Studies in Mycology 75: 213–305.

A new approach to species delimitation in *Septoria*

G.J.M. Verkley[1*], W. Quaedvlieg[1,2], H.-D. Shin[3], and P.W. Crous[1,2,4]

[1]*CBS-KNAW Fungal Biodiversity Centre, Upssalalaan 8, 3584 CT, Utrecht, the Netherlands*; [2]*Microbiology, Department of Biology, Utrecht University, Padualaan 8, 3584 CH Utrecht, the Netherlands*; [3]*Division of Environmental Science and Ecological Engineering, Korea University, Seoul 136-701, Korea*; [4]*Wageningen University and Research Centre (WUR), Laboratory of Phytopathology, Droevendaalsesteeg 1, 6708 PB Wageningen, the Netherlands*

*Correspondence: G.J.M. Verkley, g.verkleij@cbs.knaw.nl

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.

doi:10.3114/sim0018. Hard copy: June 2013.

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

Copyright CBS-KNAW Fungal Biodiversity Centre, P.O. Box 85167, 3508 AD Utrecht, The Netherlands.

You are free to share - to copy, distribute and transmit the work, under the following conditions:
Attribution: You must attribute the work in the manner specified by the author or licensor (but not in any way that suggests that they endorse you or your use of the work).
Non-commercial: You may not use this work for commercial purposes.
No derivative works: You may not alter, transform, or build upon this work.
For any reuse or distribution, you must make clear to others the license terms of this work, which can be found at http://creativecommons.org/licenses/by-nc-nd/3.0/legalcode. Any of the above conditions can be waived if you get permission from the copyright holder. Nothing in this license impairs or restricts the author's moral rights.

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

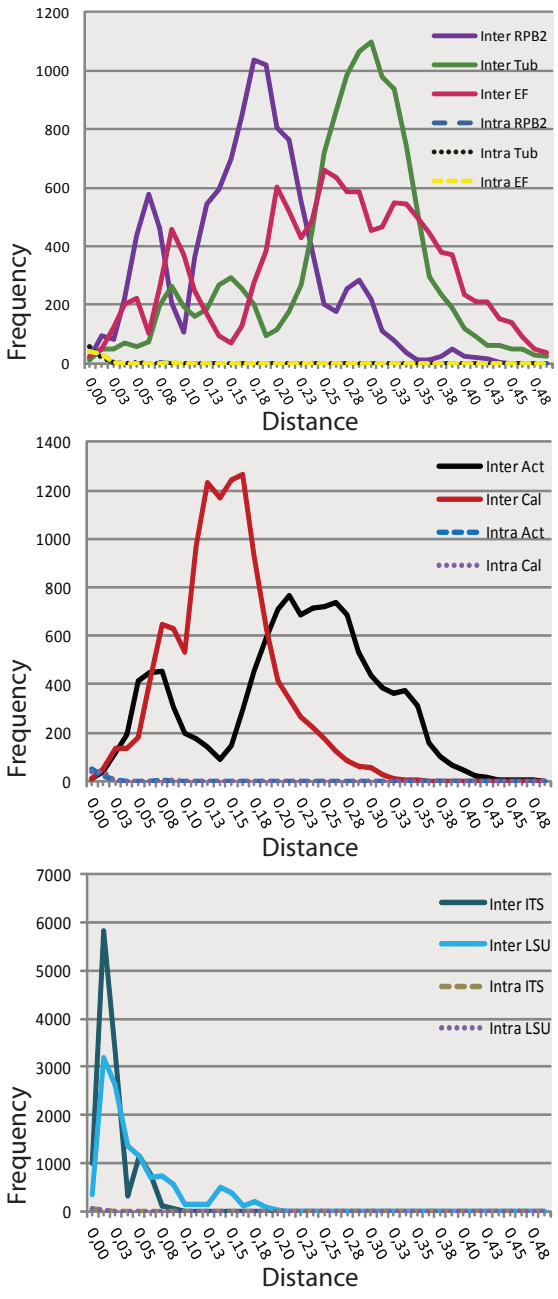

Fig. 1. Frequency distributions of the Kimura-2-parameter distances (barcoding gaps) for the seven PCR loci.

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. deamessii	–	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 comicola	*Septoria cornicola*	CBS 102324	*Cornus* sp.	Netherlands	A. van Iperen	KF253557	KF253076	KF252603	KF252115	KF251610	KF253912	KF254262
	Septoria comicola	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).

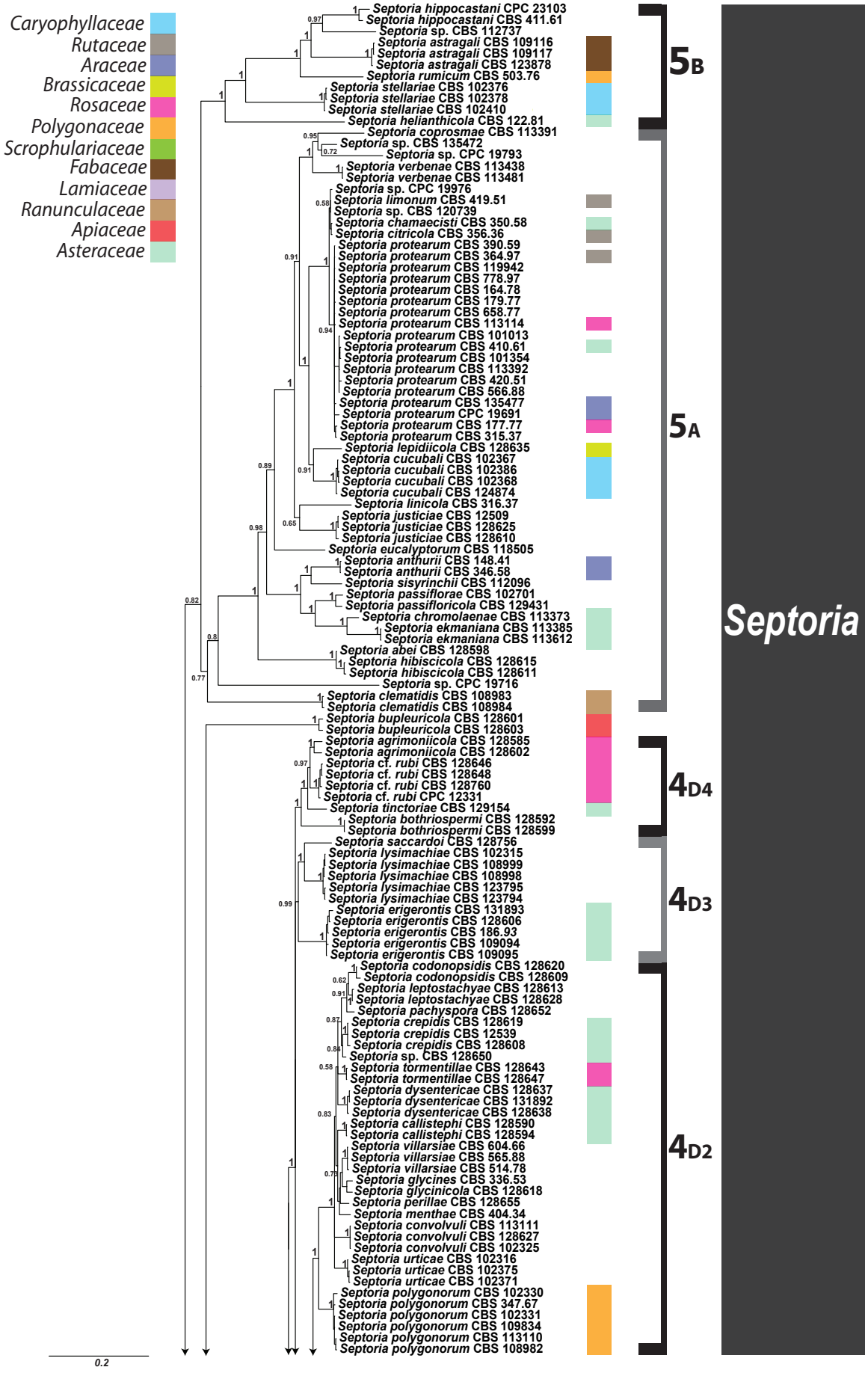

Fig. 2. Consensus phylogram (50 % majority rule) of 17 222 trees resulting from a Bayesian analysis of the combined seven loci sequence alignment using MrBayes v. 3.2.1. Bayesian posterior probabilities values are indicated on their respective branches and the scale bar indicates 0.2 expected changes 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).

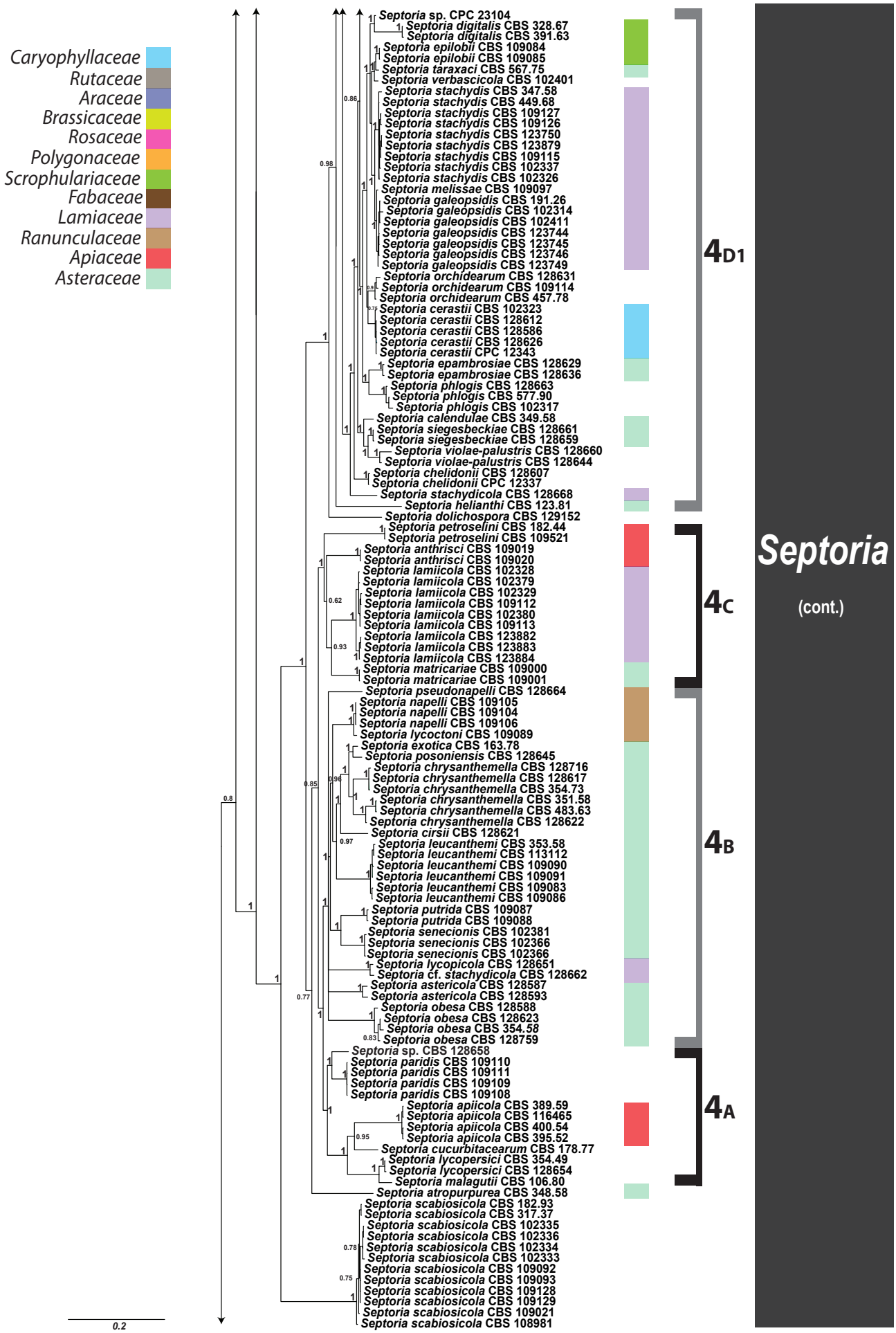

Fig. 2. (Continued).

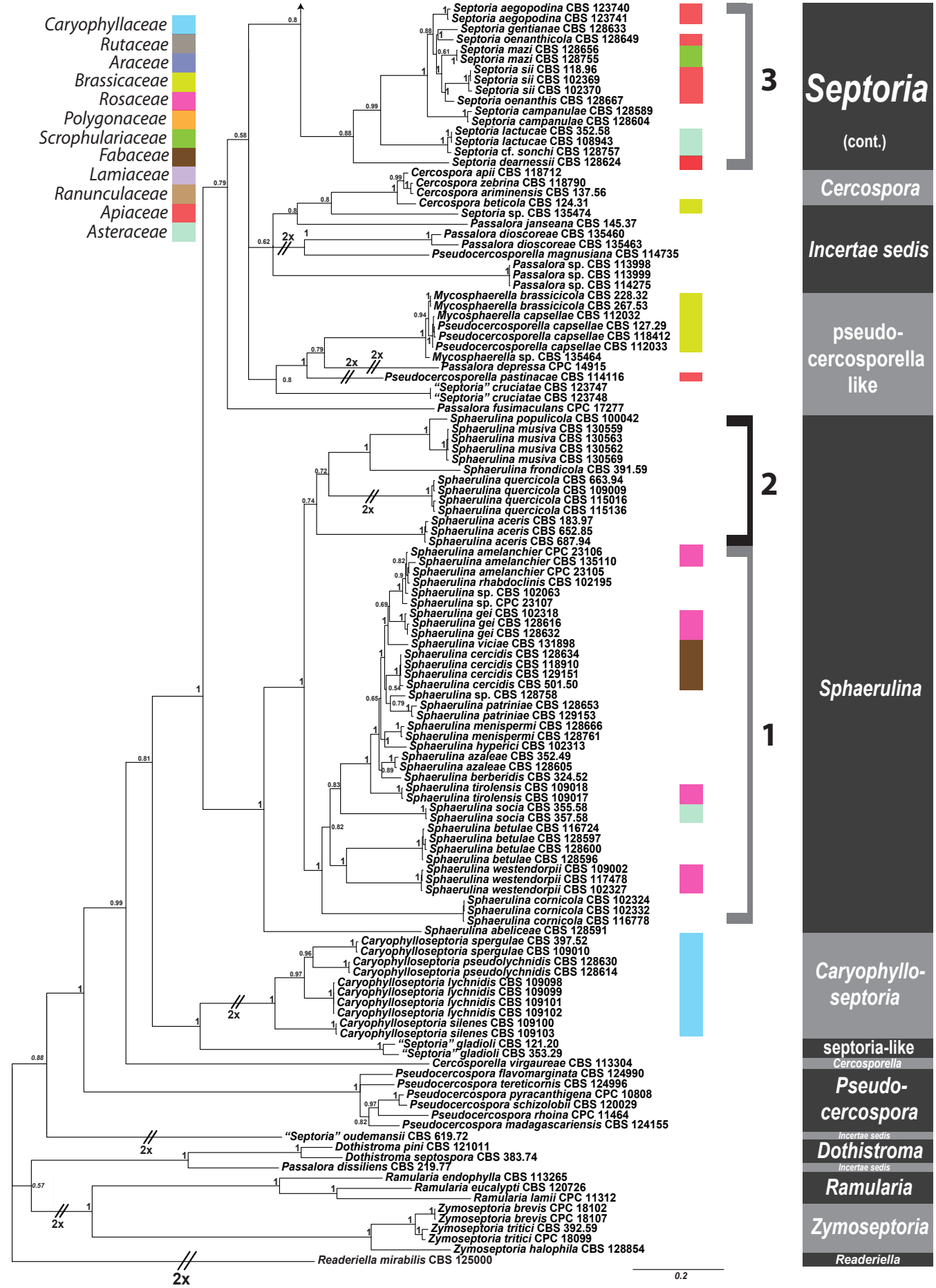

Fig. 2. (Continued).

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

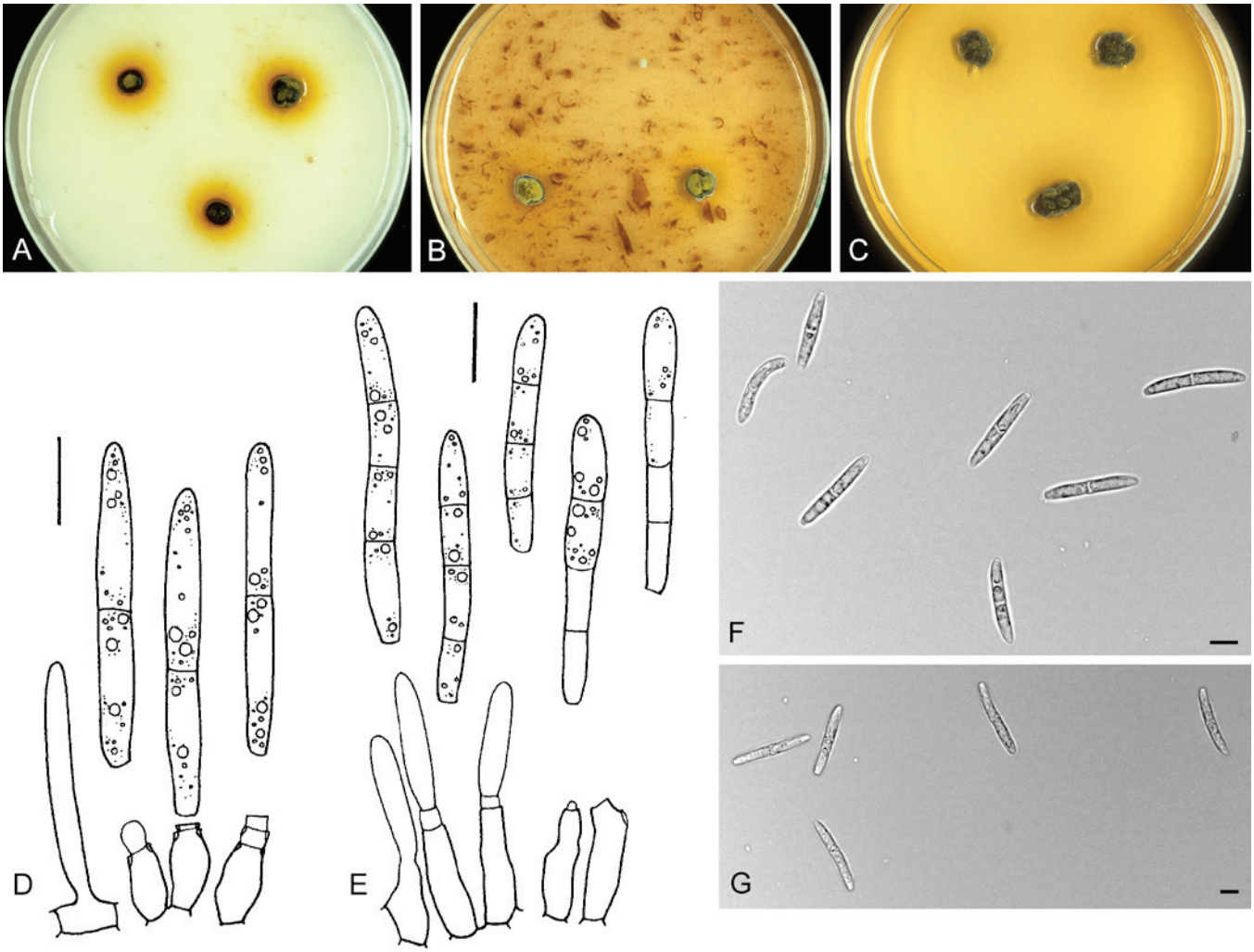

Fig. 4. *Caryophylloseptoria silenes*. A–C. Colonies CBS 109100. A. On OA. B. On CHA. C. On MEA. D. Conidia and conidiogenous cells *in planta* (CBS H-21160). E. Ibid., on OA (CBS 109100). F–G. Conidia on OA (CBS 109100). Scale bars = 10 µm.

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

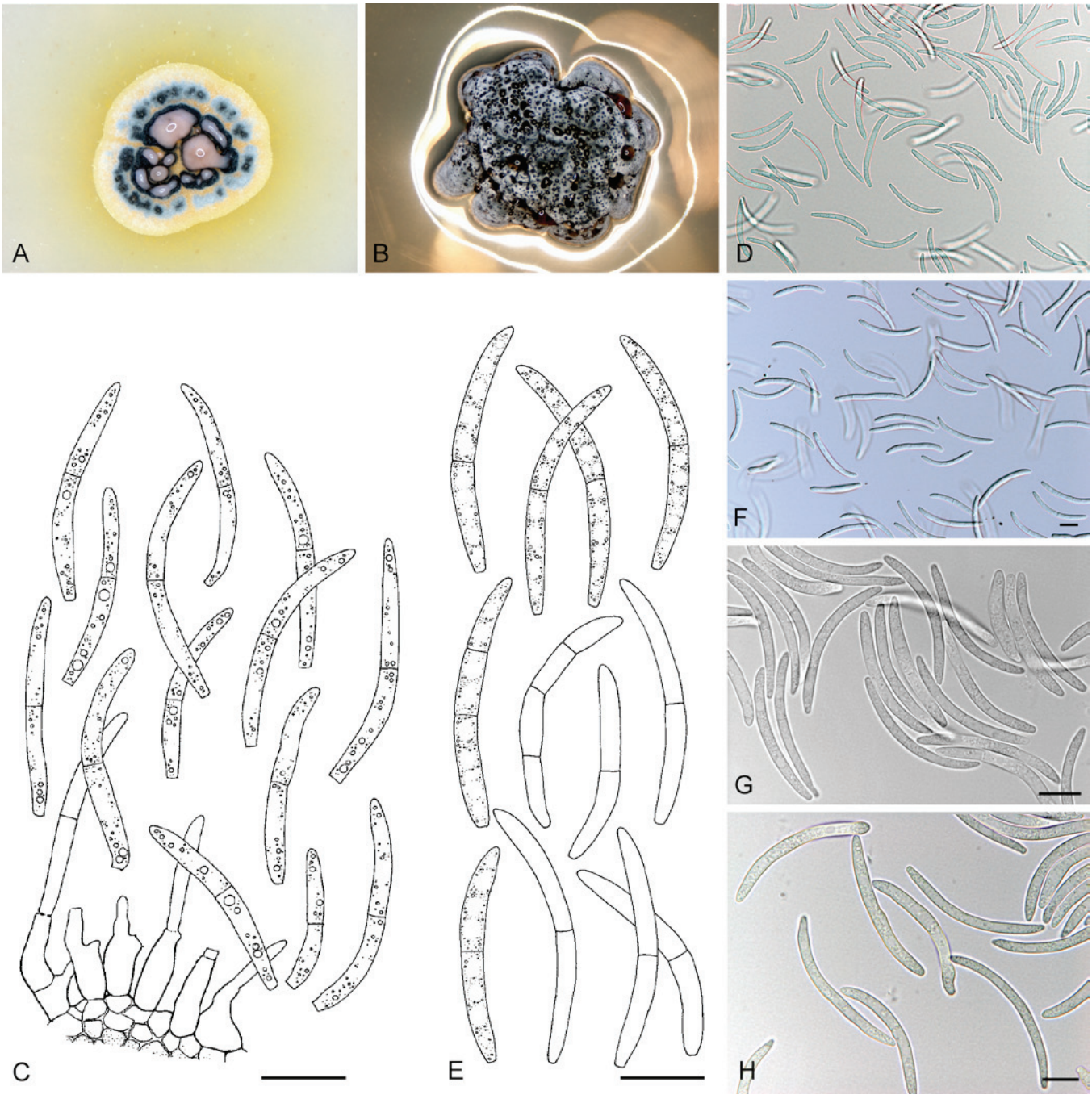

Fig. 5. *Caryophylloseptoria spergulae*. A, B. Colonies CBS 109010. A. On OA. B. On MEA. C. Conidia and conidiogenous cells *in planta* (CBS H-21150). D–H. Conidia on OA (CBS 109010). Scale bars = 10 µm.

