Pseudocercospora solanacea revisited and a survey of *Pseudocercospora* spp. on *Solanum* with a key to the species

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Abstract: Braun, U. 2017: *Pseudocercospora solanacea* revisited and a survey of *Pseudocercospora* spp. on *Solanum* with a key to the species. Schlechtendalia **32**: 51–65.

The nomenclature of *Pseudocercospora solanacea* is discussed in detail and a description, based on the re-examination of type material, is provided. The taxonomy of this species is discussed in the context of other *Pseudocercospora* species on hosts of the genus *Solanum*, and the species concerned are keyed out. *Cercospora atromarginalis*, *C. rigospora*, and *C. solani-nigri* are lectotypified. *Cercospora fuligena* (≡ *Pseudocercospora fuligena*), *C. solani-nigri*, *Pseudocercospora solani-melongenicola* are reduced to synonymy with *Pseudocercospora atromarginalis*.

Zusammenfassung: Braun, U. 2017: *Pseudocercospora solanacea* erneut aufgegriffen und eine Übersicht der *Pseudocercospora*-Arten auf *Solanum* mit einem Schlüssel zu den Arten. Schlechtendalia **32**: 51–65.

Die Nomenklatur von *Pseudocercospora solanacea* wird detailliert diskutiert und eine auf der Untersuchung von Typus-Material beruhende Beschreibung wird beigefügt. Die Taxonomie dieser Art wird im Zusammenhang mit anderen *Pseudocercospora*-Arten auf *Solanum*-Arten diskutiert und die betroffenen Arten werden aufgeschlüsselt. *Cercospora atromarginalis*, *C. rigospora* und *C. solani-nigri* werden lectotypisiert. *Cercospora fuligena* (≡ *Pseudocercospora fuligena*), *C. solani-nigri*, *Pseudocercospora solani-melongenicola* werden als Synonyme von *Pseudocercospora atromarginalis* betrachtet.

Key words: cercosporoid fungi, *Pseudocercospora*, Solanaceae.

Published online 20 Sep. 2017

Gupta & Kamal (1990) described *Pseudocercosporella leonotidis* and *P. solanacea* in Indian Phytopathology volume 42(3), dated 1989, but this issue was only effectively published in early 1990, which is of nomenclatural relevance. Gupta & Kamal (1990) cited a single collection but failed to add "holotypus/typus" or an equivalent in a modern language, required for a valid publication since 1990 (ICN, Art. 40.6). Due to these circumstances, *Pseudocercosporella leonotidis* and *P. solanacea* are invalid names. I re-examined original material of the two *Pseudocercosporella* species deposited in IMI (now K), confirmed *P. leonotidis* as *Pseudocercosporella* species (Braun 1995: 171, formal validation as *Pseudocercosporella leonotidis* B.K. Gupta & Kamal ex U. Braun), but pointed out that all structures of *P. solanacea* were pale but not quite colourless and, as I was not aware of the invalidity of *Pseudocercosporella solanacea*, proposed the new combination *Pseudocercospora solanacea* (Braun 1995: 198). Although introduced as "new combination", the latter name published with reference to a previously effectively published Latin description (Gupta & Kamal 1990: 391) and with a cited "holotype" fulfilled all conditions for a validation and introduction of a new species. Therefore, the second attempt of a validation of *Pseudocercospora solanacea* published in Braun & Urtiaga (2013: 201) is superfluous and furthermore invalid since a new registration of *P. solanacea*, required since 2013, was omitted. Braun's (1995) validation as *Pseudocercospora solanacea* was made with reference to the Latin description of *Pseudocercosporella solanacea* in Gupta & Kamal (1990), but a new description on the basis of an examination of type material was neither given in Braun (1995) nor in Braun & Urtiaga (2013). Such a description follows hereafter together with a key to *Pseudocercospora* species on hosts belonging to the genus *Solanum* including brief surveys of the taxonomy, nomenclature, host range and distribution of the species concerned, complemented by some taxonomic notes.

Pseudocercospora solanacea U. Braun, A monograph of *Cercosporella*, *Ramularia* and allied genera (phytopathogenic hyphomycetes) **1**: 198 (1995) [holotype: On *Solanum nigrum*, India, Uttar Pradesh, Gorakhpur, without date, Kamal, KS 150 (K(M) IMI 238212)]. Fig. 1

≡ *Pseudocercosporella solanacea* B.K. Gupta & Kamal, Indian Phytopathol. **42**: 391 "1989" (1990), nom. inval. (ICN, Art. 40.6).

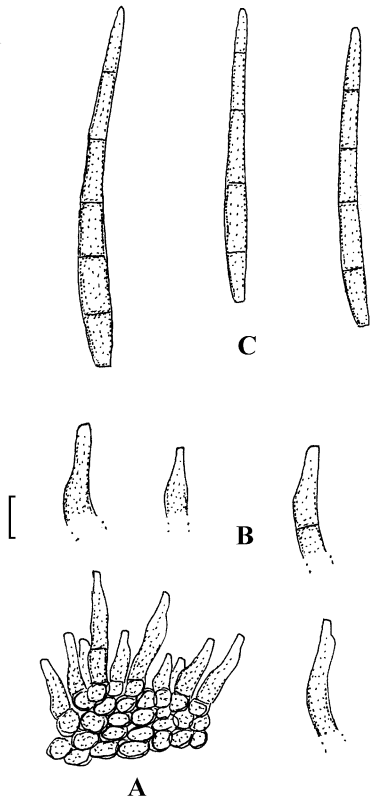


Illustration: Gupta & Kamal (1990: 390, fig. 3).

Leaf spots amphigenous, not very conspicuous, almost absent, forming pale subcircular to irregular discolorations on the upper leaf surface, dull greyish olivaceous below, 1–10 mm diam, numerous, often confluent. Caespituli amphigenous, mainly hypophyllous, punctiform to subeffuse, dense, confluent, dull greyish olivaceous. Mycelium internal; hyphae branched, 1.5–2.5 µm wide, septate, thin-walled, smooth. Stromata well-developed, substomatal to immersed, 20–80 µm diam, at first yellowish, later pale olivaceous to medium brown. Conidiophores in small to mostly large, dense fascicles, arising from stromata, through stomata or erumpent, erect, unbranched, subcylindrical to somewhat geniculate-sinuous, straight to curved, sometimes narrowed towards the apex, 5–40 × 2–5.5 µm, aseptate or occasionally with 1–2 septa near the base, subhyaline to dull greyish olivaceous, thin-walled, smooth; conidiogenous cells integrated, terminal or conidiophores mostly reduced to conidiogenous cells, 5–30 µm long, conidiogenous loci inconspicuous or visible as truncate tips, unthickened, not darkened.

Fig. 1: *Pseudocercospora solanacea*, A – Conidiophore fascicle, B – Conidiophores, C – Conidia. Bar – 10 µm. U. Braun del.

Conidia solitary, obclavate(-subcylindrical), straight to slightly curved, (30–)40–60(–75) × 2.5–5.5 µm, 3–9-septate, subhyaline to pale greyish olivaceous, thin-walled, smooth, mostly narrowed towards an obtuse apex, base short obconically truncate, 1.5–2.5 µm wide, hila neither thickened nor darkened.

Key to *Pseudocercospora* and *Paracercospora* species on *Solanum* spp.

The abbreviation "*P*." stands for "*Pseudocercospora*" (*Paracercospora* is not abridged).

1 Mycelium *in vivo* internal and external; superficial hyphae with solitary conidiophores developed 2

1* Mycelium *in vivo* consistently internal; superficial hyphae with solitary conidiophores lacking 5

2 Leaf spots lacking or indistinct; fasciculate conidiophores long, to 150 µm; conidia narrow, 20–100 × 2–4 µm [hitherto only known from the Dominican Republic on *Solanum rugosum*] ..... *P. rugosi*

2* Leaf spots usually developed and distinct; fasciculate conidiophores shorter, mostly 10–80 µm long; conidia wider, (2.5–)3–6(–7) µm 3

3 Conidia cylindrical-linear, base rounded, truncate to short obconically truncate, but not abruptly attenuated, hila ≥ 2 µm wide [hitherto only known from Taiwan on *Solanum torvum*] ..... *P. solani-torvicola*

3* Conidia cylindrical to obclavate-cylindrical, mostly distinctly attenuated towards the base (obconically truncate), often abruptly attenuated, hila 1–2 µm wide [widespread on a wide range of *Solanum* spp.] (*P. trichophila s. lat.*) 4

4 Caepituli mainly hypophyllous, effuse (not distinctly punctiform), floccose-velutinous, deep olivaceous; stromata lacking or almost so ..... *P. trichophila* var. *trichophila*

4* Caespituli amphigenous, punctiform on the upper leaf surface due to well-developed stromata, 10–60 µm diam, dark brown to blackish, with fasciculate conidiophores arising from stromata ..... *P. trichophila* var. *punctata*

5(1*) Conidiophores non-geniculate, unbranched, with conspicuous conidiogenous loci, paracercospora-like, i.e. slightly thickened and darkened at the outermost rim, visible in front view as minute circle [conidia subhyaline] 6

