| | CBS 123908; CPC 14620 | *Goniolimon tataricum* | *Plumbaginaceae* | Bulgaria | S.G. Bobev | FJ473426 | FJ473431 | FJ473436 | FJ473441 | FJ473446 |
| | CBS 124.31; CPC 5070 | *Beta vulgaris* | *Chenopodiaceae* | Romania: Hagieni | E.W. Schmidt | AY840523 | AY840490 | AY840454 | AY840421 | AY840388 |
| | CBS 125.31; CPC 5069 | *Beta vulgaris* | *Chenopodiaceae* | — | E.W. Schmidt | AY840524 | AY840491 | AY840455 | AY840422 | AY840389 |
| | CBS 126.31; CPC 5064 | *Beta vulgaris* | *Chenopodiaceae* | Germany: Klein Wanzleben | E.W. Schmidt | AY840525 | AY840492 | AY840456 | AY840423 | AY840390 |
| | CBS 132655; CPC 11341 | *Chrysanthemum segetum* (= *Ch. coronarium* var. *spatiosum*) | *Asteraceae* | South Korea: Namyangju | H.D. Shin | DQ233332 | DQ233358 | DQ233384 | DQ233410 | DQ233434 |
| | CBS 132673; CPC 14617 | *Goniolimon tataricum* | *Plumbaginaceae* | Bulgaria | S.G. Bobev | FJ473423 | FJ473428 | FJ473433 | FJ473438 | FJ473443 |
| | CBS 539.71; CPC 5062 | *Beta vulgaris* | *Chenopodiaceae* | Romania: Bucuresti | O. Constantinescu | DQ233323 | DQ233349 | DQ233375 | DQ233401 | DQ233427 |
| | CBS 548.71; IMI 161115; CPC 5065 | *Malva pusilla* | *Malvaceae* | Romania: Hagieni | O. Constantinescu & G. Negrean | DQ233324 | DQ233350 | DQ233376 | DQ233402 | DQ233428 |
| | CPC 10166 | *Beta vulgaris* | *Chenopodiaceae* | New Zealand | C.F. Hill | DQ233329 | DQ233355 | DQ233381 | DQ233407 | DQ026471 |
| | CPC 10168 | *Beta vulgaris* | *Chenopodiaceae* | New Zealand: Auckland | C.F. Hill | AY840533 | AY840500 | AY840464 | AY840431 | AY840398 |
| | CPC 10195 | *Beta vulgaris* | *Chenopodiaceae* | New Zealand | C.F. Hill | DQ233330 | DQ233356 | DQ233382 | DQ233408 | DQ026472 |
| | CPC 10197 | *Beta vulgaris* | *Chenopodiaceae* | New Zealand: Auckland | C.F. Hill | AY840535 | AY840502 | AY840466 | AY840433 | AY840400 |
| | CPC 10204 | *Beta vulgaris* | *Chenopodiaceae* | New Zealand: Auckland | C.F. Hill | DQ233331 | DQ233357 | DQ233383 | DQ233409 | DQ233433 |
| | CPC 11344 | *Chrysanthemum segetum* (= *Ch. coronarium* var. *spatiosum*) | *Asteraceae* | South Korea: Namyangju | H.D. Shin | DQ233333 | DQ233359 | DQ233385 | DQ233411 | DQ233435 |

**Table 1.** (Continued).

| Species | Culture accession number(s)[1] | Host name or isolation source | Host Family | Country | Collector | GenBank accession numbers[2] | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | | | | | | ITS | TEF | ACT | CAL | HIS |
| | CPC 12022 | *Beta vulgaris* | *Chenopodiaceae* | Germany | S. Mittler | DQ233334 | DQ233360 | DQ233386 | DQ233412 | DQ233436 |
| | CPC 12027 | *Beta vulgaris* | *Chenopodiaceae* | Germany | S. Mittler | DQ233335 | DQ233361 | DQ233387 | DQ233413 | DQ026468 |
| | CPC 12028 | *Beta vulgaris* | *Chenopodiaceae* | Egypt | M. Hasem | DQ233336 | DQ233362 | DQ233388 | DQ233414 | DQ233437 |
| | CPC 12029 | *Beta vulgaris* | *Chenopodiaceae* | Egypt | M. Hasem | DQ233337 | DQ233363 | DQ233389 | DQ233415 | DQ233438 |
| | CPC 12030 | *Beta vulgaris* | *Chenopodiaceae* | Egypt | M. Hasem | DQ233338 | DQ233364 | DQ233390 | DQ233416 | DQ233439 |
| | CPC 12031 | *Beta vulgaris* | *Chenopodiaceae* | Germany | S. Mittler | DQ233339 | DQ233365 | DQ233391 | DQ233417 | DQ026470 |
| | CPC 14618 | *Goniolimon tataricum* | *Plumbaginaceae* | Bulgaria | S.G. Bobev | FJ473424 | FJ473429 | FJ473434 | FJ473439 | FJ473444 |
| | CPC 14619 | *Goniolimon tataricum* | *Plumbaginaceae* | Bulgaria | S.G. Bobev | FJ473425 | FJ473430 | FJ473435 | FJ473440 | FJ473445 |
| | CPC 15623 | *Beta vulgaris* | *Chenopodiaceae* | Mexico: Texcoco | Ma. de Jesús Yáñez-Morales | JX143555 | JX143309 | JX143063 | JX142817 | JX142571 |
| | CPC 18813 | *Beta vulgaris* | *Chenopodiaceae* | USA: California | S.T. Koike | JX143556 | JX143310 | JX143064 | JX142818 | JX142572 |
| | CPC 5123 | *Apium graveolens* | *Apiaceae* | New Zealand: Auckland | C.F. Hill | AY752134 | AY752167 | AY752195 | AY752226 | AY752257 |
| | CPC 5125 | *Beta vulgaris* | *Chenopodiaceae* | New Zealand: Auckland | C.F. Hill | AY752137 | AY752170 | AY752198 | AY752229 | AY752260 |
| | CPC 5128 | *Beta vulgaris* | *Chenopodiaceae* | New Zealand: Auckland | C.F. Hill | AY752138 | AY752171 | AY752199 | AY752230 | AY752261 |
| | CPC 5370 | *Spinacia* sp. | *Chenopodiaceae* | Botswana: Gaborone | L. Lebogang | DQ233328 | DQ233354 | DQ233380 | DQ233406 | DQ233432 |
| | MUCC 568; MUCNS 320; MAFF 238206 | *Beta vulgaris* | *Chenopodiaceae* | Japan: Chiba | S. Uematsu | JX143557 | JX143311 | JX143065 | JX142819 | JX142573 |
| | MUCC 569; MAFF 305036 | *Beta vulgaris* | *Chenopodiaceae* | Japan: Hokkaido | K. Goto | JX143558 | JX143312 | JX143066 | JX142820 | JX142574 |
| *Cercospora* cf. *brunkii* | CBS 132657; CPC 11598 | *Geranium thunbergii* (≡ *G. nepalense* var. *thunbergii*) | *Geraniaceae* | South Korea: Namyangju | H.D. Shin | JX143559 | JX143313 | JX143067 | JX142821 | JX142575 |
| | MUCC 732 | *Datura stramonium* | *Solanaceae* | Japan: Wakayama | C. Nakashima & I. Araki | JX143560 | JX143314 | JX143068 | JX142822 | JX142576 |
| *Cercospora campi-silii* | CBS 132625; CPC 14585 | *Impatiens noli-tangere* | *Balsaminaceae* | South Korea: Inje | H.D. Shin | JX143561 | JX143315 | JX143069 | JX142823 | JX142577 |
| *Cercospora canescens* complex | CBS 111133; CPC 1137 | *Vigna* sp. | *Fabaceae* | South Africa: Potchefstroom | S. van Wyk | AY260065 | DQ835084 | DQ835103 | DQ835130 | DQ835157 |
| | CBS 111134; CPC 1138 | *Vigna* sp. | *Fabaceae* | South Africa: Potchefstroom | S. van Wyk | AY260066 | DQ835085 | DQ835104 | DQ835131 | DQ835158 |
| | CBS 132658; CPC 11626; GHA-1-0 | *Dioscorea rotundata* | *Dioscoreaceae* | Ghana | S. Nyako & A.O. Danquah | JX143562 | JX143316 | JX143070 | JX142824 | JX142578 |
| | CBS 132659; CPC 11627; GHA-1-1 | *Dioscorea alata* | *Dioscoreaceae* | Ghana | S. Nyako & A.O. Danquah | JX143563 | JX143317 | JX143071 | JX142825 | JX142579 |
| | CBS 153.55; CPC 5059 | *Phaseolus lunatus* (= *Ph. limensis*) | *Fabaceae* | USA: Georgia | E.S. Luttrell | JX143564 | JX143318 | JX143072 | JX142826 | JX142580 |
| | CPC 11628; GHA-2-1 | *Dioscorea rotundata* | *Dioscoreaceae* | Ghana | S. Nyako & A.O. Danquah | JX143565 | JX143319 | JX143073 | JX142827 | JX142581 |
| | CPC 11640; IMI 186563 | *Apium* sp. | *Apiaceae* | USA | — | JX143566 | JX143320 | JX143074 | JX142828 | JX142582 |
| | CPC 15871 | — | *Malvaceae* | Mexico: Tamaulipas | Ma. de Jesús Yáñez-Morales | JX143567 | JX143321 | JX143075 | JX142829 | JX142583 |
| | CPC 4408; Q 160 IS2 | *Citrus maxima* | *Rutaceae* | South Africa: Tsipise | K. Serfontein | AY260067 | DQ835086 | DQ835105 | DQ835132 | DQ835159 |
| | CPC 4409 | *Citrus maxima* | *Rutaceae* | South Africa: Tsipise | K. Serfontein | AY260068 | DQ835087 | DQ835106 | DQ835133 | DQ835160 |
| *Cercospora capsici* | CBS 118712 | Lesions on calyx attached to fruit | — | Fiji | P. Tyler | GU214653 | JX143322 | JX143076 | JX142830 | JX142584 |

**Table 1.** (Continued).

| Species | Culture accession number(s)[1] | Host name or isolation source | Host Family | Country | Collector | GenBank accession numbers[2] | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | | | | | | ITS | TEF | ACT | CAL | HIS |
| | CBS 132622; CPC 14520 | *Capsicum annuum* | *Solanaceae* | South Korea: Yanggu | H.D. Shin | JX143568 | JX143323 | JX143077 | JX142831 | JX142585 |
| | CPC 12307 | *Capsicum annuum* | *Solanaceae* | South Korea: Hongcheon | H.D. Shin | GU214654 | JX143324 | JX143078 | JX142832 | JX142586 |
| | MUCC 574; MUCNS 810; MAFF 238227 | *Capsicum annuum* | *Solanaceae* | Japan: Chiba | S. Uematsu | JX143569 | JX143325 | JX143079 | JX142833 | JX142587 |
| *Cercospora celosiae* | CBS 132600; CPC 10660 | *Celosia argentea* var. *cristata* (≡ *C. cristata*) | *Amaranthaceae* | South Korea: Chuncheon | H.D. Shin | JX143570 | JX143326 | JX143080 | JX142834 | JX142588 |
| *Cercospora chenopodii* | CBS 132620; CPC 14237 | *Chenopodium* cf. *album* | *Chenopodiaceae* | France: Ardeche | P.W. Crous | JX143571 | JX143327 | JX143081 | JX142835 | JX142589 |
| *Cercospora* cf. *chenopodii* | CBS 132594; CPC 10304 (TYPE) | *Chenopodium ficifolium* | *Chenopodiaceae* | South Korea: Hongcheon | H.D. Shin | JX143572 | JX143328 | JX143082 | JX142836 | JX142590 |
| | CBS 132677; CPC 15599 | *Chenopodium* sp. | *Chenopodiaceae* | Mexico: Montecillo | Ma. de Jesús Yáñez-Morales | JX143573 | JX143329 | JX143083 | JX142837 | JX142591 |
| | CPC 12450 | *Chenopodium ficifolium* | *Chenopodiaceae* | South Korea: Hongcheon | H.D. Shin | JX143574 | JX143330 | JX143084 | JX142838 | JX142592 |
| | CPC 15763 | *Chenopodium* sp. | *Chenopodiaceae* | Mexico: Montecillo | Ma. de Jesús Yáñez-Morales | JX143575 | JX143331 | JX143085 | JX142839 | JX142593 |
| | CPC 15859 | *Chenopodium* sp. | *Chenopodiaceae* | Mexico: Purificacion | Ma. de Jesús Yáñez-Morales | JX143576 | JX143332 | JX143086 | JX142840 | JX142594 |
| | CPC 15862 | *Chenopodium* sp. | *Chenopodiaceae* | Mexico: Purificacion | Ma. de Jesús Yáñez-Morales | JX143577 | JX143333 | JX143087 | JX142841 | JX142595 |
| *Cercospora chinensis* | CBS 132612; CPC 10831 | *Polygonatum humile* | *Convallariaceae* | South Korea: Pyeongchang | H.D. Shin | JX143578 | JX143334 | JX143088 | JX142842 | JX142596 |
| *Cercospora* cf. *citrulina* | CBS 119395; CPC 12682 | *Musa* sp. | *Musaceae* | Bangladesh: Western | I. Buddenhagen | EU514222 | JX143335 | JX143089 | JX142843 | JX142597 |
| | CBS 132669; CPC 12683 | *Musa* sp. | *Musaceae* | Bangladesh: Western | I. Buddenhagen | EU514223 | JX143336 | JX143090 | JX142844 | JX142598 |
| | MUCC 576; MUCNS 300; MAFF 237913 | *Citrullus lanatus* | *Cucurbitaceae* | Japan: Okinawa | T. Kobayashion *et al.* | JX143579 | JX143337 | JX143091 | JX142845 | JX142599 |
| | MUCC 577; MUCNS 254; MAFF 238205 | *Momordica charanthia* | *Cucurbitaceae* | Japan: Kagoshima | E. Imaizumi & C. Nomi | JX143580 | JX143338 | JX143092 | JX142846 | JX142600 |
| | MUCC 584; MAFF 305757 | *Psophocarpus tetragonolobus* | *Fabaceae* | Japan: Okinawa | — | JX143581 | JX143339 | JX143093 | JX142847 | JX142601 |
| | MUCC 588; MAFF 239409 | *Ipomoea pes-caprae* | *Convolvulaceae* | Japan: Okinawa | — | JX143582 | JX143340 | JX143094 | JX142848 | JX142602 |
| *Cercospora coniogrammes* | CBS 132634; CPC 17017 (TYPE) | *Coniogramme japonica* var. *gracilis* (≡ *C. gracilis*) | *Adiantaceae* | Australia: Queensland | P.W. Crous | JX143583 | JX143341 | JX143095 | JX142849 | JX142603 |
| *Cercospora corchori* | MUCC 585; MUCNS 72; MAFF 238191 (TYPE) | *Corchorus olitorius* | *Tiliaceae* | Japan: Shimane | T. Mikami | JX143584 | JX143342 | JX143096 | JX142850 | JX142604 |
| *Cercospora* cf. *coreopsidis* | CBS 132598; CPC 10648 | *Coreopsis lanceolata* | *Asteraceae* | South Korea: Seoul | H.D. Shin | JX143585 | JX143343 | JX143097 | JX142851 | JX142605 |
| | CPC 10122 | *Coreopsis lanceolata* | *Asteraceae* | South Korea: Wonju | H.D. Shin | JX143586 | JX143344 | JX143098 | JX142852 | JX142606 |
| *Cercospora delaireae* | CBS 132595; CPC 10455; GV2 PPRI number: C558 (TYPE) | *Delairea odorata* (= *Senecio mikanioides*) | *Asteraceae* | South Africa: Long Tom Pass | S. Neser | JX143587 | JX143345 | JX143099 | JX142853 | JX142607 |
| | CPC 10627 | *Delairea odorata* (= *Senecio mikanioides*) | *Asteraceae* | South Africa: Plettenberg Bay | C.L. Lennox | JX143588 | JX143346 | JX143100 | JX142854 | JX142608 |
| | CPC 10628 | *Delairea odorata* (= *Senecio mikanioides*) | *Asteraceae* | South Africa: Plettenberg Bay | C.L. Lennox | JX143589 | JX143347 | JX143101 | JX142855 | JX142609 |

**Table 1.** (Continued).

| Species | Culture accession number(s)[1] | Host name or isolation source | Host Family | Country | Collector | GenBank accession numbers[2] | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | | | | | | ITS | TEF | ACT | CAL | HIS |
| | CPC 10629 | *Delairea odorata* (= *Senecio mikanioides*) | *Asteraceae* | South Africa: Plettenberg Bay | C.L. Lennox | JX143590 | JX143348 | JX143102 | JX142856 | JX142610 |
| *Cercospora dispori* | CBS 132608; CPC 10773 | *Disporum viridescens* | *Convallariaceae* | South Korea: Pyeongchang | H.D. Shin | JX143591 | JX143349 | JX143103 | JX142857 | JX142611 |
| *Cercospora* cf. *erysimi* | CBS 115059; CPC 5361 | *Erysimum mutabile* | *Brassicaceae* | New Zealand: Manurewa | C.F. Hill | JX143592 | JX143350 | JX143104 | JX142858 | JX142612 |
| *Cercospora euphorbiae-sieboldianae* | CBS 113306 (TYPE) | *Euphorbia sieboldiana* | *Euphorbiaceae* | South Korea: Samcheok | H.D. Shin | JX143593 | JX143351 | JX143105 | JX142859 | JX142613 |
| *Cercospora fagopyri* | CBS 132623; CPC 14541 (TYPE) | *Fagopyrum esculentum* | *Polygonaceae* | South Korea: Yangpyeong | H.D. Shin | JX143594 | JX143352 | JX143106 | JX142860 | JX142614 |
| | CBS 132640; CPC 10109 | *Fallopia dumentorum* | *Polygonaceae* | South Korea: Yangpyeong | H.D. Shin | JX143595 | JX143353 | JX143107 | JX142861 | JX142615 |
| | CBS 132649; CPC 10725 | *Viola mandschurica* | *Violaceae* | South Korea: Suwon | H.D. Shin | JX143596 | JX143354 | JX143108 | JX142862 | JX142616 |
| | CBS 132671; CPC 14546 | *Cercis chinensis* | *Fabaceae* | South Korea: Yangpyeong | H.D. Shin | JX143597 | JX143355 | JX143109 | JX142863 | JX142617 |
| | MUCC 130 | *Cosmos bipinnata* | *Asteraceae* | Japan: Ehime | J. Nishikawa | JX143598 | JX143356 | JX143110 | JX142864 | JX142618 |
| | MUCC 866 | *Hibiscus syriacus* | *Malvaceae* | Japan: Ehime | J. Nishikawa | JX143599 | JX143357 | JX143111 | JX142865 | JX142619 |
| *Cercospora* cf. *flagellaris* | CBS 113127; RC3766; TX-18 | *Eichhornia crassipes* | *Pontederiaceae* | USA: Texas | D. Tessmann & R. Charudattan | DQ835075 | AF146147 | DQ835121 | DQ835148 | DQ835175 |
| | CBS 115482; A207 Bs+; CPC 4410 | *Citrus* sp. | *Rutaceae* | South Africa: Messina | M.C. Pretorius | AY260070 | DQ835095 | DQ835114 | DQ835141 | DQ835168 |
| | CBS 132637; CPC 10079 | *Trachelium* sp. | *Campanulaceae* | Israel | E. Tzul-Abad | JX143600 | JX143358 | JX143112 | JX142866 | JX142620 |
| | CBS 132646; CPC 10681 | *Cichorium intybus* | *Asteraceae* | South Korea: Suwon | H.D. Shin | JX143601 | JX143359 | JX143113 | JX142867 | JX142621 |
| | CBS 132648; CPC 10722 | *Amaranthus patulus* | *Amaranthaceae* | South Korea: Namyangju | H.D. Shin | JX143602 | JX143360 | JX143114 | JX142868 | JX142622 |
| | CBS 132653; CPC 10884 | *Dysphania ambrosioides* (≡ *Chenopodium ambrosioides*) | *Chenopodiaceae* | South Korea: Jeju | H.D. Shin | JX143603 | JX143361 | JX143115 | JX142869 | JX142623 |
| | CBS 132667; CPC 11643 | *Celosia argentea* var. *cristata* (≡ *C. cristata*) | *Amaranthaceae* | South Korea: Hoengseong | H.D. Shin | JX143604 | JX143362 | JX143116 | JX142870 | JX142624 |
| | CBS 132670; CPC 14487 | *Sigesbeckia pubescens* | *Asteraceae* | South Korea: Yanggu | H.D. Shin | JX143605 | JX143363 | JX143117 | JX142871 | JX142625 |
| | CBS 132674; CPC 14723 | *Phytolacca americana* | *Phytolaccaceae* | South Korea: Jeju | H.D. Shin | JX143606 | JX143364 | JX143118 | JX142872 | JX142626 |
| | CBS 143.51; CPC 5055 | *Bromus* sp. | *Poaceae* | — | M.D. Whitehead | JX143607 | JX143365 | JX143119 | JX142873 | JX142627 |
| | CPC 10124 | *Phytolacca americana* | *Phytolaccaceae* | South Korea: Pocheon | H.D. Shin | JX143608 | JX143366 | JX143120 | JX142874 | JX142628 |
| | CPC 1051 | *Populus deltoides* | *Salicaceae* | South Africa | P.W. Crous | AY260069 | JX143367 | JX143121 | JX142875 | JX142629 |
| | CPC 1052 | *Populus deltoides* | *Salicaceae* | South Africa | P.W. Crous | JX143609 | JX143368 | JX143122 | JX142876 | JX142630 |
| | CPC 10684 | *Phytolacca americana* | *Phytolaccaceae* | South Korea: Jinju | H.D. Shin | JX143610 | JX143369 | JX143123 | JX142877 | JX142631 |
| | CPC 4411; Q207 F5 | *Citrus* sp. | *Rutaceae* | South Africa: Messina | M.C. Pretorius | AY260071 | DQ835098 | DQ835118 | DQ835145 | DQ835172 |
| | CPC 5441 | *Amaranthus* sp. | *Amaranthaceae* | Fiji | C.F. Hill | JX143611 | JX143370 | JX143124 | JX142878 | JX142632 |
| | MUCC 127 | *Cosmos sulphureus* | *Asteraceae* | Japan: Ehime | J. Nishikawa | JX143612 | JX143371 | JX143125 | JX142879 | JX142633 |
| | MUCC 735 | *Hydrangea serrata* | *Hydrangeaceae* | Japan: Wakayama | C. Nakashima & I. Araki | JX143613 | JX143372 | JX143126 | JX142880 | JX142634 |
| | MUCC 831 | *Hydrangea serrata* | *Hydrangeaceae* | Japan: Tokyo | I. Araki & M. Harada | JX143614 | JX143373 | JX143127 | JX142881 | JX142635 |

**Table 1.** (Continued).

| Species | Culture accession number(s)[1] | Host name or isolation source | Host Family | Country | Collector | GenBank accession numbers[2] | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | | | | | | ITS | TEF | ACT | CAL | HIS |
| *Cercospora* cf. *helianthicola* | MUCC 716 | *Helianthus tuberosus* | *Asteraceae* | Japan: Wakayama | C. Nakashima & I. Araki | JX143615 | JX143374 | JX143128 | JX142882 | JX142636 |
| *Cercospora* cf. *ipomoeae* | CBS 132639; CPC 10102 | *Persicaria thunbergii* | *Polygonaceae* | South Korea: Pocheon | H.D. Shin | JX143616 | JX143375 | JX143129 | JX142883 | JX142637 |
| | CBS 132652; CPC 10833 | *Ipomoea nil* (= *I. hederacea*) | *Convolvulaceae* | South Korea: Chuncheon | H.D. Shin | JX143617 | JX143376 | JX143130 | JX142884 | JX142638 |
| | MUCC 442 | *Ipomoea aquatica* | *Convolvulaceae* | Japan: Kagawa | G. Kizaki | JX143618 | JX143377 | JX143131 | JX142885 | JX142639 |
| *Cercospora kikuchii* | CBS 128.27; CPC 5068 (TYPE) | *Glycine soja* | *Fabaceae* | Japan | T. Matsumoto | DQ835070 | DQ835088 | DQ835107 | DQ835134 | DQ835161 |
| | CBS 132633; CPC 16578 | *Glycine max* | *Fabaceae* | Argentina | — | JX143619 | JX143378 | JX143132 | JX142886 | JX142640 |
| | CBS 135.28; CPC 5067 | *Glycine soja* | *Fabaceae* | Japan | H.W. Wollenweber | DQ835071 | DQ835089 | DQ835108 | DQ835135 | DQ835162 |
| | MUCC 590; MAFF 305040 | *Glycine soja* | *Fabaceae* | Japan: Kagoshima | H. Kurata | JX143620 | JX143379 | JX143133 | JX142887 | JX142641 |
| *Cercospora lactucae-sativae* | CBS 132604; CPC 10728 | *Ixeris chinensis* subsp. *strigosa* (≡ *Ixeris strigosa*) | *Asteraceae* | South Korea: Chuncheon | H.D. Shin | JX143621 | JX143380 | JX143134 | JX142888 | JX142642 |
| | CPC 10082 | *Ixeris chinensis* subsp. *strigosa* (≡ *Ixeris strigosa*) | *Asteraceae* | South Korea: Chuncheon | H.D. Shin | JX143622 | JX143381 | JX143135 | JX142889 | JX142643 |
| | MUCC 570; MUCN S463; MAFF 238209 | *Lactuca sativa* | *Asteraceae* | Japan: Chiba | C. Nakashima | JX143623 | JX143382 | JX143136 | JX142890 | JX142644 |
| | MUCC 571; MUCNS 214; MAFF 237719 | *Lactuca sativa* | *Asteraceae* | Japan: Chiba | S. Uematsu | JX143624 | JX143383 | JX143137 | JX142891 | JX142645 |
| *Cercospora* cf. *malloti* | MUCC 575; MUCNS 582; MAFF 237872 | *Cucumis melo* | *Cucurbitaceae* | Japan: Okinawa | K. Uehara | JX143625 | JX143384 | JX143138 | JX142892 | JX142646 |
| | MUCC 787 | *Mallotus japonicus* | *Euphorbiaceae* | Japan: Okinawa | C. Nakashima & T. Akashi | JX143626 | JX143385 | JX143139 | JX142893 | JX142647 |
| *Cercospora mercurialis* | CBS 549.71 | *Mercurialis annua* | *Euphorbiaceae* | Romania: Cheia | O. Constantinescu | JX143627 | JX143386 | JX143140 | JX142894 | JX142648 |
| | CBS 550.71 (TYPE) | *Mercurialis perennis* | *Euphorbiaceae* | Romania: Cheia | O. Constantinescu | JX143628 | JX143387 | JX143141 | JX142895 | JX142649 |
| | CBS 551.71 | *Mercurialis ovata* | *Euphorbiaceae* | Romania: Hagieni | O. Constantinescu & G. Negrean | JX143629 | JX143388 | JX143142 | JX142896 | JX142650 |
| *Cercospora* cf. *modiolae* | CPC 5115 | *Modiola caroliniana* | *Malvaceae* | New Zealand | C.F. Hill | JX143630 | JX143389 | JX143143 | JX142897 | JX142651 |
| *Cercospora* cf. *nicotianae* | CBS 131.32; CPC 5076 | *Nicotiana tabacum* | *Solanaceae* | Indonesia: Medan | H. Diddens & A. Jaarsveld | DQ835073 | DQ835099 | DQ835119 | DQ835146 | DQ835173 |
| | CBS 132632; CPC 15918 | *Glycine max* | *Fabaceae* | Mexico: Tamaulipas | Ma. de Jesús Yáñez-Morales | JX143631 | JX143390 | JX143144 | JX142898 | JX142652 |
| | CBS 570.69; CPC 5075 | *Nicotiana tabacum* | *Solanaceae* | Nigeria | S.O. Alasoadura | DQ835074 | DQ835100 | DQ835120 | DQ835147 | DQ835174 |
| *Cercospora olivascens* | CBS 253.67; IMI 124975; CPC 5085 (TYPE) | *Aristolochia clematidis* | *Aristolochiaceae* | Romania: Cazanele Dunarii | O. Constantinescu | JX143632 | JX143391 | JX143145 | JX142899 | JX142653 |
| *Cercospora* cf. *physalidis* | CBS 765.79 | *Solanum tuberosum* | *Solanaceae* | Peru | L.J. Turkensteen | JX143633 | JX143392 | JX143146 | JX142900 | JX142654 |
| *Cercospora pileicola* | CBS 132607; CPC 10749 (TYPE) | *Pilea pumila* (= *P. mongolica*) | *Urticaceae* | South Korea: Dongducheon | H.D. Shin | JX143634 | JX143393 | JX143147 | JX142901 | JX142655 |
| | CBS 132647; CPC 10693 | *Pilea hamaoi* (≡ *P. pumila* var. *hamaoi*) | *Urticaceae* | South Korea: Hoengseong | H.D. Shin | JX143635 | JX143394 | JX143148 | JX142902 | JX142656 |
| | CPC 11369 | *Pilea pumila* (= *P. mongolica*) | *Urticaceae* | South Korea: Hongcheon | H.D. Shin | JX143636 | JX143395 | JX143149 | JX142903 | JX142657 |
| *Cercospora polygonacea* | CBS 132614; CPC 11318 | *Persicaria longiseta* (≡ *P. blumei*) | *Polygonaceae* | South Korea: Cheongju | H.D. Shin | JX143637 | JX143396 | JX143150 | JX142904 | JX142658 |

**Table 1.** (Continued).

| Species | Culture accession number(s)[1] | Host name or isolation source | Host Family | Country | Collector | GenBank accession numbers[2] | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | | | | | | ITS | TEF | ACT | CAL | HIS |
| *Cercospora punctiformis* | CBS 132626; CPC 14606 | *Cynanachum wilfordii* | *Asclepiadaceae* | South Korea: Bonghwa | H.D. Shin | JX143638 | JX143397 | JX143151 | JX142905 | JX142659 |
| *Cercospora* cf. *resedae* | CBS 118793 | *Reseda odorata* | *Resedaceae* | New Zealand: Auckland | C.F. Hill | JX143639 | JX143398 | JX143152 | JX142906 | JX142660 |
| | CBS 257.67; CPC 5057 | *Helianthemum* sp. | *Cistaceae* | Romania: Bucuresti | O. Constantinescu | DQ233319 | DQ233343 | DQ233369 | DQ233395 | DQ233421 |
| *Cercospora* cf. *richardiicola* | CBS 132627; CPC 14680 | *Ajuga multiflora* | *Lamiaceae* | South Korea: Incheon | H.D. Shin | JX143640 | JX143399 | JX143153 | JX142907 | JX142661 |
| | MUCC 128 | *Tagetes erecta* | *Asteraceae* | Japan: Ehime | J. Nishikawa | JX143641 | JX143400 | JX143154 | JX142908 | JX142662 |
| | MUCC 132 | *Osteospermum* sp. | *Asteraceae* | Japan: Shizuoka | J. Nishikawa | JX143642 | JX143401 | JX143155 | JX142909 | JX142663 |
| | MUCC 138 | *Fuchsia ×hybrida* | *Onagraceae* | Japan: Shizuoka | J. Nishikawa | JX143643 | JX143402 | JX143156 | JX142910 | JX142664 |
| | MUCC 578; MAFF 238210 | *Zantedeschia* sp. | *Araceae* | Japan: Ehime | J. Nishikawa | JX143644 | JX143403 | JX143157 | JX142911 | JX142665 |
| | MUCC 582; MAFF 238880 | *Gerbera hybrida* | *Asteraceae* | Japan: Shizuoka | J. Takeuchi | JX143645 | JX143404 | JX143158 | JX142912 | JX142666 |
| *Cercospora ricinella* | CBS 132605; CPC 10734 | *Ricinus communis* | *Euphorbiaceae* | South Korea: Chuncheon | H.D. Shin | JX143646 | JX143405 | JX143159 | JX142913 | JX142667 |
| | CPC 10104 | *Ricinus communis* | *Euphorbiaceae* | South Korea: Chuncheon | H.D. Shin | JX143647 | JX143406 | JX143160 | JX142914 | JX142668 |
| *Cercospora rodmanii* | CBS 113123; RC3660; 28-1 | *Eichhornia crassipes* | *Pontederiaceae* | Brazil: Rio Verde | R. Charudattan | DQ835076 | AF146136 | DQ835122 | DQ835149 | DQ835176 |
| | CBS 113124; RC2867 | *Eichhornia crassipes* | *Pontederiaceae* | Mexico: Carretero | R. Charudattan | DQ835077 | AF146137 | DQ835123 | DQ835150 | DQ835177 |
| | CBS 113125; RC4101; 400 | *Eichhornia crassipes* | *Pontederiaceae* | Zambia | M. Morris | DQ835078 | AF146146 | DQ835124 | DQ835151 | DQ835178 |
| | CBS 113126; RC3409; 62-2 | *Eichhornia crassipes* | *Pontederiaceae* | Brazil: Oroco | R. Charudattan | DQ835079 | AF146138 | DQ835125 | DQ835152 | DQ835179 |
| | CBS 113128; RC394; WH83 | *Eichhornia crassipes* | *Pontederiaceae* | USA: Florida | R. Charudattan | DQ835080 | AF146142 | DQ835126 | DQ835153 | DQ835180 |
| | CBS 113129; RC397; WH9-BR | *Eichhornia crassipes* | *Pontederiaceae* | USA: Florida | K. Conway | DQ835081 | AF146143 | DQ835127 | DQ835154 | DQ835181 |
| | CBS 113130; RC393; WHK | *Eichhornia crassipes* | *Pontederiaceae* | USA: Florida | R. Charudattan | DQ835082 | AF146144 | DQ835128 | DQ835155 | DQ835182 |
| | CBS 113131; RC395; WHV | *Eichhornia crassipes* | *Pontederiaceae* | Venezuela: Maracay | R. Charudattan | DQ835083 | AF146148 | DQ835129 | DQ835156 | DQ835183 |
| *Cercospora rumicis* | CPC 5439 | *Rumex sanguineus* | *Polygonaceae* | New Zealand: Manurewa | C.F. Hill | JX143648 | JX143407 | JX143161 | JX142915 | JX142669 |
| *Cercospora senecionis-walkeri* | CBS 132636; CPC 19196 | *Senecio walkeri* | *Asteraceae* | Laos | P. Phengsintham | JX143649 | JX143408 | JX143162 | JX142916 | JX142670 |
| *Cercospora* cf. *sigesbeckiae* | CBS 132601; CPC 10664 | *Sigesbeckia glabrescens* | *Asteraceae* | South Korea: Chuncheon | H.D. Shin | JX143650 | JX143409 | JX143163 | JX142917 | JX142671 |
| | CBS 132606; CPC 10740 | *Paulownia coreana* | *Scrophulariaceae* | South Korea: Namyangju | H.D. Shin | JX143651 | JX143410 | JX143164 | JX142918 | JX142672 |
| | CBS 132621; CPC 14489 | *Sigesbeckia pubescens* | *Asteraceae* | South Korea: Yanggu | H.D. Shin | JX143652 | JX143411 | JX143165 | JX142919 | JX142673 |
| | CBS 132641; CPC 10117 | *Persicaria orientalis* (= *P. cochinchinensis*) | *Polygonaceae* | South Korea: Chuncheon | H.D. Shin | JX143653 | JX143412 | JX143166 | JX142920 | JX142674 |
| | CBS 132642; CPC 10128 | *Pilea pumila* (= *P. mongolica*) | *Urticaceae* | South Korea: Hongcheon | H.D. Shin | JX143654 | JX143413 | JX143167 | JX142921 | JX142675 |
| | CBS 132675; CPC 14726 | *Malva verticillata* | *Malvaceae* | South Korea: Yanggu | H.D. Shin | JX143655 | JX143414 | JX143168 | JX142922 | JX142676 |
| | MUCC 587; MUCNS 197; MAFF 237690 | *Begonia* sp. | *Begoniaceae* | Japan: Chiba | S. Uematsu | JX143656 | JX143415 | JX143169 | JX142923 | JX142677 |
| | MUCC 589; MAFF 305039 | *Glycine max* | *Fabaceae* | Japan: Saitama | H. Kurata | JX143657 | JX143416 | JX143170 | JX142924 | JX142678 |
| | MUCC 849 | *Dioscorea tokoro* | *Dioscoreaceae* | Japan: Tokyo | I. Araki | JX143658 | JX143417 | JX143171 | JX142925 | JX142679 |
| *Cercospora sojina* | CBS 132018; CPC 12322 | *Glycine soja* | *Fabaceae* | South Korea: Hoengseong | H.D. Shin | GU214655 | JX143418 | JX143172 | JX142926 | JX142680 |

**Table 1.** (Continued).

| Species | Culture accession number(s)[1] | Host name or isolation source | Host Family | Country | Collector | GenBank accession numbers[2] | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | | | | | | ITS | TEF | ACT | CAL | HIS |
| | CBS 132615; CPC 11353 (TYPE) | *Glycine soja* | *Fabaceae* | South Korea: Hongcheon | H.D. Shin | JX143659 | JX143419 | JX143173 | JX142927 | JX142681 |
| | CBS 132684; CPC 17971; CCC 173-09, 09-495 | *Glycine max* | *Fabaceae* | Argentina | F. Scandiani | JX143660 | JX143420 | JX143174 | JX142928 | JX142682 |
| | CPC 11420 | *Glycine soja* | *Fabaceae* | South Korea: Hongcheon | H.D. Shin | JX143661 | JX143421 | JX143175 | JX142929 | JX142683 |
| | CPC 17964; CCC 155-09, 09-285-5 | *Glycine max* | *Fabaceae* | Argentina | F. Scandiani | JX143662 | JX143422 | JX143176 | JX142930 | JX142684 |
| | CPC 17965; CCC 156-09, 09-285-4 | *Glycine max* | *Fabaceae* | Argentina | F. Scandiani | JX143663 | JX143423 | JX143177 | JX142931 | JX142685 |
| | CPC 17966; CCC 157-09, 09-285-3 | *Glycine max* | *Fabaceae* | Argentina | F. Scandiani | JX143664 | JX143424 | JX143178 | JX142932 | JX142686 |
| | CPC 17967; CCC 158-09, 09-285-1 | *Glycine max* | *Fabaceae* | Argentina | F. Scandiani | JX143665 | JX143425 | JX143179 | JX142933 | JX142687 |
| | CPC 17968; CCC 159-09, 09-285-7 | *Glycine max* | *Fabaceae* | Argentina | F. Scandiani | JX143666 | JX143426 | JX143180 | JX142934 | JX142688 |
| | CPC 17969; CCC 167-09, 09-881 | *Glycine max* | *Fabaceae* | Argentina | N. Formento | JX143667 | JX143427 | JX143181 | JX142935 | JX142689 |
| | CPC 17970; CCC 172-09, 09-320 | *Glycine max* | *Fabaceae* | Argentina | F. Scandiani | JX143668 | JX143428 | JX143182 | JX142936 | JX142690 |
| | CPC 17972; CCC 174-09, | *Glycine max* | *Fabaceae* | Argentina | S. Piubello | JX143669 | JX143429 | JX143183 | JX142937 | JX142691 |
| | CPC 17973; CCC 176-09, 09-882 | *Glycine max* | *Fabaceae* | Argentina | N. Formento | JX143670 | JX143430 | JX143184 | JX142938 | JX142692 |
| | CPC 17974; CCC 177-09, 09-2488-1 | *Glycine max* | *Fabaceae* | Argentina | F. Scandiani | JX143671 | JX143431 | JX143185 | JX142939 | JX142693 |
| | CPC 17975; CCC 178-09, 09-1438-2 | *Glycine max* | *Fabaceae* | Argentina | F. Scandiani | JX143672 | JX143432 | JX143186 | JX142940 | JX142694 |
| | CPC 17976; CCC 179-09, 09-2591 | *Glycine max* | *Fabaceae* | Argentina | F. Scandiani | JX143673 | JX143433 | JX143187 | JX142941 | JX142695 |
| | CPC 17977; CCC 180-09, 09-2520 | *Glycine max* | *Fabaceae* | Argentina | F. Scandiani | JX143674 | JX143434 | JX143188 | JX142942 | JX142696 |
| *Cercospora* sp. A | CBS 132631; CPC 15872 | *Chenopodium* sp. | *Chenopodiaceae* | Mexico | Ma. de Jesús Yáñez-Morales | JX143675 | JX143435 | JX143189 | JX142943 | JX142697 |
| *Cercospora* sp. B | CBS 132602; CPC 10687 | *Ipomoea purpurea* | *Convolvulaceae* | South Korea: Kangnung | H.D. Shin | JX143676 | JX143436 | JX143190 | JX142944 | JX142698 |
| *Cercospora* sp. C | CBS 132629; CPC 15841 | — | *Compositae* | Mexico: Montecillo | Ma. de Jesús Yáñez-Morales | JX143677 | JX143437 | JX143191 | JX142945 | JX142699 |
| *Cercospora* sp. D | CBS 132630; CPC 15856 | — | — | Mexico | Ma. de Jesús Yáñez-Morales | JX143678 | JX143438 | JX143192 | JX142946 | JX142700 |
| *Cercospora* sp. E | CBS 132628; CPC 15632 | Unidentified wild plant | — | Mexico: Montecillo | Ma. de Jesús Yáñez-Morales | JX143679 | JX143439 | JX143193 | JX142947 | JX142701 |
| | CPC 15801 | Unidentified wild plant | — | Mexico: Montecillo | Ma. de Jesús Yáñez-Morales | JX143680 | JX143440 | JX143194 | JX142948 | JX142702 |
| *Cercospora* sp. F | CBS 132618; CPC 12062 | *Zea mays* | *Poaceae* | South Africa | P. Caldwell | DQ185071 | DQ185083 | DQ185095 | DQ185107 | DQ185119 |
| *Cercospora* sp. G | CBS 115518; CPC 5360 | *Bidens frondosa* | *Asteraceae* | New Zealand: Kopuku | C.F. Hill | JX143681 | JX143441 | JX143195 | JX142949 | JX142703 |
| | CPC 5438 | *Salvia viscosa* | *Lamiaceae* | New Zealand: Manurewa | C.F. Hill | JX143682 | JX143442 | JX143196 | JX142950 | JX142704 |
| *Cercospora* sp. H | CBS 115205; CPC 5116 | *Dichondra repens* | *Convolvulaceae* | New Zealand | C.F. Hill | JX143683 | JX143443 | JX143197 | JX142951 | JX142705 |
| | CPC 11620 | *Chamelaucium uncinatum* | *Myrtaceae* | Argentina | S. Wolcan | JX143684 | JX143444 | JX143198 | JX142952 | JX142706 |
| *Cercospora* sp. I | CBS 114815; CPC 5364 | *Deutzia purpurascens* | *Hydrangeaceae* | New Zealand: Manurewa | C.F. Hill | JX143685 | JX143445 | JX143199 | JX142953 | JX142707 |
| | CBS 114816; CPC 5363 | *Deutzia* ×*rosea* (= *D. gracilis* × *purpurascens*) | *Hydrangeaceae* | New Zealand: Manurewa | C.F. Hill | JX143686 | JX143446 | JX143200 | JX142954 | JX142708 |
| | CBS 114817; CPC 5365 | *Fuchsia procumbens* | *Onagraceae* | New Zealand: Manurewa | C.F. Hill | JX143687 | JX143447 | JX143201 | JX142955 | JX142709 |
| | CBS 114818; CPC 5362 | *Deutzia crenata* | *Hydrangeaceae* | New Zealand: Manurewa | C.F. Hill | JX143688 | JX143448 | JX143202 | JX142956 | JX142710 |

**Table 1.** (Continued).

| Species | Culture accession number(s)[1] | Host name or isolation source | Host Family | Country | Collector | GenBank accession numbers[2] | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | | | | | | ITS | TEF | ACT | CAL | HIS |
| | CBS 115117 | *Archontophoenix cunninghamiana* | *Arecaceae (Palmae)* | New Zealand: Whangarei | C.F. Hill | JX143689 | JX143449 | JX143203 | JX142957 | JX142711 |
| | CBS 115121 | *Gunnera tinctoria* | *Gunneraceae* | New Zealand: Mt Albert | C.F. Hill | JX143690 | JX143450 | JX143204 | JX142958 | JX142712 |
| | CBS 132597; CPC 10615 | *Coreopsis verticillata* | *Asteraceae* | New Zealand: Manurewa | C.F. Hill | JX143691 | JX143451 | JX143205 | JX142959 | JX142713 |
| | CBS 132643; CPC 10138 | *Ajuga multiflora* | *Lamiaceae* | South Korea: Suwon | H.D. Shin | JX143692 | JX143452 | JX143206 | JX142960 | JX142714 |
| | CPC 10616 | *Coreopsis verticillata* | *Asteraceae* | New Zealand: Manurewa | C.F. Hill | JX143693 | JX143453 | JX143207 | JX142961 | JX142715 |
| | CPC 5440 | *Nicotiana* sp. | *Solanaceae* | New Zealand: Manurewa | C.F. Hill | JX143694 | JX143454 | JX143208 | JX142962 | JX142716 |
| *Cercospora* sp. J | MUCC 541 | *Antirrhinum majus* | *Plantaginaceae* | Japan: Aichi | M.Matsusaki | JX143695 | JX143455 | JX143209 | JX142963 | JX142717 |
| *Cercospora* sp. K | CBS 132603; CPC 10719 | *Ipomoea coccinea* (≡ *Quamoclit coccinea*) | *Convolvulaceae* | South Korea: Namyangju | H.D. Shin | JX143696 | JX143456 | JX143210 | JX142964 | JX142718 |
| | CPC 10094 | *Ipomoea coccinea* (≡ *Quamoclit coccinea*) | *Convolvulaceae* | South Korea: Namyangju | H.D. Shin | JX143697 | JX143457 | JX143211 | JX142965 | JX142719 |
| | CPC 12391 | *Ipomoea coccinea* (≡ *Quamoclit coccinea*) | *Convolvulaceae* | South Korea: Namyangju | H.D. Shin | JX143698 | JX143458 | JX143212 | JX142966 | JX142720 |
| *Cercospora* sp. L | CBS 115477; CPC 5114 | *Crepis capillaris* | *Asteraceae* | New Zealand | C.F. Hill | JX143699 | JX143459 | JX143213 | JX142967 | JX142721 |
| *Cercospora* sp. M | CBS 132596; CPC 10553 | *Acacia mangium* | *Fabaceae* | Thailand: Sanamchaikhet | K. Pongpanich | JX143700 | AY752175 | AY752203 | AY752234 | AY752265 |
| *Cercospora* sp. N | CBS 132619; CPC 12684 | *Musa* sp. | *Musaceae* | Bangladesh: Western | I. Buddenhagen | EU514224 | JX143460 | JX143214 | JX142968 | JX142722 |
| *Cercospora* sp. O | CBS 132635; CPC 18636 | *Musa* sp. | *Musaceae* | Thailand: Mae Klang Loung | P.W. Crous | JX143701 | JX143461 | JX143215 | JX142969 | JX142723 |
| *Cercospora* sp. P | CBS 112649; CPC 3946 | *Citrus* sp., leaf spot | *Rutaceae* | Swaziland | M.C. Pretorius | AY260072 | DQ835090 | DQ835109 | DQ835136 | DQ835163 |
| | CBS 112722; CPC 3947 | *Citrus* sp., leaf spot | *Rutaceae* | Swaziland | M.C. Pretorius | AY260073 | DQ835091 | DQ835110 | DQ835137 | DQ835164 |
| | CBS 112728; CPC 3949 | *Citrus* × *sinensis* (≡ *C. aurantium* var. *sinensis*) | *Rutaceae* | South Africa: Komatipoort | M.C. Pretorius | AY260076 | DQ835092 | DQ835111 | DQ835138 | DQ835165 |
| | CBS 112730; CPC 3948 | *Citrus* × *sinensis* (≡ *C. aurantium* var. *sinensis*) | *Rutaceae* | South Africa: Komatipoort | M.C. Pretorius | AY260075 | DQ835093 | DQ835112 | DQ835139 | DQ835166 |
| | CBS 112894; CPC 3950 | *Citrus* × *sinensis* (≡ *C. aurantium* var. *sinensis*) | *Rutaceae* | South Africa: Komatipoort | M.C. Pretorius | AY260077 | DQ835094 | DQ835113 | DQ835140 | DQ835167 |
| | CBS 113996; CPC 5326 | *Cajanus cajan* | *Fabaceae* | South Africa: Nelspruit | L. van Jaarsveld | JX143702 | JX143462 | JX143216 | JX142970 | JX142724 |
| | CBS 115413; CPC 5328 | *Cajanus cajan* | *Fabaceae* | South Africa: Nelspruit | L. van Jaarsveld | JX143703 | JX143463 | JX143217 | JX142971 | JX142725 |
| | CBS 115609; CPC 3945 | *Citrus* sp., leaf spot | *Rutaceae* | Swaziland | M.C. Pretorius | AY260074 | DQ835096 | DQ835115 | DQ835142 | DQ835169 |
| | CBS 116365; CPC 10526 (TYPE) | *Acacia mangium* | *Fabaceae* | Thailand | M.J. Wingfield | AY752141 | AY752176 | AY752204 | AY752235 | AY752266 |
| | CBS 132645; CPC 10527 | *Acacia mangium* | *Fabaceae* | Thailand | M.J. Wingfield | AY752142 | AY752177 | AY752205 | AY752236 | AY752267 |
| | CBS 132660; CPC 11629; GHA-4-0 | *Dioscorea rotundata* | *Dioscoreaceae* | Ghana | S. Nyako & A.O. Danquah | JX143704 | JX143464 | JX143218 | JX142972 | JX142726 |
| | CBS 132662; CPC 11635; PNG-009 | *Dioscorea nummularia* | *Dioscoreaceae* | Papua New Guinea | J. Peters & A.N. Jama | JX143705 | JX143465 | JX143219 | JX142973 | JX142727 |
| | CBS 132664; CPC 11637; PNG-022 | *Dioscorea rotundata* | *Dioscoreaceae* | Papua New Guinea | J. Peters & A.N. Jama | JX143706 | JX143466 | JX143220 | JX142974 | JX142728 |
| | CBS 132665; CPC 11638; PNG-023 | *Dioscorea bulbifera* | *Dioscoreaceae* | Papua New Guinea | J. Peters & A.N. Jama | JX143707 | JX143467 | JX143221 | JX142975 | JX142729 |

**Table 1.** (Continued).

| Species | Culture accession number(s)[1] | Host name or isolation source | Host Family | Country | Collector | GenBank accession numbers[2] | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | | | | | | ITS | TEF | ACT | CAL | HIS |
| | CBS 132680; CPC 15827 | *Ricinus communis* | *Euphorbiaceae* | Mexico: Tamaulipas | Ma. de Jesús Yáñez-Morales | JX143708 | JX143468 | JX143222 | JX142976 | JX142730 |
| | CPC 10552 | *Acacia mangium* | *Fabaceae* | Thailand | K. Pongpanich | JX143709 | AY752174 | AY752202 | AY752233 | AY752264 |
| | CPC 11630; GHA-4-3 | *Dioscorea rotundata* | *Dioscoreaceae* | Ghana | S. Nyako & A.O. Danquah | JX143710 | JX143469 | JX143223 | JX142977 | JX142731 |
| | CPC 11631; GHA-5-0 | *Dioscorea rotundata* | *Dioscoreaceae* | Ghana | S. Nyako & A.O. Danquah | JX143711 | JX143470 | JX143224 | JX142978 | JX142732 |
| | CPC 11632; GHA-7-4 | *Dioscorea rotundata* | *Dioscoreaceae* | Ghana | S. Nyako & A.O. Danquah | JX143712 | JX143471 | JX143225 | JX142979 | JX142733 |
| | CPC 11633; GHA-8-4 | *Dioscorea rotundata* | *Dioscoreaceae* | Ghana | S. Nyako & A.O. Danquah | JX143713 | JX143472 | JX143226 | JX142980 | JX142734 |
| | CPC 4001 | *Citrus ×sinensis* (≡ *C. aurantium* var. *sinensis*) | *Rutaceae* | Swaziland | M.C. Pretorius | AY343372 | AY343335 | DQ835116 | DQ835143 | DQ835170 |
| | CPC 4002 | *Citrus ×sinensis* (≡ *C. aurantium* var. *sinensis*) | *Rutaceae* | Swaziland | M.C. Pretorius | DQ835072 | DQ835097 | DQ835117 | DQ835144 | DQ835171 |
| | CPC 5262 | *Hibiscus sabdariffa* | *Malvaceae* | New Zealand: Auckland (imported from Fiji) | C.F. Hill | JX143714 | JX143473 | JX143227 | JX142981 | JX142735 |
| | CPC 5327 | *Cajanus cajan* | *Fabaceae* | South Africa: Nelspruit | L. van Jaarsveld | JX143715 | JX143474 | JX143228 | JX142982 | JX142736 |
| | MUCC 771 | *Coffea arabica* | *Rubiaceae* | Japan: Okinawa | C. Nakashima | JX143716 | JX143475 | JX143229 | JX142983 | JX142737 |
| *Cercospora* sp. Q | CBS 113997; CPC 5325 | *Cajanus cajan* | *Fabaceae* | South Africa: Nelspruit | L. van Jaarsveld | JX143717 | JX143476 | JX143230 | JX142984 | JX142738 |
| | CBS 115410; CPC 5331 | *Cajanus cajan* | *Fabaceae* | South Africa: Nelspruit | L. van Jaarsveld | JX143718 | JX143477 | JX143231 | JX142985 | JX142739 |
| | CBS 115411; CPC 5332 | *Cajanus cajan* | *Fabaceae* | South Africa: Nelspruit | L. van Jaarsveld | JX143719 | JX143478 | JX143232 | JX142986 | JX142740 |
| | CBS 115412; CPC 5333 | *Cajanus cajan* | *Fabaceae* | South Africa: Nelspruit | L. van Jaarsveld | JX143720 | JX143479 | JX143233 | JX142987 | JX142741 |
| | CBS 115536; CPC 5329 | *Cajanus cajan* | *Fabaceae* | South Africa: Nelspruit | L. van Jaarsveld | JX143721 | JX143480 | JX143234 | JX142988 | JX142742 |
| | CBS 115537; CPC 5330 | *Cajanus cajan* | *Fabaceae* | South Africa: Nelspruit | L. van Jaarsveld | JX143722 | JX143481 | JX143235 | JX142989 | JX142743 |
| | CBS 132656; CPC 11536 | *Acacia mangium* | *Fabaceae* | Thailand | K. Pongpanich | JX143723 | JX143482 | JX143236 | JX142990 | JX142744 |
| | CBS 132661; CPC 11634; PNG-002 | *Dioscorea rotundata* | *Dioscoreaceae* | Papua New Guinea | J. Peters & A.N. Jama | JX143724 | JX143483 | JX143237 | JX142991 | JX142745 |
| | CBS 132663; CPC 11636; PNG-016 | *Dioscorea esculenta* | *Dioscoreaceae* | Papua New Guinea | J. Peters & A.N. Jama | JX143725 | JX143484 | JX143238 | JX142992 | JX142746 |
| | CBS 132679; CPC 15807 | *Phaseolus vulgaris* | *Fabaceae* | Mexico | Ma. de Jesús Yáñez-Morales | JX143726 | JX143485 | JX143239 | JX142993 | JX142747 |
| | CBS 132681; CPC 15844 | *Euphorbia* sp. | *Euphorbiaceae* | Mexico: Tamaulipas | Ma. de Jesús Yáñez-Morales | JX143727 | JX143486 | JX143240 | JX142994 | JX142748 |
| | CBS 132682; CPC 15850 | *Taraxacum* sp. | *Asteraceae* | Mexico: Tamaulipas | Ma. de Jesús Yáñez-Morales | JX143728 | JX143487 | JX143241 | JX142995 | JX142749 |
| | CPC 10550 | *Acacia mangium* | *Fabaceae* | Thailand | K. Pongpanich | AY752139 | AY752172 | AY752200 | AY752231 | AY752262 |
| | CPC 10551 | *Acacia mangium* | *Fabaceae* | Thailand | K. Pongpanich | AY752140 | AY752173 | AY752201 | AY752232 | AY752263 |
| | CPC 11539 | *Acacia mangium* | *Fabaceae* | Thailand | K. Pongpanich | JX143729 | JX143488 | JX143242 | JX142996 | JX142750 |
| | CPC 11639; PNG-037 | *Dioscorea rotundata* | *Dioscoreaceae* | Papua New Guinea | J. Peters & A.N. Jama | JX143730 | JX143489 | JX143243 | JX142997 | JX142751 |
| | CPC 15875 | *Euphorbia* sp. | *Euphorbiaceae* | Mexico: Tamaulipas | Ma. de Jesús Yáñez-Morales | JX143731 | JX143490 | JX143244 | JX142998 | JX142752 |
| *Cercospora* sp. R | CBS 114644 | *Myoporum laetum* | *Myoporaceae* | New Zealand: Grey Lynn | C.F. Hill | JX143732 | JX143491 | JX143245 | JX142999 | JX142753 |
| *Cercospora* sp. S | CBS 132599; CPC 10656 | *Crepidiastrum denticulatum* (≡ *Youngia denticulata*) | *Asteraceae* | South Korea: Yangpyeong | H.D. Shin | JX143733 | JX143492 | JX143246 | JX143000 | JX142754 |

**Table 1.** (Continued).

| Species | Culture accession number(s)[1] | Host name or isolation source | Host Family | Country | Collector | GenBank accession numbers[2] | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | | | | | | ITS | TEF | ACT | CAL | HIS |
| *Cercospora vignigena* | CBS 132611; CPC 10812 (TYPE) | *Vigna unguiculata* (= *V. sinensis*) | *Fabaceae* | South Korea: Jeongeup | H.D. Shin | JX143734 | JX143493 | JX143247 | JX143001 | JX142755 |
| | CPC 1134 | *Vigna unguiculata* (= *V. sinensis*) | *Fabaceae* | South Africa: Potchefstroom | S. van Wyk | JX143735 | JX143494 | JX143248 | JX143002 | JX142756 |
| | MUCC 579; MAFF 237635 | *Vigna unguiculata* (= *V. sinensis*) | *Fabaceae* | Japan: Gumma | K. Kishi | JX143736 | JX143495 | JX143249 | JX143003 | JX142757 |
| *Cercospora violae* | CBS 251.67; CPC 5079 (TYPE) | *Viola tricolor* | *Violaceae* | Romania: Cazanele Dunarii | O. Constantinescu | JX143737 | JX143496 | JX143250 | JX143004 | JX142758 |
| | CPC 5368 | *Viola odorata* | *Violaceae* | New Zealand | C.F. Hill | JX143738 | JX143497 | JX143251 | JX143005 | JX142759 |
| | MUCC 129 | *Viola* sp. | *Violaceae* | Japan: Kochi | J. Nishikawa | JX143739 | JX143498 | JX143252 | JX143006 | JX142760 |
| | MUCC 133 | *Viola tricolor* | *Violaceae* | Japan: Nagano | J. Nishikawa | JX143740 | JX143499 | JX143253 | JX143007 | JX142761 |
| | MUCC 136 | *Viola tricolor* | *Violaceae* | Japan: Shizuoka | J. Nishikawa | JX143741 | JX143500 | JX143254 | JX143008 | JX142762 |
| *Cercospora zeae-maydis* | CBS 117755; YA-03; A358 | *Zea mays* | *Poaceae* | USA: Indiana | B. Fleener | DQ185072 | DQ185084 | DQ185096 | DQ185108 | DQ185120 |
| | CBS 117756; DE-97; A359 | *Zea mays* | *Poaceae* | USA: Indiana | B. Fleener | DQ185073 | DQ185085 | DQ185097 | DQ185109 | DQ185121 |
| | CBS 117757; JV-WI-02; A360 (TYPE) | *Zea mays* | *Poaceae* | USA: Wisconsin | B. Fleener | DQ185074 | DQ185086 | DQ185098 | DQ185110 | DQ185122 |
| | CBS 117758; JH-IA-04; A361 | *Zea mays* | *Poaceae* | USA: Iowa | B. Fleener | DQ185075 | DQ185087 | DQ185099 | DQ185111 | DQ185123 |
| | CBS 117759; UC-TN-99; A362 | *Zea mays* | *Poaceae* | USA: Tennessee | B. Fleener | DQ185076 | DQ185088 | DQ185100 | DQ185112 | DQ185124 |
| | CBS 117760; NH-PA-99; A363 | *Zea mays* | *Poaceae* | USA: Pennsylvania | B. Fleener | DQ185077 | DQ185089 | DQ185101 | DQ185113 | DQ185125 |
| | CBS 117761; PR-IN-99; A364 | *Zea mays* | *Poaceae* | USA: Indiana | B. Fleener | DQ185078 | DQ185090 | DQ185102 | DQ185114 | DQ185126 |
| | CBS 117762; DEXTER-MO-00; A365 | *Zea mays* | *Poaceae* | USA: Missouri | B. Fleener | DQ185079 | DQ185091 | DQ185103 | DQ185115 | DQ185127 |
| | CBS 117763; RENBECK-IA-99; A367 | *Zea mays* | *Poaceae* | USA: Iowa | B. Fleener | DQ185080 | DQ185092 | DQ185104 | DQ185116 | DQ185128 |
| | CBS 132668; CPC 12225; CHME 52 | *Zea mays* | *Poaceae* | China: Liaoning Province | — | JX143742 | JX143501 | JX143255 | JX143009 | JX142763 |
| | CBS 132678; CPC 15602 | *Zea mays* | *Poaceae* | Mexico: Tlacotepec | Ma. de Jesús Yáñez-Morales | JX143743 | JX143502 | JX143256 | JX143010 | JX142764 |
| *Cercospora zebrina* | CBS 108.22; CPC 5091 | *Medicago arabica* (= *M. maculata*) | *Fabaceae* | — | E.F. Hopkins | JX143744 | JX143503 | JX143257 | JX143011 | JX142765 |
| | CBS 112723; CPC 3957 | *Trifolium repens* | *Fabaceae* | Canada: Ottawa | K.A. Seifert | AY260079 | JX143504 | JX143258 | JX143012 | JX142766 |
| | CBS 112736; CPC 3958 | *Trifolium repens* | *Fabaceae* | Canada: Ottawa | K.A. Seifert | AY260080 | JX143505 | JX143259 | JX143013 | JX142767 |
| | CBS 112893; CPC 3955 | *Trifolium pratense* | *Fabaceae* | Canada: Ottawa | K.A. Seifert | AY260078 | JX143506 | JX143260 | JX143014 | JX142768 |
| | CBS 113070; CPC 5367 | *Trifolium repens* | *Fabaceae* | New Zealand: Blockhouse Bay | C.F. Hill | JX143745 | JX143507 | JX143261 | JX143015 | JX142769 |
| | CBS 114359; CPC 10901 | *Hebe* sp. | *Scrophulariaceae* | New Zealand | C.F. Hill | JX143746 | JX143508 | JX143262 | JX143016 | JX142770 |
| | CBS 118789; WAC 5106 | *Trifolium subterraneum* | *Fabaceae* | Australia | M.J. Barbetti | JX143747 | JX143509 | JX143263 | JX143017 | JX142771 |
| | CBS 118790; IMI 262766; WA 2030; WAC 7973 | *Trifolium subterraneum* | *Fabaceae* | Australia | M.J. Barbetti | JX143748 | JX143510 | JX143264 | JX143018 | JX142772 |

**Table 1.** (Continued).

| Species | Culture accession number(s)[1] | Host name or isolation source | Host Family | Country | Collector | GenBank accession numbers[2] | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | | | | | | ITS | TEF | ACT | CAL | HIS |
| | CBS 118791; IMI 264190; WA2054; WAC7993 | *Trifolium cernuum* | *Fabaceae* | Australia | M.J. Barbetti | JX143749 | JX143511 | JX143265 | JX143019 | JX142773 |
| | CBS 129.39; CPC 5078 | *Trifolium subterraneum* | *Fabaceae* | USA: Wisconsin | — | JX143750 | JX143512 | JX143266 | JX143020 | JX142774 |
| | CBS 132650; CPC 10756 | *Trifolium repens* | *Fabaceae* | South Korea: Namyangju | H.D. Shin | JX143751 | JX143513 | JX143267 | JX143021 | JX142775 |
| | CBS 137.56; CPC 5118 | *Hedysarum coronarium* | *Fabaceae* | Italy | — | JX143752 | JX143514 | JX143268 | JX143022 | JX142776 |
| | CBS 537.71; IMI 161108; CPC 5089 | *Astragalus spruneri* | *Fabaceae* | Romania: Hagieni | O. Constantinescu | JX143753 | JX143515 | JX143269 | JX143023 | JX142777 |
| | CPC 5437 | *Lotus pedunculatus* | *Fabaceae* | New Zealand: Auckland | C.F. Hill | JX143754 | JX143516 | JX143270 | JX143024 | JX142778 |
| | CPC 5473 | *Jacaranda mimosifolia* | *Bignoniaceae* | New Zealand | C.F. Hill | JX143755 | JX143517 | JX143271 | JX143025 | JX142779 |
| *Cercospora zeina* | CBS 118820; CPC 11995 (TYPE) | *Zea mays* | *Poaceae* | South Africa: Pietermaritzburg | P. Caldwell | DQ185081 | DQ185093 | DQ185105 | DQ185117 | DQ185129 |
| | CBS 132617; CPC 11998 | *Zea mays* | *Poaceae* | South Africa: Pietermaritzburg | P. Caldwell | DQ185082 | DQ185094 | DQ185106 | DQ185118 | DQ185130 |
| *Cercospora* cf. *zinniae* | CBS 132624; CPC 14549 | *Zinnia elegans* | *Asteraceae* | South Korea: Yangpyeong | H.D. Shin | JX143756 | JX143518 | JX143272 | JX143026 | JX142780 |
| | CBS 132676; CPC 15075 | — | — | Brazil: Valverde | A.C. Alfenas | JX143757 | JX143519 | JX143273 | JX143027 | JX142781 |
| | MUCC 131 | *Zinnia elegans* | *Asteraceae* | Japan: Shizuoka | J. Nishikawa | JX143758 | JX143520 | JX143274 | JX143028 | JX142782 |
| | MUCC 572; MUCNS 215; MAFF 237718 | *Zinnia elegans* | *Asteraceae* | Japan: Chiba | S. Uematsu | JX143759 | JX143521 | JX143275 | JX143029 | JX142783 |
| *Septoria provencialis* | CBS 118910; CPC 12226 | *Eucalyptus* sp. | *Myrtaceae* | France | P.W. Crous | DQ303096 | JX143522 | JX143276 | JX143030 | JX142784 |

[1] CBS: CBS-KNAW Fungal Biodiversity Centre, Utrecht, The Netherlands; CPC: Culture collection of Pedro Crous, housed at CBS; IHEM: Collection of the Laboratorium voor Microbiologie en Microbiele Genetica, Rijksuniversiteit, Ledeganckstraat 35, B-9000, Gent, Belgium; IMI: International Mycological Institute, CABI-Bioscience, Egham, Bakeham Lane, U.K.; Lynfield: Private culture collection and herbarium of Frank Hill, New Zealand; MAFF: Ministry of Agticulture, Forestry and Fisheries, Tsukuba, Ibaraki, Japan; MUCC: Culture Collection, Laboratory of Plant Pathology, Mie University, Tsu, Mie Prefecture, Japan; MUCL: Université Catholique de Louvain, Louvain-la-Neuve, Belgium; MUCNS: Active cultures & specimens of Chiharu Nakashima, housed at Mie University; MUMH: Mycologicl Herbarium of Mie University, Tsu, Mie, Japan; PPRI: Plant Protection Research Institute, Pretoria, South Africa; WAC: Department of Agriculture Western Australia Plant Pathogen Collection, Perth, Australia.

[2] ITS: internal transcribed spacers and intervening 5.8S nrDNA; TEF: translation elongation factor 1-alpha; ACT: actin; CAL: calmodulin; HIS: histone H3.

cercosporin is not produced by all species (Assante *et al.* 1977, examples cited by Goodwin *et al*. 2001, see also review by Weiland *et al.* 2010). Nutritional and environmental conditions influence the production of cercosporin, making it useless for application in *Cercospora* taxonomy (Jenns *et al*. 1989). Genomic studies in recent years attempt to understand the metabolic pathway used to produce cercosporin and *C. nicotianae* has become the model organism for these studies (*e.g.* Chung *et al*. 2003, Choquer *et al.* 2005, Chen *et al.* 2007, Amnuaykanjanasin & Daub 2009).

In an attempt to address some of the shortcomings highlighted in the previous paragraph, we have obtained diseased plant material and/or cultures from as many hosts and countries as possible over several years. We sequenced the ITS locus (including ITS1, 5.8S nrRNA gene and ITS2), as well as parts of four genomic protein coding genes, namely translation elongation-factor 1-alpha, actin, calmodulin and histone H3 for each culture. Our primary objective was to re-evaluate the species concept of known *Cercospora* species by consolidating the results of multi-locus phylogenetic analyses with morphological characteristics produced on host plants and different media. A secondary objective was to test whether *Cercospora* species, in general, were host-specific.

## MATERIALS AND METHODS

### Specimens and isolates

Dried specimens and cultures used in this study are maintained in herbaria and culture collections of Genebank, National Institute of Agrobiological Sciences, Japan, (MAFF), the Mycological Herbarium and Culture Collection, laboratory of Plant Pathology, Mie University, Japan (MUMH or MUCC) and the Centraalbureau voor Schimmelcultures (CBS-KNAW Fungal Biodiversity Centre, Utrecht, The Netherlands), or the working collection of P.W. Crous (CPC), housed at CBS (Table 1). A global set of isolates (Table 1) was either obtained from personal culture collections, the culture collection of the CBS or recollected on diseased plant material, and grown in axenic culture. Symptomatic leaves with leaf spots were chosen for isolations of *Cercospora* spp. as explained in Crous (1998). To obtain ascospore isolates, excised lesions were placed in distilled water for approximately 2 h, after which they were placed on the bottom of Petri dish lids, over which the plate containing 2 % malt extract agar (MEA) (Crous *et al*. 1991, 2009c) was inverted. Germinating ascospores were examined after 24 h, and single-ascospore cultures established on MEA as explained by Crous (1998). Colonies were sub-cultured onto oatmeal agar (OA), V8-juice agar (V8), 2 % potato-dextrose agar (PDA) or MEA (Crous *et al*. 2009c) and incubated at 25 °C under continuous near-ultraviolet light, to promote sporulation.

### DNA extraction, amplification and phylogeny

Genomic DNA was isolated from fungal mycelium grown on the agar plates following the protocol of Lee & Taylor (1990) or the UltraClean™ Microbial DNA Isolation Kit (Mo Bio Laboratories, Inc., Solana Beach, CA, USA). All isolates were sequenced with five genomic loci. The primers ITS5 or ITS1 and ITS4 (White *et al*. 1990) were used to amplify the internal transcribed spacers areas as well as the 5.8S rRNA gene (ITS) of the nrDNA operon. Part of the actin gene (ACT) was amplified using the primer set ACT-512F and ACT-783R (Carbone & Kohn 1999) and part of the translation elongation factor 1-a gene (EF) using the primer set EF1-728F and EF1-986R (Carbone & Kohn 1999). The primer set CAL-228F and CAL-737R (Carbone & Kohn 1999) was used to amplify part of the calmodulin gene (CAL) whereas the primer set CylH3F and CylH3R (Crous *et al*. 2004c) was used to amplify part of the histone H3 gene (HIS). Additional degenerate primers were developed from sequences obtained from GenBank as alternative forward and reverse primers for some of the loci during the course of the study (Table 2); however, these were rarely used but based on their degenerate design could be of use to the broader scientific community. The protocols and conditions outlined by Groenewald *et al*. (2005) were followed for standard amplification and subsequent sequencing of the loci.

Sequences of *Septoria provencialis* (isolate CPC 12226) were used as outgroup based on availability and phylogenetic relationship with *Cercospora* (Crous *et al*. 2004b, 2006b). The *Cercospora* sequences were assembled and added to the outgroup sequences using Sequence Alignment Editor v. 2.0a11 (Rambaut 2002), and manual adjustments for improvement were made by eye where necessary. Gaps present in the ingroup taxa and longer than 10 characters were coded as a single event for all analyses (see TreeBASE).

Neighbour-joining analyses using the HKY85 substitution model were applied to each data partition individually to check the stability and robustness of each species clade under each data set using PAUP v. 4.0b10 (Swofford 2003) (data not shown, discussed under the species notes where applicable). Alignment gaps were treated as missing data and all characters were unordered and of equal weight. Any ties were broken randomly when encountered. The robustness of the trees obtained was evaluated by 1 000 bootstrap replications (Hillis & Bull 1993).

MrModeltest v. 2.2 (Nylander 2004) was used to determine the best nucleotide substitution model settings for each data partition. Based on the results of the MrModeltest, a model-optimised phylogenetic re-construction was performed for the aligned combined data set to determine species relationships using MrBayes v. 3.2.0 (Ronquist & Huelsenbeck 2003). The heating parameter was set at 0.3 and the Markov Chain Monte Carlo (MCMC) analysis of four chains was started in parallel from a random tree topology and lasted until the average standard deviation of split frequencies came below 0.05. Trees were saved each 1 000 generations and the resulting phylogenetic tree was printed with Geneious v. 5.5.4 (Drummond *et al*. 2011). New sequences generated in this study were deposited in NCBI's GenBank nucleotide database (www.ncbi.nlm.nih.gov; Table 1) and the alignment and phylogenetic tree in TreeBASE (www.treebase.org).

Isolates of *Cercospora* sp. Q were screened with five more loci to test whether additional loci could distinguish cryptic taxa within this species. This species was selected based on the intraspecific variation present in Fig. 2 (part 5) and also the range of host species and countries represented. The primer set GDF1 and GDR1 (Guerber *et al*. 2003) was used to amplify part of the glyceraldehyde-3-phosphate dehydrogenase (GAPDH) gene, primer set NMS1 and NMS2 (Li *et al*. 1994) for part of the mitochondrial small subunit rRNA gene and part of the chitin synthase (CHS) gene was amplified using the primers CHS-79F and CHS-354R (Carbone & Kohn 1999). Part of the gene encoding for a mini-chromosome maintenance protein (MCM7) was amplified using primers Mcm7-709for, Mcm7-1348rev, Mcm7-1447rev (Schmitt *et al*. 2009) and part of the beta-tubulin gene using mainly the primers T1, Bt2b and TUB3Rd (see Table 2 for references).

**Table 2.** Details of primers used and/or developed for this study and their relation to selected published primers. The start and end positions of the primers are derived using the GenBank accession shown next to the locus name as reference in the 5'–3' direction. See Crous *et al.* (2009a) for information on additional ITS primers.

| Name | Sequence (5' – 3') | Orientation | %GC | Tm (°C) | Start | End | Reference |
|---|---|---|---|---|---|---|---|
| **Actin (*Hypocrea orientalis* GenBank accession JQ238613)** | | | | | | | |
| ACT-512F | ATG TGC AAG GCC GGT TTC GC | Forward | 60.0 | 51.4 | 244 | 263 | Carbone & Kohn (1999) |
| ACT-783R | TAC GAG TCC TTC TGG CCC AT | Reverse | 55.0 | 47.6 | 544 | 563 | Carbone & Kohn (1999) |
| ACT1Fd | GCY GCB CTC GTY ATY GAC AAT GG | Forward | 57.2 | 45.7 - 50.6 - 54.7 | 16 | 38 | This study, see also Aveskamp *et al.* (2009) |
| ACT1Rd | CRT CGT ACT CCT GCT TBG AGA TCC AC | Reverse | 54.5 | 48.3 - 50.3 - 51.8 | 1537 | 1562 | This study |
| ACT2Fd | GTA TCG TBC TBG ACT CYG GTG AYG GTG | Forward | 56.8 | 48.1 - 52.2 - 55.4 | 854 | 880 | This study |
| ACT2Rd | ARR TCR CGD CCR GCC ATG TC | Reverse | 61.7 | 45.1 - 50.9 - 58.1 | 940 | 956 | This study, see also Quaedvlieg *et al.* (2011) |
| **Beta-tubulin (*Gibberella zeae* GenBank accession FJ214662)** | | | | | | | |
| Bt1a | TTC CCC CGT CTC CAC TTC TTC ATG | Forward | 54.2 | 50.1 | 1091 | 1114 | Glass & Donaldson (1995) |
| Bt1b | GAC GAG ATC GTT CAT GTT GAA CTC | Reverse | 45.8 | 45.1 | 1603 | 1626 | Glass & Donaldson (1995) |
| Bt2a | GGT AAC CAA ATC GGT GCT GCT TTC | Forward | 50.0 | 48.2 | 163 | 186 | Glass & Donaldson (1995) |
| Bt2b | ACC CTC AGT GTA GTG ACC CTT GGC | Reverse | 58.0 | 52.1 | 617 | 640 | Glass & Donaldson (1995) |
| CYLTUB1F | AAA TTG GTG CTG CTT TCT GG | Forward | 45.0 | 43.5 | 170 | 189 | This study |
| CYLTUB1R | AGT TGT CGG GAC GGA AGA G | Reverse | 57.9 | 46.6 | 563 | 581 | Crous *et al.* (2004c) |
| T1 | AAC ATG CGT GAG ATT GTA AGT | Forward | 38.1 | 41.5 | 1 | 17 | O'Donnell & Cigelnik (1997) |
| TUB1Fd | CAN MAT GMG KGA RAT CGT RGT | Forward | 47.6 | 36.8 - 44.5 - 51.9 | 1 | 14 | This study |
| TUB1Rd | RGC VTC YTG GTA YTG CTG GTA | Reverse | 53.2 | 43.2 - 47.4 - 51.0 | 1633 | 1652 | This study |
| TUB2Fd | GTB CAC CTY CAR ACC GGY CAR TG | Forward | 59.4 | 46.1 - 51.4 - 56.4 | 74 | 96 | This study |
| TUB2Rd | TCA CCA GTG TAC CAA TGM ARG AAA GCC | Reverse | 48.1 | 48.3 - 50.1 - 52.0 | 1545 | 1565 | This study |
| TUB3Fd | AAA THG GTG CYG CHT TCT GG | Forward | 50.8 | 42.5 - 45.9 - 50.5 | 170 | 189 | This study |
| TUB3Rd | TCV GWG TTS AGY TGA CCN GGG | Reverse | 60.3 | 46.1 - 50.5 -54.0 | 1039 | 1059 | This study |
| TUB4Fd | GGH GCY GGH AAC AAC TGG GC | Forward | 65.8 | 48.3 - 52.2 - 57.7 | 600 | 618 | This study |
| TUB4Rd | CCR GAY TGR CCR AAR ACR AAG TTG TC | Reverse | 50.0 | 44.4 - 49.4 - 54.4 | 581 | 606 | This study |
| **Calmodulin (*Colletotrichum gloeosporioides* GenBank accession HM575363)** | | | | | | | |
| CAL-228F | GAG TTC AAG GAG GCC TTC TCC C | Forward | 59.1 | 49.2 | 2 | 23 | Carbone & Kohn (1999) |
| CAL-737R | CAT CTT TCT GGC CAT CAT GG | Reverse | 50.0 | 43.4 | 439 | 458 | Carbone & Kohn (1999) |
| CAL1Rd | GCA TCA TRA GYT RGA CRA ACT CG | Reverse | 47.8 | 41.0 - 45.4 - 49.7 | 747 | 769 | This study |
| CAL2Rd | TGR TCN GCC TCD CGG ATC ATC TC | Reverse | 58.0 | 47.5 - 50.8 - 54.9 | 647 | 669 | This study |
| **Histone H3 (*Talaromyces stipitatus* GenBank accession XM_002478391)** | | | | | | | |
| CYLH3F | AGG TCC ACT GGT GGC AAG | Forward | 61.1 | 47.6 | 28 | 45 | Crous *et al.* (2004c) |
| CYLH3R | AGC TGG ATG TCC TTG GAC TG | Reverse | 55.0 | 46.6 | 361 | 380 | Crous *et al.* (2004c) |
| H3-1a | ACT AAG CAG ACC GCC CGC AGG | Forward | 66.7 | 54.2 | 10 | 30 | Glass & Donaldson (1995) |
| H3-1b | GCG GGC GAG CTG GAT GTC CTT | Reverse | 66.7 | 54.5 | 367 | 387 | Glass & Donaldson (1995) |
| HIS1Rd | RCG RAG RCG ACG GGC | Reverse | 76.7 | 45.4 - 50.0 - 54.6 | 382 | 396 | This study |
| HIS2Rd | GGA TGG TRA CAC GCT TRG CGT G | Reverse | 59.1 | 47.9 - 50.5 - 53.1 | 240 | 361 | This study |
| **ITS (*Magnaporthe grisea* GenBank accession AB026819)** | | | | | | | |
| ITS1 | TCC GTA GGT GAA CCT GCG G | Forward | 63.2 | 49.5 | 2162 | 2180 | White *et al.* (1990) |
| ITS4 | TCC TCC GCT TAT TGA TAT GC | Reverse | 45.0 | 41.6 | 2685 | 2704 | White *et al.* (1990) |
| ITS5 | GGA AGT AAA AGT CGT AAC AAG G | Forward | 40.9 | 40.8 | 2138 | 2159 | White *et al.* (1990) |
| V9G | TTA CGT CCC TGC CCT TTG TA | Forward | 45.0 | 42.8 | 2002 | 2021 | de Hoog & Gerrits van den Ende (1998) |
| **Translation elongation factor 1-alpha (*Sordaria macrospora* GenBank accession X96615)** | | | | | | | |
| CylEF-R2 | CAT GTT CTT GAT GAA RTC ACG | Reverse | 40.5 | 39.2 - 40.2 - 41.1 | 783 | 803 | Crous *et al.* (2004c) |
| EF-1 | ATG GGT AAG GAR GAC AAG AC | Forward | 47.5 | 41.2 - 42.3 - 43.4 | 190 | 209 | O'Donnell *et al.* (1998) |
| EF-2 | GGA RGT ACC AGT SAT CAT GTT | Reverse | 45.2 | 41.6 - 42.6 -43.7 | 798 | 818 | O'Donnell *et al.* (1998) |
| EF-22 | AGG AAC CCT TAC CGA GCT C | Reverse | 57.9 | 46.2 | 578 | 596 | O'Donnell *et al.* (1998) |
| EF1-1567R | ACH GTR CCR ATA CCA CCR ATC TT | Reverse | 47.1 | 43.1 - 47.2 - 52.0 | 1254 | 1276 | Designed by S. Rehner (www.aftol.org/pdfs/EF1primer.pdf) |

**Table 2.** (Continued).

| Name | Sequence (5' – 3') | Orientation | %GC | Tm (°C) | Start | End | Reference |
|---|---|---|---|---|---|---|---|
| **Translation elongation factor 1-alpha (*Sordaria macrospora* GenBank accession X96615)** | | | | | | | |
| EF1-2218R | ATG ACA CCR ACR GCR ACR GTY TG | Reverse | 54.3 | 45.6 - 50.4 - 55.1 | 1782 | 1804 | Designed by S. Rehner (www.aftol.org/pdfs/EF1primer.pdf) |
| EF1-526F | GTC GTY GTY ATY GGH CAY GT | Forward | 51.7 | 40.0 - 45.6 - 52.2 | 220 | 239 | Designed by S. Rehner (www.aftol.org/pdfs/EF1primer.pdf) |
| EF1-728F | CAT CGA GAA GTT CGA GAA GG | Forward | 50.0 | 42.2 | 306 | 325 | Carbone & Kohn (1999) |
| EF1-986R | TAC TTG AAG GAA CCC TTA CC | Reverse | 45.0 | 40.9 | 584 | 603 | Carbone & Kohn (1999) |
| EF1Fd | GTC GTT ATC GGC CAC GTC G | Forward | 63.2 | 48.5 | 223 | 241 | This study |
| EF1Rd | CGG MCT TGG TGA CCT TGC C | Reverse | 65.8 | 48.8 - 50.4 - 52.0 | 1836 | 1852 | This study |
| EF2Fd | GAT CTA CCA GTG CGG TGG | Forward | 61.1 | 45.4 | 273 | 290 | This study |
| EF2Rd | GGT GCA TYT CSA CGG ACT TGA C | Reverse | 56.8 | 48.2 - 49.1 - 49.9 | 1356 | 1377 | This study |
| EF3Fd | GAG CGT GAG CGT GGT ATC AC | Forward | 60.0 | 48.1 | 632 | 651 | This study |
| EF3Rd | GGT ACG CTK GTC RAT ACC ACC | Reverse | 57.1 | 45.5 - 47.5 - 49.6 | 286 | 306 | This study |
| EF4Fd | GGT GCA TYT CSA CGG ACT TGA C | Forward | 56.8 | 48.2 - 49.1 - 49.9 | 1356 | 1377 | This study |

## Taxonomy

Morphological descriptions are based on structures *in vivo*, with morphological structures *in vitro* noted where relevant. Structures were mounted in clear lactic acid, and 30 measurements (× 1 000 magnification) determined wherever possible, with the extremes of spore measurements given in parentheses. Observations were made with a Zeiss V20 Discovery stereo-microscope, and with a Zeiss Axio Imager 2 light microscope using differential interference contrast (DIC) illumination and an AxioCam MRc5 camera and software. Colony colours (surface and reverse) were assessed on different culture media at 25 °C in the dark, using the colour charts of Rayner (1970). All isolates obtained in this study are maintained in culture collections (Table 1). Nomenclatural novelties and descriptions were deposited in MycoBank (www.MycoBank.org; Crous *et al*. 2004a).

## RESULTS

## DNA phylogeny

Amplification products and gene sequences of similar size to that reported previously (Groenewald *et al*. 2005, 2010a) were obtained. The resulting concatenated alignment contains 361 taxa (including the outgroup taxon), and 471, 263, 199, 240 and 347 characters (including alignment gaps) were used in the ITS, TEF, ACT, CAL and HIS partitions, respectively. Based on the results of MrModeltest, the following priors were set in MrBayes for the different partitions: all partitions had dirichlet base frequencies and GTR+G models with gamma-distributed rates were implemented for ITS, ACT and CAL, and HKY+G with gamma-distributed rates for TEF while HIS required HKY+I+G with inverse gamma-distributed rates. The final aligned combined data set contained 361 ingroup taxa with a total of 1 305 characters and *Septoria provencialis* (isolate CPC 12226) served as the outgroup taxon. From this alignment 1 520 characters were used for the Bayesian analysis; these contained 588 unique site patterns (48, 172, 111, 125 and 132 for ITS, TEF, ACT, CAL and HIS, respectively). The Bayesian analysis lasted 3 995 000 generations and the consensus trees and posterior probabilities were calculated from the 5 994 trees left after discarding 1 998 trees (the first 1 000 generations) for burn-in (Fig. 2).

The ITS region has limited resolution for almost all species in *Cercospora* and therefore the results of the other gene regions were particularly useful for comparison of clade stability. Neighbour-joining analyses using the HKY85 substitution model were applied to each data partition to check the stability and robustness of each species clade under the different partitions (data not shown). The ITS region was only able to distinguish *C. zeina* and *C. zeae-maydis* from the rest of the included species. The TEF region was able to distinguish 33 of the 73 species clades and especially failed for *Cercospora* sp. M–Q (including *C.* cf. *sigesbeckiae* and *C.* cf. *richardiicola*; spanning most of Fig. 2 part 4 and the upper half of part 5), whereas ACT distinguished 43 of the 73 species clades and especially failed for *Cercospora* sp. G–I (Fig. 2 part 1) and including *C.* cf. *flagellaris* and *C. alchemillicola/C.* cf. *alchemillicola*. The ACT region also accounted for most of the variation observed for *Cercospora* sp. Q. The CAL region was able to distinguish 34 of the 73 species clades but especially failed for *Cercospora* sp. M, P and Q (including *C. kikuchii*, *C.* cf. *sigesbeckiae*, *C.* cf. *richardiicola* and C. *rodmanii*; spanning middle of Fig. 2 part 4), as well as a group consisting predominantly of *C. armoraciae*, *C. capsici*, *C. zebrina* and *C. violae* (Fig. 2 part 3). Although the locus was able to separate *C. beticola* and *C. apii*, it could not distinguish *C.* cf. *brunkii* and *C.* cf. *resedae* from *C. apii*. The HIS region distinguished 46 of the 73 species clades and especially failed for *Cercospora* sp. G–I (Fig. 2 part 1) and *Cercospora* sp. M, P and Q (including *C. kikuchii*, *C.* cf. *richardiicola* and C. *rodmanii*; spanning middle of Fig. 2 part 4). The HIS region also accounted for most of the variation observed for *C. armoraciae* and was responsible for the split of *C. beticola* into two clades. No single gene region was found which could reliably distinguish all species and, irrespective of which locus was used, occurrences of the same sequence(s) shared between multiple species were observed. If data for ITS is not taken into consideration, the remaining four loci always distinguish the following 18 species: *C. agavicola*, *C. apiicola*, *C. coniogramme*, *C.* cf. *erysimi*, *C. euphorbiae-sieboldianae*, *C. helianthicola*, *C. mercurialis*, *C. olivascens*, *C. pileicola*, *C. senecionis-walkeri*, *C. violae*, *C. zeae-maydis*, *C. zeina*, *Cercospora* sp. A, *Cercospora* sp. C, *Cercospora* sp. D, *Cercospora* sp. J, *Cercospora* sp. R. Some species are only distinguished based on a single locus and these results are discussed under the species notes, where applicable.

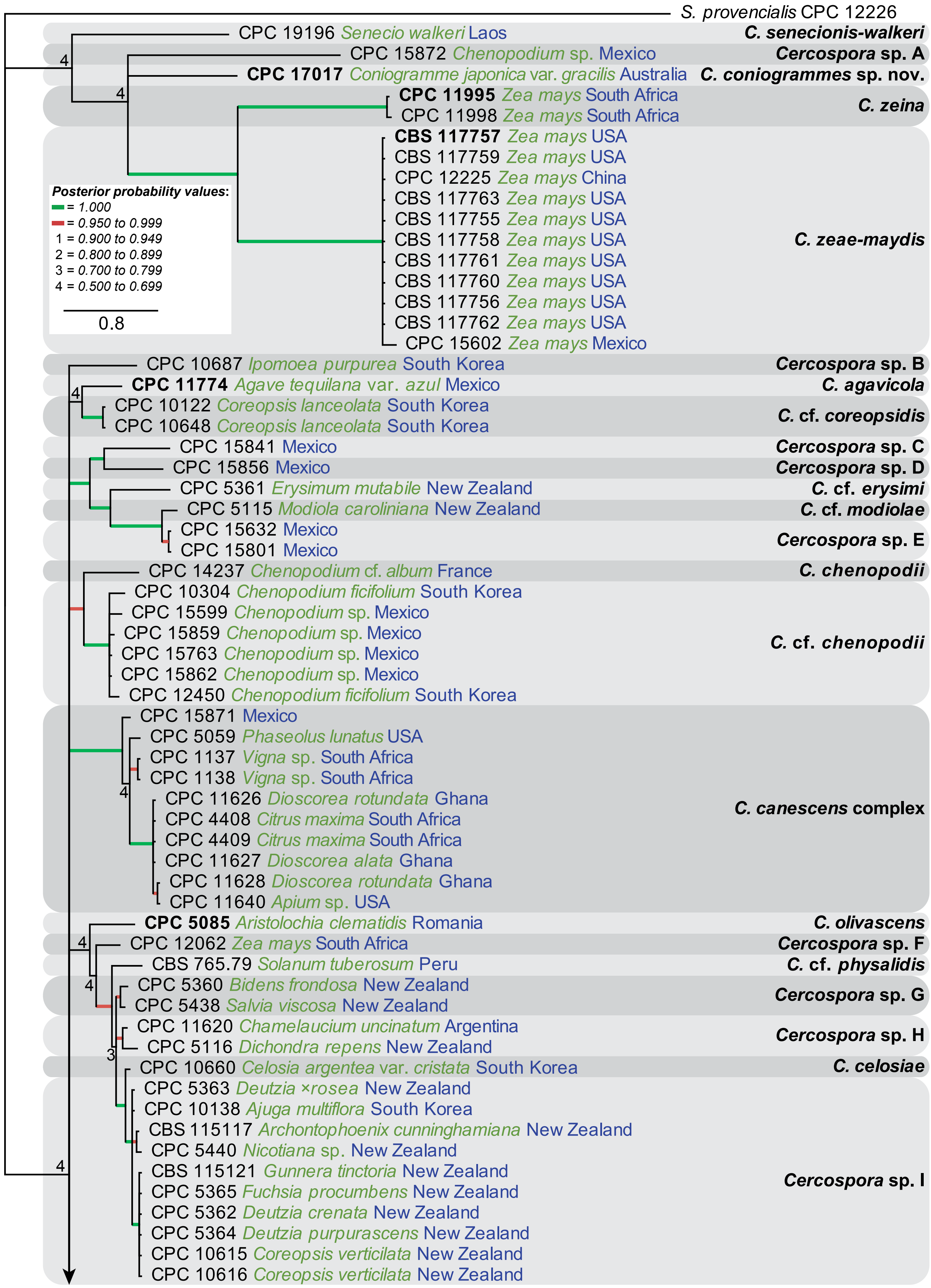



**Fig. 2.** (Part 1). Consensus phylogram (50 % majority rule) of 5 994 trees resulting from a Bayesian analysis of the combined 5-gene sequence alignment using MrBayes v. 3.2.0. Bayesian posterior probabilities are indicated with colour-coded branches and numbers (see legend) and the scale bar represents the expected changes per site. Species clades are indicated in coloured blocks and species names in black text. Hosts and countries of origin are indicated in green and blue text, respectively. The tree was rooted to *Septoria provencialis* (strain CPC 12226).

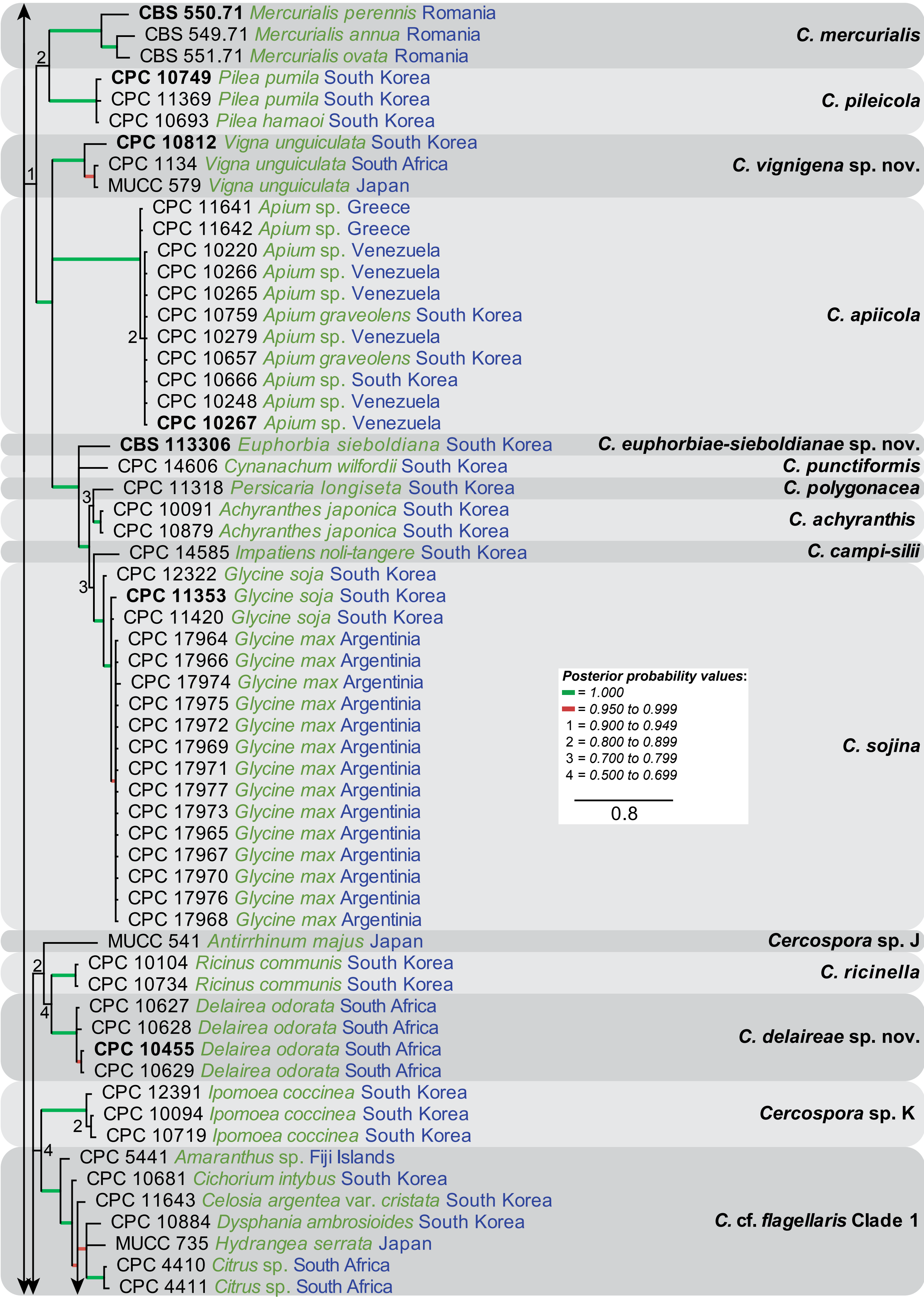

CBS 550.71 Mercurialis perennis Romania
CBS 549.71 Mercurialis annua Romania
CBS 551.71 Mercurialis ovata Romania
C. mercurialis
CPC 10749 Pilea pumila South Korea
CPC 11369 Pilea pumila South Korea
CPC 10693 Pilea hamaoi South Korea
C. pileicola
CPC 10812 Vigna unguiculata South Korea
CPC 1134 Vigna unguiculata South Africa
MUCC 579 Vigna unguiculata Japan
C. vignigena sp. nov.
CPC 11641 Apium sp. Greece
CPC 11642 Apium sp. Greece
CPC 10220 Apium sp. Venezuela
CPC 10266 Apium sp. Venezuela
CPC 10265 Apium sp. Venezuela
CPC 10759 Apium graveolens South Korea
CPC 10279 Apium sp. Venezuela
CPC 10657 Apium graveolens South Korea
CPC 10666 Apium sp. South Korea
CPC 10248 Apium sp. Venezuela
CPC 10267 Apium sp. Venezuela
C. apiicola
CBS 113306 Euphorbia sieboldiana South Korea
C. euphorbiae-sieboldianae sp. nov.
CPC 14606 Cynanachum wilfordii South Korea
C. punctiformis
CPC 11318 Persicaria longiseta South Korea
C. polygonacea
CPC 10091 Achyranthes japonica South Korea
CPC 10879 Achyranthes japonica South Korea
C. achyranthis
CPC 14585 Impatiens noli-tangere South Korea
C. campi-silii
CPC 12322 Glycine soja South Korea
CPC 11353 Glycine soja South Korea
CPC 11420 Glycine soja South Korea
CPC 17964 Glycine max Argentinia
CPC 17966 Glycine max Argentinia
CPC 17974 Glycine max Argentinia
CPC 17975 Glycine max Argentinia
CPC 17972 Glycine max Argentinia
CPC 17969 Glycine max Argentinia
CPC 17971 Glycine max Argentinia
CPC 17977 Glycine max Argentinia
CPC 17973 Glycine max Argentinia
CPC 17965 Glycine max Argentinia
CPC 17967 Glycine max Argentinia
CPC 17970 Glycine max Argentinia
CPC 17976 Glycine max Argentinia
CPC 17968 Glycine max Argentinia
C. sojina
Posterior probability values:
= 1.000
= 0.950 to 0.999
1 = 0.900 to 0.949
2 = 0.800 to 0.899
3 = 0.700 to 0.799
4 = 0.500 to 0.699
0.8
MUCC 541 Antirrhinum majus Japan
Cercospora sp. J
CPC 10104 Ricinus communis South Korea
CPC 10734 Ricinus communis South Korea
C. ricinella
CPC 10627 Delairea odorata South Africa
CPC 10628 Delairea odorata South Africa
CPC 10455 Delairea odorata South Africa
CPC 10629 Delairea odorata South Africa
C. delaireae sp. nov.
CPC 12391 Ipomoea coccinea South Korea
CPC 10094 Ipomoea coccinea South Korea
CPC 10719 Ipomoea coccinea South Korea
Cercospora sp. K
CPC 5441 Amaranthus sp. Fiji Islands
CPC 10681 Cichorium intybus South Korea
CPC 11643 Celosia argentea var. cristata South Korea
CPC 10884 Dysphania ambrosioides South Korea
MUCC 735 Hydrangea serrata Japan
CPC 4410 Citrus sp. South Africa
CPC 4411 Citrus sp. South Africa
C. cf. flagellaris Clade 1

**Fig. 2.** (Part 2).

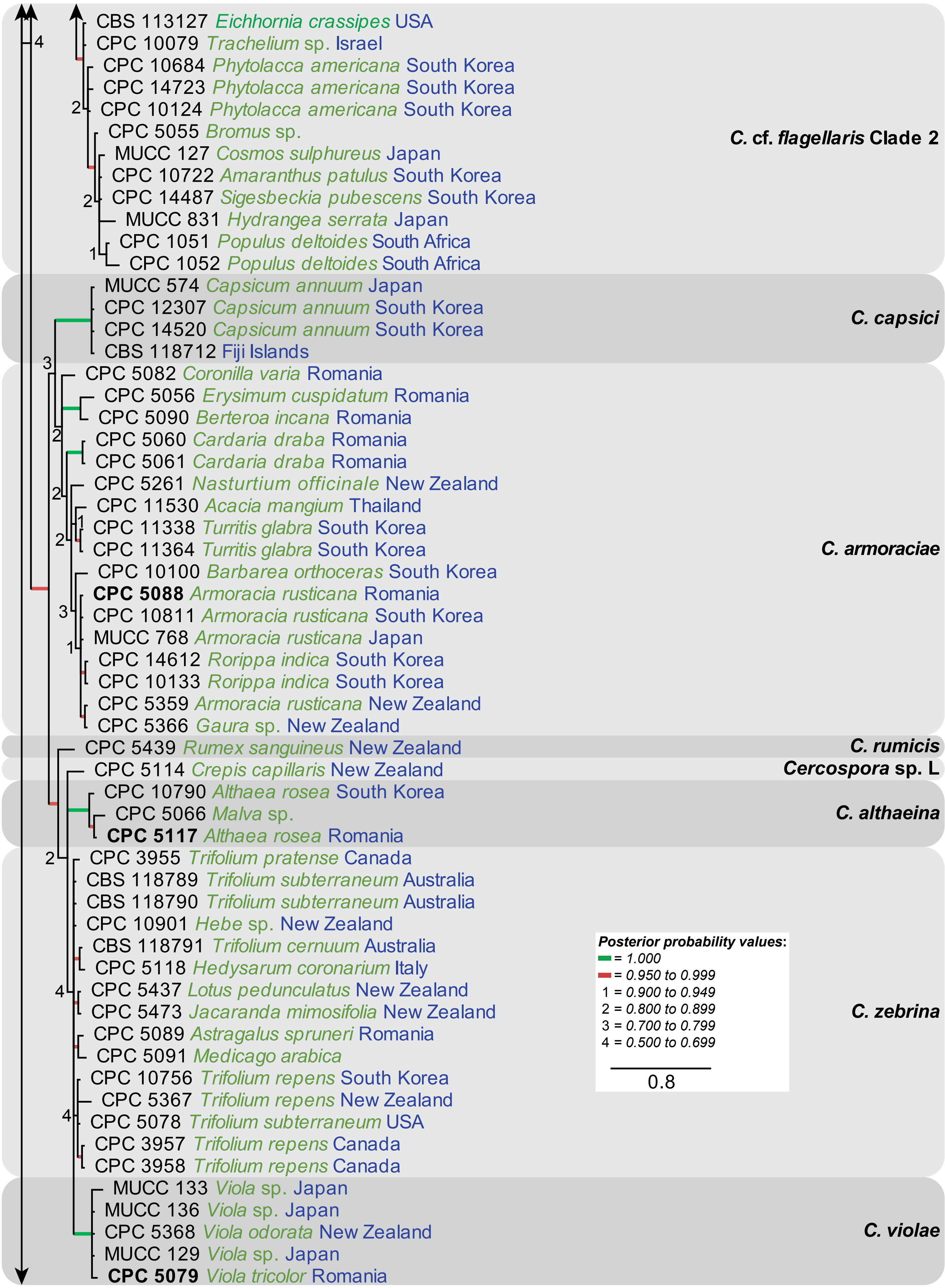
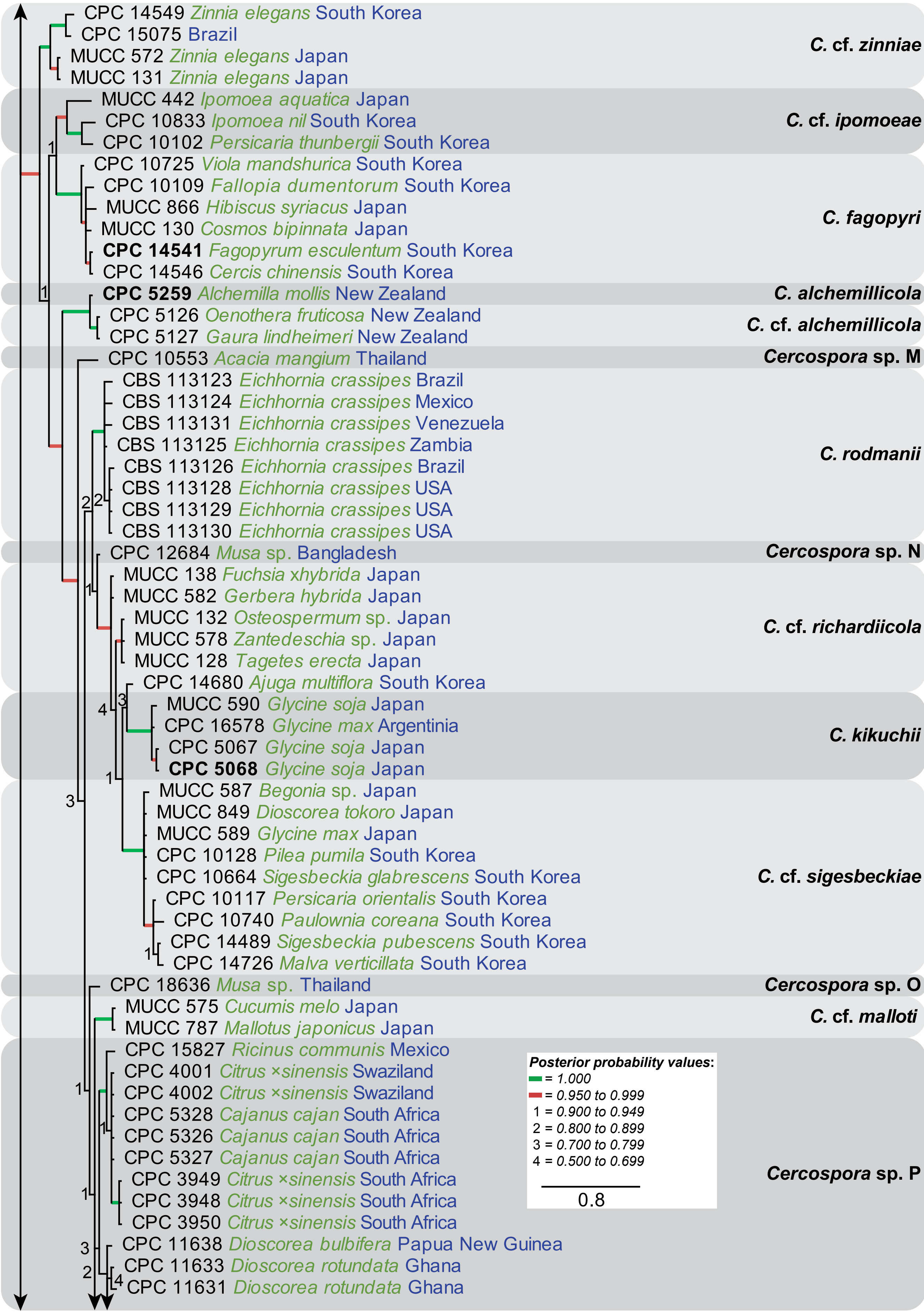
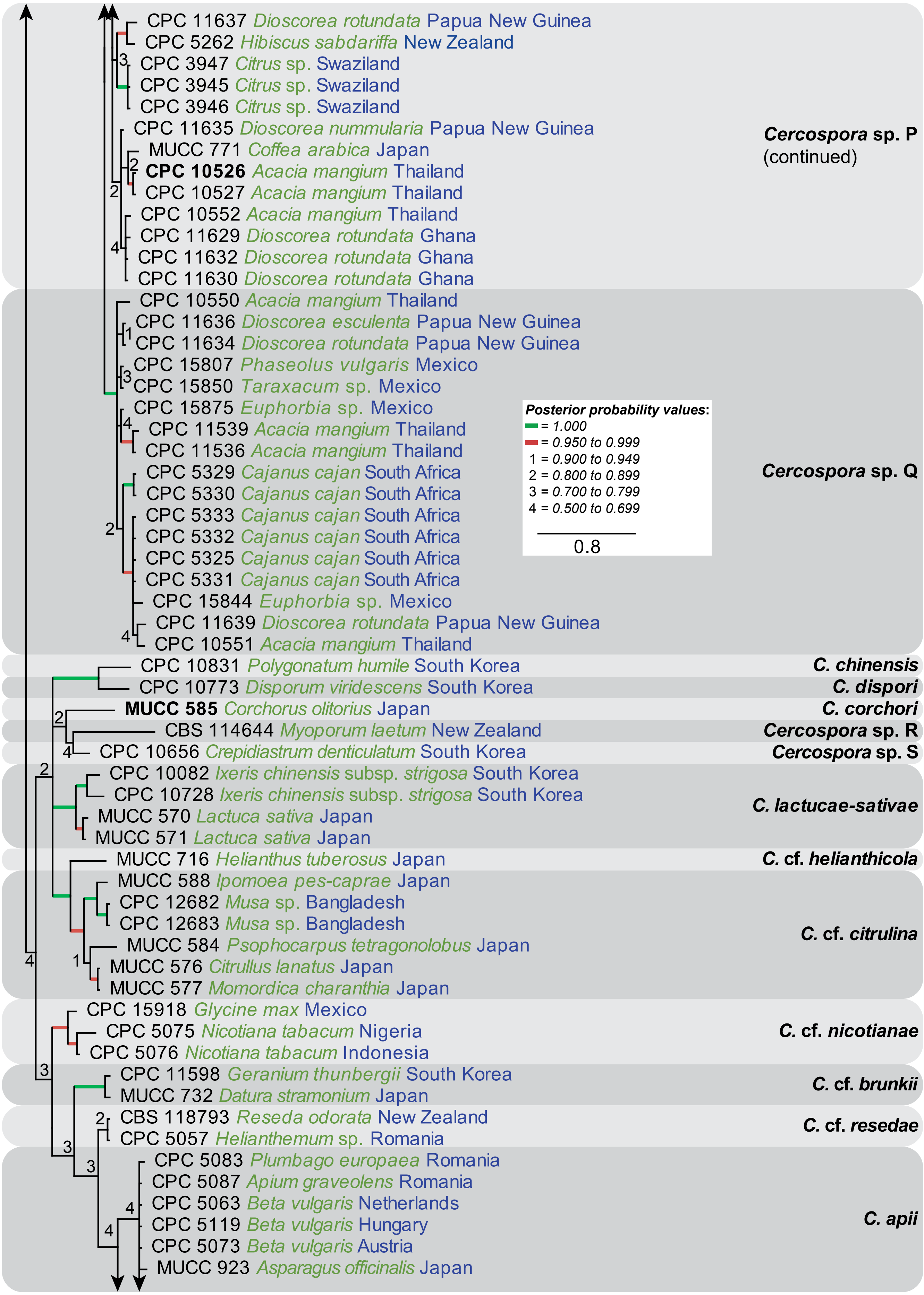

CBS 113127 Eichhornia crassipes USA
CPC 10079 Trachelium sp. Israel
CPC 10684 Phytolacca americana South Korea
CPC 14723 Phytolacca americana South Korea
CPC 10124 Phytolacca americana South Korea
CPC 5055 Bromus sp.
MUCC 127 Cosmos sulphureus Japan
CPC 10722 Amaranthus patulus South Korea
CPC 14487 Sigesbeckia pubescens South Korea
MUCC 831 Hydrangea serrata Japan
CPC 1051 Populus deltoides South Africa
CPC 1052 Populus deltoides South Africa
C. cf. flagellaris Clade 2
MUCC 574 Capsicum annuum Japan
CPC 12307 Capsicum annuum South Korea
CPC 14520 Capsicum annuum South Korea
CBS 118712 Fiji Islands
C. capsici
CPC 5082 Coronilla varia Romania
CPC 5056 Erysimum cuspidatum Romania
CPC 5090 Berteroa incana Romania
CPC 5060 Cardaria draba Romania
CPC 5061 Cardaria draba Romania
CPC 5261 Nasturtium officinale New Zealand
CPC 11530 Acacia mangium Thailand
CPC 11338 Turritis glabra South Korea
CPC 11364 Turritis glabra South Korea
CPC 10100 Barbarea orthoceras South Korea
CPC 5088 Armoracia rusticana Romania
CPC 10811 Armoracia rusticana South Korea
MUCC 768 Armoracia rusticana Japan
CPC 14612 Rorippa indica South Korea
CPC 10133 Rorippa indica South Korea
CPC 5359 Armoracia rusticana New Zealand
CPC 5366 Gaura sp. New Zealand
C. armoraciae
CPC 5439 Rumex sanguineus New Zealand
C. rumicis
CPC 5114 Crepis capillaris New Zealand
Cercospora sp. L
CPC 10790 Althaea rosea South Korea
CPC 5066 Malva sp.
CPC 5117 Althaea rosea Romania
C. althaeina
CPC 3955 Trifolium pratense Canada
CBS 118789 Trifolium subterraneum Australia
CBS 118790 Trifolium subterraneum Australia
CPC 10901 Hebe sp. New Zealand
CBS 118791 Trifolium cernuum Australia
CPC 5118 Hedysarum coronarium Italy
CPC 5437 Lotus pedunculatus New Zealand
CPC 5473 Jacaranda mimosifolia New Zealand
CPC 5089 Astragalus spruneri Romania
CPC 5091 Medicago arabica
CPC 10756 Trifolium repens South Korea
CPC 5367 Trifolium repens New Zealand
CPC 5078 Trifolium subterraneum USA
CPC 3957 Trifolium repens Canada
CPC 3958 Trifolium repens Canada
C. zebrina
MUCC 133 Viola sp. Japan
MUCC 136 Viola sp. Japan
CPC 5368 Viola odorata New Zealand
MUCC 129 Viola sp. Japan
CPC 5079 Viola tricolor Romania
C. violae
Posterior probability values:
= 1.000
= 0.950 to 0.999
1 = 0.900 to 0.949
2 = 0.800 to 0.899
3 = 0.700 to 0.799
4 = 0.500 to 0.699
0.8

**Fig. 2.** (Part 3).



CPC 14549 Zinnia elegans South Korea
CPC 15075 Brazil
MUCC 572 Zinnia elegans Japan
MUCC 131 Zinnia elegans Japan
C. cf. zinniae
MUCC 442 Ipomoea aquatica Japan
CPC 10833 Ipomoea nil South Korea
CPC 10102 Persicaria thunbergii South Korea
C. cf. ipomoeae
CPC 10725 Viola mandshurica South Korea
CPC 10109 Fallopia dumentorum South Korea
MUCC 866 Hibiscus syriacus Japan
MUCC 130 Cosmos bipinnata Japan
CPC 14541 Fagopyrum esculentum South Korea
CPC 14546 Cercis chinensis South Korea
C. fagopyri
CPC 5259 Alchemilla mollis New Zealand
C. alchemillicola
CPC 5126 Oenothera fruticosa New Zealand
CPC 5127 Gaura lindheimeri New Zealand
C. cf. alchemillicola
CPC 10553 Acacia mangium Thailand
Cercospora sp. M
CBS 113123 Eichhornia crassipes Brazil
CBS 113124 Eichhornia crassipes Mexico
CBS 113131 Eichhornia crassipes Venezuela
CBS 113125 Eichhornia crassipes Zambia
CBS 113126 Eichhornia crassipes Brazil
CBS 113128 Eichhornia crassipes USA
CBS 113129 Eichhornia crassipes USA
CBS 113130 Eichhornia crassipes USA
C. rodmanii
CPC 12684 Musa sp. Bangladesh
Cercospora sp. N
MUCC 138 Fuchsia xhybrida Japan
MUCC 582 Gerbera hybrida Japan
MUCC 132 Osteospermum sp. Japan
MUCC 578 Zantedeschia sp. Japan
MUCC 128 Tagetes erecta Japan
CPC 14680 Ajuga multiflora South Korea
C. cf. richardiicola
MUCC 590 Glycine soja Japan
CPC 16578 Glycine max Argentinia
CPC 5067 Glycine soja Japan
CPC 5068 Glycine soja Japan
C. kikuchii
MUCC 587 Begonia sp. Japan
MUCC 849 Dioscorea tokoro Japan
MUCC 589 Glycine max Japan
CPC 10128 Pilea pumila South Korea
CPC 10664 Sigesbeckia glabrescens South Korea
CPC 10117 Persicaria orientalis South Korea
CPC 10740 Paulownia coreana South Korea
CPC 14489 Sigesbeckia pubescens South Korea
CPC 14726 Malva verticillata South Korea
C. cf. sigesbeckiae
CPC 18636 Musa sp. Thailand
Cercospora sp. O
MUCC 575 Cucumis melo Japan
MUCC 787 Mallotus japonicus Japan
C. cf. malloti
CPC 15827 Ricinus communis Mexico
CPC 4001 Citrus ×sinensis Swaziland
CPC 4002 Citrus ×sinensis Swaziland
CPC 5328 Cajanus cajan South Africa
CPC 5326 Cajanus cajan South Africa
CPC 5327 Cajanus cajan South Africa
CPC 3949 Citrus ×sinensis South Africa
CPC 3948 Citrus ×sinensis South Africa
CPC 3950 Citrus ×sinensis South Africa
CPC 11638 Dioscorea bulbifera Papua New Guinea
CPC 11633 Dioscorea rotundata Ghana
CPC 11631 Dioscorea rotundata Ghana
Cercospora sp. P
Posterior probability values:
= 1.000
= 0.950 to 0.999
1 = 0.900 to 0.949
2 = 0.800 to 0.899
3 = 0.700 to 0.799
4 = 0.500 to 0.699
0.8


**Fig. 2.** (Part 4).



CPC 11637 Dioscorea rotundata Papua New Guinea
CPC 5262 Hibiscus sabdariffa New Zealand
CPC 3947 Citrus sp. Swaziland
CPC 3945 Citrus sp. Swaziland
CPC 3946 Citrus sp. Swaziland
CPC 11635 Dioscorea nummularia Papua New Guinea
MUCC 771 Coffea arabica Japan
CPC 10526 Acacia mangium Thailand
CPC 10527 Acacia mangium Thailand
CPC 10552 Acacia mangium Thailand
CPC 11629 Dioscorea rotundata Ghana
CPC 11632 Dioscorea rotundata Ghana
CPC 11630 Dioscorea rotundata Ghana
Cercospora sp. P (continued)
CPC 10550 Acacia mangium Thailand
CPC 11636 Dioscorea esculenta Papua New Guinea
CPC 11634 Dioscorea rotundata Papua New Guinea
CPC 15807 Phaseolus vulgaris Mexico
CPC 15850 Taraxacum sp. Mexico
CPC 15875 Euphorbia sp. Mexico
CPC 11539 Acacia mangium Thailand
CPC 11536 Acacia mangium Thailand
CPC 5329 Cajanus cajan South Africa
CPC 5330 Cajanus cajan South Africa
CPC 5333 Cajanus cajan South Africa
CPC 5332 Cajanus cajan South Africa
CPC 5325 Cajanus cajan South Africa
CPC 5331 Cajanus cajan South Africa
CPC 15844 Euphorbia sp. Mexico
CPC 11639 Dioscorea rotundata Papua New Guinea
CPC 10551 Acacia mangium Thailand
Cercospora sp. Q
Posterior probability values:
= 1.000
= 0.950 to 0.999
1 = 0.900 to 0.949
2 = 0.800 to 0.899
3 = 0.700 to 0.799
4 = 0.500 to 0.699
0.8
CPC 10831 Polygonatum humile South Korea
C. chinensis
CPC 10773 Disporum viridescens South Korea
C. dispori
MUCC 585 Corchorus olitorius Japan
C. corchori
CBS 114644 Myoporum laetum New Zealand
Cercospora sp. R
CPC 10656 Crepidiastrum denticulatum South Korea
Cercospora sp. S
CPC 10082 Ixeris chinensis subsp. strigosa South Korea
CPC 10728 Ixeris chinensis subsp. strigosa South Korea
MUCC 570 Lactuca sativa Japan
MUCC 571 Lactuca sativa Japan
C. lactucae-sativae
MUCC 716 Helianthus tuberosus Japan
C. cf. helianthicola
MUCC 588 Ipomoea pes-caprae Japan
CPC 12682 Musa sp. Bangladesh
CPC 12683 Musa sp. Bangladesh
MUCC 584 Psophocarpus tetragonolobus Japan
MUCC 576 Citrullus lanatus Japan
MUCC 577 Momordica charanthia Japan
C. cf. citrulina
CPC 15918 Glycine max Mexico
CPC 5075 Nicotiana tabacum Nigeria
CPC 5076 Nicotiana tabacum Indonesia
C. cf. nicotianae
CPC 11598 Geranium thunbergii South Korea
MUCC 732 Datura stramonium Japan
C. cf. brunkii
CBS 118793 Reseda odorata New Zealand
CPC 5057 Helianthemum sp. Romania
C. cf. resedae
CPC 5083 Plumbago europaea Romania
CPC 5087 Apium graveolens Romania
CPC 5063 Beta vulgaris Netherlands
CPC 5119 Beta vulgaris Hungary
CPC 5073 Beta vulgaris Austria
MUCC 923 Asparagus officinalis Japan
C. apii


**Fig. 2.** (Part 5).

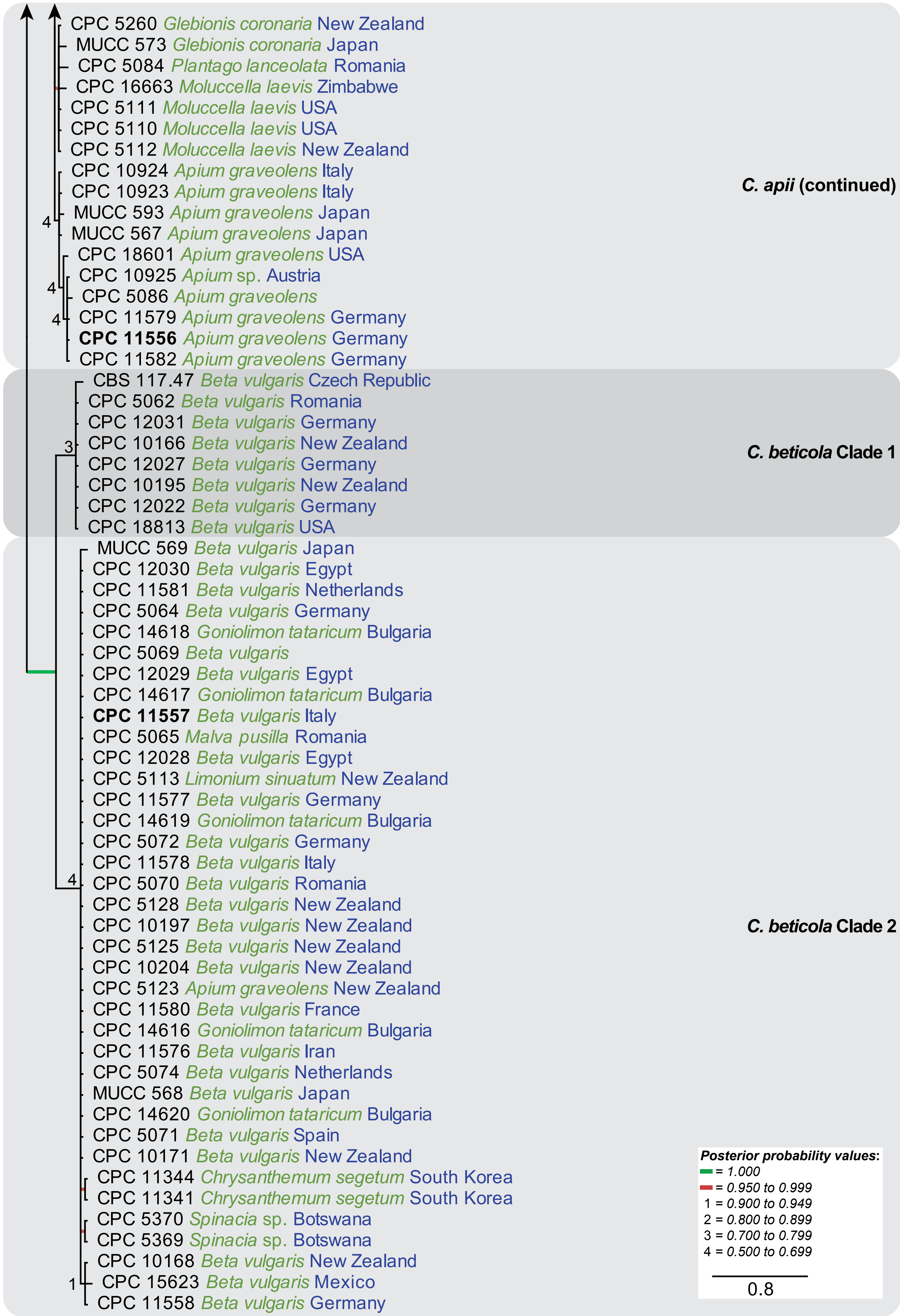

CPC 5260 Glebionis coronaria New Zealand
MUCC 573 Glebionis coronaria Japan
CPC 5084 Plantago lanceolata Romania
CPC 16663 Moluccella laevis Zimbabwe
CPC 5111 Moluccella laevis USA
CPC 5110 Moluccella laevis USA
CPC 5112 Moluccella laevis New Zealand
CPC 10924 Apium graveolens Italy
CPC 10923 Apium graveolens Italy
MUCC 593 Apium graveolens Japan
MUCC 567 Apium graveolens Japan
CPC 18601 Apium graveolens USA
CPC 10925 Apium sp. Austria
CPC 5086 Apium graveolens
CPC 11579 Apium graveolens Germany
CPC 11556 Apium graveolens Germany
CPC 11582 Apium graveolens Germany
C. apii (continued)
CBS 117.47 Beta vulgaris Czech Republic
CPC 5062 Beta vulgaris Romania
CPC 12031 Beta vulgaris Germany
CPC 10166 Beta vulgaris New Zealand
CPC 12027 Beta vulgaris Germany
CPC 10195 Beta vulgaris New Zealand
CPC 12022 Beta vulgaris Germany
CPC 18813 Beta vulgaris USA
C. beticola Clade 1
MUCC 569 Beta vulgaris Japan
CPC 12030 Beta vulgaris Egypt
CPC 11581 Beta vulgaris Netherlands
CPC 5064 Beta vulgaris Germany
CPC 14618 Goniolimon tataricum Bulgaria
CPC 5069 Beta vulgaris
CPC 12029 Beta vulgaris Egypt
CPC 14617 Goniolimon tataricum Bulgaria
CPC 11557 Beta vulgaris Italy
CPC 5065 Malva pusilla Romania
CPC 12028 Beta vulgaris Egypt
CPC 5113 Limonium sinuatum New Zealand
CPC 11577 Beta vulgaris Germany
CPC 14619 Goniolimon tataricum Bulgaria
CPC 5072 Beta vulgaris Germany
CPC 11578 Beta vulgaris Italy
CPC 5070 Beta vulgaris Romania
CPC 5128 Beta vulgaris New Zealand
CPC 10197 Beta vulgaris New Zealand
CPC 5125 Beta vulgaris New Zealand
CPC 10204 Beta vulgaris New Zealand
CPC 5123 Apium graveolens New Zealand
CPC 11580 Beta vulgaris France
CPC 14616 Goniolimon tataricum Bulgaria
CPC 11576 Beta vulgaris Iran
CPC 5074 Beta vulgaris Netherlands
MUCC 568 Beta vulgaris Japan
CPC 14620 Goniolimon tataricum Bulgaria
CPC 5071 Beta vulgaris Spain
CPC 10171 Beta vulgaris New Zealand
CPC 11344 Chrysanthemum segetum South Korea
CPC 11341 Chrysanthemum segetum South Korea
CPC 5370 Spinacia sp. Botswana
CPC 5369 Spinacia sp. Botswana
CPC 10168 Beta vulgaris New Zealand
CPC 15623 Beta vulgaris Mexico
CPC 11558 Beta vulgaris Germany
C. beticola Clade 2
Posterior probability values:
= 1.000
= 0.950 to 0.999
1 = 0.900 to 0.949
2 = 0.800 to 0.899
3 = 0.700 to 0.799
4 = 0.500 to 0.699
0.8

**Fig. 2.** (Part 6).

**Table 3.** Results from screening *Cercospora* sp. Q strains with additional loci. The percentage similarity was calculated relative to strain CPC 5325, for which sequences were generated for all loci. The number of nucleotides used for the calculation of the similarity is shown in front of the percentage. For abbreviations of loci see Table 1 and in addition: GAPDH: partial glyceraldehyde-3-phosphate dehydrogenase gene; mtSSU: partial mitochondrial small rRNA gene; CHS: partial chitin synthase gene; TUB: partial beta-tubulin gene; Mcm7: partial gene encoding a mini-chromosome maintenance protein.

| Original name | Culture accession number(s) | Host name | Percentage similarity and allele group (I-VI) designation per locus | | | | | | | | | | GenBank accession numbers |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | GAPDH | | mtSSU | | CHS | | TUB | | Mcm7 | | (GAPDH, mtSSU, CHS, TUB, Mcm7) |
| *Cercospora apii* | CBS 113997; CPC 5325 | *Cajanus cajan* | 979 nt | I | 573 nt | I | 299 nt | I | 597 nt | I | 501 nt | I | JX142521, JX142504, JX142487, JX142478, JX142473 |
| *Cercospora apii* | CBS 115410; CPC 5331 | *Cajanus cajan* | 966 nt (100 %) | I | 573 nt (100 %) | I | 299 nt (100 %) | I | 597 nt (99 %) | I | — | | JX142522, JX142505, JX142488, JX142479, — |
| *Cercospora apii* | CBS 115411; CPC 5332 | *Cajanus cajan* | 966 nt (100 %) | I | 573 nt (100 %) | I | 299 nt (100 %) | I | 597 nt (99 %) | III | — | | JX142523, JX142506, JX142489, JX142480, — |
| *Cercospora apii* | CBS 115412; CPC 5333 | *Cajanus cajan* | 966 nt (100 %) | I | 573 nt (100 %) | I | 299 nt (100 %) | I | 322 nt (9,9 %) | III | — | | JX142524, JX142507, JX142490, JX142481, — |
| *Cercospora apii* | CBS 115536; CPC 5329 | *Cajanus cajan* | 970 nt (95 %) | V | 573 nt (100 %) | I | 299 nt (99 %) | II | 597 nt (99 %) | II | — | | JX142525, JX142508, JX142491, JX142482, — |
| *Cercospora apii* | CBS 115537; CPC 5330 | *Cajanus cajan* | 970 nt (95 %) | V | 573 nt (100 %) | I | 299 nt (99 %) | II | 597 nt (99 %) | II | — | | JX142526, JX142509, JX142492, JX142483, — |
| *Cercospora acaciae-mangii* | CPC 10550 | *Acacia mangium* | 979 nt (100 %) | I | 573 nt (100 %) | I | 299 nt (99 %) | II | 450 nt (99 %) | I | 501 nt (99 %) | II | JX142533, JX142516, JX142499, JX142484, JX142475 |
| *Cercospora acaciae-mangii* | CPC 10551 | *Acacia mangium* | 979 nt (99 %) | I | 573 nt (100 %) | I | 299 nt (99 %) | II | — | | 501 nt (99 %) | III | JX142534, JX142517, JX142500, —, JX142476 |
| *Cercospora* sp. 2 | CBS 132656; CPC 11536 | *Acacia mangium* | 961 nt (96 %) | III | 573 nt (100 %) | I | 299 nt (99 %) | II | — | | — | | JX142527, JX142510, JX142493, —, — |
| *Cercospora* sp. 2 | CPC 11539 | *Acacia mangium* | 958 nt (96 %) | III | 573 nt (100 %) | I | 299 nt (99 %) | II | — | | — | | JX142535, JX142518, JX142501, —, — |
| *Cercospora dioscoreae-pyrifoliae* | CBS 132661; CPC 11634; PNG-002 | *Dioscorea rotundata* | 970 nt (95 %) | VI | 573 nt (100 %) | I | 298 nt (99 %) | II | — | | 458 nt (99 %) | III | JX142528, JX142511, JX142494, —, JX142474 |
| *Cercospora dioscoreae-pyrifoliae* | CBS 132663; CPC 11636; PNG-016 | *Dioscorea esculenta* | 969 nt (96 %) | IV | 573 nt (100 %) | I | 299 nt (99 %) | II | — | | — | | JX142529, JX142512, JX142495, —, — |
| *Cercospora dioscoreae-pyrifoliae* | CPC 11639; PNG-037 | *Dioscorea rotundata* | 969 nt (95 %) | VI | 573 nt (100 %) | I | 299 nt (99 %) | II | — | | — | | JX142536, JX142519, JX142502, —, — |
| Cercosporoid | CBS 132679; CPC 15807 | *Phaseolus vulgaris* | 954 nt (100 %) | I | 573 nt (100 %) | I | 299 nt (99 %) | III | — | | — | | JX142530, JX142513, JX142496, —, — |
| *Cercospora* sp. | CBS 132681; CPC 15844 | *Euphorbia* sp. | 956 nt (96 %) | III | 573 nt (100 %) | I | 299 nt (99 %) | III | — | | — | | JX142531, JX142514, JX142497, —, — |
| *Cercospora* sp. | CBS 132682; CPC 15850 | *Taraxacum* sp. | 960 nt (100 %) | I | 573 nt (100 %) | I | 299 nt (99 %) | II | — | | — | | JX142532, JX142515, JX142498, —, — |
| *Cercospora* sp. | CPC 15875 | *Euphorbia* sp. | 955 nt (99 %) | II | 573 nt (100 %) | I | 299 nt (99 %) | III | 597 nt (99 %) | III | — | | JX142537, JX142520, JX142503, JX142485, — |
| *Septoria provencialis* (outgroup) | CBS 118910; CPC 12226 | *Eucalyptus* sp. | 885 nt (87 %) | | — | | — | | 502 nt (82 %) | | 499 nt (81 %) | | JX142538, —, —, JX142486, JX142477 |
| ***Number of identical sequences (excl. outgroup)***: | | | 6 of 17 | | 17 of 17 | | 4 of 17 | | 0 of 8 | | 0 of 4 | | |

**Table 3.** (Continued).

| Original name | Culture accession number(s) | Host name | Percentage similarity and allele group (I-VI) designation per locus | | | | | | | | | | GenBank accession numbers |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | ITS | | TEF | | ACT | | CAL | | HIS | | (ITS, TEF, ACT, CAL, HIS) |
| *Cercospora apii* | CBS 113997; CPC 5325 | *Cajanus cajan* | 481 nt | I | 306 nt | I | 221 nt | I | 312 nt | I | 378 nt | I | JX143717, JX143476, JX143230, JX142984, JX142738 |
| *Cercospora apii* | CBS 115410; CPC 5331 | *Cajanus cajan* | 481 nt (100 %) | I | 280 nt (100 %) | I | 194 nt (100 %) | I | 280 nt (100 %) | I | 378 nt (100 %) | I | JX143718, JX143477, JX143231, JX142985, JX142739 |
| *Cercospora apii* | CBS 115411; CPC 5332 | *Cajanus cajan* | 481 nt (100 %) | I | 280 nt (100 %) | I | 194 nt (100 %) | I | 280 nt (100 %) | I | 378 nt (100 %) | I | JX143719, JX143478, JX143232, JX142986, JX142740 |
| *Cercospora apii* | CBS 115412; CPC 5333 | *Cajanus cajan* | 481 nt (100 %) | I | 280 nt (100 %) | I | 194 nt (100 %) | I | 280 nt (100 %) | I | 378 nt (100 %) | I | JX143720, JX143479, JX143233, JX142987, JX142741 |
| *Cercospora apii* | CBS 115536; CPC 5329 | *Cajanus cajan* | 481 nt (100 %) | I | 280 nt (100 %) | I | 194 nt (100 %) | I | 278 nt (100 %) | I | 378 nt (98 %) | III | JX143721, JX143480, JX143234, JX142988, JX142742 |
| *Cercospora apii* | CBS 115537; CPC 5330 | *Cajanus cajan* | 481 nt (100 %) | I | 280 nt (100 %) | I | 194 nt (100 %) | I | 280 nt (100 %) | I | 378 nt (98 %) | III | JX143722, JX143481, JX143235, JX142989, JX142743 |
| *Cercospora acaciae-mangii* | CPC 10550 | *Acacia mangium* | 481 nt (99 %) | II | 306 nt (100 %) | I | 221 nt (99 %) | II | 312 nt (100 %) | I | 377 nt (99 %) | IV | AY752139, AY752172, AY752200, AY752231, AY752262 |
| *Cercospora acaciae-mangii* | CPC 10551 | *Acacia mangium* | 481 nt (99 %) | II | 306 nt (100 %) | I | 221 nt (99 %) | IV | 305 nt (100 %) | I | 377 nt (100 %) | I | AY752140, AY752173, AY752201, AY752232, AY752263 |
| *Cercospora* sp. 2 | CBS 132656; CPC 11536 | *Acacia mangium* | 473 nt (99 %) | III | 306 nt (100 %) | I | 221 nt (99 %) | IV | 312 nt (100 %) | I | 378 nt (99 %) | IV | JX143723, JX143482, JX143236, JX142990, JX142744 |
| *Cercospora* sp. 2 | CPC 11539 | *Acacia mangium* | 481 nt (99 %) | III | 306 nt (100 %) | I | 221 nt (99 %) | IV | 312 nt (100 %) | I | 378 nt (98 %) | V | JX143729, JX143488, JX143242, JX142996, JX142750 |
| *Cercospora dioscoreae-pyrifoliae* | CBS 132661; CPC 11634; PNG-002 | *Dioscorea rotundata* | 481 nt (99 %) | III | 284 nt (100 %) | I | 221 nt (99 %) | II | 297 nt (100 %) | I | 378 nt (99 %) | VI | JX143724, JX143483, JX143237, JX142991, JX142745 |
| *Cercospora dioscoreae-pyrifoliae* | CBS 132663; CPC 11636; PNG-016 | *Dioscorea esculenta* | 481 nt (99 %) | III | 306 nt (100 %) | I | 221 nt (99 %) | II | 303 nt (100 %) | I | 378 nt (99 %) | VI | JX143725, JX143484, JX143238, JX142992, JX142746 |
| *Cercospora dioscoreae-pyrifoliae* | CPC 11639; PNG-037 | *Dioscorea rotundata* | 481 nt (99 %) | II | 306 nt (100 %) | I | 221 nt (99 %) | II | 303 nt (100 %) | I | 378 nt (99 %) | II | JX143730, JX143489, JX143243, JX142997, JX142751 |
| Cercosporoid | CBS 132679; CPC 15807 | *Phaseolus vulgaris* | 481 nt (99 %) | II | 294 nt (99 %) | II | 220 nt (99 %) | III | 312 nt (100 %) | I | 376 nt (99 %) | VI | JX143726, JX143485, JX143239, JX142993, JX142747 |
| *Cercospora* sp. | CBS 132681; CPC 15844 | *Euphorbia* sp. | 481 nt (99 %) | III | 294 nt (99 %) | II | 220 nt (99 %) | III | 312 nt (99 %) | II | 376 nt (100 %) | I | JX143727, JX143486, JX143240, JX142994, JX142748 |
| *Cercospora* sp. | CBS 132682; CPC 15850 | *Taraxacum* sp. | 481 nt (99 %) | II | 294 nt (99 %) | II | 220 nt (99 %) | III | 312 nt (100 %) | I | 377 nt (100 %) | VI | JX143728, JX143487, JX143241, JX142995, JX142749 |
| *Cercospora* sp. | CPC 15875 | *Euphorbia* sp. | 481 nt (99 %) | III | 294 nt (99 %) | II | 220 nt (99 %) | III | 312 nt (100 %) | I | 378 nt (99 %) | VI | JX143731, JX143490, JX143244, JX142998, JX142752 |
| *Septoria provencialis* (outgroup) | CBS 118910; CPC 12226 | *Eucalyptus* sp. | 483 nt (98 %) | | 317 nt (75 %) | | 227 nt (87 %) | | 329 nt (81 %) | | 386 nt (93 %) | | DQ303096, JX143522, JX143276, JX143030, JX142784 |
| ***Number of identical sequences (excl. outgroup)***: | | | 6 of 17 | | 13 of 17 | | 6 of 17 | | 16 of 17 | | 7 of 17 | | |

## Evaluation of additional loci

Isolates of *Cercospora* sp. Q were compared using the five loci used for the combined phylogeny and five additional loci as explained in the Materials and Methods. The results are summarised in Table 3 and detailed per locus below:

ITS — Three allele groups are identified based on sequence identity. The variation in this locus is based on nucleotide changes at only two positions in the second internal transcribed spacer (transitions at positions 451 and 453 compared to the sequence of isolate CPC 5325). Although allele group I was confined to isolates from *Cajanus* (*Fabaceae*), the other two groups were intermixed amongst the remaining host genera.

TEF — Two allele groups are identified based on sequence identity. The variation in this locus is based on a single nucleotide change (transitions at position 289 compared to the sequence of isolate CPC 5325). Although allele group I was confined to isolates from *Acacia* (*Fabaceae*), *Cajanus*, and *Dioscorea* (*Dioscoreaceae*), the other group represents the remaining host genera.

ACT — Four allele groups are identified based on sequence identity. The variation in this locus is based on nucleotide changes at three positions (transitions at positions 143, 166 and 173 compared to the sequence of isolate CPC 5325). Allele group I was confined to isolates from *Cajanus*, and allele group II is mainly limited to *Dioscorea* (except for one isolate from *Acacia*), allele group IV is limited to the remaining isolates from *Acacia*, and the remaining host genera belong to allele group III.

CAL — Two allele groups are identified based on sequence identity. The variation in this locus is based on a single nucleotide change (a transition at position 76 compared to the sequence of isolate CPC 5325). This single nucleotide change only occurred in isolate CPC 15844; the rest of the isolates had identical CAL sequences.

HIS — Six allele groups are identified based on sequence identity. The variation in this locus is based on nucleotide changes at 10 positions (transitions at positions 106, 112, 148, 149, 178, 205, 238, 301 and 364, as well as a transversion at position 245 compared to the sequence of isolate CPC 5325). Allele group II differs from allele group I by a unique change of C to T at position 364 and allele group V differs from allele group IV by a unique change of A to T at position 245. Even if allele group I and II and group IV and V are taken as combined groups, isolates from different hosts are intermixed and no clear association of host with allele group, as with the loci mentioned above, is possible.

GAPDH — Six allele groups are identified based on sequence identity. The variation in this locus is based on numerous nucleotide changes (transitions at positions 44, 48–49, 52–53, 56, 63–69, 110, 122, 149, 158, 206, 257, 287, 329, 335, 395, 440, 479, 530, 533, 566, 593, 596, 608, 647, 650, 674, 720, 731, 740, 747, 780, 789, 791–792, 794, 804–806, 808–809, 811–812, 817, 821–822, 824, 830, 834, 837, 839–840, 842–844, 846, 848, 852, 856, 874, 922 and 958, transversions at positions 49, 66, 233, 767, 785, 787–789, 792, 795, 797, 798, 806, 810–811, 814, 818–819, 821, 831, 833, 843, 848–849, 865 and 883, indels at positions 67, 101 and 803, as well as another indel spanning 801–811, compared to the sequence of isolate CPC 5325). Allele group II differs from allele group I by a unique change of C to T at position 530. This locus represents the largest number of nucleotide substitutions of all the loci included for *Cercospora* sp. Q in this study, and therefore has high potential for species discrimination. However, if each allele group is accepted as a distinct species, it would result in a huge proliferation of taxa within this group.

mtSSU — Only one allele group is identified based on sequence identity. No variation was observed over the 573 nucleotides sequences for the selected isolates.

CHS — Three allele groups are identified based on sequence identity. The variation in this locus is based on nucleotide changes at only three positions (transitions at positions 91, 100 and 217 compared to the sequence of isolate CPC 5325). Allele group I includes four of the six isolates from *Cajanus* and allele group III includes the isolates from *Phaseolus* (*Fabaceae*) and *Euphorbia* (*Euphorbiaceae*); the remaining isolates belong to allele group II.

TUB — This locus failed to amplify easily, even when several different primer combinations were tested. Three allele groups are identified based on sequence identity. The variation in this locus is based on nucleotide changes at six positions (transitions at positions 147 and 396, transversions at positions 172, 189, 213 and 591 compared to the sequence of isolate CPC 5325). The majority of sequences were obtained for the isolates from *Cajanus*, and these isolates end up belonging into all three allele groups.

Mcm7 — This locus failed to amplify easily, even when both available primer combinations were tested. Three allele groups are identified based on sequence identity. The variation in this locus is based on nucleotide changes at six positions (transitions at positions 60, 86, 263, 365 and 470, and a transversion at position 89, compared to the sequence of isolate CPC 5325). Due to the small number of successful sequences, a clear conclusion cannot be drawn from this dataset and it was not possible to distinguish between the isolates from *Acacia* and *Dioscorea*.

## TAXONOMY

In this paper, a polyphasic approach was taken and species are discussed and/or described with consideration to the following factors:

*Phylogenetic analyses*: Based on the clustering and support in the Bayesian tree obtained from the combined ITS, TEF, ACT, CAL and HIS alignment (Fig. 2). All genes were also assessed individually (data not shown; discussed where applicable in the species notes).

*Morphological characteristics*: A few morphological characteristics effectively distinguished species (Fig. 3). These are: conidiophores (uniform, irregular, attenuated, truncate, long or short obconically truncate), conidiogenous cells (terminal, intercalary), loci (apical, lateral, circumspersed (all around the conidiogenous cell; Hennebert & Sutton 1994); uni-local (single, terminal locus), multi-local (multiple loci); thickness, absence of protuberant loci), and conidia (dimensions, shape, hilum morphology).

A diagnostic characteristic of species with wide host ranges was circumspersed loci on tenuous conidiophores, whereas the species with narrow host ranges had a few distinct apical or lateral

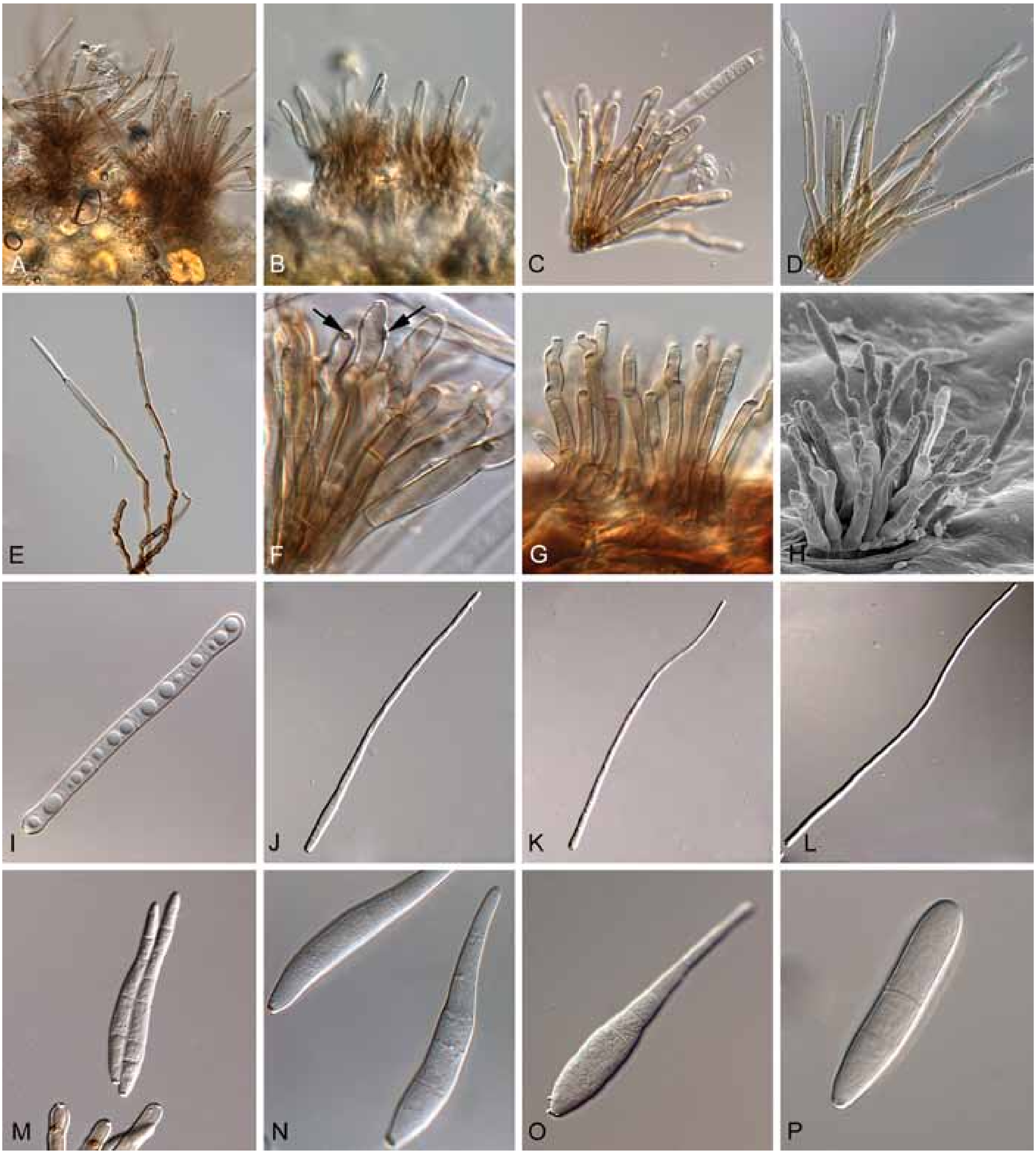



**Fig. 3.** Overview of morphological structures. A. Fasciculate conidiophores situated on a stroma. B. Conidiophores reduced to uni-local conidiogenous cells. C. Conidiophores arising from a weakly developed stroma. D. Fasciculate conidiophore with flexuous conidiophores. E. Conidiophores arising from external mycelium. F. Thickened, darkened and somewhat refractive conidial loci (arrows). G. Conidiogenous cells with multi-local loci. H. Fascicle erumpent through stoma. I. Cylindrical conidium with obtuse apex. J. Filiform conidium. K, L. Acicular, undulate conidia with subobtusely rounded apices, and truncate bases. M–O. Obclavate conidia with subobtusely rounded apices and obconically truncate bases. P. Subcylindical conidium with long obconically truncate base.

loci on moderately thick-walled to thick-walled conidiophores. These characteristics were preserved, even when the fungus was cultivated on agar medium.

The Bayesian analysis resulted in 73 species clades mapped onto the phylogenetic tree (Fig. 2); 34 of these were assigned to an existing species name, 15 more were morphologically similar to existing species but names could not be applied without doubt (indicated with "cf." in the species name, see species notes below), a further 19 could not be named unequivocally ("*Cercospora* spp. A–S") and novel species are introduced below for the remaining five clades.

***Cercospora achyranthis*** Syd. & P. Syd., Ann. Mycol. 7: 171. 1909.

*Caespituli* amphigenous, mainly hypophyllous. *Mycelium* internal. *Stromata* lacking or composed of a few brown cells, intraepiderimal or substomatal. *Conidiophores* thick-walled, dark brown, arising from internal hyphae or a few brown cells, solitary, or in loose fascicles (2–5), straight, sinuous to distinctly geniculate, flexuous, almost uniform in width, somewhat wider at the apex, often constricted at septa and proliferating point, conical at the apex, simple, sometimes branched, 31–340 × 4.5–6 µm, 2–20-septate. *Conidiogenous cells* integrated, terminal and intercalary, proliferating sympodially, multi-local; loci distinctly thickened, darkened, slightly to distinctly protuberant, apical or formed on shoulders caused by geniculation, 2–3 µm diam. *Conidia* solitary, subhyaline, acicular, cylindrical to cylindro-obclavate, straight to slightly curved, long obconically truncated and thickened at the base, obtuse at the apex, rarely constricted at the septa, 33–172 × 3.5–8 µm, 3–20-septate.

*Specimens examined*: **South Korea**, Jeju, on *Achyranthes japonica* (*Amaranthaceae*), 14 Sep. 2002, H.D. Shin, CBS H-20983, CPC 10088–10091; on *A. japonica*, 13 Nov. 2003, H.D. Shin, CBS H-20984, CBS 132613 = CPC 10879, CPC 10880–10881.

*Notes*: This species is characterised by conidiophores with a thickened, dark brown wall, vary in shape, often constricted at septa, and conical at the apex, sometimes branched, and longer than in most other species (31–340 × 4.5–6 µm, 2–20-septate). The conidia of *C. achyranthis* are not hyaline, but subhyaline to pale olivaceous and have rather small hila (*ca*. 2 µm wide), which are reminiscent of the genus *Passalora*. Nevertheless, it is a true *Cercospora*. *Cercospora achyranthis* is supported by ACT. The TEF and CAL phylogenies fail to discriminate *C. sojina* (also with subhyaline conidia and small hila) from *C. achyranthis*. On the HIS phylogeny, it is indistinguishable from *C. polygonaceae*, to which it is also a sister taxon in the combined tree (Fig. 2 part 2). The name *C. achyranthis* is based on Japanese material, and fresh collections from Japan would be required to designate an epitype for this taxon.

## ***Cercospora agavicola*** Ayala-Escobar, Mycotaxon 93: 117. 2005.

*Specimen examined*: **Mexico**, State of Guanajuato, Penjamo, on *Agave tequilana* var. *azul* (*Agavaceae*), Jan. 2003, V. Ayala-Escobar and Ma. de Jesús Yáñez-Morales, **holotype** CHAPA # 166, **isotype** HAL 1839 F, culture ex-type CBS 117292 = CPC 11774.

*Notes*: *Cercospora agavicola* is characterised by large stromata and consistently cylindrical conidia, often with swollen tips (Ayala-Escobar *et al*. 2005). In this study using a larger dataset, it is also clear that *C. agavicola*, which is supported by TEF, ACT, CAL and HIS regions, is genetically distinct from the other *Cercospora* species studied. In the combined tree (Fig. 2 part 1), it is a sister taxon to *C.* cf. *coreopsidis*.

## ***Cercospora alchemillicola*** U. Braun & C.F. Hill, Mycol. Progr. 1: 19. 2002.

*Specimens examined*: **New Zealand**, Auckland, Western Springs Gardens, on *Alchemilla mollis* (*Rosaceae*), 23 Jul. 2000, C.F. Hill, Lynfield 236 (holotype HAL, isotype PDD 73031); on *A. mollis*, C.F. Hill, Lynfield 564, **epitype designated here** CBS H-20985, culture ex-epitype CPC 5259.

*Notes*: Sequences from New Zealand on hosts of *Onagraceae* (*Gaura*, isolate CPC 5127, and *Oenothera*, isolate CPC 5126) are slightly distinct from that derived from *Alchemilla* (*Rosaceae*). The collections on *Onagraceae* (*C.* cf. *alchemillicola*) are also morphologically different from *C. alchemillicola*, and represent an undescribed species. The three isolates are identical to one another on the TEF, ACT, CAL and HIS phylogenies but also to some other species, *e.g.* to *Cercospora* sp. I, *C.* cf. *physalidis* and *C. celosiae* based on the TEF phylogeny, and *Cercospora* sp. I and *C.* cf. *physalidis* based on the ACT phylogeny. A similar mix is observed in the HIS phylogeny with *Cercospora* sp. I and *C. celosiae* and in the CAL phylogeny with *Cercospora* spp. M, O, P, Q and *C.* cf. *sigesbeckiae*. In the combined tree (Fig. 2 part 4), the three isolates represent sister taxa.

## ***Cercospora* cf. *alchemillicola***

*Specimens examined*: **New Zealand**, Auckland City, Albert Park, on *Gaura lindheimeri* (*Onagraceae*), C.F. Hill, Lynfield 545, CPC 5127; on *Oenothera fruticosa* (*Onagraceae*), C.F. Hill, Lynfield 541, CPC 5126.

*Notes*: *Cercospora* on *Gaura* and *Oenothera* in New Zealand cannot be distinguished on the individual gene trees from *C. alchemillicola* (see species notes under that species above) described from New Zealand on *Alchemilla mollis* (Braun & Hill 2002). We consider the latter two isolates to represent a distinct species, which cannot be formally named due to the absence of good specimens. In the combined tree (Fig. 2 part 4), it is a sister taxon to *C. alchemillicola*.

## ***Cercospora althaeina*** Sacc., Michelia 1: 269. 1878.

= *Cercospora kellermanii* Bubák, J. Mycol. 9: 3. 1903.
= *Cercospora althaeina* var. *praecincta* Davis, Trans. Wisconsin Acad. Sci. 18: 260. 1915.
≡ *Cercospora praecincta* (Davis) Chupp, A monograph of the fungus genus *Cercospora*: 376. 1954.
= *Cercospora ramularia* Siemaszko, Izv. Kavkazsk. Muz.12: 28. 1919, and Arch. Nauk Biol. Towarz. Nauk. Warszawsk. 1: 49. 1923.
≡ *Cercosporina ramularia* (Siemaszko) Sacc., Syll. Fung. 25: 910. 1931.
= *Cercospora althaeina* var. *althaeae-officinalis* Săvul. & Sandu, Hedwigia 73: 127. 1933.
= *Cercospora althaeicola* J.M. Yen & S.K. Sun, Cryptog. Mycol. 4: 189. 1983.

*Leaf spots* distinct, angular to irregular, mostly vein-limited, olivaceous-brown, sometimes greyish brown with dark brown margin, centre becoming pale grey with black dots (= stroma with conidiophores). *Caespituli* amphigenous, mostly epiphyllous. *Mycelium* internal. *Stromata* well-developed, emerging through stomatal openings or erumpent through the cuticle. *Conidiophores* in divergent fascicles (6–12), pale olivaceous-brown at the base, paler upwards, 0–3-septate, straight to mildly curved, 32–90 × 4–6.5 µm, conically narrowed at the apex; loci 1.5–2 µm wide, conspicuous, apical or on shoulders formed by geniculation. *Conidia* solitary, obclavate-cylindrical to filiform, not acicular, straight to mildly curved, hyaline, 1–10-septate, obtuse at the apex, subtruncate or obconically truncate at the base, 40–140 × 3.5–5 µm (adapted from Shin & Kim 2001).

*Specimens examined*: **Italy**, Selva, on *Althaea rosea*, 1876, **holotype** in PAD. **Romania**, Fundulea, on *A. rosea*, O. Constantinescu, **epitype designated here** CBS H-9811, culture ex-epitype CBS 248.67 = CPC 5117. **Unknown**, on *Malva* sp. (*Malvaceae*), C. Killian, CBS 126.26 = CPC 5066, (as *C. malvacearum*). **South Korea**, Suwon, on *Althaea rosea* (*Malvaceae*), 14 Oct. 2003, H.D. Shin, CBS H-20986, CBS 132609 = CPC 10790.

*Notes*: A true *Cercospora s. str.* close to *C. apii s. lat.*, but distinguished by obclavate-cylindrical conidia with obconically truncate bases (Crous & Braun 2003). Although only weakly supported as distinct from *C. armoraciae*, we suspect that the isolate from *Malva* sp. represents a different taxon. Further isolates and pathogenicity studies are needed to test this hypothesis. The species is distinguished in the TEF and ACT phylogenies but cannot be distinguished from *C. zebrina*, *Cercospora* sp. L and

*C. rumicis* based on the CAL phylogeny. In the HIS phylogeny the three isolates are not identical to any other species but the isolate from *Malva* sp. clusters distinct from the two *A. rosea* isolates which form a sister clade to *C. chenopodii*. In the combined tree (Fig. 2 part 3), it is a sister taxon to *C. zebrina*.

## ***Cercospora apii*** Fresen., emend. Groenewald *et al*. Phytopathology 95: 954. 2005.

*Caespituli* amphigenous. *Mycelium* internal. *Stromata* lacking or small, up to 32 µm diam, brown, substomatal or intraepidermal. *Conidiophores* arising from upper part of stromata or internal hyphae, solitary to 2–8, in loose to dense fascicles, brown, paler towards the apex, simple, mildly sinuous, moderately thick-walled to thick-walled, straight or once abruptly geniculate caused by sympodial proliferation, slightly curved, uniform in width, wider at the base, short conically truncate or truncate at the apex, 12.5–160 × 5–8 µm. *Conidiogenous cells* integrated, terminal or intercalary, proliferating sympodially, chiefly uni-local; loci distinctly thickened, not or slightly protuberant, 2–4 µm diam, apical or formed on the shoulder caused by sympodial proliferation. *Conidia* solitary, hyaline, cylindro-obclavate when shorter, longer conidia usually acicular, straight to slightly curved, subacute to obtuse at the apex, truncate to obconically truncate and thickened at the base, 35–120 × 3.5–5 µm, 3–10-septate.

*Specimens examined*: **Austria**, Wien, on *Beta vulgaris* (*Chenopodiaceae*), Jun. 1931, E.W. Schmidt, CBS 121.31 = CPC 5073; on *Apium* sp. (*Apiaceae*), 28 Aug. 2003, Institut fur Pflanzengesundheit, CBS 114416 = CPC 10925. **Germany**, Landwirtschaftsamt, Heilbron, on *Apium graveolens* (*Apiaceae*), K. Schrameyer, culture ex-type CBS 116455 = CPC 11556; CBS 116504 = CPC 11579; CBS 116507 = CPC 11582. **Hungary**, on *B. vulgaris*, Jun. 1931, E.W. Schmidt, CBS 127.31 = CPC 5119. **Italy**, on *A. graveolens*, M. Meutri, CBS 114418 = CPC 10924; CBS 114485 = CPC 10923. **Japan**, Aichi, on *A. graveolens*, 1 Nov. 1995, T. Kobayashi, MUCC 567 = MAFF 238072 = MUCNS 30 (named as *C. apii s. str.*); Shizuoka, on *A. graveolens*, 8 Jun. 2007, M. Togawa, MUMH 10802, MUCC 593; Saga, on *Asparagus officinalis* (*Asparagaceae*), 20 Sep. 1999, J. Yamaguchi, MUMH 11400, MUCC 923 = MAFF 238299; Hokkaido, on *Glebionis coronaria* (≡ *Chrysanthemum coronarium*) (*Asteraceae*), Aug. 1989, MUCC 573 = MAFF 235978. **Netherlands**, Bergen op Zoom, on *B. vulgaris*, Sep. 1951, G. van den Ende, CBS 152.52 = IMI 077043 = MUCL 16495 = CPC 5063. **New Zealand**, Auckland, on *Glebionis coronaria* (≡ *Chrysanthemum coronarium*), C.F. Hill, Lynfield 566, CPC 5260; on *Moluccella laevis* (*Lamiaceae*), C.F. Hill, Lynfield 516, CPC 5112. **Romania**, Hagieni, distr. Constanta, on *Plumbago europaea* (*Plumbaginaceae*), 13 Jun. 1970, O. Constantinescu, CBS 553.71 = IMI 161116 = CPC 5083 (as *C. plumbaginea*); Bucuresti, on *A. graveolens*, 2 Oct. 1969, O. Constantinescu, CBS H-9812, CBS 536.71 = CPC 5087; Domnesti, on *Plantago lanceolata* (*Plantaginaceae*), 3 Aug. 1965, O. Constantinescu, CBS 252.67 = CPC 5084. **Unknown**, on *A. graveolens*, Mar. 1925, L.J. Klotz, CBS 119.25 = B 42463 = IHEM 3822 = CPC 5086. **USA**, California, on *M. laevis*, S.T. Koike, CBS 110816 = CPC 5111; CBS 110813 = CPC 5110; California, on *A. graveolens*, 27 Sep. 2010, S.T. Koike, CPC 18601. **Zimbabwe**, on *M. laevis*, 13 May 2009, S. Dimbi, CBS 132683 = CPC 16663.

*Notes*: Various investigators have demonstrated that great variation in the size and shape of conidiophores and conidia (conidiophores: 25–300 × 3.5–9 µm, rarely branched, conidia: 25–315 × 3–6 µm, cylindrical, filiform to acicular) is induced by changes in environmental conditions, especially humidity. Crous & Braun (2003) pointed out these morphological ambiguities, and introduced a concept of *Cercospora apii s. lat*., for taxa morphologically indistinguishable from *Cercospora apii* on *A. graveolens*. *Cercospora apii s. str*., which is phylogenetically distinct, is characterised in that its conidiophores are almost uniform in width, moderately thick-walled or thick-walled, short obconically truncate at the apex, and with a few loci on integrated conidiogenous cells, and long-cylindrical to cylindrical-obclavate to often acicular conidia with truncate or obconically truncate basal ends and subacute to obtuse apices.

According to Crous & Braun (2003), the host plants of *C. apii s. str*. are found in more than 86 genera of several plant families. Groenewald *et al*. (2006a) concluded that *C. apii s. str*., which is mainly isolated from celery, has a wide host range, because numerous isolates of *C. apii s. lat.* originating from various host plants have similar nucleotide sequences to the type strain of *C. apii s. str*.

In principle, the phylogenetic split observed between *C. beticola* and *C. apii* is only supported by the CAL sequences, and for the other genes these two taxa cluster as a large unresolved clade. Groenewald *et al*. (2005) showed that these two species are also distinguished by their AFLP fingerprints and growth conditions, suggesting that they were operational species units with a different ecology. These results indicate that in many cases morphologically identical species occurring on different hosts in fact represent different species. The situation is complicated in that there are several species with wide host ranges. Other species can colonise dead material of non-hosts, facilitating what has been described as a pogostick hypothesis (Crous & Groenewald 2005), until they locate their ideal hosts on which they are primary pathogens. In the present study it was further found that the CAL phylogeny fails to distinguish *C. apii s. str.* from *C.* cf. *brunkii* and *C.* cf. *resedae*, which are sister taxa in the combined tree (Fig. 2 part 5).

## ***Cercospora apiicola*** M. Groenew., Crous & U. Braun, Mycologia 98: 281. 2006.

*Leaf spots* amphigenous, subcircular to irregular, 3–10 mm diam, medium brown, with a raised or inconspicuous, indefinite margin, not surrounded by a border of different colour. *Caespituli* amphigenous, but primarily hypophyllous. *Stromata* lacking to well-developed, 30–60 µm diam, medium brown. *Conidiophores* in fascicles (4–10), moderately dense, arising from stromata, emerging through stomata or erumpent through the cuticle, subcylindrical, upper part geniculate-sinuous, unbranched, 1–3-septate, 25–70 × 4–6 µm, medium brown, becoming pale brown towards the apex, smooth, wall somewhat thickened. *Conidiogenous cells* integrated, terminal, 15–30 × 4–5 µm, occasionally unilocal, usually multilocal, sympodial; loci subcircular, planate, thickened, darkened, refractive, 2.5–3 µm wide. *Conidia* solitary, cylindrical when small, obclavate-cylindrical when mature, not acicular, (50–)80–120(–150) × (3–)4–5 µm, 1–6(–18)-septate; apex subobtuse, base obconically subtruncate; hila 2–2.5 µm wide, thickened, darkened, refractive.

*Specimens examined*: **Greece**, on *Apium graveolens*, 2000, I. Vloutoglou, CBS 132666 = CPC 11642; CPC 11641. **South Korea**, Kangnung, on *A. graveolens*, 20 Sep. 2003, H.D. Shin, CPC 10666; Namyangju, on *A. graveolens*, 30 Sep. 2003, CBS 116458 = CPC 10657; on *A. graveolens*, 22 Oct. 2003, H.D. Shin, CBS 132651 = CPC 10759. **Venezuela**, La Guanota, Caripe, Edo. Monagas, 1050 m.s.n.m., on *Apium* sp., 23 Jul. 2002, N. Pons, **holotype** CBS H-18473, culture ex-type CBS 116457 = CPC 10267; CBS 132644 = CPC 10248; CPC 10220; CPC 10265–10266; CPC 10279; CPC 10666.

*Notes*: Morphologically *C. apiicola* differs from *C. apii s. str.* in having multiple conidiogenous loci and long conically truncate conidiogenous cells (Groenewald *et al*. 2006a). It has a high degree of phylogenetic independence from other species of *C. apii s. lat.* supported by TEF, ACT, CAL and HIS regions. It is also clearly distinct from *C. apii* in the combined tree (Fig. 2 part 2 vs. part 5).

## ***Cercospora armoraciae*** Sacc., Nuovo Giorn. Bot. Ital. 8: 188. 1876.

= ?*Cercospora cheiranthi* Sacc., Nuovo Giorn. Bot. Ital. 8: 187. 1876.

= *Cercospora nasturtii* Pass., Hedwigia 16: 124. 1877.
= *Cercospora nasturtii* subsp. *barbareae* Sacc., Michelia 2: 557. 1882.
≡ *Cercospora barbareae* (Sacc.) Chupp, Farlowia 1: 579. 1944.
= *Cercospora bizzozeriana* Sacc. & Berl., Malpighia 2: 248, 1888.
= *Cercospora atrogrisea* Ellis & Everh., Proc. Acad. Nat. Sci. Phiadelphia 45: 464. 1894.
= *Cercospora bizzozeriana* var. *drabae* Sausa da Câmara, Revista Agron. (Lisbon) 1: 25. 1903.
= *Cercospora berteroae* Hollós, Ann. Mus. Nat. Hung. 5: 468. 1907.
= *Cercospora drabae* Bubák & Kabát, Hedwigia 52: 362. 1912.
≡ *Cercosporina drabae* (Bubák & Kabát) Sacc., Syll. Fung. 25: 900. 1931.
= *Cercospora camarae* Curzi, Atti Ist. Bot. Univ., Pavia, III, 2: 101. 1925.
= *Cercospora cardamines* Losa (as "*cardaminae*"), Anales Jard. Bot. Madrid 6: 453. 1946.
= *Cercospora lepidii* Niessl, unknown, *in herb.*, HBG fide Chupp (1954, p. 180).

*Caespituli* amphigenous. *Mycelium* internal. *Stromata* lacking to well-developed, up to 60 µm diam, brown, substomatal or intraepidermal. *Conidiophores* arising from internal hyphae or a few brown cells, cylindrical, solitary, or in loose to divergent fascicles (2–30), pale to pale brown, paler towards apex, moderately thick-walled, simple, straight to strongly geniculate, irregular in width, often narrowed with successive geniculation, truncate or conically truncate at the tip, sometimes constricted at septa, 13–135 × 2.5–7.5 µm, 0–7-septate. *Conidiogenous cells* integrated, terminal, intercalary, proliferating sympodially, uni-local to multi-local (1–3); loci conspicuous, apical or on shoulder of conidiogenous cells caused by geniculation, rarely lateral, distinctly thickened, somewhat protuberant, refractive or darkened, 1.8–3.5 µm diam. *Conidia* solitary, hyaline, straight to mildly curved, cylindrical, cylindro-obclavate to acicular, obconically truncate or truncate, distinctly thickened at the base, obtuse at the apex, 15–125 × 2.5–6 µm, 1–11-septate.

*Specimens examined*: **Italy**, Venice, on *Armoracia rusticana* (= *A. lapathifolia*) (*Brassicaceae*), Treviso, Sep. 1874, (**syntype** Mycoth. Ven. 282, in B, HBG, S). **Japan**, Okinawa, on *A. rusticana* (= *A. lapathifolia*), 19 Nov. 2007, C. Nakashima, MUMH 10820, MUCC 768. **New Zealand**, Auckland, Grey Lynn, on *Nasturtium officinale* (= *Rorippa nasturtium-aquaticum*) (*Brassicaceae*), 14 Apr. 2002, C.F. Hill, Lynfield 576, CBS H-20988, CBS 115394 = CPC 5261 (named as *C. nasturtii*); Manurewa, on *A. rusticana* (= *A. lapathifolia*), C.F. Hill, Lynfield 622, CBS 115409 = CPC 5359 (as *C. armoraciae*); on *Gaura* sp. (*Onagraceae*), C.F. Hill, Lynfield 634, CBS 115060 = CPC 5366. **Romania**, Fundulea, on *A. rusticana* (= *A. lapathifolia*), O. Constantinescu, **epitype designated here** CBS H-20987, culture ex-epitype CBS 250.67 = CPC 5088; Fundulea, on *Cardaria draba* (*Brassicaceae*), O. Constantinescu, CBS 258.67 = CPC 5061 (as *C. bizzozeriana*); Hagieni, on *Berteroa incana* (*Brassicaceae*), O. Constantinescu, CBS 538.71 = IMI 161109 = CPC 5090 (as *C. berteroae*); Hagieni, on *C. draba*, O. Constantinescu, CBS 540.71 = IMI 161110 = CPC 5060 (as *C. bizzozeriana*); Hagieni, on *Coronilla varia* (*Fabaceae*), O. Constantinescu, CBS 555.71 = IMI 161117 = CPC 5082 (as *C. rautensis*); Valea Mraconiei, on *Erysimum cuspidatum* (*Brassicaceae*), O. Constantinescu, CBS 545.71 = CPC 5056 (as *C. erysimi*). **South Korea**, Hoengseong, on *Turritis glabra* (≡ *Arabis glabra*) (*Brassicaceae*), 23 Jun. 2004, H.D. Shin, CBS H-20989, CBS 132654 = CPC 11338 (as *C. nasturtii*); CPC 11364 (as *C. nasturtii*); Jecheon, on *Rorippa indica* (*Brassicaceae*), 19 Oct. 2007, H.D. Shin, CBS 132672 = CPC 14612 (as *C. nasturtii*); Pocheon, on *Barbarea orthoceras* (*Brassicaceae*), 23 Oct. 2002, H.D. Shin, CBS H-20990, CBS 132638 = CPC 10100 (named as *C. nasturtii*); Wonju, on *R. indica*, 18 Oct. 2002, H.D. Shin, CBS H-20991, CPC 10133 (as *C. nasturtii*); Suwon, on *A. rusticana* (= *A. lapathifolia*), 14 Oct. 2003, H.D. Shin, CBS H-20992, CBS 132610 = CPC 10811 (as *C. armoraciae*). **Thailand**, on *Acacia mangium* (*Fabaceae*), W. Himaman, CPC 11530.

*Notes*: See also *C. capsici. Cercospora armoraciae* is supported by the HIS phylogeny. In the TEF phylogeny it is part of a larger clade intermixed with *C. zebrina, Cercospora* sp. L, *C. rumicis, C. violae* and *C. althaeina*; in ACT the *C. armoraciae* clade contains some intraspecific variation and also includes *C. rumicis*. In the CAL phylogeny, it is a sister clade to *C. zebrina*, but it contains isolates from *C. capsici*. In the combined tree (Fig. 2 part 3), it is a sister taxon to *C. capsici*. Morphological characteristics of the *C. armoraciae* clade include conidiophores that are often narrowed, with successive geniculation, conically truncate at the apex, and with distinctly thickened and somewhat protuberant loci, and conidia that are cylindro-obclavate to acicular.

In this study, most *Cercospora* species on *Brassicaceae* having indistinguishable morphological characteristics are listed as synonyms under *C. armoraciae*. This treatment was proposed previously (Crous & Braun 2003). Davis (1929) pointed out that similar forms on *Brassicaceae,* namely *C. nasturtii*, *C. armoraciae*, *C. cheiranthi, etc.*, were likely conspecific. The results of this study support his prediction. *Cercospora stanleyae* Chupp ex U. Braun & Crous (Crous & Braun 2003) is tentatively maintained as a separate species due to morphological differences. *Cercospora brassicicola* differs from *C. armoraciae* in that the former has long conidiophores (up to 500 µm in length), and is pathogenic to *Brassica*. In addition, *Cercospora thlaspi* "*thlaspiae*" differs from *C. armoraciae* in that the former has long conidiophores (to 400 µm in length) and acicular conidia (40–300 × 2–4 µm).

## ***Cercospora beticola*** Sacc., emend. Groenewald *et al*., Phytopathology 95: 954. 2005.

*Caespituli* hypophyllous. *Mycelium* internal. *Stromata* lacking to well-developed, up to 60 µm diam, intraepidermal or substomatal, brown to dark brown. *Conidiophores* solitary to 2–18 in loose fascicles, slightly divergent, brown, paler towards apex, moderately thick-walled, cylindrical, almost uniform in width, simple, geniculate, 16–200(–450) × 4–6 µm, 1–6-septate, truncate at the apex, sometimes constricted at septa. *Conidiogenous cells* terminal or intercalary, proliferating sympodially, with 1–2 loci; loci distinctly thickened, not protuberant, apical or formed on shoulder of conidiogenous cells caused by geniculation and lateral, 2.5–3(–4) µm. *Conidia* solitary, filiform to acicular, straight to mildly curved, rarely cylindro-obclavate, truncate at the base, acute to subacute at the tip, 27–250 × 2–5 µm, 3–28-septate.

Description of caespituli on V8 medium; MUCC 568 (MAFF 238206): *Conidiophores* solitary to loosely fasciculate, brown, paler towards the apex, uniform in width, smooth, moderately thick-walled, straight to slightly sinuous, short conically truncate at the tip, 50–148 × 3–5 µm, multi-septate. *Conidiogenous cells* integrated, terminal; loci moderately thickened, apical, uni-local, 2–3 µm in width. *Conidia* hyaline, cylindrical to cylindro-obclavate; short obconical, slightly thickened and truncate or obconically truncate at the base, acute at the apex, 40–88 × 3–6 µm, 3–14-septate.

*Specimens examined*: **Botswana**, Gaborone, on *Spinacia* sp. (*Chenopodiaceae*), L. Lebogang, CPC 5369–5370. **Bulgaria**, on *Goniolimon tataricum* (*Plumbaginaceae*), S.G. Bobev, CBS 123907 = CPC 14616; CBS 123908 = CPC 14620; CBS 132673 = CPC 14617; CPC 14618–14619. **Czech Republic**, on *Beta vulgaris*, Sep. 1947, G.E. Bunschoten, CBS 117.47. **Egypt**, on *B. vulgaris*, 15 Apr. 2004, M. Hasem, CPC 12028–12030. **France**, Longvic, on *B. vulgaris*, S. Garressus, CBS 116505 = CPC 11580. **Germany**, on *B. vulgaris*, S. Mittler, CPC 12031; CPC 12027; CPC 12022; CBS 116502 = CPC 11577; CBS 116454 = CPC 11558; on *B. vulgaris*, Jun. 1931, E.W. Schmidt, CBS 122.31 = CPC 5072; CBS 126.31 = CPC 5064. **Iran**, Pakajik, on *B. vulgaris*, A.A. Ravanlou, CBS 116501 = CPC 11576. **Italy**, Ravenna, on *B. vulgaris*, 10 Jul. 2003, V. Rossi, culture ex-epitype CBS 116456 = CPC 11557; CBS 116503 = CPC 11578. **Japan**, Chiba, on *B. vulgaris*, 30 May 1998, S. Uematsu, MUCNS 320 = MUCC 568 = MAFF 238206; Hokkaido, on *B. vulgaris*, 1955, K. Goto, MUCC 569 = MAFF 305036. **South Korea**, Namyangju, on *Chrysanthemum segetum* (= *Ch. coronarium* var. *spatiosum*) (*Asteraceae*), 24 Jun. 2004, H.D. Shin, CBS 132655 = CPC 11341 (named as *C. chrysanthemi*); 27 Jul. 2004, H.D. Shin, CPC 11344 (named as *C. chrysanthemi*). **Mexico**, Texcoco, on *B. vulgaris*, 20 Oct. 2008, Ma. de Jesús Yáñez-Morales, CPC 15623. **Netherlands**, on *B. vulgaris*, M. Groenewald, CBS 116506 = CPC 11581; Northwest Brabant, on *B. vulgaris*, Nov. 1947, G.E. Bunschoten, CBS 116.47 = CPC 5074. **New Zealand**, Auckland, on *Limonium sinuatum* (*Plumbaginaceae*), 25 Feb. 2002, C.F. Hill, Lynfield 533, CBS 115478 = CPC 5113 (named as *C. statices*); on *B. vulgaris*, C.F. Hill, CPC 5128; Lynfield 539, CPC 5125; CPC 10197; CPC 10204; CPC 10168; CBS 117556 = CPC 10171; CPC 10168; on *Apium graveolens*, C.F. Hill, Lynfield 537a, CPC 5123. **Romania**, Bucuresti, on *B. vulgaris*, 17 Oct. 1966, O. Constantinescu, CBS 539.71 = CPC 5062; Hagieni, on *Malva pusilla* (*Malvaceae*), 15 Jul. 1970, O. Constantinescu & G. Negrean, CBS H-9847, CBS H-9849, CBS 548.71 = IMI 161115 = CPC 5065; on *B. vulgaris*, Jun. 1931, E.W. Schmidt, CBS 124.31 = CPC 5070. **Spain**, on *B. vulgaris*, Jun. 1931, E.W. Schmidt, CBS 123.31 = CPC 5071. **Unknown**, on *B. vulgaris*, Jun. 1931, E.W. Schmidt, CBS 125.31 = CPC 5069. **USA**, California, on *B. vulgaris*, S.T. Koike, CPC 18813.

*Notes*: *Cercospora beticola* is the causal agent of Cercospora leaf spot on *B. vulgaris*, which is one of the most common and destructive sugar beet diseases (Weiland & Koch 2004). Despite its importance as a plant pathogen, its actual host range remains unclear.

Initial phylogenetic analyses on the genus *Cercospora* employed ITS sequences to reveal phylogenetic relationships within the genus (Stewart *et al*. 1999, Goodwin *et al*. 2001, Pretorius *et al*. 2003). These analyses failed to discriminate all species due to the limited resolution provided by the ITS locus. Groenewald *et al*. (2005, 2006a) subsequently succeeded in using multi-locus sequence data from five gene regions to distinguish *Cercospora* species. They also expanded the host range of *C. beticola*. Although isolates of *C. beticola* have been isolated from diverse hosts, these isolates appear to have been colonising non-hosts as saprobes or secondary invaders (Crous & Groenewald 2005), and proof of their pathogenicity has not been confirmed.

Results from the phylogenetic analyses using CAL and combined multi-locus data set divide *C. beticola* and *C. apii s. str.* into two different clades, with *C. beticola* splitting further into two subclades (also see Fig. 2 part 6) based on sequence changes in HIS, probably due to intraspecific variation. The combined data clearly show that *C. apii s. str*. and *C. beticola* are related sibling species, although *C. beticola* must be retained as a separate species.

## *Cercospora* cf. *brunkii*

*Caespituli* amphigenous. *Mycelium* internal. *Stromata* lacking or composed of few dark brown cells, intraepidermal or substomatal. *Conidiophores* brown to dark brown, paler at the apex, 2–6 in loose fascicles, moderately thick-walled, straight or 1–2 times geniculate caused by sympodial proliferation, uniform in width, mildly attenuated at the apex, short obconically truncate or truncate at the apex, 30–160 × 4.5–5.5 µm, 0–9-septate. *Conidiogenous cells* integrated, terminal and intercalary, proliferating sympodially, rarely percurrently, uni- or multi-local (2–5); loci distinctly thickened, often dispersed on whole conidiophores, darkened, apical and lateral, 2–3 µm diam. *Conidia* solitary, hyaline, acicular, straight or slightly curved, thickened and truncate at the base, acute at the apex, 27–110 × 1.5–4 µm, indistinctly multi-septate, 0–9-septate.

*Specimens examined*: **Japan**, Wakayama, on *Datura stramonium* (*Solanaceae*), 30 Oct. 2007, C. Nakashima & I. Araki, MUMH 10858, MUCC 732. **South Korea**, Namyangju, on *Geranium thunbergii* (≡ *G. nepalense* var. *thunbergii*) (*Geraniaceae*), 30 Sep. 2004, H.D. Shin, CBS H-20993, CBS 132657 = CPC 11598.

*Notes*: This species is basal to *C. apii s. str*. Fresh collections from *Geranium* (*Geraniaceae*) are needed from the USA (type locality of *C. brunkii*) to determine if the latter name can be applied to this species. The two isolates representing this species are never supported in their own clade; in the TEF and ACT phylogenies they are intermixed with *C.* cf. *flagellaris*, in the CAL phylogeny with *C. apii* and in the HIS phylogeny with *C. kikuchii*, *C.* cf. *richardiicola* and *Cercospora* spp. P and Q. These different shared alleles are the likely cause for their separate position in the combined phylogeny (Fig. 2 part 5).

## *Cercospora campi-silii* Speg., Michelia 2: 171. 1880.

≡ *Cercosporidium campi-silii* (Speg.) X.J. Liu & Y.L. Guo, Acta Mycol. Sin. 1: 94. 1982.
≡ *Passalora campi-silii* (Speg.) Poonam Srivast., J. Living World 1: 114. 1994, nom. inval.
≡ *Passalora campi-silii* (Speg.) U. Braun, Mycotaxon 55: 228. 1995.
= *Cercospora impatientis* Bäumler, Verh. K. K. Zool.-Bot. Ges. Wien 38: 717. 1888.

*Leaf spots* angular to irregular, 1–3 mm diam, center greyish to pallid, surrounded by purplish brown to dark brown border lines, but brown to greyish brown without definite borders on the abaxial surface. *Caespituli* hypophyllous, but also epiphyllous in later stage of disease development. *Stromata* lacking or composed of a few brown cells. *Conidiophores* arising in fascicles of 5–12(–18), loose to moderately dense, emerging through stomata or occasionally erumpent through the cuticle, subcylindrical, 2–5 times geniculate, sometimes abruptly geniculate, unbranched, 2–4-septate, 40–110 × 4–5.5 µm, pale brown to olivaceous-brown. *Conidiogenous cells* integrated, terminal, sympodial, multi-local; loci subcircular, thickened, darkened, 2.5–3 µm wide. *Conidia* solitary, obclavate-cylindrical to elliptical, 25–60 × 4.5–6 µm, (1–)3(–6)-septate, subhyaline, apex obtuse, base obconically subtruncate; hila *ca.* 2 µm wide, thickened, darkened.

*Specimen examined*: **South Korea**, Inje, on *Impatiens noli-tangere* (*Balsaminaceae*), 29 Sep. 2007, H.D. Shin, CBS 132625 = CPC 14585.

*Notes*: Although *C. campi-silii* was transferred from *Cercospora* to *Passalora* based on its pale olivaceous conidia (Braun 1995b), as in the case of *C. sojina*, these taxa are best retained in *Cercospora*, which is fully supported by their phylogenetic position within *Cercospora*. *Cercospora campi-silii* is separated based on the TEF, ACT and HIS phylogenies in the present study. Only the CAL phylogeny failed to distinguish it from *C. sojina* and *C. achyranthis*. On the combined tree (Fig. 2 part 2), it is a sister taxon to *C. sojina*. *Cercospora campi-silii* was described from Europe and examination of European material is necessary to determine similarity with Korean collections.

## *Cercospora canescens* complex

*Cultures examined*: **Ghana**, on leaves of *Dioscorea rotundata* (*Dioscoreaceae*), 2000, S. Nyako & A.O. Danquah, CBS 132658 = CPC 11626 = GHA-1-0 (as *C. dioscoreae-pyrifoliae*); CPC 11628 = GHA-2-1; on leaves of *Dioscorea alata*, 2000, S. Nyako & A.O. Danquah, CBS 132659 = CPC 11627 = GHA-1-1. **Mexico**, Tamaulipas, unidentified *Malvaceae* host, 30 Oct. 2008, Ma. de Jesús Yáñez-Morales, CPC 15871. **South Africa**, Northwest Province, Potchefstroom, on *Vigna* sp. (*Fabaceae*), S. van Wyk, CBS 111133 = CPC 1137; CBS 111134 = CPC 1138; Tsipise, Limpopo Province, on *Citrus maxima* (*Rutaceae*) fruit spot, K. Serfontein, CPC 4408–4409. **USA**, Georgia, on *Phaseolus lunatus* (= *Ph. limensis*) (*Fabaceae*), E.S. Luttrell, CBS 153.55 = CPC 5059 (as *C. canescens*); on *Apium* sp., CPC 11640 = IMI 186563.

*Notes*: Morphologically the present clade represents isolates that correspond with the description of *C. canescens*, which was originally described from *Phaseolus* in the USA. It is possible that as more isolates are added, the lower subclade, which represents hosts in other families, may eventually split off as a distinct taxon. Epitype material from the USA is necessary to fix the application of the name *C. canescens*. The material on *Ph. lunatus* (= *Ph. limensis*) could be used in this sense, but *C. canescens* is a complicated species complex. More isolates from the USA are necessary to resolve this issue. A sequence of an isolate on *Phaseolus* from Mexico (CPC 15807) clusters in "*Cercospora* sp. Q", which might be *C. canescens*. The *C. canescens* complex is supported as a distinct clade in the ACT and CAL phylogenies. The TEF sequence of isolate CPC 15871 splits off from the rest of the isolates to cluster with *C.* cf. *coreopsidis.* In the HIS phylogeny, the isolates occur in four distinct but related clades (*C. mercurialis* occurs in an intermediate position between these clades). These four clades correspond to the intraspecific variation observed for this species in Fig. 2 (part 1).

### ***Cercospora capsici*** Heald & F.A. Wolf, Mycologia 3: 15. 1911.

*Leaf spots* circular to subcircular, more or less concentric, 2–10 mm diam. *Caespituli* amphigenous, appearing greyish brown in case of abundant sporulation. *Mycelium* internal. *Stromata* rudimentary, composed of a few swollen cells. *Conidiophores* straight to mildly curved, not branched, in divergent fascicles (3–15), mildly geniculate, 30–120 × 3–6 µm, 0–6-septate. *Conidiogenous cells* integrated, terminal, lateral, proliferating sympodially; loci distinct, slightly protuberant, apical and formed on shoulder caused by geniculation, 2–3 µm wide. *Conidia* solitary, hyaline, acicular, straight to mildly curved, 64–180 × 4–5.5 µm, 2–12-septate, subacute at the apex, obconically truncate at the base (adapted from Shin & Kim 2001).

*Description of caespituli on V8 medium*; MUCC 574 (MAFF 238227): *Conidiophores* solitary, pale brown to brown, irregular in width, wider at the base, smooth, moderately thick-walled, sinuous-geniculate, simple, conically truncated at the tip, 20–130.5 × 3.5–5 µm, multi-septate. *Conidiogenous cells* integrated, terminal; loci distinctly thickened, apical, 2–2.5 µm in width. *Conidia* solitary, hyaline, cylindro-obclavate to acicular, distinctly thickened and long obconically truncated at the base, obtuse to acute at the apex, 105–200 × 2.5–4.5 µm, 9–18-septate.

*Specimens examined*: **Fiji,** unknown host, fungus fruiting on lesions on calyx attached to fruit, 17 Aug. 2005, P. Tyler, CBS 118712. **Japan**, Chiba, on *Capsicum annuum* (*Solanaceae*), 1 Oct. 1999, S. Uematsu, MUCC 574 = MAFF 238227 = MUCNS 810. **South Korea**, Hongcheon, on *C. annuum*, 29 Aug. 2005, H.D. Shin, CBS H-20994, CPC 12307; Yanggu, on *C. annuum*, 28 Sep. 2007, H.D. Shin, CBS H-20995, CBS 132622 = CPC 14520.

*Notes*: See also *C. armoraciae*. This species is supported in the TEF (related to *Cercospora* sp. J and C. *chenopodii*), ACT (related to *Cercospora* sp. J and *C. zebrina* and *C. armoraciae*) and HIS (related to *Cercospora* spp. C and D) phylogenies and is part of the larger *C. armoraciae* clade based on CAL. In the combined tree (Fig. 2 part 3), it is a sister taxon to *C. armoraciae*. Morphological characteristics of this species on the host plant and in culture are almost similar to *C. armoraciae*. In addition, acicular conidia are formed in culture. The application of the name *C. capsici* to this clade is only tentative, since the latter species was described from the USA. North American cultures and sequences are needed to confirm their identity.

Several species of *Cercospora* occur on solanaceous host plants. Of these, *C. physalidis* has been shown to form a species complex. Braun & Mel'nik (1997) concluded many species of *Cercospora apii s. lat*. on solanaceous hosts, including *C. capsici*, were synonymous with *C. physalidis* based on their morphological characteristics. Based on the results of pathogenicity tests (C. Nakashima, unpubl. data), phylogeny, and morphology (cylindrical to obclavate, rarely acicular conidia, and conidiophores that narrow at the upper portion), *C. capsici* must be separated from the *C. physalidis* complex. Likewise, other taxa in this complex such as *C. lycii*, *C. nicandrae*, *C. sciadophila*, *C. solanacea*, and *C. solani*, which consistently have obclavate-cylindrical conidia, must be re-examined.

### ***Cercospora celosiae*** Syd., Ann. Mycol. 27: 430. 1929.

*Leaf spots* amphigenous, scattered to confluent, distinct, subcircular to irregular, small to fairly large, 1–7 mm diam, pale brown to brown, surrounded by a dark brown border. *Caespituli* amphigenous. *Stromata* small, rudimentary to slightly developed, composed of several brown, swollen hyphal cells. *Conidiophores* 3–20 in loose fascicles, emerging through stomata or erumpent through the cuticle, olivaceous-brown throughout, or paler upwards, 0–5-septate, straight to slightly curved, 1–5 times mildly geniculate, sometimes once abruptly geniculate, not branched, 25–200 × 4.5–6 µm; loci conspicuous, apical or on shoulders of conidiogenous cells caused by geniculation. *Conidia* solitary, acicular to filiform, sometimes shorter ones obclavate-cylindrical, straight to mildly curved, hyaline, 2–14-septate, slightly constricted at the septa, subacute to subobtuse at the apex, obconically truncate to subtruncate at the base, 40–150 × 3–5 µm; hilum conspicuously thickened, darkened, and non-protuberant

*Specimen examined*: **South Korea**, Chuncheon, on *Celosia argentea* var. *cristata* (≡ *C. cristata*) (*Amaranthaceae*), 7 Oct. 2003, H.D. Shin, CBS H-20996, CBS 132600 = CPC 10660.

*Notes*: The isolate representing *C. celosiae* is not supported as a separate clade; in the TEF, ACT, CAL and HIS phylogenies it is intermixed with predominantly *Cercospora* sp. I and *C. alchemillicola / C.* cf. *alchemillicola*, which is also evident from its position basal to *Cercospora* sp. I in the combined phylogeny (Fig. 2 part 1). Authentic material from China is required to determine if *C. celosiae* should be merged with what is presently treated as *Cercospora* sp. I.

### ***Cercospora chenopodii*** Fresen., Beitr. Mykol.: 92. 1863. Fig. 4

= *Ramularia dubia* Riess, Hedwigia 1: pl. 4, fig. 9. 1854.

≡ *Cercospora dubia* (Riess) G. Winter, Fungi Eur. Exs., Ed. nov., Cent. 28, No. 2780. 1882 and Hedwigia 22: 10. 1883, nom. illeg., homonym of *C. dubia* Speg., 1880.

≡ *Cercospora dubia* (Riess) Bubák, Ann. Mycol. 6: 29. 1908, nom. illeg., homonym of *C. dubia* Speg., 1880.

≡ *Cercosporidium dubium* (Riess) X.J. Liu & Y.L. Guo, Acta Mycol. Sin. 1: 95. 1982.

≡ *Passalora dubia* (Riess) Poonam Srivast., J. Living World 1: 115. 1994, comb. inval.

≡ *Passalora dubia* (Riess) U. Braun, Mycotaxon 55: 231. 1995.

= *Cercospora chenopodii* Cooke, Grevillea 12: 22. 1883, nom. illeg., homonym of *C. chenopodii* Fresen., 1863.

= *Cercospora dubia* var. *urbica* Roum., Rev. Mycol. 15: 15. 1893.

= *Cercospora dubia* var. *atriplicis* Bondartsev, Trudy Glavn. Bot. Sada 26: 51. 1910.

= *Cercospora atriplicis* Lobik, Mat. po Fl. Faun. Obsled. Terskogo Okruga: 52. 1928.

= *Cercospora chenopodii* var. *micromaculata* Dearn., Mycologia 21: 329. 1929.

= *Cercospora penicillata* f. *chenopodii* Fuckel, Fungi Rhen. Exs., Fasc. II, No. 119. 1863, nom. nud.

= *Cercospora chenopodii* var. *atriplicis patulae* Thüm., *in herb.*

= *Cercospora bondarzevii* Henn., *in herb.* B.

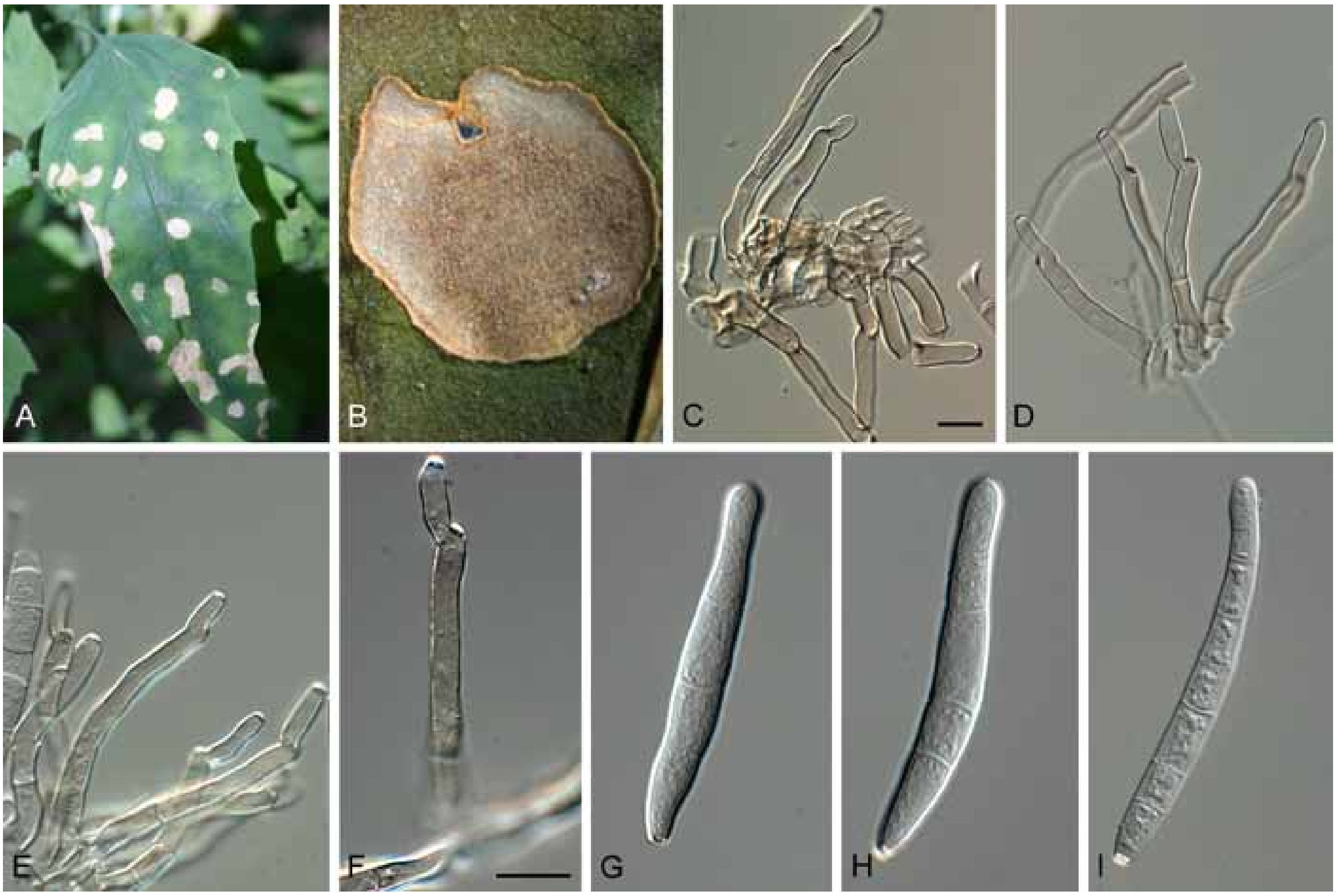



**Fig. 4.** *Cercospora chenopodii* **(**CBS 132620 = CPC 14237). A. Leaf spots. B. Close-up of lesion. C–F. Conidiophores. G–I. Conidia. Scale bars = 10 µm.

*Specimen examined*: **France**, Ardeche, N44°22'39.8" E4°26'9.1", on *Chenopodium* cf. *album* (*Chenopodiaceae*) next to river, 31 Aug. 2007, P.W. Crous, CBS H-20997, CBS 132620 = CPC 14237.

*Notes*: *Cercospora chenopodii* was transferred to the genus *Passalora* as *P. dubia* by Braun (1995a) based on broadly obclavate conidia with visible large loci. The conidia of this species are hyaline, and best retained in *Cercospora*, which has been confirmed by results of molecular sequence analyses. The species is supported as distinct in the TEF, ACT and HIS phylogenies; in the CAL phylogeny it cannot be distinguished from *C.* cf. *chenopodii*. In the combined tree (Fig. 2 part 1), it is a sister taxon to *C.* cf. *chenopodii*. Also see *C.* cf. *chenopodii*.

## *Cercospora* cf. *chenopodii* Fig. 5.

*Leaf spots* amphigenous, subcircular, circular, 3–8 mm diam, greyish brown to pale brown. *Mycelium* internal, consisting of septate, branched, smooth, pale brown hyphae. *Caespituli* in fascicles (10–40), amphigenous, brown, dense, becoming divergent, up to 150 µm wide and 50 µm high. *Conidiophores* aggregated in dense fascicles arising from the upper cells of a moderately developed brown stroma; conidiophores olivaceous-brown to brown, 2–5-septate, 1–2 times geniculate in upper part, at times apically swollen, not branched, 60–135 × 4–7 µm. *Conidiogenous cells* terminal, unbranched, pale brown, smooth, tapering to flat-tipped apical loci, proliferating sympodially, 20–40 × 4–6 µm; loci thickened, darkened, refractive, 2–4 µm diam. *Conidia* solitary, smooth, cylindrical to obclavate, straight to slightly curved, hyaline, (0–)2–4(–5)-septate, apex obtuse, base obconically truncate, (25–)40–65(–80) × (5–)6–7.5(–9) µm; hila thickened, darkened, refractive, 2–3 µm diam.

*Culture characteristics*: Colonies erumpent, spreading, with sparse aerial mycelium, and lobate, smooth margins, and folded surface; reaching 10 mm after 2 wk. On MEA iron-grey with patches of dirty white, reverse fuscous-black to greyish sepia. On OA and PDA surface mouse-grey, with patches of pale mouse-grey, reverse olivaceous-grey.

*Specimens examined*: **Mexico**, Montecillo, *Chenopodium* sp. (*Chenopodiaceae*), 9 Oct. 2008, Ma. de Jesús Yáñez-Morales, CBS 132677 = CPC 15599; CPC 15763; Purificacion, *Chenopodium* sp., 12 Oct. 2008, Ma. de Jesús Yáñez-Morales, CPC 15859; CPC 15862. **South Korea**, Hongcheon, on *Chenopodium ficifolium* (*Chenopodiaceae*), 4 Oct. 2002, H.D. Shin, CBS H-20998, culture CBS 132594 = CPC 10304; Hongcheon, on *C. ficifolium*, 27 Oct. 2005, H.D. Shin, CBS H-20999, CPC 12450.

*Notes*: The chief difference between *C. chenopodii* and *C.* cf. *chenopodii* lies in the denser fascicles observed in the former species. Otherwise, the two species are barely distinguishable, and the latter species has to be considered a cryptic taxon. In the TEF phylogeny these two species are clearly distinct, although the isolates of *C.* cf. *chenopodii* are intermixed with those of *C. delaireae*, *C. ricinella* and *Cercospora* sp. K. The ACT and HIS phylogenies separate *C.* cf. *chenopodii* from the other species included in this study, although the CAL phylogeny could not distinguish *C. chenopodii* and *C.* cf. *chenopodii*. In the combined tree (Fig. 2 part 1), it is a sister taxon to *C. chenopodii*. See the species notes for *C. chenopodii*. We refrain from describing this species as new until more isolates for *C. chenopodii* can be sequenced to determine the intraspecific variation.

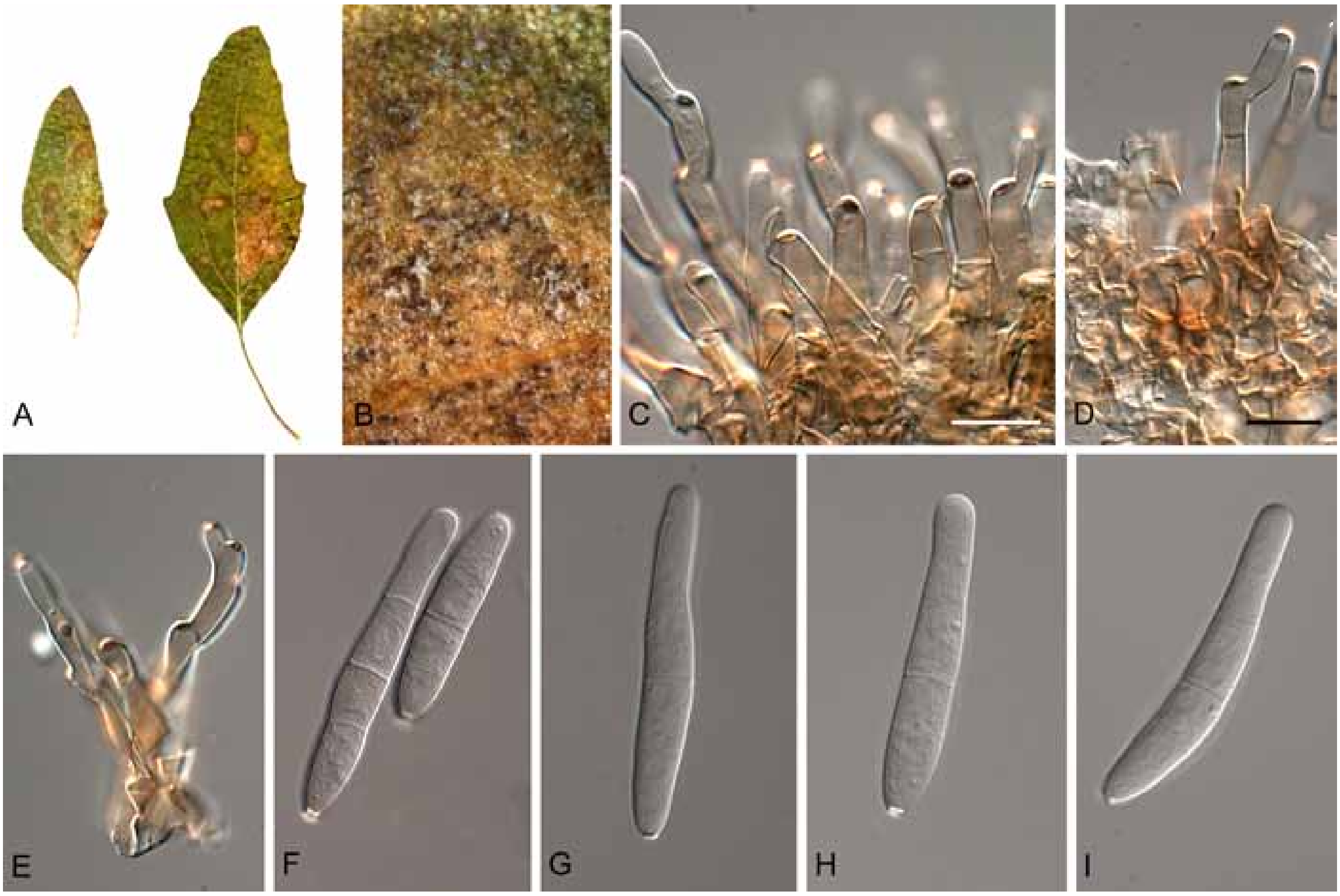



**Fig. 5.** *Cercospora* cf. *chenopodii* (CPC 10304). A. Leaf spots. B. Close-up of lesion. C–E. Fasciculate conidiophores. F–I. Conidia. Scale bars = 10 µm.

***Cercospora chinensis*** F.L. Tai, Bull. Chin. Bot. Soc. 2: 49. 1936.

*Caespituli* amphigenous. *Mycelium* internal. *Stromata* lacking to small, up to 30 µm diam, dark brown, intraepidermal or substomatal. *Conidiophores* solitary to 2–5 in loose fascicles, simple, sometimes branched, thick-walled, dark brown, paler towards the apex, mainly straight, loosely geniculate, almost uniform in width, conically truncated and somewhat wider at the apex, 61–100 × 5–6 µm, 3–6-septate. *Conidiogenous cells* integrated, proliferating sympodially or rarely percurrently, terminal and intercalary, multi-local; loci thickened, not protuberant, apical, lateral, 2.5–3 µm diam. *Conidia* solitary, hyaline, acicular to cylindro-obclavate, slightly curved, obconically truncate or subtruncate, and thickened at the base, acute at the apex, 60–210 × 3.5–5 µm, 2–16-septate.

*Specimen examined*: **South Korea**, Pyeongchang, on *Polygonatum humile* (*Convallariaceae*), 20 Sep. 2003, H.D. Shin, CBS H-21000, CBS 132612 = CPC 10831.

*Notes*: See the notes for *C. dispori* below. In the combined tree (Fig. 2 part 5), it is a sister taxon to *C. dispori* and *C. corchori*.

***Cercospora* cf. *citrulina***

*Caespituli* amphigenous. *Mycelium* internal. *Stromata* lacking or small, up to 20 µm, pale brown. *Conidiophores* pale to pale brown, paler towards the apex, irregular in width, wider at the base, narrowed successive geniculation at the apex, sinuous-geniculate to well geniculate above the middle, thin-walled when young, darker and moderately thickened in mature conidiophores, solitary or in loose fascicles (2–14), simple, truncate at the apex, 50–86 × 2.5–5 µm, 0–3-septate. *Conidiogenous cells* integrated, terminal, rarely intercalary, proliferating sympodially, multi-local; loci distinct, thickened, apical or on shoulder caused by geniculation, slightly protuberant, 2.5–3 µm diam. *Conidia* solitary, hyaline, cylindrical, filiform to acicular, straight to slightly curved, truncate to long obconically truncate and distinctly thickened at the base, apex subacute, 40–134 × 3–4 µm, multi-septate.

*Specimens examined*: **Bangladesh** (western part), on *Musa* sp. (*Musaceae*), I. Buddenhagen, CBS 119395 = CPC 12682; CBS 132669 = CPC 12683. **Japan**, Kagoshima, on *Momordica charanthia* (*Cucurbitaceae*), 20 Oct. 1997, E. Imaizumi & C. Nomi, MUCC 577 = MAFF 238205 = MUCNS 254 (as *C. citrullina*); Okinawa, on *Citrullus lanatus* (*Cucurbitaceae*), 6 Mar. 1998, T. Kobayashion *et al*., MUMH 11402, MUCC 576 = MUCNS 300 = MAFF 237913 (as *C. citrullina*); on *Psophocarpus tetragonolobus* (*Fabaceae*), MUCC 584 = MAFF 305757 (as *C. psophocarpicola*); on *Ipomoea pes-caprae* (*Convolvulaceae*), MUCC 588 = MAFF 239409 (as *C. ipomoeae*).

*Notes*: This clade is supported by the TEF, ACT and CAL phylogenies. In the HIS phylogeny, the clade is split into the two sister clades visible in the combined tree, and may eventually be shown to be a species complex. In the HIS phylogeny, MUCC 584, MUCC 576 and MUCC 577 are clustering sister to *C. chinensis* and *C. dispori* whereas the remaining isolates are sister to *C. vignigena*. In the combined tree (Fig. 2 part 5), it is a sister taxon to *C.* cf. *helianthicola*.

This taxon is distinguished from other species based on several morphological characteristics. Sporulation is mainly observed at the apex of conidiophores; slightly protuberant loci are formed on shoulders caused by geniculation; the width of conidiogenous cells immediately behind the fertile region is generally narrower, and

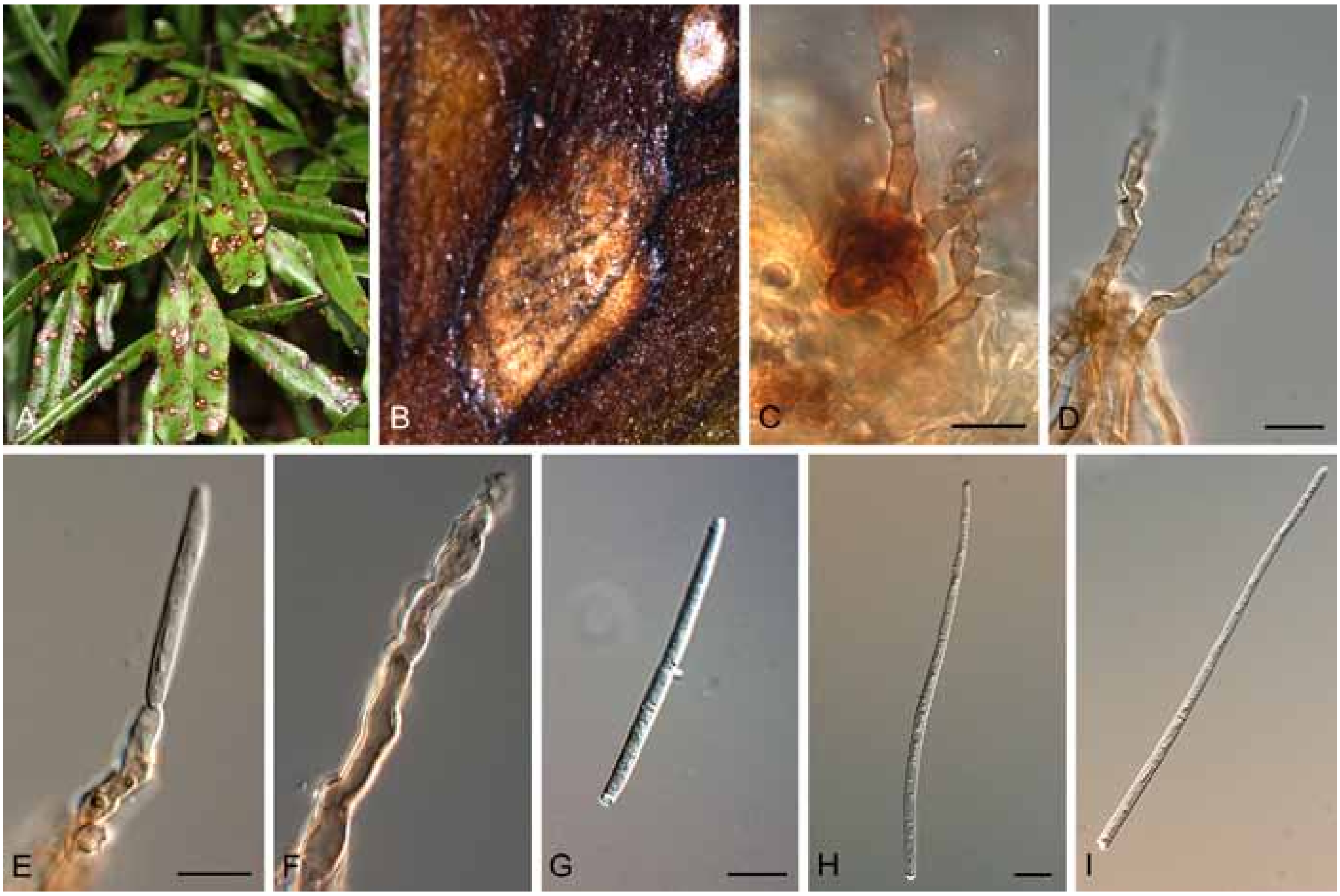



**Fig. 6.** *Cercospora coniogrammes* **(**CBS 132634 = CPC 17017). A. Leaf spots. B. Close-up of lesion. C–F. Weakly developed fascicles, showing conidiophores with sympodial proliferation and multi-local loci. G–I. Cylindrical to acicular conidia. Scale bars = 10 µm.

conidiogenous cells are truncate at the apex. An isolate obtained from *Ipomoea pes-caprae* (MUCC 588) is located in this clade (Fig. 2 part 5). It was not possible to examine its morphology in this study and thus it is not clear whether or not this fungus was saprobic. An isolate identified as *C. psophocarpicola* (MUCC 584), is also located in this clade. There is no morphological basis to divide *C. psophocarpicola* and other isolates in this clade into different species. Besides, the pathogenicity of MUCC 584 to *Psophocarpus* (*Fabaceae*) was confirmed (Ohnuki *et al*. 1989), thus showing that this species was not saprobic. Moreover, the four Japanese isolates examined in this study were obtained from the same subtropical islands in Japan. On the other hand, two isolates named as "*C. hayi*" from *Musa* sp. were also located in this clade. According to Crous *et al*. (2004b), several species of *Cercospora* are known to be able to colonise *Musa*. From the distribution of this taxon, it is natural that this species also colonised *Musa* (*Musaceae*), which grows in the same region.

***Cercospora coniogrammes*** Crous & R.G. Shivas, **sp. nov.** MycoBank MB800653. Fig. 6.

*Etymology*: Named after the host genus from which it was collected, *Coniogramme.*

*Leaf spots* amphigenous, subcircular to angular, 1–3 mm diam, grey to pale brown, surrounded by a broad brown margin, up to 4 mm diam. *Mycelium* internal. *Caespituli* predominantly epiphyllous. *Conidiophores* aggregated in loose fascicles (2–6), arising from the upper cells of a brown, weakly developed stroma, up to 20 µm diam, brown, finely verruculose in lower part, 3–7-septate, subcylindrical, straight to geniculate-sinuous, unbranched, 60–120 × 5–7 µm. *Conidiogenous cells* integrated, terminal, unbranched, brown, smooth, tapering to flat-tipped loci, proliferating sympodially, 15–35 × 3–5 µm, with numerous tightly aggregated apical loci, proliferating sympodially; loci distinct, thickened and darkened, protruding, 2–2.5 µm diam. *Conidia* solitary, hyaline, cylindrical to acicular, straight or slightly curved, apex subobtuse, base truncate, (30–)50–85(–120) × (2–)3(–3.5) µm, 1–6-septate, thin-walled, smooth; hila thickened, darkened, refractive, 1.5–2 µm diam.

*Culture characteristics*: Colonies spreading, flat, with sparse aerial mycelium, folded surface and even margins, reaching 25 mm after 2 wk. On OA blood-red in centre, red at margin. On MEA grey-olivaceous in centre, smoke-grey at margins, olivaceous-grey in reverse. On PDA umber to chestnut in centre, bay at margin, umber in reverse.

*Specimen examined*: **Australia**, Queensland, Brisbane, on *Coniogramme japonica* var. *gracilis* (≡ *C. gracilis*) (*Adiantaceae*), **holotype** CBS H-21001, Aug. 2009, P.W. Crous, culture ex-type CBS 132634 = CPC 17017.

*Notes*: The numerous, tightly aggregated loci on the conidiogenous cells, and cylindrical to acicular conidia are characteristic of this species. This species is supported on the TEF, ACT, CAL and HIS phylogenies and is basal in the combined tree (Fig. 2 part 1).

***Cercospora corchori*** Sawada, Trans. Nat. Hist. Soc. Formosa 26: 179. 1916.

*Caespituli* amphigenous. *Mycelium* internal. *Stromata* lacking to small, substomatal or intraepidermal, pale brown to brown, 16–25 µm diam. *Conidiophores* arising from upper part of stromata or internal hyphae, in loose fascicles (5–10), moderately thick-walled, pale brown to brown, uniform in width, sometimes attenuated at the apex, sinuous-geniculate, sparsely septate, conically truncate at the apex, 20–83 × 4–5 µm. *Conidiogenous cells* integrated, terminal and intercalary, proliferating sympodially, multi-local; loci distinct, thickened and darkened, apical or formed on the shoulder caused by the geniculation, 1–3 µm diam. *Conidia* hyaline to subhyaline, cylindro-obclavate to acicular, straight or slightly curved, truncate and thickened at the base, acute at the apex, 30–128 × 2.5–5 µm, 4–13-septate.

