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CONTRIBUTIONS TOWARDS A MONOGRAPH OF PHOMA (COELOMYCETES) – III

1. Section Plenodomus: Taxa often with a Leptosphaeria teleomorph

G.H. BOEREMA[1], J. DE GRUYTER[2] & H.A. VAN KESTEREN[2]

Twenty-six species of *Phoma*, characterized by the ability to produce scleroplectenchymatous pycnidia (and often also pseudothecia) are documented and described. An addendum deals with five atypical species, but which on account of literature data may be related. The following new taxa are proposed: *Phoma acuta* subsp. *errabunda* (Desm.) comb. nov. (teleomorph *Leptosphaeria doliolum* subsp. *errabunda* subsp. nov.), *Phoma acuta* subsp. *acuta* f. sp. *phlogis* (Roum.) comb. nov., *Phoma congesta* spec. nov. and *Phoma vasinfecta* spec. nov. Detailed keys and indices on host-fungus and fungus-host relations are provided and short comments on the ecology and distribution of the taxa are given.

The previously published contributions towards the planned monograph of *Phoma* refer to species of sect. *Phoma* (de Gruyter & Noordeloos, 1992; de Gruyter et al., 1993) and sect. *Peyronellaea* (Boerema, 1993).

The present paper deals primarily with all species so far placed in the section *Plenodomus* (Preuss) Boerema, van Kesteren & Loerakker (1981) (species 1–26). The members of this section are characterized by their ability to produce '*scleroplectenchyma*' (term cf. Holm, 1957: 11) in the peridium of the pycnidia, i.e. a tissue of cells with uniformly thickened walls, similar to sclerenchyma in higher plants (evolutionary convergence). The thickening of the walls may be so extensive that only a very small lumen remains as in stone cells of fruit and seed. At the base of the conidiomata the thick-walled cells are often elongated and arranged in more or less diverging rows (Fig. 1).

Most species of the section occur on herbaceous plants (Group A); the scleroplectenchymatous pycnidia then mostly develop on last year's dead stems. A few species (Group B) produce scleroplectenchymatous pycnidia on bark and bare wood of deciduous trees and shrubs.

Species of section *Plenodomus* have been attributed to four different genera by previous authors, viz. to *Plenodomus* Preuss (1851), *Diploplenodomus* Diedicke (1912), *Leptophoma* Höhnel (1915) and *Deuterophoma* Petri (1929). The type species of the section, *Plenodomus rabenhorstii* Preuss, refers to scleroplectenchymatous pycnidia of *Phoma lingam* (Tode: Fr.) Desm., the anamorph of a cosmopolitan seed-borne pathogen of brassicas. The life-cycle of this pathogen has been studied in detail by Boerema & van Kesteren (1964) and Ndimande (1976) (Fig. 1). In association with disease symptoms this fungus produces ordinary thin-walled pseudoparenchymatous pycnidia ('Type I') with late formation of an opening, i.e. a pore instead of a predetermined ostiole. In mature pycnidia the cavity is usually irregular due to the occurrence of thin-walled seriate-

1) Karel Doormanstraat 4[5], NL-2041 HD Zandvoort, The Netherlands.
2) Plant Protection Service, P.O. Box 9102, NL-6700 HC Wageningen, The Netherlands.

cellular protrusions of the proliferating layer. On last year's dead stems and roots scleroplectenchyma may develop not only in the walls of old pycnidia with pores (poroid), but also in still closed pycnidia and pycnidial primordia. This results in relatively large scleroplectenchymatous pycnidia ('Type II'), either poroid or rupturing at maturity, and sterile scleroplectenchymatous pycnosclerotia ('III'). Only a few other species of the section *Plenodomus* produce the pycnidial types in this way separately in association with a parasitic and saprophytic phase. Most species produce always more or less scleroplectenchymatous pycnidia (II) in which the formation of a pore is often accompanied by the development of a neck, but pycnosclerotia (III) may also occur. In some species the pycnidia are initially thin-walled (I), but become gradually scleroplectenchymatous (→ II). The pycnidia of most species of the section are glabrous, but in some species they may be hairy (pilose) or even setose (*Pyrenochaeta*-like).

The synonymous generic name *Leptophoma* refers to the fact that many *Phoma* species of this section, especially those occurring on herbaceous plants (Group A), are anamorphs of the Ascomycete genus *Leptosphaeria* Ces. & de Not. with a scleroplectenchymatous ascocarp wall (structure) ('Group *doliolum*' cf. Holm, 1957: 16). Heterothallism may be responsible for the great variability of the conidia in some of these species and the occasionally observed differences in the geographic distribution of pycnidia-II and teleomorph.

The generic synonym *Diploplenodomus* implies that the section also includes species producing some two-celled conidia, a common phenomenon in *Phoma* spp. (secondary septation).

Deuterophoma finally, was originally based on still closed scleroplectenchymatous pycnidia with conidia "formed outside of the mother cells by a process similar to budding" (Petri, l.c.: 394).

The formation of scleroplectenchyma may serve to carry the fungus through periods of drought caused by cold or heat. The natural distribution of most members of the section occurring on herbaceous plants (Group A) includes areas with cold winters and/or mountainous regions. Species with an explicit circumpolar-arctic or arctic-alpine distribution produce only scleroplectenchymatous pycnidia (II) and pycnosclerotia (III), even when they are parasitic. The species producing the two pycnidial phenotypes separately, i.e. type I in a parasitic phase and types II and III in a saprophytic phase, are found on plants of southern origin (*Brassica* species, *Helianthus annuus*; for more details see Boerema, 1982). Resistance to drought due to heat may be important for those species which produce their pycnidia on bark and bare wood of trees and shrubs (Group B). One of the species of that group, *Phoma tracheiphila* (Petri) Kant. & Gik., is a vascular pathogen of citrus trees in the Mediterranean and Black Sea areas. This citrus-pathogen shows another unique phenomenon in *Phoma* species, viz. the production of conidia from free conidiogenous cells formed on the aerial mycelium as in the hyphomycete genus *Phialophora* Medlar. The development of a *Phialophora*-synanamorph with occasional production of arthrospores may be an adaptation to its role as a vascular pathogen (Goidanich, Ruggieri & Gagnotto, 1948). Another species of *Phoma* with *Phialophora*-synanamorph, infecting the vascular tissues of chrysanthemums and pyrethrums, is described in the Addendum of this paper.

There does appear to be some host specialization in *Phoma* sect. *Plenodomus*, although most species are known only from dead tissue (necrophytic). This specialization and the adaptation of the scleroplectenchymatous pycnidia to low or high temperatures may ex-

plain the difficulty in getting some members of this section to grow in vitro under normal laboratory conditions. They do not grow well and do not produce pycnidia readily, often losing their ability to produce pycnidia quickly. This has a bearing on the process of the identification as discussed in the explanatory note of the key to the species and varieties.

In the Addendum five *Phoma* species (nos 27–31) which do not fit into the section *Plenodomus* are discussed, but the literature suggests they may be related to it.

All species treated have been included in the indices on host-fungus and fungus-host relations.

MATERIAL AND METHODS

The descriptions of the species of sect. *Plenodomus* are based on specimens and isolates used in previously published studies on the *Phoma* species now classified in sect. *Plenodomus* (Boerema, 1976, 1981; Boerema & van Kesteren, 1964, 1981; Boerema, van Kesteren & Loerakker, 1981; Boerema & Loerakker, 1981, 1985; Ciccarone & Russo, 1969; Graniti, 1955; Lucas, 1963; Lucas & Webster, 1967; Schwarz, 1922; Tramier & Mercier, 1963). Sections of the pycnidia were made with a freezing microtome. The presence of scleroplectenchyma, consisting of hyaline cells with thick walls and a relatively small lumen, has been observed in very thin sections and confirmed in thick sections stained with Lugol's iodine (JKJ): the thick cell-walls then become red by adsorption of the iodine (blotting-paper-effect; first noticed by Von Höhnel, 1918: 250). Oatmeal agar (OA) has been used as standard culture medium for all species of sect. *Plenodomus,* because it stimulates the production of pycnidia. Remarks as 'isolates remained sterile' or 'only sterile mycelium obtained' refer to cultural studies on OA under normal laboratory conditions. Usually also isolates were grown on malt agar (MA), to check especially pigment production and crystal formation. Growth-rates were measured after 7 days in the dark at 20–22 °C. The descriptions of the five *Phoma* species in the Addendum are mainly adopted from earlier studies by Hudson (1960), Jones & Weimer (1938), Lucas & Webster (1967), Robertson (1967), and Baker et al. (1985).

KEY TO THE SPECIES AND THE VARIETIES[3]

Differentiation based on characteristics of scleroplectenchymatous pycnidia (pycnidia-II) in vivo

Species differentiation and delimitation in the section *Plenodomus* is the same as in other sections of *Phoma,* i.e. primarily based on comparative study in vitro. However, the distinguishing character of members of the section *Plenodomus,* the development of scleroplectenchyma, is most conspicuous and marked under natural growth conditions. Therefore this key has been based on the characteristics of pycnidial type II in vivo. Determinations may be checked with the data on growth in vitro. Direct identification in vitro is difficult in this section and sometimes impossible or not workable; see 'Possibilities of identification in vitro'. Most species of sect. *Plenodomus* have a restricted host range and/or distribution; therefore the extensive and detailed host-fungus index is also very important for identification.

3) For the species treated in the Addendum (nos 27–31) see the note at the end of this key.

1a. Scleroplectenchymatous pycnidia (II) on dead stems (occasionally on roots) of herbaceous plants 2
b. Scleroplectenchymatous pycnidia (II) on dead bark or wood (occasionally petioles) of deciduous trees and shrubs 24
2a. Pycnidia-II variable in size, relatively large, often exceeding 500 µm diam.; sometimes only pycnosclerotia (III) 3
b. Pycnidia-II usually not exceeding 500 µm diam. 5
3a. All scleroplectenchyma cells in mature pycnidia having about the same wall-thickness; pycnidia-II mostly 600–700 µm diam., with convex base of elongated cells and a long broad cylindrical neck up to 700 µm, usually with a somewhat swollen top; conidia mostly 4–5 × 1.5–2 mm; on dead stems of *Mercurialis perennis* (Euphorbiaceae); specific necrophyte ..... 1. *P. macrocapsa*
[Also produces pycnidia-II in vitro, but usually with less pronounced neck.]
b. Scleroplectenchyma cells with an exceptionally thickened wall and a very small lumen (like stone cells); in addition to pycnidia-II, scleroplectenchymatous pycnosclerotia (III) frequently occur 4
4a. Conidia small, usually not exceeding 4.5 µm in length, mostly 3.5–4.5 × 1–1.5 µm; pycnidia-II mostly 300–700 µm diam., not or only slightly papillate, with narrow pore or opened by rupture; sometimes only pycnosclerotia (III); on dead stems and roots of cultivated *Brassica* spp. (Cruciferae); serious cosmopolitan pathogen
2. *P. lingam*, teleomorph *L. maculans*
[Produces only pycnidia-I in association with disease symptoms, on seed, and in vitro.]
b. Conidia up to 6 µm in length, mostly 4.5–6 × 1.5–2.5 µm; pycnidia-II mostly 350–800 µm diam., usually with long thin tubular necks of various lengths, up to 800 µm; sometimes only pycnosclerotia (III); on roots and occasionally on stems of various herbaceous plants; low temperature pathogen (especially known from the arctic regions of Eurasia and North America) ..... 3. *P. sclerotioides*
[Produces also pynidia-II and pycnosclerotia (III) in vitro.]
5a. Pycnidial base convex with conspicuous diverging rows of elongated cells 16
b. Pycnidial base less thickened, cells at base similar to scleroplectenchyma cells of side walls 6
6a. Pycnidia-II globose-papillate 7
b. Pycnidia-II with pronounced necks 13
7a. Conidia very small, mostly 2–3 × 0.5–1 µm; pycnidia-II variable, relatively large with slightly papillate pore, often aggregated or irregular with the appearance of being multilocular; on dead stems of various herbaceous plants; plurivorous necrophyte (only known from mountainous regions in SW Asia) ..... 4. *P. astragalina*
[Scleroplectenchyma not so conspicuous as in most other species of the section; isolates on OA at room temperature remain sterile.]
b. Conidia larger, length mostly between 3–9 µm 8
8a. Conidia often > 5 µm in length 9
b. Conidia usually < 5 µm in length 11

9a. Pycnidia-II often coalesced forming large elongated aggregates up to 1000 µm (pycnidial stromata); pycnidia initially relatively small, closed or papillate-poroid with somewhat protruding lip; conidia variable in shape and dimensions, mostly 4–7 × (1.5–)2 µm; dead stems of various herbaceous plants, especially Compositae; necrophyte 5. *P. agnita,* teleomorph *L. agnita*

[In vitro produces pycnidia-II, often also confluent.]

b. Pycnidia usually solitary 10

10a. Conidia uniform subcylindrical, 5–7 × 1.5–2 µm; pycnidia-II with flattened base and a papillate or truncate-conoid pore; dead stems of *Rhinanthus* species (Scrophulariaceae); probably a specific necrophyte ... 6. *P. ruttneri* [?teleomorph *L. affinis*]

[Isolates of the possible teleomorph remained sterile.]

b. Conidia variable, mostly 5–9 × 1.5–3 µm; pycnidia-II usually non-papillate with narrow pore; dead stems of *Helianthus annuus* (Compositae); specific cosmopolitan pathogen ..... 7. *P. macdonaldii,* teleomorph *L. lindquistii*

[In association with disease symptoms produces only pycnidia-I; in vitro pycnidia I→II.]

