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PHOMA EXIGUA DESM. AND ITS VARIETIES

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(With Plates 1–4 and four Text-figures)

Because of its growth features *in vitro*, pathogenicity and host relation, together with the ubiquitous wound- and weak-parasitic strains of *Phoma exigua* Desm. var. *exigua*, three more specialized pathogenic varieties of this species are distinguished: var. *linicola* (Naoum. & Vass.) Maas on flax, var. *foveata* (Foister) Boerema on potato, and var. *sambuci-nigrae* (Sacc.) comb. nov. on elder. The synonymy and the collective and differential diagnostic characteristics are discussed.

In diagnostic mycological work with diseased and dead plant material, quite often a typical pycnidial fungus with continuous and 1- (occasionally 2-) septate, hyaline spores has been isolated. The fungus occurs in association with leaf and stem lesions, rotting of fleshy roots and tubers, and is ubiquitous on dead plant material, especially herbaceous stems. It can be characterized as a weak parasite or a wound parasite, and appears to be soil-borne. The characters of this fungus correspond with the *Phoma*-"Group II" described by Dennis (1946). According to Saccardo's system of classification, it may be placed in various form-genera of the Deuteromycetes, as appears also from the "current names" listed for it by Dennis (l.c.). However, recent studies on the spore development and other microscopical characters of the type species of these genera (Brewer & Boerema, 1965; Boerema, Dorenbosch & Leffring, 1965; Boerema, 1965) make it certain that the fungus under consideration belongs to the form-genus *Phoma* Sacc. Maas (1965) has pointed out that the oldest valid name of this ubiquitous soil-born species is *Phoma exigua* Desm.

On some plants *Phoma*-like fungi are known to occur which are morphologically indistinguishable from *P. exigua*, but which can be separated by their pathogenicity or special host-relation, and their appearance in culture. This is true, for instance, for the footrot fungus of flax (*Linum usitatissimum*), generally known as *Ascochyta linicola* Naoum. & Vass., which is also included by Dennis (l.c.) in his "Group II" of *Phoma* spp. Apart from their pathogenicity to flax, isolates of this fungus can generally be recognized *in vitro* by their slow compact growth and other cultural characteristics. Maas (l.c.), regarding this parasite of flax as a variety of the ubiquitous soil-borne fungus, named it *P. exigua* var. *linicola* (Naoum. & Vass.) Maas. Another equally specific fungus, occurring on elder (*Sambucus nigra*), can be distinguished from *P. exigua* only by its growth habit *in vitro*. W. B. Grove in his herbarium (K) indicated this fungus as *P. exigua* 'f. *sambuci*'. A similar case has also been recorded for a form of dry rot of potato (*Solanum tuberosum*), called "gangrene" in the United Kingdom. In the Netherlands this disease is generally caused by a fungus, currently named *Phoma solanicola* Prill. & Del. (Boerema & van Kesteren, 1962). In no way can this species be distinguished from the ubiquitous *P. exigua*. Apparently in Scotland and Australia, however, gangrene is mostly caused by a *Phoma* which *in vitro* can at once be distinguished by its production of a yellow or red pigment diffusing in the culture medium. Malcolmson (1958a) found that this pigment-producing fungus, originally described as *Phoma foveata* Foister, is morphologically indistinguishable from *P. solanicola* (= *P. exigua*). From monospore isolations from a single pycnidium of *P. foveata*, she also obtained colonies that failed to produce any pigment. Therefore she regarded both types of colonies as referable to one species. In a later publication on gangrene, Malcolmson (1958b) referred to the pigment-producing strains as *P. solanicola* 'f. *foveata*'. Recently, J. M. Todd (Department of Agriculture and Fisheries for Scotland) pointed out (personal communication) that *P. foveata* is much more pathogenic to potato tubers than *P. solanicola* (= *P. exigua*), while the two types also differ in their temperature requirements, the former being more tolerant of lower temperatures. Boerema (1967), confirming the findings of Malcolmson (l.c.) and Todd, named the pigment-forming strains *P. exigua* var. *foveata* (Foister) Boerema.

The species and variety concept

An important criterium for the specific delimitation in the artificial system of the Deuteromycetes should be the possibility of identification independent of substratum or host. In our opinion, this means that a form-species should be based on stable and clear morphological characteristics. In *Phoma*-like fungi the number of dependable morphological characteristics is restricted. The shape and dimension of pycnidia and spores are generally highly variable. In these fungi, therefore, the species concept must be rather broad for a form-species to be readily identifiable by a taxonomist. If desirable smaller units can be distinguished within such a form-species. These can be based on growth characteristics *in vitro*, e.g. the general habitus, the production of chlamydospores, pigment, and crystals. However, there is bound to be chaos if these growth-characteristics are used for species delimitation alone. Therefore we endorse the view expressed by Maas (l.c.) and Boerema (1967) that the flax fungus and the pigment-producing gangrene fungus should be regarded as mere varieties of the ubiquitous soil-borne *P. exigua*. In the present paper the elder-fungus is also treated as a variety of *P. exigua*. It is possible that in the course of time it will be necessary to distinguish more varieties.

This concept of *P. exigua* is supported by the following typical biochemical character: it appears that the ubiquitous strains of *P. exigua*, as well as the varieties on flax and elder, are characterized by the production of a colourless metabolite "*E*" (derived from *exigua*), which can easily be oxidized to pigment "α" and pigment "β" successively. The properties of *E*, α and β will be discussed more fully in a separate chapter. In some strains of *P. exigua* var. *foveata* the oxidizable substance *E* could also be demonstrated.

It is likely that in general the occurrence of a certain fungus-metabolite is not restricted to a single species. So far, however, tests on numerous other *Phoma*-like fungi have revealed the substance *E* in cultures of five other species only; morphologically these are quite different from *P. exigua*. This has led us to believe that the oxidation reaction discussed in the next chapter is a valuable diagnostic character of *P. exigua*. The other diagnostic characters of *P. exigua* and the differentiating criteria of its varieties are summarized in Table I.

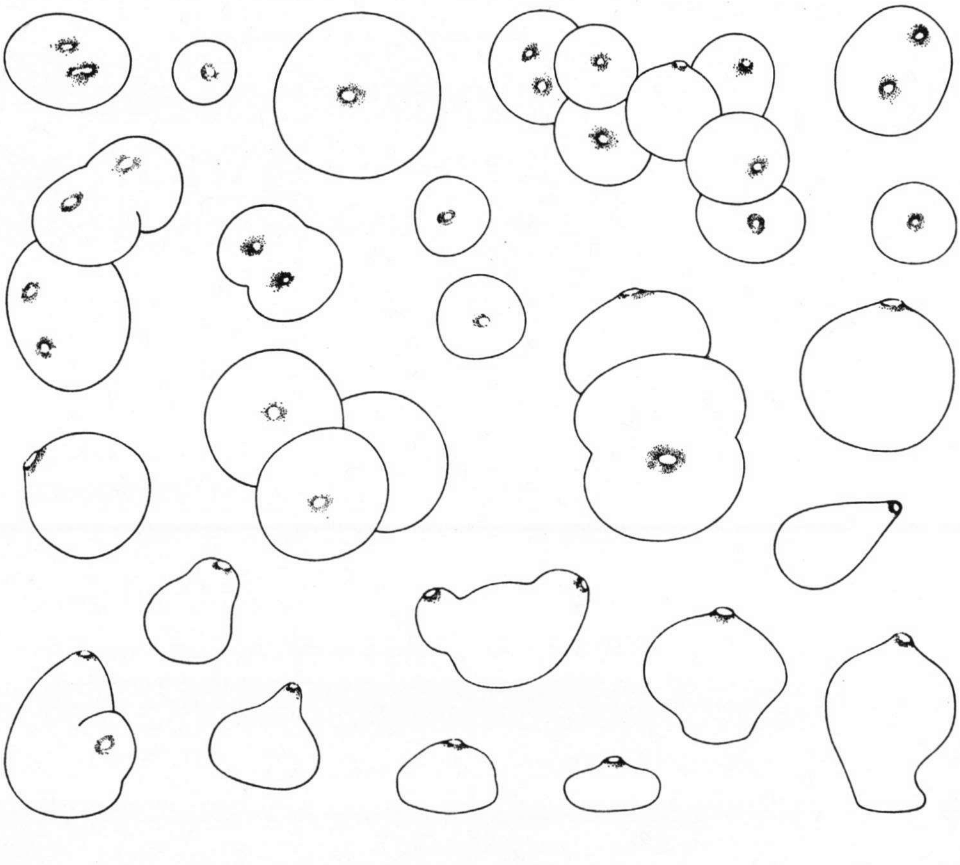


Fig. 1. *Phoma exigua* s.l. — Variation in size and shape of the pycnidia.