Description of caespituli on MEA; MUCC 585 (= MAFF 238191): *Conidiophores* solitary, brown, uniform in width, smooth, moderately thick-walled, slightly curved, simple, conically truncated at the apex, 130–230 × 3.5–4.5 µm, multi-septate. *Conidiogenous cells* integrated, terminal; loci moderately thickened, apical, 2.5–2.5 µm in width.

*Specimens examined*: **Japan**, Shimane, on *Corchorus olitorius* (*Tiliaceae*), 27 Aug. 1997, T. Mikami (**epitype designated here** – TFM:FPH-8114), culture ex-epitype MUCC 585 = MAFF 238191 = MUCNS 72. **Taiwan**, Taipei, on *C. olitorius*, 30 Jul. 1909, K. Sawada, (**isotype** – TNS-F-220392).

*Notes*: *Cercospora corchori*, which is known as the causal agent of a seed-borne disease, is distinguished from other species in that conidiophores are uniform in width, and conically truncate at the apex. Moreover, the species is supported by the ACT, CAL and HIS phylogenies. In the TEF phylogeny, it clusters on a longer branch in a clade with isolates of *Cercospora* sp. K and *C. lactucae-sativae*. In the combined tree (Fig. 2 part 5), it is a sister taxon to *Cercospora* spp. R and S.

### *Cercospora* cf. *coreopsidis*

*Leaf spots* distinct (characteristic for this species), circular to subcircular, initially pale brown, later centre grey to dirty grey with raised greyish brown margins. *Caespituli* amphigenous. *Mycelium* internal. *Stromata* lacking or small, up to 30 µm in diam, intraepidermal or substomatal, brown. *Conidiophores* solitary, or up to 2–9 in loose fascicles, irregular in width, slightly attenuated at the apex, somewhat wider at mid cells, pale brown, thick-walled, paler towards the apex, conically truncate at the apex, geniculate at the upper portion, tortuous, 30–156 × 4–5.5 µm, 1–7-septate. *Conidiogenous cells* integrated, intercalary, terminal, proliferating sympodially, multi-local; loci thickened, darkened, not protuberant, flat, apical, lateral, rarely circumspersed, 1.5–2 µm. *Conidia* solitary, hyaline, filiform to acicular, straight to curved, truncated and thickened at the base, tip acute, 40–90(–180) × (1.5–)3–5 µm, indistinctly 7–10-septate.

*Specimen examined*: **South Korea**, Seoul, *Coreopsis lanceolata* (*Asteraceae*), 17 Sep. 2003, H.D. Shin, CBS H-21002, CBS 132598 = CPC 10648; Wonju, on *C. lanceolata*, 18 Oct. 2002, H.D. Shin, CPC 10122.

*Notes*: The description of the present species is based on Korean specimens. Many species of *Cercospora* have latent pathogenicity to asteraceous plants. Although these results show that the identification of *Cercospora* species on these plants is difficult based on the host plant, the isolates originating from *Coreopsis* must be treated as a host-specific species in having an independent phylogenetic position, which is supported by the TEF, ACT, CAL and HIS phylogenies. In the combined tree (Fig. 2 part 1), it is a sister taxon to *C. agavicola*.

On the other hand, *C. beticola*, which has also been known from *Bidens* (*Asteraceae*), was also reported from *Coreopsis* (*Asteraceae*) (Thaung 1984). Morphological differences between these species were not observed. The identification of the Korean collections as *C.* cf. *coreopsidis* is only tentative and must be proven on the base of sequences derived from North American isolates, which are not yet available.

### ***Cercospora delaireae*** C. Nakash., Crous, U. Braun & H.D. Shin, **sp. nov.** MycoBank MB800654. Fig. 7.

*Etymology*: Named after the host genus from which it was collected, *Delairea.*

*Leaf spots* amphigenous, subcircular to angular, grey-brown to brown, 3–7 µm diam, surrounded by a large, brown border, 7–15 mm diam. *Caespituli* amphigenous, mainly hypophyllous. *Mycelium* internal. *Stromata* lacking or composed of few brown cells, substomatal or intraepidermal. *Conidiophores* solitary or in loose fascicles (2–4), pale brown to brown, irregular in width, narrowed at upper portion, moderately thick-walled, smooth, straight or abruptly once geniculate, truncate at the tip, 20–120 × 5–6.5 µm, 1–9-septate. *Conidiogenous cells* integrated, terminal, rarely intercalary, proliferating sympodially, 20–60 × 4–6 µm, usually unilocal, rarely multi-local; loci apical or formed on the shoulder due to sympodial proliferation, 2–4 µm diam, thickened and darkened. *Conidia* solitary, hyaline, filiform to acicular, truncate at the base, tip acute, (55–)80–150(–200) × (3.5–)4(–5) µm, 3–15-septate, thin-walled, smooth; hila thickened, darkened, 2–4 µm diam.

*Culture characteristics*: Colonies erumpent, spreading, with sparse to moderate aerial mycelium, and smooth, lobed margin and folded surface; reaching 20 mm diam after 2 wk. On MEA surface dirty white to salmon with patches of olivaceous-grey; reverse iron-grey in centre, salmon in outer region. On PDA surface dirty white with patches of pale mouse-grey, and red, diffuse pigment surrounding culture; reverse olivaceous-grey, but with prominent red pigment. On OA spreading, flat, lacking aerial mycelium, with lobate, smooth margins; surface red with diffuse red pigment surrounding colony; reverse red.

*Specimens examined*: **South Africa**, Eastern Cape Province, Plettenberg Bay, on *Delairea odorata* (= *Senecio mikaniodes*) (*Asteraceae*), C.L. Lennox, CPC 10627–10629; Mpumalanga, Long Tom Pass, on *D. odorata* (= *Senecio mikanioides*), 16 Jun. 2003, S. Neser, **holotype** CBS H-21004, culture ex-type CBS 132595 = CPC 10455.

*Notes*: *Cercospora delaireae* must be regarded as a new species based on its distinct phylogenic position (Fig. 2 part 2). In the individual gene trees it is distinguished in the ACT, CAL and HIS phylogenies; in the TEF phylogeny it cannot be distinguished from *C.* cf. *chenopodii*. In the combined tree (Fig. 2 part 2), it is a sister taxon to *C. ricinella*. It appears to be specific to *Delairea odorata* (= *Senecio mikanioides*) (Cape-ivy), and should be further evaluated as possible biocontrol agent of this host. *Delairea odorata* is an invasive perennial vine problematic in coastal riparian areas and is reported as being toxic to animals and fish. Stem, rhizome and stolon fragments resprout if left in the ground after treatment (for further information see <www.cal-ipc.org/ip/management/plant_profiles/Delairea_odorata.php>).

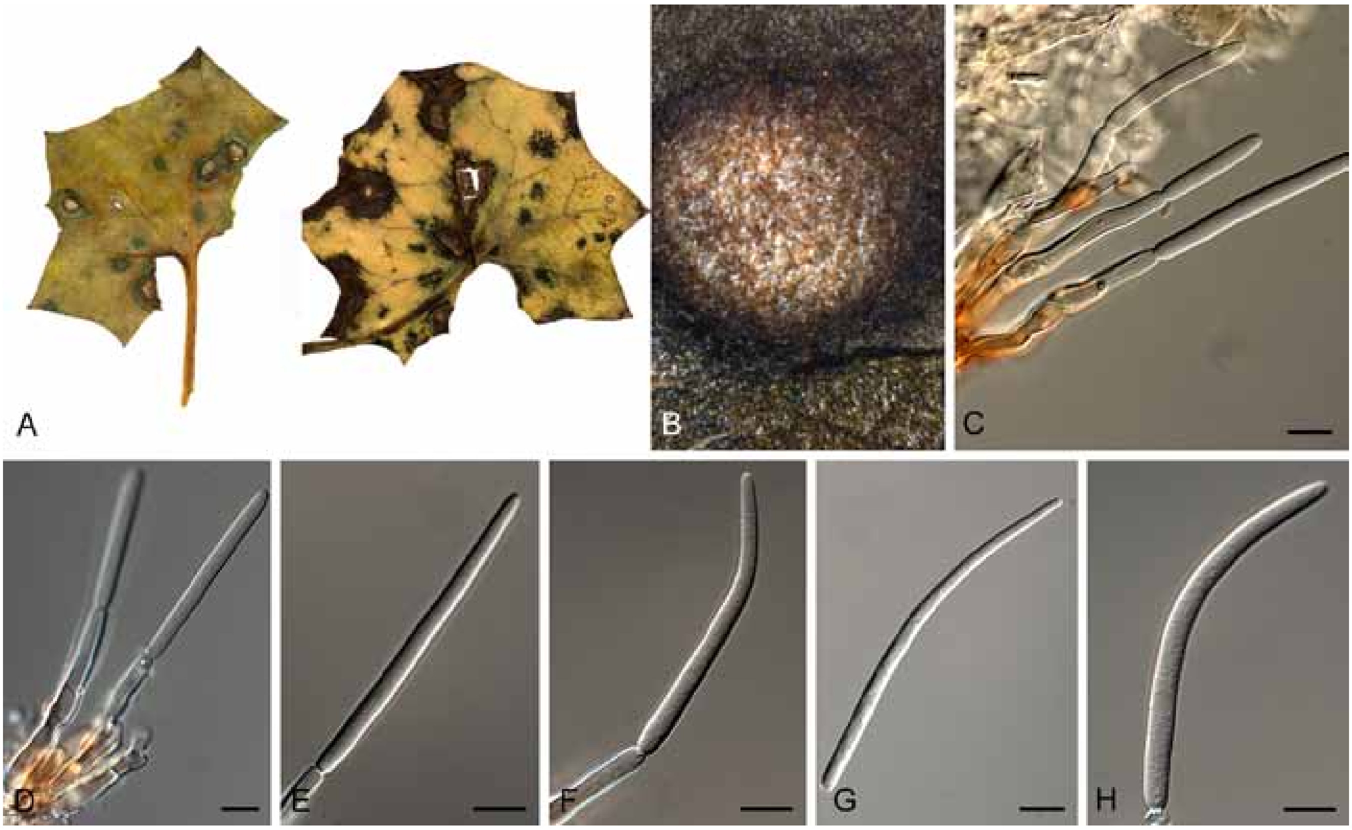



**Fig. 7.** *Cercospora delaireae* **(**CBS 132595 = CPC 10455). A. Leaf spots. B. Close-up of lesion. C–F. Conidiophores giving rise to conidia. G, H. Conidia. Scale bars = 10 µm.

## ***Cercospora dispori*** Togashi & Maki, Trans. Sapporo Nat. Hist. Soc. 17: 98. 1942.

*Caespituli* amphigenous. *Mycelium* internal. *Stromata* lacking to small, up to 40 µm diam, dark brown, intraepidermal or substomatal. *Conidiophores* solitary, or up to 2–10 in loose fascicles, thick-walled, dark brown, paler towards the apex, straight or sinuous-geniculate, almost uniform in width, conically truncate at the apex, 45–100 × 3.5–5.5 µm, 1–7-septate. *Conidiogenous cells* integrated, proliferating sympodially or rarely percurrently, terminal and intercalary, multi-local; loci thickened, not protuberant, apical, lateral. *Conidia* solitary, hyaline, acicular to cylindrical, slightly curved, obconically truncate or subtruncate, and thickened at the base, acute or obtuse at the apex, 30–85(–200) × 3.5–5 µm, 2–12-septate, thin-walled, smooth.

*Specimens examined*: **Japan**, Fukuoka, on *Disporum smilacinum* var. *ramosum* (*Convallariaceae*), 22 Sep. 1940, Y. Maki & T. Katsuki, **holotype** in SAPA? (specimen could not be located). **South Korea**, Pyeongchang, on *Disporum viridescens* (*Convallariaceae*), 20 Sep. 2003, H.D. Shin, CBS 132608 = CPC 10773; CPC 10774–10775.

*Notes*: *Cercospora chinensis* and *C. dispori* are distinguished from other *C. apii s. lat*. species in that their conidiophores are uniform in width, thick-walled, dark coloured and conically truncate at the apex. In this study, *C. chinensis* and *C. dispori* occur on *Convallariaceae*, and cluster together in a well-supported clade. On the individual gene trees, these two species (represented by isolates CPC 10831 and CPC 10773) rarely cluster and are both on long branches in the phylogenetic analyses. In the TEF phylogeny, *C. dispori* cannot be distinguished from *C. apii* / *C. beticola* whereas *C. chinensis* is a sister taxon to *C. pileicola*. In the ACT phylogeny, *C. chinensis* cannot be distinguished from *C. apii* / *C. beticola* and *C. dispori* is a sister taxon to the *C. apii* / *C. beticola* clade. In the CAL phylogeny the two species are indistinguishable and they are related to *C. lactucae-sativae*. In the HIS phylogeny the two species are sister taxa related to *C. citrullina*. In the combined tree (Fig. 2 part 5), it is a sister taxon to *C. chinensis*. Based on morphological characteristics, there is a difference between the two species in that the conidiophores of *C. chinensis* are sometimes branched. Thus, these two species are retained as separate taxa.

## ***Cercospora* cf. *erysimi***

*Specimen examined*: **New Zealand**, Manurewa, on *Erysimum mutabile* (*Brassicaceae*), 5 Dec. 2002, C.F. Hill, Lynfield 625, CBS 115059 = CPC 5361.

*Notes*: This species is phylogenetically supported by TEF, ACT, CAL and HIS. A collection on *Erysimum* (*Brassicaceae*) from Europe (isolate CPC 5056) clusters within *C. armoraciae*. The latter could also be the "true *C. erysimi*", which is still unclear. The type of *C. erysimi* is from North America. Thus, fresh material is needed from North America to resolve the application of the name "*C. erysimi*". In the combined tree (Fig. 2 part 1), it is a sister taxon to *C.* cf. *modiolae* and *Cercospora* sp. E.

## ***Cercospora euphorbiae-sieboldianae*** C. Nakash., Crous, U. Braun & H.D. Shin, **sp. nov.** MycoBank MB800655. Fig. 8.

*Etymology*: Named after the host from which it was collected, *Euphorbia sieboldiana.*

*Leaf spots* amphigenous, subcircular to irregular, 3–15 mm diam, coalenscing, up to 25 mm diam, brown to greyish brown, becoming whitish grey in centre, with blackish margins on upper surface, and greyish white to grey on lower surface. *Mycelium* internal. *Caespituli* amphigenous. *Stromata* small to well-developed, intraepidermal to


**Fig. 8.** *Cercospora euphorbiae-sieboldianae* (CBS 113306). A. Leaf spots. B. Close-up of lesion. C, D. Fasciculate conidiophores. E. Conidiophore giving rise to conidium. F–I. Conidia. Scale bars = 10 µm.

substomatal, brown to dark brown, 20–125 µm. *Conidiophores* loose to densely fasciculate in fascicles of 3–40, pale brown to brown, paler towards the apex, irregular in width, somewhat constricted at the proliferating point, conically truncate at the apex, 0–2-septate, straight or sinuous to geniculate due to sympodial proliferation, simple, rarely branched, 15–170 × 4.5–8 µm. *Conidiogenous cells* integrated, terminal, rarely intercalary, proliferating sympodially, 50–70 × 4–5 µm, multi-local; loci distinctly thickened, darkened, apical or formed on the shoulder, rarely lateral, 3–4.5 µm diam. *Conidia* solitary, hyaline to subhyaline, solitary, straight to slightly curved, obclavate to obclavate-cylindric, obconically truncated at the base, acute to obtuse at the apex, often beak-like at the apex, 38–130 × 5.5–8(–12) µm, (4–)3–6(–12)-septate, thin-walled, smooth; hila thickened, darkened, 3–4.5 µm diam.

*Culture characteristics*: Colonies erumpent, spreading, with sparse aerial mycelium and smooth, even margins, reaching 30 mm diam after 2 wk at 25 ºC in the dark. On MEA surface grey-olivaceous, reverse iron-grey. On PDA surface and reverse olivaceous-grey. Colonies forming spermatogonia in culture on both media.

*Specimen examined*: **South Korea**, Samcheok, on *Euphorbia sieboldiana* (*Euphorbiaceae*), 8 May 2003, H.D. Shin, **holotype** CBS H-21005, culture ex-type CBS 113306.

*Notes*: This species is phylogenetically distinguishable from its closest relatives in the TEF, ACT, CAL and HIS phylogenies. It is related to *C. polygonaceae* (TEF), *C. senecionis-walkeri* (ACT), *C. vignigena* (CAL) and *C. punctiformis* (HIS); therefore it is distinct from the other species occurring on *Euphorbiaceae* included in this study. In the combined tree (Fig. 2 part 2), it is a sister taxon to *C. punctiformis*. It is morphologically well distinguished from species of the *C. apii* complex and other species of *Cercospora* by its unusually broadly obclavate-cylindrical conidia (5.5–8(–12) µm) with few septa and rather broad loci and hila (3–4.5 µm).

***Cercospora fagopyri*** K. Nakata & S. Takim., J. Agric. Exp. Stat. Gov. Gen. Chosen 15: 29. 1928.

= *Cercospora fagopyri* Abramov, in Lavrov, Opred. rastit. paras. kul´t. i dikor. polezn. rast. Sibiri, Vyp. I: 22. 1932, nom. nud.

≡ *Cercospora fagopyri* Abramov, in Vasilevsky & Karakulin, Fungi imperfecti parasitici. 1. Hyphomycetes: 321. 1937, nom. illeg. (homonym).

= *Cercospora fagopyri* Chupp & A.S. Mull., Bol. Soc. Venez. Ci.. Nat. 8: 44. 1942, nom. illeg. (homonym).

*Caespituli* caulogenous, or amphigenous on leaves. *Mycelium* internal. *Stromata* intraepidermal or substomatal, pale brown, small to well-developed, 25–60 µm diam. *Conidiophores* pale brown, solitary, or in loose to dense fascicles (2–20), sinuously geniculate, rarely geniculate due to sympodial proliferation, usually irregular in width, frequently constricted due to proliferation, attenuated at the tip, truncate at the apex, multi-septate, 20–120 × 3.5–5.5 µm, 0–5-septate. *Conidiogenous cells* integrated, mainly terminal, rarely intercalary, proliferating sympodially, multi-local; loci thickened and darkened, apical and formed on the shoulder caused by sympodial proliferation, sometimes lateral, sometimes protuberant, 1.5–2.5 µm. *Conidia* solitary, hyaline, cylindrical to acicular, straight or slightly curved, long obconically truncate or truncate at the thickened and darkened base, obtuse or acute at the apex, 20–100 × 3–4 µm, 3–20-septate, thin-walled, smooth.

*Description of caespituli on V8*; (MUCC 130): *Caespituli* dimorphic, either small (common), or large (rarely observed; described in parenthesis). *Conidiophores* solitary to loosely fasciculate, arising from hyphae, subhyaline to pale brown, irregular in width, smooth, meager and thin-walled, sinuous-geniculate to geniculate (straight to geniculate), unbranched, truncated at the tip, 15–500 × 3–5 µm, multi-septate. *Conidiogenous cells* integrated, terminal or intercalary, proliferating sympodially, multi-local (uni-local); loci moderately thickened, apical, protuberant (not protuberant), 1.25–3 µm in width. *Conidia* solitary, hyaline, filiform to acicular, slightly thickened and obconically truncate (truncate) at the base, acute at the apex, 45.5–187 × 2–4.5 µm, 3–16-septate.

*Specimens examined*: **Japan**, Ehime, on *Cosmos bipinnata* (*Asteraceae*), 16 Oct. 2004, J. Nishikawa, MUMH 11394, MUCC 130; on *Hibiscus syriacus* (*Malvaceae*), MUCC 866. **South Korea**, Suwon, on *Viola mandshurica* (*Violaceae*), 14 Oct. 2003, H.D. Shin, CBS H-21006, CBS 132649 = CPC 10725; Yangpyeong, on *Cercis chinensis*, (*Fabaceae*), 19 Oct. 2007, H.D. Shin, CBS H-21007, CBS 132671 = CPC 14546; on *Fagopyrum esculentum* (*Polygonaceae*), 9 Oct. 2007, H.D. Shin, **neotype designated here** CBS H-21008, culture ex-neotype CBS 132623 = CPC 14541 (**holotype** specimen, South Korea, Suwon, on *Fag. esculentum*, Sep. 1934, K. Nakata & S. Takimoto, could not be located and is undoubtedly not preserved); on *Fallopia dumentorum* (*Polygonaceae*), 16 Oct. 2002, H.D. Shin, CBS H-21009, CBS 132640 = CPC 10109.

*Notes*: Phylogenetically the separation of *C. fagopyri* is supported by the TEF and HIS phylogenies, though it is intermixed with strains of *C.* cf. *sigesbeckiae* in the ACT phylogeny and of *C. kikuchii* in the CAL phylogeny. In the combined tree (Fig. 2 part 4), it is a sister taxon to *C.* cf. *ipomoeae*. Presently several isolates originating from diverse host families reside in this clade. However, lesions on *Viola* appear to be insect associated, and caused by a *Colletotrichum* species, with *Cercospora* colonisation being secondary. Furthermore, lesions on *Fallopia dumentorum* appear to be associated with chemical damage, not *Cercospora*, again suggestion that *Cercospora* colonisation was secondary. The fungus occurring on *Cercis chinensis* is distinct, having very long conidiophores (200–600 µm), and very long conidia. To resolve the host range of *C. fagopyri*, isolates from *Fagopyrum* need to be recollected in Korea, and pathogenicity established on the hosts listed above. Thus the name *C. fagopyri* can only be applied to other isolates than those from *Fagopyrum* tentatively, awaiting additional fresh collections.

## *Cercospora* cf. *flagellaris*

*Caespituli* amphigenous. *Mycelium* internal. *Stromata* lacking to well-developed, up to 50 µm diam, brown, intraepidermal and substomatal. *Conidiophores* straight or successively geniculate at the apex, rarely abruptly geniculate, solitary, or in loose to dense fascicles (2–23), pale brown to brown, paler towards the apex, simple, rarely branched, uniform in width up to the middle, strongly attenuated at the upper portion, sometimes constricted at septa, often constricted following sympodial proliferation, 14–140(–270) × 2.5–6.5 µm, 0–8-septate, truncate or short obconically truncated at the apex. *Conidiogenous cells* integrated, terminal and intercalary, proliferating sympodially, multi-local (2–5); loci distinctly thickened, apical or formed on the shoulders caused by geniculation, lateral, rarely protuberant, small, 1–4 µm. *Conidia* solitary, hyaline, cylindrical to acicular, sometimes obclavate, straight or slightly curved, truncate or short obconical truncate at the thickened and darkened base, acute at the apex, 18–240 (–300) × 2–4.5 µm, 1–12-septate, thin-walled, smooth.

*Description of caespituli on V8*; MUCC 127: *Conidiophores* solitary, arising from hyphae, pale brown, uniform in width, sometimes wider at the base, smooth, straight to slightly sinuous, conically truncate at the tip, 10–95 × 3–5 µm, multi-septate. *Conidiogenous cells* integrated, terminal; loci distinctly thickened, apical, 1.25–2 µm in width. *Conidia* hyaline, acicular to filiform, slightly thickened and truncate at the base, acute at the apex, 35–220 × 2–3 µm, 2–15-septate.

*Specimens examined*: **Fiji**, on *Amaranthus* sp. (*Amaranthaceae*), C.F. Hill, Lynfield 677, CPC 5441. **Israel**, on *Trachelium* sp. (*Campanulaceae*), 16 Nov. 2002, E. Tzul-Abad, CBS 132637 = CPC 10079 (as *C. campanulae*). **Japan**, Ehime, on *Cosmos sulphureus* (*Asteraceae*), 16 Oct. 2004, J. Nishikawa, MUMH 11393, MUCC 127; Tokyo, on *Hydrangea serrata* (*Hydrangeaceae*), 10 Nov. 2007, I. Araki & M. Harada, MUMH 10933, MUCC 831; Wakayama, on *H. serrata*, 30 Oct. 2007, C. Nakashima & I. Araki, MUMH 10860, MUCC 735. **South Korea**, Hoengseong, on *Celosia argentea* var. *cristata* (≡ *C. cristata*), 11 Oct. 2004, H.D. Shin, CBS 132667 = CPC 11643 (as *Cercospora* sp.); Jeju, on *Dysphania ambrosioides* (≡ *Chenopodium ambrosioides*) (*Chenopodiaceae*), 12 Nov. 2003, H.D. Shin, CBS 132653 = CPC 10884 (as *C. chenopodii-ambrosioidis*); on *Phytolacca americana* (*Phytolaccaceae*), 1 Nov. 2007, H.D. Shin, CBS 132674 = CPC 14723; CPC 14724; Jinju, on *P. americana*, 15 Oct. 2003, H.D. Shin, CPC 10684–10686; Namyangju, on *Amaranthus patulus*, 30 Sep. 2003, H.D. Shin, CBS 132648 = CPC 10722; Pocheon, on *P. americana*, 23 Oct. 2002, H.D. Shin, CPC 10124; Suwon, on *Cichorium intybus* (*Asteraceae*), 14 Oct. 2003, H.D. Shin, CBS 132646 = CPC 10681 (as *C. cichorii*); Yanggu, on *Sigesbeckia pubescens* (*Asteraceae*), 28 Sep. 2007, H.D. Shin, CBS 132670 = CPC 14487. **South Africa**, Limpopo Province, Messina, *Citrus* sp. (*Rutaceae*), M.C. Pretorius, CBS 115482 = CPC 4410; CPC 4411; on *Populus deltoides* (*Salicaceae*), P.W. Crous, CPC 1051–1052. **Unknown**, on *Bromus* sp. (*Poaceae*), M.D. Whitehead, CBS 143.51 = CPC 5055. **USA**, Texas, on *Eichhornia crassipes* (*Pontederiaceae*), R. Charudattan & D. Tessmann, 14 Sep. 1996, CBS 113127 (as *C. piaropi*).

*Notes*: The isolates from this species form a monophyletic clade identical to one another and the two isolates of *C.* cf. *brunkii* on the TEF phylogeny. In the CAL phylogeny the *C.* cf. *flagellaris* isolates form a monophyletic clade, albeit with some intraspecific variation. Based on ACT data, the clade splits into four lineages: 1. CPC 4410 and 4411, 2. CPC 1052, 1051 and 10681, 3, CPC 5441 and, 4. the remainder of the isolates. In the HIS phylogeny the species also splits into four lineages: 1. CPC 4410, 4411, 10884 and MUCC 735, 2. CPC 10681 and 11643, 3. CPC 5441 and, 4. the rest of the isolates. These splits in phylogeny (see Fig. 2 parts 2–3) are not supported by morphology: conidiophores are successively geniculate at the upper portion, strongly attenuated at the apex; conidiogenous cells are terminal and intercalary with multi-local loci, and conidia are truncate or short obconically truncate at the thickened base. We strongly suspect that this is a species complex. The latter can only be resolved once more authentic isolates for the names listed above are included (from original hosts and countries), additional DNA loci screened, and pathogenicity tests conducted. Included in this species complex is the isolate used by Tessmann *et al*. (2001) as *C. piaropi*. This isolate is indistinguishable from other isolates of *C.* cf. *flagellaris* based on the TEF, ACT, CAL and HIS phylogenies. *Cercospora flagellaris* is the older name (1882) compared to *C. piaropi* (1917) and should therefore get taxonomic preference.

## *Cercospora* cf. *helianthicola*

*Caespituli* amphigenous. *Mycelium* internal. *Stromata* brown, lacking or small, intraepidermal or substomatal, up to 25 µm diam. *Conidiophores* simple, occasionally branched, straight to geniculate, pale brown, arising from small stromata or internal hyphae, solitary or in dense fascicles (up to 15), irregular in width, narrowed at successive geniculation, truncate at the apex, moderately thick-walled, 20–180 × 3–4 µm, septate. *Conidiogenous cells* integrated, terminal, proliferating sympodially, multi-local; loci distinctly thickened, apical and formed on the shoulders caused by geniculation, rarely lateral, refractive, 1.5–2 µm. *Conidia* solitary, acicular to cylindrical, hyaline, straight or curved, truncate and distinctly thickened at the base, obtuse at the apex, 10–85 × 3–4 µm, indistinctly multi-septate, thin-walled, smooth.

*Specimen examined*: **Japan**, Wakayama, on *Helianthus tuberosus* (*Asteraceae*), 30 Oct. 2007, C. Nakashima & I. Araki, MUMH 10844, MUCC 716.

*Notes*: This species is distinguished from other taxa in that it has slightly protuberant apical loci that are at times formed on shoulders caused by geniculation. The width of its conidiogenous cells is somewhat narrower behind the fertile region, and has a truncate apex. Furthermore, its conidiophores are rarely branched. A possible name that could be applied is *C. helianthicola*, though the latter species was originally described from South America, and fresh collections would be required to confirm its phylogenetic position. The isolate used in the current study is distinct in the TEF, ACT, CAL and HIS phylogenies. In the combined tree (Fig. 2 part 5), it is a sister taxon to *C.* cf. *citrulina*.

## *Cercospora* cf. *ipomoeae*

*Caespituli* amphigenous. *Mycelium* internal. *Stromata* composed of few brown cells, or well-developed, up to 60 µm diam, intraepidermal or substomatal. *Conidiophores* in loose fascicles (2–8), pale brown, paler towards apex, straight or geniculate at the apex, irregular in width, tip conically truncate, narrowed at the apex, 22.5–92.5 × 3.5–5.5 µm, 0–4-septate. *Conidiogenous cells* integrated, terminal, proliferating sympodially, multi-local; loci thickened, darkened, apical, rarely lateral, rarely slightly protuberant, 2–2.5 µm diam. *Conidia* solitary, hyaline, filiform to acicular, slightly curved, obconically truncate or truncate, and thickened and darkened at the base, acute or obtuse at the apex, 50–135(–245) × 2.5–3(–7.5) µm, 3–19-septate, thin-walled, smooth.

*Specimens examined*: **Japan**, Kagawa, on *Ipomoea aquatica* (*Convolvulaceae*), Aug. 2005, G. Kizaki, MUMH 11203, MUCC 442; **South Korea**, Chuncheon, on *Ipomoea nil* (= *I. hederacea*) (*Convolvulaceae*), 7 Oct. 2003, H.D. Shin, CBS H-21010, CBS 132652 = CPC 10833; Pocheon, on *Persicaria thunbergii* (*Polygonaceae*), 2 Oct. 2002, H.D. Shin, CBS H-21011, CBS 132639 = CPC 10102.

*Notes*: This species is supported in the TEF phylogeny but cannot be distinguished from *Cercospora* sp. M and *C. rodmanii* in the ACT phylogeny. Isolate MUCC 442 clusters separately from the other two isolates based on the CAL and HIS phylogenies. In the combined tree (Fig. 2 part 4), it is a sister taxon to *C. fagopyri*. Sequences obtained from *Cercospora* isolates on *Ipomoea* spp. cluster in three different clades. Although the name *C. ipomoeae* is available for this clade, without sequence data from North America (and an appropriate epitype) this name cannot be applied with certainty, above all since isolates from *Ipomoea* cluster in different clades.

## *Cercospora kikuchii* (T. Matsumoto & Tomoy.) M.W. Gardner, Proc. Indian Acad. Sci. 36: 12. (1926) 1927.

*Basionym*: *Cercosporina kikuchii* T. Matsumoto & Tomoy., Ann. Phytopathol. Soc. Japan 1: 10. 1925.

*Specimens examined*: **Argentinia**, on *Glycine max* (*Fabaceae*), CBS 132633 = CPC 16578. **Japan**, Kagoshima, on *Glycine soja* (*Fabaceae*), 1952, H. Kurata, MUCC 590 = MAFF 305040; on *G. soja*, Jan. 1927, T. Matsumoto, CBS 128.27 = CPC 5068 (**ex-type** of *C. kikuchii*); on seed of *G. soja*, Jan. 1928, H.W. Wollenweber, CBS 135.28 = CPC 5067.

*Notes*: The symptoms on seeds and pods of plants inoculated with an isolate of *C. richardiicola* (MUCC 132; Nakashima, unpubl. data) originating from *Osteospermum* (*Asteraceae*) in Japan were quite similar to those caused by *C. kikuchii*. Cultures of *C. kikuchii* associated with purple seed stain symptoms cluster apart. This indicates that purple seed stain and leaf blight of *G. max* is caused by at least two different species of *Cercospora*, and that the identification of these species should not be based on disease symptoms alone. In the TEF and HIS phylogeny, the four isolates could not be distinguished from isolates of *Cercospora* sp. O, P and Q, as well as *C.* cf. *richardiicola* and *C.* cf. *sigesbeckiae*. Although these isolates clustered separate in the ACT phylogeny, intermixed in the clade was isolate CPC 14680 (*C.* cf. *richardiicola*) and isolate CPC 18636 (*Cercospora* sp. O). Similarly, the isolates clustered separate in the CAL phylogeny but intermixed with the isolates of *C. fagopyri*. In the combined tree (Fig. 2 part 4), it is a sister taxon to *C.* cf. *sigesbeckiae*.

## *Cercospora lactucae-sativae* Sawada, Rep. Gov. Agric. Res. Inst. Taiwan 35: 111. 1928.

≡ *Cercospora lactucae* Welles, Phytopathology 13: 289. 1923, nom. illeg. (homonym), non Henn.

= *Cercospora longispora* Cugini ex Trav., Malpighia 17: 217, 1902, nom. illeg. (homonym).

≡ *Cercospora longissima* Trav., Malpighia 17: correzione (correction slip) to p. 217, 1903, nom. illeg. (homonym).

≡ *Cercospora longissima* Cugini ex Sacc., Syll. Fung. 18: 607. 1906, nom. illeg. (homonym).

= *Cercospora lactucae* J.A. Stev., J. Dept. Agric. Puerto Rico 1: 105. 1917, nom. illeg. (homonym).

= *Cercospora ixeridis-chinensis* Sawada, Rep. Gov. Agric. Res. Inst. Taiwan 86: 171. 1943, nom. inval.

= *Cercospora lactucae-indicae* Sawada, Rep. Gov. Agric. Res. Inst. Taiwan 86: 172. 1943, nom. inval.

*Caespituli* amphigenous. *Mycelium* internal. *Stromata* lacking or composed from few brown cells, up to 35 µm diam. *Conidiophores* arising from internal hyphae or a few intraepidermal brown cells, brown to pale brown, solitary to loosely fasciculate (2–7), straight or mildly geniculate, moderately thick-walled, irregular in width, wider and conically truncate at the apex, constricted at proliferating point, 25–150 × 3.5–6 µm, 0–5-septate. *Conidiogenous cells* integrated, terminal and intercalary, proliferating sympodially, uni-local or multi-local (1–2); loci distinctly thickened, 2.5–3.5 µm diam, slightly protuberant, apical. *Conidia* solitary, hyaline, filiform to acicular, or obclavate, obconically truncate and distinctly thickened at the base, subacute or obtuse, often swelling at the apex, 20–125 × 2–6 µm, 4–12-septate, thin-walled, smooth, rarely catenate.

*Description of caespituli on V8 & MEA*; MUCC 570 and 571 (= MAFF 238209 and 237719): *Conidiophores* solitary to loosely fasciculate, pale brown to brown, irregular in width, wider at the apex, constricted at proliferating point, smooth, moderately thick-walled, sinuous-geniculate to geniculate, simple, conically truncate at the apex, 22.5–195 × 3–5.5 µm, multi-septate. *Conidiogenous* *cells* integrated, terminal or intercalary, proliferating sympodially; loci moderately thickened, apical, 2.5–3.7 µm in width. *Conidia* hyaline, cylindrical to cylindrical obclavate, filiform, acicular, hilum distinctly thickened and long obconically truncate at the base, obtuse to acute at the apex, 44.5–215.5 × 3–7 µm, 5–20-septate.

*Specimens examined*: **Japan**, Chiba, on *Lactuca sativa* (*Asteraceae*), 12 Sep. 1997, S. Uematsu, MUCC 571 = MAFF 237719 = MUCNS 214; 18 Sep. 1998, C. Nakashima, MUMH 11401, MUCC 570 = MAFF 238209 = MUCN S463. **South Korea**, Chuncheon, on *Ixeris chinensis* subsp. *strigosa* (≡ *Ixeris strigosa*) (*Asteraceae*), 11 Oct. 2002, H.D. Shin, CBS H-21012, CPC 10082; 7 Oct. 2003, H.D. Shin, CBS H-21013, CBS 132604 = CPC 10728. **Taiwan**, Taipei, on *L. sativa*, 9 Mar. 1924 & 5 Apr. 1924, K. Sawada (TNS-F-220470).

*Notes*: This species is characterised in that conidiophores are wide and conically truncate at the apex, and constricted at the proliferating point. Furthermore, the conidia are not strictly acicular, but range from cylindrical-obclavate to acicular and they are rather broad, 3–7 µm. This species is phylogenetically well-supported based on ACT, CAL and HIS. The species cannot be distinguished from the single isolate of *Cercospora* sp. S in the TEF phylogeny, and these two species are also sister groups, but distinct, in the ACT phylogeny. The species is distinguished based on the CAL phylogeny, and split into two groups (MUCC 571 and 571 versus CPC 10082 and 10728) in the HIS phylogeny. In the combined tree (Fig. 2 part 5), it is a sister taxon to *C.* cf. *helianthicola*.

## *Cercospora* cf. *malloti*

*Caespituli* amphigenous. *Mycelium* internal. *Stromata* lacking to well-developed, intraepidermal and substomatal, up to 65 µm diam. *Conidiophores* arising from internal hyphae or few brown cells, solitary or in loose fascicles (2–11), pale brown to brown, paler towards the apex, thick-walled, simple, rarely branched, straight or mildly geniculate, abruptly geniculate at the middle, or successively geniculate at the upper portion, irregular in width, narrowed at the apex, somewhat constricted at the part of proliferation, obconically truncate at the apex, 30–115(–250) × 2.5–5.5 µm, multi-septate. *Conidiogenous cells* integrated, terminal and intercalary, proliferating sympodially or percurrently, multi-local; loci apical or formed on the shoulders caused by geniculation, distinctly thickened, refractive, darkened, flattened, rarely protuberant at the shoulder of successive geniculation, 1–2 µm diam. *Conidia* solitary, hyaline, filiform to acicular, thickened and truncate at slightly protuberant base, obtuse or swelling at the apex, 40–90(–250) × 1.5–5 µm, 6–11(–20)-septate.

*Description of caespituli on V8*; MUCC 575 (= MAFF 237872): *Conidiophores* solitary, brown, paler at the apex, uniform in width, smooth, moderately thick-walled, simple, straight to mildly geniculate, short conically truncate at the tip, 100–465 × 1.25–3 µm, multi-septate. *Conidiogenous cells* integrated, terminal and intercalary, proliferating sympodially; loci thickened, flattened, apical or formed on the shoulders caused by geniculation, 2–3 µm in width. *Conidia* hyaline, long cylindrical to filiform, slightly thickened and truncate at the base, obtuse at the apex, 30–430 × 2–4 µm, 3–19-septate, thin-walled, smooth.

*Specimens examined*: **Japan**, Okinawa, on *Mallotus japonicus* (*Euphorbiaceae*), 19 Nov. 2007, C. Nakashima & T. Akashi, MUMH 10837, MUCC 787; on *Cucumis melo* (*Cucurbitaceae*), 20 Jan. 1999, K. Uehara, MUCC 575 = MAFF 237872 = MUCNS 582 (as *C. citrullina*).

*Notes*: This species is supported by DNA sequence data of TEF, CAL and HIS. In the ACT phylogeny, the isolates from this species are intermixed with some isolates of *C.* cf. *richardiicola* (MUCC 128, 132 and 578) and *Cercospora* sp. P (isolate MUCC 771). In the combined tree (Fig. 2 part 4), it is a sister taxon to *Cercospora* sp. P. The isolates originated from different host plants, but have identical conidiophores, which are thick-walled and with distinct loci at the apex. However, other characters, which include the pattern of geniculation and size of caespituli, are very different. More detailed studies are required to describe the morphological characters of this species. *Cercospora malloti* was originally described from *Mallotus* (*Euphorbiaceae*) collected in the USA, and fresh material needs to be recollected. The present application of this name for Japanese collections is thus only tentative.

## *Cercospora mercurialis* Pass., in Thüm., Mycoth. Univ., No. 783. 1877.

= *Cercospora fruticola* Sacc., Fungi Ital., Tab. 674. 1892.
= *Cercospora mercurialis* var. *annuae* Fautrey, in Roumeguere *et al*., Rev. Mycol. 15: 16. 1893.
= *Cercospora mercurialis* var. *latvici* Lepik, Tartu Ülik. Juures Oleva Loodusuur. Seltsi Arunded 39: 152. 1933.
= *Cercospora mercurialis* var. *multisepta* Săvul. & Sandu, Hedwigia 75: 225. 1936.

*Specimens examined*: **Italy**, Parma, on *Mercurialis annua* (*Euphorbiaceae*), 1874, Passerini, Thüm., Mycoth. Univ. 783, **isotypes** HBG, HAL. **Romania**, Distr. Prahova, Cheia, on *Mercurialis perennis* (*Euphorbiaceae*), 31 Jul. 1969, O. Constantinescu, **epitype designated here** CBS H-9850, culture ex-epitype CBS 550.71; on *M. annua*, 28 Jun. 1967, O. Constantinescu, CBS 549.71; Constanta, Hagieni, on *Mercurialis ovata* (*Euphorbiaceae*), 14 Jul. 1970, O. Constantinescu & G. Negrean, CBS H-9848, BUCM 2012, CBS 551.71.

*Notes*: *Cercospora mercurialis* is supported by TEF, ACT, CAL and HIS and can therefore be treated as an individual species. In the combined tree (Fig. 2 part 2), it is a sister taxon to *C. pileicola*.

## *Cercospora* cf. *modiolae*

*Specimen examined*: **New Zealand**, leaf spot on *Modiola caroliniana* (*Malvaceae*), 2002, C.F. Hill, Lynfield 535, CPC 5115.

*Notes*: This species is phylogenetically supported by TEF and ACT, but in the CAL and HIS phylogeny it cannot be distinguished from *Cercospora* sp. E. In the combined tree (Fig. 2 part 1), it is a sister taxon to *Cercospora* sp. E. *Cercospora modiolae* was described from North America and without sequences based on North American collections, this name can only tentatively be applied to the material from New Zealand.

## *Cercospora* cf. *nicotianae*

*Cultures examined*: **Indonesia**, Medan, leaf spot on *Nicotiana tabacum* (*Solanaceae*), Jan. 1932, H. Diddens & A. Jaarsveld, CBS 131.32 = CPC 5076. **Mexico**, southern region of Tamaulipas, on *Glycine max*, 17 Oct. 2008, Ma. de Jesús Yáñez-Morales, CBS 132632 = CPC 15918. **Nigeria**, from a leaf spot on *N. tabacum*, Jul. 1969, S.O. Alasoadura, CBS 570.69 = CPC 5075.

*Notes*: See *C. capsici.* The name *C.* cf. *nicotianae*, described from the USA, can only tentatively be applied here. North American cultures and sequence data are needed for comparison and confirmation. Phylogenetically, *C.* cf. *nicotianae* is supported by CAL and partly HIS (CPC 5075 and 5076 were separated from CPC 15918). In the TEF phylogeny, the three isolates clustered in a distinct clade with a single isolate from *C.* cf. *flagellaris* (CPC 5441) but formed three distinct lineages in the ACT phylogeny. In the combined tree (Fig. 2 part 5), it is a sister taxon to *C.* cf. *brunkii*. Notes in the CBS database report that

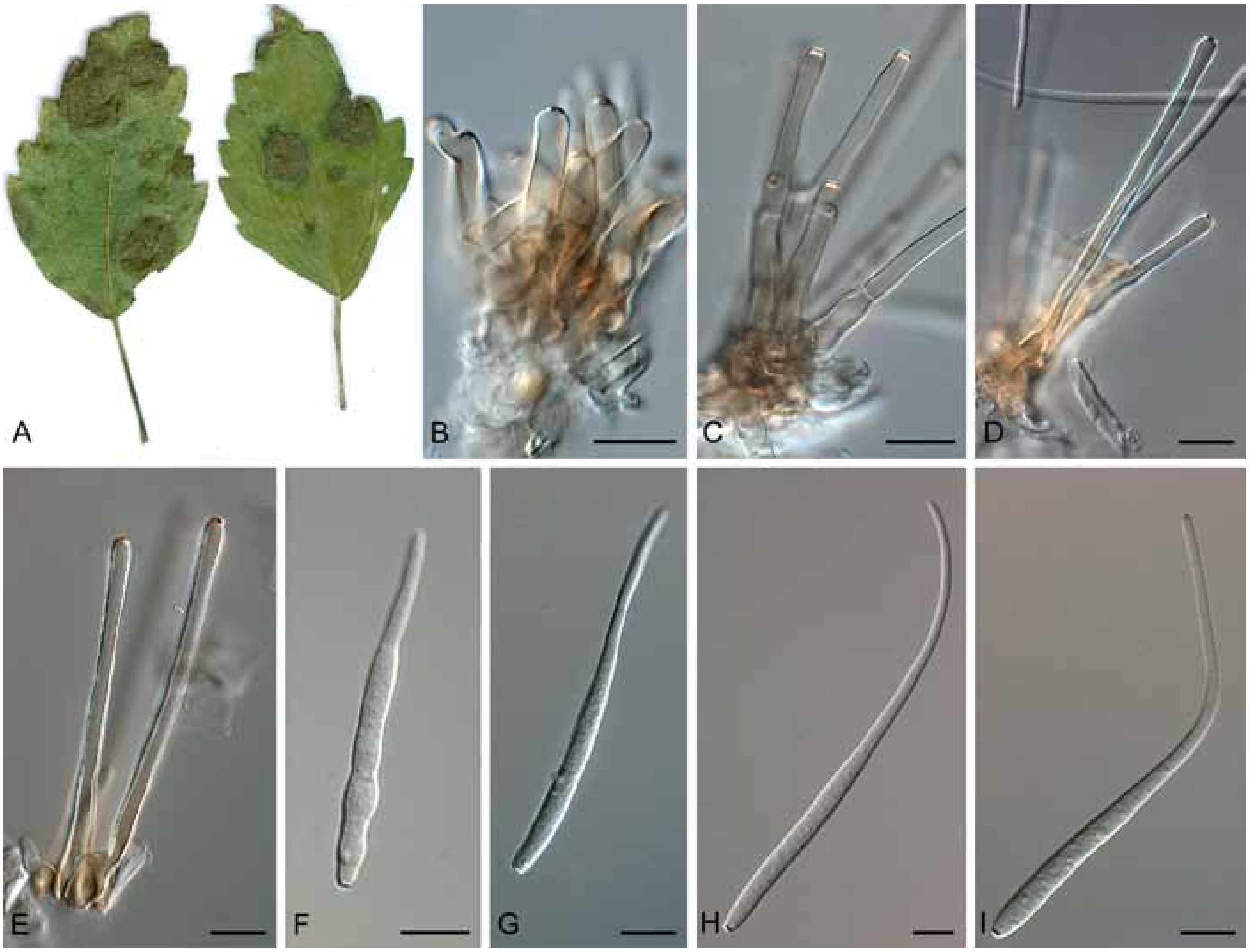



**Fig. 9.** *Cercospora pileicola* (CBS 132607 = CPC 10749). A. Leaf spots. B–E. Weakly developed, fasciculate conidiophores. F–I. Conidia. Scale bars = 10 µm.

isolate CBS 131.32 was pathogenic when inoculated onto *Nicotiana* leaves. The isolation of *C.* cf. *nicotianae* from *G. max* requires some additional explanation. Leaf spots typical of *Corynespora cassicola* were observed, and once incubated in damp chambers, a *Cercospora* sp. was found sporulating on the healthy tissue, which was identified here as *C.* cf. *nicotianae*.

### ***Cercospora olivascens*** Sacc., Michelia 1: 268. 1879.

*Specimens examined*: **Italy**, Selva, on *Aristolochia clematidis* (*Aristolochiaceae*), Aug. 1877, **isotype** distributed as Mycoth Veneta 1251, HAL. **Romania**, Cazanele Dunarii, on *A. clematidis*, 19 Oct. 1966, O. Constantinescu, **epitype designated here** CBS H-21014, culture ex-type CBS 253.67= IMI 124975 = CPC 5085.

*Notes*: This species is supported by TEF, ACT, CAL and HIS. In the combined tree (Fig. 2 part 1), it is a sister taxon to *Cercospora* sp. F.

### ***Cercospora* cf. *physalidis***

*Specimen examined*: **Peru**, on *Solanum tuberosum* (*Solanaceae*), L.J. Turkensteen, CBS 765.79.

*Notes*: This species is supported by CAL and HIS. It cannot be distinguished from *Cercospora* sp. I and *C. alchemillicola / C.* cf. *alchemillicola* based on the TEF and ACT phylogenies. In the combined tree (Fig. 2 part 1), it is a sister taxon to *Cercospora* sp. G. According to Braun & Melnik (1997), *C. physalidis* and numerous *Cercospora* spp. of *C. apii s. lat.* on various hosts of the *Solanaceae* are morphologically indistinguishable from the latter species. Fresh material on *Solanum* from North America is required to resolve this issue.

### ***Cercospora pileicola*** C. Nakash., Crous, U. Braun & H.D. Shin, **sp. nov.** MycoBank MB800656. Fig. 9.

*Etymology*: Named after the host genus from which it was collected, *Pilea.*

*Leaf spots* circular, 1–2 mm diam, center greyish to pallid, surrounded by purplish brown border lines. *Caespituli* hypogenous. *Mycelium* internal. *Stromata* lacking to small, to 30 µm diam, brown, substomatal. *Conidiophores* straight to curved, pale brown to dark brown, paler towards the apex, solitary or in loose fascicles (2–5), sometimes mildly geniculate, simple, thick-walled, uniform in width, rarely narrowed after the geniculation, conically truncate at the apex, 30–110 × 3–8.5 µm, often swelling at the base, to 9 µm, 1–3-septate. *Conidiogenous cells* integrated, terminal, proliferating sympodially; loci distinct, slightly protuberant, apical and formed on shoulder caused by geniculation, lateral, multi-local (1–2), 2.5–4 µm diam. *Conidia* hyaline, cylindrical, acicular to obclavate, straight or curved, truncate or long obconically truncate, and slightly thickened at the base, acute to obtuse at the apex, 28–175 × 4–7 µm, 0–12-septate.

*Culture characteristics*: Colonies erumpent, spreading, with moderate, fluffy aerial mycelium and lobate, even margins, reaching 25 mm diam after 1 wk at 25 ºC in the dark. On MEA surface dirty white, reverse cream; red pigment absent. On PDA surface dirty white, reverse scarlet, with diffuse red pigment in agar. On OA surface scarlet in middle (due to collapsed aerial mycelium), white in outer region (due to aerial mycelium), with diffuse red pigment surrounding colony.

*Specimens examined*: **South Korea**, Dongducheon, on *Pilea pumila* (= *P. mongolica*) (*Urticaceae*), 28 Sep. 2003, H.D. Shin, **holotype** CBS H-21015, culture **ex-type** CBS 132607 = CPC 10749; Hoengseong, on *Pilea hamaoi* (≡ *P. pumila* var. *hamaoi*) (*Urticaceae*), 10 Oct. 2003, H.D. Shin, CBS H-21016, CBS 132647 = CPC 10693; Hongcheon, on *Pilea pumila* (= *P. mongolica*), 29 Jul. 2004, H.D. Shin, CPC 11369.

*Notes*: *Cercospora pileicola* is characterised by having conidiophores that are thick-walled, almost uniform in width, conically truncate at the apex, and often swelling at the base; sporulation is restricted at the terminal part of conidiophores, and conidia are cylindrical, acicular to obclavate with long obconically truncate basal ends and rather broad, 4–7 µm. Moreover, this species is phylogenetically supported by the TEF, ACT, CAL and HIS phylogenies. In the combined tree (Fig. 2 part 2), it is a sister taxon to *C. mercurialis*. *Cercospora ganjetica* (Purkayastha & Mallik 1978), described from India on *Urtica urens* (*Urticaceae*), seems to be morphologically similar to *C. pileicola*, above all due to relatively broad conidia, but the conidia are strictly cylindrical to obclavate with obconically truncate base, i.e. acicular conidia with truncate base are not formed. Length and width of conidiophores agree with those of *C. pileicola*, but they are pluriseptate (3–6). The affinity of *C. ganjetica* is quite unclear. *Cercospora pileae* (Chupp 1954) was described from China on "*Pilea* sp." with conidia being olivaceous. This species is not included in the Chinese monograph of *Cercospora* species (Guo & Liu 2005), but Liu & Guo (1998) reduced this name to synonym with *Pseudocercospora profusa*, suggesting that the type host was misidentified, which was confirmed by Y.L. Guo (Beijing, *in litt.*). The type of *C. pileae* is not *Pilea* sp. but *Acalypha australis* (*Euphorbiaceae*). Chinese collections of *Cercospora* on various hosts of the *Urticaceae*, including *Pilea* spp., have been assigned to *Cercospora krugeriana* (= *nom. inval*.), which is a quite distinct *C. apii*-like species with narrower (2.5–5 µm), pluriseptate, acicular conidia, up to 214 µm long (Hsieh & Goh 1990, Guo & Liu 2005). In addition, the conidiophores are distinctly plurigeniculate. It is possible that the latter collections belong to the *C.* cf. *sigesbeckiae* clade as circumscribed in this study.

## ***Cercospora polygonacea*** Ellis & Everh., J. Mycol. 1: 24. 1885.

= *Cercospora avicularis* var. *sagittati* G.F. Atk., J. Elisha Mitchell Sci. Soc. 8: 48. 1892.
= *Cercospora polygoni-caespitosi* Sawada, Formosan Agric. Rev. 38: 700. 1942, nom. inval.
= *Cercospora polygoni-blumei* Sawada, nom. nud.

*Caespituli* amphigenous. *Mycelium* internal. *Stromata* lacking to small, up to 30 µm diam, pale olivaceous-brown, intraepiderimal, substomatal. *Conidiophores* successively geniculate at the upper portion, pale brown, paler towards the apex, solitary or in loose fascicles (2–5), simple, thick-walled, irregular in width, narrowed after the geniculation, conically truncated at the apex, 21–100 × 5–7 µm, 0–3-septate. *Conidiogenous cells* integrated, terminal, intercalary, proliferating sympodially, multi-local (1–6); loci distinct, protuberant, apical and formed on shoulder caused by geniculation, lateral, 2.5–3 µm diam. *Conidia* solitary, hyaline, acicular to obclavate, straight or slightly curved, truncate or obconically truncate, and thickened at the base, obtuse or acute at the apex, 60–110 × 3.5–5.5 µm, 4–9-septate, thin-walled, smooth.

*Specimen examined*: **South Korea**, Cheongju, on *Persicaria longiseta* (≡ *P. blumei*) (*Polygonaceae*), 4 Jun. 2004, H.D. Shin, CBS H-21017, CBS 132614 = CPC 11318.

*Notes*: Morphologically the Korean specimen is similar to *C. polygonaeae*, which Chupp (1954) also reported from Asia (Japan). Material from the USA on *Polygonum* (*Polygonaceae*) is required to resolve whether this taxon is the same or phylogenetically distinct. The species is phylogenetically distinct from the other species included in this study based on the TEF and ACT phylogenies, but indistinguishable from *C. achyranthis* on the HIS phylogeny and from *C. achyranthis*, *C. sojina* and *C. campi-silii* based on the CAL phylogeny. In the combined tree (Fig. 2 part 2), it is a sister taxon to *C. achyranthis*.

## ***Cercospora punctiformis*** Sacc. & Roum., Rev. Mycol. 3: 29. 1881.

= *Fusicladium cynanchi* Reichert, Bot. Jahrb. Syst. 56: 720. 1921.
= *Cercospora punctiformis* f. *catalaunica* Gonz. Frag., Mem. Real Acad. Ci. Exact. Madrid, Ser. 2, 6: 250–252. 1927.
= *Cercospora cynanchi* Lobik, Mat. Fl. Faun. Obsl. Tersk. Okr., Pjatigorsk: 53. 1928.

*Leaf spots* scattered to confluent, at first appearing as purplish spots, later greyish brown with purplish border lines, mostly vein-limited, but rather circular to irregular in case of humid and hot weather (esp. in rainy summer), mostly less than 7 mm diam. *Caespituli* amphigenous, but abundantly hypophyllous. *Mycelium* internal. *Stromata* well-developed, up to 35 µm diam, substomatal and intraepidermal, brown to dark brown. *Conidiophores* in fascicles (5–30), loose to moderately divergent, olivaceous-brown, fairly uniform in colour, but paler towards the apex in longer ones, simple, conically truncate at the apex, geniculate (0–4), 20–60(–150) × 4–7.5 µm, 0–3-septate. *Conidiogenous cells* integrated, proliferating sympodially, terminal and intercalary; loci distinctly thickened, protuberant, apical or formed on the shoulders caused by geniculation, 3–4 µm diam. *Conidia* solitary, hyaline, variable in shape and length, obclavato-cylindrical or elliptical, obconically truncate and thickened at the base, obtuse to subacute at the apex, 25–100(–175) × 4–6.5 µm, 0–8(–12)-septate, thin-walled, smooth.

*Specimen examined*: **South Korea**, Bonghwa, on *Cynanchum wilfordii* (*Asclepiadaceae*), 18 Oct. 2007, H.D. Shin, CBS H-21018, CBS 132626 = CPC 14606.

*Notes*: The Korean sample on *Cy. wilfordi* is morphologically close to *Cercospora punctiformis*, but the latter species was described from North Africa. Hence, sequence data based on North African material are needed to confirm the conspecificity of Korean collections. The ACT and HIS phylogenies separate *C. punctiformis* from the other species included in this study; in the TEF and CAL phylogenies the isolate occurs on a longer branch in a clade consisting of *C. sojina* and *C. achyranthis*. In the combined tree (Fig. 2 part 2), it is a sister taxon to *C. euphorbiae-sieboldianae*.

## ***Cercospora* cf. *resedae***

*Specimens examined*: **New Zealand**, Auckland, C.F. Hill, on *Reseda odorata* (*Resedaceae*), specimen in HAL, CBS 118793 (as *C. resedae*). **Romania**, Bucuresti, on *Helianthemum* sp. (*Cistaceae*), 15 Sep. 1966, O. Constantinescu, CBS 257.67 = CPC 5057 (as *C. cistinearum*).

*Notes*: Both the names *C. resedae* and *C. cistinearum* are available for this clade. We give preference to *C. resedae*, which is the older name. However, the application of this name is very uncertain and only tentative. Fresh European collections from *Reseda* (*Resedaceae*) are needed to designate an epitype and fix the application of the name. The TEF and ACT phylogenies could not distinguish these two isolates from *C. apii* and *C. beticola*, and the CAL phylogeny could not distinguish it from *C. apii*. The HIS phylogeny places the two isolates in the deviating *C. beticola* Clade 1. A combination of these phylogenetic positions explains the basal position of the species to the *C. apii* and *C. beticola* clades in the combined phylogeny (Fig. 2 part 5).

## *Cercospora* cf. *richardiicola*

*Caespituli* amphigenous. *Mycelium* internal. *Stromata* intraepidermal or substomatal, lacking to well-developed, up to 55 µm diam, pale brown to brown. *Conidiophores* solitary or in loose fascicles (2–15), simple, rarely branched, pale brown to reddish brown, paler towards the apex, moderately thick-walled, irregular in width, sometimes swelling at the shoulders caused by geniculation, truncate or short obconically truncate at the apex, straight to mildly geniculate, often narrowed with successive geniculation at the apex, sometimes swelling at the base to twice the width, 30–260(–360) × 2–7 µm, multi-septate (2–11). *Conidiogenous cells* integrated, terminal and intercalary, proliferating sympodially, or rarely percurrently; loci apical or formed on shoulders caused by geniculation, lateral, circumspersed, distinctly thickened and darkened, often slightly protuberant, 1.5–3.5 µm diam. *Conidia* solitary, rarely catenate, filiform, cylindrical to acicular, hyaline, thickened and truncate or rarely short obconically truncate at the base, rounded or acute at the apex, straight or slightly curved, 25–300 × 2.5–5 µm, 2–20-septate, thin-walled, smooth.

*Description of caespituli on V8*; (MUCC 128, 132, 138, 582): *Caespituli* dimorphic in culture; one type is small and commonly observed, while the other is large and rarely observed (*C. apii s. lat.* type; described in parenthesis). *Conidiophores* solitary to loosely fasciculate, arising from hyphae, subhyaline to pale brown, irregular in width, smooth, meager and thin-walled, sinuous-geniculate to geniculate (straight to geniculate), sometimes branched (unbranched), truncate or conically truncate at the tip (truncate at the tip), 6.5–60(–520) × 2.5–5 µm, multi-septate. *Conidiogenous cells* integrated, terminal or intercalary, proliferating sympodially, 1–5 multi-local (uni-local); loci moderately thickened, apical and lateral, circumspersed at the apex of conidiogenous cells, protuberant (not protuberant), 1.25–2(–4.5) µm in width. *Conidia* hyaline, filiform to acicular, slightly thickened and obconical truncate (truncate) at the base, acute at the apex, 27.5–277.5 × 2–3.5(–6.5) µm, 3–21-septate.

*Specimens examined*: **Japan**, Chiba, on *Zantedeschia* sp. (*Araceae*), S. Uematsu & C. Nakashima, MUMH 11403, MUCC 578 = MAFF 238210; Ehime, on *Tagetes erecta* (*Asteraceae*), 27 Oct. 2004, J. Nishikawa, MUMH 11392, MUCC 128; Shizuoka, on *Fuchsia* ×*hybrida* (*Onagraceae*), 22 Jun. 2006, J. Nishikawa, MUMH 11396, MUCC 138; on *Osteospermum* sp. (*Asteraceae*), 11 Sep. 2004, J. Nishikawa, MUMH 11395, MUCC 132; Tokyo, on *Gerbera hybrida* (*Asteraceae*), J. Takeuchi, MUCC 582 = MAFF 238880.

*Notes*: The name *Cercospora* cf. *richardiicola* can be applied to this clade only tentatively. The latter species was described from the USA. Hence, sequences obtained from North American collections are necessary to confirm the identity with true *C. richardiicola.* All clades within this complex (*C.* cf. *richardiicola, C. kikuchii, C.* cf. *sigesbeckiae*) are poorly resolved on TEF, ACT, CAL, and HIS regions. The TEF and HIS phylogenies could not distinguish it from *Cercospora* spp. M–Q, *C. kikuchii* and *C.* cf. *sigesbeckiae*. The ACT phylogeny split it into three clades, namely isolates MUCC 128, 132 and 578 intermixed with *C. malloti* and *Cercospora* sp. P, isolates MUCC 138 and 582 sister to *Cercospora* sp. N and isolate CPC 14680 intermixed with *C. kikuchii* and *Cercospora* sp. O. The CAL phylogeny could not distinguish the isolates from *C. rodmanii*, *C.* cf. *sigesbeckiae* and *Cercospora* sp. N. Currently this complex is split into three sister clades (Fig. 2 part 4), which could be due to a common ancestor, and an ongoing process of speciation.

*Cercospora richardiicola* is characterised in that conidiophores are sometimes swelling at the shoulders caused by geniculation, truncate or short obconically truncate at the apex, often narrowed (not attenuated) successive geniculation at the apex, and sometimes swelling at the base up to twice its median width; and loci on conidiogenous cells are circumspersed and distinctly thickened. These characteristics were sometimes difficult to find on the host plant due to the difference of maturity of the fungus. However, the morphological characteristics of this species on V8 medium were well preserved regardless of differences of host and maturity.

Isolates of *C. richardiicola* have a tendency to infect a wide host range. Isolates are frequently found together with other *Cercospora* spp. on the same leaf spots, which make identification problematic.

## ***Cercospora ricinella*** Sacc. & Berl., Atti Reale Ist. Ven. Sci. Lett. Art, Ser. 3: 721. 1885.

≡ *Cercosporina ricinella* (Sacc. & Berl.) Speg., Anales Mus. Nac. Hist. Nat. Buenos Aires 20: 429. 1910.

= *Cercospora albido-maculans* G. Winter, Hedwigia 24: 202, 1885 (also in J. Mycol. 1: 124. 1885).

= *Cercospora ricini* Speg. Anales Mus. Nac. Hist. Nat. Buenos Aires Ser. 2. 3: 343. 1899.

*Leaf spots* circular to angular, 1–10 mm diam, first appearing as brown spots, later centre becoming greyish white with reddish brown border lines. *Caespituli* amphigenous, mainly hypophyllous. *Mycelium* internal. *Stromata* lacking to well-developed, pale brown to brown, substomatal or intraepidermal, 14–50 µm. *Conidiophores* pale brown, paler towards apex, sinuous-geniculate to geniculate above the middle, in loose fascicles (2–14), slightly divergent, irregular in width, slightly attenuated at the apex, conical at the tip, sometimes constricted at proliferating point, 35–140 × 4.5–5.5 µm, 2–4-septate. *Conidiogenous cells* integrated, terminal and intercalary, proliferating sympodially; multi-local at the apex, loci distinct, slightly protuberant, mainly apical, lateral, 2–3 µm diam. *Conidia* solitary, rarely catenate, hyaline, cylindrical to cylindro-obclavate, acicular, obconically truncate or truncate and distinctly thickened at the base, acute to subacute at the apex, 20–130 × 2.5–5.5 µm, 1–8-septate, thin-walled, smooth.

*Specimens examined*: **South Korea**, Chuncheon, on *Ricinus communis* (*Euphorbiaceae*), 11 Oct. 2002, H.D. Shin, CPC 10104; 7 Oct. 2003, H.D. Shin, CBS 132605 = CPC 10734; CPC 10735–10736.

*Notes*: This species is characterised in that the conidiophores are slightly attenuated at the apex, sinuous-geniculate to geniculate above the middle, and the conidia are rarely catenate. It is supported by ACT, CAL and HIS. In the TEF phylogeny it could not be distinguished from *C. delaireae*, *C.* cf. *chenopodii* and *Cercospora* sp. K. In the combined tree (Fig. 2 part 2), it is a sister taxon to *C. delaireae*. Epitype material should be collected in Australia, where this species was described from.

### ***Cercospora rodmanii*** Conway, Canad. J. Bot. 54: 1082. 1976.

*Specimens examined*: **Brazil**, Oroco, on *Eichhornia crassipes* (*Pontederiaceae*), R. Charudattan, CBS 113126 = RC3409; Rio Verde, on *E. crassipes*, R. Charudattan, CBS 113123 = RC3660. **Mexico**, Carretero, on *E. crassipes*, R. Charudattan, CBS 113124 = RC2867. **USA**, Florida, on *E. crassipes*, R. Charudattan, CBS 113128 = RC394; CBS 113130 = RC393; K. Conway, CBS 113129 = RC397. **Venezuela**, Maracay, on *E. crassipes*, R. Charudattan, CBS 113131 = RC395. **Zambia,** on *E. crassipes*, M. Morris, CBS 113125 = RC4101.

*Notes*: *Cercospora rodmanii* is supported in the TEF phylogeny. In the ACT phylogeny, the clade includes on longer branches also *C.* cf. *ipomoeae* and *Cercospora* sp. M. and in the CAL phylogeny it was intermixed with isolates of *C.* cf. *richardiicola*, *C.* cf. *sigesbeckiae* and *Cercospora* sp. N. In the HIS phylogeny, it could not be distinguished from *Cercospora* spp. N–Q. In the combined tree (Fig. 2 part 4), it is a sister taxon to *Cercospora* sp. N. Tessmann *et al.* (2001) considered *C. rodmanii* to be a synonym of *C. piaropi* whereas Crous & Braun (2003) retained *C. rodmanii* as a separate species. From the results of the present study, we prefer to retain these as two separate species as reported previously (Groenewald *et al*. 2010a, Montenegro-Calderón *et al*. 2011). The isolate originally included as *C. piaropi* in this study (CBS 113127) is treated in the present study under *C.* cf. *flagellaris*; this isolate is also the same isolate used by Tessmann *et al.* (2001). Montenegro-Calderón *et al*. (2011) confirmed the identity of their isolates with the same genes included here, as well as beta-tubulin, and demonstrated that their isolates of *C. rodmanii* were able to also infect other important crops such as beet and sugar beet whereas *C. piaropi* (treated under *C.* cf. *flagellaris* in this study) isolate CBS 113127 and *C. rodmanii* isolate CBS 113129 were specific to water hyacinth.

### ***Cercospora rumicis*** Pavgi & U.P. Singh, Mycopathol. Mycol. Appl. 23: 191. 1964.

= *Cercospora rumicis* Ellis & Langl. ex Chupp, *A monograph of the fungus genus Cercospora*: 453. 1954, nom. inval.

*Specimen examined*: **New Zealand**, Manurewa, on *Rumex sanguineus* (*Polygonaceae*), C.F. Hill, Lynfield 671, CPC 5439.

*Notes*: *Cercospora rumicis* was treated as part of the larger *C. apii s. lat.* complex by Crous & Braun (2003). Although it clusters basal to the *C. zebrina* clade, we suspect that it may represent a distinct taxon. Fresh collections are required from India to fix the application of this name. In the TEF phylogeny, it is not distinguished from *C. zebrina* and *C. armoraciae*, and likewise not from *C. armoraciae* on the ACT phylogeny. In the CAL phylogeny, it is not distinguished from *C. zebrina* and *C. althaeina*. It is distinct from all species included in this study based on the HIS phylogeny. In the combined tree (Fig. 2 part 3), it is basal to the lineage containing *Cercospora* sp. L, *C. althaeina*, *C. zebrina* and *C. violae*.

### ***Cercospora senecionis-walkeri*** Phengsintham, Chukeatirote, McKenzie, K.D. Hyde & U. Braun, Pl. Pathol. & Quarantine 2(1): 70. 2012.

*Specimen examined*: **Laos**, on *Senecio walkeri* (*Asteraceae*), 20 Feb. 2010, P. Phengsintham, LC 0396, NUOL P567, CBS 132636 = CPC 19196.

Notes: Several *Cercospora* species have been described from *Senecio* (*Asteraceae*), but all of them are quite distinct from the species on *S. walkeri*. *Cercospora senecionis* was reduced to synonym with *C. jacquiniana* by Chupp (1954). Based on a re-examination of type material, Braun (in Braun & Mel'nik 1997) showed that *C. senecionis* represents a quite distinct true species of *Cercospora* with acicular conidia, similar to those of *C. apii s. lat*., but 80–200 × 3–6 µm in size. *Cercospora jaquiniana* is similar to *C. senecionis-walkeri* (Pheng *et al*. 2012) with regard to its conidial shape, but has much shorter conidiophores and shorter conidia, usually only 1–3-sepate, which are hyaline, subhyaline to faintly pigmented. Thus, this species was reallocated to *Passalora* by Braun (in Braun & Mel'nik 1997). The Indian taxon *C. senecionis-grahamii* is close to *C. senecionis*, but differs in having acicular to obclavate conidia, only 3–4 µm wide. The North American *C. senecionicola* is also quite distinct from *C. senecionis-walkeri* by its very narrow acicular-subcylindrical conidia, only 2–3.5 µm wide (Chupp 1954). The South American *Passalora senecionicola* (Braun *et al*. 2006) on *Senecio bonariensis* (*Asteraceae*) in Argentina is morphologically very close to *C. senecionis-walkeri* but characterised by having quite distinct lesions, larger stromata, up to 60 µm diam and short conidia that are cylindrical. *Passalora senecionicola* was assigned to *Passalora* due to subhyaline to pale olivaceous conidia, but it is possible that this species rather belongs in *Cercospora* which may be suggested by the phylogenetic position of *C. senecionis-walkeri*, which clusters within the *Cercospora* clade, although the conidia range from being almost hyaline to somewhat pigmented. *Cercospora senecionis-walkeri* is distinct from all other species included in this study based on the TEF, ACT, CAL and HIS phylogenies. In the combined tree (Fig. 2 part 1), it is basal to the other *Cercospora* spp.

### ***Cercospora* cf. *sigesbeckiae***

Morphologically similar to taxa in the *C. apii s. lat*. complex.

*Specimens examined*: **Japan**, Chiba, on *Begonia* sp. (*Begoniaceae*), 24 Jun. 1997, S. Uematsu, MUMH 11405, MUCC 587 = MAFF 237690 = MUCNS 197; Fukuoka, on *Sigesbeckia glabescens* (*Asteraceae*), 31 Oct. 1948, S. Katsuki, **holotype** in TNS; Saitama, on *Glycine max*, 1949, H. Kurata, MUCC 589 = MAFF 305039 (as *C. kikuchii*); Tokyo, on *Dioscorea tokoro* (*Dioscoreaceae*), 10 Nov. 2007, I. Araki, MUMH 10951, MUCC 849. **South Korea**, Chuncheon, on *S. glabrescens*, 7 Oct. 2003, H.D. Shin, CBS H-21019, CBS 132601 = CPC 10664 (as *C. sigesbeckiae*); on *Persicaria orientalis* (= *P. cochinchinensis*) (*Polygonaceae*), 11 Oct. 2002, H.D. Shin, CBS 132641 = CPC 10117 (as *C. polygonacea*); Hongcheon, on *Pilea pumila* (= *P. mongolica*), 3 Oct. 2002, H.D. Shin, CBS 132642 = CPC 10128 (as *C. ganjetica*); Namyangju, on *Paulownia coreana* (*Scrophulariaceae*), 22 Oct. 2003, H.D. Shin, CBS H-21020 = HAL 1863, CBS 132606 = CPC 10740; Yanggu, on *Sigesbeckia pubescens*, 28 Sep. 2007, H.D. Shin, CBS 132621 = CPC 14489 (as *C. sigesbeckiae*); on *Malva verticillata* (*Malvaceae*), H.D. Shin, CBS H-21021, CBS 132675 = CPC 14726 (as *C. malvacearum*).

*Notes*: See *Cercospora* cf. *richardiicola*. The application of the name *C.* cf. *sigesbeckiae* (based on type material from Japan), to this clade can only be tentative. Japanese cultures and sequences are needed to confirm its identity. In the TEF and CAL phylogenies, isolates are intermixed with those of *Cercospora* spp. M–Q, *C. kikuchii* and *C.* cf. *richardiicola*; in the ACT phylogeny it cannot be distinguished from *C. fagopyri*. In the HIS phylogeny the isolates form a clade on a longer branch in a clade containing *C. kikuchii* and some isolates of *C.* cf. *richardiicola*. In the combined tree (Fig. 2 part 4), it is a sister taxon to *C. kikuchii* and *C.* cf. *richardiicola*.

***Cercospora sojina*** Hara, Nogyokoku (Tokyo) 9: 28. 1915.

≡ *Cercosporina sojina* (Hara) Hara, Jitsuyo-sakumotsu-byorigaku: 112. 1925.

≡ *Cercosporidium sojinum* (Hara) X.J. Liu & Y.L. Guo, Acta Mycol. Sinica 1: 100. 1982.

≡ *Passalora sojina* (Hara) Poonam Srivast., J. Living World 1: 118. 1994, comb. inval.

≡ *Passalora sojina* (Hara) H.D. Shin & U. Braun, Mycotaxon 58: 63. 1996.

≡ *Passalora sojina* (Hara) U. Braun, Trudy Bot. Inst. im. V.L. Komarova 20: 93. 1997, comb. superfl.

= *Cercospora daizu* Miura, Manchurian R.R. Agric. Exp. Stat. Bull. 11: 25. 1920.

*Caespituli* amphigenous. *Mycelium* internal. *Stromata* small, up to 35 µm diam, intraepidermal and substomatal, brown. *Conidiophores* solitary or in loose fascicles (2–5), brown, paler towards the apex, simple, rarely branched, irregular in width, constricted at the parts of proliferation, conically truncate at the apex, straight to geniculate, 55–200 × 4.5–5 µm, 2–4-septate. *Conidiogenous cells* integrated, proliferating sympodially, terminal and intercalary, uni- or multi-local (1–2); loci distinctly thickened, protuberant, apical or formed on the shoulders caused by geniculation, 2–4 µm diam. *Conidia* solitary, hyaline, cylindrical to obclavate, fusiform, obovoid, obconically truncate and thickened at the base, obtuse at the apex, 25–70 × 5.5–9 µm, 1–5-septate, thin-walled, smooth.

*Specimens examined*: **Argentina**, on *Glycine max* (*Fabaceae*), 2009, F. Scandiani, CPC 17964 = CBS 132684 = CPC 17971 = "CCC 173-09, 09-495"; "CCC 155-09, 09-285-5"; CPC 17965 = "CCC 156-09, 09-285-4"; CPC 17966 = "CCC 157-09, 09-285-3"; CPC 17967 = "CCC 158-09, 09-285-1"; CPC 17968 = "CCC 159-09, 09-285-7"; CPC 17969 = "CCC 167-09, 09-881"; CPC 17970 = "CCC 172-09, 09-320"; CPC 17972 = CCC 174-09; CPC 17973 = "CCC 176-09, 09-882"; CPC 17974 = "CCC 177-09, 09-2488-1"; CPC 17975 = "CCC 178-09, 09-1438-2"; CPC 17976 = "CCC 179-09, 09-2591"; CPC 17977 = "CCC 180-09, 09-2520". **South Korea**, Hoengseong, on *G. soja*, 4 Sep. 2005, H.D. Shin, CBS 132018 = CPC 12322; Hongcheon, on *G. soja*, 20 Jul. 2004, H.D. Shin, **neotype designated here** CBS H-21022, culture ex-type CBS 132615 = CPC 11353; CPC 11354; CPC 11420–11423.

*Notes*: Type material of this species (Japan, Tokyo, on *G. max*, 1909, K. Hara) was not located and is probably lost. *Cercospora sojina* was transferred to the genus *Passalora* based on its distinctly thickened loci, and cylindrical and relatively wide conidia (Shin & Braun 1996). However, the hyaline conidia of this species are indicative of the fact that it is best retained in *Cercospora* (Crous & Braun 2003), which is fully supported by its position in phylogenetic trees among other *Cercospora* species. The species is supported as distinct based on the ACT and HIS phylogenies; in the TEF and CAL phylogenies the isolates of *C. achyranthis* and *C. campi-silii* are intermixed with the *C. sojina* isolates. In the combined tree (Fig. 2 part 2), it is a sister taxon to *C. campi-silii*.

## *Cercospora* sp. A

*Culture sequenced:* **Mexico**, on *Chenopodium* sp. (*Amaranthaceae*), M. de Jesus Yanez, CBS 132631 = CPC 15872.

*Notes*: This isolate is phylogenetically distinct (Fig. 2 part 1) from the other species included in this study. Unfortunately, the specimen and specimen details were not available for study.

## *Cercospora* sp. B

*Caespituli* amphigenous. *Mycelium* internal. *Stromata* lacking to developed, up to 60 µm, intraepidemal, substomatal, brown. *Conidiophores* straight or geniculate, solitary to 2–21 in dense fascicle, 0–5-septate, 20–75 × 4.5–6 µm, almost uniform in width, constricted at shoulder, conically truncate or truncate at the tip. *Conidiogenous cells* integrated, terminal, intercalary, proliferating sympodially, multilocal; loci thickened, apical, rarely lateral, 2–2.5 µm diam, slightly protuberant. *Conidia* solitary, hyaline, cylindro-obclavate to acicular, obconically truncate at thickened base, tip obtuse, 45–135 × 4–5 µm, 4–9-septate, thin-walled, smooth.

*Specimen examined*: **South Korea**, Kangnung, on *Ipomoea purpurea* (*Convolvulaceae*), 10 Sep. 2003, H.D. Shin, CBS 132602 = CPC 10687 (as *C. ipomoeae*); CPC 10688–10689 (as *C. ipomoeae*).

*Notes*: This isolate was obtained from *Ipomoea* in Korea, but differs in its phylogeny to other isolates of *C.* cf. *ipomoeae*. It has a unique position in the ACT, CAL and HIS phylogenies and is intermixed with *C. delaireae* and *Cercospora* sp. K based on the TEF phylogeny. In the combined tree (Fig. 2 part 1), it is a basal taxon to *C. agavicola*. Several species of *Cercospora* have thus far been described from *Ipomoea*, and more collections would be required to resolve the status of this collection.

## *Cercospora* sp. C

*Culture sequenced:* **Mexico**, M. de Jesus Yanez, CBS 132629 = CPC 15841.

*Notes*: This isolate is phylogenetically distinct (Fig. 2 part 1) from the other species included in this study. Unfortunately, the specimen and specimen details were not available for study.

## *Cercospora* sp. D

*Culture sequenced:* **Mexico**, M. de Jesus Yanez, CBS 132630 = CPC 15856.

*Notes*: This isolate is phylogenetically distinct (Fig. 2 part 1) from the other species included in this study. Unfortunately, the specimen and specimen details were not available for study.

## *Cercospora* sp. E

*Cultures sequenced:* **Mexico**, M. de Jesus Yanez, CBS 132628 = CPC 15632, CPC 15801.

*Notes*: These isolates are phylogenetically distinct (Fig. 2 part 1) from the other species included in this study. Unfortunately, the specimen(s) and specimen details were not available for study.

## *Cercospora* sp. F

*Specimen examined*: **South Africa**, on *Zea mays* (*Poaceae*), P. Caldwell, CBS 132618 = CPC 12062.

*Notes*: This isolate, which is supported by the CAL phylogeny, must be treated as an independent species. In the TEF and HIS phylogenies it is present on a longer branch in a clade consisting of isolates of *Cercospora* spp. G–I, *C. alchemillicola* / *C.* cf. *alchemillicola*, *C.* cf. *physalidis* and *C. celosiae*. In the ACT phylogeny it cannot be distinguished from *Cercospora* sp. Q. In the combined tree (Fig. 2 part 1), it is a sister taxon to *C.* cf. *physalidis*.

## *Cercospora* sp. G

*Caespituli* amphigenous. *Mycelium* internal. *Stromata* small to well-developed, up to 60 µm diam, brown, intraepidermal and substomatal. *Conidiophores* straight or sinuously geniculate, loosely fasciculate (3–10), pale brown to brown, paler towards the apex, moderately thick-walled, simple, irregular in width, attenuated at the apex, irregularly constricted following the proliferation, 30–50 × 3.5–4.5 µm, 0–2-septate. *Conidiogenous cells* integrated, terminal, rarely intercalary, proliferating sympodially, multi-local; loci thickened, darkened, apical or formed on the shoulders caused by geniculation, lateral, sometimes circumspersed, 1.25–2 µm in diam. *Conidia* solitary, hyaline, cylindrical to obclavate, often acicular, straight or slightly curved, truncate or subtruncate at the thickened base, obtuse or subacute at the apex, 15–165 × 2–4 µm, 1–12-septate, thin-walled, smooth.

*Specimen examined*: **New Zealand**, Manurewa, on *Salvia viscosa* (*Lamiaceae*), C.F. Hill, Lynfield 626, CPC 5438 (as *C. salviicola*); Kopuku, on *Bidens frondosa* (*Asteraceae*), C.F. Hill, Lynfield 559, CBS 115518 = CPC 5360.

*Notes*: This species is thus far only known from New Zealand. It is distinct from the other included species based on its position in the HIS phylogeny; in the TEF and ACT phylogenies it cannot be distinguished from *Cercospora* spp. F, H and I as well as *C. alchemillicola / C.* cf. *alchemillicola*, *C.* cf. *physalidis* and *C. celosiae*. In the CAL phylogeny it forms a distinct clade that cannot be distinguished from *Cercospora* sp. H. In the combined tree (Fig. 2 part 1), it is a sister taxon to *Cercospora* sp. H.

## *Cercospora* sp. H

*Specimens examined*: **Argentina**, on *Chamelaucium uncinatum* (*Myrtaceae*), S. Wolcan, CPC 11620 = 1CRI. **New Zealand**, on *Dichondra repens* (*Convolvulaceae*), C.F. Hill, Lynfield 536, CBS 115205 = CPC 5116.

*Notes*: This species is distinct from the other included species based on its position in the HIS phylogeny; in the TEF and ACT phylogenies it cannot be distinguished from *Cercospora* spp. F, G and I as well as *C. alchemillicola / C.* cf. *alchemillicola*, *C.* cf. *physalidis* and *C. celosiae*. In the CAL phylogeny it forms a distinct clade that cannot be distinguished from *Cercospora* sp. G. Whether *Cercospora* spp. G and H could be conspecific awaits collection of more isolates. In the combined tree (Fig. 2 part 1), it is a sister taxon to *C. celosiae* and *Cercospora* sp. I.

## *Cercospora* sp. I

? *Cercospora deutziae* Ellis & Everh., J. Mycol. 4: 5. 1888.
? *Cercospora guatemalensis* A.S. Mull. & Chupp, Ceiba 1: 173. 1950.

*Specimens examined*: **South Korea**, Suwon, on *Ajuga multiflora* (*Lamiaceae*), 22 Oct. 2002, H.D. Shin, CBS 132643 = CPC 10138 (as *C. guatemalensis*). **New Zealand**, Manurewa, on *Coreopsis verticillata* (*Asteraceae*), 2 Jun. 2003, C.F. Hill, Lynfield 866A, CBS 132597 = CPC 10615; Lynfield 866B, CPC 10616; on *Deutzia crenata* (*Hydrangeaceae*), 5 May 2002, C.F. Hill, Lynfield 610, CBS 114818 = CPC 5362 (named as *C. deutziae*); on *Deutzia purpurascens* (*Hydrangeaceae*), 5 May 2002, C.F. Hill, Lynfield 607, CBS 114815 = CPC 5364 (named as *C. deutziae*); on *Deutzia ×rosea* (= *D. gracilis* × *purpurascens*) (*Hydrangeaceae*), Apr. 2002, C.F. Hill, Lynfield 599, CBS 114816 = CPC 5363 (named as *C. deutziae*); on *Fuchsia procumbens* (*Onagraceae*), 5 May 2002, C.F. Hill, Lynfield 613, CBS 114817 = CPC 5365 (named as *C. fuchsia*); on *Nicotiana* sp. (*Solanaceae*), 8 Jun. 2002, C.F. Hill, Lynfield 667, CPC 5440; Mt Albert, on *Gunnera tinctoria* (*Gunneraceae*), 29 Feb. 2004, C.F. Hill, Lynfield 997, CBS 115121; Whangarei, on *Archontophoenix cunninghamiana* (*Arecaceae*), 10 Feb. 2004, C.F. Hill, CBS 115117.

*Notes*: This clade is quite distinct based on the combined tree (Fig. 2 part 1), and mainly consists of isolates from various host plants in New Zealand. In the TEF and ACT phylogenies it cannot be distinguished from *Cercospora* spp. F, G and H as well as *C. alchemillicola / C.* cf. *alchemillicola*, *C.* cf. *physalidis* and *C. celosiae*. In the CAL phylogeny it forms a distinct clade that cannot be distinguished from the single isolate of *C. celosiae*. In the HIS phylogeny it cannot be distinguished from *Cercospora* sp. F, *C. alchemillicola / C.* cf. *alchemillicola* and *C. celosiae*. In the combined tree (Fig. 2 part 1), it is a sister taxon to *C. celosiae* and *Cercospora* sp. H. Most of the *Cercospora* sp. I isolates from New Zealand would be given a species epithet based on each host plant, if these were classified with a conventional species concept. From the results of the phylogenetic tree, these isolates are recognised as belonging to a single species with a wide host range. Braun & Hill (2004) examined the collections on *Co. verticillata*, *D. crenata*, *D. purpurascens*, *D.* × *rosea*, *F. procumbens*, *Nicotiana* sp., and Braun *et al*. (2006) studied the samples on *A. cunninghamiana* and *G. tinctoria.* They referred all of them to *C. api s. lat.* as circumscribed in Crous & Braun (2003) as they are characterised by having hyaline acicular conidia formed singly, i.e. the present unnamed species is a *C. apii*-like plurivorous species.

## *Cercospora* sp. J

*Culture sequenced:* **Japan**, Aichi, on *Antirrhinum majus* (*Plantaginaceae*), 8 May 2007, M. Matsusaki, MUMH10490, MUCC 541.

*Notes*: This isolate is phylogenetically distinct (Fig. 2 part 2) from the other species included in this study. Unfortunately, the specimen was not available for study.

## *Cercospora* sp. K

*Caespituli* amphigenous. *Mycelium* internal. *Stromata* lacking or composed of a few brown cells. *Conidiophores* emerging through the cuticle or arising from stomatal openings, pale brown, paler towards the apex, almost uniform in width, sometimes narrowed at the apex following the sympodial proliferation, often constricted at septa and proliferating points, solitary or 2–3 in a loose fascicle, straight or slightly curved to sinuously geniculate, moderately thick-walled, 0–5-septate, 30–110 × 3.5–5 µm, truncate or conically truncate at the apex. *Conidiogenous cells* terminal, rarely intercalary, proliferating sympodially; loci slightly thickened, slightly protuberant (subtruncate) or flat, refractive, apical and lateral, 1.5–2.5 µm in diam. *Conidia* solitary, hyaline, filiform to acicular or obclavate, straight to slightly curved, truncate or obconically truncate at the slightly thickened at the basal end, acute at the apex, indistinctly or distinctly 1–14-septate, 35–230 × 1.5–5 µm, thin-walled, smooth.

*Specimens examined*: **South Korea,** Namyangju, on *Ipomoea coccinea* (≡ *Quamoclit coccinea*) (*Convolvulaceae*), 9 Oct. 2002, H.D. Shin, CPC 12391; 30 Sep. 2003, H.D. Shin, CBS 132603 = CPC 10719; 15 Oct. 2005, H.D. Shin, CPC 10094.

*Notes*: This species is phylogenetically supported based on DNA sequence data of ACT, CAL and HIS. In the TEF phylogeny, these isolates cannot be distinguished from *C. ricinella*, *C.* cf. *chenopodii* and *C. delaireae*. In the combined tree (Fig. 2 part 2), it is a sister taxon to *C.* cf. *flagellaris*. Different species of *Cercospora* have been described from *Ipomoea* spp. *Cercospora* *ipomoeae-pedis-caprae* was previously treated as a synonym of *C. ipomoeae* (Bagyanarayana *et al*. 1995, Shin & Kim 2001), since the length of the conidiophores and conidia in the latter species is variable. Braun *et al.* (2001) pointed out the differences among the *Cercospora* species on *Ipomoea* spp. based on the description of these species by García *et al.* (1996), and proposed that *C. ipomoeae-pedis-caprae* must be retained as a separate species. However, *Cercospora* isolates on *Ipomoea* cluster in three different places in the tree, and thus this complex remains unresolved and without epitypification the application of the names *C. ipomoeae* and *C. ipomoeae-pedis-caprae* remains unclear.

### *Cercospora* sp. L

*Specimen examined*: **New Zealand**, on *Crepis capillaris* (*Asteraceae*), C.F. Hill, Lynfield 534, CBS 115477 = CPC 5114.

*Notes*: *In vivo* material on *Crepis capillaris* from New Zealand collected by C.F. Hill, Auckland, 9 Jul. 2000, deposited at HAL has been examined and is characterised as follows: *Conidiophores* solitary or in small, loose fascicles, straight to usually geniculate-sinuous, unbranched, 20–100 × 3–6 µm, usually 1–4-septate, pale olivaceous throughout or olivaceous-brown below and paler towards the tip; *conidiogenous cells* integrated, usually terminal, sympodial, multi-local; conidiogenous loci 2–3 µm diam, thickened and darkened; *conidia* solitary, acicular, short conidia occasionally subcylindrical, straight curved to somewhat sigmoid, 60–170 × 3–4 µm, pluriseptate, apex subacute or subobtuse, base truncate, occasionally slighty attenuated at the very base (at hilum), hila 2–3 µm wide. The application of the name *Cercospora crepidis* Onděj & Zavřel, described from Europe (Czech Republic) on *Crepis capillaris*, for the fungus from New Zealand is not possible. The latter species is characterised by having obclavate conidia with distinctly obconically truncate base and short, aseptate conidiophores, only 14–22 µm long (Ondřej & Zavřel 1971). In the TEF and CAL phylogeny this isolate clusters with *C. zebrina* and *C. armoraciae* and on a longer branch in the *C. zebrina* clade in the ACT phylogeny. It is only in the HIS phylogeny that this isolate is clearly distinct, clustering as sister taxon to *C. delaireae*. In the combined tree (Fig. 2 part 3), it is a sister taxon to *C. althaeina* and *C. zebrina*.

### *Cercospora* sp. M

*Specimen examined*: **Thailand**, Chachoengsao Province, Sanamchaikhet, on leaves of *Acacia mangium* (*Fabaceae*), 28 May 2003, K. Pongpanich, CBS H-9876, CBS 132596 = CPC 10553.

*Notes*: Crous *et al.* (2004b) isolated several species of *Cercospora* from *A. mangium* in Thailand, some of which were linked to single ascospore isolates of a mycosphaerella-like telemorph (see Crous *et al*. 2004b, fig. 5). Isolate CPC 10553 (=CBS 132596) occurred on the same leaf spots with *C. acaciae-mangii* (CBS 116365 = CPC 10526), which is here treated under *Cercospora* sp. P. The TEF phylogeny could not distinguish it from *Cercospora* spp. N–Q, *C. kikuchii* and *C.* cf. *sigesbeckiae*, whereas the HIS phylogeny could not distinguish it from some isolates of *Cercospora* spp. P and Q. The ACT phylogeny places it on a longer branch with *C. rodmanii* and *C.* cf. *ipomoeae*. The CAL phylogeny could not distinguish it from *Cercospora* spp. P and Q, *C. alchemillicola / C.* cf. *alchemillicola* and *C.* cf. *sigesbeckiae*. In the combined tree (Fig. 2 part 4), it is basal to the lineage containing *C. rodmanii* and other species.

### *Cercospora* sp. N

*Specimen examined*: **Bangladesh** (western part), on *Musa* sp. (*Musaceae*), I. Buddenhagen, CBS 132619 = CPC 12684 (named as *C. hayi*).

*Notes*: *Cercospora* sp. N has shorter conidiophores than ascribed to *C. hayi*, which was described from *Musa* in Cuba. It is evident that a complex of *Cercospora* spp. occur on banana. The TEF phylogeny could not distinguish it from *Cercospora* spp. O–Q, *C. kikuchii* and *C.* cf. *sigesbeckiae*, whereas the HIS phylogeny could not distinguish it from some isolates of *Cercospora* spp. P and Q and *C. rodmanii*. The CAL phylogeny could not distinguish it from *C. rodmanii*, *C.* cf. *richardiicola* and *C.* cf. *sigesbeckiae*. The ACT phylogeny distinguishes it from the other species included in this study. In the combined tree (Fig. 2 part 4), it is a sister taxon to *C.* cf. *richardiicola* and *C. kikuchii*.

### *Cercospora* sp. O

*Specimen examined*: **Thailand**, Chiang Mai, Mae Klang Loung, N18º32.465' E98º32.874', on *Musa* sp. (*Musaceae*), 6 Oct. 2010, P.W. Crous, CBS 132635 = CPC 18636 (named as *C. hayi*).

*Notes*: Based on its shorter conidophores, *Cercospora* sp. O is distinct from *C. hayi*, and morphologically is more similar to *Cercospora* sp. N. The TEF phylogeny could not distinguish it from *Cercospora* spp. M, N and Q, *C. kikuchii* and *C.* cf. *sigesbeckiae*, whereas the HIS phylogeny could not distinguish it from some isolates of *Cercospora* spp. N, P and Q and *C. rodmanii*. The CAL phylogeny could not distinguish it from *Cercospora* spp. P and Q, *C. alchemillicola / C.* cf. *alchemillicola* and *C.* cf. *sigesbeckiae* and the ACT phylogeny from *C. kikuchii*. In the combined tree (Fig. 2 part 4), it is a sister taxon to *C.* cf. *malloti*.

### *Cercospora* sp. P

*Specimens examined*: **Ghana**, on leaves of *Dioscorea rotundata* (*Dioscoreaceae*), 2000, S. Nyako & A.O. Danquah, CBS 132660 = CPC 11629 = GHA-4-0; CPC 11630 = GHA-4-3; CPC 11631 = GHA-5-0; CPC 11632 = GHA-7-4; CPC 11633 = GHA-8-4 (as *C. dioscoreae-pyrifoliae*). **Japan**, Okinawa, on *Coffea arabica* (*Rubiaceae*), C. Nakashima, MUMH 10823, MUCC 771 (as *C. coffeicola*). **Mexico**, Tamaulipas, on *Ricinus communis*, 31 Nov. 2008, Ma. de Jesús Yáñez-Morales, CBS 132680 = CPC 15827. **New Zealand**, Auckland (imported from Fiji islands), on leaves of *Hibiscus sabdariffa* (*Malvaceae*), C.F. Hill, Lynfield 578, CPC 5262. **Papua New Guinea**, on leaves of *Dioscorea nummularia* (*Dioscoreaceae*), 2000, J. Peters & A.N. Jama, CBS 132662 = CPC 11635 = PNG-009; on leaves of *D. rotundata*, 2000, J. Peters & A.N. Jama, CBS 132664 = CPC 11637 = PNG-022; on leaves of *Dioscorea bulbifera* (*Dioscoreaceae*), 2000, J. Peters & A.N. Jama, CBS 132665 = CPC 11638 = PNG-023. **South Africa**, Nelspruit, on *Cajanus cajan* (*Fabaceae*), L. van Jaarsveld, CBS 113996 = CPC 5326; CBS 115413 = CPC 5328; CPC 5327; Komatipoort, on *Citrus* ×*sinensis* (≡ *C. aurantium* var. *sinensis*) (*Rutaceae*), M.C. Pretorius, CBS 112728 = CPC 3949; CBS 112730 = CPC 3948; CBS 112894 = CPC 3950. **Swaziland,** on *Citrus* ×*sinensis* (≡ *C. aurantium* var. *sinensis*), M.C. Pretorius, CPC 4001; CPC 4002; on *Citrus* sp. leaf spot, M.C. Pretorius, CBS 112649 = CPC 3946; CBS 112722 = CPC 3947; CBS 115609 = CPC 3945. **Thailand**, on *Acacia mangium*, M.J. Wingfield, CBS 116365 = CPC 10526; CBS 132645 = CPC 10527 (*Mycosphaerella* teleomorph ascospore isolate, **ex-type** of *Cercospora acaciae-mangii,* small colonies); on *A. mangium*, K. Pongpanich, CPC 10552.

*Notes*: Isolates of this clade were mainly obtained from *Acacia*, *Cajanus*, *Citrus* (*Rutaceae*), *Coffea* (*Rubiaceae*), *Dioscorea*, *Hibiscus* (*Malvaceae*) and *Ricinus* (*Euphorbiaceae*). Many previously described species names have in the past been applied to different isolates clustering in this clade. Based on the gene loci screened in the present study, we were unable to resolve the taxonomy of these isolates, and for now prefer to treat them as an unresolved species complex. In none of the single-gene phylogenies generated in this study did the isolates from this species form a pure monophyletic lineage, as isolates were frequently intermixed with that of *Cercospora* sp. Q, *C.* cf. *sigesbeckiae* and *C.* cf. *richardiicola*. Given this overlap in sequence identity and host species, it is possible that *Cercospora* spp. P (Fig. 2 parts 4–5) and Q (Fig. 2 part 5) could be considered as a single species complex (see species notes for *Cercospora* sp. Q below). More extensive screening of additional loci is needed to define the species boundaries in this complex. Also present in this complex are numerous isolates from *Dioscorea*, for which the name *C. dioscoreae-pyrifoliae* could have been a candidate. From the present study it is clear that several species of *Cercospora* can be isolated from this host and a more detailed study is needed to fix that name to a specific lineage.

The ex-type culture of *Cercospora acaciae-mangii* (Crous *et al*. 2004) is located in the last subclade (Fig. 2 part 5). *Cercospora acaciae-mangii* was isolated from *Acacia* leaves that also contained a *mycosphaerella*-like teleomorph that formed a *Cercospora* state in culture. However, the same leaf spots were also colonised by a second, morphologically similar species (distinguished by its ability to form larger, faster-growing colonies in agar).

## *Cercospora* sp. Q

*Specimens examined*: **Mexico**, on *Phaseolus vulgaris* (*Fabaceae*), 20 Oct. 2008, M. de Jesus Yanez, CBS 132679 = CPC 15807; Tamaulipas, on *Taraxacum* sp. (*Asteraceae*), 30 Oct. 2008, Ma. de Jesús Yáñez-Morales, CBS 132682 = CPC 15850; on *Euphorbia* sp. (*Euphorbiaceae*), 31 Oct. 2008, Ma. de Jesús Yáñez-Morales, CPC 15875; 30 Oct. 2008, Ma. de Jesús Yáñez-Morales, CBS 132681 = CPC 15844. **Papua New Guinea**, on leaves of *Dioscorea rotundata*, 2000, J. Peters & A.N. Jama, CBS 132661 = CPC 11634 = PNG-002, on leaves of *Dioscorea esculenta* (*Dioscoreaceae*), 2000, J. Peters & A.N. Jama, CBS 132663 = CPC 11636 = PNG-016; CPC 11639 = PNG-037. **South Africa**, Nelspruit, on *Cajanus cajan*, L. van Jaarsveld, CBS 113997 = CPC 5325; CBS 115410 = CPC 5331; CBS 115411 = CPC 5332; CBS 115412 = CPC 5333; CBS 115536 = CPC 5329; CBS 115537 = CPC 5330. **Thailand**, on *Acacia mangium*, K. Pongpanich, CPC 10550 (big colony on same plate as small colonies of *Cercospora acaciae-mangii*); CPC 10551 (big colony); CBS 132656 = CPC 11536; CPC 11539.

*Notes*: Several isolates from diverse hosts and families cluster in this clade, to which different names can be applied. To resolve their taxonomy, fresh collections authentic for the names (based on host and country) need to be recollected and included in future studies. Based on the genes studied here, we were unable to resolve the phylogeny of these taxa. See also the species notes for *Cercospora* sp. P. Screening the isolates from this species with five more genomic loci in this study did not clarify their potential species boundaries. By testing other candidate loci as they become available from comparative genomics and other sources we will continue to try and identify optimal genes for species recognision in this complex.

## *Cercospora* sp. R

*Specimen examined*: **New Zealand**, Auckland, Grey Lynn, on *Myoporum laetum* (*Myoporaceae*), Dec. 2003, C.F. Hill, Lynfield 186-B, CBS 114644.

*Notes*: *Pseudocercosporella myopori* is a true species of *Pseudocercosporella* (Braun & Hill 2002), which was originally described without deposting an ex-type culture. A later collection deposited at CBS (isolate CBS 114644), however, proved to be representative of an undescribed species of *Cercospora*, phylogenetically closely related to *Cercospora* sp. S and *C. corchori* (Fig. 2 part 5). This isolate has a unique phylogenetic position in the TEF, ACT, CAL and HIS phylogenies. In the combined tree (Fig. 2 part 5), it is a sister taxon to *Cercospora* sp. S.

## *Cercospora* sp. S

*Specimen examined*: **South Korea**, Yangpyeong, on *Crepidiastrum denticulatum* (≡ *Youngia denticulata*) (*Asteraceae*), 30 Sep. 2003, H.D. Shin, CBS 132599 = CPC 10656; CPC 10654–10655 (as *Cercospora lactucae-sativae*).

*Notes*: Isolate CPC 10656 is located on a slightly longer branch in the majority of genomic loci evaluated (ACT, CAL and HIS); only in the TEF phylogeny is it intermixed with isolates of *C. lactucae-sativae*. It is a close sister taxon to *Cercospora* sp. R and *C. corchori* (Fig. 2 part 5), but more isolates need to be collected to resolve its identity.

## ***Cercospora vignigena*** C. Nakash., Crous, U. Braun & H.D. Shin, **sp. nov.** MycoBank MB800657. Fig. 10.

*Etymology*: Named after the host genus from which it was collected, *Vigna*.

*Leaf spots* subcircular, amphigenous, pale to medium brown, 8–20 mm diam, with inconspicuous margin. *Caespituli* amphigenous. *Mycelium* internal. *Stromata* small to well-developed, pale brown to brown, intraepidermal and substomatal, 35–60 µm in diam. *Conidiophores* in loose to dense fascicles (2–12), straight to slightly sinuous-geniculate, pale brown, paler towards the apex, moderately thick-walled or thick-walled, cylindrical, almost uniform in width, often wider towards the apex, distinctly conical at the apex, 40–130 × 5–7(–10) µm, 0–3-septate. *Conidiogenous cells* integrated, terminal, intercalary, proliferating sympodially, 20–40 × 4–5 µm, multi-local (1–2); loci distinctly thickened, darkened, slightly protuberant, apical and lateral, 2.5–4 µm diam. *Conidia* solitary, rarely catenate, hyaline, straight to slightly curved, cylindrical to obclavate, obconically truncate and distinctly thickened at the base, subobtuse to obtuse at the apex, (35–)45–70(–150) × (2.5–)4–6(–10) µm, (3–)4–7(–14)-septate, thin-walled, smooth.

*Culture characteristics*: Colonies spreading, erumpent, with even, lobate margins and sparse to moderate aerial mycelium, reaching 25 mm diam after 2 wk. On OA olivaceous-grey in centre, pale olivaceous-grey in outer region. On MEA pale olivaceous-grey with patches of dirty white, reverse iron-grey. On PDA pale olivaceous-grey, margin submerged, grey-olivaceous; reverse olivaceous-grey.

*Specimens examined*: **Japan**, Gumma, on *Vigna unguiculata* (= *V. sinensis*) (*Fabaceae*), Sep. 1993, K. Kishi, MUCC 579 = MAFF 237635. **South Africa**, Potchefstroom, on *V. unguiculata* (= *V. sinensis*), 3 Jan. 1995, S. van Wyk, CPC 1133–1134. **South Korea**, Jeongeup, on *V. unguiculata* (= *V. sinensis*), 29 Oct. 2003, H.D. Shin, **holotype** CBS H-21023, culture ex-type CBS 132611 = CPC 10812.

*Notes*: This independent clade is supported by ACT, CAL and HIS and is composed of the isolates of *Cercospora* species that were identified as *C. canescens* on *Vigna* (*Fabaceae*) plants. In the TEF phylogeny, the clade is split into two lineages, isolates CPC 1134 and MUCC 579 as sister clade to *C. apiicola* and CPC 10812 basal to *C. apii* and *C. beticola*. In the combined tree (Fig. 2 part 2), it is basal to the lineage containing *C. apiicola* and other species. The examined isolates of *C. canescens* (the true *C. canescens* has acicular conidia), for which the original host is the genus *Phaseolus*, were located in other clades. These results show that the fungus on *Vigna* must be treated as a species distinct from *C. canescens*. *Cercospora vignicaulis* (described on *V. unguiculata* (= *V. sinensis*) collected from the USA) has in the past been listed as

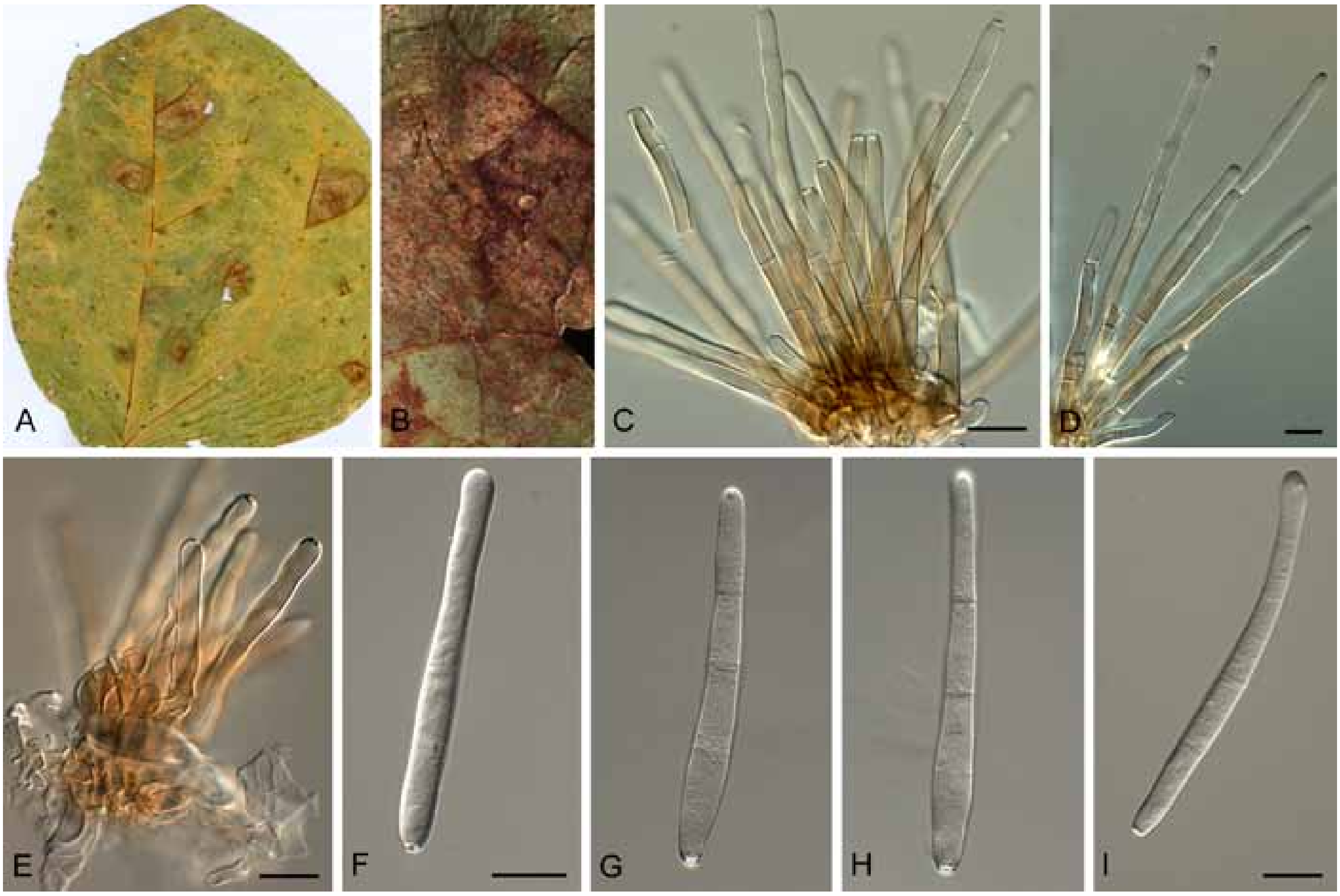


**Fig. 10.** *Cercospora vignigena* (CBS 132611 = CPC 10812). A. Leaf spots. B. Close-up of lesion. C–E. Fasciculate conidiophores. F–I. Conidia. Scale bars = 10 µm.

a synonym of *C. canescens*. However, *C. vignicaulis* has acicular conidia, which differs from the isolates studied here, and thus the present collection is described as a distinct species that appears to be specific to *Vigna*.

***Cercospora violae*** Sacc., Nuovo Giron. Bot. Ital. 8: 187. 1876.

= *Cercospora violae-tricoloris* Briosi & Cavara, Atti Ist. Bot. Univ. Pavia 2: 285. 1892.
= *Cercospora violae* var. *minor* Rota-Rossi, Atti Ist. Bot, Univ. Pavia, Ser. 2, 13: 199. 1914.
= *Cercospora violae-kiusianae* Sawada, Rep. Gov. Agric. Res. Inst. Taiwan 85: 126. 1943.
= *Cercospora difformis* Tehon, Mycologia 40: 322. 1948.
= *Cercospora trinctatis* Pass. (unpublished name cited by Chupp 1954)

*Caespituli* amphigenous. *Mycelium* internal. *Stromata* lacking to well-developed, up to 80 µm diam, brown, intraepidermal, substomatal. *Conidiophores* in dense fascicles (2–16), irregular in width, slightly attenuated at the upper portion, straight or mildly sinuous-geniculate, straight, wall moderately thickened, simple, pale brown to brown, short conically truncate at the apex, wider at the base, 20–175 × 2.5–7.5 µm, 1–10-septate, usually uni-local. *Conidiogenous cells* integrated, terminal, rarely intercalary, proliferating sympodially; loci distinct, thickened, apical, rarely lateral, 2–3 µm diam, not protuberant. *Conidia* solitary, hyaline, cylindrical to obclavate or acicular, distinctly thickened and obconically truncated at the base, obtuse at the apex, 35–195 × 2.5–5 µm, 0–18-septate, thin-walled, smooth.

*Specimens examined*: **Italy**, Selva, on *Viola odorata* (*Violaceae*), Aug. 1874, Treviso, **isotypes** distributed as Sacc. Mycotheca Veneta 279, **isotype** at HAL examined. **Japan**, Kochi, on *Viola* sp., 16 Nov. 2004, J. Nishikawa, MUMH 10333, MUCC 129; Nagano, on *V. tricolor*, 16 Feb. 2005, J. Nishikawa, MUMH 10332, MUCC 133; Shizuoka, on *V. tricolor*, 15 Jan. 2003, J. Nishikawa, MUMH 10334, MUCC 136. **Romania**, Cazanele Dunarii, on *V. tricolor*, O. Constantinescu, **epitype designated here** CBS H-21024, culture ex-epitype CBS 251.67 = CPC 5079. **New Zealand**, on *V. odorata*, C.F. Hill, CPC 5368.

*Notes*: See also *C. zebrina*. One culture that was isolated from *Viola* (strain CPC 10725) is representative of *C. fagopyri*. The original specimen of this isolate was distinguishable from *C. violae* in having circumspersed and slightly protuberant loci on its conidiophores. The isolates included here for *C. violae* are phylogenetically distinct from the other species included in this study on the basis of the TEF, ACT, CAL and HIS phylogenies. In the combined tree (Fig. 2 part 3), it is a sister taxon to *C. zebrina*.

***Cercospora zeae-maydis*** Tehon & E.Y. Daniels, Mycologia 17: 248. 1925.

*Specimens examined*: **China**, Liaoning Province, on *Zea mays* (*Poaceae*), CBS 132668 = CPC 12225 = CHME 52. **Mexico**, Tlacotepec, on *Z. mays*, 16 Sep. 2008, Ma. de Jesús Yáñez-Morales, CBS 132678 = CPC 15602. **USA**, Illinois, Alexander Co., McClure, on *Z. mays*, 29 Aug. 1924, P.A. Young, **holotype** ILLS 4276, **isotype** BPI 442569; Delaware, 1997, B. Fleener, DE-97 = A359 = CBS 117756; Indiana, Princeton, 1999, B. Fleener, PR-IN-99 = A364 = CBS 117761; Indiana, Princeton, 2003, B. Fleener, YA-03 = A358 = CBS 117755; Iowa, Johnston, 2004, B. Fleener, JH-IA-04 = A361 = CBS 117758; Iowa, Reinbeck, 1999, B. Fleener, RENBECK-IA-99 = A367 = CBS 117763; Missouri, Dexter, 2000, B. Fleener, DEXTER-MO-00 = A365 = CBS 117762; Pennsylvania, New Holland, 1999, B. Fleener, NH-PA-99 = A363 = CBS 117760; Tennessee, Union City, 1999, B. Fleener, UC-TN-99 = A362 = CBS 117759; Wisconsin, Janesville, 2002, B. Fleener, **epitype**, CBS H-17774, culture ex-epitype JV-WI-02 = A360 = CBS 117757.

*Notes*: This species is phylogenetically supported by ITS, TEF, ACT, CAL and HIS. In the combined tree (Fig. 2 part 1), it is a basal lineage. Gray leaf spot of maize was originally attributed to "group I" and "group II" siblings of *C. zeae-maydis* (Wang *et al*. 1998). More detailed information on this species was provided in Crous *et al*. (2006a).

### ***Cercospora zebrina*** Pass., Hedwigia 16: 124. 1877.

≡ *Cercosporina zebrina* (Pass.) Matsuura, J. Pl. Protect. (Tokyo) 17: 1. 1930.
= *Cercospora helvola* Sacc., Michelia 2: 556. 1882.
= *Cercospora stolziana* Magnus, Die Pilze von Tirol (*etc*.) 3: 558. 1905.
= *Cercospora helvola* var. *zebrina* Ferraris, Fl. Ital. Cryptog. 1: 423, 1910, *fide* Chupp (1954: 341).

*Specimens examined*: **Australia**, on *Trifolium cernuum* (*Fabaceae*), M.J. Barbetti, CBS 118791 = IMI 264190 = WA 2054 = WAC 7993; on *T. subterraneum*, M.J. Barbetti, CBS 118789 = WAC 5106; CBS 118790 = IMI 262766 = WA 2030 = WAC 7973. **Canada**, Ottawa, 13 Lucas lane, on *T. repens*, 1 Sep. 2000, K.A. Seifert, CBS H-21025, CBS 112723 = CPC 3957; CBS 112736 = CPC 3958; on *T. pratense*, K.A. Seifert, CBS H-21026, CBS 112893 = CPC 3955. **Italy**, on *Hedysarum coronarium* (*Fabaceae*), CBS 137.56 = CPC 5118 (as *C. ariminensis*). **New Zealand**, on *Hebe* sp. (*Scrophulariaceae*), C.F. Hill, CBS 114359 = CPC 10901; Auckland, on *Lotus pedunculatus* (*Fabaceae*), C.F. Hill, Lynfield 644, CPC 5437 (as *C. loti*); Blockhouse Bay, on *T. repens*, C.F. Hill, Lynfield 603, CBS 113070 = CPC 5367; on *Jacaranda mimosifolia* (*Bignoniaceae*), C.F. Hill, Lynfield 693, CPC 5473 (as *C. canescens*). **Romania**, Hagieni, on *Astragalus spruneri* (*Fabaceae*), O. Constantinescu, CBS 537.71 = IMI 161108 = CPC 5089 (as *C. astragali*). **South Korea**, Namyangju, on *T. repens*, 22 Oct. 2003, H.D. Shin, CBS H-21027, CBS 132650 = CPC 10756. **Unknown**, on *Medicago arabica* (= *M. maculata*) (*Fabaceae*), E.F. Hopkins, CBS 108.22 = CPC 5091 (as *C. medicaginis*). **USA**, Wisconsin, on *T. subterraneum*, CBS 129.39 = CPC 5078.

*Notes*: Morphological characteristics of the larger *C. zebrina* clade include conidiophores that are short, almost straight, slightly attenuated and distinctly conically truncate at the apex with distinctly thickened loci, and conidia, which are cylindrical to cylindro-obclavate. The type of *C. zebrina* was collected on *Trifolium* in Italy. More European collections are required to resolve this species and to delinate it from other, closely allied species.

*Cercospora althaeina*, which has wide host range on malvaceous plants, has a similar morphology to *C. zebrina. Cercospora violae*, which clusters basal to the *C. zebrina* clade, has longer and wider conidiophores, and cylindrical to acicular conidia, which separates this species from *C. zebrina*.

In the TEF phylogeny, isolates are intermixed with those of *C. armoraciae*, *C. rumicis* and *Cercospora* sp. L and in the ACT and CAL phylogenies with those of *Cercospora* sp. L and *C. althaeina*. Only in the HIS phylogeny do these isolates form a pure monophyletic clade. In the combined tree (Fig. 2 part 3), it is a sister taxon to *C. violae*.

### ***Cercospora zeina*** Crous & U. Braun, Stud. Mycol. 55: 194. 2006.

*Specimens examined*: **South Africa**, KwaZulu-Natal, Pietermaritzburg, on *Zea mays* (*Poaceae*), 2005, P. Caldwell, **holotype** CBS H-17775, culture ex-type CBS 118820 = CPC 11995; CBS 132617 = CPC 11998.

*Notes*: This species is phylogenetically supported by ITS, TEF, ACT, CAL and HIS. In the combined tree (Fig. 2 part 1), it is a basal lineage. More detailed information on this species was provided in Crous *et al*. (2006a).

### ***Cercospora* cf. *zinniae***

*Caespituli* amphigenous. *Mycelium* internal. *Stromata* lacking to small, up to 35 µm diam, intraepidermal or substomatal, pale brown to brown. *Conidiophores* in loose fascicles (3–8), pale brown to brown, straight, mildly geniculate above the middle, multi-septate, attenuated, successively geniculate, tip truncate or conically truncate, 65–300 × 3.5–5 µm, 1–12-septate. *Conidiogenous cells* integrated, proliferating sympodially, terminal and intercalary, multi-local; loci distinctly thickened, darkened, apical and lateral, sometimes circumspersed, often slightly protuberant, 2–2.5 µm diam. *Conidia* solitary, hyaline, filiform to acicular, cylindro-obclavate, straight to curved, long obconically truncate or truncate, and thickened at the base, acute at the apex, multi-septate, 30–120 × 1–4 µm, 3–13-septate.

*Description of caespituli on V8*; (MUCC 131): *Conidiophores* solitary, arising from hyphae, subhyaline to pale brown, irregular in width, smooth, meager and thin-walled, sinuous-geniculate to geniculate, unbranched, truncate or conically truncate at the tip, 13–63 × 3–5 µm, multi-septate. *Conidiogenous cells* integrated, terminal, proliferating sympodially, single to multi-local (1–2); loci moderately thickened, apical, sometimes slightly protuberant, 1.25–2 µm in width. *Conidia* hyaline, filiform to acicular, slightly thickened and long obconically truncate at the base, acute to obtuse at the apex, 25–160 × 2.5–4 µm, 3–11-septate.

*Specimens examined*: **Brazil**, Valverde, Alto Rio Doce, on unknown substrate, A.C. Alfenas, CBS 132676 = CPC 15075. **Japan**, Chiba, on *Zinnia elegans* (*Asteraceae*), 12 Sep. 1997, S. Uematsu, MUCC 572 = MAFF 237718 = MUCNS 215; Shizuoka, on *Z. elegans*, 17 Sep. 2004, J. Nishikawa, MUMH 11397, MUCC 131. **South Korea**, Yangpyeong, on *Z. elegans*, 18 Oct. 2007, H.D. Shin, CBS 132624 = CPC 14549.

*Notes*: This species is characterised in that the conidiophores are mildly geniculate above the middle, multi-septate, attenuated with successive geniculation; loci circumspersed and distinctly thickened; conidia are narrower than those of other taxa in *C. apii s. lat*. Moreover, this species is phylogenetically supported by DNA sequence data of TEF, CAL and HIS. In the ACT phylogeny, two distinct lineages are formed, namely CPC 14549 versus CPC 15075, MUCC 132 and MUCC 572. In the combined tree (Fig. 2 part 4), it is basal to the lineage containing, for example, *C.* cf. *ipomoeae*, *C. fagopyri* and *C. rodmanii*. North American cultures and sequence data are necessary to confirm the identity of Asian collections as *C. zinniae* and to designate an epitype.

## DISCUSSION

This study was initiated to resolve *Cercospora* taxonomy on the basis of morphological and DNA sequence data. Based on our earlier studies incorporating multi-gene phylogenies on smaller datasets (Crous *et al*. 2004b, 2006a, Groenewald *et al*. 2005, 2006a, 2010a), we realised this was an ambitious task. Even though a whole range of hosts and countries were included in our study, attempts to apply existing names to the different clades in the phylogenetic trees obtained proved difficult. In addition, the lack of ex-type cultures or at least reference sequences from type material, made it especially problematic to assign existing names to the derived phylogenetic clades. To our knowledge, this study presently represents the largest combination of diverse sampling of cercosporoid fungi coupled with multi-locus sequence data in a single manuscript.

One important finding is that Crous & Braun (2003) were over-optimistic when they referred 281 *Cercospora* names to *C. apii s. lat*. based on morphology alone. Of the species treated as distinct in the present paper, the following five were originally referred to *C. apii s. lat*. by Crous & Braun (2003), namely *C. beticola*, *C.*

*canescens*, *C. fagopyri*, *C. kikuchii* and *C. rumicis*. The following eight species, *C. armoraciae*, *C. corchori*, *C. lactucae-sativae*, *C. mercurialis*, *C. polygonacea*, *C. ricinella*, *C. violae* and *C. zebrina*, treated as distinct in the present study, were treated by Crous & Braun (2003) as close to or possibly identical with *C. apii s. lat*. It is evident that morphology alone provides an insufficient basis on which to establish synonymies, to describe novel species or in many cases to identify species of *Cercospora*.

In the last 10 years, 45 novel *Cercospora* names were lodged with MycoBank (Crous *et al*. 2004a). Of these, only five species are based on morphology and multi-locus sequence data, two species have morphology supplemented with ITS sequences and 38 species are based on morphology alone. Of these 45 species, only 10 species were described in culture, 26 were reported without culture characteristics and of the remaining nine it is unlikely that cultures were established. This is an alarming statistic and is something that should be addressed by the whole community working on cercosporoid fungi. If the situation is compared to that of *Colletotrichum*, it is clear that there is room for improvement. Phylogenetic studies on *Colletotrichum* species based on cultures and ITS data date back to at least 20 years, with the last 10 years showing a significant increase in species descriptions based on multi-locus sequence data (Cannon *et al*. 2012).

Groenewald *et al*. (2010a) reported on the performance of the five loci used for the phylogenetic inference in this study. They found the ITS region had limited resolution (2.7 % clade recovery) and was best be used to confirm the generic affiliation of a species, with less value when used for species comparison, specifically within the *C. apii* complex. Although CAL is necessary to distinguish *C. apii* and *C. beticola*, it only distinguished about half of the observed species clades (46.6 % clade recovery), whereas ACT was slightly more successful (58.9 % clade recovery). The HIS region compared well with ACT (63 % clade recovery), but it did split *C. beticola* into two clades. Both of these *C. beticola* clades contain isolates from the same sugar beet fields in Germany and New Zealand (Groenewald *et al*. 2006b) and whether this implies population variation or the presence of an additional cryptic species on sugar beet requires further molecular analyses of more *C. beticola* populations. The TEF region was comparable to CAL in terms of clade recovery (45 % clade recovery). Although we believe that there is still a need to identify the best barcode locus for *Cercospora*, the current multi-locus approach does enable species identification. Comparison of a few *Cercospora* genomes selected from across the phylogenetic tree might reveal a single locus with better resolution than the currently used loci.

Similar to the situation in *Pseudocercospora* (Crous *et al*. 2013), we also encountered a situation where we could not use names based on North American or European types for African or Asian cultures and *vice versa*. Based on morphological features and their distinct sequences we have chosen to treat those clades in the present study as "cf." pending comparison of those species with (epi-)type material from the original country and host as discussed under the species notes above. For numerous clades ("*Cercospora* sp. A–S"), it was not possible to unequivocally assign a species name; frequently these clades contained isolates from multiple hosts and/or countries and the same hosts occurred in multiple clades, or the host information was not available. For example, isolates from *Cajanus cajan* in South Africa can be attributed to *Cercospora* sp. P and *Cercospora* sp. Q. Crous & Braun (2003) list four *Cercospora* species associated with this host, namely *C. apii s. str.*, *C. canescens*, *C. instabilis* and *C. thirumalacharii*. The first two species were included in this study, the third is listed on *Cajanus* from numerous countries (but not including South Africa) and the last is known from India (Crous & Braun 2003). It was not possible to include authentic cultures of the latter two species, so any of these two names are potentially available for a clade. An additional complicating factor is that there are numerous sub-clades inside *Cercospora* sp. P and *Cercospora* sp. Q, which could represent either intra-specific variation or the presence of cryptic species, which are not distinguished by the loci used in this study. We sequenced five additional loci for *Cercospora* sp. Q isolates and did not find a single locus that provided better insight into this clade. Isolates from *Cajanus* also occur in the same clade with other hosts, raising the question of wide host range versus simply a chance infection (Crous & Groenewald 2005). A similar situation was observed for isolates isolated from yams (*Dioscorea*). Crous & Braun (2003) list numerous *Pseudocercospora* and *Passalora* species, and three *Cercospora* species (*C. aragonensis*, *C. dioscoreae-pyrifoliae* and *C. golaghatti*) from this host genus; of the three *Cercospora* names, *C. dioscoreae-pyrifoliae* is commonly used in literature. In this study, it was not possible to apply this name to any of the clades. Isolates from *Dioscorea* are found in the *C. canescens* complex, *Cercospora* cf. *sigesbeckiae*, *Cercospora* sp. P and *Cercospora* sp. Q, but none of these isolates were from the original host or locality of the type description for *C. dioscoreae-pyrifoliae* (based on *Dioscorea pyrifolia* in Singapore). One of the isolates included in the present study (MUCC 849, as *Cercospora* cf. *sigesbeckiae*) was treated by Nakashima *et al*. (2011) as *C. dioscoreae-pyrifoliae*. The authors noted that, although the morphological characteristics were similar to the original description, the width of the conidiophores and conidia was different. Similarly, most of the isolates from *Dioscorea* were sent to us under the name *C. dioscoreae-pyrifoliae* although we could not confirm the identification with confidence. These examples highlight the need to locate original specimens, or at least recollect material that can be used for epitypification, to fix the names used in the various phylogenetic clades. It also illustrates the importance of establishing cultures, which can be used for future molecular studies, when describing taxonomic novelties.

We believe that this study serves as a backbone for future studies on *Cercospora* taxonomy. Unfortunately, many (epi-)type cultures and adequate sequence data are lacking for a significant number of *Cercospora* species. Future studies will require the recollection of material from the original hosts and continents so that epitypes can be found and names stabilised. Furthermore, all species, especially those currently in common use, need proper molecular identification. Based on searches in Google and Google Scholar, the most commonly used *Cercospora* species names are *C. zeae-maydis*, *C. beticola*, *C. apii*, *C. canescens*, *C. kikuchii*, *C. sojina*, *C. arachidicola*, *C. coffeicola*, *C. personata* and *C. nicotianae*. Although the taxonomy of *C. apii*, *C. beticola* (Groenewald *et al*. 2005, 2006a) and *C. zeae-maydis* (Crous *et al*. 2006a) was resolved in the past, the present study resolved *C. kikuchii* and *C. sojina* but it was unable to resolve *C. canescens*. Similar studies are needed for *C. arachidicola*, *C. coffeicola*, *C. nicotianae* and *C. personata*.

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# *Alternaria* redefined

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**Abstract:** *Alternaria* is a ubiquitous fungal genus that includes saprobic, endophytic and pathogenic species associated with a wide variety of substrates. In recent years, DNA-based studies revealed multiple non-monophyletic genera within the *Alternaria* complex, and *Alternaria* species clades that do not always correlate to species-groups based on morphological characteristics. The *Alternaria* complex currently comprises nine genera and eight *Alternaria* sections. The aim of this study was to delineate phylogenetic lineages within *Alternaria* and allied genera based on nucleotide sequence data of parts of the 18S nrDNA, 28S nrDNA, ITS, GAPDH, RPB2 and TEF1-alpha gene regions. Our data reveal a *Pleospora*/*Stemphylium* clade sister to *Embellisia annulata,* and a well-supported *Alternaria* clade. The *Alternaria* clade contains 24 internal clades and six monotypic lineages, the assemblage of which we recognise as *Alternaria*. This puts the genera *Allewia*, *Brachycladium*, *Chalastospora*, *Chmelia*, *Crivellia*, *Embellisia*, *Lewia*, *Nimbya*, *Sinomyces*, *Teretispora*, *Ulocladium*, *Undifilum* and *Ybotromyces* in synonymy with *Alternaria*. In this study, we treat the 24 internal clades in the *Alternaria* complex as sections, which is a continuation of a recent proposal for the taxonomic treatment of lineages in *Alternaria*. *Embellisia annulata* is synonymised with *Dendryphiella salina*, and together with *Dendryphiella arenariae*, are placed in the new genus *Paradendryphiella*. The sexual genera *Clathrospora* and *Comoclathris*, which were previously associated with *Alternaria*, cluster within the *Pleosporaceae*, outside *Alternaria s. str.*, whereas *Alternariaster*, a genus formerly seen as part of *Alternaria*, clusters within the *Leptosphaeriaceae*. *Paradendryphiella* is newly described, the generic circumscription of *Alternaria* is emended, and 32 new combinations and 10 new names are proposed. A further 10 names are resurrected, while descriptions are provided for 16 new *Alternaria* sections.

**Key words:** *Allewia*, *Chalastospora*, *Crivellia*, *Embellisia*, *Lewia*, *Nimbya*, *Paradendryphiella, Sinomyces*, systematics, *Teretispora*, *Ulocladium*, *Undifilum*.

**Taxonomic novelties: New combinations –** *Alternaria abundans* (E.G. Simmons) Woudenb. & Crous, *Alternaria alternariae* (Cooke) Woudenb. & Crous, *Alternaria atra* (Preuss) Woudenb. & Crous, *Alternaria bornmuelleri* (Magnus) Woudenb. & Crous, *Alternaria botrytis* (Preuss) Woudenb. & Crous, *Alternaria caespitosa* (de Hoog & C. Rubio) Woudenb. & Crous, *Alternaria cantlous* (Yong Wang bis & X.G. Zhang) Woudenb. & Crous, *Alternaria caricis* (E.G. Simmons) Woudenb. & Crous, *Alternaria cinerea* (Baucom & Creamer) Woudenb. & Crous, *Alternaria didymospora* (Munt.-Cvetk.) Woudenb. & Crous, *Alternaria fulva* (Baucom & Creamer) Woudenb. & Crous, *Alternaria hyacinthi (*de Hoog & P.J. Mull. bis) Woudenb. & Crous, *Alternaria indefessa* (E.G. Simmons) Woudenberg & Crous, *Alternaria leptinellae* (E.G. Simmons & C.F. Hill) Woudenb. & Crous, *Alternaria lolii (*E.G. Simmons & C.F. Hill) Woudenb. & Crous, *Alternaria multiformis* (E.G. Simmons) Woudenb. & Crous, *Alternaria obclavata* (Crous & U. Braun) Woudenb. & Crous, *Alternaria obovoidea* (E.G. Simmons) Woudenb. & Crous, *Alternaria oudemansii* (E.G. Simmons) Woudenb. & Crous, *Alternaria oxytropis (Q. Wang, Nagao & Kakish.)* Woudenb. & Crous, *Alternaria penicillata* (Corda) Woudenb. & Crous, *Alternaria planifunda (*E.G. Simmons) Woudenb. & Crous, *Alternaria proteae (*E.G. Simmons) Woudenb. & Crous, *Alternaria scirpinfestans* (E.G. Simmons & D.A. Johnson) Woudenb. & Crous, *Alternaria scirpivora* (E.G. Simmons & D.A. Johnson) Woudenb. & Crous, *Alternaria septospora* (Preuss) Woudenb. & Crous, *Alternaria slovaca* (Svob.-Pol., L. Chmel & Bojan.) Woudenb. & Crous, *Alternaria subcucurbitae* (Yong Wang bis & X.G. Zhang) Woudenb. & Crous, *Alternaria tellustris* (E.G. Simmons) Woudenb. & Crous, *Alternaria tumida (*E.G. Simmons) Woudenb. & Crous, *Paradendryphiella salina* (G.K. Sutherl.) Woudenb. & Crous, *Paradendryphiella arenariae* (Nicot) Woudenb. & Crous. **New names –** *Alternaria aspera* Woudenb. & Crous, *Alternaria botryospora* Woudenb. & Crous, *Alternaria brassicae-pekinensis* Woudenb. & Crous, *Alternaria breviramosa* Woudenb. & Crous, *Alternaria chlamydosporigena* Woudenb. & Crous, *Alternaria concatenata* Woudenb. & Crous, *Alternaria embellisia* Woudenb. & Crous, *Alternaria heterospora* Woudenb. & Crous, *Alternaria papavericola Woudenb. & Crous, Alternaria terricola* Woudenb. & Crous. **Resurrected names –** *Alternaria cetera* E.G. Simmons, *Alternaria chartarum* Preuss, *Alternaria consortialis* (Thüm.) J.W. Groves & S. Hughes, *Alternaria cucurbitae* Letendre & Roum., *Alternaria dennisii* M.B. Ellis, *Alternaria eureka* E.G. Simmons, *Alternaria gomphrenae* Togashi, *Alternaria malorum* (Ruehle) U. Braun, Crous & Dugan, *Alternaria phragmospora* Emden, *Alternaria scirpicola* (Fuckel) Sivan. **New sections, all in *Alternaria* –** sect. *Chalastospora* Woudenb. & Crous, sect. *Cheiranthus* Woudenb. & Crous, sect. *Crivellia* Woudenb. & Crous, sect. *Dianthicola* Woudenb. & Crous, sect. *Embellisia* Woudenb. & Crous, sect. *Embellisioides* Woudenb. & Crous, sect. *Eureka* Woudenb. & Crous, sect. *Infectoriae* Woudenb. & Crous, sect. *Japonicae* Woudenb. & Crous, sect. *Nimbya* Woudenb. & Crous, sect. *Phragmosporae* Woudenb. & Crous, sect. *Pseudoulocladium* Woudenb. & Crous, sect. *Teretispora* Woudenb. & Crous, sect. *Ulocladioides* Woudenb. & Crous, sect. *Ulocladium* Woudenb. & Crous, sect. *Undifilum* Woudenb. & Crous. **New genus –** *Paradendryphiella* Woudenb. & Crous.

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## INTRODUCTION

*Alternaria* is a ubiquitous fungal genus that includes saprobic, endophytic and pathogenic species. It is associated with a wide variety of substrates including seeds, plants, agricultural products, animals, soil and the atmosphere. Species of *Alternaria* are known as serious plant pathogens, causing major losses on a wide range of crops. Several taxa are also important postharvest pathogens, causative agents of phaeohyphomycosis in immuno-compromised patients or airborne allergens. Because of the significant negative health effects of *Alternaria* on humans and their surroundings, a correct and rapid identification of *Alternaria* species would be of great value to researchers, medical mycologists and the public alike.

*Alternaria* was originally described by Nees (1816), based on *A. tenuis* as the only species. Characteristics of the genus included the production of dark-coloured phaeodictyospores in chains, and a beak of tapering apical cells. Von Keissler (1912) synonymised both *A. tenuis* and *Torula alternata* (Fries 1832) with *Alternaria alternata*, due to ambiguities in Nees's description of *A. tenuis*. Two additional genera, *Stemphylium* (Wallroth 1833) and *Ulocladium* (Preuss 1851) were subsequently described for phaeodictyosporic hyphomycetes, further complicating the taxonomic resolution in this group of fungi. Several re-descriptions and revised criteria of these genera (Saccardo 1886, Elliot 1917, Wiltshire 1933, 1938, Joly 1964) resulted in a growing number of new species. Results of a lifetime study on *Alternaria* taxonomy based upon morphological characteristics were summarised in Simmons (2007), in which 275 *Alternaria* species were recognised. One species was transferred to the genus *Prathoda* and three new genera, *Alternariaster*, *Chalastospora* and *Teretispora*, were segregated from *Alternaria*.

Molecular studies revealed multiple non-monophyletic genera within the *Alternaria* complex and *Alternaria* species clades, which do not always correlate to species-groups based upon morphological characteristics (Pryor & Gilbertson 2000, Chou & Wu 2002, de Hoog & Horré 2002, Pryor & Bigelow 2003, Hong *et al*. 2005, Inderbitzin *et al*. 2006, Pryor *et al*. 2009, Runa *et al*. 2009, Wang *et al*. 2011, Lawrence *et al*. 2012). The *A. alternata*, *A. brassicicola*, *A. infectoria*, *A. porri* and *A. radicina* species-groups were strongly supported by these studies and two new species-groups, *A. sonchi* (Hong *et al.* 2005) and *A. alternantherae* (Lawrence *et al.* 2012) and three new genera, *Crivellia* (Inderbitzin *et al.* 2006), *Undifilum* (Pryor *et al.* 2009) and *Sinomyces* (Wang *et al.* 2011), were described. The latest molecular revision of *Alternaria* (Lawrence *et al.* 2013) introduced two new species groups, *A. panax* and *A. gypsophilae*, and elevated eight species-groups to sections within *Alternaria*. The sexual phylogenetic *Alternaria* lineage, the *A. infectoria* species-group, did not get the status of section, in contrast to the eight asexual phylogenetic lineages in *Alternaria.* The *Alternaria* complex currently comprises the genera *Alternaria*, *Chalastospora* (Simmons 2007), *Crivellia*, *Embellisia*, *Nimbya*, *Stemphylium*, *Ulocladium*, *Undifilum* and the recently described *Sinomyces* together with eight sections of *Alternaria* and the *A. infectoria* species-group.

The aim of the present study was to delineate the phylogenetic lineages within *Alternaria* and allied genera, and to create a robust taxonomy. Phylogenetic inferences were conducted on sequence data of parts of the 18S nrDNA (SSU), 28S nrDNA (LSU), the internal transcribed spacer regions 1 and 2 and intervening 5.8S nrDNA (ITS), glyceraldehyde-3-phosphate dehydrogenase (GAPDH), RNA polymerase second largest subunit (RPB2) and translation elongation factor 1-alpha (TEF1) gene regions of ex-type and reference strains of *Alternaria* species and all available allied genera.

## MATERIAL AND METHODS

### Isolates

Based on the ITS sequences of all ex-type or representative strains from the *Alternaria* identification manual present at the CBS-KNAW Fungal Biodiversity Centre (CBS), Utrecht, The Netherlands (data not shown), 66 *Alternaria* strains were included in this study together with 61 ex-type or representative strains of 16 related genera (Table 1). *Alternaria* is represented by the ex-type or representative strains of the seven species-groups and species that clustered outside known *Alternaria* clades. Because of the size and complexity of the *A. alternata*, *A. infectoria* and *A. porri* species-groups, we only included known species; the complete species-groups will be treated in future studies.

Freeze-dried strains were revived in 2 mL malt/peptone (50 % / 50 %) and subsequently transferred to oatmeal agar (OA) (Crous *et al.* 2009a). Strains of the CBS collection stored in liquid nitrogen were transferred to OA directly from -80 ºC. DNA extraction was performed using the UltraClean Microbial DNA Isolation Kit (MoBio laboratories, Carlsbad, CA, USA), according to the manufacturer's instructions.

### Taxonomy

Morphological descriptions were made for isolates grown on synthetic nutrient-poor agar plates (SNA, Nirenberg 1976) with a small piece of autoclaved filter paper placed onto the agar surface. Cultures were incubated at moderate temperatures (~ 22 ºC) under CoolWhite fluorescent light with an 8 h photoperiod for 7 d. The sellotape technique was used for making slide preparations (Crous *et al.* 2009a) with Shear's medium as mounting fluid. Photographs of characteristic structures were made with a Nikon Eclipse 80i microscope using differential interference contrast (DIC) illumination. Growth rates were measured after 5 and 7 d. Colony characters were noted after 7 d, colony colours were rated according to Rayner (1970). Nomenclatural data were deposited in MycoBank (Crous *et al.* 2004).

### PCR and sequencing

The SSU region was amplified with the primers NS1 and NS4 (White *et al.* 1990), the LSU region with LSU1Fd (Crous *et al*. 2009b) and LR5 (Vilgalys & Hester 1990), the ITS region with V9G (De Hoog & Gerrits van den Ende 1998) and ITS4 (White *et al.* 1990), the GAPDH region with gpd1 and gpd2 (Berbee *et al.* 1999), the RPB2 region with RPB2–5F2 (Sung *et al.* 2007) and fRPB2–7cR (Liu *et al.* 1999) and the TEF1 gene with the primers EF1-728F and EF1-986R (Carbone & Kohn 1999) or EF2 (O'Donnell *et al.* 1998). The PCRs were performed in a MyCycler™ Thermal Cycler (Bio-Rad Laboratories B.V., Veenendaal, The Netherlands) in a total volume of 12.5 µL. The SSU and LSU PCR mixtures consisted of 1 µL genomic DNA, 1´ GoTaq® Flexi buffer (Promega, Madison, WI, USA), 2 µM $MgCl_2$, 40 µM of each dNTP, 0.2 µM of each primer and 0.25 Unit GoTaq® Flexi DNA polymerase (Promega). The ITS and GAPDH PCR mixtures differed from the original mix by containing 1 µM $MgCl_2$, the RPB2 and TEF1 PCR mixtures differed from the original mix by containing 2 µL genomic DNA and the RPB2 mixture differed from the original mix by containing 0.5 U instead of 0.25 U GoTaq® Flexi DNA polymerase. Conditions for PCR amplification consisted of an initial denaturation step of 5 min at 94 ºC followed by 35 cycles of 30 s at 94 ºC, 30 s at 48 ºC and 90 s at 72 ºC for SSU, LSU, ITS and 40 cycles of 30 s at 94 ºC, 30 s at 52 ºC / 59 ºC and 45 s at 72 ºC for TEF1 using respectively EF2 or EF1-986R as reverse primer and a final elongation step of 7 min at 72 ºC. The partial RPB2 gene was obtained by using a touchdown PCR protocol of 5 cycles of 45 s at 94 ºC, 45 s at 60 ºC and 2 min at 72 ºC, followed by 5 cycles with a 58 ºC annealing temperature and 30 cycles with a 54 ºC annealing temperature. The PCR products were sequenced in both directions using the PCR primers and the BigDye Terminator v. 3.1 Cycle Sequencing Kit (Applied Biosystems, Foster City, CA, USA), according to the manufacturer's recommendations, and analysed with an ABI Prism 3730XL Sequencer (Applied Biosystems) according to the manufacturer's instructions. Consensus sequences were computed from forward and reverse sequences using the BioNumerics v. 4.61 software package (Applied Maths, St-Martens-Latem, Belgium). All generated sequences were deposited in GenBank (Table 1).

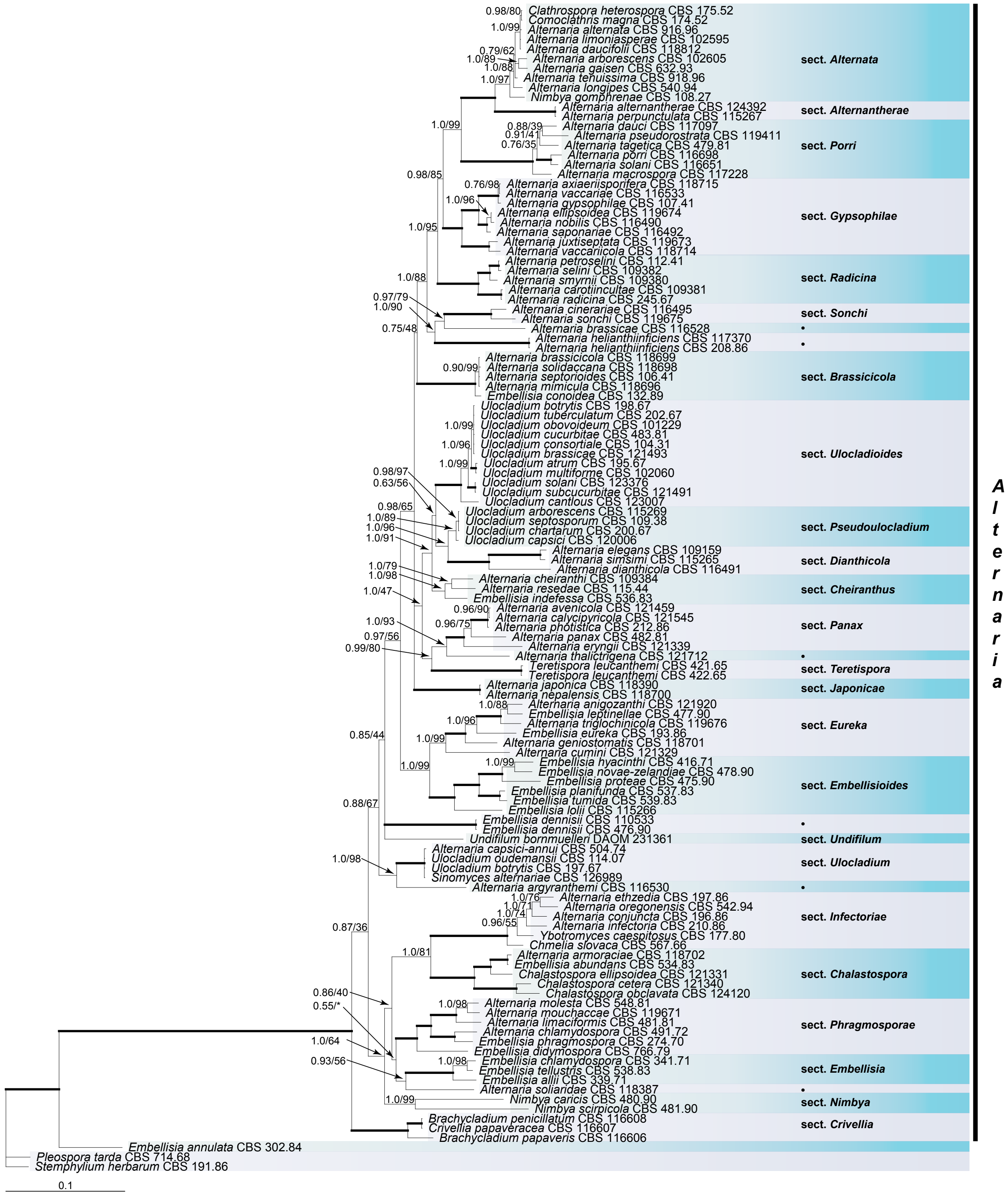


**Fig. 1.** Bayesian 50 % majority rule consensus tree based on the GAPDH, RPB2 and TEF1 sequences of 121 strains representing the *Alternaria* complex. The Bayesian posterior probabilities (PP) and RAxML bootstrap support values (ML) are given at the nodes (PP/ML). Thickened lines indicate a PP of 1.0 and ML of 100. The tree was rooted to *Stemphylium herbarum* (CBS 191.86). The monotypic lineages are indicated by black dots.

## Phylogenetic analyses

Multiple sequence alignments were generated with MAFFT v. 6.864b (http://mafft.cbrc.jp/alignment/server/index.html), and adjusted by eye. Two different datasets were used to estimate two phylogenies; an *Alternaria* complex phylogeny and a *Pleosporineae* family tree. The first tree focusses on the *Alternaria* complex, the second one was produced to place the genera *Comoclathris*, *Clathrospora* and *Alternariaster* in the context of the *Alternaria* complex. The relatives of the three genera were determined with standard nucleotide blast searches, with both the SSU and LSU sequences, against the nucleotide database in GenBank. This resulted in a selection of 35

**Table 1.** Isolates used in this study and their GenBank accession numbers. Bold accession numbers were generated in other studies.

| Old species name | New species name | *Alternaria* Section | Strain number[1] | Status[2] | Host / Substrate | Country | Other collection number[1] | GenBank accession numbers | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | | | | | SSU | LSU | RPB2 | ITS | GAPDH | TEF1 |
| *Alternaria alternantherae* | *Alternaria alternantherae* | *Althernantherae* | CBS 124392 | | *Solanum melongena* | China | HSAUP2798 | KC584506 | KC584251 | KC584374 | KC584179 | KC584096 | KC584633 |
| *Alternaria alternata* | *Alternaria alternata* | *Alternata* | CBS 916.96 | T | *Arachis hypogaea* | India | EGS 34.016 | KC584507 | **DQ678082** | KC584375 | **AF347031** | **AY278808** | KC584634 |
| *Alternaria anigozanthi* | *Alternaria anigozanthi* | *Eureka* | CBS 121920 | T | *Anigozanthus* sp. | Australia | EGS 44.066 | KC584508 | KC584252 | KC584376 | KC584180 | KC584097 | KC584635 |
| *Alternaria arborescens* | *Alternaria arborescens* | *Alternata* | CBS 102605 | T | *Lycopersicon esculentum* | USA | EGS 39.128 | KC584509 | KC584253 | KC584377 | **AF347033** | **AY278810** | KC584636 |
| *Alternaria argyranthemi* | *Alternaria argyranthemi* | | CBS 116530 | T | *Argyranthemum* sp. | New Zealand | EGS 44.033 | KC584510 | KC584254 | KC584378 | KC584181 | KC584098 | KC584637 |
| *Alternaria armoraciae* | *Alternaria armoraciae* | *Chalastospora* | CBS 118702 | T | *Armoracia rusticana* | New Zealand | EGS 51.064 | KC584511 | KC584255 | KC584379 | KC584182 | KC584099 | KC584638 |
| *Alternaria avenicola* | *Alternaria avenicola* | *Panax* | CBS 121459 | T | *Avena sp.* | Norway | EGS 50.185 | KC584512 | KC584256 | KC584380 | KC584183 | KC584100 | KC584639 |
| *Alternaria axiaeriisporifera* | *Alternaria axiaeriisporifera* | *Gypsophilae* | CBS 118715 | T | *Gypsophila paniculata* | New Zealand | EGS 51.066 | KC584513 | KC584257 | KC584381 | KC584184 | KC584101 | KC584640 |
| *Alternaria brassicae* | *Alternaria brassicae* | | CBS 116528 | R | *Brassica oleracea* | USA | EGS 38.032 | KC584514 | KC584258 | KC584382 | KC584185 | KC584102 | KC584641 |
| *Alternaria brassicicola* | *Alternaria brassicicola* | *Brassicicola* | CBS 118699 | R | *Brassica oleracea* | USA | EGS 42.002; ATCC 96836 | KC584515 | KC584259 | KC584383 | **JX499031** | KC584103 | KC584642 |
| *Alternaria calycipyricola* | *Alternaria calycipyricola* | *Panax* | CBS 121545 | T | *Pyrus communis* | China | EGS 52.071; RGR 96.0209 | KC584516 | KC584260 | KC584384 | KC584186 | KC584104 | KC584643 |
| *Alternaria capsici-annui* | *Alternaria capsici-annui* | *Ulocladium* | CBS 504.74 | | *Capsicum annuum* | – | | KC584517 | KC584261 | KC584385 | KC584187 | KC584105 | KC584644 |
| *Alternaria carotiincultae* | *Alternaria carotiincultae* | *Radicina* | CBS 109381 | T | *Daucus carota* | USA | EGS 26.010 | KC584518 | KC584262 | KC584386 | KC584188 | KC584106 | KC584645 |
| *Alternaria cheiranthi* | *Alternaria cheiranthi* | *Cheiranthus* | CBS 109384 | R | *Cheiranthus cheiri* | Italy | EGS 41.188 | KC584519 | KC584263 | KC584387 | **AF229457** | KC584107 | KC584646 |
| *Alternaria chlamydospora* | *Alternaria chlamydospora* | *Phragmosporae* | CBS 491.72 | T | Soil | Egypt | EGS 31.060; ATCC 28045; IMI 156427 | KC584520 | KC584264 | KC584388 | KC584189 | KC584108 | KC584647 |
| *Alternaria cinerariae* | *Alternaria cinerariae* | *Sonchi* | CBS 116495 | R | *Ligularia* sp. | USA | EGS 49.102 | KC584521 | KC584265 | KC584389 | KC584190 | KC584109 | KC584648 |
| *Alternaria conjuncta* | *Alternaria conjuncta* | *Infectoriae* | CBS 196.86 | T | *Pastinaca sativa* | Switzerland | EGS 37.139 | KC584522 | KC584266 | KC584390 | **FJ266475** | **AY562401** | KC584649 |
| *Alternaria cumini* | *Alternaria cumini* | *Eureka* | CBS 121329 | T | *Cuminum cyminum* | India | EGS 04.158a | KC584523 | KC584267 | KC584391 | KC584191 | KC584110 | KC584650 |
| *Alternaria dauci* | *Alternaria dauci* | *Porri* | CBS 117097 | R | *Daucus carota* | USA | EGS 46.006 | KC584524 | KC584268 | KC584392 | KC584192 | KC584111 | KC584651 |
| *Alternaria daucifolii* | *Alternaria daucifolii* | *Alternata* | CBS 118812 | T | *Daucus carota* | USA | EGS 37.050 | KC584525 | KC584269 | KC584393 | KC584193 | KC584112 | KC584652 |
| *Alternaria dianthicola* | *Alternaria dianthicola* | *Dianthicola* | CBS 116491 | R | Dianthus × allwoodii | New Zealand | EGS 51.022 | KC584526 | KC584270 | KC584394 | KC584194 | KC584113 | KC584653 |
| *Alternaria elegans* | *Alternaria elegans* | *Dianthicola* | CBS 109159 | T | *Lycopersicon esculentum* | Burkina Faso | EGS 45.072; IMI 374542 | KC584527 | KC584271 | KC584395 | KC584195 | KC584114 | KC584654 |
| *Alternaria ellipsoidea* | *Alternaria ellipsoidea* | *Gypsophilae* | CBS 119674 | T | *Dianthus barbatus* | USA | EGS 49.104 | KC584528 | KC584272 | KC584396 | KC584196 | KC584115 | KC584655 |
| *Alternaria eryngii* | *Alternaria eryngii* | *Panax* | CBS 121339 | R | *Eryngium* sp. | – | EGS 41.005 | KC584529 | KC584273 | KC584397 | **JQ693661** | **AY562416** | KC584656 |
| *Alternaria ethzedia* | *Alternaria ethzedia* | *Infectoriae* | CBS 197.86 | T | *Brassica napus* | Switzerland | EGS 37.143 | KC584530 | KC584274 | KC584398 | **AF392987** | **AY278795** | KC584657 |
| *Alternaria gaisen* | *Alternaria gaisen* | *Alternata* | CBS 632.93 | R | *Pyrus pyrifolia* cv. Nijiseiki | Japan | EGS 90.512 | KC584531 | KC584275 | KC584399 | KC584197 | KC584116 | KC584658 |

**Table 1.** (Continued).

| Old species name | New species name | *Alternaria* Section | Strain number[1] | Status[2] | Host / Substrate | Country | Other collection number[1] | GenBank accession numbers | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | | | | | SSU | LSU | RPB2 | ITS | GAPDH | TEF1 |
| *Alternaria geniostomatis* | *Alternaria geniostomatis* | *Eureka* | CBS 118701 | T | *Geniostoma* sp. | New Zealand | EGS 51.061 | KC584532 | KC584276 | KC584400 | KC584198 | KC584117 | KC584659 |
| *Alternaria gypsophilae* | *Alternaria gypsophilae* | *Gypsophilae* | CBS 107.41 | T | *Gypsophila elegans* | – | EGS 07.025; IMI 264349 | KC584533 | KC584277 | KC584401 | KC584199 | KC584118 | KC584660 |
| *Alternaria helianthiinficiens* | *Alternaria helianthiinficiens* | | CBS 117370 | R | *Helianthus annuus* | UK | EGS 50.174; IMI 388636 | KC584534 | KC584278 | KC584402 | KC584200 | KC584119 | KC584661 |
| *Alternaria helianthiinficiens* | *Alternaria helianthiinficiens* | | CBS 208.86 | T | *Helianthus annuus* | USA | EGS 36.184 | KC584535 | KC584279 | KC584403 | **JX101649** | KC584120 | **EU130548** |
| *Alternaria infectoria* | *Alternaria infectoria* | *Infectoriae* | CBS 210.86 | T | *Triticum aestivum* | UK | EGS 27.193 | KC584536 | KC584280 | KC584404 | **DQ323697** | **AY278793** | KC584662 |
| *Alternaria japonica* | *Alternaria japonica* | *Japonicae* | CBS 118390 | R | *Brassica chinensis* | USA | EGS 50.099 | KC584537 | KC584281 | KC584405 | KC584201 | KC584121 | KC584663 |
| *Alternaria juxtiseptata* | *Alternaria juxtiseptata* | *Gypsophilae* | CBS 119673 | T | *Gypsophila paniculata* | Australia | EGS 44.015; DAR 43414 | KC584538 | KC584282 | KC584406 | KC584202 | KC584122 | KC584664 |
| *Alternaria limaciformis* | *Alternaria limaciformis* | *Phragmosporae* | CBS 481.81 | T | Soil | UK | EGS 07.086; IMI 052976; QM 1790 | KC584539 | KC584283 | KC584407 | KC584203 | KC584123 | KC584665 |
| *Alternaria limoniasperae* | *Alternaria limoniasperae* | *Alternata* | CBS 102595 | T | *Citrus jambhiri* | USA | EGS 45.100 | KC584540 | KC584284 | KC584408 | **FJ266476** | **AY562411** | KC584666 |
| *Alternaria longipes* | *Alternaria longipes* | *Alternata* | CBS 540.94 | R | *Nicotiana tabacum* | USA | EGS 30.033; QM 9589 | KC584541 | KC584285 | KC584409 | **AY278835** | **AY278811** | KC584667 |
| *Alternaria macrospora* | *Alternaria macrospora* | *Porri* | CBS 117228 | T | *Gossypium barbadense* | USA | EGS 50.190 | KC584542 | KC584286 | KC584410 | KC584204 | KC584124 | KC584668 |
| *Alternaria mimicula* | *Alternaria mimicula* | *Brassicicola* | CBS 118696 | T | *Lycopersicon esculentum* | USA | EGS 01.056; QM 26a | KC584543 | KC584287 | KC584411 | **FJ266477** | **AY562415** | KC584669 |
| *Alternaria molesta* | *Alternaria molesta* | *Phragmosporae* | CBS 548.81 | T | *Phocaena phocaena* | Denmark | EGS 32.075 | KC584544 | KC584288 | KC584412 | KC584205 | KC584125 | KC584670 |
| *Alternaria mouchaccae* | *Alternaria mouchaccae* | *Phragmosporae* | CBS 119671 | T | Soil | Egypt | EGS 31.061 | KC584545 | KC584289 | KC584413 | KC584206 | **AY562399** | KC584671 |
| *Alternaria nepalensis* | *Alternaria nepalensis* | *Japonicae* | CBS 118700 | T | *Brassica* sp. | Nepal | EGS 45.073; IMI 374543 | KC584546 | KC584290 | KC584414 | KC584207 | KC584126 | KC584672 |
| *Alternaria nobilis* | *Alternaria nobilis* | *Gypsophilae* | CBS 116490 | R | *Dianthus caryophyllus* | New Zealand | EGS 51.027; NZMAF Lynfield 743 | KC584547 | KC584291 | KC584415 | KC584208 | KC584127 | KC584673 |
| *Alternaria oregonensis* | *Alternaria oregonensis* | *Infectoriae* | CBS 542.94 | T | *Triticum aestivum* | USA | EGS 29.194 | KC584548 | KC584292 | KC584416 | **FJ266478** | **FJ266491** | KC584674 |
| *Alternaria panax* | *Alternaria panax* | *Panax* | CBS 482.81 | R | *Aralia racemosa* | USA | EGS 29.180 | KC584549 | KC584293 | KC584417 | KC584209 | KC584128 | KC584675 |
| *Alternaria perpunctulata* | *Alternaria perpunctulata* | *Althernantherae* | CBS 115267 | T | *Alternanthera philoxeroides* | USA | | KC584550 | KC584294 | KC584418 | KC584210 | KC584129 | KC584676 |
| *Alternaria petroselini* | *Alternaria petroselini* | *Radicina* | CBS 112.41 | T | *Petroselinum sativum* | – | EGS 06.196 | KC584551 | KC584295 | KC584419 | KC584211 | KC584130 | KC584677 |
| *Alternaria photistica* | *Alternaria photistica* | *Panax* | CBS 212.86 | T | *Digitalis purpurea* | UK | EGS 35.172 | KC584552 | KC584296 | KC584420 | KC584212 | KC584131 | KC584678 |
| *Alternaria porri* | *Alternaria porri* | *Porri* | CBS 116698 | R | *Allium cepa* | USA | EGS 48.147 | KC584553 | KC584297 | KC584421 | **DQ323700** | KC584132 | KC584679 |

**Table 1.** (Continued).

| Old species name | New species name | *Alternaria* Section | Strain number[1] | Status[2] | Host / Substrate | Country | Other collection number[1] | GenBank accession numbers | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | | | | | SSU | LSU | RPB2 | ITS | GAPDH | TEF1 |
| *Alternaria pseudorostrata* | *Alternaria pseudorostrata* | *Porri* | CBS 119411 | T | *Euphorbia pulcherrima* | USA | EGS 42.060 | KC584554 | KC584298 | KC584422 | **JN383483** | **AY562406** | KC584680 |
| *Alternaria radicina* | *Alternaria radicina* | *Radicina* | CBS 245.67 | T | *Daucus carota* | USA | EGS 03.145; ATCC 6503; IMI 124939; QM 1301; QM 6503 | KC584555 | KC584299 | KC584423 | KC584213 | KC584133 | KC584681 |
| *"Alternaria resedae"* | *Alternaria* sp. | *Cheiranthus* | CBS 115.44 | | *Reseda odorata* | – | EGS 07.030 | KC584556 | KC584300 | KC584424 | KC584214 | KC584134 | KC584682 |
| *Alternaria saponariae* | *Alternaria saponariae* | *Gypsophilae* | CBS 116492 | R | *Saponaria officinalis* | USA | EGS 49.199 | KC584557 | KC584301 | KC584425 | KC584215 | KC584135 | KC584683 |
| *Alternaria selini* | *Alternaria selini* | *Radicina* | CBS 109382 | T | *Petroselinum crispum* | Saudi Arabia | EGS 25.198; IMI 137332 | KC584558 | KC584302 | KC584426 | **AF229455** | **AY278800** | KC584684 |
| *Alternaria septorioides* | *Alternaria septorioides* | *Brassicicola* | CBS 106.41 | T | *Reseda odorata* | Netherlands | EGS 52.089; MUCL 20298 | KC584559 | KC584303 | KC584427 | KC584216 | KC584136 | KC584685 |
| *Alternaria simsimi* | *Alternaria simsimi* | *Dianthicola* | CBS 115265 | T | *Sesamum indicum* | Argentina | EGS 13.110 | KC584560 | KC584304 | KC584428 | **JF780937** | KC584137 | KC584686 |
| *Alternaria smyrnii* | *Alternaria smyrnii* | *Radicina* | CBS 109380 | R | *Smyrnium olusatrum* | UK | EGS 37.093 | KC584561 | KC584305 | KC584429 | **AF229456** | KC584138 | KC584687 |
| *Alternaria solani* | *Alternaria solani* | *Porri* | CBS 116651 | R | *Solanum tuberosum* | USA | EGS 45.020 | KC584562 | KC584306 | KC584430 | KC584217 | KC584139 | KC584688 |
| *Alternaria soliaridae* | *Alternaria soliaridae* | | CBS 118387 | T | Soil | USA | EGS 33.024 | KC584563 | KC584307 | KC584431 | KC584218 | KC584140 | KC584689 |
| *Alternaria solidaccana* | *Alternaria solidaccana* | *Brassicicola* | CBS 118698 | T | Soil | Bangladesh | EGS 36.158; IMI 049788 | KC584564 | KC584308 | KC584432 | KC584219 | KC584141 | KC584690 |
| *Alternaria sonchi* | *Alternaria sonchi* | *Sonchi* | CBS 119675 | R | *Sonchus asper* | Canada | EGS 43.131; IMI 366167 | KC584565 | KC584309 | KC584433 | KC584220 | KC584142 | KC584691 |
| *Alternaria tagetica* | *Alternaria tagetica* | *Porri* | CBS 479.81 | R | *Tagetes erecta* | UK | EGS 33.081 | KC584566 | KC584310 | KC584434 | KC584221 | KC584143 | KC584692 |
| *Alternaria tenuissima* | *Alternaria tenuissima* | *Alternata* | CBS 918.96 | R | *Dianthus* sp. | UK | EGS 34.015 | KC584567 | KC584311 | KC584435 | **AF347032** | **AY278809** | KC584693 |
| *Alternaria thalictrigena* | *Alternaria thalictrigena* | | CBS 121712 | T | *Thalictrum* sp. | Germany | | KC584568 | KC584312 | KC584436 | **EU040211** | KC584144 | KC584694 |
| *Alternaria triglochinicola* | *Alternaria triglochinicola* | *Eureka* | CBS 119676 | T | *Triglochin procera* | Australia | EGS 41.070 | KC584569 | KC584313 | KC584437 | KC584222 | KC584145 | KC584695 |
| *Alternaria vaccariae* | *Alternaria vaccariae* | *Gypsophilae* | CBS 116533 | R | *Vaccaria hispanica* | USA | EGS 47.108 | KC584570 | KC584314 | KC584438 | KC584223 | KC584146 | KC584696 |
| *Alternaria vaccariicola* | *Alternaria vaccariicola* | *Gypsophilae* | CBS 118714 | T | *Vaccaria hispanica* | USA | EGS 46.003; ATCC 26038 | KC584571 | KC584315 | KC584439 | KC584224 | KC584147 | KC584697 |
| *Alternariaster helianthi* | *Alternariaster helianthi* | | CBS 119672 | R | *Helianthus* sp. | USA | EGS 36.007 | KC584626 | KC584368 | KC584493 | | | |
| *Alternariaster helianthi* | *Alternariaster helianthi* | | CBS 327.69 | | *Helianthus annuus* | – | | KC584627 | KC584369 | KC584494 | | | |
| *Ascochyta pisi* | *Ascochyta pisi* | | CBS 126.54 | | *Pisum sativum* | Netherlands | | **EU754038** | **DQ678070** | **DQ677967** | | | |
| *Boeremia exigua* | *Boeremia exigua* | | CBS 431.74 | | *Solanum tuberosum* | Netherlands | PD 74/2447 | **EU754084** | **EU754183** | **GU371780** | | | |
| *Brachycladium papaveris* | *Alternaria papavericola* | *Crivellia* | CBS 116606 | T | *Papaver somniferum* | USA | | KC584579 | KC584321 | KC584446 | **FJ357310** | **FJ357298** | KC584705 |
| *Brachycladium penicillatum* | *Alternaria penicillata* | *Crivellia* | CBS 116608 | T | *Papaver rhoeas* | Austria | DAOM 230457 | KC584572 | KC584316 | KC584440 | **FJ357311** | **FJ357299** | KC584698 |

**Table 1.** (Continued).

| Old species name | New species name | *Alternaria* Section | Strain number[1] | Status[2] | Host / Substrate | Country | Other collection number[1] | GenBank accession numbers | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | | | | | SSU | LSU | RPB2 | ITS | GAPDH | TEF1 |
| *Chaetodiplodia* sp. | *Chaetodiplodia* sp. | | CBS 453.68 | | *Halimione portulacoides* | Netherlands | | **DQ678001** | **DQ678054** | KC584499 | | | |
| *Chaetosphaeronema hispidulum* | *Chaetosphaeronema hispidulum* | | CBS 216.75 | | *Anthyllis vulneraria* | Germany | | **EU754045** | **EU754144** | **GU371777** | | | |
| *Chalastospora cetera* | *Alternaria cetera* | *Chalastospora* | CBS 121340 | T | *Elymus scabrus* | Australia | EGS 41.072 | KC584573 | KC584317 | KC584441 | **JN383482** | **AY562398** | KC584699 |
| *Chalastospora ellipsoidea* | *Alternaria breviramosa* | *Chalastospora* | CBS 121331 | T | *Triticum* sp. | Australia | | KC584574 | KC584318 | KC584442 | **FJ839608** | KC584148 | KC584700 |
| *Chalastospora obclavata* | *Alternaria obclavata* | *Chalastospora* | CBS 124120 | T | Air | USA | EGS 12.128 | KC584575 | **FJ839651** | KC584443 | KC584225 | KC584149 | KC584701 |
| *Chmelia slovaca* | *Alternaria slovaca* | *Infectoriae* | CBS 567.66 | T | Human | Slovakia | ATCC 24279 | KC584576 | KC584319 | KC584444 | KC584226 | KC584150 | KC584702 |
| *Clathrospora elynae* | *Clathrospora elynae* | | CBS 161.51 | | *Carex curvula* | Switzerland | | KC584628 | KC584370 | KC584495 | | | |
| *Clathrospora elynae* | *Clathrospora elynae* | | CBS 196.54 | | *Carex curvula* | Switzerland | | KC584629 | KC584371 | KC584496 | | | |
| *Clathrospora heterospora* | *Alternaria* sp. | *Alternata* | CBS 175.52 | | *Juncus mertensianus* | USA | EGS 35.1619; IMI 068085; QM 1277 | KC584577 | KC584320 | KC584445 | KC584227 | KC584151 | KC584703 |
| *Cochliobolus heterostrophus* | *Cochliobolus heterostrophus* | | CBS 134.39 | | *Zea mays* | – | DSM 1149 | **AY544727** | **AY544645** | **DQ247790** | | | |
| *Cochliobolus sativus* | *Cochliobolus sativus* | | DAOM 226212 | | *Hordeum vulgare* | Canada | | **DQ677995** | **DQ678045** | **DQ677939** | | | |
| *Comoclathris magna* | *Alternaria* sp. | *Alternata* | CBS 174.52 | | *Anemone occidentalis* | USA | EGS 39.1613; IMI 068086; QM 1278 | KC584578 | **DQ678068** | **DQ677964** | KC584228 | KC584152 | KC584704 |
| *Comoclathris compressa* | *Comoclathris compressa* | | CBS 156.53 | | *Castilleja miniata* | USA | EGS No. C-20285-I | KC584630 | KC584372 | KC584497 | | | |
| *Comoclathris compressa* | *Comoclathris compressa* | | CBS 157.53 | | *Ligusticum purpureum* | USA | EGS No. 1952a-1633 | KC584631 | KC584373 | KC584498 | | | |
| *Coniothyrium palmarum* | *Coniothyrium palmarum* | | CBS 400.71 | | *Chamaerops humilis* | Italy | | **EU754054** | **EU754153** | **DQ677956** | | | |
| *Crivellia papaveracea* | *Alternaria penicillata* | *Crivellia* | CBS 116607 | T | *Papaver rhoeas* | Austria | DAOM 230456 | KC584580 | KC584322 | KC584447 | KC584229 | KC584153 | KC584706 |
| *Dendryphiella arenariae* | *Paradendryphiella arenariae* | | CBS 181.58 | T | Coastal sand | France | DAOM 63738; IMI 067735; MUCL 4129 | KC793336 | KC793338 | **DQ470924** | | | |
| *Dendryphiella salina* | *Paradendryphiella salina* | | CBS 142.60 | | *Spartina* sp. | UK | MUCL 9639 | KC793337 | KC793339 | KC793340 | | | |
| *Embellisia abundans* | *Alternaria abundans* | *Chalastospora* | CBS 534.83 | T | *Fragaria* sp. | New Zealand | EGS 29.159 | KC584581 | KC584323 | KC584448 | **JN383485** | KC584154 | KC584707 |
| *Embellisia allii* | *Alternaria embellisia* | *Embellisia* | CBS 339.71 | R | *Allium sativum* | USA | ATCC 22412; IMI 155707; MUCL 18571; QM 8609 | KC584582 | KC584324 | KC584449 | KC584230 | KC584155 | KC584708 |
| *Embellisia annulata* | *Cicatricea salina* | | CBS 302.84 | T | *Cancer pagurus* | North Sea, Skagerrak | | KC584583 | KC584325 | KC584450 | **JN383486** | **JN383467** | KC584709 |

**Table 1.** (Continued).

| Old species name | New species name | *Alternaria* Section | Strain number[1] | Status[2] | Host / Substrate | Country | Other collection number[1] | GenBank accession numbers | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | | | | | SSU | LSU | RPB2 | ITS | GAPDH | TEF1 |
| *Embellisia chlamydospora* | *Alternaria chlamydosporigena* | *Embellisia* | CBS 341.71 | R | Air | USA | EGS 10.073; ATCC 22409; IMI 155709; MUCL 18573; QM 7287 | KC584584 | KC584326 | KC584451 | KC584231 | KC584156 | KC584710 |
| *Embellisia conoidea* | *Alternaria conoidea* | *Brassicicola* | CBS 132.89 | | *Ricinus communis* | Saudi Arabia | | KC584585 | KC584327 | KC584452 | **AF348226** | **FJ348227** | KC584711 |
| *Embellisia dennisii* | *Alternaria dennisii* | | CBS 110533 | | *Senecio jacobaea* | New Zealand | | KC584586 | KC584328 | KC584453 | KC584232 | KC584157 | KC584712 |
| *Embellisia dennisii* | *Alternaria dennisii* | | CBS 476.90 | T | *Senecio jacobaea* | Isle of Man | IMI 151744 | KC584587 | KC584329 | KC584454 | **JN383488** | **JN383469** | KC584713 |
| *Embellisia didymospora* | *Alternaria didymospora* | *Phragmosporae* | CBS 766.79 | | Seawater | Adriatic Sea | | KC584588 | KC584330 | KC584455 | **FJ357312** | **FJ357300** | KC584714 |
| *Embellisia eureka* | *Alternaria eureka* | *Eureka* | CBS 193.86 | T | *Medicago rugosa* | Australia | IMI 273162 | KC584589 | KC584331 | KC584456 | **JN383490** | **JN383471** | KC584715 |
| *Embellisia hyacinthi* | *Alternaria hyacinthi* | *Embellisioides* | CBS 416.71 | T | *Hyacinthus orientalis* | Netherlands | EGS 19.102; IMI 279179 | KC584590 | KC584332 | KC584457 | KC584233 | KC584158 | KC584716 |
| *Embellisia indefessa* | *Alternaria indefessa* | *Cheiranthus* | CBS 536.83 | T | Soil | USA | EGS 30.195 | KC584591 | KC584333 | KC584458 | KC584234 | KC584159 | KC584717 |
| *Embellisia leptinellae* | *Alternaria leptinellae* | *Eureka* | CBS 477.90 | T | *Leptinella dioica* | New Zealand | EGS 39.101 | KC584592 | KC584334 | KC584459 | KC584235 | KC584160 | KC584718 |
| *Embellisia lolii* | *Alternaria lolii* | *Embellisioides* | CBS 115266 | T | *Lolium perenne* | New Zealand | | KC584593 | KC584335 | KC584460 | **JN383492** | **JN383473** | KC584719 |
| *Embellisia novae-zelandiae* | *Alternaria botryospora* | *Embellisioides* | CBS 478.90 | T | *Leptinella dioica* | New Zealand | EGS 39.099 | KC584594 | KC584336 | KC584461 | **AY278844** | **AY278831** | KC584720 |
| *Embellisia phragmospora* | *Alternaria phragmospora* | *Phragmosporae* | CBS 274.70 | T | Soil | The netherlands | EGS 27.098; ATCC 18914 | KC584595 | KC584337 | KC584462 | **JN383493** | **JN383474** | KC584721 |
| *Embellisia planifunda* | *Alternaria planifunda* | *Embellisioides* | CBS 537.83 | T | *Triticum aestivum* | Australia | IMI 115034 | KC584596 | KC584338 | KC584463 | **FJ357315** | **FJ357303** | KC584722 |
| *Embellisia proteae* | *Alternaria proteae* | *Embellisioides* | CBS 475.90 | T | *Protea* sp. | Australia | IMI 320290; IMI 341684 | KC584597 | KC584339 | KC584464 | **AY278842** | KC584161 | KC584723 |
| *Embellisia tellustris* | *Alternaria tellustris* | *Embellisia* | CBS 538.83 | T | Soil | USA | EGS 33.026 | KC584598 | KC584340 | KC584465 | **FJ357316** | **AY562419** | KC584724 |
| *Embellisia tumida* | *Alternaria tumida* | *Embellisioides* | CBS 539.83 | T | *Triticum aestivum* | Australia | | KC584599 | KC584341 | KC584466 | **FJ266481** | **FJ266493** | KC584725 |
| *Heterospora chenopodii* | *Heterospora chenopodii* | | CBS 115.96 | | *Chenopodium album* | Netherlands | PD 94/1576 | **EU754089** | **EU754188** | **GU371775** | | | |
| *Julella avicenniae* | *Julella avicenniae* | | BCC 18422 | | Mangrove wood | Thailand | | **GU371831** | **GU371823** | **GU371787** | | | |
| *Leptosphaerulina australis* | *Leptosphaerulina australis* | | CBS 317.83 | | *Eugenia aromatica* | Indonesia | | **GU296160** | **GU301830** | **GU371790** | | | |
| *Loratospora aestuarii* | *Loratospora aestuarii* | | JK 5535B | | *Juncus roemerianus* | USA | | **GU296168** | **GU301838** | **GU371760** | | | |
| *Neophaeosphaeria filamentosa* | *Neophaeosphaeria filamentosa* | | CBS 102202 | | *Yucca rostrata* | Mexico | | **GQ387516** | **GQ387577** | **GU371773** | | | |
| *Nimbya caricis* | *Alternaria caricis* | *Nimbya* | CBS 480.90 | T | *Carex hoodii* | USA | EGS 13.094 | KC584600 | KC584342 | KC584467 | **AY278839** | **AY278826** | KC584726 |
| *“Nimbya gomphrenae”* | *Alternaria* sp. | *Alternata* | CBS 108.27 | | *Gomphrena globosa* | – | | KC584601 | KC584343 | KC584468 | KC584236 | KC584162 | KC584727 |
| *Nimbya scirpicola* | *Alternaria scirpicola* | *Nimbya* | CBS 481.90 | R | *Scirpus* sp. | UK | EGS 19.042 | KC584602 | KC584344 | KC584469 | KC584237 | KC584163 | KC584728 |

**Table 1.** (Continued).

| Old species name | New species name | *Alternaria* Section | Strain number[1] | Status[2] | Host / Substrate | Country | Other collection number[1] | GenBank accession numbers | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | | | | | SSU | LSU | RPB2 | ITS | GAPDH | TEF1 |
| *Ophiosphaerella herpotricha* | *Ophiosphaerella herpotricha* | | CBS 620.86 | | *Bromus erectus* | Switzerland | ETH 9373 | **DQ678010** | **DQ678062** | **DQ677958** | | | |
| *Paraleptosphaeria dryadis* | *Paraleptosphaeria dryadis* | | CBS 643.86 | | *Dryas octopetala* | Switzerland | ETH 9446 | KC584632 | **GU301828** | **GU371733** | | | |
| *Peyronellaea glomerata* | *Peyronellaea glomerata* | | CBS 528.66 | | *Chrysanthemum* sp. | Netherlands | PD 63/590 | **EU754085** | **EU754184** | **GU371781** | | | |
| *Peyronellaea zeae-maydis* | *Peyronellaea zeae-maydis* | | CBS 588.69 | T | *Zea mays* | USA | | **EU754093** | **EU754192** | **GU371782** | | | |
| *Phaeosphaeria ammophilae* | *Phaeosphaeria ammophilae* | | CBS 114595 | | *Ammophila arenaria* | Sweden | UPSC 3568 | **GU296185** | **GU304859** | **GU371724** | | | |
| *Phaeosphaeria avenaria* | *Phaeosphaeria avenaria* | | DAOM 226215 | | *Avena sativa* | Canada | OSC 100096 | **AY544725** | **AY544684** | **DQ677941** | | | |
| *Phaeosphaeria eustoma* | *Phaeosphaeria eustoma* | | CBS 573.86 | | *Dactylis glomerata* | Switzerland | ETH 9239 | **DQ678011** | **DQ678063** | **DQ677959** | | | |
| *Phoma complanata* | *Phoma complanata* | | CBS 268.92 | | *Anglica sylvestris* | Netherlands | PD 75/3 | **EU754081** | **EU754180** | **GU371778** | | | |
| *Phoma herbarum* | *Phoma herbarum* | | CBS 276.37 | | Wood pulp | Sweden | | **DQ678014** | **DQ678066** | **DQ677962** | | | |
| *Plenodomus lingam* | *Plenodomus lingam* | | DAOM 229267 | | *Brassica sp.* | France | | **DQ470993** | **DQ470946** | **DQ470894** | | | |
| *Pleospora betae* | *Pleospora betae* | | CBS 109410 | | *Beta vulgaris* | Netherlands | PD 77/113 | **EU754079** | **EU754178** | **GU371774** | | | |
| *Pleospora calvescens* | *Pleospora calvescens* | | CBS 246.79 | | *Atriplex hastata* | Germany | PD 77/655 | **EU754032** | **EU754131** | KC584500 | | | |
| *Pleospora chenopodii* | *Pleospora chenopodii* | | CBS 206.80 | | *Chenopodium quinoa* | Bolivia | PD 74/1022 | **JF740095** | **JF740266** | KC584501 | | | |
| *Pleospora fallens* | *Pleospora fallens* | | CBS 161.78 | | *Olea europaea* | New Zealand | | **GU238215** | **GU238074** | KC584502 | | | |
| *Pleospora halimiones* | *Pleospora halimiones* | | CBS 432.77 | | *Halimione portulacoides* | Netherlands | IMI 282137 | **JF740096** | **JF740267** | KC584503 | | | |
| *Pleospora incompta* | *Pleospora incompta* | | CBS 467.76 | | *Olea europaea* | Greece | | **GU23822** | **GU238087** | KC584504 | | | |
| *Pleospora tarda* | *Pleospora tarda* | | CBS 714.68 | T | *Medicago sativa* | Canada | EGS 04.118C; IMI 135456; MUCL 11717; QM 1379 | KC584603 | KC584345 | **AF107804** | KC584238 | **AF443881** | KC584729 |
| *Pleospora typhicola* | *Pleospora typhicola* | | CBS 132.69 | | *Typha angustifolia* | Netherlands | | **JF740105** | **JF740325** | KC584505 | | | |
| *Pyrenochaeta nobilis* | *Pyrenochaeta nobilis* | | CBS 407.76 | T | *Laurus nobilis* | Italy | | **EU754107** | **DQ678096** | **DQ677991** | | | |
| *Pyrenophora phaeocomes* | *Pyrenophora phaeocomes* | | DAOM 222769 | | *Calamagrostis villosa* | Switzerland | | **DQ499595** | **DQ499596** | **DQ497614** | | | |
| *Saccothecium sepincola* | *Saccothecium sepincola* | | CBS 278.32 | | *Ribes nigrum* | USA | | **GU296195** | **GU301870** | **GU371745** | | | |
| *Setomelanomma holmii* | *Setomelanomma holmii* | | CBS 110217 | | *Picea pungens* | USA | | **GU296196** | **GQ37633** | **GU371800** | | | |

**Table 1.** (Continued).

| Old species name | New species name | *Alternaria* Section | Strain number[1] | Status[2] | Host / Substrate | Country | Other collection number[1] | GenBank accession numbers | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | | | | | SSU | LSU | RPB2 | ITS | GAPDH | TEF1 |
| *Sinomyces alternariae* | *Alternaria alternariae* | *Ulocladium* | CBS 126989 | T | *Daucus carota* | USA | EGS 46.004 | KC584604 | KC584346 | KC584470 | **AF229485** | **AY278815** | KC584730 |
| *Stemphylium herbarum* | *Stemphylium herbarum* | | CBS 191.86 | T | *Medicago sativa* | India | EGS 36.138; IMI 276975 | **GU238232** | **GU238160** | KC584471 | KC584239 | **AF443884** | KC584731 |
| *Teretispora leucanthemi* | *Alternaria leucanthemi* | *Teretispora* | CBS 421.65 | T | *Chrysanthemum maximum* | Netherlands | ATCC 16028; IFO 9085; IMI 111986; QM 7227 | KC584605 | KC584347 | KC584472 | KC584240 | KC584164 | KC584732 |
| *Teretispora leucanthemi* | *Alternaria leucanthemi* | | CBS 422.65 | R | *Chrysanthemum maximum* | USA | EGS 17.063; ATCC 16029; IMI 111987; QM 8579 | KC584606 | KC584348 | KC584473 | KC584241 | KC584165 | KC584733 |
| *Ulocladium arborescens* | *Alternaria aspera* | *Pseudoulocladium* | CBS 115269 | T | *Pistacia vera* | Japan | IMI 369777 | KC584607 | KC584349 | KC584474 | KC584242 | KC584166 | KC584734 |
| *Ulocladium atrum* | *Alternaria atra* | *Ulocladioides* | CBS 195.67 | T | Soil | USA | ATCC 18040; IMI 124944; QM 8408 | KC584608 | KC584350 | KC584475 | **AF229486** | KC584167 | KC584735 |
| *Ulocladium botrytis* | *Alternaria botrytis* | *Ulocladium* | CBS 197.67 | T | Contaminant | USA | ATCC 18042; IMI 124942; MUCL 18556; QM 7878 | KC584609 | KC584351 | KC584476 | KC584243 | KC584168 | KC584736 |
| *Ulocladium botrytis* | *Alternaria* sp. | *Ulocladioides* | CBS 198.67 | R | Soil | USA | ATCC 18043; IMI 124949; MUCL 18557; QM 8619 | KC584610 | KC584352 | KC584477 | **AF229487** | KC584169 | KC584737 |
| *Ulocladium brassicae* | *Alternaria brassicae-pekinensis* | *Ulocladioides* | CBS 121493 | T | *Brassica pekinensis* | China | HSAUPwy0037 | KC584611 | KC584353 | KC584478 | KC584244 | KC584170 | KC584738 |
| *Ulocladium cantlous* | *Alternaria cantlous* | *Ulocladioides* | CBS 123007 | T | *Cucumis melo* | China | HSAUP0209 | KC584612 | KC584354 | KC584479 | KC584245 | KC584171 | KC584739 |
| *Ulocladium capsici* | *Alternaria concatenata* | *Pseudoulocladium* | CBS 120006 | T | – | – | HSAUPIII$_0$0035 | KC584613 | KC584355 | KC584480 | KC584246 | **AY762950** | KC584740 |
| *Ulocladium chartarum* | *Alternaria chartarum* | *Pseudoulocladium* | CBS 200.67 | T | *Populus* sp. | Canada | ATCC 18044; DAOM 59616b; IMI 124943; MUCL 18564; QM 8328 | KC584614 | KC584356 | KC584481 | **AF229488** | KC584172 | KC584741 |
| *Ulocladium consortiale* | *Alternaria consortialis* | *Ulocladioides* | CBS 104.31 | T | – | – | | KC584615 | KC584357 | KC584482 | KC584247 | KC584173 | KC584742 |
| *Ulocladium cucurbitae* | *Alternaria cucurbitae* | *Ulocladioides* | CBS 483.81 | R | *Cucumis sativus* | New Zealand | EGS 31.021; LEV 7067 | KC584616 | KC584358 | KC584483 | **FJ266483** | **AY562418** | KC584743 |
| *Ulocladium multiforme* | *Alternaria multiformis* | *Ulocladioides* | CBS 102060 | T | Soil | Canada | | KC584617 | KC584359 | KC584484 | **FJ266486** | KC584174 | KC584744 |
| *Ulocladium obovoideum* | *Alternaria obovoidea* | *Ulocladioides* | CBS 101229 | | *Cucumis sativus* | New Zealand | | KC584618 | KC584360 | KC584485 | **FJ266487** | **FJ266498** | KC584745 |
| *Ulocladium oudemansii* | *Alternaria oudemansii* | *Ulocladium* | CBS 114.07 | T | – | – | ATCC 18047; IMI 124940; MUCL 18563; QM 1744 | KC584619 | KC584361 | KC584486 | **FJ266488** | KC584175 | KC584746 |
| *Ulocladium septosporum* | *Alternaria septospora* | *Pseudoulocladium* | CBS 109.38 | | Wood | Italy | | KC584620 | KC584362 | KC584487 | **FJ266489** | **FJ266500** | KC584747 |

**Table 1.** (Continued).

| Old species name | New species name | *Alternaria* Section | Strain number[1] | Status[2] | Host / Substrate | Country | Other collection number[1] | GenBank accession numbers | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | | | | | SSU | LSU | RPB2 | ITS | GAPDH | TEF1 |
| *Ulocladium solani* | *Alternaria heterospora* | *Ulocladioides* | CBS 123376 | T | *Lycopersicon esculentum* | China | HSAUP 0521 | KC584621 | KC584363 | KC584488 | KC584248 | KC584176 | KC584748 |
| *Ulocladium subcucurbitae* | *Alternaria subcucurbitae* | *Ulocladioides* | CBS 121491 | T | *Chenopodium glaucum* | China | | KC584622 | KC584364 | KC584489 | KC584249 | **EU855803** | KC584749 |
| *Ulocladium tuberculatum* | *Alternaria terricola* | *Ulocladioides* | CBS 202.67 | T | Soil | USA | ATCC 18048; IMI 124947; MUCL 18560; QM 8614 | KC584623 | KC584365 | KC584490 | **FJ266490** | KC584177 | KC584750 |
| *Undifilum bornmuelleri* | *Alternaria bornmuelleri* | *Undifilum* | DAOM 231361 | T | *Securigera varia* | Austria | DAOM 231361 | KC584624 | KC584366 | KC584491 | **FJ357317** | **FJ357305** | KC584751 |
| *Ybotromyces caespitosus* | *Alternaria caespitosa* | *Infectoriae* | CBS 177.80 | T | Human | Spain | | KC584625 | KC584367 | KC584492 | KC584250 | KC584178 | KC584752 |

[1] ATCC: American Type Culture Collection, Manassas, VA, USA; BCC: BIOTEC Culture Collection, Thailand; CBS: Culture collection of the Centraalbureau voor Schimmelcultures, Fungal Biodiversity Centre, Utrecht, The Netherlands; DAOM: Canadian Collection of Fungal Cultures, Ottawa, Canada; DAR: Plant Pathology Herbarium, Orange Agricultural Institute, Australia; DSM: German Collection of Microorganisms and Cell Cultures, Leibniz Institute, Braunschweig, Germany; EGS: Personal collection of Dr. E.G. Simmons; ETH: Swiss Federal Institute of Technology, Switzerland; HSAUP: Department of Plant Pathology, Shandong Agricultural University, China; IFO: Institute for Fermentation Culture Collection, Osaka, Japan; IMI: Culture collection of CABI Europe UK Centre, Egham UK; JK: Personal collection of Dr. J. Kohlmeyer; LEV: Plant Health and Diagnostic Station, Levin, New Zealand; MUCL: (Agro)Industrial Fungi and Yeast Collection of the Belgian Co-ordinated Collections of Micro-organisms (BCCM), Louvain-la Neuve, Belgium; NZMAF: New Zealand Ministry of Agriculture and Forestry; OSC: Oregon State University Herbarium, USA; PD: Plant Protection Service, Wageningen, The Netherlands; RGR: Personal collection of Dr. R.G. Roberts; UPSC: Uppsala University Culture Collection, Sweden; QM: Quarter Master Culture Collection, Amherst, MA, USA.

[2] T: ex-type strain; R: representative strain.

species (Table 1) for which the SSU, LSU and RPB2 sequence data set was present or could be completed. Blast searches with *Embellisia annulata* gave hits with two marine *Dendryphiella* species, *Dendryphiella arenariae* and *Dendryphiella salina*, which we also included. Phylogenetic analyses of the sequence data consisted of Bayesian and Maximum likelihood analyses of both the individual data partitions as well as the combined aligned dataset. Bayesian analyses were performed with MrBayes v. 3.2.1 (Huelsenbeck & Ronquist 2001, Ronquist & Huelsenbeck 2003). The Markov Chain Monte Carlo (MCMC) analysis used four chains and started from a random tree topology. The sample frequency was set at 100 and the temperature value of the heated chain was 0.1. The temperature value was lowered to 0.05 when the average standard deviation of split frequencies did not fall below 0.01 after 5M generations (RPB2 and *Pleosporineae* phylogeny). Burn-in was set to 25 % after which the likelihood values were stationary. Maximum likelihood analyses including 500 bootstrap replicates were run using RAxML v. 7.2.6 (Stamatakis & Alachiotis 2010). The online tool Findmodel (http://www.hiv.lanl.gov/content/sequence/findmodel/findmodel.html) was used to determine the best nucleotide substitution model for each partition. For the SSU (*Pleosporineae* family tree), LSU, ITS, RPB2 and TEF1 partitions a GTR model with a gamma-distributed rate variation was suggested, and for the SSU (*Alternaria* complex) and GAPDH partitions a TrN model with gamma-distributed rate variation. Sequences of *Stemphylium herbarum* (CBS 191.86) were used as outgroup in the *Alternaria* phylogeny and those of *Jullella avenicae* (BCC 18422) in the *Pleosporineae* phylogeny. The resulting trees were printed with TreeView v. 1.6.6 (Page 1996) and together with the alignments deposited into TreeBASE (http://www.treebase.org).

## RESULTS

### Phylogeny

For defining the taxonomy of *Alternaria* and allied genera, 121 strains were included in the *Alternaria* complex alignment. The alignment length and unique site patterns of the different genes and gene combinations are stated in Table 2. The original ITS alignment consisted of 577 characters of which the first 78 are excluded as this contained a non-alignable region. In the original TEF1 alignment (375 characters) we coded the major inserts (Table 3), which otherwise would negatively influence the phylogeny, resulting in a TEF1 alignment of 269 characters. All phylogenies, different phylogenetic methods and gene regions or gene combinations used on this dataset (data not shown, trees and alignments lodged in TreeBASE), show a weak support at the deeper nodes of the tree. The only well-supported node (Bayesian posterior probability of 1.0, RAxML Maximum Likelihood support value of 100) in all phylogenies separates *Embellisia annulata* CBS 302.84 and the *Pleospora*/*Stemphylium* clade from the *Alternaria* complex (Fig. 1). In the *Alternaria* clade, six monotypic lineages and 24 internal clades occur consistently in the individual and combined phylogenies, although positions vary between the different gene regions or combinations used. The support values for the clades within *Alternaria* (called sections) are plotted in a heat map (Table 2) per gene and phylogenetic method used. The support values for the different phylogenetic methods vary, with the Bayesian posterior probabilities being higher than the RAxML bootstrap support values (Table 2). The SSU, LSU and ITS phylogenies display a

**Table 2.** Summary of locus and phylogenetic results as well as a heat map of the Bayesian posterior probabilities and RAxML boostrap support values per *Alternaria* section.

| | **1-region** | | | | | | **2-region** | | | **3-region** | **6-region** |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | SSU | LSU | ITS | GAPDH | RPB2 | TEF | GAPDH RPB2 | GAPDH TEF1 | RPB2 TEF1 | GAPDH RPB2 TEF1 | SSU LSU ITS GAPDH RPB2 TEF1 |
| Aligned length | 1021 | 851 | 499 | 573 | 786 | 269 | 1359 | 842 | 1055 | 1628 | 3999 |
| Unique site patterns | 45 | 57 | 148 | 272 | 296 | 224 | 568 | 496 | 520 | 792 | 1042 |
| No. of sampled trees (post burnin) | 39002 | 31578 | 75002 | 23702 | 56028 | 12452 | 10128 | 13728 | 44852 | 5778 | 16278 |
| | Bayesian Posterior Probabilities | | | | | | | | | | |
| Sect. *Alternantherae* | | * | | | | | | | | | |
| Sect. *Alternata* | | | | | | | | | | | |
| Sect. *Brassicicola* | | | | | | | | | | | |
| Sect. *Chalastospora* | * | | | | | | | | | | |
| Sect. *Cheiranthus* | * | | * | * | | | | * | | | |
| Sect. *Crivellia* | | | * | | | | | | | | |
| Sect. *Dianthicola* | * | * | | | | | | | | | |
| Sect. *Embellisia* | | * | | | | | | | | | |
| Sect. *Embellisioides* | * | * | | | * | | | | | | |
| Sect. *Eureka* | | | * | | * | * | | | | | |
| Sect. *Gypsophilae* | | | * | | | | | | | | |
| Sect. *Infectoriae* | * | * | | | | | | | | | |
| Sect. *Japonicae* | | | | | | | | | | | |
| Sect. *Nimbya* | | | | | | | | | | | |
| Sect. *panax* | * | | | | | | | | | | |
| Sect. *Phragmosporae* | | * | * | | | | | | | | |
| Sect. *Porri* | | * | | | | | | | | | |
| Sect. *Pseudoulocladium* | * | * | | | * | | * | | | | |
| Sect. *Radicina* | | | | | | | | | | | |
| Sect. *Sonchi* | * | * | | | | | | | | | |
| Sect. *Teretispora* | | | | | | | | | | | |
| Sect. *Ulocladioides* | * | * | | | | | | | | | |
| Sect. *Ulocladium* | | | * | | | | | | | | |

| | | | | |
|---|---|---|---|---|
| 1.00 | 0.95–0.99 | 0.90–0.94 | 0.80–0.89 | 0.70–0.79 |
| 0.50–0.69 | 0.25–0.49 | 0.01–0.24 | no support | |
| *= section not complete | | | | |

| | **1-region** | | | | | | **2-region** | | | **3-region** | **6-region** |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | SSU | LSU | ITS | GAPDH | RPB2 | TEF | GAPDH RPB2 | GAPDH TEF1 | RPB2 TEF1 | GAPDH RPB2 TEF1 | ALL LSU ITS GAPDH RPB2 TEF1 |
| Aligned length | 1021 | 851 | 499 | 573 | 786 | 269 | 1359 | 842 | 1055 | 1628 | 3999 |
| Unique site patterns | 45 | 57 | 148 | 272 | 296 | 224 | 568 | 496 | 520 | 792 | 1042 |
| No. of sampled trees (post burnin) | | | | | | | | | | | |
| | RAxML bootstrap support | | | | | | | | | | |
| Sect. *Alternantherae* | | * | | | | | | | | | |
| Sect. *Alternata* | | | | | | | | | | | |
| Sect. *Brassicicola* | | | | | | | | | | | |
| Sect. *Chalastospora* | * | | | | | | | | | | |
| Sect. *Cheiranthus* | * | | * | * | | | | * | | | |
| Sect. *Crivellia* | | | * | | | | | | | | |
| Sect. *Dianthicola* | * | * | | | | | | | | | |
| Sect. *Embellisia* | | * | | | | | | | | | |
| Sect. *Embellisioides* | * | * | | | * | | | | | | |
| Sect. *Eureka* | | | * | | * | * | | | | | |
| Sect. *Gypsophilae* | | | * | | | | | | | | |
| Sect. *Infectoriae* | * | * | | | | | | | | | |
| Sect. *Japonicae* | | | | | | | | | | | |
| Sect. *Nimbya* | | | | | | | | | | | |
| Sect. *panax* | * | | | | | | | | | | |
| Sect. *Phragmosporae* | | * | * | | | | | | | | |
| Sect. *Porri* | | * | | | | | | | | | |
| Sect. *Pseudoulocladium* | * | * | | | * | | * | | | | |
| Sect. *Radicina* | | | | | | | | | | | |
| Sect. *Sonchi* | * | * | | | | | | | | | |
| Sect. *Teretispora* | | | | | | | | | | | |
| Sect. *Ulocladioides* | * | * | | | | | | | | | |
| Sect. *Ulocladium* | | | * | | | | | | | | |

| | | | | |
|---|---|---|---|---|
| 100 | 95–99 | 90–94 | 80–89 | 70–79 |
| 50–69 | 25–49 | 1–24 | no support | |
| *= section not complete | | | | |

**Table 3.** Coded inserts in the TEF1 sequence alignment.

| Species | Nt position | Coded | Nt position | Coded |
|---|---|---|---|---|
| *Alternaria elegans* | 23 to 39 | TC | | |
| *Alternaria simsimi* | 23 to 39 | TCC | | |
| *Alternaria dauci* | 186 to 205 | C | 221 to 269 | TACTT |
| *Alternaria macrospora* | 186 to 205 | C | 221 to 269 | TCCCC |
| *Alternaria porri* | 186 to 205 | C | 221 to 269 | ACTTA |
| *Alternaria pseudorostrata* | 186 to 205 | C | 221 to 269 | TGGTA |
| *Alternaria solani* | 186 to 205 | C | 221 to 269 | -AAGG |
| *Alternaria tegetica* | 186 to 205 | C | 221 to 269 | CACAC |

low resolution, which reflects in poor to no support of the sections. Therefore, we chose not to include them in the multi-gene alignments, except in the all-gene alignment. In the GAPDH phylogenies, sect. *Cheiranthus*, sect. *Nimbya* and sect. *Pseudoulocladium* are poorly supported and "*A. resedae*" clusters separate from sect. *Cheiranthus*. In the RPB2 phylogenies the support values for sect. *Alternata*, sect. *Embellisioides* and sect. *Eureka* are relatively low; *A. cumini* clusters in sect. *Embellisioides* instead of sect. *Eureka* and *U. capsici* clusters separate from sect. *Pseudoulocladium*. The TEF1 phylogenies did not support sect. *Nimbya* and show relative low support for sect. *Cheiranthus*, sect. *Dianthicola*, sect. *Embellisioides*, sect. *Panax*, sect. *Phragmosporae* and sect. *Radicina*, and *A. cumini* clusters outside sect. *Eureka*. In the 2-region phylogenies *U. capsici* clusters outside sect. *Pseudoulocladium* based on GAPDH and RPB2, *E. indefessa* clusters outside sect. *Cheiranthus* based on GAPDH and TEF1, and sect. *Eureka* is poorly supported based on RPB2 and TEF1. The combined phylogeny based on the GAPDH, RPB2 and TEF1 sequences (Fig. 1) is displayed, as these are the genes with the best resolution.

The final *Pleosporineae* alignment included 74 strains, representing six families, and consisted of 2 506 characters (SSU 935, LSU 796, RPB2 775) of which 700 were unique site patterns (SSU 111, LSU 145, RPB2 444). In the SSU alignment a large insertion at position 446 in the isolates *Chaetosphaeronema hispidulum* CBS 216.75, *Pleospora fallens* CBS 161.78, *Pleospora flavigena* CBS 314.80 and *Ophiosphaerella herpotrichia* CBS 620.86 was excluded from the phylogenetic analyses. A total of 43 202 trees were sampled after the burn-in. The type species of *Clathrospora*, *C. elynae*, forms a well-supported clade, located basal to the *Pleosporaceae* (Fig. 2), outside the *Alternaria* complex. The type species of *Comoclathris*, *C. lanata*, was not available for study but the two *Comoclathris compressa* strains cluster in a well-supported clade within the *Pleosporaceae* outside *Alternaria s. str*. The genus *Alternariaster*, with *Alternariaster helianthi* as type and only species, also clusters outside the *Alternaria* complex and even outside *Pleosporaceae*; it belongs to the *Leptosphaeriaceae* instead (Fig. 2). *Embellisia annulata* is identical to *Dendryphiella salina*, and forms a well-supported clade in the *Pleosporaceae* together with *Dendryphiella arenariae*. As the type species of *Dendryphiella*, *D. vinosa*, clusters outside the *Pleosporineae* (dela Cruz 2006, Jones *et al.* 2008), *Dendryphiella salina* and *D. arenariae* are placed in a new genus, *Paradendryphiella*, below.

## Taxonomy

Based on DNA sequence data in combination with a review of literature and morphology, the species within the *Alternaria* clade are all recognised here as *Alternaria* (Fig 1). This puts the genera *Allewia*, *Brachycladium*, *Chalastospora*, *Chmelia*, *Crivellia*, *Embellisia*, *Lewia*, *Nimbya*, *Sinomyces*, *Teretispora*, *Ulocladium*, *Undifilum* and *Ybotromyces* in synonymy with *Alternaria*, resulting in the proposal of 32 new combinations, 10 new names and the resurrection of 10 names. Species of *Alternaria* were assigned to 24 *Alternaria* sections, of which 16 are newly described, and six monotypic lineages. The (emended) description of the genus *Alternaria*, the *Alternaria* sections and monotypic lineages with new *Alternaria* names and name combinations are treated below in alphabetical order. Finally the description of the new genus *Paradendryphiella* is also provided.

***Alternaria*** Nees, Syst. Pilze (Würzburg): 72. 1816 [1816–1817].

= *Elosia* Pers., Mycol. Eur. (Erlanga) 1: 12. 1822.
= *Macrosporium* Fr., Syst. Mycol. (Lundae) 3: 373. 1832.
= *Rhopalidium* Mont., Ann. Sci. Nat., Bot., Sér. 2, 6: 30. 1836.
= *Brachycladium* Corda, Icon. Fungorum hucusque Cogn. (Prague) 2: 14. 1838.
= *Ulocladium* Preuss, Linnaea 24: 111. 1851.
= *Chmelia* Svob.-Pol., Biologia (Bratislava) 21: 82. 1966.
= *Embellisia* E.G. Simmons, Mycologia 63: 380. 1971.
= *Trichoconiella* B.L. Jain, Kavaka 3: 39. 1976 [1975].
= *Botryomyces* de Hoog & C. Rubio, Sabouraudia 20: 19. 1982. (nom. illegit.)
= *Lewia* M.E. Barr & E.G. Simmons, Mycotaxon 25: 289. 1986.
= *Ybotromyces* Rulamort, Bull. Soc. Bot. Centre-Ouest, Nouv. Sér. 17: 192. 1986.
= *Nimbya* E.G. Simmons, Sydowia 41: 316. 1989.
= *Allewia* E.G. Simmons, Mycotaxon 38: 260. 1990.
= *Crivellia* Shoemaker & Inderb., Canad. J. Bot. 84: 1308. 2006.
= *Chalastospora* E.G. Simmons, CBS Biodiversity Ser. (Utrecht) 6: 668. 2007.
= *Teretispora* E.G. Simmons, CBS Biodiversity Ser. (Utrecht) 6: 674. 2007.
= *Undifilum* B.M. Pryor, Creamer, Shoemaker, McLain-Romero & Hambl., Botany 87: 190. 2009.
= *Sinomyces* Yong Wang bis & X.G. Zhang, Fungal Biol. 115: 192. 2011.

*Colonies* effuse, usually grey, dark blackish brown or black. *Mycelium* immersed or partly superficial; hyphae colourless, olivaceous-brown or brown. *Stroma* rarely formed. *Setae* and *hyphopodia* absent. *Conidiophores* macronematous, mononematous, simple or irregularly and loosely branched, pale brown or brown, solitary or in fascicles. *Conidiogenous cells* integrated, terminal becoming intercalary, polytretic, sympodial, or sometimes monotretic, cicatrized. *Conidia* catenate or solitary, dry, ovoid, obovoid, cylindrical, narrowly ellipsoid or obclavate, beaked or non-beaked, pale or medium olivaceous-brown to brown, smooth or verrucose, with transverse and with or without oblique or longitudinal septa. Septa can be thick, dark and rigid and an internal cell-like structure can be formed. Species with meristematic growth are known.
*Ascomata* small, solitary to clustered, erumpent to (nearly) superficial at maturity, globose to ovoid, dark brown, smooth, apically papillate, ostiolate. *Papilla* short, blunt. *Peridium* thin. *Hamathecium* of cellular pseudoparaphyses. *Asci* few to many per ascoma, (4–6–)8-spored, basal, bitunicate, fissitunicate, cylindrical to cylindro-clavate, straight or somewhat curved, with a short, furcate pedicel. *Ascospores* muriform, ellipsoid to fusoid, slightly constricted at septa, yellow-brown, without guttules, smooth, 3–7 transverse septa, 1–2 series of longitudinal septa through the two original central segments, end cells without septa, or with 1 longitudinal or oblique septum, or with a Y-shaped pair of septa.

*Type species*: *Alternaria alternata* (Fr.) Keissl.

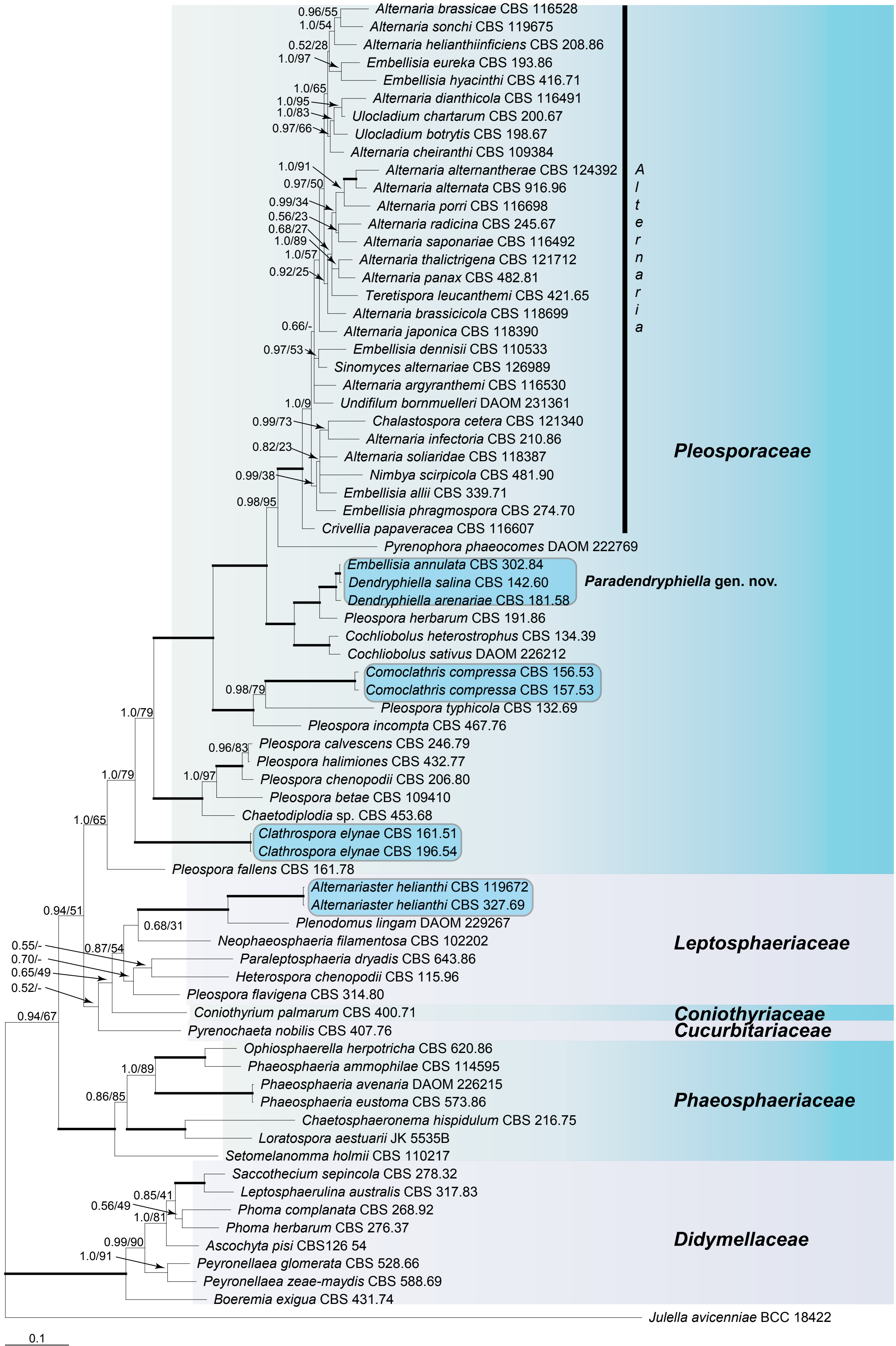


**Fig. 2.** Bayesian 50 % majority rule consensus tree based on the SSU, LSU and RPB2 sequences of 74 strains representing the *Pleosporineae*. The Bayesian posterior probabilities (PP) and RAxML bootstrap support values (ML) are given at the nodes (PP/ML). Thickened lines indicate a PP of 1.0 and ML of 100. The tree was rooted to *Julella avicenniae* (BCC 18422).

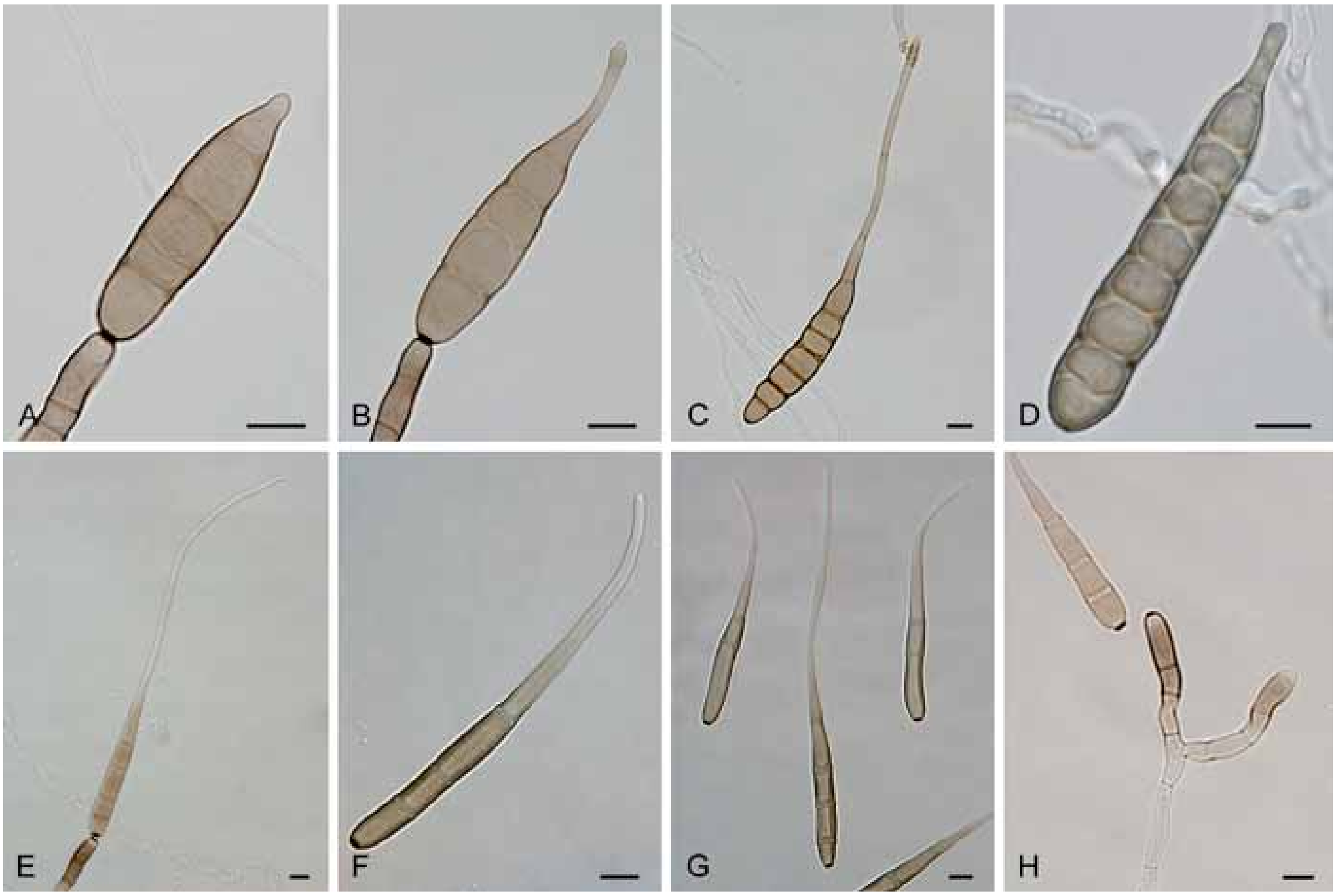


**Fig. 3.** *Alternaria* sect. *Alternantherae*: conidia and conidiophores. A–D. *A. alternantherae*. E–H. *A. perpunctulata*. Scale bars = 10 µm.

## *ALTERNARIA* SECTIONS

### Section *Alternantherae* D.P. Lawr., Gannibal, Peever & B.M. Pryor, Mycologia 105: 540. 2013. Fig. 3.

*Type species*: *Alternaria alternantherae* Holcomb & Antonop.

*Diagnosis*: Section *Alternantherae* contains short to moderately long conidiophores with a conidiogenous tip which can be enlarged. Conidia are narrowly ellipsoid or ovoid, sometimes subcylindrical, solitary or rarely paired, sometimes slightly constricted near some septa, longitudinal or oblique septa occasionally occur, disto- and euseptate, with a long apical narrow beak. The conidial beak is unbranched, septate or aseptate, long filiform, and sometimes swollen at the end. Internal compartmentation occurs, cell lumina tend to be broadly octagonal to rounded.

*Notes*: Section *Alternantherae* was recently established by Lawrence *et al.* (2013) after first being described as species-group *A. alternantherae* (Lawrence *et al.* 2012). The described section consists of three former *Nimbya* species which formed a separate clade amidst the *Alternaria* species-groups based on sequences of the GAPDH, ITS and Alt a 1 genes (Lawrence *et al.* 2012). *Nimbya celosiae* is placed in this section based on the data of Lawrence *et al*. (2012), while *N. gomphrenae* is placed in the section based on ITS sequence data from Chou & Wu (2002).

***Alternaria alternantherae*** Holcomb & Antonop., Mycologia 68: 1126. 1976.

≡ *Nimbya alternantherae* (Holcomb & Antonop.) E.G. Simmons & Alcorn, Mycotaxon 55: 142. 1995.

***Alternaria celosiicola*** Jun. Nishikawa & C. Nakash., J. Phytopathol.: doi: 10.1111/jph.12108 (p. 3). 2013.

*Basionym*: *Nimbya celosiae* E.G. Simmons & Holcomb, Mycotaxon 55: 144. 1995.

≡ *Alternaria celosiae* (E.G. Simmons & Holcomb) D.P. Lawr., M.S. Park & B.M. Pryor, Mycol. Progr. 11: 811. 2012. (nom. illegit., homonym of *Alternaria celosiae* (Tassi) O. Savul. 1950).

