MYCOTAXON

Volume 105, pp. 207-224

July-September 2008

Cercosporoid hyphomycetes on hosts of the Annonaceae: Cercospora annonaceae and Isariopsis annonarum revisited

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Abstract — Type material of *Cercospora annonaceae* and several collections assigned to this species by C. Chupp have been re-examined. The status of this species as a member of the genus *Stenella* is confirmed, but most collections in Chupp's herbarium referred to as *C. annonaceae* proved to be misidentified, and pertain to *Isariopsis annonarum*, herein reallocated to *Pseudocercospora*, and the new species *Phacellium annonae-cherimoliae*. A key to 23 cercosporoid hyphomycete species on hosts belonging to the *Annonaceae* is provided, and the taxonomy of the species concerned is briefly discussed. The following new combinations are proposed: *Pseudocercospora annonarum*, *P. asiminae* and *P. oblecta*. Furthermore, a revised, detailed description of *Pseudocercospora annonae-squamosae* is provided.

Key words — anamorphs, cercospora-like, Annona

Introduction

Cercospora annonaceae (Hennings 1909) was introduced for a cercosporoid hyphomycete on an unknown member of the Annonaceae collected in Brazil. The original data are rather scanty, simply describing hypophyllous caespituli, fasciculate 'hyphae' (i.e. conidiophores), up to $150 \times 3.5~\mu m$, septate, and cylindrical-fusiform conidia, $15\text{--}35 \times 2.5\text{--}3.5~\mu m$, 3–7-septate, brown. In his monograph of Cercospora Fresen., Chupp (1954) considered this species a coremioid hyphomycete, which has to be excluded from the latter genus. His observations were based on a revision of type material, deposited at the herbarium of the Botanical Garden and Museum in Berlin, Germany (B), and several secondary samples in his own herbarium, now maintained at the Plant Pathology Herbarium of the Cornell University, Ithaca, New York, USA (CUP). Unfortunately the type material at B has been lost. Braun (in Braun

& Mel'nik 1996) detected and examined syntype material of this species deposited at the Russian herbarium LEP. Hennings (1908) cited the following details for the type collection: 'Agua Branca in foliis Anonaceae. Majo 1903, no. 738' ['Agua Branca, São Paulo, Anonaceae, A. Puttemans, No. 738, May 10- (16?), 1903' is the altered version given in Chupp (1954), who examined this material]. The label of the syntype material at LEP deviates and reads as follows: 'Pará, Annonaceae, V 1903, Puttemans'. The whole context of the protologue and the labels concerned suggest the locality Agua Branca (or Agua Branca do Paulinho?) in the state of Pará, in which also a city with the name São Paulo exists. Braun (Braun & Mel'nik 1996) reallocated C. annonaceae to Stenella Syd., since the only discernable cercosporoid hyphomycete found in the syntype material at LEP was a member of the latter genus. However, in the latter material only solitary conidiophores arising from superficial hyphae were found, i.e. fasciculate conidiophores were lacking, which was in conflict with the original description (Hennings 1908) as well as Chupp's (1954) comments on this species, and raised the question whether a single polymorphous or two different cercosporoid taxa had been involved. Therefore, herbarium specimens referred to as C. annonaceae by C. Chupp have been re-examined in order to clarify his taxonomic decision and concept.

Materials and methods

The collections examined were described, mounted in distilled water, using oil immersion (bright field and phase contrast), but without any staining, by means of standard light microscopy (Olympus BX 50, Hamburg, Germany). 30 measurements (× 1000 magnification) of conidia and other structures were made, with the extremes given in parentheses. The collections examined are deposited at the herbaria CUP and W (abbreviations according to Holmgren et al. 1990).

Taxonomy

The examination of four specimens from CUP referred to as C. annonaceae by C. Chupp revealed them to represent several distinct taxa. A single collection from Brazil on Annona reticulata proved to be a member of Stenella conspecific with C. annonaceae, a specimen from Venezuela on A. squamosa belongs to Isariopsis annonarum [$\equiv Passalora\ annonarum$], and another one from Mexico on A. cherimolia has to be described as new species of Phacellium Bonord.

Stenella annonaceae (Henn.) U. Braun, in Braun & Mel'nik, Mikol. Fitopatol. 30(4): 3, 1996.

= Cercospora annonaceae Henn., Hedwigia 48: 18, 1908 ['1909'].

Fig. 1

MATERIAL EXAMINED: BRAZIL. Pará, on living leaves of a host belonging to the *Annonaceae* (probably *Annona* sp.), May 1903, Puttemans (LEP), lectotype of *C. annonaceae*, designated here. BRAZIL. Fungos de Minas Geraes, Viçosa-Escola, on living leaves of *Annona reticulata*, 23 Mar. 1930, A.S. Muller (CUP-MG 157).

