Species concepts in Cercospora: spotting the weeds among the roses

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

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

Taxonomic novelties: New species - Cercospora coniogrammes Crous & R.G. Shiivas, 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 vagina C. Nakash., Crous, U. Braun & H.D. Shin. Typifications: epitypifications - Cercospora alchimillicola U. Braun & C.F. Hill, Cercospora althaeina Cacc., Cercospora armoraciae Sacc., Cercospora corchor Sawada, Cercospora mercularis Pass., Cercospora olivascens Sacc., Cercospora violae Sacc.; neotypifications - Cercospora fagopyri N. Nakata & S. Takim., Cercospora agina Hara.

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INTRODUCTION

Species of the genus Cercospora belong to 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 cercosporidial 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 Fresenisus 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 conidialstomal structure, mycelium, conidiophores, conidigenous cells and conidia has been used to divide the genus into morphologically similar units. Crous & Braun (2003) used the structure of conidigenous loci and hila as well as the absence or presence of pigmentation in conidiophores and conidia in their revision of names published in Cercospora and Passalora. They recognised 659 names in the genus Cercospora, with a further 281 names referred to as C. apii s. lat. The C. apii complex represented
Fig. 1. Foliar disease symptoms associated with Cercospora spp. A. C. achyranthis on *Achyranthes japonica*. B. C. dispori on *Disporum viridescens*. C. C. chinensis on *Polygonatum humile*. D. C. cf. flagellaris on *Amaranthus patulus*. E. C. capsici on *Capsicum annuum*. F. Cercospora sp. on *Ajuga multiflora*. G. Cercospora sp. on *Cardamine leucanthemum*. H. C. cf. flagellaris on *Celtis argentea var. cristata*. I. C. zeina on *Zea mays*. J. C. beticola on *Beta vulgaris*. K. C. chrysanthemi on *Chrysanthemum*. L. C. alpina on *Aegopodium podagraria*. M. C. amoraciae on *Rorippa indica*. N. C. beticola on *Chrysanthemum segetum*. O. C. alpina on *Aegopodium podagraria*. P. C. ipomoeae on *Persicaria thunbergii*. Q. C. albicans on *Althaea rosea*. R. C. zebrina on *Trifolium repens*. S. C. sojina on *Glycine max*. T. C. brunii on *Geranium nepalense*. 
Cercospora species that were morphologically indistinguishable from *C. api* (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. api* and *C. apicola* (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. api* and *C. beticola* isolated from disease symptoms on other hosts (Groenewald et al. 2006a). *Cercospora caricus* is used as a biological control agent of *Cyperus rotundus* (*Cyperaceae*), and Inglis et al. (2001) compared Brazilian isolates with an isolate from Florida, USA. The authors used RAPDs (Randomly Amplified Polymorphic DNA), RFLPs (Restriction Fragment Length Polymorphisms) with a telomeric probe and ITS sequencing and found that a cluster of isolates from the Brazilian cerrado region showed high genetic similarity, whereas similarity between this region and others in Brazil was less that 50 %. They also found that the ITS sequence analysis did not support a division in the Brazilian isolates (99 % similar sequences) but that it did separate the Florida isolate from the Brazilian isolates (96 % similar when included with the Brazilian isolates). They concluded that the isolate from Florida probably represented cryptic speciation but that larger sampling of isolates was required from different geographical areas to address this question. Host specificity for some species appears to operate at the strain level, as for *C. rodmani*, in which the original strains of Conway (1976) were shown to be specific to water hyacinth, whereas strains identified by morphology and multi-locus sequence data as the same species, were able to infect beet and sugar beet (Montenegro-Calderón et al. 2011).