TABLE I — DELIMITATING AND DIFFERENTIATING CRITERIA

<table>
<tr><td>Pycnidia</td><td colspan="4">Thin-walled, parenchymatous with hyphal elements, brown to black, variable in size and shape, generally globose, occasionally coalesced to large, irregular fructifications (Fig. 1).
Ostioles inconspicuous, internally lined with papillate, hyaline cells (Fig. 2).</td></tr>
<tr><td>Pycnidiospores</td><td colspan="4">Hyaline, occasionally guttulate, in mass dirty white to salmon pink, ovoid to ellipsoid (Fig. 4).
Majority continuous: 2.5–12 × 1.5–5 μ, mostly (4–)5–7(–8.5) × 2(–2.5) – 3 (–3.5) μ; generally a small number are 1- (occasionally 2-) septate: 5.5–13 × 2.5–5 μ, mostly (7–)7.5 – 10(–12) × (2.5–)3 – 3.5(–4) μ.
Arising by a monopolar repetitive budding process on undifferentiated parent cells (Fig. 3, Pl. 2 fig. 1).</td></tr>
<tr><td rowspan="5">Mycelial characters</td><td>Mycelial mat extremely variable (Pl. 3 figs. 1–4).</td><td colspan="3">Mycelial mat relatively uniform.</td></tr>
<tr><td colspan="4">Generally flat and dense, white to black-coloured with various grey tinges.</td></tr>
<tr><td>Growth rate variable, very slow to very fast.</td><td>Black tinges dominating. Growth rate relatively slow (Pl. 3 fig. 5).</td><td colspan="2">Also brown tinges occur.</td></tr>
<tr><td colspan="2">Margin of the colonies irregularly scalloped or lobed (compare Pl. 3 figs. 1, 3), each prominence being based on a strongly growing leading hypha.</td><td></td><td></td></tr>
<tr><td colspan="3">Locally loose, whitish or greyish, aerial mycelial tufts (compare Pl. 3 figs. 1, 2, 4, 6), consisting of broadly swollen hyphae.</td><td></td></tr>
<tr><td>Metabolites</td><td colspan="3">Substance E always produced in various quantities; demonstrable by oxidation with alkali (compare Pl. 4 figs. 1, 2), see text.</td><td>Substance E sometimes present (Pl. 4 fig. 9). Several anthraquinone pigments produced; under strongly acid conditions yellow, at higher pH red (Pl. 4 fig. 8); in aging cultures frequently crystallized as yellow needles, see Bick & Rhee (1966).</td></tr>
<tr><td>Vars.</td><td>Phoma exigua var. exigua</td><td>var. linicola</td><td>var. sambuci-nigrae</td><td>var. foveata</td></tr>
<tr><td>Hosts</td><td>All kinds of plants.</td><td>flax.</td><td>elder.</td><td>potato.</td></tr>
</table>

The characteristic oxidation reaction

$$(E + O_2 \longrightarrow \alpha \rightleftarrows \beta)$$

in alkaline condition

From comparative experiments it appears that the production of substance E is most abundant on malt agar (formula Ainsworth, 1961: 241). On cherry agar (300 ml juice of 500 g cherries + 1300 ml H_2O + 27.5 g agar) the yield is less, while on oat agar (Ainsworth, 1961: 242) the production is scanty. At a pH lower than 5 there appears to be more E in the agar medium than at a higher pH. Further it is found that light (daylight) stimulates the production of this substance.

The oxidation products of E, the pigments α and β both act as pH-indicators. Pigment α is red-purple at pH < 10.5 and blue-green at pH > 12.5. Pigment β is yellow at pH < 3.5 and red at pH > 5.5.

DEMONSTRATION IN AGAR PLATE CULTURES (Pl. 4 figs. 1, 2)

In agar plate cultures of the ubiquitous *P. exigua* and in cultures of its varieties on flax and elder the oxidation of E to α and β can easily be produced by adding a drop of alkali, e.g. NaOH-N. The production of pigment α then promptly starts on this spot. This is shown in alkaline environment by a gradually darkening blue-green colour. The colouring is most intense at the edge of the drop, where there is a larger supply of oxygen. Subsequently pigment α passes into pigment β, which is reddish under alkaline conditions. The red colour also appears first at the edge of the drop. In the centre of the drop there is at first a mixture of bluish-green α and reddish β. The colour is, of course, also influenced by the natural colour of the agar medium, being yellow in malt agar, and red in cherry agar.

DEMONSTRATION IN CULTURE-EXTRACTS (Pl. 4 figs. 3–7)

Substance E and both pigments α and β are soluble in water. A crude solution of E can be obtained by filtering cultures of the fungus on a liquid malt medium (without agar). A solution of E can also be obtained by cutting malt agar plate cultures in small pieces, placing these in water for some days, and subsequently filtering the mixture. By adding a small amount of alkali (e.g. NaOH-N) the solution stains blue-green (α); this colour gradually passes into red (β). Shaking accelerates the reaction, but this takes place only if oxygen is present, indicating that the reaction is an oxidation process. It is not probable that the reaction is caused by an enzyme, since it is not stopped after heating at 100° C during 1/2 hour (in nitrogen atmosphere). The oxidation from α to β at first runs as an equilibrium-reaction. Ultimately, however, it becomes irreversible, since the addition of reduction substances (e.g. $Na_2S_2O_4$) does not change the colour from red (β) back into blue-green (α) or colourless (E). However, it appears possible, by adding a reduction substance, to stop the oxidation in the crude solution at a moment that chiefly only α (blue-green) is present. The final red-coloured solution (β) stains yellow on the addition of an acid (e.g. HCl–N). In this acid condition the extraction of pigment β with different extraction solvents was attempted. The process was only partly successful when 1-butanol or butanone were used. Better results were obtained, however, by adsorption in a small column of a mixture of 'Norit' and 'Hyflo Supercel'. This method can also be applied directly on the colourless substance *E*: adsorption in Norit and Hyflo Supercel, elution with aethanol, and subsequent oxidation in alkaline condition. From a purified solution of β it was established that the colour change from yellow [Munsell (1952): 2.5 Y (8/8–8/10)] to red [10. R (5/8–5/10)] and *vice versa*, occurs at the pH range of c. 3.5–5.5. Further it could be established that the pigment α changed its colour from blue-green [5.0 BG (4/4–4/6)] to red-purple [5.0 RP (5/2–5/4)] at the pH range of c. 10.5–12.5. The chemical character of *E*, α, and β has not yet been established.

Taxonomy

The synonymy of the ubiquitous *Phoma exigua* and its more specialized pathogenic varieties is discussed.

The list of synonyms quoted under *P. exigua* var. *exigua* is only provisional; many other possible synonyms are still being studied.

