

# *Species concepts in Cercospora: spotting the weeds among the roses*

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# Species concepts in *Cercospora*: spotting the weeds among the roses

J.Z. Groenewald<sup>1\*</sup>, C. Nakashima<sup>2</sup>, J. Nishikawa<sup>3</sup>, H.-D. Shin<sup>4</sup>, J.-H. Park<sup>4</sup>, A.N. Jama<sup>5</sup>, M. Groenewald<sup>1</sup>, U. Braun<sup>6</sup>, and P.W. Crous<sup>1,7,8</sup>

<sup>1</sup>CBS-KNAW Fungal Biodiversity Centre, Uppsalalaan 8, 3584 CT Utrecht, The Netherlands; <sup>2</sup>Graduate School of Bioresources, Mie University, 1577 Kurima-machiya, Tsu, Mie 514-8507, Japan; <sup>3</sup>Kakegawa Research Center, Sakata Seed Co., 1743-2 Yoshioka, Kakegawa, Shizuoka 436-0115, Japan; <sup>4</sup>Division of Environmental Science and Ecological Engineering, College of Life Sciences and Biotechnology, Korea University, Seoul 136-701, Korea; <sup>5</sup>Department of Agriculture, P.O. Box 326, University of Reading, Reading RG6 6AT, UK; <sup>6</sup>Martin-Luther-Universität, Institut für Biologie, Bereich Geobotanik und Botanischer Garten, Herbarium, Neuwerk 21, 06099 Halle (Saale), Germany; <sup>7</sup>Microbiology, Department of Biology, Utrecht University, Padualaan 8, 3584 CH Utrecht, the Netherlands; <sup>8</sup>Wageningen University and Research Centre (WUR), Laboratory of Phytopathology, Droeveendaalsesteeg 1, 6708 PB Wageningen, The Netherlands

\*Correspondence: Johannes Z. Groenewald, [egroenewald@cbs.knaw.nl](mailto:egroenewald@cbs.knaw.nl)

**Abstract:** The genus *Cercospora* contains numerous important plant pathogenic fungi from a diverse range of hosts. Most species of *Cercospora* are known only from their morphological characters *in vivo*. Although the genus contains more than 5 000 names, very few cultures and associated DNA sequence data are available. In this study, 360 *Cercospora* isolates, obtained from 161 host species, 49 host families and 39 countries, were used to compile a molecular phylogeny. Partial sequences were derived from the internal transcribed spacer regions and intervening 5.8S nrRNA, actin, calmodulin, histone H3 and translation elongation factor 1- $\alpha$  genes. The resulting phylogenetic clades were evaluated for application of existing species names and five novel species are introduced. Eleven species are *epi*-, *lecto*- or *neotypified* in this study. Although existing species names were available for several clades, it was not always possible to apply North American or European names to African or Asian strains and *vice versa*. Some species were found to be limited to a specific host genus, whereas others were isolated from a wide host range. No single locus was found to be the ideal DNA barcode gene for the genus, and species identification needs to be based on a combination of gene loci and morphological characters. Additional primers were developed to supplement those previously published for amplification of the loci used in this study.

**Key words:** *Cercospora apii* complex, co-evolution, host jumping, host specificity, speciation.

**Taxonomic novelties:** New species - *Cercospora coniogrammes* Crous & R.G. Shivas, *Cercospora delaireae* C. Nakash., Crous, U. Braun & H.D. Shin, *Cercospora euphorbiae-sieboldianae* C. Nakash., Crous, U. Braun & H.D. Shin, *Cercospora pileicola* C. Nakash., Crous, U. Braun & H.D. Shin, *Cercospora vignigena* C. Nakash., Crous, U. Braun & H.D. Shin. **Typifications:** *epitypifications* - *Cercospora alchemillicola* U. Braun & C.F. Hill, *Cercospora althaeina* Sacc., *Cercospora armoraciae* Sacc., *Cercospora corchori* Sawada, *Cercospora mercurialis* Pass., *Cercospora olivascens* Sacc., *Cercospora violae* Sacc.; **neotypifications** - *Cercospora fagopyri* N. Nakata & S. Takim., *Cercospora sojina* Hara.

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## INTRODUCTION

Species of the genus *Cercospora* belong to one of the largest genera of hyphomycetes and were often linked to the teleomorph genus *Mycosphaerella* (*Capnodiales*, *Mycosphaerellaceae*; Stewart *et al.* 1999, Crous *et al.* 2000). The genus *Mycosphaerella* was shown to be polyphyletic (Crous *et al.* 2007), and subsequently split into numerous genera, correlating with its different anamorph states (Crous *et al.* 2009a, b). The genus *Cercospora* is now considered a holomorphic genus in its own right, with some species exhibiting the ability to form mycosphaerella-like teleomorphs (Corlett 1991, Crous *et al.* 2004b). *Mycosphaerella s. str.* on the other hand, is restricted to taxa that form *Ramularia* anamorphs (Verkley *et al.* 2004). As *Mycosphaerella* has been widely applied to more than 40 different genera, Crous *et al.* (2009b) expressed their preference to use the older, recently monographed (Braun 1998) anamorph-typified name *Ramularia* (1833) for this holomorphic clade, instead of the younger, confused teleomorph-typified generic name *Mycosphaerella* (1884). This is allowed under the new, changed Article 59 of the International Code for Nomenclature of algae, fungi, and plants (ICN) (Hawksworth 2011, Norvell 2011).

Species of *Cercospora* are commonly associated with leaf spots (Fig. 1), and have also been isolated from necrotic lesions of flowers,

fruits and seeds or were associated with postharvest fruit rot disease (Silva & Pereira 2008) of hosts from across the world (Agrios 2005, To-Anun *et al.* 2011). The cercosporoid fungi have also been used as biocontrol agents (Morris & Crous 1994, Inglis *et al.* 2001, Tessman *et al.* 2001). Species of *Cercospora* were traditionally named after the host from which they were isolated, even to the extent that a species of *Cercospora* was described as new when found on a different host plant (Chupp 1954, Ellis 1971). The genus *Cercospora* was first erected by Fresenius for passalora-like fungi with pluriseptate conidia (in Fuckel 1863). Chupp's (1954) monograph accepted 1 419 *Cercospora* species and proposed a broad concept for this genus based on whether hila were thickened or not, and whether conidia were pigmented, single or in chains. The number of *Cercospora* species doubled to more than 3 000 when Pollack (1987) published her annotated list of *Cercospora* names. Since then a combination of characters such as conidiomatal structure, mycelium, conidiophores, conidiogenous cells and conidia has been used to divide the genus into morphologically similar units. Crous & Braun (2003) used the structure of conidiogenous loci and hila as well as the absence or presence of pigmentation in conidiophores and conidia in their revision of names published in *Cercospora* and *Passalora*. They recognised 659 names in the genus *Cercospora*, with a further 281 names referred to as *C. apii s. lat.* The *C. apii* complex represented

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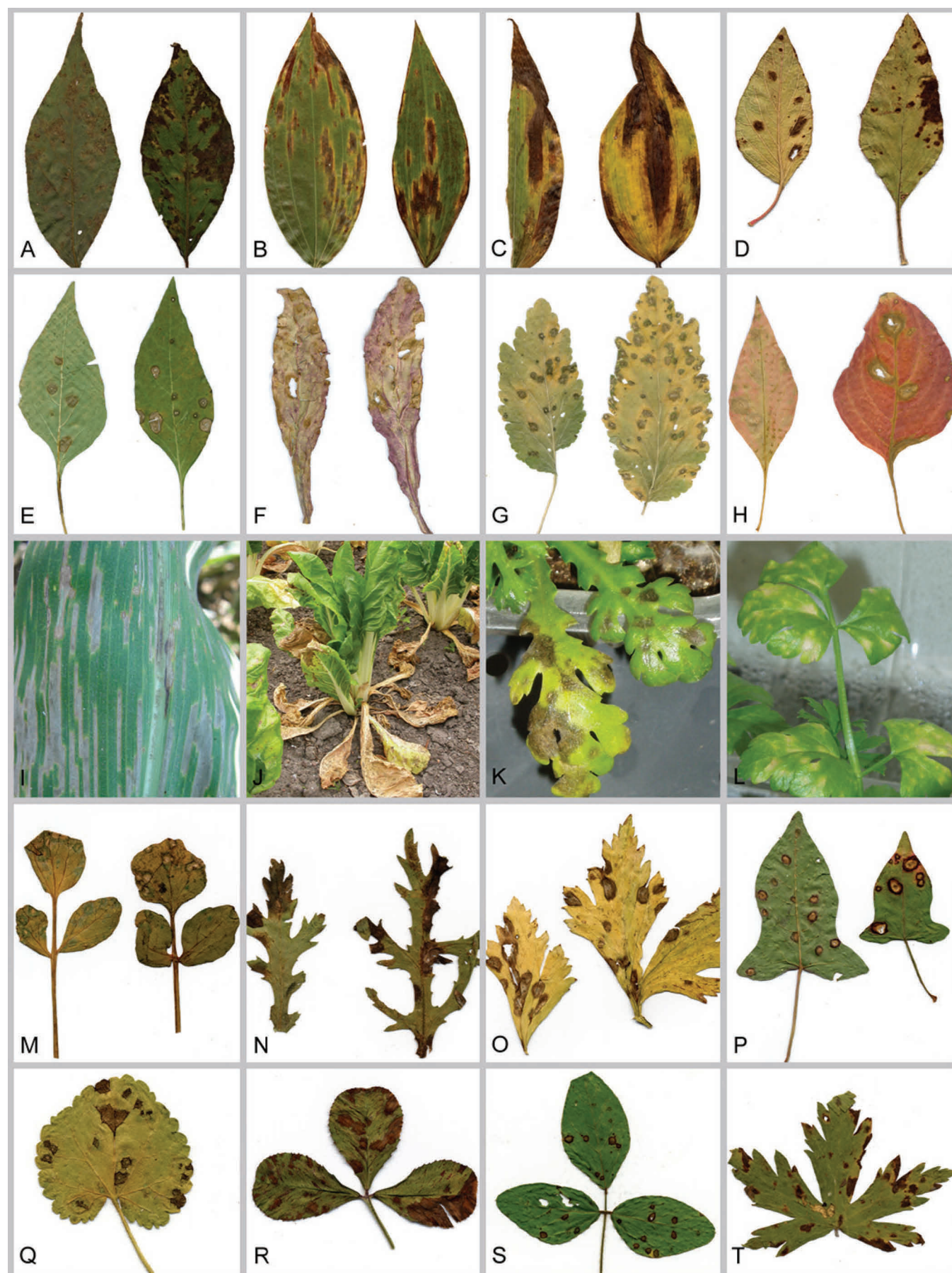
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**Fig. 1.** Foliar disease symptoms associated with *Cercospora* spp. A. *C. achyranthis* on *Achyranthes japonica*. B. *C. dispori* on *Disporum viridescens*. C. *C. chinensis* on *Polygonatum humile*. D. *C. cf. flagellaris* on *Amaranthus patulus*. E. *C. capsici* on *Capsicum annum*. F. *Cercospora* sp. on *Ajuga multiflora*. G. *Cercospora* sp. on *Cardamine leucanthae*. H. *C. cf. flagellaris* on *Celosia argentea* var. *cristata*. I. *C. zeina* on *Zea mays*. J. *C. beticola* on *Beta vulgaris*. K. *C. chrysanthemi* on *Chrysanthemum*. L. *C. apii* on *Apium*. M. *C. amoraciae* on *Rorippa indica*. N. *C. beticola* on *Chrysanthemum segetum*. O. *C. apicola* on *Apium*. P. *C. ipomoeae* on *Persicaria thunbergii*. Q. *C. althaeina* on *Althaea rosea*. R. *C. zebrina* on *Trifolium repens*. S. *C. sojae* on *Glycine max*. T. *C. brunckii* on *Geranium nepalense*.



*Cercospora* species that were morphologically indistinguishable from *C. apii* (Ellis 1971, Crous & Braun 2003). In addition, Crous & Braun (2003) introduced the concept of “compound species” which consisted of morphologically indistinguishable species with different races (host range), genetically uniform or heterogeneous, with different degrees of biological specialisation. They also proposed that genetically and morphologically clearly distinguishable taxa should be treated as separate species, although the study was confounded by the general unavailability of *Cercospora* cultures for DNA analyses. Ex-type strains mostly do not exist as such isolates were neither designated nor preserved, for the majority of *Cercospora* species (Groenewald *et al.* 2010a). For most *Cercospora* species, a sexual stage (a mycosphaerella-like state) is not known; or has been reported, but not confirmed (Goodwin *et al.* 2001). The mating type genes of some apparently asexual *Cercospora* species were recently characterised, with the discovery that *C. beticola*, *C. zeae-maydis* and *C. zeina* were heterothallic, although only one mating type was present in populations of *C. apii* and *C. apiicola* (Groenewald *et al.* 2006b, 2010b). The two mating types of *C. beticola* were distributed approximately equally in the tested populations, indicating that these genes might indeed be active, indicative of cryptic sex. More recently a skewed distribution of mating types across sugar beet fields from different localities was reported from Iran, with some fields having both mating types and others only the one or the other (Bakhshi *et al.* 2011). A further study conducted over a 3-yr period in the USA, also led to the conclusion that *C. beticola* has potential for sexual reproduction (Bolton *et al.* 2012).

Host specificity and speciation in *Cercospora* has not been studied extensively, but it is known that some species induce leaf spot symptoms when inoculated on other hosts, for example, *C. beticola* on all members of *Beta* (*Chenopodiaceae*) and other plant species (Weiland & Koch 2004) or *C. apii* and *C. beticola* isolated from disease symptoms on other hosts (Groenewald *et al.* 2006a). *Cercospora caricis* is used as a biological control agent of *Cyperus rotundus* (*Cyperaceae*), and Inglis *et al.* (2001) compared Brazilian isolates with an isolate from Florida, USA. The authors used RAPDs (Randomly Amplified Polymorphic DNA), RFLPs (Restriction Fragment Length Polymorphisms) with a telomeric probe and ITS sequencing and found that a cluster of isolates from the Brazilian cerrado region showed high genetic similarity, whereas similarity between this region and others in Brazil was less than 50 %. They also found that the ITS sequence analysis did not support a division in the Brazilian isolates (99 % similar sequences) but that it did separate the Florida isolate from the Brazilian isolates (96 % similar when included with the Brazilian isolates). They concluded that the isolate from Florida probably represented cryptic speciation but that larger sampling of isolates was required from different geographical areas to address this question. Host specificity for some species appears to operate at the strain level, as for *C. rodmanii*, in which the original strains of Conway (1976) were shown to be specific to water hyacinth, whereas strains identified by morphology and multi-locus sequence data as the same species, were able to infect beet and sugar beet (Montenegro-Calderón *et al.* 2011).

A number of molecular studies using ITS phylogenies confirmed that *Cercospora* taxa cluster in a well-supported monophyletic clade in *Mycosphaerella* (Stewart *et al.* 1999, Crous *et al.* 2000, 2009a, b, Goodwin *et al.* 2001, Pretorius *et al.* 2003), in contrast to other polyphyletic genera such as *Septoria* (Verkley *et al.* 2004; compared to the monophyletic *Zymoseptoria*, Quaedyvlieg *et al.* 2011), *Pseudocercospora*, *Passalora* and *Zasmidium* (Crous *et al.* 2009b), to name but a few. The ITS region (ITS1, 5.8S rDNA and ITS2) lacks the resolution to distinguish between most *Cercospora*

species (Groenewald *et al.* 2010a). For example, Goodwin *et al.* (2001) found a mean of 1.27 sequence changes over 18 taxa from 11 *Cercospora* species, and Pretorius *et al.* (2003) found a mean of 1.64 changes when they tested 25 taxa representing 11 *Cercospora* species. Both Goodwin *et al.* (2001) and Pretorius *et al.* (2003) observed more transitions than transversions. Only a limited number of studies utilising gene sequences other than ITS have been published thus far (for example Tessmann *et al.* 2001, Crous *et al.* 2004b, Groenewald *et al.* 2005, 2006a, 2010a, Montenegro-Calderón *et al.* 2011). Tessmann *et al.* (2001) found that 14 of the 431 aligned translation elongation factor 1- $\alpha$  characters were parsimony-informative, with only six of the 380 characters for beta-tubulin and 17 of the 309 histone H3 characters being parsimony-informative. The ITS region did not contain any differences when compared with the outgroup *C. beticola*. Crous *et al.* (2004b) used fixed nucleotide changes in aligned nucleotide characters (including alignment gaps) to discriminate *C. acaciae-mangii* from *C. apii* and *C. beticola*, and listed changes at none of 521 ITS characters (0 %), nine of 300 translation elongation factor 1- $\alpha$  characters (3 %), three of 209 actin characters (1.4 %), 10 of 312 calmodulin characters (3.2 %), and seven of 388 histone H3 characters (1.8 %). A total of 1 730 aligned characters were examined, of which 29 (1.68 %) were observed as fixed nucleotide changes. Using the same five loci, Groenewald *et al.* (2005) found 96 % similarity between *C. apii* and *C. beticola* for the calmodulin gene, with all other loci having identical sequences. Based on the differences in the calmodulin gene, distinctive AFLP banding patterns and different growth rates, the authors recognised *C. apii* s. str. and *C. beticola* s. str. as distinct species. Continuing with the same approach, Groenewald *et al.* (2006a) then proceeded to describe *C. apiicola*, a further distinct species thus far only isolated from *Apium* (*Apiaceae*). Both Groenewald *et al.* (2010a) and Montenegro-Calderón *et al.* (2011) used phylogenetic analyses of combined ITS, translation elongation factor 1- $\alpha$ , actin, calmodulin and histone H3 sequence alignments to study species boundaries and diversity in *Cercospora*. Groenewald *et al.* (2010a) concluded that although most loci tested could resolve a large number of species, the sum of the whole provided a better resolution compared to a subset of loci. In that study, the loci differed in their ability to resolve clades, with ITS and translation elongation factor 1- $\alpha$  performing worst (distinguishing three and 10 clades, respectively), while actin could distinguish 14 clades, calmodulin 13 clades and histone H3 12 clades compared to the 16 species clades recognised in the combined tree. Montenegro-Calderón *et al.* (2011) concluded that *C. rodmanii* could be distinguished from *C. piaropi* based on actin, calmodulin and histone H3, but that only calmodulin could clearly separate *C. rodmanii* from the other *Cercospora* species included in their study. These results illustrated that the phylogenetic approach using multi-locus sequences was one of the most effective ways to recognise different species of *Cercospora*. Although this approach is not suitable to recognise the true host range of a species without pathogenicity tests, it does provide a handle on the true identity of the strain being used.

Goodwin *et al.* (2001) attributed the short branch lengths observed for their ITS phylogeny to a relatively recent common ancestor that was able to, or acquired the ability to, produce cercosporin, a phytotoxic metabolite of polyketide origin (Daub & Ehrenschaft 2000). The ability to produce cercosporin probably allowed the *Cercospora* ancestor to rapidly expand its host range in a recent adaptive radiation (Goodwin *et al.* 2001). It has been suggested that this compound may enhance virulence (Upchurch *et al.* 1991), but it is not a universal pathogenicity factor as

**Table 1.** Collection details and GenBank accession numbers of isolates included in this study.

Species	Culture accession number(s) <sup>1</sup>	Host name or isolation source	Host Family	Country	Collector	GenBank accession numbers <sup>2</sup>				
						ITS	TEF	ACT	CAL	HIS
<i>Cercospora achyranthis</i>	CBS 132613; CPC 10879	<i>Achyranthes japonica</i>	Amaranthaceae	South Korea: Jeju	H.D. Shin	JX143523	JX143277	JX143031	JX142785	JX142539
	CPC 10091	<i>Achyranthes japonica</i>	Amaranthaceae	South Korea: Jeju	H.D. Shin	JX143524	JX143278	JX143032	JX142786	JX142540
<i>Cercospora agavicola</i>	CBS 117292; CPC 11774 (TYPE)	<i>Agave tequilana</i> var. <i>azul</i>	Agavaceae	Mexico: Penjamo	V. Ayala-Escobar & Ma. de Jesús Yáñez-Morales	AY647237	AY966897	AY966898	AY966899	AY966900
<i>Cercospora alchemillicola</i>	CPC 5259 (TYPE)	<i>Alchemilla mollis</i>	Rosaceae	New Zealand: Auckland	C.F. Hill	JX143525	JX143279	JX143033	JX142787	JX142541
<i>Cercospora cf. alchemillicola</i>	CPC 5126	<i>Oenothera fruticosa</i>	Onagraceae	New Zealand: Auckland	C.F. Hill	JX143526	JX143280	JX143034	JX142788	JX142542
	CPC 5127	<i>Gaura lindheimeri</i>	Onagraceae	New Zealand: Auckland	C.F. Hill	JX143527	JX143281	JX143035	JX142789	JX142543
<i>Cercospora althaeina</i>	CBS 12626; CPC 5066	<i>Malva</i> sp.	Malvaceae	—	C. Killian	JX143528	JX143282	JX143036	JX142790	JX142544
	CBS 132609; CPC 10790	<i>Althaea rosea</i>	Malvaceae	South Korea: Suwon	H.D. Shin	JX143529	JX143283	JX143037	JX142791	JX142545
	CBS 24867; CPC 5117 (TYPE)	<i>Althaea rosea</i>	Malvaceae	Romania: Fundulea	O. Constantinescu	JX143530	JX143284	JX143038	JX142792	JX142546
<i>Cercospora apii</i>	CBS 110813; CPC 5110; 01-3	<i>Moluccella laevis</i>	Lamiaceae	USA: California	S.T. Koike	AY156918	DQ233345	DQ233371	DQ233397	DQ233423
	CBS 110816; CPC 5111; 01-4	<i>Moluccella laevis</i>	Lamiaceae	USA: California	S.T. Koike	AY156919	DQ233346	DQ233372	DQ233398	DQ233424
	CBS 114416; CPC 10925	<i>Apium</i> sp.	Apiaceae	Austria	Institut für Pflanzengesundheit	AY840516	AY840483	AY840447	AY840414	AY840381
	CBS 114418; CPC 10924	<i>Apium graveolens</i>	Apiaceae	Italy	M. Meutri	AY840517	AY840484	AY840448	AY840415	AY840382
	CBS 114485; CPC 10923	<i>Apium graveolens</i>	Apiaceae	Italy	M. Meutri	AY840518	AY840485	AY840449	AY840416	AY840383
	CBS 116455; CPC 11556 (TYPE)	<i>Apium graveolens</i>	Apiaceae	Germany: Heilbron	K. Schrameyer	AY840519	AY840486	AY840450	AY840417	AY840384
	CBS 116504; CPC 11579	<i>Apium graveolens</i>	Apiaceae	Germany: Heilbron	K. Schrameyer	AY840520	AY840487	AY840451	AY840418	AY840385
	CBS 116507; CPC 11582	<i>Apium graveolens</i>	Apiaceae	Germany: Heilbron	K. Schrameyer	AY840521	AY840488	AY840452	AY840419	AY840386
	CBS 11925; B 42463; IHEM 3822; CPC 5086	<i>Apium graveolens</i>	Apiaceae	—	L. J. Klotz	AY179949	AY179915	AY840443	AY840410	AY840377
	CBS 12131; CPC 5073	<i>Beta vulgaris</i>	Chenopodiaceae	Austria: Wien	E.W. Schmidt	AY343371	AY343334	AY840444	AY840411	AY840378
	CBS 12731; CPC 5119	<i>Beta vulgaris</i>	Chenopodiaceae	Hungary	E.W. Schmidt	AY840514	AY840481	AY840445	AY840412	AY840379
	CBS 132683; CPC 16663	<i>Moluccella laevis</i>	Lamiaceae	Zimbabwe	S. Dimbi	JX143531	JX143285	JX143039	JX142793	JX142547
	CBS 15252; IMI 077043; MUCL 16495; CPC 5063	<i>Beta vulgaris</i>	Chenopodiaceae	Netherlands: Bergen op Zoom	G. van den Ende	AY840515	AY840482	AY840446	AY840413	AY840380
	CBS 25267; CPC 5084	<i>Plantago lanceolata</i>	Plantaginaceae	Romania: Domnesti	O. Constantinescu	DQ233318	DQ233342	DQ233368	DQ233394	DQ233420
	CBS 536.71; CPC 5087	<i>Apium graveolens</i>	Apiaceae	Romania: Bucuresti	O. Constantinescu	AY752133	AY752166	AY752194	AY752225	AY752256
	CBS 553.71; IMI 161116; CPC 5083	<i>Plumbago europaea</i>	Plumbaginaceae	Romania: Hagieni	O. Constantinescu	DQ233320	DQ233344	DQ233370	DQ233396	DQ233422
	CPC 18601	<i>Apium graveolens</i>	Apiaceae	USA: California	S.T. Koike	JX143532	JX143286	JX143040	JX142794	JX142548
	CPC 5112	<i>Moluccella laevis</i>	Lamiaceae	New Zealand: Auckland	C.F. Hill	DQ233321	DQ233347	DQ233373	DQ233399	DQ233425
	CPC 5260	<i>Glebionis coronaria</i> (= <i>Chrysanthemum coronarium</i> )	Asteraceae	New Zealand: Auckland	C.F. Hill	JX143533	JX143287	JX143041	JX142795	JX142549
	MUCC 567; MUCNS 30; MAFF 238072	<i>Apium graveolens</i>	Apiaceae	Japan: Aichi	T. Kobayashi	JX143534	JX143288	JX143042	JX142796	JX142550

Table 1. (Continued).

Species	Culture accession number(s) <sup>1</sup>	Host name or isolation source	Host Family	Country	Collector	GenBank accession numbers <sup>2</sup>				
						ITS	TEF	ACT	CAL	HIS
<i>Cercospora apicola</i>	MUCC 573; MAFF 235978	<i>Glebionis coronaria</i> (= <i>Chrysanthemum coronarium</i> )	Asteraceae	Japan: Hokkaido	—	JX143535	JX143289	JX143043	JX142797	JX142551
	MUCC 593	<i>Apium graveolens</i>	Apiaceae	Japan: Shizuoka	M. Togawa	JX143536	JX143290	JX143044	JX142798	JX142552
	MUCC 923; MAFF 238299	<i>Asparagus officinalis</i>	Asparagaceae	Japan: Saga	J. Yamaguchi	JX143537	JX143291	JX143045	JX142799	JX142553
	CBS 116457; CPC 10267 (TYPE)	<i>Apium</i> sp.	Apiaceae	Venezuela: Caripe	N. Pons	AY840536	AY840503	AY840467	AY840434	AY840401
	CBS 116458; CPC 10657	<i>Apium graveolens</i>	Apiaceae	South Korea: Kangnung	H.D. Shin	AY840537	AY840504	AY840468	AY840435	AY840402
	CBS 132644; CPC 10248	<i>Apium</i> sp.	Apiaceae	Venezuela: Caripe	N. Pons	AY840539	AY840506	AY840470	AY840437	AY840404
	CBS 132651; CPC 10759	<i>Apium graveolens</i>	Apiaceae	South Korea: Namyangju	H.D. Shin	AY840544	AY840511	AY840475	AY840442	AY840409
	CBS 132666; CPC 11642; GRE-4-2	<i>Apium</i> sp.	Apiaceae	Greece	I. Vlioutoglou	DQ233341	DQ233367	DQ233393	DQ233419	DQ233441
	CPC 10220	<i>Apium</i> sp.	Apiaceae	Venezuela: Caripe	N. Pons	AY840538	AY840505	AY840469	AY840436	AY840403
	CPC 10265	<i>Apium</i> sp.	Apiaceae	Venezuela: Caripe	N. Pons	AY840540	AY840507	AY840471	AY840438	AY840405
	CPC 10266	<i>Apium</i> sp.	Apiaceae	Venezuela: Caripe	N. Pons	AY840541	AY840508	AY840472	AY840439	AY840406
	CPC 10279	<i>Apium</i> sp.	Apiaceae	Venezuela: Caripe	N. Pons	AY840542	AY840509	AY840473	AY840440	AY840407
	CPC 10666	<i>Apium</i> sp.	Apiaceae	South Korea: Kangnung	H.D. Shin	AY840543	AY840510	AY840474	AY840441	AY840408
	CPC 11641; GRE-3-2	<i>Apium</i> sp.	Apiaceae	Greece	I. Vlioutoglou	DQ233340	DQ233366	DQ233392	DQ233418	DQ233440
	CBS 115060; CPC 5366	<i>Gaura</i> sp.	Onagraceae	New Zealand	C.F. Hill	JX143538	JX143292	JX143046	JX142800	JX142554
CBS 115394; CPC 5261	<i>Nasturtium officinale</i> (= <i>Rorippa nasturtium-aquaticum</i> )	Brassicaceae	New Zealand: Auckland	C.F. Hill	JX143539	JX143293	JX143047	JX142801	JX142555	
<i>Cercospora amoraciae</i>	CBS 115409; CPC 5359	<i>Armoracia rusticana</i> (= <i>A. lapathifolia</i> )	Brassicaceae	New Zealand: Manurewa	C.F. Hill	JX143540	JX143294	JX143048	JX142802	JX142556
	CBS 132610; CPC 10811	<i>Armoracia rusticana</i> (= <i>A. lapathifolia</i> )	Brassicaceae	South Korea: Suwon	H.D. Shin	JX143541	JX143295	JX143049	JX142803	JX142557
	CBS 132638; CPC 10100	<i>Barbarea orthoceras</i>	Brassicaceae	South Korea: Pocheon	H.D. Shin	JX143542	JX143296	JX143050	JX142804	JX142558
	CBS 132654; CPC 11338	<i>Turritis glabra</i> (= <i>Arabis glabra</i> )	Brassicaceae	South Korea: Hoengseong	H.D. Shin	JX143543	JX143297	JX143051	JX142805	JX142559
	CBS 132672; CPC 14612	<i>Rorippa indica</i>	Brassicaceae	South Korea: Jecheon	H.D. Shin	JX143544	JX143298	JX143052	JX142806	JX142560
	CBS 250.67; CPC 5088 (TYPE)	<i>Armoracia rusticana</i> (= <i>A. lapathifolia</i> )	Brassicaceae	Romania: Fundulea	O. Constantinescu	JX143545	JX143299	JX143053	JX142807	JX142561
	CBS 258.67; CPC 5061	<i>Cardaria draba</i>	Brassicaceae	Romania: Fundulea	O. Constantinescu	JX143546	JX143300	JX143054	JX142808	JX142562
	CBS 538.71; IMI 161109; CPC 5090	<i>Berteroa incana</i>	Brassicaceae	Romania: Hagieni	O. Constantinescu	JX143547	JX143301	JX143055	JX142809	JX142563
	CBS 540.71; IMI 161110; CPC 5060	<i>Cardaria draba</i>	Brassicaceae	Romania: Hagieni	O. Constantinescu	JX143548	JX143302	JX143056	JX142810	JX142564
	CBS 545.71; CPC 5056	<i>Erysimum cuspidatum</i>	Brassicaceae	Romania: Valea Mraconiei	O. Constantinescu	JX143549	JX143303	JX143057	JX142811	JX142565
	CBS 555.71; IMI 161117; CPC 5082	<i>Coronilla varia</i>	Fabaceae	Romania: Hagieni	O. Constantinescu	JX143550	JX143304	JX143058	JX142812	JX142566
	CPC 10133	<i>Rorippa indica</i>	Brassicaceae	South Korea: Wonju	H.D. Shin	JX143551	JX143305	JX143059	JX142813	JX142567
	CPC 11364	<i>Turritis glabra</i> (= <i>Arabis glabra</i> )	Brassicaceae	South Korea: Hoengseong	H.D. Shin	JX143552	JX143306	JX143060	JX142814	JX142568
	CPC 11530	<i>Acacia mangium</i>	Fabaceae	Thailand	W. Himaman	JX143553	JX143307	JX143061	JX142815	JX142569
	MUCC 768	<i>Armoracia rusticana</i> (= <i>A. lapathifolia</i> )	Brassicaceae	Japan: Okinawa	C. Nakashima	JX143554	JX143308	JX143062	JX142816	JX142570

Table 1. (Continued).

Species	Culture accession number(s) <sup>1</sup>	Host name or isolation source	Host Family	Country	Collector	GenBank accession numbers <sup>2</sup>				
						ITS	TEF	ACT	CAL	HIS
<i>Cercospora bellicola</i>	CBS 113069; CPC 5369	<i>Spinacia</i> sp.	Chenopodiaceae	Botswana: Gaborone	L. Lebogang	DQ233325	DQ233351	DQ233377	DQ233403	DQ233429
	CBS 115478; CPC 5113	<i>Limonium sinuatum</i>	Plumbaginaceae	New Zealand: Auckland	C.F. Hill	DQ233326	DQ233352	DQ233378	DQ233404	DQ233430
	CBS 11647; CPC 5074	<i>Beta vulgaris</i>	Chenopodiaceae	Netherlands: Northwest Brabant	G.E. Bunschoten	AY752135	AY752168	AY752196	AY752227	AY752258
	CBS 116454; CPC 11558	<i>Beta vulgaris</i>	Chenopodiaceae	Germany	S. Mittler	AY840526	AY840493	AY840457	AY840424	AY840391
	CBS 116456; CPC 11557 (TYPE)	<i>Beta vulgaris</i>	Chenopodiaceae	Italy: Ravenna	V. Rossi	AY840527	AY840494	AY840458	AY840425	AY840392
	CBS 116501; CPC 11576	<i>Beta vulgaris</i>	Chenopodiaceae	Iran: Pakajik	A.A. Ravanlou	AY840528	AY840495	AY840459	AY840426	AY840393
	CBS 116502; CPC 11577	<i>Beta vulgaris</i>	Chenopodiaceae	Germany	S. Mittler	AY840529	AY840496	AY840460	AY840427	AY840394
	CBS 116503; CPC 11578	<i>Beta vulgaris</i>	Chenopodiaceae	Italy: Ravenna	V. Rossi	AY840530	AY840497	AY840461	AY840428	AY840395
	CBS 116505; CPC 11580	<i>Beta vulgaris</i>	Chenopodiaceae	France: Longvic	S. Garressus	AY840531	AY840498	AY840462	AY840429	AY840396
	CBS 116506; CPC 11581	<i>Beta vulgaris</i>	Chenopodiaceae	Netherlands	M. Groenewald	AY840532	AY840499	AY840463	AY840430	AY840397
	CBS 11747	<i>Beta vulgaris</i>	Chenopodiaceae	Czech Republic	G.E. Bunschoten	DQ233322	DQ233348	DQ233374	DQ233400	DQ233426
	CBS 117556; CPC 10171	<i>Beta vulgaris</i>	Chenopodiaceae	New Zealand: Auckland	C.F. Hill	AY840534	AY840501	AY840465	AY840432	AY840399
	CBS 12231; CPC 5072	<i>Beta vulgaris</i>	Chenopodiaceae	Germany: Gmain	E.W. Schmidt	AY752136	AY752169	AY752197	AY752228	AY752259
	CBS 12331; CPC 5071	<i>Beta vulgaris</i>	Chenopodiaceae	Spain	E.W. Schmidt	AY840522	AY840489	AY840453	AY840420	AY840387
	CBS 123907; CPC 14616	<i>Goniolimon tataricum</i>	Plumbaginaceae	Bulgaria	S.G. Bobev	FJ473422	FJ473427	FJ473432	FJ473437	FJ473442
	CBS 123908; CPC 14620	<i>Goniolimon tataricum</i>	Plumbaginaceae	Bulgaria	S.G. Bobev	FJ473426	FJ473431	FJ473436	FJ473441	FJ473446
	CBS 12431; CPC 5070	<i>Beta vulgaris</i>	Chenopodiaceae	Romania: Hagieni	E.W. Schmidt	AY840523	AY840490	AY840454	AY840421	AY840388
	CBS 12531; CPC 5069	<i>Beta vulgaris</i>	Chenopodiaceae	—	E.W. Schmidt	AY840524	AY840491	AY840455	AY840422	AY840389
	CBS 12631; CPC 5064	<i>Beta vulgaris</i>	Chenopodiaceae	Germany: Klein Wanzleben	E.W. Schmidt	AY840525	AY840492	AY840456	AY840423	AY840390
<i>Chrysanthemum segetum</i> (= <i>Ch. coronarium</i> var. <i>spatiosum</i> )	CBS 132655; CPC 11341	<i>Chrysanthemum segetum</i> (= <i>Ch. coronarium</i> var. <i>spatiosum</i> )	Asteraceae	South Korea: Namyangju	H.D. Shin	DQ233332	DQ233358	DQ233384	DQ233410	DQ233434
	CBS 132673; CPC 14617	<i>Goniolimon tataricum</i>	Plumbaginaceae	Bulgaria	S.G. Bobev	FJ473423	FJ473428	FJ473433	FJ473438	FJ473443
	CBS 539.71; CPC 5062	<i>Beta vulgaris</i>	Chenopodiaceae	Romania: Bucuresti	O. Constantinescu	DQ233323	DQ233349	DQ233375	DQ233401	DQ233427
	CBS 548.71; IMI 161115; CPC 5065	<i>Malva pusilla</i>	Malvaceae	Romania: Hagieni	O. Constantinescu & G. Negrean	DQ233324	DQ233350	DQ233376	DQ233402	DQ233428
	CPC 10166	<i>Beta vulgaris</i>	Chenopodiaceae	New Zealand	C.F. Hill	DQ233329	DQ233355	DQ233381	DQ233407	DQ26471
	CPC 10168	<i>Beta vulgaris</i>	Chenopodiaceae	New Zealand: Auckland	C.F. Hill	AY840533	AY840500	AY840464	AY840431	AY840398
	CPC 10195	<i>Beta vulgaris</i>	Chenopodiaceae	New Zealand	C.F. Hill	DQ233330	DQ233356	DQ233382	DQ233408	DQ26472
	CPC 10197	<i>Beta vulgaris</i>	Chenopodiaceae	New Zealand: Auckland	C.F. Hill	AY840535	AY840502	AY840466	AY840433	AY840400
	CPC 10204	<i>Beta vulgaris</i>	Chenopodiaceae	New Zealand: Auckland	C.F. Hill	DQ233331	DQ233357	DQ233383	DQ233409	DQ233433
	CPC 11344	<i>Chrysanthemum segetum</i> (= <i>Ch. coronarium</i> var. <i>spatiosum</i> )	Asteraceae	South Korea: Namyangju	H.D. Shin	DQ233333	DQ233359	DQ233385	DQ233411	DQ233435



Table 1. (Continued).

Species	Culture accession number(s) <sup>1</sup>	Host name or isolation source	Host Family	Country	Collector	GenBank accession numbers <sup>2</sup>				
						ITS	TEF	ACT	CAL	HIS
<i>Cercospora cf. brunkii</i>	CPC 12022	<i>Beta vulgaris</i>	Chenopodiaceae	Germany	S. Mittler	DQ233334	DQ233360	DQ233386	DQ233412	DQ233436
	CPC 12027	<i>Beta vulgaris</i>	Chenopodiaceae	Germany	S. Mittler	DQ233335	DQ233361	DQ233387	DQ233413	DQ026468
	CPC 12028	<i>Beta vulgaris</i>	Chenopodiaceae	Egypt	M. Hasem	DQ233336	DQ233362	DQ233388	DQ233414	DQ233437
	CPC 12029	<i>Beta vulgaris</i>	Chenopodiaceae	Egypt	M. Hasem	DQ233337	DQ233363	DQ233389	DQ233415	DQ233438
	CPC 12030	<i>Beta vulgaris</i>	Chenopodiaceae	Egypt	M. Hasem	DQ233338	DQ233364	DQ233390	DQ233416	DQ233439
	CPC 12031	<i>Beta vulgaris</i>	Chenopodiaceae	Germany	S. Mittler	DQ233339	DQ233365	DQ233391	DQ233417	DQ026470
	CPC 14618	<i>Goniolimon tataricum</i>	Plumbaginaceae	Bulgaria	S.G. Bobev	FJ473424	FJ473429	FJ473434	FJ473439	FJ473444
	CPC 14619	<i>Goniolimon tataricum</i>	Plumbaginaceae	Bulgaria	S.G. Bobev	FJ473425	FJ473430	FJ473435	FJ473440	FJ473445
	CPC 15623	<i>Beta vulgaris</i>	Chenopodiaceae	Mexico: Texcoco	Ma. de Jesús Yáñez-Morales	JX143555	JX143309	JX143063	JX142817	JX142571
	CPC 18813	<i>Beta vulgaris</i>	Chenopodiaceae	USA: California	S.T. Koike	JX143556	JX143310	JX143064	JX142818	JX142572
	CPC 5123	<i>Apium graveolens</i>	Apiaceae	New Zealand: Auckland	C.F. Hill	AY752134	AY752167	AY752195	AY752226	AY752257
	CPC 5125	<i>Beta vulgaris</i>	Chenopodiaceae	New Zealand: Auckland	C.F. Hill	AY752137	AY752170	AY752198	AY752229	AY752260
	CPC 5128	<i>Beta vulgaris</i>	Chenopodiaceae	New Zealand: Auckland	C.F. Hill	AY752138	AY752171	AY752199	AY752230	AY752261
	CPC 5370	<i>Spinacia</i> sp.	Chenopodiaceae	Botswana: Gaborone	L. Lebogang	DQ233328	DQ233354	DQ233380	DQ233406	DQ233432
	MUCC 568; MUCNS 320; MAFF 238206	<i>Beta vulgaris</i>	Chenopodiaceae	Japan: Chiba	S. Uematsu	JX143557	JX143311	JX143065	JX142819	JX142573
<i>Cercospora campisilii</i>	MUCC 569; MAFF 305036	<i>Beta vulgaris</i>	Chenopodiaceae	Japan: Hokkaido	K. Goto	JX143558	JX143312	JX143066	JX142820	JX142574
	CBS 132657; CPC 11598	<i>Geranium thunbergii</i> (= <i>G. nepalense</i> var. <i>thunbergii</i> )	Geraniaceae	South Korea: Namyangju	H.D. Shin	JX143559	JX143313	JX143067	JX142821	JX142575
<i>Cercospora canescens</i> complex	MUCC 732	<i>Datura stramonium</i>	Solanaceae	Japan: Wakayama	C. Nakashima & I. Araki	JX143560	JX143314	JX143068	JX142822	JX142576
	CBS 132625; CPC 14585	<i>Impatiens noli-tangere</i>	Balsaminaceae	South Korea: Inje	H.D. Shin	JX143561	JX143315	JX143069	JX142823	JX142577
<i>Cercospora capsici</i>	CBS 111133; CPC 1137	<i>Vigna</i> sp.	Fabaceae	South Africa: Potchefstroom	S. van Wyk	AY260065	DQ835084	DQ835103	DQ835130	DQ835157
	CBS 111134; CPC 1138	<i>Vigna</i> sp.	Fabaceae	South Africa: Potchefstroom	S. van Wyk	AY260066	DQ835085	DQ835104	DQ835131	DQ835158
	CBS 132658; CPC 11626; GHA-1-0	<i>Dioscorea rotundata</i>	Dioscoreaceae	Ghana	S. Nyako & A.O. Danquah	JX143562	JX143316	JX143070	JX142824	JX142578
	CBS 132659; CPC 11627; GHA-1-1	<i>Dioscorea alata</i>	Dioscoreaceae	Ghana	S. Nyako & A.O. Danquah	JX143563	JX143317	JX143071	JX142825	JX142579
	CBS 153.55; CPC 5059	<i>Phaseolus lunatus</i> (= <i>Ph. limensis</i> )	Fabaceae	USA: Georgia	E.S. Luttrell	JX143564	JX143318	JX143072	JX142826	JX142580
<i>Cercospora capsici</i>	CPC 11628; GHA-2-1	<i>Dioscorea rotundata</i>	Dioscoreaceae	Ghana	S. Nyako & A.O. Danquah	JX143565	JX143319	JX143073	JX142827	JX142581
	CPC 11640; IMI 186563	<i>Apium</i> sp.	Apiaceae	USA	—	JX143566	JX143320	JX143074	JX142828	JX142582
	CPC 15871	—	Malvaceae	Mexico: Tamaulipas	Ma. de Jesús Yáñez-Morales	JX143567	JX143321	JX143075	JX142829	JX142583
	CPC 4408; Q 160 IS2	<i>Citrus maxima</i>	Rutaceae	South Africa: Tspise	K. Serfontein	AY260067	DQ835086	DQ835105	DQ835132	DQ835159
	CPC 4409	<i>Citrus maxima</i>	Rutaceae	South Africa: Tspise	K. Serfontein	AY260068	DQ835087	DQ835106	DQ835133	DQ835160
	CBS 118712	Lesions on calyx attached to fruit	—	Fiji	P. Tyler	GU214653	JX143322	JX143076	JX142830	JX142584

Table 1. (Continued).