A number of molecular studies using ITS phylogenies confirmed that *Cercospora* taxa cluster in a well-supported monophyletic clade in *Mycosphaerella* (Stewart et al. 1999, Crous et al. 2000, 2009a, b, Goodwin et al. 2001, Pretorius et al. 2003), in contrast to other polyphyletic genera such as *Septoria* (Verkley et al. 2004; compared to the monophyletic *Zymoseptoria*, Quaedvlieg et al. 2011), *Pseudocercospora*, *Passalora* and *Zasmidium* (Crous et al. 2009b), to name but a few. The ITS region (ITS1, 5.8S rDNA and ITS2) lacks the resolution to distinguish between most *Cercospora* species (Groenewald et al. 2010a). For example, Goodwin et al. (2001) found a mean of 1.27 sequence changes over 18 taxa from 11 *Cercospora* species, and Pretorius et al. (2003) found a mean of 1.64 changes when they tested 25 taxa representing 11 *Cercospora* species. Both Goodwin et al. (2001) and Pretorius et al. (2003) observed more transitions than transversions. Only a limited number of studies utilising gene sequences other than ITS have been published thus far (for example Tesseran 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. api* 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. api* 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. api* *s. str.* and *C. beticola* *s. str.* as distinct species. Continuing with the same approach, Groenewald et al. (2006a) then proceeded to describe *C. apicola*, 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. rodmani* could be distinguished from *C. piaropi* based on actin, calmodulin and histone H3, but that only calmodulin could clearly separate *C. rodmani* 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 & Ehrenshtaf 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
| Species                  | Culture accession number(s) | Host name or isolation source | Host Family | Country     | Collector                      | GenBank accession numbers |
|-------------------------|----------------------------|-------------------------------|-------------|-------------|--------------------------------|--------------------------|
| Cercospora achyranthis  | CBS 1338; CPC 10879        | Achyranthes japonica         | Amananthaceae | South Korea | H.D. Shin                     | JX143502 JX143503 JX143504 JX143505 JX143506 |
|                         | CPC 1091                   |                               |             |             |                                |                          |
| Cercospora agavicolca   | CBS 11729; CPC 11774 (TYPE)| Agave tequilana var. azul    | Agavaceae   | Mexico      | V. Ayala-Escobar & Ma. de Jesús Yáñez-Morales | AY467237 AY966897 AY966898 AY966899 AY966900 |
| Cercospora alchemillicola| CPC 5259 (TYPE)            | Alchemilla mollis             | Rosaceae    | New Zealand | C.F. Hill                      | JX143512 JX143513 JX143514 JX143515 JX143516 |
|                         | CPC 5126                   |                               |             |             |                                |                          |
| Cercospora althaeina    | CBS 126.26; CPC 5066       | Malva sp.                     | Malvaceae   | Romania     | C. Killian                     | JX143522 JX143523 JX143524 JX143525 JX143526 |
|                         | CPC 112609; CPC 10790      | Althaea rosea                 | Malvaceae   | New Zealand | C.F. Hill                      | JX143527 JX143528 JX143529 JX143530 JX143531 |
|                         | CPC 248.67; CPC 5117 (TYPE)| Althaea rosea                | Malvaceae   | South Korea | H.D. Shin                      | JX143532 JX143533 JX143534 JX143535 JX143536 |
|                         | CBS 110813; CPC 5110; 01-3| Moluccella laevis             | Lamiaceae   | Austria     | L. J. Klotz                     | JX143537 JX143538 JX143539 JX143540 JX143541 |
|                         | CBS 110816; CPC 5111; 01-4| Moluccella laevis             | Lamiaceae   | Italy       | M. Meutri                      | JX143542 JX143543 JX143544 JX143545 JX143546 |
|                         | CBS 114416; CPC 10925      | Apium sp.                     | Apiaceae    | Austria     | Institut für Pflanzenkunde      | JX143547 JX143548 JX143549 JX143550 JX143551 |
|                         | CBS 114418; CPC 10924      | Apium graveolens              | Apiaceae    | Italy       | M. Meutri                      | JX143552 JX143553 JX143554 JX143555 JX143556 |
|                         | CBS 114485; CPC 10923      | Apium graveolens              | Apiaceae    | Italy       | M. Meutri                      | JX143557 JX143558 JX143559 JX143560 JX143561 |
|                         | CBS 116455; CPC 11556 (TYPE)| Apium graveolens              | Apiaceae    | Germany     | K. Schrammey                    | JX143562 JX143563 JX143564 JX143565 JX143566 |
|                         | CBS 116504; CPC 11579      | Apium graveolens              | Apiaceae    | Germany     | K. Schrammey                    | JX143567 JX143568 JX143569 JX143570 JX143571 |
|                         | CBS 116507; CPC 11582      | Apium graveolens              | Apiaceae    | Germany     | K. Schrammey                    | JX143572 JX143573 JX143574 JX143575 JX143576 |
|                         | CBS 119.25; B 24263; IHEM 3822; CPC 5086 | Apium graveolens | Apiaceae | Germany | K. Schrammey | JX143577 JX143578 JX143579 JX143580 JX143581 |
|                         | CBS 121.31; CPC 5073       | Beta vulgaris                 | Chenopodiaceae | Austria     | E.W. Schmidt                    | JX143582 JX143583 JX143584 JX143585 JX143586 |
|                         | CBS 127.31; CPC 5119       | Beta vulgaris                 | Chenopodiaceae | Hungary    | E.W. Schmidt                    | JX143587 JX143588 JX143589 JX143590 JX143591 |
|                         | CBS 132683; CPC 19663      | Moluccella laevis             | Lamiaceae   | Zimbabwe   | S. Dimbi                        | JX143592 JX143593 JX143594 JX143595 JX143596 |
|                         | CBS 152.52; MI 077043; MUCL 19495; CPC 5086 | Beta vulgaris | Chenopodiaceae | Netherlands | G. van den Ende                 | JX143597 JX143598 JX143599 JX143600 JX143601 |
|                         | CBS 252.67; CPC 5084       | Plantago lanceolata           | Plantaginaceae | Romania     | O. Constantinescu               | JX143602 JX143603 JX143604 JX143605 JX143606 |
|                         | CBS 536.71; CPC 5087       | Apium graveolens              | Apiaceae    | Romania     | O. Constantinescu               | JX143607 JX143608 JX143609 JX143610 JX143611 |
|                         | CBS 553.71; IM 161116; CPC 5083 | Plumbago europaea          | Plumbaginaceae | Romania    | O. Constantinescu               | JX143612 JX143613 JX143614 JX143615 JX143616 |
|                         | CPC 18601                  | Apium graveolens              | Apiaceae    | USA         | S.T. Koike                      | JX143617 JX143618 JX143619 JX143620 JX143621 |
|                         | CPC 5112                   | Moluccella laevis             | Lamiaceae   | New Zealand | C.F. Hill                       | JX143622 JX143623 JX143624 JX143625 JX143626 |
|                         | CPC 5260                   | Glebionis coronaria (≡ Chrysanthemum coronarium) | Asteraceae | New Zealand | C.F. Hill                       | JX143627 JX143628 JX143629 JX143630 JX143631 |
|                         | MUCC 567; MUCNS 30; MAFF 238072 | Apium graveolens | Apiaceae | Japan       | T. Kobayashi                    | JX143632 JX143633 JX143634 JX143635 JX143636 |
| Species | Culture accession number(s) | Host name or isolation source | Host Family | Country | Collector | GenBank accession numbers |
|---------|-----------------------------|-------------------------------|-------------|---------|-----------|--------------------------|
| **Cercospora apiicola** | | | | | | |
| MUCC 573; MAFF 235978 | M. coronaria (≡ Chrysanthemum coronarium) | Asteraceae | Japan: Hokkaido | — | | JX143535 JX143289 JX143043 JX142797 JX142551 |
| MUCC 593 | A. graveolens | Apiaceae | Japan: Shizuoka | M. Togawa | | JX143536 JX143290 JX143044 JX142798 JX142552 |
| MUCC 923; MAFF 238299 | A. officinalis | Asparagaceae | Japan: Saga | J. Yamaguchi | | JX143537 JX143291 JX143045 JX142799 JX142553 |
| CBS 116457; CPC 10267 (TYPE) | A. apiicola | Apiaceae | Venezuela: Caripe | N. Pons | | AY840403 AY840503 AY840467 AY840435 AY840401 |
| CBS 116458; CPC 10249 | | | South Korea: Kangnun | H.D. Shin | | AY840437 AY840406 AY840370 AY840432 AY840404 |
| CBS 132651; CPC 10759 | | | | | | |
| CBS 132666; CPC 11642; GRE-4-2 | | | | | | |
| CPC 10220 | | | | | | |
| CPC 10265 | | | | | | |
| CPC 10266 | | | | | | |
| CPC 10279 | | | | | | |
| CPC 10666 | | | | | | |
| CPC 11641; GRE-3-2 | | | | | | |
| CBS 115060; CPC 5366 | G. sp. | Onagraceae | New Zealand | C.F. Hill | | JX143538 JX143292 JX143046 JX142800 JX142554 |
| CBS 115394; CPC 5261 | N. officinale (= Ropta nasturtium-aquaticum) | Brassicaceae | New Zealand: Auckland | C.F. Hill | | JX143539 JX143293 JX143047 JX142801 JX142555 |
| CBS 115409; CPC 5359 | A. rusticana (= A. lapathifolia) | Brassicaceae | New Zealand: Manurewa | C.F. Hill | | JX143540 JX143294 JX143048 JX142802 JX142556 |
| CBS 132638; CPC 10100 | B. orthoceras | Brassicaceae | South Korea: Pocheon | H.D. Shin | | JX143542 JX143296 JX143050 JX142804 JX142558 |
| CBS 132654; CPC 11338 | T. glabra (= Arabis glabra) | Brassicaceae | South Korea: Hoengseong | H.D. Shin | | JX143543 JX143297 JX143051 JX142805 JX142559 |
| CBS 132672; CPC 14612 | R. indica | Brassicaceae | South Korea: Jecheon | H.D. Shin | | JX143544 JX143298 JX143052 JX142806 JX142560 |
| CBS 220.67; CPC 5088 (TYPE) | A. rusticana (= A. lapathifolia) | Brassicaceae | Romania: Fundulea | O. Constantinescu | | JX143545 JX143299 JX143053 JX142807 JX142561 |
| CBS 225.67; CPC 5061 | C. draba | Brassicaceae | Romania: Fundulea | O. Constantinescu | | JX143546 JX143300 JX143054 JX142808 JX142562 |
| CBS 328.71; IMI 161019; CPC 5090 | B. incana | Brassicaceae | Romania: Hageri | O. Constantinescu | | JX143547 JX143301 JX143055 JX142809 JX142563 |
| CBS 540.71; IMI 161110; CPC 5060 | C. draba | Brassicaceae | Romania: Hageri | O. Constantinescu | | JX143548 JX143302 JX143056 JX142810 JX142564 |
| CBS 545.71; CPC 5056 | E. cuspidatum | Brassicaceae | Romania: Valea Mai co aci | O. Constantinescu | | JX143549 JX143303 JX143057 JX142811 JX142565 |
| CBS 555.71; IMI 161117; CPC 5082 | C. varia | Fabaceae | Romania: Hageri | O. Constantinescu | | JX143550 JX143304 JX143058 JX142812 JX142566 |
| CPC 10133 | R. indica | Brassicaceae | South Korea: Wonju | H.D. Shin | | JX143551 JX143305 JX143059 JX142813 JX142567 |
| CPC 11364 | T. glabra (= Arabis glabra) | Brassicaceae | South Korea: Hoengseong | H.D. Shin | | JX143552 JX143306 JX143060 JX142814 JX142568 |
| CPC 11530 | A. mangium | Fabaceae | Thailand | W. Himanman | | JX143553 JX143307 JX143061 JX142815 JX142569 |
| MUCC 768 | A. rusticana (= A. lapathifolia) | Brassicaceae | Japan: Okinawa | C. Nakashima | | JX143554 JX143308 JX143062 JX142816 JX142570 |
| Species | Culture accession numbers | Host name or isolation source | Host Family | Country | Collector | GenBank accession numbers |
|---------|---------------------------|------------------------------|-------------|---------|-----------|--------------------------|
| *Chrysanthemum segetum* (= *C. coronarium* var. *spatiosum*) | CBS 132673, CPC 14617 | South Korea: Namyangju | Asteraceae | H.D. Shin | DQ233332, DQ233358, DQ233384, DQ233407, DQ233434 | |
| *Chrysanthemum segetum* (= *C. coronarium* var. *spatiosum*) | CBS 132674, CPC 14618 | South Korea: Namyangju | Asteraceae | H.D. Shin | FJ47543, FJ47544, FJ47545, FJ47546, FJ47547 | |
| *Malva pusilla* | CBS 1259, CPC 11047 | Romania: Bucuresti | Malvaceae | O. Constantinescu & G. Negrean | DQ233325, DQ233350, DQ233375, DQ233402, DQ233427 | |
| *M. pusilla* | CBS 1259, CPC 11047 | Romania: Hagieni | Malvaceae | E.W. Schmidt | FJ47542, FJ47543, FJ47544, FJ47545, FJ47546 | |
| *Beta vulgaris* | CBS 116454, CPC 11558 | Germany: Northwest Brabant | Chenopodiaceae | G.E. Bunschoten | AY840526, AY840493, AY840463, AY840424, AY840391 | |
| *B. vulgaris* | CBS 116454, CPC 11558 | Germany: S. Mittler | Chenopodiaceae | AY840526, AY840493, AY840463, AY840424, AY840391 | |
| *B. vulgaris* | CBS 116454, CPC 11558 | Italy: Ravenna | Chenopodiaceae | V. Rossi | AY840527, AY840494, AY840458, AY840425, AY840392 | |
| *B. vulgaris* | CBS 116454, CPC 11558 | Iran: Pakajik | Chenopodiaceae | A.A. Ravanlou | AY840528, AY840495, AY840459, AY840426, AY840393 | |
| *B. vulgaris* | CBS 116454, CPC 11558 | Germany: S. Mittler | Chenopodiaceae | AY840529, AY840496, AY840460, AY840427, AY840394 | |
| *B. vulgaris* | CBS 116454, CPC 11558 | Italy: Ravenna | Chenopodiaceae | S. Garresus | AY840522, AY840498, AY840457, AY840424, AY840391 | |
| *B. vulgaris* | CBS 116454, CPC 11558 | Italy: Ravenna | Chenopodiaceae | S. Garresus | AY840523, AY840499, AY840463, AY840430, AY840397 | |
| *B. vulgaris* | CBS 116454, CPC 11558 | Italy: Ravenna | Chenopodiaceae | S. Garresus | AY840524, AY840501, AY840465, AY840432, AY840399 | |
| *B. vulgaris* | CBS 116454, CPC 11558 | Italy: Ravenna | Chenopodiaceae | S. Garresus | AY840525, AY840502, AY840466, AY840433, AY840400 | |
| *B. vulgaris* | CBS 122.31, CPC 11561 | New Zealand: Auckland | Chenopodiaceae | C.F. Hill | AY840530, AY840497, AY840461, AY840427, AY840395 | |
| *B. vulgaris* | CBS 122.31, CPC 11561 | New Zealand: Auckland | Chenopodiaceae | C.F. Hill | AY840532, AY840499, AY840463, AY840430, AY840397 | |
| *Beta vulgaris* | CBS 122.31, CPC 11561 | New Zealand: Auckland | Chenopodiaceae | C.F. Hill | AY840534, AY840495, AY840461, AY840430, AY840397 | |
| *Beta vulgaris* | CBS 122.31, CPC 11561 | New Zealand: Auckland | Chenopodiaceae | A.Y. Ravanlou | AY840531, AY840498, AY840462, AY840429, AY840396 | |
| *Beta vulgaris* | CBS 122.31, CPC 11561 | New Zealand: Auckland | Chenopodiaceae | G.E. Bunschoten | DQ233322, DQ233348, DQ233374, DQ233400, DQ233426 | |
| *Beta vulgaris* | CBS 122.31, CPC 11561 | New Zealand: Auckland | Chenopodiaceae | G.E. Bunschoten | DQ233322, DQ233348, DQ233374, DQ233400, DQ233426 | |
| *Cercospora beticola* | CBS 113069, CPC 11562 | Spain | Myxomycetes | F. Campoy | AY840453, AY840454, AY840455, AY840456, AY840457 | |
| *C. beticola* | CBS 113069, CPC 11562 | Spain | Myxomycetes | F. Campoy | AY840453, AY840454, AY840455, AY840456, AY840457 | |
| *C. beticola* | CBS 113069, CPC 11562 | Spain | Myxomycetes | F. Campoy | AY840453, AY840454, AY840455, AY840456, AY840457 | |
| Species | Culture accession number(s) | Host name or isolation source | Host Family | Country | Collector | GenBank accession numbers |
|---------|-----------------------------|-----------------------------|-------------|---------|-----------|-------------------------|
| CPC 12022 | Beta vulgaris | Chenopodiaceae | Germany | S. Mitter | DQ233334 DQ23336 DQ233386 DQ233412 DQ233436 |
| CPC 12027 | Beta vulgaris | Chenopodiaceae | Germany | S. Mitter | DQ23335 DQ233361 DQ233386 DQ233413 DQ233468 |
| CPC 12028 | Beta vulgaris | Chenopodiaceae | Egypt | M. Hasem | DQ23336 DQ233386 DQ233414 DQ233437 |
| CPC 12029 | Beta vulgaris | Chenopodiaceae | Egypt | M. Hasem | DQ23337 DQ233336 DQ233389 DQ233415 DQ233438 |
| CPC 12030 | Beta vulgaris | Chenopodiaceae | Egypt | M. Hasem | DQ23338 DQ233364 DQ233390 DQ233416 DQ233439 |
| CPC 12031 | Beta vulgaris | Chenopodiaceae | Germany | S. Mitter | DQ23339 DQ233365 DQ233391 DQ233417 DQ233467 |
| CPC 14618 | Gonialimon tataricum | Plumbaginaceae | Bulgaria | S.G. Bobev | FJ473424 FJ473429 FJ473434 FJ473439 FJ473444 |
| CPC 14619 | Gonialimon tataricum | Plumbaginaceae | Bulgaria | S.G. Bobev | FJ473425 FJ473430 FJ473435 FJ473440 FJ473445 |
| CPC 15623 | Beta vulgaris | Chenopodiaceae | Mexico: Texcoco | Ma. de Jesús Yáñez-Morales | JX143555 JX143309 JX143063 JX142817 JX142571 |
| CPC 18813 | Beta vulgaris | Chenopodiaceae | USA: California | S.T. Koike | JX14356 JX143310 JX143064 JX142818 JX142572 |
| CPC 5123 | Apium graveolens | Apiaceae | New Zealand: Auckland | C.F. Hill | AY752134 AY752167 AY752195 AY752226 AY752257 |
| CPC 5125 | Beta vulgaris | Chenopodiaceae | New Zealand: Auckland | C.F. Hill | AY752137 AY752170 AY752198 AY752229 AY752260 |
| CPC 5128 | Beta vulgaris | Chenopodiaceae | New Zealand: Auckland | C.F. Hill | AY752138 AY752171 AY752199 AY752230 AY752261 |
| CPC 5370 | Spinacia sp. | Chenopodiaceae | Botswana: Gaborone | L. Lebogang | DQ233328 DQ233354 DQ233380 DQ233406 DQ233432 |
| CPC 568; MUCN 320; MAFF 238206 | Beta vulgaris | Chenopodiaceae | Japan: Chiba | S. Uematsu | JX143575 JX143311 JX143065 JX142819 JX142573 |
| MUCC 569; MAFF 305066 | Beta vulgaris | Chenopodiaceae | Japan: Hokkaido | K. Goto | JX143568 JX143312 JX143066 JX142820 JX142574 |
| Cercospora cf. brunkii CBS 13285; CPC 11598 | Geranium thunbergi | Geraniaceae | South Korea: Namyangju | H.D. Shin | JX143559 JX143313 JX143067 JX142821 JX142575 |
| MUCC 732 | Datura stramonium | Solanaceae | Japan: Wakayama | C. Nakashima & I. Araki | JX143650 JX143314 JX143068 JX142822 JX142576 |
| Cercospora campi-ellii CBS 132825; CPC 14585 | Impatiens nil-tangere | Balsaminaceae | South Korea: Inje | H.D. Shin | JX143651 JX143315 JX143069 JX142823 JX142577 |
| Cercospora canescens complex CBS 111133; CPC 1137 | Vigna sp. | Fabaceae | South Africa: Potchefstroom | S. van Wyk | AY260065 DQ835084 DQ835103 DQ835153 DQ835157 |
| Cercospora capsici CBS 111134; CPC 1138 | Vigna sp. | Fabaceae | South Africa: Potchefstroom | S. van Wyk | AY260066 DQ835085 DQ835104 DQ835131 DQ835158 |
| Cercospora capsici CBS 132858; CPC 11126; GHA-1-0 | Dioscorea rotundata | Dioscoreaceae | Ghana | S. Nyako & A.O. Danquah | JX143662 JX143316 JX143070 JX142824 JX142578 |
| Cercospora capsici CBS 132859; CPC 11127; GHA-1-1 | Dioscorea alata | Dioscoreaceae | Ghana | S. Nyako & A.O. Danquah | JX143653 JX143317 JX143071 JX142825 JX142579 |
| Cercospora capsici CBS 153.55; CPC 5059 | Phaseolus lunatus (= Ph. limensis) | Fabaceae | USA: Georgia | E.S. Luttrell | JX143664 JX143318 JX143072 JX142826 JX142580 |
| Cercospora capsici CBS 11640; IMI 186563 | Apium sp. | Apiaceae | USA | — | JX143658 JX143319 JX143073 JX142827 JX142581 |
| Cercospora capsici CBS 15871 | — | Malvaceae | Mexico: Tamaulipas | Ma. de Jesús Yáñez-Morales | JX143657 JX143321 JX143075 JX142829 JX142583 |
| Cercospora capsici CBS 4408; Q 160 IS2 | Citrus maxima | Rutaceae | South Africa: Tsipline | K. Serfontein | AY260067 DQ835086 DQ835105 DQ835132 DQ835159 |
| Cercospora capsici CBS 4409 | Citrus maxima | Rutaceae | South Africa: Tsipline | K. Serfontein | AY260068 DQ835087 DQ835106 DQ835133 DQ835160 |
| Cercospora capsici CBS 118712 | Lesions on calyx attached to fruit | — | Fiji | P. Tyler | GU14653 JX143322 JX143076 JX142830 JX142584 |
| Species | Culture accession number(s) | Host name or isolation source | Host Family | Country | Collector | GenBank accession numbers |
|---------|-----------------------------|------------------------------|-------------|---------|-----------|--------------------------|
| Cercospora celosiae | CBS 132600; CPC 10660 | *Celosia argentea* var. *cristata* (≡ *C. cristata*) | Amaranthaceae | South Korea: Chuncheon | H.D. Shin | JX143570 JX143326 JX143080 JX142834 JX142588 |
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| Cercospora chenopodii | CBS 132520; CPC 14237 | *Chenopodium* cf. *album* | Chenopodiaceae | France: Ardeche | P.W. Crous | JX143571 JX143327 JX143081 JX142833 JX142587 |
| | | | | | | |
| | CBS 132677; CPC 15599 | *Chenopodium* sp. | Chenopodiaceae | South Korea: Hongcheon | H.D. Shin | JX143757 JX143324 JX143078 JX142832 JX142586 |
| | | | | | | |
| | CPC 132594; CPC 10304 (TYPE) | *Chenopodium* sp. | Chenopodiaceae | Mexico: Montecillo | Ma. de Jesús Yáñez-Morales | JX143574 JX143323 JX143079 JX142831 JX142585 |
| | | | | | | |
| | CPC 15763 | *Chenopodium* sp. | Chenopodiaceae | Mexico: Chiba | S. Uematsu | JX143569 JX143325 JX143077 JX142831 JX142585 |
| | | | | | | |
| | CPC 15859 | *Chenopodium* sp. | Chenopodiaceae | South Korea: Yanggu | H.D. Shin | JX143570 JX143322 JX143077 JX142831 JX142587 |
| | | | | | | |
| | CPC 132669; CPC 12683 | *Musa* sp. | Musaceae | Bangladesh: Western | I. Buddenhagen | EU514222 JX143335 JX143089 JX142843 JX142597 |
| | | | | | | |
| | CPC 132699; CPC 12683 | *Musa* sp. | Musaceae | Bangladesh: Western | I. Buddenhagen | EU514223 JX143336 JX143090 JX142844 JX142598 |
| | | | | | | |
| | MUCC 576; MUCNS 300; MAFF 237913 | *Citrullus lanatus* | Cucurbitaceae | Japan: Okinawa | T. Kobayashion et al. | JX143579 JX143337 JX143091 JX142845 JX142599 |
| | | | | | | |
| | MUCC 577; MUCNS 254; MAFF 232015 | *Momordica charantia* | Cucurbitaceae | Japan: Kagoshima | E. Imaizumi & C. Nomi | JX143580 JX143338 JX143092 JX142846 JX142600 |
| | | | | | | |
| | MUCC 584; MAFF 305757 | *Psophocarpus tetragonolobus* | Fabaceae | Japan: Okinawa | — | JX143581 JX143339 JX143093 JX142847 JX142601 |
| | | | | | | |
| | MUCC 598; MAFF 239409 | *Ipomoea pes-caprae* | Convolvulaceae | Japan: Okinawa | — | JX143582 JX143340 JX143094 JX142848 JX142602 |
| Cercospora coniogrammes | CBS 132634; CPC 17017 (TYPE) | *Coniogramme japonica* var. *gracilis* (≡ *C. gracilis*) | Adiantaceae | Australia: Queensland | P.W. Crous | JX143583 JX143341 JX143095 JX142849 JX142603 |
| | | | | | | |
| | MUCC 585; MUCNS 72; MAFF 238191 (TYPE) | *Corchorus olitorius* | Tiliaceae | Japan: Shimane | T. Mikami | JX143584 JX143342 JX143096 JX142850 JX142604 |
| | | | | | | |
| | CBS 132598; CPC 10648 | *Coreopsis lanceolata* | Asteraceae | South Korea: Seoul | H.D. Shin | JX143585 JX143343 JX143097 JX142851 JX142605 |
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| | CPC 10122 | *Coreopsis lanceolata* | Asteraceae | South Korea: Wonju | H.D. Shin | JX143586 JX143344 JX143098 JX142852 JX142606 |
| Cercospora delaireae | CBS 132595; CPC 10455; GV2 PPRI number: C558 (TYPE) | *Delairea odorata* (= *Senecio mikanioides*) | Asteraceae | South Africa: Long Tom Pass | S. Nesser | JX143587 JX143345 JX143099 JX142853 JX142607 |
| | | | | | | |
| | CPC 10627 | *Delairea odorata* (= *Senecio mikanioides*) | Asteraceae | South Africa: Pieterberg Bay | C.L. Lennox | JX143588 JX143346 JX143100 JX142854 JX142608 |
| | | | | | | |
| | CPC 10628 | *Delairea odorata* (= *Senecio mikanioides*) | Asteraceae | South Africa: Pieterberg Bay | C.L. Lennox | JX143589 JX143347 JX143101 JX142855 JX142609 |
| Species                      | Culture accession number(s) | Host name or isolation source | Host Family | Country                  | Collector | GenBank accession numbers |
|------------------------------|-----------------------------|-------------------------------|-------------|--------------------------|-----------|--------------------------|
| Cercospora dispori           | CBS 132608; CPC 10773       | Delairea odorata (= Senecio mikanioides) | Asteraceae  | South Korea: Plettenberg Bay | C.L. Lennox | JX143590, JX143348, JX143102, JX142856, JX142610 |
| Cercospora cf. erysimi       | CBS 115059; CPC 5361        | Erysimum mutabile             | Brassicaceae | New Zealand: Manurewa     | C.F. Hill  | JX143592, JX143350, JX143104, JX142858, JX142612 |
| Cercospora euphorbiae-sieboldiaei | CPC 113306 (TYPE) | Euphorbia sieboldiana         | Euphorbiaceae | South Korea: Samcheok    | H.D. Shin  | JX143593, JX143351, JX143105, JX142859, JX142613 |
| Cercospora fagopyri          | CBS 132623; CPC 14541 (TYPE) | Fagopyrum esculentum         | Polygonaceae | South Korea: Yangpyeong   | H.D. Shin  | JX143594, JX143352, JX143106, JX142860, JX142614 |
| Cercospora cf. flagellaris   | CBS 113127; RC3766; TX-18   | Elodea canadensis            | Pontederiaceae | USA: Texas              | D. Tessmann & R. Charudattan | DQ835075, AF146174, DQ835121, DQ835148, DQ835175 |
| Cercospora sp.               | CBS 115482; A207 Bs+; CPC 4410 | Citrus sp.                   | Rutaceae    | South Africa: Messina    | M.C. Pretorius | AY260070, DQ835095, DQ835114, DQ835145, DQ835172 |
| Cercospora sp.               | CBS 132673; CPC 10079       | Trianthema speciosissima     | Fabaceae    | South Korea: Samcheok    | H.D. Shin  | JX143595, JX143353, JX143107, JX142861, JX142615 |
| Cercospora sp.               | CBS 132646; CPC 10681       | Choripyrus affinis           | Phyllanthaceae | South Korea: Suwon       | H.D. Shin  | JX143596, JX143354, JX143108, JX142862, JX142616 |
| Cercospora sp.               | CBS 132648; CPC 10722       | Amarathus patulus            | Amaryllidaceae | South Korea: Namyangju   | H.D. Shin  | JX143597, JX143355, JX143109, JX142863, JX142617 |
| Cercospora sp.               | CBS 132653; CPC 10884       | Dysphania ambrosioides (≡ Chenopodium ambrosioides) | Chenopodiaceae | South Korea: Jeju        | H.D. Shin  | JX143598, JX143356, JX143110, JX142864, JX142618 |
| Cercospora sp.               | CBS 132663; CPC 11643       | Celosia argentea var. cristata (≡ C. cristata) | Amaryllidaceae | South Korea: Hoengseong  | H.D. Shin  | JX143604, JX143362, JX143116, JX142870, JX142624 |
| Cercospora sp.               | CBS 132670; CPC 14487       | Sisymbretia pubescens        | Asteraceae  | South Korea: Yangpyeong   | H.D. Shin  | JX143605, JX143363, JX143117, JX142871, JX142625 |
| Cercospora sp.               | CBS 132674; CPC 14723       | Phytolacca americana         | Phytolaccaceae | South Korea: Jeju        | H.D. Shin  | JX143606, JX143364, JX143118, JX142872, JX142626 |
| Cercospora sp.               | CBS 143.51; CPC 5055       | Bromus sp.                   | Poaceae     | South Korea: Pocheon     | H.D. Shin  | JX143607, JX143365, JX143119, JX142873, JX142627 |
| Cercospora sp.               | CPC 10124                   | Phytolacca americana         | Phytolaccaceae | South Africa: Pocheon    | H.D. Shin  | JX143608, JX143366, JX143120, JX142874, JX142628 |
| Cercospora sp.               | CPC 1051                    | Populus deltoides            | Salicaceae  | South Africa: P.W. Crous | P.W. Crous | AY2600069, JX143367, JX143121, JX142875, JX142629 |
| Cercospora sp.               | CPC 1052                    | Populus deltoides            | Salicaceae  | South Africa: P.W. Crous | P.W. Crous | AY2600072, JX143368, JX143122, JX142876, JX142630 |
| Cercospora sp.               | CPC 10684                   | Phytolacca americana         | Phytolaccaceae | South Korea: Jinju       | H.D. Shin  | JX143610, JX143369, JX143123, JX142877, JX142631 |
| Cercospora sp.               | CPC 4411; Q207 F5           | Citrus sp.                   | Rutaceae    | South Africa: Messina    | M.C. Pretorius | AY260071L, DQ835098, DQ835116, DQ835145, DQ835172 |
| Cercospora sp.               | CPC 5441                    | Amanathus sp.                | Amaryllidaceae | Fiji            | C.F. Hill  | JX143611, JX143370, JX143124, JX142878, JX142632 |
| Cercospora sp.               | MUCC 127                    | Cosmos sulphureus            | Asteraceae  | Japan: Ehime           | J. Nishikawa | JX143612, JX143371, JX143125, JX142879, JX142633 |
| Cercospora sp.               | MUCC 735                    | Hydrangea serrata            | Hydrangeaceae | Japan: Wakayama        | C. Nakashima & I. Araki | JX143613, JX143372, JX143126, JX142880, JX142634 |
| Cercospora sp.               | MUCC 831                    | Hydrangea serrata            | Hydrangeaceae | Japan: Tokyo           | I. Araki & M. Harada | JX143614, JX143373, JX143127, JX142881, JX142635 |
| Species | Culture accession number(s) | Host name or isolation source | Host Family | Country | Collector | GenBank accession numbers |
|---------|-----------------------------|-----------------------------|-------------|---------|-----------|-------------------------|
| Cercospora cf. helianthicola | MUCC 716 | *Helianthus tuberosus* | Asteraceae | Japan: Wakayama | C. Nakashima & I. Araki | JX143615 JX143374 JX143128 JX142882 JX142636 |
| Cercospora cf. ipomeae | CBS 1328; CPC 10102 | *Penscariella thunbergii* | Polygonaceae | South Korea: Pocheon | H.D. Shin | JX143616 JX143375 JX143129 JX142883 JX142637 |
| | CBS 1328; CPC 10833 | *Ipomoea nil* (= *I. hederacea*) | Convolvulaceae | South Korea: Chuncheon | H.D. Shin | JX143617 JX143376 JX143130 JX142884 JX142638 |
| | MUC 442 | *Ipomoea aquatica* | Convolvulaceae | Japan: Kagawa | G. Kizaki | JX143618 JX143377 JX143131 JX142885 JX142639 |
| Cercospora kikuchii | CBS 128.27; CPC 5068 (TYPE) | *Glycine soja* | Fabaceae | Japan | T. Matsumoto | DQ835070 DQ835088 DQ835107 DQ835134 DQ835161 |
| | CBS 1328; CPC 16578 | *Glycine max* | Fabaceae | Argentina | — | JX143619 JX143378 JX143132 JX142886 JX142640 |
| Cercospora lactucae-sativae | CBS 132604; CPC 10728 | *Ixeris chinensis* subsp. *strigosa* (≡ *Ixeris strigosa*) | Asteraceae | South Korea: Chuncheon | H.D. Shin | JX143621 JX143381 JX143134 JX142888 JX142641 |
| | CPC 10082 | *Ixeris chinensis* subsp. *strigosa* (≡ *Ixeris strigosa*) | Asteraceae | South Korea: Chuncheon | H.D. Shin | JX143622 JX143382 JX143135 JX142889 JX142642 |
| | MUC 570; MUCN 5463; MAFF 236209 | *Lactuca sativa* | Asteraceae | Japan: Chiba | C. Nakashima | JX143623 JX143383 JX143136 JX142890 JX142643 |
| Cercospora cf. malloti | MUC 575; MUCNS 592; MAFF 237872 | *Cucumis melo* | Cucurbitaceae | Japan: Okinawa | K. Uehara | JX143625 JX143384 JX143138 JX142892 JX142646 |
| Cercospora mercurialis | CBS 549.71 | *Malabthus japonicus* | Euphorbiaceae | Japan: Okinawa | C. Nakashima & T. Akashi | JX143626 JX143385 JX143139 JX142893 JX142647 |
| | CBS 550.71 (TYPE) | *Mercuriale annua* | Euphorbiaceae | Romania: Cheia | O. Constantinescu | JX143627 JX143386 JX143140 JX142894 JX142648 |
| | MUC 551.71 | *Mercuriale perennis* | Euphorbiaceae | Romania: Cheia | O. Constantinescu | JX143628 JX143387 JX143141 JX142895 JX142649 |
| | MUC 551.71 | *Mercuriale ovata* | Euphorbiaceae | Romania: Hagieni | O. Constantinescu & G. Negrean | JX143629 JX143388 JX143142 JX142896 JX142650 |
| Cercospora cf. modiolae | CPC 5115 | *Modiola caroliniana* | Malvaceae | New Zealand | C.F. Hill | JX143630 JX143389 JX143143 JX142897 JX142651 |
| Cercospora cf. nicotianae | CBS 131.32; CPC 5076 | *Nicotiana tabacum* | Solanaceae | Indonesia: Medan | H. Diddens & A. Jaarsveld | DQ835073 DQ835099 DQ835119 DQ835146 DQ835173 |
| | CBS 1328; CPC 15918 | *Glycine max* | Fabaceae | Mexico: Tamaulipas | Ma. de Jesús Yáñez-Morales | JX143631 JX143390 JX143144 JX142998 JX142652 |
| | CBS 570.69; CPC 5075 | *Nicotiana tabacum* | Solanaceae | Nigeria | S.O. Alasoadura | JX143632 JX143391 JX143145 JX142999 JX142653 |
| Cercospora olivascens | CBS 253.67; IMI 124975; CPC 5085 (TYPE) | *Aristolochia delatmidalis* | Aristolochiaceae | Romania: Cazanele Dunarii | O. Constantinescu | JX143632 JX143391 JX143145 JX142899 JX142653 |
| Cercospora cf. physalidis | CBS 755.79 | *Solarium tuberosum* | Solanaceae | Peru | L.J. Tukkensteen | JX143633 JX143392 JX143146 JX142900 JX142654 |
| Cercospora paxicola | CBS 132607; CPC 10749 (TYPE) | *Pilea pumila* (= *P. mongolica*) | Urticaceae | South Korea: Dongducheon | H.D. Shin | JX143634 JX143393 JX143147 JX142901 JX142655 |
| | CBS 132647; CPC 10693 | *Pilea hamae* (≡ *P. pumila var. hamae*) | Urticaceae | South Korea: Hoengseong | H.D. Shin | JX143635 JX143394 JX143148 JX142902 JX142656 |
| | CPC 11929 | *Pilea pumila* (= *P. mongolica*) | Urticaceae | South Korea: Hongcheon | H.D. Shin | JX143636 JX143395 JX143149 JX142903 JX142657 |
| Cercospora polygonaceae | CBS 132814; CPC 11318 | *Penicaria longiseta* (≡ *P. blumei*) | Polygonaceae | South Korea: Cheongju | H.D. Shin | JX143637 JX143396 JX143150 JX142904 JX142658 |
Table 1. (Continued).

