

THE NOMENCLATURE OF TWO FUNGI PARASITIZING BRASSICA

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(With three Text-figures)

The nomenclature of the perfect and imperfect stages of *Mycosphaerella brassicicola* (Duby) Lind. and *Leptosphaeria maculans* (Desm.) Ces. & De Not. is discussed.

The imperfect stages of these two parasites of *Brassica* spp. are often confused. *Mycosphaerella brassicicola* has a spermagonial stage with the characters of the form-genus *Asteromella* Pass. & Thüm. In phytopathological literature it is incorrectly known as a *Phyllosticta* species: *P. brassicicola* McAlp. A new combination for this stage is proposed: *Asteromella brassicae* (Chev.) Boerema & van Kesteren.

The pycnidial stage of *L. maculans* is known in phytopathological literature as *Phoma lingam* (Tode ex Fr.) Desm. Its characters, however, are quite different from those of the type-species of the form-genus *Phoma* Sacc. As it agrees with the type-species of the form-genus *Plenodomus* Preuss, it is concluded that the correct name is *Plenodomus lingam* (Tode ex Fr.) Höhn.

In their diagnostic mycological work the present authors have been confronted with conflicting references to the nomenclature of the perfect and imperfect stages of two fungi parasitic on *Brassica* spp., viz. *Mycosphaerella brassicicola* (Duby) Lind. and *Leptosphaeria maculans* (Desm.) Ces. & De Not. The imperfect stage of the former in phytopathological literature is mostly given as *Phyllosticta brassicicola* McAlp., while the pycnidial stage of the latter is generally known as *Phoma lingam* (Tode ex Fr.) Desm.

By comparing original herbarium material of both these fungi and studying the literature the authors have tried to clear up the confusion.

MYCOSPHAERELLA BRASSICICOLA (Duby) Lind.

Sphaeria brassicicola Duby, Bot. Gall., Ed. 2, 2: 712. 1830 ["*brassicaecola*" (Fries ined. . .)]; not *Sphaeria brassicicola* Berk. & Br. *apud* Berk., Outl. Brit. Fungol. 401. 1860. — *Sphaerella brassicicola* (Duby) Ces. & De Not. in Comment. Soc. critt. ital. No. 4: 238. 1863 ("*brassicaecola*"). — *Mycosphaerella brassicicola* (Duby) Lind. in Nat. PilFam. 1 (1): 424. Febr. 1897. — *Mycosphaerella brassicicola* (Duby) Joh. ex Oudem., Rév. Champ. 2: 210, 211. March 1897 ["*M. brassicaecola* (Duby) Johanson"].

Dothidea brassicae Desm. in Ann. Sci. nat. (Bot.), Ser. 2, 17: 113. 1842.

Sphaeria brassicae Berk. & Br. in Ann. Mag. nat. Hist., Ser. 2, 9: 384. 1852; not *Sphaeria brassicae* Dickson, Fasc. Pl. crypt. Brit. 1: 23. 1785; not *Sphaeria brassicae* Bolton, Hist. Fung. Halifax 3: 45. 1789 [= *Sclerotium semen* Tode ex Fr., the sclerotial stage of *Typhula betae* Rostrup = *Typhula brassicae* (Berg. ex Fr.) Vang]; not *Sphaeria brassicae* Schwein. in Trans. Amer. phil. Soc., N.S. 4: 222. 1834 [= *Chaetomella brassicae* (Schwein.) Starb.]; not *Sphaeria brassicae* Klotzsch, Eng. Fl. 2: 261. 1836 [= *Pleurosordaria olerum* (Fr.) Lunqvist in manuscr.]; not

Sphaeria brassicae Lasch, Exs. in Rab. Klotzsch. Herb. mycol. Ed. nov. 2, No. 550. 1885 [= *Pleospora herbarum* var. *brassicae* (Lasch) Sacc.]. — *Sphaeria brassicicola* Berk. & Br. *apud* Berk., Outl. Brit. Fungol. 401. 1860 (“*brassicaecola*”; name change); not *Sphaeria brassicicola* Duby, Bot. Gall., Ed. 2, 2: 712. 1830. — *Stigmatea brassicae* (Berk. & Br.) Kickx, Fl. cryptog. Flandres 1: 365. 1867 (incomplete reference to basionym).

SPERMAGONIAL STAGE: —

Asteromella brassicae* (Chev.) Boerema & van Kesteren, *comb. nov.

Asteromella brassicae Chev., Fl. Gén. Env. Par. 1: 449. 1826.

Phoma siliquastrum Desm. in Ann. Sci. nat. (Bot.), Ser. 3, 11: 280. 1849.

Sphaeria (Depazea) brassicae Curr. in Trans. Linn. Soc. Lond. (Bot.) 22: 334. 1859 (“Pers. in litt.”).