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,

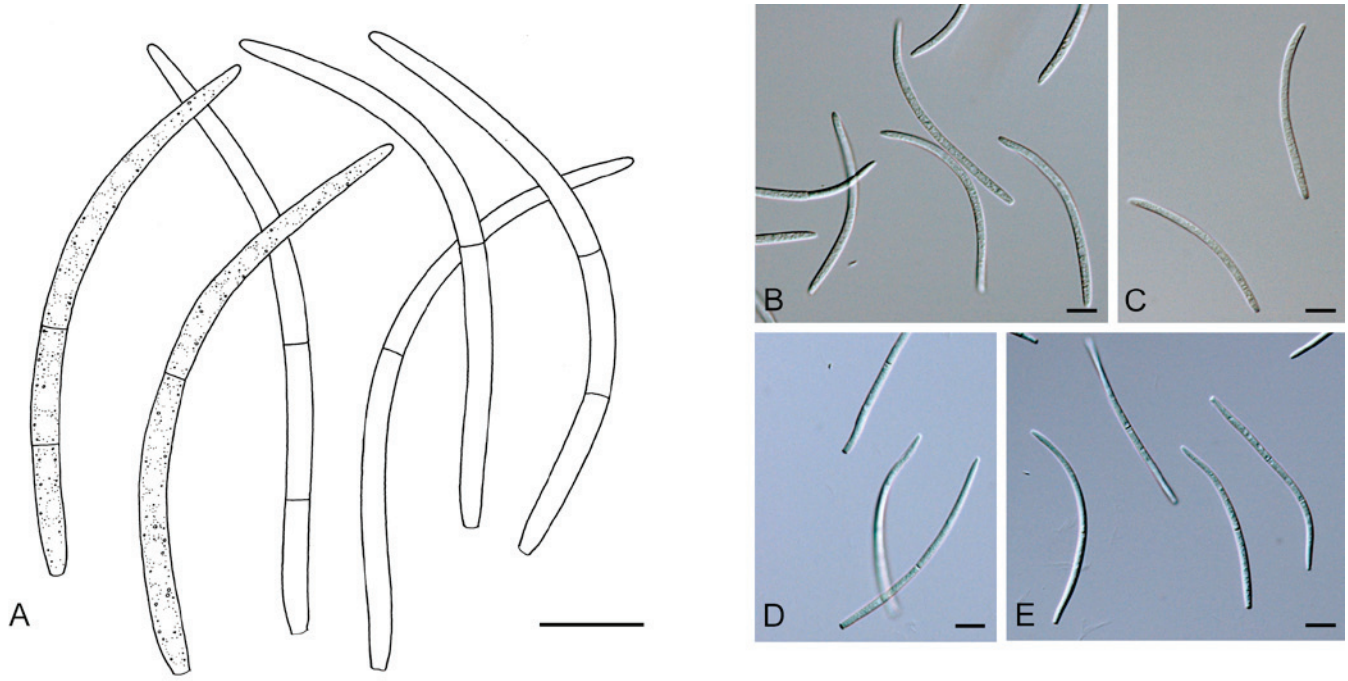

Fig. 6. *Septoria aegopodii*. A–E. Conidia *in planta*. A–C. CBS H-21262. D, E. CBS H-21199. Scale bars = 10 µm.

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.

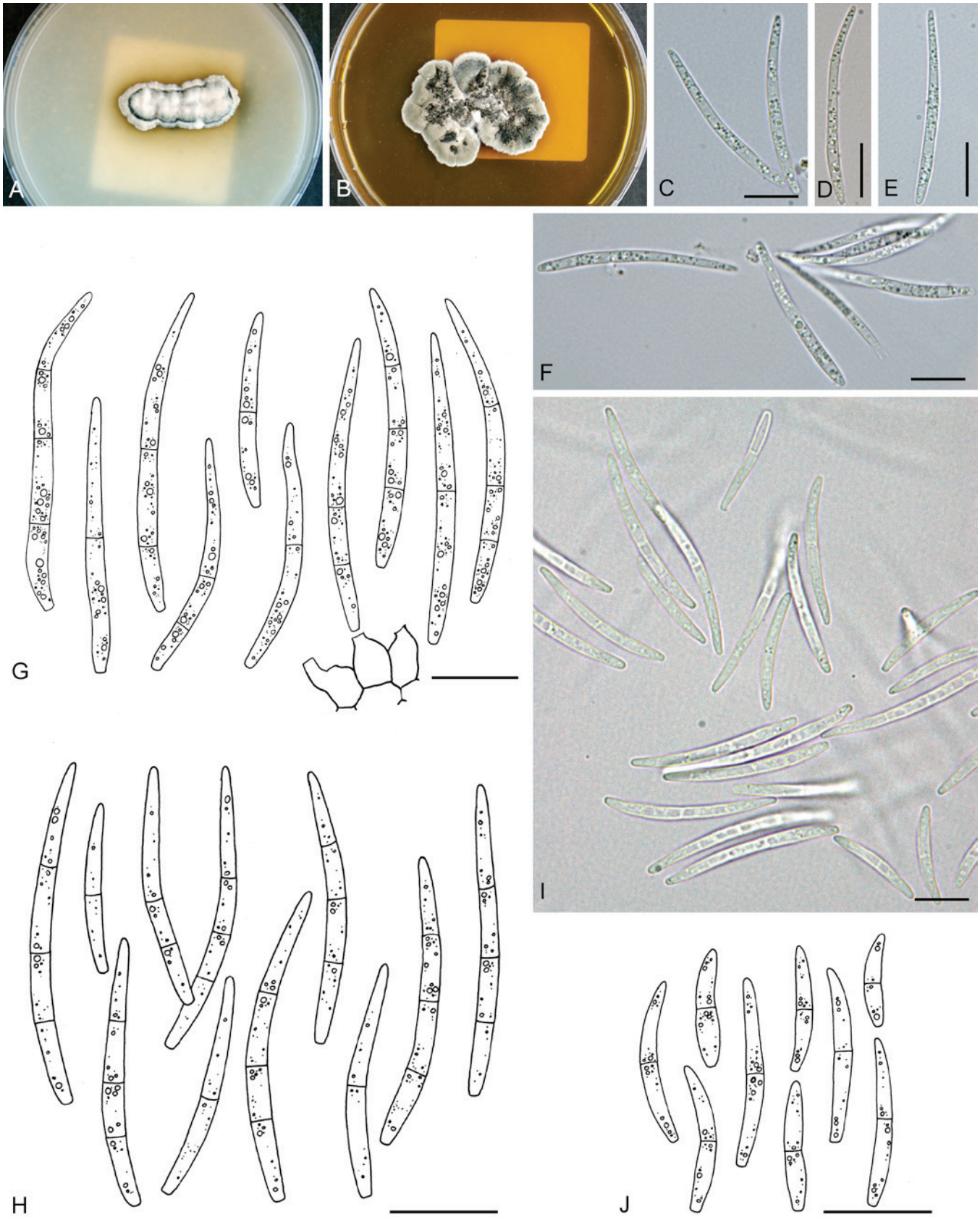

Fig. 7. *Septoria aegopodina*. A, B. Colonies CBS 123740. A. On OA. B. On MEA. C–F. Conidia *in planta* (CBS H-21249). G. Conidia and conidiogenous cells *in planta* (CBS H-21249). H, I. Conidia on OA (CBS 123741). J. Conidia on MEA (CBS 123740). Scale bars = 10 µm.

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.

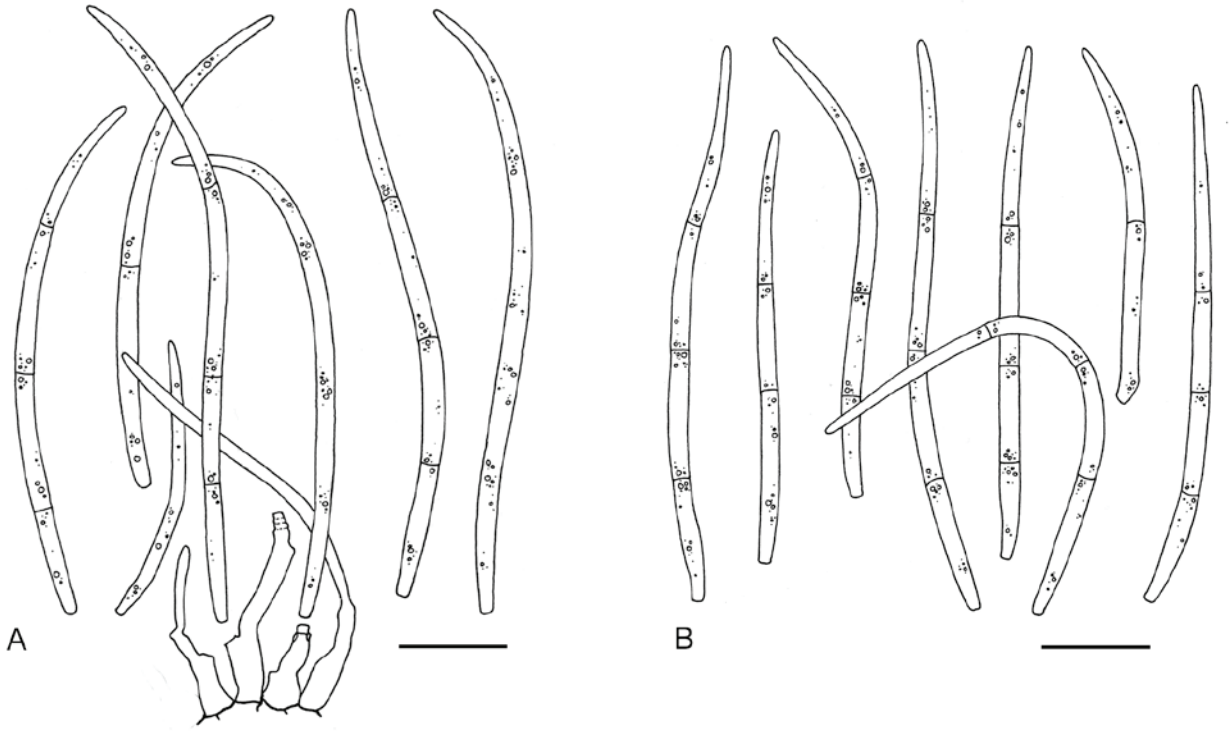

Fig. 8. *Septoria anthrisci*. A. Conidia and conidiogenous cells *in planta* (CBS H-21185). B. Conidia on OA (CBS 109020). Scale bars = 10 µm.

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

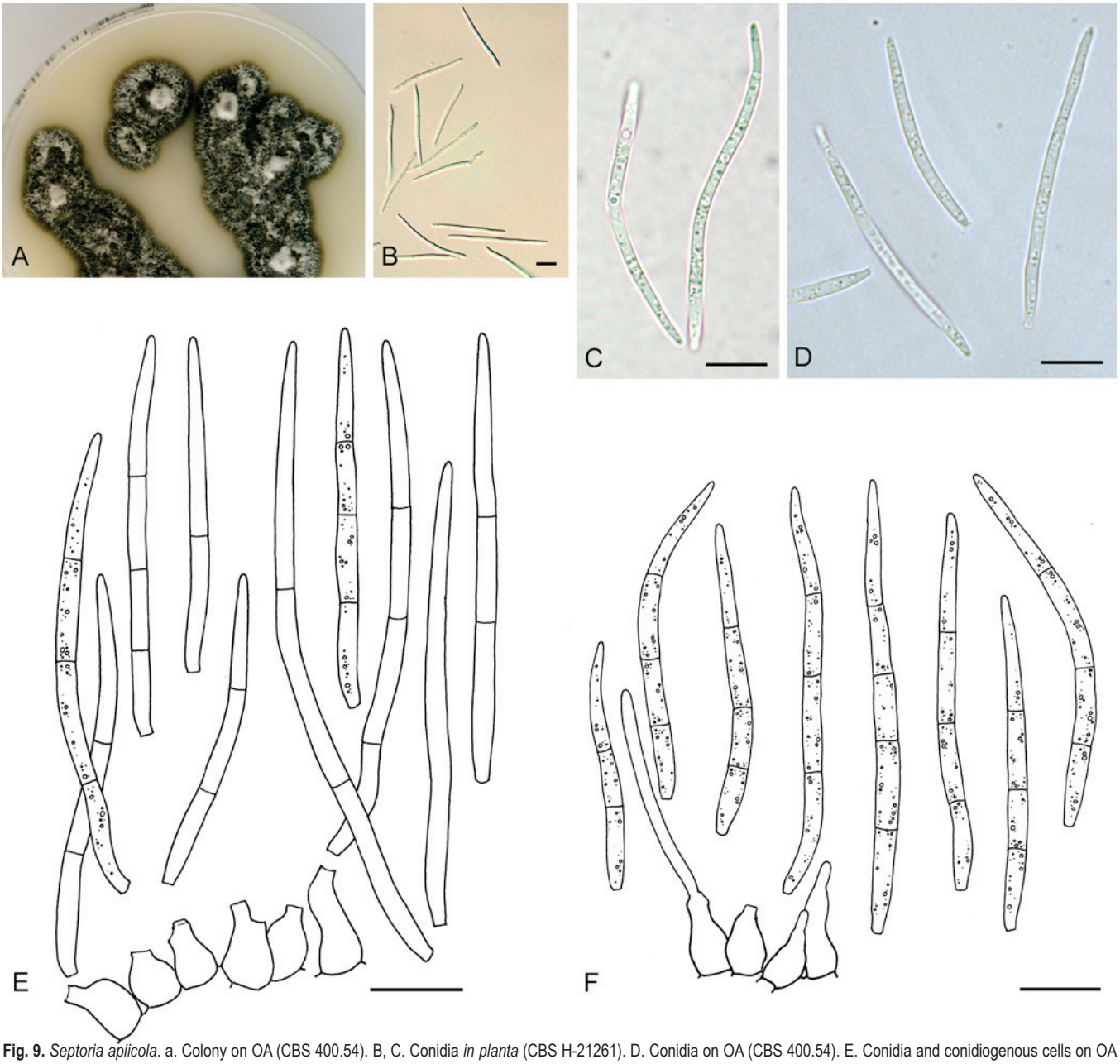

Fig. 9. *Septoria apiicola*. a. Colony on OA (CBS 400.54). B, C. Conidia *in planta* (CBS H-21261). D. Conidia on OA (CBS 400.54). E. Conidia and conidiogenous cells on OA (CBS 400.54). F. Ibid., *in planta* (CBS H-21261). Scale bars = 10 µm.

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

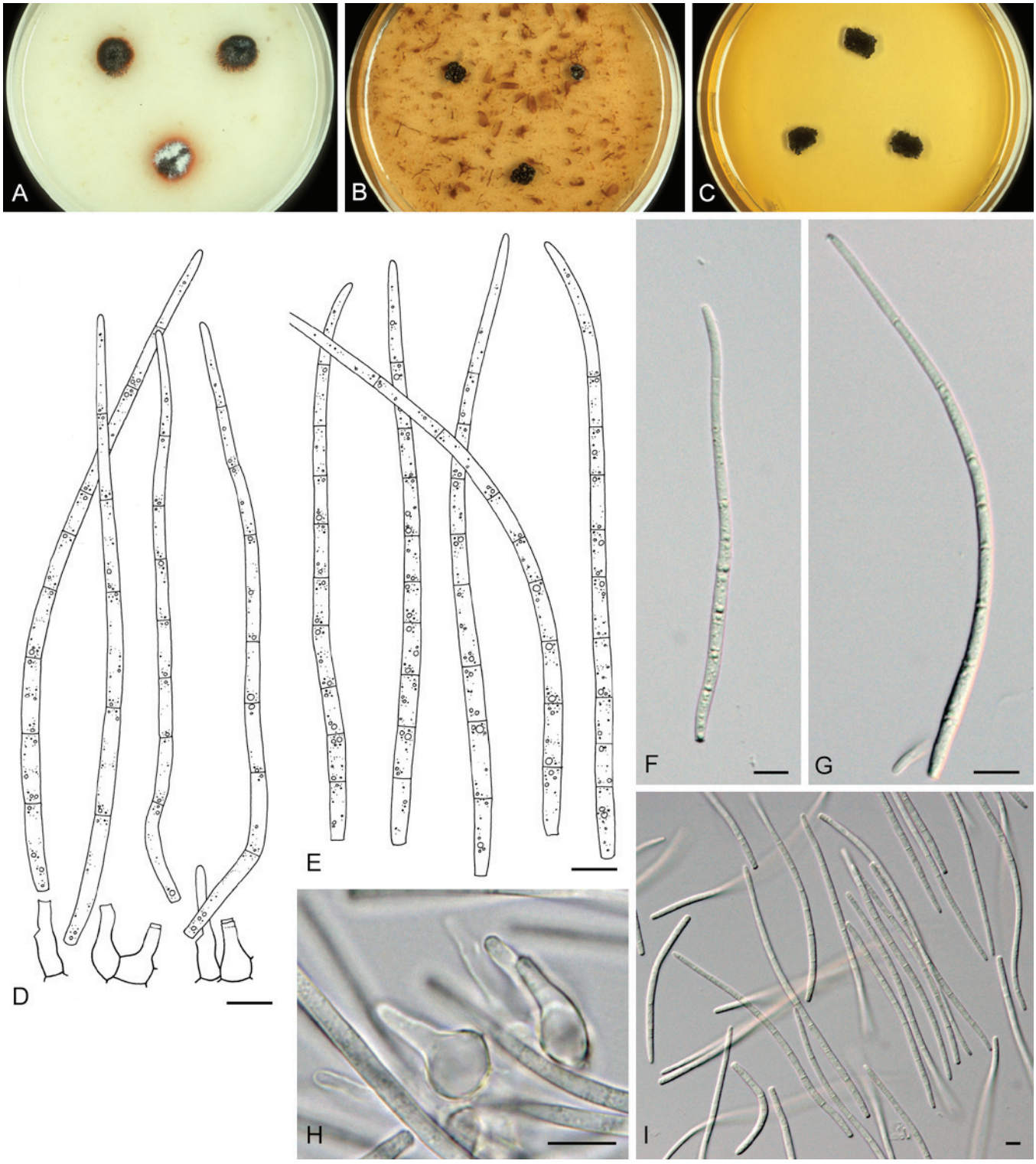

Fig. 10. *Septoria astragali*, CBS 109116. A–C. Colonies (15 C, nUV). A. On OA. B. On CHA. C. On MEA. D. Conidia and conidiogenous cells on OA (CBS 109116); E–G. Conidia *in planta* (CBS H-21258). H. Conidiogenous cells on OA (CBS 123878). I. Conidia on OA (CBS 123878). Scale bars = 10 µm.

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

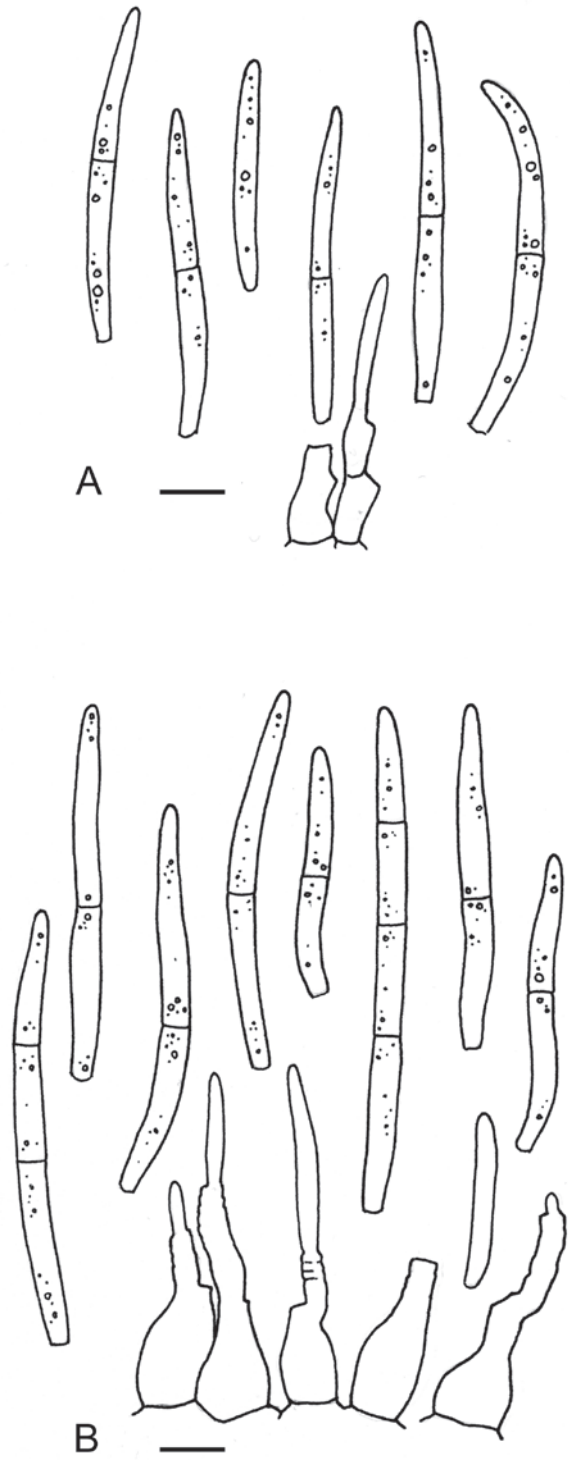

Fig. 11. *Septoria campanulae*. A. Conidia and conidiogenous cells *in planta* (CBS H-21178). B. Ibid., on CHA (CBS 109114). Scale bars = 10 µm.