***Alternaria gomphrenae*** Togashi, Bull. Imp. Coll. Agric. 9: 6. 1926.

≡ *Nimbya gomphrenae* (Togashi) E.G. Simmons, Sydowia 41: 324. 1989.

***Alternaria perpunctulata*** (E.G. Simmons) D.P. Lawr., M.S. Park & B.M. Pryor, Mycol. Progr. 11: 811. 2012.

*Basionym*: *Nimbya perpunctulata* E.G. Simmons, Stud. Mycol. 50: 115. 2004.

### Section *Alternata* D.P. Lawr., Gannibal, Peever & B.M. Pryor, Mycologia 105: 538. 2013. Fig. 4.

*Type species*: *Alternaria alternata* (Fr.) Keissl.

*Diagnosis*: Section *Alternata* contains straight or curved primary conidiophores, short to long, simple or branched, with one or several apical conidiogenous loci. Conidia are obclavate, long ellipsoid, small or moderate in size, septate, slightly constricted near some septa, with few longitudinal septa, in moderately long to long, simple or branched chains. The conidium body can narrow gradually into a tapered beak or secondary conidiophore. Secondary conidiophores can be formed apically or laterally with one or a few conidiogenous loci.

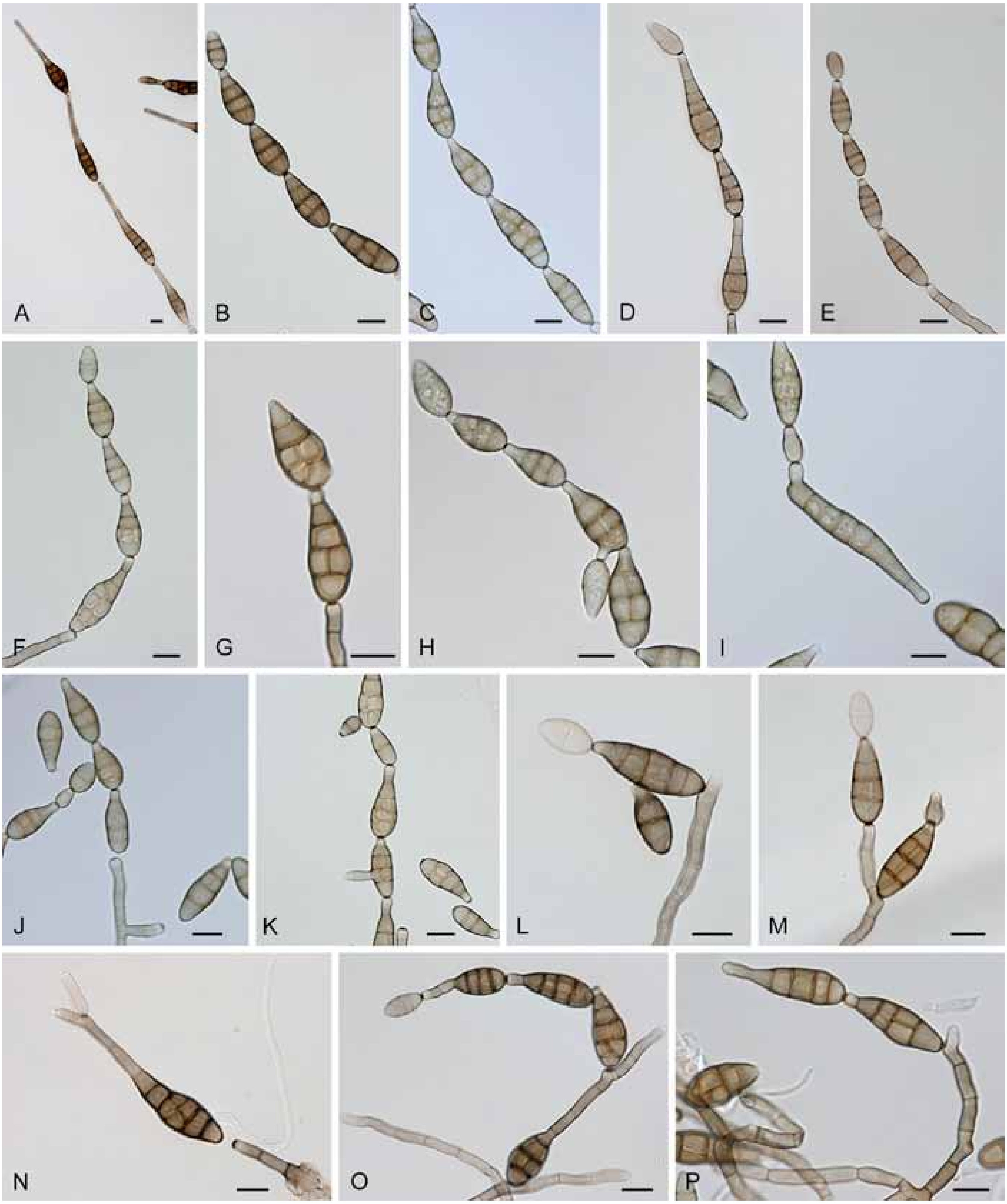


**Fig. 4.** *Alternaria* sect. *Alternata*: conidia and conidiophores. A, N. *A. daucifolii*. B, L–M. *A. arborescens*. C, H–J. *A. alternata*. D, O. *A. gaisen*. E. *A. limoniasperae*. F, K. *A. tenuissima*. G, P. *A. longipes*. Scale bars = 10 µm.

*Notes*: Next to the species that are displayed in our phylogeny, 14 more are included in sect. *Alternata* based on the study of Lawrence *et al.* (2013) and confirmed by our molecular data (not shown). We chose not to include 11 species from the study of Lawrence *et al.* (2013). The species *A. gossypina*, *A. grisae*, *A. grossulariae*, *A. iridis*, *A. lini*, *A. maritima* and *A. nelumbii* were not recognised by Simmons (2007) and the strains of *A. malvae*, *A. rhadina*, *A. resedae* and *A. tomato* used by Lawrence *et al.* (2013) were not authentic. Section *Alternata* comprises almost 60 *Alternaria* species based on ITS sequence data (data not shown). The molecular variation within this section is low.

***Alternaria alternata*** (Fr.) Keissl., Beih. Bot. Centralbl., Abt. 2, 29: 434. 1912.
*Basionym*: *Torula alternata* Fr., Syst. Mycol. (Lundae) 3: 500. 1832 (nom. sanct.).

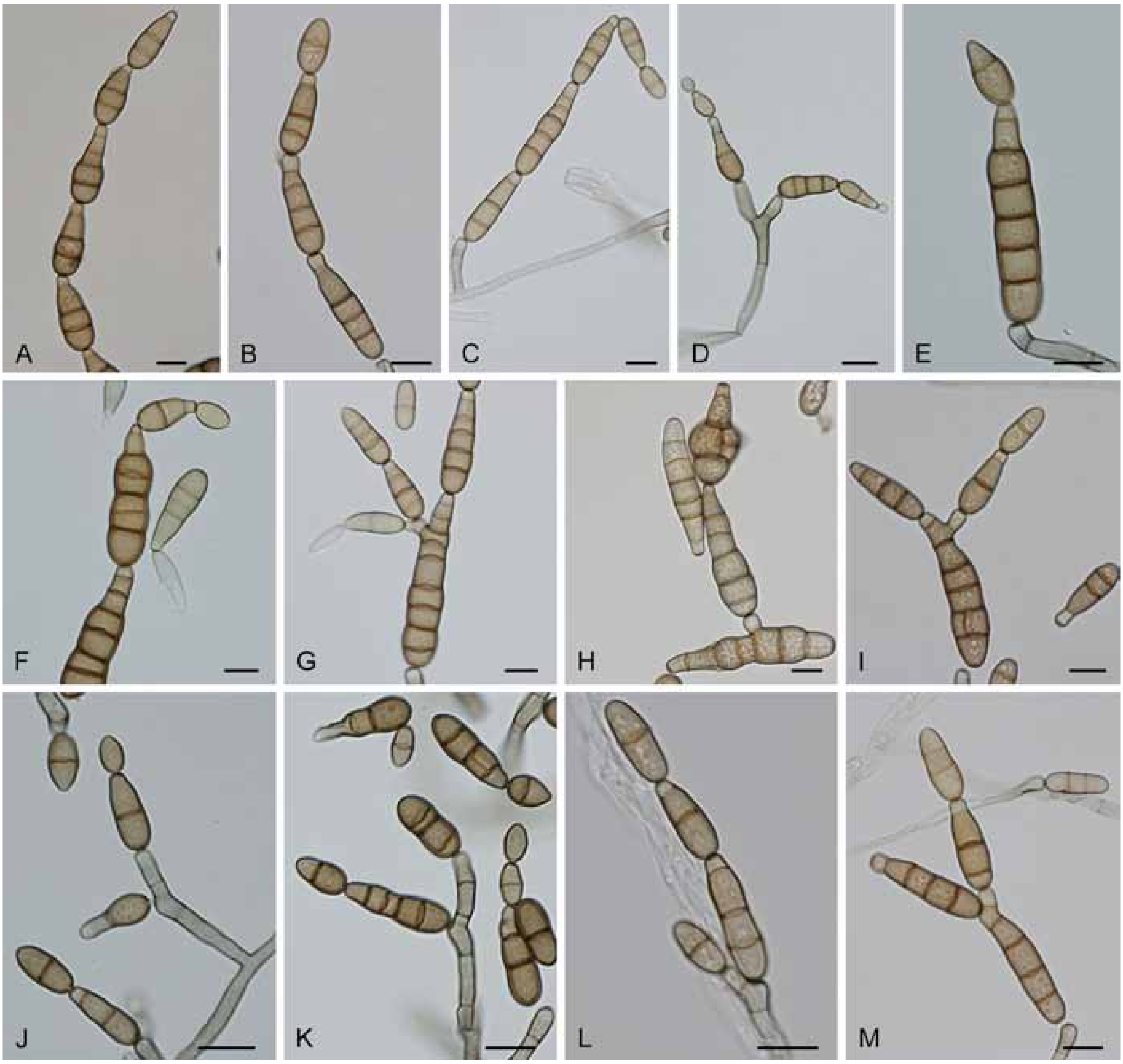


**Fig. 5.** *Alternaria* sect. *Brassicicola*: conidia and conidiophores. A, H. *A. brassicicola*. B, I, L–M. *A. mimicola*. C, G. *A. solidaccana*. D, J–K. *A. conoidea*. E–F. *A. septorioides*. Scale bars = 10 µm.

= *Alternaria tenuis* Nees, Syst. Pilze (Würzburg): 72. 1816 [1816–1817].

Additional synonyms listed in Simmons (2007)

***Alternaria angustiovoidea*** E.G. Simmons, Mycotaxon 25: 198. 1986.

***Alternaria arborescens*** E.G. Simmons, Mycotaxon 70: 356. 1999.

***Alternaria burnsii*** Uppal, Patel & Kamat, Indian J. Agric. Sci. 8: 49. 1938.

***Alternaria cerealis*** E.G. Simmons & C.F. Hill, CBS Biodiversity Ser. (Utrecht) 6: 600. 2007.

***Alternaria citriarbusti*** E.G. Simmons, Mycotaxon 70: 287. 1999.

***Alternaria citrimacularis*** E.G. Simmons, Mycotaxon 70: 277. 1999.

***Alternaria colombiana*** E.G. Simmons, Mycotaxon 70: 298. 1999.

***Alternaria daucifollii*** E.G. Simmons, CBS Biodiversity Ser. (Utrecht) 6: 518. 2007.

***Alternaria destruens*** E.G. Simmons, Mycotaxon 68: 419. 1998.

***Alternaria dumosa*** E.G. Simmons, Mycotaxon 70: 310. 1999.

***Alternaria gaisen*** Nagano ex Hara, Sakumotsu Byorigaku, Edn 4: 263. 1928.

= *Alternaria gaisen* Nagano, J. Jap. Soc. Hort. Sci. 32: 16–19. 1920. (nom. illegit.)

= *Alternaria kikuchiana* S. Tanaka, Mem. Coll. Agric. Kyoto Univ., Phytopathol. Ser. 28: 27. 1933.

= *Macrosporium nashi* Miura, Flora of Manchuria and East Mongolia, Part III Cryptogams, Fungi: 513. 1928.

***Alternaria herbiphorbicola*** E.G. Simmons, CBS Biodiversity Ser. (Utrecht) 6: 608. 2007.

***Alternaria limoniasperae*** E.G. Simmons, Mycotaxon 70: 272. 1999.

***Alternaria longipes*** (Ellis & Everh.) E.W. Mason, Mycol. Pap. 2: 19. 1928.

*Basionym*: *Macrosporium longipes* Ellis & Everh., J. Mycol. 7: 134. 1892.

= *Alternaria brassicae* var. *tabaci* Preissecker, Fachliche Mitt. Österr. Tabakregie 16: 4. 1916.

***Alternaria perangusta*** E.G. Simmons, Mycotaxon 70: 303. 1999.

***Alternaria postmessia*** E.G. Simmons, CBS Biodiversity Ser. (Utrecht) 6: 598. 2007.

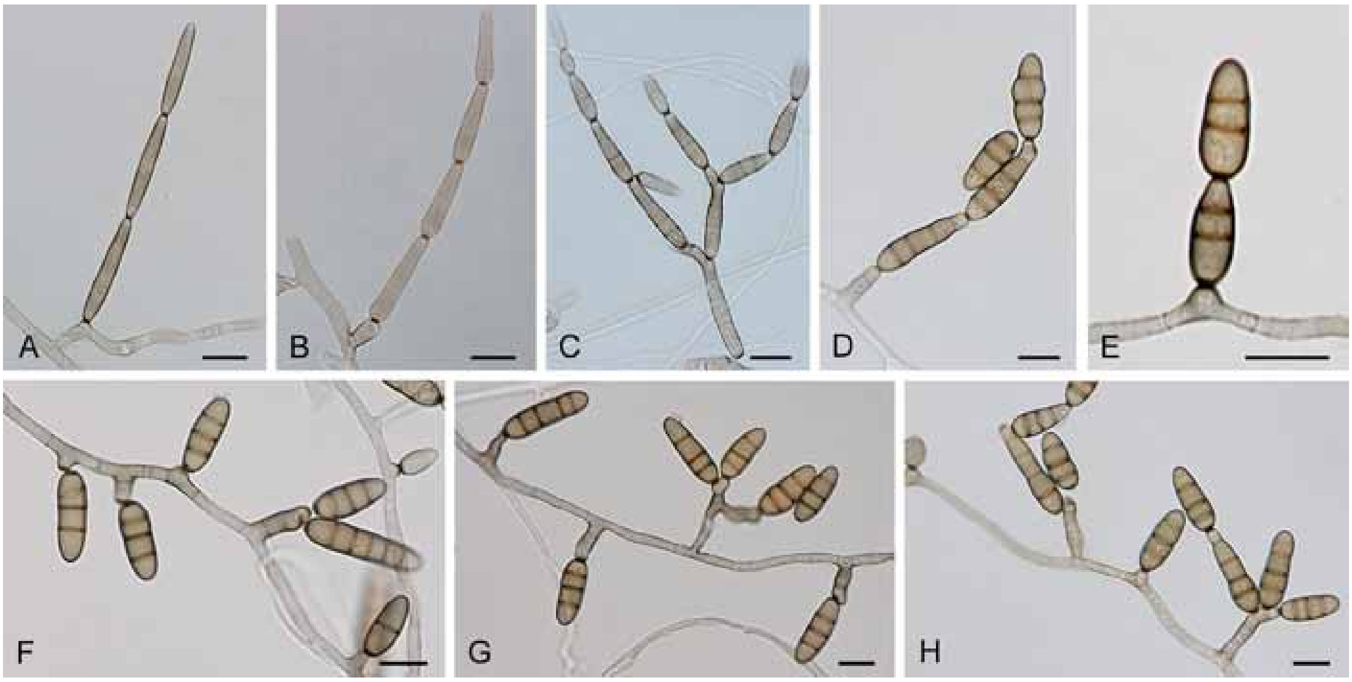


**Fig. 6.** *Alternaria* sect. *Chalastospora*: conidia and conidiophores. A. *A. cetera*. B. *A. obclavata*. C. *A. breviramosa*. D, H. *A. armoraciae*. E–G. *A. abundans*. Scale bars = 10 µm.

***Alternaria tangelonis*** E.G. Simmons, Mycotaxon 70: 282. 1999.
***Alternaria tenuissima*** (Nees & T. Nees : Fr.) Wiltshire, Trans. Brit. Mycol. Soc. 18: 157. 1933.
*Basionym*: *Macrosporium tenuissimum* (Nees & T. Nees) Fr., Syst. Mycol. (Lundae) 3: 374. 1832 (nom. sanct.).
≡ *Helminthosporium tenuissimum* Kunze ex Nees & T. Nees, Nova Acta Acad. Caes. Leop.-Carol. German. Nat. Cur. 9: 242. 1818.
Additional synonyms listed in Simmons (2007).
***Alternaria toxicogenica*** E.G. Simmons, Mycotaxon 70: 294. 1999.
***Alternaria turkisafria*** E.G. Simmons, Mycotaxon 70: 290. 1999.

## Section *Brassicicola* D.P. Lawr., Gannibal, Peever & B.M. Pryor, Mycologia 105: 541. 2013. Fig. 5.

*Type species*: *Alternaria brassicicola* (Schwein.) Wiltshire

*Diagnosis*: Section *Brassicicola* contains short to moderately long, simple or branched primary conidiophores with one or several apical conidiogenous loci. Conidia are ellipsoid, ovoid or somewhat obclavate, small or moderate in size, septate, slightly or strongly constricted at most of their transverse septa, with no to many longitudinal septa, in moderately long to long, simple or branched chains, with dark septa and cell walls. Secondary conidiophores can be formed apically or laterally with one or a few conidiogenous loci. Chlamydospores may occur.

*Notes*: Our molecular data support the morphological placement of *A. septorioides* and *A. solidaccana* in section *Brassicicola* (Simmons 2007). The other three species were already assigned to this section based on previous molecular studies (Pryor *et al.* 2009, Runa *et al.* 2009, Lawrence *et al.* 2012). *Alternaria japonica* was previously linked to the *A. brassicicola* species-group (Pryor & Gilbertson 2000, Pryor & Bigelow 2003, Lawrence *et al.* 2013), but this association was questioned by Hong *et al.* (2005). In our analyses, *A. japonica* clustered in sect. *Japonicae*.

***Alternaria brassicicola*** (Schwein.) Wiltshire, Mycol. Pap. 20: 8. 1947.
*Basionym*: *Helminthosporium brassicicola* Schwein., Trans. Amer. Philos. Soc., Ser. 2, 4: 279. 1832.
Additional synonyms listed in Simmons (2007)
***Alternaria conoidea*** (E.G. Simmons) D.P. Lawr., Gannibal, Peever & B.M. Pryor, Mycologia 105: 542. 2013.
*Basionym*: *Embellisia conoidea* E.G. Simmons, Mycotaxon 17: 226. 1983.
***Alternaria mimicula*** E.G. Simmons, Mycotaxon 55: 129. 1995.
***Alternaria septorioides*** (Westend.) E.G. Simmons, CBS Biodiversity Ser. (Utrecht) 6: 570. 2007.
*Basionym*: *Sporidesmium septorioides* Westend., Bull. Acad. Roy. Sci. Belgique., Cl. Sci., Sér. 2, 21: 236. 1854.
= *Alternaria resedae* Neerg., Annual Rep. Phytopathol. Lab. J.E. Ohlsens Enkes, Seed Growers, Copenhagen 7: 9. 1942 (nom. nud.).
= *Alternaria resedae* Neerg., Danish species of *Alternaria* & *Stemphylium*: 150. 1945.
***Alternaria solidaccana*** E.G. Simmons, CBS Biodiversity Ser. (Utrecht) 6: 572. 2007.

## Section *Chalastospora* (E.G. Simmons) Woudenb. & Crous, **comb. et stat. nov.** MycoBank MB803733. Fig. 6.

*Basionym*: *Chalastospora* E.G. Simmons, CBS Biodiversity Ser. (Utrecht) 6: 668. 2007.

*Type species*: *Alternaria cetera* E.G. Simmons

*Diagnosis*: Section *Chalastospora* contains short to long, simple or branched primary conidiophores with one or several conidiogenous loci. Conidia are pale to medium brown, narrowly ellipsoid to ellipsoid or ovoid, beakless, with no to multiple transverse eusepta and rarely longitudinal septa, solitary or in chains. Secondary conidiophores can be formed apically or laterally with one or a few conidiogenous loci.


**Fig. 7.** *Alternaria* sect. *Cheiranthus*: conidia and conidiophores. A–B. *A. indefessa*. B–C. *A. cheiranthi*. Scale bars = 10 µm.

*Notes*: Previous studies already placed *E. abundans* in the *Chalastospora*-clade (Andersen *et al.* 2009, Lawrence *et al.* 2012). Our study also placed *Alternaria armoraciae* in this section, while Crous *et al.* (2009c) showed that *Chalastospora gossypii*, formerly *Alternaria malorum*, belonged to this section based on sequences of the ITS and LSU genes.

***Alternaria abundans*** (E.G. Simmons) Woudenb. & Crous, **comb. nov.** MycoBank MB803688.
*Basionym*: *Embellisia abundans* E.G. Simmons, Mycotaxon 17: 222. 1983.
***Alternaria armoraciae*** E.G. Simmons & C.F. Hill, CBS Biodiversity Ser. (Utrecht) 6: 660. 2007.
***Alternaria breviramosa*** Woudenb. & Crous, **nom. nov.** MycoBank MB803690.
*Basionym*: *Chalastospora ellipsoidea* Crous & U. Braun, Persoonia 22: 145. 2009, non *Alternaria ellipsoidea* E.G. Simmons, 2002.
*Etymology*: Name refers to the short lateral branches.
***Alternaria cetera*** E.G. Simmons, Mycotaxon 57: 393. 1996.
≡ *Chalastospora cetera* (E.G. Simmons) E.G. Simmons, CBS Biodiversity Ser. (Utrecht) 6: 668. 2007.
***Alternaria malorum*** (Ruehle) U. Braun, Crous & Dugan, Mycol. Progr. 2: 5. 2003.
*Basionym*: *Cladosporium malorum* Ruehle, Phytopathology 21: 1146. 1931.
= *Cladosporium gossypii* Jacz., Khlopkovoe Delo, 1929 (5–6): 564. 1929, non *Alternaria gossypii* (Jacz.) Y. Nisik., K. Kimura & Miyaw., 1940.
≡ *Chalastospora gossypii* (Jacz.) U. Braun & Crous, Persoonia 22: 144. 2009.
= *Cladosporium malorum* Heald, Wash. State Agric. Exp. Sta. Bull., Special Ser. 245: 48. 1930. (nom. nud.)
Additional synonyms in Crous *et al.* (2009c).
***Alternaria obclavata*** (Crous & U. Braun) Woudenb. & Crous, **comb. nov.** MycoBank MB803689.
*Basionym*: *Chalastospora obclavata* Crous & U. Braun, Persoonia 22: 146. 2009.

## *Section Cheiranthus* Woudenb. & Crous, **sect. nov.** MycoBank MB803734. Fig. 7.

*Type species*: *Alternaria cheiranthi* (Lib.) P.C. Bolle

*Diagnosis*: Section *Cheiranthus* contains short to moderately long, simple or branched primary conidiophores with one or several conidiogenous loci. Conidia are ovoid, broadly ellipsoid with transverse and longitudinal septa, slightly or strongly constricted at the septa, in short to long, simple or branched chains. Secondary conidiophores can be formed apically or laterally with a single conidiogenous locus.

*Notes:* Next to *Alternaria cheiranthi* and *Embellisia indefessa*, sect. *Cheiranthus* contains a non-sporulating strain formerly known as *Alternaria resedae*, CBS 115.44. Because *Alternaria resedae* is synonymised with *Alternaria septorioides* (Simmons 2007), which clusters in section *Brassisicola*, CBS 115.44 will be treated as "*Alternaria* sp.". *Alternaria cheiranthi* and *E. indefessa* have been linked to *Ulocladium* (Pryor & Gilbertson 2000, Pryor & Bigelow 2003, Hong *et al.* 2005, Pryor *et al.* 2009, Runa *et al.* 2009, Lawrence *et al.* 2012), but based on morphology could not be placed here. Our extensive dataset showed that they form a sister section to section *Ulocladioides*.

***Alternaria cheiranthi*** (Lib.) P.C. Bolle, Meded. Phytopathol. Lab. "Willie Commelin Scholten" 7: 43. 1924.
*Basionym*: *Helminthosporium cheiranthi* Lib. [as "*Helmisporium*"], in Desmazières, Plantes Cryptogames du Nord de la France, edn 1: 213. 1827.
≡ *Macrosporium cheiranthi* (Lib.) Fr., Syst. Mycol. (Lundae) 3: 374. 1832.
***Alternaria indefessa*** (E.G. Simmons) Woudenberg & Crous, **comb. nov.** MycoBank MB803691.
*Basionym*: *Embellisia indefessa* E.G. Simmons, Mycotaxon 17: 228. 1983.

## Section *Crivellia* (Shoemaker & Inderb.) Woudenb. & Crous, **comb. et stat. nov.** MycoBank MB803735. Fig. 8.

*Basionym*: *Crivellia* Shoemaker & Inderb., Canad. J. Bot. 84: 1308. 2006.

*Type species*: *Alternaria penicillata* (Corda) Woudenb. & Crous (= *Cucurbitaria papaveracea* De Not.).

*Diagnosis*: Section *Crivellia* is characterised by straight or curved, simple or branched primary conidiophores, with geniculate, sympodial proliferations. Conidia are cylindrical, straight to curved to inequilateral, with transverse eusepta, rarely constricted at

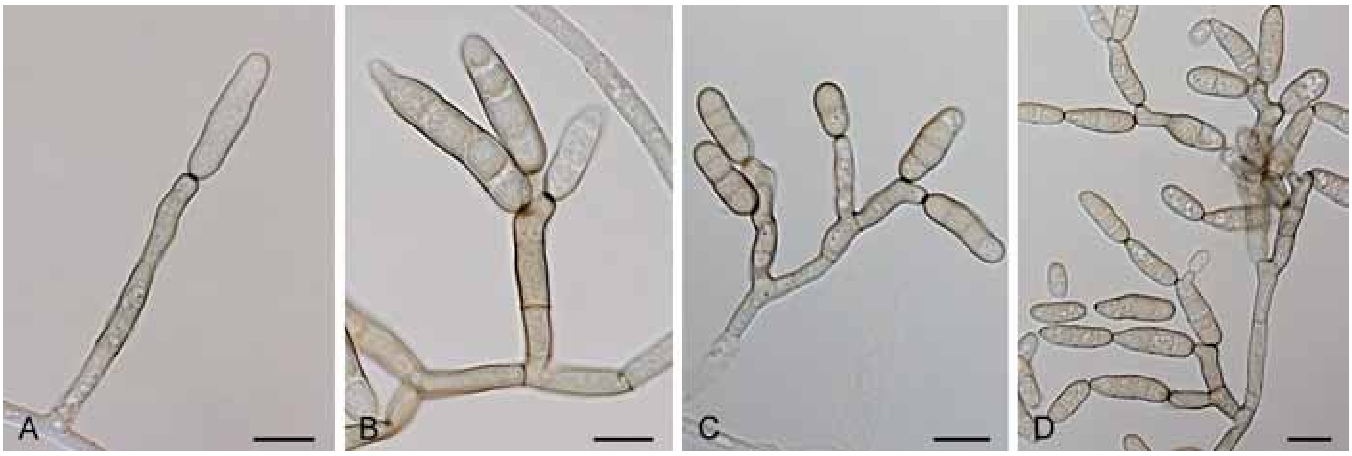


**Fig. 8.** *Alternaria* sect. *Crivellia*: conidia and conidiophores. A–B. *A. papavericola*. C–D. *A. penicillata*. Scale bars = 10 µm.

septa, single or in short, simple or branched chains. Secondary conidiophores are formed apically or laterally. Microsclerotia or chlamydospores may occur. Sexual morphs observed.

*Notes*: Section *Crivellia* contains the type species of the sexual morph *Crivellia*, *C. papaveracea*, with *Brachycladium penicillatum* asexual morph, and *Brachycladium papaveris.* The genus was established by Inderbitzin *et al.* (2006) based on the finding that *C. papaveraceae*, formerly *Pleospora papaveraceae*, belonged to the *Alternaria*-complex instead of *Pleospora s. str.* based on ITS, GAPDH and TEF1 sequences.

***Alternaria papavericola*** Woudenb. & Crous, **nom. nov.** MycoBank MB803749.
*Basionym: Helminthosporium papaveris* Sawada, J. Nat. Hist. Soc. Formosa 31: 1. 1917.
≡ *Dendryphion papaveris* (Sawada) Sawada, Special Publ. Coll. Agric. Natl. Taiwan Univ. 8: 200. 1959, non *Alternaria papaveris* (Bres.) M.B. Ellis, 1976.
≡ *Brachycladium papaveris* (Sawada) Shoemaker & Inderb., Canad. J. Bot. 84: 1310. 2006.
*Etymology*: Name refers to the host.
***Alternaria penicillata*** (Corda) Woudenb. & Crous, **comb. nov.** MycoBank MB803692.
*Basionym: Brachycladium penicillatum* Corda, Icon. Fungorum hucusque Cogn. (Prague) 2: 14. 1838.
≡ *Dendryphion penicillatum* (Corda) Fr., Summa Veg. Scand., Sect. Post. (Stockholm): 504. 1849.
= *Cucurbitaria papaveracea* De Not., Sferiacei Italici: 62. 1863.
≡ *Pleospora papaveracea* (De Not.) Sacc., Syll. Fungorum (Abellini) 2: 243. 1883.
≡ *Crivellia papaveracea* (De Not.) Shoemaker & Inderb., Canad. J. Bot. 84: 1308. 2006.
*Note*: The asexual name*, Brachycladium penicillatum* is older than the sexual name, *Cucurbitaria papaveracea*, and therefore the species epithet *penicillatum* is chosen above *papaveracea.*

## Section *Dianthicola* Woudenb. & Crous, **sect. nov.** MycoBank MB803736. Fig. 9.

*Type species*: *Alternaria dianthicola Neerg.*

*Diagnosis*: Section *Dianthicola* contains simple or branched primary conidiophores, with or without apical geniculate proliferations. *Conidia are* narrowly ovoid or narrowly ellipsoid with transverse and few longitudinal septa, slightly constricted at the septa, with a long (filamentous) beak or apical secondary conidiophore, solitary or in short chains.

*Note*: Based on the ITS sequence, *Alternaria dianthicola* clustered near *Ulocladium* (Chou & Wu 2002). Our extensive dataset places it in a sister section to section *Ulocladioides*.

***Alternaria dianthicola*** Neerg., Danish species of *Alternaria* & *Stemphylium*: 190. 1945.
***Alternaria elegans*** E.G. Simmons & J.C. David, Mycotaxon 75: 89. 2000.
***Alternaria simsimi*** E.G. Simmons, Stud. Mycol. 50: 111. 2004.

## Section *Embellisia* (E.G. Simmons) Woudenb. & Crous, **comb. et stat. nov.** MycoBank MB803737. Fig. 10.
*Basionym*: *Embellisia* E.G. Simmons, Mycologia 63: 380. 1971.

*Type species*: *Alternaria embellisia* Woudenb. & Crous (≡ *Helminthosporium allii* Campan., *Embellisia allii* (Campan.) E.G. Simmons).

*Diagnosis*: Section *Embellisia* contains simple, septate conidiophores, straight or with geniculate sympodial proliferation. Condia are solitary, ovoid to subcylindrical, straight to inequilateral, transseptate; septa can be thick, dark and rigid in contrast to the external wall. Chlamydospores may occur.

*Notes*: Section *Embellisia* contains the first two species described in the genus *Embellisia*, *Embellisia allii* (type species) and *Embellisia chlamydospora* (Simmons 1971) together with *Embellisia tellustris*. This clade is also resolved in the latest molecular revision of *Embellisia* based on sequences of the GAPDH, ITS and Alt a 1 genes as *Embellisia* group I (Lawrence *et al.* 2012).

***Alternaria chlamydosporigena*** Woudenb. & Crous, **nom. nov.** MycoBank MB803694.
*Basionym*: *Pseudostemphylium chlamydosporum* Hoes, G.W. Bruehl & C.G. Shaw, Mycologia 57: 904. 1965, non *Alternaria chlamydospora* Mouch., 1973.
≡ *Embellisia chlamydospora* (Hoes, G.W. Bruehl & C.G. Shaw) E.G. Simmons, Mycologia 63: 384. 1971.
*Etymology*: Name refers to the formation of chlamydospores during growth.

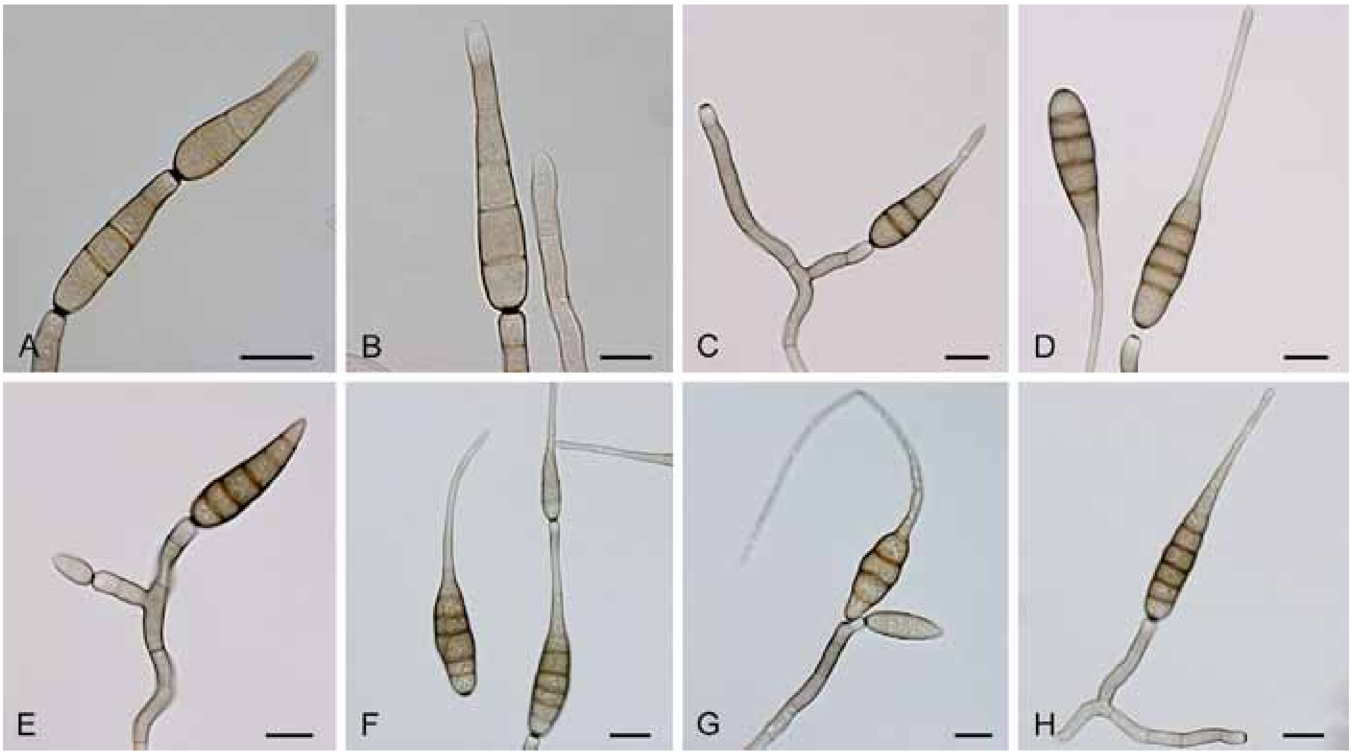


**Fig. 9.** *Alternaria* sect. *Dianthicola*: conidia and conidiophores. A–B. *A. dianthicola*. C–E. *A. simsimi*. F–H. *A. elegans*. Scale bars = 10 µm.

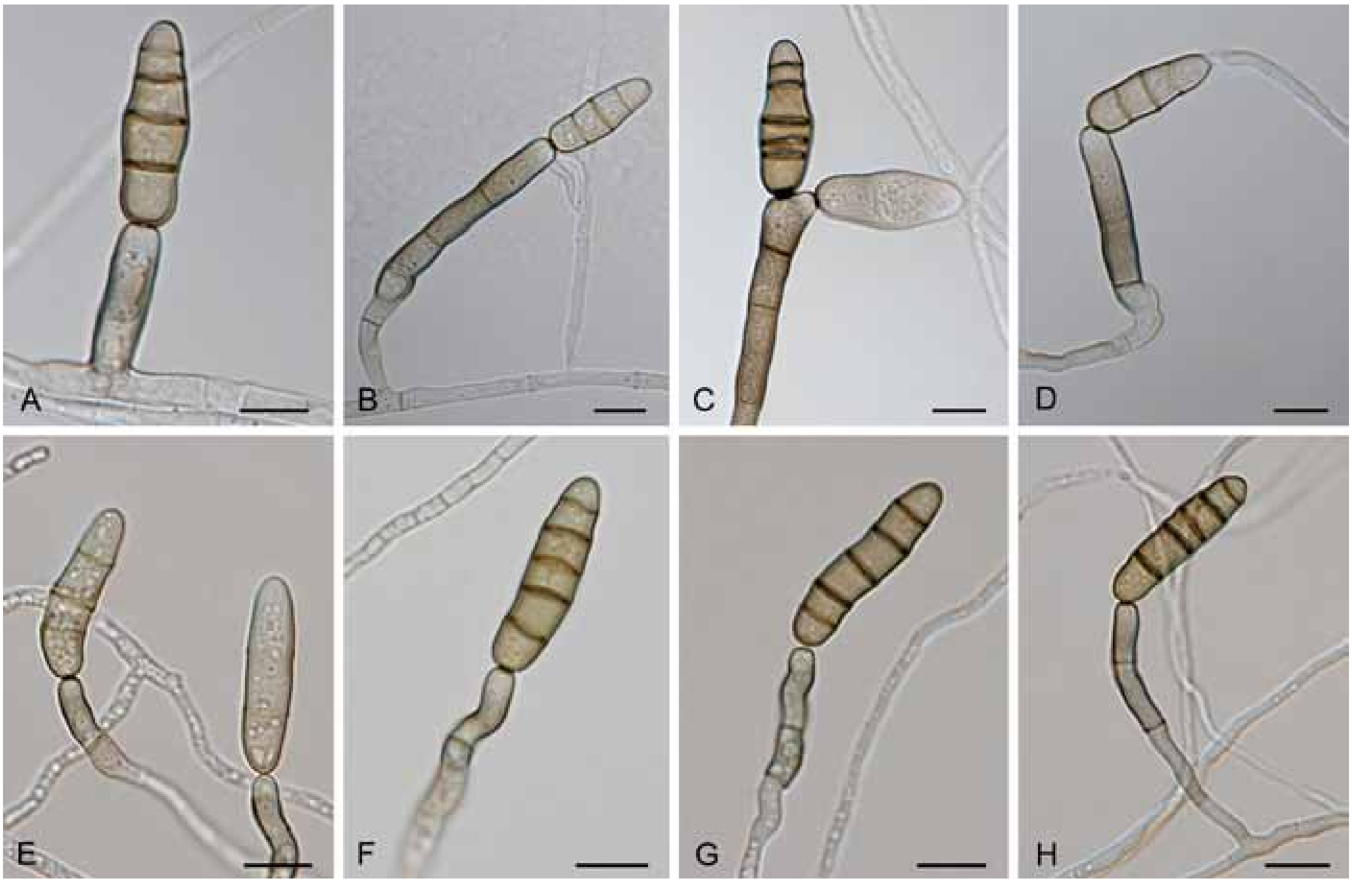


**Fig. 10.** *Alternaria* sect. *Embellisia*: conidia and conidiophores. A–D. *A. embellisia*. E–H. *A. tellustris*. Scale bars = 10 µm.

***Alternaria embellisia*** Woudenb. & Crous, **nom. nov.** MycoBank MB803693.
*Basionym*: *Helminthosporium allii* Campan., Nuovi Ann. Agric. Roma 4: 87. 1924, non *Alternaria allii* Nolla, 1927.
≡ *Embellisia allii* (Campan.) E.G. Simmons, Mycologia 63: 382. 1971.
*Etymology*: Name refers to the genus *Embellisia* for which it served as type species.

***Alternaria tellustris*** (E.G. Simmons) Woudenb. & Crous, **comb. nov.** MycoBank MB803695.
*Basionym*: *Embellisia tellustris* E.G. Simmons [as "*telluster*"], Mycotaxon 17: 234. 1983.

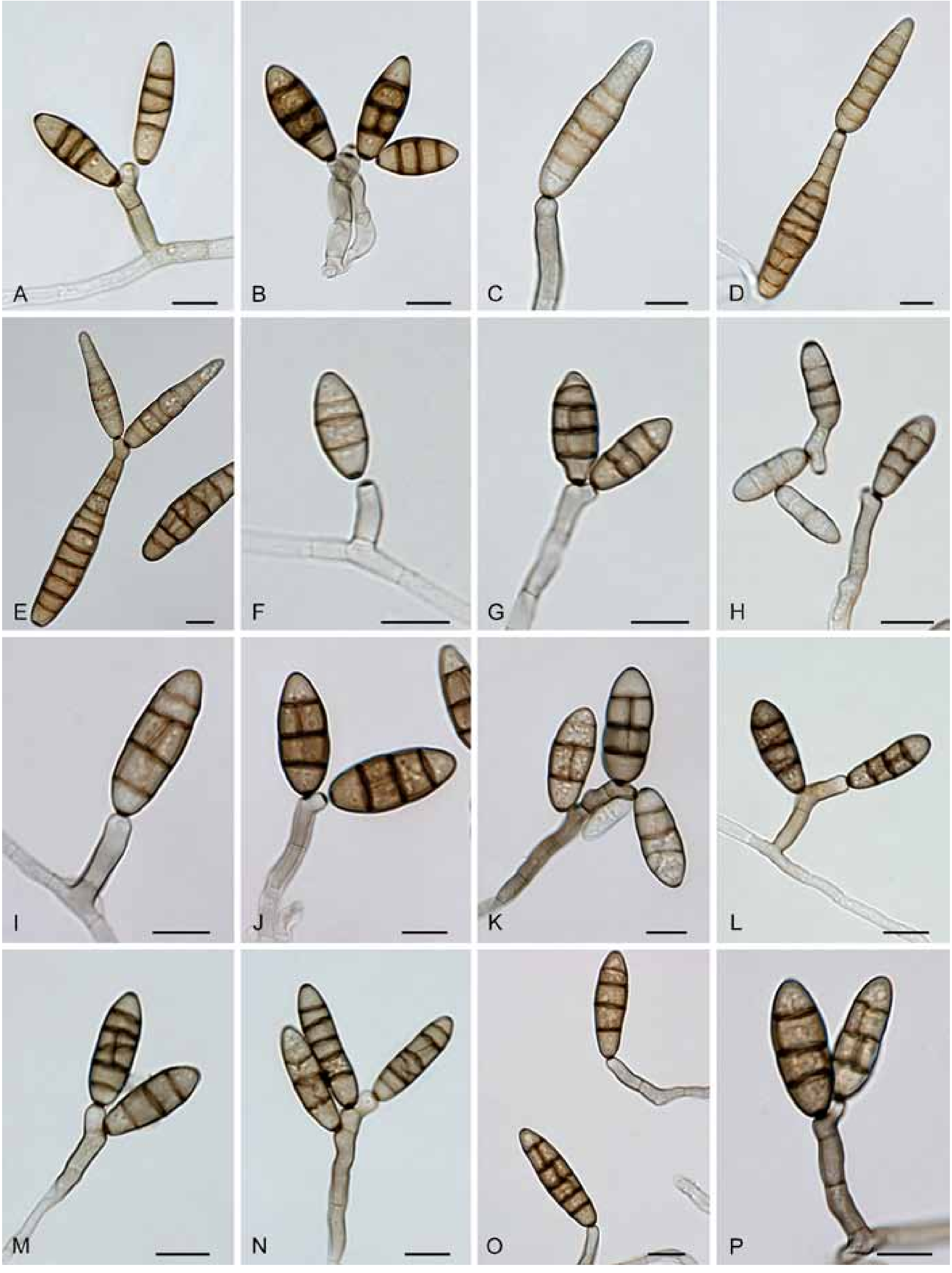


**Fig. 11.** *Alternaria* sect. *Embellisioides*: conidia and conidiophores. A–B. *A. hyacinthi*. C–E. *A. lolii*. F–H. *A. botryospora*. I–K. *A. planifunda*. L–N. *A. proteae*. O–P. *A. tumida*. Scale bars = 10 µm.

## Section *Embellisioides* Woudenb. & Crous, **sect. nov.** MycoBank MB803738. Fig. 11.

*Type species*: *Alternaria hyacinthi (*de Hoog & P.J. Mull. bis) Woudenb. & Crous

*Diagnosis*: Section *Embellisioides* contains simple, septate conidiophores, straight or with multiple, geniculate, sympodial proliferations. Apical or lateral, short secondary conidiophores may occur. Condia are solitary or in short chains, obovoid to ellipsoid, with transverse and longitudinal septa; transverse septa can be thick, dark and rigid in contrast to the external wall. Chlamydospores and a sexual morph may occur.

*Note*: In Lawrence *et al.* (2012) the section is named *Embellisia* group III.

***Alternaria botryospora*** Woudenb. & Crous, **nom. nov.** MycoBank MB803705.
*Basionym: Embellisia novae-zelandiae* E.G. Simmons & C.F. Hill, Mycotaxon 38: 252. 1990, non *Alternaria novae-zelandiae* E.G. Simmons, 2002.
*Etymology*: Name refers to the clusters of conidia.
***Alternaria hyacinthi*** (de Hoog & P.J. Mull. bis) Woudenb. & Crous, **comb. nov.** MycoBank MB803703.
*Basionym: Embellisia hyacinthi* de Hoog & P.J. Mull. bis, Netherlands J. Pl. Pathol. 79: 85. 1973.
***Alternaria lolii*** (E.G. Simmons & C.F. Hill) Woudenb. & Crous, **comb. nov.** MycoBank MB803704.
*Basionym: Embellisia lolii* E.G. Simmons & C.F. Hill, Stud. Mycol. 50: 113. 2004.
***Alternaria planifunda*** (E.G. Simmons) Woudenb. & Crous, c**omb. nov.** MycoBank MB803706.
*Basionym: Embellisia planifunda* E.G. Simmons, Mycotaxon 17: 233. 1983.
***Alternaria proteae*** (E.G. Simmons) Woudenb. & Crous, **comb. nov.** MycoBank MB803707.
*Basionym: Embellisia proteae* E.G. Simmons, Mycotaxon 38: 258. 1990.
= *Allewia proteae* E.G. Simmons, Mycotaxon 38: 262. 1990.
***Alternaria tumida*** (E.G. Simmons) Woudenb. & Crous, **comb. nov.** MycoBank MB803708.
*Basionym: Embellisia tumida* E.G. Simmons, Mycotaxon 17: 236. 1983.

## Section *Eureka* Woudenb. & Crous, **sect. nov.** MycoBank MB803739. Fig. 12.

*Type species*: *Alternaria eureka* E.G. Simmons

*Diagnosis*: Section *Eureka* contains simple, septate conidiophores, straight or with geniculate, sympodial proliferations. Apical or lateral, short secondary conidiophores may occur. Condia are solitary or in short chains, narrowly ellipsoid to cylindrical, with transverse and longitudinal septa, slighty constricted at the septa, with a blunt rounded apex. Chlamydospores and a sexual morph may occur.

*Notes*: Section *Eureka* contains four *Alternaria* species and two former *Embellisia* species. From the *Alternaria* species only the ITS sequence of *A. geniostomatis* was previously used in a molecular study (Toth *et al.* 2011), showing it to cluster separate from the other *Alternaria* spp. The two *Embellisia* species were included in the latest molecular-based revision of *Embellisia* (Lawrence *et al.* 2012) where they formed *Embellisia* group IV. A sexual morph is known for the type species of this section.

***Alternaria anigozanthi*** Priest, Australas. Pl. Pathol. 24: 239. 1995.
***Alternaria cumini*** E.G. Simmons, CBS Biodiversity Ser. (Utrecht) 6: 664. 2007.
***Alternaria eureka*** E.G. Simmons, Mycotaxon 25: 306. 1986.
≡ *Embellisia eureka* (E.G. Simmons) E.G. Simmons, Mycotaxon 38: 260. 1990.
= *Lewia eureka* E.G. Simmons, Mycotaxon 25: 304. 1986.
≡ *Allewia eureka* (E.G. Simmons) E.G. Simmons, Mycotaxon 38: 264. 1990.
***Alternaria geniostomatis*** E.G. Simmons & C.F. Hill, CBS Biodiversity Ser. (Utrecht) 6: 412. 2007.
***Alternaria leptinellae*** (E.G. Simmons & C.F. Hill) Woudenb. & Crous, **comb. nov.** MycoBank MB803696.
*Basionym*: *Embellisia leptinellae* E.G. Simmons & C.F. Hill, Mycotaxon 38: 254. 1990.
***Alternaria triglochinicola*** Alcorn & S.M. Francis, Mycotaxon 46: 359. 1993.

## Section *Gypsophilae* D.P. Lawr., Gannibal, Peever & B.M. Pryor, Mycologia 105: 541. 2013. Fig 13

*Type species*: *Alternaria gypsophilae Neerg.*

*Diagnosis*: Section *Gypsophilae* contains simple, or occasionally branched, primary conidiophores, with one or a few conidiogenous loci. Conidia are ellipsoid to long ovoid, with multiple transverse and longitudinal septa, conspicuously constricted near some transverse septa, solitary or in short chains. Secondary conidiophores are formed apically with one or two conidiogenous loci or laterally with a single conidiogenous locus. Species from this section occur on *Caryophyllaceae.*

*Notes:* Section *Gypsophilae* was recently established by Lawrence et al. (2013) containing the four *Alternaria* species, *A. gypsophilae*, *A. nobilis*, *A. vaccariae* and *A. vaccariicola*. Our dataset adds four *Alternaria* species, *A. axiaeriisporifera*, *A. ellipsoidea*, *A. saponariae*, and *A. juxtiseptata* to this section. Simmons (2007) noted the similarity of the primary conidia of *A. ellipsoidea* to *A. gypsophilae*, *A. nobilis*, *A. saponariae* and *A. vaccariae*. This section contains all *Alternaria* species that occur on *Caryophyllaceae* (Simmons 2002), except *A. dianthicola* which resides in sect. *Dianthicola*.

***Alternaria axiaeriisporifera*** E.G. Simmons & C.F. Hill, CBS Biodiversity Ser. (Utrecht) 6: 662. 2007.
***Alternaria ellipsoidea*** E.G. Simmons, Mycotaxon 82: 31. 2002.
***Alternaria gypsophilae*** Neerg., Danish species of *Alternaria* & *Stemphylium*: 207. 1945.
***Alternaria juxtiseptata*** E.G. Simmons, Mycotaxon 82: 32. 2002.
***Alternaria nobilis*** (Vize) E.G. Simmons, Mycotaxon 82: 7. 2002.
*Basionym*: *Macrosporium nobile* Vize, Grevillea 5(35): 119. 1877.
***Alternaria saponariae*** (Peck) Neerg., Annual Rep. Phytopathol. Lab. J.E. Ohlsens Enkes, Seed Growers, Copenhagen 3: 6. 1938 [1937–1938].
*Basionym*: *Macrosporium saponariae* Peck, Rep. (Annual) NewYork State Mus. Nat. Hist. 28: 62. 1876 [1875].


**Fig. 12.** *Alternaria* sect. *Eureka*: conidia and conidiophores. A–B. *A. anigozanthi*. C–D. *A. cumini*. E–F. *A. leptinellae*. G–H. *A. triglochinicola*. I–J. *A. geniostomatis*. K–L. *A. eureka*. Scale bars = 10 µm.

***Alternaria vaccariae*** (Săvul. & Sandu) E.G. Simmons & S.T. Koike, Mycotaxon 82: 21. 2002.
*Basionym*: *Macrosporium vaccariae* Săvul. & Sandu, Hedwigia 73: 130. 1933.
***Alternaria vaccariicola*** E.G. Simmons, CBS Biodiversity Ser. (Utrecht) 6: 594. 2007.

## Section *Infectoriae* Woudenb. & Crous, sect. nov. MycoBank MB803740. Fig. 14.

*Type species*: *Alternaria infectoria* E.G. Simmons

*Diagnosis*: Section *Infectoriae* contains short to long, simple or branched primary conidiophores with one or several conidiogenous loci. Conidia are obclavate, long-ellipsoid, small or moderate in size, septate, slightly constricted near some septa, with few longitudinal septa, in moderately long to long, branched chains. Long, geniculate, multi-locus secondary conidiophores can be formed apically or laterally. Sexual morphs are known, and meristematic growth has been reported.

*Notes*: In addition to the six species that are displayed in our phylogeny, 19 more are included based on the study of Lawrence *et al.* (2013), confirmed with our molecular data (not shown). From these 25 species, nine species have a known sexual morph in *Lewia*. Three species from the study of Lawrence *et al.* (2013) are not included; *A. photistica* (sect. *Panax*) and *A. dianthicola* (sect. *Dianthicola*) cluster elsewhere in our phylogenies and *A. peglionii* is marked as a taxon *incertae sedis* by Simmons (2007). The human pathogenic genera *Ybotromyces* and *Chmelia* are also embedded in sect. *Infectoriae*.

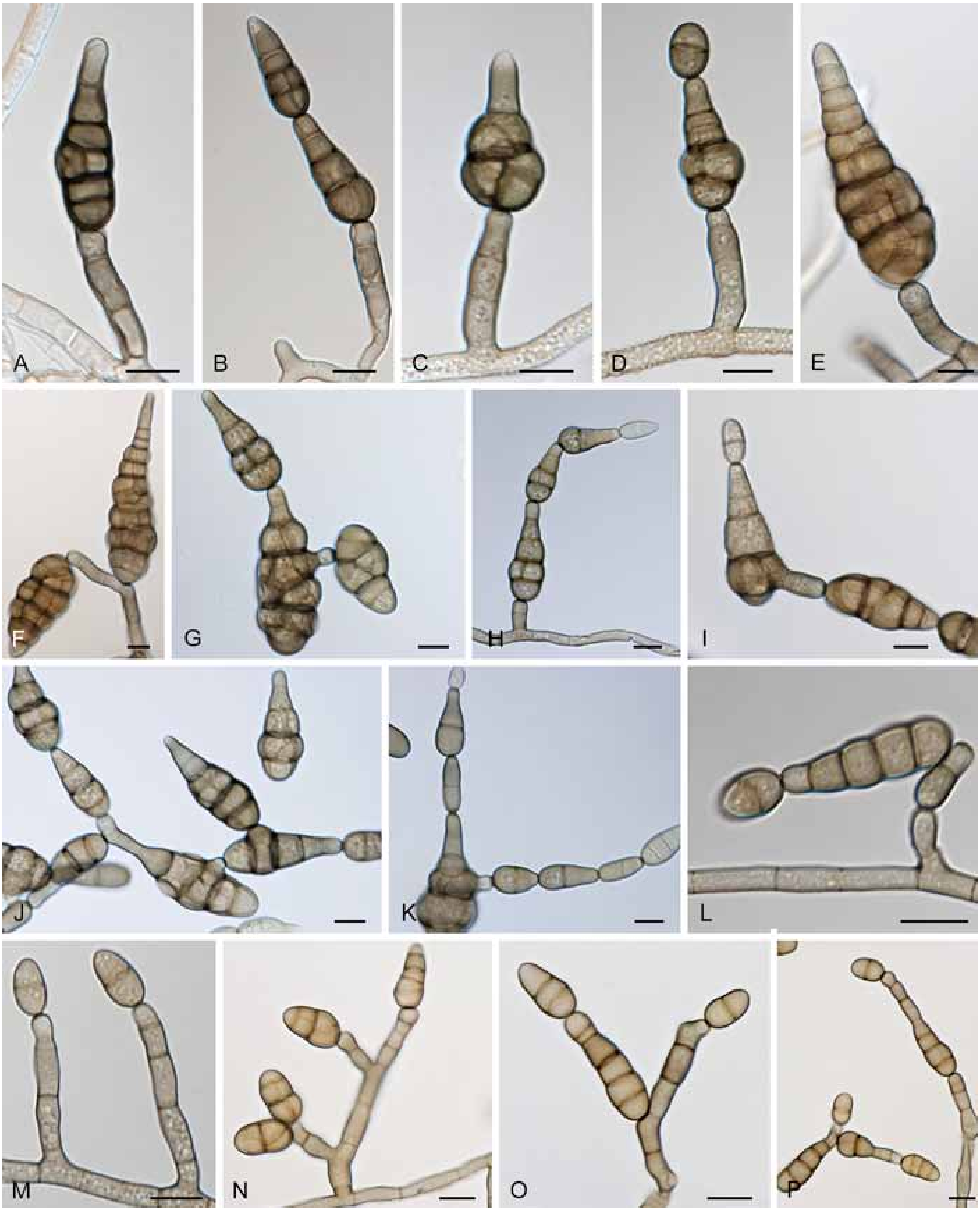


**Fig. 13.** *Alternaria* sect. *Gypsophilae*: conidia and conidiophores. A–B. *A. axiariisporifera*. C–D. *A. ellipsoidea*. E–G. *A. saponariae*. H–I. *A. vaccariae*. J–K. *A. nobilis*. L–M. *A. juxtiseptata*. N–P. *A. vaccariicola*. Scale bars = 10 µm.

***Alternaria alternarina*** E.G. Simmons, CBS Biodiversity Ser. (Utrecht) 6: 644. 2007.

= *Pyrenophora alternarina* M.D. Whitehead & J. Dicks., Mycologia 44: 748. 1952.

≡ *Lewia alternarina* (M.D. Whitehead & J.G. Dicks.) E.G. Simmons, CBS Biodiversity Ser. (Utrecht) 6: 644. 2007.

***Alternaria arbusti*** E.G. Simmons, Mycotaxon 48: 103. 1993.

***Alternaria caespitosa*** (de Hoog & C. Rubio) Woudenb. & Crous, **comb. nov.** MycoBank MB803698.

*Basionym*: *Botryomyces caespitosus* de Hoog & C. Rubio, Mycotaxon 14: 19. 1982.

≡ *Ybotromyces caespitosus* (de Hoog & C. Rubio) Rulamort, Bull. Soc. Bot. Centre-Ouest, Nouv. Sér. 21: 512. 1990.

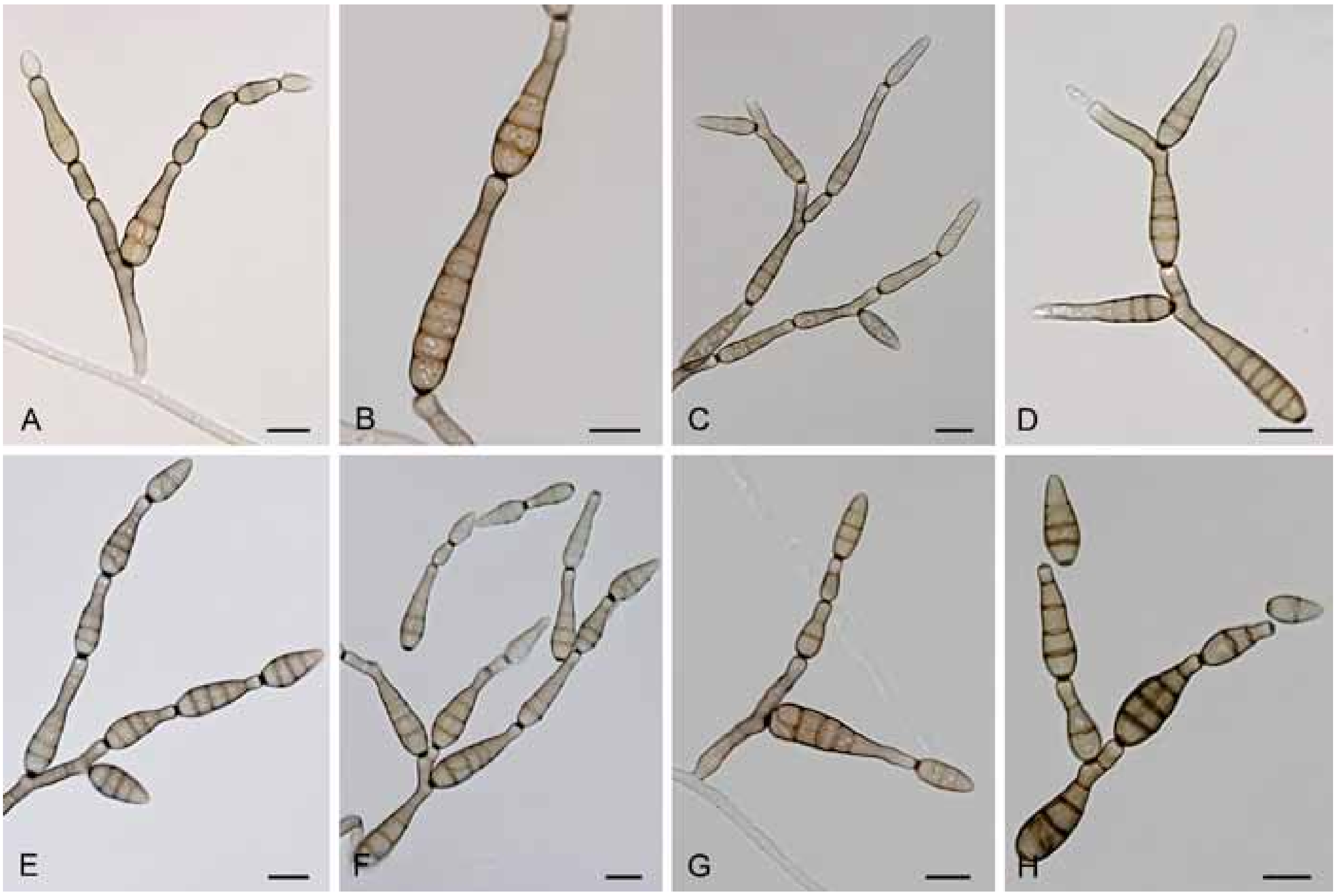


**Fig. 14.** *Alternaria* sect. *Infectoriae*: conidia and conidiophores. A–B. *A. ethzedia*. C–D. *A. infectoria*. E–F. *A. conjuncta*. G–H. *A. oregonensis*. Scale bars = 10 µm.

***Alternaria californica*** E.G. Simmons & S.T. Koike, CBS Biodiversity Ser. (Utrecht) 6: 602. 2007.

***Alternaria conjuncta*** E.G. Simmons, Mycotaxon 25: 294. 1986.

= *Sphaeria scrophulariae* Desm., Ann. Sci. Nat., Bot., Sér. 2, 6: 245. 1836.

≡ *Leptosphaeria scrophulariae* (Desm.) Sacc., Syll. Fungorum (Abellini) 2: 57. 1883.

≡ *Heptameria scrophulariae* (Desm.) Cooke, Grevillea 18(no. 86): 31. 1889.

≡ *Pleospora scrophulariae* (Desm.) Höhn., Sitzungsber. Kaiserl. Akad. Wiss., Math.-Naturwiss. Cl., Abt. 1. 126(4–5): 374. 1917.

≡ *Lewia scrophulariae* (Desm.) M.E. Barr & E.G. Simmons, Mycotaxon 25: 294. 1986.

***Alternaria daucicaulis*** E.G. Simmons, CBS Biodiversity Ser. (Utrecht) 6: 640. 2007.

= *Lewia daucicaulis* E.G. Simmons, CBS Biodiversity Ser. (Utrecht) 6: 640. 2007.

***Alternaria ethzedia*** E.G. Simmons, Mycotaxon 25: 300. 1986.

= *Lewia ethzedia* E.G. Simmons, Mycotaxon 25: 299. 1986.

***Alternaria frumenti*** E.G. Simmons & C.F. Hill, CBS Biodiversity Ser. (Utrecht) 6: 620. 2007.

***Alternaria graminicola*** E.G. Simmons, CBS Biodiversity Ser. (Utrecht) 6: 626. 2007.

***Alternaria hordeiaustralica*** E.G. Simmons & Alcorn, CBS Biodiversity Ser. (Utrecht) 6: 614. 2007.

= *Lewia hordeiaustralica* E.G. Simmons & Alcorn, CBS Biodiversity Ser. (Utrecht) 6: 614. 2007.

***Alternaria hordeicola*** E.G. Simmons & Kosiak, CBS Biodiversity Ser. (Utrecht) 6: 630. 2007.

= *Lewia hordeicola* Kwaśna & Kosiak, Mycologia 98: 663. 2006.

***Alternaria humuli*** E.G. Simmons, Mycotaxon 83: 139. 2002.

***Alternaria incomplexa*** E.G. Simmons, Mycotaxon 57: 394. 1996.

***Alternaria infectoria*** E.G. Simmons, Mycotaxon 25: 298. 1986.

= *Pleospora infectoria* Fuckel, Jahrb. Nassauischen Vereins Naturk. 23–24: 132. 1870 [1869–70].

≡ *Sphaeria infectoria* (Fuckel) Cooke, Handb. Brit. Fungi 2: 897. 1871.

≡ *Pleospora phaeocomoides* var. *infectoria* (Fuckel) Wehm., A World Monograph of the Genus *Pleospora* and its Segregates: 121. 1961.

≡ *Lewia infectoria* (Fuckel) M.E. Barr & E.G. Simmons, Mycotaxon 25: 296. 1986.

***Alternaria intercepta*** E.G. Simmons, Mycotaxon 83: 134. 2002.

= *Lewia intercepta* E.G. Simmons & McKemy, Mycotaxon 83: 133. 2002.

***Alternaria merytae*** E.G. Simmons, Mycotaxon 83: 136. 2002.

***Alternaria metachromatica*** E.G. Simmons, Mycotaxon 50: 418. 1994.

***Alternaria novae-zelandiae*** E.G. Simmons, Mycotaxon 83: 142. 2002.

***Alternaria oregonensis*** E.G. Simmons, Mycotaxon 50: 417. 1994.

***Alternaria slovaca*** (Svob.-Pol., L. Chmel & Bojan.) Woudenb. & Crous, **comb. nov.** MycoBank MB803699.

*Basionym*: *Aureobasidium slovacum* Svob.-Pol., L. Chmel & Bojan., Conspect. Verruc. 5: 116. 1966.

≡ *Chmelia slovaca* (Svob.-Pol., L. Chmel & Bojan.) Svob.-Pol., Biologia (Bratislava) 21: 83. 1966.

***Alternaria triticimaculans*** E.G. Simmons & Perelló, Mycotaxon 50: 413. 1994.

***Alternaria triticina*** Prasada & Prabhu, Indian Phytopathol. 15 (3–4): 292. 1963. [1962]

***Alternaria ventricosa*** R.G. Roberts, Mycotaxon 100: 164. 2007.

***Alternaria viburni*** E.G. Simmons, Mycotaxon 83: 132. 2002.

= *Lewia viburni* E.G. Simmons & McKemy, Mycotaxon 83: 130. 2002.

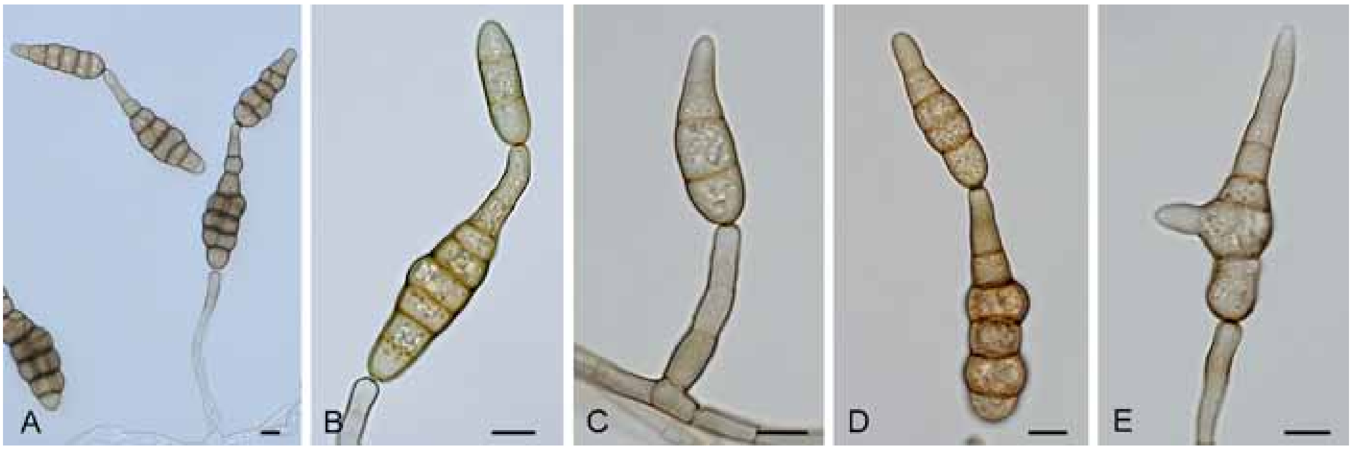


**Fig. 15.** *Alternaria* sect. *Japonicae*: conidia and conidiophores. A–B. *A. japonica*. C–E. *A. nepalensis*. Scale bars = 10 µm.

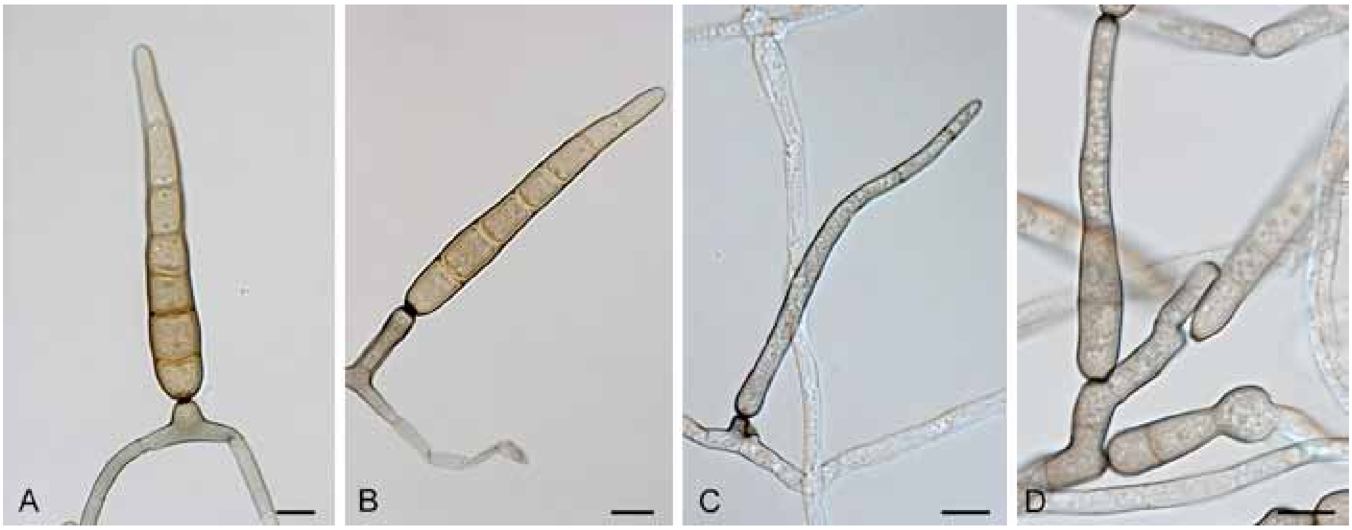


**Fig. 16.** *Alternaria* sect. *Nimbya*: conidia and conidiophores. A–B. *A. caricis*. C–D. *A. scirpicola*. Scale bars = 10 µm.

## Section *Japonicae* Woudenb. & Crous, sect. nov. MycoBank MB803741. Fig. 15.

*Type species*: *Alternaria japonica* Yoshii

*Diagnosis*: Section *Japonicae* contains short to long, simple or occasionally branched primary conidiophores with a single conidiogenous locus. Conidia are short, to long-ovoid with transverse and longitudinal septa, conspicuously constricted at most of the transverse septa, in short chains. Apical secondary conidiophores are produced with a single conidiogenous locus. The species within this section occur on *Brassicaceae.*

*Note*: *Alternaria japonica* was previously connected to the *A. brassicicola* species-group (Pryor & Gilbertson 2000, Pryor & Bigelow 2003, Lawrence *et al.* 2013), but this association was questioned by Hong *et al.* (2005).

***Alternaria japonica*** Yoshii, J. Pl. Protect. 28: 17. 1941.
= *Alternaria matthiolae* Neerg., Danish species of *Alternaria* and *Stemphylium*: 184. 1945.

***Alternaria nepalensis*** E.G. Simmons, CBS Biodiversity Ser. (Utrecht) 6: 480. 2007.

## Section *Nimbya* (E.G. Simmons) Woudenb. & Crous, comb. et stat. nov. MycoBank MB803742. Fig. 16.

*Basionym*: *Nimbya* E.G. Simmons, Sydowia 41: 316. 1989.

*Type species*: *Alternaria scirpicola* (Fuckel) Sivan.

*Diagnosis*: Section *Nimbya* contains simple, short to moderately long conidiophores, which may form one or a few short to long, geniculate, sympodial proliferations. Conidia are narrowly elongate-obclavate, gradually tapering apically, solitary or in short chains, with transverse disto- and eusepta, sometimes slightly constricted near eusepta. Apical condiophores with a single conidiogenous locus can be formed. Internal compartmentation occurs, cell lumina tend to be broadly octagonal to rounded. A sexual morph may occur.

*Notes*: Section *Nimbya* contains the type species of *Nimbya*, *N. scirpicola*, and *N. caricis* (Simmons 1989). A more extensive study on *Nimbya* (Lawrence *et al.* 2012) found that *N. scirpinfestans* and *N. scirpivora* also belonged to this section based on sequences of the GAPDH, ITS and Alt a 1 genes.

***Alternaria caricis*** (E.G. Simmons) Woudenb. & Crous, **comb. nov.** MycoBank MB803700.
*Basionym*: *Nimbya caricis* E.G. Simmons, Sydowia 41: 328. 1989.

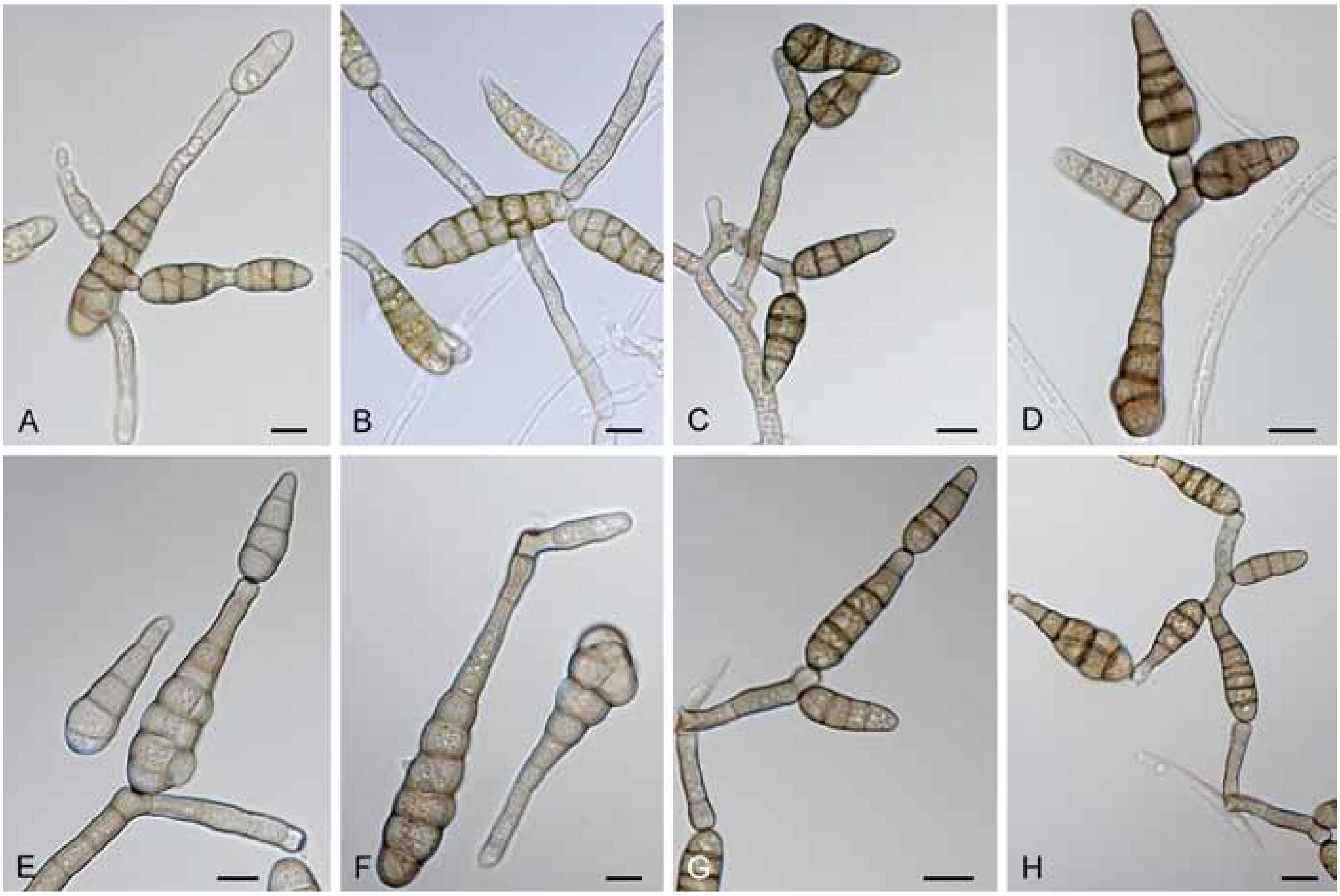


**Fig. 17.** *Alternaria* sect. *Panax*: conidia and conidiophores. A–B. *A. avenicola*. C–D. *A. calycipyricola*. E–F. *A. panax*. G–H. *A. photistica*. Scale bars = 10 µm.

***Alternaria scirpicola*** (Fuckel) Sivan., Bitunicate Ascomycetes and their Anamorphs (Vaduz): 526. 1984.
*Basionym*: *Sporidesmium scirpicola* Fuckel, Jahrb. Nassauischen Vereins Naturk. 23–24: 140. 1870 [1869–70].

≡ *Clasterosporium scirpicola* (Fuckel) Sacc., Syll. Fungorum (Abellini) 4: 393. 1886.
≡ *Cercospora scirpicola* (Fuckel) Zind.-Bakker, Rev. Mycol. (Paris) 5: 66. 1940.
≡ *Alternaria scirpicola* (Fuckel) M.T. Lucas & J. Webster, Čas. Slez. Mus., Ser. A, Hist. Nat. 23: 151. 1974 (nom. inval.).
≡ *Nimbya scirpicola* (Fuckel) E.G. Simmons, Sydowia 41: 316. 1989.
= *Sphaeria scirpicola* DC., in Lamarck & de Candolle, Fl. Franç., Edn 3 (Paris) 2: 300. 1805.
≡ *Clathrospora scirpicola* (DC.) Höhn., Ann. Mycol. 18(1/3): 77. 1920.
≡ *Macrospora scirpicola* (DC.) Fuckel, Jahrb. Nassauischen Vereins Naturk. 23–24: 139. 1870 [1869–70].
≡ *Pyrenophora scirpicola* (DC.) E. Müll., Sydowia 5(3–6): 256. 1951.

*Note*: Although *Sphaeria scirpicola* DC. (de Candolle 1805) predates *Sporidesmium scirpicola* Fuckel (Fuckel 1870), a valid combination in *Alternaria* already exists, thus we choose to retain *Alternaria scirpicola* (Fuckel) Sivan., which is also a well established name.

***Alternaria scirpinfestans*** (E.G. Simmons & D.A. Johnson) Woudenb. & Crous, **comb. nov.** MycoBank MB803701.
*Basionym*: *Nimbya scirpinfestans* E.G. Simmons & D.A. Johnson, Mycotaxon 84: 420. 2002.

= *Macrospora scirpinfestans* E.G. Simmons & D.A. Johnson, Mycotaxon 84: 417. 2002.

***Alternaria scirpivora*** (E.G. Simmons & D.A. Johnson), Woudenb. & Crous, **comb. nov.** MycoBank MB803702.
*Basionym*: *Nimbya scirpivora* E.G. Simmons & D.A. Johnson, Mycotaxon 84: 424. 2002.

= *Macrospora scirpivora* E.G. Simmons & D.A. Johnson, Mycotaxon 84: 422. 2002.

## Section *Panax* D.P. Lawr., Gannibal, Peever & B.M. Pryor, Mycologia 105: 541. 2013. Fig. 17.

*Type species*: *Alternaria panax* Whetzel

*Diagnosis*: Section *Panax* contains simple or branched, short to moderately long primary conidiophores, with one or a few conidiogenous loci. Conidia are obclavate to ovoid, with multiple transverse and longitudinal septa, conspicuously constricted near several transverse septa, solitary or in simple or branched, short chains. Apical secondary conidiophores are formed with one or several conidiogenous loci, multiple lateral secondary conidiophores with a single conidiogenous locus may occur.

*Notes*: Section *Panax* was recently described by Lawrence *et al.* (2013) and consists of *A. calycipyricola*, *A. eryngii* and *A. panax*. Our extended dataset added the species *A. avenicola* and *A. photistica* to this section. Three species, *A. avenicola, A. calycipyricola*, and *A. photistica* have earlier been placed in the *A. infectoria* species-group based on their morphological characters (Simmons 2007), and two of them have a known sexual morph; *Lewia avenicola* (Simmons 2007) and *Lewia photistica* (Simmons 1986). A phylogenetic study based on Alt a 1 and GAPDH sequences placed *A. photistica* in the *A. infectoria* species-group (Hong *et al.* 2005) but an extensive study on the *A. infectoria* species-group (Andersen *et al*. 2009) confirmed our finding, and placed this species outside the *A. infectoria* species-group. Additional research performed on multiple *A. photistica* strains support our sequence data (data not shown).

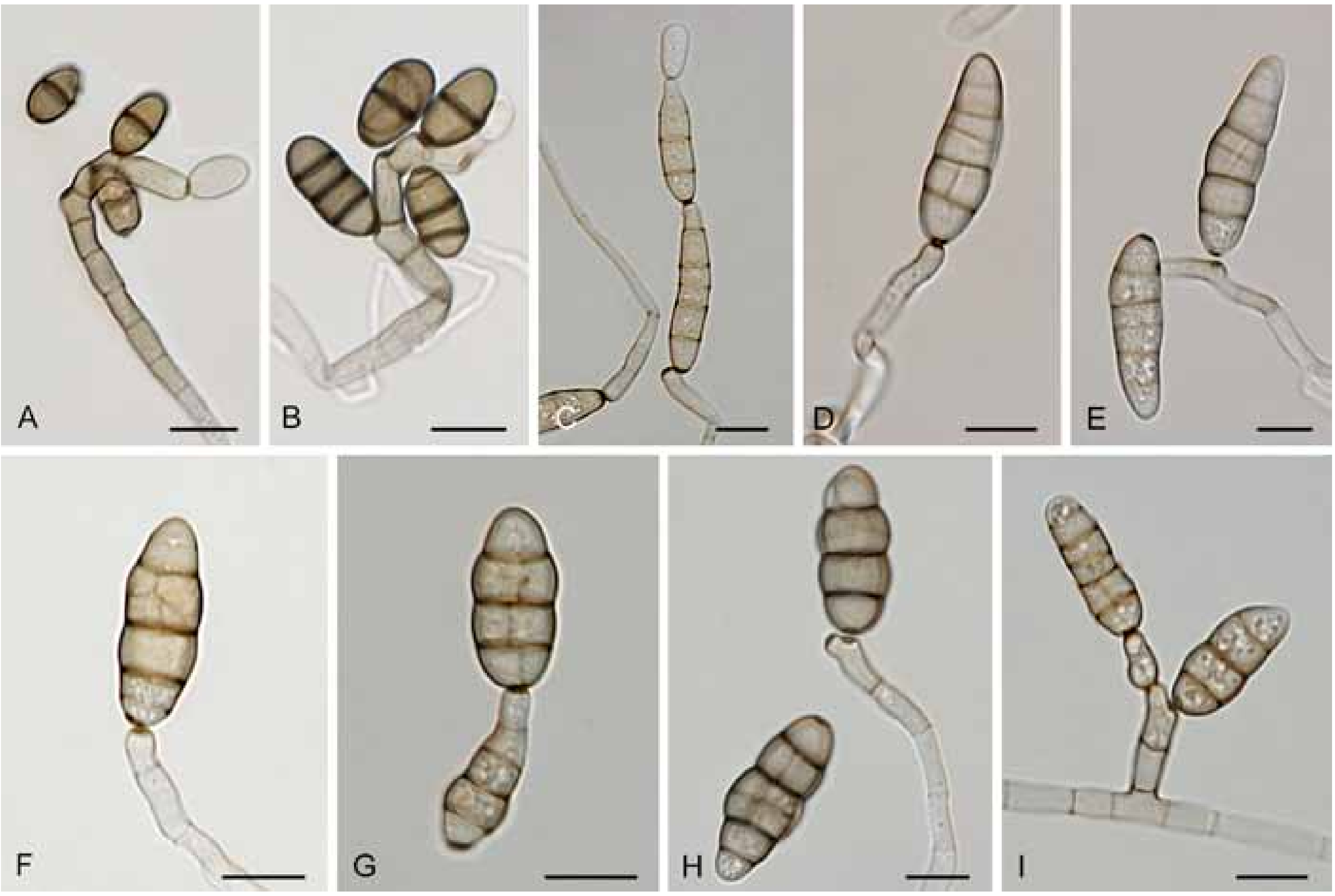


**Fig. 18.** *Alternaria* sect. *Phragmosporae*: conidia and conidiophores. A–B. *A. didymospora*. C. *A. phragmospora*. D–E. *A. limaciformis*. F–G. *A. molesta*. H–I. *A. mouchaccae*. Scale bars = 10 µm.

***Alternaria avenicola*** E.G. Simmons, Kosiak & Kwaśna, in Simmons, CBS Biodiversity Ser. (Utrecht) 6: 114. 2007.

= *Lewia avenicola* Kosiak & Kwaśna, Mycol. Res. 107: 371. 2003.

***Alternaria calycipyricola*** R.G. Roberts, Mycotaxon 100: 162. 2007.

***Alternaria eryngii*** (Pers.) S. Hughes & E.G. Simmons, Canad. J. Bot. 36: 735. 1958.

*Basionym*: *Conoplea eryngii* Pers., Mycol. Eur. (Erlanga) 1: 11. 1822.

≡ *Exosporium eryngianum* (Pers.) Chevall., Flore Générale des Environs de Paris 1: 39. 1826.

≡ *Exosporium eryngii* (Pers.) Duby, Bot. Gallicum., Edn 2 (Paris) 2: 882. 1830.

≡ *Helminthosporium eryngii* (Pers.) Fr., Syst. Mycol. (Lundae) 3: 361. 1832.

***Alternaria panax*** Whetzel, Bull. U.S.D.A. 250: 11. 1912.

= *Macrosporium araliae* Dearn. & House, Circ. New York State Mus. 24: 58. 1940.

= *Alternaria araliae* H.C. Greene, Trans. Wisconsin Acad. Sci. 42: 80. 1953.

***Alternaria photistica*** E.G. Simmons, Mycotaxon 25: 304. 1986.

= *Lewia photistica* E.G. Simmons, Mycotaxon 25: 302. 1986.

## Section *Phragmosporae* Woudenb. & Crous, **sect. nov.** MycoBank MB803743. Fig. 18.

*Type species*: *Alternaria phragmospora* Emden

*Diagnosis*: Section *Phragmosporae* contains simple, short to moderately long, primary conidiophores, with one or multiple geniculate, sympodial proliferations. Conidia are (broad) ovoid to long ovoid, ellipsoid, curved, or limaciform, with multiple transverse and few to multiple longitudinal septa, some septa darkened, slightly to conspicuously constricted near several transverse septa, solitary or in simple short chains. Apical secondary conidiophores are formed with one or several conidiogenous loci. All species within the section are known from soil and seawater environments.

*Note*: Section *Phragmosporae* contains six species of which two were linked to *Embellisia.*

***Alternaria chlamydospora*** Mouch. [as "*chlamydosporum*"], Mycopathol. Mycol. Appl. 50: 217. 1973.

***Alternaria didymospora*** (Munt.-Cvetk.) Woudenb. & Crous, **comb. nov.** MycoBank MB803709.

*Basionym*: *Embellisia didymospora* Munt.-Cvetk., Mycologia 68: 49. 1976.

***Alternaria limaciformis*** E.G. Simmons, Mycotaxon 13: 24. 1981.

***Alternaria molesta*** E.G. Simmons, Mycotaxon 13: 17. 1981.

***Alternaria mouchaccae*** E.G. Simmons, Mycotaxon 13: 18. 1981.

≡ *Ulocladium chlamydosporum* Mouch., Rev. Mycol. (Paris) 36: 114. 1971, non *Alternaria chlamydospora* Mouch., 1973.

***Alternaria phragmospora*** Emden, Acta Bot. Neerl. 19: 393. 1970.

≡ *Embellisia phragmospora* (Emden) E.G. Simmons, Mycotaxon 17: 232. 1983.

## Section *Porri* D.P. Lawr., Gannibal, Peever & B.M. Pryor, Mycologia 105: 541. 2013. Fig 19

*Type species*: *Alternaria porri* (Ellis) Cif.


**Fig. 19.** *Alternaria* sect. *Porri*: conidia and conidiophores. A–C. *A. daucii*. D–F. *A. pseudorostrata*. G–H. *A. solani*. Scale bars = 10 µm.

*Diagnosis*: Section *Porri* is characterised by broadly ovoid, obclavate, ellipsoid, subcylindrical or obovoid (medium) large conidia, disto- and euseptate, solitary or in short to moderately long chains, with a simple or branched, long to filamentous beak. Conidia contain multiple transverse and longitudinal septa and are slightly constricted near some transverse septa. Secondary conidiophores can be formed apically or laterally.

*Notes*: In addition to the six species that are displayed in our phylogeny, 40 more are included based on the study of Lawrence *et al.* (2013), confirmed with own molecular data (not shown). With almost 80 species section *Porri* is the largest *Alternaria* section (data not shown). The section displays a higher level of genetic variation than the second largest section; section *Alternata*.

***Alternaria acalyphicola*** E.G. Simmons, Mycotaxon 50: 260. 1994.

***Alternaria agerati*** Sawada ex E.G. Simmons, Mycotaxon 65: 63. 1997.

= *Alternaria agerati* Sawada, Rep. Dept. Agric. Gov. Res. Inst. Formosa 86: 165. 1943. (nom. inval., Art. 36.1)

***Alternaria agripestis*** E.G. Simmons & K. Mort., Mycotaxon 50: 255. 1994.

***Alternaria anagallidis*** A. Raabe, Hedwigia 78: 87. 1939.

***Alternaria aragakii*** E.G. Simmons, Mycotaxon 46: 181. 1993.

***Alternaria argyroxiphii*** E.G. Simmons & Aragaki, Mycotaxon 65: 40. 1997.

***Alternaria bataticola*** Ikata ex W. Yamam., Trans. Mycol. Soc. Japan 2(5): 89. 1960.

= *Macrosporium bataticola* Ikata, Agric. Hort. (Tokyo) 22: 241. 1947 (nom. inval., Art. 36.1).

***Alternaria blumeae*** E.G. Simmons & Sontirat, Mycotaxon 65: 81. 1997.

***Alternaria calendulae*** Ondřej, Čas. Slez. Mus. v Opavě, Ser. A, Hist. Nat. 23(2): 150. 1974.

= *Alternaria calendulae* W. Yamam. 1939 (nom. nud.).

= *Macrosporium calendulae* Nelen, Bull. Centr. Bot. Gard. (Moscow) 35: 90. 1959 (nom. inval., Art. 36.1).

= *Macrosporium calendulae* Nelen, Bot. Mater. Otd. Sporov. Rast. Bot. Inst. Akad. Nauk S.S.S.R. 15: 144. 1962.

= *Alternaria calendulae* Nirenberg, Phytopathol. Z. 88(2): 108. 1977 (nom. illegit., Art. 53.1).

***Alternaria capsici*** E.G. Simmons, Mycotaxon 75: 84. 2000.

***Alternaria carthami*** S. Chowdhury, J. Indian Bot. Soc. 23: 65. 1944.

= *Macrosporium anatolicum* A. Săvul., Bull. Sect. Sci. Acad. Roumaine 26: 709. 1944.

***Alternaria cassiae*** Jurair & A. Khan, Pakistan J. Sci. Industr. Res. 3(1): 72. 1960.

***Alternaria cichorii*** Nattrass, First List of Cyprus Fungi: 29. 1937.

≡ *Alternaria porri* f.sp. *cichorii* (Natrass) T. Schmidt, Pflanzenschutz-berichte 32: 181. 1965.

≡ *Macrosporium cichorii* (Nattrass) Gordenko, Mikol. Fitopatol. 9(3): 241. 1975.

***Alternaria cirsinoxia*** E.G. Simmons & K. Mort., Mycotaxon 65: 72. 1997.

***Alternaria crassa*** (Sacc.) Rands, Phytopathology 7: 337. 1917.

*Basionym*: *Cercospora crassa* Sacc., Michelia 1(no. 1): 88. 1877.

***Alternaria cretica*** E.G. Simmons & Vakal., Mycotaxon 75: 64. 2000.

***Alternaria cucumerina*** (Ellis & Everh.) J.A. Elliott, Amer. J. Bot. 4: 472. 1917.

*Basionym*: *Macrosporium cucumerinum* Ellis & Everh., Proc. Acad. Nat. Sci. Philadelphia 47: 440. 1895.

**Alternaria cyphomandrae** E.G. Simmons, Mycotaxon 75: 86. 2000.
**Alternaria danida** E.G. Simmons, Mycotaxon 65: 78. 1997.
**Alternaria dauci** (J.G. Kühn) J.W. Groves & Skolko, Canad. J. Res., Sect. C, Bot. Sci. 22: 222. 1944.
*Basionym*: *Sporidesmium exitiosum* var. *dauci* J.G. Kühn, Hedwigia 1: 91. 1855.
Additional synonyms in Simmons 2007.
**Alternaria dichondrae** Gambogi, Vannacci & Triolo, Trans. Brit. Mycol. Soc. 65(2): 323. 1975.
**Alternaria euphorbiicola** E.G. Simmons & Engelhard, Mycotaxon 25: 196. 1986.
≡ *Macrosporium euphorbiae* Reichert, Bot. Jahrb. Syst. 56: 723. 1921. (nom. illegit., Art 53.1).
**Alternaria grandis** E.G. Simmons, Mycotaxon 75: 96. 2000.
**Alternaria hawaiiensis** E.G. Simmons, Mycotaxon 46: 184. 1993.
**Alternaria limicola** E.G. Simmons & M.E. Palm, Mycotaxon 37: 82. 1990.
**Alternaria linicola** J.W. Groves & Skolko, Canad. J. Res., Sect. C, Bot. Sci. 22: 223. 1944.
**Alternaria macrospora** Zimm., Ber. Land-Forstw. Deutsch-Ostafrika 2: 24. 1904.
≡ *Macrosporium macrosporum* (Zimm.) Nishikado & Oshima, Agric. Res. (Kurashiki) 36: 391. 1944.
= *Sporidesmium longipedicellatum* Reichert, Bot. Jahrb. Syst. 56: 723. 1921.
≡ *Alternaria longipedicellata* (Reichert) Snowden, Rep. Dept. Agric. Uganda: 31. 1927 [1926].
**Alternaria multirostrata** E.G. Simmons & C.R. Jacks., Phytopathology 58: 1139. 1968.
**Alternaria nitrimali** E.G. Simmons & M.E. Palm, Mycotaxon 75: 93. 2000.
**Alternaria passiflorae** J.H. Simmonds, Proc. Roy. Soc. Queensland. 49: 151. 1938.
**Alternaria poonensis** Ragunath, Mycopathol. Mycol. Appl. 21: 315. 1963.
**Alternaria porri** (Ellis) Cif., J. Dept. Agric. Porto Rico 14: 30. 1930 [1929].
*Basionym*: *Macrosporium porri* Ellis, Grevillea 8 (no. 45): 12. 1879.
**Alternaria protenta** E.G. Simmons, Mycotaxon 25: 207. 1986.
**Alternaria pseudorostrata** E.G. Simmons, Mycotaxon 57: 398. 1996.
**Alternaria ricini** (Yoshii) Hansf., Proc. Linn. Soc. Lond. : 53. 1943.
*Basionym*: *Macrosporium ricini* Yoshii, Bult. Sci. Fak. Terk. Kjusu Imp. Univ. 3(4): 327. 1929.
**Alternaria rostellata** E.G. Simmons, Mycotaxon 57: 401. 1996.
**Alternaria scorzonerae** (Aderh.) Loer., Netherlands J. Pl. Pathol. 90(1): 37. 1984.
*Basionym*: *Sporidesmium scorzonerae* Aderh.,Arbeiten Kaiserl. Biol. Anst. Land-Forstw . 3: 439. 1903.
**Alternaria sesami** (E. Kawam.) Mohanty & Behera, Curr. Sci. 27: 493. 1958.
*Basionym*: *Macrosporium sesami* E. Kawam., Fungi 1(2): 27. 1931.
**Alternaria solani** Sorauer, Z. Pflanzenkrankh. Pflanzenschutz 6: 6. 1896.
= *Macrosporium solani* Ellis & G. Martin, Amer. Naturalist 16(12): 1003. 1882
≡ *Alternaria solani* (Ellis & G. Martin) L.R. Jones & Grout, Vermont Agric. Exp. Sta. Annual Rep. 9: 86. 1896.
Additional synonyms in Simmons (2007).
**Alternaria solani-nigri** R. Dubey, S.K. Singh & Kamal [as "*solani-nigrii*"], Microbiol. Res. 154(2): 120. 1999.
**Alternaria steviae** Ishiba, T. Yokoy. & Tani, Ann. Phytopathol. Soc. Japan 48(1): 46. 1982.
**Alternaria subcylindrica** E.G. Simmons & R.G. Roberts, Mycotaxon 75: 62. 2000.
**Alternaria tagetica** S.K. Shome & Mustafee, Curr. Sci. 35: 370. 1966.
**Alternaria tomatophila** E.G. Simmons, Mycotaxon 75: 53. 2000.
**Alternaria tropica** E.G. Simmons, Mycotaxon 46: 187. 1993.
**Alternaria zinniae** H.Pape ex M.B. Ellis, Mycol. Pap. 131: 22. 1972.
= *Alternaria zinniae* H. Pape, Angew. Bot. 24: 61. 1942. (nom. inval., Art. 36.1)

## Section *Pseudoulocladium* Woudenb. & Crous, sect. nov. MycoBank MB803744. Fig. 20.

*Type species*: *Alternaria chartarum* Preuss

*Diagnosis*: Section *Pseudoulocladium* is characterised by simple or branched conidiophores with short, geniculate, sympodial proliferations. Conidia are obovoid, non-beaked with a narrow base, in simple or (mostly) branched chains. Apical secondary conidiophores with multiple conidiogenous loci and lateral secondary conidiophores with a single conidiogenous locus can be formed.

*Note*: It forms a sister clade to section *Ulocladioides.*

**Alternaria aspera** Woudenb. & Crous, **nom. nov.** MycoBank MB803712.
*Basionym*: *Ulocladium arborescens* E.G. Simmons, Stud. Mycol. 50: 117. 2004, non *Alternaria arborescens* E.G. Simmons, 1999.
*Etymology*: Name refers to the conspicuously ornamented conidia.
**Alternaria chartarum** Preuss, Bot. Zeitung 6: 412, 1848.
≡ *Sporidesmium polymorphum* var. *chartarum* (Preuss) Cooke, Fungi Brit. Exs., ser. 2: 329. 1875.
≡ *Ulocladium chartarum* (Preuss) E.G. Simmons, Mycologia 59: 88. 1967.
= *Alternaria stemphylioides* Bliss, Mycologia 36: 538. 1944.
≡ *Alternaria chartarum* f. *stemphylioides* (Bliss) P. Joly, Encycl. Mycol. (Paris) 33: 161. 1964.
**Alternaria concatenata** Woudenb. & Crous, **nom. nov.** MycoBank MB803713.
*Basionym*: *Ulocladium capsici* F. Xue & X.G. Zhang [as "*capsicuma*"], Sydowia 59: 174. 2007, non *Alternaria capsici* E.G. Simmons, 2000.
*Eymology*: Name refers to the concatenated conidia.
**Alternaria septospora** (Preuss) Woudenb. & Crous, **comb. nov.** MycoBank MB803714.
*Basionym*: *Helminthosporium septosporum* Preuss, Linnaea 24: 117. 1851.
≡ *Macrosporium septosporum* (Preuss) Rabenh., Bot. Zeitung 9: 454. 1851.
≡ *Ulocladium septosporum* (Preuss) E.G. Simmons, Mycologia 59: 87. 1967.

## Section *Radicina* D.P. Lawr., Gannibal, Peever & B.M. Pryor, Mycologia 105: 541. 2013. Fig. 21.

*Type species*: *Alternaria radicina* Meier, Drechsler & E.D. Eddy

*Diagnosis*: Section *Radicina* contains straight, simple or branched, short or long, primary conidiophores with multiple, short geniculate, sympodial proliferations with single or a few conidiogenous loci at the apex. Sporulation resembles a cluster or clumps of conidia. Conidia are widely ovoid to narrowly


**Fig. 20.** *Alternaria* sect. *Pseudoulocladium*: conidia and conidiophores. A–B. *A. aspera*. C–D. *A. concatenata*. E–F. *A. chartarum*. G–H. *A. septospora*. Scale bars = 10 µm.

ellipsoid, moderate in size, beakless, with several transverse and longitudinal septa, solitary or in short chains. Solitary, short, apical secondary conidiophores may occur. The species from this section occur on *Umbelliferae*.

*Note*: This section was first recognised by Pryor & Gilbertson (2000) based on sequence data of the ITS and mitochondrial SSU.

***Alternaria carotiincultae*** E.G. Simmons, Mycotaxon 55: 103. 1995.
***Alternaria petroselini*** (Neerg.) E.G. Simmons, More dematiaceous hyphomycetes (Kew): 417. 1976.
*Basionym*: *Stemphylium petroselini* Neerg., Zentralbl. Bakteriol., 2. Abt., 104: 411. 1942.

≡ *Stemphylium radicinum* var. *petroselini* (Neerg.) Neerg., Danish species of *Alternaria* & *Stemphylium*: 357. 1945.

≡ *Alternaria radicina* var. *petroselini* (Neerg.) Neerg., Encycl. Mycol. 33: 123. 1964.

***Alternaria radicina*** Meier, Drechsler & E.D. Eddy, Phytopathology 12: 157. 1922.

≡ *Stemphylium radicinum* (Meier, Drechsler & E.D. Eddy) Neerg., Annual Rep. Phytopathol. Lab. J.E. Ohlsens Enkes, Seed Growers, Copenhagen 4: 14. 1939.

≡ *Thyrospora radicina* (Meier, Drechsler & E.D. Eddy) Neerg., Bot. Tidsskr. 44: 361. 1939.

≡ *Pseudostemphylium radicinum* (Meier, Drechsler & E.D. Eddy) Subram., Curr. Sci. 30: 423. 1961.

***Alternaria selini*** E.G. Simmons, Mycotaxon 55: 109. 1995.
***Alternaria smyrnii*** (P. Crouan & H. Crouan) E.G. Simmons, Mycotaxon 55: 41. 1995.
*Basionym*: *Helminthosporium smyrnii* P. Crouan & H. Crouan, Florule Finistère (Paris): 11. 1867.

≡ *Macrosporium smyrnii* (P. Crouan & H. Crouan) Sacc., Syll. Fungorum (Abellini) 4: 527. 1886.

## Section *Sonchi* D.P. Lawr., Gannibal, Peever & B.M. Pryor, Mycologia 105: 542. 2013. Fig. 22.

*Type species*: *Alternaria sonchi* Davis

*Diagnosis*: Section *Sonchi* is characterised by subcylindrical, broadly ovoid, broadly ellipsoid or obclavate, (medium) large conidia, single or in short chains, with multiple transverse and few longitudinal septa, slightly constricted at the septa, with a blunt taper which can form secondary conidiophores.

*Notes*: The species-group was described by Hong *et al.* (2005) based on molecular data of the GAPDH and Alt a 1 regions. Lawrence *et al.* (2013) included *A. brassicae* as a basal lineage in sect. *Sonchi*, which is supported as a monotypic lineage in our analyses. The species from section *Sonchi* occur on multiple hosts within the *Compositae*.

***Alternaria cinerariae*** Hori & Enjoji, J. Pl. Protect. 18: 432. 1931.
***Alternaria sonchi*** Davis, in Elliott, Bot. Gaz. 62: 416. 1916.

## Section *Teretispora* (E.G. Simmons) Woudenb. & Crous, **comb. et stat. nov.** MycoBank MB803745. Fig. 23.

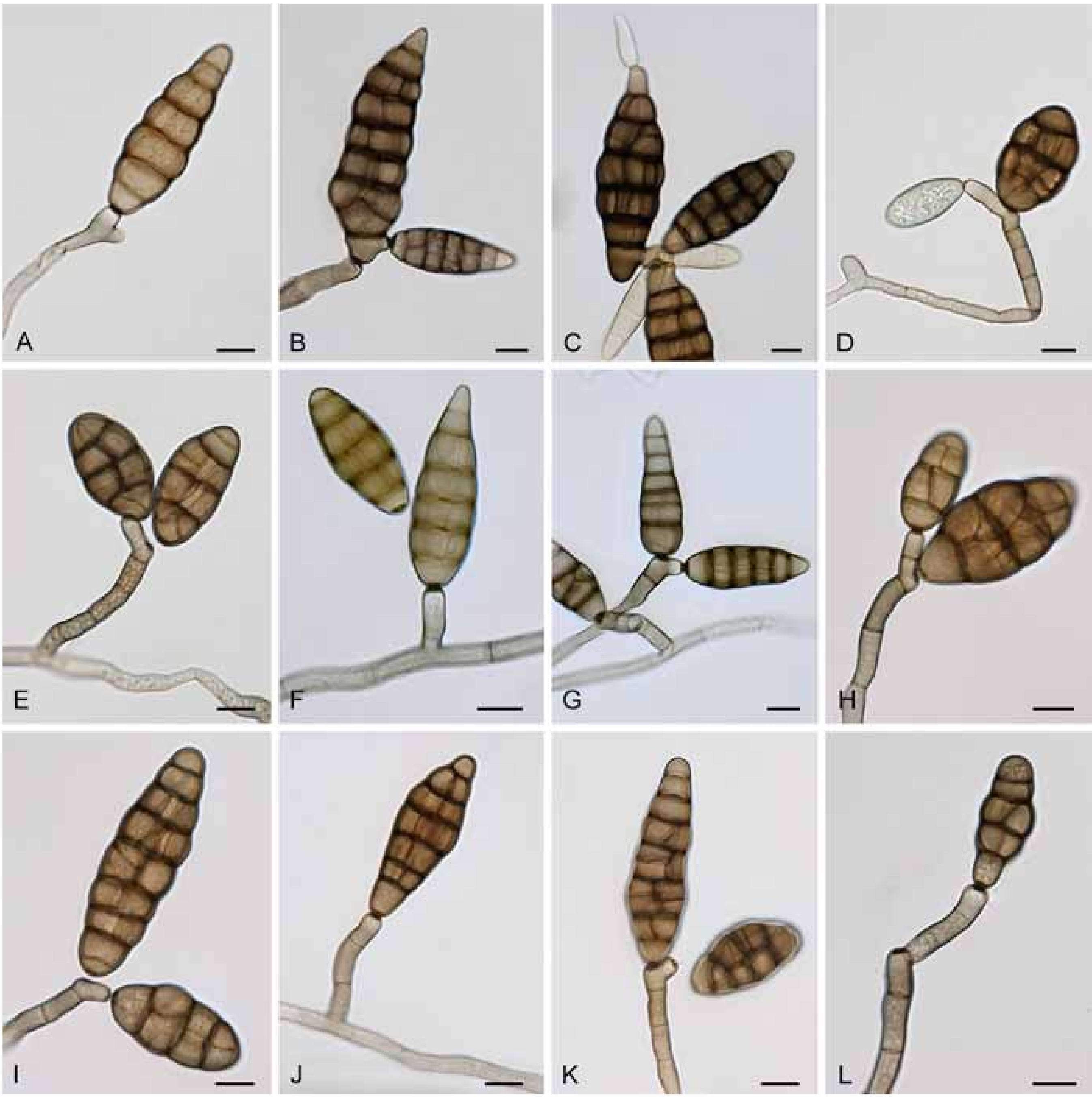


**Fig. 21.** *Alternaria* sect. *Radicina*: conidia and conidiophores. A–C. *A. carotiincultae*. D–E. *A. petroselini*. F–G. *A. radicina*. H–I. *A. selini*. J–L. *A. smyrnii*. Scale bars = 10 µm.

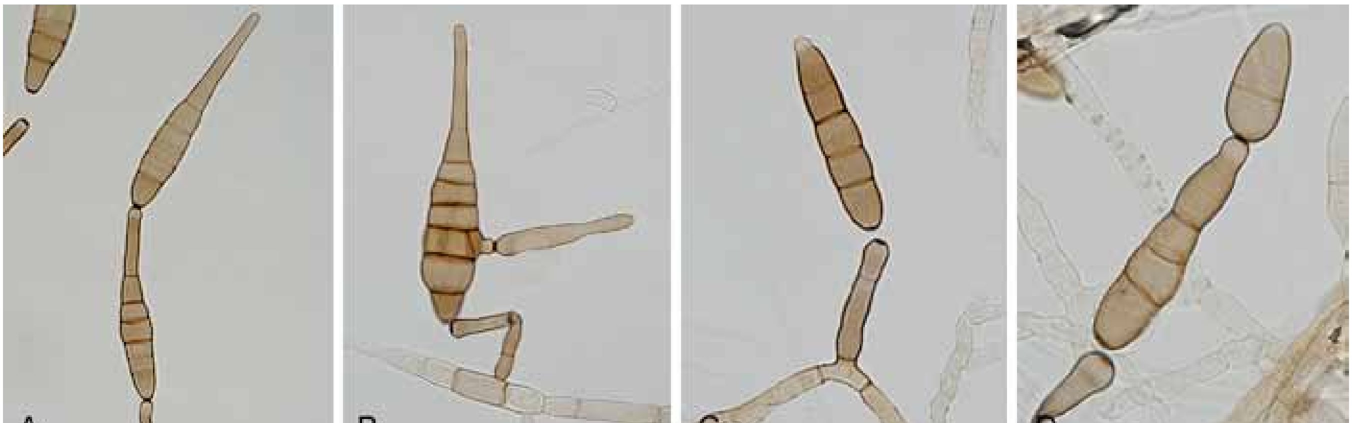


**Fig. 22.** *Alternaria* sect. *Sonchi*: conidia and conidiophores. A–B. *A. cinerariae*. C–D. *A. sonchi*. Scale bars = 10 µm.

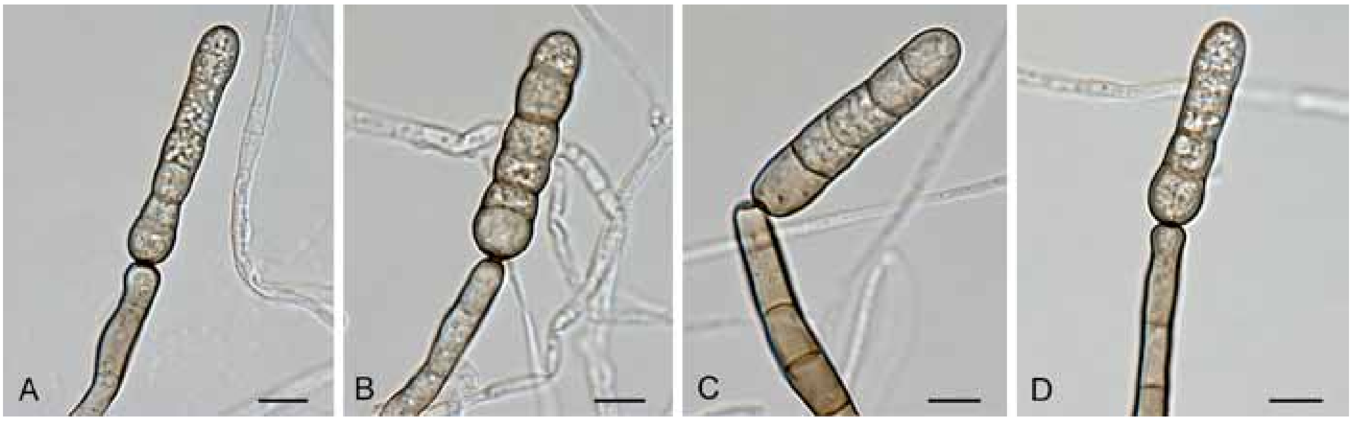


**Fig. 23.** *Alternaria* sect. *Teretispora*: conidia and conidiophores. A–D. *A. leucanthemi*. Scale bars = 10 µm.

*Basionym*: *Teretispora* E.G. Simmons, CBS Biodiversity Ser. (Utrecht) 6: 674. 2007.

*Type species*: *Alternaria leucanthemi* Nelen

*Diagnosis*: Section *Teretispora* is characterised by simple conidiophores, sometimes extending at the apex with one or two, geniculate, sympodial proliferations, bearing single, long cylindrical mature conidia lacking a beak portion, with many transverse and a few longitudinal septa, constricted at most of the transverse septa. Secondary conidiophores with a single conidium are rarely formed at the apex; instead, they may form from the base of the primary conidium.

*Notes*: The genus *Teretispora* had *Teretispora leucanthemi,* formerly *Alternaria leucanthemi* (= *Alternaria chrysanthemi*)*,* as type and only species (Simmons 2007). We choose to treat this as a section, which retains the name *Teretispora*, rather than a monotypic lineage.

***Alternaria leucanthemi*** Nelen, in Nelen & Vasiljeva, Bot. Mater. Otd. Sporov. Rast. Bot. Inst. Akad. Nauk S.S.S.R. 15: 148. 1962.

≡ *Teretispora leucanthemi* (Nelen) E.G. Simmons, CBS Biodiversity Ser. (Utrecht) 6: 674. 2007.

= *Alternaria leucanthemi* Nelen, Bull. Centr. Bot. Gard. (Moscow) 35: 83. 1959. (nom. inval., Art. 36.1)

= *Alternaria chrysanthemi* E.G. Simmons & Crosier, Mycologia 57: 142. 1965.

## Section *Ulocladioides* Woudenb. & Crous, **sect. nov.** MycoBank MB803746. Fig. 24.

*Type species*: *Alternaria cucurbitae* Letendre & Roum.

*Diagnosis*: Section *Ulocladioides* is characterised by conidiophores with short, geniculate, sympodial proliferations. Conidia are obovoid, non-beaked with a narrow base, single or in chains, which may form secondary conidiophores at the apex.

*Note*: Section *Ulocladioides* resembles section *Ulocladium* and contains the majority of the species included in this study from the genus *Ulocladium* (11/17).

***Alternaria atra*** (Preuss) Woudenb. & Crous, **comb. nov.** MycoBank MB803717.

*Basionym*: *Ulocladium atrum* Preuss, Linnaea 25: 75. 1852.

≡ *Stemphylium atrum* (Preuss) Sacc., Syll. Fungorum (Abellini) 4: 520. 1886.

***Alternaria brassicae-pekinensis*** Woudenb. & Crous, **nom. nov.** MycoBank MB803723.

*Basionym*: *Ulocladium brassicae* Yong Wang bis & X.G. Zhang, Mycologia 100: 457. 2008, non *Alternaria brassicae* (Berk.) Sacc., 1880.

*Etymology*: Name refers to the host from which it was originally isolated.

***Alternaria cantlous*** (Yong Wang bis & X.G. Zhang) Woudenb. & Crous, **comb. nov.** MycoBank MB803719.

*Basionym*: *Ulocladium cantlous* Yong Wang bis & X.G. Zhang, Mycologia 102: 376. 2010.

***Alternaria consortialis*** (Thüm.) J.W. Groves & S. Hughes [as "*consortiale*"], Canad. J. Bot. 31: 636. 1953.

*Basionym*: *Macrosporium consortiale* Thüm., Herb. Mycol. Oecon. 9: no. 450. 1876.

≡ *Stemphylium consortiale* (Thüm.) J.W. Groves & Skolko, Canad. J. Res., Sect. C, Bot. Sci.: 196. 1944.

≡ *Pseudostemphylium consortiale* (Thüm.) Subram., Curr. Sci. 30: 423. 1961.

≡ *Ulocladium consortiale (Thüm.)* E.G. Simmons, Mycologia 59: 84. 1967.

= *Stemphylium ilicis* Tengwall, Meded. Phytopathol. Lab. "Willie Commelin Scholten" 6: 44. 1924.

***Alternaria cucurbitae*** Letendre & Roum., in Roumeguère, Rev. Mycol. (Toulouse) 8 (no. 30): 93. 1886.

≡ *Ulocladium cucurbitae* (Letendre & Roum.) E.G. Simmons, Mycotaxon 14: 48. 1982.

***Alternaria heterospora*** Woudenb. & Crous, **nom. nov.** MycoBank MB803724.

*Basionym*: *Ulocladium solani* Yong Wang bis & X.G. Zhang, Mycol. Progr. 8: 209. 2009, non *Alternaria solani* Sorauer, 1896.

*Etymology*: Name refers to the various conidial morphologies observed during growth.

***Alternaria multiformis*** (E.G. Simmons) Woudenb. & Crous, **comb. nov.** MycoBank MB803720.

*Basionym*: *Ulocladium multiforme* E.G. Simmons, Canad. J. Bot. 76: 1537. 1999 [1998].

***Alternaria obovoidea*** (E.G. Simmons) Woudenb. & Crous, **comb. nov.** MycoBank MB803721.

*Basionym*: *Ulocladium obovoideum* E.G. Simmons, Mycotaxon 37: 104. 1990.

***Alternaria subcucurbitae*** (Yong Wang bis & X.G. Zhang) Woudenb. & Crous, **comb. nov.** MycoBank MB803722.

*Basionym*: *Ulocladium subcucurbitae* Yong Wang bis & X.G. Zhang, Mycologia 100: 456. 2008.

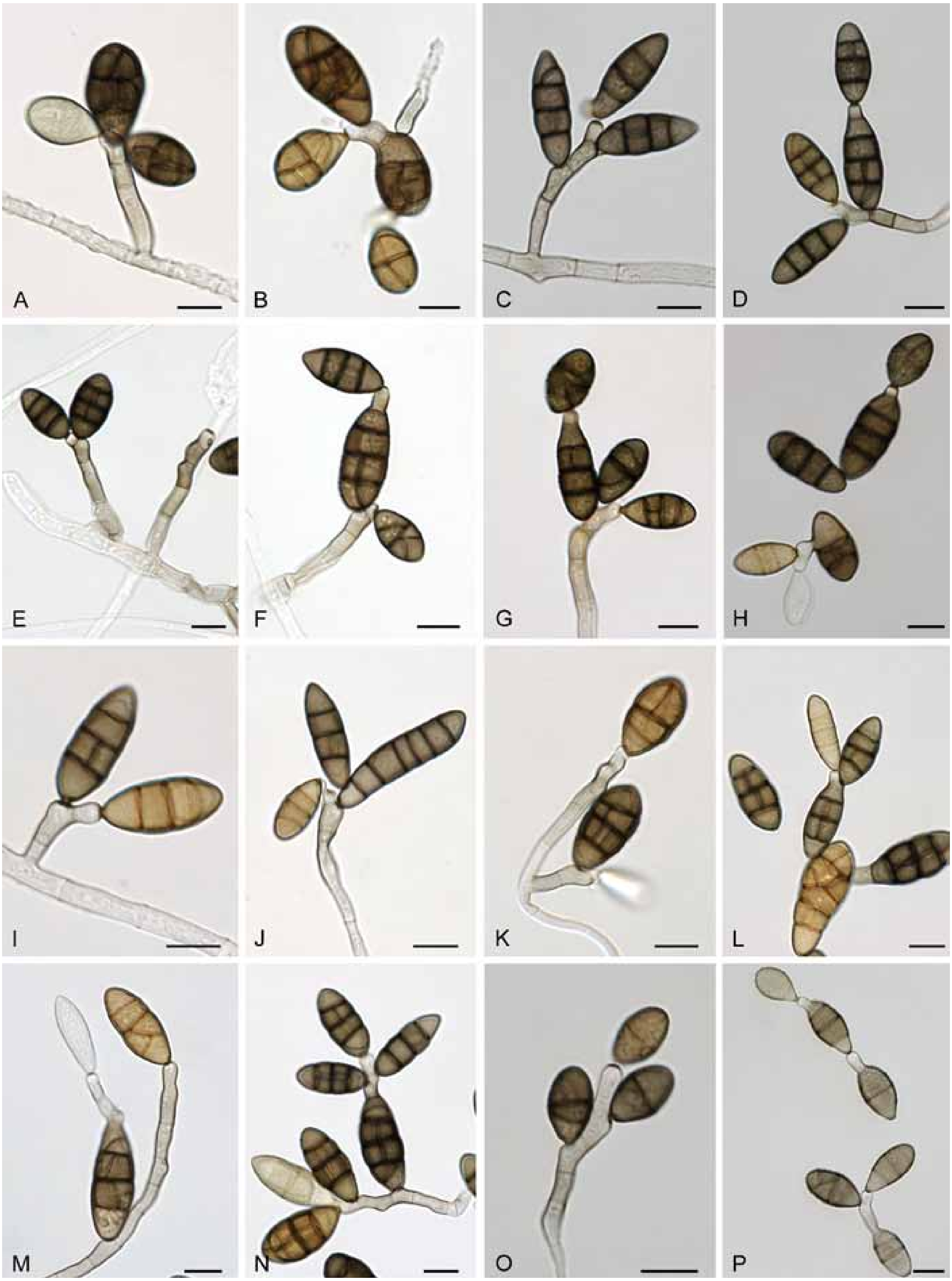


**Fig. 24.** *Alternaria* sect. *Ulocladioides*: conidia and conidiophores. A–B. *A. atra*. C–D. *A. brassicae-pekinensis*. E–F. *A. cantlous*. G–H. *A. multiformis*. I–J. *A. obovoidea*. K–L. *A. heterospora*. M–N. *A. subcucurbitae*. O–P. *A. terricola*. Scale bars = 10 µm.

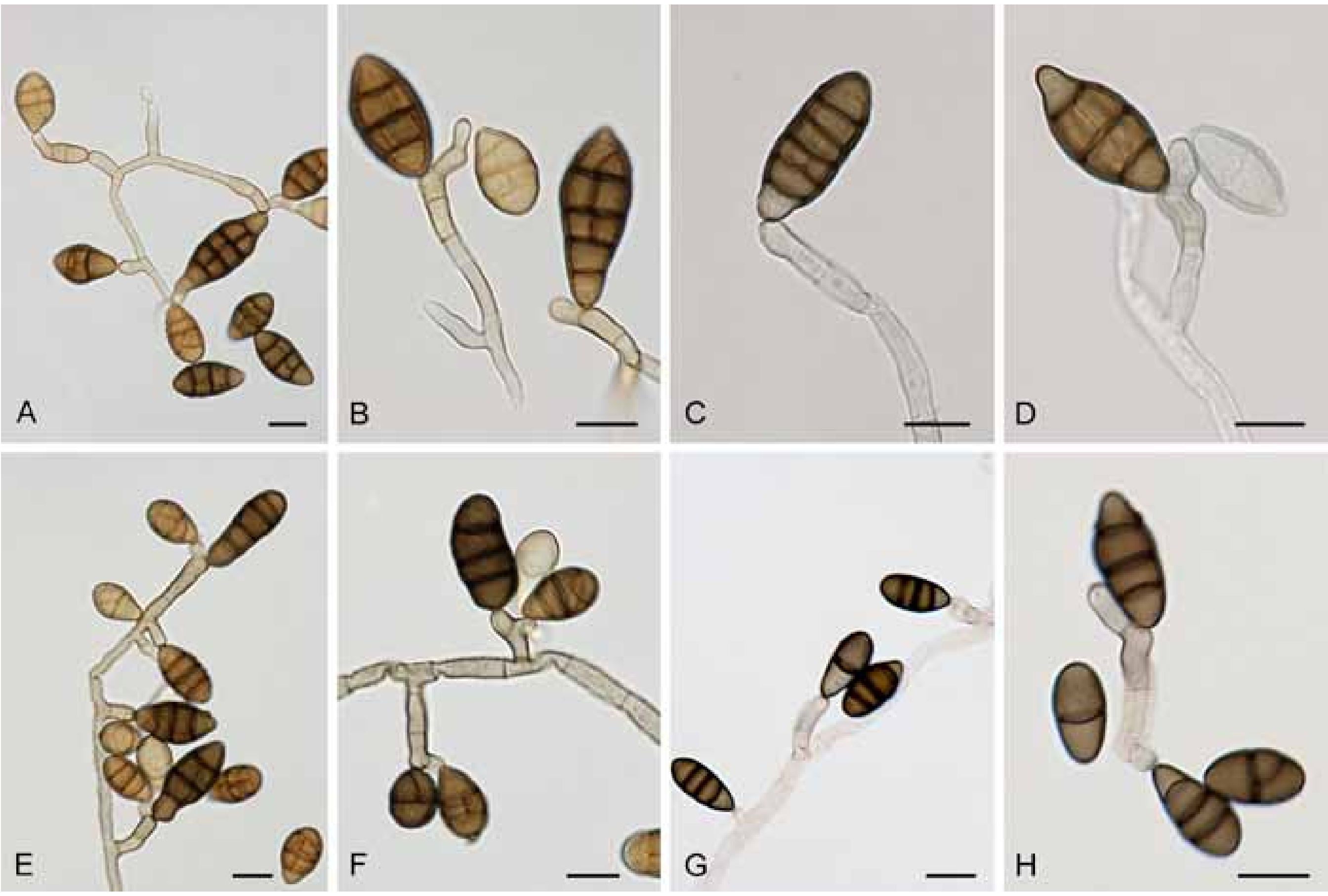


**Fig. 25.** *Alternaria* sect. *Ulocladium*: conidia and conidiophores. A–B. *A. capsici-annui*. C–D. *A. oudemansii*. E–F. *A. alternariae*. G–H. *A. botrytis*. Scale bars = 10 µm.

***Alternaria terricola*** Woudenb. & Crous, **nom. nov.** MycoBank MB803725.
*Basionym*: *Ulocladium tuberculatum* E.G. Simmons, Mycologia 59: 83. 1967, non *Alternaria tuberculata* M. Zhang & T.Y. Zhang, 2006.
*Etymology*: Name refers to soil from which it was originally isolated.

## Section *Ulocladium* (Preuss) Woudenb. & Crous, **comb. et stat. nov.** MycoBank MB803747. Fig. 25.

*Basionym*: *Ulocladium* Preuss, Linnaea 24: 111. 1851.

*Type species*: *Alternaria botrytis* (Preuss) Woudenb. & Crous

*Diagnosis*: Section *Ulocladium* is characterised by simple conidiophores, or with one or two short, geniculate, sympodial proliferations, with (mostly) single, obovoid, non-beaked conidia with a narrow base.

*Notes*: Section *Ulocladium* resembles sect. *Ulocladioides*. The epitype of *Ulocladium*, *U. botrytis* CBS 197.67, and the isotype of *U. oudemansii* (CBS 114.07) cluster with the *Sinomyces* representative, as do many other strains stored as *U. botrytis* in the CBS collection (data not shown). Furthermore, a strain stored as *A. capsici-annui* (CBS 504.74) in the CBS collection clusters within the *Sinomyces* clade and displays identical morphological features.

***Alternaria alternariae*** (Cooke) Woudenb. & Crous, **comb. nov.** MycoBank MB803716.
*Basionym*: *Sporidesmium alternariae* Cooke, Handb. Brit. Fungi 1: 1440. 1871.

≡ *Stemphylium alternariae* (Cooke) Sacc., Syll. Fungorum (Abellini) 4: 523. 1886.
≡ *Ulocladium alternariae* (Cooke) E.G. Simmons, Mycologia 59: 82. 1967.
≡ *Sinomyces alternariae* (Cooke) Yong Wang bis & X.G. Zhang, Fungal Biol. 115: 194. 2011.

***Alternaria botrytis*** (Preuss) Woudenb. & Crous, **comb. nov.** MycoBank MB803718.
*Basionym*: *Ulocladium botrytis* Preuss, Linnaea 24: 111. 1851.

≡ *Stemphylium botryosum* var. *ulocladium* Sacc. (nom. nov.), Syll. Fungorum (Abellini) 4: 522. 1886.
≡ *Stemphylium botryosum* var. *botrytis* (Preuss) Lindau, Rabenhorst's. Kryptog.-Fl., Edn 2 (Leipzig) 1(9): 219. 1908.

***Alternaria capsici-annui*** Săvul. & Sandu, Hedwigia 75: 228. 1936.
***Alternaria oudemansii*** (E.G. Simmons) Woudenb. & Crous, **comb. nov.** MycoBank MB803715.
*Basionym*: *Ulocladium oudemansii* E.G. Simmons, Mycologia 59: 86. 1967.

## Section *Undifilum* (B.M. Pryor, Creamer, Shoemaker, McLain-Romero & Hambl.) Woudenb. & Crous, **comb. et stat. nov.** MycoBank MB803748. Fig. 26.

*Basionym*: *Undifilum* B.M. Pryor, Creamer, Shoemaker, McLain-Romero & Hambl., Botany 87: 190. 2009.

*Type species*: *Alternaria bornmuelleri* (Magnus) Woudenb. & Crous

*Diagnosis*: Section *Undifilum* is characterised by ovate to obclavate to long ellipsoid, straight to inequilateral, single, transseptate conidia;

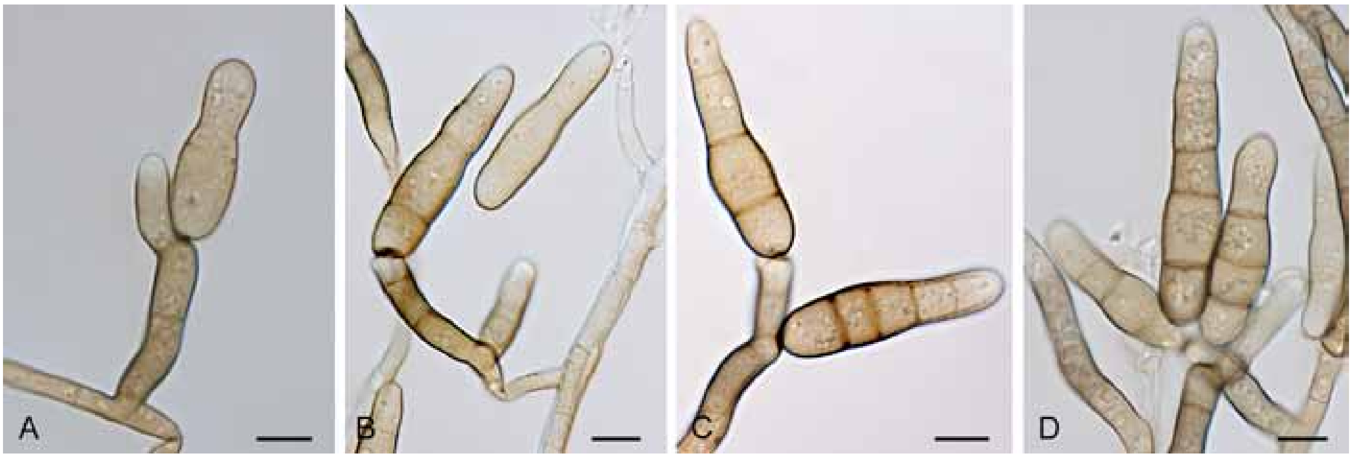


**Fig. 26.** *Alternaria* sect. *Undifilum*: conidia and conidiophores. A–D. *A. bornmuelleri*. Scale bars = 10 µm.

septa can be thick, dark and rigid, and form unique germ tubes, which are wavy or undulate until branching. Species of this section occur on *Fabaceae* and almost all produce the toxic compound swaisonine.

*Notes:* Section *Undifilum* shares morphological features with section *Embellisia*, but is characterised by the formation of a wavy germ tube upon germination (Pryor *et al.* 2009). Based on previous studies, the swaisonine producing species *U. oxytropis* (Pryor et al. 2009, Lawrence *et al.* 2012), *U. fulvum* and *U. cinereum* (Baucom *et al.* 2012) also belong to this section, although the type species, *A. bornmuelleri*, does not produce swaisonine.

***Alternaria bornmuelleri*** (Magnus) Woudenb. & Crous, **comb. nov.** MycoBank MB803726.
*Basionym*: *Helminthosporium bornmuelleri* Magnus, Hedwigia 38 (Beibl.): 73. 1899.
≡ *Undifilum bornmuelleri* (Magnus) B.M. Pryor, Creamer, Shoemaker, McLain-Romero & Hambl., Botany 87: 190. 2009.
***Alternaria cinerea*** (Baucom & Creamer) Woudenb. & Crous, **comb. nov.** MycoBank MB803731.
*Basionym*: *Undifilum cinereum* Baucom & Creamer, Botany 90: 872. 2012
***Alternaria fulva*** (Baucom& Creamer) Woudenb. & Crous, **comb. nov.** MycoBank MB803732.
*Basionym*: *Undifilum fulvum* Baucom & Creamer, Botany 90: 871. 2012
***Alternaria oxytropis*** (Q. Wang, Nagao & Kakish.) Woudenb. & Crous, **comb. nov.** MycoBank MB803727.
*Basionym*: *Embellisia oxytropis* Q. Wang, Nagao & Kakish., Mycotaxon 95: 257. 2006.
≡ *Undifilum oxytropis* (Q. Wang, Nagao & Kakish.) B.M. Pryor, Creamer, Shoemaker, McLain-Romero & Hambl., Botany 87: 191. 2009.

## Monotypic lineages

The following six species are not assigned to one of the 24 above described *Alternaria* sections and are treated as separate, single species, lineages in this study. Future studies, including more and/or new *Alternaria* species, might eventually give rise to the formation of new sections, when these new species show to be closely related to one of these monotypic lineages.

***Alternaria argyranthemi*** E.G. Simmons & C.F. Hill, Mycotaxon 65: 32. 1997.
***Alternaria brassicae*** (Berk.) Sacc., Michelia 2(no. 6): 129. 1880.
*Basionym*: *Macrosporium brassicae* Berk., Engl. Fl., Fungi (Edn 2) (London) 5: 339. 1836.
Additional synonyms listed in Simmons (2007).
***Alternaria dennisii*** M.B. Ellis, Mycol. Pap. 125: 27. 1971.
≡ *Embellisia dennisii* (M.B. Ellis) E.G. Simmons, Mycotaxon 38: 257. 1990.
***Alternaria helianthiinficiens*** E.G. Simmons, Walcz & R.G. Roberts [as "*helianthinficiens*"], Mycotaxon 25: 204. 1986.
***Alternaria soliaridae*** E.G. Simmons, CBS Biodiversity Ser. (Utrecht) 6: 374. 2007.
***Alternaria thalictrigena*** K. Schub. & Crous, Fungal Planet No. 12: 2. 2007.

## *Paradendryphiella* Woudenb. & Crous, gen. nov. MycoBank MB803750. Fig. 27.

*Colonies* on SNA effuse, entire, velvety, olivaceous. Reverse olivaceous-grey to iron-grey. *Mycelium* consisting of branched, septate hypha, (sub)hyaline, smooth. *Conidiophores* subhyaline, simple or branched, septate or not, straight or flexuous, often nodose with conspicuous, brown pigmentation at the apical region; at times reduced to conidiogenous cells. *Conidiogenous cells* terminal or lateral, with denticles aggregated at apex, with prominent conidial scars, thickened but not darkened; sometimes proliferating with a new head or a short, inconspicuous sympodial rachis. *Conidia* produced holoblastically, on narrow denticle, smooth, cylindrical to obclavate, straight or slightly flexuous, 1–7 transverse septa, pale to medium brown, often with dark septa (often constricted), and a darkened zone of pigmentation at the apex, and at the hilum, which is thickened, and somewhat protruding, with a minute marginal frill. *Chlamydospores* and sexual state not observed.

*Type species*: *Paradendryphiella salina* (G.K. Sutherl.) Woudenb. & Crous

***Paradendryphiella salina*** (G.K. Sutherl.) Woudenb. & Crous, **comb. nov.** MycoBank MB803751.
*Basionym*: *Cercospora salina* G.K. Sutherl., New Phytol. 15: 43. 1916.
≡ *Dendryphiella salina* (G.K. Sutherl.) Pugh & Nicot, Trans. Brit. Mycol. Soc. 47(2): 266. 1964.
≡ *Scolecobasidium salinum* (G.K. Sutherl.) M.B. Ellis, More dematiaceous hyphomycetes (Kew): 192. 1976.

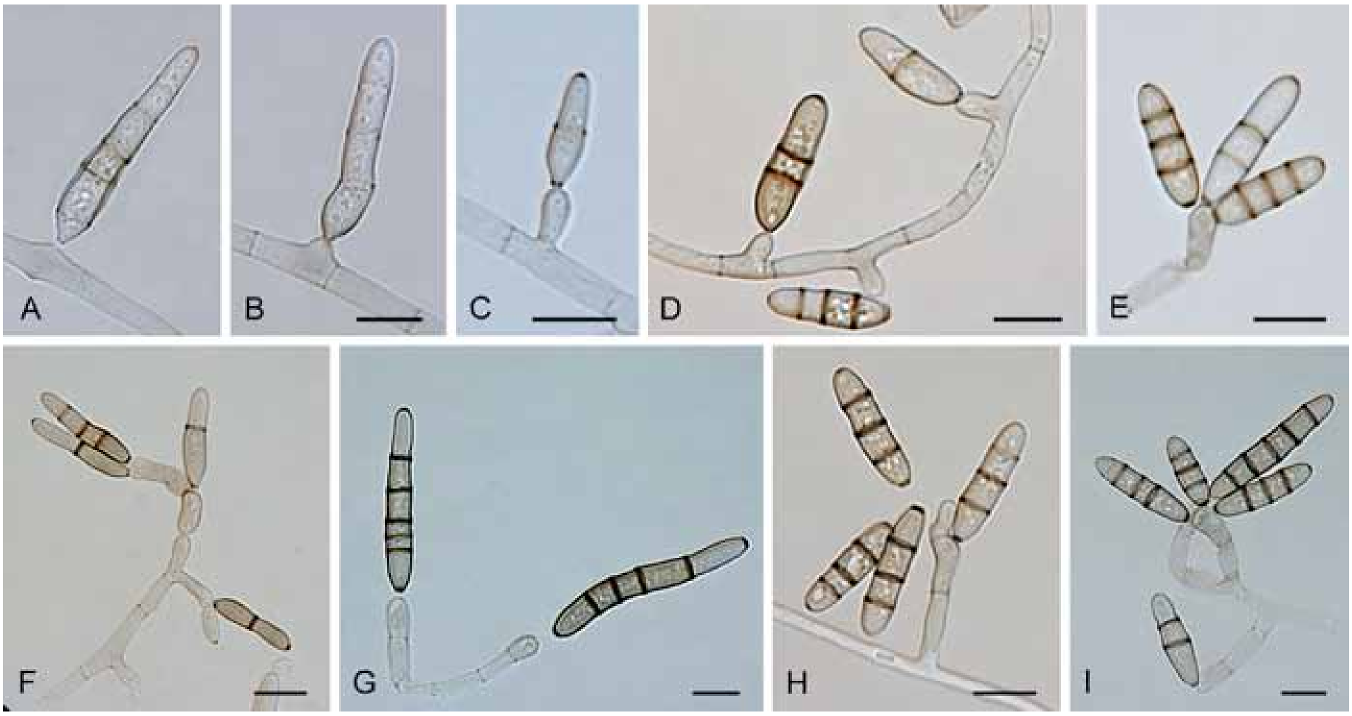


**Fig. 27.** *Paradendryphiella* gen. nov.: conidia and conidiophores. A–B, D–E, G–I. *P. salina*. C, F. *P. arenariae*. Scale bars = 10 µm.

= *Embellisia annulata* de Hoog, Seigle-Mur., Steiman & K.-E. Erikss., Antonie van Leeuwenhoek J. Microbiol. Serol. 51: 409. 1985.

***Paradendryphiella arenariae*** (Nicot) Woudenb. & Crous, **comb. nov.** MycoBank MB803752.

*Basionym*: *Dendryphiella arenariae* Nicot, [as "arenaria"] Rev. Mycol. (Paris) 23: 93. 1958.

≡ *Scolecobasidium arenarium* (Nicot) M.B. Ellis, More dematiaceous hyphomycetes (Kew): 194. 1976.

## DISCUSSION

The well-supported node for the *Alternaria* clade obtained in the present study, and the low bootstrap support at the deeper nodes within the *Alternaria* complex is also consistently seen in previous phylogenetic studies published on these genera (Pryor & Bigelow 2003, Inderbitzin *et al.* 2006, Pryor *et al.* 2009, Runa *et al.* 2009, Wang *et al.* 2011, Lawrence *et al.* 2012). The only phylogenetic study which displays a second fully supported node is based on a five-gene combined dataset of GAPDH, Alt a 1, actin, plasma membrane ATPase and calmodulin (Lawrence *et al.* 2013). This node, called clade A by the authors, supports eight "asexual" *Alternaria* species-groups and an *Ulocladium* (sect. *Ulocladioides* in our phylogenies) clade. By resolving these eight asexual phylogenetic lineages of *Alternaria* together with *Ulocladium*, which is sister to the sexual *A. infectoria* species-group and other sexual genera, Lawrence *et al.* (2013) elevated the asexual species-groups to sections within *Alternaria*. If we take this node as cut-off for the genus *Alternaria* in our phylogenies, this would leave an *Alternaria* clade with 14 internal clades (sections) and three monotypic lineages. In order to create a stable phylogenetic taxonomy, seven new genera need to be described of which three would be monotypic; *E. dennissii*, *A. argyranthemi* and *A. soliaridae*. *Embellisia* species would be assigned to five different genera of which four would be new, leaving only *E. allii*, *E. chlamydospora* and *E. tellustris* in the genus *Embellisia*. The well-known (medical) *A. infectoria* species-group would also have to be transferred to a new genus. This node is not supported in our study (0.98 PP /65 ML Fig 1) and also the strict asexual/sexual division is not supported as two sexual morphs are found in section *Panax*. This approach would therefore give rise to multiple small genera, and would not end up in a logical and workable situation.

Based on our phylogenetic study on parts of the SSU, LSU, ITS, GAPDH, RPB2 and TEF1 gene regions of ex-type and reference strains of *Alternaria* species and all available allied genera, we resolved a *Pleospora*/*Stemphylium*-clade sister to *Embellisia annulata*, and a well-supported *Alternaria* clade. The *Alternaria* clade contains 24 internal clades and six monotypic lineages. In combination with a review of literature and morphology, the species within the *Alternaria* clade are all recognised here as *Alternaria s. str*. This puts the genera *Allewia*, *Brachycladium*, *Chalastospora*, *Chmelia*, *Crivellia*, *Embellisia*, *Lewia*, *Nimbya*, *Sinomyces*, *Teretispora*, *Ulocladium*, *Undifilum* and *Ybotromyces* in synonymy with *Alternaria*.

The support values for the different sections described in this study are plotted in a heatmap per gene/gene combination and phylogenetic method used (Table 2). This shows that the Bayesian method provides greater support than the Maximum Likelihood bootstrap support values, which is in congruence with previous reports (*e.g.* Douady *et al.* 2003). The sections *Cheiranthus*, *Eureka* and *Nimbya* have the lowest support values. For sect. *Eureka* this is mainly caused by the position of *A. cumini*, which clusters within sect. *Embellisioides* based on its RPB2 sequence and as a monotypic lineage based on its TEF1 sequence. Section *Cheiranthus* and *Nimbya* are small sections, with relative long branches. Future studies, including more strains and/or species in these sections, are necessary to check the stability of these long branches.

The sexual genus ***Crivellia*** with its ***Brachycladium*** asexual morph was described by Inderbitzin *et al.* (2006) with *Crivellia papaveraceae* (asexual morph *Brachycladium penicillatum*) as type species and *B. papaveris*, with an unnamed sexual morph, as second species. The genus *Brachycladium*, which was synonymised with *Dendryphion* (Ellis 1971), was resurrected for the non-sexual stage based on polyphyly within *Dendryphion* and morphological distinction from its type species, *D. comosum*. The type species of *Brachycladium*, *B. penicillatum*, resides in *Alternaria* sect. *Crivellia*, which places *Brachycladium* in synonymy with *Alternaria* instead of *Dendryphion*.

The genus ***Chalastospora*** was established by Simmons (2007) based on *Chalastospora cetera,* formerly *Alternaria cetera.* Two new *Chalastospora* species*, C. ellipsoidea* and *C. obclavata*, and *A. malorum* as *C. gossypii* were later added to the genus, based on sequence data of the ITS and LSU regions (Crous *et al.* 2009c). The genus is characterised by conidia which are almost always narrowly ellipsoid to narrowly ovoid with 1–6 transverse eusepta, generally lacking oblique or longitudinal septa (Crous *et al.* 2009c). Our study shows that *Alternaria armoraciae* and *Embellisia abundans* also belong to this clade. Juvenile conidia of *A. armoraciae* are ovoid, but vary from being narrow to broadly ovoid and ellipsoid, with 3–5 transverse septa and a single longitudinal septum in up to four of the transverse segments (Simmons 2007). *Embellisia abundans* was already mentioned as part of the *Chalastospora* clade (Andersen *et al.* 2009, Lawrence *et al.* 2012), and has long ovoid or obclavate conidia with 3–6 transverse septa and rarely any longitudinal septa (Simmons 1983). The description of sect. *Chalastospora* does therefore not completely follow the original description of the genus *Chalastospora*.

The genus ***Embellisia*** is characterised by the thick, dark, rigid conidial septa and the scarcity of longitudinal septa (Simmons 2007). It was first described by Simmons (1971), with *Embellisia allii* as type and *E. chlamydospora* as second species. Multiple *Embellisia* species followed after the description of the genus, which was later linked to the sexual genus *Allewia* (Simmons 1990). The latest molecular-based revision was performed based on sequences of the GAPDH, ITS and Alt a 1 genes (Lawrence *et al.* 2012). They found that *Embellisia* split into four clades and multiple species, which clustered individually amidst *Alternaria*, *Ulocladium* or *Stemphylium* spp. Our results mostly support these data, but with the inclusion of more ex-type/representative strains of *Alternaria* some additions were made to the different *Embellisia* groups mentioned by Lawrence *et al.* (2012). Group I (sect. *Embellisia*) and III (sect. *Embellisioides*) are identical to the treatment of Lawrence *et al.* (2012) but group II (section *Phragmosporae*) and IV (section *Eureka*) are both expanded with four *Alternaria* species. As not all species from group II and IV display the typical morphological characters of *Embellisia*, we chose to name these *Alternaria* sections based on the oldest species residing in the respective sections. *Embellisia abundans* was already mentioned as being part of the *Chalastospora*-clade and *E. indefessa* formed a clade close to *Ulocladium*, which we now assign to sect. *Cheiranthus*. *Embellisia dennisii* also forms a separate lineage in our phylogenies; therefore the old name *Alternaria dennissii* is resurrected. Furthermore, the clustering of *E. conoidea* within the *A. brassicicola* species-group and *E. annulata* close to *Stemphylium*, now assigned as *Paradendryphiella* gen. nov., is confirmed by our phylogenetic data. The morphological character of thick, dark, rigid septa seems to have evolved multiple times and does not appear to be a valid character for taxonomic distinction at generic level.

The sexual morphs ***Lewia*** (Simmons 1986) and ***Allewia*** (Simmons 1990) were linked to *Alternaria* and *Embellisia* respectively, with the only difference between these genera being the morphology of their asexual morphs. *Lewia chlamidosporiformans* and *L. sauropodis* are transferred to the genus *Leptosphaerulina* (Simmons 2007), which leaves 11 *Lewia* species with a known *Alternaria* anamorph. Most of them (9/11) reside in sect. *Infectoriae,* the others are found in sect. *Panax*. *Allewia* only contains two species of which one resides in sect. *Eureka* and one in sect. *Embellisioides*. With the establishment of the new International Code of Nomenclature for algae, fungi and plants (ICN), the dual nomenclature system for sexual and asexual fungal morphs was abandoned and replaced by a single-name nomenclature (Hawksworth *et al.* 2011, Norvell 2011). In order to implement the new rules of the ICN, we synonymised *Lewia* and *Allewia* with *Alternaria*.

Although multiple molecular studies included ***Nimbya*** isolates in their phylogenies (Chou & Wu 2002, Pryor & Bigelow 2003, Hong *et al.* 2005, Inderbitzin *et al.* 2006, Pryor *et al.* 2009), a more extensive molecular-based study was recently published by Lawrence *et al.* (2012). Based on sequences of the GAPDH, ITS and Alt a 1 genes, the authors found a *Nimbya* clade which contained the type species *N. scirpicola* together with *N. scirpinfestans*, *N. scirpivora* and *N. caricis.* The *N. scirpicola* isolate which we included in our study, was assigned to this genus by Simmons (1989) based on morphological characters, as is the one used in other molecular studies (Pryor & Bigelow 2003, Hong *et al.* 2005, Lawrence *et al.* 2012). The sequences of the ITS, GAPDH and Alt a 1 genes of these isolates are however not identical, but do cluster in the same clade in the two phylogenies (data not shown), together with the isolate of *N. caricis*. The *N. gomphrenae* isolate we included in our phylogeny was not representative of the name. Simmons mentioned in 1989 that Togashi (1926) described two different fungi and deposited the small-spored species in the CBS collection, instead of the large-spored *N. gomphrenae* isolate. *Nimbya gomphrenae* CBS 108.27, which does not sporulate anymore, will therefore be treated as "*Alternaria* sp.", and resides in sect. *Alternata*. The ITS sequence of *N. gomphrenae* from Chou & Wu (2002) actually clusters within sect. *Alternantherae*. This section was described by Lawrence *et al.* (2012) and consists of three *Nimbya* species, which they renamed to *Alternaria* based on the position of the clade amidst the *Alternaria* species-groups. Based on the data from Chou & Wu (2002), the name *Alternaria gomphrenae* is resurrected and placed in sect. *Alternantherae*.

The genus ***Sinomyces*** was described in by Wang *et al.* (2011) to accommodate *Ulocladium alternariae* and two new species from China, *S. obovoideus* and *S. fusoides* (type). The genus was differentiated from *Ulocladium* based on its simple conidiophores with a single apical pore or 1–2 short, uniperforate, geniculate sympodial proliferations. Unfortunately, our DNA sequence analyses of the ex-type cultures of the two new species from China (CBS 124114 and CBS 123375) were not congruent with the GAPDH (both species) and Alt a 1 (*S. obovoideus*) sequences deposited in GenBank (data not shown), leading us to doubt the authenticity of these strains. This matter could not be resolved in spite of contacting the original depositors. The ex-type strain of *S. alternariae* (CBS 126989) was therefore included as representative of the genus *Sinomyces*. The presence of the epitype of *Ulocladium*, *U. botrytis* CBS 197.67, in this section resulted in us rejecting the name *Sinomyces*, and calling this sect. *Ulocladium.* In addition, the presence of *U. oudemansii* in this section, with conidiophores with 1–5 uniperforate geniculations (Simmons 1967), also disagrees with the mentioned differentiation of *Sinomyces* from *Ulocladium*.

The type species of ***Ulocladium***, *U. botrytis*, was typified by two representative strains QM 7878 (CBS 197.67) and QM 8619 (CBS 198.67) (Simmons 1967). Molecular studies performed afterwards showed that these strains are not identical (de Hoog & Horré 2002). Most molecular studies performed used CBS 198.67

as representative of *U. botrytis* (Pryor & Gilbertson 2000, Pryor & Bigelow 2003, Hong *et al.* 2005, Xue & Zhang 2007, Pryor *et al.* 2009, Runa *et al.* 2009, Wang *et al.* 2010, Wang *et al.* 2011, Lawrence *et al.* 2012), which clusters in section *Ulocladioides*. However, de Hoog & Horré (2002) epitypified *U. botrytis* with CBS 197.67, which clusters with *Sinomyces* strains, as does *Ulocladium oudemansii*, now named sect. *Ulocladium*. Extended phylogenetic analyses on all *U. botrytis* strains present in the CBS culture collection (16 isolates) also highlight this issue as they cluster either within sect. *Ulocladium* or sect. *Ulocladioides* (data not shown), both with one of the representative strains described by Simmons (1967). The suggestion to synonymise *Ulocladium* with *Alternaria* has been made several times in the past (Pryor & Gilbertson 2000, Chou & Wu 2002). The latest systematic revision of the genus *Ulocladium* (Runa *et al.* 2009) based on sequences from the ITS, GAPDH and Alt a 1 genes supported previous findings of poly- and paraphyletic relationships of *Ulocladium* among *Alternaria*, *Embellisia* and *Stemphylium* spp. (de Hoog & Horré 2002, Pryor & Bigelow 2003, Hong *et al.* 2005). *Ulocladium alternariae* and *U. oudemansii*, now known as sect. *Ulocladium*, cluster separately. The core *Ulocladium* clade, containing the two sister clades now called sect. *Ulocladioides* and sect. *Pseudoulocladium*, was confirmed by later studies (Wang *et al.* 2010, Lawrence *et al.* 2012). *Alternaria cheiranthi* and *Embellisia indefessa* have been linked to *Ulocladium* (Pryor & Gilbertson 2000, Pryor & Bigelow 2003, Hong *et al.* 2005, Pryor *et al.* 2009, Runa *et al.* 2009, Lawrence *et al.* 2012), but missed the diagnostic feature of *Ulocladium*. Our study showed that they form a sister section, sect. *Cheiranthus*, to sect. *Ulocladioides*. The confusing taxonomy in this genus strengthens our decision to reduce *Ulocladium* to synonymy with *Alternaria*. The characteristics of the former genus *Ulocladium* are added to the new broader *Alternaria* generic circumscription.

The genus ***Undifilum*** was described by Pryor *et al.* (2009) to accommodate the species *U. oxytropis* and *U. bornmuelleri*. It shares the morphological feature of thick, dark and rigid septa with the genus *Embellisia*, but was characterised by the formation of a wavy germ-tube upon germination (Pryor *et al.* 2009). A recent study on fungal endophytes in locoweeds in the US described two new *Undifilum* species (Baucom *et al.* 2012). Both new species produce the toxic compound swaisonine, which is also produced by *U. oxytropis*. Swaisonine is the cause of a neurological disease, locism, of grazing animals, resulting in economic losses in livestock (James & Panter 1989). The production of swaisonine seems to be related to this section, although the type-species, *U. bornmuelleri*, does not produce this toxin.

The genus ***Ybotromyces*** contains one species, *Y. caespitosus* (originally *Botryomyces caespitosus*), which was isolated from a skin lesion of a human patient (de Hoog & Rubio 1982). De Hoog *et al.* (1997) discovered a high similarity to *Alternaria* spp. based on restriction patterns of the ITS and SSU rDNA. A phylogeny study of melanised meristematic fungi based on their SSU and ITS rDNA sequences (Sterflinger *et al.* 1999) placed *Y. caespitosus* within the *Pleosporales* together with *Alternaria* and *Pleospora*. De Hoog & Horré (2002) hypothesized that the ex-type strain of *Y. caespitosus*, CBS 177.80, is likely a synanamorph of a yet undescribed *Alternaria* species. Our phylogeny supports this hypothesis, and places the genus in sect. *Infectoriae*.

***Chmelia*** *slovaca*, described from dermatic lesions of a human (Svobodová 1966), also clusters with sect. *Infectoriae* as was shown previously (de Hoog & Horré 2002). The genus produces different types of chlamydospores and sporadically blastospores, but no conidia or conidiophores, which makes it difficult to identify based on morphology. De Hoog & Horré (2002) were confident that *Chmelia* is a sterile member of *A. infectoria*, which is in agreement with our results.

## Genera unrelated to *Alternaria*

The placement of the sexual genus ***Pleospora*** (1863) with ***Stemphylium*** (1833) asexual morphs as basal sister clade to the *Alternaria* complex is well-documented in multiple molecular studies (Chou & Wu 2002, Pryor & Bigelow 2003, Hong *et al.* 2005, Pryor *et al.* 2009, Lawrence *et al.* 2012). Therefore, we only included the type species of both genera in our phylogenies and used them as outgroup in the *Alternaria* phylogeny. *Pleospora herbarum* with its *Stemphylium herbarum* (CBS 191.86) asexual morph is the type species of the genus *Pleospora*. *Stemphylium botryosum* with its *Pleospora tarda* (CBS 714.68) sexual morph is the type species of the genus *Stemphylium*.

*Embellisia annulata* proved to be identical to the marine species ***Dendryphiella*** *salina*, and forms a well-supported clade in the *Pleosporaceae* together with *D. arenariae*. Several DNA-based studies (dela Cruz 2006, Jones *et al.* 2008, Zhang *et al.* 2009) concluded that the marine *Dendryphiella* species, *D. arenariae* and *D. salina*, belonged to the *Pleosporaceae* as sister clade to the *Pleospora*/*Stemphylium* complex. Furthermore, they showed the type species of *Dendryphiella*, *D. vinosa*, to be only distantly related, based on sequences of the ITS, SSU, LSU (Jones *et al.* 2008) and ITS, TEF1, RPB2 (dela Cruz 2006) gene regions. The transfer of the marine *Dendryphiella* species to *Scolecobasidium* (Ellis 1976), was also disputed. *Scolecobasidium* does not belong to the *Pleosporales* based on ITS, TEF1, and RPB2 sequences (dela Cruz 2006) and the morphology of the two *Dendryphiella* species does not fit the generic circumscription of *Scolecobasidium* (dela Cruz 2006, Jones *et al.* 2008). Ellis (1976) described denticles on the conidiogenous cells when the conidia become detached. However other observers describe a marginal basal frill on the conidia after detachment, leaving a scar on the conidiophore. We propose to place the two species in the new genus *Paradendryphiella* as *C. arenariae* and *C. salina*. The need for a new genus to accommodate the two species was already suggested by Jones *et al.* (2008).

A recent study on *Diademaceae*, a family which is characterised by a flat circular operculum and bitunicate asci (Shoemaker & Babcock 1992), excluded the sexual genera ***Comoclathris*** and ***Clathrospora***, and (provisionally) placed them in the *Pleosporaceae* with alternaria-like asexual morphs (Zhang *et al.* 2011). Molecular data of two strains (Dong *et al.* 1998, Schoch *et al.* 2009) placed them within the *Pleosporaceae*. A confusing factor is that Dong *et al.* (1998) use the name *Comoclathris baccata* in their paper for strain CBS 175.52, but submitted their sequences under the name *Clathrospora diplospora* to GenBank. Shoemaker & Babcock (1992) synonymised *Clathrospora diplospora* with *Comoclathris baccata*, which renders *Comoclathris* as the correct generic name. The confusion around these genera is illustrated by the fact that the CBS collection currently harbours six strains named as *Clathrospora* species of which four were renamed by Shoemaker & Babcock in 1992 based on morphological studies, and three of these four strains were even transferred to the genus *Comoclathris*. The type species of *Clathrospora*, *C. elynae* is represented by two strains of which one, CBS 196.54, was also studied morphologically by Shoemaker and Babcock (1992). They form a well-supported clade, located basal to the *Pleosporaceae*

(Fig. 2), outside the *Alternaria* complex. The type species of *Comoclathris*, *Comoclathris lanata*, was not available to us, but the two *Comoclathris compressa* strains cluster together in a well-supported clade within the *Pleosporaceae*, also outside the *Alternaria* complex, which we believe to be the correct phylogenetic placement of the genus. Two other strains, named *Comoclathris magna* (CBS 174.52) and *Clathrospora heterospora* (CBS 175.52) by Shoemaker and Babcock (1992), cluster amidst sect. *Alternata*. Culture studies performed by Simmons (1952) showed the presence of alternaria-like conidia in these cultures and no (mature) ascospore formation. Presumably the species observed by Shoemaker and Babcock (1992) on plant material were lost during cultivation and became replaced by *A. alternata* species-group isolates. Both strains will be treated as "*Alternaria* sp."

The genus ***Alternariaster*** was first described by Simmons (2007) with *Alternariaster helianthi*, formerly *Alternaria helianthi* or *Helminthosporium helianthi*, as type and only species. It is distinct from *Alternaria* by the lack of a pigmented conspicuous internal, circumhilar ring in its conidia and conidiophores. Our study showed that this genus is clearly not part of the *Alternaria* complex and belongs to the *Leptosphaeriaceae* (Fig. 2) (Alves *et al.* 2013).

In the recently published book "The genera of Hyphomycetes" (Seifert *et al.* 2011) three more genera are linked to *Alternaria*, namely ***Pantospora***, ***Briansuttonia*** and ***Rhexoprolifer***. A recent study on *Pantospora* included ITS and LSU sequence data of the type species *Pantospora guazumae*, which placed the genus in *Mycosphaerellaceae* (Minnis *et al.* 2011). This refutes the link with *Alternaria*. The genus *Rhexoprolifer* was described in 1996 by Matsushima with *R. variabilis* as type and only species, isolated from South Africa. *Rhexoprolifer variabilis* has rhexolytic conidial liberation and proliferating conidiophores with both phragmosporous and dictyosporous conidia. *Briansuttonia* was described in 2004 to accommodate *Corynespora alternarioides* (Castañeda Ruiz *et al.* 2004). The distoseptate muriform conidia of *Briansuttonia* do resemble *Alternaria* and *Stemphylium*, but the conidiogenous loci and euseptate conidia of *Alternaria* and holoblastic conidial ontogeny and euseptate muriform conidia of *Stemphylium* were enough for the authors to regard their taxon as a different genus. Both asexual genera presently lack molecular data, and we were unable to obtain any living specimens of these taxa. It would be valuable to include both genera in a future study to resolve the connection among genera with muriform conidia and *Alternaria*.

The description of *Alternaria s. str.* in the present study is supported by i) a well-supported phylogenetic node in multiple analyses, ii) high similarity of clades within *Alternaria* based on SSU, LSU and ITS data, and iii) variation in the order of the clades between the different gene phylogenies, which is in congruence with low support values at these deeper nodes. We follow the precedence introduced by Lawrence *et al.* (2013) to assign the taxonomic status of sections of *Alternaria* for the different clades found, thus allowing us to retain the former generic names but associated with a different taxonomic status. For end-users, this also results in a more stable and understandable taxonomy and nomenclature.

## DEDICATION

We would like to dedicate this manuscript to the late Dr E.G. Simmons, who spent over 50 years of his life researching the systematics of the genus *Alternaria*. Without the time EGS spent on characterising the species included in this study, and his impeccable strain collection, which he placed in CBS for preservation and further study, the present study would not have been possible.

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# A new approach to species delimitation in *Septoria*

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**Abstract:** *Septoria* is a large genus of asexual morphs of *Ascomycota* causing leaf spot diseases of many cultivated and wild plants. Host specificity has long been a decisive criterium in species delimitation in *Septoria*, mainly because of the paucity of useful morphological characters and the high level of variation therein. This study aimed at improving the species delimitation of *Septoria* by adopting a polyphasic approach, including multilocus DNA sequencing and morphological analyses on the natural substrate and in culture. To this end 365 cultures preserved in CBS, Utrecht, The Netherlands, among which many new isolates obtained from fresh field specimens were sequenced. Herbarium material including many types was also studied. Full descriptions of the morphology *in planta* and *in vitro* are provided for 57 species. DNA sequences were generated for seven loci, viz. nuclear ITS and (partial) LSU ribosomal RNA genes, RPB2, actin, calmodulin, Btub, and EF. The robust phylogeny inferred showed that the septoria-like fungi are distributed over three main clades, establishing the genera *Septoria s. str.*, *Sphaerulina*, and *Caryophylloseptoria* gen. nov. Nine new combinations and one species, *Sphaerulina tirolensis* sp. nov. were proposed. It is demonstrated that some species have wider host ranges than expected, including hosts from more than one family. *Septoria protearum*, previously only associated with *Proteaceae* was found to be also associated with host plants from six additional families of phanerogams and cryptogams. To our knowledge this is the first study to provide DNA-based evidence that multiple family-associations occur for a single species in *Septoria*. The distribution of host families over the phylogenetic tree showed a highly dispersed pattern for 10 host plant families, providing new insight into the evolution of these fungi. It is concluded that trans-family host jumping is a major force driving the evolution of *Septoria* and *Sphaerulina*.

**Key words:** Evolution, host jumping, host specificity, Multilocus Sequence Typing (MLST), *Mycosphaerella*, *Mycosphaerellaceae,* new genus, new species, *Pleosporales, Phloeospora*, *Septoria*, *Sphaerulina*, taxonomy, systematics..

**Taxonomic novelties: New genus** – *Caryophylloseptoria* Verkley, Quaedvlieg & Crous; **New species** – *Sphaerulina tirolensis* Verkley, Quaedvlieg & Crous; **New combinations** – *Caryophylloseptoria lychnidis* (Desm.) Verkley, Quaedvlieg & Crous, *Caryophylloseptoria silenes* (Westend.) Verkley, Quaedvlieg & Crous, *Caryophylloseptoria spergulae* (Westend.) Verkley, Quaedvlieg & Crous, *Sphaerulina aceris* (Lib.) Verkley, Quaedvlieg & Crous, *Sphaerulina cornicola* (DC. : Fr.) Verkley, Quaedvlieg & Crous, *Sphaerulina gei* (Roberge ex Desm.) Verkley, Quaedvlieg & Crous, *Sphaerulina hyperici* (Roberge ex Desm.) Verkley, Quaedvlieg & Crous, *Sphaerulina frondicola* (Fr.) Verkley, Quaedvlieg & Crous, *Sphaerulina socia* (Pass.) Quaedvlieg, Verkley & Crous; **Epitypifications (basionyms)** – *Ascochyta lysimachiae* Lib., *Septoria astragali* Roberge ex Desm., *Septoria cerastii* Roberge ex Desm., *Septoria clematidis* Roberge ex Desm., *Septoria cruciatae* Roberge ex Desm., *Septoria spergulae* Westend., *Septoria epilobii* Westend., *Septoria galeopsidis* Westend., *Septoria gei* Roberge ex Desm., *Septoria hyperici* Roberge ex Desm., *Septoria rubi* Westend., *Septoria senecionis* Westend., *Septoria urticae* Roberge ex Desm.

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## INTRODUCTION

Fungi classified in the genus *Septoria* Sacc. are asexual morphs of *Ascomycota* causing leaf spot diseases on many cultivated and wild plants. Some 3000 *Septoria* names have been described in literature (Verkley *et al.* 2004a, b). Sexual morphs are unknown for most taxa, but those reported were mostly classified in *Mycosphaerella* and *Sphaerulina* (Von Arx 1983, Sutton & Hennebert 1994, Crous *et al.* 2000, Verkley & Priest 2000, Crous *et al.* 2001, Aptroot 2006). Several overviews of the taxonomic work done on these fungi have been provided in the literature (Shin & Sameva 2004, Priest 2006, Quaedvlieg *et al.* 2013). Priest (2006) discussed the complex nomenclatural history of *Septoria*. The type species of *Septoria*, *S. cytisi*, is a fungus occurring on the woody legume *Cytisus laburnum* (= *Laburnum anagyroides*) and several other, mostly herbaceous *Fabaceae* (Farr 1992, Muthumary 1999). The phylogenetic position of this species for which no cultures are available has for long been uncertain. However, using well-identified herbarium material, Quaedvlieg *et al*. (2011) were able to extract DNA and successfully amplify and sequence nuclear ribosomal RNA genes to determine its position in a comprehensive phylogeny inferred for *Mycosphaerellaceae*.

Most taxonomists adopted a generic concept of *Septoria* that included fungi forming pycnidial conidiomata with holoblastic, hyaline, smooth-walled conidiogenous cells with sympodial and/or percurrent proliferation and hyaline, smooth, filiform to cylindrical multi-septate conidia (Sutton 1980, Constantinescu 1984, Sutton & Pascoe 1987, 1989, Farr 1991, 1992). Similar fungi forming acervular conidiomata were classified in *Phloeospora*, with *Phloeospora ulmi* as the type species, yet some researchers adopted a broader concept to include *Phloeospora* in *Septoria* (Jørstad 1965, Von Arx 1983, Andrianova 1987, Braun 1995). Recent DNA-sequencing studies have shown that the morphological characters that were used to delimit coelomycete genera in the past, in particular those pertaining to conidiomatal structure and conidiogenesis, did not correlate well with the sequence-inferred phylogenies (Crous *et al.* 2001, Verkley *et al.* 2004a, b). Quaedvlieg *et al.* (2013) present in their broad-scope study the results of an in-depth morphological and multi-gene sequence analyses of the septoria-like genera based on numerous isolates (including *S. cytisi*). In their study, they resolve the affinities and settle the nomenclature of all important septoria-like genera in the *Dothideales* and *Pleosporales*.

Host specificity has long been a decisive criterium in species delimitation in *Septoria*, mainly because of the paucity of useful morphological characters and the high level of variation therein. Traditionally, species of *Septoria* that were morphologically very similar but found on plants of different host families, were regarded as distinct taxa. Material from the same genus or from closely related host genera from the same plant family that could be distinguished by features such as conidial length and/or width and septation were usually also considered to belong to separate species. Most taxonomists revising *Septoria* lacked facilities to thoroughly investigate host ranges. A number of economically important *Septoria* species and species complexes have been subjected to infection experiments on various hosts, viz. the pathogens of *Apium* (Cochran 1932, Sheridan 1968) and cultivated *Chrysanthemum* (Waddell & Weber 1963, Punithalingam & Wheeler 1965). The results of these studies largely seemed to confirm the general belief that *Septoria* species have host ranges that are limited to a single genus of plants and in relatively few cases, also include a few closely related genera from the same plant family (Priest 2006). Molecular phylogenetic studies on *Septoria* species infecting *Asteraceae* (Verkley & Starink-Willemse 2004) and woody perennials (Feau *et al.* 2006) showed that species that are capable of infecting hosts of the same plant family do not (always) cluster in monophyletic groups, which is indicative of disjunct evolutionary patterns of these pathogens and their hosts. To explain these patterns, it has been postulated that "host jumping" occurs from typical (susceptible) hosts to "non-host" plants through asymptomatic tissue infection and subsequent exploration of new susceptible hosts. Examples of this were found in certain *Mycosphaerella* species and their *Acacia* hosts (Crous *et al.* 2004b, Crous & Groenewald 2005), but the mechanisms driving host jumping are not yet understood. With our study in which we investigate the phylogenetic relationships of species from a wider spectrum of host families we hope to provide more insight into the evolution of these fungal pathogens and their host plants and to contribute to understanding such mechanisms.

Early molecular phylogenetic studies have confirmed the relationships of septoria-like fungi with sexual morphs within *Mycosphaerellaceae*, and that the septoria-like fungi are of poly- and paraphyletic origins (Stewart *et al.* 1999, Crous *et al.* 2001, Goodwin *et al.* 2001, Verkley *et al.* 2004a, b, Verkley & Starink-Willemse, 2004). The ITS and/or LSU nrDNA sequence data used in those studies did not provide sufficient phylogenetic information to discriminate closely related species nor resolve most of the internal nodes in the trees. Verkley *et al.* (2004a, b) already concluded that groups within the then known "*Mycosphaerella* clade" showed no correlation to conidiomatal structure or conidiogenesis, confirming the conclusions drawn by Crous *et al.* (2001). Feau *et al.* (2006) sequenced the ITS, partial β-tubulin gene, and a proportion of the mitochondrial small subunit ribosomal gene (mtSSU) to infer a phylogeny for *Septoria* associated with diseases of woody perennials (many of which are here transferred to *Sphaerulina*). Although their inferred trees provided improved resolution, it was clear that even more DNA loci would be needed to fully resolve closely related species and species complexes within *Septoria s. str.*

The primary goal of our work was to improve the taxonomy of *Septoria* by adopting a polyphasic approach to taxon delimitation. To this end we studied cultures preserved in CBS, Utrecht, the Netherlands and material freshly collected in the field, did a full characterisation of the morphology *in planta* and *in vitro*, and sequenced seven DNA loci, viz. nuclear ITS and (partial) LSU ribosomal RNA genes, and RPB2, actin (Act), calmodulin (Cal), β-tubulin (Btub), and translation elongation factor 1-alpha (EF) genes. The obtained datasets of the seven loci were also evaluated for PCR amplification success rates and barcode gaps in order to determine which individual, or combination of loci, would be best suited for fast and reliable species resolution and identification.

Most students of *Septoria* have focused on material on the natural substrate and did not isolate and deposit cultures in public culture collections. Of all material we were able to successfully isolate, cultures were deposited in CBS-KNAW Fungal Biodiversity Centre (CBS) in Utrecht, The Netherlands. To assess the nomenclature this material was compared to type material as far as it could be obtained for study. Where useful new material and associated pure cultures were designated as epitypes, to facilitate future work. This study supplements the work of Quaedvlieg *et al.* (2013), who attain a broader perspective and address the complicated taxonomy and polyphyly of septoria-like fungi, proposing several new genera for taxa that are distantly related to *Septoria cytisi* and allied species.

## MATERIAL AND METHODS

### Collecting, isolating and morphological comparison

Infected plant material was collected in the field and taken to the laboratory. Leaves were examined directly under a stereomicroscope to observe sporulating structures, or when insufficiently developed, incubated in a Petri-dish with wetted filter paper for 1–2 d to enhance the development of fruiting bodies. Cirrhi of spores were removed and mounted in tapwater for the microscopic examination of conidia. Isolates were obtained by either transferring cirrhi directly onto 3 % malt extract agar (MEA, Oxoid) plates with 50 ppm penicillin and streptomycin, and streaked over the agar surface with an inoculation loop and some sterile water. Sometimes conidia in water from slide preparations were taken with a loop and streaked directly onto a plate. After 1–3 d at room temperature, germinated conidia were transferred on to fresh media without antibiotics. New isolates were deposited in the CBS. Cultures taken from the CBS Collection were activated from lyophilised or cryopreserved material and inoculated on oatmeal (OA) and MEA plates. A complete overview of the material used in this study is presented in Table 1.

For the morphological study *in planta* hand sections were made from infected leaves, mounted in water and examined under an Olympus BX 50 microscope equipped with bright field and differential interference contrast (DIC) objectives, and photographed using a mounted Nikon Digital Sight DS-5M camera. Conidial masses were mounted in water and 30 spores measured. For culture studies, 7–14-d-old cultures were transferred to fresh OA, MEA and cherry decoction agar (CHA) plates and placed in an incubator under n-UV light (12 h light, 12 h dark) at 15 ºC to promote sporulation (if otherwise, this is indicated in the descriptions). Media were prepared according to Crous *et al.* (2009). Colony colours were described according to Rayner (1970). Sporulating structures obtained from cultures were used for the morphological description *in vitro*. Photographs of culture plates were taken after 2–3 wk on a photo stand with daylight tubes with a Pentax K110 D digital camera. Cultures were incubated up to 40 d to observe sporulation and other features.

## DNA isolation, PCR and sequencing

Genomic DNA was extracted from fungal mycelium growing on MEA, using the UltraClean® Microbial DNA Isolation Kit (Mo Bio Laboratories, Inc., Solana Beach, CA, USA). Strains (Table 1) were sequenced for seven loci: Actin (Act), calmodulin (Cal), β-tubulin (Btub), internal transcribed spacer (ITS), Translation elongation factor 1-alpha (EF) 28S nrDNA (LSU) and RNA polymerase II second largest subunit (RPB2); the primer sets listed in Table 2 were used. The PCR amplifications were performed in a total volume of 12.5 µL solution containing 10–20 ng of template DNA, 1 × PCR buffer, 0.7 µL DMSO (99.9 %), 2 mM $MgCl_2$, 0.4 µM of each primer, 25 µM of each dNTP and 1.0 U Taq DNA polymerase (GoTaq, Promega). PCR amplification conditions were set as follows: an initial denaturation temperature of 96 °C for 2 min, followed by 40 cycles at the denaturation temperature of 96 °C for 45 s, primer annealing at the temperature stipulated in Table 2, primer extension at 72 °C for 90 s and a final extension step at 72 °C for 2 min. The resulting fragments were sequenced using the PCR primers together with a BigDye Terminator Cycle Sequencing Kit v. 3.1 (Applied Biosystems, Foster City, CA). Sequencing reactions were performed as described by Cheewangkoon *et al*. (2008). All novel sequences were deposited in NCBI's GenBank database and alignments and phylogenetic trees in TreeBASE.

## Sequence alignement and phylogenetic analyses

A basic alignment of the obtained sequence data was first done using MAFFT v. 7 (http://mafft.cbrc.jp/alignment /server/index. html; Katoh *et al*. 2002) and if necessary, manually improved in BioEdit v. 7.0.5.2 (Hall 1999). To check the congruency of the multigene dataset, a 70 % neighbour-joining (NJ) reciprocal bootstrap method with maximum likelihood distance was performed (Mason-Gamer & Kellogg 1996, Lombard *et al.* 2010). Bayesian analyses (critical value for the topological convergence diagnostic set to 0.01) were performed on the concatenated loci using MrBayes v. 3.2.1 (Huelsenbeck & Ronquist 2001) as described by Crous *et al.* (2006a) using nucleotide substitution models that were selected using MrModeltest (Table 3) (Nylander 2004).

### Kimura-2-parameter values

The inter-and intraspecific distances for each individual dataset were calculated using MEGA v. 4.0 (Tamura *et al*. 2007) with the Kimura-2-parameter (pairwise deletion) model.

## RESULTS

## Identification of the best DNA barcode loci for *Septoria* species

### Amplification success

The PCR amplification success rates were very high for all seven loci, varying from 97 % for RPB2 to 100 % for ITS and LSU (Table 3). Good amplification reactions of RPB2 required a 2–3 times higher DNA input then the other loci and this locus is therefore less favorable for easy identification. The other six loci amplified without problems.

### Kimura-2-parameter values

The Kimura-2-parameter (K2P) distribution graphs are depicted in Fig. 1. They visualise the inter- and intraspecific distances per locus (barcoding gap). A good barcoding locus should have no overlap between the inter- and intraspecific K2P distances and should have an average interspecific distance that is at least 10 times as high as the average intraspecific distance of that locus (Hebert *et al*. 2003). The seven loci show a rather constant degree of intraspecific variation of 0.01 in their K2P distribution graphs, however their interspecific variations shows considerable differences. The average interspecific variation in both ITS and LSU datasets is very low (0.015) compared to their intraspecific variation (0.01), leading to a very low inter- to intraspecific variation ratios of 1.5 : 1 for these two loci (Fig. 1). These low ratios are far below the required 10 : 1 ratio, indicating a general lack of natural variation within these two loci, making them ill-suited for effective identification of the individual species used in this dataset. These low K2P results for ITS and LSU are consistent with

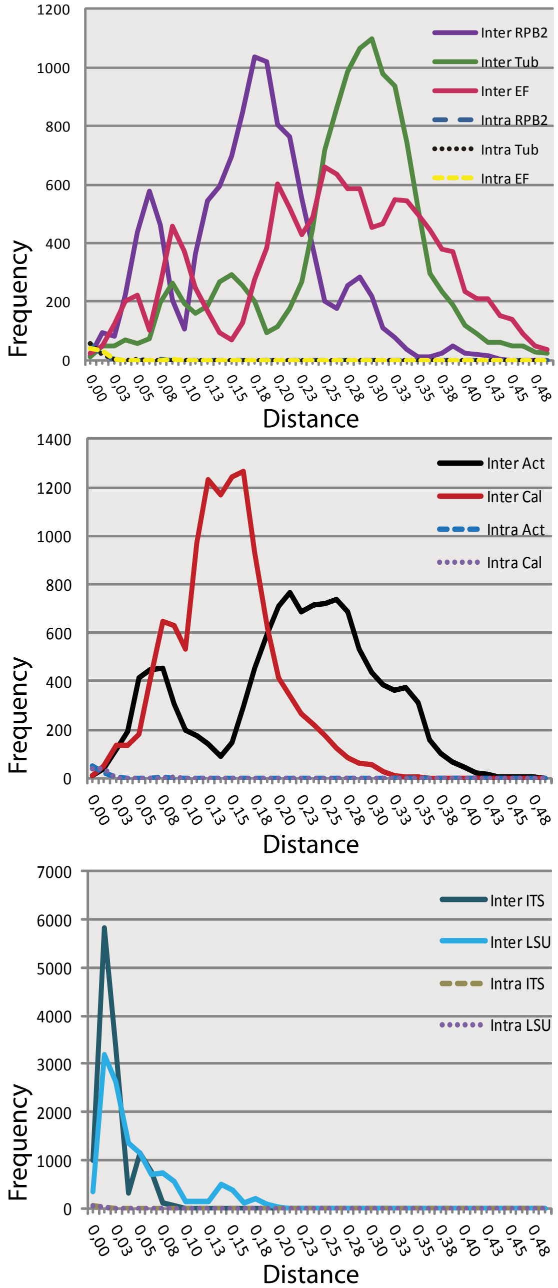


**Fig. 1.** Frequency distributions of the Kimura-2-parameter distances (barcoding gaps) for the seven PCR loci.

**Table 1.** Isolates used during this study.

| Species | Old name | Isolate no[1] | Host | Location | Collector | GenBank Accession no[2] | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | | | EF | Tub | RPB2 | LSU | ITS | Act | Cal |
| *Caryophylloseptoria lychnidis* | *Septoria lychnidis* | CBS 109098 | *Silene pratensis* | Austria | G.J.M. Verkley | KF253234 | KF252768 | KF252292 | KF251790 | KF251286 | KF253595 | KF253949 |
| | *Septoria lychnidis* | CBS 109099 | *Silene pratensis* | Austria | G.J.M. Verkley | KF253235 | KF252769 | KF252293 | KF251791 | KF251287 | KF253596 | KF253950 |
| | *Septoria lychnidis* | CBS 109101 | *Silene pratensis* | Austria | G.J.M. Verkley | KF253236 | KF252770 | KF252294 | KF251792 | KF251288 | KF253597 | KF253951 |
| | *Septoria lychnidis* | CBS 109102 | *Silene pratensis* | Austria | G.J.M. Verkley | KF253237 | KF252771 | KF252295 | KF251793 | KF251289 | KF253598 | KF253952 |
| *Car. pseudolychnidis* | *Septoria lychnidis* | CBS 128614 | *Lychnis cognata* | South Korea | H.D. Shin | KF253238 | KF252772 | KF252296 | KF251794 | KF251290 | KF253599 | KF253953 |
| | *Septoria lychnidis* | CBS 128630 | *Lychnis cognata* | South Korea | H.D. Shin | KF253239 | KF252773 | KF252297 | KF251795 | KF251291 | KF253600 | KF253954 |
| *Car. silenes* | *Septoria silenes* | CBS 109100 | *Silene nutans* | Austria | G.J.M. Verkley | KF253240 | KF252774 | KF252298 | KF251796 | KF251292 | KF253601 | KF253955 |
| | *Septoria silenes* | CBS 109103 | *Silene pratensis* | Austria | G.J.M. Verkley | KF253241 | KF252775 | KF252299 | KF251797 | KF251293 | KF253602 | KF253956 |
| *Car. spergulae* | *Septoria* sp. | CBS 109010 | *Spergula morisonii* | Netherlands | A. Aptroot | KF253242 | KF252776 | KF252300 | KF251798 | KF251294 | KF253603 | KF253957 |
| | *Septoria dianthi* | CBS 397.52 | *Dianthus caryophyllus* | Netherlands | Schouten | KF253243 | KF252777 | KF252301 | KF251799 | KF251295 | KF253604 | KF253958 |
| *Cercospora apii* | – | CBS 118712 | – | Fiji | P. Tyler | KF253244 | KF252778 | KF252302 | KF251800 | KF251296 | KF253605 | KF253959 |
| *Cer. ariminensis* | – | CBS 137.56 | *Hedysarum coronarium* | Italy | M. Ribaldi | KF253245 | KF252779 | KF252303 | KF251801 | KF251297 | KF253606 | KF253960 |
| *Cer. beticola* | – | CBS 124.31 | – | Romania | E.W. Schmidt | KF253246 | KF252780 | KF252304 | KF251802 | KF251298 | KF253607 | KF253961 |
| *Cercospora* sp. | – | CBS 112737 | *Rhus typhina* | Canada | K.A. Seifert | KF253247 | KF252781 | – | KF251803 | KF251299 | KF253608 | KF253962 |
| *Cer. zebrina* | – | CBS 118790 | *Trifolium subterraneum* | Australia | M.J. Barbetti | KF253248 | KF252782 | KF252305 | KF251804 | KF251300 | KF253609 | KF253963 |
| *Cercosporella virgaureae* | – | CBS 113304 | *Erigeron annuus* | South Korea | H.D. Shin | KF253249 | – | KF252306 | KF251805 | KF251301 | KF253610 | KF253964 |
| *Dothistroma pini* | – | CBS 121011 | *Pinus palassiana* | Ukraine | A.C. Usichenko | KF253250 | – | KF252307 | KF251806 | KF251302 | KF253611 | KF253965 |
| *Dot. septosporum* | – | CBS 383.74 | *Pinus coulteri* | France | M. Morelet | KF253251 | – | KF252308 | KF251807 | KF251303 | KF253612 | KF253966 |
| *Mycosphaerella brassicicola* | – | CBS 228.32 | *Brassica oleracea* | Denmark | C.A. Jörgensen | KF253252 | KF252783 | KF252309 | KF251808 | KF251304 | KF253613 | KF253967 |
| | – | CBS 267.53 | *Brassica oleracea* | Netherlands | F. Quak | KF253253 | KF252784 | KF252310 | KF251809 | KF251305 | KF253614 | KF253968 |
| *Myc. capsellae* | – | CBS 112033 | *Brassica* sp. | UK | R. Evans | KF253254 | KF252785 | KF252311 | KF251810 | KF251306 | KF253615 | KF253969 |
| | *Mycosphaerella* sp. | CBS 135464; CPC 11677 | *Brassica* sp. | UK | R. Evans | – | KF252786 | KF252312 | KF251811 | KF251307 | KF253616 | KF253970 |
| *Passalora depressa* | – | CPC 14915 | *Angelica gigas* | South Korea | H.D. Shin | KF253256 | KF252788 | KF252314 | KF251813 | KF251309 | – | KF253972 |
| *Pas. dioscoreae* | – | CBS 135460; CPC 10855 | *Dioscorea tokora* | South Korea | H.D. Shin | KF253257 | KF252789 | KF252315 | KF251814 | KF251310 | KF253618 | – |
| | – | CBS 135463; CPC 11513 | *Dioscorea tenuipes* | South Korea | H.D. Shin | KF253258 | KF252790 | KF252316 | KF251815 | KF251311 | KF253619 | – |
| *Pas. dissiliens* | – | CBS 219.77 | *Vitis vinifera* | Iraq | M.S.A. Al-Momen | KF253259 | KF252791 | KF252317 | KF251816 | KF251312 | KF253620 | – |
| *Pas. fusimaculans* | – | CPC 17277 | *Agrostis* sp. | Thailand | Pheng Pheng | KF253260 | KF252792 | KF252318 | KF251817 | KF251313 | KF253621 | KF253973 |
| *Pas. janseana* | – | CBS 145.37 | – | – | E.C. Tullis | KF253261 | KF252793 | – | KF251818 | KF251314 | KF253622 | KF253974 |

**Table 1.** (Continued).

| Species | Old name | Isolate no[1] | Host | Location | Collector | GenBank Accession no[2] | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | | | EF | Tub | RPB2 | LSU | ITS | Act | Cal |
| *Passalora* sp. | – | CBS 113998 | *Cajanus cajan* | South Africa | L. van Jaarsveld | KF253262 | KF252794 | KF252319 | KF251819 | KF251315 | KF253623 | – |
| *Passalora* sp. | – | CBS 113999 | *Cajanus cajan* | South Africa | L. van Jaarsveld | KF253263 | KF252795 | KF252320 | KF251820 | KF251316 | KF253624 | – |
| *Passalora* sp. | – | CBS 114275 | *Cajanus cajan* | South Africa | L. van Jaarsveld | KF253264 | KF252796 | KF252321 | KF251821 | KF251317 | – | – |
| *Pseudocercospora madagascariensis* | – | CBS 124155 | *Eucalyptus camaldulensis* | Madagascar | M.J. Wingfield | KF253265 | – | KF252322 | KF251822 | KF251318 | KF253625 | – |
| *Pse. pyracanthae* | – | CPC 10808 | *Pyracantha angustifolia* | South Korea | H.D. Shin | KF253266 | – | KF252323 | KF251823 | KF251319 | KF253626 | – |
| *Pse. pyracanthigena* | – | CBS 112032 | *Pyracantha angustifolia* | South Korea | M.J. Park | KF253267 | KF252797 | KF252324 | KF251824 | KF251320 | KF253627 | KF253975 |
| *Pse. rhoina* | – | CPC 11464 | *Rhus chinensis* | South Korea | H.D. Shin | KF253268 | – | KF252325 | KF251825 | KF251321 | – | – |
| *Pse. schizolobii* | – | CBS 120029 | *Schizolobium parahybum* | Ecuador | M.J. Wingfield | KF253269 | KF252798 | KF252326 | KF251826 | KF251322 | KF253628 | – |
| | – | CBS 124990 | *Eucalyptus camaldulensis* | Thailand | W. Himaman | KF253270 | – | KF252327 | KF251827 | KF251323 | KF253629 | – |
| *Pse. tereticornis* | – | CBS 124996 | *Eucalyptus nitens* | Australia | A.J. Cargenie | KF253271 | KF252799 | KF252328 | KF251828 | KF251324 | KF253630 | KF253976 |
| *Pseudocercosporella capsellae* | – | CBS 118412 | *Brassica* sp. | New Zealand | C.F. Hill | KF253272 | KF252800 | KF252329 | KF251829 | KF251325 | KF253631 | KF253977 |
| | – | CBS 127.29 | – | – | K. Togashi | KF253273 | KF252801 | KF252330 | KF251830 | KF251326 | KF253632 | KF253978 |
| *Pella. magnusiana* | – | CBS 114735 | *Geranium silvaticum* | Sweden | E. Gunnerbeck | KF253274 | KF252802 | – | KF251831 | KF251327 | – | KF253979 |
| *Pella. pastinacae* | – | CBS 114116 | *Laserpitium latifolium* | Sweden | K. & L. Holm | KF253275 | KF252803 | KF252331 | KF251832 | KF251328 | KF253633 | KF253980 |
| *Ramularia endophylla* | – | CBS 113265 | *Quercus robur* | Netherlands | G.J.M. Verkley | KF253276 | – | KF252332 | KF251833 | KF251329 | KF253634 | KF253981 |
| *Ram. eucalypti* | – | CBS 120726 | *Eucalyptus grandiflora* | Italy | W. Gams | KF253277 | – | KF252333 | KF251834 | KF251330 | KF253635 | KF253982 |
| *Ram. lamii* | – | CPC 11312 | *Leonurus sibiricus* | South Korea | H.D. Shin | KF253278 | – | KF252334 | KF251835 | KF251331 | KF253636 | KF253983 |
| *Readeriella mirabilis* | – | CBS 125000 | *Eucalyptus globulus* | Australia | I.W. Smith | KF253279 | KF252804 | KF252335 | KF251836 | KF251332 | KF253637 | KF253984 |
| *Septoria abei* | – | CBS 128598 | *Hibiscus syriacus* | South Korea | H.D. Shin | KF253280 | KF252805 | KF252336 | KF251837 | KF251333 | KF253638 | KF253985 |
| *Sep. aegopodina* | – | CBS 123740 | *Aegopodium podagraria* | Czech Republic | G.J.M. Verkley | KF253281 | KF252806 | – | KF251838 | KF251334 | KF253639 | KF253986 |
| | – | CBS 123741 | *Aegopodium podagraria* | Czech Republic | G.J.M. Verkley | KF253282 | KF252807 | – | KF251839 | KF251335 | KF253640 | KF253987 |
| *Sep. agrimoniicola* | – | CBS 128585 | *Agrimonia pilosa* | South Korea | H.D. Shin | KF253283 | KF252808 | KF252337 | KF251840 | KF251336 | KF253641 | KF253988 |
| | – | CBS 128602 | *Agrimonia pilosa* | South Korea | H.D. Shin | KF253284 | KF252809 | KF252338 | KF251841 | KF251337 | – | KF253989 |
| *Sep. anthrisci* | – | CBS 109019 | *Anthriscus* sp. | Austria | G.J.M. Verkley | KF253285 | KF252810 | KF252339 | KF251842 | KF251338 | KF253642 | KF253990 |
| | – | CBS 109020 | *Anthriscus* sp. | Austria | G.J.M. Verkley | KF253286 | KF252811 | KF252340 | KF251843 | KF251339 | KF253643 | KF253991 |
| *Sep. anthurii* | – | CBS 148.41 | *Anthurium* sp. | – | P. Kotthoff | KF253287 | KF252812 | KF252341 | KF251844 | KF251340 | KF253644 | KF253992 |
| | – | CBS 346.58 | *Anthurium* sp. | Germany | R. Schneider | KF253288 | KF252813 | KF252342 | KF251845 | KF251341 | KF253645 | KF253993 |
| *Sep. apiicola* | – | CBS 116465 | *Apium graveolens* | Netherlands | R. Munning | KF253289 | KF252814 | KF252343 | KF251846 | KF251342 | KF253646 | KF253994 |
| | – | CBS 389.59 | *Apium graveolens* | Italy | M. Ribaldi | KF253290 | KF252815 | KF252344 | KF251847 | KF251343 | KF253647 | KF253995 |
| | – | CBS 395.52 | *Apium* sp. | Netherlands | G. van den Ende | KF253291 | KF252816 | KF252345 | KF251848 | KF251344 | KF253648 | KF253996 |

**Table 1.** (Continued).

| Species | Old name | Isolate no[1] | Host | Location | Collector | GenBank Accession no[2] | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | | | EF | Tub | RPB2 | LSU | ITS | Act | Cal |
| | – | CBS 400.54 | *Apium graveolens* | Netherlands | J.A. von Arx | KF253292 | KF252817 | KF252346 | KF251849 | KF251345 | KF253649 | KF253997 |
| *Sep. astericola* | – | CBS 128587 | *Aster tataricus* | South Korea | H.D. Shin | KF253293 | KF252818 | KF252347 | KF251850 | KF251346 | KF253650 | KF253998 |
| | – | CBS 128593 | *Aster yomena* | South Korea | H.D. Shin | KF253294 | KF252819 | KF252348 | KF251851 | KF251347 | KF253651 | KF253999 |
| *Sep. astragali* | – | CBS 109117 | *Astragalus glycyphyllos* | Austria | G.J.M. Verkley | KF253296 | KF252821 | KF252350 | KF251853 | KF251349 | KF253653 | KF254001 |
| | – | CBS 123878 | *Astragalus glycyphyllos* | Czech Republic | G.J.M. Verkley | KF253297 | KF252822 | KF252351 | KF251854 | KF251350 | KF253654 | KF254002 |
| | – | CBS 109116 | *Astragalus glycyphyllos* | Austria | G.J.M. Verkley | KF253298 | KF252823 | KF252352 | KF251855 | KF251351 | KF253655 | KF254003 |
| *Sep. atropurpurea* | – | CBS 348.58 | *Aster canus* | Germany | R. Schneider | KF253299 | KF252824 | KF252353 | KF251856 | KF251352 | KF253656 | KF254004 |
| *Sep. bothriospermi* | – | CBS 128592 | *Bothriospermum tenellum* | South Korea | H.D. Shin | KF253300 | KF252825 | KF252354 | KF251857 | KF251353 | KF253657 | KF254005 |
| | – | CBS 128599 | *Bothriospermum tenellum* | South Korea | H.D. Shin | KF253301 | KF252826 | KF252355 | KF251858 | KF251354 | KF253658 | KF254006 |
| *Sep. bupleuricola* | – | CBS 128601 | *Bupleurum longiradiatum* | South Korea | H.D. Shin | KF253302 | KF252827 | KF252356 | KF251859 | KF251355 | KF253659 | KF254007 |
| | – | CBS 128603 | *Bupleurum falcatum* | South Korea | H.D. Shin | KF253303 | KF252828 | KF252357 | KF251860 | KF251356 | KF253660 | KF254008 |
| *Sep. calendulae* | – | CBS 349.58 | *Calendula arvensis* | Italy | R. Schneider | KF253304 | KF252829 | KF252358 | KF251861 | KF251357 | KF253661 | KF254009 |
| *Sep. callistephi* | – | CBS 128590 | *Callistephus chinensis* | South Korea | H.D. Shin | KF253305 | KF252830 | KF252359 | KF251862 | KF251358 | KF253662 | KF254010 |
| | – | CBS 128594 | *Callistephus chinensis* | South Korea | H.D. Shin | KF253306 | KF252831 | KF252360 | KF251863 | KF251359 | KF253663 | KF254011 |
| *Sep. campanulae* | – | CBS 128589 | *Campanula takesimana* | South Korea | H.D. Shin | KF253307 | KF252832 | KF252361 | KF251864 | KF251360 | KF253664 | KF254012 |
| | – | CBS 128604 | *Campanula takesimana* | South Korea | H.D. Shin | KF253308 | KF252833 | KF252362 | KF251865 | KF251361 | KF253665 | KF254013 |
| *Sep. cerastii* | – | CBS 102323 | *Cerastium fontanum* | Netherlands | G.J.M. Verkley | KF253309 | KF252834 | KF252363 | KF251866 | KF251362 | KF253666 | KF254014 |
| | – | CBS 128586 | *Cerastium holosteoides* | South Korea | H.D. Shin | KF253310 | KF252835 | KF252364 | KF251867 | KF251363 | KF253667 | KF254015 |
| | – | CBS 128612 | *Cerastium holosteoides* | South Korea | H.D. Shin | KF253311 | KF252836 | KF252365 | KF251868 | KF251364 | KF253668 | KF254016 |
| | – | CBS 128626 | *Cerastium holosteoides* | South Korea | H.D. Shin | KF253312 | KF252837 | KF252366 | KF251869 | KF251365 | KF253669 | KF254017 |
| | – | CPC 12343 | *Cerastium holosteoides* | South Korea | H.D. Shin | KF253313 | KF252838 | KF252367 | KF251870 | KF251366 | KF253670 | KF254018 |
| *Sep.* cf. *rubi* | *Septoria* sp. | CPC 12331 | *Rubus crataegifolius* | South Korea | H.D. Shin | KF253317 | KF252842 | KF252371 | KF251874 | KF251370 | KF253674 | KF254022 |
| | *Septoria rubi* | CBS 128646 | *Rubus crataegifolius* | South Korea | H.D. Shin | KF253314 | KF252839 | KF252368 | KF251871 | KF251367 | KF253671 | KF254019 |
| | *Septoria rubi* | CBS 128648 | *Rubus crataegifolius* | South Korea | H.D. Shin | KF253315 | KF252840 | KF252369 | KF251872 | KF251368 | KF253672 | KF254020 |
| | *Septoria rubi* | CBS 128760 | *Rubus crataegifolius* | South Korea | H.D. Shin | KF253316 | KF252841 | KF252370 | KF251873 | KF251369 | KF253673 | KF254021 |
| *Sep.* cf. *sonchi* | – | CBS 128757 | *Sonchus asper* | South Korea | H.D. Shin | KF253500 | KF253020 | KF252546 | KF252057 | KF251552 | KF253855 | KF254204 |
| *Sep.* cf. *stachydicola* | *Septoria lycopicola* | CBS 128662 | *Stachys riederi* | South Korea | H.D. Shin | KF253513 | KF253034 | KF252559 | KF252071 | KF251566 | KF253867 | KF254218 |
| *Sep. chamaecisti* | – | CBS 350.58 | *Helianthemum hybridum* | Germany | R. Schneider | KF253318 | KF252843 | KF252372 | KF251875 | KF251371 | KF253675 | KF254023 |
| *Sep. chelidonii* | – | CBS 128607 | *Chelidonium majus* | South Korea | H.D. Shin | KF253319 | KF252844 | KF252373 | KF251876 | KF251372 | KF253676 | KF254024 |
| | – | CPC 12337 | *Chelidonium majus* | South Korea | H.D. Shin | KF253320 | KF252845 | KF252374 | KF251877 | KF251373 | KF253677 | KF254025 |
| *Sep. chromolaenae* | – | CBS 113373 | *Chromolaena odorata* | Cuba | S. Neser | KF253321 | KF252846 | KF252375 | KF251878 | KF251374 | KF253678 | KF254026 |

**Table 1.** (Continued).

| Species | Old name | Isolate no[1] | Host | Location | Collector | GenBank Accession no[2] | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | | | EF | Tub | RPB2 | LSU | ITS | Act | Cal |
| *Sep. chrysanthemella* | – | CBS 128617 | *Chrysanthemum morifolium* | South Korea | H.D. Shin | KF253322 | KF252847 | KF252376 | KF251879 | KF251375 | KF253679 | KF254027 |
| | – | CBS 128622 | *Chrysanthemum boreale* | South Korea | H.D. Shin | KF253323 | KF252848 | KF252377 | KF251880 | KF251376 | KF253680 | KF254028 |
| | – | CBS 483.63 | *Chrysanthemum* sp. | Netherlands | H.A. van der Aa | KF253324 | KF252849 | KF252378 | KF251881 | KF251377 | KF253681 | KF254029 |
| | – | CBS 128716 | – | South Africa | E. Oh | KF253325 | KF252850 | KF252379 | KF251882 | KF251378 | KF253682 | KF254030 |
| | – | CBS 351.58 | *Chrysanthemum indicum* | Germany | R. Schneider | KF253326 | KF252851 | KF252380 | KF251883 | KF251379 | KF253683 | KF254031 |
| | – | CBS 354.73 | *Chrysanthemum morifolium* | New Zealand | G.F. Laundon | KF253327 | KF252852 | KF252381 | KF251884 | KF251380 | KF253684 | KF254032 |
| *Sep. cirsii* | – | CBS 128621 | *Cirsium setidens* | South Korea | H.D. Shin | KF253328 | KF252853 | KF252382 | KF251885 | KF251381 | KF253685 | KF254033 |
| *Sep. citri* (= *protearum* complex) | | | | | | | | | | | | |
| | *Septoria orchidearum* | CBS 101013 | *Masdevallia* sp. | Netherlands | W. Veenbaas-Rijks | KF253457 | KF252978 | KF252504 | KF252013 | KF251508 | KF253812 | KF254161 |
| | *Septoria* sp. | CBS 101354 | *Gevuina avellana* | New Zealand | S. Ganev | KF253458 | KF252979 | KF252505 | KF252014 | KF251509 | KF253813 | KF254162 |
| | *Septoria lobeliae* | CBS 113392 | *Lobelia erinus* | – | S. Wolcon | KF253460 | KF252981 | KF252507 | KF252016 | KF251511 | KF253815 | KF254164 |
| | *Septoria aciculosa* | CBS 177.77 | *Fragaria* sp. | New Zealand | H.J. Boesewinkel | KF253463 | KF252984 | KF252509 | KF252019 | KF251514 | KF253818 | KF254167 |
| | *Septoria citri* | CBS 315.37 | – | – | L.L. Huillier | KF253465 | – | KF252511 | KF252021 | KF251516 | KF253820 | KF254169 |
| | *Septoria gerberae* | CBS 410.61 | *Gerbera jamesonii* | Italy | W. Gerlach | KF253468 | KF252988 | KF252514 | KF252024 | KF251519 | KF253823 | KF254172 |
| | *Septoria hederae* | CBS 566.88 | *Hedera helix* | France | H.A. van der Aa | KF253470 | KF252990 | KF252515 | KF252026 | KF251521 | KF253825 | KF254174 |
| *Sep. citricola* | – | CBS 356.36 | *Citrus sinensis* | Italy | G. Ruggieri | KF253329 | KF252854 | KF252383 | KF251886 | KF251382 | KF253686 | KF254034 |
| *Sep. clematidis* | – | CBS 108983 | *Clematis vitalba* | Germany | G.J.M. Verkley | KF253330 | KF252855 | KF252384 | KF251887 | KF251383 | KF253687 | KF254035 |
| | – | CBS 108984 | *Clematis vitalba* | Germany | G.J.M. Verkley | KF253331 | KF252856 | KF252385 | KF251888 | KF251384 | KF253688 | KF254036 |
| *Sep. codonopsidis* | – | CBS 128609 | *Codonopsis lanceolata* | South Korea | H.D. Shin | KF253332 | KF252857 | KF252386 | KF251889 | KF251385 | KF253689 | KF254037 |
| | – | CBS 128620 | *Codonopsis lanceolata* | South Korea | H.D. Shin | KF253333 | KF252858 | KF252387 | KF251890 | KF251386 | KF253690 | KF254038 |
| *Sep. convolvuli* | – | CBS 102325 | *Calystegia sepium* | Netherlands | G.J.M. Verkley | KF253334 | KF252859 | KF252388 | KF251891 | KF251387 | KF253691 | KF254039 |
| | – | CBS 113111 | *Calystegia sepium* | New Zealand | G.J.M. Verkley | KF253335 | KF252860 | KF252389 | KF251892 | KF251388 | KF253692 | KF254040 |
| | – | CBS 128627 | *Calystegia soldanella* | South Korea | H.D. Shin | KF253336 | KF252861 | KF252390 | KF251893 | KF251389 | KF253693 | KF254041 |
| *Sep. coprosmae* | – | CBS 113391 | *Coprosma robusta* | New Zealand | G.J.M. Verkley | KF253255 | KF252787 | KF252313 | KF251812 | KF251308 | KF253617 | KF253971 |
| *Sep. crepidis* | – | CPC 12539 | *Crepis japonica* | South Korea | H.D. Shin | KF253339 | KF252864 | KF252393 | KF251896 | KF251392 | KF253696 | KF254044 |
| | – | CBS 128608 | *Youngia japonica* | South Korea | H.D. Shin | KF253337 | KF252862 | KF252391 | KF251894 | KF251390 | KF253694 | KF254042 |
| | – | CBS 128619 | *Youngia japonica* | South Korea | H.D. Shin | KF253338 | KF252863 | KF252392 | KF251895 | KF251391 | KF253695 | KF254043 |

**Table 1.** (Continued).

| Species | Old name | Isolate no[1] | Host | Location | Collector | GenBank Accession no[2] | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | | | EF | Tub | RPB2 | LSU | ITS | Act | Cal |
| *Sep. cruciatae* | *Septoria* sp. | CBS 123747 | *Galium odoratum* | Czech Republic | G.J.M. Verkley | KF253340 | KF252865 | KF252394 | KF251897 | KF251393 | KF253697 | KF254045 |
| | *Septoria* sp. | CBS 123748 | *Galium odoratum* | Czech Republic | G.J.M. Verkley | KF253341 | KF252866 | KF252395 | KF251898 | KF251394 | KF253698 | KF254046 |
| *Sep. cucubali* | – | CBS 102367 | *Cucubalus baccifer* | Netherlands | G.J.M. Verkley | KF253342 | KF252867 | KF252396 | KF251899 | KF251395 | KF253699 | KF254047 |
| | – | CBS 102368 | *Cucubalus baccifer* | Netherlands | G.J.M. Verkley | KF253343 | KF252868 | KF252397 | KF251900 | KF251396 | KF253700 | KF254048 |
| | – | CBS 102386 | *Saponaria officinalis* | Netherlands | G.J.M. Verkley | KF253344 | KF252869 | KF252398 | KF251901 | KF251397 | KF253701 | KF254049 |
| | *Septoria* sp. | CBS 124874 | *Fagus sylvatica* | Germany | M. Unterseher | KF253345 | KF252870 | KF252399 | KF251902 | KF251398 | KF253702 | KF254050 |
| *Sep. cucurbitacearum* | – | CBS 178.77 | *Cucurbita maxima* | New Zealand | H.J. Boesewinkel | KF253346 | – | KF252400 | KF251903 | KF251399 | KF253703 | KF254051 |
| *Sep. dearnessii* | – | CBS 128624 | *Angelica dahurica* | South Korea | H.D. Shin | KF253347 | KF252871 | KF252401 | KF251904 | KF251400 | KF253704 | KF254052 |
| *Sep. digitalis* | – | CBS 328.67 | *Digitalis lanata* | Netherlands | H.A. van der Aa | KF253348 | KF252872 | KF252402 | KF251905 | KF251401 | KF253705 | KF254053 |
| | – | CBS 391.63 | *Digitalis lanata* | Czech Republic | V. Holubová | KF253349 | KF252873 | KF252403 | KF251906 | KF251402 | KF253706 | KF254054 |
| *Sep. dolichospora* | – | CBS 129152 | *Solidago virgaurea* | South Korea | H.D. Shin | KF253350 | KF252874 | – | KF251907 | KF251403 | KF253707 | KF254055 |
| *Sep. dysentericae* | – | CBS 128637 | *Inula britannica* | South Korea | H.D. Shin | KF253351 | KF252875 | KF252404 | KF251908 | KF251404 | KF253708 | KF254056 |
| | – | CBS 128638 | *Inula britannica* | South Korea | H.D. Shin | KF253352 | KF252876 | KF252405 | KF251909 | KF251405 | KF253709 | KF254057 |
| | – | CBS 131892; CPC 12328 | *Inula britannica* | South Korea | H.D. Shin | KF253353 | KF252877 | KF252406 | KF251910 | KF251406 | KF253710 | KF254058 |
| *Sep. ekmaniana* | – | CBS 113385 | *Chromolaena odorata* | Mexico | M.J. Morris | KF253354 | KF252878 | – | KF251911 | KF251407 | KF253711 | KF254059 |
| | – | CBS 113612 | *Chromolaena odorata* | Mexico | M.J. Morris | KF253355 | KF252879 | – | KF251912 | KF251408 | KF253712 | KF254060 |
| *Sep. epambrosiae* | – | CBS 128629 | *Ambrosia trifida* | South Korea | H.D. Shin | KF253356 | KF252880 | KF252407 | KF251913 | KF251409 | KF253713 | KF254061 |
| | – | CBS 128636 | *Ambrosia trifida* | South Korea | H.D. Shin | KF253357 | KF252881 | KF252408 | KF251914 | KF251410 | KF253714 | KF254062 |
| *Sep. epilobii* | – | CBS 109084 | *Epilobium fleischeri* | Austria | G.J.M. Verkley | KF253358 | KF252882 | KF252409 | KF251915 | KF251411 | KF253715 | KF254063 |
| | – | CBS 109085 | *Epilobium fleischeri* | Austria | G.J.M. Verkley | KF253359 | KF252883 | KF252410 | KF251916 | KF251412 | KF253716 | KF254064 |
| *Sep. erigerontis* | – | CBS 109094 | *Erigeron annuus* | Austria | G.J.M. Verkley | KF253360 | KF252884 | KF252411 | KF251917 | KF251413 | KF253717 | KF254065 |
| | – | CBS 109095 | *Erigeron annuus* | Austria | G.J.M. Verkley | KF253361 | KF252885 | KF252412 | KF251918 | KF251414 | KF253718 | KF254066 |
| | – | CBS 128606 | *Erigeron annuus* | South Korea | H.D. Shin | KF253362 | KF252886 | KF252413 | KF251919 | KF251415 | KF253719 | KF254067 |
| | – | CBS 131893; CPC 12340 | *Erigeron annuus* | South Korea | H.D. Shin | KF253363 | KF252888 | KF252414 | KF251920 | KF251416 | KF253720 | KF254068 |
| | *Septoria schnabliana* | CBS 186.93 | *Erigeron annuus* | Italy | M. Vurro | KF253364 | KF252887 | KF252537 | KF252048 | KF251543 | KF253893 | KF254244 |
| *Sep. eucalyptorum* | – | CBS 118505 | *Eucalyptus* sp. | India | W. Gams | KF253365 | KF252889 | KF252415 | KF251921 | KF251417 | KF253721 | KF254069 |
| *Sep. exotica* | – | CBS 163.78 | *Hebe speciosa* | New Zealand | H.J. Boesewinkel | KF253366 | KF252890 | KF252416 | KF251922 | KF251418 | KF253722 | KF254070 |

**Table 1.** (Continued).

| Species | Old name | Isolate no[1] | Host | Location | Collector | GenBank Accession no[2] | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | | | EF | Tub | RPB2 | LSU | ITS | Act | Cal |
| *Sep. galeopsidis* | – | CBS 123744 | *Galeopsis* sp. | Czech Republic | G.J.M. Verkley | KF253367 | KF252891 | KF252417 | KF251923 | KF251419 | KF253723 | KF254071 |
| | – | CBS 123746 | *Galeopsis* sp. | Czech Republic | G.J.M. Verkley | KF253368 | KF252892 | KF252418 | KF251924 | KF251420 | KF253724 | KF254072 |
| | – | CBS 123749 | *Galeopsis* sp. | Czech Republic | G.J.M. Verkley | KF253369 | KF252893 | KF252419 | KF251925 | KF251421 | KF253725 | KF254073 |
| | – | CBS 191.26 | *Galeopsis* sp. | – | C. Killian | KF253370 | KF252894 | KF252420 | KF251926 | KF251422 | KF253726 | KF254074 |
| | – | CBS 102314 | *Galeopsis tetrahit* | Netherlands | G.J.M. Verkley | KF253371 | KF252895 | KF252421 | KF251927 | KF251423 | KF253727 | KF254075 |
| | – | CBS 102411 | *Galeopsis tetrahit* | Netherlands | G.J.M. Verkley | KF253372 | KF252896 | KF252422 | KF251928 | KF251424 | KF253728 | KF254076 |
| | – | CBS 123745 | *Galeopsis* sp. | Czech Republic | G.J.M. Verkley | KF253373 | KF252897 | KF252423 | KF251929 | KF251425 | KF253729 | KF254077 |
| *Sep. gentianae* | – | CBS 128633 | *Gentiana scabra* | South Korea | H.D. Shin | KF253374 | KF252898 | KF252424 | KF251930 | KF251426 | KF253730 | KF254078 |
| *Sep. gladioli* | – | CBS 121.20 | – | – | – | KF253375 | KF252899 | KF252425 | KF251931 | KF251427 | KF253731 | KF254079 |
| | – | CBS 353.29 | – | Netherlands | J.C. Went | KF253376 | KF252900 | KF252426 | KF251932 | KF251428 | KF253732 | KF254080 |
| *Sep. glycines* | – | CBS 336.53 | – | Japan | H. Kurata | KF253377 | KF252901 | – | KF251933 | KF251429 | KF253733 | KF254081 |
| *Sep. glycinicola* | – | CBS 128618 | *Glycine max* | South Korea | H.D. Shin | KF253378 | KF252902 | KF252427 | KF251934 | KF251430 | KF253734 | KF254082 |
| *Sep. helianthi* | – | CBS 123.81 | *Helianthus annuus* | – | M. Muntañola | KF253379 | KF252903 | KF252428 | KF251935 | KF251431 | KF253735 | KF254083 |
| *Sep. helianthicola* | – | CBS 122.81 | *Helianthus annuus* | – | M. Muntañola | KF253380 | KF252904 | KF252429 | KF251936 | KF251432 | KF253736 | KF254084 |
| *Sep. hibiscicola* | – | CBS 128611 | *Hibiscus syriacus* | South Korea | H.D. Shin | KF253381 | KF252905 | KF252430 | KF251937 | KF251433 | KF253737 | KF254085 |
| | – | CBS 128615 | *Hibiscus syriacus* | South Korea | H.D. Shin | KF253382 | KF252906 | KF252431 | KF251938 | KF251434 | KF253738 | KF254086 |
| *Sep. hippocastani* | – | CBS 411.61 | *Aesculus hippocastanum* | Germany | W. Gerlach | KF253383 | KF252907 | KF252432 | KF251939 | KF251435 | KF253739 | KF254087 |
| *Sep. justiciae* | – | CPC 12509 | *Justicia procumbens* | South Korea | H.D. Shin | KF253386 | KF252910 | KF252435 | KF251942 | KF251438 | KF253742 | KF254090 |
| | – | CBS 128610 | *Justicia procumbens* | South Korea | H.D. Shin | KF253384 | KF252908 | KF252433 | KF251940 | KF251436 | KF253740 | KF254088 |
| | – | CBS 128625 | *Justicia procumbens* | South Korea | H.D. Shin | KF253385 | KF252909 | KF252434 | KF251941 | KF251437 | KF253741 | KF254089 |
| *Sep. lactucae* | – | CBS 108943 | *Lactuca sativa* | Netherlands | P. Grooteman | KF253387 | KF252911 | KF252436 | KF251943 | KF251439 | KF253743 | KF254091 |
| | – | CBS 352.58 | *Lactuca sativa* | Germany | G. Sörgel | KF253388 | KF252912 | KF252437 | KF251944 | KF251440 | KF253744 | KF254092 |
| *Sep. lamiicola* | – | CBS 102328 | *Lamium album* | Netherlands | G.J.M. Verkley | KF253389 | KF252913 | KF252438 | KF251945 | KF251441 | KF253745 | KF254093 |
| | – | CBS 102329 | *Lamium album* | Netherlands | G.J.M. Verkley | KF253390 | KF252914 | KF252439 | KF251946 | KF251442 | KF253746 | KF254094 |
| | – | CBS 102379 | *Lamium* sp. | Netherlands | G.J.M. Verkley | KF253391 | KF252915 | KF252440 | KF251947 | KF251443 | KF253747 | KF254095 |
| | – | CBS 102380 | *Lamium* sp. | Netherlands | G.J.M. Verkley | KF253392 | KF252916 | KF252441 | KF251948 | KF251444 | KF253748 | KF254096 |
| | – | CBS 109112 | *Lamium album* | Austria | G.J.M. Verkley | KF253393 | KF252917 | KF252442 | KF251949 | KF251445 | KF253749 | KF254097 |
| | – | CBS 109113 | *Lamium album* | Austria | G.J.M. Verkley | KF253394 | KF252918 | KF252443 | KF251950 | KF251446 | KF253750 | KF254098 |
| | – | CBS 123882 | *Lamium* sp. | Czech Republic | G.J.M. Verkley | KF253395 | KF252919 | KF252444 | KF251951 | KF251447 | KF253751 | KF254099 |

