

## Taxonomic problems of the *Ramularia/Cercospora* complex

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A generic concept for the *Ramularia/Cercospora* complex is proposed, based upon pigmentation, structure of caespituli, conidial scars, and conidial formation. The genera *Ramularia*, *Cercospora*, *Pseudocercospora*, *Theclonia*, and *Phacellium* are discussed and described in detail. A key to the discussed and some related genera is added.

Key words: *Ramularia/Cercospora* complex, generic concept, key

The *Ramularia/Cercospora* complex (Hyphomycetes) comprises genera with colourless conidiophores and conidia. They are anamorphs of *Mycosphaerella* (Ascomycetes). The delimitation and circumscription of some genera are still debated and cause taxonomic problems. As a solution a generic concept is presented. As a rule closely allied genera with either colourless or coloured conidiophores and conidia are not to be merged (the traditional, well established limits between such genera would be dropped). All genera of the *Ramularia/Cercospora* complex have 'coloured counterparts' within the *Cercospora* complex (*Ramularia/Phaeoramularia* and *Mycovellosiella*; *Cercospora/Cercospora*; *Pseudocercospora/Pseudocercospora*, incl. *Cercoseptoria*; *Phacellium/Phaeoisariopsis* and *Tandonella*). The main characteristics for generic delimitation include structure of the caespituli (fasciculate/synnematous), structure of the conidial scars (thickened, conspicuous/unthickened, obscure), and conidial formation (in connection with conidial shape and septation).

### The recognized genera

#### 1. *Ramularia* emend. U. Braun

***Ramularia*** Unger, Die Exantheme der Pflanzen, p. 169, Wien 1833 emend. U. Braun (to be proposed as nom. cons.) [non Roussel 1806, Algae].

*Didymaria* Corda, Anleit. Stud. Mycol., p. 32, Prag, 1842.

*Septocylindrium* Bon., Handb. allg. Mykol., p. 35, Stuttgart, 1851 (nom. inval.).

*Septocylindrium* Bon. ex Sacc., Michelia 2: 15. 1880.

*Acrotheca* Fuckel, Jb. Ver. Naturk. Nassau 15: 43. 1860.

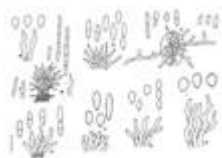
*Ovularia* Sacc., Michelia 2: 17. 1880.

*Ophiocladium* Cav., Z. Pflkrh. 3: 26. 1893. [p. 66]

*Pseudovularia* Speg., An. Mus. Nac. B. Aires 20: 418. 1910.

*Tretovularia* Deighton, Trans. Br. mycol. Soc. 82: 743. 1984.

*Mycovellosiella* sensu Deighton (1974, 1979) p.p.



**Fig. 1.**

Different species of *Ramularia*, conidiophores, fascicles, conidia.

A. *Ramularia pusilla* Unger,

B. *R. trollii* Ivanov,

C. *R. arachidis* Bond.-Mont.,

D. *R. buniadis* Vest.,

E. *R. cardui-personatae* Höhnelt,

F. *R. compacta* (Ellis & Everh.) U. Braun,

G. *R. daronici* Pass. & Thümen,

H. *R. pseudoglobosa* U. Braun.

U. Braun del., scale bar = 20 µm.

Lectotype species: *Ramularia pusilla* Unger.

Phytoparasitic, mostly causing leaf spots, sometimes chlorosis, or without visible symptoms, occasionally saprophytic; vegetative hyphae immersed in the host tissue, septate, hyaline to faintly coloured, sometimes with internal primary mycelium and superficial-aerial secondary mycelium, internal mycelium often forming stroma-like hyphal aggregations, especially in the sub-stomatal cavities; conidiophores solitary, arising from the superficial hyphae, or mostly fasciculate, arising through stomata, from the inner hyphae or stomata, rarely erumpent through the epidermis; conidiophores straight to geniculate–sinuous, continuous or septate, hyaline (rarely faintly coloured at the base in species with coloured stromata, very rarely with a faint greenish tinge throughout), simple or occasionally branched; conidiogenous cells integrated, sympodially elongating, polyblastic, cicatrized, conidial scars conspicuous, small, refractive, mostly slightly thickened; conidia formed singly or catenulate, sometimes in branched chains, solitary conidia 0–1-septate, mostly ellipsoid–ovoid to subglobose, catenate conidia aseptate to multiseptate, mostly 0–4-septate, usually ellipsoid, cylindrical, fusiform, rarely filiform, occasionally constricted at the septa, smooth to verruculose–echinulate, hilum distinct, usually slightly [p. 67] thickened, refractive, darkened; teleomorphic states belonging to *Mycosphaerella* ([Fig. 1](#)).