LEAF SPOTS amphigenous, subcircular to angular-irregular, 1-25 mm diam., sometimes confluent, pale to dull dark brown, later grayish to dingy grayish white, margin indefinite or with a narrow darker border or marginal line. COLONIES amphigenous, mainly hypophyllous, inconspicuous, effuse to punctiform, brown to grayish brown. Mycelium internal and external; superficial hyphae emerging through stomata, 1.5–3 μm wide, branched, septate, subhyaline, pale to medium olivaceous, olivaceous-brown or yellowish brown, thin-walled, verruculose. STROMATA lacking or small, not very conspicuous, 10-40 μm diam., immersed, brown. Conidiophores solitary, arising from superficial hyphae or in small to moderately large fascicles, loose to usually rather dense, occasionally even coremioid, arising from immersed stromatic hyphal aggregations, erect, unbranched, subcylindrical, straight to somewhat flexuous-sinuous, upper fertile part usually geniculate-sinuous, sometimes strongly so, $20-150 \times (2.5-)3-4(-4.5)$ µm, pluriseptate, pale to dark brown, yellowish brown or olivaceous-brown, smooth, wall thin to slightly thickened (< 1 μm). Conidiogenous cells integrated, terminal and intercalary, 5–20 μm long, occasionally longer, with several conspicuous conidiogenous loci, slightly thickened and darkened, 1-1.5 µm diam. CONIDIA solitary, subcylindricalfiliform, acicular to narrowly obclavate, $20-100 \times 2.5-4.5 \mu m$, 2-8-septate, pale olivaceous, yellowish brown to brown, verruculose, wall thin (ca. 0.5 μm wide), apex obtuse to subacute, base truncate to usually obconically truncate, 1-1.5 (-2) μm wide, hila slightly thickened and darkened.

COMMENTS: The collection on *Annona reticulata* agrees well with the original description of *C. annonaceae* as well as the lectotype of this species in that solitary as well as fasciculate conidiophores are formed. Fasciculate conidiophores were described by Hennings (1908) and observed by Chupp (1954), whereas solitary conidiophores arising from superficial hyphae were found by Braun & Mel'nik (1996) in the lectotype sample.

Phacellium annonae-cherimoliae U. Braun, sp. nov.

FIG. 2

Mycobank MB 511858.

Phacellio sessili simile, sed conidiis longioribus et angustioribus, 8–25 \times 2–4(–5) μm , 0–1(–2)-septatis, levibus.

MATERIAL EXAMINED: MEXICO. Jalapa, Vera Cruz, on living leaves of Annona cherimolia (Annonaceae), 19 Jul. 1932, O.A. Plunkett 143 (CUP 60731), holotype. Isotype: CUP 39057.

LEAF SPOTS amphigenous, subcircular to angular-irregular, 1–5 mm diam., occasionally confluent, pale to dark brown, later grayish brown to dingy gray,



Fig. 1. Stenella annonaceae. A. Conidiophore fascicle. B. Superficial hyphae with or without solitary conidiophores. C. Tips of conidiophores with conidiogenous cells. D. Conidia. Scale bar = $10~\mu m$ (fig. A based on CUP-MG 157, figs B–G based on type material from LEP). U. Braun del.

on the lower leaf surface usually much paler, margin conspicuous, narrow, dark brown to blackish. Mycelium internal, forming immersed stromatic hyphal aggregations at the base of synnemata, 20–50 μ m diam., brown. Conidiomata synnematous, erect, straight, occasionally slightly curved to sinuous, subcylindrical or somewhat attenuated towards the apex, 150–400 \times 10–40 μ m, medium brown, composed of a firm stipe of densely appressed parallel threads (conidiophores) and a rather compact, often poorly developed capitulum, barely or only slightly splaying out. Individual conidiophores 1-4 µm wide, pale to mid olivaceous, olivaceous-brown or brown, pluriseptate throughout, smooth, thin-walled. Conidiogenous cells integrated, terminal, intercalary and pleurogenous, 5-20 \times 2-5 μ m, subhyaline to very pale olivaceous or olivaceous-brown, with a single to usually several conspicuous conidiogenous loci, 1–1.5 µm diam., slightly thickened and darkened. Conidia catenate, in simple or occasionally branched chains, ellipsoid-ovoid, cylindrical, 8–25 \times 2-4(-5) µm, 0-1(-2)-septate, hyaline or subhyaline, thin-walled, smooth or almost so, ends obtuse to somewhat attenuated, hila 1–1.5 µm diam., slightly thickened and darkened.

COMMENTS: Due to synnematous conidiomata with integrated, terminal as well as pleurogenous, cicatrized, hyaline or only pale conidiogenous cells, and hyaline or subhyaline conidia formed in chains, the new cercosporoid species on Annona cherimolia fits the concept of the hyphomycete genus Phacellium as circumscribed by Braun (1998). Phacellium annonae-cherimoliae, the first species of *Phacellium* on a host belonging to the *Annonaceae*, is morphologically close to *P. sessile* U. Braun, but differs in having longer and narrower, 0-1(-2)septate, smooth conidia. P. sessile, on Sanguisorba canadensis in North America, possesses very similar synnemata with numerous pleurogenous conidiogenous cells, but the conidia are $10-16(-18) \times 4-6(-8)$ µm, aseptate and verruculose (Braun 1998). The South American *P. paspali* (Syd.) U. Braun is a further similar species, also characterized by having slender, pigmented synnemata, often somewhat narrowed towards the apex, with little differentiated capitula and abundant pleurogenous conidiogenous cells, but the synnemata are pale reddish to pink and the conidia are aseptate. The type species of *Phacellium*, *P. inhonestum* Bonord. [= *P. alborosellum* (Desm.) U. Braun], is, except for the synnematous conidiomata, close to Ramularia Unger. Other species with distinctly pigmented synnemata and conidiophores are more cercosporoid, resembling phaeoramularia-like *Passalora* Fr. species, but differ in having pleurogenous, hyaline or subhyaline conidiogenous cells and colourless conidia. The taxonomy of this genus within the complex of cercosporoid *Mycosphaerella* anamorphs is still unclear. Cultures of the type species and molecular sequence analyses of various *Phacellium* species, including those with colorless and pigmented synnemata, are not yet available. Thus, we prefer to maintain Phacellium tentatively.