| Species | Culture accession number(s) | Host name or isolation source | Host Family | Country | Collector | GenBank accession numbers |
|---------|-----------------------------|------------------------------|-------------|---------|-----------|--------------------------|
|         |                             |                              |             |         |           | ITS | TEF | ACT | CAL | HIS       |
| **Cercospora punctiformis** | CBS 132626; CPC 14600 | Cynanchum wilfordii | Asclepiadaceae | South Korea: Bonghwa | H.D. Shin | JX143638 | JX143397 | JX143151 | JX142905 | JX142659 |
| **Cercospora cf. reesae**   | CBS 118793 | Reseda odorata | Resedaceae | New Zealand: Auckland | C.F. Hill | JX143639 | JX143398 | JX143152 | JX142906 | JX142660 |
| **Cercospora cf. richarditica** | CBS 132627; CPC 14680 | Ajuga multiflora | Lamiaceae | South Korea: Incheon | H.D. Shin | JX143640 | JX143399 | JX143153 | JX142907 | JX142661 |
| **Cercospora cf. richarditica** | CBS 132; CPC 10734 | Tagetes erecta | Asteraceae | Japan: Ehime | J. Nishikawa | JX143641 | JX143400 | JX143154 | JX142908 | JX142662 |
| **Cercospora cf. richarditica** | CPC 10104 | Fuchsia ×hybrida | Onagraceae | Japan: Shizuoka | J. Nishikawa | JX143642 | JX143401 | JX143155 | JX142909 | JX142663 |
| **Cercospora cf. richarditica** | CPC 10104 | Zantedeschia sp. | Araceae | Japan: Ehime | J. Nishikawa | JX143643 | JX143402 | JX143156 | JX142910 | JX142664 |
| **Cercospora cf. richarditica** | CPC 10104 | Gerbera hybrida | Asteraceae | Japan: Shizuoka | J. Takeuchi | JX143644 | JX143403 | JX143157 | JX142911 | JX142665 |
| **Cercospora cf. richarditica** | CPC 10104 | Zantedeschia sp. | Araceae | Japan: Ehime | J. Nishikawa | JX143645 | JX143404 | JX143158 | JX142912 | JX142666 |
| **Cercospora cf. richarditica** | CPC 10104 | Fuchsia ×hybrida | Onagraceae | Japan: Shizuoka | J. Nishikawa | JX143646 | JX143405 | JX143159 | JX142913 | JX142667 |
| **Cercospora cf. richarditica** | CPC 10104 | Zantedeschia sp. | Araceae | Japan: Ehime | J. Nishikawa | JX143647 | JX143406 | JX143160 | JX142914 | JX142668 |
| **Cercospora cf. richarditica** | CPC 10104 | Fuchsia ×hybrida | Onagraceae | Japan: Shizuoka | J. Takeuchi | JX143648 | JX143407 | JX143161 | JX142915 | JX142669 |
| **Cercospora cf. richarditica** | CPC 10104 | Zantedeschia sp. | Araceae | Japan: Ehime | J. Nishikawa | JX143649 | JX143408 | JX143162 | JX142916 | JX142670 |
| **Cercospora cf. richarditica** | CPC 10104 | Gerbera hybrida | Asteraceae | Japan: Shizuoka | J. Takeuchi | JX143650 | JX143409 | JX143163 | JX142917 | JX142671 |
| **Cercospora cf. richarditica** | CPC 10104 | Zantedeschia sp. | Araceae | Japan: Ehime | J. Nishikawa | JX143651 | JX143410 | JX143164 | JX142918 | JX142672 |
| **Cercospora cf. richarditica** | CPC 10104 | Gerbera hybrida | Asteraceae | Japan: Shizuoka | J. Takeuchi | JX143652 | JX143411 | JX143165 | JX142919 | JX142673 |
| **Cercospora cf. richarditica** | CPC 10104 | Zantedeschia sp. | Araceae | Japan: Ehime | J. Nishikawa | JX143653 | JX143412 | JX143166 | JX142920 | JX142674 |
| **Cercospora cf. richarditica** | CPC 10104 | Gerbera hybrida | Asteraceae | Japan: Shizuoka | J. Takeuchi | JX143654 | JX143413 | JX143167 | JX142921 | JX142675 |
| **Cercospora cf. richarditica** | CPC 10104 | Zantedeschia sp. | Araceae | Japan: Ehime | J. Nishikawa | JX143655 | JX143414 | JX143168 | JX142922 | JX142676 |
| **Cercospora cf. richarditica** | CPC 10104 | Gerbera hybrida | Asteraceae | Japan: Shizuoka | J. Takeuchi | JX143656 | JX143415 | JX143169 | JX142923 | JX142677 |
| **Cercospora cf. richarditica** | CPC 10104 | Zantedeschia sp. | Araceae | Japan: Ehime | J. Nishikawa | JX143657 | JX143416 | JX143170 | JX142924 | JX142678 |
| **Cercospora cf. richarditica** | CPC 10104 | Gerbera hybrida | Asteraceae | Japan: Shizuoka | J. Takeuchi | JX143658 | JX143417 | JX143171 | JX142925 | JX142679 |
| **Cercospora cf. richarditica** | CPC 10104 | Zantedeschia sp. | Araceae | Japan: Ehime | J. Nishikawa | JX143659 | JX143418 | JX143172 | JX142926 | JX142680 |
Table 1. (Continued).

| Species            | Culture accession number(s) | Host name or isolation source | Country      | Collector | GenBank accession numbers |
|--------------------|-----------------------------|------------------------------|--------------|-----------|----------------------------|
| *Cercospora* sp. A | CBS 132615, CPC 11353 (TYPE) | Glycine soja Fabaceae        | South Korea: Hongcheon | H.D. Shin | JX14369 JX143419 JX143437 JX143227 JX142881 |
| *Cercospora* sp. B | CBS 132620, CPC 11337      | Glycine max Fabaceae         | Argentina    | F. Scandiani | JX143621 JX143422 JX143438 JX143230 JX142883 |
| *Cercospora* sp. C | CBS 132619, CPC 11336      | Glycine soja Fabaceae        | South Korea: Hongcheon | H.D. Shin | JX143621 JX143422 JX143438 JX143230 JX142883 |
| *Cercospora* sp. D | CBS 132622, CPC 11335      | Glycine max Fabaceae         | Argentina    | F. Scandiani | JX143621 JX143422 JX143438 JX143230 JX142883 |
| *Cercospora* sp. E | CBS 132621, CPC 11334      | Glycine max Fabaceae         | Argentina    | F. Scandiani | JX143621 JX143422 JX143438 JX143230 JX142883 |
| *Cercospora* sp. F | CBS 132618, CPC 11329      | Glycine max Fabaceae         | Argentina    | F. Scandiani | JX143621 JX143422 JX143438 JX143230 JX142883 |
| *Cercospora* sp. G | CBS 132617, CPC 11328      | Glycine max Fabaceae         | Argentina    | F. Scandiani | JX143621 JX143422 JX143438 JX143230 JX142883 |
| *Cercospora* sp. H | CBS 132623, CPC 11333      | Glycine max Fabaceae         | Argentina    | F. Scandiani | JX143621 JX143422 JX143438 JX143230 JX142883 |
| *Cercospora* sp. I | CBS 132616, CPC 11332      | Glycine max Fabaceae         | Argentina    | F. Scandiani | JX143621 JX143422 JX143438 JX143230 JX142883 |
| *Cercospora* sp. J | CBS 132614, CPC 11331      | Glycine max Fabaceae         | Argentina    | F. Scandiani | JX143621 JX143422 JX143438 JX143230 JX142883 |