The complicated history of *Ramularia* was discussed by Hughes (1949), Braun (1988a), and Sutton and Waller (1988). Unger (1833) described *Ramularia* with two original species, *R. pusilla* and *R. didyma*. A type species was not indicated. *R. pusilla* was later selected by Unger (1836) as lectotype (Hughes, 1949). Corda (1842) described *Didymaria*, with *R. didyma* Unger as the only species of his new genus, and emended the circumscription of *Ramularia* with *R. pusilla* as the only species. This treatment must be considered as indirect typification agreeing with Unger's intentions. Unger's original material is not preserved. Therefore, Braun (1988a) proposed the following lectotypification: *R. pusilla* Unger, lectotype – Unger (1833, pl. II, fig. 12), original drawing, type host, *Poa nemoralis*. Clements and Shear (1931) suggested *R. urticae* Ces. as neotype and Von Arx (1970, 1983) proposed a third typification (lectotype = *R. didyma* Unger). These neotypifications have no justification because they do not conform to Art. 8.1 of the Code.

Saccardo (1880) redescribed *Ramularia* and introduced the new genus *Ovularia* with two original species, *O. sphaeroidea* (Sacc.) Sacc. and *O. obovata* (Fuckel) Sacc. (the lectotype species, cf. Oudemans 1883). Saccardo (1886) emended the generic circumscription of *Ovularia* and included the lectotype species of *Ramularia*. He published the combination *O. pusilla* (Unger) Sacc. but described this species on *Alchemilla*. Saccardo & D. Saccardo (1906) proposed the combination *O. pusilla* (Unger) Sacc. & D. Sacc. for the fungus on *Poa nemoralis* (superfluous combination). As no convincing criteria are available to separate the taxa *pusilla* and *obovata* generically, *Ramularia* is the correct name for *Ovularia* sensu Saccardo. *Didymaria* Corda is applicable to the '*Ramularia* group' sensu Saccardo. Subramanian (1971) used *Ramularia* in the correct sense and reintroduced *Septocylindrium* Bon. ex Sacc. for *Ramularia* sensu Sacc.

The genera *Ramularia*, *Didymaria* and *Ovularia* cannot be upheld as separate genera (e.g. Hughes, 1949; Nannfeldt, 1950; Savile, 1957; Hughes, 1958; Gunnerbeck, 1967; Hawksworth, 1980; Poelt, 1983; Braun, 1988a; Sutton and Waller, 1988). Several concepts have been applied to *Ovularia*. Originally, it only comprised species with aseptate conidia produced singly. Saccardo (1886) and many subsequent authors referred to *Ovularia* species with aseptate conidia either formed singly or in chains. Von Arx (1983) put special emphasis on conidial formation and included species with 1- and 2-celled conidia, but always produced singly. The distinction between *Ramularia* and *Ovularia* was based on three main characteristics, viz. conidial formation (formed singly or in chains), septation, and conidial

shape. There are, however, very numerous intermediates between all versions of *Ramularia* and *Ovularia* (Hughes, 1949; Braun, 1988a; Sutton and Waller, 1988).

The following genera are considered synonyms of *Ramularia* because their type species belong to *Ramularia*: [p. 68]

*Septocylindrium* Bon. ex Sacc. (Subramanian, 1971; Braun, 1988a)

Type species: *Ramularia septata* (Bon.) Bubák (= *Cylindrium septatum* Bon., *Septocylindrium bonordenii* Sacc., *Septocylindrium septatum* (Bon.) Pound, *Ramularia bonordenii* (Sacc.) Höhnel). Saccardo (1886) reduced *Tapeinosporium* Bon. (Bot. Ztg. 11: 285. 1853) to synonymy with *Septocylindrium*. Various authors followed this treatment (e.g. Subramanian, 1971; Carmichael *et al.*, 1980; Hawksworth *et al.*, 1983), but *Tapeinosporium* Bon. (nom. dub.), described from potato tubers, is not congeneric with *Septocylindrium*.