The names of authors are abbreviated as recommended in the 'Index of Plant Diseases in the United States' (Agric. Handb. U.S. Dep. Agric. 165. 1960). Herbaria and culture collections are coded according to Lanjouw & Stafleu (1959) and the list of abbreviations in the catalogue of the American Type Culture Collection (Ed. 7, 1964), respectively.

PHOMA EXIGUA Desm. var. EXIGUA — Pls. 1, 2 fig. 1; Pl. 3 figs. 1–4; Pl. 4 figs. 1–7

Phoma exigua Desm. *in* Annls Sci. nat. (Bot.) III, **11**: 282, 283. 1849. — Holotype: Pl. cryptog. N. France, Ed. 1, Fasc. 38, No. 1869a. 1849 on *Polygonum tataricum* L. = *Fagopyrum tataricum* (L.) Gaertn. (PC; isotype K).

Phyllosticta sambuci Desm. *in* Annls Sci. nat. (Bot.) III, **8**: 34. 1847.

Phyllosticta hortorum Speg. *in* Atti Soc. crittogam. ital. **3**: 67. 1881. — *Ascochyta hortorum* (Speg.) C. O. Sm. *in* Bull. Del. Univ. agric. Exp. Stn **63**: 19–23. 1904.

Phyllosticta decidua Ell. & Kell. *in* Am. Nat. **17**: 1165. 1883.

Phoma herbarum West. f. *brassicae* Sacc. *in* Sylloge Fung. **3**: 133. 1884.

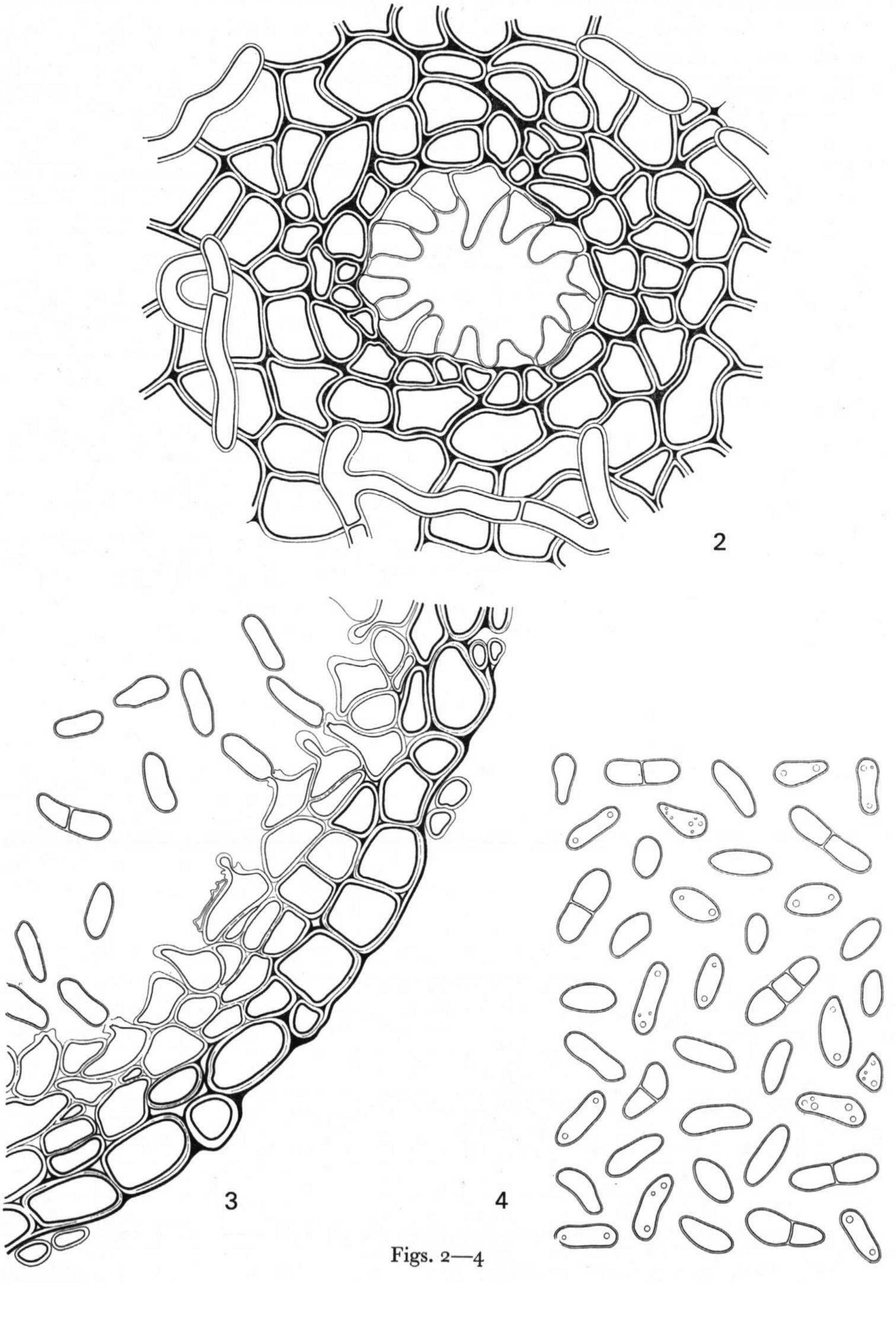
Phoma herbarum West. f. *hyoscyami* Sacc. in Sylloge Fung. **3**: 133. 1884.

Phoma herbarum West. f. *schoberiae* Sacc. *in* Sylloge Fung. **3**: 133. 1884.

Phoma solanicola Prill. & Del. *in* Bull. Soc. mycol. Fr. **6**: 179. 1890.

EXPLANATION OF FIGURES 2—4

Figs. 2–4. *Phoma exigua* s.l. — 2. Superficial view of an ostiolum; note the structure of the wall and the papillous cells surrounding the opening. — 3. Cross section of the pycnidial wall, showing various stages of the spore-forming process (monopolar repetitive budding; compare Boerema, 1965). Diagrams made by camera lucida or drawn after electronmicrographs. — 4. Pycnidiospores, showing variation in shape, size, septation and presence of guttules.



Figs. 2—4

Phoma solaniphila Oud. *in* Versl. gewone Vergad. wis- en natuurk. Afd. K. Akad. Wet. Amst. **9**: 297. 1900.

Phyllosticta vincae-minoris Bres. & Krieger *in* Hedwigia **39**: 325. 1900.

Phyllosticta vincae-majoris Allesch. *in* Rab. KryptogFlora, Pilze **6**: 155. 1901.

Phyllosticta mulgedii J. J. Davis *in* Trans. Wis. Acad. Sci. Arts Lett. **16**: 761. 1909.

Phoma linicola Bub. *in* Annln naturh. Mus. Wien **28**: 203. 1914; not *Phoma linicola* Em. Marchal & Verpl. *in* Bull. Soc. r. Bot. Belg. **59**: 22. 1926 (= *P. exigua* var. *linicola*); not *Phoma linicola* Naoum. *in* Mater. Mikol. Fitopat. Ross. **5**: 3. 1926 (= *Macrophoma* [?], fide Maas, 1965).

Phoma tuberosa Melhus, Rosenb. & E. S. Schultz *in* J. agric. Res. **7**: 251. 1916.

Phoma herbarum West. var. *dulcamaricola* Bub. *in* Bot. Közl. **1915**: 63. 1915.

DESCRIPTIONS & ILLUSTRATIONS.—Köhler *in* Angew. Bot. **10**: 113–139, figs. 1–9. 1928 (*Phoma solanicola*); Dennis *in* Trans. Br. mycol. Soc. **29**: 21–26, text-figs. 1 C-G, 3 E2–7, pl. 1 figs. 4–6. 1946 (group II, strain 2–7); Malcolmson *in* Trans. Br. mycol. Soc. **41**: 415–417, pl. 22 figs. 1, 2. 1958 (*Phoma solanicola, P. tuberosa*); Maas *in* Neth. J. Pl. Path. **71**: 114, 115, fig. 1 D-F. 1965 (*Phoma exigua*).