Pseudocercospora annonarum (Petr. & Cif.) U. Braun & Crous, comb. nov. Fig. 3 Mycobank MB 511859.

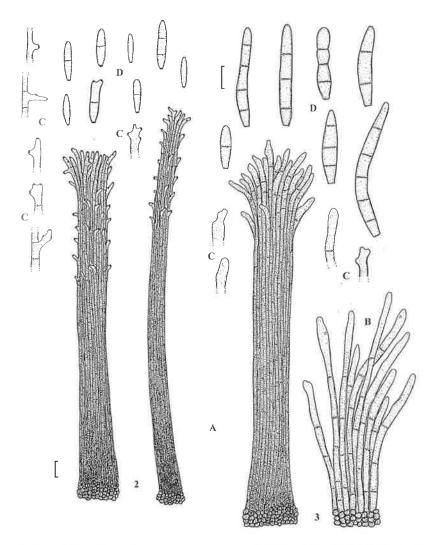
Bas.: Isariopsis annonarum ['anonarum'] Petr. & Cif., Ann. Mycol. 30: 235, 1932.

- = Phaeoisariopsis annonarum (Petr. & Cif.) U, Braun, Nova Hedwigia 50: 511, 1990.
- = Passalora annonarum (Petr. & Cif.) U. Braun & Crous, in Crous & Braun, Mycosphaerella and its anamorphs: 1. Names published in Cercospora and Passalora. CBS Biodiversity Series 1: 438, 2003.

MATERIAL EXAMINED: DOMINICAN REPUBLIC. Prov. Santiago, Santiago, Valle del Ciboa, on living leaves of *Annona squamosa* (*Annonaceae*), 22 Dec. 1930, Ekman (W, No. 10913), type of *I. annonarum*. VENEZUELA. Caracas, Los Chorros, on living leaves of *Annona squamosa*, Mar, 1939, Muller & Whetzl (CUP-VZ 2892), as *Cercospora annonaceae*.

LEAF SPOTS amphigenous, subcircular to angular-irregular, 1-10 mm diam., occasionally confluent, pale to dark brown, later grayish brown to dingy gray, on the lower leaf surface usually much paler, margin conspicuous, dark brown to blackish, narrow. Conidiomata hypophyllous, synnematous, scattered, rather inconspicuous to punctiform, brown to dark brown. Mycelium internal. Stromata immersed, $20-60 \,\mu\text{m}$ diam., brown. Synnemata $80-250 \times 20-50 \,\mu\text{m}$, brown, composed of a mostly firm subcylindrical stipe of numerous, densely appressed parallel conidiophores and a more or less loose apical capitulum, often somewhat wider at the very base, occasionally with conidiophores in dense fascicles, i.e. not distinctly synnematous, individual conidiophores $40-250 \times 2-5$ μm, terminal cells (conidiogenous cells) up to 7 μm wide, olivaceous to medium brown, pluriseptate throughout, thin-walled, smooth. Conidiogenous Cells integrated, terminal, rarely intercalary or pleurogenous, 10-25(-35) µm long; conidiogenous loci inconspicuous to subconspicuous by being subdenticulate or by having an unthickened, but slightly darkened-refractive ultimate rim (paracercospora-like), visible in front view as minute circle, 1-2 µm diam. CONIDIA solitary, obclavate-cylindrical, occasionally subclavate, short conidia sometimes ellipsoid-ovoid, straight to curved, $(15-)25-70(-80) \times (3.5-)4-8$ (-9) μ m, (0-)1-7(-10)-septate, occasionally constricted at the septa, pale to medium olivaceous or olivaceous-brown, thin-walled (ca. 0.5 µm), smooth, apex obtuse, base obconically truncate to somewhat convex, (1.5-)2-2.5(-3)μm wide, unthickened, not darkened, at most slightly refractive.

Comments: During the course of a revision and reassessment of the genus *Phacellium* (= *Isariopsis* Fresen.), Braun (1990) reallocated cercosporoid species with pigmented, scolecoid conidia, including *Isariopsis annonarum*, to *Phaeoisariopsis* Ferraris. Later it turned out that the formation of synnematous conidiomata is of little taxonomic relevance at generic level in cercosporoid anamorphs. Furthermore, the genus *Phaeoisariopsis* proved to be heterogeneous, encompassing passalora-like species with conspicuous, thickened and darkened conidiogenous loci as well as pseudocercospora-like taxa with inconspicuous loci (Deighton 1990, Crous & Braun 2003).



Figs 2–3. 2. Phacellium annonae-cherimoliae. 3. Pseudocercospora annonarum. A. Synnemata. B. Conidiophores in a dense fascicle. C. Conidiogenous cells. D. Conidia (based on type material, except for fig. B of P. annonarum which is based on CUP-VZ 2892). Scale bars = $10~\mu m$. U. Braun del.