11a. Pycnidia occasionally setose, i.e. with a number of stiff setae around the pore, but often also without any trace of setae; pycnidia papillate and initially thin-walled: I→II; conidia mostly 3.5–4.5 × 1.5 µm; dead stems of *Gentiana* species (Gentianaceae); noxious pathogen (so far only known from Europe) 8. *P. drobnjacensis*

[In association with disease symptoms produces only pycnidia-I (often setose around the pore); in vitro pycnidia-I→II, mostly with pilose neck.]

b. Pycnidia glabrous 12

12a. Pycnidia-II subglobose-conical with broad base and usually slightly papillate pore, mostly 150–250 µm diam., conidia mostly 4 × 1.5 µm; dead stems of Cruciferae, especially *Berteroa incana*; necrophyte .... 9. *P. conferta,* teleomorph *L. conferta*

[In vitro also produces pycnidia-II, but more irregular in shape.]

b. Pycnidia-II depressed globose with flattened base, explicitly papillate, usually with a dark-lined tube-shaped pore, mostly 200–350 µm diam.; conidia mostly 4–5 × 1–1.5 µm; on dead stems of *Melampyrum* species (Scrophulariaceae); specific necrophyte ..... 10. *P. petrakii* [?teleomorph *L. suffulta*]

[Isolates on OA at room temperature remained sterile.]

13a. Neck up to 500 µm long, pilose; conidia mostly 4–5.5 × 1.5–2.5 µm; on dead stems of Labiatae, especially *Leonura cardiaca* and *Ballota nigra*; necrophyte 11. *P. leonuri,* teleomorph *L. slovacica*

[In vitro produces pycnidia-II with very long pilose necks.]

b. Neck up to 200 µm long, bare or semi-pilose 14

14a. Conidia usually exceeding 5 µm in length, mostly 5–6 × 1.5–2 µm; on dead stems of *Achillea* species (Compositae); specific(?) necrophyte (so far only known from southern Europe) ..... 12. *P. congesta,* teleomorph *L. congesta*

[In vitro also produces pycnidia-II, usually with semi-pilose neck.]

b. Conidia usually not exceeding 5 µm in length 15

15a. Conidia conspicuous 2–4 guttulate, mostly 4–5 × 1.5–2 mm, but occasionally up to 6 µm long; on dead stems of *Veronica* species (Scrophulariaceae); specific necrophyte ..... 13. *P. veronicicola*
[In vitro also produces pycnidia-II, sometimes with pilose neck.]

b. Conidia eguttulate or with 2 inconspicuous small guttules, mostly 3–4 × 1–1.5 µm; on dead stems of Ranunculaceae, especially *Aconitum* and *Ranunculus* spp.; specific necrophyte (only known from southern Europe) ..... 14. *P. longirostrata*
[In vitro usually produces pycnidia-II with several necks, transfers soon become sterile.]

16a. Conidia relatively small, not exceeding 5 µm in length and 2 µm in width 17

b. Conidia usually larger 19

17a. Pycnidia-II depressed globose with flattened base and rather sharply delimited papillate neck of variable length; conidia mostly 3.5–5 × 1–1.5 µm; on dead stems of various herbaceous plants; necrophyte
15b. *P. acuta* subsp. *errabunda*, teleomorph *L. doliolum* subsp. *errabunda*
[In vitro also produces pycnidia-II, usually with somewhat pilose necks.]

b. Pycnidia-II usually more globose and less depressed, mostly with a conspicuous neck 18

18a. Pycnidia-II more or less subglobose with elongated neck up to 400 µm; conidia eguttulate, mostly 3.5–5 × 1.5 µm; dead stems of *Urtica* spp. (Urticaceae); specific necrophyte .. 15a. *P. acuta* subsp. *acuta*, teleomorph *L. doliolum* subsp. *doliolum*
[In vitro also produces pycnidia-II, but usually they remain very small with pilose necks; transfers soon become sterile. A specific pathogenic form commonly occurs on cultivated phloxes (Polemoniaceae): f. sp. *phlogis* (teleomorph unknown).]

b. Pycnidia-II depressed globose to subglobose with flattened base and a pronounced neck up to 200 µm; conidia mostly 4–4.5 × 1–1.5 µm with 1–2 small guttules; dead stems of Cruciferae, especially *Sisymbrium* spp.; pathogen (distribution not clear)
16. *P. sublingam*, teleomorph *L. submaculans*
[Produces only pycnidia-I in association with disease symptoms and in vitro.]

19a. Conidia aseptate 20

b. Conidia occasionally also 1-septate 23

20a. Conidia mostly not exceeding 8 µm in length 21

b. Conidia (6–)8–10(–12) × 2–2.5 µm; usually aseptate but occasionally 1-septate and longer up to 16 µm; pycnidia-II variable in shape with flattened base, often subglobose-papillate, but also with a long neck, usually at one side; dead stems of *Urtica* spp. (Urticaceae); specific necrophyte ..... 17. *P. piskorzii*, teleomorph *L. acuta*
[Only rarely recorded because of its common development at the inside hollow stems; isolates on OA at room temperature remained sterile.]

21a. Conidia often pluriguttulate, variable in shape and dimensions, usually oblong to ellipsoidal and always one-celled, mostly 5–8 × 2–2.5 µm; pycnidia-II with flattened base and pronounced cylindrical neck; dead stems of *Senecio* spp., occasionally other Compositae; specific necrophyte
18. *P. sydowii* [?teleomorph *L. senecionis*]
[Produces pycnidia-II in vitro.]

b. Conidia eguttulate or inconspicuously biguttulate 22

22a. Pycnidia-II depressed globose, usually with irregular deformed flattened base and short papillate neck; conidia variable in dimensions, mostly (4–)5–7 × 2–2.5 mm, sometimes much larger, (7–)8–12(–16) × 2–3 mm and then often 1-septate; on dead stems of various herbaceous plants; plurivorous necrophyte
19. *P. doliolum*, teleomorph *L. conoidea*
[Produces pycnidia-II in vitro with conidia of the more common, smaller dimensions; neck usually somewhat pilose.]

b. Pycnidia-II conoid with flattened base and conspicuous beak-like elongated neck, initially subglobose-papillate and thin-walled: I→II; conidia variable 4–8 × 2–3 µm and/or 4–6 × 2.5–4 µm; dead stems, leaves and seed capsules of various herbaceous plants; necrophyte (so far only known from arctic-alpine regions in Europe)
20. *P. pedicularis*
[In vitro produces pycnidia-I→II, which remain subglobose-papillate and small.]

23a. Pycnidia-II with flattened base and long neck, usually at one side 20b

b. Pycnidia-II with irregular base and short papillate neck 22a

24a. Pycnidia-II mostly < 250 µm in diam. 25

b. Pycnidia-II commonly > 250 µm in diam. 26

25a. Conidia very small, mostly 2–3 × 1–1.5 µm; pycnidia-I→II, subglobose with gradually developing cylindrical neck; subepidermal on stems of *Citrus* trees; noxious pathogen (only known from Mediterranean and Black Sea areas) 21. *P. tracheiphila*
[In vitro produces mostly only incomplete thin-walled pycnidia, but usually abundant development of conidia from free conidiogenous cells formed on the aerial mycelium: *Phialophora*-synanamorph.]

b. Conidia longer, 4.5–6.5 × 1–2 µm; pycnidia-II subglobose with flattened or somewhat pointed base and broad papillate pore, often with a protruding lip; bark and wood of *Malus pumila*; opportunistic pathogen (only known from North America and Japan) ..... 22. *P. coonsii*
[Produces pycnidia-II in vitro.]

26a. Pycnidia-II mostly 250–350 µm diam. 27

b. Pycnidia-II larger, often 400–500 µm diam. 28

27a. Pycnidia globose-papillate with flattened or somewhat pointed base, initially thin-walled and gradually becoming scleroplectenchymatous: I→II; conidia mostly 3–4 × 1–2 µm; bark and wood of various deciduous trees and shrubs; opportunistic pathogen ..... 23a, b. *P. enteroleuca* vars *enteroleuca* and *influorescens*
[Produces pycnidia-I→II in vitro. Varieties with or without production of a fluorescing metabolite.]

b. Pycnidia very thick-walled, mostly irregular-subglobose with flattened, often somewhat elongated base; even protopycnidia thick-walled and scleroplectenchymatous: II; conidia 2.5–4 × 1–1.5 µm; especially on bark of *Salix alba* (Salicaceae), occasionally other trees; opportunistic pathogen ..... 24. *P. intricans*
[Produces similar, but smaller pycnidia-II in vitro.]

28a. Pycnidia globose-papillate or with a short cylindrical neck, initially thin-walled: I→II; conidia mostly 3.5–5 × 2–2.5 µm; bark and wood of various deciduous trees and shrubs; necrophyte ..... 25. *P. rubefaciens*
[In vitro also produces pycnidia-I→II.]

b. Pycnidia usually globose-papillate with flattened base, at length often collapsing and becoming discoid or pezizoid; protopycnidia already scleroplectenchymatous: II, sometimes remaining sterile: pycnosclerotia (III); conidia very variable, often 4.5–6 × 2–3 and/or 6–10 × 2–3 mm, occasionally 1-septate; wood, occasionally petioles of various deciduous trees and shrubs; necrophyte (mostly recorded in the vicinity of rivers, especially near river banks in Europe and North America)
26. *P. pezizoides*

[Isolates on OA at room temperature remained sterile.]

Note

The five *Phoma* species with 'common' pseudoparenchymatous pycnidia, discussed in the Addendum (nos 27–31) can be differentiated on account of their conidial dimensions and specific hosts: 27. *P. annullata,* teleomorph *L. sacchari* produces large conidia, usually 9–15 × 2–4 mm. This fungus is well-known in Africa, Asia and South America as a pathogen of sugar-cane leaves (Ring Spot). 28. *P. meliloti,* conidia mostly 4–6 × 2–3 µm, occurs at low temperatures as a microform of the *Stagonospora*-anamorph of *L. weimeri,* recorded widely in temperate regions on various Leguminosae (Leaf Spot, Stem Canker and Root Rot of forage legumes). Similar, but somewhat smaller conidia are produced by: 29. *P. rostrupii,* conidia (4–)5–6(–6.5) × 1.5–2.5 µm, teleomorph *L. libanotis,* recorded in Europe on stems and roots of various Umbelliferae (Phoma Root Rot of carrots) and 30. *P. sanguinolenta,* conidia 4.5–5 × 1.5–2.5 µm, teleomorph *L. purpurea,* found in Europe and North America in reddened or purple coloured patches on dead stems of Compositae. Finally, 31. *P. vasinfecta* produces relatively small conidia, mostly 2.5–4 × 1–1.5 µm. This vascular pathogen of chrysanthemums and pyrethrums (Phoma Decline Disease, Slow Wilt) is characterized by a *Phialophora*-synanamorph just like *P. tracheiphila* (no. 21).