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*

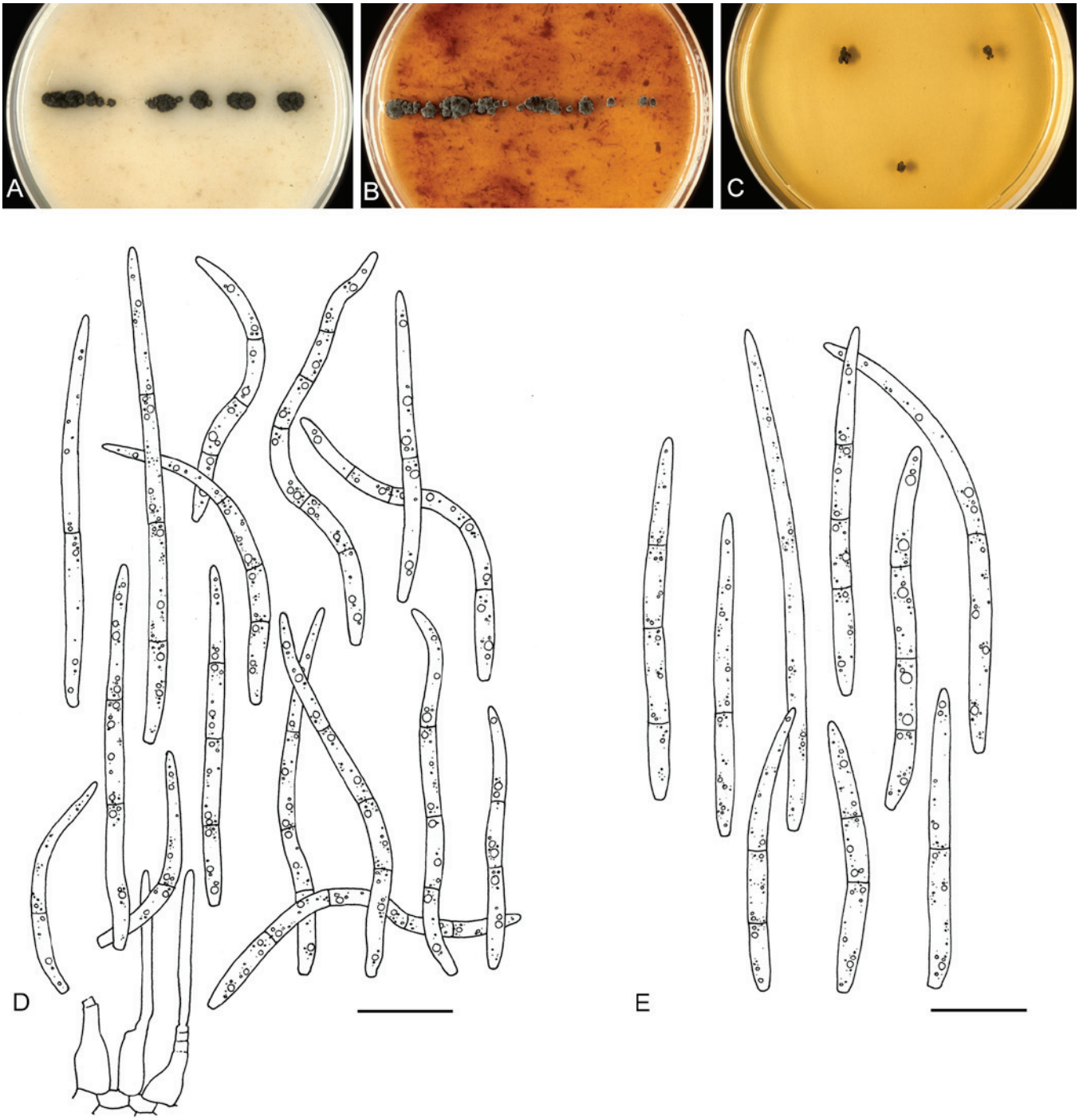

Fig. 12. *Septoria cerastii*, CBS 102323. A–C. Colonies (15 ºC, nUV). A. On OA. B. On CHA. C. On MEA. D. Conidia and conidiogenous cells *in planta* (CBS H-21158, epitype). E. Conidia on OA (CBS 102323). Scale bars = 10 µm.

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

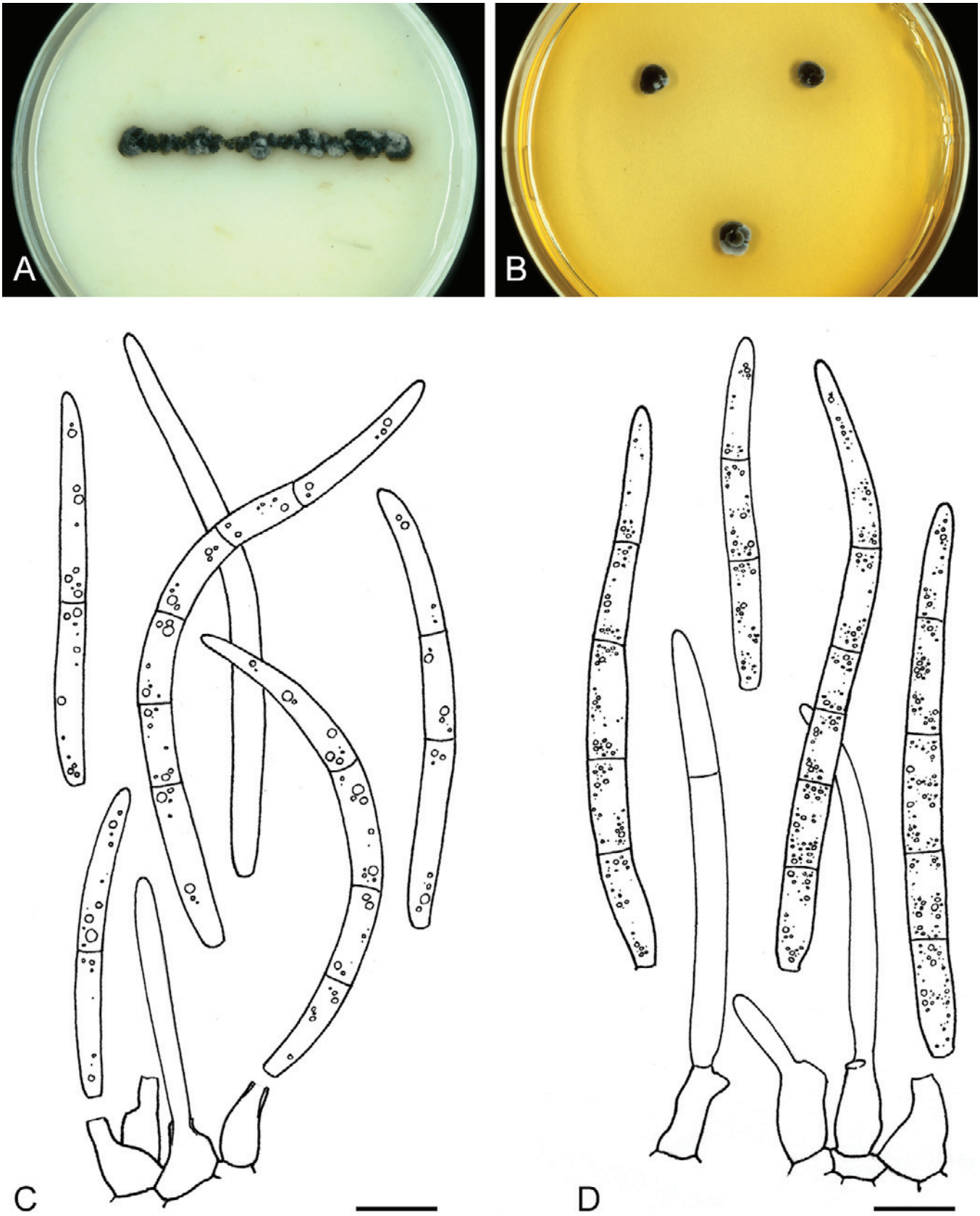

Fig. 13. *Septoria clematidis*. A, B. Colonies CBS 108983 (15 ºC, nUV). A. On OA. B. On MEA. C. Conidia and conidiogenous cells *in planta* (CBS H-21182, epitype). D. Ibid., CBS 108983 on OA. Scale bars = 10 µm.

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

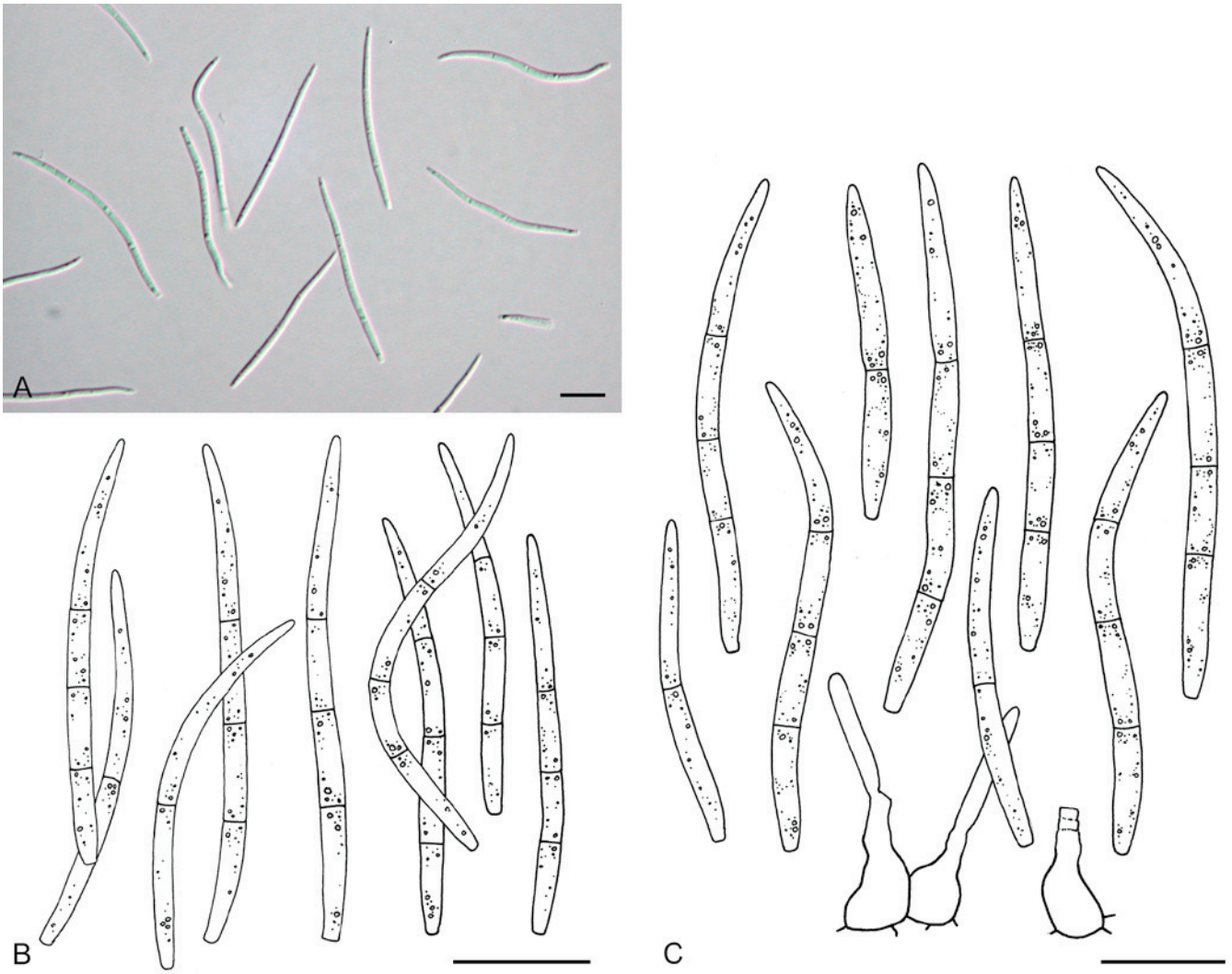

Fig. 14. *Septoria convolvuli*. A, B. Conidia *in planta* (CBS H-21244). C. Conidia and conidiogenous cells on OA (CBS 102325). Scale bars = 10 µm.

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,

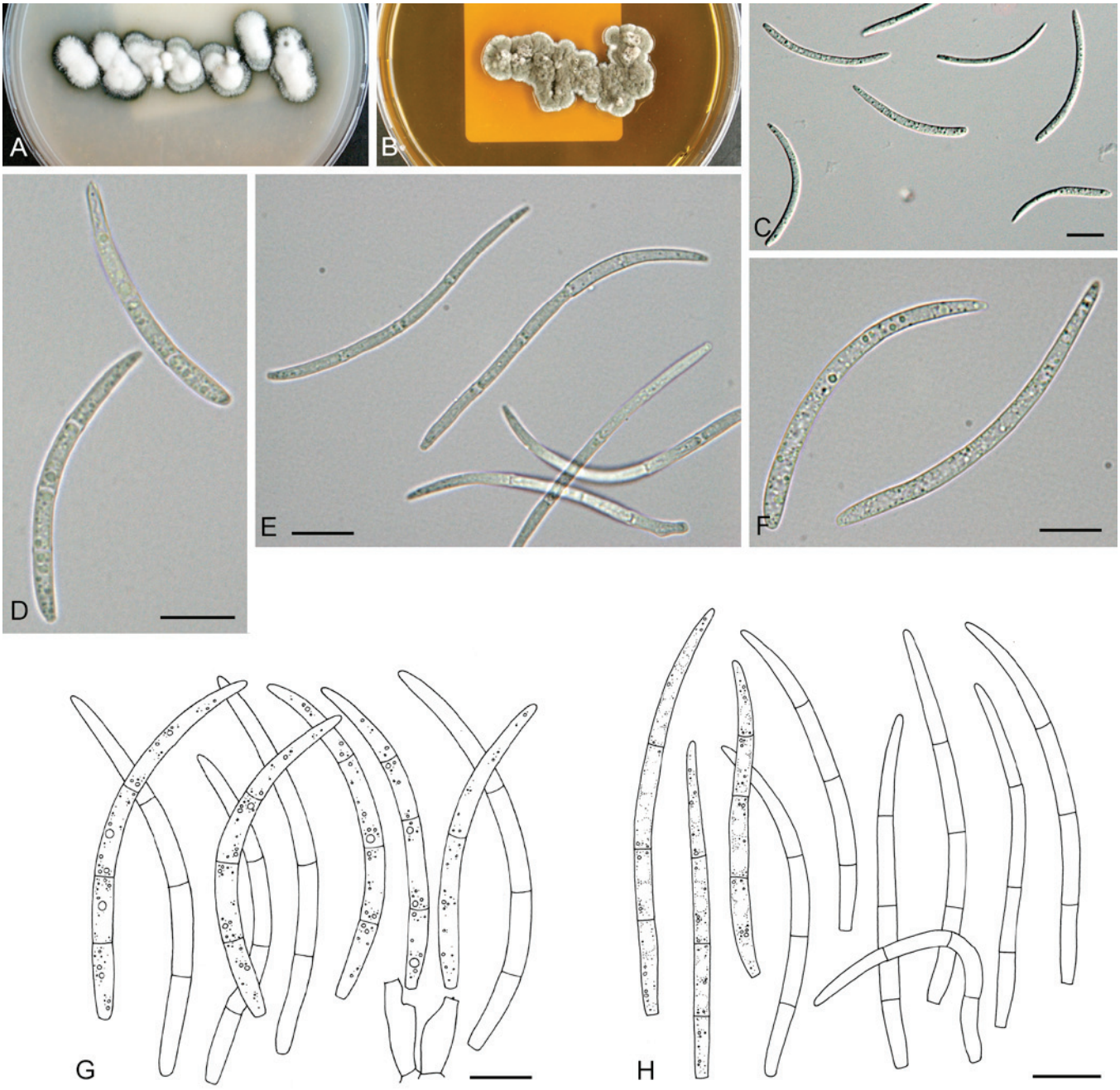

Fig. 15. *Septoria cruciatae*. A, B. Colonies CBS 123747. A. On OA. B. On MEA. C, D. Conidia *in planta* (CBS H-21250, epitype). E. Conidia on OA (CBS 123748). F. Conidia *in planta* (CBS H-21250). G. Conidia and conidiogenous cells *in planta* (CBS H-21250). H. Conidia on OA (CBS 123747). Scale bars = 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

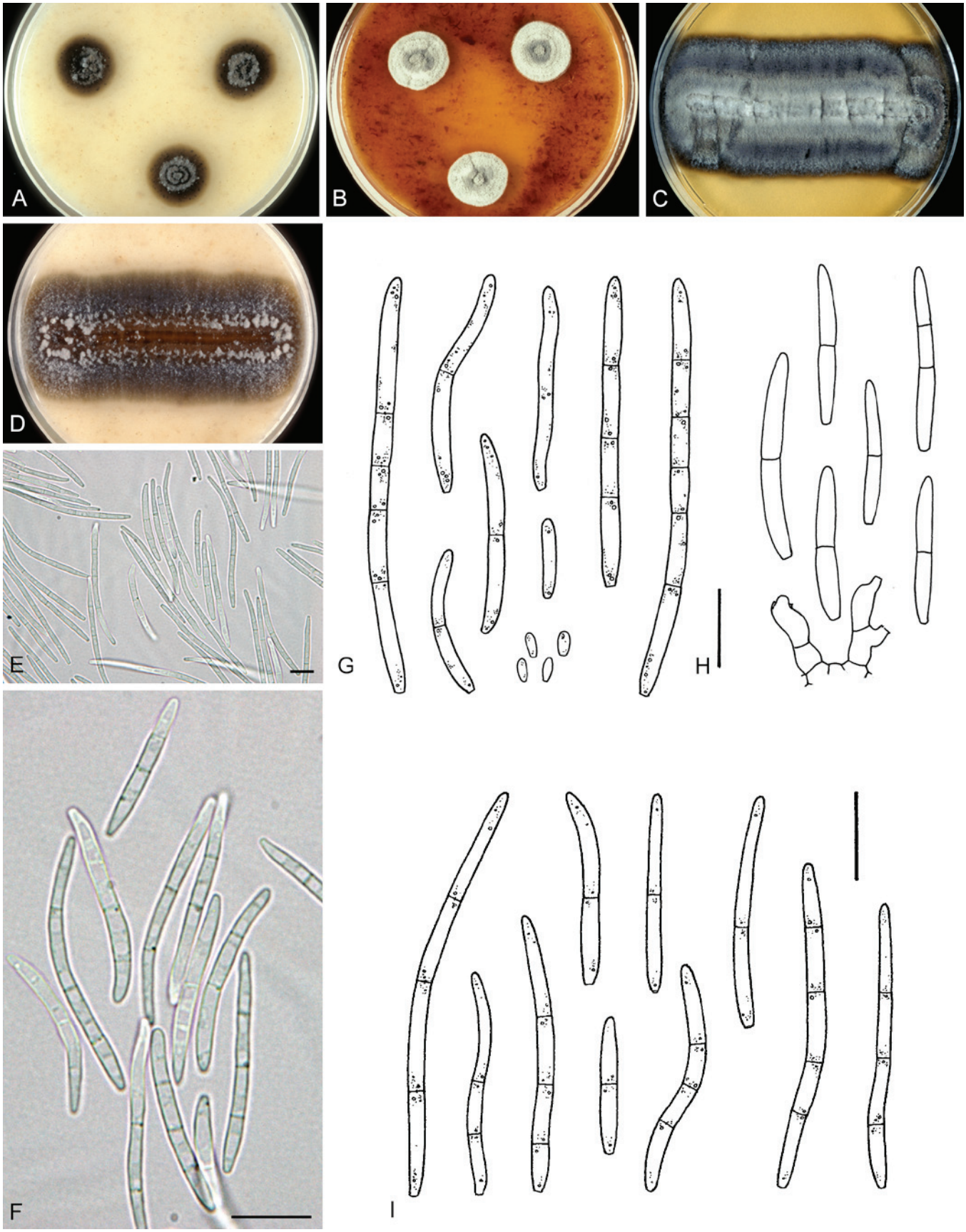

Fig. 16. *Septoria cucubali*. A–C. Colonies. A. CBS 102367, on OA. B. Ibid., on CHA. C, D. CBS 102386. C. On MEA. D. On OA. E, F. Conidia on OA (CBS 102386). G. Conidia and spermatia on OA (CBS 102367). H. Conidia and conidiogenous cells *in planta* (CBS H-21159). I. Conidia on OA (CBS 102386). Scale 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

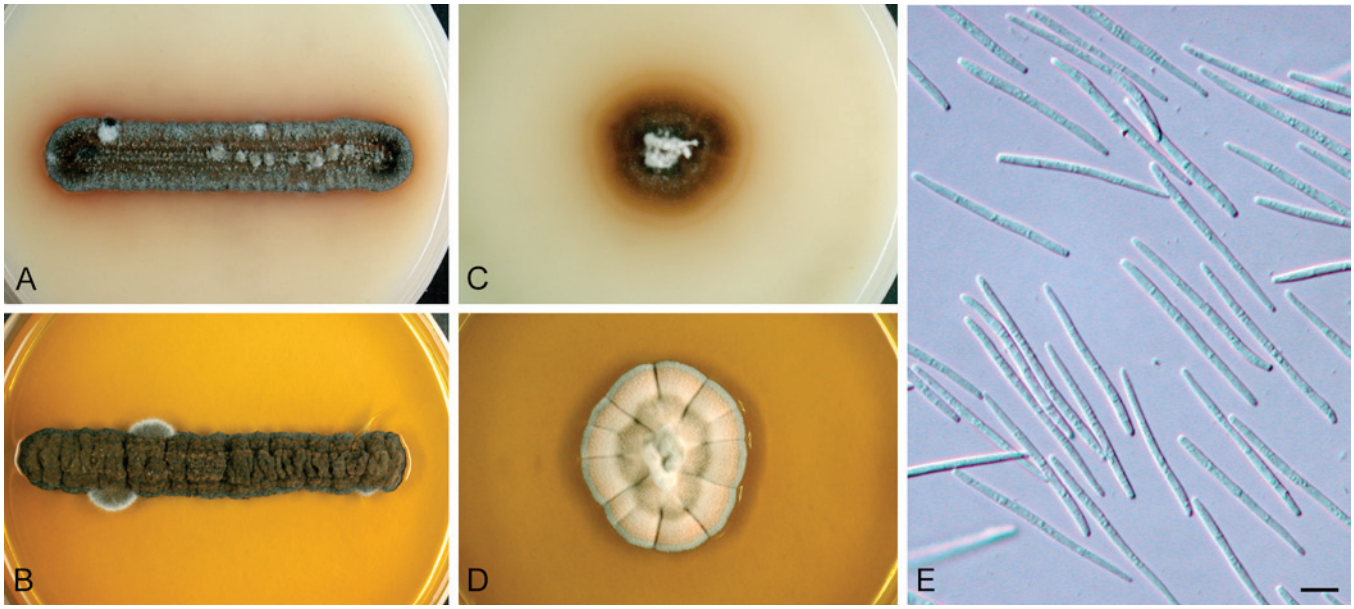

Fig. 17. *Septoria digitalis*. A, B. Colonies CBS 328.67 (15 ºC, nUV). A. On OA. B. On MEA. C, D. Colonies CBS 391.63 (15 ºC, nUV). C. On OA. D. On MEA. E. Conidia on OA (CBS 328.67). Scale bars = 10 µm.

