Cercosporoid fungi (*Mycosphaerellaceae*) 1. Species on other fungi, *Pteridophyta* and *Gymnospermae*

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Abstract: Cercosporoid fungi (former *Cercospora* s. lat.) represent one of the largest groups of hyphomycetes belonging to the *Mycosphaerellaceae* (Ascomycota). They include asexual morphs, asexual holomorphs or species with mycosphaerella-like sexual morphs. Most of them are leaf-spotting plant pathogens with special phytopathological relevance. The only monograph of *Cercospora* s. lat., published by Chupp (1954), is badly in need of revision. However, the treatment of this huge group of fungi can only be accomplished stepwise on the basis of treatments of cercosporoid fungi on particular host plant families. The present first part of this series comprises an introduction, a survey on currently recognised cercosporoid genera, a key to the genera concerned, a discussion of taxonomically relevant characters, and descriptions and illustrations of cercosporoid species on other fungi (mycohyphal taxa), *Pteridophyta* and *Gymnospermae*, arranged in alphabetical order under the particular cercosporoid genera, which are supplemented by keys to the species concerned. The following taxonomic novelties are introduced: *Passalora austroplenckiae* comb. nov., *P. backmanii* comb. nov., *P. condensata* comb. nov., *P. gymnocladi* comb. nov., *P. thalictri* comb. nov., *Pseudocercospora davalliiicola* sp. nov., *P. chamaeyparidis* comb. nov., *P. cratevicola* nom. nov., *P. gleicheniae* comb. nov., *P. lygodicola* sp. nov., *P. lygodigina* nom. nov., *P. nephrolepidigina* sp. nov., *P. paraxenosporoides* sp. nov., *P. pini-densiflorae* var. *montantiana* comb. et stat. nov., *P. pteridigena* sp. nov., *P. ptisanae* sp. nov., *P. sciadopityos* sp. nov., *P. subramanianii* nom. nov., *P. thuina* comb. nov., and *Zasmidium australiense* comb. nov.

Key words: Ascomycota
*Cercospora* s. lat.
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INTRODUCTION

Cercospora-like fungi are one of the largest groups of mostly plant pathogenic, leaf-spotting hyphomycetes, comprising more than 2000 names (Crous & Braun 2003). Numerous economically relevant plant diseases are involved, as for instance angular leaf spot of bean (*Pseudocercospora griseola*). Numerous economically relevant plant diseases comprising more than 2000 names (Crous & Braun 2004, Hernández-Gutiérrez & Dianese 2008, 2009). They are dematiaceous hyphomycetes characterised by having mycosphaerella-like sexual morphs. Most of them are leaf-spotting plant pathogens with special phytopathological relevance. The only monograph of *Cercospora* s. lat., published by Chupp (1954), is badly in need of revision. However, the treatment of this huge group of fungi can only be accomplished stepwise on the basis of treatments of cercosporoid fungi on particular host plant families. The present first part of this series comprises an introduction, a survey on currently recognised cercosporoid genera, a key to the genera concerned, a discussion of taxonomically relevant characters, and descriptions and illustrations of cercosporoid species on other fungi (mycohyphal taxa), *Pteridophyta* and *Gymnospermae*, arranged in alphabetical order under the particular cercosporoid genera, which are supplemented by keys to the species concerned. The following taxonomic novelties are introduced: *Passalora austroplenckiae* comb. nov., *P. backmanii* comb. nov., *P. condensata* comb. nov., *P. gymnocladi* comb. nov., *P. thalictri* comb. nov., *Pseudocercospora davalliiicola* sp. nov., *P. chamaeyparidis* comb. nov., *P. cratevicola* nom. nov., *P. gleicheniae* comb. nov., *P. lygodicola* sp. nov., *P. lygodigina* nom. nov., *P. nephrolepidigina* sp. nov., *P. paraxenosporoides* sp. nov., *P. pini-densiflorae* var. *montantiana* comb. et stat. nov., *P. pteridigena* sp. nov., *P. ptisanae* sp. nov., *P. sciadopityos* sp. nov., *P. subramanianii* nom. nov., *P. thuina* comb. nov., and *Zasmidium australiense* comb. nov.

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*In memoriam Charles D. Chupp (1886–1967), the author of the first monograph of *Cercospora*.**
The present work is a compilation based on papers and unpublished data of the authors as well as global literature. Details on methods are to be found in the papers cited. As far as new examinations are concerned, fungal structures have been examined on the base of standard methods of light microscopy, using an Olympus BX50 microscope, with distilled water and lactic acid as media, but without any staining. If possible, measurements of 30 conidia and other structures have been made at a magnification of ×1000. The following abbreviations are used: author names follow Brumpt & Powell (1992), journals Bridson (2004a, b), and exsiccatea http://www.botanischesstaatsammlung.de/DatabaseClient/IndExs/index.jsp (IndExs – Index of Exsiccatae). Taxonomy and nomenclature of plant families, genera and species are based on the "Angiosperm Phylogeny Website" (http://www.mobot.org/mobot/research/apweb/). Tropicos database (http://www. Tropicos.org/), and The Plant List (http://www.theplantlist.org).

**Taxonomically relevant characters**

Basic characters at generic rank (for the discrimination of genera) are mainly confined to colour of conidiophores (hyaline or pigmented) and the structure of the conidiogenous loci and conidial hila (conspicuous by being thickened and darkened versus inconspicuous, neither thickened nor darkened, or at least unthickened). Other features previously used to distinguish number of additional species have been described since Chupp’s (1954) monograph, and numerous comprehensive taxonomic treatments and works dealing with particular areas, including large countries, have been published, e.g., Viégas (1945, Brazil), Muntañola (1960), Deighton (1967, 1971, 1974, 1976, 1979, 1983, 1987, 1990), Katsuki (1965, Japan), Yen & Lim (1980, Singapore and the Malay Peninsula), Hsieh & Goh (1990, Taiwan), Guo & Hsieh (1995, China, *Pseudocercospora*), Crous & Braun (1996, South Africa), Braun & Mel’nik (1997, Russia and adjacent countries), Shin & Kim (2001, Korea), Guo et al. (2005, China, *Cercospora*), Guo et al. (2003, China, *Passalora s. lat.*), Kamal (2010, India) and Phengsinthat et al. (2013a, b, Laos, Thailand). Hence, Chupp’s (1954) monograph is badly out of date. There is no modern comprehensive treatment of cercosporoid species, and taxonomic work on this fungal group is complicated and time-consuming due to the large number of species involved, and descriptions scattered throughout the mycological and phytopathological literature. Therefore, a new “Chupp” summarising all taxa of and data on cercosporoid hyphomycetes is urgently required. To accomplish a comprehensive treatment of all taxa concerned in a monograph as in Chupp (1954), we have decided to treat the cercosporoids occurring on particular host families, i.e., in principle following Chupp’s (1954) concept, but supplemented by keys to the species and illustrations for most taxa. In the present first contribution, hyperparasitic cercosporoid species and taxa on hosts belonging to *Pteridophyta* and *Gymnospermae* are treated. After comprehensive treatments of cercosporoids of all host families, it will be possible to supplement the individual publications and compile a monograph.

**MATERIAL AND METHODS**

The history and the evolution of concepts of cercosporoid genera was later questioned due to numerous morphologically intermediate taxa and a continuum in several previously applied generic characters as well as the first phylogenetic results based on DNA sequence data (Crous et al. 2000, Crous & Braun 2003), which again lead to a reduction of recognised cercosporoid genera. Most of these changes in generic circumscriptions have recently been confirmed during the course of various molecular DNA studies, although a few newly segregated cercosporoid genera have been introduced to reflect monophyletic, morphologically separated clades, e.g. *Phaeocercospora* (Crous et al. 2012), *Palidocercospora* and *Phaeomyccentrospora* (Crous et al. 2013). Other genera, previously sometimes considered to be synonyms, have been confirmed as separate genera, e.g. *Pantospora* (Minnis et al. 2011), *Paracercospora s. str.* and *Scolecostigmina s. str.* (Crous et al. 2013).

The history and the evolution of concepts of cercosporoid genera was comprehensively discussed in Deighton (1976), Braun (1995a) and Crous & Braun (2003) as well as recently in Crous et al. (2013) and Groenewald et al. (2013) with special emphasis on *Pseudocercospora* and *Cercospora*, respectively. These treatments may be consulted for further details.

Beside numerous, partly controversial treatments of cercosporoid hyphomycetes at generic level, a very large
smaller generic units (segregated genera) proved to be of little relevance at generic level, e.g. absence or formation of external mycelium in vivo, arrangement and formation of conidiophores in vivo (formed singly on superficial hyphae, fasciculate, in sporodochia or synnemata). However, these characters are useful at species rank, i.e. for the differentiation of allied, morphologically similar species. The following additional characters are useful and applicable for the characterisation of species and their discrimination from allied taxa: shape and size, septation, pigmentation (pale to dark brown), wall thickness and surface structure (smooth to verrucose) of conidiophores; shape, size, integration and proliferation mode of conidiogenous cells; location, size (diameter) and shape of conidiogenous loci (scars) (e.g. inconspicuous, on shoulders caused by sympodial proliferation, denticle-like, etc.); formation of conidia (solitary or in simple or branched chains), shape, size, septation (eu- or distoseptate, transversely or longitudinally to obliquely septate, amero- to scolecosporous), colourless or pigmented, wall smooth or sculptured; shape and size, number and location of hila.

SEXUAL MORPHS AND CURRENTLY RECOGNISED CERCOSPOROID GENERA

Mycosphaerella and mycosphaerella-like sexual morphs

Sexual morphs of various cercosporoid hyphomycetes were traditionally referred to as Mycosphaerella. Ascomata of the latter genus are morphologically rather uniform and provide few characters to support further splitting. The associated asexual morphs are, in contrast, morphologically strongly differentiated and better reflect genotypic variation. The type species of Mycosphaerella, M. punctiformis, has an asexual morph described as Ramularia endophylla and clusters together with other Ramularia species in a monophyletic Ramularia clade within the Mycosphaerellaceae (Verkley et al. 2004, Crous et al. 2007), so that Mycosphaerella s. str. becomes a facultative synonym of Ramularia according to the new rules of the ICN (Art. 59). The older name Ramularia has priority and should be applied as holomorph name for this monophyletic unit composed of asexual or sexual morphs, or Ramularia species with Mycosphaerella sexual morphs in their life cycles. The further splitting of ascomycetes with mycosphaerella-like sexual morphs is closely connected with and based on assemblages of certain species with particular asexual morphs for which asexual morph-typified generic names are available. Ramularia (Mycosphaerella) as mucedineaceous genus, characterised by having colourless conidiophores and conidia, does not belong to the complex of cercosporoid genera, and is hence not treated in this series. Ramularia and allied mucedineaceous genera have been monographed by Braun (1995a, 1998), and a detailed molecular phylogeny will be published elsewhere (Videira et al., in prep.).

CERCOSPORA S. STR.

The genus Cercospora was introduced by Fresenius (in Fuckel 1863) for passalora-like species with pluriseptate conidia. The typification of a genus is essential for further taxonomic treatments, i.e. for changed generic circumscriptions s. str. or s. lat. However, the typification of Cercospora was previously controversially handled and discussed. Cercospora apii was usually considered as type species (or lectotype species) of Cercospora (Solheim 1930, Clements & Shear 1931, Ellis 1971, etc.), based on the assumption that the first description of this genus dates back to Fresenius (1863). This typification was accepted by most subsequent authors, including Sutton & Pons (1988), but proved to be wrong, which was pointed out by Braun (1995a) who showed that the first valid description of Cercospora was published somewhat earlier in Fückel (1863) and simultaneously in Fückel, Fungi Rhen. Exs., Fasc. II, No. 117, 1863 with Cercospora penicillata (C. depazoides) as only and hence type species. Fückel (1863) only added a new forma (f. apii), which is, however, irrelevant for the typification. Early circumscriptions of Cercospora comprised Cercospora ferruginea, a species with thickened, darkened conidigenous loci and pigmented conidia, which was later reallocated to Mycovellulosiella and belongs now to Passalora emend. During the course of the following 100 years, the application of Cercospora had been continuously widened (Saccardo 1880, Solheim 1930, etc.). All kinds of superficially similar species, with or without conspicuous conidigenous loci, with hyaline or pigmented conidia, formed singly or in chains, were assigned to this genus. This broad generic concept was used and applied by Chupp (1954) in his monograph of Cercospora s. lat., in which he treated 1 419 species. The number of species assigned to Cercospora increased rapidly in the following decades. Pollack (1987) listed more than 3 000 names. Several early attempts to split Cercospora s. lat. into smaller generic units had been made, e.g. by Earle (1901) (Cercosporidium), Ferraris (1909) (Phaeoisariopsis), Spegazzini (1910) (Cercosporina, Pseudocercospora), Maublanc (1913a, b) (Asperisporium), Rangel (1917) (Mycovellosiella), Miura (1928) (Cercosporiopsis), Sydow (1930) (Stenella), Petrak (1951) (emendation of Chaetotrichum to include some cercosporid taxa), Muntanofila (1960) (Phaeoramularia), etc. However, the genera concerned did not gain wide acceptance and application until Deighton’s (1967, 1971, 1974, 1976, 1979, 1983, 1987, 1990) comprehensive studies on cercosporid hyphomycetes, and his new generic concepts and splitting of Cercospora s. lat. Ellis (1971, 1976) followed Deighton’s concepts and accepted Cercosporidium, Mycovellulosiella, Phaeoramularia and other cercosporid genera segregated from Cercospora. Deighton (1976) re-introduced Pseudocercospora and widened its circumscription to all kinds of cercosporid hyphomycetes with inconspicuous (unthickened, not darkened) conidigenous loci, i.e. he finished the gradual reduction of the application of the genus Cercospora and confined it (s. str.) to species resembling C. apii, i.e. to taxa with pigmented conidiophores, thickened and darkened conidigenous loci (scars) and colourless, pluriseptate, scolecosporous conidia formed singly, a concept accepted up to now and confirmed by molecular sequence analyses in which Cercospora s. str. proved to represent a monophyletic clade (Crous et al. 2000, Groenewald et al. 2013). Numerous molecular examinations of Cercospora species have been carried out, based on rDNA ITS data as well as multilocus approaches (Stewart et al. 1999, Crous et al. 2000, 2004a, 2009a, b, Goodwin et al. 2007 volume 4 · no. 2
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2001, Tessmann et al. 2001, Pretorious et al. 2003, Groenewald et al. 2005, 2006a, b, 2010, 2013, Montenegro-Calderón et al. 2011). Crous & Braun (2003) published an annotated list of Cercospora and Passalora emend. names, including 659 recognised species of Cercospora s. str. and further 281 species names reduced to synonymy with C. apii s. lat. since they were morphologically not or barely distinguishable from C. apii s. str. on celery. This concept was influenced by assumptions as well as proven results suggesting that C. apii s. lat. comprises specialised as well as plurivorous races (Ellis 1971). Crous & Braun (2003) provided a morphological circumscription of Cercospora apii s. lat. and recommended to assign new collections on hosts of new families or genera to C. apii s. lat. if morphologically indistinguishable and if not proven by means of molecular sequence analyses and/or inoculation experiments that distinct species are involved. However, the speciation within Cercospora s. str., above all with regard to C. apii s. lat., is more complicated than previously assumed and far from being comprehensively perceived. Detailed molecular examination of Cercospora s. str. based on a multilocus DNA approach (ITS, actin, calmodulin, histone H3, and translation elongation factor 1-alpha genes) has recently been carried out by Groenewald et al. (2013). The monophyly of Cercospora s. str. was verified, but the speciation within this genus proved to be very complicated. Cercospora apii s. lat. as plurivorous monophyletic species could not be confirmed. Cercospora apii s. lat. is rather a complicated complex composed of specialised as well as numerous species with wide host range, often with overlapping host ranges between particular taxa. The problem is that most of the taxa involved, including various plurivorous ones, are morphologically barely distinguishable. Certain hosts or host ranges are also not reliable for taxonomic purposes within C. apii s. lat. Cercospora collections on certain hosts with agreeing morphology found in different geographical regions do often not belong to a single species, i.e. it is usually not possible to simply apply old names of Cercospora species described from Europe or North America to taxa in Africa, Asia, Australia or South America and vice versa. Therefore, descriptions of new species on new hosts morphologically indistinguishable from C. apii s. lat. should be avoided without support by molecular sequence analyses. The collections concerned should be simply referred to as C. apii s. lat. (C. apii complex) as recommended by Crous & Braun (2003).

Attempts to separate Cercospora into several subgeneric units have been made by Penzes (1927) (three sections: Brachycercosporae, Macrocercosporae and Mediocercosporae) and Solheim (1930) (21 sections based on mycelium internal/external, conidiophores simple/branched, stroma and conidium shape), which are, however, barely practicable and not useful since these classifications were derived from a wide range of species of Cercospora s. lat. that now belong to different genera. Therefore, it is not surprising that these subgeneric concepts have never been applied by other authors.

A special problem concerns Cercospora species with colourless but passalora-like conidia, i.e. broadly ellipsoid-ovoid to obclavate-cylindrical, only with few septa, e.g. Cercospora chenopodii (Passalora dubia) and C. sojina (P. sojina). In this case, the generic relevance of the conidial shape versus conidial colour was unclear and differently evaluated. However, this problem has recently been clearly solved on the basis of molecular sequence analyses (Groenewald et al. 2012), which showed that species with hyaline conidia, independent of the conidial shape, cluster within the Cercospora clade. Other Cercospora species are characterised by having colourless or very pale conidiophores. They are superficially similar to Cercospora species, but species of the latter genus have quite distinct conidiogenous loci (Braun 1995a). Braun (1993) introduced Cercospora subgen. Hyalocercospora for such species. Molecular data for Cercospora cercosporelloidies, the type species of this subgenus, or any other species assigned to it in Braun (1995a) are not yet available, i.e. it is still unresolved if they cluster in the monophyletic Cercospora clade.

The following description circumscribes Cercospora as currently perceived and phylogenetically confirmed as monophyletic genus:

**Cercospora** Frese., in Fuckel, **Hedwigia** 2: 133 (1863) [and in Fuckel, Fungi Rhen. Exs., Fasc. II, No. 117, 1863].

Type species: *Cercospora penicillata* (Ces.) Fresen. 1863 (C. depazeoides (Desm.) Sacc. 1876).

Synonyms: *Virgasporium* Cooke, *Grevillea* 3: 182 (1875) [type species: *V. maculatum* Cooke 1875].


**Description** [emend. Crous&Braun (2003:16)]: Hyphomycetes (asexual morphs, asexual holomorphs) or Cercospora with mycosphaerella-like sexual morphs; *Mycosphaerellaceae*. Saprobic, secondary invaders or mostly plant pathogenic, symptomless or usually causing distinct lesions (leaf-spotting fungi). Mycelium internal, rarely external; hyphae branched, septate, colourless or almost so to usually pigmented, thin-walled, smooth, rarely faintly rough-walled. *Stromata* lacking to well-developed, substomatal, intaepidermal to deeply immersed, mostly pigmented, composed of *textura angulata* or *globosa*. *Conidiophores* mononematous, macronematous, solitary or fasciculate, in small to large fascicles, rarely in sporodochial conidiomata, emerging through stomata or erumpent, very rarely arising from superficial hyphae, erect, continuous to pluriseptate, hyaline or almost so (subgen. *Hyalo cercospora*) to mostly pigmented, pale olivaceous to dark brown (subgen. *Cercospora*), wall smooth to somewhat rough, thin to moderately thick; conidiogenous cells integrated, terminal or intercalary, sometimes conidiophores aseptate, i.e. reduced to conidiogenous cells, monoblastic, determinate to usually polyblastic, proliferation sympodial, rarely percurrent, conidiogenous loci (scars) conspicuous, thickened and darkened-refractive, planate with minute central pore. *Conidia* solitary, rarely in short chains (mainly under high humidity), mostly scolecosporous, obclavate-cylindrical, acicular, filiform and plurieuseptate, rarely amero- to phragmosporous, broadly ellipsoid-ovoid to broadly...
obclavate-cylindrical, but always hyaline or subhyaline (with a pale greenish tinge), thin-walled, smooth or almost so, hila thickened and darkened, conidial secession schizolytic.

**DISTOCERCOSPORA**

The genus *Distocercospora* is passalora-like (thickened and darkened loci and hila and pigmented conidia), but differs in having distoseptate conidia. The meaning of distosepation as character on generic level within the complex of cercosporoid genera is, however, unclear. Distosepta may occasionally occur intermixed between genuine septa in some *Passalora* species (Crous & Braun 2003) as well as in *Pseudocercospora cryptomericola* (Nakashima et al. 2007). It is possible that distosepta mixed with eusepta are more common in cercosporoid fungi than hitherto known as it is often rather difficult to discern such septa in taxa with thin walls. However, cultures and molecular data based on Japanese material of the type species of *Distocercospora, D. pachyderma,* and *D. livistonae* have recently been examined by C. Nakashima (unpubl. data), which showed that these species cluster within the *Mycosphaerellaceae* clade in a more basal and separate position. These results indicate that *Distocercospora* has to be maintained as separate genus, distinguished from *Passalora* by having consistently distoseptate conidia.


*Type species:* *Distocercospora pachyderma* (Syd. & P. Syd.) Pons & B. Sutton 1988.


*Description:* *Folicolous,* plant pathogenic, leaf spotting hyphomycetes (asexual morphs), sexual morphs unknown. *Mycelium in vivo* internal; hyphae branched, septate, subhyaline to pigmented, thin-walled, smooth. *Stromata* lacking to well-developed, pigmented, *textura angulata* to *globosa.* *Conidiophores* macronematous, mononematous, simple to branched, often strongly branched, septate, pigmented, thin-walled, smooth to rough-walled; conidigenous cells integrated, terminal, occasionally intercalary, proliferation sympodial, conidigenous loci conspicuous, somewhat thickened and darkened. *Conidia* formed singly, rarely in short chains, scolcosporous, mostly obclavate to cylindrical, with a single to several transverse distosepta, subhyaline to pigmented, wall smooth to rough, hila somewhat thickened and darkened, conidial secession schizolytic.

**PASSALORA EMEND. CROUS & BRAUN (2003)**

*Passalora,* described by Fries (1849), was the first genus introduced for cercosporoid hyphomycetes. Fresenius (in Fuckel 1863) introduced *Cercospora* for passalora-like species with pluriseptate conidia. Later the concept of *Cercospora* was considerably widened, and culminated in Chupp’s (1954) monograph of *Cercospora s. lat.* with very broad generic concept. Several attempts to segregate smaller generic units from *Cercospora s. lat.* for cercosporoids with thickened and darkened conidigenous loci were made in the 20th century, but attracted little attention and were rarely used, e.g. *Cercospirdium* (Earle 1901), *Mycovellosiella* (Rangel 1917), *Ragnhildiana* (Solheim 1930), *Cercodeuterospora* (Ceruzzi 1932), *Berteromycetes* (Ciferri 1954), *Fulvia* and *Oreophylla* (Ciferri 1954), *Phaeoramularia* (Muntafola 1960), *Tandonella* (Prasad & Verma 1970).

Deighton (1967) reintroduced *Cercospirdium* for cercosporoid-like hyphomycetes with internal mycelium, usually well-developed stromata, fasciculate conidiophores and solitary, non-scolecosporous, mostly pale conidia and maintained *Passalora,* although very similar, as separate genus based on “lacking” stromata and pale brown conidia. For similar species characterised by conidia formed in chains, Ellis (1971, 1976) and Deighton (1979) accepted and used *Phaeoramularia,* and for those with solitary conidiophores arising from superficial mycelium the old name *Mycovellosiella* was reintroduced (Deighton 1974, 1979, 1983; Ellis 1971, 1976). This splitting of the *Passalora* complex had been the generally recognised genus concept in the following about 25 years, recognised by most subsequent authors (e.g., von Arx 1983, Pons & Sutton 1988, Hsieh & Goh 1990, Braun 1995a, Braun & Mel’nik 1997, Shin & Kim 2001, Guo et al. 2003, etc.).

First doubts with regard to the acceptance and rationality of the differentiation between *Passalora* and *Cercospirdium,* as made in Deighton (1967), were expressed in Deighton’s (1990) reassessment of the synnematous genus *Phaeoisariopsis* in which he confined the latter genus to a few species around *P. griseola,* the type species, characterised by having subconspicuous, non-protuberant conidigenous loci on non-geniculate conidigenous cells. Other former *Phaeoisariopsis* species with inconspicuous (unthickened, not darkened) loci were assigned to *Pseudocercospora,* and the remaining species with thickened, darkened loci on distinctly geniculate conidigenous cells were proposed to be candidates for *Passalora.* Braun (1995b) reassessed the *Passalora* complex and proposed to reduce *Cercospirdium,* *Mycovellosiella* and *Phaeoramularia* to synonymy with *Passalora.* Crous & Braun (2003) discussed this generic complex in detail and came to the conclusion that these genera and various additional ones should better be merged under the oldest name *Passalora.* There is a continuum of all relevant morphological characters between species of the genera involved. Numerous examples of intermediate species were cited and discussed in Crous & Braun (2003). Neither the conidial formation, solitary or in chains, nor the presence or absence of superficial mycelium represent reliable features on generic rank. With regard to morphological features reliably applicable for the discrimination on generic level, *Passalora* is comparable with other cercosporoid and ramularioid genera like *Pseudocercospora,* *Pseudocercosorella,* *Ramularia* and *Zasmidium.* Thus, the new emended circumscription of *Passalora* (according to Crous & Braun 2003) encompassed cercosporoid species with internal and external or only internal mycelium, solitary, fasciculate to synnematous conidiophores.
and conidia formed singly or in chains, but in all cases with conspicuous (thickened and darkened) conidigenous loci (scar) and mostly non-scolecosporous, pigmented conidia. This new concept was also supported by first molecular sequence analyses (Crous et al. 2000, 2001). Hernández-Gutiérrez & Dianese (2009) divided *Passalora* in sections, viz. sect. *Passalora*, *Mycovelloisella*, *Phaeoramularia*, and *Pseudophaeoisariopsis*, which can be seen as morphological, non-monophyletic groups, which are, however, connected by numerous morphologically intermediate species. Sequences of *Passalora fulva* (*Cladosporion fulvum, Fulvia fulva*), type species of the genus *Fulvia*, with a special habit of conidiophores, are close to those of other *Passalora* species in the *Mycosphaerellaceae* clade (Thomma et al. 2005), which supported the reduction of *Fulvia* to synonym with *Passalora* as proposed in Crous & Braun (2003). In this wide concept of *Passalora*, some species with hyaline passalora-like conidia (non-scolecosporous, broad, only with few septa) were included, as for instance *Passalora dubia* and *P. jasenea*. However, in molecular sequence analyses, such species clustered within the *Cercospora* clade (Groenewald et al. 2012), i.e. the colour of the conidia (absence or presence of pigmentation) is more important than the conidial shape, although most *Passalora* species are characterised by having non-scolecosporous conidia and most *Cercospora* species by scolecosporous ones.

The currently applied wide concept of *Passalora* introduced by Braun (1995b) and Crous & Braun (2003) is not generally accepted and was questioned by some authors. For instance, Guo et al. (2003) treated Chinese species of the *Passalora* s. lat. complex and recognised three genera, namely *Mycovelloisella, Passalora* (including *Cercosporidium*) and *Phaeoramularia*. Baker et al. (2000) discussed the intricate, controversial history of *Passalora* and *Cercosporidium* in detail, admitted a morphological continuum between the two genera, but considered the merging of these genera as undesirable. They discussed morphological differences between these genera, and considered them to be sufficiently distinct to be maintained until more profound examinations will be available. With the increasing application of molecular methods in the *Cercospora* complex, more profound approaches are now given, but corresponding analyses of sequence data do not support a clear separation of *Cercosporidium, Passalora* and other genera involved.

The phylogenetic structure of *Passalora* is, however, complicated and causes severe problems. Numerous available phylogenetic examinations based on rDNA ITS data and other markers indicate that *Passalora* s. lat. is not monophyletic (Crous et al. 2000, 2001, 2009b, c, 2013; Thomma et al. 2005). Taxa within the *Mycosphaerellaceae* are at least paraphyletic, if not polyphyletic. Comprehensive phylogenetic analyses based on a much broader sampling, including the type species of *Passalora* and its synonymised genera, are necessary for a better understanding of the generic structure of *Passalora* s. lat. However, a severe problem is that clades or subclades spread within the *Mycosphaerellaceae* are not clearly connected with morphological groups within *Passalora*, i.e. *mycovelloisella*-like, *phaeoramularia*-like groups of species and other morphological types are not reflected in phylogenetic assemblages. Hence, a comprehensive phylogenetic reassessment and further splitting of *Passalora* is currently not possible based on available data, and it has to be accepted as a para- or polyphyletic genus, at least for the present.

**Passalora** Fr., *Summa Veg. Scand.* 2: 500 (1849).

Type species: *Passalora bacilligera* (Mont. & Fr.) Mont. & Fr. 1849.

Synonyms: *Cercosporidium* E. Earle, *Muhlenbergia* 1: 16 (1901) [type species: *C. helleri* E. Earle 1901].


*Berteromyces* Cif., *Sydowia* 8: 267 (1954) [type species: *B. aeneus* Cif. 1954].

*Oreophyllum* Cif., *Sydowia* 8: 253 (1954) [type species: *O. angelaemariae* Cif. 1954].