Species	Culture accession number(s) <sup>1</sup>	Host name or isolation source	Host Family	Country	Collector	GenBank accession numbers <sup>2</sup>				
						ITS	TEF	ACT	CAL	HIS
<i>Cercospora celosiae</i>	CBS 132622; CPC 14520	<i>Capsicum annuum</i>	<i>Solanaceae</i>	South Korea: Yanggu	H.D. Shin	JX143568	JX143323	JX143077	JX142831	JX142585
	CPC 12307	<i>Capsicum annuum</i>	<i>Solanaceae</i>	South Korea: Hongcheon	H.D. Shin	GU214654	JX143324	JX143078	JX142832	JX142586
	MUCC 574; MUCNS 810; MAFF 238227	<i>Capsicum annuum</i>	<i>Solanaceae</i>	Japan: Chiba	S. Uematsu	JX143569	JX143325	JX143079	JX142833	JX142587
<i>Cercospora celosiae</i>	CBS 132600; CPC 10660	<i>Celosia argentea</i> var. <i>cristata</i> (= <i>C. cristata</i> )	<i>Amaranthaceae</i>	South Korea: Chuncheon	H.D. Shin	JX143570	JX143326	JX143080	JX142834	JX142588
<i>Cercospora chenopodii</i>	CBS 132620; CPC 14237	<i>Chenopodium</i> cf. <i>album</i>	<i>Chenopodiaceae</i>	France: Ardeche	P.W. Crous	JX143571	JX143327	JX143081	JX142835	JX142589
<i>Cercospora</i> cf. <i>chenopodii</i>	CBS 132594; CPC 10304 (TYPE)	<i>Chenopodium ficifolium</i>	<i>Chenopodiaceae</i>	South Korea: Hongcheon	H.D. Shin	JX143572	JX143328	JX143082	JX142836	JX142590
	CBS 132677; CPC 15599	<i>Chenopodium</i> sp.	<i>Chenopodiaceae</i>	Mexico: Montecillo	Ma. de Jesús Yáñez-Morales	JX143573	JX143329	JX143083	JX142837	JX142591
	CPC 12450	<i>Chenopodium ficifolium</i>	<i>Chenopodiaceae</i>	South Korea: Hongcheon	H.D. Shin	JX143574	JX143330	JX143084	JX142838	JX142592
<i>Cercospora chinensis</i>	CPC 15763	<i>Chenopodium</i> sp.	<i>Chenopodiaceae</i>	Mexico: Montecillo	Ma. de Jesús Yáñez-Morales	JX143575	JX143331	JX143085	JX142839	JX142593
	CPC 15859	<i>Chenopodium</i> sp.	<i>Chenopodiaceae</i>	Mexico: Purificacion	Ma. de Jesús Yáñez-Morales	JX143576	JX143332	JX143086	JX142840	JX142594
	CPC 15862	<i>Chenopodium</i> sp.	<i>Chenopodiaceae</i>	Mexico: Purificacion	Ma. de Jesús Yáñez-Morales	JX143577	JX143333	JX143087	JX142841	JX142595
	CBS 132612; CPC 10831	<i>Polygonatum humile</i>	<i>Convallariaceae</i>	South Korea: Pyeongchang	H.D. Shin	JX143578	JX143334	JX143088	JX142842	JX142596
	CBS 119395; CPC 12682	<i>Musa</i> sp.	<i>Musaceae</i>	Bangladesh: Western	I. Buddenhagen	EU514222	JX143335	JX143089	JX142843	JX142597
	CBS 132669; CPC 12683	<i>Musa</i> sp.	<i>Musaceae</i>	Bangladesh: Western	I. Buddenhagen	EU514223	JX143336	JX143090	JX142844	JX142598
	MUCC 576; MUCNS 300; MAFF 237913	<i>Citullus lanatus</i>	<i>Cucurbitaceae</i>	Japan: Okinawa	T. Kobayashion <i>et al.</i>	JX143579	JX143337	JX143091	JX142845	JX142599
<i>Cercospora conioagrammes</i>	MUCC 577; MUCNS 254; MAFF 238205	<i>Momordica charantia</i>	<i>Cucurbitaceae</i>	Japan: Kagoshima	E. Imaizumi & C. Nomi	JX143580	JX143338	JX143092	JX142846	JX142600
<i>Cercospora conioagrammes</i>	MUCC 584; MAFF 305757	<i>Psophocarpus tetragonolobus</i>	<i>Fabaceae</i>	Japan: Okinawa	—	JX143581	JX143339	JX143093	JX142847	JX142601
	MUCC 588; MAFF 239409	<i>Ipomoea pes-caprae</i>	<i>Convolvulaceae</i>	Japan: Okinawa	—	JX143582	JX143340	JX143094	JX142848	JX142602
	CBS 132634; CPC 17017 (TYPE)	<i>Coniogramme japonica</i> var. <i>gracilis</i> (= <i>C. gracilis</i> )	<i>Adiantaceae</i>	Australia: Queensland	P.W. Crous	JX143583	JX143341	JX143095	JX142849	JX142603
<i>Cercospora corchori</i>	MUCC 585; MUCNS 72; MAFF 238191 (TYPE)	<i>Corchorus olitorius</i>	<i>Tiliaceae</i>	Japan: Shimane	T. Mikami	JX143584	JX143342	JX143096	JX142850	JX142604
<i>Cercospora</i> cf. <i>coreopsidis</i>	CBS 132598; CPC 10648	<i>Coreopsis lanceolata</i>	<i>Asteraceae</i>	South Korea: Seoul	H.D. Shin	JX143585	JX143343	JX143097	JX142851	JX142605
	CPC 10122	<i>Coreopsis lanceolata</i>	<i>Asteraceae</i>	South Korea: Wonju	H.D. Shin	JX143586	JX143344	JX143098	JX142852	JX142606
<i>Cercospora delaireae</i>	CBS 132595; CPC 10455; GV2 PPRI number: C558 (TYPE)	<i>Delairea odorata</i> (= <i>Senecio mikanioides</i> )	<i>Asteraceae</i>	South Africa: Long Tom Pass	S. Naser	JX143587	JX143345	JX143099	JX142853	JX142607
	CPC 10627	<i>Delairea odorata</i> (= <i>Senecio mikanioides</i> )	<i>Asteraceae</i>	South Africa: Plettenberg Bay	C.L. Lennox	JX143588	JX143346	JX143100	JX142854	JX142608
	CPC 10628	<i>Delairea odorata</i> (= <i>Senecio mikanioides</i> )	<i>Asteraceae</i>	South Africa: Plettenberg Bay	C.L. Lennox	JX143589	JX143347	JX143101	JX142855	JX142609

Table 1. (Continued).

Species	Culture accession number(s) <sup>1</sup>	Host name or isolation source	Host Family	Country	Collector	GenBank accession numbers <sup>2</sup>			
						ITS	TEF	ACT	CAL HIS
<i>Cercospora dispersi</i>	CPC 10629	<i>Delairea odorata</i> (= <i>Senecio mikanioides</i> )	Asteraceae	South Africa: Plettenberg Bay	C.L. Lennox	JX143590	JX143348	JX143102	JX142856 JX142610
	CBS 132608; CPC 10773	<i>Disporum viridescens</i>	Convallariaceae	South Korea: Pyeongchang	H.D. Shin	JX143591	JX143349	JX143103	JX142857 JX142611
<i>Cercospora cf. erysimi</i>	CBS 115059; CPC 5361	<i>Erysimum mutabile</i>	Brassicaceae	New Zealand: Manurewa	C.F. Hill	JX143592	JX143350	JX143104	JX142858 JX142612
<i>Cercospora euphorbiae-sieboldianae</i>	CBS 113306 (TYPE)	<i>Euphorbia sieboldiana</i>	Euphorbiaceae	South Korea: Samcheok	H.D. Shin	JX143593	JX143351	JX143105	JX142859 JX142613
<i>Cercospora fagopyri</i>	CBS 132623; CPC 14541 (TYPE)	<i>Fagopyrum esculentum</i>	Polygonaceae	South Korea: Yangpyeong	H.D. Shin	JX143594	JX143352	JX143106	JX142860 JX142614
	CBS 132640; CPC 10109	<i>Fallopia dumetorum</i>	Polygonaceae	South Korea: Yangpyeong	H.D. Shin	JX143595	JX143353	JX143107	JX142861 JX142615
	CBS 132649; CPC 10725	<i>Viola mandshurica</i>	Violaceae	South Korea: Suwon	H.D. Shin	JX143596	JX143354	JX143108	JX142862 JX142616
	CBS 132671; CPC 14546	<i>Cercis chinensis</i>	Fabaceae	South Korea: Yangpyeong	H.D. Shin	JX143597	JX143355	JX143109	JX142863 JX142617
	MUCC 130	<i>Cosmos bipinnata</i>	Asteraceae	Japan: Ehime	J. Nishikawa	JX143598	JX143356	JX143110	JX142864 JX142618
<i>Cercospora cf. flagellaris</i>	MUCC 866	<i>Hibiscus syriacus</i>	Malvaceae	Japan: Ehime	J. Nishikawa	JX143599	JX143357	JX143111	JX142865 JX142619
	CBS 113127; RC3766; TX-18	<i>Eichhornia crassipes</i>	Pontederiaceae	USA: Texas	D. Tessmann & R. Charudattan	DQ835075	AF146147	DQ835121	DQ835148 DQ835175
	CBS 115482; A207 Bs+; CPC 4410	<i>Citrus</i> sp.	Rutaceae	South Africa: Messina	M.C. Pretorius	AY260070	DQ835095	DQ835114	DQ835141 DQ835168
	CBS 132637; CPC 10079	<i>Trachelium</i> sp.	Campanulaceae	Israel	E. Tzul-Abad	JX143600	JX143358	JX143112	JX142866 JX142620
	CBS 132646; CPC 10681	<i>Cichorium intybus</i>	Asteraceae	South Korea: Suwon	H.D. Shin	JX143601	JX143359	JX143113	JX142867 JX142621
	CBS 132648; CPC 10722	<i>Amaranthus patulus</i>	Amaranthaceae	South Korea: Namyangju	H.D. Shin	JX143602	JX143360	JX143114	JX142868 JX142622
	CBS 132653; CPC 10884	<i>Dysphania ambrosioides</i> (= <i>Chenopodium ambrosioides</i> )	Chenopodiaceae	South Korea: Jeju	H.D. Shin	JX143603	JX143361	JX143115	JX142869 JX142623
	CBS 132667; CPC 11643	<i>Celosia argentea</i> var. <i>cristata</i> (= <i>C. cristata</i> )	Amaranthaceae	South Korea: Hoengseong	H.D. Shin	JX143604	JX143362	JX143116	JX142870 JX142624
	CBS 132670; CPC 14487	<i>Sigesbeckia pubescens</i>	Asteraceae	South Korea: Yanggu	H.D. Shin	JX143605	JX143363	JX143117	JX142871 JX142625
	CBS 132674; CPC 14723	<i>Phytolacca americana</i>	Phytolaccaceae	South Korea: Jeju	H.D. Shin	JX143606	JX143364	JX143118	JX142872 JX142626
	CBS 143.51; CPC 5055	<i>Bromus</i> sp.	Poaceae	—	M.D. Whitehead	JX143607	JX143365	JX143119	JX142873 JX142627
	CPC 10124	<i>Phytolacca americana</i>	Phytolaccaceae	South Korea: Pocheon	H.D. Shin	JX143608	JX143366	JX143120	JX142874 JX142628
	CPC 1051	<i>Populus deltoides</i>	Salicaceae	South Africa	P.W. Crous	AY260069	JX143367	JX143121	JX142875 JX142629
	CPC 1052	<i>Populus deltoides</i>	Salicaceae	South Africa	P.W. Crous	JX143609	JX143368	JX143122	JX142876 JX142630
	CPC 10684	<i>Phytolacca americana</i>	Phytolaccaceae	South Korea: Jinju	H.D. Shin	JX143610	JX143369	JX143123	JX142877 JX142631
	CPC 4411; Q207 F5	<i>Citrus</i> sp.	Rutaceae	South Africa: Messina	M.C. Pretorius	AY260071	DQ835098	DQ835118	DQ835145 DQ835172
	CPC 5441	<i>Amaranthus</i> sp.	Amaranthaceae	Fiji	C.F. Hill	JX143611	JX143370	JX143124	JX142878 JX142632
	MUCC 127	<i>Cosmos sulphureus</i>	Asteraceae	Japan: Ehime	J. Nishikawa	JX143612	JX143371	JX143125	JX142879 JX142633
	MUCC 735	<i>Hydrangea serrata</i>	Hydrangeaceae	Japan: Wakayama	C. Nakashima & I. Araki	JX143613	JX143372	JX143126	JX142880 JX142634
	MUCC 831	<i>Hydrangea serrata</i>	Hydrangeaceae	Japan: Tokyo	I. Araki & M. Harada	JX143614	JX143373	JX143127	JX142881 JX142635

Table 1. (Continued).

Species	Culture accession number(s) <sup>1</sup>	Host name or isolation source	Host Family	Country	Collector	GenBank accession numbers <sup>2</sup>			
						ITS	TEF	ACT	HIS
<i>Cercospora cf. helianthicola</i>	MUCC 716	<i>Helianthus tuberosus</i>	Asteraceae	Japan: Wakayama	C. Nakashima & I. Araki	JX143615	JX143374	JX143128	JX142882
<i>Cercospora cf. ipomoeae</i>	CBS 132639; CPC 10102	<i>Persicaria thunbergii</i>	Polygonaceae	South Korea: Pocheon	H.D. Shin	JX143616	JX143375	JX143129	JX142883
	CBS 132652; CPC 10833	<i>Ipomoea nil</i> (= <i>I. hederacea</i> )	Convolvulaceae	South Korea: Chuncheon	H.D. Shin	JX143617	JX143376	JX143130	JX142884
	MUCC 442	<i>Ipomoea aquatica</i>	Convolvulaceae	Japan: Kagawa	G. Kizaki	JX143618	JX143377	JX143131	JX142885
<i>Cercospora kikuchii</i>	CBS 128.27; CPC 5068 (TYPE)	<i>Glycine soja</i>	Fabaceae	Japan	T. Matsumoto	DQ835070	DQ835088	DQ835107	DQ835134
	CBS 132633; CPC 16578	<i>Glycine max</i>	Fabaceae	Argentina	—	JX143619	JX143378	JX143132	JX142886
	CBS 135.28; CPC 5067	<i>Glycine soja</i>	Fabaceae	Japan	H.W. Wollenweber	DQ835071	DQ835089	DQ835108	DQ835135
	MUCC 590; MAFF 305040	<i>Glycine soja</i>	Fabaceae	Japan: Kagoshima	H. Kurata	JX143620	JX143379	JX143133	JX142887
<i>Cercospora lactucae-sativae</i>	CBS 132604; CPC 10728	<i>Ixeris chinensis</i> subsp. <i>strigosa</i> (= <i>Ixeris strigosa</i> )	Asteraceae	South Korea: Chuncheon	H.D. Shin	JX143621	JX143380	JX143134	JX142888
	CPC 10082	<i>Ixeris chinensis</i> subsp. <i>strigosa</i> (= <i>Ixeris strigosa</i> )	Asteraceae	South Korea: Chuncheon	H.D. Shin	JX143622	JX143381	JX143135	JX142889
	MUCC 570; MUCN S463; MAFF 238209	<i>Lactuca sativa</i>	Asteraceae	Japan: Chiba	C. Nakashima	JX143623	JX143382	JX143136	JX142890
	MUCC 571; MUCNS 214; MAFF 237719	<i>Lactuca sativa</i>	Asteraceae	Japan: Chiba	S. Uematsu	JX143624	JX143383	JX143137	JX142891
<i>Cercospora cf. malloti</i>	MUCC 575; MUCNS 582; MAFF 237872	<i>Cucumis melo</i>	Cucurbitaceae	Japan: Okinawa	K. Uehara	JX143625	JX143384	JX143138	JX142892
<i>Cercospora mercurialis</i>	MUCC 787	<i>Mallotus japonicus</i>	Euphorbiaceae	Japan: Okinawa	C. Nakashima & T. Akashi	JX143626	JX143385	JX143139	JX142893
	CBS 549.71	<i>Mercurialis annua</i>	Euphorbiaceae	Romania: Cheila	O. Constantinescu	JX143627	JX143386	JX143140	JX142894
	CBS 550.71 (TYPE)	<i>Mercurialis perennis</i>	Euphorbiaceae	Romania: Cheila	O. Constantinescu	JX143628	JX143387	JX143141	JX142895
	CBS 551.71	<i>Mercurialis ovata</i>	Euphorbiaceae	Romania: Hagieni	O. Constantinescu & G. Negrean	JX143629	JX143388	JX143142	JX142896
<i>Cercospora cf. modiolae</i>	CPC 5115	<i>Modiola caroliniana</i>	Malvaceae	New Zealand	C.F. Hill	JX143630	JX143389	JX143143	JX142897
<i>Cercospora cf. nicotianae</i>	CBS 131.32; CPC 5076	<i>Nicotiana tabacum</i>	Solanaceae	Indonesia: Medan	H. Diddens & A. Jaarsveld	DQ835073	DQ835099	DQ835119	DQ835146
	CBS 132632; CPC 15918	<i>Glycine max</i>	Fabaceae	Mexico: Tamaulipas	Ma. de Jesús Yáñez-Morales	JX143631	JX143390	JX143144	JX142898
<i>Cercospora olivascens</i>	CBS 570.69; CPC 5075	<i>Nicotiana tabacum</i>	Solanaceae	Nigeria	S.O. Alasoadura	DQ835074	DQ835100	DQ835120	DQ835147
	CBS 253.67; IMI 124975; CPC 5085 (TYPE)	<i>Aristobolchia clematidis</i>	Aristobolchiaceae	Romania: Cazanele Dunarii	O. Constantinescu	JX143632	JX143391	JX143145	JX142899
<i>Cercospora cf. physalidis</i>	CBS 765.79	<i>Solanum tuberosum</i>	Solanaceae	Peru	L.J. Turkensteen	JX143633	JX143392	JX143146	JX142900
<i>Cercospora pileicola</i>	CBS 132607; CPC 10749 (TYPE)	<i>Pilea pumila</i> (= <i>P. mongolica</i> )	Urticaceae	South Korea: Dongducheon	H.D. Shin	JX143634	JX143393	JX143147	JX142901
	CBS 132647; CPC 10693	<i>Pilea hamaoi</i> (= <i>P. pumila</i> var. <i>hamaoi</i> )	Urticaceae	South Korea: Hoengseong	H.D. Shin	JX143635	JX143394	JX143148	JX142902
	CPC 11369	<i>Pilea pumila</i> (= <i>P. mongolica</i> )	Urticaceae	South Korea: Hongcheon	H.D. Shin	JX143636	JX143395	JX143149	JX142903
<i>Cercospora polygonaceae</i>	CBS 132614; CPC 11318	<i>Persicaria longiseta</i> (= <i>P. blumei</i> )	Polygonaceae	South Korea: Cheongju	H.D. Shin	JX143637	JX143396	JX143150	JX142904



Table 1. (Continued).

Species	Culture accession number(s) <sup>1</sup>	Host name or isolation source	Host Family	Country	Collector	GenBank accession numbers <sup>2</sup>			
						ITS	TEF	ACT	CAL
<i>Cercospora punctiformis</i>	CBS 132626; CPC 14606	<i>Cynanachum wilfordii</i>	Asclepiadaceae	South Korea: Bonghwa	H.D. Shin	JX143638	JX143397	JX143151	JX142905
<i>Cercospora cf. resedae</i>	CBS 118793	<i>Reseda odorata</i>	Resedaceae	New Zealand: Auckland	C.F. Hill	JX143639	JX143398	JX143152	JX142906
<i>Cercospora cf. richardicola</i>	CBS 257.67; CPC 5057	<i>Helianthemum</i> sp.	Cistaceae	Romania: Bucuresti	O. Constantinescu	DQ233319	DQ233343	DQ233369	DQ233395
	CBS 132627; CPC 14680	<i>Ajuga multiflora</i>	Lamiaceae	South Korea: Incheon	H.D. Shin	JX143640	JX143399	JX143153	JX142907
	MUCC 128	<i>Tagetes erecta</i>	Asteraceae	Japan: Ehime	J. Nishikawa	JX143641	JX143400	JX143154	JX142908
	MUCC 132	<i>Osteospermum</i> sp.	Asteraceae	Japan: Shizuoka	J. Nishikawa	JX143642	JX143401	JX143155	JX142909
	MUCC 138	<i>Fuchsia × hybrida</i>	Onagraceae	Japan: Shizuoka	J. Nishikawa	JX143643	JX143402	JX143156	JX142910
<i>Cercospora ricinella</i>	MUCC 578; MAFF 238210	<i>Zantedeschia</i> sp.	Araceae	Japan: Ehime	J. Nishikawa	JX143644	JX143403	JX143157	JX142911
	MUCC 582; MAFF 238880	<i>Gerbera hybrida</i>	Asteraceae	Japan: Shizuoka	J. Takeuchi	JX143645	JX143404	JX143158	JX142912
	CBS 132605; CPC 10734	<i>Ricinus communis</i>	Euphorbiaceae	South Korea: Chuncheon	H.D. Shin	JX143646	JX143405	JX143159	JX142913
	CPC 10104	<i>Ricinus communis</i>	Euphorbiaceae	South Korea: Chuncheon	H.D. Shin	JX143647	JX143406	JX143160	JX142914
	CBS 113123; RC3660; 28-1	<i>Eichhomia crassipes</i>	Pontederiaceae	Brazil: Rio Verde	R. Charudattan	DQ835076	AF146136	DQ835122	DQ835149
<i>Cercospora rodmanii</i>	CBS 113124; RC2867	<i>Eichhomia crassipes</i>	Pontederiaceae	Mexico: Carretero	R. Charudattan	DQ835077	AF146137	DQ835123	DQ835150
	CBS 113125; RC4101; 400	<i>Eichhomia crassipes</i>	Pontederiaceae	Zambia	M. Morris	DQ835078	AF146146	DQ835124	DQ835151
	CBS 113126; RC3409; 62-2	<i>Eichhomia crassipes</i>	Pontederiaceae	Brazil: Orocó	R. Charudattan	DQ835079	AF146138	DQ835125	DQ835152
	CBS 113128; RC394; WH83	<i>Eichhomia crassipes</i>	Pontederiaceae	USA: Florida	R. Charudattan	DQ835080	AF146142	DQ835126	DQ835153
	CBS 113129; RC397; WH9-BR	<i>Eichhomia crassipes</i>	Pontederiaceae	USA: Florida	K. Conway	DQ835081	AF146143	DQ835127	DQ835154
	CBS 113130; RC393; WHK	<i>Eichhomia crassipes</i>	Pontederiaceae	USA: Florida	R. Charudattan	DQ835082	AF146144	DQ835128	DQ835155
	CBS 113131; RC395; WHV	<i>Eichhomia crassipes</i>	Pontederiaceae	Venezuela: Maracay	R. Charudattan	DQ835083	AF146148	DQ835129	DQ835156
	CPC 5439	<i>Rumex sanguineus</i>	Polygonaceae	New Zealand: Manurewa	C.F. Hill	JX143648	JX143407	JX143161	JX142915
	CBS 132636; CPC 19196	<i>Senecio walkeri</i>	Asteraceae	Laos	P. Phengsintham	JX143649	JX143408	JX143162	JX142916
	CBS 132601; CPC 10664	<i>Sigesbeckia glabrescens</i>	Asteraceae	South Korea: Chuncheon	H.D. Shin	JX143650	JX143409	JX143163	JX142917
<i>Cercospora cf. sigesbeckiae</i>	CBS 132606; CPC 10740	<i>Paulownia coreana</i>	Scrophulariaceae	South Korea: Namyangju	H.D. Shin	JX143651	JX143410	JX143164	JX142918
<i>Cercospora rumicis</i>	CBS 132621; CPC 14489	<i>Sigesbeckia pubescens</i>	Asteraceae	South Korea: Yanggu	H.D. Shin	JX143652	JX143411	JX143165	JX142919
	CBS 132641; CPC 10117	<i>Pericaria orientalis</i> (= <i>P. cochinchinensis</i> )	Polygonaceae	South Korea: Chuncheon	H.D. Shin	JX143653	JX143412	JX143166	JX142920
	CBS 132642; CPC 10128	<i>Pilea pumila</i> (= <i>P. mongolica</i> )	Urticaceae	South Korea: Hongcheon	H.D. Shin	JX143654	JX143413	JX143167	JX142921
	CBS 132675; CPC 14726	<i>Malva verticillata</i>	Malvaceae	South Korea: Yanggu	H.D. Shin	JX143655	JX143414	JX143168	JX142922
	MUCC 587; MUCNS 197; MAFF 237690	<i>Begonia</i> sp.	Begoniaceae	Japan: Chiba	S. Uematsu	JX143656	JX143415	JX143169	JX142923
<i>Cercospora soja</i>	MUCC 589; MAFF 305039	<i>Glycine max</i>	Fabaceae	Japan: Saitama	H. Kurata	JX143657	JX143416	JX143170	JX142924
	MUCC 849	<i>Dioscorea tokoro</i>	Dioscoreaceae	Japan: Tokyo	I. Araki	JX143658	JX143417	JX143171	JX142925
	CBS 132018; CPC 12322	<i>Glycine soja</i>	Fabaceae	South Korea: Hoengseong	H.D. Shin	GU214655	JX143418	JX143172	JX142926

Table 1. (Continued).

Species	Culture accession number(s) <sup>1</sup>	Host name or isolation source	Host Family	Country	Collector	GenBank accession numbers <sup>2</sup>				
						ITS	TEF	ACT	CAL	HIS
<i>Cercospora</i> sp. A	CBS 132615; CPC 11353 (TYPE)	<i>Glycine soja</i>	Fabaceae	South Korea: Hongcheon	H.D. Shin	JX143659	JX143419	JX143173	JX142927	JX142681
	CBS 132684; CPC 17971; CCC 173-09, 09-495	<i>Glycine max</i>	Fabaceae	Argentina	F. Scandiani	JX143660	JX143420	JX143174	JX142928	JX142682
	CPC 11420	<i>Glycine soja</i>	Fabaceae	South Korea: Hongcheon	H.D. Shin	JX143661	JX143421	JX143175	JX142929	JX142683
	CPC 17964; CCC 155-09, 09-285-5	<i>Glycine max</i>	Fabaceae	Argentina	F. Scandiani	JX143662	JX143422	JX143176	JX142930	JX142684
	CPC 17965; CCC 156-09, 09-285-4	<i>Glycine max</i>	Fabaceae	Argentina	F. Scandiani	JX143663	JX143423	JX143177	JX142931	JX142685
	CPC 17966; CCC 157-09, 09-285-3	<i>Glycine max</i>	Fabaceae	Argentina	F. Scandiani	JX143664	JX143424	JX143178	JX142932	JX142686
	CPC 17967; CCC 158-09, 09-285-1	<i>Glycine max</i>	Fabaceae	Argentina	F. Scandiani	JX143665	JX143425	JX143179	JX142933	JX142687
	CPC 17968; CCC 159-09, 09-285-7	<i>Glycine max</i>	Fabaceae	Argentina	F. Scandiani	JX143666	JX143426	JX143180	JX142934	JX142688
	CPC 17969; CCC 167-09, 09-881	<i>Glycine max</i>	Fabaceae	Argentina	N. Formento	JX143667	JX143427	JX143181	JX142935	JX142689
	CPC 17970; CCC 172-09, 09-320	<i>Glycine max</i>	Fabaceae	Argentina	F. Scandiani	JX143668	JX143428	JX143182	JX142936	JX142690
<i>Cercospora</i> sp. B	CPC 17972; CCC 174-09,	<i>Glycine max</i>	Fabaceae	Argentina	S. Piubello	JX143669	JX143429	JX143183	JX142937	JX142691
	CPC 17973; CCC 176-09, 09-882	<i>Glycine max</i>	Fabaceae	Argentina	N. Formento	JX143670	JX143430	JX143184	JX142938	JX142692
	CPC 17974; CCC 177-09, 09-2488-1	<i>Glycine max</i>	Fabaceae	Argentina	F. Scandiani	JX143671	JX143431	JX143185	JX142939	JX142693
	CPC 17975; CCC 178-09, 09-1438-2	<i>Glycine max</i>	Fabaceae	Argentina	F. Scandiani	JX143672	JX143432	JX143186	JX142940	JX142694
	CPC 17976; CCC 179-09, 09-2591	<i>Glycine max</i>	Fabaceae	Argentina	F. Scandiani	JX143673	JX143433	JX143187	JX142941	JX142695
	CPC 17977; CCC 180-09, 09-2520	<i>Glycine max</i>	Fabaceae	Argentina	F. Scandiani	JX143674	JX143434	JX143188	JX142942	JX142696
	CBS 132631; CPC 15872	<i>Chenopodium</i> sp.	Chenopodiaceae	Mexico	Ma. de Jesús Yáñez-Morales	JX143675	JX143435	JX143189	JX142943	JX142697
	CBS 132602; CPC 10687	<i>Ipomoea purpurea</i>	Convolvulaceae	South Korea: Kangnung	H.D. Shin	JX143676	JX143436	JX143190	JX142944	JX142698
	CBS 132629; CPC 15841	—	Compositae	Mexico: Montecillo	Ma. de Jesús Yáñez-Morales	JX143677	JX143437	JX143191	JX142945	JX142699
	CBS 132630; CPC 15856	—	—	Mexico	Ma. de Jesús Yáñez-Morales	JX143678	JX143438	JX143192	JX142946	JX142700
<i>Cercospora</i> sp. C	CBS 132628; CPC 15632	Unidentified wild plant	—	Mexico: Montecillo	Ma. de Jesús Yáñez-Morales	JX143679	JX143439	JX143193	JX142947	JX142701
	CPC 15801	Unidentified wild plant	—	Mexico: Montecillo	Ma. de Jesús Yáñez-Morales	JX143680	JX143440	JX143194	JX142948	JX142702
	CBS 132618; CPC 12062	<i>Zea mays</i>	Poaceae	South Africa	P. Caldwell	DQ185071	DQ185083	DQ185095	DQ185107	DQ185119
	CBS 115518; CPC 5360	<i>Bidens frondosa</i>	Asteraceae	New Zealand: Kopuku	C.F. Hill	JX143681	JX143441	JX143195	JX142949	JX142703
	CPC 5438	<i>Salvia viscosa</i>	Lamiaceae	New Zealand: Manurewa	C.F. Hill	JX143682	JX143442	JX143196	JX142950	JX142704
	CBS 115205; CPC 5116	<i>Dichondra repens</i>	Convolvulaceae	New Zealand	C.F. Hill	JX143683	JX143443	JX143197	JX142951	JX142705
	CPC 11620	<i>Chamaelium uncinatum</i>	Myrtaceae	Argentina	S. Wolcan	JX143684	JX143444	JX143198	JX142952	JX142706
	CBS 114815; CPC 5364	<i>Deutzia purpurascens</i>	Hydrangeaceae	New Zealand: Manurewa	C.F. Hill	JX143685	JX143445	JX143199	JX142953	JX142707
	CBS 114816; CPC 5363	<i>Deutzia × rosea</i> (= <i>D. gradilis</i> × <i>purpurascens</i> )	Hydrangeaceae	New Zealand: Manurewa	C.F. Hill	JX143686	JX143446	JX143200	JX142954	JX142708
	CBS 114817; CPC 5365	<i>Fuchsia procumbens</i>	Onagraceae	New Zealand: Manurewa	C.F. Hill	JX143687	JX143447	JX143201	JX142955	JX142709
<i>Cercospora</i> sp. D	CBS 114818; CPC 5362	<i>Deutzia crenata</i>	Hydrangeaceae	New Zealand: Manurewa	C.F. Hill	JX143688	JX143448	JX143202	JX142956	JX142710

Table 1. (Continued).

Species	Culture accession number(s) <sup>1</sup>	Host name or isolation source	Host Family	Country	Collector	GenBank accession numbers <sup>2</sup>				
						ITS	TEF	ACT	CAL	HIS
<i>Cercospora</i> sp. J	CBS 115117	<i>Archontophoenix cunninghamiana</i>	Arecaceae (Palmae)	New Zealand: Whangarei	C.F. Hill	JX143689	JX143449	JX143203	JX142957	JX142711
	CBS 115121	<i>Gunnera tinctoria</i>	Gunneraceae	New Zealand: Mt Albert	C.F. Hill	JX143690	JX143450	JX143204	JX142958	JX142712
	CBS 132597; CPC 10615	<i>Coreopsis verticillata</i>	Asteraceae	New Zealand: Manurewa	C.F. Hill	JX143691	JX143451	JX143205	JX142959	JX142713
	CBS 132643; CPC 10138	<i>Ajuga multiflora</i>	Lamiaceae	South Korea: Suwon	H.D. Shin	JX143692	JX143452	JX143206	JX142960	JX142714
	CPC 10616	<i>Coreopsis verticillata</i>	Asteraceae	New Zealand: Manurewa	C.F. Hill	JX143693	JX143453	JX143207	JX142961	JX142715
	CPC 5440	<i>Nicotiana</i> sp.	Solanaceae	New Zealand: Manurewa	C.F. Hill	JX143694	JX143454	JX143208	JX142962	JX142716
	MUCC 541	<i>Antirrhinum majus</i>	Plantaginaceae	Japan: Aichi	M. Matsusaki	JX143695	JX143455	JX143209	JX142963	JX142717
	CBS 132603; CPC 10719	<i>Ipomoea coccinea</i> (= <i>Quamoclit coccinea</i> )	Convolvulaceae	South Korea: Namyangju	H.D. Shin	JX143696	JX143456	JX143210	JX142964	JX142718
	CPC 10094	<i>Ipomoea coccinea</i> (= <i>Quamoclit coccinea</i> )	Convolvulaceae	South Korea: Namyangju	H.D. Shin	JX143697	JX143457	JX143211	JX142965	JX142719
	CPC 12391	<i>Ipomoea coccinea</i> (= <i>Quamoclit coccinea</i> )	Convolvulaceae	South Korea: Namyangju	H.D. Shin	JX143698	JX143458	JX143212	JX142966	JX142720
<i>Cercospora</i> sp. L	CBS 115477; CPC 5114	<i>Crepis capillaris</i>	Asteraceae	New Zealand	C.F. Hill	JX143699	JX143459	JX143213	JX142967	JX142721
	CBS 132596; CPC 10553	<i>Acacia mangium</i>	Fabaceae	Thailand: Sanamchaikhet	K. Pongpanich	JX143700	AY752175	AY752203	AY752234	AY752265
	CBS 132619; CPC 12684	<i>Musa</i> sp.	Musaceae	Bangladesh: Western	I. Buddenhagen	EU514224	JX143460	JX143214	JX142968	JX142722
	CBS 132635; CPC 18636	<i>Musa</i> sp.	Musaceae	Thailand: Mae Klang Loun	P.W. Crous	JX143701	JX143461	JX143215	JX142969	JX142723
<i>Cercospora</i> sp. P	CBS 112649; CPC 3946	<i>Citrus</i> sp., leaf spot	Rutaceae	Swaziland	M.C. Pretorius	AY260072	DQ835090	DQ835109	DQ835136	DQ835163
	CBS 112722; CPC 3947	<i>Citrus</i> sp., leaf spot	Rutaceae	Swaziland	M.C. Pretorius	AY260073	DQ835091	DQ835110	DQ835137	DQ835164
	CBS 112728; CPC 3949	<i>Citrus</i> × <i>sinensis</i> (= <i>C. aurantium</i> var. <i>sinensis</i> )	Rutaceae	South Africa: Komatipoort	M.C. Pretorius	AY260076	DQ835092	DQ835111	DQ835138	DQ835165
	CBS 112730; CPC 3948	<i>Citrus</i> × <i>sinensis</i> (= <i>C. aurantium</i> var. <i>sinensis</i> )	Rutaceae	South Africa: Komatipoort	M.C. Pretorius	AY260075	DQ835093	DQ835112	DQ835139	DQ835166
<i>Cercospora</i> sp. O	CBS 112894; CPC 3950	<i>Citrus</i> × <i>sinensis</i> (= <i>C. aurantium</i> var. <i>sinensis</i> )	Rutaceae	South Africa: Komatipoort	M.C. Pretorius	AY260077	DQ835094	DQ835113	DQ835140	DQ835167
	CBS 113996; CPC 5326	<i>Cajanus cajan</i>	Fabaceae	South Africa: Nelspruit	L. van Jaarsveld	JX143702	JX143462	JX143216	JX142970	JX142724
	CBS 115413; CPC 5328	<i>Cajanus cajan</i>	Fabaceae	South Africa: Nelspruit	L. van Jaarsveld	JX143703	JX143463	JX143217	JX142971	JX142725
	CBS 115609; CPC 3945	<i>Citrus</i> sp., leaf spot	Rutaceae	Swaziland	M.C. Pretorius	AY260074	DQ835096	DQ835115	DQ835142	DQ835169
	CBS 116365; CPC 10526 (TYPE)	<i>Acacia mangium</i>	Fabaceae	Thailand	M.J. Wingfield	AY752141	AY752176	AY752204	AY752235	AY752266
	CBS 132645; CPC 10527	<i>Acacia mangium</i>	Fabaceae	Thailand	M.J. Wingfield	AY752142	AY752177	AY752205	AY752236	AY752267
	CBS 132660; CPC 11629; GHA-4-0	<i>Dioscorea rotundata</i>	Dioscoreaceae	Ghana	S. Nyako & A.O. Danquah	JX143704	JX143464	JX143218	JX142972	JX142726
	CBS 132662; CPC 11635; PNG-009	<i>Dioscorea nummularia</i>	Dioscoreaceae	Papua New Guinea	J. Peters & A.N. Jama	JX143705	JX143465	JX143219	JX142973	JX142727
	CBS 132664; CPC 11637; PNG-022	<i>Dioscorea rotundata</i>	Dioscoreaceae	Papua New Guinea	J. Peters & A.N. Jama	JX143706	JX143466	JX143220	JX142974	JX142728
	CBS 132665; CPC 11638; PNG-023	<i>Dioscorea bulbifera</i>	Dioscoreaceae	Papua New Guinea	J. Peters & A.N. Jama	JX143707	JX143467	JX143221	JX142975	JX142729

Table 1. (Continued).

Species	Culture accession number(s) <sup>1</sup>	Host name or isolation source	Host Family	Country	Collector	GenBank accession numbers <sup>2</sup>				
						ITS	TEF	ACT	CAL	HIS
<i>Cercospora</i> sp. Q	CBS 132680; CPC 15827	<i>Ricinus communis</i>	Euphorbiaceae	Mexico: Tamaulipas	Ma. de Jesús Yáñez-Morales	JX143708	JX143468	JX143222	JX142976	JX142730
	CPC 10552	<i>Acacia mangium</i>	Fabaceae	Thailand	K. Pongpanich	JX143709	AY752174	AY752202	AY752233	AY752264
	CPC 11630; GHA-4-3	<i>Dioscorea rotundata</i>	Dioscoreaceae	Ghana	S. Nyako & A.O. Danquah	JX143710	JX143469	JX143223	JX142977	JX142731
	CPC 11631; GHA-5-0	<i>Dioscorea rotundata</i>	Dioscoreaceae	Ghana	S. Nyako & A.O. Danquah	JX143711	JX143470	JX143224	JX142978	JX142732
	CPC 11632; GHA-7-4	<i>Dioscorea rotundata</i>	Dioscoreaceae	Ghana	S. Nyako & A.O. Danquah	JX143712	JX143471	JX143225	JX142979	JX142733
	CPC 11633; GHA-8-4	<i>Dioscorea rotundata</i>	Dioscoreaceae	Ghana	S. Nyako & A.O. Danquah	JX143713	JX143472	JX143226	JX142980	JX142734
	CPC 4001	<i>Citrus × sinensis</i> (≡ <i>C. aurantium</i> var. <i>sinensis</i> )	Rutaceae	Swaziland	M.C. Pretorius	AY343372	AY343335	DQ835116	DQ835143	DQ835170
	CPC 4002	<i>Citrus × sinensis</i> (≡ <i>C. aurantium</i> var. <i>sinensis</i> )	Rutaceae	Swaziland	M.C. Pretorius	DQ835072	DQ835097	DQ835117	DQ835144	DQ835171
	CPC 5262	<i>Hibiscus sabdariffa</i>	Malvaceae	New Zealand: Auckland (imported from Fiji)	C.F. Hill	JX143714	JX143473	JX143227	JX142981	JX142735
	CPC 5327	<i>Cajanus cajan</i>	Fabaceae	South Africa: Nelspruit	L. van Jaarsveld	JX143715	JX143474	JX143228	JX142982	JX142736
	MUCC 771	<i>Coffea arabica</i>	Rubiaceae	Japan: Okinawa	C. Nakashima	JX143716	JX143475	JX143229	JX142983	JX142737
	CBS 113997; CPC 5325	<i>Cajanus cajan</i>	Fabaceae	South Africa: Nelspruit	L. van Jaarsveld	JX143717	JX143476	JX143230	JX142984	JX142738
	CBS 115410; CPC 5331	<i>Cajanus cajan</i>	Fabaceae	South Africa: Nelspruit	L. van Jaarsveld	JX143718	JX143477	JX143231	JX142985	JX142739
	CBS 115411; CPC 5332	<i>Cajanus cajan</i>	Fabaceae	South Africa: Nelspruit	L. van Jaarsveld	JX143719	JX143478	JX143232	JX142986	JX142740
	CBS 115412; CPC 5333	<i>Cajanus cajan</i>	Fabaceae	South Africa: Nelspruit	L. van Jaarsveld	JX143720	JX143479	JX143233	JX142987	JX142741
	CBS 115536; CPC 5329	<i>Cajanus cajan</i>	Fabaceae	South Africa: Nelspruit	L. van Jaarsveld	JX143721	JX143480	JX143234	JX142988	JX142742
	CBS 115537; CPC 5330	<i>Cajanus cajan</i>	Fabaceae	South Africa: Nelspruit	L. van Jaarsveld	JX143722	JX143481	JX143235	JX142989	JX142743
	CBS 132656; CPC 11536	<i>Acacia mangium</i>	Fabaceae	Thailand	K. Pongpanich	JX143723	JX143482	JX143236	JX142990	JX142744
	CBS 132661; CPC 11634; PNG-002	<i>Dioscorea rotundata</i>	Dioscoreaceae	Papua New Guinea	J. Peters & A.N. Jama	JX143724	JX143483	JX143237	JX142991	JX142745
	CBS 132663; CPC 11636; PNG-016	<i>Dioscorea esculenta</i>	Dioscoreaceae	Papua New Guinea	J. Peters & A.N. Jama	JX143725	JX143484	JX143238	JX142992	JX142746
<i>Cercospora</i> sp. R	CBS 132679; CPC 15807	<i>Phaseolus vulgaris</i>	Fabaceae	Mexico	Ma. de Jesús Yáñez-Morales	JX143726	JX143485	JX143239	JX142993	JX142747
	CBS 132681; CPC 15844	<i>Euphorbia</i> sp.	Euphorbiaceae	Mexico: Tamaulipas	Ma. de Jesús Yáñez-Morales	JX143727	JX143486	JX143240	JX142994	JX142748
	CBS 132682; CPC 15850	<i>Taraxacum</i> sp.	Asteraceae	Mexico: Tamaulipas	Ma. de Jesús Yáñez-Morales	JX143728	JX143487	JX143241	JX142995	JX142749
	CPC 10550	<i>Acacia mangium</i>	Fabaceae	Thailand	K. Pongpanich	AY752139	AY752172	AY752200	AY752231	AY752262
	CPC 10551	<i>Acacia mangium</i>	Fabaceae	Thailand	K. Pongpanich	AY752140	AY752173	AY752201	AY752232	AY752263
	CPC 11539	<i>Acacia mangium</i>	Fabaceae	Thailand	K. Pongpanich	JX143729	JX143488	JX143242	JX142996	JX142750
	CPC 11639; PNG-037	<i>Dioscorea rotundata</i>	Dioscoreaceae	Papua New Guinea	J. Peters & A.N. Jama	JX143730	JX143489	JX143243	JX142997	JX142751
<i>Cercospora</i> sp. S	CPC 15875	<i>Euphorbia</i> sp.	Euphorbiaceae	Mexico: Tamaulipas	Ma. de Jesús Yáñez-Morales	JX143731	JX143490	JX143244	JX142998	JX142752
	CBS 114644	<i>Myoporum laetum</i>	Myoporaceae	New Zealand: Grey Lynn	C.F. Hill	JX143732	JX143491	JX143245	JX142999	JX142753
<i>Cercospora</i> sp. S	CBS 132559; CPC 10656	<i>Crepidiasium denticulatum</i> (≡ <i>Youngia denticulata</i> )	Asteraceae	South Korea: Yangpyeong	H.D. Shin	JX143733	JX143492	JX143246	JX143000	JX142754



Table 1. (Continued).