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*

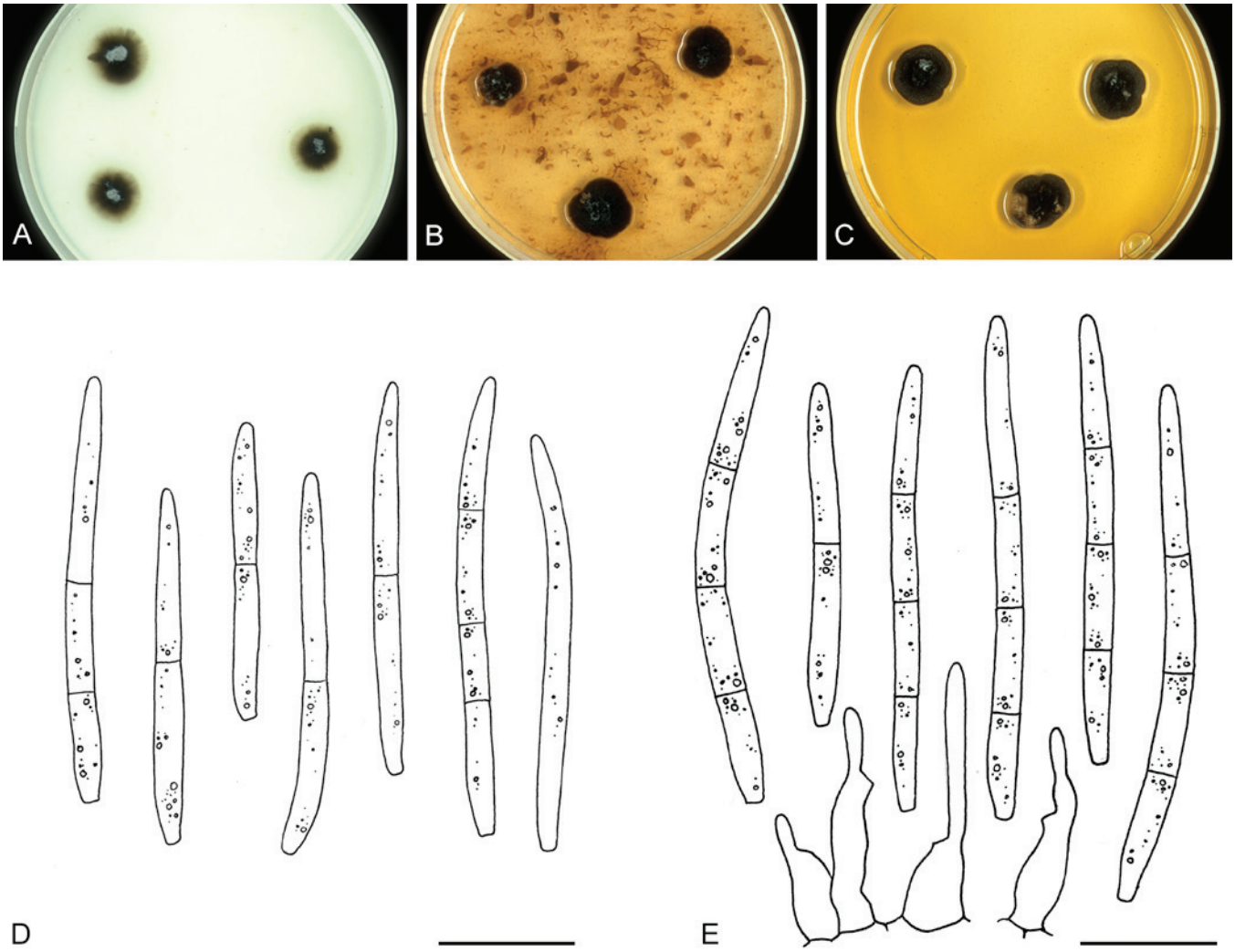

Fig. 18. *Septoria epilobii*. A–C. Colonies CBS 109084 (15 ºC, nUV). A. On OA. B. On CHA. C. On MEA. D. Conidia *in planta* (CBS H-21171, epitype). E. Conidia and conidiogenous cells on OA (CBS 109094). Scale bars = 10 µm.

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.*

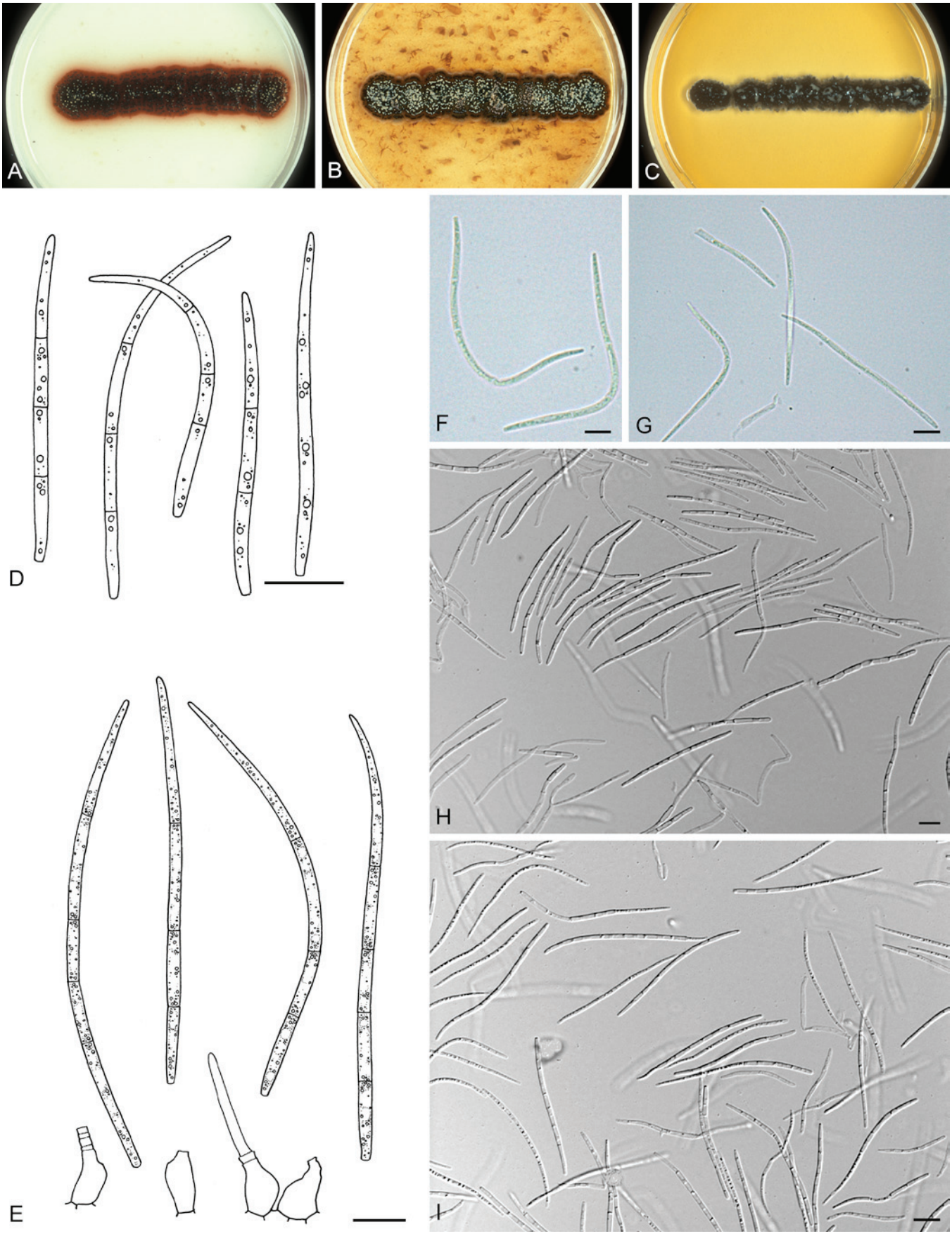

Fig. 19. *Septoria erigerontis*. A–C. Colonies CBS 109094 (15 ºC, nUV). A. On OA. B. On CHA. C. On MEA. D. Conidia *in planta* (CBS H-21176). E. Conidia and conidiogenous cells on OA (CBS 109094). F, G. Conidia *in planta* (CBS H-21176). H, I. Conidia on OA (CBS 186.93). Scale bars = 10 µm.

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

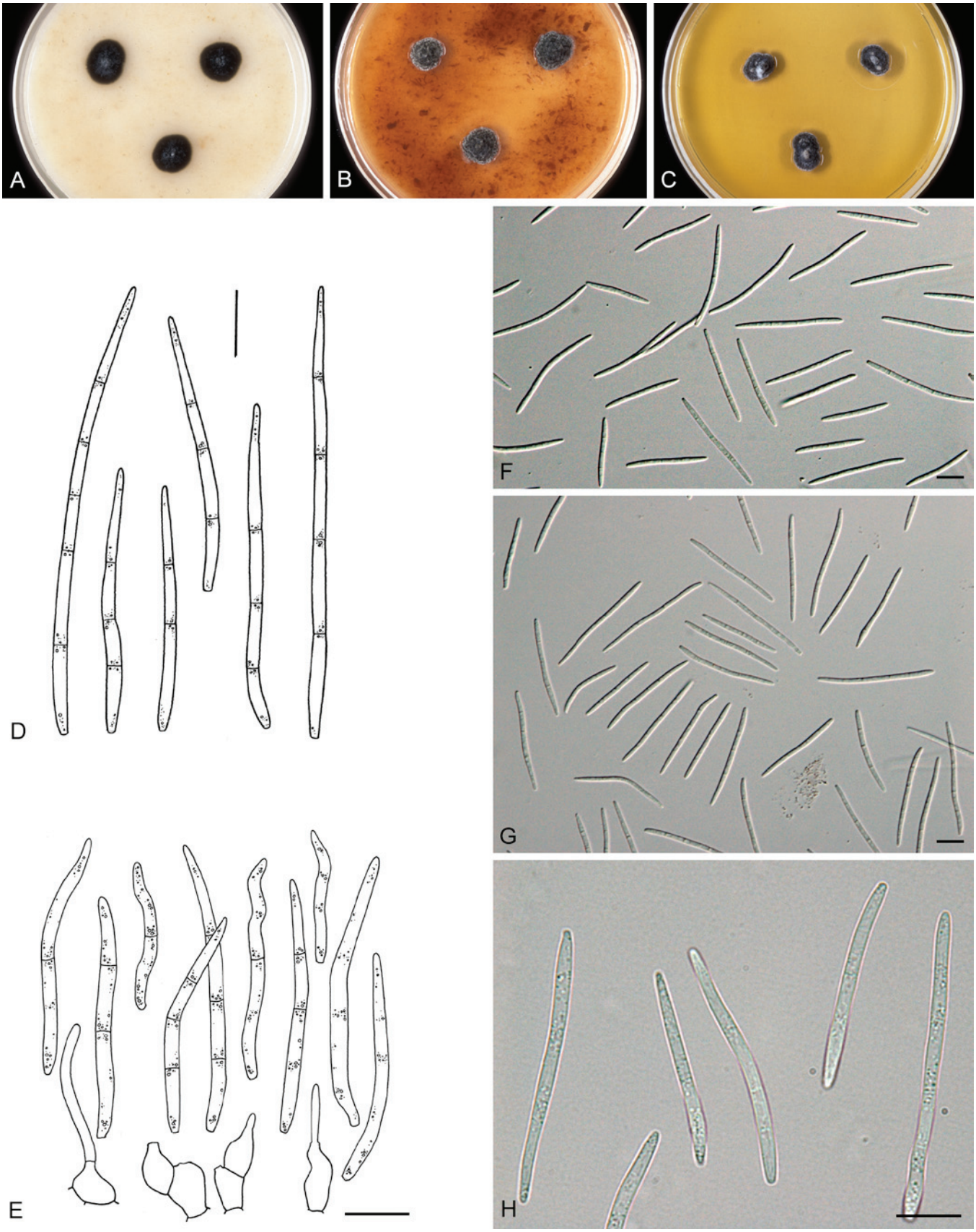

Fig. 20. *Septoria galeopsidis*, CBS 102314. A–C. Colonies (15 ºC, nUV). A. On OA. B. On CHA. C. On MEA. D. Conidia on OA. E. Conidia and conidiogenous cells *in planta* (CBS H-21195). F–H. Conidia on OA (CBS 123744). Scale bars = 10 µm.

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,

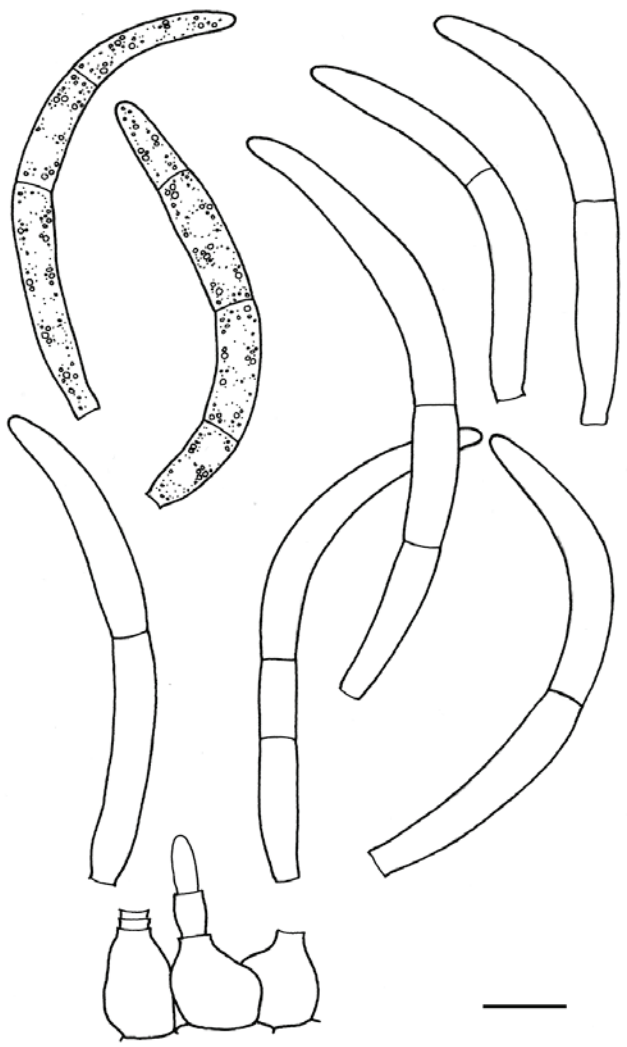

Fig. 21. *Septoria heraclei*, conidia and conidiogenous cells *in planta* (CBS H-21224). Scale bars = 10 µm.

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.

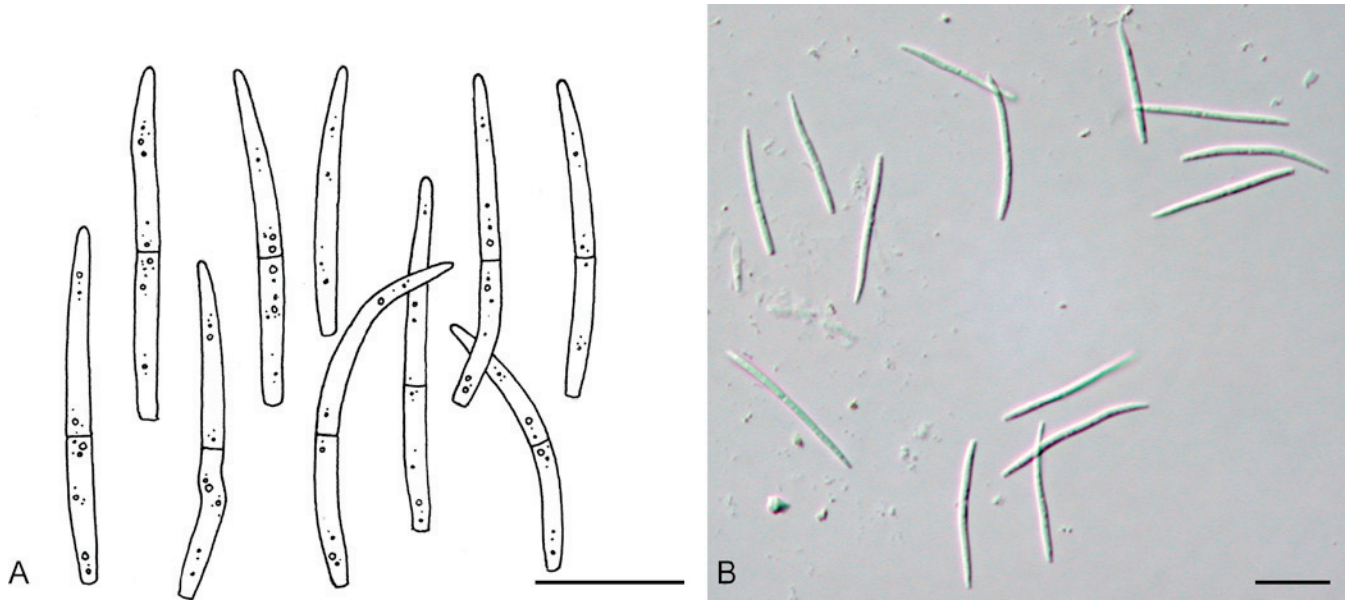

Fig. 22. *Septoria hypochoeridis*, CBS H-21234. A, B. Conidia *in planta*. Scale bars = 10 µm.

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

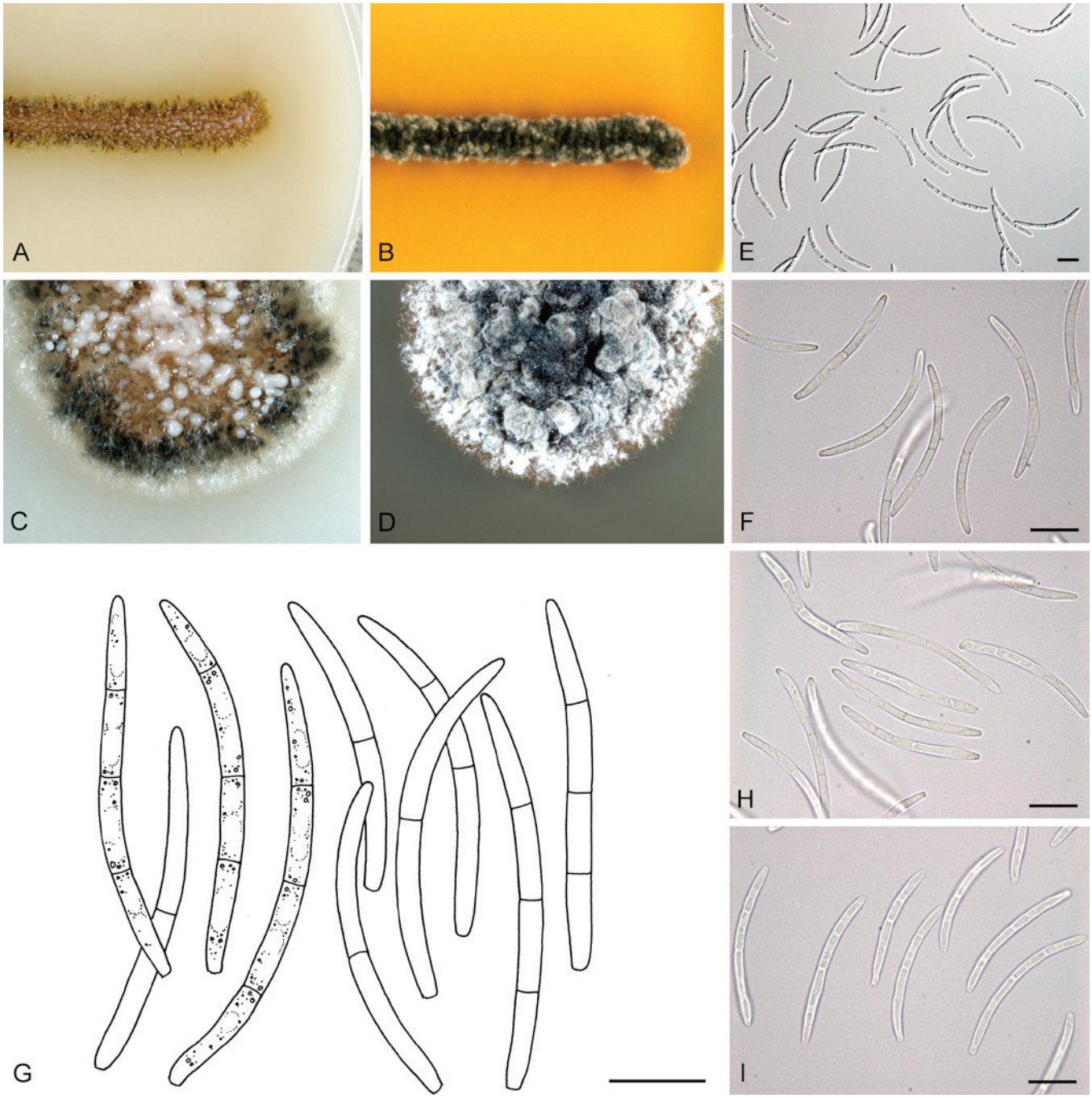

Fig. 23. *Septoria lactucae*. A–D. Colonies CBS 108943 (15 °C, nUV). A. On OA. B. On MEA. C. Colony margin on OA. D. Colony margin on MEA. E–I. Conidia on OA (CBS 108943). Scale bars = 10 µm.

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

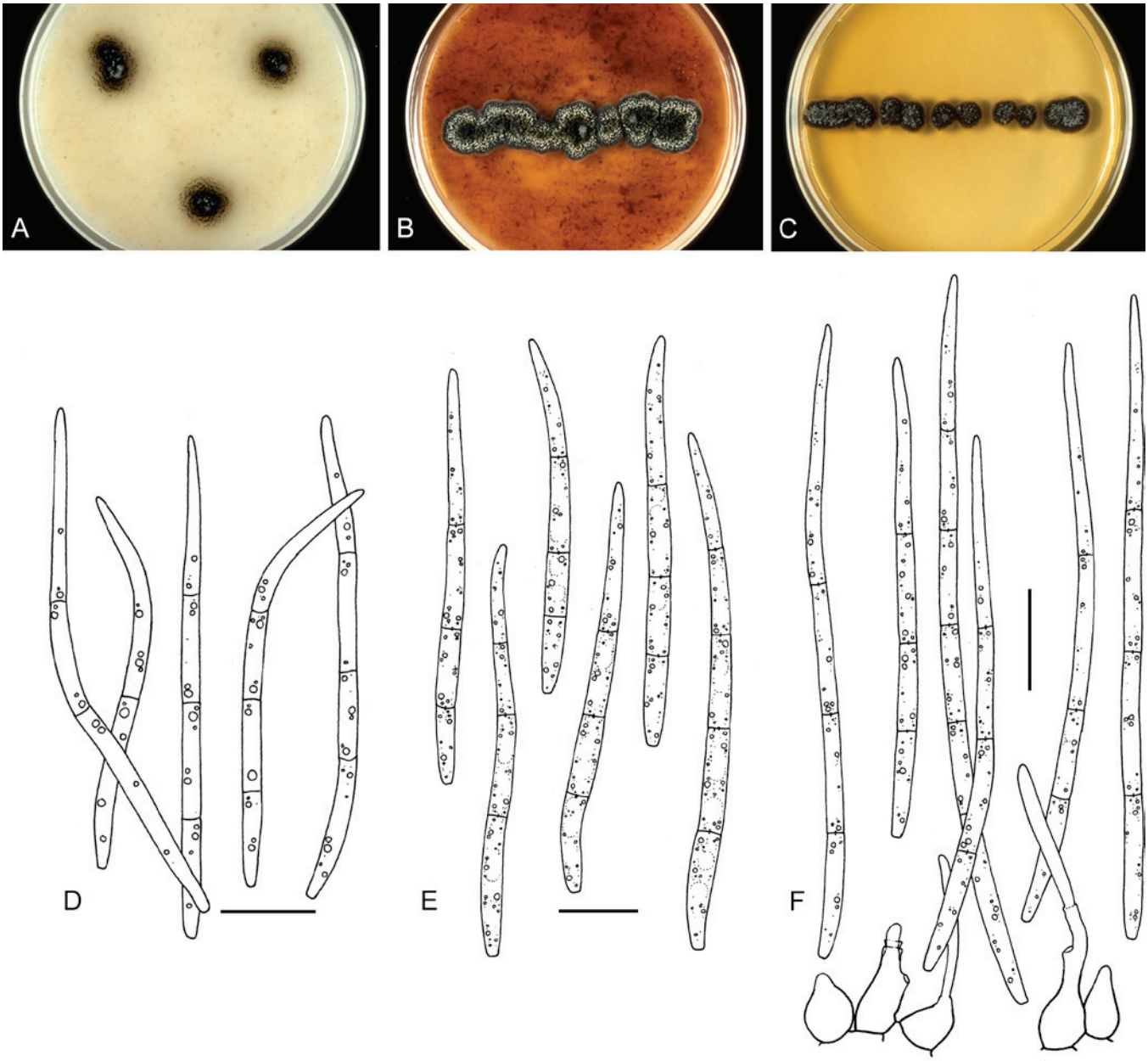

Fig. 24. *Septoria lamiicola*, CBS 102329. A–C. Colonies (15 °C, nUV). A. On OA. B. On CHA. C. On MEA. D. Conidia *in planta* (CBS H-21181). E. Ibid. (CBS H-21216). F. Conidia and conidiogenous cells on OA (CBS 102380). Scale bars = 10 µm.