Hence, most species of *Phaeoisariopsis* were reallocated to *Passalora* and *Pseudocercospora*, respectively. Due to subconspicuous conidiogenous loci (ultimate rim unthickened, but somewhat darkened-refractive, scars visible in

front view as minute circles), Crous & Braun (2003) assigned *I. annonarum* to *Passalora*. Based on a molecular and morphological reassessment of *Phaeoisariopsis griseola* (Sacc.) Ferraris, the type species, Crous et al. (2006) reduced the genus *Phaeoisariopsis* to synonymy with *Pseudocercospora*. *P. griseola* is characterized by having conidiogenous loci ranging from being quite inconspicuous to subconspicuous by being unthickened, but slightly darkened-refractive, at least with regard to the ultimate rim. Since *P. griseola* clustered within a subclade formed by other *Pseudocercospora* species, it became clear that taxa with minutely thickened and slightly darkened conidiogenous loci have to be placed in *Pseudocercospora*. The recent examination of the rich collection of *I. annonarum* from Venezuela showed that this species has a similar morphological range of the conidiogenous loci as in *P. griseola*. Thus, *I. annonarum* is better placed in *Pseudocercospora*.

Key to cercosporoid hyphomycete species on hosts of the Annonaceae

Numerous cercosporoid hyphomycete species, including the taxa treated herein, have been described on host species belonging to the *Annonaceae*. The following key and brief discussions on some of the species listed have been prepared to render the differences between the taxa concerned palpable.

1	Conidiophores in distinct synnemata
1*	Conidiophores mononematous, solitary or fasciculate
2	Synnemata composed of a firm stipe and a \pm loose capitulum; conidiogenous cells usually integrated, terminal; conidiogenous loci inconspicuous or only ultimate rim slightly darkened-refractive (visible in front view as minute circle); conidia solitary, pigmented, $(15-)25-70(-80)\times(3.5-)4-8(-9)$ µm; on Annona squamosa Pseudocercospora annonarum
2*	Synnemata composed of a firm stipe and a compact, little differentiated capitulum; conidiogenous cells frequently pleurogenous; conidiogenous loci minute, but conspicuous, thickened and darkened; conidia catenate, hyaline or subhyaline, $8-25\times 2-4(-5)$ µm, $0-1(-2)$ -septate; on Annona cherimolia
	Phacellium annonae-cherimoliae
3	Conidiogenous loci conspicuous, thickened and darkened 4
3*	Conidiogenous loci inconspicuous, at most subconspicuous by being denticle-
	like, but neither thickened nor darkened
4	Superficial mycelium present; hyphae distinctly verruculose
4*	Superficial mycelium smooth or lacking
5	Conidiophores solitary, arising from superficial hyphae, as well as fasciculate; on Annona spp., Brazil
5*	Conidiophores consistently solitary, arising from superficial hyphae; on <i>Polyalthia suberosa</i> , India

6	Conidiophores fasciculate, pigmented; conidia solitary, acicular when mature, pluriseptate, hyaline; on <i>Annona</i> spp
6*	Conidiophores fasciculate or solitary, pigmented; conidia not acicular, solitary and pigmented or catenate and \pm hyaline (<i>Passalora</i>)
7	Conidia catenate 8
7*	Conidia solitary
8	Conidiophores 120–200(–250) µm long; conidia $30-70\times3-4$ µm, 2–7-septate, subhyaline to pale brown; on <i>Isolona cauliflora</i> , Kenya <i>Passalora isolonae</i>
8*	Conidiophores 30–150 μ m long; conidia 20–40(–65) × 2–4.5 μ m, 0–3(–5)-septate, hyaline or subhyaline; on <i>Annona dioica</i> and <i>Xylopia grandiflora</i> , Brazil
- (-)	
9(7)	Conidiophores solitary and fasciculate, ca. 60–210 \times 5.5–9 μm ; conidia ca. 35–130 \times 7–9 μm , 1–4-septate; on <i>Miliusa</i> sp., India
	····· Passalora annonacearum
9*	Conidiophores much shorter and narrower, up to $80\times 6~\mu m$
10	Conidiophores solitary, arising from superficial hyphae; conidia 14.5–50 μ m long, up to 4-septate; on <i>Miliusa tomentosa</i> , India <i>Passalora miliusae</i>
10*	Conidiophores fasciculate, emerging through stomata; conidia 25–80 µm long, 3–8-septate; on <i>Annona</i> spp., Brazil
11(3)	Superficial mycelium present; conidiophores solitary as well as fasciculate, sometimes even in sporodochial conidiomata
11*	Superfical mycelium lacking; conidiophores consistently in loose to dense, almost sporodochial fascicles
12	Conidia very broad, $20-80\times 4-12~\mu m$, with $1-9$ transverse and occasionally $1(-2)$ oblique or longitudinal septa; on <i>Asimina triloba</i> , North America
	Pseudocercospora asiminae
12*	Conidia much narrower, up to 7 μm wide, only transversely septate
13	Conidiophores consistently solitary, arising from superficial hyphae, distinct fascicles lacking, $12-70\times3.5-5~\mu m$; conidia narrowly obclavate-cylindrical, $40-156\times2.5-3.5~\mu m$, $3-13$ -septate; on <i>Polyalthia suberosa</i> , India
13*	
14	Conidia very long and wide, $50-150\times 5-7$ µm, densely pluriseptate (6–18), hila 2.5–3.5 µm wide; conidiophores usually fasciculate, occasionally solitary, arising from superficial hyphae; on <i>Annona</i> spp. and <i>Rollinia</i> sp., Asia, West Indies, Central to South America <i>Pseudocercospora annonae</i>
14*	Conidia narrower, 1.5–6(–7) µm wide, up to 10-septate, hila narrower, 1–2.5 µm
15	Conidia 25–140 × 3–6(–7) μ m, very pale, mostly subhyaline; on <i>Asimina</i> spp.,
15*	North America
IJ	Conidia narrower, 1.5–4 µm, subhyaline to pale brown; on <i>Annona</i> and <i>Rollinia</i> spp