Species	Culture accession number(s) <sup>1</sup>	Host name or isolation source	Host Family	Country	Collector	GenBank accession numbers <sup>2</sup>				
						ITS	TEF	ACT	CAL	HIS
<i>Cercospora vignigena</i>	CBS 132611; CPC 10812 (TYPE)	<i>Vigna unguiculata</i> (= <i>V. sinensis</i> )	Fabaceae	South Korea: Jeongeup	H.D. Shin	JX143734	JX143493	JX143247	JX143001	JX142755
	CPC 1134	<i>Vigna unguiculata</i> (= <i>V. sinensis</i> )	Fabaceae	South Africa: Potchefstroom	S. van Wyk	JX143735	JX143494	JX143248	JX143002	JX142756
<i>Cercospora violae</i>	MUCC 579; MAFF 237635	<i>Vigna unguiculata</i> (= <i>V. sinensis</i> )	Fabaceae	Japan: Gumma	K. Kishi	JX143736	JX143495	JX143249	JX143003	JX142757
	CBS 251.67; CPC 5079 (TYPE)	<i>Viola tricolor</i>	Violaceae	Romania: Cazanele Dunarii	O. Constantinescu	JX143737	JX143496	JX143250	JX143004	JX142758
<i>Cercospora zeae-maydis</i>	CPC 5368	<i>Viola odorata</i>	Violaceae	New Zealand	C.F. Hill	JX143738	JX143497	JX143251	JX143005	JX142759
	MUCC 129	<i>Viola</i> sp.	Violaceae	Japan: Kochi	J. Nishikawa	JX143739	JX143498	JX143252	JX143006	JX142760
	MUCC 133	<i>Viola tricolor</i>	Violaceae	Japan: Nagano	J. Nishikawa	JX143740	JX143499	JX143253	JX143007	JX142761
	MUCC 136	<i>Viola tricolor</i>	Violaceae	Japan: Shizuoka	J. Nishikawa	JX143741	JX143500	JX143254	JX143008	JX142762
	CBS 117755; YA-03; A358	<i>Zea mays</i>	Poaceae	USA: Indiana	B. Fleener	DQ185072	DQ185084	DQ185096	DQ185108	DQ185120
	CBS 117756; DE-97; A359	<i>Zea mays</i>	Poaceae	USA: Indiana	B. Fleener	DQ185073	DQ185085	DQ185097	DQ185109	DQ185121
	CBS 117757; JV-WI-02; A360 (TYPE)	<i>Zea mays</i>	Poaceae	USA: Wisconsin	B. Fleener	DQ185074	DQ185086	DQ185098	DQ185110	DQ185122
	CBS 117758; JH-IA-04; A361	<i>Zea mays</i>	Poaceae	USA: Iowa	B. Fleener	DQ185075	DQ185087	DQ185099	DQ185111	DQ185123
	CBS 117759; UC-TN-99; A362	<i>Zea mays</i>	Poaceae	USA: Tennessee	B. Fleener	DQ185076	DQ185088	DQ185100	DQ185112	DQ185124
	CBS 117760; NH-PA-99; A363	<i>Zea mays</i>	Poaceae	USA: Pennsylvania	B. Fleener	DQ185077	DQ185089	DQ185101	DQ185113	DQ185125
<i>Cercospora zebrina</i>	CBS 117761; PR-IN-99; A364	<i>Zea mays</i>	Poaceae	USA: Indiana	B. Fleener	DQ185078	DQ185090	DQ185102	DQ185114	DQ185126
	CBS 117762; DEXTER-MO-00; A365	<i>Zea mays</i>	Poaceae	USA: Missouri	B. Fleener	DQ185079	DQ185091	DQ185103	DQ185115	DQ185127
	CBS 117763; RENBECK-IA-99; A367	<i>Zea mays</i>	Poaceae	USA: Iowa	B. Fleener	DQ185080	DQ185092	DQ185104	DQ185116	DQ185128
	CBS 132668; CPC 12225; CHME 52	<i>Zea mays</i>	Poaceae	China: Liaoning Province	—	JX143742	JX143501	JX143255	JX143009	JX142763
	CBS 132678; CPC 15602	<i>Zea mays</i>	Poaceae	Mexico: Tlaxcopec	Ma. de Jesús Yáñez-Morales	JX143743	JX143502	JX143256	JX143010	JX142764
	CBS 108.22; CPC 5091	<i>Medicago arabica</i> (= <i>M. maculata</i> )	Fabaceae	—	E.F. Hopkins	JX143744	JX143503	JX143257	JX143011	JX142765
	CBS 112723; CPC 3957	<i>Trifolium repens</i>	Fabaceae	Canada: Ottawa	K.A. Seifert	AY260079	JX143504	JX143258	JX143012	JX142766
	CBS 112736; CPC 3958	<i>Trifolium repens</i>	Fabaceae	Canada: Ottawa	K.A. Seifert	AY260080	JX143505	JX143259	JX143013	JX142767
	CBS 112893; CPC 3955	<i>Trifolium pratense</i>	Fabaceae	Canada: Ottawa	K.A. Seifert	AY260078	JX143506	JX143260	JX143014	JX142768
	CBS 113070; CPC 5367	<i>Trifolium repens</i>	Fabaceae	New Zealand: Blockhouse Bay	C.F. Hill	JX143745	JX143507	JX143261	JX143015	JX142769
<i>Cercospora zebrina</i>	CBS 114359; CPC 10901	<i>Hebe</i> sp.	Scrophulariaceae	New Zealand	C.F. Hill	JX143746	JX143508	JX143262	JX143016	JX142770
	CBS 118789; WAC 5106	<i>Trifolium subterraneum</i>	Fabaceae	Australia	M.J. Barbetti	JX143747	JX143509	JX143263	JX143017	JX142771
	CBS 118790; IMI 262766; WA 2030; WAC 7973	<i>Trifolium subterraneum</i>	Fabaceae	Australia	M.J. Barbetti	JX143748	JX143510	JX143264	JX143018	JX142772

Table 1. (Continued).

Species	Culture accession number(s) <sup>1</sup>	Host name or isolation source	Host Family	Country	Collector	GenBank accession numbers <sup>2</sup>				
						ITS	TEF	ACT	CAL	HIS
<i>Cercospora zeina</i>	CBS 118791; IMI 264190; WA2054; WAC7993	<i>Trifolium cernuum</i>	Fabaceae	Australia	M.J. Barbetti	JX143749	JX143511	JX143265	JX143019	JX142773
	CBS 129.39; CPC 5078	<i>Trifolium subterraneum</i>	Fabaceae	USA: Wisconsin	—	JX143750	JX143512	JX143266	JX143020	JX142774
	CBS 132650; CPC 10756	<i>Trifolium repens</i>	Fabaceae	South Korea: Namyangju	H.D. Shin	JX143751	JX143513	JX143267	JX143021	JX142775
	CBS 137.56; CPC 5118	<i>Hedysarum coronarium</i>	Fabaceae	Italy	—	JX143752	JX143514	JX143268	JX143022	JX142776
	CBS 537.71; IMI 161108; CPC 5089	<i>Astragalus sprunerii</i>	Fabaceae	Romania: Hagieni	O. Constantinescu	JX143753	JX143515	JX143269	JX143023	JX142777
	CPC 5437	<i>Lotus pedunculatus</i>	Fabaceae	New Zealand: Auckland	C.F. Hill	JX143754	JX143516	JX143270	JX143024	JX142778
	CPC 5473	<i>Jacaranda minosifolia</i>	Bigoniaceae	New Zealand	C.F. Hill	JX143755	JX143517	JX143271	JX143025	JX142779
	CBS 118820; CPC 11995 (TYPE)	<i>Zea mays</i>	Poaceae	South Africa: Pietermaritzburg	P. Caldwell	DQ185081	DQ185093	DQ185105	DQ185117	DQ185129
	CBS 132617; CPC 11998	<i>Zea mays</i>	Poaceae	South Africa: Pietermaritzburg	P. Caldwell	DQ185082	DQ185094	DQ185106	DQ185118	DQ185130
	CBS 132624; CPC 14549	<i>Zinnia elegans</i>	Asteraceae	South Korea: Yangpyeong	H.D. Shin	JX143756	JX143518	JX143272	JX143026	JX142780
<i>Cercospora cf. zinniae</i>	CBS 132676; CPC 15075	—	—	Brazil: Valverde	A.C. Alfenas	JX143757	JX143519	JX143273	JX143027	JX142781
	MUCC 131	<i>Zinnia elegans</i>	Asteraceae	Japan: Shizuoka	J. Nishikawa	JX143758	JX143520	JX143274	JX143028	JX142782
	MUCC 572; MUCNS 215; MAFF 237718	<i>Zinnia elegans</i>	Asteraceae	Japan: Chiba	S. Uematsu	JX143759	JX143521	JX143275	JX143029	JX142783
	CBS 118910; CPC 12226	<i>Eucalyptus</i> sp.	Myrtaceae	France	P.W. Crous	DQ303096	JX143522	JX143276	JX143030	JX142784

<sup>1</sup> CBS: CBS-KNAW Fungal Biodiversity Centre, Utrecht, The Netherlands; CPC: Culture collection of Pedro Crous, housed at CBS; IHM: Collection of the Laboratorium voor Microbiologie en Microbiële Genetica, Rijksuniversiteit, Ledeganckstraat 35, B-9000, Gent, Belgium; IMI: International Mycological Institute, CAB International, Egham, Surrey, UK; Lynfield: Private culture collection and herbarium of Frank Hill, New Zealand; MAFF: Ministry of Agriculture, Forestry and Fisheries, Tsukuba, Ibaraki, Japan; MUCC: Culture Collection, Laboratory of Plant Pathology, Mie University, Tsu, Mie Prefecture, Japan; MUCL: Université Catholique de Louvain, Louvain-la-Neuve, Belgium; MUCNS: Active cultures & specimens of Chiharu Nakashima, housed at Mie University; MUMH: Mycological Herbarium of Mie University, Tsu, Mie, Japan; PPRI: Plant Protection Research Institute, Pretoria, South Africa; WAC: Department of Agriculture Western Australia Plant Pathogen Collection, Perth, Australia.

<sup>2</sup> ITS: internal transcribed spacers and intervening 5.8S rDNA; TEF: translation elongation factor 1- $\alpha$ ; ACT: actin; CAL: calmodulin; HIS: histone H3.

cercosporin is not produced by all species (Assante *et al.* 1977, examples cited by Goodwin *et al.* 2001, see also review by Weiland *et al.* 2010). Nutritional and environmental conditions influence the production of cercosporin, making it useless for application in *Cercospora* taxonomy (Jenks *et al.* 1989). Genomic studies in recent years attempt to understand the metabolic pathway used to produce cercosporin and *C. nicotianae* has become the model organism for these studies (e.g. Chung *et al.* 2003, Choquer *et al.* 2005, Chen *et al.* 2007, Amnuaykanjanasin & Daub 2009).

In an attempt to address some of the shortcomings highlighted in the previous paragraph, we have obtained diseased plant material and/or cultures from as many hosts and countries as possible over several years. We sequenced the ITS locus (including ITS1, 5.8S nrRNA gene and ITS2), as well as parts of four genomic protein coding genes, namely translation elongation-factor 1- $\alpha$ , actin, calmodulin and histone H3 for each culture. Our primary objective was to re-evaluate the species concept of known *Cercospora* species by consolidating the results of multi-locus phylogenetic analyses with morphological characteristics produced on host plants and different media. A secondary objective was to test whether *Cercospora* species, in general, were host-specific.

## MATERIALS AND METHODS

### Specimens and isolates

Dried specimens and cultures used in this study are maintained in herbaria and culture collections of Genebank, National Institute of Agrobiological Sciences, Japan, (MAFF), the Mycological Herbarium and Culture Collection, laboratory of Plant Pathology, Mie University, Japan (MUMH or MUCC) and the Centraalbureau voor Schimmelcultures (CBS-KNAW Fungal Biodiversity Centre, Utrecht, The Netherlands), or the working collection of P.W. Crous (CPC), housed at CBS (Table 1). A global set of isolates (Table 1) was either obtained from personal culture collections, the culture collection of the CBS or recollected on diseased plant material, and grown in axenic culture. Symptomatic leaves with leaf spots were chosen for isolations of *Cercospora* spp. as explained in Crous (1998). To obtain ascospore isolates, excised lesions were placed in distilled water for approximately 2 h, after which they were placed on the bottom of Petri dish lids, over which the plate containing 2 % malt extract agar (MEA) (Crous *et al.* 1991, 2009c) was inverted. Germinating ascospores were examined after 24 h, and single-ascospore cultures established on MEA as explained by Crous (1998). Colonies were sub-cultured onto oatmeal agar (OA), V8-juice agar (V8), 2 % potato-dextrose agar (PDA) or MEA (Crous *et al.* 2009c) and incubated at 25 °C under continuous near-ultraviolet light, to promote sporulation.

### DNA extraction, amplification and phylogeny

Genomic DNA was isolated from fungal mycelium grown on the agar plates following the protocol of Lee & Taylor (1990) or the UltraClean™ Microbial DNA Isolation Kit (Mo Bio Laboratories, Inc., Solana Beach, CA, USA). All isolates were sequenced with five genomic loci. The primers ITS5 or ITS1 and ITS4 (White *et al.* 1990) were used to amplify the internal transcribed spacers areas as well as the 5.8S rRNA gene (ITS) of the nrDNA operon. Part of the actin gene (ACT) was amplified using the primer set

ACT-512F and ACT-783R (Carbone & Kohn 1999) and part of the translation elongation factor 1- $\alpha$  gene (EF) using the primer set EF1-728F and EF1-986R (Carbone & Kohn 1999). The primer set CAL-228F and CAL-737R (Carbone & Kohn 1999) was used to amplify part of the calmodulin gene (CAL) whereas the primer set CylH3F and CylH3R (Crous *et al.* 2004c) was used to amplify part of the histone H3 gene (HIS). Additional degenerate primers were developed from sequences obtained from GenBank as alternative forward and reverse primers for some of the loci during the course of the study (Table 2); however, these were rarely used but based on their degenerate design could be of use to the broader scientific community. The protocols and conditions outlined by Groenewald *et al.* (2005) were followed for standard amplification and subsequent sequencing of the loci.

Sequences of *Septoria provencialis* (isolate CPC 12226) were used as outgroup based on availability and phylogenetic relationship with *Cercospora* (Crous *et al.* 2004b, 2006b). The *Cercospora* sequences were assembled and added to the outgroup sequences using Sequence Alignment Editor v. 2.0a11 (Rambaut 2002), and manual adjustments for improvement were made by eye where necessary. Gaps present in the ingroup taxa and longer than 10 characters were coded as a single event for all analyses (see TreeBASE).

Neighbour-joining analyses using the HKY85 substitution model were applied to each data partition individually to check the stability and robustness of each species clade under each data set using PAUP v. 4.0b10 (Swofford 2003) (data not shown, discussed under the species notes where applicable). Alignment gaps were treated as missing data and all characters were unordered and of equal weight. Any ties were broken randomly when encountered. The robustness of the trees obtained was evaluated by 1 000 bootstrap replications (Hillis & Bull 1993).

MrModeltest v. 2.2 (Nylander 2004) was used to determine the best nucleotide substitution model settings for each data partition. Based on the results of the MrModeltest, a model-optimised phylogenetic re-construction was performed for the aligned combined data set to determine species relationships using MrBayes v. 3.2.0 (Ronquist & Huelsenbeck 2003). The heating parameter was set at 0.3 and the Markov Chain Monte Carlo (MCMC) analysis of four chains was started in parallel from a random tree topology and lasted until the average standard deviation of split frequencies came below 0.05. Trees were saved each 1 000 generations and the resulting phylogenetic tree was printed with Geneious v. 5.5.4 (Drummond *et al.* 2011). New sequences generated in this study were deposited in NCBI's GenBank nucleotide database ([www.ncbi.nlm.nih.gov](http://www.ncbi.nlm.nih.gov); Table 1) and the alignment and phylogenetic tree in TreeBASE ([www.treebase.org](http://www.treebase.org)).

Isolates of *Cercospora* sp. Q were screened with five more loci to test whether additional loci could distinguish cryptic taxa within this species. This species was selected based on the intraspecific variation present in Fig. 2 (part 5) and also the range of host species and countries represented. The primer set GDF1 and GDR1 (Guerber *et al.* 2003) was used to amplify part of the glyceraldehyde-3-phosphate dehydrogenase (GAPDH) gene, primer set NMS1 and NMS2 (Li *et al.* 1994) for part of the mitochondrial small subunit rRNA gene and part of the chitin synthase (CHS) gene was amplified using the primers CHS-79F and CHS-354R (Carbone & Kohn 1999). Part of the gene encoding for a mini-chromosome maintenance protein (MCM7) was amplified using primers MCM7-709for, MCM7-1348rev, MCM7-1447rev (Schmitt *et al.* 2009) and part of the beta-tubulin gene using mainly the primers T1, Bt2b and TUB3Rd (see Table 2 for references).

**Table 2.** Details of primers used and/or developed for this study and their relation to selected published primers. The start and end positions of the primers are derived using the GenBank accession shown next to the locus name as reference in the 5'–3' direction. See Crous *et al.* (2009a) for information on additional ITS primers.

Name	Sequence (5' – 3')	Orientation	%GC	Tm (°C)	Start	End	Reference
<b>Actin (<i>Hypocrea orientalis</i> GenBank accession JQ238613)</b>							
ACT-512F	ATG TGC AAG GCC GGT TTC GC	Forward	60.0	51.4	244	263	Carbone & Kohn (1999)
ACT-783R	TAC GAG TCC TTC TGG CCC AT	Reverse	55.0	47.6	544	563	Carbone & Kohn (1999)
ACT1Fd	GCY GCB CTC GTY ATY GAC AAT GG	Forward	57.2	45.7 - 50.6 - 54.7	16	38	This study, see also Aveskamp <i>et al.</i> (2009)
ACT1Rd	CRT CGT ACT CCT GCT TBG AGA TCC AC	Reverse	54.5	48.3 - 50.3 - 51.8	1537	1562	This study
ACT2Fd	GTA TCG TBC TBG ACT CYG GTG AYG GTG	Forward	56.8	48.1 - 52.2 - 55.4	854	880	This study
ACT2Rd	ARR TCR CGD CCR GCC ATG TC	Reverse	61.7	45.1 - 50.9 - 58.1	940	956	This study, see also Quaedvlieg <i>et al.</i> (2011)
<b>Beta-tubulin (<i>Gibberella zeae</i> GenBank accession FJ214662)</b>							
Bt1a	TTC CCC CGT CTC CAC TTC TTC ATG	Forward	54.2	50.1	1091	1114	Glass & Donaldson (1995)
Bt1b	GAC GAG ATC GTT CAT GTT GAA CTC	Reverse	45.8	45.1	1603	1626	Glass & Donaldson (1995)
Bt2a	GGT AAC CAAATC GGT GCT GCT TTC	Forward	50.0	48.2	163	186	Glass & Donaldson (1995)
Bt2b	ACC CTC AGT GTA GTG ACC CTT GGC	Reverse	58.0	52.1	617	640	Glass & Donaldson (1995)
CYLUB1F	AAA TTG GTG CTG CTT TCT GG	Forward	45.0	43.5	170	189	This study
CYLUB1R	AGT TGT CGG GAC GGA AGA G	Reverse	57.9	46.6	563	581	Crous <i>et al.</i> (2004c)
T1	AAC ATG CGT GAG ATT GTA AGT	Forward	38.1	41.5	1	17	O'Donnell & Cigelnik (1997)
TUB1Fd	CAN MAT GMG KGA RAT CGT RGT	Forward	47.6	36.8 - 44.5 - 51.9	1	14	This study
TUB1Rd	RGC VTC YTG GTA YTG CTG GTA	Reverse	53.2	43.2 - 47.4 - 51.0	1633	1652	This study
TUB2Fd	GTB CAC CTY CAR ACC GGY CAR TG	Forward	59.4	46.1 - 51.4 - 56.4	74	96	This study
TUB2Rd	TCA CCA GTG TAC CAA TGM ARG AAA GCC	Reverse	48.1	48.3 - 50.1 - 52.0	1545	1565	This study
TUB3Fd	AAA THG GTG CYG CHT TCT GG	Forward	50.8	42.5 - 45.9 - 50.5	170	189	This study
TUB3Rd	TCV GWG TTS AGY TGA CCN GGG	Reverse	60.3	46.1 - 50.5 - 54.0	1039	1059	This study
TUB4Fd	GGH GCY GGH AAC AAC TGG GC	Forward	65.8	48.3 - 52.2 - 57.7	600	618	This study
TUB4Rd	CCR GAY TGR CCR AAR ACR AAG TTG TC	Reverse	50.0	44.4 - 49.4 - 54.4	581	606	This study
<b>Calmodulin (<i>Colletotrichum gloeosporioides</i> GenBank accession HM575363)</b>							
CAL-228F	GAG TTC AAG GAG GCC TTC TCC C	Forward	59.1	49.2	2	23	Carbone & Kohn (1999)
CAL-737R	CAT CTT TCT GGC CAT CAT GG	Reverse	50.0	43.4	439	458	Carbone & Kohn (1999)
CAL1Rd	GCA TCA TRA GYT RGA CRAACT CG	Reverse	47.8	41.0 - 45.4 - 49.7	747	769	This study
CAL2Rd	TGR TCN GCC TCD CGG ATC ATC TC	Reverse	58.0	47.5 - 50.8 - 54.9	647	669	This study
<b>Histone H3 (<i>Talaromyces stipitatus</i> GenBank accession XM_002478391)</b>							
CYLH3F	AGG TCC ACT GGT GGC AAG	Forward	61.1	47.6	28	45	Crous <i>et al.</i> (2004c)
CYLH3R	AGC TGG ATG TCC TTG GAC TG	Reverse	55.0	46.6	361	380	Crous <i>et al.</i> (2004c)
H3-1a	ACT AAG CAG ACC GCC CGC AGG	Forward	66.7	54.2	10	30	Glass & Donaldson (1995)
H3-1b	GCG GGC GAG CTG GAT GTC CTT	Reverse	66.7	54.5	367	387	Glass & Donaldson (1995)
HIS1Rd	RCG RAG RCG ACG GGC	Reverse	76.7	45.4 - 50.0 - 54.6	382	396	This study
HIS2Rd	GGA TGG TRA CAC GCT TRG CGT G	Reverse	59.1	47.9 - 50.5 - 53.1	240	361	This study
<b>ITS (<i>Magnaporthe grisea</i> GenBank accession AB026819)</b>							
ITS1	TCC GTA GGT GAA CCT GCG G	Forward	63.2	49.5	2162	2180	White <i>et al.</i> (1990)
ITS4	TCC TCC GCT TAT TGA TAT GC	Reverse	45.0	41.6	2685	2704	White <i>et al.</i> (1990)
ITS5	GGAAGT AAAAGT CGT AAC AAG G	Forward	40.9	40.8	2138	2159	White <i>et al.</i> (1990)
V9G	TTA CGT CCC TGC CCT TTG TA	Forward	45.0	42.8	2002	2021	de Hoog & Gerrits van den Ende (1998)
<b>Translation elongation factor 1-alpha (<i>Sordaria macrospora</i> GenBank accession X96615)</b>							
CylEF-R2	CAT GTT CTT GAT GAA RTC ACG	Reverse	40.5	39.2 - 40.2 - 41.1	783	803	Crous <i>et al.</i> (2004c)
EF-1	ATG GGT AAG GAR GAC AAG AC	Forward	47.5	41.2 - 42.3 - 43.4	190	209	O'Donnell <i>et al.</i> (1998)
EF-2	GGA RGT ACC AGT SAT CAT GTT	Reverse	45.2	41.6 - 42.6 - 43.7	798	818	O'Donnell <i>et al.</i> (1998)
EF-22	AGG AAC CCT TAC CGA GCT C	Reverse	57.9	46.2	578	596	O'Donnell <i>et al.</i> (1998)
EF1-1567R	ACH GTR CCR ATA CCA CCR ATC TT	Reverse	47.1	43.1 - 47.2 - 52.0	1254	1276	Designed by S. Rehner ( <a href="http://www.aftol.org/pdfs/EF1primer.pdf">www.aftol.org/pdfs/EF1primer.pdf</a> )



Table 2. (Continued).

Name	Sequence (5' – 3')	Orientation	%GC	Tm (°C)	Start	End	Reference
Translation elongation factor 1-alpha ( <i>Sordaria macrospora</i> GenBank accession X96615)							
EF1-2218R	ATG ACA CCR ACR GCR ACR GTY TG	Reverse	54.3	45.6 - 50.4 - 55.1	1782	1804	Designed by S. Rehner (www.aftol.org/pdfs/EF1primer.pdf)
EF1-526F	GTC GTY GTY ATY GGH CAY GT	Forward	51.7	40.0 - 45.6 - 52.2	220	239	Designed by S. Rehner (www.aftol.org/pdfs/EF1primer.pdf)
EF1-728F	CAT CGA GAA GTT CGA GAA GG	Forward	50.0	42.2	306	325	Carbone & Kohn (1999)
EF1-986R	TAC TTG AAG GAA CCC TTA CC	Reverse	45.0	40.9	584	603	Carbone & Kohn (1999)
EF1Fd	GTC GTT ATC GGC CAC GTC G	Forward	63.2	48.5	223	241	This study
EF1Rd	CGG MCT TGG TGA CCT TGC C	Reverse	65.8	48.8 - 50.4 - 52.0	1836	1852	This study
EF2Fd	GAT CTA CCA GTG CGG TGG	Forward	61.1	45.4	273	290	This study
EF2Rd	GGT GCA TYT CSA CGG ACT TGA C	Reverse	56.8	48.2 - 49.1 - 49.9	1356	1377	This study
EF3Fd	GAG CGT GAG CGT GGT ATC AC	Forward	60.0	48.1	632	651	This study
EF3Rd	GGT ACG CTK GTC RAT ACC ACC	Reverse	57.1	45.5 - 47.5 - 49.6	286	306	This study
EF4Fd	GGT GCA TYT CSA CGG ACT TGA C	Forward	56.8	48.2 - 49.1 - 49.9	1356	1377	This study

## Taxonomy

Morphological descriptions are based on structures *in vivo*, with morphological structures *in vitro* noted where relevant. Structures were mounted in clear lactic acid, and 30 measurements ( $\times 1\,000$  magnification) determined wherever possible, with the extremes of spore measurements given in parentheses. Observations were made with a Zeiss V20 Discovery stereo-microscope, and with a Zeiss Axio Imager 2 light microscope using differential interference contrast (DIC) illumination and an AxioCam MRc5 camera and software. Colony colours (surface and reverse) were assessed on different culture media at 25 °C in the dark, using the colour charts of Rayner (1970). All isolates obtained in this study are maintained in culture collections (Table 1). Nomenclatural novelties and descriptions were deposited in MycoBank (www.Mycobank.org; Crous *et al.* 2004a).

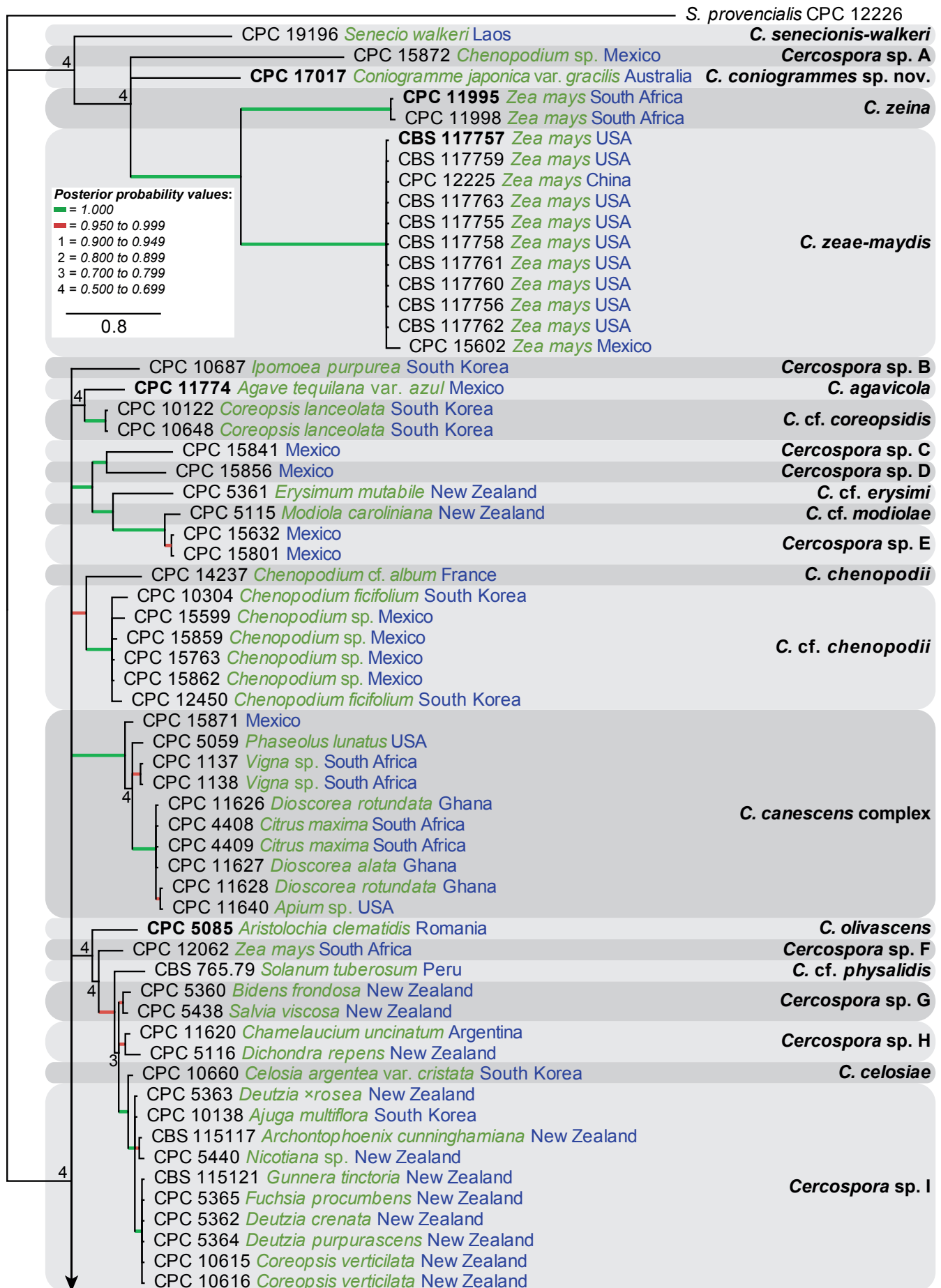
## RESULTS

### DNA phylogeny

Amplification products and gene sequences of similar size to that reported previously (Groenewald *et al.* 2005, 2010a) were obtained. The resulting concatenated alignment contains 361 taxa (including the outgroup taxon), and 471, 263, 199, 240 and 347 characters (including alignment gaps) were used in the ITS, TEF, ACT, CAL and HIS partitions, respectively. Based on the results of MrModeltest, the following priors were set in MrBayes for the different partitions: all partitions had dirichlet base frequencies and GTR+G models with gamma-distributed rates were implemented for ITS, ACT and CAL, and HKY+G with gamma-distributed rates for TEF while HIS required HKY+I+G with inverse gamma-distributed rates. The final aligned combined data set contained 361 ingroup taxa with a total of 1 305 characters and *Septoria provincialis* (isolate CPC 12226) served as the outgroup taxon. From this alignment 1 520 characters were used for the Bayesian analysis; these contained 588 unique site patterns (48, 172, 111, 125 and 132 for ITS, TEF, ACT, CAL and HIS, respectively). The Bayesian analysis lasted 3 995 000 generations and the consensus trees and posterior probabilities were calculated from the 5 994

trees left after discarding 1 998 trees (the first 1 000 generations) for burn-in (Fig. 2).

The ITS region has limited resolution for almost all species in *Cercospora* and therefore the results of the other gene regions were particularly useful for comparison of clade stability. Neighbour-joining analyses using the HKY85 substitution model were applied to each data partition to check the stability and robustness of each species clade under the different partitions (data not shown). The ITS region was only able to distinguish *C. zeina* and *C. zeae-maydis* from the rest of the included species. The TEF region was able to distinguish 33 of the 73 species clades and especially failed for *Cercospora* sp. M–Q (including *C. cf. sigesbeckiae* and *C. cf. richardiicola*; spanning most of Fig. 2 part 4 and the upper half of part 5), whereas ACT distinguished 43 of the 73 species clades and especially failed for *Cercospora* sp. G–I (Fig. 2 part 1) and including *C. cf. flagellaris* and *C. alchemillicola/C. cf. alchemillicola*. The ACT region also accounted for most of the variation observed for *Cercospora* sp. Q. The CAL region was able to distinguish 34 of the 73 species clades but especially failed for *Cercospora* sp. M, P and Q (including *C. kikuchii*, *C. cf. sigesbeckiae*, *C. cf. richardiicola* and *C. rodmanii*; spanning middle of Fig. 2 part 4), as well as a group consisting predominantly of *C. armoraciae*, *C. capsici*, *C. zebrina* and *C. violae* (Fig. 2 part 3). Although the locus was able to separate *C. beticola* and *C. apii*, it could not distinguish *C. cf. brunii* and *C. cf. resedae* from *C. apii*. The HIS region distinguished 46 of the 73 species clades and especially failed for *Cercospora* sp. G–I (Fig. 2 part 1) and *Cercospora* sp. M, P and Q (including *C. kikuchii*, *C. cf. richardiicola* and *C. rodmanii*; spanning middle of Fig. 2 part 4). The HIS region also accounted for most of the variation observed for *C. armoraciae* and was responsible for the split of *C. beticola* into two clades. No single gene region was found which could reliably distinguish all species and, irrespective of which locus was used, occurrences of the same sequence(s) shared between multiple species were observed. If data for ITS is not taken into consideration, the remaining four loci always distinguish the following 18 species: *C. agavicola*, *C. apicola*, *C. coniogramme*, *C. cf. erysimi*, *C. euphorbiae-sieboldianae*, *C. helianthicola*, *C. mercurialis*, *C. olivascens*, *C. pileicola*, *C. senecionis-walkerii*, *C. violae*, *C. zeae-maydis*, *C. zeina*, *Cercospora* sp. A, *Cercospora* sp. C, *Cercospora* sp. D, *Cercospora* sp. J, *Cercospora* sp. R. Some species are only distinguished based on a single locus and these results are discussed under the species notes, where applicable.



**Fig. 2.** (Part 1). Consensus phylogram (50 % majority rule) of 5 994 trees resulting from a Bayesian analysis of the combined 5-gene sequence alignment using MrBayes v. 3.2.0. Bayesian posterior probabilities are indicated with colour-coded branches and numbers (see legend) and the scale bar represents the expected changes per site. Species clades are indicated in coloured blocks and species names in black text. Hosts and countries of origin are indicated in green and blue text, respectively. The tree was rooted to *Septoria provencialis* (strain CPC 12226).

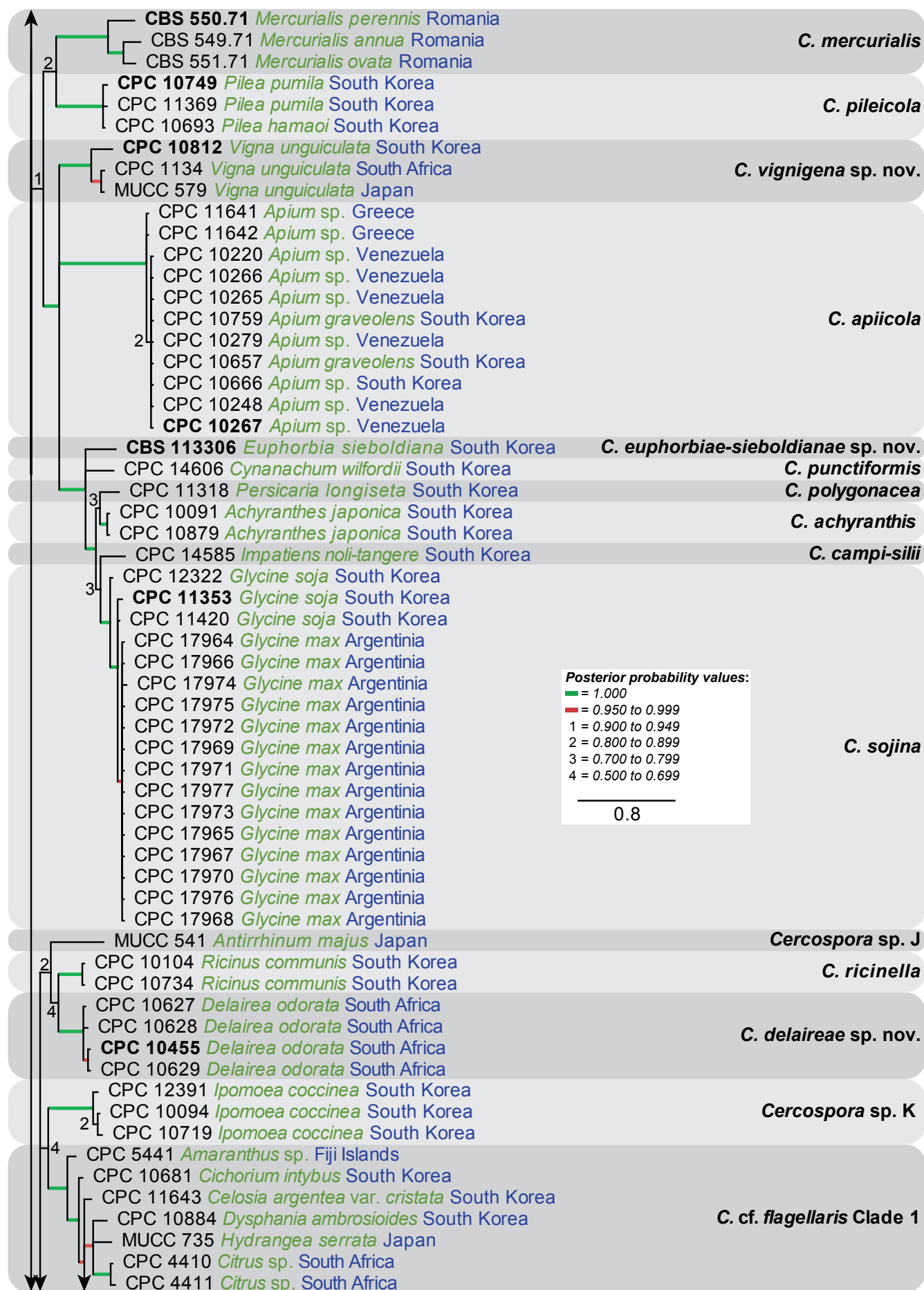


Fig. 2. (Part 2).

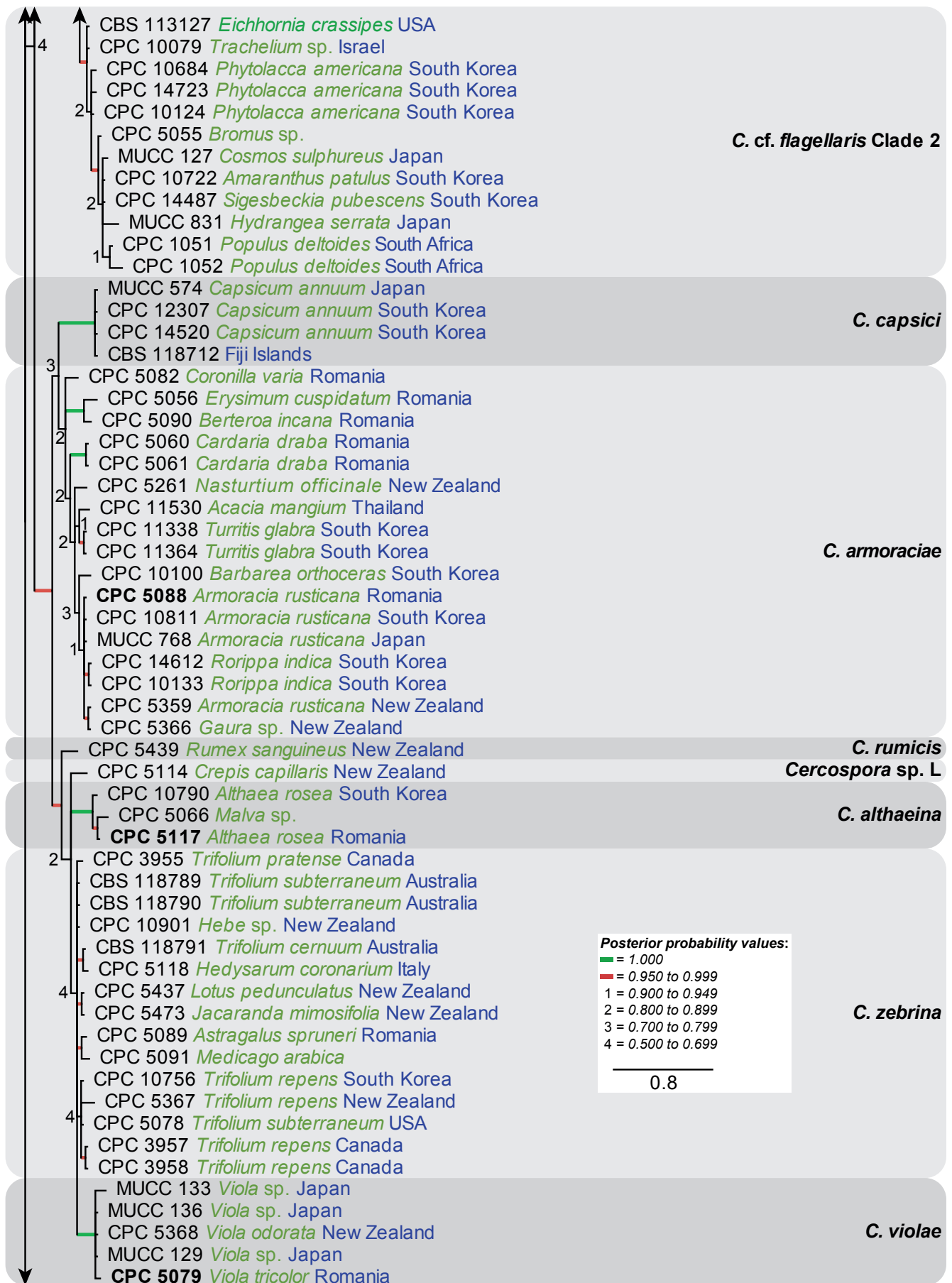


Fig. 2. (Part 3).



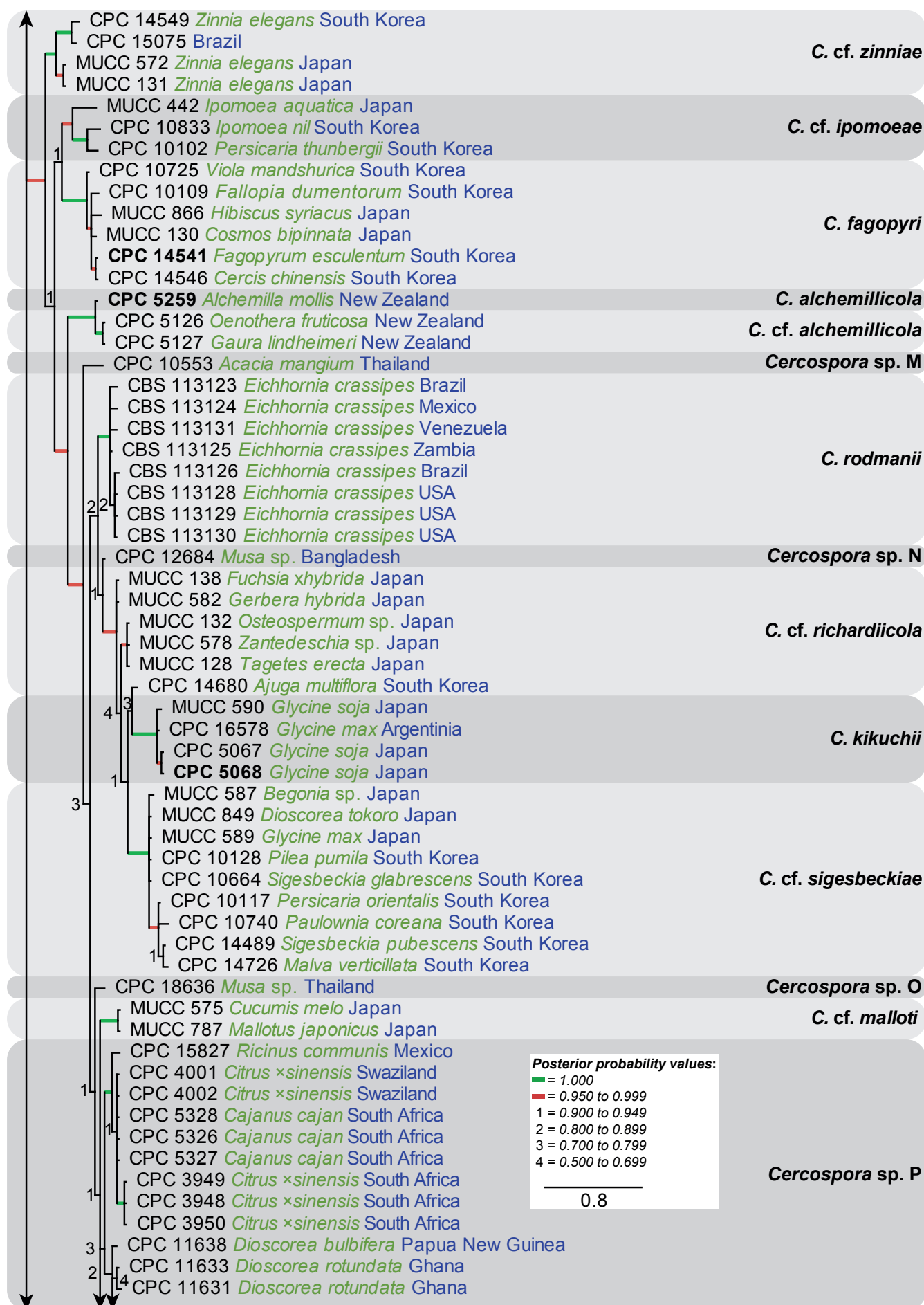


Fig. 2. (Part 4).

