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Two leaf pathogens of *Ribes* spp. in North America, *Quasiphloeospora saximontanensis* and *Phloeosporella ribis*

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The generic name *Quasiphloeospora*, type species *Q. saximontanensis* comb. nov., is introduced for a species associated with foliar lesions on the forest weed *Ribes viscosissimum* and other species of *Ribes*. It is compared with similar genera and species of hyphomycetes and coelomycetes, especially *Phloeosporella ribis* comb. nov. with which it has been confused.

Competing weeds in the forest renewal sites of British Columbia (B.C.) are important reservoirs of plant pathogenic fungi. Traditionally, chemical herbicides, manual cutting and controlled burning have been used to control the growth of forest weeds, but increasing public opposition to these methods has caused much research to be directed toward development of biological control agents (mycoherbicides) (Dorworth, 1990; Wall & Shamoun, 1990; Wall, Prasad & Shamoun, 1992).

In the summer of 1993, the junior author (S.F.S.) and his colleagues at the Pacific Forestry Centre conducted a field survey and collected fungi from diseased forest weeds and shrubs for screening and evaluation of their use as potential biocontrol agents against these weeds. Disease symptoms associated with a fungal infection were observed on foliage of sticky currant (*Ribes viscosissimum* Pursh) and the causal fungus identified as *Cercospora saximontanensis* Deighton. The weed is considered to be a major competitor with respect to moisture, nutrients and space in the reforestation sites of coastal and interior B.C. It also acts as an alternate host to white pine (*Pinus monticola* Dougl. ex D. Don) blister rust disease caused by *Cronartium ribicola* J. C. Fisch., and is therefore an important limiting factor to the regeneration of these trees. The aim of the present study was to characterize this species and distinguish it from other known species on this host substratum as a prerequisite to any strategies for its potential use as a biocontrol agent.