16	Superficial mycelium with solitary conidiophores abundant, fascicles of conidiophores variable, small and loose to rich and dense, occasionally in almost sporodochial conidiomata; apex of conidia obtuse in cylindrical conidia to subacute in obclavate conidia; on <i>Annona</i> spp. and <i>Rollinia mucosa</i> , Asia, West Indies, Central to South America <i>Pseudocercospora annonae-squamosae</i>
16*	Mycelium internal and external, but conidiophores in dense fascicles, solitary conidiophores lacking; apex of conidia obtuse; on <i>Annona purpurea</i> , Brazil
17(11	1)Conidiophores in sporodochial conidiomata; conidiogenous cells monoblastic, percurrent, with distinct annellations; conidia rough-walled
17*	Conidiogenous cells monoblastic to usually polyblastic, sympodial, annellations lacking; conidia smooth or almost so
18	Conidiophores 30–50 μm long, verruculose; conidia 40–120 \times 4.5–8 μm , obclavate-cylindrical; on <i>Annona senegalensis</i> , South Africa
18*	Pseudocercospora oblecta Conidiophores shorter, 5–20(–30) μm long, smooth; conidia narrower, 20–220 × 3.5–5 μm, cylindrical-vermiform; on Annona crassifolia, Brazil Pseudocercospora annonifolii
19(1)	7)Conidia broad, 5–8 μ m; conidiophores in small, \pm loose fascicles
19*	Conidia narrower, 2–5 µm; conidiophores usually numerous, in ± dense, often sporodochial fascicles
20	Conidiophores fasciculate, very long, 60–220 µm; conidia obclavate, 50–110 µm long, base obconically truncate; on <i>Annona senegalensis</i> and <i>Annona</i> sp., Africa, Asia <i>Pseudocercospora scitula</i>
20*	Conidiophores much shorter, up to 100 µm long, fasciculate, occasionally solitary, arising from superficial hyphae; conidia broadly acicular-obclavate, base truncate to slightly obconically truncate; on <i>Annona</i> spp. and <i>Rollinia</i> sp., Asia, West Indies, Central to South America <i>Pseudocercospora annonae</i>
21(19	9)Conidia subcylindrical-filiform to subacicular, 57.5–115 × 3.5–4.5 μm,
	hyaline; on Miliusa sp., India Pseudocercospora annonacea
21*	Conidia obclavate-cylindrical, narrower, 2–3 µm wide, olivaceous to olivaceous-brown
22	Conidia (30–)50–80(–100) µm long; mycelium internal and external; on <i>Annona montana</i> , Brazil <i>Pseudocercospora xenoannonicola</i>
22*	Conidia shorter, 30–65 µm long; mycelium consistently internal;
	on Xylopia aethiopica, Africa Pseudocercospora aethiopicae

Cercospora apii Fresen. s. lat. (sensu Crous & Braun 2003).

COMMENT: C. apii s. lat. (incl. C. canescens Ellis & G. Martin) has been recorded on Annona 'odorata' (Crous & Braun 2003).

Passalora annonacearum ['anonacearum'] A.N. Rai & Kamal,

Kavaka 14: 33, 1988 ['1986'].

ILLUSTRATION: Rai & Kamal (1988: 34, Fig. 2).

On Miliusa sp., Asia, India.

Passalora annonigena U. Braun & F.O. Freire,

Cryptog. Mycol. 23: 297, 2003 ['2002'].

ILLUSTRATION: Braun & Freire (2003: 298, Fig. 2).

On Annona sp., South America, Brazil.

Passalora isolonae (Siboe, P.M. Kirk & P.F. Cannon) U. Braun & Crous,

in Crous & Braun, *Mycosphaerella* and its anamorphs. 1. Names published in *Cercospora* and *Passalora*. CBS Biodiversity Series 1: 457, 2003.

■ Phaeoramularia isolonae Siboe, P.M. Kirk & P.F. Cannon, in Siboe et al., Sydowia 52(2): 299, 2000.

ILLUSTRATION: Siboe et al. (2000: 300, Fig. 6).

On Isolona cauliflora, Africa, Kenya.

Passalora miliusae U. Braun & Crous,

in Crous & Braun, *Mycosphaerella* and its anamorphs. 1. Names published in *Cercospora* and *Passalora*. CBS Biodiversity Series 1: 460, 2003.

■ Mycovellosiella indica P. Kumar & Kamal, Curr. Sci. 51: 846, 1982, non Passalora indica Kamal & P. Kumar, 1981.

ILLUSTRATION: Kumar & Kamal (1982: 846, Figs 1-2).

On Miliusa tomentosa, Asia, India.

Passalora xylopiae (Viégas & Chupp) U. Braun & Crous,

in Crous & Braun, *Mycosphaerella* and its anamorphs. 1. Names published in *Cercospora* and *Passalora*. CBS Biodiversity Series 1: 432, 2003.

■ Cercospora xylopiae Viégas & Chupp, in Viégas, Bol. Brasil. Agron. 8: 58, 1945.
LITERATURE: Chupp (1954: 46).

On Annona dioica and Xylopia grandiflora, South America, Brazil.