**Table 1.** (Continued).

| Species | Old name | Isolate no[1] | Host | Location | Collector | GenBank Accession no[2] | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | | | EF | Tub | RPB2 | LSU | ITS | Act | Cal |
| | – | CBS 123883 | *Lamium* sp. | Czech Republic | G.J.M. Verkley | KF253396 | KF252920 | KF252445 | KF251952 | KF251448 | KF253752 | KF254100 |
| | – | CBS 123884 | *Lamium* sp. | Czech Republic | G.J.M. Verkley | KF253397 | KF252921 | KF252446 | KF251953 | KF251449 | KF253753 | KF254101 |
| *Sep. lepidiicola* | – | CBS 128635 | *Lepidium virginicum* | South Korea | H.D. Shin | KF253398 | KF252922 | KF252447 | KF251954 | KF251450 | KF253754 | KF254102 |
| *Sep. leptostachyae* | – | CBS 128613 | *Phryma leptostachya* | South Korea | H.D. Shin | KF253399 | KF252923 | KF252448 | KF251955 | KF251451 | KF253755 | KF254103 |
| | – | CBS 128628 | *Phryma leptostachya* | South Korea | H.D. Shin | KF253400 | KF252924 | KF252449 | KF251956 | KF251452 | KF253756 | KF254104 |
| *Sep. leucanthemi* | – | CBS 109083 | *Chrysanthemum leucanthemum* | Austria | G.J.M. Verkley | KF253401 | KF252925 | KF252450 | KF251957 | KF251453 | KF253757 | KF254105 |
| | – | CBS 109086 | *Chrysanthemum leucanthemum* | Austria | G.J.M. Verkley | KF253402 | KF252926 | KF252451 | KF251958 | KF251454 | KF253758 | KF254106 |
| | – | CBS 109090 | *Chrysanthemum leucanthemum* | Austria | G.J.M. Verkley | KF253403 | KF252927 | KF252452 | KF251959 | KF251455 | KF253759 | KF254107 |
| | – | CBS 109091 | *Chrysanthemum leucanthemum* | Austria | G.J.M. Verkley | KF253404 | KF252928 | KF252453 | KF251960 | KF251456 | KF253760 | KF254108 |
| | – | CBS 113112 | *Chrysanthemum leucanthemum* | New Zealand | G.J.M. Verkley | KF253405 | KF252929 | KF252454 | KF251961 | KF251457 | KF253761 | KF254109 |
| | – | CBS 353.58 | *Chrysanthemum maximum* | Germany | R. Schneider | KF253406 | KF252930 | KF252455 | KF251962 | KF251458 | KF253762 | KF254110 |
| *Sep. limonum* | – | CBS 419.51 | *Citrus limonium* | Italy | G. Goidánich | KF253407 | KF252931 | KF252456 | KF251963 | KF251459 | KF253763 | KF254111 |
| *Sep. linicola* | – | CBS 316.37 | *Linum usitatissimum* | – | H.W. Hollenweber | KF253408 | KF252932 | KF252457 | KF251964 | KF251460 | KF253764 | KF254112 |
| *Sep. lycoctoni* | – | CBS 109089 | *Aconitum vulparia* | Austria | G.J.M. Verkley | KF253409 | KF252933 | KF252458 | KF251965 | KF251461 | KF253765 | KF254113 |
| *Sep. lycopersici* | – | CBS 128654 | *Lycopersicon esculentum* | South Korea | H.D. Shin | KF253410 | KF252934 | KF252459 | KF251966 | KF251462 | KF253766 | KF254114 |
| | – | CBS 354.49 | *Lycopersicon esculentum* | Canada | B.H. MacNeil | KF253411 | KF252935 | KF252460 | KF251967 | KF251463 | KF253767 | KF254115 |
| *Sep. lycopicola* | – | CBS 128651 | *Lycopus ramosissimus* | South Korea | H.D. Shin | KF253412 | KF252936 | KF252461 | KF251968 | KF251464 | KF253768 | KF254116 |
| *Sep. lysimachiae* | – | CBS 102315 | *Lysimachia vulgaris* | Netherlands | G.J.M. Verkley | KF253413 | KF252937 | KF252462 | KF251969 | KF251465 | KF253769 | KF254117 |
| | – | CBS 108998 | *Lysimachia vulgaris* | Netherlands | G.J.M. Verkley | KF253414 | KF252938 | KF252463 | KF251970 | KF251466 | KF253770 | KF254118 |
| | – | CBS 108999 | *Lysimachia vulgaris* | Netherlands | G.J.M. Verkley | KF253415 | KF252939 | KF252464 | KF251971 | KF251467 | KF253771 | KF254119 |
| | – | CBS 123794 | *Lysimachia* sp. | Czech Republic | G.J.M. Verkley | KF253416 | KF252940 | KF252465 | KF251972 | KF251468 | KF253772 | KF254120 |
| | – | CBS 123795 | *Lysimachia* sp. | Czech Republic | G.J.M. Verkley | KF253417 | KF252941 | KF252466 | KF251973 | KF251469 | KF253773 | KF254121 |
| *Sep. malagutii* | – | CBS 106.80 | *Solanum* sp. | Peru | G.H. Boerema | KF253418 | – | KF252467 | KF251974 | KF251470 | KF253774 | KF254122 |
| *Sep. matricariae* | – | CBS 109000 | *Matricaria discoidea* | Netherlands | G.J.M. Verkley | KF253419 | KF252942 | KF252468 | KF251975 | KF251471 | KF253775 | KF254123 |
| | – | CBS 109001 | *Matricaria discoidea* | Netherlands | G.J.M. Verkley | KF253420 | KF252943 | KF252469 | KF251976 | KF251472 | KF253776 | KF254124 |
| *Sep. mazi* | – | CBS 128656 | *Mazus japonicus* | South Korea | H.D. Shin | KF253421 | KF252944 | KF252470 | KF251977 | KF251473 | KF253777 | KF254125 |

**Table 1.** (Continued).

| Species | Old name | Isolate no[1] | Host | Location | Collector | GenBank Accession no[2] | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | | | EF | Tub | RPB2 | LSU | ITS | Act | Cal |
| | – | CBS 128755 | *Mazus japonicus* | South Korea | H.D. Shin | KF253422 | KF252945 | KF252471 | KF251978 | KF251474 | KF253778 | KF254126 |
| *Sep. melissae* | – | CBS 109097 | *Melissa officinalis* | Netherlands | H.A. van der Aa | KF253423 | KF252946 | KF252472 | KF251979 | KF251475 | KF253779 | KF254127 |
| *Sep. menthae* | – | CBS 404.34 | – | Japan | T. Hemmi | KF253424 | KF252947 | – | KF251980 | KF251476 | KF253780 | KF254128 |
| *Sep. napelli* | – | CBS 109104 | *Aconitum napellus* | Austria | G.J.M. Verkley | KF253425 | KF252948 | KF252473 | KF251981 | KF251477 | KF253781 | KF254129 |
| | – | CBS 109105 | *Aconitum napellus* | Austria | G.J.M. Verkley | KF253426 | KF252949 | KF252474 | KF251982 | KF251478 | KF253782 | KF254130 |
| | – | CBS 109106 | *Aconitum napellus* | Austria | G.J.M. Verkley | KF253427 | KF252950 | KF252475 | KF251983 | KF251479 | KF253783 | KF254131 |
| *Sep. obesa* | *Septoria artimisiae* | CBS 128588 | *Artemisia lavandulaefolia* | South Korea | H.D. Shin | KF253428 | KF252951 | KF252476 | KF251984 | KF251480 | KF253784 | KF254132 |
| | *Septoria chrysanthemella* | CBS 128623 | *Chrysanthemum indicum* | South Korea | H.D. Shin | KF253429 | KF252952 | KF252477 | KF251985 | KF251481 | KF253785 | KF254133 |
| | – | CBS 128759 | *Chrysanthemum morifolium* | South Korea | H.D. Shin | KF253430 | – | KF252478 | KF251986 | KF251482 | KF253786 | KF254134 |
| | – | CBS 354.58 | *Chrysantemum indicum* | Germany | R. Schneider | KF253431 | – | KF252479 | KF251987 | KF251483 | KF253787 | KF254135 |
| *Sep. oenanthis* | – | CBS 128667 | *Cicuta virosa* | South Korea | H.D. Shin | KF253432 | KF252953 | KF252481 | KF251989 | KF251485 | KF253788 | KF254136 |
| *Sep. oenanthicola* | *Septoria oenanthis* | CBS 128649 | *Oenanthe javanica* | South Korea | H.D. Shin | KF253433 | KF252954 | KF252480 | KF251988 | KF251484 | KF253789 | KF254137 |
| *Sep. orchidearum* | *Septoria cyclaminis* | CBS 128631 | *Cyclamen fatrense* | South Korea | H.D. Shin | KF253434 | KF252955 | KF252482 | KF251990 | KF251486 | KF253790 | KF254138 |
| | – | CBS 457.78 | *Listera ovata* | France | H.A. van der Aa | KF253435 | KF252956 | KF252483 | KF251991 | KF251487 | KF253791 | KF254139 |
| *Sep. oudemansii* | – | CBS 619.72 | *Poa pratensis* | Germany | R. Schneider | KF253436 | KF252957 | KF252484 | KF251992 | KF254299 | – | KF254140 |
| *Sep. pachyspora* | – | CBS 128652 | *Zyathoxylum schinifolium* | South Korea | H.D. Shin | KF253437 | KF252958 | KF252485 | KF251993 | KF251488 | KF253792 | KF254141 |
| *Sep. paridis* | – | CBS 109111 | *Paris quadrifolia* | Austria | G.J.M. Verkley | KF253438 | KF252959 | KF252486 | KF251994 | KF251489 | KF253793 | KF254142 |
| | – | CBS 109110 | *Paris quadrifolia* | Austria | G.J.M. Verkley | KF253439 | KF252960 | KF252487 | KF251995 | KF251490 | KF253794 | KF254143 |
| | *Septoria violae-palustris* | CBS 109108 | *Viola* sp. | Austria | G.J.M. Verkley | KF253440 | KF252961 | KF252488 | KF251996 | KF251491 | KF253795 | KF254144 |
| | *Septoria violae-palustris* | CBS 109109 | *Viola* sp. | Austria | G.J.M. Verkley | KF253441 | KF252962 | KF252489 | KF251997 | KF251492 | KF253796 | KF254145 |
| *Sep. passifloricola* | *Sep. passiflorae* | CBS 102701 | *Passiflora edulis* | New Zealand | C.F. Hill | KF253442 | KF252963 | KF252490 | KF251998 | KF251493 | KF253797 | KF254146 |
| | – | CBS 129431 | *Passiflora edulis* | South Korea | H.D. Shin | KF253443 | KF252964 | – | KF251999 | KF251494 | KF253798 | KF254147 |
| *Sep. perillae* | – | CBS 128655 | *Perilla frutescens* | South Korea | H.D. Shin | KF253444 | KF252965 | KF252491 | KF252000 | KF251495 | KF253799 | KF254148 |
| *Sep. petroselini* | – | CBS 109521 | – | Netherlands | H.A. van der Aa | KF253445 | KF252966 | KF252492 | KF252001 | KF251496 | KF253800 | KF254149 |
| | – | CBS 182.44 | *Petroselinum sativum* | Netherlands | S.D. de Wit | KF253446 | KF252967 | KF252493 | KF252002 | KF251497 | KF253801 | KF254150 |
| *Sep. phlogis* | – | CBS 102317 | *Phlox* sp. | Netherlands | G.J.M. Verkley | KF253447 | KF252968 | KF252494 | KF252003 | KF251498 | KF253802 | KF254151 |
| | – | CBS 128663 | *Phlox paniculata* | South Korea | H.D. Shin | KF253448 | KF252969 | KF252495 | KF252004 | KF251499 | KF253803 | KF254152 |
| | – | CBS 577.90 | *Phlox* sp. | Netherlands | H.A. van der Aa | KF253449 | KF252970 | KF252496 | KF252005 | KF251500 | KF253804 | KF254153 |
| *Sep. polygonorum* | – | CBS 102330 | *Polygonum persicaria* | Netherlands | G.J.M. Verkley | KF253450 | KF252971 | KF252497 | KF252006 | KF251501 | KF253805 | KF254154 |

**Table 1.** (Continued).

| Species | Old name | Isolate no[1] | Host | Location | Collector | GenBank Accession no[2] | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | | | EF | Tub | RPB2 | LSU | ITS | Act | Cal |
| | – | CBS 102331 | *Polygonum persicaria* | Netherlands | G.J.M. Verkley | KF253451 | KF252972 | KF252498 | KF252007 | KF251502 | KF253806 | KF254155 |
| | – | CBS 108982 | *Polygonum persicaria* | Germany | G.J.M. Verkley | KF253452 | KF252973 | KF252499 | KF252008 | KF251503 | KF253807 | KF254156 |
| | – | CBS 109834 | *Polygonum persicaria* | Netherlands | G.J.M. Verkley | KF253453 | KF252974 | KF252500 | KF252009 | KF251504 | KF253808 | KF254157 |
| | – | CBS 113110 | *Polygonum persicaria* | New Zealand | C.F. Hill | KF253454 | KF252975 | KF252501 | KF252010 | KF251505 | KF253809 | KF254158 |
| | – | CBS 347.67 | *Polygonum persicaria* | Netherlands | H.A. van der Aa | KF253455 | KF252976 | KF252502 | KF252011 | KF251506 | KF253810 | KF254159 |
| *Sep. posoniensis* | – | CBS 128645 | *Chrysosplenium japonicum* | South Korea | H.D. Shin | KF253456 | KF252977 | KF252503 | KF252012 | KF251507 | KF253811 | KF254160 |
| *Sep. protearum* | *Septoria* sp. | CPC 19691 | *Zanthedeschia aethiopica* | South Africa | P.W. Crous | KF253474 | KF252994 | KF252519 | KF252030 | KF251525 | KF253829 | KF254178 |
| | *Septoria* sp. | CBS 113114 | *Geum* sp. | New Zealand | G.J.M. Verkley | KF253459 | KF252980 | KF252506 | KF252015 | KF251510 | KF253814 | KF254163 |
| | *Septoria* sp. | CBS 119942 | *Asplenium ruta-muraria* | Germany | G.J.M. Verkley | KF253461 | KF252982 | – | KF252017 | KF251512 | KF253816 | KF254165 |
| | *Septoria* sp. | CBS 135477; CPC 19675 | *Zanthedeschia aethiopica* | South Africa | P.W. Crous | KF253473 | KF252993 | KF252518 | KF252029 | KF251524 | KF253828 | KF254177 |
| | *Septoria* sp. | CBS 164.78 | *Nephrolepis* sp. | New Zealand | H.J. Boesewinkel | KF253462 | KF252983 | KF252508 | KF252018 | KF251513 | KF253817 | KF254166 |
| | *Septoria* sp. | CBS 179.77 | *Myosotis* sp. | New Zealand | H.J. Boesewinkel | KF253464 | KF252985 | KF252510 | KF252020 | KF251515 | KF253819 | KF254168 |
| | *Septoria* sp. | CBS 364.97 | *Skimmia* sp. | Netherlands | J. de Gruyter | KF253466 | KF252986 | KF252512 | KF252022 | KF251517 | KF253821 | KF254170 |
| | *Septoria ligustri* | CBS 390.59 | *Ligustrum vulgare* | Italy | M. Ribaldi | KF253467 | KF252987 | KF252513 | KF252023 | KF251518 | KF253822 | KF254171 |
| | *Septoria pistaciae* | CBS 420.51 | *Pistacia vera* | Italy | G. Goidánich | KF253469 | KF252989 | – | KF252025 | KF251520 | KF253824 | KF254173 |
| | *Septoria* sp. | CBS 658.77 | *Boronia denticulata* | New Zealand | H.J. Boesewinkel | KF253471 | KF252991 | KF252516 | KF252027 | KF251522 | KF253826 | KF254175 |
| | – | CBS 778.97 | *Protea cynaroides* | South Africa | L. Viljoen | KF253472 | KF252992 | KF252517 | KF252028 | KF251523 | KF253827 | KF254176 |
| *Sep. pseudonapelli* | *Septoria napelli* | CBS 128664 | *Aconitum pseudolaeve* | South Korea | H.D. Shin | KF253475 | KF252995 | KF252520 | KF252031 | KF251526 | KF253830 | KF254179 |
| *Sep. putrida* | – | CBS 109087 | *Senecio nemorensis* | Austria | G.J.M. Verkley | KF253476 | KF252996 | KF252521 | KF252032 | KF251527 | KF253831 | KF254180 |
| | – | CBS 109088 | *Senecio nemorensis* | Austria | G.J.M. Verkley | KF253477 | KF252997 | KF252522 | KF252033 | KF251528 | KF253832 | KF254181 |
| *Sep. rumicum* | *Septoria acetosae* | CBS 503.76 | *Rumex acetosa* | France | H.A. van der Aa | KF253478 | KF252998 | KF252523 | KF252034 | KF251529 | KF253833 | KF254182 |
| *Sep. saccardoi* | – | CBS 128756 | *Lysimachia vulgaris* | South Korea | H.D. Shin | KF253479 | KF252999 | KF252524 | KF252035 | KF251530 | KF253834 | KF254183 |
| *Sep. scabiosicola* | – | CBS 102333 | *Knautia arvensis* | Netherlands | G.J.M. Verkley | KF253480 | KF253000 | KF252525 | KF252036 | KF251531 | KF253835 | KF254184 |
| | – | CBS 102334 | *Knautia arvensis* | Netherlands | G.J.M. Verkley | KF253481 | KF253001 | KF252526 | KF252037 | KF251532 | KF253836 | KF254185 |
| | – | CBS 102335 | *Knautia arvensis* | Netherlands | G.J.M. Verkley | KF253482 | KF253002 | KF252527 | KF252038 | KF251533 | KF253837 | KF254186 |
| | – | CBS 102336 | *Knautia arvensis* | Netherlands | G.J.M. Verkley | KF253483 | KF253003 | KF252528 | KF252039 | KF251534 | KF253838 | KF254187 |
| | – | CBS 108981 | *Knautia arvensis* | Germany | G.J.M. Verkley | KF253484 | KF253004 | KF252529 | KF252040 | KF251535 | KF253839 | KF254188 |
| | – | CBS 109021 | *Knautia arvensis* | Austria | G.J.M. Verkley | KF253485 | KF253005 | KF252530 | KF252041 | KF251536 | KF253840 | KF254189 |

**Table 1.** (Continued).

| Species | Old name | Isolate no[1] | Host | Location | Collector | GenBank Accession no[2] | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | | | EF | Tub | RPB2 | LSU | ITS | Act | Cal |
| | – | CBS 109092 | *Knautia dipsacifolia* | Austria | G.J.M. Verkley | KF253486 | KF253006 | KF252531 | KF252042 | KF251537 | KF253841 | KF254190 |
| | – | CBS 109093 | *Knautia dipsacifolia* | Austria | G.J.M. Verkley | KF253487 | KF253007 | KF252532 | KF252043 | KF251538 | KF253842 | KF254191 |
| | – | CBS 109128 | *Knautia dipsacifolia* | Austria | G.J.M. Verkley | KF253488 | KF253008 | KF252533 | KF252044 | KF251539 | KF253843 | KF254192 |
| | – | CBS 109129 | *Knautia dipsacifolia* | Austria | G.J.M. Verkley | KF253489 | KF253009 | KF252534 | KF252045 | KF251540 | KF253844 | KF254193 |
| | – | CBS 182.93 | *Succissa pratensis* | France | H.A. van der Aa | KF253490 | KF253010 | KF252535 | KF252046 | KF251541 | KF253845 | KF254194 |
| | – | CBS 317.37 | – | – | – | KF253491 | KF253011 | KF252536 | KF252047 | KF251542 | KF253846 | KF254195 |
| *Sep. senecionis* | – | CBS 102366 | *Senecio fluviatilis* | Netherlands | G.J.M. Verkley | KF253492 | KF253012 | KF252538 | KF252049 | KF251544 | KF253847 | KF254196 |
| | – | CBS 102381 | *Senecio fluviatilis* | Netherlands | G.J.M. Verkley | KF253493 | KF253013 | KF252539 | KF252050 | KF251545 | KF253848 | KF254197 |
| *Sep. siegesbeckiae* | – | CBS 128659 | *Siegesbeckia glabrescens* | South Korea | H.D. Shin | KF253494 | KF253014 | KF252540 | KF252051 | KF251546 | KF253849 | KF254198 |
| | – | CBS 128661 | *Siegesbeckia pubescens* | South Korea | H.D. Shin | KF253495 | KF253015 | KF252541 | KF252052 | KF251547 | KF253850 | KF254199 |
| *Sep. sii* | – | CBS 102369 | *Berula erecta* | Netherlands | G.J.M. Verkley | KF253496 | KF253016 | KF252542 | KF252053 | KF251548 | KF253851 | KF254200 |
| | – | CBS 102370 | *Berula erecta* | Netherlands | G.J.M. Verkley | KF253497 | KF253017 | KF252543 | KF252054 | KF251549 | KF253852 | KF254201 |
| | – | CBS 118.96 | *Berula erecta* | Netherlands | H.A. van der Aa | KF253498 | KF253018 | KF252544 | KF252055 | KF251550 | KF253853 | KF254202 |
| *Sep. sisyrinchii* | – | CBS 112096 | *Sysirinchium* sp. | New Zealand | C.F. Hill | KF253499 | KF253019 | KF252545 | KF252056 | KF251551 | KF253854 | KF254203 |
| *Septoria* sp. | *Pseudocercospora* sp. | CPC 19976 | *Feijoa sellowiana* | Italy | G. Polizzy | KF253509 | KF253030 | – | KF252067 | KF251562 | KF253863 | KF254214 |
| *Septoria* sp. | – | CPC 23104 | – | Italy | E. van Agtmaal | KF253511 | KF253032 | KF252557 | KF252069 | KF251564 | KF253865 | KF254216 |
| *Septoria* sp. | – | CBS 109114 | *Campanula glomerata* | Austria | G.J.M. Verkley | KF253501 | KF253021 | KF252547 | KF252058 | KF251553 | KF253856 | KF254205 |
| *Septoria* sp. | – | CBS 120739 | *Eucalyptus* sp. | Italy | W. Gams | KF253503 | KF253023 | KF252549 | KF252060 | KF251555 | KF253858 | KF254207 |
| *Septoria* sp. | *Septoria taraxaci* | CBS 128650 | *Taraxacum officinale* | South Korea | H.D. Shin | KF253504 | KF253024 | KF252550 | KF252061 | KF251556 | KF253859 | KF254208 |
| *Septoria* sp. | *Septoria posoniensis* | CBS 128658 | *Chrysoplenium japonicum* | South Korea | H.D. Shin | KF253505 | KF253025 | KF252551 | KF252062 | KF251557 | KF253860 | KF254209 |
| *Septoria* sp. | – | CBS 135472; CPC 19304 | *Vigna unguiculata ssp. sesquipedalis* | Austria | P.W. Crous | KF253506 | KF253026 | KF252552 | KF252063 | KF251558 | KF253861 | KF254210 |
| *Septoria* sp. | – | CBS 135474; CPC 19485 | *Conyza canadensis* | Brazil | R.W. Barreto | KF253507 | KF253027 | KF252553 | KF252064 | KF251559 | KF253862 | KF254211 |
| *Septoria* sp. | – | CBS 135478; CPC 19716 | *Searsia laevigatum* | South Africa | A. Wood | KF253508 | KF253028 | KF252554 | KF252065 | KF251560 | – | KF254212 |
| *Septoria* sp. | – | CBS 135479; CPC 19793 | Syzygium cordatum | South Africa | P.W. Crous | – | KF253029 | KF252555 | KF252066 | KF251561 | – | KF254213 |
| *Septoria* sp. | – | CPC 23103; MP11 | *Aesculus* sp. | Netherlands | S.I.R. Videira | KF253510 | KF253031 | KF252556 | KF252068 | KF251563 | KF253864 | KF254215 |
| *Sep. stachydicola* | – | CBS 128668 | *Stachys riederi* | South Korea | H.D. Shin | KF253512 | KF253033 | KF252558 | KF252070 | KF251565 | KF253866 | KF254217 |
| *Sep. stachydis* | – | CBS 109115 | *Campanula glomerata* | Austria | G.J.M. Verkley | KF253502 | KF253022 | KF252548 | KF252059 | KF251554 | KF253857 | KF254206 |
| | – | CBS 102326 | *Stachys sylvatica* | Netherlands | G.J.M. Verkley | KF253514 | KF253035 | KF252560 | KF252072 | KF251567 | KF253868 | KF254219 |
| | – | CBS 102337 | *Stachys sylvatica* | Netherlands | G.J.M. Verkley | KF253515 | KF253036 | KF252561 | KF252073 | KF251568 | KF253869 | KF254220 |

**Table 1.** (Continued).

| Species | Old name | Isolate no[1] | Host | Location | Collector | GenBank Accession no[2] | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | | | EF | Tub | RPB2 | LSU | ITS | Act | Cal |
| | – | CBS 109126 | *Stachys sylvatica* | Austria | G.J.M. Verkley | KF253516 | KF253037 | KF252562 | KF252074 | KF251569 | KF253870 | KF254221 |
| | – | CBS 109127 | *Stachys sylvatica* | Austria | G.J.M. Verkley | KF253517 | KF253038 | KF252563 | KF252075 | KF251570 | KF253871 | KF254222 |
| | – | CBS 123750 | *Stachys* sp. | Czech Republic | G.J.M. Verkley | KF253518 | KF253039 | KF252564 | KF252076 | KF251571 | KF253872 | KF254223 |
| | – | CBS 123879 | *Stachys* sp. | Czech Republic | G.J.M. Verkley | KF253519 | KF253040 | KF252565 | KF252077 | KF251572 | KF253873 | KF254224 |
| | – | CBS 449.68 | *Stachys sylvatica* | Netherlands | H.A. van der Aa | KF253520 | KF253041 | KF252566 | KF252078 | KF251573 | KF253874 | KF254225 |
| | *Sep. astericola* | CBS 347.58 | *Aster canus* | Germany | R. Schneider | KF253295 | KF252820 | KF252349 | KF251852 | KF251348 | KF253652 | KF254000 |
| *Sep. stellariae* | – | CBS 102376 | *Stellaria media* | Netherlands | G.J.M. Verkley | KF253521 | KF253042 | KF252567 | KF252079 | KF251574 | KF253875 | KF254226 |
| | – | CBS 102378 | *Stellaria media* | Netherlands | G.J.M. Verkley | KF253522 | KF253043 | KF252568 | KF252080 | KF251575 | KF253876 | KF254227 |
| | – | CBS 102410 | *Stellaria media* | Netherlands | G.J.M. Verkley | KF253523 | KF253044 | KF252569 | KF252081 | KF251576 | KF253877 | KF254228 |
| *Sep. taraxaci* | – | CBS 567.75 | *Taraxacum* sp. | Armenia | H.A. van der Aa | KF253524 | KF253045 | KF252570 | KF252082 | KF251577 | KF253878 | KF254229 |
| *Sep. tinctoriae* | – | CBS 129154 | *Serratula coronata* | South Korea | H.D. Shin | KF253525 | KF253046 | KF252571 | KF252083 | KF251578 | KF253879 | KF254230 |
| *Sep. tormentillae* | – | CBS 128643 | *Potentilla fragarioides* | South Korea | H.D. Shin | KF253526 | KF253047 | KF252572 | KF252084 | KF251579 | KF253880 | KF254231 |
| | – | CBS 128647 | *Potentilla fragarioides* | South Korea | H.D. Shin | KF253527 | KF253048 | KF252573 | KF252085 | KF251580 | KF253881 | KF254232 |
| *Sep. urticae* | *Septoria glechomatis* | CBS 102316 | *Glechoma hederacea* | Netherlands | G.J.M. Verkley | KF253528 | KF253049 | KF252574 | KF252086 | KF251581 | KF253882 | KF254233 |
| | – | CBS 102371 | *Urtica dioica* | Netherlands | G.J.M. Verkley | KF253529 | KF253050 | KF252575 | KF252087 | KF251582 | KF253883 | KF254234 |
| | – | CBS 102375 | *Urtica dioica* | Netherlands | G.J.M. Verkley | KF253530 | KF253051 | KF252576 | KF252088 | KF251583 | KF253884 | KF254235 |
| *Sep. verbascicola* | – | CBS 102401 | *Verbascum nigrum* | Netherlands | G.J.M. Verkley | KF253531 | KF253052 | KF252577 | KF252089 | KF251584 | KF253885 | KF254236 |
| *Sep. verbenae* | – | CBS 113438 | *Verbena officinalis* | New Zealand | G.J.M. Verkley | KF253532 | KF253053 | KF252578 | KF252090 | KF251585 | KF253886 | KF254237 |
| | – | CBS 113481 | *Verbena officinalis* | New Zealand | G.J.M. Verkley | KF253533 | KF253054 | KF252579 | KF252091 | KF251586 | KF253887 | KF254238 |
| *Sep. villarsiae* | – | CBS 514.78 | *Nymphoides peltata* | Netherlands | H.A. van der Aa | KF253534 | KF253055 | KF252580 | KF252092 | KF251587 | KF253888 | KF254239 |
| | – | CBS 565.88 | *Nymphoides peltata* | Netherlands | H.A. van der Aa | KF253535 | KF253056 | KF252581 | KF252093 | KF251588 | KF253889 | KF254240 |
| | – | CBS 604.66 | *Nymphoides peltata* | Netherlands | L. Marvanová | KF253536 | KF253057 | KF252582 | KF252094 | KF251589 | KF253890 | KF254241 |
| *Sep. violae-palustris* | – | CBS 128644 | *Viola selkirkii* | South Korea | H.D. Shin | KF253537 | KF253058 | KF252583 | KF252095 | KF251590 | KF253891 | KF254242 |
| | – | CBS 128660 | *Viola yedoensis* | South Korea | H.D. Shin | KF253538 | KF253059 | KF252584 | KF252096 | KF251591 | KF253892 | KF254243 |
| *Sphaerulina abeliceae* | *Septoria abeliceae* | CBS 128591 | *Zelkova serrata* | South Korea | H.D. Shin | KF253539 | – | KF252585 | KF252097 | KF251592 | KF253894 | KF254245 |
| *Sphaerulina aceris* | *Mycosphaerella latebrosa* | CBS 183.97 | *Acer pseudoplatanus* | Netherlands | H.A. van der Aa | KF253540 | – | KF252586 | KF252098 | KF251593 | KF253895 | KF254246 |
| | *Mycosphaerella latebrosa* | CBS 652.85 | *Acer pseudoplatanus* | Netherlands | H.A. van der Aa | KF253541 | KF253060 | KF252587 | KF252099 | KF251594 | KF253896 | KF254300 |
| | *Mycosphaerella latebrosa* | CBS 687.94 | *Acer pseudoplatanus* | Netherlands | G.J.M. Verkley | KF253542 | KF253061 | KF252588 | KF252100 | KF251595 | KF253897 | KF254247 |

**Table 1.** (Continued).

| Species | Old name | Isolate no[1] | Host | Location | Collector | GenBank Accession no[2] | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | | | EF | Tub | RPB2 | LSU | ITS | Act | Cal |
| *Sphaerulina amelanchier* | – | CBS 135110 | *Amelanchier* sp. | Netherlands | S.I.R. Videira | KF253543 | KF253062 | KF252589 | KF252101 | KF251596 | KF253898 | KF254248 |
| | *Septoria* sp. | CPC 23107; MP9 | *Betula* sp. | Netherlands | S.I.R. Videira | KF253583 | KF253098 | KF252626 | KF252139 | KF251634 | KF253937 | KF254288 |
| | *Septoria* sp. | CPC 23105; MP22 | *Quercus* sp. | Netherlands | S.I.R. Videira | KF253544 | KF253063 | KF252590 | KF252102 | KF251597 | KF253899 | KF254249 |
| | – | CPC 23106; MP7 | *Castanea* sp. | Netherlands | S.I.R. Videira | KF253545 | KF253064 | KF252591 | KF252103 | KF251598 | KF253900 | KF254250 |
| *Sphaerulina azaleae* | *Septoria azaleae* | CBS 128605 | *Rhododendron* sp. | South Korea | H.D. Shin | KF253546 | KF253065 | KF252592 | KF252104 | KF251599 | KF253901 | KF254251 |
| | *Septoria azaleae* | CBS 352.49 | *Rhododendron* sp. | Belgium | J. van Holder | KF253547 | KF253066 | KF252593 | KF252105 | KF251600 | KF253902 | KF254252 |
| *Sphaerulina berberidis* | *Mycosphaerella berberidis* | CBS 324.52 | *Berberis vulgaris* | Switzerland | E. Müller | KF253548 | KF253067 | KF252594 | KF252106 | KF251601 | KF253903 | KF254253 |
| *Sphaerulina betulae* | *Septoria betulae* | CBS 116724 | *Betula pubescens* | Scotland | S. Green | KF253549 | KF253068 | KF252595 | KF252107 | KF251602 | KF253904 | KF254254 |
| | *Septoria betulae* | CBS 128596 | *Betula platyphylla* | South Korea | H.D. Shin | KF253550 | KF253069 | KF252596 | KF252108 | KF251603 | KF253905 | KF254255 |
| | *Septoria betulae* | CBS 128597 | *Betula schmidtii* | South Korea | H.D. Shin | KF253551 | KF253070 | KF252597 | KF252109 | KF251604 | KF253906 | KF254256 |
| | *Septoria betulae* | CBS 128600 | *Betula platyphylla* | South Korea | H.D. Shin | KF253552 | KF253071 | KF252598 | KF252110 | KF251605 | KF253907 | KF254257 |
| *Sphaerulina cercidis* | *Septoria provencialis* | CBS 118910 | *Eucalyptus* sp. | France | P.W. Crous | KF253553 | KF253072 | KF252602 | KF252114 | KF251609 | KF253908 | KF254258 |
| | *Septoria cercidis* | CBS 128634 | *Cercis siliquastrum* | South Korea | H.D. Shin | KF253554 | KF253073 | KF252599 | KF252111 | KF251606 | KF253909 | KF254259 |
| | *Septoria cercidis* | CBS 129151 | *Cercis siliquastrum* | South Korea | H.D. Shin | KF253555 | KF253074 | KF252600 | KF252112 | KF251607 | KF253910 | KF254260 |
| | *Septoria cercidis* | CBS 501.50 | *Cercis siliquastrum* | Netherlands | G. van den Ende | KF253556 | KF253075 | KF252601 | KF252113 | KF251608 | KF253911 | KF254261 |
| *Sphaerulina cornicola* | *Septoria cornicola* | CBS 102324 | *Cornus* sp. | Netherlands | A. van Iperen | KF253557 | KF253076 | KF252603 | KF252115 | KF251610 | KF253912 | KF254262 |
| | *Septoria cornicola* | CBS 102332 | *Cornus* sp. | Netherlands | A. van Iperen | KF253558 | KF253077 | KF252604 | KF252116 | KF251611 | KF253913 | KF254263 |
| | *Septoria cornicola* | CBS 116778 | *Cornus sanguinea* | USA | A.Y. Rossman | KF253559 | KF253078 | – | KF252117 | KF251612 | KF253914 | KF254264 |
| *Sphaerulina frondicola* | *Septoria populi* | CBS 391.59 | *Populus pyramidalis* | Germany | R. Schneider | KF253572 | – | KF252617 | KF252130 | KF251625 | KF253927 | KF254277 |
| *Sphaerulina gei* | *Septoria gei* | CBS 102318 | *Geum urbanum* | Netherlands | G.J.M. Verkley | KF253560 | KF253079 | KF252605 | KF252118 | KF251613 | KF253915 | KF254265 |
| | *Septoria gei* | CBS 128616 | *Geum japonicum* | South Korea | H.D. Shin | KF253561 | KF253080 | KF252606 | KF252119 | KF251614 | KF253916 | KF254266 |
| | *Septoria gei* | CBS 128632 | *Geum japonicum* | South Korea | H.D. Shin | KF253562 | KF253081 | KF252607 | KF252120 | KF251615 | KF253917 | KF254267 |
| *Sphaerulina hyperici* | *Septoria hyperici* | CBS 102313 | *Hypericum* sp. | Netherlands | G.J.M. Verkley | KF253563 | KF253082 | KF252608 | KF252121 | KF251616 | KF253918 | KF254268 |
| *Sphaerulina menispermi* | *Septoria menispermi* | CBS 128666 | *Menispermum dauricum* | South Korea | H.D. Shin | KF253564 | KF253083 | KF252609 | KF252122 | KF251617 | KF253919 | KF254269 |
| | *Septoria menispermi* | CBS 128761 | *Menispermum dauricum* | South Korea | H.D. Shin | KF253565 | KF253084 | KF252610 | KF252123 | KF251618 | KF253920 | KF254270 |
| *Sphaerulina musiva* | *Septoria musiva* | CBS 130559 | *Populus* sp. | Canada | J. LeBoldus | KF253566 | – | KF252611 | KF252124 | KF251619 | KF253921 | KF254271 |
| | *Septoria musiva* | CBS 130562 | *Populus* sp. | Canada | J. LeBoldus | KF253567 | KF253085 | KF252612 | KF252125 | KF251620 | KF253922 | KF254272 |
| | *Septoria musiva* | CBS 130563 | *Populus deltoides* × *P. balsamifera* | Canada | J. LeBoldus | KF253568 | – | KF252613 | KF252126 | KF251621 | KF253923 | KF254273 |

**Table 1.** (Continued).

| Species | Old name | Isolate no[1] | Host | Location | Collector | GenBank Accession no[2] | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | | | EF | Tub | RPB2 | LSU | ITS | Act | Cal |
| | *Septoria musiva* | CBS 130569 | *Populus deltoides* | Canada | J. LeBoldus | KF253569 | KF253086 | KF252614 | KF252127 | KF251622 | KF253924 | KF254274 |
| *Sphaerulina patriniae* | *Septoria patriniae* | CBS 128653 | *Patrinia scabiosaefolia* | South Korea | H.D. Shin | KF253570 | KF253087 | KF252615 | KF252128 | KF251623 | KF253925 | KF254275 |
| | *Septoria patriniae* | CBS 129153 | *Patrinia villosa* | South Korea | H.D. Shin | KF253571 | KF253088 | KF252616 | KF252129 | KF251624 | KF253926 | KF254276 |
| *Sphaerulina populicola* | *Mycosphaerella populicola* | CBS 100042 | *Populus trichocarpa* | USA | G. Newcombe | KF253573 | – | KF252618 | KF252131 | KF251626 | KF253928 | KF254278 |
| *Sphaerulina quercicola* | *Septoria quercicola* | CBS 109009 | *Quercus rubra* | Netherlands | G.J.M. Verkley | KF253574 | KF253089 | KF252619 | KF252132 | KF251627 | KF253929 | KF254279 |
| | *Septoria quercicola* | CBS 115016 | *Quercus robur* | Netherlands | G.J.M. Verkley | KF253575 | KF253090 | KF252620 | KF252133 | KF251628 | KF253930 | KF254280 |
| | *Septoria quercicola* | CBS 115136 | *Quercus robur* | Netherlands | G.J.M. Verkley | KF253576 | KF253091 | KF252621 | KF252134 | KF251629 | KF253931 | KF254281 |
| | *Septoria quercicola* | CBS 663.94 | *Quercus robur* | Netherlands | H.A. van der Aa | KF253577 | KF253092 | KF252622 | KF252135 | KF251630 | KF253932 | KF254282 |
| *Sphaerulina rhabdoclinis* | *Dothistroma rhabdoclinis* | CBS 102195 | *Pseudotsuga menziesii* | Germany | H. Butin | KF253578 | KF253093 | KF252623 | KF252136 | KF251631 | – | KF254283 |
| *Sphaerulina socia* | *Septoria rosae* | CBS 355.58 | *Rosa* sp. | – | – | KF253579 | KF253094 | KF252624 | KF252137 | KF251632 | KF253933 | KF254284 |
| | *Septoria socia* | CBS 357.58 | *Chrysanthemum leucanthemum* | Germany | R. Schneider | KF253580 | KF253095 | KF252625 | KF252138 | KF251633 | KF253934 | KF254285 |
| *Sphaerulina* sp. | *Septoria* sp. | CBS 102063 | *Actinidia deliciosa* | New Zealand | C.F. Hill | KF253581 | KF253096 | KF252627 | KF252140 | KF251635 | KF253935 | KF254286 |
| *Sphaerulina* sp. | *Septoria lysimachiae* | CBS 128758 | *Lysimachia clethroides* | South Korea | H.D. Shin | KF253582 | KF253097 | KF252628 | KF252141 | KF251636 | KF253936 | KF254287 |
| *Sphaerulina tirolensis* | *Septoria rubi* | CBS 109017 | *Rubus idaeus* | Austria | G.J.M. Verkley | KF253584 | KF253099 | KF252629 | KF252142 | KF251637 | KF253938 | KF254289 |
| | *Mycosphaerella rubi* | CBS 109018 | *Rubus idaeus* | Austria | G.J.M. Verkley | KF253585 | KF253100 | KF252630 | KF252143 | KF251638 | KF253939 | KF254290 |
| *Sphaerulina viciae* | – | CBS 131898 | *Vicia amurense* | South Korea | H.D. Shin | KF253586 | KF253101 | KF252631 | KF252144 | KF251639 | KF253940 | KF254291 |
| *Sphaerulina westendorpii* | *Septoria rubi* | CBS 102327 | *Rubus* sp. | Netherlands | G.J.M. Verkley | KF253587 | KF253102 | KF252632 | KF252145 | KF251640 | KF253941 | KF254292 |
| | *Mycosphaerella rubi* | CBS 109002 | *Rubus* sp. | Netherlands | G.J.M. Verkley | KF253588 | KF253103 | KF252633 | KF252146 | KF251641 | KF253942 | KF254293 |
| | *Septoria rubi* | CBS 117478 | *Rubus fruticosus* | Netherlands | G.J.M. Verkley | KF253589 | KF253104 | KF252634 | KF252147 | KF251642 | KF253943 | KF254294 |
| *Zymoseptoria brevis* | – | CPC 18102 | *Phalaris paradoxa* | Iran | M. Razavi | KF253590 | – | KF252635 | KF252148 | KF251643 | KF253944 | KF254295 |
| | – | CPC 18107 | *Phalaris minor* | Iran | M. Razavi | KF253591 | – | KF252636 | KF252149 | KF251644 | KF253945 | KF254296 |
| *Zymoseptoria halophila* | – | CBS 128854 | *Hordeum glaucum* | Iran | M. Razavi | KF253592 | – | – | KF252150 | KF251645 | KF253946 | KF254297 |
| *Zymoseptoria tritici* | – | CPC 18099 | *Aegilops tauschii* | Iran | M. Razavi | KF253594 | – | KF252638 | KF252152 | KF251647 | KF253948 | KF254299 |
| | – | CBS 392.59 | *Triticum aestivum* | Switzerland | E. Becker | KF253593 | – | KF252637 | KF252151 | KF251646 | KF253947 | KF254298 |

[1]CBS: CBS Fungal Biodiversity Centre, Centraalbureau voor Schimmelcultures, Utrecht, The Netherlands; CPC: Collection Pedro Crous, housed at CBS; S: William Quaedvlieg working collection (will be merged into the CPC collection); MP: Sandra Isabel Rodrigues Videira working collection (will be merged into the CPC collection).

[2]Act:: Actin, Cal: Calmodulin, EF: Translation elongation factor 1-alpha, RPB2: RNA polymerase II second largest subunit, Btub: β-tubulin LSU: 28S large subunit of the nrRNA gene and ITS: internal transcribed spacer regions of the nrDNA operon.

previous results by Verkley *et al.* (2004a, b) which showed that both loci could not resolve the lower phylogenetic relationships between closely related *Septoria* species. Due to the presence of intron regions in the five remaining protein coding loci, these genes provide much higher interspecific variation than the more conserved ITS and LSU loci. These protein coding genes thus have (much) higher K2P inter- to intraspecific variation ratios: for Cal 14 : 1, RPB2 17 : 1, Act 23 : 1, EF 26 : 1 and for Btub 29 : 1 (Fig. 1), making them all suitable for reliable species resolution throughout the range of septoria-like fungi. As the EF and Btub have the largest barcoding gap, these loci should give the highest species resolution and preferably be used for identifying species.

## Phylogeny

Basal to the seven-locus tree are the outgroup taxon *Readeriella mirabilis* (CBS 125000), and a monophyletic group comprising 11 strains, viz. *Dothistroma pini* (CBS 121011), *D. septospora*, (CBS 383.74), *Passalora dissiliens* (CBS 219.77), three *Ramularia* species (*Mycosphaerella s. str.*, see Quaedvlieg *et al.* 2013) and three *Zymoseptoria* species, including its type species *Z. tritici* (syn. *Mycosphaerella graminicola*, *Septoria tritici*). The basal ingroup taxa include CBS 619.72 identified as *Septoria oudemansii*, a *Pseudocercospora* clade with six strains, and *Cercosporella virgaureae* (CBS 113304). A well-supported cluster of two basal lineages (bootstrap support 100 %) comprises a cluster (100 %) of two isolates identified as *S. gladioli*, and a second cluster (100 %) containing 10 strains representing four septoria-like species that are all associated with leaf spots on plants of the family *Caryophyllaceae*, and for which the new generic name *Caryophylloseptoria* is proposed below. These include *C. silenes* (CBS 109100, 109103), *C. lychnidis* (CBS 109098–109102), two isolates originating from *Lychnis cognata* in Korea for which the new species *C. pseudolychnidis* is proposed by Quaedvlieg *et al.* (2013) (CBS 128614, 128630), and two isolates of *C. spergulae* (CBS 397.52, 109010).

The remaining ingroup can be devided into a *Sphaerulina* clade (100 %, 51 strains including the basal strain of *Sph. abeliceae*, CBS 128591) and main *Septoria* clade (80 %, 259 strains) with, positioned in between smaller groups comprised of "*Septoria*" *cruciatae* (CBS 123747, 123748), a small pseudocercosporella-like clade comprising *Passalora fusimaculans* (CPC 17277), a clade with *Passalora depressa* (CPC 14915), *"Mycosphaerella" brassicicola* and affiliated taxa with *Pseudocercosporella* asexual morphs (100 %, 9 strains), and a miscellaneous clade containing "*Passalora*" sp. (100 %, CBS 113989, 113999, 114275), *Passalora dioscoreae* (CPC 10855, 11513), *Pseudocercosporella magnusiana* (CBS 114735), *Passalora janseana* (CBS 145.37), "*Septoria erigerontis*" (CPC 19485), and a *Cercospora* clade (100 %, 4 strains).

The ***Sphaerulina* clade** comprises the aforementioned CBS 128591 identified as *S. abelicaea* (from *Zelkova serrata*) and **clades 1 and 2.** Clade 1 (100 %, 37 strains) includes at its base three strains of *Sph. cornicola*, the sister taxa *Sph. betulae* and *S. westendorpii* (syn. *S. rubi*) on *Rubus fruticosus* (CBS 102327, 109002, 117478), and *Sph. socia* (CBS 355.58, CBS 357.58). The remainder of clade 1 contains a well-supported cluster of 25 strains with various species infecting herbaceous and woody hosts. CBS 109017 and 19018, originating from *Rubus idaeus* in Austria, represent a species for which *Sphaerulina tirolensis* sp. nov. is introduced below. Furthermore this cluster contains *Sphaerulina berberidis* (syn. *Mycosphaerella berberidis*, *S. berberidis* Niessl), *Sph. azaleae*, *Sph. hyperici*, *Sph. menispermi*, *Sph. patriniae*, *Sph. cercidis*, and *Sph. gei*. Clade 2 (74 %, 13 strains) of the *Sphaerulina* clade includes only species infecting tree, the poplar pathogens *Sph. populicola* (syn. *Mycosphaerella populicola*, CBS 100042), *Sph. musiva* (syn. *Septoria musiva*, four strains), and *Sph. frondicola* (syn. *Mycosphaerella populi*, *S. populi*, CBS 391.59), and furthermore *Sphaerulina aceris* (syn. *Mycosphaerella latebrosa*, *Phloeospora aceris*, asexual morph *S. aceris*, three strains), which causes leaf spot on *Acer* spp., and *Sph. quercicola* (syn. *S. querciola*).

At the base of the **main *Septoria* clade**, a well-supported clade 3 (88 %, 16 strains) includes several species associated with hosts in the *Apiaceae*, viz., *S. oenanthis* (CBS 128667) and *S. oenanthicola* (CBS 128649; a new species proposed by Quaedvlieg *et al.* (2013), *S. sii* (CBS 118.96, 102369, 102370), and *S. aegopodii* (CBS 123740, 123741), and associated with other plant families, *S. dearnessii* (CBS 128624), a cluster of two strains of *S. lactucae* (CBS 352.58, 108943) and *S. sonchi* (CBS 128757), *S. campanulae* (CBS 128589, 128604), *S. mazi* (CBS 128656, 128755), and *S. gentianae* (CBS 128633). In **clade 4** (100 %, 183 strains) *S. bupleuricola* (CBS 128601, 128603) and *S. scabiosicola* (100 %, 12 strains) occupy a basal position and **subclades 4a–d** can be distinguished. **Subclade 4a** (100 %, 46 strains) comprises of a group of 13 strains of miscellaneous host plants, mostly with smaller conidia, viz., two *Solanum* pathogens *S. lycopersici* (CBS 354.49, 128654) and *S. malagutii* (CBS 106.80), *S. apiicola* (4 strains), *S. cucurbitacearum* (CBS 178.77), and *S. aridis* (4 strains), and a second strain identified as *S.posonniensis* (CBS 128658). **Subclade 4b** (100 %, 33 strains) harbours several taxa infecting *Asteraceae*, among others *S. obesa* (four strains), *S. senecionis* (three strains), *S. putrida* (CBS 109087, 109088), *S. leucanthemi* (6 strains), *S.cirsii* (CBS 128621), six strains of the *S. chrysanthemella* complex, *S. exotica* (CBS 163.78), and *S. posoniensis* (CBS 128645). Furthermore this group of 33 comprises taxa with relatively large conidia capable of infecting *Ranunculaceae*, viz. *S.lycoctoni*, *S. napelli* (CBS 109104–109106) from Austria and *S. pseudonapelli* (CBS 128664; a new species proposed by Quaedvlieg *et al.* 2013) from Korea. It also includes *S. lycopicola* (128651), CBS 128662 identified as *S. stachydicola* (probably misidentified), and two strains of *S. astericola* (CBS 128587, 128593). **Subclade 4c** (99 %, 15 strains) contains *S. matricariae* (CBS 109000, 109001), *S. lamiicola* (8 strains), *S. anthrisci* (CBS 109019, 109020), and *S. petroselini* (CBS 182.44, 109521), and **subclade 4d** (100 %, 103 strains) shows four subgroups, 4d-1–4. Basic to these are found *S. dolichospora* (CBS 129152) and *S. helianthi* (CBS 123.81). **Subclade 4d-1** (100 %, 45 strains) contains *S.* cf. *stachydicola* (CBS 128668 ; see Quaedvlieg *et al.* 2013), and many other species infecting herbaceous plants, among others *S. stachydis* (nine strains), *S. phlogis* (three strains), *S. epambrosiae* (CBS 128629, 128636), *S. cerastii* (five strains), *S. galeopsidis* (seven strains), *S. stachydis* (9 strains), *S. epilobii* (CBS 109084, 109085) and *S. digitalis* (CBS 391.63, 328.67). **Subclade 4d-2** (100 %, 35 strains) comprises among others *S. polygonorum* (six strains), *S. urticae* and *S convolvuli* (three strains each), *S.villarsiae*, *S. crepidis*, and *S. codonopsidis*. **Subclade 4d-3** (99 %, 11 strains) containing *S. erigerontis* (five strains), *S. lysimachii* (five strains), and *S. saccardoi* (CBS 128756). **Subclade 4d-4** (100 %, 9 strains) contains *S. bothriospermi* (CBS 128592, 128599), *S. tinctoriae* (CBS 129154), four strains identified as *S. rubi* that need to be re-named, and *S.agrimoniicola* (CBS 128585, 128602).

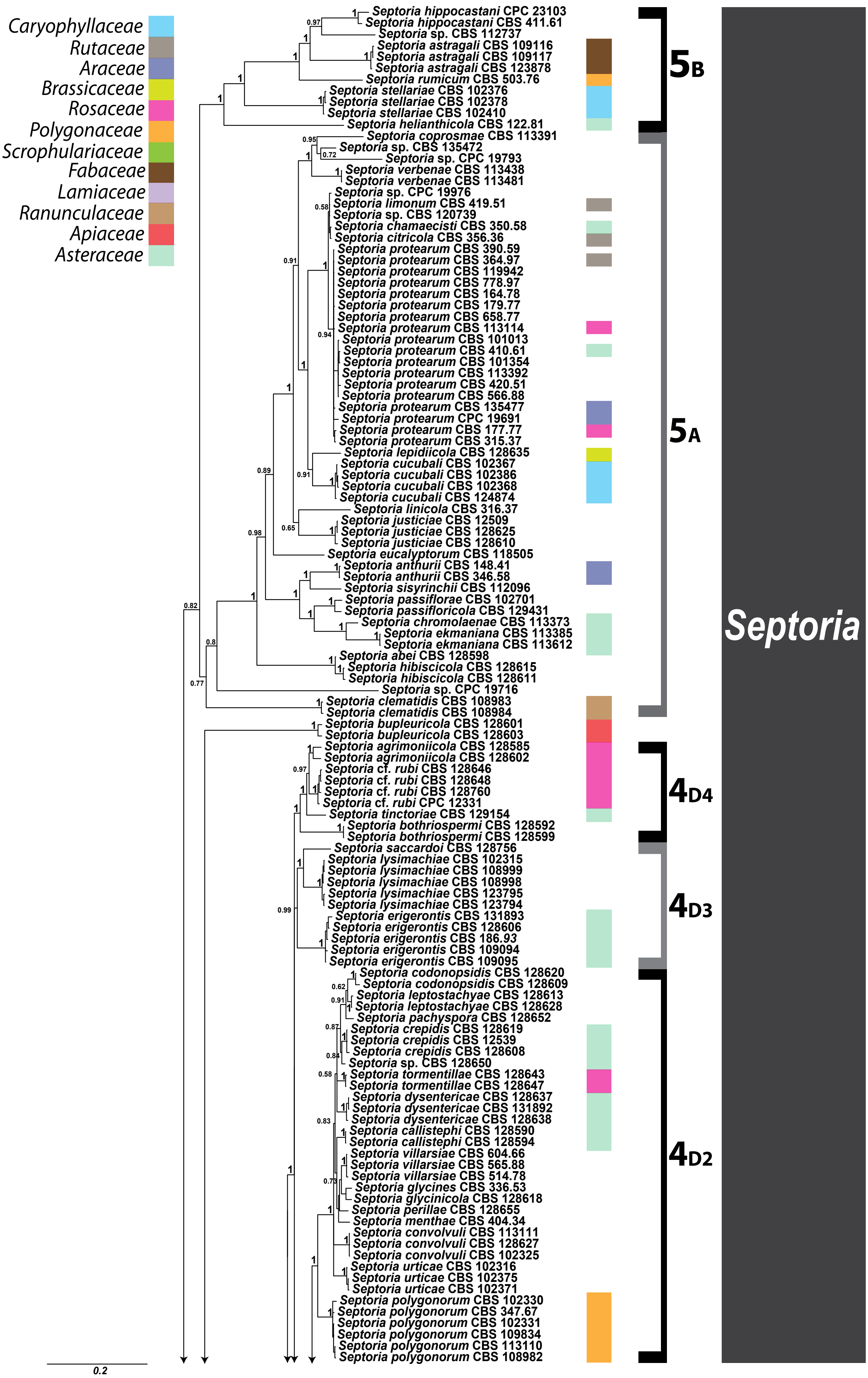


**Fig. 2.** Consensus phylogram (50 % majority rule) of 17 222 trees resulting from a Bayesian analysis of the combined seven loci sequence alignment using MrBayes v. 3.2.1. Bayesian posterior probabilities values are indicated on their respective branches and the scale bar indicates 0.2 expected changes per site. The tree was rooted to *Readeriella mirabilis* (*Teratosphaeriaceae*) (CBS 125000). The family of the host plant from which the strain was isolated is indicated for 12 most prevalently occurring host families in our dataset (colour bar according to the legend).

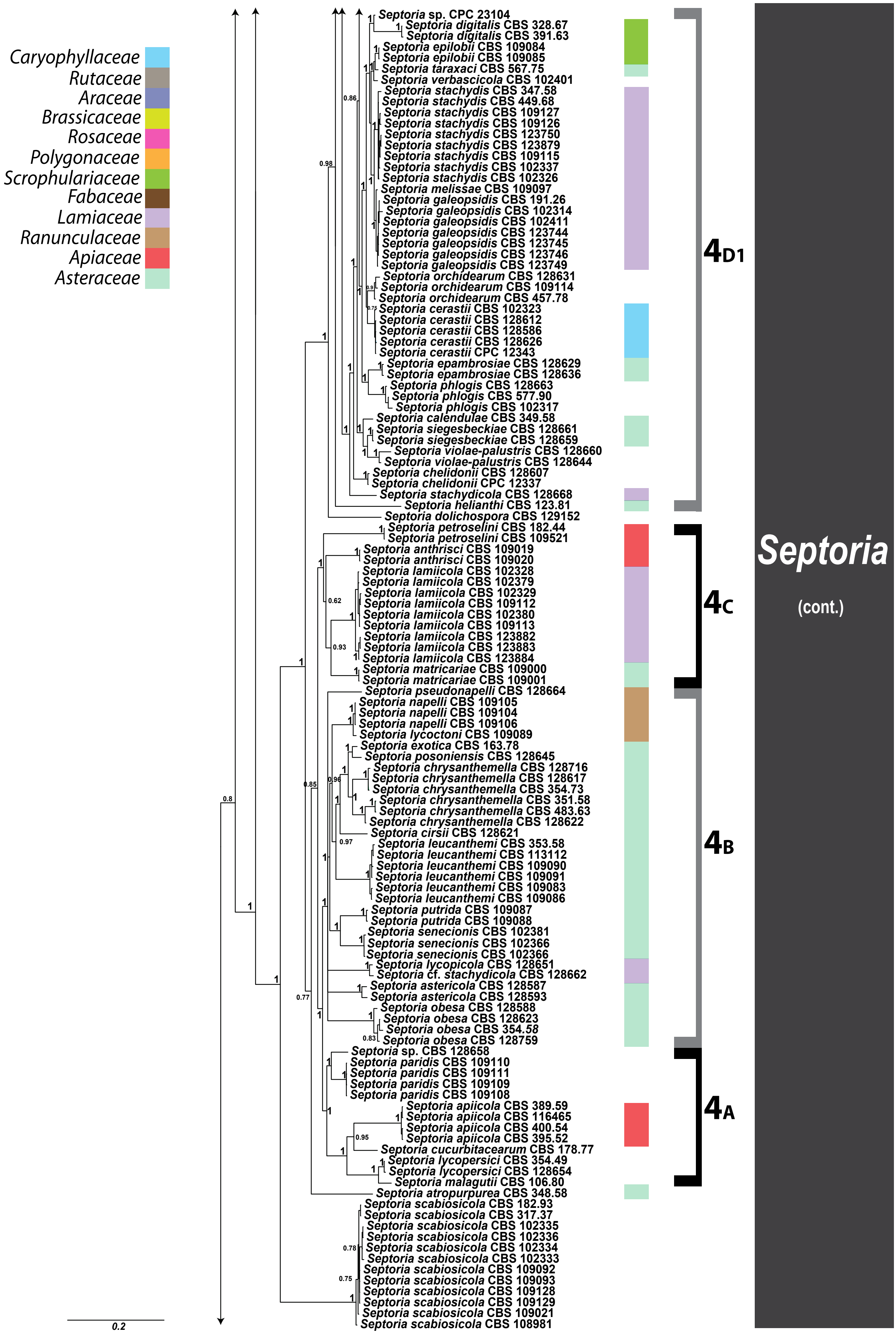


**Fig. 2.** (Continued).

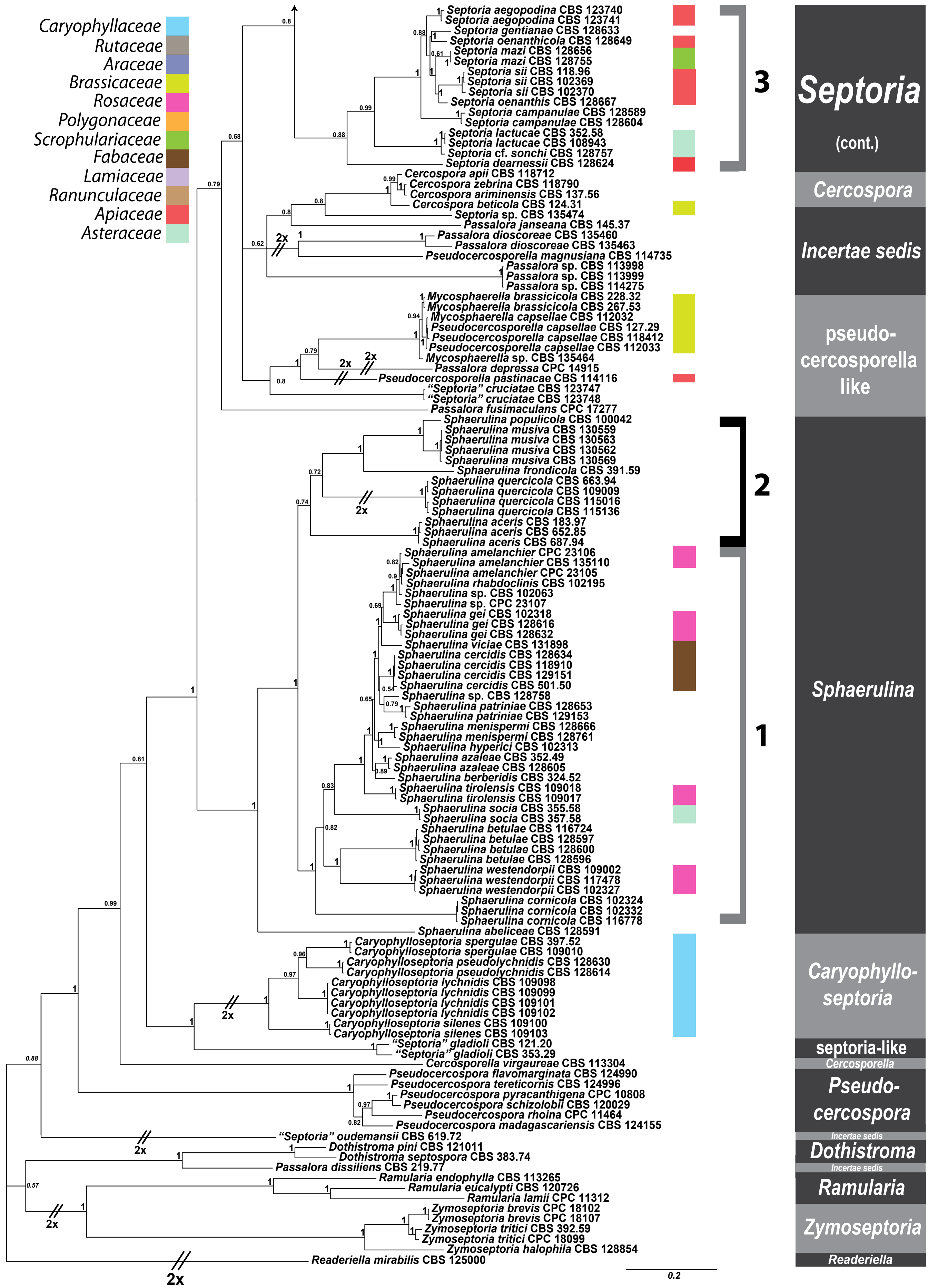


**Fig. 2.** (Continued).

**Table 2.** Primer combinations used during this study for generic amplification and sequencing.

| Locus | Primer | Primer sequence 5' to 3': | Annealing temperature (°C) | Orientation | Reference |
|---|---|---|---|---|---|
| Translation elongation factor-1α | EF1-728F | CATCGAGAAGTTCGAGAAGG | 52 | Forward | Carbone & Kohn (1999) |
| | EF-2 | GGARGTACCAGTSATCATGTT | 52 | Reverse | O'Donnell *et al.* (1998) |
| β-tubulin | T1 | AACATGCGTGAGATTGTAAGT | 52 | Forward | O'Donnell & Cigelnik (1997) |
| | β-Sandy-R | GCRCGNGGVACRTACTTGTT | 52 | Reverse | Stukenbrock *et al.* (2012) |
| RNA polymerase II second largest subunit | fRPB2-5F | GAYGAYMGWGATCAYTTYGG | 49 | Forward | Liu *et al.* (1999) |
| | fRPB2-414R | ACMANNCCCCARTGNGWRTTRTG | 49 | Reverse | Quaedvlieg *et al.* (2011) |
| LSU | LSU1Fd | GRATCAGGTAGGRATACCCG | 52 | Forward | Crous *et al.* (2009a) |
| | LR5 | TCCTGAGGGAAACTTCG | 52 | Reverse | Vilgalys & Hester (1990) |
| ITS | ITS5 | GGAAGTAAAAGTCGTAACAAGG | 52 | Forward | White *et al.* (1990) |
| | ITS4 | TCCTCCGCTTATTGATATGC | 52 | Reverse | White *et al.* (1990) |
| Actin | ACT-512F | ATGTGCAAGGCCGGTTTCGC | 52 | Forward | Carbone & Kohn (1999) |
| | ACT2Rd | ARRTCRCGDCCRGCCATGTC | 52 | Reverse | Groenewald *et al.* (2012) |
| Calmodulin | CAL-235F | TTCAAGGAGGCCTTCTCCCTCTT | 50 | Forward | Quaedvlieg *et al.* (2012) |
| | CAL2Rd | TGRTCNGCCTCDCGGATCATCTC | 50 | Reverse | Groenewald *et al.* (2012) |

**Table 3.** Amplification success, phylogenetic data and the substitution models used in the phylogenetic analysis, per locus.

| Locus | Act | Cal | EF1 | RPB2 | Btub | ITS | LSU |
|---|---|---|---|---|---|---|---|
| Amplification succes (%) | 99 | 100 | 100 | 97 | 100 | 100 | 100 |
| Number of characters | 304 | 601 | 619 | 354 | 565 | 574 | 853 |
| Unique site patterns | 234 | 407 | 507 | 198 | 380 | 261 | 147 |
| Substitution model used | GTR-I-gamma | HKY-I-gamma | GTR-I-gamma | GTR-I-gamma | HKY-I-gamma | GTR-I-gamma | GTR-I-gamma |
| Number of generations (1000×) | | | | 10 197 | | | |
| Total number of trees (n) | | | | 22 962 | | | |
| Sampled trees (n) | | | | 17 222 | | | |

In **clade 5** (92 %, 63 strains) of the main *Septoria* clade two main clusters are found. At the base of the **subclade 5a** (77 %, 52 strains), two strains of *S. clematidis* (CBS 108983–4) and *Septoria* sp. (CPC 19716) originating from *Searsia laevigatum* in South Africa. This cluster furthermore comprises three strains isolated from *Hibiscus* spp., viz., *S. hibiscicola* (CBS 128611, 128615) and *S. abei* (CBS 128598), and two main groups, one with *S. anthurii* (CBS 148.41, 346.58), *S. sisyrinchii* (CBS 112096), the *Chromolaena* fungi *S. chromolaenae* (CBS 113373) and *S. ekmanniana* (CBS 113385, 113612), and *S. passiflorae* (CBS 102701) and *S. passifloricola* (CBS 129431), and a second group comprising at the base *S. eucalyptorum* (CBS 118505; Crous *et al*. 2006b), and furthermore *S. justiciae* (CBS 128610, 128625, and CPC 12509), *S. linicola* (CBS 316.37), *S. cucubali* (3 strains, including CBS 124874, an endophytic isolate from *Fagus* leaf litter), *S. lepidiicola* (CBS 128635) and and a partially unresolved cluster of 23 strains comprising the plurivorous *S. protearum* and *S. citri* complex. A small well-supported cluster (100 %) contains *S. verbenae* (CBS 113438, 113481), two unidentified species of *Septoria* (CPC 19304, from *Vigna unguiculata* subsp. *sesquipedalis* and CPC 19793, from *Syzygium cordatum*), and *M. coacervata* (CBS 113391). **Subclade 5b** (100 %, 11 strains) comprises *S. helianthicola* (CBS 122.81), three strains of *S. stellariae*, CBS 503.76 identified as *S. acetosae*, three strains of *S. astragali*, "*Cercospora* sp." (CBS 112737), and furthermore *S. hippocastani* (CBS 411.61 and MP11).

Examining the distribution of host families throughout the tree, an interesting disjunct pattern is found for the families that are represented by more than a few specimens (see legend in Fig. 2). For example, the 28 species infecting *Asteraceae* are found in all clades and most subclades of the tree, including *Sphaerulina*; nine species infecting *Apiaceae* are found in clade 3 and subclades 4a–d of *Septoria*; 10 species of *Rosaceae* in *Septoria* clades 4, 5 and *Sphaerulina* (clades 1 and 2); six species infecting *Lamiaceae* are dispersed in subclades 4b, c, and d-1.

## TAXONOMY

***Caryophylloseptoria*** Verkley, Quaedvlieg & Crous, **gen. nov.** MycoBank MB804469.

*Etymology*: Named after the plant family on which these taxa occur, *Caryophyllaceae*.

*Conidiomata* pycnidial, epiphyllous or predominantly epiphyllous, globose to subglobose, or slightly depressed, with a central ostiolum. *Conidiomatal wall* composed of *textura angularis* or *globulosa-angularis. Conidiogenous cells* hyaline, holoblastic, proliferating percurrently 1–many times with indistinct annellations,

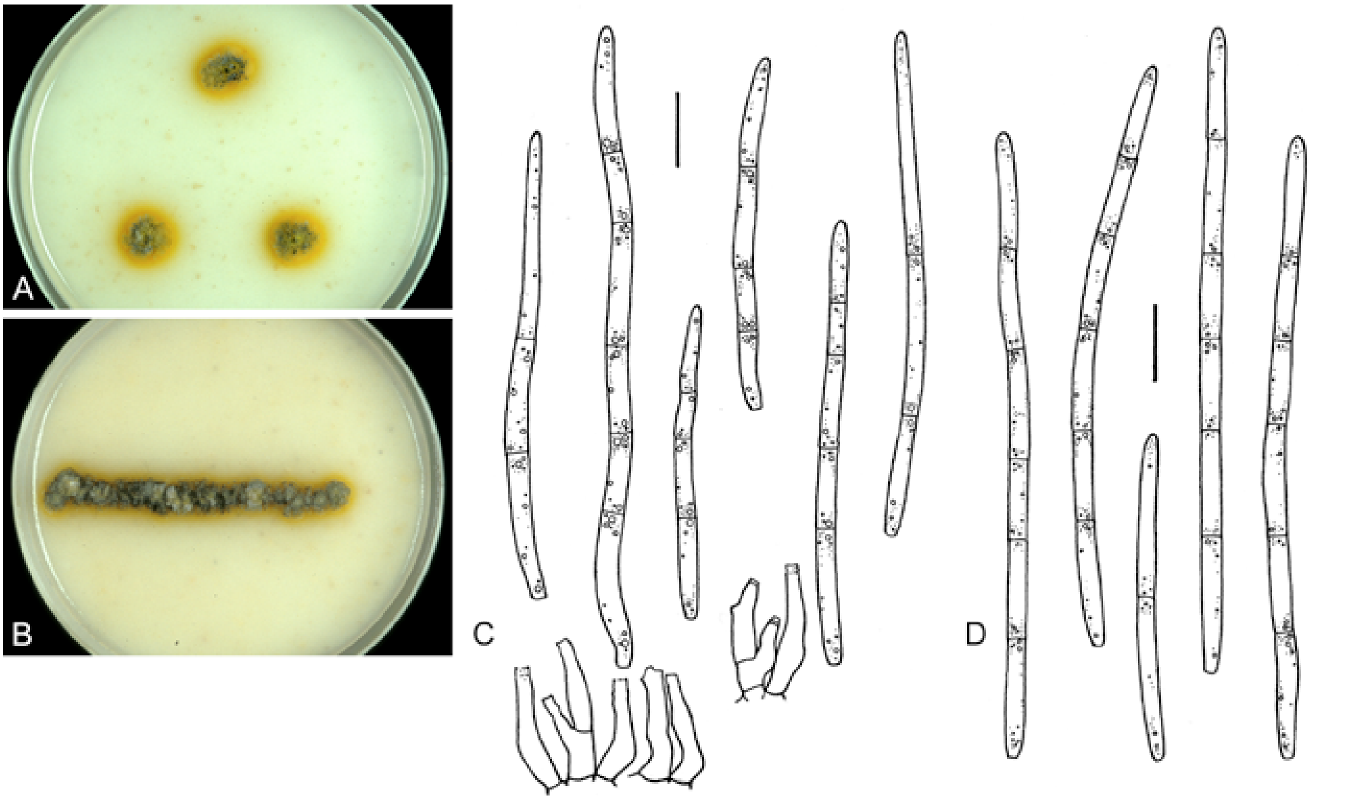


**Fig. 3.** *Caryophylloseptoria lychnidis*. A. CBS 109098, colony on OA. B. Ibid., on CMA. C. Conidia and conidiogenous cells *in planta* (CBS 109098). D. Conidia on OA (CBS 109098). Scale bars = 10 µm.

or (in addition) proliferating sympodially. *Conidia* cylindrical, straight, curved or flexuous, multiseptate, not or somewhat constricted around the septa, hyaline, contents with several oil-droplets and granular material in each cell.

*Type species*: *Caryophylloseptoria lychnidis* (Desm.) Verkley, Quaedvlieg & Crous.

***Caryophylloseptoria lychnidis*** (Desm.) Verkley, Quaedvlieg & Crous, **comb. nov.** MycoBank MB804470. Fig. 3.
*Basionym*: *Septoria lychnidis* Desm., Annls Sci. Nat., sér. 3, Bot. 11: 347. 1849.

For extended synonymy see Shin & Sameva (2004).

Description *in planta*: *Symptoms* leaf spots circular, whitish to pale yellow, surrounded by a brown border; *Conidiomata* pycnidial, epiphyllous, several in each leaf spot, globose to subglobose, dark brown, semi-immersed, 50–100(–120) µm diam; *ostiolum* central, initially circular, 25–45 µm wide, later more irregular and up to 100 µm wide, surrounding cells concolorous or somewhat darker; *conidiomatal wall* 10–20µm thick, composed of *textura angularis* without distinctly differentiated layers, the cells 3–5 µm diam, the outer cells with brown, somewhat thickened walls, the inner cells with hyaline and thinner walls; *Conidiogenous cells* hyaline, cylindrical and tapering gradually towards the apex, or narrowly ampulliform with a relatively wide and long neck, holoblastic, proliferating percurrently 1–many times with indistinct annellations, rarely also proliferating sympodially, 6–17.5(–22) × 3–4(–5) µm. *Conidia* cylindrical, straight, more often slightly curved or flexuous, with a narrowly to broadly rounded, sometimes more distinctly pointed apex, towards the broadly truncate base barely attenuated, (0–)3–5(–7)-septate, not constricted around the septa, hyaline, contents with several oil-droplets and minute granular material in each cell in the living state, with inconspicuous oil-droplets and granular contents in the rehydrated state, (22–)39–75(–85) × 2–3 µm (rehydrated). *Sexual morph* unknown.

*Description in vitro*: *Colonies* on OA (3–)4–6 mm diam in 12 d (7–11 mm in 3 wk), with an even, pure yellow to straw, glabrous margin, the pigment diffusing into the surrounding medium; colonies spreading, but in the centre quite distinctly elevated, immersed mycelium pure yellow to straw, later locally citrine-green or citrine; after 10–15 d darkened by numerous immersed or superficial pycnidia arranged in random patterns, the outer wall of the superficial pycinidia entirely covered by white to glaucous hyphae, tardily releasing initially buff to straw, later salmon conidial slime; reverse pure yellow, but centre olivaceous and citrine to greenish olivaceous after 3 wk. After incubation over about 7 wk olivaceous-black sectors become visible in the colony consisting mostly of immersed strands of dark-walled hyphae, alternating with yellow sectors; some colonies develop wider sectors that remain yellow above, but more ochreous on reverse. *Colonies* on CMA 4–6 mm diam in 12 d (9–12 mm in 3 wk), as on OA, but sporulating earlier. *Colonies* on MEA 2–4 mm diam in 12 d (5–7(–9) mm in 3 wk; 17–24 mm in 7 wk), with an even to ruffled, colourless to buff, glabrous margin; no diffusing pigment seen; colonies restricted, irregularly pustulate up to 3 mm high, the surface dark, blackish or chestnut, covered by a short, dense mat of white to glaucous-grey, after 7 wk straw to pale yellow, aerial mycelium; conidiomata releasing droplets, later larger masses of first whitish, then salmon conidial slime; reverse brown-vinaceous in the centre, surrounded by hazel or cinnamon areas. *Colonies* on CHA 4.5 mm diam in 3 wk (24 mm in 7 wk); colony as on MEA, but the surface almost entirely hidden under a dense mat of woolly, white aerial mycelium, locally with a pure yellow to straw haze which later becomes more intense, and a yellowish pigment diffusing into the surrounding medium; reverse

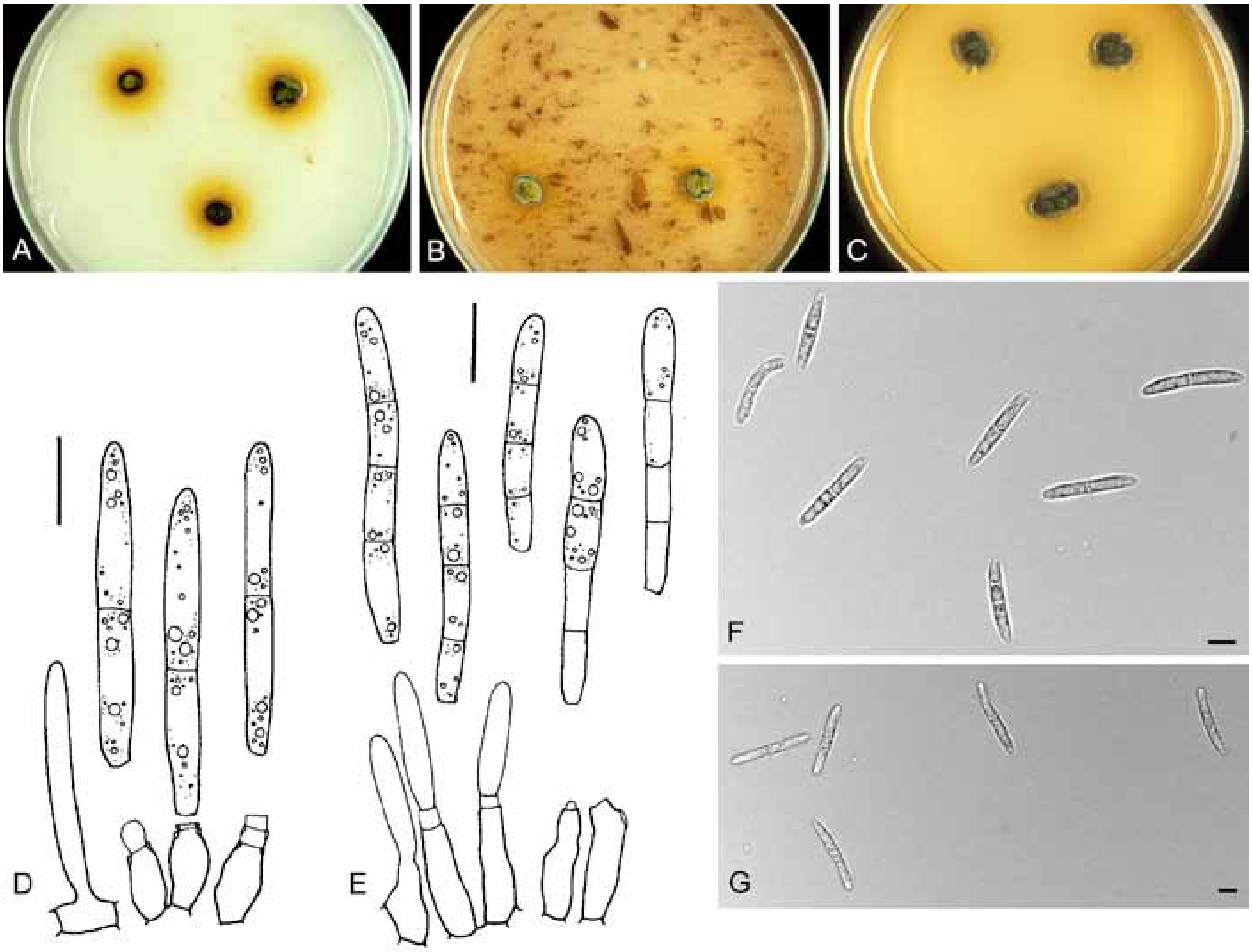


**Fig. 4.** *Caryophylloseptoria silenes*. A–C. Colonies CBS 109100. A. On OA. B. On CHA. C. On MEA. D. Conidia and conidiogenous cells *in planta* (CBS H-21160). E. Ibid., on OA (CBS 109100). F–G. Conidia on OA (CBS 109100). Scale bars = 10 µm.

umber to sienna; densely aggregated superficial conidiomata in the centre releasing masses of amber to pale salmon conidial slime. *Conidiomata* pycnidial, as *in planta*, but somewhat larger, 70–145 µm diam, mostly single, sometimes merged into complexes, without differentiated ostiolum; *conidiogenous cells* as *in planta*, proliferating percurrently with distinct annellations or sympodially, 8.5–25 × 3.5–6 µm; *conidia* cylindrical, straight, slightly curved or flexuous, with a rounded apex, lower part barely attenuated into a broad truncate base, (0–)1–5-septate, not constricted around the septa, hyaline, with several oil-droplets and minute granular material in each cell, (44–)77–94.5 × (2–)2.5–3 µm.

*Hosts*: *Lychnis* spp. and *Silene* spp. (incl. *Melandrium*).

*Material examined*: **Austria**, Tirol, Inntal, near Telfs, on living leaves of *Silene pratensis* (syn. *M. album*), 4 Aug. 2000, G. Verkley 1047, CBS H-21161, living culture CBS 109098, 109102; same loc., host, date, G. Verkley 1048, CBS H-21162, living culture CBS 109099, 109101; **Netherlands**, Hilversum, on living leaves of *Silene dioica* (syn. *Melandrium rubrum*), 22 June 1985, H.A. van der Aa 9524, CBS H-18112.

*Notes*: This fungus has been reported from several species of *Lychnis* and *Silene* (including *Melandrium*), and the size ranges of conidia given by various authors differ considerably. In the original description by Desmazières, the fungus was characterised as having 5–7-septate conidia, measuring 50–70 ×2.5–3 µm, in widely opening pycnidia. Diedicke (1915) gave the same spore measurements, but Grove (1935) reported 30–50 × 2–3 µm, while Jørstad (1965) gave different ranges on different hosts (overall extremes 27–72 × 2–3 µm). Radulescu *et al.* (1973) reported 30–76 × 2.2–3.3 µm, and Vanev *et al.* (1997) 26–93.5 × 1.5–3.2 µm. The characters of the Austrian material studied here generally agree well with previous records, and the range of conidial sizes agrees best with that given by Vanev *et al.* (1997). The authors cited above have listed various names as synonyms of *S. lychnidis*, including *S. lychnidis* var. *pusilla* (= *S. pusilla*). Two strains isolated from *Lychnis cognata* in South Korea (CBS 128614, 128630) first also identitifed as *S. lychnidis*, were shown by sequence analyses to belong to a distinct species, for which the name *C. pseudolychnidis* is introduced by Quaedvlieg *et al.* (2013).

***Caryophylloseptoria silenes*** (Westend.) Verkley, Quaedvlieg & Crous, **comb. nov.** MycoBank MB804471. Fig. 4.

*Basionym*: *Septoria silenes* Westend., in Westendorp & Wallays, Herb. crypt. Belge, Fasc. 19, no 955. 1854; Bull. Acad. R. Belg. Cl. Sci., Sér. 2, 2: 575. 1857.

*Description in planta*: *Symptoms* leaf spots circular or elliptical, pale yellow to pale brown, surrounded by a dark purplish border; *Conidiomata* pycnidial, amphigenous but predominately epiphyllous, numerous in each leaf spot, globose to subglobose, immersed, 50–80(–100) µm diam; *ostiolum* central, initially circular, 20–45 µm wide, later more irregular and up to 50 µm wide, surrounding cells somewhat darker; *conidiomatal wall* only 10–15 µm thick, composed of *textura angularis* without distinctly differentiated layers, the outer cells with brown, somewhat thickened walls and 4–7.5 µm diam, the inner cells hyaline and thin-walled and 3.5–5 µm diam; *Conidiogenous cells* hyaline, ampuliform, or cylindrical and widest near the apex, hyaline, holoblastic, proliferating percurrently 1–several times with distinct scars (annellations), sympodial proliferation not observed, 4–10 × 3–5 µm. *Conidia* cylindrical, straight or slightly curved, with a rounded apex, lower part attenuated more or less abruptly into a broad truncate base, (0–)1(–4)-septate, somewhat constricted around the septa, hyaline, contents with several oil-droplets in each cell in the living state, with conspicuous oil-droplets and granular contents in the rehydrated state, 21–37 × 2–3.5(–4) µm (rehydrated; in turgescent state up to 4.5 µm wide). *Sexual morph* unknown.

*Description in vitro*: *Colonies* on OA 7–9 mm diam in 12 d (7–10 mm in 3 wk; 21–23 mm in 7 wk), with an even, later undulating, pure yellow to luteous, glabrous margin, the pigment diffusing into the medium around the colony; colonies spreading, but in the centre quite distinctly elevated, immersed mycelium luteous to ochreous-orange, darkened by numerous simple, first brownish, then black pycnidia arranged in concentric patterns, releasing droplets of initally milky white, later pale pure yellow conidial slime; immersed mycelium later mostly luteous to sienna, much darker after 7 wk; most of the colony covered by a high, woolly-floccose mat of pale grey, later straw to pure yellow aerial mycelium; reverse luteous, in the centre umber, ultimately becoming almost black. *Colonies* on CMA 5–7 mm diam in 12 d (7–9 mm in 3 wk; 18–19 mm in 7 wk), as on OA, but immersed mycelium and (more scarce) aerial mycelium more intensely pigmented, immersed mycelium appearing rust to sienna after 3, but mostly black after 7 wk, and conidial slime earlier pure yellow. *Colonies* on MEA 3–5 mm diam in 12 d (5–9 mm in 3 wk; 17–20 mm in 7 wk), with a ruffled, yellowish, glabrous margin; diffusing yellow pigment distinct around the colony; colonies restricted, irregularly pustulate up to 3 mm high, the surface dark, blackish or chestnut, covered by a short, dense, almost pruinose mat of grey to pure yellow aerial mycelium; conidiomata releasing droplets of initially pale pure yellow, later almost amber conidial slime; reverse chestnut or blood. *Colonies* on CHA 3.5–5 mm diam in 12 d (7–8 mm in 3 wk; 12–17 mm in 7 wk), with an even or irregular margin, mostly hidden underneath white aerial hyphae; yellow pigment very clear diffusing beyond the colony margin after 3 wk; colonies restricted, conical or hemispherical, the surface very dark, but mostly covered by a dense mat of woolly, initially white, then pure yellow aerial mycelium; reverse sienna to fulvous. Sporulating scarcely after 3, but more intensely after 7 wk, cirrhi or droplets of pale pure yellow, later amber conidial slime released by superficial conidiomata.

*Conidiomata* pycnidial, as *in planta*, but larger, 90–155 µm diam, mostly single, sometimes merged into complexes with several ostioli; *conidiogenous cells* as *in planta*, but often with a more elongated neck, proliferating percurrently with distinct annellations or sympodially, 7–17 × 3–5 µm; *conidia* cylindrical, straight or slightly curved, with a rounded apex, lower part attenuated more or less abruptly into a broad truncate base, (0–)1–3(–4)-septate, somewhat constricted around the septa, hyaline, with several oil-droplets in each cell, (24–)26.5–35(–42) × 3–4(–5) µm.

*Hosts*: *Silene* spp.

*Material examined*: **Austria**, Tirol, Ötztal, Horlachtal, Mühl near Niederthai, alt. 1500 m, on living leaves of *Siline nutans*, 3 Aug. 2000, G. Verkley 1041, CBS H-21160, living cultures CBS 109100, 109103.

*Notes*: Jørstad (1965) examined type material from BR in Westend., Herb. crypt. Belge 955, on *Silene armeria*. He reported that among numerous immature pycnidia were a few thin-walled pycnidia with 0-septate conidia measuring 21–24 × 2–2.5 µm, but in his opinion there was no doubt that collections from other hosts like *Silene cucubalus* (= *S. inflata*), and from *Silene rupestris* with predominantly 1-septate spores up to 31 µm in length belonged to the same species. In the material collected in Austria, we have observed predominantly 1-septate conidia, but conidial length did vary in different fruitbodies: some pycnidia produced conidia 21–28 µm in length, others conidia measuring 26–37 µm in length. However, isolates from these pycnidia were similar in colony characters and conidia produced did not show such differences in size range.

Priest (2006) noted that there are at least two taxa of *Septoria* occurring on *Silene*, a short-spored taxon represented by *S. silenes*, and a long-spored taxon for which the name *S. silenicola* applies. This author referred all collections from Australia on this host genus to *S. silenicola,* for which conidia measure (34–)48–65(–85) × 2–2.5(–3) µm.

As pointed out by Petrak (1925) and Jørstad (1965), several of the *Septoria* described on *Silene* spp. (and *Melandrium*) are likely to be conspecific with *S. silenes*. *Septoria dominii* Bubák 1905 was already placed in the synonymy of *S. silenes* by Jørstad (1965), and the same could be correct for *S. dimera* from *Silene nutans*. According to the original diagnosis, the conidia of *S. dimera* are 1-septate and measure 28–32 × 4 µm. Radulescu *et al.* (1973) and Markevičius & Treigienė (2003) treated *S. dimera* as a separate species next to *S. silenes*, reporting measurements for conidia of *S. dimera* as 25–40 × 3–4 µm, and 21–35 × 3.2–4.3 µm, respectively. Vanev *et al.* (1997) also treated *S. dimera*, reporting conidial measurements 26–65 × 2.5–4 µm, but they included material from *Silene* spp. and *Cucubalus baccifer*.

***Caryophylloseptoria spergulae*** **(**Westend.) Verkley, Quaedvlieg & Crous, **comb. nov.** MycoBank MB804472. Fig. 5.

*Basionym*: *Septoria spergulae* Westend., in Westendorp & Wallays, Herb. crypt. Belge, Fasc. 23-24, no. 1155. 1857; Bull. Acad. R. Belg. Cl. Sci., Sér. 2, 2: 576. 1857.

*Description in planta*: Symptoms absent. *Conidiomata* pycnidial, black, in dense groups on dead stems and leaves, only partly immersed in the host tissue, globose or slightly depressed, (50–)75–150 µm diam; *ostiolum* circular, central, 10–12.5 µm wide, without distinctly differentiated cells; *pycnidial wall* with an outer layer of *textura globulosa-angularis* containing cells 8–12 µm diam with brown walls, thickened unevenly up to 3µm, and an inner layer of *textura globulosa-angularis* containing cells 5–8 µm diam with hyaline or pale brown walls. *Conidiogenous cells* hyaline, ampuliform, or elongated ampulliform with a distinct neck, hyaline or very pale brown near the base, holoblastic, proliferating percurrently 1–many times with indistinct annellations, also sympodially, 5–10(–16) × 3–5 µm. *Conidia* cylindrical, regularly curved, or abruptly bent in the lower cell, gradually attenuated to the rounded apex, gradually or more abruptly attenuated into a truncate base, 1(–2)-septate, not or indistinctly constricted around the septum, hyaline, contents rich in small guttulae, minutely

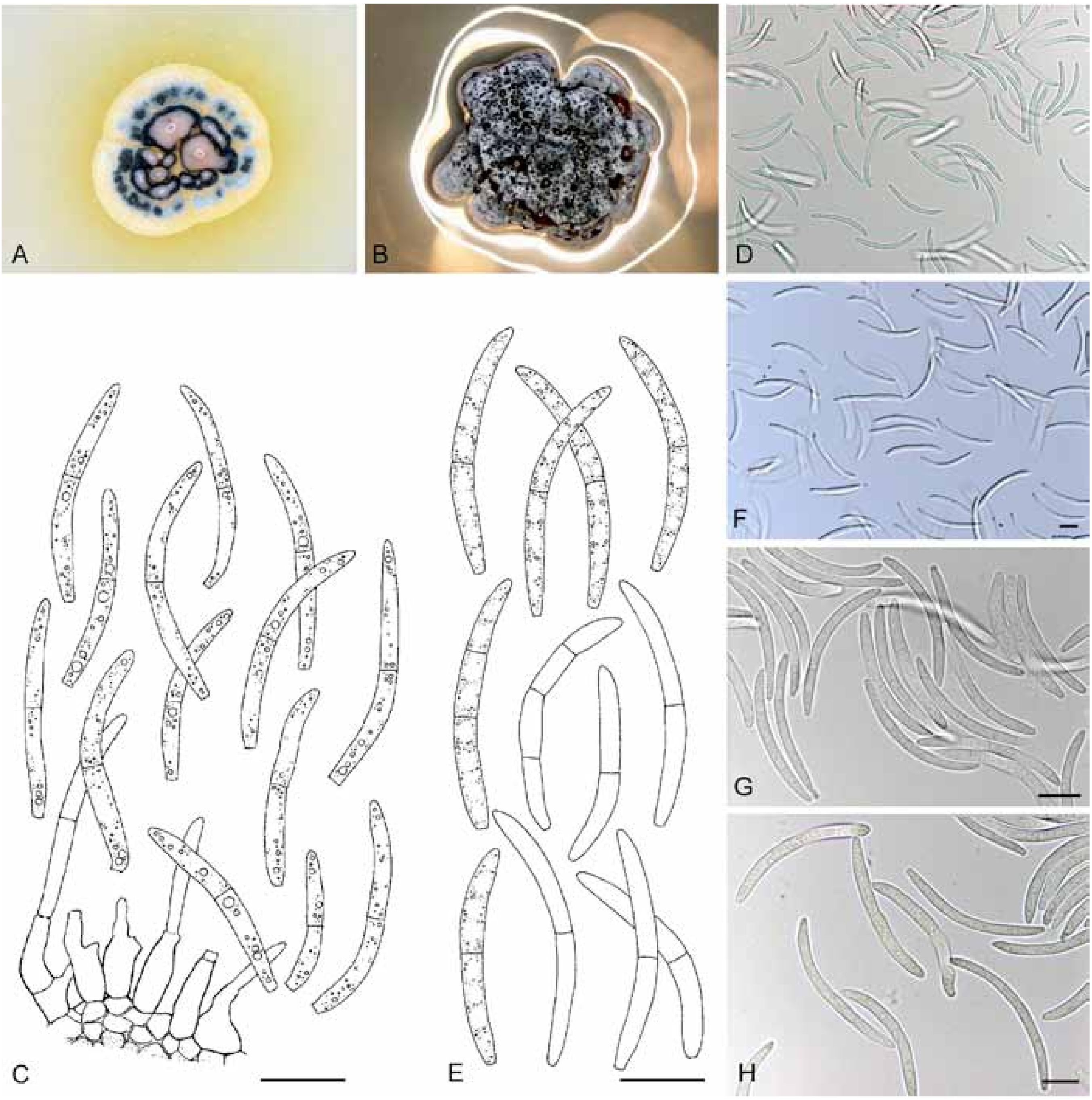


**Fig. 5.** *Caryophylloseptoria spergulae*. A, B. Colonies CBS 109010. A. On OA. B. On MEA. C. Conidia and conidiogenous cells *in planta* (CBS H-21150). D–H. Conidia on OA (CBS 109010). Scale bars = 10 µm.

granular material and large vacuoles in the living state, oil-droplets merged into larger guttules in the rehydrated state, (18–)24–33 (–40) × 2.0–2.5(–3.0) µm (rehydrated). *Sexual morph* unknown.

*Description in vitro*: *Colonies* on OA less than 2 mm diam after 2 wk (6–8 mm in 28 d), restricted, though not much elevated, with an even, colourless, glabrous margin; colony surface covered by a dense continuous or discontinuous mat of grey, finely felted to somewhat woolly, low aerial mycelium, agar around the colony showing a yellow diffusing pigment; immersed mycelium pale luteous to saffron, reverse concolorous, but olivaceous-black under areas with well-developed aerial mycelium or conidiomata. Colony sporulating in the centre after about 2 wk, with spores in large pale salmon droplets oozing from pycnidioid complexes. *Colonies* on CMA 8–10 mm diam in 28 d, as on OA, but immersed mycelium soon darkening and olivaceous-black, while the aerial mycelium is somewhat more greenish, and the mat denser and more continuous; reverse olivaceous-black. *Colonies* on MEA 5 mm diam in 2 wk (8–10 mm in 28 d), restricted, with an even, buff, glabrous margin; colony surface black, but with a diffuse mat of greyish white, often with some sulphur yellow (centre), woolly aerial mycelium; fruitbodies developing tardily on the colony surface, sporulating with large, dirty white to pale reddish masses in watery droplets; reverse dark brick to olivaceous-black. *Colonies* on CHA 7–9 mm diam in 2 wk, as on MEA, but aerial mycelium higher and denser, in the centre also conspicuously yellowish-pale citrine. No sporulation observed.

*Conidiomata* mostly olivaceous-brown, irregular merged complexes of initially closed, but soon widely opening stromata, only rarely pycnidial and structurally similar to those on the natural substratum. *Conidiogenous cells* hyaline, ampuliform, or elongated ampulliform with a relatively long neck, hyaline or very pale brown near the base, holoblastic, proliferating percurrently 1–many times with indistinct annellations, also sympodially, mostly after one or more percurrent proliferations, 7– 14(–22) × 3–5 µm. *Conidia* on OA hyaline, pale salmon in mass, cylindrical and regularly curved, or abruptly bent in the lower or upper cell, gradually attenuated to the rounded apex, more abruptly attenuated into a truncate base, contents granular with large vacuoles, 1(–3)-septate, not or indistinctly constricted around the septa, contents rich in minute guttulae and granular material, 25.5–41 × (2.0–)2.5–3.0(–4.5) µm.

*Hosts*: On dead leaves and stems of *Spergula* spp.

*Material examined*: **Belgium**, Beverloo, on dry leaves and stems of *Spergula arvensis*, M. Torquinet *s.n.*, **isotype** BR-MYCO 159328-54, also distributed in Westendorp & Wallay, Herb.crypt.Belg., Fasc. 23-24: no.1155. **Germany**, Brandenburg, Kreis Nieder-Barnim, near Prenden, on leaves and stems of *Spergula vernalis*, 24 July 1920, H. & P. Sydow *s.n.*, distributed in Sydow, Mycotheca germanica 1688, CBS H-4765. **Netherlands**, on *Dianthus caryophyllus*, Schouten *s.n.*, CBS 397.52 (sub *S. dianthi* Desm.); Prov. Gelderland, 't Harde, Doornspijkse Heide, De Zanden, on decaying leaves of *Spergula morisonii*, A. Aptroot 48300, 13 June 2000, **epitype designated here** CBS H-21150 "MBT175350", living culture ex-epitype CBS 109010.

*Notes*: This fungus was originally described from dry leaves and stems of *Spergula arvensis* by Westendorp, who described the conidia as 30 × 2.5 µm. The type from BR is well-preserved and rich in fruitbodies on leaves and stems, where conidia are 1(–2)-septate, 20–38 × 2–2.5(–3) µm. The collection Aptroot 48300 from *Spergula morisonii* agrees in morphology and can be identified as conspecific, although it contains a larger proportion of 2-septate conidia (that are mostly 30–40 µm long) than in the type. The material on *Spergula vernalis* that was distributed as Mycotheca germanica 1688 morphologically also agrees with these collections.

Other names were later introduced for *Septoria* on members of the plant genus *Spergularia* (= *Alsine*), which is closely related to *Spergula*: *S. alsines* Rostr. 1903 from *Spergularia* sp., conidia 20–31 × 2–3 µm formed in 55–120 µm wide pycnidia (Teterevnikova-Babayan 1987; conidia 20–25 × 2–3 µm and 3-septate, in the original diagnosis of Rostrup 1903, based on material from *Alsine verna* non *Spergula vernalis*), *S. spergulariae* 1903, on *Spergularia rubra* (conidia 30–45 × 2.5–3 µm, "multiseptate"), *S. vandasii* 1906, on *Alsine glomerata*, and *S. spergularina* 1945, on *Spergularia longipes* (no conidial measurements available). Some of these names could be synonymous with *S. spergulae* or perhaps *S. alsines*, but in order to corroborate this, new material needs to be collected and compared to the types. According to Teterevnikova-Babayan (1987), *S. alsines* differs from *S. spergulae* in conidial shape in that the conidial base is more truncate than in *S. spergulae*, and in that it is capable of also killing *Minuartia glomerata*. *Rhabdospora alsines* Mont. 1892, which was described from dead stems of *Alsine tenuifolia*, is unlikely to be conspecific with *S. spergulae*, as its conidia were described as 16–18 × 2 µm and 1-septate.

Muthumary (1999) studied type material of *S. dianthi* 1849 (PC 344) and by the drawings he made of it the conidia of this fungus and those of *S. spergulae* appear very similar in shape. Muthumary reported that the conidia of *S. dianthi* were 32–48 (av. 40) × 3–4 (av. 3) µm, and mostly 1-, rarely 2-septate. Given these measurements, on average, the conidia in the type of *S. dianthi* are clearly longer than in *S. spergulae* (on average below or around 30). Moreover, *S. dianthi* is a fungus causing leaf spots on several *Dianthus* spp., while *S. spergulae* is only known from dry and dead host tissues, and is therefore believed to be saprobic (and possibly endophytic). CBS 109010 and the only strain available for *S. dianthi* (CBS 397.52) show 100 % sequence homology of the LSU, ITS, Btub and Cal, while there are only minor differences in Act (99.25 %), EF (97.54 %), and RPB2 (99.42 %). Further work is required to establish that *S. dianthi* and *S. spergulae* are truely distinct taxa.

## ***Septoria*** Sacc., Syll. Fung. 3 : 474. 1884. nom. cons.

*Type species* : *S. cytisi* Desm.

A generic description is provided by Quaedvlieg *et al.* (2013, this volume).

## ***Septoria aegopodii*** Desm. ex J. Kickx, Pl. Crypt. Fland. 1: 427. 1876 [Annls Sci. Nat., sér. 6, 7: no 616. 1878?]. Fig. 6.

= *Septoria podagrariae* Lasch, in Rabenh., Herb. mycol. I, no 458. 1843. nomen nudum.
= *Sphaeria podagrariae* Roth, Catal. Bot. 1: 230. 1797.
≡ *Mycosphaerella podagrariae* (Roth : Fr.) Petr., Annls mycol. 19 (3/4): 203. 1921.
= *Cryptosporium aegopodii* Preuss, Linnaea 24: 719 (Fungi Hoyersw., no. 322). 1853.
≡ *Phloeospora aegopodii* (Preuss) Grove, British Stem- and Leaf-fungi (Coelomycetes) 1: 434. 1935.
≡ *Septoria aegopodii* (Preuss) Sacc., Syll. Fung. 3: 529. 1884 [non Desm. 1878].
?= *Septoria podagrariae* var. *pimpinellae-magnae* Kabát & Bubák, in Bubák & Kabát, Ber. naturw.-med. Ver. Innsbruck 30: 19-36 (extr. 11). 1906.
= *Mycosphaerella aegopodii* Potebnia, Annls mycol. 8(1): 49. 1910.

*Description in planta*: *Symptoms* leaf spots numerous but small, angular and delimited by veinlets, visible on both sides of the leaf, white to pale yellow. *Conidiomata* pycnidial, developing soon after first discolouration of the host tissue, predominantly epiphyllous, mostly also visible from the underside of the lesion, several scattered in each leaf spot, globose to subglobose, pale to dark brown (drying black), immersed, 125–190 µm diam, releasing conidia in white cirrhi; *ostiolum* central, initially circular and 17–35 µm wide, later becoming more irregular and up to 100 µm wide, surrounding cells dark brown, with thickened cell walls; *conidiomatal wall* except for the part surrounding the ostiolum poorly developed, about 10–20 µm thick, composed of pale brown to hyaline angular cells 3.5–8 µm diam with thin walls. *Conidiogenous cells* hyaline, discrete, cylindrical to narrowly or broadly ampulliform, holoblastic, proliferating sympodially, 8–15(–18) × 2.5–4.5 µm. *Conidia* filiform-cylindrical, straight, curved to somewhat flexuous, attenuated gradually to a relatively broadly rounded apex and broadly truncate base often provided with a collar of gelatinous material, (0–)1–2(–3)-septate (second and later septa very thin and easily overlooked), not constricted around the septa, hyaline, contents with numerous minute oil-droplets and granular material in each cell in the living state, with minute oil-droplets and granular contents in the rehydrated state, (30–)55–95(–115) × 3.5–4 µm (living; 30–72(–80) × 2.5–4 µm, rehydrated).

*Description in vitro*: All attempts to grow the isolates from conidia failed. Some conidia germinated at the apical cells, but mycelia died within 1–2 d after germination.

*Hosts*: *Aegopodium podagraria* and *Pimpinella* sp.

*Material examined*: **Austria**, Tirol, Ötztal, Ötz near Habichen, on living leaves of *Pimpinella* sp., 24 July 2000, G. Verkley 1001, CBS H-21187. **Netherlands**, Prov. Overijssel, Losser, in garden at Mollenbergstraat, on living leaves of *Aegopodium podagraria*, June 1999, G. Verkley 800, CBS H-21192; same substr., Prov. Overijssel,

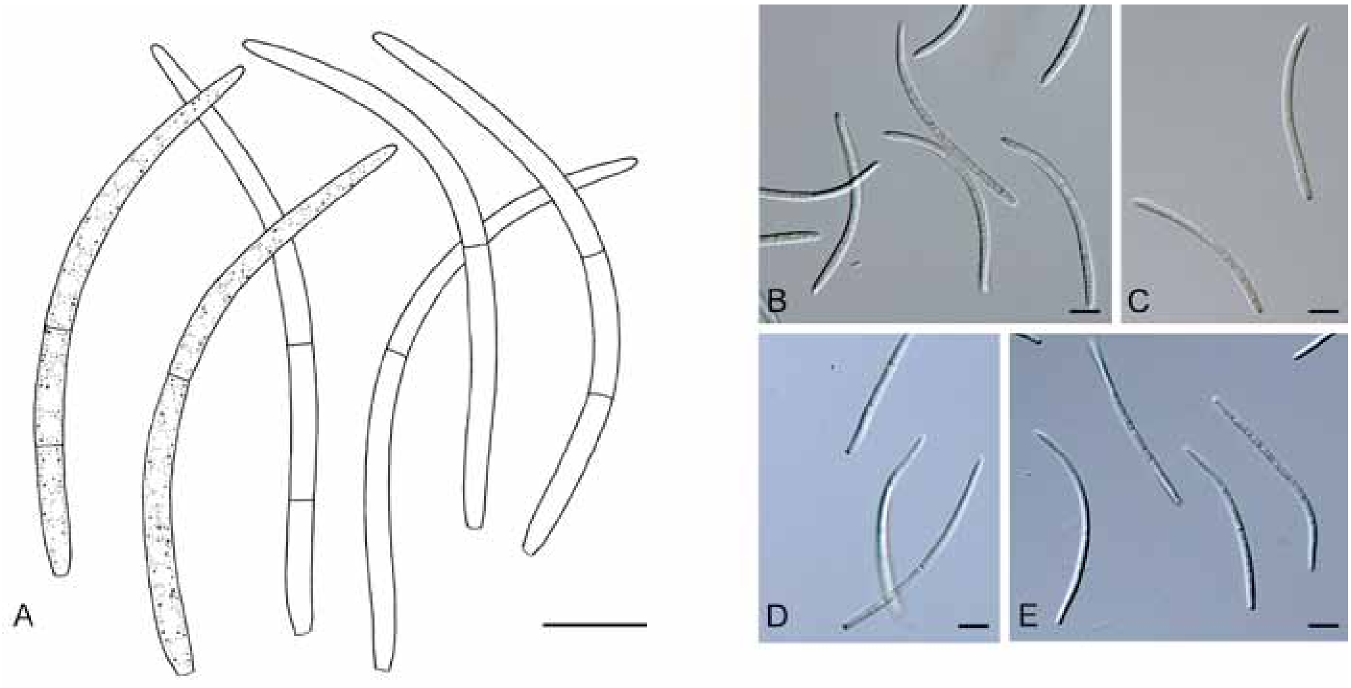


**Fig. 6.** *Septoria aegopodii*. A–E. Conidia *in planta*. A–C. CBS H-21262. D, E. CBS H-21199. Scale bars = 10 µm.

Losser, Arboretum Poort-Bulten, June 1999, G. Verkley 801, CBS H-21193; same substr., Prov. Utrecht, 's Graveland, Gooilust, 5 Sep. 1999, G. Verkley 916, CBS H-21199; same substr., Prov. Limburg, St. Jansberg, near Plasmolen, 9 Sep. 1999, G. Verkley 931, CBS H-21211; same substr., Prov. Zeeland, Zuid-Beveland, Community of Borsele, Schouwersweel near Nisse, 27 Aug. 2001, G. Verkley 1116, CBS H-21165; same substr., Prov. Utrecht, Soest, 29 July 2008, G. Verkley 5020, CBS H-21262.

*Notes*: This species is common on *Aegopodium podagraria*, especially on plants growing under less favourable conditions. Jørstad (1965) noted that in autumn the pycnidia are commonly accompanied by immature perithecia (or by "sclerotia") of *Mycosphaerella aegopodii* in Sweden, but we have not found any in The Netherlands. According to van der Aa (pers. comm.), the sexual morph only matures in montane habitats. Aptroot (2006), who studied herbarium specimens collected at high altitudes in several localities in Europe also did not observe any mature ascomata. Type material of *M. podagrariae* could not be located (Aptroot 2006). Simon *et al.* (2009) studied the cellular interactions between *M. podagrariae* and *Aegopodium podagraria* based on German material (no cultures preserved).

We have not seen the type of *S. podagrariae* var. *pimpinellae-magnae* 1906 described from *Pimpinella magna* (= *P. major*?) in Tirol, but since the conidial characters given by Saccardo & Trotter (1913, 45–60 × 2.5–4 µm, 3-septate) are well within the range of *S. aegopodii*, it is placed here tentatively as a synonym. On *Pimpinella*, eight other *Septoria* species or varieties have been described in the literature, but these could not be studied here. The oldest available name would be *S. pimpinellae* Ellis 1893 (later homonyms Laubert 1920 and Hollós 1926). According to the diagnoses the conidial sizes described for these taxa largely overlap, and range from 15–35 × 1–1.5(–2) µm, thus all considerably smaller than in *S. aegopodii*.

***Septoria aegopodina*** Sacc., Michelia 1: 185. 1878. Fig. 7.

= *Septoria aegopodina* var. *villosa* Gonz. Frag., Assoc. españ. Progr. Cienc. Congr. Oporto, 6. Cienc. natur.: 47. 1921.

= *Septoria aegopodina* var. *trailii* Grove, British Stem-and Leaf-Fungi (Coelomycetes) 1: 396. 1935.

*Description in planta*: *Symptoms* leaf spots numerous, indefinite and soon covering large parts of the leaf lamina, visible on both sides of the leaf, first yellow then pale orange-brown. *Conidiomata* pycnidial, predominantly hypophyllous, scattered or gregarious, globose to subglobose, pale to dark brown, immersed, 90–160 µm diam, releasing conidia in white cirrhi; *ostiolum* central, circular and 15–25 µm wide, surrounded by cells with dark brown to almost black, thickened walls; *conidiomatal wall* 10–28 µm thick, composed of an outer cell layer of pale brown to hyaline isodiametric angular or globose cells, 3.5–8 µm diam with thickened walls, and an inner layer of one or more hyaline cells with not or only slightly thickened walls. *Conidiogenous cells* hyaline, discrete, mostly broadly ampulliform, holoblastic, rarely proliferating sympodially, possibly also percurrently but no annellations visible, 4–7(–8) × 3–4.5 µm. *Conidia* filiform to filiform-cylindrical, straight or curved, attenuated gradually to a narrowly rounded to somewhat pointed apex, and attenuated gradually or more abruptly to a narrowly truncate base, (0–)1–3-septate, not constricted around the septa, hyaline, with numerous minute and several larger oil-droplets in each cell in the living state, and minute oil-droplets and granular contents in the rehydrated state, (22–)30–42.5 × 1.5–2(–2.5) µm (rehydrated). *Sexual morph* unknown.

*Description in vitro* (20 ºC, diffuse daylight): *Colonies* on OA 7–10 mm diam in 2 wk, with a very narrow, glabrous and rosy-buff margin; colony restricted, somewhat elevated, immersed mycelium colourless to faintly brick, or much darker, brown-vinaceous, but mostly hidden under a dense, woolly mat of pure white to faintly yellow aerial mycelium; reverse olivaceous-black to dark brick; a vinaceous pigment diffusing into the surrounding medium. *Colonies* on MEA 8–15 mm diam in 2 wk, the margin covered by pure white aerial hyphae; colony restricted, irregularly postulate in the central area, mostly covered by a dense woolly-floccose mat of smoke grey aerial mycelium, but after 2 wk numerous glabrous, black conidiomata appear on the colony surface in the centre, releasing milky white conidial slime. Reverse of colony olivaceous-black.

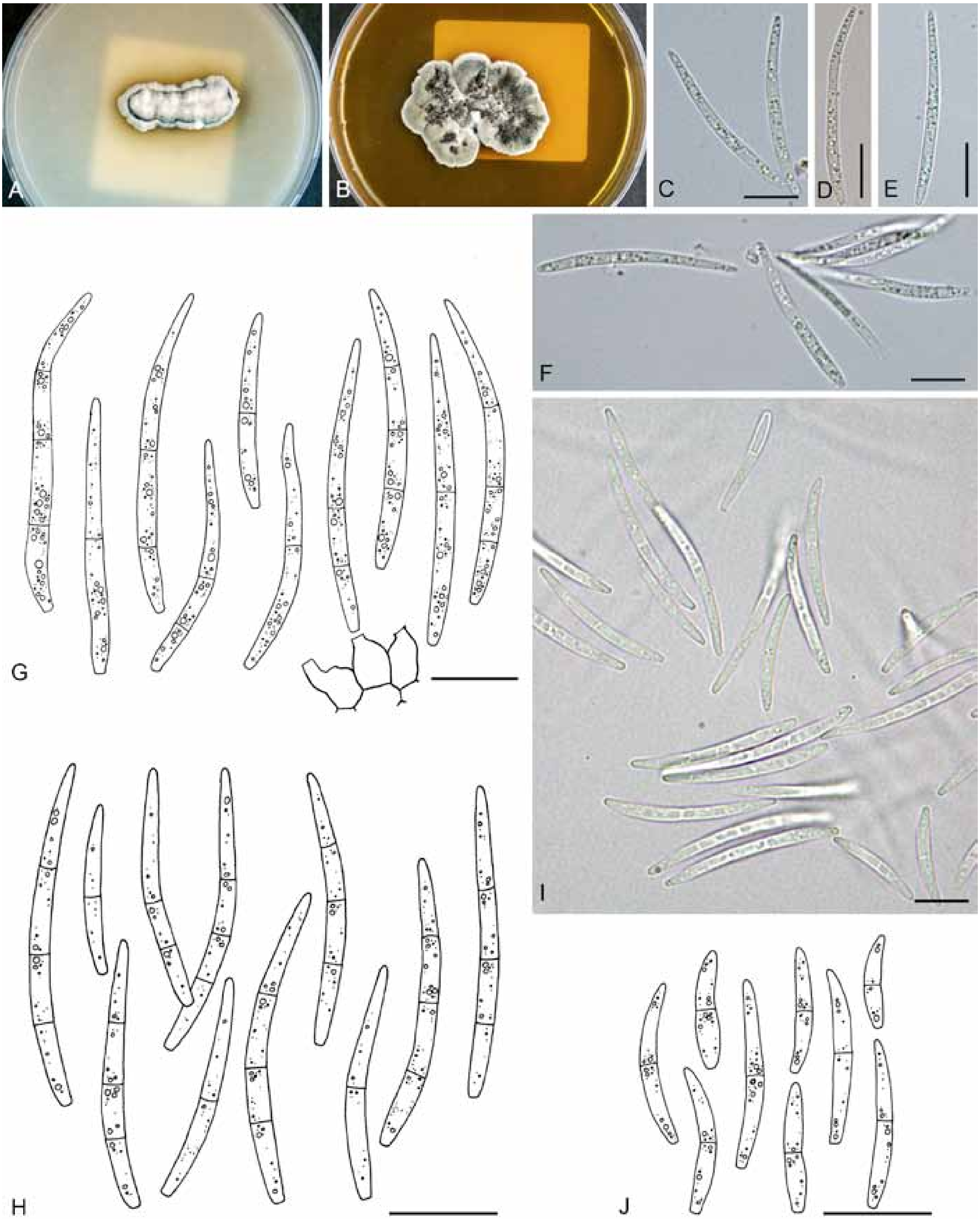


**Fig. 7.** *Septoria aegopodina*. A, B. Colonies CBS 123740. A. On OA. B. On MEA. C–F. Conidia *in planta* (CBS H-21249). G. Conidia and conidiogenous cells *in planta* (CBS H-21249). H, I. Conidia on OA (CBS 123741). J. Conidia on MEA (CBS 123740). Scale bars = 10 µm.

*Conidia* on MEA elongated ellipsoidal to cylindrical, straight to distinctly curved, rounded to narrowly pointed at the apex, attenuated gradually to a narrowly truncate base, 0–1-septate, 0-septate 8–12 × 2–2.5(–3), 1-septate 10–21 × 2–2.5 µm; *Conidia* on OA cylindrical, straight or slightly to distinctly curved, narrowly rounded to slightly pointed at the apex, attenuated gradually to a narrowly truncate base, 1–3-septate, (16–)20–32 × 1.5–2 µm.

*Hosts*: *Aegopodium podagraria* and *Pimpinella* spp.

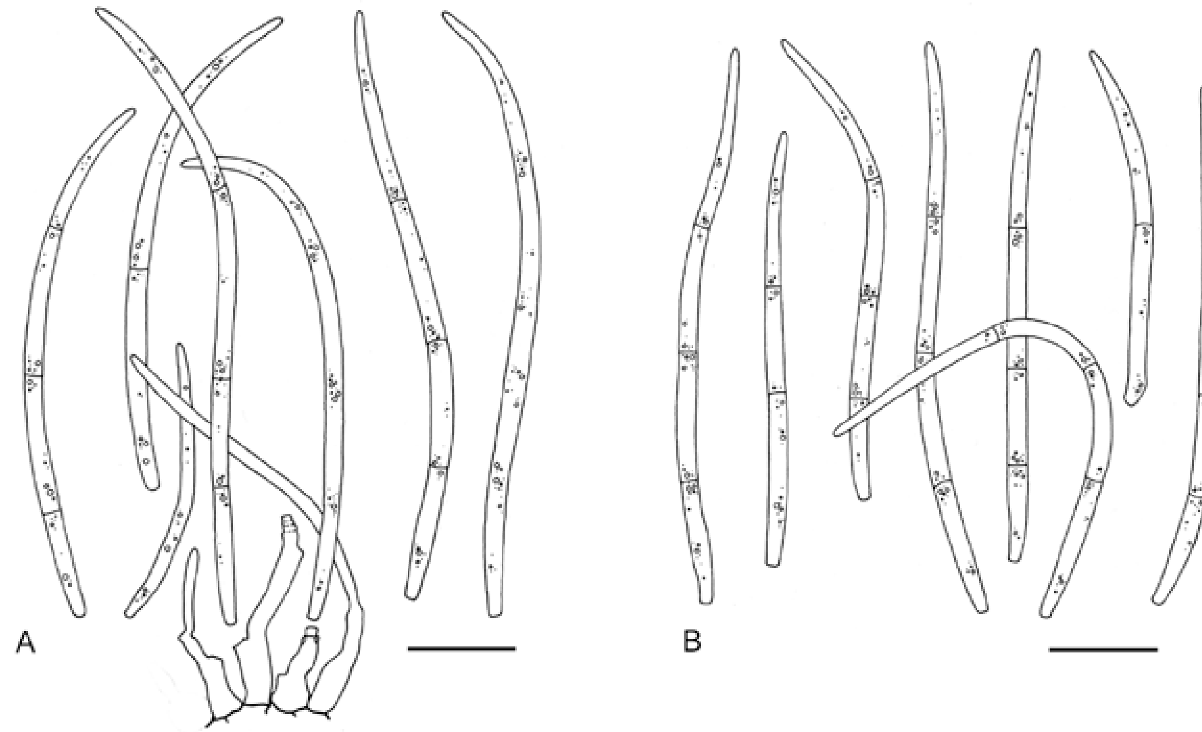


**Fig. 8.** *Septoria anthrisci*. A. Conidia and conidiogenous cells *in planta* (CBS H-21185). B. Conidia on OA (CBS 109020). Scale bars = 10 µm.

*Material examined*: **Czech Republic**, Moravia, Veltice, Forest of Rendez Vous, on living leaves of *Aegopodium podagraria*, 16 Sep. 2008, G. Verkley 6013, CBS H-21249, living cultures CBS 123740, 123741.

*Notes*: Morphologically, the material from the Czech Republic available here agrees well with *S. aegopodina* as described by Vanev *et al.* (1997) and Shin & Sameva (2004), although the pycnidia are larger than described by these authors (55–85 µm diam). The species can easily be distinguished from *S. aegopodii* occurring on the same host plant, as the conidia of that fungus are considerably larger (30–115 × 3.5–4 µm), and appear predominantly 1-septate. The conidia more closely resemble those of *S. anthrisci*. The diagnoses of *S. aegopodina* var. *trailii* based on material on *Pimpinella saxifraga*, and of *S. aegopodina* var. *villosa* on *Pimpinella villosa*, agree with the description of the type variety. Both varieties are therefore considered synonyms of *S. aegopodina*. In the multigene phylogeny *S. aegopodina* groups fairly closely with *S. oenanthicola*, *S. sii* and *S. oenanthis* from the same host family (*Apiaceae*), but other taxa from that family like *S. anthrisci* are relative distant and belong elsewhere the *Septoria* clade (Fig. 2). Other isolates grouping with *S. aegopodii* include those of *S. mazi* from *Mazus japonicus* (*Scrophulariaceae*), *S. campanulae* from *Campanula takesimana* (*Campanulaceae*), and *S. gentianae* from *Gentiana scabra* var. *buergeri* (*Gentianaceae*).

***Septoria anthrisci*** Pass. & Brunaud, Rev. Mycol. (Toulouse) 5: 250. 1883 [non P. Karst., Meddn Soc. Fauna Flora fenn. 13: 10. 1884]. Fig. 8.

*Description in planta*: *Symptoms* leaf spots numerous but small, circular to elliptical, visible on both sides of the leaf, the centre white to pale ochreous, surrounded by a relatively narrow, somewhat elevated, dark reddish brown to black margin. *Conidiomata* pycnidial, epiphyllous, sometimes also visible from the underside of the lesion, mostly one, rarely up to three in each leaf spot, subglobose to lenticular, sometimes becoming cupulate, brown to black, immersed, 115–190 µm diam; *ostiolum* central, initially circular and 30–55 µm wide, later becoming more irregular and up to 100 µm wide, surrounding cells concolorous; *conidiomatal wall* about 12–20 µm thick, composed of an outer layer of pale brown angular cells 4.5–7 µm diam with somewhat thickened walls, and an inner layer of thin-walled, pale yellow angular to globose cells 2.5–5 µm diam. *Conidiogenous cells* hyaline, discrete, rarely integrated in 1-septate conidiophores, globose or narrowly or broadly ampulliform, holoblastic, mostly with a relatively narrow elongated neck, proliferating percurrently several times with distinct annellations, often also sympodially after or in between a few percurrent proliferations, 6–14(–18) × 2.5–5(–6) µm. *Conidia* filiform, straight, curved to flexuous, attenuated gradually to a narrowly pointed apex and narrowly truncate base, (0–)1–3(–4)-septate (septa very thin and easily overlooked), not constricted around the septa, hyaline, contents with several minute oil-droplets and granular material in each cell in the living state, with minute oil-droplets and granular contents in the rehydrated state, (18–)25–59 (–65) × 1–2 µm (living; rehydrated, 1–1.8 µm wide). *Sexual morph* unknown.

*Description in vitro*: *Colonies* on OA 4–6(–9) mm diam in 1 wk (18–22 mm in 22 d), with an even, glabrous, peach, later coral margin, with a concolorous pigment diffusing beyond the colony margin; colonies after 1 wk restricted, distinctly elevated in the centre, immersed mycelium first peach to pale coral, then deep coral, the colony already appearing darker in the centre after 1 wk due to numerous almost black pycnidial conidiomata in part merging into large complexes, releasing pale whitish or rosy-buff droplets of conidial slime from one to several short-papillate or more elongated neck-like openings; reverse in the centre blood colour, surrounded by a first intense peach, later scarlet or coral area. *Colonies* on CMA 7–8(–9) mm diam in 1 wk (18–21 mm in 22 d), as on OA. *Colonies* on MEA 6–11 mm diam in 1 wk (24–29 mm in 22 d), with an even, almost glabrous, buff margin, without a diffusing pigment; colonies restricted, irregularly pustulate to hemispherical, already up to 4 mm high after 1 wk, immersed mycelium leaden grey to olivaceous-grey, covered by well-developed white to greyish, appressed, woolly aerial mycelium; conidiomata abundantly developing at the surface in the central area, releasing cirrhi of buff to pale luteous to rosy-buff conidial slime; reverse fuscous black to brown-vinaceous, surrounded by a narrow pale luteous marginal zone. *Colonies* on CHA 7–12 mm diam in 1 wk (29–31 mm in 22 d), as on MEA, but the surface more glaucous to glaucous blue green, the margin rosy-buff, and the conidial slime pale flesh.

*Conidiomata* pycnidial, single, brown to black, 100–250 μm diam, *conidiogenous cells* as *in planta*; *conidia* as *in planta*, 25–55(–69) × 1.2–2 μm.

*Hosts*: *Anthriscus* spp., and also *Chaerophyllum* spp. (Teterevnikova-Babayan 1987; Vanev *et al.* 1997).

*Material examined*: **Austria**, Tirol, Ötztal, Sautens, on living leaves of *Anthriscus* sp., 30 July 2000, G. Verkley 1022, CBS H-21185, living culture CBS 109019, 109020.

*Notes*: According to the short and incomplete original diagnosis, the conidia of *S. anthrisci* are continuous, 40–50 μm long. The type host is *Anthriscus vulgaris*. The description of the species on the host agrees well with those provided by Vanev *et al*. (1997) and Teterevnikova-Babayan (1987), although the latter reported conidia up to 75 μm long. The species is close to *S. petroselini* (CBS 182.44 and CBS 109521), from which it cannot be distinguished by ITS sequence, but the EF and Act sequences proved to differ by 4 and 27 %, respectively.

Of other *Septoria* species found on the family *Apiaceae*, only *S. petroselini* is relatively closely related. *Septoria petroselini* can be distinguished from *S. anthrisci* by the larger conidia (29-80 × 1.9-2.5 mm) with up to 7 septa on the host plant, usually species of *Petroselinum* or *Coriandrum*.

***Septoria apiicola*** Speg., Boln Acad. nac. Cienc. Córdoba 11: 294. 1888. Fig. 9.

≡ *Rhabdospora apiicola* (Speg.) Kuntze, Revisio generum plantarum 3 (2): 509. 1898.

= *Septoria apii* Chester, Bull. Torrey Bot. Club 18: 371. 1891 [non Rostr., Gartn. Tidende 180. 1893, later homonym].

= *Septoria petroselini* var. *apii* Briosi & Cavara, I funghi parassiti delle piante coltivate de utili essicati, delineati e descritti, Fasc. 6, no 144. 1891.

= *Septoria apii-graveolentis* Dorogin, Mater. Mikol. Fitopat. Ross. 1 (4): 72. 1915.

*Description in planta*: *Symptoms* on leaves numerous spots, scattered, separate but not well-delimited, circular to elliptical, or confluent, yellowish or pale brown and in dry conditions also with a white centre, visible on both sides of the leaf. *Conidiomata* pycnidial, amphigenous, single, numerous in each lesion, scattered, in small clusters or in more or less distinct concentric patterns, globose to subglobose, dark brown to black, immersed, (60–)75–170 μm diam; *ostiolum* circular, central, somewhat papillate, 15–45(–55) μm wide, surrounded by darker cells with thickened walls; *conidiomatal wall* composed of *textura angularis*, 12.5–20 μm thick, with an outer layer of cells, 4–6.5(–8) μm diam with brown, thickened walls, and an inner layer of hyaline and thin-walled cells 3.5–4 μm diam. *Conidiogenous cells* cylindrical, or broadly to elongated ampulliform mostly without distinct neck, hyaline, holoblastic, proliferating percurrently, annellations indistinct, rarely also sympodially, 4–8(–10) × 3.5–5 μm. *Conidia* filiform, straight, curved, or flexuous, gradually attenuated to a narrowly rounded to more or less pointed apex, more or less abruptly attenuated into a truncate base, (1–)2–3(–5)-septate, not or only inconspicuously constricted around the septa in the living state, hyaline, containing one to several relatively small oil-droplets in each cell, in the rehydrated state with larger oil-masses, 20–48(–56) × 2–2.5 μm (living; rehydrated, NT 1.5–2 μm wide). *Sexual morph* unknown.

*Description in vitro (based on CBS 400.54)*: *Colonies* on OA 12–18 mm diam in 2 wk, with an even to slightly ruffled, glabrous, colourless margin; colonies spreading, remaining almost plane, immersed mycelium dull green to dark herbage green; aerial mycelium moderately to well-developed, woolly-floccose, white; dark brown to black single globose pycnidia developing after 7–10 d scattered over the agar surface, more rarely immersed in the agar, 70–100(–140) μm diam, ostioli often reduced or absent, releasing droplets of milky white conidial slime; reverse dark bluish green to black, diffusing pigment absent. *Conidiogenous cells* as *in planta*, but more often proliferating sympodially, 4–12.5 × 3.5–4.5 μm. *Conidia* as *in planta*, mostly 30–55(–68) × 2–2.5 μm.

*Hosts*: *Apium australe*, *A. graveolens* var. *graveolens* (celery), *A. graveolens* var. *rapaceum* (celeriac), *A. prostratum*.

*Material examined*: **Italy**, Perugia, culture ex leaf of *Apium graveolens*, deposited June 1959, M. Ribaldi *s.n.*, CBS 389.59; **Netherlands**, culture ex *Apium* sp., deposited Aug. 1952, isolated by G. van den Ende *s.n.*, CBS 395.52; Prov. Utrecht, Baarn, Cantonspark, culture ex living leaves of *A.graveolens*, 1953, deposited Oct. 1954, J.A. von Arx *s.n.*, CBS 400.54 = IMI 092628; Prov. Limburg, Venray, Vreedepeel, on living leaves of *A. graveolens* var. *graveolens*, Aug. 2004, collector unknown (G. Verkley 3046), CBS H-21261; same substr., Noord-Brabant, between Zevenbergen and Zevenbergschen Hoek, 26 Aug. 2004, R. Munning (G. Verkley 3048), CBS H-21163, living culture CBS 116465.

*Notes*: According to Priest (2006), it is apparent that at least two species of *Septoria* occur on *Apium* spp. worldwide. Earlier studies demonstrated considerable variation in the dimensions of conidia in material on *Apium* spp. especially in conidial width, along with other minor morphological differences, and differences in leaf spot type (Cochran 1932, Sheridan 1968). Gabrielson & Grogan (1964) concluded that there was just one species involved, characterised by pycnidia 55–190 μm diam and conidia 10–72 × 0.9–3.0 μm. They accepted the name *S. apiicola*, and placed *S. apii* and *S. apii-graveolentis* in its synonymy. Jørstad (1965) placed *S. apii* in the synonymy of *S. petroselini*, while Sutton & Waterston (1966) followed Gabrielson & Grogan but described the conidia as 22–56 × 2–2.5 μm. As was the case in the material from Australia studied more recently by Priest (2006; conidia 30–48 × 2–2.5 μm), most conidia in the collections available for the present study are 2–2.5 μm wide. These collections proved highly homogenous in DNA sequences of the genes investigated and in most morphological characters. However, morphological and molecular investigations of more material on *Apium* from various host species and geographical regions is required before conclusions can be drawn about the number of taxa involved on this host genus.

According to Sutton & Waterston (1966) and also Priest (2006), the conidiogenous cells of *S. apiicola* are phialidic, producing several conidia enteroblastically and seceding at the same level, and these authors did not report sympodial proliferation. In the material we were able to examine however, percurrent proliferation was mostly seen and rarely also sympodial *in planta*, while sympodially proliferating conidiogenous cells were more common *in vitro*. The difference may result from the fact that here we studied

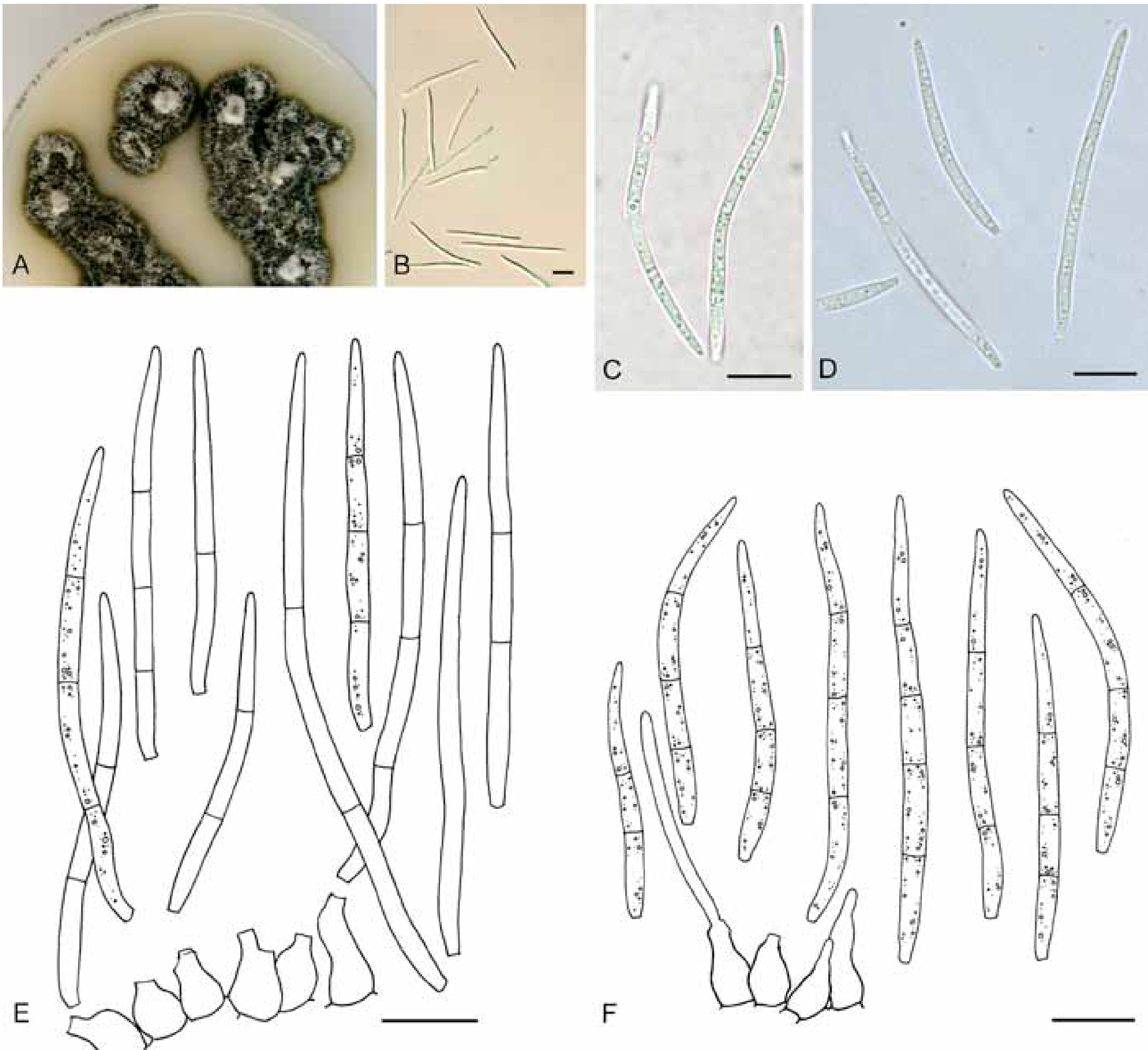


**Fig. 9.** *Septoria apiicola*. a. Colony on OA (CBS 400.54). B, C. Conidia *in planta* (CBS H-21261). D. Conidia on OA (CBS 400.54). E. Conidia and conidiogenous cells on OA (CBS 400.54). F. Ibid., *in planta* (CBS H-21261). Scale bars = 10 µm.

living material, as we noted that after rehydration of the herbarium vouchers it is indeed very difficult to still see the details, in particular progressive annellations.

***Septoria astragali*** Roberge ex Desm., Annls Sci. Nat., sér. 2, Bot. 19: 345. 1843. Fig. 10.

?= *Septoria astragali* var. *brencklei* Sacc., Atti Memorie Accad. patavina 33: 171 (as 'brinklei'). 1917.

*Description in planta*: *Symptoms* leaf spots circular or more irregular, often indefinite or delimited by a dark brown border, white, pale ochreous to yellowish brown, usually several on each leaflet. *Conidiomata* pycnidial, often visible on both sides of the leaf, amphigenous, but either predominantly hypo- (V6023) or epiphyllous (V1036), scattered, globose, immersed to semi-immersed, 125–170 µm diam; *ostiolum* circular, central, 20–55 µm wide, surrounding cells somewhat darker; *conidiomatal wall* up to 30 µm thick, composed of an outer layer of isodiametric to irregular cells 3.5–8.5 µm diam with brown walls which are thickened up to 1 µm, and an inner layer of hyaline, thin-walled cells 3–7 µm diam. *Conidiogenous cells* hyaline, ampuliform, or elongated ampulliform with a distinct neck, hyaline, holoblastic, proliferating sympodially, and sometimes (also) percurrently 1–2 times with indistinct annellations, 10–17 × 5–8 µm. *Conidia* cylindrical, straight, curved, or flexuous, gradually attenuated to a narrowly rounded to somewhat pointed apex and a truncate base, (5–)7–9(–11)-septate, somewhat constricted around the septa in the living state ("T"), not constricted in the rehydrated state, hyaline, contents granular or with numerous small and a few larger oil-droplets in each cell, (85–) 105–145 × 3.5–4 µm (living; rehydrated, 3–3.5 µm wide). *Sexual morph* unknown.

*Description in vitro*: *Colonies* on OA 2–4 mm diam in 10 d (34–37 mm in 7 wk), with an even or irregular, glabrous, colourless margin; colonies spreading, the surface plane, immersed mycelium mostly colourless to buff with very diffuse, short, whitish aerial mycelium, the centre of the colony darkened by numerous superficial and immersed, separate or confluent pycnidial conidiomata, the outer

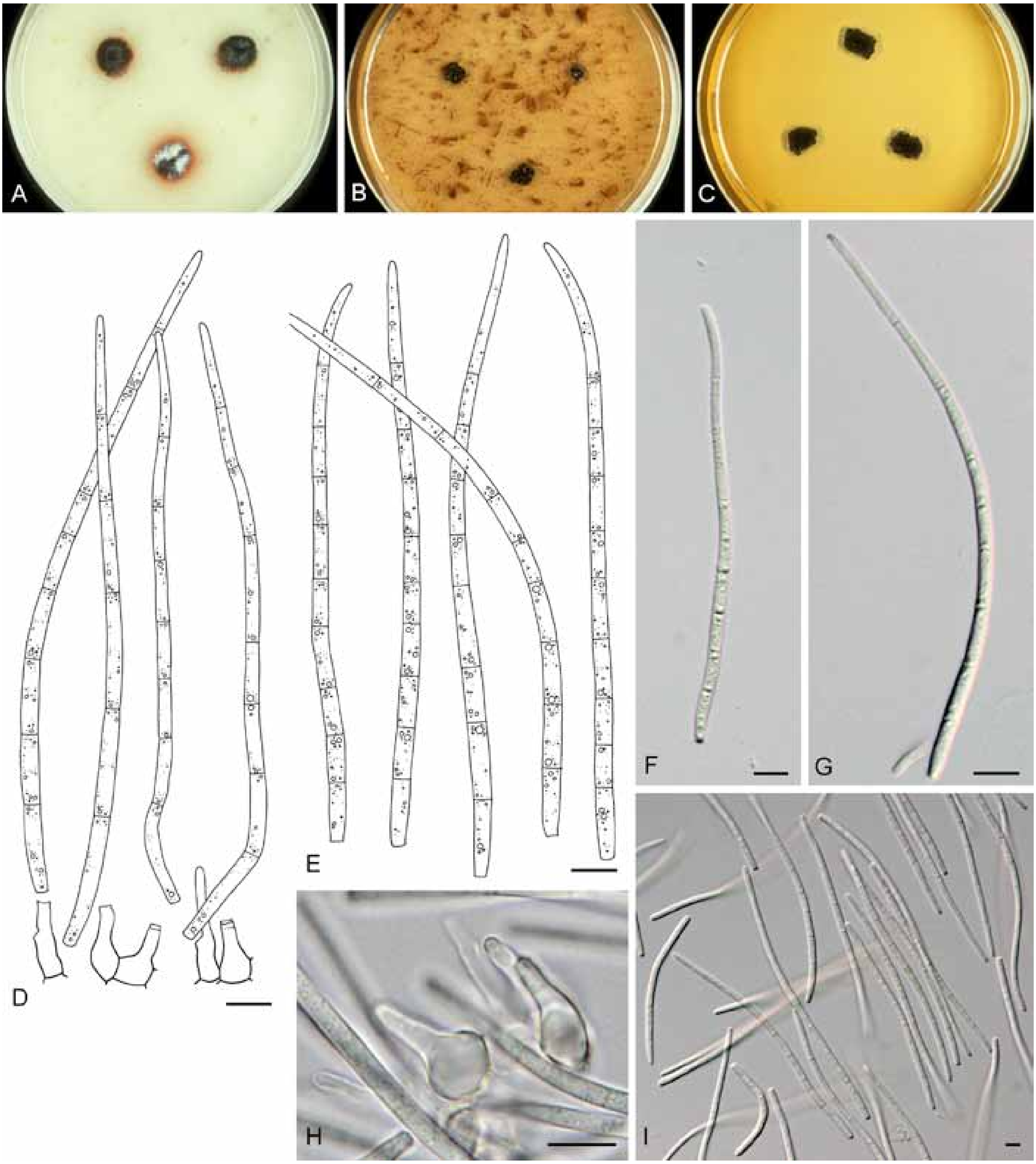


**Fig. 10.** *Septoria astragali*, CBS 109116. A–C. Colonies (15 C, nUV). A. On OA. B. On CHA. C. On MEA. D. Conidia and conidiogenous cells on OA (CBS 109116); E–G. Conidia *in planta* (CBS H-21258). H. Conidiogenous cells on OA (CBS 123878). I. Conidia on OA (CBS 123878). Scale bars = 10 µm.

walls covered with short mycelial outgrowth, with a single opening releasing a stout cirrhus of pale whitish to rosy-buff conidial slime; reverse mostly olivaceous-black due to the conidiomata; after incubation of 5–7 wk, more of the immersed mycelium darkens to olivaceous-black, with traces of a red pigment especially near the margin, and the aerial mycelium becomes more dominant, white or grey. *Colonies* on CMA 2–3 mm diam in 10 d (27–28 mm in 7 wk), as on OA, but the reddish pigment at the margin more conspicuous in old cultures. *Colonies* on MEA 1.5–3 mm diam in 10 d ((8–)14–17 mm in 7 wk), with an even to irregular, glabrous, buff margin; colonies first restricted, while later faster growing hyphal strands colonize the medium underneath the surface of the agar, pustulate to hemispherical, the surface first ochreous or amber, later olivaceous-grey or black covered by fairly dense, short, white aerial mycelium; some superficial or immersed pycnidial conidiomata formed, releasing cirrhi of pale buff conidial slime; reverse dark umber to brown-vinaceous. *Colonies* on CHA 1.5–3 mm diam in 10 d (15–17 mm in 7 wk), with an irregular margin which is hardly visible from above; colonies restricted, irregularly pustulate to hemispherical, the surface dark brick to dark slate blue, covered by a diffuse, very short, felty, white aerial mycelium; abundant superficial conidiomata releasing stout cirrhi of rosy-buff conidial slime; reverse blood colour.

*Hosts*: *Astragalus* spp.

*Material examined*: **Austria**, Tirol, Ötztal, Ötz, near Habichen W of Ötztaler Aache, 1 Aug. 2000, on living leaves of *Astragalus glycyphyllos*, G. Verkley 1036, **epitype designated here** CBS H-21151 "MBT175673", living cultures ex-epitype CBS 109116, 109117; Carinthia, near Töschling at Wörthersee, on living leaves of *A. glycyphyllos*, July (year not indicated), Keissler, distributed in Keissler, Kryptogam. exsicc. 1331, PC 0084566. **Czech Republic**, Moravia, Pavlov, forest around ruin, 18 Sep. 2008, on living leaves of *A. glycyphyllos*, G. Verkley 6023, CBS H-21258, living culture CBS 123878. **France**, Lower Normandy, Calvados, Baynes near Forêt de Cerisy, 20-21 Sep. 1842, on leaves of *A. glycyphyllos*, Roberge, "Col. Desmazieres 1863, no. 8, 59", **isotype** PC 0084563; Côte-d'Or, Montagne de Bard, same substr., June 1901, Fautrey, PC 0084565 (herb. Mussat); same substr., Pinsguel, near Toulouse, 30 Aug. 1935, Moesz, PC 0084564. **Poland**, Puszcza Bialowieska, Aug. 1922, on living leaves of *A. glycyphyllos*, W. Siemaszko, distributed in W. Siemaszko, Fung. Bialowiezenses exsicc. 73, PC 0084569. **Romania**, Transsilvania, distr. Istriţa-Năsăud, Arcalia Arboretum, 1 July 1966, on living leaves of *A. glycyphyllos*, A. Crişan, distributed in Flora Romania exsicc 3127, PC 0084567; same substr., Muntenia, distr. Ilfov, Pantelimon, 18 July 1926, T. Săvulescu & C. Sandhu, distributed in Săvulescu, Herb. Mycol. Romanicum 4, 166, PC 0084568 (sub *S. astragali* f. *santonensis*).

*Notes*: The type specimen in PC of *S. astragali* contains several mounted leaves and is provided with a hand-written description in French. Conidia observed in this material are mostly 7–9-septate, 85–130 × 2.5–3.5 µm. The type thus agrees well with the original description which indicated conidia 120 × 3 µm, with 9–10 septa. Of the other collections available for this study that generally all agree with the type in morphology and leaf symptoms, 1036 from Tirol is chosen as epitype. Various authors have reported comparable conidial measurements for this large-spored *Septoria*. Jørstad (1965) reported conidial measurements 48–128 × 3–3.5 µm, Teterevnikova-Babayan (1987) 60–140 × 3–4 µm, Vanev *et al.* (1997), 58–112 × 2.5–3.5 µm. According to the original diagnosis, *S. astragali* var. *brencklei*, described from *Lathyrus venosus* in North Dakota, has 8–10-septate conidia, 130–150 × 4–5 µm, and Teterevnikova-Babayan (1987) placed it in synonymy with *S. astragali*. *Septoria astragali* is one of the first of over 200 *Septoria* that were described from plants of the family *Fabaceae*.

***Septoria campanulae*** (Lév.) Sacc., Syll. Fung. 3: 544. 1884. Fig. 11.
*Basionym*: *Ascochyta campanulae* Lév., Annls Sci. Nat., sér. 3, Bot. 5: 277. 1846.

*Description in planta*: *Symptoms* definite, circular to irregular, pale to dark brown leaf spots, epigenous, usually delimited by blackened veinlets. *Conidiomata* pycnidial, predominantly ephiphyllous, rarely hyphyllous, scattered, globose to subglobose, immersed to semi-immersed, 40–125 µm diam; *ostiolum* circular, central, 10–20 µm wide, surrounding cells darker; *conidiomatal wall* 10–20 µm diam, composed of an outer layer of brown-walled cells 3.5–10 µm diam, and an inner layer of hyaline cells 3.5–6 µm diam. *Conidiogenous cells* discrete or integrated in 1–2-septate conidiophores, cylindrical, or ampuliform, sometimes with an elongated neck, hyaline, holoblastic, proliferating sympodially, and often in the same cell also percurrently showing indistinct annellations, 5–15 × 3–5 µm. *Conidia* filiform, straight or slightly curved, gradually attenuated to a narrowly rounded or somewhat pointed apex, gradually or more abruptly attenuated into a narrowly truncate base, 0–1(–3)-septate, not or indistinctly constricted around the septa, hyaline, contents

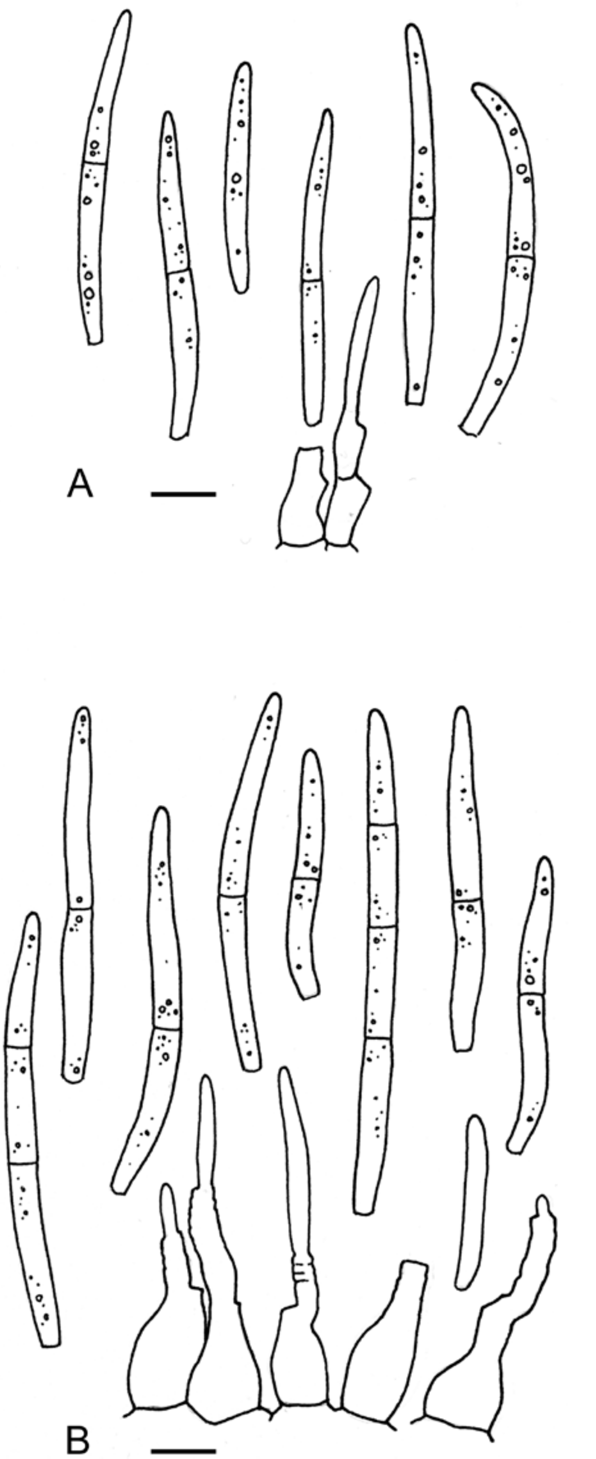


**Fig. 11.** *Septoria campanulae*. A. Conidia and conidiogenous cells *in planta* (CBS H-21178). B. Ibid., on CHA (CBS 109114). Scale bars = 10 µm.

with small oil-droplets and minutely granular material in the living state and rehydrated state, (12.5–)15–25(–32) × 1.5–2 µm (rehydrated). *Sexual morph* unknown.

*Description in vitro*: *Colonies* on OA 6–9 mm diam in 10 d (28–32 mm in 3 wk; > 65 mm in 7 wk), with an even, somewhat undulating, glabrous, colourless margin; colonies spreading, the surface plane, immersed mycelium pale luteous to ochreous, but radiating greenish or olivaceous hyphal strands soon developing, which later dominate the olivaceous-black colonies, then also a distinct red pigment is produced which diffuses beyond the colony margin; scattered, mostly superficial pycnidial conidiomata, which are first dark olivaceous, then almost black, glabrous, with a single or up to 5 ostioli placed on short papillae or more elongated necks, that release pale whitish conidial slime; aerial mycelium scanty, diffuse, woolly-floccose, white; reverse in the centre most dark slate blue, first surrounded and intermixed with ochreous to rust, later more coral. *Colonies* on CMA 5–9 mm diam in 10 d (24–28 mm in 3 wk; > 70 mm in 7 wk), with an even, glabrous margin; as on OA but immersed mycelium with a greenish haze throughout, later almost entirely olivaceous-black; aerial mycelium even more scanty, but higher and reverse darker, dark slate blue throughout most of the colony; conidiomata similar as on OA, but necks shorter or absent. *Colonies* on MEA 7–9 mm diam in 2 wk (24–30 mm in 3 wk; > 70 mm in 7 wk), with an even, undulating to ruffled, glabrous, buff to honey margin; colonies first more restricted, pustulate to almost conical, but later growing faster with a plane submarginal area; immersed mycelium rather dark, near the margin covered by woolly to felty white aerial mycelium; mostly composed of spherical conidiomatal initials, superficial mature conidiomata releasing milky white conidial slime; reverse first dark brick in the centre, near the margin locally grey-olivaceous or cinnamon, later sepia to brown-vinaceous, the margin honey. *Colonies* on CHA 4–10 mm diam in 10 d (17–32 mm in 3 wk; 45–65 mm in 7 wk), with an irregular or even, buff margin covered by a diffuse, felty white, later grey aerial mycelium; further as on MEA, but the colony surface less elevated and especially near the margin with greyish, felty to tufty aerial mycelium; in the centre numerous conidiomata develop at the surface, after 3 wk releasing milky white to rosy-buff droplets of conidial slime; reverse in the centre blood colour, dark brick to cinnamon at the margin.

*Conidiogenous cells* as *in planta*, but often with relatively longer necks due to repetitive percurrent proliferation. *Conidia* as *in planta*, but more often 2 and also 3-septate, and mostly 18–34.5 × 1.5–2 µm (OA), 13–32 × 1.5–2 µm (CHA).

*Hosts*: *Campanula glomerata*, *C. takesimana*.

*Material examined*: **Austria**, Tirol, Ötztal, Sulztal, Gries, along the river in the village, on living leaves of *Campanula glomerata*, 1 Aug. 2000, G. Verkley 1034, CBS H-21178, living cultures CBS 109114, 109115. **Korea**, Taean, on living leaves of *C. takesimana*, H.D. Shin, living culture SMKC 21949 = KACC 42622 = CBS 128589; Daejeon, same substr., H.D. Shin, living culture SMKC 24476 = KACC 44787 = CBS 128604.

*Notes*: The first species described on *Campanula* is *S. campanulae*, for which Shin & Sameva (2004) provided a detailed description based on material occurring in Korea on *C. punctata* and *C. takeshimana* (conidia mostly 1-septate, 13–24 × 1.5–2 µm). Shin & Sameva summerised the history of the *Septoria* species on the genus *Campanula*. Of the three species most often accepted, viz., *S. campanulae*, *S. obscura*, and *S. trachelii*, *S. campanulae* fits the current material best. *Septoria arcautei* was not mentioned by Shin & Sameva. This species was described from *C. glomerata* in Spain, and according to the original description by Unanumo, the pycnidia are predominantly epiphyllous, 55.8–74.8 µm diam, and the conidia continuous, 20–25.7 × 0.8 µm. *Septoria campanulae* is closely related to several species from hosts in *Apiaceae*, including *S. aegopodina*, *S. oenanthis*, and *S. sii* (Fig. 2). Sequencing results of CBS 109114 and 109115 were puzzling, suggesting possible contamination.

### ***Septoria cerastii*** Roberge ex Desm., Annls Sci. Nat., sér. 3, Bot. 11: 347. 1849. Fig. 12.

*Description in planta*: *Symptoms* indefinite, yellow to brown leaf spots, but more often on withering parts of leaves, stems and bracts. *Conidiomata* pycnidial, on leaves amphigenous but predominately epiphyllous, scattered or aggregated, globose, semi-immersed, 80–125(–150) µm diam; *ostiolum* circular, central, 20–45 µm wide, surrounding cells somewhat darker; *conidiomatal wall* composed of *textura angularis* without distinctly differentiated layers, the outer cells with brown, somewhat thickened walls and 4–6.5 µm diam, the inner cells hyaline and thin-walled and 3.5–6 µm diam. *Conidiogenous cells* ampulliform, or elongated ampulliform with a distinct neck, hyaline, holoblastic, proliferating percurrently 1–many times with indistinct annellations, also sympodially, 5–10 × 3–5 µm. *Conidia* filiform to filiform-cylindrical, straight, curved, or flexuous, gradually attenuated to a rounded or more or less pointed apex, abruptly attenuated into a truncate base, (1–)2–4(–5)-septate, not or indistinctly constricted around the septa, hyaline, contents moderately rich in small guttulae, minutely granular material and large vacuoles in the living state, in the rehydrated state with inconspicuous contents and no oil-droplets, (21–)30–52(–57) × 1.5–2 µm (rehydrated). *Sexual morph* unknown.

*Description in vitro*: *Colonies* on OA 2–4 mm diam in 2 wk (10–13 mm in 6 wk), the margin irregular to ruffled, almost as dark as rest of the colony, covered by diffuse, grey aerial mycelium; the colony spreading, almost plane to somewhat irregularly lifted and pustulate, immersed mycelium olivaceous-black to black, covered with dense, grey, woolly aerial mycelium; conidiomata starting to develop at the surface after 10–15 d; reverse olivaceous-black. *Colonies* on CMA 2–5 mm diam in 2 wk (13–17 mm in 6 wk), as on OA; conidial slime milky white; reverse greenish grey to almost black. *Colonies* on MEA 0.5–1.5 mm diam in 2 wk (4–6 mm in 6 wk), as on OA, with equally dense and long, woolly, grey aerial mycelium; colony hemispherical, with scarce pycnidial conidiomata developing tardily; reverse dark slate blue to black. *Colonies* on CHA 1–3 mm diam in 2 wk (8–12 mm in 6 wk), as on OA, but colonies more distinctly lifted above the agar surface, hemispherical, and aerial mycelium denser but shorter; conidiomata developing scarcely at the surface.

*Conidiomata* pycnidial and similar as *in planta*, 100–150 µm diam, or merged into larger complexes especially on the agar surface, dark olivaceous-black to black, up to 250 µm diam; *ostiolum* as *in planta*, or absent; *Conidiogenous cells* hyaline, ampuliform, or elongated ampulliform to cylindrical, with a distinct neck, holoblastic, proliferating percurrently 1–many times with indistinct scars (annellations), also sympodially, 5–12(–15) × 3–5(–6.5) µm. *Conidia* on OA similar as *in planta*, 1–3(–5)-septate, indistinctly constricted around the septa, hyaline, contents moderately rich in small guttulae, minutely granular material and large vacuoles in the living state, (26–)35–50(–57) × 1.5–2.5 µm (T), released from superficial conidiomata in whitish cirrhi or slimy masses.

*Hosts*: In leaf spots and on withering leaves, stems and bracts of *Cerastium* spp. According to Markevičius & Treigienė (2003), also on *Stellaria holostea*.

*Material examined*: **Korea**, Hoengseong, on *C. holosteoides* var. *hallaisanense*, 14 May 2006, H.D. Shin, CBS 128586 = KACC 42367 = SMKC 21781; same loc., substr., H.D. Shin, CBS 128612 = KACC 42831 = SMKC 22609; Jeju, on *C. holosteoides*, 1 Nov. 2007, H.D. Shin, CBS 128626 = KACC 43220 = SMKC 23137. **Netherlands**, prov. Utrecht, Baarn, on living leaves of *Cerastium* sp., 9 Aug. 1968, H.A. van der Aa 731, CBS H-18069; same loc., substratum, 18 Oct. 1962, H.A. van der Aa, CBS H-18070, and 19 Oct. 1963, CBS H-18071; Prov. Noord Holland, Amsterdamse Waterleidingduinen, near Ruigeveld, on withering leaves of *Cerastium fontanum* subsp. *vulgare*, 31 Aug. 1999, G. Verkley & A. van Iperen 915, epitype **designated here** CBS H-21158 "MBT175351", living culture ex-epitype CBS 102323. **Romania**, distr. Ilfov, Malu-Spart, on living leaves of *C. fontanum*

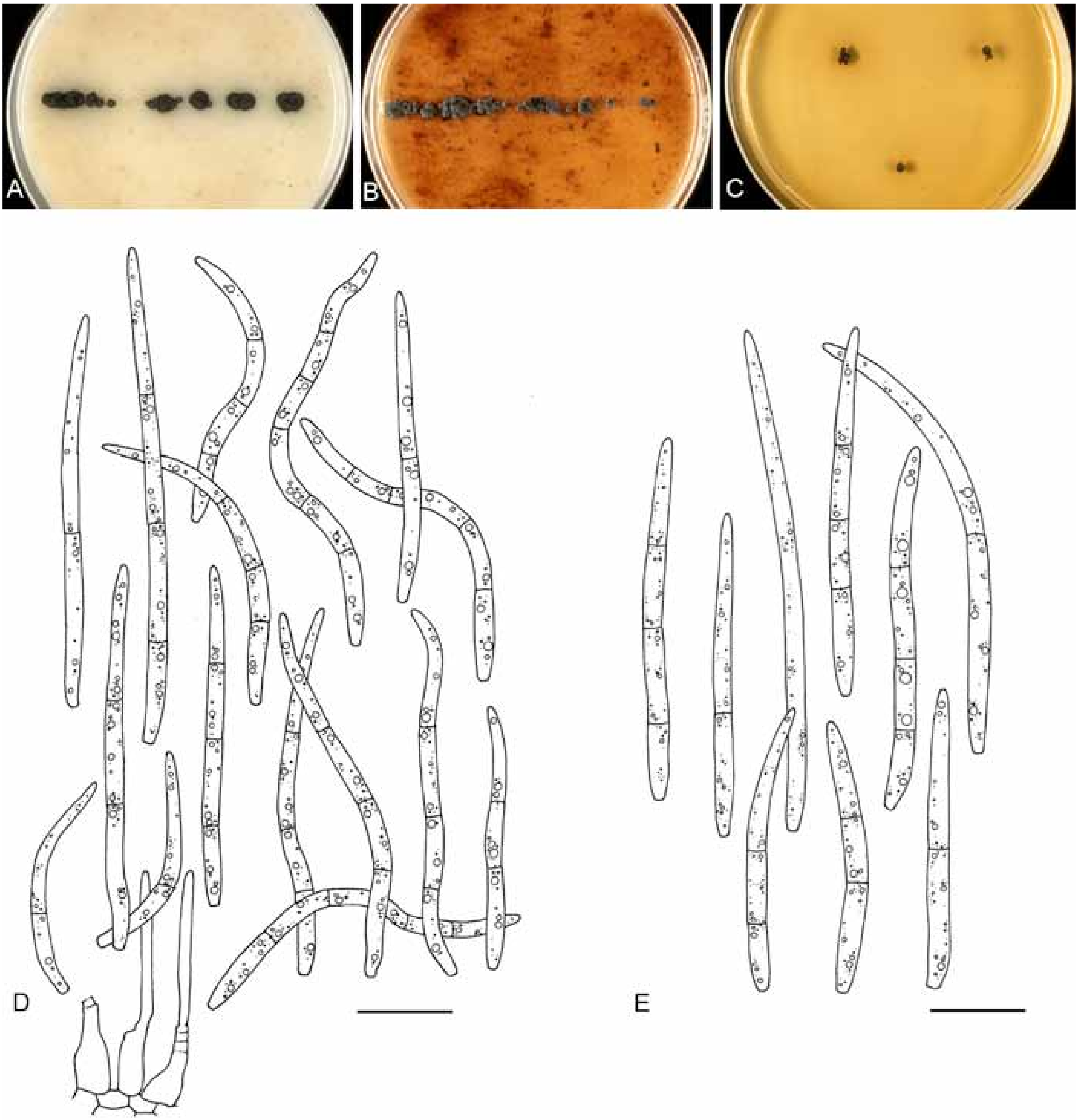


**Fig. 12.** *Septoria cerastii*, CBS 102323. A–C. Colonies (15 °C, nUV). A. On OA. B. On CHA. C. On MEA. D. Conidia and conidiogenous cells *in planta* (CBS H-21158, epitype). E. Conidia on OA (CBS 102323). Scale bars = 10 µm.

subsp. *triviale*, 20 May 1973, G. Negrean, CBS H-18072, distributed in Herb. Mycol. Romanicum, fasc. 50, no. 2475.

*Notes*: The material on *Cerastium fontanum* examined here agrees in morphology with the detailed description of Muthumary (1999), who studied type material of *S. cerastii* (PC 1324) and also provided excellent illustrations. The type host was identified as *C. vulgatum*, which is a synonym of *C. fontanum* subsp. *vulgare* (and *C. holosteoides*). According to Muthumary, no definite spots are on the leaves in this collection, but the fungus is nonetheless interpreted as parasitic. We have the impression from our collection that it may be endophytic or a very weak pathogen, but in Korea the fungus causes very characteristic symptoms on *C. holosteoides* var. *hallaisanense* (Shin & Sameva 2004).

This species and *S. stellariae* occur on two very closely related host genera, *Cerastium* and *Stellaria* (Smissen *et al.* 2002), but the two can be distinguished morphologically by conidiogenesis and conidial morphology *in planta*, and the cultures also differ considerably in pigmentation and growth speed especially on OA. DNA sequence data also support the hypothesis that *S. cerastii* and *S. stellariae* are distinct species, as they differ for example by 6 base positions on ITS 1, and the distance in the multilocus tree is considerable. Jørstad (1965) also regarded *S. cerastii* and *S. stellariae* as distinct species, indicating that on average the spores in the latter were much longer (22–96 µm) than in the former (20–43 µm). He mentioned that in two collections of *S. cerastii* from Iceland the conidia reached lengths of 57–60 µm, whereas in collections from Norway attributed to the same species conidia were no longer than 43 µm. In the Dutch collection studied here, conidia also reached 57 µm in length.

***Septoria chromolaenae*** Crous & den Breeÿen, Fungal Diversity 23: 90. 2006.

A detailed description of the species *in planta* and *in vitro* was given by Den Breeÿen *et al.* (2006).

*Material examined*: **Cuba**, near Havana, *Chromolaena odorata*, S. Neser, 28 Oct. 1997, **holotype** CBS H-19756, culture ex-type CBS 113373.

*Notes*: This species is closely related to two strains identified as *S. ekmanniana* (CBS 113385, 113612) originating from *Chromolaena odorata* (*Asteraceae*) in Mexico. The two species can readily be distinguished by conidial sizes, particularly in culture (Den Breeÿen *et al.* 2006). Other species in this clade include *S. passiflorae* (CBS 102701) and *S. passifloricola* (CBS 129431), and *S. anthurii* (CBS 148.41, 346.58) and *S. sisyrinchii* (CBS 112096).

### *Septoria chrysanthemella* complex

*Septoria chrysanthemella* Sacc., Syll. Fung. 11: 542. 1895. nom. nov. pro *S. chrysanthemi* Cavara, Atti Ist. bot. Univ. Lab. crittogam. Pavia, Ser. 2, 2: 266. 1892 [non Allesch., 1891].

A description *in planta* was provided by Punithalingam (1967a) and Priest (2006). *Sexual morph*: unknown.

Multilocus sequencing revealed that five of the isolates studied here that were identified as *S. chrysanthemella* belong to a species complex, showing the presence of two cryptic sister species. The first group includes CBS 354.73, 128616 and 128617, originating from *Chrysanthemum morifolium* in New Zealand and Korea, respectively. The second group comprises the two European isolates CBS 351.58 and 483.63, and CBS 128622 from Korea, from various *Chrysanthemum* spp. A description of the isolates is provided below.

Group 1: Description *in vitro (CBS 354.73)*: *Colonies* on OA 20–23 mm diam in 2 wk, with an even, glabrous margin; colonies spreading, immersed mycelium grey-olivaceous and in the centre with a brown haze, mostly glabrous but locally with some tufts of pure white aerial mycelium; reverse greenish grey to olivaceous-grey. Pycnidia developing immersed and on the agar surface after 10–12 d, releasing pale white conidial slime. *Colonies* on MEA 17–20 mm diam in 2 wk, with an even, colourless to buff margin; colonies restricted to spreading, in the centre irregularly pustulate, the surface dark, provided with diffuse or more dense mat of grey, appressed aerial mycelium; reverse brown-vinaceous. Conidiomata developing on the agar surface in the centre, releasing milky white masses of conidial slime.

*Material examined*: **New Zealand**, Taranaki, *Chrysanthemum morifolium*, G.F. Laundon, 24 Nov. 1972, LEV 6807, living culture CBS 354.73. **South Korea**, Hongcheon, *Chr. morifolium*, H.D. Shin, 10 Sep. 2007, living culture SMKC 22860 = KACC 43086 = CBS 128617.

Group 2: Description *in vitro (CBS 351.58)*: *Colonies* on OA reaching 32–36 mm diam in 2 wk, with an even, glabrous margin; colonies spreading, immersed mycelium pale luteous to faintly saffron, mostly glabrous but locally with some tufts of pure white aerial mycelium; reverse flesh to saffron. Pycnidia formed immersed or on the agar surface after 10–12 d, releasing pale white conidial slime. *Colonies* on MEA reaching 36–40 mm diam in 2 wk, with an even, cvolourless to buff margin; colonies spreading, the surface entirely covered by a dense mat of pure white to rose, woolly aerial mycelium; reverse fulvous to ochreous, dark brick in the centre. Pycnidia formed mostly on the agar surface after 10–2 wk, releasing pale white conidial slime.

*Material examined*: **Germany**, Berlin, *Chrysanthemum indicum*, R. Schneider, June 1957, living culture BBA 8432 = CBS 351.58. **Netherlands**, Baarn, on *Chr ysanthemum* sp., isol. H.A. van der Aa, dep. J.A. von Arx Nov. 1963, living culture CBS 483.63. **South Korea**, Hoengseong, on *Chr. boreale*, H.D. Shin, 16 Oct. 2007, living culture SMKC 23025 = KACC 43191 = CBS 128622.

*Notes*: Saccardo (1895) did not specify the host species of *S. chrysanthemella*, but in the original diagnosis of Cavara (for which Saccardo proposed a nomen novum to replace the name *S. chrysanthemi* because it was antedated by *S. chrysanthemi* Allesch. 1891), the host was indicated to be *Chrysanthemum indicum*. The fungus was described to produce conidia 55–65 × 1.5–2 µm, and lacking septa. It will have to be resolved to which group of the complex the name *S. chrysanthemella* should be applied.

***Septoria clematidis*** Roberge ex Desm., Annls Sci. Nat., sér. 3, Bot. 20: 93. 1853 [non Pandotra & K.S.M. Sastry, nom. illeg., Art. 53]. Fig. 13.

*Description in planta*: *Symptoms* leaf spots angular to circular, initially mostly pale yellowish brown, then greyish brown, sometimes surrounded by a darker border, visible on both sides of the leaf. *Conidiomata* pycnidial, epiphyllous, several in each leaf spot, globose to subglobose, dark brown, immersed, 65–120(–160) µm diam; *ostiolum* central, circular, 55–80(–100) µm wide, surrounding cells concolorous or somewhat darker; *conidiomatal wall* 20–35 µm thick, composed of *textura angularis* without distinctly differentiated layers, the cells 3–10 µm diam, the outer cells with brown, somewhat thickened walls, the inner cells with hyaline and thinner walls. *Conidiogenous cells* hyaline, narrowly to broadly ampulliform with a relatively wide and sometimes elongated neck, holoblastic, proliferating sympodially and possibly also percurrently in some cells but annellations not observed, 8–12.5 × 4–5(–6) µm. *Conidia* cylindrical to filiform-cylindrical, straight, more often curved or slightly flexuous, with a relatively broadly rounded, sometimes somewhat pointed apex, barely attenuated towards the broadly truncate base, (1–)4–5(–6)-septate, not or indistinctly constricted around the septa, hyaline, contents with a few oil-droplets and minute granular material in each cell in the living state, with inconspicuous oil-droplets and granular contents in the rehydrated state, (40–)47–67(–80) × (3–)3.5–4 µm (rehydrated). *Sexual morph* unknown.

*Description in vitro*: *Colonies* on OA 3–6(–8) mm diam in 3 wk (12–15 mm in 7 wk), the margin irregular to ruffled, colourless, glabrous; the colony almost plane to somewhat irregularly lifted and pustulate, immersed mycelium initially in the centre pale grey-olivaceous with some long aerial hyphae, darkening entirely in older colonies to olivaceous-black, this darkening starting where pycnicial stromata are formed releasing milky white droplets of conidial slime after about 3 wk; reverse of colony dark slate blue to olivaceous-black. *Colonies* on CMA 4–7(–9) mm diam in 3 wk (12–17 mm in 7 wk), as on OA, but aerial mycelium denser

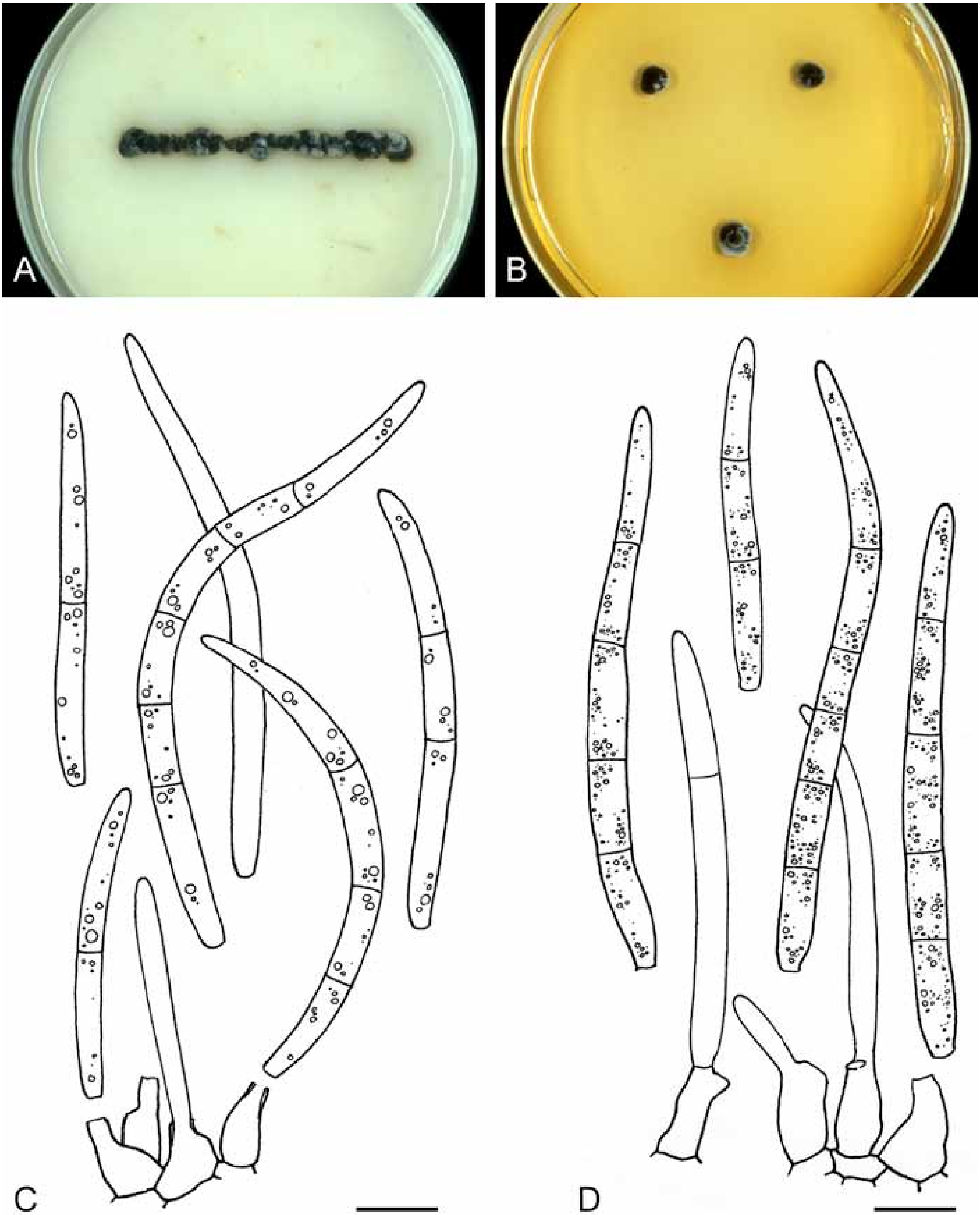


**Fig. 13.** *Septoria clematidis*. A, B. Colonies CBS 108983 (15 ºC, nUV). A. On OA. B. On MEA. C. Conidia and conidiogenous cells *in planta* (CBS H-21182, epitype). D. Ibid., CBS 108983 on OA. Scale bars = 10 µm.

on sterile parts of the colony. Numerous pycnidial conidiomata developing after 2 wk in the agar, on its surface, and also in the aerial mycelium, but no fertile ones observed. *Colonies* on MEA 4.5–7 mm diam in 3 wk (11–18(–22) mm in 7 wk), with a barely visible margin; colony restricted, hemispherical, the surface very dark or black, covered by short, diffuse to dense white or grey aerial hyphae; pycnidial conidiomata at the surface releasing clear droplets without conidial slime after 3 wk, and later first buff, then dirty luteous droplets with conidia; reverse dark slate blue to black, margin pale luteous or buff. *Colonies* on CHA 4.5–7 mm diam in 3 wk (15–18 mm in 7 wk), as on MEA, but aerial mycelium denser with longer hyphae; conidiomatal initials developing scarcely at the surface, still sterile after 3 wk, but later on releasing dirty buff to pale ochreous droplets of conidial slime. In older colonies on MEA and CHA a grey or greyish white, dense mat of aerial hyphae may cover small or larger sectors.

*Conidiomata* as *in vitro*, pycnidial, often merged to complex stromata, first brownish, then black, glabrous or the surface covered by short white hyphae; *conidiogenous cells* as *in planta*, but larger, 7.5–20 × 3–5(–6) µm, holoblastic, proliferating sympodially, no percurrent proliferation observed; *conidia* similar in shape as *in planta* but mostly 3–7-septate, (45–)55–85(–105) × 4–5(–7) µm.

*Hosts*: *Clematis* spp.

*Material examined*: **Austria**, Tirol, Ötztal, Brunau, on living leaves of *Clematis vitalba*, 30 July 2000, G. Verkley 1025, **epitype designated here** CBS H-21182 "MBT175353", living cultures ex-epitype CBS 108983, 108984; same loc., substr., date, G. Verkley 1026, CBS H-21183; same substr., S. Tirol, Eggenthal, Birchabruck, 23 July 1904, J. Kabát, distributed in Kabát & Bubák, Fungi imperfecti exsicc. 163, PC 0084599. **France**, Parc de Lébisey, 27 July 1848, Roberge (?), 'Col. Desmazieres 1863, no. 8, 448', **isotype** PC 0084593; same loc., substr., June 1848, Roberge, PC 0084596; same substr., Paris, Parc de St Cloud, Aug. 1908, Ludwig, PC 0084607; same substr., Fontainebleau forest, Aug. 1885, PC 0084604; same substr., Clères, 27 Aug. 1896 (herb. Mussat), PC 0084598; same substr., Seine-et-Oise, Meudon, 15 Nov. 1844, Roussel (Herb. Roussel), PC 0084594, PC 0084595. **Romania**, distr. Iaşi, Moldova, Bârnova, same substr., 30 Aug. 1934, T. Săvulescu & C. Sandhu, distributed in Săvulescu, Herb. Mycol. Romanicum 24, 1160, PC 0084603, 0084608, 0084597.

*Notes*: This is one of the large-spored species of *Septoria* from the genus *Clematis*. Teterevnikova-Babayan (1987), who studied collections from several species of *Clematis* observed, 4–6-septate conidia 60–90 × 3–5 µm. Vanev *et al.* (1997) reported conidia as 39–100 × 2.5–4 µm. The type of *S. clematidis* in PC showed 4-7-septate conidia 52–78 × 3–3.5 µm, in good agreement with the ones observed in the Austrian material (CBS H-21182), which is designated above as epitype.

The taxonomy of the 15 described species of *Septoria* on *Clematis* is still unresolved (Shin & Sameva 2004), and would certainly benefit from study of additional fresh material and cultures which could be compared with type material. *Septoria clematidis* Roberge is probably distinct from *S. clematidis* Pandotra & K.S.M. Sastry, a taxon described on *Clematis grata* in India that should be renamed because it is a later homonym. According to Muthumary (1999), the conidia in the type of *S. clematidis* Pan. & Sastry are 1–3-septate, 38–66 × 2.5–3 µm, whereas in the original diagnosis the conidia are described as " septate", 25.6–44.8 (av. 36.3) × 2.3–3.2 (av. 2.7). Two other large-spored species are *S. jackmanii* Ellis & Everh. 1892, which was described from *Clematis jackmanii* in Geneva, New York and, according to the diagnosis, has conidia 40–70 × 2.5–3 µm (number of septa not given), and also *S. williamsiae* Priest, based on material on *C. aristata* in Australia, which has (1–)3(–4)-septate conidia 20–45(–55) × (1.5–)2 µm (Priest 2006).

***Septoria convolvuli*** Desm., Annls Sci. Nat., sér. 2, Bot.17: 108. 1842. Fig. 14.

*Description in planta*: *Symptoms* leaf lesions circular, single or confluent to form irregular extended lesions, pale to dark brown, showing one to several concentric lines and a dark brown, slightly raised line or zone delimiting the lesion, visible on both sides of the leaf. *Conidiomata* pycnidial, epiphyllous, several in each lesion, immersed, subglobose to globose, brown to black, (65–)90–120(–145) µm diam; *ostiolum* central, circular to irregular, initially 20–40 µm wide, later becoming more irregular and up to 70 µm wide, surrounding cells somewhat darker; *conidiomatal wall* 10–15 µm thick, composed of a homogenous tissue of hyaline, angular cells, 2.5–4.5 µm diam, the outermost cells pale brown with slightly thickened walls, the inner cells thin-walled. *Conidiogenous cells* hyaline, discrete, rarely integrated in 1-septate conidiophores, narrowly to broadly ampulliform, holoblastic, proliferating percurrently several times, with indistinct annellations on a relatively elongated neck, or sympodially, 6–10(–17) × 2.5–3.5(–4) µm. *Conidia* filiform to filiform-cylindrical, slightly to strongly curved, often elegantly flexuous, attenuated in the upper cell to a narrowly rounded to pointed tip, narrowly truncate at the base, 1–3(–4)-septate, not constricted around the septa, hyaline, contents minute oil-droplets and granular material in the rehydrated state, (15–)23–42(–50) × 1.5–2 µm (rehydrated). *Sexual morph* unknown.

*Description in vitro*: *Colonies* on OA 3–5 mm diam in 1 wk (16–20 mm in 25 d; 40–48 mm in 33 d), with an even, glabrous margin, which is colourless, or faintly salmon due to a diffusable pigment already visible after 1 wk (but fading after 3 wk); colonies first restricted, conical to irregularly pustulate, but later spreading, immersed mycelium in the centre becoming first yellowish or citrine, then herbage green or darker olivaceous, surrounded by a more palid, rosy-buff or pale salmon, later hazel outer zone; pycnidia already developing in clusters or radiating rows at the colony surface, but they remain scarce, later releasing pale rosy-buff or whitish droplets of conidial slime; aerial mycelium remaining scanty, but in the centre it may be well-developed, white, woolly; reverse in the centre olivaceous-black to olivaceous-grey, surrounded by a first salmon or rosy-buff zone where the diffusable pigment is formed, but this becomes hazel. *Colonies* on CMA 3–5 mm diam in 1 wk [(15–)18–21 mm in 25 d; 38–40 mm in 33 d], as on OA, but salmon pigment only faintly visible after 20 d, the margin becoming rosy-buff; centre much darker earlier on, entirely olivaceous-black, numerous black papillate to rostrate pycnidia developing after 21 d, releasing pale whitish to buff droplets of conidial slime. *Colonies* on MEA 2–5 mm diam in 1 wk [5–11 mm in 25 d; 16–18(– 23) mm in 33 d], with a ruffled, mostly colourless margin already covered by white aerial hyphae after 1 wk; a halo of a diffusing pigment is visible after 1 wk, which fades later on; colonies restricted, irregularly pustulate and up to 3 mm high after 1 wk, immersed mycelium dark, but mostly invisible from above due to well-developed, white to greyish, dense and short-felted aerial mycelium; black conidiomata already developing after 1 wk, releasing large masses of buff conidial slime; reverse mostly sepia to isabelline. Some colonies may show a more spreading growth after 2 wk in sectors, that are glabrous, immersed mycelium almost black. *Colonies* on CHA 3–5 mm diam in 1 wk (18–30 mm in 25 d; 30–34 in 33 d), with an even, glabrous, colourless margin; colonies irregularly pustulate, up to 3 mm high after 1 wk, immersed mycelium colourless to pale ochreous, but in the centre the surface may be already almost black, while after 25 d the entire colony attains that colour, the larger part covered by well-developed, low, dense, pure white, later smoke-grey to grey-olivaceous, felty to woolly-floccose, aerial mycelium; conidiomatal initials developing mainly in the centre after 1 wk; reverse mostly fawn, but later almost entirely brown-vinaceous.

*Conidiomata* single, 60–150 µm diam, or merged to small clusters of up to 350 µm diam, olivaceous to brown, formed mostly on the agar surface; *conidiogenous cells* as *in planta*, 6–20 × 2.5–4(–5) µm; *conidia* as *in planta*, but often some conidia with

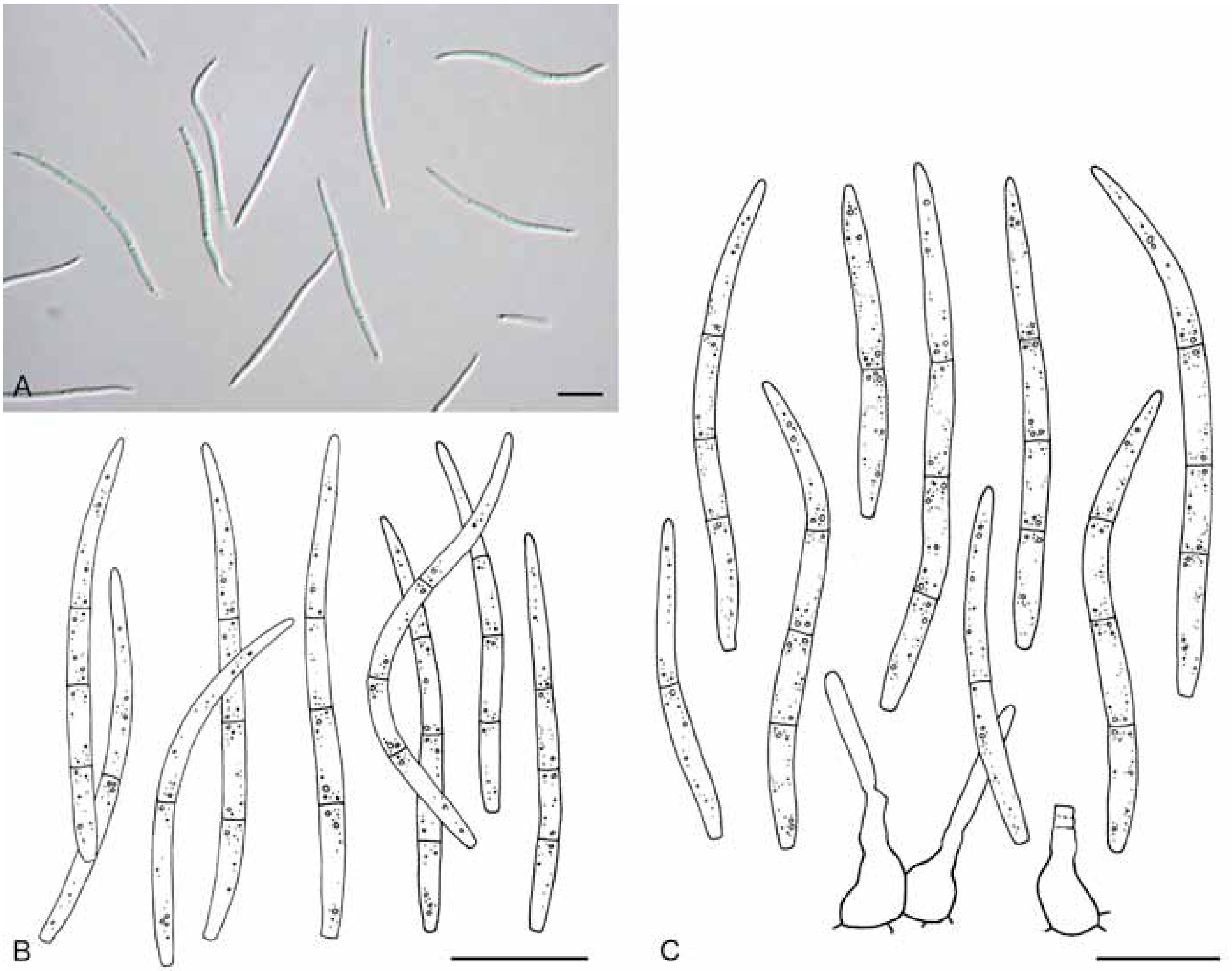


**Fig. 14.** *Septoria convolvuli*. A, B. Conidia *in planta* (CBS H-21244). C. Conidia and conidiogenous cells on OA (CBS 102325). Scale bars = 10 µm.

cells that are somewhat inflated, and constricted around septa, (22–)30–45(–55) × 1.8–2.5 µm.

*Hosts*: *Calystegia* spp. and *Convolvulus* spp.

*Material examined*: **Germany**, Eiffel, Schalkenmehren near Maar, Daun, on living leaves of *Convolvulus arvensis*, 16 Sep. 1970, H.A. van der Aa 2276, CBS H-18082. **Netherlands**, Prov. Hoord-Holland, Laren, on living leaves of *Calystegia sepium*, 18 July 1970, H.A. van der Aa 2198, CBS H-18081; Prov. Flevoland, Erkemeder beach, in edge of marshland bordering the lake, on living leaves of *Ca. sepium*, 8 Sep. 1999, G. Verkley 927, CBS H-21209, living culture CBS 102325. **New Zealand**, North Island, Coromandel, Tairua Forest, along roadside of St. Hway 25, near crossing 25A, on living leaves of *Ca. sepium*, 21 Jan. 2003, G. Verkley 1844, CBS H-21244, living culture CBS 113111; same substr., North Isl., Waikato, Taupiri, Bob Byrne Memorial Park, 27 Jan. 2003, G. Verkley 1896, CBS H-21248; same substr., North Isl., Northland, Russell, 30 Jan. 2003, G. Verkley 2014, CBS H-21245. **South Korea**, Kangnung, isolated from *Ca. soldanella*, H.D. Shin, 8 Nov. 2007, KACC 43226 = CBS 128627.

*Notes*: Morphologically and genetically the collections available proved highly homogeneous. Muthumary (1999) and Priest (2006) both reported sympodial conidiogenesis for this species, but did not observe annellidic conidiogenesis. According to Shin & Sameva (2004), the conidia can be up to 68 µm long and 7-septate. Jørstad (1965) listed several *Septoria* names that were based on material from *Convolvulaceae* in the synonymy of *S. convolvuli*, including *S. septulata*. Beach (1919) reported physiological differences for the species on *Convolvulus arvensis*, but whether this correlates with genetic differences still remains to be investigated. Moreover, as already pointed out by Priest (2006), a number of species on *Calystegia* and *Convolvulus* still have to be critically re-examined, which would have to include studies in culture.

## *Septoria coprosmae* Cooke, Grevillea 14: 129. 1886.

*Description in vitro*: *Colonies* on OA 32 mm diam in 28 d (45 mm in 38 d), with a glabrous, colourless, even margin; colony spreading, the surface glabrous with only a few tufts of pure white aerial mycelium near the centre, immersed mycelium mostly cinnamon, but brick in the centre, reverse concolorous; no diffusing pigments observed. Conidiomata formed after 3–10 d, on the agar surface or submerged, simple or complex, with dark, first reddish-brown, then black walls, preformed opening undifferentiated or lacking, tardily releasing pale salmon to whitish conidial slime (after 30 d or later). *Colonies* on MEA (Oxoid, 3 %) 35 mm diam in 28 d (45 mm in 38 d), spreading but slightly elevated in the centre, with a colourless to rosy-buff, glabrous, even margin; colony surface leaden-grey to black, but with a fine felt coverage of minute, white aerial hyphae, reverse mostly dark brick to sepia, surrounded by cinnamon near the margin; no diffusing pigments observed. Conidiomata formed from 10 d onwards, mostly superficial, complex, opening by tearing of the upper wall and releasing milky white conidial slime. Spermatogonia of an *Asteromella*-state also formed.

*Conidiomata* simple or complex, with several merging cavities, lacking a differentiated ostiolum, opening by tearing of the wall; conidiomatal wall composed of a single layer of isodiametric cells, 6–13 µm diam. *Conidiogenous cells* discrete, or integrated in short, 1–2-septate conidiophores, hyaline, cylindrical, holoblastic, sympodial; *conidia* cylindrical, hyaline, smooth-walled, mostly curved, rounded at the tip, attenuated to a truncate base, (0–)1–3-septate , not or only slightly constricted around the septa, with minute oil-droplets near the ends and the septa, 9–31 × 1.8–2.2 µm (MEA), 17–30 × 1.7–2.0(–2.5) µm (OA); *Spermatia* hyaline, ellipsoid, with rounded ends and minutely granular contents, 3–5 × 0.8–1.2 µm.

*Hosts*: *Coprosma robusta*, *Coprosma* sp.

*Material examined*: **New Zealand**, North Island, Bay of Islands area, N. of Russell, mycosphaerella-like sexual morph on living leaves of *Coprosma robusta*, G. Verkley 2020, CBS H-21246, living single ascospore isolate CBS 113391.

*Notes*: CBS 113391 was obtained from rehydrated spotted leaves of *Coprosma robusta* collected in New Zealand that contained a mycosphaerella-like sexual morph. No mature asci were observed in this material, nor a septoria-like morph, but the isolate obtained developed pycnidia agreeing with conidia described for *S. coprosmae* (30 × 2 µm). In the multilocus phylogeny CBS 113391 groups with CPC 19304, originating from *Vigna unguiculata* subsp. *sesquipedalis* in Australia, and CPC 19793, isolated from *Syzygium cordatum* in Australia, and is also relatively closely related to *S. verbenae* (CBS 113438, 113481) isolated from *Verbena officinalis* in New Zealand. Aptroot (2006) investigated an isotype of *Mycosphaerella coacervata* from BPI and could only find "various coelomycetes". It is unclear whether it contained a *Septoria*. Sydow (1924) provided a description of the sexual morph of *M. coacervata* and an associated spermatial state, but not of a *Septoria*.

***Septoria cruciatae*** Roberge ex Desm., Annls Sci. Nat., sér. 3, Bot. 8: 20. 1847. Fig. 15.

= *Septoria urens* Pass., Atti Soc. crittog. ital. 2: 31. 1879.
= *Septoria aparines* Ellis & Kellerm., J. Mycol. 5: 143. 1889.
≡ *Rhabdospora aparines* (Ellis & Kellerm.) Kuntze, Revisio generum plantarum 3 (2): 509. 1898.
= *Septoria asperulae* Bäumler, Verh. zool.-bot. Ges. Wien 40: 142. 1890.
= *Septoria galii-borealis* Henn., Bot. Jahrb. Syst. 37: 163. 1905 [non Bubák & Kabát].
= *Septoria galii-borealis* Bubák & Kabát, Hedwigia 52: 350. 1912 [non Henn., later homonym].
?= *Phleospora bresadolae* Allesch., Ber. bot. Ver. Landshut 12: 60. 1892.
?= *Septoria relicta* Bubák, Annls mycol. 4: 116. 1906.

For more synonyms see Jørstad (1965).

*Description in planta*. *Symptoms* leaf lesions indefinite, usually a single one on each leaf expanding to ultimately cover the entire lamina, brown. *Conidiomata* pycnidial, epiphyllous, numerous, semi-immersed to immersed, subglobose to globose, dark brown to black, 170–240 µm diam; *ostiolum* central, circular, initially 25–55 µm wide, later becoming more irregular and up to 90 µm wide, surrounding cells concolourous; *conidiomatal wall* 20–35 µm thick, composed of an inner layer of isodiametric to irregular cells mostly 2.5–4.5 µm diam with hyaline cell walls up to 2 µm thick, and an outer layer of hyphal cells, 8–15 × 5–6.5 µm with orange brown walls thickened up to 2 µm, well developed and up to 15 µm thick in the upper part of the pycnidium wall. *Conidiogenous cells* hyaline, discrete, rarely integrated in 1-septate conidiophores, cylindrical, or narrowly to broadly ampulliform, holoblastic, proliferating rarely percurrently showing 1–2 indistinct annellations, sometimes (also) proliferating sympodially, 10–15(–22) × 3–5.5 (–6) µm. *Conidia* filiform, curved to flexuous, rounded to somewhat pointed at the apex, attenuated modestly towards the truncate base, (0–)2–3-septate, not constricted around the septa, hyaline, containing several large oil-droplets and granular material in the living state and rehydrated state, (30–)42–54(–60) × 2.5–3.2 µm (living; rehydrated, 2.0–2.5 µm wide), released in white cirrhi.

*Description in vitro (20 ºC, diffuse daylight)*. *Colonies* on OA 8–12 mm diam in 2 wk, with a glabrous, colourless, even margin; colony restricted, the surface mostly covered by pure white, woolly-floccose aerial mycelium, immersed mycelium mostly bright or darker herbage-green, brick in the centre, reverse dark green to black; a red pigment diffuses into the medium. Conidiomata developing in the centre on the surface of the colony or in the aerial mycelium, releasing pale milky white to rosy-buff conidial slime. *Colonies* on MEA 5–7 mm diam in 2 wk, with a barely visible, irregularly ruffled margin; colony restricted, hemispherical to irregularly pustulate, the surface entirely covered by a dense felty to woolly mat of pale olivaceous-grey, locally reddish, aerial mycelium, immersed mycelium almost black; reverse olivaceous-black to black; conidiomata developing on the surface in the centre of colonies, releasing milky white to rosy-buff conidial slime. *Conidiomata* on OA olivaceous-brown to olivaceous, globose, single or aggregated, 200–380 µm diam, on the agar mostly without a well-developed ostiolum, the wall composed of a rather undifferentiated outer layer of loosely interwoven, pale brown hyphae with barely thickened walls, and an inner layer of globose to angular cells with hyaline walls up to 2 µm thick. *Conidia* as *in planta*, mostly 3-septate, 35–65 × 2–2.5(–3) µm (OA).

*Hosts*: *Galium* spp.

*Material examined*: **Czech Republic**, Moravia, Milovice, forest Milovika stran, 15 Sep. 2008, on living or decaying leaves of *Galium odoratum*, G. Verkley 6007, **epitype designated here** CBS H-21250 "MBT175354", living cultures ex-epitype CBS 123747, 123748. **France**, Libisey near Caen, on living leaves of *G. cruciatum*, Jul.-Sep. 1844, M. Roberge, "Col. Desmazieres 1863, no. 8, 200", **isotype** PC 0084552, with handwritten description in French; Libisey near Caen, on living leaves of *G. cruciatum*, July 1844, M. Roberge, PC 0084551; Puy-de-Dôme, Ambert, on *G. cruciatum*, 23 Aug. 1903, L. Brevière, PC 0084553. **Germany**, Thüringen, Berka a. Ilm, on leaves of *G. rotundifolium*, 21 July 1912, H. Diedicke, distributed in Sydow, Mycotheca germanica 1132, PC 0084548. **Iran**, Pass Ghaleh, on *G. coronatum*, 10 July 1968, Sharif, PC 0084549. **Romania**, Bucharest, on *G. mollugo*, 4 Oct. 1974, G. Negrean, distributed in Herb. Mycol. Romanicum 50, 2476, PC 0084550.

*Notes*: The description given above is based on the collections on *Galium odoratum* and *G. cruciatum*, including the well-preserved type specimen from PC and the collection V6007, which agrees well with this type material. Although the latter is from Czech Republic and another host species than the type, it is selected here as epitype as two cultures derived from it are also preserved in CBS. According to Jørstad (1965), on *G. boreale* conidia are 23–73 × (1–)1.5–2(–2.5) µm (with mostly 3 septa), and on *G. aparine* 37–88 × 1–1.5 µm (with up to 5 septa). Jørstad placed five names in the synonymy of *S. cruciatae*, including *S. asperulae* from *G. odoratum*. He reported limited differences between material on different species of *Galium*, and it is not unlikely that there is just one species capable of infecting several species of *Galium*. In addition to the names he listed as synonyms of *S. cruciatae*, *S. relicta* and *Phleospora bresadolae*, both described from *G. odoratum* (syn. *Asperula odorata*) in Czech Republic and Germany, respectively,

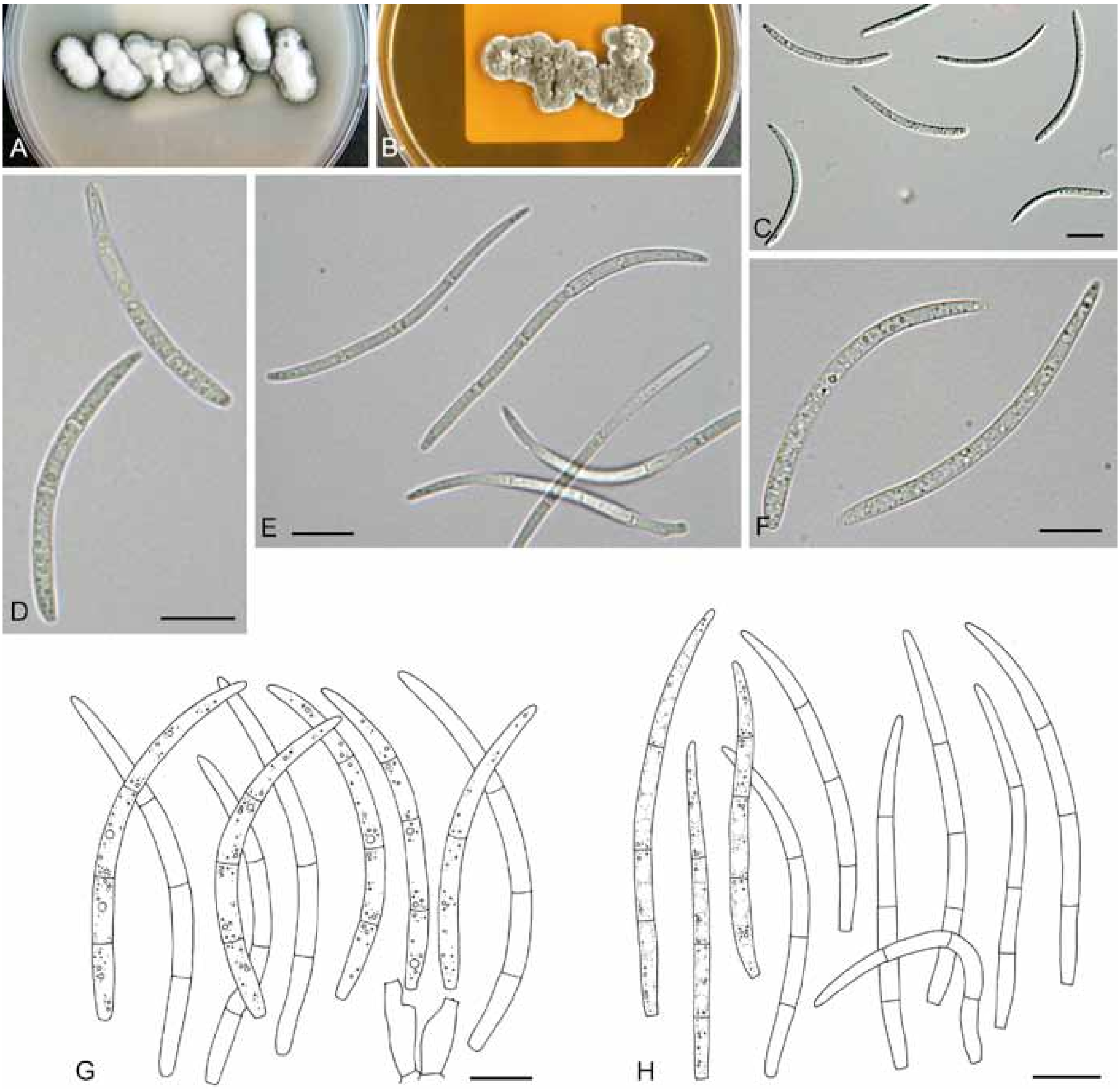


**Fig. 15.** *Septoria cruciatae*. A, B. Colonies CBS 123747. A. On OA. B. On MEA. C, D. Conidia *in planta* (CBS H-21250, epitype). E. Conidia on OA (CBS 123748). F. Conidia *in planta* (CBS H-21250). G. Conidia and conidiogenous cells *in planta* (CBS H-21250). H. Conidia on OA (CBS 123747). Scale bars = 10 µm.

may also be regarded as synonyms, but we have not studied type material for those (conidia reported 38–60 × 3–3.5 µm and 40–60 × 2.5–3.5 µm for these two respectively). The multigene phylogeny shows that the epitype of *S. cruciatae* is not part of the main *Septoria* clade (Fig 1), but basal to a clade of pseudocercosporella-like fungi. A new genus may have to be proposed for it in future.

***Septoria cucubali*** Lebedeva, Materialy po mikol. obsled. Rossii 5, 3: 3. 1921. Fig. 16.

*Description in planta*: *Symptoms* indefinite colourless to pale yellowish brown lesions, both on the lamina and along the leaf margins. *Conidiomata* pycnidial, epiphyllous, mostly gregarious, globose, black, semi-immersed, 50–95 µm diam; *osiolum* central, circular, 20–35 µm wide, provided with slightly darker cells; *conidiomatal wall* relatively thin, composed of *textura angularis*, the outer cells 3.5–5 µm diam, with brown, somewhat thickened walls, the inner cells 2.5–4.5 µm diam, with hyaline and thin walls. *Conidiogenous cells* ampulliform to cylindrical, without a distinct neck, hyaline, holoblastic, appearing to be phialidic, but proliferating percurrently with indistinct and close annellations, rarely also proliferating sympodially, 5–8(–10) × 2–3 µm. *Conidia* fusiform-cylindrical to cylindrical, weakly curved, gradually attenuated to a rounded or more or less pointed apex, abruptly attenuated into a narrow, truncate base, mostly 0–1(–3)-septate, not or indistinctly constricted around the septa, hyaline, contents minutely granular in the living state, in the rehydrated state with no distinct contents, (9–)15–42(–52) × 2–2.5 µm (rehydrated). *Sexual morph* unknown.

*Description in vitro*: *Colonies* on OA 13–18 mm diam in 2 wk (50–55 mm in 6 wk), with an even, glabrous, first colourless margin; colony spreading, immersed mycelium in the centre pale ochreous to

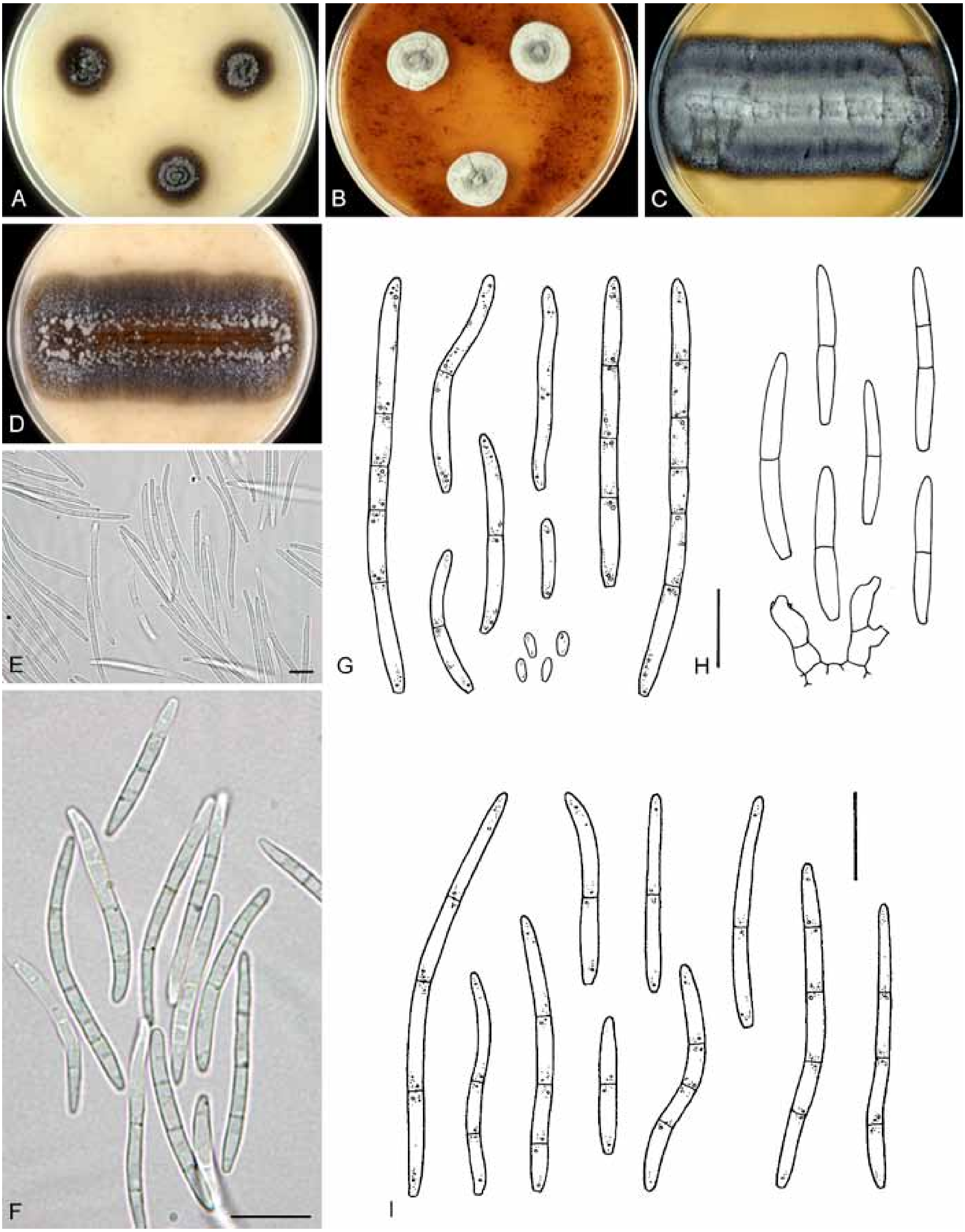


**Fig. 16.** *Septoria cucubali*. A–C. Colonies. A. CBS 102367, on OA. B. Ibid., on CHA. C, D. CBS 102386. C. On MEA. D. On OA. E, F. Conidia on OA (CBS 102386). G. Conidia and spermatia on OA (CBS 102367). H. Conidia and conidiogenous cells *in planta* (CBS H-21159). I. Conidia on OA (CBS 102386). Scale bars = 10 µm.

sienna with a distinct citrine to olivaceous tone especially towards the margin, or a faint salmon haze; aerial mycelium scanty to well-developed, woolly-floccose, greyish white, gradually attaining a reddish haze; reverse rust to bay, with olivaceous-black areas. Surface of the colony first plane, but later irregularly lifted, with blackish stromata developing on the surface and immersed in the agar, first spherical, closed, later opening widely to expose a milky white to luteous conidial slime. *Colonies* on CMA 9–15 mm diam in 2 wk (43–45 mm in 6 wk), with an even, glabrous, colourless to buff margin; further as on OA, but immersed mycelium only in the centre sienna, for the most olivaceous to almost dull green; aerial mycelium similar in colour and texture, but scarcer; reverse olivaceous-black, with distinct rust central areas; conidiomata less developed. *Colonies* on MEA 9–16 mm diam in 2 wk, with an even, buff or peach to scarlet margin, mostly hidden under tufts of aerial mycelium; colonies hemispherical, sometimes radially striate, immersed mycelium dark ochreous to greyish brown or olivaceous-black, mostly covered by finely felty or floccose-tufty, white, greyish or scarlet aerial mycelium; luteous to reddish diffusable pigment sometimes present; reverse rust to chestnut, margin apricot; stromata scarcely developing, releasing milky white to rosy-buff conidial slime. *Colonies* on CHA (4–)6–9 mm diam in 2 wk [(30–)40–46 mm in 6 wk], as on MEA, conidial slime first rosy-buff, later ochreous.

*Conidiomata* pycnidial, as *in planta* but often larger, 100–175µm, or merging into larger complexes; *conidiogenous cells* as *in planta*, but annellations more distinct. *Conidia* fusiform-cylindrical to cylindrical, straight or weakly curved, gradually attenuated to a rounded or more or less pointed apex, abruptly attenuated into a narrow, truncate base, (0–)1–3(–4)-septate, not or indistinctly constricted around the septa, hyaline, contents minutely granular with small oil-droplets, (9–)15–29(–52) × 2–2.5 µm.

Both on the plant and in culture spermatogonia of an *Asteromella* state were produced, in which 0-septate, ellipsoid spermatia were formed 2–3 × 1–1.5 µm. No sexual morph was observed.

*Hosts*: on living leaves of *Cucubalus baccifer* and *Saponaria officinalis*.

*Material examined*: **Germany**, isolated from leaf litter of *Fagus sylvatica*, M. Unterseher, living culture CBS 124874. **Netherlands**, Prov. Gelderland, Millingen aan de Rijn, Millingerwaard, on living leaves of *Cucubalus baccifer*, 6 Oct. 1999, G. Verkley 941, CBS H-21159, living cultures CBS 102367, 102368; same loc., date, brown leaf margin on living leaves of *Saponaria officinalis*, 6 Oct. 1999, G. Verkley 938, CBS H-21218, living culture CBS 102386.

*Notes*: The material on *Cucubalus* available for this study showed conidia (9–)15–19(–23) × 2–2.5 µm, thus much shorter and somewhat narrower than reported for *S. cucubali* in the original diagnosis (34–50 × 1.5–2 µm; based on material collected in July), and by Teterevnikova-Babayan (1987). This Dutch material was collected much later in the season than the type, and under relatively dry conditions. Averages of conidial width and especially lengths seen in specimens collected under adverse conditions such as drought or cold can be lower as compared to material collected under optimal conditions. The isolates obtained from this material were, however, capable of producing conidia up to 52 µm in length. This would be in good agreement with *S. cucubali*, as are the morphology of the pycnidia, the shape and width of the conidia, as well as the symptoms on the plant described by Teterevnikova-Babayan (1987) for *S. cucubali*. Markevičius & Treigiene (2003) reported *S. dimera* on *Cucubalus*, and that species is characterised by conidia that are wider (21–35 × 3.2–4.3 µm; Vanev *et al.* 1997 report 26–65 × 2.5–4 µm for that species).

The isolates from *Cucubalus* were also very similar to those obtained from the material collected in the same area on *Saponaria*, and the sequences obtained indicate that these isolates all belong to a single species. The material on the plant studied here differs from the description of *S. saponariae* provided by Teterevnikova-Babayan (1987), who describes conidia as 1–3-septate, 25–59 × 3.3–4.5 µm. That species thus has much wider conidia. Host range of *S. cucubali* in literature only mentions *Cucubalus*, but it is clear from the present study that it also includes *Saponaria officinalis*. The strain isolated from beech leaf litter may be an accidental dweller and originate from a *Caryophyllaceae* host growing in the vicinity. That the fungus would be capable of infecting *Fagus* leaves as an endophyte seems unlikely but cannot be excluded.

## ***Septoria cucurbitacearum*** Sacc., Nuovo G. bot. ital. 8: 205. 1876.

*Description in vitro*: *Colonies* on OA 38 mm diam in 5 wk, with an even, or slightly undulating, colourless, glabrous margin; colonies restricted to moderately spreading, almost entirely olivaceous-black, due to brown-walled immersed hyphae, the surface mostly glabrous, yet in the centre and around pycnidia often with greyish white, pruinose aerial hyphae. *Conidiomata* numerous, scattered or gregarious, black, pycnidial, with a single often quite long ostiolate neck, but fruitbodies often bursting somewhere in the lower wall, conidial slime pale white; reverse concolourous. *Conidiogenous cells* hyaline, discrete, ampulliform to cylindrical, holoblastic, with 1–3 percurrent proliferations, 8–16 × 3.5–5 µm. *Conidia* filiform, curved or flexuous, hyaline, 3–5(–7)-septate, not constricted around the septa, narrowly rounded at the top, slighty attenuating to a narrowly truncate base, with minute oil-droplets, (30–)35–55 (–72) × 1.5–2(–2.5) µm.

*Hosts*: *Cucurbita* spp., *Cucumis* spp. and *Citrullus vulgaris*.

*Material examined*: **New Zealand**, culture isolated from living leaves of *Cucurbita maxima*, date of collection and isolation unknown (deposited in Feb. 1977), H. J. Boesewinkel *s.n.*, CBS 178.77.

*Notes*: No specimens on plant material were available for this study. A description based on specimens from *Cucumis*, *Cucurbita* and *Citrullus* collected in Australia is provided by Priest (2006), and the sporulating structures observed in CBS 178.77 on OA agree well with that description. *Septoria cucurbitacearum* is the oldest name on plants of the family *Cucurbitaceae*, and Punithalingam (1982) discussed the relationship with the other taxa on the host genera *Cucurbita* and *Cucumis*. On the basis of the multilocus sequence analysis it can be concluded that *S. cucurbitacearum* is closely related to *S. lycospersici* (CBS 354.49 and 128654), *S. malagutii* (CBS 106.80), and *S. apiicola*.

## ***Septoria digitalis*** Pass., Atti Soc. crittog. ital. 2: 36. 1879. Fig. 17.

*Description in planta (based on CBS H-18090)*: *Symptoms* leaf spots hologenous, scattered, circular to elliptical, pale yellowish brown, definite with a dark brown border, or indefinite, surrounded by a larger area of the leaf which turns reddish purple. *Conidiomata* pycnidial, epiphyllous, numerous scattered in each leaf spot, subglobose to globose, immersed, brown to black, (70–)85–130 µm diam; *ostiolum* central, initially circular and 20–45 µm wide, later more irregular and up to 60 µm wide, surrounding cells undifferentiated; *conidiomatal wall* about 12.5–20 µm thick, composed of an outer layer of isodiametric cells 4.5–8(–10) µm diam or more irregular cells with brown walls 1–2 µm thick, and an inner layer of angular to globose cells 2.5–4(–6) µm diam with relatively thin, hyaline walls. *Conidiogenous cells* hyaline, discrete, rarely integrated in 1-septate conidiophores, globose, doliiform or

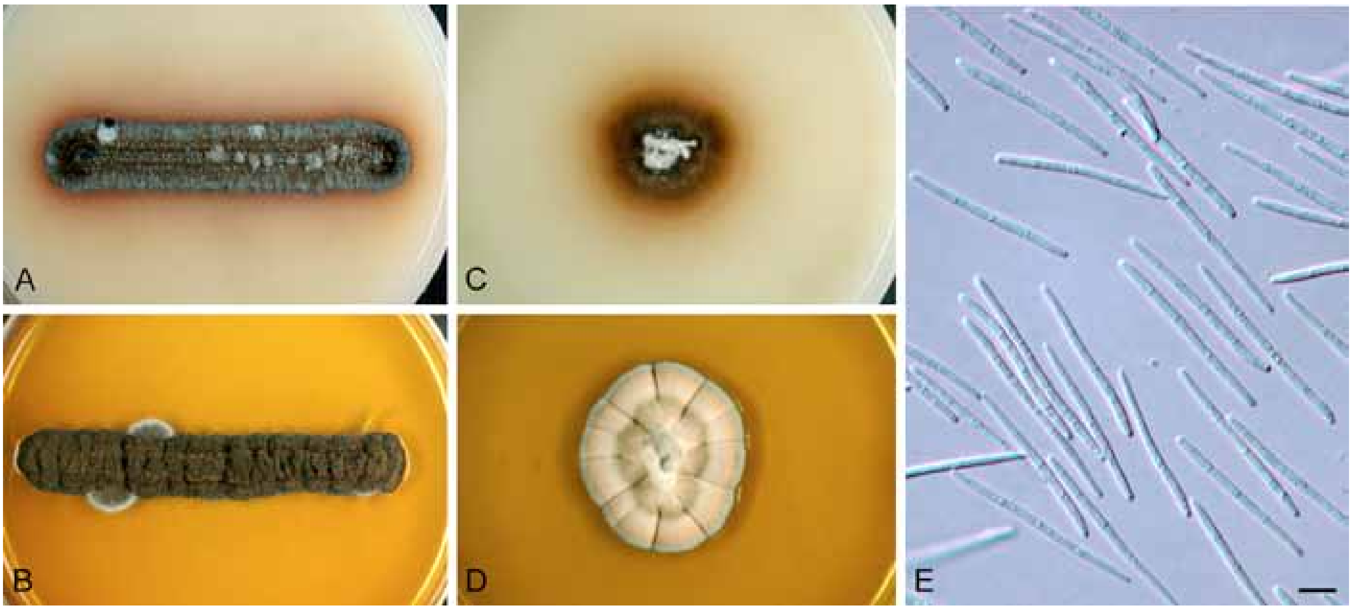


**Fig. 17.** *Septoria digitalis*. A, B. Colonies CBS 328.67 (15 ºC, nUV). A. On OA. B. On MEA. C, D. Colonies CBS 391.63 (15 ºC, nUV). C. On OA. D. On MEA. E. Conidia on OA (CBS 328.67). Scale bars = 10 µm.

ampulliform, holoblastic, proliferating sympodially and often also percurrently, with close indistinct annellations on an elongated neck, 3–8.5(–10) × 2–3.5(–4.5) µm. *Conidia* filiform-cylindrical to cylindrical, straight to slightly curved, rarely somewhat flexuous, attenuated gradually to a narrowly rounded to pointed apex, and attenuated gradually or more abruptly to a narrowly truncate base, 1–3(–4)-septate, not constricted around the septa, hyaline, contents with minute oil-droplets and granular contents in the rehydrated state, (16.5–)22–44 × 1.5–2(–2.5) µm (rehydrated). *Sexual morph* unknown.