MATERIALS AND METHODS

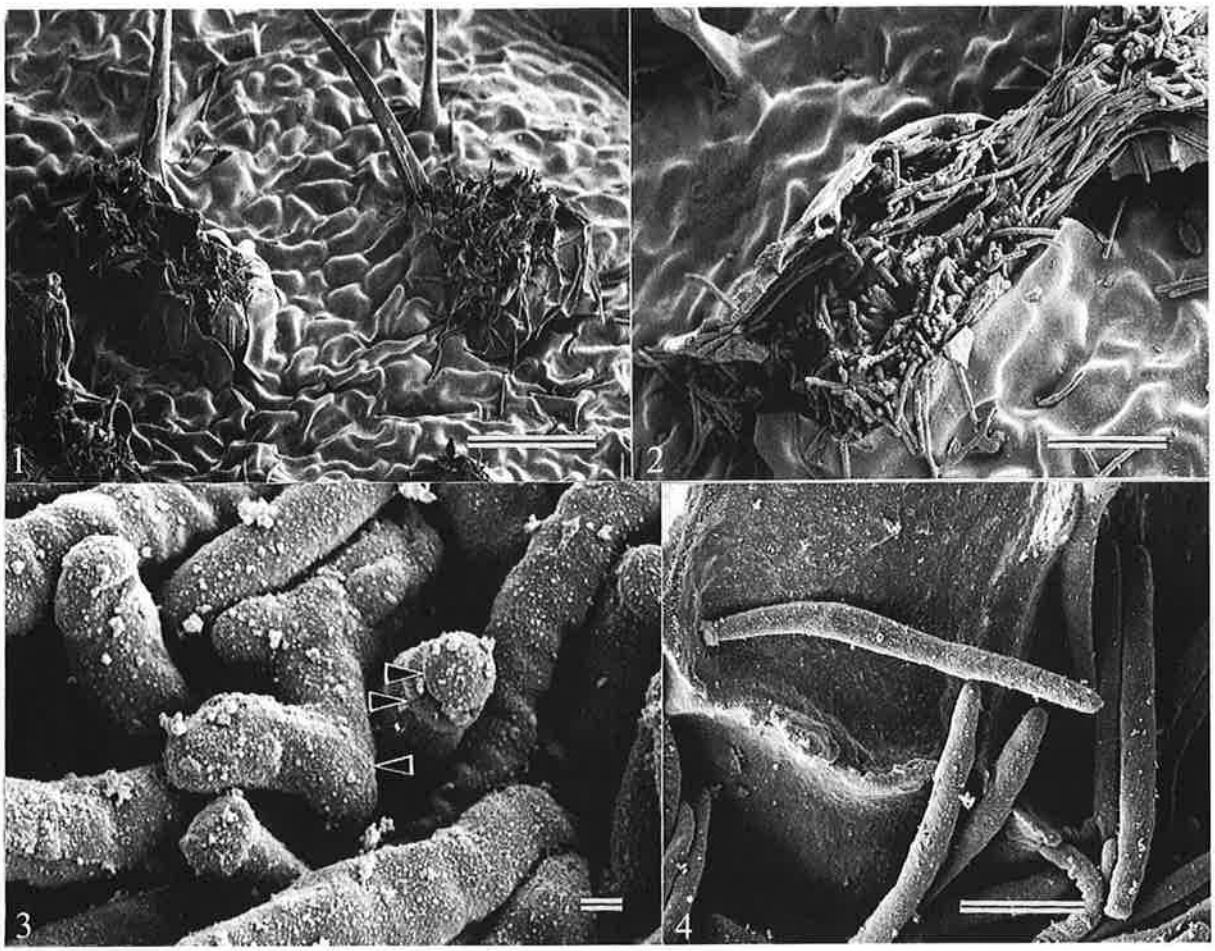
Diseased leaf samples of sticky currant were collected and conidium development was examined by SEM. Leaf discs bearing conidiomata (approximately 7 × 7 mm) were fixed in glutaraldehyde, followed by 1% osmium tetroxide in a 0·1 M phosphate buffer, dehydrated in a graded acetone series, critical point dried and mounted. Specimens were coated with gold–palladium and viewed with a JSM 6400 scanning electron microscope. All measurements were obtained by mounting specimens in lactophenol cotton blue, and observing them under the 100 × (oil) objective of a light microscope. Material was compared and contrasted with holdings in herb. IMI.

Quasiphloeospora B. Sutton, Crous & Shamoun, gen. nov. (Figs 1–7)

Foliicola, laesionibus consociatus. *Mycelium* internum, brunneum, ramosum, septatum. *Conidiomata* separata, acervularia vel sporodochialia, epidermalia vel subepidermalia, ad basim ex textura angulari brunnea et supra ex textura prismatica composita. *Conidiophora* brunnea, ad basim irregulariter ramosa et verruculosa, septata, cylindrica, ex cellulis superioribus conidiomatum formata. *Cellulae conidiogenae* in conidiophoris incorporatae, terminales vel laterales, laeves, brunneae, cylindricae, rectae, proliferationibus percurrentibus et enteroblasticis et aliquot annellationibus, vel proliferationibus sympodialibus et holoblasticis. *Loci conidiogeni* atri et incrassati. *Conidia* holoblastica, pallide brunnea, laevia, cylindrica, septata, ad apicem obtusa et ad basim truncata, cicatrice basali incrassata et atra.

Typus generis: *Quasiphloeospora saximontanensis* (Deighton) B. Sutton, Crous & Shamoun.