POSSIBILITIES OF IDENTIFICATION IN VITRO

Direct and exact determination of isolates is only feasible with a limited number of species in section *Plenodomus*. On the usual agar media fewer than half the taxa described in this paper form the scleroplectenchymatous pycnidia (type II) characteristic of sect. *Plenodomus*. Some species, including the type species of the section, produce in vitro thin-walled pseudoparenchymatous pycnidia (type I), which may be recognized as *Plenodomus*-like only by the late development of a pore and the occurrence of thin-walled seriate cellular protrusions in the pycnidial cavity. Other species remain sterile on the usual agar media, or develop some pycnidia only after a long time (months). One species usually produces in vitro only a few abnormal pycnidial bodies, but commonly forms a *Phialophora*-synanamorph. Table I displays some diagnostic features of the species which produce pycnidia readily on OA. More information on their cultural characteristics can be found in the synoptic tables published by Boerema (1976), Boerema, van Kesteren & Loerakker (1981), and Boerema & Loerakker (1985). For the pathogens included in section *Plenodomus* the disease symptoms may be an important indication of the identity of isolates.

Table I. Diagnostic features in vitro of some species and varieties of *Phoma* sect. *Plenodomus*, sporulating well on OA at 20–22°C.

Pycnidia I(→II) (pycnidia initially always type I)		*Pycnidia II* (scleroplectenchymatous from the start)	
Growth-rate **10–15 mm** diam. (after 7 days in darkness)			
yellow-red pigment (discolouration at reverse) *P. rubefaciens* (no. 25)		pycnidia small, often only after 1–2 months; with rubigenous grains *P. coonsii* (no. 22)	pycnidia large, developing quickly *P. macrocapsa* (no. 1)
Growth-rate **15–25 mm**			
red pigment purplish-blue with NaOH *P. enteroleuca* var. *enteroleuca* (no. 23a)	no pigmentation *P. lingam* (no. 2; teleomorph *L. maculans*) *P. sublingam* (no. 16; teleomorph *L. submalans*) (very similar in vitro)	cultures more or less yellow coloured growth-rate on MA reduced (10–18 mm) *P. sydowii* (no. 18; teleomorph *L. senecionis*)	yellow pigment in cell walls *P. veronicicola* (no. 13) yellow pigment fading in daylight *P. pedicularis* (no. 20)
		pycnidia with long necks necks semi-pilose *P. congesta* (no. 12; teleomorph *L. congesta*)	necks setose *P. leonuri* (no. 11; teleomorph *L. slovacica*)
		necks bare, often *pycnosclerotia (III)* E+ reaction with NaOH *P. sclerotioides* (no. 3)	
Growth-rate **25–45 mm**			
red pigment, purplish-blue with NaOH with crystals *P. macdonaldii* (no. 7; teleomorph *L. lindquistii*)	without crystals *P. enteroleuca* var. *influorescens* (no. 23b)	red pigment *P. agnita* (no. 5; teleomorph *L. agnita*)	yellow pigment *P. conferta* (no. 9; teleomorph *L. conferta*)
		no pigmentation relatively long necks *P. longirostrata* (no. 14)	papillate conidia relatively large *P. doliolum* (no. 19; teleomorph *L. conoidea*)
		small pycnidia *P. acuta* subsp. *acuta* (no. 15a; teleomorph *L. doliolum* subsp. *doliolum*)	conidia relatively small *P. acuta* subsp. *errabunda* (no. 15b; teleomorph *doliolum* subsp. *errabunda*)
Growth-rate **50–70 mm**			
yellow-brown diffusible pigment *P. lingam*, non aggressive strains (no. 2; teleomorph *L. maculans*)		red pigment, purplish-blue with NaOH *P. intricans* (no. 24)	

FUNGUS–HOST INDEX

With reference to the numbers of the species in the descriptive part and additional data on distribution. Species of sect. *Plenodomus* are provided with the pycnidial designations I, II or III; the five *Phoma* species treated in the Addendum are indicated by 'add.'.

A. on **herbaceous plants**

Plurivorous species: (but often with host-preference, see below)	no. 4 *P. astragalina* (II) [in mountainous regions of SW Asia] no. 15b *P. acuta* subsp. *errabunda* (II) (teleom. *L. doliolum* subsp. *errabunda*) no. 19 *P. doliolum* (II) (teleom. *L. conoidea*) [both widespread in temperate regions of Europe and N America] no. 20 *P. pedicularis* (I→II) [in arctic-alpine regions of Europe] no. 3 *P. sclerotioides* (II, III) [in arctic regions of Eurasia and N America: Brown Root Rot]
With specific or preferred host	
Compositae esp. *Achillea* spp.	no. 12 *P. congesta* (II) (teleom. *L. congesta*) [only known from southern Europe]
Chrysanthemum spp. (Disease: Phoma Decline, Slow Wilt)	no. 31 *P. vasinfecta* (add.) [recorded in Europe, N America and Australia]
esp. *Cirsium* spp.	no. 30 *P. sanguinolenta* (add.) (teleom. *L. purpurea*) [known from Europe and N America]
esp. *Eupatorium cannabinum*	no. 5 *P. agnita* (II) (teleom. *L. agnita*) [occasionally also recorded on hosts other than composites; possibly exclusively in Europe]
Helianthus annuus (Disease: Black Stem, Black Spot)	no. 7 *P. macdonaldii* (I + II) (teleom. *L. lindquistii*) [not known from other composites; world-wide on commercial sunflower]
esp. *Senecio* spp.	no. 18 *P. sydowii* (II) (?teleom. *L. senecionis*) [only recorded in Europe]

esp. *Solidago* spp.	no. 15b *P. acuta* subsp. *errabunda* (II) (teleom. *L. doliolum* subsp. *errabunda*)
	no. 19 *P. doliolum* (II) (teleom. *L. conoidea*)
	[both plurivorous in temperate regions of Europe and N America]
Cruciferae	
esp. *Berteroa incana*	no. 9 *P. conferta* (II) (teleom. *L. conferta*)
	[occasionally also recorded on hosts other than crucifers; only known from Europe]
esp. *Brassica* spp. (Disease: Black Leg, Dry Rot or Canker)	no. 2 *P. lingam* (I + II, III) (teleom. *L. maculans*)
	[world-wide seed-borne pathogen]
esp. *Sisymbrium* spp.	no. 16 *P. sublingam* (I + II) (teleom. *L. submaculans*)
	[known from Europe and N America]
Euphorbiaceae	
Mercurialis perennis	no. 1 *P. macrocapsa* (II)
	[only recorded in Europe]
Gentianaceae	
Gentiana spp. (Disease: Leaf Spot)	no. 8 *P. drobnjacensis* (I + II)
	[so far only known from Europe]
Gentiana spp.	no. 20 *P. pedicularis* (I→II)
	[plurivorous in arctic-alpine regions of Europe]
Gramineae	
Saccharum officinarum (Disease: Ring Spot)	no. 27 *P. annullata* (add.) (teleom. *L. sacchari*)
	[recorded in Africa, Asia and S America]
Labiatae	
esp. *Ballota nigra* and *Leonuris cardiaca*	no. 11 *P. leonuri* (II) (teleom. *L. slovacica*)
	[only recorded in Europe]
Leguminosae	
Astragalus spp.	no. 4 *P. astragalina* (II)
	[plurivorous in mountainous regions of SW Asia]
esp. *Melilotus* spp.	no. 28 *P. meliloti* (add.) (teleom. *L. weimeri*)
	[recorded on various legumes in Australia, Europe and N America]

idem (Disease: Brown Root Rot)	no. 3 *P. sclerotioides* (II, III) [plurivorous in arctic regions of Eurasia and N America; most pathogenic records refer to legumes]
Polemoniaceae	
Phlox spp. (Disease: Dieback)	no. 15a *P. acuta* subsp. *acuta* f. sp. *phlogis* (II) [only recorded in Europe; teleom. unknown]
Ranunculaceae	
esp. *Aconitum* and *Ranunculus* spp.	no. 14 *P. longirostrata* (II) [only recorded in southern Europe]
Scrophulariaceae	
Melampyrum spp.	no. 10 *P. petrakii* (II) (?teleom. *L. suffulta*) [only recorded in Europe]
Pedicularis spp.	no. 20 *P. pedicularis* (I→II) [plurivorous in arctic-alpine regions of Europe]
Rhinanthus spp.	no. 6 *P. ruttneri* (II) (?teleom. *L. affinis*) [only known from Europe]
Veronica spp.	no. 13 *P. veronicicola* (II) [only recorded in Europe]
Umbelliferae	
esp. *Angelica* spp.	no. 15b *P. acuta* subsp. *errabunda* (II) (teleom. *L. doliolum* subsp. *errabunda*) [plurivorous in temperate regions of Europe and N America]
e.g. *Daucus carota*	no. 29 *P. rostrupii* (add.) (teleom. *L. libanotis*) [only recorded in Europe]
esp. *Foeniculum vulgare*	no. 19 *P. doliolum* (II) (teleom. *L. conoidea*) [plurivorous in temperate regions of Europe and N America]
Urticaceae	
esp. *U. dioica*	no. 15a *P. acuta* subsp. *acuta* (II) (teleom. *L. doliolum* subsp. *doliolum*) [known from Europe and N America] no. 17 *P. piskorzii* (II) (teleom. *L. acuta*) [known from Europe and N America]

B. on **deciduous trees** and **shrubs**

Plurivorous species: (but often with some host-preference see below)	no. 23a/b *P. enteroleuca* var. *enteroleuca* and var. *influorescens* (I→II) [widespread in Europe and apparently also common in N America] no. 26 *P. pezizoides* (II) [especially near river banks in Europe (central and southern regions) and N America (north-west USA)] no. 25 *P. rubefaciens* (I→II) [widespread in Europe]
With specific or preferred host	
Bignoniaceae *Catalpa bignonioides*	no. 23a *P. enteroleuca* var. *enteroleuca* (I→II) [plurivorous in Europe and N America]
Caprifoliaceae *Lonicera caprifolia* *Sambucus nigra*	idem
Rosaceae *Malus pumila* (Disease: Bark Canker)	no. 22 *P. coonsii* (II) [so far only known from N America and Japan]
Malus pumila and *Pyrus communis*	no. 23a *P. enteroleuca* var. *enteroleuca* (I→II) [plurivorous in Europe and N America]
Rutaceae *Citrus* spp. esp. *C. limonia* (Disease: 'Mal Secco')	no. 21 *P. tracheiphila* (I→II) [throughout the Mediterranean and Black Sea areas]
Salicaceae *Salix alba*	no. 24 *P. intricans* (II) [incidentally also isolated from trees of other genera; only known from Europe]
Salix spp.	no. 26 *P. pezizoides* (II) [plurivorous; esp. recorded near river banks in central and southern Europe and north-west USA]
Ulmaceae *Ulmus* spp.	no. 23a/b *P. enteroleuca* var. *enteroleuca* and var. *influorescens* (I→II) [plurivorous in Europe and N America]