Phyllosticta nabi Sacc. in *Michelia* 1: 532. 1879.

Phyllosticta brassicicola McAlp. in Bull. Victoria agric. Dep. 27. 1901 (“*brassicaecola*”).

Phyllosticta brassicicola Grove in J. R. hort. Soc. 40: 76. 1914.

Phyllosticta brassicina Sacc. in Ann. mycol., Berl. 11: 16. 1913. — *Asteromella brassicina* (Sacc.) Rupperecht in *Sydowia* 13: 11. 1959.

MISAPPLICATIONS. — *Phoma siliquastrum* Desm. *sensu* Henderson in *Phytopathology* 8: 389, 390. 1918; *sensu* Cunningham in Bull. New Zeal. Dep. Agric. 133: 38. 1927; *sensu* Grove, Brit. Coelomycetes 1: 70. 1935 (= *Plenodomus lingam*, see this paper under *Leptosphaeria maculans*).

Depazea brassicae Curr. *sensu* Sacc., Syll. Fung. 3: 38, 39. 1884, pro syn. (= *Plenodomus lingam*, see this paper under *Leptosphaeria maculans*).

DESCRIPTIONS & ILLUSTRATIONS. — Dring in Trans. Brit. mycol. Soc. 44: 253–264. 1961 (both stages).

SPECIMENS EXAMINED. — Berkeley herb. (*Sphaeria brassicae*; K); Desmazières, Pl. crypt. N. France Ed. 1, 119 (*Phoma siliquastrum*; PC; type); Desmazières, Pl. crypt. France Ed. 2, 95 (*Dothidea brassicae*; FI); Greville herb. (*Phyllosticta brassicae* “Pers. in litt.”; E); Hooker herb. [*Phyllosticta brassicae* “Pers. in litt.”; K; type of *Sphaeria (Depazea) brassicae* Curr.]; Persoon herb. (*Phyllosticta brassicae* “Moug. in hb. Pers.”; L 910. 261–906); Roumeguère, Fungi gall. exs. in herb. Roussel (*Asteroma brassicae*; PC); Saccardo, Mycoth. ital. 1269 (*Phyllosticta brassicina*; PAD; type); Saccardo, Mycoth. ital. 1326 (*Phyllosticta nabi*; PAD; type).

This fungus is the cause of a typical leafspot, known as Ringspot, of *Brassica* spp., especially of varieties of *Brassica oleracea*. Apart from the leaves all other aerial parts of the plant may be infected. For description of the disease symptoms, see Weimer (1926).

At first there appear on the spots little pycnidia which are to be characterized as spermagonia (Snyder, 1946; Dring, 1961). Later on perithecia develop. As these two stages often occur together on the spots, the connection between them has long been known.

The nomenclature of the perfect stage has recently been worked out by Dring (1961). We agree with the synonymy given, but cannot follow him as far as the author citation of the species is concerned. Dring, being aware of the fact that Oudemans and Lindau had independently transferred the species in the same year to *Mycosphaerella*, thought “the actual priority would be difficult to establish, as ‘Engler & Prantl’ bears no date other than ‘1897.’” However, Oudemans published the recombination (which he ascribed to Johanson and subsequently to Johanson &

Magnus; see Oudemans, 1921) in March 1897. It is remarkable that Dring overlooked the indication "Gedruckt im Februar 1897" in Lindau's publication.

Duby named the species *Sphaeria brassicaecola* Fr. ined., which is the cause that herbarium material is often cited as *Sphaeria brassicaecola* Fr. However, Fries never described this species.

The identity of *Sphaeria brassicae* Dickson and *Sphaeria brassicae* Bolton with the sclerotial stage of *Typhula brassicae* (*Sclerotium semen*) is based on data of Vang (1945) and Fries (Syst. mycol. 2: 249. 1822).

The identity of *Sphaeria brassicae* Klotzsch (see also Dring, 1961) is based on notes by Cl. Moreau and Nils Lunqvist on the holotype of *Sphaeria olerum* Fr. in Herb. E. Fries at Uppsala.

In phytopathological literature the imperfect stage of the present fungus is mostly called *Phyllosticta brassicicola*. However, it represents not a conidial stage but a spermatial one which should be placed in the form-genus *Asteromella* Pass. & Thüm. (type-species: *Asteromella ovata* Thüm., see Batista, Peres & Maia, 1960).

In old herbarium material the imperfect stage is often indicated as *Depazea brassicaecola* Fr., a name not found in literature and apparently derived from Duby's name of the perfect stage, *Sphaeria brassicaecola* Fr. ined., discussed above.

The synonymy of the imperfect stage is mainly based on the investigation of original herbarium material as listed above. As we had no opportunity to examine original herbarium material of *Asteroma brassicae* (not known to be in existence), *Phyllosticta brassicicola* McAlp., and *Phyllosticta brassicicola* Grove, we had to rely on original descriptions. In our opinion these names may also refer to the spermagonial stage of *Mycosphaerella brassicicola* which is completely in accordance with the views of other authors.