Foliicolous, associated with lesions. *Mycelium* internal, brown, branched, septate. *Conidiomata* separate, acervular to sporodochial, epidermal to subepidermal, composed of brown *textura angularis* at the base and *textura prismatica* above. *Conidiophores* brown, verruculose, irregularly branched at the base, septate, cylindrical, formed from the upper cells of the conidiomata. *Conidiogenous cells* integrated, terminal or lateral, smooth or verruculose, brown, cylindrical, straight, proliferating percurrently and enteroblastically to form annellations

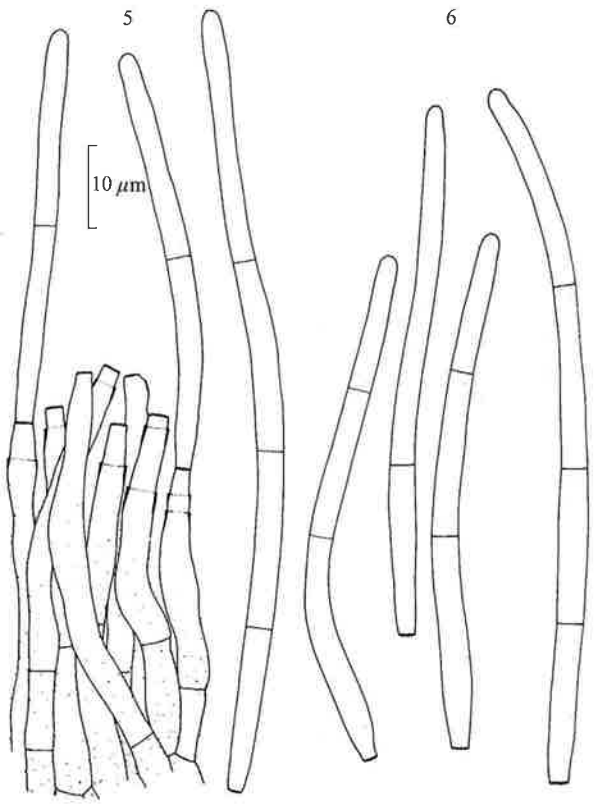


Figs 1–4. Scanning electron micrographs of *Quasiphloeospora saximontanensis*. **Figs 1, 2.** Erumpent acervular conidiomata. **Fig. 3.** Conidiogenous cells with sympodial (arrow) or enteroblastic (double arrow) proliferation. **Fig. 4.** Cylindrical conidia with obtuse apices and truncate, thickened bases (bars, 100, 50, 1 and 10 µm, respectively).

or sympodially and holoblastically. *Conidiogenous loci* dark and thickened. *Conidia* holoblastic, pale brown, smooth, cylindrical, septate, obtuse at the apex and truncate at the base; basal scar dark and thickened.

This newly described genus occupies a position intermediate between the sporodochial hyphomycetes and acervular coelomycetes, but neither Sutton (1973, 1980) nor Nag Raj (1981) consider conidiomatal structure to be of primary systematic significance in these groups. In determining the relationships of this species account should be taken of the published literature in both groups. The more compact arrangement of conidiophores suggests placement of *Quasiphloeospora* in the coelomycetes rather than the hyphomycetes. However, there are many species of *Pseudocercospora* Speg. (a genus usually placed in the hyphomycetes) where this type of conidiomatal structure also occurs.

In contrast, the nature of scars left on conidiogenous cells and those on conidial hila after secession are increasingly being recognized as vital clues to fundamental relationships in hyphomycetes, and this is especially relevant in the many genera surrounding the *Cercospora* complex (Luttrell, 1963; Deighton, 1973, 1976, 1979; Mangenot & Reisinger, 1976; Pons, Sutton & Gay, 1985; David, 1993). Ultrastructurally the basal scar is composed of only a single-layered wall derived from one half of the secession septum whereas the periclinal wall is double-layered (Cole & Samson, 1980). This sort of arrangement is basic to both unthickened and thickened scars, but in the latter, additional wall material and/or melanin is laid down before, during and after the events leading to secession. The thickened scar at the conidial base in *Quasiphloeospora* is the character which really distinguishes this genus from others. In the coelomycetes there is no parallel at all. In genera such as *Colletogloeum* Petr., *Phloeospora* Wallr., *Ahmadia* Syd., *Anaphysmene* Bubák and others (Sutton, 1980) where there is a basic similarity in conidiogenous events and conidial morphology, all have thin, unthickened basal scars which show no differences from the periclinal walls of the conidia in examination by optical microscopy. In the hyphomycetes there are many genera in the *Cercospora* complex where conidial scars are thickened in different ways and Deighton (1973, 1976, 1979) has separated a number of genera such as *Cercosporella* Sacc. and *Pseudocercosporidium* Deighton (highly thickened and refractive), and *Paracercospora* Deighton (thickening confined to the rim), on this basis. *Pseudocercospora* and *Paracercospora* appear closely related to *Quasiphloeospora*, but the conidial scars in *Pseudocercospora* are unthickened, and in *Paracercospora* the thickening is restricted to the rim of the conidiogenous cell. In *Cercospora* Fresen., where the species on