*Acrotheca* Fuckel (Hughes, 1958; Braun, 1988a)

Type species: *Acrotheca gei* Fuckel (= *Ramularia gei*). Hughes (1958) investigated type material of *A. gei* and stated that this species belongs to *Ramularia*. I have examined original material of *A. gei*, distributed by Fuckel in *Fungi rhen.*, Suppl., Fasc. VIII, No. 2229 (ex herb. HAL) and can confirm his observations.

*Ophiocladium* Cav. (Braun, 1988a; Sutton and Waller, 1988)

Type species: *Ophiocladium hordei* Cav. (= *Ramularia collo-cygni* Sutton & Waller). Sprague (1946) referred the type species of *Ophiocladium* to *Ovularia*.

*Pseudovularia* Speg. (Deighton, 1972; Braun, 1988a)

Type species: *Pseudovularia trifolii* Speg. (= *Ramularia argentinensis* Deighton). Clements & Shear (1931) cited *Pseudovularia* as synonym of *Ovularia*.

*Tretovularia* Deighton (Braun, 1990)

Type species: *Tretovularia villiana* (Magnus) Deighton (= *Ovularia villiana* Magnus, *Ramularia villiana* (Magnus) Nannf.). This genus was introduced for *Ovularia villiana* Magnus. Deighton (1984) distinguished his new genus from *Ramularia* by polytretic conidiogenous cells and by the unthickened hilum of the conidia. Most *Ramularia* (incl. *Ovularia*) species with subglobose conidia resemble *Tretovularia villiana* in these features (e.g. *Ramularia viciae* (Frank) Sacc., *R. schwarziana* (Magnus) Gunnerb., *R. sphaeroidea* Sacc., *R. tuberculiformis* (Höhnel) U. Braun, *R. vogeliana* (Sacc. & Sydow) U. Braun, etc.). The conidial hilum is, indeed, unthickened or hardly thickened, but it is refractive and conspicuous. Conidiogenesis in *R. villiana* and in numerous morphologically closely related species has not been studied in detail. Additional investigations, especially in culture, are urgently needed. Therefore, at present I prefer to include *Tretovularia* in *Ramularia*.

Braun (1990) discussed the relationship between *Ramularia* and *Mycovellosiella*. Deighton (1974, 1979) included some *Ramularia* species with superficial hyphae in *Mycovellosiella*. Deighton (1979, p. 14) stated: 'It may be more convenient to separate the colourless species into a distinct genus or subgenus, but for the present I prefer not to do so ...'. *Mycovellosiella* is a genus for species with coloured superficial hyphae and conidiophores and should not be lumped with similar *Ramularia* species (Ellis, 1971; Von Arx, 1983). *Ramularia* species with external hyphae are not uncommon and they usually are included in the generic circumscription (e.g. Von Arx, 1983; Braun, 1988a). The conidiogenesis, structure of the conidiophores, conidial scars, and conidia agree perfectly with *Ramularia*. There are intermediates between 'typical' *Ramularia* species with internal mycelium and fasciculate conidiophores and *Ramularia* species with superficial hyphae (Braun, 1990). Therefore, the introduction of a new genus for 'Mycovellosiella-like' *Ramularia* species would hardly be tenable and I prefer to maintain those species in *Ramularia*. [p. 68]

There are *Ramularia*-like species with synnematosus conidiophores. They are excluded (cf. *Phacellium* below). *Ramularia* (*Ovularia*)-like species on lichens are not congeneric and must be excluded (Braun, 1988a). *Ovularia peltigerae* Keissler belongs to *Refractohilum* [*R. peltigerae* (Keissler) D. Hawksw.], and *Ramularia peltigericola* D. Hawksw. was transferred

to the new genus *Hawksworthiana* U. Braun (1988a, p. 276). Braun (1990) discussed the distinction between *Ramularia* and *Cercosporiella*. The conidia of *Cercosporiella* are formed singly, they are long, *Cercospora*-like, and multiseptate. Long, multiseptate conidia in *Ramularia* are always catenate. Solitary *Ramularia* conidia are ellipsoid-ovoid to subglobose and only 0–1-septate. Furthermore, there are obvious differences in the structure of the conidial scars (Deighton, 1973). *Ramulariopsis* Speg. (cf. Deighton, 1972, 1974) is very similar to *Ramularia*, but it differs by conidiophores with terminal as well as lateral conidiogenous cells. The lateral ones are short patent branches.