On the type material of *Phyllosticta napi* no fructifications have been observed (see also Dring, 1961), but in view of the symptoms and the description of this fungus it can be said with certainty that this name refers to the spermagonial stage of *Mycosphaerella brassicicola*.

There is much confusion about the fungus described by Currey as *Sphaeria* (*Depazea*) *brassicae* Pers. in litt. This name has to be attributed to Currey. Examination of an original exsiccatum in the Herbarium at Kew shows that this name is based on material collected by Mougeot with his indication "*Phyllosticta brassicae* Pers. in litt." In Persoon's herbarium at Leyden and in Greville's herbarium at Edinburgh paratype material also collected by Mougeot is present. However, Persoon never described this stage. *Sphaeria brassicae* Curr. is inexactly cited in several books as *Depazea brassicae* Curr., but Currey mentioned *Depazea* in parentheses as he considered it a subdivision of the genus *Sphaeria*. Saccardo (Syll. Fung. 3) supposed that *Phyllosticta brassicae* as described by Westendorp (in Bull. Acad. Belg. Cl. Sci. 10: 397. 1851) was a new combination of Currey's *Sphaeria* (*Depazea*) *brassicae* (1859). The dates of publication, however, clearly show this to be impossible. Westendorp's name is based on and a name change of *Depazea brassicaecola* Desm. = *Plenodomus lingam* (Tode ex Fr.) Höhn.

LEPTOSPHERA MACULANS (Desm.) Ces. & De Not.

Sphaeria maculans Desm. in Ann. Sci. nat. (Bot.), Ser. 3, 6: 77. 1846; not *Sphaeria maculans* Sow. ex Berk. & Br. in Ann. Mag. nat. Hist., Ser. 2, 9: 378. 1852 [= *Phaeosphaeria sowerbyi* (Fuck.) Holm]. — *Leptosphaeria maculans* (Desm.) Ces. & De Not. in Comment. Soc. critt. ital. No. 4: 235. 1863. — *Pleospora maculans* (Desm.) Tul., Sel. Fung. Carp. 2: 274. 1863.

Sphaeria napi Fuck., Exs. Fungi rhen. No. 895. 1864 (nomen dubium). — *Leptosphaeria napi* (Fuck.) Sacc., Syll. Fung. 2: 45. 1883.

Pleospora napi Fuck., Symb. mycol. 136. 1870 [nomen dubium, fide Holm in Symb. bot. Upsal. 14 (3): 36. 1957].

MISAPPLICATIONS. — See discussion.

PYCNIDIAL STAGE: —

PLENODOMUS LINGAM (Tode ex Fr.) Höhn.

Sphaeria lingam Tode, Fung. Mecklenb. Sel. 2: 51. 1791 (devaliated name). — *Sphaeria lingam* Tode ex Fr., Syst. mycol. 2: 507, 508. 1823. — *Phoma lingam* (Tode ex Fr.) Desm. in Ann. Sci. nat. (Bot.), Ser. 3, 11: 281. 1849. — *Plenodomus lingam* (Tode ex Fr.) Höhn. in S. B. Akad. Wiss. Wien (Math.-nat. Kl., Abt. I) 120: 463. 1911.

Depazea brassicaecola Desm., Exs. Pl. crypt. N. France, Ed. 1 (Fasc. 4), No. 185. 1826. — *Depazea vagans* var. ("y") *brassicae* Kickx, Fl. crypt. Env. Louv. 125. 1835 (name change). — *Septoria brassicae* Westend. & Wall., Exs. Herb. crypt. Belge (Fasc. 6), No. 294. 1847 (name change). — *Phyllosticta brassicae* Westend. in Bull. Acad. Belg. Cl. Sci. 10: 397. 1851 (name change).

Sclerotium sphaeriaeforme Lib., Exs. Pl. crypt. Ard. (Fasc. 3), No. 237. 1834.

Plenodomus rabenhorstii Preuss in Linnæa 24: 145. 1851.

Aposphaeria brassicae Thüm. in Hedwigia 12: 189, 190. 1880. — *Phoma brassicae* (Thüm.) Sacc., Syll. Fung. 3: 119. 1884.

Phoma napobrassicae Rostrup in Tidsskr. Landøkon. 11: 330. 1892. — *Phoma lingam* var. *napobrassicae* (Rostrup) Grove, Brit. Coelomycetes 1: 70. 1935.

MISAPPLICATIONS. — *Polydesmus exitiosus* Kühn *sensu* Fuck., Symb. mycol. 136. 1870 (= p.p. *Alternaria brassicae*, fide Neergaard, Danish *Alternaria* and *Stemphylium* 218. 1945).

