Systematics and diversity of the Phyllachoraceae associated with Rosaceae, with a monograph of *Polystigma*

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Biotrophic members of the Phyllachoraceae are described and illustrated, and their nomenclature assessed. *Isothea* is considered to be a monotypic genus with close affinities to *Phyllachora*. Four species of *Phyllachora* are accepted; some have distinctive features which may provide evidence for subdivision of that genus. Two species currently referred to *Plectosphaera* are studied; neither is a typical biotroph. *Polystigma* is formally monographed. Five species are accepted, all on species of *Prunus*, including the previously undescribed *P. amygdalinum*, an economically important pathogen of almond (*Prunus dulcis*). An eastern Russian species originally described in *Polystigmella* is treated as a subspecies of the widespread plum pathogen *Polystigma rubrum*. A number of species names is excluded from the Phyllachoraceae.

Biotrophic representatives of the Phyllachoraceae associated with species of Rosaceae appear to be relatively small in number (12 species of fungi known from 3100 plant species), but include a number of economically important taxa. The important genus *Glomerella* (anamorph *Colletotrichum*) also has several important representatives associated with Rosaceae, but species of this genus are necrotrophic or saprobic for at least most of their life cycle, and species concepts as currently recognized are not comparable (Cannon, in press). They are, therefore, not included in this survey.

The apparent lack of diversity of Phyllachoraceae associated with the Rosaceae can partly be explained by the predominantly temperate distribution of the plant family; about 80% of known species of Phyllachoraceae are tropical (Cannon, in press). A notable exception is *Isothea rhytismoides* (see below), which extends at least to 83° N in the Canadian Arctic.

MATERIALS AND METHODS

Dried reference specimens of Phyllachoraceae were examined from a wide range of herbaria. Some were collected by various collaborators at the request of the author to ensure the availability of material in the correct state of maturity.

Stromata from the dried collections were dissected in situ, in a drop of water. The contents were allowed to swell before being removed from the specimen using the tip of a scalpel blade. Squash mounts were made and examined in water and lactofuchsin, and sections cut using a freezing microtome. Nomarski and phase optics were employed. All photographs and measurements are of material mounted in lactofuchsin unless specified otherwise.

ISOTHEA

Isothea Fr., Summa Vegetabilium Scandinaviae: 421, 1849.

Isothea was erected for the single species Sphaeria rhytismoides C. Bab. ex Berk. (non Corda). Five or six further taxa have been transferred to Isothea by different authors, but none is wellknown. It is not obvious from the original description why Fries regarded the genus as distinct, but at that period many of the genera now currently accepted were either not yet recognized, or poorly delimited. Isothea is clearly closely related to Phyllachora, but seems to differ primarily in having peridial cells which are large and thick-walled. The ostiolar structure with clavate pigmented peridial cells outside of true periphyses is not known in Phyllachora, although interestingly both Phyllachora physocarpi and Plectosphaera fragariae (see below) have ostioles surrounded by conic-papillate cells. Ostiolar structure has not been studied in depth in Phyllachora. An anamorph is not present in Isothea.

The transfer of *Isothea rhytismoides* to *Phyllachora* by Vasil'eva (1987) is unjustified, and is formally incorrect as *Isothea* predates *incluchora*. The two genera may ultimately be found to be ose relatives, but more studies in the variation within *Phyllachora* are required before this hypothesis can be properly tested.

Isothea rhytismoides Fr., Summa Vegetabilium Scandinaviae: 421, 1849.

Sphaeria rhytismoides C. Bab. ex Berk., Ann. Mag. Nat. Hist. 6: 361, 1841, non Sphaeria rhytismoides Corda, Icones Fungorum 4: 42, 1840.

Sphaerella rhytismoides (Fr.) De Not., Comm. Soc. Critt. Ital. 2 (3): 488, 1867.

Laestadia rhytismoides (Fr.) Sacc., Sylloge Fungorum 1: 424, 1882.

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- *Hypospila rhytismoides* (Fr.) Niessl, in Rabenhorst, *Fungi Europaei* no. 3261, 1885, *in sched*.
- Carlia rhytismoides (Fr.) Kuntze, Revisio Generis Plantarum 2: 846, 1891.
- Guignardia rhytismoides (Fr.) Zahlbr., Krypt. exs. Mus. Palat. Vindob. no. 618, 1901, in sched.; Ann. k.k. Naturh. Hofmus. Wien 16: 66, 1901.
- Phyllachora rhytismoides (Fr.) Lar. N. Vassiljeva, Pirenomitsety i Lokuloaskomitsety Severa Dal'nego Vostoka: 225, 1987.

Sphaeria dryadis Fuckel, Fungi Rhenani no. 2161, 1868, in sched.

Description

Anamorph: not known.

Infected areas 1-2.5 mm diam., the included leaf tissue sometimes reddish brown. Stromata hologenous (though usually not visible from the lower surface due to leaf tomentum), the ostioles epigenous. Blackened tissue sometimes spreading between ascomata below the cuticle but much more heavily developed above and below ascomata (in roughly circular regions 120–200 µm diam.), restricted to an upper and lower layer, subcuticular, composed of heavily melanized epidermal and some palisade cells, fungal tissue not clearly visible, eventually covering almost the whole of the infected area. Ascomata usually strongly aggregated, clearly distinguishable from the surface even in old colonies, from the surface usually strongly domed, the ostiole inconspicuous; 200–320 μm diam., usually slightly oblate; peridium 8–14 μm thick, composed of 4-5 layers of strongly compressed hyaline pseudoparenchymatous cells with walls to nearly 1 µm thick, sometimes apparently merging with compressed host tissue at the sides of the ascomata, in the ostiolar region forming swollen and pigmented clavate periphysis-like elements with cells to $18 \times 4 \,\mu\text{m}$, merging into true hyaline periphyses within (Fig. 1). Centrum formed from a thin layer of very thinwalled pseudoparenchymatous tissue lining the lower part of the wall. Paraphyses inconspicuous, formed (sometimes in pairs) from \pm globose cells and with at least the lower septa often constricted, to 8 µm diam., gradually tapering, very thinwalled, about as long as the asci. Asci 67-95 × 16-22.5 μm, clavate, short- to long-stalked (occasionally to ca 40 µm), swelling significantly just before ascospore release, thinwalled at all stages, the apex obtuse to rounded, with a small sometimes inconspicuous apical ring ca 4 μm diam. and 0.5 μm thick, usually 8-spored but ascospores frequently aborting. Ascospores arranged irregularly, $(9.5-)12.5-16 \times 5-6.5 \mu m$, usually \pm cylindrical with round ends, sometimes cylindricellipsoidal or ovoid, often slightly larger and/or irregularly shaped in asci with fewer than 8 ascospores; thin- and

smooth-walled, aseptate, often strongly guttulate, without a gelatinous sheath. *Appressoria* to 7 μ m long, widely clavate, mid brown, formed directly from germinating ascospores, occasionally while still in the ascoma.

Typification: **United Kingdom**: Scotland: Sutherland, Assynt, Inchnadamph, on *Dryas octopetala*, Sep. 1838, *C. Babington* (K! – holotype of *Sphaeria rhytismoides* C. Bab. ex Berk.). **Germany**: in Bavariae superioris alpibus, on *Dryas octopetala*, aestate, *s. coll*. (Fuckel, *Fungi Rhenani* no. 2161, ?G – holotype, IMI! – isotype of Sphaeria dryadis).

Host species: Dryas integrifolia, D. octopetala.

Distribution: Austria, Canada, Faeroe Islands, Germany, Greenland, Iceland, Italy, Norway, Romania, Russia, Sweden, Switzerland, United Kingdom (Scotland).

Illustrations: Figs 1-2.

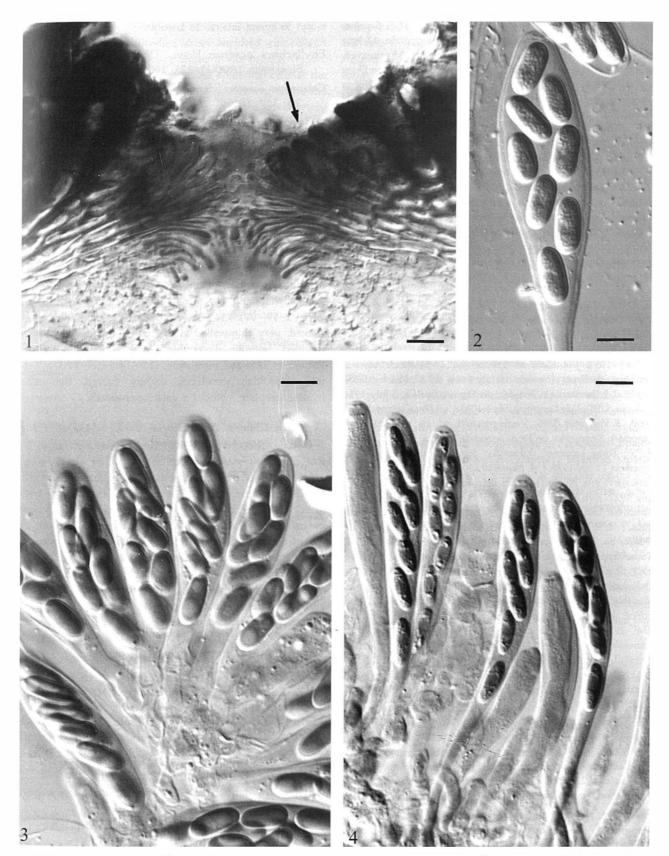
This arctic-alpine species is common throughout most of the range of its host genus *Dryas*, though it appears not to extend southwards along the Rocky Mountain range in Western Canada and the U.S.A. Collections from central Europe appear to have slightly longer ascospores than those from more northerly latitudes, but the number of specimens examined in detail was insufficient to confirm this impression. Canadian collections seem more or less identical to those from northern Europe.

The name on which *Isothea rhytismoides* is based, *Sphaeria rhytimoides* C. Bab. ex Berk., appears to be a later homonym of *S. rhytismoides* Corda (1840). Berkeley (1841) referred to a publication by Babington (in *Abstr. Linn. Trans.* p. 32) in his description of *Sphaeria rhytismoides*. This publication has not been traced, but if the name was validly published there it might predate Corda's homonym. The only effect would be a change of author citation.

Specimens examined: Austria: Tirol, Innsbruck, Hafelkar, 2400 m, on Dryas octopetala, July 1940, F. Petrak (WSP 31563; IMI 22034, IMI 236494 as Petrak, Reliquiae Petrakianae no. 238). Canada: North West Territories, Baffin Island, Inugsuin Fiord, Geog. Survey Site, on dry lower slopes below cliffs 1 mile S of Inugsuin site, 69° 37' N, 70° 02' W, on Dryas integrifolia, 29 July 1967, J. A. Parmelee & J. R. Seaborn (UPS, ex DAOM 117822); North West Territories, Ellesmere Island, Franklin District, Hazen Camp: in small area on S slope, 2 miles WNW of camp, 81° 49' N, 71° 21' W, 1200 m, on Dryas integrifolia, 3 July 1962, D. B. O. Savile 4534 (UPS, ex DAOM 92320); North West Territories, district of Franklin, Somerset Island, Aston Bay, 73° 39' N, 94° 45' W, on Dryas integrifolia, 10 Aug. 1958, D. B. O. Savile 3767 (UPS, ex DAOM 60075); North West Territories, Mackenzie District, DEW Line site, pin 1, Clinton Point, 69° 35' N, 120° 44' W, on Dryas integrifolia, 8 Aug. 1963, J. A. Parmelee 3145a (IMI 137877, ex DAOM 115769); North West Territories, Ellesmere Island, Hazen Camp, 81° 49' N, 71° 21' W, on

Key to genera included

1.	Stromata poorly developed; probably primarily saprobic	
1'.	Stromata well-developed; biotrophic for at least a large part of the life cycle	
	2. Stromata brightly coloured	
	2'. Stromata black	
3.	Ascomatal walls composed of thin-walled compressed cells; ostioles \pm simple	
3'.	Ascomatal walls composed of large rather thick-walled cells; ostiole surrounded by clavate pigmented cells derived	
	from the periphyses	



Figs 1–4. Figs 1–2. *Isothea rhytismoides.* **Fig. 1.** Vertical section through ostiolar region, with clavate pigmented cells derived from periphyses (arrow) (IMI 346091; bar = 10 μ m). **Fig. 2.** Ascus and ascospores (IMI 295585; bar = 10 μ m). **Fig. 3.** *Phyllachora physocarpi*. Asci and ascospores (IMI 367563; bar = 10 μ m). **Fig. 4.** *Polystigma rubrum*. Asci and ascospores. (Capron *s.n.*, ex K; bar = 10 μ m).

Dryas integrifolia, 16 July 1962, D. B. O. Savile 4642 (IMI 105169, ex DAOM 92315). Faeroe Islands: Oesterö, in monte Kodlen prope Eide, 300 m, on Dryas octopetala, 17 Aug. 1895, H. G. Simmons 438Fung (UPS). Greenland: Ivigtut, on Dryas integrifolia, 22 June 1883, A. Berlin (UPS). Iceland: Sudur-Pingeyjarsysla, Mjvatnssveit, ca 500 m S of Haganes (at western shore of Lake Myvatn), on Dryas octopetala, 28 July 1971, K. Holm & L. Holm 43c-71 (UPS); Hóf in Horgárdal, on Dryas octopetala, 24 June 1902, O. Davidsson (UPS); N Iceland, Husavik, on Dryas octopetala, 25 June 1903, O. Paulsen (UPS). Italy: Sud-Tirol, Radein, E of Auer in Etschtal, 1600 m, on Dryas octopetala, 29 Oct. 1989, A. Nograsek (IMI 356695). Norway: Sör-Tröndelag, Opdal h:d, Knudshö, on Dryas octopetala, 28 July 1899. A. T. Fredriksson (UPS); Sör-Tröndelag, Opdal h:d, Kongsvoll on Dryas octopetala, 20 Aug. 1884, O. Juel (UPS); Opland, Lom h:d, Röisheim, on Dryas octopetala, 8 July 1894, O. Juel (UPS); Svalbard, Bellsound, on Dryas octopetala, 30 June 1883, A. G. Nathorst (UPS); Svalbard, Tempelbay, on Dryas octopetala, 17 July 1882, A. G. Nathorst (UPS); Svalbard, s. loc., on Dryas octopetala, 1861, s. coll. (UPS). Romania: Hunedoara, Muntii Retezatului, Piule, on Dryas octopetala, 30 Sep. 1974, G. Negrean (IMI 200910; Herbarium Mycologicum Romanicum no. 2487). Russia: Novaya Zemlya, Sinus Bessimanaja, on Dryas octopetala, July 1875, F. R. Kjellman & A. N. Lundstrom (UPS). Sweden: Härjeladen, Tännäs s:n, Hammafjället, 1000 m, on Dryas octopetala, 30 July 1933, J. A. Nannfeldt 4802a (UPS); Jämtland, Åre s:n, Snasahögarna, below Täljbilfanen, 750 m, on Dryas octopetala, 27 July 1951, J. A. Nannfeldt 11606b (UPS); Jämtland, Åre s:n, Renfjället, on Dryas octopetala, 13 July 1884, M. M. Floderus (UPS); Jämtland, Frostviken s:n, Raudek, on Dryas octopetala, 2 July 1914, E. Borner (UPS); Lule Lappmark, Skaitetjåkko, on Dryas octopetala, July 1900, T. Vestergren (UPS, Vestergren, M. sel. exs. no. 405); Lule Lappmark, Koratjokka, on Dryas octopetala, 14 Aug. 1912, T. Lindfors (UPS); Torne Lappmark, Jukkasjärvi parish, Kartimvare, on Dryas octopetala, 11 July 1928, J. A. Nannfeldt 1203b (UPS); Torne Lappmark, Jukkasjärvi s:n, Nuolja, towards Björkliden, on Dryas octopetala, 6 July 1927, J. A. Nannfeldt 833a (UPS); Torne Lappmark, Jukkasjärvi parish, Mt Låktatjåkko, NE slope, 900 m, on Dryas octopetala, 7 July 1928, J. A. Nannfeldt 1617b (UPS); Torne Lappmark, Jukkasjärvi s:n, Nualju, on Dryas octopetala, 23 Aug. 1946, L. Holm 50/a (UPS); Torne Lappmark, Jukkasjärvi s:n, Nuolja, on Dryas octopetala, 10 July 1927, R. Olsen (UPS). Switzerland: Graubünden, prope Arosa, on Dryas octopetala, s.d., P. Magnus (IMI 11252; Kryptog. exs. Mus. Palat. Vindobon, no. 618). United Kingdom: Scotland: Sutherland, Loch Eriboll, Kempie, on Dryas octopetala, 14 May 1985, S. M. Francis (IMI 295585); Sutherland, 3 km S of Inchnadamph, on Dryas octopetala, 13 Aug. 1990, P. F. Cannon (IMI 346091); Sutherland, Bettyhill, Strathnaver NNR, NC7060, on Dryas octopetala, 12 May 1985, P. F. Cannon (IMI 304687); Sutherland, Loch Eriboll, Ard Neackie, NC4459, on Dryas octopetala, 13 May 1985, P. F. Cannon (IMI 304696).