**Cercospora** sp. B and *Cercospora* sp. C are from the same collection of Glycine soja in Argentina. *Cercospora* sp. A and *Cercospora* sp. D are from different collections of Glycine soja in South Korea. *Cercospora* sp. E and *Cercospora* sp. F are from the same collection of Glycine max in Argentina. *Cercospora* sp. G and *Cercospora* sp. H are from the same collection of Glycine max in Argentina. *Cercospora* sp. I and *Cercospora* sp. J are from different collections of Glycine max in Argentina.
| Species | Culture accession number(s) | Host name or isolation source | Host Family | Country | Collector | GenBank accession numbers |
|---------|----------------------------|-------------------------------|-------------|---------|-----------|-------------------------|
|         |                            |                               |             |         |           | ITS TEF ACT CAL HIS     |
| Cercospora sp. J | CBS 115117 | Archontophoenix cunninghamiana | Arecaceae (Palmae) | New Zealand: Whangarei | C.F. Hill | JX143689 JX143449 JX143203 JX142957 JX142711 |
|         | CBS 115121 | Gunnera tinctoria | Gunneraceae | New Zealand: Mt Albert | C.F. Hill | JX143690 JX143450 JX143204 JX142958 JX142712 |
| Cercospora sp. | CBS 132643; CPC 10138 | Coreopsis verticillata | Asteraceae | South Korea: Suwon | H.D. Shin | JX143692 JX143452 JX143206 JX142960 JX142715 |
|         | CPC 5440 | Nicotiana sp. | Solanaceae | New Zealand: Manurewa | C.F. Hill | JX143694 JX143454 JX143208 JX142962 JX142716 |
| Cercospora sp. K | CBS 132603; CPC 10719 | Ipomoea coccinea (≡ Quamoclit coccinea) | Convolvulaceae | New Zealand: Manurewa | C.F. Hill | JX143695 JX143455 JX143209 JX142961 JX142717 |
|         | CBS 132643; CPC 10138 | Ipomoea coccinea (≡ Quamoclit coccinea) | Convolvulaceae | South Korea: Suwon | H.D. Shin | JX143696 JX143456 JX143210 JX142963 JX142718 |
| Cercospora sp. L | CBS 132597; CPC 10615 | Antirrhinum majus | Plantaginaceae | Japan: Aichi | M.M. Matsusaki | JX143698 JX143458 JX143212 JX142964 JX142720 |
|         | CBS 132643; CPC 10138 | Ipomoea coccinea (≡ Quamoclit coccinea) | Convolvulaceae | South Korea: Suwon | H.D. Shin | JX143699 JX143459 JX143213 JX142965 JX142721 |
| Cercospora sp. M | CBS 132596; CPC 10553 | Acacia mangium | Fabaceae | Thailand: Sanamchakhet | K. Pongpanich | JX143700 AY752175 AY752203 AY752234 AY752265 |
|         | CBS 132619; CPC 12684 | Musa sp. | Musaceae | Thailand: Namyangju | P.W. Crous | JX143701 JX143461 JX143215 JX142969 JX142723 |
| Cercospora sp. O | CBS 132635; CPC 18636 | Musa sp. | Musaceae | Thailand: Namyangju | P.W. Crous | JX143702 JX143462 JX143216 JX142970 JX142724 |
| Cercospora sp. P | CBS 112649; CPC 3946 | Citrus sp., leaf spot | Rutaceae | Swaziland | M.C. Pretorius | AY260072 DG835090 DG835109 DG835113 DG835163 |
|         | CBS 112722; CPC 3947 | Citrus sp., leaf spot | Rutaceae | Swaziland | M.C. Pretorius | AY260073 DG835091 DG835110 DG835137 DG835164 |
|         | CBS 112728; CPC 3949 | Citrus × sinensis (≡ C. aurantium var. sinensis) | Rutaceae | South Africa: Komatiport | M.C. Pretorius | AY260076 DG835092 DG835111 DG835138 DG835165 |
|         | CBS 112730; CPC 3948 | Citrus × sinensis (≡ C. aurantium var. sinensis) | Rutaceae | South Africa: Komatiport | M.C. Pretorius | AY260075 DG835093 DG835112 DG835139 DG835166 |
|         | CBS 112894; CPC 3950 | Citrus × sinensis (≡ C. aurantium var. sinensis) | Rutaceae | South Africa: Komatiport | M.C. Pretorius | AY260077 DG835094 DG835113 DG835140 DG835167 |
| Cercospora sp. | CBS 113996; CPC 5326 | Cajanus cajan | Fabaceae | South Africa: Nelspruit | L. van Jaarsveld | JX143702 JX143462 JX143216 JX142970 JX142724 |
|         | CBS 115413; CPC 5328 | Cajanus cajan | Fabaceae | South Africa: Nelspruit | L. van Jaarsveld | JX143703 JX143463 JX143217 JX142971 JX142725 |
|         | CBS 115699; CPC 3945 | Citrus sp., leaf spot | Rutaceae | Swaziland | M.C. Pretorius | AY260074 DG835096 DG835115 DG835142 DG835169 |
|         | CBS 116365; CPC 10526 | Acacia mangium | Fabaceae | Thailand | M.J. Wingfield | AY752141 AY752176 AY752204 AY752235 AY752266 |
|         | CBS 132645; CPC 10527 | Acacia mangium | Fabaceae | Thailand | M.J. Wingfield | AY752142 AY752177 AY752205 AY752236 AY752267 |
|         | CBS 132660; CPC 11062; GHA-4-0 | Dioscorea rotundata | Dioscoreaceae | Ghana | S. Nyako & A.O. Danquah | JX143704 JX143464 JX143218 JX142972 JX142726 |
|         | CBS 132662; CPC 11065; PNG-009 | Dioscorea nummularia | Dioscoreaceae | Papua New Guinea | J. Peters & A.N. Jama | JX143705 JX143465 JX143219 JX142973 JX142727 |
|         | CBS 132664; CPC 11637; PNG-022 | Dioscorea nummularia | Dioscoreaceae | Papua New Guinea | J. Peters & A.N. Jama | JX143706 JX143466 JX143220 JX142974 JX142728 |
|         | CBS 132665; CPC 11638; PNG-023 | Dioscorea bulbifera | Dioscoreaceae | Papua New Guinea | J. Peters & A.N. Jama | JX143707 JX143467 JX143221 JX142975 JX142729 |
| Species | Culture accession number(s) | Host name or isolation source | Host Family | Country | Collector | GenBank accession numbers |
|---------|-----------------------------|------------------------------|------------|---------|-----------|--------------------------|
| **CBS 138580; CPC 15827** | *Ricinus communis* | **Euphorbiaceae** | Mexico: Tamaulipas | Ma. de Jesús Yáñez-Morales | JX143708 JX143468 JX143222 JX142976 JX142730 |
| CPC 10552 | *Acacia mangium* | **Fabaceae** | Thailand | K. Pongpanich | JX143709 AY752174 AY752202 AY752233 AY752264 |
| CPC 11630; GHA-4-3 | *Dioscorea rotundata* | **Dioscoreaceae** | Ghana | S. Nyako & A.O. Danquah | JX143710 JX143469 JX143223 JX142977 JX142731 |
| CPC 11631; GHA-5-0 | *Dioscorea rotundata* | **Dioscoreaceae** | Ghana | S. Nyako & A.O. Danquah | JX143711 JX143470 JX143224 JX142978 JX142732 |
| CPC 11632; GHA-7-4 | *Dioscorea rotundata* | **Dioscoreaceae** | Ghana | S. Nyako & A.O. Danquah | JX143712 JX143471 JX143225 JX142979 JX142733 |
| CPC 4001 | *Citrus ×sinensis* (≡ *C. aurantium* var. *sinensis*) | **Rutaceae** | Swaziland | M.C. Pretorius | JX143372 AY343335 DQ835116 DQ835143 DQ835170 |
| CPC 4002 | *Citrus ×sinensis* (≡ *C. aurantium* var. *sinensis*) | **Rutaceae** | Swaziland | M.C. Pretorius | JX143715 JX143474 JX143229 JX142982 JX142736 |
| CPC 5262 | *Hibiscus sabdariffa* | **Malvaceae** | New Zealand: Auckland (imported from Fiji) | C.F. Hill | JX143714 JX143473 JX143227 JX142981 JX142735 |
| CPC 5327 | *Cajanus cajan* | **Fabaceae** | South Africa: Nelspruit | L. van Jaarsveld | JX143716 JX143475 JX143229 JX142983 JX142737 |
| MUCC 771 | *Coffea arabica* | **Rubiaceae** | Japan: Okinawa | C. Nakashima | JX143717 JX143476 JX143230 JX142984 JX142738 |
| **Cercospora sp. Q** | *Cajanus cajan* | **Fabaceae** | South Africa: Nelspruit | L. van Jaarsveld | JX143718 JX143477 JX143231 JX142985 JX142739 |
| CBS 113997; CPC 5325 | *Cajanus cajan* | **Fabaceae** | South Africa: Nelspruit | L. van Jaarsveld | JX143719 JX143478 JX143232 JX142986 JX142740 |
| CBS 115410; CPC 5331 | *Cajanus cajan* | **Fabaceae** | South Africa: Nelspruit | L. van Jaarsveld | JX143720 JX143479 JX143233 JX142987 JX142741 |
| CBS 115411; CPC 5332 | *Cajanus cajan* | **Fabaceae** | South Africa: Nelspruit | L. van Jaarsveld | JX143721 JX143480 JX143234 JX142988 JX142742 |
| CBS 115412; CPC 5333 | *Cajanus cajan* | **Fabaceae** | South Africa: Nelspruit | L. van Jaarsveld | JX143722 JX143481 JX143235 JX142989 JX142743 |
| CBS 115536; CPC 5329 | *Cajanus cajan* | **Fabaceae** | South Africa: Nelspruit | L. van Jaarsveld | JX143723 JX143482 JX143236 JX142990 JX142744 |
| CBS 115537; CPC 5330 | *Cajanus cajan* | **Fabaceae** | South Africa: Nelspruit | L. van Jaarsveld | JX143724 JX143483 JX143237 JX142991 JX142745 |
| CBS 138586; CPC 11536 | *Acacia mangium* | **Fabaceae** | Thailand | K. Pongpanich | JX143725 JX143484 JX143238 JX142992 JX142746 |
| CBS 138581; CPC 15844 | *Phaseolus vulgaris* | **Fabaceae** | Mexico | Ma. de Jesús Yáñez-Morales | JX143726 JX143485 JX143239 JX142993 JX142747 |
| CBS 138582; CPC 15850 | *Euphorbia sp.* | **Euphorbiaceae** | Mexico: Tamaulipas | Ma. de Jesús Yáñez-Morales | JX143727 JX143486 JX143240 JX142994 JX142748 |
| CPC 10550 | *Taraxacum sp.* | **Asteraceae** | Thailand | K. Pongpanich | AY752139 AY752172 AY752202 AY752233 AY752264 |
| CPC 10551 | *Acacia mangium* | **Fabaceae** | Thailand | K. Pongpanich | AY752140 AY752173 AY752201 AY752232 AY752265 |
| CPC 11539 | *Acacia mangium* | **Fabaceae** | Thailand | K. Pongpanich | AY752141 AY752174 AY752202 AY752233 AY752266 |
| CPC 11639; PNG-037 | *Dioscorea rotundata* | **Dioscoreaceae** | Papua New Guinea | J. Peters & A.N. Jama | JX143730 JX143489 JX143243 JX142997 JX142751 |
| CPC 15875 | *Euphorbia sp.* | **Euphorbiaceae** | Malaysia: Tamaulipas | Ma. de Jesús Yáñez-Morales | JX143731 JX143490 JX143244 JX142998 JX142752 |
| CPC 11644 | *Myoporum laetum* | **Myoporaceae** | New Zealand: Grey Lynn | C.F. Hill | JX143732 JX143491 JX143245 JX142999 JX142753 |
| CPC 13509 | *Crepis denticulata* (≡ *Youngia denticulata*) | **Asteraceae** | South Korea: Yangpyeong | H.D. Shin | JX143733 JX143492 JX143246 JX143000 JX142754 |
| Species Concept | Culture Accession Numbers | ACT | CAL | ITS | TEF | ACT | HIS |
|-----------------|---------------------------|-----|-----|-----|-----|-----|-----|
| **Cercospora anisopliae** | CBS 123860, CPC 13813 | JX143734 | | JX143433 | JX143247 | | |
| **Cercospora violae** | CBS 251.67, CPC 5079 | JX143737 | | JX143496 | JX143250 | | |
| **Cercospora zeae-maydis** | CBS 117755, CPC 5079 | JX143738 | | JX143497 | JX143251 | | |
| **Cercospora zebrina** | CBS 108.22, CPC 5079 | JX143739 | | JX143498 | JX143252 | | |
| **Cercospora zebrina** | CBS 108.22, CPC 5079 | JX143740 | | JX143499 | JX143253 | | |
| **Cercospora zebrina** | CBS 108.22, CPC 5079 | JX143741 | | JX143500 | JX143254 | | |
| **Cercospora zebrina** | CBS 108.22, CPC 5079 | JX143742 | | JX143501 | JX143255 | | |
| **Cercospora zebrina** | CBS 108.22, CPC 5079 | JX143743 | | JX143502 | JX143256 | | |
| **Cercospora zebrina** | CBS 108.22, CPC 5079 | JX143744 | | JX143503 | JX143257 | | |
| **Cercospora zebrina** | CBS 108.22, CPC 5079 | JX143745 | | JX143504 | JX143258 | | |
| **Cercospora zebrina** | CBS 108.22, CPC 5079 | JX143746 | | JX143505 | JX143259 | | |
# Table 1. (Continued)

| Species | Culture accession number(s) | Host name or isolation source | Host Family | Country | Collector | GenBank accession numbers |
|---------|-----------------------------|------------------------------|-------------|---------|-----------|---------------------------|
| Trifolium cernuum | CBS 118791; IMI 264190; WA2054; WAC7993 | | Fabaceae | Australia | M.J. Barbetti | JX143749, JX143511, JX143265, JX143019, JX142773 |
| Trifolium subterraneum | CBS 129.39; CPC 5078 | USA: Wisconsin | Fabaceae | — | — | JX143750, JX143512, JX143266, JX143020, JX142774 |
| Trifolium repens | CBS 132650; CPC 10756 | South Korea: Namyangju | Fabaceae | H.D. Shin | — | JX143751, JX143513, JX143267, JX143021, JX142775 |
| Hedysarum coronarium | CBS 137.56; CPC 5118 | Italy | Fabaceae | — | — | JX143752, JX143514, JX143268, JX143022, JX142776 |
| Astragalus spruneri | CBS 537.71; IMI 161108; CPC 5099 | Romania: Hagieni | Fabaceae | O. Constantinescu | — | JX143753, JX143515, JX143269, JX143023, JX142777 |
| Lotus pedunculatus | CPC 5437 | New Zealand: Auckland | Fabaceae | C.F. Hill | — | JX143754, JX143516, JX143270, JX143024, JX142778 |
| Jacaranda mimosiformis | CPC 5473 | New Zealand | Fabaceae | C.F. Hill | — | JX143755, JX143517, JX143271, JX143025, JX142779 |
| Zinnia elegans | CBS 118820; CPC 11995 (TYPE) | South Africa: Pietermaritzburg | Asteraceae | P. Caldwell | — | DQ185081, DQ185093, DQ185105, DQ185117, DQ185129 |
| Zea mays | CBS 13617; CPC 11998 | South Africa: Pietermaritzburg | Poaceae | P. Caldwell | — | DQ185082, DQ185094, DQ185106, DQ185118, DQ185130 |
| Zinnia elegans | CBS 13324; CPC 14549 | South Korea: Yangpyeong | Asteraceae | H.D. Shin | — | JX143756, JX143518, JX143272, JX143026, JX142780 |
| — | CBS 132676; CPC 15075 | Brazil: Valverde | — | A.C. Alfenas | — | JX143757, JX143519, JX143273, JX143027, JX142781 |
| Zinnia elegans | MUCC 131 | Japan: Shizuoka | Asteraceae | J. Nishikawa | — | JX143758, JX143520, JX143274, JX143028, JX142782 |
| Zinnia elegans | MUCC 572; MUCNS 215; MAFF 237718 | Japan: Chiba | Asteraceae | S. Uematsu | — | JX143759, JX143521, JX143275, JX143029, JX142783 |
| Eucalyptus sp. | CBS 118910; CPC 12226 | France | Myrtaceae | P.W. Crous | — | DQ303096, JX143522, JX143276, JX143030, JX142784 |

1 CBS: CBS-KNAW Fungal Biodiversity Centre, Utrecht, The Netherlands; CPC: Culture collection of Pedro Crous, housed at CBS; IHEM: Collection of the Laboratorium voor Microbiologie en Microbiële Genetica, Rijksuniversiteit, Ledeganckstraat 35, B-9000, Gent, Belgium; IMI: International Mycological Institute, CABI-Bioscience, Egham, Bakeham Lane, U.K.; Lynfield: Private culture collection and herbarium of Frank Hill, New Zealand; MAFF: Ministry of Agriculture, Forestry and Fisheries, Tsukuba, Ibaraki, Japan; MUCC: Culture Collection, Laboratory of Plant Pathology, Mie University, Tsu, Mie Prefecture, Japan; MUGL: 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; PPRRI: Plant Protection Research Institute, Pretoria, South Africa; WAC: Department of Agriculture Western Australia Plant Pathogen Collection, Perth, Australia.