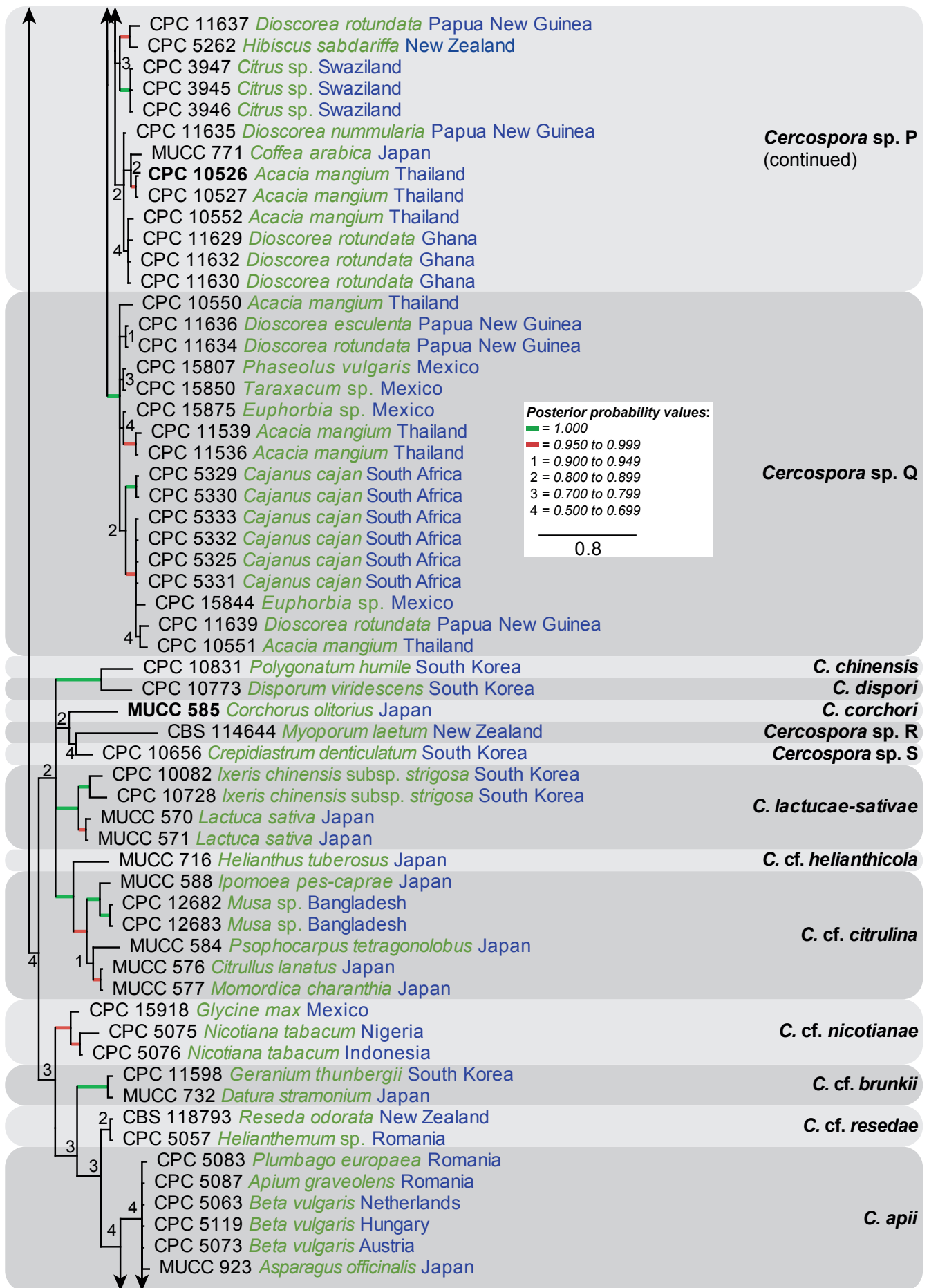


Fig. 2. (Part 5).

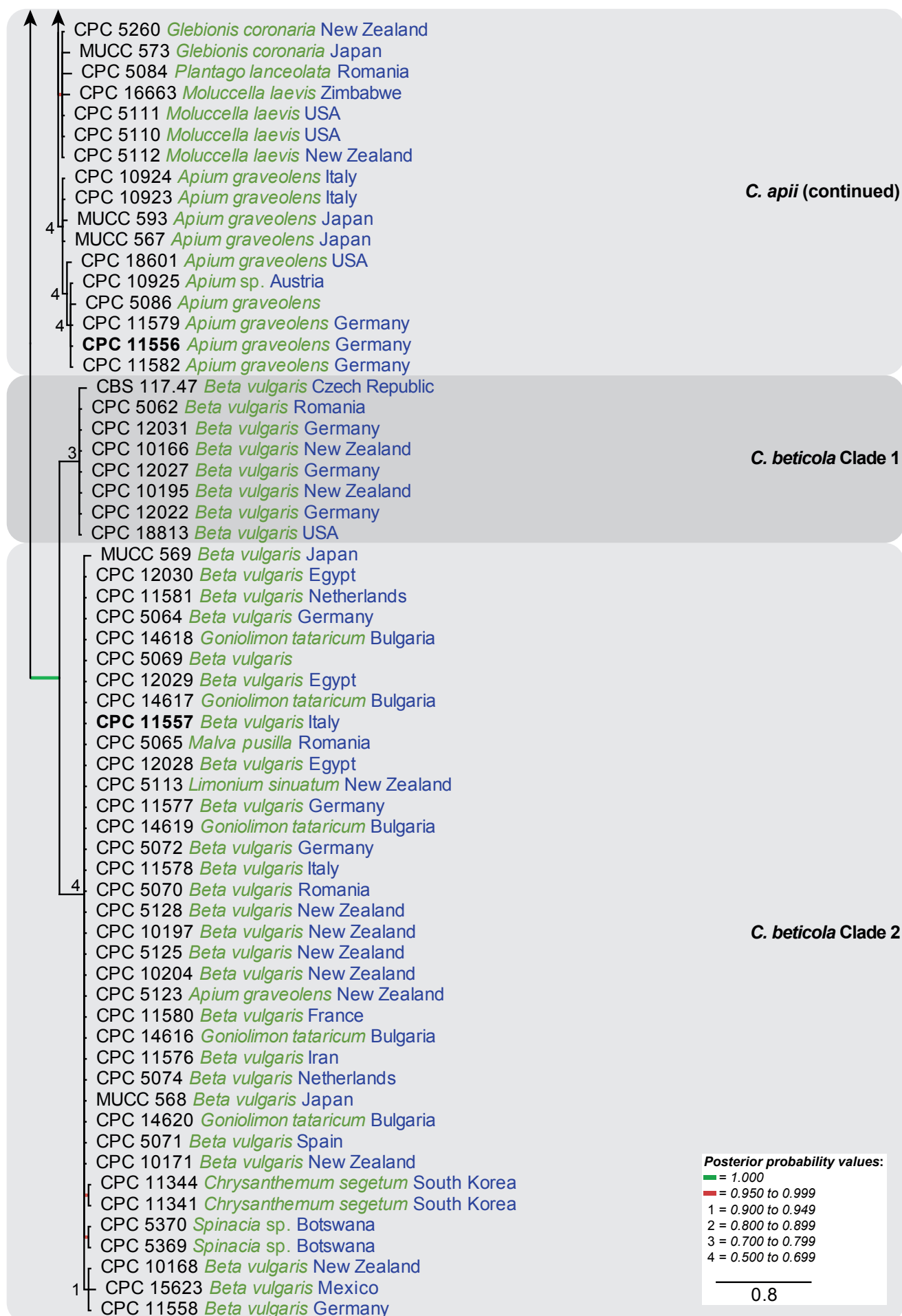


Fig. 2. (Part 6).

**Table 3.** Results from screening *Cercospora* sp. Q strains with additional loci. The percentage similarity was calculated relative to strain CPC 5325, for which sequences were generated for all loci. The number of nucleotides used for the calculation of the similarity is shown in front of the percentage. For abbreviations of loci see Table 1 and in addition: GAPDH: partial glyceraldehyde-3-phosphate dehydrogenase gene; mtSSU: partial mitochondrial small rRNA gene; CHS: partial chitin synthase gene; TUB: partial beta-tubulin gene; Mcm7: partial gene encoding a mini-chromosome maintenance protein.

Original name	Culture accession number(s)	Host name	Percentage similarity and allele group (-VI) designation per locus						GenBank accession numbers	
			GAPDH	mtSSU	CHS	TUB	Mcm7		(GAPDH, mtSSU, CHS, TUB, Mcm7)	
<i>Cercospora apii</i>	CBS 113997; CPC 5325	<i>Cajanus cajan</i>	979 nt	I	573 nt	I	597 nt	I	501 nt	JX142521, JX142504, JX142487, JX142478, JX142473
<i>Cercospora apii</i>	CBS 115410; CPC 5331	<i>Cajanus cajan</i>	966 nt (100 %)	I	573 nt (100 %)	I	597 nt (99 %)	I	—	JX142522, JX142505, JX142488, JX142479, —
<i>Cercospora apii</i>	CBS 115411; CPC 5332	<i>Cajanus cajan</i>	966 nt (100 %)	I	573 nt (100 %)	I	597 nt (100 %)	III	—	JX142523, JX142506, JX142489, JX142480, —
<i>Cercospora apii</i>	CBS 115412; CPC 5333	<i>Cajanus cajan</i>	966 nt (100 %)	I	573 nt (100 %)	I	322 nt (9.9 %)	III	—	JX142524, JX142507, JX142490, JX142481, —
<i>Cercospora apii</i>	CBS 115536; CPC 5329	<i>Cajanus cajan</i>	970 nt (95 %)	V	573 nt (100 %)	I	597 nt (99 %)	II	—	JX142525, JX142508, JX142491, JX142482, —
<i>Cercospora apii</i>	CBS 115537; CPC 5330	<i>Cajanus cajan</i>	970 nt (95 %)	V	573 nt (100 %)	I	597 nt (99 %)	II	—	JX142526, JX142509, JX142492, JX142483, —
<i>Cercospora acaciae-mangii</i>	CPC 10550	<i>Acacia mangium</i>	979 nt (100 %)	I	573 nt (100 %)	I	450 nt (99 %)	I	501 nt (99 %)	JX142533, JX142516, JX142499, JX142484, JX142475
<i>Cercospora acaciae-mangii</i>	CPC 10551	<i>Acacia mangium</i>	979 nt (99 %)	I	573 nt (100 %)	I	—	III	501 nt (99 %)	JX142534, JX142517, JX142500, —, JX142476
<i>Cercospora</i> sp. 2	CBS 132656; CPC 11536	<i>Acacia mangium</i>	961 nt (96 %)	III	573 nt (100 %)	I	—	—	—	JX142527, JX142510, JX142493, —, —
<i>Cercospora</i> sp. 2	CPC 11539	<i>Acacia mangium</i>	958 nt (96 %)	III	573 nt (100 %)	I	—	—	—	JX142535, JX142518, JX142501, —, —
<i>Cercospora dioscoreae-pyrifoliae</i>	CBS 132661; CPC 11634; PNG-002	<i>Dioscorea rotundata</i>	970 nt (95 %)	VI	573 nt (100 %)	I	—	III	458 nt (99 %)	JX142528, JX142511, JX142494, —, JX142474
<i>Cercospora dioscoreae-pyrifoliae</i>	CBS 132663; CPC 11636; PNG-016	<i>Dioscorea esculenta</i>	969 nt (96 %)	IV	573 nt (100 %)	I	—	—	—	JX142529, JX142512, JX142495, —, —
<i>Cercospora dioscoreae-pyrifoliae</i>	CPC 11639; PNG-037	<i>Dioscorea rotundata</i>	969 nt (95 %)	VI	573 nt (100 %)	I	—	—	—	JX142536, JX142519, JX142502, —, —
<i>Cercosporoid</i>	CBS 132679; CPC 15807	<i>Phaseolus vulgaris</i>	954 nt (100 %)	I	573 nt (100 %)	I	—	—	—	JX142530, JX142513, JX142496, —, —
<i>Cercospora</i> sp.	CBS 132681; CPC 15844	<i>Euphorbia</i> sp.	956 nt (96 %)	III	573 nt (100 %)	I	—	—	—	JX142531, JX142514, JX142497, —, —
<i>Cercospora</i> sp.	CBS 132682; CPC 15850	<i>Taraxacum</i> sp.	960 nt (100 %)	I	573 nt (100 %)	I	—	—	—	JX142532, JX142515, JX142498, —, —
<i>Cercospora</i> sp.	CPC 15875	<i>Euphorbia</i> sp.	955 nt (99 %)	II	573 nt (100 %)	I	597 nt (99 %)	III	—	JX142537, JX142520, JX142503, JX142485, —
<i>Septoria provencialis</i> (outgroup)	CBS 118910; CPC 12226	<i>Eucalyptus</i> sp.	885 nt (87 %)	—	—	—	502 nt (82 %)	—	499 nt (81 %)	JX142538, —, —, JX142486, JX142477
Number of identical sequences (excl. outgroup):			6 of 17	17 of 17	4 of 17	0 of 8	0 of 4			

Table 3. (Continued).

Original name	Culture accession number(s)	Host name	Percentage similarity and allele group (I-VI) designation per locus					GenBank accession numbers					
			ITS	TEF	ACT	CAL	HIS	(ITS, TEF, ACT, CAL, HIS)					
<i>Cercospora apii</i>	CBS 113997; CPC 5325	<i>Cajanus cajan</i>	481 nt	I	306 nt	I	221 nt	I	312 nt	I	378 nt	I	JX143717, JX143476, JX143230, JX142984, JX142738
<i>Cercospora apii</i>	CBS 115410; CPC 5331	<i>Cajanus cajan</i>	481 nt (100 %)	I	280 nt (100 %)	I	194 nt (100 %)	I	280 nt (100 %)	I	378 nt (100 %)	I	JX143718, JX143477, JX143231, JX142985, JX142739
<i>Cercospora apii</i>	CBS 115411; CPC 5332	<i>Cajanus cajan</i>	481 nt (100 %)	I	280 nt (100 %)	I	194 nt (100 %)	I	280 nt (100 %)	I	378 nt (100 %)	I	JX143719, JX143478, JX143232, JX142986, JX142740
<i>Cercospora apii</i>	CBS 115412; CPC 5333	<i>Cajanus cajan</i>	481 nt (100 %)	I	280 nt (100 %)	I	194 nt (100 %)	I	280 nt (100 %)	I	378 nt (100 %)	I	JX143720, JX143479, JX143233, JX142987, JX142741
<i>Cercospora apii</i>	CBS 115536; CPC 5329	<i>Cajanus cajan</i>	481 nt (100 %)	I	280 nt (100 %)	I	194 nt (100 %)	I	278 nt (100 %)	I	378 nt (98 %)	III	JX143721, JX143480, JX143234, JX142988, JX142742
<i>Cercospora apii</i>	CBS 115537; CPC 5330	<i>Cajanus cajan</i>	481 nt (100 %)	I	280 nt (100 %)	I	194 nt (100 %)	I	280 nt (100 %)	I	378 nt (98 %)	III	JX143722, JX143481, JX143235, JX142989, JX142743
<i>Cercospora acaciae-mangii</i>	CPC 10550	<i>Acacia mangium</i>	481 nt (99 %)	II	306 nt (100 %)	I	221 nt (99 %)	II	312 nt (100 %)	I	377 nt (99 %)	IV	AY752139, AY752172, AY752200, AY752231, AY752262
<i>Cercospora acaciae-mangii</i>	CPC 10551	<i>Acacia mangium</i>	481 nt (99 %)	II	306 nt (100 %)	I	221 nt (99 %)	IV	305 nt (100 %)	I	377 nt (100 %)	I	AY752140, AY752173, AY752201, AY752232, AY752263
<i>Cercospora</i> sp. 2	CBS 132656; CPC 11536	<i>Acacia mangium</i>	473 nt (99 %)	III	306 nt (100 %)	I	221 nt (99 %)	IV	312 nt (100 %)	I	378 nt (99 %)	IV	JX143723, JX143482, JX143236, JX142990, JX142744
<i>Cercospora</i> sp. 2	CPC 11539	<i>Acacia mangium</i>	481 nt (99 %)	III	306 nt (100 %)	I	221 nt (99 %)	IV	312 nt (100 %)	I	378 nt (98 %)	V	JX143729, JX143488, JX143242, JX142996, JX142750
<i>Cercospora dioscoreae-pyritifoliae</i>	CBS 132661; CPC 11634; PNG-002	<i>Dioscorea rotundata</i>	481 nt (99 %)	III	284 nt (100 %)	I	221 nt (99 %)	II	297 nt (100 %)	I	378 nt (99 %)	VI	JX143724, JX143483, JX143237, JX142991, JX142745
<i>Cercospora dioscoreae-pyritifoliae</i>	CBS 132663; CPC 11636; PNG-016	<i>Dioscorea esculenta</i>	481 nt (99 %)	III	306 nt (100 %)	I	221 nt (99 %)	II	303 nt (100 %)	I	378 nt (99 %)	VI	JX143725, JX143484, JX143238, JX142992, JX142746
<i>Cercospora dioscoreae-pyritifoliae</i>	CPC 11639; PNG-037	<i>Dioscorea rotundata</i>	481 nt (99 %)	II	306 nt (100 %)	I	221 nt (99 %)	II	303 nt (100 %)	I	378 nt (99 %)	II	JX143730, JX143489, JX143243, JX142997, JX142751
<i>Cercosporoid</i>	CBS 132679; CPC 15807	<i>Phaseolus vulgaris</i>	481 nt (99 %)	II	294 nt (99 %)	II	220 nt (99 %)	III	312 nt (100 %)	I	376 nt (99 %)	VI	JX143726, JX143485, JX143239, JX142993, JX142747
<i>Cercospora</i> sp.	CBS 132681; CPC 15844	<i>Euphorbia</i> sp.	481 nt (99 %)	III	294 nt (99 %)	II	220 nt (99 %)	III	312 nt (99 %)	II	376 nt (100 %)	I	JX143727, JX143486, JX143240, JX142994, JX142748
<i>Cercospora</i> sp.	CBS 132682; CPC 15850	<i>Taraxacum</i> sp.	481 nt (99 %)	II	294 nt (99 %)	II	220 nt (99 %)	III	312 nt (100 %)	I	377 nt (100 %)	VI	JX143728, JX143487, JX143241, JX142995, JX142749
<i>Cercospora</i> sp.	CPC 15875	<i>Euphorbia</i> sp.	481 nt (99 %)	III	294 nt (99 %)	II	220 nt (99 %)	III	312 nt (100 %)	I	378 nt (99 %)	VI	JX143731, JX143490, JX143244, JX142998, JX142752
<i>Septoria provencialis</i> (outgroup)	CBS 118910; CPC 12226	<i>Eucalyptus</i> sp.	483 nt (98 %)		317 nt (75 %)		227 nt (87 %)		329 nt (81 %)		386 nt (93 %)		DQ303096, JX143522, JX143276, JX143030, JX142784
Number of identical sequences (excl. outgroup):			6 of 17	13 of 17	6 of 17	16 of 17	7 of 17						



## Evaluation of additional loci

Isolates of *Cercospora* sp. Q were compared using the five loci used for the combined phylogeny and five additional loci as explained in the Materials and Methods. The results are summarised in Table 3 and detailed per locus below:

**ITS** — Three allele groups are identified based on sequence identity. The variation in this locus is based on nucleotide changes at only two positions in the second internal transcribed spacer (transitions at positions 451 and 453 compared to the sequence of isolate CPC 5325). Although allele group I was confined to isolates from *Cajanus* (*Fabaceae*), the other two groups were intermixed amongst the remaining host genera.

**TEF** — Two allele groups are identified based on sequence identity. The variation in this locus is based on a single nucleotide change (transitions at position 289 compared to the sequence of isolate CPC 5325). Although allele group I was confined to isolates from *Acacia* (*Fabaceae*), *Cajanus*, and *Dioscorea* (*Dioscoreaceae*), the other group represents the remaining host genera.

**ACT** — Four allele groups are identified based on sequence identity. The variation in this locus is based on nucleotide changes at three positions (transitions at positions 143, 166 and 173 compared to the sequence of isolate CPC 5325). Allele group I was confined to isolates from *Cajanus*, and allele group II is mainly limited to *Dioscorea* (except for one isolate from *Acacia*), allele group IV is limited to the remaining isolates from *Acacia*, and the remaining host genera belong to allele group III.

**CAL** — Two allele groups are identified based on sequence identity. The variation in this locus is based on a single nucleotide change (a transition at position 76 compared to the sequence of isolate CPC 5325). This single nucleotide change only occurred in isolate CPC 15844; the rest of the isolates had identical CAL sequences.

**HIS** — Six allele groups are identified based on sequence identity. The variation in this locus is based on nucleotide changes at 10 positions (transitions at positions 106, 112, 148, 149, 178, 205, 238, 301 and 364, as well as a transversion at position 245 compared to the sequence of isolate CPC 5325). Allele group II differs from allele group I by a unique change of C to T at position 364 and allele group V differs from allele group IV by a unique change of A to T at position 245. Even if allele group I and II and group IV and V are taken as combined groups, isolates from different hosts are intermixed and no clear association of host with allele group, as with the loci mentioned above, is possible.

**GAPDH** — Six allele groups are identified based on sequence identity. The variation in this locus is based on numerous nucleotide changes (transitions at positions 44, 48–49, 52–53, 56, 63–69, 110, 122, 149, 158, 206, 257, 287, 329, 335, 395, 440, 479, 530, 533, 566, 593, 596, 608, 647, 650, 674, 720, 731, 740, 747, 780, 789, 791–792, 794, 804–806, 808–809, 811–812, 817, 821–822, 824, 830, 834, 837, 839–840, 842–844, 846, 848, 852, 856, 874, 922 and 958, transversions at positions 49, 66, 233, 767, 785, 787–789, 792, 795, 797, 798, 806, 810–811, 814, 818–819, 821, 831, 833, 843, 848–849, 865 and 883, indels at positions 67, 101 and 803, as well as another indel spanning 801–811, compared to the sequence of isolate CPC 5325). Allele group II differs from allele group I by a

unique change of C to T at position 530. This locus represents the largest number of nucleotide substitutions of all the loci included for *Cercospora* sp. Q in this study, and therefore has high potential for species discrimination. However, if each allele group is accepted as a distinct species, it would result in a huge proliferation of taxa within this group.

**mtSSU** — Only one allele group is identified based on sequence identity. No variation was observed over the 573 nucleotides sequences for the selected isolates.

**CHS** — Three allele groups are identified based on sequence identity. The variation in this locus is based on nucleotide changes at only three positions (transitions at positions 91, 100 and 217 compared to the sequence of isolate CPC 5325). Allele group I includes four of the six isolates from *Cajanus* and allele group III includes the isolates from *Phaseolus* (*Fabaceae*) and *Euphorbia* (*Euphorbiaceae*); the remaining isolates belong to allele group II.

**TUB** — This locus failed to amplify easily, even when several different primer combinations were tested. Three allele groups are identified based on sequence identity. The variation in this locus is based on nucleotide changes at six positions (transitions at positions 147 and 396, transversions at positions 172, 189, 213 and 591 compared to the sequence of isolate CPC 5325). The majority of sequences were obtained for the isolates from *Cajanus*, and these isolates end up belonging into all three allele groups.

**Mcm7** — This locus failed to amplify easily, even when both available primer combinations were tested. Three allele groups are identified based on sequence identity. The variation in this locus is based on nucleotide changes at six positions (transitions at positions 60, 86, 263, 365 and 470, and a transversion at position 89, compared to the sequence of isolate CPC 5325). Due to the small number of successful sequences, a clear conclusion cannot be drawn from this dataset and it was not possible to distinguish between the isolates from *Acacia* and *Dioscorea*.

## TAXONOMY

In this paper, a polyphasic approach was taken and species are discussed and/or described with consideration to the following factors:

**Phylogenetic analyses:** Based on the clustering and support in the Bayesian tree obtained from the combined ITS, TEF, ACT, CAL and HIS alignment (Fig. 2). All genes were also assessed individually (data not shown; discussed where applicable in the species notes).

**Morphological characteristics:** A few morphological characteristics effectively distinguished species (Fig. 3). These are: conidiophores (uniform, irregular, attenuated, truncate, long or short obconically truncate), conidiogenous cells (terminal, intercalary), loci (apical, lateral, circumspersed (all around the conidiogenous cell; Hennebert & Sutton 1994); uni-local (single, terminal locus), multi-local (multiple loci); thickness, absence of protuberant loci), and conidia (dimensions, shape, hilum morphology).

A diagnostic characteristic of species with wide host ranges was circumspersed loci on tenuous conidiophores, whereas the species with narrow host ranges had a few distinct apical or lateral



**Fig. 3.** Overview of morphological structures. A. Fasciculate conidiophores situated on a stroma. B. Conidiophores reduced to uni-local conidiogenous cells. C. Conidiophores arising from a weakly developed stroma. D. Fasciculate conidiophore with flexuous conidiophores. E. Conidiophores arising from external mycelium. F. Thickened, darkened and somewhat refractive conidial loci (arrows). G. Conidiogenous cells with multi-local loci. H. Fascicle erupting through stoma. I. Cylindrical conidium with obtuse apex. J. Filiform conidium. K, L. Acicular, undulate conidia with subobtusely rounded apices, and truncate bases. M–O. Oblavate conidia with subobtusely rounded apices and obconically truncate bases. P. Subcylindrical conidium with long obconically truncate base.

loci on moderately thick-walled to thick-walled conidiophores. These characteristics were preserved, even when the fungus was cultivated on agar medium.

The Bayesian analysis resulted in 73 species clades mapped onto the phylogenetic tree (Fig. 2); 34 of these were assigned to an existing species name, 15 more were morphologically similar to existing species but names could not be applied without doubt (indicated with “cf.” in the species name, see species notes below), a further 19 could not be named unequivocally (“*Cercospora* spp.

A–S”) and novel species are introduced below for the remaining five clades.

***Cercospora achyranthis*** Syd. & P. Syd., Ann. Mycol. 7: 171. 1909.

*Caespituli* amphigenous, mainly hypophyllous. *Mycelium* internal. *Stromata* lacking or composed of a few brown cells, intraepidermal or substomatal. *Conidiophores* thick-walled, dark brown, arising from



internal hyphae or a few brown cells, solitary, or in loose fascicles (2–5), straight, sinuous to distinctly geniculate, flexuous, almost uniform in width, somewhat wider at the apex, often constricted at septa and proliferating point, conical at the apex, simple, sometimes branched,  $31\text{--}340 \times 4.5\text{--}6 \mu\text{m}$ , 2–20-septate. *Conidiogenous cells* integrated, terminal and intercalary, proliferating sympodially, multi-local; loci distinctly thickened, darkened, slightly to distinctly protuberant, apical or formed on shoulders caused by geniculation,  $2\text{--}3 \mu\text{m}$  diam. *Conidia* solitary, subhyaline, acicular, cylindrical to cylindro-obclavate, straight to slightly curved, long obconically truncated and thickened at the base, obtuse at the apex, rarely constricted at the septa,  $33\text{--}172 \times 3.5\text{--}8 \mu\text{m}$ , 3–20-septate.

*Specimens examined:* **South Korea**, Jeju, on *Achyranthes japonica* (Amaranthaceae), 14 Sep. 2002, H.D. Shin, CBS H-20983, CPC 10088–10091; on *A. japonica*, 13 Nov. 2003, H.D. Shin, CBS H-20984, CBS 132613 = CPC 10879, CPC 10880–10881.

*Notes:* This species is characterised by conidiophores with a thickened, dark brown wall, vary in shape, often constricted at septa, and conical at the apex, sometimes branched, and longer than in most other species ( $31\text{--}340 \times 4.5\text{--}6 \mu\text{m}$ , 2–20-septate). The conidia of *C. achyranthis* are not hyaline, but subhyaline to pale olivaceous and have rather small hila (ca.  $2 \mu\text{m}$  wide), which are reminiscent of the genus *Passalora*. Nevertheless, it is a true *Cercospora*. *Cercospora achyranthis* is supported by ACT. The TEF and CAL phylogenies fail to discriminate *C. sojina* (also with subhyaline conidia and small hila) from *C. achyranthis*. On the HIS phylogeny, it is indistinguishable from *C. polygonaceae*, to which it is also a sister taxon in the combined tree (Fig. 2 part 2). The name *C. achyranthis* is based on Japanese material, and fresh collections from Japan would be required to designate an epitype for this taxon.

***Cercospora agavicola*** Ayala-Escobar, Mycotaxon 93: 117. 2005.

*Specimen examined:* **Mexico**, State of Guanajuato, Penjamo, on *Agave tequilana* var. *azul* (Agavaceae), Jan. 2003, V. Ayala-Escobar and Ma. de Jesús Yáñez-Morales, **holotype** CHAPA# 166, **isotype** HAL 1839 F, culture ex-type CBS 117292 = CPC 11774.

*Notes:* *Cercospora agavicola* is characterised by large stromata and consistently cylindrical conidia, often with swollen tips (Ayala-Escobar *et al.* 2005). In this study using a larger dataset, it is also clear that *C. agavicola*, which is supported by TEF, ACT, CAL and HIS regions, is genetically distinct from the other *Cercospora* species studied. In the combined tree (Fig. 2 part 1), it is a sister taxon to *C. cf. coreopsidis*.

***Cercospora alchemillicola*** U. Braun & C.F. Hill, Mycol. Progr. 1: 19. 2002.

*Specimens examined:* **New Zealand**, Auckland, Western Springs Gardens, on *Alchemilla mollis* (Rosaceae), 23 Jul. 2000, C.F. Hill, Lynfield 236 (holotype HAL, isotype PDD 73031); on *A. mollis*, C.F. Hill, Lynfield 564, **epitype designated here** CBS H-20985, culture ex-epitype CPC 5259.

*Notes:* Sequences from New Zealand on hosts of *Onagraceae* (*Gaura*, isolate CPC 5127, and *Oenothera*, isolate CPC 5126) are slightly distinct from that derived from *Alchemilla* (Rosaceae). The collections on *Onagraceae* (*C. cf. alchemillicola*) are also morphologically different from *C. alchemillicola*, and represent an undescribed species. The three isolates are identical to one another on the TEF, ACT, CAL and HIS phylogenies but also to

some other species, e.g. to *Cercospora* sp. I, *C. cf. physalidis* and *C. celosiae* based on the TEF phylogeny, and *Cercospora* sp. I and *C. cf. physalidis* based on the ACT phylogeny. A similar mix is observed in the HIS phylogeny with *Cercospora* sp. I and *C. celosiae* and in the CAL phylogeny with *Cercospora* spp. M, O, P, Q and *C. cf. sigesbeckiae*. In the combined tree (Fig. 2 part 4), the three isolates represent sister taxa.

### ***Cercospora cf. alchemillicola***

*Specimens examined:* **New Zealand**, Auckland City, Albert Park, on *Gaura lindheimeri* (Onagraceae), C.F. Hill, Lynfield 545, CPC 5127; on *Oenothera fruticosa* (Onagraceae), C.F. Hill, Lynfield 541, CPC 5126.

*Notes:* *Cercospora* on *Gaura* and *Oenothera* in New Zealand cannot be distinguished on the individual gene trees from *C. alchemillicola* (see species notes under that species above) described from New Zealand on *Alchemilla mollis* (Braun & Hill 2002). We consider the latter two isolates to represent a distinct species, which cannot be formally named due to the absence of good specimens. In the combined tree (Fig. 2 part 4), it is a sister taxon to *C. alchemillicola*.

***Cercospora althaeina*** Sacc., *Michelia* 1: 269. 1878.

= *Cercospora kellermanii* Bubák, *J. Mycol.* 9: 3. 1903.

= *Cercospora althaeina* var. *praecincta* Davis, *Trans. Wisconsin Acad. Sci.* 18: 260. 1915.

≡ *Cercospora praecincta* (Davis) Chupp, *A monograph of the fungus genus Cercospora*: 376. 1954.

= *Cercospora ramularia* Siemaszko, *Izv. Kavkazsk. Muz.* 12: 28. 1919, and *Arch. Nauk Biol. Towarz. Nauk. Warszawsk.* 1: 49. 1923.

≡ *Cercosporina ramularia* (Siemaszko) Sacc., *Syll. Fung.* 25: 910. 1931.

= *Cercospora althaeina* var. *althaeae-officinalis* Săvul. & Sandu, *Hedwigia* 73: 127. 1933.

= *Cercospora althaeicola* J.M. Yen & S.K. Sun, *Cryptog. Mycol.* 4: 189. 1983.

*Leaf spots* distinct, angular to irregular, mostly vein-limited, olivaceous-brown, sometimes greyish brown with dark brown margin, centre becoming pale grey with black dots (= stroma with conidiophores). *Caespituli* amphigenous, mostly epiphyllous. *Mycelium* internal. *Stromata* well-developed, emerging through stomatal openings or erumpent through the cuticle. *Conidiophores* in divergent fascicles (6–12), pale olivaceous-brown at the base, paler upwards, 0–3-septate, straight to mildly curved,  $32\text{--}90 \times 4\text{--}6.5 \mu\text{m}$ , conically narrowed at the apex; loci  $1.5\text{--}2 \mu\text{m}$  wide, conspicuous, apical or on shoulders formed by geniculation. *Conidia* solitary, obclavate-cylindrical to filiform, not acicular, straight to mildly curved, hyaline, 1–10-septate, obtuse at the apex, subtruncate or obconically truncate at the base,  $40\text{--}140 \times 3.5\text{--}5 \mu\text{m}$  (adapted from Shin & Kim 2001).

*Specimens examined:* **Italy**, Selva, on *Althaea rosea*, 1876, **holotype** in PAD. **Romania**, Fundulea, on *A. rosea*, O. Constantinescu, **epitype designated here** CBS H-9811, culture ex-epitype CBS 248.67 = CPC 5117. **Unknown**, on *Malva* sp. (Malvaceae), C. Killian, CBS 126.26 = CPC 5066, (as *C. malvacearum*). **South Korea**, Suwon, on *Althaea rosea* (Malvaceae), 14 Oct. 2003, H.D. Shin, CBS H-20986, CBS 132609 = CPC 10790.

*Notes:* A true *Cercospora* s. str. close to *C. apii* s. lat., but distinguished by obclavate-cylindrical conidia with obconically truncate bases (Crous & Braun 2003). Although only weakly supported as distinct from *C. armoraciae*, we suspect that the isolate from *Malva* sp. represents a different taxon. Further isolates and pathogenicity studies are needed to test this hypothesis. The species is distinguished in the TEF and ACT phylogenies but cannot be distinguished from *C. zebrina*, *Cercospora* sp. L and

*C. rumicis* based on the CAL phylogeny. In the HIS phylogeny the three isolates are not identical to any other species but the isolate from *Malva* sp. clusters distinct from the two *A. rosea* isolates which form a sister clade to *C. chenopodii*. In the combined tree (Fig. 2 part 3), it is a sister taxon to *C. zebrina*.

***Cercospora apii*** Fresen., emend. Groenewald *et al.* Phytopathology 95: 954. 2005.

*Caespituli* amphigenous. *Mycelium* internal. *Stromata* lacking or small, up to 32 µm diam, brown, substomatal or intraepidermal. *Conidiophores* arising from upper part of stromata or internal hyphae, solitary to 2–8, in loose to dense fascicles, brown, paler towards the apex, simple, mildly sinuous, moderately thick-walled to thick-walled, straight or once abruptly geniculate caused by sympodial proliferation, slightly curved, uniform in width, wider at the base, short conically truncate or truncate at the apex, 12.5–160 × 5–8 µm. *Conidiogenous cells* integrated, terminal or intercalary, proliferating sympodially, chiefly uni-local; loci distinctly thickened, not or slightly protuberant, 2–4 µm diam, apical or formed on the shoulder caused by sympodial proliferation. *Conidia* solitary, hyaline, cylindro-obclavate when shorter, longer conidia usually acicular, straight to slightly curved, subacute to obtuse at the apex, truncate to obconically truncate and thickened at the base, 35–120 × 3.5–5 µm, 3–10-septate.

*Specimens examined:* **Austria**, Wien, on *Beta vulgaris* (*Chenopodiaceae*), Jun. 1931, E.W. Schmidt, CBS 121.31 = CPC 5073; on *Apium* sp. (*Apiaceae*), 28 Aug. 2003, Institut für Pflanzengesundheit, CBS 114416 = CPC 10925. **Germany**, Landwirtschaftsamt, Heilbronn, on *Apium graveolens* (*Apiaceae*), K. Schrameyer, culture ex-type CBS 116455 = CPC 11556; CBS 116504 = CPC 11579; CBS 116507 = CPC 11582. **Hungary**, on *B. vulgaris*, Jun. 1931, E.W. Schmidt, CBS 127.31 = CPC 5119. **Italy**, on *A. graveolens*, M. Meutri, CBS 114418 = CPC 10924; CBS 114485 = CPC 10923. **Japan**, Aichi, on *A. graveolens*, 1 Nov. 1995, T. Kobayashi, MUCC 567 = MAFF 238072 = MUCNS 30 (named as *C. apii* s. str.); Shizuoka, on *A. graveolens*, 8 Jun. 2007, M. Togawa, MUMH 10802, MUCC 593; Saga, on *Asparagus officinalis* (*Asparagaceae*), 20 Sep. 1999, J. Yamaguchi, MUMH 11400, MUCC 923 = MAFF 238299; Hokkaido, on *Glebionis coronaria* (= *Chrysanthemum coronarium*) (*Asteraceae*), Aug. 1989, MUCC 573 = MAFF 235978. **Netherlands**, Bergen op Zoom, on *B. vulgaris*, Sep. 1951, G. van den Ende, CBS 152.52 = IMI 077043 = MUCL 16495 = CPC 5063. **New Zealand**, Auckland, on *Glebionis coronaria* (= *Chrysanthemum coronarium*), C.F. Hill, Lynfield 566, CPC 5260; on *Moluccella laevis* (*Lamiaceae*), C.F. Hill, Lynfield 516, CPC 5112. **Romania**, Hagieni, distr. Constanta, on *Plumbago europaea* (*Plumbaginaceae*), 13 Jun. 1970, O. Constantinescu, CBS 553.71 = IMI 161116 = CPC 5083 (as *C. plumbaginea*); Bucuresti, on *A. graveolens*, 2 Oct. 1969, O. Constantinescu, CBS H-9812, CBS 536.71 = CPC 5087; Domnesti, on *Plantago lanceolata* (*Plantaginaceae*), 3 Aug. 1965, O. Constantinescu, CBS 252.67 = CPC 5084. **Unknown**, on *A. graveolens*, Mar. 1925, L.J. Klotz, CBS 119.25 = B 42463 = IHEM 3822 = CPC 5086. **USA**, California, on *M. laevis*, S.T. Koike, CBS 110816 = CPC 5111; CBS 110813 = CPC 5110; California, on *A. graveolens*, 27 Sep. 2010, S.T. Koike, CPC 18601. **Zimbabwe**, on *M. laevis*, 13 May 2009, S. Dimbi, CBS 132683 = CPC 16663.

*Notes:* Various investigators have demonstrated that great variation in the size and shape of conidiophores and conidia (conidiophores: 25–300 × 3.5–9 µm, rarely branched, conidia: 25–315 × 3–6 µm, cylindrical, filiform to acicular) is induced by changes in environmental conditions, especially humidity. Crous & Braun (2003) pointed out these morphological ambiguities, and introduced a concept of *Cercospora apii* s. *lat.*, for taxa morphologically indistinguishable from *Cercospora apii* on *A. graveolens*. *Cercospora apii* s. *str.*, which is phylogenetically distinct, is characterised in that its conidiophores are almost uniform in width, moderately thick-walled or thick-walled, short obconically truncate at the apex, and with a few loci on integrated conidiogenous cells, and long-cylindrical to cylindrical-obclavate to often acicular conidia with truncate or obconically truncate basal ends and subacute to obtuse apices.

According to Crous & Braun (2003), the host plants of *C. apii* s. *str.* are found in more than 86 genera of several plant families. Groenewald *et al.* (2006a) concluded that *C. apii* s. *str.*, which is mainly isolated from celery, has a wide host range, because numerous isolates of *C. apii* s. *lat.* originating from various host plants have similar nucleotide sequences to the type strain of *C. apii* s. *str.*

In principle, the phylogenetic split observed between *C. beticola* and *C. apii* is only supported by the CAL sequences, and for the other genes these two taxa cluster as a large unresolved clade. Groenewald *et al.* (2005) showed that these two species are also distinguished by their AFLP fingerprints and growth conditions, suggesting that they were operational species units with a different ecology. These results indicate that in many cases morphologically identical species occurring on different hosts in fact represent different species. The situation is complicated in that there are several species with wide host ranges. Other species can colonise dead material of non-hosts, facilitating what has been described as a pogostick hypothesis (Crous & Groenewald 2005), until they locate their ideal hosts on which they are primary pathogens. In the present study it was further found that the CAL phylogeny fails to distinguish *C. apii* s. *str.* from *C. cf. brunkii* and *C. cf. resedae*, which are sister taxa in the combined tree (Fig. 2 part 5).

***Cercospora apiicola*** M. Groenew., Crous & U. Braun, Mycologia 98: 281. 2006.

*Leaf spots* amphigenous, subcircular to irregular, 3–10 mm diam, medium brown, with a raised or inconspicuous, indefinite margin, not surrounded by a border of different colour. *Caespituli* amphigenous, but primarily hypophyllous. *Stromata* lacking to well-developed, 30–60 µm diam, medium brown. *Conidiophores* in fascicles (4–10), moderately dense, arising from stromata, emerging through stomata or erumpent through the cuticle, subcylindrical, upper part geniculate-sinuous, unbranched, 1–3-septate, 25–70 × 4–6 µm, medium brown, becoming pale brown towards the apex, smooth, wall somewhat thickened. *Conidiogenous cells* integrated, terminal, 15–30 × 4–5 µm, occasionally unilocal, usually multilocal, sympodial; loci subcircular, planate, thickened, darkened, refractive, 2.5–3 µm wide. *Conidia* solitary, cylindrical when small, obclavate-cylindrical when mature, not acicular, (50–)80–120(–150) × (3–)4–5 µm, 1–6(–18)-septate; apex subobtuse, base obconically subtruncate; hila 2–2.5 µm wide, thickened, darkened, refractive.

*Specimens examined:* **Greece**, on *Apium graveolens*, 2000, I. Voutoglou, CBS 132666 = CPC 11642; CPC 11641. **South Korea**, Kangnung, on *A. graveolens*, 20 Sep. 2003, H.D. Shin, CPC 10666; Namyangju, on *A. graveolens*, 30 Sep. 2003, CBS 116458 = CPC 10657; on *A. graveolens*, 22 Oct. 2003, H.D. Shin, CBS 132651 = CPC 10759. **Venezuela**, La Guanota, Caripe, Edo. Monagas, 1050 m.s.n.m., on *Apium* sp., 23 Jul. 2002, N. Pons, **holotype** CBS H-18473, culture ex-type CBS 116457 = CPC 10267; CBS 132644 = CPC 10248; CPC 10220; CPC 10265–10266; CPC 10279; CPC 10666.

*Notes:* Morphologically *C. apiicola* differs from *C. apii* s. *str.* in having multiple conidiogenous loci and long conically truncate conidiogenous cells (Groenewald *et al.* 2006a). It has a high degree of phylogenetic independence from other species of *C. apii* s. *lat.* supported by TEF, ACT, CAL and HIS regions. It is also clearly distinct from *C. apii* in the combined tree (Fig. 2 part 2 vs. part 5).

***Cercospora armoraciae*** Sacc., Nuovo Giorn. Bot. Ital. 8: 188. 1876.

= ?*Cercospora cheiranthi* Sacc., Nuovo Giorn. Bot. Ital. 8: 187. 1876.



- = *Cercospora nasturtii* Pass., Hedwigia 16: 124. 1877.  
 = *Cercospora nasturtii* subsp. *barbareae* Sacc., Michelia 2: 557. 1882.  
     ≡ *Cercospora barbareae* (Sacc.) Chupp, Farlowia 1: 579. 1944.  
 = *Cercospora bizzozeriana* Sacc. & Berl., Malpighia 2: 248. 1888.  
 = *Cercospora atrogrisea* Ellis & Everh., Proc. Acad. Nat. Sci. Philadelphia 45: 464. 1894.  
 = *Cercospora bizzozeriana* var. *drabae* Sausa da Câmara, Revista Agron. (Lisbon) 1: 25. 1903.  
 = *Cercospora berteroeae* Hollós, Ann. Mus. Nat. Hung. 5: 468. 1907.  
 = *Cercospora drabae* Bubák & Kabát, Hedwigia 52: 362. 1912.  
     ≡ *Cercosporina drabae* (Bubák & Kabát) Sacc., Syll. Fung. 25: 900. 1931.  
 = *Cercospora camarae* Curzi, Atti Ist. Bot. Univ., Pavia, III, 2: 101. 1925.  
 = *Cercospora cardamines* Losa (as "*cardaminae*"), Anales Jard. Bot. Madrid 6: 453. 1946.  
 = *Cercospora lepidii* Niessl, unknown, in herb., HBG fide Chupp (1954, p. 180).

*Caespituli* amphigenous. *Mycelium* internal. *Stromata* lacking to well-developed, up to 60 µm diam, brown, substomatal or intraepidermal. *Conidiophores* arising from internal hyphae or a few brown cells, cylindrical, solitary, or in loose to divergent fascicles (2–30), pale to pale brown, paler towards apex, moderately thick-walled, simple, straight to strongly geniculate, irregular in width, often narrowed with successive geniculation, truncate or conically truncate at the tip, sometimes constricted at septa, 13–135 × 2.5–7.5 µm, 0–7-septate. *Conidiogenous cells* integrated, terminal, intercalary, proliferating sympodially, uni-local to multi-local (1–3); loci conspicuous, apical or on shoulder of conidiogenous cells caused by geniculation, rarely lateral, distinctly thickened, somewhat protuberant, refractive or darkened, 1.8–3.5 µm diam. *Conidia* solitary, hyaline, straight to mildly curved, cylindrical, cylindro-obclavate to acicular, obconically truncate or truncate, distinctly thickened at the base, obtuse at the apex, 15–125 × 2.5–6 µm, 1–11-septate.