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,

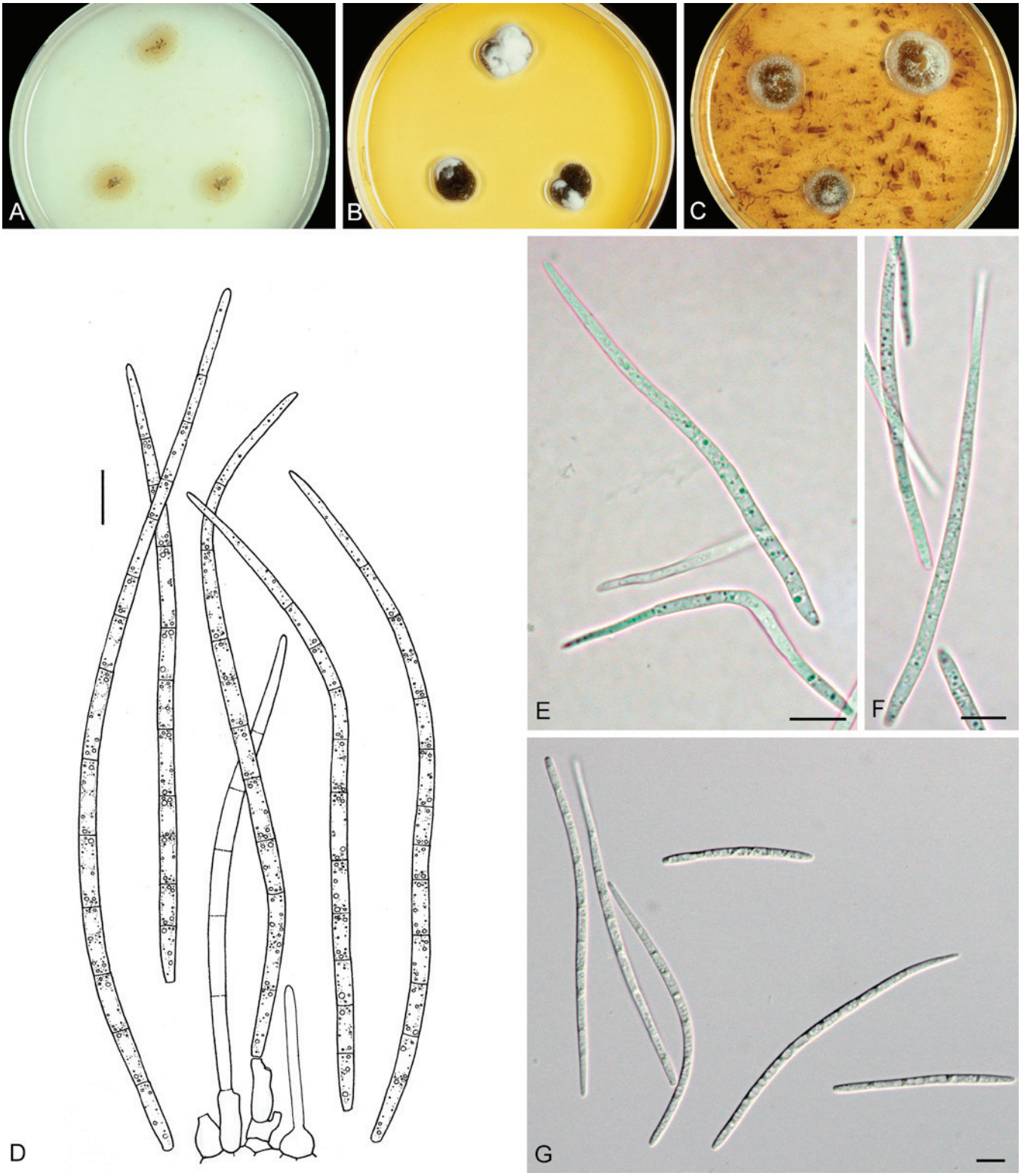

Fig. 25. *Septoria leucanthemi*. A–C. Colonies CBS 109090 (15 °C, nUV). A. On OA. B. On MEA. C. On CHA. D. Conidia and conidiogenous cells on OA (CBS 109090). E, F. Conidia *in planta* (CBS H-21243). G. Conidia on MEA (CBS 109090). Scale bars = 10 µm.

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

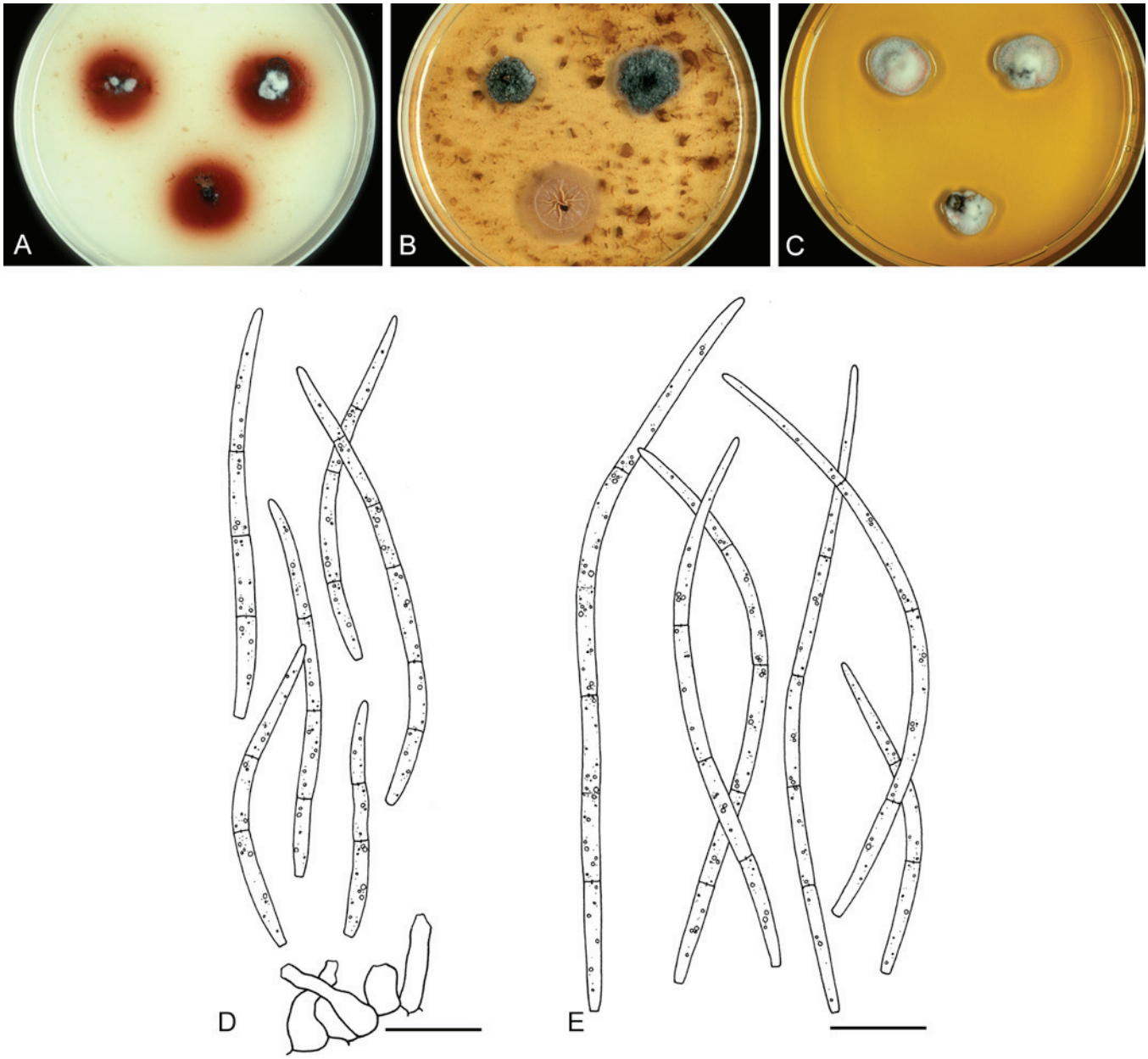

Fig. 26. *Septoria lycoctoni*. A–C. Colonies CBS 109089 (15 °C, nUV). A. On OA. B. On CHA. C. On MEA. D. Conidia and conidiogenous cells *in planta* (CBS H-21155). E. Conidia on OA (CBS 109089). Scale bars = 10 µm.

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.

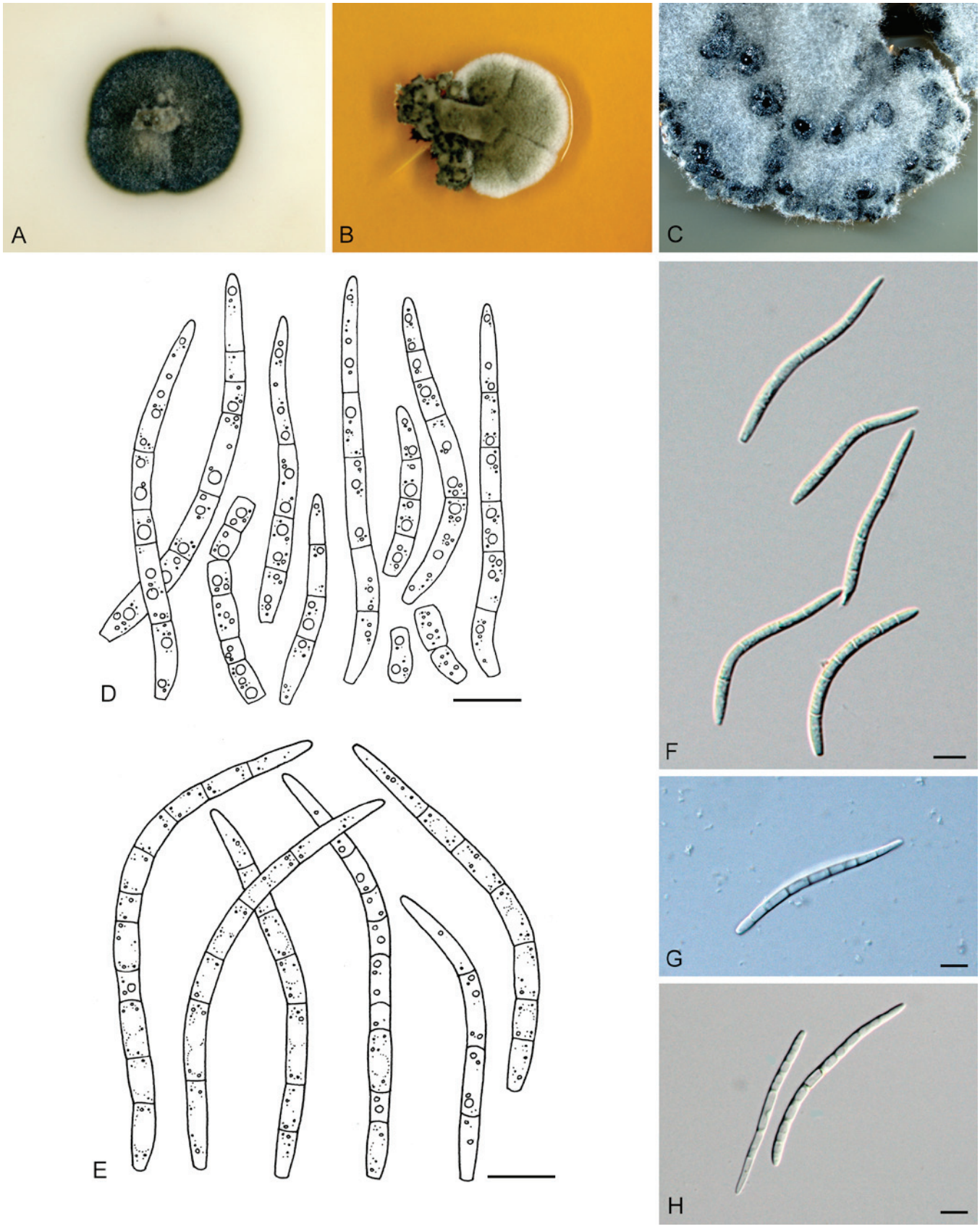

Fig. 27. *Septoria lysimachiae*. A–C. Colonies (15 °C, nUV). A. CBS 123794 on OA. B. CBS 108998 on MEA. C. Ibid., colony margin on MEA. D. Conidia *in planta* (CBS H-21196). E. Conidia on OA (CBS 108998). F. Conidia *in planta* (CBS H-21196). G. Conidia on OA (CBS 108998). H. Conidia on OA (CBS 108999). 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

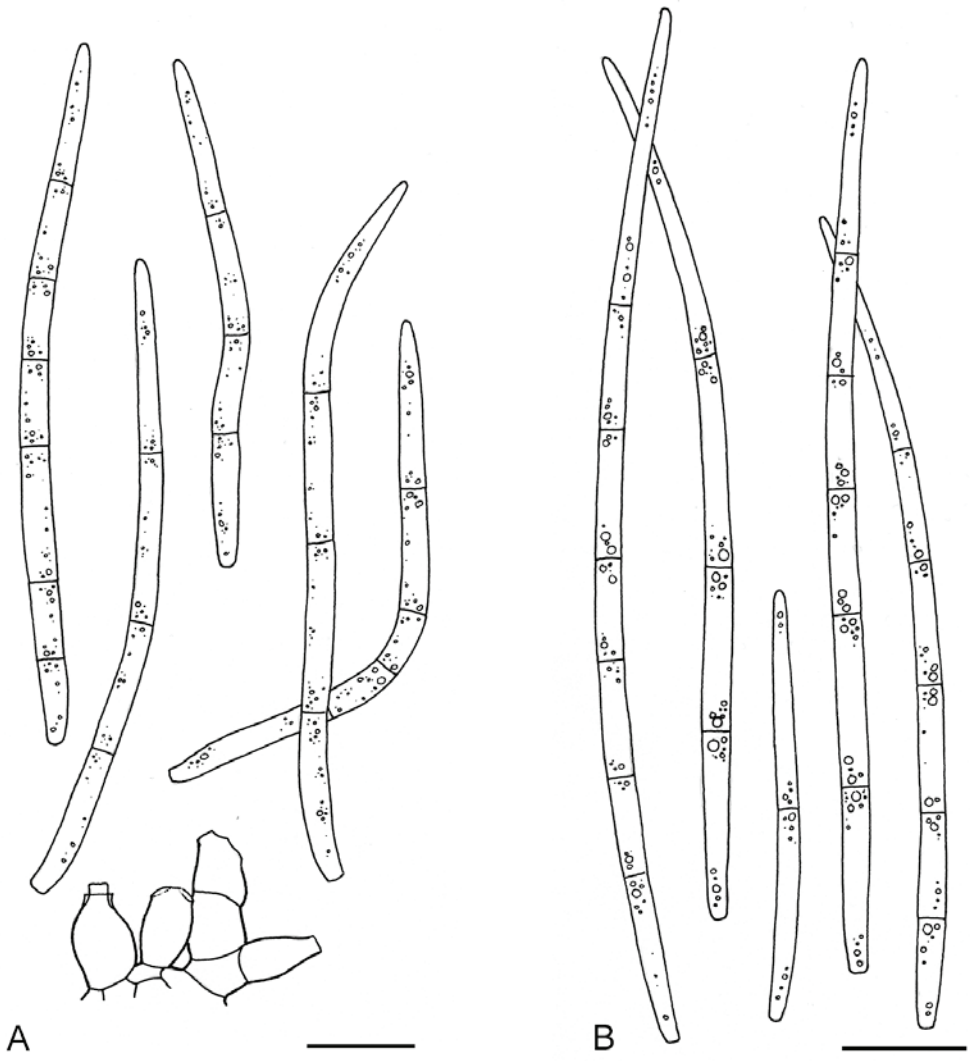

Fig. 28. *Septoria matricariae*. A. Conidia and conidiogenous cells *in planta* (CBS H-21228). B. Conidia on OA (CBS 109001). Scale bars = 10 µm.

(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 hypophyllous, 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

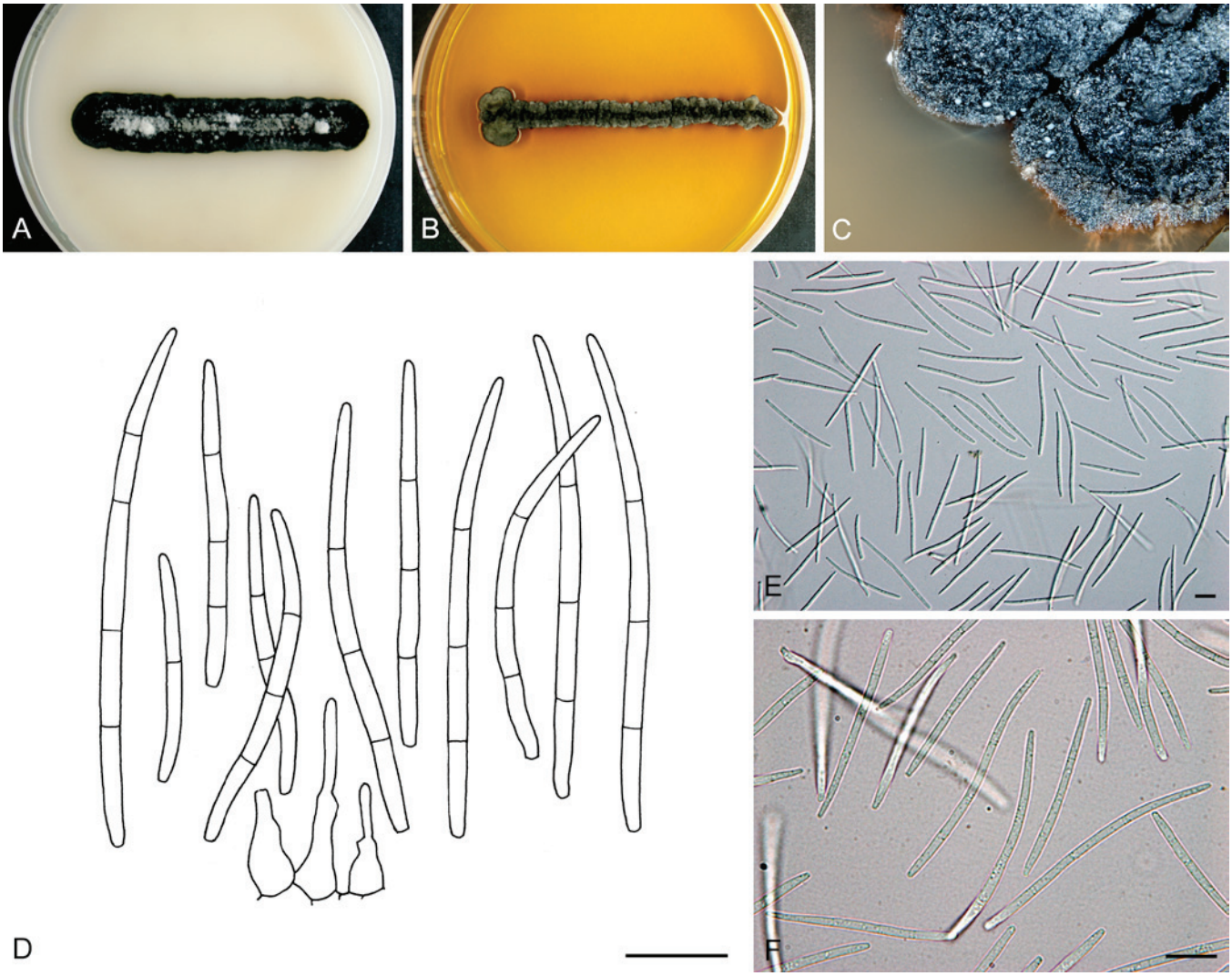

Fig. 29. *Septoria melissae*, CBS 109097. A–C. Colonies (15 °C, nUV). A. On OA. B. On MEA. C. On MEA, detail of colony margin. D. Conidia and conidiogenous cells on OA. E–F. Conidia on OA. Scale bars = 10 µm.

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.

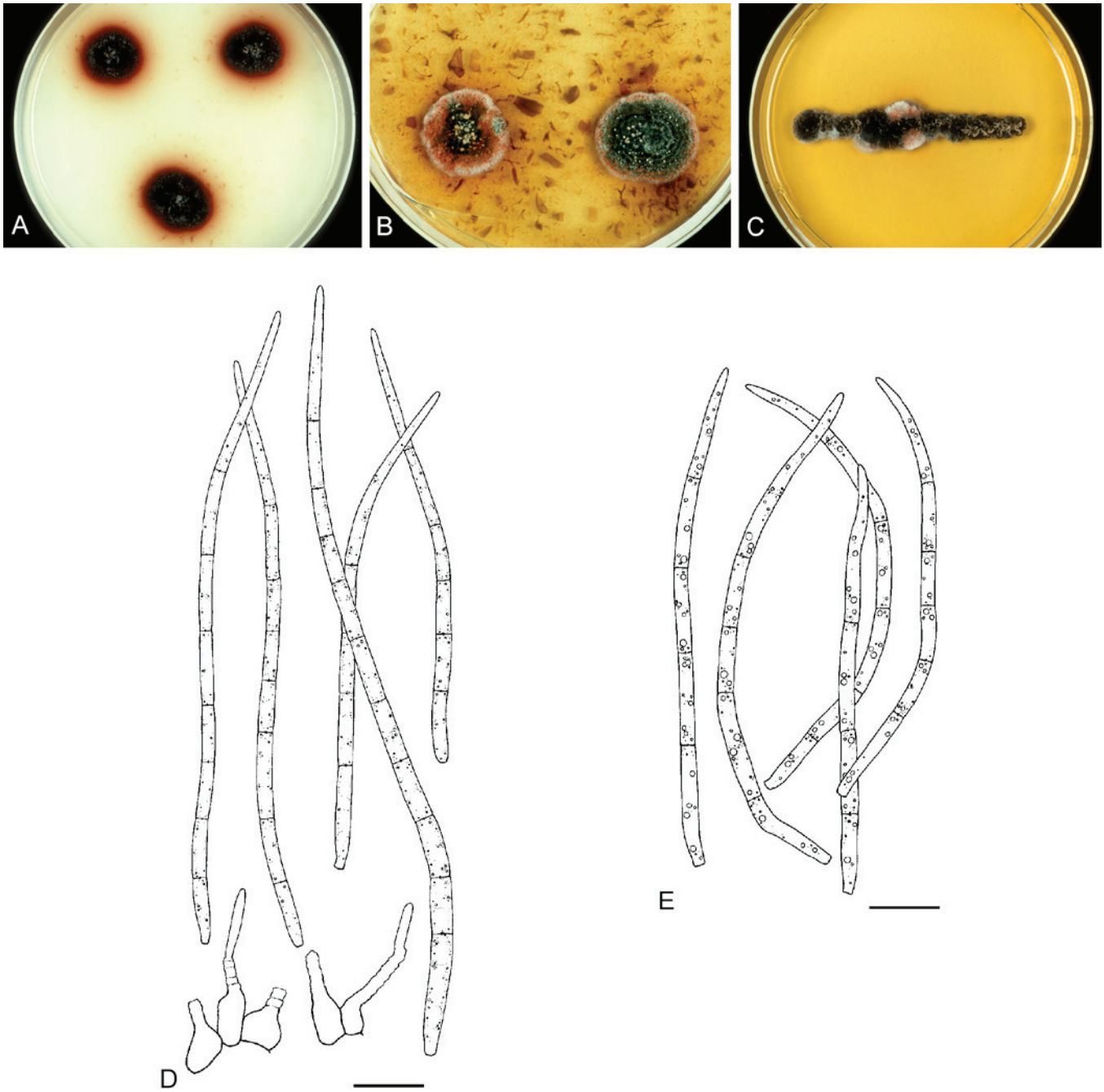

Fig. 30. *Septoria napelli*. A–C. Colonies CBS 109104 (15 °C, nUV). A. On OA. B. On CHA. C. On MEA. D. Conidia and conidiogenous cells on OA (CBS 109104). E. Conidia *in planta* (CBS H-21153). Scale bars = 10 µm.