5* Conidiogenous loci quite inconspicuous or subdenticulate, but always unthickened, not darkened, not paracercospora-like, i.e. in front view not visible as minute circles 7

6 Conidia more or less cylindrical, (25–)30–70(–80) × 3–5 µm, base truncate to short obconically truncate, loci and hila about 2–3 µm diam; on various *Solanum* spp., including *S. melongena* ..... *Paracercospora egenula*

6* Conidia obclavate-cylindrical, (30–)40–90(–130) × 2.5–5 µm, base distinctly obconically truncate, loci and hila 1–2 µm diam; hitherto only known from North America on *Solanum carolinense* ..... *P. carolinensis*

7(5*) Stromata lacking or small, only formed as small substomatal aggregations of swollen hyphal cells, to about 30 µm diam; conidiophores loosely fasciculate 8

7* Stromata well-developed, 10–80 µm diam; often forming sporodochial conidiomata 9

8 Conidia (2.5–)3–5 µm wide; on a wide range of *Solanum* species, incl. former *Lycopersicon* species, almost worldwide ..... *P. atromarginalis* (incl. *P. fuligena* and *P. solani-melongenicola*)

8* Conidia narrower, 2–3.5 µm; on *Solanum pseudocapsicum*, Brazil ..... *P. solani-pseudocapsicicola*

9(7*) Conidiophores long and narrow, to 110 × 2–3 µm, very pale olivaceous; conidia narrowly obclavate-cylindrical, 60–110 × 2–3 µm, very pale olivaceous; hitherto only know from Argentina on *Solanum pseudocapsicum* ..... *P. fasciculata*

9* Conidiophores much shorter, 5–60 µm long, or conidiophores and conidia much wider, 2.5–6 µm 10

10 Conidiophores and conidia narrow, 1.5–4 µm, on average < 3 µm 11

10* Conidiophores and conidia broader, 2.5–6 µm, on average > 3 µm 12

11 Conidiophores uniformly short, 5–25 µm; conidiogenous loci inconspicuous or visible as truncate tip, but not denticle-like ..... *P. marcelliana*

11* Conidiophores 8–60 µm long; conidiogenous loci often denticle-like ..... *P. venezuelae*

12(10*) Caespituli epiphyllous; conidiophores 15–75 µm long, not geniculate, septa indistinct, olivaceous brown; conidia pale fuliginous ..... *P. modesta*

12* Caespituli amphigenous; conidiophores either aseptate or distinctly septate, conidiophores and conidia very pale, subhyaline to pale olivaceous 13

13 Caespituli mainly epiphyllous; conidiophores 1–6-septate throughout; hitherto only known from India on *Solanum lasiocarpum* ..... "*P. venezuelae* var. *indica*"

13* Caespituli mainly hypophyllous; conidiophores usually aseptate, occasionally with 1–2 septa at the base; hitherto only known from India on *Solanum nigrum* ..... *P. solanacea*

List of species

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

≡ *Cercospora atromarginalis* G.F. Atk. (*atramarginalis*), J. Elisha Mitchell Sci. Soc. **8**: 59 (1892) [lectotype (designated here, MycoBank, MBT378765): on *Solanum* (?) *nigrum*, USA, Alabama, Auburn, 1890, G.F. Atkinson (CUP-A-001359#1(AL); isolectotypes: CUP-A-001359#2(AL), CUP-040793].

= *Cercospora rigospora* G.F. Atk., J. Elisha Michell Sci. Soc. **8**: 65 (1892) [lectotype (designated here, MycoBank, MBT378766): on *Solanum* (?) *nigrum*, USA, Alabama, Auburn, 5 Jul. 1890, G.F. Atkinson (CUP-A-001225#1(AL); isolectotypes: CUP-A-001225#2(AL), CUP-040819].

= *Cercospora tosensis* Henn., Bot. Jahrb. Syst. **34**: 605 (1905) [holotype: on living leaves of *Solanum nigrum*, Japan, Akamachi, Tosa, Oct. 1903, T. Yoshinaga 43 (B700015016)].

= *Cercospora nigri* Tharp, Mycologia **9**: 112 (1917) [holotype: on *Solanum nigrum*, USA, Texas, Palestine, 30 Oct. 1914, Lewis & B.C. Tharp 192 (BPI 438897)].

= *Cercospora fuligena* Roldan, Philipp. J. Sci. **66**: 8 (1938) [type: on living leaves of *Solanum lycopersicum*, Philippines, Laguna, Luzon, College of Agriculture, Campus, 5 Mar. 1934, E.F. Roldan 32 (not seen, probably not preserved)].

≡ *Pseudocercospora fuligena* (Roldan) Deighton, Mycol. Pap. **140**: 144 (1976).

= *Cercospora solani-biflori* Sawada, Formosan Agric. Rev. **39**: 701 (1942) and Taiwan Agric. Res. Inst. Rep. **85**: 123 (1943), *nom. inval*. (Art. 39.1) [authentic material: on *Lycianthes biflora* (≡ *Solanum biflorum*), Taiwan, Taichung, 10 Oct. 1910, K. Sawada (NTU-PPE)].

= *Cercospora solani-nigri* Chidd., Mycopathol. Mycol. Appl. **17**: 76 (1962) [lectotype (designated here, MycoBank, MBT378767): on living leaves of *Solanum nigrum*, India, Poona, near Mulha river bed, 10 Dec. 1957, P.P. Chiddarwar 27 (BPI 441404)].

= *Pseudocercospora solani-melongenicola* Goh & W.H. Hsieh, *Cercospora* and similar genera from Taiwan: 318 (1990) [holotype: on living leaves of *Solanum melongena*, Taiwan, Hsinchu, 2 Dec. 1920, K. Sawada (NTU-PPE)].

Leaf spots lacking or almost so, diffuse greenish, yellowish to ochraceous discolorations, when developed subcircular to angular-irregular, 2–7 mm diam, margin indefinite or with narrow dark border, at first yellowish, later brown, finally greyish brown to dingy grey, mainly epiphyllous, less conspicuous and usually without distinct border on the lower leaf surface. Caespituli usually hypophyllous, occasionally amphigenous, scattered, effuse to gregarious, punctiform (above all on distinct leaf spots and on the upper leaf surface) or forming velutinous patches, often vein-limited, or even extended covers in the case of heavy infections, dark, often dingy olivaceous to brown. Mycelium internal. Stromata lacking or small, composed of a few swollen hyphal cells in the substomatal cavities, rarely somewhat larger, to 30 µm diam, above all in the case of epiphyllous caespituli. Conidiophores in small to moderately large fascicles (about 2–30 conidiophores), loose and divergent to moderately dense, arising from internal hyphae or small stromatic hyphal aggregations, emerging through stomata, erect, straight, curved to moderately geniculate-sinuous, unbranched or occasionally branched, 5–60(–100) × 2–6 µm, 0–3(–4)-septate, pale to medium olivaceous, olivaceous brown to brown throughout or paler towards the tip, wall thin, smooth to somewhat rough; conidiogenous cells integrated, terminal or conidiophores aseptate, i.e. conidiophores reduced to conidiogenous cells, 5–25 µm long, conidiogenous loci inconspicuous, unthickened, not darkened, sometimes visible as truncate tip or lateral "shoulder" caused by sympodial proliferation. Conidia solitary, cylindrical, obclavate-cylindrical, short conidia sometimes ellipsoid or fusoid, (15–)20–110(–120) × (2.5–)3–5 µm, (1–)2–9(–11)-septate, occasionally slightly constricted at the septa, subhyaline to pale olivaceous or olivaceous brown, thin-walled, smooth or almost so, apex obtuse, rounded, rarely subacute, base usually short obconically truncate, sometimes rounded or long obconically truncate, hila 1–2 µm wide, unthickened, not darkened.

(1) Host range, distribution, literature and illustrations recorded under *P. atromarginalis*: *Capsicum annuum*; *Lycianthes biflora* (≡ *Solanum biflorum*); *Nicandra physalodes*; *Physalis peruviana*; *Solanum aethiopicum*, *S. americanum* [= *S. nodiflorum*, *S. photeinocarpum*], *S. aviculare*, *S. chenopodioides* [= *S. gracile*], *S. elaeagnifolium*, *S. laciniatum*, *S. mammosum*, *S. nigrum* [= *S. alatum*], *S. pseudocapsicum*, *S. torvum*, *S. xanthocarpum* (Solanaceae), worldwide, Africa (Canary Islands, Ethiopia, Kenya, Libya, Mauritius, Malawi, Senegal, Sudan, Uganda, Zambia, Zimbabwe), Asia (China, India, Iran, Japan, Korea, Myanmar, Pakistan, Philippines, Sri Lanka, Taiwan, Thailand), Australia, New Zealand, North America (USA, Alabama, Florida, Georgia, Texas, Wisconsin), Central and South America (Brazil, Colombia, Costa Rica, Honduras, Panama, Venezuela), Oceania (Cook Islands, Fiji, Hawaii, New Caledonia, Niue, Solomon Islands, Vanuatu), West Indies (Barbados, Bermuda, Cuba, Dominican Republic, Jamaica, Puerto Rico, Trinidad and Tobago, Virgin Islands).