FUNGUS–HOST INDEX

A. on **herbaceous plants**

P. acuta subsp. *acuta* (15a) (teleom. *L. doliolum* subsp. *doliolum*)	*Urtica* spp. (Urticaceae)
f. sp. *phlogis*	*Phlox* spp. (Polemoniaceae)
P. acuta subsp. *errabunda* (15b) (teleom. *L. doliolum* subsp. *errabunda*)	e.g. *Angelica sylvestris* (Umbelliferae) and *Solidago* spp. (Compositae)
P. agnita (5) (teleom. *L. agnita*)	e.g. *Eupatorium cannabinum* (Compositae)
P. annullata (27) (teleom. *L. sacchari*)	*Saccharum officinarum* (Gramineae)
P. astragalina (4)	e.g. *Astragalus* spp. (Leguminosae)
P. conferta (9) (teleom. *L. conferta*)	e.g. *Berteroa incana* (Cruciferae)
P. congesta (12) (teleom. *L. congesta*)	e.g. *Achillea* spp. (Compositae)
P. doliolum (19) (teleom. *L. conoidea*)	e.g. *Angelica sylvestris* (Umbelliferae), *Foeniculum vulgare* (id.) and *Solidago* spp. (Compositae)
P. drobnjacensis (8)	*Gentiana* spp. (Gentianaceae)
P. leonuri (11) (teleom. *L. slovacica*)	e.g. *Ballota nigra* (Labiatae) and *Leonuris cardiaca* (id.)
P. lingam (2) (teleom. *L. maculans*)	*Brassica* spp. (Cruciferae)
P. longirostrata (14)	*Aconitum* and *Ranunculus* spp. (Ranunculaceae)
P. macdonaldii (7) (teleom. *L. lindquistii*)	*Helianthus annuus* (Compositae)
P. macrocapsa (1)	*Mercurialis perennis* (Euphorbiaceae)
P. meliloti (28) (teleom. *L. weimeri*)	e.g. *Melilotus* spp. (Leguminosae)
P. pedicularis (20)	e.g. *Pedicularis* spp. (Scrophulariaceae) and *Gentiana* spp. (Gentianaceae)
P. petrakii (10) (?teleom. *L. suffulta*)	*Melampyrum* spp. (Scrophulariaceae)
P. piskorzii (17) (teleom. *L. acuta*)	*Urtica* spp. (Urticaceae)
P. rostrupii (29) (teleom. *L. libanotis*)	e.g. *Daucus carota* (Umbelliferae)
P. ruttneri (6) (?teleom. *L. affinis*)	*Rhinanthus* spp. (Scrophulariaceae)
P. sanguinolenta (30) (teleom. *L. purpurea*)	e.g. *Cirsium* spp. (Compositae)
P. sclerotioides (3)	e.g. *Melilotus* spp. (Leguminosae)

P. sublingam (16) (teleom. *L. submaculans*)	e.g. *Sisymbrium* spp. (Cruciferae)
P. sydowii (18) (?teleom. *L. senecionis*)	*Senecio* spp. (Compositae)
P. vasinfecta (31)	*Chrysanthemum* spp. (Compositae)
P. veronicicola (13)	*Veronica* spp. (Scrophulariaceae)

B. on **deciduous trees** and **shrubs**

P. coonsii (22)	*Malus pumila* (Rosaceae)
P. enteroleuca and varieties (23)	e.g. *Catalpa bignonioides* (Bignoniaceae), *Lonicera caprifolia* (Caprifoliaceae), *Malus pumila* (Rosaceae) and *Ulmus* spp. (Ulmaceae)
P. intricans (24)	*Salix alba* (Salicaceae)
P. pezizoides (26)	e.g. *Salix* spp. (Salicaceae)
P. rubefaciens (25)	e.g. *Malus pumila* (Rosaceae)
P. tracheiphila (21)	*Citrus* spp., esp. *C. limonia* (Rutaceae)

DESCRIPTIVE PART

Section Plenodomus (1–26)

1. **Phoma macrocapsa** Trail — Fig. 2A

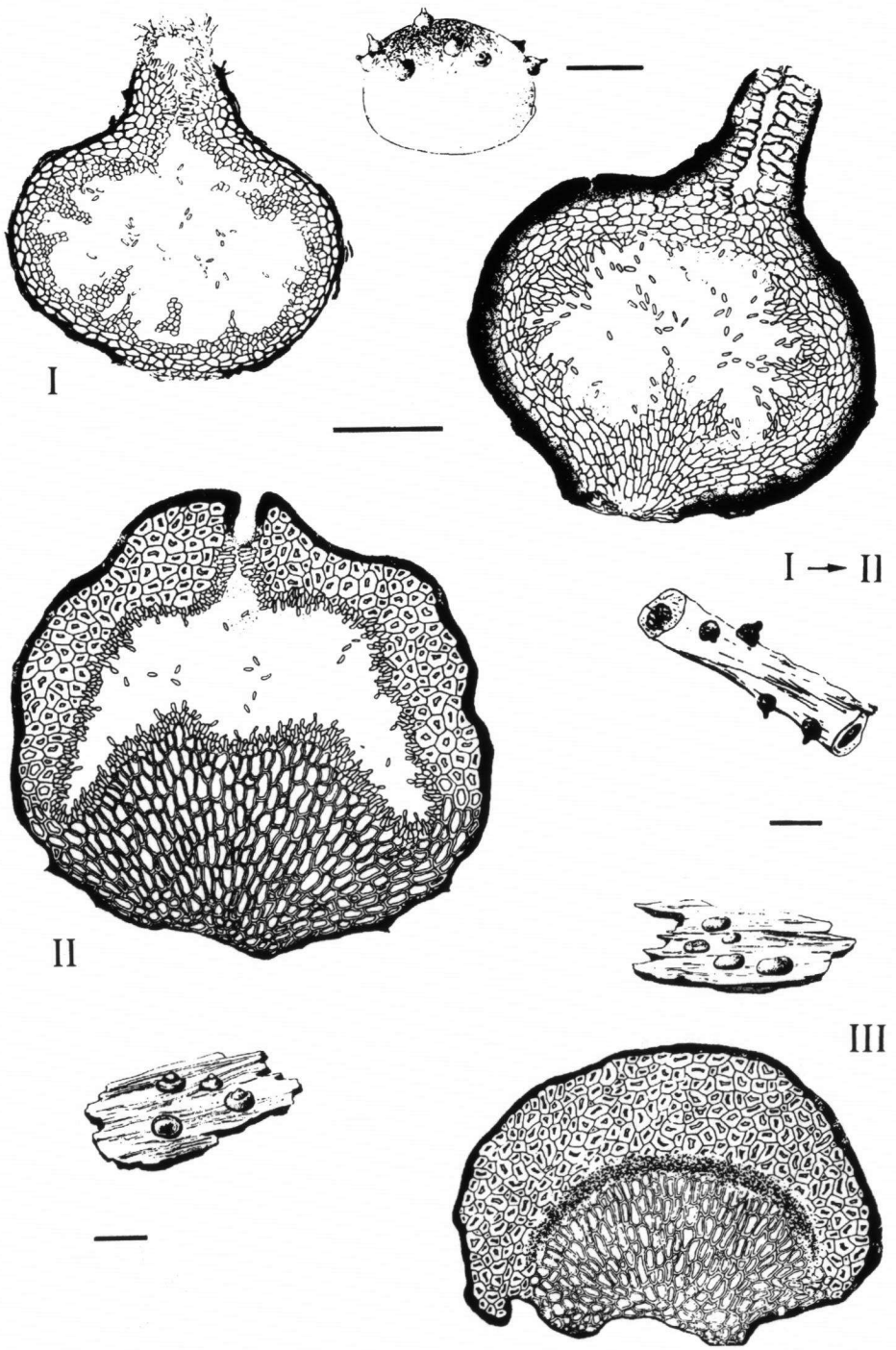
Phoma macrocapsa Trail, Scott. Nat. 8 [II, 2] (1886) 237. — *Plenodomus macrocapsa* (Trail) Rupprecht, Sydowia 13 (1959) 20–21.

Description in vivo (*Mercurialis perennis*)

Pycnidia-II only (on dead stems, scattered or in groups), relatively large, (400–)600–700 µm diam., depressed globose, with flattened base and a conspicuous broad and long cylindrical neck, usually with a somewhat swollen top (phallus-like), the neck reaching to a height of 400–700 µm. Wall explicitly scleroplectenchymatous with a convex thickening consisting of diverging rows of somewhat elongated cells at the base. The cell walls of the scleroplectenchyma have the same thickness throughout. Exudate cream or whitish. Conidia ellipsoidal to subcylindrical, (3–)4–5 × (1–)1.5–2 µm, usually with two conspicuous polar guttules.

Description in vitro

OA: growth-rate 12–15(–20) µm, regular with fine, compact, dark olivaceous grey or greenish grey aerial mycelium; reverse greenish olivaceous with primrose margin. In fresh isolates numerous scattered relatively large scleroplectenchymatous pycnidia-II develop on the agar, resembling the pycnidia in vivo, but usually with a less pronounced neck. Conidia as in vivo.


I
I → II
II
III

Ecology and distribution. Very common in Europe on dead stems of *Mercurialis perennis* (Euphorbiaceae). Regarded as a harmless specialized necrophyte, but under some conditions the fungus apparently causes damage to the host. The fungus probably occurs everywhere on the host. "Remarkable for its large pycnidia" (Grove, 1935).

Representative culture. CBS 640.93.

2. **Phoma lingam** (Tode: Fr.) Desm. — Figs 1, 2B

Teleomorph: *Leptosphaeria maculans* (Desm.) Ces. & de Not.

Phoma lingam (Tode: Fr.) Desmazières, Annls Sci. nat. (Bot.) III, 11 (1849) 281. — *Sphaeria lingam* Tode, Fungi mecklenb. 2 (1791) 51; Tode: Fr., Syst. mycol. 2 (2) (1823) 507. — *Plenodomus lingam* (Tode: Fr.) Höhnel, Sber. Akad. Wiss. Wien (Math.-naturw. Kl., Abt. 1) 120 (1911) 463.

Depazea brassicicola Desmazières, Pl. cryptog. N. France [ed. 1] Fasc. 3 (1826) No. 185 [as '*brassicaecola*']. — *Depazea vagans* var. *brassicae* Kickx, Fl. crypt. Env. Louv. 125 (1835) 125 [as '*γ Brassicae*'; name change]. — *Septoria brassicae* Westendorp & Wallays, Herb. crypt. Belg. Fasc. 6 (1847) No. 294 [name change]. — *Phyllosticta brassicae* Westendorp, Bull. Acad. r. Sci. Lett. Beaux Arts Belg. 18 (1851) 397 [name change].

Sclerotium sphaeriaeforme Libert, Pl. cryptog. Ard. Fasc. 3 (1834) No. 237.

Plenodomus rabenhorstii Preuss, Linnaea, Halle 24 (1851) 145.

Aposphaeria brassicae Thümen, Hedwigia 12 (1880) 189–190. — *Phoma brassicae* (Thümen) Saccardo, Sylloge Fung. 3 (1884) 119.

Phoma densiuscula Saccardo & Roumeguère, Revue mycol. 6 (1884) 30 [as '*Phoma* (Aposph.)'] [= Reliq. Libert Ser. IV No. 86; holotype in herb. Saccardo, PAD].