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

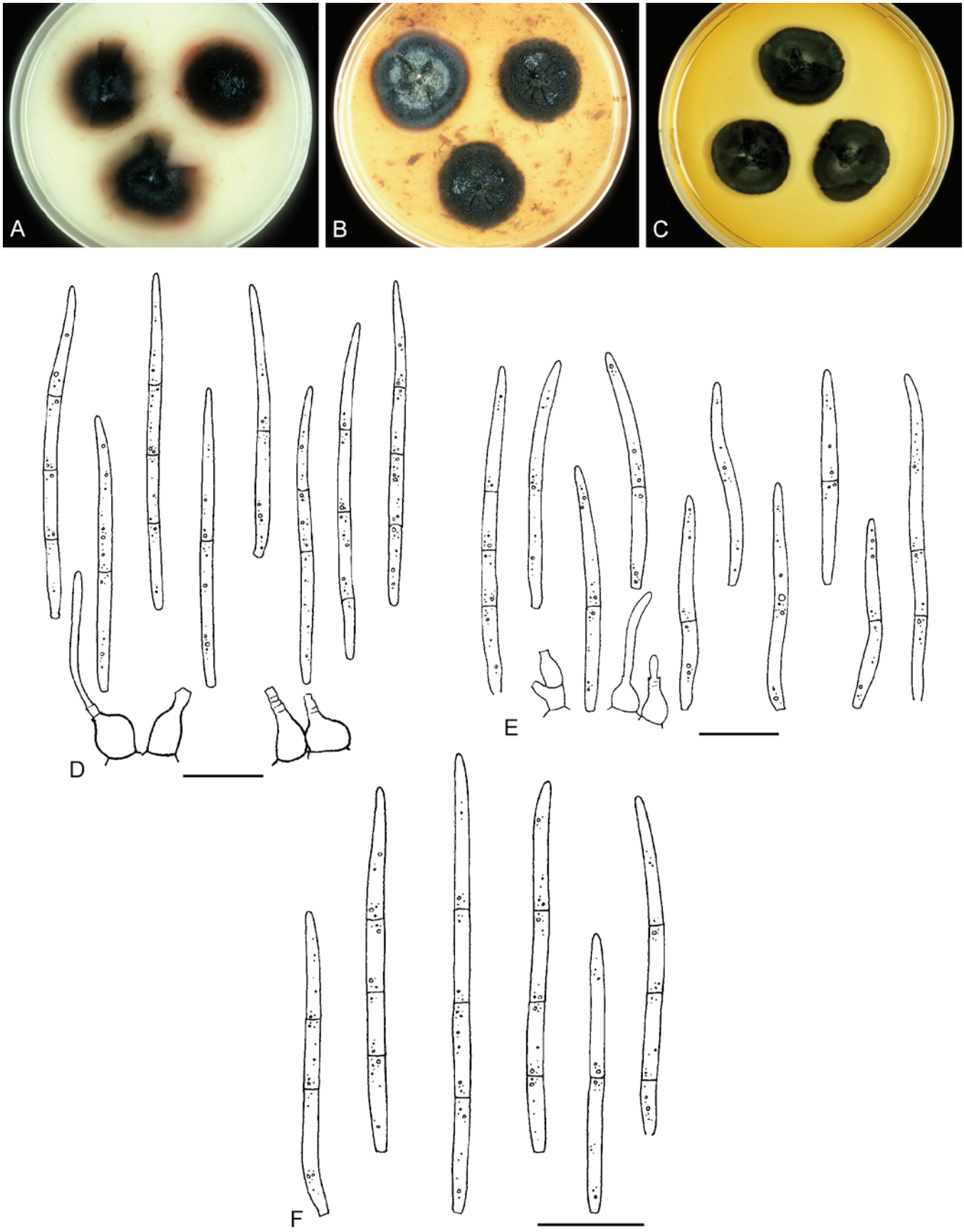

Fig. 31. *Septoria paridis*. A–C. Colonies (15 °C, nUV). A. On OA (CBS 109110). B. On CHA (CBS 109110). C. On MEA (CBS 109108). D. Conidia and conidiogenous cells *in planta* (CBS H-21177, *Paris quadrifolia*). E. Ibid. (CBS H-21152, *Viola palustris*). F. Conidia on OA (CBS 109108). Scale bars = 10 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.

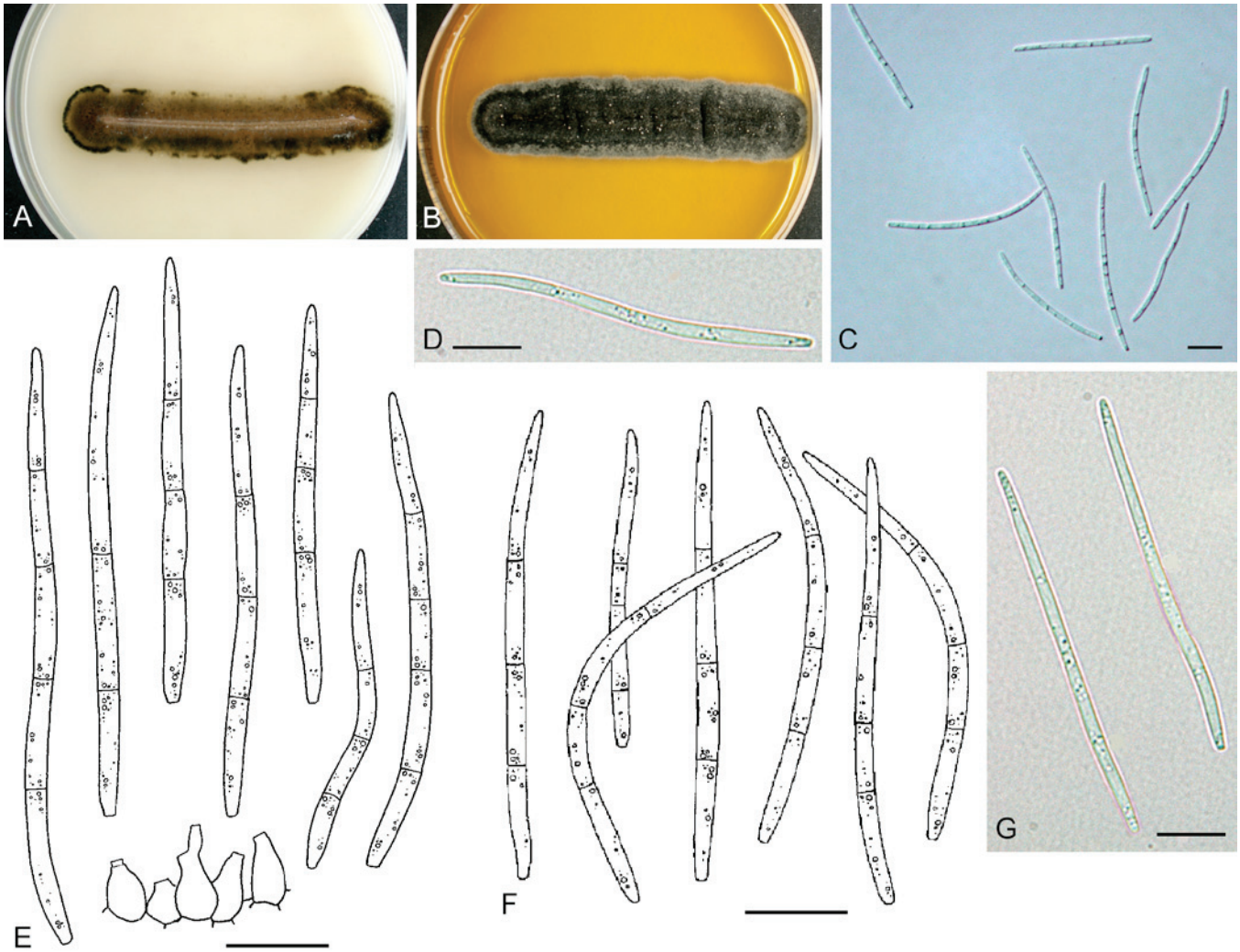

Fig. 32. *Septoria petroselini*. A, B. Colonies CBS 109521 (15 °C, nUV). A. On OA. B. On MEA. C, D. Conidia on OA (CBS 109521). E. Conidia and conidiogenous cells *in planta* (CBS H-21166). F. Conidia on OA (CBS 182.44). G. Conidia on OA (CBS 109521). Scale bars = 10 µm.

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,

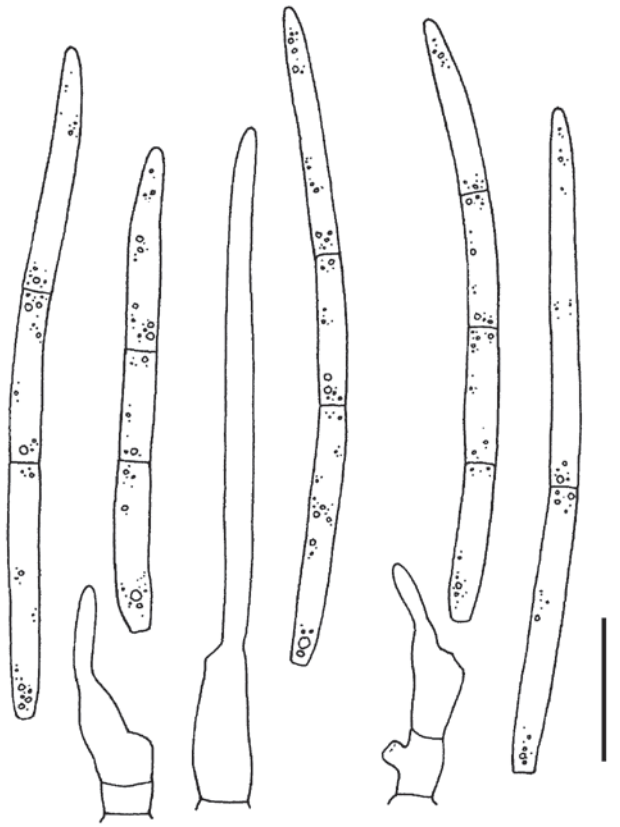

Fig. 33. *Septoria phlogis*. Conidia and conidiogenous cells *in planta* (CBS H-21198). Scale bars = 10 µm.

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

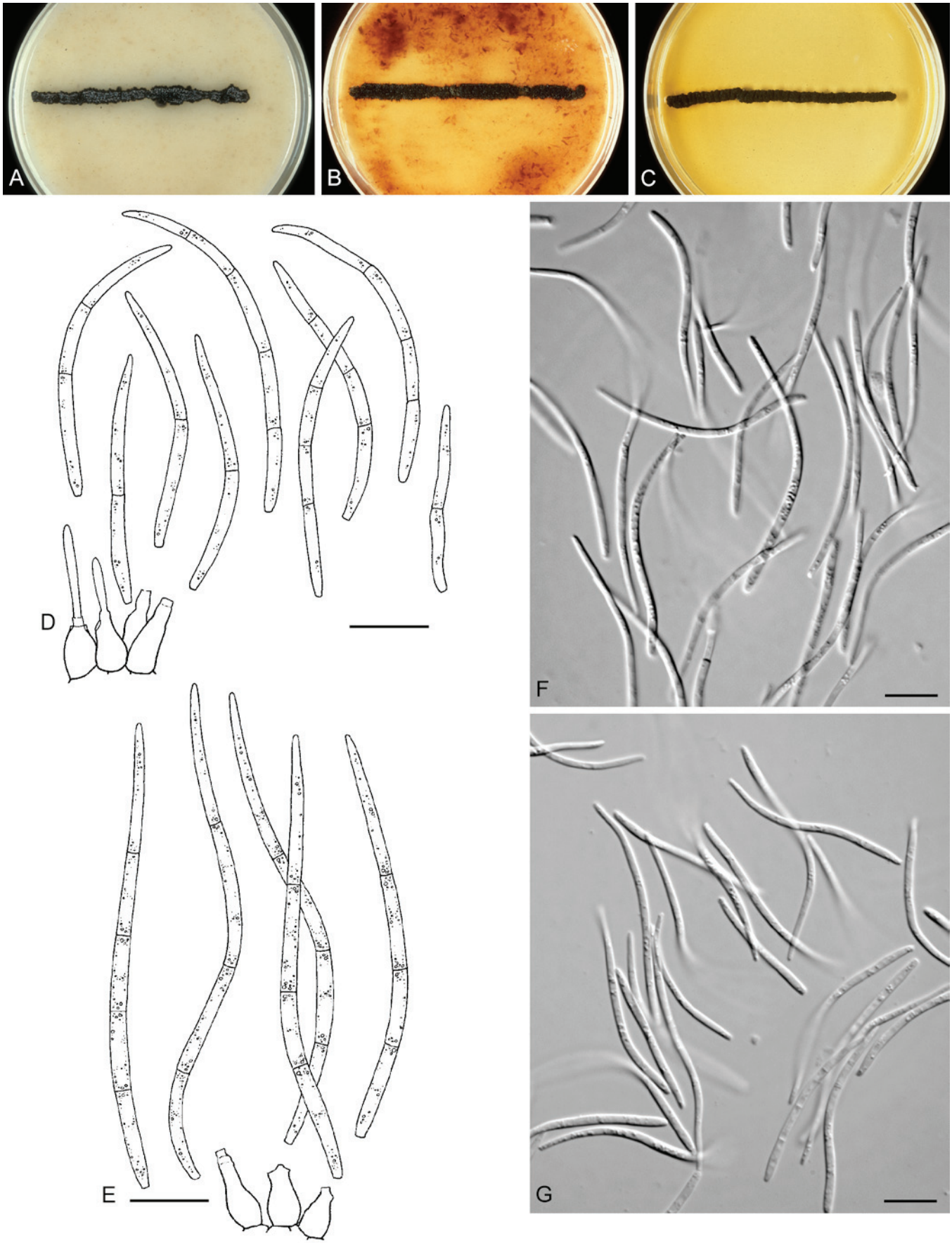

Fig. 34. *Septoria polygonorum*. A–C. Colonies CBS 102331 (15 °C, nUV). A. On OA. B. On CHA. C. On MEA. D. Conidia and conidiogenous cells *in planta* (CBS H-21212). E. Ibid., on OA (CBS 108982). F, G. Conidia on OA (CBS 347.67). Scale bars = 10 µm.

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,

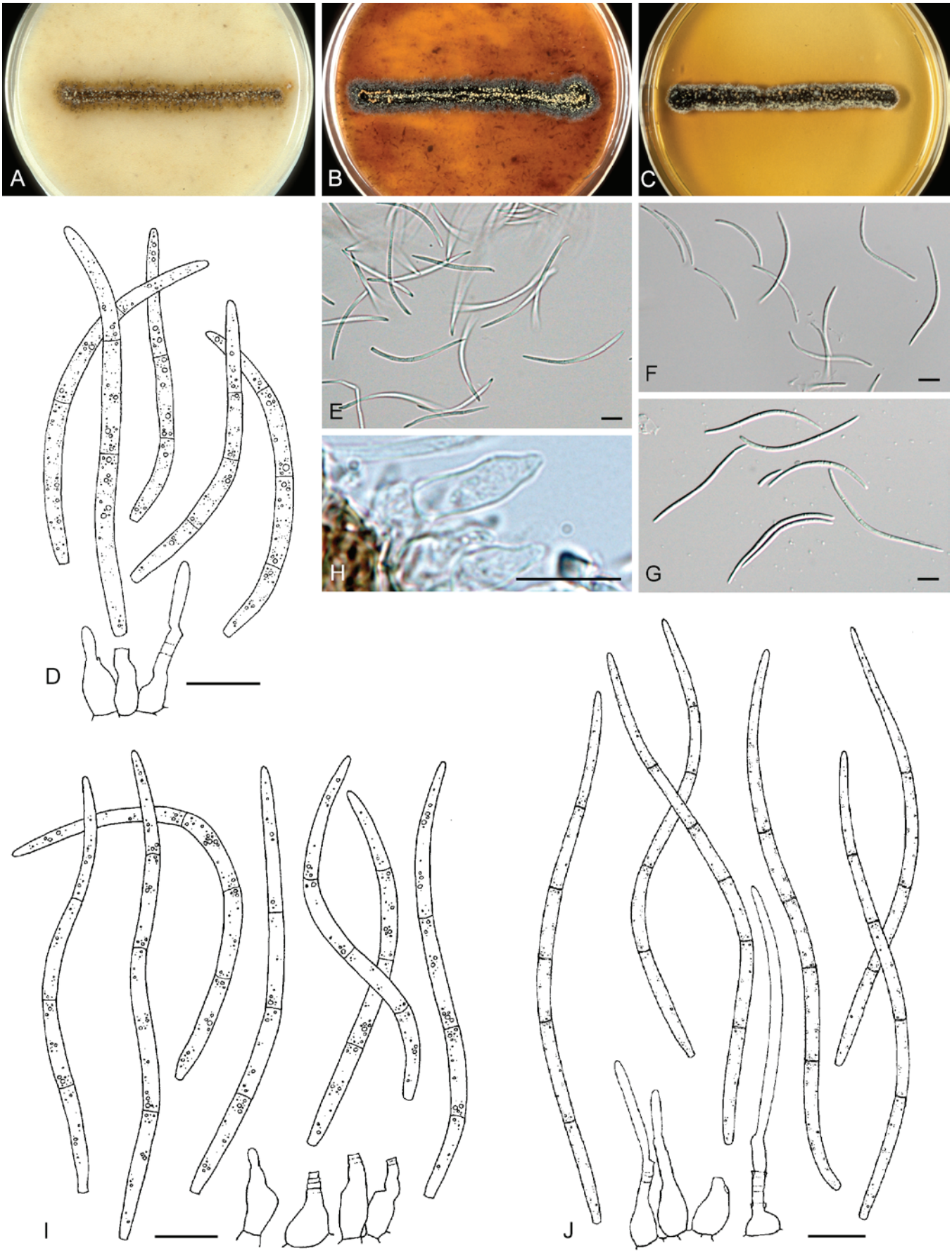

Fig. 35. A–E. *Septoria senecionis*. A–C. Colonies CBS 102381 (15 °C, nUV). A. On OA. B. On CHA. C. On MEA. D. Conidia and conidiogenous cells *in planta* (CBS H-21219, epitype). E. Conidia *in planta* (CBS H-21219). F–J. *Septoria putrida*. F, G. Conidia *in planta* (CBS H-21174). H. Conidiogenous cells *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.

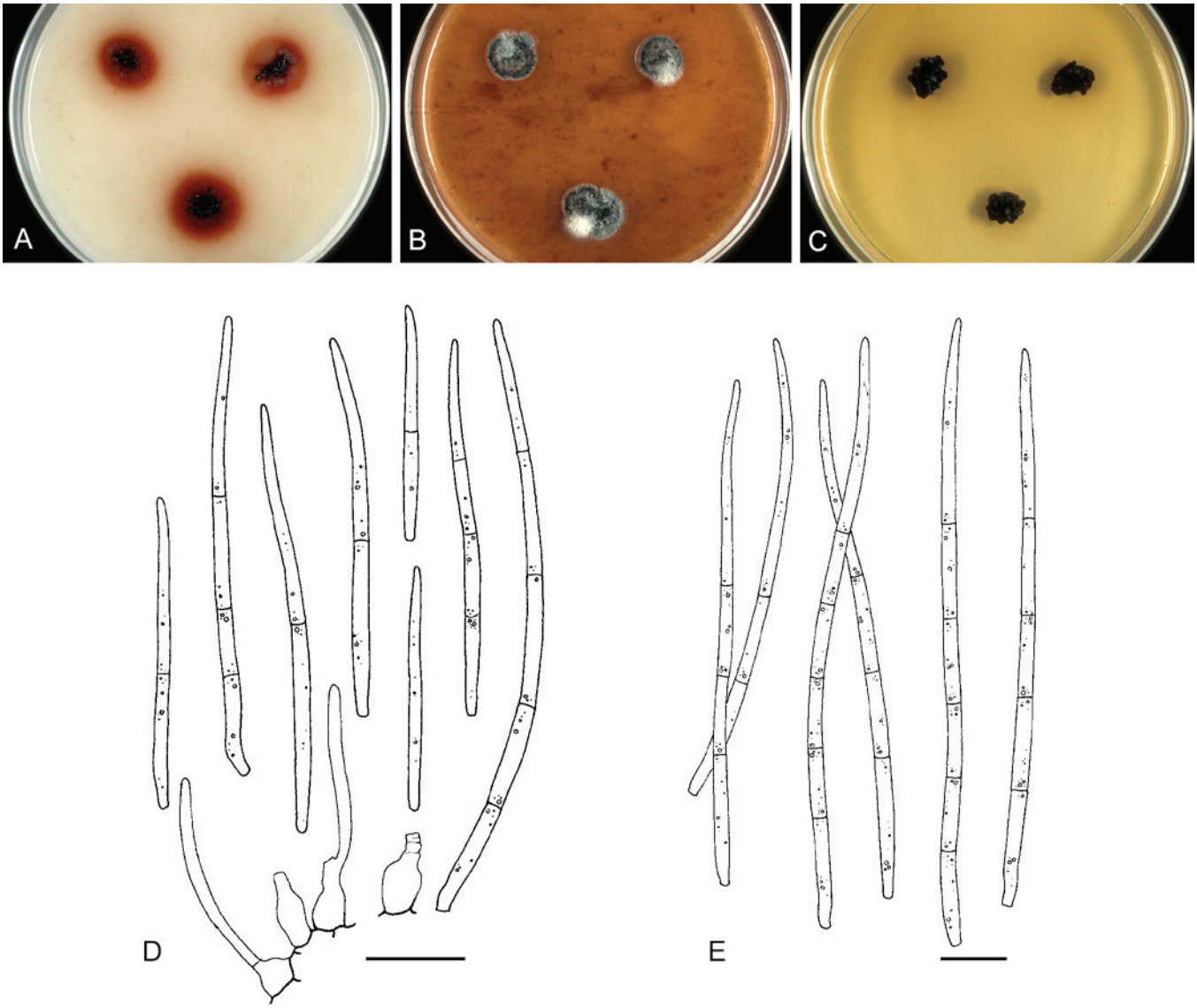

Fig. 36. *Septoria scabiosicola*, CBS 102333. A–C. Colonies (15 °C, nUV). A. On OA. B. On CHA. C. On MEA. D. Conidia and conidiogenous cells *in planta* (CBS H-21180). E. Conidia on OA (CBS 109021). Scale bars = 10 µm.