Literature: Saccardo (1892: 635; 1906, 604; 1931, 891), Chupp (1954: 532), Vasudeva (1963: 150), Katsuki (1965: 60), Ellis (1976: 287), Williams (1987), Hsieh & Goh (1990: 312), Guo & Hsieh (1995: 315), Guo *et al.* (1998: 329), Shin & Kim (2001: 164), Crous & Braun (2003: 71–72), Kamal (2010: 151–152), Pirnia et al. (2012), Phengsintham et al. (2013b: 103–104), Bakhshi et al. (2014: 250).

Illustrations: Chupp (1954: 532, fig. 187); Ellis (1976: 288, fig. 218 C), Williams (1987: 187, unnumbered figure), Hsieh & Goh (1990: 313, fig. 237), Guo & Hsieh (1995: 315, fig. 264), Guo *et al.* (1998: 329, fig. 269), Shin & Kim (2001: 165, fig. 70), Phengsintham et al. (2013b: 105, figs 52 and 53), Bakhshi et al. (2014: 252, fig. 3).

(2) Host range, distribution, literature and illustrations recorded under *P. fuligena*: *Capsicum annuum* (= *C. frutescens*), *C. chinense*, *C. baccatum*; *Solanum aethiopicum*, *S chilense*, *S. chmielewskii*, *S. habrochaites* (≡ *Lycopersicon hirsutum*), *S. lasiocarpum* (= *S. indicum*, nom. rej.), *S. lycopersicum* (≡ *Lycopersicon esculentum*), *S. macrocarpon*, *S. melongena*, *S. neorickii* [≡ *Lycopersicum parviflorum*], *S. nigrum*, *S. pennellii*, *S. peruvianum* [= *L. glandulosum*], *S. pimpinellifolium*, *Withania somnifera*, Africa (Gabon, Gambia, Ivory Coast, Maldives, Nigeria, Senegal, Somalia, Tanzania, Togo, Uganda), Asia (Bangladesh, Brunei, Cambodia, China, India, Japan, Korea, Malaysia, Papua New Guinea, Philippines, Taiwan, Thailand, Vietnam), North America (Mexico; USA, Florida, Ohio), South America (Brazil, Chile), Australia, New Zealand, Oceania (Cook Islands, New Caledonia, Palau, Solomon Islands, Vanuatu), West Indies (Cuba, Netherlands Antilles).

Literature: Chupp (1954: 540), Vasudeva (1963: 111), Katsuki (1965: 61), Mulder & Holliday (1975), Ellis (1976: 287), Hsieh & Goh (1990: 314), Guo & Hsieh (1995: 318), Wang et al. (1995), Guo *et al.* (1998: 332), Kamal (2010: 177), Lee et al. (2012), Phengsintham et al. (2012: 58–59; 2013a: 104–104), Subhedi et al. (2015).

Illustrations: Mulder & Holliday (1975: unnumbered figure), Ellis (1976: 288, fig. 218 B), Hsieh & Goh (1990: 316, fig. 239), Guo & Hsieh (1995: 319, fig. 267), Guo *et al.* (1998: 333, fig. 272), Phengsintham et al. (2012: 58–60, figs 1–3; 2013a: 104, fig. 94, 105, fig. 95).

Material examined (selection – collections deposited at HAL): Brazil, Ceará, Monsenhor Tabosa City, on *S. nigrum*, 10 Sep. 2004, F. Freire (HAL 3225 F). Brunei, Kilanas, on *S. lycopersicum*, 26 May 1997, A. Ali (HAL 3226 F). Canary Islands, La Palma, Cubo de la Galga, on *S. nigrum*, 16 Aug. 2015, V. Kummer (HAL 3217 F). Cuba, Pinar del Río, on *Solanum americanum*, 13 Apr. 1988, R.F. Castañeda C88/94 (HAL 3219 F); Gramna, on *Solanum americanum*, 15 June 1987, R.F. Castañeda C87/174 (HAL 3223 F). India, A.P., Mahabubnagar, Mannanore Forest, on *S. nigrum*, Dec. 1990, J. Jagadeeswar (HAL 3216 F). New Zealand, Auckland, Mount Albert, on *Nicandra physalodes*, 28 Jul. 2002, C.F. Hill (HAL 3218 F); Auckland, Mount Albert, on *Solanum aviculare*, 20 Oct. 2002, C.F. Hill (HAL 3221 F); Waikato Region, Whangamarino Wetland, Kopuku, on *S. chenopodioides*, 21 Apr. 2002, C.F. Hill (HAL 3222 F); Auckland, Blockhouse Bay, on *S. nigrum*, 10 Apr. 2000, C.F. Hill (HAL 3220 F); Auckland, Mount Albert, Phyllis Reserve, on *S. pseudocapsicum*, 12 Mar. 2007, C.F. Hill (HAL 2151 F). Thailand, Bangkok, greenhouse, on *S. lycopersicum*, 2 Jul. 2004, S. Kandziora (HAL 3227 F). Venezuela, Lara, Río Claro, on *S. nigrum*, Jone 2007, R. Urtiaga (HAL 3215 F); Lara, Sanare, Sabana Redonda Arriba, on *S. nigrum*, June 2010, R. Urtiaga (HAL 2497 F).

Notes: *Solanum nigrum* is one of the most common hosts of *P. atromarginalis*. Collections from Brazil, the Canary Islands, Costa Rica, Cuba, India, New Zealand, Pakistan, and Venezuela, deposited in B, BPI, HAL, and NY, have been examined. *Nicandra physalodes* infected by *P. atromarginalis* was found in New Zealand (see material examined). *Solanum nigrum* plants heavily infected by *P. atromarginalis* were present in the vicinity of the infected *Nicandra* plants. Type material of *Cercospora solani-nigri* has been re-examined and proved to be a synonym of *P. atromarginalis*. Chiddarwar (1962) mentioned that type material of the species described in his paper was deposited in BPI, HCIO and IMI, but he failed to designate holotypes for the species concerned. Therefore, the examined syntype of *C. solani-nigri* deposited in BPI is designated as lectotype.

Pseudocercospora fuligena is traditionally used for the common Tomato Black Leaf Mould. This species is morphologically indistinguishable from *P. atromarginalis*. Furthermore, it is genetically almost identical with the latter species (see Crous et al. 2013, combined ITS, ACT, and EF-1α tree; Silva et al. 2016). Wang et al. (1995) carried out comprehensive inoculation experiments. A total of 137 accessions representing 26 species and five solanaceous genera were inoculated with *P. fuligena*. A wide range of former *Lycopersicon* species, *Capsicum annuum*, *C. chinense* and *C. baccatum*, and *Solanum nigrum*, *S. aethiopicum*, *S. lasiocarpum* (= *S. indicum*, nom. rej.), *S. macrocarpon* and *S. melongena* were susceptible (development of lesions with sporulation), i.e. these species belong to the host range of Tomato Black Leaf Mould. *Solanum nigrum* and *S. aethiopicum* are common hosts of *P. atromarginalis*. *Pseudocercospora* on *S. melongena* was described from Taiwan as *P. solani-melongenicola*. This species is morphologically barely distinct from *P. atromarginalis* and *P. fuligena* (Hsieh & Goh 1990) except for slightly larger stromata on the upper leaf surface. On the basis of the proven wide host range of *P. fuligena*, including *Solanum nigrum*, one of the principal hosts of *P. atromarginalis*, in addition to isozyme and polymerase chain reaction (PCR) studies (Ho

1993), Wang et al. (1995) concluded that *P. atromarginalis* is synonymous with *P. fuligena*. This conclusion is supported by results of molecular sequence analyses (see Crous et al. 2013). However, the nomenclatural consequences taken by Wang et al. (1995) were wrong. *P. atromarginalis* is older than *P. fuligena* and takes priority, i.e. *P. fuligena* has to be reduced to synonymy with *P. atromarginalis*. Designations of epitypes for *Cercospora atromarginalis* (North American material on *Solanum nigrum* or *S. americanum*) and *C. fuligena* (material from the Philippines on *Solanum lycopersicum*), including cultures and retrieved sequence data, will be final steps to clarify the taxonomy of *P. atromarginalis* emend.

Tomato is traditionally referred to as *Lycopersicon esculentum*, but the genus *Lycopersicon* is phylogenetically not tenable. Tomatoes cluster within the genus *Solanum* (Asamizu & Ezura 2009), i.e. they are true *Solanum* species. Based on morphology and ITS sequence data, Saroj et al. (2014) identified a leaf-spotting fungus on *Withania somnifera* in India as *Pseudocercospora fuligena*, which seems to be an additional indication of a wider host range of the *P. atromarginalis*/*P. fuligena* complex. *Withania* is allied with *Physalis*, and *Physalis peruviana* has been recorded as host of *P. atromarginalis*. Saroj et al. (2014) examined and compared only ITS data which were 99% identical with *P. fuligena*. To sum up, *P. atromarginalis* emend. occurs on host species of the following solanaceous host genera: *Capsicum*, *Lycianthes*, *Nicandra*, *Physalis*, *Solanum* (incl. *Lycopersicon*), and *Withania*.