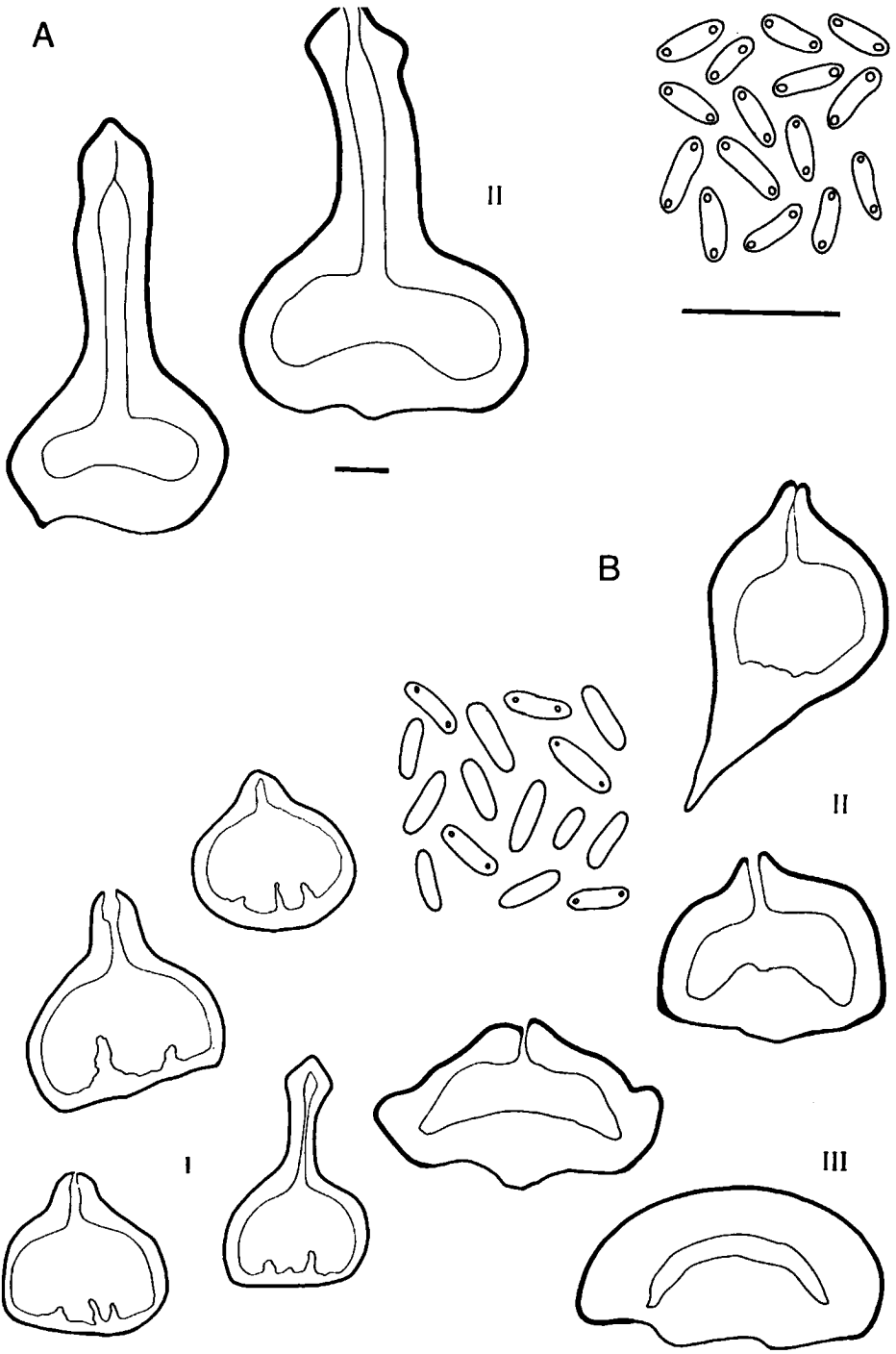
Phoma napobrassicae Rostrup, Tidsskr. Landøkon. 11 (1892) 330. — *Phoma lingam* var. *napobrassicae* (Rostrup) Grove, Br. Coelomycetes 1 (1935) 70.

Selected literature. Boerema & van Kesteren (1964).

Description in vivo (especially *Brassica* spp.)

Pycnidia-I (on leaf spots, stem- and pod lesions, seed, usually solitary and arranged in rows) variable in dimensions, mostly 150–350(–400) µm diam., generally subglobose or flask-shaped with broad base, at maturity usually with 1 distinct poroid papilla (occasionally more) which may grow out into a long neck; sometimes confluent becoming irregular, up to 600 µm diam. with several papillae (or necks); mostly black but sometimes noticeably lighter, greyish-brown [pycnidia then often with a somewhat swollen or club-like neck]. Pycnidia-II (on woody parts of last year's dead stems, occasionally roots) relatively large, (200–)300–700(–1000) µm diam., mostly subglobose with an irregular flattened base, but sometimes beetroot-like, not or only slightly papillate; with narrow pore or opened by rupture. At length the pycnidia often collapse and become discoid or

Fig. 1. *Phoma lingam*, type species of section *Plenodomus*. Vertical sections of its pycnidial types on cabbage. Thin-walled pycnidia-I occur on seed and in association with disease symptoms. Note the series of cells protruding into the pycnidial cavity. On old stem lesions the pycnidia may become thick-walled by the development of new cell layers, I→II. Note the fan-like arrangement of elongated cells at the base of the pycnidium and the hyphal outgrowths in the papilla. Secondary thickening of the cell walls in the peridium results in scleroplectenchyma as in the relatively large pycnidia-II found on old dead stems or roots at the end of the next season. Note the resemblance with stone cells in higher plants. The process of wall thickening may also occur in pycnidial initials: development of sterile pycnosclerotia, III (Drawings partly after Boerema & van Kesteren, 1964, partly original).


A
II
B
II
I
III

turban-like. Sometimes they remain closed and sterile: pycnosclerotia (III). Wall ± explicitly scleroplectenchymatous: above and around polygonal thick-walled cells with a very small lumen (like stone cells), at the base a convex thickening consisting of diverging rows of less-thickened elongated cells. Exudate mostly red-violet (amethyst coloured) but also whitish or pinkish. Conidia ellipsoidal to subcylindrical, occasionally with two small polar guttules, (2.5–)3.5–4.5(–5) × 1–1.5(–2) µm.

Pseudothecia (subepidermal on stems during overwintering) up to 600 µm diam., depressed globose with flattened base and inconspicuous conical neck. Wall more or less scleroplectenchymatous. Asci 120–135 × 12–16 µm, 8-spored, quadriseriate above, biseriate below. Ascospores 45–55 × 6–7 µm, narrowly fusiform, 5-septate, yellowish-brown with guttules (for a recent detailed description see Shoemaker, 1984). Occasionally multiloculate pycnidia, containing microconidia, c. 1.5–3 × 1–1.5 µm, occur side by side with young pseudothecia. [The former look like spermogonia, but the microconidia are able to germinate and give rise to normal pycnidial cultures; compare Smith & Sutton, 1964 and Ndimande, 1976.]

Description in vitro

OA: growth-rates clearly different and related to the virulence of the isolates.

Slow-growing isolates ['aggressive (virulent) strains'], growth-rate c. (15–)25 mm diam., often irregular with dendritic pattern but also regular; usually copious aerial mycelium varying in colour, white, grey, greenish (dull green-dark herbage green), yellowish (straw, amber, luteous) or brown (fulvous, amber). Usually abundant production of pycnidia-I on and in the agar, mostly solitary, globose-papillate, black and relatively small, 150–250 µm diam., sometimes larger and/or confluent.

Fast-growing isolates ['weakly aggressive (avirulent) strains'], growth-rate c. 50(–70) mm diam., characterized by a yellow-brown diffusible pigment with intensity of colour varying from pale straw to cinnamon; horizontal growth regular with a little white or greyish aerial mycelium, often sectoring with pycnidia of different dimensions. Pycnidia-I developing on and in the agar, black, relatively large, globose-papillate, up to 350–400 µm diam., or smaller and then often flask-shaped, 150–250 µm diam., black or greyish-brown.

In old cultures of both types of isolates the pycnidia occasionally show a thickening of the cell walls in the peridium (→II: ± scleroplectenchymatous). Swollen cells, which are terminal or intercalary, solitary or in clusters and one- or more-celled arthrospores (Ndimande, 1976) may occur in the aerial mycelium.

Ecology and distribution. A cosmopolitan pathogen of cultivated *Brassica* spp.: Dry Rot and Canker (Am.: Black Leg) attacking cotyledons, leaves, stems, roots and pods. From pod lesions the fungus may spread into the seeds. The fungus is also recorded on

Fig. 2. A. *Phoma macrocapsa.* Remarkable for its large pycnidia, characterized by long broad cylindrical necks with somewhat swollen tops. Conidia usually with two conspicuous polar guttules. — B. *Phoma lingam.* The cabbage pathogen displays a wide diversity in pycnidial types. Pycnidia-I are mostly globose-papillate, but some strains produce pycnidia with elongated swollen necks. The shape of the relatively large scleroplectenchymatous pycnidia-II is variable, sometimes beetroot-like or turban-like, but always neck-less. Pycnidia and pycnosclerotia bar 100 µm, conidia bar 10 µm.

various other cultivated and wild crucifers. The pseudoparenchymatous pycnidial type I occurs in association with the disease symptoms and in vitro. The fungus is heterothallic and displays considerable variability in morphology of anamorph and teleomorph, cultural characteristics and pathogenicity. This is probably favoured by the world-wide domestication of the brassicas and explains why at present the intraspecific variability of this fungus is much wider than the interspecific differences between some allied scleroplectenchyma producing *Phoma/Leptosphaeria* species [compare *P. sublingam* (no. 16; teleomorph *L. submaculans*) with *P. conferta* (no. 9; teleomorph *L. conferta*) and compare the intraspecific differences within the dog with the interspecific differences between the wolf and jackal]. For literature references on recent pathogenicity studies of this *Brassica* pathogen, see Boerema, Pieters & Hamers (1993) sub *Leptosphaeria maculans*.

Representative cultures. CBS 532.66, CBS 156.94, CBS 260.94.

Note. Not included in the above description are strains producing only scleroplectenchymatous pycnidia and pycnosclerotia, and strains producing pseudothecia with extremely large ascospores with more septa than usual [formerly differentiated as a separate species: *Leptosphaeria napi* (Fuckel) Sacc.]. Finally it should be noted that all records of the fungus on non-cruciferous plants appeared to be based on misidentifications. The statement in old literature that the scleroplectenchymatous pycnidia of *P. lingam* also occur on old wet wood refers to their superficial resemblance to pycnidia of *Phoma pezizoides* (no. 26).

3. **Phoma sclerotioides** Preuss ex Sacc. — Fig. 3A

Phoma sclerotioides Preuss ex Saccardo, Fungi Herb. Brux. (1892) 21; Sylloge Fung. 11 (1895) 492. — *Plenodomus sclerotioides* Preuss in Rabenh., Klotzschii Herb. mycol. Cent. 13 (1849) No. 1281 [nomen nudum].

Plenodomus meliloti Markova-Letova, Bolez. Rast. 16 (1928) 195.

Plenodomus meliloti Dearness & Sandford, Annls mycol. 28 (1930) 324–325 [homonym].

Plenodomus sorghi Morochkovskii, Trudy bot. Inst. Akad. Nauk SSSR 1 (1933) 277–278.

Selected literature. Boerema & van Kesteren (1981), Boerema & Loerakker (1985).

Description in vivo (especially on *Melilotus alba*)

Only pycnidia-II (mainly on roots, occasionally on basal stem parts, usually in dense clusters and nearly superficial), relatively large, (200–)350–800(–1000) µm diam., subglobose to depressed globose with flattened base (occasionally thickened at basal margin), initially closed, pores developing as short papillae or, usually, as long thin tubular necks of various lengths (up to 800 µm). Sometimes the pycnidia remain closed and sterile: pycnosclerotia (III). Wall of mature pycnidia shows different scleroplectenchymatous cell structures; on the outside polygonal thick-walled cells with a very small lumen (like stone cells) and on the inside similar polygonal cells with relatively thin walls; at the central base the latter cells may be elongated and form a palisade. Protopycnidia are at first completely filled with relatively large polygonal thin-walled cells; the proliferate layer, made up of very small cells, arises in the centre and has initially a cap-like shape, the resulting central cavity gradually enlarges, apparently at the cost of the large thin-walled cells. Conidiogenous cells well-differentiated, cone-shaped. Exudate cream or yellowish. Conidia ellipsoidal to subcylindrical, 4.5–6 × 1.5–2.5(–3) µm, eguttulate or with 1–4 polar guttules.

Description in vitro

OA: growth-rate 15–24 mm, aerial mycelium scarce, cottony or fluffy, green-yellowish; reverse ochraceous, sometimes with a luteous or amber zone. All strains tested produced antibiotic E: on application of a drop of NaOH green → red (E+ reaction). Fresh isolates usually produce abundant pycnidia-II and pycnosclerotia (III), often covered with hyaline, ochraceous or brownish droplets. Conidia as in vivo.

Ecology and distribution. Northern parts of Eurasia and North America, common on roots and occasional on lower stems of various herbaceous plants. Well-known as plurivorous low temperature parasite: Brown Root Rot. The fungus is particularly destructive on herbage legumes, notably sweet clover, *Melilotus alba* and lucerne, *Medicago sativa,* following winter dormancy. It may also be pathogenic on grasses and cereals exposed to low temperature (Smith, 1987).

Representative culture. CBS 144.84.