*Specimens examined:* **Italy**, Venice, on *Armoracia rusticana* (= *A. lapathifolia*) (*Brassicaceae*), Treviso, Sep. 1874, (*syntype* Mycoth. Ven. 282, in B, HBG, S). **Japan**, Okinawa, on *A. rusticana* (= *A. lapathifolia*), 19 Nov. 2007, C. Nakashima, MUMH 10820, MUCC 768. **New Zealand**, Auckland, Grey Lynn, on *Nasturtium officinale* (= *Rorippa nasturtium-aquaticum*) (*Brassicaceae*), 14 Apr. 2002, C.F. Hill, Lynfield 576, CBS H-20988, CBS 115394 = CPC 5261 (named as *C. nasturtii*); Manurewa, on *A. rusticana* (= *A. lapathifolia*), C.F. Hill, Lynfield 622, CBS 115409 = CPC 5359 (as *C. armoraciae*); on *Gaura* sp. (*Onagraceae*), C.F. Hill, Lynfield 634, CBS 115060 = CPC 5366. **Romania**, Fundulea, on *A. rusticana* (= *A. lapathifolia*), O. Constantinescu, *epitype designated here* CBS H-20987, culture ex-epitype CBS 250.67 = CPC 5088; Fundulea, on *Cardaria draba* (*Brassicaceae*), O. Constantinescu, CBS 258.67 = CPC 5061 (as *C. bizzozeriana*); Hagieni, on *Berteroa incana* (*Brassicaceae*), O. Constantinescu, CBS 538.71 = IMI 161109 = CPC 5090 (as *C. berteroeae*); Hagieni, on *C. draba*, O. Constantinescu, CBS 540.71 = IMI 161110 = CPC 5060 (as *C. bizzozeriana*); Hagieni, on *Coronilla varia* (*Fabaceae*), O. Constantinescu, CBS 555.71 = IMI 161117 = CPC 5082 (as *C. rautensis*); Valea Mraconiei, on *Erysimum cuspidatum* (*Brassicaceae*), O. Constantinescu, CBS 545.71 = CPC 5056 (as *C. erysimi*). **South Korea**, Hoengseong, on *Turritis glabra* (= *Arabis glabra*) (*Brassicaceae*), 23 Jun. 2004, H.D. Shin, CBS H-20989, CBS 132654 = CPC 11338 (as *C. nasturtii*); CPC 11364 (as *C. nasturtii*); Jecheon, on *Rorippa indica* (*Brassicaceae*), 19 Oct. 2007, H.D. Shin, CBS 132672 = CPC 14612 (as *C. nasturtii*); Pocheon, on *Barbarea orthoceras* (*Brassicaceae*), 23 Oct. 2002, H.D. Shin, CBS H-20990, CBS 132638 = CPC 10100 (named as *C. nasturtii*); Wonju, on *R. indica*, 18 Oct. 2002, H.D. Shin, CBS H-20991, CPC 10133 (as *C. nasturtii*); Suwon, on *A. rusticana* (= *A. lapathifolia*), 14 Oct. 2003, H.D. Shin, CBS H-20992, CBS 132610 = CPC 10811 (as *C. armoraciae*). **Thailand**, on *Acacia mangium* (*Fabaceae*), W. Himaman, CPC 11530.

*Notes:* See also *C. capsici*. *Cercospora armoraciae* is supported by the HIS phylogeny. In the TEF phylogeny it is part of a larger clade intermixed with *C. zebrina*, *Cercospora* sp. L., *C. rumicis*, *C. violae* and *C. althaeina*; in ACT the *C. armoraciae* clade contains some intraspecific variation and also includes *C. rumicis*. In the CAL phylogeny, it is a sister clade to *C. zebrina*, but it contains isolates from *C. capsici*. In the combined tree (Fig. 2 part 3), it is a sister taxon to *C. capsici*. Morphological characteristics of the

*C. armoraciae* clade include conidiophores that are often narrowed, with successive geniculation, conically truncate at the apex, and with distinctly thickened and somewhat protuberant loci, and conidia that are cylindro-obclavate to acicular.

In this study, most *Cercospora* species on *Brassicaceae* having indistinguishable morphological characteristics are listed as synonyms under *C. armoraciae*. This treatment was proposed previously (Crous & Braun 2003). Davis (1929) pointed out that similar forms on *Brassicaceae*, namely *C. nasturtii*, *C. armoraciae*, *C. cheiranthi*, etc., were likely conspecific. The results of this study support his prediction. *Cercospora stanleyae* Chupp ex U. Braun & Crous (Crous & Braun 2003) is tentatively maintained as a separate species due to morphological differences. *Cercospora brassicicola* differs from *C. armoraciae* in that the former has long conidiophores (up to 500 µm in length), and is pathogenic to *Brassica*. In addition, *Cercospora thlaspi* "*thlaspieae*" differs from *C. armoraciae* in that the former has long conidiophores (to 400 µm in length) and acicular conidia (40–300 × 2–4 µm).

*Cercospora beticola* Sacc., emend. Groenewald *et al.*, Phytopathology 95: 954. 2005.

*Caespituli* hypophyllous. *Mycelium* internal. *Stromata* lacking to well-developed, up to 60 µm diam, intraepidermal or substomatal, brown to dark brown. *Conidiophores* solitary to 2–18 in loose fascicles, slightly divergent, brown, paler towards apex, moderately thick-walled, cylindrical, almost uniform in width, simple, geniculate, 16–200(–450) × 4–6 µm, 1–6-septate, truncate at the apex, sometimes constricted at septa. *Conidiogenous cells* terminal or intercalary, proliferating sympodially, with 1–2 loci; loci distinctly thickened, not protuberant, apical or formed on shoulder of conidiogenous cells caused by geniculation and lateral, 2.5–3(–4) µm. *Conidia* solitary, filiform to acicular, straight to mildly curved, rarely cylindro-obclavate, truncate at the base, acute to subacute at the tip, 27–250 × 2–5 µm, 3–28-septate.

Description of caespituli on V8 medium; MUCC 568 (MAFF 238206): *Conidiophores* solitary to loosely fasciculate, brown, paler towards the apex, uniform in width, smooth, moderately thick-walled, straight to slightly sinuous, short conically truncate at the tip, 50–148 × 3–5 µm, multi-septate. *Conidiogenous cells* integrated, terminal; loci moderately thickened, apical, uni-local, 2–3 µm in width. *Conidia* hyaline, cylindrical to cylindro-obclavate; short obconical, slightly thickened and truncate or obconically truncate at the base, acute at the apex, 40–88 × 3–6 µm, 3–14-septate.

*Specimens examined:* **Botswana**, Gaborone, on *Spinacia* sp. (*Chenopodiaceae*), L. Lebogang, CPC 5369–5370. **Bulgaria**, on *Gonolimon tataricum* (*Plumbaginaceae*), S.G. Bobev, CBS 123907 = CPC 14616; CBS 123908 = CPC 14620; CBS 132673 = CPC 14617; CPC 14618–14619. **Czech Republic**, on *Beta vulgaris*, Sep. 1947, G.E. Bunschoten, CBS 117.47. **Egypt**, on *B. vulgaris*, 15 Apr. 2004, M. Hasem, CPC 12028–12030. **France**, Longvic, on *B. vulgaris*, S. Garressus, CBS 116505 = CPC 11580. **Germany**, on *B. vulgaris*, S. Mittler, CPC 12031; CPC 12027; CPC 12022; CBS 116502 = CPC 11577; CBS 116454 = CPC 11558; on *B. vulgaris*, Jun. 1931, E.W. Schmidt, CBS 122.31 = CPC 5072; CBS 126.31 = CPC 5064. **Iran**, Pakajik, on *B. vulgaris*, A.A. Ravanlou, CBS 116501 = CPC 11576. **Italy**, Ravenna, on *B. vulgaris*, 10 Jul. 2003, V. Rossi, culture ex-epitype CBS 116456 = CPC 11557; CBS 116503 = CPC 11578. **Japan**, Chiba, on *B. vulgaris*, 30 May 1998, S. Uematsu, MUCNS 320 = MUCC 568 = MAFF 238206; Hokkaido, on *B. vulgaris*, 1955, K. Goto, MUCC 569 = MAFF 305036. **South Korea**, Namyangju, on *Chrysanthemum segetum* (= *Ch. coronarium* var. *spatiosum*) (*Asteraceae*), 24 Jun. 2004, H.D. Shin, CBS 132655 = CPC 11341 (named as *C. chrysanthemi*); 27 Jul. 2004, H.D. Shin, CPC 11344 (named as *C. chrysanthemi*). **Mexico**, Texcoco, on *B. vulgaris*, 20 Oct. 2008, Ma. de Jesús Yáñez-Morales, CPC 15623. **Netherlands**, on *B. vulgaris*, M. Groenewald, CBS 116506 = CPC 11581; Northwest Brabant, on *B. vulgaris*, Nov. 1947, G.E. Bunschoten, CBS 116.47 = CPC 5074. **New Zealand**, Auckland, on *Limonium sinuatum* (*Plumbaginaceae*), 25 Feb. 2002, C.F. Hill, Lynfield 533,



CBS 115478 = CPC 5113 (named as *C. stances*); on *B. vulgaris*, C.F. Hill, CPC 5128; Lynfield 539, CPC 5125; CPC 10197; CPC 10204; CPC 10168; CBS 117556 = CPC 10171; CPC 10168; on *Apium graveolens*, C.F. Hill, Lynfield 537a, CPC 5123. **Romania**, Bucuresti, on *B. vulgaris*, 17 Oct. 1966, O. Constantinescu, CBS 539.71 = CPC 5062; Hagieni, on *Malva pusilla* (Malvaceae), 15 Jul. 1970, O. Constantinescu & G. Negrean, CBS H-9847, CBS H-9849, CBS 548.71 = IMI 161115 = CPC 5065; on *B. vulgaris*, Jun. 1931, E.W. Schmidt, CBS 124.31 = CPC 5070. **Spain**, on *B. vulgaris*, Jun. 1931, E.W. Schmidt, CBS 123.31 = CPC 5071. **Unknown**, on *B. vulgaris*, Jun. 1931, E.W. Schmidt, CBS 125.31 = CPC 5069. **USA**, California, on *B. vulgaris*, S.T. Koike, CPC 18813.

**Notes:** *Cercospora beticola* is the causal agent of *Cercospora* leaf spot on *B. vulgaris*, which is one of the most common and destructive sugar beet diseases (Weiland & Koch 2004). Despite its importance as a plant pathogen, its actual host range remains unclear.

Initial phylogenetic analyses on the genus *Cercospora* employed ITS sequences to reveal phylogenetic relationships within the genus (Stewart *et al.* 1999, Goodwin *et al.* 2001, Pretorius *et al.* 2003). These analyses failed to discriminate all species due to the limited resolution provided by the ITS locus. Groenewald *et al.* (2005, 2006a) subsequently succeeded in using multi-locus sequence data from five gene regions to distinguish *Cercospora* species. They also expanded the host range of *C. beticola*. Although isolates of *C. beticola* have been isolated from diverse hosts, these isolates appear to have been colonising non-hosts as saprobes or secondary invaders (Crous & Groenewald 2005), and proof of their pathogenicity has not been confirmed.

Results from the phylogenetic analyses using CAL and combined multi-locus data set divide *C. beticola* and *C. apii* s. str. into two different clades, with *C. beticola* splitting further into two subclades (also see Fig. 2 part 6) based on sequence changes in HIS, probably due to intraspecific variation. The combined data clearly show that *C. apii* s. str. and *C. beticola* are related sibling species, although *C. beticola* must be retained as a separate species.

### *Cercospora* cf. *brunkii*

*Caespituli* amphigenous. *Mycelium* internal. *Stromata* lacking or composed of few dark brown cells, intraepidermal or substomatal. *Conidiophores* brown to dark brown, paler at the apex, 2–6 in loose fascicles, moderately thick-walled, straight or 1–2 times geniculate caused by sympodial proliferation, uniform in width, mildly attenuated at the apex, short obconically truncate or truncate at the apex, 30–160 × 4.5–5.5 µm, 0–9-septate. *Conidiogenous cells* integrated, terminal and intercalary, proliferating sympodially, rarely percurrently, uni- or multi-local (2–5); loci distinctly thickened, often dispersed on whole conidiophores, darkened, apical and lateral, 2–3 µm diam. *Conidia* solitary, hyaline, acicular, straight or slightly curved, thickened and truncate at the base, acute at the apex, 27–110 × 1.5–4 µm, indistinctly multi-septate, 0–9-septate.

**Specimens examined:** **Japan**, Wakayama, on *Datura stramonium* (Solanaceae), 30 Oct. 2007, C. Nakashima & I. Araki, MUMH 10858, MUCC 732. **South Korea**, Namyangju, on *Geranium thunbergii* (= *G. nepalense* var. *thunbergii*) (Geraniaceae), 30 Sep. 2004, H.D. Shin, CBS H-20993, CBS 132657 = CPC 11598.

**Notes:** This species is basal to *C. apii* s. str. Fresh collections from *Geranium* (Geraniaceae) are needed from the USA (type locality of *C. brunkii*) to determine if the latter name can be applied to this species. The two isolates representing this species are never supported in their own clade; in the TEF and ACT phylogenies they are intermixed with *C. cf. flagellaris*, in the CAL phylogeny with *C.*

*apii* and in the HIS phylogeny with *C. kikuchii*, *C. cf. richardiicola* and *Cercospora* spp. P and Q. These different shared alleles are the likely cause for their separate position in the combined phylogeny (Fig. 2 part 5).

### *Cercospora campi-silii* Speg., *Michelia* 2: 171. 1880.

= *Cercosporidium campi-silii* (Speg.) X.J. Liu & Y.L. Guo, *Acta Mycol. Sin.* 1: 94. 1982.

= *Passalora campi-silii* (Speg.) Poonam Srivast., *J. Living World* 1: 114. 1994, nom. inval.

= *Passalora campi-silii* (Speg.) U. Braun, *Mycotaxon* 55: 228. 1995.

= *Cercospora impatientis* Bäumler, *Verh. K. K. Zool.-Bot. Ges. Wien* 38: 717. 1888.

*Leaf spots* angular to irregular, 1–3 mm diam, center greyish to pallid, surrounded by purplish brown to dark brown border lines, but brown to greyish brown without definite borders on the abaxial surface. *Caespituli* hypophyllous, but also epiphyllous in later stage of disease development. *Stromata* lacking or composed of a few brown cells. *Conidiophores* arising in fascicles of 5–12(–18), loose to moderately dense, emerging through stomata or occasionally erumpent through the cuticle, subcylindrical, 2–5 times geniculate, sometimes abruptly geniculate, unbranched, 2–4-septate, 40–110 × 4–5.5 µm, pale brown to olivaceous-brown. *Conidiogenous cells* integrated, terminal, sympodial, multi-local; loci subcircular, thickened, darkened, 2.5–3 µm wide. *Conidia* solitary, obclavate-cylindrical to elliptical, 25–60 × 4.5–6 µm, (1–)3(–6)-septate, subhyaline, apex obtuse, base obconically subtruncate; hila ca. 2 µm wide, thickened, darkened.

**Specimen examined:** **South Korea**, Inje, on *Impatiens noli-tangere* (Balsaminaceae), 29 Sep. 2007, H.D. Shin, CBS 132625 = CPC 14585.

**Notes:** Although *C. campi-silii* was transferred from *Cercospora* to *Passalora* based on its pale olivaceous conidia (Braun 1995b), as in the case of *C. sojae*, these taxa are best retained in *Cercospora*, which is fully supported by their phylogenetic position within *Cercospora*. *Cercospora campi-silii* is separated based on the TEF, ACT and HIS phylogenies in the present study. Only the CAL phylogeny failed to distinguish it from *C. sojae* and *C. achyranthis*. On the combined tree (Fig. 2 part 2), it is a sister taxon to *C. sojae*. *Cercospora campi-silii* was described from Europe and examination of European material is necessary to determine similarity with Korean collections.

### *Cercospora canescens* complex

**Cultures examined:** **Ghana**, on leaves of *Dioscorea rotundata* (Dioscoreaceae), 2000, S. Nyako & A.O. Danquah, CBS 132658 = CPC 11626 = GHA-1-0 (as *C. dioscoreae-pyrifoliae*); CPC 11628 = GHA-2-1; on leaves of *Dioscorea alata*, 2000, S. Nyako & A.O. Danquah, CBS 132659 = CPC 11627 = GHA-1-1. **Mexico**, Tamaulipas, unidentified *Malvaceae* host, 30 Oct. 2008, Ma. de Jesús Yáñez-Morales, CPC 15871. **South Africa**, Northwest Province, Potchefstroom, on *Vigna* sp. (*Fabaceae*), S. van Wyk, CBS 111133 = CPC 1137; CBS 111134 = CPC 1138; Tshipise, Limpopo Province, on *Citrus maxima* (*Rutaceae*) fruit spot, K. Serfontein, CPC 4408–4409. **USA**, Georgia, on *Phaseolus lunatus* (= *Ph. limensis*) (*Fabaceae*), E.S. Luttrell, CBS 153.55 = CPC 5059 (as *C. canescens*); on *Apium* sp., CPC 11640 = IMI 186563.

**Notes:** Morphologically the present clade represents isolates that correspond with the description of *C. canescens*, which was originally described from *Phaseolus* in the USA. It is possible that as more isolates are added, the lower subclade, which represents hosts in other families, may eventually split off as a distinct taxon. Epitype material from the USA is necessary to fix the application

of the name *C. canescens*. The material on *Ph. lunatus* (= *Ph. limensis*) could be used in this sense, but *C. canescens* is a complicated species complex. More isolates from the USA are necessary to resolve this issue. A sequence of an isolate on *Phaseolus* from Mexico (CPC 15807) clusters in "*Cercospora* sp. Q", which might be *C. canescens*. The *C. canescens* complex is supported as a distinct clade in the ACT and CAL phylogenies. The TEF sequence of isolate CPC 15871 splits off from the rest of the isolates to cluster with *C. cf. coreopsidis*. In the HIS phylogeny, the isolates occur in four distinct but related clades (*C. mercurialis* occurs in an intermediate position between these clades). These four clades correspond to the intraspecific variation observed for this species in Fig. 2 (part 1).

***Cercospora capsici*** Heald & F.A. Wolf, Mycologia 3: 15. 1911.

*Leaf spots* circular to subcircular, more or less concentric, 2–10 mm diam. *Caespituli* amphigenous, appearing greyish brown in case of abundant sporulation. *Mycelium* internal. *Stromata* rudimentary, composed of a few swollen cells. *Conidiophores* straight to mildly curved, not branched, in divergent fascicles (3–15), mildly geniculate, 30–120 × 3–6 µm, 0–6-septate. *Conidiogenous cells* integrated, terminal, lateral, proliferating sympodially; loci distinct, slightly protuberant, apical and formed on shoulder caused by geniculation, 2–3 µm wide. *Conidia* solitary, hyaline, acicular, straight to mildly curved, 64–180 × 4–5.5 µm, 2–12-septate, subacute at the apex, obconically truncate at the base (adapted from Shin & Kim 2001).

*Description of caespituli on V8 medium*; MUCC 574 (MAFF 238227): *Conidiophores* solitary, pale brown to brown, irregular in width, wider at the base, smooth, moderately thick-walled, sinuous-geniculate, simple, conically truncated at the tip, 20–130.5 × 3.5–5 µm, multi-septate. *Conidiogenous cells* integrated, terminal; loci distinctly thickened, apical, 2–2.5 µm in width. *Conidia* solitary, hyaline, cylindro-obclavate to acicular, distinctly thickened and long obconically truncated at the base, obtuse to acute at the apex, 105–200 × 2.5–4.5 µm, 9–18-septate.

*Specimens examined*: Fiji, unknown host, fungus fruiting on lesions on calyx attached to fruit, 17 Aug. 2005, P. Tyler, CBS 118712. Japan, Chiba, on *Capsicum annuum* (Solanaceae), 1 Oct. 1999, S. Uematsu, MUCC 574 = MAFF 238227 = MUCNS 810. South Korea, Hongcheon, on *C. annuum*, 29 Aug. 2005, H.D. Shin, CBS H-20994, CPC 12307; Yanggu, on *C. annuum*, 28 Sep. 2007, H.D. Shin, CBS H-20995, CBS 132622 = CPC 14520.

*Notes*: See also *C. armoraciae*. This species is supported in the TEF (related to *Cercospora* sp. J and *C. chenopodii*), ACT (related to *Cercospora* sp. J and *C. zebrina* and *C. armoraciae*) and HIS (related to *Cercospora* spp. C and D) phylogenies and is part of the larger *C. armoraciae* clade based on CAL. In the combined tree (Fig. 2 part 3), it is a sister taxon to *C. armoraciae*. Morphological characteristics of this species on the host plant and in culture are almost similar to *C. armoraciae*. In addition, acicular conidia are formed in culture. The application of the name *C. capsici* to this clade is only tentative, since the latter species was described from the USA. North American cultures and sequences are needed to confirm their identity.

Several species of *Cercospora* occur on solanaceous host plants. Of these, *C. physalidis* has been shown to form a species complex. Braun & Mel'nik (1997) concluded many species of *Cercospora* *apii* s. lat. on solanaceous hosts, including *C. capsici*, were synonymous with *C. physalidis* based on their morphological

characteristics. Based on the results of pathogenicity tests (*C. Nakashima*, unpubl. data), phylogeny, and morphology (cylindrical to obclavate, rarely acicular conidia, and conidiophores that narrow at the upper portion), *C. capsici* must be separated from the *C. physalidis* complex. Likewise, other taxa in this complex such as *C. lycii*, *C. nicandrae*, *C. sciadophila*, *C. solanacea*, and *C. solani*, which consistently have obclavate-cylindrical conidia, must be re-examined.

***Cercospora celosiae*** Syd., Ann. Mycol. 27: 430. 1929.

*Leaf spots* amphigenous, scattered to confluent, distinct, subcircular to irregular, small to fairly large, 1–7 mm diam, pale brown to brown, surrounded by a dark brown border. *Caespituli* amphigenous. *Stromata* small, rudimentary to slightly developed, composed of several brown, swollen hyphal cells. *Conidiophores* 3–20 in loose fascicles, emerging through stomata or erumpent through the cuticle, olivaceous-brown throughout, or paler upwards, 0–5-septate, straight to slightly curved, 1–5 times mildly geniculate, sometimes once abruptly geniculate, not branched, 25–200 × 4.5–6 µm; loci conspicuous, apical or on shoulders of conidiogenous cells caused by geniculation. *Conidia* solitary, acicular to filiform, sometimes shorter ones obclavate-cylindrical, straight to mildly curved, hyaline, 2–14-septate, slightly constricted at the septa, subacute to subobtuse at the apex, obconically truncate to subtruncate at the base, 40–150 × 3–5 µm; hilum conspicuously thickened, darkened, and non-protuberant

*Specimen examined*: South Korea, Chuncheon, on *Celosia argentea* var. *cristata* (= *C. cristata*) (Amaranthaceae), 7 Oct. 2003, H.D. Shin, CBS H-20996, CBS 132600 = CPC 10660.

*Notes*: The isolate representing *C. celosiae* is not supported as a separate clade; in the TEF, ACT, CAL and HIS phylogenies it is intermixed with predominantly *Cercospora* sp. I and *C. alchemillicola* / *C. cf. alchemillicola*, which is also evident from its position basal to *Cercospora* sp. I in the combined phylogeny (Fig. 2 part 1). Authentic material from China is required to determine if *C. celosiae* should be merged with what is presently treated as *Cercospora* sp. I.

***Cercospora chenopodii*** Fresen., Beitr. Mykol.: 92. 1863. Fig. 4

= *Ramularia dubia* Riess, Hedwigia 1: pl. 4, fig. 9. 1854.

= *Cercospora dubia* (Riess) G. Winter, Fungi Eur. Exs., Ed. nov., Cent. 28, No. 2780. 1882 and Hedwigia 22: 10. 1883, nom. illeg., homonym of *C. dubia* Speg., 1880.

= *Cercospora dubia* (Riess) Bubák, Ann. Mycol. 6: 29. 1908, nom. illeg., homonym of *C. dubia* Speg., 1880.

= *Cercosporidium dubium* (Riess) X.J. Liu & Y.L. Guo, Acta Mycol. Sin. 1: 95. 1982.

= *Passalora dubia* (Riess) Poonam Srivast., J. Living World 1: 115. 1994, comb. inval.

= *Passalora dubia* (Riess) U. Braun, Mycotaxon 55: 231. 1995.

= *Cercospora chenopodii* Cooke, Grevillea 12: 22. 1883, nom. illeg., homonym of *C. chenopodii* Fresen., 1863.

= *Cercospora dubia* var. *urbica* Roum., Rev. Mycol. 15: 15. 1893.

= *Cercospora dubia* var. *atriplicis* Bondartsev, Trudy Glavn. Bot. Sada 26: 51. 1910.

= *Cercospora atriplicis* Lobik, Mat. po Fl. Faun. Obsled. Terskogo Okrug: 52. 1928.

= *Cercospora chenopodii* var. *micromaculata* Dearn., Mycologia 21: 329. 1929.

= *Cercospora penicillata* f. *chenopodii* Fuckel, Fungi Rhen. Exs., Fasc. II, No. 119. 1863, nom. nud.

= *Cercospora chenopodii* var. *atriplicis patulae* Thüm., in herb.

= *Cercospora bondarzewii* Henn., in herb. B.



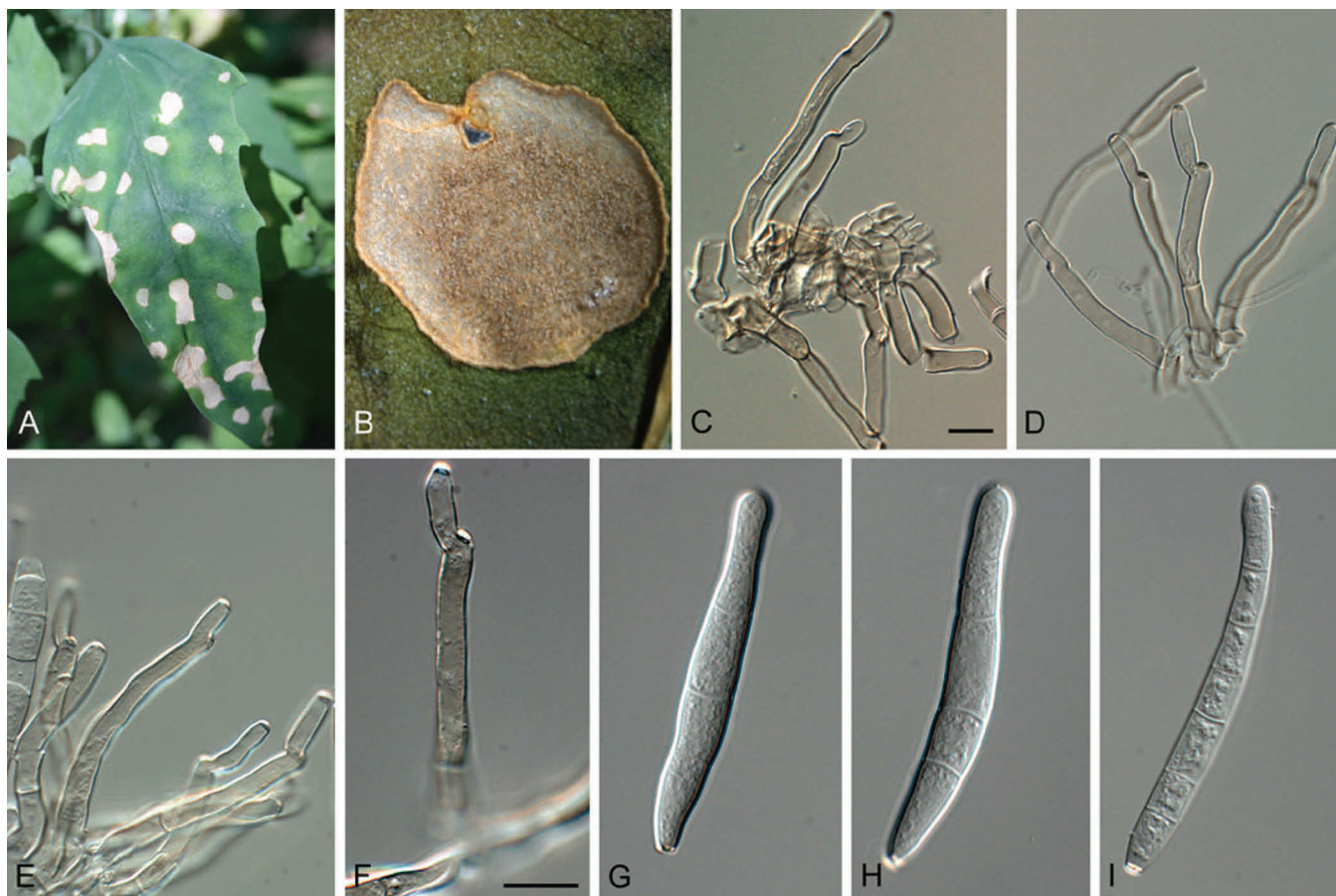


Fig. 4. *Cercospora chenopodii* (CBS 132620 = CPC 14237). A. Leaf spots. B. Close-up of lesion. C–F. Conidiophores. G–I. Conidia. Scale bars = 10 µm.

Specimen examined: **France**, Ardeche, N44°22'39.8" E4°26'9.1", on *Chenopodium* cf. *album* (*Chenopodiaceae*) next to river, 31 Aug. 2007, P.W. Crous, CBS H-20997, CBS 132620 = CPC 14237.

**Notes:** *Cercospora chenopodii* was transferred to the genus *Passalora* as *P. dubia* by Braun (1995a) based on broadly obclavate conidia with visible large loci. The conidia of this species are hyaline, and best retained in *Cercospora*, which has been confirmed by results of molecular sequence analyses. The species is supported as distinct in the TEF, ACT and HIS phylogenies; in the CAL phylogeny it cannot be distinguished from *C. cf. chenopodii*. In the combined tree (Fig. 2 part 1), it is a sister taxon to *C. cf. chenopodii*. Also see *C. cf. chenopodii*.

#### *Cercospora cf. chenopodii* Fig. 5.

**Leaf spots** amphigenous, subcircular, circular, 3–8 mm diam, greyish brown to pale brown. **Mycelium** internal, consisting of septate, branched, smooth, pale brown hyphae. **Caespituli** in fascicles (10–40), amphigenous, brown, dense, becoming divergent, up to 150 µm wide and 50 µm high. **Conidiophores** aggregated in dense fascicles arising from the upper cells of a moderately developed brown stroma; conidiophores olivaceous-brown to brown, 2–5-septate, 1–2 times geniculate in upper part, at times apically swollen, not branched, 60–135 × 4–7 µm. **Conidiogenous cells** terminal, unbranched, pale brown, smooth, tapering to flat-tipped apical loci, proliferating sympodially, 20–40 × 4–6 µm; loci thickened, darkened, refractive, 2–4 µm diam. **Conidia** solitary, smooth, cylindrical to obclavate, straight to slightly curved, hyaline, (0–)2–4(–5)-septate, apex obtuse, base obconically truncate,

(25–)40–65(–80) × (5–)6–7.5(–9) µm; hila thickened, darkened, refractive, 2–3 µm diam.

**Culture characteristics:** Colonies erumpent, spreading, with sparse aerial mycelium, and lobate, smooth margins, and folded surface; reaching 10 mm after 2 wk. On MEA iron-grey with patches of dirty white, reverse fuscous-black to greyish sepia. On OA and PDA surface mouse-grey, with patches of pale mouse-grey, reverse olivaceous-grey.

**Specimens examined:** **Mexico**, Montecillo, *Chenopodium* sp. (*Chenopodiaceae*), 9 Oct. 2008, Ma. de Jesús Yáñez-Morales, CBS 132677 = CPC 15599; CPC 15763; Purificación, *Chenopodium* sp., 12 Oct. 2008, Ma. de Jesús Yáñez-Morales, CPC 15859; CPC 15862. **South Korea**, Hongcheon, on *Chenopodium ficifolium* (*Chenopodiaceae*), 4 Oct. 2002, H.D. Shin, CBS H-20998, culture CBS 132594 = CPC 10304; Hongcheon, on *C. ficifolium*, 27 Oct. 2005, H.D. Shin, CBS H-20999, CPC 12450.

**Notes:** The chief difference between *C. chenopodii* and *C. cf. chenopodii* lies in the denser fascicles observed in the former species. Otherwise, the two species are barely distinguishable, and the latter species has to be considered a cryptic taxon. In the TEF phylogeny these two species are clearly distinct, although the isolates of *C. cf. chenopodii* are intermixed with those of *C. delaireae*, *C. ricinella* and *Cercospora* sp. K. The ACT and HIS phylogenies separate *C. cf. chenopodii* from the other species included in this study, although the CAL phylogeny could not distinguish *C. chenopodii* and *C. cf. chenopodii*. In the combined tree (Fig. 2 part 1), it is a sister taxon to *C. chenopodii*. See the species notes for *C. chenopodii*. We refrain from describing this species as new until more isolates for *C. chenopodii* can be sequenced to determine the intraspecific variation.

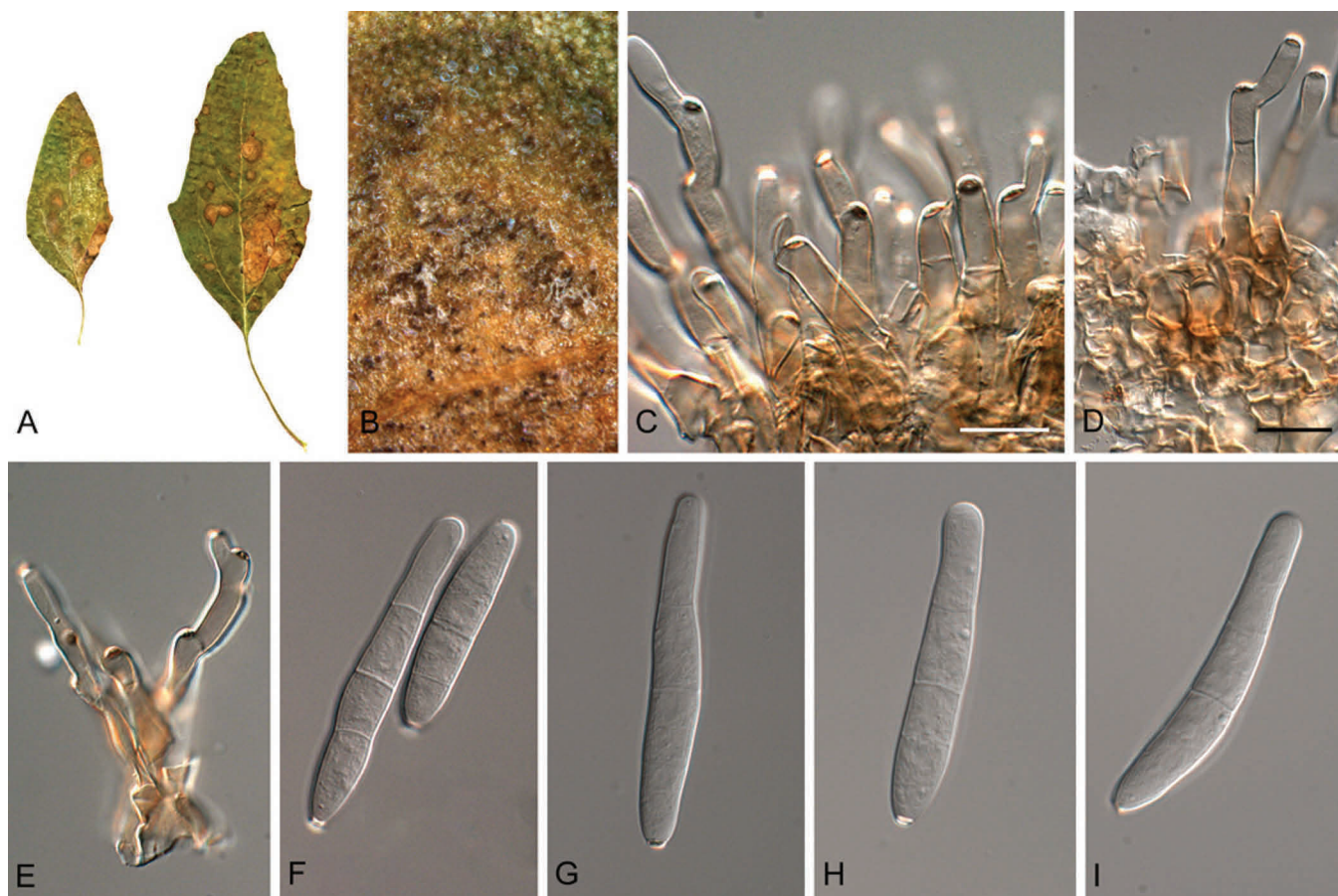


Fig. 5. *Cercospora* cf. *chenopodii* (CPC 10304). A. Leaf spots. B. Close-up of lesion. C–E. Fasciculate conidiophores. F–I. Conidia. Scale bars = 10 µm.

***Cercospora chinensis*** F.L. Tai, Bull. Chin. Bot. Soc. 2: 49. 1936.

*Caespituli* amphigenous. *Mycelium* internal. *Stromata* lacking to small, up to 30 µm diam, dark brown, intraepidermal or substomatal. *Conidiophores* solitary to 2–5 in loose fascicles, simple, sometimes branched, thick-walled, dark brown, paler towards the apex, mainly straight, loosely geniculate, almost uniform in width, conically truncated and somewhat wider at the apex, 61–100 × 5–6 µm, 3–6-septate. *Conidiogenous cells* integrated, proliferating sympodially or rarely percurrently, terminal and intercalary, multi-local; loci thickened, not protuberant, apical, lateral, 2.5–3 µm diam. *Conidia* solitary, hyaline, acicular to cylindro-obclavate, slightly curved, obconically truncate or subtruncate, and thickened at the base, acute at the apex, 60–210 × 3.5–5 µm, 2–16-septate.

*Specimen examined*: South Korea, Pyeongchang, on *Polygonatum humile* (Convallariaceae), 20 Sep. 2003, H.D. Shin, CBS H-21000, CBS 132612 = CPC 10831.

*Notes*: See the notes for *C. dispori* below. In the combined tree (Fig. 2 part 5), it is a sister taxon to *C. dispori* and *C. corchori*.

***Cercospora* cf. *citrullina***

*Caespituli* amphigenous. *Mycelium* internal. *Stromata* lacking or small, up to 20 µm, pale brown. *Conidiophores* pale to pale brown, paler towards the apex, irregular in width, wider at the base, narrowed successive geniculation at the apex, sinuous-geniculate to well geniculate above the middle, thin-walled when young, darker and moderately thickened in mature conidiophores, solitary

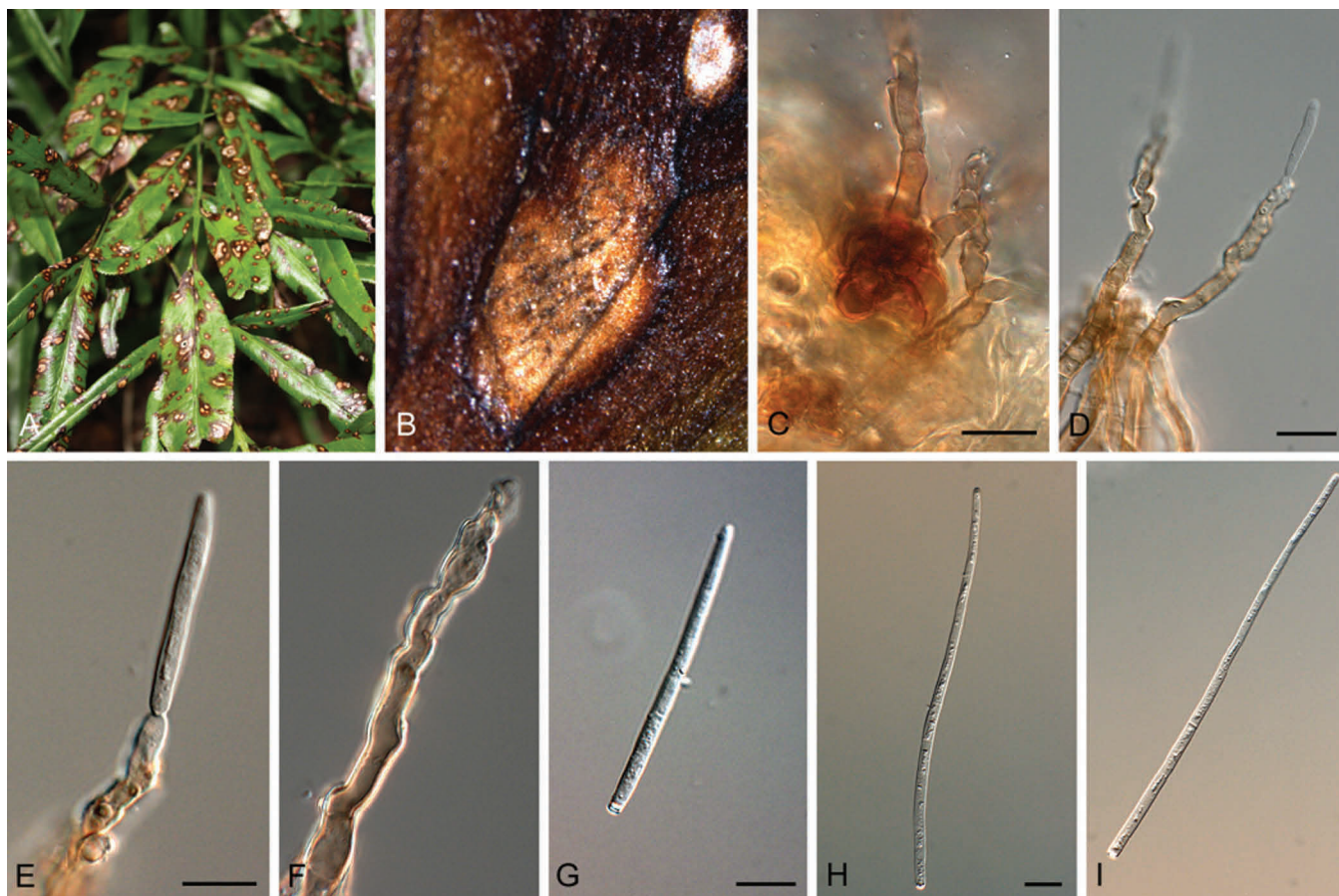
or in loose fascicles (2–14), simple, truncate at the apex, 50–86 × 2.5–5 µm, 0–3-septate. *Conidiogenous cells* integrated, terminal, rarely intercalary, proliferating sympodially, multi-local; loci distinct, thickened, apical or on shoulder caused by geniculation, slightly protuberant, 2.5–3 µm diam. *Conidia* solitary, hyaline, cylindrical, filiform to acicular, straight to slightly curved, truncate to long obconically truncate and distinctly thickened at the base, apex subacute, 40–134 × 3–4 µm, multi-septate.

*Specimens examined*: Bangladesh (western part), on *Musa* sp. (Musaceae), I. Buddenhagen, CBS 119395 = CPC 12682; CBS 132669 = CPC 12683. Japan, Kagoshima, on *Momordica charantia* (Cucurbitaceae), 20 Oct. 1997, E. Imaizumi & C. Nomi, MUCC 577 = MAFF 238205 = MUCNS 254 (as *C. citrullina*); Okinawa, on *Citrullus lanatus* (Cucurbitaceae), 6 Mar. 1998, T. Kobayashion et al., MUMH 11402, MUCC 576 = MUCNS 300 = MAFF 237913 (as *C. citrullina*); on *Psophocarpus tetragonolobus* (Fabaceae), MUCC 584 = MAFF 305757 (as *C. psophocarpicola*); on *Ipomoea pes-caprae* (Convolvulaceae), MUCC 588 = MAFF 239409 (as *C. ipomoeae*).

*Notes*: This clade is supported by the TEF, ACT and CAL phylogenies. In the HIS phylogeny, the clade is split into the two sister clades visible in the combined tree, and may eventually be shown to be a species complex. In the HIS phylogeny, MUCC 584, MUCC 576 and MUCC 577 are clustering sister to *C. chinensis* and *C. dispori* whereas the remaining isolates are sister to *C. vignigena*. In the combined tree (Fig. 2 part 5), it is a sister taxon to *C. cf. helianthicola*.

This taxon is distinguished from other species based on several morphological characteristics. Sporulation is mainly observed at the apex of conidiophores; slightly protuberant loci are formed on shoulders caused by geniculation; the width of conidiogenous cells immediately behind the fertile region is generally narrower, and





**Fig. 6.** *Cercospora coniogrammes* (CBS 132634 = CPC 17017). A. Leaf spots. B. Close-up of lesion. C–F. Weakly developed fascicles, showing conidiophores with sympodial proliferation and multi-local loci. G–I. Cylindrical to acicular conidia. Scale bars = 10 µm.

conidiogenous cells are truncate at the apex. An isolate obtained from *Ipomoea pes-caprae* (MUCC 588) is located in this clade (Fig. 2 part 5). It was not possible to examine its morphology in this study and thus it is not clear whether or not this fungus was saprobic. An isolate identified as *C. psophocarpicola* (MUCC 584), is also located in this clade. There is no morphological basis to divide *C. psophocarpicola* and other isolates in this clade into different species. Besides, the pathogenicity of MUCC 584 to *Psophocarpus* (*Fabaceae*) was confirmed (Ohnuki *et al.* 1989), thus showing that this species was not saprobic. Moreover, the four Japanese isolates examined in this study were obtained from the same subtropical islands in Japan. On the other hand, two isolates named as “*C. hayi*” from *Musa* sp. were also located in this clade. According to Crous *et al.* (2004b), several species of *Cercospora* are known to be able to colonise *Musa*. From the distribution of this taxon, it is natural that this species also colonised *Musa* (*Musaceae*), which grows in the same region.