2 ITS: internal transcribed spacers and intervening 5.8S nrDNA; TEF: translation elongation factor 1-alpha; ACT: actin; CAL: calmodulin; HIS: histone H3.
 cercosporin is not produced by all species (Assante et al. 1977, examples cited by Goodwin et al. 2001, see also review by Weiland et al. 2010). Nutritional and environmental conditions influence the production of cercosporin, making it useless for application in Cercospora taxonomy (Jenns et al. 1989). Genomic studies in recent years attempt to understand the metabolic pathway used to produce cercosporin and C. nicotiana has become the model organism for these studies (e.g. Chung et al. 2003, Choquer et al. 2005, Chen et al. 2007, Amnuaykanjanas & 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 isolation 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 plated 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 or recollected on diseased plant material, and grown in axenic culture. Symptoms 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 plated 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 rDNA 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 (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 CyIIH3F and CyIIH3R (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 procvncialis (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 every 1 000 generations and the resulting phylogenetic tree was printed with Geneious v. 5.5.4 (Drummond et al. 2011). New sequences generated in this study were deposited in NCBI’s GenBank nucleotide database (www.ncbi.nlm.nih.gov; Table 1) and the alignment and phylogenetic tree in TreeBASE (www.treebase.org).

Isolates of Cercospora sp. Q were screened with five more loci to test whether additional loci could distinguish cryptic taxa within this species. This species was selected based on the intraspecific variation present in Fig. 2 (part 5) and also the range of host species and countries represented. The primer set GDF1 and GDR1 (Guerry 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 chin synthesize (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, Mmc7-1348rev, Mmc7-1447rev (Schmitt et al. 2009) and part of the beta-tubulin gene using mainly the primers T1, Bi2b and TUB3Rd (Table 2 for references).
| Name Sequence (5' – 3') | Orientation | %GC | Tm (°C) | Start | End | Reference |
|-------------------------|-------------|------|---------|-------|-----|-----------|
| 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 GCT GCB GTG GTY ATY GAC ATG GG | Forward | 57.2 | 45.7 - 50.6 - 54.7 | 16 | 38 | This study, see also Aveskamp et al. (2009) |
| ACT1Rd CRT CGT ACT CCT GCT TGB AGA TCA AC | Reverse | 54.5 | 48.3 - 50.3 - 51.8 | 1537 | 1562 | This study |
| ACT2Fd GTA TCG TBC TGB ACT CGY GTG AVG GTG | Forward | 56.8 | 48.1 - 52.2 - 55.4 | 854 | 880 | This study |
| ACT2Rd ACH TCR CCG CRR GCC ATG TC | Reverse | 61.7 | 51.5 - 50.9 - 58.1 | 940 | 956 | This study, see also Quaedvlieg et al. (2011) |

**Beta-tubulin (Gibberella zeae GenBank accession FJ214662)**

| Name Sequence (5' – 3') | Orientation | %GC | Tm (°C) | Start | End | Reference |
|-------------------------|-------------|------|---------|-------|-----|-----------|
| Bt1a TTC CCC CTC CTC TTC TCC ATG | Forward | 54.2 | 50.1 | 1091 | 1114 | Glass & Donaldson (1995) |
| Bt1b GAC GAG ATC CAT GTT GAA CAC TCT | Reverse | 45.8 | 45.1 | 1603 | 1626 | Glass & Donaldson (1995) |
| Bt2a GGT AAC CAA ATC GGT GCT GCT TTC | Forward | 50.0 | 48.2 | 163 | 186 | Glass & Donaldson (1995) |
| Bt2b ACC CTC AGT GTA GTG ACC CTT CGC | Reverse | 58.0 | 52.1 | 617 | 640 | Glass & Donaldson (1995) |

**Calmodulin (Colletotrichum gloeosporioides GenBank accession HM573633)**

| Name Sequence (5' – 3') | Orientation | %GC | Tm (°C) | Start | End | Reference |
|-------------------------|-------------|------|---------|-------|-----|-----------|
| 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 G | Reverse | 50.0 | 43.4 | 439 | 458 | Carbone & Kohn (1999) |
| CAL1Rd GCA TCA TRA GYT RGA CRA ACT GTG | Reverse | 47.8 | 41.0 - 45.4 - 49.7 | 747 | 769 | This study |
| CAL2Rd TCA CCA GTG TAC CAA TGM ARG AAA GCC | Reverse | 48.1 | 48.3 - 50.1 - 52.0 | 1545 | 1565 | This study |
| CAL3F CAL3R GGC TGG TRA CAC GGY AAC GCC | Reverse | 50.8 | 42.6 - 45.0 - 50.5 | 170 | 189 | This study |
| H3-1a ACT AAG CAG ACC GCC CGC AGG | Forward | 66.7 | 54.2 | 10 | 30 | Glass & Donaldson (1995) |
| HIS1Rd RCG RAG RCG ACG GCC | Reverse | 76.7 | 45.4 - 50.0 - 54.6 | 382 | 396 | This study |

**ITS (Magnaporthe grisea GenBank accession AB026819)**

| Name Sequence (5' – 3') | Orientation | %GC | Tm (°C) | Start | End | Reference |
|-------------------------|-------------|------|---------|-------|-----|-----------|
| ITS1 TCC GTA GGA AAC CTT CGG G | Forward | 63.3 | 49.2 | 2162 | 2180 | White et al. (1990) |
| ITS4 TCC TCC GCT TAT TGA TAT GC | Reverse | 45.0 | 41.6 | 2685 | 2704 | White et al. (1990) |
| ITS5 GGA AGT AAA AGT GCG ACG AAG | Forward | 40.9 | 40.8 | 2138 | 2159 | White et al. (1990) |
| ITS7A TTA GTG CTC TGC CCT TTG TA | Forward | 45.0 | 42.8 | 2002 | 2021 | de Hoog & Gerrits van den Ende (1998) |

**Translation elongation factor 1-alpha (Sordaria macrospora GenBank accession X96615)**

| Name Sequence (5' – 3') | Orientation | %GC | Tm (°C) | Start | End | Reference |
|-------------------------|-------------|------|---------|-------|-----|-----------|
| CyEF-R2 CAT GTT CTT GAT GAA RTC ACG | Reverse | 40.5 | 39.2 - 40.2 - 41.1 | 783 | 803 | Carbone et al. (2004c) |
| EF-1 ATG GGT AAG GAR GAC AAG AC | Forward | 47.5 | 41.2 - 42.3 - 43.4 | 190 | 209 | O'Donnell et al. (1998) |
| EF-2 GGA RGT ACC AGT SAT CAT GTT | Reverse | 45.2 | 41.6 - 42.6 - 43.7 | 798 | 818 | O'Donnell et al. (1998) |
| EF-22 AGG AAC CAC TAC CGA GCT C | Reverse | 57.9 | 46.2 | 578 | 596 | O'Donnell et al. (1998) |
| EF1-1567R ACH GTR CCA CTA CCA CCR ATC TT | Reverse | 47.1 | 43.1 - 47.2 - 52.0 | 1254 | 1276 | Designed by S. Rehner (www.afbol.org/pdfs/EF1primer.pdf) |
Table 2. (Continued).

| Name | Sequence (5' – 3') | Orientation | %GC | Tm (°C) | Start | End | Reference |
|------|--------------------|-------------|------|---------|-------|-----|-----------|
| EF1-2218R | ATG ACA CCR ACR ACR 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 TGG 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 TTY 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 CTG GTC RAT ACC ACC | Reverse | 57.1 | 45.5 - 47.5 - 49.6 | 286 | 306 | This study |
| EF4Fd | GGT GCA TTG CSA CGG ACT TGA C | Forward | 56.8 | 48.2 - 49.1 - 49.9 | 1356 | 1377 | This study |

Taxonomy

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

RESULTS

DNA phylogeny

Amplification products and gene sequences of similar size to that reported previously (Groenewald et al. 2005, 2010a) were obtained. The resulting concatenated alignment contains 361 taxa (including the outgroup taxon), and 471, 263, 199, 240 and 347 characters (including alignment gaps) were used in the ITS, TEF, ACT, CAL and HIS partitions, respectively. Based on the results of MrModeltest, the following priors were set in MrBayes for the different partitions: all partitions had dirichlet base frequencies and distributed rates. The final aligned combined data set 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. flagellariis 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. rodmani, 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 2). Although the locus was able to separate C. beticola and C. apii, it could not distinguish C. cf. brunkii and C. cf. resedae from C. apii. The HIS region distinguished 46 of the 73 species clades and especially failed for Cercospora sp. G–I (Fig. 2 part 1) and Cercospora sp. M, P and Q (including C. kikuchii, C. cf. richardiicola and C. rodmani; 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 shared between multiple species were observed. If data for ITS is not
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. 3.2.6. 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)

| Strain Code | Species/Type | Country |
|-------------|--------------|---------|
| CPC 113127  | *Eichhornia crassipes* | USA     |
| CPC 10079   | *Trachelium* sp. | Israel  |
| CPC 10684   | *Phytolacca americana* | South Korea |
| CPC 14723   | *Phytolacca americana* | South Korea |
| CPC 10124   | *Phytolacca americana* | South Korea |
| CPC 5055    | *Bromus* sp. |          |
| MUCC 127    | *Cosmos sulphureus* | Japan |
| CPC 10722   | *Amaranthus patulus* | South Korea |
| CPC 14487   | *Sigesbeckia pubescens* | South Korea |
| MUCC 831    | *Hydrangea serrata* | Japan |
| CPC 1051    | *Populus deltoides* | South Africa |
| CPC 1052    | *Populus deltoides* | South Africa |
| MUCC 574    | *Capsicum annuum* | Japan |
| CPC 12307   | *Capsicum annuum* | South Korea |
| CPC 14520   | *Capsicum annuum* | South Korea |
| CBS 118712  | *Eichhornia crassipes* | Fiji Islands |
| CPC 5082    | *Coronilla varia* | Romania |
| CPC 5056    | *Erysimum cuspidatum* | Romania |
| CPC 5090    | *Berteroa incana* | Romania |
| CPC 5060    | *Cardaria draba* | Romania |
| CPC 5061    | *Cardaria draba* | Romania |
| CPC 5261    | *Nasturtium officinale* | New Zealand |
| CPC 11530   | *Acacia mangium* | Thailand |
| CPC 11338   | *Turritis glabra* | South Korea |
| CPC 11364   | *Turritis glabra* | South Korea |
| CPC 10100   | *Barbarea orthoceras* | South Korea |
| CPC 5088    | *Armoracia rusticana* | Romania |
| CPC 10811   | *Armoracia rusticana* | South Korea |
| MUCC 768    | *Armoracia rusticana* | Japan |
| CPC 14612   | *Rorippa indica* | South Korea |
| CPC 10133   | *Rorippa indica* | South Korea |
| CPC 5359    | *Armoracia rusticana* | New Zealand |
| CPC 5366    | *Gauro* sp. | New Zealand |
| CPC 5439    | *Rumex* sanguineus | New Zealand |
| CPC 5114    | *Crepis capillaris* | New Zealand |
| CPC 10790   | *Althaea rosea* | South Korea |
| CPC 5066    | *Malva* sp. |          |
| CPC 5117    | *Althaea rosea* | Romania |
| CPC 3955    | *Trachelium pratense* | Canada |
| CBS 118789  | *Trachelium subterraneum* | Australia |
| CBS 118790  | *Trachelium subterraneum* | Australia |
| CPC 10901   | *Hebe* sp. | New Zealand |
| CBS 118791  | *Trachelium cernuum* | Australia |
| CPC 5118    | *Hedysarum coronarium* | Italy |
| CPC 5437    | *Lotus pedunculatus* | New Zealand |
| CPC 5473    | *Jacaaranda mimosa* | New Zealand |
| CPC 5089    | *Astragalus spruneri* | Romania |
| CPC 5091    | *Medicago arabica* |          |
| CPC 10756   | *Trachelium repens* | South Korea |
| CPC 5367    | *Trachelium repens* | New Zealand |
| CPC 5078    | *Trachelium subterraneum* | USA |
| CPC 3957    | *Trachelium repens* | Canada |
| CPC 3958    | *Trachelium repens* | Canada |
| MUCC 133    | *Viola* sp. | Japan |
| MUCC 136    | *Viola* sp. | Japan |
| CPC 5368    | *Viola odorata* | New Zealand |
| MUCC 129    | *Viola* sp. | Japan |
| CPC 5079    | *Viola tricolor* | Romania |

*Posterior probability values:*

- **1** = 1.000
- **2** = 0.950 to 0.999
- **3** = 0.900 to 0.949
- **4** = 0.800 to 0.899
- **5** = 0.700 to 0.799
- **6** = 0.500 to 0.699

- **0.8**
Fig. 2. (Part 4).
**Fig. 2.** (Part 5).

| CPC | Scientific Name | Country/Region |
|-----|----------------|----------------|
| CPC 11637 | Dioscorea rotundata | Papua New Guinea |
| CPC 11636 | Dioscorea esculenta | Papua New Guinea |
| CPC 11634 | Dioscorea rotundata | Papua New Guinea |
| CPC 15807 | Phaseolus vulgaris | Mexico |
| CPC 15850 | Taraxacum sp. | Mexico |
| CPC 15875 | Euphorbia sp. | Mexico |
| CPC 11539 | Acacia mangium | Thailand |
| CPC 11536 | Acacia mangium | Thailand |
| CPC 5329 | Cajanus cajan | South Africa |
| CPC 5330 | Cajanus cajan | South Africa |
| CPC 5333 | Cajanus cajan | South Africa |
| CPC 5332 | Cajanus cajan | South Africa |
| CPC 5325 | Cajanus cajan | South Africa |
| CPC 5331 | Cajanus cajan | South Africa |
| CPC 15844 | Euphorbia sp. | Mexico |
| CPC 11639 | Dioscorea rotundata | Papua New Guinea |
| CPC 10551 | Acacia mangium | Thailand |
| CPC 10831 | Polygonatum humile | South Korea |
| CPC 10773 | Disporum viridescens | South Korea |
| CPC 10656 | Crepidastrum denticulatum | South Korea |
| CPC 10082 | Ixeris chinensis subsp. strigosa | South Korea |
| CPC 10728 | Ixeris chinensis subsp. strigosa | South Korea |
| MUCC 570 | Lactuca sativa | Japan |
| MUCC 571 | Lactuca sativa | Japan |
| MUCC 716 | Helianthus tuberosus | Japan |
| MUCC 588 | Ipomoea pes-caprae | Japan |
| CPC 12682 | Musa sp. | Bangladesh |
| CPC 12683 | Musa sp. | Bangladesh |
| MUCC 584 | Psophocarpus tetragonolobus | Japan |
| MUCC 576 | Citrullus lanatus | Japan |
| MUCC 577 | Momordica charantia | Japan |
| CPC 15918 | Glycine max | Mexico |
| CPC 5075 | Nicotiana tabacum | Nigeria |
| CPC 5076 | Nicotiana tabacum | Indonesia |
| CPC 11598 | Geranium thunbergii | South Korea |
| MUCC 732 | Datura stramonium | Japan |
| CBS 118793 | Reseda odorata | New Zealand |
| CPC 5057 | Helianthemum sp. | Romania |
| CPC 5083 | Plumbago europaea | Romania |
| CPC 5087 | Apium graveolens | Romania |
| CPC 5063 | Beta vulgaris | Netherlands |
| CPC 5119 | Beta vulgaris | Hungary |
| CPC 5073 | Beta vulgaris | Austria |
| MUCC 923 | Asparagus officinalis | Japan |