Phoma oleracea Sacc. *sensu* Ritzema Bos in Tijdschr. PlZiekt. 10: 61. 1904; 11: 106. 1905 and Z. PflKrankh. 16: 269. 1906; *sensu* Henderson in Phytopathology 8: 392. 1918, pro syn.; *sensu* Cunningham in Bull. New Zeal. Dep. Agric. 133: 38, 39. 1927, pro syn.; *sensu* Nielsen in Tidsskr. Planteavl. 38: 147. 1932, pro syn.; *sensu* Grove, Brit. Coelomycetes 1: 70. 1935, pro syn. (= *Phoma herbarum* Westend., fide Boerema, 1964).

Phoma incrustans Sacc. *sensu* Höhn. in S. B. Akad. Wiss. Wien (Math.-nat. Kl., Abt. I) 118: 890. 1909, pro syn. [= *Phomopsis incrustans* (Sacc.) Died., the imperfect stage of *Diaporthe incrustans* Nits., fide Wehmeyer, Genus *Diaporthe* 1933].

Sphaeria olerum Mougeot *sensu* Höhn. in S. B. Akad. Wiss. Wien (Math.-nat. Kl., Abt. I) 120: 463. 1911, pro syn. [= *Pleurosordaria olerum* (Fr.) Lunqvist in manuscr., fide Herb. E. Fries in Uppsala, *Sphaeria olerum* Fr.].

Phoma siliquastrum Desm. *sensu* Henderson in Phytopathology 8: 389, 390. 1918, pro syn.; *sensu* Cunningham in Bull. New Zeal. Dep. Agric. 133: 38, 39. 1927, pro syn.; *sensu* Grove, Brit. Coelomycetes 1: 70. 1935, pro syn. (= *Asteromella brassicae*, see this paper under the spermatogonial stage of *Mycosphaerella brassicicola*).

DESCRIPTIONS & ILLUSTRATIONS. —

Perfect stage: Müller in Sydowia 4: 244. 1950; Holm in Symb. bot. upsal. 14: 36, 37. 1957.

Imperfect stage: Tode, Fung. Mecklenb. Sel. 2: 51, pl. 16 fig. 126. 1791

(*Sphaeria lingam*); Ritzema Bos in Tijdschr. PlZiekt. **10**: pl. 2, 3 figs. 3-7. 1904 (*Phoma oleracea*); Diedicke in Ann. mycol., Berl. **9**: 138, pl. 8 figs. 1, 2. 1911 (*Phoma lingam*, *Plenodomus rabenhorstii*); Cunningham in Bull. New Zeal. Dep. Agric. **133**: 41, 42, figs. 28, 29. 1927 (*Phoma lingam*).

SPECIMENS EXAMINED. — Desmazières, Pl. crypt. N. France Ed. 1, 185 (*Depazea brassicaecola*; FI, PC, L; type); 1784 (*Sphaeria maculans*; PC; type); 1877 (*Phoma lingam*; PC); Funck, Cryptog. Gew. 379 (*Sphaeria lingam*; L); Jaap, Fungi sel. Exs. 541 (*Plenodomus rabenhorstii*; L); Libert herb. (*Sclerotium sphaeriaeforme*; BR; type); Libert, Pl. crypt. Ard., 237 (*Sclerotium sphaeriaeforme*; BR); Persoon herb. (*Sphaeria lingam*; L 910. 267-174, -175, -179); Rostrup herb. (*Phoma napobrassicae*; CP; type); Saccardo, Mycoth. ven. (*Leptosphaeria napi*; PAD); Sydow, Mycoth. germ. 1123 (*Plenodomus lingam*; PAD); Westendorp herb. (*Phyllosticta brassicae*; BR); Westendorp & Wallays, Herb. crypt. belge 294 (*Septoria brassicae*; BR).

This fungus causes leafspots, lesions and discolorations on the stems, siliques and 'bulbs' of *Brassica* spp. The disease is known as Dryrot and Canker or Black leg and occurs especially on turnip, swede, broccoli and cabbage. For description of the disease symptoms see Henderson (1918), Cunningham (1927), and Buddin (1934).

The conspecificity of the perfect and imperfect stages has already been recorded as probable in much of the old systematic literature. In Switzerland, Müller and Tomašević (1957) were able to prove this connection by single ascospore isolations. It had already been proved in 1956 by Smith in New Zealand who identified the perfect stage at first as *Leptosphaeria napi* (nomen dubium). Recently the connection between the perfect and imperfect stages has been established in England (written information of Dr. B. C. Sutton, IMI).

When one consults the systematic literature concerning the perfect stage (see among others Müller, 1950 and Holm, 1957), the general opinion appears to be that apart from *Brassica* spp. the fungus also inhabits other Cruciferae. The data, however, are often conflicting and doubtful, as is seen from the following account.