***Cercospora coniogrammes*** Crous & R.G. Shivas, **sp. nov.**  
Mycobank MB800653. Fig. 6.

**Etymology:** Named after the host genus from which it was collected, *Coniogramme*.

**Leaf spots** amphigenous, subcircular to angular, 1–3 mm diam, grey to pale brown, surrounded by a broad brown margin, up to 4 mm diam. **Mycelium** internal. **Caespituli** predominantly epiphyllous. **Conidiophores** aggregated in loose fascicles (2–6), arising from the upper cells of a brown, weakly developed stroma, up to 20 µm diam, brown, finely verruculose in lower part, 3–7-septate, subcylindrical, straight to geniculate-sinuous, unbranched, 60–120

× 5–7 µm. **Conidiogenous cells** integrated, terminal, unbranched, brown, smooth, tapering to flat-tipped loci, proliferating sympodially, 15–35 × 3–5 µm, with numerous tightly aggregated apical loci, proliferating sympodially; loci distinct, thickened and darkened, protruding, 2–2.5 µm diam. **Conidia** solitary, hyaline, cylindrical to acicular, straight or slightly curved, apex subobtuse, base truncate, (30–)50–85(–120) × (2–)3(–3.5) µm, 1–6-septate, thin-walled, smooth; hila thickened, darkened, refractive, 1.5–2 µm diam.

**Culture characteristics:** Colonies spreading, flat, with sparse aerial mycelium, folded surface and even margins, reaching 25 mm after 2 wk. On OA blood-red in centre, red at margin. On MEA grey-olivaceous in centre, smoke-grey at margins, olivaceous-grey in reverse. On PDA umber to chestnut in centre, bay at margin, umber in reverse.

**Specimen examined:** **Australia**, Queensland, Brisbane, on *Coniogramme japonica* var. *gracilis* (= *C. gracilis*) (*Adiantaceae*), **holotype** CBS H-21001, Aug. 2009, P.W. Crous, culture ex-type CBS 132634 = CPC 17017.

**Notes:** The numerous, tightly aggregated loci on the conidiogenous cells, and cylindrical to acicular conidia are characteristic of this species. This species is supported on the TEF, ACT, CAL and HIS phylogenies and is basal in the combined tree (Fig. 2 part 1).

***Cercospora corchori*** Sawada, Trans. Nat. Hist. Soc. Formosa 26: 179. 1916.

**Caespituli** amphigenous. **Mycelium** internal. **Stromata** lacking to small, substomatal or intraepidermal, pale brown to brown, 16–25



µm diam. *Conidiophores* arising from upper part of stromata or internal hyphae, in loose fascicles (5–10), moderately thick-walled, pale brown to brown, uniform in width, sometimes attenuated at the apex, sinuous-geniculate, sparsely septate, conically truncate at the apex, 20–83 × 4–5 µm. *Conidiogenous cells* integrated, terminal and intercalary, proliferating sympodially, multi-local; loci distinct, thickened and darkened, apical or formed on the shoulder caused by the geniculation, 1–3 µm diam. *Conidia* hyaline to subhyaline, cylindro-obclavate to acicular, straight or slightly curved, truncate and thickened at the base, acute at the apex, 30–128 × 2.5–5 µm, 4–13-septate.

Description of caespituli on MEA; MUCC 585 (= MAFF 238191): *Conidiophores* solitary, brown, uniform in width, smooth, moderately thick-walled, slightly curved, simple, conically truncated at the apex, 130–230 × 3.5–4.5 µm, multi-septate. *Conidiogenous cells* integrated, terminal; loci moderately thickened, apical, 2.5–2.5 µm in width.

*Specimens examined*: **Japan**, Shimane, on *Corchorus olitorius* (Tiliaceae), 27 Aug. 1997, T. Mikami (epitype designated here – TFM:FPH-8114), culture ex-epitype MUCC 585 = MAFF 238191 = MUCNS 72. **Taiwan**, Taipei, on *C. olitorius*, 30 Jul. 1909, K. Sawada, (isotype – TNS-F-220392).

*Notes*: *Cercospora corchori*, which is known as the causal agent of a seed-borne disease, is distinguished from other species in that conidiophores are uniform in width, and conically truncate at the apex. Moreover, the species is supported by the ACT, CAL and HIS phylogenies. In the TEF phylogeny, it clusters on a longer branch in a clade with isolates of *Cercospora* sp. K and *C. lactucae-sativae*. In the combined tree (Fig. 2 part 5), it is a sister taxon to *Cercospora* spp. R and S.

### *Cercospora* cf. *coreopsisidis*

*Leaf spots* distinct (characteristic for this species), circular to subcircular, initially pale brown, later centre grey to dirty grey with raised greyish brown margins. *Caespituli* amphigenous. *Mycelium* internal. *Stromata* lacking or small, up to 30 µm in diam, intraepidermal or substomatal, brown. *Conidiophores* solitary, or up to 2–9 in loose fascicles, irregular in width, slightly attenuated at the apex, somewhat wider at mid cells, pale brown, thick-walled, paler towards the apex, conically truncate at the apex, geniculate at the upper portion, tortuous, 30–156 × 4–5.5 µm, 1–7-septate. *Conidiogenous cells* integrated, intercalary, terminal, proliferating sympodially, multi-local; loci thickened, darkened, not protuberant, flat, apical, lateral, rarely circumsperised, 1.5–2 µm. *Conidia* solitary, hyaline, filiform to acicular, straight to curved, truncated and thickened at the base, tip acute, 40–90(–180) × (1.5–)3–5 µm, indistinctly 7–10-septate.

*Specimen examined*: **South Korea**, Seoul, *Coreopsis lanceolata* (Asteraceae), 17 Sep. 2003, H.D. Shin, CBS H-21002, CBS 132598 = CPC 10648; Wonju, on *C. lanceolata*, 18 Oct. 2002, H.D. Shin, CPC 10122.

*Notes*: The description of the present species is based on Korean specimens. Many species of *Cercospora* have latent pathogenicity to asteraceous plants. Although these results show that the identification of *Cercospora* species on these plants is difficult based on the host plant, the isolates originating from *Coreopsis* must be treated as a host-specific species in having an independent phylogenetic position, which is supported by the TEF, ACT, CAL and HIS phylogenies. In the combined tree (Fig. 2 part 1), it is a sister taxon to *C. agavicola*.

On the other hand, *C. beticola*, which has also been known from *Bidens* (Asteraceae), was also reported from *Coreopsis* (Asteraceae) (Thaung 1984). Morphological differences between these species were not observed. The identification of the Korean collections as *C. cf. coreopsisidis* is only tentative and must be proven on the base of sequences derived from North American isolates, which are not yet available.

***Cercospora delaireae*** C. Nakash., Crous, U. Braun & H.D. Shin, **sp. nov.** MycoBank MB800654. Fig. 7.

*Etymology*: Named after the host genus from which it was collected, *Delairea*.

*Leaf spots* amphigenous, subcircular to angular, grey-brown to brown, 3–7 µm diam, surrounded by a large, brown border, 7–15 mm diam. *Caespituli* amphigenous, mainly hypophyllous. *Mycelium* internal. *Stromata* lacking or composed of few brown cells, substomatal or intraepidermal. *Conidiophores* solitary or in loose fascicles (2–4), pale brown to brown, irregular in width, narrowed at upper portion, moderately thick-walled, smooth, straight or abruptly once geniculate, truncate at the tip, 20–120 × 5–6.5 µm, 1–9-septate. *Conidiogenous cells* integrated, terminal, rarely intercalary, proliferating sympodially, 20–60 × 4–6 µm, usually unilocal, rarely multi-local; loci apical or formed on the shoulder due to sympodial proliferation, 2–4 µm diam, thickened and darkened. *Conidia* solitary, hyaline, filiform to acicular, truncate at the base, tip acute, (55–)80–150(–200) × (3.5–)4(–5) µm, 3–15-septate, thin-walled, smooth; hila thickened, darkened, 2–4 µm diam.

*Culture characteristics*: Colonies erumpent, spreading, with sparse to moderate aerial mycelium, and smooth, lobed margin and folded surface; reaching 20 mm diam after 2 wk. On MEA surface dirty white to salmon with patches of olivaceous-grey; reverse iron-grey in centre, salmon in outer region. On PDA surface dirty white with patches of pale mouse-grey, and red, diffuse pigment surrounding culture; reverse olivaceous-grey, but with prominent red pigment. On OA spreading, flat, lacking aerial mycelium, with lobate, smooth margins; surface red with diffuse red pigment surrounding colony; reverse red.

*Specimens examined*: **South Africa**, Eastern Cape Province, Plettenberg Bay, on *Delairea odorata* (= *Senecio mikanioides*) (Asteraceae), C.L. Lennox, CPC 10627–10629; Mpumalanga, Long Tom Pass, on *D. odorata* (= *Senecio mikanioides*), 16 Jun. 2003, S. Naser, **holotype** CBS H-21004, culture ex-type CBS 132595 = CPC 10455.

*Notes*: *Cercospora delaireae* must be regarded as a new species based on its distinct phylogenetic position (Fig. 2 part 2). In the individual gene trees it is distinguished in the ACT, CAL and HIS phylogenies; in the TEF phylogeny it cannot be distinguished from *C. cf. chenopodii*. In the combined tree (Fig. 2 part 2), it is a sister taxon to *C. ricinella*. It appears to be specific to *Delairea odorata* (= *Senecio mikanioides*) (Cape-ivy), and should be further evaluated as possible biocontrol agent of this host. *Delairea odorata* is an invasive perennial vine problematic in coastal riparian areas and is reported as being toxic to animals and fish. Stem, rhizome and stolon fragments resprout if left in the ground after treatment (for further information see <[www.cal-ipc.org/ip/management/plant\\_profiles/Delairea\\_odorata.php](http://www.cal-ipc.org/ip/management/plant_profiles/Delairea_odorata.php)>).

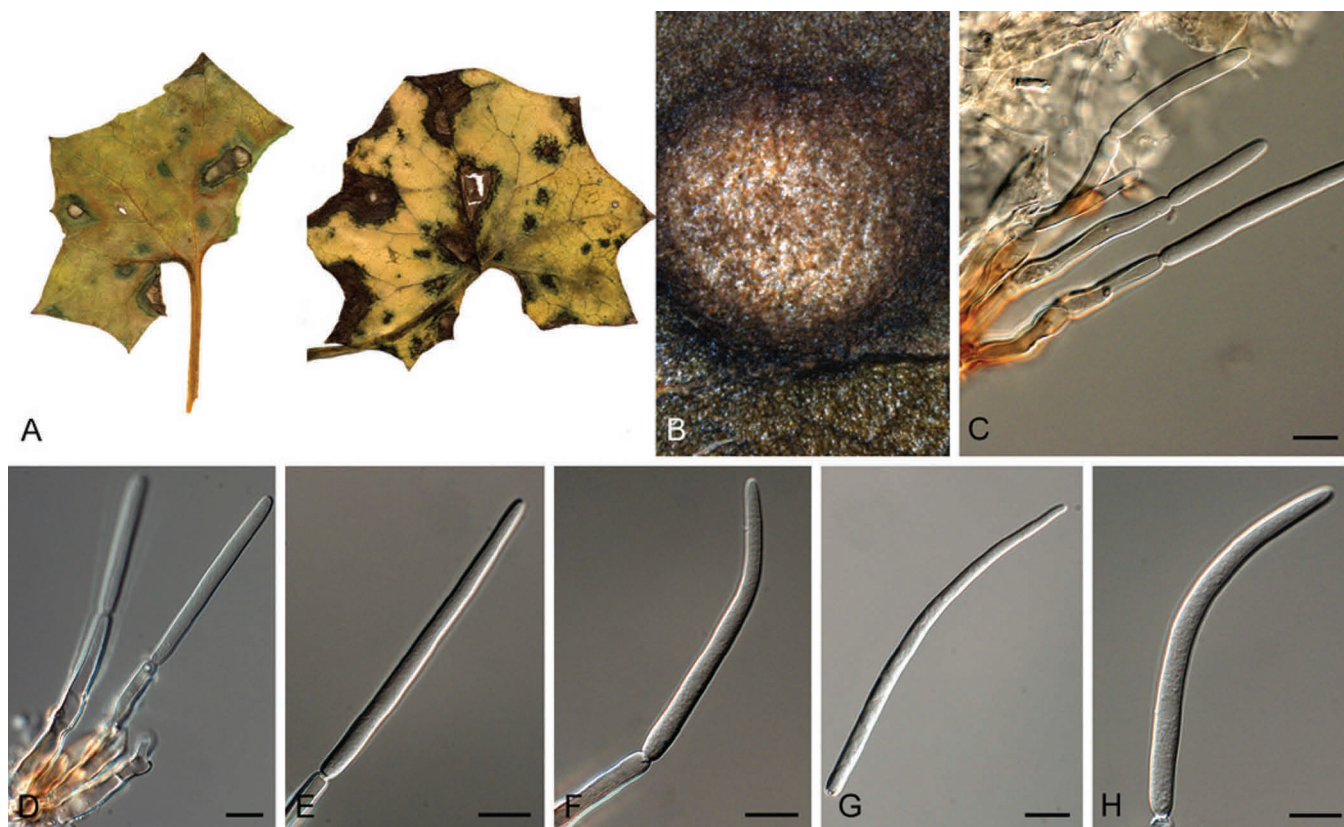


Fig. 7. *Cercospora delaireae* (CBS 132595 = CPC 10455). A. Leaf spots. B. Close-up of lesion. C–F. Conidiophores giving rise to conidia. G, H. Conidia. Scale bars = 10 µm.

***Cercospora dispori*** Togashi & Maki, Trans. Sapporo Nat. Hist. Soc. 17: 98. 1942.

*Caespituli* amphigenous. *Mycelium* internal. *Stromata* lacking to small, up to 40 µm diam, dark brown, intraepidermal or substomatal. *Conidiophores* solitary, or up to 2–10 in loose fascicles, thick-walled, dark brown, paler towards the apex, straight or sinuous-geniculate, almost uniform in width, conically truncate at the apex, 45–100 × 3.5–5.5 µm, 1–7-septate. *Conidiogenous cells* integrated, proliferating sympodially or rarely percurrently, terminal and intercalary, multi-local; loci thickened, not protuberant, apical, lateral. *Conidia* solitary, hyaline, acicular to cylindrical, slightly curved, obconically truncate or subtruncate, and thickened at the base, acute or obtuse at the apex, 30–85(–200) × 3.5–5 µm, 2–12-septate, thin-walled, smooth.

*Specimens examined*: **Japan**, Fukuoka, on *Disporum smilacinum* var. *ramosum* (Convallariaceae), 22 Sep. 1940, Y. Maki & T. Katsuki, **holotype** in SAPA? (specimen could not be located). **South Korea**, Pyeongchang, on *Disporum viridescens* (Convallariaceae), 20 Sep. 2003, H.D. Shin, CBS 132608 = CPC 10773; CPC 10774–10775.

*Notes*: *Cercospora chinensis* and *C. dispori* are distinguished from other *C. apii* s. lat. species in that their conidiophores are uniform in width, thick-walled, dark coloured and conically truncate at the apex. In this study, *C. chinensis* and *C. dispori* occur on Convallariaceae, and cluster together in a well-supported clade. On the individual gene trees, these two species (represented by isolates CPC 10831 and CPC 10773) rarely cluster and are both on long branches in the phylogenetic analyses. In the TEF phylogeny, *C. dispori* cannot be distinguished from *C. apii* / *C. beticola* whereas *C. chinensis* is a sister taxon to *C. pileicola*. In the ACT phylogeny, *C. chinensis* cannot be distinguished from *C. apii* / *C. beticola* and *C. dispori* is a sister taxon to the *C. apii* / *C. beticola* clade. In the

CAL phylogeny the two species are indistinguishable and they are related to *C. lactucae-sativae*. In the HIS phylogeny the two species are sister taxa related to *C. citrullina*. In the combined tree (Fig. 2 part 5), it is a sister taxon to *C. chinensis*. Based on morphological characteristics, there is a difference between the two species in that the conidiophores of *C. chinensis* are sometimes branched. Thus, these two species are retained as separate taxa.

### ***Cercospora* cf. *erysimi***

*Specimen examined*: **New Zealand**, Manurewa, on *Erysimum mutabile* (Brassicaceae), 5 Dec. 2002, C.F. Hill, Lynfield 625, CBS 115059 = CPC 5361.

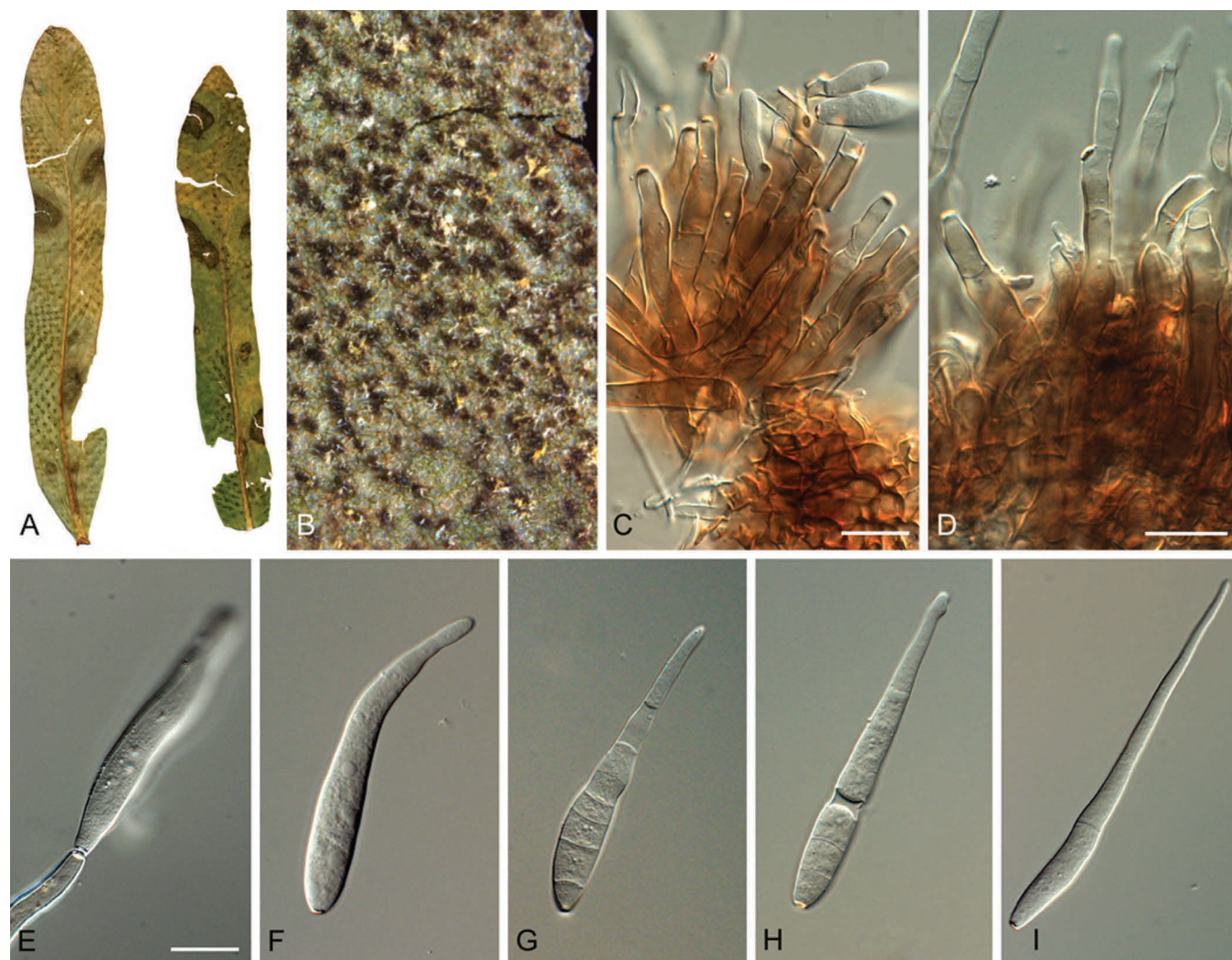
*Notes*: This species is phylogenetically supported by TEF, ACT, CAL and HIS. A collection on *Erysimum* (Brassicaceae) from Europe (isolate CPC 5056) clusters within *C. armoraciae*. The latter could also be the “true *C. erysimi*”, which is still unclear. The type of *C. erysimi* is from North America. Thus, fresh material is needed from North America to resolve the application of the name “*C. erysimi*”. In the combined tree (Fig. 2 part 1), it is a sister taxon to *C. cf. modiolae* and *Cercospora* sp. E.

***Cercospora euphorbiae-sieboldianae*** C. Nakash., Crous, U. Braun & H.D. Shin, **sp. nov.** MycoBank MB800655. Fig. 8.

*Etymology*: Named after the host from which it was collected, *Euphorbia sieboldiana*.

*Leaf spots* amphigenous, subcircular to irregular, 3–15 mm diam, coalenscing, up to 25 mm diam, brown to greyish brown, becoming whitish grey in centre, with blackish margins on upper surface, and greyish white to grey on lower surface. *Mycelium* internal. *Caespituli* amphigenous. *Stromata* small to well-developed, intraepidermal to





**Fig. 8.** *Cercospora euphorbiae-sieboldianae* (CBS 113306). A. Leaf spots. B. Close-up of lesion. C, D. Fasciculate conidiophores. E. Conidiophore giving rise to conidium. F–I. Conidia. Scale bars = 10  $\mu$ m.

substomatal, brown to dark brown, 20–125  $\mu$ m. *Conidiophores* loose to densely fasciculate in fascicles of 3–40, pale brown to brown, paler towards the apex, irregular in width, somewhat constricted at the proliferating point, conically truncate at the apex, 0–2-septate, straight or sinuous to geniculate due to sympodial proliferation, simple, rarely branched, 15–170  $\times$  4.5–8  $\mu$ m. *Conidiogenous cells* integrated, terminal, rarely intercalary, proliferating sympodially, 50–70  $\times$  4–5  $\mu$ m, multi-local; loci distinctly thickened, darkened, apical or formed on the shoulder, rarely lateral, 3–4.5  $\mu$ m diam. *Conidia* solitary, hyaline to subhyaline, solitary, straight to slightly curved, obclavate to obclavate-cylindric, obconically truncated at the base, acute to obtuse at the apex, often beak-like at the apex, 38–130  $\times$  5.5–8(–12)  $\mu$ m, (4–)3–6(–12)-septate, thin-walled, smooth; hila thickened, darkened, 3–4.5  $\mu$ m diam.

**Culture characteristics:** Colonies erumpent, spreading, with sparse aerial mycelium and smooth, even margins, reaching 30 mm diam after 2 wk at 25  $^{\circ}$ C in the dark. On MEA surface grey-olivaceous, reverse iron-grey. On PDA surface and reverse olivaceous-grey. Colonies forming spermatogonia in culture on both media.

**Specimen examined:** South Korea, Samcheok, on *Euphorbia sieboldiana* (*Euphorbiaceae*), 8 May 2003, H.D. Shin, **holotype** CBS H-21005, culture ex-type CBS 113306.

**Notes:** This species is phylogenetically distinguishable from its closest relatives in the TEF, ACT, CAL and HIS phylogenies. It is related to *C. polygonaceae* (TEF), *C. senecionis-walkerii* (ACT), *C. vignigena* (CAL) and *C. punctiformis* (HIS); therefore it is distinct from the other species occurring on *Euphorbiaceae* included in this study. In the combined tree (Fig. 2 part 2), it is a sister taxon to *C. punctiformis*. It is morphologically well distinguished from species of the *C. apii* complex and other species of *Cercospora* by its unusually broadly obclavate-cylindrical conidia (5.5–8(–12)  $\mu$ m) with few septa and rather broad loci and hila (3–4.5  $\mu$ m).

***Cercospora fagopyri* K. Nakata & S. Takim., J. Agric. Exp. Stat. Gov. Gen. Chosen 15: 29. 1928.**

= *Cercospora fagopyri* Abramov, in Lavrov, Opređ. rastit. paras. kul't. i dikor. polezn. rast. Sibiri, Vyp. I: 22. 1932, nom. nud.

≡ *Cercospora fagopyri* Abramov, in Vasilevsky & Karakulin, Fungi imperfecti parasitici. 1. Hyphomycetes: 321. 1937, nom. illeg. (homonym).

= *Cercospora fagopyri* Chupp & A.S. Mull., Bol. Soc. Venez. Ci.: Nat. 8: 44. 1942, nom. illeg. (homonym).

*Caespituli* caulogenous, or amphigenous on leaves. *Mycelium* internal. *Stromata* intraepidermal or substomatal, pale brown, small to well-developed, 25–60  $\mu$ m diam. *Conidiophores* pale brown, solitary, or in loose to dense fascicles (2–20), sinuously geniculate, rarely geniculate due to sympodial proliferation, usually irregular in width, frequently constricted due to proliferation,

attenuated at the tip, truncate at the apex, multi-septate, 20–120 × 3.5–5.5 µm, 0–5-septate. *Conidiogenous cells* integrated, mainly terminal, rarely intercalary, proliferating sympodially, multi-local; loci thickened and darkened, apical and formed on the shoulder caused by sympodial proliferation, sometimes lateral, sometimes protuberant, 1.5–2.5 µm. *Conidia* solitary, hyaline, cylindrical to acicular, straight or slightly curved, long obconically truncate or truncate at the thickened and darkened base, obtuse or acute at the apex, 20–100 × 3–4 µm, 3–20-septate, thin-walled, smooth.

*Description of caespituli on V8*; (MUCC 130): *Caespituli* dimorphic, either small (common), or large (rarely observed; described in parenthesis). *Conidiophores* solitary to loosely fasciculate, arising from hyphae, subhyaline to pale brown, irregular in width, smooth, meager and thin-walled, sinuous-geniculate to geniculate (straight to geniculate), unbranched, truncated at the tip, 15–500 × 3–5 µm, multi-septate. *Conidiogenous cells* integrated, terminal or intercalary, proliferating sympodially, multi-local (uni-local); loci moderately thickened, apical, protuberant (not protuberant), 1.25–3 µm in width. *Conidia* solitary, hyaline, filiform to acicular, slightly thickened and obconically truncate (truncate) at the base, acute at the apex, 45.5–187 × 2–4.5 µm, 3–16-septate.

*Specimens examined*: **Japan**, Ehime, on *Cosmos bipinnata* (Asteraceae), 16 Oct. 2004, J. Nishikawa, MUMH 11394, MUCC 130; on *Hibiscus syriacus* (Malvaceae), MUCC 866. **South Korea**, Suwon, on *Viola mandshurica* (Violaceae), 14 Oct. 2003, H.D. Shin, CBS H-21006, CBS 132649 = CPC 10725; Yangpyeong, on *Cercis chinensis*, (Fabaceae), 19 Oct. 2007, H.D. Shin, CBS H-21007, CBS 132671 = CPC 14546; on *Fagopyrum esculentum* (Polygonaceae), 9 Oct. 2007, H.D. Shin, **neotype designated here** CBS H-21008, culture ex-neotype CBS 132623 = CPC 14541 (**holotype** specimen, South Korea, Suwon, on *Fag. esculentum*, Sep. 1934, K. Nakata & S. Takimoto, could not be located and is undoubtedly not preserved); on *Fallopia dumentorum* (Polygonaceae), 16 Oct. 2002, H.D. Shin, CBS H-21009, CBS 132640 = CPC 10109.

*Notes*: Phylogenetically the separation of *C. fagopyri* is supported by the TEF and HIS phylogenies, though it is intermixed with strains of *C. cf. sigesbeckiae* in the ACT phylogeny and of *C. kikuchii* in the CAL phylogeny. In the combined tree (Fig. 2 part 4), it is a sister taxon to *C. cf. ipomoeae*. Presently several isolates originating from diverse host families reside in this clade. However, lesions on *Viola* appear to be insect associated, and caused by a *Colletotrichum* species, with *Cercospora* colonisation being secondary. Furthermore, lesions on *Fallopia dumentorum* appear to be associated with chemical damage, not *Cercospora*, again suggesting that *Cercospora* colonisation was secondary. The fungus occurring on *Cercis chinensis* is distinct, having very long conidiophores (200–600 µm), and very long conidia. To resolve the host range of *C. fagopyri*, isolates from *Fagopyrum* need to be recollected in Korea, and pathogenicity established on the hosts listed above. Thus the name *C. fagopyri* can only be applied to other isolates than those from *Fagopyrum* tentatively, awaiting additional fresh collections.

### *Cercospora cf. flagellaris*

*Caespituli* amphigenous. *Mycelium* internal. *Stromata* lacking to well-developed, up to 50 µm diam, brown, intraepidermal and substomatal. *Conidiophores* straight or successively geniculate at the apex, rarely abruptly geniculate, solitary, or in loose to dense fascicles (2–23), pale brown to brown, paler towards the apex, simple, rarely branched, uniform in width up to the middle, strongly attenuated at the upper portion, sometimes constricted at septa, often constricted following sympodial proliferation, 14–140(–270) ×

2.5–6.5 µm, 0–8-septate, truncate or short obconically truncated at the apex. *Conidiogenous cells* integrated, terminal and intercalary, proliferating sympodially, multi-local (2–5); loci distinctly thickened, apical or formed on the shoulders caused by geniculation, lateral, rarely protuberant, small, 1–4 µm. *Conidia* solitary, hyaline, cylindrical to acicular, sometimes obclavate, straight or slightly curved, truncate or short obconical truncate at the thickened and darkened base, acute at the apex, 18–240 (–300) × 2–4.5 µm, 1–12-septate, thin-walled, smooth.

*Description of caespituli on V8*; MUCC 127: *Conidiophores* solitary, arising from hyphae, pale brown, uniform in width, sometimes wider at the base, smooth, straight to slightly sinuous, conically truncate at the tip, 10–95 × 3–5 µm, multi-septate. *Conidiogenous cells* integrated, terminal; loci distinctly thickened, apical, 1.25–2 µm in width. *Conidia* hyaline, acicular to filiform, slightly thickened and truncate at the base, acute at the apex, 35–220 × 2–3 µm, 2–15-septate.

*Specimens examined*: **Fiji**, on *Amaranthus* sp. (Amaranthaceae), C.F. Hill, Lynfield 677, CPC 5441. **Israel**, on *Trachelium* sp. (Campanulaceae), 16 Nov. 2002, E. Tzul-Abad, CBS 132637 = CPC 10079 (as *C. campanulae*). **Japan**, Ehime, on *Cosmos sulphureus* (Asteraceae), 16 Oct. 2004, J. Nishikawa, MUMH 11393, MUCC 127; Tokyo, on *Hydrangea serrata* (Hydrangeaceae), 10 Nov. 2007, I. Araki & M. Harada, MUMH 10933, MUCC 831; Wakayama, on *H. serrata*, 30 Oct. 2007, C. Nakashima & I. Araki, MUMH 10860, MUCC 735. **South Korea**, Hoengseong, on *Celosia argentea* var. *cristata* (= *C. cristata*), 11 Oct. 2004, H.D. Shin, CBS 132667 = CPC 11643 (as *Cercospora* sp.); Jeju, on *Dysphania ambrosioides* (= *Chenopodium ambrosioides*) (Chenopodiaceae), 12 Nov. 2003, H.D. Shin, CBS 132653 = CPC 10884 (as *C. chenopodii-ambrosioidis*); on *Phytolacca americana* (Phytolaccaceae), 1 Nov. 2007, H.D. Shin, CBS 132674 = CPC 14723; CPC 14724; Jinju, on *P. americana*, 15 Oct. 2003, H.D. Shin, CPC 10684–10686; Namyangju, on *Amaranthus patulus*, 30 Sep. 2003, H.D. Shin, CBS 132648 = CPC 10722; Pocheon, on *P. americana*, 23 Oct. 2002, H.D. Shin, CPC 10124; Suwon, on *Cichorium intybus* (Asteraceae), 14 Oct. 2003, H.D. Shin, CBS 132646 = CPC 10681 (as *C. cichorii*); Yanggu, on *Sigesbeckia pubescens* (Asteraceae), 28 Sep. 2007, H.D. Shin, CBS 132670 = CPC 14487. **South Africa**, Limpopo Province, Messina, *Citrus* sp. (Rutaceae), M.C. Pretorius, CBS 115482 = CPC 4410; CPC 4411; on *Populus deltoides* (Salicaceae), P.W. Crous, CPC 1051–1052. **Unknown**, on *Bromus* sp. (Poaceae), M.D. Whitehead, CBS 143.51 = CPC 5055. **USA**, Texas, on *Eichhornia crassipes* (Pontederiaceae), R. Charudattan & D. Tessmann, 14 Sep. 1996, CBS 113127 (as *C. piaropi*).

*Notes*: The isolates from this species form a monophyletic clade identical to one another and the two isolates of *C. cf. brunkii* on the TEF phylogeny. In the CAL phylogeny the *C. cf. flagellaris* isolates form a monophyletic clade, albeit with some intraspecific variation. Based on ACT data, the clade splits into four lineages: 1. CPC 4410 and 4411, 2. CPC 1052, 1051 and 10681, 3. CPC 5441 and, 4. the remainder of the isolates. In the HIS phylogeny the species also splits into four lineages: 1. CPC 4410, 4411, 10884 and MUCC 735, 2. CPC 10681 and 11643, 3. CPC 5441 and, 4. the rest of the isolates. These splits in phylogeny (see Fig. 2 parts 2–3) are not supported by morphology: conidiophores are successively geniculate at the upper portion, strongly attenuated at the apex; conidiogenous cells are terminal and intercalary with multi-local loci, and conidia are truncate or short obconically truncate at the thickened base. We strongly suspect that this is a species complex. The latter can only be resolved once more authentic isolates for the names listed above are included (from original hosts and countries), additional DNA loci screened, and pathogenicity tests conducted. Included in this species complex is the isolate used by Tessmann *et al.* (2001) as *C. piaropi*. This isolate is indistinguishable from other isolates of *C. cf. flagellaris* based on the TEF, ACT, CAL and HIS phylogenies. *Cercospora flagellaris* is the older name (1882) compared to *C. piaropi* (1917) and should therefore get taxonomic preference.



***Cercospora* cf. *helianthicola***

*Caespituli* amphigenous. *Mycelium* internal. *Stromata* brown, lacking or small, intraepidermal or substomatal, up to 25 µm diam. *Conidiophores* simple, occasionally branched, straight to geniculate, pale brown, arising from small stromata or internal hyphae, solitary or in dense fascicles (up to 15), irregular in width, narrowed at successive geniculation, truncate at the apex, moderately thick-walled, 20–180 × 3–4 µm, septate. *Conidiogenous cells* integrated, terminal, proliferating sympodially, multi-local; loci distinctly thickened, apical and formed on the shoulders caused by geniculation, rarely lateral, refractive, 1.5–2 µm. *Conidia* solitary, acicular to cylindrical, hyaline, straight or curved, truncate and distinctly thickened at the base, obtuse at the apex, 10–85 × 3–4 µm, indistinctly multi-septate, thin-walled, smooth.

*Specimen examined*: Japan, Wakayama, on *Helianthus tuberosus* (Asteraceae), 30 Oct. 2007, C. Nakashima & I. Araki, MUMH 10844, MUCC 716.

*Notes*: This species is distinguished from other taxa in that it has slightly protuberant apical loci that are at times formed on shoulders caused by geniculation. The width of its conidiogenous cells is somewhat narrower behind the fertile region, and has a truncate apex. Furthermore, its conidiophores are rarely branched. A possible name that could be applied is *C. helianthicola*, though the latter species was originally described from South America, and fresh collections would be required to confirm its phylogenetic position. The isolate used in the current study is distinct in the TEF, ACT, CAL and HIS phylogenies. In the combined tree (Fig. 2 part 5), it is a sister taxon to *C. cf. citrulina*.

***Cercospora* cf. *ipomoeae***

*Caespituli* amphigenous. *Mycelium* internal. *Stromata* composed of few brown cells, or well-developed, up to 60 µm diam, intraepidermal or substomatal. *Conidiophores* in loose fascicles (2–8), pale brown, paler towards apex, straight or geniculate at the apex, irregular in width, tip conically truncate, narrowed at the apex, 22.5–92.5 × 3.5–5.5 µm, 0–4-septate. *Conidiogenous cells* integrated, terminal, proliferating sympodially, multi-local; loci thickened, darkened, apical, rarely lateral, rarely slightly protuberant, 2–2.5 µm diam. *Conidia* solitary, hyaline, filiform to acicular, slightly curved, obconically truncate or truncate, and thickened and darkened at the base, acute or obtuse at the apex, 50–135(–245) × 2.5–3(–7.5) µm, 3–19-septate, thin-walled, smooth.

*Specimens examined*: Japan, Kagawa, on *Ipomoea aquatica* (Convolvulaceae), Aug. 2005, G. Kizaki, MUMH 11203, MUCC 442; South Korea, Chuncheon, on *Ipomoea nil* (= *I. hederacea*) (Convolvulaceae), 7 Oct. 2003, H.D. Shin, CBS H-21010, CBS 132652 = CPC 10833; Pocheon, on *Persicaria thunbergii* (Polygonaceae), 2 Oct. 2002, H.D. Shin, CBS H-21011, CBS 132639 = CPC 10102.

*Notes*: This species is supported in the TEF phylogeny but cannot be distinguished from *Cercospora* sp. M and *C. rodmanii* in the ACT phylogeny. Isolate MUCC 442 clusters separately from the other two isolates based on the CAL and HIS phylogenies. In the combined tree (Fig. 2 part 4), it is a sister taxon to *C. fagopyri*. Sequences obtained from *Cercospora* isolates on *Ipomoea* spp. cluster in three different clades. Although the name *C. ipomoeae* is available for this clade, without sequence data from North America (and an appropriate epitype) this name cannot be applied with certainty, above all since isolates from *Ipomoea* cluster in different clades.

***Cercospora kikuchii*** (T. Matsumoto & Tomoy.) M.W. Gardner, Proc. Indian Acad. Sci. 36: 12. (1926) 1927.

*Basionym*: *Cercosporina kikuchii* T. Matsumoto & Tomoy., Ann. Phytopathol. Soc. Japan 1: 10. 1925.

*Specimens examined*: Argentina, on *Glycine max* (Fabaceae), CBS 132633 = CPC 16578. Japan, Kagoshima, on *Glycine soja* (Fabaceae), 1952, H. Kurata, MUCC 590 = MAFF 305040; on *G. soja*, Jan. 1927, T. Matsumoto, CBS 128.27 = CPC 5068 (ex-type of *C. kikuchii*); on seed of *G. soja*, Jan. 1928, H.W. Wollenweber, CBS 135.28 = CPC 5067.

*Notes*: The symptoms on seeds and pods of plants inoculated with an isolate of *C. richardiicola* (MUCC 132; Nakashima, unpubl. data) originating from *Osteospermum* (Asteraceae) in Japan were quite similar to those caused by *C. kikuchii*. Cultures of *C. kikuchii* associated with purple seed stain symptoms cluster apart. This indicates that purple seed stain and leaf blight of *G. max* is caused by at least two different species of *Cercospora*, and that the identification of these species should not be based on disease symptoms alone. In the TEF and HIS phylogeny, the four isolates could not be distinguished from isolates of *Cercospora* sp. O, P and Q, as well as *C. cf. richardiicola* and *C. cf. sigesbeckiae*. Although these isolates clustered separate in the ACT phylogeny, intermixed in the clade was isolate CPC 14680 (*C. cf. richardiicola*) and isolate CPC 18636 (*Cercospora* sp. O). Similarly, the isolates clustered separate in the CAL phylogeny but intermixed with the isolates of *C. fagopyri*. In the combined tree (Fig. 2 part 4), it is a sister taxon to *C. cf. sigesbeckiae*.

***Cercospora lactucae-sativae*** Sawada, Rep. Gov. Agric. Res. Inst. Taiwan 35: 111. 1928.

= *Cercospora lactucae* Welles, Phytopathology 13: 289. 1923, nom. illeg. (homonym), non Henn.

= *Cercospora longispora* Cugini ex Trav., Malpighia 17: 217, 1902, nom. illeg. (homonym).

= *Cercospora longissima* Trav., Malpighia 17: correzione (correction slip) to p. 217, 1903, nom. illeg. (homonym).

= *Cercospora longissima* Cugini ex Sacc., Syll. Fung. 18: 607. 1906, nom. illeg. (homonym).

= *Cercospora lactucae* J.A. Stev., J. Dept. Agric. Puerto Rico 1: 105. 1917, nom. illeg. (homonym).

= *Cercospora ixeridis-chinensis* Sawada, Rep. Gov. Agric. Res. Inst. Taiwan 86: 171. 1943, nom. inval.

= *Cercospora lactucae-indicae* Sawada, Rep. Gov. Agric. Res. Inst. Taiwan 86: 172. 1943, nom. inval.

*Caespituli* amphigenous. *Mycelium* internal. *Stromata* lacking or composed from few brown cells, up to 35 µm diam. *Conidiophores* arising from internal hyphae or a few intraepidermal brown cells, brown to pale brown, solitary to loosely fasciculate (2–7), straight or mildly geniculate, moderately thick-walled, irregular in width, wider and conically truncate at the apex, constricted at proliferating point, 25–150 × 3.5–6 µm, 0–5-septate. *Conidiogenous cells* integrated, terminal and intercalary, proliferating sympodially, uni-local or multi-local (1–2); loci distinctly thickened, 2.5–3.5 µm diam, slightly protuberant, apical. *Conidia* solitary, hyaline, filiform to acicular, or obclavate, obconically truncate and distinctly thickened at the base, subacute or obtuse, often swelling at the apex, 20–125 × 2–6 µm, 4–12-septate, thin-walled, smooth, rarely catenate.

*Description of caespituli on V8 & MEA*; MUCC 570 and 571 (= MAFF 238209 and 237719): *Conidiophores* solitary to loosely fasciculate, pale brown to brown, irregular in width, wider at the apex, constricted at proliferating point, smooth, moderately thick-walled, sinuous-geniculate to geniculate, simple, conically truncate at the apex, 22.5–195 × 3–5.5 µm, multi-septate. *Conidiogenous*



cells integrated, terminal or intercalary, proliferating sympodially; loci moderately thickened, apical, 2.5–3.7 µm in width. *Conidia* hyaline, cylindrical to cylindrical obclavate, filiform, acicular, hilum distinctly thickened and long obconically truncate at the base, obtuse to acute at the apex, 44.5–215.5 × 3–7 µm, 5–20-septate.

*Specimens examined:* **Japan**, Chiba, on *Lactuca sativa* (Asteraceae), 12 Sep. 1997, S. Uematsu, MUCC 571 = MAFF 237719 = MUCNS 214; 18 Sep. 1998, C. Nakashima, MUMH 11401, MUCC 570 = MAFF 238209 = MUCN S463. **South Korea**, Chuncheon, on *Ixeris chinensis* subsp. *strigosa* (= *Ixeris strigosa*) (Asteraceae), 11 Oct. 2002, H.D. Shin, CBS H-21012, CPC 10082; 7 Oct. 2003, H.D. Shin, CBS H-21013, CBS 132604 = CPC 10728. **Taiwan**, Taipei, on *L. sativa*, 9 Mar. 1924 & 5 Apr. 1924, K. Sawada (TNS-F-220470).

*Notes:* This species is characterised in that conidiophores are wide and conically truncate at the apex, and constricted at the proliferating point. Furthermore, the conidia are not strictly acicular, but range from cylindrical-obclavate to acicular and they are rather broad, 3–7 µm. This species is phylogenetically well-supported based on ACT, CAL and HIS. The species cannot be distinguished from the single isolate of *Cercospora* sp. S in the TEF phylogeny, and these two species are also sister groups, but distinct, in the ACT phylogeny. The species is distinguished based on the CAL phylogeny, and split into two groups (MUCC 571 and 571 versus CPC 10082 and 10728) in the HIS phylogeny. In the combined tree (Fig. 2 part 5), it is a sister taxon to *C. cf. helianthicola*.

### *Cercospora cf. malloti*

*Caespituli* amphigenous. *Mycelium* internal. *Stromata* lacking to well-developed, intraepidermal and substomatal, up to 65 µm diam. *Conidiophores* arising from internal hyphae or few brown cells, solitary or in loose fascicles (2–11), pale brown to brown, paler towards the apex, thick-walled, simple, rarely branched, straight or mildly geniculate, abruptly geniculate at the middle, or successively geniculate at the upper portion, irregular in width, narrowed at the apex, somewhat constricted at the part of proliferation, obconically truncate at the apex, 30–115(–250) × 2.5–5.5 µm, multi-septate. *Conidiogenous cells* integrated, terminal and intercalary, proliferating sympodially or percurrently, multi-local; loci apical or formed on the shoulders caused by geniculation, distinctly thickened, refractive, darkened, flattened, rarely protuberant at the shoulder of successive geniculation, 1–2 µm diam. *Conidia* solitary, hyaline, filiform to acicular, thickened and truncate at slightly protuberant base, obtuse or swelling at the apex, 40–90(–250) × 1.5–5 µm, 6–11(–20)-septate.