Description [emend. Crous & Braun (2003: 21)]: *Hypomyces* (asexual morphs or asexual holomorphs) or *Passalora* species with mycosphaerella-like sexual morphs; *Mycosphaerellaceae*. *Folicolus*, occasionally also caulicolous or on fruits, usually phytopathogenic, causing leaf-spots or other lesions, occasionally symptomless, rarely hyperparasitic or saprobic. *Mycelium in vivo* internal and external, superficial; hyphae branched, septate, colourless or almost so to pigmented, thin-walled, smooth or almost so. *Stromata* absent to well-developed, substomatal, intraepidermal to deeply immersed, apllanate to subglobose.
subhyaline to usually pigmented. Conidiophores *in vivo* solitary, arising from superficial hyphae, lateral, occasionally terminal, or loosely to densely fasciculate, arising from internal hyphae or stroma, sometimes in sporodochia or synnemata, macronematous, cylindrical, filiform to strongly geniculate-sinuous, unbranched or sometimes branched, pale to distinctly pigmented, olivaceous to medium dark brown, continuous to pluriseptate, wall thin to somewhat thickened, smooth, occasionally somewhat rough; conidiogenous cells integrated, terminal, occasionally intercalary or pleurogenous, or conidiophores aseptate, i.e. conidiophores reduced to conidiogenous cells, mono- to mostly polyblastic, pleurogenous, or conidiophores aseptate, i.e. conidiophores cells integrated, terminal, occasionally intercalary or smooth, occasionally somewhat rough; conidiogenous continuous to pluriseptate, wall thin to somewhat thickened, to distinctly pigmented, olivaceous to medium dark brown, geniculate-sinuous, unbranched or sometimes branched, pale synnemata, macronematous, cylindrical, filiform to strongly internal hyphae or stromata, sometimes in sporodochia or terminal, or loosely to densely fasciculate, arising from solitary, arising from superficial hyphae, lateral, occasionally

**PSEUDOCERCOSPORA EMEND. CROUS ET AL. (2013), PALLIDOCERCOSPORA AND PHAEOCERCOSPORA**

The genus *Pseudocercospora* was introduced by Spegazzini (1910) in order to accommodate *Septotema vitis* (Cercospora vitis). This genus name was little used until Deighton (1976) reintroduced it in the course of his splitting of *Cercospora s. lat.* into smaller generic units. He used *Pseudocercospora* for cercosporoid hyphomycetes with unthickened “conidial scars” (i.e. conidiogenous loci), widened its circumscription and added a large number of species. Unthickened conidiogenous loci are characterised by having locus walls not thicker than the walls of the surrounding conidiogenous cells. Such loci are often inconspicuous, but may be more rigid and conspicuous in other species by being more or less denticle-like. The unthickened nature of the conidiogenous loci is, indeed, the fundamental character of *Pseudocercospora*, although in almost all species of this genus the loci are in addition not darkened-refractive, i.e. not darker than the surrounding wall of the conidiogenous cells (the darker pigmentation of conidiogenous loci, which is diagnostic for species of other cercosporoid genera like *Cercospora*, *Passalora* and *Zasmidium*, is generally caused by a combination of darker pigmentation and sometimes structural differences that may cause altered refraction of the light). The basic importance of unthickened conidiogenous loci as generic character for *Pseudocercospora* is supported by several “abnormal” species with more conspicuous loci which are unthickened but darker by being somewhat refractive or even slightly darkened (Crous & Braun 2003). Nevertheless such species belong in *Pseudocercospora*, which has been confirmed in several studies based on molecular sequence analyses (e.g., Crous et al. 2001, 2012).

Another problem concerns conidial formation. In almost all *Pseudocercospora* species, the conidia are consistently formed singly, but conidial catenation may occasionally occur, e.g. in *Pseudocercospora nyctanthis*, *P. millettiensis* and *P. noveboracensis* (Hsieh & Goh 1990, Braun & Mel’nik 1997, Crous & Braun 2003, Crous et al. 2013). Some other pseudocercospora-like species, characterised by subconspicuous conidiogenous loci (unthickened or almost so, but somewhat refractive or darkened-refractive) giving rise to short conidial chains or disarticulating conidia, were considered to be intermediate between *Passalora* and *Pseudocercospora* and assigned to the new genus *Pseudophaeoramularia* (Braun & Mel’nik 1997). However, the phylogenetic position of species with *Pseudophaeoramularia* morphology within the *Pseudocercospora* (*s. str.*) clade revealed that catenate conidia and somewhat darkened-refractive loci and hila are acceptable variation within *Pseudocercospora*.

*Prathigada* is another example for a misinterpreted and confused genus. Due to at least partly conspicuous conidiogenous loci, it has previously been interpreted as close to *Passalora*, but distinct by having obclavate, relatively thick-walled, often apically rostrate conidia. Beside type material, a collection on *Crataeva formosensis*, collected in Japan, has been examined and compared. The Japanese material agrees perfectly with the type material. The conidia do not exceed 50 µm in length and three septa in both specimens. Results of molecular sequence analyses based on the Japanese material (C. Nakashima, unpubl. data) showed that *Prathigada cratevae*, the type species of *Prathigada*, clusters within the *Pseudocercospora* *s. str.* clade near to *P. fijienensis*, i.e. *Prathigada* has to be reduced to synonym with *Pseudocercospora*. The molecular data are supported by morphological characters of *P. cratevae*. The conidiogenous loci and conidial hila are somewhat intermediate between the *Passalora* and *Pseudocercospora* type by ranging from inconspicuous to conspicuous by being denticulate- or peg-like or by being somewhat refractive to slightly darkened-refractive, but on the other hand they are always unthickened and thus not in conflict with the current concept of *Pseudocercospora* *s. str.* (Crous et al. 2013). Unthickened conidiogenous loci which are more conspicuous by being somewhat darkened-refractive are known in other proven *Pseudocercospora* species, e.g. in *Pseudophaeoramularia*, which has been reduced to synonymy with the latter genus (Crous et al. 2013). Due to the discussed results, *Prathigada cratevae* has to be reallocated to *Pseudocercospora*. The following redescription is based on the re-examination of type material and an additional Japanese sample:

*Pseudocercospora cratevicola* C. Nakash. & U. Braun, nom. nov.

MycoBank MB805517

(Fig. 1)

**Basionym:** Napiladium *cratevae* Syd. & P. Syd. (*cratevae*), *An. Mycol.* 11: 329 (1913), non *Pseudocercospora* *cratevae* Phengsintham et al. (2013).


Description: Leaf spots almost lacking to well-developed, amphigenous, subcircular to angular-irregular, 1–10 mm diam or confluent and larger, yellowish, ochraceous, pale to medium brown, later dark brown by abundant fructification, lesions uniform or with a paler centre, finally sometimes greyish white, surrounded by a darker border, often with a diffuse yellowish to ochraceous halo. *Caespitulis* amphigenous, scattered, punctiform, sometimes pustulate, later confluent and dense, forming larger layers, dark brown. Mycelium internal. **Stromata** lacking or almost so to well-developed, substomatal to intraepidermal or deeply immersed, subcircular in outline, 10–80 µm diam, or oblong, up to 150 × 50 µm, olivaceous-brown, yellowish brown to medium brown, composed of swollen hyphal cells, subcircular to angular-irregular in outline, 3–8 µm diam, wall somewhat thickened. Arrangement of conidiophores variable, ranging from small fascicles arising from internal hyphae or small stromata, rarely even solitary, to well-developed, large, dense fascicles, forming sporodochial conidiomata, emerging through stomata or erumpent, erect, straight to somewhat curved, subcylindrical to mostly attenuated towards the tip, conical or somewhat irregularly shaped, unbranched, 10–35 × 5–10 µm, 0–1-septate, pale olivaceous to olivaceous-brown or light brown, wall thin, about 0.5–0.75 µm, smooth or almost so to verruculose; conidiophores mostly reduced to conidiogenous cells, occasionally integrated, terminal, 10–30 µm long, proliferation sympodial, rarely punctiform, with a single or few conidiogenous loci, inconspicuous to conspicuous by being denticile-like (peg-like) or by being somewhat refractive or slightly darkened-refractive, but always unthickened, 1.5–3 µm diam. Conidia solitary, 15–50 × 5–9 µm, 0–3-septate, young small conidia ellipsoid-ovoid, obvoid or subcylindrical, 0–1-septate, thin-walled, subhyaline or pale, uniformly pigmented, mostly verruculose, fully developed older conidia obclavate, straight to often curved, above all at the apex, 2–3-septate, pale olivaceous to medium brown dark brown, above all in the lower part, uniformly pigmented or often distinctly paler towards the tip, wall thickened, up to 1.5 µm, smooth or almost so to verruculose, apex obtuse to somewhat pointed, base short obconically truncate, sometimes abruptly attenuated, peg-like, 1.5–3 µm diam, hila neither thickened nor darkened, at most somewhat refractive.


**Notes:** Subramanian (1953) introduced *Micaraea* for *Napicladium cratevae* as type species and added the new species *M. punjabensis* distinguished from the latter species by having longer conidia, about 30–70 µm, with mostly 3–6 septa. Later he assigned the two species to *Prathigada*.
introduced as replacement name since *Micarea* proved to be a younger homonym. The source for the description and illustration of *Prathigada cratevae* in Ellis (1971) is unclear, but undoubtedly covers *P. cratevae* as well as *P. punjabensis*, although the latter name is not cited as synonym. The re-examination of type material of *Napicladium cratevae* (S., F42112) showed that this collection perfectly coincides with Subramanian’s (1953) description and illustration. Mature, fully developed conidia do not exceed a length of 50 µm and are consistently 0–3-septate, and the examined and sequenced Japanese collection on *Crataeva formosensis* (F42112) showed that this collection perfectly coincides with examination of type material of *Pseudocercospora* *condensata* (Passalora *condensata* (Ellis & Kellerm.) U. Braun, *MycoBank* MB805521 *Basionym*: *Cercospora condensata* Ellis & Kellerm., *J. Mycol.* 1(1): 2 (1885). *Synonym*: *Prathigada condensata* (Ellis & Kellerm.) U. Braun, *Cryptog. Mycol.* 20: 166 (1999).


Notes: Other species assigned to *Prathigada* do not agree with *Passalora*, belong elsewhere or they are doubtful and unclear. The status of *Prathigada bauhiniae* (Rao *et al.* 1975) is unclear. *Stenellopsis shoreae* was reallocaated to *Prathigada* by Kamal (2010), but due to unthickened hila it is possible that this species belongs to *Pseudocercospora*. *Prathigada tamarindii* (Muthappa 1968) is a doubtful species characterised by its unusual conidia which are about 20–30 × 8.5–11 µm and 1–2-septate. A re-examination of type material or examinations of new collections are necessary to reassess this species. *Prathigada terminaliae* (Sutton 1994) is better considered a species of *Pseudocercospora* (*P. terminaliae*). *Prathigada terminaliae-bellericae* (Kamal 2010) is tentatively reduced to synonymy with *P. terminaliae*. The significance of differences in the length of conidiophores and conidia between *P. terminaliae* and *P. terminaliae-bellericae* is unclear and doubtful as the values for these structures of the latter species are intermediate between *P. terminaliae* and *P. kenemensis*, which has been reduced to synonym with the former species as well (Crous & Braun 2003). *Prathigada ziziphi* (Rao & Ramakrishnan 1965) is tentatively reduced to synonymy with *Pseudocercospora jujubae*. Type material was not available, but the shape and size of the conidia agree well.

There are several other morphological characteristics which were proposed for a further splitting of *Pseudocercospora* into smaller generic units, but all of them failed due to a morphological continuum between the particular morphological types and numerous intermediate taxa. Furthermore, there is no molecular (phylogenetic) evidence for and support of genera to be segregated based on morphology (Crous *et al.* 2000, 2001, 2013). Braun (1998) tried to use morphological characters for a separation of *Pseudocercospora* into morphological, non-phylogenetic sections, which are, however, little useful. *Pseudocercospora*...
(Crous et al. 2013), recently introduced for the "Mycosphaerella heimi" complex (Crous et al. 2004a), is a segregation from Pseudocercospora mainly based on its distinct phylogenetic position and culture characteristics (formation of red crystals on MEA, PDA, SNA and WA), whereas the morphology of the asexual and sexual morphs is pseudocercospora- and mycosphaerella-like, respectively.

Cercoseptoria was recognised and reintroduced in Deighton (1976) for pseudocercosporoid species with acicular conidia. Most of the species assigned to Cercoseptoria are distinctly sporodochial. Deighton (1987) and Braun (1988) questioned Cercoseptoria as properly distinguished genus and reduced it to synonymy with Pseudocercospora. Absence or presence of stromata and conidial shape are too variable in Pseudocercospora to be used for the discrimination of smaller units on generic rank. Braun's (1993) introduction of Cercostigmina for pseudocercospora-like former Stigmina species (conidiophores and conidia thin-walled, conidia scleosporous) with consistently percurrently proliferating conidiogenous cells, partly associated with mycosphaerella-like sexual morphs, is another example. Sympodial and percurrent proliferations of conidiogenous cells are often mixed in particular Pseudocercospora species, and species with consistently percurrent proliferation cluster within the big Pseudocercospora clade as well (Crous et al. 2001, 2013; Taylor et al. 2003).

The conidiogenous loci of Phaeoisariopsis griseola, type species of Phaeoisariopsis, were previously considered to be passalora-like, i.e. slightly thickened and darkened. However, the loci in P. griseola range from being quite inconspicuous (neither thickened nor darkened), as exhibited in the type material of Pseudocercospora columnaris (Cercospora columnaris), one of the synonyms of P. griseola, to subconspicuous (i.e. non-protuberant, lying flat around the conidiogenous cells, unthickened, but slightly darkened-refractive). Deighton (1990) maintained Phaeoisariopsis as separate genus, but confined it to a few species with scars similar to those of its type species, P. griseola. He reallocated synnematous species with inconspicuous conidiogenous loci to Pseudocercospora and those with distinctly sympodial conidiogenous cells and conspicuously thickened and darkened loci to Passalora, whereas Braun (1992) considered Phaeoisariopsis a synnematous counterpart of Passalora. However, the locus type of Phaeoisariopsis griseola, type species of Phaeoisariopsis, falls within the range of loci in Pseudocercospora, which has been proven by means of results of molecular sequence analyses (Crous et al. 2006). These comprehensive examinations of angular leaf spot of bean (P. griseola) showed that this species clusters within the Pseudocercospora clade and revealed that the formation of synnematous conidiomata does not play any taxonomic role on generic level within the Pseudocercospora complex (Crous et al. 2006, 2013). Hence, this species was reallocated to the latter genus and Phaeoisariopsis was reduced to synonym with Pseudocercospora, which was proposed to be conserved as the former genus name is older (Braun & Crous 2006), i.e. former Phaeoisariopsis species with subconspicuous, P. griseola-like scars as well as inconspicuous loci are now part of Pseudocercospora and those with conspicuously thickened loci belong to Passalora. Furthermore, Crous et al. (2006) demonstrated the unexpected phylogenetic position of Stigmina platana, type species of Stigmina, within the Pseudocercospora clade. Although older than Pseudocercospora, the latter genus name was conserved over that of Stigmina (Braun & Crous 2006).

Paracercospora (Deighton 1979), with P. egenula as type species, was introduced for former pseudocercosporid hyphomycetes characterised by having a special type of conidiogenous loci, viz. the scars are only visible by a ring-like structure formed by a slightly thickened and darkened rim. P. fijensis was originally assigned to Pseudocercospora, a position later confirmed in molecular sequence analyses (Crous et al. 2000, 2001, Stewart et al. 1999, Arzanlou et al. 2008). Therefore, Crous & Braun (2003) reduced Paracercospora to synonymy with Pseudocercospora, but the situation is more complicated as P. fijensis is, indeed, a species of the latter genus, but P. egenula, the type species of Paracercospora, does not cluster within the Pseudocercospora clade and is tentatively maintained as separate genus (Crous et al. 2013). The problem is that the scar structure (Paracercospora type) is not informative and distinctive in this case, i.e. Paracercospora is confined to its type species and only phylogenetically distinguished from Pseudocercospora. Phaeocercospora (Crous et al. 2013) is another pseudocercospora-like genus just based on its separate phylogenetic position.

Based on detailed multilocus phylogenetic examinations, Crous et al. (2013) revealed a large monophyletic Pseudocercospora (s. str.) clade, including the type species of this genus, representing Pseudocercospora emend., which is now a holomorph genus in its own right. Beside species of the "Mycosphaerella heimi" complex, forming a separate clade that is now treated as Pallidocercospora, and Phaeocercospora, there are some additional species morphologically indistinguishable from Pseudocercospora which cluster, however, apart from Pseudocercospora (s. str.) in other clades. Such phylogenetically unresolved species, as for instance P. colombiensis on Eucalyptus (Crous 1998), P. thailandica on Acacia (Crous et al. 2004b), and P. tibouchinigena on Tibuchina (Crous et al. 2013), are tentatively retained in Pseudocercospora. Pseudocercospora s. str. is characterised as follows:

Type species: Pseudocercospora vitis (Lév.) Spreg. 1910.
[Type species: S. platani (Fuckel) Sacc. 1880.]
[Type species: Ph. griseola (Sacc.) Ferraris 1909.]
Paraceratoceraspora p.p. [see Crous et al. (2013)].


Description [emend. Crous et al. (2013)]: Hyphomycetes (asexual morphs or asexual holomorphs) or Pseudocercospora with mycosphaerella-like sexual morphs; Mycosphaerellaceae. Folicolous, occasionally also caulicolous or on fruits, usually phytopathogenic, causing leaf spots or other lesions, occasionally symptomless or endophytic. Mycelium in vivo internal and/or external, superficial, sometimes climbing leaf hairs; hyphae branched, septate, hyaline to pigmented, mostly thin-walled, smooth or faintly rough-walled, mostly about 1–6 μm wide, external hyphae emerging through stomata, rarely erumpent. Stromata lacking to well-developed, small to large, substomatal, intraepidermal to deeply immersed, mostly between 10 and 120 μm diam, pale olivaceous to dark brown. Colonies on leaves, amphiogenous, sometimes also on fruits and stems, almost colourless to dark brown, scattered to dense. Conidiophores semimacronematous to mostly macronematous, in small to large, dense fascicles, arising from internal hyphae or stomata, emerging through stomata or erumpent, and/or conidiophores solitary, arising from superficial hyphae, lateral or occasionally terminal, sometimes forming sporodochial conidiomata (numerous conidiogenous cells or short conidiophores arising from well-developed stomata) or distinct synnemata, conical, cylindrical, filiform to strongly geniculate-sinuous, unbranched to branched, aseptate (conidiophores reduced to conidiogenous cells) to pluriseptate, subhyaline to dark brown, wall thin to moderately thick, smooth to somewhat rough-walled, occasionally with annelations caused by rejuvenation; conidiogenous cells integrated, terminal, occasionally intercalary, or conidiophores often reduced to conidiogenous cells, mono- to polyblastic, sympodially or percurrently proliferating, sometimes both types of proliferation mixed, conidiogenous loci inconspicuous or conspicuous by being more or less denticile-like, but locus wall always unthickened or almost so, usually neither darkened nor refractive, rarely more rigid and more conspicuous by being somewhat darkened-refractive or slightly thickened along the rim, but not thickened throughout. Conidia usually formed singly, rarely disarticulating or in short acropetal chains, usually scolecosporous, i.e. obclavate, cylindrical, filiform, acicular and pluriseptate, rarely amero- to phragmosporous, i.e. ellipsoid-ovoid, short cylindrical, fusiform, aseptate or with few septa, euseptate, rarely eusepta mixed with few distosepta, but not consistently distoseptate, hyaline or subhyaline, olivaceous, olivaceous-brown to medium dark brown, wall thin to somewhat thickened, smooth to faintly verruculose, ends rounded, truncate to obconically truncate, hila unthickened or almost so, planate, rarely slightly bulging, without marginal frill or rarely with minute frill, conidial secession schizolytic.

Type species: Palolidoceraspora heimii (Crous) Crous 2013. Pseudoceraspora p.p. [see Crous et al. (2013)].

Description: Hyphomycetes (asexual morphs or asexual holomorphs) or Palolidoceraspora with mycosphaerella-like sexual morphs; Mycosphaerellaceae. Phylogenetically distinct from Pseudocercospora, forming a separate clade. In vivo morphologically indistinguishable from Pseudocercospora, but in vitro forming red crystals on MEA, PDA, SNA and WA.

Type species: Phaecercospora colophospherum Crous 2012.

Description: Hyphomycetes (asexual morphs or asexual holomorphs); Mycosphaerellaceae. Phylogenetically distinct from Pseudocercospora, belonging to the "Dothistroma" clade". Morphologically close to and barely distinguishable from former Cercostigmata species (Cercostigmata-like Pseudocercospora species), i.e. with unilocular, determinate to percurrent conidiogenous cells. Hitherto monotypic (the type species occurs in South Africa on the legume Colophospherum mopane).

STENELLA AND ZASMIDIUM

Stenella was introduced by Sydow (1930) as monotypic genus for S. araguata, a species with conspicuously thickened, darkened conidiogenous loci and hila. However, this genus was little applied until Ellis (1976) and Deighton (1979) widened its concept and added numerous morphologically similar species, previously mostly assigned to Cercospora, characterised by forming distinctly verruculose superficial mycelium in vivo and verruculose conidia, formed singly or in chains. The number of new and reallocated species increased rapidly, encompassing a wide range of morphological types, i.e. species with exclusively solitary conidiophores arising from superficial hyphae to taxa with solitary as well as fasciculate conidiophores, with or without stromata, with catenate or solitary amero- to scolecosporous conidia or both types mixed in particular species. Similar species with stenella-like conidia, but without any verruculose superficial hyphae in vivo have previously been placed in Stenellopsis, but Braun & Crous (2005) reduced the latter genus to synonymy with Stenella, a conclusion supported by results of molecular sequence.
analyses (Shivas et al. 2009). The presence of superficial mycelium in *Stenella* is not essential on generic rank, which is comparable to the situation in other cercosporoid genera like *Passalora* and *Pseudocercospora*. *Verrucisporota*, introduced by Shaw & Alcorn (1993) as replacement for the illegitimate *Verrucospora*, with *V. proteacearum* as type species, is morphologically very close to *Zasmidium* and barely distinguishable. Previous attempts to distinguish this genus from *Stenellopsis* on the base of differences in the stroma structure, broad loci and rugose conidia (Ellis 1971, David 1997) are neither practicable nor tenable. New species of this genus described by Beilharz & Pascoe (2002) are rather *zasmidium-like*. One of these species, *V. proteacearum* (asexual morphs or asexual holomorphs) or *Zasmidium* with mycosphaerella-like sexual morphs; *Mycosphaerellaceae*. Saprobic or mostly biotrophic, usually foliculous, symptomless or causing various lesions, ranging from yellowish discolorations to distinct leaf spots. In plant pathogenic species, mycelium mostly immersed as well as superficial, rarely only immersed; hyphae branched, septate, colourless or almost so to pigmented, pale olivaceous to brown, wall thin to somewhat thickened, immersed hyphae smooth or almost so to faintly rough, external hyphae distinctly verruculose to verrucose (in culture immersed hyphae usually smooth or almost so, aerial hyphae verruculose). Stromata lacking to well-developed, pigmented. Conidiophores solitary, arising from superficial hyphae, lateral, occasionally terminal, in vivo (in plant pathogenic taxa) sometimes also fasiculate, arising from internal hyphae or stromata, semimacronematous to macronematous, in culture occasionally micronematous, cylindrical, filiform, subuliform, straight to strongly geniculate-sinuous, mostly unbranched, asceptate, i.e. reduced to conidigenous cells, to plurisepate, subhyaline to pigmented, pale olivaceous to medium dark brown, wall thin to somewhat thickened, smooth to verruculose; conidigenous cells integrated, terminal, occasionally intercalary, rarely pleurogenous, or conidiophores reduced to conidigenous cells, mostly polyblastic, sympodial, conidigenous loci conspicuous, somewhat thickened and darkened-refractive, planate. *Conidia* solitary or catenate, in simple or branched acropetal chains, shape and size variable, ranging from amoerato scolecosporous, asceptate to transversely plurisepate, subhyaline to pigmented, pale olivaceous to brown, wall thin to somewhat thickened, smooth or almost so to usually distinctly verruculose (in plant pathogenic species without superficial mycelium always verruculose), hila somewhat thickened and darkened-refractive, planate, conidial secession schizolytic.

**Type species**: *Stenella araguata* Syd. 1930.

**Description** [emend. Braun et al. (2010a)]: *Hyphomycetes* (asexual morphs or asexual holomorphs) or *Zasmidium* with mycosphaerella-like sexual morphs; *Mycosphaerellaceae*. Saprobic or mostly biotrophic, usually foliculous, symptomless or causing various lesions, ranging from yellowish discolorations to distinct leaf spots. In plant pathogenic species, mycelium mostly immersed as well as superficial, rarely only immersed; hyphae branched, septate, colourless or almost so to pigmented, pale olivaceous to brown, wall thin to somewhat thickened, immersed hyphae smooth or almost so to faintly rough, external hyphae distinctly verruculose to verrucose (in culture immersed hyphae usually smooth or almost so, aerial hyphae verruculose). Stromata lacking to well-developed, pigmented. Conidiophores solitary, arising from superficial hyphae, lateral, occasionally terminal, in vivo (in plant pathogenic taxa) sometimes also fasiculate, arising from internal hyphae or stromata, semimacronematous to macronematous, in culture occasionally micronematous, cylindrical, filiform, subuliform, straight to strongly geniculate-sinuous, mostly unbranched, asceptate, i.e. reduced to conidigenous cells, to plurisepate, subhyaline to pigmented, pale olivaceous to medium dark brown, wall thin to somewhat thickened, smooth to verruculose; conidigenous cells integrated, terminal, occasionally intercalary, rarely pleurogenous, or conidiophores reduced to conidigenous cells, mostly polyblastic, sympodial, conidigenous loci conspicuous, somewhat thickened and darkened-refractive, planate. *Conidia* solitary or catenate, in simple or branched acropetal chains, shape and size variable, ranging from amoerato scolecosporous, asceptate to transversely plurisepate, subhyaline to pigmented, pale olivaceous to brown, wall thin to somewhat thickened, smooth or almost so to usually distinctly verruculose (in plant pathogenic species without superficial mycelium always verruculose), hila somewhat thickened and darkened-refractive, planate, conidial secession schizolytic.

**TENTATIVELY RECOGNISED CERCOSPOROID GENERA**

**Type species**: *Asperisporium caricae* (Speg.) Maubl. 1913.


**Description:** Usually foliicolous, leaf-spotting hyphomycetes, *Mycosphaerellaceae*. *Mycelium* in vivo internal; hyphae branched, septate, colourless to pigmented, thin-walled, smooth or almost so. *Stromata* usually well-developed, substomatal to intraepidermal, often somewhat erumpent. Conidiogenous cells integrated, terminal or formed as lateral branchlets, arising from superficial hyphae, conidiogenous loci conspicuous, thickened and darkened, conidia catenate, pigmented. Myosphaerella-like clade close to several *Passalora* species, including *P. brachycarpa*. According to this result, *Asperisporium* is undoubtedly a potential synonym of *Passalora*. However, its type species, *P. brachycarpa*, is morphologically very close to *Passalora*, as already emphasized by Crous & Braun (2003), except for verrucosus conidia. The phylogenetic position of *A. caricae*, its type species, has recently been elucidated in Minnis et al. (2011), based on DNA sequences from the ITS region and LSU. Although it is supposed that the genus *Asperisporium* is polyphyletic and the phylogenetic position of its type species is still unknown, a formal reassessment of *Asperisporium* was postponed by Minnis et al. (2011) until the whole *Passalora* complex will be phylogenetically examined and reassessed. However, the postponed reassessment of the genus *Asperisporium* does only concern its type species. Other species assigned to *Asperisporium* have to be individually reassessed, if possible based on molecular sequence data. *Asperisporium sequoiae* and *A. juniperinum*, two species on Gymnosperms with relatively delicately rough-walled conidia, are typical examples. However, it is still unclear and unproven whether this genus belongs in the *Mycosphaerellaceae*. Therefore, *Denticularia* is tentatively retained as genus on its own.

**Notes:** Morphologically close to *Cladosporium* and *mycovelllosiella-like Passalora* species (with superficial hyphae, conidiophores fasciculate or solitary, arising from superficial hyphae, conidiogenous loci conspicuous, thickened and darkened, conidia catenate, pigmented), but the loci and hila are not cladosporium-like (not coronate) and all species assigned to this genus are hyperparasitic. The hyperparasitic habit as single character is barely acceptable and usable to discriminate this genus from *Passalora*, but since the phylogenetic position of *Cladosporiella* and its relation to the *Mycosphaerellaceae* is still unclear and unproven, we tentatively prefer to maintain it as separate genus.


**Type species:** *Denticularia modesta* (Syd.) Deighton 1972.

**Notes:** Morphologically close to *Pseudocercospora* (leaf spotting hyphomycetes with unthickened, not darkened conidiogenous loci and hila), but the conidiogenous loci are distinctly denticle-like, and the catenate conidia are nontocolosporous, only with 0–1–3 septa. Cultures of the type species of this genus and results of molecular sequence analyses are necessary to resolve its phylogenetic position and clarify its relation to *Pseudocercospora*. It is still unclear and unproven if this genus belongs in the *Mycosphaerellaceae*. Therefore, *Denticularia* is tentatively retained as genus on its own.


**Type species:** *Elletevera parasitica* (Ellis & Everh.) Deighton 1969.

**Notes:** This genus was introduced for hyperparasitic cercosporoid hyphomycetes with “distinct” conidiogenous loci, morphologically resembling species of the former genus *Mycovelllosiella*. However, the re-examination of several collections of the type species of *Elletevera* showed that Deighton’s (1969) original description of the conidiogenous
loci (scars) is misleading (Crous & Braun 2003). Due to
denticle-like loci with unthickened, not darkened walls, 
Elettevera is possibly related to Pseudocercospora or perhaps
not cercosporoid at all. But this question cannot be answered
without knowledge of the phylogenetic affinity of this genus,
which is still unproven and unclear. The hyperparasitic habit
alone is insufficient to uphold Elettevera as separate genus,
but until its phylogenetic position is proven the latter genus
is tentatively maintained.

*Type species*: *Eriocercosporella balladynae* (Hansf.) Deighton
1969.