PHYLLACHORA

Phyllachora Nitschke ex Fuckel, Jahrb. Nassauischen Vereins Naturk. 23–24: 216, 1870, non Phyllachora Nitschke ex Fuckel, Fungi Rhenani no. 2056, 1867, in sched., nom. cons.
Phyllachora is a large genue with people 200 species genue has

Phyllachora is a large genus, with nearly 900 species currently recognized. The exclusively biotrophic nature of most of its species means that host specificity has played a major role in species definition. Species on Gramineae and Leguminosae have been the subjects of at least reasonably modern monographic treatment (Parbery, 1967, 1971; Cannon, 1991), but for species associated with most other host families the most useful study remains that of Theissen & Sydow (1915). This

is a small further contribution to understanding of the genus, but all species studied in detail show unusual features.

- Phyllachora acaenae Henn., Öfvers, K. Vet.-Akad. Förh. Stockholm 1900(2): 325, 1900.
- Catacauma acaenae (Henn.) Theiss. & Syd., Annls Mycol. 13: 387, 1915.

Anamorph: not known.

Infected areas not differentiated. Blackened regions 350-1000 µm diam., irregular in shape, very strongly raising the substrate surface, 2- to 10-loculate, the individual ascomata easily distinguishable from the surface, shining black, appearing slightly roughened due to the leaf epidermal architecture, ostioles usually conspicuous. Ascomata shallowly conical, to 250 µm diam. Upper wall composed of leaf epidermal tissue infiltrated by strongly melanized textura epidermoidea. Lower wall hardly developed. Paraphyses copious when immature but many deliquescing at maturity, to 2.5 µm diam., thin-walled, gradually tapering, the apex swollen, about as long as the asci. Asci 42–59(–67) × 14·5–19 μ m, clavate, usually very shortstalked, very thin-walled at all stages, the apex objuse to rounded, without discernible apical structures, 8-spored. Ascospores arranged biseriately, $(12-)14\cdot 5-16(-17\cdot 5) \times 7-8\cdot 5$ µm, ellipsoidal, sometimes slightly curved, thin-walled, hyaline, aseptate, without a gelatinous sheath.

Typification: Chile: ad Concepción, on Acaena ovalifolia, s.d., F. Neger 122 (B - holotype, lost and presumed destroyed).

Host species: Acaena ovalifolia, A. ovalifolia var. insulae-exterioris, A. stangii.

Distribution: Chile, Tristan da Cunha.

The type has been destroyed, and none of the specimens examined is suitable as a neotype, as the only Chilean one lacks mature spores. Further collections around the type locality should be made in order that the application of the name *Phyllachora acaenae* may be properly fixed, which will allow confirmation or otherwise of the identity of the specimens from Tristan da Cunha. The paraphyses with distinctly swollen tips are unusual for the genus.

Other specimens examined: Chile: Masafuera, Q. de las Casas, on Acaena ovalifolia var. insulae-exterioris, 11 Feb. 1917, C. Skottsberg (S). Tristan da Cunha: Hottentot Gulch, 650 m, on Acaena stangii, 23 Mar. 1938, Y. Mejland 1760 (O); Inaccessible Island, above Blenden Hall, 400 m, on Acaena stangii, 19 Feb. 1938, E. Christopherson 2357 (O).

- Phyllachora dalibardae (Peck) Sacc., Sylloge Fungorum 2: 600, 1883.
- Dothidea dalibardae Peck, Ann. Rep. NY St. Mus. 27: 109, 1875.

Anamorph: not known.

Infected areas hardly delimited, though some discoloration of leaf tissue around effete ascomata is apparent. Blackened regions $180-320 \mu m$ diam., roughly circular, hologenous, the ostioles epigenous, inconspicuous, the surface \pm flat, shining

black but the pigmentation poorly developed except around the ostioles until a late stage of development, 1- to 8-loculate. Upper and lower walls composed of several layers of rather irregular mid brown thin-walled textura angularis with cells to 9 µm diam., more strongly pigmented in the ostiolar region, covered with more or less unmodified epidermal cells at the periphery and sometimes between the ostiolar regions of the ascomata; lateral walls similar in construction but less strongly pigmented. Periphyses well-developed, to 15 µm long, septate, tapering, merging into the paraphysis layer. Paraphyses welldeveloped, to 4 µm diam., thin-walled, rather irregular, sometimes slightly swollen between the septa (possibly an effect of secondary invaders), roughly the same length as the asci. Asci 64–79 × 8·5–9·5 μm, narrowly clavate, short-stalked, thin-walled at all stages, the apex obtuse, with an inconspicuous apical ring ca 2.5 µm diam. and 0.5 µm thick, 8-spored. Ascospores arranged biseriately, (14.5-)17.5-19 $\times 3.5-4.5 \,\mu$ m, narrowly fusiform, usually slightly curved (with one + flat face), thin-walled, aseptate, eventually becoming very slightly pigmented and verrucose (perhaps a degradation effect), without a gelatinous sheath.

Typification: **U.S.A.**: New York State, Sullivan Co., Forestburgh, on *Dalibarda repens*, Sep. 1873, *C. H. Peck* (NYS!, holotype of *Dothidea dalibardae*).

Host species: Dalibarda repens L.

Distribution: U.S.A.; only known from New York State.

This is an inconspicuous species, and poorly known. It appears rarely to have been collected since Peck's original work, and the ambiguity of its host identity no doubt has contributed to its relative obscurity. The species is easily distinguished from other *Phyllachora* taxa on Rosaceae using ascospore characters. It is the only true species of *Phyllachora* on that host family known from North America.

Giant spores, which are presumably multinucleate, occur occasionally in asci containing fewer than eight ascospores. A small proportion of asci also contains ascospores which develop abnormally, becaoming almost globose rather than fusiform. Neither of these phenomena is particularly unusual within the Phyllachoraceae.

Other specimens examined: U.S.A.: New York State, Essex Co., Newcomb, on Dalibarda repens, 22 July 1922, H. D. House (NYS); New York State, Mud Pond, on Dalibarda repens, July, C. H. Peck (NYS).

- Phyllachora negeriana Henn. & Lindau, *Hedwigia* 36: 225, 1897.
- Pleuroplacosphaeria negeriana Syd., Annls Mycol. **26**: 114, 1928 [anamorph].
- Infected areas to 10 mm diam., the included leaf tissue hardly modified.

Anamorph: Blackened regions 250–1000 µm diam, irregularly shaped and often coalescing, intraepidermal, hardly raising the substrate surface, possibly ostiolate through the host stomata, some of which have much more melanized fungal tissue associated with them than others. *Upper wall* composed of conspicuously thick host cuticle and the upper part of the epidermis, slightly melanized but with little evidence of fungal tissue. *Lower wall* to 15 μ m thick, composed of flattened host cells pervaded by dark brown thick-walled *textura epidermoidea*, the cells 2–3 μ m diam. *Fertile layer* not clearly differentiated from the lower wall. *Conidiophores* usually present, to 35 μ m long and *ca* 2 μ m diam., cylindrical, hyaline, thin-walled, formed directly from the strongly contorted cells of the lower wall. *Conidiogenous cells* usually formed laterally but occasionally in small terminal clusters, 18–26 μ m long, 2–2·5 μ m diam., gradually tapering, sometimes slightly irregular in form, proliferating percurrently; periclinal thickening often obvious, collarettes lacking. *Conidia* 4–6 × *ca* 1·5 μ m, clavate, the base slightly attenuated, hyaline, aseptate, apparently smooth-walled.

Teleomorph: Blackened regions 500-2500 µm diam., amphigenous, sometimes coalescing, often irregularly shaped, eventually strongly raising the substrate surface, containing 1-3 ascomata. Ascomata conic-oblate, the ostiolar region distinctly elongate in transverse section. Upper wall very welldeveloped, to 120 µm thick in the ostiolar region, decreasing in thickness gradually towards the edge of the blackened region, with an outer layer of host cuticle and the outer part of the epidermal cells, and a wide inner layer of very strongly melanized flattened fungal tissue, the lumina completely occluded except for the very innermost layers, which merge into periphyses in the ostiolar region. Lower wall 20-30 µm thick, composed of a number of layers of strongly melanized flattened fungal cells. Periphyses well-developed, hyaline, apparently immersed in a mucous coating. Paraphyses copious, to 6 µm diam., very thin-walled, gradually tapering, septate, branching not seen, enveloped in a mucous coat. Asci 116–146 \times 28–37 μ m, clavate-ellipsoidal but often rather irregularly shaped, thin-walled at all stages of development, short-stalked, the apex acute to obtuse, slightly thicker-walled but without obvious apical structures, 8-spored. Ascospores arranged obliquely uniseriately to biseriately, 20-23.5 \times 12–13 µm, ellipsoidal to cylindric-ellipsoidal, rarely slightly ovoid, guite thick-walled, hyaline, aseptate, smooth-walled, with a thin to thick epispore-like layer (apparently not mucous) which quickly degenerates, the spore eventually becoming pale brown and slightly rough-walled.

Typification: Chile: Andenthal Los Condos, on Kageneckia oblonga, s.d., F. Neger (B – holotype of *Phyllachora negeriana*, lost and presumed destroyed; UPS (F-06052) 102945! – isotype, here designated lectotype). Chile: Cordillera de Santiago, Salto de Agua, on *Kageneckia oblonga*, June 1925, *E. Werdermann* 1745 (Sydow, *Fungi exotici exsiccati* no. 932; B – holotype of *Pleuroplacosphaeria negeriana*, lost and presumed destroyed; K! – isotype, here designated lectotype).

Host species: Kageneckia oblonga Ruiz & Pavon.

Distribution: Chile.

As Sydow (1928) noted, the ascospores of *Phyllachora negeriana* may eventually become brown and slightly rough-walled, prompting Sydow's comparison with *Sphaerodothis*. It is not uncommon for *Phyllachora* ascospores to become brown, but this appears to be a degeneration of the ascospores rather than part of the normal maturation process (Cannon, 1989).

Genuine *Sphaerodothis* species have ascospores which become dark brown before release from the ascus.

The anamorph of *Phyllachora negeriana* is somewhat unusual amongst the *Phyllachora* group, but this perhaps represents a developmental exteme rather than a major evolutionary branch. Distinctive features include the large size of the conidiomata, the very large numbers of conidiogenous cells which are usually formed laterally from conidiophores, and the narrowly clavate rather than filiform conidia. It is not unlike the anamorph of *Phyllachora pterocarpi*, for example, and this fungus also has amphigenous ascomata. Although early workers (e.g. Theissen & Sydow, 1915) considered ascomatal position within the leaf to be an important generic character which separated *Phyllachora* from *Catacauma*, recent researchers (e.g. Cannon, 1991) have considered that ascomatal position is more to do with the physical characteristics of the host than the relationships of the fungus.

The ascospores with a distinct epispore layer are also unusual for the genus, but the systematic significance of this structure is unclear. This is because collections of Phyllachoraceae frequently degenerate rapidly in storage if they are not preserved very carefully (Pascoe, 1990) and ascospore sheaths and epispores may frequently break down to a degree beyond recognition. The rough-walled appearance of old ascospores of this species may be a result of epispore degeneration rather than wall ornamentation.

Phyllachora physocarpi Jacz., in Jaczewski, Komarov & Tranzschel, Fungi Rossiae Exsiccati no. 290, 1899, in sched. Anamorph: unknown.

Infected areas 0.7-4 mm diam., the included leaf surface distinctly browned, usually roughly circular, often coalescing. Blackened regions 150-350 µm diam., 10-50 per infected area, hypogenous, sometimes coalescing (to 6-loculate), irregular but usually roughly circular, usually not strongly domed, matt black especially when immature, the ostiole relatively large, easily visible when wet. In section ascomata spherical to oblate, occupying the lower epidermis and mesophyll. Upper wall 15-20 µm thick, slightly thicker in the vicinity of the ostiole, composed primarily of strongly melanized textura epidermoidea, the epidermis strongly degraded and the cuticle apparently missing. Lower wall poorly developed, composed of compressed host tissue filled with strongly contorted fungal cells, the palisade layer sometimes slightly melanized but not disrupted. Ostiole surrounded by melanized conicpapillate cells. Periphyses well-developed, to 35 µm long, hyaline, thin-walled, gradually tapering. Paraphyses absent, at least at maturity. Asci 60–77 \times 13.5–16 µm, clavate-cylindrical, the stalk rather variable in length, thin-walled at all stages, the apex obtuse, with a small apical ring 2.5-3 µm diam. and ca 0.5 µm thick, 8-spored. Ascospores arranged biseriately, $12.5-14 \times 4.5-5.5 \ \mu m$, cylindrical with rounded ends, often slightly curved (fabiform), occasionally slightly ovoid, fairly thin-walled, hyaline, aseptate, without a gelatinous sheath.

Typification: **Russia**: Russian Far East, 'in saxosis montibus Londoko ad ripas fl. Kirma, fl. Amur influentis, in regione montium Burejensium', on *Physocarpus amurensis*, 20 Aug.–1 Sep. 1895, Komarov (Fungi Rossiae Exsiccati no. 290, LE – holotype, not seen; K! – isotype of Phyllachora physocarpi).

Host species: Physocarpus amurensis Maxim., P. opulifolia (L.) Maxim.

Distribution: Russia (Russian Far East).

This species does not have the shining black stromata of a typical *Phyllachora*, but this may be at least partly due to its hypogenous placement within the leaf and the apparent breakdown of the covering cuticle. The absence of paraphyses is unusual for the genus, but is not unparalleled (Cannon, 1991). Judging from the appearance of the dried host leaves, the fungus has some deleterious effect, but this may be insignificant as the host is deciduous, the browning of the leaf in the vicinity of the ascomata coinciding with natural senescence.

Other specimen examined: Russia: Primorskii Krai, Vladivostok, on Physocarpus opulifolia, Sep. 1986, L. N. Vasil'eva (IMI 367563).

PLECTOSPHAERA

Plectosphaera Theiss., Annls Mycol. 14: 413, 1916.

Plectosphaera was used by von Arx & Müller (1954) to accommodate non- or weakly stromatic *Phyllachora* species. This concept of the genus is unfortunately untenable, as the type species *P. bersamae* (Lingelsh.) Theiss. is a typical stromatic member of *Phyllachora*. Von Arx & Müller's concept of *Plectosphaera* seems to include a rather disparate array of fungi. Some have clear affinities to *Phyllachora* and its relatives, but others probably have closer links to the *Glomerella* aggregate, or to the fungi currently placed in the Hyponectriaceae.

Plectosphaera fragariae (Willi Krieg. & Rehm) Arx & E. Müll., Beitr. Kryptogfl. Schweiz **11** (1): 208, 1954.

Phomatospora fragariae Willi Krieg. & Rehm, Annls Mycol. 4: 39, 1906.

Physosporella fragariae (Willi Krieg. & Rehm) Höhn., Annls Mycol. 16: 61, 1918.

Stromata absent. Ascomata immersed in leaf tissue, 120–200 µm diam., \pm globose, with a slightly papillate ostiole surrounded by a patch *ca* 50 µm diam. of almost black thick-walled, often curved cells to 15 µm in length and 4–5 µm wide, giving the appearance of blunt spines. *Peridium* thin, membranous, with outer layers of pale brown *textura globulosa-angularis* with cells up to 12 µm diam., and inner layers of thin-walled hyaline flattened cells. *Paraphyses* not seen; perhaps evanescent at maturity. *Periphyses* very well-developed, to 2.5 µm diam., rather thick-walled. *Asci* 62–74 × 12–15 µm, clavate, short-stalked, very thin-walled, the apex obtuse, apical structures not clearly visible, 8-spored. Ascospores 10.5–12(–14) × 5.5–6.5 µm, ellipsoidal-fusiform to ovoid, occasionally slightly papillate, hyaline, aseptate, thin- and smooth-walled, apparently without a gelatinous sheath.

Typification: Germany: Königstein, on dry leaves of Fragaria vesca, Apr.-May 1898–1900, W. Krieger (Krieger, Fungi Saxonici no. 1929, IMI! – isotype of Phomatospora fragariae).

Host: Fragaria vesca L.

Distribution: Germany.