HABITAT & OCCURRENCE.—Ubiquitous soil-born fungus, occurring on various parts of all kinds of plants (see table II). Very often associated with distinct disease symptoms, such as leafspots, lesions on stems and roots (tubers), damping off, dieback, and so on. In all these cases the fungus generally behaves like a weak parasite or a wound parasite, exactly like *Botrytis cinerea*. At the time of leaf fall and natural dying-off of herbaceous plants it is generally the most frequently-occurring pycnidial fungus. In mycological diagnostic work of diseased plants it is also one of the most common fungi isolated.

SPECIMENS EXAMINED.—

Exsiccata: *Phoma exigua* var. *a*, Desmazières, Pl. cryptog. N. France, Ed. 1, Fasc. 38, No. 1869a, holotype (PC; see Plate 1), and isotype (K); *Phoma linicola*, type (Herb. Bubak, BKL); *Phoma solanicola*, type (Herb. Delacroix, VER [1]); *Phoma solaniphila*, type (Herb. Oudemans, GRO); *Phyllosticta decidua*, Ellis, N. Am. Fungi, No. 307, syntype on *Leonurus cardiaca* (NY); N. Am. Fungi, No. 1165, syntype on *Nepeta cataria* (L 910.243–492); *Phyllosticta mulgedii*, type (NY); *Phyllosticta sambuci* Desm., Pl. cryptog. N. France, Ed. 1, Fasc. 33, No. 1638, holotype (PC); Pl. cryptog. France, Ed. 2, Fasc. 25, No. 1238 (PC); *Phyllosticta vincae-minoris*, Petrak, Kryptog. exs. No. 2417 (L 922.54–79).

Cultures: *Phoma solanicola*, isolate from potato tuber (CBS 236.28); *Phoma tuberosa*, isolate from cysts of *Heterodera rostochiensis* (CBS 369.45); *Phyllosticta hortorum*, isolate made by Togashi, Japan (CBS 289.29).

Desmazières already considered *Phoma exigua* a "polyphagous" species. However, examination of the exsiccata he distributed under *P. exigua* reveal that he used this name in a very wide sense, including quite different *Phoma*-species. He underestimated the sporological characters, paying more attention to the features of the pycnidia; on account of the shape and dimensions of the pycnidia he distinguished two varieties. Only the one first treated, 'var. *a*', should be considered typical to the species *P. exigua* (var. *exigua*). Maas (1965) pointed out that the holotype (PC; Plate 1 above), as well as an isotype (K) of variety *a* on buckwheat refers to the

[1] Station centrale de Pathologie Végétale, Versailles; not listed by Lanjouw & Stafleu (1959).

fungus discussed in this paper. As will be clear we completely support this conclusion.

It should be noted that the exsiccata subsequently distributed by Desmazières under the name *P. exigua* var. *a* (on vetchling: Pl. cryptog. France II, Ed. 3, Fasc. 2, No. 57. 1853) represents a quite different species, viz. *Phoma medicaginis* Malbr. & Roum. var. *pinodella* (L. K. Jones) Boerema (see Boerema & al., 1965).

The original exsiccata of the second variety of *P. exigua*, distinguished by Desmazières and indicated as var. '*b*' or '*minor*' [2] [Pl. cryptog. N. France, Ed. 9, Fasc. 38, No. 1869b. 1849, holotype (PC; Plate 1 below), and isotype (K) on *Ranunculus* sp.; and Pl. cryptog. France II, Ed. 3, Fasc. 16, No. 759. 1860, specimen on *Thalictrum* sp.] appear to contain a species similar to the ubiquitous saprophyte *Phoma herbarum* West. (see Boerema, 1964).

Phoma exigua and *P. herbarum* have also in later periods often been confused. The latter, however, has substantially smaller spores, which are generally continuous (Boerema, 1964; Sutton, 1964). Further, the species is much less common on herbaceous stems than *P. exigua*. On account of these differences, four forms and one variety taken to belong to *P. herbarum* have been listed above as synonyms of *P. exigua*. Of these infraspecific taxa no original material is known to exist, but their spore-dimensions are too large for *P. herbarum*. Their identity with *P. exigua* is further in accordance with the original opinion that they represent only variants of a single ubiquitous species occurring on different hosts.

The original material of *Phyllosticta sambuci* contains pycnidia, which could not be distinguished microscopically from *P. exigua*. The pycnidia occur on small whitish spots situated along fold lines and lines of rupture in the leaves of elder (injury caused by the wind). From Dutch material with the same type of injury-lesions, strains of the ubiquitous *P. exigua* were repeatedly isolated. The separate particular elder-variety of *P. exigua* (discussed on p. 26), on the other hand, is generally associated with true leaf spots. *Phyllosticta sambuci* antedates the name *Phoma exigua*; however it is not available to replace the latter, since the transfer to *Phoma* would result in a later homonym of *Phoma sambuci* Pass. (*in* J. Hist. nat. Bord. **1885**: 135. 1885).

The synonymy of *Phyllosticta decidua*, *Phoma solanicola*, *Phoma solaniphila*, *Phyllosticta vincae-minoris*, and *Phyllosticta mulgedii* with *P. exigua* is also based on comparative examination of original herbarium material and the study of fresh isolates from the corresponding hosts or related species.

In the literature *Phyllosticta decidua* is reputed to be a polyphagous species with relatively small, continuous pycnidiospores (3–5 × 2 μ, compare Seaver, 1961). However, in the two original exsiccata of this species the spores were larger — of the same size as those of *P. exigua* — and, moreover, sometimes 1-septate.

The original descriptions of the remaining species are, broadly speaking, in accordance with the characteristics of *P. exigua*, except that the occurrence of 1-septate spores was overlooked.

[2] Afterwards cited by Saccardo (*in* Sylloge Fung. **3**: 134. 1884) as *P. exigua* var. *ranunculorum* Desm.