**Description**: Fungicolous, hyperparasitic dematiaceous
hyphomycetes. *Myccelium* superficial; hyphae branched, 
septate, pigmented, thin-walled, smooth. *Stromata* lacking. 
*Conidiophores* macronematous, mononematous, solitary, *in vivo*
 arising from superficial hyphae, lateral, erect, usually
unbranched, continuous to septate, pigmented, thin-
walled, smooth; *conidiogenous cells* integrated, terminal
and intercalary, sympodially proliferating, but usually not
distinctly geniculate, conidiogenous loci subconspicuous, i.e.
unthickened, not or barely protuberant, not or only slightly
darkened-refractive. *Conidia* solitary, scolecosporous,
transversely euseptate, pigmented, thin-walled, smooth or
almost so, hila unthickened, not or barely darkened-refractive.

**Notes**: Due to the conidiogenesis, the structure of the
conidiogenous cells and the thick-walled conidia, this
genus seems to be allied to the *Sporidesmium* complex,
but an affinity to *Pseudocercospora* can also not be
excluded with certainty. However, the phylogenetic affinity of
Eriocercosporella and its relation to the Mycosphaerellaceae
are currently quite unclear. Molecular examinations of the
phylogenetic position of the type species of this genus are
necessary to decide if Eriocercosporella belongs to the
cercosporoid or to the sporidesmioid complex. Therefore,
this genus is only tentatively treated in the present context of
cercosporoid genera.

*Type species*: *Pantospora guazumae* Cif. 1938.

373: 13 (1962) [*type species*: *D. ulmifolia* (Obreg.-Bot.)
A.G. Medeiros 1962].

*Literature*: Deighton (1976: 156–159), Crous & Braun (2003:

**Description**: Fungicolous hyphomycetes, associated with leaf
spots. *Myccelium* internal and external, superficial hyphae
emerging through stomata, branched, pigmented, septate,
thin-walled, smooth. *Stromata* lacking. *Conidiophores* 
macronematous, mononematous, *in vivo* solitary, arising from
superficial hyphae, lateral, simple, occasionally branched,
pigmented, septate, thick-walled, smooth; conidiogenous
cells integrated, terminal, uni- to multilocular, sympodially
or occasionally percurrently proliferating, loci truncate, flat,
broad, neither thickened nor darkened, conidiogenesis
thalloblastic, i.e. at first blastic, then thalic (base of
conidia ± agreeing in width with the diameter of the broad
conidiogenous loci). *Conidia* solitary, cylindrical to clavate,
oncasionally disarticulating, pluriseptate, occasionally with
1–2 additional distosepta, thick-walled, brown, smooth, not
attenuated at the base, hila truncate, broad, width ± agreeing
with the diameter of the conidiogenous loci, neither thickened
nor darkened, conidial secession schizolytic.

**Notes**: The genus *Pantospora* was described by Ciferri
(1938). *Pantospora guazumae*, the type species, is a leaf-
spotting hyphomycete on *Guazuma ulmifolia*. Dictyocephala,
based on *Cercospora ulmifolia* described from Colombia on
G. ulmifolia, is undoubtedly a synonym of Pantospora as already pointed out by Deighton (1976), who recognised the latter genus although its type species is very similar to the type species of Pseudocercospora by forming conidiophores in dense corymbose fascicles or distinct synnemata and sympodially to percurrently proliferating conidigenous cells with unthickened, not darkened conidigenous loci. The regular formation of oblique to longitudinal conidial septa was considered to be the only difference, although a few non-horizontal septa may also occur in some Pseudocercospora species, including P. vitis, its type species. As there is no rational base for a morphological discrimination between the two genera, Crous & Braun (2003) reduced Pantospora to synonymy with Pseudocercospora. However, sequence analyses based on data from the rDNA ITS and nLSU region, recently carried out by Minnis et al. (2011), showed that Pantospora guazumae did neither cluster within the Pseudocercospora s. str. clade [= clade 16, including the type species P. vitis, according to Crous et al. (2009b)] nor in clade 14 with other pseudocercospora-like species. The closest relatives were rather passalora-like. These results suggest that Pantospora cannot be considered a synonym of Pseudocercospora. This genus is, at least tentatively, maintained as separate genus until a better resolution of the assemblage of species around P. guazumae will be available.


Type species: Paracercospora egenula (Syd.) Deighton 1979.

**Description:** Dematiaceous hyphomycete genus morphologically barely distinguishable from Pseudocercospora, but phylogenetically distinct; Mycosphaerellaceae. Mycelium in vivo internal. Conidiophores macronematous, fasciculate, pigmented; conidigenous cells integrated, terminal or conidiophores reduced to conidiogenous cells, conidiogenous loci subconspicuous by being circular with very slightly thickened and darkened-refractive rim. Conidia solitary, scoccosporous, subhyaline to very pale olivaceous, hila very slightly thickened and darkened-refractive along the rim.

**Notes:** The phylogenetic position and taxonomy of Paracercospora is complicated and not yet fully understood. Based on early phylogenetic analyses, Stewart et al. (1999) considered Paracercospora a synonym of Pseudocercospora and concluded that conidigenous loci (scars) only slightly thickened and darkened around the rim are not sufficiently different from quite unthickened loci to be used as distinctive character on generic level, which was supported by additional rDNA ITS examinations (Crous et al. 2000, 2001). Therefore, Crous & Braun (2003) followed this conclusion and treated Paracercospora as synonym of Pseudocercospora. However, the reassessment of Paracercospora was based on data derived from non-type species, mainly P. fijiensis and P. basiramifera (Crous 1998, Arzaniou et al. 2008), which indeed cluster within the big Pseudocercospora clade. Paracercospora egenula, the type species of Paracercospora, has recently been included in molecular sequence analyses, but clustered apart of the Pseudocercospora clade in a not yet fully understood clade together with Passalora brachybarca, a species with catenate conidia, Pseudocercospora tibuchigina, which is morphologically indistinguishable from genuine Pseudocercospora spp., and several Mycosphaerella spp. (Crous et al. 2012). Hence, Paracercospora is currently confined to its type species, characterised by circular conidigenous loci with slightly thickened, darkened-refractive rim and very pale conidia. Since such paracercosporid loci as well as subhyaline or pale conidia are also known in several genuine Pseudocercospora species, there is no rational base for a morphological discrimination of the two genera, i.e. Paracercospora s. str. is currently just a phylogenetically differentiated monotypic genus.


**Type species:** Parastenella magnoliae (Weedon) J.C. David 1991.

**Synonym:** Stenellopsis Morgan-Jones, Mycotaxon 10: 405 (1980), nom illeg. (Art. 53.1).


**Description:** Dematiaceous hyphomycete genus resembling Zasmidium in vivo with superficial mycelium, hyphae, conidiophores and solitary conidia pigmented, distinctly verruculose to verrucose), but the conidigenous cells are terminal and intercalary, denticulate, with lateral short peg-like protuberances, conidigenous loci inconspicuous, neither thickened nor darkened.

**Notes:** The phylogenetic position of this genus is unknown. It is quite unclear if it is part of the Capnodiales and Mycosphaerellaceae at all.


**Type species:** Pseudoasperisporium tupae (Speg.) U. Braun 2000.

**Literature:** Seifert et al. (2011: 363).

**Notes:** Morphologically close to Asperisporium, but the conidigenous loci and hila at the base of conidia are unthickened and not darkened. Species of Pseudoasperisporium are distinguished from superficially similar Fusicladium species (Venturiaceae) by having coarsely verruculose conidia. The phylogenetic affinity of this genus is, however, unclear and unproven.


**Type species:** Pseudocercosporidium venezuelanum (Syd.) Deighton 1973.

Description: Foliicolous, plant pathogenic, leaf spotting hyphomycetes, telemorph unknown. Mycelium internal. Stromata lacking. Conidiophores in vivo solitary or in small loose fascicles (groups) emerging through stomata, laxly erect, macronematous, frequently branched, septate, pigmented (very pale brown), thin-walled, smooth; conidiogenous cells integrated, terminal, intercalary or pleurogenous (as lateral branchlets), sympodial, polyblastic, conidiogenous loci conspicuous, protruding, convex (papilla-like), but wall of the loci neither thickened nor darkened, only somewhat refractive. Conidia solitary, didymous to scolecosporous, pigmented (deeper in pigmentation than the conidiophores), thin-walled, smooth or almost so, hila neither thickened nor darkened.

Notes: The phylogenetic affinity of *P. venezuelanum* and its relation to the *Mycosphaerellaceae* are unknown. *Pseudocercosporidium* resembles *Passalora*, but the structure of the conidiogenous loci is quite distinct and closer to scars of genera like *Neoovularia* and *Pseudodidymaria* (Braun 1998).


Type species: *Quasiphloeospora saximontanensis* (Deighton) B. Sutton, Crous & Shamoun 1996.


Description: Cercosporoid hyphomycetes characterised by forming large immersed sporodochia-like conidiomata with filiform, somewhat pigmented, irregularly verruculose conidiophores, aseptate, i.e. reduced to conidiogenous cells, monoblastic, determinate or sympodially to percurrently proliferating, with slightly thickened and darkened conidiogenous loci, and very pale to somewhat pigmented scolecosporous conidia formed singly.

Notes: *Quasiphloeospora* is a cercosporoid genus with intricate morphology and complex morphological relations to several other genera, including *Cercospora*, *Passalora* and *Pseudocercospora* (Crous & Braun 2003), but due to very pale, almost colourless structures also to genera like *Pseudocercospora*. Sutton et al. (1996) classified the conidiomata as acervuli, although they may better be referred to as sporodochia. The particular characters of *Q. saximontanensis*, above all the structure of the conidiogenous loci, are intermediate between the three similar genera cited above. A clear affiliation to one of these genera, just based on morphology, is not possible. It is also possible that this species is unrelated to any of the cercosporoid genera. Affinity and position of *Quasiphloeospora* can only be proven by means of results of molecular sequence analyses, which are, however, not yet available. This genus might belong in the *Mycosphaerellaceae*, but this is unproven. Thus, *Quasiphloeospora* is only tentatively maintained as separate cercosporoid genus.


Type species: *Scolecostigmina mangiferae* (Koord.) U. Braun & Mouch. 1999.

*Stigmina* p.p. [see Braun (1999), Crous et al. (2013)].


Description: *Scolecostigmina* is morphologically close to *Pseudocercospora*, above all to former *Cercostigmina* species (leaf spotting dematiaceous hyphomycetes with sporodochial conidiomata, macronematous densely fasciculate conidiophores, percurrently proliferating conidiogenous cells, neither thickened nor darkened applanate loci, and scolecosporous, plurieuseptate, pigmented conidia formed singly), but the wall of the conidiophores is somewhat thickened and mostly verruculose, possesses conspicuous, coarse annellations and the conidia are transversely and occasionally also obliquely or longitudinally septate.

Notes: *S. mangiferae*, the type species, which belongs in the *Mycosphaerellaceae*, does not cluster within the *Pseudocercospora* clade, i.e. it is phylogenetically distinct, supporting *Scolecostigmina* as separate genus. The correct placement of numerous additional species in *Scolecostigmina* is, however, phylogenetically unproven and quite unclear. Sequence data derived from cultures of *Scolecostigmina chibaensis* on *Pinus* spp. in Japan (Nakashima et al. 2007) have been analysed and showed that this species is not allied to the type species of *Scolecostigmina* and does not belong to the *Mycosphaerellaceae* at all. It takes an isolated position with unclear affinity on family level, and does not belong to any other families containing cercosporoid hyphomycetes as for instance *Cladosporiaceae*, *Dissoconiacaeae* or *Teratosphaeriacae* (Nakashima, unpubl. data). Due to the phylogenetic position of *Cercospora cryptomeriicola* within the *Pseudocercospora* clade, this species has been reallocated to the latter genus, although its morphology is rather scolecostigmina-like. The conidiomata are sporodochial, conidiogenous cells proliferate percurrently with conspicuous annellations, and the walls of the conidia are thickened (Nakashima et al. 2007). These data indicate that the typical “Scolecostigmina” morphology is unreliable, i.e. all species assigned to *Scolecostigmina* have to be re-examined and reassessed once molecular data are available.


Description: Morphologically close to *Pseudocercospora* (leaf spotting hyphomycetes with unthickened, not darkened conidiogenous loci and hila), but the conidiogenous cells are not geniculate, i.e. not distinctly sympodially proliferating, the conidiogenous loci are distinctly denticle-like, and the solitary conidia are didymous to phragmosporous, i.e. not scolecosporous.

Notes: The phylogenetic position of the type species of this genus and its relation to the *Mycosphaerellaceae* as well as to the genus *Pseudocercospora* are still unknown.
and unproven. Therefore, *Semipseudocercospora* is only tentatively maintained as separate cercosporoid genus.

**Sirosporium** Bubák & Serebrian., *Hedwigia* 52: 272 (1912).

*Type species*: *Sirosporium antenniforme* (Berk. & M.A. Curtis) Bubák & Serebrian. 1912.


*Description*: Morphologically close to *Passalora*, i.e. above all mycocellulosa-like (leaf spotting dematiaceous hyphomycetes with internal and external mycelium, superficial hyphae giving rise to solitary conidiophores, lateral and terminal, conidiophores may also be formed in fascicles, conspicuous conidiogenous loci and hila, thickened and darkened, conidia solitary, size, shape and septation variable), but the conidia are relatively thick-walled and at least partly dictyosporous.

*Notes*: The morphological differentiation between *Sirosporium* and mycocellulosa-like *Passalora* species is vague. The phylogenetic meaning and value of thick conidial walls and oblique to longitudinal septa as distinguishing characters between *Sirosporium* and *Passalora* is unclear. The phylogenetic position of the type species of *Sirosporium* is still unknown. As already proposed in Braun (1995a) as well as Crous & Braun (2003), *Sirosporium* is tentatively treated as separate genus and should be confined to species with dictyosporous conidia with thick walls.

**Doubtful and Excluded Genera**

Several hyphomycete genera have previously been considered to be and treated as cercosporoid genera, but based on modern phylogenetic examinations they are not part of the family *Mycosphaerellaceae* and the corresponding clade, i.e. they belong elsewhere and are not cercosporoid *s. lat.*. Species of such genera are not treated here:


*Type species*: *Miuraea degenerans* (Syd. & P. Syd.) Hara 1948.


*Notes*: Statements that *Miuraea* is associated with mycosphaerella-like teleomorphs and belongs to the *Mycosphaerellaceae* were based on *Miuraea persicae* (sexual morph: *Mycosphaerella pruni-persicae*). This species clusters together with *Pseudocercospora* species within the *Mycosphaerellaceae* (Crous *et al.* 2013) and should rather be assigned to the latter genus, which is in its current circumscription non-monophyletic. It is quite unclear and phylogenetically unproven if *M. persicae* is congeneric with *M. degenerans*, the type species of *Miuraea*. The latter species differs from *M. persicae* in having thin-walled, hyaline hyphae and conidia, which become thick-walled and pigmented with age. Longitudinal and oblique septa are rather common. *Miuraea s. str.* does possibly not belong to the *Mycosphaerellaceae* at all, but this is not yet proven. *Miuraea asiminae*, another species treated under *Miuraea* in Braun (1995a), was later reallocated to *Pseudocercospora* (Braun & Crous 2008).


*Notes*: The type species, originally described as species of *Cercospora*, was later reallocated to *Pseudocercospora* (Braun 1993). However, based on molecular sequence analyses, recently carried out by Crous *et al.* (2013), it was demonstrated that it represents an undescribed genus belonging to the *Pleosporales*.


*Type species*: *Thedgonia ligustrina* (Boerema) B. Sutton 1973.


*Notes*: *Thedgonia* was previously considered a cercosporoid genus with a type species originally assigned to *Cercospora s. lat.* (von Arx 1983, Braun 1995a), which was seemingly supported by the finding of the sexual morph of *T. lupini*, described as *Mycosphaerella lupini* (Kaiser & Crous 1998), and the phylogenetic position of this species in the *Mycosphaerellaceae* (Crous & Braun 2003). However, *T. ligustrina*, the type species of *Thedgonia*, and *T. lupini* are not congeneric and phylogenetically distinct since *T. ligustrina* clusters within the *Helotiales* (Crous *et al.* 2009a, 2013). *Thedgonia lupini* has to be reassessed and reallocated to a genus within the *Mycosphaerellaceae*, maybe to the non-monophyletic genus *Pseudocercospora* to which this species roughly fits. The affinity of other species assigned to *Thedgonia* is unclear and unproven.


*Notes*: *Xenostigmina* and its synanamorphs in *Mycopappus* belong to the *Pleosporales* (Crous *et al.* 2013), i.e. they are not part of the *Mycosphaerellaceae*, in contrast to *Stigmina s. str.* which has been reduced to synonym with *Pseudocercospora* (Crous *et al.* 2006).
# KEY TO CURRENTLY RECOGNISED CERCOSPOROID GENERA

Expanded keys to cercosporoid genera and morphologically similar and confusable genera have been published in Braun (1995a: 23–36), Crous & Braun (2003: 28–32) and Braun in Seifert et al. (2011: 887–893).

<table>
<thead>
<tr>
<th>Key</th>
<th>Description</th>
<th>Notes</th>
</tr>
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<tbody>
<tr>
<td>1</td>
<td>Saprobiic or biotrophic, plant pathogenic hyphomycetes, causing various lesions, mostly leaf-spotting</td>
<td>2</td>
</tr>
<tr>
<td>2</td>
<td>Very large immersed sporodochium-like conidiomata, about 40–130 μm diam, with filiform, somewhat pigmented, irregularly verruculose conidiophores, aseptate, i.e. reduced to conidiogenous cells, monoblastic, determinate or sympodially to percurrently proliferating, with slightly thickened and darkened conidiogenous loci, and pale (subhyaline) to somewhat pigmented scolecosporous conidia formed singly; on <em>Ribes saximontanensis</em> in North America</td>
<td>Quasiphielospora</td>
</tr>
<tr>
<td>3</td>
<td>Stromata lacking; conidiophores in vivo solitary or in small loose fascicles (groups) emerging through stomata, laxly erect, frequently branched, very pale brown; conidiogenous cells integrated, terminal, intercalary or pleurogenous (as lateral branchlets), conidiogenous loci conspicuous, protruding, convex (papilla-like), but wall of the loci neither distinctly thickened nor darkened, only somewhat refractive; conidia solitary, didymo- to scolecosporous, pigmented (deeper in pigmentation than the conidiophores), hilum neither thickened nor darkened</td>
<td>Pseudocercosporidium</td>
</tr>
<tr>
<td>4</td>
<td>Conidiogenous loci inconspicuous, neither thickened nor darkened or subconspicuous by being more rigid or denticile-like, but wall of the loci always unthickened and not darkened, at most somewhat refractive, or only slightly thickened and darkened around the rim (formed as minute somewhat darker rim visible as darker circle)</td>
<td>Parastenella</td>
</tr>
<tr>
<td>5</td>
<td>Conidiogenous loci conspicuous, thickened and darkened throughout, except for a very minute centre pore (in front view visible as minute dark circle)</td>
<td></td>
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<tr>
<td>6</td>
<td>Forming superficial mycelium in vivo, hyphae verruculose-verrucose; conidiogenous cells terminal and intercalary, denticulate, with lateral short peg-like protuberances, conidiogenous loci inconspicuous, neither thickened nor darkened</td>
<td>Parastenella</td>
</tr>
<tr>
<td>7</td>
<td>Conidiophores in vivo in synnematous conidiomata</td>
<td></td>
</tr>
<tr>
<td>8</td>
<td>Conidiophores in sporodochial conidiomata; wall of the densely arranged conidiophores somewhat thickened and mostly distinctly verruculose, forming conspicuous, coarse annellations; conidia transversely and occasionally also obliquely or longitudinally septate, wall often somewhat thickened</td>
<td>Scolecostigmina</td>
</tr>
<tr>
<td>9</td>
<td>Conidiophores thin-walled, rarely somewhat thickened, but then always smooth, annellations lacking or if present fine and rather inconspicuous; conidia usually thin-walled and transversely septate</td>
<td></td>
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<tr>
<td>10</td>
<td>Conidiogenous cells with distinct denticles; conidia amero- to phragmosporous, i.e. not scolecosporous</td>
<td>Pseudoasperisporium</td>
</tr>
<tr>
<td>11</td>
<td>Conidiogenous cells not denticulate or only subdenticulate (conidiogenous loci on shoulders caused by sympodial proliferation) and then scolecosporous</td>
<td>Pseudocercospora</td>
</tr>
</tbody>
</table>

- *Ribes saximontanensis* in North America
- *Quasiphielospora*
- *Pseudocercosporidium*
- *Parastenella*
- *Scolecostigmina*
- *Pseudoasperisporium*
- *Pseudocercospora* (synnematous species)
11 (10) Conidiogenous cells not geniculate, i.e. not distinctly sympodially proliferating, conidiogenous loci formed as distinct terminal to lateral denticles; conidia solitary, didymo- to phragmosporous; on *Peristrophe*, Asia .......................................................... *Semipseudocercospora*

Conidiogenous cells sympodially proliferating; conidia catenate, 0–1(–3)-septate ............................................... *Denticularia*

12 (10) Conidiophores fasciculate and solitary, arising from superficial hyphae; conidiogenesis thalloblastic; conidiogenous loci truncate, flat, broad, loci and conidium initials of similar width, conidial base not or barely constricted; conidia thick-walled; on *Marsdenia* in India ...................................................... *Eriocercospora*

Conidiogenesis holoblastic; width of loci and conidium initials different, narrowed at the attachment point between conidiogenous cells and conidium initial .......................................................... 13

13 (12) Conidiophores solitary, arising from superficial hyphae, fasciculate, in sporodochia or even synnemata; conidiogenous loci inconspicuous or conspicuous by being more or less denticle-like, but locus wall always unthickened or almost so, usually neither darkened nor refractive, rarely more rigid and more conspicuous by being somewhat darkened-refractive or slightly thickened and darkened along the rim [loci ring-like, slightly thickened and darkened along the rim, on *Solanum*, see *Paracercospora* s. str.]; conidia solitary, rarely in short chains, usually scolecosporous, rarely amero- to phragmosporous, subhyaline to usually pigmented [in *vitro* without red crystals] .......................................................... *Pseudocercospora*  

[On *Colophospermum copane*, South Africa; conidiogenous cells unilocal, determinate to percurrent, *Cercostigmata*; phylogenetically distinct from *Pseudocercospora* s. str., see *Phaeocercospora*]

Conidiophores solitary or fasciculate; morphologically barely distinguishable from *Pseudocercospora*, but phylogenetically distinct and with red crystals *in vitro* (*P. heimii* complex) ........................................... *Pallidocercospora*

14 (4) *In vivo* with distinctly verruculose-verrucose superficial hyphae (aerial mycelium *in vitro* also verruculose); conidia smooth or almost so to mostly verruculose-verrucose as well .......................................................... 15

Superficial hyphae *in vivo* lacking or, if present, smooth or almost so .......................................................... 16

15 (14) Conidiogenous loci pileate; conidiophores *in vivo* solitary as well as fasciculate; conidia catenate; on *Pithecellobium*, South America (*Teratosphaeriaceae*) .......................................................... *Stenella*

Conidiogenous loci planate (*Cercospora*-like) (*Mycosphaerellaceae*) .......................................................... *Zasmidium*

16 (14) Conidiophores pigmented, rarely hyaline or subhyaline [subgen. *Hyalocercospora*]; conidia always colourless, usually scolecosporous, acicular, filiform, obclavate-cylindrical, and pluriseptate, rarely amero- to phragmosporous .................................................. *Cercospora*

Conidiophores and conidia pigmented, at least faintly olivaceous .......................................................... 17

17 (16) Conidia consistently distoseptate; conidiophores mostly frequently branched ...................................... *Distocercospora*

Conidia aseptate to euseptate or at most few distosepta mixed with eusepta .................................................. 18

18 (17) Conidia distinctly (usually coarsely) verruculose-verrucose .......................................................... 19

Conidia smooth or almost so .......................................................... 20

19 (18) Conidiophores mostly numerous in dense sporodochial conidiomata; conidia solitary, usually amero- to phragmosporous, occasionally with longitudinal or oblique septa ........................................... *Asperisporium*

Conidiophores fasciculate; conidia solitary, but scolecosporous, only transversely septate  

.................................................................................. *Zasmidium* (p.p., species without superficial hyphae *in vivo*)

20 (18) Conidia solitary, ± scolecosporous, fully developed conidia usually attenuated towards the tip, somewhat rostrate, often somewhat curved, wall thickened; conidiogenous loci subconspicuous, ranging from inconspicuous to conspicuous by being denticle-like or somewhat darkened-refractive, but always unthickened; *in vivo* without superficial mycelium .... see *Pseudocercospora* p.p. (incl. *Prathigada*)

Conidia solitary to catenate, amero- to scolecosporous, not rostrate, usually thin-walled; *in vivo*

with or without superficial mycelium .......................................................... 21

21 (20) *In vivo* with solitary conidiophores arising from superficial hyphae; conidia scolecosporous, fairly thick-walled, with transverse and occasionally also longitudinal and oblique septa ...................................... *Sirosporium*

*In vivo* with internal or internal and external hyphae; conidia amero- to scolecosporous, thin-walled, transversely septate .................................................. 22
22 (21) Conidia solitary or catenate; conidiogenous loci and conidial hila always distinctly thickened and darkened .................................................. Passalora
Conidia catenate; conidiogenous loci subconspicuous, ranging from inconspicuous to conspicuous by being somewhat darkened-refractive, but always unthickened
.............................................................................................. see Pseudocercospora p.p. (incl. Pseudophaeoramularia)

23 (1) Conidiophores laxly fasciculate, often branched; conidiogenous cells denticulate, but conidiogenous loci not thickened and not darkened; hyperparasitic on ascomycetes (Phyllachora) .................................................. Elletevera
In vivo with solitary conidiophores arising from superficial hyphae; conidiogenous loci not denticle-like ................... 24

24 (23) Conidia catenate; conidiogenous loci somewhat thickened and darkened; on cercosporoid hyphomycetes and rusts  .............................................................. Cladosporiella

Conidia solitary; conidiogenous loci subconspicuous, unthickened, not or only slightly darkened-refractive; on sooty moulds .............................................................. Eriocercospora

TAXONOMIC TREATMENT

Fungicolous cercosporoid species

The genera Cladosporiella, Elletevera and Eriocercospora, which may have affinity to cercosporoid genera, are treated in this chapter. However, the phylogenetic positions of these genera are quite unclear. Molecular data are not yet known. Elletevera and Eriocercospora species are rather pseudocercospora-like, but might also be related to similar denticulate hyphomycete genera or to the Sporidesmium complex. Affinity and position of Cladosporiella, morphologically superficially similar to the Cladosporium complex, is also quite unclear. This genus is treated here due to rough similarity to phaeoramularia-like Passalora species. All hyperparasitic taxa are only tentatively included in this work on cercosporoids. The name Cercospora uredinophila (Deighton 1969) suggests a hyperparasitic habit, but proved to be a common phytopathogenic fungus on various Scirpus spp. A comprehensive treatment of this species with full synonymy was published in Braun (1995a). Cercospora uromycestri and C. acori, reallocated to Passalora in Crous & Braun (2003), seems to be the only true cercosporoid species hyperparasitic or at least fungicolous on rust fungi.

CLADOSPORIELLA

Key to the species of Cladosporiella

1 Conidiophores very long, about 25–500 µm; on rust fungi .......................................................... 2
Conidiophores much shorter, about 8–40 µm; on cercosporoid hyphomycetes ............................................. 3

2 (1) Stromata lacking; conidia (7–)15–40(–50) × 3.5–4.5 µm, (0–)1–2(–5)-septate .................. C. uredinicola
Stromata well-developed and large, 20–90(–150) µm diam; conidia broader, 4–6.5 µm, (0–)1(–3)-septate .................. C. uredines

3 (1) Conidia 20–135 × 2–5 µm, 0–9-septate ........................................... C. cercosporicola
Conidia much shorter, 9–15 × 3–4 µm, 0–3-septate .................................................. C. deightonii

List of Cladosporiella species

(Fig. 2)

Illustrations: Deighton (1965: 36, fig. 14), Ellis (1971: 303, fig. 209), Seifert et al. (2011: 709, fig. 227B).


Description: Colonies hyperparasitic on Passalora koepkei, loosely floccose, pale. Mycelium superficial, some pale hyphae tightly coiled around conidiophores and conidia, branched, septate, thin-walled, smooth. Stromata none. Conidiophores arising from superficial hyphae, erect, straight to flexuous, unbranched, 8–40 × 3–4 µm, continuous or sparingly septate, pale olivaceous, thin-walled, smooth; conidiogenous cells integrated, terminal or conidiophores reduced to conidiogenous cells, about 5–20 µm long, conidiogenous loci conspicuous, slightly thickened and darkened, small, about 0.8–1 µm diam. Conidia catenate, in branched chains, subcylindrical to filiform or somewhat obclavate, 20–135 × 2–4.5(–5) µm, 0–9-septate, pale olivaceous, smooth, thin-walled, ends short obconical, occasionally slightly swollen, hila slightly thickened and darkened.

Holotype: Sabah; on Passalora koepkei, Mycosphaerellaceae, on Saccharum officinarum, Poaceae, 1964, J. Solomon (K(M) IMI 107538b).
**Host range and distribution:** Only known from the type collection.

(Fig. 3)

**Illustration:** Castañeda & Braun (1989: 45, fig. 9).

**Description:** Colonies on leaf spots of and associated with *Cercospora coffeicola*, hypophyllous, pale. *Mycelium* superficial; hyphae flexuous, richly branched, 1–4 µm wide, pale olivaceous-brown, septate, thin-walled, smooth. *Stromata* lacking. **Conidiophores** arising from superficial hyphae, lateral, erect, almost straight to geniculate-sinuous, narrowed towards the apex, unbranched, 8–30 × 2–3 µm, aseptate, rarely with 1–2 septa, olivaceous, thin-walled, smooth; conidiophores usually reduced to conidiogenous cells, rarely with integrated, terminal conidiogenous cells, conidiogenous loci conspicuous, minute, about 1 µm diam, slightly thickened and darkened, often situated on short peg-like protuberances or shoulders caused by sympodial proliferation near the apex. **Conidia** formed singly or in short chains, ellipsoid, subcylindrical, subclavate, 9–15 × 3–4 µm, 0–3-septate, pale olivaceous to brownish, thin-walled, smooth, ends rounded to attenuated, hila slightly thickened and darkened, about 1–1.5 µm wide.