4. **Phoma astragalina** (Gonz.-Frag.) Boerema & v. Kest. — Fig. 3B

Phoma astragalina (Gonz.-Frag.) Boerema & van Kesteren, Persoonia 11 (3) (1981) 317. — *Ceuthospora astragalina* Gonzáles-Fragoso, Boln. R. Soc. esp. Hist. nat. 18 (1918) 84. — *Plenodomus astragalinus* (Gonz.-Frag.) Petrak in Rechinger, Baumgartner, Petrak & Szatala, Annln naturh. Mus. Wien 50 (1940) 498–499.

Plenodomus dianthi Bubák, Annln K.K. naturh. Hofmus. Wien [Annln Naturh. Mus. Wien] 28 (1914) 204. — *Phoma dianthi* (Bubák) Bubák, Annls mycol. 13 (1915) 30; not *Phoma dianthi* Saccardo & Malbranche, Atti R. Ist. veneto Sci. VI, 1 (1883) 1276 [= *Phomopsis* sp.]; not *Phoma dianthi* Ellis & Everhart, Langl. Cat. Pl. Basse-La (1887) 32 [nomen nudum]; not *Phoma dianthi* Lagiere, Annls Ec. natn. Agric. Grignon III, 5 (1946) 160 [= *Phomopsis* sp.].

Plenodomus khorasanicus Petrak in Rechinger, Baumgartner, Petrak & Szatala, Annln naturh. Mus. Wien 50 (1940) 499–500.

Selected literature. Boerema & van Kesteren (1981).

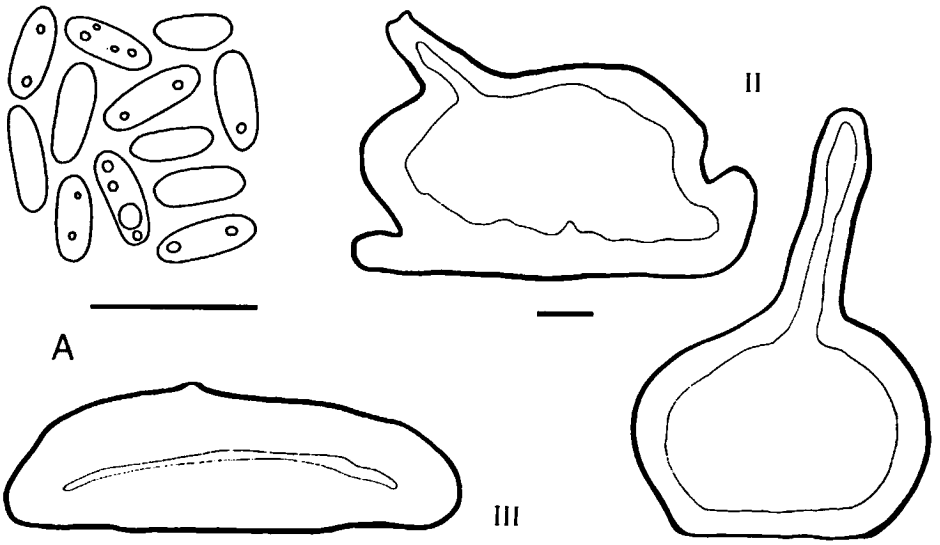
Description in vivo (especially on *Astragalus* spp.)

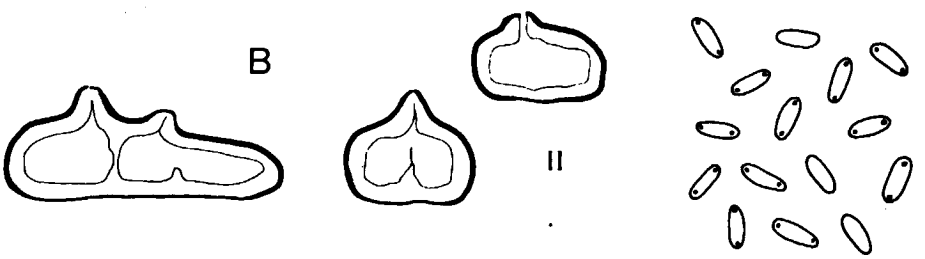
Only pycnidia-II (mostly on dead stems, scattered or in groups, subepidermal or subcortical), but scleroplectenchyma not as conspicuous as in most other species of the section, 150–300 µm diam., extremely variable, sometimes mainly depressed globose to ellipsoidal, but also more irregular in shape and larger, up to 600 µm diam., usually with a flattened base and slightly papillated pore, often aggregated or confluent. Wall of mature pycnidia sometimes with irregular outgrowths bulging into the cavity giving it a multilocular appearance. Young pycnidia (protopycnidia) are initially completely filled with more or less parallel rows of somewhat elongated cells. Exudate whitish. Conidia small, ellipsoidal, 2–3 × 0.5–1 µm, usually with two minute polar guttules.

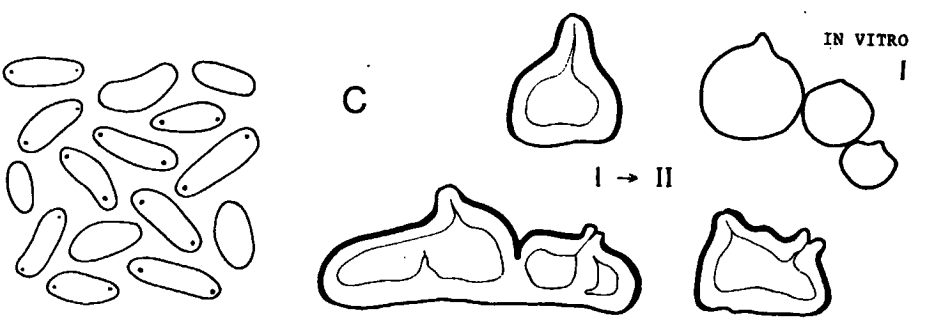
Description in vitro

OA: freshly isolated cultures only produce sterile mycelium at room temperature. The fungus probably requires a period of low temperature and/or special nutritional conditions for fructification.

Ecology and distribution. Found on various herbaceous plants (dead stems and occasionally petioles) in the higher mountainous regions of south-western Asia (Iran, Turkey, Afghanistan). Most host records refer to *Astragalus* spp.


II
A
III


B
II


IN VITRO
I
C
I → II

5. **Phoma agnita** Gonz.-Frag. — Fig. 3C

Teleomorph: *Leptosphaeria agnita* (Desm.) Ces. & de Not.

Phoma agnita Gonzáles-Fragoso, Mems R. Acad. Cienc. Artes Barcelona 15 (1920) 432.

Plenodomus chondrillae Diedicke, Annls mycol. 9 (1911) 140; Krypt.-Fl. Mark Brandenb. 9, Pilze 7 (2) (1912; vol. dated '1915') 236; not *Phoma chondrillae* Hollós, Annls hist.-nat. Mus. natn. hung. 4 (1906) 337 [= *Phomopsis chondrillae* (Hollós) S. Dias & Lucas in Agronomia lusit. 37 (1975) 99].

Phoma acuta f. *petasites* Roumeguère, Fungi gall. exs. Cent. 11 (1881) No. 1007; Revue mycol. 3 (1881) 30 [nomen nudum].

Description in vivo (especially *Eupatorium cannabinum*)

Pycnidia-II only (on dead stems, usually densely crowded, first immersed, later superficial), mostly 125–250 µm diam., depressed globose and relatively small, closed or with a sharply delimited papillate pore with somewhat protruding lip; later often coalescing to large flattened-elongated or irregular, more or less multilocular pycnidial 'stromata', up to 1000 µm diam. Wall made up of polygonal scleroplectenchyma cells of variable dimensions, parallel rows of elongated cells usually occur around the party-walls. Exudate (pale) reddish or amethyst coloured. Conidia variable, 4–7 × (1.5–)2 µm, usually oblong-ellipsoidal, straight or slightly curved, with two inconspicuous guttules.

Pseudothecia (also on dead stems), 350–500 µm diam., depressed globose with a strong ridge, flattened base and a short strongly papillate pore. Wall scleroplectenchymatous. Asci 110–125 × 9–11 µm, 8-spored, ± biseriate. Ascospores 31–35 × 4–5 µm, narrowly subcylindrical, 6-septate, third cell from above slightly swollen, yellowish brown with 2 guttules per cell (for recent description see Shoemaker, 1984).

Description in vitro

OA: growth-rate 30–40 mm diam.; greenish-transparent; aerial mycelium sparse, tenuous-felted, whitish to yellowish-grey; reverse vinaceous buff, pale salmon, but in the centre yellow or greenish olivaceous. On application of a drop of NaOH the reddish diffusible pigments turn blue. Thick-walled pycnidia, type II, usually occur in abundance on and in the agar; they are more or less pilose but otherwise resemble those in vivo, also often confluent, forming irregular or catenate aggregates. Small pycnidia sometimes occur in aerial mycelium. In vitro the conidia are even more variable in shape and dimensions than those in vivo; being ellipsoidal, oval to ovoid or pyriform, and commonly straight, (3.5–)4–6(–7.5) × (1.5–)2(–3) µm.

Ecology and distribution. Common in Europe on dead stems of Compositae, especially *Eupatorium cannabinum,* but also reported and isolated from members of various other herbaceous plant families (e.g. Labiatae, Papilionaceae and Umbelliferae). Possibly exclusive to Europe; North American records of this fungus are in doubt (Shoemaker, 1984).

Representative culture. CBS 121.89.

Fig. 3. A. *Phoma sclerotioides.* This low temperature pathogen produces large scleroplectenchymatous pycnidia-II and pycnosclerotia-III. The pores of the pycnidia usually develop on long thin tubular necks. — B. *Phoma astragalina.* Characterized by very small conidia and extremely variable pycnidia-II, often aggregated, or irregular with the appearance of being multilocular. — C. *Phoma agnita.* Pycnidia-II initially relatively small, closed or papillate-poroid with somewhat protruding lip, often coalescing to large multilocular pycnidial stromata. Note the variable shape of the conidia.

6. **Phoma ruttneri** (Petrak) Boerema & v. Kest. — Fig. 4A

Possible teleomorph: *Leptosphaeria affinis* P. Karsten.

Phoma ruttneri (Petrak) Boerema & van Kesteren, Persoonia 11 (3) (1981) 324. — *Plenodomus ruttneri* Petrak, Sydowia 8 (1955) 582–583.
Selected literature. Boerema & van Kesteren, 1981.

Description in vivo (*Rhinanthus* spp.)

Pycnidia-II only (on dead stems, scattered, subepidermal), mostly 250–350 µm diam., depressed globose with a distinct papillate or truncate-conical pore. Wall uniform in thickness and made up of several layers of polygonal scleroplectenchyma cells of variable sizes. Conidia 5–7 × 1.5–2 µm, subcylindrical, usually somewhat curved, eguttulate.

[Pseudothecia (also on dead stems) up to 400 µm diam., conic with a flattened base and a short truncate-conical neck. Wall ± scleroplectenchymatous. Asci 85–100 × 5–6 µm, 4-spored, biseriate or triseriate above. Ascospores 40–60 × 5–6 µm, narrowly fusiform and somewhat clavate, 3-septate, yellow or nearly colourless, without guttules (for recent description of this teleomorph, see Shoemaker, 1984).]

Description in vitro

OA: cultures made from the supposed teleomorph produced only sterile mycelium.

Ecology and distribution. In Europe (Austria, Germany) found on dead stems of *Rhinanthus* spp. On the type substratum the pycnidia occur together with pseudothecia of *Leptosphaeria affinis,* which is widespread in Europe on *Rhinanthus minor.* The single identity of both morphs is plausible but has not yet been proved by comparison of cultures.

7. **Phoma macdonaldii** Boerema — Fig. 4B

Teleomorph: *Leptosphaeria lindquistii* Frezzi.

Phoma macdonaldii Boerema, Persoonia 6 (1) (1970) 20–21.
Selected literature. Boerema, van Kesteren & Loerakker (1981).

Description in vivo (*Helianthus annuus*)

Pycnidia-I (lesions on stems, leaves etc., solitary, scattered or in rows) mostly 70–170(–200) µm diam., subglobose, not or only slightly papillate. Exudate dirty whitish or red-violet coloured. Conidia highly variable in shape and dimensions, (4.5–)5–9(–10) × 1.5–3(–4) µm, eguttulate. Pycnidia-II (on last year's dead stems) usually larger, 100–300 µm diam., also subglobose, usually non-papillate with narrow pores. Conidia as in pycnidia-I.