## 2. *Cercosporiella* Sacc. emend. Deighton

***Cercosporiella*** Sacc., *Michelia* 2(6): 20. 1880, emend. Deighton (1973).

Lectotype species: *Cercosporiella cana* (Sacc.) Sacc. [= *C. virgaureae* (Thümen) Allescher]



**Fig. 2.**

Other genera, conidiophores, fascicles (synnema in B), conidia.

A. *Cercosporiella virgaureae* (Thümen) Allescher,

B. *Phacellium alborosellum* (Desm.) U. Braun,

C. *Thedgonia pavoniae* (Deighton) U. Braun,

D. *Thedgonia ligustrina* (Boerema) B. Sutton,

E. *Pseudocercosporiella capsellae* (Ell. & Ev.) Deighton,

F. *Pseudocercosporiella trollii* (Sacc. & Winter) U. Braun.

U. Braun del., scale bar = 20 µm. [p. 71]

Phytoparasitic, mostly causing leaf spots; vegetative hyphae internal, septate, colourless to faintly coloured, often forming substomatal stromata, composed of hyaline to olivaceous hyphae, rarely with a secondary superficial mycelium; conidiophores usually fasciculate, arising through stomata from the inner mycelium or from the stromata, straight and subcylindric to geniculate–sinuous, aseptate to septate, hyaline, rarely faintly coloured at the very base or with a faint greenish tinge throughout; conidiogenous cells integrated, polyblastic, sympodial, cicatrized, old conidial scars conspicuous, thickened, colourless, refractive, the thickening extending beyond the area originally occupied by the base of the conidium; conidia formed singly, hyaline, occasionally faintly greenish, usually subcylindric to obclavate, sometimes fusiform, 1- to pluriseptate, apex obtuse, base narrowed, rounded or truncate, hilum mostly slightly thickened, refractive ([Fig. 2A](#)).

Deighton (1973) redescribed *Cercosporiella* and excluded species with unthickened, obscure conidial scars. He discussed and described the structure of the conidial scars and the conidiogenesis in detail. Braun (1990) discussed the differentiation between *Cercosporiella* and *Ramularia*. *Cercosporiella* in general appearance resembles *Cercospora*, but the latter genus is distinguished by coloured conidiophores and the conidial scars are more conspicuously thickened.

## 3. *Pseudocercosporiella* Deighton emend. U. Braun

***Pseudocercosporiella*** Deighton, *Mycol. Pap.* 133: 38, 1973, emend. U. Braun

*Cercosporiella* auct. p.p.

*Cylindrosporium* auct. p.p.

*Cercoseptoria* auct. p.p.

Type species: *Pseudocercosporiella ipomoeae* Deighton

Phytoparasitic, mostly causing leaf spots; vegetative hyphae internal, colourless to faintly coloured; stromata absent to well developed, substomatal, intraepidermal, large stromata often rupturing the stomata and cells, sometimes erumpent, hyaline to faintly coloured; conidiophores (or conidiogenous cells) solitary to fasciculate, emerging through stomata or erumpent through the cuticle, arising from the inner hyphae or stromata, hyaline (sometimes faintly greenish), continuous or with a few septa, usually very short; conidiogenous cells integrated, sympodial, polyblastic, conidial scars inconspicuous, unthickened, \*+ truncate, conidia formed singly, \*+ cylindrical, filiform, slightly obclavate, pluriseptate, hyaline, with a truncate, unthickened hilum ([Fig. 2 E, F](#)).

Deighton (1973) described the new genus *Pseudocercosporella*, characterized by unthickened, inconspicuous conidial scars. He transferred several species of *Cercosporella* and *Cylindrosporium* (sensu Sacc.). Petrak (1925) introduced the generic name *Cercoseptoria* (nom. nov. for *Septoriopsis* [p. 71] Stev. & Dalbey) and referred various species with hyaline conidiophores and conidia to it, although the type species of this genus is characterized by coloured structures. *Cercoseptoria* is, indeed, close to *Pseudocercosporella* and Von Arx (1983) merged both genera. But genera with colourless and coloured structures should not be lumped. *Cercoseptoria* is hardly separable from *Pseudocercospora* and should be reduced to synonymy with the latter genus (Deighton, 1987).