This may not be a member of the Phyllachoraceae, as von Arx & Müller (1954) implied when they transferred Krieger & Rehm's name into *Plectosphaera*. The apparently saprobic nutritional status and the blackened tissue which is confined to blunt spine-like processes in *Phomatospora fragariae* precludes placement in *Phyllachora*. The genus name *Physosporella* Höhn. may need to be resurrected for this species, and perhaps also other saprobic taxa formerly placed in *Plectosphaera* such as *P. spartii* E. Müll. Relationships with *Glomerella*, as well as the Hyponectriaceae, need exploration. The apparent similarity of the ostiolar processes to the spines surrounding the ostiole in *Acanthorhynchus vaccinii* Shear (syn. *Physalospora vaccinii* (Shear) Arx & E. Müll.; Hyponectriaceae) needs further investigation.

The material examined has degenerated, and some structures were difficult to intepret. Modern collections are needed. As the various examples of the exsiccatum set were gathered at different times (to judge from the label), the specimen examined may not technically constitute isotype material.

- Plectosphaera rosae Arx & E. Müll., Beitr. Kryptogfl. Schw. 11 (1): 206, 1954.
- ?Sphaeria rosicola Fuckel, Jahrb. Nassauischen Vereins Naturk. 23–24: 114, 1870.
- ?Physalospora rosicola (Fuckel) Sacc., Sylloge Fungorum 1: 435, 1882.

Stromata absent. Ascomata 300-400 µm diam., strongly aggregated, usually \pm circular when viewed from above, with a poorly-defined outer ring of blackened tissue, a central black dot where the ostiole penetrates the plant epidermis, and the intervening tissue appearing hardly differentiated from the surrounding substratum; inserted beneath the epidermal layer, oblate to shallowly conical. Upper wall composed of brown thick-walled textura angularis with cells to 9 µm diam. around the ostiole and at the edge of the ascoma, merging into largercelled textura globulosa with cells to 17 µm diam. in the middle portion, and in the lower wall. Ostiole well-developed, not papillate, lined with hyaline periphyses to ca 10 µm long and 2 µm diam. Paraphyses well-developed, to 4 µm diam., very thin-walled, gradually tapering, ? deliquescing at maturity. Asci 84–94 \times 11·5–14 µm, cylindric-clavate, very thin-walled at all stages, \pm short-stalked but tending to break down near the base making measurement difficult, the apex rounded, ? with a small apical ring 2–3 μ m diam. and ca 0.5 μ m thick, 8-spored. Ascospores arranged \pm biseriately, 17.5–21.5 \times 6.5–7.5 µm, fusiform-ellipsoidal, often slightly curved (fabiform), thin-walled, hyaline, aseptate, mucous sheath not seen.

Typification: Italy: Treviso, Cansiglio, on dead stems of *Rosa canina*, Aug. 1898, *s. coll*. (D. Saccardo, *Mycotheca Italica* no. 287, as *Physalospora rosicola* (Fuckel) Sacc.; PAD! – syntype of *Plectosphaera rosae*).

Host species: Rosa canina.

Distribution: Italy; perhaps also from Germany (see below).

Von Arx & Müller did not specify the source of the material of this species that they examined, so although the specimen from Padova is authentic material, it is not clear whether it is the holotype. The sample examined is very small, and further collections are needed in order that a complete examination of this species may take place. Von Arx & Müller apparently relied upon the opinion of Petrak (1929) as to the identity of *Sphaeria rosicola*; he suggested that it was a synonym of *Pringsheimia sepincola* (Fr.) Höhn. (= *Saccothecium sepincola* (Fr.) Fr.). Judging from Fuckel's original description, this was not the case, and his species name may in fact be an earlier and priorable synonym of *Plectosphaera rosae*. Unusually, Fuckel did not cite type material from his exsiccatum series *Fungi Rhenani* in the original publication, and no type material has been located.

Plectosphaera rosae appears very similar to *Glomerella cingulata*, but appears to have at least primarily biotrophic nutrition. *Glomerella* species often have a period of biotrophic nutrition immediately following infection of the host, but become necrotrophs well before ascoma formation. The links between generic placement and mode of nutrition need further study, especially because of the considerable significance of *Glomerella* to plant pathologists.

POLYSTIGMA

- **Polystigma** Pers. ex DC., in Lamarck & de Candolle, *Flore Française* 6: 164, 1815. Lectotype: *Polystigma rubrum* (Pers.) DC. (Clements & Shear, 1931).
- Polystigma Pers., in Mougeot & Nestler, Stirpes Cryptogamae Vogeso-Romanae nos 270–1, 1812, in sched. Nom. inval. (Art. 32).
- Polystigmella Jacz. & Natalyina, in Natal'ina, Mater. Mikol. Fitopatol. Leningrad 8: 163, 1929. Holotype: P. ussuriensis Jacz. & Natalyina.
- Polystigmina Sacc., Sylloge Fungorum 3: 622, 1884 [anamorph]. Holotype: Polystigmina rubra (Pers.) Sacc.
- Rhodoseptoria Naumov, Bull. trimest. Soc. mycol. Fr. 29: 279, 1913 [anamorph]. Holotype: Rhodoseptoria ussuriensis Naumov.

Polystigma has been recognized as a genus since the early days of systematic mycology, but this contribution appears to be the first attempt at a formal monograph. The genus is characterized principally by its brightly coloured stromata, which occur on living leaves of *Prunus* spp. in the Euro-Asiatic region. The genus is probably a close relative of *Phyllachora*, as there are few distinguishing characteristics apart from the stromatal pigmentation. A possible further delimiting character is that *Polystigma* anamorphs have conidiogenous cells which at least mostly proliferate sympodially rather than percurrently, as is usual in the Phyllachoraceae. Observation is difficult due to the small size of the conidial structures, and the distinction does not appear to be absolute.

Polystigma species are temperate in distribution, and their host leaves are deciduous. In most species therefore conidial stromata are formed on living leaves throughout the summer, and overwinter on the ground after leaf fall. Ascomata are formed within the stromata during early spring, and ascospores are released to infect emerging leaves. *Polystigma* is one of the

few genera of Phyllachoraceae which appears to cause economic damage to its host plants, causing among other symptoms premature leaf fall (e.g. Banihashemi, 1990; Kranz, 1962). The deleterious effect apparently has not been quantified.

Müller (1986) noted that at least in some instances the stromata of *Polystigma* species accumulate starch, presumably as energy reserves for ascomatal formation, in common with species of *Diachora*. This feature may well serve as a further distinguishing characteristic from *Phyllachora*, but the blue staining in iodine of *Polystigma* stromata does not occur reliably. It is possible that significant starch reserves also build up within *Phyllachora* stromata, but the blueing might be masked by melanin deposits. Starch accumulation is likely to be correlated with the deciduous nature of the host leaves of *Polystigma* and *Diachora* species. The coloration of the stromata has in the past resulted in *Polystigma* being separated at ordinal level from *Phyllachora* and its relatives (e.g. Chadefaud, 1960), but the almost complete lack of melanin pigments does not in itself preclude placement in the Phyllachoraceae.

Polystigma is a small genus, apparently restricted to Prunus. Species such as P. astragali on Leguminosae are here referred to Stigmatula (Sacc.) Syd. & P. Syd. (Cannon, 1991); they differ in anamorph characteristics and stromatal characters as well as in host preference. A number of other species has been referred to the genus in the past which probably do not belong; for example Polystigma adenostomatis (referred to Hyponectria in this publication), and P. montserratis which is believed to be a species of Phyllachora with reduced melanin pigmentation and which causes death of host cells immediately surrounding the stromata (Cannon, 1991). P. sonneratiae probably does not belong in Polystigma, though its affinities are not yet fully established (Hyde & Cannon, 1992), and P. pusillum again does not belong to the genus sensu stricto but waits for relatives to be identified (Cannon, 1991). A complex of species on leafy and phyllodinous Australasian Acacia

Key to species of Polystigma

species belongs to yet a further assemblage. Link (1833) accepted a greatly expanded concept of *Polystigma*, with rather nebulous boundaries. His work on the genus appears not to have been accepted either by his contemporaries or by subsequent authors.

Article 59 of the International Code of Botanical Nomenclature rears its ugly head again for Polystigma. The names currently used for the anamorph and teleomorph of the type species *P. rubrum* are linked to the same basionym, Sphaeria rubra Pers. There seems little point in expending energy deciding whether the name Polystigma should refer to the teleomorph or the anamorph when there is ample evidence linking the two morphs. Applying the rules strictly would probably necessitate the use of the poorly-known name Polystigmella for the teleomorph. The name Polystigma was apparently first introduced by Persoon on an exsiccatum label in 1812, but no description of the genus was provided. The name was validated three years later by de Candolle (in Lamarck & de Candolle, 1815).

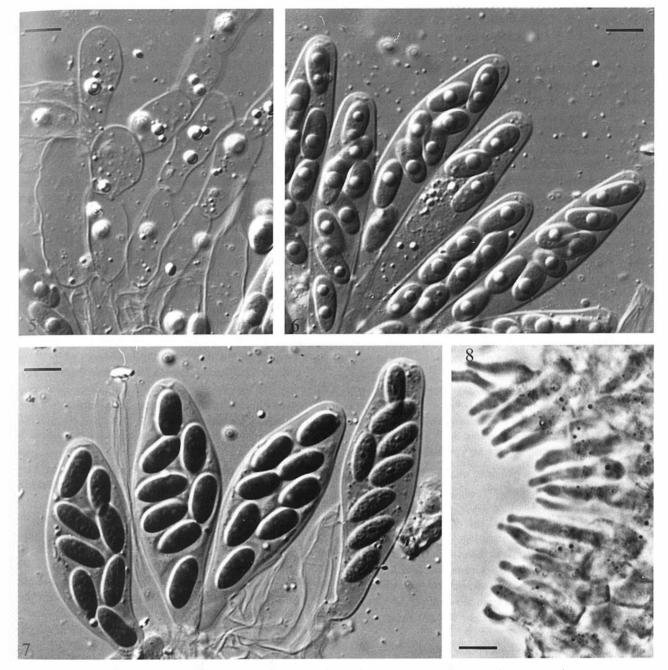
Polystigma amygdalinum P. F. Cannon, sp. nov. (Fig. 7) Septoria rubra β amygdali Desm., Ann. Sci. Nat., Bot. sér. 2, 19: 343, 1843.

- Polystigmina rubra var. amygdali (Desm.) Sacc., Sylloge Fungorum **3**: 622, 1884, as "amygdalinum".
- Polystigma rubrum var. amygdali Rehm, Annls. Mycol. 4: 70, 1906, nom. nud.

Stromata primo ochracea deinde atropurpurascentia, crassa; conidiomata sparsa; *cellulae conidiogenae* $12-22 \times 2-2.5 \mu m$, laterales vel terminales, *conidia* sympodialia efficientia; *conidia* $22-34 \times 0.75-1 \mu m$, filiformia, sigmoidea, ad apicem angustata; ascomata numerosa, hologena, leniter papillata; paraphyses sparsae, tenuitunicatae; asci $74-97 \times 18-23 \mu m$, clavati, brevistipitati, tenuitunicati, cum apparatu apicali *ca* 4 μm diam., octospori; *ascosporae* (13–)14–16.5 \times 5.5–6.5 μm , cylindricae, ad centrum minutus constrictae, aspetatae, hyalinae, laeves, sina vagina gelatinosa.

1.	Anamorph present
1'.	Teleomorph present
	2. Stromata yellowish, at least when young
	2′. Stromata reddish brown at all stages
3.	Stromata at first pale yellow, becoming orange; conidia 55-120 µm long; on Prunus cornuta, Himalayas Polystigmina pallescens
3'.	
	4. Stromata becoming yellowish brown, causing inrolling of leaves but not significant distortion; conidiomata sparse; conidia
	22–34 µm long; on <i>Prunus dulcis</i> , widely distributed
	4'. Stromata initially pale yellow, becoming orange-red, causing significant distortion of young shoots; conidiomata abundant;
	conidia 38–53 µm long; on Prunus armeniaca, China
5.	Conidia 22–42 µm long; on Prunus domestica and P. spinosa, widespread
5'.	
5.	6. Stromata yellowish, mature in autumn or spring without a preceding anamorphic stage; ascospores $13.5-15.5 \times 5.5-7 \mu m$; on
-	6'. Stromata reddish or brown to black, at least when mature; anamorphic stage always present
7.	Stromata brown to purplish black when mature, thick, causing inrolling of the leaf; ascospores $13-16.5 \times 5.5-6.5 \mu m$, \pm cylindrical;
	on Prunus dulcis, widespread
7'.	
	8. Stromata reddish brown, causing deformation of shoots and leaves; ascospores $12-15 \times 5-6 \mu m$, ovoid-cylindrical to
	ellipsoidal; on Prunus armeniaca, China
	8'. Stromata dark reddish brown to black, causing some hypertrophy but not inrolling
9.	Stromata almost black when mature, the ostioles inconspicuous; on Prunus domestica and P. spinosa, widespread
	Polystigma rubrum subsp. rubrum
9'.	Stromata reddish brown when mature, with black pigmentation around the ostioles; on various Prunus spp., eastern Russia

9. Stromata reddish brown when mature, with black pigmentation around the ostioles; on various Prunus spp., eastern Russia Polystigma rubrum subsp. ussuriense



Figs 5–8. Figs 5–6. Polystigma fulvum (IMI 163055). Fig. 5. Paraphyses; bar = 10 μ m. Fig. 6. Asci and ascospores; bar = 10 μ m. Fig. 7. Polystigma amygdalinum. Asci and ascospores (IMI 343415; bar = 10 μ m). Fig. 8. Polystigma rubrum. Periphyses. (Capron s.n., ex K; bar = 10 μ m).

Stromata: developing through late spring and summer on living leaves, producing conidia in summer and autumn, and ascospores from fallen overwintered leaves the following spring.

Conidial stromata to 40×15 mm diam., irregularly shaped, at first yellow-brown to orange-brown but soon darkening in the central portion, hologenous, crinkling the leaf but not causing noticeable hypertrophy; composed of two outer layers of epidermal tissue and strongly tanned parenchyma cells, and a hyaline inner layer.

Conidiomata sparse, very inconspicuous, $80-120 \mu m$ diam., \pm globose, the ostiolar region slightly papillate, hypogenous.

Conidiomatal wall poorly differentiated, composed of a narrow layer of small hyaline thick-walled *textura angularis*, from which the conidiogenous cells are directly derived. Conidiogenous cells arising as lateral or terminal branches from short relatively undifferentiated conidiophores, $12-22 \times 2-2.5 \mu m$, almost cylindrical but usually gradually tapering from the base, the upper portion (up to 5 μm) often slightly irregular due to successive conidial scars, proliferating sympodially. Conidia 22--34 × 0.75-1 μm , the widest point usually almost at the base, usually tapering smoothly towards the sigmoidally curved filiform apex; hyaline, aseptate, apparently smoothwalled.

Ascostromata extensive, sometimes covering large portions of the leaf, apparently causing leaf curl, purplish black (dark red when fresh; Ghazanfari & Banihashemi, 1976), 1.5-2 mm thick. Ascomata very numerous, shallowly domed, hologenous, the ostioles epigenous, inconspicuous, very slightly papillate. Paraphyses rather sparse, composed of chains of very thinwalled textura globulosa, branched at the base, to 18 µm wide at the base, tapering towards the acute apex. Asci $74-97 \times 18-23 \mu m$, clavate, short-stalked, very thin-walled at all stages, the apex obtuse to truncate, with an apical ring ca 4 μm diam. and 1 μm deep, usually 8-spored but occasionally 4-spored. Ascospores arranged biseriately, (13-)14-16.5 \times 5·5–6·5 µm, \pm cylindrical, one end rounded and the other obtuse to acute, usually slightly constricted in the central region, quite thin-walled, smooth, hyaline, aseptate, without a gelatinous sheath. Ascospores in some only of the 4-spored asci are larger (16–18 \times 6·5–7 μ m), and similarly shaped.

Typification: **Israel**: Kibbutz Givat Oz, on *Prunus dulcis*, 28 Feb. 1992, *A. Lin* (IMI 353415, holotype of *Polystigma amygdalinum*).

Host species: Prunus dulcis (syn. P. amygdalus, Amygdalus communis, A. webbii), Amygdalus nana, A. ledebouriana.

Distribution: Afghanistan (Gattani, 1962 as P. rubrum), Cyprus, Greece (Alexopoulos, 1940 as P. rubrum), India, Iran, Israel, Italy, Kazakhstan (Byzova & Vasyagina, 1981; Byzova, 1983 as P. rubrum), Lebanon (Khatib et al., 1969 as P. ochraceum), Libya (Kranz, 1962 as P. rubrum), Morocco, Portugal, Romania, Spain (Gonzales Fragoso, 1927), Tadzhikistan (Stepanov, 1966 as P. rubrum), Turkey, Ukraine.