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

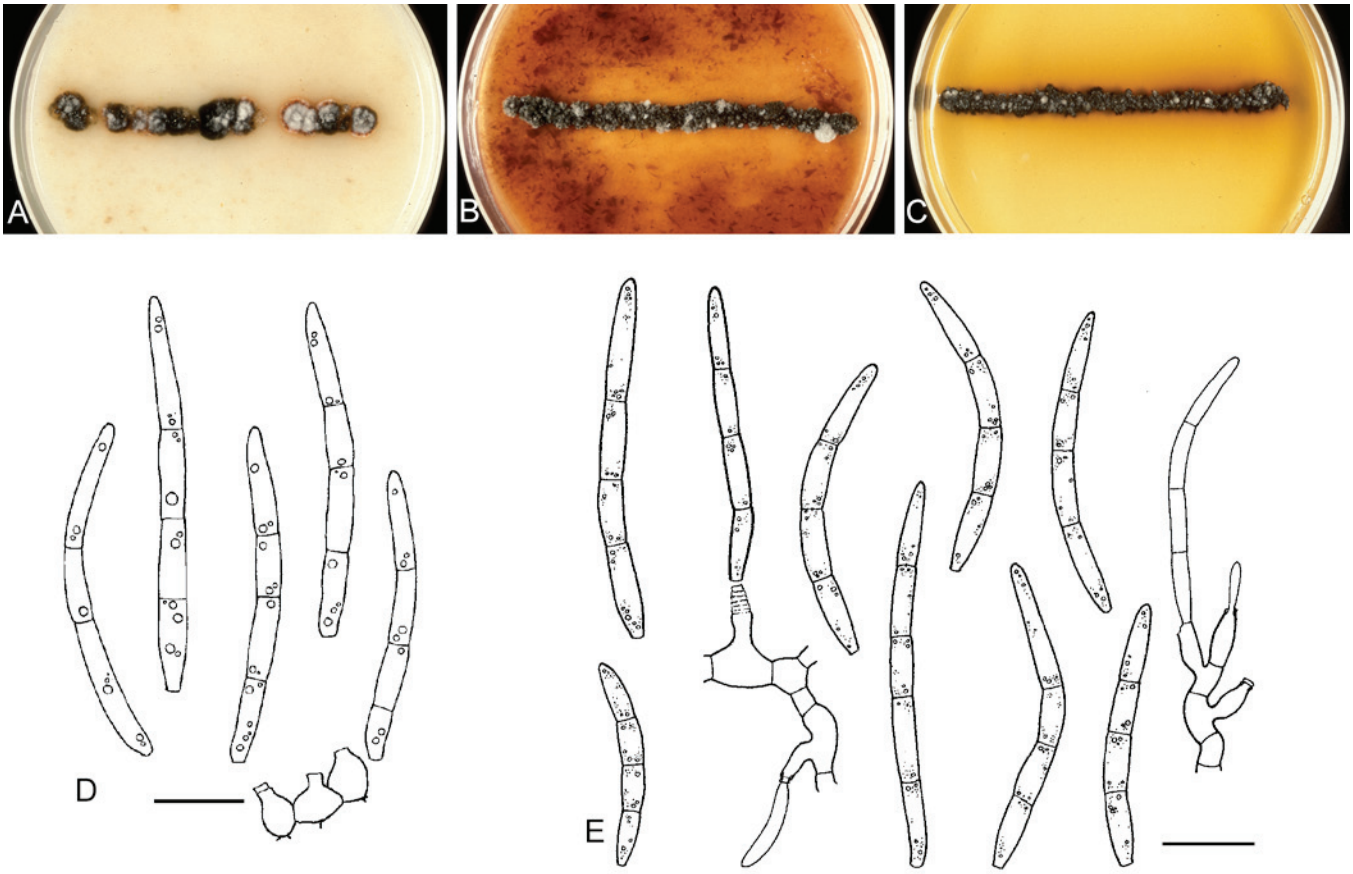

Fig. 37. *Septoria sii*. A–C. Colonies CBS 102370 (15 °C, nUV). A. On OA. B. On CHA. C. On MEA. D. Conidia and conidiogenous cells *in planta* (CBS H-21223). E. Ibid., on OA (CBS 102369). Scale bars = 10 µm.

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

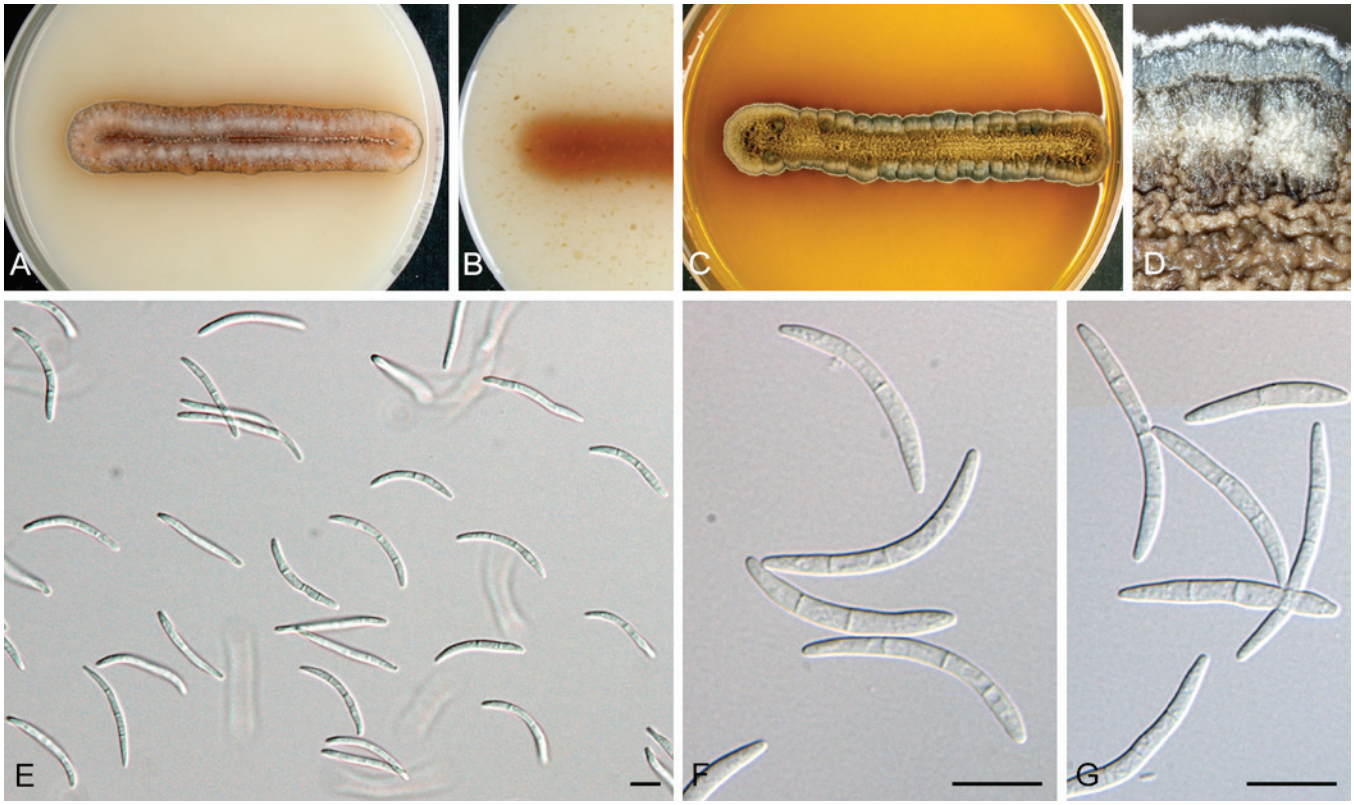

Fig. 38. *Septoria sisyrinchii*, CBS 112096. A–D. Colonies (15 °C, nUV). A. On OA. B. Ibid., reverse. C. On MEA. D. Ibid., detail of colony margin. E–G. Conidia on OA. Scale bars = 10 µm.

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

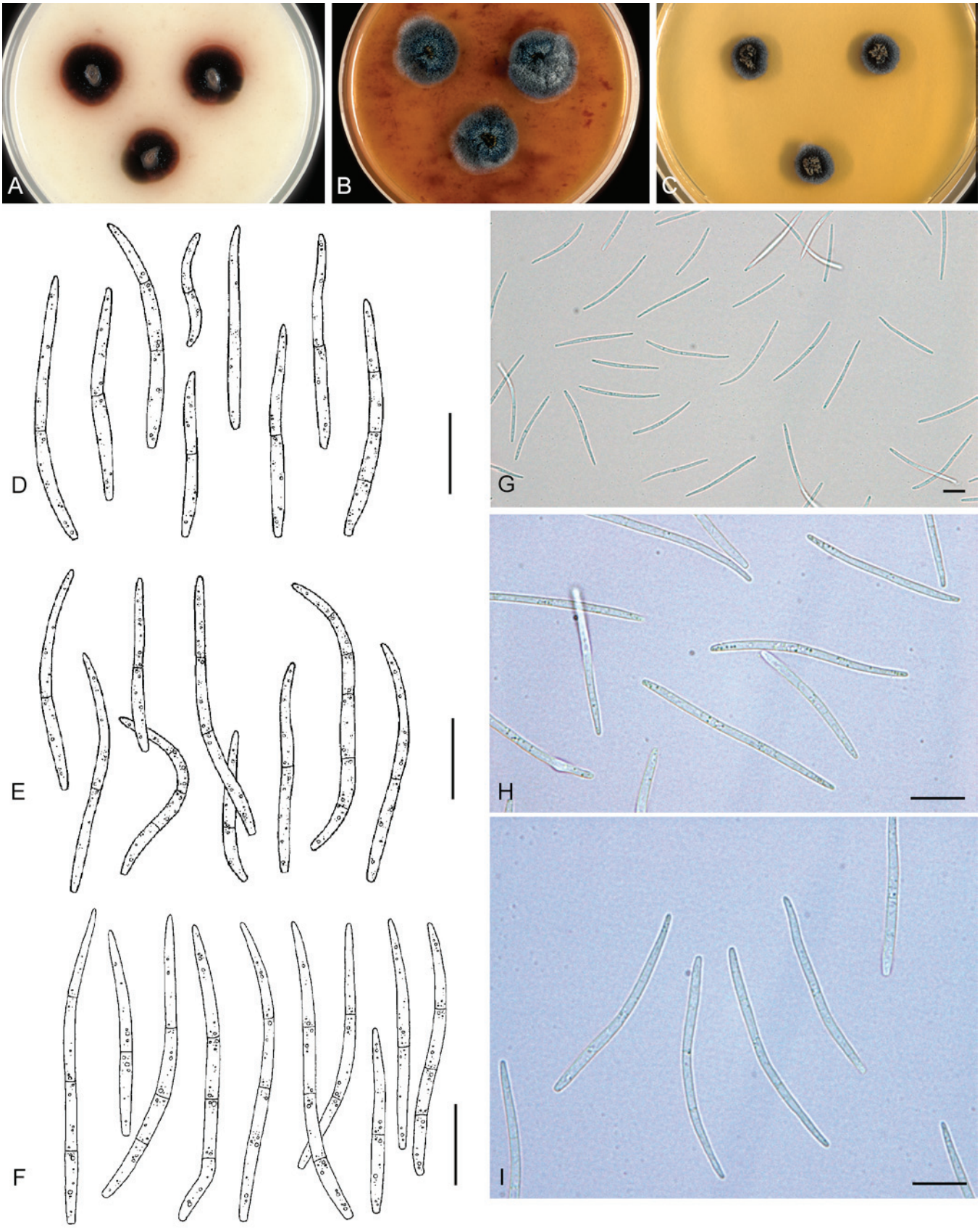

Fig. 39. *Septoria stachydis*. A–C. Colonies CBS 102337 (15 °C, nUV). A. On OA. B. On CHA. C. On MEA. D. Conidia *in planta* (CBS H-21226). E. Conidia *in planta* (CBS H-21175). F–I. Conidia on OA (CBS 123750). Scale bars = 10 µm.

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

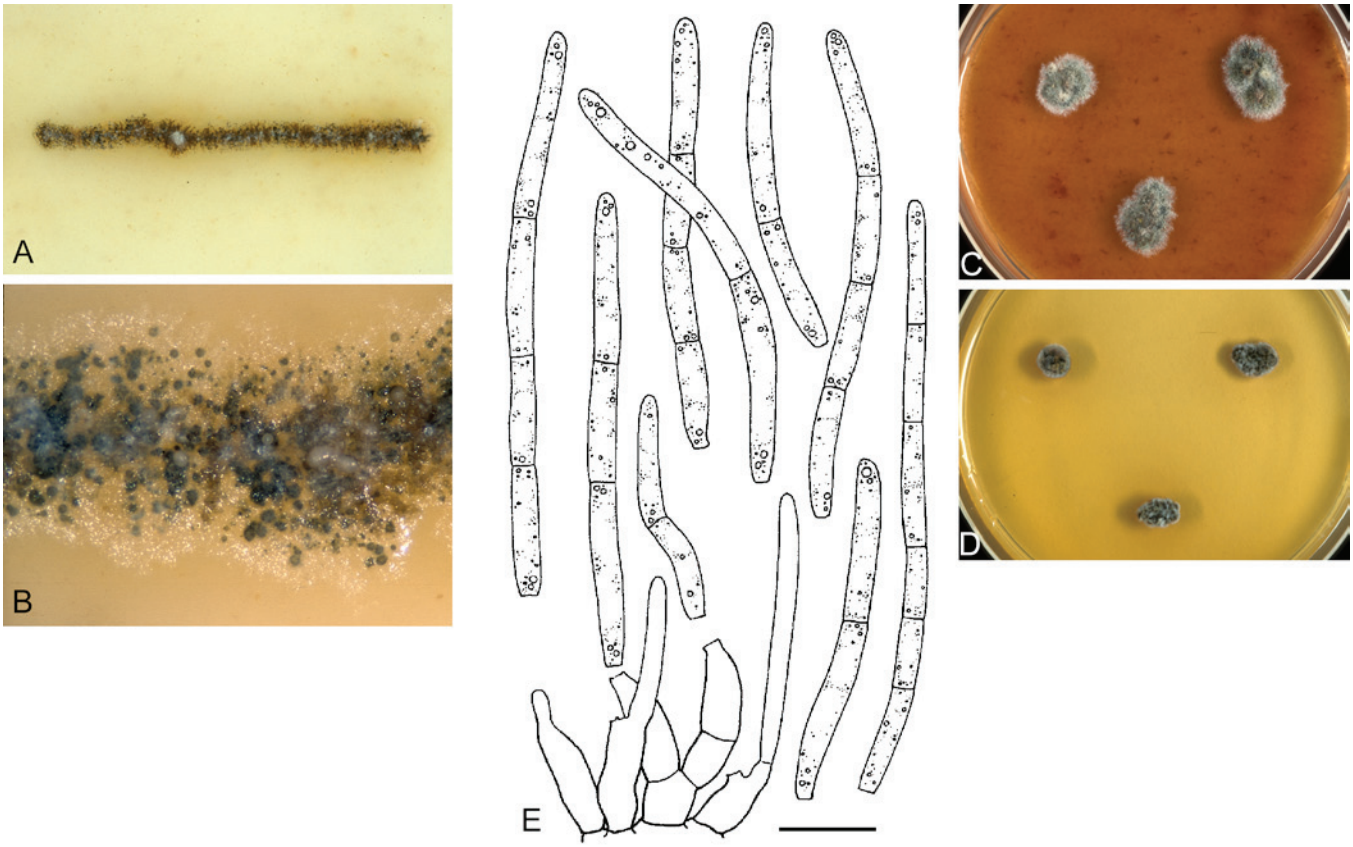

Fig. 40. *Septoria stellariae*. A–D. Colonies CBS 102364. A, B. On OA. C. On CHA. D. On MEA. E. Conidia and conidiogenous cells on OA (CBS 102364). Scale bars = 10 µm.

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,

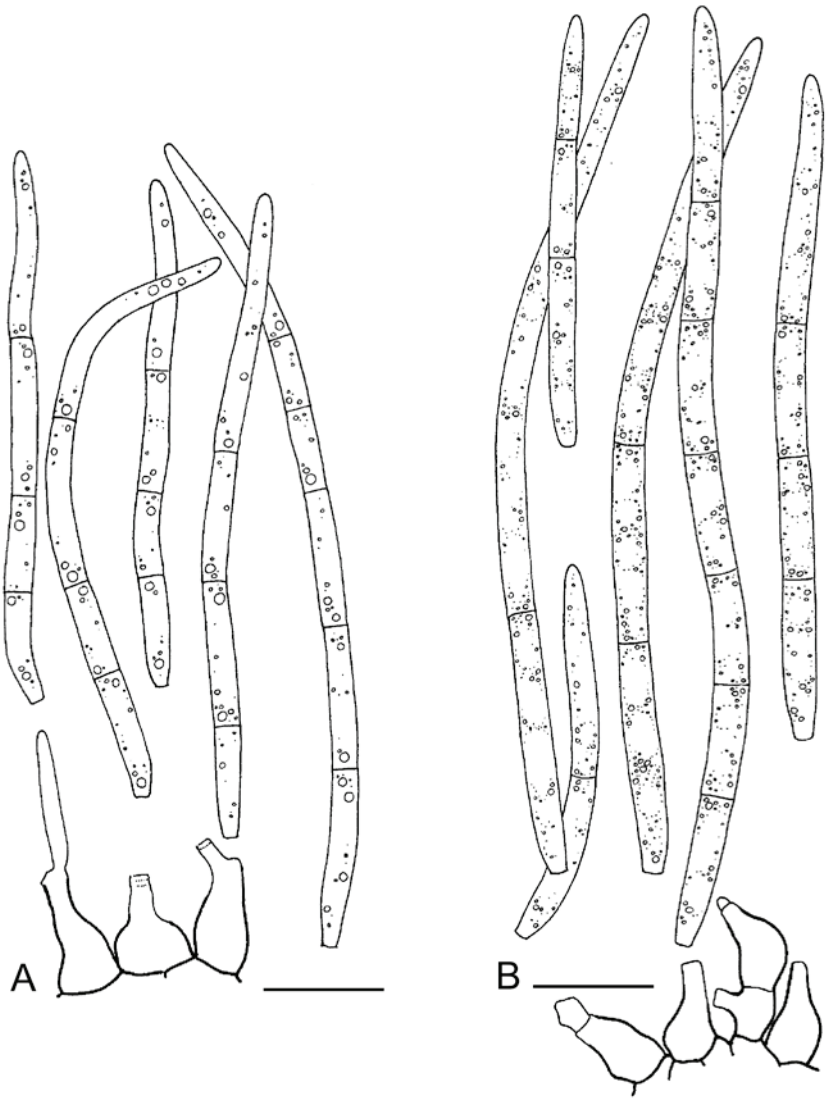

Fig. 41. *Septoria urticae*, epitype. A. Conidia and conidiogenous cells *in planta* (CBS H-21221). B. Ibid., on OA (CBS 102371). Scale bars = 10 µm.

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.

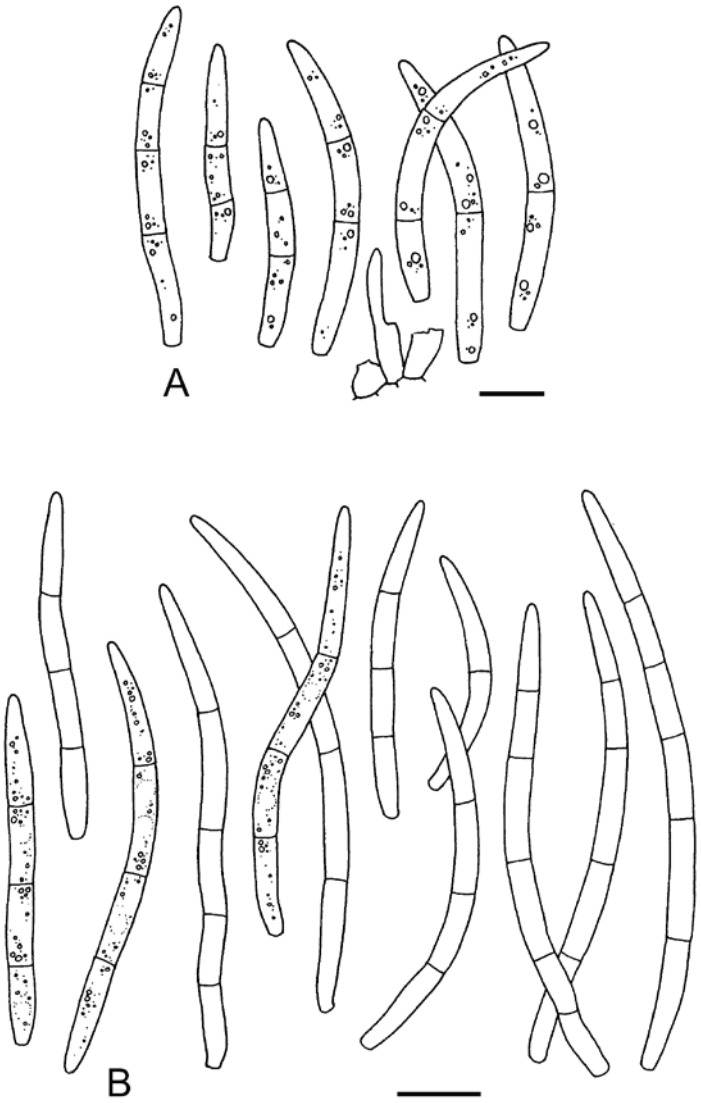

Fig. 42. *Septoria verbenae*. A. Conidia and conidiogenous cells *in planta* (CBS H-21241). B. Conidia on OA (CBS 113438). Scale bars = 10 µm.

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*

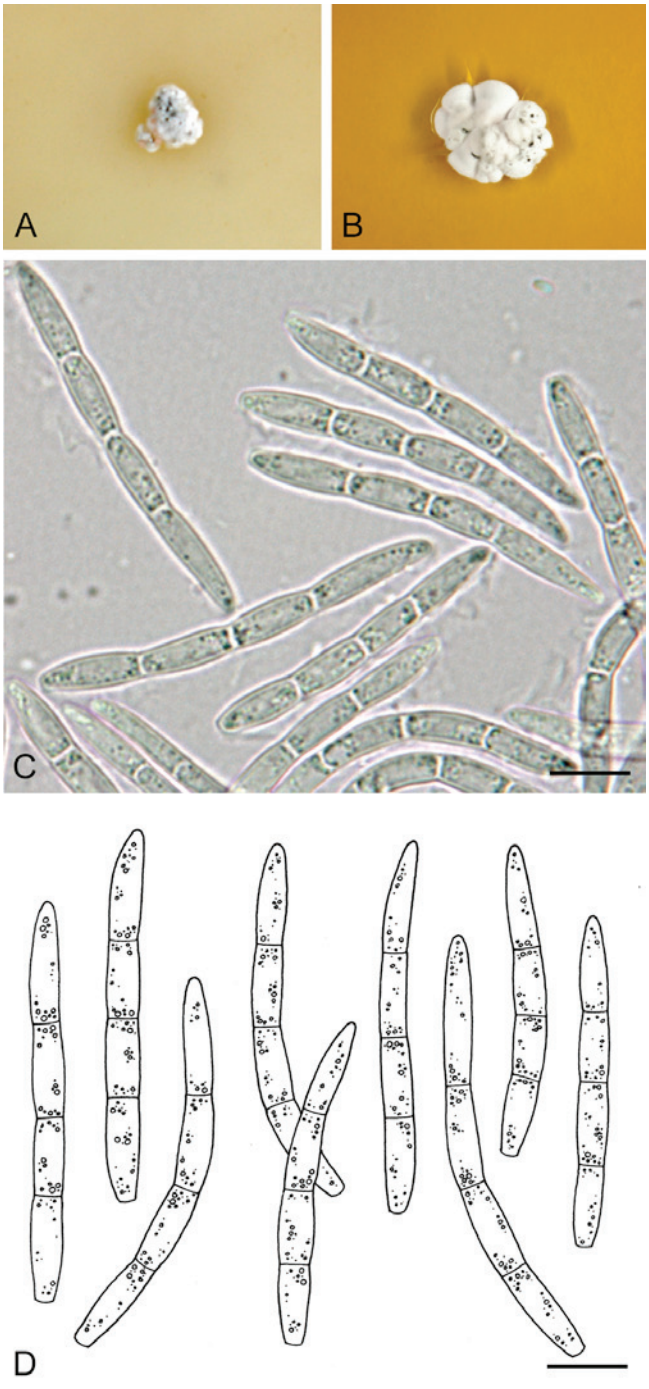

Fig. 43. *Sphaerulina aceris*. A, B. Colonies CBS 183.97. A. On OA. B. On MEA. C, D. Conidia *in planta* (CBS H-21239). Scale bars = 10 µm.