Figs 5, 6. *Quasiphloeospora saximontanensis*. **Fig. 5.** Developing conidia, conidiophores and conidiogenous cells. **Fig. 6.** Mature conidia.

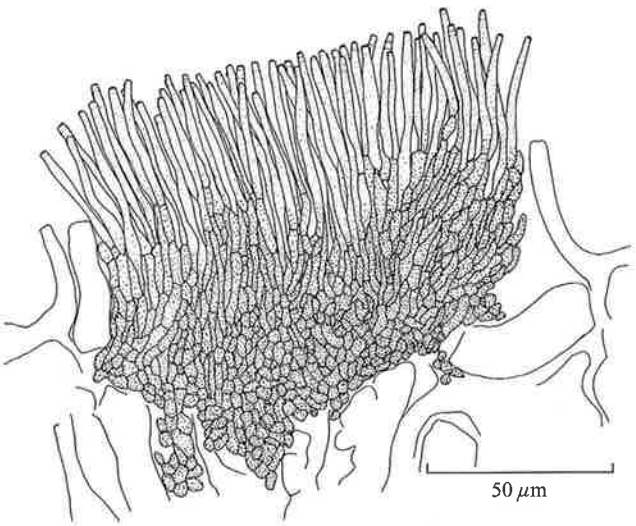


Fig. 7. *Quasiphloeospora saximontanensis*. Vertical section of a conidioma.

Ribes spp. was originally described by Deighton (1983), the scars are very prominently thickened and protuberant but these features are unlike those in *Quasiphloeospora*.

In *Quasiphloeospora* the very pale brown, smooth conidia are formed from verruculose conidiogenous cells. In *Cercospora* (Pons & Sutton, 1988) conidia are hyaline and conidiogenous cells show sympodial enteroblastic proliferation associated with conidiogenesis, but in *Quasiphloeospora* percurrent enteroblastic proliferation results in a series of annellations associated with conidial formation as do a limited number of sympodial holoblastic proliferations. In this respect *Quasiphloeospora* resembles *Pseudocercospora* where both types of proliferation are commonly found (Sutton, Pascoe & Sharma, 1987; Sutton & Pascoe, 1988).

Quasiphloeospora saximontanensis (Deighton) B. Sutton, Crous & Shamoun, comb. nov.

Cercospora saximontanensis Deighton, *Mycol. Pap.* 151: 7 (1983).