Pseudothecia (on dead stems) 130–230 µm diam., depressed globose, not or only slightly papillate. Wall ± scleroplectenchymatous. Asci 70–145 × 7.5–10.5 µm, 8-spored, irregularly uniseriate. Ascospores 12.5–25 × 3.5–8.5 µm, irregularly fusiform, 1–3-(often 2-)septate, pale yellow with guttules (for detailed description see Frezzi, 1968).

Description in vitro

OA: growth-rate 25–45 mm, aerial mycelium cottony, mostly whitish, greyish or greenish-olivaceous; reverse olivaceous greenish-yellow or glaucous tinged, often with white granular or flaky crystals. Old colonies may show a pink or red discolouration of agar becoming purplish or blue with a drop of NaOH (the presence of anthraquinone

cynodontin has been demonstrated together with some unknown yellow pigments). Usually abundant production of subglobose, non-papillate pycnidia, I→II. Conidia highly variable, as in vivo.

Ecology and distribution. A pathogen of the 'American' sunflower, *Helianthus annuus,* causing lesions on stems, petioles, leaves and inflorescences: Black Stem, Black Spot, see e.g. Marić & Schneider (1979). At present the fungus probably occurs wherever the commercial sunflower is cultivated; the records are from Europe (France, Romania, former Yugoslavia), North America (Canada, USA) and South America (Argentine).

Representative culture. CBS 386.80.

Note. In the past the anamorph has been erroneously referred to *Phoma oleracea* var. *helianthi-tuberosi* Sacc., a synonym of the ubiquitous saprophyte *Phoma herbarum* Westend. [described in Contributions I–2; de Gruyter et al., 1993].

8. **Phoma drobnjacensis** Bubák — Fig. 4C

Phoma drobnjacensis Bubák, Bot. Kozl. 14 (1915) 63. [Holotype, BPI, originally labelled as *Plenodomus drobnjacensis.*]

Pyrenochaeta gentianae Chevassut, Bull. Soc. mycol. Fr. 81 (1965) 36.

Selected literature. Boerema, van Kesteren & Loerakker (1984).

Description in vivo (*Gentiana* spp.)

Pycnidia-I (leaf spots and basal stem rot, usually aggregated in short rows) relatively small, (100–)150–200 µm diam.; subglobose with a short papillate neck, neck of mature pycnidia black and semi-setose, i.e. often with a number of setae around the pore, setae rigid and septate, usually 45–60 × 3–4 µm. Pycnidia-II (superficial on dead stems) larger, 200–500 µm diam., also subglobose-papillate, but often without any trace of setae. Wall of full-grown pycnidium shows randomly polygonal scleroplectenchyma cells and is about the same thickness throughout. Exudate whitish. Conidia (3–)3.5–4.5(–5) × (1–)1.5(–2) µm, oblong-ellipsoidal, sometimes curved, usually biguttulate.

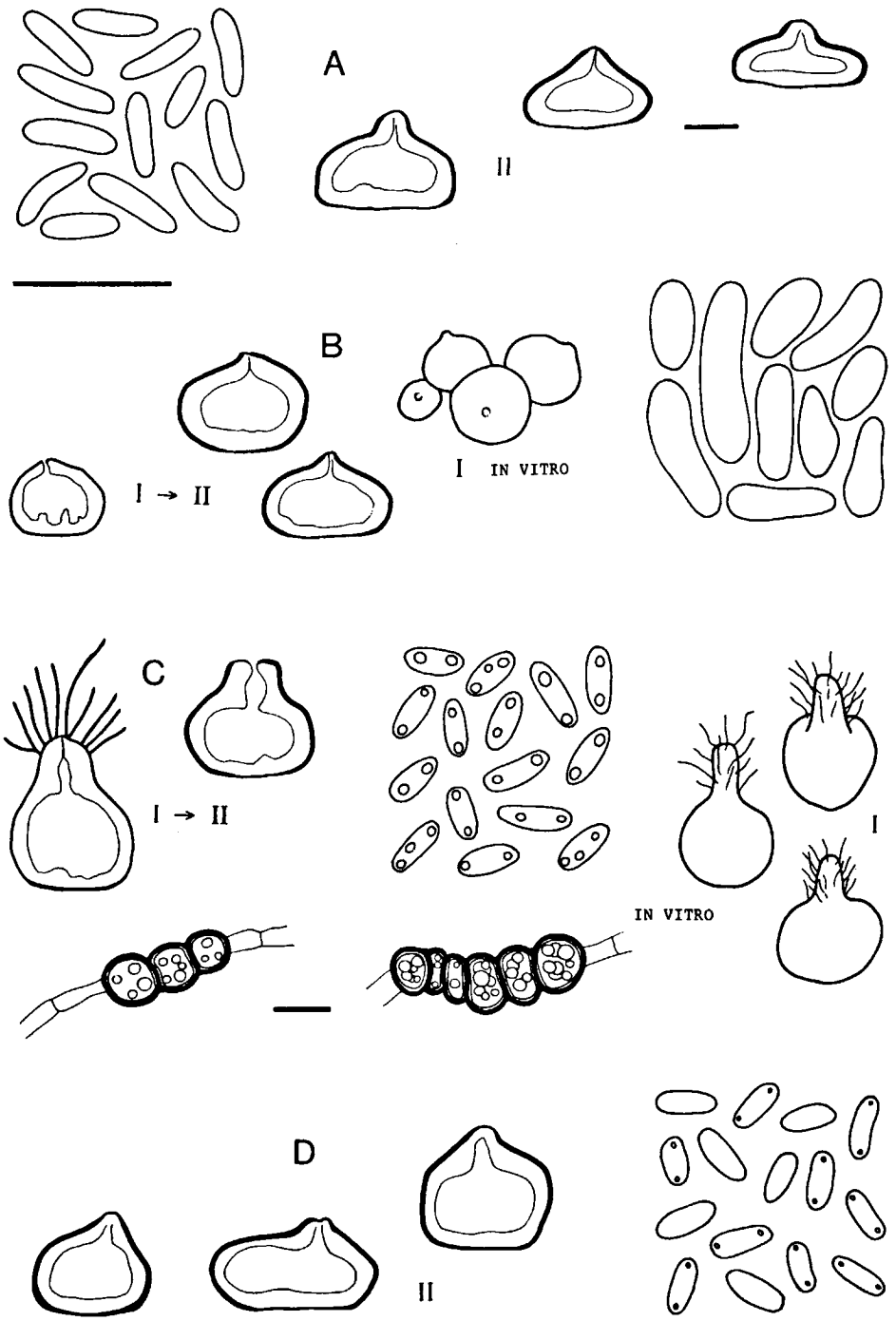
Description in vitro

OA: growth-rate 35–47 mm, aerial mycelium very tenuous, low, somewhat felted, greyish; reverse conspicuous sulphur yellow to citrine green. With addition of a drop of NaOH the yellowish pigment quickly turns red. Pycnidia may develop abundantly on the agar, I→II, usually with a short cylindrical neck, glabrous or hairy at the apex, i.e. semi-pilose (not setose as in vivo), mostly solitary connected by superficial hyphae. Occasional aberrant small pycnidia occur in aerial mycelium. Conidia as in vivo.

MA: cultures show clearly that the yellowish pigment diffuses from the hyphae into the agar and crystallizes out as complexes of needles; on the surface of the agar they may form greenish yellow scales, 200–600 µm diam. In old cultures there is a natural change from yellow to red.

Chlamydospores commonly occur in the agar; they are unicellular, mostly 10–15 µm diam., usually intercalary in short or long, sometimes branching chains, relatively thick-walled, and olivaceous with one or more greenish guttules.

Ecology and distribution. Originally described from *Gentiana asclepidea* in the mountains of Montenegro, former Yugoslavia (semi-setose pycnidia). Recently repeatedly re-


A
II
B
I → II
I IN VITRO
C
I → II
IN VITRO
I
D
II

corded as a pathogen on different cultivated species of *Gentiana* in England, France, Germany and the Netherlands: Leaf Spot. The fungus has occasionally been isolated from a cultivar of *Lisianthus russellianus*.

Representative cultures. CBS 270.92, CBS 269.92.

9. **Phoma conferta** P. Sydow ex Died. — Fig. 4D

Teleomorph: *Leptosphaeria conferta* Niessl ex Sacc.

Phoma conferta P. Sydow ex Diedicke, Krypt.-Fl. Mark Brandenb. 9, Pilze 7 (2) (1912 [vol. dated '1915']) 142; not *Phoma conferta* Ellis & Everhart, H.L. Jones, Bull. Oberlin Coll. Lab. 9 (1898) 7; [nomen nudum; as '*confertum*']. — *Phoma conferta* P. Sydow, Mycoth. March. Cent. 43 (1895) No. 4291 [nomen nudum].

Description in vivo (especially *Berteroa incana*)

Pycnidia-II only (on dead stems, scattered or seriate, at first covered by the epidermis, later superficial), 150–250(–400) µm diam., subglobose-conical with broad base and usually slightly papillate pore. Wall consisting of polygonal scleroplectenchyma cells of variable dimensions; cells at base similar to those at side walls, but with more or less parallel arrangement. Exudate whitish. Conidia oblong-ellipsoidal (3.5–)4(–5) × (1–)1.5(–2) µm, usually with two small guttules.

Pseudothecia (also on dead stems) up to 380 µm diam., conical to subglobose. Wall scleroplectenchymatous. Asci 100–140 × 14–18 µm, 8-spored, irregularly quadriseriate. Ascospores 44–52 × 6–7 µm, fusiform, mostly curved, 3-septate, yellowish, guttulate [for recent detailed description see Lucas, 1963].

Description in vitro

OA: growth-rate 30–40 mm, cream white; aerial mycelium tenuous, yellow-green; reverse grey with yellow zones. Pycnidia-II in concentric zones both on and in the agar and in aerial mycelium, resembling those in vivo, but more irregular in shape. Conidia as in vivo.

Ecology and distribution. Common in Europe on dead stems of various wild Cruciferae, but occasionally also on plants of other families (e.g. Compositae). It is often confused with *Phoma sublingam* (no. 16; teleomorph *Leptosphaeria submaculans*). Both fungi commonly occur together on *Berteroa (Farsetia) incana*. They can be easily differentiated by their teleomorphs [*L. conferta* is distinctive in having neck-less pseudothecia and 3-septate ascospores]. The conidia of their anamorphs are similar but the pycnidia of

Fig. 4. A. *Phoma ruttneri*. Pycnidia-II depressed globose with a flattened base and a papillate or truncate-conical pore. Conidia uniform subcylindrical. — B. *Phoma macdonaldii*. This pathogen of the commercial sunflower produces pycnidia-I in association with disease symptoms; pycnidia-II occur on dead stems. Both pycnidial types are subglobose and not or only slightly papillate. Conidia are highly variable in shape and dimensions. — C. *Phoma drobnjacensis*. Pycnidia initially thin-walled I→II; in association with disease symptoms on gentians sometimes with rigid setae on the papilla; in vitro (right) usually with a pilose neck. The fungus produces chains of thick-walled chlamydospores, diam. 10–15 µm. — D. *Phoma conferta*. Pycnidia-II subglobose-conical with broad base and usually slightly papillate pore.

P. conferta are always scleroplectenchymatous, type II, and nearly neck-less, whereas the pycnidial types I and II of *P. sublingam* usually have a pronounced neck.

Representative culture. CBS 375.64.

Note. The scleroplectenchymatous pycnidia of *P. conferta* may develop simultaneously with the pseudothecia of its teleomorph, but on *Berteroa incana* they are more often found together with the pseudothecia of *L. submaculans* [!: such a confusing coexistence also occurs with the pycnidia of *Phoma acuta* subsp. *acuta* (no. 15a; teleomorph *L. doliolum* subsp. *doliolum*) and the pseudothecia of *Leptosphaeria acuta* (anamorph *Phoma piskorzii*, no. 17) on *Urtica dioica*]. It should be noted that *Phoma berteroae* Hollós, described in Annls hist.-nat. Mus. natn. hung. 6 (1908) 529 may be conspecific with *P. conferta*, but the original material of *P. berteroae* appears to have been destroyed during the Second World War (information from Museum of Natural History, Budapest) and therefore could not be checked for the presence of scleroplectenchyma.