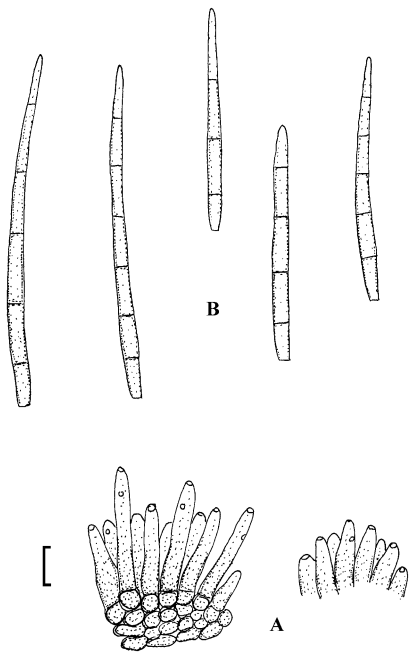
Pseudocercospora carolinensis (Tharp) U. Braun & Crous, in Crous & Braun, CBS Biodiversity Ser. **1**: 106 (2003). Fig. 2

≡ *Cercospora carolinensis* Tharp, Mycologia **9**: 109 (1917) [lectotype (designated here, MycoBank, MBT378768): on *Solanum carolinense*, USA, Texas, Palestine, 30 Oct. 1914, Lewis & Tharp 176 (BPI 434272); isolectotypes: BPI 434271, NY 936952, 936953].

≡ *Cercosporina carolinensis* (Tharp) Sacc., Syll. Fung. **25**: 916. 1931.

Literature: Chupp (1954: 535).

Leaf spots circular to angular-irregular, 2–5 mm diam, brown, margin indefinite. Caespituli usually epiphyllous, punctiform, dark brown. Mycelium internal. Stromata 15–75 µm diam, immersed, brown. Conidiophores in moderately large fascicles, dense, arising from stromata, erumpent, erect, straight to slightly curved, not geniculate, unbranched, 10–35 × 3.5–6 µm, 0(–1)-septate, pale olivaceous brown, thin-walled, smooth; conidiophores usually reduced to conidiogenous cells, conidiogenous loci paracercospora-like, 1–3 per conidiogenous cell, only ultimate rim slightly thickened and darkened, in front view visible as minute ring, 1–2 µm diam. Conidia solitary, obclavate-subcylindrical to subacicular, (30–)40–90(–130) × 2.5–5 µm, 3–10(–12)-septate, subhyaline to very pale yellowish green or olivaceous, thin-walled, smooth, apex subobtuse to subacute, base short obconically truncate, truncate in subacicular conidia, 1.5–2 µm wide, hila unthickened, not darkened, at most ultimate rim very slightly thickened and darkened.



Host range and distribution: on *Solanum carolinense* (Solanaceae), North America (USA, Texas).

Notes: This species is a typical '*Paracercospora*' with conspicuous circular conidiogenous loci (only ultimate rim slightly thickened and darkened). The taxonomic value of paracercospora-like conidiogenous loci was called into question by Stewart et al. (1999), and Crous & Braun (2003) formally reduced *Paracercospora* to synonymy with *Pseudocercospora*.

Fig. 2: *Pseudocercospora carolinensis*, A – Conidiophore fascicles, B – Conidia. Bar – 10 µm. U. Braun del.

Paracercospora-like conidiogenous loci are, indeed, not taxonomically relevant on generic level, but they are not confined to a single cercosporoid genus. Crous et al. (2013) confirmed *Paracercospora s. str.* (type species: *P. egenula*) as a genus of its own, phylogenetically clearly separated from *Pseudocercospora*. However, *Paracercospora fijiensis* (Morelet) Deighton proved to be a species of *Pseudocercospora* (Arzanlou et al. 2008). Thus, the true generic affinity of *Cercospora carolinensis* needs to be confirmed by molecular sequence analyses.

P. carolinensis is morphologically very close to *Paracercospora egenula*, but differs in having smaller conidiogenous loci (1–2 µm wide) and smaller conidial hila (1.5–2 µm wide). The loci in *P. egenula* are 2–3 µm wide. Furthermore, the conidia of the latter species are usually cylindrical, whereas the conidia of *P. carolinensis* are usually distinctly obclavate with obconically truncate bases.

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

≡ *Cercoseptoria egenula* Syd., Ann. Mycol. **33**: 885 (1935) [holotype: on *Solanum panduriforme*, South Africa, E. Transvaal, Barberton District, Nelspruit, Research Station, May 1931, L.C.C. Liebenberg D93 (PREM 25999); isotype K(M) IMI 89597].

≡ *Cercospora egenula* (Syd.) Chupp & Doidge, Bothalia **4**: 885 (1948).

≡ *Pseudocercospora egenula* (Syd.) U. Braun & Crous, in Crous & Braun, CBS Biodiversity Ser. **1**: 171 (2003).

= *Cercospora solani-melongenae* Chupp, Bothalia 4: 892. 1948 [holotype: on *Solanum melongena*, Japan, Chiba Pref., Matsudo, 5 Oct. 1916, S. Hori (BPI 441399); isotype: K(M) IMI 90165].

Host range and distribution: on *Solanum cerasiferum*, *S. dubium*, *S. incanum*, *S. marginatum*, *S. melongena*, *S. panduriforme*, *S. schimperianum* (Solanaceae), Africa (Ethiopia, Kenya, Malawi, Mozambique, Seychelles, Somalia, South Africa, South Korea, Sudan, Tanzania,), Asia (China, India, Indonesia, Japan, Korea, Malaysia, Saudi-Arabia, Taiwan), Oceania (Fiji, Hawaii, New Caledonia, Samoa, Tonga).

Literature: Chupp (1954: 551), Katsuki (1965: 62), Ellis (1976: 288), Deighton (1979: 48), Crous & Braun (2003: 171), Kamal (2010: 172), Crous et al. (2013: 65).

Illustrations: Chupp (1954: 538, fig. 193; 551, fig. 207), Ellis (1976: 288, fig. 218 D), Deighton (1979: 49, fig. 25), Crous et al. (2013: 66, fig. 9).

Notes: See notes under *Pseudocercospora carolinensis*.

Pseudocercospora fasciculata (Speg.) Deighton, Mycol. Pap. 1**40**: 104 (1976).

≡ *Septocylindrium fasciculatum* Speg., Anales Soc. Cient. Argent. **13**: 23 (1882) [holotype: on *Solanum pseudocapsicum*, Argentina, Buenos Aires, near San José de Flores, Feb. 1881, S. Spegazzini (LPS 10861); isotype: K(M) IMI 120632].

Illustration: Deighton (1976: 105, fig. 62).

Host range and distribution: on *Solanum pseudocapsicum* (Solanaceae), South America (Argentina).

Pseudocercospora marcelliana (Chupp) U. Braun & Crous, in Crous & Braun, CBS Biodiversity Ser. **1**: 267 (2003). Fig. 3

≡ *Cercospora marcelliana* Chupp, Monograph of *Cercospora*: 543 (1954) [holotype: on *Solanum nudum* (= *S. micranthum*), Venezuela, near Barcelona, banks of Neveri, 26 May 1938, C.F. Chardon (CUP-VZ 2670)].

Literature: Crous & Braun (2003: 267), Braun & Urtiaga (2012: 315).

Illustration: Chupp (1954: 543, fig. 198), Braun & Urtiaga (2012: 317, fig. 11).

Leaf spots amphigenous, subcircular to angular-irregular, 1–12 mm diam, yellowish, brown, greyish brown, finally dingy grey to greyish white, leaf spots less conspicuous below, margin indefinite or occasionally darker, ferruginous. Caespituli amphigenous, mainly epiphyllous, punctiform, scattered, brown. Mycelium internal. Stromata lacking or almost so to well-developed, subglobose to somewhat irregular, substomatal to immersed, 15–75 µm diam, olivaceous brown. Conidiophores mostly in large, dense fascicles, arising from stromata, through stomata or erumpent, sometimes solitary or in small fascicles, 2–4 conidiophores, arising from substomatal hyphae, emerging through stomata, erect, straight to curved,

subcylindrical, conical, not or somewhat geniculate-sinuous, simple, rarely branched, 5–30 × 1.5–3.5(–4) µm, mostly aseptate, occasionally 1(–2)-septate, subhyaline to pale olivaceous, thin-walled, smooth; conidiophores mostly reduced to conidiogenous cells, conidiogenous loci inconspicuous or visible as truncate tip, unthickened, not darkened. Conidia solitary, narrowly cylindrical-obclavate, long conidia sometimes subcylindrical-filifiorm or subacicular, 15–110 × 2–3.5 µm, (1–)3–11-septate, subhyaline to pale olivaceous, apex obtuse to subacute, thin-walled, smooth, base short to long obconically truncate, occasionally truncate, 1–1.5 µm wide, hila unthickened, not darkened.