Deighton (1973) included two species in *Pseudocercosporella* with catenulate conidia, often in branched chains. The conidia often possess short, protuberant lateral branchlets. These species do not match the generic concept of *Pseudocercosporella* very well. I prefer to confine *Pseudocercosporella* to species with solitary conidia. *Theadgonia* B. Sutton, discussed below, is an appropriate genus for related species with catenulate conidia.

#### 4. *Theadgonia* B. Sutton emend. U. Braun

***Theadgonia*** B. Sutton, Trans. Br. mycol. Soc. 61: 426. 1973, emend. U. Braun.

Syn.: *Cercoseptoria* sensu Von Arx (1981, 1983) p.p.

Type species: *Theadgonia ligustrina* (Boerema) B. Sutton

Phytoparasitic, causing leaf spots; mycelium internal, colourless to faintly coloured, greenish; stromata usually well developed, substomatal; conidiophores fasciculate, arising from the stromata, subcylindric, straight to curved, geniculate–sinuous, simple or branched at the base, aseptate to septate, hyaline or almost so (faintly greenish), smooth; conidiogenous cells integrated, terminal, polyblastic, sympodial, conidial scars flat or inconspicuous, unthickened; conidia in simple or branched chains, \*+ cylindrical, hyaline, sometimes faintly greenish, septate, disarticulating or intact; conidia from branched chains often with short, lateral, protuberant branchlets, hilum \*+ truncate, unthickened ([Fig. 2 C, D](#)).

Von Arx (1981, 1983) reduced *Theadgonia* to synonymy with *Cercoseptoria*. This treatment was not accepted by Deighton (1983). *Cercoseptoria* is congeneric with *Pseudocercospora* (Deighton, 1987; Braun, 1988b). The conidia of *Pseudocercosporella* species are formed singly. *Theadgonia* is characterized by catenulate conidia. *Pseudocercosporella dioscoreae* Deighton and *P. pavoniae* Deighton resemble *Theadgonia*. The conidia are produced in chains and the conidial scars are unthickened and flat. The conidial chains are often branched, the conidia frequently possess short, protuberant, lateral branchlets and the conidiophores are mostly simple, only rarely branched at the base. Nevertheless, I prefer to transfer these species to *Theadgonia*. A new genus would hardly be tenable.

***Theadgonia dioscoreae*** (Deighton) U. Braun, *comb. nov.*

Basionym: *Pseudocercosporella dioscoreae* Deighton, Mycol. Pap. 133: 49. 1973. [p. 72]

***Thedgonia pavoniae*** (Deighton) U. Braun, *comb. nov.*

Basionym: *Pseudocercospora pavoniae* Deighton, Mycol. Pap. 133: 50–51. 1973.

## 5. *Phacellium* Bon. emend. U. Braun

***Phacellium*** Bonorden, in Rabenh., Fungi eur. exs., ed. nov., ser. 2, cent. III, No. 288, Dresden 1860 (with description!) and Bot. Ztg. 19: 203, 1861, emend. U. Braun.

Syn.: *Isariopsis* Fres., Beitr. Mykol. 3: 87–88. 1863, type species *I. pusilla* Fres.

*Ramulaspera* Lindr., Acta Soc. Fauna Fl. Fenn. 22: 5. 1902, type species *Ovularia salicina* Vesterg.

*Isariopsella* Höhnelt, Ber. dt. bot. Ges. 35: 357. 1917, type species *Ramularia vossiana* Thümen.

Type species: *Phacellium dishonestum* Bon. = *Ph. alborosellum* (Desm.) U. Braun (1990).

Phytoparasitic, mostly causing leaf spots; mycelium internal, colourless or faintly coloured, often forming stromata in the substomatal cavities, colourless to faintly coloured; conidiophores macronematous, synnematous, individual conidiophores simple, rarely branched, continuous to septate, hyaline or almost so, apically and partly laterally splaying out; synnemata at first hyaline, later coloured, at least in the lower part, yellowish, yellowish-brown, brown, reddish-brown, flesh-coloured; free ends of the conidiophores hyaline; conidiogenous cells integrated, terminal, polyblastic, sympodial, cicatrized, scars conspicuous, small, somewhat thickened, refractive; conidia formed singly or catenate, sometimes in branched chains, 0–1-septate, hyaline, smooth to verruculose, shape variable, ellipsoid–ovoid, fusiform, subcylindric, subglobose, irregular, hilum conspicuous, often slightly thickened, refractive ([Fig. 2B](#)).