Lesions amphigenous, light brown to dark red, angular, vein-limited, up to 5 mm diam., occasionally associated with chlorosis extending beyond the areas of sporulation. *Mycelium* immersed, consisting of smooth, olivaceous to brown inter- and intra-cellular, branched, septate hyphae 1·5–2·5 μm wide. *Conidiomata* epigenous and hypogenous, abundant, separate, dark brown to black, acervular, sporodochial and hyphal (fasciculate), epidermal to subepidermal, composed at the base of brown *textura angularis* becoming paler and increasingly more like *textura prismatica* towards the conidiophore-bearing region, or emerging as fascicles of up to 20 through stomata, 40–130 μm diam. × 50–110 μm high (including the conidiophores). *Conidiophores* olivaceous to medium brown, irregularly verruculose and branched at the base, becoming less rough above, 1–4 septate, cylindrical, erect, formed from the upper cells of the conidiomata, 35–70 × 3–4·5 μm. *Conidiogenous cells* integrated, mostly terminal, occasionally lateral, irregularly verruculose, pale brown to olivaceous, cylindrical, straight or slightly flexuous, proliferating percurrently and enteroblastically to form up to 3 annellations, or sympodially and holoblastically to form 2–3 loci, 15–45 × 3–4·5 μm. *Conidiogenous loci* non-protuberant, non-geniculate, dark and thickened, 2–2·5 μm wide. *Conidia* holoblastic, pale brown to olivaceous, smooth, cylindrical, straight or gently curved, obtuse at the apex and truncate at the gradually or occasionally abruptly tapered base, eguttulate, 1–4 septate, 40–100 × 2·5–3·5 μm; basal scar darker and more thickened than the periclinal wall.

On leaves of *Ribes* spp., Wyo., Idaho, Wash., Calif., U.S.A., and B.C., Canada.

Specimens examined: On leaves of *Ribes viscosissimum*, Indian Paintbrush Trail, Grand Teton National Park, Wyo., U.S.A., 16 Aug. 1937, W. G. & R. Solheim & H. F. House 5369, W. G. Solheim, *Mycoflora Saximontanensis Exsiccata* 1191, sub nom., *Cercoseptoria ribis* (Davis) Dearn. & House, IMI 98069, holotype; Signal Mountain, Grand Teton National Park, Wyo., U.S.A., 22 July 1955, W. G. & R. Solheim 4080, W. G. Solheim, *Mycoflora Saximontanensis Exsiccata* 1396, sub nom. *Cercospora septoriopsis* Chupp, IMI 169953; Priest River Experimental Station, Idaho, U.S.A., 3 Aug. 1931, G. G. Hedgcock, USDA Forest Pathology 54910, sub nom. *Cercoseptoria ribis* (Davis) Dearn. & House (det. Dearness), IMI 92408; Trail to Cathedral Lakes region, B. C., Canada, 1 Aug. 1956, J. A. Calder, J. A. Parmelee & R. L. Taylor 19577, DAOM 54335 sub nom. *Cercospora septoriopsis* Chupp, IMI 76263; Lardeau River, Benton Creek, Nelson Forest Region, B. C., Canada, 27 Aug. 1993, A. Erickson 141, IMI 363488; on *Ribes speciosum*, Topanga Canyon, Santa Monica Mountains, Calif., U.S.A., 31 Mar. 1935, *Southern Californian Fungi*, O. A. Plunkett, sub nom. *Cercospora ribicola* Ellis & Everh., IMI 154326; on *Ribes sanguineum*, Duckabush River, Wash.,

U.S.A., 9 Aug. 1912, E. Bartholomew, *Fungi Columbiani*, E. Bartholomew 4907, sub nom. *Cercospora ribicola* Ellis & Everh., IMI 8453.

This species was originally described by Deighton (1983) from *Ribes viscosissimum*, *R. sanguineum* Pursh and *R. speciosum* Pursh in North America from material misidentified as *Cercospora ribicola* Ellis & Everh. and *Cercospora septoriopsis* Chupp or its synonym *Cercoseptoria ribis* (Davis) Dearn. & House. It only has a tenuous relationship to *Cercospora* in having cicatrized conidiogenous loci and filiform conidia. It differs from this genus by the pale brown conidia, the percurrently and sympodially proliferating conidiogenous cells, conidiogenesis associated with such proliferations, verruculose conidiophores and conidiogenous cells, the non-protuberant, non-geniculate conidiogenous loci, and the acervular to sporodochial conidiomata.