This species is a serious pathogen of almonds in the Middle East, often causing premature defoliation (e.g. Kranz, 1962). It has been referred to in the past both as *Polystigma ochraceum* (a synonym of *P. fuloum*) and *P. rubrum*, but is distinct from these species in stromatal morphology and ascospore shape. The development and ascoma formation of *P. amygdalinum* (as *P. ochraceum*) was studied by Ghazanfari & Banihashemi (1976). They found that mature ascomata were formed most plentifully in leaves collected from affected trees in October, and their formation was dependent on a sufficiently low incubation temperature.

The fungus appears to be susceptible to various fungicides, although these are only efficaceous when applied at petal fall, when the ascospores are being transmitted from overwintered stromata to young leaves (Banihashemi, 1990). Control can also be effected by burning of fallen leaves in the autumn and winter.

This taxon is described as a new species due to the difficulties of typifying unequivocally Desmazières' name *Septoria rubra* β *amygdali*, and confusion over the application of Article 59.

Other specimens examined: Cyprus: unlocalized, on almond, comm. 19 Nov. 1930, H. M. Morris (IMI 16910); Agros, on Prunus amygdalus, Sept. 1937, R. M. Nattrass 869 (IMI 16898). India: Shalimar, on Prunus amygdalus, 12 Aug. 1987, V. K. Razdan (IMI 321486). Iran: 40 km SE of Shiraz, Maharlou, on Prunus dulcis, 28 May 1993, Z. Banihashemi (IMI 358821). Israel: Kibbutz Gazit, on Prunus dulcis, 20 Mar. 1992, A. Lin (IMI 353416); near Tel Aviv, Ben Sherman, 6 Aug. ????, I. Reichert (IMI 16897); Givat Oz, on Prunus dulcis, 4 Dec. 1992, A. Sztejnberg (IMI 355456); Givat Oz, Emek Yizre'el, on Prunus dulcis, 1 Jan. 1993, A. Sztejnberg (IMI 358797); same locality and host, 19 Feb. 1993, s. coll. (IMI 358816); Lower Galilee, Gazit, on Prunus dulcis, 1 Jan. 1993, A. Sztejnberg (IMI 358796); same locality and host, 19 Feb. 1993, s. coll. (IMI 358817); Golan Heights, Kefar Haruv, on Prunus dulcis, 1 Jan. 1993, A. Sztejnberg (IMI 358798).
Italy: dintorni di Bologna, on Amygdalus communis, estate 1889, G. E. Mattei (IMI 16905; Briosi & Cavara, Funghi Parassiti delle Piante Coltivate ed Utili no. 145). Morocco: El Hadjeb, on Amygdalus communis, 15 Sep. 1937, R. Delécluse (IMI 16908, UPS; Mycotheca generalis; exs. Rev. Mycol. no. 19). Portugal: Azores, unlocalized, on almond, comm. Nov. 1924, Bensanda (IMI 16908). Romania: reg. Dobrogea-Ostrov, 1957, M. Olangiu (IMI 150579; Savulescu, Herbarium Mycologicum Romanicum no. 1765). Turkey: Ankara, on Amygdalus webbii, 22 Oct. 1944, collector indecipherable (WSP 30529).

Polystigma deformans Syd., Annls Mycol. 34: 417, 1936.

Stromata to 30 mm diam., restricted to emerging leaves and apparently arresting development of young shoots, sometimes occupying almost the whole of the leaf, the surface pale ochre to reddish brown (dried material), often causing the leaf to incurl, to *ca* 1 mm thick, inner tissues hyaline to pale yellow, composed of hypertrophied leaf cells filled with crystalline material interspersed with ramifying hyphae.

Anamorph: conidiomata 150–250 µm diam., \pm spherical to flattened, the wall poorly developed, difficult to distinguish from the stromatal tissue. Conidiogenous cells arranged over \pm the whole of the inner surface, $15-21 \times 2 \cdot 5-3 \cdot 5$ µm, rather irregular, \pm cylindrical, sometimes swollen at the base, often curved, apparently proliferating at least sometimes periclinally. Conidia $38-53 \times ca$ 1 µm, \pm cylindrical, the basal portion usually slightly swollen, fusiform, often sigmoidally curved, hyaline, aseptate.

Teleomorph: ascomata immersed within the stroma, the ostioles epigenous, visible from the surface only as slightly sunken dark brown to black spots *ca* 25 μ m diam., \pm spherical, the wall fairly thin, \pm hyaline, difficult to distinguish from the stromatal tissue, composed of very thin-walled pseudo-parenchymatous cells, the ostioles periphysate. Paraphyses tapering gradually, very thin-walled. Asci cylindric-clavate, very thin-walled at all observed stages, without developed apical structures. Ascospores not seen [12–15 × 5–6 μ m, ovoid-cylindrical to ellipsoidal, narrower at the base, sometimes slightly curved; Sydow, 1936].

Typification: **China**: Beijing, Prince park, on *Prunus armeniaca*, 15 Sept. 1935, Y. C. *Wang* (B – holotype, lost and presumed destroyed); same locality and host, 1932, Y. C. *Wang* 233 (B, lost and presumed destroyed; HMAS 132821), anamorphic stage cited by Sydow.

Host species: Prunus armeniaca, P. davidiana.

Distribution: China.

The material examined contains only conidiomata and immature ascomata. Its identity, therefore, could not be unequivocally established, nor could its relationships. The species as interpreted here might be close to *Polystigma amygdalinum*, but the blackish pigmentation around the ostioles and the very long conidia serve as distinguishing features.

The restriction of stromata to young leaves seems diagnostic, a feature noted in the original description, and their at least almost complete maturation while still attached to the tree is also noteworthy.

Other specimens examined: China: prov. Shansi austr., Yüan-ch'ü distr., ad pag. Wu-li-Tsun, ca 900 m, on Prunus davidiana, 12 July 1924, H. Smith (Plantae sinenses no. 8298; UPS); Hebei Province, Pingshang county, on Prunus armeniaca, May 1990, S. M. Tian (IMI); Liaoning, Xingcheng, on Prunus armeniaca, 12 July 1955, Guang-zheng Jiang 6036 (HMAS 13334); Shandong, Muping, on Prunus armeniaca, 28 May 1930, T. N. Liou 6669 (HMAS 161); Beijing, Fangshan, on Prunus armeniaca, 26 June 1935, Fong-yan Huang (HMAS 1615); Liaoning, on Prunus armeniaca, 19 May 1950, T. N. Liou 259 (HMAS 1614).

- Polystigma fulvum DC., in Lamarck & de Candolle, Flore Française 6: 164, 1815. (Figs 5–6)
- Dothidea fulva (DC.) Fr., Systema Mycologicum 2: 554, 1823.
- Hypocrea fulva (DC.) De Not., Erb. Critt. Ital. no. 1473, 1865, in sched.
- Polystigma fulvum Pers., in Mougeot & Nestler, Stirpes Cryptogamae Vogeso-Romanae no. 271, 1812, in sched. Nom. inval. (Art. 32).
- Polystigma fulvum (Fr.) Tomilin, Botanicheskii Materialy 16: 137, 1963. Based on Dothidea fulva (DC.) Fr. Nom. inval., Art. 33.2; full reference to basionym not cited, and now unnecessary under the modern nomenclatural rules.
- Xyloma rubrum β padi Funck, Cryptog. Gewächse des Fichtelgebirg's no. 322, 1801; in sched. Nom. inval. (Art. 32).
- Xyloma aurantiacum Schleich., Plantae Cryptogamae Helveticae no. 487, 1807. Nom. inval. (Art. 32).
- Sphaeria ochracea Wahlenb., Flora Lapponica: 518, 1812.
- Dothidea ochracea (Wahlenb.) Fr., Summa Vegetabilium Scandinaviae **2**: 387, 1849.
- Polystigma ochraceum (Wahlenb.) Sacc., Nuovo Giorn. Bot. Ital. 8: 181, 1876.
- Sphaeria padi J. C. Schmidt & Kunze, in Holl, Schmidt & Kunze, Deutschland Schwämme: 1, 1815, in sched. Nom. inval. (Art. 32).
- Sphaeria xantha Fr., Observationes Mycologici 1: 172, 1815, nom. illeg. (Art. 63).
- Polystigma aurantiacum Pers. ex Fr., Systema Mycologicum 2: 554, 1823, nom. inval. (Art. 34); apparently erroneously attributed in synonymy to Persoon, Mycologia Europaea t. 5, f.1, 1822.
- Libertella fulva Thüm., Mycotheca Universalis no. 1195, 1878, in sched.

Immature stromata (in summer and autumn) without a delimited infected area, at first hardly causing hypertrophy of the leaf, to *ca* 10 mm diam., roughly circular, hologenous, the adaxial surface yellow to pale brown, quickly becoming orangebrown and rather thicker due to the development of fungal tissue, the adaxial surface sometimes appearing minutely punctate (perhaps due to leaf glands), and the abaxial surface strongly punctate due to the development of sunken ostioles.

Mature stromata (in late autumn and spring) similar in size

to the immature stromata, but conspicuously thickened (*ca* 1 mm), at first bulging around developing ascomata but eventually becoming more uniformly thickened, at first reddish orange but eventually becoming dark orange-brown, the leaf cuticle eventually peeling away, with 30-200 ascomata, visible as black patches $80-100 \mu m$ diam. on the adaxial surface, and sunken ostioles on the abaxial one. Outer layer of stroma $30-40 \mu m$ thick at the abaxial surface, somewhat thinner at the adaxial one, dark orange-brown, composed primarily of strong tanned leaf tissue. Inner layer at first white but becoming pale brown, composed almost entirely of fungal tissue.

Conidiomata absent.

Ascomata roughly spherical but sometimes slightly flattened, the walls not well differentiated from stromatal tissue, the ostioles not conspicuous, at first clearly sunken but eventually becoming very slightly protuberant. Paraphyses to 12 µm diam., tapering gradually to an acute tip, septate, sometimes inflated between the septa, extremely thin-walled. Periphyses to 20 µm long, 3–4 µm wide at the base, gradually tapering towards the apex. Asci 98–128 × 14·5–16(–18·5) µm, narrowly clavate, long-stalked (to ca 50 µm) the apex obtuse, thin-walled at all stages, with a subapical ring 3–3·5 µm diam. and ca 1 µm thick, 8-spored. Ascospores arranged biseriately, 13·5–15·5 × 5·5–6·5(–7) µm, cylindric-ellipsoidal to obovoid, thin- and smooth-walled, hyaline, aseptate, often guttulate, without a gelatinous sheath.

Typification: **Finland**: Lapponia: Komenji ad Sodankylä, on *Padus*, 5 Sept. 1802, *s. coll*. (UPS; ex herb Wahlenberg, authentic and probably type material of *Sphaeria ochracea* Wahlenb., here designated neotype); Lapponia, Komenji, host not specified. s.d., *Wahlenberg* (K; authentic material of *Sphaeria ochracea* Wahlenb.). **Germany**: unlocalized, on *Prunus padus*, Sept. [year unknown], *s. coll*. (K; Funck, Cryptog. Gewächse des Fichtelgebirg's no. 322, authentic material of *Xyloma rubrum* β *padi* Funck). **Germany**: unlocalized, host not specified, s.d., *s. coll*. (K; Schmidt & Kunze, *Deutschlands Schwämme* no. 1, authentic material of *Sphaeria padi* Schmidt & Kunze).

Host species: Prunus padus L. (syn. Cerasus padus, Padus racemosa), Prunus asiatica (syn. Padus asiatica), Prunus maximowiczii. Records on Prunus grayana (e.g. Anon., 1965) have not been verified.

Distribution: Austria, Belgium [?], China (unverified record cited by Eriksson & Yue, 1988), Czechoslovakia, Finland, France, Germany, Hungary, India, Italy, Japan (Anon., 1965, unverified), Latvia, Norway, Romania, Russia, Sweden, Switzerland, Ukraine, United Kingdom.

Stromata are formed on living leaves in the spring and summer, ascomata developing during the summer and autumn. An anamorph is apparently not produced. Immature asci are present in material collected in September (IMI 12760, 30184), and apparently mature ones in an autumn Italian collection (de Notaris, *Erb. Crittog. Ital.* no. 1473). Ascospore release is probably delayed until the following spring, at least in most regions. Relatively few collections have been seen which bear the mature teleomorph. The described variation of features such as ascus and ascospore size and shape may not therefore adequately reflect their true extent.

Sphaeria ochracea Wahlenb. appears to have been described as a composite of *Polystigma fulvum* and *P. rubrum*. It is here

neotypified as a synonym of *P. fulvum*, in accordance with long-established practice; Fries (1815) appears to have been the first to implicitly restrict application of the name to the fungus on *Prunus padus*. The heterogeneity of Wahlenberg's species concept was apparently one reason why Fries adopted the name *Sphaeria xantha* (here interpreted as superfluous and thus illegitimate) instead of Wahlenberg's name, but he also seemed to consider the first-published name inappropriate bearing in mind the coloration of the fungus.

Fries (1823) adopted de Candolle's name Polystigma fulvum and transferred it to Dothidea; that name is therefore sanctioned and takes precedence over the earlier name Sphaeria ochracea Wahlenb. Fries cited the name Polystigma aurantiacum in synonymy with Dothidea fulva, giving a figure in Persoon (1822) as a source. Although the fungus depicted appears to be Polystigma fulvum, the name is apparently never referred to in Persoon (1822), and is not included in the index to that work (Rogers, Rogers & Seeler, 1942). The epithet presumably originated from Schleicher's nom. nud. Sphaeria aurantiaca (see above). Material has not been seen of Libertella fulva Thüm. Saccardo (1884) stated that the exsiccatum he saw contained asci, and placed the name into synonymy with Polystigma fulvum. If the taxon is conidial as Thümen intimated by his choice of name, synonymy with P. rubrum is more likely.

Limin (1986) investigated the host range of this species (referred to as Polystigma ochraceum) and P. rubrum subsp. ussuriense, and found that P. fulvum would form mature stromata on Padus asiatica, though development was slower than that of Polystigma rubrum subsp. ussuriense. Yellowishorange stromata were also formed on Padus maackii, but little development of the fungus occurred after inoculation onto Prunus dulcis (syn. Amygdalus communis), Cerasus fruticosa, Prunus domestica \times P. ussuriensis, Prunus americana or P. nigra. Limin referred to an anamorphic stage forming on Padus asiatica, but none was found on the only collection seen on that host from eastern Russia (IMI 367561). This is of stromata on senescing leaves collected in September, and contains mature asci. It is possible that there is a further eastern Asiatic form of that species which has an anamorph, so more research is needed.

The collection seen from *Prunus maximowiczii* (LE 146582) is immature, containing only asci in early stages of development. Other features are consistent with identification as *Polystigma fulvum*.

A widely distributed collection on *Pyrus communis* labelled as *Polystigma ochraceum* var. *aurantiacum* Westend., the name perhaps based on *Polystigma aurantiacum* Pers. ex Fr. (Herbier Barbey-Boissier no. 890; ex herb Müller Arg. 1896, K!, UPS!), is actually *Venturia pyrina* Aderh.