In the synonymy of *Leptosphaeria maculans* Müller (1950) cited also *Leptosphaeria cylindrospora* Auersw. & Niessl ex Sacc. on *Chamaerion angustifolium* and *Epilobium* species. According to Holm (1957), however, *L. cylindrospora*, differs clearly from *L. maculans* by the ascospores being 4-septate instead of 5-septate. *Leptosphaeria alliariae* (Auersw.) Rehm described from *Alliaria officinalis* is cited as a synonym of *L. maculans* both by Müller and Holm. The latter, however, mentions that the fungus occurring on *Alliaria* is of a distinct type with "despores plus petites et un peu plus grossières," so *L. alliariae* seems to be a distinct species. Holm also mentions *Leptosphaeria virginica* (Cooke & Ellis) Sacc. as a synonym albeit with a question mark.

In view of the above contrarities and uncertainties we have not reported these names and their basionyms in the synonymy. In our opinion we shall only be able to solve these questions after comparative infection trials and a comparative study of the imperfect stages. In connection with this it is worth noting that Müller and Tomašević (1957) found pycnidia of the *Camarosporium*-type in addition to pycnidia of the *Plenodomus* (= *Leptophoma*)-type in a culture of a fungus, which they identified as *L. maculans* and isolated from *Artemisia campestris*. The former type, however,

has never been observed in the life history of the fungus parasitizing *Brassica* spp. Indeed, Dr. E. Müller informed us that in his opinion it is just possible that only one specialized form of *L. maculans* parasitizes *Brassica* spp.

Leptosphaeria napi (Fuck.) Sacc. mentioned above in the synonymy of the perfect stage is to be characterized as a nomen dubium. Holm (l.c.) stated that the type material of this fungus is absolutely identical with *L. maculans*. However, in the description of *L. napi* 6–10-celled spores are mentioned whereas *L. maculans* always has 6-celled spores. See also Winter (1887). Neergaard (1945) mentions *Leptosphaeria exitiosa* Rostrup [“(Kühn) Rostrup”] as a synonym of *L. napi*. The description of *L. exitiosa* given by Rostrup (1902) makes it clear that this is incorrect.

The imperfect stage of *Leptosphaeria maculans* is mostly regarded as a member of the form-genus *Phoma* Sacc. and called *Phoma lingam*. With regard to the vague original description of that genus this looks correct. However, comparison with the type-species of the genus *Phoma* (*P. herbarum* Westend.; see Boerema, 1964) shows this to be a pycnidial stage with quite different characteristics. First a description of the imperfect stage of *L. maculans* is given.

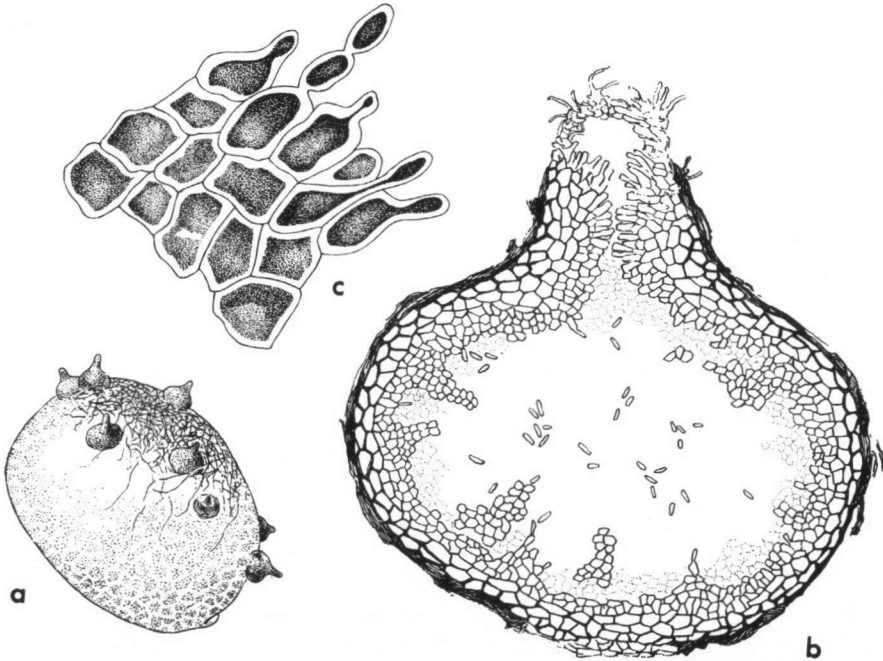


Fig. 1. *Leptosphaeria maculans* (Desm.) Ces. & De Not., stat. con. *Plenodomus lingam* (Tode ex Fr.) Höhn.: the 'normal' pycnidial phaenotype (type I). — a. Habitus on cabbage seed ($\times 16$). — b. Vertical section ($\times 225$, somewhat simplified). — c. Detail of wall structure and origin of the spores ($\times 2300$).