Quasiphloeospora saximontanensis has frequently been misidentified as what was originally known as *Cylindrosporium ribis* Davis, which was later placed in *Cercoseptoria* Petr. by Dearness & House (1940) and *Cercospora* by Chupp (1954). Since there are no modern accounts of this species and *Cylindrosporium*, *Cercoseptoria* and *Cercospora* are not appropriate placements for it, a description with revised nomenclature follows.

Phloeosporella ribis (Davis) B. Sutton, Crous & Shamoun, comb. nov. (Figs 8–10)

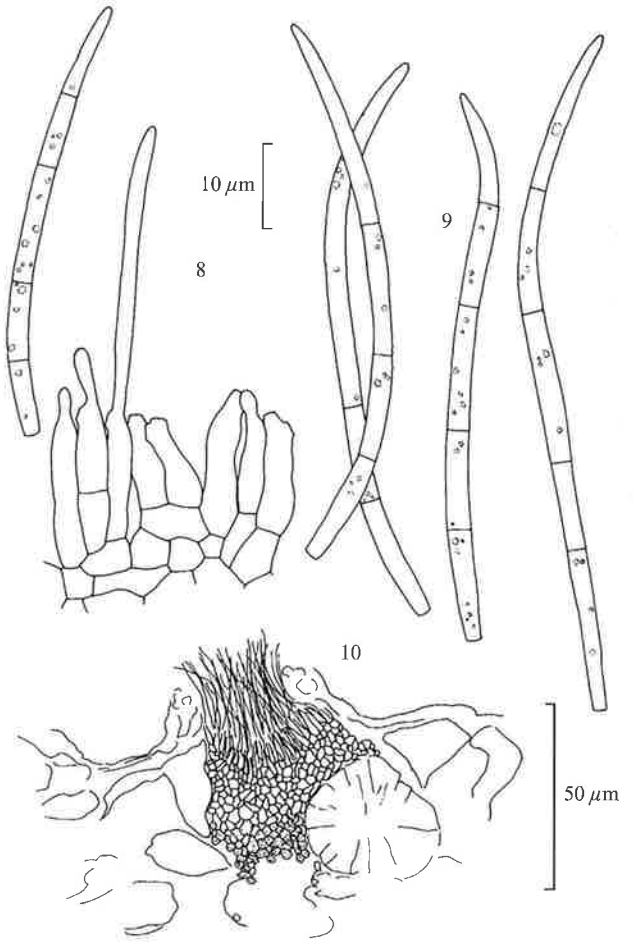
Cylindrosporium ribis Davis, *Trans. Wisc. Acad. Sci., Arts Lett.* 16: 759 (1910).

Cercoseptoria ribis (Davis) Dearness & House, *Circ. NY State Mus.* 24: 56 (1940).

Cercospora septoriopsis Chupp, *A monograph of the fungus genus Cercospora*: 520 (1954).

Lesions amphigenous, pale to medium brown with a narrow purple-brown raised margin, circular to elliptical or irregular, not vein-limited, up to 5 mm diam. *Mycelium* immersed, consisting of smooth, hyaline inter- and intra-cellular, branched, septate hyphae 1·5–2·5 µm wide. *Conidiomata* mostly epigenous but a few hypogenous, abundant, separate, white to cream, acervular, epidermal to subepidermal, composed of hyaline *textura angularis* which is very pale brown at the base of the conidiomata, up to 50 µm diam. × 35 µm high (including the conidiophores). *Conidiophores* hyaline, smooth, branched sparingly at the base, 1–2-septate, mostly cylindrical, erect, formed from the upper cells of the conidiomata, 40 × 3–4 µm. *Conidiogenous cells* integrated or discrete, smooth, hyaline, cylindrical, straight or slightly flexuous, proliferating sympodially and holoblastically to form up to 2 loci, 15–45 × 3–4·5 µm. *Conidiogenous loci* non-protuberant, non-geniculate, hyaline, 2 µm wide. *Conidia* holoblastic, hyaline, smooth, filiform, irregularly curved, obtuse to acute at the apex and truncate at the gradually tapered base, irregularly guttulate, 1–4-septate, 40–85 × 2–2·5 µm; basal scar hyaline.