*Description of caespituli on V8:* MUCC 575 (= MAFF 237872): *Conidiophores* solitary, brown, paler at the apex, uniform in width, smooth, moderately thick-walled, simple, straight to mildly geniculate, short conically truncate at the tip, 100–465 × 1.25–3 µm, multi-septate. *Conidiogenous cells* integrated, terminal and intercalary, proliferating sympodially; loci thickened, flattened, apical or formed on the shoulders caused by geniculation, 2–3 µm in width. *Conidia* hyaline, long cylindrical to filiform, slightly thickened and truncate at the base, obtuse at the apex, 30–430 × 2–4 µm, 3–19-septate, thin-walled, smooth.

*Specimens examined:* **Japan**, Okinawa, on *Mallotus japonicus* (Euphorbiaceae), 19 Nov. 2007, C. Nakashima & T. Akashi, MUMH 10837, MUCC 787; on *Cucumis melo* (Cucurbitaceae), 20 Jan. 1999, K. Uehara, MUCC 575 = MAFF 237872 = MUCNS 582 (as *C. citrullina*).

*Notes:* This species is supported by DNA sequence data of TEF, CAL and HIS. In the ACT phylogeny, the isolates from this species

are intermixed with some isolates of *C. cf. richardiicola* (MUCC 128, 132 and 578) and *Cercospora* sp. P (isolate MUCC 771). In the combined tree (Fig. 2 part 4), it is a sister taxon to *Cercospora* sp. P. The isolates originated from different host plants, but have identical conidiophores, which are thick-walled and with distinct loci at the apex. However, other characters, which include the pattern of geniculation and size of caespituli, are very different. More detailed studies are required to describe the morphological characters of this species. *Cercospora malloti* was originally described from *Mallotus* (Euphorbiaceae) collected in the USA, and fresh material needs to be recollected. The present application of this name for Japanese collections is thus only tentative.

### *Cercospora mercurialis* Pass., in Thüm., Mycoth. Univ., No. 783. 1877.

- = *Cercospora fruticola* Sacc., Fungi Ital., Tab. 674. 1892.
- = *Cercospora mercurialis* var. *annuae* Fautrey, in Roumeguere *et al.*, Rev. Mycol. 15: 16. 1893.
- = *Cercospora mercurialis* var. *latvici* Lepik, Tartu Ülik. Juures Oleva Loodusuur. Seltsi Arundel 39: 152. 1933.
- = *Cercospora mercurialis* var. *multisepta* Săvul. & Sandu, Hedwigia 75: 225. 1936.

*Specimens examined:* **Italy**, Parma, on *Mercurialis annua* (Euphorbiaceae), 1874, Passerini, Thüm., Mycoth. Univ. 783, **isotypes** HBG, HAL. **Romania**, Distr. Prahova, Cheia, on *Mercurialis perennis* (Euphorbiaceae), 31 Jul. 1969, O. Constantinescu, **epitype designated here** CBS H-9850, culture ex-epitype CBS 550.71; on *M. annua*, 28 Jun. 1967, O. Constantinescu, CBS 549.71; Constanta, Hagieni, on *Mercurialis ovata* (Euphorbiaceae), 14 Jul. 1970, O. Constantinescu & G. Negrean, CBS H-9848, BUCM 2012, CBS 551.71.

*Notes:* *Cercospora mercurialis* is supported by TEF, ACT, CAL and HIS and can therefore be treated as an individual species. In the combined tree (Fig. 2 part 2), it is a sister taxon to *C. pileicola*.

### *Cercospora cf. modiolae*

*Specimen examined:* **New Zealand**, leaf spot on *Modiola caroliniana* (Malvaceae), 2002, C.F. Hill, Lynfield 535, CPC 5115.

*Notes:* This species is phylogenetically supported by TEF and ACT, but in the CAL and HIS phylogeny it cannot be distinguished from *Cercospora* sp. E. In the combined tree (Fig. 2 part 1), it is a sister taxon to *Cercospora* sp. E. *Cercospora modiolae* was described from North America and without sequences based on North American collections, this name can only tentatively be applied to the material from New Zealand.

### *Cercospora cf. nicotianae*

*Cultures examined:* **Indonesia**, Medan, leaf spot on *Nicotiana tabacum* (Solanaceae), Jan. 1932, H. Diddens & A. Jaarsveld, CBS 131.32 = CPC 5076. **Mexico**, southern region of Tamaulipas, on *Glycine max*, 17 Oct. 2008, Ma. de Jesús Yáñez-Morales, CBS 132632 = CPC 15918. **Nigeria**, from a leaf spot on *N. tabacum*, Jul. 1969, S.O. Alasoadura, CBS 570.69 = CPC 5075.

*Notes:* See *C. capsici*. The name *C. cf. nicotianae*, described from the USA, can only tentatively be applied here. North American cultures and sequence data are needed for comparison and confirmation. Phylogenetically, *C. cf. nicotianae* is supported by CAL and partly HIS (CPC 5075 and 5076 were separated from CPC 15918). In the TEF phylogeny, the three isolates clustered in a distinct clade with a single isolate from *C. cf. flagellaris* (CPC 5441) but formed three distinct lineages in the ACT phylogeny. In the combined tree (Fig. 2 part 5), it is a sister taxon to *C. cf. brunckii*. Notes in the CBS database report that

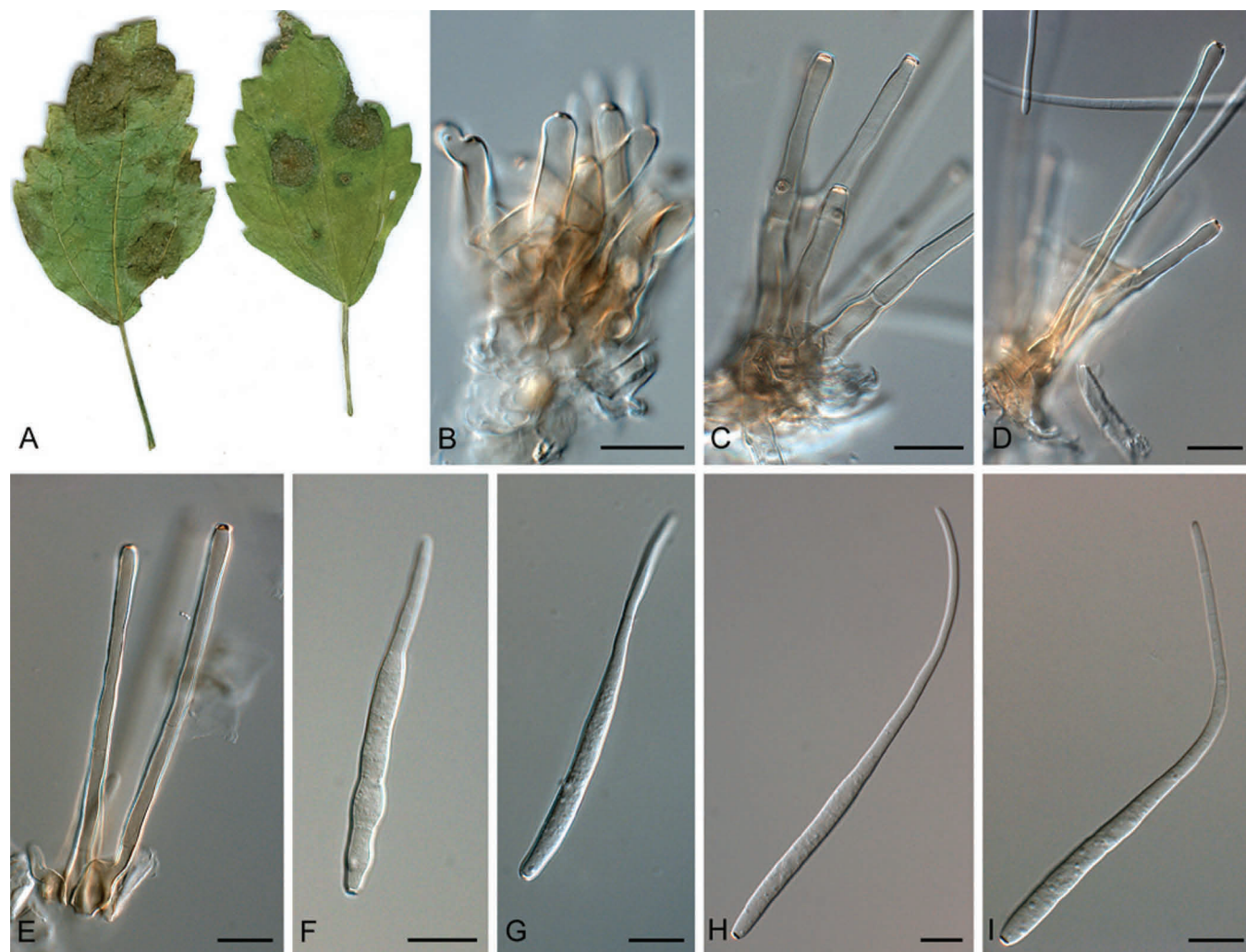


Fig. 9. *Cercospora pileicola* (CBS 132607 = CPC 10749). A. Leaf spots. B–E. Weakly developed, fasciculate conidiophores. F–I. Conidia. Scale bars = 10 µm.

isolate CBS 131.32 was pathogenic when inoculated onto *Nicotiana* leaves. The isolation of *C. cf. nicotianae* from *G. max* requires some additional explanation. Leaf spots typical of *Corynespora cassicola* were observed, and once incubated in damp chambers, a *Cercospora* sp. was found sporulating on the healthy tissue, which was identified here as *C. cf. nicotianae*.

### *Cercospora olivascens* Sacc., Michelia 1: 268. 1879.

**Specimens examined:** Italy, Selva, on *Aristolochia clematidis* (Aristolochiaceae), Aug. 1877, **isotype** distributed as Mycoth Veneta 1251, HAL. Romania, Cazanele Dunarii, on *A. clematidis*, 19 Oct. 1966, O. Constantinescu, **epitype designated here** CBS H-21014, culture ex-type CBS 253.67= IMI 124975 = CPC 5085.

**Notes:** This species is supported by TEF, ACT, CAL and HIS. In the combined tree (Fig. 2 part 1), it is a sister taxon to *Cercospora* sp. F.

### *Cercospora cf. physalidis*

**Specimen examined:** Peru, on *Solanum tuberosum* (Solanaceae), L.J. Turkensteen, CBS 765.79.

**Notes:** This species is supported by CAL and HIS. It cannot be distinguished from *Cercospora* sp. I and *C. alchemillicola* / *C. cf. alchemillicola* based on the TEF and ACT phylogenies. In the combined tree (Fig. 2 part 1), it is a sister taxon to *Cercospora* sp. G. According to Braun & Melnik (1997), *C. physalidis* and

numerous *Cercospora* spp. of *C. apii* s. lat. on various hosts of the Solanaceae are morphologically indistinguishable from the latter species. Fresh material on *Solanum* from North America is required to resolve this issue.

***Cercospora pileicola*** C. Nakash., Crous, U. Braun & H.D. Shin, **sp. nov.** MycoBank MB800656. Fig. 9.

**Etymology:** Named after the host genus from which it was collected, *Pilea*.

**Leaf spots** circular, 1–2 mm diam, center greyish to pallid, surrounded by purplish brown border lines. **Caespituli** hypogenous. **Mycelium** internal. **Stromata** lacking to small, to 30 µm diam, brown, substomatal. **Conidiophores** straight to curved, pale brown to dark brown, paler towards the apex, solitary or in loose fascicles (2–5), sometimes mildly geniculate, simple, thick-walled, uniform in width, rarely narrowed after the geniculation, conically truncate at the apex, 30–110 × 3–8.5 µm, often swelling at the base, to 9 µm, 1–3-septate. **Conidiogenous cells** integrated, terminal, proliferating sympodially; loci distinct, slightly protuberant, apical and formed on shoulder caused by geniculation, lateral, multi-local (1–2), 2.5–4 µm diam. **Conidia** hyaline, cylindrical, acicular to obclavate, straight or curved, truncate or long obconically truncate, and slightly thickened at the base, acute to obtuse at the apex, 28–175 × 4–7 µm, 0–12-septate.



**Culture characteristics:** Colonies erumpent, spreading, with moderate, fluffy aerial mycelium and lobate, even margins, reaching 25 mm diam after 1 wk at 25 °C in the dark. On MEA surface dirty white, reverse cream; red pigment absent. On PDA surface dirty white, reverse scarlet, with diffuse red pigment in agar. On OA surface scarlet in middle (due to collapsed aerial mycelium), white in outer region (due to aerial mycelium), with diffuse red pigment surrounding colony.

**Specimens examined:** **South Korea**, Dongducheon, on *Pilea pumila* (= *P. mongolica*) (*Urticaceae*), 28 Sep. 2003, H.D. Shin, **holotype** CBS H-21015, culture **ex-type** CBS 132607 = CPC 10749; Hoengseong, on *Pilea hamaoi* (= *P. pumila* var. *hamaoi*) (*Urticaceae*), 10 Oct. 2003, H.D. Shin, CBS H-21016, CBS 132647 = CPC 10693; Hongcheon, on *Pilea pumila* (= *P. mongolica*), 29 Jul. 2004, H.D. Shin, CPC 11369.

**Notes:** *Cercospora pileicola* is characterised by having conidiophores that are thick-walled, almost uniform in width, conically truncate at the apex, and often swelling at the base; sporulation is restricted at the terminal part of conidiophores, and conidia are cylindrical, acicular to obclavate with long obconically truncate basal ends and rather broad, 4–7 µm. Moreover, this species is phylogenetically supported by the TEF, ACT, CAL and HIS phylogenies. In the combined tree (Fig. 2 part 2), it is a sister taxon to *C. mercurialis*. *Cercospora ganjetica* (Purkayastha & Mallik 1978), described from India on *Urtica urens* (*Urticaceae*), seems to be morphologically similar to *C. pileicola*, above all due to relatively broad conidia, but the conidia are strictly cylindrical to obclavate with obconically truncate base, i.e. acicular conidia with truncate base are not formed. Length and width of conidiophores agree with those of *C. pileicola*, but they are pluriseptate (3–6). The affinity of *C. ganjetica* is quite unclear. *Cercospora pileae* (Chupp 1954) was described from China on "*Pilea* sp." with conidia being olivaceous. This species is not included in the Chinese monograph of *Cercospora* species (Guo & Liu 2005), but Liu & Guo (1998) reduced this name to synonym with *Pseudocercospora profusa*, suggesting that the type host was misidentified, which was confirmed by Y.L. Guo (Beijing, *in litt.*). The type of *C. pileae* is not *Pilea* sp. but *Acalypha australis* (*Euphorbiaceae*). Chinese collections of *Cercospora* on various hosts of the *Urticaceae*, including *Pilea* spp., have been assigned to *Cercospora krugeriana* (= *nom. inval.*), which is a quite distinct *C. apii*-like species with narrower (2.5–5 µm), pluriseptate, acicular conidia, up to 214 µm long (Hsieh & Goh 1990, Guo & Liu 2005). In addition, the conidiophores are distinctly plurigeniculate. It is possible that the latter collections belong to the *C. cf. sigesbeckiae* clade as circumscribed in this study.

***Cercospora polygonacea* Ellis & Everh., J. Mycol. 1: 24. 1885.**

- = *Cercospora avicularis* var. *sagittati* G.F. Atk., J. Elisha Mitchell Sci. Soc. 8: 48. 1892.
- = *Cercospora polygoni-caespitosi* Sawada, Formosan Agric. Rev. 38: 700. 1942, *nom. inval.*
- = *Cercospora polygoni-blumei* Sawada, *nom. nud.*

**Caespituli** amphigenous. **Mycelium** internal. **Stromata** lacking to small, up to 30 µm diam, pale olivaceous-brown, intraepidermal, substomatal. **Conidiophores** successively geniculate at the upper portion, pale brown, paler towards the apex, solitary or in loose fascicles (2–5), simple, thick-walled, irregular in width, narrowed after the geniculation, conically truncated at the apex, 21–100 × 5–7 µm, 0–3-septate. **Conidiogenous cells** integrated, terminal, intercalary, proliferating sympodially, multi-local (1–6); loci distinct, protuberant, apical and formed on shoulder caused by geniculation,

lateral, 2.5–3 µm diam. **Conidia** solitary, hyaline, acicular to obclavate, straight or slightly curved, truncate or obconically truncate, and thickened at the base, obtuse or acute at the apex, 60–110 × 3.5–5.5 µm, 4–9-septate, thin-walled, smooth.

**Specimen examined:** **South Korea**, Cheongju, on *Persicaria longisetia* (= *P. blumei*) (*Polygonaceae*), 4 Jun. 2004, H.D. Shin, CBS H-21017, CBS 132614 = CPC 11318.

**Notes:** Morphologically the Korean specimen is similar to *C. polygonaceae*, which Chupp (1954) also reported from Asia (Japan). Material from the USA on *Polygonum* (*Polygonaceae*) is required to resolve whether this taxon is the same or phylogenetically distinct. The species is phylogenetically distinct from the other species included in this study based on the TEF and ACT phylogenies, but indistinguishable from *C. achyranthis* on the HIS phylogeny and from *C. achyranthis*, *C. sojina* and *C. campii-silii* based on the CAL phylogeny. In the combined tree (Fig. 2 part 2), it is a sister taxon to *C. achyranthis*.

***Cercospora punctiformis* Sacc. & Roum., Rev. Mycol. 3: 29. 1881.**

- = *Fusicladium cynanchi* Reichert, Bot. Jahrb. Syst. 56: 720. 1921.
- = *Cercospora punctiformis* f. *catalaunica* Gonz. Frag., Mem. Real Acad. Ci. Exact. Madrid, Ser. 2, 6: 250–252. 1927.
- = *Cercospora cynanchi* Lobik, Mat. Fl. Faun. Obsl. Tersk. Okr., Pjatigorsk: 53. 1928.

**Leaf spots** scattered to confluent, at first appearing as purplish spots, later greyish brown with purplish border lines, mostly vein-limited, but rather circular to irregular in case of humid and hot weather (esp. in rainy summer), mostly less than 7 mm diam. **Caespituli** amphigenous, but abundantly hypophyllous. **Mycelium** internal. **Stromata** well-developed, up to 35 µm diam, substomatal and intraepidermal, brown to dark brown. **Conidiophores** in fascicles (5–30), loose to moderately divergent, olivaceous-brown, fairly uniform in colour, but paler towards the apex in longer ones, simple, conically truncate at the apex, geniculate (0–4), 20–60(–150) × 4–7.5 µm, 0–3-septate. **Conidiogenous cells** integrated, proliferating sympodially, terminal and intercalary; loci distinctly thickened, protuberant, apical or formed on the shoulders caused by geniculation, 3–4 µm diam. **Conidia** solitary, hyaline, variable in shape and length, obclavato-cylindrical or elliptical, obconically truncate and thickened at the base, obtuse to subacute at the apex, 25–100(–175) × 4–6.5 µm, 0–8(–12)-septate, thin-walled, smooth.

**Specimen examined:** **South Korea**, Bonghwa, on *Cynanchum wilfordii* (*Asclepiadaceae*), 18 Oct. 2007, H.D. Shin, CBS H-21018, CBS 132626 = CPC 14606.

**Notes:** The Korean sample on *Cy. wilfordii* is morphologically close to *Cercospora punctiformis*, but the latter species was described from North Africa. Hence, sequence data based on North African material are needed to confirm the conspecificity of Korean collections. The ACT and HIS phylogenies separate *C. punctiformis* from the other species included in this study; in the TEF and CAL phylogenies the isolate occurs on a longer branch in a clade consisting of *C. sojina* and *C. achyranthis*. In the combined tree (Fig. 2 part 2), it is a sister taxon to *C. euphorbiae-sieboldianae*.

***Cercospora cf. resedae***

**Specimens examined:** **New Zealand**, Auckland, C.F. Hill, on *Reseda odorata* (*Resedaceae*), specimen in HAL, CBS 118793 (as *C. resedae*). **Romania**, Bucuresti,

on *Helianthemum* sp. (Cistaceae), 15 Sep. 1966, O. Constantinescu, CBS 257.67 = CPC 5057 (as *C. cistinearum*).

**Notes:** Both the names *C. resedae* and *C. cistinearum* are available for this clade. We give preference to *C. resedae*, which is the older name. However, the application of this name is very uncertain and only tentative. Fresh European collections from *Reseda* (*Resedaceae*) are needed to designate an epitype and fix the application of the name. The TEF and ACT phylogenies could not distinguish these two isolates from *C. apii* and *C. beticola*, and the CAL phylogeny could not distinguish it from *C. apii*. The HIS phylogeny places the two isolates in the deviating *C. beticola* Clade 1. A combination of these phylogenetic positions explains the basal position of the species to the *C. apii* and *C. beticola* clades in the combined phylogeny (Fig. 2 part 5).

### *Cercospora* cf. *richardiicola*

*Caespituli* amphigenous. *Mycelium* internal. *Stromata* intraepidermal or substomatal, lacking to well-developed, up to 55 µm diam, pale brown to brown. *Conidiophores* solitary or in loose fascicles (2–15), simple, rarely branched, pale brown to reddish brown, paler towards the apex, moderately thick-walled, irregular in width, sometimes swelling at the shoulders caused by geniculation, truncate or short obconically truncate at the apex, straight to mildly geniculate, often narrowed with successive geniculation at the apex, sometimes swelling at the base to twice the width, 30–260(–360) × 2–7 µm, multi-septate (2–11). *Conidiogenous cells* integrated, terminal and intercalary, proliferating sympodially, or rarely percurrently; loci apical or formed on shoulders caused by geniculation, lateral, circumsperised, distinctly thickened and darkened, often slightly protuberant, 1.5–3.5 µm diam. *Conidia* solitary, rarely catenate, filiform, cylindrical to acicular, hyaline, thickened and truncate or rarely short obconically truncate at the base, rounded or acute at the apex, straight or slightly curved, 25–300 × 2.5–5 µm, 2–20-septate, thin-walled, smooth.

**Description of caespituli on V8;** (MUCC 128, 132, 138, 582): *Caespituli* dimorphic in culture; one type is small and commonly observed, while the other is large and rarely observed (*C. apii* s. lat. type; described in parenthesis). *Conidiophores* solitary to loosely fasciculate, arising from hyphae, subhyaline to pale brown, irregular in width, smooth, meager and thin-walled, sinuous-geniculate to geniculate (straight to geniculate), sometimes branched (unbranched), truncate or conically truncate at the tip (truncate at the tip), 6.5–60(–520) × 2.5–5 µm, multi-septate. *Conidiogenous cells* integrated, terminal or intercalary, proliferating sympodially, 1–5 multi-local (uni-local); loci moderately thickened, apical and lateral, circumsperised at the apex of conidiogenous cells, protuberant (not protuberant), 1.25–2(–4.5) µm in width. *Conidia* hyaline, filiform to acicular, slightly thickened and obconical truncate (truncate) at the base, acute at the apex, 27.5–277.5 × 2–3.5(–6.5) µm, 3–21-septate.

**Specimens examined:** **Japan**, Chiba, on *Zantedeschia* sp. (*Araceae*), S. Uematsu & C. Nakashima, MUMH 11403, MUCC 578 = MAFF 238210; Ehime, on *Tagetes erecta* (*Asteraceae*), 27 Oct. 2004, J. Nishikawa, MUMH 11392, MUCC 128; Shizuoka, on *Fuchsia × hybrida* (*Onagraceae*), 22 Jun. 2006, J. Nishikawa, MUMH 11396, MUCC 138; on *Osteospermum* sp. (*Asteraceae*), 11 Sep. 2004, J. Nishikawa, MUMH 11395, MUCC 132; Tokyo, on *Gerbera hybrida* (*Asteraceae*), J. Takeuchi, MUCC 582 = MAFF 238880.

**Notes:** The name *Cercospora* cf. *richardiicola* can be applied to this clade only tentatively. The latter species was described from the

USA. Hence, sequences obtained from North American collections are necessary to confirm the identity with true *C. richardiicola*. All clades within this complex (*C. cf. richardiicola*, *C. kikuchii*, *C. cf. sigesbeckiae*) are poorly resolved on TEF, ACT, CAL, and HIS regions. The TEF and HIS phylogenies could not distinguish it from *Cercospora* spp. M–Q, *C. kikuchii* and *C. cf. sigesbeckiae*. The ACT phylogeny split it into three clades, namely isolates MUCC 128, 132 and 578 intermixed with *C. malloti* and *Cercospora* sp. P, isolates MUCC 138 and 582 sister to *Cercospora* sp. N and isolate CPC 14680 intermixed with *C. kikuchii* and *Cercospora* sp. O. The CAL phylogeny could not distinguish the isolates from *C. rodmanii*, *C. cf. sigesbeckiae* and *Cercospora* sp. N. Currently this complex is split into three sister clades (Fig. 2 part 4), which could be due to a common ancestor, and an ongoing process of speciation.

*Cercospora richardiicola* is characterised in that conidiophores are sometimes swelling at the shoulders caused by geniculation, truncate or short obconically truncate at the apex, often narrowed (not attenuated) successive geniculation at the apex, and sometimes swelling at the base up to twice its median width; and loci on conidiogenous cells are circumsperised and distinctly thickened. These characteristics were sometimes difficult to find on the host plant due to the difference of maturity of the fungus. However, the morphological characteristics of this species on V8 medium were well preserved regardless of differences of host and maturity.

Isolates of *C. richardiicola* have a tendency to infect a wide host range. Isolates are frequently found together with other *Cercospora* spp. on the same leaf spots, which make identification problematic.

### *Cercospora ricinella* Sacc. & Berl., Atti Reale Ist. Ven. Sci. Lett. Art, Ser. 3: 721. 1885.

= *Cercosporina ricinella* (Sacc. & Berl.) Speg., Anales Mus. Nac. Hist. Nat. Buenos Aires 20: 429. 1910.

= *Cercospora albido-maculans* G. Winter, Hedwigia 24: 202, 1885 (also in J. Mycol. 1: 124. 1885).

= *Cercospora ricini* Speg. Anales Mus. Nac. Hist. Nat. Buenos Aires Ser. 2: 3: 343. 1899.

**Leaf spots** circular to angular, 1–10 mm diam, first appearing as brown spots, later centre becoming greyish white with reddish brown border lines. *Caespituli* amphigenous, mainly hypophyllous. *Mycelium* internal. *Stromata* lacking to well-developed, pale brown to brown, substomatal or intraepidermal, 14–50 µm. *Conidiophores* pale brown, paler towards apex, sinuous-geniculate to geniculate above the middle, in loose fascicles (2–14), slightly divergent, irregular in width, slightly attenuated at the apex, conical at the tip, sometimes constricted at proliferating point, 35–140 × 4.5–5.5 µm, 2–4-septate. *Conidiogenous cells* integrated, terminal and intercalary, proliferating sympodially; multi-local at the apex, loci distinct, slightly protuberant, mainly apical, lateral, 2–3 µm diam. *Conidia* solitary, rarely catenate, hyaline, cylindrical to cylindro-obclavate, acicular, obconically truncate or truncate and distinctly thickened at the base, acute to subacute at the apex, 20–130 × 2.5–5.5 µm, 1–8-septate, thin-walled, smooth.

**Specimens examined:** **South Korea**, Chuncheon, on *Ricinus communis* (*Euphorbiaceae*), 11 Oct. 2002, H.D. Shin, CPC 10104; 7 Oct. 2003, H.D. Shin, CBS 132605 = CPC 10734; CPC 10735–10736.

**Notes:** This species is characterised in that the conidiophores are slightly attenuated at the apex, sinuous-geniculate to geniculate above the middle, and the conidia are rarely catenate. It is supported by ACT, CAL and HIS. In the TEF phylogeny it could not be



distinguished from *C. delaireae*, *C. cf. chenopodii* and *Cercospora* sp. K. In the combined tree (Fig. 2 part 2), it is a sister taxon to *C. delaireae*. Epitype material should be collected in Australia, where this species was described from.

***Cercospora rodmanii*** Conway, Canad. J. Bot. 54: 1082. 1976.

*Specimens examined*: **Brazil**, Oroco, on *Eichhornia crassipes* (Pontederiaceae), R. Charudattan, CBS 113126 = RC3409; Rio Verde, on *E. crassipes*, R. Charudattan, CBS 113123 = RC3660. **Mexico**, Carretero, on *E. crassipes*, R. Charudattan, CBS 113124 = RC2867. **USA**, Florida, on *E. crassipes*, R. Charudattan, CBS 113128 = RC394; CBS 113130 = RC393; K. Conway, CBS 113129 = RC397. **Venezuela**, Maracay, on *E. crassipes*, R. Charudattan, CBS 113131 = RC395. **Zambia**, on *E. crassipes*, M. Morris, CBS 113125 = RC4101.

*Notes*: *Cercospora rodmanii* is supported in the TEF phylogeny. In the ACT phylogeny, the clade includes on longer branches also *C. cf. ipomoeae* and *Cercospora* sp. M. and in the CAL phylogeny it was intermixed with isolates of *C. cf. richardiicola*, *C. cf. sigesbeckiae* and *Cercospora* sp. N. In the HIS phylogeny, it could not be distinguished from *Cercospora* spp. N–Q. In the combined tree (Fig. 2 part 4), it is a sister taxon to *Cercospora* sp. N. Tessmann *et al.* (2001) considered *C. rodmanii* to be a synonym of *C. piaropi* whereas Crous & Braun (2003) retained *C. rodmanii* as a separate species. From the results of the present study, we prefer to retain these as two separate species as reported previously (Groenewald *et al.* 2010a, Montenegro-Calderón *et al.* 2011). The isolate originally included as *C. piaropi* in this study (CBS 113127) is treated in the present study under *C. cf. flagellaris*; this isolate is also the same isolate used by Tessmann *et al.* (2001). Montenegro-Calderón *et al.* (2011) confirmed the identity of their isolates with the same genes included here, as well as beta-tubulin, and demonstrated that their isolates of *C. rodmanii* were able to also infect other important crops such as beet and sugar beet whereas *C. piaropi* (treated under *C. cf. flagellaris* in this study) isolate CBS 113127 and *C. rodmanii* isolate CBS 113129 were specific to water hyacinth.

***Cercospora rumicis*** Pavgi & U.P. Singh, Mycopathol. Mycol. Appl. 23: 191. 1964.

= *Cercospora rumicis* Ellis & Langl. ex Chupp, *A monograph of the fungus genus Cercospora*: 453. 1954, nom. inval.

*Specimen examined*: **New Zealand**, Manurewa, on *Rumex sanguineus* (Polygonaceae), C.F. Hill, Lynfield 671, CPC 5439.

*Notes*: *Cercospora rumicis* was treated as part of the larger *C. apii* s. lat. complex by Crous & Braun (2003). Although it clusters basal to the *C. zebrina* clade, we suspect that it may represent a distinct taxon. Fresh collections are required from India to fix the application of this name. In the TEF phylogeny, it is not distinguished from *C. zebrina* and *C. armoraciae*, and likewise not from *C. armoraciae* on the ACT phylogeny. In the CAL phylogeny, it is not distinguished from *C. zebrina* and *C. althaeina*. It is distinct from all species included in this study based on the HIS phylogeny. In the combined tree (Fig. 2 part 3), it is basal to the lineage containing *Cercospora* sp. L, *C. althaeina*, *C. zebrina* and *C. violae*.

***Cercospora senecionis-walkerii*** Phengsintham, Chukeatirote, McKenzie, K.D. Hyde & U. Braun, Pl. Pathol. & Quarantine 2(1): 70. 2012.

*Specimen examined*: **Laos**, on *Senecio walkeri* (Asteraceae), 20 Feb. 2010, P. Phengsintham, LC 0396, NUOL P567, CBS 132636 = CPC 19196.

*Notes*: Several *Cercospora* species have been described from *Senecio* (Asteraceae), but all of them are quite distinct from the species on *S. walkeri*. *Cercospora senecionis* was reduced to synonym with *C. jacquiniana* by Chupp (1954). Based on a re-examination of type material, Braun (in Braun & Mel'nik 1997) showed that *C. senecionis* represents a quite distinct true species of *Cercospora* with acicular conidia, similar to those of *C. apii* s. lat., but 80–200 × 3–6 µm in size. *Cercospora jacquiniana* is similar to *C. senecionis-walkerii* (Pheng *et al.* 2012) with regard to its conidial shape, but has much shorter conidiophores and shorter conidia, usually only 1–3-sepate, which are hyaline, subhyaline to faintly pigmented. Thus, this species was reallocated to *Passalora* by Braun (in Braun & Mel'nik 1997). The Indian taxon *C. senecionis-grahamii* is close to *C. senecionis*, but differs in having acicular to obclavate conidia, only 3–4 µm wide. The North American *C. senecionicola* is also quite distinct from *C. senecionis-walkerii* by its very narrow acicular-subcylindrical conidia, only 2–3.5 µm wide (Chupp 1954). The South American *Passalora senecionicola* (Braun *et al.* 2006) on *Senecio bonariensis* (Asteraceae) in Argentina is morphologically very close to *C. senecionis-walkerii* but characterised by having quite distinct lesions, larger stromata, up to 60 µm diam and short conidia that are cylindrical. *Passalora senecionicola* was assigned to *Passalora* due to subhyaline to pale olivaceous conidia, but it is possible that this species rather belongs in *Cercospora* which may be suggested by the phylogenetic position of *C. senecionis-walkerii*, which clusters within the *Cercospora* clade, although the conidia range from being almost hyaline to somewhat pigmented. *Cercospora senecionis-walkerii* is distinct from all other species included in this study based on the TEF, ACT, CAL and HIS phylogenies. In the combined tree (Fig. 2 part 1), it is basal to the other *Cercospora* spp.

### ***Cercospora cf. sigesbeckiae***

Morphologically similar to taxa in the *C. apii* s. lat. complex.

*Specimens examined*: **Japan**, Chiba, on *Begonia* sp. (Begoniaceae), 24 Jun. 1997, S. Uematsu, MUMH 11405, MUCC 587 = MAFF 237690 = MUCNS 197; Fukuoka, on *Sigesbeckia glabescens* (Asteraceae), 31 Oct. 1948, S. Katsuki, **holotype** in TNS; Saitama, on *Glycine max*, 1949, H. Kurata, MUCC 589 = MAFF 305039 (as *C. kikuchii*); Tokyo, on *Dioscorea tokoro* (Dioscoreaceae), 10 Nov. 2007, I. Araki, MUMH 10951, MUCC 849. **South Korea**, Chuncheon, on *S. glabescens*, 7 Oct. 2003, H.D. Shin, CBS H-21019, CBS 132601 = CPC 10664 (as *C. sigesbeckiae*); on *Persicaria orientalis* (= *P. cochinchinensis*) (Polygonaceae), 11 Oct. 2002, H.D. Shin, CBS 132641 = CPC 10117 (as *C. polygonacea*); Hongcheon, on *Pilea pumila* (= *P. mongolica*), 3 Oct. 2002, H.D. Shin, CBS 132642 = CPC 10128 (as *C. ganjetica*); Namyangju, on *Paulownia coreana* (Scrophulariaceae), 22 Oct. 2003, H.D. Shin, CBS H-21020 = HAL 1863, CBS 132606 = CPC 10740; Yanggu, on *Sigesbeckia pubescens*, 28 Sep. 2007, H.D. Shin, CBS 132621 = CPC 14489 (as *C. sigesbeckiae*); on *Malva verticillata* (Malvaceae), H.D. Shin, CBS H-21021, CBS 132675 = CPC 14726 (as *C. malvacearum*).

*Notes*: See *Cercospora cf. richardiicola*. The application of the name *C. cf. sigesbeckiae* (based on type material from Japan), to this clade can only be tentative. Japanese cultures and sequences are needed to confirm its identity. In the TEF and CAL phylogenies, isolates are intermixed with those of *Cercospora* spp. M–Q, *C. kikuchii* and *C. cf. richardiicola*; in the ACT phylogeny it cannot be distinguished from *C. fagopyri*. In the HIS phylogeny the isolates form a clade on a longer branch in a clade containing *C. kikuchii* and some isolates of *C. cf. richardiicola*. In the combined tree (Fig. 2 part 4), it is a sister taxon to *C. kikuchii* and *C. cf. richardiicola*.



***Cercospora sojina* Hara, Nogoyokoku (Tokyo) 9: 28. 1915.**

≡ *Cercosporina sojina* (Hara) Hara, Jitsuyo-sakumotsu-byorigaku: 112. 1925.

≡ *Cercosporidium sojinum* (Hara) X.J. Liu & Y.L. Guo, Acta Mycol. Sinica 1: 100. 1982.

≡ *Passalora sojina* (Hara) Poonam Srivast., J. Living World 1: 118. 1994, comb. inval.

≡ *Passalora sojina* (Hara) H.D. Shin & U. Braun, Mycotaxon 58: 63. 1996.

≡ *Passalora sojina* (Hara) U. Braun, Trudy Bot. Inst. im. V.L. Komarova 20: 93. 1997, comb. superfl.

= *Cercospora daizu* Miura, Manchurian R.R. Agric. Exp. Stat. Bull. 11: 25. 1920.

*Caespituli* amphigenous. *Mycelium* internal. *Stromata* small, up to 35 µm diam, intraepidermal and substomatal, brown. *Conidiophores* solitary or in loose fascicles (2–5), brown, paler towards the apex, simple, rarely branched, irregular in width, constricted at the parts of proliferation, conically truncate at the apex, straight to geniculate, 55–200 × 4.5–5 µm, 2–4-septate. *Conidiogenous cells* integrated, proliferating sympodially, terminal and intercalary, uni- or multi-local (1–2); loci distinctly thickened, protuberant, apical or formed on the shoulders caused by geniculation, 2–4 µm diam. *Conidia* solitary, hyaline, cylindrical to obclavate, fusiform, obovoid, obconically truncate and thickened at the base, obtuse at the apex, 25–70 × 5.5–9 µm, 1–5-septate, thin-walled, smooth.

*Specimens examined*: **Argentina**, on *Glycine max* (*Fabaceae*), 2009, F. Scandiani, CPC 17964 = CBS 132684 = CPC 17971 = "CCC 173-09, 09-495"; "CCC 155-09, 09-285-5"; CPC 17965 = "CCC 156-09, 09-285-4"; CPC 17966 = "CCC 157-09, 09-285-3"; CPC 17967 = "CCC 158-09, 09-285-1"; CPC 17968 = "CCC 159-09, 09-285-7"; CPC 17969 = "CCC 167-09, 09-881"; CPC 17970 = "CCC 172-09, 09-320"; CPC 17972 = CCC 174-09; CPC 17973 = "CCC 176-09, 09-882"; CPC 17974 = "CCC 177-09, 09-2488-1"; CPC 17975 = "CCC 178-09, 09-1438-2"; CPC 17976 = "CCC 179-09, 09-2591"; CPC 17977 = "CCC 180-09, 09-2520". **South Korea**, Hoengseong, on *G. soja*, 4 Sep. 2005, H.D. Shin, CBS 132018 = CPC 12322; Hongcheon, on *G. soja*, 20 Jul. 2004, H.D. Shin, **neotype designated here** CBS H-21022, culture ex-type CBS 132615 = CPC 11353; CPC 11354; CPC 11420–11423.

*Notes*: Type material of this species (Japan, Tokyo, on *G. max*, 1909, K. Hara) was not located and is probably lost. *Cercospora sojina* was transferred to the genus *Passalora* based on its distinctly thickened loci, and cylindrical and relatively wide conidia (Shin & Braun 1996). However, the hyaline conidia of this species are indicative of the fact that it is best retained in *Cercospora* (Crous & Braun 2003), which is fully supported by its position in phylogenetic trees among other *Cercospora* species. The species is supported as distinct based on the ACT and HIS phylogenies; in the TEF and CAL phylogenies the isolates of *C. achyranthis* and *C. campisillii* are intermixed with the *C. sojina* isolates. In the combined tree (Fig. 2 part 2), it is a sister taxon to *C. campisillii*.

***Cercospora* sp. A**

*Culture sequenced*: **Mexico**, on *Chenopodium* sp. (*Amaranthaceae*), M. de Jesus Yanez, CBS 132631 = CPC 15872.

*Notes*: This isolate is phylogenetically distinct (Fig. 2 part 1) from the other species included in this study. Unfortunately, the specimen and specimen details were not available for study.

***Cercospora* sp. B**

*Caespituli* amphigenous. *Mycelium* internal. *Stromata* lacking to developed, up to 60 µm, intraepidermal, substomatal, brown. *Conidiophores* straight or geniculate, solitary to 2–21 in dense

fascicle, 0–5-septate, 20–75 × 4.5–6 µm, almost uniform in width, constricted at shoulder, conically truncate or truncate at the tip. *Conidiogenous cells* integrated, terminal, intercalary, proliferating sympodially, multilocal; loci thickened, apical, rarely lateral, 2–2.5 µm diam, slightly protuberant. *Conidia* solitary, hyaline, cylindro-obclavate to acicular, obconically truncate at thickened base, tip obtuse, 45–135 × 4–5 µm, 4–9-septate, thin-walled, smooth.

*Specimen examined*: **South Korea**, Kangnung, on *Ipomoea purpurea* (*Convolvulaceae*), 10 Sep. 2003, H.D. Shin, CBS 132602 = CPC 10687 (as *C. ipomoeae*); CPC 10688–10689 (as *C. ipomoeae*).

*Notes*: This isolate was obtained from *Ipomoea* in Korea, but differs in its phylogeny to other isolates of *C. cf. ipomoeae*. It has a unique position in the ACT, CAL and HIS phylogenies and is intermixed with *C. delaireae* and *Cercospora* sp. K based on the TEF phylogeny. In the combined tree (Fig. 2 part 1), it is a basal taxon to *C. agavicola*. Several species of *Cercospora* have thus far been described from *Ipomoea*, and more collections would be required to resolve the status of this collection.

***Cercospora* sp. C**

*Culture sequenced*: **Mexico**, M. de Jesus Yanez, CBS 132629 = CPC 15841.

*Notes*: This isolate is phylogenetically distinct (Fig. 2 part 1) from the other species included in this study. Unfortunately, the specimen and specimen details were not available for study.

***Cercospora* sp. D**

*Culture sequenced*: **Mexico**, M. de Jesus Yanez, CBS 132630 = CPC 15856.

*Notes*: This isolate is phylogenetically distinct (Fig. 2 part 1) from the other species included in this study. Unfortunately, the specimen and specimen details were not available for study.

***Cercospora* sp. E**

*Cultures sequenced*: **Mexico**, M. de Jesus Yanez, CBS 132628 = CPC 15632, CPC 15801.

*Notes*: These isolates are phylogenetically distinct (Fig. 2 part 1) from the other species included in this study. Unfortunately, the specimen(s) and specimen details were not available for study.

***Cercospora* sp. F**

*Specimen examined*: **South Africa**, on *Zea mays* (*Poaceae*), P. Caldwell, CBS 132618 = CPC 12062.

*Notes*: This isolate, which is supported by the CAL phylogeny, must be treated as an independent species. In the TEF and HIS phylogenies it is present on a longer branch in a clade consisting of isolates of *Cercospora* spp. G–I, *C. alchemillicola* / *C. cf. alchemillicola*, *C. cf. physalidis* and *C. celosiae*. In the ACT phylogeny it cannot be distinguished from *Cercospora* sp. Q. In the combined tree (Fig. 2 part 1), it is a sister taxon to *C. cf. physalidis*.

***Cercospora* sp. G**

*Caespituli* amphigenous. *Mycelium* internal. *Stromata* small to well-developed, up to 60 µm diam, brown, intraepidermal and substomatal. *Conidiophores* straight or sinuously geniculate, loosely fasciculate (3–10), pale brown to brown, paler towards the apex, moderately thick-walled, simple, irregular in width, attenuated at the apex, irregularly constricted following the proliferation, 30–50 × 3.5–4.5 µm, 0–2-septate. *Conidiogenous cells* integrated, terminal, rarely intercalary, proliferating sympodially, multi-local; loci thickened, darkened, apical or formed on the shoulders caused by geniculation, lateral, sometimes circumsperised, 1.25–2 µm in diam. *Conidia* solitary, hyaline, cylindrical to obclavate, often acicular, straight or slightly curved, truncate or subtruncate at the thickened base, obtuse or subacute at the apex, 15–165 × 2–4 µm, 1–12-septate, thin-walled, smooth.

*Specimen examined:* **New Zealand**, Manurewa, on *Salvia viscosa* (Lamiaceae), C.F. Hill, Lynfield 626, CPC 5438 (as *C. salviicola*); Kopuku, on *Bidens frondosa* (Asteraceae), C.F. Hill, Lynfield 559, CBS 115518 = CPC 5360.

*Notes:* This species is thus far only known from New Zealand. It is distinct from the other included species based on its position in the HIS phylogeny; in the TEF and ACT phylogenies it cannot be distinguished from *Cercospora* spp. F, H and I as well as *C. alchemillicola* / *C. cf. alchemillicola*, *C. cf. physalidis* and *C. celosiae*. In the CAL phylogeny it forms a distinct clade that cannot be distinguished from *Cercospora* sp. H. In the combined tree (Fig. 2 part 1), it is a sister taxon to *Cercospora* sp. H.

***Cercospora* sp. H**

*Specimens examined:* **Argentina**, on *Chamelaurium uncinatum* (Myrtaceae), S. Wolcan, CPC 11620 = 1CRI. **New Zealand**, on *Dichondra repens* (Convolvulaceae), C.F. Hill, Lynfield 536, CBS 115205 = CPC 5116.

*Notes:* This species is distinct from the other included species based on its position in the HIS phylogeny; in the TEF and ACT phylogenies it cannot be distinguished from *Cercospora* spp. F, G and I as well as *C. alchemillicola* / *C. cf. alchemillicola*, *C. cf. physalidis* and *C. celosiae*. In the CAL phylogeny it forms a distinct clade that cannot be distinguished from *Cercospora* sp. G. Whether *Cercospora* spp. G and H could be conspecific awaits collection of more isolates. In the combined tree (Fig. 2 part 1), it is a sister taxon to *C. celosiae* and *Cercospora* sp. I.