In vivo the imperfect stage shows a variable habit apparently depending on the season (different phenotypes). The pycnidia *in vitro* generally resemble those associated with spots on living leaves, siliques, stems and 'bulbs' of *Brassica* spp. in summer (Fig. 1). The primordium of this type of pycnidium, which also occurs on the seeds (Fig. 1a), arises by the simple or compound meristogenous method (Kempton, 1919).¹

In the gradually enlarging pseudoparenchymatic mass soon one or more cavities develop, filled with spores embedded in a gelatinous matrix. These cavities evidently originate by histolysis of the central cells (lysigenetic origin, cf. Dodge, 1923). The origin of the first spores is not clear. Probably they are of endogenous origin (Klebahn, 1933). The fruit-bodies remain long closed. The opening is formed toward the end of the growing process (Cunningham, 1927) and is preceded by rapid cell divisions at the top of the fruit-body. As a result a papilla develops which often grows out into a long cylindrical neck (Fig. 1a). Sometimes several papillae occur on one fruit-body. The central cells of the papillate beak gradually disintegrate, thus providing a narrow passage-way. In contrast with the predetermined opening or *ostiole* of the form-genus *Phoma* (Boerema, 1964), this opening may be called a *porus*. The cells lining the cavity in the papilla or neck mostly bud into short hyphae (Fig. 1b) which usually desintegrate, so that in a fully mature fruit-body little of them remains (cf. Dodge, 1923: 753). They are homologous with periphyses (Cunningham, 1927).

The peridium of a mature pycnidium consists of an outer and an inner wall and is made up of several cell layers. The outer wall shows three or four layers of relatively large, somewhat dark-walled cells which gradually pass into the smaller hyaline cells of the inner wall. These cells are somewhat radially arranged and their contents generally show a striking colour when stained with cotton blue. This layer varies considerably in thickness and sometimes series of cells stretch into the centre of the pycnidium (Fig. 1b), which makes the pycnidia sometimes seem divided into several loculi (Cunningham, 1927). The spores filling the whole cavity of the mature pycnidium arise directly from the meristematic hyaline cells (Fig. 1c). They are produced by budding, not only of the cells lining the cavity but also of more deeply situated cells. The latter form long narrow protuberances on which the spores are produced. This process of spore-forming may be referred to as *murogenous* (Luttrell, 1963) in contrast with the *porogenous* origin of the spores in the type species of the form-genus *Phoma* (Boerema, 1964).

The pycnidia described above are in phytopathological literature designated as type I (Henderson, 1918; Cunningham, 1927).

The imperfect stage of the fungus may occur in a different phase on dead overwintered cabbage stems and mummified swede 'bulbs' and the like (Fig. 2). Generally this consists of relatively big pycnidia with a thick wall, indicated in phytopathological literature as type II (Henderson, 1918; Cunningham, 1927). This type originates from a pycnidium of type I (Cunningham, 1927), through the formation of a thick layer of typically sclerenchymatous cells between the large dark-coloured outer cells and the small hyaline meristematic cells. The shape of the thick-walled pycnidia is variable, sometimes turban-like (Fig. 2a). The elongated top with porus is not so striking as in the case of type I on account of the thick wall. At the base of the fruit-body the sclerenchymatous cells, arranged in the shape of a fan, clearly originate from the substrate (Fig. 2b).

¹ It should be noted that Calvert & Pound (1949) by pairing two distinct types of the fungus obtained in the merger zone between the colonies a heavy line of "conjuncture" pycnidia which in their opinion were of symphogenous origin.

Sclerenchymatous cells sometimes also develop in immature pycnidia of type I which have not yet developed a porus. This results in a relatively big pycnidium, completely closed in the beginning, but rupturing irregularly without a definite porus (Fig. 3a).

Sclerenchymatous cells may also occur in pycnidial knots in which a distinct cavity is not yet present, giving rise to a sterile body, the *pycno-sclerotium* (Fig. 3a), the centre of which often shows a dish-shaped zone of small-celled tissue (Fig. 3b).

Incidentally, sclerotoid bodies with or without spore formation are also found to develop *in vitro* (Pound, 1947, isolate s39).

Finally it should be noted that in the development of the sclerenchymatous cells the pycnidia of type II resemble the perfect stage, which in fact has the same wall texture (Holm, 1957: 37).