**Types:** Cuba: Los Corrales de Guisa, Granma, on *Cercospora coffeicola*, Mycosphaerellaceae, on *Coffea arabica*, Rubiaceae, 24 June 1987, R. F. Castañeda (INIFAT C87/171 - holotype; HAL 1649 F – isotype).

**Host range and distribution:** Only known from the type collection.

(Fig. 4)


**Description:** Colonies on uredosori, effuse, subvelutinous, grey-brown to brown. *Mycelium* immersed in the sori as well as superficial; hyphae 2–3 µm wide, sparingly branched, olivaceous, thin-walled, smooth. *Stromata* lacking. **Conidiophores** arising from superficial hyphae, lateral or sometimes terminal, erect, straight to curved or somewhat...
geniculate-sinuous, unbranched or branched, 25–500 × 2.5–4 µm, pluriseptate, moderately olivaceous, paler towards the tip, thin-walled, smooth; conidiogenous cells integrated, terminal to intercalary, about 10–30 µm long, proliferation sympodial; conidiogenous loci conspicuous, mostly slightly prominent or on peg-like protuberances, slightly thickened and darkened. Conidia in simple or occasionally branched chains, ellipsoid-ovoid, subcylindrical, fusiform, obclavate, (7–)15–40(–50) × (3.5–)4–4.5 µm, (0–)1–2(–5)-septate, pale olivaceous, thin-walled, smooth, ends rounded to narrowed, hila slightly thickened and darkened.

Holotype: Sierra Leone: Dodo, on uredosori of Puccinia eucomi, Pucciniaceae, on Andropogon auriculatus, Poaceae, 15 Apr. 1940, F. C. Deighton (K(M) IMI 43280b).

Host range and distribution: On uredo- and teleutosori of rust fungi, on Puccinia eucomi, Pucciniaceae, and Ravenelia zygiae, Raveneliaceae, Africa (Sierra Leone).


Exsiccatae: Sydow, Fungi Exot. Exs. 444.

Description: Colonies on uredo- and teleutosori, pale to deep grey-green, short and densely velutinous-floccose to densely floccose, sometimes forming dense round to elliptic masses up to 4 mm diam. Mycelium immersed within the sorus and extending into the surrounding leaf-tissue; hyphae branched, 1.5–2 µm diam, septate, pale olivaceous, thin-walled, smooth, sometimes completely suppressing the formation of uredosores. Stromata small to well-developed, immediately above the sorus hyphae aggregated, forming dense stromata, often 25–80 µm wide and 20–90 µm deep, occasionally up to 150 µm diam, composed of densely packed, ascending, sparingly branched hyphae developing to conidiophores. Conidiophores in smaller to mostly large or very large, dense fascicles, arising from stromata, laxly erect, straight or almost so to flexuous, filiform, simple or occasionally with short branchlets, 60–350 × 2.5–4 µm, pluriseptate, pale yellowish olivaceous to medium olivaceous, paler towards the tip, thin-walled, smooth; conidiogenous cells integrated, terminal to intercalary, conidiogenous loci truncate, occasionally subdenticulate, 1–1.5(–2) µm diam, very slightly thickened and darkened-refractive. Conidia in simple or branched acropetal chains, ellipsoid-ovoid, fusiform, subcylindrical, straight to somewhat curved, (12–)15–35(–45) × 4–6.5 µm, (0–)1(–3)-septate, pale olivaceous, thin-walled, smooth, primary conidia with broadly rounded apex, otherwise both ends short obconically truncate, hila 1–1.5 µm wide, very slightly thickened, darkened-refractive.

Types: Philippines: on uredosori (uredosp.) on Scirpus grossus, Cyperaceae, 20 Mar. 1913, P. W. Graff, Sydow, Fungi Exot. Exs. 444 (p.p.) (K(M) IMI 164332b – holotype; Sydow, Fungi Exot. Exs. 444 (e.g. BPI 420980) – isotypes).

Host range and distribution: On uredo- and teleutosori of rust fungi, on Puccinia (polygono-ampibi, scleriae, solmsii, thaliae) and Uredo sp., Pucciniaceae, Asia (India, Malaysia, Philippines), West Indies (Trinidad).

Excluded Cladosporiella species


Illustration: Castañeda (1988: fig. 2).


Notes: This is a foliicolous species with very long, simple or branched, pigmented, 8–15-septate conidiophores, 180–300 × 6–7 µm, ramoconidia and extremely long, brown conidia, 100–310 × 4–5 µm, with 15–30(–35) septa. The generic affinity of this unusual species is quite unclear.

ELLETEVERA

Key to the species of Elletevera

1 Conidiophores very long, 100–250 µm, frequently branched; conidia 12–60 × (4–)5–7.5(–10) µm, (0–)2–4(–6)-septate, very pale olivaceous; on Phyllachora parasitica and Phyllachora sp., Africa, North and South America ...................................................... E. parasitica
Conidiophores shorter, 85–120 µm, unbranched; conidia 17–23 × 7–9 µm, (1–)2(–3)-septate, pale olivaceous-ochraceous; on Phyllachora shiraiana, Asia, Japan ...................................................... E. ochracea

Illustration: Katumoto (1988: 110, fig. 2).

List of Elletevera species

Elletevera ochracea Katum., Bull. Fac. Agric. Yamaguchi Univ. 35: 110 (1988). (Fig. 6)

Description: Colonies hypophyllous, on stromata of Phyllachora shiraiana, ochraceous to brownish, elliptical to oblong in shape, 1.5–7 × 1.5–3.5 mm. Mycelium immersed; hyphae 2.5–3 µm wide, branched, septate, subhyaline to

Illustration: Deighton (1969: fig. 5).
very pale olivaceous. **Conidiophores** numerous, arising from superficial stromata, flat, pseudoparenchymatous, 35–40 µm diam, olivaceous-ochraceous, erect, divergent, cylindrical, straight to sinuous, sometimes geniculate in the upper portion, unbranched, 85–120 × 4.5–6.5 µm, attenuated towards the tip (to about 2.5 µm), 1–2-septate in the lower portion, pale olivaceous, thin-walled, smooth; conidiogenous cells integrated, terminal, long, conidiogenous loci visible, subdenticulate. **Conidia** solitary, short cylindrical-obovoid, 17–23 × 7–9 µm, (1–)2(–3)-septate, pale olivaceous-ochraceous, thin-walled, smooth, apex broadly rounded, base short obconically truncate, hila 0.8–1 µm wide.

**Holotype**: Japan: Yamaguchi Pref.: Nishiki-cho, Mt. Jakuchi, on stromata of *Phyllachora shiraiana*, Phyllachoraceae, on leaves of *Sasa palmata*, Poaceae, 6 May 1985, K. Katumoto (YAM 24294).

**Host range and distribution**: Only known from the type collection.

**Elletevera parasitica** (Ellis & Everh.) Deighton, *Mycol. Pap.* 118: 19 (1969). (Fig. 7)  

**Illustrations**: Deighton (1969: 19, fig. 11 and pl. 1), Seifert et al. (2011: 701, fig. 219C).

**Exsiccate**: Davis, Fungi Wiscon. Exs. 152.

**Description**: Colonies amphigenous, mainly hypophyllous, on and around *Phyllachora* spp., pale greenish, floccose, often contiguous. *Myceum* immersed in ascomata of the host fungus; hyphae 1.5–3 µm wide, branched, septate, subhyaline to faintly olivaceous, thin-walled, smooth.
Stromata formed by aggregated pale olivaceous, ascending hyphae, about 3–4 µm wide, in ostioles of the ascomata, 40–50 µm diam. Conidiophores numerous, in divergent floccose fascicles, arising from stromata, through ostioles, also erumpent through the wall of ascomata and from repent external hyphae, erect, cylindrical-filiform, 100–250 × 4–5 µm, sometimes narrowed towards the tip and 2.5–4 µm wide, simple or branched, with 1–2 main branches and short lateral branchlets, about 20–25 µm long, pluriseptate, very pale olivaceous, thin-walled, smooth; conidiogenous cells integrated, terminal, conidiogenous loci neither thickened nor darkened, but distinct by being denticle-like and somewhat refractive, about 1–1.5 µm diam. Conidia solitary, broadly ellipsoid-ovoid, obovoid, fusiform, obclavate, cylindrical-clavate, occasionally rostrate, straight to somewhat curved, 12–60 × (4–)5–7.5 (–10) µm, (0–)2–4 (–6)-septate, very pale olivaceous, thin-walled, smooth, apex broadly rounded, more attenuated in conidia with rostrate apex, base short obconically truncate, hila about 1–2 µm wide.

**ERIOCERCOSPORA**

**Key to the species of Eriocercospora**

1 Conidiophores up to 600 µm long and (3.5–)5–9 (–13) µm wide; conidia (3.5–)5–9 (–13) µm wide; on various hosts belonging to the *Asterinaceae*, *Englerulaceae* and *Parodiopsidaceae* …………….. E. balladynae

Conidiophores shorter, up to 120 µm long, and only 2.5–4 µm wide; conidia narrower, only up to 4.5 µm; on *Meliolina molle*, *Meliolinae* …………………………………………………………………………………………………………………………………………………. E. olivacea

**List of Eriocercospora species**


(Fig. 8)


Description: Colonies overgrowing those of the host fungi, olivaceous, velutinous to woolly. *Mycelium* superficial; hyphae growing between host hyphae, branched, 2–3.5 µm diam, occasionally swollen, up to 5 µm wide, septate, pale olivaceous, darker around conidiophores. *Conidiophores* arising from superficial hyphae, erect or almost so, straight to curved, flexuous, sinuous or somewhat geniculate, simple or branched, length very variable, 15–600 × 4–7.5 (–10.5) µm, width often variable throughout their length, pluriseptate, pale to medium olivaceous, thin-walled, smooth; conidiogenous cells integrated, terminal or intercalary, about 10–30 µm long, conidiogenous loci subconspicuous, i.e. unthickened, not or barely protuberant, not or only slightly darkened-refractive, about 1.5–2.5 µm diam. *Conidia* solitary, shape rather variable, ellipsoid-ovoid, obovoid, fusiform, subclavate to obclavate, (15–)25–70 (–135) × (3.5–)5–9 (–13) µm, (1–)3–6 (–9)-septate, occasionally slightly constricted at the septa, very pale olivaceous to medium pale olivaceous, thin-walled, smooth, apex obtuse, broadly rounded to somewhat attenuated, base obconically truncate, hila about 1–2.5 µm wide, not to slightly darkened-refractive, barely thickened.

Holotype: *Uganda*: Entebbe road, on *Balladynopsis entebbeensis*, on leaves of *Grumilea suculenta*, Nov. 1943, C. G. Hansford 3264 (K(M) IMI 562c).


(Fig. 9)

Illustration: Pirozynski (1974: 39, fig. 3).

Description: Colonies confined to colonies of *Meliolina molle*, olivaceous, feltly, 1–2 mm thick, completely obscuring...
the host fungus. Mycelium superficial; hyphae appressed to host hyphae but not penetrating them, often toruloid, 2.5–5 µm wide, septate, pale olivaceous, thin-walled, smooth. Conidiophores arising from superficial hyphae, lateral, occasionally terminal, erect, geniculate-sinuous, simple or branched, up to 120 µm long and 2.5–4 µm wide, pluriseptate, pale olivaceous, thin-walled, smooth; conidiogenous cells integrated, terminal and intercalary, 10–20 µm long; conidiogenous loci truncate, about 1.8–2.5 µm diam, neither thickened nor darkened or at most refractive or very slightly darkened. Conidia solitary, long, cylindrical-vermiform or filiform to somewhat obclavate, up to 150 µm long and 4.5 µm wide, pluriseptate (up 22 septa), pale olivaceous to olivaceous, thin-walled, smooth, apex obtuse, rounded, base truncate to short obconically truncate, about 2–2.5 µm, hila neither thickened nor darkened.

Types: **India**: Tamil Nadu: Nilgiris, Gudalpur, on Meliolina molle, Meliolinaceae, on Syzygium cf. grande (S. cf. montanum), Myrtaceae, 22 Feb. 1966, K. A. Pirozynski (K(M) 120229b – holotypes; DAOM 145763 – isotype).

Host range and distribution: Only known from the type collection.

**Excluded Eriocercospora species**


*Notes:* This is a saprobic mucedineous hyphomycete of unknown generic affinity, in any case not belonging to *Eriocercospora*. It is superficially somewhat reminiscent of plant pathogenic species of *Pseudocercosporella*.


**Key to fungiicolous *Passalora* species**

1 Mycelium internal and external, superficial; stromata lacking; conidiophores consistently solitary, arising from superficial hyphae; on *Uromyces sparganii*, Asia ................................................................. *P. acori*

Mycelium immersed; stromata present, dark brown, columnar, globose to linear, often confluent to form continuous stromatic areas over and within aecia; conidiophores arising from stromatic structures, in small to moderately large fascicles; on aecia of *Uromyces cestri*, North America ................................................................. *P. uromycestri*

**List of fungiicolous *Passalora* species**


(Fig. 10)


*Illustration*: Yen & Lim (1980: 205, fig. 8).

*Description*: Leaf spots indistinct, sometimes forming dark grey specks. Colonies on uredospores, amphigenous, effuse, dark brown. *Mycelium* internal and external, hyphae branched, septate, 2.5–5 µm wide, yellowish brown to brown, thin-walled, smooth. *Conidiophores* consistently
solitary, arising from superficial hyphae, erect, cylindrical, not geniculate, unbranched, 20–190 × 4–5 µm, 2–6(–8)-septate, brown to dark brown, tips rounded to conical; conidiogenous cells integrated, terminal, with several minute brown conidiogenous loci. Conidia solitary, obclavate to obclavate-subcylindrical, 40–120 × 2–2.5 µm, 4–9(–12)-septate, pale olivaceous-brown, thin-walled, smooth, apex pointed, base obconically truncate, hila slightly thickened and darkened.


Host range and distribution: Only known from the type collection.

(Fig. 11)

Illustrations: Pollack (1971: 690, figs 1–8).

Description: Colonies formed as dark brown to blackish felt-like growth on aecial pustules of Uromyces cestri, which formed small, swollen punctiform spots, 1–3 mm diam, surrounded by a yellowish halo. Mycelium immersed. Stromata dark brown, columnar, globose to linear, often confluent to form continuous stromatic areas over and within the aecia. Conidiophores arising from stromatic structures, in small to moderately large fascicles, loose to rather dense, erect, straight to slightly geniculate-sinuous, mostly unbranched, about (15–)20–110(–130) × 4–6 µm, pluriseptate, light to dark brown, wall thin to slightly thickened, smooth or almost so; conidiogenous cells integrated, terminal, about 10–30 µm long, conidiogenous loci conspicuous, thickened and darkened, slightly protuberant or often lateral and flat, appressed, 1–2 µm diam. Conidia solitary, obclavate, 30–125 × 1.5–3.5 µm, 1–2 µm wide; conidia acicular, base truncate; on Asplenium spp., Europe, North America ................................................................. C. asplenii

Cercospora

Tabular key to Cercospora species on ferns

Most species on ferns belong to the Cercospora apii complex (sensu Crous & Braun 2003), i.e. they are morphologically very similar and morphologically little differentiated, so that it is barely possible to key out the species concerned just based on morphology. Phylogenetic data are not yet available. Therefore, we prefer to list these species in form of a tabular key based on host genera and families.

Adiantaceae = Pteridaceae subfam. Vittarioideae

Aspleniaceae
1 Conidia acicular, base truncate; on Asplenium spp., Europe, North America ........................................... C. asplenii
Conidia narrowly obclavate-filiform, base obconically truncate; on Asplenium radicans .......... Cercospora camptosori

Cheilanthaceae = Pteridaceae subfam. Cheilanthoideae

Cyatheaceae
On Alsophila, North America ....................................................................................................................... C. asplenii

Dryopteridaceae
1 Stromata 20–50 µm diam; conidia 30–125 × 1.5–3.5 µm, base obconically truncate, 1–2 µm wide;
on Dryopteris sp., North America ................................................................. C. camptosori
Stromata lacking or very small; conidia 95–250 × 3.5–5 µm, base truncate, wider, about 3–4 µm wide;
on Dryopteris polyphodioides, China ................................................................. C. dryopteridis

Lygodiaceae
On Lygodium japonicum, India ............................................................................................................. C. lygodiicola
Marsileaceae
On Marsilea quadrifolia, India ................................................................. C. marsileae

Polypodiaceae
1 Stromata lacking or almost so; on Platycerium spp., North America ................................................................. P. platyeri
Stromata 20–45 µm diam; on Microsorum membranaceum (Platyptysis membranaceae), Asia (India) .......... P. pleopeltidis

Pteridaceae subfam. Cheilanthonoidea (= Cheilanthaceae)
On Aleuritopteris farinosa (Cheilanthes farinosa), India .......................................................................................... C. cheilanthis

Pteridaceae subfam. Vittarioidea (= Adiantaceae)
1 Conidia broadly obclavate-cylindrical, short conidia sometimes fusiform, 40–90 × (4–)5–8 µm; on Adiantum, Tanzania ........................................................................................................ C. adianticola
Conidia acicular, only 2–5 µm wide ......................................................................................................................... 2
2 (1) Conidia 145.5–455.5 × 3.5–4 µm; on Adiantum, India .................................................................................. C. pteridigena
Conidia much shorter and narrower, up to 120 µm long and 2–4 µm wide ......................................................... 3
3 (2) Stromata lacking or very small; on Adiantum, Asia ................................................................................ C. adianticola
Stromata well-developed, up to 75 µm diam; on Adiantum, North America ......................................................... C. asplenii

Selaginellaceae
On Selaginella spp., Europe, North America ....................................................................................................... C. selaginiellorum

Thelypteridaceae
1 Conidia long, 60–400 × 2–4 µm, 1–35-septate; on Abacopteris, Singapore ....................................................... C. abacopteridis
Conidia shorter, 50–110 × 3–4 µm, usually 4–10-septate; on Cyclosorus, India, Taiwan ............................................ C. cyclosor

Woodsiaceae
1 Conidia acicular, 20–90 µm long, base truncate; on Diplazium esculentum, Philippines ........................................ C. athyrii
Conidia acicular to narrowly obclavate, 45–155(–230) µm, base truncate to short obconically truncate; 
on Diplazium esculentum, India .................................................................................................................... C. diplaziicola

List of Cercospora species on ferns

(Fig. 12)


Illustrations: Yen & Lim (1980: 204, fig. 7C–E).

Description: Leaf spots amphigenous, vein-limited, brown, later confluent. Caespituli hypophyllous, inconspicuous. Mycelium internal. Stromata lacking. Conidiophores in relatively small fascicles, 2–18, divergent or somewhat denser, arising from internal hyphae, emerging through stomata, erect, straight, subcylindrical to somewhat sinuous, 0–2 times geniculate above, unbranched, 15–120 × 4–5 µm, 1–5-septate, dark brown, paler towards the tip, wall thin to slightly thickened, smooth; conidiogenous cells integrated, terminal, occasionally intercalary, conidiogenous loci conspicuous, 2–2.5 µm wide, darkened and thickened. Conidia solitary, acicular to filiform, straight to somewhat curved, 60–400 × 2–4 µm, 1–35-septate, hyaline, thin-walled, smooth, apex acute, base truncate, hilum about 2–3 µm wide, thickened and darkened.


Host range and distribution: Only known from the type collection.

Cercospora adianticola R.K. Srivast., A.K. Srivast. & Kamal, Kavaka 20/21: 38 “1992/1993” (1995); as "adiantiicola". (Fig. 13)


Illustration: Srivastava et al. (1995: 38, fig. 1).

Description: Leaf spots amphigenous, 0.5–3 mm diam, irregular, streak-like, sometimes confluent, spread over the whole leaf surface. Mycelium internal; hyphae septate, branched. Stromata lacking or poorly developed. Conidiophores in small fascicles, erect, straight, subcylindrical to 1–3 times geniculate, unbranched, 70–140 × 3–6 µm, septate, olivaceous; conidiogenous cells integrated, terminal and intercalary, conidiogenous loci conspicuous, 2–4.5 µm diam, thickened and darkened. Conidia solitary, acicular, 50–100 × 2–4 µm, 3–11-septate, hyaline, thin-walled, smooth, apex acute, base truncate or
slightly atenuated, hila about 1.5–2.5 µm wide, thickened and darkened.


Host range and distribution: only known from the type collection.

Notes: This species belongs to the C. api s. lat. complex. Thaung (1984) recorded “Cercospora asplenii” on Adiantum sp. from Myanmar, but this collection seems to belong to C. adianticola.

Cercospora adiantigena U. Braun & Crous, in Crous & Braun, Mycosphaerella and Anam. 1: 44 (2003). (Fig. 14)

Literature: To-anun et al. (2011: 32), Begum et al. (2012).

Illustrations: Crous & Braun (2003: 45, fig. 2), To-anun et al. (2011: 32, fig. 14).

Description: Leaf spots amphigenous, oblong, linear, spread between veins, 2–15 × 0.5–1.5 mm or confluent, forming larger patches, brown. Caespituli amphigenous, punctiform to subeffuse, greyish brown to dingy greyish white. Mycelium internal. Stromata well-developed, immersed, 10–50 µm diam, subhyaline to pale olivaceous-brown. Conidiophores in small to moderately large fascicles, loose to fairly dense, arising from stromata, erumpent, erect, straight, subcylindrical to moderately geniculate-sinuous, unbranched, 25–150 × 4–10 µm, plurisepate, subhyaline, occasionally with a faintly greenish to olivaceous tinge, thin-walled, smooth; conidiogenous cells integrated, terminal or occasionally intercalary, 10–35 µm long, conidiogenous loci conspicuous, planate, thickened and darkened throughout, 2.5–4 µm diam. Conidia solitary, broadly obclavate-cylindrical, short conidia sometimes fusiform, 40–90 × (4–)5–8 µm, (1–)3–6(–8)-septate, colourless, thin-walled, smooth, apex
obtuse, base short obconically truncate, 3–4 µm wide, hila thickened and darkened.

Holotype: Tanzania: Kigoma, Kakombe, on Adiantum philippense, 21 Feb. 1964, K. A. Pirozynski (K(M) IMI 106709b).

Host range and distribution: On Adiantum philippense and Doryopteris sp., Pteridaceae subfam. Vittarioideae (Adiantaceae), Africa (Tanzania), Asia (Philippines, Thailand).

Notes: This species is reminiscent of Cercosporella, but the conidiogenous loci are planate, thickened and darkened throughout, i.e. they are cercosporoid. Thus this species rather pertains to Cercospora subgen. Hyalocercospora.


Fig. 14. Cercospora adiantigena (K(M) IMI 106709b). A. Conidiophore fascicle. B. Conidiogenous cells. C. Conidia. Bar = 10 µm.

Fig. 15. Cercospora asplenii (HBG, holotype). A. Conidiophore fascicle. B. Conidia. Bar = 10 µm.


Description: Leaf spots variable in shape and size, small to relatively large, pale to dark brown or almost blackish, centre later paler, pale brown to dingy grey. Caespituli amphigenous. Stromata subglobose, small to large, up to 75 µm diam, brown to almost blackish brown. Conidiophores in small to moderately large fascicles, 2–20, occasionally solitary, divergent, straight, subcylindrical to geniculate-sinuous. 0–5 times geniculate, usually unbranched, 20–120 × 4–5.5 µm, pluriseptate, medium olivaceous-brown throughout, wall slightly thickened, smooth; conidiogenous cells integrated, mostly terminal, conidiogenous loci conspicuous, thickened and darkened. Conidia solitary, acicular, 20–120 × 2–4 µm, indistinctly pluriseptate, hyaline, thin-walled, smooth, apex subacute, base truncate, hilum about 2–2.5 µm wide, thickened and darkened.
Holotype: Croatia: Dalmatia, Lapad near Ragusa, on Asplenium trichomanes, 16 Mar. 1914, O. Jaap (HBG).

Host range and distribution: On ?Adiantum sp., Pteridaceae subfam. Vittarioideae (Adiantaceae); ?Alsophila australis, Cyatheaceae; Asplenium (nidus [antiquum], trichomanes, Asplenium sp.), Aspleniaceae; North America (Canada, USA, Florida), Asia (India, Japan, Myanmar), Europe (Czech Republic, Germany, Croatia, Switzerland).

Cercospora athyrii Mendoza, Philipp. J. Sci. 75: 165 (1941).


Description: Leaf spots subcircular, 1–8 mm diam, brown, somewhat sunken on the upper surface. Mycelium internal. Stromata small, only filling the substomatal cavity, brown.

Conidiophores in dense fascicles, arising from stromata, emerging through stomata, erect, subcylindrical or somewhat attenuated towards the tip, or only 1–2 times geniculate, unbranched, 30–105 × 3.5–5 µm, pluriseptate, medium to dark olivaceous-brown, paler towards the tip; conidiogenous loci conspicuous, thickened and darkened.

Conidia solitary, acicular, straight to curved, 20–90 × 3–5 µm, distinctly pluriseptate, hyaline, thin-walled, smooth, apex acute, base truncate.

Holotype: Philippines: Luzon, Manila, on Diplazium esculentum (Athyrium esculentum), Woodsiaiceae, Mendoza, No. 55483 (not seen).

Host range and distribution: Only known from the type collections.


(Fig. 16)


Description: Leaf spots amphigenous, circular to angular-irregular, small to large, sometimes covering large leaf segments, brown, margin indefinite. Caespituli amphigenous, punctiform. Mycelium internal. Stromata 20–50 µm diam, dark brown. Conidiophores in dense fascicles, arising from stromata, erect, subcylindrical or somewhat attenuated towards the tip, straight to somewhat geniculate near the apex, unbranched, 20–60 × 4–5 µm, septate, pale olivaceous-brown, paler towards the tip, thin-walled, smooth; conidiogenous cells integrated, terminal, conidiogenous loci conspicuous, thickened and darkened, 1–2 µm diam. Conidia solitary, narrowly obclavate-filiform, 30–125 × 1.5–3.5 µm, indistinctly pluriseptate, hyaline, thin-walled, smooth, apex acute or subacute, base obconically truncate, 1–2 µm wide, hila somewhat thickened and darkened.

Lectotype (designated here, MycoBank, MBT176146): USA: Wisconsin: Grant County, Marquette State Park, on Asplenium radicans (Camptosorus rhizophyllus), 1 Aug. 1914, J. J. Davis (WIS). Isolectotype: BPI 433994.


Notes: This species differs from fern-inhabiting species belonging to the C. apii complex in having narrowly obclavate-filiform conidia with obconically truncate base and narrow conidiogenous loci and hila, only 1–2 µm diam.

Cercospora cheilanthis Chowdhry, D. Gupta & Padhi, Indian Phytopathol. 36: 624 (1983); as “cheilanther”. (Fig. 17)
**Description:** Leaf spots amphigenous, circular to elongated, 1–3 mm diam, blackish brown, Caespituli amphigenous, mainly epiphyllous. Mycelium internal. Stromata well-developed, 15–45 µm diam, globular, dark brown. Conidiophores in large, dense fascicles, arising from stromata, about 10–40, erect, straight to somewhat curved, cylindrical, 1–3 times geniculate above, unbranched, 30–165 × 3–5.5 µm, 2–6-septate, deep olivaceous-brown; conidiogenous cells integrated, terminal and intercalary, conidiogenous loci conspicuous, thickened and darkened. Conidia solitary, acicular, about 10–130 × 1.5–3 µm, 1–19-septate, hyaline, thin-walled, smooth, apex acute, base truncate, hila thickened and darkened.

**Holotype:** India: Odisha (Orissa): Bhubaneswar, on leaves of Aleuritopteris farinosa (Cheilanthes farinosa), Pteridaceae subfam. Cheilanthoideae (= Cheilanthaceae), 30 Nov. 1977, D. Gupta (HCIO 32848).

**Host range and distribution:** Only known from the type collection.

**Note:** This species belongs to *Cercospora apii* s. lat. (*sensu* Crous & Braun 2003).


(Fig. 18)

**Synonym:** *Cercospora cyclosori* Sarbajna & Chattopadh, J. Mycopathol. Res. 28: 14 (1990), nom. illeg. (Art. 53.1) [type: on Cyclosorus sp., India, West Bengal, Hooghly, India, 23 Jan. 1990, Goh & Hsieh (K(M) IMI 312082)].

**Fig. 17.** *Cercospora cheilanthis* (based on the original illustration). A. Conidiophore fascicle. B. Conidia. Bar = 10 µm.

**Fig. 18.** *Cercospora cyclosori* (K(M) IMI 312082). A. Conidiophore fascicle. B. Conidia. Bar = 10 µm.

(Fig. 19)


**Illustrations**: Das (1989: 38, fig. 1), Phengsintham *et al.* (2013a: 38, figs 20–21).

**Description**: Leaf spots subcircular to irregular, 1–5 mm diam, grey-brown to dark brown in the centre, margin indefinite to dark brown. *Caespituli* amphigenous, scattered, dark brown. *Mycelium* internal; hyphae branched, 2–3 µm wide, septate, constricted at the septa, distance between septa 5–10 µm, brownish or green-hyaline, wall thin, smooth, forming plate-like plectenchymatous stromatic hyphal aggregations. *Stromata* small to well-developed, oval to ellipsoidal, 15–25 µm diam, brown, substomatal or intraepidermal, composed of swollen hyphal cells, subglobose, rounded to angular in outline, 6–17 µm wide, brown to dark brown, wall thin. *Conidiophores* formed singly or fasciculate, arising from stromata (2–12 per fascicle), emerging through stomata, unbranched, straight to curved, cylindrical, 40–190 × 4–6.5 µm, 2–8-septate, distance between septa 8–28 µm long, medium brown or olivaceous-brown, paler at the apex, wall 0.5–0.8 µm wide, smooth, slightly to strongly geniculate, width ± uniform; conidiogenous cells integrated, terminal or intercalary, cylindrical, 10–20 × 3–5 µm, pale brown; conidiogenous loci conspicuous, subcircular, 2–3 µm wide, brown. *Conidia* solitary, acicular to narrowly oblanceolate, straight to curved, 45–155(−230) × 3–5(−6) µm, 3–20-septate, hyaline, thin-walled, smooth, tip acute, base truncate to short obconically truncate, 2–3 µm wide, hila thickened and darkened.