**Posterior probability values:**

- 1.000 = 1.000
- 0.950 to 0.999
- 0.900 to 0.949
- 0.800 to 0.899
- 0.700 to 0.799
- 0.500 to 0.699

Cercospora sp. P

Cercospora sp. Q

Cercospora sp. R

Cercospora sp. S

C. chinensis

C. dispersi

C. corchori

C. helianthicola

C. citrulina

C. cf. brunkii

C. cf. resedae

C. apii
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 glycerolaldehyde-3-phosphate dehydrogenase gene; mtSSU: partial mitochondrial small rRNA gene; CHS: partial chitin synthase gene; TUB: partial beta-tubulin gene; Mcm7: partial gene encoding a mini-chromosome maintenance protein.

| Original name | Culture accession number(s) | Host name | Percentage similarity and allele group (I-VI) designation per locus | GenBank accession numbers |
|---------------|-----------------------------|-----------|-------------------------------------------------------------------|--------------------------|
| Cercospora apii | CBS 113997; CPC 5325 | Cajanus cajan | GAPDH 979 nt I, mtSSU 573 nt I, CHS 299 nt I, TUB 597 nt I, Mcm7 501 nt I | JX142521, JX142504, JX142467, JX142478, JX142473 |
| Cercospora apii | CBS 115410; CPC 5331 | Cajanus cajan | GAPDH 966 nt (100 %) I, mtSSU 573 nt (100 %) I, CHS 299 nt (100 %) I, TUB 597 nt (99 %) I, Mcm7 — | JX142522, JX142505, JX142468, JX142479, — |
| Cercospora apii | CBS 115411; CPC 5332 | Cajanus cajan | GAPDH 966 nt (100 %) I, mtSSU 573 nt (100 %) I, CHS 299 nt (100 %) I, TUB 597 nt (99 %) I, Mcm7 — | JX142523, JX142506, JX142469, JX142480, — |
| Cercospora apii | CBS 115412; CPC 5333 | Cajanus cajan | GAPDH 970 nt (95 %) V, mtSSU 573 nt (100 %) I, CHS 299 nt (99 %) II, TUB 597 nt (99 %) II, Mcm7 — | JX142524, JX142507, JX142490, JX142481, — |
| Cercospora sp. 2 | CPC 10551 | Acacia mangium | GAPDH 979 nt (99 %) I, mtSSU 573 nt (100 %) I, CHS 299 nt (99 %) I, TUB —, Mcm7 501 nt (99 %) II | JX142525, JX142516, JX142499, JX142484, JX142475 |
| Cercospora dioscoreae-pyrifoliae | CBS 132661; CPC 11634; PNG-002 | Dioscorea rotundata | GAPDH 970 nt (95 %) VI, mtSSU 573 nt (100 %) I, CHS 298 nt (99 %) II, TUB 458 nt (99 %) III, Mcm7 — | JX142528, JX142511, JX142494, —, JX142474 |
| Cercospora dioscoreae-pyrifoliae CPC 11639; PNG-037 | Dioscorea esculenta | 969 nt (96 %) I, mtSSU 573 nt (100 %) I, CHS 299 nt (99 %) I | JX142529, JX142512, JX142495, —, JX142476 |
| Cercospora dioscoreae-pyrifoliae CPC 11633; CPC 5329 | Dioscorea rotundata | 969 nt (96 %) I, mtSSU 573 nt (100 %) I, CHS 299 nt (99 %) I | JX142526, JX142509, JX142492, JX142483, — |
| Cercospora dioscoreae-pyrifoliae CPC 15807 | Phaseolus vulgaris | 954 nt (100 %) I, mtSSU 573 nt (100 %) I, CHS 299 nt (99 %) I | JX142530, JX142513, JX142496, —, JX142489 |
| Cercospora sp. 2 CPC 15844 | Euphorbia sp. | 956 nt (96 %) I, mtSSU 573 nt (100 %) I, CHS 299 nt (99 %) I | JX142531, JX142514, JX142497, —, JX142489 |
| Cercospora sp. CPC 15850 | Taraxacum sp. | 960 nt (100 %) I, mtSSU 573 nt (100 %) I, CHS 299 nt (99 %) II | JX142532, JX142515, JX142498, —, JX142489 |
| Cercospora sp. CPC 15875 | Euphorbia sp. | 955 nt (99 %) II, mtSSU 573 nt (100 %) I, CHS 299 nt (99 %) III | JX142533, JX142517, JX142500, —, JX142476 |
| Septoria provencialis (outgroup) CBS 118910; CPC 12226 | Eucalyptus sp. | 885 nt (57 %) — | JX142534, JX142517, JX142500, —, JX142476 |

Number of identical sequences (excl. outgroup): 6 of 17 17 of 17 4 of 17 0 of 8 0 of 4
| Original name          | Culture accession number(s) | Host name      | Percentage similarity and allele group (I-VI) designation per locus | GenBank accession numbers |
|------------------------|----------------------------|----------------|-----------------------------------------------------------------------|---------------------------|
|                        |                            |                | ITS         TEF     ACT     CAL     HIS                                      | (ITS, TEF, ACT, CAL, HIS) |
| **Cercospora apii**    | CBS 113997; CPC 5325       | Cajanus cajan  | 481 nt     306 nt  221 nt  312 nt  378 nt                                 | JX143717, JX143476, JX143230, JX142984, JX142738 |
|                        | CBS 115410; CPC 5331       | Cajanus cajan  | 481 nt (100 %) 280 nt (100 %) 194 nt (100 %) 280 nt (100 %) 378 nt (100 %) | JX143718, JX143477, JX143231, JX142985, JX142739 |
|                        | CBS 115411; CPC 5332       | Cajanus cajan  | 481 nt (100 %) 280 nt (100 %) 194 nt (100 %) 280 nt (100 %) 378 nt (100 %) | JX143719, JX143478, JX143232, JX142986, JX142740 |
|                        | CBS 115412; CPC 5333       | Cajanus cajan  | 481 nt (100 %) 280 nt (100 %) 194 nt (100 %) 280 nt (100 %) 378 nt (100 %) | JX143720, JX143479, JX143233, JX142987, JX142741 |
|                        | CBS 115536; CPC 5330       | Cajanus cajan  | 481 nt (100 %) 280 nt (100 %) 194 nt (100 %) 280 nt (100 %) 378 nt (100 %) | JX143721, JX143480, JX143234, JX142988, JX142742 |
| Cercospora acaciae-mangii | CPC 10550 | Acacia mangium | 481 nt (99 %) II 306 nt (100 %) I 221 nt (99 %) II 312 nt (100 %) I 377 nt (99 %) IV | AY752139, AY752172, AY752200, AY752231, AY752262 |
| Cercospora acaciae-mangii | CPC 10551 | Acacia mangium | 481 nt (99 %) II 306 nt (100 %) I 221 nt (99 %) IV 305 nt (100 %) I 377 nt (100 %) I | AY752140, AY752173, AY752201, AY752232, AY752263 |
| Cercospora sp. 2       | CBS 132656; CPC 11536     | Acacia mangium | 473 nt (99 %) III 306 nt (100 %) I 221 nt (99 %) IV 312 nt (100 %) I 378 nt (99 %) IV | JX143723, JX143482, JX143236, JX142990, JX142744 |
| Cercospora sp. 2       | CPC 11539                | Acacia mangium | 481 nt (99 %) III 306 nt (100 %) I 221 nt (99 %) IV 312 nt (100 %) I 378 nt (99 %) IV | JX143729, JX143488, JX143242, JX142996, JX142750 |
| Cercospora dioscoreae-pyrifoliae | CBS 132661; CPC 11634; PNG-002 | Dioscorea rotundata | 481 nt (99 %) III 284 nt (100 %) I 221 nt (99 %) II 297 nt (100 %) I 378 nt (99 %) VI | JX143724, JX143483, JX143237, JX142991, JX142745 |
| Cercospora dioscoreae-pyrifoliae | CBS 132663; CPC 11636; PNG-016 | Dioscorea esculenta | 481 nt (99 %) III 306 nt (100 %) I 221 nt (99 %) II 303 nt (100 %) I 378 nt (99 %) VI | JX143725, JX143484, JX143238, JX142992, JX142746 |
| Cercospora dioscoreae-pyrifoliae | CPC 11639; PNG-037 | Dioscorea rotundata | 481 nt (99 %) III 306 nt (100 %) I 221 nt (99 %) II 303 nt (100 %) I 378 nt (99 %) II | JX143730, JX143489, JX143243, JX142997, JX142751 |
| Cercosporoid           | CBS 132679; CPC 15807     | Phaseolus vulgaris | 481 nt (99 %) II 294 nt (99 %) II 220 nt (99 %) II 220 nt (99 %) I 376 nt (99 %) VI | JX143726, JX143485, JX143239, JX142993, JX142747 |
| Cercospora sp.         | CBS 132681; CPC 15844     | Euphorbia sp.  | 481 nt (99 %) III 294 nt (99 %) II 220 nt (99 %) II 312 nt (99 %) II 376 nt (100 %) I | JX143727, JX143486, JX143240, JX142994, JX142748 |
| Cercospora sp.         | CBS 132682; CPC 15850     | Taraxacum sp.  | 481 nt (99 %) II 294 nt (99 %) II 220 nt (99 %) II 312 nt (100 %) I 377 nt (100 %) VI | JX143728, JX143487, JX143241, JX142995, JX142749 |
| Cercospora sp.         | CPC 15875                | Euphorbia sp.  | 481 nt (99 %) III 294 nt (99 %) II 220 nt (99 %) II 312 nt (100 %) I 378 nt (99 %) VI | JX143731, JX143490, JX143244, JX142998, JX142752 |
| Septoria provencialis  | CBS 118910; CPC 12226    | Eucalyptus sp.  | 483 nt (98 %) III 317 nt (75 %) II 227 nt (67 %) 329 nt (81 %) 386 nt (93 %) | DQ930306, 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 5325). Although allele group I was confined to isolates from CPC 5325). Although allele group I was confined to isolates from Cajanus and allele group IV is limited to Dioscorea, the remaining host genera belong to allele group III.

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). This single nucleotide change only occurred in isolate CPC 15844; the rest of the isolates had identical CAL sequences.

CHS — 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 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
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

Fig. 3. Overview of morphological structures. A. Fasciculate conidiophores situated on a stroma. B. Conidiophores reduced to uni-local conidiogenous cells. C. Conidiophores arising from a weakly developed stroma. D. Fasciculate conidiophore with flexuous conidiophores. E. Conidiophores arising from external mycelium. F. Thickened, darkened and somewhat refractive conidial loci (arrows). G. Conidiogenous cells with multi-local loci. H. Fascicle erumpent through stoma. I. Cylindrical conidium with obtuse apex. J. Filiform conidium. K, L. Acicular, undulate conidia with subobtusely rounded apices, and truncate bases. M–O. Obclavate conidia with subobtusely rounded apices and obconically truncate bases. P. Subcylindrical conidium with long obconically truncate base.
internal hyphae or a few brown cells, solitary, or in loose fascicles (2–5), straight, sinuous to distinctly geniculate, flexuous, almost uniform in width, somewhat wider at the apex, often constricted at septa and proliferating point, conical at the apex, simple, sometimes branched, 31–340 × 4.5–6 µm, 2–20-septate. Conidiogenous cells integrated, terminal and intercalary, proliferating sympodially, multi-local; loci distinctly thickened, darkened, slightly to distinctly protuberant, apical or formed on shoulders caused by geniculation, 2–3 µm diam. Conidia solitary, subhyaline, acicular, cylindrical to cylindro-obclavate, straight to slightly curved, long obconically truncate and thickened at the base, obtuse at the apex, rarely constricted at the septa, 33–172 × 3.5–8 µm, 3–20-septate.

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

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

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

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

Notes: *Cercospora agavicola* is characterised by large stromata and consistently cylindrical conidia, often with swollen tips (Ayala-Escobar et al. 2005). In this study using a larger dataset, it is also a sister taxon to *C. cf. physalidis* and *C. cf. physalidis* based on the ACT phylogeny. A similar mix is observed in the HIS phylogeny with *Cercospora* sp. I and *C. cf. physalidis* and in the CAL phylogeny with *Cercospora* spp. M, O, P and *C. cf. sipesbeckiae*. In the combined tree (Fig. 2 part 4), the three isolates represent sister taxa.

*Cercospora cf. alchemillilicola*

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. alchemillilicola* (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. alchemillilicola*. 

*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* amphiogenous, mostly epiphyllous. **Mycelium** internal. **Stromata** well-developed, emerging through stomatal openings or erumpent through the cuticle. **Conidiophores** in divergent fascicles (6–12), pale olivaceous-brown at the base, paler upwards, 0–3-septate, straight to mildly curved, 32–90 × 4.6–5.5 µm, conically narrowed at the apex; loci 1.5–2 µm wide, conspicuous, apical or on shoulders formed by geniculation. **Conidia** solitary, obclavate-cylindrical to filiform, not acicular, straight to mildly curved, hyaline, 1–10-septate, obtuse at the apex, subtruncate or obconically truncate at the base, 40–140 × 3.5–5 µm (adapted from Shin & Kim 2001).

*Cercospora alchearnea* 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 964, 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. *alchearnea* are also morphologically different from *C. alchemillilicola* 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 and Q and *C. cf. sipesbeckiae*. In the combined tree (Fig. 2 part 4), the three isolates represent sister taxa.

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

*Caespituli* amphiogenous. *Myceillum* internal. *Stromata* lacking or small, up to 32 µm diam, brown, subostomal 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 symiodial proliferation, slightly curved, uniform in width, wider at the base, short conically truncate or truncate at the apex, 12.5–160 × 5–8 µm. *Conidigenous cells* integrated, terminal or intercalary, proliferating symiodially, chiefly uni-local; loci distinctly thickened, not or slightly protuberant, 2–4 µm diam, apical or formed on the shoulder caused by symiodial proliferation. *Conidia* solitary, hyaline, cylindro-oblackate when shorter, longer conidia usually acicular, straight to slightly curved, subacute to obtuse at the apex, truncate to obconically truncate and thickened at the base, 35–120 × 3.5–5 µm, 3–10-septate.

*Specimens examined*. **Austria**, Wien, on *Beta vulgaris* (Chenopodiaceae), Jun. 1931, E.W. Schmidt, CBS 121.31 = CPC 5073; on *Apium sp.* (Apiaceae), 28 Aug. 2003, Institut fur Pflanzensundheit, CBS 114416 = CPC 10923. **Germany**, Landwirtschaftsamt, Heilbron, on *Apium graveolens* (Apiaceae), K. Schrameyer, culture ex-type CBS 116455 = CPC 11565; 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, MUC 567 = MAFF 238072 = MUCNS 30 (named as *C. api s. str.*); Shizuoka, on *A. graveolens*, 8 Jun. 2007, M. Togawa, MUMH 10802, MUC 503; Saga, on *Asparagus oﬃnalis* (Asparagaceae), 20 Sep. 1999, J. Yamaguchi, MUMH 11400, MUC 923 = MAFB 238299; Hokkaido, on *Glebionis coronaria* (≡ *Zinnia elegans*), Aug. 1989, MUC 573 = MAFB 235978. **Netherlands**, Bergen op Zoom, on *B. vulgaris*, Sep. 1951, G. van den Ende, CBS 152.52 = IMI 070703 = MUC 16495 = CPC 5063. **New Zealand**, Auckland, on *Glebionis coronaria* (≡ *Zinnia elegans*), C.F. Hilt, Lyntield 566, CPC 5260. **Romania**, Constanța, CBS 553.71 = IMI 161116 = CPC 5053 (as *C. plumaginea*); București, on *A. graveolens*, 2 Oct. 1969, O. Constantinescu, CBS 9812 = CPC 5084. **South Africa**, Durban, on *Plantago lanceolata* (Plantaginaceae), 21 Nov. 2005, M. Schramm, CBS 125.21 = CPC 5079. **United States of America**, California, on *M. resedae*, 20 Oct. 1970, J.J. Ito, CBS 116229 = CPC 5067; **U.S.A.**, USA, California, on *M. resedae*, S.T. Koike, CBS 110816 = CPC 5084. **Zimbabwe**, on *M. resedae*, 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 api s. lat.*, for taxa morphologically indistinguishable from *Cercospora api* on *A. graveolens*. *Cercospora api 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-oblackate 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. api s. str.* are found in more than 86 genera of several plant families. Groenewald et al. (2006a) concluded that *C. api s. str.*, which is mainly isolated from celery, has a wide host range, because numerous isolates of *C. api s. lat.* originating from various host plants have similar nucleotide sequences to the type strain of *C. api s. str.*.