*Description in vitro (18 ºC, near UV light) CBS 328.67*: *Colonies* on OA 12–13 mm diam in 2 wk, with an even to slightly ruffled, glabrous margin; colonies restricted to spreading, with some irregular pustulate elevations in the centre, immersed mycelium dark rust to chestnut, mostly covered by a more or less dense mat of low, woolly to woolly-floccose, greyish to somewhat reddish aerial mycelium, with scattered higher tufts, reverse blood colour; producing a red pigment diffusing into the surrounding agar medium. *Colonies* on MEA 10–13 mm diam in 2 wk, with an even margin which is mostly covered by aerial mycelium; colonies restricted, irregularly pustulate and up to 2 mm high in the centre, immersed mycelium dark, entirely covered by a dense mat of appressed, finely felted, grey to ochreous or rust aerial mycelium, the surface showing numerous sterile black stromata; reverse dark brick or sepia in the centre, surrounded by dark violet slate. No sporulation or diffusing pigment observed. *CBS 391.63*: *Colonies* on OA 23–25 mm diam in 2 wk, with an even, glabrous margin; colonies spreading, immersed mycelium fulvous to rust, or some brown-vinaceous, glabrous, or with barely any aerial mycelium, no sporulation observed; reverse blood colour in centre, fading to red or coral towards the margin; producing some red pigment diffusing into the surrounding agar medium. *Colonies* on MEA 25–30 mm diam in 2 wk, with an even, undulating, glabrous, buff margin; colonies restricted to spreading, radially striate, up to 2 mm high in the centre, immersed mycelium dark, entirely covered by a dense mat of appressed, finely felted, rosy vinaceous to flesh aerial mycelium with greysih or white zones ; reverse brown-vinaceous to blood colour. No sporulation or diffusing pigment observed.

*Conidia* (OA) as *in planta*, 20–48(–52) × 1.5–2.5 µm.

*Hosts*: *Digitalis* spp.

*Material examined*: **Czech Republic**, South Bohemia, Písek, on *Digitalis lanata*, Sep. 1962 V. Holubová-Jechová, living culture CBS 391.63. **Netherlands**, Doornspijk, herbal garden, in leaf spot on *D. lanata*, 22 June 1967, H.A. van der Aa 72, CBS H-18090, and dried culture on OA CBS H-18092, living culture CBS 328.67.

*Notes*: The two strains investigated here showed some notable differences in colony features, and they are therefore described separately above. Nonetheless, these strains showed highly homologous sequences of all loci investigated here. The strains are relatively distant from the closest relatives in the *Septoria*-clade, viz., among others, *S. epilobii* (CBS 109084, 109085), *S. verbascicola* (CBS 102401), and the strains of *S. stachydis* and *S. galeopsidis*. According to the original diagnosis, based on material on *Digitalis lutea*, the conidia of *S. digitalis* are continuous, 25–30 × 1.5 µm (also in Radulescu *et al.* 1973, Teterevnikova-Babayan 1983). Although conidia observed in the material on *D. lanata* studied here are up to 44 µm long and provided with up to 4 septa, it is concluded that the name *S. digitalis* can be applied to this material.

***Septoria epilobii*** Westend., Bull. Acad. r. Belg., Cl. Sci., Sér. 2, 19: 120. 1852 [non Roberge ex Desm. 1853]. Fig. 18.

= *S. epilobii* Roberge ex Desm., Annls Sci. Nat., ser. 3, 20 : 94. 1853 [Nom. illeg., later homonym].

?= *S. epilobii* Westend. var. *durieui* Unamuno, Boln R. Soc. esp. Hist. nat. 34: 250. 1934.

*Description in planta*: *Symptoms* leaf lesions sparse to numerous, single, circular to irregular, rarely entended to the margin of the leaf, brown, often with a greyish centre, well-delimited by a dark brown elevated line, visible on both sides of the leaf. *Conidiomata* pycnidial, epiphyllous, several in each lesion, subglobose to globose, brown to black, 48–75 µm diam; *ostiolum* central, circular, initially 15–24 µm wide, later becoming more irregular and up to 40 µm wide, surrounding cells dark brown; *conidiomatal wall* 12–20 µm thick, composed of a homogenous tissue of hyaline, angular cells, 3–6.5 µm diam, the outermost cells pale brown with slightly thickened walls, the inner cells hyaline and thin-walled. *Conidiogenous cells*

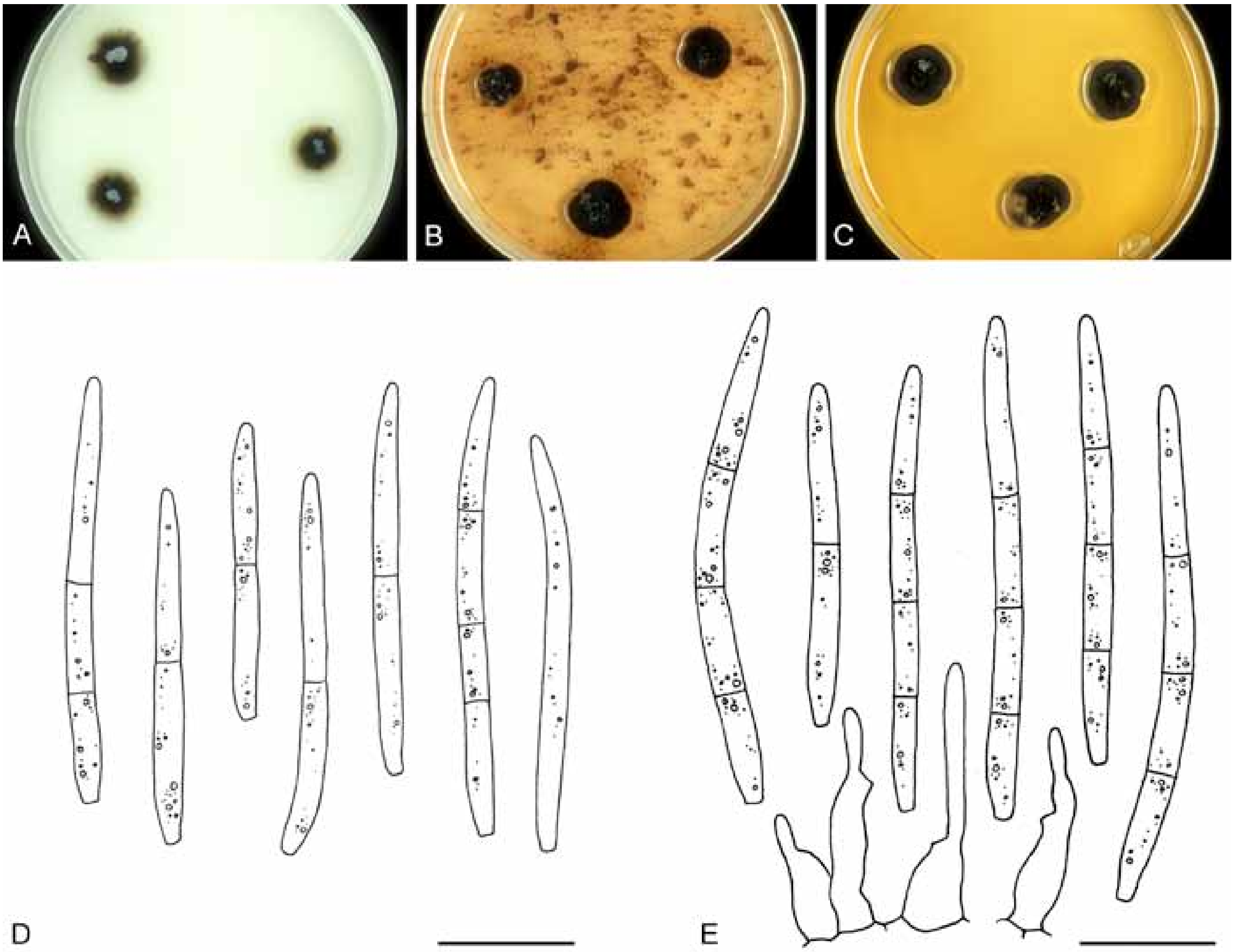


**Fig. 18.** *Septoria epilobii*. A–C. Colonies CBS 109084 (15 ºC, nUV). A. On OA. B. On CHA. C. On MEA. D. Conidia *in planta* (CBS H-21171, epitype). E. Conidia and conidiogenous cells on OA (CBS 109094). Scale bars = 10 µm.

hyaline, discrete, rarely also integrated in 1-septate conidiophores, cylindrical, or narrowly to broadly ampulliform, holoblastic, proliferating sympodially, sometimes with a relatively narrow and elongated neck (no annellations seen), 5–14 × 3.5–6 µm. *Conidia* cylindrical or filiform-cylindrical, straight to slightly curved, narrowly to broadly rounded at the apex, narrowing slightly or more distinctly to a truncate base, (0–)1–3-septate, not or slightly constricted around the septa, hyaline, contents with few minute oil-droplets and granular material in each cell in the rehydrated state, 25–35(–40) × 1.5–2(–2.5) µm (rehydrated). *Sexual morph* unknown.

*Description in vitro*: *Colonies* on OA 12–15(–17) mm diam in 3 wk (45–48 mm in 7 wk), with an even, glabrous, colourless or vaguely buff margin; colonies spreading, plane, in the centre olivaceous-black, surrounded by olivaceous radiating hyphal strands; reverse concolourous; aerial mycelium absent, or a tuft of white or grey woolly aerial mycelium in the centre; abundant olivaceous to brown, then black, pycnidial conidiomata developing after 3 wk, releasing milky white droplets of conidial slime. *Colonies* on CMA 12–14(–16) mm diam in 3 wk (45–50 mm in 7 wk), as on OA, but centre more homogeneous olivaceous-black after 3 wk; after 7 wk larger outer area saffron to pale ochreous, margin buff; reverse concolourous; sporulation as on OA, but older conidial slime pale saffron. *Colonies* on MEA (7–)10–16 mm diam in 3 wk (46–50 mm in 7 wk), with an even, glabrous, rosy-buff or buff margin; colonies restricted, conical, in the centre with more irregular pustulate protruberances, after about 4 wk becoming more spreading, the surface brown-vinaceous to almost black, locally ochreous to dirty peach, covered by a diffuse, low, minutely felty whitish to grey aerial mycelium; reverse brown-vinaceous to dark slate blue, locally cinnamon to ochreous; conidiomatal initials developing from 3 wk onwards in most of the colonies, but sporulation occurs sparsely in submarginal pycnidia after 7 wk in dirty white to rosy-buff droplets. *Colonies* on CHA 7–12(–16) mm diam in 3 wk (34–38 mm in 7 wk), as on MEA, including sporulation.

*Conidiomata* as *in planta*, single or merged, with a single or a few papillate openings, which can be positioned on an elongated neck; conidiogenous cells as *in planta*, proferating sympodially and possibly also percurrently, but the presence of annellations could not be confirmed, 5–18 × 3.5–6 µm; *conidia* as *in planta*, 24–41 × 1.8–2.5 µm.

*Hosts*: *Chamaenerion angustifolium* and *Epilobium* spp.

*Material examined*: **Austria**, Tirol, Ober Inntal, Samnaun Gruppe, Zanderstal near Spiss, alt. 1800 m, on rocky bank of Zandersbach, on living leaves of *Epilobium fleischeri*, 11 Aug. 2000, G. Verkley 1068, **epitype designated here** CBS H-21171 "MBT175355", living cultures ex-epitype CBS 109084, 109085. **Belgium**, on the bank of river Wépion, near Namur, on leaves of *E. spicatum* (= *E. angustifolium, Chamaenerion angustifolium*), 1829, Bellynck, "Westendorp & Wallay Herb. Crypt. no. 727", **isotype** BR-MYCO 158690-95. **Netherlands**, prov. Utrecht, Baarn, Baarnsche bos, ex leaf spot of *E. angustifolium*, 17 Sep. 1967, L. Marvanová *s.n.*, living culture CBS 435.67 no longer available (infected with basidiomycete).

*Notes*: In the type specimen of *S. epilobii* on *Epilobium angustifolium* (= *Chamaenerion angustifolium*), from BR, 1–3-septate conidia, 20–40 × 1–1.5 µm are observed. Although the collection of *S. epilobii* from Tirol was collected on another host species, *E. fleischeri*, it agrees morphologically well with the type material, and therefore this Austrian collection is chosen here as epitype. It is considered likely that a single taxon is capable of infecting various members of the genera *Epilobium* and its sister-genus *Chamaenerion*. The concept of *S. epilobii* maintained here concurs with that of most authors (Radulescu *et al.* 1973, Teterevnikova-Babayan 1987), except Vanev *et al.* (1997), who gave a much wider length range of conidia, viz., 12–72 ×1–2 µm, but their concept of *S. epilobii* may erroneously have been based in part on specimens of *S. alpicola*. *Septoria epilobii* is very distinct from *S. alpicola* Sacc. 1897, a species causing systemic infections in *Epilobium* spp. in alpine and boreal regions (type host *E. alpinum*), developing pycnidia on symptomless leaves as well as stems that produce conidia, 24–95 × 0.7–1.5(–2) µm, with up to 7 septa (Jørstad 1965).

*Septoria epilobii* var. *durieui* Unamuno, which has been described from *E. duriaei* in Spain, with conidia 30–55 × 1.5 µm, is tentatively placed here in the synonymy of *S. epilobi*.

As can be seen in the multilocus phylogeny (Fig. 2), the strains of *Septoria epilobii* are closely related to CBS 102401, which was isolated from *Verbascum nigrum*, and preliminarily identified as *S. verbascicola* Berk. & M.A. Curtis. This name is a *nomen nudum* and the type should be studied. Other closely related species include *S. taraxaci* (CBS 567.75), *S. stachydis*, *S. galeopsidis*, and *S. digitalis*.

***Septoria erigerontis*** Peck, Rep. N.Y. St. Mus. nat. Hist. 24: 87. 1872 [non Berk. & M.A. Curtis 1874; nec Hollós 1926, later homonyms]. Fig. 19.

≡ *Septoria erigerontea* Sacc., Syll. Fung. 3: 547. 1884 [nom. illeg., Art. 52. superfluous nom. nov.].

= *Septoria erigeronata* Thüm., Bull. Soc. Imp. Nat. Moscou 56: 132. 1881.

= *Septoria schnabliana* (Allesch.) Died., KryptogFl. M. Brandenb. 9: 454. 1914.

≡ *Rhabdospora schnabliana* Allesch., Hedwigia 34: 273. 1895.

= *Septoria chanousii* Ferraris, Malpighia 16: 27. 1902.

= *Septoria stenactidis* Vill, in Sydow, Annls mycol. 8: 493. 1910.

?= *Septoria bosniaca* Picb., Glasnik Zemal. Muz. Bosn. Herceg. 45: 68. 1933.

*Description in planta*: *Symptoms* leaf spots hologenous, scattered, circular to irregular, pale brown, indefinite or surrounded by a slightly darker margin. *Conidiomata* pycnidial, epiphyllous, numerous scattered in each leaf spot, subglobose to globose, brown to black, semi-immersed, 75–130 µm diam; *ostiolum* central, initially circular and 15–35 µm wide, later more irregular, up to 55 µm wide, surrounding cells dark brown and with more thickened walls; *conidiomatal wall* about 8–12.5 µm thick, composed of a homogenous tissue of hyaline, angular cells 2.5–4 µm diam with relatively thin, hyaline walls, surrounded by a layer of pale to dark brown cells, 2–5 µm diam, with somewhat thickened walls. *Conidiogenous cells* hyaline, discrete, rarely integrated in 1–2-septate conidiophores, cylindrical to doliiform, or narrowly to broadly ampulliform, holoblastic, proliferating mostly sympodially, rarely also percurrently with indistinct annellations, 6–10 × 2.5–4.5 µm. *Conidia* filiform, straight, slightly curved to flexuous, attenuated gradually to a narrowly rounded to pointed apex and narrowly truncate base, (0–)1–3(–5)-septate, not constricted around the septa, hyaline, contents with several minute oil-droplets and granular material in each cell in the living state, with minute oil-droplets and granular contents in the rehydrated state, (17–)25–50(–62.5) × 1–1.5(–2) µm (rehydrated). *Sexual morph* unknown.

*Description in vitro*: *Colonies* on OA 8–11 mm diam in 12 d (42–44 mm in 7 wk), with an even, glabrous, colourless to pale red or coral margin, the pigment also clearly diffusing beyond the margin; colonies spreading, the surface almost plane, immersed mycelium translucent and red everywhere (12 d), in the centre with densely aggregated superficial pycnidial conidiomata often with distinct papillate to rostrate openings, which later may elongate further, pycnidia elsewhere in radiating rows, later also in concentric rings, releasing milky white to pale buff droplets of conidial slime; aerial mycelium white, felty, scanty, mostly in the centre; reverse concolorous. *Colonies* on CMA 7–10 mm diam in 12 d (50–59 mm in 7 wk), as on OA, but immersed hyphae darker and olivaceous, but red pigmentation still distinct, especially around the colony margin. *Colonies* on MEA 4–7 mm diam in 12 d (45–48 mm in 7 wk), with a ruffled, colourless to pale buff, plane marginal zone; colony initially restricted, hemispherical after 12 d, with an irregularly pustulate-worty surface, later for the most plane and spreading, immersed mycelium very dark chestnut to black, aerial mycelium on elevated surface almost absent, but near margin forming short-tufty mat of pure white hyphae; superficial pycnidial conidiomata releasing pale flesh or milky white droplets of conidial slime. *Colonies* on CHA 6–8 mm diam in 12 d (29–36 mm in 7 wk), as on MEA, but in some sectors with an even, rosy-buff margin; colonies less elevated in the centre than on MEA, covered with diffuse, woolly, greyish aerial mycelium in the centre, and a low, dense mat of reddish hyphae near the margin; pycnidial conidiomata more numerous than on MEA, later in distinct, concentric patterns, producing flesh, later salmon droplets of conidial slime.

*Conidiogenous cells* (OA) as *in planta*, but more frequently proliferating percurrently and with distinct annellations. *Conidia* as *in planta*, up to 85 µm long and 2.5 µm wide.

*Hosts*: *Conyza* spp. and *Erigeron* spp.

*Material examined*: **Austria**, Tirol, Inntal W of Innsbruck, S of Telfs, along road 171, on living leaves of *Erigeron annuus*, 4 Aug. 2000, G. Verkley 1045, CBS H-21176, living culture CBS 109094, 109095; same substr., country unknown, M. Vurro, living culture CBS 186.93 (sub *S. schnabliana*). **South Korea**, Namyangju, same substr., H.D. Shin, 3 May 2006, living culture SMKC 21739 = KACC 42356 = CBS 128606; same country, loc. unknown, same substr., living culture CPC 12340 = CBS 131893.

*Notes*: The material available for this study agreed generally well with the detailed descriptions given for this species in recent literature (Shin & Sameva 2004, Priest 2006). However, Priest (2006) did not observe sympodial proliferation in the conidiogenous cells. Shin & Sameva (2004) reported conidia up to 70 µm long in material from South Korea. Verkley & Starink-Willemse (2004) already showed that the ITS sequence of CBS 186.93 identified as *S. schnabliana* is identical to that in *S. erigerontis* (CBS 109094), and suspected the conspecificity of this material. Strong evidence for this conspecificity is provided here, as the additional genes sequenced were all (almost) identical for the three isolates investigated, and also for CBS 128606 (= KACC 42356) and CBS 131893 (= CPC 12340) from the same host in South Korea.

According to the diagnosis, *Septoria stenactidis*, described from *Stenactis annua* (= *E. annuum*), has continuous (or indistinctly septate) conidia, 35–40 × 1 µm, which agrees well with *S. erigerontis* on the type host, and it was already placed in the synonymy by Jørstad (1965), and recently also by Priest (2006). Priest also included *S. chanousii* in the synonymy of *S. erigerontis.*

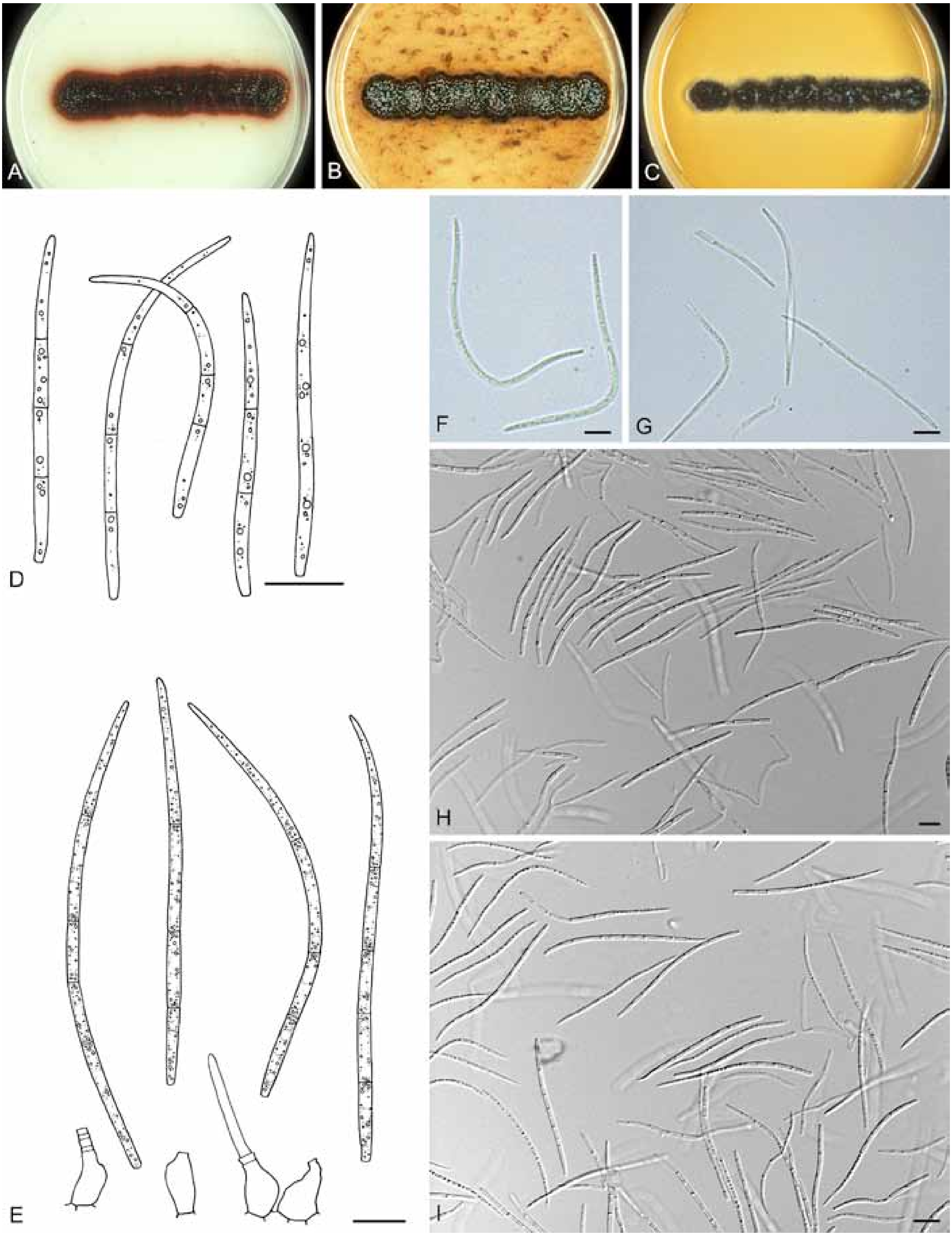


**Fig. 19.** *Septoria erigerontis*. A–C. Colonies CBS 109094 (15 ºC, nUV). A. On OA. B. On CHA. C. On MEA. D. Conidia *in planta* (CBS H-21176). E. Conidia and conidiogenous cells on OA (CBS 109094). F, G. Conidia *in planta* (CBS H-21176). H, I. Conidia on OA (CBS 186.93). Scale bars = 10 µm.

This fungus was originally decribed on *E. uniflora* in Italy, with 3–4-septate conidia measuring 45–50 × 1.5 µm. Likewise, *S. bosniaca* from *Erigeron polymorphus* described in the diagnosis as a fungus with 0(–3)-septate conidia, 19–42 × 1.3–1.9 µm, is probably also a synonym.

***Septoria galeopsidis*** Westend., Bull. Acad. r. Belg., Cl. Sci., Sér. 2, 2: 577. 1857. Fig. 20.

= *Ascochyta galeopsidis* Lasch in Rabenh., Herb. Myc. I, 1058. 1846 [nom. nud.].

= *Septoria cotylea* Pat. & Har., Bull. Soc. Mycol. France 21: 85. 1905.

*Description in planta*: *Symptoms* leaf spots irregular or angular, becoming dark brown, in yellow parts of the leaf lamina. *Conidiomata* pycnidial, hypophyllous, often numerous in each leaf spot, globose to subglobose, dark brown, almost completely immersed, 75–100(–130) µm diam; *ostiolum* central, initially circular, 15–25 µm wide, surrounding cells somewhat darker; *conidiomatal wall* 10–22 µm thick, composed of *textura angularis* without distinctly differentiated layers, the cells 3–8 µm diam, the outer cells with brown, somewhat thickened walls, the inner cells with hyaline and thinner walls. *Conidiogenous cells* discrete, sometimes integrated into 1–2-septate conidiophores, hyaline, narrowly or broadly ampulliform with a relatively narrow neck, holoblastic, proliferating percurrently with indistinct annellations, and also sympodially, 6–12(–15) × 3.5–5(–6) µm. *Conidia* filiform, straight or slightly curved, sometimes flexuous, with a rounded or somewhat pointed apex, attenuated towards the narrowly truncate base, (0–)3(–5)-septate, not constricted around the septa, hyaline, contents with several minute oil-droplets and granular material in each cell in the living state, with inconspicuous oil-droplets and granular contents in the rehydrated state, 20.5–44 × 1.5–2.5 µm (living; rehydrated, 1–2 µm wide). *Sexual morph* unknown.

*Description in vitro*: *Colonies* on OA 7–13 mm diam in 2 wk (35–43 mm in 6 wk), with an even, glabrous, colourless margin; colonies almost plane, immersed mycelium homogeneously olivaceous-black to greenish black (also near the margin); aerial mycelium scanty, woolly-floccose, white or greyish; superficial pycnidial conidiomata scanty, scattered over the central aerea, releasing milky white droplets of conidial slime; reverse dark slate blue to black. *Colonies* on CMA 7–13 mm diam in 2 wk (33–37 mm in 6 wk), as on OA, but concentration of conidiomatal development in elevated pustules on the elsewhere flat colony. *Colonies* on MEA 6–11 mm diam in 2 wk (33–39(–46) mm in 6 wk), the margin even, later undulating, buff, narrow and glabrous; colonies hemispherical, often irregularly pustulate or with columnar outgrowths up to 5 mm high, immersed mycelium olivaceous-black to black, mostly covered by a dense mat of finely velted, greyish aerial mycelium; faster growing, glabrous sectors with buff immersed mycelium may appear after several weeks; conidiomata starting to develop on the (dark) colony surface, tardily sporulating with whitish to flesh droplets of conidial slime; reverse brown-vinaceous or olivaceous-black. *Colonies* on CHA 5–10(–15) mm diam in 2 wk (20–29 mm in 6 wk), with an even, glabrous to nearly so, buff margin; colonies irregularly pustulate, immersed mycelium olivaceous-black, mostly covered by a dense but appressed mat of woolly-floccose, grey aerial mycelium, in some slightly faster growing sectors pure white; scattered but scarce superficial conidiomata releasing pale flesh droplets of conidial slime; reverse blood colour to black.

*Conidiomata* pycnidial and similar as *in planta*, 100–150 µm diam, or merged into larger complexes especially on the agar surface, dark brown, up to 200 µm diam; *ostiolum* as *in planta*, or absent. *Conidiogenous cells* hyaline, ampuliform, or elongated ampulliform to cylindrical, with a distinct neck, holoblastic, proliferating percurrently with indistinct scars (annellations), or sympodially, 8–13(–15) × 3–4.5(–5) µm. *Conidia* cylindrical, straight or slightly curved, tapering to a rounded or somewhat pointed apex, lower part slightly or more clearly attenuated into a broad truncate base, (0–)1–3(–5)-septate, not constricted around the septa, hyaline, with several oil-droplets and minute granular material in each cell, (37–)50–65 (–70) × 2–2.5 µm.

*Hosts*: *Galeopsis angustifolia*, *G. ladanum*, *G. pubescens*, *G. speciosa* and *G. tetrahit*.

*Material examined*: **Belgium**, in the vicinity of Mons, on leaves of *Galeopsis tetrahit*, R. P. Clém. Dumont, distributed in Westendorp & Wallays, Herb. crypt. Belge, Fasc. 23-24, no 1134, **isotype** BR-MYCO 158116-06. **Czech Republic**, Moravia, Mikulov, on living leaves of *Galeopsis* sp., 15 Sep. 2008, G. Verkley 6003, CBS H-21256, living cultures CBS 123744, 123749; same substr., date, Moravia, Milovice, forest Milovika stran, G. Verkley 6006, CBS H-21254, living cultures CBS 123745, 123746. **France**, Corrèze, Prât Alleyrat, on living leaves of *G. tetrahit*, 25 July 1976, H.A. van der Aa 5344, CBS H-18099; loc. unknown, isol. C. Killian ex *Galeopsis* sp., living culture CBS 191.26. **Netherlands**, prov. Noord-Brabant, Cromvoirt, on living leaves of *G. tetrahit*, 2 June 1963, H.A. van der Aa *s.n.*, CBS H-18097; prov. Gelderland, Putten, on living leaves of *G. tetrahit*, 8 Aug. 1984, G. de Hoog *s.n.*, CBS H-18100; prov. Utrecht, Soest, on living leaves of *G. tetrahit*, 4 Aug. 1999, G. Verkley 902, CBS H-21195, living culture CBS 102314; prov. Limburg, St. Jansberg near Plasmolen, on living leaves of *G. tetrahit*, 9 Sep. 1999, G. Verkley 934, **epitype designated here** CBS H-21215 "MBT175356", living culture ex-epitype CBS 102411. **Romania**, distr. Satu-Mare, Pir, on living leaves of *G. ladanum*, 27 Aug. 1973, G. Negrean *s.n.*, CBS H-18098.

*Notes*: Jørstad (1965) reported comparable conidial size ranges in specimens on different host species, viz. *G. speciosa* (extreme values 20–64 × 1–2.5 µm) and *G. tetrahit* (28–60 × 1–2 µm), although in most Norwegian collections on *G. tetrahit*, the maximum conidial length varied downwards to 48 µm. In the original diagnosis of *S. galeopsidis* conidia are described as 30–40 × 1–1.5 µm (Saccardo 1884), while Radulescu *et al.* (1973) reported measurements ranging between 20–45 µm in length in collections on various hosts. In the type material from BR investigated here conidia are mostly 3–5-septate, 19–40 × 1.5–2 µm. In other material available for the present study, maximum length of conidia was only 44 µm *in planta*, whereas the strains obtained from it were capable of forming conidia with a maximum length of 70 µm on OA. The differences with *S. lamiicola* are discussed under that species.

*Septoria galeopsidis* is closely related to only some of the other *Septoria* species occurring on plants from the family *Lamiaceae*, especially *S. melissae* (CBS 109097) and *S. stachydis*. *Septoria lamiicola* on *Lamium* spp., which is morphologically quite similar to *S. galeopsidis*, proves genetically very distinct, although these taxa can barely be distinguished by their ITS sequence (99.5 %). Several house-keeping genes do allow an easy identification of these species.

***Septoria heraclei*** (Lib.) Desm., Pl. crypt. Fr., Fasc. 11, no 534. 1831. Fig. 21.

*Basionym*: *Ascochyta heraclei* Lib., Pl. crypt. Ard., Cent. 1: no. 51. 1830.

≡ *Cylindrosporium heraclei* (Lib.) Höhn., Sber. Akad. Wiss. Wien, Math.-naturw. Kl. 115, I: 378. 1906 [non Oudem. 1873, nec Ellis & Everh. 1888].

≡ *Phloeospora heraclei* (Lib.) Petr., Annls mycol. 17: 71. 1919 [non (Lib.) Maire, Bull. Soc. Mycol. France 46: 241. 1930].

≡ *Cylindrosporium umbelliferarum* Wehm., Mycologia 39: 475. 1947. nom. nov.

= *Septoria heraclei-palmati* Maire, Bull. Soc. Mycol. France 21: 167. 1905.

*Description in planta*: *Symptoms* leaf spots numerous but small, irregular in outline, best visible on the upper side of the leaf, initially yellowish or ochreous, later becoming pale to dark brown, in places white due to loosening of the epidermis. *Conidiomata* pseudopycnidial, hypophyllous, one, rarely up to three in each

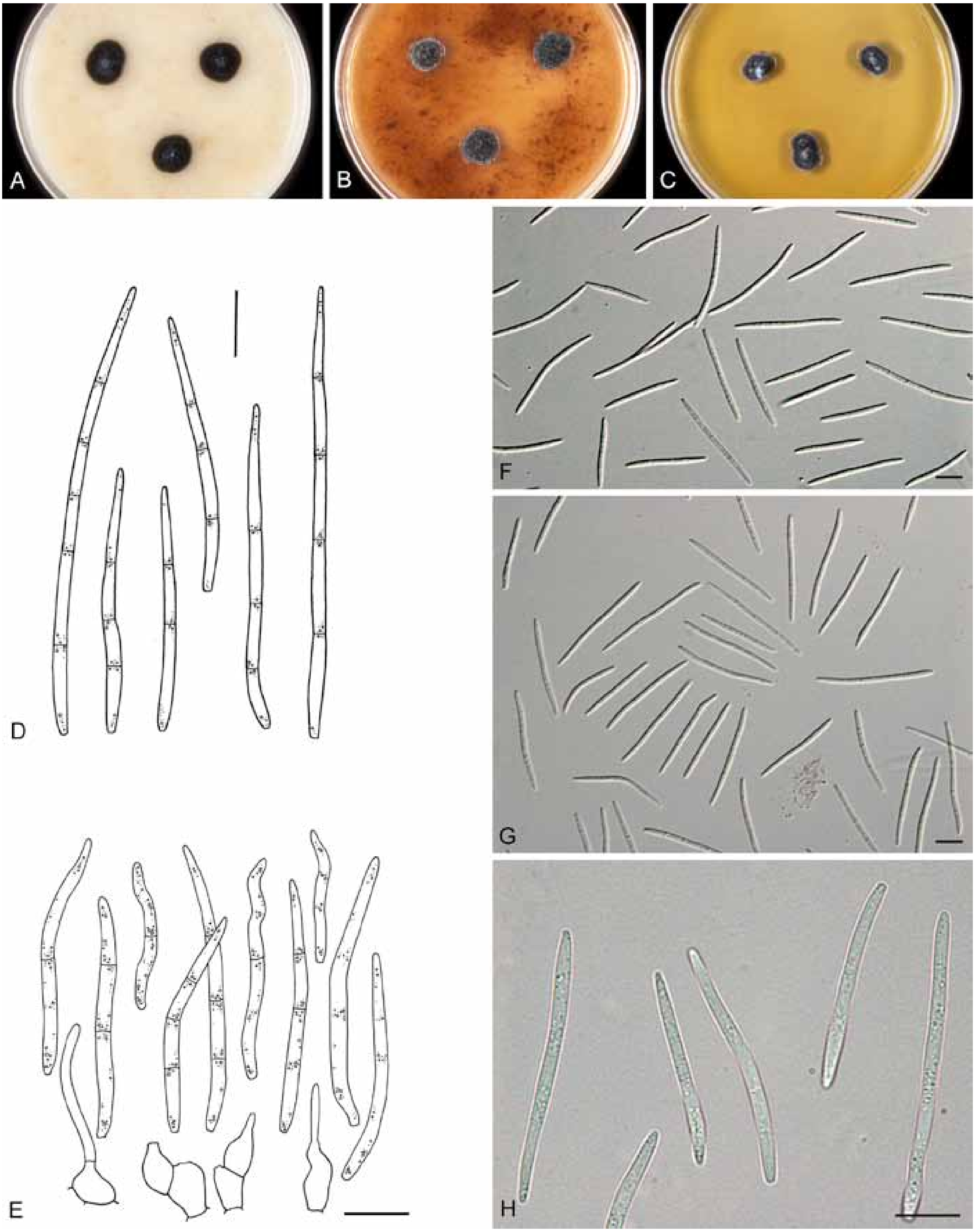


**Fig. 20.** *Septoria galeopsidis*, CBS 102314. A–C. Colonies (15 ºC, nUV). A. On OA. B. On CHA. C. On MEA. D. Conidia on OA. E. Conidia and conidiogenous cells *in planta* (CBS H-21195). F–H. Conidia on OA (CBS 123744). Scale bars = 10 µm.

leaf spot, lenticular, immersed, the upper wall rupturing in an early stage and conidial masses breaking through the leaf epidermis, pale brown, 115–200 µm diam; *ostiolum* absent; *conidiomatal wall* about 15–28 µm thick, composed of an outer layer of pale brown angular cells, 5–10 µm diam with somewhat thickened walls, and an inner layer of thin-walled, pale yellow angular to globose cells, 4.5–8 µm diam. *Conidiogenous cells* hyaline, discrete, rarely integrated in 1-septate conidiophores, cylindrical, or broadly ampulliform, holoblastic, proliferating percurrently one to several times with distinct annellations, sometimes also sympodially,

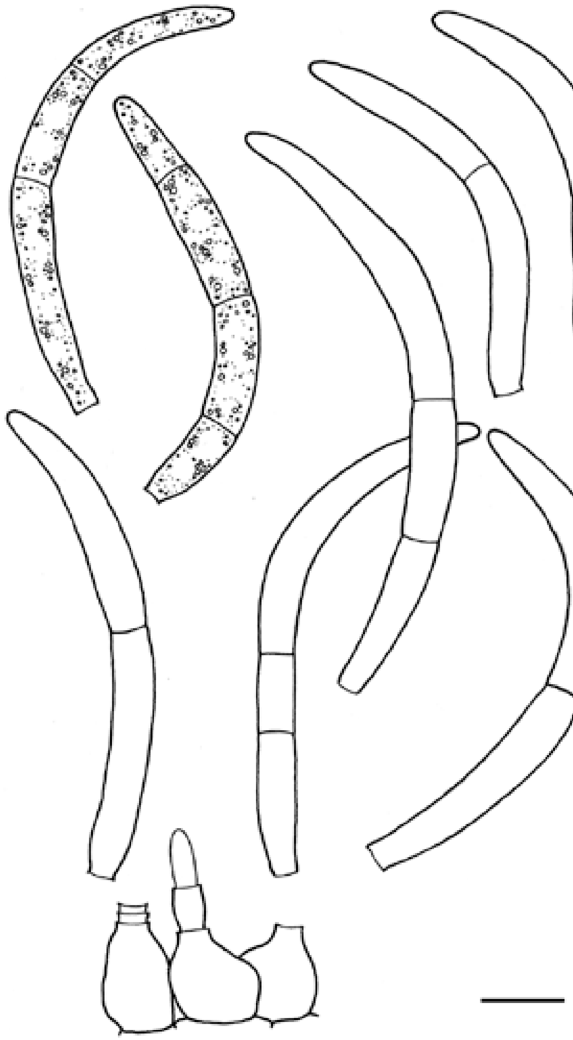

**Fig. 21.** *Septoria heraclei*, conidia and conidiogenous cells *in planta* (CBS H-21224). Scale bars = 10 µm.

10–25 × 5–7(–8) µm. *Conidia* cylindrical, usually strongly curved, attenuated gradually to a blunt to somewhat pointed apex, attenuated gradually, or more abruptly just above the broadly truncate base, (0–)1–2(–4)-septate, not or indistinctly constricted around the septa, hyaline, contents with numerous small oil-droplets and granular material in each cell in the living state, with amorphous granular contents in the rehydrated state, 40–55(–70) × 4–6 µm (living; rehydrated, 3–5 µm wide).

*Description in vitro*: Several attempts were made to isolate this species but unfortunately no conidia survived after germination.

*Hosts*: *Heracleum* spp.

*Material examined*: **Austria**, Tirol, Ötztal, Ötz near Habichen, on living leaves of *Heracleum sphondylium*, 24 July 2000, G. Verkley 1002, CBS H-21186. **Netherlands**, Prov. Limburg, Gulpen, near Stokhem, on living leaves of *H. sphondylium*, 28 June 2000, G. Verkley 957, CBS H-21224; same substr., Prov. Limburg, upper edge of Savelsbos, G. Verkley 959, CBS H-21225.

*Notes*: The conidia of this fungus are much wider than in most other *Septoria* species on *Apiaceae*. Jørstad (1965) reported conidia 35–57 × 3–5 µm, usually with 1 septum. Vanev *et al.* (1997) observed conidia up to 85 µm long, and 1.8–3.5 µm wide. *Septoria heraclei-palmati* was originally described from *Heracleum palmatum* in Greece, with 1-septate conidia, 50–70 × 3 µm. Jørstad (1965) already considered this name as a synonym of *S. heraclei*. Other authors have mostly accepted *S. heracleicola* as a further *Septoria* species on *Heracleum*, describing the conidia as continuous and ranging roughly in size 20–40 × 1–2 µm (Radulescu *et al.* 1973, Teterevnikova-Babayan 1987, Vanev *et al.* 1997). Four further *Septoria* and two *Rhabdospora* species have been described in the literature based on material found on various members of the genus *Heracleum*, all of which according to their original descriptions have conidia more or less within this range, so with much narrower conidia than *S. heraclei*.

***Septoria hypochoeridis*** Petrov, Materialy po mikol. i fitopat. Rossii (Leningrad) 6 (1): 55. 1927. Fig. 22.

*Description in planta*: *Symptoms* leaf spots scattered, 2–5 mm diam, definite, circular, hologenous, grey to white in the centre, surrounded by a slightly elevated, dark reddish purple or black zone. *Conidiomata* pycnidial, hypophyllous, one to a few in each leaf spot, (sub)globose, immersed, dark brown, 60–95 µm diam; *ostiolum* central, circular, 15–28 µm diam, surrounded by darker cells; *conidiomatal wall* about 10–20 µm thick, composed of an outer layer isodiametric or more irregular cells, 5–10 µm diam, with somewhat thickened, pale brown walls, and an inner layer of thin-walled, hyaline angular to globose cells, 4.5–7 µm diam. *Conidiogenous cells* hyaline, discrete, cylindrical, or broadly ampulliform, holoblastic, proliferating sympodially, percurrent proliferation not observed, 8–15 × 3.5–4(–5.5) µm. *Conidia* filiform, straight to slightly curved, attenuated gradually to a somewhat pointed apex, or more abruptly just above the broadly truncate base, 0–1(–2)-septate, not constricted at the septum, hyaline, contents with granular material in the rehydrated state, 15–24 × 1–1.5 µm (rehydrated). *Sexual morph* unknown.

*Description in vitro*: No cultures could be obtained. Conidia placed on MEA and OA died shortly after germination.

*Hosts*: *Hypochoeris radicata* and other *Hypochoeris* spp.

*Material examined*: **New Zealand**, North Island, Taupo distr., Tongariro Nat. Park, Taurewa, along road 47, on decaying leaf base of *Hypochoeris radicata*, 25 Jan. 2003, G. Verkley 1871, CBS H-21234.

*Additional material examined*: **New Zealand**, North Island, Taupo distr., Lake Taupo, shoreline E of Motutaiko Island, on living leaves of *Crepis capillaris*, 25 Jan. 2003, G. Verkley 1870, CBS H-21235.

*Notes*: The material on *Hypochoeris radicata* from New Zealand agrees well with the original description and drawing of *Septoria hypochoeridis*; conidia are reported as continuous to 1-septate, 19–22 × 1.5 µm. According to Teterevnikova-Babayan (1987), the conidia of this species can be somewhat larger, 20–25 × 1.5–2 µm, and *Hypochoeris grandiflora* is also infected. *Rhabdospora hypochoeridis* was described from dead stems of *H. radicata* in Germany, with curved conidia, 16–30 × 0.6–1 µm, which, according to Priest (2006), is suggestive of a *Phomopsis* with β-conidia rather than a *Septoria*. Another species ocurring on this host and other *Asteraceae* is *Septoria lagenophorae*, which occurs in association with *Puccinia* spp. and other fungi (Priest 2006). This fungus can be distinguished from *S. hypochoeridis* by 1–2-septate conidia, 15–32 µm long, and conidiogenous cells which are not proliferating sympodially but produce successive conidia enteroblastically at the same level through a narrow opening (Priest 2006), so appearing phialidic.

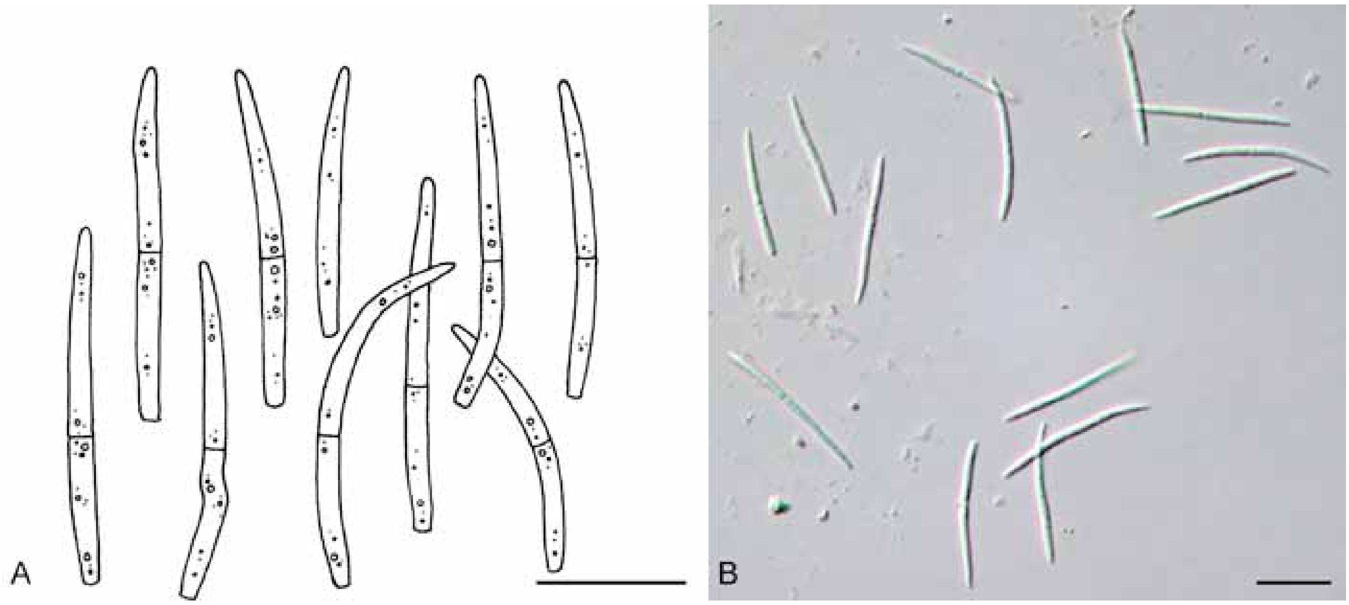


**Fig. 22.** *Septoria hypochoeridis*, CBS H-21234. A, B. Conidia *in planta*. Scale bars = 10 µm.

The collection on *Crepis capillaris* studied here may also belong to *S. hypochoeridis*, but no earlier reports from the host genus *Crepis* have been documented. This material agrees in all morphological characters with the collection on *Hypochoeris*, but the conidia lack septa. It is certainly morphologically different from *Septoria crepidis*, which produces much larger, mostly 3-septate conidia [22–55 × 1.5–2(–2.5) cf. Shin & Sameva 2004]. The *S. crepidis* strains CBS 128608 (= KACC 42396), 128619 (= KACC 43092) and 131895 (= CPC 12539) isolated from *Crepis japonica* (syn. *Youngia japonica*) in South Korea, group with CBS 128650, *Septoria* sp. (originally identified as *S. taraxaci*), but by lack of cultures and molecular data for *S. hypochoeridis* the phylogenetic relationship with *S. crepidis* and allied *Septoria* remains to be resolved.

***Septoria lactucae*** Pass., Atti Soc. crittog. ital. 2: 34. 1879 [non Peck, Bot. Gaz. 4: 170. 1879. Later homonym, nom. illeg. Art. 53]. Fig. 23.

*Description in vitro*: *Colonies* on OA 8–9 mm diam in 2 wk, with an even to undulating, colourless margin; colonies spreading to restricted, immersed mycelium pale luteous, without aerial mycelium, conidiomata developing immersed and on the agar surface, mostly in the centre and in radiating rows, conidiomata releasing milky white to rosy-buff conidial masses; reverse hazel with a tinge of ochreous. *Colonies* on MEA 4.5–6 mm diam in 2 wk, with a minutely ruffled, buff margin; colonies restricted, irregularly pustulate, the surface almost black, with low and weakly developed, finely felted, white to grey aerial mycelium but also glabrous areas occur; reverse chestnut to brown-vinaceous. No sporulation observed.

*Conidia* (OA) filiform to cylindrical, weakly to strongly curved, attenuated gradually towards the relatively broadly, more rarely narrowly rounded apex, attenuated gradually or more abruptly to a truncate base, hyaline, (0–)1–3-septate, contents granular and sometimes also with minute oil-droplets, (22–)28–38.5(–46) × 2–2.5 µm (living). Sexual morph unknown.

*Hosts*: *Lactuca sativa* and *L. serriola*.

*Material examined*: **Germany**, Potsdam, on leaf of *Lactuca sativa*, 20 Nov. 1958, G. Sörgel 628, living culture CBS 352.58. **Netherlands**, on seed of *L. sativa*, Sep. 2000, P. Grooteman *s.n.*, living culture CBS 108943.

*Notes*: *Septoria lactucae* is the oldest name described in *Septoria* from the host *Lactuca sativa*. Three others have been described from lettuce (including two later homonyms), and another eight from other species of the genus *Lactuca*. Symptoms of the minor leaf spot disease of lettuce were described by Punithalingam & Holiday (1972). They describe the conidia as 1–2(–3)-septate, 25–40 × 1.5–2 µm. Muthumary (1999) examined the type and described the conidia as fusiform, straight to slightly curved, narrowed at the tip, truncate at the base, 1–3 septate, 32–52 (av. 35) × 2–2.5 µm. According to Jørstad (1965), conidia of *S. lactucae* are 19–48 × 1.5–2 µm with up to 2 septa, while Priest (2006) describes them as 1–3-septate, 22–33(–36) × 2–2.5(–3) µm. CBS 128757 (KACC 43221) isolated from *Sonchus asper* in South Korea, and identified as *Septoria sonchi*, is very closely related and groups in a cluster with 100 % bootstrap support with the strains of *S. lactucae* (Fig. 2).

***Septoria lamiicola*** Sacc., Syll. Fung. 3: 358. 1884. nom. nov. pro *S. lamii* Sacc., Michelia 1: 180. 1878. Fig. 24.

≡ *Septoria heterochroa* Roberge ex Desm. f. *lamii* Desm., Annls Sci. Nat., sér. 3, Bot. 8: 22. 1847.
= *Septoria lamii* Westend., in Bellynck, Bull. Acad. Roy. Sci. Belgique 19: 63. 1852.
= *Septoria lamii* Pass., in Thüm., Mycoth. univ., Cent. 12, no 1183. 1878; Atti Soc. crittog. ital. 2: 37. 1879.

*Description in planta*: *Symptoms* leaf spots circular to angular, white to pale brown, surrounded by a dark brown border. *Conidiomata* pycnidial, epiphyllous, several in each leaf spot, globose to subglobose, dark brown, immersed to semi-immersed, 65–100 µm diam; *ostiolum* central, initially circular, 20–35 µm wide, later up to 50 µm wide, surrounding cells concolorous or somewhat darker; *conidiomatal wall* 12–25 µm thick, composed of *textura angularis* without distinctly differentiated layers, the cells 3.5–8 µm diam, the outer cells with brown, somewhat thickened walls, the inner cells with hyaline and thinner walls. *Conidiogenous cells* hyaline, narrowly or broadly ampulliform with a relatively narrow

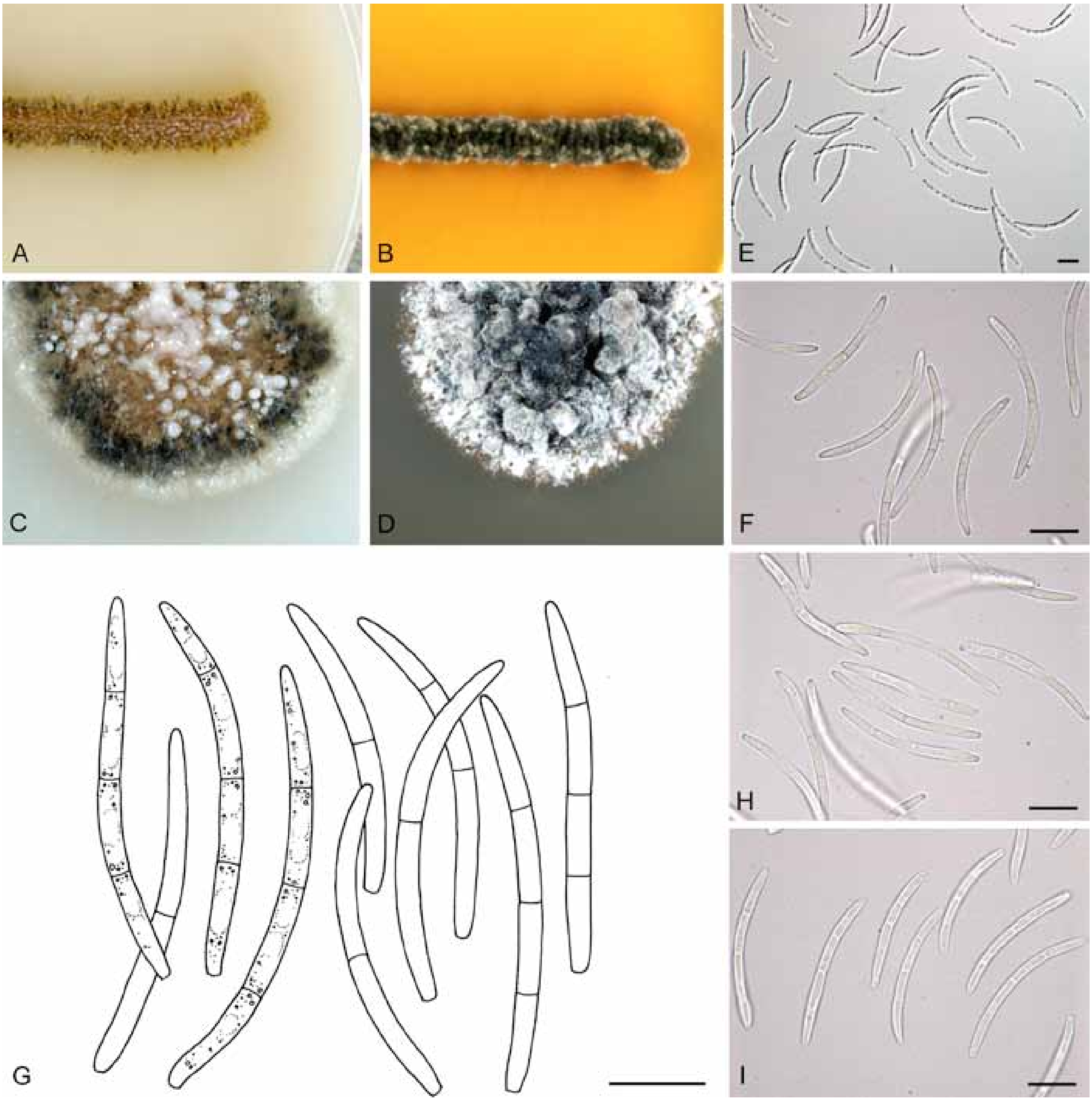


**Fig. 23.** *Septoria lactucae*. A–D. Colonies CBS 108943 (15 °C, nUV). A. On OA. B. On MEA. C. Colony margin on OA. D. Colony margin on MEA. E–I. Conidia on OA (CBS 108943). Scale bars = 10 µm.

neck, holoblastic, proliferating sympodially, and towards the apex often also percurrently 1–many times with indistinct annellations, 5–10(–12) × 3.5–4(–5) µm. *Conidia* filiform to filiform-cylindrical, straight or slightly curved, rarely flexuous, with a rounded or somewhat pointed apex, attenuated towards the narrowly truncate base, (0–)3(–5)-septate, not constricted around the septa, hyaline, contents with several minute oil-droplets and granular material in each cell in the living state, with inconspicuous oil-droplets and granular contents in the rehydrated state, (26–)35–50(–54) × 1.5–2.5(–3) µm (living; rehydrated, 1–2 µm wide; V1032, rehydrated, 33–52 × 1.5–2). *Sexual morph* unknown.

*Description in vitro*: *Colonies* on OA 8–14 mm diam in 2 wk (40–45 mm in 6 wk), with an even, glabrous, colourless margin; colonies plane, immersed mycelium colourless to pale primrose or buff, later becoming homogeneously dark herbage green, soon appearing darker by numerous immersed and superficial pycnidial conidiomata, that release dirty white to rosy-buff conidial slime; aerial mycelium absent, only developing in the centre after several wk as a sharply delimited, dense, white, woolly floccose mat; reverse buff at the margin, inwards dark olivaceous-grey. *Colonies* on CMA 4–8 mm diam in 2 wk (20–27 mm in 6 wk), with an even, glabrous margin; as on OA but immersed mycelium more honey to pale luteous throughout, later becoming more greenish, the pycnidial conidiomata as on OA, but in more regular concentric rings, releasing rosy-buff, later salmon conidial slime. *Colonies* on MEA 7–9 mm diam in 2 wk (28–33 mm in 6 wk), with an even (later undulating), glabrous, buff to honey margin; colonies pustulate to almost hemispherical, immersed mycelium rather dark, locally covered by woolly to felty white aerial mycelium; mostly composed of spherical conidiomatal

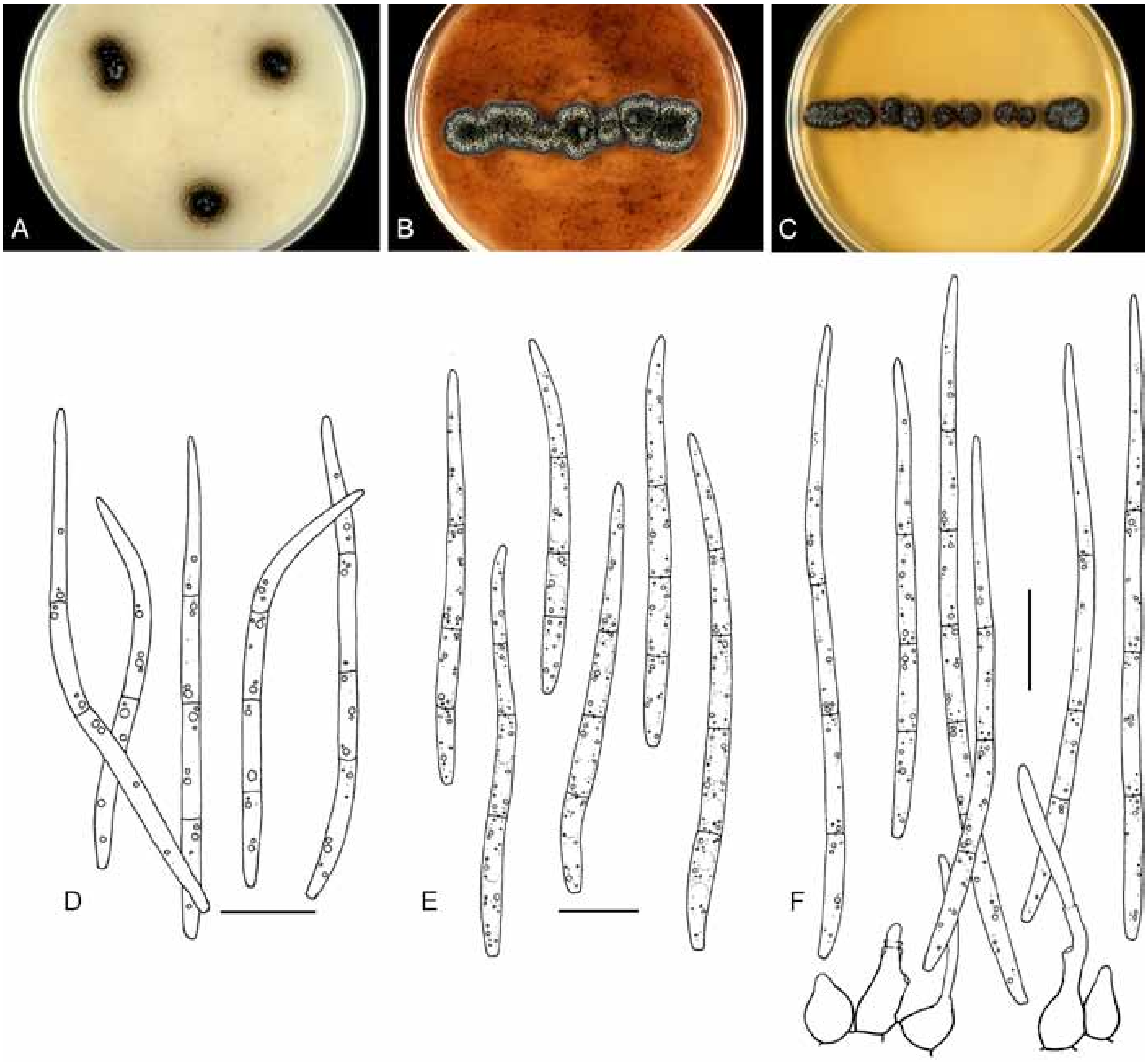


**Fig. 24.** *Septoria lamiicola*, CBS 102329. A–C. Colonies (15 °C, nUV). A. On OA. B. On CHA. C. On MEA. D. Conidia *in planta* (CBS H-21181). E. Ibid. (CBS H-21216). F. Conidia and conidiogenous cells on OA (CBS 102380). Scale bars = 10 µm.

initials, superficial mature conidiomata releasing a dirty white, later buff conidial slime; reverse dark brick in the centre, near the margin cinnamon to honey. *Colonies* on CHA 8–14 mm diam in 2 wk (35–42 mm in 6 wk), with an even, but later irregular, buff margin covered by a diffuse, felty white aerial mycelium; further as on MEA, but the colony surface less elevated, and more homogeneously covered by diffuse, felty, white aerial mycelium; conidial slime abundantly produced, first milky white, later dirty honey; reverse in the centre blood colour, dark brick at the margin.

*Conidiomata* pycnidial, first olivaceous, then almost black, glabrous, 150–450 µm diam, with 1–5 ostioli placed on short papillae or more elongated necks up to 350 µm long; *conidiogenous cells* as *in planta*, proliferating sympodially and mostly also percurrently with distinct annellations, 8–16 × 3–8 µm; *conidia* cylindrical, straight or slightly curved, tapering to a rounded apex, lower part slightly attenuated into a broad truncate base, (0–)1–5-septate, not constricted around the septa, hyaline, with several oil-droplets and minute granular material in each cell, (34–)50–65(–70) × 2–3 µm.

*Hosts*: *Lamium album*, *L. maculatum*, *L. purpureum* and several other *Lamium* spp.

*Material examined*: **Austria**, Tirol, Ötztal, Sulztal, Gries, alt. 1570 m, on living leaves of *Lamium album*, 1 Aug. 2000, G. Verkley 1032, CBS H-21181, living cultures CBS 109112, 109113. **Czech Republic**, Moravia, Pavlov, forest around ruin, on living leaves of *Lamium* sp., 18 Sep. 2008, G. Verkley 6020, CBS H-21251, living cultures CBS 123882, 123883, and 6021, CBS H-21252, living culture CBS 123884. **Netherlands**, prov. Limburg, St. Jansberg near Plasmolen, on living leaves of *L. album*, 9 Sep. 1999, G. Verkley 925, CBS H-21207, living cultures CBS 102328, 102329; prov. Gelderland, Millingen aan den Rijn, Millingerwaard, on living leaves of *L. album*, 6 Oct. 1999, G. Verkley 936, CBS H-21216, living cultures CBS 102379, 102380.

*Notes*: According to Jørstad (1965), conidia of *S. lamiicola* are 3-septate, 24–60 × 1–2 µm, while Teterevnikova-Babayan (1987) reported 35–50 × 0.75–1.5 µm from seven *Lamium* species. For the current study, only fresh material on *Lamium album* was available. Jørstad (1965) mentioned the resemblance of the conidia with those in *S. galeopsidis*, but also noted a difference in the wall thickness of the pycnidia, which we did not observe. A much more profound difference is seen between cultures of the two species, with colonies of *S. galeopsidis* on OA being opaque and dark olivaceous-black even at the margin, while colonies of *S. lamiicola* are more translucent yellowish to ochreous, becoming darker only due to the formation of pycnidia. Priest (2006) pointed towards differences in conidial width and conidiogenesis between *S. lamiicola* and *S. galeopsidis*, but having compared both species morphologically *in planta* and *in vitro*, we conclude that these species cannot be distinguished using these criteria. These two species are, however, readily distinguished by DNA sequence data, and the multilocus phylogeny provides evidence for a close relationship with *S. matricariae* (CBS 109000, CBS 109001), while other *Septoria* occurring on the same plant family as *S. lamiicola* (*Lamiaceae*) are all much more distant (Fig. 2). The Austrian and Dutch collections of *S. lamiicola* on *L. album* are sufficiently homogenous to consider them conspecific.

***Septoria leucanthemi*** Sacc. & Speg., in Saccardo, Michelia 1: 191. 1878. Fig. 25.

≡ *Rhabdospora leucanthemi* (Sacc. & Speg.) Petr., Sydowia 11: 351. 1957.

For addditional synonyms see Punithalingam (1967b).

*Description in planta*: *Symptoms* leaf spots hologenous or epigenous, scattered, circular to irregular, pale to dull brown throughout or with whitish central area, indefinite with concentric zones or delimited by a slightly darker margin. *Conidiomata* pycnidial, predominantly epiphyllous, numerous scattered in each leaf spot, subglobose to globose, brown to black, semi-immersed, 130–220(–240) µm diam; *ostiolum* central, circular, 35–100 µm wide, surrounding cells dark brown and with more thickened walls; *conidiomatal wall* about 8–12.5 µm thick, composed of a homogenous tissue of hyaline, angular cells, 2.5–5 µm diam with relatively thin, hyaline walls, surrounded by a layer of pale to dark brown angular to more irregular cells, 3–6.5 µm diam with slightly thickened walls. *Conidiogenous cells* hyaline, discrete, rarely integrated in 1–2-septate conidiophores, cylindrical to doliiform, or ampulliform, holoblastic, proliferating percurrently with indistinct annellations, or sympodially, 6–18 × 4–6.5(–7.5) µm. *Conidia* filiform to filiform-cylindrical, straight, curved, sometimes slightly flexuous, attenuated gradually to a narrowly rounded to pointed apex, widest near the base, where attenuating abruptly or more gradually into a narrowly truncate base, (5–)6–13-septate (later secondary septa are developed in some cells), not constricted around the septa, hyaline, contents with several minute oil-droplets and granular material in each cell in the living state, with minute oil-droplets and granular contents in the rehydrated state, (67–)80–100(–125) × 2.5–3.0(–3.5) µm (rehydrated). *Sexual morph* unknown.

*Description in vitro*: *Colonies* on OA 6–8(–11) mm diam in 2 wk (11–14(–17) mm in 3 wk), with an even, glabrous, colourless margin; colonies spreading, the surface plane, immersed mycelium pale buff, later more or less rosy-buff; in the centre complexes of pycnidial conidiomata with pale brown or olivaceous walls release masses of pale whitish to buff conidial slime; reverse concolorous, but honey in the centre. *Colonies* on CMA 9–11(–13) mm diam in 2 wk (15–18 mm in 3 wk), as on OA, but with some white diffuse and high aerial hyphae in the centre, and later more elevated in the centre; reverse in the centre hazel to fawn after 3 wk; conidiomata much more numerous and larger than on OA, developing in concentric or random patterns as discrete, large acervuloid (later almost discoid to cupulate) stromata with olivaceous sterile tissues, releasing large masses of pale white to pale buff conidial slime. *Colonies* on MEA 7–10 mm diam in 2 wk (14–17 mm in 3 wk), with an even, colourless, glabrous margin; colonies restricted, irregularly pustulate to hemispherical, the bumpy surface consisting of numerous protruding conidiomatal initials, appearing dark, with sepia, dark brick and cinnamon tinges, aerial mycelium mostly absent, locally dense, pure white and woolly; reverse mostly sepia to fawn or vinaceous buff. Sporulation only observed after about 7 wk. *Colonies* on CHA 7–13 mm diam in 2 wk (15–20 mm in 3 wk), with an even, glabrous, pale vinaceous buff margin; colonies restricted, irregularly pustulate to conical, the surface bumpy, immersed mycelium honey to hazel, covered by dense to diffuse, pure white, woolly aerial mycelium; conidiomata sparsely developing at the surface after 2 wk, the wall slightly darker than the surrounding hyphae, releasing pale white conidial slime (even after 3 wk); reverse cinnamon in the centre, vinaceous buff or pale ochreous at the margin.

*Conidiomata* and conidiogenous cells as *in planta*. *Conidia* as *in planta*, 5–13(–17)-septate, 70–125(–175) × 3–4 µm (OA).

*Hosts*: Various species of the genera *Chrysanthemum*, *Tagetes*, *Achillea*, *Centaurea* and *Helianthus* (Waddell & Weber 1963, Punithalingam 1967b, c).

*Material examined*: **Austria**, Tirol, Ober Inntal, Samnaun Gruppe, Böderweg on Lazidalm, on living leaves of *Chrysanthemum leucanthemum*, 8 Aug. 2000, G. Verkley 1055, CBS H-21173, living cultures CBS 109090, 109091; Same substr., Tirol, Zanderstal near Spiss, 11 Aug. 2000, G. Verkley 1069, CBS H-21170, living cultures CBS 109083, 109086. **Germany**, Hamburg, on living leaves of *Chr. maximum*, Sep. 1958, R. Schneider *s.n.* CBS H-18111, living culture CBS 353.58 = BBA 8504 = IMI 91322. **New Zealand**, Coromandel distr., Coromandel peninsula, Waikawau, coast along St. Hwy 25, on living leaves of *Chr. leucanthemum*, 22 Jan. 2003, G. Verkley 1826, CBS H-21247; same substr., North Island, Coromandel, Tairua Forest, along roadside of St. Hway 25, near crossing 25A, 23 Jan. 2003, G. Verkley 1842b, CBS H-21243, living culture CBS 113112.

*Notes*: The six strains studied here showed minor differences in morphological characters and DNA sequences, which show highest similarity to sequences of CBS 128621, an isolate originating from *Cirsium setidens* in South Korea, and identified as *S. cirsii* (Fig. 2). *Septoria leucanthemi* is also closely related to a number of other *Septoria* species from *Asteraceae*, such as *S. senecionis* and *S. putrida* (*Senecio* spp.), *S. obesa* (*Chrysanthemum* spp., *Artemisia*) and *S. astericola* (*Aster* sp.). It is confirmed here that *Septoria obesa*, which has been regarded as a synonym of *S. leucanthemi* by Jørstad (1965), should be treated as a separate species (see also the note on *S. obesa*).

***Septoria lycoctoni*** Speg. ex Sacc., Michelia 2 : 167. 1880. Fig. 26.

*Description in planta*: *Symptoms* leaf spots epigenous, numerous, circular to irregular, single or confluent, white to pale greyish, surrounded by an initially red, then dark brown to black and thickened border. *Conidiomata* pycnidial, epiphyllous, inconspicuous, up to a few in each leaf spot, globose to subglobose, brown, immersed, 90–145(–220) µm diam; *ostiolum* central, circular, more or less papillate, 25–55 µm wide; *conidiomatal wall* 17–35 µm thick, composed of *textura angularis*, differentiated layers absent, the cells mostly 3.5–5(–11) µm diam, the outer cells with brown, somewhat thickened walls, the inner cells with thinner, hyaline walls. *Conidiogenous cells* hyaline, cylindrical, or elongated ampulliform with a relatively narrow neck which widens at the top,

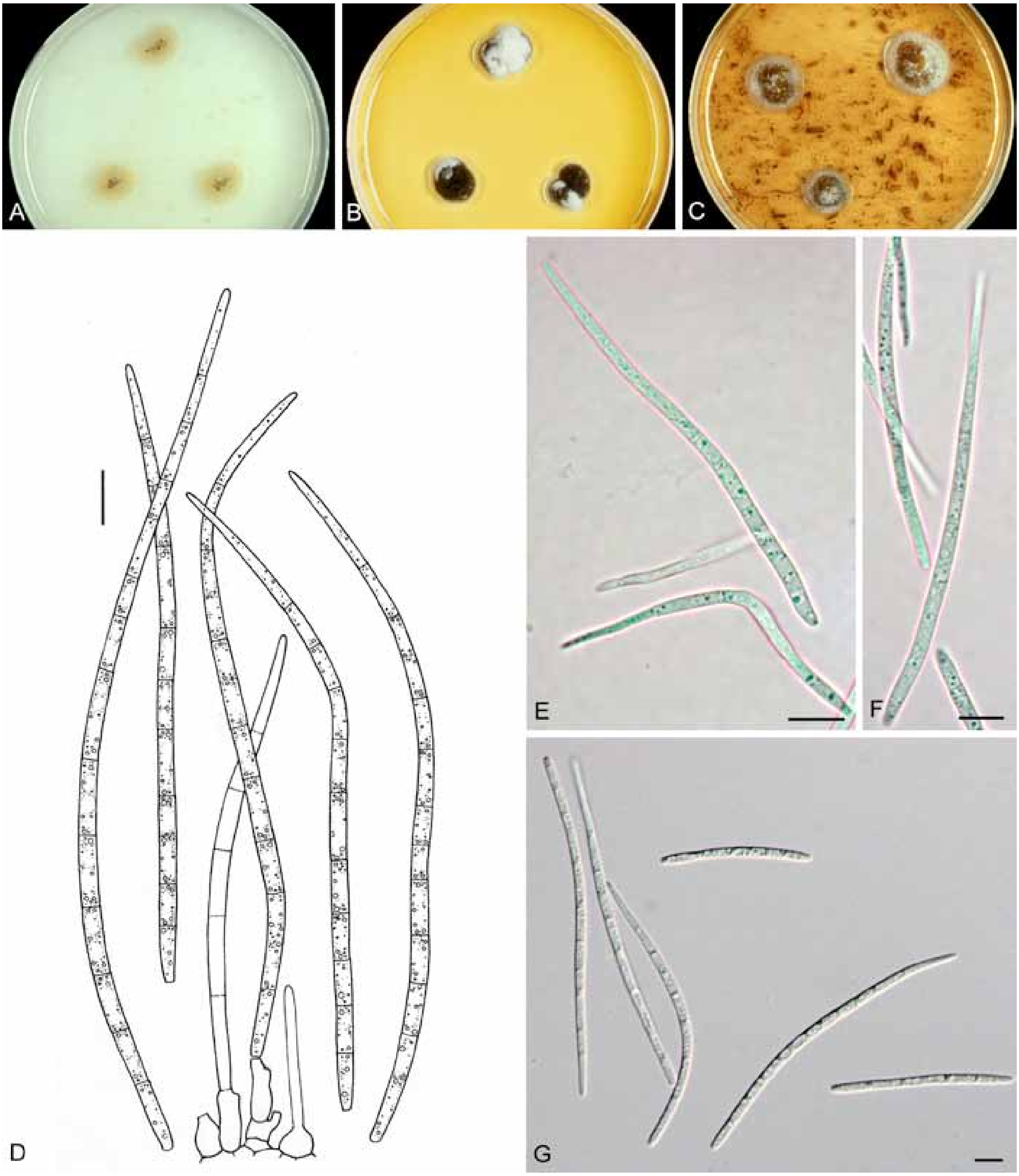


**Fig. 25.** *Septoria leucanthemi*. A–C. Colonies CBS 109090 (15 °C, nUV). A. On OA. B. On MEA. C. On CHA. D. Conidia and conidiogenous cells on OA (CBS 109090). E, F. Conidia *in planta* (CBS H-21243). G. Conidia on MEA (CBS 109090). Scale bars = 10 µm.

hyaline, holoblastic, proliferating sympodially, 7–18 × 3.5–6 µm. *Conidia* filiform, straight, more often curved, sometimes flexuous, gradually attenuated to the pointed apex, more or less attenuated towards the broadly truncate base, (0–)2–5(–6)-septate, not or indistinctly constricted around the septa, hyaline, with several oil-droplets and granular contents in each cell in the rehydrated state, 26–47 × 1.5–2 µm (rehydrated; up to 2.5 µm wide in the living state). *Sexual morph* unknown.

*Description in vitro*: *Colonies* on OA 9–11 mm diam in 2 wk (18–20 mm in 3 wk), with an even, glabrous, colourless margin; immersed mycelium mostly coral to scarlet, the pigment diffusing into the surrounding medium; in the centre black and slightly elevated with mostly superficial, glabrous pycnidia, surrounded by an area with more scattered pycnidia, releasing pale white to pale flesh droplets of conidial slime; aerial mycelium only present in the centre, but well-developed, dense, appressed, woolly, white or greyish, locally with a flesh haze; reverse scarlet to coral, the centre darker, blood

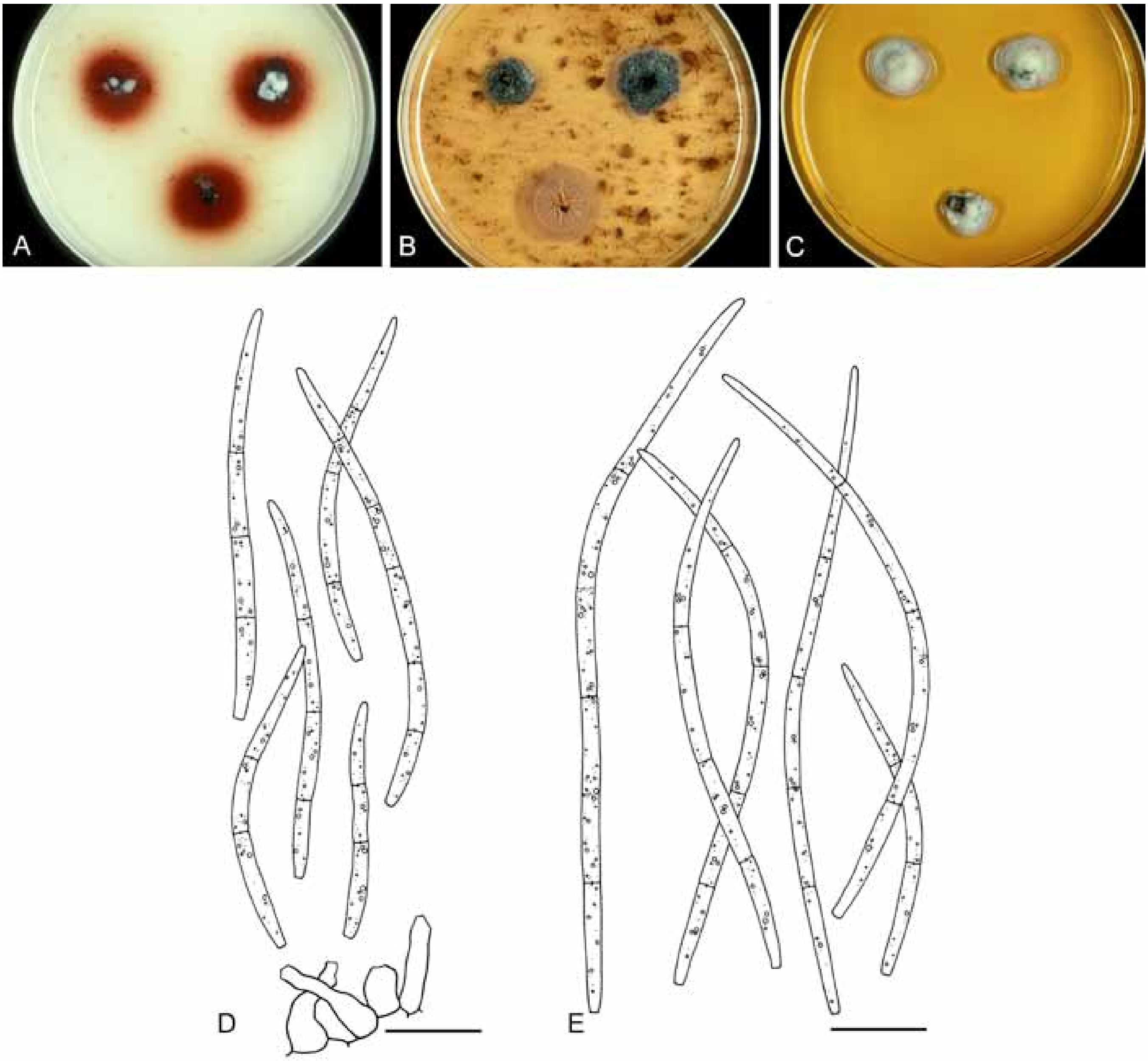


**Fig. 26.** *Septoria lycoctoni*. A–C. Colonies CBS 109089 (15 °C, nUV). A. On OA. B. On CHA. C. On MEA. D. Conidia and conidiogenous cells *in planta* (CBS H-21155). E. Conidia on OA (CBS 109089). Scale bars = 10 µm.

colour. *Colonies* on CMA 9–12 mm diam in 2 wk (17–19 mm in 3 wk), as on OA, but pycnidia more numerous, usually only formed in the centre of the colony. *Colonies* on MEA (3–)5–9 mm diam in 2 wk (13–18 mm in 3 wk), with an irregular margin; colonies restricted, the surface cerebriform to irregularly pustulate, up to 3 mm high, the surface pale brown, later black, at first almost glabrous, or (especially in brighter-coloured faster growing sectors/colonies) already covered by dense mat of pure white to flesh, woolly aerial mycelium, that later covers most of the colony surface; large masses of honey or pale amber conidial slime locally emerging from immersed conidiomata; reverse of the colony either dark brick or luteous to ochreous, paler towards the margin. *Colonies* on CHA 8–13 mm diam in 2 wk (15–19(–22) mm in 3 wk), with an even or undulating, colourless margin mostly hidden under aerial hyphae; immersed mycelium greenish grey, grey-olivaceous to olivaceous-black, throughout covered by well-developed, tufty whitish grey aerial mycelium that later shows a reddish haze; reverse blood colour, but margin paler; in the central part of the colony numerous pycnidia develop, releasing pale whitish to rosy-buff conidial slime; in older colonies the central surface becomes cerebriform and about 3 mm high, much like on MEA.

*Conidiomata* as *in planta*, pycnidial with barely protruding ostioli, which later often grow out to elongated necks up 50–150 µm long; on CMA less differentiated and fairly large, opening by tearing of the upper wall; *conidiogenous cells* as *in planta*, but larger, 9–25 × 3.5–7.5 µm, proliferating sympodially and also percurrently, but annellations on the necks are inconspicuous; *conidia* similar in shape as *in planta* but longer, 3–5(–6)-septate, 30–75 × 1.5–2.5 µm.

*Hosts*: *Aconitum vulparia* (= *A. lycoctoni*), *A. anthora*, *A. conversiflorum* and several other *Aconitum* spp.

*Material examined*: **Austria**, Ober Inntal, Samnaun Gruppe, Lawenalm near Serfaus, alt. 2000 m., on living leaves of *Aconitum vulparia* (syn. *A. lycoctonum*), 8 Aug. 2000, G. Verkley 1053, CBS H-21155, living culture CBS 109089.

*Notes*: In the diagnosis of *S. lycoctoni*, the conidia were described as “indistinctly multiseptate”, measuring 25–35 × 1.5–2 (Saccardo 1884). This fungus was found on *A. lycoctonum* in Italy. Teterevnikova-Babayan (1987) gave conidial size ranges of 25–70 × 1–2 µm for this species, and she included several of the varieties which were described after 1880, viz., var. *sibirica* 1896, var. *macrospora* 1909, var. *anthorae* 1928. Petrak (1957) observed conidia 20–60 (rarely 70 to 80) × 1.5–2 µm in his collection on *Aconitum moldavicum*.

The colonies of *Septoria lycoctoni* and *S. napelli* look very similar on all media tested, although in *S. napelli* more red pigment seems to be produced than in *S. lycoctoni*, and the conidial slime is salmon rather than flesh. The two species can more readily be distinguished from each other by the shape of their conidia. In *S. lycoctoni*, the mature conidia only attenuate towards the apex above the uppermost septum, while in *S. napelli*, the tapering of the conidium walls is visible below the second septum from the top. The difference between the conidia of these species is also clear on the plant. Because the conidia of *S. napelli* are wider, the septa and the attenuations are easier to observe. In the case of *S. lycoctoni* the apical attenuation of conidia is not so clear, which may explain why Petrak (1957), who compared this species also to collections identified as *S. napelli* (but for reasons explained below probably misidentified), circumscribed the conidia of *S. lycoctoni* as not-attenuated.

The strains of *S. napelli* (CBS 109104–109106) originating from *Aconitum napellus* and CBS 109089 of *S. lycoctoni* are very closely related and form a monophyletic group in the multilocus phylogeny (Fig. 2).

***Septoria lysimachiae*** (Lib.) Westend., Bull. Acad. r. Belg., Cl. Sci., Sér. 2, 19: 120. 1852. Fig. 27.
*Basionym*: *Ascochyta lysimachiae* Lib., Pl. Crypt. Ard. Fasc. 3, 252. 1834.

*Description in planta*: *Symptoms* leaf lesions indefinite, usually only a few scattered over the leaf lamina, or a single one, most often developing from the tip to the petiole, greyish to reddish brown. *Conidiomata* pycnidial, epiphyllous, immersed, subglobose to globose, black, 95–120(–165) µm diam; *ostiolum* central, circular, initially 25–35 µm wide, later becoming more irregular and up to 90 µm wide, surrounding cells concolourous; *conidiomatal wall* 10–20 µm thick, composed of an outer layer of angular to irregular cells mostly 4.5–10 µm diam with pale to orange brown walls, and an inner layer of isodiametric, hyaline cells 3–6 µm diam. *Conidiogenous cells* hyaline, discrete, rarely integrated in 1-septate conidiophores, cylindrical, or narrowly to broadly ampulliform, holoblastic, proliferating sympodially, and often also percurrently showing 1–3 indistinct annellations on a neck-like protrusion, 8–15 × 3–5(–6) µm. *Conidia* cylindrical to filiform-cylindrical, slightly to strongly curved, rarely somewhat flexuous, narrowly rounded to pointed at the apex, attenuated gradually or more abruptly towards a narrowly truncate base, (0–)3–5, later with secondary septa dividing the cells, conidia sometimes breaking up into smaller fragments in the cirrhus, not or slightly constricted around the septa, hyaline, containing several large oil-droplets and granular material in the living and rehydrated state, (28–)35–70(–88) × 2.5–3.5(–4) µm (living; rehydrated, 2.0–3 µm wide). *Sexual morph* unknown.

*Description in vitro*: *Colonies* on OA rather variable in growth speed and pigmentation, 3.5–7 mm diam in 1 wk (20–26 mm in 2 wk), with an even, glabrous, colourless margin; colonies spreading, flat,immersed mycelium first mostly buff, then either rosy-buff to pale salmon turning olivaceous or hazel, or long colourless and later becoming olivaceous-black to greenish black; aerial mycelium woolly-floccose, white or greyish, mostly developing only in the centre; reverse olivaceous-black to greenish grey or dark slate blue to black. Conidiomata developing scarcely immersed in the agar, producing small amounts of conidia that are released as rosy-buff droplet. *Colonies* on CMA 2–4 mm diam in 1 wk (15–20 mm in 3 wk), as on OA, but centre of the colony somewhat elevated, and colourlous marginal zone narrow, immersed mycelium becoming more rapidly pigmented with a vinaceous buff tint, in the centre becoming brown-vinaceous; reverse hazel, in the centre almost black. *Colonies* on MEA 3.5–6 mm diam in 1 wk (8–17(–19) mm in 3 wk), with an even to slightly ruffled, buff to rosy-buff, glabrous margin; some strains with a more uneven outline, strongly fimbriate, with faster growing deeply immersed mycelium often extending well beyond the colony margin at the level of the agar surface; colonies spreading, but often distinctly elevated or irregularly pustulate in the centre; immersed mycelium variable in colour, buff, ochreous or brownish, and in the faster growing sectors often with a glaucous haze; aerial mycelium diffuse to dense, pure white, (vinaceous) greyish or brownish, finely felted to woolly; reverse versicoloured, margin and parts of faster growing sectors buff to honey, in other parts darker, hazel to brown-vinaceous, sometimes mostly olivaceous-black. Some strains show a conspicuous halo of diffusing reddish pigment (CBS 108996, 108997). Scarce dark conidiomata beginning to develop in the centre after 1 wk, releasing pale white droplets of conidial slime after about 3 wk. *Colonies* on CHA 2–4(–6) mm diam in 1 wk [18–24(–26) mm in 21 d], with an even or slightly ruffled, glabrous, colourless to buff margin; colonies irregularly pustulate, immersed mycelium olivaceous-black; aerial mycelium soon covering most of the colony, woolly-floccose, smoke grey with an olivaceous haze, locally grey-olivaceous, in slightly faster growing sectors sometimes pure white; reverse mostly brown-vinaceous. Superficial, blackish conidiomata in the centre releasing pale rosy-buff to white masses of conidial slime after 1 wk; reverse mostly blood colour, or fawn and brown-vinaceous in the centre.

*Conidia* (OA) cylindrical, slightly to strongly curved to flexuous, narrowly rounded to somewhat pointed at the apex, attenuated gradually or more abruptly towards a truncate base, mostly 3–7(–11)-septate, including the soon formed secondary septa, cells soon loosing their turgesence and often separating into smaller fragments, in the turgescent state constricted around the septa, hyaline, with many vacuuoles and also containing several large oil-droplets and granular material in the living state and rehydrated state, (30–)40–80–(90) × 2.5–3.5(–4) µm (living; rehydrated NT 2.0–3 µm wide).

*Hosts*: *Lysimachia* spp.

*Material examined*: **Belgium**, near Namur, on leaves of *Lysimachia vulgaris*, Bellynck, **isotype** BR-MYCO 145978-90, also distributed in M. A. Libert, Pl. Crypt. Ard. Fasc. 3, no. 253. **Czech Republic**, Mikulov, on living leaves of *Lysimachia* sp., 15 Sep. 2008, G. Verkley 6004, CBS H-21255, living cultures CBS 123794, 123795. **Netherlands**, Prov. Utrecht, Baarn, De Hooge Vuursche, in the forest, on *L. vulgaris*, 22 June 2000, G. Verkley 955, **epitype designated here** CBS H-21227 “MBT175357”, living cultures ex-epitype CBS 108998, 108999; Prov. Utrecht, Soest, Stadhouderslaan near monument “De Naald”, on living leaves of *L.vulgaris*, 4 Aug. 1999, G. Verkley 903, CBS H-21196, living culture CBS 102315; Prov. Gelderland, Amerongen, Park Kasteel Amerongen, on living leaves of *L. vulgaris*, 11 July 2000, G. Verkley 971, CBS H-21230, living culture CBS 108996, 108997.

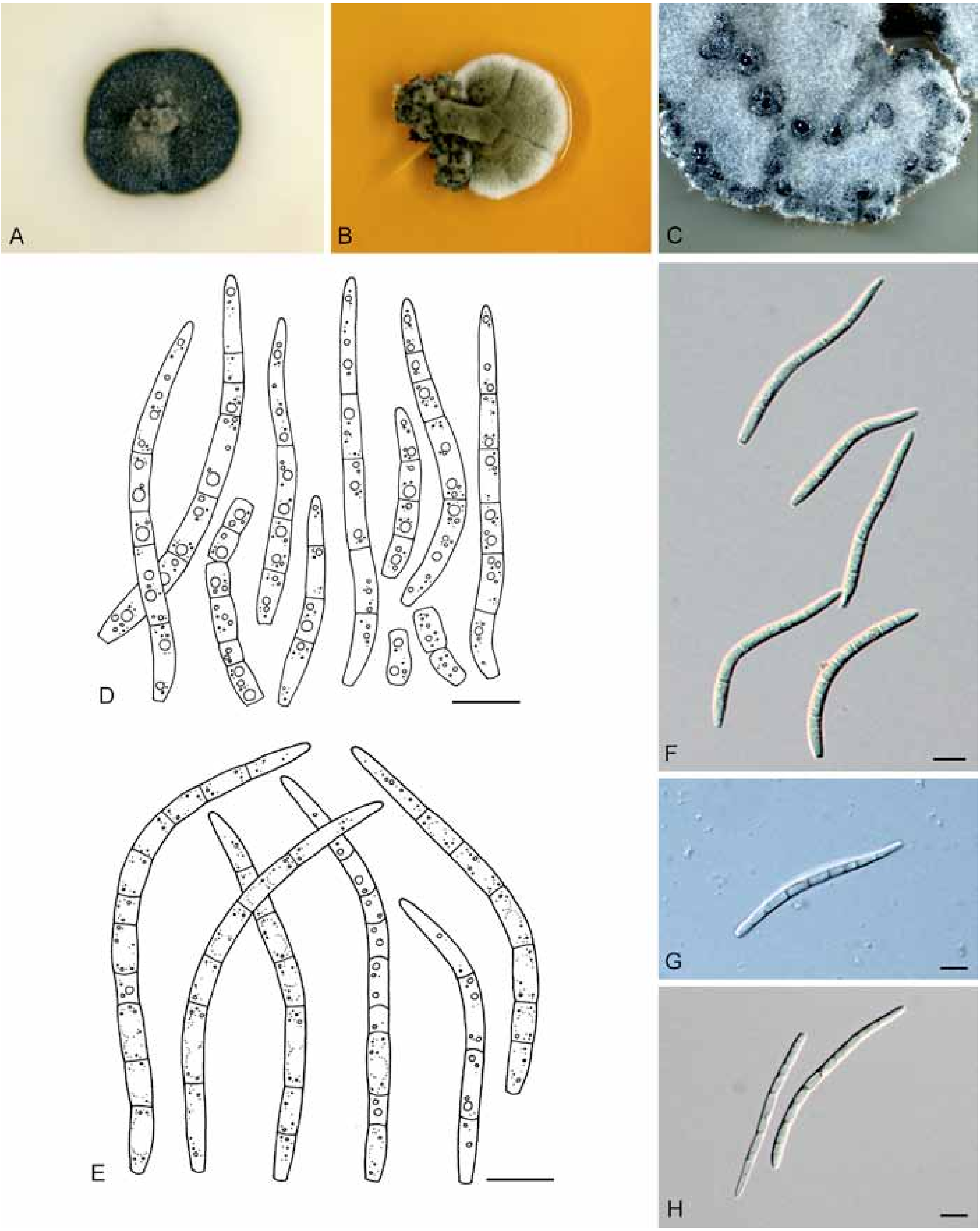


**Fig. 27.** *Septoria lysimachiae*. A–C. Colonies (15 °C, nUV). A. CBS 123794 on OA. B. CBS 108998 on MEA. C. Ibid., colony margin on MEA. D. Conidia *in planta* (CBS H-21196). E. Conidia on OA (CBS 108998). F. Conidia *in planta* (CBS H-21196). G. Conidia on OA (CBS 108998). H. Conidia on OA (CBS 108999). Scale bars = 10 µm.

*Notes*: Shin & Sameva (2003) provided a detailed description of *S. lysimachiae* (conidia 35–80 × 1.5–2.5 µm, 3–7-septate). In the type material from BR the conidia are mostly 3–5-septate, 25–72 × 2.5–3.5 µm, and very similar in shape to those observed in the material that was collected from the field for the present study. The isolates show more variation in colony characters than observed in most other species of *Septoria*, but this phenotypic heterogeneity is neither reflected in the sporulating structures nor in the sequence data obtained. The EF, Btub and RPB2 gene sequences proved 100 % identical among strains originating from the Netherlands

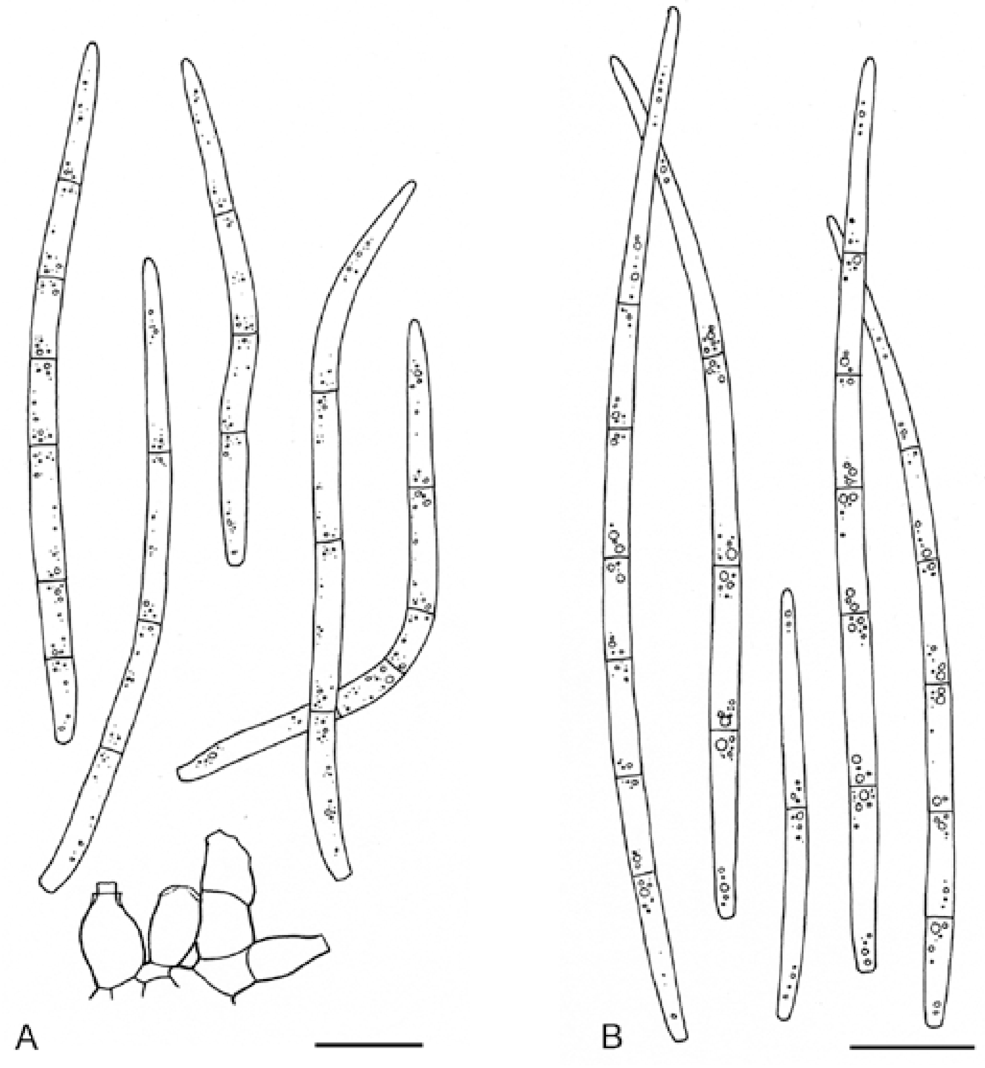


**Fig. 28.** *Septoria matricariae*. A. Conidia and conidiogenous cells *in planta* (CBS H-21228). B. Conidia on OA (CBS 109001). Scale bars = 10 µm.

(CBS 102315, 108998 and 108999) and Czech Republic (CBS 123794, 123795), while differences found between the Dutch and Czech isolates for Cal and Act were only 3 (99.3 % similarity) and 1 bp (99.6 %), respectively. It is concluded therefore that the material studied belongs to a single species. *Septoria saccardoi*, based on material from *Lysimachia vulgaris* in Italy, is characterised by cylindrical, curved, 3-septate conidia, 38–40 × 3.5 µm (Saccardo 1906). Quaedvlieg *et al.* (2013) describe this species in detail based on an isolate originating from of *Lysimachia vulgaris* var. *davuricai* in Korea (CBS 128665 = KACC 43962) and because it is distant to other septoria-like fungi, they propose a new genus name to accommodate it, *Xenoseptoria*. CBS 128758, isolated from *L. clethoroides* in Korea was identified as *S. lysimachiae*, but based on sequence analyses it is a distant fungus belonging in the genus *Sphaerulina*.

***Septoria matricariae*** Hollós, Annls Mus. nat. Hung. 8: 5. 1910 [non Syd. 1921; nec Cejp, Fassatiova & Zavrel, Zpravy 153: 13. 1971; later homonyms]. Fig. 28.

= *S. chamomillae* Andrian., Mikol. i Fitopat. 30: 10. 1996. Nom. nov. pro *S. matricariae* Syd., Annls mycol. 19: 143. 1921; nom. illeg. Art. 53 [non Marchal & Sternon, 1923].

?= *S. chamomillae* Marchal & Sternon, Bull. Soc. r. Bot. Belg. 55: 50. 1922.

*Description in planta*: *Symptoms* lesions indefinite, leaves becoming affected from the top towards base, discolouring to yellow and brown. *Conidiomata* pycnidial, amphigenous, numerous, more or less evenly dispersed over the affected area, globose to subglobose, dark brown to black, immersed, 75–125(–150) µm diam; *ostiolum* central, circular, often papillate, breaking through the leaf epidermis, 25–43(–50) µm wide, surrounding cells concolorous or somewhat darker; *conidiomatal wall* 10–20 µm thick, composed of *textura angularis* without distinctly differentiated layers, the cells 2–6 µm diam, the outer cells with yellowish brown, thickened walls, the inner cells with hyaline, also relatively thick walls; *Conidiogenous cells* hyaline, discrete or integrated in 1–2-septate conidiophores up to 17.5 µm long, doliiform, narrowly to broadly ampulliform, holoblastic, proliferating sympodially and/or also percurrently with one or two indistinct annellations, 3.5–10 × 3–4.5(–5.5) µm. *Conidia* filiform, straight, curved or slightly flexuous, attenuated gradually towards a relatively narrowly rounded to pointed apex, barely attenuated towards the broadly truncate base, indistinctly (1–)2–3(–6)-septate, not or indistinctly constricted around septa, hyaline, contents with a few minute oil-droplets and granular material in each cell in the living state, with inconspicuous oil-droplets and granular contents in the rehydrated state, 41–58 × 2–3 µm (living; rehydrated, 1.5–2.4 µm wide). *Sexual morph* unknown.

*Description in vitro*: *Colonies* on OA 19–24 mm diam in 3 wk (44–48 mm in 6 wk), with an even, glabrous, colourless margin; colonies spreading, the surface plane, immersed mycelium olivaceous-black to very dark dull green, with numerous dark, radiating hyphae, almost entirely glabrous, few tufts of greyish aerial mycelium in the centre; numerous scattered single or complex pycnidial conidiomata developed already after 1 wk, with a single ostiole or several papillate or rostrate openings, from which pale rosy-buff droplets of conidial slime are released; reverse concolourous. *Colonies* on CMA 16–18(–20) mm diam in 3 wk (38–50 mm in 6 wk), as on OA. *Colonies* on MEA 9–12(–14) mm diam in 3 wk (27–39 mm in 6 wk), with an even to slightly ruffled buff margin; colonies restricted, conical and up to 3 mm high after 3 wk, immersed mycelium near the margin grey-olivaceous, but most of the colony surface iron grey to greenish black, the outer areas mostly covered by a low but dense, finely felted, grey aerial mycelium, the centre almost glabrous; superficial semi-immersed conidiomata releasing pale whitish droplets of conidial slime after 2–3 wk; reverse mostly dark slate blue with olivaceous areas. *Colonies* on CHA 16–22 mm diam in 3 wk (39–46 mm in 6 wk), as on MEA, but conidiomata more numerous, releasing pale whitish to pale rosy-buff droplets or cirrhi of conidial slime, and reverse with a brown-vinaceous tinge.

*Conidiomata* as *in planta*, pycnidial with a single ostiolum, dark brown to black, rarely merged into complex fruitbodies; *conidiogenous cells* as *in planta*, but larger and more often integrated in 1–3-septate conidiophores, 10–15(–23) × 3–6(–7) µm; *conidia* as *in planta*, but longer, 36–78(–90) × (1.6–)1.7–2.2 µm, contents several oil-droplets in each cell.

*Hosts*: *Matricaria* spp.

*Material examined*: **Netherlands**, prov. Limburg, Zuid-Limburg, along roadside near Savelsbos, on living leaves of *Matricaria discoidea* (= *M. matricarioides*), 28 June 2000, G. Verkley 960, CBS H-21228, living cultures CBS 109000, 109001. **Romania**, Suceava, Siret, on leaves of *M. discoidea*, 7 July 1969, distributed in Contantinescu & Negrean, Herb. mycol. Romanicum Fasc. 40, no. 199, CBS H-18115.

*Notes*: The phylogenetic analyses indicate that *S. matricariae* is closest to *S. lamiicola*, yet rather distant from other *Septoria* occurring on *Asteraceae*. The indefinite lesions caused by this species are reminiscent of those developed by *S. stellariae* on *Stellaria media*. The leaves seem to whither more rapidly and pycnidia develop soon after discolouration of the leaf tissues starts. Stems are not affected. In the original diagnosis of *S. matricariae*, based on material from *Matricaria discoidea* in Hungary, the conidia are described as continuous and 40–60 × 2–2.5 µm. The Dutch and also the Romanian material studied here contain conidia with mostly 1–3 septa, but otherwise agree well with Hollós' description of the type. According to Radulescu *et al.* (1973) the conidia in material from the same host plant are also continuous, measuring 25–50 × 1.5–2 µm. As in several other *Septoria* spp., the septa in *S. matricariae* are not easy to observe, and Hollós and others may have overlooked them.

Sydow described a *Septoria* under the same name from *Matricaria chamomilla* in Germany with multiseptate conidia 30–60 × 1–1.5 µm. The name he proposed was illegitimate because it is a later homonym of *S. matricariae* Hollós, as is also *S. matricariae* Cejp *et al.*. *Septoria chamomillae* was also described from *M. chamomillae* in Belgium and has 3–5-septate conidia 35–52 × 1–2 µm. Although we have not seen the types of either of these names, we consider them tentatively as synonyms of *S. matricariae*.

***Septoria melissae*** Desm., Annls Sci. Nat., sér. 3, Bot., 20: 87. 1853. Fig. 29.

≡ *Phloeospora melissae* (Desm.) Parisi, Bull. Bot. R. Univ. Napoli 6: 292. 1921.

*Description in vitro*: *Colonies* on OA 12–13 mm diam in 2 wk, with an even to slightly ruffled, mostly colourless margin; colonies restricted to spreading, somewhat elevated in the centre, immersed mycelium greenish black, with greenish hyphal strands radiating into or even beyond the colourless margin, the surface mostly glabrous or provided with very diffuse, finely felted, grey aerial hyphae, the elevations in the centre bearing tufts of more well-developed, grey aerial mycelium; conidiomata developing mostly in the centre immersed or on the agar surface, releasing pale rosy to rosy-buff conidial slime. No diffusing pigment observed. *Colonies* on MEA 5–7(–9) mm diam in 2 wk, with a slightly ruffled margin; colonies restricted, pustulate with cerebriform elevations in the centre, the surface black, covered by a diffuse to dense mat of finely felted, mostly grey aerial mycelium; reverse very dark brown-vinaceous. Conidiomata sparsely developing on the colony surface, releasing dirty reddish brown conidial slime. A very faint pigment is visible around the colony.

*Conidiogenous cells* (OA) globose to ampulliform, holoblastic, hyaline, discrete or integrated in 1(–2)-septate conidiophores, proliferating sympodially, percurrent proliferation not observed, 4–10 × 3–5 µm. *Conidia* filiform, straight to flexuous, weakly to more strongly curved, attenuated gradually to a narrowly rounded, typically pointed apex, attenuated gradually to a narrowly truncate to somewhat rounded base, hyaline, with fine granular material and minute oil-droplets, (0–)3(–5)-septate, (22–)30–50(–61) × 1.5–2 µm. *Sexual morph* unknown.

*Host*: *Melissa officinalis*.

*Material examined*: **Netherlands**, Baarn, garden Eemnesserweg, on living leaves of *Melissa officinalis*, 11 Sep. 2000, H.A. van der Aa *s.n.* (G. Verkley 1073), CBS H-21169, living cultures CBS 109096, 109097.

*Notes*: This species is the only *Septoria* described from the genus *Melissa*. The type material originates from *Melissa officinalis* in France (not seen). According to the short original diagnosis, *S. melissae* produces conidia 30 × 1.6 µm, and no septa were reported. Radulescu *et al.* (1973) described the conidia as continuous or with 1–3 septa, 25–38 × 1.6 µm. These measurements agree quite well with those given by Teterevnikova-Babayan (1987; 28–38 × 1.5 µm), but Vanev *et al.* (1997) gave a much wider range of measurements, 20.5–58 × 1.5–2.2 µm (septa 2–5). Genetically CBS 109097 is very closely related to *S. galeopsidis*, but a 5 bp insertion found in the Btub gene is absent in all sequenced strains of *S. galeopsidis*. *Septoria melissae* can furthermore be distinguished in culture from *S. galeopsidis* by the narrower conidia on OA (1.5–2 µm, in *S. galeopsidis* 2–2.5 µm), and the conidiogenous cells, which only proliferate sympodially and not percurrently.

***Septoria napelli*** Speg, Decades mycologicae italicae I-XII: no. 117. 1879; Atti Soc. crittog. ital., Ser. 2, 3: 69. 1880. Fig. 30.

≡ *Rhabdospora napelli* (Speg.) Petr., Sydowia 11: 376. 1957 [misapplication].

*Description in planta*: *Symptoms* leaf spots hologenous, circular to irregular, single, white to pale greyish, surrounded by a first red, then black, relatively wide border, often completely blackening the narrow leaflets. *Conidiomata* pycnidial, epiphyllous, rarely also hypohyllous, conspicuous, one to many in each leaf spot, globose to subglobose, black, semi-immersed, 100–150(–200) µm diam; *ostiolum* central, circular, initially 15–25 µm wide, later opening

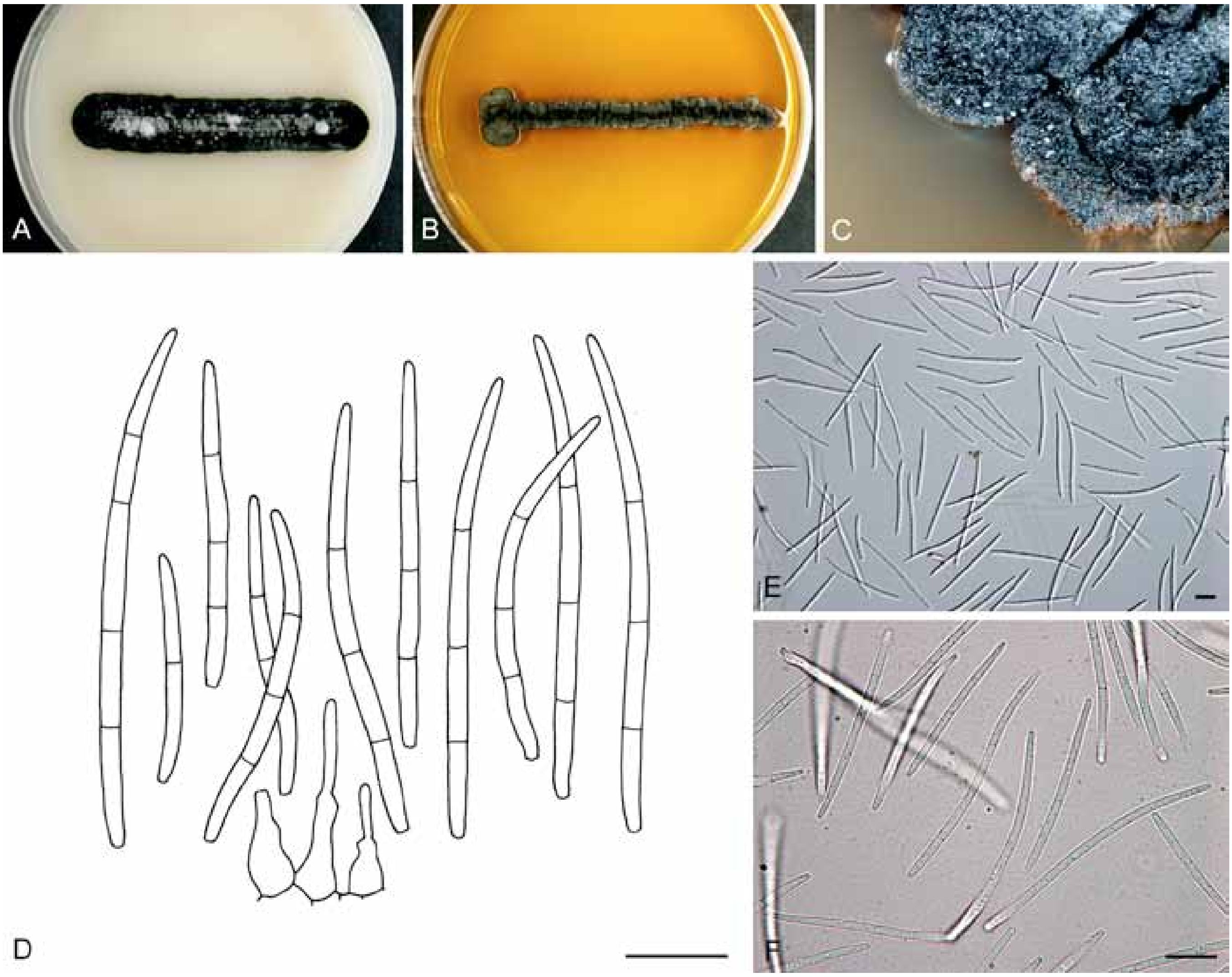


**Fig. 29.** *Septoria melissae*, CBS 109097. A–C. Colonies (15 °C, nUV). A. On OA. B. On MEA. C. On MEA, detail of colony margin. D. Conidia and conidiogenous cells on OA. E–F. Conidia on OA. Scale bars = 10 µm.

more widely; *conidiomatal wall* 15–28 µm thick, composed of *textura angularis*, differentiated layers absent, the cells mostly 4–10 µm diam, the outer cells with brown, somewhat thickened walls, the inner cells with hyaline and thinner walls. *Conidiogenous cells* hyaline, cylindrical, broadly to narrowly ampulliform, with a distinct neck of variable length, hyaline, holoblastic, with several distinct percurrent proliferations, more rarely also sympodial after a sequence of percurrent proliferations of the same cell, 10–22 × 3.5–8 µm. *Conidia* filiform, straight, more often irregularly curved, gradually attenuated to the pointed apex, weakly or more distinctly attenuated towards the broadly truncate base, (3–)4–5(–7)-septate, not constricted around the septa, hyaline, with several relatively large oil-droplets and also minute granular contents in each cell in the rehydrated state, 59–80 × (1.5–)2–3.5 µm (rehydrated; up to 4 µm wide in the living state). *Sexual morph* unknown.

*Description in vitro*: *Colonies* on OA 9–15 mm diam in 2 wk (45–53 mm in 49 d), with an even, glabrous, colourless margin; immersed mycelium coral to scarlet, with pigment diffusing beyond the colony margin; colony becoming black in the centre and somewhat elevated due to superficial pycnidia, surrounded by an area with more scattered pycnidia, releasing flesh to salmon droplets of conidial slime; aerial mycelium well-developed and dense in the centre, appressed, woolly, white to pale grey; reverse scarlet to coral, in the centre blood colour. *Colonies* on CMA 8–12 mm diam in 2 wk (62–65 mm in 49 d), as on OA. *Colonies* on MEA 5–9 mm diam in 2 wk (38–44 mm in 49 d), the margin irregular; colonies restricted, with a cerebriform surface, becoming about 5 mm high, the surface soon black, first almost glabrous, later mostly covered by a dense mat of white to flesh, woolly aerial mycelium; honey or amber conidial slime masses are released from immersed pycnidia; reverse of the colony dark brick or luteous, paler towards the margin. *Colonies* on CHA 8–13 mm diam in 2 wk (55–58 mm in 49 d), with an even or undulating, colourless margin, partly hidden under aerial hyphae; immersed mycelium grey-olivaceous or olivaceous-black, covered with well-developed, grey and partly greenish glaucous, later reddish, aerial mycelium; reverse blood colour, the margin paler; in the central part of the colony numerous pycnidia develop, releasing rosy-buff conidial slime.

*Conidiomata* as *in vitro* pycnidial, ostioli initially barely protruding, but later often growing out to form elongated necks up to 100 µm long; on CMA conidiomata less differentiated, sometimes without ostiolum and opening by tearing of the upper wall; *conidiogenous cells* as *in planta*, but larger, 10–32 × 3.5–8.5(–10) µm, proliferating sympodially and also percurrently, with distinct annellations on the elonated necks. *Conidia* similar in shape as *in planta* but longer, 5–7(–11)-septate, 64–95(–118) × 2–3.5(–4) µm.

*Hosts*: *Aconitum* spp.

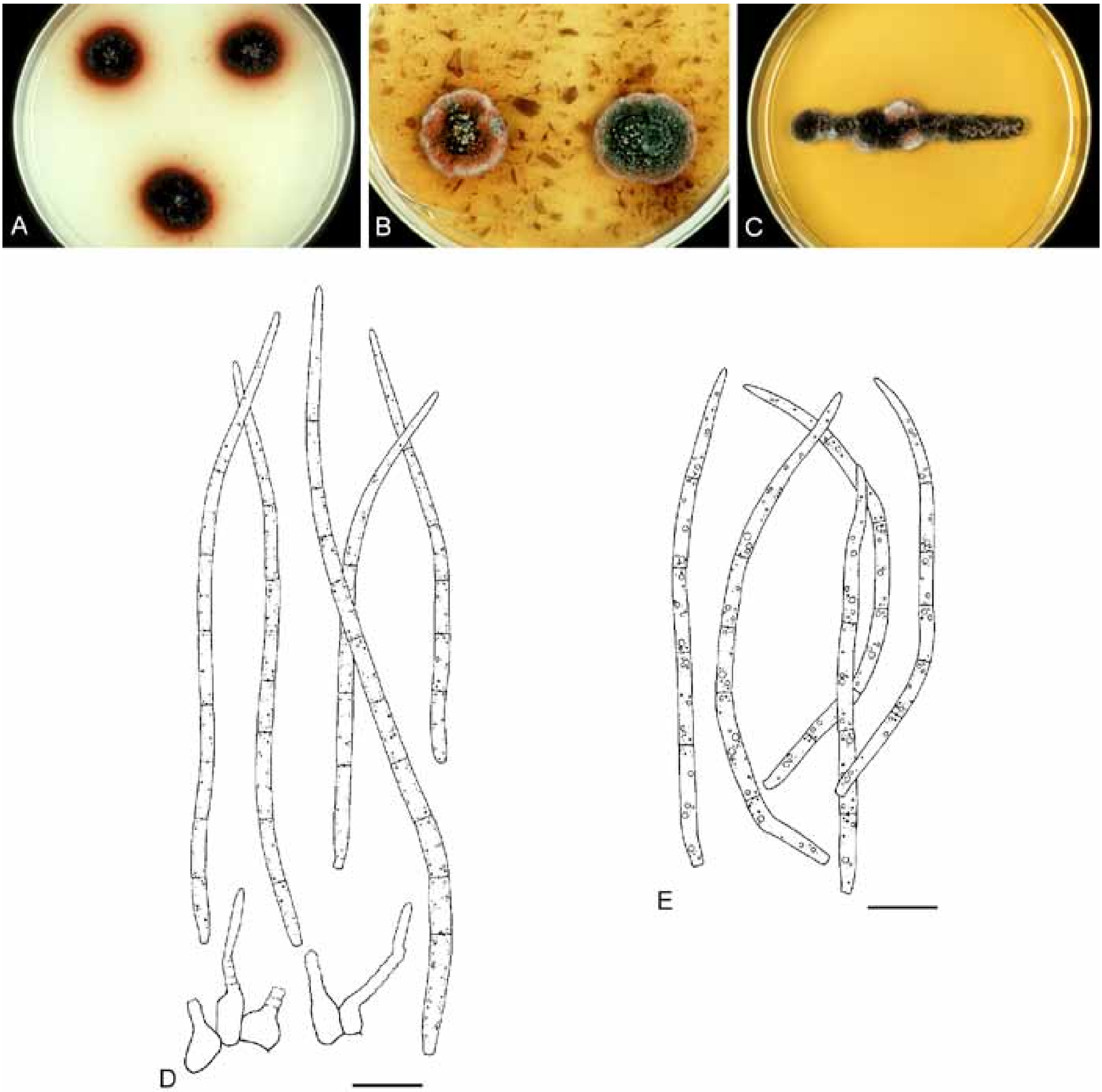


**Fig. 30.** *Septoria napelli*. A–C. Colonies CBS 109104 (15 °C, nUV). A. On OA. B. On CHA. C. On MEA. D. Conidia and conidiogenous cells on OA (CBS 109104). E. Conidia *in planta* (CBS H-21153). Scale bars = 10 µm.

*Material examined*: **Austria**, Ober Inntal, Samnaun Gruppe, Zanderstal near Spiss, alt. 1800 m., on living leaves of *Aconitum napellus*, 11 Aug. 2000, G. Verkley 1070, CBS H-21153, living cultures CBS 109104, 109105; same loc., host, date, G. Verkley 1071, CBS H-21154, living culture CBS 109106. **Romania**, reg. Mureş-Autonomă Maghiară, on living leaves of *A. degenii*, 25 Aug. 1953, C. Sandu-Ville *s.n.*, CBS H-18117, distributed in Herb. Mycol. Romanicum, fasc. 35, no. 1742.

*Notes*: According to the brief original diagnosis, *S. napelli* is characterised by 120–130 µm wide hypophyllous pycnidia, and indistinctly septate conidia measuring 50–100 × 2–4 µm. Teterevnikova-Babayan (1987) reported up to 9-septate conidia measuring 40–100 × 3–4 µm, and Shin & Sameva (2004) 3–9-septate conidia, 40–105 × (2.5–)3–5 µm in Korean material. It is doubtful whether the description by Petrak (1957) of *S. napelli* was based on correctly identified material. Pycnidia of that fungus were mostly hypophyllous, with 3–7, rarely 8–9-septate conidia measuring 40–70 (rarely up to *ca.* 100) × 3–4 µm, arising from septate and branched conidiophores. The pycnidial wall was composed of globose to angular cells 5–8(–10) µm diam, with walls thickened to an extent which would avoid any compression. Petrak (1957) also observed young fruitbodies of a sexual morph on dead leaves in between old and empty conidiomata. Although this sexual morph was immature, in his opinion it was "undoubtedly *Pleosporaceae*, perhaps a species of *Leptosphaeria,* but certainly not *Mycosphaerella*". Certain similarities in the walls of the asexual and sexual morph, made him suspect that they were produced in different stages in the life-cycle of a single fungus. Because of the large size of the pycnidia of Petrak's *S. napelli*, the structure of the pycnidial wall and conidial ontogeny, which were unlike typical *Septoria*, he proposed the combination *Rhabdospora napelli*. Petrak's observations of *S. napelli* probably pertained to a different septoria-like fungus (*Stagonospora*?), probably with pleosporalean affinities, but of which the exact identity remains unclear.

The fungus studied in the present study, which is a member of the *Septoria* clade, generally agrees with the original description of *S. napelli*. It is unknown whether *S. napelli* has a sexual morph. Two *Mycosphaerella* names have been published from *Aconitum*, *M. antonovii* on *Aconitum excelsum* in Siberia, and *M. aconitorum*, on *Aconitum* sp. in Austria. Both names were introduced by Petrak, who did not observe associated asexual morphs for these *Mycosphaerella* spp. A comparison with *S. lycoctoni*, including the molecular results, is provide above in the notes on *S. lycoctoni*.

CBS 128664 isolated from *Aconitum pseudolaeve* var. *erectum* in Korea, is genetically distinct from both *Septoria* spp. on *Aconitum* in Europe. The new name *S. pseudonapelli* is proposed for this fungus by Quaedvlieg *et al.* (2013, this volume).

***Septoria obesa*** Syd., in Syd. & P. Syd., Annls mycol. 12: 163. 1914.

= *S. artemisiae* Unamuno, Assoc. españ. Progr. Cienc. Congr. Salamanca: 46. 1923 [nom. illeg., later homonym, non Passerini, 1879].

Descriptions *in planta* are provided by Punithalingam (1967c) and Priest (2006). Sexual morph unknown.

*Hosts*: *Artemisia lavandulaefolia* and *Chrysanthemum* spp.

*Material examined*: **Germany**, Weihenstephan, on *Chrysanthemum indicum*, R. Schneider Sep. 1957, living culture CBS 354.58 = BBA 8554 = IMI 091324. **South Korea**, Hongcheon, on *Artemisia lavandulaefolia*, H.D. Shin, 28 June 2006, living culture SMKC 21934 = KACC 42453 = CBS 128588; Bonghwa, on *Chr. indicum*, H.D. Shin, 18 Oct. 2007, living culture SMKC 23048 = KACC 43193 = CBS 128623; Jeju, on *Chr. morifolium*, 5 July 2008, living culture KACC 43858 = CBS 128759.

*Notes*: Jørstad (1965) regarded *S. obesa* as a synonym of *S. leucanthemi*, as both have similar conidial morphologies and occur on several *Chrysanthemum* spp. Punithalingam (1967b, c), however, recognised *S. obesa* and *S. leucanthemi* as separate species, noting that the conidia of *S. obesa* are consistently wider than those of *S. leucanthemi*. Verkley & Starink-Willemse (2004) found additional, molecular support for the treatment.as separate species in eight polymorphisms found on the ITS sequences of strains representing these species. Further evidence is now provided here based on sequences of six other loci. The host ranges of the two species are also different: *S. leucanthemi* is capable of infecting various species of a wide range plant genera, viz. *Chrysanthemum*, *Tagetes*, *Achillea*, *Centaurea* and *Helianthus* (Waddell & Weber 1963, Punithalingam 1967b). *Septoria obesa* seems to mainly infect *Chrysanthemum* spp., but it does also infect *Artemisia lavendulaefolia*, as could be demonstrated in this study with CBS 128588, a strain originally identified as *S. artemisiae*. The strain is genetically very close to the other strains of *S. obesa* studied here and therefore regarded as conspecific. The conidia produced by CBS 128588 are in good agreement with *S. obesa* as well, being much larger than in *S. artemisiae* (30–33 × 1.5 µm, according to the original diagnosis of *S. artemisiae* Passerini). The later homonym *S. artemisiae* described by Unamuno based on material on *Artemisia vulgaris* in Spain with 4-septate conidia 35.5–52.5 × 2.5–3 µm, is placed here in the synonymy of *S. obesa*.

The conidia of the sunflower pathogen *S. helianthi* (50–85 × 2–3 µm) are similar to those of *S. obesa* (50–90 × 2.5–3.5 µm, cf. Priest 2006), but they can be distinguished by the number of septa formed, viz., seldom more than 5 in *S. helianthi* and 5–11 septa in *S. obesa*. Verkley & Starink already showed that ITS sequences of these species differ by more than 20 base positions, which is also supported by the results found in the present study for other genes (Fig. 2).

***Septoria paridis*** Pass., Atti Soc. crittog. ital. 2: 41. 1879. Fig. 31.

*Description in planta*: *Symptoms* leaf spots single, scarce, circular to irregular, white to pale ochreous, surrounded by a vague orange to reddish brown zone, visible on both sides of the leaf, decaying to shot-holes. *Conidiomata* pycnidial, epiphyllous, one to a few in each leaf spot, globose, black, immersed, 60–100 µm diam; *ostiolum* central, circular and 35–40 µm wide, surrounding cells concolorous to slightly darker; *conidiomatal wall* up to 15 µm thick, composed throughout of hyaline, angular cells, 2.5–5 µm diam, the outermost cells brown with somewhat thickened walls, the inner cells hyaline and thin-walled. *Conidiogenous cells* hyaline, discrete, globose, doliiform, or broadly ampulliform, holoblastic, proliferating percurrently several times with distinct annellations thus forming a relatively narrow neck, rarely also sympodially, 5–8(–11) × 2.5–5 µm. *Conidia* filiform, straight, or slightly curved, attenuated gradually to a narrowly pointed apex and a narrowly truncate base, 0–3-septate (septa very thin and easily overlooked), not constricted around the septa, contents with several minute oil-droplets and granular material in each cell in the living state, with minute oil-droplets and granular contents in the rehydrated state, (18–)20–28.5(–34) × 1–1.5(–2) µm (living; rehydrated, 1 µm wide). *Sexual morph* unknown.

*Description in vitro*: *Colonies* on OA 8–11 mm diam in 10 d (30–35 mm in 3 wk; more than 75 mm in 7 wk), with an even, glabrous, colourless margin; immersed mycelium mostly homogeneously pale coral to pale red, some pigment diffusing beyond the colony margin, olivaceous to greenish hyphal radial strands also weakly or more strongly developing in some sectors or entire colonies (especially after 7 wk, when most of the red pigment is no longer visible); in the centre olivaceous-black and slightly elevated due to superficial and immersed pycnidia, surrounded by an area with more scattered pycnidia, releasing pale whitish droplets of conidial slime; aerial mycelium very scanty, few minute white tufts; reverse olivaceous-black to greenish grey, surrounded by coral to sienna areas. *Colonies* on CMA 7–10 mm diam in 10 d (28–33 mm in 3 wk; more than 75 mm in 7 wk), as on OA, but the colonies sooner pigmented, dark green, dark blueish green or olivaceous, and a red pigment tardily formed, but more persistent and still well visible after 7 wk. Sporulation as on OA. *Colonies* on MEA 6–11 mm diam in 10 d (23–30 mm in 3 wk; 64–75 mm in 7 wk), the margin even, glabrous, buff; colonies spreading, but the centre elevated, irregularly pustulate, up to 2 mm high, the surface dark greyish brown, later black, covered by short felty white aerial mycelium, or higher tufts; reverse of the colony brown-vinaceous or sepia, paler towards the margin. Pycnidia mostly superficial, in dense groups. *Colonies* on CHA 5–8 mm diam in 10 d (28–35 mm in 3 wk; 45–55 mm in 7 wk), with an even to ruffled, glabrous, colourless to buff margin; immersed mycelium in areas where first sporulation occurs becoming dark, greenish grey to dark slate blue, later more throughout colony, covered by well-developed, tufty whitish grey aerial mycelium that later shows a reddish haze; reverse olivaceous-black to sepia, but margin paler; in the central part of the colony numerous pycnidia develop; in older colonies the centre becomes up to 3 mm high.

*Conidiomata* (OA) as *in planta*, immersed or developing on the agar surface, single or merged into complexes 100–220 µm

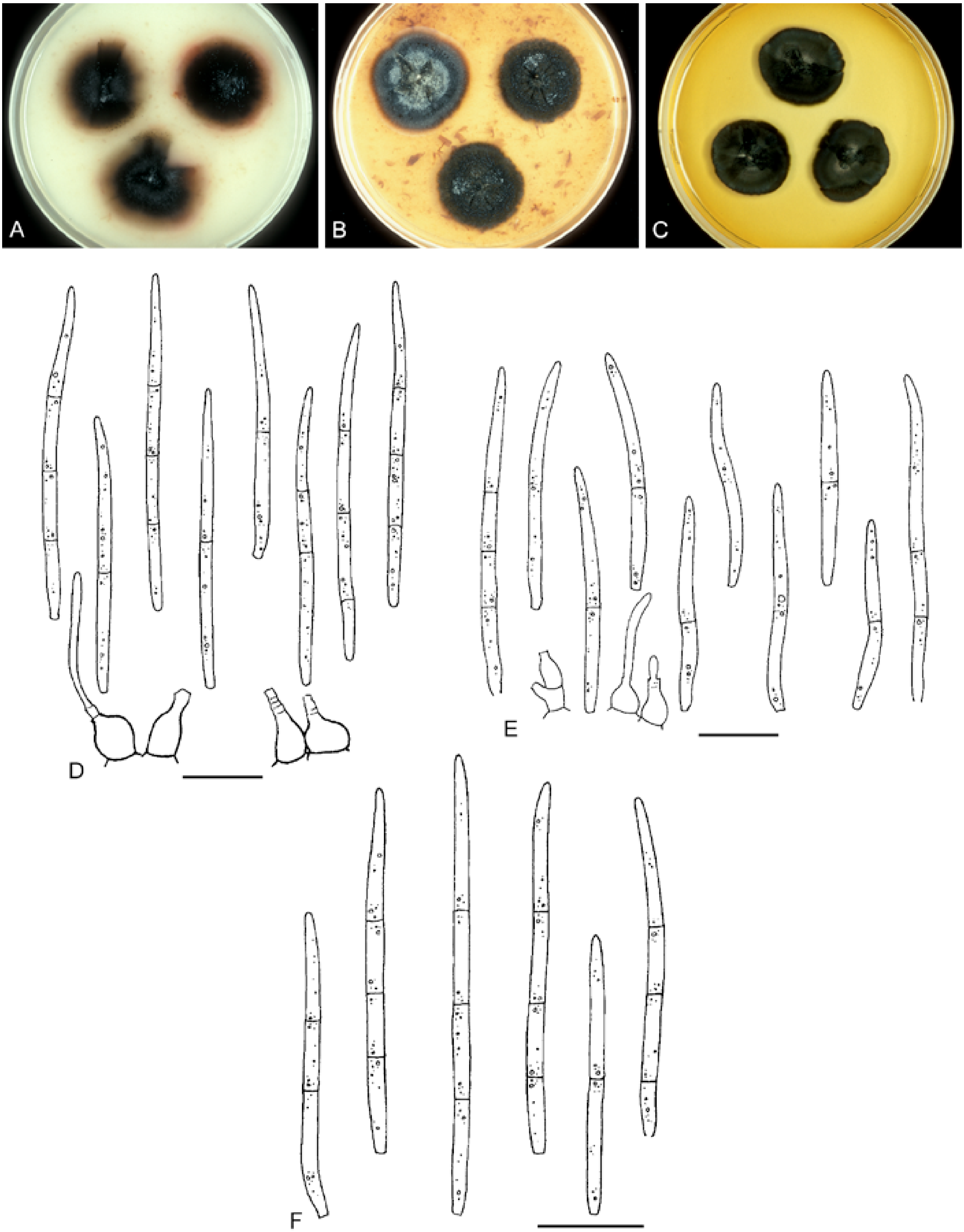


**Fig. 31.** *Septoria paridis*. A–C. Colonies (15 °C, nUV). A. On OA (CBS 109110). B. On CHA (CBS 109110). C. On MEA (CBS 109108). D. Conidia and conidiogenous cells *in planta* (CBS H-21177, *Paris quadrifolia*). E. Ibid. (CBS H-21152, *Viola palustris*). F. Conidia on OA (CBS 109108). Scale bars = 10 µm.

diam, superficial pycnidia mostly forming one to several elongated necks, initially pale brown, then almost black, releasing pale whitish conidial slime, later becoming rosy-buff. *Conidiogenous cells* as *in planta*, 7–12(–14) × 2.5–5 µm. *Conidia* as *in planta* but some considerably longer, 22–38(–45) × 1–1.5 µm.

*Hosts*: *Paris quadrifolia*, *P. incompleta* and *Viola palustris.*

*Material examined*: **Austria**, Tirol, Leutaschtal Weidach, on river bank, on living leaves of *Paris quadrifolia*, 2 Aug. 2000, G. Verkley 1038, CBS H-21177, living cultures CBS 109110, 109111; Tirol, Ötztal, Sölden, near Hoch-Sölden, on living leaves of *Viola palustris*, 31 July 2000, G. Verkley 1037, CBS H-21152, living cultures CBS 109108, 109109.

*Notes*: According to the original description, conidia of *S. paridis* are 20 × 1 µm and aseptate. Vanev *et al.* (1997) describe the conidia as 18–25 × 1–1.3 µm, Teterevnikova-Babayan (1983), 20–25 × 1 µm. As is seen in several other *Septoria*, the conidia can reach considerably greater length in culture than on the natural host plant. In shape of the conidia the species strongly resembles *S. galeopsidis* and *S. scabiosicola*, as do the cultures, although *S. galeopsidis* does not produce a red pigment on OA. The material on *Viola palustris* (*Violaceae*) collected in Tirol was initially identified as *S. violae-palustris*, but based on the DNA sequence analyses of seven loci (Fig. 2) and the agreeing phenotype it is concluded that the material is conspecific with *S. paridis*. This is the first report of this fungus on another host genus than *Paris*, and also outside the *Liliaceae*. A second *Septoria* occurring on *Paris quadrifolia* is *S. umbrosa*. That species differs from *S. paridis* by much larger conidia, 30–85 × 3–4.5 µm, which are 5–7-septate.

***Septoria passifloricola*** Punith., CMI Descr. Pathogenic Fungi & Bacteria no. 670. 1980.

≡ *S. passiflorae* Louw, Sci. Bull. Dept. Agric. For. Un. S. Africa 229: 34. 1941. Nom. illeg. Art 53 [non Syd., Annls mycol. 37: 408. 1939].

*Description in vitro*: *Colonies* on OA 12–15 mm diam in 2 wk, with an even, glabrous, buff margin; colonies spreading, immersed mycelium mostly homogeneous orange, but no diffusion of pigments beyond the margin observed; the surface covered by appressed, greyish white to grey aerial mycelium developing in concentric areas, beneath which mostly superficial, dark brown to almost black pycnidia or more complex conidiomata develop, releasing pale whitish to dirty greyish droplets of conidial slime; reverse orange to sienna. *Colonies* on CMA 10–14 mm diam in 2 wk, as on OA. *Colonies* on MEA 5–7(–10) mm diam in 2 wk, with an even, weakly lobed, black margin, which may be covered by short fluffy, pure white aerial mycelium; colonies spreading but elevated at the centre, the surface almost black, with immersed conidiomatal complexes soon covered by masses of first pale white, buff, and then brick conidial slime; the central area later entirely covered by cerebriform, brick masses of slime; reverse brick to almost vinaceous, and fawn. *Colonies* on CHA 8–10(–14) mm diam in 2 wk, with an even, buff margin covered by a diffuse, felty aerial mycelium; further as on MEA, but surface less elevated, and largely covered by diffuse, felty, grey-white aerial mycelium; conidial slime as on MEA abundantly produced from similar conidiomatal complexes, but more intensely pigmented, deep scarlet; reverse blood colour.

*Conidiogenous cells* (OA) hyaline, discrete, broadly ampulliform to cylindrical, holoblastic, with one or two indistinct percurrent proliferations (sympodial proliferation not observed), 8–14 × 3–6 µm; *conidia* filiform, hyaline, narrowly rounded at the top, attenuated to a truncate base, straight to somewhat curved, 1–2(–3)-septate, not constricted around the septa, mostly 10–30(–35) × 1.5–2(–2.5) µm.

*Host*: *Passiflora edulis*.

*Material examined*: **Australia**, Victoria, Wonthaggi, on *Passiflora edulis*, Mar. 2011, C. Murdoch, living culture CBS 129431. **New Zealand**, Auckland, Mt Albert, on living leaves of *P. edulis*, 21 Feb. 2000, C. F. Hill MAF LYN-118a, living culture CBS 102701.

*Notes*: Priest (2006) provided a description of the fungus on the host, and discussed the nomenclature. He also mentioned the anonymous reporting of a *Septoria* state observed in ascospore isolates from a *Mycosphaerella* sp. found on fruits lesions, but whether this truly is the sexual morph of *S. passifloricola* remains to be corroborated. The multilocus phylogeny (Fig. 2) provides evidence of a close relationship with *S. ekmanniana* (CBS 113385, 113612) and *S. chromolaenae* (CBS 113373), and also *S. sisyrinchii* (CBS 112096) and *S. anthurii* (CBS 148.41, 346.58).

***Septoria petroselini*** (Lib.) Desm., Mem. Soc. Roy. Sci. Lille 1843: 97. 1843. Fig. 32.

*Basionym*: *Ascochyta petroselini* Lib., Pl. Crypt. Arduenna 3: 252. 1834.

≡ *Phleospora petroselini* (Lib.) Westend., Bull. Acad. r. Bruxelles 12 (9): 252. 1845.

*Description in planta*: *Symptoms* leaf spots indefinite, without a distinct border, pale brown, visible on both sides in green parts of leaves or barely discoloured petioles. *Conidiomata* pycnidial, numerous, mostly epiphyllous, semi-immersed, black, mostly 80–200 mm diam, with a central, first narrow, later wider opening, releasing pale white cirrhi of conidia; *conidiomatal wall* composed of one or two layers of brown-walled, angular cells, lined by a layer of hyaline cells. *Conidiogenous cells* hyaline, discrete, holoblastic, sympodially or percurrently proliferating, ampulliform, 6–10 × 3–6 mm. *Conidia* hyaline, filiform, straight to somewhat flexuous, the upper cell tapered into the obtuse apex, relatively widely truncate at the base, (1–)3–5(–7) septate, not or only indistinctly constricted at the septa, contents granular or with minute oil-droplets around the septa and at the ends, 29–80 × 1.9–2.5 mm (living; rehydrated, 1.2–1.5 mm wide). *Sexual morph* unknown.

*Description in vitro (18 °C, near UV) CBS 109521*: *Colonies* on OA 13–16 mm diam in 2 wk, with an even, colourless margin; colonies spreading, immersed mycelium mostly pale ochreous, soon appearing dull green due to the development of dark green hyphal strands, particularly in a discontinuous submarginal zone; reverse in the centre ochreous to fulvous, surrounded by olivaceous-grey. Conidiomata developing after 5–7 d immersed in the agar or on its surface, most numerous in the centre of the colony, releasing milky white to rosy-buff conidial slime. Conidia also produced directly from mycelium near the centre of the colony. *Colonies* on MEA 17–20 mm diam in 2 wk, with an even to somewhat ruffled, buff margin; colonies spreading to restricted, somewhat elevated towards the centre, the surface black with many stromata developing and releasing milky white droplets of conidial slime, aerial mycelium diffuse to more dense and low, grey; reverse mostly greenish grey to iron-grey, in the centre with fawn to dark brick haze.

*Conidiomata* and conidiogenous cells as *in planta*. *Conidia* (OA) filiform to filiform-cylindrical, straight, flexuous or curved, attenuated gradually to the narrowly rounded to pointed apex, attenuated gradually or more abruptly to the narrowly truncate base, (0–)3–5(–7)-septate, 30–54(–65) × 2–2.5(–3) µm.

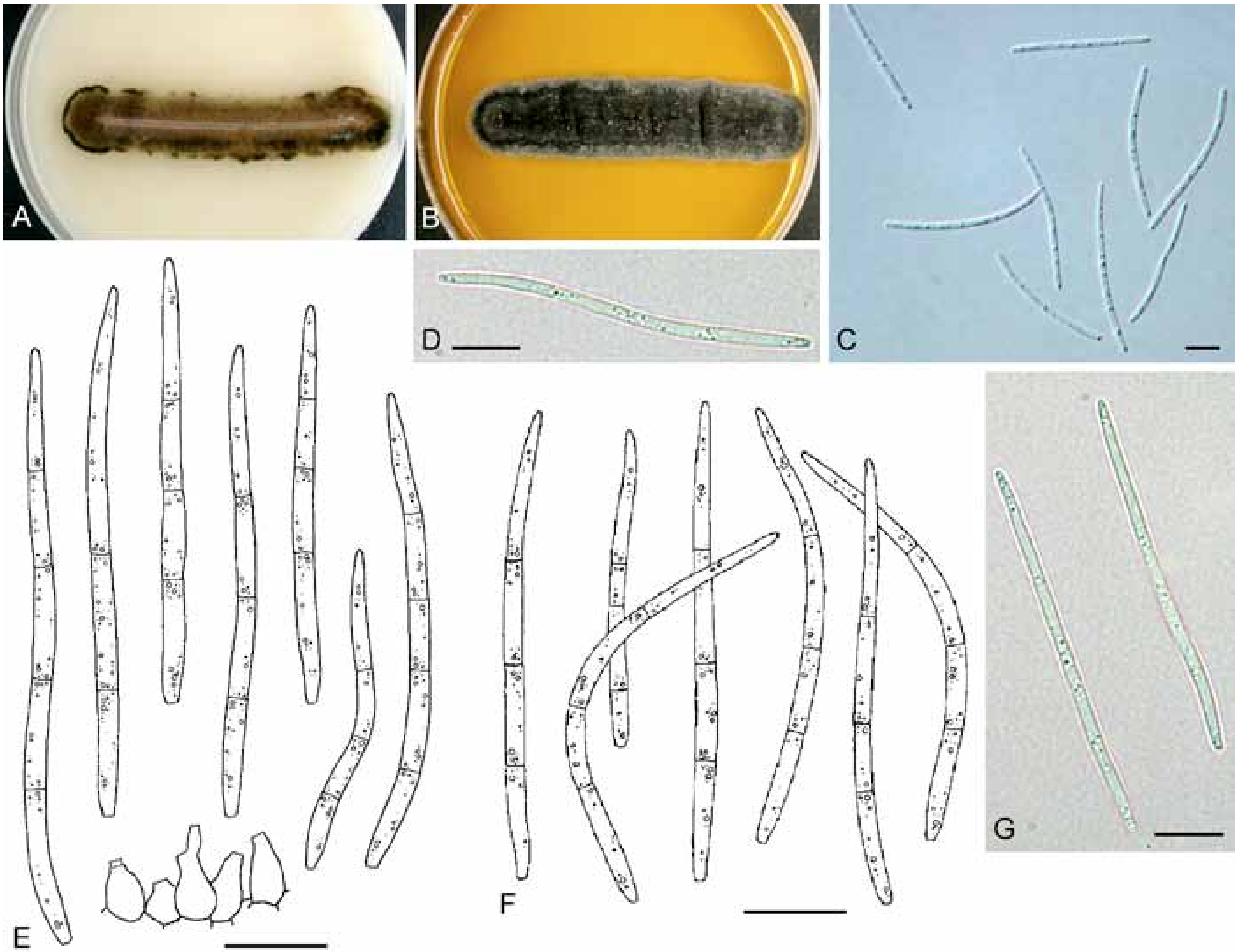


**Fig. 32.** *Septoria petroselini*. A, B. Colonies CBS 109521 (15 °C, nUV). A. On OA. B. On MEA. C, D. Conidia on OA (CBS 109521). E. Conidia and conidiogenous cells *in planta* (CBS H-21166). F. Conidia on OA (CBS 182.44). G. Conidia on OA (CBS 109521). Scale bars = 10 µm.

*Hosts*: *Petroselinum crispum* (syn. *Apium petroselinum*), other *Petroselinum* spp. and *Coriandrum sativum* (Priest 2006).

*Material examined*: **Netherlands**, Prov. Utrecht, Baarn, garden Eemnesserweg 90, on living leaves of *Petroselinum crispum*, 29 Mar. 2001, H.A. van der Aa 12642, CBS H-21166, living culture CBS 109521; Laren, on living leaves of *P. sativum*, June 1944, S. Dudok de Wit *s.n.*, living culture CBS 182.44 = IMI 100279, dried specimen of culture on CMA, CBS H-18128.

*Notes*: CBS 182.44, isolated from *Petroselinum sativum*, produces conidia 29–49 × 1–2 µm, and this range of sizes agrees with those given for *S. petroselini* by most authors [26–45(–52) × (1–)1.5–2 µm cf. Priest 2006; 16–46 × 1–2 mm cf. Jørstad 1965 on *Petroselinum*]. In contrast, the conidia in the collection on *P. crispum* (CBS H-21166), as well as in the isolate CBS 109521 derived from it, were up to 80 µm long and 2.5 µm wide, and the pycnidia were also larger than described for *S. petroselini*, for which this material was initially identified as *S. apiicola*, but the molecular data provide evidence that it also belongs to *S. petroselini*. The material is 100 % homologous on ITS, Act, RPB2 and EF, and 99.7 % on Cal with CBS 182.44. The range of conidial sizes for *S. petroselini* is therefore expanded here, although it should be noted that the conidia formed *in vitro* are not over 65 µm in length in the material available. The ITS sequence of *S. anthrisci* is distinct from that of *S. apiicola*, but identical to that of *S. petroselini* and other species. *Septoria anthrisci* can be distinguished from *S. petroselini* by the Act, EF and RPB2 sequences.

***Septoria phlogis*** Sacc. & Speg., in Sacc., Michelia 1: 184. 1878 [as "phlocis"; non Ellis & Everh., in G. Martin, J. Mycol. 3: 85. 1887; nec P. Syd., Mycoth. March., Cent. 18, no 1757; Cent. 23, no 2278. 1887; later homonyms]. Fig. 33.

*Description in planta*: *Symptoms* leaf lesions developing in areas of the leaf lamina that first turn yellow, indefinite or delimited by darkening veinlets, hologenous, pale to dark brown. *Conidiomata* pycnidial, epiphyllous, numerous, semi-immersed to immersed, subglobose to globose, dark brown to black, 100–160 µm diam; *ostiolum* central, circular, initially 25–35 µm wide, later becoming more irregular and up to 70 µm wide, surrounding cells concolourous; *conidiomatal wall* 15–28 µm thick, composed of an outer layer of isodiametric to irregular cells mostly 5–9 µm diam with pale brown cell walls up to 2 µm thick, and an inner layer of hyphal to isodiametric cells 3–5 µm diam with thin, hyaline walls. *Conidiogenous cells* hyaline, discrete or integrated in 1–2-septate conidiophores up to 22 µm long, cylindrical, or narrowly to broadly ampulliform, holoblastic, often proliferating percurrently with indistinct annellations as well as sympodially, 5–7.5(–8) × 2.5–4(–5) µm. *Conidia* cylindrical, filiform, straight to slightly curved,

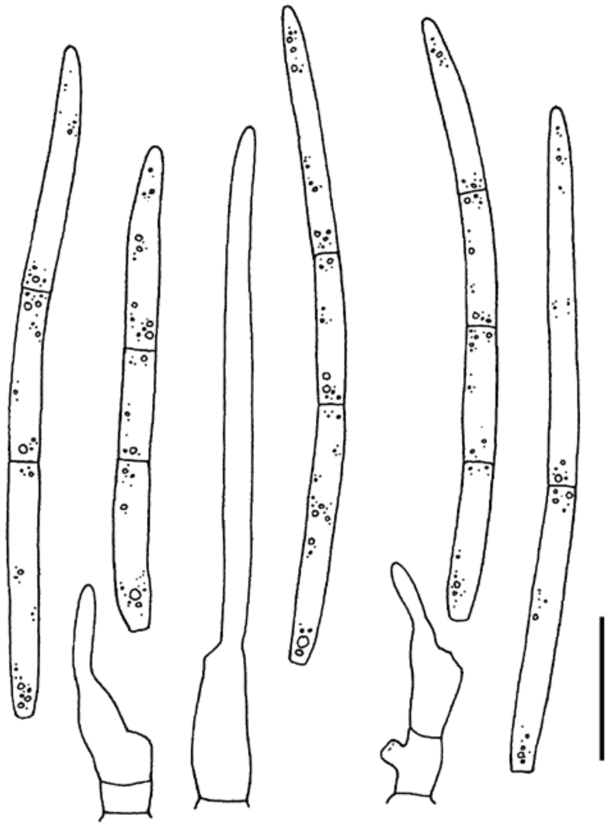

**Fig. 33.** *Septoria phlogis*. Conidia and conidiogenous cells *in planta* (CBS H-21198). Scale bars = 10 µm.

narrowly rounded to somewhat pointed at the apex, attenuated gradually or more abruptly towards the narrowly truncate base, (0–)1–3(–4)-septate, not constricted around the septa, hyaline, containing minute oil-droplets and granular material in the living and rehydrated state, (22–)32–50(–60) × 1.5–2 µm (rehydrated; living, 2–2.5 µm wide). *Sexual morph* unknown.

*Description in vitro*: *Colonies* on OA 15–18 mm diam in 19 d, with an even, glabrous, buff to rosy-buff margin; colonies spreading, plane; immersed mycelium variably pigmented over sectors, usually either brownish olivaceous, or cinnamon to saffron (honey with a reddish haze); aerial mycelium scanty, white, locally forming a diffuse woolly-floccose mat; reverse olivaceous-black and cinnamon or saffron. *Colonies* on CMA 13–18 mm diam in 19 d, as on OA. *Colonies* on MEA 12–17 mm diam in 19 d, with an even, glabrous, buff margin; colonies spreading, the surface mostly plane, only somewhat elevated or folded towards the centre; immersed mycelium mostly dark salmon to olivaceous-black, covered by a dense, appressed mat of woolly, mostly white to faintly rosy-buff aerial mycelium; an ochreous pigment diffuses into the surrounding medium; reverse mostly sienna or blood colour, with an ochreous to saffron margin. *Colonies* on CHA 12–18 mm diam in 19 d, as on MEA.

*Hosts*: *Phlox* spp.

*Material examined*: **Netherlands**, Prov. Noord-Holland, Enkhuizen, on living leaves of *Phlox* sp., 6 Sep. 1949, J.A. von Arx *s.n.*, CBS H-4862; Prov. Utrecht, Baarn, Cantonspark, on living leaves of *Phlox* sp., 27 Aug. 1999, G. Verkley 911, CBS H-21198, living culture CBS 102317; same substr., Jan. 1932, D. Moll *s.n.*, living culture CBS 312.32; Garden in Baarn, same substr., 16 Oct. 1990, H.A. van der Aa 10919, CBS H-18130, living culture CBS 577.90; same substr., loc., 27 Aug. 1997, H.A. van der Aa 12302, CBS H-18131.

*Notes*: Priest (2006) described the conidia of *S. phlogis* as filiform, 1–4-septate, straight to curved, (35–)50–73 × (1–)1.5–2 µm, hyaline, with a truncate base and obtuse apex. He accepted *S. divaricatae* as a separate species, with *Phlox drummondi* (syn. *P. divaricata*) as the only known host plant, and *S. drummondi* as a synonym. *Septoria divaricatae* has similarly shaped but smaller conidia than *S. phlogis*, 1–3-septate, (13–)25–40(–45) × 1–1.5 µm. The overlap in length of the conidia of the two is minimal, at least on the host plant, indicating that they might be truly separate taxa. Several other authors have also accepted *S. divaricatae* as a distinct entity (Teterevnikova-Babayan 1987, Muthumary 1999). However, Jørstad (1965) considered *S. divaricatae* a synonym of *S. phlogis*, and also *S. phlogina*. Both *S. phlogis* and *S. divaricatae* occur on *P. drummondi* and this may have contributed to the confusion. Investigations based on fresh material on different *Phlox* species, and studies of cultures derived thereof, as well as type material of the names mentioned above, will be required in order to settle the complicated taxonomy of *Septoria* on *Phlox*.

Molecular identification of *S. phlogis* is straight-forward, as all protein-coding genes investigated here, particularly Btub, Cal and RPB2, show unique diagnostic sequences. *Septoria epambrosiae* (CBS 128629, 128636) is a sister species to *S. phlogis*. *Septoria epambrosiae* is a pathogen of *Ambrosia artemisiifolia* (*Asteraceae*), which today is the prime cause of hay fever in many areas where this weed occurs.

***Septoria polygonorum*** Desm., Annls Sci. Nat., sér. 2, Bot.17: 108. 1842. Fig. 34.

≡ *Spilosphaeria polygonorum* (Desm.) Rabenh., Herb. Mycol. II, no. 442a. 1856.

*Description in planta*: *Symptoms* leaf spots small, circular, hologenous, ochreous to brown, sharply delimited by a dark red-brown zone. *Conidiomata* pycnidial, mainly epiphyllous, several to many developed in each leaf spot after some time, subglobose to lenticular, not protruding strongly, brown to almost black, 50–120 µm diam; *ostiolum* central, initially circular and 25–45 µm wide, surrounding cells concolorous to somewhat darker brown; *conidiomatal wall* about 10–25 µm thick, composed of angular cells 2.0–6.5 µm diam, the outermost cells pale yellowish brown with somewhat thickened walls, the inner cells thin-walled. *Conidiogenous cells* hyaline, discrete, narrowly or broadly ampulliform with a relatively wide neck, holoblastic, often first proliferating sympodially, and later also percurrently 1–several times with distinct annellations, 5–10(–14) × 3.–5.5(–6.5) µm. *Conidia* filiform to filiform-cylindrical, straight or slightly curved, or flexuous, attenuated gradually to a narrowly rounded to pointed apex, attenuated more abruptly towards the truncate base, 1–4-septate, not or only inconspicuously constricted around the septa, hyaline, contents with several minute oil-droplets and granular material in each cell in the living state, with inconspicuous oil-droplets and granular contents in the rehydrated state, (17–)22–45(–53) × 1.5–2 µm (living; rehydrated, 1.2–1.8 µm wide). *Sexual morph* unknown.

*Description in vitro*: *Colonies* normally slow-growing, but sometimes with fast-growing sectors (diam including these between brackets) on all media except MEA. On OA 3–5 [6–7] mm diam in 2 wk [6–7 (22–30) mm in 6 wk], the margin regular, glabrous, colourless; colonies spreading, plane, immersed mycelium olivaceous-black, but grey-olivaceous to greenish grey in faster growing sectors that sometimes develop from typically slow-growing colonies; aerial mycelium generally absent or very scanty, but woolly-floccose

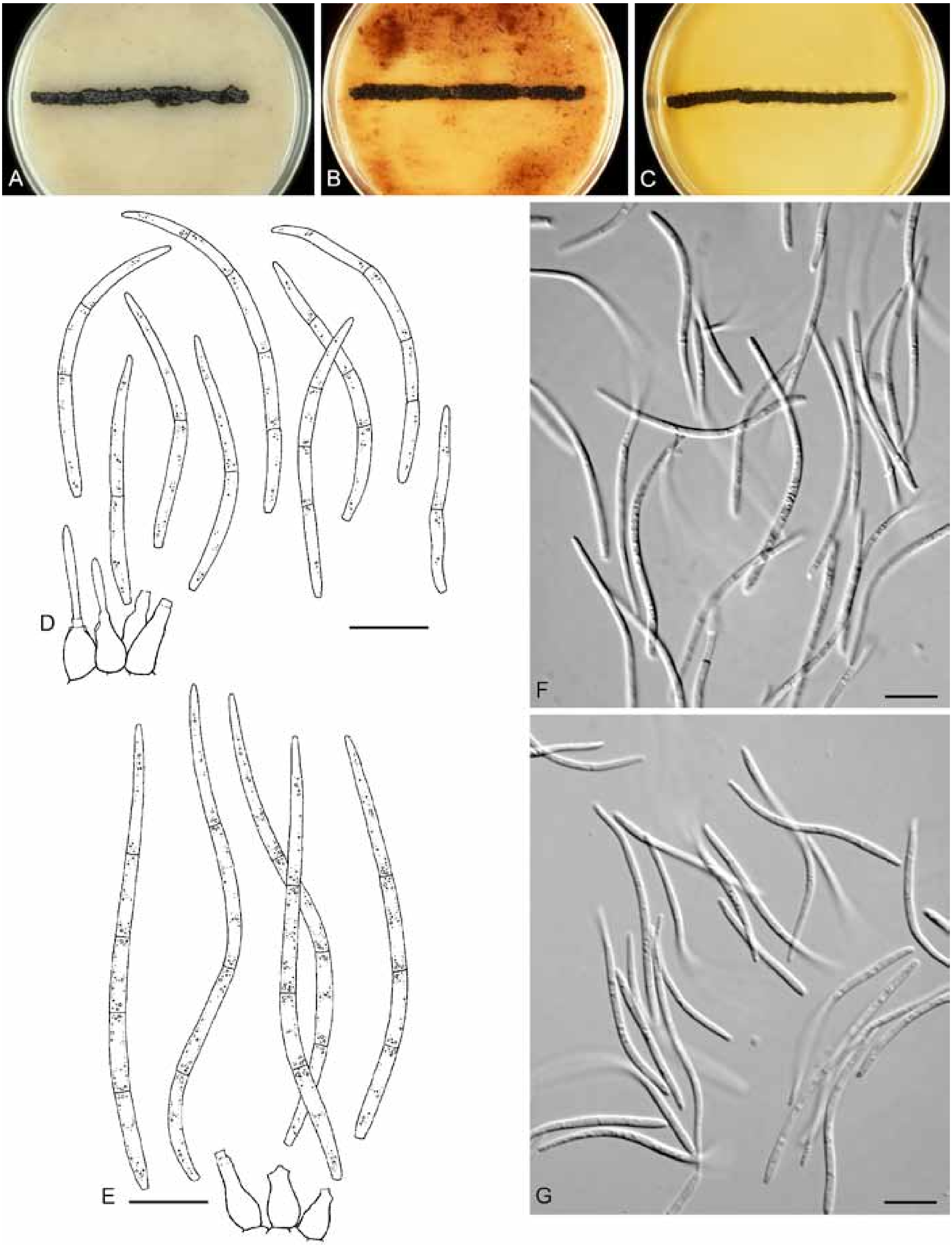


**Fig. 34.** *Septoria polygonorum*. A–C. Colonies CBS 102331 (15 °C, nUV). A. On OA. B. On CHA. C. On MEA. D. Conidia and conidiogenous cells *in planta* (CBS H-21212). E. Ibid., on OA (CBS 108982). F, G. Conidia on OA (CBS 347.67). Scale bars = 10 µm.

appressed on the above mentioned sectors; white conidial slime produced from numerous, scattered pycnidial or stromatic conidiomata; reverse dark slate blue to olivaceous-black. *Colonies* on CMA 4–5 (6–7) mm diam in 2 wk [5–7 (22–27) mm in 6 wk], as on OA, with similar fast-growing sectors. *Colonies* on MEA 3–4 mm diam in 2 wk (6–8 mm in 6 wk), the margin regular, glabrous, barely visible; colonies irregularly pustulate to hemispherical, immersed mycelium olivaceous-black to black, glabrous, the surface bearing numerous droplets of milky white to dirty buff conidial slime emerging from scattered pycnidial conidiomata; reverse olivaceous-black to black. *Colonies* on CHA 3–5 mm diam in 2 wk [7–10 (22–26) mm in 6 wk], the margin distinctly ruffled, glabrous, ochreous to greyish; colonies irregularly pustulate, immersed mycelium olivaceous-black, lacking aerial mycelium; milky white to dirty buff conidial slime emerging from scattered pycnidial conidiomata; reverse blood colour.

*Conidiomata* (OA) as *in planta*, single and pycnidial, brown to black, glabrous, 85–150 µm diam, with a single ostiolum up to 50 µm wide, rarely also merged into multilocular stromata up to 300 µm diam which may have several openings; conidiogenous cells as *in planta*, proliferating sympodially and/or percurrently, 9–20 × 4–7 µm; *conidia* as *in planta* but longer, 30–65(–72) × 1.5–2(–2.2) µm.

*Hosts*: *Polygonum* spp.

*Material examined*: **Austria**, Tirol, Ötztal, Sautens, on living leaves of *Polygonum persicaria*, 30 July 2000, G. Verkley 1024, CBS H-21213, living culture CBS 108982. **Netherlands**, prov. Utrecht, Baarn, Zandvoordtweg, same substr., 9 July 1967, H.A. van der Aa 98, CBS H-18695, living culture CBS 347.67; same substr., prov. Limburg, St. Jansberg, near Plasmolen, 9 Sep. 1999, G. Verkley 926, CBS H-21208, living cultures CBS 102330, 102331; same substr., prov. Limburg, Savelsbos, 28 June 2000, G. Verkley 967, CBS H-21212, living cultures CBS 109007, 109008; Prov. Zeeland, Zuid-Beveland, community of Borsele, Valdijk near Nisse, 27 Aug. 2001, G. Verkley 1110, CBS H-21164, living culture CBS 109834. **New Zealand**, North Island, Coromandel, Tairua Forest, along roadside of St. Hway 25, near crossing 25A, 23 Jan. 2003, G. Verkley 1843, CBS H-21242, living culture CBS 113110.

*Notes*: More than ten *Septoria* species have been described from the host genus *Polygonum*, of which *S. polygonorum* is the oldest one. The material available for the present study agrees generally well in morphology with the description of *S. polygonorum* provided by other authors. Priest (2006) described the conidiogenous cells as holoblastic (first conidium), producing subsequent conidia enterobastically, seceding at the same level (mode “Event 13: enteroblastic non-progressive”). Muthumary (1999), who studied type material of *S. polygonorum* from PC, observed sympodially proliferated cells. Priest may have overlooked the sympodial conidiogenesis, as in the present study sympodially proliferating cells were also observed in field specimens of *S. polygonorum*. The strains available from distant geographical origins showed highly similar sequences for seven loci. The multilocus phylogeny indicates a rather isolated position of *S. polygonorum* (Fig. 2).

## ***Septoria protearum*** Viljoen & Crous, S. Afr. J. Bot. 64: 144. 1998.

*Description in planta*: *Symptoms* leaf spots varied according to the host. *Conidiomata* pycnidial, epiphyllous or amphigenous, semi-immersed or becoming erumpent, subglobose to globose, dark brown to black, 65–200 µm diam; *ostiolum* central, circular, slightly papillate, 18–30(–60) µm wide, surrounding cells concolourous, releasing white cirrhi of conidial slime; *conidiomatal wall* 10–22 µm thick, composed of 3–4 layers of brown, isodiametric to irregular cells mostly 5–10 µm diam with dark brown cell walls up to 2 µm thick, sometimes with an an inner layer of hyphal to isodiametric cells 3.5–5 µm diam with thin, hyaline walls. *Conidiogenous cells* hyaline, discrete and globose or doliiform often with an elongated neck, or integrated in 1–5-septate conidiophores up to 30 µm long and narrowly to broadly ampulliform, holoblastic, proliferating percurrently with indistinct annellations as well as sympodially, 4–12 × 1.5–3.5(–5) µm. *Conidia* hyaline, cylindrical, subcylindrical to obclavate, straight to curved, rounded to somewhat pointed at the apex, attenuated gradually or more abruptly towards the truncate base, (0–)1–3(–4)-septate, not constricted around the septa, containing minute oil-droplets and granular material in rehydrated state, (6–)12–22(–30) × 1.5–2 µm (rehydrated). *Sexual morph* unknown.

*Description in vitro (18 ºC, near UV)*: *Colonies* on OA 11–16 mm diam in 1 wk, 23–30 mm in 2 wk, with an even, slightly undulating, colourless margin; colonies plane, spreading, immersed mycelium ochreous to pale luteous or rosy-buff and rarely also with greenish tinges, aerial mycelium absent or scarce with few grey to rosy-buff tufts; conidiomata developing mostly immersed in the agar, scattered or in concentric zones, olivaceous-black, releasing droplets of milky white to pale salmon conidial slime. Reverse cinnamon to hazel or fawn, or rosy-buff. *Colonies* on MEA 32–36 mm diam in 2 wk, with an even, (vinaceous) buff to colourless undulating margin; colonies restricted with a cerebriform elevated central area or lower and more spreading, radially striate, the entire surface covered by a dense mat of finely felted, somewhat woolly, white to greysh, or salmon to flesh aerial mycelium; reverse dark, fawn to brown-vinaceous, or olivaceous-black mixed with bright rust to coral. Conidiomata developing after 1 wk, mostly immersed and releasing whitish conidial slime. *Colonies* on CHA 17–19 mm diam in 1 wk, 25–31 mm in 2 wk, with an even, saffron margin with some diffuse white aerial mycelium; colonies spreading but slightly elevated in the centre, entirely covered by a dense mat of pure white, locally weakly salmon, woolly and somewhat sticky aerial mycelium, in the marginal area later with a glaucous haze; reverse in the centre chestnut, surrounded by rust and apricot zones, margin saffron. Sporulation as on MEA.

*Conidiomata* (OA) pycnidial, globose, single or merging into complexes up to 220 µm diam, brown to black, the wall composed of pale brown *textura angularis* with cells up to 10 µm diam, inner cells smaller and hyaline. *Conidiogenous cells* hyaline, discrete or integrated in simple, 1(–2)-septate conidiophores, cylindrical or narrowly to broadly ampulliform, holoblastic, proliferating sympodially, and/or percurrently with indistinct annellations, and then often showing a narrow neck of variable length, 5–10(–13.5) × 2.5–3(–3.5) µm. *Conidia* filiform to cylindrical, straight, more often curved or flexuous, or bent irregularly, rounded to somewhat pointed at the apex, attenuated gradually or more abruptly towards the narrowly truncate base, (0–)1–3-septate, not constricted at the septa, hyaline, contents as *in planta*, (8–)12–22(–25) × 1.5–2 µm (CBS 119942), (12–)15–23.5(–31) × 1–1.5 µm (CBS 179.77), 17–35 × 1–1.5(–2) µm (CBS 658.77).

*Hosts*: *Asplenium ruta-muraria*, *Boronia denticulata*, *Geum* sp., *Ligustrum vulgare*, *Myosotis* sp., *Nephrolepis* sp., *Pistacia vera*, *Protea cynaroides*, *Protea* sp., *Skimmia* sp. and *Zanthedeschia aethiopica*.

*Material examined*: **Germany**, Potsdam, Maulbeerallee beneath the Orangerie, on living leaves of *Asplenium ruta-muraria*, 17 Nov. 2005, V. Kummer 0045/3, CBS H-19729, living culture CBS 119942. **Italy**, details of loc. unknown, on *Pistacia vera*, June 1951, deposited by G. Goidánich, living culture CBS 420.51; on *Ligustrum vulgare*, June 1959, M. Ribaldi, living culture CBS 390.59. **Netherlands**, Reeuwijk, in leaf spot of *Skimmia* sp., commercially cultivated under plastic ‘tunnels’, 1996, J. de Gruyter, CBS H-21190, PD 96/11330 = CBS 364.97. **New Zealand**, Auckland, on *Myosotis* sp., Dec. 1976, H.J. Boesewinkel, CBS H=18209, living culture

CBS 179.77; same area, on *Nephrolepis* sp., Sep. 1977, H.J. Boesewinkel, CBS H-18211, living culture CBS 164.78; same area, on leaves and stems of *Boronia denticulata*, 5 Apr. 1977, H. J. Boesewinkel, CBS H-18120, living culture isolated, CBS 658.77; same area, Albert Park, on leaves of *Geum* sp., 21 Jan. 2003, G. Verkley V1821, CBS H-21233, living culture CBS 113114. **South Africa**, Gauteng Province, on leaves of *Protea cynaroides*, Sep. 1996, L. Viljoen, living ex-type culture of *Septoria protearum* STE-U 1470 = CBS 778.97; Pilgrims Rest, on *Zanthedeschia aethiopica*, 15 July 2011, P.W. Crous, living culture CPC 19675.

*Notes*: The description of *S. protearum* given by Crous *et al.* (2004) has been emended here using observations on material isolated from other hosts than *Protea*. These fungi are, despite minor differences in colony characteristics, genetically very similar, and therefore regarded as conspecific. The name *S. protearum* is adopted as it is based on well-decribed type material and ex-type cultures. The distinction with a number of strains isolated from *Citrus* spp., *Fragaria* sp., *Gerbera jamesonii*, *Gevuina avellana*, *Hedera helix*, *Lobelia erinus*, and *Masdevallia* sp. is doubtful but, based on the morphological differences in combination with a limited number of polymorphisms on the house-keeping genes, they are treated here as part of *Septoria citri* (which clusters in the *S. protearum* complex), which is a species complex that needs to be further resolved. Material studied and some cultural characters of CBS 113392 are provided below.

*Additional material of the Septoria citri complex examined*: Country and host unknown, May 1937, L.L. Huiller, living culture CBS 315.37 (sub *Septoria citri*). **Argentina**, in leaf spot of *Lobelia erinus*, S. Wolcon *s.n.*, 'V1466', living culture CBS 113392. **Italy**, Sicilia, on *Gerbera jamesonii*, Nov. 1961, W. Gerlach, living cultures CBS 410.61 = BBA 9588 (sub *S. gerberae*). **Netherlands**, Paterwolde, in glasshouse, in leaf spots of *Masdevallia* sp., Feb. 1998, W. Veenbaas-Rijks (CBS H-18124), living culture CBS 101013 (sub *S. orchidacearum*). **New Zealand**, leaf of *Gevuina avellana*, Nov. 1998, S. Ganev, living culture CBS 101354; Waitakere, culture isolated from leaf of *Fragaria* sp., Nov. 1975, H. J.Boesewinkel, living culture CBS 177.77 (sub *Septoria aciculosa*). **Portugal**, Algarve, Monchique, in leaf spot on *Hedera helix*, 14 June 1988, H.A. van der Aa 10494, living culture CBS 566.88 (sub *S. hederae* Desm.).

*Description in vitro (18 ºC, near UV, CBS 113392)*: *Colonies* 23–26 mm diam in 2 wk, with an even, glabrous colourless margin; colonies spreading, immersed mycelium orange, lacking aerial mycelium; reverse bay to scarlet. Conidiomata developing in concentric patterns, immersed and on the agar surface, releasing milky white masses of conidial slime. *Colonies* on MEA 17–23 mm diam in 2 wk, with an even colourless margin mostly covered by white aerial hyphae; colonies spreading but developing cerebriform elevations in the centre, immersed mycelium livid vinaceous to vinaceous buff, with diffuse to dense, appressed, whitish to vinaceous buff aerial mycelium.

*Conidiogenous cells* (OA) varied in shape, globose, doliiform to ampulliform or cylindrical, discrete, rarely integrated in 1-septate conidiophores, holoblastic, proliferating sympodially, and also percurrently with several close and indisctinct annellations, hyaline, 4.5–8(–10) × 3–5 µm. *Conidia* filiform to cylindrical, straight to flexuous, often weakly curved, attenuated gradually to a narrowly rounded to somewhat pointed apex, attenuated gradually or more abruptly to a narrowly truncate to almost rounded base, contents granular with few minute oil-droplets in the living state, (0–)1–3-septate, (12–)15–28 × 1.5–2 µm (living); CBS 177.77 (OA) 17–35.5 × 1–2 µm (living).

***Septoria putrida*** Strasser, Verh. zool.-bot. Ges. Wien 65: 180. 1915. Fig. 35F–J.

*Description in planta*: *Symptoms* definite leaf spots, hologenous or epigenous, scattered or in clusters, initially pale yellowish, later grey to white, surrounded by a black elevated zone or merely delimited by leaf veins. *Conidiomata* pycnidial, one to several in each leaf spot, scattered, semi-immersed, predominantly epiphyllous, pale brown, lenticular to globose, 80–180 µm diam; *ostiolum* circular, central, initially 25–50 µm wide, later opening to 80 µm diam, lacking distinctly differentiated cells; *conidiomatal wall* composed of *textura angularis* without distinctly differentiated layers, mostly 10–20 µm thick, the outer cells with brown, somewhat thickened walls and 4.5–10 µm diam, the inner cells hyaline, thin-walled, 4–9 µm diam. *Conidiogenous cells* hyaline, discrete or integrated in short, 1-septate conidiophores, cylindrical, or ampuliform with a mostly relatively short, but sometimes strongly elongated neck (8–10 µm long), hyaline, holoblastic, proliferating percurrently with distinct annellations, sometimes also sympodially, 6.5–12(–19.5) × 3.5–5 µm. *Conidia* cylindrical, usually strongly curved or flexuous, gradually attenuated to a rounded apex, gradually attenuated into a broadly truncate base, (0–)3–5-septate, not or indistinctly constricted around the septa, hyaline, contents with several small guttulae and numerous granules in each cell in the living state, oil-droplets rarely merged into larger guttules in the rehydrated state, (32–)40–70(–85) × 2–2.5(–3.0) µm (rehydrated). *Sexual morph* unknown.

*Description in vitro*: *Colonies* on OA 5.5–8.5 mm diam in 12 d (13–15 mm in 3 wk; 50–55 mm in 7 wk), with an even, somewhat undulating, glabrous, colourless margin; colonies plane, immersed mycelium buff to primrose, in some sectors also with dark herbage green to dull green radiating hyphal stands, after 7 wk mostly dark greenish; pycnidial conidiomata scattered immersed and superficial, which are first dark olivaceous, then almost black, glabrous or beset with short hyphal protrusions, 150–450 µm diam, mostly with a single ostiolum placed on short papillae, that releases pale whitish or buff conidial slime; aerial mycelium diffuse, woolly-floccose, white to grey; reverse dull green to olivaceous-black in the centre. *Colonies* on CMA 4–7 mm diam in 12 d (11–14 mm in 3 wk; 50–55 mm in 7 wk), with an even, glabrous, colourless margin; immersed mycelium apart from margin olivaceous-black, at the margin with some local production of a coral pigment after 7 wk; aerial mycelium higher, diffuse woolly, greyish; reverse darker as on OA; conidiomata similar as on OA. *Colonies* on MEA 2.5–5 mm diam in 12 d (11–13 mm in 3 wk; 42–46 mm in 7 wk), with an even to ruffled, glabrous, colourless to buff margin, which may be irregularly lobate after 7 wk; colonies restricted, pustulate to almost hemispherical, immersed mycelium rather dark, aerial mycelium diffuse, short, felty white, behind the margin denser and higher; superficial mature conidiomata releasing first milky white, later pale luteous to saffron, then salmon conidial slime; reverse olivaceous-black in the centre, near the margin honey. *Colonies* on CHA 5–7 mm diam in 12 d (8–11 mm in 3 wk), with an irregular, ruffled, colourless margin, older colonies distinctly lobate; the surface mostly covered by a low, dense to diffuse, felty white, later grey aerial mycelium, near the margin pure white felty to tufty; further as on MEA; conidial slime abundantly produced, first milky white, later salmon or saffron; reverse in the centre blood colour, dark brick to cinnamon at the margin.

*Conidia* as *in planta*, (0–)3–5(–6)-septate, 40–85(–97) × 2–2.5(–3) µm.

*Host*: *Senecio nemorensis*.

*Material examined*: **Austria,** Tirol, Ober Inntal, Samnaun Gruppe, Lawenalm, on living leaves of *Senecio nemorensis* subsp. *fuchsii*, 8 Aug. 2000, G. Verkley 1052a,

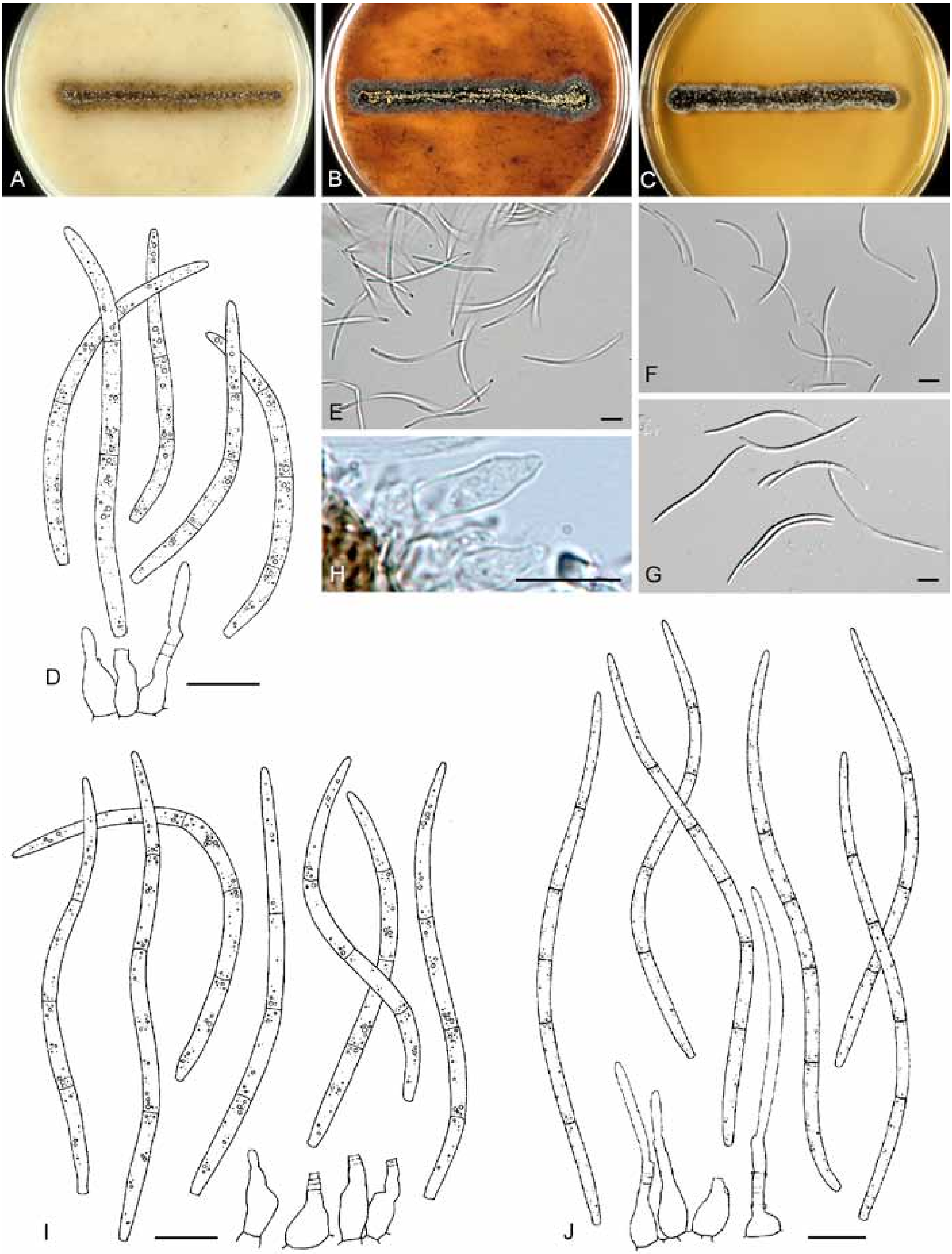


**Fig. 35.** A–E. *Septoria senecionis*. A–C. Colonies CBS 102381 (15 °C, nUV). A. On OA. B. On CHA. C. On MEA. D. Conidia and conidiogenous cells *in planta* (CBS H-21219, epitype). E. Conidia *in planta* (CBS H-21219). F–J. *Septoria putrida*. F, G. Conidia *in planta* (CBS H-21174). H. Conidiogenous cells *in planta* (CBS H-21174). I. Conidia and conidiogenous cells *in planta* (CBS H-21174). J. Ibid., on OA (CBS 109088). Scale bars = 10 µm.

CBS H-21174, living cultures CBS 109087, 109088.

*Notes*: *Septoria putrida* was originally described from *Senecio nemorensis* found in Austria (Sonntagberg), reportedly with

0(–9–11?)-septate conidia, 70–80 × 2 µm. The multilocus sequence analysis indicates that *S. putrida* and *S. senecionis* are closely related but genetically distinct species (Fig. 2). Morphologically these sister taxa can best be distinguished based on conidial length; conidia in *S. putrida* can be up to 85 µm long *in planta* and even longer (up to 97 µm) in culture, whereas those of *S. senecionis* are rarely longer than 65 *in planta* and not over 70 µm long in culture.

Thirteen more taxa have been described in *Septoria* on *Senecio*, of which *S. anaxaea* Sacc. is another distinctive, long-spored species described from *Senecio grandidentatus* (?= *S. praealtus*), and recently also from several other *Senecio* spp. in Australia. According to Priest (2006), conidia are 3(–6)-septate, 28–75 × 2.5–3 µm (50–130 × 3.5–5 µm, Teterevnikova-Babayan 1987). Most other *Septoria* spp. on *Senecio* may be synonyms of *S. senecionis*, and this needs to be confirmed by study of the type material.

***Septoria rumicum*** Sacc. & Paol., in Saccardo, Bull. Soc. r. Bot. Belg. 28: 23. 1889.

*Description in vitro*: *Colonies* on OA 3–5 mm diam in 3 wk, with an even colourless margin; colonies restricted, irregularly pustulate, immersed mycelium olivaceous-black mostly hidden under a low, dense mat of felty grey to white aerial mycelium; reverse olivaceous-grey. *Colonies* on MEA 6–10(–12) mm diam in 3 wk, with an even or lobed, colourless margin; colonies restricted, irregularly pustulate, immersed mycelium appearing olivaceous-grey under a dense mat of woolly-floccose, white to grayish aerial mycelium; reverse olivaceous-black. No sporulation observed.

*Conidia* (OA) cylindrical, filiform, straight or slightly curved, attenuated gradually towards a narrowly rounded to almost pointed apex, attenuated gradually or more abruptly towards the narrowly truncate base, 3–5(–7)-septate, mostly 60–82 × 2–3 µm.

*Hosts*: *Rumex* spp. (*R. acetosa*, *R. alpinum*).

*Material examined*: **France**, Corrèze, Roumignac, on leaves of *Rumex acetosa*, H.A. van der Aa 5338, CBS H-18050, living culture CBS 503.76 ; Haute-Savoie, Mt. Beaudin, on stem of *R. alpinus*, July 1978, H.A. van der Aa 9594c, CBS H-18163, living culture CBS 522.78.

*Notes*: Jørstad (1965) noted that *S. rumicis* Trail, which was published in the same year as *S. rumicum*, may be conspecific. *Septoria acetosae* Oud. was also regarded as a synonym. According to Saccardo (1892, Syll. Fung. 10: 380), *S. rumicum* produces mostly epiphyllous pycnidia 100–125 µm diam, and continuous (?) conidia 50–68 × 3 µm. *Septoria rumicis* produces chiefly epiphyllous pycnidia 90–100 µm diam and conidia 24–40 × 2–2.5 µm (Teterevnikova-Babayan 1987), according to Jørstad (1965), 20–50 × 2.5–3.5, with 2–3(–5) septa. *Septoria acetosae* was treated as a separate species by Teterevnikova-Babayan (1987). According to the latter author, it is characterised by 1–3-septate conidia, 28–50 × 3–5 µm. As the conidial sizes of the material available here agree best with the original description of *S. rumicum*, this name is adopted here. Several other species of *Septoria* have been described from *Rumex*, most of which need to be restudied to assess their status.

***Septoria scabiosicola*** (Desm.) Desm., Annls Sci. Nat., sér. 3, Bot. 20: 96. 1853. Fig. 36.
*Basionym*: *Depazea scabiosicola* Desm., Annls Sci. Nat., sér. 2, Bot. 6: 247. 1836.

*Description in planta*: *Symptoms* leaf spots numerous but small, circular, some merging to irregular patterns, centre white, surrounded by a relatively broad, dark margin with a distinct red or purple periphery. *Conidiomata* pycnidial, epiphyllous but sometimes also visible from the underside of the lesion, one to a few in each leaf spot, subglobose to globose, brown to black, usually fully immersed, 65–130 µm diam; *ostiolum* central, initially circular and 35–60 µm wide, later becoming more irregular and up to 80 µm wide, surrounding cells concolorous to pale brown; *conidiomatal wall* about 10–15 µm thick, composed of a homogenous tissue of hyaline, angular cells 2.5–6.5 µm diam, the outermost cells pale brown with somewhat thickened walls, the inner cells thin-walled. *Conidiogenous cells* hyaline, discrete, doliiform, or narrowly to broadly ampulliform, holoblastic, with a relatively narrow elongated neck, proliferating percurrently several times with distinct annellations, often also sympodially after a few percurrent proliferations, 6–9(–12) × 2.5–3(–5) µm. *Conidia* filiform to filiform-cylindrical, straight, slightly curved to flexuous, attenuated gradually to a narrowly pointed apex and narrowly truncate base, (0–)3–5(–6)-septate (septa very thin and easily overlooked), not constricted around the septa, hyaline, contents with several minute oil-droplets and granular material in each cell in the living state, with minute oil-droplets and granular contents in the rehydrated state, (17–)30–55 (–79) × 1–2 µm (living; rehydrated, 1–1.8 µm wide). *Sexual morph* unknown.

*Description in vitro*: *Colonies* on OA 9–13 mm diam in 2 wk, with an even, glabrous, colourless margin; immersed mycelium mostly homogeneously coral to scarlet, the pigment diffusing beyond the colony margin; in the centre black and slightly elevated due to immersed and more frequently superficial pycnidia, surrounded by an area with more scattered pycnidia, releasing pale flesh droplets of conidial slime; aerial mycelium scanty, consisting of minute white tufts; reverse scarlet to coral, the centre darker, blood colour. Colonies may develop sectors that are unpigmented and glabrous. *Colonies* on CMA 8–11 mm diam in 2 wk; similar as on OA, but generally less strongly pigmented. *Colonies* on MEA 6–9 mm diam in 2 wk, the margin irregular; colonies restricted, the centre elevated and cerebriform to irregularly pustulate, up to 2 mm high, the surface pale brown, later black, with scanty white areal mycelium; reverse of the colony dark brick, paler towards the margin. *Colonies* on CHA 6–11 mm diam in 2 wk, with an even, glabrous, colourless margin; immersed mycelium greenish grey to dark slate blue, throughout covered by well-developed, tufty whitish grey arial mycelium that later attains a reddish haze; reverse blood colour, but margin paler; in the central part of the colony numerous pycnidia develop, releasing pale vinaceous to rosy-buff conidial slime; in older colonies the centre becomes cerebriform and up to 3mm high, much as on MEA.

*Conidiomata* (OA) as *in planta*, pycnidial, sometimes merged into larger complex stromata dark brown, glabrous, 80–180 µm diam, with a single ostiolum, or without preformed opening and simply bursting open; *conidiogenous cells* as *in planta*, but more often integrated in 1–2-septate conidiophores, often only proliferating percurrently and/or sympodially, 6–15 × 3–7.5 µm; *conidia* as *in planta*, 1–6(–7)-septate, not constricted around the septa, hyaline, with several minute oil-droplets and numerous granules in each cell, (30–)40–80(–100) ×1.5–2(–2.5) µm.

*Hosts*: *Knautia* spp., *Succisa* spp. and *Scabiosa* spp.

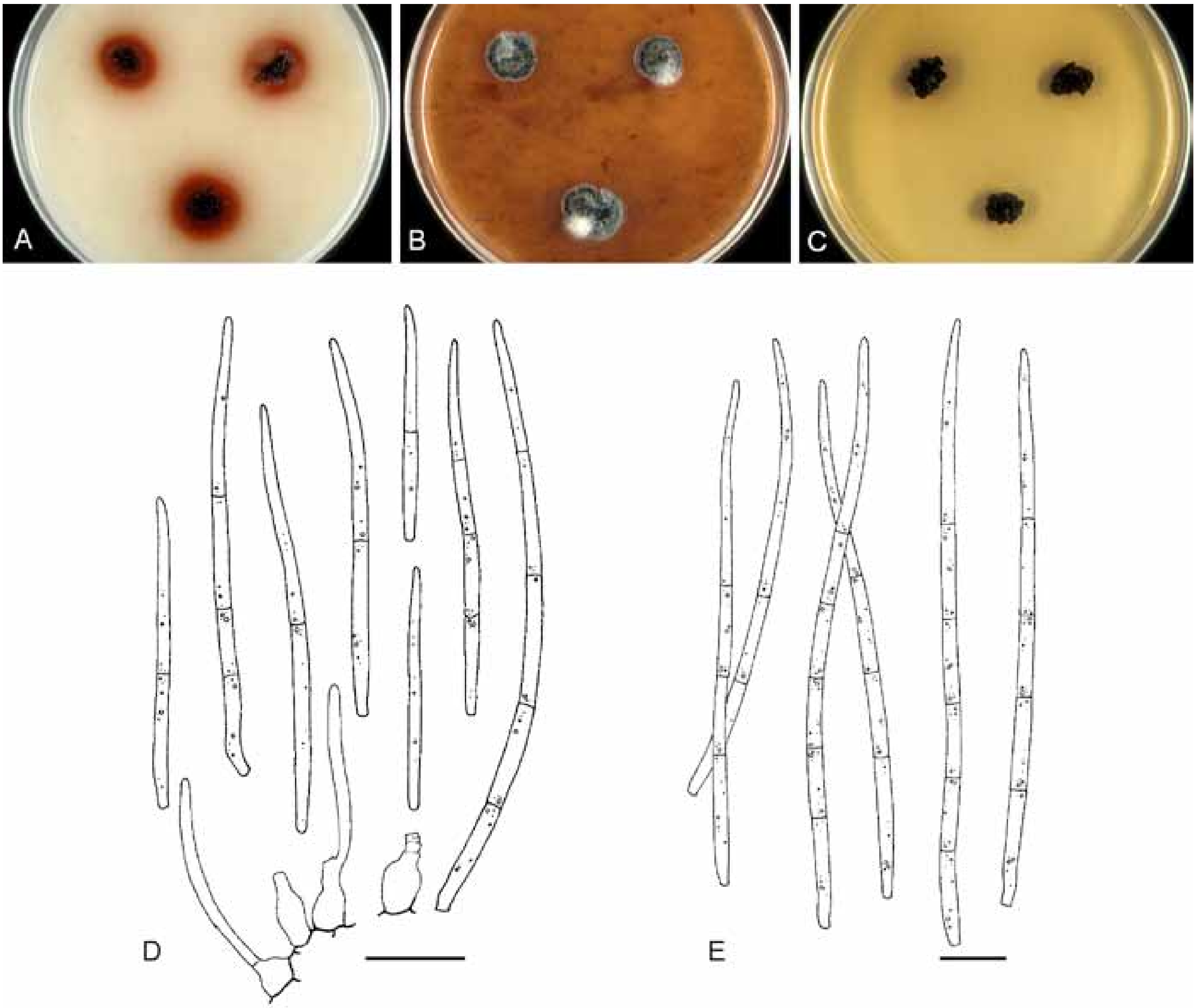


**Fig. 36.** *Septoria scabiosicola*, CBS 102333. A–C. Colonies (15 °C, nUV). A. On OA. B. On CHA. C. On MEA. D. Conidia and conidiogenous cells *in planta* (CBS H-21180). E. Conidia on OA (CBS 109021). Scale bars = 10 µm.

*Material examined*: **Austria**, Tirol, Ötztal, Brunau, along roadside, on living leaves of *Knautia arvensis*, 30 July 2000, G. Verkley 1023, CBS H-21184, living cultures CBS 108981, 109021; Tirol, Ötztal, Sautens, in meadow, 30 July 2000, G. Verkley 1030, CBS H-21180, living cultures CBS 108985, 108986; Tirol, Ötztal, Ötz, near Piburger See along forest road, on living leaves of *K. dipsacifolia*, 1 Aug. 2000, G. Verkley 1033, CBS H-21179, living cultures CBS 109092, 109093; Tirol, Ober Inntal, Samnaun Gruppe, Serfaus, on living leaves of *K. dipsacifolia*, 9 Aug. 2000, G. Verkley 1062, CBS H-21172, living cultures CBS 109128, 109129. **France**, on living leaves of *Succissa pratensis,* H.A. van der Aa 11375, living culture CBS 182.93. **Germany**, on living leaves of *Scabiosa lucida,* R. Schneider, living culture CBS 356.58. **Netherlands**, prov. Gelderland, near Winssen, along Waalbanddijk, on living leaves of *K. arvensis*, 9 Sep. 1999, G. Verkley 919, CBS H-21201, living cultures CBS 102333, 102334; same loc., host, date, G. Verkley 920, CBS H-21203, living cultures CBS 102335, 102336; same loc., host, date, G. Verkley 921, CBS H-21202; unknown host, July 1937, living culture CBS 317.37.

*Notes*: Jørstad (1965) and Radulescu *et al.* (1973) reported variability in the maximum length of conidia on the host plant. This is confirmed in the present study, where the highest and lowest maximum lengths observed in specimens were 79 and 42 µm, in specimens CBS H-21184 and CBS H-21180, respectively. Both specimens were collected from the same host at comparable altitudes (ca. 700 m), from localities in Tirol, Austria less than three kilometers apart. Isolates obtained from these two collections proved equally capable of producing conidia up 100 µm long under standard conditions of incubation.

These isolates as well as other from *Knautia arvensis*, and strains originating from *Scabiosa* and *Succissa* showed no correlation between conidial sizes and host, and although some variation in gene sequences was observed, especially in Act and EF, the data firmly support the hypothesis that they belong to a single taxon. Several *formae* have been described in *S. scabiosicola*, but evidence to support these as separate entities is wanting. *Septoria scabiosicola* is relatively distantly related from other members of the *Septoria* clade (Fig. 2).

***Septoria senecionis*** Westend., Bull. Acad. r. Belg., Cl. Sci., Sér. 2, 19: 121. 1851. Fig. 35A–E.

*Description in planta*: *Symptoms* indefinite, hologenous leaf lesions, often eventually affecting large parts of the leaf lamina, initially pale yellowish, later pale to dark brown. *Conidiomata* pycnidial, numerous, scattered, immersed, mostly epiphyllous, pale brown, lenticular to globose, (45–)65–120(–160) µm diam; *ostiolum* circular, central, initially 20–35 µm wide, later opening to 60 µm diam, lacking distinctly differentiated cells; *conidiomatal wall* composed of *textura angularis* without distinctly differentiated layers, mostly 15–20 µm thick, the outer cells with brown, somewhat thickened walls and 4.5–10 µm diam, the inner cells hyaline and thin-walled and of comparable diam. *Conidiogenous cells* hyaline, discrete or integrated in short, 1–2-septate conidiophores, cylindrical, or ampuliform with a relatively short neck, hyaline, holoblastic, proliferating sympodially, and sometimes also percurrently with indistinct annellations, 6.5–10(–12.5) × 2.5–4.5 µm. *Conidia* cylindrical, weakly to strongly curved, or flexuous, gradually attenuated to a rounded apex, gradually or more abruptly attenuated into a broadly truncate base, (0–)2–5(–6)-septate, not or indistinctly constricted around the septa, hyaline, contents with several small guttules and numerous granules in each cell in the living state, oil-droplets rarely merged into larger guttules in the rehydrated state, (20–)40–65 × 2–2.5(–3) µm (rehydrated). *Sexual morph* unknown.

*Description in vitro*: *Colonies* on OA 7–10 mm diam in 2 wk (22–26 mm in 6 wk), with an even, somewhat undulating, glabrous, colourless margin; colonies spreading, the surface plane, immersed mycelium pale luteous or buff, with scattered immersed and superficial pycnidial conidiomata, which are first dark olivaceous, then almost black, glabrous, 150–450 µm diam, with a single or several (up to 5!) ostioli placed on short papillae or more elongated necks (up to 350 µm), that release buff to rosy-buff later salmon conidial slime; aerial mycelium diffuse, woolly-floccose, white; reverse honey, but isabelline to hazel in the centre. *Colonies* on CMA 6–8 mm diam in 2 wk (18–23 mm in 6 wk), with an even, glabrous margin; as on OA but immersed mycelium with a greenish haze; aerial mycelium higher and reverse darker, later hazel with olivaceous and yellow tinges; conidiomata similar as on OA. *Colonies* on MEA 7–9 mm diam in 2 wk (18–21 mm in 6 wk), with an even or somewhat undulating, glabrous, buff to honey margin; colonies pustulate to almost hemispherical, immersed mycelium rather dark, near the margin covered by woolly to felty white aerial mycelium; mostly composed of spherical conidiomatal initials, superficial mature conidiomata releasing rosy-buff to salmon, later honey conidial slime; reverse dark brick in the centre, near the margin cinnamon to honey. *Colonies* on CHA 7–14 mm diam in 2 wk (20–28 mm in 6 wk), with an irregular, buff margin covered by a diffuse, felty white, later grey aerial mycelium; further as on MEA, but the colony surface less elevated and especially near the margin with greyish felty to tufty aerial mycelium; conidial slime abundantly produced, first rosy-buff, later salmon to ochreous; reverse in the centre blood colour, dark brick to cinnamon at the margin.

*Conidiomata* on OA see above. Conidia as *in planta*, mostly (0–)3–5(–6)-septate, 44–63(–70) × 2.5–3 µm.

*Hosts*: *Senecio fluviatilis* and *S. nemorensis*.

*Material examined*: **Belgium**, Château de Namur, on leaves of *Senecio sarracenica*, 1829, A. Bellynck, **isotype** BR-MYCO 155500-09. **Netherlands**, Prov. Gelderland, Millingen a/d Rijn, Millingerwaard, on living leaves of *S. fluviatilis*, 6 Oct. 1999, G. Verkley 939, **epitype designated here** CBS H-21219 "MBT175358", living cultures ex-epitype CBS 102366, 102381.

*Notes*: The first *Septoria* that was described on the genus *Senecio* was *S. senecionis*. The type host is *Senecio sarracenica* (= *Senecio fluviatilis*), and in later literature it has also been reported from several other species of *Senecio* (Radulescu *et al.* 1973). According to the diagnosis by Westendorp, the conidia are 40 × 1.5 µm and 3–4-septate. Vanev *et al.* (1997) described the conidia of *S. senecionis* as 2–6-septate, 29–68 × 2–2.5 µm, Radulescu *et al.* (1973) as 3–4-septate, 33–57 × 1.2–2 µm. By examining the type specimen from BR it is here confirmed that conidia are in fact wider than described by Westendorp. It contains a single leaf with a few lesions, and conidia observed are 30–55 × 1.5–2.5 µm, and mostly 3–5-septate. The fresh material that was collected in the Netherlands from the same host species, *Senecio fluviatilis*, and from which CBS 102366 and 102381 were isolated, is in sufficient agreement with the type and is therefore designated here as epitype of *S. senecionis*. Differences with *Septoria putrida* are discussed under that species.

***Septoria sii*** Roberge ex Desm., Pl. crypt. Fr., Fasc. 44, no 2185; Annls Sci. Nat., sér. 3, Bot. 20: 92. 1853. Fig. 37.

*Description in planta*: *Symptoms* leaf spots, yellow to brown, initially vaguely delimited but later well-delimited by veinlets, scattered, later often confluent over large areas, visible on both sides of the leaf. *Conidiomata* pycnidial, epiphyllous, rarely also hypophyllous, single, scattered or in small clusters, globose to subglobose, immersed, (60–)80–110 µm diam; ostiolum circular, central, 12.5–25(–35) µm wide, surrounding cells concolorous; conidiomatal wall composed of *textura angularis* 5–10 µm thick, with an outer layer of cells 3–4.5 µm diam with brown, thickened walls, and an inner layer of hyaline and thin-walled cells, 2.5–4 µm diam. *Conidiogenous cells* hyaline, broadly or elongated ampulliform, normally with a distinct neck, hyaline, holoblastic, proliferating percurrently, annellations indistinct, 5–8.5 × 3–5 µm. *Conidia* cylindrical, straight, curved, or flexuous, gradually attenuated to a relatively broadly rounded apex, more or less abruptly attenuated into a truncate base, 1–3(–4)-septate, slightly to distinctly constricted around the septa in the fresh, fully hydrated state, hyaline, containing one to several relatively large oil-droplets in each cell, in the rehydrated state with irregular oil-masses (20–)29–35(–42) × 2–2.5(–3) µm (living; rehydrated, 1.5–2 µm wide). *Sexual morph* unknown.

*Description in vitro*: *Colonies* on OA 4–9 mm diam in 2 wk [(15–) 19–23 mm in 6 wk], with an even, glabrous, colourless margin; colonies remaining almost plane, immersed mycelium olivaceous-black, locally however peach is dominant, which becomes scarlet after several wk; aerial mycelium mostly well-developed, woolly-floccose, white; scattered, mostly immersed pycnidial to stromatic conidiomata developing in the centre, releasing droplets of milky white to rosy-buff conidial slime; reverse dark slate blue to olivaceous-black, and locally peach, the pigment not diffusing into the medium. *Colonies* on CMA up to 1.5 mm diam in 2 wk [7–10 (–25) mm in 6 wk], as on OA, but peach pigment diffusing into the medium, while the colony itself is predominantly olivaceous-black. Colonies frequently develop faster growing sectors that first are buff and sporulate directly from the mycelium, later become pale luteous with a distinct scarlet pigmentation and forming numerous mostly superficial pycnidia. *Colonies* on MEA 3–6 mm diam in 2 wk [12–14(–26) mm in 6 wk], the margin ruffled, olivaceous-black; colony concolorous, irregularly pustulate-worty, covered by diffuse to dense felty white or greyish aerial mycelium; numerous conidiomatal initials developing at the surface, mature ones releasing cirrhi of conidia that first are milky white, later salmon, sometimes merging to form slimy masses covering areas of the colony surface; the agar surrounding the colony slightly discoloured by diffusing pigment(s). *Colonies* on CHA 5–6 mm diam in 2 wk [8–13(–15) mm in 6 wk], as on MEA; some parts of the colonies

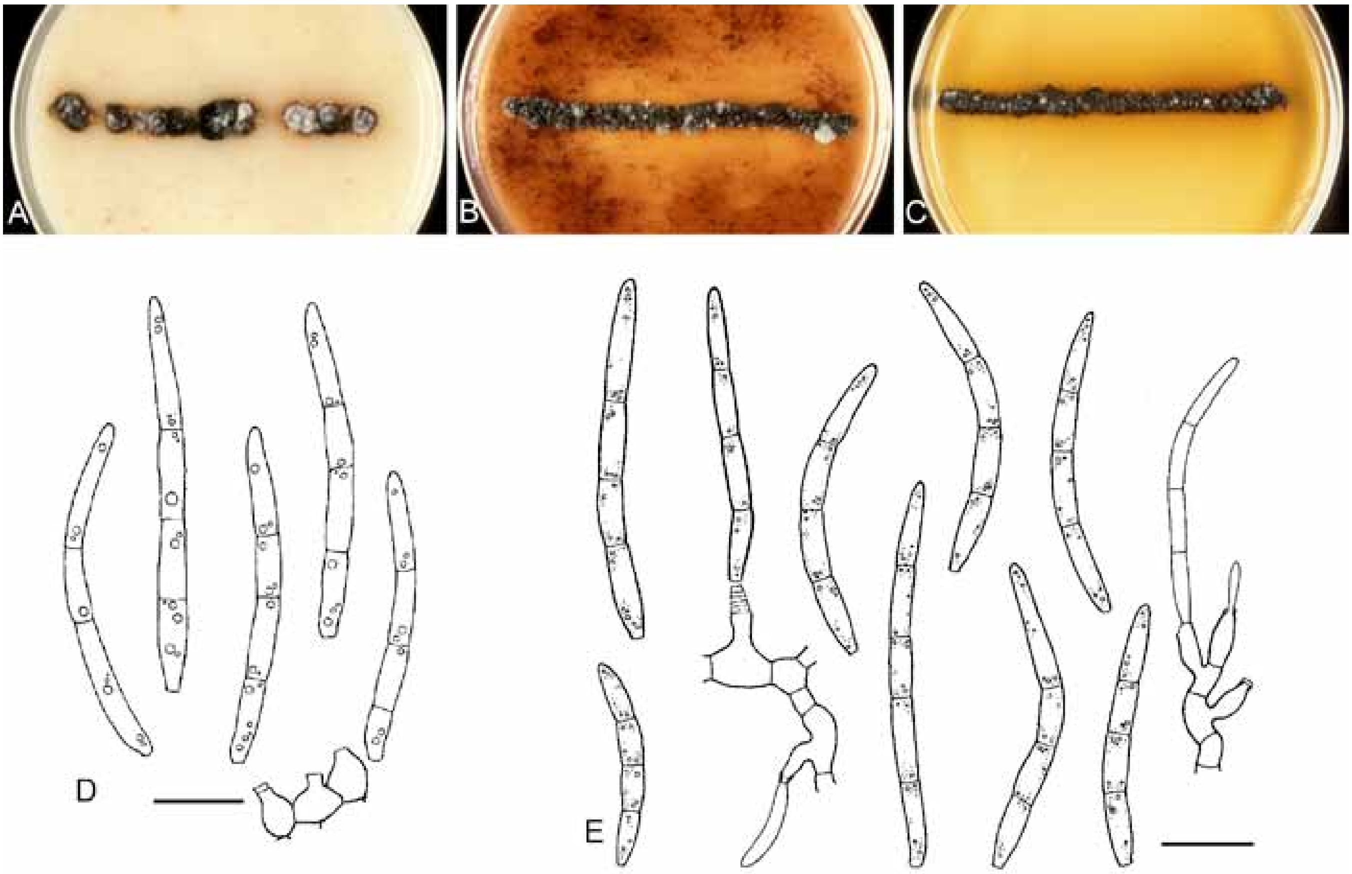


**Fig. 37.** *Septoria sii*. A–C. Colonies CBS 102370 (15 °C, nUV). A. On OA. B. On CHA. C. On MEA. D. Conidia and conidiogenous cells *in planta* (CBS H-21223). E. Ibid., on OA (CBS 102369). Scale bars = 10 µm.

pale ochreous, tardily sporulating, releasing pale flesh to salmon droplets of conidial slime from superficial pycnidial conidiomata.

Cultures sporulating with conidiogenous cells developing in (superficial) mycelial hyphae, solitary or in sequences, in addition to c*onidiomata*. *Conidiomata* on OA pycnidial, single, dark brown to black, 80–185 µm diam, ostiolum single 30–60 µm diam, or stromatic without a differentiated opening and up to 220 µm diam; conidiogenous cells inside pycnidia as *in planta* but often with more elongated neck, holoblastic, percurrently proliferating one to several times with indistinct annellations, 7–12.5 × 3–6 µm. *Conidia* as *in planta*, 22–43 × 2.2–2.5 µm.

*Hosts*: *Sium latifolium*, other *Sium* spp. and *Berula erecta* (syn. *Sium erectum*).

*Material examined*: **Netherlands**, Prov. Friesland, Terschelling, ditch in polder S of Hoorn, on living leaves of *Berula erecta*, 19 Aug. 1995, H.A. van der Aa 12029, CBS H-18173, living culture CBS 118.96; same substr., Prov. Utrecht, 's Graveland, Kortenhoefse plassen, "Oppad", 14 Oct. 1999, G. Verkley & H.A. van der Aa 945, CBS H-21223, living culture CBS 102369; same loc., substr., date, G. Verkley & H.A. van der Aa 946, CBS H-21222, living culture CBS 102370.

*Notes*: The stout conidia with blunt apices and distinct constrictions around the septa (at least in the living, turgescent state) and the absence of sympodial proliferation in conidiogenesis distinguish this species from most other *Septoria* on *Apiaceae* here investigated, including *S. apiicola*. According to the original diagnosis, based on material from *Sium latifolium* in France, the conidia are 30–40 × 2.5 µm. Most later authors have reported somewhat different size ranges; for example Teterevnikova-Babayan (1985) observed conidia 20–60 × 1–1.5 µm, Vanev *et al.* (1997) 20–41 × 1.5–2.2 µm, and Radulescu *et al.* (1973) reported 30–40 × 2–3 µm. The material available for this study proved homogeneous in morphology and genotype. The phylogenetic data indicate that this species is very closely related to *S. mazi*, a fungus occurring on *Mazus japonica* (*Scrophulariaceae*), but also to *S. aegopodina* on *Aegopodium* sp. (*Apiaceae*). The conidia of *S. mazi* morphologically resemble those of *S. sii*, but they are narrower and the septa normally indistinct [15–42 × 1.5–2(–2.5) µm, Shin & Sameva 2004].

## ***Septoria sisyrinchii*** Speg., An. Mus. nac. Hist. nat. B. Aires, 6: 324. 1899. Fig. 38.

*Description in planta*: *Symptoms* leaf lesions developing in large areas of the leaf lamina that first turn yellow, indefinite, hologenous, pale to dark brown, appearing black due to numerous conidiomata. *Conidiomata* pycnidial, amphigenous, numerous, semi-immersed to immersed, subglobose to globose, black, 70–100(–120) µm diam; *ostiolum* central, circular, 15–35 µm wide, sometimes opening more widely, releasing white to pale yellowish cirrhi of conidial slime, surrounding cells concolourous or somewhat darker; *conidiomatal wall* 15–20 µm thick, composed of an outer layer of isodiametric cells 5–8 µm diam with brown, slightly thickened cell walls up to 1 µm thick, and an inner layer of globose to isodiametric cells 3–6 µm diam with thin, hyaline walls. *Conidiogenous cells* hyaline, discrete or integrated in 1-septate conidiophores up 15 µm long, cylindrical, or ampulliform, holoblastic, proliferating sympodially, percurrent proliferations not observed, 5–10 × 2.5–3.5 µm. *Conidia* cylindrical to cylindrical-filiform, slightly to strongly curved, sometimes flexuous, narrowly rounded to somewhat pointed at the apex, attenuated gradually or more abruptly towards

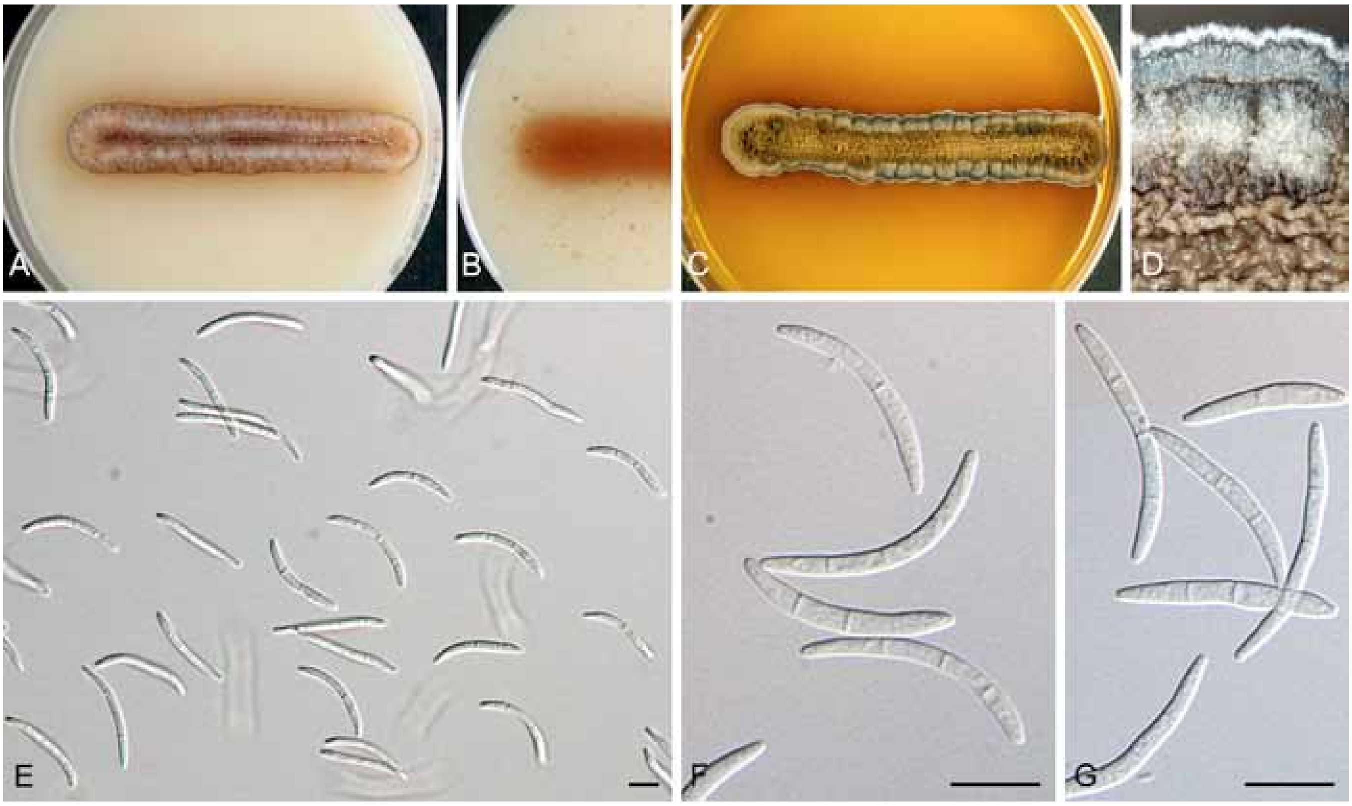


**Fig. 38.** *Septoria sisyrinchii*, CBS 112096. A–D. Colonies (15 °C, nUV). A. On OA. B. Ibid., reverse. C. On MEA. D. Ibid., detail of colony margin. E–G. Conidia on OA. Scale bars = 10 µm.

the truncate base, (0–)1–3-septate, not constricted around the septa, hyaline, containing minute oil-droplets and granular material in the rehydrated state, (15.5–)20–30 × 1.5–2(–2.5) µm (rehydrated). *Sexual morph* unknown.

*Description in vitro (18 ºC, near UV)*: *Colonies* on OA 11–15 mm diam in 2 wk, with an even, buff margin; colonies restricted to spreading, immersed mycelium a mixture of luteous and saffron, the surface provided with a very diffuse, white fluffy to woolly aerial mycelium, which is denser in zones; reverse sienna; numerous conidiomata developing after 5–7 d especially in the centre, releasing milky white rosy-buff conidial slime. *Colonies* on MEA 10–14 mm diam in 2 wk, with a buff, minutely ruffled margin; colonies restricted, radially striate and somewhat elevated in the centre, the surface dirty greyish brown, soon covered by large masses ochreous to pale brown masses of conidia. Reverse chestnut to blood color, or brown-vinaceous.

Conidiomata and conidiogenous cells as *in planta*. Conidia as *in planta*, mostly 18–35× 1.5–2.5 µm.

*Hosts*: *Sisyrinchum* spp.

*Material examined*: **New Zealand**, Auckland, Manurewa, Auckland Botanical Gardens, on leaf of *Sisyrinchum* sp., 28 Dec. 2002, C. F. Hill LYN 755, CBS H-21259, living culture CBS 112096.

*Notes*: The material from Auckland agrees well with the original diagnosis of *S. sisyrinchii*, which was based on material from *Sisyrinchium bonariense* in Argentina. Conidia were described as 0–3-septate, 15–24 × 2.5 µm. The multilocus phylogeny indicates that *S. anthurii* of the genus *Anthurium* (*Araceae*) is a closely related species (Fig. 2).

***Septoria stachydis*** Roberge ex Desm., Annls Sci. Nat., sér. 3, Bot. 8: 19. 1847. Fig. 39.

*Description in planta*: *Symptoms* leaf spots angular or irregular, greyish to yellowish brown, with a somewhat darker to black border. *Conidiomata* pycnidial, epiphyllous, rarely also hypophyllous, mostly 1–5 in each leaf spot, globose to subglobose, dark brown, semi-immersed, 65–100(–125) µm diam; *ostiolum* central, circular, 12–20 µm wide, later opening more widely up to 50 µm, surrounding cells somewhat darker; *conidiomatal wall* 12–18 µm thick, composed of angular and irregular cells 2.5–6 µm diam, the outer cells with brown, somewhat thickened walls, the inner cells with hyaline and thinner walls. *Conidiogenous cells* discrete, sometimes integrated into 1–septate conidiophores, hyaline, broadly ampulliform with a relatively narrow neck, holoblastic, proliferating percurrently with indistinct annellations, rarely also sympodially, 5–8(–10) × 2.5–3.5(–5) µm. *Conidia* filiform to filiform-cylindrical, curved or irregularly bent, rarely straight or flexuous, with a narrowly rounded or somewhat pointed apex, with a truncate base, (0–)1–3(–5)-septate, not constricted around the septa, hyaline, contents with several minute oil-droplets and granular material in each cell in the living state, with inconspicuous oil-droplets and granular contents in the rehydrated state, (17–)20–42 × 1–2 µm (living; rehydrated, 1–1.5 µm wide). *Sexual morph* unknown.