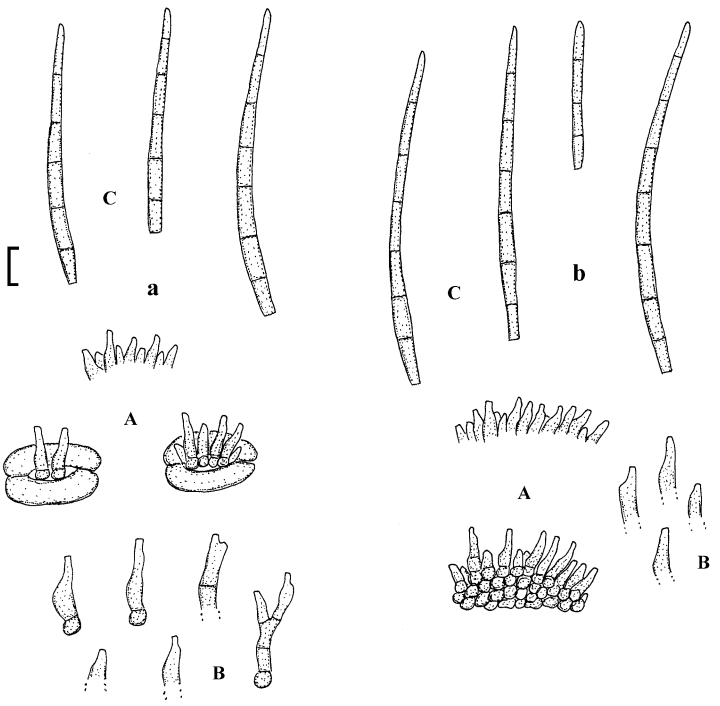


Fig. 3: *Pseudocercospora marcelliana* (a – holotype, b – HAL 2486 F, on *Solanum torvum* var. *hartwegianum*, Venezuela), A – Conidiophore fascicles, B – Conidiophores, C – Conidia. Bar – 10 µm. U. Braun del.

Host range and distribution: on *Solanum nudum*, *S. torvum* var. *hartwegianum* (Solanaceae), South America, Venezuela.

Notes: Braun & Urtiaga (2012) examined a new collection of this species from Venezuela on *S. torvum* var. *hartwegianum* and published an illustration. The present redescription of *P. marcelliana* and the new illustrations were prepared on the basis of re-examinations of type material and a new Venezuelan collection on *S. torvum* var. *hartwegianum*. Chupp (1954) described "nonfasciculate conidiophores (branched from procumbent threads)", but I have not found any superficial hyphae with solitary conidiophores, neither in the type material nor in the new collection from Venezuela.

Pseudocercospora modesta (Syd.) Deighton, Mycol. Pap. **140**: 148 (1976).

≡ *Cercospora modesta* Syd., Ann. Mycol. **25**: 141 (1927) [lectotype (designated here, MycoBank, MBT378769): on *Solanum* sp., Costa Rica, San José, La Caja, 3 Jan 1925, H. Sydow, Fungi Exot. Exs. 711 (S-F37421); isolectotyes: e.g., BPI 438551, CUP, FH 1012303, HBG, K(M) IMI 8505, LSUM 156954, MICH 15335, MIN 497726, WIS-F-6649].

Literature: Chupp (1954: 545), Crous & Braun (2003: 278).

Illustration: Chupp (1954: 543, fig. 200).

Host range and distribution: on *Solanum stramoniifolium*, *Solanum* sp. (Solanaceae), Central and South America (Costa Rica, Venezuela).

Notes: This species was recorded from India on *Solanum torvum* (Kamal 2010: 198) and from Myanmar on *S. lasiocarpum* [= *S. indicum*, nom. rej.] (Thaung 1984: 448). These records are

unclear, doubtful and in need to be proven. The record from Myanmar might belong to *Pseudocercospora venezuelae* var. *indica*.

Pseudocercospora rugosi (Chupp) U. Braun & Crous, in Crous & Braun, CBS Biodiversity Ser. **1**: 360 (2003) Fig. 4

≡ *Cercospora rugosi* Chupp, Monograph of *Cercospora*: 548 (1954) [holotype: on *Solanum rugosum*, Dominican Republic, La Vega, Trail cfrom Jarabacoa to Constanra, 13 Sep. 1037, C.E. Chardon (CUP 1156)].

Illustration: Chupp (1954: 548, fig. 203).

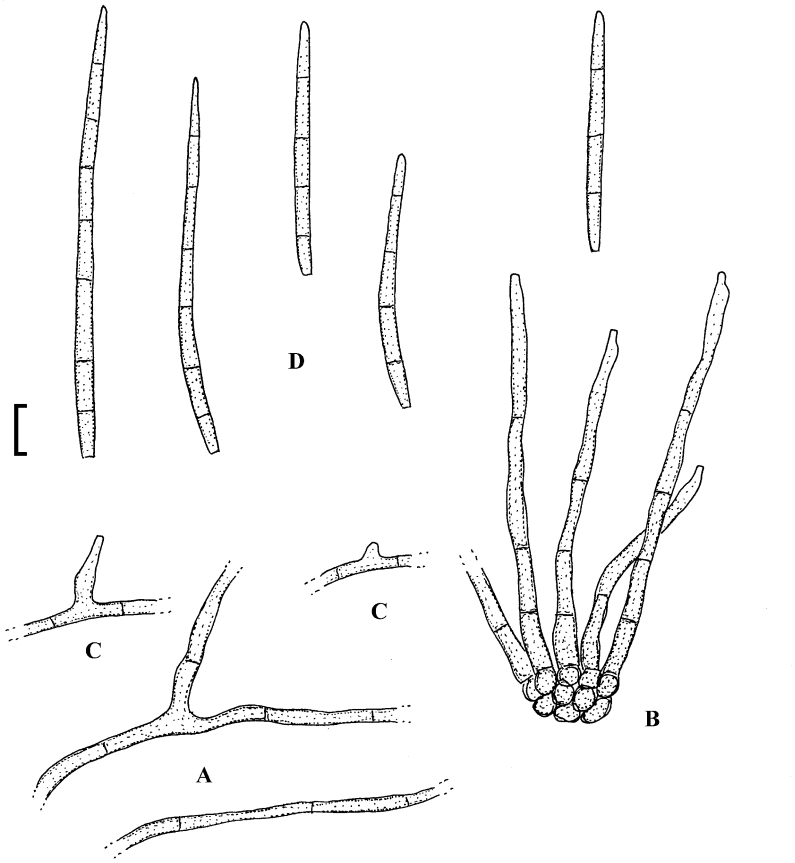


Fig. 4: *Pseudocercospora rugosi* (holotype), A – Superficial hyphae, B – Solitary conidiophores arising from superficial hyphae, C – Conidiophore fascicle, D – Conidia. Bar – 10 µm. U. Braun del.

Leaf spots lacking or almost so. Caespitili amphigenous, effuse, forming small olivaceous patches, 1–4 mm diam. Mycelium internal and external; superficial hyphae scantily branched, 1.5–3 µm wide, septate, pale olivaceous to olivaceous brown, thin-walled, smooth. Stromata lacking or only formed as small hyphal aggregations, 10–20 µm diam, olivaceous brown. Conidiophores in small, loose fascicles, 2–8, arising from internal hyphae or small hyphal aggregations, through stomata or erumpent, and solitary, arising from superficial hyphae, erect, straight to sinuous, occasionally geniculate, tortuous, simple or rarely branched, somewhat attenuated from base to top, 5–150 × 3–5 µm, aseptate to pluriseptate, pale to medium olivaceous to brown, thin-walled, smooth; conidiogenous cells integrated, terminal or conidiophores aseptate, i.e. reduced to conidiogenous cells, conidiophores arising from superficial hyphae usually formed as peg-like to cylindrical-conical protuberances of hyphal cells, not cut off by a basal septum, conidiogenous loci inconspicuous or visible as truncate tip, unthickened, not darkened. Conidia solitary, narrowly obclavate-cylindrical, straight to somewhat curved, 20–100 × 2–4 µm, 2–10-septate, subhyaline to very pale olivaceous, thin-walled, smooth, apex subobtuse to subacute, base short to long obconically truncate, 1–1.5 µm wide, hila unthickend, not darkened.

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

Notes: Type material of this species has been re-examined. Chupp's (1954) description is incomplete. Superficial mycelium with solitary conidiophores was not described. Braun and Crous (in Crous & Braun 2003) reallocated *Cercospora rugosi* to *Pseudocercospora*, but without redescription and without new illustration.

Pseudocercospora solani-pseudocapsicicola Meir. Silva, R.W. Barreto & Crous, Persoonia **37**: 164 (2016) [holotype: on *Solanum pseudocapsicum*, Brazil, Minas Gerais, Viçosa, Sítio Criciúma, 23 Jan. 2014, M. Silva (VIC 42807)].

Illustration: Silva et al. (2016: 164, fig. 20).

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

Notes: *P. solani-pseudocapsicicola* is morphologically very close to *P. atromarginalis*, but differs in having narrower conidia, and the two species are, in addition, genetically clearly distinct and not closely allied.