***Cercospora* sp. I**

? *Cercospora deutziae* Ellis & Everh., J. Mycol. 4: 5. 1888.

? *Cercospora guatemalensis* A.S. Mull. & Chupp, Ceiba 1: 173. 1950.

*Specimens examined:* **South Korea**, Suwon, on *Ajuga multiflora* (Lamiaceae), 22 Oct. 2002, H.D. Shin, CBS 132643 = CPC 10138 (as *C. guatemalensis*). **New Zealand**, Manurewa, on *Coreopsis verticillata* (Asteraceae), 2 Jun. 2003, C.F. Hill, Lynfield 866A, CBS 132597 = CPC 10615; Lynfield 866B, CPC 10616; on *Deutzia crenata* (Hydrangeaceae), 5 May 2002, C.F. Hill, Lynfield 610, CBS 114818 = CPC 5362 (named as *C. deutziae*); on *Deutzia purpurascens* (Hydrangeaceae), 5 May 2002, C.F. Hill, Lynfield 607, CBS 114815 = CPC 5364 (named as *C. deutziae*); on *Deutzia × rosea* (= *D. gracilis* × *purpurascens*) (Hydrangeaceae), Apr. 2002, C.F. Hill, Lynfield 599, CBS 114816 = CPC 5363 (named as *C. deutziae*); on *Fuchsia procumbens* (Onagraceae), 5 May 2002, C.F. Hill, Lynfield 613, CBS 114817 = CPC 5365 (named as *C. fuchsia*); on *Nicotiana* sp. (Solanaceae), 8 Jun. 2002, C.F. Hill, Lynfield 667, CPC 5440; Mt Albert, on *Gunnera tinctoria* (Gunneraceae), 29 Feb. 2004, C.F. Hill, Lynfield 997, CBS 115121; Whangarei, on *Archontophoenix cunninghamiana* (Arecaceae), 10 Feb. 2004, C.F. Hill, CBS 115117.

*Notes:* This clade is quite distinct based on the combined tree (Fig. 2 part 1), and mainly consists of isolates from various host plants in New Zealand. In the TEF and ACT phylogenies it cannot be distinguished from *Cercospora* spp. F, G and H as well as *C. alchemillicola* / *C. cf. alchemillicola*, *C. cf. physalidis* and *C. celosiae*. In the CAL phylogeny it forms a distinct clade that cannot be distinguished from the single isolate of *C. celosiae*. In the HIS phylogeny it cannot be distinguished from *Cercospora* sp. F, *C. alchemillicola* / *C. cf. alchemillicola* and *C. celosiae*. In the combined tree (Fig. 2 part 1), it is a sister taxon to *C. celosiae* and *Cercospora* sp. H. Most of the *Cercospora* sp. I isolates from New Zealand would be given a species epithet based on each host plant, if these were classified with a conventional species concept. From the results of the phylogenetic tree, these isolates are recognised as belonging to a single species with a wide host range. Braun & Hill (2004) examined the collections on *Co. verticillata*, *D. crenata*, *D. purpurascens*, *D. × rosea*, *F. procumbens*, *Nicotiana* sp., and Braun *et al.* (2006) studied the samples on *A. cunninghamiana* and *G. tinctoria*. They referred all of them to *C. api* s. lat. as circumscribed in Crous & Braun (2003) as they are characterised by having hyaline acicular conidia formed singly, i.e. the present unnamed species is a *C. api*-like plurivorous species.

***Cercospora* sp. J**

*Culture sequenced:* **Japan**, Aichi, on *Antirrhinum majus* (Plantaginaceae), 8 May 2007, M. Matsusaki, MUMH10490, MUCC 541.

*Notes:* This isolate is phylogenetically distinct (Fig. 2 part 2) from the other species included in this study. Unfortunately, the specimen was not available for study.

***Cercospora* sp. K**

*Caespituli* amphigenous. *Mycelium* internal. *Stromata* lacking or composed of a few brown cells. *Conidiophores* emerging through the cuticle or arising from stomatal openings, pale brown, paler towards the apex, almost uniform in width, sometimes narrowed at the apex following the sympodial proliferation, often constricted at septa and proliferating points, solitary or 2–3 in a loose fascicle, straight or slightly curved to sinuously geniculate, moderately thick-walled, 0–5-septate, 30–110 × 3.5–5 µm, truncate or conically truncate at the apex. *Conidiogenous cells* terminal, rarely intercalary, proliferating sympodially; loci slightly thickened, slightly protuberant (subtruncate) or flat, refractive, apical and lateral, 1.5–2.5 µm in diam. *Conidia* solitary, hyaline, filiform to acicular or obclavate, straight to slightly curved, truncate or obconically truncate at the slightly thickened at the basal end, acute at the apex, indistinctly or distinctly 1–14-septate, 35–230 × 1.5–5 µm, thin-walled, smooth.

*Specimens examined:* **South Korea**, Namyangju, on *Ipomoea coccinea* (= *Quamoclit coccinea*) (Convolvulaceae), 9 Oct. 2002, H.D. Shin, CPC 12391; 30 Sep. 2003, H.D. Shin, CBS 132603 = CPC 10719; 15 Oct. 2005, H.D. Shin, CPC 10094.

*Notes:* This species is phylogenetically supported based on DNA sequence data of ACT, CAL and HIS. In the TEF phylogeny, these isolates cannot be distinguished from *C. ricinella*, *C. cf. chenopodii* and *C. delaireae*. In the combined tree (Fig. 2 part 2), it is a sister taxon to *C. cf. flagellaris*. Different species of *Cercospora* have been described from *Ipomoea* spp. *Cercospora*

*ipomoeae-pedis-caprae* was previously treated as a synonym of *C. ipomoeae* (Bagyanarayana *et al.* 1995, Shin & Kim 2001), since the length of the conidiophores and conidia in the latter species is variable. Braun *et al.* (2001) pointed out the differences among the *Cercospora* species on *Ipomoea* spp. based on the description of these species by García *et al.* (1996), and proposed that *C. ipomoeae-pedis-caprae* must be retained as a separate species. However, *Cercospora* isolates on *Ipomoea* cluster in three different places in the tree, and thus this complex remains unresolved and without epitypification the application of the names *C. ipomoeae* and *C. ipomoeae-pedis-caprae* remains unclear.

### *Cercospora* sp. L

*Specimen examined:* **New Zealand**, on *Crepis capillaris* (Asteraceae), C.F. Hill, Lynfield 534, CBS 115477 = CPC 5114.

*Notes:* *In vivo* material on *Crepis capillaris* from New Zealand collected by C.F. Hill, Auckland, 9 Jul. 2000, deposited at HAL has been examined and is characterised as follows: *Conidiophores* solitary or in small, loose fascicles, straight to usually geniculate-sinuous, unbranched, 20–100 × 3–6 µm, usually 1–4-septate, pale olivaceous throughout or olivaceous-brown below and paler towards the tip; *conidiogenous cells* integrated, usually terminal, sympodial, multi-local; *conidiogenous loci* 2–3 µm diam, thickened and darkened; *conidia* solitary, acicular, short conidia occasionally subcylindrical, straight curved to somewhat sigmoid, 60–170 × 3–4 µm, pluriseptate, apex subacute or subobtuse, base truncate, occasionally slightly attenuated at the very base (at hilum), hila 2–3 µm wide. The application of the name *Cercospora crepidis* Ondřej & Zavrěš, described from Europe (Czech Republic) on *Crepis capillaris*, for the fungus from New Zealand is not possible. The latter species is characterised by having obclavate conidia with distinctly obconically truncate base and short, aseptate conidiophores, only 14–22 µm long (Ondřej & Zavrěš 1971). In the TEF and CAL phylogeny this isolate clusters with *C. zebrina* and *C. armoraciae* and on a longer branch in the *C. zebrina* clade in the ACT phylogeny. It is only in the HIS phylogeny that this isolate is clearly distinct, clustering as sister taxon to *C. delaireae*. In the combined tree (Fig. 2 part 3), it is a sister taxon to *C. althaeina* and *C. zebrina*.

### *Cercospora* sp. M

*Specimen examined:* **Thailand**, Chachoengsao Province, Sanamchaikhet, on leaves of *Acacia mangium* (Fabaceae), 28 May 2003, K. Pongpanich, CBS H-9876, CBS 132596 = CPC 10553.

*Notes:* Crous *et al.* (2004b) isolated several species of *Cercospora* from *A. mangium* in Thailand, some of which were linked to single ascospore isolates of a mycosphaerella-like teleomorph (see Crous *et al.* 2004b, fig. 5). Isolate CPC 10553 (=CBS 132596) occurred on the same leaf spots with *C. acaciae-mangii* (CBS 116365 = CPC 10526), which is here treated under *Cercospora* sp. P. The TEF phylogeny could not distinguish it from *Cercospora* spp. N–Q, *C. kikuchii* and *C. cf. sigesbeckiae*, whereas the HIS phylogeny could not distinguish it from some isolates of *Cercospora* spp. P and Q. The ACT phylogeny places it on a longer branch with *C. rodmanii* and *C. cf. ipomoeae*. The CAL phylogeny could not distinguish it from *Cercospora* spp. P and Q, *C. alchemillicola* / *C. cf. alchemillicola* and *C. cf. sigesbeckiae*. In the combined tree (Fig. 2 part 4), it is basal to the lineage containing *C. rodmanii* and other species.

### *Cercospora* sp. N

*Specimen examined:* **Bangladesh** (western part), on *Musa* sp. (Musaceae), I. Buddenhagen, CBS 132619 = CPC 12684 (named as *C. hayi*).

*Notes:* *Cercospora* sp. N has shorter conidiophores than ascribed to *C. hayi*, which was described from *Musa* in Cuba. It is evident that a complex of *Cercospora* spp. occur on banana. The TEF phylogeny could not distinguish it from *Cercospora* spp. O–Q, *C. kikuchii* and *C. cf. sigesbeckiae*, whereas the HIS phylogeny could not distinguish it from some isolates of *Cercospora* spp. P and Q and *C. rodmanii*. The CAL phylogeny could not distinguish it from *C. rodmanii*, *C. cf. richardiicola* and *C. cf. sigesbeckiae*. The ACT phylogeny distinguishes it from the other species included in this study. In the combined tree (Fig. 2 part 4), it is a sister taxon to *C. cf. richardiicola* and *C. kikuchii*.

### *Cercospora* sp. O

*Specimen examined:* **Thailand**, Chiang Mai, Mae Klang Loung, N18°32.465' E98°32.874', on *Musa* sp. (Musaceae), 6 Oct. 2010, P.W. Crous, CBS 132635 = CPC 18636 (named as *C. hayi*).

*Notes:* Based on its shorter conidiophores, *Cercospora* sp. O is distinct from *C. hayi*, and morphologically is more similar to *Cercospora* sp. N. The TEF phylogeny could not distinguish it from *Cercospora* spp. M, N and Q, *C. kikuchii* and *C. cf. sigesbeckiae*, whereas the HIS phylogeny could not distinguish it from some isolates of *Cercospora* spp. N, P and Q and *C. rodmanii*. The CAL phylogeny could not distinguish it from *Cercospora* spp. P and Q, *C. alchemillicola* / *C. cf. alchemillicola* and *C. cf. sigesbeckiae* and the ACT phylogeny from *C. kikuchii*. In the combined tree (Fig. 2 part 4), it is a sister taxon to *C. cf. malloti*.

### *Cercospora* sp. P

*Specimens examined:* **Ghana**, on leaves of *Dioscorea rotundata* (Dioscoreaceae), 2000, S. Nyako & A.O. Danquah, CBS 132660 = CPC 11629 = GHA-4-0; CPC 11630 = GHA-4-3; CPC 11631 = GHA-5-0; CPC 11632 = GHA-7-4; CPC 11633 = GHA-8-4 (as *C. dioscoreae-pyrifoliae*). **Japan**, Okinawa, on *Coffea arabica* (Rubiaceae), C. Nakashima, MUMH 10823, MUCC 771 (as *C. coffeicola*). **Mexico**, Tamaulipas, on *Ricinus communis*, 31 Nov. 2008, Ma. de Jesús Yáñez-Morales, CBS 132680 = CPC 15827. **New Zealand**, Auckland (imported from Fiji islands), on leaves of *Hibiscus sabdariffa* (Malvaceae), C.F. Hill, Lynfield 578, CPC 5262. **Papua New Guinea**, on leaves of *Dioscorea nummularia* (Dioscoreaceae), 2000, J. Peters & A.N. Jama, CBS 132662 = CPC 11635 = PNG-009; on leaves of *D. rotundata*, 2000, J. Peters & A.N. Jama, CBS 132664 = CPC 11637 = PNG-022; on leaves of *Dioscorea bulbifera* (Dioscoreaceae), 2000, J. Peters & A.N. Jama, CBS 132665 = CPC 11638 = PNG-023. **South Africa**, Nelspruit, on *Cajanus cajan* (Fabaceae), L. van Jaarsveld, CBS 113996 = CPC 5326; CBS 115413 = CPC 5328; CPC 5327; Komatipoort, on *Citrus × sinensis* (≡ *C. aurantium* var. *sinensis*) (Rutaceae), M.C. Pretorius, CBS 112728 = CPC 3949; CBS 112730 = CPC 3948; CBS 112894 = CPC 3950. **Swaziland**, on *Citrus × sinensis* (≡ *C. aurantium* var. *sinensis*), M.C. Pretorius, CPC 4001; CPC 4002; on *Citrus* sp. leaf spot, M.C. Pretorius, CBS 112649 = CPC 3946; CBS 112722 = CPC 3947; CBS 115609 = CPC 3945. **Thailand**, on *Acacia mangium*, M.J. Wingfield, CBS 116365 = CPC 10526; CBS 132645 = CPC 10527 (Mycosphaerella teleomorph ascospore isolate, *ex-type* of *Cercospora acaciae-mangii*, small colonies); on *A. mangium*, K. Pongpanich, CPC 10552.

*Notes:* Isolates of this clade were mainly obtained from *Acacia*, *Cajanus*, *Citrus* (Rutaceae), *Coffea* (Rubiaceae), *Dioscorea*, *Hibiscus* (Malvaceae) and *Ricinus* (Euphorbiaceae). Many previously described species names have in the past been applied to different isolates clustering in this clade. Based on the gene loci screened in the present study, we were unable to resolve the taxonomy of these isolates, and for now prefer to treat them as an unresolved species complex. In none of the single-gene phylogenies generated in this study



did the isolates from this species form a pure monophyletic lineage, as isolates were frequently intermixed with that of *Cercospora* sp. Q, *C. cf. sigesbeckiae* and *C. cf. richardiicola*. Given this overlap in sequence identity and host species, it is possible that *Cercospora* spp. P (Fig. 2 parts 4–5) and Q (Fig. 2 part 5) could be considered as a single species complex (see species notes for *Cercospora* sp. Q below). More extensive screening of additional loci is needed to define the species boundaries in this complex. Also present in this complex are numerous isolates from *Dioscorea*, for which the name *C. dioscoreae-pyrifoliae* could have been a candidate. From the present study it is clear that several species of *Cercospora* can be isolated from this host and a more detailed study is needed to fix that name to a specific lineage.

The ex-type culture of *Cercospora acaciae-mangii* (Crous *et al.* 2004) is located in the last subclade (Fig. 2 part 5). *Cercospora acaciae-mangii* was isolated from *Acacia* leaves that also contained a *mycosphaerella*-like teleomorph that formed a *Cercospora* state in culture. However, the same leaf spots were also colonised by a second, morphologically similar species (distinguished by its ability to form larger, faster-growing colonies in agar).

### *Cercospora* sp. Q

**Specimens examined:** **Mexico**, on *Phaseolus vulgaris* (Fabaceae), 20 Oct. 2008, M. de Jesus Yanez, CBS 132679 = CPC 15807; Tamaulipas, on *Taraxacum* sp. (Asteraceae), 30 Oct. 2008, Ma. de Jesús Yáñez-Morales, CBS 132682 = CPC 15850; on *Euphorbia* sp. (Euphorbiaceae), 31 Oct. 2008, Ma. de Jesús Yáñez-Morales, CPC 15875; 30 Oct. 2008, Ma. de Jesús Yáñez-Morales, CBS 132681 = CPC 15844. **Papua New Guinea**, on leaves of *Dioscorea rotundata*, 2000, J. Peters & A.N. Jama, CBS 132661 = CPC 11634 = PNG-002, on leaves of *Dioscorea esculenta* (Dioscoreaceae), 2000, J. Peters & A.N. Jama, CBS 132663 = CPC 11636 = PNG-016; CPC 11639 = PNG-037. **South Africa**, Nelspruit, on *Cajanus cajan*, L. van Jaarsveld, CBS 113997 = CPC 5325; CBS 115410 = CPC 5331; CBS 115411 = CPC 5332; CBS 115412 = CPC 5333; CBS 115536 = CPC 5329; CBS 115537 = CPC 5330. **Thailand**, on *Acacia mangium*, K. Pongpanich, CPC 10550 (big colony on same plate as small colonies of *Cercospora acaciae-mangii*); CPC 10551 (big colony); CBS 132656 = CPC 11536; CPC 11539.

**Notes:** Several isolates from diverse hosts and families cluster in this clade, to which different names can be applied. To resolve their taxonomy, fresh collections authentic for the names (based on host and country) need to be recollected and included in future studies. Based on the genes studied here, we were unable to resolve the phylogeny of these taxa. See also the species notes for *Cercospora* sp. P. Screening the isolates from this species with five more genomic loci in this study did not clarify their potential species boundaries. By testing other candidate loci as they become available from comparative genomics and other sources we will continue to try and identify optimal genes for species recognition in this complex.

### *Cercospora* sp. R

**Specimen examined:** **New Zealand**, Auckland, Grey Lynn, on *Myoporium laetum* (Myoporaceae), Dec. 2003, C.F. Hill, Lynfield 186-B, CBS 114644.

**Notes:** *Pseudocercospora myopori* is a true species of *Pseudocercospora* (Braun & Hill 2002), which was originally described without depositing an ex-type culture. A later collection deposited at CBS (isolate CBS 114644), however, proved to be representative of an undescribed species of *Cercospora*, phylogenetically closely related to *Cercospora* sp. S and *C. corchori* (Fig. 2 part 5). This isolate has a unique phylogenetic position in the TEF, ACT, CAL and HIS phylogenies. In the combined tree (Fig. 2 part 5), it is a sister taxon to *Cercospora* sp. S.

### *Cercospora* sp. S

**Specimen examined:** **South Korea**, Yangpyeong, on *Crepidiastrum denticulatum* (= *Youngia denticulata*) (Asteraceae), 30 Sep. 2003, H.D. Shin, CBS 132599 = CPC 10656; CPC 10654–10655 (as *Cercospora lactucae-sativae*).

**Notes:** Isolate CPC 10656 is located on a slightly longer branch in the majority of genomic loci evaluated (ACT, CAL and HIS); only in the TEF phylogeny is it intermixed with isolates of *C. lactucae-sativae*. It is a close sister taxon to *Cercospora* sp. R and *C. corchori* (Fig. 2 part 5), but more isolates need to be collected to resolve its identity.

***Cercospora vignigena*** C. Nakash., Crous, U. Braun & H.D. Shin, **sp. nov.** MycoBank MB800657. Fig. 10.

**Etymology:** Named after the host genus from which it was collected, *Vigna*.

**Leaf spots** subcircular, amphigenous, pale to medium brown, 8–20 mm diam, with inconspicuous margin. **Caespituli** amphigenous. **Mycelium** internal. **Stromata** small to well-developed, pale brown to brown, intraepidermal and substomatal, 35–60 µm in diam. **Conidiophores** in loose to dense fascicles (2–12), straight to slightly sinuous-geniculate, pale brown, paler towards the apex, moderately thick-walled or thick-walled, cylindrical, almost uniform in width, often wider towards the apex, distinctly conical at the apex, 40–130 × 5–7(–10) µm, 0–3-septate. **Conidiogenous cells** integrated, terminal, intercalary, proliferating sympodially, 20–40 × 4–5 µm, multi-local (1–2); loci distinctly thickened, darkened, slightly protuberant, apical and lateral, 2.5–4 µm diam. **Conidia** solitary, rarely catenate, hyaline, straight to slightly curved, cylindrical to obclavate, obconically truncate and distinctly thickened at the base, subobtuse to obtuse at the apex, (35–)45–70(–150) × (2.5–)4–6(–10) µm, (3–)4–7(–14)-septate, thin-walled, smooth.

**Culture characteristics:** Colonies spreading, erumpent, with even, lobate margins and sparse to moderate aerial mycelium, reaching 25 mm diam after 2 wk. On OA olivaceous-grey in centre, pale olivaceous-grey in outer region. On MEA pale olivaceous-grey with patches of dirty white, reverse iron-grey. On PDA pale olivaceous-grey, margin submerged, grey-olivaceous; reverse olivaceous-grey.

**Specimens examined:** **Japan**, Gumma, on *Vigna unguiculata* (= *V. sinensis*) (Fabaceae), Sep. 1993, K. Kishi, MUCC 579 = MAFF 237635. **South Africa**, Potchefstroom, on *V. unguiculata* (= *V. sinensis*), 3 Jan. 1995, S. van Wyk, CPC 1133–1134. **South Korea**, Jeongeup, on *V. unguiculata* (= *V. sinensis*), 29 Oct. 2003, H.D. Shin, **holotype** CBS H-21023, culture ex-type CBS 132611 = CPC 10812.

**Notes:** This independent clade is supported by ACT, CAL and HIS and is composed of the isolates of *Cercospora* species that were identified as *C. canescens* on *Vigna* (Fabaceae) plants. In the TEF phylogeny, the clade is split into two lineages, isolates CPC 1134 and MUCC 579 as sister clade to *C. apiicola* and CPC 10812 basal to *C. apii* and *C. beticola*. In the combined tree (Fig. 2 part 2), it is basal to the lineage containing *C. apiicola* and other species. The examined isolates of *C. canescens* (the true *C. canescens* has acicular conidia), for which the original host is the genus *Phaseolus*, were located in other clades. These results show that the fungus on *Vigna* must be treated as a species distinct from *C. canescens*. *Cercospora vignicaulis* (described on *V. unguiculata* (= *V. sinensis*) collected from the USA) has in the past been listed as



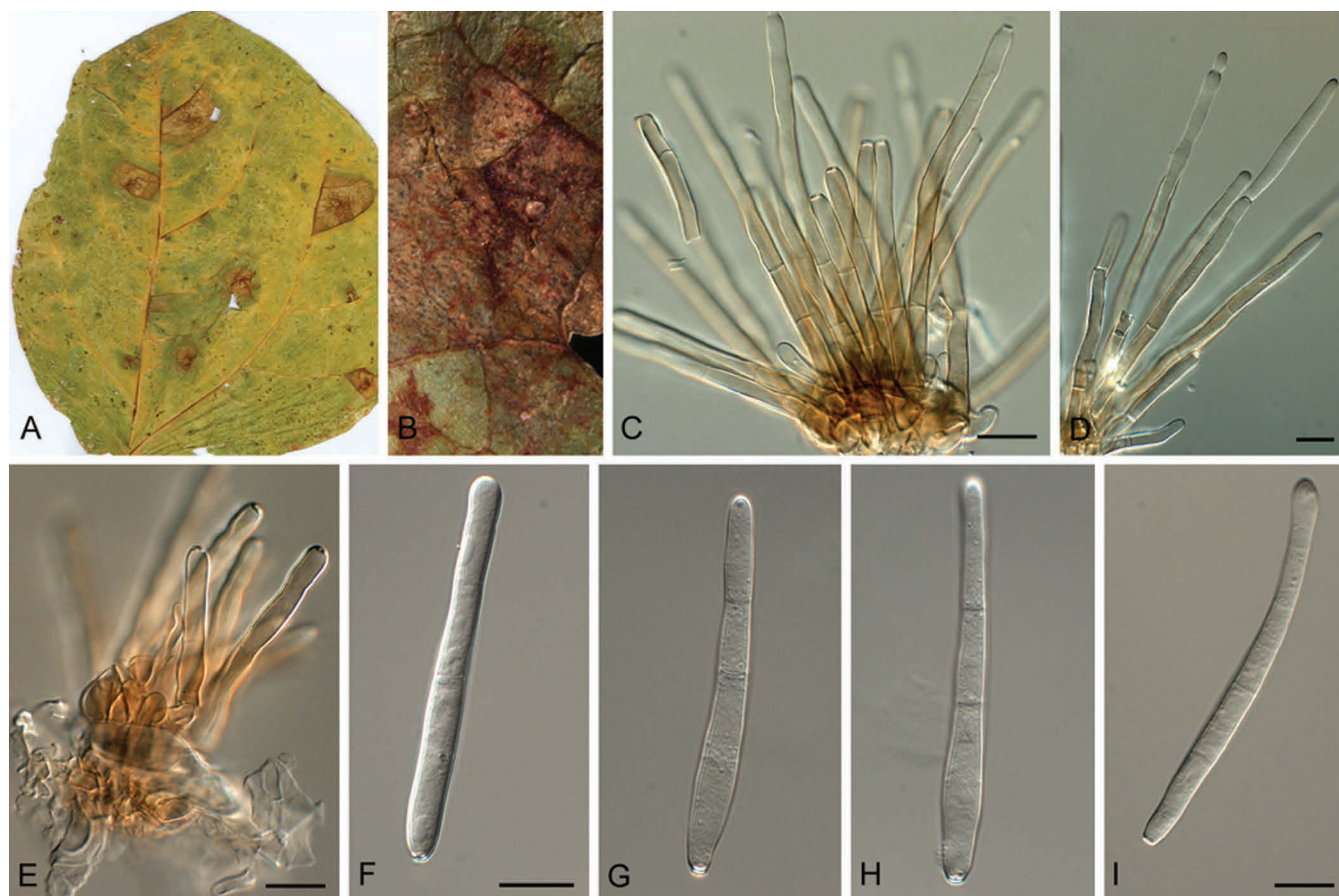


Fig. 10. *Cercospora vignigena* (CBS 132611 = CPC 10812). A. Leaf spots. B. Close-up of lesion. C–E. Fasciculate conidiophores. F–I. Conidia. Scale bars = 10 µm.

a synonym of *C. canescens*. However, *C. vignicaulis* has acicular conidia, which differs from the isolates studied here, and thus the present collection is described as a distinct species that appears to be specific to *Vigna*.

***Cercospora violae* Sacc., Nuovo Giron. Bot. Ital. 8: 187. 1876.**

- = *Cercospora violae-tricoloris* Briosi & Cavara, Atti Ist. Bot. Univ. Pavia 2: 285. 1892.
- = *Cercospora violae* var. *minor* Rota-Rossi, Atti Ist. Bot. Univ. Pavia, Ser. 2, 13: 199. 1914.
- = *Cercospora violae-kiusianae* Sawada, Rep. Gov. Agric. Res. Inst. Taiwan 85: 126. 1943.
- = *Cercospora difformis* Tehon, Mycologia 40: 322. 1948.
- = *Cercospora trinctatis* Pass. (unpublished name cited by Chupp 1954)

*Caespituli* amphigenous. *Mycelium* internal. *Stromata* lacking to well-developed, up to 80 µm diam, brown, intraepidermal, substomatal. *Conidiophores* in dense fascicles (2–16), irregular in width, slightly attenuated at the upper portion, straight or mildly sinuous-geniculate, straight, wall moderately thickened, simple, pale brown to brown, short conically truncate at the apex, wider at the base, 20–175 × 2.5–7.5 µm, 1–10-septate, usually unilocal. *Conidiogenous cells* integrated, terminal, rarely intercalary, proliferating sympodially; loci distinct, thickened, apical, rarely lateral, 2–3 µm diam, not protuberant. *Conidia* solitary, hyaline, cylindrical to obclavate or acicular, distinctly thickened and obconically truncated at the base, obtuse at the apex, 35–195 × 2.5–5 µm, 0–18-septate, thin-walled, smooth.

*Specimens examined*: **Italy**, Selva, on *Viola odorata* (Violaceae), Aug. 1874, Treviso, **isotypes** distributed as Sacc. Mycotheca Veneta 279, **isotype** at HAL examined. **Japan**, Kochi, on *Viola* sp., 16 Nov. 2004, J. Nishikawa, MUMH 10333,

MUCC 129; Nagano, on *V. tricolor*, 16 Feb. 2005, J. Nishikawa, MUMH 10332, MUCC 133; Shizuoka, on *V. tricolor*, 15 Jan. 2003, J. Nishikawa, MUMH 10334, MUCC 136. **Romania**, Cazanele Dunarii, on *V. tricolor*, O. Constantinescu, **epitype designated here** CBS H-21024, culture ex-epitype CBS 251.67 = CPC 5079. **New Zealand**, on *V. odorata*, C.F. Hill, CPC 5368.

*Notes*: See also *C. zebrina*. One culture that was isolated from *Viola* (strain CPC 10725) is representative of *C. fagopyri*. The original specimen of this isolate was distinguishable from *C. violae* in having circumscribed and slightly protuberant loci on its conidiophores. The isolates included here for *C. violae* are phylogenetically distinct from the other species included in this study on the basis of the TEF, ACT, CAL and HIS phylogenies. In the combined tree (Fig. 2 part 3), it is a sister taxon to *C. zebrina*.

***Cercospora zeae-maydis* Tehon & E.Y. Daniels, Mycologia 17: 248. 1925.**

*Specimens examined*: **China**, Liaoning Province, on *Zea mays* (Poaceae), CBS 132668 = CPC 12225 = CHME 52. **Mexico**, Tlacotepec, on *Z. mays*, 16 Sep. 2008, Ma. de Jesús Yáñez-Morales, CBS 132678 = CPC 15602. **USA**, Illinois, Alexander Co., McClure, on *Z. mays*, 29 Aug. 1924, P.A. Young, **holotype** ILLS 4276, **isotype** BPI 442569; Delaware, 1997, B. Fleener, DE-97 = A359 = CBS 117756; Indiana, Princeton, 1999, B. Fleener, PR-IN-99 = A364 = CBS 117761; Indiana, Princeton, 2003, B. Fleener, YA-03 = A358 = CBS 117755; Iowa, Johnston, 2004, B. Fleener, JH-IA-04 = A361 = CBS 117758; Iowa, Reinbeck, 1999, B. Fleener, RENBECK-IA-99 = A367 = CBS 117763; Missouri, Dexter, 2000, B. Fleener, DEXTER-MO-00 = A365 = CBS 117762; Pennsylvania, New Holland, 1999, B. Fleener, NH-PA-99 = A363 = CBS 117760; Tennessee, Union City, 1999, B. Fleener, UC-TN-99 = A362 = CBS 117759; Wisconsin, Janesville, 2002, B. Fleener, **epitype**, CBS H-17774, culture ex-epitype JV-WI-02 = A360 = CBS 117757.

*Notes*: This species is phylogenetically supported by ITS, TEF, ACT, CAL and HIS. In the combined tree (Fig. 2 part 1), it is a basal

lineage. Gray leaf spot of maize was originally attributed to "group I" and "group II" siblings of *C. zeae-maydis* (Wang *et al.* 1998). More detailed information on this species was provided in Crous *et al.* (2006a).

### ***Cercospora zebrina* Pass., Hedwigia 16: 124. 1877.**

= *Cercosporina zebrina* (Pass.) Matsuura, J. Pl. Protect. (Tokyo) 17: 1. 1930.

= *Cercospora helvola* Sacc., Michelia 2: 556. 1882.

= *Cercospora stolziana* Magnus, Die Pilze von Tirol (*etc.*) 3: 558. 1905.

= *Cercospora helvola* var. *zebrina* Ferraris, Fl. Ital. Cryptog. 1: 423, 1910, *fide* Chupp (1954: 341).

*Specimens examined*: **Australia**, on *Trifolium cernuum* (Fabaceae), M.J. Barbeti, CBS 118791 = IMI 264190 = WA 2054 = WAC 7993; on *T. subterraneum*, M.J. Barbeti, CBS 118789 = WAC 5106; CBS 118790 = IMI 262766 = WA 2030 = WAC 7973. **Canada**, Ottawa, 13 Lucas lane, on *T. repens*, 1 Sep. 2000, K.A. Seifert, CBS H-21025, CBS 112723 = CPC 3957; CBS 112736 = CPC 3958; on *T. pratense*, K.A. Seifert, CBS H-21026, CBS 112893 = CPC 3955. **Italy**, on *Hedysarum coronarium* (Fabaceae), CBS 137.56 = CPC 5118 (as *C. ariminensis*). **New Zealand**, on *Hebe* sp. (Scrophulariaceae), C.F. Hill, CBS 114359 = CPC 10901; Auckland, on *Lotus pedunculatus* (Fabaceae), C.F. Hill, Lynfield 644, CPC 5437 (as *C. loti*); Blockhouse Bay, on *T. repens*, C.F. Hill, Lynfield 603, CBS 113070 = CPC 5367; on *Jacaranda mimosifolia* (Bignoniaceae), C.F. Hill, Lynfield 693, CPC 5473 (as *C. canescens*). **Romania**, Hagieni, on *Astragalus spruneri* (Fabaceae), O. Constantinescu, CBS 537.71 = IMI 161108 = CPC 5089 (as *C. astragali*). **South Korea**, Namyangju, on *T. repens*, 22 Oct. 2003, H.D. Shin, CBS H-21027, CBS 132650 = CPC 10756. **Unknown**, on *Medicago arabica* (= *M. maculata*) (Fabaceae), E.F. Hopkins, CBS 108.22 = CPC 5091 (as *C. medicaginis*). **USA**, Wisconsin, on *T. subterraneum*, CBS 129.39 = CPC 5078.

*Notes*: Morphological characteristics of the larger *C. zebrina* clade include conidiophores that are short, almost straight, slightly attenuated and distinctly conically truncate at the apex with distinctly thickened loci, and conidia, which are cylindrical to cylindro-obclavate. The type of *C. zebrina* was collected on *Trifolium* in Italy. More European collections are required to resolve this species and to delineate it from other, closely allied species.

*Cercospora althaeina*, which has wide host range on malvaceous plants, has a similar morphology to *C. zebrina*. *Cercospora violae*, which clusters basal to the *C. zebrina* clade, has longer and wider conidiophores, and cylindrical to acicular conidia, which separates this species from *C. zebrina*.

In the TEF phylogeny, isolates are intermixed with those of *C. armoraciae*, *C. rumicis* and *Cercospora* sp. L and in the ACT and CAL phylogenies with those of *Cercospora* sp. L and *C. althaeina*. Only in the HIS phylogeny do these isolates form a pure monophyletic clade. In the combined tree (Fig. 2 part 3), it is a sister taxon to *C. violae*.

### ***Cercospora zeina* Crous & U. Braun, Stud. Mycol. 55: 194. 2006.**

*Specimens examined*: **South Africa**, KwaZulu-Natal, Pietermaritzburg, on *Zea mays* (Poaceae), 2005, P. Caldwell, **holotype** CBS H-17775, culture ex-type CBS 118820 = CPC 11995; CBS 132617 = CPC 11998.

*Notes*: This species is phylogenetically supported by ITS, TEF, ACT, CAL and HIS. In the combined tree (Fig. 2 part 1), it is a basal lineage. More detailed information on this species was provided in Crous *et al.* (2006a).

### ***Cercospora* cf. *zinniae***

*Caespituli* amphigenous. *Mycelium* internal. *Stromata* lacking to small, up to 35 µm diam, intraepidermal or substomatal, pale brown

to brown. *Conidiophores* in loose fascicles (3–8), pale brown to brown, straight, mildly geniculate above the middle, multi-septate, attenuated, successively geniculate, tip truncate or conically truncate, 65–300 × 3.5–5 µm, 1–12-septate. *Conidiogenous cells* integrated, proliferating sympodially, terminal and intercalary, multi-local; loci distinctly thickened, darkened, apical and lateral, sometimes circumspersed, often slightly protuberant, 2–2.5 µm diam. *Conidia* solitary, hyaline, filiform to acicular, cylindro-obclavate, straight to curved, long obconically truncate or truncate, and thickened at the base, acute at the apex, multi-septate, 30–120 × 1–4 µm, 3–13-septate.

*Description of caespituli on V8*; (MUCC 131): *Conidiophores* solitary, arising from hyphae, subhyaline to pale brown, irregular in width, smooth, meager and thin-walled, sinuous-geniculate to geniculate, unbranched, truncate or conically truncate at the tip, 13–63 × 3–5 µm, multi-septate. *Conidiogenous cells* integrated, terminal, proliferating sympodially, single to multi-local (1–2); loci moderately thickened, apical, sometimes slightly protuberant, 1.25–2 µm in width. *Conidia* hyaline, filiform to acicular, slightly thickened and long obconically truncate at the base, acute to obtuse at the apex, 25–160 × 2.5–4 µm, 3–11-septate.

*Specimens examined*: **Brazil**, Valverde, Alto Rio Doce, on unknown substrate, A.C. Alfenas, CBS 132676 = CPC 15075. **Japan**, Chiba, on *Zinnia elegans* (Asteraceae), 12 Sep. 1997, S. Uematsu, MUCC 572 = MAFF 237718 = MUCNS 215; Shizuoka, on *Z. elegans*, 17 Sep. 2004, J. Nishikawa, MUMH 11397, MUCC 131. **South Korea**, Yangpyeong, on *Z. elegans*, 18 Oct. 2007, H.D. Shin, CBS 132624 = CPC 14549.

*Notes*: This species is characterised in that the conidiophores are mildly geniculate above the middle, multi-septate, attenuated with successive geniculation; loci circumspersed and distinctly thickened; conidia are narrower than those of other taxa in *C. apii* s. lat. Moreover, this species is phylogenetically supported by DNA sequence data of TEF, CAL and HIS. In the ACT phylogeny, two distinct lineages are formed, namely CPC 14549 versus CPC 15075, MUCC 132 and MUCC 572. In the combined tree (Fig. 2 part 4), it is basal to the lineage containing, for example, *C. cf. ipomoeae*, *C. fagopyri* and *C. rodmanii*. North American cultures and sequence data are necessary to confirm the identity of Asian collections as *C. zinniae* and to designate an epitype.

## **DISCUSSION**

This study was initiated to resolve *Cercospora* taxonomy on the basis of morphological and DNA sequence data. Based on our earlier studies incorporating multi-gene phylogenies on smaller datasets (Crous *et al.* 2004b, 2006a, Groenewald *et al.* 2005, 2006a, 2010a), we realised this was an ambitious task. Even though a whole range of hosts and countries were included in our study, attempts to apply existing names to the different clades in the phylogenetic trees obtained proved difficult. In addition, the lack of ex-type cultures or at least reference sequences from type material, made it especially problematic to assign existing names to the derived phylogenetic clades. To our knowledge, this study presently represents the largest combination of diverse sampling of cercosporoid fungi coupled with multi-locus sequence data in a single manuscript.

One important finding is that Crous & Braun (2003) were over-optimistic when they referred 281 *Cercospora* names to *C. apii* s. lat. based on morphology alone. Of the species treated as distinct in the present paper, the following five were originally referred to *C. apii* s. lat. by Crous & Braun (2003), namely *C. beticola*, *C.*



*canescens*, *C. fagopyri*, *C. kikuchii* and *C. rumicis*. The following eight species, *C. armoraciae*, *C. corchori*, *C. lactucae-sativae*, *C. mercurialis*, *C. polygonacea*, *C. ricinella*, *C. violae* and *C. zebrina*, treated as distinct in the present study, were treated by Crous & Braun (2003) as close to or possibly identical with *C. apii* s. lat. It is evident that morphology alone provides an insufficient basis on which to establish synonymies, to describe novel species or in many cases to identify species of *Cercospora*.

In the last 10 years, 45 novel *Cercospora* names were lodged with MycoBank (Crous *et al.* 2004a). Of these, only five species are based on morphology and multi-locus sequence data, two species have morphology supplemented with ITS sequences and 38 species are based on morphology alone. Of these 45 species, only 10 species were described in culture, 26 were reported without culture characteristics and of the remaining nine it is unlikely that cultures were established. This is an alarming statistic and is something that should be addressed by the whole community working on cercosporoid fungi. If the situation is compared to that of *Colletotrichum*, it is clear that there is room for improvement. Phylogenetic studies on *Colletotrichum* species based on cultures and ITS data date back to at least 20 years, with the last 10 years showing a significant increase in species descriptions based on multi-locus sequence data (Cannon *et al.* 2012).

Groenewald *et al.* (2010a) reported on the performance of the five loci used for the phylogenetic inference in this study. They found the ITS region had limited resolution (2.7 % clade recovery) and was best be used to confirm the generic affiliation of a species, with less value when used for species comparison, specifically within the *C. apii* complex. Although CAL is necessary to distinguish *C. apii* and *C. beticola*, it only distinguished about half of the observed species clades (46.6 % clade recovery), whereas ACT was slightly more successful (58.9 % clade recovery). The HIS region compared well with ACT (63 % clade recovery), but it did split *C. beticola* into two clades. Both of these *C. beticola* clades contain isolates from the same sugar beet fields in Germany and New Zealand (Groenewald *et al.* 2006b) and whether this implies population variation or the presence of an additional cryptic species on sugar beet requires further molecular analyses of more *C. beticola* populations. The TEF region was comparable to CAL in terms of clade recovery (45 % clade recovery). Although we believe that there is still a need to identify the best barcode locus for *Cercospora*, the current multi-locus approach does enable species identification. Comparison of a few *Cercospora* genomes selected from across the phylogenetic tree might reveal a single locus with better resolution than the currently used loci.

Similar to the situation in *Pseudocercospora* (Crous *et al.* 2013), we also encountered a situation where we could not use names based on North American or European types for African or Asian cultures and *vice versa*. Based on morphological features and their distinct sequences we have chosen to treat those clades in the present study as “cf.” pending comparison of those species with (epi-)type material from the original country and host as discussed under the species notes above. For numerous clades (“*Cercospora* sp. A–S”), it was not possible to unequivocally assign a species name; frequently these clades contained isolates from multiple hosts and/or countries and the same hosts occurred in multiple clades, or the host information was not available. For example, isolates from *Cajanus cajan* in South Africa can be attributed to *Cercospora* sp. P and *Cercospora* sp. Q. Crous & Braun (2003) list four *Cercospora* species associated with this host, namely *C. apii* s. str., *C. canescens*, *C. instabilis* and *C. thirumalacharii*. The first two species were included in this study, the third is listed on *Cajanus* from numerous countries (but not including South Africa)

and the last is known from India (Crous & Braun 2003). It was not possible to include authentic cultures of the latter two species, so any of these two names are potentially available for a clade. An additional complicating factor is that there are numerous sub-clades inside *Cercospora* sp. P and *Cercospora* sp. Q, which could represent either intra-specific variation or the presence of cryptic species, which are not distinguished by the loci used in this study. We sequenced five additional loci for *Cercospora* sp. Q isolates and did not find a single locus that provided better insight into this clade. Isolates from *Cajanus* also occur in the same clade with other hosts, raising the question of wide host range versus simply a chance infection (Crous & Groenewald 2005). A similar situation was observed for isolates isolated from yams (*Dioscorea*). Crous & Braun (2003) list numerous *Pseudocercospora* and *Passalora* species, and three *Cercospora* species (*C. aragonensis*, *C. dioscoreae-pyrifoliae* and *C. golaghatti*) from this host genus; of the three *Cercospora* names, *C. dioscoreae-pyrifoliae* is commonly used in literature. In this study, it was not possible to apply this name to any of the clades. Isolates from *Dioscorea* are found in the *C. canescens* complex, *Cercospora* cf. *sigesbeckiae*, *Cercospora* sp. P and *Cercospora* sp. Q, but none of these isolates were from the original host or locality of the type description for *C. dioscoreae-pyrifoliae* (based on *Dioscorea pyrifolia* in Singapore). One of the isolates included in the present study (MUCC 849, as *Cercospora* cf. *sigesbeckiae*) was treated by Nakashima *et al.* (2011) as *C. dioscoreae-pyrifoliae*. The authors noted that, although the morphological characteristics were similar to the original description, the width of the conidiophores and conidia was different. Similarly, most of the isolates from *Dioscorea* were sent to us under the name *C. dioscoreae-pyrifoliae* although we could not confirm the identification with confidence. These examples highlight the need to locate original specimens, or at least recollect material that can be used for epitypification, to fix the names used in the various phylogenetic clades. It also illustrates the importance of establishing cultures, which can be used for future molecular studies, when describing taxonomic novelties.

We believe that this study serves as a backbone for future studies on *Cercospora* taxonomy. Unfortunately, many (epi-)type cultures and adequate sequence data are lacking for a significant number of *Cercospora* species. Future studies will require the recollection of material from the original hosts and continents so that epitypes can be found and names stabilised. Furthermore, all species, especially those currently in common use, need proper molecular identification. Based on searches in Google and Google Scholar, the most commonly used *Cercospora* species names are *C. zeae-maydis*, *C. beticola*, *C. apii*, *C. canescens*, *C. kikuchii*, *C. sojina*, *C. arachidicola*, *C. coffeicola*, *C. personata* and *C. nicotianae*. Although the taxonomy of *C. apii*, *C. beticola* (Groenewald *et al.* 2005, 2006a) and *C. zeae-maydis* (Crous *et al.* 2006a) was resolved in the past, the present study resolved *C. kikuchii* and *C. sojina* but it was unable to resolve *C. canescens*. Similar studies are needed for *C. arachidicola*, *C. coffeicola*, *C. nicotianae* and *C. personata*.

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