Phacellium annonae-cherimoliae, see above.

Pseudocercospora aethiopicae Deighton, Mycol. Pap. 140: 13, 1976.

Illustration: Deighton (1976: 14, Fig. 3).

On *Xylopia aethiopica*, Africa, Sierra Leone.

Pseudocercospora annonacea (Kamal, Narayan & R.P. Verma) U. Braun, Nova Hedwigia 58(1–2): 209, 1994.

≡ Cercoseptoria annonacea ['anonacea'] Kamal, Narayan & R.P. Verma, Indian Phytopathol.
39(3): 455, 1987 ['1986'].

= Pseudocercosporella miliusae M.D. Mehrotra & R.K. Verma, Mycol. Res. 95: 1168, 1991. LITERATURE: Braun (1995: 194).

ILLUSTRATION: Kamal et al. (1987: 455, Fig. 2).

On Miliusa velutina, Asia, India.

Pseudocercospora annonae U. Braun & Crous, in Braun et al.,

Feddes Repert. 113: 117, 2002.

≡ Cercospora annonae ['anonae'] A,S. Mull. & Chupp, Arq. Inst. Biol., Veg. Rio de Janeiro 1:
214, 1935, nom. inval.

LITERATURE: Chupp (1954: 45), Crous & Braun (2003: 59).

ILLUSTRATION: Braun et al. (2002: 115, Fig. 5).

On Annona cherimolia, A. muricata, A. reticulata, A. squamosa, Annona sp., Asia, West Indies, Central to South America (Brazil, Cuba, Guatemala, India, Panama, Philippines, Venezuela).

Pseudocercospora annonae-squamosae U. Braun & R.F. Castañeda,

in Castañeda & Braun, Cryptog. Bot. 1: 50, 1989. Fig. 4

- = Cercospora caracasensis Chupp & A.S. Mull., Bol. Soc. Venez. Ci. Nat. 8: 39, 1942, nom. inval.
- = Pseudocercospora annonicola Goh & W.H. Hsieh, in Hsieh & Goh, Cercospora and similar fungi from Taiwan: 22, 1990.

LITERATURE: Chupp (1954: 45), Vasudeva (1963: 67).

ILLUSTRATIONS: Vasudeva (1963: 68, Fig. 33), Castañeda & Braun (1989: 48, Fig. 19), Hsieh & Goh (1990: 22, Fig. 10).

MATERIAL EXAMINED: CUBA. Santiago de las Vegas, on living leaves of Annona squamosa, 29 Dec. 1987, R.F. Castañeda C87/376 (HAL 1650 F), holotype of P. annonae-squamosae. BRAZIL. State of Ceará, Paraipaba City, on living leaves of Annona cherimolia × squamosa, 19 May 2003, E. Cordoso (HAL 2219 F); State of Ceará, Pacajus County, on living leaves of Annona muricata, 19 Sep. 1999, F. Freire (HAL 2222 F); State of Pará, Amazonian Region, Belém City, on living leaves of Annona pygmaea, 30 Aug. 2003, L. Poltronieri (HAL 2220 F); State of Ceará, Pacajus County, on living leaves of Annona squamosa, 11 May 1999, F. Freire (HAL 2223 F); State of Ceará, Cascavel County, Preaoca District, on living leaves of Annona sp., 16 Mar. 2000, F. Freire (HAL 2224 F); State of Pará, Amazonian Region, Belém City, on living leaves of Rollinia mucosa, 28 Aug. 2003, L. Poltonieri (HAL 2221 F). VENEZUELA. Caracas, on living leaves of Annona purpurea, 1 Mar. 1938, A.S. Muller (CUP-VZ 2111), holotype of C. caracasensis.

On Annona atemoya, A. cherimolia × squamosa, A. muricata, A. purpurea, A. pygmaea, A. reticulata, A. squamosa, Annona sp., Rollinia mucosa, Asia, West Indies, central to South America (Brazil, Cuba, India, Japan, Panama, Taiwan, Venezuela).

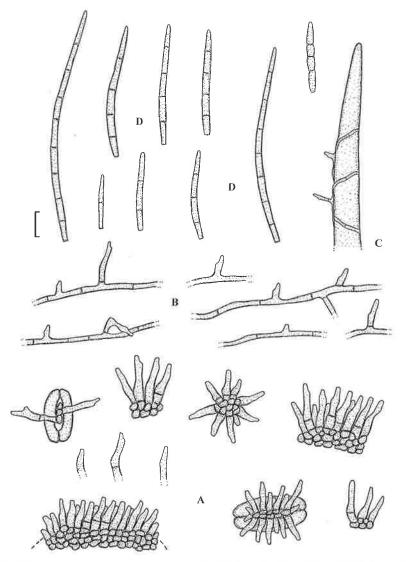


Fig. 4. *Pseudocercospora annonae-squamosae*. A. Conidiophore fascicles. B. Superficial hyphae with solitary conidiophores. C. Hyphae climbing a leaf hair. D. Conidia (A based CUP-VZ 2111, B–D based on type material. Scale bar = 10 µm. U. Braun *del*.