In principle, the phylogenetic split observed between *C. beticola* and *C. api* 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. api s. str.* from *C. cf. brunkii* and *C. cf. resedae*, which are sister taxa in the combined tree (Fig. 2 part 5).

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

*Leaf spots* amphiogenous, 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* amphiogenous, but primarily hypophyllous. *Stromata* lacking to well-developed, 30–60 µm diam, brown. *Conidiophores* in fascicles (4–10), moderately dense, arising from stromata, emerging through stoma 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 unilocular, usually multilocular, 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 × (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. Vloutigouli, CBS 132666 = CPC 11642; **South Korea**, on *A. graveolens*, 20 Sep. 2003, H.D. Shin, CBS 10646; Namyangju, on *A. graveolens*, 30 Sep. 2003, CBS 116459 = 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 *A. graveolens*, 23 Jul. 2002, N. Pons, holotype CBS H-18473, culture ex-type CBS 116457 = CPC 10267; CBS 132664 = CPC 10248; CPC 10220; CPC 10265–10266; CPC 10279; CPC 10666.

**Notes**: Morphologically *C. apicola* differs from *C. api 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. api s. lat.* supported by TEF, ACT, CAL and HIS regions. It is also clearly distinct from *C. api* 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 amphigenous. Mycelium internal. Stromata lacking to well-developed, up to 60 μm diam, brown, subostomal or intrapaeridial. Conidiophores arising from internal hyphae or a few brown cells, cylindrical, solitary, or in loose to divergent fascicles (2–30), pale to brown paler towards apex, moderately thick-walled, simple, straight to slightly 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-oblaccular to aciculate, 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, HBO, S), Japan. Okinawa, on A. rusticana (= A. lapathifolia), 19 Nov. 2007, C. Nakashima, MUMH 10820, MUCC 768. New Zealand, Auckland, Grey Lynn, on A. rusticana, MUCC 768. South Africa, northern Cape, on A. rusticana, 10 Jul. 2007, H. Dhauw

Notes: See also C. capsici. Cercospora armoricaceae is supported by the HIS phylogeny. In the TEF phylogeny it is a sister clade to C. zebrina, Cercospora sp. L. C. rumicis, C. violae and C. althaeina; in ACT the C. armoricaceae 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. armoricaceae 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 cilindro-oblaccular to aciculate.

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

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

Cercospora amphigenous. Mycelium internal. Stromata lacking to well-developed, up to 60 μm diam, subostomal or intrapaeridial. Conidiophores arising from internal hyphae or a few brown cells, cylindrical, solitary, or in loose to divergent fascicles (2–30), pale to brown paler towards apex, moderately thick-walled, simple, straight to slightly 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-oblaccular to aciculate, 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, HBO, S), Japan. Okinawa, on A. rusticana (= A. lapathifolia), 19 Nov. 2007, C. Nakashima, MUMH 10820, MUCC 768. New Zealand, Auckland, Grey Lynn, on A. rusticana, MUCC 768. South Africa, northern Cape, on A. rusticana, 10 Jul. 2007, H. Dhauw...
CBS 115478 = CPC 5113 (named as *C. statices*); on *B. vulgaris*, C.F. Hill, CPC 5128; Lyndfield 539, CPC 5125; CPC 10197; CPC 10204; CPC 10168; CBS 117556 = CPC 10171; CPC 10168; on *Apium graveolens*, C.F. Hill, CPC 5737a, CPC 5123. *Romania*, Brăuleni, on *B. vulgaris*, 17 Oct. 1966, O. Constantinescu, CBS 539.71 = CPC 5062; Hagener, on *Malva pusilla* (Malvaceae), 15 Jul. 1970, O. Constantinescu & G. Negrean, CBS H-9847, CBS H-9849, CBS 547.71 = 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, Pretorious 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 2003). These analyses failed to discriminate all species due to the limited resolution provided by the ITS locus.

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Results from the phylogenetic analyses using CAL and combined multi-locus data set divide *C. beticola* and *C. api 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. api 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 and sometimes abruptly geniculate, unbranched, 2–4–septate, 40–110 × 4.5–5.5 µm, 0–9-septate. *Conidiogenous cells* attenuated at the apex, short obconically truncate or truncate at the base, acute at the apex, 30–160 × 4.5–5.5 µm, pale brown to olivaceous-brown.

*Conidia*: 110 × 1.5–4 µm, indistinctly multi-septate, 0–9-septate. *Curved, thickened and truncate at the base, acute at the apex, 27–110 × 1.5–4 µm, indistinctly multi-septate, 0–9-septate.

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

**Notes:** Although *C. campi-sili* was transferred from *Cercospora* to *Passalora* based on its pale olivaceous conidia (Braun 1995b), as in the case of *C. sojina*, these taxa are best retained in *Cercospora*, which is fully supported by their phylogenetic position within *Cercospora*. *Cercospora campi-sili* is separated based on the TEF, ACT and HIS phylogeny in the present study. Only the CAL phylogeny failed to distinguish it from *C. sojina* and *C. achyranthis*. On the combined tree (Fig. 2 part 2), it is a sister taxon to *C. sojina*. *Cercospora campi-sili* 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 = GAHA-1-0 (as *C. dianthae-pyrifoliae*); CPC 11626 = GAHA-2-1; on leaves of Dioscorea alata 2000, S. Nyako & A.O. Danquah, CBS 132659 = CPC 11627 = GAHA-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; CPC 111134 = CPC 1138; Tspise, 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 *Aipomi 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 HIS phylogeny with *C. kikuchi*, *C. cf. richardicola* 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).
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. coreopsisid*. 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* amphiogenous, appearing greyish brown in case of abundant sporulation. *Myccelium* 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 truncate 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 fructing on lesions on calyx attached to fruit, 17 Aug, 2005, P. Tyler, CBS 115712. Japan, Chiba, on *Capsicum annuum* (Solanaceae), 1 Oct. 1999, S. Umemoto, 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 145220.

**Notes**: See also *C. armoracae*. 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. armoracae*) and HIS (related to *Cercospora* spp. C and D) phylogenies and is part of the larger *C. armoracae* clade based on CAL. In the combined tree (Fig. 2 part 3), it is a sister taxon to *C. armoracae*. Morphological characteristics of this species on the host plant and in culture are almost similar to *C. armoracae*. 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. physalisid* has been shown to form a species complex. Braun & Melnik (1997) concluded many species of *Cercospora apii s. lat.* on solanaceous hosts, including *C. capsici*, were synonymous with *C. physalisid* 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. physalisid* complex. Likewise, other taxa in this complex such as *C. lycii*, *C. nicandreae*, *C. sciadophila*, *C. solanacea*, and *C. solani*, which consistently have obclavate-cylindrical conidia, must be re-examined.

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

Leaf spots amphiogenous, 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* amphiogenous. *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, Chunchon, on *Celisia argentea* var. *cristata* (= *C. cristata*) (Amaranthaceae), 7 Oct. 2003, H.D. Shin, CBS H-20996, CBS 132600 = CPC 10660.

**Notes**: The isolates representing *C. celosiæ* 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. 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. celosiæ* should be merged with what is presently treated as *Cercospora* sp. I.

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

≡ *Ramularia dubia* Rubia, Hedwigia 1: pl. 4, fig. 9. 1854.
≡ *Cercospora dubia* (Riess) G. Winter, Fungi Eur. Exs., Ed. nov., Cent. 28, No. 2760. 1882 and Hedwigia 22: 10. 1883, nom. illeg., homonym of *C. dubia* Speg., 1880.
≡ *Cercospora dubia* (Riess) Bubak, Ann. Mycol. 6: 29. 1906, 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) Poornam 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. atropilos Bondartsev, Trudy Glavn. Bl. Sada 26: 51. 1910.
≡ *Cercospora atropilos* Lobik, Mat. po Fl. Faun. Obsled. Terskogo Okruga: 52. 1928.
≡ *Cercospora chenopodii* var. micromaculae Deam., Mycologia 21: 329. 1929.
≡ *Cercospora penicillata* f. *chenopodii* Fukiel, Fung. Rhen. Exs., Fasc. II, No. 119, 1863, nom. nud.
≡ *Cercospora chenopodii* var. atropilos Thüm., in herb.
≡ *Cercospora borerzervii* Henno., in herb. B.
Specimen examined: France, Ardeche, N 44º22’39.8” E 4º26’9.1”, on Chenopodium cf. album (Chenopodiaceae) next to river, 31 Aug. 2007, P.W. Crous, CBS H-20997, CBS 132620 = CPC 14237.

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

Cercospora cf. chenopodii Fig. 5.

Leaf spots amphigenous, subcircular, circular, 3–8 mm diam, greyish brown to pale brown. Mycelium internal, consisting of septate, branched, smooth, pale brown hyphae. Caespituli in fascicles (10–40), amphigenous, brown, dense, becoming divergent, up to 150 µm wide and 50 µm high. Conidiophores aggregated in dense fascicles arising from the upper cells of a moderately developed brown stroma; conidiophores olivaceous-brown to brown, 2–5-septate, 1–2 times geniculate in upper part, at times apically swollen, not branched, 60–135 × 4–7 µm. Conidiogenous cells terminal, unbranched, pale brown, smooth, tapering to flat-tipped apical loci, proliferating sympodially, 20–40 × 4–6 µm; loci thickened, darkened, refractive, 2–4 µm diam. Conidia solitary, smooth, cylindrical to obclavate, straight to slightly curved, hyaline, (0–)2–4–(5–)septate, apex obtuse, base obconically truncate, (25–)40–65(–80) × (5–)6–7.5(–9) µm; hila thickened, darkened, refractive, 2–3 µm diam.

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

Specimens examined: Mexico, Montecillo, Chenopodium sp. (Chenopodiaceae), 9 Oct. 2008, Ma. de Jesús Yáñez-Morales, CBS 132677 = CPC 15599; CPC 15763; Purificacion, Chenopodium sp., 12 Oct. 2008, Ma. de Jesús Yáñez-Morales, CPC 15859; CPC 15862. South Korea, Hongcheon, on Chenopodium ficifolium (Chenopodiaceae), 4 Oct. 2002, H.D. Shin, CBS H-20998, culture CBS 132594 = CPC 10304; Hongcheon, on C. ficifolium, 27 Oct. 2005, H.D. Shin, CBS H-20999, CPC 12459.

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

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

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

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

**Cercospora cf. citrulina**

*Caepticul*i 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 *Citrus lanatus* (*Cucurbitaceae*), 6 Mar. 1998, T. Kobayashion et al., MUMH 11402, MUCC 576 = MUCNS 300 = MAFF 237913 (as *C. citrullina*); *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...
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 verrucose 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
**Cercospora delaireae**

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

Leaves spots: amphigenous, subcircular to angular, grey-brown to brown, 3–7 μm diam, surrounded by a large, brown border, 7–17 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 unicellular, 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 mikanioiodes*) (Asteraceae), C.L. Lennox, CPC 10627–10629; Mpumalanga, Long Tom Pass, on *D. odorata* (= *Senecio mikanioiodes*), 16 Jun. 2003, S. Nesper, *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 *Cercospora coreopsidis*. In the combined tree (Fig. 2 part 2), it is a sister taxon to *C. beticola*, which has also been known from *Bidens* (Asteraceae), was also reported from *Coreopsis* (Asteraceae) (Thueng 1984). Morphological differences between these species were not observed. The identification of the Korean collections as *C. cf. coreopsidis* is only tentative and must be proven on the base of sequences derived from North American isolates, which are not yet available.

**Cercospora coreopsidis**

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

Specimens 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) (Thueng 1984). Morphological differences between these species were not observed. The identification of the Korean collections as *C. cf. coreopsidis* is only tentative and must be proven on the base of sequences derived from North American isolates, which are not yet available.

**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) (Thueng 1984). Morphological differences between these species were not observed. The identification of the Korean collections as *C. cf. coreopsidis* is only tentative and must be proven on the base of sequences derived from North American isolates, which are not yet available.

**Cercospora coreopsidis**

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

Specimens examined: **Japan**, Shimane, on Coreuchos olitorius (Tiliaceae), 27 Aug. 1997, T. Mikami (*epitype designated here – TFM:FPH-8114*), culture ex-*epitype* MUC 585 = MAFF 238191. *Cercospora coreopsidis* 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.

**Notes**: *Cercospora korinchii*, 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* spp. K and *C. lactuceae-sativae*. In the combined tree (Fig. 2 part 5), it is a sister taxon to *Cercospora* spp. R and S.
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 phylogenoy, the two species are indistinguishable and 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-sieboldiana 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, coalasencing, 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

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

Culture characteristics: Colonies erumpent, spreading, with sparse aerial mycelium and smooth, even margins, reaching 30 mm diam after 2 wk at 25 °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-walkeri (ACT), C. vignigena (CAL) and C. punctiformis (HIS); therefore it is distinct from the other species occurring on Euphorbiaceae included in this study. In the combined tree (Fig. 2 part 2), it is a sister taxon to C. punctiformis. It is morphologically well distinguished from species of the C. api complex and other species of Cercospora by its unusually broadly obclavate-cylindrical conidia (5.5–8(–12) μm) with few septa and rather broad loci and hila (3–4.5 μm).

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

Caespituli caulogenous, or amphigenous on leaves. Mycelium internal. Stromata intraepidermal or substomatal, pale brown, small to well-developed, 25–60 μm diam. Conidiophores pale brown, solitary, or in loose to dense fascicles (2–20), sinuously geniculate, rarely geniculate due to sympodial proliferation, usually irregular in width, frequently constricted due to proliferation.
attenuated at the tip, truncate at the apex, multi-septate, 20–120 × 3.5–5.5 μm, 0–5-septate. Conidiogenous cells integrated, mainly terminal, rarely intercalary, proliferating sympodially, multi-local; loci thickened and darkened, apical and formed on the shoulder caused by sympodial proliferation, sometimes lateral, sometimes protuberant, 1.5–2.5 μm. Conidia solitary, hyaline, cylindrical to acicular, straight or slightly curved, long obconically truncate or truncate at the thickened and darkened base, obtuse or acute at the apex, 20–100 × 3–4 μm, 3–20-septate, thin-walled, smooth.

Description of caespituli on V8; (MUC 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, MUC 130; on Hibiscus syriacus (Malvaceae), MUC 866. South Korea, Suwon, on Vioa manshurica (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 132626 = CPC 14541 (holotype) specimen, South Korea, Suwon, on Fag. esculentum, Sep. 1934, K. Nakata & S. Takimoto, could not be located and is undoubtly 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. flagellaris is supported by the TEF and HIS phylogenies, though it is intermittently mixed 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. flagellaris, isolates from Fagopyrum need to be re-collected in Korea, and pathogenicity established on the hosts listed above. Thus the name C. flagellaris can only be applied to other isolates than those from Fagopyrum tentatively, awaiting additional fresh collections.

Cercospora cf. flagellaris

Caespituli amphiogenous. 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; (MUC 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 apex, 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, Lyndfield 677, CPC 5441, Israel, on Trachellium sp. (Campnanulaceae), 16 Nov. 2002, E. Tzu-Abad, CBS 132637 = CPC 10079 (as C. campanulata), Japan, Ehime, on Cosmos sulphureus (Asteraceae), 16 Oct. 2004, J. Nishikawa, MUMH 11393, MUC 127; Tokyo, on Hydrangea serrata (Hydrangeaceae), 10 Nov. 2007, I. Araki & M. Harada, MUMH 10933, MUC 831, Wakayama, on H. serrata, 30 Oct. 2007. C. Nakashima & I. Araki, MUMH 10860, MUC 735, South Korea, Hoengseong, on Celastrus argenteus 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. ambrosioides); on Phytolacca americana (Phytolaccaeaceae), 1 Nov. 2007, H.D. Shin, CBS 132674 = CPC 14723; CPC 14724; Jinu, on A. campanulata, 15 Oct. 2003, H.D. Shin, CBS 10864–10866; Nanyangju, on Amaranthus patulus, 30 Sep. 2003, H.D. Shin, CBS 132648 = CPC 10722; Pocheon, on A. campanulata, 20 Feb. 2002, H.D. Shin, CPC 10124; Suwon, on Cichorium intybus (Asteraceae), 14 Oct. 2003, H.D. Shin, CBS 132646 + CPC 10681 (= C. cichorii); Yangyu, on Sigsbeckia pubescens (Asteraceae), 28 Sep. 2007, H.D. Shin, CBS 132670 = CPC 14847.