TABLE II

HOSTPLANTS FROM WHICH PHOMA EXIGUA VAR. EXIGUA HAS BEEN ISOLATED

Apocynaceae	3	Cucurbitaceae	7	Polemoniaceae	3
Nerium (1)		*Cucumis* (7)		*Phlox* (3)	
Vinca (2)		Cupressaceae	1	Primulaceae	5
Aceraceae	2	*Juniperus* (1)		*Cyclamen* (2)	
Acer (1)		Ericaceae	2	*Lysimachia* (1)	
Anthurium (1)		*Rhododendron* (2)		*Primula* (2)	
Begoniaceae	2	Geraniaceae	3	Ranunculaceae	13
Begonia (2)		*Geranium* (1)		*Anemone* (6)	
Berberidaceae	2	*Pelargonium* (2)		*Cimicifuga* (1)	
Berberis (1)		Gramineae	3	*Clematis* (2)	
Mahonia (1)		*Triticum* (3)		*Paeonia* (1)	
Bignoniaceae	3	Hydrophyllaceae	1	*Ranunculus* (3)	
Incarvillea (3)		*Nemophila* (1)		Rosaceae	27
Cactaceae	1	Iridaceae	5	*Fragaria* (6)	
Cactus (1)		*Crocus* (1)		*Malus* (12)	
Campanulaceae	3	*Freesia* (1)		*Prunus* (4)	
Campanula (1)		*Gladiolus* (1)		*Pyrus* (3)	
Platycodon (2)		*Iris* (1)		*Rosa* (1)	
Caprifoliaceae	11	*Ixia* (1)		*Sorbus* (1)	
Lonicera (2)		Labiatae	1	Salicaceae	6
Sambucus (3)		*Monarda* (1)		*Populus* (2)	
Viburnum (6)		Liliaceae	9	*Salix* (4)	
Caryophyllaceae	2	*Allium* (2)		Saxifragaceae	3
Dianthus (2)		*Colchicum* (1)		*Philadelphus* (1)	
Chenopodiaceae	3	*Hosta* (1)		*Ribes* (1)	
Beta (2)		*Lilium* (1)		*Saxifraga* (1)	
Spinacia (1)		*Tulipa* (2)		Scrophulariaceae	1
Compositae	58	*Yucca* (2)		*Rhinanthus* (1)	
Ageratum (1)		Lobeliaceae	1	Solanaceae	21
Buphthalmum (1)		*Lobelia* (1)		*Solanum* (21)	
Chrysanthemum (16)		Magnoliaceae	1	Taxaceae	1
Cichorium (15)		*Magnolia* (1)		*Taxus* (1)	
Dahlia (13)		Malvaceae	1	Thymelaeaceae	1
Doronicum (1)		*Malva* (1)		*Daphne* (1)	
Erigeron (1)		Oleaceae	7	Ulmaceae	8
Lactuca (3)		*Forsythia* (1)		*Ulmus* (8)	
Liatris (6)		*Ligustrum* (5)		Umbelliferae	11
Solidago (1)		*Syringa* (1)		*Anthriscus* (3)	
Corylaceae	1	Papaveraceae	3	*Apium* (2)	
Corylus (1)		*Dicentra* (1)		*Carum* (3)	
Cruciferae	9	*Papaver* (2)		*Daucus* (3)	
Aubrietia (1)		Papilionaceae	13	Valerianaceae	1
Cheiranthus (1)		*Medicago* (2)		*Valeriana* (1)	
Brassica (4)		*Phaseolus* (3)		Vitaceae	1
Hesperis (1)		*Pisum* (5)		*Vitis* (1)	
Lunaria (2)		*Trifolium* (2)			
		Vicia (1)			

The synonymy of *Phyllosticta hortorum* with *P. exigua* is based on the study of a living culture from leafspots of an eggplant in Japan (obtained from the CBS), which has been compared with the original diagnosis. It must be noted that by Italian workers (see Ciferri, 1957) *P. hortorum* is declared to be identical with the pycnidial state of *Didymella lycopersici* Kleb., the causal organism of tomato stemrot or cancer. However, this is not justified by the original diagnosis of *P. hortorum* and has not been based on a comparative study of fungal isolates.

Regarding *Phyllosticta vincae-majoris* and its variant on *Vinca minor* mentioned above, we may refer to Jansen (1965). The data on *Phoma linicola* are quoted from Maas (1965). For a discussion of *Phoma tuberosa*, see Malcolmson (1958a).

PHOMA EXIGUA Desm. var. LINICOLA (Naoum. & Vass.) Maas—Pl. 3 fig. 5

Ascochyta linicola Naoum. & Vass. *apud* Naoum. *in* Mater. Mikol. Fitopat. Ross. **5**: 3. 1926. — *Phoma exigua* Desm. var. *linicola* (Naoum. & Vass.) Maas *in* Neth. J. Pl. Path. **71**: 118. 1965.

Phoma linicola Em. Marchal & Verpl. *in* Bull. Soc. r. Bot. Belg. **59**: 22. 1926; not *Phoma linicola* Bub. *in* Annln naturh. Mus. Wien **28**: 203. 1914 (= *P. exigua* var. *exigua*); not *Phoma linicola* Naoum. *in* Mater. Mikol. Fitopat. Ross. **5**: 3. 1926 (= *Macrophoma* [?] fide Maas, 1965).

Diplodina lini Moesz *in* Magy. bot. Lap. **29**: 35–38. 1930.

DESCRIPTIONS & ILLUSTRATIONS.—Kerr *in* Trans. Br. mycol. Soc. **36**: 61–73. fig. 1, pl. 4 figs. 1–4, 6. 1953 (*Ascochyta linicola*); Breyer *in* Wiss. Z. Martin-Luther-Univ. Halle-Wittenb. **12**: 155–164 (Isol. 1, 3, 4), figs. 1, 2, 4–9. 1963; Maas *in* Neth. J. Pl. Path. **71**: 114–115, fig. 1 A-C. 1965 (*Phoma exigua* var. *linicola*).

HABITAT.—Associated with damping-off of flax seedlings and brown discoloration of the root collar and stem bases of flax (*Linum usitatissimum*). For description of the disease symptoms, see e.g. Breyer (1963).

SPECIMENS EXAMINED.—

Exsiccatum: *Phoma exigua* on *Linum usitatissimum* L., Westendorp, Herb. Cryptog. belge, Fasc. 23, No. 1137 (BR).

Cultures: *Ascochyta linicola*, three isolates made by Dr. H. Diddens, 1929 (CBS 112.28 = culture of Russian herb. material, CBS 113.28, CBS 114.28); isolate made by Dr. A. Kerr, 1953 (CBS 109.49); five isolates made by Dr. J. van der Spek (IPO[3]).

For a detailed discussion of the synonymy of this footrot fungus of flax, see Maas (1965).

[3] Institute of Phytopathological Research, Wageningen.

EXPLANATION OF TABLE II

The ciphers in the table refer to the number of isolates made. In the periode 1961–1965, 260 isolates were made from diseased or dead plant material distributed over 46 families and 99 genera of Phanerogams. These isolates were obtained from stems (156), leaves (52), roots (41), and seeds or fruits (11).

PHOMA EXIGUA Desm.
var. **sambuci-nigrae** (Sacc.) Boerema & Höw., *comb. nov.*—Pl. 3 fig. 6; Pl. 2 fig. 2

Phoma herbarum West. f. *sambuci-nigrae* Sacc. *in* Sylloge Fung. **3**: 133. 1884 (basionym).
Phyllosticta sambucina Allesch. *ex* Mig. *in* Thomé KryptogFlora, Pilze **4**(1): 33. 1921.

DESCRIPTIONS.—Allescher ex Migula, l.c. (*Phyllosticta sambucina*); Grove, Br. Coelomycetes **1**: 104. 1935 (*Phoma exigua*).

HABITAT.—Associated with leaf spots (Pl. 4) and dead shoots of elder (*Sambucus nigra*).

SPECIMENS EXAMINED.—
Exsiccata: *Phoma herbarum* f. *sambuci-nigrae*, holotype (Herb. Saccardo, PAD); *Phoma exigua* 'f. *sambuci*' (Herb. Grove, K).

There are various *Phoma* spp. described from branches of elder, but only the spore dimensions of the above cited form of *Phoma herbarum* are in accordance with those of this parasite of elder. Of the leafspot-fungi from elder mentioned in literature, only the name *Phyllosticta sambucina* Allescher as published by Migula can be applied to this fungus. Allescher himself withdrew this name (see Rab. KryptogFlora, Pilze **6**: 87. 1901), on second thoughts considering that it belonged to *Phyllosticta sambuci* Desm. But after having examined the original material of the latter we have concluded that this is not correct; see further the discussion of *P. exigua* var. *exigua*.

PHOMA EXIGUA Desm. var. FOVEATA (Foister) Boerema—Pl. 4 figs. 8, 9

Phoma foveata Foister *in* Trans. Proc. bot. Soc. Edinb. **33**: 66. 1940. — *Phoma solanicola* Prill. & Del. f. *foveata* (Foister) Malcolmson *in* Ann. appl. Biol. **46**: 639. 1958. — *Phoma exigua* Desm. var. *foveata* (Foister) Boerema *in* Neth. J. Pl. Path. **73**: 192. 1967.