*Description in vitro*: *Colonies* on OA 13–16 mm diam in 2 wk (V1049: 8–10 mm in 12 d, 16–18 mm in 3 wk; > 50 mm in 7 wk), with an even, glabrous, colourless margin; immersed mycelium mostly homogeneously coral after 2 wk, the centre of the colony already appearing almost black by numerous superficial and immersed pycnidia; olivaceous-black sectors with dark

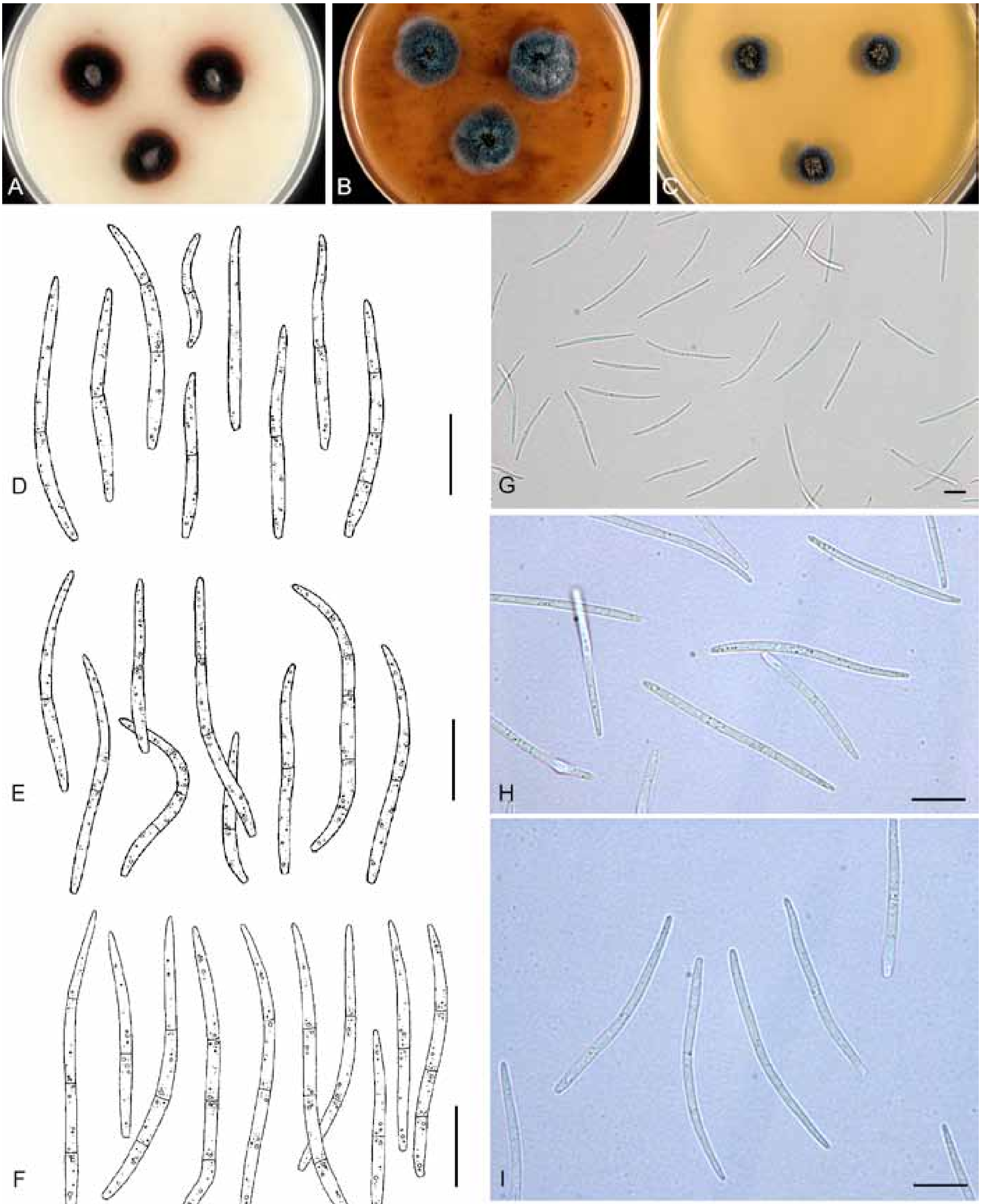


**Fig. 39.** *Septoria stachydis*. A–C. Colonies CBS 102337 (15 °C, nUV). A. On OA. B. On CHA. C. On MEA. D. Conidia *in planta* (CBS H-21226). E. Conidia *in planta* (CBS H-21175). F–I. Conidia on OA (CBS 123750). Scale bars = 10 µm.

pigmented radiating sterile hyphae also present, later becoming more dominant, or sectors covered by salmon masses of conidia formed directly from mycelial hyphae; aerial mycelium absent; reverse concolorous, but blood colour in the centre, later mainly olivaceous-black or dark slate blue. Surface of the colony smooth. Pycnidia numerous after 2 wk, superficial or immersed, releasing salmon or rosy-buff droplets of conidial slime. *Colonies* on CMA 8–12 mm diam in 2 wk (11–14 mm in 12 d, 14–24 mm in 3 wk), as on OA, but olivaceous-black sectors more dominant, sometimes colony almost entirely so. *Colonies* on MEA 8–10 (slow growing sectors) to 12–16 (fast growing sectors) in 2 wk (18–21 mm in 3 wk; 43–58 mm in 7 wk), with an even, glabrous, honey to buff margin; immersed mycelium very dark blood colour; centre of the colony rising high above the agar surface, cerebriform, covered by dirty ochreous conidial slime formed from separate or fused pycnidial conidiomata. Aerial mycelium in slow-growing sectors scanty, scattered minute tufts of white aerial mycelium, in faster growing sectors well-developed, dense, woolly-cottony, first white, later olivaceous-grey to glaucous grey, locally with a reddish discoloration; some colonies with a more homogeneous, olivaceous-black felty surface, sporulating after 3 wk in the centre, with superficial black pycnidial conidiomata releasing milky white masses of conidial slime. *Colonies* on CHA 12–18 mm in 2 wk (15–18 mm in 3 wk; 34–38 mm in 7 wk), with an even, glabrous, colourless margin; immersed mycelium greenish grey to dark slate blue, the outer zone covered by well-developed, tufty whitish grey aerial mycelium; reverse blood colour, but margin paler; in the central part of the colony numerous pycnidia develop, releasing pale vinaceous to rosy-buff conidial slime; in older colonies the centre becomes cerebriform, much as on MEA.

*Conidiomata* (OA) immersed in the agar or on the agar surface, black, single, globose, 100–175 µm diam, or irregular, and merged into large complexes 190–350 µm diam, with relatively thick walls; *ostiolum* as *in planta*, or absent; *Conidiogenous cells* as *in planta*, but more often integrated in 1–3-septate conidiophores. *Conidia* as *in planta*, 22–47(–54.5) × 1–2 µm.

*Hosts*: *Stachys* spp.

*Material examined*: **Austria**, Tirol, Ober Inntal, Lawenwald near Serfaus, on living leaves of *Stachys sylvatica*, 8 Aug. 2000, G. Verkley 1049, CBS H-21175, living cultures CBS 109126, 109127. **Czech Republic**, Moravia, Veltice, Forest of Rendez Vous, on living leaves of *Stachys* sp., 16 Sep. 2008, G. Verkley 6008, CBS H-21253, living cultures CBS 123750, 123879. **Netherlands**, prov. Utrecht, Baarn, Kasteel Groeneveld, on living leaves of *St. sylvatica*, 7 July 1968, H.A. van der Aa 685, CBS H-18175, living culture CBS 449.68; prov. Gelderland, Wageningen, Binnenveld, on living leaves of *Stachys* sp., 23 July 1981, H.A. van der Aa 7952, CBS H-18176; prov. Gelderland, Winssen, Kasteel Doddendael, on living leaves of *St. sylvatica*, 9 Sep. 1999, G. Verkley 922, CBS H-21204, living cultures CBS 102326, 102337; prov. Limburg, Gulpen, near Stokhem, on living leaves of *St. sylvatica*, 28 June 2000, G. Verkley 965, CBS H-21226, living cultures CBS 109005, 109006. **Romania**, distr. Ilfov, pădurea Malu Spart, on living leaves of *St. sylvatica*, 27 June 1971, G. Negrean & A. Voicu *s.n.*, CBS H-18178, distributed in Herb. Mycol. Romanicum, fasc. 41, no. 2001; distr. Prahova, Sinaia, Valea Peleşului, on living leaves of *St. sylvatica*, 4 Sep. 1971, G. Negrean *s.n.*, CBS H-18177, distributed in Herb. Mycol. Romanicum, fasc. 41, no. 2002.

Additional material examined – **Germany**, loc. unknown, isol. Ziekler, living culture CBS 307.31, preserved as *S. stachydis*, identity uncertain.

*Notes*: According to Jørstad (1965), the conidia of *S. stachydis* on *Stachys sylvatica* are 16–57 × 1–1.5(–2) µm, with a lowest maximum length for any collection of 32 µm. In the collections available for the present study, conidia are up to 42 µm in length *in planta*, and 54.5 µm long *in vitro*. The species differs morphologically from *S. stachydicola* (Bubák. ex Serebrian.) Jacz., which occurs on the same host genus. Shin & Sameva (2004) gave a description of *S. stachydicola*, based on two collections of *Stachys riederi* var. *japonica* from Korea. According to these authors, the conidia of that species are 38–72 × 2–3 µm (3–7-septate), so longer and wider than those of *S. stachydis*. Also, the pycnidia are smaller in diam (40–80 µm) and ostioli much wider (20–36 µm) than in *S. stachydis*. CBS 128668 (= KACC 44796) is described by Quaedvlieg *et al.* (2013) as *Septoria* cf. *stachydicola*. This isolate, and also CBS 128662 (=KACC 43871) are both distant from European isolates of *S. stachydis.*

***Septoria stellariae*** Roberge ex Desm., Annls Sci. Nat., sér. 3, Bot. 8: 22. 1847. Fig. 40.

? = *Sphaeria isariphora* Desm., Annls Sci. Nat., sér. 2, Bot. 19: 358. 1843.
≡ *Mycosphaerella isariphora* (Desm.) Johanson, Öfvers. K. Svensk. Vetensk.-Akad. Förhandl. 41 (no. 9): 165. 1884.

*Description in planta*: *Symptoms* indefinite white or pale yellow to pale brown leaf lesions on lower leaves of plants, often starting at the leaf margin, extending rapidly over the lamina and leading to complete withering of leaves and their petioles. *Conidiomata* pycnidial, brown, in dense groups on withering petioles and leaves, where mostly epiphyllous, only partly immersed in the host tissue, globose or lenticular, (85–)120–160(–210) µm diam; *ostiolum* circular, central, initially 20–35 µm wide, later opening to 80 µm diam, without distinctly differentiated cells; *conidiomatal wall* composed of *textura angularis* without distinctly differentiated layers, mostly 15–25 µm thick, the outer cells with brown, somewhat thickened walls and 4.5–8 µm diam, the inner cells hyaline and thin-walled and 3.5–6.5 µm diam; conidiogenous cells lining the whole inner surface of the pycnidium. *Conidiogenous cells* hyaline, discrete or integrated in short simple, 1–2-septate conidiophores, cylindrical, or ampuliform to elongated ampulliform with a relatively short neck, hyaline, holoblastic, proliferating sympodially, 5–12(–15) × 2.5–4 µm. *Conidia* cylindrical to filiform, weakly curved or abruptly bent in the lower cell, sometimes flexuous, gradually attenuated to the rounded apex, gradually or more abruptly attenuated into a broadly truncate base, (0–)1–3(–5)-septate, not or indistinctly constricted around the septa, hyaline, contents with several small guttulae and numerous granules in each cell in the living state, oil-droplets rarely merged into larger guttules in the rehydrated state, (21–)30–64 (–70) × 1.5–2.5(–3) µm (living; rehydrated, 1–2 µm wide).

*Description in vitro*: *Colonies* on OA 3–5 mm diam in 2 wk, with an even, glabrous, colourless margin; a yellow pigment diffusing into the agar beyond the margin; immersed mycelium mostly colourless to buff or saffron with scanty, whitish aerial mycelium, the centre of the colony darkened by numerous superficial and immersed, separate or confluent pycnidial conidiomata, releasing rosy-buff to salmon conidial slime; reverse pale luteous to saffron, but olivaceous-black in areas with numerous conidiomata. *Colonies* on CMA 3–6 mm diam in 2 wk, as on OA. *Colonies* on MEA 2–5 mm diam in 2 wk, with an even, glabrous, colourless margin, locally with rapidly outgrowing hyphae forming superficial pycnidial conidiomata; colonies pustulate to hemispherical, the surface greenish grey to olivaceous-black covered by fairly dense greyish to saffron, woolly aerial mycelium; some superficial or immersed pycnidial conidiomata formed; reverse dark umber to blood colour. *Colonies* on CHA 4–8 mm diam in 2 wk, remaining almost plane, with an irregular margin; immersed mycelium greenish grey to dark slate-blue in the centre, buff near the margin; aerial mycelium well-developed, greyish to white, with a distinct flesh discoloration especially at the margin; reverse blood colour; abundant immersed and superficial pycnidial conidiomata formed, releasing a buff to saffron conidial slime.

*Conidiomata* (OA) pycnidial and similar as *in planta*, single, 100–250 µm diam, but more often merged into larger complexes, brown to olivaceous brown, and up to 350 µm diam; *ostiolum* as *in planta*, or absent. *Conidiogenous cells* hyaline, as *in planta* but

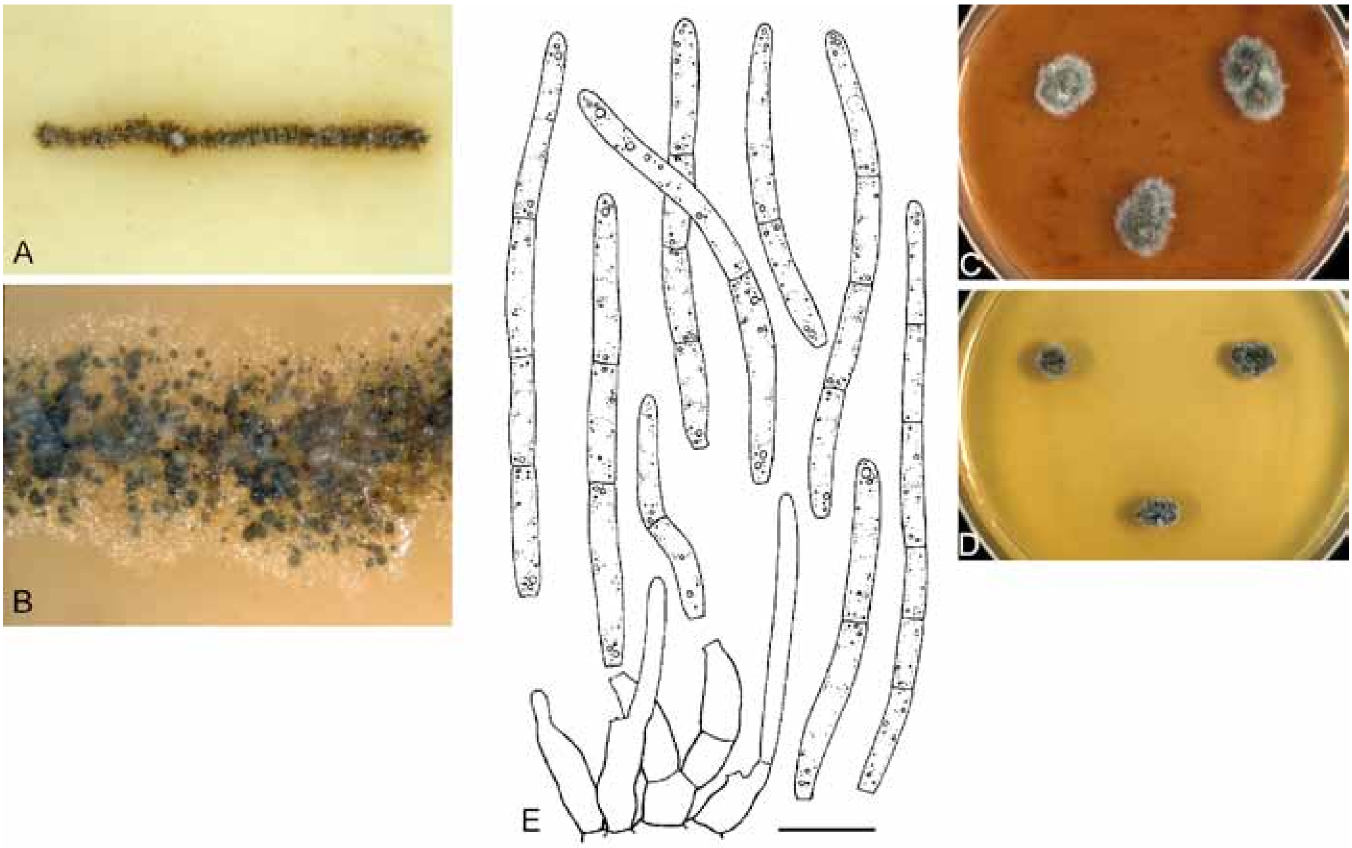


**Fig. 40.** *Septoria stellariae*. A–D. Colonies CBS 102364. A, B. On OA. C. On CHA. D. On MEA. E. Conidia and conidiogenous cells on OA (CBS 102364). Scale bars = 10 µm.

predominantly cylindrical, holoblastic, proliferating sympodially, rarely percurrently with indistinct annellations, 5–15(–22) × 2.5–4.5 µm. *Conidia* similar as *in planta*, (0–)3–5-septate, not or indistinctly constricted around the septa, hyaline, contents with several small guttules and numerous granules in each cell, (20–)30–75(–84) × 2–2.5(–3.0) µm.

*Hosts*: *Stellaria* spp. and *Myosoton* spp.

*Material examined*: **Germany**, Eifel, Gunderath, near Heilbachsee, on living leaves of *Stellaria media*, 22 June 1992, H.A. van der Aa 11341, CBS H-5333. **Netherlands**, Prov. Utrecht, Baarn, on leaves of *S. media*, 18 May 1985, H.A. van der Aa 9492, CBS H-18179; Prov. Noord-Holland, Laren, on leaves of *S. media*, 18 Feb. 1967, H.A. van der Aa *s.n.*, CBS H-18180; prov. Noord-Brabant, Valkenswaard, on withering leaves and stems of *St. media*, 1 May 1967 , H.A. van der Aa *s.n.*, CBS H-18179; Ameland, Nes, on leaves of *St. media*, 27 May 1967 , H.A. van der Aa *s.n.*, CBS H-18182; Prov. Gelderland, Landgoed Staverden, on withering leaves and petioles of *St. media*, 1 Aug. 1999, G. Verkley 901, CBS H-21156, living cultures CBS 102364, 102410; Prov. Limburg, Mook en Middelaar, St. Jansberg, near Plasmolen, on withering leaves and petioles of *St. media*, 9 Sept 1999, G. Verkley 933, CBS H-21157, living culture CBS 102378; Prov. Flevoland, Erkemeder strand, on withering leaves and petioles of *St. media*, 8 Sept 1999, G. Verkley 929, CBS H-21217, living culture CBS 102376; Prov. Flevoland, Ketelmeer, IJsseloog, on withering leaves and petioles of *St. media*, 22 May 2002, G. Verkley 1141, CBS H-21260. **Romania**, distr. Vîlcea, Muntele Cozia, Stîna Foarfeca, on living leaves of *S. media*, 14 Oct. 1976, G. Negrean *s.n.*, CBS H-18183, distributed in Herb. Mycol. Romanicum, fasc. 60, no. 2990.

*Notes*: This fungus is a weak pathogen of *Stellaria media* in the Netherlands, on which it is only seen under very humid conditions. Especially the lower parts of plants that are sheltered by the surrounding vegetation are affected. Jørstad (1965) observed conidia up to 82 µm in length on *Stellaria crassifolia*, and up to 96 µm long on *Stellaria media*, the type host. It has also been reported from other *Stellaria* spp., and *Myosoton* (Radulescu *et al.* 1973, Vanev *et al.* 1997, Markevičius & Treigienė 2003). *Septoria stellariae* var. *macrospora* was originally described from the same host as *S. stellariae*, *Stellaria media*. According to Teterevnikova-Babayan (1987), conidia of this variety measure 50–120 × 2.5–4 µm. On fresh plant material studied here conidia longer than 70 µm were not observed, but the isolates obtained thereof did produce conidia up to 84 µm long. Sequence analyses of CBS 102376, 102378, and 102410 originating from three different localities showed no significant polymorphisms in the seven loci, indicating that material belongs to a single taxon. Whether the variety *macrospora* is tenable, is unclear at this point. We agree with Jørstad (1965), that the connection with the sexual morph *Mycosphaerella isariphora* suggested in the literature, requires confirmation. It is therefore listed as a tentative synonym of *S. stellariae*.

## ***Septoria urticae*** Roberge ex Desm., Annls Sci. Nat., sér. 3, Bot. 8: 24. 1847. Fig. 41.

*Description in planta*: *Symptoms* leaf spots small, angular, often merging to irregular patterns, initially pale yellowish brown, partly becoming dark greyish brown later, with a dark border. *Conidiomata* pycnidial, epiphyllous, several in each leaf spot, subglobose to lenticular, pale brown, usually fully immersed, 70–120 µm diam; *ostiolum* central, initially circular and 30–45 µm wide, later becoming more irregular and up to 80 µm wide, surrounding cells concolorous to pale brown; *conidiomatal wall* about 10–17 µm thick, composed of a homogenous tissue of hyaline, angular cells 2.5–6.5 µm diam, the outermost cells pale yellowish brown with somewhat thickened walls, the inner cells thin-walled. *Conidiogenous cells* hyaline, mostly discrete, narrowly or broadly ampulliform with a relatively narrow neck, holoblastic,

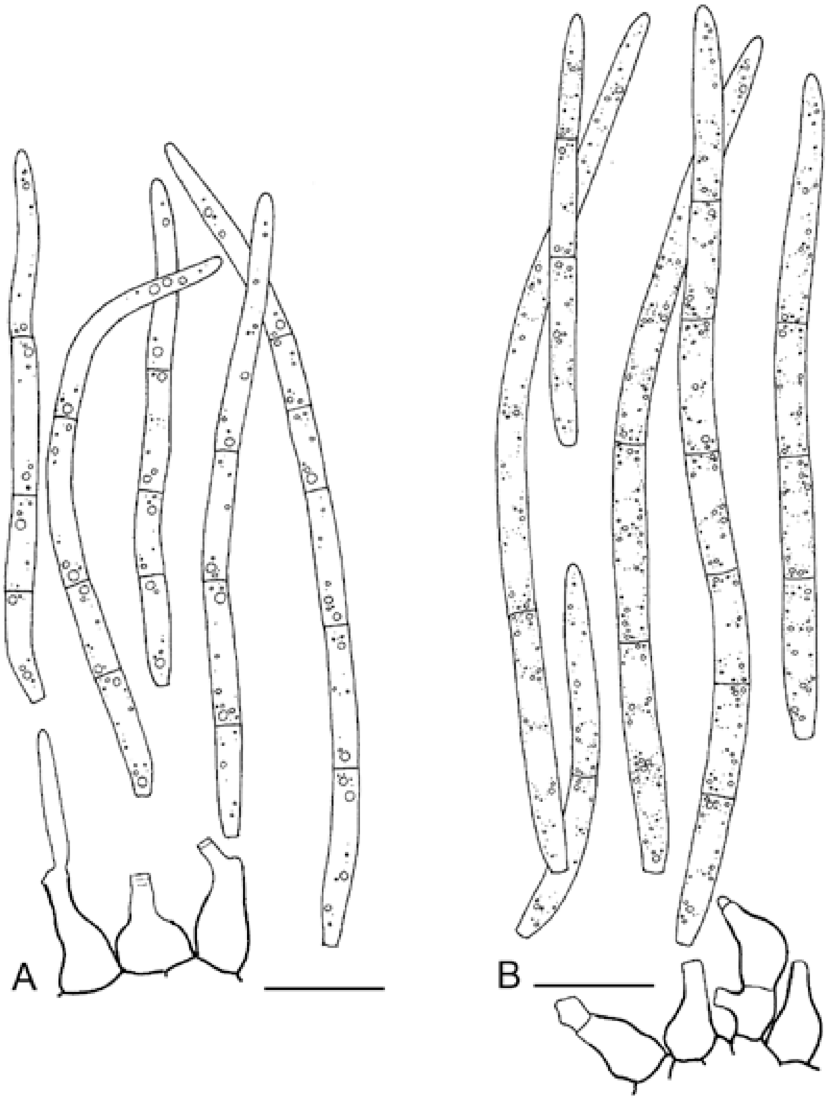


**Fig. 41.** *Septoria urticae*, epitype. A. Conidia and conidiogenous cells *in planta* (CBS H-21221). B. Ibid., on OA (CBS 102371). Scale bars = 10 µm.

often first proliferating sympodially, and later also percurrently 1–several times with distinct annellations, 6–12(–16) × 4–5.5(–7) µm. *Conidia* cylindrical, straight or slightly curved, flexuous, or irregularly bent, with a narrowly rounded apex, attenuated towards the narrowly truncate base, (0–)1–5(–7)-septate, not constricted around the septa, hyaline, contents with several oil-droplets and granular material in each cell in the living state, with inconspicuous oil-droplets and granular contents in the rehydrated state, (18–)30–57(–75) × 2–3 µm (living; rehydrated, 2–2.5 µm wide). *Sexual morph* unknown.

*Description in vitro*: *Colonies* on OA 6–7 mm diam in 2 wk (19–22 mm in 6 wk), with an even, glabrous, red to coral margin, the pigment also clearly diffusing beyond the margin; colonies almost plane, immersed mycelium near the margin red, in the centre very dark, blood colour to black, also due to mostly superficial pycnidial conidiomata releasing pale flesh droplets of conidial slime; white, felty aerial mycelium scanty, mostly only just behind the margin; reverse concolorous. *Colonies* on CMA 4-6 mm diam in 2 wk (16–17 mm in 6 wk), as on OA. *Colonies* on MEA 6–7(–9) mm diam in 2 wk [20–22(–28) mm in 6 wk], with an even, buff to very pale flesh plane marginal zone; the pigment diffusing into the medium; colony often hemispherical with an irregularly pustulate-worty surface, immersed mycelium very dark chestnut to black, aerial mycelium absent, except in faster growing sectors, which are entirely covered by a dense, felty mat of reddish aerial mycelium; superficial pycnidial conidiomata releasing dirty white to flesh droplets of conidial slime. *Colonies* on CHA 4–6 mm diam in 2 wk (17–22 mm in 6 wk), as on MEA, but with an initially ruffled (later more even), rather dark margin and more numerous conidiomata producing flesh droplets of conidial slime.

*Conidiomata* (OA) pycnidial, pale brown to dark brown, glabrous, 100–230 µm diam, with a single ostiolum as *in planta*, or ostioli barely differentiated; *conidiogenous cells* as *in planta*, but more often integrated in 1–2-septate conidiophores, often only proliferating percurrently with distinct annellations on an elongated neck, 6–14 × 3–7.5 µm; *conidia* cylindrical, straight or slightly curved, tapering to a rounded apex, lower part attenuated into a broad truncate base, 1–7(–9)-septate, not constricted around the septa, hyaline, with several minute oil-droplets and numerous granulae in each cell, (34–)40–70(–90) ×2.5–3(–3.5) µm.

*Hosts*: *Urtica* spp. and *Glechoma hederacea*.

*Material examined*: **Netherlands**, Prov. Utrecht, Soest, Overhees, on living leaves of *Glechoma hederacea*, in leaf spots associated with *Puccinia glechomatis*, 8 Aug. 1999, G. Verkley 904, CBS H-21197, living culture CBS 102316; Prov. Utrecht, 's Graveland, Kortenhoefse plassen, "Oppad", on living leaves of *Urtica dioica*, 14 Oct. 1999, H.A. van der Aa & G. Verkley 947, **epitype designated here** CBS H-21221 "MBT175359", living cultures ex-epitype CBS 102371, 102375.

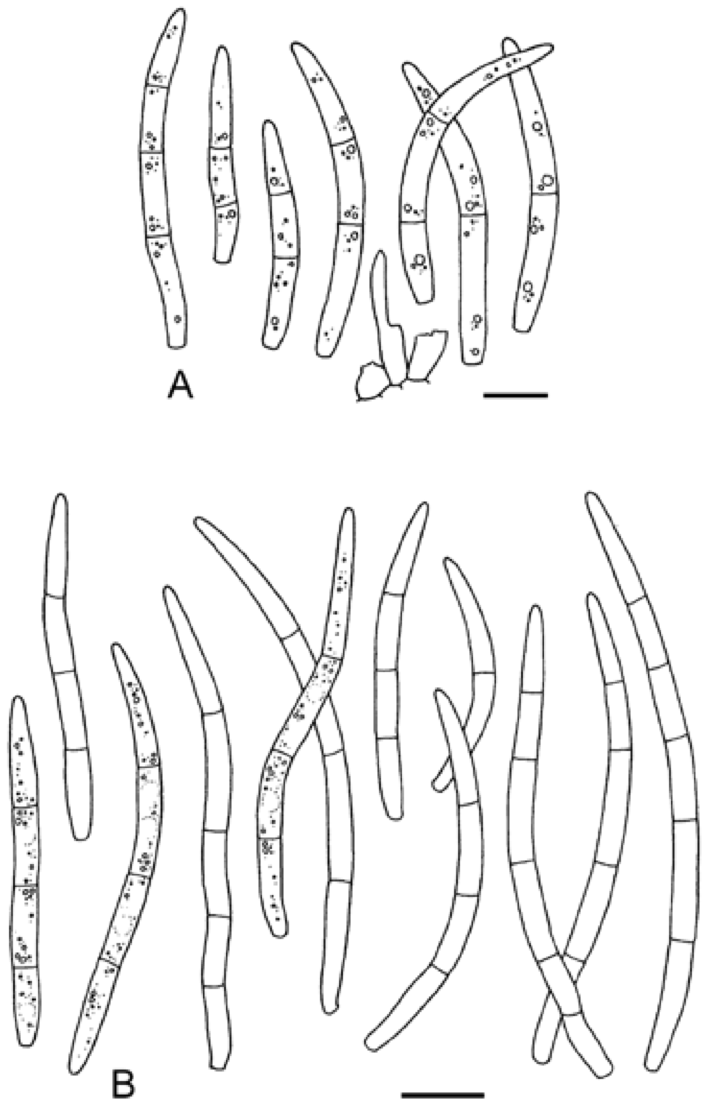


**Fig. 42.** *Septoria verbenae*. A. Conidia and conidiogenous cells *in planta* (CBS H-21241). B. Conidia on OA (CBS 113438). Scale bars = 10 µm.

*Notes*: Muthumary (1999) provided a description and illustration of type material of *S. urticae* (PC 1309). Because there are only insignificant differences between his observations of the type and those observed here in the Dutch collection on the same host, *Urtica dioica*, the latter is selected as epitype. Muthumary reported ostioli 20–40 µm wide, while in the Dutch material the ostioli eventually open up further to about 80 µm wide. Muthumary observed conidia 35–50 × 2–2.5 µm with 3–4 septa, but other authors have found that conidia *in planta* can be much longer and have more septa. Jørstad (1965) found that conidia in Norwegean material on *U. dioica* were 22–81 × 1–1.5 µm, with up to 6 septa. Priest (2006), who studied material on *U. insidia* and *U. urens* in Australia reported conidia (26–)35–50(–70) × 1.5–2 µm, 3–5-septate. The present study shows that *in vitro* conidia can even be up to 90 µm long in this species. The material from *Glechoma hederaceae* sporulating in association with the rust *Puccinia glechomatis*, proved morphologically in good agreement with that on *Urtica dioica*, and since it is also genetically similar to the material from that host, it is regarded conspecific. Other *Septoria* species have also occasionally been found in association with rust sori, viz., *S. lagenophorae*, which is regarded to be a hyperparasite of rusts, and occasionally also other leaf-spotting fungi (Priest 2006).

According to Muthumary, the conidiogenous cells of *S. urticae* each produce a solitary terminal conidium and often also proliferate sympodially. It is established here that *S. urticae* is also capable of proliferating percurrently, and that this mode of proliferation is more frequent in pure culture. In contrast, Priest (2006) observed conidiogenous cells that first produced a conidium holoblastically, and subsequent conidia enteroblastically at the same level from a narrow conidiogenous locus, viz. like in phialidic conidiogenesis. It is unclear whether this is truly phialidic conidiogenesis, or just cryptic percurrent proliferation as observed in *S. chrysanthemella*, where the scars of the subsequent secessions are indistinguishable due to the limitations in the resolution of the light microscope (Verkley 1998a).

***Septoria verbenae*** Roberge ex Desm., Annls Sci. Nat., sér. 3, Bot., 8: 19. 1847. Fig. 42.

*Description in planta*: *Symptoms* stem lesions and leaf spots small, angular to irregular, and merging to elongated areas, initially red to purplish red, then becoming pale in the centre with a darker border. *Conidiomata* pycnidial, epiphyllous, one to a few in each lesion, globose, dark brown, immersed, 70–140 µm diam; *ostiolum* central, circular, 25–40 µm wide, surrounding cells dark; *conidiomatal wall* about 12.5–20 µm thick, composed of a homogenous tissue of *textura angularis* with hyaline cells 2.5–7.5 µm diam, the outermost cells mid brown with somewhat thickened walls, the inner cells thin-walled and pale yellowish brown. *Conidiogenous cells* hyaline, discrete, or integrated in 1–2-septate conidiophores, narrowly ampulliform to almost cylincrical, often with a relatively narrow neck, holoblastic, first proliferating sympodially, and in some cells later also percurrently 1–several times with indistinct annellations, 12–18(–20) × 2.5–6 µm. *Conidia* cylindrical, straight or slightly curved, flexuous, with a narrowly rounded to somewhat pointed apex, attenuated towards the narrowly truncate base, (1–)3(–5)-septate, not constricted around the septa, hyaline, contents with several oil-droplets and granular material in each cell in the living state, with inconspicuous oil-droplets and granular contents in the rehydrated state, (22–)16–48 × (1–)1.5–2 µm (rehydrated). *Sexual morph* unknown.

*Description in vitro*: *Colonies* on OA 10–13 mm diam in 2 wk, with an even, colourless margin; colonies restricted to spreading, immersed mycelium citrine to grey-olivaceous, locally soon darker radiating strands occur, glabrous but in the centre of colonies, where irregular elevations are formed, covered by well-developed, grey to white finely felted aerial mycelium; reverse greenish grey to olivaceous-black. Conidiomata developing immersed or on the agar surface after 10–2 wk. *Colonies* on MEA 10–13 mm diam in 2 wk, with a slighlty ruffled, buff to amber margin; colonies restricted, irregularly pustulate, the surface entirely covered by a low, dense mat of whitish to grey finely felted aerial mycelium; reverse dark brown to almost black, locally fulvous to sienna. No sporulation observed.

*Conidia* (OA) filiform to cylindrical, typically weakly to strongly curved, sometimes straight or flexuous, attenuated gradually to a somewhat pointed apex, attenuated gradually or more abruptly to the narrowly truncate to almost rounded base, hyaline, with granular contents and minute oil droplets, (1–)3–5(–7)-septate, (22–)28–46(–54) × 1.5–2(–2.5) µm.

*Host*: *Verbena officinalis.*

*Material examined*: **New Zealand**, North Isl., Northland, Bay of Islands area, Manawaora along roadside, on living leaves of *Verbena officinalis*, 30 Jan. 2003, G. Verkley 2017, CBS H-21240; same loc., date, on stems of *V. officinalis*, G. Verkley 2023, CBS H-21241, living culture CBS 113438, 113481.

*Notes*: Priest (2006) gave a detailed description based on a collection from New South Wales, Australia [conidia (1–)3-septate, 26–48 × 1.5(–2) µm]. The two strains available proved morphologically similar. These New Zealand strains proved to have identical Act, Btub, Cal, EF, and RPB2 sequences, distinct from other *Septoria*.

## *Sphaerulina*

*Type species*: *Sphaerulina myriadea* (DC.) Sacc., Michelia 1 : 399. 1878.

Quaedvlieg *et al.* (2013, this volume) provide a description based on the sexual morph and treat several additional species with septoria-like asexual morphs.

***Sphaerulina aceris*** (Lib.) Verkley, Quaedvlieg & Crous, **comb. nov.** MycoBank MB804473. Fig. 43.

*Basionym*: *Ascochyta aceris* Lib., Pl. crypt. Ard., Cent. 1: no. 54. 1830.

≡ *Septoria aceris* (Lib.) Berk. & Broome, Ann. Mag. Nat. Hist. Ser. 2, 5: 379. 1850.

≡ *Phloeospora aceris* (Lib.) Sacc., Syll. Fung. 3: 577. 1884.

= *Septoria pseudoplatani* Roberge ex Desm., Annls Sci. Nat., sér. 3, Bot. 8: 21. 1847.

≡ *Cylindrosporium pseudoplatani* (Roberge ex Desm.) Died., Annls mycol. 10: 486. 1912.

= *Sphaerella latebrosa* Cooke, Handb. Brit. Fungi 2: no. 2754. 1871.

≡ *Mycosphaerella latebrosa* (Cooke) J. Schröt., in Cohn, Krypt.-Fl. Schlesien (Breslau) 3.2(3): 334. 1894 [1908].

≡ *Carlia latebrosa* (Cooke) Höhn., Hedwigia 62: 73. 1920.

= *Septoria seminalis* var. *platanoidis* Allesch., Hedwigia 35: 34. 1896.

≡ *Cylindrosporium platanoidis* (Allesch.) Died., Annls mycol. 10(5): 486. 1912.

= *Septoria epicotylea* Sacc., Malpighia 11: 314. 1897.

= *Phloeospora pseudoplatani* Bubák & Kabát in Bubák, Sber. K. böhm. Ges. Wiss., Math.-naturw, Kl., 7: 16. 1903.

*Description in planta*: *Symptoms* small (0.2–0.5 mm diam), circular to angular, hologenous reddish brown leaf spots. *Conidiomata* acervular, epi- or hypophyllous, one to a few in each leaf spot, pale brown (drying dark brown), 105–180(–220) µm diam, releasing conidia in white columnar masses; *conidiomatal wall*

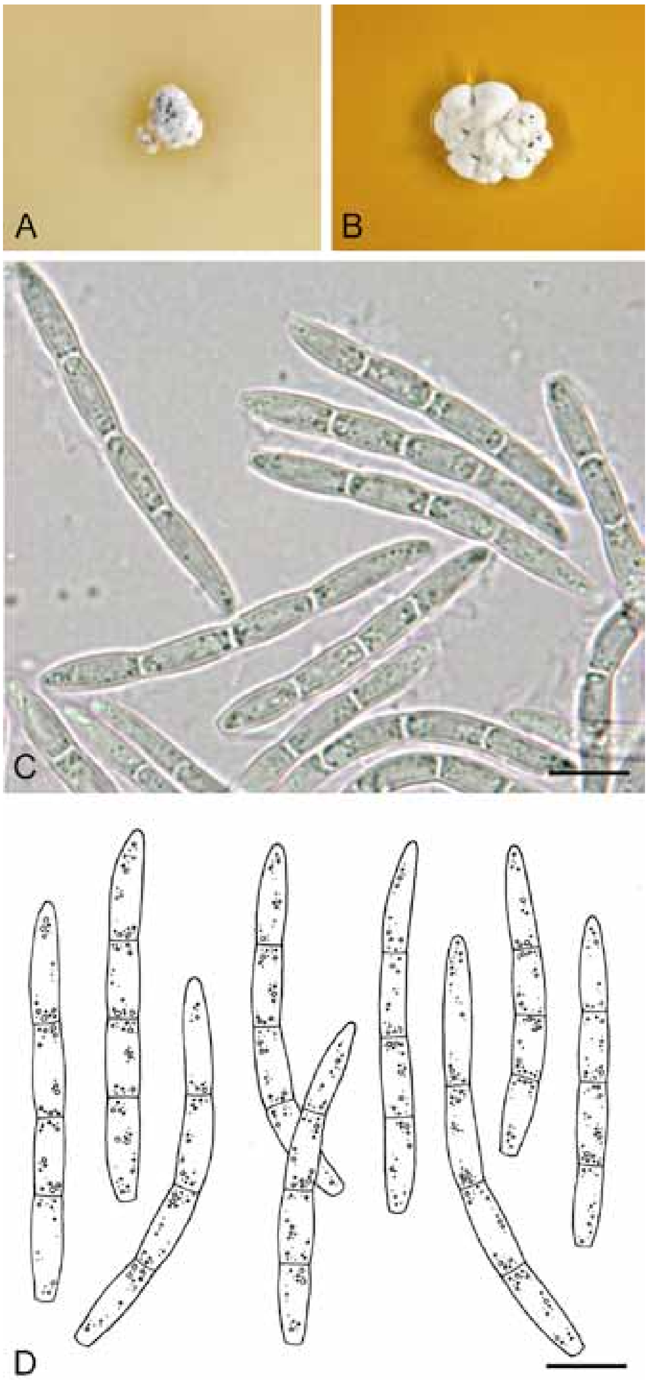


**Fig. 43.** *Sphaerulina aceris*. A, B. Colonies CBS 183.97. A. On OA. B. On MEA. C, D. Conidia *in planta* (CBS H-21239). Scale bars = 10 µm.

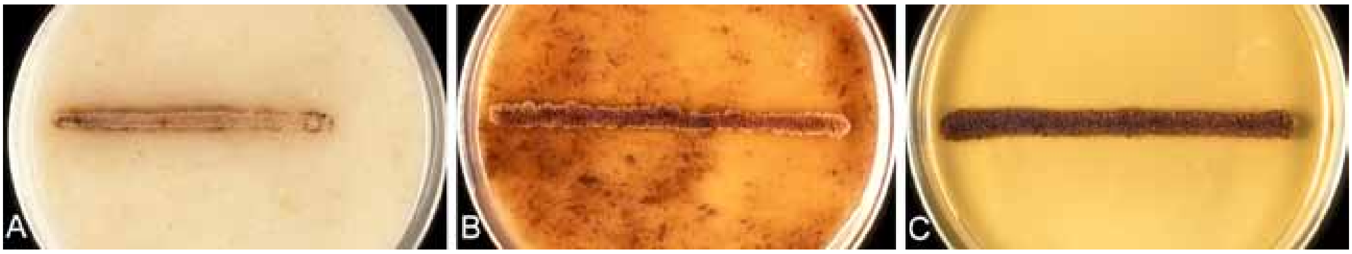


**Fig. 44.** *Sphaerulina cornicola*. A–C. Colonies CBS 102324. A. On OA. B. On CHA. C. On MEA.

mainly consisting of a basal 15–25(–35) µm thick layer of angular to subglobose, subhyaline to pale brown cells 5–10 µm diam, lateral wall absent or very poorly developed, composed of similar, somewhat darker cells. *Conidiogenous cells* hyaline, discrete or integrated in 1(–2)-septate conidiophores, subglobose, doliiform or ampulliform, holoblastic, proliferating percurrently with one to several disctinct annellations, or sympodially, sometimes both types of proliferation occur in a single conidiogenous cell, 8–15 (–20) × 2.5–4 µm. *Conidia* cylindrical, straight or more or less curved, attenuated gradually to a broadly rounded apex, attenuated more or less abruptly to a truncate base, (1–)3-septate, conspicuously constricted around the septa in fresh and rehydrated state, hyaline, contents with numerous minute oil-droplets and granular material in each cell in the living state, with minute oil-droplets and granular contents in the rehydrated state, (32–)37–47(–50) × 3–4 µm (living; rehydrated, 2–3 µm wide).

*Description in vitro*. *Colonies* on OA 3–4 mm diam in 2 wk, with a undulating even margin; colonies restricted, irregularly pustulate, the surface buff or much darker grey to brown, locally glabrous but mostly covered by a dense mat of finely felted white aerial mycelium, conidiomata developing on the surface releasing conidia in clear droplets, or in milky white to rosy-buff masses; reverse dark greyish or brown-vinaceous. *Colonies* on MEA 3–4(–8) mm diam in 2 wk, with a undulating even margin; colonies restricted, irregularly pustulate, the surface almost black provided with low and finely felted, diffuse, grey to white aerial mycelium, conidiomata developing just beneath the colony surface, releasing white cirrhi of conidia; reverse a palet of brown-vinaceous, cinnamon and olivaceous-grey.

*Conidia* (OA) as *in planta*, (31–)34–50(–58) × 3.5–5 µm. Microconidia (spermatia of the *Asteromella* state) ellipsoid, hyaline, 0-septate, 3–4 × 1.5 µm.

*Hosts*: *Acer campestre*, *A. circinatum*, *A. hyrcanum* (Vanev *et al.* 1997) and *A. pseudoplatanus*.

*Material examined*: **France**, locality unknown, on leaves of *Acer campestre*, distributed in Libert, Pl. Cryptog. Ard. Fasc. 1 (1830): no. 54, **isotype** BR–MYCO 153858-16, type of *Ascochyta aceris* Lib. **Netherlands**, prov. Utrecht, Baarn, on *Acer pseudoplatanus*, July 1969, I. Blok, living culture CBS 514.69; Baarn, garden WCS, on living leaves of *Acer pseudoplatanus*, 23 July 1985, H.A. van der Aa 9537, CBS H-14666, living culture CBS 652.85; same substr., prov. Zuid-Holland, Wassenaar, Hollandsch Duin, 14 Aug. 1994, G. Verkley 227, CBS H-18040, living culture CBS 687.94; same substr., prov. Zuid-Holland, Wassenaar, Ganzenhoek, 8 Aug. 1995, G. Verkley 307, CBS H-21239, living culture CBS 187.96; same substr., prov. Utrecht, Baarn, Eemnesserweg, 7 May 1996, H.A. van der Aa 12120, CBS H-14665, living culture CBS 183.97; **USA**, Oregon, Lane Co., Proxy Falls Trail, on living leaves of *Acer circinatum*, 11 Oct. 1996, J. K. Stone & G. Verkley 480, CBS H-21236, living culture CBS 655.97.

*Notes*: This is the oldest septoria-like species described from members of the family *Aceraceae*. It occurs on several species of the genus *Acer*. In the original diagnosis of Libert, three host species were mentioned, viz., *A. campestre*, *A. pseudoplatanus* and *A. platanoides*. Jørstad (1965) treated forms on *A. platanoides* with conidia 26–60 × 2–2.5 µm as *S. apatela* All. (synonyms *S. seminalis* var. *platanoidis* All., *Phleospora platanoidis* Kabát & Bubák, *Phloeospora samarigena* Bubák & Krieg.), while those on *A. campestre* remained unsettled. According to Jørstad (1965) conidia of *S. aceris* are 24–43 × 2–3 µm, with 3 septa, which agrees well with the sizes observed in the type specimen available in the present study. This material also showed a small proportion of 4-septate conidia in one of the fruitbodies. More species with conidia longer than 60 µm have been described from *A. platanoides*, and these need to be critically assessed in a comprehensive study including isolates of all *Septoria* occurring on the genus *Acer*. No isolates from the the type host *A. campestre* that would be most suitable as epitype, were available, hence no epitypification is proposed here. The ultrastructure of conidiogenesis and conidia of *S. aceris* was studied by Verkley (1998b), who showed that in a single cell percurrent as well as sympodial proliferation can occur.

A description of the sexual morph known as *Mycosphaerella latebrosa* was provided by Kuijpers & Aptroot (2002), but their species concept included several discrete entities that are distinguishable by their conidial states and occur on distantly related host plants. It is unlikely that these entities can be distinguished at all by the morphology of the sexual state (Verkley & Starink-Willemse 2004).

***Sphaerulina cornicola*** (DC.: Fr.) Verkley, Quaedvlieg & Crous, **comb. nov.** MycoBank MB804474. Fig. 44.

*Basionym*: *Depazea cornicola* DC.: Fr., in De Candolle & Lamarck, Flore Française VI: 146. 1815.

≡ *Septoria cornicola* (DC.: Fr.) Desm., Pl. crypt. Fr., Fasc. 7, no 342. 1828; Index Pl. crypt. Fr.: 24. 1851.

= *S. cornicola* var. *ampla* H. C. Greene, Amer. Midl. Nat. 41: 755. 1949 (fide Farr 1991).

For extended synonymy see Farr (1991). Neotype on *Cornus sanguinea*, France (BPI, designated by Farr 1991), not seen.

*Description in planta*: *Symptoms* starting as red discolorations of the leaf lamina and margin, which develop to scattered, circular to irregular, hologenous leaf spots, that later become pale brown, and surrounded by a dark brown to black bordering zone and a distinct red or purple periphery. *Conidiomata* pycnidial, epiphyllous, numerous scattered in each leaf spot, subglobose to globose, brown to black, immersed or semi-immersed, 55–100(–120) µm diam; *ostiolum* central, initially circular and 25–40 µm wide, later becoming more irregular and up to 60 µm wide, surrounding cells concolorous to pale brown. *Conidiomatal wall* about 10–15 µm thick, composed of a outer layer of hyphal to irregular cells 3.0–8 µm diam with brown walls, and an inner layer of hyaline cells 3–5 µm diam; *Conidiogenous cells* hyaline, discrete, doliiform, or narrowly to broadly ampulliform, holoblastic, proliferating sympodially, sometimes also percurrently with indistinct annellations, 5–12.5(–15) × 3–4(–8) µm. *Conidia* cylindrical, regularly curved, attenuated gradually to a rounded or somewhat pointed apex and a narrowly truncate base, (0–)1–3(–5)-septate, distinctly constricted around the septa only in the fresh state, hyaline, contents with several minute oil-droplets and granular material in each cell in the living state, with amorphous material and granular contents in the rehydrated state, (20–)24–40 × 3–4 µm (living; rehydrated, 2–3 µm wide). *Sexual morph* unknown.

*Description in vitro*: *Colonies* on OA 4–7mm diam in 2 wk (12–16 mm in 6 wk), with an even, glabrous, buff margin; colonies spreading, the surface first plane, then somewhat pustulate, immersed mycelium a mixture of fawn and rosy-buff tinges, locally darker olivaceous, the surface largely covered by a rosy-buff to vinaceous buff masses or a film of conidial slime produced directly by the mycelium; reverse rosy-buff with isabelline to hazel areas, later darker in the centre. *Colonies* on CMA 3–4 mm diam in 2 wk (8–12 mm in 6 wk), as on OA. *Colonies* on MEA 4.5–7 mm diam in 2 wk (9–14(–16) mm in 6 wk), restricted, the entire surface of the colony regularly cerebriform with large masses of conidial slime (also covering the margin), first salmon, later darkening to ochreous or umber, eventually even chestnut; reverse sienna to bay. *Colonies* on CHA 4–6 mm diam in 2 wk (11–14 mm in 6 wk), as on MEA.

*Conidia* (OA) as *in planta*, but showing secondary conidiation, 1–8(–16)-septate, conidia germinating from intermediate cells (laterally) or the basal cells (axially) to form new conidial fragments of variable length, or branched complexes, rendering a heterogeneous mixture.

*Host*: *Cornus sanguinea*.

*Material examined*: **Germany**, Baden-Württemberg, Kussa-Rheinheim, 3 Sep. 1999, A. Aptroot 46371, CBS H-21191. **Netherlands**, Prov. Noord Brabant, Eindhoven, Milieu- & Educatiecentrum Eindhoven, on living leaves of *Cornus sanguinea*, 4 Sep. 1999, A. van Iperen (G. Verkley 918), CBS H-21237, living cultures CBS 102324, 102332; same substr., prov. Limburg, Gulpen, near Stokhem, 28 June 2000, G. Verkley 963, CBS H-21238. **USA**, Maryland, Prince Georges Co., on *C. sanguinea*, 14 Sep. 2004, A. Y. Rossman 4089 (BPI), living culture CBS 116778.

*Notes*: The material examined has the typical conidia of *Sphaerulina cornicola*, agreeing with those described by Farr (1991). *Septoria cornina* can be distinguished from *Sphaer. cornicola* by more variously curved, most commonly hooked, falcate or lunate conidia (23–)32–90(–110) × 2–4(–5) µm with rounded apex (Farr 1991, Shin & Sameva 2004). The phylogenetic relationship with *S. cornina* remains to be clarified.

***Sphaerulina frondicola*** (Fr.) Verkley, Quaedvlieg & Crous, **comb. nov.** MycoBank MB804477.
Basionym: *Septoria populi* Desm, Annls Sci. Nat., sér 2, Bot., 19: 345. 1843. nom. nov. pro *Depazea frondicola* Fr., Observationes mycologicae, 2: 365, t. 5: 6–7. 1818.

≡ *Sphaeria frondicola* (Fr.) Fr., Syst. Mycol. 2: 529. 1822.

= *Sphaerella populi* Auersw., in Gonnermann & Rabenhorst, Mycol. eur. Abbild. Sämmtl. Pilze Eur. 5–6: 11 .1869.

≡ *Mycosphaerella populi* (Auerw.) J. Schroet., in Cohn, Krypt.-Fl. Schlesien (Breslau) 3.2 (3): 336. 1894.

*Description in vitro (CBS 391.59)*: *Colonies* on OA 3–5 mm diam in 2 wk, with an even or slightly ruffled, colourless, glabrous margin; colonies restricted and up to 2 mm high after 2 wk, immersed mycelium mostly olivaceous to dark herbage green, with moderately developed, greyish white, woolly-floccose aerial mycelium; numerous large, simple or complex, olivaceous to reddish brown stromatic conidiomata formed that open widely to release masses of rosy-buff conidial slime; reverse mostly olivaceous-black. *Colonies* on MEA 2–3(–4) mm diam in 2 wk, with a ruffled, buff, glabrous margin; colonies restricted, up to 2 mm high, irregularly pustulate, the surface appearing dark brown to black, but with numerous hemispherical stromata at the surface which are fawn to vinaceous brown, some of which start sporulating directly from the surface forming masses of rosy-buff conidial slime after 2 wk; aerial mycelium scarce, locally denser, white; reverse almost black. *Colonies* on CHA 4–6 mm diam in 2 wk, with an even, rosy-buff margin covered by pure white, woolly aerial mycelium; colonies restricted, up to 2 mm high, immersed mycelium entirely hidden under a dense mat of pure white, high, woolly aerial mycelium; reverse brown-vinaceous in the centre, surrounded by a rosy-buff to buff marginal zone.*Conidiomata* not well-developed. *Conidiogenous cells* observed holoblastic, some cells with a single percurrent proliferation. *Conidia* showing signs of degeneration. In addition, cylindrical to dumpbell-shaped spermatia or microconidia, (5.5–)7.5–13.5(–14.5) × 1.2–1.7 mm, are formed from phialides in the same fruitbodies.

*Host*: *Populus pyramidalis*.

*Material examined*: **Germany**, Berlin-Kladow, on living leaves of *Populus pyramidalis*, Dec. 1959, R. Schneider *s.n.*, BBA 8987, CBS H-18150, living culture CBS 391.59

*Notes*: CBS 391.59 groups in a subclade of the *Sphaerulina*-clade (Fig. 2), that was named after the type species *Sphaerulina myriadea* that resides in it (Quaedvlieg *et al.* 2013). Closest relatives are the other poplar pathogens *Sphaer. populicola* (syns *Septoria populicola* Peck, *Mycosphaerella populicola*, CBS 100042) and several isolates of *Sphaer. musiva* (synonyms *Septoria musiva*, *Mycosphaerella populorum*). CBS 391.59 now only develops atypical sporulating structures not described in detail here.

***Sphaerulina gei*** (Roberge ex Desm.) Verkley, Quaedvlieg & Crous, **comb. nov.** MycoBank MB804475. Fig. 45E–G.
*Basionym*: *Septoria gei* Roberge ex Desm., Annls Sci. Nat., sér. 2, Bot. 19: 343. 1843.

*Description in planta*: *Symptoms* leaf lesions irregular, greyish brown, well-delimited by a dark brown line, surrounding leaf tissue often yellowish; *Conidiomata* pycnidial, amphigenous though predominantly epiphyllous, numerous in each lesion, subglobose to cupulate, brown to black, 35–80 µm diam; *ostiolum* central, circular, initially 35–60 µm wide, later becoming more irregular and up to 80 µm wide, surrounding cells dark brown; *conidiomatal wall* 10–15 µm thick, composed of a homogenous tissue of hyaline, angular cells 2.5–6.5 µm diam, the outermost cells pale brown with slightly thickened walls, the inner cells thin-walled. *Conidiogenous cells* hyaline, discrete, rarely also integrated in 1–2-septate conidiophores, cylindrical or narrowly to broadly ampulliform, holoblastic, often with a relatively narrow and elongated neck, proliferating percurrently several times with distinct annellations, rarely also sympodially, 6–10(–15) × 3.5–5(–6) µm. *Conidia* filiform, slightly curved to flexuous, rarely straight, narrowly rounded at the apex, narrowly truncate at the base, (0–)2–5(–8)-septate (septa

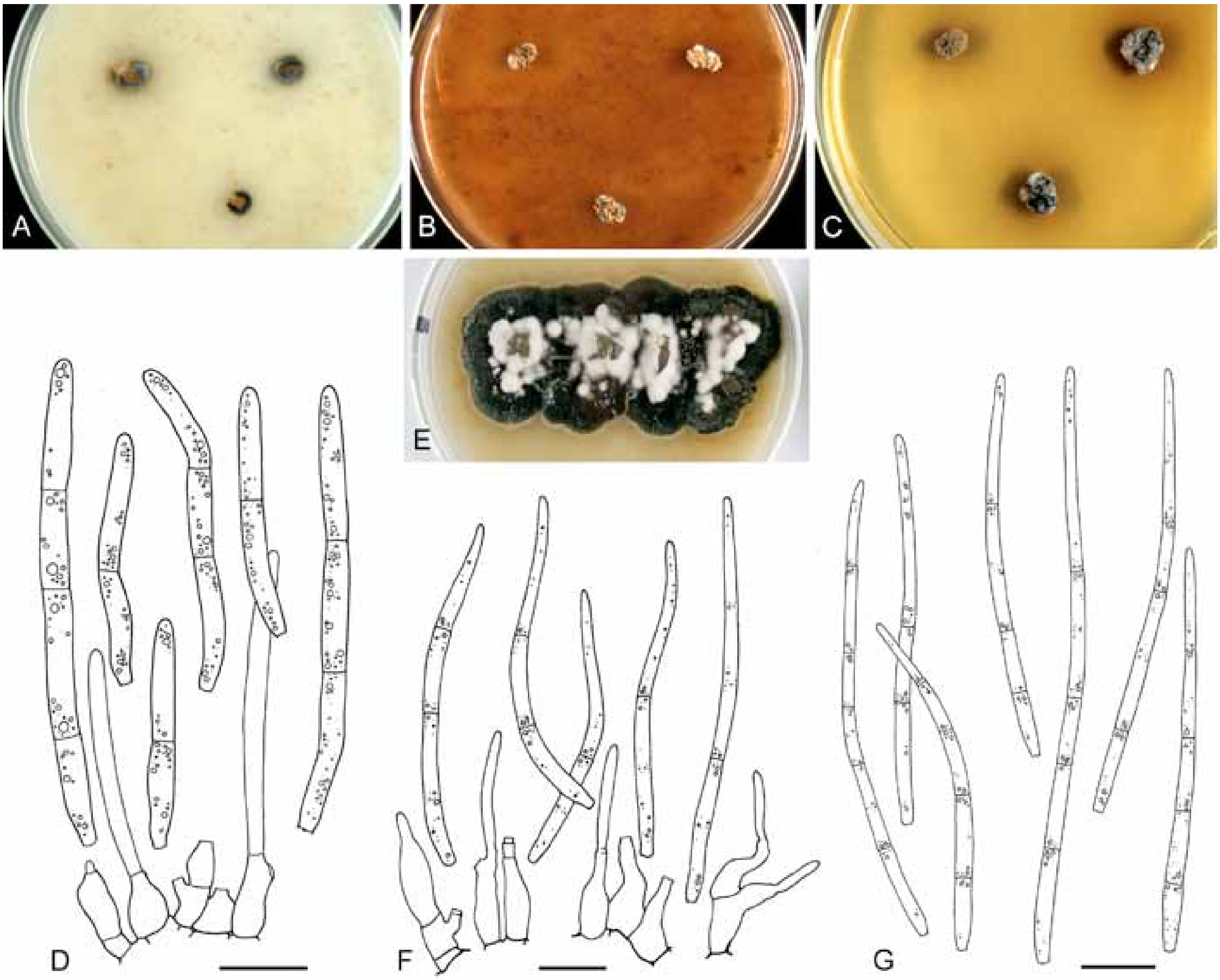

**Fig. 45.** A–D. *Sphaerulina hyperici*. A–C. Colonies CBS 102313. A. On OA. B. On CHA. C. On MEA. D. Conidia and conidiogenous cells *in planta* (CBS H-21194, epitype). E–G. *Sphaerulina gei*. E. Colony on OA (KACC 44051 = CBS 128632). F. Conidia and conidiogenous cells *in planta* (CBS H-21194, epitype). G. Ibid., on OA (CBS 102318). Scale bars = 10 µm.

very thin and easily overlooked), not constricted around the septa, hyaline, contents with several minute oil-droplets and granular material in each cell in the living state, with minute oil-droplets and granular contents in the rehydrated state, 33–65(–75) × 2–2.8(–3) µm (living; rehydrated, 1.8–2.5 µm wide). *Sexual morph* unknown.

*Description in vitro*: *Colonies* on OA 6–8(–15) mm diam in 3 wk, with an even, glabrous, colourless to buff margin; colonies spreading, immersed mycelium at first buff to rosy-buff, tardily becoming olivaceous to olivaceous-black, occassionally some sectors remaining buff; aerial mycelium mostly wanting, but sometimes with a few greyish tufts, the surface of the colony centre soon covered by rosy-buff masses of conidial slime, produced from conidiogenous cells directly on the mycelium or in pycnidial conidiomata; reverse olivaceous-black, margin buff. *Colonies* on CMA 7–9 mm diam in 3 wk, as on OA, but green pigmentation developing more rapidly. *Colonies* on MEA 7–9(–11) mm diam in 3 wk, with an irregular, glabrous, rosy-buff margin; a reddish pigment diffusing into the agar; colony spreading to restricted, the surface cerebriform to irregularly lobed, up to 2 mm high, very dark, but locally covered either by grey, felted aerial mycelium or masses of salmon conidial slime, produced directly from hyphae or in superficial stromatal conidiomata; reverse rust to chestnut. *Colonies* on CHA 6–7(–10) mm diam in 3 wk, colony features and sporulation as on MEA, but the margin covered by whitish aerial mycelium; diffusing pigment also present. Sporulating structures on OA very similar to those *in planta*, but conidia up to 85 µm long.

*Hosts*: *Geum* spp.

*Material examined*: **Czech Republic**, Bohemia, near Tábor, on living leaves of *Geum urbanum*, 20 July 1903, F. Bubák, distributed in Kabát & Bubák, Fungi imperfecti exsicc. 114, PC 0084558. **France**, Caen, on living leaves of *G. urbanum,* “Col. Desmazieres 1863, no. 8, 58”, “Jun-Sep. 1842”, **isotype** PC 0084556; forest near Caen, on living leaves of *G. urbanum,* 1841, Roberge, PC 0084555. **Germany**, Brandenburg, Buchmühle near Lagow, on living leaves of *G. urbanum*, 10 Sep. 1909, P. Sydow, PC 0084559. **Korea**, Hoengseong, on living leaves of *G. japonicum*, H.D. Shin, living culture CBS 128616 = KACC 43029 = SMKC 22748; same substr., Pyeongchang, H.D. Shin, living culture CBS 128632 = KACC 44051 = SMKC 23686. **Latvia**, prov. Vidzeme, Kr. Riga, Ogre, on living leaves of *G. urbanum*, 19 July 1936, J. Smarods, PC 0084557. **Netherlands**, Prov. Limburg, Schimperbosch, SW of Vaals, on the same substr., 29 Aug. 1999. H.A. van der Aa *s.n.*, CBS H-21168; Prov. Noord Holland, Amsterdamse Waterleidingduinen, Panneland, on living leaves of *G. urbanum*, 31 Aug. 1999, G. Verkley & A. van Iperen 914, **epitype designated here** CBS H-21167 “MBT175360”, living culture ex-epitype CBS 102318. **Romania**, distr. Prahova, Muntenia, Cheia, on living leaves of *G. rivale*, T. Săvulescu & C. Sandhu, distributed in Săvulescu, Herb. Mycol. Romanicum 8, 377, PC 0084560. **Sweden**, Gotland, Endre parish, Hulte, on living leaves of *G. urbanum*, 16 July 1898, T. Vestergren, PC 0084561.

*Notes*: The type material from PC studied contains one leaf showing the typical symptoms, and although only old empty fruitbodies were observed in it, it is almost certain that these are the product of this well-known and common "*Septoria"* species. The other material studied here was in much better condition and proved highly homogeneous in both symptoms and morphology of the sporulating structures, including the collection from *Geum rivale,* with most conidia observed below 70 µm long. Some authors found conidia up to about 75 µm long in various European collections (Jørstad 1965, Vanev *et al.* 1997). In the fresh material from The Netherlands, conidia were no longer than 65 µm on the host plant, but the isolates obtained from it produced conidia up to 85 µm long. This material is chosen here to epitypify *Sphaer. gei* because it is geographically the closest one for which also a culture is available.

Several authors have recognised *Septoria gei* f. *immarginata* for material on *Geum urbanum* with smaller conidia, *viz.* Radulescu *et al.* (1973), reporting conidia as continuous, 33–56 × 1.1–1.5 µm (in majority 40–46 × 1.5 µm), and Teterevnikova-Babayan (1983), reporting 20–33 × 1.5 µm. Shin & Sameva (2004) considered this *forma* a synonym of *S. gei*, for which they noted the wide range of conidial sizes. In Asian collections identified as *S. gei* the conidia appear to be longer than in material from elsewhere (Shin & Sameva 2004), but the Korean isolates included here are genetically very close to the ex-epitype strain CBS 102318, and regarded as conspecific. Sequence analyses of the cultures of *Sphaer. gei* indicate a close relationship with species such as *Sphaer. patriniae* (CBS 128653, 129153), from *Patrinia scabiosaefolia* and *P. villosa* (*Valerianaceae*) and *Sphaer. cercidis* (Quaedvlieg *et al.* 2013).

***Sphaerulina hyperici*** **(**Roberge ex Desm.) Verkley, Quaedvlieg & Crous, **comb. nov.** MycoBank MB804476. Fig. 45A–D.

*Basionym*: *Septoria hyperici* Roberge ex Desm., Annls Sci. Nat., sér. 2, Bot.17: 110. 1842.

≡ *Phleospora hyperici* (Roberge ex Desm.) Westend., Bull. Acad. r. Bruxelles 12 (9): 251. 1845.

*Description in planta*: *Symptoms* leaf lesions indefinite, usually starting to develop from the tip of leaf lamina and progressing towards the basis, irregular, reddish brown, surrounding leaf tissue often yellowish; *Conidiomata* pycnidial, amphigenous, densly dispersed in each lesion, only partly immersed, subglobose to globose or flask-shaped, brown to black, 55–90(–130) µm diam; *ostiolum* central, circular, often lifted above the leaf surface, 25–35(–50) µm wide, surrounded by concolorous or somewhat darker cells; *conidiomatal wall* 10–22 µm thick, composed of a homogenous tissue of hyaline, angular cells 2–5.5 µm diam, the outermost cells pale brown with slightly thickened walls, the inner cells thin-walled. *Conidiogenous cells* hyaline, discrete or integrated in 1–2-septate conidiophores, terminal ones narrowly to broadly ampulliform, holoblastic, producing a single conidium or proliferating sympodially, 6–8(–10) × 3.5–5 µm. *Conidia* cylindrical, straight, more often slightly curved or flexuous, broadly rounded at the apex, narrowing slightly to the truncate base, 1–3(–5)-septate, not or slightly constricted around the septa, hyaline, contents with a few oil-droplets and minute granular material in each cell in the living state, with oil-droplets and granular contents in the rehydrated state, 24–55(–63) × 2.5–3.5 µm (living; rehydrated, 1.8–2.8 µm wide). *Sexual morph* unknown (see notes).

*Description in vitro*: *Colonies* on OA 4–7 mm diam in 2 wk, with an even, glabrous, colourless margin; centre and some outgrowing sectors entirely pale luteous to buff, where conidia are formed directly on the immersed and superficial mycelium; submarginal area blackish, due to dark pigmented hyphae and superficial pycnidia, covered by diffuse, white tufty to woolly aerial mycelium; reverse concolourous. *Colonies* on CMA as on OA. *Colonies* on MEA 3–7 mm diam in 2 wk (32–40 mm in 6 wk), with an irregular, glabrous margin; a reddish pigment diffusing into the agar; colony restricted, the surface cerebriform to irregularly lobed, up to 2 mm high, immersed mycelium dark, mostly covered by dense, pure white, woolly aerial mycelium, or salmon to saffron by masses of conidia; reverse cinnamon to brick. *Colonies* on CHA 3–5 mm diam in 2 wk, with an irregular, glabrous margin; colony restricted, the surface cerebriform to irregularly lobed, up to 2 mm high, dark but mostly covered by salmon to saffron conidial masses, and some areas with a dense, pure white, woolly-floccose aerial mycelium; reverse dark brick.

*Hosts*: *Hypericum* spp.

*Material examined*: **Bulgaria**, Camkorije, on leaves of *Hypericum quadrangulum*, 31 Aug. 1907, Fr. Bubák, distributed in Kabát & Bubák, Fungi imperfecti exsicc. 469 (PC 0084544). **Czech Republic**, Bohemia, Bukovina, on leaves of *H. perforatum*, 9 June 1906, J. Kabát, distributed in Kabát & Bubák, Fungi imperfecti exsicc. 421 (PC 0084542); same substr., E. Moravia, M. Weisskirchen, Aug. 1941, F. Petrak (PC 0084545). **France**, loc. unknown, on leaves of *H. perforatum*, **isotype** PC 0084532; Lighhouse of Libisey near Caen, same substr., June 1841, M. Roberge, PC 0084531; same substr., Bois de Plaisir, 16 July 1935 (Herb. G. Viennot-Bourgin), PC 0084533; same substr., Allier, Gennetines, 5 Apr. 1959, A. Lachmann, PC 0084535; Landes, Etang near Seignosse, on *H. helodes*, 5 Aug. 1964, G. Durrieu, PC 0084536; Seine-et-Marne, Fontainebleau forest, on leaves of *H. hirsutum*, July 1888, Feuilleaubols, PC 0084537, 0084540. **Germany**, Hessen-Nassau, Dillkreis, Langenaubach, on leaves of *H. quadrangulum*, 12 July 1931, A. Ludwig, distributed in Sydow, Mycotheca germanica 2570, PC 0084538; Brandenburg, Sadowa, on leaves of *H. perforatum*, 4 Aug. 1907, P. Sydow, distributed in Sydow, Mycotheca germanica 625, PC 0084543. **Netherlands**, Prov. Utrecht, Soest, along railroad between Lange Duinen and De Zoom, on living leaves of *Hypericum* sp., 28 July 1999, G. Verkley 900, **epitype designated here** CBS H-21194 "MBT175361", living culture ex-epitype CBS 102313. **Romania,** Moldova, distr. Iaşi, Poeni, on leaves of *H. hirsutum*, 1 Aug. 1948, C. Sandu-Ville & I. Rădulescu, distributed in Tr. Săvulescu, Herb. Mycol. Romanicum, fasc. 29, no. 1445, PC 0084534, 0084546. **Sweden**, E. Götland, Gryt parish, ca. 300 m E.-S.E. of Strömmen, on leaves of *H. maculatum*, 18 July 1947, J.A. Nannfeldt 9386, distributed in S. Lundell & J.A. Nannfeldt, Fungi exsicc. Suecici, praes. Upsal. 1910, PC 0084547.

*Notes*: According to Jørstad (1965), the pycnidia of *Sphaer. hyperici* are immersed hypophylously, but in most collections investigated here they protrude with their ostioli from either side of the leaf in about equal numbers. Jørstad (1965) further noted that the conidial sizes varied considerably between collections, with extreme values ranging between 15 and 57 µm for length and 1.5–2.5 µm for width of conidia. Vanev *et al.* (1997) reported conidia 21.5–54 × 2–3.2 µm. In the type specimen, which is rich in conidiomata with protruding dry spore-masses, conidia are mostly 1–3-septate, 25–50 × 2–2.5 µm, thus in good agreement with the collection V900, which is designated as epitype.

Four varieties of *Septoria hyperici* and a few more *Septoria* species have been described on species of the genus *Hypericum*. Most of these taxa have conidia in the size range given here for *Sphaer. hyperici*, indicating that these might be conspecific. However, more strains should be isolated from the different species of *Hypericum* and compared with type material of these taxa, before firm conclusions about their status can be drawn. *Septoria hypericorum*, which was described from *H. perforatum* with conidia reported 15–35 × 4–6 µm, is likely to belong in *Stagonospora* or another related asexual morph. The ex-epitype strain of *Sphaer. hyperici* CBS 102313 is closely related to strains identified as *S.*

*menispermi* (CBS 128666, 128761), and somewhat more distant from species such as *Sphaer. gei*, and *Sphaer. cercidis* (CBS 501.50).

Petrak (1925) stated that *Mycosphaerella hyperici* is the sexual morph of *Septoria hyperici*, but this has not been confirmed by culture studies. The only culture available of *M. hyperici* for comparison, CBS 280.49, was sequenced by Zalar *et al*. (2007) and shown to group with isolates of *Cladosporium halotolerans*, so it may be a culture contaminant. No strain is available for *M. hypericina*, a species originally described from *Hypericum prolificum* in the US. No asexual morph is known for this taxon which, according to Aptroot (2006), is morphologically indistinguishable from *M. punctiformis* (anam. *Ramularia endophylla*; Verkley *et al.* 2004c).

***Sphaerulina socia*** (Pass.) Quaedvlieg, Verkley & Crous, **comb. nov.** MycoBank MB804478.

*Basionym*: *Septoria socia* Pass., Funghi Parm. Septor.: no. 74; Atti Soc. crittog. ital. 2: 33. 1879.

*Description in planta*: *Symptoms* leaf lesions circular to irregular, single or confluent to form irregular extended lesions, pale to dark brown, usually surrounded by a red or purple zone, mostly visible on both sides of the leaf. *Conidiomata* pycnidial, mostly epiphyllous, a few to many in each lesion, immersed, globose, brown to black, 80–100(–110) µm diam; *ostiolum* central, circular, 15–25 µm wide, surrounding cells darker; *conidiomatal wall* 10–17 µm thick, composed 2–3 layers of isodiametric cells, 2–3.5(–5) µm diam, the cells in the outermost layer(s) pale brown with slightly thickened walls, the inner cells thin-walled. *Conidiogenous cells* hyaline, discrete, rarely integrated in 1(–2)-septate conidiophores, globose, or narrowly to broadly ampulliform, holoblastic, proliferating percurrently and/or sympodially, sometimes with indistinct annellations on an elongated neck, 4–8.5(–12) × 2–3(–3.5) µm. *Conidia* cylindrical, straight to slightly curved, rarely flexuous, attenuated in the upper cell to a pointed to narrowly rounded tip, attenuated gradually or more abruptly towards a sub-truncate base, 1–3(–5)-septate, not constricted around the septa, hyaline, contents minute oil-droplets and granular material in the rehydrated state, (19–)22–34 × 1–1.5(–2) µm (rehydrated). *Sexual morph* unknown.

*Hosts*: *Chrysanthemum leucanthemum* and other wild or cultivated *Chrysanthemum* spp.

*Material examined*: **Germany**, Torstedt near Harburg, Sep. 1957, R. Schneider *s.n.*, BBA 8514, living culture CBS 357.58. **New Zealand**, North Island, Coromandel, Tairua Forest, along roadside of St. Hway 25, near crossing 25A, on living leaves of *Chrysanthemum leucanthemum*, 23 Jan. 2003, G. Verkley 1842a, CBS H-21243.

*Additional material examined*: **Netherlands**, on leaf of *Rosa* sp., isolated June 1958 by Plant Protection Service, Wageningen, CBS 355.58 (preserved as *S. rosae*; possibly infection of a fungus originally identified as *S. rosae*).

*Notes*: Punithalingam (1967d) described the conidiogenous cells as obpyriform, undifferentiated cells producing blastospores, while Muthumary (1999) also observed sympodially proliferating cells in a collection from India; the present material from New Zealand clearly showed both percurrent and sympodial conidiogenesis, even in a single conidiogenous cell. In this respect, *S. socia* is similar to *S. chrysanthemella*, for which both these proliferations were observed with transmission electron microscopy (Verkley 1998a).

According to Teterevnikova-Babayan (1987) conidia are 21–35 × 1–1.5 µm, so with these measurements the present observations are in good agreement. Verkley & Starink-Willemse (2004) noted that the ITS sequence of CBS 357.58 identified as *S. socia* suggested a relatively distant relationship with other *Septoria* species on the family *Asteraceae*, and that it was more closely related to species such as the maple pathogen *Sphaerulina aceris* (syn. *Septoria aceris, Mycosphaerella latebrosa)* and poplar pathogen *Sphaerulina populicola*. Multilocus sequencing performed here confirms that CBS 357.58 groups in the *Sphaerulina*-clade, and that CBS 355.58 originally identified as *S. rosae* likely got infected with *S. socia*. *Septoria rosae* is a large spored species (70–90 × 3.5–4 µm) for which the name of the presumed sexual morph *Sphaerulina rehmiana* would be accepted (Quaedvlieg *et al*. 2013). Based on the huge difference in conidial size it seems very unlikely that it was confused with *S. socia.* The material from New Zealand studied here failed to grow in culture, so a genetic comparison was not possible. More isolates will be required to determine the affinities of *Sphaerulina rehmiana*.

***Sphaerulina tirolensis*** Verkley, Quaedvlieg & Crous, **sp. nov.** MycoBank MB804479. Fig. 46.

*Etymology*: named after the region in Austria where the type material was collected, Tirol.

*Description in planta*: *Symptoms* leaf lesions numerous, circular to irregular, mostly single, or confluent, dull brown, amphigenous but on the lower surface barely visible due to the white hairs of the host; *Conidiomata* pycnidial, epiphyllous, many in each lesion, immersed, subglobose to globose, brown to black, 55–100 µm diam; *ostiolum* central, circular, initially 15–30 µm wide, later up to 50 µm wide, surrounding cells somewhat darker; *conidiomatal wall* 15–22 µm thick, composed of an outer layer of pale brown angular to irregular cells, 8–12 µm wide with walls thickened to 1.5 µm, and an inner layer of hyaline, angular to globose, thin-walled cells. *Conidiogenous cells* hyaline, discrete, rarely integrated in 1-septate conidiophores, cylindrical or narrowly to broadly ampulliform, holoblastic, some proliferating percurrently 1–several times with indistinct annellations and forming an elongated neck, rarely proliferating sympodially, 5–12.5(–15) × 3.5–4(–5) µm. *Conidia* cylindrical, straight, slightly curved to flexuous, narrowly to broadly rounded at the apex, truncate or slightly narrowed at the base, (1–)3–7(–9)-septate, not constricted around the septa, hyaline, with granular contents and minute oil-droplets, 40–70(–78) × 2.5–3(–3.5) µm (rehydrated). *Sexual morph* not observed.

*Description in vitro*: *Colonies* on OA 2.5–4(–5) mm diam in 2 wk; 16–20 mm in 7 wk), with an even, glabrous, colourless or buff to rosy-buff margin; immersed mycelium dark green or dull green, showing some salmon or rosy-buff colours only after more than 6 wk of incubation; colonies restricted, but with irregular elevations in the centre on which complexes of stromatic conidiomata and single pycnidia are formed, releasing whitish conidial slime; aerial mycelium variable, almost wanting, to well developed as a dense, white, woolly-floccose mat; reverse mostly olivaceous-black, locally buff to rosy-buff. *Colonies* on CMA 3–4.5(–5) mm daim in 2 wk, 6–8 mm in 3 wk (22–25 mm in 7 wk), as on OA, but with a narrower colourless margin. Conidial slime also milky white, as on OA. *Colonies* on MEA 2–4(–6) mm diam in 2 wk, 6–9 mm in 3 wk (16–22 mm in 7 wk), with an even, glabrous colourless to buff margin; colonies restricted, irregularly pustulate to hemispherical, sometimes with rather high, subglobose outgrowths; immersed mycelium buff to honey usually only near the margin, olivaceous-black in the centre; almost entirely covered by a dense, appressed

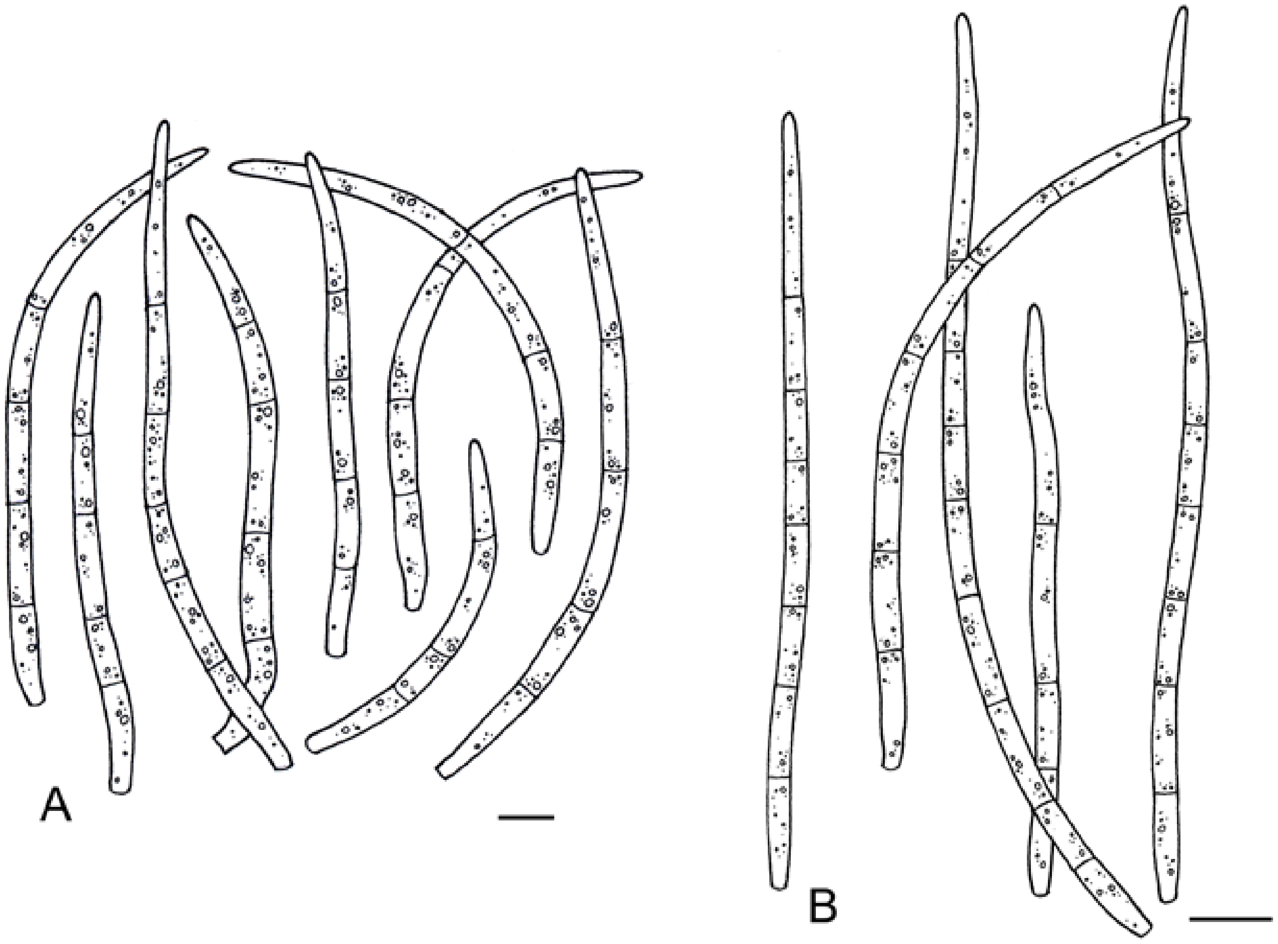


**Fig. 46.** *Sphaerulina tirolensis*. A. Conidia *in planta* (CBS H-21232, holotype). B. Conidia on OA (CBS 109017). Scale bars = 10 µm.

mat of white or grey aerial mycelium; a diffusable pigment staining the surrounding agar more or less ochreous; reverse usually dark umber or olivaceous-black in the centre, surrounded by ochreous, which later becomes fulvous to apricot. *Colonies* on CHA 3–4 mm diam in 2 wk, 5–6 mm in 3 wk (12–16 mm in 7 wk), with an even but later more irregular, glabrous, buff, rosy-buff or flesh margin; colonies pustulate to almost hemispherical, the surface olivaceous-black to dark slate blue, glabrous, or covered by diffuse, greyish or flesh aerial mycelium, some colonies later covered by a pure white, dense mat of aerial mycelium; diffusable pigment not observed; reverse blood colour to umber. Cultures produce large masses of pale flesh conidial slime, aggregating around the colony margin.

*Conidiomata* pycnidial or merged into stromatic complexes. *Conidiogenous cells* as *in planta*. *Conidia* straight to curved or flexuous, narrowly to broadly rounded at the apex, narrowly truncate at the base, 3–7(–9)-septate, not constricted around the septa, hyaline, contents granular with minute oil-droplets, 54–96(–108) × 2.5–3 µm.

*Host*: *Rubus idaeus*.

*Material examined*: **Austria**, Tirol, Pitztal, Arzl, on living leaves of *Rubus idaeus*, 30 July 2000, G. Verkley 1021, **holotype** CBS H-21232, living cultures ex-type CBS 109017, 109018.

*Notes*: *Sphaerulina tirolensis* differs from another septoria-like fungus described on *R. idaeus*, *viz. Rhabdospora rubi* var. *rubi-idaei* described from stems of *R. idaeus* in Romania, with conidia (36–)40–50(–60) × 2(–2.5) µm. Demaree & Wilcox (1943) studied Septoria leaf-spot diseases of raspberry (*R. idaeus*) in North America. *Cylindrosporium rubi,* of which the sexual morph is *Sphaerulina rubi* cf. Demaree & Wilcox (1943), is also different. The sequences of the various protein-coding genes fully support *Sphaer. tirolensis* as a separate species from the next taxon, *Sphaer. westendorpii*. The latter can be distinguished from *Sphaer. tirolensis* by the smaller conidia *in planta* [24–45(–50) × 1.8–2.2 µm] and also in culture [30–68(–80) × 1.5–2(–2.5) µm].

***Sphaerulina westendorpii*** Verkley, Quaedvlieg & Crous, **comb. et nom. nov.** MycoBank MB804480. Fig. 47.

*Basionym*: *Septoria rubi* Westend., in Westend. & Wallay, Herb. crypt. Belge, Fasc. 19, no. 938. 1854; Kickx, Fl. crypt. Flandr. 1: 432. 1867.

= *Mycosphaerella rubi* Roark, Phytopathology 11: 329. 1921.

*Description in planta*: *Symptoms* leaf lesions numerous, circular to irregular, single or confluent, pale yellowish brown to greyish brown, partly well-delimited by a dark red brown line or zone. *Conidiomata* pycnidial, epiphyllous, several in each lesion, immersed, subglobose to globose, brown to black, 55–90 µm diam; *ostiolum* central, circular, initially 20–40 µm wide, later becoming more irregular and up to 70 µm wide, surrounding cells somewhat darker; *conidiomatal wall* 10–15 µm thick, composed of a homogenous tissue of hyaline, angular cells 2.5–3.5 µm diam, the outermost cells pale brown with slightly thickened walls, the inner cells thin-walled. *Conidiogenous cells* hyaline, discrete, rarely integrated in 1-septate conidiophores, narrowly to broadly

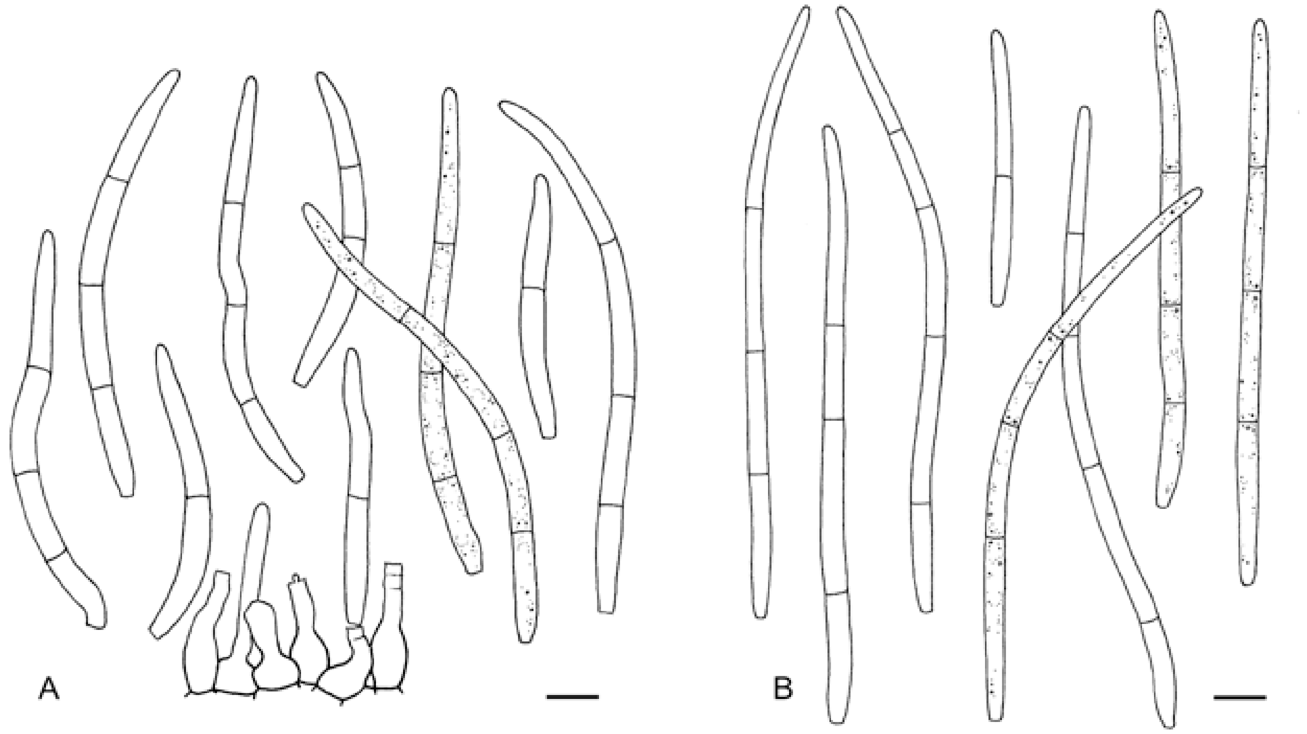


**Fig. 47.** *Sphaerulina westendorpii*. A. conidia *in planta* (CBS H-21229, epitype); B. conidia on OA (CBS 102327). Scale bars = 10 µm.

ampulliform, holoblastic, proliferating percurrently several times with indistinct annellations thus forming a relatively elongated neck, rarely also sympodially, 5–10(–15) × 2.5–3.5(–4) µm. *Conidia* filiform-cylindrical, straight, slightly curved to flexuous, narrowly to broadly rounded at the apex, narrowly truncate at the base, (0–)2–3(–5)-septate, not constricted around the septa, hyaline, contents granular material, sometimes with minute oil-droplets both in the living and rehydrated state, 24–45(–50) × 1.8–2.2 µm (living; rehydrated, 1.5–2.0 µm wide).

*Description in vitro*: *Colonies* on OA 8–10 mm diam in 19 d, with an even, glabrous, colourless or buff to rosy-buff margin; immersed mycelium dark green or dull green, but sectors or other parts of colonies may be only olivaceous-buff or rosy-buff to salmon; colonies spreading, with irregular elevations in the centre on which conidiomata are formed, releasing a whitish conidial slime; aerial mycelium almost absent to well developed and forming a dense, white, woolly-floccose mat; reverse olivaceous-black, locally buff to rosy-buff. *Colonies* on CMA 5–7(–10) mm diam in 19 d, as on OA, but more distinctly elevated and restricted. In faster growing sectors salmon to ochreous pigmentation (due to weak production of red pigment?) in a peripheral zone preceedes the formation a dominant greens. Conidial slime also milky white, as on OA. *Colonies* on MEA 9–12 mm diam in 19 d, with an even, glabrous colourless to buff margin; colonies restricted, irregularly pustulate to hemispherical; immersed mycelium buff to honey near the margin, olivaceous-black in the centre, sometimes mostly honey; almost entirely covered by a dense, appressed mat of white or grey aerial mycelium; a diffusable pigment staining the surrounding agar more or less ochreous; reverse usually dark umber or olivaceous-black in the centre, surrounded by ochreous, which later becomes fulvous to apricot. *Colonies* on CHA 7–9 mm diam in 19 d, with an even but later more irregular, glabrous, buff, rosy-buff or flesh margin; colonies pustulate to almost hemispherical, the surface ochreous to sienna, glabrous, or covered by diffuse, greyish or flesh aerial mycelium; diffusable pigment not observed; reverse blood colour to umber.

*Conidiomata* pycnidial or merged into stromatic complexes, as *in planta*. *Conidiogenous cells* as *in planta*, mostly cylindrical and proliferating percurrently, rarely also sympodially, 7–15(–18) × 2.5–3.5(–4) µm; *Conidia* as *in planta* but mostly 3–5-septate and considerably longer, 30–68(–80) × 1.5–2(–2.5) µm.

*Hosts*: *Rubus* spp.

*Material examined*: **Belgium**, Oostacker, near Gand, on leaves of *Rubus* sp., **isotype** BR-MYCO 159265-88, also distributed in Westend. & Wallay, Herb. crypt. Belge, Fasc. 19, no. 938. **Czech Republic**, Mikulov, on living leaves of *Rubus* sp., 15 Sep. 2008, G. Verkley 6002, CBS H-21257. **Netherlands**, prov. Limburg, Gerendal, on living leaves of *R. fruticosus s.l.*, 28 June 2000, G. Verkley 964, **epitype designated here** CBS H-21229 "MBT175362", living cultures ex-epitype CBS 109002, 109003; Prov. Limburg, Mookerheide, in mixed forest, on living leaves of *R. fruticosus s.l.*, 9 Sep. 1999, G. Verkley 923, CBS H-21205, living culture CBS 102327; same loc. and substr., 23 Aug. 2004, G. Verkley & M. Starink 3036, CBS H-21263, living culture CBS 117478; same substr., Prov. Limburg, St. Jansberg near Plasmolen, in mixed forest, G. Verkley 924, CBS H-21206; Prov. Flevoland, Erkemeder strand, in sandy dunes, on living leaves of *R. fruticosus s.l.*, 8 Sep. 1999, G. Verkley 930, CBS H-21210.

*Notes*: Jørstad (1965) discussed the problems regarding the taxonomy of *Septoria* species described from *Rubus*. Some of the later described taxa have been placed in synonymy with *Septoria rubi*, but most still need to be reevaluated based on fresh material, culture studies, and molecular characterisation. The type material in BR contains several well-preserved leaves of the *R. fruticosus* complex, showing typical symptoms. Fruitbodies investigated contained mostly 1–3-septate conidia, 17.5–40 × 1–1.5 µm, and with the typical shape of this common fungus on *Rubus* spp. The specimen CBS H-21229 from *R. fruticosus* in the south of the Netherlands, is chosen as epitype. This species is nested within the *Sphaerulina*-clade, and a new name in *Sphaerulina* should therefore be proposed for it. *Sphaerulina rubi* Demaree & Wilcox is already in use for another fungus with a *Cylindrosporium* sexual state (*C. rubi* Ellis & Morgan, conidia 40–55 × 2.5 µm cf. Saccardo), so *Sphaer. westendorpii* is proposed here as nomen novum. *Sphaerulina rehmiana* has been associated with *Septoria rosae* CBS 355.58, which has been identified as *S. rosae*, is genetically distinct from *Sphaer. westendorpii* (Quaedvlieg *et al.* 2013).

## Insufficiently known species

For the following species no host material was available and these have only been studied in culture, mostly based on older isolates, for which details are not described when the strain is regarded as degenerate.

***Septoria hippocastani*** Berk. & Broome, Ann. Mag. nat. Hist., Ser. 2, 5: 379. 1850.

*Material examined*: **Germany**, Pfälzer Wald, on *Aesculus hippocastanum*, Sep 1961, deposited Nov 1961, W. Gerlach, living culture CBS 411.61 (= BBA 9619).

*Note*: CBS 411.61 is degenerated and sterile, but based on multilocus sequence analysis it can be concluded that it is a *Septoria s. str.* (Fig. 2).

***Septoria limonum*** Pass., Atti Soc. crittog. ital., 2: 23. 1879.

*Description in vitro (18 ºC, near UV)*: *Colonies* on OA 20–29 mm diam in 3 wk, with an even, colourless margin; colonies plane, spreading, immersed mycelium in the centre flesh, surrounded by a broad zone of dark vinaceous to brown-vinaceous, aerial mycelium absent, or scarce, with few tufts of pure white aerial hyphae; reverse concolorous. No sporulation observed. *Colonies* on MEA 25–32 mm diam in 3 wk, with an even to somewhat ruffled, buff to colourless margin; colonies spreading, somewhat elevated in the centre, immersed mycelium appearing grayish, the colony surface almost entirely covered by a dense mat of white to grey, woolly-floccose aerial mycelium; reverse in the centre rust, surrounded by a broad zone of olivaceous-grey to greenish grey, which is sharply bordered by the narrow buff to luteous margin. No sporulation observed.

*Material examined*: **Italy**, *Citrus limonium*, isolated Mar. 1951, deposited by G. Goidanich, living culture CBS 419.51.

*Notes*: In the multilocus sequence analysis (Fig. 2) this strain groups with CBS 356.36 (*S. citricola*) and few other strains in a weakly supported clade close to the plurivorous *Septoria protearum* and isolates of *Septoria citri*. Due to the lack of morphological information linked to this strain, its identity remains uncertain.

## DISCUSSION

The type species of the genus *Septoria*, *S. cytisi*, could not be included in the multilocus analysis due to the fact that only LSU and ITS sequences were available for this species. However, as shown by Quaedvlieg *et al.* (2011), the position of this taxon is beyond doubt central to the clade indicated here as the main *Septoria* clade. Several “typical” *Septoria* species infecting herbaceous plants proved genetically distant from *S. cytisi* and its relatives, and can best be classified in separate genera, *Sphaerulina* (Quaedvlieg *et al.* 2013) and *Caryophylloseptoria*.

The identification of *Septoria* has thus far mainly relied on host taxonomy and morphological characters of the shape, size, and septation of conidia (Jørstad 1965, Teterevnikova-Babayan 1987, Andrianova 1987, Vanev *et al.* 1997, Muthumary 1999, Shin & Sameva 2004, Priest 2006). Taxonomists have noted that conidial width is generally a more reliable character for species identification than conidial length, which is more variable. Some also noticed that *Septoria* material collected from the same location and host species, but under different environmental conditions or at different times in the same season, can differ considerably in average conidial sizes, particularly length (Jørstad 1965). These findings are also confirmed in our study. Reliable identification based on morphological comparison alone is not possible for many *Septoria* species, and reference sequences will have to be produced for many more taxa in future. This will require critical studies of type specimens and also require the recollection of fresh material. It is crucial that the types of the oldest names available for *Septoria* on certain hosts will need to be studied as part of such work, and where necessary epitypes designated to fix the genetic application of these names. Although hardly practised thus far by taxonomists, isolation and study in culture is a valuable and indispensable tool for *Septoria* species delimitation and identification. We noted that the shape of conidia on OA generally agree best with those in the source material on the natural substrate. Under standardised incubation conditions on standard media cultures originating from deviant voucher material, for example because it developed under adverse conditions, show again their “normal” phenotypes which is better for comparison purposes. Extracting DNA from axenic cultures is straight-forward and less prone to errors caused by contaminants, a problem often encountered when extracting DNA from plant tissue.

The K2P results show that the five protein coding genes used during this research should all theoretically be able to distinquish every species in this dataset as their average inter- to intraspecific distance ration is over 10:1. The problem is that these are average numbers, not absolute numbers. For example, the Btub K2P graph in Fig. 1 starts at 0 and not at at 0.29, meaning that there actually are a few species in our dataset that are not distinguishable by Btub alone (although obviously by far most species in fact are). To avoid this, we recommend using at least two of the protein coding loci used in this study for identification of *Septoria* and allied genera. Because EF and Btub both have very high PCR success rates and have the highest species resolution percentage of all the loci used in this study, we recommend using these two loci for species identification purposes. It is advisable, however, to first sequence the ITS and LSU for a preliminary genus identification by blasting in GenBank and other useful databases.

The multilocus sequence dataset generally provided good resolution, with maximum to high bootstrap support for almost all terminal and most of the deeper nodes of the phylogenetic tree. The intraspecific variation in the genes investigated is limited for most taxa, even if specimens originate from such distant geographic origins as New Zealand, Korea and Europe (*S. convolvuli*, *S. leucanthemi*, *S. polygonorum*). Strains assigned to *Septoria citri* possibly represent a species complex, one of few groups within the main *Septoria* clade that was not resolved. One case of cryptic speciation is revealed in the *S. chrysanthemella* complex, where at least two genetically discrete entities can be found that are phenotypically difficult to distinguish.

Our results confirm that most species of *Septoria* have narrow host ranges, being limited to a single genus or a few genera of the same plant family. There were a few notable exceptions, however. We demonstrated that the supposed single-family host ranges of *Septoria paridis* (*Liliaceae*) and *S. urticae* (*Urticaceae*), each actually included one additional family (*Violaceae* and *Lamiaceae*, respectively). More surprisingly *Septoria protearum*, previously only associated with *Proteaceae* (*Protea*) (Crous *et al.* 2004), was now found to be also associated with *Araceae* (*Zanthedeschia*), *Aspleniaceae* (*Asplenium*), *Rutaceae* (*Boronia*), *Boraginaceae* (*Myosotis*), *Oleandraceae* (*Nephrolepis*), and *Rosaceae* (*Geum*). To our knowledge this is the first study to provide DNA-based evidence confirming that multiple family-associations occur for a single species in *Septoria*. It is to be expected that collecting and sequencing of more material will show more taxa to be plurivorous, and perhaps *S. paridis* and *S. urticae* will be among those.

Coevolution of plant pathogenic fungi and their hosts has been documented for several groups. Other possible patterns of evolution have already been suggested for septoria-like fungi in previous studies but the data available were not sufficient to fully understand the evolution of these fungi (Feau *et al.* 2006). The robust phylogeny we inferred revealed polyphyletic distribution patterns over the entire range of the *Septoria* clade for no less than 10 (singletons excluded) of the host families represented. These results clearly reject the coevolution hypothesis for *Septoria*, as species do not seem to consistently coevolve with hosts from a single host family but frequently jump successfully to hosts in new families. *Caryophylloseptoria* seems an exceptional genus in that it only comprises species infecting *Caryophyllaceae*, but it should be noted that it now only contains four species, as three other species infecting this family cluster distant within the *Septoria* clade (*S. cucubali*, *S. cerastii*, and *S. stellariae*). In the other clades some single-host family clusters can be found, but they do not comprise more than six fungal species (*S. chrysanthemella* and close relatives of *Asteraceae* within subclade 4b).

We conclude that trans-family host jumping must be a major force driving the evolution of *Septoria* and *Sphaerulina*. Species like *S. paridis* and *S. urticae* infecting (at least) two plant families may in fact be cases in point, as they could be in a transitional period of gradually changing from one principal host family to another, unrelated one. The genetic basis for successful host jumping is unclear. It may involve horizontal gene transfer, transient phases of endophytic infections in “non-hosts” as a first step in a process of genetic adaptation to new optimal hosts, or perhaps a combination of both. Plant pathological research may shed more light on the mechanisms driving *Septoria* evolution which would be important, as it may in future allow accurate assessment of risks involved with the introduction of new crops in areas where *Septoria* species occur on the local flora.

## HOST FAMILY INDEX

The taxa fully described in the Taxonomy section of this study are listed below according to the host family.

*Aceraceae*
- *Sphaerulina aceris*

*Apiaceae*
- *Septoria aegopodii*
- *S. aegopodina*
- *S. anthrisci*
- *S. apiicola*
- *S. heraclei*
- *S. petroselini*
- *S. sii*

*Araceae*
- *Septoria protearum*

*Aspleniaceae*
- *Septoria protearum*

*Asteraceae*
- *Septoria chromolaenae*
- *S. chrysanthemella*
- *S. ekmanniana*
- *S. erigerontis*
- *S. hypochoeridis*
- *S. lactucae*
- *S. leucanthemi*
- *S. matricariae*
- *S. putrida*
- *S. senecionis*
- *Sphaerulina socia*

*Betulaceae*
- *Sphaerulina betulae*

*Boraginaceae*
- *Septoria protearum*

*Campanulaceae*
- *Septoria campanulae*
- *S. citri* complex

*Caryophyllaceae*
- *Caryophylloseptoria lychnidis*
- *C. silenes*
- *C. spergulae*
- *Septoria cerastii*
- *S. cucubali*
- *S. stellariae*

*Convolvulaceae*
- *Septoria convolvuli*

*Cornaceae*
- *Sphaerulina cornicola*

*Cucurbitaceae*
- *Septoria cucurbitacearum*

*Dipsacaceae*
- *Septoria scabiosicola*

*Fabaceae*
- *Septoria astragali*

*Hypericaceae*
- *Septoria hyperici*

*Iridaceae*
- *Septoria sisyrinchii*

*Lamiaceae*
- *Septoria galeopsidis*
- *S. lamiicola*
- *S. melissae*
- *S. stachydis*

*Liliaceae*
- *Septoria paridis*

*Oleandraceae*
- *Septoria protearum*

*Onagraceae*
- *Septoria epilobii*

*Passifloraceae*
- *Septoria passifloricola*

*Polemoniaceae*
- *Septoria phlogis*

*Polygonaceae*
- *Septoria polygonorum*

*S. rumicum*
*Primulaceae*
*Septoria lysimachiae*
*Ranunculaceae*
*Septoria clematidis*
*S. lycoctoni*
*S. napelli*
*Rosaceae*
*Septoria citri* complex
*Sphaerulina gei*
*Sphaer. tirolensis*
*Sphaer. westendorpii*
*Rubiaceae*
*Septoria cruciatae*
*S. coprosmae*
*Rutaceae*
*Septoria protearum*
*Salicaceae*
*Sphaerulina frondicola*
*Scrophulariaceae*
*Septoria digitalis*
*Urticaceae*
*Septoria urticae*
*Verbenaceae*
*Septoria verbenae*
*Violaceae*
*Septoria paridis*

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# Sizing up *Septoria*

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**Abstract:** *Septoria* represents a genus of plant pathogenic fungi with a wide geographic distribution, commonly associated with leaf spots and stem cankers of a broad range of plant hosts. A major aim of this study was to resolve the phylogenetic generic limits of *Septoria*, *Stagonospora*, and other related genera such as *Sphaerulina*, *Phaeosphaeria* and *Phaeoseptoria* using sequences of the the partial 28S nuclear ribosomal RNA and RPB2 genes of a large set of isolates. Based on these results *Septoria* is shown to be a distinct genus in the *Mycosphaerellaceae*, which has mycosphaerella-like sexual morphs. Several septoria-like species are now accommodated in *Sphaerulina*, a genus previously linked to this complex. *Phaeosphaeria* (based on *P. oryzae*) is shown to be congeneric with *Phaeoseptoria* (based on *P. papayae*), which is reduced to synonymy under the former. *Depazea nodorum* (causal agent of nodorum blotch of cereals) and *Septoria avenae* (causal agent of avenae blotch of barley and rye) are placed in a new genus, *Parastagonospora*, which is shown to be distinct from *Stagonospora* (based on *S. paludosa*) and *Phaeosphaeria*. Partial nucleotide sequence data for five gene loci, ITS, LSU, EF-1α, RPB2 and Btub were generated for all of these isolates. A total of 47 clades or genera were resolved, leading to the introduction of 14 new genera, 36 new species, and 19 new combinations.

**Key words:** *Capnodiales*, Multi-Locus Sequence Typing (MLST), *Mycosphaerella*, *Mycosphaerellaceae, Phaeoseptoria*, *Phaeosphaeria*, *Phaeosphaeriaceae, Pleosporales, Septoria*, *Sphaerulina*, *Stagonospora*, systematics.

**Taxonomic novelties: New genera –** *Acicuseptoria* Quaedvlieg, Verkley & Crous, *Cylindroseptoria* Quaedvlieg, Verkley & Crous, *Kirstenboschia* Quaedvlieg, Verkley & Crous, *Neoseptoria* Quaedvlieg, Verkley & Crous, *Neostagonospora* Quaedvlieg, Verkley & Crous, *Parastagonospora* Quaedvlieg, Verkley & Crous, *Polyphialoseptoria* Quaedvlieg, R.W. Barreto, Verkley & Crous, *Ruptoseptoria* Quaedvlieg, Verkley & Crous, *Septorioides* Quaedvlieg, Verkley & Crous, *Setoseptoria* Quaedvlieg, Verkley & Crous, *Stromatoseptoria* Quaedvlieg, Verkley & Crous, *Vrystaatia* Quaedvlieg, W.J. Swart, Verkley & Crous, *Xenobotryosphaeria* Quaedvlieg, Verkley & Crous, *Xenoseptoria* Quaedvlieg, H.D. Shin, Verkley & Crous. **New species –** *Acicuseptoria rumicis* Quaedvlieg, Verkley & Crous, *Caryophylloseptoria pseudolychnidis* Quaedvlieg, H.D. Shin, Verkley & Crous, *Coniothyrium sidae* Quaedvlieg, Verkley, R.W. Barreto & Crous, *Corynespora leucadendri* Quaedvlieg, Verkley & Crous, *Cylindroseptoria ceratoniae* Quaedvlieg, Verkley & Crous, *Cylindroseptoria pistaciae* Quaedvlieg, Verkley & Crous, *Kirstenboschia diospyri* Quaedvlieg, Verkley & Crous, *Neoseptoria caricis* Quaedvlieg, Verkley & Crous, *Neostagonospora caricis* Quaedvlieg, Verkley & Crous, *Neostagonospora elegiae* Quaedvlieg, Verkley & Crous, *Paraphoma dioscoreae* Quaedvlieg, H.D. Shin, Verkley & Crous, *Parastagonospora caricis* Quaedvlieg, Verkley & Crous, *Parastagonospora poae* Quaedvlieg, Verkley & Crous, *Phlyctema vincetoxici* Quaedvlieg, Verkley & Crous, *Polyphialoseptoria tabebuiae-serratifoliae* Quaedvlieg, Alfenas & Crous, *Polyphialoseptoria terminaliae* Quaedvlieg, R.W. Barreto, Verkley & Crous, *Pseudoseptoria collariana* Quaedvlieg, Verkley & Crous, *Pseudoseptoria obscura* Quaedvlieg, Verkley & Crous, *Sclerostagonospora phragmiticola* Quaedvlieg, Verkley & Crous, *Septoria cretae* Quaedvlieg, Verkley & Crous, *Septoria glycinicola* Quaedvlieg, H.D. Shin, Verkley & Crous, *Septoria oenanthicola* Quaedvlieg, H.D. Shin, Verkley & Crous, *Septoria pseudonapelli* Quaedvlieg, H.D. Shin, Verkley & Crous, *Setophoma chromolaenae* Quaedvlieg, Verkley, R.W. Barreto & Crous, *Setoseptoria phragmitis* Quaedvlieg, Verkley & Crous, *Sphaerulina amelanchier* Quaedvlieg, Verkley & Crous, *Sphaerulina pseudovirgaureae* Quaedvlieg, Verkley & Crous, *Sphaerulina viciae* Quaedvlieg, H.D. Shin, Verkley & Crous, *Stagonospora duoseptata* Quaedvlieg, Verkley & Crous, *Stagonospora perfecta* Quaedvlieg, Verkley & Crous, *Stagonospora pseudocaricis* Quaedvlieg, Verkley, Gardiennet & Crous, *Stagonospora pseudovitensis* Quaedvlieg, Verkley & Crous, *Stagonospora uniseptata* Quaedvlieg, Verkley & Crous, *Vrystaatia aloeicola* Quaedvlieg, Verkley, W.J. Swart & Crous, *Xenobotryosphaeria calamagrostidis* Quaedvlieg, Verkley & Crous, *Xenoseptoria neosaccardoi* Quaedvlieg, H.D. Shin, Verkley & Crous. **New combinations –** *Parastagonospora avenae* (A.B. Frank) Quaedvlieg, Verkley & Crous, *Parastagonospora nodorum* (Berk.) Quaedvlieg, Verkley & Crous, *Phaeosphaeria papayae* (Speg.) Quaedvlieg, Verkley & Crous, *Pseudocercospora domingensis* (Petr. & Cif.) Quaedvlieg, Verkley & Crous, *Ruptoseptoria unedonis* (Roberge ex Desm.) Quaedvlieg, Verkley & Crous, *Septorioides pini-thunbergii* (S. Kaneko) Quaedvlieg, Verkley & Crous, *Sphaerulina abeliceae* (Hiray.) Quaedvlieg, Verkley & Crous, *Sphaerulina azaleae* (Voglino) Quaedvlieg, Verkley & Crous, *Sphaerulina berberidis* (Niessl) Quaedvlieg, Verkley & Crous, *Sphaerulina betulae* (Pass.) Quaedvlieg, Verkley & Crous, *Sphaerulina cercidis* (Fr.) Quaedvlieg, Verkley & Crous, *Sphaerulina menispermi* (Thüm.) Quaedvlieg, Verkley & Crous, *Sphaerulina musiva* (Peck) Quaedvlieg, Verkley & Crous, *Sphaerulina oxyacanthae* (Kunze & J.C. Schmidt) Quaedvlieg, Verkley & Crous, *Sphaerulina patriniae* (Miura) Quaedvlieg, Verkley & Crous, *Sphaerulina populicola* (Peck) Quaedvlieg, Verkley & Crous, *Sphaerulina quercicola* (Desm.) Quaedvlieg, Verkley & Crous, *Sphaerulina rhabdoclinis* (Butin) Quaedvlieg, Verkley & Crous, *Stromatoseptoria castaneicola* (Desm.) Quaedvlieg, Verkley & Crous. **Typifications: Epitypifications –** *Phaeosphaeria oryzae* I. Miyake, *Phaeoseptoria papayae* Speg.; **Neotypification –** *Hendersonia paludosa* Sacc. & Speg.

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## INTRODUCTION

Fungal species belonging to *Septoria* are among the most common and widespread leaf-spotting fungi worldwide. *Septoria* Sacc. (*Mycosphaerella*, *Capnodiales*, *Dothideomycetes*) is based on *Septoria cytisi*, which was first described by Desmazières (1847) as a pathogen of *Cytisus laburnum* (= *Laburnum anagyroides*). The genus *Septoria* is extremely large, and during the past 150 years more than 2000 taxa have been ascribed to this asexual genus (Verkley & Priest 2000, Verkley *et al*. 2004). Presently, *Septoria s.lat*. represents a polyphyletic assembly of genera that cluster mostly in the *Mycosphaerellaceae* (a family incorporating many plant pathogenic coelomycetes), although fungi with septoria-like morphology have also evolved outside this family



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(Crous *et al.* 2009a, c). Although many species of *Septoria* have mycosphaerella-like sexual states, the name *Mycosphaerella* does not apply to them, and should not be used in this context.

Following a proposal accepted by the International Code of Nomenclature for algae, fungi and plants (ICN), the generic name *Septoria* Sacc. was conserved over the older synonym *Septaria* Fr. (original spelling). The arguments preceding the typification of *Septoria* and subsequent proposals for name conservation by Wakefield (1940), Rogers (1949) and Donk (1964) between *Septoria sensu* Saccardo or *Septaria* Fries were various. In the end the committee for fungi appointed by the ICN followed the recommendation of Donk (1964), and decided on *Septoria* Sacc. over *Septaria* Fr., arguing that *Septoria* Sacc. had already been in prevalent use for many years, and should therefore be accepted as the correct name.

After examining several herbarium specimens of *S. cytisi*, Sutton (1980) circumscribed *Septoria* as follows: *Mycelium* immersed, branched, septate, pale brown. *Conidiomata* pycnidial, immersed, separate or aggregated (but not confluent), globose, papillate (or not), brown, thin-walled of pale brown *textura angularis*, often with a smaller-celled inner layer, somewhat darker and more thick-walled around the ostiole. *Conidiophores* reduced to conidiogenous cells. *Conidiogenous cells* holoblastic, either determinate or indeterminate, with a limited number of sympodial proliferations. Each locus has a broad, flat, unthickened scar, discrete, hyaline, smooth, ampulliform, doliiform or lageniform to short cylindrical. *Conidia* hyaline, multiseptate, filiform, smooth and either continuous or constricted at septa. Later work by Constantinescu (1984), Sutton & Pascoe (1987, 1989) and Farr (1991, 1992) augmented Sutton's previous generic circumscription by also including species with sympodial, enteroblastic and percurrent conidial proliferation. Furthermore, based on similarities in conidiomatal development, von Arx (1983) and Braun (1995) adopted an even wider concept of *Septoria* that included the acervular forms normally accommodated in *Phloeospora.*

Morphological traits in *Septoria* are generally conserved, and specific morphological characters by which to describe and identify *Septoria* and septoria-like species are limited. This lack of specific morphological characters caused *Septoria* taxonomy to be largely dependent on associated host data, leading to many of the described species only being identifiable by host plant, and by variation in informative supplementary characters like conidial length, width and septation (Jørstad 1965, 1967, Sutton 1980). Of these supplementary characters, conidial width appears to be the most stable (i.e. it shows the least amount of intraspecific variation) and in most *Septoria* species, intraspecific conidial width rarely varies more than 1 µm (Priest 2006).

This reliance on host data in *Septoria* taxonomy is far from perfect, and should be avoided for identification purposes (see Verkley *et al.* 2013, this volume). Extensive host inoculation experiments by Beach (1919) and Teterevnikova-Babayan (1987) have shown that identification of *Septoria* spp. by host specificity alone is error prone because many *Septoria* species are not restricted to a single specific host (i.e. several taxa have broader host ranges). *Septoria* species like *S. lactucicola* and *S. lycopersici* can not only infect multiple plant species within the same genus, but can also infect plants belonging to closely allied families and genera. In contrast to this, morphologically well distinguishable *Septoria* species can also parasitise the same hosts (*e.g.* multiple distinct *Septoria* species can be found on both *Chrysanthemum* and *Rubus* hosts) (Demaree & Wilcox 1943, Punithalingam 1976, Shin & Sameva 2004). Because host specificity has been one of the main criteria used for describing new, morphologically indistinguishable *Septoria* species over the past 150 years, one can expect that a certain number of described taxa are in fact synonyms of species from related hosts.

## *Septoria* and septoria-like genera in the molecular era

Although it had previously been speculated by Sutton (1980) that *Septoria* was in fact polyphyletic, definitive proof of this hypothesis awaited the introduction of molecular techniques. Cunfer & Ueng (1999) were the first to use rDNA sequence data of the internal transcribed spacer region (ITS) to postulate that *Zymoseptoria tritici* (then known as *Septoria tritici*) and several *Stagonospora* spp. (a morphologically similar genus, previously linked to *Septoria*) actually belonged to two distinct genera. Verkley *et al.* (2004) extended this study by employing a combination of 28S nrDNA (LSU) and ITS data to prove that *Septoria* was in fact both poly- and paraphyletic. Their work showed that septoria-like species such as *Z. tritici* and *Z. passerinii* were more closely related to *Ramularia* than to the majority of the other *Septoria* species used in their datasets.

Feau *et al.* (2006) were the first to use a multi-locus polyphasic sequencing approach to reliably identify *Septoria* spp. Besides ITS and LSU sequence data, they also used β-tubulin (Btub) sequence data to separate closely related species into distinct monophyletic groups that frequently correlated with their respective host families. These results supported the approach of using multi-gene sequence data for studying a large collection of *Septoria* strains at species level.

*Septoria s. str.* was finally demarcated when Quaedvlieg *et al.* (2011) managed to obtain both ITS and LSU sequence data from *S. cytisi* herbarium specimens. Phylogenetic analysis of the obtained *S. cytisi* LSU sequence data clearly proved that *Z. tritici* and *Z. passerinii* [as previously indicated by Cunfer & Ueng (1999) and Verkley *et al.* (2004)] did not belong to *Septoria s. str*., but in fact belonged to a separate genus, closely related to *Ramularia*. These two species were subsequently split off from *Septoria* and placed in a new genus, *Zymoseptoria* (named for the yeast-like state produced in culture). Since the initial *Zymoseptoria* paper, five additional species from members of *Poaceae* have been described in this genus (Crous *et al*. 2012a, Stukenbrock *et al*. 2012).

## Septoria-like asexual genera

Since the description of *Septoria* by Desmazières (1847), several additional septoria-like genera (pycnidial/acervular/stromatic conidioma with filiform conidia) have been described which could be mistaken for *Septoria s. str*.

The two economically most important septoria-like genera are probably *Zymoseptoria* (sexual morph mycosphaerella-like) and *Parastagonospora* (sexual morph phaeosphaeria-like; see below). Both of these genera are pathogenic on *Poaceae* (grasses) and are directly or indirectly responsible for significant annual crop losses worldwide on cereals such as barley and wheat (Eyal et al. 1987). Quaedvlieg *et al*. (2011) determined that *Zymoseptoria* formed a distinct clade in the *Mycosphaerellaceae*, while *Stagonospora* was found to cluster in the *Phaeosphaeriaceae* within the *Pleosporales,* near other genera like *Phoma* and *Phaeosphaeria* (Cunfer & Ueng 1999, Solomon *et al*. 2006) which contain important plant pathogens. However, besides *Zymoseptoria* and *Parastagonospora* there are many other, lesser-known septoria-like genera awaiting elucidation. The goal of the present study is therefore to conduct an in-depth morphological and molecular analysis of these septoria-like genera, and resolve the affinities of *Stagonospora* and its purported sexual morph, *Phaeosphaeria*. To this end a collection of 370 *Septoria* and septoria-like isolates (Table 1) were subjected to morphological examination and multi-gene DNA analyses.

## MATERIALS AND METHODS

### Isolates

Symptomatic leaves were incubated in moist chambers for up to 1 wk to enhance sporulation before single conidial colonies were established on 2 % malt extract agar (MEA) (Crous *et al*. 2009d). Leaf spots bearing ascomata were soaked in water for approximately 2 h, after which they were attached to the inner surface of Petri dish lids over plates containing MEA. Ascospore germination patterns were examined after 24 h, and single ascospore cultures established as described previously (Crous *et al*. 1991, Crous 1998). Colonies were sub-cultured onto synthetic nutrient-poor agar (SNA) containing sterile *Hordeum vulgare* (barley) and *Urtica dioica* (stinging nettle) stems, potato-dextrose agar (PDA), oatmeal agar (OA), and MEA (Crous *et al.* 2009d), and incubated at 25 °C under continuous near-ultraviolet light to promote sporulation. Isolates were also obtained from the culture collections of the CBS-KNAW Fungal Biodiversity Centre (CBS) in Utrecht, and the working collection of Pedro Crous (CPC). Reference strains were deposited CBS (Table 1).

### DNA extraction, amplification and sequencing

Genomic DNA was extracted from fungal mycelium growing on MEA, using the UltraClean® Microbial DNA Isolation Kit (Mo Bio Laboratories, Inc., Solana Beach, CA, USA). Strains (Table 1) were screened for five loci (β-tubulin (Btub), internal transcribed spacer (ITS), Translation elongation factor 1-alpha (EF-1α) 28S nrDNA (LSU) and RNA polymerase II second largest subunit (RPB2) using the primer sets listed in Table 2. The PCR amplifications were performed in a total volume of 12.5 μL solution containing 10–20 ng of template DNA, 1 × PCR buffer, 0.7 μL DMSO (99.9 %), 2 mM $MgCl_2$, 0.4 μM of each primer, 25 μM of each dNTP and 1.0 U Taq DNA polymerase (GoTaq, Promega). PCR amplification conditions were set as follows: an initial denaturation temperature of 96 °C for 2 min, followed by 40 cycles of denaturation temperature of 96 °C for 45 s, primer annealing at the temperature stipulated in Table 2, primer extension at 72 °C for 90 s and a final extension step at 72 °C for 2 min. The resulting fragments were sequenced using the PCR primers together with a BigDye Terminator Cycle Sequencing Kit v. 3.1 (Applied Biosystems, Foster City, CA). Sequencing reactions were performed as described by Cheewangkoon *et al*. (2008). All novel sequences were deposited in NCBI's GenBank database and alignments and phylogenetic trees in TreeBASE.

### Phylogenetic analyses

A basic alignment of the obtained sequence data was first done using MAFFT v. 7 [(http://mafft.cbrc.jp/alignment /server/index. html) (Katoh *et al*. 2002)] and if necessary, manually improved in BioEdit v. 7.0.5.2 (Hall 1999). To check the congruency of the RPB2 and LSU dataset, a 70 % neighbour-joining (NJ) reciprocal bootstrap method with maximum likelihood distance was performed (Mason-Gamer & Kellogg 1996, Lombard *et al.* 2010). Bayesian analyses (critical value for the topological convergence diagnostic set to 0.01) were performed on the concatenated loci using MrBayes v. 3.2.1 (Huelsenbeck & Ronquist 2001) as described by Crous *et al.* (2006) using nucleotide substitution models that were selected using MrModeltest v.2.3 (Table 3) (Nylander 2004). In order to keep the trees manageable for publication, two separate Bayesian trees were run. The first tree was run with all the *Septoria* and septoria-like isolates that either belonged to, or where more closely related to the *Mycosphaerellaceae* (Fig. 1) while the second tree contained all the septoria-like isolates either belonging to, or being more closely related to the *Phaeosphaeriaceae* (Fig. 2). *Parastagonospora nodorum* (CBS 259.49) was used as outgroup for the *Mycosphaerellaceae* dataset, while *Dothistroma pini* (CBS 121005) was used as outgroup for the *Phaeosphaeriaceae* dataset. As the novel genera and species described in this study were already clearly distinquishable in the LSU/RPB2 trees, the ITS, EF-1α and Btub sequence data of these isolates were deposited in GenBank without their subsequent trees being published in this paper.

### Taxonomy

Taxonomic descriptions were based on isolates sporulating in culture. Diseased leaf tissue was viewed under a Zeiss V20 Discovery stereo-microscope, while a Zeiss Axio Imager 2 light microscope with differential interference contrast (DIC) illumination and an AxioCam MRc5 camera with Zen software was used to capture morphological structures. Adobe Photoshop CS3 was used for the final editing of acquired images and photographic preparations. For measurements, 30–50 replicates of all relevant morphological features were made at ×1000 magnification. Colony characters and pigment production were noted after 2–4 wk of growth on MEA, PDA and OA (Crous *et al.* 2009d) incubated at 25 ºC in the dark. Colony colours (surface and reverse) were rated according to the colour charts of Rayner (1970).

## RESULTS

### DNA sequencing and phylogenetic analysis

The RPB2 and LSU sequence datasets did not show any conficts in both the *Mycosphaerellaceae* and *Phaeosphaeriaceae* tree topologies for the 70 % reciprocal bootstrap trees, allowing us to combine them in the multigene analyses. For the *Mycosphaerellaceae* tree, the gene boundaries were: 1–327 bp for RPB2 and 332–1120 bp for LSU. For the *Phaeosphaeriaceae* tree (Fig. 2), the gene boundaries were 1–777 bp for LSU and 782–1108 bp for RPB2. During the generation of the *Mycosphaerellaceae* tree (Fig. 1), a total of 57 048 trees were sampled out of the generated 76 062 trees (75 %). During the generation of the *Phaeosphaeriaceae* tree (Fig. 2), a total of 2844 trees were sampled out of the generated 3792 trees (75 %).

### Taxonomy

A total of 347 isolates representing 170 species were subjected to DNA analysis and morphological comparison. Phylogenetic analyses based on the LSU and RPB2 genes resolved a total of 47 clades of

**Table 1.** Collection details and GenBank accession numbers of isolates included in this study.

| Species | Isolate no.[1] | Host | Location | Collector | GenBank accession no.[2] | | | | |
|---|---|---|---|---|---|---|---|---|---|
| | | | | | EF-1α | Btub | RPB2 | LSU | ITS |
| *Acicuseptoria rumicis* | CBS 522.78 | *Rumex alpinus* | France | H.A. van der Aa | KF253105 | KF252643 | KF252153 | KF251648 | KF251144 |
| *Boeremia telephii* | CBS 135415; S670 | *Lavatera thuringiaca* | Germany | U. Damm | – | KF252644 | KF252154 | KF251649 | KF251145 |
| *Caryophylloseptoria lychnidis* | CBS 109098 | *Silene pratensis* | Austria | G.J.M. Verkley | KF253234 | KF252768 | KF252292 | KF251790 | KF251286 |
| | CBS 109099 | *Silene pratensis* | Austria | G.J.M. Verkley | KF253235 | KF252769 | KF252293 | KF251791 | KF251287 |
| | CBS 109101 | *Silene pratensis* | Austria | G.J.M. Verkley | KF253236 | KF252770 | KF252294 | KF251792 | KF251288 |
| | CBS 109102 | *Silene pratensis* | Austria | G.J.M. Verkley | KF253237 | KF252771 | KF252295 | KF251793 | KF251289 |
| *Car. pseudolychnidis* | CBS 128614 | *Lychnis cognata* | South Korea | H.D. Shin | KF253238 | KF252772 | KF252296 | KF251794 | KF251290 |
| | CBS 128630 | *Lychnis cognata* | South Korea | H.D. Shin | KF253239 | KF252773 | KF252297 | KF251795 | KF251291 |
| *Car. silenes* | CBS 109100 | *Silene nutans* | Austria | G.J.M. Verkley | KF253240 | KF252774 | KF252298 | KF251796 | KF251292 |
| | CBS 109103 | *Silene pratensis* | Austria | G.J.M. Verkley | KF253241 | KF252775 | KF252299 | KF251797 | KF251293 |
| *Car. spergulae* | CBS 397.52 | *Dianthus caryophyllus* | Netherlands | Schouten | KF253243 | KF252777 | KF252301 | KF251799 | KF251295 |
| | CBS 109010 | *Spergula morisonii* | Netherlands | A. Aptroot | KF253242 | KF252776 | KF252300 | KF251798 | KF251294 |
| *Cercospora beticola* | CBS 124.31; CPC 5070 | *Beta vulgaris* | Romania | – | KF253106 | KF252645 | KF252155 | KF251650 | KF251146 |
| *Cer. capsici* | CBS 118712 | – | Fiji | P. Tyler | KF253244 | KF252778 | KF252302 | KF251800 | KF251296 |
| *Cer. zebrina* | CBS 137.56 | *Hedysarum coronarium* | Italy | M. Ribaldi | KF253245 | KF252779 | KF252303 | KF251801 | KF251297 |
| | CBS 118790; IMI 262766 | *Trifolium subterraneum* | Australia | M.J. Barbetti | KF253107 | KF252646 | KF252156 | KF251651 | KF251147 |
| *Chaetosphaeronema hispidulum* | CBS 216.75 | *Anthyllis vulneraria* | Germany | R. Schneider | KF253108 | KF252647 | KF252157 | KF251652 | KF251148 |
| *Coniothyrium carteri* | CBS 105.91 | *Quercus robur* | Germany | H. Schill | KF253165 | KF252700 | KF252214 | KF251712 | KF251209 |
| | CBS 101633 | *Quercus* sp. | Netherlands | – | KF253166 | KF252701 | KF252215 | KF251713 | KF251210 |
| *Con. glycinicola* | CBS 124141 | *Glycine max* | Zimbabwe | C. Lavy | KF253167 | KF252702 | KF252216 | KF251714 | KF251211 |
| *Con. sidae* | CBS 135108; CPC 19602 | *Sida* sp. | Brazil | R.W. Barreto | KF253109 | KF252648 | KF252158 | KF251653 | KF251149 |
| *Corynespora leucadendri* | CBS 135133; CPC 19345 | *Leucadendron* sp. | South Africa | S. Lee | KF253110 | KF252639 | KF252159 | KF251654 | KF251150 |
| *Cylindroseptoria ceratoniae* | CBS 477.69 | *Ceratonia siliqua* | Spain | H.A. van der Aa | KF253111 | KF252649 | KF252160 | KF251655 | KF251151 |
| *Cyl. pistaciae* | CBS 471.69 | *Pistacia lentiscus* | Spain | H.A. van der Aa | KF253112 | KF252650 | KF252161 | KF251656 | KF251152 |
| *Cytostagonospora martiniana* | CBS 135102; CPC 17727 | *Acacia pycnantha* | Australia | P.W. Crous | KF253113 | KF252651 | KF252162 | KF251657 | KF251153 |
| *Dissoconium commune* | CPC 12397 | *Eucalyptus globulus* | Australia | I. Smith | KF253190 | KF252724 | KF252242 | KF251740 | KF251237 |
| *Dothistroma pini* | CBS 116484 | *Pinus nigra* | USA | G. Adams | JX901622 | JX902193 | JX901948 | JX901824 | JX901736 |
| | CBS 116485 | *Pinus nigra* | USA | G. Adams | JX901625 | JX902196 | JX901951 | JX901827 | JX901739 |
| | CBS 116487 | *Pinus nigra* | USA | G. Adams | JX901620 | JX902191 | JX901946 | JX901822 | GU214532 |
| | CBS 121005 | *Pinus pallasiana* | Russia | T. S. Bulgakov | KF253115 | KF252653 | – | KF251659 | KF251155 |
| | CBS 121011 | *Pinus pallasiana* | Russia | A.C. Usichenko | KF253250 | – | KF252307 | KF251806 | KF251302 |
| *Dot. septosporum* | CBS 383.74 | *Pinus coulteri* | France | M. Morelet | KF253251 | – | KF252308 | KF251807 | KF251303 |

**Table 1.** (Continued).

| Species | Isolate no.[1] | Host | Location | Collector | GenBank accession no.[2] | | | | |
|---|---|---|---|---|---|---|---|---|---|
| | | | | | EF-1α | Btub | RPB2 | LSU | ITS |
| | CPC 16798 | *Pinus mugo* 'Rostrata' | Netherlands | W. Quaedvlieg | JX901627 | JX902198 | JX901953 | JX901829 | JX901741 |
| | CPC 16799 | *Pinus mugo* | Netherlands | W. Quaedvlieg | JX901628 | JX902199 | JX901954 | JX901830 | JX901742 |
| *Kirstenboschia diospyri* | CBS 134911; CPC 19869 | *Diospyros whyteana* | South Africa | P.W. Crous | KF253116 | KF252640 | KF252164 | KF251660 | KF251156 |
| | CPC 19870 | *Diospyros whyteana* | South Africa | P.W. Crous | KF253117 | KF252641 | KF252165 | KF251661 | KF251157 |
| *Lecanosticta acicola* | CBS 322.33 | – | – | P.V. Siggers | JX901639 | JX902213 | JX901968 | JX901844 | JX901755 |
| | CBS 133791 | *Pinus strobus* | USA | B. Ostrofsky | KC013002 | KC013008 | KC013014 | KC013017 | KC012999 |
| *Lec. brevispora* | CBS 133601 | *Pinus* sp. | Mexico | J.Y. Morales | JX901649 | JX902224 | JX901979 | JX901855 | JX901763 |
| *Lec. guatamalensis* | IMI 281598 | *Pinus oocarpa* | Guatemala | H.C. Evans | JX901650 | JX902225 | JX901980 | JX901856 | JX901764 |
| *Lec. longispora* | CBS 133602 | *Pinus* sp. | Mexico | J.Y. Morales | JX901651 | JX902227 | JX901982 | JX901858 | JX901766 |
| *Leptosphaeria albopunctata* | CBS 254.64 | *Spartina alterniflora* | USA | J. Kohlmeyer | KF253118 | KF252654 | KF252166 | KF251662 | KF251158 |
| *Mycosphaerella brassicicola* | CBS 228.32 | *Brassica oleracea* | Denmark | C.A. Jörgensen | KF253252 | KF252783 | KF252309 | KF251808 | KF251304 |
| | CBS 267.53 | *Brassica oleracea* | Netherlands | F. Quak | KF253253 | KF252784 | KF252310 | KF251809 | KF251305 |
| *Mycosphaerella* sp. | CBS 135464; CPC 11677 | *Draba nemorosa* var. *hebecarpa* | South Korea | H.D. Shin | – | KF252786 | KF252312 | KF251811 | KF251307 |
| *Neoseptoria caricis* | CBS 135097; S653 | *Carex acutiformis* | Netherlands | W. Quaedvlieg | – | – | KF252167 | KF251663 | KF251159 |
| *Neosetophoma samarorum* | CBS 138.96 | *Phlox paniculata* | Netherlands | – | KF253119 | KF252655 | KF252168 | KF251664 | KF251160 |
| | CBS 139.96 | *Poa* sp. | Netherlands | – | KF253120 | KF252656 | KF252169 | KF251665 | KF251161 |
| | CBS 568.94 | *Urtica dioica* | Netherlands | G.J.M. Verkley | KF253121 | KF252657 | KF252170 | KF251666 | KF251162 |
| *Neostagonospora caricis* | CBS 135092; S616 | *Carex acutiformis* | Netherlands | W. Quaedvlieg | – | KF252658 | KF252171 | KF251667 | KF251163 |
| *Neost. elegiae* | CBS 135101; CPC 16977 | *Elegia cuspidata* | South Africa | S. Lee | KF253122 | KF252659 | KF252172 | KF251668 | KF251164 |
| *Paraphoma chrysanthemicola* | CBS 172.70 | *Chrysanthemum morifolium* | Netherlands | R. Schneider | KF253123 | KF252660 | KF252173 | KF251669 | KF251165 |
| | CBS 522.66 | *Chrysanthemum morifolium* | UK | – | KF253124 | KF252661 | KF252174 | KF251670 | KF251166 |
| *Parap. dioscoreae* | CBS 135100; CPC 11357 | *Dioscorea tokoro* | South Korea | H.D. Shin | KF253125 | KF252662 | KF252175 | KF251671 | KF251167 |
| | CPC 11355 | *Dioscorea tokoro* | South Korea | H.D. Shin | KF253126 | KF252663 | KF252176 | KF251672 | KF251168 |
| | CPC 11361 | *Dioscorea tokoro* | South Korea | H.D. Shin | KF253127 | KF252664 | KF252177 | KF251673 | KF251169 |
| *Parap. fimeti* | CBS 170.70 | *Apium graveolens* | Netherlands | M.A. de Waard | KF253128 | KF252665 | KF252178 | KF251674 | KF251170 |
| | CBS 368.91 | *Juniperus communis* | Switzerland | – | KF253129 | KF252666 | KF252179 | KF251675 | KF251171 |
| *Parap. radicina* | CBS 111.79 | *Malus sylvestris* | Netherlands | G.H. Boerema | KF253130 | KF252667 | KF252180 | KF251676 | KF251172 |
| | CBS 102875 | *Lycopersicon esculentum* | Germany | – | KF253131 | KF252668 | KF252181 | KF251677 | KF251173 |
| *Parastagonospora avenae* | CBS 289.69 | *Lolium perenne* | Germany | U.G. Schlösser | KF253132 | KF252669 | KF252182 | KF251678 | KF251174 |
| | CBS 290.69 | *Lolium perenne* | Germany | U.G. Schlösser | KF253133 | KF252670 | KF252183 | KF251679 | KF251175 |
| *Paras. caricis* | CBS 135671; S615 | *Carex acutiformis* | Netherlands | W. Quaedvlieg | KF253134 | KF252671 | KF252184 | KF251680 | KF251176 |

**Table 1.** (Continued).

| Species | Isolate no.[1] | Host | Location | Collector | GenBank accession no.[2] | | | | |
|---|---|---|---|---|---|---|---|---|---|
| | | | | | EF-1α | Btub | RPB2 | LSU | ITS |
| *Paras. nodorum* | CBS 110109 | *Lolium perenne* | Denmark | M.P.S. Câmara | KF253135 | KF252672 | KF252185 | KF251681 | KF251177 |
| *Paras. "nodorum"* | CBS 259.49 | *Triticum* sp. | Canada | – | KF253143 | KF252679 | KF252192 | KF251688 | KF251185 |
| *Paras. poae* | CBS 135089; S606 | *Poa* sp. | Netherlands | S.I.R. Videira | KF253136 | KF252673 | KF252186 | KF251682 | KF251178 |
| | CBS 135091; S613 | *Poa* sp. | Netherlands | S.I.R. Videira | KF253137 | KF252674 | KF252187 | KF251683 | KF251179 |
| *Passalora depressa* | CPC 14915 | *Angelica gigas* | South Korea | H.D. Shin | KF253256 | KF252788 | KF252314 | KF251813 | KF251309 |
| *Pas. dioscoreae* | CBS 135460; CPC 10855 | *Dioscorea tokoro* | South Korea | H.D. Shin | KF253257 | KF252789 | KF252315 | KF251814 | KF251310 |
| | CBS 135463; CPC 11513 | *Dioscorea tenuipes* | South Korea | H.D. Shin | KF253258 | KF252790 | KF252316 | KF251815 | KF251311 |
| *Phaeophleospora eugeniae* | CPC 15143 | *Eugenia uniflora* | Brazil | A.C. Alfenas | KF253138 | KF252642 | – | JX901875 | KF251180 |
| | CPC 15159 | *Eugenia uniflora* | Brazil | A.C. Alfenas | JX901667 | JX902245 | JX901999 | JX901876 | FJ493189 |
| *"Phaeosphaeria" alpina* | CBS 456.84 | *Phleum alpinum* | Switzerland | A. Leuchtmann | KF253139 | KF252675 | KF252188 | KF251684 | KF251181 |
| *Phaeos. caricicola* | CBS 603.86 | *Carex pendula* | Switzerland | A. Leuchtmann | KF253140 | KF252676 | KF252189 | KF251685 | KF251182 |
| *Phaeos. juncicola* | CBS 110108 | *Phlox* sp. | Netherlands | M.P.S. Câmara | KF253141 | KF252677 | KF252190 | KF251686 | KF251183 |
| *Phaeos. nigrans* | CBS 307.79 | *Zea mays* | Switzerland | – | KF253142 | KF252678 | KF252191 | KF251687 | KF251184 |
| *Phaeos. oryzae* | CBS 110110 | *Oryza sativa* | South Korea | L. Hausch | – | KF252680 | KF252193 | KF251689 | KF251186 |
| *Phaeos. papayae* | CBS 135416 | *Carica papaya* | Brazil | A.C. Alfenas | – | KF252681 | KF252194 | KF251690 | KF251187 |
| *"Phaeos." phragmiticola* | CBS 459.84 | *Phragmites australis* | Switzerland | A. Leuchtmann | KF253144 | KF252682 | KF252195 | KF251691 | KF251188 |
| *"Phaeos." pontiformis* | CBS 117487 | – | Netherlands | J. Harrak | KF253145 | KF252683 | KF252196 | KF251692 | KF251189 |
| *Phaeosphaeria* sp. | CBS 206.87 | *Zea mays* | Gabon | J.L. Notteghem | KF253146 | KF252684 | KF252197 | KF251693 | KF251190 |
| | CBS 135465; CPC 11894 | *Zea mays* | South Africa | P.W. Crous | KF253147 | KF252685 | KF252198 | KF251694 | KF251191 |
| *"Phaeos." typharum* | CBS 296.54 | *Nardus stricta* | Switzerland | L.E. Wehmeyer | KF253148 | KF252686 | KF252199 | KF251695 | KF251192 |
| *"Phaeos." vagans* | CBS 604.86 | *Calamagrostis arundinacea* | Sweden | A. Leuchtmann | KF253149 | KF252687 | KF252200 | KF251696 | KF251193 |
| phaeosphaeria-like sp. | CBS 123.76 | *Prunus domestica* | Serbia | M. Arseijevic | KF253150 | KF252688 | KF252201 | KF251697 | KF251194 |
| | CBS 135461; CPC 11231 | *Musa* sp. | Mauritius | Y. Jaufeerally-Fakim | KF253151 | KF252689 | KF252202 | KF251698 | KF251195 |
| | CBS 135466; CPC 12131 | *Acacia crassicarpa* | Thailand | W. Himaman | KF253153 | KF252691 | KF252204 | KF251700 | KF251197 |
| | CBS 135469; CPC 12881 | *Pinus monticola* | USA | G. Newcombe & R.G. Ganley | KF253154 | KF252692 | KF252205 | KF251701 | KF251198 |
| | CPC 12130 | *Acacia crassicarpa* | Thailand | W. Himaman | KF253152 | KF252690 | KF252203 | KF251699 | KF251196 |
| *Phaeosphaeriopsis glaucopunctata* | CBS 653.86 | *Ruscus aculeatus* | Switzerland | A. Leuchtmann | KF253155 | KF252693 | KF252206 | KF251702 | KF251199 |
| *Phloeospora ulmi* | CBS 344.97 | *Ulmus glabra* | Austria | W. Gams | KF253158 | KF252696 | – | KF251705 | KF251202 |
| | CBS 613.81 | *Ulmus* sp. | Austria | H.A. van der Aa | KF253159 | KF252697 | KF252208 | KF251706 | KF251203 |
| | CBS 101564 | *Ulmus* sp. | Netherlands | H.A. van der Aa | KF253156 | KF252694 | KF252207 | KF251703 | KF251200 |
| | CBS 109835 | *Ulmus* sp. | Netherlands | G.J.M. Verkley | KF253157 | KF252695 | – | KF251704 | KF251201 |
| *Phlogicylindrium eucalyptorum* | CBS 111680 | *Eucalyptus nitens* | Australia | P.W. Crous | KF253160 | KF252698 | KF252209 | KF251707 | KF251204 |

**Table 1.** (Continued).

| Species | Isolate no.[1] | Host | Location | Collector | GenBank accession no.[2] | | | | |
|---|---|---|---|---|---|---|---|---|---|
| | | | | | EF-1α | Btub | RPB2 | LSU | ITS |
| | CBS 111689 | *Eucalyptus nitens* | Australia | P.W. Crous | KF253161 | – | KF252210 | KF251708 | KF251205 |
| *Phlyctema vincetoxici* | CBS 123726 | *Vincetoxicum officinale* | Czech Republic | G.J.M. Verkley | KF253162 | KF252699 | KF252211 | KF251709 | KF251206 |
| | CBS 123727 | *Vincetoxicum officinale* | Czech Republic | G.J.M. Verkley | KF253163 | – | KF252212 | KF251710 | KF251207 |
| | CBS 123743 | *Vincetoxicum officinale* | Czech Republic | G.J.M. Verkley | KF253164 | – | KF252213 | KF251711 | KF251208 |
| *Phoma herbarum* | CBS 615.75 | *Rosa multiflora* | Netherlands | G.H. Boerema | KF253168 | KF252703 | KF252217 | KF251715 | KF251212 |
| *Polyphialoseptoria tabebuiae-serratifoliae* | CBS 112650 | *Tabebuia serratifolia* | Brazil | A.C. Alfenas | KF253169 | KF252704 | KF252218 | KF251716 | KF251213 |
| *Pol. terminaliae* | CBS 135106; CPC 19611 | *Terminalia catappa* | Brazil | R.W. Barreto | KF253170 | KF252705 | KF252219 | KF251717 | KF251214 |
| | CBS 135475; CPC 19487 | *Terminalia catappa* | Brazil | R.W. Barreto | KF253171 | – | KF252220 | KF251718 | KF251215 |
| *Pseudocercospora chiangmaiensis* | CBS 123244 | *Eucalyptus camaldurensis* | Thailand | R. Cheewangkoon | JX901676 | JX902254 | JX902008 | JX901885 | JX901781 |
| *Pse. eucalyptorum* | CBS 116303 | *Eucalyptus nitens* | South Africa | P.W. Crous | KF253172 | KF252706 | KF252221 | KF251719 | KF251216 |
| | CPC 13816 | *Eucalyptus glaucescens* | UK | S. Denman | KF253230 | KF252764 | KF252288 | KF251786 | KF251282 |
| *Pse. madagascariensis* | CBS 124155 | *Eucalyptus camaldulensis* | Madagascar | M.J. Wingfield | KF253265 | – | KF252322 | KF251822 | KF251318 |
| *Pse. natalensis* | CBS 111069 | *Eucalyptus nitens* | South Africa | T. Coutinho | KF302389 | KF302384 | KF302393 | KF302405 | KF302399 |
| *Pse. norchiensis* | CBS 120738 | *Eucalyptus* sp. | Italy | W. Gams | JX901684 | JX902263 | JX902017 | JX901894 | JX901785 |
| *Pse. robusta* | CBS 111175 | *Eucalyptus robur* | Malaysia | M.J. Wingfield | JX901694 | JX902273 | JX902027 | JX901904 | DQ303081 |
| *Pse. schizolobii* | CBS 120029 | *Schizolobium parahybum* | Ecuador | M.J. Wingfield | KF253269 | KF252798 | KF252326 | KF251826 | KF251322 |
| *Pse. tereticornis* | CPC 13299 | *Eucalyptus tereticornis* | Australia | P.W. Crous | JX901701 | JX902280 | JX902034 | JX901911 | GQ852770 |
| *Pseudocercosporella capsellae* | CBS 127.29 | – | – | K. Togashi | KF253273 | KF252801 | KF252330 | KF251830 | KF251326 |
| | CBS 112032 | *Brassica* sp. | UK | R. Evans | KF253267 | KF252797 | KF252324 | KF251824 | KF251320 |
| | CBS 112033 | *Brassica* sp. | UK | R. Evans | KF253254 | KF252785 | KF252311 | KF251810 | KF251306 |
| | CBS 118412 | *Brassica* sp. | New Zealand | C.F. Hill | KF253272 | KF252800 | KF252329 | KF251829 | KF251325 |
| *"Pella." magnusiana* | CBS 114735 | *Geranium silvaticum* | Sweden | E. Gunnerbeck | KF253274 | KF252802 | – | KF251831 | KF251327 |
| *Pella. pastinacae* | CBS 114116 | *Laserpitium latifolium* | Sweden | L. Holm | KF253275 | KF252803 | KF252331 | KF251832 | KF251328 |
| *Pseudoseptoria collariana* | CBS 135104; CPC 18119 | *Bambusoideae* sp. | Iran | A. Mirzadi Gohari | KF253174 | KF252707 | KF252223 | KF251721 | KF251218 |
| *Pseudos. obscura* | CBS 135103; CPC 18118 | *Bambusoideae* sp. | Iran | A. Mirzadi Gohari | KF253175 | KF252708 | KF252224 | KF251722 | KF251219 |
| *Ramularia endophylla* | CBS 113265 | *Quercus robur* | Netherlands | G.J.M. Verkley | KF253176 | KF252709 | KF252225 | KF251723 | KF251220 |
| *Ram. eucalypti* | CBS 120726 | *Eucalyptus grandis* var. *grandiflora Maiden* | Italy | W. Gams | KF253177 | KF252710 | KF252226 | KF251724 | KF251221 |
| *Ram. lamii* | CPC 11312 | *Leonurus sibiricus* | South Korea | H.D. Shin | KF253178 | KF252711 | KF252227 | KF251725 | KF251222 |
| *Ram. pratensis* | CPC 11294 | *Rumex crispus* | South Korea | – | KF253179 | KF252712 | KF252228 | KF251726 | KF251223 |
| *Ramularia* sp. | CBS 115913 | *Cerastium semidecandrum* | Netherlands | A. Aptroot | KF253180 | – | KF252229 | KF251727 | KF251224 |
| *Readeriella angustia* | CBS 124998 | *Eucalyptus delegatensis* | Australia | B.A. Summerel | KF253181 | KF252713 | KF252230 | KF251728 | KF251225 |
| *Rea. eucalypti* | CPC 13401 | *Eucalyptus* sp. | Portugal | P.W. Crous | KF253173 | – | KF252222 | KF251720 | KF251217 |

**Table 1.** (Continued).

| Species | Isolate no.[1] | Host | Location | Collector | GenBank accession no.[2] | | | | |
|---|---|---|---|---|---|---|---|---|---|
| | | | | | EF-1α | Btub | RPB2 | LSU | ITS |
| *Rea. readeriellophora* | CPC 12920 | *Eucalyptus sp.* | Australia | A. Carnegie | KF253114 | KF252652 | KF252163 | KF251658 | KF251154 |
| *Ruptoseptoria unedonis* | CBS 355.86 | *Arbutus unedo* | France | H.A. van der Aa | – | KF252715 | KF252233 | KF251731 | KF251228 |
| | CBS 755.70 | *Arbutus unedo* | Croatia | J.A. von Arx | – | KF252716 | KF252234 | KF251732 | KF251229 |
| *Sclerostagonospora phragmiticola* | CBS 338.86 | *Phragmites australis* | France | H.A. van der Aa | KF253184 | KF252717 | KF252235 | KF251733 | KF251230 |
| *Septoria abei* | CBS 128598 | *Hibiscus syriacus* | South Korea | H.D. Shin | KF253280 | KF252805 | KF252336 | KF251837 | KF251333 |
| *Sep. "agropyrina"* | CBS 387.64 | – | Japan | – | KF302392 | KF302387 | KF302398 | KF302410 | KF302404 |
| *Sep. anthrisci* | CBS 109020 | *Anthriscus* sp. | Austria | G.J.M. Verkley | KF253286 | KF252811 | KF252340 | KF251843 | KF251339 |
| *Sep. anthurii* | CBS 346.58 | *Anthurium scherzerianum* | Germany | R. Schneider | KF253288 | KF252813 | KF252342 | KF251845 | KF251341 |
| *Sep. apiicola* | CBS 400.54 | *Apium graveolens* | Netherlands | J.A. von Arx | KF253292 | KF252817 | KF252346 | KF251849 | KF251345 |
| *"Sep." arundinacea* | CBS 133.68 | *Phragmites australis* | Netherlands | H.A. van der Aa | KF253185 | KF252718 | KF252236 | KF251734 | KF251231 |
| | CBS 281.72 | *Phragmites australis* | Netherlands | J.W. Veenbaas-Rijks | KF253186 | KF252719 | KF252237 | KF251735 | KF251232 |
| *Sep. astericola* | CBS 128593 | *Aster yomena* | South Korea | H.D. Shin | KF253294 | KF252819 | KF252348 | KF251851 | KF251347 |
| *Sep. astragali* | CBS 109116 | *Astragalus* sp. | Austria | G.J.M. Verkley | KF253298 | KF252823 | KF252352 | KF251855 | KF251351 |
| | CBS 123878 | *Astragalus glycyphyllos* | Czech Republic | G.J.M. Verkley | KF253297 | KF252822 | KF252351 | KF251854 | KF251350 |
| *Sep. atropurpurea* | CBS 348.58 | *Aster canus* | Germany | R. Schneider | KF253299 | KF252824 | KF252353 | KF251856 | KF251352 |
| *Sep. bothriospermi* | CBS 128599 | *Bothriospermum tenellum* | South Korea | H.D. Shin | KF253301 | KF252826 | KF252355 | KF251858 | KF251354 |
| *Sep. bupleuricola* | CBS 128603 | *Bupleurum falcatum* | South Korea | H.D. Shin | KF253303 | KF252828 | KF252357 | KF251860 | KF251356 |
| *Sep. calendulae* | CBS 349.58 | *Calendula arvensis* | Italy | R. Schneider | KF253304 | KF252829 | KF252358 | KF251861 | KF251357 |
| *Sep. callistephi* | CBS 128590 | *Callistephus chinensis* | South Korea | H.D. Shin | KF253305 | KF252830 | KF252359 | KF251862 | KF251358 |
| *Sep. campanulae* | CBS 128604 | *Campanula takesimana* | South Korea | H.D. Shin | KF253308 | KF252833 | KF252362 | KF251865 | KF251361 |
| *Sep. cerastii* | CBS 128612 | *Cerastium holosteoides* | South Korea | H.D. Shin | KF253311 | KF252836 | KF252365 | KF251868 | KF251364 |
| *Sep.* cf. *agrimoniicola* | CBS 128585 | *Agrimonia pilosa* | South Korea | H.D. Shin | KF253283 | KF252808 | KF252337 | KF251840 | KF251336 |
| | CBS 128602 | *Agrimonia pilosa* | South Korea | H.D. Shin | KF253284 | KF252809 | KF252338 | KF251841 | KF251337 |
| *Sep.* cf. *rubi* | CBS 128646 | *Rubus crataegifolius* | South Korea | H.D. Shin | KF253314 | KF252839 | KF252368 | KF251871 | KF251367 |
| *Sep.* cf. *stachydicola* | CBS 128668 | *Stachys riederi* var. *japonica* | South Korea | H.D. Shin | KF253512 | KF253033 | KF252558 | KF252070 | KF251565 |
| *Sep. chelidonii* | CBS 128607 | *Chelidonium majus* | South Korea | H.D. Shin | KF253319 | KF252844 | KF252373 | KF251876 | KF251372 |
| *Sep. chromolaenae* | CBS 113373 | *Chromolaena odorata* | Cuba | S. Neser | KF253321 | KF252846 | KF252375 | KF251878 | KF251374 |
| *Sep. chrysanthemella* | CBS 128622 | *Chrysanthemum boreale* | South Korea | H.D. Shin | KF253323 | KF252848 | KF252377 | KF251880 | KF251376 |
| | CBS 128716 | – | South Africa | E. Oh | KF253325 | KF252850 | KF252379 | KF251882 | KF251378 |
| *Sep. cirsii* | CBS 128621 | *Cirsium setidens* | South Korea | H.D. Shin | KF253328 | KF252853 | KF252382 | KF251885 | KF251381 |
| *Sep. citricola* | CBS 356.36 | *Citrus sinensis* | Italy | G. Ruggieri | KF253329 | KF252854 | KF252383 | KF251886 | KF251382 |
| *Sep. clematidis* | CBS 108983 | *Clematis vitalba* | Germany | G.J.M. Verkley | KF253330 | KF252855 | KF252384 | KF251887 | KF251383 |
| *Sep. codonopsidis* | CBS 128620 | *Codonopsis lanceolata* | South Korea | H.D. Shin | KF253333 | KF252858 | KF252387 | KF251890 | KF251386 |

**Table 1.** (Continued).

| Species | Isolate no.[1] | Host | Location | Collector | GenBank accession no.[2] | | | | |
|---|---|---|---|---|---|---|---|---|---|
| | | | | | EF-1α | Btub | RPB2 | LSU | ITS |
| *Sep. convolvuli* | CBS 128627 | *Calystegia soldanella* | South Korea | H.D. Shin | KF253336 | KF252861 | KF252390 | KF251893 | KF251389 |
| *Sep. coprosma* | CBS 113391 | *Coprosma robusta* | New Zealand | G.J.M. Verkley | KF253255 | KF252787 | KF252313 | KF251812 | KF251308 |
| *Sep. crepidis* | CBS 128608 | *Youngia japonica* | South Korea | H.D. Shin | KF253337 | KF252862 | KF252391 | KF251894 | KF251390 |
| | CBS 128619 | *Youngia japonica* | South Korea | H.D. Shin | KF253338 | KF252863 | KF252392 | KF251895 | KF251391 |
| *Sep. cretae* | CBS 135095; CPC 651 | *Nerium oleander* | Greece | U. Damm | – | KF252720 | KF252238 | KF251736 | KF251233 |
| *Sep. cruciatae* | CBS 123747 | *Galium odoratum* | Czech Republic | G.J.M. Verkley | KF253340 | KF252865 | KF252394 | KF251897 | KF251393 |
| *Sep. cucubali* | CBS 102386 | *Saponaria officinalis* | Netherlands | G.J.M. Verkley | KF253344 | KF252869 | KF252398 | KF251901 | KF251397 |
| *Sep. cucurbitacearum* | CBS 178.77 | *Cucurbita maxima* | New Zealand | H.J. Boesewinkel | KF253346 | – | KF252400 | KF251903 | KF251399 |
| *Sep. dearnessii* | CBS 128624 | *Angelica dahurica* | South Korea | H.D. Shin | KF253347 | KF252871 | KF252401 | KF251904 | KF251400 |
| *Sep. digitalis* | CBS 391.63 | *Digitalis lanata* | Czech Republic | V. Holubová | KF253349 | KF252873 | KF252403 | KF251906 | KF251402 |
| *Sep. dysentericae* | CBS 131892; CPC 12328 | *Inula britannica* | South Korea | H.D. Shin | KF253353 | KF252877 | KF252406 | KF251910 | KF251406 |
| *Sep. epambrosiae* | CBS 128629 | *Ambrosia trifida* | South Korea | H.D. Shin | KF253356 | KF252880 | KF252407 | KF251913 | KF251409 |
| *Sep. epilobii* | CBS 109084 | *Epilobium fleischeri* | Austria | G.J.M. Verkley | KF253358 | KF252882 | KF252409 | KF251915 | KF251411 |
| | CBS 109085 | *Epilobium fleischeri* | Austria | G.J.M. Verkley | KF253359 | KF252883 | KF252410 | KF251916 | KF251412 |
| *Sep. erigerontis* | CBS 186.93 | *Erigeron annuus* | Italy | M. Vurro | KF253364 | KF252887 | KF252537 | KF252048 | KF251543 |
| | CBS 109094 | *Erigeron annuus* | Austria | G.J.M. Verkley | KF253360 | KF252884 | KF252411 | KF251917 | KF251413 |
| | CBS 131893; CPC 12340 | *Erigeron annuus* | South Korea | H.D. Shin | KF253363 | KF252888 | KF252414 | KF251920 | KF251416 |
| *Sep. eucalyptorum* | CBS 118505 | *Eucalyptus* sp. | India | W. Gams | KF253365 | KF252889 | KF252415 | KF251921 | KF251417 |
| *Sep. exotica* | CBS 163.78 | *Hebe speciosa* | New Zealand | H.J. Boesewinkel | KF253366 | KF252890 | KF252416 | KF251922 | KF251418 |
| *Sep. galeopsidis* | CBS 191.26 | *Galeopsis* sp. | – | C. Killian | KF253370 | KF252894 | KF252420 | KF251926 | KF251422 |
| | CBS 102314 | *Galeopsis tetrahit* | Netherlands | G.J.M. Verkley | KF253371 | KF252895 | KF252421 | KF251927 | KF251423 |
| | CBS 102411 | *Galeopsis tetrahit* | Netherlands | G.J.M. Verkley | KF253372 | KF252896 | KF252422 | KF251928 | KF251424 |
| *Sep. gentianae* | CBS 128633 | *Gentiana scabra* | South Korea | H.D. Shin | KF253374 | KF252898 | KF252424 | KF251930 | KF251426 |
| "*Sep.*" *gladioli* | CBS 121.20 | – | – | W.J. Kaiser | KF253375 | KF252899 | KF252425 | KF251931 | KF251427 |
| | CBS 353.29 | – | Netherlands | J.C. Went | KF253376 | KF252900 | KF252426 | KF251932 | KF251428 |
| *Sep. glycinicola* | CBS 128618 | *Glycine max* | South Korea | H.D. Shin | KF253378 | KF252902 | KF252427 | KF251934 | KF251430 |
| *Sep. helianthi* | CBS 123.81 | *Helianthus annuus* | – | M. Muntañola | KF253379 | KF252903 | KF252428 | KF251935 | KF251431 |
| *Sep. hibiscicola* | CBS 128615 | *Hibiscus syriacus* | South Korea | H.D. Shin | KF253382 | KF252906 | KF252431 | KF251938 | KF251434 |
| *Sep. hippocastani* | CBS 411.61 | *Aesculus hippocastanum* | Germany | W. Gerlach | KF253383 | KF252907 | KF252432 | KF251939 | KF251435 |
| | CPC 23103; MP11 | *Aesculus* sp. | Netherlands | S.I.R. Videira | KF253510 | KF253031 | KF252556 | KF252068 | KF251563 |
| *Sep. justiciae* | CBS 128625 | *Justicia procumbens* | South Korea | H.D. Shin | KF253385 | KF252909 | KF252434 | KF251941 | KF251437 |
| *Sep. lactucae* | CBS 352.58 | *Lactuca sativa* | Germany | G. Sörgel | KF253388 | KF252912 | KF252437 | KF251944 | KF251440 |

**Table 1.** (Continued).

| Species | Isolate no.[1] | Host | Location | Collector | GenBank accession no.[2] | | | | |
|---|---|---|---|---|---|---|---|---|---|
| | | | | | EF-1α | Btub | RPB2 | LSU | ITS |
| | CBS 108943 | *Lactuca sativa* | Netherlands | P. Grooteman | KF253387 | KF252911 | KF252436 | KF251943 | KF251439 |
| *Sep. lamiicola* | CBS 123884 | *Lamium* sp. | Czech Republic | G.J.M. Verkley | KF253397 | KF252921 | KF252446 | KF251953 | KF251449 |
| *Sep. lepidiicola* | CBS 128635 | *Lepidium virginicum* | South Korea | H.D. Shin | KF253398 | KF252922 | KF252447 | KF251954 | KF251450 |
| *Sep. leptostachyae* | CBS 128613 | *Phryma leptostachya* | South Korea | H.D. Shin | KF253399 | KF252923 | KF252448 | KF251955 | KF251451 |
| | CBS 128628 | *Phryma leptostachya* | South Korea | H.D. Shin | KF253400 | KF252924 | KF252449 | KF251956 | KF251452 |
| *Sep. leucanthemi* | CBS 109090 | *Chrysanthemum leucanthemum* | Austria | G.J.M. Verkley | KF253403 | KF252927 | KF252452 | KF251959 | KF251455 |
| *Sep. limonum* | CBS 419.51 | *Citrus limonum* | Italy | G. Goidánich | KF253407 | KF252931 | KF252456 | KF251963 | KF251459 |
| *Sep. linicola* | CBS 316.37 | *Linum usitatissimum* | – | H.W. Hollenweber | KF253408 | KF252932 | KF252457 | KF251964 | KF251460 |
| *Sep. lycoctoni* | CBS 109089 | *Aconitum vulparia* | Austria | G.J.M. Verkley | KF253409 | KF252933 | KF252458 | KF251965 | KF251461 |
| *Sep. lycopersici* | CBS 128654 | *Lycopersicon esculentum* | South Korea | H.D. Shin | KF253410 | KF252934 | KF252459 | KF251966 | KF251462 |
| *Sep. lycopicola* | CBS 128651 | *Lycopus ramosissimus* | South Korea | H.D. Shin | KF253412 | KF252936 | KF252461 | KF251968 | KF251464 |
| *Sep. lysimachiae* | CBS 102315 | *Lysimachia vulgaris* | Netherlands | G.J.M. Verkley | KF253413 | KF252937 | KF252462 | KF251969 | KF251465 |
| | CBS 123795 | *Lysimachia* sp. | Czech Republic | G.J.M. Verkley | KF253417 | KF252941 | KF252466 | KF251973 | KF251469 |
| *Sep. malagutii* | CBS 106.80 | *Solanum* sp. | Peru | G.H. Boerema | KF253418 | – | KF252467 | KF251974 | KF251470 |
| *Sep. matricariae* | CBS 109001 | *Matricaria discoidea* | Netherlands | G.J.M. Verkley | KF253420 | KF252943 | KF252469 | KF251976 | KF251472 |
| *Sep. mazi* | CBS 128755 | *Mazus japonicus* | South Korea | H.D. Shin | KF253422 | KF252945 | KF252471 | KF251978 | KF251474 |
| *Sep. melissae* | CBS 109097 | *Melissa officinalis* | Netherlands | H.A. van der Aa | KF253423 | KF252946 | KF252472 | KF251979 | KF251475 |
| *Sep. napelli* | CBS 109105 | *Aconitum napellus* | Austria | G.J.M. Verkley | KF253426 | KF252949 | KF252474 | KF251982 | KF251478 |
| *Sep. obesa* | CBS 354.58 | *Chrysanthemum indicum* | Germany | R. Schneider | KF253431 | – | KF252479 | KF251987 | KF251483 |
| | CBS 128588 | *Artemisia lavandulaefolia* | South Korea | H.D. Shin | KF253428 | KF252951 | KF252476 | KF251984 | KF251480 |
| | CBS 128623 | *Chrysanthemum indicum* | South Korea | H.D. Shin | KF253429 | KF252952 | KF252477 | KF251985 | KF251481 |
| *Sep. oenanthicola* | CBS 128649 | *Oenanthe javanica* | South Korea | H.D. Shin | KF253187 | KF252721 | KF252239 | KF251737 | KF251234 |
| *Sep. oenanthis* | CBS 128667 | *Cicuta virosa* | South Korea | H.D. Shin | KF253432 | KF252953 | KF252481 | KF251989 | KF251485 |
| *Sep. orchidearum* | CBS 457.78 | *Listera ovata* | France | H.A. van der Aa | KF253435 | KF252956 | KF252483 | KF251991 | KF251487 |
| | CBS 128631 | *Cyclamen fatrense* | South Korea | H.D. Shin | KF253434 | KF252955 | KF252482 | KF251990 | KF251486 |
| *Sep. pachyspora* | CBS 128652 | *Zyathoxylum schinifolium* | South Korea | H.D. Shin | KF253437 | KF252958 | KF252485 | KF251993 | KF251488 |
| *Sep. paridis* | CBS 109108 | *Viola* sp. | Austria | G.J.M. Verkley | KF253440 | KF252961 | KF252488 | KF251996 | KF251491 |
| | CBS 109111 | *Paris quadrifolia* | Austria | G.J.M. Verkley | KF253438 | KF252959 | KF252486 | KF251994 | KF251489 |
| *Sep. passiflorae* | CBS 102701 | *Passiflora edulis* | New Zealand | C.F. Hill | KF253442 | KF252963 | KF252490 | KF251998 | KF251493 |
| *Sep. perillae* | CBS 128655 | *Perilla frutescens* | South Korea | H.D. Shin | KF253444 | KF252965 | KF252491 | KF252000 | KF251495 |
| *Sep. petroselini* | CBS 182.44 | *Petroselinum sativum* | Netherlands | S.D. de Wit | KF253446 | KF252967 | KF252493 | KF252002 | KF251497 |
| *Sep. phlogis* | CBS 128663 | *Phlox paniculata* | South Korea | H.D. Shin | KF253448 | KF252969 | KF252495 | KF252004 | KF251499 |

**Table 1.** (Continued).

| Species | Isolate no.[1] | Host | Location | Collector | GenBank accession no.[2] | | | | |
|---|---|---|---|---|---|---|---|---|---|
| | | | | | EF-1α | Btub | RPB2 | LSU | ITS |
| *Sep. polygonorum* | CBS 347.67 | *Polygonum persicaria* | Netherlands | H.A. van der Aa | KF253455 | KF252976 | KF252502 | KF252011 | KF251506 |
| | CBS 109834 | *Polygonum persicaria* | Netherlands | G.J.M. Verkley | KF253453 | KF252974 | KF252500 | KF252009 | KF251504 |
| *Sep. posoniensis* | CBS 128645 | *Chrysosplenium japonicum* | South Korea | H.D. Shin | KF253456 | KF252977 | KF252503 | KF252012 | KF251507 |
| *Sep. protearum* | CBS 177.77 | *Fragaria* sp. | New Zealand | H.J. Boesewinkel | KF253463 | KF252984 | KF252509 | KF252019 | KF251514 |
| | CBS 390.59 | *Ligustrum vulgare* | Italy | M. Ribaldi | KF253467 | KF252987 | KF252513 | KF252023 | KF251518 |
| | CBS 566.88 | *Hedera helix* | France | H.A. van der Aa | KF253470 | KF252990 | KF252515 | KF252026 | KF251521 |
| | CBS 778.97 | *Protea cynaroides* | South Africa | L. Viljoen | KF253472 | KF252992 | KF252517 | KF252028 | KF251523 |
| | CBS 135477; CPC 19675 | *Zantedeschia aethiopica* | South Africa | P.W. Crous | KF253473 | KF252993 | KF252518 | KF252029 | KF251524 |
| *Sep. pseudonapelli* | CBS 128664 | *Aconitum pseudolaeve* var. *erectum* | South Korea | H.D. Shin | KF253475 | KF252995 | KF252520 | KF252031 | KF251526 |
| *Sep. putrida* | CBS 109088 | *Senecio nemorensis* | Austria | G.J.M. Verkley | KF253477 | KF252997 | KF252522 | KF252033 | KF251528 |
| *Sep. rumicum* | CBS 503.76 | *Rumex acetosa* | France | H.A. van der Aa | KF253478 | KF252998 | KF252523 | KF252034 | KF251529 |
| *Sep. saccardoi* | CBS 128756 | *Lysimachia vulgaris* | South Korea | H.D. Shin | KF253479 | KF252999 | KF252524 | KF252035 | KF251530 |
| *Sep. scabiosicola* | CBS 102334 | *Knautia arvensis* | Netherlands | G.J.M. Verkley | KF253481 | KF253001 | KF252526 | KF252037 | KF251532 |
| | CBS 102336 | *Knautia arvensis* | Netherlands | G.J.M. Verkley | KF253483 | KF253003 | KF252528 | KF252039 | KF251534 |
| | CBS 108981 | *Knautia arvensis* | Germany | G.J.M. Verkley | KF253484 | KF253004 | KF252529 | KF252040 | KF251535 |
| | CBS 109093 | *Knautia dipsacifolia* | Austria | G.J.M. Verkley | KF253487 | KF253007 | KF252532 | KF252043 | KF251538 |
| *Sep. senecionis* | CBS 102366 | *Senecio fluviatilis* | Netherlands | G.J.M. Verkley | KF253492 | KF253012 | KF252538 | KF252049 | KF251544 |
| | CBS 102381 | *Senecio fluviatilis* | Netherlands | G.J.M. Verkley | KF253493 | KF253013 | KF252539 | KF252050 | KF251545 |
| *Sep. siegesbeckiae* | CBS 128659 | *Siegesbeckia glabrescens* | South Korea | H.D. Shin | KF253494 | KF253014 | KF252540 | KF252051 | KF251546 |
| | CBS 128661 | *Siegesbeckia pubescens* | South Korea | H.D. Shin | KF253495 | KF253015 | KF252541 | KF252052 | KF251547 |
| *Sep. sii* | CBS 102370 | *Berula erecta* | Netherlands | G.J.M. Verkley | KF253497 | KF253017 | KF252543 | KF252054 | KF251549 |
| *Sep. sisyrinchii* | CBS 112096 | *Sysirinchium* sp. | New Zealand | C.F. Hill | KF253499 | KF253019 | KF252545 | KF252056 | KF251551 |
| *Septoria* sp. | CBS 128650 | *Taraxacum officinale* | South Korea | H.D. Shin | KF253504 | KF253024 | KF252550 | KF252061 | KF251556 |
| | CBS 128658 | *Chrysosplenium japonicum* | South Korea | H.D. Shin | KF253505 | KF253025 | KF252551 | KF252062 | KF251557 |
| | CBS 128757 | *Sonchus asper* | South Korea | H.D. Shin | KF253500 | KF253020 | KF252546 | KF252057 | KF251552 |
| | CBS 135472; CPC 19304 | *Vigna unguiculata* ssp. *sesquipedalis* | Austria | P.W. Crous | KF253506 | KF253026 | KF252552 | KF252063 | KF251558 |
| | CBS 135474; CPC 19485 | *Conyza canadensis* | Brazil | R.W. Barreto | KF253507 | KF253027 | KF252553 | KF252064 | KF251559 |
| | CBS 135478; CPC 19716 | *Eucalyptus* sp. | India | W. Gams | KF253188 | KF252722 | KF252240 | KF251738 | KF251235 |
| | CBS 135479; CPC 19793 | *Syzygium cordatum* | South Africa | P.W. Crous | – | KF253029 | KF252555 | KF252066 | KF251561 |
| | CPC 19976 | *Feijoa sellowiana* | Italy | G. Polizzi | KF253509 | KF253030 | – | KF252067 | KF251562 |

**Table 1.** (Continued).

| Species | Isolate no.[1] | Host | Location | Collector | GenBank accession no.[2] | | | | |
|---|---|---|---|---|---|---|---|---|---|
| | | | | | EF-1α | Btub | RPB2 | LSU | ITS |
| | CPC 21105 | *Cluvia* sp. | South Africa | P.W. Crous | – | – | KF302396 | KF302408 | KF302402 |
| | CPC 23104 | – | Italy | E. van Agtmaal | KF253511 | KF253032 | KF252557 | KF252069 | KF251564 |
| *Sep. stachydis* | CBS 347.58 | *Aster canus* | Germany | R. Schneider | KF253295 | KF252820 | KF252349 | KF251852 | KF251348 |
| | CBS 102326 | *Stachys sylvatica* | Netherlands | G.J.M. Verkley | KF253514 | KF253035 | KF252560 | KF252072 | KF251567 |
| | CBS 109115 | *Campanula glomerata* | Austria | G.J.M. Verkley | KF253502 | KF253022 | KF252548 | KF252059 | KF251554 |
| | CBS 109127 | *Stachys sylvatica* | Austria | G.J.M. Verkley | KF253517 | KF253038 | KF252563 | KF252075 | KF251570 |
| *Sep. stellariae* | CBS 102376 | *Stellaria media* | Netherlands | G.J.M. Verkley | KF253521 | KF253042 | KF252567 | KF252079 | KF251574 |
| *"Sep." steviae* | CBS 120132 | *Stevia rebaudiana* | Japan | J. Ishiba | KF253191 | – | KF252243 | KF251741 | KF251238 |
| *"Sep." tanaceti* | CBS 358.58 | *Tanacetum vulgare* | Germany | R. Schneider | KF253192 | – | KF252244 | KF251742 | KF251239 |
| *Sep. taraxaci* | CBS 567.75 | *Taraxacum* sp. | Armenia | H.A. van der Aa | KF253524 | KF253045 | KF252570 | KF252082 | KF251577 |
| *Sep. tinctoriae* | CBS 129154 | *Serratula coronata* | South Korea | H.D. Shin | KF253525 | KF253046 | KF252571 | KF252083 | KF251578 |
| *Sep. tormentillae* | CBS 128643 | *Potentilla fragarioides* | South Korea | H.D. Shin | KF253526 | KF253047 | KF252572 | KF252084 | KF251579 |
| | CBS 128647 | *Potentilla fragarioides* | South Korea | H.D. Shin | KF253527 | KF253048 | KF252573 | KF252085 | KF251580 |
| *Sep. urticae* | CBS 102316 | *Glechoma hederacea* | Netherlands | G.J.M. Verkley | KF253528 | KF253049 | KF252574 | KF252086 | KF251581 |
| | CBS 102375 | *Urtica dioica* | Netherlands | G.J.M. Verkley | KF253530 | KF253051 | KF252576 | KF252088 | KF251583 |
| *Sep. verbascicola* | CBS 102401 | *Verbascum nigrum* | Netherlands | G.J.M. Verkley | KF253531 | KF253052 | KF252577 | KF252089 | KF251584 |
| *Sep. verbenae* | CBS 113438 | *Verbena officinalis* | New Zealand | G.J.M. Verkley | KF253532 | KF253053 | KF252578 | KF252090 | KF251585 |
| *Sep. villarsiae* | CBS 514.78 | *Nymphoides peltata* | Netherlands | H.A. van der Aa | KF253534 | KF253055 | KF252580 | KF252092 | KF251587 |
| *Sep. violae-palustris* | CBS 128644 | *Viola selkirkii* | South Korea | H.D. Shin | KF253537 | KF253058 | KF252583 | KF252095 | KF251590 |
| | CBS 128660 | *Viola yedoensis* | South Korea | H.D. Shin | KF253538 | KF253059 | KF252584 | KF252096 | KF251591 |
| septoria-like sp. | CBS 134910; CPC 19500 | *Tibouchina herbacea* | Brazil | D.F. Parreira | KF302391 | KF302386 | KF302397 | KF302409 | KF302403 |
| | CBS 135471; CPC 19294 | *Corymbia gummifera* | Australia | P.W. Crous | KF253193 | KF252725 | KF252245 | KF251743 | KF251240 |
| | CBS 135473; CPC 19311 | *Phragmites* sp. | USA | – | KF253194 | KF252726 | KF252246 | KF251744 | KF251241 |
| | CBS 135481; CPC 22154; S672 | *Polygonatum* sp. | Netherlands | U. Damm | – | – | KF252247 | KF251745 | KF251242 |
| *Septorioides pini-thunbergii* | CBS 473.91 | *Pinus thunbergii* | Japan | S. Kaneko & Y. Zinno | – | KF252727 | KF252248 | KF251746 | KF251243 |
| *Setophoma chromolaenae* | CBS 135105; CPC 18553 | *Chromolaena odorata* | Brazil | R.W. Barreto | KF253195 | KF252728 | KF252249 | KF251747 | KF251244 |
| *Setop. sacchari* | CBS 333.39 | *Saccharum officinarum* | Brazil | A.A. Bitancourt | – | – | KF252250 | KF251748 | KF251245 |
| *Setop. terrestris* | CBS 335.29 | *Allium sativum* | USA | H.N. Hansen | KF253196 | KF252729 | KF252251 | KF251749 | KF251246 |
| | CBS 335.87 | *Allium cepa* | Senegal | – | KF253197 | KF252730 | KF252252 | KF251750 | KF251247 |
| | CBS 377.52 | *Allium cepa* | – | R.H. Larson | KF253198 | KF252731 | KF252253 | KF251751 | KF251248 |
| | CBS 135470; CPC 18417 | *Zea mays* | South Africa | S. Lamprecht | KF253189 | KF252723 | KF252241 | KF251739 | KF251236 |

**Table 1.** (Continued).

| Species | Isolate no.[1] | Host | Location | Collector | GenBank accession no.[2] | | | | |
|---|---|---|---|---|---|---|---|---|---|
| | | | | | EF-1α | Btub | RPB2 | LSU | ITS |
| *Setoseptoria phragmitis* | CBS 114802 | *Phragmites australis* | Hong Kong | K.D. Hyde | KF253199 | KF252732 | KF252254 | KF251752 | KF251249 |
| | CBS 114966 | *Phragmites australis* | Hong Kong | K.D. Hyde | KF253200 | KF252733 | KF252255 | KF251753 | KF251250 |
| *Sphaerulina abeliceae* | CBS 128591 | *Zelkova serrata* | South Korea | H.D. Shin | KF253539 | – | KF252585 | KF252097 | KF251592 |
| *Sph. aceris* | CBS 687.94 | *Acer pseudoplatanus* | Netherlands | G.J.M. Verkley | KF253542 | KF253061 | KF252588 | KF252100 | KF251595 |
| *Sph. amelanchier* | CBS 102063 | *Actinidia deliciosa* | New Zealand | C.F. Hill | KF253581 | KF253096 | KF252627 | KF252140 | KF251635 |
| | CBS 135110; MP8 | *Amelanchier* sp. | Netherlands | S.I.R. Videira | KF253543 | KF253062 | KF252589 | KF252101 | KF251596 |
| | CPC 23105; MP22 | *Quercus* sp. | Netherlands | S.I.R. Videira | KF253544 | KF253063 | KF252590 | KF252102 | KF251597 |
| | CPC 23106; MP7 | *Castanea* sp. | Netherlands | S.I.R. Videira | KF253545 | KF253064 | KF252591 | KF252103 | KF251598 |
| | CPC 23107; MP9 | *Betula* sp. | Netherlands | S.I.R. Videira | KF253583 | KF253098 | KF252626 | KF252139 | KF251634 |
| *Sph. azaleae* | CBS 352.49 | *Rhododendron* sp. | Belgium | J. van Holder | KF253547 | KF253066 | KF252593 | KF252105 | KF251600 |
| | CBS 128605 | *Rhododendron* sp. | South Korea | H.D. Shin | KF253546 | KF253065 | KF252592 | KF252104 | KF251599 |
| *Sph. berberidis* | CBS 324.52 | *Berberis vulgaris* | Switzerland | E. Müller | KF253548 | KF253067 | KF252594 | KF252106 | KF251601 |
| *Sph. betulae* | CBS 116724 | *Betula pubescens* | Netherlands | S. Green | KF253549 | KF253068 | KF252595 | KF252107 | KF251602 |
| | CBS 128600 | *Betula platyphylla* var. *japonica* | South Korea | H.D. Shin | KF253552 | KF253071 | KF252598 | KF252110 | KF251605 |
| *Sph. cercidis* | CBS 501.50 | *Cercis siliquastrum* | Netherlands | G. van den Ende | KF253556 | KF253075 | KF252601 | KF252113 | KF251608 |
| | CBS 118910 | *Eucalyptus* sp. | France | P.W. Crous | KF253553 | KF253072 | KF252602 | KF252114 | KF251609 |
| | CBS 128634 | *Cercis siliquastrum* | Argentina | H.D. Shin | KF253554 | KF253073 | KF252599 | KF252111 | KF251606 |
| | CBS 129151 | *Cercis siliquastrum* | Argentina | H.D. Shin | KF253555 | KF253074 | KF252600 | KF252112 | KF251607 |
| *Sph. cornicola* | CBS 102324 | *Cornus* sp. | Netherlands | A. van Iperen | KF253557 | KF253076 | KF252603 | KF252115 | KF251610 |
| | CBS 102332 | *Cornus* sp. | Netherlands | A. van Iperen | KF253558 | KF253077 | KF252604 | KF252116 | KF251611 |
| *Sph. frondicola* | CBS 391.59 | *Populus pyramidalis* | Germany | R. Schneider | KF253572 | – | KF252617 | KF252130 | KF251625 |
| *Sph. gei* | CBS 102318 | *Geum urbanum* | Netherlands | G.J.M. Verkley | KF253560 | KF253079 | KF252605 | KF252118 | KF251613 |
| | CBS 128632 | *Geum japonicum* | South Korea | H.D. Shin | KF253562 | KF253081 | KF252607 | KF252120 | KF251615 |
| *Sph. hyperici* | CBS 102313 | *Hypericum* sp. | Netherlands | G.J.M. Verkley | KF253563 | KF253082 | KF252608 | KF252121 | KF251616 |
| *Sph. menispermi* | CBS 128666 | *Menispermum dauricum* | South Korea | H.D. Shin | KF253564 | KF253083 | KF252609 | KF252122 | KF251617 |
| | CBS 128761 | *Menispermum dauricum* | South Korea | H.D. Shin | KF253565 | KF253084 | KF252610 | KF252123 | KF251618 |
| *Sph. musiva* | CBS 130570 | *Populus deltoides* | Canada | J. LeBoldus | JX901725 | JX902304 | JX902058 | JX901935 | JX901812 |
| *Sph. myriadea* | CBS 124646 | *Quercus dentata* | Japan | K. Tanaka | KF253201 | KF252734 | KF252256 | KF251754 | KF251251 |
| *Sph. oxyacanthae* | CBS 135098; S654 | *Crataegus* sp. | Netherlands | W. Quaedvlieg | KF253202 | KF252735 | KF252257 | KF251755 | KF251252 |
| *Sph. patriniae* | CBS 128653 | *Patrinia scabiosaefolia* | South Korea | H.D. Shin | KF253570 | KF253087 | KF252615 | KF252128 | KF251623 |
| *Sph. populicola* | CBS 100042 | *Populus trichocarpa* | USA | G. Newcombe | KF253573 | – | KF252618 | KF252131 | KF251626 |
| *Sph. pseudovirgaureae* | CBS 135109; S669 | *Solidago gigantea* | Netherlands | S.I.R. Videira | KF253203 | KF252736 | KF252258 | KF251756 | KF251253 |

**Table 1.** (Continued).

| Species | Isolate no.[1] | Host | Location | Collector | GenBank accession no.[2] | | | | |
|---|---|---|---|---|---|---|---|---|---|
| | | | | | EF-1α | Btub | RPB2 | LSU | ITS |
| *Sph. quercicola* | CBS 663.94 | *Quercus robur* | Netherlands | H.A. van der Aa | KF253577 | KF253092 | KF252622 | KF252135 | KF251630 |
| | CBS 109009 | *Quercus rubra* | Netherlands | G.J.M. Verkley | KF253574 | KF253089 | KF252619 | KF252132 | KF251627 |
| | CBS 115016 | *Quercus robur* | Netherlands | G.J.M. Verkley | KF253575 | KF253090 | KF252620 | KF252133 | KF251628 |
| | CBS 115136 | *Quercus robur* | Netherlands | G.J.M. Verkley | KF253576 | KF253091 | KF252621 | KF252134 | KF251629 |
| | CBS 115137 | *Quercus robur* | Netherlands | G.J.M. Verkley | KF302390 | KF302385 | KF302394 | KF302406 | KF302400 |
| *Sph. socia* | CBS 355.58 | *Rosa* sp. | – | – | KF253579 | KF253094 | KF252624 | KF252137 | KF251632 |
| | CBS 357.58 | *Chrysanthemum leucanthemum* | Germany | R. Schneider | KF253580 | KF253095 | KF252625 | KF252138 | KF251633 |
| *Sph. tirolensis* | CBS 109017 | *Rubus idaeus* | Austria | G.J.M. Verkley | KF253584 | KF253099 | KF252629 | KF252142 | KF251637 |
| | CBS 109018 | *Rubus idaeus* | Austria | G.J.M. Verkley | KF253585 | KF253100 | KF252630 | KF252143 | KF251638 |
| *Sph. viciae* | CBS 131898 | *Vicia amurense* | South Korea | H.D. Shin | KF253586 | KF253101 | KF252631 | KF252144 | KF251639 |
| *Sph. westendorpii* | CBS 117478 | *Rubus fruticosus* | Netherlands | G.J.M. Verkley | KF253589 | KF253104 | KF252634 | KF252147 | KF251642 |
| *Stagonospora* cf. *paludosa* | CBS 130005 | *Carex* sp. | Russia | – | KF253204 | KF252737 | KF252259 | KF251757 | KF251254 |
| *Sta. duoseptata* | CBS 135093; S618 | *Carex acutiformis* | Netherlands | W. Quaedvlieg | KF253205 | KF252738 | KF252260 | KF251758 | KF251255 |
| *"Sta." foliicola* | CBS 110111 | *Phalaris arundinacea* | USA | N. O'Neil | KF253206 | KF252739 | KF252261 | KF251759 | KF251256 |
| *Sta. paludosa* | CBS 135088; S601 | *Carex acutiformis* | Netherlands | W. Quaedvlieg | KF253207 | KF252740 | KF252262 | KF251760 | KF251257 |
| *Sta. perfecta* | CBS 135099; S656 | *Carex acutiformis* | Netherlands | W. Quaedvlieg | KF253208 | – | KF252263 | KF251761 | KF251258 |
| *Sta. pseudocaricis* | CBS 135132; S610 | *Carex acutiformis* | France | A. Gardiennet | KF253210 | KF252742 | KF252265 | KF251763 | KF251260 |
| | CBS 135414; S609 | *Carex acutiformis* | France | A. Gardiennet | – | KF302383 | KF302395 | KF302407 | KF302401 |
| *Sta. pseudovitensis* | CBS 135094; S620 | *Carex acutiformis* | Netherlands | W. Quaedvlieg | KF253211 | KF252743 | KF252266 | KF251764 | KF251261 |
| | S602 | *Carex acutiformis* | Netherlands | W. Quaedvlieg | KF253212 | KF252744 | KF252267 | KF251765 | KF251262 |
| *Stagonospora* sp. | CBS 135096; 652 | *Carex acutiformis* | France | A. Gardiennet | – | – | KF252268 | KF251766 | KF251263 |
| *Sta. uniseptata* | CBS 135090; S611 | *Carex acutiformis* | Netherlands | W. Quaedvlieg | – | KF252745 | KF252269 | KF251767 | KF251264 |
| | CPC 22150; S608 | *Carex acutiformis* | Netherlands | W. Quaedvlieg | KF253214 | KF252747 | KF252271 | KF251769 | KF251266 |
| | CPC 22151; S607 | *Carex acutiformis* | Netherlands | W. Quaedvlieg | KF253213 | KF252746 | KF252270 | KF251768 | KF251265 |
| stagonospora-like sp. | CBS 516.74 | *Triticum aestivum* | Brazil | Y.R. Mehta | KF253215 | KF252748 | KF252272 | KF251770 | KF251267 |
| | CBS 135482; CPC 22155; S526 | *Poa* sp. | Netherlands | W. Quaedvlieg | KF253216 | KF252749 | KF252273 | KF251771 | KF251268 |
| | CBS 135483; CPC 22157; S617 | *Carex acutiformis* | Netherlands | W. Quaedvlieg | KF253217 | KF252750 | KF252274 | KF251772 | KF251269 |
| | S619 | *Carex acutiformis* | Netherlands | W. Quaedvlieg | KF253218 | KF252751 | KF252275 | KF251773 | KF251270 |
| *Stromatoseptoria castaneicola* | CBS 102322 | *Castanea sativa* | Netherlands | G.J.M. Verkley | KF253219 | KF252752 | KF252276 | KF251774 | KF251271 |
| | CBS 102377 | *Castanea sativa* | Netherlands | G.J.M. Verkley | KF253220 | KF252753 | KF252277 | KF251775 | KF251272 |
| *Teratosphaeria juvenalis* | CBS 111149 | *Eucalyptus cladocalyx* | South Africa | P.W. Crous | KF253221 | KF252754 | KF252278 | KF251776 | KF251273 |

**Table 1.** (Continued).

| Species | Isolate no.[1] | Host | Location | Collector | GenBank accession no.[2] | | | | |
|---|---|---|---|---|---|---|---|---|---|
| | | | | | EF-1α | Btub | RPB2 | LSU | ITS |
| *Ter. molleriana* | CBS 111164 | *Eucalyptus globulus* | Portugal | M.J. Wingfield | KF253222 | KF252755 | KF252279 | KF251777 | KF251274 |
| *Ter. parva* | CBS 119901 | *Eucalyptus globulus* | Ethiopia | A. Gezahgne | KF253223 | KF252756 | KF252280 | KF251778 | KF251275 |
| *Ter. pseudoeucalypti* | CBS 124577 | *Eucalyptus grandis* × *E. camaldulensis* | Australia | V. Andjic | KF253224 | KF252757 | KF252281 | KF251779 | KF251276 |
| *Ter. suberosa* | CPC 13106 | *Eucalyptus dunnii* | Australia | A.J. Carnegie | KF253183 | – | KF252232 | KF251730 | KF251227 |
| *Ter. toledana* | CBS 113313 | *Eucalyptus* sp. | Spain | P.W. Crous & G. Bills | KF253225 | KF252758 | KF252282 | KF251780 | KF251277 |
| *Vrystaatia aloeicola* | CBS 135107; CPC 20617 | *Aloe maculata* | South Africa | P.W. Crous & W.J. Swart | – | KF252759 | KF252283 | KF251781 | KF251278 |
| *Xenobotryosphaeria calamagrostidis* | CBS 303.71 | *Calamagrostis* sp. | Italy | G.A. Hedjaroude | KF253226 | KF252760 | KF252284 | KF251782 | KF251279 |
| *Xenoseptoria neosaccardoi* | CBS 120.43 | *Cyclamen persicum* | Netherlands | Roodenburg | KF253227 | KF252761 | KF252285 | KF251783 | KF251280 |
| | CBS 128665 | *Lysimachia vulgaris* var. *davurica* | South Korea | H.D. Shin | KF253228 | KF252762 | KF252286 | KF251784 | KF251281 |
| *Zasmidium anthuriicola* | CBS 118742 | *Anthurium* sp. | Thailand | C.F. Hill | KF253229 | KF252763 | KF252287 | KF251785 | FJ839626 |
| *Zas. citri* | CPC 13467 | *Eucalyptus* sp. | Thailand | W. Himaman | KF253182 | KF252714 | KF252231 | KF251729 | KF251226 |
| *Zas. lonicericola* | CBS 125008 | *Lonicera japonica* | South Korea | H.D. Shin | KF253231 | KF252765 | KF252289 | KF251787 | KF251283 |
| *Zas. nocoxi* | CBS 125009 | Twig debris | USA | P.W. Crous | KF253232 | KF252766 | KF252290 | KF251788 | KF251284 |
| *Zas. scaevolicola* | CBS 127009 | *Scaevola taccada* | Australia | R.G. Shivas & P.W Crous | KF253233 | KF252767 | KF252291 | KF251789 | KF251285 |
| *Zymoseptoria brevis* | CBS 128853 | *Phalaris minor* | Iran | – | JQ739777 | JF700968 | JF700799 | JQ739833 | JF700867 |
| | CPC 18109 | *Phalaris paradoxa* | Iran | – | JQ739779 | JF700970 | JF700801 | JQ739835 | JF700869 |
| | CPC 18112 | *Phalaris paradoxa* | Iran | – | JQ739782 | JF700973 | JF700804 | JQ739838 | JF700872 |
| *Zym. halophila* | CBS 128854; CPC 18105 | *Hordeum glaucum* | Iran | M. Razavi | KF253592 | – | JF700808 | KF252150 | KF251645 |
| *Zym. passerinii* | CBS 120384 | *Hordeum vulgare* | USA | S. Ware | JQ739788 | JF700878 | JF700979 | JQ739844 | JF700810 |
| | CBS 120385 | *Hordeum vulgare* | USA | S. Ware | JQ739789 | JF700980 | JF700811 | JQ739845 | JF700879 |
| *Zym. pseudotritici* | CBS 130976 | *Dactylis glomerata* | Iran | M. Javan-Nikkhah | JQ739772 | JN982484 | JN982482 | JQ739828 | JN982480 |
| *Zym. tritici* | CPC 18117 | *Avena* sp. | Iran | – | JQ739801 | JF700986 | JF700817 | JQ739857 | JF700885 |

[1]CBS: CBS-KNAW Fungal Biodiversity Centre, Utrecht, The Netherlands; CPC: Culture collection of Pedro Crous, housed at CBS; IMI: International Mycological Institute, CABI-Bioscience, Egham, Bakeham Lane, U.K.; MP: Working collection of Sandra Videira; S: Working collection of William Quaedvlieg.

[2]Btub: β-tubulin; EF-1α: Translation elongation factor 1-alpha; ITS: internal transcribed spacers and intervening 5.8S nrDNA; LSU: 28S large subunit of the nrRNA gene; RPB2: RNA polymerase II second largest subunit.

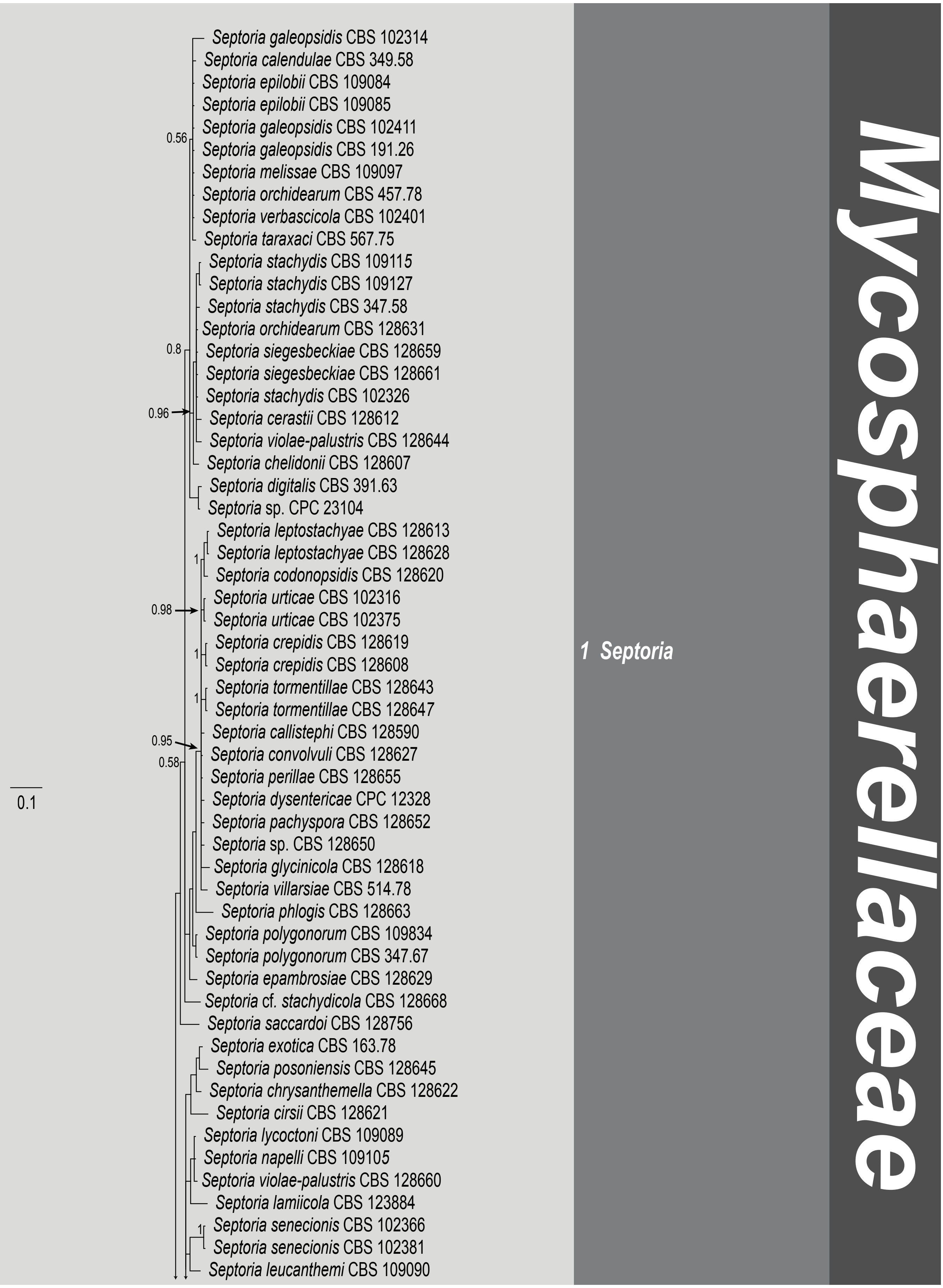


**Fig. 1.** A Bayesian 50 % majority rule RPB2/LSU consensus tree containing all *Septoria* and septoria-like taxa available at the CBS, which cluster in or near the *Mycosphaerellaceae*. Bayesian posterior probabilities support values for the respective nodes are displayed in the tree. A stop rule (set to 0.01) for the critical value for the topological convergence diagnostic was used for the Bayesian analysis. The tree was rooted to *Phaeosphaeria nodorum* (CBS 259.49). The scalebar indicates 0.1 expected changes per site.

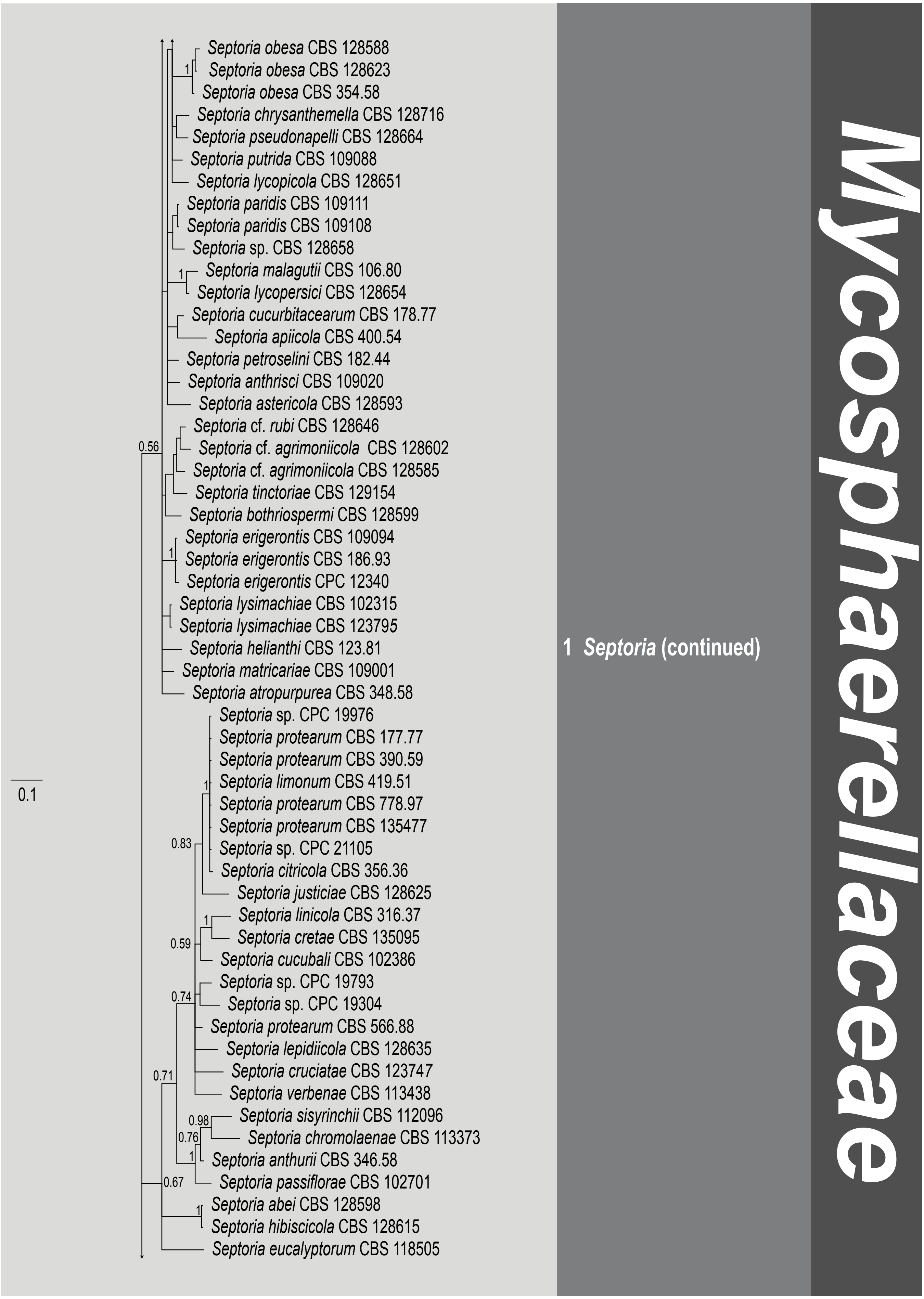


**Fig. 1.** (Continued).

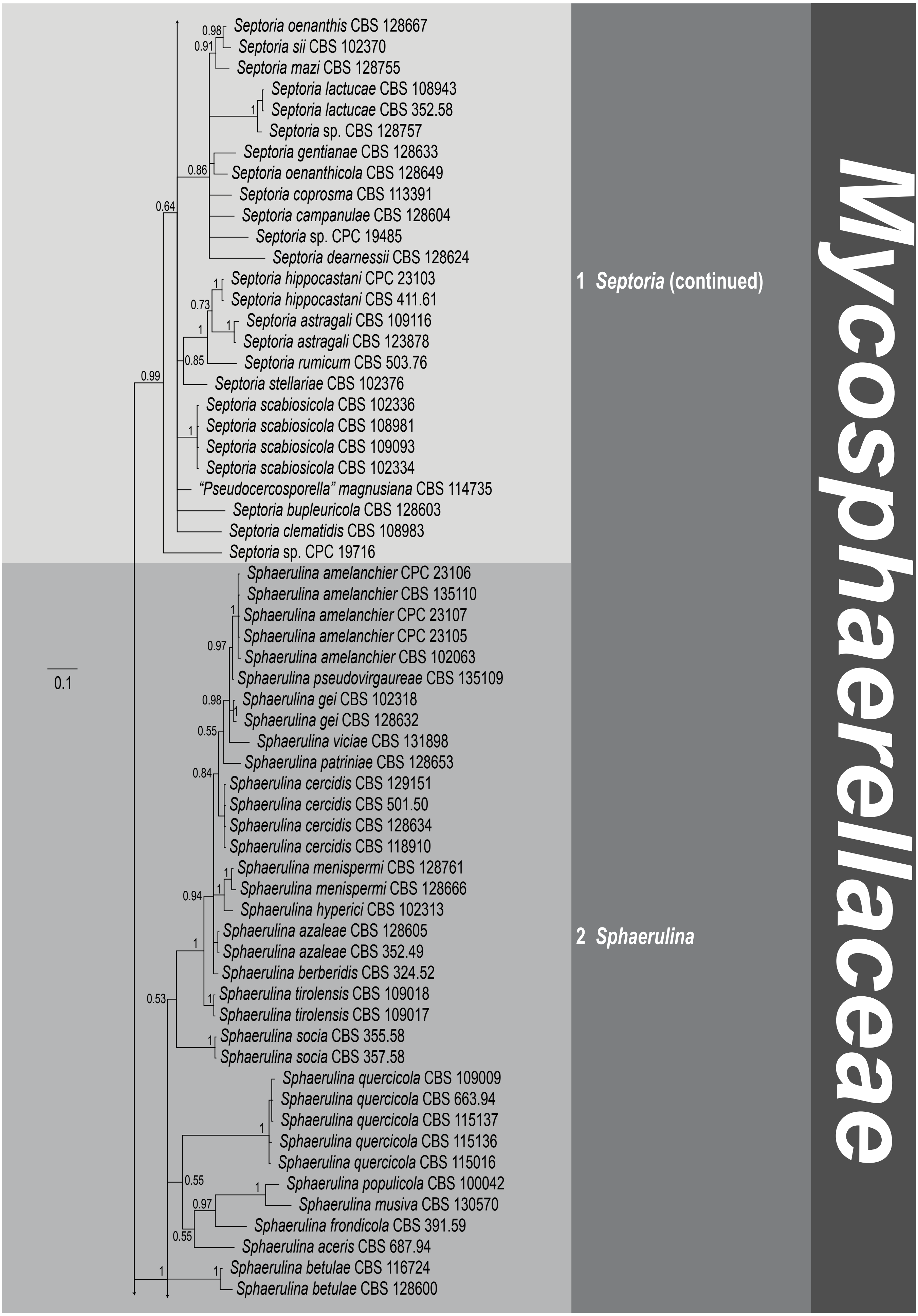


**Fig. 1.** (Continued).

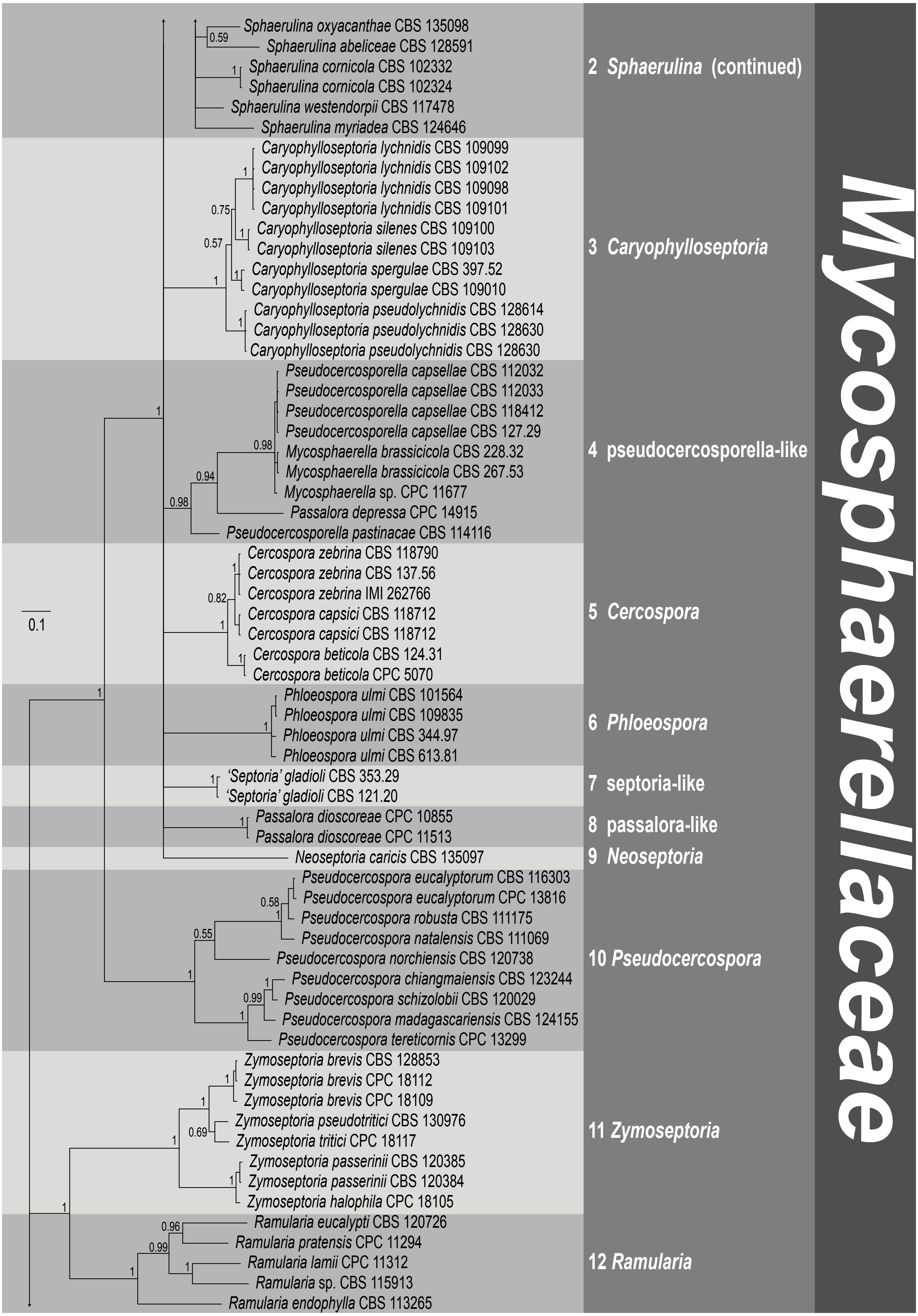


**Fig. 1.** (Continued).

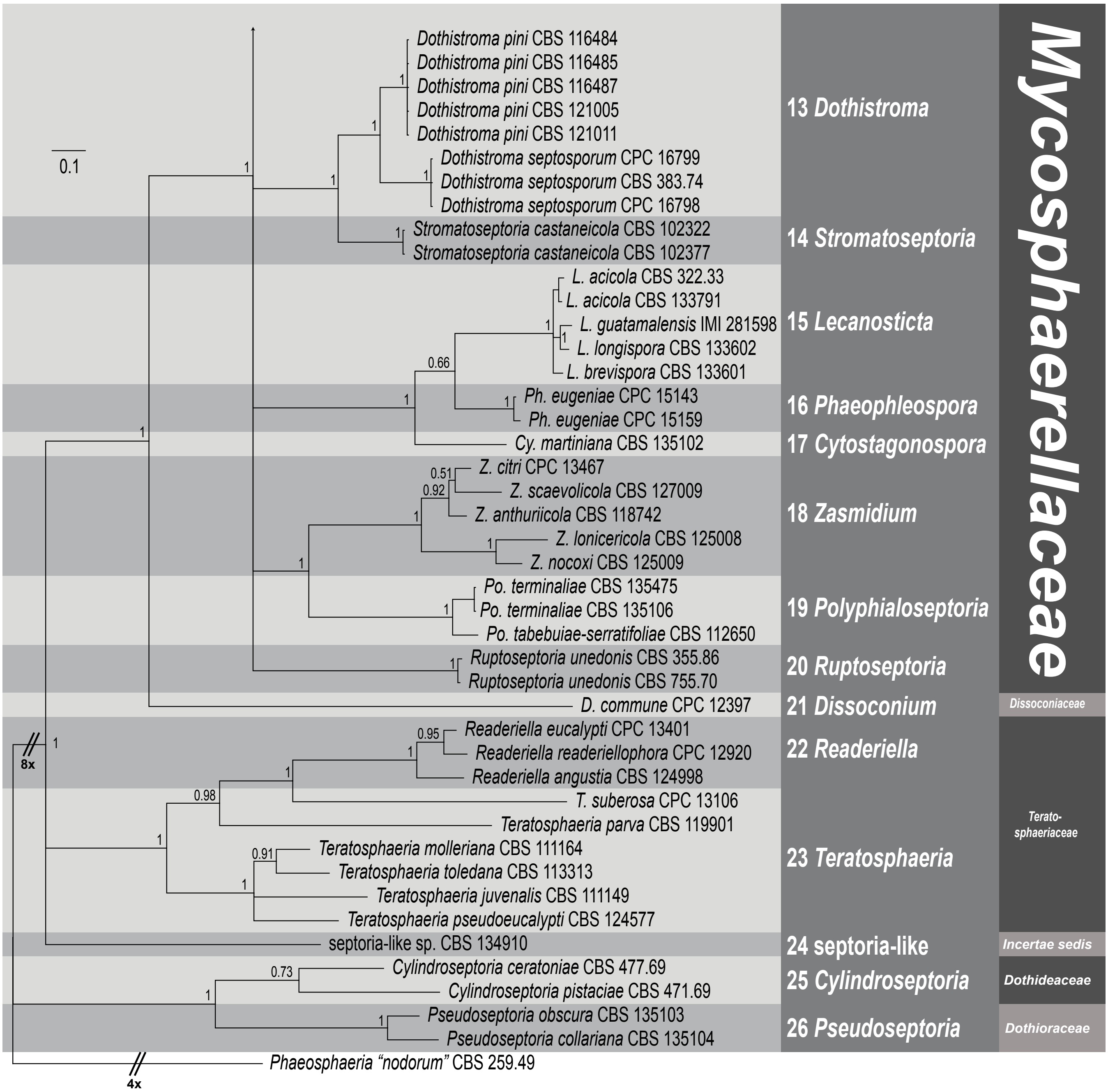


**Fig. 1.** (Continued).

**Table 2.** Primer combinations used during this study for generic amplification and sequencing.

| Locus | Primer | Primer sequence 5' to 3' | Annealing temperature (°C) | Orientation | Reference |
|---|---|---|---|---|---|
| Translation elongation factor-1α | EF1-728F | CATCGAGAAGTTCGAGAAGG | 52 | Forward | Carbone & Kohn (1999) |
| | EF-2 | GGARGTACCAGTSATCATGTT | 52 | Reverse | O'Donnell *et al.* (1998) |
| β-tubulin | T1 | AACATGCGTGAGATTGTAAGT | 52 | Forward | O'Donnell & Cigelnik (1997) |
| | β-Sandy-R | GCRCGNGGVACRTACTTGTT | 52 | Reverse | Stukenbrock *et al.* (2012) |
| RNA polymerase II second largest subunit | fRPB2-5F | GAYGAYMGWGATCAYTTYGG | 49 | Forward | Liu *et al.* (1999) |
| | fRPB2-414R | ACMANNCCCCARTGNGWRTTRTG | 49 | Reverse | Quaedvlieg *et al.* (2011) |
| LSU | LSU1Fd | GRATCAGGTAGGRATACCCG | 52 | Forward | Crous *et al.* (2009a) |
| | LR5 | TCCTGAGGGAAACTTCG | 52 | Reverse | Vilgalys & Hester (1990) |
| ITS | ITS5 | GGAAGTAAAAGTCGTAACAAGG | 52 | Forward | White *et al.* (1990) |
| | ITS4 | TCCTCCGCTTATTGATATGC | 52 | Reverse | White *et al.* (1990) |

**Table 3.** Amplification success, phylogenetic data and the substitution models used in the phylogenetic analysis, per locus.

| Locus | RPB2 | LSU |
|---|---|---|
| Amplification succes (%) | 99.20 % | 100 % |
| Number of characters | 327 | 792 |
| Unique site patterns | 197 | 216 |
| Substitution model used | GTR-I-gamma | GTR-I-gamma |
| Number of generations (1000×) | 2575 | |
| Total number of trees (n) | 5152 | |
| Sampled trees (n) | 3864 | |

which 26 contained species belonging to the *Septoria* (-like) complex. These 47 resolved clades belong to a multitude of different families within the *Dothidiomycetes* ranging from the *Mycosphaerellaceae* in the *Capnodiales* to the *Lentitheciaceae* in the *Pleosporales*. It is still unclear within the *Dothidiomycetes* where the phylogenetic family borders are located, or even how many phylogenetically substainable families there actually are. The family annotation in the phylogenetic trees (Figs 1, 2) is therefore based on the closest LSU neighbour that was available in GenBank, with clades treated as *incertae sedis* if no closer relationship than 97 % could be found.

## *Septoria* and septoria-like genera

In addition to *Septoria s. str.*, numerous septoria-like genera (pycnidial/acervular/stromatic conidioma with filiform conidia) have since been described. Although the majority of these have no ex-type culture available for DNA analysis, many have type material deposited in herbaria, which were available for morphological examination. A summary of these genera is provided below.