Other specimens examined: Austria: Carinthia, pr. Greifenburg, on Prunus padus, Sept. ????, F. von Höhnel (IMI 12670; Crypt. Exs. ed. Mus. Hist. Nat. Vindob. no. 3272); same locality and host, Sept. 1901, von Höhnel (IMI 22222); Niederösterreich, Purkersdorf, on Prunus padus, July 1940, F. Petrak (IMI 330066; Reliquiae Petrakianae no. 716); Austria inferior, Krems, on Prunus padus, June 1871, Thümen (K; Thümen, Fungi Austriaci no. 178); Carinthia, Bleiburg, on Prunus padus, s.d., Kristof (K, WSP; Flora Exsiccata Austro-Hungarica no. 1577); Austria inf., Senftonberg, host not specified, s.d., s. coll. (K; ex herb Thümen). Belgium [?]: unlocalized, on Prunus padus, s.d., s. coll.,

(K; Mougeot & Nestler, Stirp. Crypt. Voges. no. 271). Czechoslovakia: am Sattler, in montibus sudeticis, host not specified, s.d., T. Bail (K; Rabenhorst, Herb. Mycol. edn 2, no. 579) [mature asci]. Czechoslovakia [?]: Sachsen, Erzgebirge, bei Bockau, on Prunus padus, 28 July 1885, W. Krieger (K; Krieger, Fungi Saxonici no. 229a); same locality and host, 27 Sep. 1886, W. Krieger (K; Krieger, Fungi Saxonici no. 229b) [mature asci]. Finland: Ob, Sdeni, Ajos, on Prunus padus, 22 July 1959, E. R. Julin (UPS); Ostrobotnia borealis: Ii, Maakrunni, on Prunus padus, 6 Aug. 1933, J. I. Liro & H. Roivanen (IMI 60898, UPS; Liro, Mycotheca Fennica no. 870); Karelia ladogensis: Suistamo, Jalonvaara, Tupinmylly, on Prunus padus, 13 Aug. 1937, J. I. Liro & H. Roivanen (UPS; Liro, Mycotheca Fennica no. 477); Ostrobotnia australis: Maalahti, Storskär, on Prunus padus, July 1962, L. Roivanen & H. Roivanen (UPS); Ks Posio Pernu, riverside grove by Kurttajoki (2 km upstream of Koivuköngäs falls), on Prunus padus, 23 Aug. 1964, T. Ulvinen (UPS; ex herb Univ. Oulu); Regio Aboensis: Iniö, Lökholm, on Prunus padus, 22 July 1932, L. E. Kari (IMI 16896). France : Jura, on Prunus padus, s.d., Morthier 889 (UPS; ex herb Fuckel 1894; ex herb Barbey-Boissier); Jura, on Prunus padus, s.d., Morthier (K; Fuckel, Fungi Rhenani no. 1826). Germany: Driesen, on Prunus padus, s.d., Lasch (K; Rabenhorst, Herb. Mycol. edn 2, no. 69); Franconia, Eschenau, on Prunus padus, autumn 1864, P. Reinsch (K; Rabenhorst, Fungi Europaei no. 1036); Reichenhall, on Prunus padus, Aug. 1869, A. Braun (K; Rabenhorst, Fungi Europaei no. 1358); Dresden, host not specified, s.d., Rabenhorst (K; ex herb Cooke); unlocalized, on Prunus padus, s.d., s. coll. (K; Knieff & Hartm., Pl. Crypt. Badens. no. 65); Göttingen, host not specified, 1835, Wissmann (K); ca. Östrich, host not specified, s.d., s. coll.. (K; Fuckel, Fungi Rhenani no. 2664, originally identified as Polystigma rubrum) [mature ascomata]; Eisleben, on Prunus domestica, 1875, J. Kunze (K; ex herb Kunze) [mature ascomata; the host is probably misidentified]. Hungary: Comit. Szepes: Iglofüred, on Prunus padus, Sept. 1905, F. Filarsky (IMI 30184, UPS, WSP 18151; Petrak, Mycotheca generalis no. 284). India: Kanawar, Punang Forest, 8500', on Prunus padus, 8 Oct. 1890, A. Barclay (K). Italy: Val Anzasca, Macugnaga, on Cerasus sp. ('un ciliegio'), autumn 1865, de Notaris (K; Erbar. Crittogam, Ital. no. 1473) [mature teleomorph]; Sudtyrol, Predazzo, on Prunus padus, 1885-6, Arnold (K; Rehm, Ascomyceten no. 872). Latvia: Zemgale: distr. Dobele, Telrvete, in silvam ad cementario, on Prunus racemosa, 27 July 1956, E. Vimba (UPS; Fungi Latvici no. 6). Norway: Troms: Nordreisa, Bilto, ca 200m, on Prunus padus, 6 Aug. 1960, L. Roivanen & H. Roivanen (UPS; ex H); Vesterålen: Hadselöy, Ongstad, vid stigen till Storvand, ca 100m, on Prunus padus, 21 Aug. 1966, H. Smith 4826:2 (UPS); Hordaland: Kvam hd., Karpedammen ved Porsmyr, on Prunus padus, 17 Aug. 1975, F.-E. Eckblad (UPS: ex herb Univ. Bergen); Gtta. [?], on Prunus padus, 28 July 1947, F. J. Newhook (IMI 16833); Kongsvoll, near Oppdal, on Prunus padus, Aug. 1985, S. M. Francis (IMI 314478). Romania: Moldova: distr. Neamt, Piatra Neamt, pe muntele Cozla, on Prunus padus, 30 July 1954, T. Savulescu (IMI 28934; Herbarium Mycologicum Romanicum no. 1301). Russia: Siberia, Krasnoyarsk, Minusinsk, on Prunus padus, s.d., Martianoff (UPS; ex herb Thümen); European Russia, Novgorod, ad fluv. Tigoda, on Prunus padus, 1894, V. Komarov (K; Jaczewski, Komarov & Tranzschel, Fungi Rossiae Exsiccati no. 82); Khabarovsk, Bolshekhekhzirski Reservation, on Padus asiatica, 16 Sep. 1982, L. N. Vasil'eva (IMI 367561); Dal'nevostochnyi Krai, Vladivostokskii okrug, Poluostov Murav'eva Amurskogo, on Prunus maximowiczii, 19 Aug. 1929, V. Transhel' (LE 146582). Sweden: Åre, on Prunus padus, 23 July 1950, G. M. Waterhouse (IMI 42334); unlocalized, host not specified, s.d., s. coll. (K; Fries, Scleromyci Sueciae no. 241, as Sphaeria xantha); ad Jonsered Vestrog, on Prunus padus, 28 Aug. 1889, L. Romell (K; Romell, Fungi Exsiccati Praesertim Scandinavici no. 77); Hosjö, DLr Vika, Karlslund, on Prunus padus, 5 Aug. 1977, R. Morander 3215 (UPS); Gästrikland: Hille parish, Iggön, near the

village on the central part of the island, on Prunus padus, 30 July 1972, R. Santesson 24173 (UPS); Småland: Nöbbele s:n, Orraryd, host not specified, 1881, C. J. Johanson (UPS); Småland: Gränna, Gyllene, Uttern, on Prunus padus, 14 July 1945, K. V. O. Dahlgren (UPS); Småland: Vrigstad, on Prunus padus, July 1887, R. Tolf (UPS); VG Skopde, host not specified, Aug. 1880, J. Carlson (UPS); VG Henneberg: Bårsled, on Prunus padus, 23 July 1889, A. G. Eliasson (UPS); Mössekeys [?], host not specified, 13 Aug. 1869, J. E. Zetterstedt (UPS); VG Finnerödja, on Prunus padus, s.d., G. Neander (UPS); ad Tjufordei in paroecia Åstra Karup, Hallendil, on Prunus padus, 11 Aug. 1927, A. G. Eliasson (UPS); Halland: Getinge, host not specified, s.d., s. coll. (UPS, ex herb Fries); Värmland: Långserud par., Norra Botten, on Prunus padus, 29 July 1889, H. Dahlstedt (UPS); Södermanland: Soderstelje, Hall, on Prunus padus, July 1895, T. Vestergren (UPS); Sdm Allhelgona s:n, Bullersta, on Prunus padus, Aug. 1892 G. V. Schotte (UPS); Södermanland: Strängnäs parish, Hospitalet, on Prunus padus, 12 Aug. 1931, J. A. Nannfeldt 4288 (UPS); Uppland: Hånäs par., Fågeln, on Prunus padus, 2 Sept. 1975, S. Ryman 3629 (UPS); Uppland: Fuubo s:n, Marichued [?] gård, on Prunus padus, 8 Oct. 1928, N. Hyalnder (UPS); Uppland: Vendels s:n, Tomsarbo, on Prunus padus, 19 Sept. 1970, K. Holm & L. Holm (UPS); Uppland: Uppsala, Slattobacken, on Prunus padus, 20 Sept. 1892, A. G. Eliasson (UPS); Uppland; Alvkarleby par., Billudden Peninsula, Billskaten, on Prunus padus, 30 Aug. 1974, N. Lundqvist 9466 (UPS); Uppland: Stockholm, Nacka, on Prunus padus, 2 Aug. 1882, J. Eriksson (UPS; Eriksson, Fungi parasitici scandinaviae no. 198); Uppland: Elfkarelby, Tanunsberg, on Prunus padus, 31 July 1886, E. Henning (UPS); Uppsala, on Prunus padus, 20 Sept. 1884, A. Nilsson (UPS); Uppland: Uppsala (Bondyrka) at the river Hågaån ca 1 km S of Norby, on Prunus padus, 26 Aug. 1927, J. A. Nannfeldt 15790 (UPS); Holmiae, ad Bellevue, host not specified, 23 Sept. 1882, K. J. Haeggblom (UPS); Uppland: Alsihe I, Kungshann, on Prunus padus, 18 Sept. 1898, R. Sernand (UPS); Uppland: Bondkyrka s:n, Fabordarna, on Prunus padus, 20 Sept. 1928, J. A. Nannfeldt 3762 (UPS); Dalarna: Husby parish, N of Flinsberget, on Prunus padus, 1 Sept. 1973, L. Junell 2179 (UPS); Dalarna: Husby par., E of Lövnäs (= 6 km SE of Husby) at the edge of the wood, on *Prunus padus*, 1 Sept. 1973, N. Lundqvist 8714 (UPS); Gästrikland: Hamrånge s:n, Axmar bruk, Overhammar, host not specified, 19 Aug. 1942, G. Lohammar (UPS); Gästrikland: Valbo s:n, Turuvik, Gärrmarkuna W om jainvagstationen, on Prunus padus, 29 July 1938, J. A. Nannfeldt 5591 (UPS), Gästrikland: Hille s:n, Gålgrund, on Prunus padus, 10 Aug. 1972, S. Ahlner (UPS); Dalarna: Transtrand, on Prunus padus, Sept. 1911, N. Sylvén (UPS; Lagerberg & Sylvén, Skogens skadesv. no. 23); Medelpad: Torp s:n, Torpshammar, on Prunus padus, 9 Aug. 1933, J. A. Nannfeldt 4922 (UPS); Ångermanland : Ytterlännäs socken, Sel, on Prunus padus, 13 July 1970, N. Lundqvist 6720 (UPS); Ångermanland: Vitryggeia s:n, Skuleberget, O-siden, on Prunus padus, 14 July 1932, G. B. E. Hasselberg (UPS); Jämtland: ad cataractam Rista in paroecia Undersåker, on Prunus padus, 12 Aug. 1925, A. G. Eliasson (UPS); Jämtland: Frösö, Valla, strandsnår vid Storsjöstranden, on Prunus padus, 22 Sept. 1923, R. Sernander (UPS); Jämtland: Åre, on Prunus padus, 7 Sept. 1885, C. J. Johanson (UPS); Norrbotten: Nedertornea, Laivandden i Vuono, on Prunus padus, 6 Sept. 1942, E. R. Julin (UPS); Norrbotten: Karl Gustav par., Kukkola, on Prunus padus, 11 Aug. 1960, E. R. Julin (UPS). Switzerland: Graubünden: Klosters, Novai, on Prunus padus, 17 July 1970, E. Müller (IMI 163055a, WSP 89027) [mature asci]; Berner Oberland: Kiental, on Prunus padus, 15 Aug. 1926, W. Ryby (IMI 22223, ex hort. bot. Bernensis); Zürich, host not specified, s.d., Müller (K; ex herb Shuttleworth); in montibus prope Neuchâtel, on Cerasus padus, Aug. 1869; P. Morthier (K). United Kingdom: England: near Ilkley, Middleton, on Prunus padus, Sep. 1893, H. T. Soppitt (K; ex herb Crossland); Scotland: banks of the Clunie, on Prunus padus, July 1895,

W. Gardiner (K); Scotland: near Aberdeen, host not specified, 1869, s. coll. (K; Cooke, Fungi Britannici Exsiccati no. 464); unlocalized, host not specified, s.d., s. coll. (IMI 16899, K; Cooke, Fungi Britannici Exsiccati edn 2, no. 578).

Polystigmina pallescens Petr., in Petrak & Ahmad, Sydowia 8: 183, 1954.

Stromata formed on living leaves in the spring and summer, conidiomata developing during the summer and autumn. Ascomata formed in mature stromata; immature asci are present in material collected late in the season. Ascospore release is probably delayed until the following spring.

Stromata without a delimited infected area, at first hardly causing hypertrophy of the leaf, to *ca* 17 mm diam., roughly circular, sometimes coalescing, hologenous, pale yellow to pale brown, quickly becoming bright orange to orange-brown and rather thicker due to the development of fungal tissue, the adaxial surface with minute brown spots to 50 μ m diam. where the conidiomatal ostioles emerge and the abaxial surface with ill-defined greyish-brown blotches to 250 μ m diam. where the ascomata are developing, with darker sunken ostiolar regions to 75 μ m diam.

Anamorph: Conidiogenous cells arising from a poorly defined layer of small-celled hyaline *textura angularis*, sometimes in fascicles but even short conidiophores almost never developed; $24-32 \times 2\cdot 5-3 \mu m$, almost cylindrical, the apex acute, proliferation unclear. Conidia 55–120 μm in length, filiform (*ca* 0.5 μm wide), very flexible, often with a very inconspicuous globose knob at the base, hyaline, apparently smooth and aseptate.

Typification: **Pakistan**: Kagan Valley, on *Prunus cornuta*, 26 July 1951, *S. Ahmad* 4427 (GZU – holotype of *Polystigmina pallescens*, not seen).

Host species: Cerasus sp., Prunus cornuta.

Distribution: India, Nepal, Pakistan.

This species was described as an anamorph, but is clearly refrable to *Polystigma*, and some specimens examined (e.g. IMI 71436) have immature asci. The coloration of the young stromata suggests affinities with *Polystigma fulvum*, but that species does not produce an anamorph. The conidia of *Polystigmina pallescens* are significantly longer than those of other known species of *Polystigma*. The holotype has not been seen, but several of Ahmad's collections from similar localities are in IMI, and Petrak's description is comprehensive. There is little doubt as to the identity of the species.

Other specimens examined: India: unlocalized, on Prunus cornuta, 8 July 1973, R. D. Ram 2 (IMI 185885); Garwhal Himalaya, on Betula alnoides (probably actually Prunus sp.), Aug.–Sept. 1983, R. D. Gaur R-76 (IMI 280952); same data, R. D. Gaur R-80 (IMI 280956). Nepal: below Mugu, Mugu Khola, 3500 m, on Cerasus sp., 24 Aug. 1952, O. Polunin, W. R. Sykes & L. H. J. Williams 3019 (K). Pakistan: Shogran, on Prunus cornuta, 27 July 1956, S. Ahmad 14149 (IMI 81154); same locality and host, 25 July 1956, S. Ahmad 14148 (IMI 81153); Swat, Kalam, on Prunus cornuta, 21 Aug. 1952, S. Ahmad (IMI 236615; Reliquiae Petrakianae no. 360); Kamal Ban Forest, on

Prunus cornuta, 20 Oct. 1954, A. H. Khan (IMI 71436, ex herb. Pakistan Forest Institute no. 400; immature asci).

Polystigma rubrum (Pers.) DC., in Lamarck & de Candolle,Flore Française 6: 164, 1815.(Fig. 8)

subsp. rubrum

Xyloma rubrum Pers., Observationes Mycologiae 2: 101, 1799.

- Polystigma rubrum Pers., in Mougeot & Nestler, Stirpes Cryptogamae Vogeso-Romanae no. 270, 1812, nom. inval. (Art. 32).
- Sphaeria rubra (Pers.) Fr., Observationes Mycologicae 1: 172, 1815.
- Dothidea rubra (Pers.) Fr., Systema Mycologicum 2: 553, 1823.
- Septoria rubra (Pers.) Desm., Ann. Sci. Nat., Bot. sér. 2, **19**: 343, 1843 [anamorph].
- Libertella rubra (Pers.) Bonord., Handbuch der Allgemeine Mykologie 1: 55, 1851 [anamorph].
- Polystigmina rubra (Pers.) Sacc., Sylloge Fungorum 3: 622, 1884 [anamorph].
- Sphaeria hyetospilus Mart., Flore Cryptogamica Erlangensis: 478, 1817, nom. illeg., Art. 63. Xyloma rubrum Pers. and Sphaeria padi Duv. cited in synonymy; apparently a composite of the two taxa.
- Polystigma rubrum forma pruni-spinosae Sacc., Mycotheca Veneta no. 637, 1876; in sched. Nom. inval. (Art. 32).
- Polystigma rubrum forma pruni-domesticae Sacc., Mycotheca Veneta no. 638, 1876; in sched. Nom. inval. (Art. 32).
- Polystigmina rubra forma ramipetiolicola Sacc., Annls Mycol. 1: 26, 1903 [anamorph].

Stromata: developing throughout late spring and summer on living leaves, producing conidia in summer and autumn, and ascospores from fallen overwintered leaves the following spring; the conidiomata sometimes persisting in an apparently viable condition until the ascomata are mature.

Conidial stromata to 10(-35) mm diam., irregularly shaped but usually roughly circular, yellowish-brown in very young lesions but quickly becoming orange to reddish brown, becoming darker in the central region, hologenous, the surrounding leaf tissue hardly affected, containing a large number of conidiomata; composed of an upper layer of plant tissue 40–50 µm thick whose cells are filled with bright orange-brown material, an intermediate layer 300–500 µm thick of almost completely occluded angular to vertically elongated fungal cells, and a lower layer similar to the upper one.