DESCRIPTIONS & ILLUSTRATIONS.—Dennis *in* Trans. Br mycol. Soc. **29**: 17–21, text-figs. 1 A, B, 3 E1, pl. 1 figs. 1, 2. 1946 (group I, *Phoma foveata*); Malcolmson *in* Trans. Br. mycol. Soc. **41**: 415–417. 1958 (*Phoma foveata*); Kranz *in* Sydowia **16**: 12, 13, figs. 5, 7. 1963 (Isol. 1, 2, 4); Bick & Rhee *in* Biochem. J. **98**: 112–116. 1966 (study of the characteristic anthraquinone pigments).

HABITAT.—In certain regions associated with tuber rot ("gangrene") and stem lesions of potatoes (*Solanum tuberosum*). Also occurring incidentally on other plants. For description of the symptoms of potato gangrene, see e.g. Advis. Leafl. Minist. Agric. Fish. 545. 1966.

SPECIMENS EXAMINED.—
Cultures: *Phoma foveata*, culture of type (CBS 155.45 = NCTC 6113); isolate made by Dr. J. Kranz, 1963, Isol. 4 (IP-BONN [4]); two isolates made by Mr. J. M. Todd, 1963; *Phoma solanicola* f. *foveata*, two isolates made by Dr. J. F. Malcolmson, 1958.

[4] Institut für Pflanzenkrankheiten der Universität Bonn; not listed by Lanjouw & Stafleu (1959).

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REFERENCES

AINSWORTH, G. C. (1961). Ainsworth & Bisby's dictionary of the fungi. Kew.

BICK, I. R. C. & C. RHEE (1966). Anthraquinone pigments from *Phoma foveata* Foister. *In* Biochem. J. **98**: 112–116.

BOEREMA, G. H. (1964). *Phoma herbarum* Westend., the type-species of the form-genus *Phoma* Sacc. *In* Persoonia **3**: 9–16.

—— (1965). Spore development in the form-genus *Phoma*. *In* Persoonia **3**: 413–417.

—— (1967). The *Phoma* organisms causing gangrene of potatoes. *In* Neth. J. Pl. Path. **73**: 190–192.

——, M. M. J. DORENBOSCH & L. LEFFRING (1965). A comparative study of the black stem fungi on lucerne and red clover and the footrot fungus on pea. *In* Neth. J. Pl. Path. **71**: 79–89.

—— & H. A. VAN KESTEREN (1962). *Phoma*-achtige schimmels bij aardappel. *In* Versl. Meded. plziektenk. Dienst Wageningen **136** (Jaarb. 1961): 201–209.

BREWER, J. G. & G. H. BOEREMA (1965). Electron microscope observations on the development of pycnidiospores in *Phoma* and *Ascochyta* spp. *In* Proc. K. Ned. Akad. Wet. (Sect. C) **68**: 86–97.

BREYER, H. (1963). Beiträge zur Kenntnis von *Phoma* spec. an *Linum usitatissimum* L. *In* Wiss. Z. Martin-Luther-Univ. Halle-Wittenb. **12**: 153–183.

CIFERRI, R. (1957). *Phoma – Phyllosticta* e *Diplodina – Ascochyta* sul pomodoro e sinonimia di *Ascochyta hortorum*. *In* Atti Ist. bot. Univ. Lab. crittogam. Pavia V, **14**: 99–106.

DENNIS, R. W. G. (1946). Notes on some British fungi ascribed to *Phoma* and related genera. *In* Trans. Br. mycol. Soc. **29**: 11–42.

JANSEN, M. J. C. M. (1965). Bladvlekken en scheutsterfte bij *Vinca* species veroorzaakt door *Phoma exigua*. *In* Versl. Meded. plziektenk. Dienst Wageningen **142** (Jaarb. 1964): 153–154.

LANJOUW, J. & F. A. STAFLEU (1959). Index Herbariorum. Part 1. The herbaria of the world. Ed. 4 (Regnum vegetabile **15**). Utrecht.

MAAS, P. W. TH. (1965). The identity of the footrot fungus of flax. *In* Neth. J. Pl. Path. **71**: 113–121.

MALCOLMSON J. F. (1958a). A consideration of the species of *Phoma* which parasitize potatoes. *In* Trans. Br. mycol. Soc. **41**: 413–418.

—— (1958b). Some factors affecting the occurrence and development in potatoes of gangrene caused by *Phoma solanicola* Prill. & Delacr. *In* Ann. appl. Biol. **46**: 639–650.

MUNSELL (1952). Color charts for plant tissues. Munsell Color Comp. Maryland. U.S.A.

SEAVER, F. J. (1961). Phyllostictales Phyllostictaceae (pars). *In* N. Am. Flora **6**(1).

SUTTON, B. C. (1964). *Phoma* and related genera. *In* Trans. Br. mycol. Soc. **47**: 497–509.

EXPLANATION OF PLATES 1–4

PLATE 1

Phoma exigua, type; var. '*a*' on buckwheat, var. '*b*' (or '*minor*') on *Ranunculus* (PC).

PLATE 2

Fig. 1. *Phoma exigua*, electron micrograph showing characteristic stages of the spore-forming process.

VP = "virginal" parent cell just before the detachment of the first spore; note the thick fold of the wall in the process of abstricting a spore.

RP = parent cell, which has previously produced a series of spores, at a stage just after detachment of a new spore; note the thick collar at the top of the parent cell.

In both cases, the wall of the spore-initial has not yet been differentiated; compare the wall of the mature spore (MSp) produced before by RP. For further details, see Brewer & Boerema (1965).

Fig. 2. *Phoma exigua* var. *sambuci-nigrae*. Leaves of elder showing brown spots with some concentric rings and numerous pycnidia, the leaf tissue encircling the spot being more or less yellow discoloured.

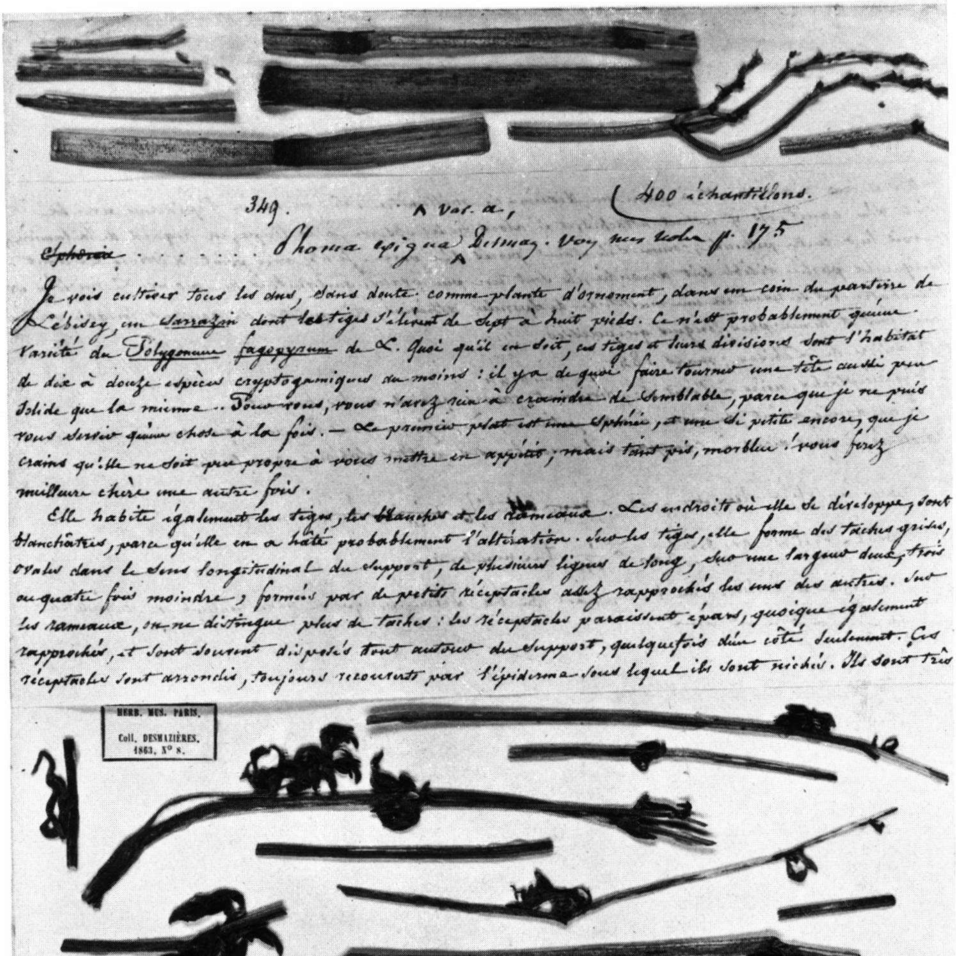
PLATE 3

Figs. 1–6. *Phoma exigua*. — 1–4. Var. *exigua*. — 5. Var. *linicola*. — 6. Var. *sambuci-nigrae*. Cultures showing the variation in growth habit; 1, 2 on malt agar, 3–6 on cherry agar.