Specimens examined: On *Ribes triste*, La Pointe, Bayfield Co., Wis., U.S.A., 10 July 1908, J. J. Davis, ex Univ. Wisc. Herb., IMI 194769, lectotype of *Cylindrosporium ribis* Davis; *Ribes vulgare*, Madison, Wisc., U.S.A., 28 July 1914, J. J. Davis, E. Bartholomew, *Fungi Columbiani* 4625 sub nom. *Cylindrosporium ribis* Davis, IMI 21475.



Figs 8–10. *Phloeosporella ribis*. **Fig. 8.** Conidiogenous cells and developing conidia. **Fig. 9.** Conidia. **Fig. 10.** Vertical section of a conidioma.

The placement of this species in *Cylindrosporium* Grev. is not tenable on account of the lack of unicellular conidia formed from phialides (Sutton, 1980). Rawlinson, Sutton & Muthyalu (1978) showed that the genus is currently monotypic and restricted to *C. concentricum* Grev., the anamorph of *Pyrenopeziza brassicae* B. Sutton & Rawl. *Cercoseptoria*, another genus in which this pathogen of *Ribes* spp. has been placed, is inappropriate because the conidia in *Cercoseptoria* are brown and often verruculose. Deighton (1976) at first accepted this genus but later (Deighton, 1987) regarded it as a synonym of *Pseudocercospora*. *Cercospora* is also unsuitable because of its hyphomycetous habit and the fact that both conidiogenous loci and conidial scars are prominently thickened (Pons & Sutton, 1988).

Cylindrosporium ribis is more correctly placed in *Phloesporella* Höhn. The only modern account of *Pholoeosporella* is by Sutton (1980) who redescribed the type species, *P. ceanothi* (Ell. & Everh.) Höhn. and accepted five species, four of which had been formerly placed in *Cylindrosporium*. Characters of the genus are the filiform hyaline septate conidia formed from holoblastic sympodially proliferating conidiogenous cells in acervular conidiomata.

CONCLUSIONS

There have been several fungi referable to the '*Cercospora* complex' described from foliage of *Ribes* spp. (Chupp, 1954; Pollack, 1987). Revision of these has been piecemeal. Chupp (1954) thought that *C. magellanica* Speg. described on *R. magellanicum* Poir. from Argentina might be classed as a *Polythrincium* Kunze. Braun & Rogerson (1993) dealt with *C. coalescens* Davis on *R. inerme* from Utah, U.S.A. and referred it to *Phaeoramularia* Munt.-Cvetk. Deighton (1983) dealt with *C. septoriopsis* Chupp (a nomen novum for *Cylindrosporium ribis* Davis) and concluded that under this name a number of collections had been misidentified. He accepted the name *Cylindrosporium ribis* for some material and segregated the remainder as a new taxon, *Cercospora saximontanensis* Deighton. It has been shown that these two taxa are indeed distinct but neither are correctly placed in *Cercospora*. *Cylindrosporium ribis* (*Cercospora septoriopsis*) is referred to *Phloeosporella* and *Cercospora saximontanensis* is placed in a new genus *Quasiphloeospora*. They differ in symptoms, conidiomatal structure, some aspects of conidiogenous events, conidial morphology and scar structure. For the purposes of quick identification *Q. saximontanensis* has vein-limited lesions, mostly epigenous sporulation, dark brown to black conidiomata, and the conidia are pale brown with a thickened basal scar. *P. ribis* has lesions surrounded by a purple raised margin, sporulation is mostly epigenous, conidiomata are white to cream, and conidia are hyaline with no thickened basal scar.

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