The above description of the development of the imperfect stage of *Leptosphaeria maculans* clearly indicates that this state cannot belong to the form-genus *Phoma*

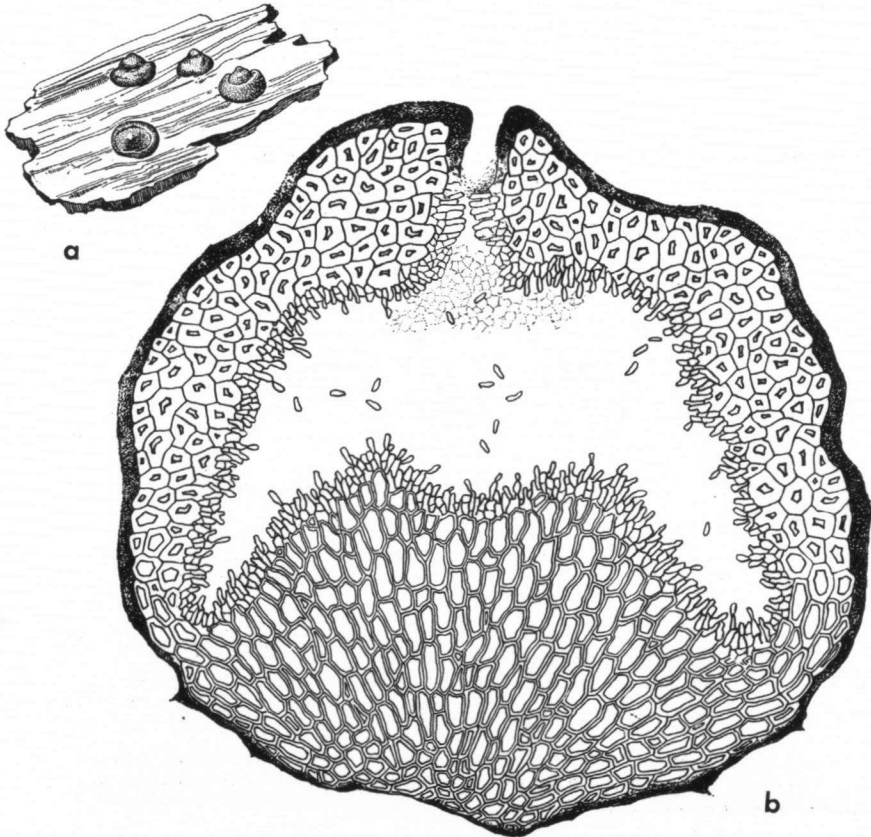


Fig. 2. *Leptosphaeria maculans* (Desm.) Ces. & De Not., stat. con. *Plenodomus lingam* (Tode ex Fr.) Höhn.: the 'sclerenchymatous' pycnidial phaenotype (type II). — a. Surface view on dead cabbage stem ($\times 11$). — b. Vertical section ($\times 225$, somewhat simplified).

Sacc. (cf. Boerema, 1964). However, it fits the form-genus *Plenodomus* Preuss and agrees with the type species, *P. rabenhorstii* Preuss. The original description of this species concerns the closed sclerotoid form where spores are liberated by rupture of the fruit-body. Later, Preuss (1862) included in the description the sclerotoid pycnidial form where the spores are set free through a porus. Of course, a name given to a certain phaenotype of a fungus imperfectus must also be applied to other phaenotypes of the same stage. Thus, the name *P. rabenhorstii* also fits the non-sclerotoid phaenotype of this stage.

The current name for this stage, *Phoma lingam*, was also first applied to the sclerotoid form (with and without a distinct porus) and not to the non-sclerotoid form. This follows from Tode's description and the figures of *Sphaeria lingam*.

That *Plenodomus rabenhorstii* and *Sphaeria lingam* were synonymous was proved independently by Dedicke (1911) and von Höhnel (1911). It was Dedicke who studied the original material of *Plenodomus rabenhorstii*. It is a pity that this type material (Botanisches Museum Berlin) was lost during the last war. The combination *Plenodomus lingam* published by von Höhnel is in our opinion the correct name for the imperfect stage of *Leptosphaeria maculans*.

The original description of the genus *Plenodomus* did not cover the whole range of phaenotypes of the type species. Also the additional descriptions by Dedicke (1911) and Bubák (1915: 29) did not complete the picture especially because these authors did not mention the non-sclerotoid form. However, for the time being we do not intend to improve this description. In our opinion it is necessary to have more information on related species of *Plenodomus* before a diagnosis can be made. It is also necessary to consider the generic characters and differences from related genera of the Sphaeropsidales.²

Original material of the synonyms of the imperfect stage was examined with the exception of *Aposphaeria brassicae* Thüm., of which no material was available. However, the description of *Aposphaeria brassicae*, as given by Saccardo (*Phoma brassicae*), clearly indicates that this refers to the imperfect stage of *Leptosphaeria maculans*. This is in accordance with the opinion of other authors (Henderson, 1918; Cunningham, 1927).