Pseudocercospora solani-torvicola Goh & W.H. Hsieh, Trans. Mycol. Soc. Republ. China **4**(2): 9 (1989) [holotype: on *Solanum torvum*, Taiwan, Taichung, 23 Aug. 1944, K. Sawada (NTU-PPE)].

Misapplied name: *Cercospora solani-torvi* sensu Sawada, Taiwan Agric. Res. Inst. Rep. **87**: 88 (1944).

Literature: Hsieh & Goh (1990: 319), Guo & Hsieh (1995: 321), Guo et al. (1998: 335).

Illustrations: Hsieh & Goh (1990: 320, fig. 242), Guo & Hsieh (1995: 322, fig. 270), Guo et al. (1998: 336, fig. 275).

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

Pseudocercospora trichophila (F. Stevens) Deighton, Mycol. Pap. **140**: 106 (1976).
var. ***trichophila***

≡ *Cercospora trichophila* F. Stevens, Trans. Illinois Acad. Sci. **10**: 212 (1917) [lectotype (designated by Deighton 1976: 112): on *Solanum* sp. (as "*Helicteres* sp."), Puerto Rico, Peñuelas, 11 Aug. 1913, F.L. Stevens (ILL 15333, secondary catalogue number); isolectotype: K(M) IMI 119606; syntypes (on *Solanum torvum*): CUP 016952, ILL 10728, 10729, 10732, MICH 15377, RMS 3289, 3291].

= *Cercospora brachyclada* Syd., Ann. Mycol. **23**: 422 (1925) [lectotype (designated here, MycoBank, MBT378770): on *Solanum umbellatum*, Costa Rica, La Caja near San José, 24 Dec. 1924, H. Sydow, Syd., Fungi Exot. Exs. 707 (S-F23389); isolectotypes: CUP 39232, FH, GZU, K(M) IMI 8503, LSU 156950, MICH 15261, MIN 512609, PDD 61553, WIS-F-66519, also distributed as Reliq. Petrak. 1148].

= *Cercospora costeroana* Petr. & Cif., Ann. Mycol. **30**: 311 (1932) [lectotype (designated by Braun 2001: 68): on *Solanum verbascifolium*, Dominican Republic, Llano Costero, 10 Feb. 1930, E.L. Ekman 3649 (W, Acqu. 1973, no. 10388); isolectotype: BPI 435259, PAV; topotype material (Feb. 1930): Cif., Mycofl. Doming. Exs. 343 (e.g., CUP, K(M) IMI 59291, MICH 328146, 328167, NY 936985, RMS 24303, 24304].

≡ *Mycovellosiella costeroana* (Petr. & Cif.) X.J. Liu & Y.L. Guo, Mycosystema **1**: 246 (1988).

= *Cercospora solani-asperi* R.E.D. Baker & W.T. Dale, Mycol. Pap. **33**: 105 (1951) [holotype: on *Solanum asperum*, Trinidad, Arima Forest reserve, 25 Oct. 1947, W.T. Dale, I.C.T.A. Fungi of Trinidad 1729 (K(M) IMI 24507).

≡ *Pseudocercospora solani-asperi* (R.E.D. Baker & W.T. Dale) Deighton, Mycol. Pap. **140**: 113 (1976).

≡ *Pseudocercospora trichophila* var. *solani-asperi* (R.E.D. Baker & W.T. Dale) U. Braun, Mycosphere **3**: 324 (2012).

= *Cercospora solani-hirti* R.E.D. Baker & W.T. Dale, Mycol. Pap. **33**: 105 (1951) [holotype: on *Solanum hirtum*, Trinidad, Grande Riviera, 15 June 1947, R.E.D. Baker, I.C.T.A. Fungi of Trinidad 1521 (K(M) IMI 24493); isotype: CUP 37171].

= *Cercospora pariensis* Chupp, Monograph of *Cercospora*: 546 (1954). [holotype: on *Solanum* sp., Trinidad, Chacachacare Island, Gulf of Paria, 20 Dec. 1944, C.E. Chardon 33 (CUP 37477); isotype: K(M) IMI 191832].

= *Cercospora solani-longispora* J.M. Yen, Bull. Trimestriel Soc. Mycol. France **93**: 158 (1977) [type: on *Solanum* sp., Taiwan, Taichung, 29 Oct. 1971, J.M. Yen 71260, not traced, probably not preserved].

≡ *Pseudocercospora solani-longispora* (J.M. Yen) J.M. Yen, Bull. Trimestriel Soc. Mycol. France **94**: 388 (1978).

Literature: Saccardo (1931: 892), Chupp (1954: 558), Vasudeva (1963: 225), Ellis (1976: 179), Braun (2001: 68), Crous & Braun (2003: 409–410), Kamal (2010: 228).

Illustrations: Deighton (1976: 107–113, figs 63–68), Ellis (1976: 179: fig. 128).

Leaf spots almost lacking, diffuse yellowish discolorations or forming brown spots, subcircular to angular-irregular, 0.5–5 mm diam, occasionally larger, to 15 mm, margin mostly indefinite, sometimes vein-limited. Caespituli usually hypophyllous, epiphyllous colonies less common, effuse, floccose-velutinous, pale to mostly dark olivaceous, occasionally paler and less conspicuous. Mycelium internal and external; internal hyphae 1.5–4 µm wide, pale, septate, thin-walled; superficial hyphae emerging through stomata, appressed to the leaf surface and often ascending leaf hairs, scantily branched, pale olivaceous, 1.5–4 µm wide, septate, thin-walled, smooth. Stromata lacking or only with a few swollen hyphal cells in the substomatal cavities. Conidiophores solitary, arising from superficial hyphae, lateral, occasionally terminal, occasionally in small, loose fascicles, emerging through stomata, arising from internal hyphae or small substomatal hyphal aggregations, erect to decumbent, subcylindrical-conical, straight, curved to strongly geniculate-sinuous, unbranched, rarely once branched, 5–80 × 2.5–5 µm, 0–4-septate, pale olivaceous to olivaceous brown, thin-walled, smooth; conidiogenous cells integrated, terminal or conidiophores reduced to conidiogenous cells, 5–25 µm long, conidiogenous loci inconspicuous or visible as truncate tips or lateral shoulders formed by sympodial proliferation, unthickened, not darkened. Conidia solitary, subcylindrical to obclavate-cylindrical, straight to curved, 20–110(–165) × 3–5(–7) µm, 1–10(–15)-septate, subhyaline to pale olivaceous, apex obtuse, rounded, base obconically truncate, 1–2 µm wide, hila unthickened, not darkened.

Host range and distribution: on *Lycianthes biflora* (= *S. biflorum*), *Solanum aturense* (= *S. asperrimum*), *S. asperum*, *S. americanum*, *S. erianthum* (= *S. verbascifolium* auct., nom. rej.), *S. ferox*, *S. hirtum*, *S. jamaicense*, *S. melongena*, *S. nigrum*, *S. surattense*, *S. torvum*, *S. umbellatum* (Solanaceae), Asia (Brunei, China, India, Japan, Malaysia, Papua New Guinea, Taiwan), Central and South America (Brazil, Colombia, Costa Rica, Ecuador [Galapagos], Guyana, Panama, Venezuela), North America (USA, Florida), West Indies (Cuba, Dominican Republic, Jamaica, Puerto Rico, Trinidad and Tobago, Virgin Islands), Oceania (Solomon Islands).

Pseudocercospora trichophila var. ***punctata*** U. Braun, in Braun & Urtiaga, Mycosphere **3**: 322 (2012) [holotype: on *Solanum hirtum*, Venezuela, Lara, Sanare, Sabana Redonda Arriba, June 2010, R. Urtiaga 377 (HAL 2498 F)].

= *Cercospora solanacea* Sacc. & Berl., Atti Reale Ist. Veneto Sci. Lett. Arti **VI**, 3: 721 (1885) [holotype: on *Solanum erianthum* (= *S. verbascifolium* auct.), Australia, Logan 34 (PAD)].

Literature: Chupp (1954: 549), Hsieh & Goh (1990: 322), Guo & Hsieh (1995: 322–324), Guo et al. (1998: 336–337), Braun & Urtiaga (2013: 202), Phengsintham et al. (2013a: 133).

Illustrations: Chupp (1954: 548, fig. 204), Hsieh & Goh (1990: 321, 322, figs 243, 244), Guo & Hsieh (1995: 323, fig. 271), Guo et al. (1998: 337, fig. 276), Braun & Urtiaga (2012: 225, fig. 16; 2013: 201, fig. 14), Phengsintham et al. (2013a: 135, figs 144, 145).

Distinguished from var. *trichophila* by the formation of amphigenous colonies, caespituli punctiform on the upper leaf surface, stromata developed, 10–60 µm diam, conidiophores solitary, arising from superficial hyphae, as well as fasciculate, arising from substomatal hyphae or stromata.