**Fig. 19. Cercospora diplaziicola** (K(M) IMI 292584). A. Conidiophore fascicle. B. Conidiogenous cells. C. Conidia. Bar = 10 µm.

Host range and distribution: On Diplazium esculentum, Woodsiaceae, Asia (India, Laos, Thailand).

Notes: Cercospora diplaziicola with acicular to obclavate conidia is very close to C. athyrii, which was described to have acicular conidia. However, type material of the latter species could not be traced, is probably not maintained and thus cannot be re-examined to prove the variation of the conidial shape. It is possible that the two species described from Diplazium esculentum in Asia are conspecific. Cercospora diplaziicola is only tentatively maintained as separate species.

(Fig. 20)


Illustration: Guo (1997: 2, fig. 1).

Description: Leaf spots amphigenous, subcircular to angular-irregular, 1–3 mm diam, often confluent, greyish white to pale yellowish brown, with dark brown halo on the upper side, paler on the lower side. Caespituli mainly hypophyllous. Mycelium internal. Stromata lacking or only with a few aggregated swollen hyphal cells. Conidiophores solitary or in small fascicles, 2–12, divergent, erect, straight, subcylindrical to 1–4 times geniculate, usually unbranched, 40–150(–210) × 4–6 µm, 1–5-septate, olivaceous-brown to medium brown, paler towards the tip; conidiogenous cells integrated, terminal and intercalary, conidiogenous loci conspicuous, thickened and darkened, 2.5–3.5 µm diam. Conidiophores solitary, acicular, 95–250 × 3.5–5 µm, pluriseptate, hyaline, thin-walled, smooth, apex acute, base truncate, about 3–4 µm wide, hila somewhat thickened and darkened.


Host range and distribution: Only known from the type collection.

Note: This species is part of the Cercospora apii complex.


Illustration: Lall et al. (1964: 182, fig. 1).

Description: Leaf spots amphigenous, irregularly shaped, 2–15 mm diam, fuliginous, margin paler, sometimes covering the whole surface of leaflets. Caespituli amphigenous. Stromata lacking or small, composed of a few swollen hyphal cells.

Conidiophores solitary or few to many in loose fascicles, arising from internal hyphae or small stromatic hyphal aggregations, erect, subcylindrical to somewhat geniculate, unbranched, about 15–50 × 4–5 µm, continuous to sparingly septate, olivaceous-brown below, paler towards the apex; conidiogenous cells integrated, terminal or conidiophores reduced to conidiogenous cells, conidiogenous loci thickened and darkened. Conidia solitary, narrowly obclavate, 25–130 × 3–4 µm, indistinctly pluriseptate, subhyaline, thin-walled, smooth, apex subacute or acute, base short obconically truncate.


Host range and distribution: Only known from the type collection.
(Fig. 21)

*Description:* Leaf spots brown to rusty brown, with chlorotic halo, 2–14 mm in length, sometimes spreading over the whole leaflet. *Caespituli* amphigenous. *Mycelium* internal. *Stromata* well-developed, consisting of brown cells. *Conidiophores* in fascicles, 2–10, erect, straight, subcylindrical, unbranched, apical part geniculate, about 50–110 × 3.5–5 µm, 1–3-septate, brown, paler towards the tip, thin-walled, smooth; conidiogenous cells integrated, terminal, conidiogenous loci thickened and darkened. *Conidia* formed singly, acicular, about 45–225 × 3–5.5 µm, 4–26-septate, hyaline, thin-walled, smooth, apex pointed, base truncate.

*Holotype:* India: Tamil Nadu: Annamalainagar, on living leaves of *Marsilea quadrifolia*, 5 Nov. 1965, V. Ragunathan (HCIO 29330).

*Host range and distribution:* On *Marsilea quadrifolia*, Marsileaceae, Asia (India, Myanmar).

*Note:* This species belongs to the *Cercospora apii* complex.


(Fig. 22)

(Fig. 23)


**Types:** India: Bombay, Mahabaleshwar, on leaves of Microsorum membranaceum, 14 Oct. 1955, P. P. Chiddarwar (K (M) IMI 83185 – holotype; BPI 439783 – isotype).

**Host range and distribution:** on Microsorum (bifurcata, grande, Platycerium sp.), Polypodiaceae, Asia (India, M.S., U.P.).

**Notes:** A morphologically similar Cercospora was found on Nephrolepis cordifolia (Polypodium cordifolium), Davalliaeae, in Venezuela (Lara, La Cuchilla, Dec. 2006, R. Urtiaga, HAL 2601 F, deposited as Cercospora sp.). The sample concerned is, however, too meager for a final determination and description.

**Cercospora pteridigena** M.K. Khan, R.K. Verma & Kamal, *Indian Phytopathol.* 45: 26 (1994). (Fig. 24)
Cercosporoid fungi

**Description:** Lesions amphigenous, mainly on young leaves and leaflets, 2.5–15 mm diam, scattered, sometimes covering the whole leaf surface, light yellow to dark brown. Mycelium internal; hyphae up to 2.5 µm wide, septate, smooth. Stromata lacking or only poorly developed, small aggregations of swollen hyphal cells, about 10–20 µm diam, olivaceous. Conidiophores solitary or in small fascicles, arising from internal hyphae or small stromata, erect, straight to somewhat geniculate-sinuous, length variable, about 150–400 µm long and 4.5–6 µm wide, pluriseptate, brown; conidiogenous cells integrated, terminal and intercalary, conidiogenous loci conspicuous, thickened and darkened. Conidia solitary, acicular, up to 300 µm long, pluriseptate, hyaline, thin-walled, apex pointed, base truncate, hila thickened and darkened.

**Syntypes:** France: on leaves of Selaginella denticulata and S. helvetica (details not indicated).

**Host range and distribution:** on leaves of Selaginella (apoda, helvetica, kruassiana [denticulata]), Selaginellaceae, Europe (France), North America (USA, Minnesota).

**Notes:** This species belongs to the *C. apii* complex. Cour & Joly (1965) compared *C. selaginellarum* with the latter species and discussed the morphological similarity of the two species. Type material was not indicated in the original publication, and two different host species were cited, Selaginella helvetica and *S. denticulata*. Original material could not be traced. Jaap, Fungi Sel. Exs. 619, issued as Leptosphaeria helvetica var. major, on Selaginella helvetica, Italy, Liguria, Portofino, 26 Mar. 1913, O. Jaap (material deposited at HAL examined) contains conidiophores and conidia of *Cercospora* sp., but the latter material does not belong to *C. selaginellarum*. The conidia are much shorter, narrower and obclavate, and the conidiogenous loci are rather small, 1.5–2 µm diam (stromata immersed, about 10–40 µm diam, brown; conidiophores fasciculate, straight, subcylindrical, 80–150 × 3–6 µm, pluriseptate, medium to darker brown, tips much paler, conidiogenous loci 1.5–2 µm wide, slightly thickened and darkened; conidia solitary, obclavate, about 40–90 × 4–5 µm, 3–8-septate, hyaline or almost so, smooth, apex subobtuse, base rounded to short obconically truncate, 2 µm wide, hila slightly thickened and darkened). However, the material from Italy is not sufficient for a final taxonomic conclusion.
**Key to the species of Passalora on ferns**

1. Conidiophores 30–80 × 3–5 µm; conidia obclavate, long and narrow, 40–210 × 2–4 µm, subhyaline to pale olivaceous; on *Pteridium aquilinum*, widespread .............................. P. *pteridis*

Conidiophores longer and broader, about 25–350 × 4–7.5 µm; conidia obclavate-cylindrical, shorter and broader, 25–100 × 4–6 µm, olivaceous-brown or brown; on *Pyrrosia lingua*, Japan .............................. P. *pyrrosiae*

**List of Passalora species on ferns**


(Fig. 25)


Illustrations: Lall et al. (1964: 182, fig. 3), Braun & Mel’nik (1997: 121, fig. 49).

Description: Leaf spots amphigenous, formed as irregular discolorations, yellowish brown, brown, later darker, margin indefinite. *Caespituli* hypophyllous, subeffuse, not very conspicuous. *Mycelium* internal and external; superficial hyphae branched, septate, 2–6 µm wide, smooth, thin-walled, subhyaline to olivaceous. *Stromata* lacking or only formed as small substomatal hyphal aggregations. *Conidiophores* in small, loose fascicles, arising from internal hyphae or hyphal aggregations, or solitary, arising from superficial hyphae, erect to decumbent, flexuous, simple or occasionally branched, subcylindrical to somewhat clavate, to geniculate-sinuous, 20–100 × 5–10 µm, continuous to pluriseptate, olivaceous to brownish, thin-walled, smooth; conidiogenous cells integrated, terminal, often somewhat swollen, subclavate, about 20–40 µm long, conidiogenous loci conspicuous, somewhat thickened and darkened. *Conidia* solitary, broadly obclavate-subcylindrical, (30–)40–120(–140) × 5–8 µm, pluriseptate, hyaline, subhyaline to pale olivaceous, thin-walled, smooth, apex obtuse, base obconically truncate, hila slightly thickened and darkened.

Holotype: Russia: Pskhu, Caucasus Mts., on *Pteridium aquilinum*, 1917, W. Siemaszko (not seen).

Host range and distribution: On *Pteridium* (aquilinum, *Pteridium* sp.), *Dennstaedtiaceae*, Asia (India, Japan), Caucasus (Georgia), Europe (Russia, Spain), North America (USA, Wisconsin).

Notes: Type material of *C. pteridis* could not be traced in Siemaszko’s herbarium at WA. The reallocation of this species to *Mycovellosiella* and *Passalora*, respectively, was based on the examination of type material of *Cercospora pteridicola*. The identity of a Japanese collection on *Pteridium aquilinum* subsp. *japonicum* (*P. aquilinum* var. *latiusculum*), Iwate, 31 Aug. 1947, K. Sawada (IUM-FS79), recorded by Sawada (1958) as *Cercospora pteridis*, is unclear and remains unproven as this sample is devoid of any fructification, which has been confirmed by a recently made re-examination. Records of this species from India and Myanmar on *Pteridium* sp. (Lall et al. 1964, Thaung 1984) are also unclear and unproven. Material was not available for a re-examination. A previous record from Colombia on *Pteridium aquilinum* subsp. *japonicum* (P. aquilinum var. *latiusculum*), Iwate, 31 Aug. 1947, K. Sawada (IUM-FS79), recorded by Sawada (1958) as *Cercospora pteridis*, is unclear and remains unproven as this sample is devoid of any fructification, which has been confirmed by a recently made re-examination. Records of this species from India and Myanmar on *Pteridium* sp. (Lall et al. 1964, Thaung 1984) are also unclear and unproven. Material was not available for a re-examination. A previous record from Colombia on

Fig. 25. *Passalora pteridis* (MA, holotype of *Cercospora pteridicola*).

Pteris sp. (Chupp 1954) was based on a misidentification and belongs to a Pseudocercospora described in this paper as *P. pteridigena*.

(Fig. 26)


*Literature:* Katsuki (1965: 76).

*Illustration:* Motohashi et al. (2008: 143, fig. 6).

**Description:** Lesions indistinct or with distinct discolorations, 3–8 mm diam, greyish brown to reddish brown above, with darker border line and greyish brown or brown below, sometimes covering the whole surface. *Caespituli* hypophyllous, fuliginous. *Mycelium* internal. *Stromata* intraepidermal, small to large, up to 135 μm diam, olivaceous-brown to dark brown. *Conidiophores* solitary or in moderately large fascicles, 2–18, loose to dense, arising from stromata, erumpent, erect, straight to slightly curved, subcylindrical to genulate-sinuous, unbranched, about 25–350 × 4–7.5 μm, 4–10-septate, pale olivaceous-brown to brown, thick-walled, asperulate; conidiogenous cells integrated, terminal, sympodially or percurrently proliferating, conidiogenous loci thickened and darkened, 2.5–5 μm diam. *Conidia* solitary, obclavate-cylindrical, straight to curved, 25–100 × 4–6 μm, 1–11-euseptate, rarely distoseptate, occasionally constricted at the septa, olivaceous-brown or brown, wall thickened, asperulate, base obconically truncate, apex obtuse, hila somewhat thickened and darkened.


**Host range and distribution:** On *Pyrrosia lingua*, Polypodiaceae; Asia (Japan).
**Pseudocercospora**

**Key to the species of Pseudocercospora on ferns**

1. Mycelium internal and external; superficial hyphae usually with solitary conidiophores ........................................ 2
   Mycelium internal; superficial hyphae with solitary conidiophores lacking ........................................................... 14

2 (1) Stromata lacking; conidiophores only solitary, arising from superficial hyphae ......................................................... 3
   Stromata mostly present, small to large; conidiophores fasciculate, arising from internal hyphae or stromata as well as solitary, arising from superficial hyphae .................................................. 6

3 (2) Conidiophores very long, 100–300 µm, pluriseptate (10–30 septa); conidia subcylindrical, ellipsoid to short obclavate-ovoid, 12–25 × 4.5–6 µm, (2–)3–4(–5)-septate; on Dictyophora dichotoma, Africa, Gabon .......................................................... P. gleicheniae
   Conidiophores much shorter, 2–40 µm, 0–2-septate; conidia acicular-filiform or narrowly obclavate-cylindrical, much longer and narrower; on other hosts .................................................. 4

4 (3) Conidia narrowly cylindrical to obclavate-cylindrical, 30–80 × 2–3 µm; on Abacopteris nephrolepidigera, Singapore ........................................................................................................................................ P. abacopteridis
   Conidia acicular-filiform, 60–120 × 2–3.5 µm; on other hosts ........................................................................................ 5

5 (4) Conidia 3–3.5 µm wide, hila 2.5–3 µm wide; on Rumohra adiantiformis, Taiwan ......................................................... P. rumohrae
   Conidia narrower, 2–3 µm, hila 1.5–2 µm wide; on Ptisana salicina, New Zealand .......................................................... P. ptisanae

6 (2) Stromata lacking; forming fasciculate conidiophores arising from internal hyphae, emerging through stomata;
   conidia short, only 10–35 × 1.5–4 µm, 1–3-septate; on Lygodium japonicum, Asia .................................................. P. lygonii
   Stromata developed, giving rise to fasciculate conidiophores; conidia longer, pluriseptate ........................................... 7

7 (6) Stromata very large, up to 150 µm diam; on Nephrolepis falcata, Australia .......................................................... P. nephrolepidicola
   Stromata much smaller, 10–80 µm diam ...................................................................................................................... 8

8 (7) Superficial hyphae present, but without solitary conidiophores; on Davallia fejeensis, Brazil ......................... P. davalliicola
   Superficial hyphae with solitary conidiophores present and usually abundant ...................................................... 9

9 (8) Conidia narrow, only 2–4 µm wide; on Lygodium, Nephrolepis or Pteris spp. .................................................. 10
   Conidia wider, 3–5.5 µm; on other hosts .................................................................................................................. 13

10 (9) Conidiophores very long, 30–150 µm; conidia acicular to narrowly obclavate, very long, 40–250 µm;
   on Pteris sp., Colombia .......................................................... P. pteridigena
   Conidiophores much shorter, 5–70 µm; conidia much shorter, up to 125 µm ........................................................ 11

11 (10) Conidia acicular to narrowly cylindrical, base truncate; on Nephrolepis spp., Asia ........................................ P. nephrolepidicola
   Conidia obclavate-cylindrical, base obconically truncate; on Lygodium or Pteris spp. .............................................. 12

12 (11) Hyphae subhyaline; conidiophores thin-walled; on Pteris sp., Asia .......................................................... P. pteridigena
   Hyphae subhyaline, but distinctly pigmented where conidiophores arise; wall of longer conidiophores somewhat thickened; on Lygodium sp., Asia ................................................................. P. lygodigena

13 (9) Leaf spots lacking or indistinct; colonies hypophyllous; stromata small, 10–20 µm diam;
   conidiophores up to 150 × 7 µm; on Adiantum, Asia, South America ................................................................. P. adianti
   Leaf spots developed; colonies amphigenous; with large epiphyllous stromata, 20–60 µm diam;
   conidiophores up to 100 × 5 µm; on Lorchites hirsuta, Venezuela ................................................................. P. lonchitidis

14 (1) Stromata lacking or almost so ......................................................................................................................... 15
   Stromata developed, 10–110 µm diam .................................................................................................................. 16

15 (14) Conidiophores 60–180 × 4–7 µm; conidia 3–5 µm wide; on Plagiopyrya euphlebia, Taiwan ..................... P. plagiopyrae
Conidiophores much shorter and narrower, 7–35 × 2.5–3 µm; conidia only 2–3 µm wide;  
on *Nephrolepis auriculata*, Taiwan ................................................................. P. nephrolepidis

16 (14) Stromata epiphyllous, immersed, very large, 60–110 µm diam; on *Cyathea* sp., Japan ..................... P. cyatheae  
Stromata much smaller, 10–75 µm diam ................................................................. 17

17 (16) Conidia acicular-filiform .................................................................................................................. 18  
Conidia obclavate-cylindrical ................................................................................................. 22

18 (17) Conidia very narrow, 1–1.5 µm wide; on *Cyclosorus acuminatus*, Taiwan ......................... P. pteridophytophila  
Conidia wider, 1.5–4 µm; on other hosts .................................................................................. 19

19 (18) Conidiophores relatively short, 5–30 µm; on *Arachniodes or Microsorum* spp. ....................... 20  
Conidiophores longer, up to 70 µm; on other hosts ................................................................. 21

20 (19) Colonies hypophyllous; conidiophores usually aseptate; on *Arachniodes* sp., China ............... P. arachnioidis  
Colonies amphigenous; conidiophores 1–5-septate; on *Microsorum* ........................................... P. microsori

21 (19) Conidiophores usually aseptate; conidia 50–120 µm long; on *Metathelypteris laxa*, Taiwan ...... P. thelypteridis  
Conidiophores 0–2-septate; conidia 60–80 µm long; on *Deparia japonica*, Taiwan ...................... P. atheryi

22 (17) Conidiophores very short, 9–14 × 2–4 µm; on *Christella parasitica*, Thailand ......................... P. christellae  
Conidiophores longer, (5–)10–280 µm; on other hosts ............................................................. 23

23 (22) Conidiophores very long, 160–280 µm; on *Lygodium* sp., India ............................................. P. polypodiacearum  
Conidiophores shorter, 5–150 µm; on other hosts ....................................................................... 24

24 (23) Conidiophores long, up to 150 µm; on *Angiopteris or Pityrogramma* ........................................... 25  
Conidiophores shorter, 10–75 µm; on other hosts ........................................................................ 26

25 (24) Conidiophores 2–6 µm wide; conidia 30–60 × 3–5 µm; on *Angiopteris* sp., Asia .................. P. angiopteridis  
Conidiophores 5–7 µm wide; conidia 25–200 × 5–7.5 µm; on *Pityrogramma*, Ecuador ....................... (?)*Cercospora trismeriae* (see “Doubtful, excluded and insufficiently known species”)

26 (24) Superficial hyphae present, but without solitary conidiophores; on *Davallia fejeensis*, Brazil ...... P. davalliicola  
Superficial hyphae lacking ........................................................................................................... 27

27 (26) Conidia narrow, 2–4 µm ........................................................................................................... 28  
Conidia wider, 3–6 µm ............................................................................................................... 30

28 (27) Conidia 20–80 µm long, only 3–5-septate; on diverse ferns of different families;  
North and South America and Europe (introduced) ................................................................. P. phyllitidis  
Conidia 20.5–110 µm long, 2–12-septate ......................................................................................... P. phyllitidis

29 (28) Conidia never acicular, base short obconically truncate; on *Odontosoria chinensis*, India .......... P. davalliae  
Conidia acicular to somewhat obclavate-cylindrical, base mostly truncate or only slightly obconically truncate; on *Microsorum pustulatum*, Australia ................................................. P. microsori

30(27) Stromata 20–75 µm diam; conidiophores 10–70 µm long, 0–3-septate; conidia 4–7 µm wide;  
on *Tectaria zeylanica*, Asia ................................................................................................. P. helminhostachydis  
Stromata smaller, 10–40 µm diam; conidiophores 15–40 µm long, 0–1-septate; conidia 3–5 µm wide;  
on *Lygodium japonicum*, China .............................................................................................. P. lygodiicola

**Tabular key to Pseudocercospora species on ferns**

**Adiantaceae** (Pteridaceae subfam. Vittarioideae)

**Athyriaceae**

On *Deparia japonica* (*Athryrum japonicum*), Taiwan .................................................................................................................. P. atheryi
**Cyatheaceae**

1. Distinct leaf spots formed; colonies epiphyllous; stromata very large, 60–110 µm diam; conidiophores 25–50 × 3–5 µm; conidia cylindrical-obclavate, 30–50 × 3.5–5.5 µm, base rounded to distinctly obconically truncate; on *Cyathea* sp., Japan ......................................................... P. cyatheae

On dead fronds; colonies amphigenous; stromata smaller, up to 60 µm diam; conidiophores longer and narrower, 30–70 × 2–3 µm; conidia subcylindrical or subacicular, width often irregular, base truncate to somewhat obconically truncate; on *Cyathea australis*, Australia ........................................... P. cyatheicola

**Davalliacae**

1. Superficial hyphae with solitary conidiophores present ................................................................. 2

Superficial hyphae lacking, if present without solitary conidiophores ............................................. 3

2 (1) Stromata large, up to 130 µm diam; on *Nephrolepis falcata*, Australia .................................... P. nephrolepidicola

Stromata smaller, 10–80 µm diam; on *Nephrolepis biserrata* and *Nephrolepis* sp., Brunei, Thailand ................................................................. P. nephrolepidigena

3 (1) Stromata lacking or small, up to 35 µm diam; conidia subcylindrical-acicular, usually 65–100 µm long, base truncate; on *Nephrolepis auriculata*, Taiwan ................................................................. P. nephrolepidis

Stromata larger, up to 75 µm diam; conidia obclavate-subcylindrical, 12–80 µm long, base obconically truncate ........................................................................ 4

4 (3) Mycelium internal and external, but superficial hyphae without solitary conidiophores;

conidia 3–5 µm wide, hila (1.5–2)(–2.5) µm diam; on leaves of *Davallia fejeensis*, Brazil ................ P. davalliiola

Mycelium only internal; conidia 2–3.5 µm wide, hila 1–1.5 µm diam; on *Davallia trichomanoides* and *Nephrolepis exaltata*, North America ....................................... P. phyllitidis

**Dennstadiaceae**

On *Lonicitis hirsuta*, Venezuela ........................................................................................................ P. lonchitidis

**Dryopteridaceae**

1. Stromata lacking; with solitary conidiophores arising from superficial hyphae; conidia acicular,

60–120 µm long; on *Rumohra adiantiformis*, Taiwan ................................................................. P. rumohrae

Stromata small to well-developed; solitary conidiophores lacking ................................................. 2

2 (1) Conidiophores 6.5–30 µm long; fully developed conidia acicular, short conidia sometimes obclavate;

on *Arachniodes* sp., China ................................................................. P. arachnioidis

Conidiophores 10–75 µm long; conidia always obclavate; on *Rumohra adiantiformis*, North America .... P. phyllitidis

**Gleicheniaceae**

On *Dicranopteris linearis*, Africa, Gabon ....................................................................................... P. gleichneniace

**Lindseaceae**

On leaves of *Odontosoria chinensis* [Davallia tenuifolia], India ................................................................ P. davalliae

**Lygodiacae**

1. Superficial hyphae present ............................................................................................................... 2

Mycelium only internal, superficial hyphae lacking ........................................................................... 3

2 (1) Stromata lacking; conidia small, 10–35 × 1.5–4 µm, 1–3-septate; on *Lygodium* spp. .............. P. lygodii

Stromata present; conidia 40–115.5 µm long, pluriseptate; on *Lygodium* sp. ................................. P. lygodigena

3 (1) Conidiophores short, 15–40 µm, 0–1-septate; on leaves of *Lygodium japonicum* .................. P. lygodiicola

Conidiophores much longer, 160–280 µm, pluriseptate; on *Lygodium* sp., India ......................... P. polypodiaceaerum

**Marattiacae**

1. Superficial mycelium with solitary conidiophores developed; stromata lacking;

conidia acicular-filiform; on *Ptisana salicina*, New Zealand ......................................................... P. ptisanae

Superficial mycelium with solitary conidiophores lacking; stromata well-developed; conidia obclavate-cylindrical ....... 2
2 (1) Conidia 3–5 µm wide, hila (1.5–)2(–2.5) µm wide; on Angiopteris spp., Asia ........................................ P. angiopteridis
Conidia narrower, 2–3.5 µm, hila 1–1.5 µm wide; on Angiopteris sp., North America ........................................ P. phyllitidis

Osmundaceae
On Osmunda regalis, North America ................................................................. P. phyllitidis

Plagiogyriaceae
On Plagiogryya euphlebia, Taiwan ................................................................. P. plagiogyriae

Polypodiaceae
1 Conidia distinctly obclavate, base distinctly obconically truncate, 20–80 × 2–3.5 µm, 3–5-septate;
on Camptoleonum phyllitidis and Polypodium polypodioides, North America .............................................. P. phyllitidis
Conidia acicular to somewhat obclavate-cylindrical, base usually truncate or only slightly
obconically truncate, longer, 50–110 µm, with 2–12 septa; on Microsorum pustulatum, Australia ........ P. microsori

Pteridaceae subfam. Pteridoideae
1 Mycelium internal; superficial hyphae with solitary conidiophores lacking; conidiophores only in fascicles ........... 2
Mycelium internal and external; superficial hyphae with solitary conidiophores present ........................................ 3

2 (1) Conidiophores up to 150 × 7 µm; conidia up to 200 µm long and 5–7.5 µm wide; on Pityrogramma, Ecuador
................................................................. (?). Cercospora trismeriae (see “Doubtful, excluded and insufficiently known species”)
Conidiophores up to 100 × 3–5 µm; conidia 20–80 × 2–5 µm; on Pteris spp., North America ................................ P. phyllitidis

2 (2) Conidia 3–5 µm wide, hila (1.5–)2(–2.5) µm wide; on Cyclosorus acuminatus, Taiwan ......................... P. pteridophytophila
Conidia longer and wider, 50–120 × 2.5–3 µm, subhyaline to pale olivaceous;
on Metathelypteris laxa (Thelypteris laxa), Taiwan ................................................................. P. thelypteridis

3 Conidiophores longer, 30–150 µm, medium dark brown, wall somewhat thickened; conidia longer, 40–250 µm;
on Pteris sp., Colombia ................................................................. P. pteridigena

Pteridaceae subfam. Vittarioideae (= Adiantaceae)
On Adiantum spp., Asia (India), South America (Venezuela) ............................................................... P. adianti

Tectariaceae
On Tectaria zeylanica (Helminthostachys zeylanica), Asia ................................................................. P. helminthostachydis

Thelypteridaceae
1 Stroma lacking; superficial hyphae developed, giving rise to solitary conidiophores, fasciculate
conidiophores not formed; on Abacopteris urophylla, Singapore ................................................. P. abacopteridicola
Stroma developed; superficial hyphae and solitary conidiophores lacking; conidiophores fasciculate .................... 2

2 (1) Conidia acicular-filiform, base ± truncate ................................................................. 3
Conidia obclavate, base distinctly obconically truncate ......................................................... 4

2 (2) Conidia narrow, 30–70 × 1–1.5 µm, hyaline; on Cyclosorus acuminatus, Taiwan ......................... P. pteridophytophila
Conidia longer and wider, 50–120 × 2.5–3 µm, subhyaline to pale olivaceous;
on Metathelypteris laxa (Thelypteris laxa), Taiwan ................................................................. P. thelypteridis

4 (2) Conidiophores very short, 9–15 µm, 0–1-septate; conidia long, 50–105 µm;
on leaves of Christella parasitica, Thailand ................................................................. P. christellae
Caeptistui epiphyllous; conidiophores longer, 10–75 µm, aseptate or with several septa;
conidia shorter, 20–80 µm; on Thelypteris tetragona, North America ........................................ P. phyllitidis

List of Pseudocercospora species on ferns

(Fig. 27)


Illustration: Yen & Lim (1980: 204, fig. 7 A–B).

Description: Leaf spots amphigenous, vein-limited, brown, later confluent. Caesptitui hypophyllous, vein-limited, brown,
later confluent. Mycelium internal and external, superficial
hyphae branched, septate, pale olivaceous-brown, 1.5–2.5 µm wide, thin-walled, smooth. Stromata lacking.
Conidiophores solitary, arising from superficial hyphae, lateral, occasionally terminal, erect, straight, subcylindrical or slightly attenuated towards the tip, unbranched, short, about 5–15 × 2.5–3 µm, 0–1-septate, concolorous with the hyphae, thin-walled, smooth; conidiophores reduced to conidiogenous cells, conidiogenous loci inconspicuous, neither thickened nor darkened. Conidia solitary, narrowly cylindrical to obclavate-cylindrical, 30–80 × 2–3 µm, 1–7(–9)-septate, pale olivaceous-brown, thin-walled, smooth, tips obtuse or subobtuse, base truncate, hilum neither thickened nor darkened.


Host range and distribution: Only known from the type collection.


(Fig. 28)
sinuous, sometimes tortuous, usually unbranched, 20–150 × 4–7 µm, continuous to pluriseptate, mostly 2–8-septate, pale to medium brown, wall thin to slightly thickened, smooth; conidiogenous cells integrated, terminal to intercalary, 10–35 µm long, conidiogenous loci inconspicuous to distinctly denticile-like, but wall always unthickened and not darkened. Conidia solitary, obclavate to cylindrical-obclavate, occasionally broadly subacicular, straight to curved, occasionally sinuous-sigmoid, 40–120 × 4–5.5 µm, 5–15-septate, subhyaline to pale olivaceous, thin-walled, smooth, apex obtuse to subacute, base short obconically truncate, about 2–2.5 µm wide, hila neither thickened nor darkened.