PLATE 4

Figs. 1–7. *Phoma exigua* var. *exigua*. — Figs. 1–2. The oxidation-reaction in a two-weeks-old plate culture on cherry agar; 1. photographed five min. after addition of a drop of NaOH-N: conspicuous production of bluish green α on the spot; 2. photographed one hour later: α completely oxidized to reddish β. — Figs. 3–7. The oxidation-reaction in purified extract; 3. nearly colourless *E*; 4. the oxidation-product α at a pH of c. 10 (red-purple); 5. α in strongly alkaline condition (dark blue-green); 6. the final oxidation-product β in strongly alkaline condition (red); 7. β in strongly acid condition (yellow).

Figs. 8, 9. *Phoma exigua* var. *foveata*. — Fig. 8. On oat agar (pH c. 6); red discolouration of the medium by the production of anthraquinone pigments. — Fig. 9. On cherry agar (pH c. 5); production of greenish-blue α after addition of a drop of NaOH-N.



349. ^var. a,
(400 échantillons.
~~Sphoeria~~ . . . . Phoma exigua ^Desmaz. Voy mes notes p. 175

Je vois cultiver tous les ans, sans doute comme plante d'ornement, dans un coin du parterre de Lébisey, un sarrazin dont les tiges s'élèvent de sept à huit pieds. Ce n'est probablement qu'une variété du Polygonum fagopyrum de L. Quoi qu'il en soit, ces tiges et leurs divisions sont l'habitat de dix à douze espèces cryptogamiques au moins : il y a de quoi faire tourner une tête aussi peu solide que la mienne. Pour vous, vous n'avez rien à craindre de semblable, parce que je ne puis vous servir qu'une chose à la fois. — Le premier plat est une Sphérie, et une si petite encore, que je crains qu'elle ne soit peu propre à vous mettre en appétit ; mais tant pis, morbleu ! vous ferez meilleure chère une autre fois.

Elle habite également les tiges, les branches et les rameaux. Les endroits où elle se développe, sont blanchâtres, parce qu'elle en a hâté probablement l'altération. Sur les tiges, elle forme des taches grises, ovales dans le sens longitudinal du support, de plusieurs lignes de long, sur une largeur deux, trois ou quatre fois moindre, formées par de petits réceptacles assez rapprochés les uns des autres. Sur les rameaux, on ne distingue plus de taches : les réceptacles paraissent épars, quoique également rapprochés, et sont souvent disposés tout autour du support, quelquefois d'un côté seulement. Ces réceptacles sont arrondis, toujours recouverts par l'épiderme sous lequel ils sont nichés. Ils sont très

HERB. MUS. PARIS.
Coll. DESMAZIÈRES,
1863, N° 8.

372. (300 échantillons.
Sphoria minuscula (Nob.) Phoma exigua, b. Voy mes notes p. 175

Il faut de bons yeux, mon bon ami, pour apercevoir cette petite espèce sans le secours de la loupe ; il faut une bonne loupe pour la voir d'une manière satisfaisante ; il faut une bonne dose de courage pour user ses yeux, perdre son temps, et lasser sa patience avec une pareille misère. Vive la Cryptogamie pour la patience et le temps perdu !

Cette misère, puisque misère y a, habite les tiges et les feuilles mortes de diverses renoncules : elle est ici sur le Ranunculus bulbosus ; mais je l'ai remarquée aussi chez le R. acris. Dès que les tiges commencent à s'altérer, on voit s'y former de place en place des taches d'un roux terreux, sur lesquelles se montrent bientôt les réceptacles, qui s'étendent avec elles, et finissent par envahir les branches, les rameaux, les pédoncules, et la face inférieure des feuilles. Le support a parcouru alors le cercle de son existence, car les graines sont mûres et tombent : il ne paraît plus exister que pour le parasite, qui l'assiège de toutes parts. Il blanchit en se desséchant, et alors les réceptacles, pâles dans

1869 PHOMA EXIGUA, *Desmaz. Ann. des Sc. nat.* 1849.

a, Peritheciis rotundatis. Occurrit in foliis Polygoni tatarici?
b, Minor ; peritheciis sæpe ovatis. Occurrit in foliis Ranunculorum.

Cette espèce est quelquefois caulicole ; on la distinguera alors et au premier coup d'œil, du *Phoma Desmazieri*, Dur. et Mont. Fl. d'Alg., en ce qu'elle est beaucoup plus petite dans toutes ses parties.

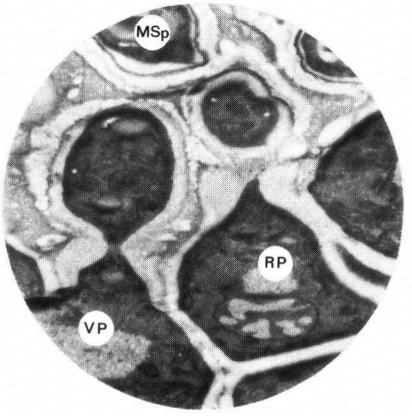


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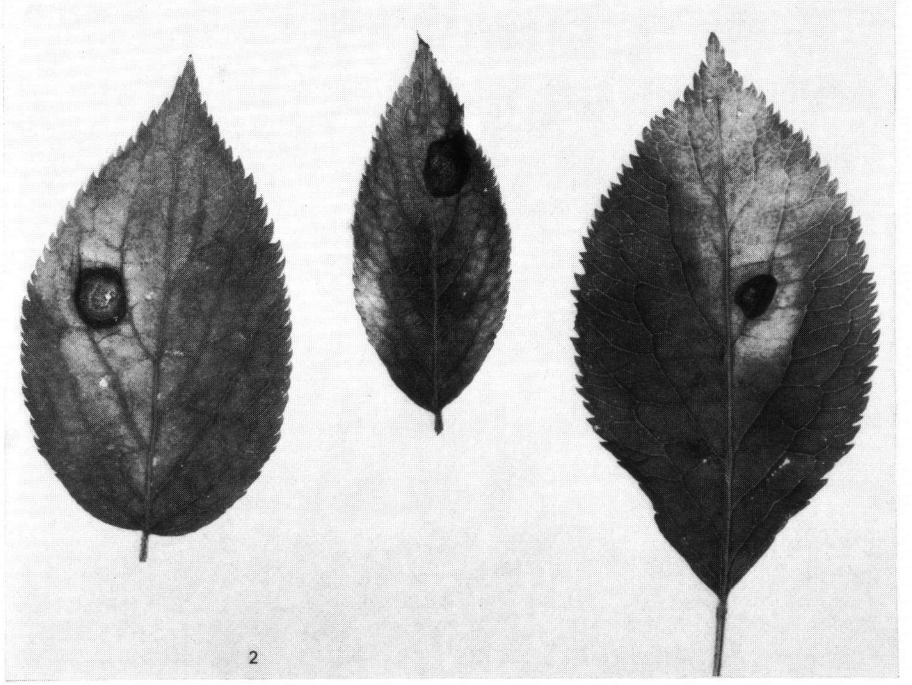
Photo Electron microscopy section of the Service Institute for Applied Mechanics and Technical Physics in Agriculture, Wageningen