Anamorph: conidiomata 150–250 μ m diam., roughly spherical, epigenous or hologenous, the ostiole epigenous, very inconspicuous. Conidiomatal wall very poorly developed, not clearly distinguishable from the stromatal tissue. Conidiogenous cells developing over the entire inner surface of the wall, often laterally from sequential cells of short conidiophores to 10 μ m long and *ca* 2 μ m wide; derived from a thin layer of *textura angularis* with hyaline thin-walled cells 3–5 μ m diam. Conidiogenous cells 13–24 × 2–3 μ m, at first usually cylindrical but gradually tapering towards the upper region, which is slightly irregular in appearance due to successive conidial scars; usually proliferating sympodially. Conidia (22–) $28-42 \times 0.5-0.75 \mu m$, the lower part (to approximately the mid point) very narrowly lanceolate to fusiform, the upper part filiform (*ca* 0.25 μm wide), sigmoidally curved, the base \pm truncate, hyaline, aseptate, apparently smooth-walled.

Teleomorphic stromata 1–5 mm diam., irregularly shaped but usually roughly circular, strongly raising the adaxial surface of the leaf, flat or slightly concave on the abaxial surface, hologenous, reddish brown to black, sometimes faintly verrucose (a feature of the leaf epidermal architecture), the ostioles sometimes inconspicuous but appearing as small black dots on paler stromata, often somewhat sunken; composed of pigmented outer layers 20–40 μ m thick and a hyaline inner layer containing the ascomata.

Ascomata \pm spherical. Paraphyses rather sparse, to 7 µm diam., gradually tapering towards the apex, very thin-walled, strongly inflated between the septa: Asci 94–118×10^{.5}– 12 µm, narrowly clavate, very long-stalked (to *ca* 60 µm), very thin-walled at all stages, the apex obtuse, with an apical ring 2–3 µm diam. and *ca* 0^{.5} µm thick, 8-spored. Ascospores arranged biseriately, 10^{.5}–14×3^{.5}–4^{.5}(–5^{.5}) µm, cylindricellipsoidal, occasionally obovoid, occasionally slightly curved (fabiform), hyaline, aseptate, thin- and smooth-walled, without a gelatinous sheath.

Typification: 'Utplurimum automno, in foliis Pruni domesticae, rarius Pr. spinosae' (typification statement of Xyloma rubrum). Belgium [?], unlocalized, 'in foliis Pruni domesticae et spinosae, autunno', s. coll. (IMI!, K!; Mougeot & Nestler, Stirp. Crypt. Vogesorum no. 270, authentic material of Polystigma rubrum Pers., nom inval.). Italy: Belluno, Cadore, on Prunus spinosa, 1874, S. Venzo (K!; Saccardo, Mycotheca Veneta no. 637, authentic material for Polystigma rubrum forma pruni-spinosae). Italy: Treviso, Vittorio, on Prunus domestica, 1875, s. coll. (K!; Saccardo, Mycotheca Veneta no. 638, authentic material for Polystigma rubrum forma pruni-domesticae). Italy: Treviso, Volpago, Montello, in ramulis tenellis Pruni spinosae, Sept. 1902, s. coll. (?PAD – holotype of Polystigmina rubra forma ramipetiolicola, not seen).

Host species: Prunus domestica L., Prunus institia L. (syn. Prunus domestica subsp. institia), Prunus spinosa L. Records on Prunus salicina (e.g. Anon., 1965, 1972) have not been verified, and may refer to subsp. ussuriense. The host cited as Malus baccata (see below) is probably misidentified.

Distribution: Armenia, Austria, Belgium (Grove, 1937), Bulgaria (Yossifovitch, 1937), Channel Islands, China, Cyprus, Czechoslovakia, Denmark, Finland, France, Germany, Greece (Pantidou, 1973), Hungary, India (Bilgrami et al., 1979), Iran, Iraq, Ireland, Italy, Japan (Anon., 1965), Kazakhstan (Byzova & Vasyagina, 1981), Kirghizia (Byzova & Vasyagina, 1981, unverified), Korea (Anon, 1972, unverified), Lebanon (Khatib et al., 1969), Lithuania (Brundza, 1961), Moldova (Fatina, 1989), Netherlands (Oudemans, 1897), Poland, Portugal (Sousa de Câmara, 1916), Romania, Russia, Serbia, Spain (Gonzales Fragoso, 1927), Sweden, Switzerland, Tadzhikistan (Stepanov, 1966), Turkey, Ukraine, United Kingdom, Uzbekistan (Byzova & Vasyagina, 1981, unverified). The records cited by Byzova & Vasyagina (1981) from countries other than Kazakhstan do not cite host names; they may thus refer to Polystigma amygdalinum instead. Their statement that the species occurs in North America has not been substantiated.

The typification of *Polystigma rubrum* presents problems if application of the name is to continue with current practice,

not least because the teleomorph and anamorph names have the same basionym, as discussed above. There are only two collections identified as Xyloma rubrum in Persoon's herbarium in L, neither being definite type material as minimal collection data are given. L 910263-760 contains two portions of leaves, containing what may be developing ascomata of Polystigma rubrum. It is inscribed 'Hb. Pers. ded. Letellier' and (in a different hand) 'Dothidea rubra Fr.'). The material is in poor condition, and its identity has not been unequivocally established. L 910263-779 contains several leaves with welldeveloped stromata, but the host is given as Prunus padus and two subsequent annotations (in unknown hands) re-identify the collection as Polystigma fulvum. Clearly, neither of these collections is suitable either as a lectotype or a neotype of Polystigma rubrum. Neotypification with a collection from another source is not carried out here, pending rationalization of Art. 59 with its implications for the generic name.

From evidence provided by serial collections in Serbia, mature ascospores are present in stromata between March and May. In collections from *Prunus domestica*, conidia tend to be shorter and often have shorter apical filiform regions than those from *P. spinosa*, but there is considerable variation between specimens, and the effect if it is statistically significant might be geographical rather than host-related.

There are many literature records of *Polystigma rubrum* on almond (*Prunus dulcis*, syn. *P. amygdalinum*). These are referred here to the newly described species *Polystigma amygdalinum*. The material distributed in Fuckel's *Fungi Rhenani* no. 2664 as *Polystigma rubrum* is in fact *P. fulvum*.

Laestadia circumscissa Sacc. (Saccardo, 1903), was placed into synonymy with *Polystigma rubrum* by von Arx & Müller (1954). No material has been seen, but the fact that ascomata mature in autumn and the stromata form shot-holes in the host leaves suggests that the affinities of this species lie elsewhere. It might be yet another synonym of *Glomerella cingulata*, or indeed a composite of that species and *Polystigma rubrum*; a collection examined from Serbia (IMI 368472) includes both species and exhibits apparently similar symptoms.

Other specimens examined : Armenia : near Erevan, on Prunus domestica, Sep. 1956, K. Abakyan & D. Babayan (IMI 75984; Griby SSSR (Moskovskoe Obshchetvo Ispytatelei Prirody) no. 120). Austria: Carinthia, prope Bleiburg, on Prunus domestica, s.d., Kristof (UPS; Flora exsiccata Austro-Hungarica no. 1981); Mähr.-Weisskirchen, on Prunus domestica, Aug. 1929, F. Petrak (IMI 30800, WSP 18577; Petrak, Mycotheca Generalis no. 700); Austria inf., Dross, on Prunus spinosa, s.d., s. coll. (K, ex herb Thümen, Plowright). Channel Islands: Guernsey: Petit Port, on Prunus spinosa, 16 Sep. 1948, M. B. Ellis & J. P. Ellis (IMI 31818, K); Guernsey, unlocalized, on Prunus spinosa, 1847, s. coll. (K). China: Shansi austr., Yüan-ch'iü district, Hsiung-shanting, ca 800 m, on 'Malus baccata' [probably actually Prunus sp.], 10 July 1924, H. Smith (Plantae sinenses no. 8299, UPS). Cyprus: Trikoukhia, on Prunus domestica, comm. 3 Nov. 1929, H. M. Morris (IMI 16909; very immature, identification doubtful). Czechoslovakia: Bohemia, Teplitz Schönau, on Prunus domestica, July 1901, Eichler [?] (IMI 16901); Brno, on Prunus domestica, Sep. 1924, R. Picbauer (IMI 16904; Baudys & Picbauer, Phytopathologicky Herbár Pestovanych Rostlin no. 30). Denmark: Fyen Skaarup, on Prunus institia, 7 Sep. 1882, C. J. Johanson (UPS); Micus Klink [?], host not specified, 3 Aug. 1873, O. Thoen (UPS). Finland: ad Panckoco, on Prunus domestica, 27 Aug. 1811, s. coll., (UPS; ex herb Wahlenberg, authentic material of

Sphaeria ochracea Wahlenb.). France: Var, Le Luc, on Prunus spinosa, s.d., s. coll (K; ex herb Shuttleworth); Puy de Dôme, Royat, on Prunus spinosa, Aug. 1890, A. Héribaud (K); unlocalized, on Prunus spinosa, s.d., Fautrey 1627 (UPS); Colmar, on Prunus domestica, 1869, Kaufmann (UPS); unlocalized, on Prunus spinosa, Fautrey 1068 UPS: unlocalized, on Prunus sp., s.d., Ripart (UPS); Germany: Westfalen: Siegen, Gaiargründ [?], bei Hainiken, on Prunus spinosa, 8 Oct. 1922, A. Ludwig (IMI 16911, ex herb Ludwig); Westfalen: Siegen, Hainiken, on Prunus spinosa, 16 July 1922, A. Ludwig (IMI 16912, ex herb Ludwig); unlocalized, on various Prunus species, s.d., s. coll. (K; Fuckel, Fungi Rhenani no. 1003); Berlin, on Prunus domestica, Aug. 1882, P. Sydow (K; Sydow, Mycotheca Marchica no. 958); Sachsen, Halle, bei Oberröblingen, on Prunus domestica, Aug. 1877, R. Staritz (UPS; ex herb Staritz); Mittelfranken: Hersbruck, Aschbach, on Prunus spinosa, 4 July 1948, K. Starcs 6997 (UPS); Mittelfranken: Hersbruck, Ellenbach, on Prunus spinosa, 8 Sep. 1948, K. Starcs 9337 (UPS); bei Dresden, on Prunus domestica, Oct. 1882, P. Magnus (UPS); Haut Rhin, Websheim, 210m, sur pruniers, 20 Aug. 1869, J. P. Becker (UPS; ex herb Becker). Hungary: Transilvania australis, ad pagam Giregrace, on Prunus sp., 25 Sep. 1875, F. Michael (UPS; ex herb Richter); Iran: Lorestan, Khorram Abad, on Prunus domestica, 20 Feb. 1989, V. Minassian (IMI 358822); Lorestan, Hamedan, on Prunus domestica, 4 Mar. 1991, V. Minassian (IMI 358824); same locality and host, 14 Mar. 1990, V. Minassian (IMI 358825); same locality and host, 10 Apr. 1991, V. Minassian (IMI 358826); Lorestan, Tooysarkan, on Prunus domestica, 4 May 1991, V. Minassian (IMI 358823); Lorestan, Hamedan, on Prunus domestica, 10 May 1991, V. Minassian (IMI 358827, mature ascospores); same locality and host, 10 June 1991, V. Minassian (IMI 358828). Iraq: Shaklaurh, on Prunus ?domestica (misidentified as Morus sp.), 22 Oct. 1976, A. A. Attrackchi (IMI 214602; ex herb. Dep. Pl. Prot., Hammam Al-Alil no. 28). Ireland: Co. Tipperary, shore of Lough Derg, near Gortmore Point, on Prunus spinosa, 10 July 1967, M. P. Scannell (K); Co. Mayo, Lough Carra, on Prunus spinosa, 20 July 1966, M. Scannell (K); Co. Clare, Burren, N of Leamanah Castle, by Lough Aleenaun, on Prunus spinosa, 12 July 1966, M. J. P. Scannell; 1 mile W of Sligo town, 7 July 1962, M. Scannell (K). Italy: Serra-Pamparato, on Prunus domestica, 1888, Mondovì (IMI 16900; Briosi & Cavara, I Funghi Parassiti delle Piante Coltivate ed Utili no. 12); ad Oldenico, presso Vercelli, on Prunus spinosa, 1858, Malinverni (K; de Notaris, Erb. Critt. Ital. no. 240). Romania: Oltenia, Segarcea, prope pagum Tîmburesti, 90m, on Prunus domestica, 10 Sep. 1963, I. Comes, I. Ene, M. Costescu & I. Terbea (IMI 120527; Flora Oltenia Exsiccata no. 132); Muntenia, distr. Ilfov, Buceresti, on Prunus domestica, 22 Oct. 1924, T. Savulescu & C. Sandu (IMI 16902, 16913; Herbarium Mycologicum Romanicum no. 556). Russia: Chuvashskaya ASSR, Il'inka, Zelenaya Stoyanka, banks of river Volga, 4 Aug. 1978, V. A. Mel'nik (IMI 249345); Primorskii Krai, environs of Vladivostok, on cultivated plum, 6 Apr. 1993, L. N. Vasil'eva (IMI 367564; teleomorph); prov. Kursk, distr. Dmitriewsk., Derjutschino, on Prunus domestica, July-Aug. 1911, A. Bondarzew (WSP 14193; Bucholtz, Fungi Rossiae exsiccati ser A., no 92). Serbia: Valjevo, on Prunus domestica, June 1986, M. Arsenijevic (IMI 368472); Valjevo, Jovanja, on Prunus domestica, Mar. 1994, M. Arsenijevic (IMI 368473); same locality and host, 17 Feb. 1995, S. Stojanovic (IMI 368474); same locality and host, 10 Mar. 1995, S. Stojanovic (IMI 368475); same locality and host, 8 Apr. 1995, S. Stojanovic (IMI 368476); same locality and host, 8 May 1995, S. Stojanovic (IMI 368477). Sweden: Göteborg, on Prunus spinosa, 17 Aug. 1895, K. L. Larsen (IMI 207794; ex herb LD); Bergiiland, unlocalized, host not specified, 5 Aug. 1889, collector indecipherable (UPS); Skåne: Kullen, host not specified, 18 July 1909, H. Du Rietz (UPS); Skåne: ad Apelryd, prope Bånad, on Prunus spinosa, 14 Sep. 1925, A. G. Eliasson (UPS); Skåne: Dalby, on Prunus spinosa, 15 Oct. 1890, L. Romell (UPS; Eriksson, Fungi parasitici scandinaviae no. 345);