Leaf spots amphigenous, conspicuous on the upper leaf side, lacking or less conspicuous below, subcircular to angular-irregular, 1–8 mm diam, or confluent and larger, pale to medium dark brown, reddish brown to almost black, greyish brown to dingy grey, often vein-limited, with distinct narrow darker border or halo above, margin indefinite below. Caespituli amphigenous, more or less effuse on the lower leaf surface and punctiform above, dark brown. Mycelium internal and external; superficial hyphae mainly hypophyllous, emerging through stomata, sparingly branched, 1–5 µm wide, septate, hyaline, subhyaline to pale olivaceous or olivaceous brown, thin-walled, smooth or almost so. Stromata small to well-developed, mainly epiphyllous,

intraepidermal, occasionally substomatal, 10–60 µm diam, medium to dark olivaceous brown, lacking or very small below. Conidiophores on the upper side in small to moderately large fascicles, loose to dense, arising from stromata, erect, straight, subcylindrical to geniculate-sinuous, unbranched, 10–70 × 3–7 µm, pale olivaceous to medium olivaceous brown, 0–4-septate, thin-walled, smooth, on the lower leaf surface conidiophores solitary, arising from superficial hyphae, lateral, occasionally terminal, shorter, 3–25 × 2.5–5 µm, 0–1-septate; conidiogenous cells intergrated, terminal or conidiophores reduced to conidiogenous cells, 3–25 µm long, conidiogenous loci inconspicuous to subdenticulate, unthickened, not darkened. Conidia solitary, subcylindrical or obclavate-cylindrical, (10–)20–90(–110) × (2.5–)3–5(–6) µm, (1–)2–10(–12)-septate, distance between septa 6–18 µm, subhyaline to pale olivaceous, apex obtuse, rounded to subacute, base obconically truncate, 1–2 µm wide, hila unthickened, not darkened.

Host range and distribution: on *Solanum aculeatissimum*, *S. erianthum*, *S. hirtum*, *S. undatum* (Solanaceae), Asia (China, India, Laos, Taiwan), Australia, South America (Venezuela), West Indies (Puerto Rico, Trinidad).

Notes: *Pseudocercospora trichophila* is a common and widespread cercosporoid species on a wide range of hosts. This species is polymorphous which is reflected in various described species which have been reduced to synonymy with *P. trichophila* on the basis of agreeing or strongly overlapping morphological characters. Deighton (1976) maintained *Cercospora solani-asperi* as a species of its own, distinguished from *Pseudocercospora trichophila* by having narrower conidia, and reallocated it to *Pseudocercospora*. Braun (in Braun & Urtiaga 2012) introduced the combination *P. trichophila* var. *solani-asperi*. However, the conidial size of *Pseudocercospora* on *Solanum asperum* falls within the range of *P. trichophila*. Therefore, I prefer to reduce this taxon to synonymy with *P. trichophila* var. *trichophila*. In some collections, including type material, the colonies are strictly hypophyllous, more or less effuse, and stromata and conidiophore fascicles are lacking or almost so. There are other collections with superficial hyphae and solitary conidiophores as well as fasciculate conidiophores and small stromata. The colonies in such collections are usually amphigenous, and fascicles and stromata are chiefly formed on the upper leaf surface where they often form characteristically punctiform colonies. Braun & Urtiaga (2012) introduced the new variety *P. trichophila* var. *punctata* for such collections. Such differences between epiphyllous and hypophyllous colonies are not unusual in *Pseudocercospora* species. Yen's (1977) description of *Cercospora solani-longispora* agrees well with *P. trichophila* except for somewhat longer conidia, 30–210 × 3.5–5 µm. The conidial length is often strongly influenced by external conditions, e.g., humidity and temperature. Therefore, *C. solani-longispora* should better be considered a synonym of *P. trichophila*, at least tentatively until cultures and results of molecular sequence analyses will be available.

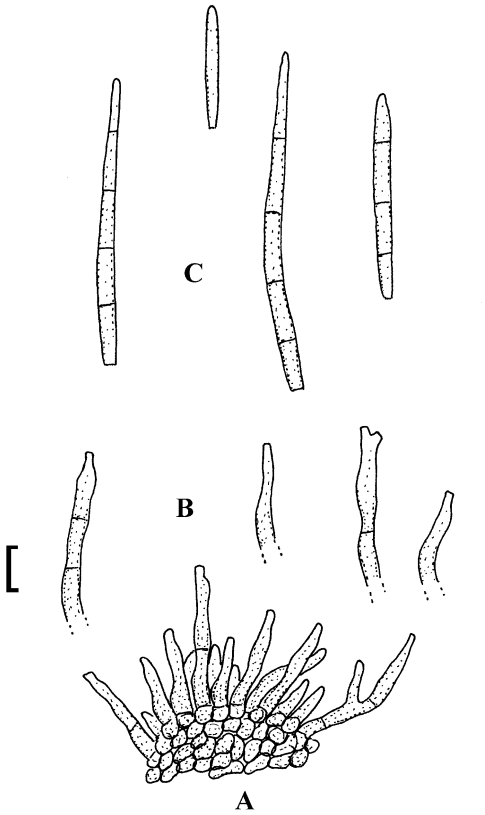
The destiny of the lectotype material of *Cercopsora trichophila* is not quite clear. *C. trichophila* was described with three different host species, *Helicteres*, *Solanum torvum* and *S. verbascifolium*. Chupp (1954) cited *Helicteres jamaicensis* as host and argued that the fungus on this host should be considered the true *C. trichophila*. Deighton (1976) followed Chupp's (1954) arguments and designated the material deposited at ILL as *C. trichophila* on *Helicteres* (identification corrected to *Solanum* sp.) as lectotype. However, this material, re-examined by Deighton (Puerto Rico, Peñuelas, 11 Aug. 1913, F.L. Stevens, ILL 15333 – secondary catalogue number) is not listed in Crane & Jones (1997) and not present among ILL collections in the database "Mycology Collections Portal".

Pseudocercospora venezuelae (Chupp) Deighton, Mycol. Pap. **140**: 113 (1976) Fig. 5

≡ *Cercospora venezuelae* Chupp, Monogr. Univ. Porto Rico, Ser. B, **2**: 254 (1934) [lectotype (designated here, MycoBank, MBT378771: on *Solanum* sp., Venezuela, Est. Táchira, La Mulera, 17 Sep. 1932, C.E. Chardon 1238 (CUP-VZ 1238); isolectotypes: FH 1012423, K(M) IMI 105212a].

Literature: Chupp (1954: 553), Deighton (1976: 113), Braun & Freire (2003: 323–324; 2006: 244), Crous & Braun (2003: 419).

Illustrations: Chupp (1954: 551, fig. 209), Deighton (1976: 114, fig. 69).



Host range and distribution: on *Solanum* "*aculeatum*", *S. aethiopicum* (= *S. gilo*), *S. argenteum*, *Solanum* sp. (Solanaceae), South America (Brazil, Venezuela).

Notes: Deighton (1976) provided a detailed description and a drawing based on type material of *C. venezuelae*. In addition, he examined material from Brazil on *Solanum argenteum* and from Venezuela on *Solanum aculeatum* (Jacq.) O.E. Schultz (nom. illeg.). The latter name is unresolved. Braun & Freire (2003, 2006) reported collections on *Solanum* sp. and *S. aethiopicum* (= *S. gilo*) from Brazil, which are characterised as follows: Leaf spots amphigenous, subcircular to angular-irregular, 2–10 mm diam or confluent and larger, brown, later greyish brown to greyish white, margin indefinite or narrow and darker.

Fig. 5: *Pseudocercospora venezuelae* (HAL 3234 F, on *Solanum aethiopicum*, Brazil), A – Conidiophore fascicle, B – Conidiophores, C – Conidia. Bar – 10 µm. U. Braun del.

Caespituli amphigenous, punctiform and dark brown to blackish on the upper leaf surface, less conspicuous below. Mycelium internal (a few superficial hyphae have been observed, but it is unclear if they actually pertain to the present species). Stromata substomatal, 15–40 µm diam, pale olivaceous to olivaceous brown. Conidiophores usually in moderately large, dense fascicles, arising from stromata, through stomata, erect, straight to slightly curved or sinuous, rarely geniculate, sometimes apex subdenticulate, unbranched, 10–70 × 2–4 µm, 0–1(–2)-septate, pale olivaceous, thin-walled, smooth; conidiogenous cells integrated, terminal or conidiophores reduced to conidiogenous cells, 10–35 µm long, conidiogenous loci inconspicuous or subdenticulate, but always unthickened and not darkened. Conidia solitary, cylindrical to obclavate-cylindrical, straight, occasionally curved, (15–)30–65 × 3–5 µm, (0–)3–6-septate, subhyaline to pale olivaceous, thin-walled, smooth, apex obtuse to subacute, base short obconically truncate, 1–1.5 µm wide, hila unthickened, not darkened.

Pseudocercospora venezuelae var. *indica* (Govindu & Thirum.) Kamal, Cercosporoid Fungi of India: 230 (2010), nom. inval.

≡ *Cercospora venezuelae* var. *indica* Govindu & Thirum., Sydowia **9**: 223 (1955), nom. inval. (Art. 39.1) [type: on *Solanum lasiocarpum* (= *S. indicum*, nom. rej.), India, Tamil Nadu, Nilgiris, Hosamande, 19 June 1953, H. C. Govindu (not preserved)].