COMMENTS: With regard to the formation of solitary and fasciculate conidiophores, *P. annonae-squamosae* is rather polymorphous. Relatively large, dense, sometimes almost sporodochial fascicles of conidiophores with well-

developed stromata, are usually epiphyllously formed, whereas on the lower leaf side the conidiophores are usually solitary arising from superficial hyphae, and only arranged in smaller fascicles with lacking or small stromata. The development of superficial hyphae with solitary conidiophores on the one hand and well-developed fascicles on the other hand is rather variable. Superficial mycelium may be sparsely developed in some collections, as for instance in the type material of C. caracasensis, and well-developed conidiophore fascicles may be lacking in other specimens, as in the holotype of this species. Therefore, the following redescription of this species based on a wider range of collections on various host species is necessary in order to demonstrate its variability: LEAF SPOTS amphigenous, subcircular to angular-irregular, 1-30 mm diam., occasionally confluent, reddish brown, medium to dark or blackish brown, later often grayish brown to dingy gray, finally sometimes grayish white, often vein-limited, margin indefinite or with a darker marginal line. CAESPITULI amphigenous, on the upper side conspicuous, punctiform, scattered, dark brown to blackish, but soon turning grayish by abundant conidial formation, on the lower leaf surface subeffuse and less conspicuous, dingy grayish olivaceous to olivaceous-brown. Mycelium internal and external; superficial hyphae variable, ranging from almost lacking to well-developed, usually hypophyllous, emerging through stomata, occasionally climbing leaf hairs, branched, septate, 1-3.5 μm wide, thin-walled, pale olivaceous to olivaceousbrown, smooth. Stromata almost lacking to well-developed, above all on the upper side, 10–80 μm diam., substomatal to intraepidermal, olivaceous-brown. CONIDIOPHORES in small, loose to large and dense, almost sporodochial fascicles, arising from internal hyhae or stromata, emerging through stomata or erumpent, and solitary, arising from superficial hyphae, lateral, rarely terminal (on the upper side usually in well-developed, sometimes almost sporodochial fascicles, on the lower side in small, loose fascicles and solitary, arising from superficial hyphae), erect, straight, subcylindrical, conical to distinctly geniculate-sinuous, usually unbranched, 5–30(–45) \times 2–4(–5) μ m, 0-1(-2)-septate, subhyaline to pale olivaceous or olivaceous-brown, medium olivaceous-brown in mass, thin-walled, smooth. Conidiogenous cells integrated, terminal or conidiophores reduced to conidiogenous cells, 5-20 μm long; conidiogenous loci inconspicuous to subconspicuous by being truncate or subdenticulate, but always unthickened and not darkened. Conidia solitary, narrowly obclavate-cylindrical, (15-)20-75(-85) × (1.5-)2-4(-5) μm, (1-)2-6 (-8)-septate, occasionally slightly constricted at the septa, subhyaline to pale olivaceous, thin-walled, smooth, apex obtuse, above all in cylindrical conidia, to subacute, above all in obclavate conidia, base short obconically truncate, 1-2 um wide, hila unthickened, neither darkened nor refractive.

Pseudocercospora annonarum, see above.

Pseudocercospora annonifolii (Bat. & Peres) U. Braun & O.F. Freire,

in Braun, Bibl. Lichenol. 86: 82, 2003.

= Cercospora annonifolii Bat, & Peres, Anais do XIII Congresso da Sociedad Botânica do Brasil: 374, 1964 ['1962'].

Illustration: Braun (2003: 93, Fig. 4).

On Annona crassifolia, South America, Brazil.

Pseudocercospora asiminae (Ellis & Morgan) U. Braun & Crous, comb. nov. MycoBank, MB 511860.

Bas: Phloeospora ['Phleospora'] asiminae Ellis & Morgan, in Martin, J. Mycol. 3: 88, 1887.

- = Rhopaloconidium asiminae (Ellis & Morgan) Petr., Sydowia 6: 301, 1952.
- Miuraea asiminae (Ellis & Morgan) Arx & Constant., in Arx, Proc. Kon. Ned. Akad. Wetensch., C 86: 39, 1983.
- = Cercospora asiminae Ellis & Kellerm., J. Mycol. 3: 103, 1887.
- Centrospora asiminae (Ellis & Kellerm.) Deighton, Mycol. Pap. 124: 5, 1971
- = Mycocentrospora asiminae (Ellis & Kellerm.) Deighton, Taxon 21: 716, 1972. Literature: Chupp (1954: 45), Braun (1995: 223), Crous & Braun (2003: 68). Illustration: Braun (1995: 222, Fig. 211a).

On Asimina parviflora, 'A. obtusa' and A. triloba, North America, USA.