## Pycnidial forms

***Cytostagonospora*** Bubák, Ann. Mycol. 14: 150. 1916. Fig. 3.

*Mycelium* immersed, dark brown, branched, septate. *Conidiomata* pycnidial, amphigenous, separate, globose, dark brown to black, immersed, unilocular, thick-walled, clypeate; walls of dark brown, thick-walled *textura angularis* to *textura globulosa*, becoming hyaline towards the conidiogenous region, extending in the upper part to become a circular clypeus of similar thickness to the wall. *Ostiole* central, circular, papillate to shortly rostrate, depressed, situated immersed within the clypeus. *Conidiophores* reduced to conidiogenous cells. *Conidiogenous cells* holoblastic, determinate, discrete, lageniform, hyaline, smooth, formed from the inner cells of the pycnidial wall. *Conidia* hyaline, 0–2-euseptate, not constricted at septa, base truncate, apex obtuse, thin-walled, eguttulate, smooth, filiform, often curved (Sutton 1980).

*Type species*: *C. photiniicola* Bubák, Ann. Mycol. 14(3–4): 150. 1916.

*Notes*: Von Arx (1983) and Sutton (1980) disagreed about the link of *Cytostagonospora* to *Septoria*. Von Arx treated it as a synonym of *Septoria,* while Sutton retained it as a separate genus.

***Dearnessia*** Bubák, Hedwigia 58: 25. 1916.

*Mycelium* hyaline to brown, branched, septate. *Conidiomata* pycnidial, amphigenous, separate, globose, immersed, brown; wall of thin-walled *textura angularis*. *Ostiole* central, circular, papillate. *Setae* ostiolar, approximately straight, unbranched, tapered towards apex, dark brown, smooth, thin-walled, septate. *Conidiogenous cells* holoblastic, determinate, discrete, doliiform to ampulliform, hyaline, smooth and formed from the inner layer of the pycnidial wall. *Conidia* cylindrical to irregular, hyaline, 1–multi-transversely euseptate, rarely with 1–2 longitudinal eusepta, continuous or constricted, often tapered at the apex, base truncate, thin-walled, smooth, guttulate or not (Sutton 1980).

*Type species*: *D. apocyni* Bubák, Hedwigia 58: 25. 1916.

***Dearnessia apocyni*** Bubák, Hedwigia 58: 25. 1916. Figs 4, 5.

*Leaf spots* amphigenous, irregular, feathery to angular, dark brown, 3–6 mm diam, surrounded by a wide chlorotic zone up to 3 mm diam. *Conidiomata* epiphyllous, pycnidial, erumpent, up to 150 µm diam, with central ostiole; wall of 3–6 layers of brown *textura angularis*. *Conidiogenous cells* doliiform, globose to subcylindrical, hyaline, smooth, thin-walled, mode of proliferation obscure, 5–10 × 4–6 µm. *Conidia* hyaline, smooth, subcylindrical to obclavate, apex obtuse, base truncate to subobtuse, straight to irregular (lateral swellings?), 1–4-septate, 16–33 × 5–8 µm.

*Specimen examined*: **Canada**, Ontario, London, on leaves of *Apocynum androsaemifolium* (*Apocynaceae*), 11 Aug. 1910, J. Dearness, **holotype** F43227.

*Notes*: Because the specimen is in poor condition, no definite conclusion could be reached about its potential relationships. However, *D. apocyni* does appear septoria-like in general morphology.

***Jahniella*** Petr., Ann. Mycol. 18: 123. 1921. [1920]. Figs 6, 7.

*Mycelium* branched, immersed, septate, brown. *Conidiomata* pycnidial, superficial on epidermis, immersed, separate, globose, papillate, dark brown, thick-walled, sclerenchymatic; wall consisting of an outer layer of dark brown, thick-walled *textura angularis*, a middle layer of 8 cells thick, of hyaline to pale brown, thick-walled cells, and an inner layer of thin-walled, hyaline, irregular cells. *Ostiole* single, circular, with a distinct channel and hyaline

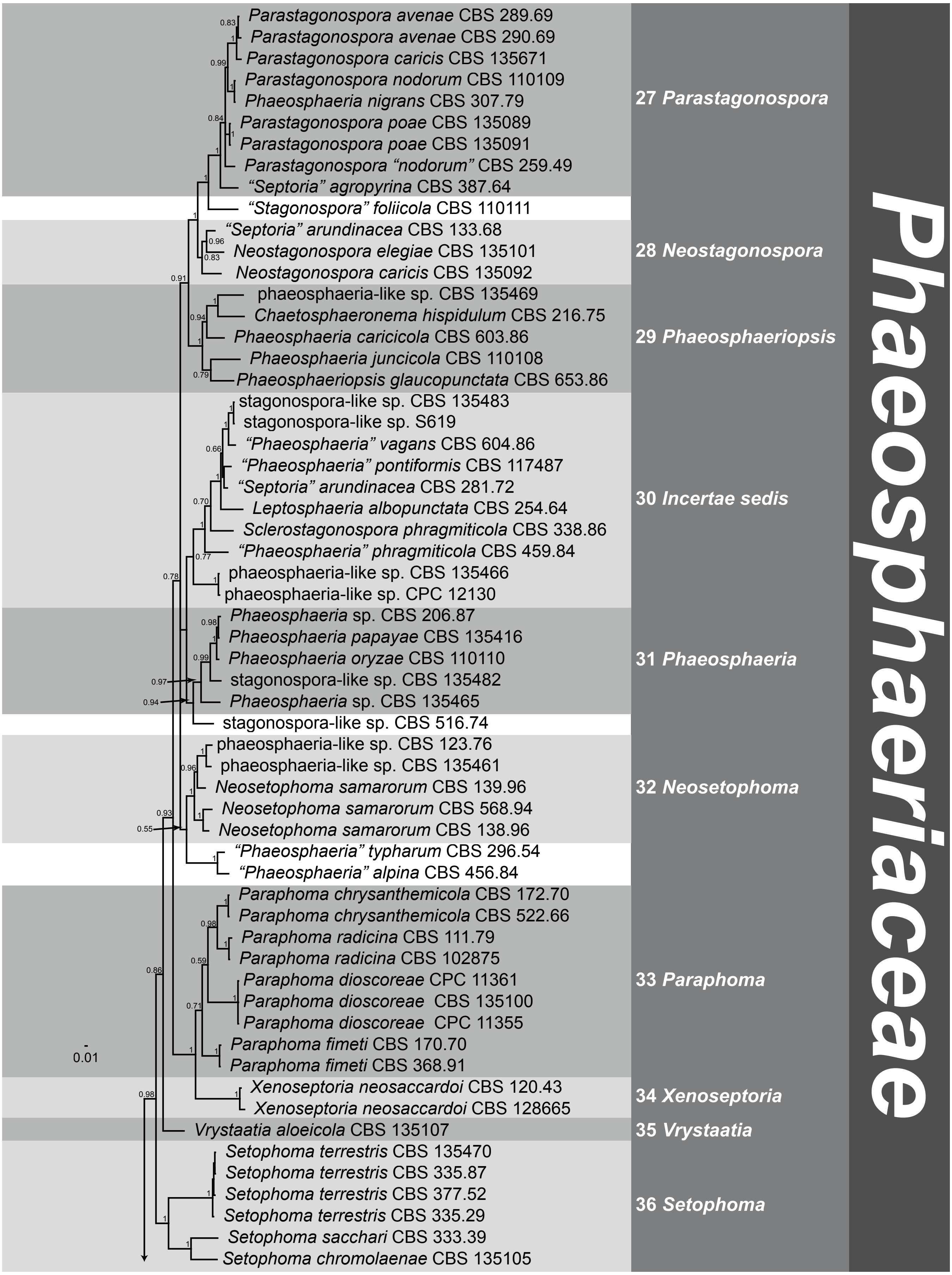


**Fig. 2.** A Bayesian 50 % majority rule RPB2/LSU consensus tree containing all *Septoria* and septoria-like taxa available at the CBS, which cluster in or near the *Phaeosphaeriaceae*. Bayesian posterior probabilities support values for the respective nodes are displayed in the tree. A stop rule (set to 0.01) for the critical value for the topological convergence diagnostic was used for the Bayesian analysis. The tree was rooted to *Dothistroma pini* (CBS 121005). The scalebar indicates 0.01 expected changes per site.

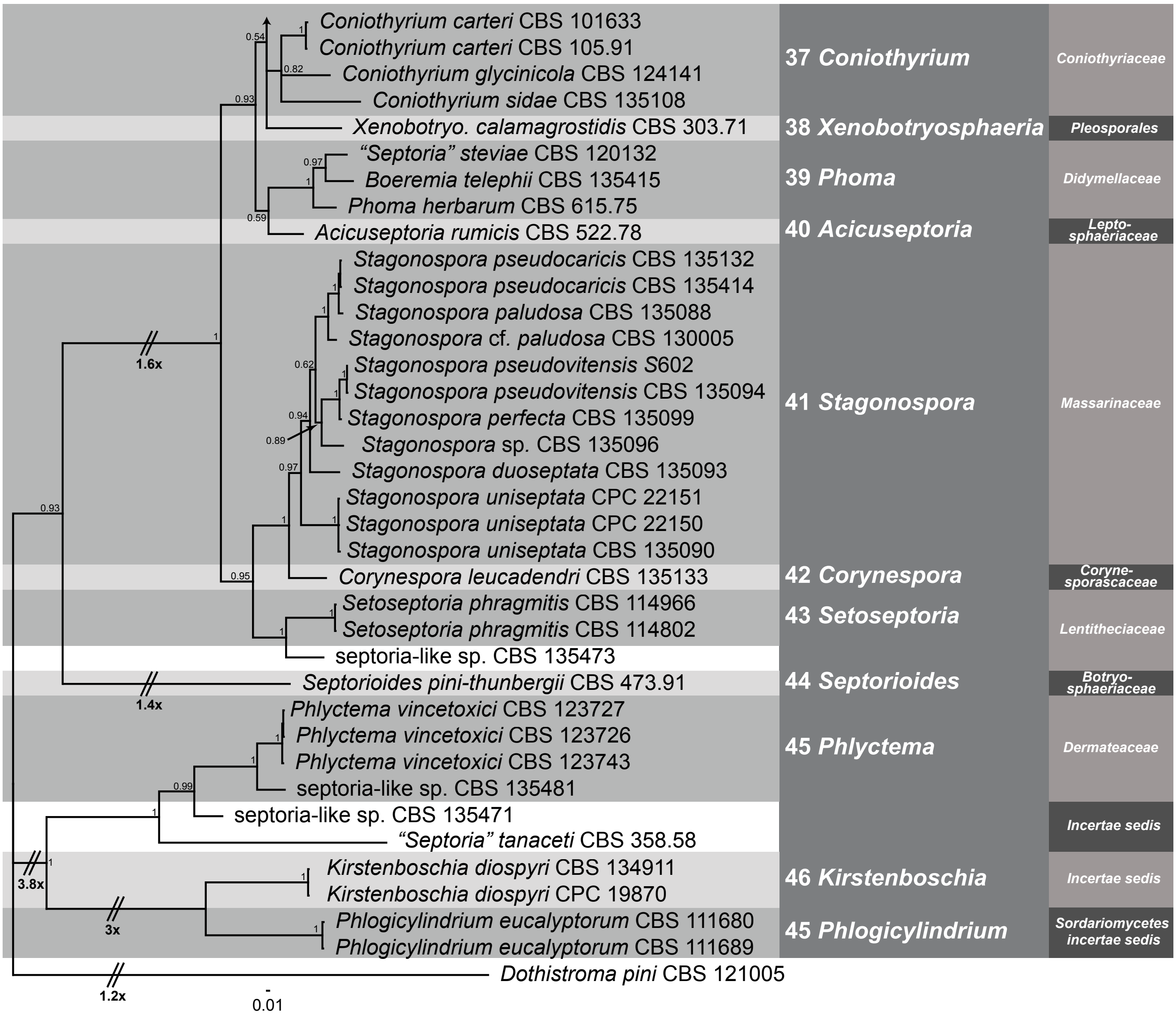


**Fig. 2.** (Continued).

periphysoid cells. *Conidiophores* reduced to conidiogenous cells. *Conidiogenous cells* holoblastic, determinate, discrete, hyaline, ampulliform, lining the wall of the pycnidium. *Conidia* straight or slightly curved, hyaline, thin-walled, smooth, 3–4-euseptate, eguttulate, truncate at the base, slightly tapered to the apex (Sutton 1980).

*Type species*: *J. bohemica* Petr., Ann. Mycol. 18(4–6): 123. 1921. [1920]

*Specimen examined*: **Czech Republic**, Bohemia, on stems of *Scrophularia nodosa* (*Scrophulariaceae*), 18 Mar. 1916, J. Jahn, **holotype** K(M) 180917, slides ex BPI.

*Note*: The specimen correlates closely with the description provided by Sutton (1980), except that the conidiomata are superficial, not immersed in the epidermis.

***Megaloseptoria*** Naumov, Morbi Plantarum 14: 144. 1925. Figs 8, 9.

*Mycelium* immersed, branched, septate, brown. *Conidiomata* pycnidial, separate, globose, slightly papillate, dark brown to black, superficial, sessile, often aggregated in groups, unilocular, thick-walled; wall of several cell layers of brown *textura angularis*, more darkly pigmented on the outside. *Ostiole* single, circular. *Conidiophores* hyaline, branched, septate (mainly at the base), smooth, straight or irregular, formed from the inner cells of the pycnidial wall. *Conidiogenous cells* enteroblastic, determinate, discrete or integrated, doliiform, ampulliform or irregularly cylindrical, hyaline, smooth, collarette evident, channel wide, periclinal thickening present. *Conidia* hyaline to pale brown with several transverse eusepta, continuous, tapered near the obtuse apex and truncate base, thin-walled, smooth, cylindrical, straight or slightly curved, often with 2 guttules in each cell (Sutton 1980).

*Type species*: *M. mirabilis* Naumov, Morbi Plant. Script. Sect. Phytopath. Hort. Bot. Prince. USSR 14: 144. 1925.

***Megaloseptoria mirabilis*** Naumov, Morbi Plantarum 14: 144. 1925.

*Conidiomata* aggregated in a black stroma at the ends of branchlets, globose, black, smooth, with central ostiole, up to 600 µm diam, papillate; wall of 3–8 layers of dark brown *textura*

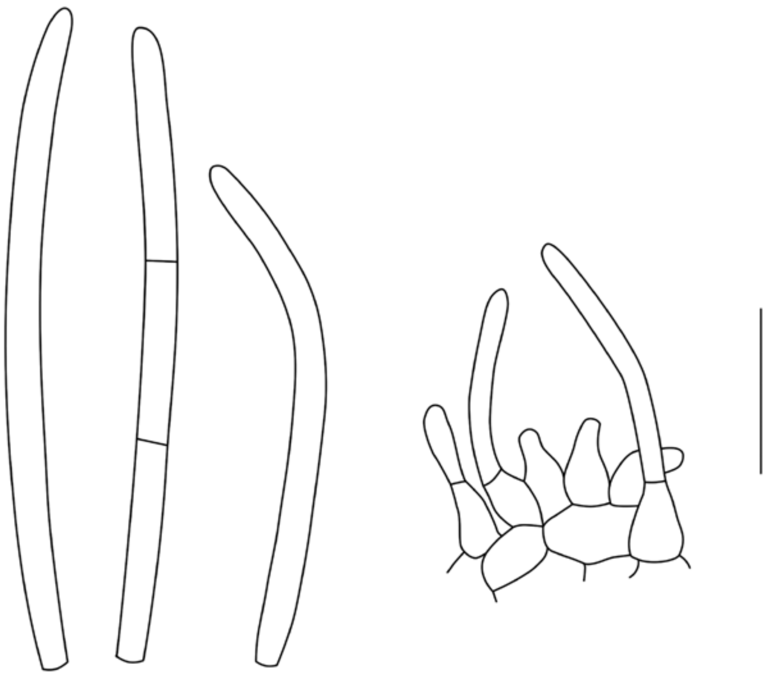

**Fig. 3.** Conidia and conidiogenous cells of *Cytostagonospora photiniicola* (redrawn from Sutton 1980). Scale bar = 10 µm.

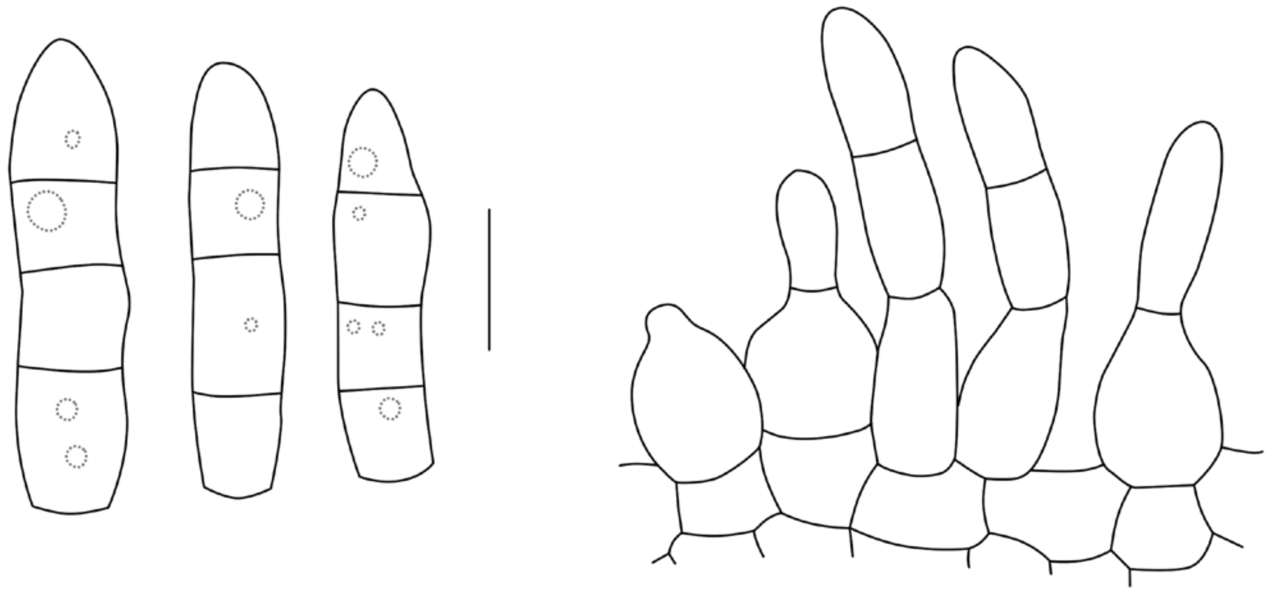

**Fig. 4.** Conidia and conidiogenous cells of *Dearnessia apocyni* (F43227). Scale bars = 10 µm.


**Fig. 5.** *Dearnessia apocyni* (F43227). A. Leaf spot. B, C. Conidiogenous cells. D. Conidia. Scale bars = 10 µm.

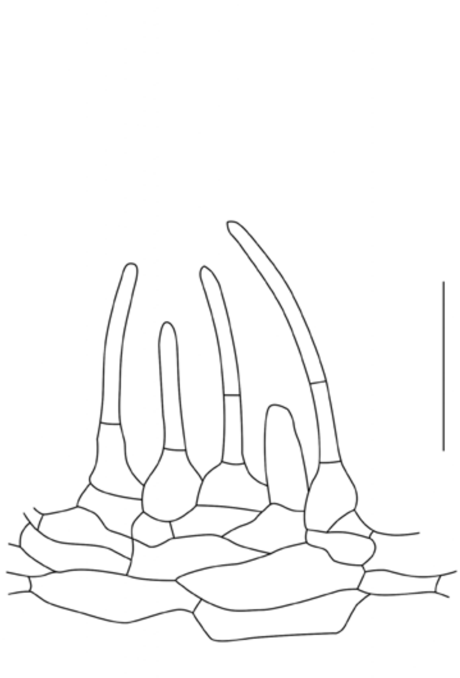

**Fig. 6.** Conidia and conidiogenous cells of *Jahniella bohemica* (redrawn from Sutton 1980). Scale bar = 10 µm.

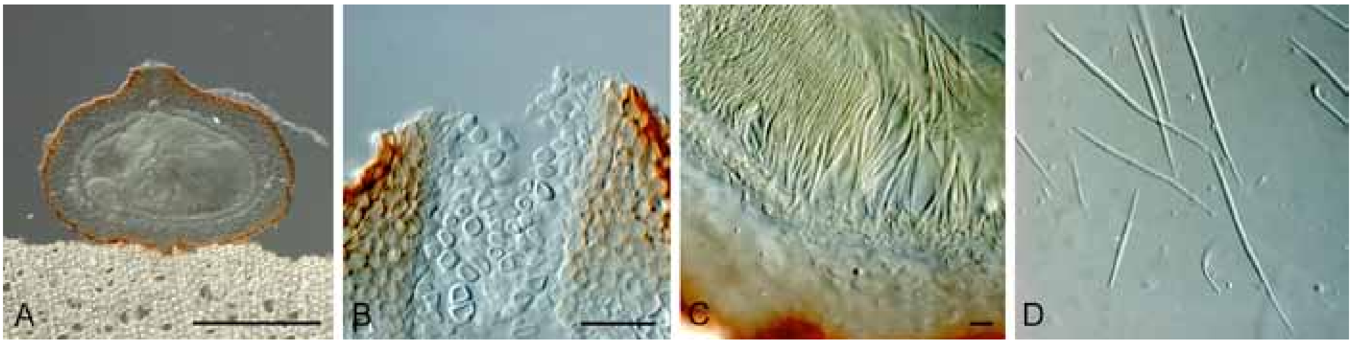


**Fig. 7.** *Jahniella bohemica* [K(M) 180917]. A. Vertical section through conidioma. B. Ostiolar region with loose cells. C. Conidiogenous cells. D. Conidia. Scale bars = 10 µm.

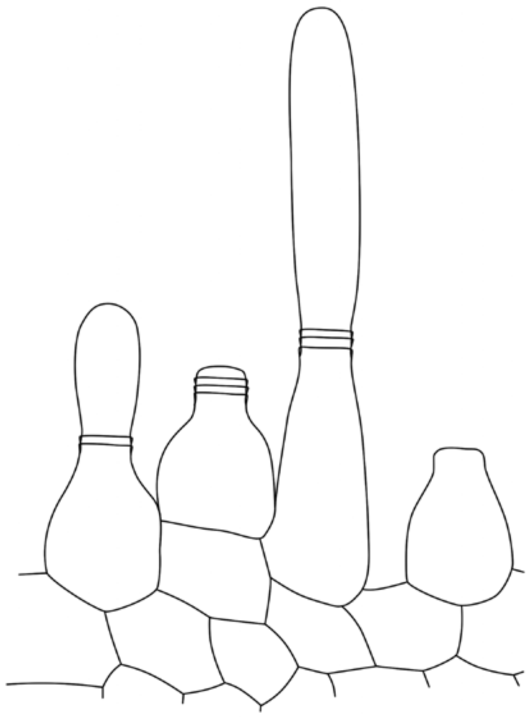

**Fig. 8.** Conidia and conidiogenous cells of *Megaloseptoria mirabilis* (MA-Fungi 6978-1). Scale bars = 10 µm.

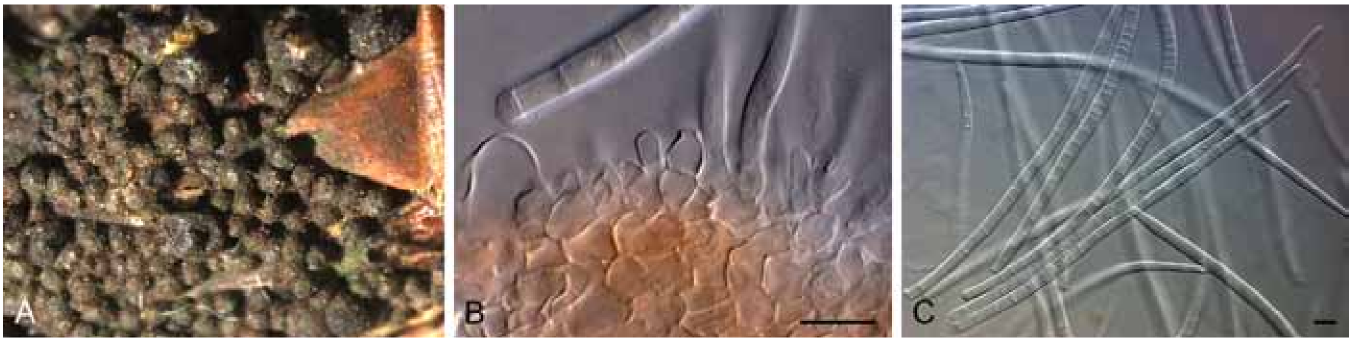


**Fig. 9.** *Megaloseptoria mirabilis* (MA-Fungi 6978-1). A. Conidiomata on host tissue. B. Conidiogenous cells. C. Conidia. Scale bars = 10 µm.

*angularis*. *Conidiogenous cells* lining the cavity, subcylindrical to ampulliform, hyaline, smooth, 7–15 × 4–8 µm; proliferating percurrently near apex. *Conidia* solitary, scolecosporous, variously curved, subcylindrical, tapering in upper third to obtuse apex, base truncate, 3–4 µm diam, transversely 30–40-septate, (170–)200–250 × (5–)6(–7) µm.

*Specimen examined*: **Switzerland**, Zürich, St. Schnach., on branchlets of *Pinus pungens* var. *glauba* (*Pinaceae*), 10 July 1951, E. Müller, **holotype** MA-Fungi 6978-1.

*Note*: *Megaloseptoria* differs from *Septoria* in that the conidiomata are aggregated in a black stroma, which is not the case in *Septoria s. str*.

***Phaeoseptoria*** Speg., Revista Mus. La Plata 15(2): 39. 1908.

*Leaf spots* angular-subcircular, 0.5–3 mm diam, becoming confluent. *Conidiomata* pycnidial, epiphyllous, subepidermal, black, 60–90 µm diam. *Conidiogenesis cells* hyaline, smooth, holoblastic (?). *Conidia* filiform, obclavate, smooth, 1–3-euseptate, medium brown, 30 × 3 µm (Saccardo & Trotter 1913, Walker *et al.* 1992, Crous *et al.* 1997).

*Type species*: *P. papayae* Speg., Revista Mus. La Plata 15(2): 39. 1908.

*Notes*: *Phaeoseptoria papayae* was originally described from leaf spots on *Carica papaya* collected in the São Paulo Botanical Garden, Brazil. Presently there are numerous clades that contain isolates conforming to this morphology, and this matter can only be resolved once fresh material of *P. papayae* has been recollected to clarify its phylogeny (see below).

***Pseudoseptoria*** Speg., Ann. Mus. Nac. B. Aires, Ser. 3 13: 388. 1910.

*Mycelium* immersed, branched, septate, pale brown. *Conidiomata* pycnidial, solitary or linearly aggregated, immersed, brown, globose, unilocular; walls thin, of pale brown *textura angularis*. *Ostiole* distinct, central, circular. *Conidiophores* reduced to conidiogenous cells. *Conidiogenous cells* discrete, determinate or indeterminate, hyaline, smooth, ampulliform with a prominent cylindrical papilla with several percurrent proliferations at the apex. *Conidia* falcate, fusoid, acutely rounded at each end, hyaline, aseptate, guttulate, smooth, thin-walled (Sutton 1980).

*Type species*: *P. donacicola* Speg., Ann. Mus. Nac. B. Aires, Ser. 3 13: 388. 1910.

*Note*: Species of *Pseudoseptoria* are plant pathogenic to members of *Poaceae*.

***Rhabdospora*** (Durieu & Mont. ex Sacc.) Sacc., Syll. Fung. (Abellini) 3: 578. 1884. nom. cons.
*Basionym*: *Septoria* sect. *Rhabdospora* Durieu & Mont., in Durieu, Expl. Sci. Alg. 1 (livr. 15): 592. 1849. [1846–1849].

*Type species*: *R. oleandri* Durieu & Mont., in Durieu, Expl. Sci. Alg. 1 (livr. 15): 593. 1849 [1846–1849].

*Notes*: *Rhabdospora* is a poorly defined genus, originally established to accommodate septoria-like species occurring on stems (Priest 2006). Of the 11 species treated by Sutton (1980), most are currently placed in *Septoria*. This genus is in need of revision pending the recollection of fresh material (on *Nerium oleander* from Algeria).

***Sclerostagonospora*** Höhn., Hedwigia 59: 252. 1917.

*Conidiomata* pycnidial, immersed, separate, dark brown to black, globose, unilocular; walls thin, composed of thick-walled, dark brown *textura angularis*; ostiole single, circular, central, papillate. *Conidiophores* reduced to conidiogenous cells. *Conidiogenous cells* holoblastic, determinate, discrete, hyaline, smooth, ampulliform to irregular, formed from the inner cells of the pycnidial wall. *Conidia* subcylindrical, pale brown, thin-walled, minutely verruculose, 3-euseptate, sometimes slightly constricted at the septa (from Sutton 1980).

*Type species*: *S. heraclei* (Sacc.) Höhn., Hedwigia 59: 252. 1917.

*Note*: *Sclerostagonospora* differs from *Stagonospora* in having pigmented conidia.

***Septoria*** (Sacc.) Sacc., Syll. Fung 3: 474. 1884. nom. cons. Figs 10, 11.
= *Septaria* Fr., Novit. Fl. Svec. 5: 78. 1819. nom. rejic.

*Mycelium* slow-growing, pale brown, septate, immersed. *Conidiomata* pycnidial, immersed, separate or aggregated (but not confluent), globose, papillate (or not), brown, wall of thin, pale

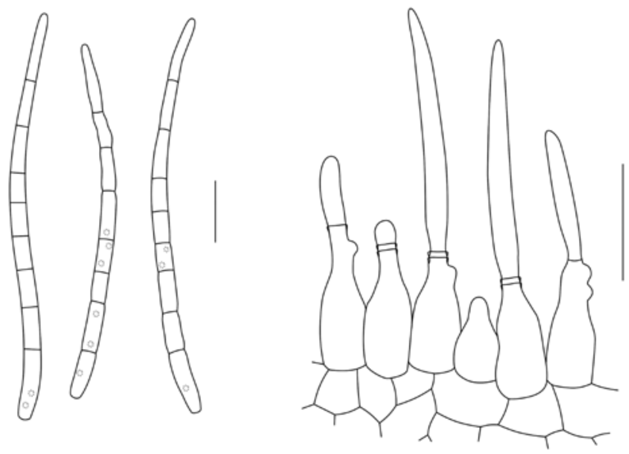

**Fig. 10.** Conidia and conidiogenous cells of *Septoria cytisi* (BPI USO 378994). Scale bars = 10 µm.

brown *textura angularis*, inner layer of flattened, hyaline *textura angularis*, frequently somewhat darker and more thick-walled around the ostiole. *Ostiole* single, circular, central. *Conidiophores* reduced to conidiogenous cells. *Conidiogenous cells* holoblastic, either determinate or indeterminate, proliferating sympodially and/or percurrently, hyaline, smooth, ampulliform, dolliform or lageniform to short cylindrical; scars unthickened. *Conidia* hyaline, multiseptate, filiform, smooth, continuous or constricted at septa. Sexual states are mycosphaerella-like.

*Type species*: *S. cytisi* Desm., Ann. Sci. Nat. Bot. 8: 24. 1847.

*Specimen examined*: **Slovakia**, Muehlthal near Bratislava (Pressburg), on leaves of *Laburnum anagyroides* (*Leguminosae*), 1884, J.A. Baeumler, BPI USO 378994.

*Note*: The ITS and LSU sequences of this specimen were published respectively under GenBank accession numbers JF700932 and JF700954.

***Stagonospora*** (Sacc.) Sacc., Syll. Fung. (Abellini) 3: 445. 1884. nom. cons.

*Basionym*: *Hendersonia* subgen. *Stagonospora* Sacc., Michelia 2 (no. 6): 8. 1880.

*Conidiomata* pycnidial, immersed, unilocular, globose, separate, ostiolate; walls of dark brown, thick-walled *textura angularis*, and on the inside of hyaline, thin-walled, flattened cells. *Conidiophores* reduced to conidiogenous cells. *Conidiogenous cells* doliiform, hyaline, with several percurrent proliferations at the apex, formed from the inner cells of the pycnidial wall. *Conidia* hyaline, smooth to finely verruculose, 1–multiseptate, cylindrical or fusoid-ellipsoidal, straight or slightly curved, often guttulate, constricted or not at septa.

*Type species*: *S. paludosa* (Sacc. & Speg.) Sacc., Syll. Fung. (Abellini) 3: 453. 1884.

***Stenocarpella*** Syd. & P. Syd., Ann. Mycol. 15(3–4): 258. 1917. Fig. 12.

*Mycelium* immersed, brown, branched, septate. *Conidiomata* pycnidial, separate or sometimes confluent, globose or elongated, dark brown, subepidermal, unilocular, thick-walled; walls composed of dark brown, thick-walled *textura angularis*. Ostiole single, circular, papillate, protruding. *Conidiophores* usually absent. *Conidiogenous cells* cylindrical, hyaline, determinate, discrete, phialidic, with collarette and minute periclinal thickening, lining the inner layer of the pycnidial wall. *Conidia* subcylindrical, straight or curved, fusiform, apex obtuse, base tapered, truncate, thick-walled, smooth-walled, granular, pale to medium brown, 0–3-euseptate. Beta conidia hyaline, scolecosporous, curved (Crous *et al.* 2006, Lamprecht *et al.* 2011).

*Type species*: *S. zeae* Syd. & P. Syd., Ann. Mycol. 15(3–4): 258. 1917. [= *S. macrospora* (Earle) B. Sutton]

*Specimens examined*: **South Africa**, KwaZulu-Natal, Hlabisa, rain-damaged Bt *Zea mays* hybrid (*Poaceae*), 2003-04 season, J. Rheeder (**ex-epitype**, CBS 117560 = MRC 8615, designated in Crous *et al.* 2006); KwaZulu-Natal, *Zea mays* kernels, 2005, P. Caldwell, CPC 11863 = CBS 128560.

*Notes*: *Stenocarpella* presently contains two species, *S. macrospora* and *S. maydis*, both causing "Diplodia ear rot of maize". These two taxa were previously assigned to *Diplodia* and *Macrodiplodia*, respectively (Petrak & Sydow 1927, Sutton 1964). Several years later, Sutton re-examining these taxa and placed them in their own genus, *Stenocarpella* (Sutton 1977, 1980). Recent phylogenetic studies confirmed that these taxa indeed cluster by themselves

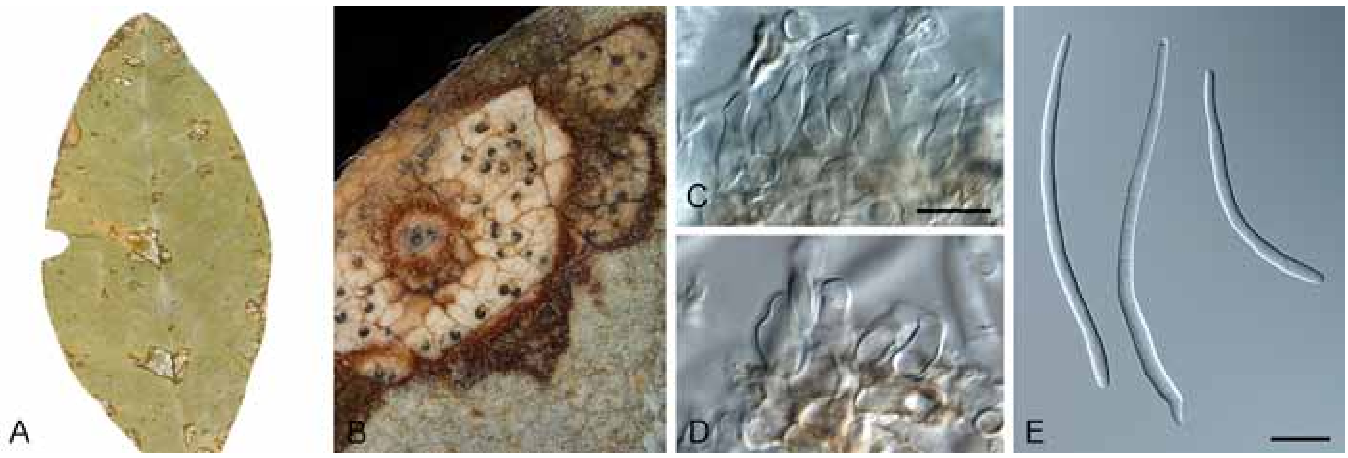


**Fig. 11.** *Septoria cytisi* (BPI USO 378994). A. Leaf with symptoms. B. Close-up of leaf spot with conidiomata. C, D. Conidiogenous cells giving rise to conidia. E. Conidia. Scale bars = 10 µm.

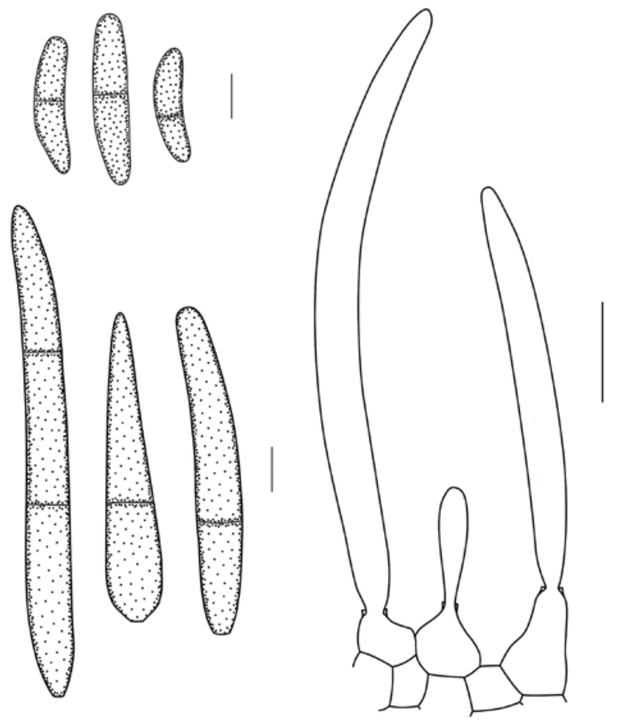

**Fig. 12.** *Stenocarpella maydis* (top) and *S. macrospora* (bottom) (redrawn from Sutton 1980). Scale bars = 10 µm.

within the *Diaporthales* (Crous *et al*. 2006, Lamprecht *et al.* 2011), supporting the decision of Sutton (1980).

***Trichoseptoria*** Cavara, Atti Ist. Bot. Univ. Lab. Crittog. Pavia 2: 40. 1892.

*Type species*: *T. alpei* Cavara, Atti Ist. Bot. Univ. Lab. Crittog. Pavia 2: 40. 1892.

*Notes*: Not much is known about this septoria-like genus, except that it is distinguished from *Septoria* by having setae on its pycnidia with 1–2-septate, hyaline conidia. This genus is in further need of revision once fresh material has been recollected (*Citrus vulgaris*, Belgiojoso, Alps).

***Zymoseptoria*** Quaedvlieg & Crous, Persoonia 26: 64. 2011.

*Conidiomata* pycnidial, semi-immersed to erumpent, dark brown to black, subglobose, with central ostiole; wall of 3–4 layers of brown *textura angularis*. *Conidiophores* hyaline and smooth, 1–2-septate, or reduced to conidiogenous cells, lining the inner cavity. *Conidiogenous cells* are tightly aggregated and ampulliform to doliiform or subcylindrical, phialidic with periclinal thickening, or with 2–3 inconspicuous, percurrent proliferations at the apex. *Conidia* (Type I) solitary, hyaline, smooth, guttulate, narrowly cylindrical to subulate, tapering towards acutely rounded apex, with bluntly rounded to truncate base, transversely euseptate; hila not thickened nor darkened. On OA and PDA media plates the aerial hyphae disarticulate into phragmospores (Type II conidia) that again give rise to Type I conidia via microcyclic conidiation; yeast-like growth and microcyclic conidiation (Type III conidia) common on agar media (Quaedvlieg *et al*. 2011).

*Type species*: *Z. tritici* (Desm.) Quaedvlieg & Crous, Persoonia 26: 67. 2011.

*Notes*: *Zymoseptoria* was split off from *Septoria s. str.* and redescribed by Quaedvlieg *et al*. (2011) based on LSU sequence data when said authors delimitated *Septoria s. str*. by sequencing the ITS and LSU sequences out of *S. cytisi* herbarium material. Phylogenetic analysis showed that *Zymoseptoria* species cluster within a distinct clade inside the *Mycosphaerellaceae* that is closely related to *Ramularia*, but located distant from *Septoria s. str*.

## Acervular forms

***Asteromidium*** Speg., Ann. Soc. cient. argent. 26(1): 66. 1888. Figs 13, 14.

*Mycelium* immersed, branched, septate, hyaline. *Conidiomata* acervular, subcuticular, separate or confluent, pulvinate to doliiform, at the base, composed of hyaline to pale brown, thin-walled *textura angularis* which extends laterally, finally with separate cells dispersed in a mucilaginous matrix to form the overlying wall; cuticle discoloured and occasionally pseudoparenchymatous, walls adjacent to the upper epidermal wall also discoloured; dehiscence irregular. *Conidiogenous cells* holoblastic, discrete, indeterminate, ± cylindrical, hyaline, smooth, with 1–2 sympodial proliferations, scars unthickened, flat, formed from the basal and lateral walls. *Conidia* cylindrical to fusoid, gently tapered at each end, apex obtuse, base truncate, thin-walled, guttulate to granular, hyaline, 3-septate (Sutton 1980).

*Type species*: *A. imperspicuum* Speg., Ann. Soc. cient. argent. 26(1): 66. 1888.

*Specimen examined*: **Paraguay**, on leaves of *Sapindaceae*, 1883, **isotype** K(M) 180228, ex B. Balansa Pl. du Paraguay No. 4085.

*Notes*: This genus has to be recollected (*Sapindaceae*, Paraguay) to allow for a molecular comparison to other existing genera in this

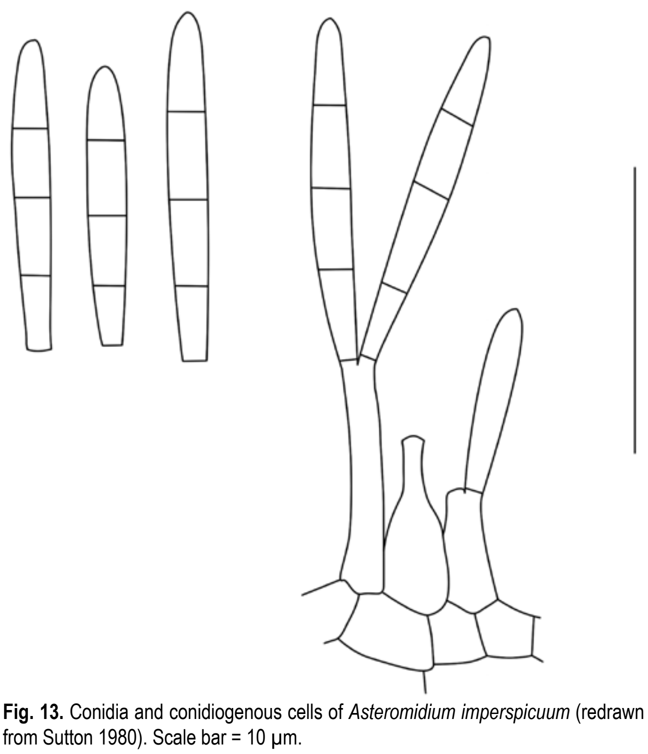

**Fig. 13.** Conidia and conidiogenous cells of *Asteromidium imperspicuum* (redrawn from Sutton 1980). Scale bar = 10 µm.

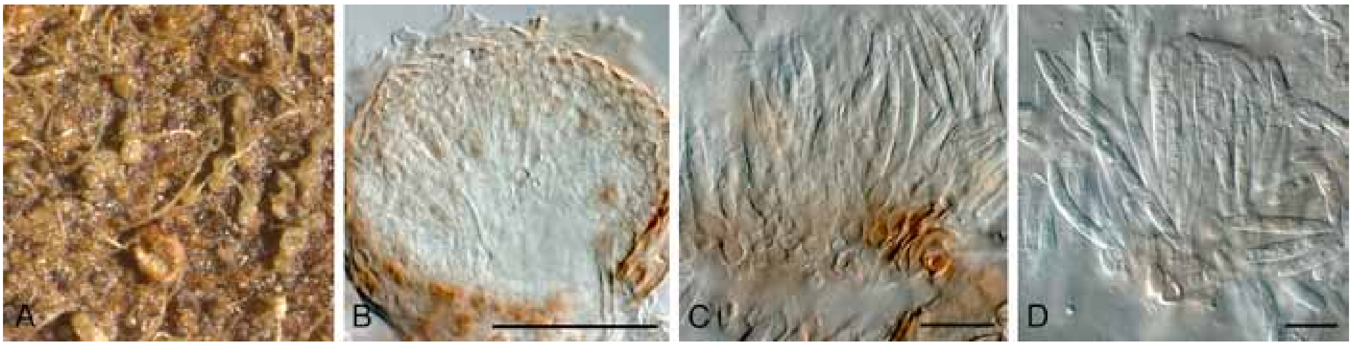


**Fig. 14.** *Asteromidium imperspicuum* [K(M) 180228]. A. Conidiomata on host surface. B. Section through conidioma. C, D. Conidiogenous cells and conidia. Scale bars: B = 75 µm, all others = 10 µm.

complex. The morphology of the specimen examined correlates well with the description provided by Sutton (1980).

### ***Ciferriella*** Petr., Ann. Mycol. 28(5/6): 409. 1930.

*Type species*: *C. domingensis* Petr. & Cif., Ann. Mycol. 28(5/6): 409. 1930.

= ***Pseudocercospora*** Speg., Anales Mus. Nac. Hist. Nat. B. Aires, Ser. 3, 20: 437. 1910.

### ***Pseudocercospora domingensis*** (Petr. & Cif.) Quaedvlieg, Verkley & Crous, **comb. nov.** MycoBank MB804401. Figs 15, 16.

*Basionym*: *Ciferriella domingensis* Petr. & Cif., Ann. Mycol. 28(5/6): 409. 1930.

*Leaf spots* amphigenous, subcircular, medium brown with dark purple margin, 1.5–6 mm diam. Sporulation hypophyllous, fasciculate to sporodochial, brown, arising from a brown stroma, up to 50 µm diam. *Conidiophores* medium brown, smooth, subcylindrical, 0–2-septate, straight to once geniculate, 15–20 × 3–5 µm. *Conidiogenous cells* terminal, brown, smooth to finely verruculose, ampulliform to subcylindrical, proliferating sympodially or percurrently, tapering to a truncate apex, 2 µm diam, 10–15 × 3–4 µm. *Conidia* brown, smooth, straight to slightly curved, obclavate, apex subobtuse, base obconically truncate, 0–3-septate, 35–60 × 3–4 µm.

*Specimen examined*: **Dominican Republic**, on *Vitex umbrosa* (*Lamiaceae*), 26 May 1929, coll. R. Ciferri, det. F. Petrak, **holotype** ex N.Y. Bot. Gard. No 01048475.

*Notes*: The dimensions of the conidia and conidiophores correlate with the observations of Sutton (1980). However, the conidiomata are sporodochial to fasciculate, and not acervular. *Ciferriella domingensis* is a typical *Pseudocercospora sensu* Crous *et al.* (2013). Based on the species presently known from *Vitex* (Crous & Braun 2003), it appears to represent a distinct taxon, for which a new combination in *Pseudocercospora* is proposed.

### ***Colletogloeum*** Petr., Sydowia 7: 368. 1953.

*Mycelium* immersed, branched, septate, hyaline to pale brown. *Conidiomata* acervular, epidermal to subepidermal, separate, occasionally confluent, composed of hyaline to pale brown, thin-walled *textura angularis*. *Conidiophores* hyaline to pale brown, sparsely branched, septate, smooth, cylindrical or slightly irregular, formed from the upper cells of the acervulus. *Conidiogenous cells* integrated or discrete, indeterminate, cylindrical or doliiform, with several percurrent proliferations at apex. *Conidia* hyaline to pale brown, 0-multiseptate, straight, curved or irregular, truncate at the base, obtuse at the apex, usually thin-walled, smooth, guttulate or not.

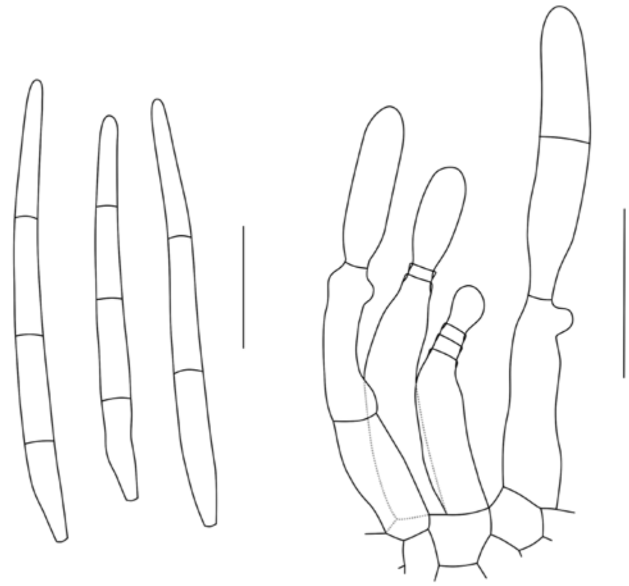

**Fig. 15.** Conidia and conidiogenous cells of *Pseudocercospora domingensis* (NY No 01048475). Scale bars = 10 µm.

*Type species*: *C. dalbergiae* (S. Ahmad) Petr., Sydowia 7: 369. 1953. [= *C. sissoo* (Syd.) B. Sutton, Mycol. Pap. 97: 14. 1964.]

*Notes*: The exact taxonomic position of *Colletogloeum* was unclear for a long time as it included many species that appear to represent asexual morphs of *Teratosphaeria.* Crous *et al.* (2009a–c) used ITS sequence data from a specimen representative of *C. sissoo* (IMI 119162) to demonstate that the type of *Colletogloeum* clustered near the *Pseudocercospora* complex within the *Mycosphaerellaceae*.

### ***Cylindrosporium*** Grev., Scott. crypt. fl. (Edinburgh) 1: pl. 27. 1822.

= *Cylindrodochium* Bonord., Handb. Allgem. mykol. (Stuttgart): 132. 1851.

*Mycelium* immersed, branched, septate, hyaline. *Conidiomata* acervular, white, slimy, subcuticular, separate or confluent, formed of pale brown to hyaline, thin-walled *textura angularis*; dehiscence irregular. *Conidiophores* hyaline, parallel, branched


**Fig. 16.** *Pseudocercospora domingensis* (NY No 01048475). A. Leaf spot. B, C. Conidiogenous cells. D. Conidia. Scale bars = 10 µm.

only at the base, 1–2-septate, smooth, formed from the upper pseudoparenchyma. *Conidiogenous cells* enteroblastic, phialidic, integrated, cylindrical, hyaline, smooth. *Conidia* straight or slightly curved, aseptate, cylindrical, thin-walled, smooth, hyaline, eguttulate (Sutton 1980).

*Type species*: *C. concentricum* Unger, Exanth. Pflanzen (Wien) 2: 9. 1833.

*Notes*: Sutton (1980), Von Arx (1983), Deighton (1987) and Braun (1990) could not agree on the taxonomic status of this genus, which is associated with light leaf spot of oil seed rape (sexual morph *Pyrenopeziza brassicae*). This genus is in need of revision, awaiting the recollection of fresh material of *C. concentricum* (on *Pulmonaria officinalis*, Germany).

## ***Phloeospora*** Wallr., Fl. Crypt. Germ. (Norimbergae) 2: 176. 1833.

*Mycelium* immersed, septate, hyaline. *Conidiomata* acervular, subepidermal, circular, discrete or confluent, composed of hyaline to pale brown, thin-walled *textura angularis*; dehiscence irregular. *Conidiophores* reduced to conidiogenous cells or with one or two supporting cells, branched at base or not. *Conidiogenous cells* holoblastic, annellidic, occasionally also sympodial, discrete, indeterminate hyaline, smooth, cylindrical, with several apical inconspicuous annellations, formed from the upper cells of the acervuli. *Conidia* hyaline, septate, smooth, guttulate or not, cylindrical, curved, attenuated towards the apices, apex obtuse to subobtuse, base truncate, with minute marginal frill.

*Type species*: *P. ulmi* (Fr.) Wallr., Fl. Crypt. Germ. (Norimbergae) 2: 177. 1833.

*Notes*: Sexual morphs of *Phloeospora* have been linked to genera that resemble the concepts of *Mycosphaerella, Didymella* and *Sphaerulina*. Verkley & Priest (2000) already noted that this genus is heterogeneous and in need of revision. The phylogenetic analysis performed in this study confirmed that *Phloeospora* (based on *P. ulmi*) clusters close to, but separate from *Septoria s. str*. (Fig. 1).

## ***Phloeosporella*** Höhn., Ann. Mycol. 22: 201. 1924. Fig. 17.

*Mycelium* immersed, branched, septate, hyaline. *Conidiomata* acervular, subepidermal, ± circular, discrete, composed of hyaline to pale brown, thin-walled *textura angularis*. *Conidiogenous cells* holoblastic, sympodial, discrete, indeterminate, hyaline, smooth, lageniform to cylindrical, with 1–2 broad, flat unthickened apical scars, formed from the upper pseudoparenchyma. *Conidia* hyaline, 2-euseptate, thin-walled, smooth, guttulate, straight, curved or irregular, tapered gradually to an obtuse apex and abruptly to a truncate base (Sutton 1980).

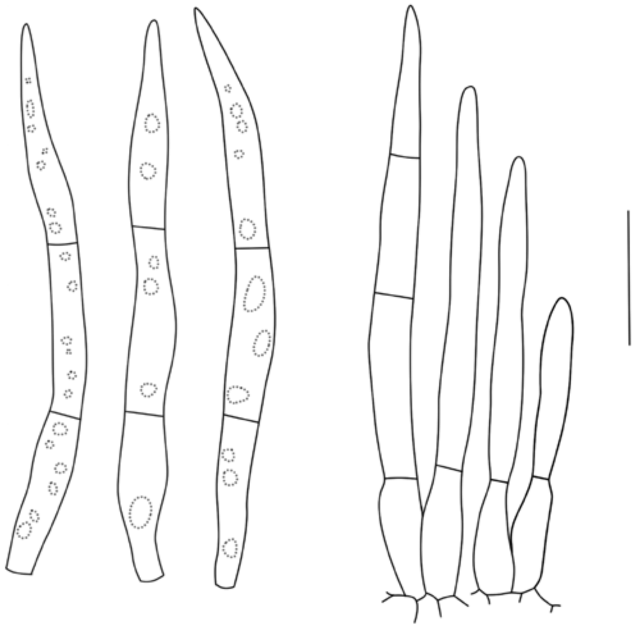

**Fig. 17.** Conidia and conidiogenous cells of *Phloeosporella ceanothi* (redrawn from Sutton 1980). Scale bar = 10 µm.

*Type species*: *P. ceanothi* (Ellis & Everh.) Höhn., Ann. Mycol. 22(1–2): 201. 1924.

*Notes*: Not much is known of the sexual state of this genus, but *P. padi* has been linked to *Blumeriella jaapii* (Sutton 1980). A phylogenetic analysis performed on available isolates (unpubl. data) indicated that *Phloeosporella* is polyphyletic. However, as the type is not known from culture (on *Ceanothus*, California, USA), this matter could not be resolved.

## ***Septogloeum*** Sacc., Michelia 2(6): 11. 1880.

*Mycelium* immersed, branched, septate, hyaline. *Conidiomata* acervular, epidermal to subepidermal, separate or confluent, formed of pale brown thin-walled pseudoparenchyma. *Conidiophores* short, stout, 1–2-septate, hyaline, smooth, branched at the base, formed from the upper pseudoparenchyma. *Conidiogenous cells* phialidic, discrete or integrated, determinate, cylindrical, doliiform to obpyriform, hyaline, smooth, with minute collarette and prominent periclinal thickening. *Conidia* hyaline, 1–3-euseptate, thin-walled, smooth, eguttulate, base truncate, apex obtuse, straight or curved, constricted, obovoid (Sutton 1980).

*Type species*: *S. carthusianum* (Sacc.) Sacc., Michelia 2(6): 11. 1880.

*Notes*: Although more than 120 species of *Septogloeum* have been described, the genus was reduced to just two species by Sutton & Pollack (1974). Sexual morphs have been linked to *Pleuroceras* in the *Diaporthales* (Monod 1983). The genus is in need of revision pending fresh collections.

***Xenocylindrosporium*** Crous & Verkley, Fungal Planet 44. 2009.

*Conidiomata* immersed, black, opening by irregular rupture, acervuloid, up to 300 µm diam; wall consisting of 3–4 layers of pale brown *textura angularis*. *Conidiophores* hyaline, smooth, subcylindrical, branched, septate, or reduced to ampulliform conidiogenous cells. *Conidiogenous cells* hyaline, smooth, ampulliform to subcylindrical, terminal or lateral on septate conidiophores, monophialidic with minute periclinal thickening. *Conidia* solitary, hyaline, smooth, curved, widest in middle, tapering to acutely rounded apex and truncate base, 0 –1-septate.

*Type species*: *X. kirstenboschense* Crous & Verkley, Fungal Planet 44. 2009.

## Stromatic forms

***Dothistroma*** Hulbary, Bull. Ill. Nat. Hist. Surv. 21: 235. 1941.

*Mycelium* immersed, branched, septate, pale brown to hyaline. *Conidiomata* sometimes acervular, initially subepidermal later erumpent, composed of pale brown, thin-walled *textura angularis*, sometimes eustromatic, multilocular and of darker brown, thick-walled tissue. *Stromata* are strongly erumpent and finally pulvinate. *Conidiogenous cells* holoblastic, discrete, determinate, ampulliform, hyaline, smooth, non-proliferating, formed from the upper cells of stroma or from inner cells of the locular walls. *Conidia* hyaline, straight or curved, filiform, 1–5-euseptate, continuous, thin-walled and smooth (Barnes *et al.* 2004).

*Type species*: *D. pini* Hulbary, Bull. Ill. Nat. Hist. Surv. 21: 235. 1941.

*Notes*: *Dothistroma* sexual morphs are mycosphaerella-like (Evans 1984), and the two species of *Dothistroma* that have been subjected to DNA sequencing (*D. septosporum* and *D. pini*) cluster together in the *"Dothistroma* clade" as described by Crous *et al*. (2009a, c). Because of a lack of recognisable morphological characteristics, it is virtually impossible to discriminate between *D. septosporum* and *D. pini* without molecular tools (Barnes *et al.* 2004). Multiple morphological varieties of both *D. septosporum* and *D. pini* have

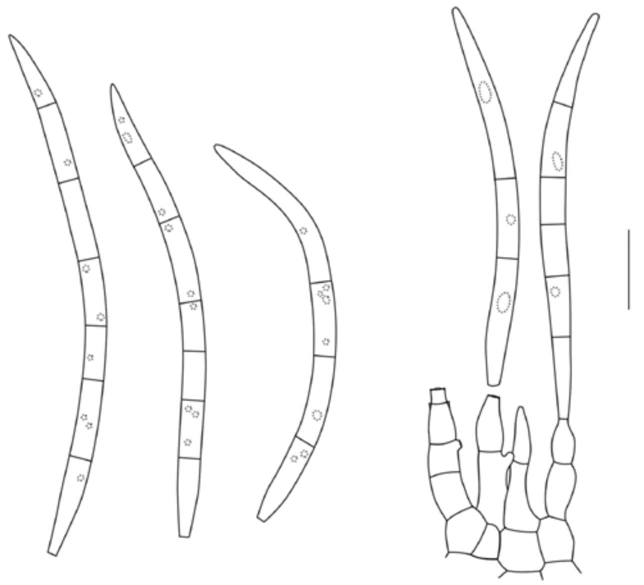

**Fig. 18.** Conidia and conidiogenous cells of *Phlyctaeniella humuli* (IMI 202260) (redrawn from Sutton 1980). Scale bar = 10 µm.

been described based on differences in conidia length alone (*e.g. D. septosporum* var. *keniense*). However, controversy exists as to whether spore size represents an adequate characteristic to distinguish among these *Dothistroma* varieties, as since the introduction of molecular tools only *D. septosporum* and *D. pini* have been confirmed as distinct species.

***Phlyctaeniella*** Petr., Ann. Mycol. 20: 323. 1922. Fig. 18.

Mycelium immersed, branched, septate, hyaline. *Conidiomata* eustromatic, separate, immersed, pale brown, globose, unilocular, scarcely erumpent; side wall and base of several cell layers of hyaline, thin-walled *textura angularis*, above of larger pale brown tissue. *Ostiole* indistinct, and dehiscence by rupture of the upper wall. *Conidiophores* hyaline, smooth, septate, irregularly branched, especially at the base, formed from the inner cells of the stroma wall. *Conidiogenous cells* phialidic, integrated or discrete, determinate, hyaline, markedly tapered at the apices, smooth, with apical or lateral apertures, collarette minute, with periclinal thickening; only rarely becoming percurrent. *Conidia* hyaline, smooth, thin-walled, irregularly guttulate, filiform, straight, curved or irregular, multiseptate (Sutton 1980).

*Type species*: *P. polonica* Petr., Ann. Mycol. 20: 323. 1922.

*Note*: Fresh material needs to be collected of this taxon (on *Aruncus silvestris*, Austria), before its taxonomy can be resolved.

***Septocyta*** Petr., Ann. Mycol. 25: 330. 1927. Figs 19, 20.

*Mycelium* immersed, branched, septate, hyaline to pale brown. *Conidiomata* eustromatic, immersed, separate, erumpent, dark brown to black, finally opening widely, unilocular, multilocular or convoluted, thick-walled; wall of pale brown, thin-walled *textura angularis* except in the dehiscent region which is darker brown and more thick-walled. *Ostiole* absent, dehiscence by breakdown of the upper wall. *Conidiogenous cells* are holoblastic, sympodial with 1–3

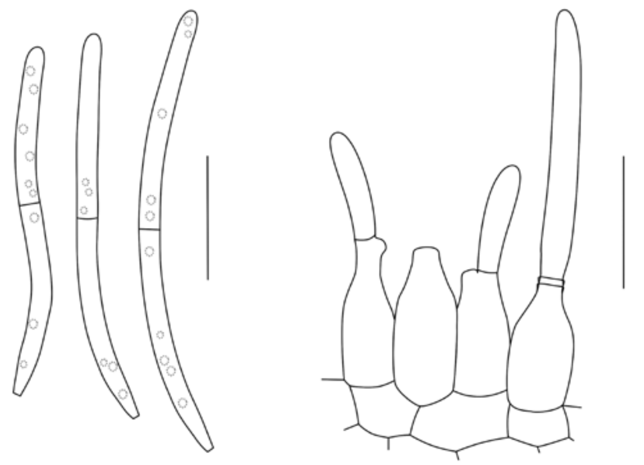

**Fig. 19.** Conidia and conidiogenous cells of *Septocyta ramealis* (PDD 51271). Scale bars = 10 µm.

apical, scarcely protruding, unthickened denticles, indeterminate, discrete, ampulliform to lageniform, hyaline, smooth, formed from the inner cells of the locular walls. *Conidia* hyaline, 1–3 euseptate, smooth, straight or slightly curved, acicular, apex obtuse, base truncate, often with minute guttules associated with septa (Sutton 1980).

*Type species*: *S. ramealis* (Roberge ex Desm.) Petr., Ann. Mycol. 25: 330. 1927.

### ***Septocyta ramealis*** (Roberge ex Desm.) Petr., Ann. Mycol. 25: 330. 1927.

*Conidiomata* eustromatic to pycnidial, black, up to 160 µm diam, aggregated in clusters, erumpent through ruptures in epidermis, convulated; wall of 3–8 layers of brown *textura angularis*. *Conidiophores* lining the inner cavity, reduced to conidiogenous cells, or one or two supporting cells. *Conidiogenous cells* hyaline, smooth, ampulliform, proliferating sympodially and percurrently near apex, also with lateral denticle-like protrusions, 6–12 × 2.5–4 µm. *Conidia* hyaline, smooth, guttulate, (9–)20–30(–35) × 1.5(–2) µm, 1(–3)-septate, irregularly curved, subcylindrical, apex obtuse, base tapering slightly to truncate hilum, 0.5 µm diam.

*Specimen examined*: **Germany**, Brandenberg, on *Rubus fructicosus* (*Rosaceae*), 7 June 1923, coll. P. Sydow, det. H. Sydow, Sydow Mycoth. Germ. PDD 51271.

*Notes*: *Septocyta ramealis*, the type of *Septocyta*, has a long list of synonyms. The specimen examined here (PDD 51271), differs somewhat from the description provided by Sutton (1980), and appears to represent a species of *Septoria s. str*., as the mode of conidiogenesis is not that different. Presently there is a single ITS sequence labelled as *S. ruborum* available on GenBank (JN133277.1), placing it in the middle of *Septoria s. str*. As no type material of *S. ramealis* could be located, this matter remains unresolved.

### ***Septopatella*** Petr., Ann. Mycol. 23: 128. 1925.

*Mycelium* immersed, branched, septate, hyaline to subhyaline. *Conidiomata* superficial, often subtended by a superficial, pale brown, septate, branched mycelium, pulvinate, separate to occasionally aggregated, dark brown to black, finally opening widely, cupulate; basal wall of small-celled, brown, thin-walled *textura angularis,* becoming *textura porrecta* as it merges into the periclinal walls; a hypostroma attaches the conidioma to the substrate; *Ostiole* absent. *Conidiophores* hyaline, septate, branched at the base, thin-walled, cylindrical, formed from the gelatinized basal wall of the conidioma. *Conidiogenous cells* holoblastic, sympodial, integrated, indeterminate, cylindrical, hyaline, smooth, produced as 2–3 branches from the apex of the conidiophores. *Conidia* hyaline, 3–4-euseptate, thin-walled, smooth, minutely guttulate, straight or curved, occasionally irregularly filiform (Dyko & Sutton 1979, Sutton 1980).

*Type species: S. septata* (Jaap) Petr., Ann. Mycol. 23: 129. 1925.

*Note*: Not much is known about this genus, and as no cultures of *S. septata* are presently available (on *Pinus montana*, Czech Republic) this matter cannot be resolved.

### ***Stictosepta*** Petr., Sydowia 17: 230. 1964. [1963]. Fig. 21.

*Mycelium* immersed, branched, septate, hyaline. *Conidiomata* eustromatic, immersed, globose to collabent, papillate, unilocular, often convoluted, hyaline; walls thick, of hyaline, thin-walled

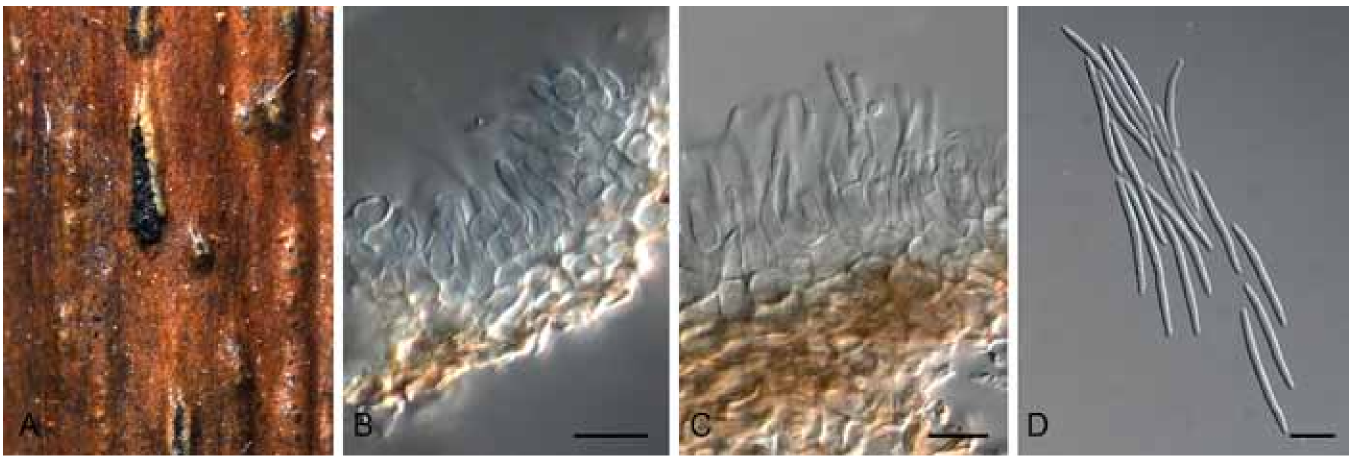


**Fig. 20.** *Septocyta ramealis* (PDD 51271). A. Conidiomata on host tissue. B, C. Conidiogenous cells. D. Conidia. Scale bar = 10 µm.

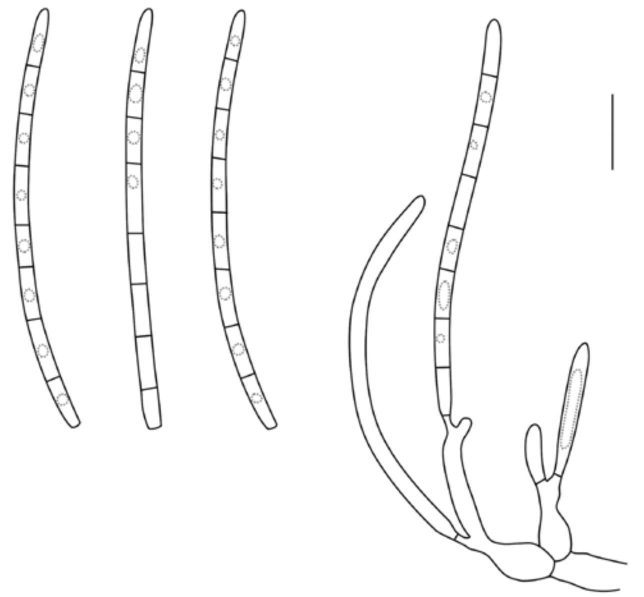

**Fig. 21.** Conidia and conidiogenous cells of *Stictosepta cupularis* (redrawn from Sutton 1980). Scale bar = 10 µm.

*textura intricata*. *Ostiole* central and circular, single, furfuraceous. *Conidiophores* hyaline, septate, branched, anastomosing, formed from the inner cells of the locular wall. *Conidiogenous cells* sympodial or synchronous, integrated, indeterminate, hyaline, thin-walled, with usually two small, unthickened, apical, slightly protuberant conidiogenous loci. *Conidia* hyaline, thin-walled, smooth, multiseptate, slightly constricted at the septa, each cell medianly guttulate, straight or curved, base truncate, apex obtuse (Sutton 1980).

*Type species*: *S. cupularis* Petr., Sydowia 17: 230. 1964. [1963].

*Note*: Not much is known about this genus, but as no isolate of *S. cupularis* is presently available (on stems of *Fraxinus*, Czech Republic), it will not be treated here.

## Sexual morphs linked to *Septoria*

Several sexual genera have been linked to *Septoria* and allied genera in literature, but very few have been confirmed in culture. Most sexual states cluster in the *Mycosphaerella* complex.

***Mycosphaerella*** Johanson, Öfvers. K. Svensk. Vetensk.-Akad. Förhandl. 41(no. 9): 163. 1884.
= *Ramularia* Unger, Exanth. Pflanzen (Wien): 119. 1833.

*Mycelium* immersed to superficial, septate, hyaline, branched. *Caespituli* usually whitish to greyish on host tissue. *Conidiophores* fasciculate to synnematal, rarely solitary, or forming small sporodochia, emerging through stomata, from inner hyphae or stromata; conidiophores straight, subcylindric to geniculate-sinuous, aseptate or septate, hyaline, occasionally branched, smooth, rarely rough. *Conidiogenous cells* integrated, terminal, polyblastic, elongating sympodially, apex more or less straight to geniculate-sinuous or strongly curved, cicatrized, conidial scars hardly to conspicuously thickened, but always darkened, refractive. *Conidia* solitary to catenate, sometimes in branched chains, 0–4(–multi)-septate, hyaline, ellipsoid-ovoid to cylindrical-fusoid, rarely filiform, occasionally constricted at the septa, smooth to verruculose-echinulate; hila distinct, slightly to conspicuously thickened, darkened, refractive; conidial secession schizolytic. *Ascomata* immersed to superficial, uniloculate, globose to subglobose with papillate, central, periphysate ostiole, dark brown to black, scattered or gregarious. *Peridium* of 3–6 layers of thin- to thick-walled *textura angularis*, dark brown to black. *Hamathecium* dissolves at maturity, and no stromatic tissue remains between the asci. *Asci* bitunicate, fissitunicate, 8-spored, cylindrical to cylindric-clavate, ovoid to ampulliform or saccate, sessile to subsessile, apex rounded with distinct or indistinct ocular chamber. *Ascospores* bi- to tri- or multiseriate, ellipsoid-fusoid to obclavate or subcylindrical, hyaline, medianly 1-septate, often constricted at the septum, smooth-walled, granular to guttulate, mostly lacking any sheath.

*Type species*: *Ramularia pusilla* Unger, Exanth. Pflanzen (Wien): 169. 1833.

*Notes*: Species of *Ramularia* (including the *Mycosphaerella* sexual morph) have evolved over a broad developmental and physiological adaptation range that includes endophytes, saprophytes and symbionts. However, for a major part *Ramularia* consists of a wide range of narrow host range, foliicolous plant pathogens which are the cause of significant economical losses in both temperate and tropical crops worldwide (Crous *et al.* 2001). Verkley *et al*. (2004) showed that *Mycosphaerella s. str.* (linked to *M. punctiformis*) was in fact restricted to species with *Ramularia* anamorphs, leaving many "*Mycosphaerella"* species to be disposed to other genera. In employing the one fungus = one name concept (Hawksworth *et al.* 2011, Wingfield *et al*. 2012), the choice is to use *Ramularia* over *Mycosphaerella*, as the former is monophyletic and recently monographed (Braun 1995, 1998), while *Mycosphaerella* is poly- and paraphyletic, and consists of more than 40 genera, many as yet untreated (Crous *et al.* 2009c)

***Sphaerulina*** Sacc., Michelia 1(no. 4): 399. 1878.

*Ascomata* pseudothecial, immersed, subepidermal, erumpent at the top, single to clustered, globose, papillate. *Ostiole* central, with hyaline periphyses; wall of *textura angularis*, composed of 2–4 layers of brown cells. *Hamathecium* dissolving at maturity. *Asci* bitunicate, fissitunicate, clustered, cylindrical to obclavate, rounded at apex, with or without a shallow apical chamber, short-stipitate or sessile, with 8 biseriate to triseriate ascospores. *Ascospores* subcylindrical to fusiform, rounded at ends, slightly tapered, straight or slightly curved, 1–3-septate, with a primary septum nearly median, hyaline, smooth, without sheath or appendages.

*Type species*: *Sphaerulina myriadea* (DC.) Sacc., Michelia 1(no. 4): 399. 1878.

*Notes*: The genus *Sphaerulina* was chiefly separated from *Mycosphaerella* on the basis of ascospore septation (Crous *et al.* 2011). *Sphaerulina myriadea*, which occurs on hosts in the *Fagaceae*, appears to be a species complex. Results in this paper show that *Sphaerulina myriadea* clusters together with many septoria-like species in a clade that is distinct, but very closely related to *Septoria s. str.* The septoria-like species in this *Sphaerulina* clade were subsequently rediscribed in *Sphaerulina*. Species including ones with 1-septate ascospores and septoria-like asexual morphs are treated below and by Verkley *et al.* (2013).

## Treatment of phylogenetic clades

Based on the phylogenetic data generated in this study, we were able to delineate several clades in the *Septoria* complex. Recognised clades, as well as novel species and genera, are described and discussed below. Taxa with descriptions that are freely available online in MycoBank or open access journals, are not repeated here.

## Clade 1: *Septoria*

*Description*: See above.

*Type species*: *S. cytisi* Desm., Ann. Sci. Nat. Bot. 8: 24. 1847.

***Septoria* cf. *agrimoniicola*** Bondartsev, Mater. mikol. obslêed. Ross. 2: 6. 1921.

*Leaf spots* on the upper leaf surface, distinct, scattered, brown with purplish margin, circular to angular, sometimes vein-limited, discrete lesions 2–4 mm diam, reaching 10 mm wide when confluent, finally the center becoming pale colored to nearly whitish; on the lower leaf surface similar but discoloured (Shin & Sameva 2004). On sterile *Carex* leaves on WA. *Conidiomata* pycnidial, separate but frequently aggregated and linked by brown stromatic tissue in a stroma; globose, black, exuding a creamy conidial mass via a central ostiole; conidiomata up to 350 µm diam; wall of 6–12 layers of dark brown, thick-walled *textura angularis*. *Conidiophores* reduced to conidiogenous cells or 1–2 supporting cells, hyaline, subcylindrical, lining the inner layer of conidioma. *Conidiogenous cells* hyaline, smooth, subcylindrical to ampulliform, 10–17 × 3–4 µm; proliferating sympodially but also percurrently near apex. *Conidia* hyaline, smooth, guttulate, filiform, apex subobtuse, base long obconically truncate, 1–4-septate, (20–)25–35(–40) × 1.5–2(–2.5) µm; microcyclic conidiation observed.

*Culture characteristics*: Colonies on PDA flat, undulate with sparse, white aerial mycelium, surface olivaceous-black, reverse olivaceous-black, after 14 d, 3.5 cm diam; on MEA with sparse white aerial mycelium, surface olivaceous-black, reverse olivaceous-black, after 14 d, 5 cm diam; on OA with sparse white aerial mycelium, surface olivaceous, reverse olivaceous, after 14 d, 3 cm diam.

*Specimen examined*: **South Korea**, Guri, on leaves of *Agrimonia pilosa* (*Rosaceae*), 11 Jul. 2009, H.D. Shin (CBS H-21279, culture CBS 128602 = KACC 44644 = SMKC 24292).

*Notes*: This fungus was first reported from Korea by Shin & Sameva (2002) as *S. agrimoniicola*, and fits well with the original description of this European taxon. However, fresh European collections and cultures are required for comparison, as *S. agrimoniicola* may well be restricted to Europe.

***Septoria* cf. *stachydicola*** Hollós, Mathem. Természettud. Közlem. Magg. Tudom. Akad. 35(1): 60. 1926.

*Leaf spots* on the upper leaf surface distinct, scattered, brown with purplish margin, circular to angular, sometimes vein-limited, discrete lesions 2–4 mm diam, reaching 10 mm wide when confluent, finally the center becoming paler or nearly whitish; on the lower leaf surface similar but discoloured (Shin & Sameva 2004). On OA. *Conidiomata* solitary to aggregated, black, globose, becoming somewhat papillate, up to 250 µm diam, opening by means of central ostiole, up to 40 µm diam; wall of 6–8 layers of thick-walled, brown *textura angularis*; exuding a creamy conidial mass. *Conidiophores* reduced to conidiogenous cells. *Conidiogenous cells* lining the inner wall layer, hyaline, discrete, ampulliform to lageniform, 4–10 × 3–5 µm, proliferating sympodially or percurrently with inconspicuous proliferations. *Conidia* filiform, curved or flexuous, rarely straight, (60–)65–75(–90) × 1.5–2(–3) µm, hyaline, guttulate, 4–7(–11)–septate, apex subobtuse, slightly tapering from basal septum to truncate base, 1.5–2 µm.

*Culture characteristics*: Colonies on PDA erumpent, with feathery margin, with sparse white aerial mycelium, surface greenish-black, reverse olivaceous-black, after 14 d, 2.5 cm diam; on MEA with sparse white aerial mycelium, surface cinnamon to olivaceous-black in the younger patches, reverse cinnamon to olivaceous-black in patches, after 14 d, 4 cm diam; on OA with sparse white aerial mycelium, surface greenish-black, reverse fuscous-black, after 14 d, 3 cm diam.

*Specimen examined*: **South Korea**, Incheon, leaf of *Stachys riederi* var. *japonica* (*Lamiaceae*), 14 Aug. 2008, H.D. Shin (CBS H-21278, culture CBS 128668 = KACC 44796 = SMKC 24663).

*Note*: The Korean collection was originally identified as *Septoria stachydicola*, which fits the original description provided for this taxon (Shin & Sameva 2004). However, authentic European material is required for a comparison to confirm this identification, as we suspect *S. stachydicola* may be restricted to Europe.

***Septoria cretae*** Quaedvlieg, Verkley & Crous, **sp. nov.** MycoBank MB804402. Figs 22, 23.

*Etymology*: Named after Crete, the island from where it was collected.

On sterile *Carex* leaves on WA. *Conidiomata* up to 250 µm diam, brown, immersed, subepidermal, pycnidial, subglobose with central

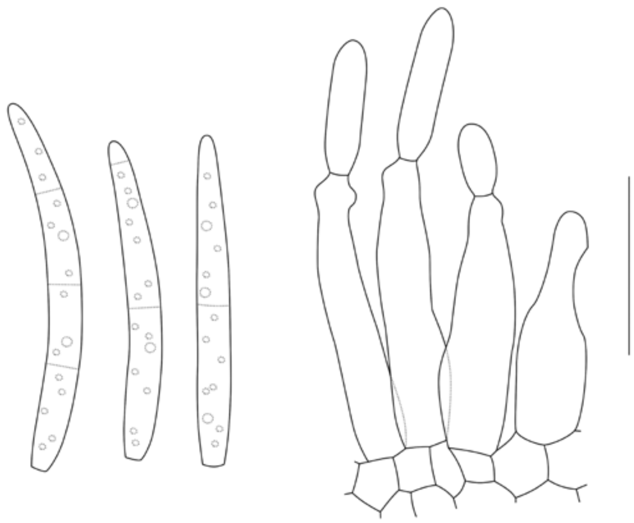

**Fig. 22.** Conidia and conidiogenous cells of *Septoria cretae* (CBS 135095). Scale bar = 10 µm.

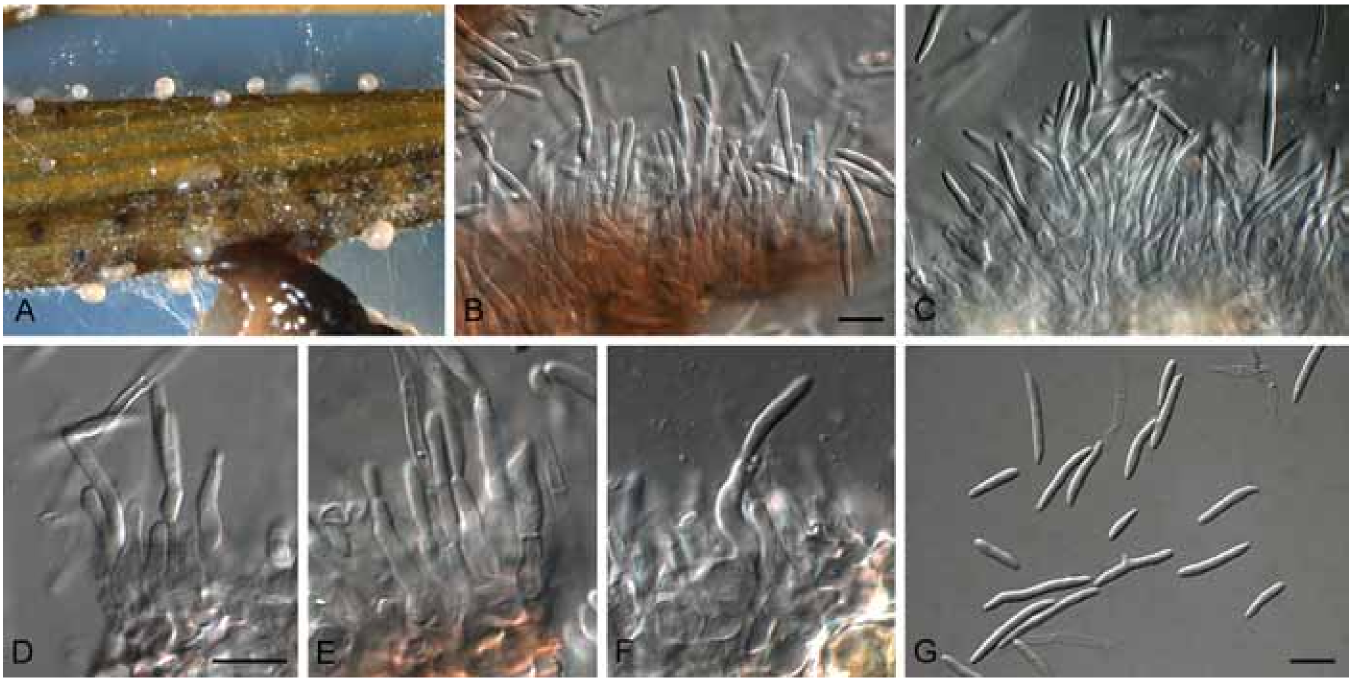


**Fig. 23.** *Septoria cretae* (CBS 135095). A. Colony sporulating in culture. B–F. Conidiophores and conidiogenous cells giving rise to conidia. G. Conidia. Scale bars = 10 µm.

ostiole, exuding creamy conidial mass; wall of 2–3 layers of brown *textura angularis*. *Conidiophores* reduced to conidiogenous cells, or with a supporting cell that gives rise to several conidiogenous cells. *Conidiogenous cells* phialidic, hyaline, smooth, aggregated, lining the inner cavity, ampulliform to subcylindrical, straight to curved, proliferating sympodially near apex, 10–20 × 2–3.5 µm. *Conidia* hyaline, smooth, thin-walled, subcylindrical to narrowly obclavate, granular, with subobtuse apex and obconically truncate to truncate base, 1–3-septate, (8–)15–22(–27) × 2(–3) µm.

*Culture characteristics*: Colonies on PDA erumpent, with feathery margin, lacking aerial mycelium, surface fuscous-black, reverse olivaceous-black, after 14 d, 3.5 cm diam; on MEA surface fuscous-black, reverse olivaceous-black, after 14 d, 4 cm diam; on OA surface fuscous-black, reverse fuscous-black, after 14 d, 3.5 cm diam.

*Specimen examined*: **Greece**, Crete, on leaves of *Nerium oleander* (*Apocynaceae*), 7 Jul. 2012, U. Damm, (**holotype** CBS H-21277, culture ex-type CBS 135095).

*Notes*: Several species of *Septoria* are known on *Nerium oleander*, namely *S. juliae* [conidia 1–6(–7)-septate, 26–54 × 2.5–5.5 µm], *S. neriicola* (conidia 1-septate, 30–40 × 0.7–1 µm), *S. oleandriicola* [conidia 1–3-septate, 12.5–22.5–37.5(–40) × 2.5–3(–4.5) µm], *S. oleandrina* (conidia 0–1-septate, 9–19 × 1–1.5 µm), and *S. roll-hansenii* (conidia 0–4-septate, 25–39 × 3–4 µm) (Bedlan 2011), which differ from *S. cretae* based on conidial dimensions and septation.

***Septoria glycinicola*** Quaedvlieg, H.D. Shin, Verkley & Crous, **sp. nov.** MycoBank MB804403. Fig. 24.

*Etymology*: Named after the host genus on which it was collected, *Glycine*.

On OA. *Conidiomata* forming in concentric circles, pycnidial, separate, black, globose, up to 150 µm diam, opening by a central ostiole, up to 30 µm diam, exuding a creamy conidial mass; wall consisting of 3–6 layers of brown *textura angularis*. *Conidiophores* reduced to conidiogenous cells. *Conidiogenous cells* lining the inner cavity, hyaline, smooth, ampulliform, 10–16 × 2.5–3.5 µm, proliferating sympodially near apex, holoblastic.

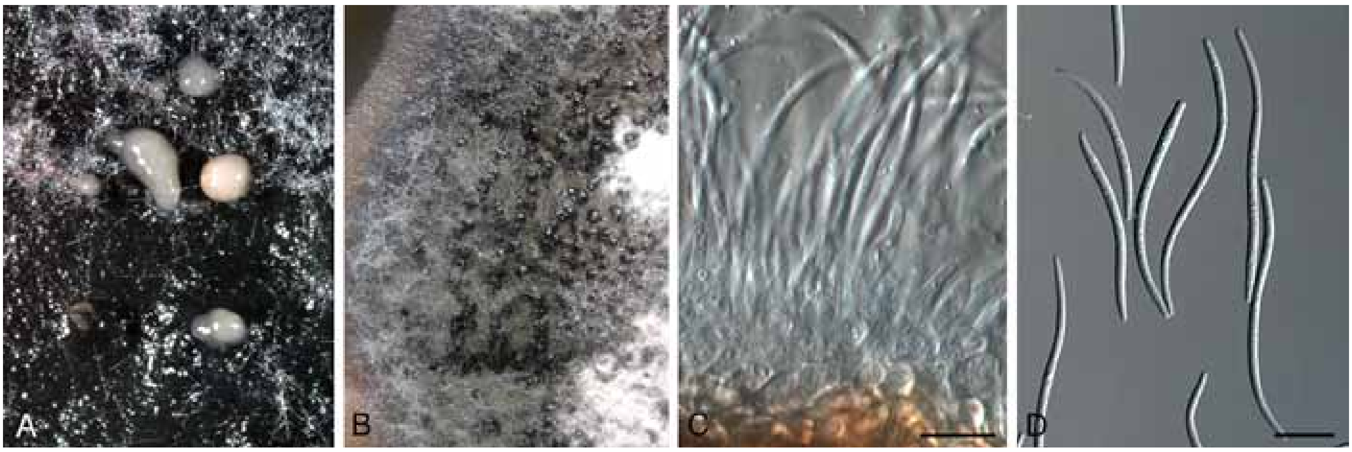


**Fig. 24.** *Septoria glycinicola* (CBS 128618). A, B. Colonies sporulating on PDA. C. Conidiogenous cells. D. Conidia. Scale bars = 10 µm.

*Conidia* hyaline, smooth, guttulate to granular, subcylindrical to narrowly obclavate, irregularly to gently curved, apex subobtuse, base long obconically truncate, 3–6-septate, (33–)45–55(–65) × (1.5–)2 µm.

*Culture characteristics*: Colonies on PDA flat, circular, with sparse black aerial mycelium with black tufts, surface patches of olivaceous-black to fawn in the younger parts, reverse with patches of olivaceous-black in the older parts to mouse-grey and pale purplish grey in the younger mycelium, after 14 d, 6.5 cm diam, pinkish exudate; on OA lobate, with sparse white aerial mycelium, surface patches of vinaceous to olivaceous-black, reverse fuscous-black to vinaceous-buff; after 14 d, 8.5 cm diam, pinkish exudate; on MEA with radial lobes, very short white aerial mycelium, surface fuscous-black, reverse olivaceous-black; after 14 d, 4.5 cm diam.

*Specimen examined*: **South Korea**, Namyangju, on leaves of *Glycine max* (*Fabaceae*), 22 Sep. 2008, H.D. Shin (**holotype** CBS H-21270, culture ex-type CBS 128618 = KACC 43091 = SMKC 22879).

*Notes*: *Septoria glycines* is the common *Septoria* species associated with brown spot of soybeans. *Septoria glycinicola* is distinct from *S. glycines* (conidia 1–4 septate, 21–45 × 1.5–2 µm) in that it has larger conidia.

***Septoria oenanthicola*** Quaedvlieg, H.D. Shin, Verkley & Crous, **sp. nov.** MycoBank MB804405. Fig. 25.

*Etymology*: Named after the host genus from which it was collected, *Oenanthe.*

On sterile *Carex* leaves on WA. *Conidiomata* pycnidial, separate but aggregated, black, globose, up to 200 µm diam, opening by central ostiole, up to 20 µm diam, exuding a creamy conidial mass; wall consisting of dark brown, thickened, 6–10 layers of *textura angularis*. *Conidiophores* reduced to conidiogenous cells or to one supporting cell. *Conidiogenous cells* hyaline, smooth, 3–5 × 3–7 µm, ampulliform, proliferating sympodially near apex, holoblastic. *Conidia* hyaline, smooth, guttulate, subcylindrical to narrowly obclavate, apex subobtuse, base long obconically truncate, 1–6-septate, (17–)25–45(–55) × (2–)2.5(–3) µm.

*Culture characteristics*: Colonies on PDA flat, undulate with sparse, white aerial mycelium, surface olivaceous-grey, reverse olivaceous, after 14 d, 2.5 cm diam; on MEA with sparse, white aerial mycelium, surface olivaceous-grey, reverse olivaceous-black, after 14 d, 5 cm diam; on OA with sparse white aerial mycelium, surface olivaceous-grey, reverse olivaceous, after 14 d, 3 cm diam.

*Specimen examined*: **South Korea**, Yangpyeong, on leaves of *Oenanthe javanica* (*Apiaceae*), 25 May 2006, H.D. Shin (**holotype** CBS H-21281, culture ex-type CBS 128649 = KACC 42394 = SMKC 21807).

*Notes*: This fungus was originally recorded from Korea by Shin (1998) as *Septoria oenanthis*. However, conidia of Korean specimens (30–60 ×1.5–2.5 µm; Shin & Sameva 2004) are much larger than that of the American type collection (20–35 × 1.5–2 µm; Saccardo 1895), and therefore better treated as a separate taxon.

***Septoria pseudonapelli*** Quaedvlieg, H.D. Shin, Verkley & Crous, **sp. nov.** MycoBank MB804404. Fig. 26.

*Etymology*: Named after its morphological similarity to *Septoria napelli*.

*Leaf spots* on the upper leaf surface, scattered to confluent, distinct, angular to irregular, usually vein-limited, small to large, up to 30 mm when confluent, at first appearing small angular brown discoloration, later turning blackish brown with or without distinct border line, finally central area becoming blackish and surrounded by pale greenish margin; on the lower leaf surface similar but discoloured (Shin

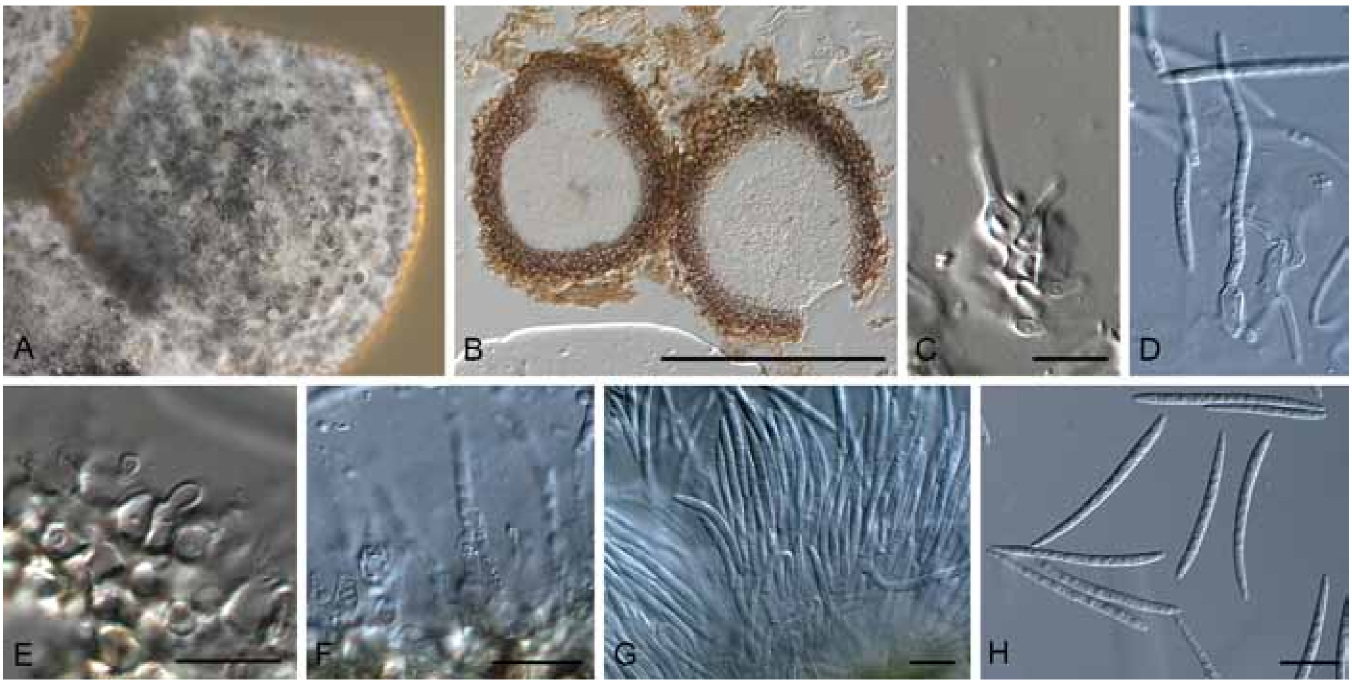


**Fig. 25.** *Septoria oenanthicola* (CBS 128649). A. Colony sporulating on MEA. B. Section through conidiomata. C–G. Conidiogenous cells. H. Conidia. Scale bars: B = 200 µm, all others = 10 µm.

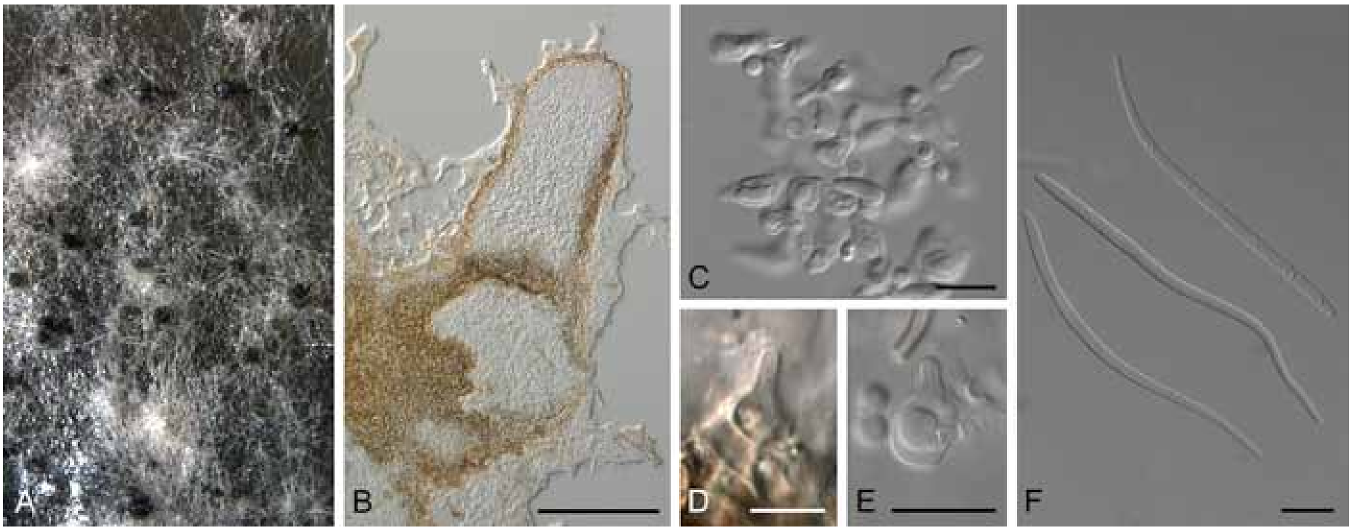


**Fig. 26.** *Septoria pseudonapelli* (CBS 128664). A. Colony sporulating on PDA. B. Section through conidioma. C–E. Conidiogenous cells. F. Conidia. Scale bars: B = 125 µm, all others = 10 µm.

& Sameva 2004). On sterile *Carex* leaves on WA. *Conidiomata* pycnidial, separate, black, globose, papillate with short neck (at times 1–2 necks develop), up to 250 µm wide, 500 µm high with central ostiole; wall of 5–7 layers of brown *textura angularis*. *Conidiophores* reduced to conidiogenous cells. *Conidiogenous cells* ampulliform, lining the inner cavity, hyaline, smooth, with sympodial or apical percurrent proliferation, 10–13 × 5–7 µm. *Conidia* filiform, curved to flexuous, (50–)75–90(–100) × (2.5–)3(–3.5) µm, hyaline, guttulate, 4–10-septate, apex subobtuse, base obconically truncate, 2 µm diam.

*Culture characteristics*: Colonies on PDA flat, undulate with sparse, white aerial mycelium, surface olivaceous-black, reverse olivaceous-black, after 14 d, 2 cm diam; on MEA with sparse white aerial mycelium, surface olivaceous-black, reverse olivaceous-black, after 14 d, 4 cm diam; on OA with sparse white aerial mycelium, surface olivaceous, reverse olivaceous, after 14 d, 2 cm diam.

*Specimen examined*: **South Korea**, Chuncheon, on leaves of *Aconitum pseudolaeve* var. *erectum* (*Ranunculaceae*), 4 Sep. 2008, H.D. Shin (**holotype** CBS H-21280, culture ex-type CBS 128664 = KACC 43952 = SMKC 23638).

*Notes*: This taxon was originally reported as *Septoria napelli* from Korea by Shin & Sameva (2004), and broadly corresponds with the original description provided for this taxon (Petrak 1957). However, we have examined European material authentic for the name (see Verkley *et al*. 2013, this issue), from which the Korean fungus is genetically different. Based on these observations we describe the Korean collection as new.

## Clade 2: *Sphaerulina*

***Sphaerulina*** Sacc., Michelia 1(no. 4): 399. 1878.

*Description*: See above.

*Type species*: *Sphaerulina myriadea* (DC.) Sacc., Michelia 1(no. 4): 399. 1878.

*Specimens examined*: **Germany**, Driesen, Lasch [Rabenhorst, Fungi Eur. no. 149] (L). **Japan**, Aomori, Tsugaru, Kidukuri, Bense-marsh (40°51'53" N, 140°17'42"E), on leaves of *Q. dentata*, 21 Apr. 2007, K. Tanaka 2243 (HHUF 29940; single ascospore culture CBS 124646 = JCM 15565). **UK**, on leaves of *Quercus robur* (*Fagaceae*), J.E. Vize [Microfungi Brit. Ex. No. 195] (ex IMI 57186, K(M) 167735). **USA**, California: Sequoia National Park. alt. 2590 m, on leaves of *Castanopsis sempervirens*, 18 Jun. 1931, H.E. Parks (BPI 623686); Lake Co., Hoberg's Resort, on leaves of *Q. kelloggii*, 15 May 1943, V. Miller (BPI 623707); Maryland, Marlboro, on leaves of *Q. alba*, 26 Apr. 1929, C.L. Shear ( BPI 623705); Texas, Houston, on leaves of *Q. alba*, 8 Apr. 1869, H.W. Ravenel (BPI 623704).

*Notes*: Sivanesan (1984) linked *Sphaerulina* to *Septoria*, *Cercospora* and *Cercosporella* asexual morphs, though these were never confirmed based on DNA data. The latter two genera have since been shown to be distinct (Crous *et al*. 2013, Groenewald *et al*. 2013; this volume), which leaves septoria-like asexual morphs such as *Sphaerulina rubi* Demaree & Wilcox (linked to *Cylindrosporium rubi* Ellis & Morgan), and *S. rehmiana* (linked to *Septoria rosae*), which confirms the results obtained here (Fig. 1).

***Sphaerulina abeliceae*** (Hiray.) Quaedvlieg, Verkley & Crous, **comb. nov.** MycoBank MB804406.
*Basionym*: *Septoria abeliceae* Hiray., Mem. Col. Agr. Kyoto. Imp. Univ. 13(3): 33. 1931.

*Specimen examined*: **South Korea**, Jeonju, on leaves of *Zelkova serrata* (*Ulmaceae*), 29 Oct. 2006, H.D. Shin, CBS 128591 = KACC 42626.

***Sphaerulina amelanchier*** Quaedvlieg, Verkley & Crous, **sp. nov.** MycoBank MB804407. Figs 27, 28.

*Etymology*: Named after the host genus from which it was collected, *Amelanchier*.

On sterile *Carex* leaves on WA. *Conidiomata* pycnidial, brown, separate, immersed, globose, up to 150 µm diam, exuding a creamy conidial mass via central ostiole; wall of 3–6 layers of brown *textura angularis*. *Conidiophores* reduced to conidiogenous cells. *Conidiogenous cells* hyaline, smooth, subcylindrical, irregularly curved, branched to once geniculate-sinuous, 5–20 × 3–4 µm; proliferating sympodially. *Conidia* hyaline, smooth, guttulate, filiform, narrowly obclavate, apex subacutely rounded, base long obconically truncate, 1–8-septate, (25–)40–55(–60) × (1.5–)2(–2.5) µm; microcyclic conidiation common. *Ascomata* globose, brown,

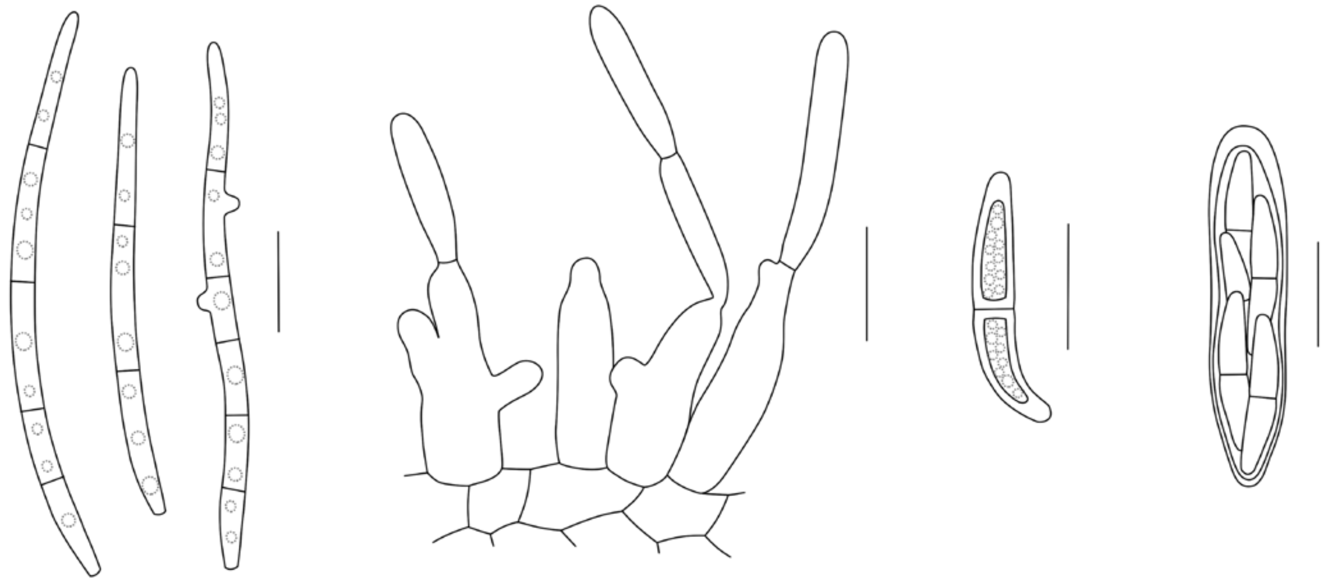

**Fig. 27.** Conidia, conidiogenous cells, ascospore and ascus of *Sphaerulina amelanchier* (CBS 135110). Scale bars = 10 µm.

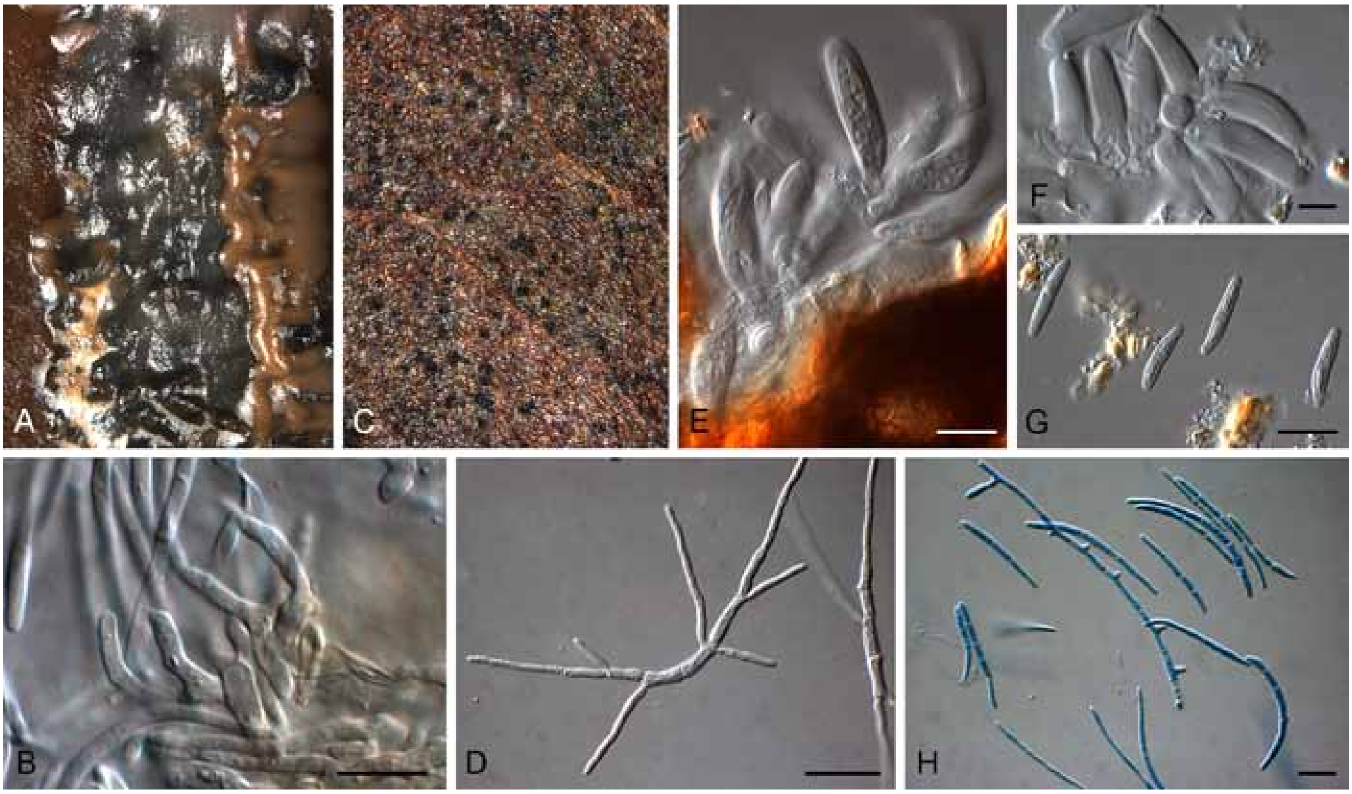


**Fig. 28.** *Sphaerulina amelanchier* (CBS 135110). A. Colony on PDA. B. Conidiogenous cells. C. Ascomata on host tissue. D. Germinating ascospore. E, F. Asci. G. Ascospores. H. Conidia. Scale bars = 10 µm.

separate, immersed to erumpent, up to 150 µm diam. *Asci* broadly ellipsoid to obclavate, 22–35 × 7–9 µm; apical chamber visible, 1–1.5 µm diam. *Ascospores* fusoid-ellipsoid, hyaline, smooth, granular, not to slightly constricted at median septum, widest just above septum, prominently curved, (13–)17–20(–25) × (2.5–)3(–3.5) µm. *Ascospores* germinating from both ends, with germ tubes parallel to the long axis, developing lateral branches and becoming constricted at septum, 3–4 µm diam.

*Culture characteristics*: Colonies on PDA radially striate with lobate edge, sparse white aerial mycelium, surface fuscous-black to buff for the younger tissue, reverse cinnamon to olivaceous-black, after 14 d, 3 cm diam; on MEA surface patches of hazel to fawm to fuscous-black, reverse sepia to olivaceous-black, after 14 d, 4.5 cm diam; on OA surface pale-vinaceous to fuscous-black, reverse cinnamon to fuscous-black, after 14 d, 3 cm diam.

*Specimen examined*: **Netherlands**, Houten, on leaf litter of *Amelanchier* sp. (*Rosaceae*), 28 Mar. 2012, S. Videira (**holotype** CBS H-21282, culture ex-type CBS 135110 = MP8 = S544).

*Note*: Presently there are no known species of septoria-like fungi known from *Amelanchier.* Phylogenetically, it is similar to *Sphaerulina rhabdoclinis* (conidia 8–30 × 1.5–2 µm), which infects needles of *Pseudotsuga menziesii*. Phylogenetically similar isolates occur on *Betula*, *Castanea* and *Quercus*. More isolates and molecular data are required to resolve this complex.

***Sphaerulina azaleae*** (Voglino) Quaedvlieg, Verkley & Crous, **comb. nov.** MycoBank MB804408.
*Basionym*: *Septoria azaleae* Voglino, Syll. Fung. (Abellini) 14(2): 976. 1899.
≡ *Phloeospora azaleae* (Voglino) Priest, Fungi of Australia: 224. 2006.

*Specimens examined*: **Belgium**, on leaves of *Rhododendron* sp. (*Ericaceae*), J. van Holder, CBS 352.49. **South Korea**, Hongcheon, on leaves of *Rhododendron* sp., 18 Oct. 2009, H.D. Shin, KACC 44865 = CBS 128605.

***Sphaerulina berberidis*** (Niessl) Quaedvlieg, Verkley & Crous, **comb. nov.** MycoBank MB804409.
*Basionym*: *Septoria berberidis* Niessl, in Rabenhorst, Bot. Ztg. 24: 411. 1866.
= *Sphaerella berberidis* Auersw., in Gonnermann & Rabenhorst, Mycol. eur. Abbild. Sämmtl. Pilze Eur. 5-6: 3. 1869 (nom. nov. for *Sphaeria berberis* Nitschke ex Fuckel).
≡ *Mycosphaerella berberidis* (Auersw.) Lindau, in Engler & Prantl, Nat. Pflanzenfam., Teil. I (Leipzig) 1(1): 424. 1897.

*Description in vitro* (CBS 116724): *Colonies* on OA 16–20 mm diam after 14 d, with an even, colourless margin; colonies spreading to restricted, somewhat elevated in the centre, the surface covered by a dense mat of pure white, woolly aerial mycelium; reverse in the centre dark brick to brown vinaceous, surrounded by cinnamon tinges; small amounts of a yellow to greenish pigment diffusies into the surrounding medium. *Colonies* on MEA 8–10 mm diam after 14 d, with an even to slighlty ruffled vinaceous buff margin; colonies restricted, pustulate, the surface ochraceous or darker, with diffuse to locally more dense finely felted grey aerial mycelium; reverse brown vinaceous to vinaceous buff. Culture remained sterile.

*Specimen examined*: **Switzerland**, Kt. Graubünden, Rodels-Realta, on *Berberis vulgaris* (*Berberidaceae*), 2 Jun. 1951, E. Müller, specimen CBS-H4984, culture CBS 324.52.

***Sphaerulina betulae*** (Pass.) Quaedvlieg, Verkley & Crous, **comb. nov.** MycoBank MB804410.
*Basionym*: *Septoria betulae* Pass., Primo Elenc. Funghi Parm.: no. 52. 1867.

*Specimens examined*: **Netherlands**, Olst, leaves of *Betula pubescens* (*Betulaceae*), Sep. 2004, S. Green, CBS 116724. **South Korea**, Hongcheon, leaves of *B. platyphylla* var. *japonica*, 27 May 2008, H.D. Shin, CBS 128600 = KACC 43769.

***Sphaerulina cercidis*** (Fr.) Quaedvlieg, Verkley & Crous, **comb. nov.** MycoBank MB804411.
*Basionym*: *Septoria cercidis* Fr., in Léveillé, Ann. Sci. Nat., Bot., Sér. 3 9: 251. 1848.
= *Septoria provencialis* Crous, Stud. Mycol. 55: 127. 2006.

*Specimens examined*: **Argentina**, La Plata, on *Cercis siliquastrum* (*Caesalpiniaceae*), 12 Feb. 2008, H.D. Shin, KACC 43596 = CBS 129151; on *C. siliquastrum*, 1 Sep. 2007, H.D. Shin, KACC 44497 = CBS 128634. **France**, Provence, Cheval Blanc camping site, on leaves of *Eucalyptus* sp., 29 Jul. 2005, P.W. Crous, **holotype** of *S. provincialis*, CBS H-19701, culture ex-type CBS 118910. **Netherlands**, on *C. siliquastrum*, Sep. 1950, G. van den Ende, CBS 501.50.

***Sphaerulina menispermi*** (Thüm.) Quaedvlieg, Verkley & Crous, **comb. nov.** MycoBank MB804412.
*Basionym*: *Septoria menispermi* Thüm., Pilzflora Siber.: no. 818. 1880.

*Specimens examined*: **South Korea**, Chuncheon, on leaves of *Menispermum dauricum* (*Menispermaceae*), 16 Jun. 2008, H.D. Shin, KACC 43848 = CBS 128761; Pyeongchang, on leaves of *M. dauricum*, 23 Sep. 2008, H.D. Shin, KACC 43968 = CBS 128666.

***Sphaerulina musiva*** (Peck) Quaedvlieg, Verkley & Crous, **comb. nov.** MycoBank MB804413.
*Basionym*: *Septoria musiva* Peck, Ann. Rep. N.Y. St. Mus. Nat. Hist. 35: 138. 1883 [1881]
= *Mycosphaerella populorum* G.E. Thomps., Phytopathology 31: 246. 1941.
≡ *Davidiella populorum* (G.E. Thomps.) Aptroot, CBS Diversity Ser. (Utrecht) 5: 164. 2006.
= *Cylindrosporium oculatum* Ellis & Everh., J. Mycol. 5(3): 155. 1889.

*Specimen examined*: **Canada**, Quebec, leaf spot of *Populus deltoids* (*Salicaceae*), J. LeBoldus, CBS 130570.

***Sphaerulina oxyacanthae*** (Kunze & J.C. Schmidt) Quaedvlieg, Verkley & Crous, **comb. nov.** MycoBank MB804414. Figs 29, 30.
*Basionym*: *Septoria oxyacanthae* Kunze & J.C. Schmidt, Myk. Hefte (Leipzig) 2: 108. 1823.
≡ *Phloeospora oxyacanthae* (Kunze & J.C. Schmidt) Wallr., Fl. Crypt. Germ. (Norimbergae) 2: 117. 1833.

*Leaf spots* amphigenous, medium to dark brown, subcircular to angular, 1–6 mm diam, with dark brown border. *Conidiomata* epiphyllous, up to 150 µm diam, brown, immersed, subepidermal, opening by irregular rupture of upper layer, with 3–4 apical flaps, exuding a long crystalline flame-like cirrhus of conidia; wall 3–8 layers of brown *textura angularis*. On sterile *Carex* leaves on WA. *Conidiophores* reduced to conidiogenous cells, or with one supporting cell that can become fertile, forming a lateral conidiogenous locus just below the septum, 10–20 × 2.5–4 µm. *Conidiogenous cells* hyaline, smooth, aggregated, lining the inner cavity, terminal and lateral, ampulliform, 5–10 × 2.5–3.5 µm; proliferating several times percurrently near apex. *Conidia* hyaline, smooth, guttulate, 6–12-septate, falcate, widest in lower third of conidium, flexuous, apical cell tapering to subacute apex, forming a curved apical appendage-like elongation, 10–17 µm long, median cells are 5–10 µm long, basal cell forming an eccentric appendage that tapers to a subacutely rounded base, scar approximately 2–4

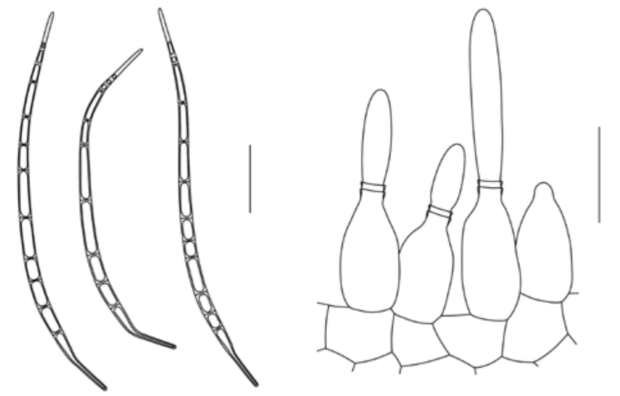

**Fig. 29.** Conidia and conidiogenous cells of *Sphaerulina oxyacanthae* (CBS 135098). Scale bars = 10 µm.


**Fig. 30.** *Sphaerulina oxyacanthae* (CBS 135098). A. Leaves with leaf spots. B. Close-up of conidiomata. C. Section though conidioma. D–F. Conidiogenous cells. G. Conidia (note appendages). Scale bars: C = 150 µm, all others = 10 µm.

µm below basal septum; basal cell (incl. appendage) 11–20 µm long, conidia (60–)75–90(–100) × 2(–2.5) µm.

*Culture characteristics*: Colonies on PDA umbonate with undulate edge and sparse, white aerial mycelium, surface isabelline, reverse greyish sepia, after 14 d, 3 cm diam; similar on MEA and PDA.

*Specimen examined*: **Netherlands**, Wageningen, 51°57'50.43"N 5°41'0.41"E, on leaves of *Crataegus* sp. (*Rosaceae*), Sep. 2012, W. Quaedvlieg (CBS H-21291, culture CBS 135098 = S654).

*Notes*: Several septoria-like species have been described from leaves of *Crataegus* (Farr & Rossman 2013). The present collection matches the description of *Septoria oxyacanthae* (leaf spots on *Crataegus oxyacantha* in Germany, conidia 8–12-septate; conidial dimensions not given). Unfortunately we have been unable to locate type material of this species.

***Sphaerulina patriniae*** (Miura) Quaedvlieg, Verkley & Crous, **comb. nov.** MycoBank MB804415.
*Basionym*: *Septoria patriniae* Miura, Flora of Manchuria and East Mongolia, III Cryptogams, Fungi (Industr. Contr. S. Manch. Rly 27) 3: 465. 1928.

*Specimen examined*: **South Korea**, Pocheon, on leaves of *Patrinia scabiosaefolia* (*Valerianaceae*), 20 Aug. 2006, H.D. Shin, KACC 42518 = CBS 128653.

***Sphaerulina populicola*** (Peck) Quaedvlieg, Verkley & Crous, **comb. nov.** MycoBank MB804416.
*Basionym*: *Septoria populicola* Peck, Ann. Rep. N.Y. St. Mus. 40: 59. 1887.

= *Septoria populicola* House, Bull. N.Y. St. Mus.: 59. 1920. (nom. illegit.)
= *Mycosphaerella populicola* C.H. Thomps., Phytopathology 31: 251. 1941.

*Specimen examined*: **USA**, Washington, Puyallup, on *Populus trichocarpa* (*Salicaceae*), 2 May 1997, G. Newcombe, CBS 100042.

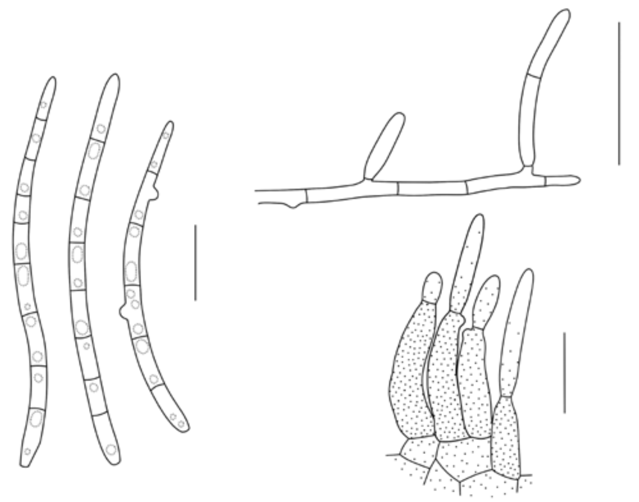

**Fig. 31.** Conidia, conidiogenous loci on a hypha, and conidiogenous cells of *Sphaerulina pseudovirgaureae* (CBS 135109). Scale bars = 10 µm.

***Sphaerulina pseudovirgaureae*** Quaedvlieg, Verkley & Crous, **sp. nov.** MycoBank MB804417. Figs 31, 32.

*Etymology*: Named after its similarity to *Septoria virgaureae*.

Conidiomata pycnidial, separate, erumpent, globose, up to 120 µm diam, dark brown, exusing a creamy conidial cirrhus through central ostiole, somewhat papillate; wall of 2–3 laters of brown textura angularis. Conidiophores reduced to conidiogenous cells or with one supporting cell, subcylindrical, 0–1-septate, branched below or not, pale brown at base, 10–20 × 3–5 µm. Conidiogenous cells integrated, hyaline, but pale brown at base, smooth, proliferating sympodially near apex, 7–17 × 2–3 µm. Conidia solitary, hyaline, smooth, guttulate, subcylindrical to narrowly obclavate, scolecosporous, irregularly curved, apex subobtuse, base truncate or narrowly obconically truncate, 3–10-septate, (30–)40–60(–80) × 2.5(–3) µm.

*Culture characteristics*: Colonies spreading, erumpent with sparse aerial mycelium and smooth, lobate margin and folded surface; reaching 13 mm diam after 2 wk. On MEA surface saffron with

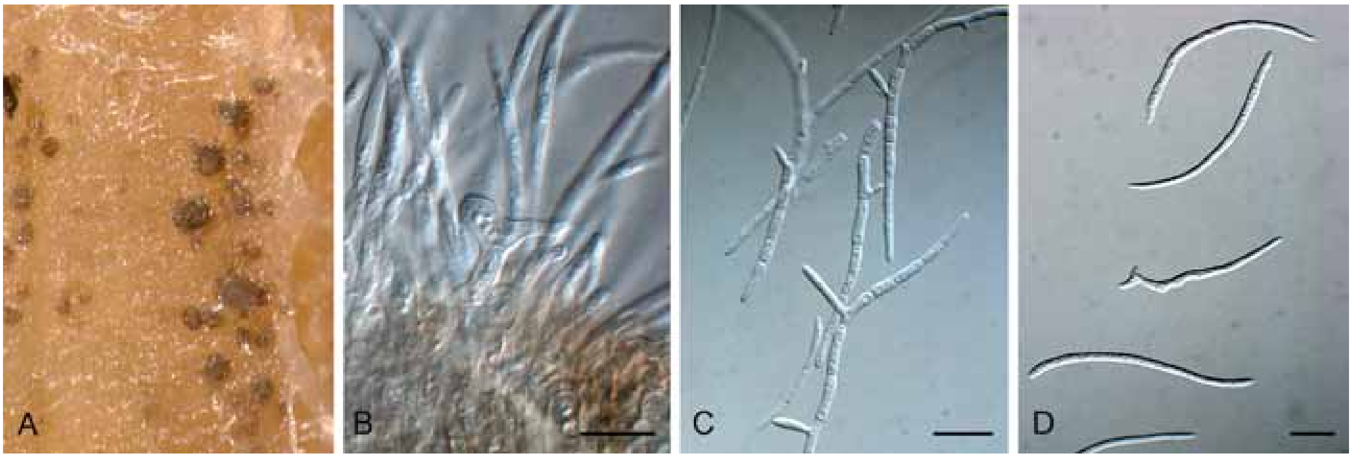


**Fig. 32.** *Sphaerulina pseudovirgaureae* (CBS 135109). A. Conidiomata forming in culture. B. Conidiogenous cells. C. Microcyclic conidiation. D. Conidia. Scale bars = 10 µm.

patches of dirty white, reverse saffron to orange; on PDA surface and reverse saffron; on OA surface saffron.

*Specimen examined*: **Netherlands**, Nijmegen, de Duffelt, on leaves of *Solidago gigantea* (*Asteraceae*), Aug. 2012, S. Videira (**holotype** CBS H-21327, culture ex-type CBS 135109 = S669).

*Notes*: Several septoria-like species have been recorded on *Solidago* (Farr & Rossman 2013). Of these taxa *Sphaerulina pseudovirgaureae* is most similar to *Septoria virguareae* (conidia 80–100 × 1.5 µm) except that its conidia are shorter and wider.

***Sphaerulina quercicola*** (Desm.) Quaedvlieg, Verkley & Crous, **comb. nov.** MycoBank MB804419. Figs 33, 34.

*Basionym*: *Septoria incondita* var. *quercicola* Desm., Ann. Sci. nat., Sér. 3, Bot. 20: 95. 1853.

≡ *Septoria quercicola* (Desm.) Sacc., Michelia 1: 174. 1879.

≡ *Phleospora quercicola* (Desm.) Sacc., in P. A. Saccardo & D. Saccardo, 1906. Syll. Fung. 18: 490. 1906.

= *Septoria quercina* Fautr., in Fautrey & Lambotte, Revue Mycol. 17: 170. 1895 (nom. illeg., art. 53; non Desmazières, 1847). Nom. nov. pro *Septoria quercicola* f. *macrospora* Roum., Revue Mycol. 13: 80. 1891.

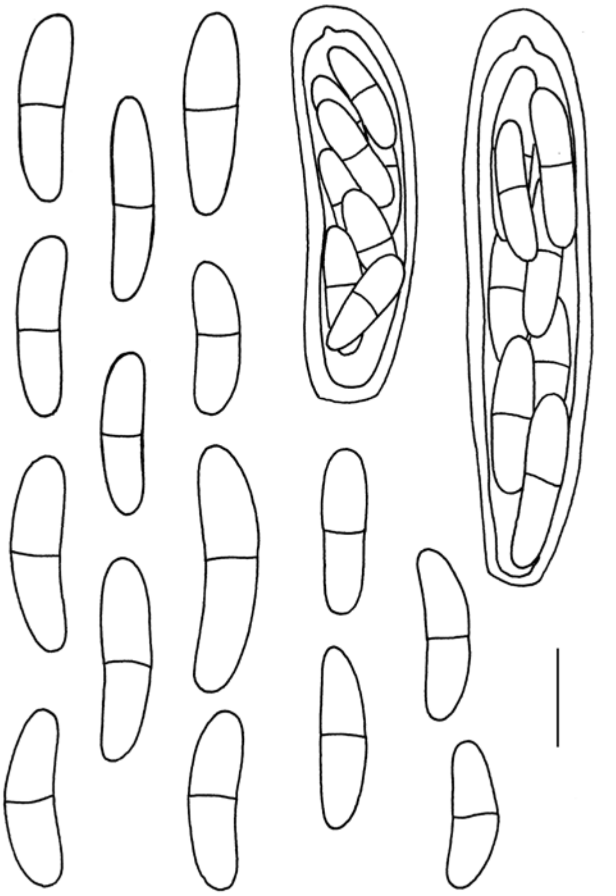

**Fig. 33.** Ascospores and asci of *Sphaerulina quercicola* (CBS 113266). Scale bar = 10 µm.

Description *in vivo*. *Symptoms* definite, small hologenous leaf spots, scattered or in clusters, in the centre orange brown, pale yellowish brown to white, usually delimited by a blackened, somewhat elevated zone, the surrounding leaf tissues becoming red or yellow. *Conidiomata* pycnidial or acervuloid, one to a few in each leafspot, scattered, semi-immersed, predominantly hypophyllous, pale to dark brown, lenticular to globose, 100–200 µm diam; *ostiolum* often not well-developed, initially circular, central, soon opening widely, lacking distinctly differentiated cells; *conidiomatal wall* composed of *textura angularis* without distinctly differentiated layers and sometimes only well-developed in the lower part of the conidioma, mostly 10–15 µm thick, the outer cells with brown, somewhat thickened walls and 4.5–8 µm diam, the inner cells hyaline, thin-walled, 3–8 µm diam. *Conidiogenous cells* hyaline, discrete or integrated in simple, short, (1–)3–5-septate conidiophores which may be branched at the base, doliiform, cylindrical, or ampuliform, hyaline, holoblastic, proliferating percurrently with one to several, more or less distinct annellations, or sympodially, sometimes both types of proliferation occurring in a single conidiogenous cell, 4.5–16(–22.5) × 3–4.5 µm. *Conidia* cylindrical, curved or flexuous, broadly rounded at the apex which is provided with a cap of mucilaginous material, attenuated gradually to a broadly or more narrowly truncate base which often is also provided with an amorphous mass of mucilaginous material, hyaline, (0–)1–3-septate, constricted around the septa, sometimes at one or more septa also some amorphous mucilaginous material may be present, contents with numerous small oil droplets, (32.5–)38–50(–65) × 3–4 µm. *Ascomata* not clearly associated with leaf spots, pseudothecial, predominantly hypophyllous, black, subepidermal, erumpent to superficial, globose, 100–150 µm diam; apical ostiole 5–10 µm wide; wall consisting of 2–3 layers of medium brown *textura angularis*. *Asci* aparaphysate, fasciculate, bitunicate, subsessile, broadly ellipsoidal to subcylindrical, straight to slightly curved, 8-spored, 35–50 × 9–12 µm. *Ascospores* tri- to


**Fig. 34.** *Sphaerulina quercicola* (CBS 663.94). A. Leaves with leaf spots. B. Close-up of lesion. C. Conidiogenous cells. D. Conidia. Scale bars = 10 µm.


**Fig. 35.** *Sphaerulina rhabdoclinis* (CBS 102195). A. Conidiomata forming in culture. B. Sporulation on PDA. C. Conidia. Scale bar = 10 µm.

multiseriate, overlapping, hyaline, guttulate, thin-walled, curved, rarely straight, fusoid-ellipsoidal with obtuse ends, widest at septum or just above, medianly 1-septate, not constricted at the septum, tapering towards both ends, (13–)15–18(–20) × (3.5–)4–4.5(–5) µm (av. 17 × 4.5 µm).

*Culture characteristics*: Colonies on OA reaching 5–7 mm diam in 21 d, with an even to undulating, colourless margin; colonies restricted, irregularly pustulate, immersed mycelium appearing dark greyish to olivaceous black, rosy buff near the margin, covered mostly with a dense mat of woolly, pure white or greyish aerial mycelium; reverse in the centre brown vinaceous or more greyish black, surrounded by brick to rosy buff. Pycnidia developing on the agar surface in the centre, releasing droplets of rosy-buff conidial slime. *Colonies* on MEA reaching 4–6(–8) mm diam in 21 d, with an even, to irregularly undulating margin which is mostly hidden under the aerial mycelium; colonies restricted, irregularly pustulate, the surface mostly blackish or very dark grey, covered by dense to diffuse, finely felted, white aerial mycelium; reverse mostly olivaceous black, near the margin cinnamon to buff. Numerous single and aggregated pycnidia developing on the colony surface in the centre, releasing milky white to rosy buff conidial slime. *Conidia* as *in planta* (CBS 663.94) though on average considerably longer, 51.5–74.5 × 3–4(–4.5) µm (OA), the apex, base and area around septa normally both provided with mucilaginous material as described above, (0–)1–3(–5)-septate.

*Specimens examined*: **Austria**, endophyte culture ex twig of *Quercus petraea* (*Fagaceae*), Aug. 1991, E. Halmschlager 212 (H. A. van der Aa 10986), CBS 456.91. **France**, loc. unknown, on leaves of *Quercus* sp. (“divers Chênes”), distributed in Desmazières, Pl. crypt. Fr., Fasc. 43, no. 2193 (PC, type of *Septoria incondita* var. *quercicola* Desm.). **Netherlands**, Utrecht, Baarn, on living leaves of *Q. robur*, 11 Aug. 1994, G. Verkley 225 (CBS H-21188), living culture CBS 663.94; prov. Utrecht, Soest, De Stompert, on living leaves of *Q. rubra*, 15 Aug. 1995, G. Verkley 310 (CBS H-21189), CBS 791.95; Same loc., dead fallen leaves of *Q. robur*, Apr. 2003, G. Verkley *s.n.*, single ascospore-isolate CBS 113266 (‘Crous 3’); Same loc., G. Verkley & I. van Kempen, endophyte isolates ex green leaves of *Q. robur* CBS 115016, 115136, 115137; Prov. Gelderland, Amerongen, Park Kasteel Amerongen, leaf spot of *Q. rubra*, 11 Jul. 2000, G. Verkley 973 (CBS H-21231), living culture CBS 109009; Prov. Utrecht, Amelisweerd, on dead leaves of *Q. robur*, 25 Apr. 2005, G. Verkley 3108A, culture CBS 117803, CPC 12097.

***Sphaerulina rhabdoclinis*** (Butin) Quaedvlieg, Verkley & Crous, **comb. nov.** MycoBank MB804420. Fig. 35.
*Basionym*: *Dothistroma rhabdoclinis* Butin, For. Path. 30: 196. 2000.

*Specimen examined*: **Germany**, Wolfenbüttel, on needles of *Pseudotsuga menziesii* (*Pinaceae*), 24 May 1998, H. Butin, culture ex-type CBS 102195.

*Note*: *Sphaerulina rhabdoclinis* is phylogenetically closely related to *S. amelanchier*, which appears to be a species complex occurring on unrelated hosts (see Verkley *et al*. 2013).

***Sphaerulina viciae*** Quaedvlieg, H.D. Shin, Verkley & Crous, **sp. nov.** MycoBank MB804418. Figs 36, 37.

*Etymology*: Named after the host genus from which it was collected, *Vicia*.

On *Anthriscus* stem. Conidiomata pycnidial, solitary, erumpent, brown, globose, up to 150 µm diam, with central ostiole; wall of 3–6 layers of textura angularis. Conidiophores reduced to conidiogenous cells. Conidiogenous cells lining the inner cavity, hyaline, smooth, subcylindrical, tapering and proliferating sympodially at apex, 5–10 × 3–4 µm. Conidia hyaline, smooth, guttulate, subcylindrical, irregularly curved, apex obtuse, base truncate, (3–)6–multiseptate, not or slightly constricted at septa (especially constricted on SNA, OA and MEA), (45–)55–75(–110) × (2.5–)3(–3.5) µm.

*Culture characteristics*: Colonies erumpent, spreading with folded surface and sparse aerial mycelium, and smooth, lobate margin; reaching 12 mm diam after 2 wk. On MEA and PDA surface and reverse olivaceous-grey. On OA surface pale olivaceous-grey.

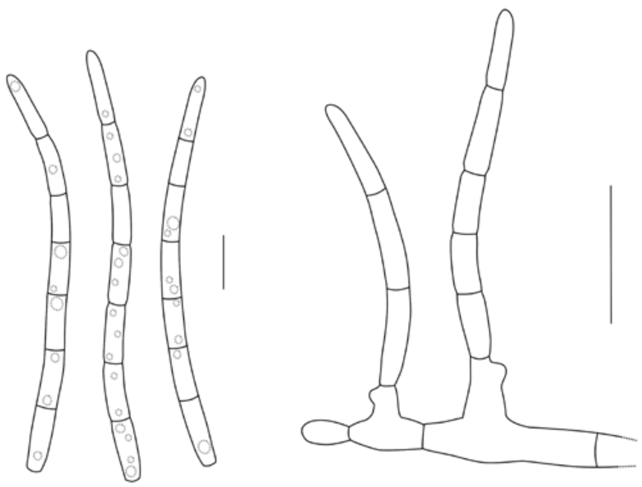

**Fig. 36.** Conidia and conidiogenous cells of *Sphaerulina viciae* (CBS 131898). Scale bars = 10 µm.

*Specimen examined*: **South Korea**, on leaves of *Vicia amurense* (*Fabaceae*), 12 Aug. 2004, H.D. Shin (**holotype** CBS H-21283, culture ex-type CPC 11414, 11416, 11415 = CBS 131898).

*Notes*: Several septoria-like species are known from *Vicia* (Farr & Rossman 2013). Of these, *Sphaerulina viciae* is most similar to *Septoria viceae* (conidia 30–60 × 2.5 µm), but distinct in having longer and wider conidia.

## Clade 3: *Caryophylloseptoria*

*Description*: See Verkley *et al.* (2013)

*Type species*: *Caryophylloseptoria lychnidis* (Desm.) Verkley, Quaedvlieg & Crous.

***Caryophylloseptoria pseudolychnidis*** Quaedvlieg, H.D. Shin, Verkley & Crous, **sp. nov.** MycoBank MB804481. Fig. 38.

*Etymology*: Named after its morphological similarity to *Septoria lychnidis*.

*Leaf spots* on the upper leaf surface, scattered to confluent, distinct, circular, angular to irregular, usually very large, reaching up to 20 mm diam, often surrounded with yellow halo, lacking concentric rings, initially dark brown with pale green border, becoming brown to dark brown, finally turning greyish brown to pallid in the centre; on the lower leaf surface greyish brown to brown with yellowish margin (Shin & Sameva 2004). On sterile *Carex* leaves on WA. *Conidiomata* pycnidial, globose, up to 250 µm diam, black with central ostiole, but frequently splitting open at maturity, appearing acervular; wall of 6–8 layers of dark brown *textura angularis*. *Conidiophores* subcylindrical, lining the inner cavity, hyaline, smooth, reduced to conidiogenous cells, or with 1–2 supporting cells, frequently branched at base, 10–25 × 3–5 µm. *Conidiogenous cells* subcylindrical to ampulliform, 7–15 × 3–5 µm; proliferating sympodially or percurrently near apex. *Conidia*

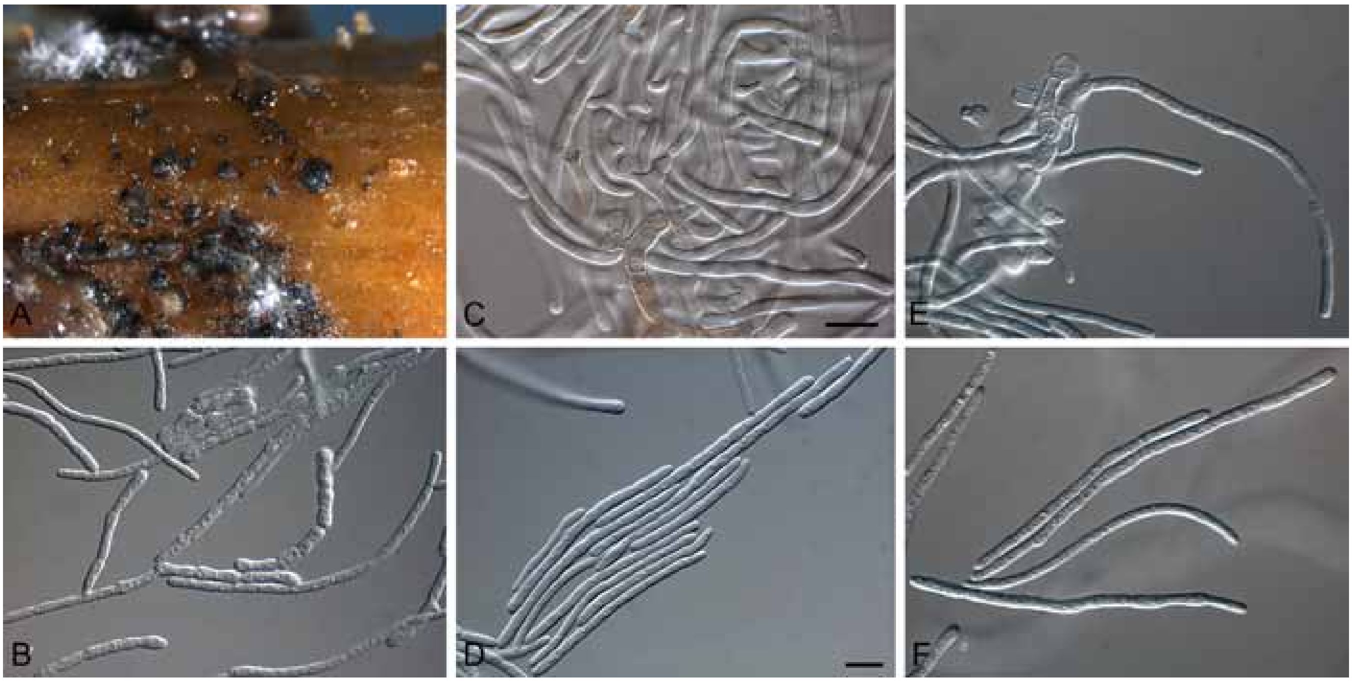


**Fig. 37.** *Sphaerulina viciae* (CBS 131898). A. Conidiomata forming in culture. B, C, E. Conidiogenous cells. D, F. Conidia. Scale bars = 10 µm.

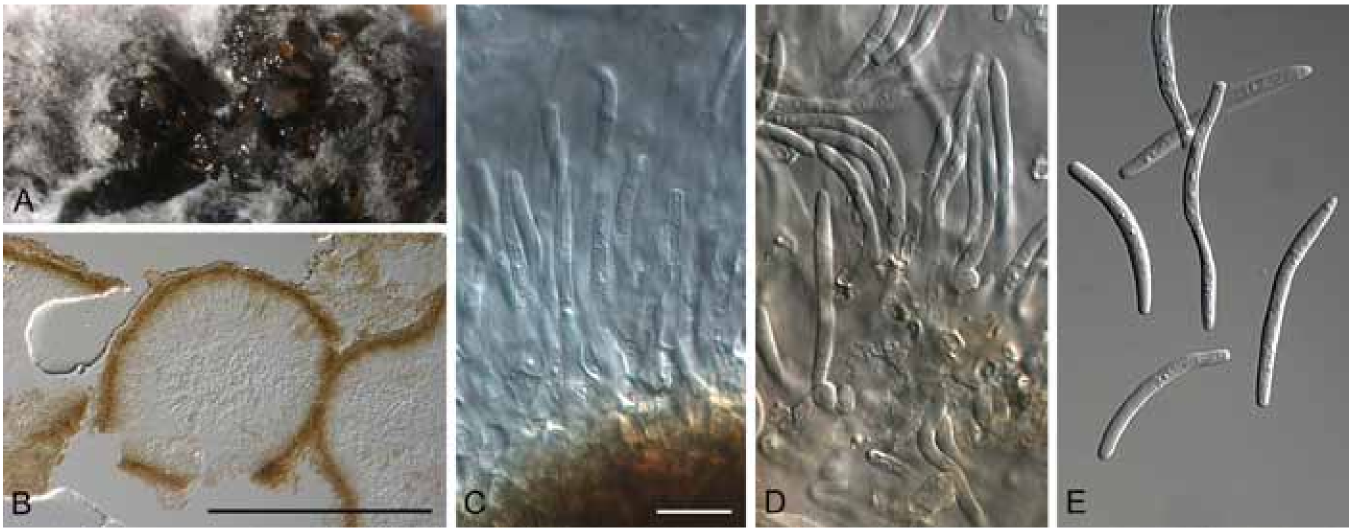


**Fig. 38.** *Caryophylloseptoria pseudolychnidis* (CBS 128630). A. Colony sporulating on MEA. B. Vertical section through conidiomata. C, D. Conidiogenous cells. E. Conidia. Scale bar: B = 250 µm, others = 10 µm.

hyaline, smooth, guttulate, cylindrical, apex obtuse to subobtuse, base truncate, 3–3.5 µm; 1–3(–5)-septate, (25–)32–45(–50) × (2–)2.5–3(–3.5) µm.

*Culture characteristics*: Colonies on PDA flat, undulate, very sparse, mixed grey and white aerial mycelium, surface isabelline to fuscous-black, reverse olivaceous-black to isabelline for the younger tissue, after 14 d, 3 cm diam; on MEA umbonate, striate, undulate, surface fuscous-black to honey for the younger tissue after 14 d 3.5 cm diam; on OA surface dark-mouse-grey, reverse iron-grey to mouse-grey.

*Specimen examined*: **South Korea**, Yangpyeong, Jungmi mountain, on leaves of *Lychnis cognata* (*Caryophyllaceae*), 27 May 2007, H.D. Shin (**holotype** CBS H-21292, culture ex-type CBS 128630 = KACC 43866 = SMKC 23519).

*Notes*: Shin (1995) recorded this species for the first time in Korea, while Shin & Sameva (1999) provided a full morphologial description. Although it compared well with the original description of this European taxon, its conidia tend to be smaller than those of *S. lychnidis* (50–70 × 2.5–3 µm), of which we have also examined European material (see Verkley *et al*. 2013, this issue).

## Clade 4: pseudocercosporella-like

*Note*: See Frank *et al.* (2010).

## Clade 5: *Cercospora*

*Note*: See Groenewald *et al.* (2013).

## Clade 6: *Phloeospora*

*Description*: See above.

*Type species*: *P. ulmi* (Fr.) Wallr., Fl. Crypt. Germ. (Norimbergae) 2: 177. 1833.

***Phloeospora ulmi*** (Fr.) Wallr., Fl. Crypt. Germ. (Norimbergae) 2: 177. 1833. Figs 39, 40.

≡ *Septoria ulmi* Fr. [as '*Septaria*'], Novit. Fl. Svec. 5(cont.): 78. 1819.

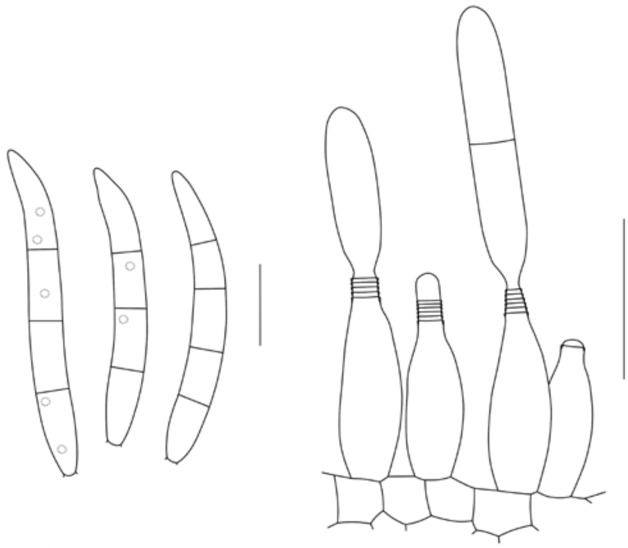

**Fig. 39.** Conidia and conidiogenous cells of *Phloeospora ulmi* (CBS 613.81). Scale bars = 10 µm.

≡ *Septogloeum ulmi* (Fr. & Kunze) Died., Krypt. Fl. Brandenburg (Leipzig) 9: 836. 1915.
≡ *Cylindrosporium ulmi* (Fr.) Vassiljevsky, Fungi Imperfecti Parasitici 2: 580. 1950.
= *Mycosphaerella ulmi* Kleb., Z. PflKrankh. 12: 257. 1902.
= *Sphaerella ulmi* (Kleb.) Sacc. & D. Sacc., Syll. Fung. (Abellini) 17: 642. 1905.

*Leaf spots* angular, vein limited, separate, becoming somewhat confluent, initially small yellow-green spots that finally turn brown. *Conidiomata* acervular, hypophyllous, separate, subepidermal, composed of thin-walled, medium brown *textura angularis*, up to 200 µm diam, opening by irregular rupture, and exuding a prominent cirrhus of orange to yellow-orange conidia. *Conidiophores* reduced to conidiogenous cells, or with 1–2 supporting cells, branched below or not, subcylindrical, 10–30 × 4–5 µm. *Conidiogenous cells* hyaline, smooth, subcylindrical, straight to once geniculate, with numerous prominent percurrent proliferations at apex, 10–15 × 4–5 µm. *Conidia* solitary, hyaline, smooth, straight to curved, guttulate or not, fusiform, tapering towards an obtuse or subobtuse apex, and truncate base, 2–3 µm diam, with minute marginal frill,

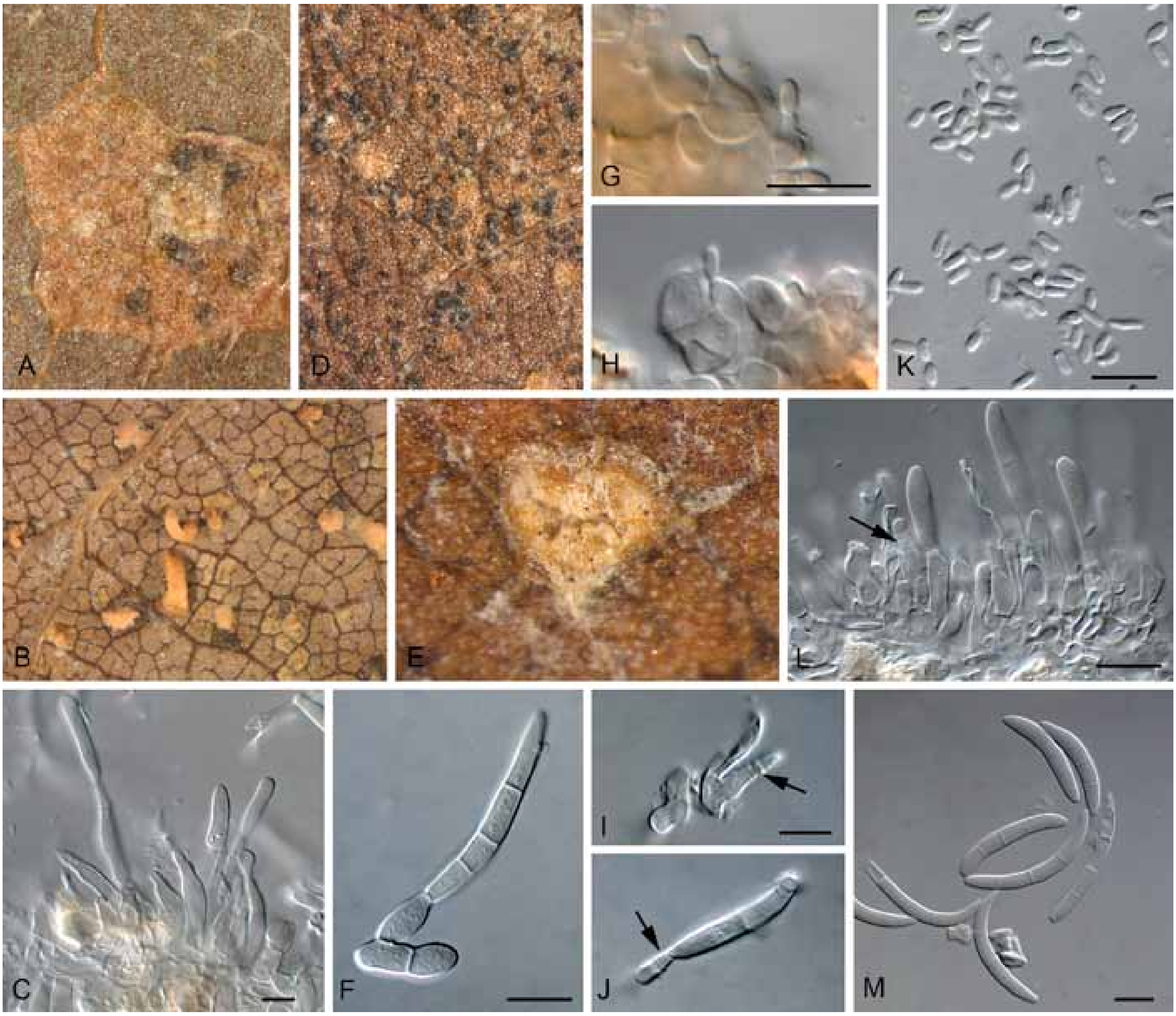


**Fig. 40.** *Phloeospora ulmi* (CBS 613.81). A, B, D, E. Conidiomata bursting through host tissue. G, H. Microconidiogenous cells. K. Spermatia. C, F, I, J, L. Macroconidiogenous cells (arrows denote percurrent proliferation). M. Conidia. Scale bars = 10 µm.

3–5-septate, (20–)30–50(–60) × (3.5–)4–5(–6) µm. Leaf spots also contain black spermatogonia and ascomata.

*Specimens examined*: **Austria**, Innsbruck, near Hungerburg, on leaves of *Ulmus* sp. (*Ulmaceae*), 21 Sep. 1981, H.A. van der Aa, CBS H-14740, H-14861, culture CBS 613.81; Innsbruck, road to Hungerburg, on leaves of *Ulmus glabra*, 20 Oct. 1996, W. Gams, CBS 344.97. **Netherlands**, Baarn, garden of CBS, Oosterstraat 1, on leaves of *Ulmus* sp., 26 Aug. 1998, H.A. van der Aa, CBS H-14739, culture CBS 101564. **Unknown**, on leaves of *Ulmus pedunculata*, 15 Jul. 1901, A. van Luijk, CBS H-920.

*Note*: Distinct from *Septoria s. str.* by having acervuli, and conidiogenous cells with prominent percurrent proliferation.

## Clade 7: septoria-like

***Septoria gladioli*** Pass., in Rabenhorst, Fungi europ. exsicc.: no. 1956. 1875. Passerini, Atti Soc. crittog. ital. 2: 41. 1879.

*Descripton in vitro* (18 ºC, NUV). *CBS 121.20*: *Colonies* on OA 15–18 mm diam after 21 d, with an even to slightly ruffled, colourless margin; colonies plane, immersed mycelium olivaceous black, fading over amber towards the margin, aerial mycelium absent; reverse concolorous. No sporulation observed. *Colonies* on MEA 10–15 mm diam after 21 d, with an even, pale luteous to amber margin; colonies restricted, irregularly pustulate to cerebriform, immersed mycelium ochreous to salmon, covered by diffuse, finely felted, white aerial mycelium; reverse in the centre rust, fading towards the margin over apricot to pale luteous. No sporulation observed. *CBS 353.29*: *Colonies* on OA 16–20 mm diam after 21 d, with an even to slightly ruffled, colourless margin; colonies plane, immersed mycelium rosy buff mixed with some olivaceous grey, aerial mycelium absent; reverse mainly pale purplish grey to pale mouse grey. No sporulation observed. *Colonies* on MEA 14–22(–26) mm diam after 21 d, with an even to lobed, buff margin; colonies restricted, elevated towards the centre, radially striate, immersed mycelium greenish olivaceous fading to ochreous or buff salmon, the central part mostly covered by diffuse, finely felted, white aerial mycelium; reverse in the centre dark brick to isabelline or hazel, fading towards the margin over pale cinnamon to buff. No sporulation observed.

*Specimen examined*: **Netherlands**, Mar. 1929, J.C. Went, CBS 353.29. Unknown location and host, 1920, W.J. Kaiser, CBS 121.20.

*Notes*: Priest (2006) provided a complete description of *S. gladioli* on host material, based on observations of an isotype in MEL, and several specimens on *Gladiolus* cultivars collected in Australia. The two strains available from the CBS are old and sterile, and show some differences that also seem to be reflected in the DNA data obtained. *Septoria gladioli* is the only species of septorioid fungi described from the genus *Gladiolus*. An unusual feature of the species is that it overwinters as "sclerotia", that cause leaf infections in the next season (Priest 2006). The conidiogenous cells are holoblastic and very distinctly proliferate percurrently to form subsequent conidia, but no sympodial proliferation has been reported. Based on the multilocus phylogeny, the aforementioned isolates should be placed in their own genus, with the genus *Phloeospora* as its closest relative. Recollecting material will be required to determine the generic disposition, the delimitation of the taxa (as there seem to be at least two) and to which of these taxa the name *Septoria gladioli* should be applied.

## Clade 8: passalora-like

***Passalora dioscoreae*** (Ellis & G. Martin) U. Braun & Crous, in Crous & Braun, CBS Biodiversity Ser. (Utrecht) 1: 162. 2003.

*Specimen examined*: **South Korea**, on leaves of *Dioscorea tokoro* (*Dioscoreaceae*), 24 Oct. 2003, H.D. Shin (CPC 10855); *ibid*., on leaves of *Dioscorea tenuipes*, 1 Jan. 2004, H.D. Shin (CPC 11513).

*Notes*: *Passalora dioscoreae* is not congeneric with the type species of the genus, *P. bacilligera*. The taxonomy of *Passalora* and its relatives will be treated in a future publication (Videira *et al*., in prep.).

## Clade 9: *Neoseptoria*

***Neoseptoria*** Quaedvlieg, Verkley & Crous, **gen. nov.** MycoBank MB804421.

*Etymology*: Resembling the genus *Septoria*.

*Foliicolous*. *Conidiomata* black, immersed, subepidermal, pycnidial, subglobose with central ostiole, exuding creamy conidial mass; wall of 2–3 layers of brown *textura angularis*. *Conidiophores* 0–2-septate, subcylindrical, hyaline to pale brown at base, smooth, straight to geniculate-sinuous. *Conidiogenous cells* phialidic, hyaline, smooth, aggregated, lining the inner cavity, subcylindrical to ampulliform, straight to geniculate-sinuous; proliferating several times percurrently near apex, rarely sympodially. *Conidia* scolecosporous, hyaline, smooth, flexuous, rarely straight, granular, thin-walled, narrowly obclavate, apex subobtuse, base long obconically truncate, tapering to a truncate hilum, 3–multiseptate.

*Type species*: *Neoseptoria caricis* Quaedvlieg, Verkley & Crous.

*Note*: The genus *Neoseptoria* is morphologically similar to *Septoria*, but distinct in having mono- to polyphialidic conidiogenous cells that proliferate percurrently at the apex.

***Neoseptoria caricis*** Quaedvlieg, Verkley & Crous, **sp. nov.** MycoBank MB804422. Figs 41, 42.

*Etymology*: Named after the host genus on which it occurs, *Carex*.

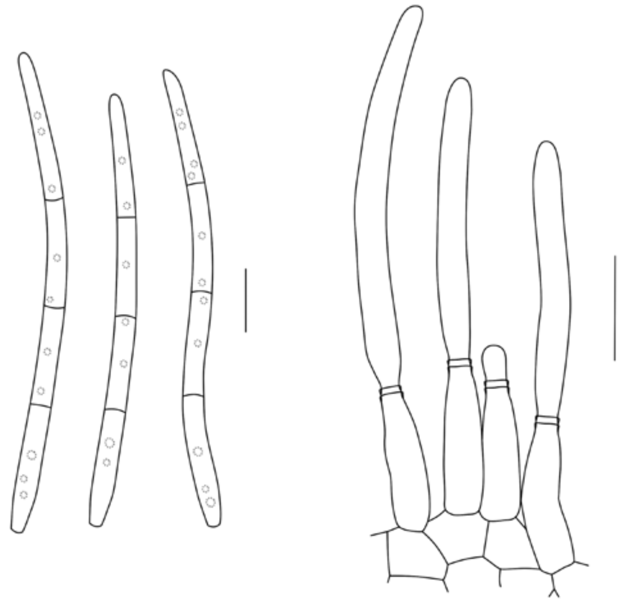

**Fig. 41.** Conidia and conidiogenous cells of *Neoseptoria caricis* (CBS 135097). Scale bars = 10 µm.

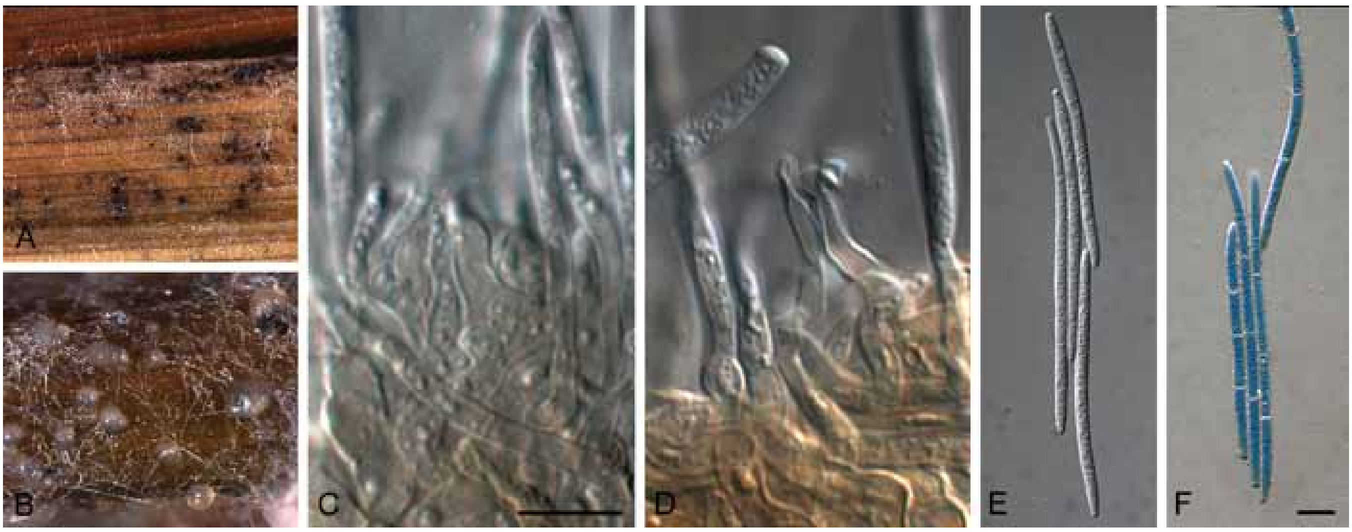


**Fig. 42.** *Neoseptoria caricis* (CBS 135097). A, B. Conidiomata developing in culture. C, D. Conidiogenous cells. E, F. Conidia. Scale bars = 10 µm.

On sterile *Carex* leaves on WA. *Conidiomata* up to 150 µm diam, black, immersed, subepidermal, pycnidial, subglobose with central ostiole, exuding creamy conidial mass; wall of 2–3 layers of brown *textura angularis*. *Conidiophores* reduced to conidiogenous cells, or 0–2-septate, subcylindrical, hyaline to pale brown at base, smooth, straight to geniculate-sinuous, 10–30 × 2.5–3.5 µm. *Conidiogenous cells* phialidic, hyaline, smooth, aggregated, lining the inner cavity, subcylindrical to ampulliform, straight to geniculate-sinuous, 8–15 × 2.5–3 µm; proliferating several times percurrently near apex, rarely sympodially. *Conidia* scolecosporous, hyaline, smooth, flexuous, rarely straight, granular, thin-walled, narrowly obclavate, apex subobtuse, base long obconically truncate, tapering to a truncate hilum, 1.5–2 µm diam, 3(–5)-septate, (40–)55–68(–80) × (2.5–)3(–3.5) µm.

*Culture characteristics*: Colonies on PDA erumpent, undulate, lacking aerial mycelium, reverse iron-grey, after 14 d, 3 cm diam; on MEA reverse greyish sepia, after 14 d, 3 cm diam, with fine, pale pink to orange aerial mycelium; on OA similar to MEA, but with pinkish tufts of aerial mycelium.

*Specimen examined*: **Netherlands**, Wageningen, on leaves of *Carex acutiformis* (*Cyperaceae*), Aug. 2012, W. Quaedvlieg (**holotype** CBS H-21293, culture ex-type CBS 135097 = S653).

*Notes*: Several septoria-like species have been described from *Carex* (Farr & Rossman 2013). Of these, *N. caricis* is most similar to *S. caricicola* (conidia 25–55 × 4 µm; (6–)7(–8)-septate), but distinct in having longer and narrower conidia with less septa.

## Clade 10: *Pseudocercospora*

*Note*: See Crous *et al*. (2013)

## Clade 11: *Zymoseptoria*

*Note*: See Quaedvlieg *et al.* (2011).

## Clade 12: *Ramularia*

*Note*: See Crous *et al.* (2009a, c).

## Clade 13: *Dothistroma*

*Note*: See Barnes *et al.* (2004).

## Clade 14: *Stromatoseptoria*

***Stromatoseptoria*** Quaedvlieg, Verkley & Crous, **gen. nov.** MycoBank MB804423.

*Etymology*: Stroma = referring to central stoma in pycnidium that gives rise to conidiophores; *Septoria* = septoria-like morphology.

*Foliicolous*, plant pathogenic. *Conidiomata* pycnidial, hypophyllous, subglobose to lenticular, very pale brown to dark brown, immersed to erumpent, exuding conidia in white cirrhus; *ostiolum* central, circular, surrounding cells concolorous; *conidiomatal wall* composed of a homogenous tissue of hyaline to very pale brown, angular to irregular cells. *Conidiophores* subcylindrical, branched, hyaline, septate. *Conidiogenous cells* hyaline, discrete or integrated, cylindrical or narrowly ampulliform, holoblastic, often also proliferating percurrently. *Conidia* cylindrical, slightly to distinctly curved, broadly rounded apex, attenuated towards a truncate base, transversely euseptate, mostly constricted at septa.

*Type species*: *Stromatoseptoria castaneicola* (Desm.) Quaedvlieg, Verkley & Crous.

*Notes*: *Stromatoseptoria* is distinguished from *Septoria* based on the central cushion or stroma that gives rise to its conidiophores (*sensu Coniella* and *Pilidiella*; van Niekerk *et al*. 2004), and conidia that tend to be olivaceous-brown in mass, and also turn olivaceous and verruculose with age.

***Stromatoseptoria castaneicola*** (Desm.) Quaedvlieg, Verkley & Crous, **comb. nov.** MycoBank MB804424. Fig. 43.
*Basionym*: *Septoria castaneicola* Desm., Ann. Sci. Nat., Sér. 3, Bot. 8: 26. 1847.

≡ (?) *Phleospora castanicola* (Desm.) D. Sacc., Mycoth. Ital., Cent. 1-2, no. 173.
= *Septoria gilletiana* Sacc., Michelia 1: 359. 1878.
? = *Septoria castaneae* Lév., Ann. Sci. Nat., Sér. 3, Bot. 5: 278. 1846.
≡ *Cylindrosporium castaneae* Krenner, Bot. Közl. 41(3-4): 126. 1944.

Description *in vivo. Leaf spots* numerous, small, angular, and often merging to irregular patterns, visible on both sides of the leaf, initially pale yellowish brown, later reddish brown with a narrow, darker border; *Conidiomata* pycnidial, hypophyllous, several in each

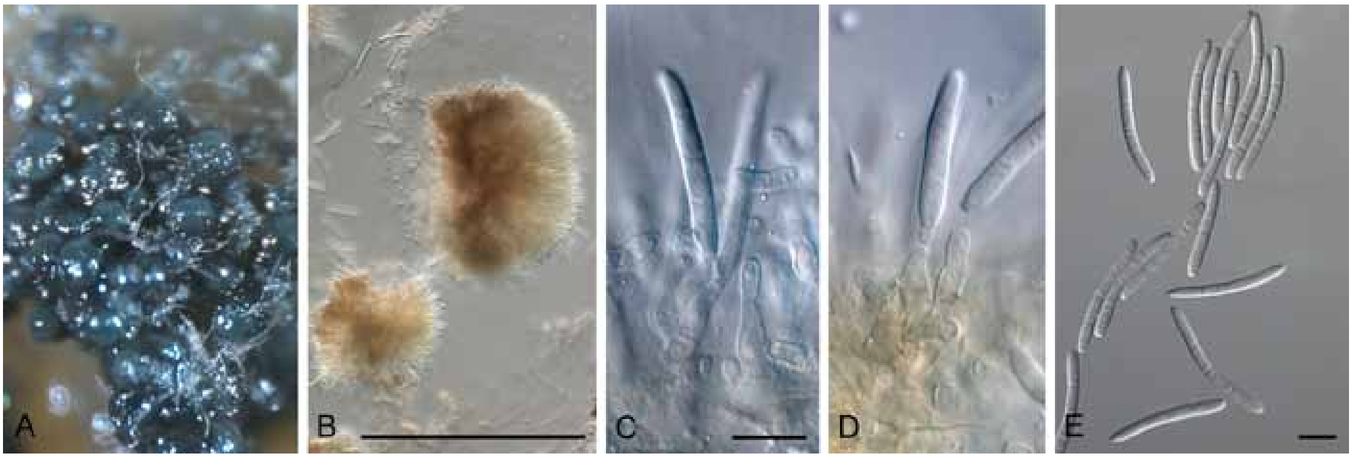


**Fig. 43.** *Stromatoseptoria castaneicola* (CBS 102320). A. Colony sporulating on MEA. B. Stroma giving rise to conidiogenous cells. C, D. Conidiogenous cells. E. Conidia. Scale bars: B = 200 µm, all others = 10 µm.

leaf spot, subglobose to lenticular, very pale brown to dark brown, usually fully immersed, 80–150(–200) µm diam, releasing conidia in white cirrhi; *ostiolum* not well-differentiated, central, circular, 18–50 µm wide, surrounding cells concolorous; *conidiomatal wall* about 10–17 µm thick, composed of a homogenous tissue of hyaline to very pale brown, angular to irregular cells 4–10 µm diam; *Conidiophores* subcylindrical, branched at base, hyaline, smooth, 1–2-septate; base frequently brown, verruculose. *Conidiogenous cells* hyaline, discrete or integrated in conidiophores cylindrical or narrowly ampulliform, holoblastic, often also proliferating percurrently with up to 3 closely positioned annellations, 7–17(–20) × 3–4(–5) µm. *Conidia* cylindrical, slightly to distinctly curved, irregularly bent or flexuous, with a relatively broadly rounded apex, attenuated towards a truncate base, basal and apical cell often both wider than intermediate cells, (0–)2–3(–4)-septate, mostly constricted around the septa in the living state, hyaline, contents with several oil-droplets and granular material in each cell in the living state, with granular contents in the rehydrated state, 30–46 × 3–4 µm ("T"; rehydrated, "NT" 2–3 µm wide). Conidia are olivaceous-brown in mass, and older conidia also turn olivaceous and verruculose, and at times anastomose in culture.

*Culture characteristics*: Colonies (CBS 102322) on OA reaching 4–8 mm diam in 25 d (9–12 mm in 33 d), with an even, glabrous, buff margin; colonies restricted, up to 1 mm high, immersed mycelium homogeneously buff, where conidiomatal complexes develop dark brick to black, in part covered by pure white, dense, appressed and woolly aerial mycelium, later a salmon haze occurs in the immersed mycelium; reverse buff, locally cinnamon to sepia. *Colonies* on CMA reaching (4–)7–11 mm diam in 25 d (8–12 mm in 33 d), as on OA, but with a halo of reddish to salmon, diffusing pigment, which becomes more intense after 33 d, and immersed mycelium in the centre darker, and aerial mycelium more strongly developed, later becoming locally salmon or citrine; reverse brick and dark brick, surrounded by a reddish to salmon zone. Colonies on MEA reaching 6.5–9 mm diam in 25 d (9–11.5 mm in 33 d), with an even, buff to cinnamon margin, entirely hidden under the aerial mycelium, with a very faint halo of diffusing pigment; colonies restricted, up to 4 mm high, hemispherical to irregularly pustulate, entirely covered by a dense mat of felted aerial mycelium, which, especialy in the centre, attains a rosy buff or primrose to citrine haze; reverse cinnamon to hazel, around a brick to dark brick centre. Colonies on CHA reaching 7–9 mm diam in 25 d (9–11 mm in 33 d), as on MEA, but no diffusing pigment observed around the colonies. *Conidiomata* on OA developing after 10–15 d, black, globose, single or merged to complexes up to 250 µm diam, releasing milky white conidial slime. *Conidiogenous cells* as *in planta*. *Conidia* as *in planta*, mostly 3-septate, 30–45 × 3.5–4.5 µm (CBS 102320, OA, "T"; "NT" 3 µm wide).

*Specimens examined*: **Austria**, Tirol, Klausen, on leaves of *Castanea vesca* (*Fagaceae*), Aug., distributed in F. von Höhnel, Krypt. exsicc. no. 415, (PC0084576, PC0084583). **France**, Lébisey, Aug. and Sep. 1843, M. Roberge, 'Coll. Desmazières 1863, no. 8', on leaves of *Castanea sativa* (PC0084574, type of *Septoria castanicola* Desm.); same substr., Meudon, 1 Aug. 1849 (PC0084571, PC0084589, PC0084590, PC0084591) and Jul. 1852 (PC0084572); same substr., loc. and date unknown, 'Coll. Desmazières 1863, no. 8' (PC0084570); Seine-et-Marne, Fontainebleau, Sep 1881, distributed in Roumeguère, Fungi Gallici exsicc. no. 2029 (PC0084575). **Netherlands**, prov. Utrecht, Baarn, Lage Vuursche, on living leaves of *Castanea sativa*, 29 Aug. 1999, G. Verkley 912 (CBS H-21200), cultures CBS 102320–102322; same substr., prov. Limburg, St. Jansberg, 9 Sep. 1999, G. Verkley 932 (CBS H-21214), culture CBS 102377; same substr., prov. Limburg, Molenhoek, Heumense Schans (46-12-55), 23 Aug. 2004, G. Verkley & M. Starink 3040, culture CBS 116464.

*Notes*: According to the original diagnosis that Desmazières published in 1847 based on material on *Castanea* collected in autumn, the conidia are elongated, thin and curved, and about 40 µm in length. No further details like conidial septa were given. The material PC0084574 is the only collection received from PC that antidates the publication and assumedly is the type. It consists of several leaves with numerous pycnidia in leaf spots, some of which belong to *Septoria castaneicola* with the characteristic conidia, but most are a spermatial state of most likely the *Mycosphaerella punctiformis* complex (= *Ramularia*, Verkley *et al.* 2004).

Teterevnikova-Babayan (1987) treated *S. castaneicola* Desm. as a synonym of *S. castaneae* Lév., and both originally were described from the same host, *Castanea sativa* (syn. *C. vesca*). Teterevnikova-Babayan (1987) described the conidia as 3-septate, 25–40 × 2.5–4.5 µm, which is in fairly good agreement with present observations. The type of *S. castanaea* Lév. could not be studied and the name remains doubtful. Even though Léveillé described symptoms that match those of *S. castaneicola* fairly well, he described the conidia as aseptate, and failed to give information about their size.

## Clade 15: *Lecanosticta*

*Note*: See Quaedvlieg *et al*. (2012).

## Clade 16: *Phaeophleospora*

*Note*: See Crous et al. (2009b, c).

## Clade 17: *Cytostagonospora*

***Cytostagonospora*** Bubák, Ann. Mycol. 14: 150. 1916.

Description: See above.

*Type species*: *Cytostagonospora photiniicola* Bubák [as "*photinicola*"], Ann. Mycol. 14: 150. 1916.

***Cytostagonospora martiniana*** (Sacc.) B. Sutton & H.J. Swart, Trans. Br. mycol. Soc. 87: 99. 1986. Figs 44, 45.
*Basionym*: *Septoria martiniana* Sacc., Syll. Fung. (Abellini) 10: 351. 1892.

= *Septoria phyllodiorum* Cooke & Massee, Grevillea 19(90): 47. 1890, non *S. phyllodiorum* Sacc., Hedwigia 29: 156. 1890.

On sterile *Carex* leaves on WA. *Leaf spots* amphigenous, circular, grey to brown with raised dark brown border, 1–3 mm diam. *Conidiomata* immersed, subepidermal, epiphyllous, solitary to aggregated with stromatic tissue, with central ostiolar opening exuding a creamy to white conidial mass, rupturing at maturity (pycnidial to acervular), brown, globose, up to 400 µm diam; wall of 3–6 layers of brown *textura angularis*. *Conidiophores* hyaline, smooth, subcylindrical, 0–5-septate, branched or not, 10–15(–50) × 3–4 µm, giving rise to terminal and lateral conidiogenous cells. *Conidiogenous cells* hyaline, smooth, subcylindrical or ampulliform, 4–8 × 3–4 µm, polyphialidic, with apical and lateral loci, with visible periclinal thickening, at times also proliferating percurrently (both modes can also be present on the same conidiogenous cell). *Conidia* hyaline, smooth, granular, irregularly curved, subcylindrical to narrowly obclavate, apex subobtuse, base long, obconically truncate, (1–)3-septate, (18–)32–45(–50) × (1.5–)2(–3) µm; base not thickened, 0.5–1 µm diam.

*Culture characteristics*: Colonies on PDA convex, erumpent with feathery margin, lacking aerial mycelium, surface fuscous-black, reverse olivaceous-black, after 14 d, 4 cm diam, with a beautifull purple exudate at the outer edges; on MEA, after 14 d, 3.5 cm diam, lacking any exudate; on OA surface fuscous-black, reverse olivaceous-grey, after 14 d, 4 cm diam, purplish-red coloured exudate.

*Specimen examined*: **Australia**, Warneet close to Melbourne, S38º13'37.8" E145º18'25.4", on leaves of *Acacia pycnantha* (*Mimosaceae*), 21 Oct. 2009, P.W. Crous (specimen CBS H-21297, culture CBS 135102 = CPC 17727).

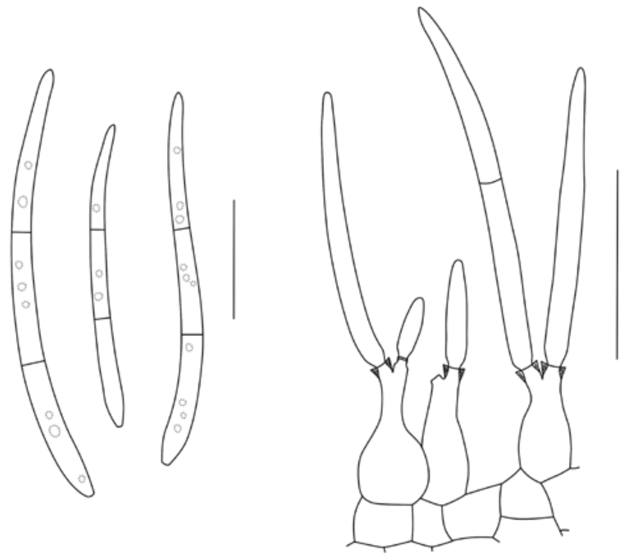

**Fig. 44.** Conidia and conidiogenous cells of *Cytostagonospora martiniana* (CBS 135102). Scale bars = 10 µm.

*Notes*: The present collection matches the description of *Cytostagonospora martiniana* provided by Sutton & Swart (1986). As discussed by the authors, this genus is distinct from *Septoria s. str*. based on its conidiomata aggregated in stromatic tissue, and unique mode of conidiogenesis. In culture conidiogenous cells exhibited a mixture of sympodial proliferation, or were polyphialidic with periclinal thickening, but also proliferated percurrently. Species of *Septoria* occurring on *Acacia* were treated by Sutton & Pascoe (1987).

## Clade 18: *Zasmidium*

*Note*: See Crous *et al.* (2007a, b, 2009c).

## Clade 19: *Polyphialoseptoria*

***Polyphialoseptoria*** Quaedvlieg, R.W. Barreto, Verkley & Crous, **gen. nov.** MycoBank MB804425.

*Etymology*: Polyphialo = polyphialides; *Septoria* = septoria-like.

*Foliicolous,* plant pathogenic. *Conidiomata* brown, erumpent, pycnidial (acervular in culture), globose, brown; wall of 3–6 layers of pale brown *textura angularis*. *Conidiophores* reduced to conidiogenous cells. *Conidiogenous cells* hyaline, smooth, subcylindrical to ampulliform; proliferating sympodially at apex, forming polyphialides with minute periclinal thickening, or as solitary loci on superficial mycelium in culture. *Conidia* hyaline, smooth, granular to guttulate, scolecosporous, irregularly curved, apex subobtuse, base long obconically truncate, transversely multi-euseptate, in older cultures disarticulating at septa; microcyclic conidiation also common in older cultures.

*Type species*: *Polyphialoseptoria terminaliae* Quaedvlieg, R.W. Barreto, Verkley & Crous.

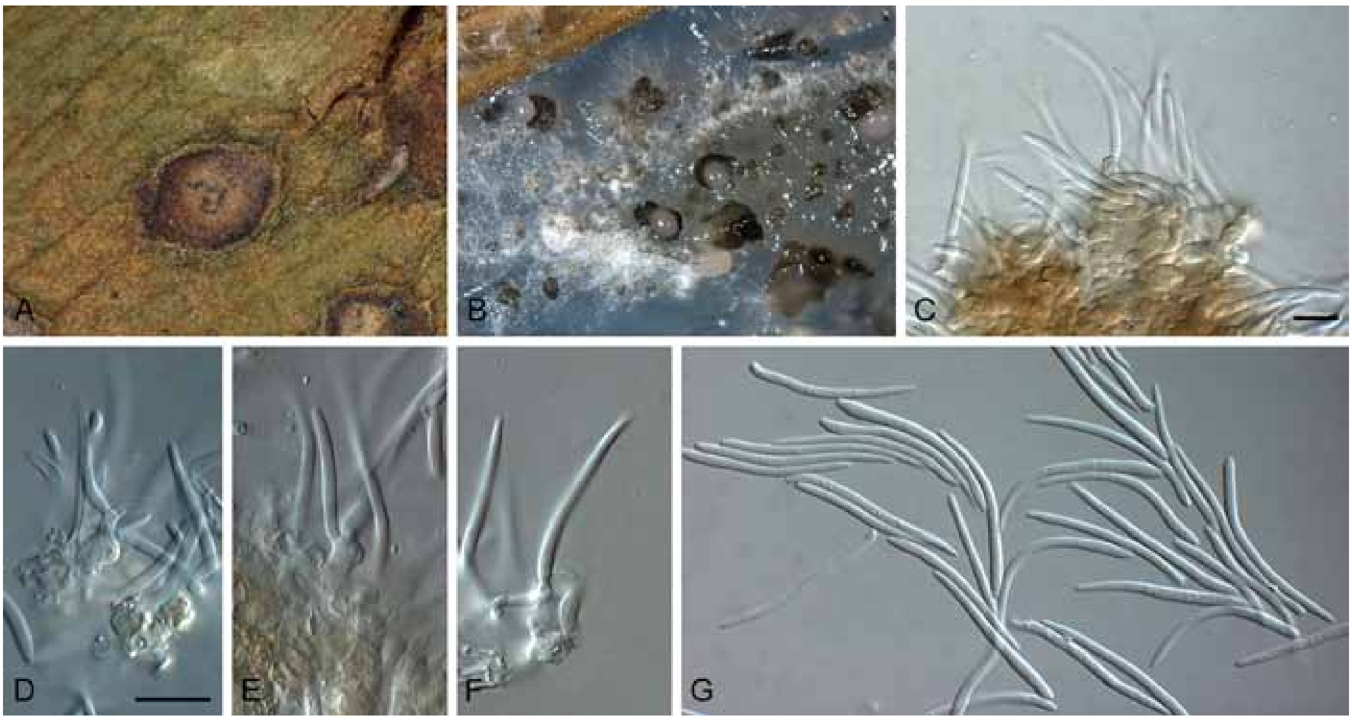


**Fig. 45.** *Cytostagonospora martiniana* (CBS 135102). A. Leaf spot. B. Conidiomata forming in culture. C–F. Conidiogenous cells. G. Conidia. Scale bars = 10 µm.

***Polyphialoseptoria tabebuiae-serratifoliae*** Quaedvlieg, Alfenas & Crous, **sp. nov.** MycoBank MB804427. Figs 46, 47.

*Etymology*: Named after its host, *Tabebuia serratifolia.*

*Leaf spots* variable in number on mature leaves; initially as small spots or purple-brown areas, with the inner part becoming grey-white with age, surrounded by a purple-brown halo. *Conidiomata* developing on sterile barley leaves on WA, pale cream in colour, erumpent, globose, up to 180 µm diam; wall of 2–3 layers of pale brown *textura angularis*. *Conidiophores* hyaline, smooth, cylindrical, septate, branched, 10–35 × 1.5 µm. *Conidiogenous cells* terminal and lateral, cylindrical, hyaline, smooth, proliferating sympodially, 10–15 × 1.5 µm. *Conidia* solitary, hyaline, smooth, granular, irregularly curved, subcylindrical, apex subobtuse, base truncate, (0–)1–3(–4)-septate, (15–)25–35(–55) × 1.5(–2) µm.

*Culture characteristics*: Colonies flat, spreading, with sparse aerial mycelium and smooth, even margins, reaching 40 mm diam after 2 wk. On OA surface dirty pink; on PDA surface and reverse dirty white. On MEA surface folded, dirty white, reverse cinnamon.

*Specimen examined*: **Brazil**, Minas Gerais, Viçosa, on leaves of *Tabebuia serratifolia* (*Bignoniaceae*), 1999, A.C. Alfenas (**holotype** CBS H-21299, culture ex-type CBS 112650).

*Notes*: Inácio & Dianese (1998) described *Septoria tabebuiae-impetiginosae* on *T. impetiginosa* (conidia 25–67 × 2–4 µm, 2–6-septate), and also compared this species to *S. tabebuiae* (18–40 × 1.7–2.5 µm, aseptate conidia) on *T. berteroi,* and *S. cucutana* (34–40 × 0.8–1 µm) on *T. pentaphylla* and *T. spectabilis*. Furthermore, they also referred to an undescribed species Ferreira (1989) mentioned on *T. serratifolia* in Viçosa, Minas Gerais, which is named as *S. tabebuiae-serratifoliae* in the present study.

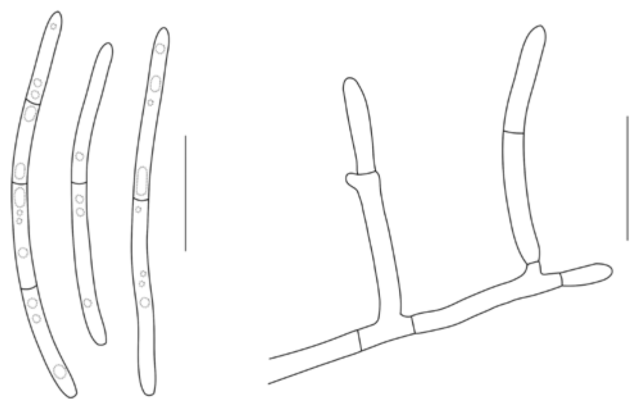

**Fig. 46.** Conidia and conidiogenous loci on hypha of *Polyphialoseptoria tabebuiae-serratifoliae* (CBS 112650). Scale bars = 10 µm.

*Polyphialoseptoria tabebuiae-serratifoliae* is distinct from species of *Septoria* known from *Tabebuia* based on its conidial morphology.

***Polyphialoseptoria terminaliae*** Quaedvlieg, R.W. Barreto, Verkley & Crous, **sp. nov.** MycoBank MB804426. Fig. 48.

*Etymology*: Named after the host genus from which it was collected, *Terminalia*.

*Leaf spots* irregular to subcircular, amphigenous, mostly aggregated along leaf veins, pale brown, 3–8 mm diam, surrounded by a prominent, wide, red-purple border. On sterile *Carex* leaves on WA. *Conidiomata* brown, erumpent, pycnidial (acervular in culture), up to 600 µm diam, globose, brown, exuding a crystalline cirrhus of conidia; wall of 3–6 layers of pale brown *textura angularis*. *Conidiophores* reduced to conidiogenous cells. *Conidiogenous cells* hyaline, smooth, subcylindrical to ampulliform, 5–10 × 3–4 µm; proliferating sympodially at apex, forming polyphialides with minute periclinal thickening, or as solitary loci on superficial mycelium in culture. *Conidia* hyaline, smooth, granular to guttulate, scolecosporous, irregularly curved, apex subobtuse, base long obconically truncate (1–1.5 µm diam), multiseptate (–16), in older cultures disarticulating at septa; microcyclic conidiation also common in older cultures, (40–)75–120(–140) × 2–3(–3.5) µm.

*Culture characteristics*: Colonies on PDA erumpent with feathery margin, lacking aerial mycelium, surface fuscous-black, reverse olivaceous-black to buff in the younger tissue, after 14 d, 1 cm diam; on MEA surface and reverse isabelline to greyish-sepia; on OA surface pale-vinaceous, reverse rosy-buff to buff.

*Specimen examined*: **Brazil**, Minas Gerais, Viçosa, on leaves of *Terminalia catappa* (*Combretaceae*), 18 May 2010, R.W. Barreto (**holotype** CBS H-21298, culture ex-type CBS 135106 = CPC 19611); ibed., (CBS 135475 = CPC 19487)

*Notes*: As far as we could establish there are presently no species of *Septoria* described from *Terminalia*, and as this taxon is distinct from all taxa in GenBank, we herewith describe it as a novel species. A *Septoria* sp. has been reported on leaves of *Terminalia* sp. in Florida and Venezuela (Farr & Rossman 2013). *Polyphialoseptoria* is distinct from *Septoria* based on the presence of polyphialides. *Neoseptoria* also has phialides as observed in *Polyphialoseptoria*, but these tend to chiefly be monophialides.

## Clade 20: *Ruptoseptoria*

***Ruptoseptoria*** Quaedvlieg, Verkley & Crous, **gen. nov.** MycoBank MB804428.


**Fig. 47.** *Polyphialoseptoria tabebuiae-serratifoliae* (CBS 112650). A. Conidiomata forming in culture. B. Conidiogenous cells. C. Conidia. Scale bars = 10 µm.

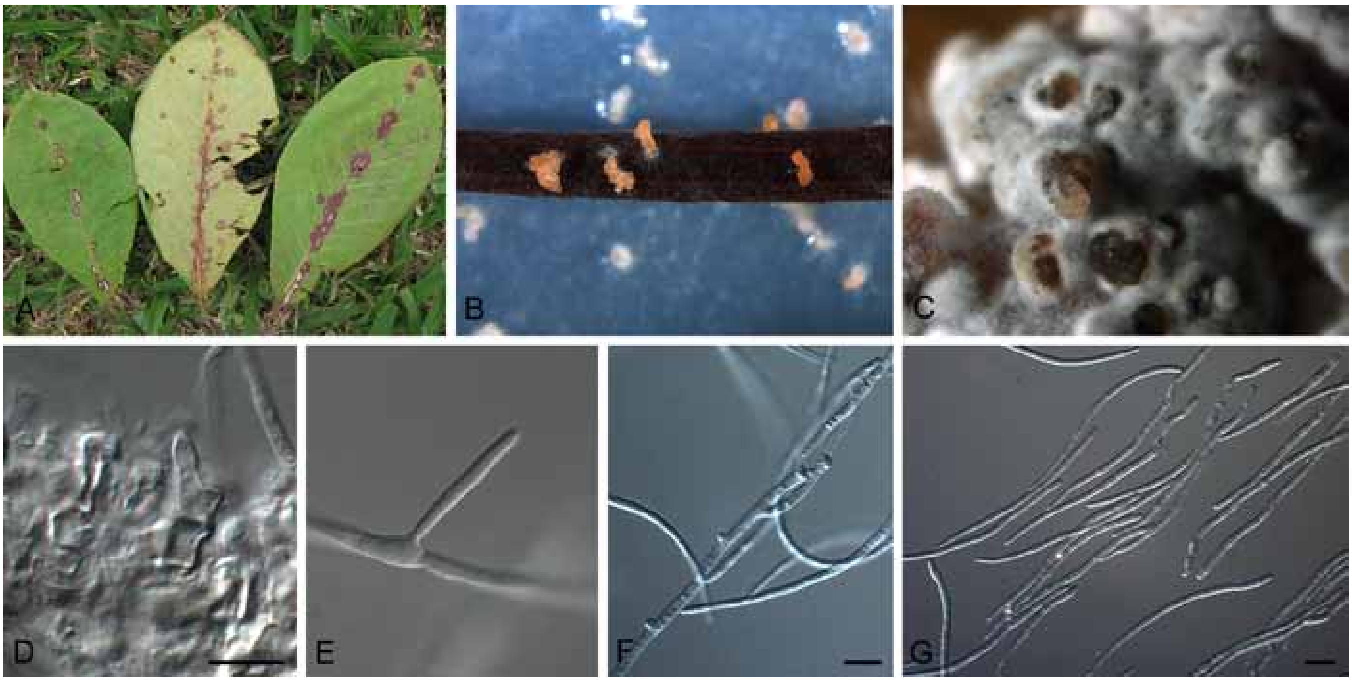


**Fig. 48.** *Polyphialoseptoria terminaliae* (CBS 135106). A. Leaves with leaf spots. B, C. Conidiomata sporulating in culture. D–F. Conidiogenous cells and loci. G. Conidia. Scale bars = 10 µm.

*Etymology*: Rupto = irregular rupture of conidiomata; *Septoria* = septoria-like.

*Foliicolous,* plant pathogenic. *Conidiomata* black, appressed, elongated, pycnidial, but opening via irregular rupture, convulated; exuding a creamy white conidial mass; outer wall dark brown, crusty, consisting of 6–8 layers of dark brown *textura angularis*; giving rise to 2–3 inner layers of pale brown to hyaline *textura angularis*. *Conidiophores* lining the inner cavity, hyaline, smooth or pale brown, verruculose at base, branched below, septate, subcylindrical. *Conidiogenous cells* integrated, terminal, subcylindrical, smooth; proliferating sympodially at apex, or apex phialidic with minute periclinal thickening. *Conidia* solitary, hyaline, smooth, guttulate, subcylindrical to narrowly obclavate, gently to irregularly curved, apex subobtuse, base truncate to narrowly obovoid, transversely septate.

*Type species*: *Ruptoseptoria unedonis* (Roberge ex Desm.) Quaedvlieg, Verkley & Crous.

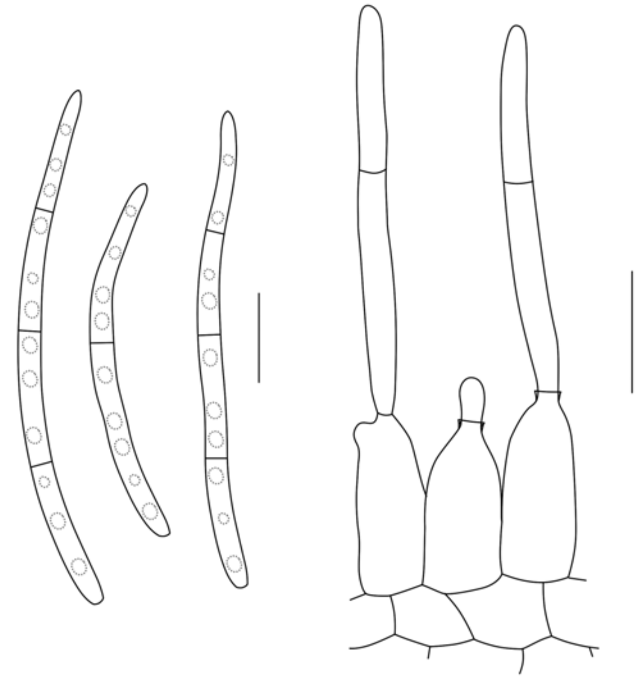

**Fig. 49.** Conidia and conidiogenous cells of *Ruptoseptoria unedonis* (CBS 355.86). Scale bars = 10 µm.

***Ruptoseptoria unedonis*** (Roberge ex Desm.) Quaedvlieg, Verkley & Crous, **comb. nov.** MycoBank MB804429. Figs 49, 50.

*Basionym*: *Septoria unedonis* Roberge ex Desm., Ann. Sci. Nat., Bot., Sér. 3(8): 20. 1847.

= *Sphaerella arbuticola* Peck, Bull. Torrey Bot. Club 10(7): 75. 1883.

≡ *Mycosphaerella arbuticola* (Peck) Jaap, Ann. Mycol. 14(1/2): 13. 1916.

≡ *Mycosphaerella arbuticola* (Peck) House, Contr. Univ. Mich. Herb. 9(8): 587. 1972.

*Leaf spots* numerous, small, amphigenous, irregular to subcircular, whitish in the middle, with very broad, purple borders. *Conidiomata* black, appressed, elongated, pycnidial, but opening via irregular rupture, convulated, up to 450 µm diam, exuding a creamy white conidial mass; outer wall dark brown, crusty, consisting of 6–8 layers of dark brown *textura angularis*; giving rise to 2–3 inner layers of pale brown to hyaline *textura angularis*. *Conidiophores* lining the inner cavity, hyaline, smooth or pale brown, verruculose at base, branched below, 1–2-septate, subcylindrical, 10–15 × 2–4 µm. *Conidiogenous cells* integrated, terminal, subcylindrical, smooth, 6–12 × 2.5–3.5 µm; proliferating sympodially at apex, or apex phialidic with minute periclinal thickening. *Conidia* solitary, hyaline, smooth, guttulate, subcylindrical to narrowly obclavate, gently to irregularly curved, apex subobtuse, base truncate to narrowly obovoid, 1–3(–6)-septate, (25–)30–47(–56) × 2(–3) um.

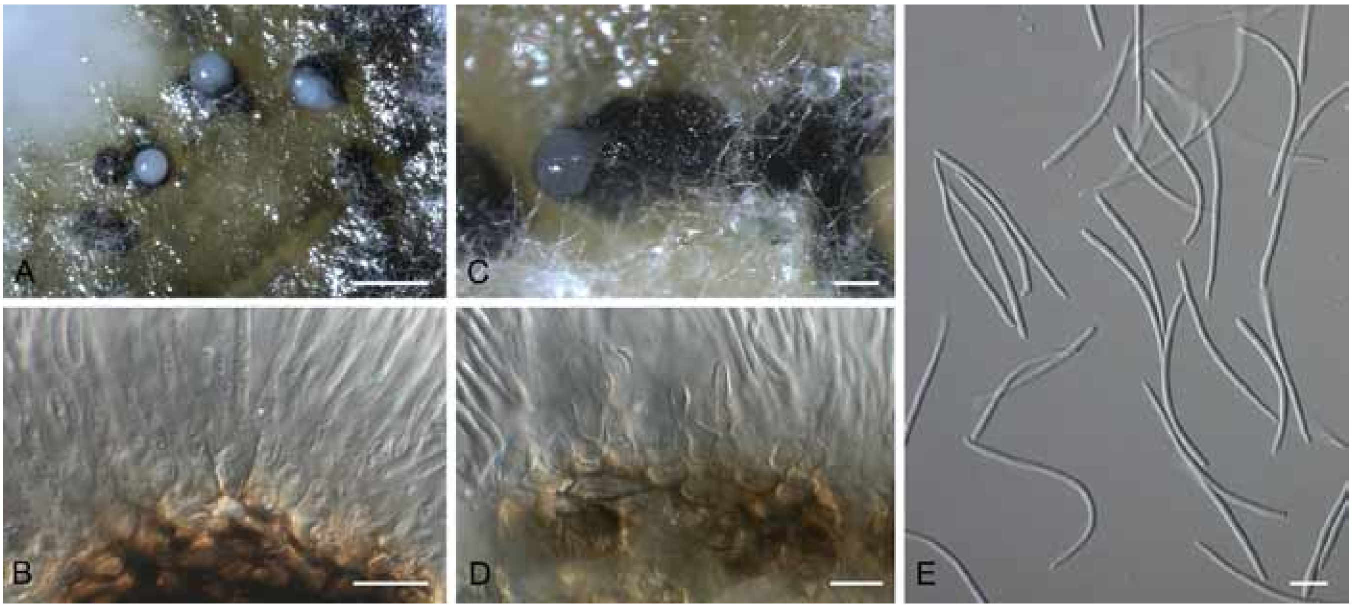


**Fig. 50.** *Ruptoseptoria unedonis* (CBS 355.86). A, C. Conidiomata forming in culture. B, D. Conidiogenous cells. E. Conidia. Scale bars: A = 450 µm, C = 110 µm, all others = 10 µm.

*Culture characteristics*: Colonies on OA spreading with moderate aerial mycelium and smooth, even margins; surface olivaceous-grey in outer region, centre dirty white to pale pink, reverse iron grey; on MEA surface dark-mouse-grey to mouse-grey, reverse greenish-black; on PDA surface mouse-grey to dark-mouse-grey, reverse greenish-black.

*Specimen examined*: **France**, Seignosse le Penon, Lamdes, Forest communale de Seignosse, on leaves of *Arbutus unedo* (*Ericaceae*), Aug. 1986, H.A. van der Aa (CBS H-14645, culture CBS 355.86).

*Notes*: *Mycosphaerella arbuticola* (CBS 355.86) is a species pathogenic to *Arbutus menziesii* in California (Aptroot 2006), clusters with "*Septoria*" *unedonis* (CBS 755.70, CBS H-18192), which is associated with leaf spots on *Arbutus unedo* in Croatia, and elsewhere in Europe. Based on these results, the sexual-asexual link between these two names is confirmed. Morphologically, however, *Ruptoseptoria* is similar to *Septoria*, and can only be distinguished based on its conidiomata that are convulated, opening by irregular rupture, and conidiogenous cells that are frequently phialidic.

## Clade 21: *Dissoconium* (*Dissoconiaceae*)

*Note*: See Li *et al.* (2012).

## Clade 22: *Readeriella* (*Teratosphaeriaceae*)

*Note*: See Crous *et al.* (2007a, 2009a–c).

## Clade 23: *Teratosphaeria*

*Note*: See Crous *et al.* (2007, 2009c).

## Clade 24: septoria-like

*Specimen examined*: **Brazil**, Nova Friburgo, on leaves of *Tibouchina herbacea* (*Melastomataceae*), 15 Dec. 2007, D.F. Parreira (CBS 134910 = CPC 19500).

*Note*: The taxonomy of this species could not be resolved, as isolate CPC 19500 proved to be sterile.

## Clade 25: *Cylindroseptoria*

***Cylindroseptoria*** Quaedvlieg, Verkley & Crous, **gen. nov.** MycoBank MB804430.

*Etymology*: Cylindro = cylindrical conidia; *Septoria* = septoria-like.

*Conidiomata* pycnidial with central ostiole, or cupulate, separate, brown, short-stipitate, tapering towards base; rim with elongated brown, thick-walled cells with obtuse ends; rim covered with mucoid layer that flows over from conidiomatal cavity, filled with conidial mass; wall of 3–4 layers of medium brown *textura angularis*, becoming hyaline towards inner region. *Conidiogenous cells* hyaline, smooth, ampulliform, lining inner cavity, with prominent periclinal thickening at apex. *Conidia* solitary, hyaline, smooth, granular or not, cylindrical with obtuse apex, tapering at base to truncate scar, aseptate.

*Type species*: *Cylindroseptoria ceratoniae* Quaedvlieg, Verkley & Crous.

***Cylindroseptoria ceratoniae*** Quaedvlieg, Verkley & Crous, **sp. nov.** MycoBank MB804431. Figs 51, 52.

*Etymology*: Named after the host genus on which it occurs, *Ceratonia*.

*Conidiomata* separate, brown, cupulate, short-stipitate, rim up to 300 µm diam, 100–180 µm tall, tapering towards base, 20–50 µm diam (on *Anthriscus sylvestris* stems, not on OA or PDA, where they appear more flattened with agar surface); rim with elongated brown, thick-walled cells with obtuse ends, 5–12 × 4–5 µm; rim covered with mucoid layer that flows over from conidiomatal cavity, filled with conidial mass; wall of 3–4 layers of medium brown *textura angularis*, becoming hyaline towards inner region. *Conidiogenous cells* hyaline, smooth, ampulliform, lining inner cavity, 7–12 × 4–6 µm; apex 2 µm diam, with prominent periclinal thickening. *Conidia* solitary, hyaline, smooth, granular or not, cylindrical with obtuse apex, tapering at base to truncate scar 1 µm diam, aseptate, (10–)12–14(–16) × 3(–3.5) µm.

*Culture characteristics*: Colonies spreading, reaching 28 mm diam after 2 wk, with sparse aerial mycelium and even, lobate margins. On MEA surface iron-grey, reverse olivaceous-grey. On OA surface olivaceous-grey. On PDA surface and reverse iron-grey.

*Specimen examined*: **Spain**, Mallorca, Can Pastilla, on leaves of *Ceratonia siliqua* (*Caesalpinaceae*), 24 May 1969, H.A. van der Aa (**holotype** CBS H-21300, culture ex-type CBS 477.69).

*Notes*: *Cylindroseptoria ceratoniae* is quite distinct in that it has cup-shaped acervuli, ampilliform conidiogenous cells with periclinal thickening, and hyaline, aseptate, cylindrical conidia. *Cylindroseptoria* needs to be compared with *Satchmopsis* (infundibular conidiomata), *Cornucopiella* (tubular conidiomata) and *Thaptospora* (cylindrical / lageniform / campanulate conidiomata), but the combination of cupulate conidiomata and cylindrical, and aseptate conidia is distinct.

***Cylindroseptoria pistaciae*** Quaedvlieg, Verkley & Crous, **sp. nov.** MycoBank MB804432. Figs 53, 54.

*Etymology*: Named after the host genus on which it occurs, *Pistacia*.

*Conidiomata* pycnidial, erumpent, globose, black, separate, with black crusty outer layer of cells, up to 200 µm diam, with central ostiole; wall of 3–6 layers of brown *textura angularis*. *Conidiophores* reduced to conidiogenous cells. *Conidiogenous cells* phialidic (mostly monophialidic, but a few observed to also be polyphialidic), lining the inner cavity, hyaline, smooth, ampulliform, 5–8 × 3–4 µm, proliferating percurrently (inconspicuous) or with periclinal thickening at apex (also occurring as solitary loci on superficial hyphae surrounding pycnidia). *Conidia* hyaline, smooth, cylindrical, mostly straight, rarely slightly curved, apex subobtuse, base truncate, guttulate, aseptate, (9–)11–13(–18) × 2.5–3(–3.5) µm.

*Culture characteristics*: Colonies on PDA flat, circular, lacking aerial mycelium, surface fuscous-black, reverse olivaceous-black, after 14 d, 3.5 cm diam; on MEA surface fuscous-black, reverse olivaceous-black, after 14 d, 4.5 cm diam; on OA similar to PDA.

*Specimen examined*: **Spain**, Mallorca, El Arenal, on leaves of *Pistacia lentiscus* (*Anacardiaceae*), 25 May 1969, H.A. van der Aa (**holotype** CBS H-21301, culture CBS 471.69).

*Notes*: *Cylindroseptoria pistaciae* is tentatively placed in *Cylindroseptoria*, as it has pycnidial rather than cupulate conidiomata. However, synapomorphies with *Cylindroseptoria* include phialides with periclinal thickening, and cylindrical, aseptate conidia. Further collections are required to determine if conidiomatal anatomy is more important than conidiogenesis and conidial morphology. For the present, however, the generic circumscription

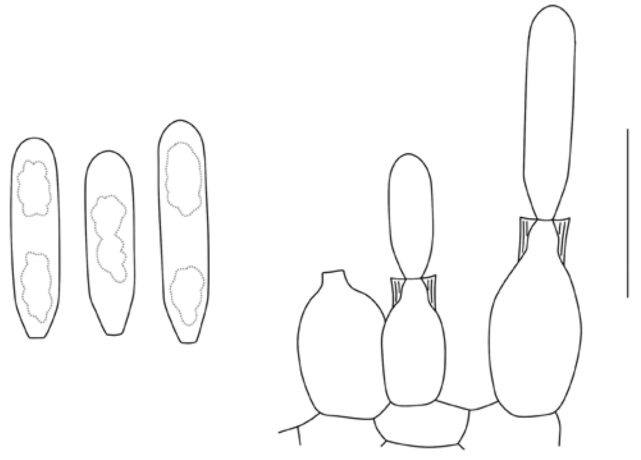

**Fig. 51.** Conidia and conidiogenous cells of *Cylindroseptoria ceratoniae* (CBS 477.69). Scale bar = 10 µm.

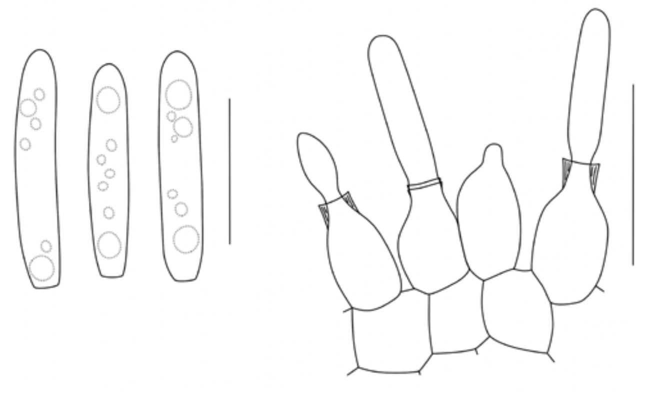

**Fig. 53.** Conidia and conidiogenous cells of *Cylindroseptoria pistaciae* (CBS 471.69). Scale bars = 10 µm.

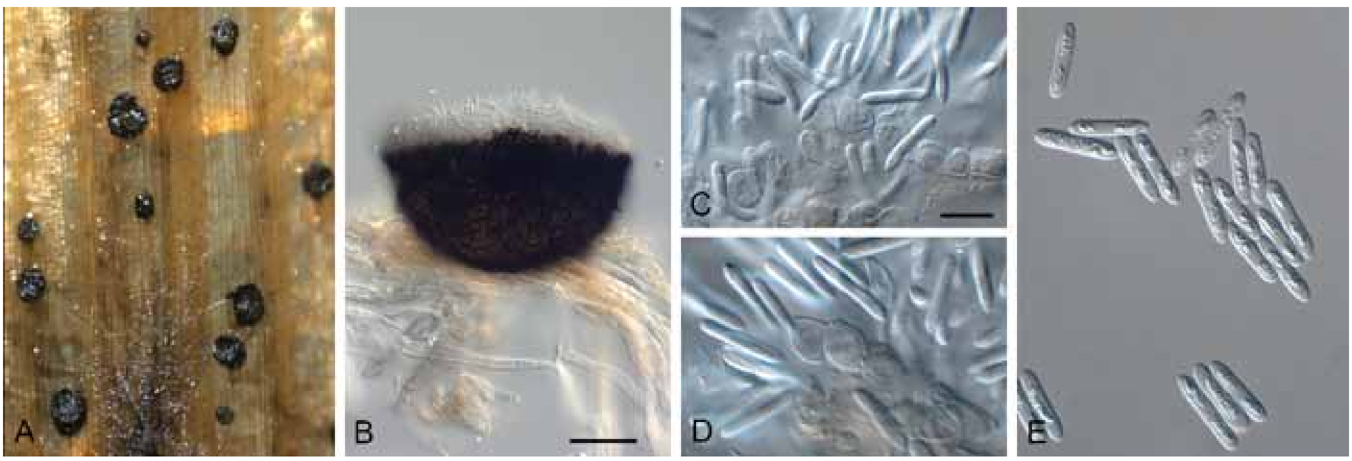


**Fig. 52.** *Cylindroseptoria ceratoniae* (CBS 477.69). A, B. Conidiomata forming in culture. C, D. Conidiogenous cells giving rise to conidia. E. Conidia. Scale bars: B = 45 µm, all others = 10 µm.

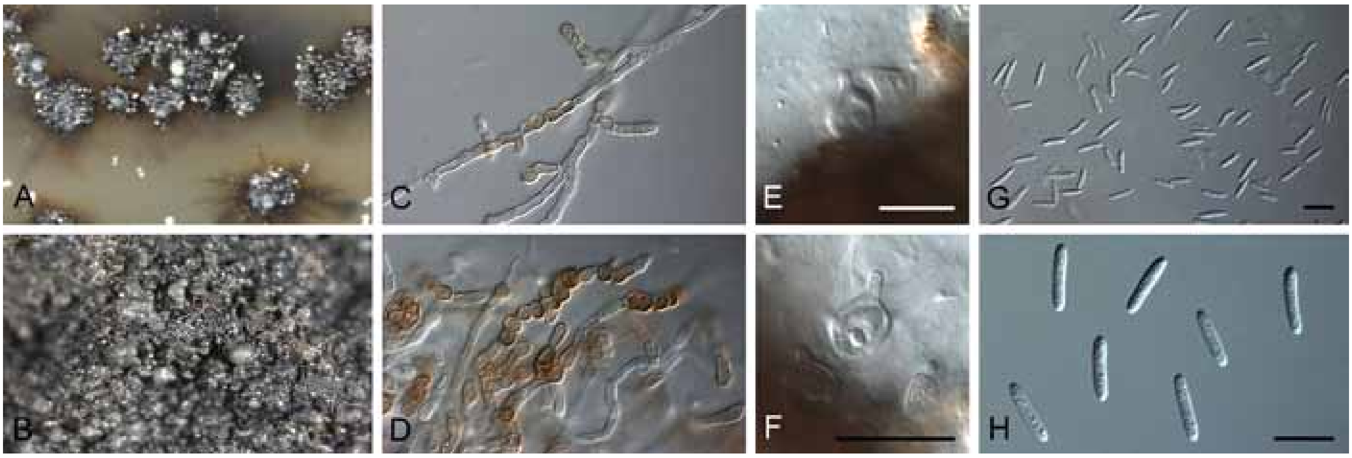


**Fig. 54.** *Cylindroseptoria pistaciae* (CBS 471.69). A, B. Conidiomata sporulating in culture. C, D. Intercalary chains of chlamydospore-like cells. E, F. Conidiogenous cells. G, H. Conidia. Scale bars = 10 µm.

of *Cylindroseptoria* has been widened to include taxa with pycnidial conidiomata. *Cylindroseptoria pistaciae* could be confused with *Septoria pistaciae*, though conidia of the latter are 20–30 × 1.6 µm, and are 1(–3)-septate (Chitzanidis & Michaelides 2002).

## Clade 26: *Pseudoseptoria*

***Pseudoseptoria*** Speg., Ann. Mus. Nac. B. Aires, Ser. 3 13: 388. 1910.

= *Aphanofalx* B. Sutton, Trans. Brit. Mycol. Soc. 86: 21. 1986.

*Caulicolous* and *foliicolous*, plant pathogenic or saprobic. Conidiomata stromatic, pycnidioid, unilocular, glabrous, black, ostiolate; wall of *textura angularis*, in some cases cells in the upper wall larger and darker than cells in the lower wall. *Conidiophores* reduced to conidiogenous cells lining the cavity of the conidioma. *Conidiogenous cells* discrete or integrated, cylindrical or lageniform, colourless, smooth-walled, invested in mucus, with a prominent cylindrical papilla with several percurrent proliferations at the apex; collarette prominent and extanding past conidia, or reduced and inconspicuous. *Conidia* fusiform, lunate or irregular, curved, unicellular, colourless, smooth-walled with or without an excentric basal appendage, continuous with conidium body, plectronoid to podiform, or with a blunt or spathulate distal end.

*Type species*: *P. donacicola* Speg., Ann. Mus. Nac. B. Aires, Ser. 3 13: 388. 1910. [= *P. donacis* (Pass.) B. Sutton].

***Pseudoseptoria collariana*** Quaedvlieg, Verkley & Crous, **sp. nov.** MycoBank MB804433. Fig. 55.

*Etymology*: Named after its prominently flared collarettes, forming a sleeve.

On sterile *Carex* leaves on WA. *Conidiomata* immersed to erumpent, globose, dark brown, up to 400 µm diam, unilocular, opening via central ostiole; wall of 6–10 layers of brown *textura angularis*. *Conidiophores* reduced to conidiogenous cells, or branched at the base with one supporting cell that is dark brown, encased

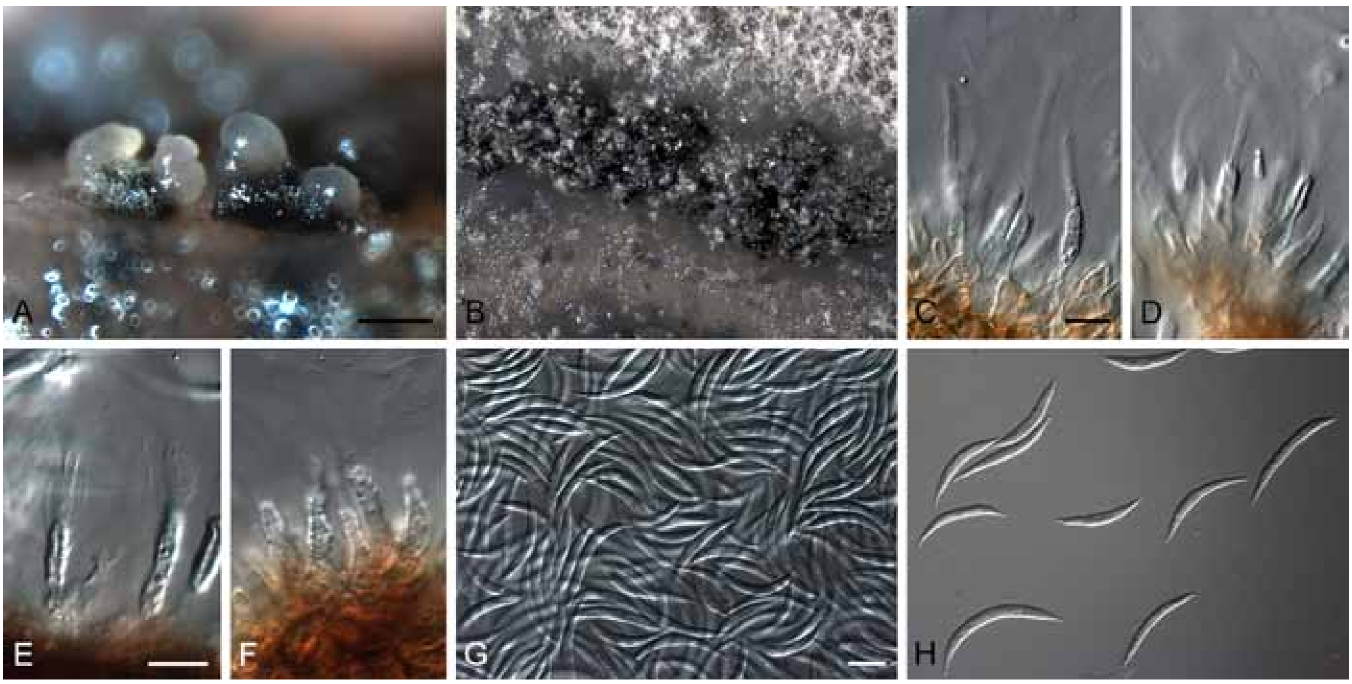


**Fig. 55.** *Pseudoseptoria collariana* (CBS 135104). A, B. Colonies sporulating in culture. C–F. Conidiogenous cells with prominent collarettes. G, H. Conidia. Scale bars: A = 400 µm, all others = 10 µm.