**Lectotype (designated here, MycoBank, MBT176147):** Venezuela: El Limon, near Puerto La Cruz, on Adiantum tetraphyllum, 15 Jan. 1928, H. Sydow, Syd., Fungi Exot. Exs. 884 (HBG). Isolectotypes: Syd., Fungi Exot. Exs. 884 (e.g. B, BPI 432406, CUP, MICH 15252, S, UPS, etc.).

**Host range and distribution:** On Adiantum (latifolium, lunulatum, tetraphyllum, Adiantum sp.), Pteridaceae subfam. Vittarioideae (= Adiantaceae), Asia (India, Maharashtra, West Bengal), South America (Venezuela).


**Description:** Leaf spots amphigenous, subcircular to angular-irregular, often confluent, forming larger patches, up to 10 mm diam, brown, margin indefinite. Caespituli ephylloous, punctiform, dark brown to blackish. Mycelium internal. Stromata immersed, well-developed, 20–70 µm diam, dark brown. Conidiophores in larger fascicles, loose to dense, erect, straight, subcylindrical to sinuous or somewhat geniculate, unbranched, 10–140 × 2–6 µm, continuous to pluriseptate, brown throughout or paler towards the tip, thin-walled, smooth; conidiogenous cells integrated, terminal, about 10–30 µm long, conidiogenous loci inconspicuous, neither thickened nor darkened. Conidia solitary, obclavate-cylindrical, straight to somewhat curved, 30–60 × 3–5 µm, 3–6-septate, subhyaline to pale olivaceous or olivaceous-brown, thin-walled, smooth, apex obtuse to subacute, base obconically truncate, (1.5–)2(–2.5) µm wide, hila neither thickened nor darkened.

**Types:** Taiwan: Hwalien Hsieh, Taluke, on Angiopteris lygodiiifolia, 1 Feb. 1985, T. K. Goh (NCHUPP-148a – holotype; K(M) IMI 312070 – isotype).

Host range and distribution: On Angiopteris (evecta, lygodiiifolia), Marattiaceae, Asia (Indonesia, Taiwan).

Notes: Braun (2001) re-examined type material of Cercospora angiopteridis and reduced this species to synonym with Pseudocercospora angiopteridis.

**Pseudocercospora arachniodis** Y.L. Guo, *Mycosystema* 6: 103 (1993). (Fig. 30)


**Illustrations:** Guo (1993: 104, fig. 1), Guo & Hsieh (1995: 88, fig. 80), Guo et al. (1998: 104, fig. 84).

**Description:** Leaf spots amphigenous, at first elliptical to angular, 0.5–1 mm diam, later oblong, 1–4 × 0.5–1 mm, often
confluent, reddish brown, with dark brown halo on the upper side, paler brown below. Caespituli hypophyllous. Mycelium internal. Stromata substomatal, small, composed of a few swollen, olivaceous-brown cells or globose, 10–30 µm diam. Conidiophores in small to moderately large fascicles, usually dense, arising from stromata, emerging thought stomata, straight to curved, subcylindrical, rarely geniculate, unbranched, 6.5–30 × 2.5–4 µm, 0(–1)-septate, uniformly pale olivaceous to olivaceous, thin-walled, smooth, apex conic to conically truncate; conidiophores usually reduced to conidiogenous cells, conidiogenous loci inconspicuous, unthickened and not darkened, sometimes visible as truncate tip. Conidia solitary, acicular, shorter conidia obclavate, 30–110 × 1.5–3 µm, 3–11-septate, pale olivaceous, thin-walled, smooth, apex obtuse to subacute, base truncate to short obconically truncate, about 1–2 µm wide, hila unthickened, not darkened.


Host range and distribution: Only known from the type collection.


Illustrations: Hsieh & Goh (1990: 38, fig. 23), Guo & Hsieh (1995: 34, fig. 32), Guo et al. (1998: 45, fig. 32).

Description: Leaf spots amphigenous, angular-irregular, up to 3 mm diam, brown, margin indefinite. Caespituli
epiphyllous, punctiform, dark brown to blackish. Mycelium internal. Stromata epiphyllous, immersed to somewhat erumpent, subcircular to irregularly shaped, 20–50 µm diam, dark brown. Conidiophores numerous, in dense fascicles arising from stromata, erect, subcylindrical-filiform, geniculate-sinuous, usually simple, rarely branched, 10–70 × 2–3 µm, 0–2-septate, subhyaline to pale olivaceous, thin-walled, smooth; conidiogenous cells integrated, terminal or conidiophores reduced to conidiogenous cells, 10–25 µm long, conidiogenous loci inconspicuous, neither thickened nor darkened. Conidia solitary, acicular, almost straight to usually curved-sinuous, 60–80 × 2–3 µm, indistinctly pluriseptate, subhyaline, thin-walled, smooth, apex acute, base truncate, 2–2.5 µm wide, hila neither thickened nor darkened.


Host range and distribution: Only known from the type collection.


Literature: Phengsintham et al. (2013a: 60–61).

Description: Leaf spots subcircular to irregular, 3–9 mm diam, at first brownish, later becoming brown to dark yellowish brown at the margin. Caespituli epiphyllous, conspicuous. Mycelium internal; hyphae branched, 2–3 µm wide, septate, constricted at the septa, distance between septa 6–8 µm, subhyaline to brownish, wall 0.3–0.5 µm wide, smooth, forming plate-like plectenchymatous stromatic hyphal aggregations. Stromata oval to ellipsoidal, 20–40 µm diam, brown to dark brown, stroma cells oval, ellipsoidal and angular, 3–10 µm wide, dark brown, wall 0.5–0.8 µm wide, smooth. Conidiophores fasciculate, arising from stromata (3–16 per fascicle), geniculate, unbranched, 9–15 × 2–4 µm, 0–1-septate, slightly constricted at the septa, distance between septa 3–12 µm, uniformly pale to medium brown, paler and narrower towards the tip, wall 0.3–0.5 µm wide, smooth. Conidiogenous cells terminal, 8–12 × 2–4 µm, obtuse; conidiogenous loci inconspicuous, unthickened, not darkened. Conidia solitary, obclavate, straight to slightly curved, 50–105 × 2–4 µm, 3–9-septate, pale olivaceous-brown, wall 0.3–0.5 µm wide, smooth, tip subacute, base obconically truncate, hila 1–2 µm wide.

In vitro: Colonies on PDA after 3 wk at 25 C dark grey, reaching 10–15 mm diam, hyphae 2–7 µm wide, septate, constricted at the septa, distance between septa 9–19 µm, brownish or subhyaline, wall 0.3–0.8 µm wide, smooth. Colonies sterile.

Holotype: Thailand: Chiang Rai Province: Muang District, Mae Chan Village, on leaves of Christella parasitica,
µm diam, pale brown to brown. Conidiophores in large, dense fascicles, arising from stromata, erumpent, erect, straight to somewhat sinuous, subcylindrical or attenuated towards the tip, unbranched, 25–50 × 3–5 µm, 0–3-septate, pale brown to brown, paler towards the tip, thin-walled, smooth; conidiophores reduced to conidiogenous cells or conidiogenous cells integrated, terminal, proliferation sympodial or sometimes percurrent, conidiogenous loci inconspicuous, unthickened, not darkened or rim-like. Conidia solitary, cylindrical to obclavate, mildly curved to sigmoid, 30–50 × 3.5–5.5 µm, 3–8-septate, pale brown, thin-walled, smooth, apex attenuated, obtuse to subacute, base rounded to obconically truncate, hila unthickened, not darkened.

Holotype: Japan: Okinawa Pref.: Ishigaki, Tomigusuku, on leaves of Cyathea sp., Cyatheaceae, 28 Mar. 2003, S. Inaba

Host range and distribution: Only known from the type collection.

Pseudocercospora cyatheicola Crous & R.G. Shivas, Persoonia 26: 121 (2011); as “cyathicola”. (Fig. 34)

Illustration: Crous et al. (2011: 120).

Description: On dead fronds, associated with a mycosphaerella-like teleomorph. Mycelium internal; hyphae septate, branched, 2.5–3 µm wide, pale brown, smooth, thin-walled. Stromata amphigenous on fronds, well-developed, erumpent, up to 60 µm diam and 40 µm high, brown. Conidiophores arising from stromata, in loose to
rather dense well-developed fascicles, erect, subcylindrical, straight to geniculate-sinuous, unbranched, 30–70 × 2–3 µm, 1–3-septate, pale to medium brown, smooth, thin-walled; conidiogenous cells integrated, terminal, pale brown, proliferation sympodial and percurrent, conidiogenous loci visible as truncate ends, unthickened and not darkened, 1.5–2 µm wide. Conidia solitary, subcylindrical to subacicular, somewhat irregular in width, straight to irregularly curved, (35–)60–80 (–90) × (2–)3 (–3.5) µm, 3–9-septate, pale brown, smooth, thin-walled, guttulate, apex obtuse to subacute, base truncate to somewhat obconically truncate, hila about 2 µm wide, unthickened, not darkened.

In vitro (in the dark, 25 °C after 1 mo): Colonies spreading, somewhat erumpent, with moderate aerial mycelium and smooth, lobate margins, reaching 35–45 mm diam. On malt extract agar surface olivaceous-grey, with patches of smoke-grey, reverse iron-grey; on potato-dextrose agar surface pale olivaceous-grey, margin olivaceous-grey, reverse iron-grey; on oatmeal agar surface pale olivaceous-grey, margin olivaceous-grey.


Host range and distribution: Only known from the type collection.

(Fig. 35)


Illustration: Kar & Mandal (1969: 355, fig. 17).

Description: Leaf spots amphigenous, irregular in shape, 1–5 mm diam, dingy brown to darker brown, margin indefinite. Mycelium internal. Stromata substomatal, 15–50 µm diam, dark olivaceous, composed of swollen hyphal cells, about 2–5 µm diam. Conidiophores fasciculate, in small to moderately large, loose to dense fascicles, arising from stromata, emerging through stomata, erect, straight, subcylindrical to attenuated towards the tip, mostly geniculate-sinuous, unbranched, about 5–65 × 2.5–5.5 µm, 0–6-septate, uniformly very pale olivaceous-brown, thin-walled, smooth; conidiophores reduced to conidiogenous cells or conidiogenous cells integrated, terminal, occasionally intercalary, about 5–25 µm long, conidiogenous loci inconspicuous or visible by being truncate or rarely subdenticulate. Conidia solitary, narrowly obclavate-subcylindrical or linear, 20.5–105.5 × 2–3.5 µm, 2–11-septate, pale olivaceous, thin-walled, smooth, apex obtuse to subacute, base short obconically truncate, about 1–1.5 µm wide, hila unthickened, not darkened.

Types: India: West Bengal: Darjeeling, Kalimpong, 1372 m alt., on leaves of Odontosoria chinensis (Davallia tenuifolia), Lindseaeaceae, 8 May 1967, A. K. Kar & M. Mandal (K(M) IMI 135178 – holotype; BPI 435482 – isotype).

Host range and distribution: Only known from the type collection.

Notes: Braun & Freire (2004: 229–230) recorded this species on Davallia fejeensis from Brazil, which represents, however, a distinct species described below as Pseudocercospora davalliacola.

Pseudocercospora davalliacola U. Braun, sp. nov. MycoBank MB805524 (Fig. 36)

Etymology: Derived from its host genus (inhabitant of Davallia).
**Diagnosis:** Pseudocercosporae davalliae similis, sed hyphis superficialibus cum conidiophoris solitariis formatibus, conidiophoris saepe 0–1-septatis et conidiis brevioribus, 12–70 µm, subhyaline to pale olivaceous, thin-walled, smooth. Stromata substomatal, 10–50 µm diam, olivaceous-brown, composed of swollen hyphal cells, about 2–5 µm diam. Conidiophores in small to moderately large fascicles, loose to mostly dense, arising from stromata, through stomata, erect, straight, subcylindrical to distinctly geniculate-sinuous, unbranched, 5–40 × 2–4.5 µm, 0–1–(2–)septate, subhyaline to pale olivaceous or olivaceous-brown, thin-walled, smooth; conidiophores reduced to conidiogenous cells or conidiogenous cells integrated, terminal, 5–25 µm long, conidiogenous loci inconspicuous. Conidia solitary or in short chains, occasionally even in branched chains, short conidia subcylindrical-fusoid, longer conidia narrowly obclavate-cylindrical, 12–70 × 2–4 µm, 1–7-septate, subhyaline to pale olivaceous, thin-walled, smooth, apex obtuse to pointed, base obconically truncate, 1–1.5 µm wide, hila unthickened, not darkened.


**Host range and distribution:** Only known from the type collection.

**Notes:** Braun & Freire (2004) recorded this collection as Pseudocercospora davalliae. Davallia fejeensis and the type host of the latter species, Odontosoria chinensis [Davallia tenuifolia] are, however, not allied and belong in different families. Furthermore, there are various morphological differences between collections on the two hosts. The conidia in P. davalliae are consistently formed singly and much longer, up to about 100 µm, and pluriseptate. The conidiophores are also longer and up to 6-septate, and superficial hyphae with solitary conidiophores are lacking.

**Pseudocercospora gleicheniae** (J.M. Yen) U. Braun, **comb. nov.**

MycoBank MB805525 (Fig. 37)


**Literature:** Crous & Braun (2003: 198).

**Illustration:** Yen (1974: 42, fig. 1).

**Description:** Lesions lacking. Caespituli hypophyllous. Mycelium internal and external; hyphae emerging through stomata, superficial, branched, septate, pale olivaceous-brown, 1.5–2 µm wide, thin-walled, smooth. Stromata lacking or small, substomatal, somewhat pigmented. Conidiophores solitary, arising from superficial hyphae, lateral or occasionally terminal, erect, very long and filiform, straight to somewhat sinuous, unbranched or branched, about 100–300 µm long and 3.5–5 µm wide, pluriseptate throughout (about 10–30 septa), dark brown, wall thickened, smooth; conidiogenous cells integrated, terminal or intercalary, 10–30 µm long, conidiogenous loci conspicuous by being ± denticle-like, but wall neither thickened nor darkened, about 1–2 µm broad. Conidia solitary, subcylindrical, ellipsoid, short subclavate-obovoid, 12–25 × 4.5–6 µm, (2–)3–4(–5)-septate,
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subhyaline, pale olivaceous to olivaceous-brown, thin-walled, smooth or almost so, apex rounded, base short obconically truncate to somewhat peg-like, hila neither thickened nor darkened.

Holotype: Gabon: Libreville, 16.3 km sur route de Kongo, on Dicranopteris linearis, Gleicheniaceae, 23 Feb. 1969, G. Gilles 139 (PC).

Host range and distribution: Only known from the type collection.

Notes: This is a very unusual species. The generic affinity is not quite clear. Crous & Braun (2003) excluded this species. Denticulate conidiogenous cells and phragmosporous conidia resemble species of the Dactylaria complex. However, the very long thick-walled conidiophores are not dactylarioid. The type of loci (neither thickened nor darkened, subdenticulate loci caused by geniculation due to sympodial proliferation to distinctly dentic-like) are within the range of Pseudocercospora loci. Phragmosporous conidia are unusual for the latter genus but may occur. Therefore, this species is tentatively assigned to Pseudocercospora.


(Basionym: Cercospora helminthostachydis Henn., Hedwigia 47: 265 (1908).


Description: Leaf spots amphigenous, small indistinct or irregular spots on the upper side, 2–5 mm diam, on the lower side dark, blackish by dense colonies. Caespituli hypophyllous, pustulate, dark brown to black. Mycelium internal. Stromata small to well-developed, substomatal to intraeidermal, 20–75 µm diam, brown, composed of swollen hyphal cells, 2–7 µm diam. Conidiophores in moderately large to large fascicles, arising from stromata, emerging through stomata or erumpent, dense, sometimes very dense, erect, unbranched, straight, subcylindrical to somewhat attenuated towards the tip, slightly geniculate-sinuous, 10–70 × 3–6 µm, 0–3-septate, pale to medium olivaceous-brown, thin-walled, smooth; conidiogenous cells integrated, terminal, 10–30 µm long, conidiogenous loci unthickened, not darkened. Conidia solitary, obclavate-cylindrical, straight to somewhat curved,
40–100 × 4–6 µm, 3–7-septate, olivaceous to olivaceous-brown, thin-walled, smooth, apex obtuse, rounded, base short obconically truncate, hila 1.5–2 µm wide, neither thickened nor darkened.

**Types:** Philippines: Mindanao, Davao, on *Tectaria zeylanica*, 15 Mar. 1904, E. B. Copeland 543 (B – holotype; BPI 437080 – isotype [date given as "15 Mar. 1906"]).

**Host range and distribution:** On *Tectaria zeylanica* (*Helminthostachys zeylanica*), *Tectariaceae*, Asia (India, Philippines, Myanmar).


(Fig. 39)


**Literature:** Crous & Braun (2003: 255).

**Description:** Leaf spots amphigenous, irregularly shaped, 3–8 mm diam, dull red above, below often only with a narrow marginal line surrounding a greenish area. *Caespituli* amphigenous, punctiform on the upper side, effuse below, grey to dark brown. *Mycelium* internal and external, superficial hyphae only formed on the lower side, branched, septate, subhyaline to pale olivaceous, 1–4 µm diam, thin-walled, smooth. *Stromata* only epiphyllous, immersed, subglobose, 20–60 µm diam, brown to dark brown. *Conidiophores* on the upper side in larger fascicles, loose to mostly dense, arising from stromata, erumpent, on the lower side in small, loose fascicles and solitary, arising from superficial hyphae, lateral or occasionally terminal, conidiophores erect, straight, subcylindrical to geniculate-sinuous, unbranched or occasionally branched, 10–100 × 3–5 µm, continuous to pluriseptate throughout, subhyaline to pale olivaceous-brown throughout, thin-walled, smooth; conidiogenous cells integrated, terminal, about 10–30 µm long, conidiogenous loci inconspicuous to subdenticulate, but always unthickened and not darkened. *Conidia* solitary, acicular to obclavate, 30–160 × 3–5 µm, 3- to pluriseptate, subhyaline to pale olivaceous, thin-walled, smooth, apex obtuse to subacute, base obconically truncate, about 2–3.5 µm wide, hila neither thickened nor darkened.

**Holotype:** Venezuela: Aragua, road Maracaya Choroni, on *Lonchitis hirsuta*, *Dennstediaceae*, 9 Apr. 1939, H. H. Whetzel & A. S. Muller (CUP-VZ-3385).

**Host range and distribution:** Only known from the type collection.


(Fig. 40)


**Description:** Leaf spots amphigenous, circular to elliptical, scattered, 2–30 mm diam, greyish to dark brown, centre becoming paler, margin indefinite. *Colonies* amphigenous, mainly hypophyllous. *Mycelium* internal and external; superficial hyphae creeping and climbing setae of the leaf surface, branched, septate, 2–5 µm wide, olivaceous to pale brown. *Conidiophores* in small fascicles (2–10), divergent, arising from internal hyphae, emerging through stomata, or solitary, arising from superficial hyphae, lateral, erect, straight, subcylindrical to slightly geniculate-sinuous, unbranched, 20–90 × 3–4 µm, 2–7-septate, yellowish ochraceous to medium brown, thin-walled, smooth; conidiogenous cells integrated, terminal, conidiophores occasionally reduced to conidiogenous cells, about 20–35 µm long, conidiogenous loci inconspicuous to subdenticulate, but always unthickened and not darkened. *Conidia* solitary, obclavate-cylindrical, straight to somewhat curved, 10–35 × 1.5–4 µm, 1–3-septate, colourless, thin-walled, smooth, apex acute to subobtuse, base obconically truncate, about 1–2 µm wide, hila unthickened, not darkened.

**Fig. 39. Pseudocercospora lonchitidis** (CUP-VZ-3385). A. Superficial hyphae. B. Solitary conidiophores arising from superficial hyphae. C. Conidiophore fascicle. D. Conidia. Bar = 10 µm.
Holotype: Taiwan: Hsinchu Hsien, Hsinpu, on Lygodium japonicum, 2 May 1920, K. Sawada (NTU-PPE).

Host range and distribution: On Lygodium (flexuosum, japonicum [microstachyum]). Lygodiaceae, Asia (Taiwan, Thailand).

Pseudocercospora lygodicola Y.L. Guo & U. Braun, sp. nov.
MycoBank, MB805526 (Fig. 41)

Etymology: Epithet derived from its host genus (inhabitant of Lygodium).


Diagnosis: Pseudocercosporae polypodiacearum similis, sed conidiophoris brevioribus, 15–40 µm, 0–1-septatis, apice non inflatis.

Description: Leaf spots amphigenous, irregularly shaped, 1–6 mm diam, often confluent and larger, covering up to half of a leaf, greyish brown above, greyish black below. Caespituli amphigenous, mainly hypophyllous. Mycelium immersed. Stromata substomatal, subglobose, 10–40 µm diam, dark brown. Conidiophores in dense fascicles, arising from stromata, through stomata, erect, straight, subcylindrical to geniculate-sinuous, 15–40 × 2.5–5 µm, 0–1-septate, uniformly olivaceous to olivaceous-brown, thin-walled, smooth, apex obtuse to conic; conidiophores reduced to conidiogenous cells or conidiogenous cells integrated, terminal, about 10–25 µm long, conidiogenous loci inconspicuous or subdenticulate, but always unthickened and not darkened. Conidia solitary, obclavate, occasionally subcylindrical, 40–115 × 3–5 µm, 3–13-septate, olivaceous-brown, thin-walled, smooth, apex obtuse to subacute, base subtruncate to usually short obconically truncate, about 1.5–2 µm wide, hila unthickened, not darkened.

Types: China: Guangdong Province: Guangzhou, on leaves of Lygodium japonicum, Lygodiaceae, 8 VI 1962, Q. M. Ma & X. J. Liu 1439 (HAMAS 59148 – holotype; BPI 1109717 – isotype).

Host range and distribution: Only known from the type collection.

Notes: This species was previously recorded, described and illustrated from China as Pseudocercospora polypodiacearum (Guo & Hsieh 1995, Guo et al. 1998), but differs from the latter species in having much shorter, 0–1-septate, apically usually not inflated conidiophores, and is thus better considered a separate species.

Pseudocercospora lygodiigena U. Braun, nom. nov.
MycoBank MB806067 (Fig. 42)

Illustration: Sarbajna (1990: 488, fig. 1).

Description: Leaf spots amphigenous, subcircular to angular-irregular, 1–4 mm diam., sometimes vein-limited, centre greyish, margin darker, brown. Caespituli amphigenous, mostly hypophyllous, punctiform, scattered to aggregated, brown or greyish by abundant sporulation. Mycelium internal and external; superficial hyphae emerging through
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stomata, branched, 1–4 µm wide, septe, pigmented near conidiophores, otherwise hyaline, subhyaline or very pale olivaceous, thin-walled, smooth or almost so, occasionally faintly rough-walled. Stromata lacking to well-developed, mostly substomal, 10–30 µm diam., pigmented. Conidiophores in small to moderately large, loose fascicles, 3–30, arising from internal hyphae or stromata and solitary, arising from superficial hyphae, lateral, erect, straight, subcylindrical to somewhat sinuous or subgeniculate, unbranched, 5–55 × 2–4 µm, 0–3(–5)-septate, pale to medium brown or olivaceous-brown, wall thin to somewhat thickened, up to 0.8 µm, smooth; conidiogenous cells integrated, terminal, 5–25 µm long, conidiogenous loci inconspicuous, neither thickened nor darkened. Conidia solitary, narrowly obclavate-subcylindrical, occasionally subacicular, straight to curved, 30–115.5 × 2–4 µm, 2–14-septate, hyaline to faintly pigmented, thin-walled, smooth or almost so to somewhat rough, apex subobtuse to pointed, base short obconically truncate, 1–1.5 µm wide, hila neither thickened nor darkened.


**Host range and distribution:** On Lygodium sp., Lygodiaceae, Asia (India).

**Notes:** This species does neither belong to *Stenella* nor to *Zasmidium*. Due to inconspicuous conidiogenous loci and unthickened, non-pigmented hila of the conidia, it has to be reallocated to *Pseudocercospora*. Sarbajna (1990) cited IMI 288612 as number of the holotype, but the data (locality, collector and date) specified in the original description for the holotype do not agree with the data on the label of the material deposited at Kew (K) under this number. The search for another collection of this species (under another IMI number) corresponding to the data cited in Sarbajna’s (1990) failed. Thus, type material of this species is undoubtedly not preserved. The material deposited as *Stenella lygodii* under IMI 288612 agrees with Sarbajna’s (1990) original description, but it cannot be considered the

**Fig. 41.** *Pseudocercospora lygodiicola* (HMAS 59148). A. Conidiophore fascicle. B. Conidiophore tips. C. Conidia. Bar = 10 µm.

**Fig. 42.** *Pseudocercospora lygodiigena* (K(M) IMI 288612). A. Conidiophores arising from superficial hyphae. B. Fasciculate conidiophores. C. Conidia. Bar = 10 µm.
Holotype. Therefore, we propose to designate this material as neotype of *S. lygodii*.


*(Fig. 43)*

*Description:* Leaves on fonds, amphigenous, scattered to confluent, often covering much of the fond surface, circular to irregular, 5–15 mm diam, dark reddish brown, centre becoming grey, margin conspicuous, uneven, with chlorotic halo, vein-limited. *Caespituli* amphigenous. *Mycelium* internal. *Stromata* well-developed, 20–60 µm diam, substomatal, brown. *Conidiophores* in loose to dense fascicles, 5–30, arising from stromata, through stomata, forming sporodochial conidiomata, erect, unbranched, geniculate-sinuous, 30–65 × 3–5 µm, reddish brown, paler towards the apex, 1–5-septate, thin-walled, smooth; conidiogenous cells integrated, terminal, subcylindrical, 10–35 × 2.5–4 µm, conidiogenous loci inconspicuous or visible as truncate tip, unthickened, not darkened. *Conidia* solitary, acicular to narrowly obclavate-subcylindrical, curved to flexuous, 50–110 × 2.5–4 µm, 2–12-septate, pale brown, thin-walled, smooth, apex rounded or subacute, base truncate to slightly obconically truncate, hila neither thickened nor darkened.

*Holotype:* **Australia:** Queensland: Brisbane, West End, Doris Street, on *Microsorum pustulatum* Copel., *Polypodiaceae*, 6 Aug. 2010, B. C. McNeil (BRISP 53617).

*Host range and distribution:* Only known from the type collection.


*(Fig. 44)*

*Description:* Leaves amphigenous, shape and size irregular, 2–12 mm diam, medium brown, margin indefinite. *Mycelium* internal and external; hyphae branched, 2–3 µm wide, septate, brown, thin-walled, smooth. *Stromata* well-developed, subepidermal, up to 150 µm diam and 50 µm high,
medium brown. Conidiophores arising from stromata in loose fascicles, or solitary, arising from superficial hyphae, erect, subcylindrical, irregularly geniculate-sinuous, unbranched or branched below, 25–45(–90) × 2.5–3(–3.5) µm, 1–4-septate, medium brown, thin-walled, smooth; conidiogenous cells integrated, terminal, subcylindrical, 15–25(–40) × (2–)2.5(–3) µm, sympodially and 1–2 times percurrently proliferating, conidiogenous loci neither thickened nor darkened. Conidia solitary, subcylindrical-filiform, occasionally slightly aciculare (somewhat attenuated towards the tip), straight to irregularly flexuous, (40–)50–60(–95) × (2.5–)3.5(–4) µm, 3–6(–9)-septate, pale brown, thin-walled, smooth, apex obtuse, rounded, base truncate, hila neither thickened nor darkened. Ascomata globose, erumpent, up to 80 µm diam, brown, with a central ostiole; asci subcylindrical to narrowly ovoid, 35–50 × 8–10 µm. Ascospores fusiform-ellipsoid, widest in the middle of the apical cell, tapering towards both ends, 9–11 × 2.5–3.5 µm, colourless, apex acutely rounded, constricted at the septum.

In vitro (in the dark at 25 °C, after 2 wk): Colonies spreading, erumpent, with folded surface and even, lobate margins, up to 15 mm diam. On potato-dextrose agar surface smoke-grey with patches of grey-olivaceous, iron-grey in reverse; on oatmeal agar olivaceous-grey with patches of pale olivaceous-grey.


Host range and distribution: Only known from the type collection.

Notes: Pseudocercospora nephrolepidis, described from Taiwan on Nephrolepis auriculata, differs from P. nephroleplicola in lacking or much smaller stromata, lacking superficial hyphae, shorter, only 0–1-septate conidiophores and shorter conidia.

Pseudocercospora nephrolepidigena U. Braun, Meeboon & C. Nakash., sp. nov.
MycoBank MB805527 (Fig. 45)

Etymology: Derived from its host genus, Nephrolepis.

Literature: Braun & Sivapalan (1999: 21, as "P. thelypteridis"), Nakashima et al. (2007: 265, as "P. phyllitidis"), Meeboon et al. (2007, as "P. phyllitidis").

Illustration: Braun & Sivapalan (1999: 20, fig. 12, as "P. thelypteridis").

Fig. 45. Pseudocercospora nephrolepidigena (HAL 2602 F). a. Based on type material. b. Based on material from Brunei at HAL. A. Solitary conidiophores arising from superficial hyphae. B. Superficial hyphae. C. Conidiophore fascicles. D. Conidiophores. E. Conidia. Bar = 10 µm.
Diagnosis: Pseudocercosporae nephrolepidis et P. phyllitidis similis, sed hyphis superficialibus cum conidiophoris solitariis crescentibus.