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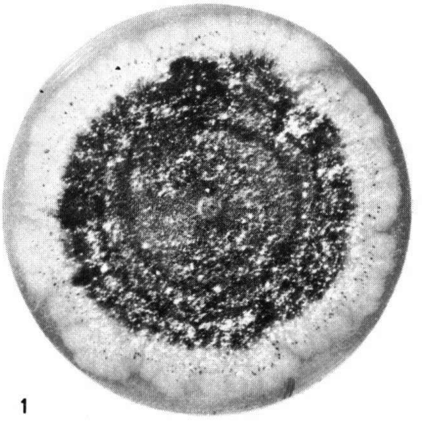

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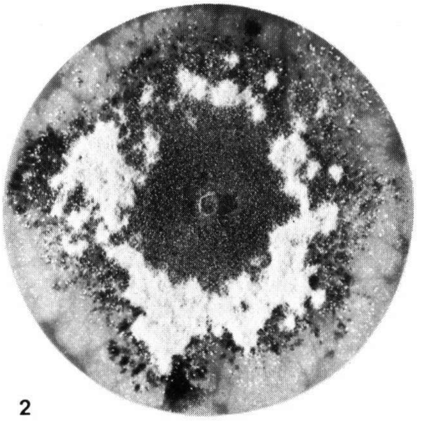

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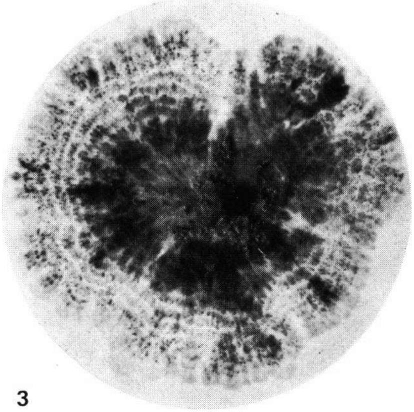

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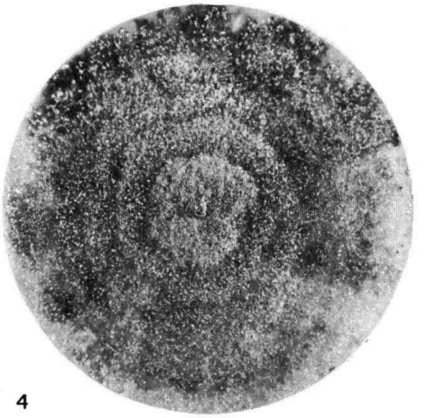

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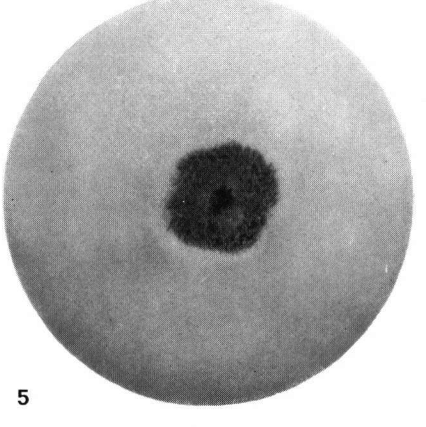

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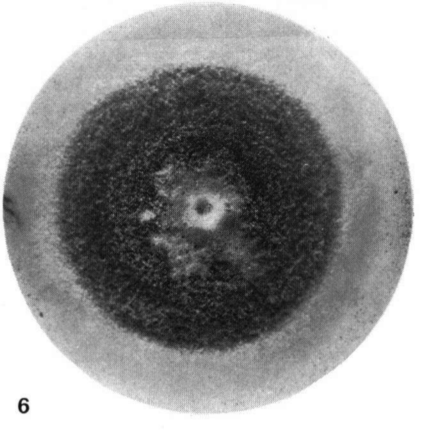

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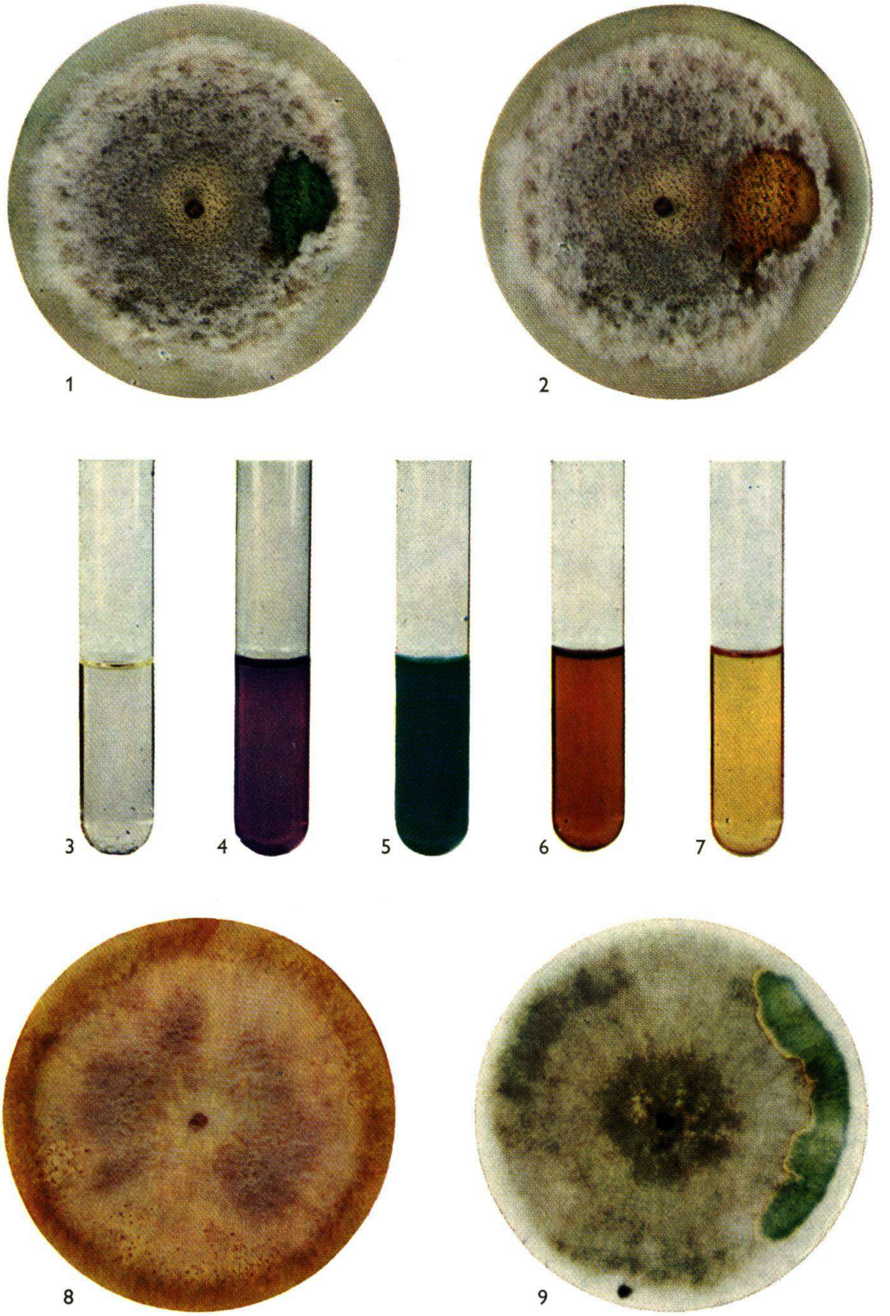
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