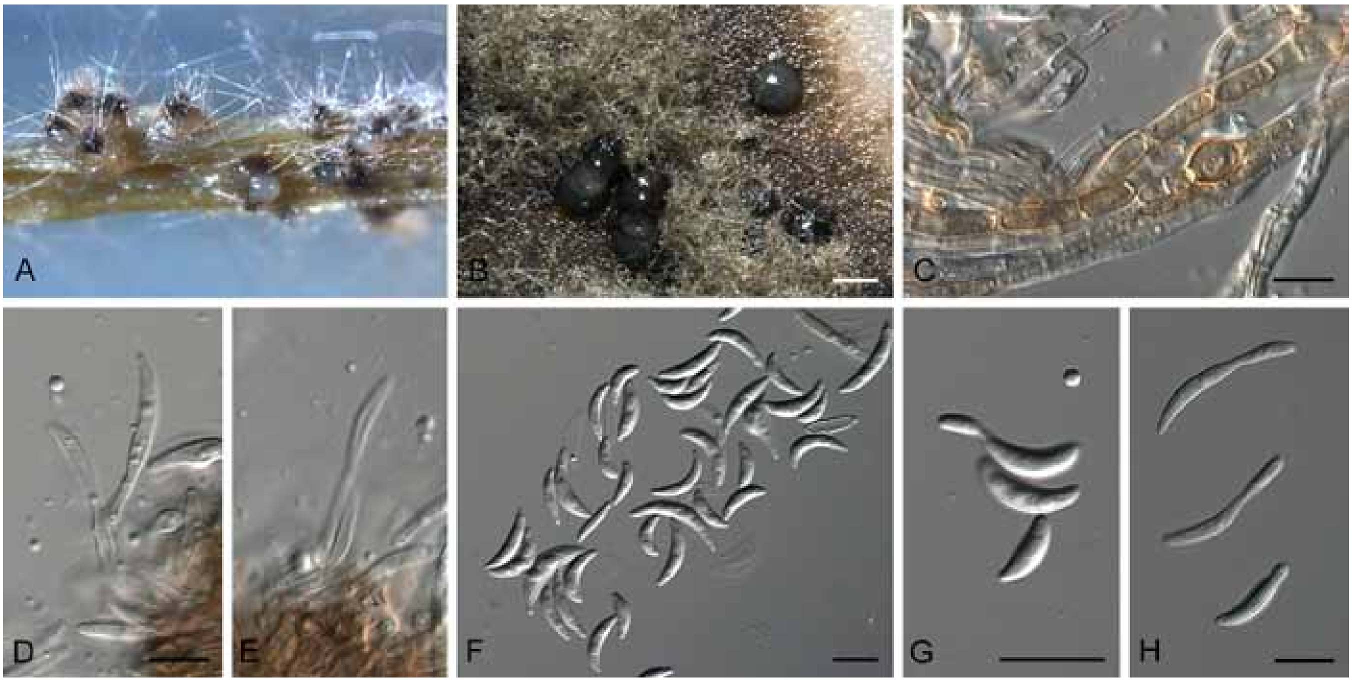


**Fig. 56.** *Pseudoseptoria obscura* (CBS 135103). A, B. Colony sporulating in culture. C. Chlamydospore-like cells developing. D, E. Conidiogenous cells. F–H. Conidia. Scale bars: B = 250 µm, all others = 10 µm.

in a mucilaginous matrix. *Conidiogenous cells* subcylindrical to ampulliform, hyaline, smooth to pale brown, finely verruculose, 18–35 × 3.5–8 µm; apical region with numerous conspicuous percurrent proliferations, with long, prominent collarettes that completely enclose and extend above young, developing conidia, but disintegrating into a mucoid mass with age. *Conidia* fusiform, lunate, curved, aseptate, hyaline, smooth, tapering to an subobtuse to spathulate apex, base truncate (1 µm diam), with a single, unbranched, eccentric basal appendage, 2–4 µm long; conidia (from apex to hilum) (24–)26–28(–30) × (2.5–)3 µm.

*Culture characteristics*: Colonies on PDA flat, round with feathery margins, lacking aerial mycelium, surface olivaceous-black to rosy-buff for younger tissue, reverse olivaceous-black, to rosy-buff for younger tissue, after 14 d 1.5 cm diam; on MEA surface olivaceous-black to buff for younger tissue, reverse olivaceous-black to brick for younger tissue, after 14 d, 2 cm diam; on OA similar to MEA.

*Specimen examined*: **Iran**, Golestan Province, on leaves of Bamboo (*Poaceae*), 12 May 2009, A. Mirzadi Gohari (**holotype** CBS H-21302, culture ex-type CBS 135104 = CPC 18119).

***Pseudoseptoria obscura*** Quaedvlieg, Verkley & Crous, **sp. nov.** MycoBank MB804434. Fig. 56.

*Etymology*: Named after the obscure basal appendage that occurs on some conidia.

On sterile *Carex* leaves on WA. *Conidiomata* immersed to erumpent, globose, dark brown, up to 250 µm diam (smaller than in 18119), unilocular, opening via central ostiole; wall of 3–6 layers of brown *textura angularis*. *Conidiophores* reduced to conidiogenous cells. *Conidiogenous cells* subcylindrical to doliiform, hyaline, smooth to pale brown, finely verruculose, 6–12 × 2–5 µm; apical region with numerous inconspicuous to conspicuous percurrent proliferations; collarettes absent to prominent. *Conidia* fusiform, lunate, curved, aseptate, hyaline, smooth, tapering to an subobtuse apex; base truncate, rarely with a single, unbranched, eccentric basal appendage, 1–2 µm long; conidia (from apex to hilum) (8–)12–14(–15) × (2–)2.5(–3) µm.

*Culture characteristics*: Colonies on PDA flat, undulate with feathery margins, lacking aerial mycelium, surface concentric rings of fuscous-black to pale purplish grey to fuscous-black, reverse concentric rings of greyish-sepia to fawn to fuscous-black, after 14 d, 2 cm diam; on MEA similar to PDA; OA flat, undulate, lacking aerial mycelium, surface fuscous-black to purplish grey for the younger tissue, reverse greyish-sepia to vinaceous-buff for the younger tissue.

*Specimen examined*: **Iran**, Golestan Province, on leaves of Bamboo (*Poaceae*), 12 May 2009, A. Mirzadi Gohari (**holotype** CBS H-21303, culture ex-type CBS 135103 = CPC 18118).

*Notes*: Species of the genus *Aphanofalx* occur on members of *Poaceae*, presumably as saprobes. The genus is characterised by having taxa with pycnidial conidiomata, and percurrently proliferating conidiogenous cells, and hyaline, aseptate conidia with a basal, excentric appendage. In contrast, species of *Pseudoseptoria* are known to occur on members of *Poaceae* as plant pathogens. The genus is also characterised by having taxa with pycnidial conidiomata, and percurrently proliferating conidiogenous cells, and hyaline, aseptate conidia that lack basal appendages. During this study we also investigated three strains identified as *P. donasis* (CBS 291.69, 313.68 and 417.51), the type species of *Pseudoseptoria*. Much to our surprise they formed a monophyletic lineage (results not shown) with the two strains described here (which have basal appendages), suggesting that *Pseudoseptoria* represents an older name for *Aphanofalx*, and that the basal appendage is a species-specific character, as also found in other groups of coelomycetes (Crous *et al.* 2012b).

*Aphanofalx* is presently known from two species, *A. mali* (conidia 26–33 × 2–2.5 µm), and *A. irregularis* (conidia 12–28(–31) × (2–)2.5–

3(–3.5) µm (Nag Raj 1993). *Pseudoseptoria collariana* [conidia (24–)26–28(–30) × (2.5–)3 µm] and *P. obscura* [conidia (8–)12–14(–15) × (2–)2.5(–3) µm] are easily distinguished from these taxa based on their conidial dimensions. The three species of *Pseudoseptoria* treated by Sutton (1980), namely *P. donacis* (conidia 20–23 × 2–2.5 µm), *P. stromaticola* (conidia 16–18.5 × 2 µm) and *P. bromigena* (conidia 20–23 × 2–2.5 µm) can be distinguished from *P. collorata* and *P. obscura* by conidial dimensions, and lacking basal conidial appendages.

## Clade 27: *Parastagonospora*

***Parastagonospora*** Quaedvlieg, Verkley & Crous, **gen. nov.** MycoBank MB804435.

*Etymology*: Resembling the genus *Stagonospora*.

*Foliicolous*, plant pathogenic. Ascocarps immersed, globose, becoming depressed, medium brown to black; wall of 3–6 layers of thick-walled, brown *textura angularis*; ostiole slightly papillate. Asci clavate, cylindrical or curved, shortly stipitate, 8-spored; ascus wall thick, bitunicate. Ascospores fusoid, subhyaline to pale brown, transversely euseptate (–3), constricted at the septa, penultimate cell swollen. Pseudoparaphyses filiform, hyaline, septate. *Conidiomata* black, immersed, subepidermal, pycnidial, subglobose with central ostiole, exuding creamy conidial mass; wall of 2–3 layers of brown *textura angularis*. *Conidiophores* reduced to conidiogenous cells. *Conidiogenous cells* phialidic, hyaline, smooth, aggregated, lining the inner cavity, ampulliform to subcylindrical, with percurrent proliferation near apex. *Conidia* hyaline, smooth, thin-walled, cylindrical, granular to multi-guttulate, with obtuse apex and truncate base, transversely euseptate.

*Type species*: *Parastagonospora nodorum* (Berk.) Quaedvlieg, Verkley & Crous.

*Notes*: The genus *Parastagonospora* is introduced to accommodate several serious cereal pathogens that were formerly accommodated in either *Septoria/Stagonospora*, or *Leptosphaeria/Phaeosphaeria*. As shown previously, *Septoria* is not available for these fungi (Quaedvlieg *et al*. 2011), and neither is *Leptosphaeria* (de Gruyter *et al*. 2013). Furthermore, in the present study we also clarify the phylogenetic positions of *Stagonospora* and *Phaeosphaeria*, which cluster apart from this group of cereal pathogens, which are best accommodated in their own genus, *Parastagonospora*.

*Parastagonospora* is distinguished from *Stagonospora* in that *Stagonospora* has conidiogenous cells that proliferate percurrently, or via phialides with periclinal thickening, and conidia that are subcylindrical to fusoid-ellipsoidal. Sexual morphs known for species of *Parastagonospora* are phaeosphaeria-like, whereas those observed for *Stagonospora s. str.* are didymella-like.

***Parastagonospora avenae*** (A.B. Frank) Quaedvlieg, Verkley & Crous, **comb. nov.** MycoBank MB804436.
*Basionym*: *Septoria avenae* A.B. Frank, Ber. Dt. Bot. Ges. 13: 64. 1895.

≡ *Stagonospora avenae* (A.B. Frank) Bissett [as 'avena'], Fungi Canadenses, Ottawa 239: 1. 1982
= *Leptosphaeria avenaria* G.F. Weber, Phytopath. 12: 449. 1922.
≡ *Phaeosphaeria avenaria* (G.F. Weber) O.E. Erikss., Ark. Bot., Ser. 2 6: 408. 1967.
= *Pleospora tritici* Garov., Arch. Triennale Lab. Bot. Crittog. 1: 123. 1874.

*Specimens examined*: **Germany**, Kiel-Kitzeberg, on *Lolium multiflorum*, 1968, U.G. Schlösser, CBS 290.69, CBS 289.69.

*Notes*: Although the oldest epithet for this taxon is *Pleospora tritici* (1874), "*avenae*" has been well established in literature, and accepted by the community. We thus recommend that this epithet be retained for this pathogen. Parastagonospora avenae leaf blotch of barley and rye (f.sp. *tritici*), appears distinct from the pathogen on oats (f.sp. *avenaria*) (Cunfer 2000), and further research is required to resolve this issue.

***Parastagonospora caricis*** Quaedvlieg, Verkley & Crous, **sp. nov.** MycoBank MB804437. Figs 57, 58.

*Etymology*: Named after the host genus from which it was collected, *Carex*.

On sterile *Carex* leaves on WA. *Conidiomata* up to 250 µm diam, black, immersed, subepidermal, pycnidial, subglobose with central ostiole, exuding pale pink conidial cirrhus; wall of 2–3 layers of brown *textura angularis*. *Conidiophores* reduced to conidiogenous cells. *Conidiogenous cells* phialidic, hyaline, smooth, aggregated, lining the inner cavity, ampulliform, 8–15 × 4–6 µm, with percurrent proliferation at apex. *Conidia* hyaline, smooth, thin-walled, scolecosporous, subcylindrical, with subobtuse apex and truncate base, 7–15-septate, (50–)60–70(–75) × (5–)6 µm.

*Culture characteristics*: Colonies on PDA flat, undulate, with short, white aerial mycelium, surface olivaceous-black in the older parts, vinaceous-buff in the younger mycelium, reverse olivaceous-black in the older parts, brick in the younger mycelium, after 14 d, 4 cm diam; on MEA convex, fimbriate, surface fawn to hazel, reverse fusceous-black to cinnamon, after 14 d, 3 cm diam; on OA similar to MEA.

*Specimen examined*: **Netherlands**, Veenendaal, de Blauwe Hel, on leaves of *Carex acutiformis* (*Cyperaceae*), 25 Jul. 2012, W. Quaedvlieg (**holotype** CBS H-21304, culture ex-type CBS 135671 = S615).

*Note*: Conidia of *P. caricis* are larger than those of *P. avenae*, which are (1–)3(–7)-septate, 17–46 × 2.5–4.5 µm (Bissett 1982), and narrower than those of *Stagonospora gigaspora*, which are 58–84 × 10–14 µm (Ellis & Ellis 1997).

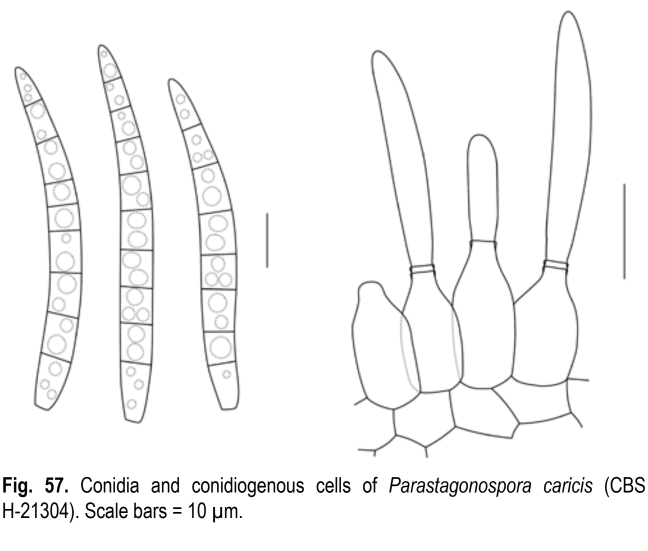

**Fig. 57.** Conidia and conidiogenous cells of *Parastagonospora caricis* (CBS H-21304). Scale bars = 10 µm.

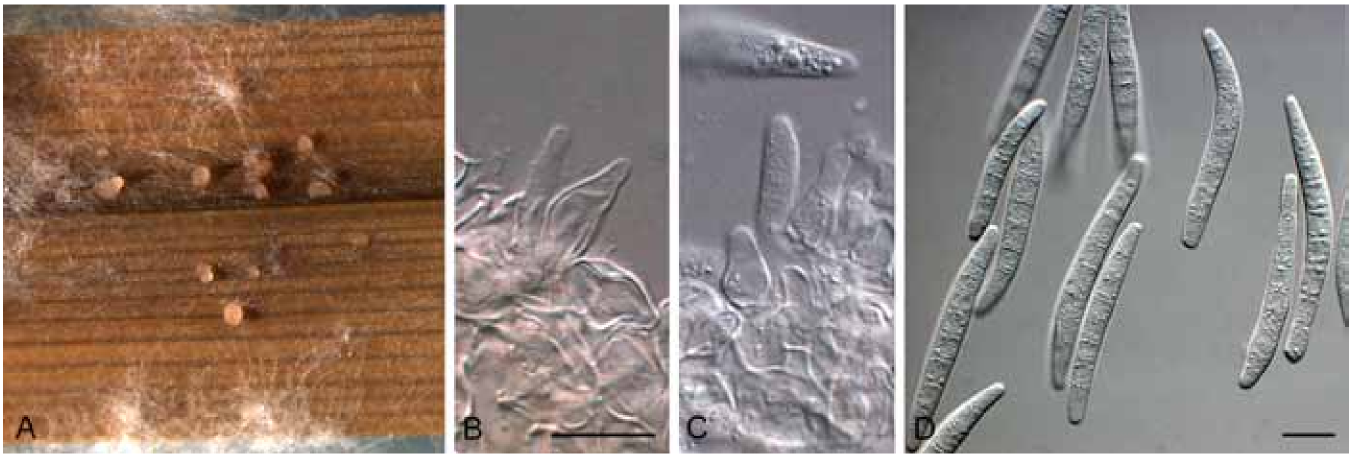

**Fig. 58.** *Parastagonospora caricis* (CBS H-21304). A. Colony sporulating in culture. B, C. Conidiogenous cells. D. Conidia. Scale bars = 10 µm.

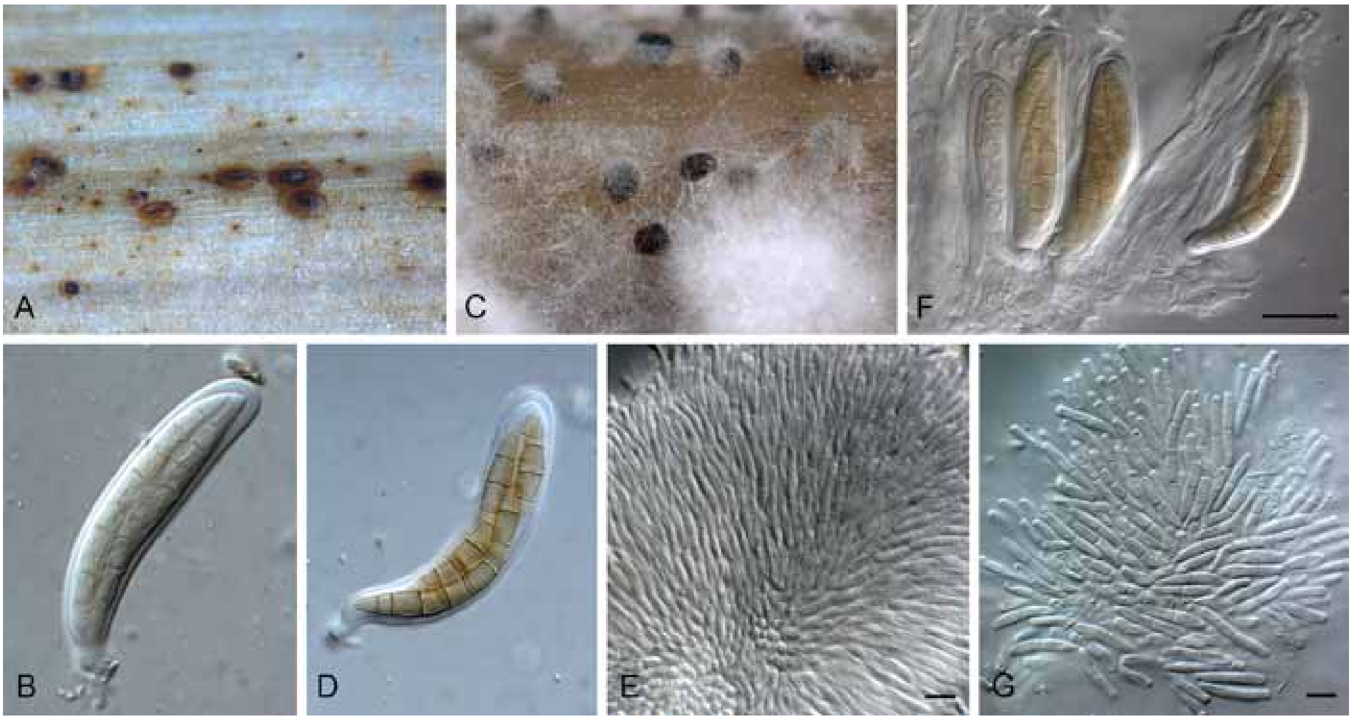

**Fig. 59.** *Parastagonospora nodorum* (CBS H-13909). A, C. Ascomata and conidiomata forming in culture. B, D, F. Asci with ascospores. E, G. Conidia. Scale bars = 10 µm.

***Parastagonospora nodorum*** (Berk.) Quaedvlieg, Verkley & Crous, **comb. nov.** MycoBank MB804438. Fig. 59.
*Basionym*: *Depazea nodorum* Berk., Gard. Chron., London: 601. 1845.

≡ *Septoria nodorum* (Berk.) Berk., Gard. Chron., London: 601. 1845.
≡ *Stagonospora nodorum* (Berk.) E. Castell. & Germano, Annali Fac. Sci. Agr. Univ. Torino 10: 71. 1977. [1975–76]
= *Leptosphaeria nodorum* E. Müll., Phytopath. J. 19: 409. 1952.
≡ *Phaeosphaeria nodorum* (E. Müll.) Hedjar., Sydowia 22: 79. 1969. [1968]

*Specimen examined*: **Denmark**, on *Lolium perenne*, Feb. 2002, M.P.S. Câmara, CBS 110109.

*Notes*: Parastagonospora nodorum blotch is an important disease of cereals, having been reported from barley and wheat in most countries where these crops are cultivated (Cunfer 2000). Recent studies have also indicated that *P. nodorum* probably resembles a species complex, awaiting further morphological characterisation (McDonald *et al.* 2013).

***Parastagonospora poae*** Quaedvlieg, Verkley & Crous, **sp. nov.** MycoBank MB804439. Figs 60, 61.

*Etymology*: Named after the host genus from which it was collected, *Poa*.

On sterile *Carex* leaves on WA. *Conidiomata* up to 250 µm diam, black, immersed, subepidermal, pycnidial, subglobose with central ostiole, exuding creamy conidial mass; wall of 2–3 layers of brown *textura angularis*. *Conidiophores* reduced to conidiogenous cells. *Conidiogenous cells* phialidic, hyaline, smooth, aggregated, lining the inner cavity, ampulliform to subcylindrical, with percurrent proliferation near apex, 6–10 × 3–4(–5) µm. *Conidia* hyaline, smooth, thin-walled, cylindrical, granular, with obtuse apex and truncate base, medianly 1-septate, (20–)25–27(–32) × (2–)2.5(–2.5) µm; ends becoming swollen and guttulate with age.

*Culture characteristics*: Colonies on PDA flat, circular, with sparse, white aerial mycelium, surface dark-mouse-grey, reverse black, after 14 d, 8.5 cm diam; on MEA surface hazel, reverse dark-brick to sepia; OA similar to MEA.

*Specimens examined*: **Netherlands**, Wageningen, on leaves of *Poa* sp. (*Poaceae*), 2 Aug. 2012, S. Videira J (**holotype** CBS H-21305, culture ex-type CBS 135089 = S606); Wageningen, on leaves of *Poa* sp., 2 Aug. 2012, S. Videira CBS 135091 = S613).

*Note*: Conidia of *P. poae* are narrower than those of *P. nodorum*, which are (0–)1–3-septate, 13–28 × 2.8–4.6 µm (Bissett 1982).

## Clade 28: *Neostagonospora*

***Neostagonospora*** Quaedvlieg, Verkley & Crous, **gen. nov.** MycoBank MB804440.

*Etymology*: Resembling the genus *Stagonospora*.

*Foliicolous. Conidiomata* immersed, pycnidial, globose, exuding a pale luteous to creamy conidial mass; wall of 2–3 layers of pale brown *textura angularis*. *Conidiophores* reduced to conidiogenous cells. *Conidiogenous cells* phialidic, hyaline, smooth, aggregated, lining the inner cavity, ampulliform to doliiform, tapering at apex with prominent periclinal thickening. *Conidia* hyaline, smooth, granular, thin-walled, narrowly fusoid-ellipsoidal to subcylindrical, apex subobtusely rounded, base truncate, widest in middle, transversely euseptate, becoming constricted with age.

*Type species*: *Neostagonospora caricis* Quaedvlieg, Verkley & Crous.

*Note*: *Neostagonospora* is similar to *Stagonospora* by having pycnidial conidiomata with euseptate, hyaline, fusoid-ellipsoidal to subcylindrical conidia, but distinct in having conidiogenous cells that are phialidic, with prominent periclinal thickening.

***Neostagonospora caricis*** Quaedvlieg, Verkley & Crous, **sp. nov.** MycoBank MB804441. Figs 62, 63.

*Etymology*: Named after the host genus on which it occurs, *Carex*.

On sterile *Carex* leaves on WA. *Conidiomata* immersed, pycnidial, globose, up to 200 µm diam, exuding a pale luteous to creamy conidial mass; wall of 2–3 layers of pale brown *textura angularis*. *Conidiophores* reduced to conidiogenous cells. *Conidiogenous cells* phialidic, hyaline, smooth, aggregated, lining the inner cavity, ampulliform to doliiform, 5–7 × 5–7 µm; tapering at apex with prominent periclinal thickening. *Conidia* hyaline, smooth, granular, thin-walled, narrowly fusoid-ellipsoidal, apex subobtusely rounded, base truncate, widest in middle, 1-septate, becoming constricted with age, (10–)13–16(–19) × (3–)3.5(–4) µm.

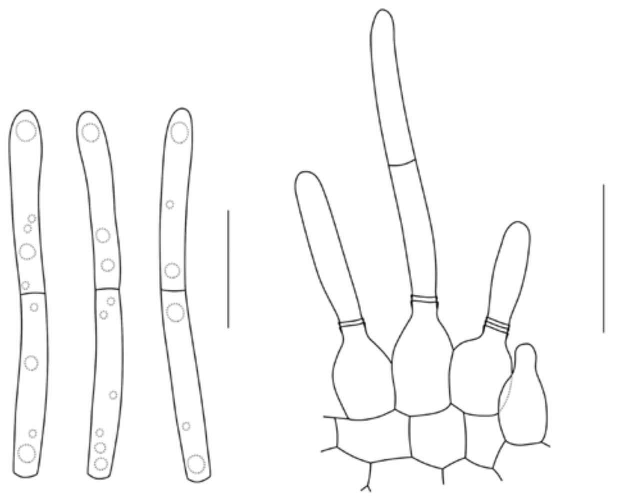

**Fig. 60.** Conidia and conidiogenous cells of *Parastagonospora poae* (CBS 135091). Scale bars = 10 µm.

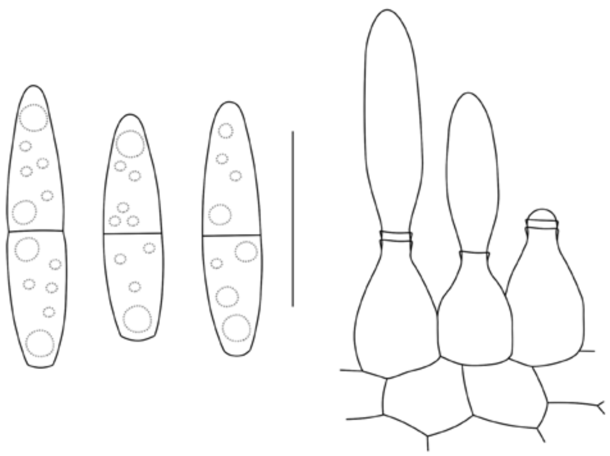

**Fig. 62.** Conidia and conidiogenous cells of *Neostagonospora caricis* (CBS 135092). Scale bars = 10 µm.

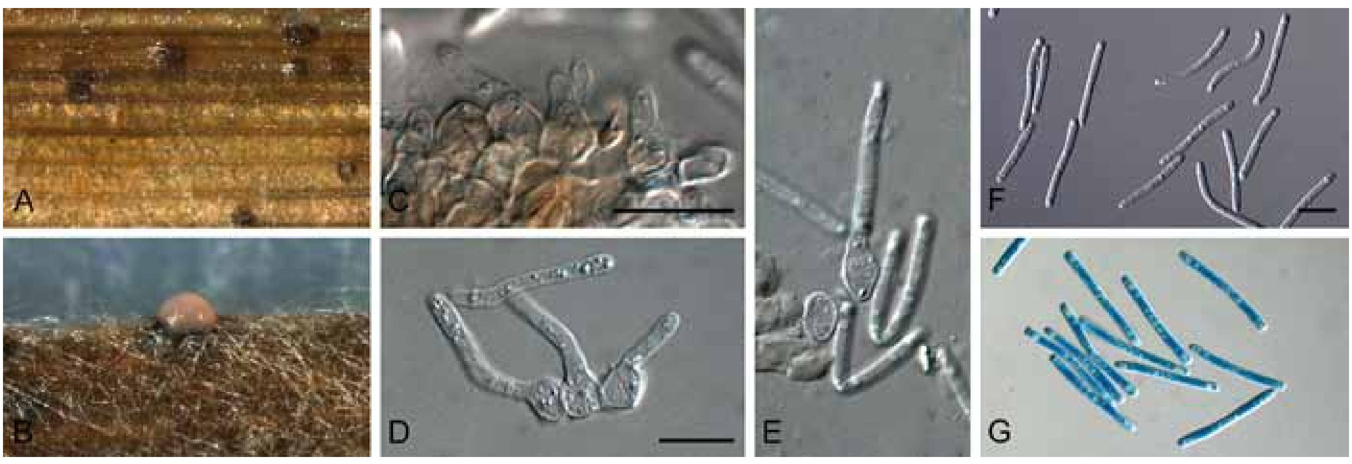


**Fig. 61.** *Parastagonospora poae* (CBS 135091). A, B. Conidiomata forming in culture. C–E. Conidiogenous cells. F, G. Conidia. Scale bars = 10 µm.

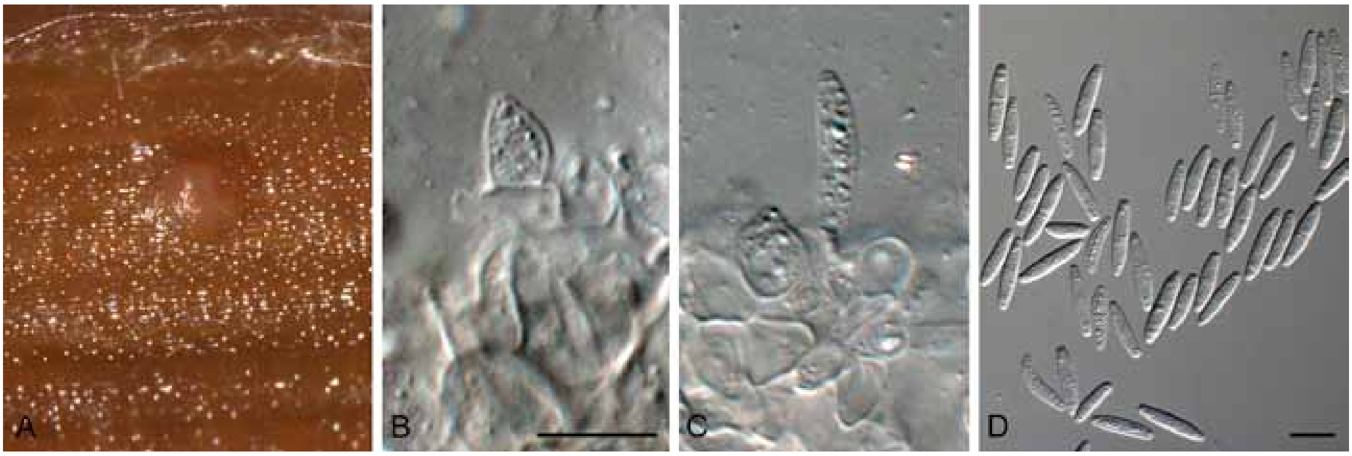


**Fig. 63.** *Neostagonospora caricis* (CBS 135092). A. Conidioma forming in culture. B, C. Conidiogenous cells. D. Conidia. Scale bars = 10 µm.

*Culture characteristics*: Colonies on PDA flat, undulate, with sparse, powdery white aerial mycelium, surface greyish-sepia to isabelline, reverse olivaceous-grey to pale olivaceous-grey, after 14 d, 8.5 cm diam; on MEA erumpent, circular, with fine white aerial mycelium, surface honey, reverse cinnamon, after 14 d, 6 cm diam; on OA similar to PDA but surface honey, reverse cinnamon.

*Specimen examined*: **Netherlands**, Veenendaal, de Blauwe Hel, on leaves of *Carex acutiformis* (*Cyperaceae*), Aug. 2012, W. Quaedvlieg (**holotype** CBS H-21306, culture ex-type CBS 135092 = S616).

*Note*: *Neostagonospora caricis* is similar to *Septoria caricis* (conidia 1-septate, 20–35 × 2.5–3 µm; Ellis & Ellis 1997), although its conidia are shorter.

***Neostagonospora elegiae*** Quaedvlieg, Verkley & Crous, **sp. nov.** MycoBank MB804442. Figs 64, 65.

*Etymology*: Named after the host genus from which it was collected, *Elegia.*

On *Anthriscus* stem. *Conidiomata* pycnidial, up to 150 µm diam, erumpent, globose, brown, opening by a central ostiole, exuding a crystalline conidial mass; wall consisting of 3–6 layers of pale brown *textura angularis*. *Conidiophores* reduced to conidiogenous cells. *Conidiogenous cells* phialidic, lining the inner cavity, hyaline, smooth, ampulliform, 4–7 × 4–6 µm; apex with prominent periclinal thickening. *Conidia* hyaline, smooth, guttulate to granular, scolecosporous, irregularly curved, subcylindrical, apex subobtuse, base truncate (slight taper from apical septum to apex and basal septum to hilum visible in some conidia), (0–)3-septate, (20–)50–65(–70) × (2.5–)3 µm.

*Culture characteristics*: Colonies spreading, erumpent with moderate aerial mycelium and smooth, even margins; reaching 35 mm diam after 2 wk. On OA pale luteous. On MEA dirty white on surface, luteous in reverse. On PDA dirty white on surface, pale luteous in reverse.

*Specimen examined*: **South Africa**, Western Cape Province, Harold Porter Botanical Garden, on leaves of *Elegia cuspidata* (*Restionaceae*), 30 Nov. 2001, S. Lee (**holotype** CBS H-21307, culture ex-type CBS 135101 = CPC 16977).

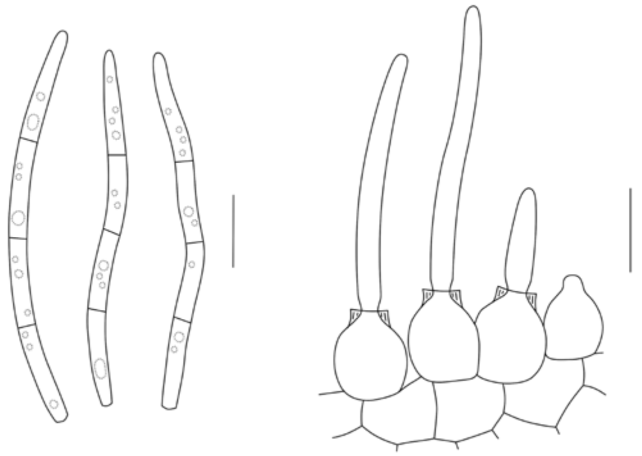

**Fig. 64.** Conidia and conidiogenous cells of *Neostagonospora elegiae* (CBS 135101). Scale bars = 10 µm.

*Notes*: No septoria-like fungi are presently known from *Elegia* (Lee *et al*. 2004). *Neostagonospora elegiae* is distinguished from *N. caricis* based on its conidial morphology.

## Clade 29: *Phaeosphaeriopsis*

***Phaeosphaeriopsis*** M.P.S. Câmara, M.E. Palm & A.W. Ramaley, Mycol. Res. 107: 519. 2003.

*Saprobic* or *plant pathogenic. Ascomata* solitary or aggregated, immersed, subepidermal to erumpent, pushing up flaps of the epidermis, globose to pyriform, often papillate, solitary or gregarious in a stroma of scleroplectenchyma or dark brown *textura angularis*, often surrounded by septate, brown hyphae extending into the host tissues. *Asci* 8-spored, bitunicate, cylindrical to broadly fusoid, short stipitate, with visible apical chamber. *Ascospores* uni- to triseriate, cylindrical, broadly rounded at apex, tapering to narrowly rounded base, 4–5-septate, first septum submedian, often constricted, medium brown, echinulate, punctate or verrucose. Asexual morph coniothyrium-like or phaeostagonospora-like. *Conidiomata* pseudoparenchymatous, sometimes of scleroplectenchyma. *Conidiogenous cells* lining locule, ampulliform, hyaline, proliferating percurrently, resulting in inconspicuous annellations. *Conidia* cylindrical, with bluntly rounded ends, 0–3-septate, yellowish brown, punctate (Câmara *et al*. 2003, Zhang *et al*. 2012).

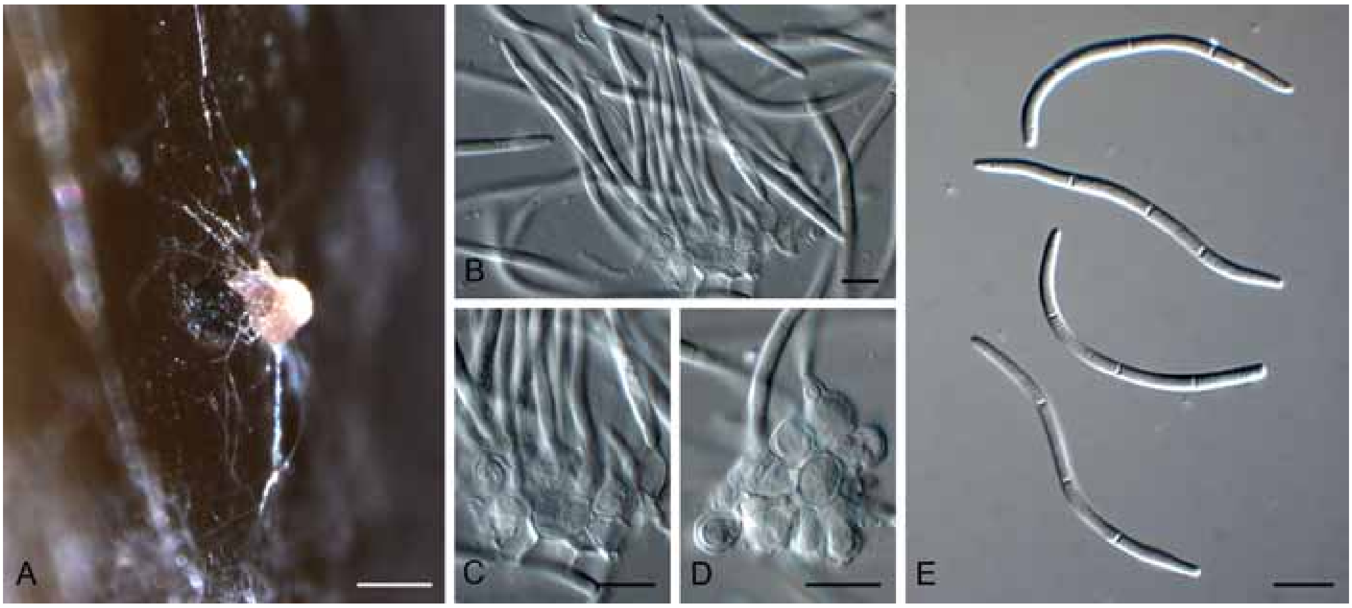


**Fig. 65.** *Neostagonospora elegiae* (CBS 135101). A. Conidioma forming in culture. B–D. Conidiogenous cells. E. Conidia. Scale bars: A = 150 µm, all others = 10 µm.

*Type species*: *Phaeosphaeriopsis glaucopunctata* (Grev.) M.P.S. Câmara, M.E. Palm & A.W. Ramaley, Mycol. Res., 107: 519. 2003.

***Phaeosphaeriopsis glaucopunctata*** (Grev.) M.P.S. Câmara, M.E. Palm & A.W. Ramaley, Mycol. Res. 107: 519. 2003. Figs 66, 67.
*Basionym*: *Cryptosphaeria glaucopunctata* Grev., Fl. Edin.: 362. 1824.

≡ *Paraphaeosphaeria glaucopunctata* (Grev.) Shoemaker & C. E. Babc., Can. J. Bot. 63: 1286. 1985.
= *Sphaeria rusci* Wallr., Fl. Crypt. Germ. 2: 776. 1833.
≡ *Leptosphaeria rusci* (Wallr.) Sacc., Syll. Fung. 2: 74. 1883.
≡ *Paraphaeosphaeria rusci* (Wallr.) O. E. Erikss., Ark. Bot., Ser. 2 6: 406. 1967.

*Ascomata* scattered or aggregated, immersed, globose to subglobose, up to 250 µm diam; peridium up to 25 µm wide, of thick-walled *textura angularis*; *hamathecium* of dense, wide, cellular pseudoparaphyses, 3–5 µm diam. *Asci* 8-spored, bitunicate, cylindrical to broadly fusoid, with a short pedicel and small apical chamber, 50–110 × 10–16 µm. *Ascospores* uni- to triseriate, cylindrical, medium brown, 4(−5)-septate, without constriction or slightly constricted at the basal septum, the forth cell from the apex usually slightly inflated, the basal cell often longer, 14–28 × (3.5–)5–7.5 µm. *Conidiomata* pycnidial, immersed, scattered or aggregated, dark brown, subglobose, ostiolate, up to 200 µm diam. *Conidiophores* reduced to conidiogenous cells. *Conidiogenous cells* lining the inner cavity, ampulliform, hyaline, smooth, 5–10 × 3–6 µm; proliferating percurrently at apex. *Conidia* aseptate, smooth to finely verruculose, medium brown, subcylindrical, straight to reniform with obtuse ends, (5–)7–9(–10) × (2.5–)3(–5) µm.

*Culture characteristics*: On PDA colonies flat, spreading, with sparse aerial mycelium and smooth, lobate, even margins, surface primrose, reverse olivaceous-buff, On OA buff with patches of isabelline due to sporulating conidiomata. On MEA dirty white on surface, isabelline in reverse (centre), cinnamon in outer region.

*Specimen examined*: **Switzerland**, Kt. Basel-Stadt, Park Basel, on *Ruscus aculeatus* (*Ruscaceae*), 25 Sep. 1980, *A. Leuchtmann* (CBS H-21308, culture CBS 653.86).

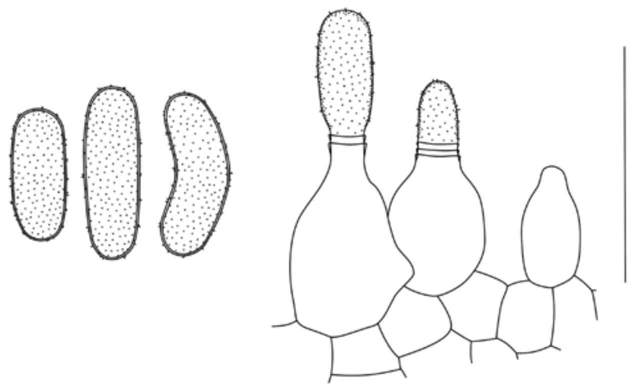

**Fig. 66.** Conidia and conidiogenous cells of *Phaeosphaeriopsis glaucopunctata* (CBS 653.86). Scale bar = 10 µm.

*Notes*: The genus *Phaeosphaeriopsis* is characterised by having uni- or multiloculate stromata and 4–5-septate ascospores. It presently contains species with coniothyrium-like, and phaeostagonospora-like asexual morphs (*e.g. P. musae*; Arzanlou & Crous 2006). The type species, *Phaeosphaeriopsis glaucopunctata*, is associated with leaf spot and necrosis on *Ruscus aculeatus* (Câmara *et al*. 2003, Golzar & Wang 2012). The fact that an isolate identified as *Chaetosphaeronema hispidulum* (lectotype of *Chaetosphaeronema*) clusters in this clade is puzzling. The genus *Chaetosphaeronema* is characterised by setose, dark brown pycnidia with thick-walled outer cell layers, producing hyaline, 1-septate conidia (Sutton 1980). Isolate CBS 216.75 proved to be sterile, however, so this matter could unfortunately not be resolved.

## Clade 30: *Sclerostagonospora*

*Description*: See above.

*Type species*: *S. heraclei* (Sacc.) Höhn., Hedwigia 59: 252. 1917.

***Sclerostagonospora phragmiticola*** Quaedvlieg, Verkley & Crous, **sp. nov.** MycoBank MB804443. Fig. 68.

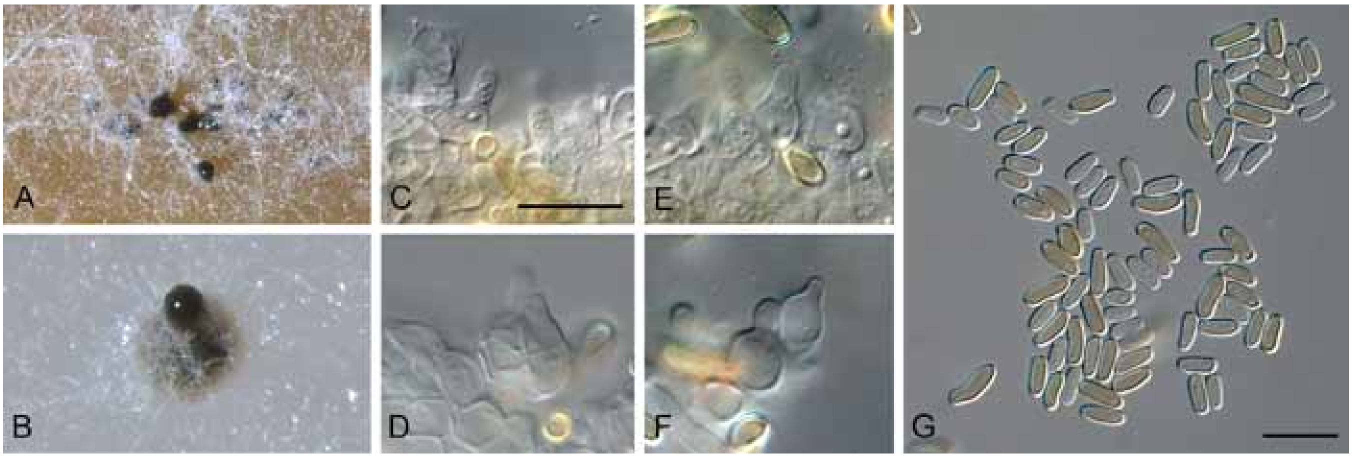


**Fig. 67.** *Phaeosphaeriopsis glaucopunctata* (CBS 653.86). A. Colony on MEA. B. Colony on OA. C–F. Conidiogenous cells giving rise to conidia. G. Conidia. Scale bars = 10 µm

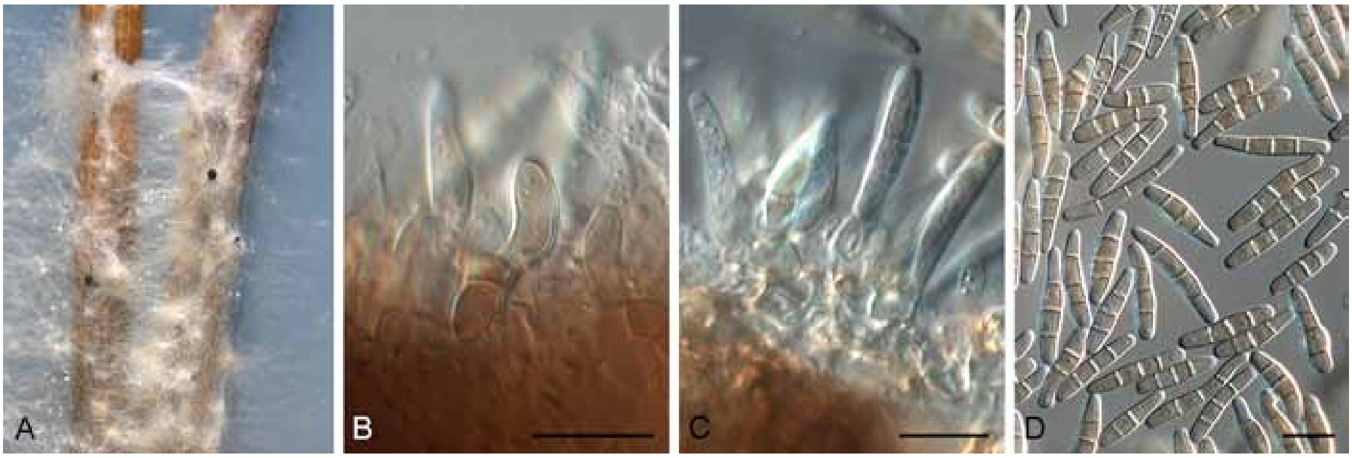


**Fig. 68.** *Sclerostagonospora phragmiticola* (CBS 338.86). A. Colony sporulating in culture. B, C. Conidiogenous cells. D. Conidia. Scale bars = 10 µm.

*Etymology*: Named after the host genus from which it was collected, *Phragmites.*

On sterile *Carex* leaves on WA. *Conidiomata* pycnidial, brown, globose, immersed to erumpent, up to 400 µm diam with central ostiole; wall of 6–8 layers of brown *textura angularis*. *Conidiophores* reduced to conidiogenous cells. *Conidiogenous cells* lining the inner cavity of conidioma, hyaline to pale olivaceous, smooth, subcylindrical to doliiform, 6–15 × 3–4 µm, proliferating several times percurrently at apex. *Conidia* brown, smooth, subcylindrical, apex obtuse, base truncate, straight to gently curved, (1–)3(–5)-euseptate, older conidia swelling, becoming widest in second or third cell from base, (15–)20–25(–27) × (3–)3.5(–4) µm.

*Specimen examined*: **France**, Landes, Seignosse, Étang d'Hardy, on leaves of *Phragmites australis* (*Poaceae*), 11 June 1986, H.A. van der Aa (**holotype** CBS H-21309, culture ex-type CBS 338.86).

*Notes*: *Sclerostagonospora caricicola* fits the concept of *Sclerostagonospora* by having pycnidial conidiomata that give rise to hyaline conidiogenous cells that proliferate percurrently, and subcylindrical, pigmented conidia. Until fresh material of the type species, *S. heraclei* has been recollected and subjected to DNA analysis, the application of this generic name will remain tentative. Several other species cluster in this clade, suggesting that the sexual morph is phaeosphaeria-like.

## Clade 31: *Phaeosphaeria*

***Phaeosphaeria*** I. Miyake, Bot. Mag., Tokyo 23: 93. 1909.
= *Phaeoseptoria* Speg., Revta Mus. La Plata 15: 39. 1908.

*Foliicolous. Ascomata* immersed, subepidermal, ellipsoidal to globose, glabrous; ostiole central, devoid of periphyses; wall of 2–3 layers of brown *textura angularis*. *Pseudoparaphyses* transversely septate, guttulate, encased in mucous. *Asci* stipitate, clavate to cylindrical, stalked, biseriate. *Ascospores* brown, narrowly fusiform, straight or slightly curved, transversely septate, smooth to verruculose, enclosed in a mucoid sheath or not. *Conidiomata* pycnidial, immersed, becoming erumpent, brown, with central ostiole; wall of 2–3 layers of brown *textura angularis*. *Conidiophores* reduced to conidiogenous cells. *Conidiogenous cells* hyaline, ampulliform to subcylindrical or doliiform; proliferating inconspicuously percurrently near apex. *Conidia* solitary, pale brown, smooth, guttulate, subcylindrical to narrowly obclavate, apex obtuse, base truncate, straight to curved, transversely euseptate, at times slightly constricted at septa; hilum not darkened nor thickened.

*Type species*: *P. oryzae* I. Miyake, Bot. Mag. Tokyo, 23(266): 93. 1909.

*Notes*: *Phaeosphaeria* (1909; based on *P. oryzae*) is congeneric with *Phaeoseptoria* (1908; based on *P. papayae*). We choose to use the sexual name *Phaeosphaeria*, as it is well established, and less confused than *Phaeoseptoria*, which has become a confused concept applied to numerous septoria-like taxa with pigmented conidia (see Walker *et al*. 1992).

***Phaeosphaeria oryzae*** I. Miyake, Bot. Mag. Tokyo, 23(266): 93. 1909. Figs 69, 70.

≡ *Pleospora oryzae* (I. Miyake) Hara, J. Agric. Soc. Japan 31(361): 17. 1927.
≡ *Trematosphaerella oryzae* (I. Miyake) Padwick, A manual of rice diseases: 153. 1950.
≡ *Leptosphaerella oryzae* (I. Miyake) Hara, A monograph of rice diseases: 53. 1959.
≡ *Leptosphaerulina oryzae* (I. Miyake) Karan, Mycopath. Mycol. Appl. 24: 88. 1964.
= *Phaeoseptoria oryzae* I. Miyake, J. Coll. Agric. Imp. Univ. Tokyo 2(4): 260. 1910.

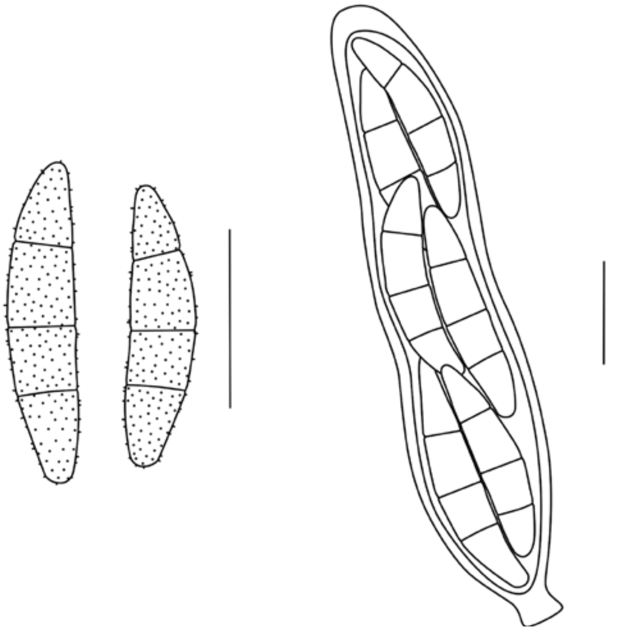

**Fig. 69.** Asci and ascospores of *Phaeosphaeria oryzae* (BPI 744438). Scale bars = 10 µm.

*Ascomata* immersed, subepidermal, ellipsoidal to globose, glabrous, up to 150 µm diam, ostiole central, up to 20 µm diam, devoid of periphyses; wall of 2–3 layers of brown *textura angularis*. *Pseudoparaphyses* 2–3 µm diam, transversely septate, guttulate, encased in mucous. *Asci* stipitate, cylindrical, 30–55 × 7–9 µm, stalked, biseriate. *Ascospores* brown, narrowly fusiform, straight or slightly curved, (15–)17–20(–23) × 4(–5) µm, 3-septate, uniformly verruculose, enclosed in a mucoid sheath; after discharge, ascospores become prominently swollen, up to 33 µm long and 8 µm wide.

*Specimens examined*: **Japan**, No. 196178, on 2, Prov. Susuya Shizuoka, Sep. 1907, ex Herb. Sydow, ex S., as *Leptosphaeria oryzae* Hori = *Phaeosphaeria oryzae* I. Miyake, slides prepared by O. Eriksson, **lectotype** (UPS). **Korea**, on leaf of *Oryza sativa* (*Poaceae*), intercepted at Port San Francisco, CA, 29 Dec. 1997, coll. L. Hausch, det. M.E. Palm, **epitype** designated here as BPI 744438, culture ex-epitype CBS 110110 (MBT175330).

*Notes*: Several detailed accounts of this species are available (Eriksson 1967, Shoemaker & Babcock 1989, Fukuhara 2002). The epitype chosen here closely matches the lectotype in morphology.

***Phaeosphaeria papayae*** (Speg.) Quaedvlieg, Verkley & Crous, **comb. nov.** MycoBank MB804444. Figs 71, 72.
*Basionym*: *Phaeoseptoria papayae* Speg., Revta Mus. La Plata: 39. 1908.

*Leaf spots* associated with infections of *Asperisporium caricae*, amphigenous, pale brown to grey-white, subcircular to angular, 1–5 mm diam, with red-purple margin; conidiomata developing

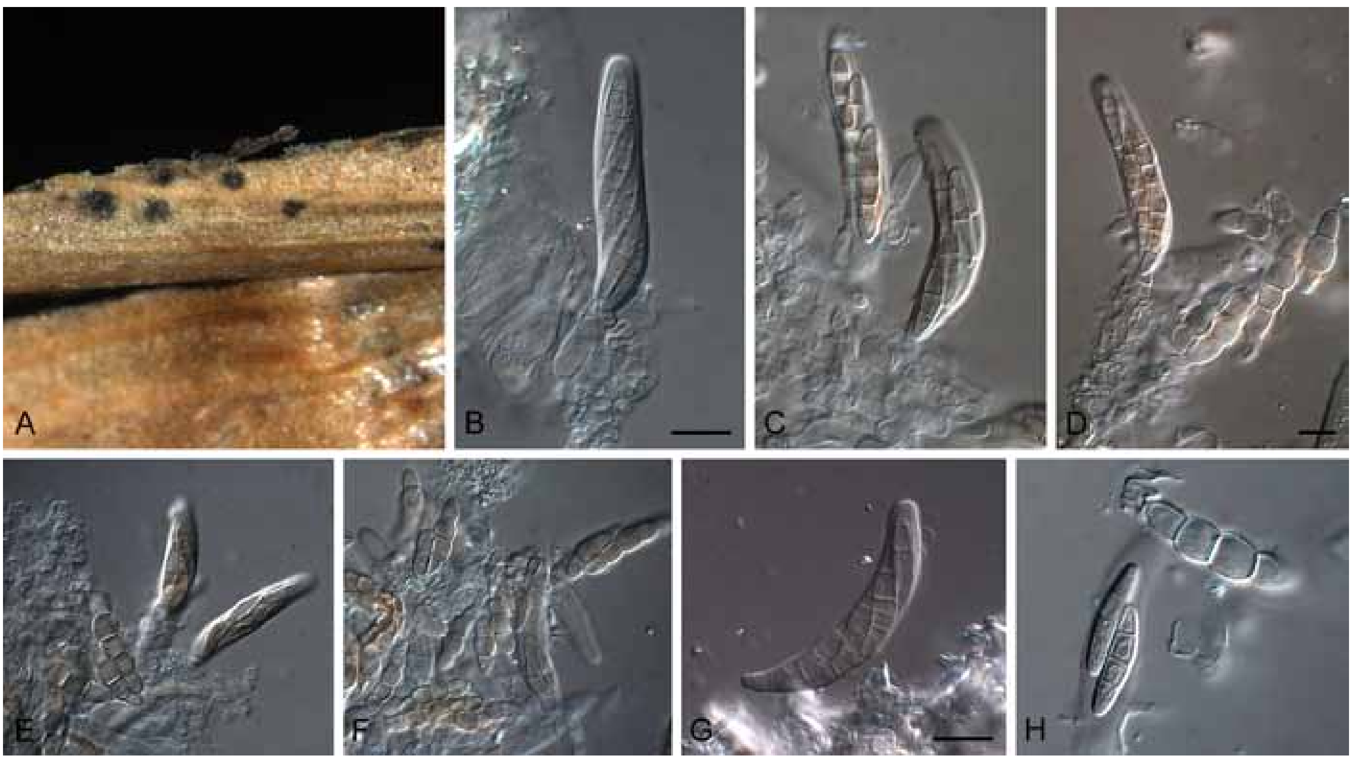


**Fig. 70.** *Phaeosphaeria oryzae* (BPI 744438). A. Ascomata on host tissue. B–G. Asci. H. Ascospores. Scale bars = 10 µm.

and sporulating on leaves when incubated in moist chambers, with white, fluffy mycelium erumpting from lesions. *Conidiomata* amphigenous, pycnidial, brown, globose, up to 120 µm diam, with central ostiole, exuding a brown conidial cirrhus; wall of 3–4 layers of brown *textura angularis*. *Conidiophores* reduced to conidiogenous cells. *Conidiogenous cells* lining the inner cavity, hyaline, smooth, ampulliform to subcylindrical or doliiform, 5–12 × 4–6 µm; proliferating inconspicuously percurrently near apex (conidiogenous cells disintegrating at maturity). *Conidia* solitary, pale brown, smooth, guttulate, subcylindrical to narrowly obclavate, apex obtuse, base truncate, (1–)3(–4)-septate, at times slightly constricted at septa, straight to slightly curved, (15–)26–32(–35) × (2.5–)3 µm; hilum not darkened nor thickened, 2 µm diam. *Ascomata* developed after 4 wk in culture on sterile nettle stems: aggregated in black clusters, globose, up to 150 µm diam, with central ostiole; wall of 2–3 layers of brown *textura angularis*. *Asci* bitunicate, curved to straight, fasciculate, short stipitate with ocular chamber, 40–60 × 8–11 µm. *Pseudoparaphyses* hyaline, smooth, 2–3 µm, septate, constricted at septa, not anastomosing, hypha-like with obtuse ends, distributed among asci. *Ascospores* tri to multiseriate, fusoid, curved to straight, brown, verruculose throughout, somewhat constricted at septa with age, second cell from apex swollen, (18–)24–26(–29) × (3–)4(–5) µm.

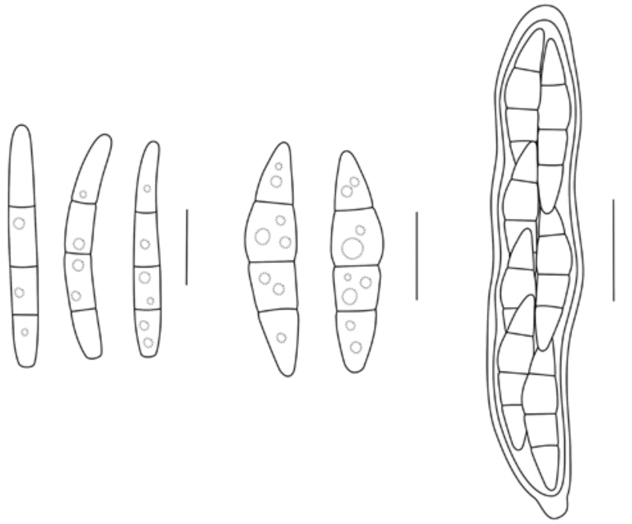

**Fig. 71.** Conidia, ascospores and ascus of *Phaeosphaeria papayae* (CBS H-21310). Scale bars = 10 µm.

*Culture characteristics*: Colonies with abundant aerial mycelium, covering dish within 2 wk at 24 ºC, fast growing, olivaceous-grey on MEA (surface and reverse); margins smooth, even, sterile on MEA, PDA and OA, as well as on SNA with sterile barley leaves.

*Specimens examined*: **Brazil**, São Paulo, Botanical Garden, on leaves of *Carica papaya* (*Caricaceae*), Sep. 1908, IMI 246301, slide ex-holotype; Minas Gerais, Viçosa, UFV campus, on leaves of *Carica papaya*, Mar. 2013, A.C. Alfenas, **epitype** designated here as CBS H-21310, culture ex-epitype CBS 135416 (MBT175331).

*Notes*: It is interesting to note that Walker *et al*. (1992) also observed *Phaeoseptoria papayae* to co-occur with *Asperisporium*

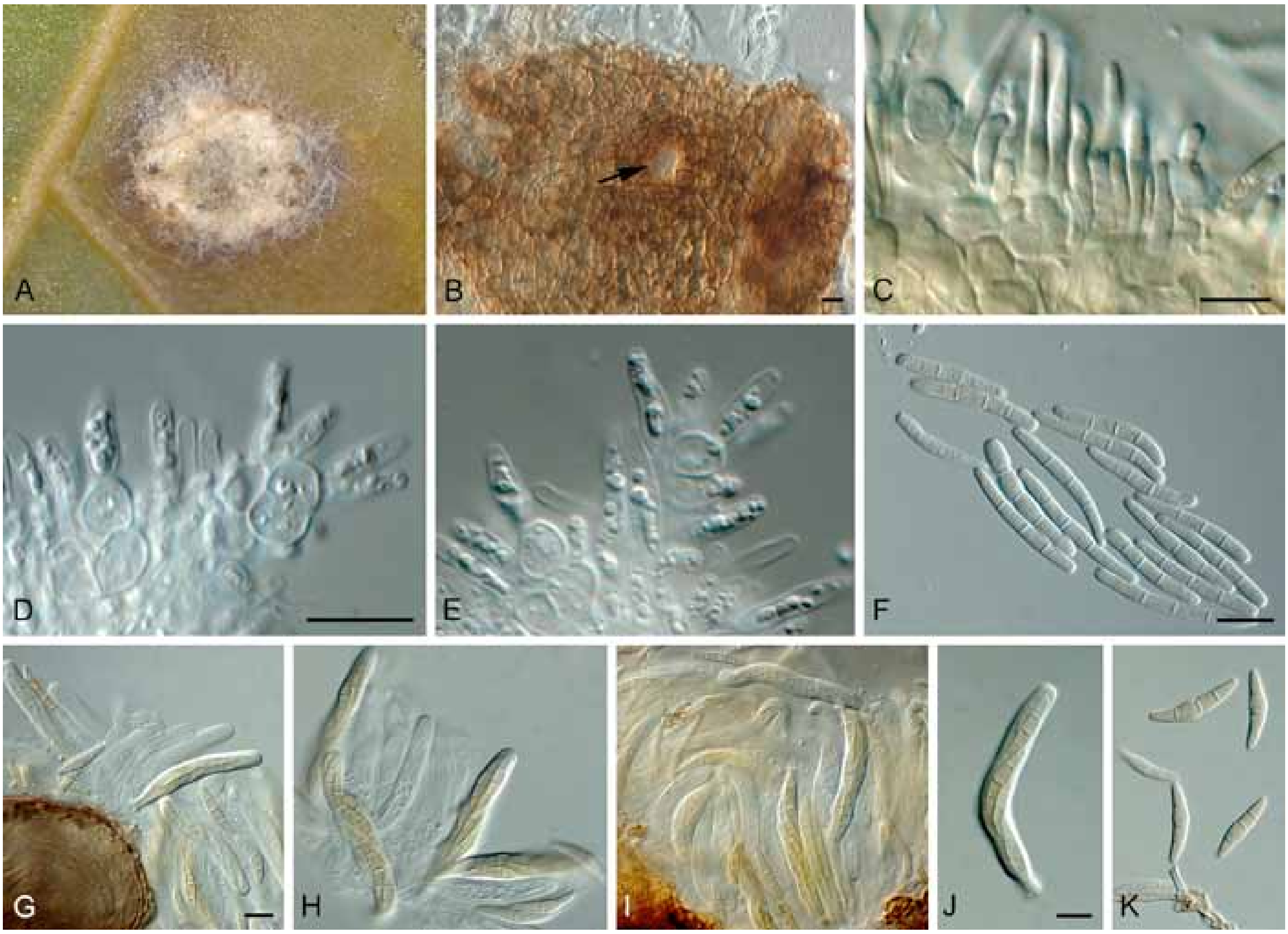


**Fig. 72.** *Phaeosphaeria papayae* (CBS H-21310). A. Leaf spot. B. Conidioma with ostiole (arrow). C–E. Conidiogenous cells. F. Conidia. G–K. Asci and ascospores. Scale bars = 10 µm.

*caricae* on the holotype specimen (noted by Spegazzini as *Cercospora caricae*), suggesting that the co-occurrence of these two pathogens is quite common. The fresh collection obtained in this study enabled us to elucide the conidiogenesis of the fungus (not observed by Walker *et al*. 1992), and also designate an epitype specimen. Phylogenetically it is closely related to *Phaeosphaeria oryzae*, which has *Phaeoseptoria oryzae* as asexual morph.

## Clade 32: *Neosetophoma*

***Neosetophoma*** Gruyter, Aveskamp & Verkley, Mycologia 102(5): 1075. 2010.

*Foliicolous,* plant pathogenic. *Conidiomata* pycnidial, solitary to confluent, on upper surface of agar, globose to irregular, with mycelial outgrowths, or confluent, with papillate ostioles, sometimes developing long necks, honey to olivaceous or olivaceous-black, with up to 10 layers of pseudoparenchymatal cells. *Conidiogenous cells* hyaline, monophyalidic. *Conidia* slightly yellowish, 0–1(–3)-septate, ellipsoidal to cylindrical, usally attenuate at one end, often guttulate.

*Type species*: *N. samarorum* Gruyter, Aveskamp & Verkley, Mycologia 102(5): 1075. 2010.

*Note*: The fact that several strains with a phaeosphaeria-like morphology cluster in this clade, suggests that sexual states do exist for species of *Neosetophoma.*

## Clade 33: *Paraphoma*

***Paraphoma*** Morgan-Jones & J.F. White, Mycotaxon 18: 58. 1983.

*Mycelium* consisting of branched, septate, subhyaline to pale brown, smooth hyphae. *Conidiomata* pycnidial, solitary to aggregated, superficial to immersed, dark brown, globose to subglobose, papillate, uniloculate, setose; ostiole circular, single; wall of 3–6 layers of brown *textura angularis*. *Setae* copious, straight to flexuous, smooth to verruculose, thick-walled, septate, pale brown to brown. *Conidiogenous cells* lageniform, monophalidic, formed from inner layer of conidiomatal wall, hyaline to subhyaline, discrete. *Conidia* ellipsoid, aseptate, hyaline, smooth, guttulate. *Chlamydospores* if present unicellular.

*Type species*: *P. radicina* (McAlpine) Morgan-Jones & J.F. White, Mycotaxon 18: 60. 1983.

***Paraphoma dioscoreae*** Quaedvlieg, H.D. Shin, Verkley & Crous, **sp. nov.** MycoBank MB804445. Figs 73, 74.

*Etymology*: Named after the host genus from which it was collected, *Dioscorea.*

On *Anthriscus* stem. *Conidiomata* pycnidial, separate, immersed becoming erumpent, globose, with papillate neck and central ostiole exuding a crystalline conidial mass; conidiomata up to 350 µm diam, neck up to 150 µm diam, of darker brown cells than body, which is pale brown; wall of 3–6 layers of pale brown *textura angularis*. *Conidiophores* hyaline, smooth, subcylindrical, reduced to conidiogenous cells, 1–5-septate, irregularly branched, 5–20 × 3–5 µm. *Conidiogenous cells* phialidic, hyaline, smooth, ampulliform to subcylindrical (long, elongated neck on *Anthriscus* stem, but not on MEA), 5–15 × 2–3 µm; apex with prominent periclinal thickening, or with several percurrent prolferations (especially on conidiogenous cells with elongated necks). *Conidia* solitary, straight to slightly curved, hyaline, smooth, aseptate, cylindrical with obtuse ends and a guttule at each end, (5–)6(–7) × 2(–2.5) µm.

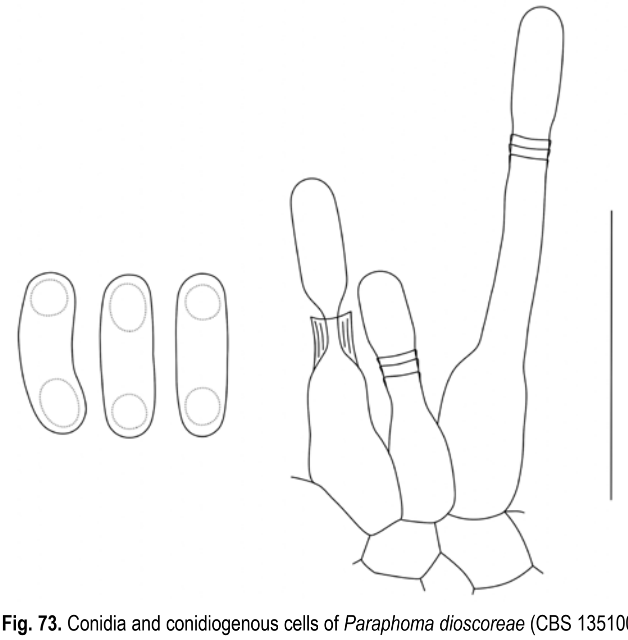

**Fig. 73.** Conidia and conidiogenous cells of *Paraphoma dioscoreae* (CBS 135100). Scale bar = 10 µm.

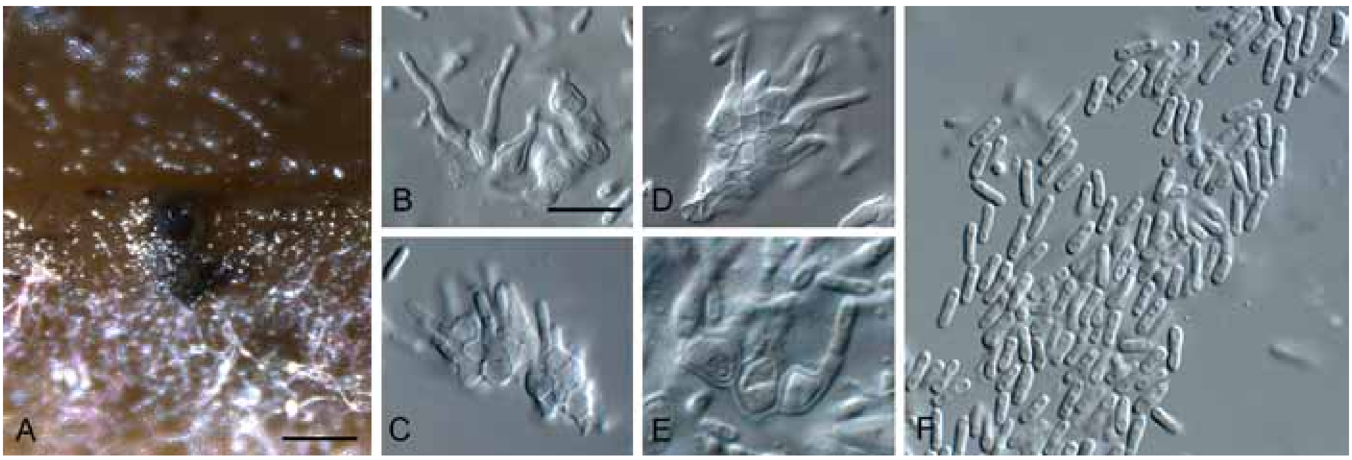


**Fig. 74.** *Paraphoma dioscoreae* (CBS 135100). A. Conidioma forming in culture. B–E. Conidiogenous cells. F. Conidia. Scale bars: B = 350 µm, all others = 10 µm.

*Culture characteristics*: Colonies flat, spreading with sparse aerial mycelium and even, smooth margins; after 2 wk reaching 30 mm diam on MEA, 40 mm on PDA and 50 mm on OA. On PDA dark brick, reverse fuscous-black. On OA dark brick with patches of sienna and ochreous. On MEA surface dirty white (due to aerial mycelium), also somewhat sectored, reverse umber.

*Specimen examined*: **South Korea**, on leaves of *Dioscorea tokoro* (*Dioscoreaceae*), 24 Oct. 2003, H.D. Shin (**holotype** CBS H-21311, culture ex-type CPC 11357 = CBS 135100).

*Note*: *Paraphoma dioscoreae* is phylogenetically distinct from the three other species presently known in the genus (de Gruyter *et al.* 2010).

## Clade 34: *Xenoseptoria*

***Xenoseptoria*** Quaedvlieg, H.D. Shin, Verkley & Crous, **gen. nov.** MycoBank MB804446.

*Etymology*: Similar to the genus *Septoria s. str.*, but distinct.

*Foliicolous,* plant pathogenic. *Conidiomata* separate, pycnidial, immersed becoming erumpent, globose, brown, developing 1–3 papillate necks, exuding a pink to orange conidial mass; wall of 4–8 layers of brown *textura angularis*. *Conidiophores* hyaline, smooth, reduced to conidiogenous cells or septate, branched below. *Conidiogenous cells* lining the inner cavity, hyaline, smooth, ampulliform to doliiform or subcylindrical, mono- to polyphialidic, with prominent periclinal thickening, but also with percurrent proliferation. *Conidia* hyaline, smooth, guttulate, scolecosporous, straight to irregularly curved, cylindrical to obclavate, transversely euseptate, tapering to subobtuse apex, base obtuse.

*Type species*: *Xenoseptoria neosaccardoi* Quaedvlieg, Verkley & Crous.

***Xenoseptoria neosaccardoi*** Quaedvlieg, H.D. Shin, Verkley & Crous, **sp. nov.** MycoBank MB804447. Figs 75, 76.

*Etymology*: Resembling *Septoria saccardoi*, but morphologically distinct.

*Leaf spots* on the upper leaf surface, scattered, distinct, circular, 2–4 mm diam, initially appearing as reddish brown discolouration, later turning brown to reddish brown without a distinct border line, finally central area becoming greyish brown to dull grey and surrounded by reddish to dark brown margin, reddish pigments may diffuse outward to form a halo; on the lower leaf surface initially showing reddish discolouration, later becoming brown with distinct border line, center greyish brown to grey with indistinct border (Shin & Sameva 2004). On sterile *Carex* leaves on WA. *Conidiomata* separate, pycnidial, immersed becoming erumpent, globose, up to 350 µm diam, brown, becoming ostiolate, developing 1–3 papillate necks, exuding a pink to orange conidial mass; wall of 4–8 layers of brown *textura angularis*. *Conidiophores* hyaline,

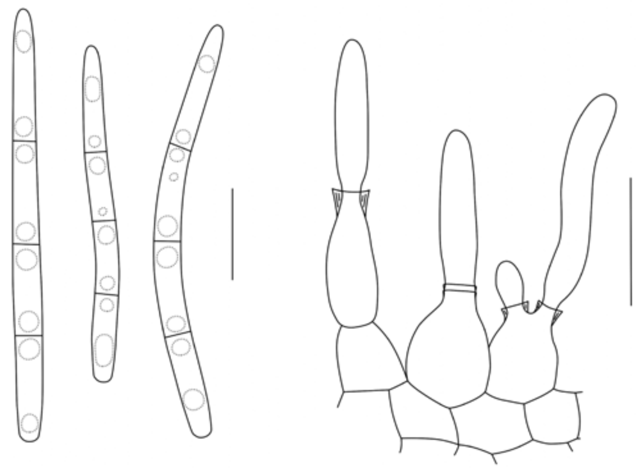

**Fig. 75.** Conidia and conidiogenous cells of *Xenoseptoria neosaccardoi* (CBS 128665). Scale bars = 10 µm.

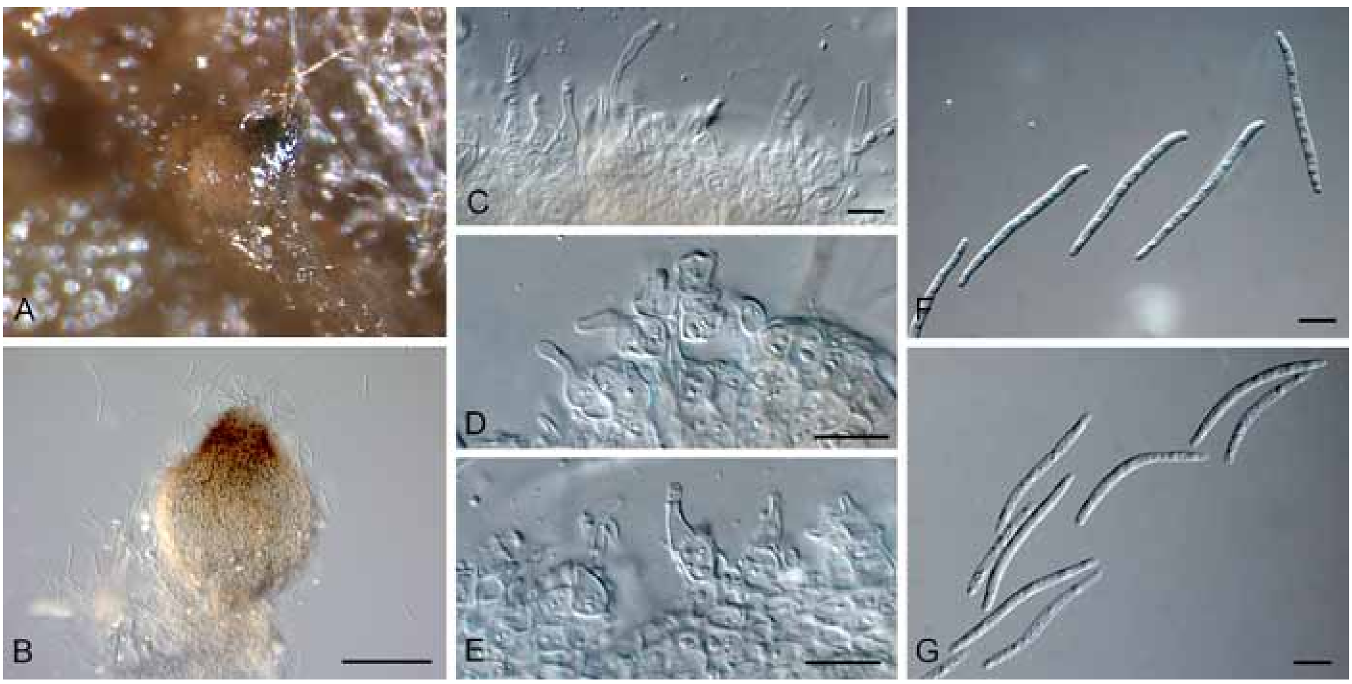


**Fig. 76.** *Xenoseptoria neosaccardoi* (CBS 128665). A, B. Pycnidia forming in culture. C–E. Conidiogenous cells. F, G. Conidia. Scale bars: B = 170 µm, all others = 10 µm.

smooth, reduced to conidiogenous cells or 1–2-septate, branched below, 10–20 × 4–6 µm. *Conidiogenous cells* lining the inner cavity, hyaline, smooth, ampulliform to doliiform or subcylindrical, mono- to polyphialidic, with prominent periclinal thickening, but also with percurrent proliferation, 5–15 × 3–5 µm. *Conidia* hyaline, smooth, guttulate, scolecosporous, straight to irregularly curved, cylindrical to obclavate, (1–)3-septate, (23–)33–45(–48) × (2.5-)3(–4) µm, tapering to subobtuse apex, base obtuse, 2–2.5 µm diam.

*Culture characteristics*: Colonies flat, spreading, with sparse aerial mycelium and lobate, feathery mergins, reaching 30 mm after 2 wk. On PDA surface iron-grey, reverse olivaceous-grey; on OA surface olivaceous-grey; on MEA surface folded, bay, reverse umber.

*Specimen examined*: **South Korea**, Pyeongchang, on leaves of *Lysimachia vulgaris* var. *davurica* (*Primulaceae*), 30 May 2007, H.D. Shin (**holotype** CBS H-21312, culture ex-type CBS 128665 = KACC 43962 = SMKC 23666).

*Notes*: An isolate of *Septoria saccardoi* (CBS 128756) clusters in *Septoria s. str*., thus well apart from this taxon, which was collected in Korea. The Korean collection closely matches that of the original description of *Septoria saccardoi* (on *Lysimachia vulgaris* in Italy), having 3-septate, curved, cylindrical conidia, 38–40 × 3.5 µm, 3-septate (Saccardo & Saccardo 1906). *Xenoseptoria* is however distinct from *Septoria s. str*. in forming pycnidia with multiple papillate necks, and having conidiogenous cells that are mono- or polyphialidic.

## Clade 35: *Vrystaatia*

***Vrystaatia*** Quaedvlieg, W.J. Swart, Verkley & Crous, **gen. nov.** MycoBank MB804448.

*Etymology*: Named after the Free State Province in South Africa, "Vrystaat" in Afrikaans, where this fungus was collected.

*Foliicolous*. *Conidiomata* black, globose, pycnidial with central, dark brown ostiolar area, substomatal on host, erumpent in culture; wall of 6–8 layers of pale brown *textura angularis*; exuding cirrhus of orange conidia. *Conidiophores* reduced to conidiogenous cells. *Conidiogenous cells* lining the inner cavity of conidioma, globose to ampulliform, rarely allantoid, hyaline, smooth; with prominent periclinal thickening, or proliferating several times percurrently near apex, giving rise to macro- and microconidia. *Macroconidia* solitary, hyaline, smooth, guttulate, subcylindrical to narrowly obclavate or acicular, apex obtuse to subobtuse, base truncate to long obconically truncate, conidia widest at or just above basal septum, transversely euseptate. *Microconidia* hyaline, smooth, aseptate, pear-shaped to globose or ellipsoid, apex obtuse, base truncate.

*Type species*: *Vrystaatia aloeicola* Quaedvlieg, Verkley, W.J. Swart & Crous.

***Vrystaatia aloeicola*** Quaedvlieg, Verkley, W.J. Swart & Crous, **sp. nov.** MycoBank MB804449. Figs 77, 78.

*Etymology*: Named after the host genus from which it was collected, *Aloe*.

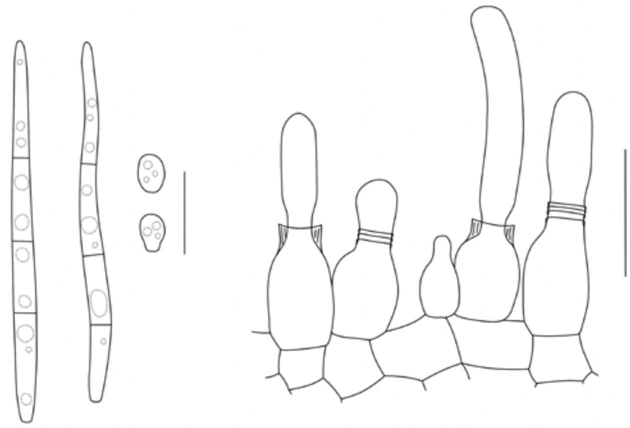

**Fig. 77.** Macro- and microconidia and conidiogenous cells of *Vrystaatia aloeicola* (CBS 135107). Scale bars = 10 µm.

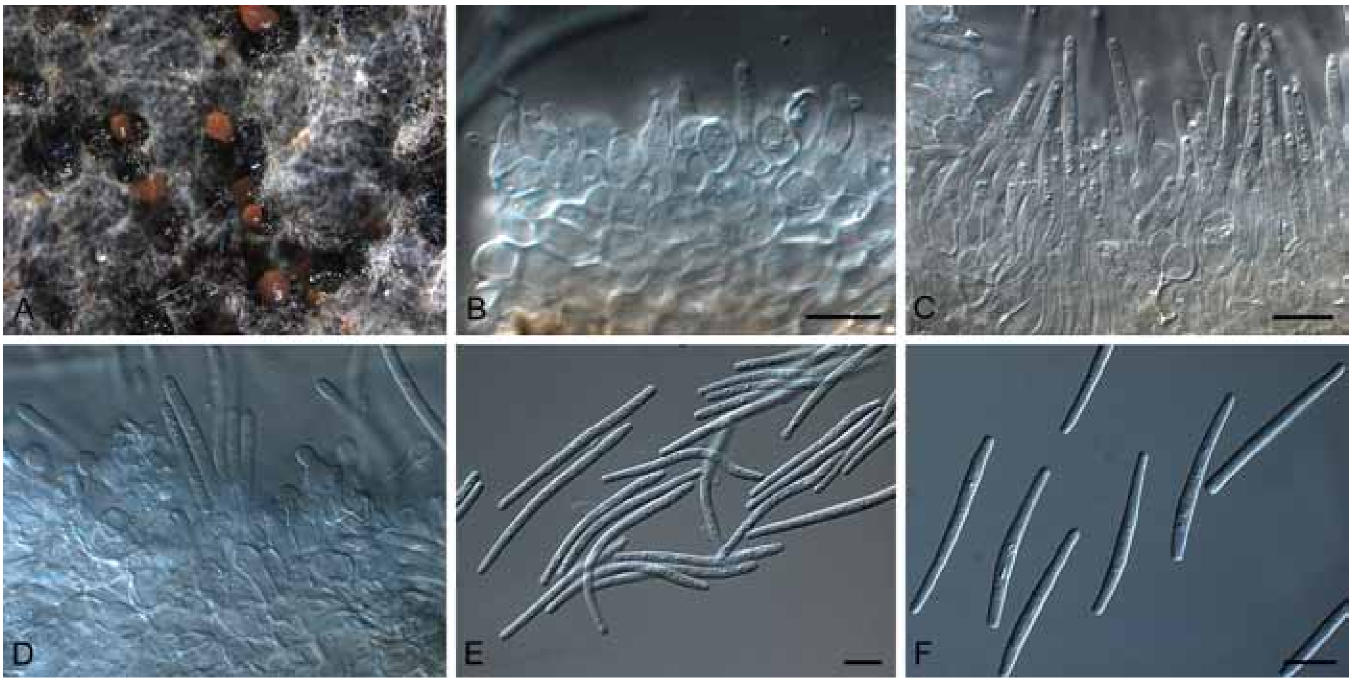


**Fig. 78.** *Vrystaatia aloeicola* (CBS 135107). A. Conidiomata sporulating on PDA, with characteristic orange conidial cirrhi. B–D. Conidiogenous cells. E, F. Conidia. Scale bars = 10 µm.

On sterile *Carex* leaves on WA. *Conidiomata* black, globose, pycnidial with central, dark brown ostiolar area, substomatal on host, erumpent in culture; wall of 6–8 layers of pale brown *textura angularis*; exuding cirrhus of orange conidia. *Conidiophores* reduced to conidiogenous cells. *Conidiogenous cells* lining the inner cavity of conidioma, globose to ampulliform, rarely allantoid, hyaline, smooth, 5–12 × 4–6 µm; with prominent periclinal thickening, or proliferating several times percurrently near apex, 2–2.5 µm diam, giving rise to macro- and microconidia. *Macroconidia* solitary, hyaline, smooth, guttulate, subcylindrical to narrowly obclavate or acicular, apex obtuse to subobtuse, base truncate to long obconically truncate, conidia widest at or just above basal septum, (1–)3-septate, (30–)40–52(–65) × (2.5–)3(–3.5) µm. *Microconidia* hyaline, smooth, aseptate, pear-shaped to globose or ellipsoid, apex obtuse, base truncate, 4–6 × 3–3.5 µm.

*Culture characteristics*: On MEA colonies spreading fast, with moderate aerial mycelium and smooth, even margin, reaching 30 mm diam after 2 wk; surface with concentric zones of umber and apricot; reverse umber, produces brown exudates; on PDA round lobate margins, lacking aerial mycelium, reaching 20 mm diam after 2 wk, surface fuscous-black to greyish-sepia for younger mycelium, reverse fuscous-black to greyish-sepia for younger mycelium; on OA round, lobate, lacking aerial mycelium, reaching 30 mm diam after 2 wk, surface vinaceous-grey, reverse greyish sepia.

*Specimen examined*: **South Africa**, Orange Free State, Bloemfontein, Free State National Botanical Garden, on dead leaf tips of *Aloe maculata* (*Aloaceae*), 7 May 2012, P.W. Crous & W.J. Swart (**holotype** CBS H-21313, culture ex-type CBS 135107 = CPC 20617).

*Notes*: *Vrystaatia* is distinct from *Septoria s. str.* in that it has phialidic conidiogenous cells that proliferate percurrently or with prominent periclinal thickening, and form macro- as well as microconidia in culture, which is not typical of *Septoria*. *Rhabdospora aloetica* was described from stems of *Aloe* sp. in Portugal, with aseptate conidia, 12–16 × 1.5 µm (Saccardo & Saccardo 1906); it is likely this is an asexual morph of *Diaporthe*. As far as we could establish, no septoria-like fungi have thus far been described from *Aloe*.

## Clade 36: *Setophoma*

***Setophoma*** Gruyter, Aveskamp & Verkley, Mycologia 102: 1077. 2010.

*Conidiomata* pycnidial, solitary to confluent, superficial or submerged in agar, globose to subglobose, setose, with papillate ostioles, honey to olivaceous to olivaceous-black, with 2–7(–11) layers of pseudoparenchymatal cells. *Conidiogenous cells* hyaline, monophyalidic. *Conidia* aseptate, ellipsoidal to subcylindrical to subfusoid, guttulate.

*Type species*: *S. terrestris* (H.N. Hansen) Gruyter, Aveskamp & Verkley, Mycologia 102: 1077. 2010.

***Setophoma chromolaenae*** Quaedvlieg, Verkley, R.W. Barreto & Crous, **sp. nov.** MycoBank MB804450. Figs 79, 80.

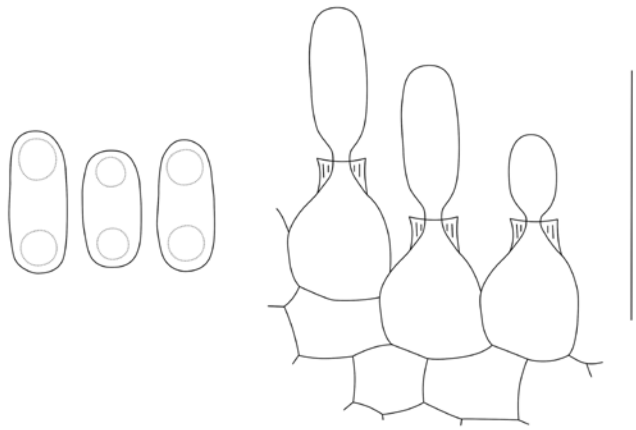

**Fig. 79.** Conidia and conidiogenous cells of *Setophoma chromolaenae* (CBS 135105). Scale bar = 10 µm.


**Fig. 80.** *Setophoma chromolaenae* (CBS 135105). A. Conidiomata forming on OA. B, C, F. Conidiomata with setae. D, E. Conidiogenous cells. G. Conidia. Scale bars: B = 22 µm, C, F = 45 µm, all others = 10 µm.

*Etymology*: Named after the host genus from which it was collected, *Chromolaena.*

*Conidiomata* pycnidial, brown, globose, separate, erumpent, up to 90 µm diam; outer surface covered in brown setae, up to 80 µm long, brown, thick-walled, 3–5 µm diam, 1–4-septate, with slight apical taper to obtuse apex; conidial wall of 3–6 layers of brown *textura angularis*. *Conidiophores* reduced to conidiogenous cells. *Conidiogenous cells* lining the inner cavity, ampulliform, hyaline, smooth, 4–6 × 3–6 µm, with prominent periclinal thickening at apex. *Conidia* hyaline, smooth, subcylindrical, somewhat narrowly ellipsoid when old, with two prominent guttules at ends, (4.5–)5–6 (–7) × (2–)2.5(–3) µm.

*Culture characteristics*: On MEA spreading, with sparse aerial mycelium, folded surface, margin smooth, lobate; surface umber with patches of apricot and dirty white, reverse ochreous. On PDA surface iron-grey, reverse olivaceous-grey. On OA surface iron-grey, surrounded by orange to apricot diffuse pigment layer in agar; reaching 55 mm diam after 2 wk.

*Specimen examined*: **Brazil**, Rio de Janeiro, Fazenda Santa Rosa, Ponte das Laranjeiras, on leaves of *Chromolaena odorata* (*Asteraceae*), 6 Apr. 2010, R.W. Barreto (**holotype** CBS H-21314, culture ex-type CBS 135105 = CPC 18553).

*Note*: *Setophoma chromolaenae* is phylogenetically distinct from *S. sacchari* and *S. terrestris*, the two other species presently known from the genus (de Gruyter *et al.* 2010).

## Clade 37: *Coniothyrium* (*Coniothyriaceae*)

***Coniothyrium*** Corda, Icon. Fung. (Prague) 4: 38. 1840.

*Mycelium* immersed, consisting of septate, hyaline to brown, branched hyphae. *Conidiomata* pycnidial, separate, globose, pale to dark brown, immersed, unilocular, thin-walled; wall of brown, thick-walled *textura angularis*. *Ostiole* circular, central, papillate or not. *Conidiophores* reduced to conidiogenous cells. *Conidiogenous cells* lining the inner cavity, phialidic, annellidic, indeterminate, discrete, doliiform to cylindrical, hyaline to pale brown, smooth, several annellations at apex. *Conidia* subcylindrical, spherical, ellipsoid or broadly clavate, brown, thick-walled, 0(–1)-euseptate, smooth to verruculose, apex obtuse, base truncate, at times with minute marginal frill (Sutton 1980).

*Type species*: *C. palmarum* Corda, Icon. Fung. (Prague) 4: 38. 1840.

***Coniothyrium sidae*** Quaedvlieg, Verkley, R.W. Barreto & Crous, **sp. nov.** MycoBank MB804451. Figs 81, 82.

*Etymology*: Named after the host genus from which it was collected, *Sida*.

*Conidiomata* pycnidial, globose, immersed becoming erumpent, up to 200 µm diam; wall consisting of 3–4 layers of subhyaline to pale brown *textura angularis*. *Ostiole* central, papillate, dark brown, up to 30 µm diam, surrounded by a whorl of brown setae, smooth, thick-walled, 4–8-septate, straight to curved, tapering to subobtuse apices, up to 130 µm long, 5–8 µm diam at base. *Conidiogenous cells* hyaline, smooth, lining the inner cavity, ampulliform to globose, 4–7 × 4–6 µm; apex with prominent periclinal thickening. *Conidia* solitary, hyaline, smooth, aseptate, granular (in Shear's medium, prominently guttulate in lactic acid), fusoid-ellipsoidal, straight to slightly curved, apex obtuse, base truncate to bluntly rounded, (9–)10–12(–13) × (2.5–)3 µm. *Ascomata* developing after several weeks on MEA, separate, pseudothecial, erumpent, uniloculate, papillate, brown, up to 300 µm diam; wall of 4–8 layers of brown *textura angularis*. *Asci* fasciculate, 8-spored, short papillate, hyaline, smooth, subcylindrical, bitunicate, with well-developed apical chamber, 2 µm diam, 55–65 × 8–11 µm. *Ascospores* bi- to triseriate, brown, smooth, guttulate, straight to slightly curved, (3–)5-septate, apical cell obtusely rounded, basal cell somewhat elongated and subobtuse; in ascospores that are 4-septate, the second cell from the apex is markedly swollen, in 5-septate ascospores the third cell from the apex is markedly swollen, (18–)20–24(–26) × (4–)5(–5.5) µm. *Pseudoparaphyses* hyaline, smooth, intermingled among asci, anastomosing, cellular, constricted at septa, up to 80 µm long, 2–4 µm diam.

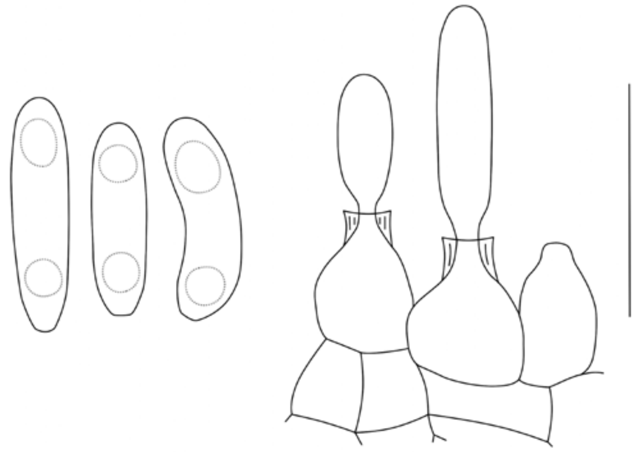

**Fig. 81.** Conidia and conidiogenous cells of *Coniothyrium sidae* (CBS 135108). Scale bar = 10 µm.

*Culture characteristics*: Colonies erumpent, spreading, moderate aerial mycelium even, lobate margins. On MEA surface olivaceous-grey, reverse umber. On OA suface olivaceous-grey with diffuse umber pigment in agar. On PDA surface and reverse olivaceous-grey.

*Specimen examined*: **Brazil**, Rio de Janeiro, Nova Friburgo, Riograndina, along roadside on *Sida* sp. (*Malvaceae*), 24 Feb. 2008, R.W. Barreto (**holotype** CBS H-21315, culture ex-type CPC 19602 = RWB 866 = CBS 135108).

*Note*: De Gruyter *et al*. (2013) placed several phoma-like species with a similar morphology in the genus *Coniothyrium*, to which *C. sidae* is allied. Of interest is the paraphaeosphaeria-like sexual morph that developed in culture, which is newly linked here to *Coniothyrium*. The genus *Paraphaeosphaeria* is linked to *Paraconiothyrium* (Verkley *et al.* 2004).

## Clade 38: *Xenobotryosphaeria*

***Xenobotryosphaeria*** Quaedvlieg, Verkley & Crous, **gen. nov.** MycoBank MB804452.

*Etymology*: Resembling the genus *Botryosphaeria*, but distinct.

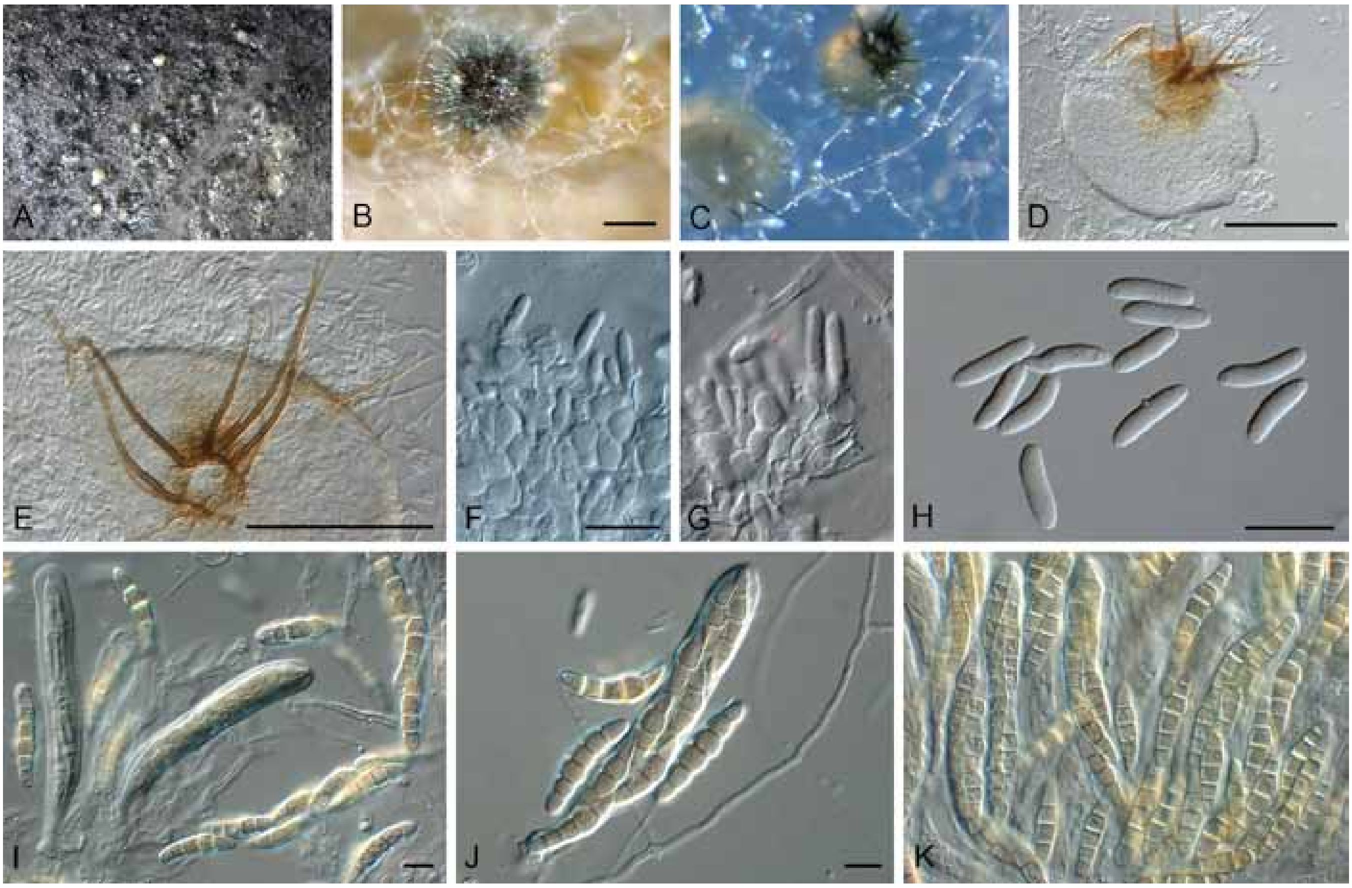


**Fig. 82.** *Coniothyrium sidae* (CBS 135108). A–E. Conidiomata forming in culture, showing setae. F, G. Conidiogenous cells. H. Conidia. I–K. Asci and ascospores. Scale bars: B, D, E = 100 µm, all others = 10 µm.

*Ascomata* brown, globose, smooth, ostiolate, superficial on stems; wall of 3–4 layers of brown *textura angularis*. *Asci* clavate, hyaline, smooth, short stipitate, fasciculate, bitunicate, thin-walled, apical chamber not visible, 6–8-spored. *Ascospores* multiseriate, hyaline, smooth and thin-walled, granular, broadly ellipsoid, ends obtuse, aseptate. *Pseudoparaphyses* not seen.

*Type species*: *Xenobotryosphaeria calamagrostidis* Quaedvlieg, Verkley & Crous.

***Xenobotryosphaeria calamagrostidis*** Quaedvlieg, Verkley & Crous, **sp. nov.** MycoBank MB804453. Figs 83, 84.

*Etymology*: Named after the host genus from which it was collected, *Calamagrostis.*

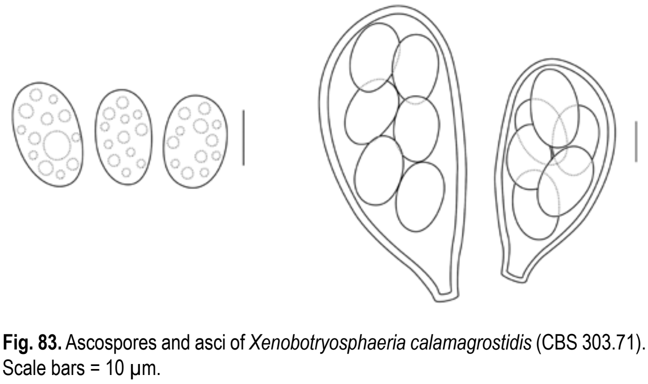

**Fig. 83.** Ascospores and asci of *Xenobotryosphaeria calamagrostidis* (CBS 303.71). Scale bars = 10 µm.

On *Anthriscus* stem. *Ascomata* brown, globose, smooth, superficial on stems, ostiolate, up to 180 µm diam; wall of 3–4 layers of brown *textura angularis*. *Asci* clavate, hyaline, smooth, short stipitate, fasciculate, bitunicate, thin-walled, apical chamber not visible, 6–8-spored, 60–80 × 30–40 µm. *Ascospores* multiseriate, hyaline, smooth and thin-walled, granular, broadly ellipsoid, ends obtuse, aseptate, (17–)18–20(–24) × (11–)12–13(–14) µm. *Pseudoparaphyses* not seen.

*Culture characteristics*: Colonies flat, spreading, with sparse to no aerial mycelium. On PDA surface and reverse dirty white; on MEA concolorous with agar; on OA pale pink on surface.

*Specimen examined*: **Italy**, Bergamo Vigolo, on *Calamagrostis* sp. (*Poaceae*), 20 Jun. 1967, G.A. Hedjaroude (**holotype** CBS H-21316, culture ex-type CBS 303.71).

*Notes*: Hedjaroude (1968) studied the specimen (ETH 7131; as *Phaeosphaeria silvatica*), but obviously the incorrect fungus was cultivated, as *X. calamagrostidis* is quite distinct from *P. silvatica*, which has cylindrical-fusoid, brown, 6–8-septate ascospores, 18–18 × 4–5 µm. *Xenobotryosphaeria* is reminiscent of genera in the *Botryosphaeriales*, but is phylogenetically distinct (Crous *et al.* 2006, Phillips *et al.* 2008, Liu *et al*. 2012). It also resembles species of *Muyocopron* (*Muyocopronaceae*), but the latter genus differs in that it has circular, flattened ascomata, as well as prominent pseudoparaphyses, which are absent in *Xenobotryosphaeria.*

## Clade 39: *Phoma*

*Note*: See Aveskamp *et al*. (2010), de Gruyter *et al*. (2009, 2013).

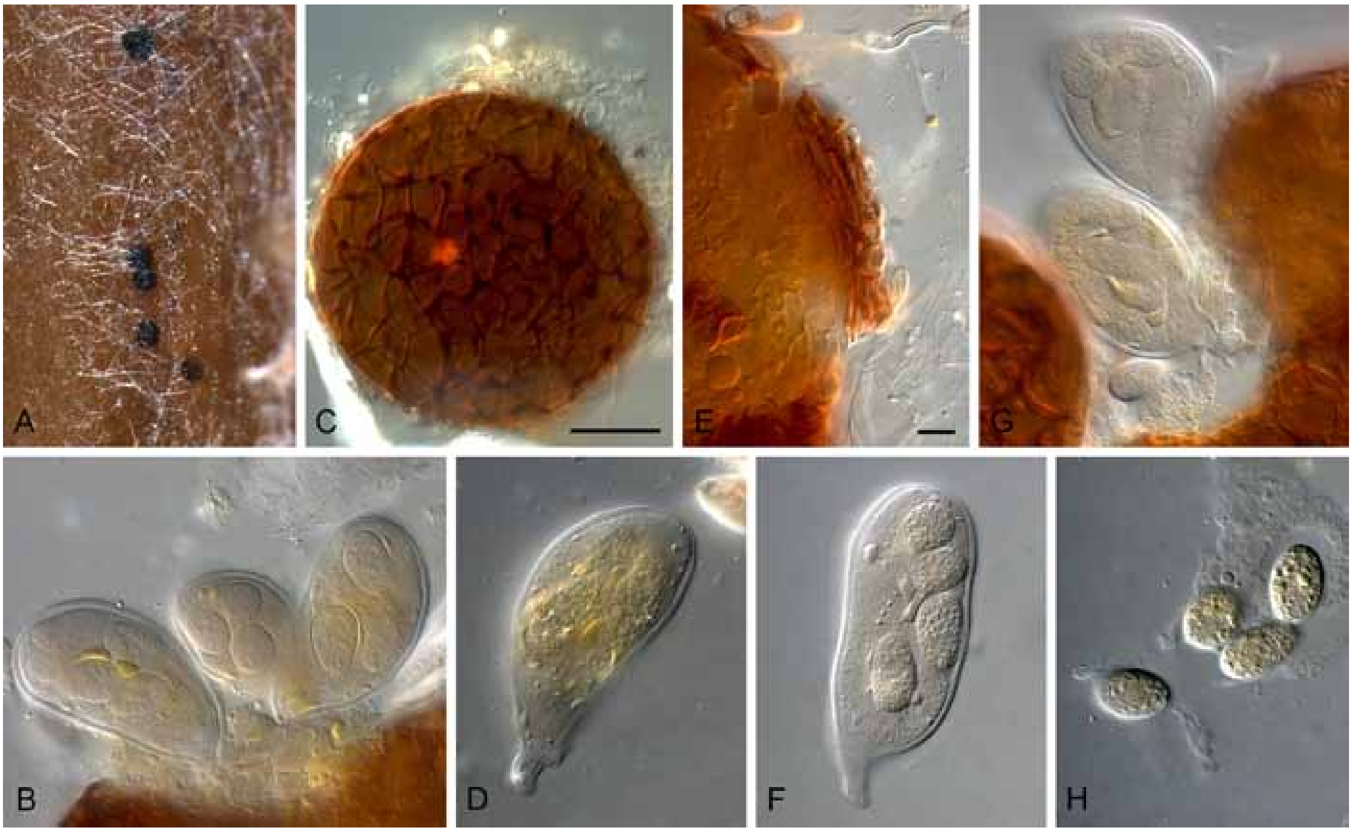


**Fig. 84.** *Xenobotryosphaeria calamagrostidis* (CBS 303.71). A, C. Ascomata forming in culture. E, G. broken wall with asci. B, D, F. Asci. H. Ascospores. Scale bars: C = 45 µm, all others = 10 µm.

## Clade 40: *Acicuseptoria*

***Acicuseptoria*** Quaedvlieg, Verkley & Crous, **gen. nov.** MycoBank MB804454.

*Etymology*: *Acicu*- from acicular (conidia), and *Septoria* = septoria-like.

*Conidiomata* pycnidial, erumpent, brown, globose, with central ostiole, exuding a cream conidial mass; wall consisting of 3–6 layers of thin, brown *textura angularis*. *Conidiophores* reduced to conidiogenous cells. *Conidiogenous cells* hyaline, smooth, ampulliform; proliferating inconspicuously and percurrently at apex, or simply appearing holoblastic. *Conidia* solitary, hyaline, granular, acicular, straight to gently curved, tapering towards apex that is acutely rounded, base truncate, transversely euseptate.

*Type species*: *Acicuseptoria rumicis* Quaedvlieg, Verkley & Crous.

***Acicuseptoria rumicis*** Quaedvlieg, Verkley & Crous, **sp. nov.** MycoBank MB804455. Fig. 85.

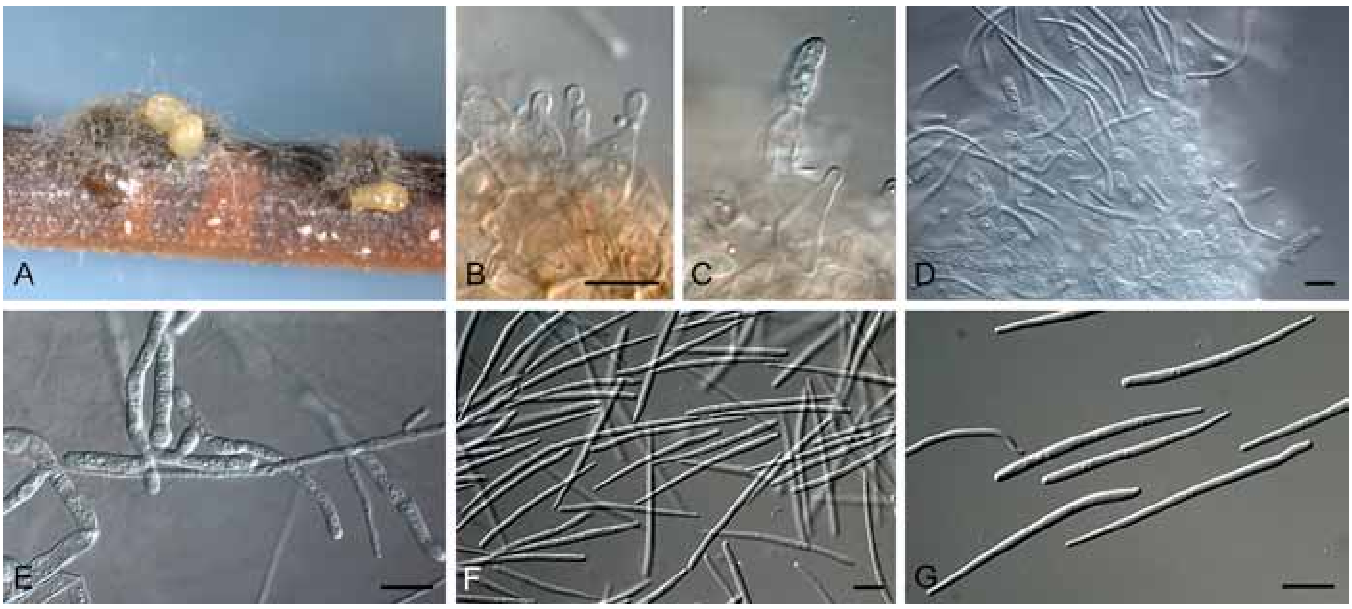


**Fig. 85.** *Acicuseptoria rumicis* (CBS 522.78). A. Conidiomata sporulating in culture. B–E. Conidiogenous cells. F, G. Conidia. Scale bars = 10 µm.

*Etymology*: Named after the host genus from which it was collected, *Rumex*.

On sterile *Carex* leaves on WA. *Conidiomata* pycnidial, erumpent, brown, globose, up to 300 µm diam, with central ostiole, exuding a cream conidial mass; wall consisting of 3–6 layers of thin, brown *textura angularis*. *Conidiophores* reduced to conidiogenous cells. *Conidiogenous cells* hyaline, smooth, ampulliform, 7–15 × 5–7 µm; proliferating inconspicuously and percurrently at apex, or simply appearing holoblastic. *Conidia* solitary, hyaline, granular, acicular, straight to gently curved, tapering towards apex that is acutely rounded, base truncate, 1.5–2 µm diam, up to 8-septate, (32–)40–60(–70) × 2(–2.5) µm.

*Culture characteristics*: Colonies lobate, flat with little appressed, white aerial mycelium. On MEA surface olivaceous-grey, reverse umber. On OA suface olivaceous-grey. On PDA surface and reverse olivaceous-grey.

*Specimen examined*: **France**, Haute Savoie, Mt. Beaudin, 2000 m alt., stem of *Rumex alpinus* (*Polygonaceae*), Oct. 1978, H.A. van der Aa (**holotype** CBS H-18163, culture ex-type CBS 522.78).

*Notes*: *Acicuseptoria rumicis* was originally deposited as *Septoria rumicum*, but is distinct from the latter in having acicular, narrower conidia. *Acicuseptoria* is distinct from *Septoria s. str.* in having acicular conidia.

## Clade 41: *Stagonospora*

***Stagonospora*** (Sacc.) Sacc., Syll. Fung. (Abellini) 3: 445. 1884.

*Description*: See above.

*Type species*: *S. paludosa* (Sacc. & Speg.) Sacc., Syll. Fung. (Abellini) 3: 453. 1884.

***Stagonospora duoseptata*** Quaedvlieg, Verkley & Crous, **sp. nov.** MycoBank MB804459. Figs 86, 87.

*Etymology*: Named after the fact that conidia are 2-septate.

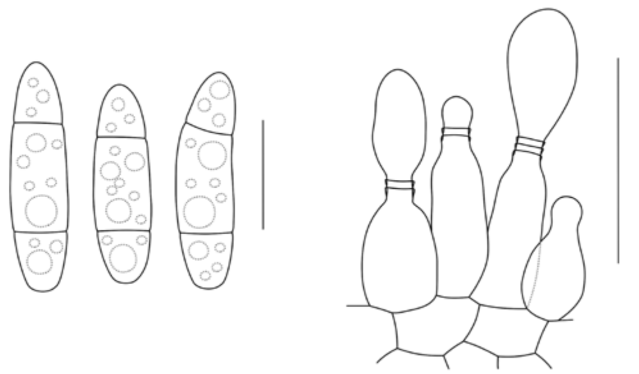

**Fig. 86.** Conidia and conidiogenous cells of *Stagonospora duoseptata* (CBS 135093). Scale bars = 10 µm.

On sterile *Carex* leaves on WA. *Conidiomata* dark brown, immersed, subepidermal, pycnidial, globose, up to 400 µm diam, exuding a short, hyaline cirrhus of conidia; wall of 3–4 layers of medium brown *textura angularis*. *Conidiophores* hyaline, smooth, lining inner cavity, 0–1-septate, subcylindrical, 10–20 × 4–5 µm. *Conidiogenous cells* phialidic, hyaline, smooth, aggregated, lining the inner cavity, subcylindrical to ampulliform or doliiform, 6–8 × 3–4 µm; phialidic with several apical percurrent proliferations. *Conidia* hyaline, smooth, thin-walled, granular, fusoid-ellipsoidal, 2-septate, with septa 4–6 µm inwards from both obtuse conidial ends; conidia widest in middle, (18–)20–23(–25) × (5–)6(–7) µm.

*Culture characteristics*: Colonies on PDA flattened, circular with lobate edges, and fine grey aerial mycelium, surface mouse-grey, reverse olivaceous-black, after 14 d, 4 cm diam; on MEA after 14 d, 4.5 cm diam; on OA similar to MEA.

*Specimen examined*: **Netherlands**, Nijmegen, de Duffelt, on leaves of a *Carex acutiformis* (*Cyperaceae*), 29 Jul. 2012, W. Quaedvlieg (**holotype** CBS H-21321, culture ex-type CBS 135093 = S618).

*Notes*: *Stagonospora duoseptata* is distinct from other species occurring on *Carex* in that it has fusoid-ellipsoidal, 2-septate conidia, (18–)20–23(–25) × (5–)6(–7) µm, with septa positioned 4–6 µm inwards from its obtuse conidial ends. *Stagonospora biseptata* (occurring on *Carex lanuginosa*, Wisconsin, USA) has conidia that are larger, (35–)40–50(–55) × (2–)10–11(–13) µm (Greene 1961).


**Fig. 87.** *Stagonospora duoseptata* (CBS 135093). A. Conidiomata forming in culture. B, C. Conidiogenous cells. D. Conidia. Scale bars = 10 µm.

***Stagonospora paludosa*** (Sacc. & Speg.) Sacc., Syll. Fung. (Abellini) 3: 453. 1884. Figs 88, 89.
*Basionym*: *Hendersonia paludosa* Sacc. & Speg., Michelia 1(no. 3): 353. 1878.

On sterile *Carex* leaves on WA. *Conidiomata* black, immersed, subepidermal, pycnidial, globose, up to 400 µm diam, exuding a short, hyaline cirrhus of conidia; wall of 3–4 layers of medium brown *textura angularis*. *Conidiophores* reduced to conidiogenous cells. *Conidiogenous cells* phialidic, hyaline, smooth, aggregated, lining the inner cavity, ampulliform to doliiform, 5–10 × 5–10 µm; tapering at apex with prominent periclinal thickening or 1–2 inconspicuous percurrent proliferations visible at apex. *Conidia* hyaline, smooth, thin-walled, granular, or each cell with a large central guttule, subcylindrical to fusoid, apex subobtusely to obtusely rounded, base truncate (4–7 µm diam), (6–)7–8-septate (becoming constricted at septa with age), (45–)55–63(–65) × (9–)10–11 µm.

*Culture characteristics*: Colonies on PDA flat, circular, with grey aerial mycelium, reverse olivaceous-black to buff at the margins, after 14 d, 8.5 cm diam; on MEA umbonate, round, with appressed, grey aerial mycelium, with white patches; OA similar to PDA, but reverse buff with iron-grey patches at the outer region.

*Specimens examined*: **Italy**, on *Carex riparia* (*Cyperaceae*), Feb. 1878, holotype (presumably lost). **Netherlands**, Utrecht, Veenendal, de Blauwe Hel, *Carex acutiformis* (*Cyperaceae*), 23 Jul. 2012, W. Quaedvlieg (**neotype** designated here CBS H-21317, culture ex-type S601 = CBS 135088) (MBT175339).

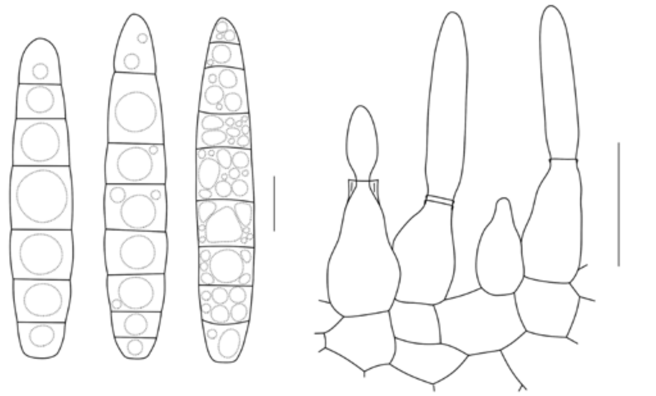

**Fig. 88.** Conidia and conidiogenous cells of *Stagonospora paludosa* (CBS 135088). Scale bars = 10 µm.

*Notes*: For more than a century, *Stagonospora* was confused with *Septoria.* The introduction of molecular techniques around the turn of the century made it possible to definitively establish that *Stagonospora* was not linked to *Septoria*, and that it in fact clusters with other important plant pathogenic genera like *Phoma* and *Leptosphaeria* in the *Pleosporales* (Cunfer & Ueng 1999, Solomon *et al*. 2006). The type of *Stagonospora* (*S. paludosa*) was recollected from a *Carex* during this study and phylogenetic analyses showed that this species clustered separately from most other known "*Stagonospora"* spp. (mostly isolated from *Poaceae*), but together with several other *Stagonospora* species that were also collected from *Carex*. This led to the conclusion that *Stagonospora s. str*. was limited to *Carex*, and that other commercially important stagonospora-like species on *Poaceae* (*e.g. S. avenae* and *S. nodorum*) in fact belonged to different genera.

***Stagonospora perfecta*** Quaedvlieg, Verkley & Crous, **sp. nov.** MycoBank MB804458. Figs 90, 91.

*Etymology*: Named after the fact that both sexual and asexual morphs of the fungus developed in culture.

On sterile *Carex* leaves on SNA. *Ascomata* developing on SNA, solitary, globose, brown, erumpent, up to 300 µm diam, with central ostiole; wall of 3–4 layers of brown *textura angularis*. *Pseudoparaphyses* intermingled among asci, hyaline, smooth, guttulate, multi-septate, constricted at septa, branched, hyphal-like, 4–6 µm diam, filling entire cavity. *Asci* stipitate, hyaline, smooth, clavate to fusoid-ellipsoidal, bitunicate, with prominent apiculus, 1.5–2.5 µm diam, 8-spored, 45–100 × 12–18 µm. *Ascospores* hyaline, smooth, 3- to multi-seriate in ascus,

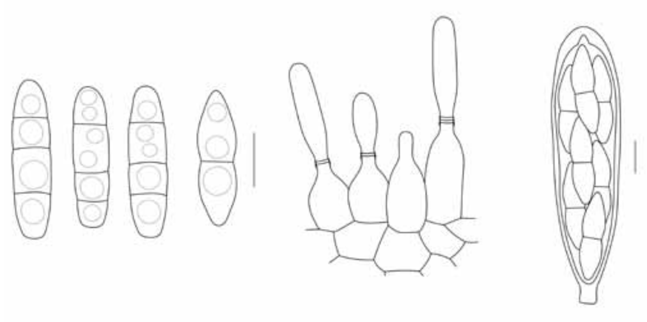

**Fig. 90.** Conidia, conidiogenous cells and ascus with ascospores of *Stagonospora perfecta* (CBS 135099). Scale bars = 10 µm.

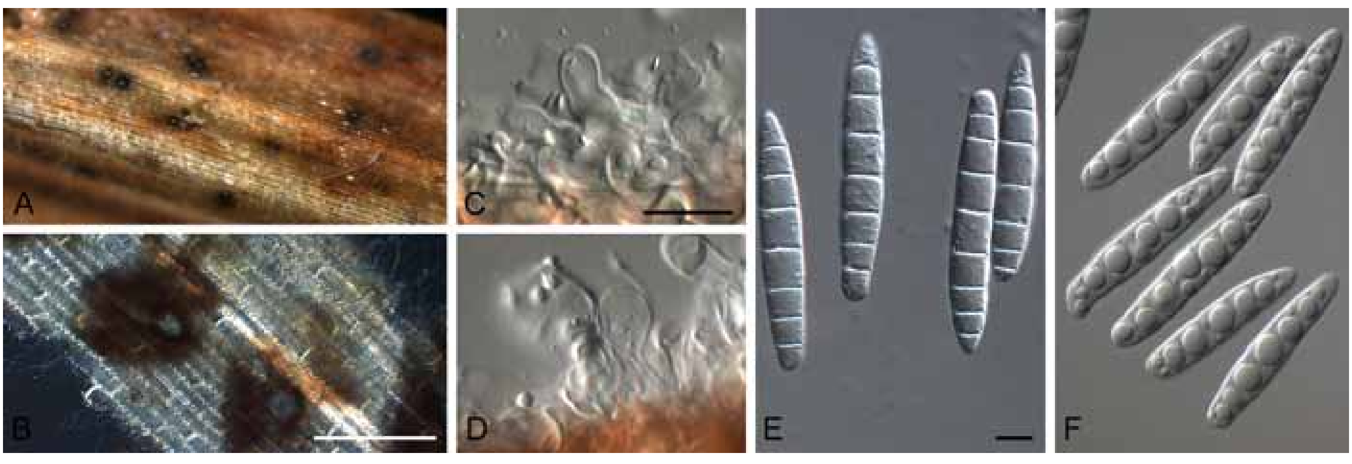


**Fig. 89.** *Stagonospora paludosa* (CBS 135088). A, B. Conidiomata forming in culture. C, D. Conidiogenous cells. E, F. Conidia. Scale bars: B = 400 µm, all others = 10 µm.

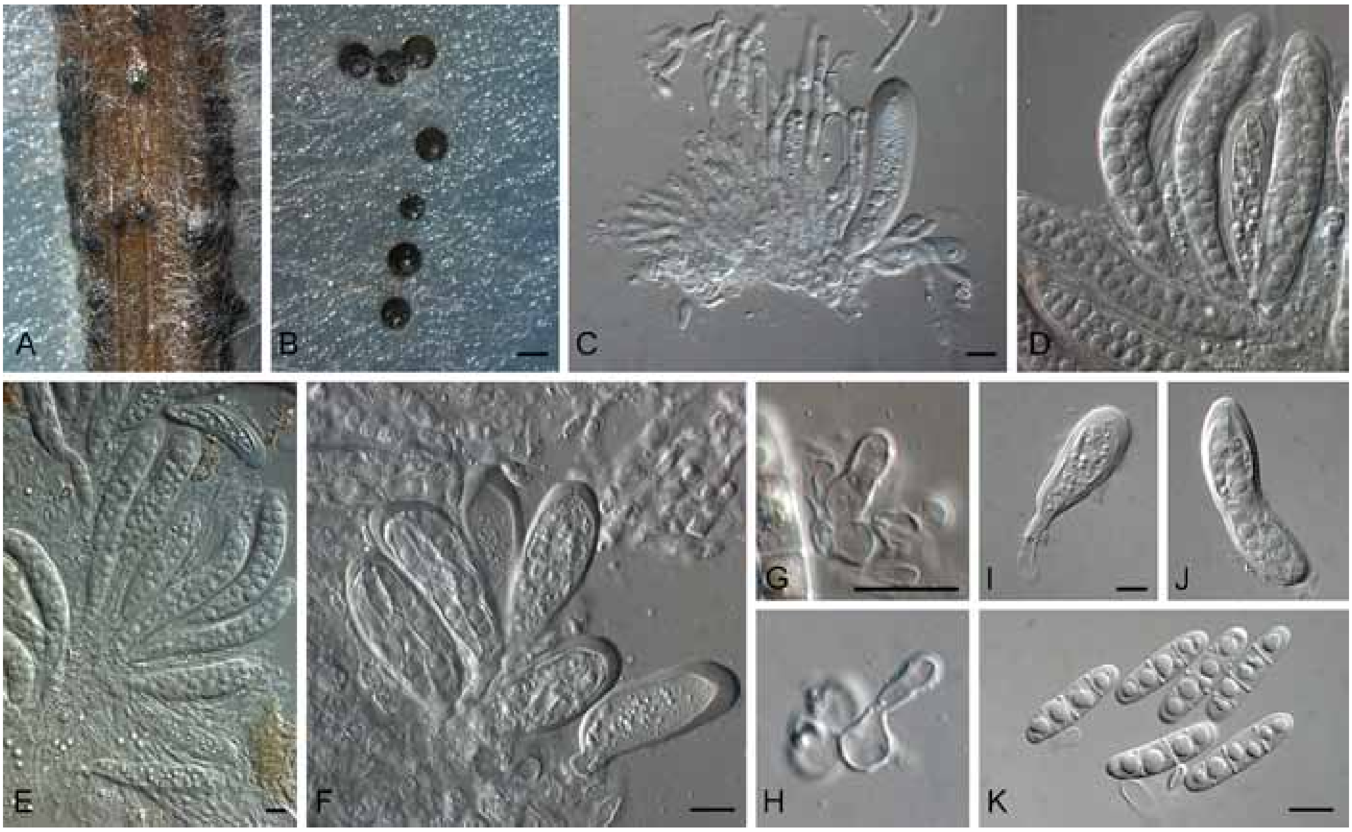


**Fig. 91.** *Stagonospora perfecta* (CBS 135099). A. Conidiomata forming in culture. B. Ascomata forming in culture. C–F, I, J. Asci and pseudoparaphyses. G, H. Conidiogenous cells. K. Conidia. Scale bars: B = 300 µm, all others = 10 µm.

fusoid-ellipsoidal with median septum, prominently constricted at septum, tapering towards subobtuse apices, with 1–2 large guttules per cell, thin-walled, widest just above septum in upper cell, (20–)23–25(–27) × (5–)6–7(–8) µm. *Conidiomata* up to 300 µm diam, brown, immersed, subepidermal, pycnidial, subglobose with central ostiole, exuding crystalline to creamy conidial mass; wall of 2–3 layers of brown *textura angularis*. *Conidiophores* reduced to conidiogenous cells. *Conidiogenous cells* phialidic, hyaline, smooth, aggregated, lining the inner cavity, ampulliform to doliiform or subcylindrical, with several percurrent proliferations near apex, 5–12 × 4–6 µm. *Conidia* hyaline, smooth, thin-walled, subcylindrical to narrowly fusoid-ellipsoidal, with obtuse apex and bluntly rounded base, 2–3-septate, slightly constricted at septa, with 1–2 large guttules per cell, (19–)25–29(–32) × (6–)7(–8) µm.

*Culture characteristics*: Colonies on PDA flattened, convex, circular, with white aerial mycelium, surface fuscous-black, reverse iron-grey to black, after 14 d, 8.5 cm diam; on MEA surface fuscous-black, reverse olivaceous-black; on OA surface isabelline, reverse fuscous-black.

*Specimen examined*: **Netherlands**, Limburg, Weert, Moerselpeel, on leaves of *Carex acutiformis* (*Cyperaceae*), Sep. 2012, W. Quaedvlieg (**holotype** CBS H-21320, culture ex-type CBS 135099 = S656).

*Notes*: *Stagonospora perfecta* is the first species with a confirmed sexual state in the genus *Stagonospora*. Of interest is the fact that it is didymella-like, rather than phaeosphaeria-like in morphology, which also explains it clustering in the *Didymellaceae*. Morphologically *S. perfecta* resembles *S. vitensis* (18–32 × 4–6 µm, 2–3(–4)-septate; Ellis & Ellis 1997), but conidia are wider. *Stagonospora perfecta* is closely related to *S. pseudovitensis*, though in the latter conidia are slightly longer, more fusoid-ellipsoidal in shape, and lack a sexual morph in culture.

***Stagonospora pseudocaricis*** Quaedvlieg, Verkley, Gardiennet & Crous, **sp. nov.** MycoBank MB804456. Figs 92, 93.

*Etymology*: Named after the species that it resembles, *Stagonospora caricis*.

On sterile *Carex* leaves on WA. *Conidiomata* black, immersed, subepidermal, pycnidial, globose, up to 400 µm diam, exuding a short, hyaline cirrhus of conidia; wall of 3–4 layers of medium brown *textura angularis*. *Conidiophores* reduced to conidiogenous cells. *Conidiogenous cells* phialidic, hyaline, smooth, aggregated, lining the inner cavity, ampulliform to doliiform, 5–9 × 5–8 µm; tapering at apex with prominent periclinal thickening or 1–2 inconspicuous percurrent proliferations visible at apex. *Conidia* hyaline, smooth, thin-walled, granular, or each cell with a large central guttule, subcylindrical to fusoid, apex subobtusely to obtusely rounded, base truncate, (5–)6(–7)-septate, (35–)42–48(–50) × (6–)7–8 µm.

*Culture characteristics*: Colonies on PDA flat, circular, with appressed, grey aerial mycelium, surface sepia, reverse olivaceous-black to buff, after 14 d, 8.5 cm diam; on MEA umbonate, round, with appressed, grey aerial mycelium with white patches, surface greyish sepia, reverse fuscous-black to olivaceous-black; OA similar to PDA.

*Specimens examined*: **France**, Foncegrive, Rive de la Venelle, on *Carex acutiformis* (*Cyperaceae*), Oct. 2012, A. Gardiennet (**holotype** CBS H-21318, culture ex-type CBS 135132 = S610); *ibed*., S609 = CBS 135414).

*Note*: Conidia of *S. pseudocaricis* closely resemble those of *S. caricis* (25–45 × 4–8 µm, 5–7-septate; Ellis & Ellis 1997), but are longer.

**_Stagonospora pseudovitensis_** Quaedvlieg, Verkley & Crous, **sp. nov.** MycoBank MB804457. Figs 94, 95.

*Etymology*: Named after the species that it resembles, *Stagonospora vitensis*.

On sterile *Carex* leaves on WA. *Conidiomata* black, immersed, subepidermal, pycnidial, globose with central ostiole, up to 180 µm diam; wall of 3–4 layers of pale brown *textura angularis*. *Conidiophores* reduced to conidiogenous cells. *Conidiogenous cells* phialidic, hyaline, smooth, aggregated, lining the inner cavity, ampulliform to doliiform, 5–7 × 4–5 µm; tapering at apex with inconspicuous periclinal thickening or percurrent proliferation. *Conidia* hyaline, smooth, thin-walled, granular, subcylindrical with obtuse apex and truncate to bluntly rounded base, 3–4 µm diam, 3-septate, with large central guttule in each cell, (25–)28–33(–36) × (6–)7(–8) µm.

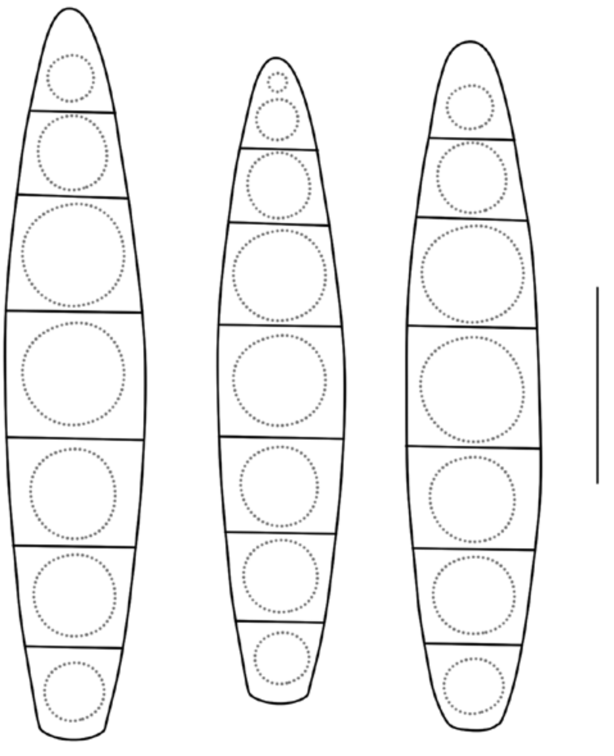

**Fig. 92.** Conidia of *Stagonospora pseudocaricis* (CBS 135132). Scale bar = 10 µm.

*Culture characteristics*: Colonies on PDA flat, circular, aerial mycelium consisting of some grey tufts, surface pale mouse-grey, reverse olivaceous-black, after 14 d, 8.5 cm diam; on MEA similar to PDA, but with appressed, white aerial mycelium, and with some grey tufts; OA similar to MEA, but reverse olivaceous-grey.

*Specimens examined*: **Netherlands**, Veenendaal, de Blauwe Hel, on leaves of *Carex acutiformis* (*Cyperaceae*), 23 Jul. 2012, W. Quaedvlieg (**holotype** CBS H-21319, culture ex-type CBS 135094 = S620); *ibed*., S602.

*Note*: Conidia of *S. pseudovitensis* differ from that of *S. vitensis* (18–32 × 4–6 µm, 2–3(–4)-septate; Ellis & Ellis 1997), by having consistently 3-septate, wider conidia.

**_Stagonospora uniseptata_** Quaedvlieg, Verkley & Crous, **sp. nov.** MycoBank MB804460. Figs 96, 97.

*Etymology*: Named after the fact that conidia are 1-septate.

On sterile *Carex* leaves on WA. *Conidiomata* up to 150 µm diam, black, immersed, subepidermal, pycnidial, globose with central ostiole, exuding yellow conidial masses; wall of 3–4 layers of red-brown *textura angularis*. *Conidiophores* reduced to conidiogenous cells. *Conidiogenous cells* phialidic, hyaline, smooth, aggregated, lining the inner cavity, ampulliform to subcylindrical, 5–8 × 3–4 µm, with percurrent proliferation at apex. *Conidia* hyaline, smooth, thin-walled, fusoid-ellipsoidal, with obtuse apex and truncate to bluntly rounded base (2 µm diam), medianly 1-septate, prominently constricted at septum, straight to irregularly curved, widest in middle of either apical or basal cell, granular, including yellow-green reflective guttules, (13–)16–20(–22) × (5–)5.5(–6) µm.

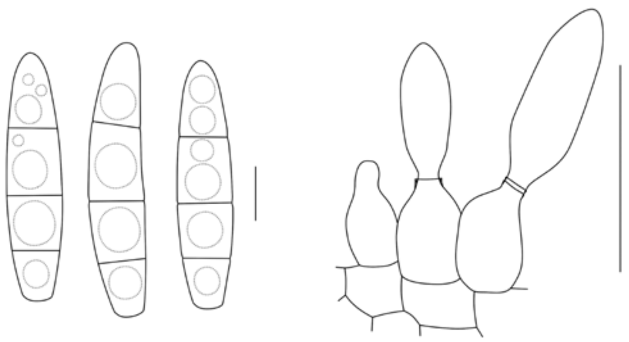

**Fig. 94.** Conidia and conidiogenous cells of *Stagonospora pseudovitensis* (CBS 135094). Scale bars = 10 µm.

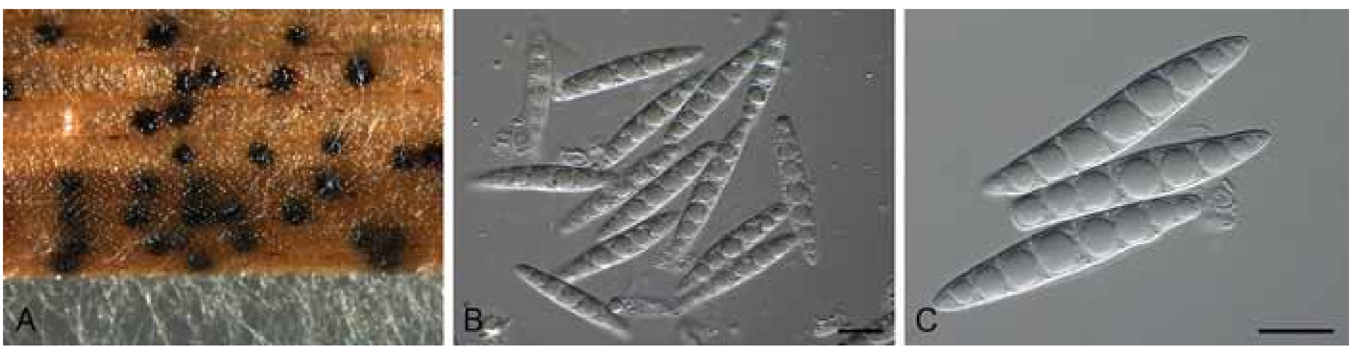


**Fig. 93.** *Stagonospora pseudocaricis* (CBS 135132). A. Conidiomata forming in culture. B, C. Conidia. Scale bars = 10 µm.

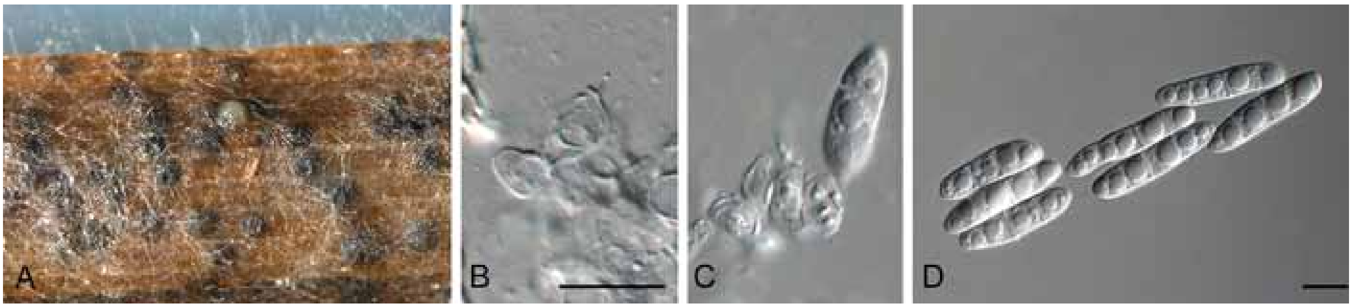


**Fig. 95.** *Stagonospora pseudovitensis* (CBS 135094). A. Conidiomata forming in culture. B, C. Conidiogenous cells. D. Conidia. Scale bars = 10 µm.

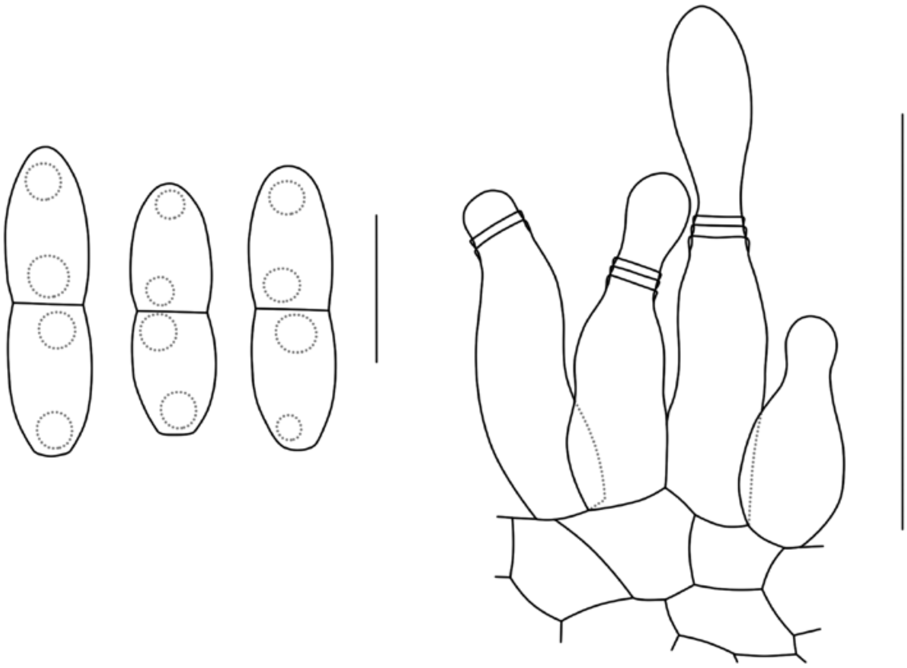

**Fig. 96.** Conidia and conidiogenous cells of *Stagonospora uniseptata* (CBS 135090). Scale bars = 10 µm.

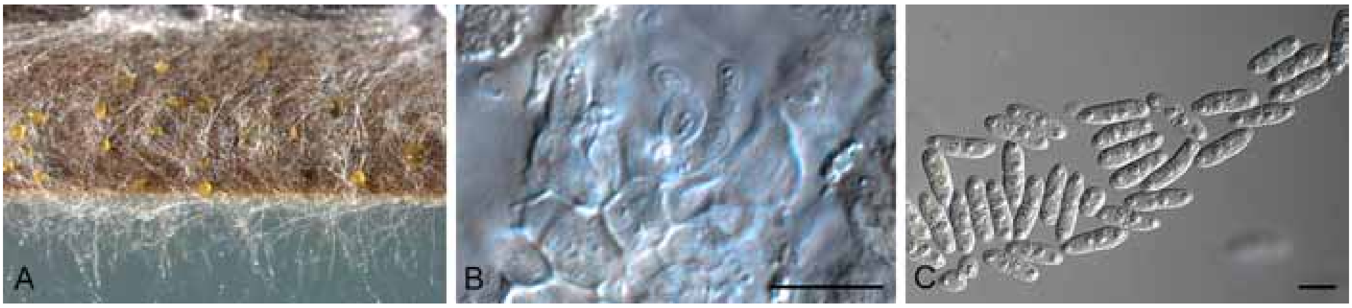


**Fig. 97.** *Stagonospora uniseptata* (CBS 135090). A. Conidiomata sporulating in culture. B. Conidiogenous cells. C. Conidia. Scale bars = 10 µm.

*Culture characteristics*: Colonies on PDA appressed, circular, with short, greyish-white aerial mycelium, surface fusous-black, reverse olivaceous-black to hazel, after 14 d, 8.5 cm diam; on MEA surface hazel, reverse cinnamon; on OA with patches of white aerial mycelium, surface isabelline, reverse olivaceous to fuscous-black.

*Specimens examined*: **Netherlands**, Nijmegen, de Duffelt, on leaves of a *Carex acutiformis* (*Cyperaceae*), 29 Jul. 2012, W. Quaedvlieg, (**holotype** CBS H-21322, culture ex-type CBS 135090 = S611); *ibed*., S607, S608 = CPC 22151 and CPC 22150.

*Notes*: Of the *Stagonospora* and *Septoria* species occurring on *Carex*, *Stagonospora uniseptata* is most similar to *Septoria caricis* (conidia 20–35 × 2.5–3 µm, 1-septate; Ellis & Ellis 1997), but distinct in that conidia are shorter and wider.

## Clade 42: *Corynespora*

***Corynespora*** Güssow, Z. PflKrankh. PflPath. PflSchutz 16: 10. 1906.

*Mycelium* immersed or superficial. *Stroma* present in some species. *Setae* and hyphopodia absent. *Conidiophores* macronematous, mononematous, straight or flexuous, unbranched, brown or olivaceous brown, smooth. *Conidiogenous cells* monotretic, integrated, terminal, percurrent, cylindrical or doliiform. *Conidia* solitary or catenate, dry, acrogenous, simple, obclavate, rarely cylindrical, subhyaline, pale to dark brown or olivaceous brown or straw-coloured, euseptate or distoseptate, smooth, rarely verruculose (Ellis 1971).

*Type species*: *C. mazei* Güssow, Consp. Regni Veget. (Leipzig) 16: 13. 1906. [= *C. cassiicola* (Berk. & M.A. Curtis) C.T. Wei, Mycol. Pap. 34: 5. 1950.]

***Corynespora leucadendri*** Quaedvlieg, Verkley & Crous, **sp. nov.** MycoBank MB804461. Figs 98, 99.

*Etymology*: Named after the host genus from which it was collected, *Leucadendron.*

On MEA and PDA after 2 wk. *Mycelium* consisting of creeping, branched, septate, hyaline, smooth, 3–4(–5) µm diam hyphae that become brown close to conidiophores; stroma lacking. *Conidiophores* subcylindrical, erect, medium brown, 100–300 µm tall, 4–6(–7) µm diam, thick-walled, transversely multiseptate, with several swollen nodes of conidiophore rejuvenation (up to 12 µm diam). *Conidiogenous cells* terminal, cylindrical, medium brown, smooth, ends swollen or not, central locus somewhat darkened or inconspicuous, 15–40 × 5–6(–7) µm. *Conidia* medium brown, obclavate to subcylindrical, straight to slightly curved, thick-walled, (3–)4–6(–10)-distoseptate, basal locus thickened, darkened, protruding, 2–3 µm diam, (35–)70–110(–170) × (6–)7–8(–11) µm.

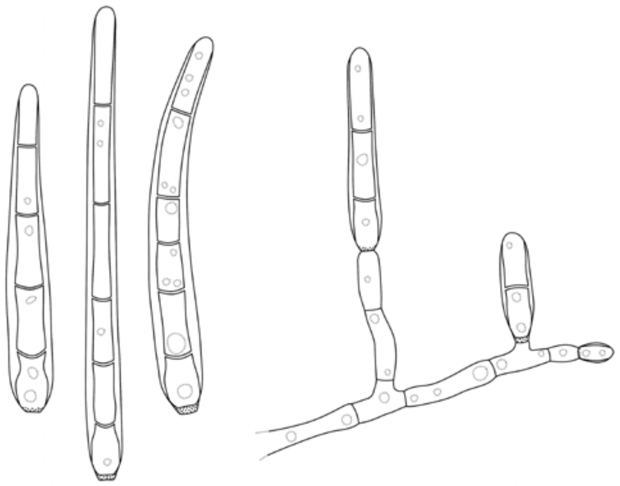

**Fig. 98.** Conidia and conidiogenous loci of *Corynespora leucadendri* (CBS 135133). Scale bar = 10 µm.

*Culture characteristics*: Colonies erumpent, spreading with moderate aerial mycelium and smooth, even margin; reaching 25 mm diam after 2 wk. On MEA surface dirty white, reverse cinnamon. On PDA surface dirty white, reverse buff to rosy buff with diffuse rosy buff pigment. On OA surface dirty white with diffuse rosy buff pigment in agar.

*Specimen examined*: **South Africa**, Western Cape Province, Helderberg Nature Reserve, from the leaves of *Leucadendron* sp. (*Proteaceae*), 14 Aug. 2000, S. Lee (**holotype** CBS H-21323, culture ex-type CBS 135133 = CPC 19345).

*Notes*: This species was not treated by Marincowitz *et al*. (2008), and presently no species of *Corynespora* are known from *Leucadendron*. Furthermore, based on conidial morphology, none of the species treated by Ellis (1971, 1976) resemble *C. leucadendri*, nor is it similar to any *Corynespora* sequence presently deposited in GenBank. For these reasons we thus introduce *C. leucadendri* as a new taxon.

## Clade 43: *Setoseptoria*

***Setoseptoria*** Quaedvlieg, Verkley & Crous, **gen. nov.** MycoBank MB804462.

*Etymology*: Named after its conidiomata which are septoria-like, but setose.

*Conidiomata* pycnidial, brown, immersed, globose with central ostiole, somewhat papillate, apical erumpent part at times with brown, verruculose to warty setae; wall of 6–8 layers of brown *textura angularis*; inner layer of 6–10 layers of hyaline *textura angularis*. *Conidiophores* lining the inner cavity, reduced to conidiogenous cells, or with one supporting cell. *Conidiogenous cells* hyaline, smooth, subcylindrical to doliiform; apical region with several inconspicuous percurrent proliferations, or with periclinal thickening; collarette inconspicuous, or prominent, flared. *Conidia* hyaline, smooth, becoming somewhat olivaceous and verruculose in older cultures, subcylindrical, tapering in apical part to obtuse or subobtuse apex, base truncate, transversely euseptate, straight to somewhat curved, mostly with one large central guttule per cell, older conidia becoming constricted at septa, disarticulating into phragmospores.

*Type species*: *Setoseptoria phragmites* Quaedvlieg, Verkley & Crous.

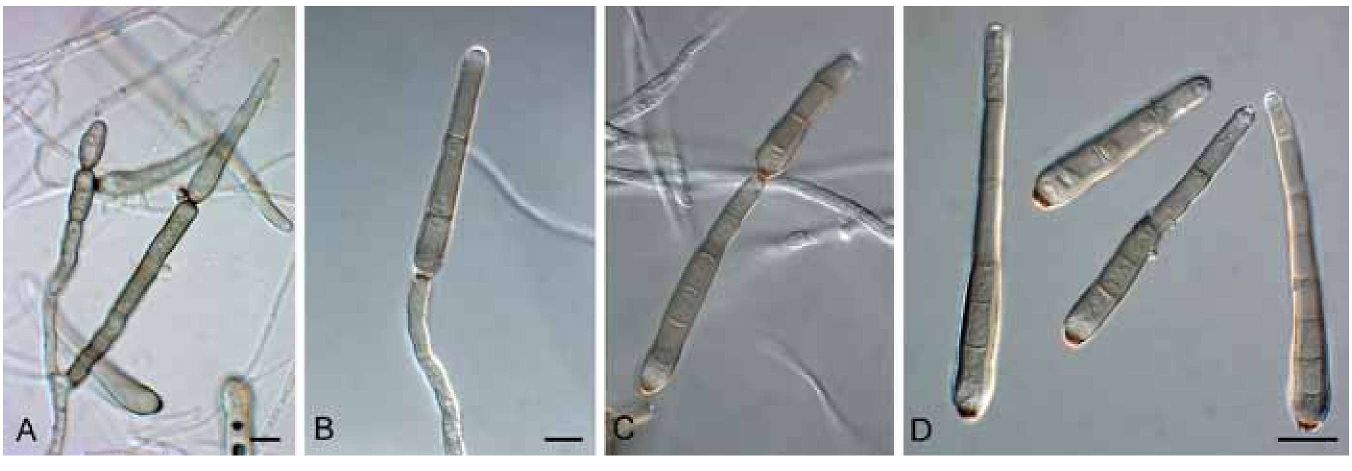


**Fig. 99.** *Corynespora leucadendri* (CBS 135133). A–C. Conidiogenous cells giving rise to conidia. D. Conidia. Scale bars = 10 µm.

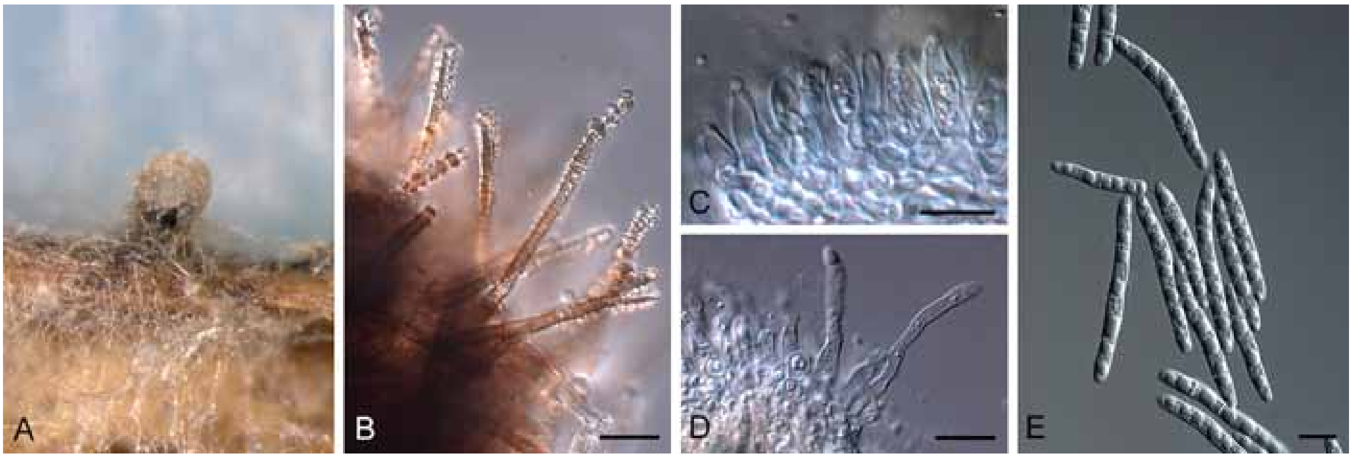


**Fig. 100.** *Setoseptoria phragmitis* (CBS 114802). Conidioma sporulating in culture. B. Setae. C, D. Conidiogenous cells. E. Conidia. Scale bars = 10 µm.

***Setoseptoria phragmitis*** Quaedvlieg, Verkley & Crous, **sp. nov.** MycoBank MB804463. Fig. 100.

*Etymology*: Named after the host genus from which it was collected, *Phragmites.*

On sterile *Carex* leaves on WA. *Conidiomata* pycnidial, brown, immersed, globose with central ostiole, up to 30 µm diam, somewhat papillate, up to 200 µm diam, apical erumpent part at times with brown, verruculose to warty setae; wall of 6–8 layers of brown *textura angularis*; inner layer of 6–10 layers of hyaline *textura angularis*. *Conidiophores* lining the inner cavity, reduced to conidiogenous cells, or with one supporting cell. *Conidiogenous cells* hyaline, smooth, subcylindrical to doliiform, 7–12 × 3–4 µm; apical region with several inconspicuous percurrent proliferations, or with periclinal thickening; collarette inconspicuous, or prominent, flared. *Conidia* hyaline, smooth, becoming somewhat olivaceous and verruculose in older cultures, subcylindrical, (1–)3-septate, (19–)25–35(–38) × (3.5–)4 µm, tapering in apical part to obtuse or subobtuse apex, base truncate, 1.5–2.5 µm diam, straight to somewhat curved, mostly with one large central guttule per cell, older conidia becoming constricted at septa, disarticulating into phragmospores.

*Culture characteristics*: Colonies on PDA umbonate, round, fluffy grey white aerial mycelium on the younger parts with longer grey blackish tufts on the older parts, surface olivaceous-black to buff at the younger mycelium, reverse olivaceous-black at the older parts to buff at the younger mycelium, after 14 days 6 cm diam; on MEA similar toPDA but after 14 d, 7 cm diam; on OA similar to PDA.

*Specimens examined*: **Hong Kong**, Mai Po Mangrove, from the leaves of *Phragmites australis* (*Poaceae*), 12 Mar. 1998, K.D. Hyde (**holotype** CBS H-21324, culture ex-type CBS 114802 = HKUCC 2689); *ibid*., 3 Feb. 2000, K.D. Hyde (CBS 114966 = HKUCC 6029).

*Notes*: *Setoseptoria* needs to be compared to *Dearnessia* and *Trichoseptoria* (see above). The genus *Trichoseptoria* is poorly known, and details about its conidiogenesis is lacking, and thus it cannot be compared until it has been recollected. *Setoseptoria* is distinct from *Dearnessia* in that it has conidiogenous cells with prominent percurrent proliferation, and conidia that tend to become olivaceous and verruculose in older cultures, and disarticulate into phragmospores. Several *Septoria* species have been described from *Phragmites*, including *S. phragmitis* (conidia 20–30 × 1.5–2 µm), *S. arundinacea* (conidia 6–7-septate, 60–70 × 5–6 µm), *S. curva* (conidia 14–20 × 3.5–4.5 µm), and *S. graminum* (conidia multiseptate, 55–75 × 1–1.3 µm), all of which appear to differ from *Setoseptoria phragmitis* based on its conidial morphology.

## Clade 44: *Septorioides*

***Septorioides*** Quaedvlieg, Verkley & Crous, **gen. nov.** MycoBank MB804464.

*Etymology*: Resembling the genus *Septoria*.

*Foliicolous. Conidiomata* black, unilocular, globose, flattened, opening by means of irregular rupture; wall consisting of 6–10 layers of dark brown *textura irregularis* to *angularis*, exuding a crystal conidial mass. *Paraphyses* intermingled among conidiophores, hyaline, cylindrical, branched at base, septate with obtuse ends. *Microconidia* hyaline, smooth, cylindrical, mostly straight, apex obtuse, base truncate. *Conidiophores* reduced to conidiogenous cells or with a supporting cell. *Conidiogenous cells* lining the inner cavity in basal layer, hyaline, smooth, subcylindrical to ampulliform, giving rise to macro- and microconidia. *Spermatia* formed in conidiomata, cylindrical, hyaline, smooth, straight to curved. *Macroconidia* hyaline, smooth, guttulate, subcylindrical, straight to irregularly curved, tapering in apical cell to subobtuse apex, base truncate, transversely euseptate.

*Type species*: *Septorioides pini-thunbergii* (S. Kaneko) Quaedvlieg, Verkley & Crous.

***Septorioides pini-thunbergii*** (S. Kaneko) Quaedvlieg, Verkley & Crous, **comb. nov.** MycoBank MB804465. Fig. 101.
*Basionym*: *Septoria pini-thunbergii* S. Kaneko, Trans. Mycol. Soc. Japan 30(4): 463. 1989.

Associated with needle blight, or isolated as endophyte. On PDA. *Conidiomata* black, unilocular, globose, flattened, up to 400 µm diam, opening by means of irregular rupture; wall consisting of 6–10 layers of dark brown *textura irregularis* to *angularis*, exuding a crystal conidial mass. *Paraphyses* intermingled among conidiophores, hyaline, cylindrical, branched at base, septate with obtuse ends, 2–2.5 µm diam, up to 80 µm long. *Microconidia* hyaline, smooth,

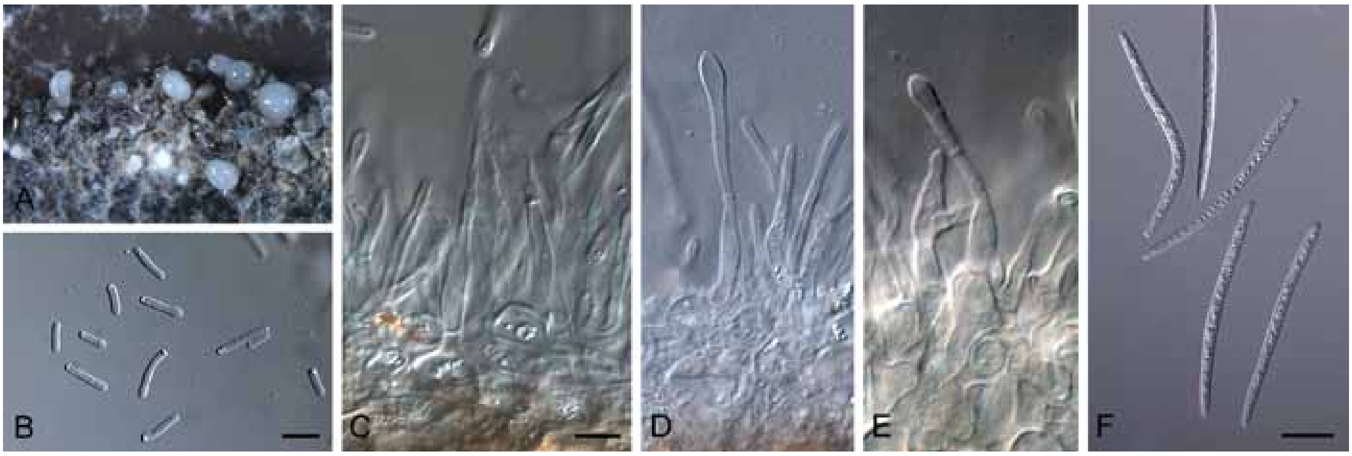


**Fig. 101.** *Septorioides pini-thunbergii* (CBS 473.91). A. Colony sporulating on PDA. B. Spermatia. C–E. Conidiogenous cells. F. Conidia. Scale bars = 10 µm.

cylindrical, mostly straight, apex obtuse, base truncate, 5–15 × 2–2.5 µm. *Conidiophores* reduced to conidiogenous cells or with a supporting cell. *Conidiogenous cells* lining the inner cavity in basal layer, hyaline, smooth, subcylindrical to ampulliform, 10–15 × 4–6 µm, giving rise to macro- and microconidia. *Spermatia* formed in conidiomata, cylindrical, hyaline, smooth, straight to curved, 3–7 × 2 µm. *Macroconidia* hyaline, smooth, guttulate, subcylindrical, straight to irregularly curved, tapering in apical cell to subobtuse apex, base truncate, (60–)70–80(–110) × 3.5(–4) µm, (1–)3–6(–10)-septate.

*Specimen examined*: **Japan**, Akita Prefecture, Tenno-cho, on needles of *Pinus thunbergii* (*Pinaceae*), Aug. 1984, S. Kaneko & Y. Zinno, culture ex-type of *Septoria pini-thunberghii* (CBS 473.91).

*Note*: *Septorioides* is distinguished from *Septoria* by having conidiomata that open by means of an irregular split (acervular), and having paraphyses intermingled among its conidiophores. *Septorioides pini-thunbergii* was originally described from blighted needles of *Pinus thunbergii* in Japan (Kaneko *et al.* 1989). It was also recently isolated as endophyte from needles of *P. densiflora* in Korea (Yoo & Eom 2012).

## Clade 45: *Phlyctema*

***Phlyctema*** Desm., Ann. Sci. Nat., Sér. 3, 8: 16. 1847.
= *Allantozythia* Höhn., Mykol. Unters. 3: 322. 1923.

*Mycelium* immersed, branched, septate, hyaline. *Conidiomata* eustromatic, immersed, erumpent, sporodochial, separate, yellowish brown, pulvinate, circular, unilocular but convoluted, thick-walled; wall of *textura angularis*, darker brown and thicker-walled at base than at the sides. *Ostiole* absent, dehiscence by irregular rupture. *Conidiophores* hyaline, septate, branched irregularly, cylindrical to filiform, formed from the wall lining the conidiomata. *Conidiogenous cells* enteroblastic, phialidic, integrated or discrete, determinate, hyaline, with minute collarette and periclinal thickening. *Conidia* hyaline, aseptate, fusiform, eguttulate, straight to slightly curved or irregular (Sutton 1980).

*Type species*: *P. vagabunda* Desm., Ann. Sci. Nat., Bot., Sér. 3, 8: 16. 1847.

*Notes*: *Phlyctema* is characterised by having eustromatic, convulated, pulvinate to sporodochial conidiomata, branched, hyaline conidiophores, and phialidic conidiogenous cells that give rise to hyaline, aseptate, fusiform, straight to curved conidia. The genus has more than 80 names, and is in need of revision. . The type species is linked to a sexual morph known as *Neofabraea alba* (Verkley 1999).

***Phlyctema vincetoxici*** Quaedvlieg, Verkley & Crous, **sp. nov.** MycoBank MB804466. Figs 102, 103.

*Etymology*: Named after the host genus from which it was collected, *Vincetoxicum.*

*Conidiomata* immersed, separate, eustromatic, unilocular, convulated, opening by irregular rupture, becoming acervular to sporodochial, up to 450 µm diam; wall of 3–6 layers of brown *textura angularis*; outer surface covered in brown, warty hyphae. *Conidiophores* hyaline, smooth, subcylindrical, lining the inner layer, branched, 1–4-septate, 15–50 × 4–5 µm. *Conidiogenous cells* phialidic, hyaline, smooth, subcylindrical to cymbiform or doliiform, with apical periclinal thickening and minute, non-flaring collarette, 7–18 × 3.5–5 µm. *Conidia* hyaline, smooth, guttulate, aseptate, fusiform, curved, tapering to subobtuse apex and truncate base, (27–)33–37(–40) × 3(–3.5) µm.

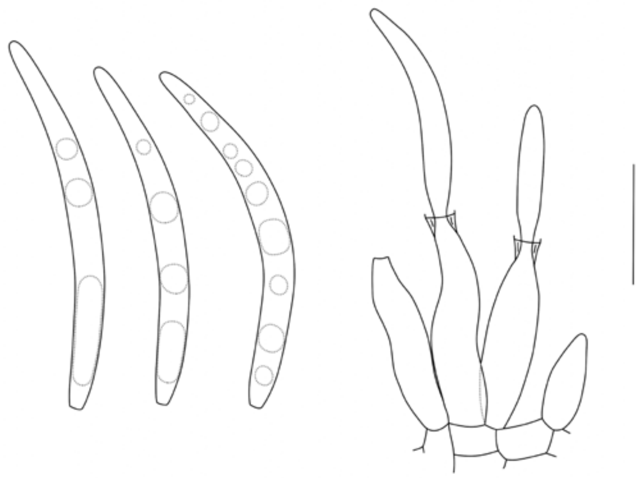

**Fig. 102.** Conidia and conidiogenous cells of *Phlyctema vincetoxici* (CBS 123727). Scale bar = 10 µm.

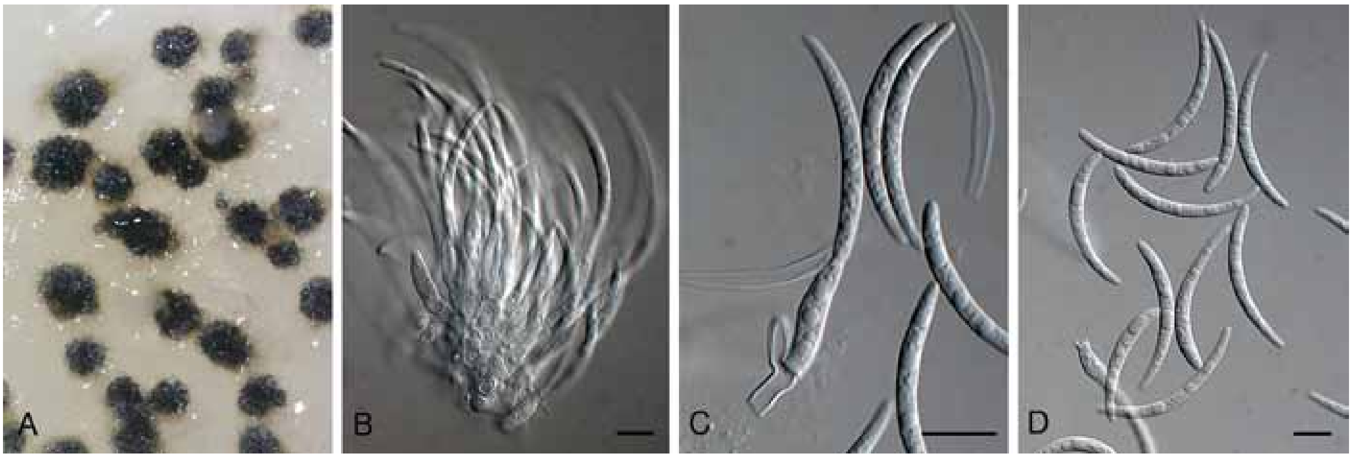


**Fig. 103.** *Phlyctema vincetoxici* (CBS 123727). A. Colonies forming on OA. B, C. Conidiogenous cells. D. Conidia. Scale bars = 10 µm.

*Culture characteristics*: Colonies on PDA flat, circular, with sparse, white aerial mycelium, surface dark-brick, reverse greyish sepia, after 14 d, 7 cm diam; on MEA undulate, lacking aerial mycelium, after 14 d, 6 cm diam; on OA flat, circular, lacking aerial mycelium, after 14 d, 8.5 cm diam.

*Specimen examined*: **Czech Republic**, Moravia, Podyji National Park, Masovice, Klinka area, on leaves of *Vincetoxicum officinale* (*Asclepiadaceae*), 17 Sep. 2008, G. Verkley (**holotype** CBS H-21325, culture ex-type CBS 123727 = V6015.2).

*Notes*: No species of *Phlyctema* has thus far been described on *Vincetoxicum. Septoria vincetoxici* (conidia 30–50 × 1–1.5 µm; Saccardo 1884) has somewhat longer, narrower conidia. *Phlyctema vincetoxici* was found sporulating in leaf spots showing numerous hypophyllous teleospore sori of the rust fungus *Cronartium flaccidum* (identified by H.A. van der Aa).

## Clade 46: *Kirstenboschia*

***Kirstenboschia*** Quaedvlieg, Verkley & Crous, **gen. nov.** MycoBank MB804467.

*Etymology*: Kirstenbosch National Botanical Garden is one of the most acclaimed botanical gardens of the world, set against the foot of Cape Town's Table Mountain. With more than 7000 plant species, it has also proven to be a source of numerous undescribed fungal species. Kirstenbosch was established in 1913, and to celebrate its centenary (2013), the fungal genus *Kirstenboschia* is named after this beautiful garden.

*Foliicolous. Conidiomata* erumpent, sporodochial, separate, with slightly raised outer margin of 3–10 layers of *textura intricata*. *Conidiophores* lining the inner cavity, hyaline, smooth, septate, subcylindrical, branched below and above. *Conidiogenous cells* terminal and lateral, hyaline, smooth, ampulliform to subcylindrical, proliferating sympodially, apical loci truncate, at times appearing subdenticulate. *Conidia* solitary, hyaline, scolecosporous, smooth, granular, thin-walled, acicular to narrowly obclavate with subobtuse apex and truncate to long obconically truncate base, 3-septate, irregularly curved.

*Type species*: *K. diospyri* Quaedvlieg, Verkley & Crous.

***Kirstenboschia diospyri*** Quaedvlieg, Verkley & Crous, **sp. nov.** MycoBank MB804468. Figs 104, 105.

*Etymology*: Named after the host genus from which it was collected, *Diospyros.*

*Conidiomata* erumpent, sporodochial, up to 300 µm diam, separate, appearing creamy to pale yellow when sporulating on SNA with barley leaves, with slightly raised outer margin of 3–10 layers of *textura intricata*. *Conidiophores* lining the inner cavity, hyaline, smooth, 0–4-septate, subcylindrical, branched below and above, 5–15 × 2–4 µm. *Conidiogenous cells* 5–10 × 2–3 µm, terminal and lateral, hyaline, smooth, ampulliform to subcylindrical, proliferating sympodially, apical loci truncate, at times appearing subdenticulate, 1 µm diam. *Conidia* solitary, hyaline, scolecosporous, smooth, granular, thin-walled, acicular to narrowly obclavate with subobtuse apex and truncate to long obconically truncate base, 3-septate, irregularly curved, (40–)60–70(–75) × (1.5–)2 µm.

*Culture characteristics*: Colonies on PDA erumpent, with moderate aerial mycelium, and smooth, lobate margin; surface and reverse dirty white. On OA dirty white with diffuse brown pigment in agar. On MEA surface folded, irregular, strongly erumpent, dirty white, reverse sienna.

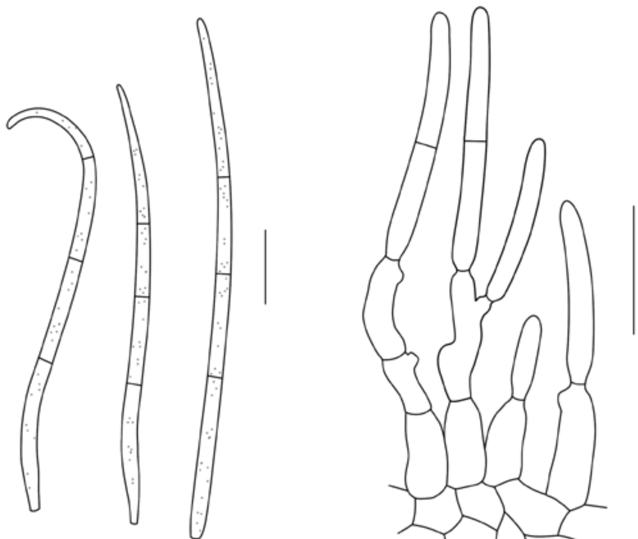

**Fig. 104.** Conidia and conidiogenous cells of *Kirstenboschia diospyri* (CBS 134911). Scale bars = 10 µm.

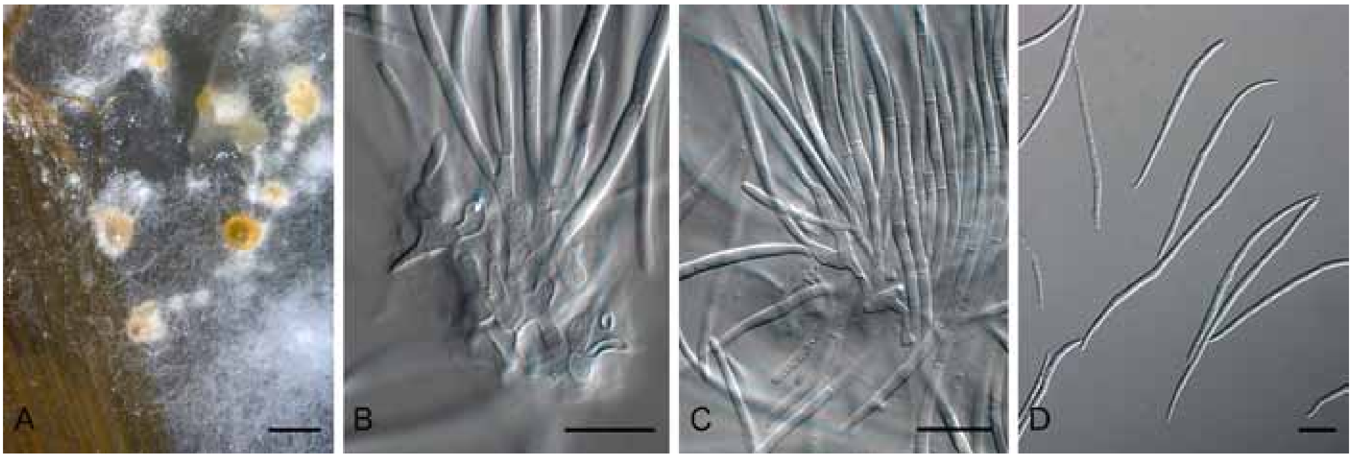


**Fig. 105.** *Kirstenboschia diospyri* (CBS 134911). A. Conidiomata forming in culture. B, C. Conidiogenous cells. D. Conidia. Scale bars: A = 300 µm, all others = 10 µm.

*Specimen examined*: **South Africa**, Western Cape Province, Kirstenbosch Botanical Garden, on leaves of *Diospyros whyteana* (*Ebenaceae*), 9 Aug. 2011, P.W. Crous (**holotype** CBS H-21326, culture ex-type CBS 134911 = CPC 19869).

*Note*: *Kirstenboschia* is distinguished from *Septoria s. str*. and allied genera based on its distinctive, sporodochial conidiomata, and conidiogenous cells that proliferate sympodially, but at times are subdenticulate.

## Clade 47: *Phlogicylindrium*

***Phlogicylindrium*** Crous, Summerb. & Summerell, Fungal Diversity 23: 340. 2006.

*Foliicolous. Conidiomata* synnematal to sporodochial, pale brown. *Macroconidiophores* arising from a brown stroma of 3–6 layers of *textura angularis*, giving rise to subcylindrical, hyaline (dark brown at the base), smooth, frequently branched conidiophores, 0–2(–6)-septate. *Macroconidiogenous cells* hyaline, smooth, subcylindrical, proliferating sympodially and percurrently near apex. *Macroconidia* hyaline, smooth, subcylindrical, transversely septate, apex obtusely rounded, base truncate, slightly curved. *Microconidia* formed in acervular conidiomata together with macroconidia. *Microconidiophores* intermingled among macroconidiophores, hyaline, smooth, subcylindrical, branched, 1–4-septate. *Microconidiogenous cells* terminal and lateral, hyaline, smooth, ampulliform, phialidic, solitary or in penicillate clusters. *Microconidia* hyaline, smooth, hamate, curved, apex subobtuse, base truncate, widest in upper third, aseptate (Summerell *et al*. 2006).

*Type species*: *P. eucalypti* Crous, Summerb. & Summerell, Fungal Diversity 23: 340. 2006.

***Phlogicylindrium eucalyptorum*** Crous, Fungal Planet 20. 2007. Figs 106, 107.

On OA. *Conidiomata* synnematal to sporodochial, pale brown up to 300 µm diam. *Macroconidiophores* arising from a brown stroma of 3–6 layers of textura angularis, giving rise to subcylindrical, hyaline (dark brown at the base), smooth, frequently branched conidiophores, 0–2(–6)-septate, 15–25(–45) × 3–4 µm. *Macroconidiogenous cells* hyaline, smooth, subcylindrical, 10–15 × 2–4 µm, proliferating sympodially and percurrently near apex. *Macroconidia* hyaline, smooth, subcylindrical, 1(–3)-septate, apex obtusely rounded, base truncate, slightly curved, (27–)40–50(–55) × 2–2.5(–3) µm. *Microconidia* formed in acervular conidiomata together with macroconidia. *Microconidiophores* intermingled among macroconidiophores, hyaline, smooth, subcylindrical, branched, 1–4-septate, 20–40 × 2–2.5 µm. *Microconidiogenous cells* terminal and lateral, hyaline, smooth, ampulliform, phialidic, 5–16 × 2–2.5 µm, solitary or in penicillate clusters of up to 3. *Microconidia* hyaline, smooth, hamate, curved, apex subobtuse, base truncate, widest in upper third, aseptate, (16–)17–20(–24) 1.5(–2) µm.

*Specimens examined*: **Australia**, Victoria, Otway Ranges, (near Gellibrand), latitude: -38.568412, longitude: 143.539586, elevation: 175 m, on leaves of *Eucalyptus globulus* (*Myrtaceae*), Sep. 2005, I. Smith, **holotype** CBS H-19771, cultures ex-type CPC 12429 = CBS 120221; New South Wales, on leaves of *E. nitens*, 22 Nov. 1996, P.W. Crous (CBS 111689 = CPC 1547 = STE-U 1547).

*Notes*: The present strain represents the second collection of this fungus. Isolates from this collection formed a microconidial state not observed in the type (Crous *et al*. 2007c), and novel for species of *Phlogicylindrium*.

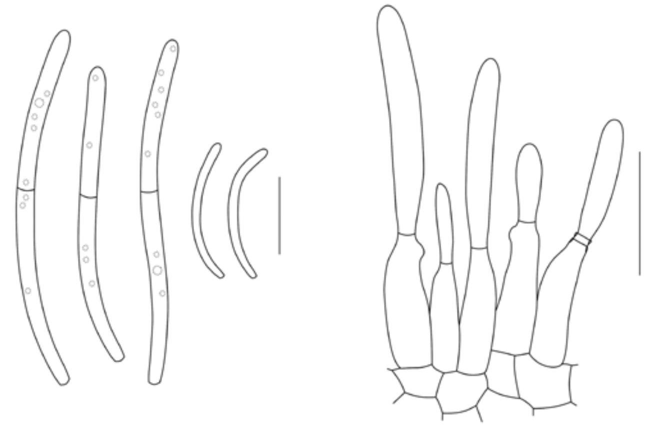

**Fig. 106.** Macro- and microconidia and conidiogenous cells of *Phlogicylindrium eucalyptorum* (CBS 111689). Scale bars = 10 µm.

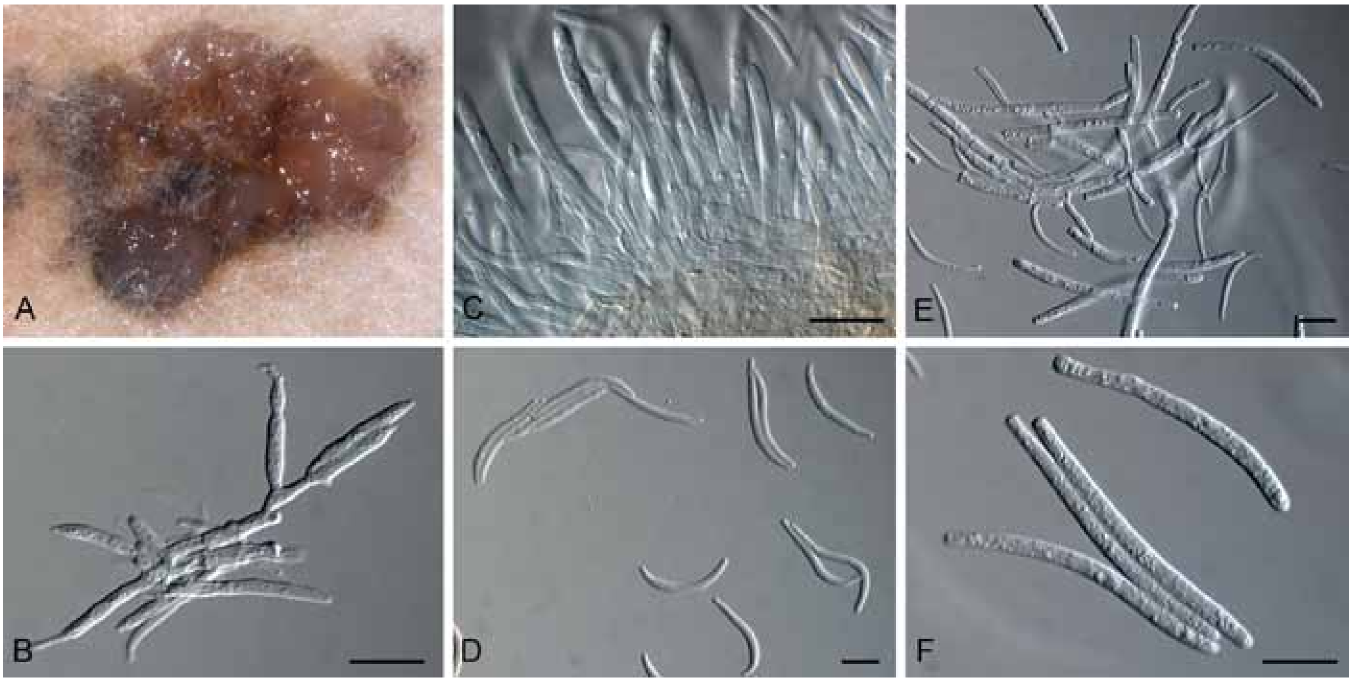


**Fig. 107.** *Phlogicylindrium eucalyptorum* (CBS 111689). A. Colony on OA. B, E. Microcyclic conidiation with macro- and macroconidia. C. Macroconidiogenous cells. D. Microconidia. F. Macroconidia. Scale bars = 10 µm.

## DISCUSSION

The main question considered in the present study was: what is *Septoria*? To address this we included 370 isolates representing 170 species, sampled from six continents. Furthermore, we also generated several phylogenetic datasets based on partial sequences of the ITS, LSU, Btub, RPB2 and EF-1α loci. In the final analysis, it was clear that *Septoria* is a well-defined genus and phylogenetic clade, with pycnidial, ostiolate conidiomata, conidiophores reduced to conidiogenous cells that proliferate sympodially, and hyaline, filiform conidia with transverse eusepta, fitting the original concept of Sutton (1980). However, when host material has been incubated for a while, several pycnidial species tend to form acervuli (also not clearly defined when studied in culture on normal agar media), and conidiogenous cells could have a combination of sympodial and percurrent proliferation (as observed in *Pseudocercospora*; Crous *et al.* 2013).

The present study, including that of Verkley *et al*. (2013) defined an additional 15 genera that were formerly treated as "septoria" in the widest sense. Although it has recently been shown that *Phoma* is a generic complex representing many morphologic and phylogenetic genera (Aveskamp et al. 2010, de Gruyter et al. 2010, 2013), this was not expected to also be the case for *Septoria*. Furthermore, many of the septoria-like genera discussed earlier in this paper are presently still not known from sequence, and thus their phylogeny remains to be resolved, meaning that they could add futher entities to the list of acknowledged septoria-like genera.

Although *Septoria s. str*. is a genus in the *Mycosphaerellaceae* (*Capnodiales*), several of the septoria-like genera clustered outside this family. Species of *Septoria* are morphologically conserved, and in the past many taxa were identified based on host, which has been shown to be unreliable (see Verkley *et al*. 2013), as several taxa have wide host ranges. Another complication revealed in the present study is that many septoria-like genera cluster in different phylogenetic clades, but have still retained the *Septoria* morphological characters, which means that as in *Phoma*, future identifications in this complex will also have to rely on DNA sequence data to support morphological conclusions.

The genus *Stagonospora* has always been separated from *Septoria* on the basis that *Septoria* has conidiogenous cells with sympodial proliferation, whereas in *Stagonospora* they proliferate percurrently. As shown in the present study, however, conidiogenesis is far too broad a feature to define all genera that express these modes of proliferation in their conidiogenous cells. *Stagonospora*, which is based on *S. paludosa*, was epitypified in this study, and shown to cluster apart from *Septoria s. str.* Another major surprise lies in the fact that Septoria nodorum blotch, caused by "*Stagonospora*" *nodorum*, clusters in a distinct genus, unrelated to *Stagonospora s. str*., and also separate from *Phaeosphaeria s. str*. A repercussion from these findings is the fact that the common cereal pathogens, which are neither *Stagonospora*, *Septoria*, *Phaeosphaeria* or *Leptosphaeria* (see de Gruyter *et al*. 2013), now have to be accommodated in a new genus, *Parastagonospora*. Furthermore, it appears that *Stagonospora s. str*. occurs on *Poaceae*, but has thus far only been confirmed from *Carex*, though further sampling will undoubtedly extend the host range of this genus. *Parastagonospora* is thus a novel, distinct stagonospora-like genus, which has sexual morphs that are phaeosphaeria-like in morphology, thus quite unlike those of *Stagonospora s. str*., which are more didymella-like in morphology.

The genus *Phaeosphaeria* is based on *P. oryzae* (asexual morph *Phaeoseptoria oryzae*), for which we could designate an epitype in this study. Furthermore, we also recollected the type species of *Phaeoseptoria*, *P. papayae*, for which we also designated an epitype. As expected, *Phaeoseptoria* clusters with *Phaeosphaeria*, for which we choose the name of the sexual morph, *Phaeosphaeria*, on the basis that it is clearly resolved, and well established in literature. In contrast, *Phaeoseptoria* has in recent years become a muddled concept harbouring unrelated coelomycetes with pigmented conidia.

Obtaining a culture of *Cytostagonospora martiniana* clarified the phylogenetic position of the genus as distinct from *Septoria*, resolving the difference of opinion between von Arx (1983), who regarded it as synonym of *Septoria*, versus Sutton (1980), who retained it as separate genus. Of interest is the unique mode of conidiogenesis, ranging from holoblastic sympodial to polyphialides with periclinal thickening to percurrent proliferation. It should be noted, however, that although this is a distinct genus, *C. mariniana* is not the type of *Cytostagonospora*, and *C. photiniicola* (occurring on *Photinia serrulata*, Austria) will have to be recollected to confirm that these two fungi are congeneric.

The genus *Phloeospora* (based on *P. ulmi*) has for long been assumed to be a synonym of *Septoria* based on morphology. It is thus good to finally see it resolved as separate phylogenetic lineage, which is also supported morphologically based on its acervular conidiomata and conidiogenous cells with prominent percurrent proliferation. In spite of resolving 21 genera, several lineages remain unresolved, and are simply treated as “septoria-like” awaiting the recollection of additional material.

It is surprising that so many of the cereal pathogens actually have a confused taxonomy. Eyespot disease of wheat, formely treated as *Tapesia* (*Ramulispora* asexual states), was shown to represent a distinct genus *Oculimacula* (*Helgardia* asexual states) (Crous *et al*. 2003), while Quaedvlieg *et al.* (2011) determined that Septoria tritici blotch, caused by “*Septoria*” *tritici*, is in fact better accommodated in a new genus, *Zymoseptoria*, which appears to be restricted to members of *Poaceae*. The present study also resolved the phylogenetic position of Septoria nodorum blotch, which proved to not represent a member of *Septoria*, *Stagonospora*, or *Phaeosphaeria*, but to represent a distinct genus, described here as *Parastagonospora*. Clearly more attention should be directed towards resolving the taxonomy of the pathogens of agricultural crops of major economic importance in future, as these findings also have implications for genomic studies, where organisms from different genera, and even families get compared to one another, and new evolutionary hypotheses are proposed on the assumption that these taxa are congeneric. To clarify the taxonomy of well-known plant pathogens, however, many species will have to be recollected, and epitypified, so that authentic cultures and DNA barcodes will become available to fix the genetic application of these names.

## General conclusions

The genus *Septoria* is defined by having pycnidial to acervular conidiomata, and hyaline conidiophores that give rise to conidiogenous cells that proliferate sympodially and percurrently, forming hyaline, filiform conidia with transverse eusepta. Many species have wide host ranges, and host occurrence should not be used as primary character for identification (see Verkley *et al*. 2013, this issue). Although species of *Septoria* and several of the novel genera introduced here have mycosphaerella-like sexual states, the name *Mycosphaerella* is restricted to the genus *Ramularia*, and is unavailable for species of *Septoria* and related genera.

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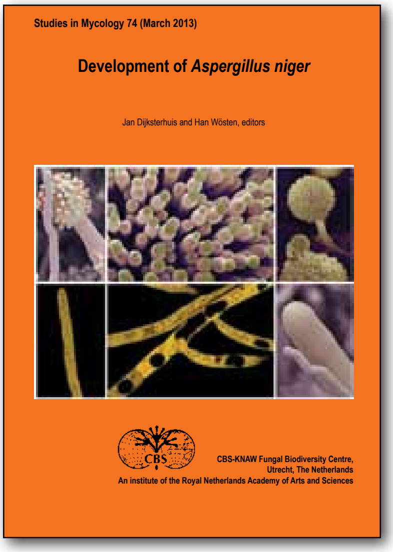
# INDEX OF FUNGAL NAMES

Alphabetical list of fungal species, genera and families treated in the Taxonomy sections of the included manuscripts.

**A**

**M**

**R**




## Studies in Mycology 74: Development of *Aspergillus niger*

J. Dijksterhuis and H.A.B. Wösten (eds)

This issue of Studies in Mycology deals with vegetative growth and development of *Aspergillus* in general and *A. niger* in particular. *Aspergillus* niger is a member of the *Aspergillus* section *Nigri*, a group of 26 species that are dubbed "the black Aspergilli". *Aspergillus niger* is a cosmopolitan fungus. It can be isolated from all continents and is not very selective with respect to environmental conditions. *Aspergillus niger* is used as a cell factory for the production of enzymes and metabolites such as organic acids.

The issue starts with a review on molecular mechanisms underlying differentiation processes in the vegetative mycelium and during asexual and sexual development of aspergilli.

The articles of van Leeuwen *et al*. show that the RNA composition of dormant conidia is highly different from that of germinating conidia (i.e. of conidia during isotropic and polarized growth). The transcriptome of conidia changes most dramatically during the first two hours of germination enabling initiation of protein synthesis and respiration. The antifungal natamycin does neither affect differential expression of genes nor germination of *A. niger* conidia during the first 2 h of the process. Notably, subsequent stages of germination were effectively blocked by the anti-fungal compound, and the transcriptome inside the cells had changed thoroughly. The article of van Veluw *et al*. focusses on stages following germination namely the formation of micro-colonies. It is shown that micro-colonies of a control strain are smaller and more heterogeneous in size when compared to strains in which pigmentation genes are inactivated. These results are of interest from a biotechnological point of view since productivity is related to the morphology of micro-colonies. The results of Van Veluw *et al*. also indicate the existence of transcriptionally and translationally highly active and lowly active hyphae in 1 mm wide micro-colonies of *A. niger* as was previously shown in macro-colonies with a diameter of about 5–7 cm. However, the existence of distinct populations of hyphae with high and low transcriptional and translational activity seems to be less robust when compared to macro-colonies. Why colonies have hyphae with different transcriptional and translational activity is still not clear but it may have a role in survival in an environment where conditions are dynamic. The article of Bleichrodt *et al*. focusses on sporulating colonies. Evidence is presented that GFP but not mRNA streams from the vegetative mycelium to conidiophores. Apparently, flow of molecules to the reproductive structure is selective. Absence of RNA streaming would explain why distinct RNA profiles were found in the aerial mycelium when compared to the vegetative mycelium. Future studies should reveal why GFP flows but mRNA does not.

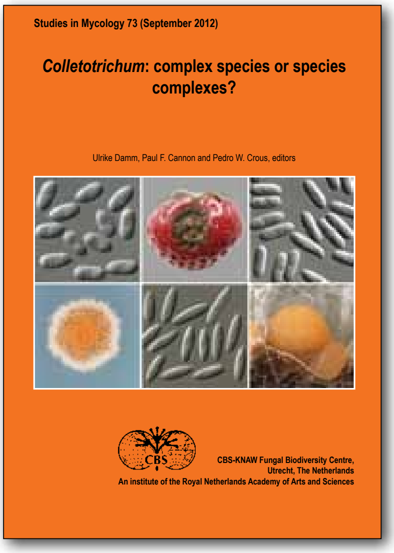
**85 pp., fully illustrated with colour pictures (A4 format), paperback, 2013. € 40**

## Studies in Mycology 73: *Colletotrichum*: complex species or species complexes?

U. Damm, P.F. Cannon and P.W. Crous (eds)

This volume of Studies in Mycology is dedicated to Brian C. Sutton, in honour of his scientific contributions to our present understanding of the genus *Colletotrichum*, and for providing a framework for morphology-based identification of taxa in the genus. The volume consists of contributions that revise three of the major *Colletotrichum* species complexes, and a concluding paper that summarises the present situation. It provides an online identification tool to all presently recognised species, and also gives insight into future research directions. The research papers continue the trend of applying multi-locus phylogenetics to elucidate cryptic species complexes, and in the process designates numerous epitype specimens to fix the genetic application of names. Furthermore, numerous novel taxa are introduced in the *C. acutatum* (treating 31 taxa, and introducing 21 novel species), *C. boninense* (treating 17 taxa, and introducing 12 novel species), and *C. gloeosporioides* (treating numerous taxa of which 22 are accepted, and introducing 9 novel taxa, as well as one novel subspecies) species complexes. Although some species appear to have preferences to specific hosts or geographical regions, others are plurivorous and are present in multiple regions. The future for *Colletotrichum* biology will thus have to rely on consensus classification and robust online identification tools. In support of these goals, a Subcommission on *Colletotrichum* has been formed under the auspices of the International Commission on Taxonomy of Fungi, which will administer a carefully curated barcode database for sequence-based identification of species within the BioloMICS web environment.

**213 pp., fully illustrated with colour pictures (A4 format), paperback, 2012. € 65**





## Studies in Mycology 72: The genus *Cladosporium*

K. Bensch, U. Braun, J.Z. Groenewald and P.W. Crous

A monographic revision of the hyphomycete genus *Cladosporium s. lat.* (*Cladosporiaceae*, *Capnodiales*) is presented. It includes a detailed historic overview of *Cladosporium* and allied genera, with notes on their phylogeny, systematics and ecology. True species of *Cladosporium s. str.* (anamorphs of *Davidiella*), are characterised by having coronate conidiogenous loci and conidial hila, i.e., with a convex central dome surrounded by a raised periclinal rim. Recognised species are treated and illustrated with line drawings and photomicrographs (light as well as scanning electron microscopy). Species known from culture are described *in vivo* as well as *in vitro* on standardised media and under controlled conditions. Details on host range/substrates and the geographic distribution are given based on published accounts, and a re-examination of numerous herbarium specimens. Various keys are provided to support the identification of *Cladosporium* species *in vivo and in vitro*. Morphological datasets are supplemented by DNA barcodes (nuclear ribosomal RNA gene operon, including the internal transcribed spacer regions ITS1 and ITS2, the 5.8S nrDNA, as well as partial actin and translation elongation factor 1-α gene sequences) diagnostic for individual species. In total 993 names assigned to *Cladosporium s. lat.*, including *Heterosporium* (854 in *Cladosporium* and 139 in *Heterosporium*), are treated, of which 169 are recognised in *Cladosporium s. str.* The other taxa are doubtful, insufficiently known or have been excluded from *Cladosporium* in its current circumscription and re-allocated to other genera by the authors of this monograph or previous authors.

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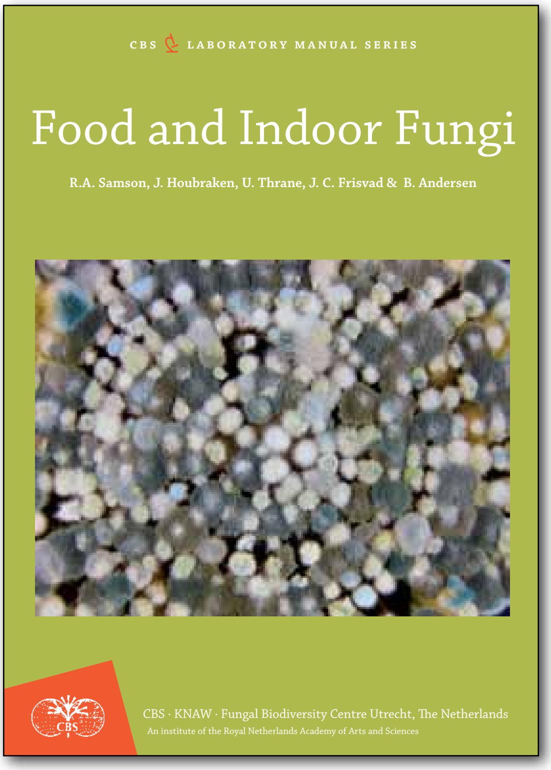
# CBS Laboratory Manual Series




## CBS Laboratory Manual Series 2: Food and Indoor Fungi

R.A. Samson, J. Houbraken, U. Thrane, J.C. Frisvad and B. Andersen

This book is the second in the new CBS Laboratory Manual Series and is based on the seventh edition of INTRODUCTION TO FOOD AND AIRBORNE FUNGI. This new version, FOOD AND INDOOR FUNGI, has been transformed into a practical user's manual to the most common micro-fungi found in our immediate environment – on our food and in our houses. The layout of the book starts at the beginning with the detection and isolation of food borne fungi and indoor fungi in chapters 1 and 2, describing the different sampling techniques required in the different habitats. Chapter 3 deals with the three different approaches to identification: morphology, genetics and chemistry. It lists cultivation media used for the different genera and describes step by step how to make microscope slides and tape preparations for morphological identification. The chapter also describes how to do molecular and chemical identification from scratch, how to evaluate the results and warns about pitfalls. Chapter 4 gives all the identification keys, first for the major phyla (*Ascomycetes*, *Basidiomycetes* and *Zygomycetes*) common on food and indoors, then to the different genera in the *Zygomycetes* and the *Ascomycetes*, with a large section on the anamorphic fungi and a section for yeasts. The section on anamorphic fungi contains two keys to the different genera: a dichotomous key and a synoptic key. For each genus a key to the species treated is provided, followed by entries on the different species. For each species colour plates are accompanied by macro- and a micro-morphological descriptions, information on molecular and chemical identification markers, production of mycotoxins, habitats and physiological and ecological characteristics. The book is concluded with an extensive reference list and appendices on the associated mycobiota on different food types and indoor environments, mycotoxins and other secondary metabolites, a glossary on the mycological terms used in the book and lastly a detailed appendix on the media used for detection and identification.

**390 pp., fully illustrated with colour pictures (A4 format). Hardbound, 2010. € 70**

## CBS Laboratory Manual Series 1: Fungal Biodiversity

P.W. Crous, G.J.M. Verkley, J.Z. Groenewald and R.A. Samson (eds)

This book is the first in the new "CBS Laboratory Manual Series", and focuses on techniques for isolation, cultivation, molecular and morphological study of fungi and yeasts. It has been developed as a general text, which is based on the annual mycology course given at the CBS-KNAW Fungal Biodiversity Centre (Centraalbureau voor Schimmelcultures). It provides an introductory text to systematic mycology, starting with a concise treatise of *Hyphochytridiomycota* and *Oomycota*, which have long been subject of study by mycologists, but are now classified in the Kingdom *Chromista*. These are followed by sections on the groups of "true fungi": *Chytridiomycota*, *Zygomycota*, *Ascomycota* and *Basidiomycota*. This descriptive part is illustrated by figures of life-cycles and schematic line-drawings as well as photoplates depicting most of the structures essential for the study and identification of these fungi. Special attention is given to basic principles of working with axenic cultures, good morphological analysis, and complicated issues for beginners such as conidiogenesis and the understanding of life-cycles. Exemplar taxa for each of these fungal groups, in total 37 mostly common species in various economically important genera, are described and illustrated in detail. In a chapter on general methods a number of basic techniques such as the preparation and choice of media, microscopic examination, the use of stains and preparation of permanent slides, and herbarium techniques are explained. Further chapters deal with commonly used molecular and phylogenetic methods and related identification tools such as BLAST and DNA Barcoding, fungal nomenclature, ecological groups of fungi such as soil-borne and root-inhabiting fungi, water moulds, and fungi on plants and of quarantine importance. Some topics of applied mycology are also treated, including fungi in the air- and indoor environment and fungi of medical importance. Common mycological terminology is explained in a glossary, with reference to illustrations in the book. A chapter providing more than 60 mycological media for fungal cultivation, and a comprehensive list of cited references are also provided. The book is concluded with an index, and dendrograms reflecting our current understanding of the evolutionary relationships within the *Fungi*.

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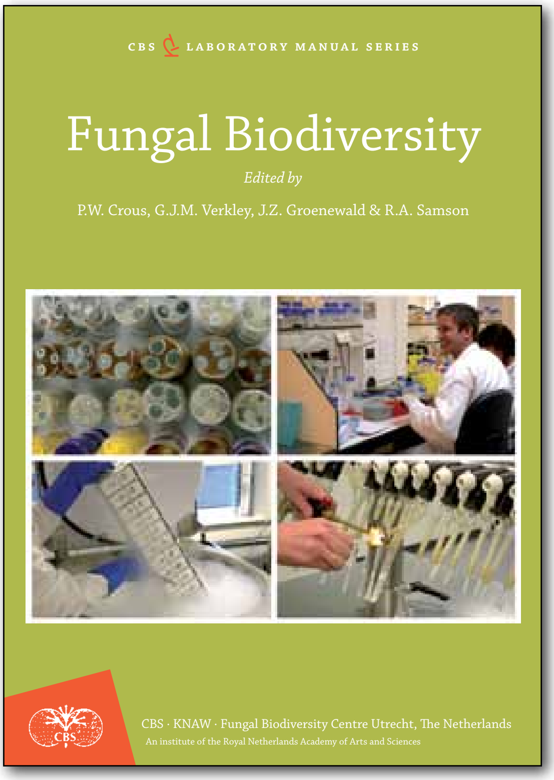


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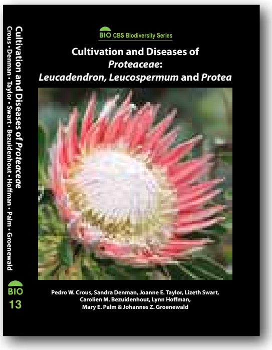


### No. 13: Cultivation and Diseases of *Proteaceae*: *Leucadendron*, *Leucospermum* and *Protea*

Pedro W. Crous, Sandra Denman, Joanne E. Taylor, Lizeth Swart, Carolien M. Bezuidenhout, Lynn Hoffman, Mary E. Palm and Johannes Z. Groenewald

*Proteaceae* represent a prominent family of flowering plants in the Southern Hemisphere. Because of their beauty, unique appearance, and relatively long shelf life, *Proteaceae* cut-flowers have become a highly desirable crop for the export market. The cultivation of *Proteaceae* is a thriving industry that provides employment in countries where these flowers are grown, often in areas that are otherwise unproductive agriculturally. Diseases cause a loss in yield, and also limit the export of these flowers due to strict phytosanitary regulations. In this publication the fungi that cause leaf, stem and root diseases on *Leucadendron*, *Leucospermum* and *Protea* are treated. Data are provided pertaining to the taxonomy, identification, host range, distribution, pathogenicity, molecular characteristics and control of these pathogens. Taxonomic descriptions and illustrations are provided and keys are included to distinguish species in genera where a number of species affect *Proteaceae*. Disease symptoms are described and colour photographs are included. Where known, factors that affect disease epidemiology are discussed. Disease management strategies are also presented that will assist growers and advisors in making appropriate choices for reducing disease in specific areas. Information is also provided relating to crop improvement, cultivation techniques, harvesting and export considerations. Further development and expansion of this industry depends on producing and obtaining disease-free germplasm from countries where these plants are indigenous. For that reason it is important to document the fungi that occur on *Proteaceae*, and to establish the distribution of these fungi. These data are essential for plant quarantine services for use in risk assessments.

**360 pp., fully illustrated (A4 format). Hardbound, 2013. € 75**


### No. 12: Ophiostomatoid Fungi: Expanding Frontiers

Keith A. Seifert, Z. Wilhelm de Beer and Michael J. Wingfield (eds)

The 1992 Convention on Biological Diversity created a new awareness of the economic impact of living organisms. Regulators and quarantine specialists in governments all over the world now scrutinise dots on maps, as real-time online disease mapping and prediction models allow us to track (and try to prevent) the spread of diseases across borders. Woodlands are more managed, include less genetic diversity, and seem to be more susceptible to rapidly spreading disease. Different jurisdictions use different terminology, Biosecurity, Alien Invasive Species, Quarantine, but it is now commonplace to see large signs in airports, along highways, and on public hiking trails, warning citizens not to accidentally or deliberately facilitate the spread of unwanted pests or microbes. With the ophiostomatoid fungi, scientists have to cope with the overlapping behaviour of a triumvirate of kingdoms, the fungi, the animals (bark beetles, mites or nematodes), and how all of these impact trees in our forests and cities.

This book includes 21 papers divided among five themes, plus an appendix. It is a sequel to *Ceratocystis* and *Ophiostoma*: Taxonomy, Ecology, and Pathogenicity, published by the APS Press in 1993, and like that book is derived from an international symposium, this one held on North Stradbroke Island, Australia prior to the 9th International Mycological Congress. A year before this volume was completed, mycological taxonomy formally abandoned the historical two name system, known as dual nomenclature, and we are now adopting a single name binomial system. The appendix to this book provides a preliminary view of the nomenclature of the ophiostomatoid fungi using the new single name system. In an attempt at consistency, this naming system is used in all chapters.

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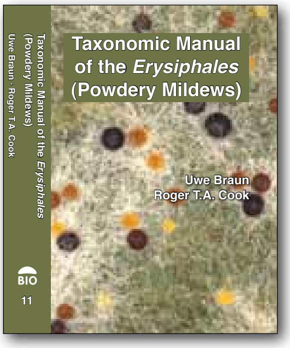
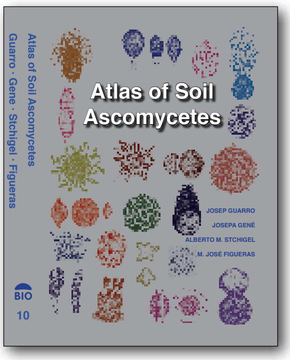



### No. 11: Taxonomic Manual of the *Erysiphales* (Powdery Mildews)

Uwe Braun and Roger T.A. Cook

The "Taxonomic Manual of the *Erysiphales* (Powdery Mildews)" is a fully revised, expanded new version of U. Braun's former monograph from 1987, which is out of print. The present book covers the taxonomy of all powdery mildew fungi. New chapters have been prepared for phylogenetic relationships, conidial germination, conidia as viewed by Scanning Electron Microscopy, fossil powdery mildews, and holomorph classification. The treatment of the *Erysiphales*, its tribes and genera are based on recent molecular phylogenetic classifications. A key to the genera (and sections), based on teleomorph and anamorph characters is provided, supplemented by a key solely using anamorph features. Keys to the species are to be found under the particular genera. A special tabular key to species based on host families and genera completes the tools for identification of powdery mildew taxa. In total, 873 powdery mildew species are described and illustrated in 853 figures (plates). The following data are given for the particular species and subspecific taxa: bibliographic data, synonyms, references to descriptions and illustrations in literature, full descriptions, type details, host range, distribution and notes. A further 236 taxonomic novelties are introduced, comprising the new genus *Takamatsuella*, 55 new species, four new varieties, six new names and 170 new combinations. A list of excluded and doubtful taxa with notes and their current status is attached, followed by a list of references and a glossary. This manual deals with the taxonomy of the *Erysiphales* worldwide, and provides an up-todate basis for the identification of taxa, as well as comprehensive supplementary information on their biology, morphology, distribution and host range. This monograph is aimed at biologists, mycologists and phytopathologists that encounter or study powdery mildew diseases.

**707 pp., fully illustrated with 853 pictures and line drawings (A4 format). Hardbound, 2012. € 80**




### No. 10: Atlas of Soil Ascomycetes

Josep Guarro, Josepa Gené, Alberto M. Stchigel and M. José Figueras

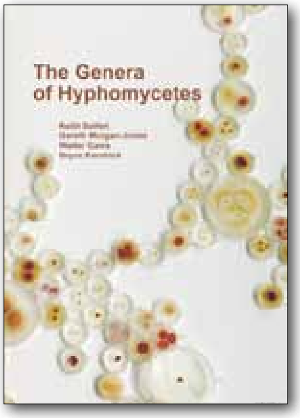
This compendium includes almost all presently known species of ascomycetes that have been reported in soil and which sporulate in culture. They constitute a very broad spectrum of genera belonging to very diverse orders, but mainly to the *Onygenales*, *Sordariales*, *Eurotiales*, *Thelebolales*, *Pezizales*, *Melanosporales*, *Pleosporales*, *Xylariales*, *Coniochaetales* and *Microascales*. The goal of this book is to provide sufficient data for users to recognise and identify these species. It includes the description of 146 genera and 698 species. For each genus a dichotomous key to facilitate species identification is provided and for each genus and species the salient morphological features are described. These descriptions are accompanied by line drawings illustrating the most representative structures. Light micrographs, supplemented by scanning electron micrographs and Nomarski interference contrast micrographs of most of the species treated in the book are also included. In addition, numerous species not found in soil but related to those included in this book are referenced or described. This book will be of value not only to soil microbiologists and plant pathologists concerned with the soilborne fungi and diseases, but also to anyone interested in identifying fungi in general, because many of the genera included here are not confined to soil. Since most of the fungi of biotechnological or clinical interest (dermatophytes, dimorphic fungi and opportunists) are soil-borne ascomycetes, the content of this book is of interest for a wide range of scientists.

**486 pp., fully illustrated with 322 pictures and line drawings (A4 format). Hardbound, 2012. € 70**

## CBS Biodiversity Series

### No. 9: The Genera of Hyphomycetes

Keith Seifert, Gareth Morgan-Jones, Walter Gams and Bryce Kendrick




The Genera of Hyphomycetes is the essential reference for the identification of moulds to all those who work with these fungi, including plant pathologists, industrial microbiologists, mycologists and indoor environment specialists, whether they be professionals or students. The book compiles information on about 1480 accepted genera of hyphomycetes, and about 1420 genera that are synonyms or names of uncertain identity. Each accepted genus is described using a standardized set of key words, connections with sexual stages (teleomorphs) and synanamorphs are listed, along with known substrates or hosts, and continental distribution. When available, accession numbers for representative DNA barcodes are listed for each genus. A complete bibliography is provided for each genus, giving the reader access to the literature necessary to identify species. Most accepted genera are illustrated by newly prepared line drawings, including many genera that have never been comprehensively illustrated before, arranged as a visual synoptic key. More than 200 colour photographs supplement the line drawings. Diagnostic keys are provided for some taxonomic and ecological groups. Appendices include an integrated classification of hyphomycete genera in the phylogenetic fungal system, a list of teleomorph-anamorph connections, and a glossary of technical terms. With its combination of information on classical morphological taxonomy, molecular phylogeny and DNA diagnostics, this book is an effective modern resource for researchers working on microfungi.

**997 pp., fully illustrated with colour pictures and line drawings (A4 format). Hardbound, 2011. € 80**

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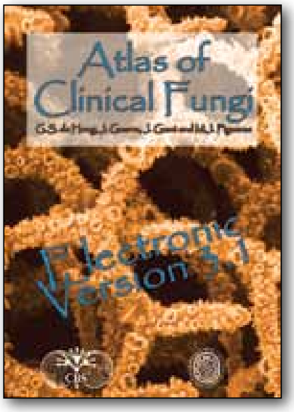



### Atlas of Clinical Fungi CD-ROM version 3.1

G.S. de Hoog, J. Guarro, J. Gené and M.J. Figueras (eds)

A new electronic version of the 3rd edition is available since November 2011. It will allows fast and very comfortable search through the entire Atlas text the engine is fully equiped for simple as well as advanced search. Items are strongly linked enabling direct use of the electronic version as a benchtool for identification and comparison. Text boxes with concise definitions appear explaining all terminology while reading. Illustrations are of highest quality and viewers are provided for detailed observation. The Atlas is interactive in allowing personal annotation which will be maintained when later versions will be downloaded.

The electronic version has been developed by T. Weniger. The third edition will contain about 530 clinically relevant species, following all major developments in fungal diagnostics. Regular electronic updates of the Atlas are planned, which should include numerous references to case reports, as well as full data on antifungals. Future features will include links to extended databases with verified molecular information. Note: The Atlas runs on Windows only! Not compatible with Mac

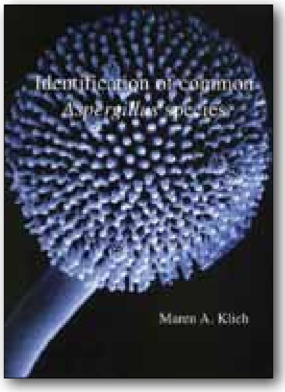
**Atlas of Clinical Fungi version 3.1, interactive CD-ROM, 2011. € 105**

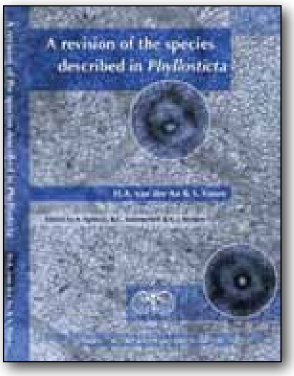
### Identification of Common *Aspergillus* Species

Maren A. Klich

Descriptions and identification keys to 45 common *Aspergillus* species with their teleomorphs (*Emericella*, *Eurotium*, *Neosartorya* and *Sclerocleista*). Each species is illustrated with a one page plate and three plates showing the most common colony colours.

**116 pp., 45 black & white and 3 colour plates (Letter format), paperback, 2002. € 45**




### A revision of the species described in *Phyllosticta*

Huub A. van der Aa and Simon Vanev

2936 taxa are enumerated, based on the original literature and on examination of numerous herbarium (mostly type) specimens and isolates. 203 names belong to the genus *Phyllosticta s.str.*, and are classified in 143 accepted species. For seven of them new combinations are made and for six new names are proposed. The great majority, 2733 taxa, were redisposed to a number of other genera. A complete list of these novelties, as included in the book's abstract, can also be consulted on the web-site of CBS.

**510 pp. (17 x 25 cm), paperback, 2002. € 55**

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