Literature: Vasudeva (1963: 209), Crous & Braun (2003: 419).

Illustration: Govindu & Thirumalachar (1955: plate 4, fig. 7).

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

Notes: *Cercospora venezuelae* var. *indica* is an invalid name published without Latin description or diagnosis. Kamal (2010) reallocated this invalid variety to *Pseudocercospora venezuelae*, but failed to validate this name. According to the English description and illustration, the Indian material is well characterised by having relatively large stromata and fasciculate, 1–6-septate conidiophores. The septation of the conidiophores clearly differentiate the Indian fungus on *Solanum lasiocarpum* from *P. venezuelae* and suggests a species of its

own, but owing to lacking type material a validation and a final reassessment of this taxon are currently not possible.

Literature

Arzanlou, M., Groenewald, J. Z., Fullerton, R. A., Abeln, E. C. A., Carlier J., et al. 2008: Multiple gene genealogies and phenotypic characters differentiate several novel species of *Mycosphaerella* and related anamorphs on banana. Persoonia **20**: 19–37.

Asamizu, E. & Ezura, H. 2009: Inclusion of Tomato in the genus *Solanum* as "*Solanum lycopersicum*" is Evident from Phylogenetic Studies. Journal of the Japanese Society for Horticultural Science **78**(1): 3–5.

Bakhshi, M., Arzanlou M., Babai-Ahari, A., Groenewald, J. Z. & Crous, P. W. 2014: Multi-gene analysis of *Pseudocercospora* spp. from Iran. Phytotaxa **184**(5): 245–265.

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

Braun, U. 2001: Taxonomic notes on some species of the *Cercospora* complex (VII). Fungal Diversity **8**: 41–71.

Braun, U. & Freire, F. C. O. ["2002"] 2003: Some cercosporoid hyphomycetes from Brazil – II. Cryptogamie Mycologie **23**: 295–328.

Braun, U. & Freire, F. C. O. 2006: Some cercosporoid hyphomycetes from Brazil – IV. Cryptogamie Mycologie **27**: 231–248.

Braun, U. & Urtiaga. R. 2012: New species and new records of cercosporoid hyphomycetes from Cuba and Venezuela (Part 1). Mycosphere **3**: 301–329.

Braun, U. & Urtiaga, R. 2013: New species and new records of cercosporoid hyphomycetes from Cuba and Venezuela (Part 2). Mycosphere **4**: 165–205.

Chiddarwar, P. P. 1962: Contributions to our knowledge of the Cercosporae of Bombay State-III. Mycopathologia et Mycologia Applicata **17**: 71–78.

Chupp, C. 1954: A Monograph of the fungus genus *Cercospora.* Ithaca, NY, published by the author.

Crane, J. L. & Jones, A. G. 1997: An Annotated Catalogue of Types of the University of Illinois Mycological Collections (ILL). Illinois Biological Monographs **58**: 1–165.

Govindu, H. C. & Thirumalachar, M. J. 1955: Notes on some Indian Cercosporae-VI. Sydowia **9**: 221–228.

Crous, P. W. & Braun, U. 2003: *Mycosphaerella* and its Anamorphs: 1. Names published in *Cercospora* and *Passalora*. CBS Biodiversity Series no. 1. Utrecht.

Crous, P. W., Braun, U., Hunter, G. C., Wingfield, M. J., Verkley, G .J. M., Shin, H.-D., Nakashima, C. & Groenewald, J. Z. 2013: Phylogenetic lineages in *Pseudocercospora*. Studies in Mycology **75**: 37–114.

Deighton, F. C. 1976: Studies on *Cercospora* and allied genera. VI. *Pseudocercospora* Speg., *Pantospora* Cif. and *Cercoseptoria* Petr. Mycological Papers **140**: 1–168.

Deighton, F. C. 1979: Studies on *Cercospora* and allied genera. VII. New species and redispositions. Mycological Papers **144**: 1–56.

Ellis, M. B. 1976: More Dematiaceous Hyphomycetes. Kew, Commonwealth Mycological Institute.

Guo, Y. L. & Hsieh, W. H. 1995: The genus *Pseudocercospora* in China. Mycosystema Monographicum Series **2**: 1–388.

Guo, Y. L., Liu, X. J. & Hsieh, W. H. 1998. *Pseudocercospora*. Flora Fungorum Sinicorum, Vol. 9. Beijing.

Gupta, B. K. & Kamal ["1989"] 1990: New species of *Pseudocercosporella*. Indian Phytopathology **42(**3): 388–392.

Ho, M. L. 1993: Use of isozyme and polymerase chain reaction to detect the differences between *Pseudocercospora atromarginalis* and *P. fuligena.* M.S. Thesis, National Chungshin University, Taichung, Taiwan.

Hsieh, W. H. & Goh, T. K. 1990: *Cercospora* and similar Fungi from Taiwan. Taipei.

Kamal 2010: Cercosporoid fungi of India. Dehra Dun.

Katsuki, S. 1965: Cercosporae of Japan. Transactions of the Mycological Society of Japan, Extra Issue **1**: 1–100.

Lee, M. H., Lee, S. S., Kim, H. G., Lee, Y. S., Lee, J. H. & Yu, S. H. 2012: Black leaf mold of tomato caused by *Pseudocercospora fuligena* in Korea. Research in Plant Disease **18**(3): 255–258.

Mulder, J. L. & Holliday, P. 1975: *Cercospora elaeidis*. CMI Descriptions of Pathogenic Fungi and Bacteria **465**: 1–2.

Phengsintham, P., Chukeatirote, E., McKenzie, E. H. C., Hyde, K. D. & Braun, U. 2012: Tropical phytopathogens 2: *Pseudocercospora fuligena*. Plant Pathology & Quarantine **2**(1): 57–62.

Phengsintham, P., Chukeatirote, E., McKenzie, E. H. C., Hyde, K. D. & Braun, U. 2013a: Monograph of Cercosporoid fungi from Laos**.** Current Research in Environmental & Applied Mycology **3**(1): 34–158.

Phengsintham, P., Braun, U., McKenzie, E. H. C., Chukeatirote, E., Cai, L. & Hyde, K. D. 2013b: Monograph of Cercosporoid fungi from Thailand. Plant Pathology & Quarantine **3**(2): 67–138.

Pirnia, M., Zare, R., Zamanizadeh, H. R., Khodaparast, A. & Djavadi, B. 2012: Contribution to the identification of *Pseudocercospora* species in Iran. Iranian Journal of Plant Pathology **48**(3): 29–37.

Saccardo, P. A. 1892: Sylloge Fungorum omnium hucusque cognitum. Vol. 10. Padova.

Saccardo, P. A. 1906: Sylloge Fungorum omnium hucusque cognitum, Vol. 18. Supplementum Universal Pars VII. [Saccardo PA, Saccardo D, eds]. Padova.

Saccardo, P. A. 1931: Sylloge Fungorum omnium hucusque cognitum. Vol. 25 [Trotter A, ed.]. Avellino.

Saroj, A., Mumar, A. Srivastava, A. K., Khaliq, A., Absar, N., Akam, M. & Samad, A. 2014: New Report of Black Leaf Spot Mold (*Pseudocercospora fuligena*) on *Withania somnifera* from India. Plant Disease **98**: 1275.

Shin, H. D. & Kim, J. D. 2001: *Cercospora* and allied genera from Korea. Plant Pathogens of Korea **7**: 1–303.

Silva, M., Barreto, R. W., Pereira, O. L., Freitas, N. M., Groenewald, J. Z. & Crous, P. W. 2016: Exploring fungal mega-diversity: *Pseudocercospora* from Brazil. Persoonia **37**: 142–172.

Stewart, E. L, Liu Z., Crous, P. W., Szabo, L. 1999: Phylogenetic relationships among some cercosporoid anamorphs of *Mycosphaerella* based on rDNA sequence analysis. Mycological Research **103**: 1491–1499.

Subedi, N., Testen, A. L., Baysal-Gurel, F. & Miller, S. A. 2015: First report of black mold of tomato caused by *Pseudocercospora fuligena* in Ohio. Plant Disease **99**(2): 285.

Thaung, M. M. 1984: Some fungi of *Cercospora* complex from Burma. Mycotaxon **19**: 425–452.

Vasudeva, R. S. 1963: Indian Cercosporae. New Delhi.

Williams M. A. J. 1987: *Pseudocercospora atromarginalis*. CMI Descriptions of Pathogenic Fungi and Bacteria No. 940. Mycopathololog**i**a **100**: 187–188.

Wang, T. C., Hartman, G. L., Hsieh, W. H. & Black, L. L. 1995: Reactions of Solanaceous Species to *Pseudocercospora fuligena*, the Causal Agent of Tomato Black Leaf Mold. Plant Disease **79**: 661–665.

Yen. J. M. 1977: Étude sur les champignons parasites du Sud-Est Asiatique. XXVI. Les *Cercospora* de Formose II. Bulletin Trimestriel de la Société Mycologique de France **93**: 145–164.

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