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, 10684 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. piaori. 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. piaori (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, 10–65 × 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. citrulina.

Cercospora cf. ipomeae

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 distinctly thickened, 2.5–2.5 µm diam, slightly protuberant, apical. 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, Chunchon, on Ipomoea nil (= I. nedericae) (Convolvulaceae), 7 Oct. 2003, H.D. Shin, CBS H-21010, CBS 132652 = CPC 10833; Pocheon, on Ipomoea, 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: 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. citrulina.

Cercospora kikuchii

(T. Matsumoto & Tomoy.) M.W. Gardner, Proc. Indian Acad. Sci. 36: 12. (1926) 1927. Basionym: Cercospora 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 305940; 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 Osteospernum (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. richardiicola and C. sigesbeckiae. Although these isolates clustered separate in the ACT phylogeny, intermixed in the clade was isolate CPC 14680 (C. 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. 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 Honn.
≡ 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 lactucae-Indicae 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, subacutte 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, MUCU 571 = MAFF 237719 = MUCNS 214; 18 Sep. 1998, C. Nakashima, MUMH 11401, MUCU 570 = MAFF 238209 = MUCN S463. South Korea, Chuncheon, on Ixeris chinensis subsp. strigosus (I. Ixeris strigosus) (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 (MUCU 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. heliantichola.

Cercospora cf. malloti

Caespituli amphiogenous. 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 shoulder of successive geniculation, 1–2 μm diam. Conidia, 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. Description of caespituli on V8: MUCU 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, MUCU 787; on Cucumis melo (Cucurbitaceae), 20 Jan. 1999, K. Uehara, MUCU 575 = MAFF 237872 = MUCNS 582 (as C. citrinula).

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 (MUCU 128, 132 and 578) and Cercospora sp. P (isolate MUCU 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 Roumeguer et al., Rev. Mycol. 15: 16. 1893.
= Cercospora mercurialis var. lativic Lepik, Tartu Ülik. Juures Oleva Loodusuur. Seltsi Arunded 39: 152. 1933.
= Cercospora mercurialis var. multisepta Sävull & 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 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. 1992, 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. flagellariis (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. brunii. Notes in the CBS database report that...
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. physalisid**

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. alchemilllicola* / *C. cf. alchemilllicola* 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. physalisid* 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, substomal. *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.
**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 & Mallick 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 synonymy 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. api*-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 plurigeneric. 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. rud.*  

*Caespituli* amphiogenous. *Myelium* 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 truncate 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.

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

Notes: Morphologically the Korean specimen is similar to *C. polygonae*, 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* from the HIS phylogeny and from *C. achyranthis*, *C. sojina* and *C. campsi-sili* 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* amphiogenous, but abundantly hyphopilous. *Myelium* 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, conicallytruncate 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**, Tonghwa, on Cynanchum wilfordii (*Asclepiadaceae*), 19 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,
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 epithete 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 amphiogenous. 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 genulate, 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, circumserpens, thickened and distinctly 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: (MUC 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 concically truncate at the tip (truncatae 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, circumserpens 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 obconically truncate (truncatae) 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. Uenatsu & C. Nakashima, MUMH 11403, MUC 575 = MAFF 238210; Ehime, on Tagetes erecta (Asteraceae), 27 Oct. 2004, J. Nishikawa, MUMH 11392, MUC 128; Shizuoka, on Fuchsia ×hybrida (Onagraceae), 22 June, 2004, J. Nishikawa, MUMH 11396, MUC 138; on Osteospermum sp. (Asteraceae), 11 Sep. 2004, J. Nishikawa, MUMH 11395, MUC 132; Tokyo, on Gerbera ×hybrida (Asteraceae), J. Takeuchi, MUC 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 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 MUC 128, 132 and 578 intermixed with C. malloti and Cercospora sp. P, isolates MUC 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 circumserpens 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 riciella Sacc. & Berl., Atti Reale Ist. Ven. Sci. Lett. Art, Ser. 3: 721. 1885.

≡ Cercospora riciella (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 ricii 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 amphiogenous, mainly hypophyllous. Mycelium internal. Stromata lacking to well-developed, pale brown to brown, subepidermal 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 132805 = 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 rodmani** 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 = RC3867. **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 rodmani* 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. rodmani* to be a synonym of *C. piaropi* whereas Crous & Braun (2003) retained *C. rodmani* 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. rodmani* 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. rodmani* isolate CBS 113129 were specific to water hyacinth.

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

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

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

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

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

**Cercospora cf. sigesbeckiae**

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

Specimens examined: **Japan**, Chiba, on *Begonia sp.* (Begoniaceae), 24 Jun. 1997, S. Uematsu, MUMH 11405, MUCC 587 = MAFF 237690 = MUCNS 197; Fukuoeka, on *Sagesbeckia glutinosa* (Asteraceae), 31 Oct. 1948, S. Katsuki, holotype in TNS, Saitama, on *Glycine max* max, 1949, H. Kurata, MUCC 589 = MAFF 305039 (as *C. kikuchii*). Tokyo, on *Dioscorea tokoro* (Dioscoreaceae), 10 Nov. 2007, I. Araki, MUMH 10955, MUCC 849. **South Korea**, Chuncheon, on *S. glutinosa*, 7 Oct. 2003, H.D. Shin, CBS H-31010, CBS 132621 = CPC 10664 (as *C. sigesbeckiae*); on *Persicaria orientalis* (= *P. cochinichinensis* (Polygonaceae)), 11 Oct. 2002, H.D. Shin, CBS 132641 = CPC 10117 (as *C. polygonaceae*); Hongcheon, on *Pilea pumila* (= *P. mongolica*), 3 Oct. 2002, H.D. Shin, CBS 132642 = CPC 10128 (as *C. gangeticola*); Namyangju, on *Paulownia cornaca* (Scrophulariaceae), 22 Oct. 2003, H.D. Shin, CBS H-21020 = HAL 1863, CBS 132606 = CPC 10740; Yanggu, on *Sagesbeckia 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. 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*. 

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**Cercospora sojina** Hara, Nogyokoku (Tokyo) 9: 28. 1915.
≡ Cercospora sojina (Hara) Hara, Ōtsuyo-sakumotsu-byōryokaku: 112. 1925.
≡ Cercosporidium sojina (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** 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 132628 = CPC 17964 = "CCC 156-09, 09-285-4"; CPC 17965 = "CCC 156-09, 09-285-5"; CPC 17966 = "CCC 157-09, 09-285-3"; CPC 17967 = "CCC 158-09, 09-285-1"; CPC 17668 = "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, 09-882"; 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, 09-2520"; South Korea: Hoengseong, on G. soja, 2004, 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**: This isolate was obtained from Ipomoea in Korea, but differs in its phylogenetic trees 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. agavicolae*. 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 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. C–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. 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, solitarily 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, multilocular; loci thickened, apical, rarely lateral, 2–2.5 µm diam, slightly protuberant. **Conidia** solitarily, hyaline, cylindrical-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 10667 (as C. ipomoeae); CPC 10688–10689 (as C. ipomoeae).

**Notes**: This isolate is phylogenetically distinct from *Ipomoea* in Korea, but differs in its phylogenetic trees 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. agavicolae*. 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. G

_Caespituli_ amphiogenus. _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, relatively 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. _Conidigenous_ cells integrated, terminal, rarely intercalary, proliferating sympodially, multi-local; loci thickened, darkened, apical or formed on the shoulders caused by geniculation, lateral, sometimes circumpersed, 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.

Specimens examined: _New Zealand_, Manurewa, on *Salvia viscosa* (Lamiaceae), C.F. Hill, Lynfield 626, CPC 5438 (as C. salviicola); Kopuku, on *Bollea 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, 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.

Cercospora sp. H

Specimens examined: _Argentina_, on _Chameleacium uncinatum_ (Myrtaceae), S. Wolcan, CPC 11620 = ICR. _New Zealand_, on _Dichondra repens_ (Comovulaceae), C.F. Hill, Lynfield 536, CBS 115025 = 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 deutiae_ 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 _Corokia 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. deutiae_); on _Deutzia purpurascens_ (Hydrangeaceae), 5 May 2002, C.F. Hill, Lynfield 607, CBS 114815 = CPC 5364 (named as _C. deutiae_); on _Deutzia ×rosea_ (= _D. gracilis × purpurascens_) (Hydrangeaceae), Apr. 2002, C.F. Hill, Lynfield 599, CBS 114816 = CPC 5363 (named as _C. deutiae_); on _Fuchsia procumbens_ (Onagraceae), 5 May 2002, C.F. Hill, Lynfield 613, CBS 114817 = CPC 5365 (named as _C. fuchiae_); 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. alchemillicola_, _C. cf. physalidis_ 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 _Ca. 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. Matussaki, 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_ amphiogenus. _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 sinusously 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. chenopodii_. In the combined tree (Fig. 2 part 2), it is a sister taxon to _C. 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 Garcia 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; conidioseptum loci 2–3 µm diam, thickened and darkened; conidia solitary, acicular, short conidia occasionally subcyindrical, 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 & Zavrěl, 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 & Zavrěl 1971). In the TEF and CAL phylogeny this isolate clusters with C. zebrina and C. armoracae 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 113635 = CPC 10526), which is here treated under Cercospora sp. P. The TEF phylogeny could not distinguish it from Cercospora sp. N–Q, C. kikuchi 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 sp. P and Q, C. alchemilllicola / C. cf. alchemilllicola 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 sp. O–Q, C. kikuchi 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. richardicola 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. richardicola and C. kikuchi.

**Cercospora sp. O**

Specimen examined: **Thailand**, Chiang Mai, Mae Klang Loung, N18º32.465' E98º32.874', on Musa sp. (Musaceae), 6 Oct. 2010, P.W. Crous, CBS 132635 = CPC 18636 (named as C. hayi).

**Notes:** Based on its shorter 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 sp. M, N and Q, C. kikuchi 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 sp. P and Q, C. alchemilllicola / C. cf. alchemilllicola and C. cf. sigesbeckiae and the ACT phylogeny from C. kikuchi. In the combined tree (Fig. 2 part 4), it is a sister taxon to C. cf. malloii.

**Cercospora sp. P**

Specimens examined: **Ghana**, on leaves of Dioscorea rotundata (Dioscoreaceae), 2000, S. Nyako & A.O. Damquah, CBS 132660 = CPC 11629 = GHA-4-6; CPC 11630 = GHA-4-3; CPC 11631 = GHA-5-0; CPC 11632 = GHA-7-4; CPC 11633 = GHA-8-4 (as C. dioscoreae-pyrolifolia). **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. rodontata, 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 113596 = CPC 5326; CBS 115413 = CPC 5326; 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 colonymised 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 132670 = CPC 15807; Tamaulipas, on Taraxacum sp. (Asteraceae), 30 Oct. 2008, Ma. de Jesus Yáñez-Morales, CBS 132682 = CPC 15850; on Esphorbia sp. (Esphorbiaceae), 31 Oct. 2008, Ma. de Jesus Yáñez-Morales, CPC 15875; 30 Oct. 2008, Ma. de Jesus 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 132661 = CPC 11635 = PNG-016; CPC 11639 = PNG-007. South Africa, Nelspruit, on Cajanus cajan, L. van Jaarsveld, CBS 115997 = CRL 3252; CBS 115410 = CRL 3531; CBS 115411 = CRL 3532; CBS 115536 = CRL 3532; CBS 115537 = CRL 3530. *Thailand*, on Acacia mangium, K. Pongpanich, CPC 10590 (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 below. More extensive screening of additional loci is needed to resolve the phylogeny of these taxa. See also the species notes below. More extensive screening of additional loci is needed to resolve the phylogeny of these taxa.

**Cercospora sp. R**

Specimen examined: New Zealand, Auckland, Grey Lynn, on Myoporum lautum (Myoporaceae), Dec. 2003, C.F. Hill, Lynfield 186-8, CBS 114644.

*Notes*: Pseudocercospora myoporii is a true species of *Pseudocercospora* (Braun & Hill 2002), which was originally described without deposing 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**

Specimens examined: South Korea, Yangpyeong, on Cephalidium dentriculatum (= Youngia dentriculata) (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, amphiogenous, pale to medium brown, 8–20 mm diam, with inconspicuous margin. *Caespituli* amphiogenous. *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 sinous-guniculate, 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. *Conidigenous 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, subbotubus 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, margin submerged, grey-olivaceous; reverse iron-grey. On PDA pale olivaceous-grey, margin submersed, grey-olivaceous; reverse olivaceous-grey.

Specimens examined: Japan, Gunma, on Vigna unguiculata (= *V. sinensis*) (Fabaceae), Sep. 1993, K. Kishi, MUCC 579 = MAFF 237635. *South Africa*, Potchefstroom, on V. unguiculata (= *V. sinensis*), 3 Jan. 1985, 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). In the TEF phylogeny, the clade is split into two lineages, isolates CPC 1134 and MUCC 579 as sister clade to *C. apiocola* and CPC 10812 basal to *C. apiola* and *C. beticola*. In the combined tree (Fig. 2 part 2), it is basal to the lineage containing *C. apiocola* 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 vignigena* (described on *V. unguiculata* (= *V. sinensis*) collected from the USA) has in the past been listed as...
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 violae-kiusianae S. Sawada, Rep. Gov. Agric. Res. Inst. Taiwan 85: 126. 1943.
- = 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 unicellular. 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, MUC 129; Nagano, on V. tricolor, 16 Feb. 2005, J. Nishikawa, MUMH 10332, MUC 133; Shizuoka, on V. tricolor, 15 Jan. 2003, J. Nishikawa, MUMH 10334, MUC 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 5968.

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

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

Specimens examined: China, Liaoning Province, on Zea mays (Poaceae), CBS 132668 = CPC 12225 = CHME 52. Mexico, Tlacotepac, 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 442566; 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-17747, 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 3), it is a basal
lineage. Gray leaf spot of maize was originally attributed to “group I” and “group II” siblings of *C. zae-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.

≡ *Cercosporella 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 var. zebrina* Ferraris, Fl. Ital. Cryptog. 1: 423,1910, fide Chupp (1954: 341).

Specimens examined: Australia, on *Trifolium cernuum* (Fabaceae), M.J. Barbetti, CBS 118791 = IMI 264190 = WA 2054 = WA 7993; on *T. subterraneum*, M.J. Barbetti, CBS 116789 = WAC 5106; CBS 116790 = WA 262766 = WA 2030 = WA 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 10001; 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 5347; on *Jacaranda mimosaefolia* (*Bignoniaceae*), C.F. Hill, Lynfield 693, CPC 5473 (as *C. canescens*). *Romania*, Hagieri, on *Astragalus spinuni* (*Fabaceae*), O. Constantinescu, O. CBS 53.71.7 = IMI 161108 = CPC 5089 (as *C. australis*). *South Korea*, Namyangju, on *T. repens*, 22 Oct. 2003, H.D. Shin, CBS H-21027, CBS 132650 = CPC 10756. *Unknown*, on *Medicago arabica* (= *M. malacata*) (*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 malvacaceous 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 other, closely allied species.

In the TEF phylogeny, isolates are intermixed with those of *C. armoricana*, *C. ruminicis* 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**

*Caeasputuli* amphibogenous. *Mycelium* internal. Stromata lacking to small, up to 35 µm diam, intraepidermal or subrostomal, 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. *Conidigenous 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, filamentous 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 caesputuli on *V8*; (MUCC 131): *Cercosporioides* 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. *Conidigenous 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, filamentous 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. Afrenas, 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. api* 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. ipomoeae*, *C. fagopyri* and *C. rodmani*. 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 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.
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 synonyms, 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. thirumalachaini. 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-pyrfoliae and C. golaghatti) from this host genus; of the three Cercospora names, C. dioscoreae-pyrfoliae 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-pyrfoliae (based on Dioscorea pyrfolia 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-pyrfoliae. 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-pyrfoliae 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. arachidica, 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. 2008a) 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. arachidica, C. coffeicola, C. nicotianae and C. personata.

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