COMMENTS: Based on a re-examination of type material of Phloeospora asiminae and Cercospora asiminae, Braun (1995) confirmed that the two taxa are conspecific and, due to the occurrence of some conidia with oblique or longitudinal septa, followed Arx & Constantinescu (in Arx 1983) in placing this species in Miuraea Hara. The latter genus is insufficiently known and undoubtedly heterogeneous (Braun 1995). Cultures and molecular sequence analyses of M. degenerans (Syd. & P. Syd.) Hara, the type species, are not yet available. This species is characterized by having pigmented, thick-walled, $dictyos porous conidia. \it Miuraea per sicae (Sacc.) Hara is a color less \it My cosphaerella \it Miuraea per sicae (Sacc.) Hara is a color less \it My cosphaerella \it Miuraea per sicae (Sacc.) Hara is a color less \it My cosphaerella \it Miuraea per sicae (Sacc.) Hara is a color less \it My cosphaerella \it Miuraea per sicae (Sacc.) Hara is a color less \it My cosphaerella \it Miuraea per sicae (Sacc.) Hara is a color less \it My cosphaerella \it Miuraea per sicae (Sacc.) Hara is a color less \it My cosphaerella \it Miuraea per sicae (Sacc.) Hara is a color less \it My cosphaerella \it Miuraea per sicae (Sacc.) Hara is a color less \it My cosphaerella \it Miuraea per sicae (Sacc.) Hara is a color less \it My cosphaerella \it Miuraea per sicae (Sacc.) Hara is a color less \it My cosphaerella \it Miuraea per sicae (Sacc.) Hara is a color less \it My cosphaerella \it Miuraea per sicae (Sacc.) Hara is a color less \it My cosphaerella \it Miuraea per sicae (Sacc.) Hara is a color less \it My cosphaerella \it Miuraea per sicae (Sacc.) Hara is a color less \it My cosphaerella \it Miuraea per sicae (Sacc.) Hara is a color less \it My cosphaerella \it Miuraea per sicae (Sacc.) Hara is a color less \it My cosphaerella \it Miuraea per sicae (Sacc.) Hara is a color less \it My cosphaerella \it Miuraea per sicae (Sacc.) Hara is a color less \it My cosphaerella \it Miuraea per sicae (Sacc.) Hara is a color less \it My cosphaerella \it Miuraea per sicae (Sacc.) Hara is a color less \it My cosphaerella \it Miuraea per sicae (Miuraea per sicae (Miu$ anamorph probably closely related to the genus Pseudocercosporella Deighton. The fungus on Asimina species is, however, better placed in Pseudocercospora. The conidiophores are formed singly, arising from superficial hyphae, as well as fasciculate, pigmented, with unthickened, neither darkened nor refractive conidiogenous loci. The conidia are only slightly thickened, transversely septate, only occasionally with 1(-2) oblique or longitudinal septa (Braun 1995). The formation of oblique or longitudinal septa in conidia of Pseudocercospora is unusual, but may occur, even in P. vitis (Lév.) Speg. (Deighton 1976), the type species, i.e. this feature does not exclude this cercosporoid Asimina species from the latter genus.

Pseudocercospora asiminae-pygmaeae U. Braun, A monograph of Cercosporella, Ramularia and allied genera (phytopathogenic hyphomycetes), Vol. 1: 223, 1995. Illustration: Braun (1995: 222, Fig. 211b).

On Asimina angustifolia, A. incana and A. pygmaea, North America, USA.

Pseudocercospora oblecta (Syd.) Crous & U. Braun, comb. nov.

Мусованк МВ 511861.

Bas.: Cercospora oblecta Syd., Ann. Mycol. 33: 235, 1935.

≡ Stigmina oblecta (Syd.) Crous & U. Braun, Mycotaxon 57: 285, 1996.

Literature: Chupp (1954: 45).

Illustration: Crous & Braun (1996: 286, Fig. 8).

On Annona senegalensis, South Africa.

COMMENTS: On account of rather coarse conidiophores with percurrently proliferating conidiogenous cells, Crous & Braun (1996) assigned C. oblecta to the genus Stigmina Sacc. in the broad sense of Ellis (1971, 1976). The conidiogenous loci in this species are pseudocercospora-like, i.e. unthickened and non-pigmented. Braun (1993) introduced the genus Cercostigmina U. Braun for stigmina-like Mycosphaerella anamorphs with thin-walled, euseptate, scolecosporous conidia, which was later reduced to synonymy with Pseudocercospora based on a molecular and morphological reassessment (Crous & Braun 2003). Scolecostigmina U. Braun (Braun et al. 1999) was proposed for similar anamorphs with coarse, thick- and often rough-walled conidiophores formed in sporodochial conidiomata and relatively broad conidia, with slightly thickened, relatively dark conidia. The status of this genus is unclear. Cultures of the type species and molecular sequence analyses are not yet available. But most species assigned to this genus are probably Mycosphaerella anamorphs that should better be accommodated in Pseudocercospora. Crous et al. (2006) demonstrated that even Stigmina platani (Fuckel) Sacc., the type species of Stigmina, characterized by having phragmosporous, distoseptate conidia, represents a Mycosphaerella anamorph clustering in the Pseudocercospora clade. Braun & Crous (2006) proposed to conserve Pseudocercospora against Stigmina and Phaeoisariopsis. Cercospora oblecta is morphologically similar to Pseudocercospora annonifolii.

Pseudocercospora polyalthiae J.M. Yen, A.K. Kar & B.K. Das,

Mycotaxon 16(1): 43, 1982.

Illustration: Yen et al. (1982: 44, Fig. 4 E–G).

On Polyalthia suberosa, Asia, India.

Pseudocercospora xenoannonicola Crous & Bench.,

in Crous et al., Sydowia 52(2): 88, 2000.

Illustration: Crous et al. (2000: 87, Fig. 10).

On Annona montana, South America, Brazil.

Stenella annonaceae, see above.

Stenella polyalthiae ['polylathiae'] S. Chaudhary, N. Sharma & Kamal,

Indian Phytopathol. 55(1): 58, 2002.

Illustration: Chaudhary et al. (2002: 58, Fig. 2).

On Polyalthia suberosa, Asia, India.

Acknowledgements

Thanks are due to the curators of the herbaria CUP and W for the possibility to examine type material in their keeping. We are much obliged to Chiharu Nakashima, Mie University, Japan, and Roland Kirschner, J. W. Goethe University Frankfurt a. M., Germany, for providing presubmission reviews.

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