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

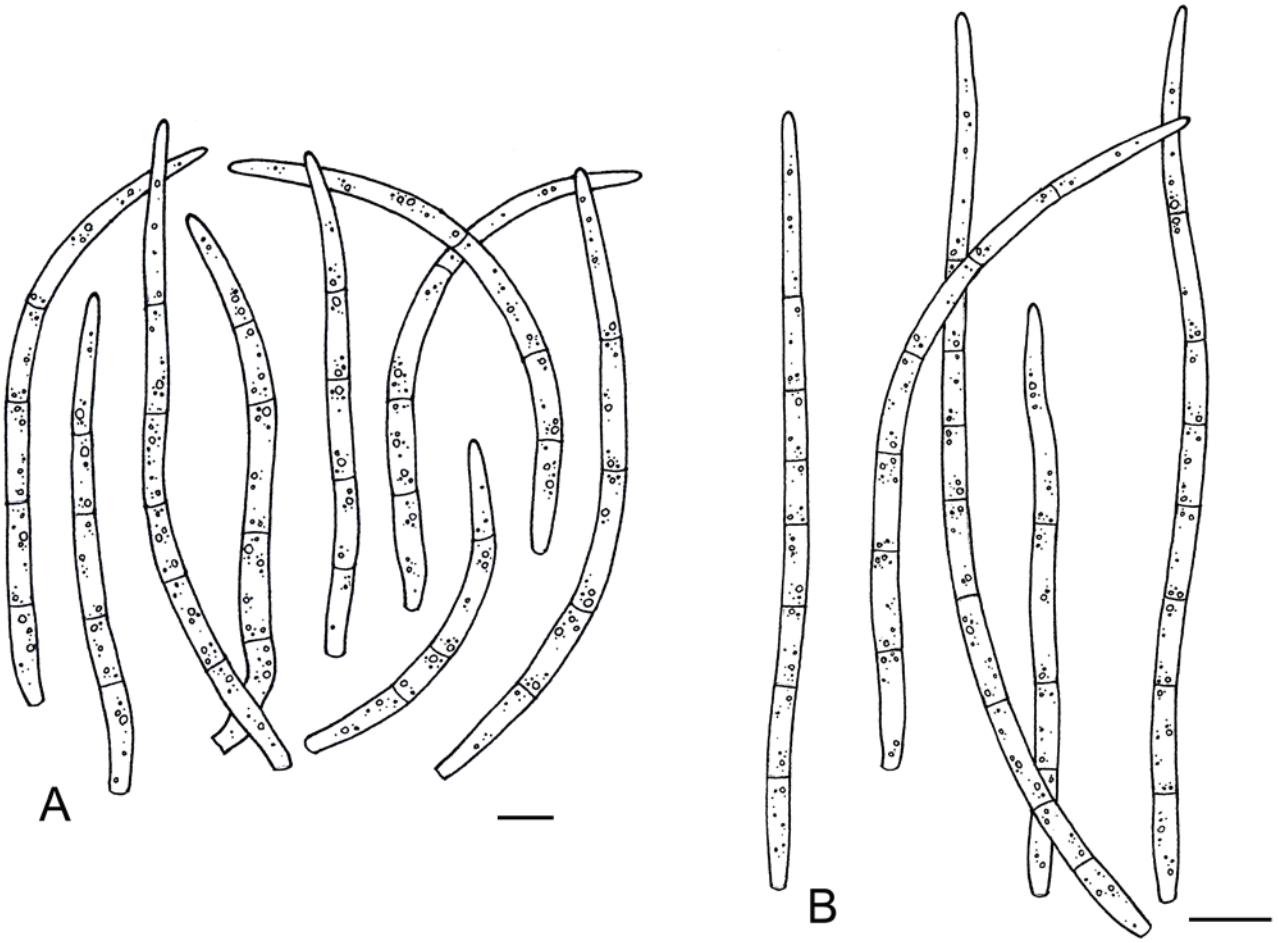

Fig. 46. *Sphaerulina tirolensis*. A. Conidia *in planta* (CBS H-21232, holotype). B. Conidia on OA (CBS 109017). Scale bars = 10 µm.

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

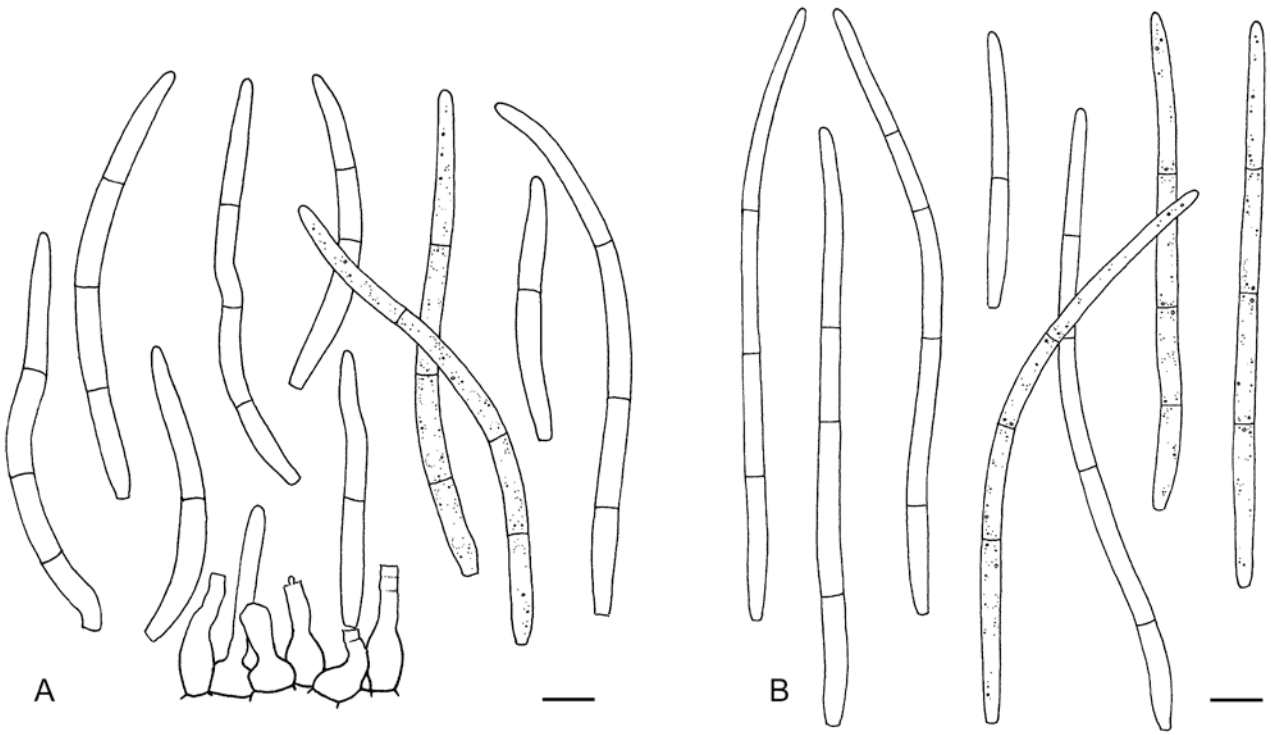

Fig. 47. *Sphaerulina westendorpii*. A. conidia *in planta* (CBS H-21229, epitype); B. conidia on OA (CBS 102327). Scale bars = 10 µm.

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

ACKNOWLEDGEMENTS

We thank the technical staff of the CBS Collection for their support during this project. Arien van Iperen (cultures) and Marjan Vermaas (photographic plates) are acknowledged for their invaluable assistance. Huub van der Aa is thanked for his help during collecting and identifying material. Simeon Vanev is gratefully acknowledged for his support with collecting bibliographic data and translating Russian diagnoses. Part of the DNA barcode sequencing results used in this study was financially supported by the Fonds Economische Structuurversterking (FES, Dutch Ministery of Education, Culture and Science grant BEK/BPR-2009/137964-U, "Making the Tree of Life Work").

REFERENCES

Andrianova TV (1987). Problems of classification and phylogeny of *Septoria* species. *Mikologiya i Fitopatologiya* **21**: 393–399.

Aptroot A (2006). *Mycosphaerella* and its anamorphs 2. Conspectus of *Mycosphaerella*. *CBS Biodiversity Series* **5**. CBS-KNAW Fungal Biodiversity Centre, Utrecht, The Netherlands.

Arx JA von (1983). *Mycosphaerella* and its anamorphs. *Proceedings Koninklijke Nederlandse Akademie van Wetenschappen, Series C - Biological and Medical Sciences* **86** (1): 15–54.

Beach WS (1919). Biological spezialization in the genus *Septoria*. *American Journal of Botany* **6**: 1–33.

Braun U (1995). A monograph of *Cercosporella*, *Ramularia* and allied genera (Phytopathogenic Hyphomycetes). Vol. 1. IHW-Verlag, Eching.

Breeÿen A den, Groenewald JZ, Verkley GJM, Crous PW (2006). Morphological and molecular characterisation of *Mycosphaerellaceae* associated with the invasive weed, *Chromolaena odorata*. *Fungal Diversity* **23**: 89–110.

Cheewangkoon R, Crous PW, Hyde KD, Groenewald JZ, To-anan C (2008). Species of *Mycosphaerella* and related anamorphs on *Eucalyptus* leaves from Thailand. *Persoonia* **21**: 77–91.

Cochran LC (1932). A study of two Septoria leaf spots of celery. *Phytopathology* **22**: 791–812.

Constantinescu O (1984). Taxonomic revision of *Septoria*-like fungi parasitic on *Betulaceae*. *Transactions of the British Mycological Society* **83**: 383–398.

Crous PW, Aptroot A, Kang J-C, Braun U, Wingfield MJ (2000). The genus *Mycosphaerella* and its anamorphs. *Studies in Mycology* **45**: 107–121.

Crous PW, Groenewald JZ (2005). Hosts, species and genotypes: opinions versus data. *Australasian Plant Pathology* **34**: 463–470.

Crous PW, Denman S, Taylor JE, Swart L, Palm, ME (2004a).Cultivation and diseases of *Proteaceae*: *Leucadendron*, *Leucospermum* and *Protea*. *CBS Biodiversity Series* **2**: 1–228.

Crous PW, Groenewald JZ, Pongpanich K, Himaman W, Arzanlou M, Wingfield MJ (2004b). Cryptic speciation and host specificity among *Mycosphaerella* spp. occurring on Australian *Acacia* species grown as exotics in the tropics. *Studies in Mycology* **50**: 457–469.

Crous PW, Kang J-C, Braun U (2001). A phylogenetic redefinition of anamorph genera in *Mycosphaerella* based on ITS rDNA sequences and morphology. *Mycologia* **93**: 1081–1101.

Crous PW, Slippers B, Wingfield MJ, Rheeder J, Marasas WFO, *et al*. (2006a). Phylogenetic lineages in the *Botryosphaeriaceae*. *Studies in Mycology* **55**: 235–253.

Crous PW, Verkley GJM, Groenewald JZ, Samson RA (2009). *CBS Laboratory Manual Series* **1**. CBS-KNAW Fungal Biodiversity Centre, Utrecht, The Netherlands.

Crous PW, Wingfield MJ, Mansilla JP, Alfenas AC, Groenewald JZ (2006b). Phylogenetic reassessment of *Mycosphaerella* spp. and their anamorphs occurring on *Eucalyptus*. II. *Studies in Mycology* **55**: 99–131.

Demaree JB, Wilcox MS (1943). The fungus causing the so-called "Septoria leaf-spot disease" of raspberry. *Phytopathology* **33**: 986–1003.

Diedicke H (1915). Pilze VII, *Sphaeropsidaea*, *Melanconiae*,. Kryptogamenfl. Mark Brandenburg **9**: 1–962.

Farr DF (1991). *Septoria* species on *Cornus*. *Mycologia* **83**: 611–623.

Farr DF (1992). Species of *Septoria* on the *Fabaceae*, subfamily *Faboidae*, tribe *Genistae*. *Sydowia* **44**: 13–31.

Feau N, Hamelin RC, Bernier L (2006). Attributes and congruence of three molecular data sets: inferring phylogenies among *Septoria*-related species from woody perennial plants. *Molecular Phylogenetics and Evolution* **40**: 808–829.

Gabrielson RL, Grogan RG (1964). The late blight organism *Septoria apiicola*. *Phytopathology* **54**: 1251–1257.

Goodwin SB, Dunkle LD, Zismann VL (2001). Phylogenetic analysis of *Cercospora* and *Mycosphaerella* based on the internal transcribed spacer region of ribosomal DNA. *Phytopathology* **91**: 648–658.

Grove WB (1935). British stem and leaf fungi (*Coelomycetes*). Vol. I: *Sphaeropsidales*, *Sphaerioideae* with hyaline conidia: 1–488.

Hall TA (1999). BioEdit: A user-friendly biological sequence alignment editor and analysis program for Windows 95/98/NT. *Nucleic Acids Symposium Series* **41**: 95–98.

Hebert PDN, Cywinska A, Ball SL, DeWaard JR (2003). Biological identifications through DNA barcodes. *Proceedings of the Royal Society of London Series B* **270**: 313–321.

Huelsenbeck JP, Ronquist F (2001). MRBAYES: Bayesian inference of phylogenetic trees. *Bioinformatics* **17**: 754–755.

Jørstad I (1965). *Septoria* and septoroid fungi on dicotyledones in Norway. *Skrifter utgitt av Det Norske Videnskaps-Akademi i Oslo, I: Mat-Naturv. Klasse* **22**:1-110.

Katoh K, Misawa K, Kuma K, Miyata T (2002). MAFFT: a novel method for rapid multiple sequence alignment based on fast Fourier transform. *Nucleic Acids Research* **30**: 3059–3066.

Kuijpers AFA, Aptroot A (2004). A revision of *Mycosphaerella* section *Longispora* (Ascomycetes). *Nova Hedwigia* **75**: 451–468.

Lombard L, Crous PW, Wingfield BD, Wingfield MJ (2010). Species concepts in *Calonectria* (*Cylindrocladium*). *Studies in Mycology* **66**: 1–13.

Markevičius V, Treigienė A (2003). Sphaeropsidales. Genus *Septoria*. *Mycota Lithuaniae* **10**, 3: 1–199.

Mason-Gamer RJ, Kellogg EA (1996). Testing for phylogenetic conflict among molecular data sets in the tribe *Triticeae* (*Gramineae*). *Systematic Biology* **45**: 524–545.

Muthumary J (1999). First contribution to a monograph of *Septoria* species in India. Madras: Centre for advanced studies in Botany.

Nylander JAA (2004). MrModeltest v2. Program distributed by the author. *Evolutionary Biology Centre Uppsala University*.

Petrak F (1925). Beiträge zur Pilzflora Südost-Galiziens und der Zentralkarpathen. *Hedwigia* **65**: 179–330.

Petrak F (1957). Die auf Aconiten vorkommenden Arten der Gattung *Septoria*. *Sydowia* **11**: 375–379.

Priest MJ (2006). Fungi of Australia. *Septoria*. ABRS, Canberra: CSIRO Publishing, Melbourne.

Punithalingam E (1967a). *Septoria chrysanthemella*. *CMI Descriptions of Pathogenic Fungi and Bacteria* **137**. Commonwealth Mycological Institute, Kew.

Punithalingam E (1967b). *Septoria leucanthemi*. *CMI Descriptions of Pathogenic Fungi and Bacteria* **138**. Commonwealth Mycological Institute, Kew

Punithalingam E (1967c). *Septoria obesa*. *CMI Descriptions of Pathogenic Fungi and Bacteria* **139**. Commonwealth Mycological Institute, Kew.

Punithalingam E (1967d). *Septoria socia*. *CMI Descriptions of Pathogenic Fungi and Bacteria* **140**. Commonwealth Mycological Institute, Kew.

Punithalingam E (1982). *Septoria cucurbitacearum*. *CMI Descriptions of Pathogenic Fungi and Bacteria* **740**. Commonwealth Mycological Institute, Kew.

Punithalingam E, Holiday P (1972). *Septoria lactucae*. *CMI Descriptions of Pathogenic Fungi and Bacteria* **335**. Commonwealth Mycological Institute, Kew.

Punithalingam E, Wheeler BEJ (1965). *Septoria* spp. occurring on species of *Chrysanthemum*. *Transactions of the British Mycological Society* **48**: 423–439.

Quaedvlieg W, Kema GHJ, Groenewald JZ, Verkley GJM, Seifbarghi S, Razavi M, Gohari A, Mirzadi, Mehrabi R, Crous PW (2011). *Zymoseptoria* gen. nov.: a new genus to accommodate *Septoria*-like species occurring on graminicolous hosts. *Persoonia* **26**: 57–69.

Quaedvlieg W, Groenewald JZ, Jesús Yáñez-Morales M, Crous PW (2012). DNA barcoding of *Mycosphaerella* species of quarantine importance to Europe. *Persoonia* **29**: 101–115.

Quaedvlieg W, Verkley GJM, Shin H-D, Barreto RW, Algenas AC, Swart WJ, Groenewald JZ, Crous PW (2013). Sizing up *Septoria*. *Studies in Mycology* **75**: 307–390. (this volume).

Radulescu E, Negru A, Docea E (1973). Septoriozele din România. Bucureşti: Editura Academiei Republicii Socialiste România.

Rayner RW (1970). A mycological colour chart. CMI and British Mycological Society. Kew, UK.

Saccardo PA (1884). *Sylloge Fungorum: Sylloge Sphaeropsidearum et Melanconiearum*. **3**: 542. Padova, Italy.

Saccardo PA (1895). *Sylloge fungorum: Supplemental Universale, Pars III* **11**: 1–753. Padova, Italy.

Saccardo PA (1906). *Sylloge fungorum: Supplemental Universale, Pars VII* **18**: 1–838. Padova, Italy.

Saccardo PA, Sydow P (1899). *Sylloge Fungorum: Supplemental Universale, Pars IV* **14**: 1–1316. Padova, Italy.

Sheridan JE (1968). Conditions for infection of celery by *Septoria apiicola*. *Plant Disease Report* **52**: 142–145.

Shin HD, Sameva EF (2004). *Septoria* in Korea (Plant Pathogens of Korea 11). National Institute of Agricultural Science and Technology, Republic of Korea.

Simon UK, Groenewald JZ, Stierhof Y-D, Crous PW, Bauer R (2009). A necrotrophic phytopathogen forming a special cellular interaction with its host *Aegopodium podagraria*. *Mycological Progress* **9**: 49–56.

Smissen RD, Clement JC, Garnock-Jones PJ, Chambers JK (2002). Subfamilial relationships within *Caryophyllaceae* as inferred from 5' *ndhF* sequences. *American Journal of Botany* **89**: 1336–1341.

Stewart EL, Liu Z, Crous PW, Szabo LJ (1999). Phylogenetic relationships among some cercosporoid anamorphs of *Mycosphaerella* based on rDNA sequence analysis. *Mycological Research* **103**: 1491–1499.

Sutton BC (1980). The Coelomycetes. Fungi imperfecti with Pycnidia, Acervuli and Stromata. Commonwealth Mycological Institute, Kew, Surrey, England.

Sutton BC, Pascoe IG (1987). *Septoria* species on *Acacia*. *Transactions of the British Mycological Society* **89**: 521–532.

Sutton BC, Pascoe IG (1989). Some *Septoria* species on native Australian plants. *Studies in Mycology* **31**: 177–186.

Sutton BC, Hennebert GL (1994). Interconnections amongst anamorphs and their possible contribution to ascomycete systematics. In A*scomycete systematics: problems and perspectives in the nineties* (Hawksworth DL, ed.), pp. 77–98. Plenum Press, New York, USA.

Sutton BC, Waterston JM (1966) Septoria apiicola. *CMI Descriptions of Pathogenic Fungi and Bacteria* **88**. Commonwealth Mycological Institute, Kew.

Sydow H von (1924). Beiträge zur Kenntnis der Pilzflora Neu-Seelands. I. *Annales Mycologici* **22**: 299–317.

Tamura K, Dudley J, Nei M, Kumar S (2007). MEGA4: Molecular evolutionary genetics analysis (MEGA) software version 4.0. *Molecular Biology and Evolution* **24**: 1596–1599.

Teterevnikova-Babayan DN (1987). Fungi of the genus *Septoria* in the U.S.S.R. Yerevan: Akademia Nauk Armyanskoi SSR.

Vanev SG, Sameva EF, Bakalova GG (1997). Fungi Bulgaricae 3. Ordo *Sphaeropsidales*. Sofia: Editio Academica Prof. Marin Drinov.

Verkley GJM (1998a). Ultrastructural evidence for two types of proliferation in a single conidiogenous cell of *Septoria chrysanthemella*. *Mycological Research* **102**: 368–372.

Verkley GJM (1998b). Ultrastructure of conidiogenesis and conidia in two species of *Septoria* sensu lato. *Mycologia* **90**: 189–198.

Verkley GJM, Priest MJ (2000). *Septoria* and similar coelomycetous anamorphs of *Mycosphaerella*. *Studies in Mycology* **45**: 123–128.

Verkley GJM, Starink-Willemse M (2004a). A phylogenetic study of some *Septoria* species pathogenic to *Asteraceae* based on ITS ribosomal DNA sequences. *Mycological Progress* **3**: 315–322.

Verkley GJM, Starink-Willemse M, Iperen A van, Abeln ECA (2004b). Phylogenetic analyses of *Septoria* species based on the ITS and LSU-D2 regions of nuclear ribosomal DNA. *Mycologia* **96**: 558–571.

Verkley GJM, Crous PW, Groenewald JZ, Braun U, Aptroot A (2004c). *Mycosphaerella punctiformis* revisited: morphology, phylogeny, and epitypification of the type species of the genus *Mycosphaerella* (*Dothideales*, *Ascomycota*). *Mycological Research* **108**: 1271–1282.

Waddell HT, Weber GF (1963). Physiology and pathology of *Septoria* species on *Chrysanthemum*. *Mycologia* **55**: 442–452.

White TJ, Bruns T, Lee S, Taylor JW (1990). Amplification and direct sequencing of fungal ribosomal RNA genes for phylogenetics. In: *PCR protocols: a guide to methods and applications* (Innis MA, Gelfland DH, Sininsky JJ, White TJ, eds). Academic Press, San Diego, USA: 315–322.

Zalar P, Hoog GS de, Schroers H-J (2007). Phylogeny and ecology of the ubiquitous saprobe *Cladosporium sphaerospermum*, with descriptions of seven new species from hypersaline environments. *Studies in Mycology* **58**: 157–183.