Description: Leaf spots amphigenous, subcircular to angular-irregular, 1–15 mm diam, or oblong, up to 20 mm, sometimes confluent, forming large blotches or entire leaf segments becoming necrotic, pale to dark brown, margin indefinite or somewhat darker, sometimes with yellowish halo, occasionally somewhat zonate. Caespituli amphigenous, conspicuous on the upper side, punctiform, scattered, blackish or greyish by abundant conidial formation, less conspicuous on the lower side. Mycelium internal and external; superficial hyphae amphigenous, abundant on the lower side, less developed but also present on the upper side, branched, 1.5–4.5 µm wide, septate, subhyaline to pale olivaceous, thin-walled, smooth. Stromata small to well-developed, immersed, 10–80 µm diam, pale to dark olivaceous-brown, cells 2.5–8 µm diam. Conidiophores in small to rather large, loose to mostly dense fascicles, arising from stromata, erumpent, or solitary, arising from superficial hyphae, lateral, erect, straight, subcylindrical or somewhat attenuated towards the tip, unbranched, occasionally somewhat geniculate, 5–50 × 1.5–4 µm (with attached persistent conidia up to about 80 µm long), 0–3-septate, subhyaline to pale olivaceous or brownish, thin-walled, smooth; conidiophores often aseptate, i.e. reduced to conidiogenous cells, or conidiogenous cells integrated, terminal, 5–25 µm long, often monoblastic, determinate, sometimes polyblastic, sympodially proliferating, conidiogenous loci inconspicuous or visible as truncate tips, about 1.5–2.5 µm wide, neither thickened nor darkened. Conidia solitary, persistent, i.e. attached to the conidiogenous cells for a longer time, cylindrical, long conidia filiform to subacicular, i.e. somewhat attenuated towards the tip, straight to somewhat curved, 25–115 × (1.5–)2–3.5(–4) µm, 2–10-septate, septa not very distinct, subhyaline to very pale olivaceous, thin-walled, smooth, apex obtuse to subacute, base truncate, about 1.5–2.5 µm wide, hila neither thickened nor darkened.


Host range and distribution: On Nephrolepis (biserrata, cordifolia, Nephrolepis sp.), Davalliaceae, Asia (Brunei, Thailand).

Notes: Nakashima et al. (2007) recorded collections on this host from Thailand as Pseudocercospora phyllitidis, but the latter American species differs in lacking superficial hyphae and in having much longer conidiophores. Furthermore, the type host of P. phyllitidis, Campyloneurum phyllitidis, belongs to the Polypodiaceae. Pseudocercospora phyllitidis, recorded on various ferns belonging to different families, is probably heterogeneous. “Pseudocercospora thelypteridis” on Nephrolepis from Brunei, described and illustrated in Braun & Sivapalan (1999), agrees well with P. nephrolepidigena.


Illustration: Kirschner & Chen (2007: 224, fig. 2).
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fasciculate, up to 22, arising from internal hyphae or stromata, emerging through stomata, straight, subcylindrical to slightly geniculate, unbranched (7–)13–28(–35) × 2.5–3 µm, 0–1-septate, pale brown, thin-walled, smooth; conidiogenous cells integrated, terminal or conidiophores mostly aseptate, i.e. reduced to conidiogenous cells, conidiogenous loci broadly truncate, neither thickened nor darkened. Conidia solitary, subcylindrical to acicular, i.e. somewhat tapering from base to top, straight to curved or sinuous, about (30–)65–100(–115) × 2–3 µm, inconspicuously 2–9-septate, subhyaline to pale brown (paler than the conidiophores), thin-walled, smooth, apex subobtuse to subacute, base truncate, hila neither thickened nor darkened.

Holotype: Taiwan: Taipei County, Yangmingshan, ca. 800 m alt., on living leaves of Nephrolepis auriculata, 2 Mar. 2006, R. Kirschner 2555 (TNM).

Host range and distribution: on Nephrolepis auriculata, Davalliaceae, Asia (Taiwan).

Note: Differences between this species and the Australian P. nephrolepidicola are discussed under the latter species.

Pseudocercospora phyllitidis (H.H. Hume) U. Braun & Crous, in Crous & Braun, Mycosphaerella and Anam. 1: 321 (2003). (Fig. 47)


Description: Leaf spots amphigenous, angular-irregular, 2–18 mm diam, brown, margin usually indefinite. Caespituli hypophyllous. Mycelium internal; rarely with a few superficial hyphae, but without conidiophores. Stromata small to large, only filling the substomatal cavity or larger, 10–80 µm diam, subglobose, brown. Conidiophores in small to rather large fascicles, arising from stromata, emerging through stomata, erect, straight to somewhat curved or sinuous, subcylindrical, barely geniculate, unbranched, 10–75(–100) × 3–5 µm, continuous to pluriseptate, uniformly subhyaline, pale to medium olivaceous-brown or brown, wall thin to somewhat thickened, smooth; conidiogenous cells integrated, terminal or conidiophores reduced to conidiogenous cells, conidiogenous loci inconspicuous, neither thickened nor darkened. Conidia solitary, obclavate, 20–80 × 2–5 µm, 3–5-septate, subhyaline to pale olivaceous, thin-walled, smooth, apex subacute or obtuse, base obconically truncate, about 1.5–2.5 µm wide, hila neither thickened nor darkened.


Host range and distribution: On Angyopteris sp., Marattiaceae; Campyloneurum phyllitidis, Polypodium polypodioides, Polypodiaceae; Davallia trichomanoides, Nephrolepis exaltata, Davalliaceae; Osmunda regalis, Osmundaceae; Pteris (P. biaurita, P. ensifolia), Pteridaceae; Rumohra adiantiformis, Dryopteridaceae; Thelypteris tetragona, Thelypteridaceae; non-identified fern, North America (Canada; USA, Florida, Indiana), Jamaica, Panama, Puerto Rico, Europe (UK, in a botanical garden).

Notes: Records of this species from Asia, India (Lall et al. 1964, Kamal 2010) are doubtful and seem to belong to P. pteridicola. There are various records on ferns belonging to different families, suggesting that P. phyllitidis is probably heterogeneous.


Description: Leaf spots amphigenous, subcircular, 7–10 mm diam, dark brown, centre becoming grey, zonate. Caespituli amphigenous. Mycelium internal. Stromata lacking or only few swollen hyphal cells in the substomatal cavity. Conidiophores fasciculate, 3–20, loose, arising from swollen substomatal hyphal cells, emerging through stomata, erect, straight to usually geniculate-sinuous, occasionally subnodulose, unbranched, 60–180 × 4–7 µm, indistinctly 3–8-septate, brown, paler towards the tip, almost hyaline at the apex, thin-walled, smooth; conidiogenous cells integrated, terminal and intercalary, conidiogenous loci inconspicuous to visible by being truncate or subdenticulate. Conidia solitary obclavate, straight to somewhat curved, 50–85 × 3–5 µm, 5–7-septate, pale olivaceous, thin-walled, smooth, apex pointed, base short obconically truncate, about 1.5–2 µm wide, hila neither thickened nor darkened.

Types: Taiwan: Taipei Hsieh, Shihting, on Plagiogyria euphlebia, Plagiogryraeaceae, 6 Nov. 1927, K. Sawada (NTU-PPE – holotype; HMAS 05180 – isotype).

Host range and distribution: Only known from the type collection.

Pseudocercospora polypodiacearum D.N. Shukla, A.K. Singh, P. Kumar & Kamal, Indian Phytopathol. 35: 86 (1982). (Fig. 49)


Illustration: Shukla et al. (1982: 85, fig. 1).
through stomata or erumpent, erect, straight to flexuous, geniculate-sinuous, unbranched, 60–280 × 3–7 µm, sometimes swollen at the apex, pluriseptate throughout, brown, thin-walled, smooth; conidiogenous cells integrated, terminal, 10–30 µm long, mono- to polyblastic, sympodially proliferating, conidiogenous loci inconspicuous, unthickened, not darkened. Conidia solitary, obclavate-cylindrical, 30–130 × 3–7.5 µm, (1–)4–8–(12)-septate, pale olivaceous to light brown, thin-walled, smooth, apex obtuse to subacute, base obconically truncate, occasionally somewhat peg-like, 1.5–2.5 µm wide, hila unthickened, not darkened.


Host range and distribution: On Lygodium (flexuosum, sp.), Schizaeaceae, Asia (India, Karnataka, U.P.).

Notes: A Chinese collection on Lygodium japonicum was described and illustrated by Guo & Hsieh (1995) and Guo et al. (1998) as P. polypodiacearum. However, this collection is morphologically quite distinct by its much shorter, 0–1-septate and apically unswollen conidiophores, and thus better separated and described as new species (see P. lygodiicola).


(Fig. 50)


Description: Leaf spots amphigenous, subcircular, 1–6 mm diam, often confluent, yellowish brown, pale brown to greyish brown, with purplish to dark brown margin. Caespituli amphigenous, mostly hypophyllous. Mycelium internal and external; superficial hyphae branched, septate, 1.5–2.5 µm, subhyaline, thin-walled, smooth. Stromata lacking, small or well-developed, 15–30 µm diam, substomatal, brown. Conidiophores in small to large fascicles, loose to dense, arising from stromata, emerging through stomata, or solitary, arising from superficial hyphae, lateral, rarely terminal, erect, straight, subcylindrical to geniculate-sinuous, usually unbranched, rarely branched, 10–70 × 2.5–4 µm, 0–7-septate, pale olivaceous, olivaceous-brown to medium brown, thin-walled, smooth; conidiogenous cells integrated, terminal, about 10–25 µm long, conidiogenous loci inconspicuous, neither thickened nor darkened. Conidia solitary, narrowly obclavate-subcylindrical, attenuated towards the tip, 40–125 × 2–4 µm, 2- to pluriseptate, subhyaline, thin-walled, smooth, apex subacute, base obconically truncate, 1–2 µm wide, hila neither thickened nor darkened.

Holotype: China: Sichuan Province: Chongqing, on Pteris vittata, 31 Aug. 1962, Q. M. Ma & S. J. Han 1740 (HMAS 59158).

Host range and distribution: On Pteris (biaurita, vittata), Pteridaceae, Asia (China, India).

Notes: Braun & Mel’nik (1997) assigned a collection on Pteris sp. from Colombia to P. pteridicola, which is, however, morphologically deviating, geographically isolated, and therefore described as P. pteridigena. “Cercospora phyllitidis” on Pteris biaurita in India (Lall et al. 1964: 182, fig. 2; Kamal 2010) and on Pteris sp. in India (Kakoti et al. 1998) belong
probably to *P. pteridicola*, but material was not available for a re-examination.

**Pseudocercospora pteridigena** U. Braun, *sp. nov.*

*MycoBank MB805528 (Fig. 51)*

*Etymology:* Derived from its host genus, *Pteris*.

*Diagnosis:* Pseudocercosporae pteridicolae valde similis, sed conidiophoris longioribus, ad 150 µm, parietibus atrioribus et leviter incrassatis, conidiis longioribus, ad 250 µm longis.

*Description:* Leaf spots amphigenous, subcircular to somewhat irregular, 3–6 mm diam, yellowish brown to grey, with a wide dark reddish brown border. *Caespituli* hypophyllous, scattered, fine, brownish. Mycelium internal and external; superficial hyphae emerging through stomata, sparingly branched, 1.5–3 µm wide, subhyaline to pale olivaceous, septate, thin-walled, smooth. Stromata small, substomatal, 10–35 µm diam, brown, composed of swollen hyphal cells, 2–5 µm diam. *Conidiophores* in small fascicles, loose to moderately dense, arising from stroma, emerging through stomata or solitary, arising from superficial hyphae, erect, straight, subcylindrical to somewhat sinuous or slightly geniculate, unbranched, 30–150 × 3–5 µm, continuous to pluriseptate, medium dark brown below, paler towards the apex, wall somewhat thickened, smooth; conidiogenous cells integrated, terminal, about 10–30 µm long, conidiogenous loci unthickened, not darkened, but sometimes subdenticulate. *Conidia* solitary, acicular to narrowly obclavate, 40–250 × 2–4 µm, 4-septate to pluriseptate, subhyaline to pale olivaceous, thin-walled, smooth, apex pointed, base short obconically truncate, 1–1.5 µm wide, hila neither thickened nor darkened.


*Host range and distribution:* Only known from the type collection.

*Notes:* The Asian *Pseudocercospora pteridicola* resembles *P. pteridigena* but differs in having much shorter, paler, thin-walled conidiophores, 10–70 µm, and shorter conidia, 40–125 µm. The collection from Colombia was tentatively assigned to *P. pteridicola* in Braun & Mel’nik (1987: 84), and morphological differences between this collection and the Chinese type were discussed.


(Fig. 52)
**Pseudocercospora ptisanae** U. Braun, sp. nov.

*MycoBank MB805529* (Fig. 53)

**Literature**: Braun & Hill (2002: 29, as *Pseudocercospora cf. rumohrae*).

**Illustration**: Braun & Hill (2002: 27, fig. 10).

**Etymology**: Epithet derived from its host genus, *Ptisana*.

**Diagnosis**: *Pseudocercospora rumohrae* valde similis, sed hospite divergenti (*Ptisana, Marattiaceae*) et hilis multo angustioribus, 1.5–2 μm diam.

**Description**: Leaf spots amphigenous, shape and size variable, brown, margin indefinite. *Caesipultii* hypophyllous, not very conspicuous. *Mycelium* internal and external; superficial hyphae emerging through stomata, branched, septate, 1–4 μm wide, thin-walled, subhyaline to pale olivaceous, smooth. *Stromata* lacking. *Conidiophores* usually solitary, arising from superficial hyphae, lateral, rarely terminal, occasionally in small, loose fascicles, emerging through stomata, erect, straight, subcylindrical to geniculate-sinuous, unbranched, 5–40 × 2–3 μm, 0–1-septate, subhyaline to pale olivaceous, thin-walled, smooth; conidiophores usually reduced to conidiogenous cells or conidiogenous cells sometimes integrated, terminal, conidiogenous loci inconspicuous. *Conidia* solitary, acicular to filiform, 80–100 × 2–3 μm, indistinctly pluriseptate, subhyaline to pale olivaceous, thin-walled, smooth, apex subacute, base truncate, 1.5–2 μm wide, hila unthickened, not darkened.

**Holotype**: New Zealand: Auckland, Auckland Domain, FERNZ Fernery, on leaves of *Ptisana salicina* (*Marattia salicina*), Marattiaceae, 6 Mar. 2005, C. F. Hill (PDD 82345), ex-type culture: ICMP 15860.

**Notes**: This species was described and illustrated by Braun & Hill (2002) as *Pseudocercospora cf. rumohrae*, based on a collection from 2000 (New Zealand, Auckland, Auckland University, 30 Apr. 2000, C.F. Hill 185). This collection, originally deposited at HAL, is not maintained. It was lost in June 2013 during a big flood that caused damage in the herbarium HAL. *Pseudocercospora on Ptisana salicina* is, indeed, morphologically very close to *P. rumohrae*, but it occurs on a fern of another family, and the conidia and hila are distinctly narrower.
Description: Leaf spots amphigenous, angular-irregular, size variable, centre brown, yellowish or paler brown towards the periphery, margin indefinite. Colonies hypophyllous, not very conspicuous. Mycelium internal and external, superficial hyphae emerging through stomata: branched, septate, very pale olivaceous, thin-walled, smooth. Stromata lacking. Conidiophores solitary, arising from superficial hyphae, occasionally a few conidiophores emerging through stomata, forming small, loose fascicles, erect, straight to slightly curved, subcylindrical to slightly clavate, at most slightly geniculate-sinuous, 2–25 × 2.5–4 µm, 0–2-septate, subhyaline to pale brownish, thin-walled, smooth; conidiogenous cells integrated, terminal or conidiophores reduced to conidiogenous cells, 2–20 µm long, conidiogenous loci inconspicuous, neither thickened nor darkened. Conidia solitary, acicular, 60–120 × 3–3.5 µm, indistinctly plurisepitate, hyaline to very pale olivaceous, thin-walled, smooth; apex acute or subacute, base truncate, about 2.5–3 µm wide, hila neither thickened nor darkened.


Host range and distribution: Only known from the type collection.


Description: Leaf spots amphigenous, angular-irregular, up to 3 mm diam, brown, margin indefinite. *Caespituli* epiphyllous, punctiform, dark brown to blackish. *Mycelium* internal. Stromata immersed, irregularly shaped, 20–35 µm diam, dark brown. *Conidiophores* numerous, densely fasciculate, arising from stromata, erumpent, erect, straight to curved, cylindrical-filiform, not geniculate, simple or sometimes branched, somewhat narrowed towards the apex, 10–60 × 2–3 µm, continuous, rarely septate, subhyaline to pale olivaceous, paler towards the apex, tips rounded to truncate, thin-walled, smooth; conidiogenous cells integrated, terminal or conidiophores reduced to conidiogenous cells, conidiogenous loci inconspicuous. *Conidia* solitary, acicular-filiform, 50–120 × 2.5–3 µm, 5–12-septate, subhyaline to pale olivaceous, thin-walled, smooth, apex pointed, base truncate or subtruncate, about 1.5–2 µm wide, hila neither thickened nor darkened.


Host range and distribution: Only known from the type collection.

**Zasmidium**

A single species.

**Zasmidium australiense** (J.L. Mulder) U. Braun & Crous, comb. nov.

MycoBank MB805530 (Fig. 56)


Description: Leaf spots lacking, attacked areas only chlorotic corresponding to the areas delimited by veins, similar chlorotic areas also on the upper surface. Colonies hypophyllous, effuse, forming greyish brown patches. *Mycelium* internal and external; superficial hyphae forming mycelial mats or a loose reticulum on the leaf surface, becoming darker brown with age, branched, septate, rarely constricted at septa, about 4–5 µm wide, strongly echinulate, rarely smooth. Stromata absent. *Conidiophores* solitary, arising from superficial hyphae, lateral, rarely terminal, erect, straight, subcylindrical, usually unbranched, at most apically somewhat geniculate, up to 160 × 3.5–5.5 µm, septate, dark brown, conspicuously echinulate with crested type projections, denser than in conidia; conidiogenous cells integrated, terminal, proliferation sympodial, occasionally percurrent; conidiogenous loci distinct, non-protuberant, thickened and darkened-refractive, about 1.5–1.5 µm diam. *Conidia* solitary, cylindrical, straight to distinctly curved, about 30–70 × 3–5.5 µm, (1–)3–4(–5)-septate, brown, wall thin, echinulate (crested projections), less dense than in conidiophores and lacking around hila, apex obtuse, rounded, base rounded to truncate, hila slightly thickened and darkened.

Holotype: Australia: Peregian beach, on leaves of *Blechnum serrulatum* (*B. indicum*), Blechnaceae, 3 Dec. 1982, J. L. Alcorn 8240b (K(M) IMI 273944).

Host range and distribution: Only known from the type collection.

Notes: Due to scolecosporous conidia formed singly and truncate scars and hila, this species is reallocated to *Zasmidium*.
CERCOSPOROID SPECIES ON GYMNOSPERMAE

Passalora species on Gymnospermae

Key to the species of Passalora on Gymnospermae

1 Stromata 20–80 µm diam; conidiophores fasciculate, 20–90 µm long, 2–5-septate; conidia 30–65 × 4–6 µm, 1–6-septate; on hosts of various genera of the Cupressaceae, including Juniperus, Asia, North and South America .......................................................... P. sequoiae

Stromata larger, up to 150 µm wide and 120 µm deep; conidiophores in sporodochial conidiomata, shorter, about 10–40 µm long, 0–1-septate; conidia about 15–45 × 4–5 µm, 0–4-septate; on Juniperus communis, Europe, North America ......................................................... P. juniperina

List of Passalora species on Gymnospermae

(Fig. 57)

Illustrations: Ellis (1976: 120, fig. 84B), Hodges (1962: 65, fig. 2C), Sutton & Hodges (1990: 318, fig. 2), Solheim (2013: figs 2–5).

Description: Causinig needle blight, attacked hosts only partly with dead needles or needles almost completely necrotic, needles at first light brown, later greyish brown to grey. Colonies amphigenous, mainly epiphyllous, scattered or in lines, dark brown to blackish, punctiform to pustulate. Mycelium internal, usually epidermal and subepidermal; hyphae branched, septe, 2–6 µm wide, brown, thin-walled, smooth. Stromata substomatal, intraepidermal to deeply immersed, finally also erumpent, often expended and large, up to 150 µm diam and 120 µm deep, medium to dark brown, composed of dense, rounded to mostly angular cells, about 2.5–8 µm diam, wall somewhat thickened. Conidiomata sporodochial, composed of large stromata and numerous, densely arranged conidiophores, emerging through stomata or erumpent, erect, straight to slightly curved, subcylindrical, unbranched, (5–)10–35(–40) × 3–7(–9) µm, 0–1-septate, olivaceous-brown, yellowish brown, thin-walled, smooth or almost so; conidiophores mostly reduced to conidigenous cells or conidigenous cells integrated, terminal, proliferation sympodial, occasionally percurrent, conidigenous loci 1–3, rather inconspicuous to conspicuous, slightly thickened and somewhat refractive, little darkened, (1.5–)2(–2.2) µm wide. Conidia solitary, cylindrical to obclavate-cylindrical of fusiform, 15–45 × (3–)4–5(–6.5) µm, 0–3(–4)-septate, without constrictions at septa, olivaceous to yellowish brown, thin-walled, delicately verruculose, apex obtuse, base rounded to short obconically truncate, 1.5–2.2 µm wide, hila rarely or only slightly thickened, refractive, barely darkened.


Host range and distribution: on Juniperus communis [var. communis, var. depressa (J. intermedia), var. saxatilis (J. nana)], Cupressaceae, Europe (Finland, Norway, Romania, Sweden, Russia), North America (Canada, Ontario; USA, Iowa, Michigan, Wisconsin).

Note: Material recently collected in Russia, Novgorod Oblast, 2002, by V.A. Mel’nik has been distributed in Mycotheca Graecensia 249 (e.g. BPI 688449, GZU, HAL).

(Fig. 58)
Basionym: Cercospora sequoiae Ellis & Everh., J. Mycol. 3(2): 13 (1887).


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Illustrations: Hodges (1962: 63, figs. 1A, 2A), Hsieh & Goh (1990: 326, fig. 247), Sutton & Hodges (1990: 315, fig. 1), Baker et al. (2000: 251, fig. 1), Guo et al. (2003: 121, fig. 78).


Description: Leaves (needles, scale leaves) at first with small, subcircular lesions, yellowish brown to medium reddish or dark brown, scattered, later enlarged and confluent, finally entire leaves becoming necrotic, brown or greyish brown; twig symptoms visible as pale brown, irregular lesions, later enlarged and confluent, finally turning reddish brown towards the tips. Caespituli punctiform-pustulate, scattered, brown or visible as dark greyish masses of conidia. Mycelium internal. Stromata substomatal to immersed, intraepidermal to deeply immersed, erumpent, subglobose to hemispherical or somewhat irregular, 25–100 µm diam, dark brown, composed of swollen hyphal cells, rounded to isodiametric, 2.5–8 µm diam. Conidiophores in small to usually large fascicles, loose to usually dense, arising from stromata, through stomata or erumpent, erect, straight to curved or frequently geniculate-sinuous, above all in the upper half, unbranched, 20–90 × 2.5–8 µm, 2–5-septate, medium brown to dark brown throughout or paler towards the tip, olivaceous-brown, thin-walled, smooth or almost so, occasionally somewhat verruculose; conidiogenous cells integrated, terminal, about 10–40 µm long, polyblastic, proliferating sympodially, rarely percurrently, with 1–6 distinctly thickened and darkened conidiogenous loci, 2–2.5 µm diam, mostly on shoulders formed by sympodial proliferation. Conidia solitary, obclavate-cylindrical, straight to somewhat curved, 30–80 × 4–9 µm, 1–15-septate, occasionally somewhat constricted at the septa, yellowish to pale olivaceous-brown or brown, thin-walled, verruculose-echinulate, apex obtuse, rounded, base short obconically truncate, about 2–2.5 µm wide, hila slightly thickened and darkened.

Host range and distribution: On Cryptomeria japonica, Cupressocyparis leylandica, Cupressus (lusitanica, macrocarpa, sempervirens), Gymnosporangium manazanica, Hesperocyparis arizonica (Cupressus arizonica), Juniperus (communis, chinensis, virginiana), Platycladus orientalis (Thuja orientalis), Sequoia (sequoiae, sempervirens), Taxodium (distichum, mucronatum), Cupressaceae, Asia (China, Japan), North America (Canada; USA, Alaska, North Carolina, Louisiana, Oklahoma, Pennsylvania), South America (Brazil, Guatemala), Caribbean (Jamaica), Hawaii.

Notes: A specimen on Cryptomeria japonica from Taiwan (24 Sep. 1928, K. Sawada, TNS-F220395) and various Japanese collections on C. japonica (IUM-FS58, IUM-FS61, MUMH10801, TFM:FPH-41, TFM:FPH-67) and Taxodium mucronatum (TFM:FPH-3395) have been re-examined. Furthermore, cultures ex Cryptomeria japonica (MAFF237184, MAFF410035, MAFF410800, MAFF 410802, MUCC780 ex MUMH 10801) and ex Taxodium mucronatum (MAFF410034) exist. ITS1-5.8S-ITS2 (V9G/ITS4) & ACT (ACT512F/ACT783R) sequences obtained from these isolates are identical, suggesting that this fungus, at least in Japan, represents a uniform species. Sequences derived from cultures of Cercospora juniperina cluster close to P. sequoiae with various other Passalora species, which supports the position of the two species in Passalora, at least tentatively as the latter genus is not monophyletic.

In Japan, the causal agent of needle blight of Cryptomeria japonica was described by Shirai (in Kitajima 1916) as Cercospora cryptomeriae, which was already reduced to synonymy with Cercospora sequoiae by Ito et al. (1958, 1967) based on agreeing morphological characteristics.

Pseudocercospora species on Gymnospermae

Key to the species of Pseudocercospora on Gymnospermae

1  Conidia very broad, 5–8 µm ............................................................... 2
   Conidia narrower, 2–5 µm .......................................................... 5

2 (1) Conidiophores very long, 50–120 µm; on Cryptomeria, Japan ............................................................... P. cryptomerica
   Conidiophores much shorter, 10–60 µm; on other hosts .......................................................... 3

3 (2) Conidia very long and broad, 65–135 × 9–13 µm; on twigs of Pinus, Japan .................... [Scolecostigmina chibaensis]
   Conidia shorter and narrower, 18–55 × 2–8 µm; on leaves .................................................. 4

4 (3) Stromata well-developed, 150–250 µm diam and 70–130 µm deep or oblong, up to 500 µm in length;
   conidia smooth; on Thuja plicata, North America, and Chaemaecyparis lawsoniana, Hawaii ....................... P. thujina
   Stromata lacking or small, up to 30 µm diam; conidia rough-walled; on Chamaecyparis obtusa, Japan ........................................................................................................ P. chamaecyparidis

5 (1) Stromata almost lacking or relatively small, 10–50 µm; conidiophores fasciculate ................... 6
   Stromata large, 20–150(–300) µm diam; conidiomata sporodochial ........................................ 9

6 (5) Stromata lacking or small, up to 30 µm; conidiophores usually percurrently proliferating,
   with up to five fine annellations; conidia 18–50 µm long and 5–10-septate;
   on Chamaecyparis obtusa, Japan ................................................................................................. P. chamaecyparidis
   Stromata 20–50 µm diam; conidiophores sympodially proliferating; conidia mostly longer,
   exceeding 50 µm; on other hosts .......................................................................................... 7

7 (6) Conidiophores often branched; conidia pale brown; leaf lesions characteristically marginal;
   on Ginkgo biloba, Taiwan ........................................................................................................... P. ginkgoana
   Conidiophores usually unbranched; conidia subhyaline to pale olivaceous; lesions not confined
   to leaf margins; on other hosts ............................................................................................... 8

8 (7) Stromata 20–50 µm diam; on Sequoia sempervirens (in inoculation experiments also on Larix kaempferi),
   Japan ............................................................................................................................... P. paraxeroxsporoides
   Stromata 20–150 µm diam; on Pinus spp., Africa, Asia, Central and South America, Caribbean ...... P. pini-densiflorae

9 (5) Conidia acicular or narrowly cylindrical, 35–93 × 2–3 µm, only 3–5-septate, base truncate;
   on Sciadoply is verticillata, Japan ............................................................................................... P. sciadopytios
   Conidia cylindrical or obclavate-cylindrical, shorter, (10)–20–65(–80) µm long, at least partly short
   obconically truncate at the base; on other hosts ................................................................. 10
Conidia obclavate-cylindrical, usually (10–)20–60(–80) µm; on *Pinus* spp., Africa, Asia, Central and South America, Caribbean ................................................. P. pini-densiflora

Tabular key to the species of *Pseudocercospora* on Gymnospermae

**Cupressaceae**

1 Conidia very broad, 5–8 µm .......................................................................................................................... 2
Conidia narrower, 2–5 µm ............................................................................................................................... 4

2 (1) Conidiophores very long, 50–120 µm; on *Cryptomeria*, Japan .......................................................... P. cryptomeriicola
Conidiophores much shorter, 10–60 µm; on other hosts ............................................................................. 3

3 (2) Stromata well-developed, 150–230 µm diam and 70–120 µm deep; conidia smooth; on *Thuja plicata*, North America ......................................................................................................................... 3
Stromata lacking or small, up to 30 µm diam; conidia rough-walled; on *Chamaecyparis obtusa*, Japan ................................................................................................................................. P. chamaeyparidis

4 (1) Stromata lacking or small, up to 30 µm; conidiophores fasciculate, usually percurrently proliferating, with up to five fine annellations; conidia cylindrical to obclavate, 5–10-septate; on *Chamaecyparis obtusa*, Japan ......................................................................................................................... P. chamaeyparidis
Stromata large, 30–150 µm diam; conidiomata sporodochial; conidiogenous cells sympodially and often also percurrently proliferating, with fine annellations; conidia more or less cylindrical, 3–5-septate, base truncate to short obconically truncate; on *Cryptomeria*, *Hesperocyparis* and *Juniperus*, *Cupressaceae*, Asia and North America ......................................................................................... P. juniperi

**Ginkgoaceae**

On *Ginkgo biloba*, Taiwan ......................................................................................................................... P. ginkgoana

**Pinaceae**

1 Conidia very long and broad, 65–135 × 9–13 µm; on twigs of *Pinus*, Japan ........................................... [Scolecostigmina chibaensis]
Conidia narrower, 2–5 µm; on leaves ........................................................................................................... 2

2 (1) Conidia cylindrical, relatively short, (15–)20–40(–50); on *Larix decidua*, Europe ............................. P. exosporioides
Conidia obclavate-cylindrical, longer, (10–)20–80 µm; on *Pinus* (or *Larix* but only in inoculation experiments) ................. 3

3 (2) Stromata 20–150 µm diam; on *Pinus* spp., Africa, Asia, Central and South America, Caribbean ......................... P. pini-densiflora
Stromata 20–50 µm diam; usually on *Sequoia sempervirens*, *Cupressaceae* (in inoculation experiments also on *Larix kaempferi*), Japan ............................................................................................................. P. paraexosporioides

**Sciadopityaceae**

On *Sciadopitys verticillata*, Japan ................................................................................................................ P. sciadopytios

**List of Pseudocercospora species on Gymnospermae**

*Pseudocercospora chamaeyparidis* (Sawada) C. Nakash. & U. Braun, comp. nov.
MycoBank MB805531 (Fig. 59)

Description: Leaves turning pale brown to brown, finally grey. *Caespituli* hypophyllous, formed as scattered, blackish sporodochia, erumpent. Stromata lacking or small, up to 30 µm, brown to blackish brown. *Conidiophores* fasciculate, arising from internal mycelium or stromata, straight, subcylindrical, 10–50 × 2.5–5 µm, aseptate or septate, brown to blackish brown, wall thin or only slightly thickened, smooth; conidiogenous cells integrated, terminal, proliferating percurrently or occasionally sympodially, often with...
annellations, loci thin, unthickened to somewhat protuberant. Conidia solitary, cylindrical to obclavate, straight, curved or sigmoid, 18–50 × 2–8 μm, 5–10-septate, brown to reddish brown, smooth to faintly rough-walled (light microscopy), verruculose under SEM, thin, apex obtuse, rounded, base truncate and unthickened, 2–3.8 μm wide.