Blek, Karlehamn, on Prunus spinosa, Aug. 1883, C. J. Johanson (UPS); Öland, ad Fariestaden, on Prunus spinosa, 30 Aug. 1914, A. G. Eliasson (UPS); Öland, Torslunda socken, Arontorp, on Prunus spinosa, 6 Sep. 1963, L. Junell 1622 (UPS); Gotland: Visby, Galybeigu, on Prunus spinosa, 14 July 1895, A. G. Eliasson (UPS); Gotland, norr om Visby, on Prunus spinosa, July 1895, T. Vestergren (UPS); Halland, unlocalized, host not specified, s.d., s. coll. (UPS; ex herb Fries); Halland, ad Godhem in paroecia Oustala, on Prunus spinosa, 17 June 1914, A. G. Eliasson (UPS); Getange, host not specified, s.d., s. coll. (UPS; ex herb Fries); Halland, host not specified, s.d., s. coll. (UPS; ex herb Fries); Bohuslan, Ljungs s:n, Aufacterod, on Prunus spinosa, 28 July 1887, A. G. Eliasson (UPS); Bohuslan, Storon ex Gaderoa, on Prunus spinosa, 30 Aug. 1911, A. G. Eliasson (UPS); Bohuslan, in Lindholen ad Skafioland, on Prunus spinosa, 2 Aug. 1911, A. G. Eliasson (UPS); Bohuslan, Spekeröd s:n, 0.5 km NO om Röd, on Prunus spinosa, 8 Sep. 1946, F. Karlvall (UPS); Bohuslan, Spekeröd s:n, 0.5 km NO om Röra gård, on Prunus spinosa, 10 Sep. 1947, F. Karlvall 3249 (UPS); Bohuslan, rod prope Hallevikstrand, on Prunus spinosa, 16 Aug. 1882, O. Nordstedt (UPS); Göteborg, on Prunus spinosa, 17 Aug. 1895, A. L. Larsen (UPS); Osterg. Tåby, Beateborg, host not specified, 11 Aug. 1913, P. A. Issen (UPS); Uppland: Overgran parish, Arnö, on Prunus spinosa, 14 July 1936, S. Junell (UPS). Switzerland: Vaud, Valleyres, on Prunus spinosa, 15 Sep. 1886, J. Veller (K; Barbey, Société Dauphinoise no. 4385 bis). Turkey: Kütahya, on Prunus domestica, 13 Aug. 1968, H. K. Wagnan 29 (IMI 135768). United Kingdom: England: Cornwall, near Perranporth, Lambourne, on Prunus spinosa, 16 Oct. 1926, F. Rilstone (K, LIV); England: Porlock Beach, on Prunus spinosa, 25 May 1957, P. K. Austwick (IMI 69433); England: Bungay, host not specified, s.d., Stock (K); Northamptonshire, host not specified, July 1848, s. coll. (K; ex herb Broome); England: North Wootton, on Prunus spinosa, s.d., C. B. Plowright (K; Sphaeriacei Britannici no. 15); England: near Ryde, host not specified, Sep. 1843, s.d., s. coll. (K; ex herb Broome); England: Bungay, host not specified, Sep. 1865, M. C. Cooke (K; Cooke, Fungi Britannici Exsiccati no. 182); England: Weymouth, near Portisham, 15 Aug. 1890, s. coll. (K; ex herb Grove); England: Brixham, on Prunus spinosa, Aug. 1889, W. R. Hughes (K); England: Scarborough, Hayburn Wyke, on Prunus spinosa, 14 Aug. 1892, s. coll. (K; ex herb Grove); England: near Weymouth, on Prunus spinosa, 10 Aug. 1890, s. coll. (K; ex herb Grove); England: Cornwall, Saltash, on Prunus spinosa, 8 Sep. 1932, s. coll. (K; ex herb Grove); England: North Wootton, Lex's [?] Wood, host not specified, Sep. 1871, C. B. Plowright (K); England: Isleworth, host not specified, s.d., Murray (K); England: Oxfordshire, Crowell Hill, on Prunus spinosa, July 1844, s. coll. (K; ex herb Ayres); England: East Bergholt, host not specified, Sep. 1855, s. coll. (K; ex herb Currey); England: Weymouth, on Prunus spinosa, 15 Aug. 1890, s. coll. (K; ex herb Grove); England: Devon, cliffs W of Ilfracombe, on Prunus spinosa, Aug. 1930, R. W. G. Dennis (K); England: Ilfracombe, Cairn Top, on Prunus spinosa, 30 Aug. 1908, R. H. Philip 1438 (K); England: Shere, host not specified, s.d., Capron (K; ex herb Cooke) [mature ascomata]; England: Hampshire, Basingstoke, near Oakley, on Prunus spinosa, July 1871, R. S. Hill (K); Wales: Anglesey, near Bryn Siencyn, on Prunus spinosa, 19 July 1927, P. G. M. Rhodes 3009 (K); Wales: Lampeter, host not specified, 1841, S. Ralfs (K); Wales: Aberystwyth, on Prunus spinosa, 3 Sep. 1905, s. coll. (K; ex herb Grove); Wales: Abergele, on Prunus spinosa, 26 Aug. 1882, s. coll. (K; ex herb Grove); Wales: Tenby, on Prunus spinosa, Aug. 1925, E. M. Wakefield (IMI 12792); Wales: Aberystwyth, on Prunus spinosa, 3 Sep. 1905, s. coll. (K; ex herb Grove); Wales: Glamorgan, Gower, Mewslade, 17 July 1953, s. coll. 61 (K); Scotland: Dunbartonshire, on Prunus spinosa, s.d., s. coll. (K); Scotland: Midlothian, Auchendinny Woods, s.d., s. coll. (K); unlocalized, host not specified, s.d., s. coll. (IMI 16977; Cooke, Fungi Britannici Exsiccati no. 577, identification doubtful, immature).

subsp. ussuriense (Jacz. & Natalyina) P. F. Cannon, comb. et

Polystigmella ussuriensis Jacz. & Natalyina, in Natal'ina, Mater. Mikol. Fitopatol. Leningrad **8**: 162, 1929.

stat. nov.

Polystigma ussuriense (Jacz. & Natalyina) Prots., Sad i Ogorod 7: 35, 1957.

Rhodoseptoria ussuriensis Naumov, Bull. trimest. Soc. mycol. Fr. 29: 278, 1913 [anamorph].

Differs from subsp. *rubrum* by: ascostromata reddish brown rather than dark brown, with the ostioles distinctly visible and surrounded by a small melanized region; and the conidia which are 38–63 µm long.

Typification: **Russia**: Russian Far East: in prov. Austro-Ussuriensi, on *Prunus* sp. (a Manchurian species), s.d., s. coll. (holotype of *Rhodoseptoria ussuriensis*, not seen; see probable type material cited below). **Russia**: Russian Far East: Shkotovskogo Raiona, near Petrovka, on *Prunus triflora* var. *koreana*, May 1928, s. coll. (holotype of *Polystigmella ussuriensis*, not seen; see possible type material cited below).

Host species: Prunus mandschurica, P. maximowiczii, P. triflora, P. triflora var. koreana, Prunus ussuriensis.

Distribution: Russia (Dalny Vostok region).

Polystigma rubrum subsp. *ussuriense* was originally described as the only representative of the separate genus *Polystigmella*. The stated difference between it and *Polystigma* was that *Polystigmella* had ascospores which were septate. The fungus otherwise appears very similar to *Polystigma rubrum*. The observed septum within the ascospores was presumably an observational error for the juxtaposition of oil droplets, a not uncommon phenomenon when spores are examined in certain mounting media. Some of the specimens examined have poor documentation; two of the collections cited below are possible type material, but it is not easy to reconcile them with the collection data given in the original publications. Only one collection, itself rather sparse, showed mature ascomata.

Polystigma rubrum subsp. *ussuriense* is probably an eastern Asian variant of subsp. *rubrum*, restricted to *Prunus triflora* and immediate relatives. It is possible that there is clinal variation at least in conidium length between the subspecies in northern Europe and eastern Asia, but suitable collections from localities in central Russia have not been seen in order to test this hypothesis. The collection on *Prunus mandschurica* seen has conidia which are slightly shorter on average than those from collections on *Prunus triflora*, but there is insufficient evidence to support the erection of a further taxon. That sample contains semi-mummified fruit infected by the fungus, as well as affected leaves. Subsp. *rubrum* also occurs in eastern Asia, presumably introduced with cultivated plums.

Limin (1986) studied the host specificity of this subspecies (under the synonym *Polystigma ussuriense*), though it is not certain that he was working with subsp. *ussuriense* rather than subsp. *rubrum*. He found that the fungus would cause infections of *Prunus besseyi*, *P. domestica* \times *P. ussuriensis*, *P. americana*, *P. nigra*, *P. salicina*, *P. salicina* \times *P. americana*, *P. calycina* \times *P. nigra* and *P. ussuriensis*. Host species from *Prunus* sections *Armeniaca* and *Cerasus* showed some evidence of

parasitism, but the lesions did not develop fully, although comparatively large yellowish stromata were formed on *Cerasus tomentosa, Prunus spinosa* and *P. cerasifera*. Negligible pathogenic effect was observed on *Spiraea salicifolia* or *Padus asiatica*, and none at all on *Padus maackii* and *Amygdalus communis*. These experiments are in general supportive of subspecific status for *Polystigma rubrum* subsp. *ussuriense*. There is considerable diversity among *Prunus* species from eastern Asia, and their classification needs reinterpretation. It is not improbable that further *Polystigma* taxa remain to be discovered in this region.

Specimens examined: Russia: Dal'nevostochnyi Krai, locality indecipherable, on Prunus triflora, 17 May, O. Natal'ina (LE 146853; possible type material of Polystigmella ussuriensis); Dal'nevostochnyi Krai, Vladivostokskii okrug., okrestnosti g. Vladivostoka, on Prunus triflora, 23 July 1927, V. Transhel' (LE 146588); Dal'nevostochnyi Krai, Primorskaya oblast', Dolina r. Surgan, c Vladimiro Aleksandrov'ske, on Prunus triflora, 13 Sep. 1938, V. I. Protsenko (LE 146581); locality indeciperable, on 'sliva usyrskaya', 5 Aug. 1932, s. coll. (LE 146580); Amur, Blagovestshenk, on Prunus mandschurica, 27 July 1924, Aleksahine (LEP); Primorskii Krai, Spasskii Raion, near Nakhimovskii, on Prunus ussuriensis, 23 Sep. 1981, V. A. Limin (LEP); Yuzhno-ussuriskii Krai, Spasskoe, host not specified, 11 June 1912, Naumov (LEP; probable type material of Rhodoseptoria ussuriensis).

EXCLUDED AND DOUBTFUL SPECIES

- Polystigma adenostomatis Farl., in Ellis & Everh., Fungi Columbiani no. 2049, 1905, in sched.
- = Hyponectria adenostomatis (Farl.) P. F. Cannon, comb. nov.

Infected areas not clearly delimited. Blackened regions to 1 mm diam., rather irregular, the individual ascomata not completely coalescing, containing 1-5 ascomata. Ascomata hologenous, the ostioles epigenous, 250-350 µm diam., spherical to slightly oblate, the ostiolar region shallowly conical. Ascomatal walls poorly developed. Upper wall reduced to a clypeus, 100-140 µm diam., composed of several layers of very degenerate plant cells \pm filled with fairly strongly melanized textura epidermoidea. Lower and side walls almost absent, composed of a narrow layer of almost hyaline fungal tissue surrounded by strongly tanned host cells. Periphyses not seen. Paraphyses well-developed, copious, to 4 µm diam., fairly thinwalled, slightly tapering, septate, branching not seen. Asci formed from a crozier system, 58-66 × 18-22 µm, saccate, short-stalked, thin-walled at all stages of development, the apex rounded, without clearly-defined apical structures, 8-spored. Ascospores arranged biseriately, $13.5-15.5(-18) \times 8-$ 9.5 µm, ellipsoidal to ovoid-ellipsoidal, thin-walled, hyaline, smooth, aseptate, without a mucous sheath.

Typification: U.S.A.: California: San Mateo County, on Adenostoma fasciculatum, 12 April 1903, C. H. Thompson (FH – holotype, K!, WSP 5935! – isotypes of Polystigma adenostomatis).

Host species: Adenostoma fasciculatum Hook. & Arn.

Distribution: U.S.A. (California); only known from the type collection.

The transfer to *Hyponectria* is made with reservations, as that genus is in need of revision, and its taxonomic position relative to the Phyllachoraceae reassessed. Nevertheless, the much-reduced ascomatal wall with melanized material restricted to only a small clypeus is not typical of *Phyllachora*, the other obvious placement for the species.

Phyllachora beaumontii Cooke, Grevillea 13: 63, 1885.

- ? = Auerswaldiella puccinioides (Speg.) Theiss. & Syd., Annls Mycol. **12**: 278, 1914:
- Auerswaldia puccinioides Speg., An. Soc. Cient. Argentina 19: 247, 1885.

Typification: U.S.A.: Alabama, on ?Prunus caroliniana [given as in Ceraso carolia], Beaumont, ex herb. Berkeley no. 4893 (K! – probable syntype of Phyllachora beaumontii, here designated neotype). Unlocalized, ex herb. Berkeley no. 4635 (K! – probable syntype of Phyllochora beaumontii). Unlocalized, ex herb. Berkeley no. 4891 (K! – probable syntype of Phyllachora beaumontii). Unlocalized, ex herb. Cooke (K! – probable syntype of Phyllachora beaumontii). Unlocalized, ex herb. Cooke (K! – probable syntype of Phyllachora beaumontii). Paraguay: Mbocaiate, prope Villa Rica, on leaves of ?Prunus sp., 15 Jan. 1882, B. Balansa (Plantes du Paraguay no. 3443, IMI 158813! – isotype of Auerswaldia puccinioides).

The type material studied of *Auerswaldiella puccinioides* is immature, but appears to belong to the same species as *Phyllachora beaumontii*, as was suspected by Theissen & Sydow (1915). Cooke's name would appear to be published a few weeks previous to that of Spegazzini; the issue of *Grevillea* containing Cooke's paper is dated March 1885, and according to Farr (1973) Spegazzini's work was not published until June of that year. Bearing in mind the lack of complete certainty of publication dates, the immaturity of one of the type specimens and lack of research into species concepts, a new combination is not appropriate.

Phyllachora fructigena (Schwein.) Sacc., Sylloge Fungorum 2: 622, 1883.

- Dothidea fructigena Schwein., Trans. Amer. Phil. Soc. Philadelphia 4: 232, 1832.
- = Botryosphaeria obtusa (Schwein.) Shoemaker, Can. Jour. Bot. 42: 1298, 1964.

Typification: 'in pomis putridissimis in campo dejectis prope Camden' [see below].

None of the collections cited below is adequately documented, and it is possible that they are all authentic material. The only one found to contain spores is the one from Bloxam's herbarium, which could have originated from Schweinitz's collections via Berkeley. This is in poor condition, but almost certainly represents the *Sphaeropsis* anamorph of *Botryosphaeria obtusa*. See Shoemaker (1964) and Sivanesan (1984) for further information. The Schweinitz name probably represents the earliest available name for the anamorph. Bearing in mind the poor condition of the material examined and its dubious type status, not to mention the highly questionable need for a separate name for the anamorph, no new combination is made.

Materials examined; **U.S.A.**: Massachusetts, on 'decaying apples', ex herb. Currey (K); Massachusetts, on 'decaying apple', ex herb. Cooke

(K). Unlocalized, on 'decaying apples', ex herb. Bloxam (K); unlocalized, on 'old apples', misit Curtis, ex herb. Ravenel (K); unlocalized, 'in poma', *M. A. Curtis*, ex herb. Berkeley (K). No information, ex herb Schweinitz, ex herb. Berkeley ['no fruit'] (K).

Phyllachora impressa (Fr.) Sacc., Sylloge Fungorum 2: 609, 1883.

Dothidea impressa Fr., Systema Mycologicum 2: 564, 1823.

Discosia impressa (Fr.) Fr., Summa Vegetabilium Scandinaviae: 423, 1849.

= Diplocarpon impressum (Fr.) L. Holm & K. Holm, Kew Bull. 31: 568, 1977.

Typification: Sweden: Femsjö [?], on decaying leaves of Rubus chamaemorus, s.d., E. M. Fries (Fries, Scleromyci Sueciae no. 152, UPS – holotype of Dothidea impressa).

Phyllachora pomigena (Schwein.) Sacc., Sylloge Fungorum **2**: 622, 1883.

DOTHIDEA POMIGENA Schwein., Trans. Amer. Phil. Soc. n.s., 4:232, 1832.

= Gloeodes pomigena (Schwein.) Colby, Trans. Illin. St. Acad. Sci. 13: 157, 1920.

Typification: 'frequens in maturis pomis dictis "Newton Pippins", Pennsylv.', not seen.

The genus *Gloeodes* (of which this is the type) appears not to have been examined recently. The fungus as interpreted by Colby (1920) may represent an immature species of *Schizothyrium* (Ascomycota), rather than a coelomycete, the structures shown as conidia actually being immature asci. However, there is a complex of fungal species on this substratum which needs systematic study (Johnson, Sutton & Hodges, 1996).

Phyllachora potentillae (Schwein.) Peck ex Seym., Host Index of the Fungi of North America: 388, 1929.

Sphaeria potentillae Schwein., Schriften der naturforschenden Gesellschaft zu Leipzig 1: 46, 1822.

? = Nodulosphaeria sp.

Typification: **U.S.A.**: Pennsylvania, Bethlehem, host not cited [*Potentilla* sp. presumed], s.d., *s. coll*. (Collins Collection no. 378, **PH**!, possible type material of *Sphaeria potentillae*); same locality, host not cited, 1826, *s. coll*. (**PH**! – authentic material of *Sphaeria potentillae*).

The name *Phyllachora potentillae* was cited in the host index published by Seymour (1929), and no other reference has been found (J. H. Haines, *pers. comm.* 12 May 1995). Examination of authentic material of *Sphaeria potentillae* shows a member of the Dothideales, possibly referable to *Nodulosphaeria* Rabenh. (Shoemaker, 1984; Shoemaker & Babcock, 1987). The collections studied are unfortunately slightly immature, which makes their disposition uncertain. Unusual features of this species include a distinctly setose ascoma which is almost completely superficial (presumably more or less unavoidable when developing in a leaf), well-developed cellular pseudoparaphyses, and ascospores which appear to have a distinctly swollen section. Mature ascospores were not seen; immature ones measured $26-29 \times 3\cdot 5-4$ µm, were completely hyaline and appeared to be becoming at least 3-septate. Phyllachora rosae (Schwein.) Sacc., Sylloge Fungorum 2: 611, 1883.

Dothidea rosae Schwein., Trans. Amer. Philos. Soc. Philadelphia, n.s., 4: 235, 1832.

= Diplocarpon rosae F. A. Wolf, Bot. Gaz. 54: 231, 1912.

The Schweinitz fungus appears to represent the anamorphic state of *Diplocarpon rosae*, so the name does not threaten that of Wolf under the current nomenclatural rules. The fungus is the common black spot of cultivated roses.