The synonym *Depazea brassicicola* ("brassicaecola") was described for the non-sclerotoid stage as it occurs on leaves of cabbage (type I). This explains why the author of this name, Desmazières, described the same fungus imperfectus a second time as *Phoma lingam* (sclerotoid, type II) 23 years later. We confirmed this by comparison of the type material of *Depazea brassicicola* and Desmazières' material of *Phoma lingam*. The synonym *Depazea brassicicola* was redescribed by Belgian authors successively as a variety of *Depazea vagans* (Kickx); a *Septoria* species (Westendorp &

² Some later synonyms exist of the genus *Plenodomus* Preuss, e.g. *Leptophoma* Höhn. [in S.B. Akad. Wiss. Wien (Math.-nat. Kl., Ab. I) 124: 73. 1915]. The type species of this genus, *Leptophoma acuta* (Fuck.) Höhn. [= *Phoma acuta* Fuck., the imperfect stage of *Leptosphaeria acuta* (Fuck.) Karst.], shows the same characters as *Plenodomus lingam*. In 1918 von Höhnel also came to this conclusion (see also Petrak, 1921: 192, and 1924: 101).

Wallays) and a *Phyllosticta* species (Westendorp). In the descriptions they changed the specific epithet "*brassicaecola*" to "*brassicae*". We also confirmed this by comparing their original material with that of Desmazières. However, it seems that the Belgian synonyms are often misused for the spermagonial stage of *Mycosphaerella brassicicola* as appears from exsiccata in various herbaria. The main reason of this error might be that Saccardo in his "Sylloge Fungorum" erroneously indicated *Phyllosticta brassicae* Westend. as a transfer of *Sphaeria brassicae* Curr. instead of *Depazea brassicicola* (*Sphaeria brassicae* Curr. is a synonym of the spermagonial stage of *Mycosphaerella brassicicola*, which see above).

It may be remarked that *Sclerotium sphaeriaeforme* is based on the pycnosclerotial phaenotype of the imperfect stage. This was already mentioned by Desmazières in his description of *Phoma lingam*.

The misapplication of the name *Phoma incrustans* as a synonym of *Plenodomus rabenhorstii* by von Höhnel (1909) was later on redressed by himself (von Höhnel, 1911; cf. Diedicke, 1911).

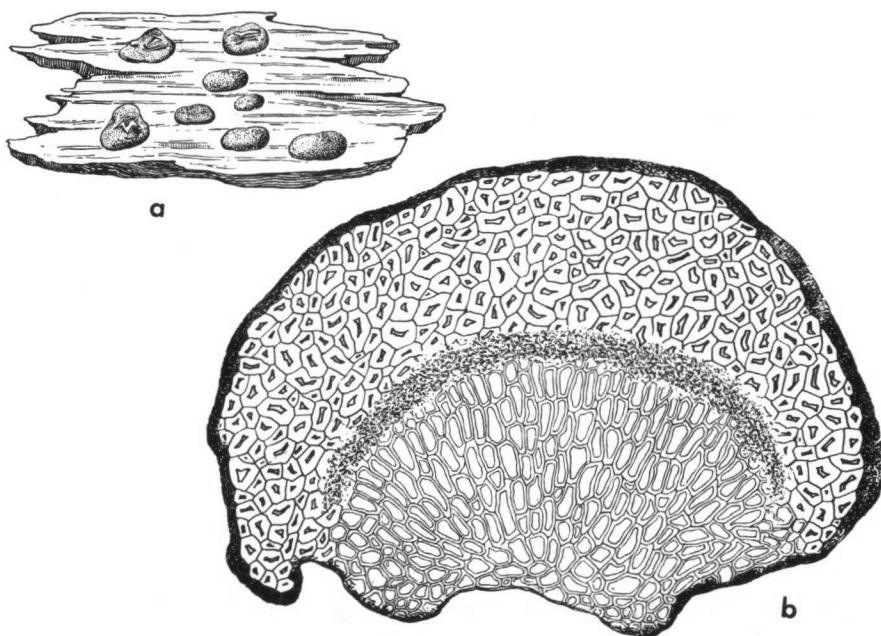


Fig. 3. *Leptosphaeria maculans* (Desm.) Ces. & De Not., stat. con. *Plenodomus lingam* (Tode ex Fr.) Höhn.: exceptional phaenotypes of the pycnidial stage. — a. Surface view of a part of a dead cabbage stem with 'sclerenchymatous' pycnidial knots (pycnosclerotia) and 'sclerenchymatous' pycnidia without porus and opened by rupture of the wall ($\times 11$). — b. Vertical section of a pycnosclerotium (approx. $\times 225$, somewhat simplified).

Finally it should be noted that *Phoma oleracea*, a synonym of *Phoma herbarum* (see also under misapplications) which is of general occurrence as a saprophyte on the seedcoats of *Brassica* spp., has often been mistaken for *Plenodomus* (*Phoma*) *lingam*.

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