Host range and distribution: On Chamaecyparis obtusa, Cupressaceae, Asia (Japan).

Notes: Cercospora chamaecyparidis was described by Sawada based on Japanese material on Chamaecyparis obtusa. The type material, which has been re-examined, is morphologically close to the North American Pseudocercospora thujina (Stigmina thujina) on Thuja plicata, but

beside a different host it is distinguished by having much smaller or even lacking stromata. Thus it is better to retain this fungus as separate species.

Pseudocercospora cryptomeriicola (Sawada) C. Nakash., Akashi & Akiba, in Nakashima et al., Mycoscience 48: 254 (2007). (Fig. 60)


Illustrations: Nakashima et al. (2007: 252, fig. 2; 253, figs 3–12).

Description: Causing black line needle blight of Cryptomeria, leaves and stems discoloured, yellowish to brown, at first with smaller spots, finally entire needles affected. Colonies visible as fungal masses consisting of olivaceous conidiophores and conidia in lines from base to top on necrotic needles. Mycelium internal. Stromata well-developed, immersed, later erumpent, subglobose, about 90–275 μm diam, dark olivaceous-brown to black, composed of swollen hyphal cells, rounded to angular or oblong. Conidiophores in large, loose to dense fascicles, arising from stromata, forming sporodochial conidiomata, erumpent, simple or rarely branched, subcylindrical, straight to slightly sinuous, 50–120 × 3–5 μm, 1–7-septate, dark brown to blackish, wall smooth,
Conidiogenous cells integrated, terminal, percurrently proliferating, with conspicuous annellations, conidiogenous loci neither thickened nor darkened. *Conidia* solitary, cylindrical-obclavate, straight to slightly curved, 50–80 × 5–8 µm, 7–13-septate, occasionally distosepta mixed with eusepta, pale brown to brown, wall somewhat thickened, smooth or almost so, apex rounded, base truncate to obconically truncate, 2.5–3.8 µm wide, hila neither thickened nor darkened.

**Holotype:** Japan: Yamagata, Kamabuchi, on *Cryptomeria japonica*, 8 Aug. 1949, Sato (Herbarium, Museum of Iwate University, Japan).

**Host range and distribution:** On leaves and stems of *Cryptomeria japonica*, Japan, *Cupressaceae*, Asia (Japan, endemic).

**Notes:** A culture (NBRC 102150) and several collections of this species, which is endemic in Japan, have been examined (TFM:FPH-1085, 1088, 7850 and 7851). Due to unthickened conidiogenous loci and conidial hila as well as its proven phylogenetic position in the *Pseudocercospora* clade, Nakashima et al. (2007) reallocated this species to *Pseudocercospora*, although the formation of well-developed sporodochia, percurrently proliferating conidiogenous cells and large, above all broad, dark and thick-walled conidia are rather *Scolecostigmina*-like.


**Illustration:** Sutton & Hodges (1990: 321, fig. 4).


**Description:** Causing needle blight, at first forming small brown to reddish brown discolorations, later expanded, often at tips, finally entire needles discoloured, nectric, dead and shed. *Colonies* amphigenous, punctiform to pustulate, dark. *Mycelium* internal; hyphae branched, septate, 2–10 µm diam, brown, smooth or almost so. *Stromata* well-developed, immersed, large, sometimes confluent, about 50–150 µm diam, sometimes up to 300 µm in length, dark brown, sometimes with a reddish tinge, composed of swollen hyphal cells, 2–8 µm diam, rounded in outline to angular. *Conidiophores* numerous to very numerous, arising from stromata, erumpent, forming large, dense sporodochial conidiomata, erect, straight to somewhat curved-sinuous, subcylindrical to somewhat conical (attenuated towards the tip), not, barely or only slightly geniculate, unbranched, 5–30 × 2–4.5 µm, 0–1(–2)-septate, pale yellowish to olivaceous-brown throughout or paler towards the tip, thinned-walled, smooth or almost so; conidiophores reduced to conidiogenous cells or conidiogenous cells integrated, terminal, 5–25 µm long, conidiogenous loci inconspicuous, neither thickened nor darkened. *Conidia* solitary, cylindrical-obclavate-cylindrical, somewhat attenuated towards the tip, straight to slightly curved, (15–)20–40(–50) × 2–3.5 µm, (1–)3–4(–5)-septate, subhyaline to pale olivaceous, thin-walled, smooth or almost so to somewhat rough-walled, apex obtuse, base short obconically truncate, 1.5–2 µm wide, hila neither thickened nor darkened.

**Lectotype (designated here, MycoBank, MBT176151):** Czech Republic: Moravia, Hranice (Mährisch Weisskirchen), Ludinabach, on needles of *Larix decidua*, 8 Oct. 1914, F. Petrak (BPI 436251); islectotypes: K(M) IMI 24163, LEP; Petr., Fl. Bohem. Morav. Exs. 1351, e.g. HBG.

**Host range and distribution:** On needles of *Larix decidua*, *Pinaceae*, Europe (Czech Republic).
Notes: The material deposited at BPI is marked as “holotype”, but there are several duplicates of the type collection (syntypes) housed in several other herbaria. Therefore, it is proposed to designate the BPI material as lectotype.


(Fig. 62)

*Illustration*: Kirschner & Okuda (2013: 423, fig. 1A–E).

*Description*: Lesions marginal, visible as necrotic, brown leaf margins with yellowish border towards the healthy green leaf blade. *Caespituli* amphigenous. *Mycelium* internal; hyphae intercellular, 2–3 µm wide, hyaline to pale brown, smooth. *Stromata* developed, amphigenous, about 30–40 µm diam, immersed, erumpent through the epidermis, composed of brown swollen hyphal cells, 3–11 × 3–5 µm. *Conidiophores* numerous, in dense fascicles, arising from stromata, erumpent, erect, straight, subcylindrical, somewhat curved to distinctly geniculate, simple or branched, (12–)26–57(–78) × 3–5(–7) µm, continuous or 1- to pluriseptate, pale to medium brown, thin-walled, smooth; conidiophores reduced to conidiogenous cells or conidiogenous cells integrated, terminal, occasionally pleurogenous, (8–)9.5–16.5(–21) × 2.5–4 µm, conidiogenous loci inconspicuous to subdenticulate, truncate and 1–1.5 µm wide, but always unthickened and not darkened. *Conidia* solitary, subcylindrical to narrowly obclavate, i.e. narrowed towards the apex and obconically truncate at the base, straight or occasionally curved, (11–)33–65(–75) × 2–2.5(–3) µm, 1–9-septate, pale brown, thin-walled, smooth, apex obtuse to subacute, base short obconically truncate, 1.5 µm wide, hila neither thickened nor darkened.

*Holotype*: Taiwan: Taoyuan County, Lasashan, New Century Resort Farm with tea and fruit plantations, ca. 1,500 m alt., on leaves of *Ginkgo biloba*, 22 Oct. 2011, R. Kirschner et al. 3561 (TNM).

*Host range and distribution*: On leaves of *Ginkgo biloba*, Ginkgoaceae, Asia (Taiwan).

*Notes*: This is the first *Pseudocercospora* on *Ginkgo*. Kirschner & Okuda (2013) cultivated this fungus, and derived ITS DNA sequence data. A comparison showed a 99 % similarity with sequences of *Pseudocercospora chiangmaiensis*.


(Fig. 63)


*Illustration*: Sutton & Hodges (1990: 320, fig. 3).

*Description*: Causing needle blight, with discolorations and leaf spots, yellowish to brown, finally entire leaves discoloured, necrotic; often occurring in young plantations and windbreaks. *Colonies* punctiform to pustulate, paler or dark by abundant conidial formation. *Mycelium* internal; hyphae mainly intraepidermal, but also in the mesophyll, branched, septate, 2–5 µm wide, brown. *Stromata* well-developed, substomatal to deeply immersed, about 30–150 µm diam, medium to dark brown, composed of swollen hyphal cells, about 3–6 µm diam, wall somewhat thickened. *Conidiophores* in small to usually larger, often almost sporodochial fascicles, loose to moderately dense, arising from stromata, through stromata or erumpent, erect, straight, subcylindrical to somewhat geniculate-sinuous, unbranched or rarely branched, 15–40 × 2.5–3.5 µm, 0–3-septate, olivaceous-brown, paler towards the tip, thin-walled, smooth; conidiogenous cells integrated, terminal, 10–25 µm long, proliferation sympodial or percurrent, with fine annellations, conidiogenous loci
truncate, neither thickened nor darkened. Conidia solitary, cylindrical, subcylindrical to slightly obclavate-cylindrical, straight to somewhat curved, 30–60 × 2.5–3 µm, 3–5-septate, not constricted at the septa, pale olivaceous to olivaceous-brown in mass, thin-walled, almost smooth to rough-walled, apex obtuse, base truncate or slightly obconically truncate, about 2 µm wide, hila unthickened, not darkened.


Host range and distribution: On Cryptomeria japonica, Hesperocyparis arizonica (Cupressus arizonica), Juniperus (communis, virginiana, Juniperus sp.), Cupressaceae, Asia (Japan), North America (Canada, Ontario; USA, Arizona, Connecticut, Florida, Georgia, Kentucky, Missouri, North Carolina, Nebraska, Oklahoma, South Carolina, Virginia, Wisconsin).

Notes: This species was previously confused with Cercospora juniperina (see Chupp 1954), but it is easily distinguishable from the latter species by having unthickened, not darkened conidiogenous loci as pointed out by Sutton & Hodges (1990).

Pseudocercospora paraexosporioides C. Nakash. & U. Braun, sp. nov.
MycoBank MB805532 (Fig. 64)

Etymology: Named for its resemblance to Pseudocercospora exosporioides.

Pseudonym: Cercospora exosporioides sensu auct.

Diagnosis: Differt a P. exosporioides stromatibus minoribus, 20–50 µm diam, conidiophoris in fasciculis minoribus et conidiis longioribus, 25–80 µm, pluriseptatis (3–10).

Description: Leaf spot scattered, brown, later enlarged and confluent, yellowish brown to reddish brown or dark brown. Caespituli hypophyllous, punctiform, dark olivaceous. Mycelium internal. Stromata hypophyllous, substomatal to immersed, pale to dark brown, 20–50 µm diam. Conidiophores in small to moderately large, dense fascicles, arising from stromata, through stomata or erumpent, straight, subcylindrical or narrower towards the apex to geniculate, unbranched, 22–48 × 2–3 µm, 0–2-septate, pale to brown, thin-walled, smooth; conidiogenous cells integrated, terminal, proliferating sympodially, conidiogenous loci truncate, unthickened, not darkened. Conidia solitary, cylindrical to obclavate, straight or mildly curved, 25–80 × 2–4 µm, 3–10-septate, pale to olive-brown, thin-walled, smooth to rough-walled, apex obtuse to subacute, base obconically truncate, about 2–2.5 µm wide, hila unthickened, not darkened.

Holotype: Japan: Tokushima Pref.: on leaves of Sequoia sempervirens, 4 Sept. 1959, K. Ito (TFM:FPH-551).
Host range and distribution: On Larix kaempferi (only in inoculation tests), Pinaceae and Sequoia sempervirens, Cupressaceae, Asia (Japan, endemic).

Notes: Additional material has been examined: on leaves of Sequoia sempervirens, Japan, Ibaraki Pref., Tsukuba, 11 Sep. 1998, T. Kobayashi & C. Nakashima (CNS 448, herb. Nakashima); Japan, Fukuoka Pref., Tanushimaru, 20 June 2000, T. Kobayashi & Y. Ono (CNS 970, herb. Nakashima); culture ex Sequoia sempervirens (MAFF237788, ex CNS 448).

Hashimoto (1959) observed and collected a species of Cercospora on Sequoia sempervirens in a nursery in Fukuoka Prefecture, Japan. The specimen concerned was sent to C. Chupp, who identified it as Cercospora exosporioides. To confirm the pathogenicity, mycelial suspensions were used to inoculate Larix kaempferi, Sequoia sempervirens, Pinus densiflora, Pinus thunbergii, and Cryptomeria japonica. Three weeks later, symptoms and conidial masses were observed on L. kaempferi and S. sempervirens (Hashimoto 1959).

Natural infections are only known from S. sempervirens, which seems to be the principal host of this species. The identification of the Japanese species as P. exosporioides is, however, not tenable since collections from Japan on S. sempervirens and the type material of the latter species from Europe are morphologically rather different. True P. exosporioides differs from P. paraexosporioides in having much larger stromata, up to 300 µm diam, large sporodochial conidiomata, and much shorter, usually subcylindrical conidia with few septa. The Japanese collections of “P. exosporioides” represent undoubtedly a separate species described as P. paraexosporioides. Reports of P. exosporioides from Japan (e.g. Crous & Braun 2003) refer to the new species.

var. pini-densiflorae
(Fig. 65)


Description: Causing needle blight, i.e. needles with yellowish, yellowish brown to later greyish to blackish brown lesions, finally becoming necrotic. Colonies punctiform to pustulate, greyish to greyish brown. Mycelium internal; hyphae branched, septate, pale olivaceous to olivaceous-brown, thin-walled, smooth. Stromata substomatal, subglobose, 20–150 µm diam, brown to dark brown, composed of thick-walled, swollen hyphal cells, 2–6 µm diam. Conidiophores in rich, dense to very dense fascicles, often forming sporodochial conidiomata, arising from stromata, through stomata or erumpent, erect, straight, subcylindrical or narrowed towards the tip to geniculate-sinuous, unbranched, 5–50 × 2.5–4 µm, subhyaline to uniformly olivaceous or olivaceous-brown, 0–3-septate, thin-walled, smooth; conidiophores reduced to conidiogenous cells or conidiogenous cells integrated, terminal, 5–25 µm long, sympodially or occasionally percurrently proliferating, with fine, not very conspicuous annellations, conidiogenous loci inconspicuous or at least neither thickened nor darkened. Conidia solitary, obclavate or obclavate-cylindrical, straight to somewhat curved, (10–)20–65(–80) × 2–5 µm, (1–)3–7(–10)-septate, subhyaline to pale olivaceous, thin-walled, smooth, apex obtuse to subacute, base obconically truncate, 1.5–2.5 µm wide, hila.

Fig. 65. Pseudocercospora pini-densiflorae (BPI 1109716). A. Conidiophore fascicles. B. Conidiophore tips. C. Conidia. Bar = 10 µm.
unthickened, not darkened; with Asteromella state. Sexual morph forming variable ascostromata, dark brown to black, discrete, immersed, subepidermal, globose, unilocular, (50–)70–90(–120) µm diam to erumpent, linear, multilocular, 150–800(–1400) µm long, 70–125(–160) µm wide and 90–150 µm deep, occasionally laterally united in bands, stromata pseudoparenchymatous, cells 3–8(–12) µm diam, with thickened walls, locules globose to flask-shaped, (45–)50–75(–95) × 55–75 µm, ostiolate, paraphyses, often with an apical stromatic shield, 70–90 µm diam, in longitudinal series, ascites bitunicaten, clavate to cylindrical, (33–)35–38 × 5.5–7 µm, with a thickened bluntly rounded apex, rarely saccate, 32–36 × 6–8 µm, 8-spored, ascospores ellipsoid, cuneate, (7.5–)8.5–11(–12.5) × (1.8–)2.2–2.8 µm, 1-septate, hyaline, guttulate.

In vitro: Colonies grey to greyish green or blackish, attending 1.8–2.2 cm after 15 d on PCA-UV at 25 °C, with compact, grey mycelium in the centre, becoming pulvinate, black reverse (conidia in culture up to 90 µm long and 1.8–2.5 µm wide).

Type: Japan: Kagoshima, Magome, on needles of Pinus densiflora, 20 Sep. 1915 [not preserved]; Japan: Kagoshima, Magome, on needles of Pinus densiflora, 1 Oct. 1915, identified by Hara (NIAES C-511 – neotype designated here, MycoBank, MBT176152).

Host range and distribution: On needles of Pinus (ayacahuite, canariensis, caribaea, cembra, clausa, contorta, contorta var. murreyana, densiflora, echinata, elliottii, flexilis, greggii, halepensis, hartwegii [rudis], jeffreyi, kesiya, lambertiana, luchensis, massoniana, merkusii, mugo, muricata, nigra, oocarpa, patula, parviflora, pentaphylla, pinaster, pinea, ponderosa, pseudostrubos, radiata, resinosa, rigida, roxburghii, strobus, sylvestris, taeda, taiwanensis, thunbergii, tubuliformis, and wallichiana [griffithii]), Pinaceae. Africa (Kenya, Madagascar, Malawi, South Africa, Swaziland, Tanzania, Zambia, Zimbabwe), Asia (Bangladesh, China, India, Japan, Korea, Malaysia, Nepal, Papua New Guinea, Philippines, Sri Lanka, Thailand, Vietnam), Australia and New Zealand, Central and South America (Brazil, Nicaragua), West Indies (Jamaica, Netherlands Antilles). The following species were susceptible in inoculation experiments carried out by Suto (1979) in Japan: Abies veitchii, A. sachalinensis, Cedrus deodara, Picea glehni, P. jezoensis, Pseudotsuga menziesii, and Larix kaempferi (L. leptolepis).

var. montantiana (M.D. Mehrotra) U. Braun, comb. et stat. nov.
MycoBank MB805533


Diagnosis: Conidia narrowly obclavate-subcylindrical to subacicular, only 1.5–2.5 µm wide, but otherwise morphologically fully agreeing with var. pini-densiflorae.

Holotype: India: Assam: on needles of Pinus kesiya, Pinaceae, Apr. 1984, M. D. Mehrotra (K(M) IMI 286975).

Notes: Pseudocercospora pini-densiflorae is the causal agent of a common, widespread disease of Pinus spp. causing needle blight. Type material is not preserved, but toptype material has been found in the Herbarium of the National Institute for Agro-Environmental Science, Japan, which is proposed to serve as neotype.

Pseudocercospora montantiana was described from India on Pinus kesiya and distinguished from P. pini-densiflorae by its narrower acicular conidia, only 1.8–2.5 µm wide (Mehrotra 1987). However, type material of the latter species was examined and proved to be very close to P. pini-densiflorae. The conidia are, indeed, narrower than in common collections of P. pini-densiflorae, but the conidia are not consistently acicular. Shorter conidia are narrowly obclavate-subcylindrical with short obconically truncate base, which agrees with typical conidia of P. pini-densiflorae. Only some very long conidia may be subacicular. Otherwise P. montantiana on Pinus kesiya, which has been recorded as host species of P. pini-densiflorae, is morphologically indistinguishable from the latter species and barely more than a morphological variety of the common pine needle blight. Stromata are variable, 10–80 µm diam or oblong and up to 150 µm in length, the conidiophores are numerous, in dense fascicles, 10–50 × 2–4 µm, and the conidia are mostly 25–70 µm long and 3–7-septate. Mehrotra (1987) described conidiophores up to 100 µm long, which possibly refers to conidiophores with attached conidia, and he described conidia up to 105 µm in length.

Pseudocercospora sciadopityos C. Nakash. & Tak. Kobay., sp. nov.
MycoBank MB805534
(Fig. 66)


Diagnosis: Pseudocercospora juniperi, P. exosporoides et P. pini-densiflorae similis, sed conidiales acicularibus vel anguste cilindraceis, ad 83 µm longis, sed etiam 3–5-septatis, basi truncata.

Description: Leaf symptoms visible as brown to yellowish brown discolorations. Caespituli hypophyllous, punctiform, formed as olivaceous masses of conidia and conidiophores. Mycelium internal. Stromata immersed, intraepidermal to substomatal, erumpent, brown to dark brown, 45–75 µm diam. Conidiophores arising from stromata, densely fasciculate, through stomata or erumpent, erect, straight to slightly curved, 35–85 × 2–3 µm (on average 55 × 2 µm), plurisepate, pale brown, thin-walled, smooth; conidiogenous cells integrated, terminal, proliferating sympodially or percurrently, with unthickened, not darkened conidiogenous loci. Conidia solitary, mildly curved, acicular to narrowly cylindrical, 63–83 × 2–3
μm (on average 71 × 3 μm), 3–5-septate, pale, smooth, base truncate, 2–3.8 μm wide, hila neither thickened nor darkened.


Host range and distribution: On Sciadopitys verticillata, Sciadopityaceae, Asia (Japan, Tochigi, Tokyo, Chiba).

Note: A first description of this species, which caused early defoliation of Sciadopitys several times in Japan, has been published by Kobayashi (2007) as Cercospora sp.

Pseudocercospora thujina (Dearn.). U. Braun & C. Nakash., comb. nov.
MycoBank MB805535 (Fig. 67)


Illustrations: Morgan-Jones (1971: 1006, fig. 10), Hodges (1982: 868, fig. 1A–D).

Description: Leaves turning pale brown to brown, later greyish brown or grey, finally they become necrotic and die, in severe cases entire branches or twigs may die. Conidiomata hypophyllous, scattered, blackish, sporodochial, erumpent. Mycelium immersed; hyphae branched, septate, 2–4 μm wide, brown, wall smooth. Stromata well-developed, at first immersed, later often rupturing the epidermis, dark brown to black, 150–270 μm diam and 60–170 μm deep, or oblong, up to 500 μm in length, composed of swollen hyphal cells, rounded to angular in outline, about 2–6 μm diam. Conidiophores numerous, in loose to usually dense fascicles, arranged in palisade-like layers, arising from stromata, forming sporodochial conidioports, erumpent, erect, straight to curved or somewhat flexuous, subcylindrical or somewhat attenuated towards the tip, unbranched, 10–80 × 3–7 μm, aseptate to sparingly septate, light brown, yellowish brown or pale olivaceous-brown throughout or usually somewhat paler towards the tip, darker in mass, wall thin to slightly thickened, smooth or somewhat rough; conidiophores
reduced to conidiogenous cells or conidiophores septate and conidiogenous cells integrated, terminal, monoblastic, determinate or percurrently proliferating, with up to five fine anellations, sometimes also sympodially proliferating, with two loci, conidiogenous loci unthickened, not darkened, about 2–4 µm wide, sometimes with minute frill. **Conidia** solitary, straight to mostly curved or sigmoid, often abruptly curved at the apex or sometimes at the base, subcylindrical-vermiform to clavate, occasionally obclavate, 30–70 × (5–)6–9(–11) µm, 4–16-septate, usually without constrictions at the septa or only slightly constricted, cells often with distinct central lumen, medium brown to medium dark brown, wall thin to slightly thickened, up to 1 µm, smooth to faintly rough, apex obtuse, rounded, base short obconically truncate, 2–5 µm wide, hila unthickened, not darkened, often with minute frill.


**Host range and distribution:** On *Chamaecyparis lawsoniana*, *Thuja plicata*, *Cupressus*, North America (Canada, British Columbia; USA, Idaho, North Carolina, Oregon, Washington), introduced in Europe (Austria and Croatia), Hawaii and New Zealand.

**Notes:** Based on the phylogenetic position of its type species, Crous et al. (2006) reduced *Stigmina* to synonymy with *Pseudocercospora*. Therefore, the generic position of *Stigmina thujina* has to be reassessed. Due to its sporodochial conidiomata with frequently percurrently proliferating conidiogenous cells and relatively thin-walled conidia, this species is rather *Cercostigmina*-like (Braun 1993), but the latter genus was reduced to synonymy with *Pseudocercospora*. The type species of *Cercostigmina* and additional species assigned to this genus cluster within the big *Pseudocercospora* clade (Crous et al. 2001, 2013; Taylor et al. 2003). Furthermore, the conidiogenous cells of *S. thujina* are percurrent as well as sometimes sympodial. Therefore, this species is better reallocated to *Pseudocercospora*.

*Pseudocercospora thujina* is also known on *Chamaecyparis lawsoniana* and has been introduced on this host in Europe, Hawaii and New Zealand (Hodges 1982, Dick 1998, Cech 2008, Cech & Diminić (2008). Two samples from Hawaii have been re-examined (BPI 428035, 428036). The first European observation was from 2002 in Austria, Salzburg. *Cercospora chamaecyparidis*, described from Japan, is morphologically very close to *P. thujina*, but occurs on the Asian *Chamaecyparis obtusa* and differs in having much smaller or even lacking stromata and verruculose conidia. Therefore, *C. chamaecyparidis* is maintained as a separate species and reallocated to *Pseudocercospora* as well.

**Doubtful, excluded and insufficiently known species**

*Cercospora filicum* Henn., *Hedwigia* 41: 310 (1902).

**Literature:** Saccardo (1906: 611), Chupp (1954: 455).

**Holotype:** Brazil: São Paulo, Botanical Garden, on *Nephrodium* sp., *Dryopteridaceae*, A. Puttemans No. 258 [not preserved].

**Notes:** Due to rather broad, densely septate cylindrical conidia with thick walls, this species is rather helminthosporioid, but not cercosporoid (see Chupp 1954).

*Cercospora equiseti* Dobrozr., *Bolez.* Rast. 16: 202 (1927).


**Literature:** Vassiljevsky & Karakulin (1937: 219), Braun (1998: 360).

**Illustration:** Braun (1998: 362, fig. 618).

**Holotype:** Russia: Leningrad Oblast’, on *Equisetum arvense*, *Equisetaceae*, 23 Jul. 1927, Dobrozrakova (LE 40397).

*Cercospora trismeriae* Petr., *Sydowia* 2: 379 (1948)

**Literature:** Chupp (1954: 457), Crous & Braun (2003: 411).

**Description:** Leaf spots narrow, oblong between secondary veins and often extending from the midrib to the leaf margin, in severe infections covering large portions of the leaf blade, dull yellow to greyish brown on both surfaces. *Caespituli* mainly hypophyllous. *Mycelium* internal. *Stromata* substomatal, globose, dark olivaceous. *Conidiophores* straight, curved to sinuous, 40–150 × 5–7 µm, pale olivaceous, sparingly septate. *Conidia* obclavate, straight to curved, rarely sigmoid, 25–200 × 5–7.5 µm, 2–9-septate, subhyaline to pale olivaceous-brown, base subtruncate, apex subobtuse to somewhat attenuated.

**Holotype:** Ecuador: Pichinicha Province: Mindo, on living leaves of *Pityrogramma* sp. (*Trismeria* sp.), 5 Nov. 1937, H. Sydow, No. 1937.

**Host range and distribution:** Only known from the type collection.

**Notes:** The generic affinity of this species is unclear and could not be proven since it was not possible to trace type material, neither in Petrak’s herbarium at W nor at GZU. Based on the original description, *C. trismeriae* is probably a species of *Pseudocercospora*.

Illustration: Nakashina et al. (2007: 251, fig. 1).

Description: Twig symptoms visible as swellings, finally cracking. Stromata lacking or small, blackish brown to black, erumpent, small aggregations of swollen hyphal cells, 2–13 µm diam. Conidiophores solitary to densely fasciculate, straight, olivaceous-brown to blackish brown, subcylindrical, 30–90 × 4–10 µm, pluriseptate, wall thickened, up to about 2 µm, smooth or almost so, occasionally rough; conidiogenous cells integrated, terminal, determinate or percurrently proliferating, with truncate, unthickened, not darkened terminal locus with distinct, relatively large porus, up to 2 µm diam (conidiogenesis probably tretic). Conidia solitary, occasionally in short chains, phragmo- to scclecosporous, broadly obclavate-subcylindrical, 65–135 × 9–13 µm, 5–13-euseptate or eu- and distosepta mixed, often somewhat constricted at septa, brown to blackish brown, wall thick, up to 2 µm, smooth to somewhat verruculose, apex sometimes somewhat rostrate, tips obtuse, base obconically truncate, 4–5.5 µm wide, hila neither thickened nor darkened or entire base somewhat darker.


Host range and distribution: On Pinus (ayacahuite, parviflora var. parviflora, parviflora var. pentaphylla, peuce, strobiformis, wallichiana, strobus, Pinus sp.), Pinaceae, Asia (Japan).

Notes: In preliminary phylogenetic analyses using rDNA ITS data, S. chibaensis did neither cluster with Pseudocercospora species (including Stigmina s. str. [type species: S. platani]) nor Scolecostigma mangiferae, the type species of Scolecostigma. This species does not belong to the Mycosphaerellaceae at all. The conidiogenous cells possess a conspicuous, relatively large porus, and the conidiogenesis seems to be tretic. Scolecostigma chibaensis is morphologically rather corynesporid. It has to be excluded from Scolecostigma in any case, but a final conclusion must be postponed as its phylogenetic affinity to a specific order and family is not yet clear.

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