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REFERENCES

- Alexopoulos, C. J. (1940). Some fungi from Greece. Mycologia 32, 336–358. Arx, J. A. von & Müller, E. (1954). Die Gattungen der amerosporen
- Pyrenomyceten. Beiträge zur Kryptogamenflora der Schweiz **11** (1), pp. 434. Anon. (1965). [Common Names of Economic Plant Diseases in Japan]. Vol. **3**, pp. 218. Phytopathological Society of Japan: Tokyo.
- Anon. (1972). [A List of Plant Diseases, Insect Pests and Weeds in Korea], pp. 424. Korean Society for Plant Protection: Korea.
- Banihashemi, Z. (1990). Biology and control of *Polystigma ochraceum*, the cause of almond red leaf blotch. *Plant Pathology* **39**, 309–315.
- Berkeley, M. J. (1841). Notices of British fungi. XLIII. Annals & Magazine of Natural History 6, 355-365.
- Bilgrami, K. S., Jamaluddin & Rizwi, M. A. (eds) (1979). Fungi of India. Part 1. List and References, pp. 467. Today & Tomorrow's Printers & Publishers: New Delhi.
- Brundza, K. (1961). Parazitnye Griby Kul'tiviruemykh Rastenii Litovskoi SSR i Nekotorye Voprosy Biologii Parazitnykh Gribov, pp. 302. Lithuanian Academy of Sciences: Vilnius.
- Byzova, Z. M. (1983). Mikromitsety na nekotorykh reliktovykh kustarnikakh. Botanicheskie Materialy Gerbariya Instituta Botaniki Akademii Nauk Kazakhkoi SSR 13, 89–91.

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- Byzova, Z. M. & Vasyagina, M. P. (1981). Sumchatye Griby 1. Protoaskomitsety (Protoascomycetes) – Euaskomitsety (Euascomycetes). In Flora Sporovykh Rastenii Kazakhstana (ed. Anon.), 12. pp. 244. Akademiya Nauk Kazakhskoi SSR: Alma Ata, Kazakhstan.
- Cannon, P. F. (1989). Notes on *Sphaerodothis* species parasitic on Gramineae. *Studies in Mycology* **31**, 49–59.
- Cannon, P. F. (1991). A revision of *Phyllachora* and some similar genera on the host family Leguminosae. Mycological Papers no. 163, pp. 302.
- Cannon, P. F. (in press). Diversity of the *Phyllachoraceae* with special reference to the tropics. In *Diversity of Fungi in the Tropics and Subtropics* (ed. K. D. Hyde). University of Hong Kong Press: Hong Kong.
- Chadefaud, M. (1960). Les végétaux non vasculaires (Cryptogamie). In Chadefaud, M. & Emberger, L., Traité de Botanique Systématique. Vol. 2, pp. 1018. Masson: Paris.
- Clements, F. L. & Shear, C. L. (1931). The Genera of Fungi, pp. 496. Wilson: New York.
- Colby, A. S. (1920). Sooty blotch of pomaceous fruits. Transactions of the Illinois State Academy of Science 13, 139–175.
- Corda, A. C. J. (1840). Icones Fungorum Hucusque Cognitorum. Vol. 4, pp. 53. Calve: Prague.
- Eriksson, O. E. & Yue, Jing-zhu (1988). The Pyrenomycetes of China, an Annotated Checklist, pp. 88. University of Umeå: Umeå, Sweden and Academia Sinica: Beijing.
- Farr, M. L. (1973). An annotated list of Spegazzini's Gungus taxa. Bibliotheca Mycologica 35, pp. 1661.
- Fatina, E. Sh. (1989). Bolezni i Vrediteli Slivy v Moldavii, pp. 206. Shtiintsa: Kishinev.
- Fries, E. M. (1815). Observationes Mycologicae. Vol. 1, pp. 230 pp. Bonnier: Hafniae.
- Fries, E. M. (1823). Systema Mycologicum. Vol. 2, pp. 620. Berlingiana: Lund.

Gattani, M. L. (1962). Plant diseases of economic importance in Afghanistan. FAO Plant Protection Bulletin 10, 30–35.

Ghazanfari, J. & Banihashemi, Z. (1976). Factors influencing ascocarp formation in Polystigma ochraceum. Transactions of the British Mychological Society 66, 401–406 (1976).

- Gonzales Fragoso, R. (1927). Enumeración y distribución geográfica de los esferopsidales conocidos de la península lbérica. *Trabajos del Museo* Nacional de Ciencias Naturales Madrid, ser. Bot., **23**, pp. 59.
- Grove, W. B. (1937). British Stem- and Leaf-Fungi (Coelomycetes). Vol. 2, pp. 406. Cambridge University Press: Cambridge.
- Hyde, K. D. & Cannon, P. F. (1992). Polystigma sonneratiae causing leaf spots on the mangrove genus Sonneratia. Australian Journal of Botany 5, 415–420.
- Johnson, E. M., Sutton, T. B. & Hodges, C. S. (1996). Peltaster fructicala: a new species in the complex of fungi causing apple sooty blotch disease. *Mycologia* 88, 114–120.
- Khatib, H., Davet, P. & Sardy, G. (1969). Liste des Maladies des Plantes au Liban 1959–1969, pp. 44. Institute of Agricultural Research: Fanar, Lebanon.
- Kranz, J. (1962). Plant diseases in Cyrenaica. FAO Plant Protection Bulletin 10, 121–125.
- Lamarck, J. B. de & Candolle, A. P. de (1915). *Flore Française*. Vol. 5, pp. 662. Desray: Paris.
- Limin, V. A. (1986). Spetsializatsiya Polystigma ussuriensis (Jacz. & Nat.) A. Prots. i P. ochraceum (Wahl.) Sacc. v usloviyakh Primorskogo Kraya. In

(Accepted 25 March 1996)

- Link, D. H. F. (1833). Handbuch zur Erkennung der Nutzbarsten und am Häufigsten Vorkommenden Gewächse. Vol. 3, pp. 536. Haude und Spenerschen Buchhandlung (Joseephy): Berlin.
- Müller, E. (1986). On the genus Diachora J. Müller (Ascomycetes). Transactions of the Botanical Society of Edinburgh 150th Anniversary Supplement, 69–75.
- Oudemans, C. A. J. A. (1897). Révision des Champignons tant Supérieurs qu'Inférieurs Trouvés jusqu'à ce Jour dans les Pays-Bas. Vol. 2, pp. 491. J. Müller: Amsterdam.
- Pantidou, M. A. (1973). Fungus-Host Index for Greece, pp. 382. Benaki Phytopathological Institute: Kifissia, Greece.
- Parbery, D. G. (1967). Studies on graminicolous species of *Phyllachora* Nke. in Fckl. V. A taxonomic monograph. *Australian Journal of Botany* 15, 271–375.
- Parbery, D. G. (1971). Studies on graminicolous species of *Phyllachora* Nke. in Fckl. VI. Additions and corrections to Part V. *Australian Journal of Botany* 19, 207–235.
- Pascoe, I. G. (1990). Observations on the ascus structure of *Plectosphaera* eucalypti (Phyllachoraceae). Mycological Research **94**, 675–684.
- Persoon, C. H. (1822). Mycologia Europaea. Vol. 1, pp. 351. J. J. Palmius: Erlangae.
- Petrak, F. (1929) Mykologische Notizen X. Nos. 601–700. Annales Mycologici 27, 324–410.
- Rogers, D. P., Rogers, A. M. & Seeler, E. V. (1942). Index Botanicus Sistens Omnes Fungorum Species in C. H. Persoonii Mycologia Europaea...Farlow Library: Cambridge, Massachusetts.
- Saccardo, P. A. (1884). Sylloge Fungorum ... Vol. 3, pp. 860. Saccardo: Padova.
- Saccardo, P. A. (1903). Notae mycologicae. Series III. Annales Mycologicae 1, 24–29.
- Seymour, A. B. (1929). *Host Index of the Fungi of North America*, pp. 732. Harvard University Press: Cambridge, Mass.
- Shoemaker, R. A. (1964). Conidial states of some *Botryosphaeria* species on *Vitis* and *Quercus. Canadian Journal of Botany* **42**, 1297–1301.
- Shoemaker, R. A. (1984). Canadian and some extralimital Nodulosphaeria species. Canadian Journal of Botany 62, 2730–2753.
- Shoemaker, R. A. & Babcock, C. E. (1987). Additions to Nodulosphaeria. Canadian Journal of Botany 65, 1921–1926.
- Sivanesan, A. (1984). The Bitunicate Ascomycetes and their Anamorphs, pp. 701. J. Cramer: Vaduz.
- Sousa da Câmara, E. de (1916). Contributiones ad Mycofloram Lusitaniae. Centuria VII. Boletim da Direccao Geral de Agricultura Lisboa 13(3), 1–28.
- Stepanov, P. M. (1966). Ozhog lit'ev Mindalya. Byulleten' Nauchno-Issledovatel'skogo Informatsii Tadzhikistanogo Nauchno-Issledovatel'skogo Instituta Sel'skogo Khozyaistva 4, 51–53.
- Sydow, H. (1928). Fungi chilenses a cl. E. Werdermann lecti. Pars prima. Annales Mycologici 26, 100–126.
- Sydow, H. (1936). Novae fungorum species XXIV. Annales Mycologici 34, 411–422.
- Theissen, F. & Sydow, H. (1915). Die Dothideales. Kritisch-systematische Originaluntersuchungen. Annales Mycologici 13, 147–746+6 pl.
- Vasil'eva, L. N. (1987). Pirenomitsety i Lokuloaskomitsety Severa Dal'nego Vostoka, pp. 255. Nauka: Leningrad.
 Yossifovitch, M. (1937). Contribution de l'étude de la protection du prunier

contre Polystigma rubrum (Pers.) DC. Revue de Pathologie Végétale 24, 18-31.

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Reaction-diffusion model of mycelial growth

substrate is continuously replaced, sub-apical branches are produced at approximately regular intervals behind the growing tip. Such regularity is a consequence of the constant drop-off in inhibitor concentration with distance from the growing tip. In our model, where substrate is not replaced, the *s* concentration in subapical regions of the filament far from the tip is not sufficient to support an activator peak and hence the formation of a lateral branch fails. Sub-apical branching may be produced by invoking a mechanism for substrate independent activator and inhibitor production.

Alternative mechanisms which lead to the production of subapical branches are possible. As stated above, subapical localized accumulations of activator are prevented by rapid consumption of substrate. However, the presence of a physical barrier such as a septum, may lead to an accumulation of diffusing activator which, according to the model, would be autocatalytic. Branching which results from this process would, therefore, be coincident with the position of septa. A potentially important omission in the model is the translocation of nutrients within the mycelium. This important phenomenon may also contribute to the production of subapical branches which we are currently assessing.

It is clear that vegetative growth in mycelia involves many more mechanisms than are represented by the model presented here. However, an important conclusion of this work, is that fractal structure and the response to nutritional heterogeneity can be reproduced by invoking only a few simple mechanisms.

The above mechanisms for colony growth and morphology are testable indirectly as discussed, and in principle directly, once the activator and inhibitor are identified. If the activator is indeed calcium, then calcium peaks should occur in advance of morphogenetic changes and should persist at growing tips. Significant problems have been encountered in attempting to measure cytosolic free Ca^{2+} in filamentous fungi because of the rapid sequestration of Ca^{2+} -sensitive dyes within organelles (Read *et al.*, 1992; Knight *et al.*, 1993). However, new methods for Ca^{2+} measurement in fungi are being developed (Read, N. D., pers. comm.) which should provide suitable protocols to test the hypothesis proposed in this paper.

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REFERENCES

- Bartnicki-Garcia, S. (1990). Role of vesicles in apical growth and a new mathematical model of hyphal morphogenesis. In *Tip Growth in Plant and Fungal Cells* (ed. I. B. Heath), pp. 211–232. Academic Press: London.
- Berridge, M. J. (1975). The interaction of cyclic nucleotides and calcium in the control of cellular activity. *Advances in Cyclic Nucleotide Research* 6, 1–98.
- Crawford, J. W. & Ritz, K. (1994). Origin and consequences of colony form in fungi: A reaction-diffusion mechanism for morphogenesis. In *Shape and Form in Plants and Fungi* (ed. D. S. Ingram & A. Hudson), pp. 311-327. Academic Press: London.

(Accepted 13 March 1996)

- Crawford, J. W., Ritz, K. & Young, I. M. (1993). Quantification of fungal morphology, gaseous transport and microbial dynamics in soil: an integrated framework utilising fractal geometry. *Geoderma* 56, 157–172.
- Dicker, J. W. & Turian, G. (1990). Calcium deficiencies and apical hyperbranching in wild type and the 'frost' and 'spray' morphological mutants of *Neurospora crassa*. Journal of General Microbiology 136, 1413–1420.
- Ermentrout, G. B. & Edelstein-Keshet, L. (1993). Cellular automata approaches to biological modelling. *Journal of Theoretical Biology* **196**, 97–133.
- Gierer, A. & Meinhardt, H. (1972). A theory of biological pattern formation. *Kybernetik* 12, 30–39.
- King, S. B. & Alexander, L. J. (1969). Nuclear behaviour, septation and hyphal growth of Alternaria solani. American Journal of Botany 56, 249–253.
- Knight, H., Trewavas, A. J. & Read, N. D. (1993). Confocal microscopy of living fungal hyphae microinjected with Ca²⁺-sensitive fluorescent dyes. *Mycological Research* 97, 1505–1515.
- Meakin, P. (1986). A new model for biological formation. Journal of Theoretical Biology 118, 101–113.
- Meinhardt, H. (1976). Morphogenesis of lines and nets. Differentiation 6, 117-123.
- Meinhardt, H. (1982). Models of Biological Pattern Formation. Academic Press: London.
- Murray, J. D. (1982). Parameter space for Turing instability in reaction diffusion mechanisms: A comparison of models. *Journal of Theoretical Biology* 98, 143-163.
- Niemeyer, L., Pietronero, L. & Wiesmann, J. (1984). Fractal dimension of dielectric breakdown. *Physical Review Letters* 52, 1033-1036.
- Obert, M., Pfeifer, P. & Sernetz, M. (1990). Microbial growth patterns described by fractal geometry. *Journal of Bacteriology* **172**, 1180–1185.
- Orbach, R. (1986). Dynamics of fractal networks. Science 231, 814–819.
- Patankar, D. B., Liu, T. & Oolman, T. (1993). A fractal model for the characterization of mycelial morphology. *Biotechnology and Bioengineering* 42, 571-578.
- Prosser, J. L. & Trinci, A. P. J. (1979). A model for hyphal growth and branching. *Journal of General Microbiology* 111, 153-164.
- Rasmussen, H. & Goodman, D. B. P. (1977). Relationships between calcium and cyclic nucleotides in cell activation. *Physiological Reviews* 57, 421–509.
- Read, N. D., Allan, W. T. G., Knight, H., Knight, M. R., Malho, R., Russell, A., Shacklock, P. S. & Trewavas, A. J. (1992). Imaging and measurement of cytosolic free calcium in plant and fungal cells. *Journal of Microscopy* 166, 57-86.
- Reissig, J. L. & Kinney, S. G. (1983). Calcium as a branching signal in Neurospora crassa. Journal of Bacteriology 154, 1397-1402.
- Ritz, K. (1995). Growth responses of some soil fungi to spatially heterogeneous nutrients. FEMS Microbiology Ecology 16, 269–280.
- Ritz, K. & Crawford, J. (1990). Quantification of the fractal nature of Trichoderma viride. Mycological Research 98, 1138–1152.
- Robson, G. D., Wiebe, M. G. & Trinci, A. P. J. (1991a). Exogenous cAMP and cGMP modulate branching in *Fusarium graminearum*. Journal of General Microbiology 137, 963–969.
- Robson, G. D., Wiebe, M. G. & Trinci, A. P. J. (1991b). Low calcium concentrations induce increased branching in *Fusarium graminearum*. *Mycological Research* 95, 561–565.
- Taylor, C. C. & Taylor, S. J. (1991). Estimating the dimension of a fractal. Journal of the Royal Statistical Society B 53, 353-364.
- Trinci, A. P. J. (1970). Kinetics of apical and lateral branching in Aspergillus nidulans and Geotrichum lactis. Transactions of the British Mycological Society 55, 17–28.
- Trinci, A. P. J. (1979). The duplication cycle and vegetative development in moulds. In *Fungal Walls and Hyphal Growth* (ed. J. H. Burnett & A. P. J. Trinci), pp. 132–163. Cambridge University Press: Cambridge, UK.
- Witten, T. A. & Sander, L. M. (1983). Diffusion limited aggregation. Physical Review B 27, 5686-5697.
- Wolfram, S. (1984). Cellular automata as models of complexity. *Nature* **311**, 419-424.
- Zalokar, M. (1959). Growth and differentiation of *Neurospora* hyphae. *American Journal of Botany* **46**, 602–610.