Some *Ramularia*-like fungi are well characterized by synnematous conidiophores. The individual conidiophores are colourless or almost so, but the synnemata are always coloured, at least in the lower part. The conidia are colourless, solitary or catenate, 0–1-septate. *Isariopsis* Fres. has often been used to accommodate this group of synnematous *Ramularia*-like fungi. Braun (1988b) discussed and redescribed this genus. Braun (1990) discussed the nomenclature of *Phacellium* and *Isariopsis* and reintroduced the older, valid name *Phacellium*. Various authors proposed to reduce *Isariopsis* to synonymy with *Ramularia* (e.g. Gunnerbeck, 1967; Gjaerum, 1968), but the latter genus can be clearly distinguished from *Isariopsis* (= *Phacellium*) by fasciculate, free conidiophores, separated from base to apex. They are neither tightly adpressed nor fused. [p. 73]

Key to the genera of the *Ramularia/Cercospora* complex and some related genera with hyaline conidiophores and conidia

1. Lichenicolous, on *Peltigera*; conidiophores ampulliform, solitary; stroma-like structures absent *Hawksworthiana* U. Braun
- 1\*. On host plants of the Pteridophyta and Spermatophyta, with other features 2
2. Conidiophores synnematous; synnemata at first hyaline, later coloured in the lower half, free ends of the individual conidiophores hyaline, cicatrized; conidia formed singly or in chains, 0–1-septate, hyaline, mostly verruculose *Phacellium* Bon.
- 2\*. Conidiophores solitary or fasciculate, not synnematous, neither tightly adpressed nor fused 3

- |     |  |                                     |
|-----|--|-------------------------------------|
| 3.  | Conidia in chains  | 4                                   |
| 3*. | Conidia formed singly  | 6                                   |
| 4.  | Conidial scars flat or inconspicuous, unthickened; conidia in simple chains, disarticulating, or in branched chains, conidia often with short, protuberant, lateral branchlets   | <i>Thedegonia</i> B. Sutton         |
| 4*. | Conidial scars conspicuous, small, thickened, refractive   | 5                                   |
| 5.  | Mycelium internal, some species also with external secondary mycelium; conidiophores fasciculate or solitary, arising from superficial hyphae; conidiogenous cells integrated, terminal  | <i>Ramularia</i> Unger              |
| 5*. | Mycelium internal; conidiophores fasciculate, simple to branched; conidiogenous cells integrated, terminal and intercalary, as short lateral branches<br><br>(hardly separable from <i>Ramularia</i> and perhaps congeneric)   | <i>Ramulariopsis</i> Speg           |
| 6.  | Conidial scars conspicuous, thickened, refractive  | 7                                   |
| 6*. | Conidial scars inconspicuous, unthickened  | 8                                   |
| 7.  | Conidia ± ellipsoid–ovoid to subglobose, 0–1-septate; scars small, slightly thickened, refractive  | <i>Ramularia</i> Unger              |
| 7*. | Conidia subcylindric, obclavate, long, 'Cercospora-like', pluriseptate; scars usually conspicuously thickened, the thickening extending beyond the area originally occupied by the base of the conidium  | <i>Cercosporella</i> Sacc.          |
| 8.  | Mycelium internal and external, superficial; conidiophores with broad, flat scars, hyaline, conidia very long, obclavate, multiseptate, rostrate, base truncate, broad, unthickened, hyaline or central cells fairly thick-walled and coloured; conidia often with appendage-like branches at the base | <i>Mycocentrospora</i> Deighton     |
| 8*. | Mycelium internal; conidia without thick-walled, coloured central cells  | 9                                   |
| 9.  | Parasitic on Poaceae; conidia often with some lateral branches; conidiogenous cells often with protuberant scars   | <i>Ramulispora</i> Miura            |
| 9*. | Parasitic on Dicotyledons; conidia unbranched;   | <i>Pseudocercosporella</i> Deighton |

conidiogenous cells with non-protuberant scars

[p. 74]

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