10. **Phoma petrakii** Boerema & v. Kest. — Fig. 5A

Possible teleomorph: *Leptosphaeria suffulta* (Nees : Fr.) Niessl.

Phoma petrakii Boerema & van Kesteren, Persoonia 11 (3) (1981) 321[–322]. — *Plenodomus niesslii* Petrak, Annls mycol. 20 (1922) 322–323; not *Phoma niesslii* Saccardo, Michelia 2 (3) (1882) 618 [= probably *Phoma exigua* Desm. var. *exigua*, sect. *Phyllostictoides*, see van der Aa et al., 1990].

'*Plenodomus sylvaticus*' sensu Rupprecht, Sydowia 13 (1959) 21 [as '*sylvatica*'; misapplied, see Note below].

Selected literature. Boerema & van Kesteren (1981).

Description in vivo (*Melampyrum* spp.)

Pycnidia-II only (on dead stems, solitary, scattered or in groups), 200–350 µm diam., depressed globose, with flattened base and a distinct papillate neck, usually with dark lined tube-shaped pore. The pycnidia show much resemblance with those of the plurivorous *Phoma acuta* subsp. *errabunda* (no. 15b; teleomorph *Leptosphaeria doliolum* subsp. *errabunda*), but differ by the absence of a convex basal wall thickening; the explicitly scleroplectenchymatous wall has uniform thickness. Exudate salmony coloured. Conidia (3.5–)4–5 × 1–1.5(–2) µm, ellipsoidal to subcylindrical, straight or slightly curved, usually with two polar guttules.

[Pseudothecia (also on dead stems) up to 450 µm diam., truncate-conical. Wall scleroplectenchymatous. Asci 80–100 × 6–8 µm, 8-spored, biseriate. Ascospores 25–30 × 4–4.5 µm, narrowly fusiform, 3-septate, central cell nearly as long as end cells, yellowish without guttules (for recent description of this supposed teleomorph see Shoemaker, 1984)].

Description in vitro

OA: repeated attempts to isolate this fungus at room temperature have been not successful. [Also an obvious difference with the plurivorous *P. acuta* subsp. *errabunda* which can always be grown easily in culture.]

Ecology and distribution. Widespread in Europe on species of *Melampyrum* (semi-parasitic, especially on roots of Gramineae). The scleroplectenchymatous pseudothecia of *Leptosphaeria suffulta* frequently occur in close association with the pycnidia, but a single identity must still be proved.

Note. Phoma petrakii has often been confused with *P. sylvatica* Sacc. [sect. *Sclerophomella,* compare de Gruyter & Noordeloos (1992: 89)]. The pycnidia of *P. sylvatica* are smaller than those of *P. petrakii* and not scleroplectenchymatous, but their conidia have approximately the same dimensions. The combination *Plenodomus sylvaticus* (Sacc.) Rupprecht was based on a misidentified collection of *P. petrakii.*

11. **Phoma leonuri** Let. — Fig. 5B

Teleomorph: *Leptosphaeria slovacica* Picb.

Phoma leonuri Letendre in Roum., Fungi gall. exs. (1884) No. 3068; Revue mycol. 6 (1884) 229. — *Plenodomus leonuri* (Let.) Moesz & Smarods in Moesz, Magy. bot. Lap. 31 (1932) 38.

Phoma complanata var. *acuta* Auerswald, Fungi europ. exs./Klotzschii Herb. mycol. Cont. Cent. 4 (1861) No. 343 [as '*complanatum*' and var. '*acatum*'; obviously introduced as a new variety ("A typica specie non nisi ostiolo elongato diversa") representing '*Sphaeria acutum* Pers. p.p.' on *Ballota nigra* subsp. *foetida*].

Phoma acuta f. *ballotae* Thümen, Verh. K.K. zool.-bot. Ges. Wien 25 (1875) 550 [as '*acutum* Awd', see above].

Phoma acuta f. *ballotae* P. Sydow, Mycoth. March. (1889) No. 2571 [as '*acutum*'; nomen nudum].

Phoma acuta f. *ballotae* Allescher, Rabenh. Krypt.-Flora [ed. 2], Pilze 6 [Lief. 63] (1898 [vol. dated '1901']) 271 [nomen nudum].

Selected literature. Boerema, van Kesteren & Loerakker (1981).

Description in vivo (especially *Leonurus cardiaca*)

Pycnidia-II only (on dead stems, usually aggregated in short rows, subepidermal, later superficial), mostly 200–300 µm diam., subglobose with flattened base, and cylindrical semi-pilose necks, often up to c. 500 µm long. Wall at the flattened base and in the 'shoulder'-region strongly thickened, but otherwise uniformly made up of polygonal scleroplectenchyma cells of differing dimensions. Exudate white-yellowish. Conidia oblong to ellipsoidal, (3.5–)4–5.5 × 1.5–2.5 µm, usually with two minute polar guttules.

Pseudothecia (also on dead stems) mostly 275–375 µm diam., subglobose, non-sulcate, with distinct, occasionally papillate pore. Wall ± scleroplectenchymatous. Asci (60–) 75–100 × 5.5–7.5 µm, 8-spored, biseriate in the upper part, uniseriate below. Ascospores 18–22(–28) × 4.5–5.5 µm, broadly fusiform, 3-septate with acute end cells, olivaceous yellow (for detailed description see the original diagnosis in Trotter, 1972: 405).

Description in vitro

OA: growth-rate 11–27 mm, aerial mycelium absent or scarce, lanose in the centre, whitish or (pale)olivaceous grey, sometimes with dark olivaceous felted sectors; reverse mostly ochraceous or yellow-red due to a somewhat diffusible pigment [no reaction with addition of a drop of NaOH]. Variable production of pycnidia with conspicuous long pilose necks, at first pale brown, ultimately dark with greenish tinge. Conidia as in vivo.

Ecology and distribution. In continental Europe common on dead stems of the perennial labiate herbs *Leonurus cardiaca* and *Ballota nigra* subsp. *nigra* and subsp. *foetida.* The fungus is occasionally recorded on dead stems of other Labiatae. Specimens of the anamorph on *Ballota* are usually referred to '*Phoma acuta*' or '*Plenodomus acutus*' as commonly occurring on nettle stems (compare the documentation above). The nettle pathogen – correct citation *Phoma acuta* (Hoffm.: Fr.) Fuckel subsp. *acuta* (see no. 15a; teleo-

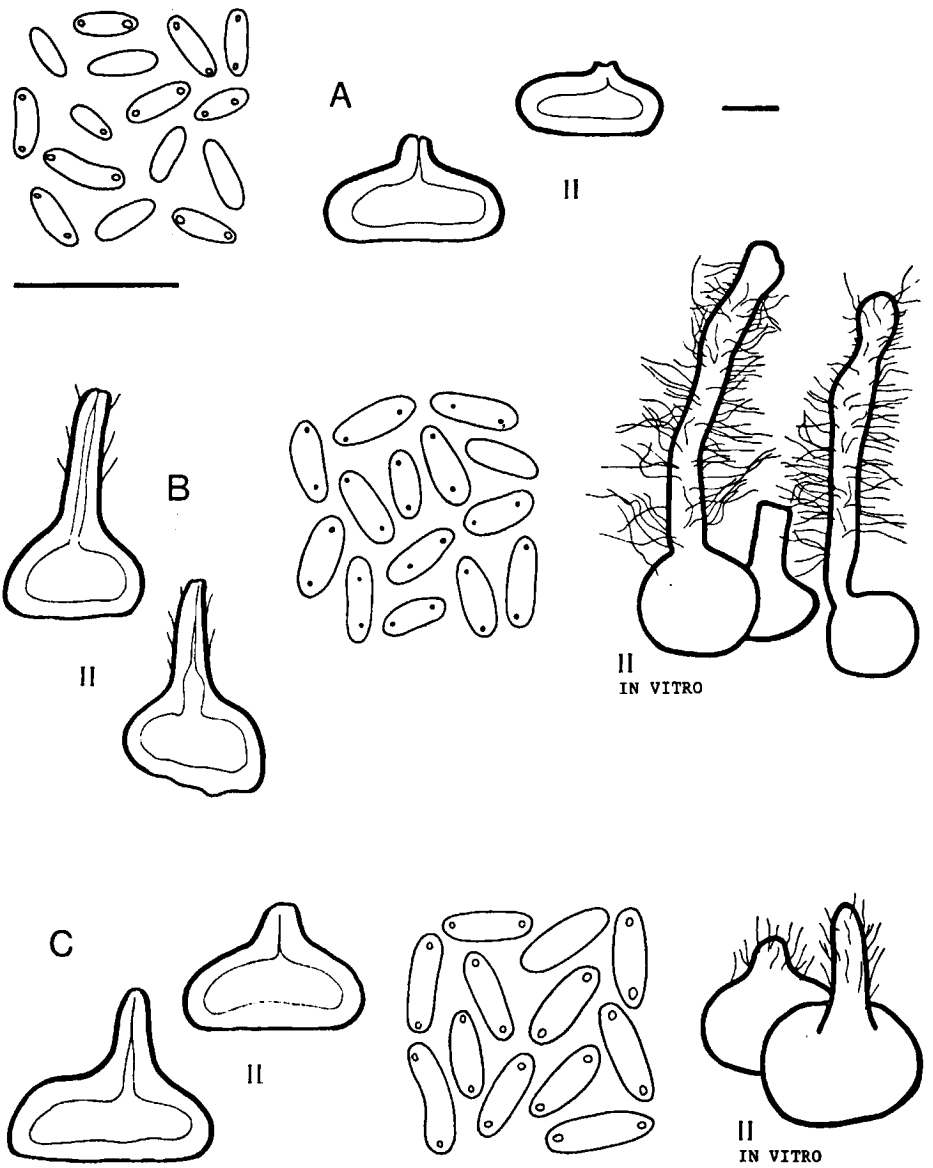


Fig. 5. A. *Phoma petrakii*. Pycnidia-II depressed globose with flattened base and distinctly papillate, usually with a dark-lined tube-shaped pore. — B. *Phoma leonuri*. Characterized by pycnidia-II with conspicuous long cylindrical necks; in vivo semi-pilose but in vitro explicitly pilose. — C. *Phoma congesta*. Pycnidia-II depressed globose with flattened base and conspicuous beak-like papilla which gradually may develop into a long neck. In vitro (left) neck usually pilose.

morph *Leptosphaeria doliolum* subsp. *doliolum*) – produces similar pycnidia in vivo, but these have a convex base of diverging rows of elongated cells. In vitro the pycnidia of *P. acuta* are small and quite different from those of *P. leonuri*.

Representative culture. CBS 389.80.

12. **Phoma congesta** Boerema, de Gruyter & van Kesteren, *spec. nov.* — Fig. 5C

Teleomorph: *Leptosphaeria congesta* Lucas.

Isolatus ex ascosporis, cultus in agaro farina avenae confecto (Lucas, 1963: 363): Pycnidia copiosa, superficialia, plerumque 240–480 µm diam., subglobosa, papilla conspicua rostrata saepe collum longum formante praedita, fere crassitunicata. Conidia oblonga-ellipsoidea, plerumque 5–6 × 1.5–2 µm. Holotypus colonia exsiccata LISE 1638, isolata e caulibus mortuis *Erigerontis canadensis*, Póvoa de Santa Iria, Estremadura in Lusitania, Martius 1961.

Selected literature. Lucas (1963).

Description in vivo (especially on *Achillea* spp.)

Pycnidia-II only (on woody parts of dead stems, gregarious and occasionally confluent), mostly 250–500 µm diam., depressed globose with flattened broad base and conspicuous beak-like papilla which gradually may develop into a long neck. The wall has a somewhat convex thickening at the base, but similar polygonal scleroplectenchyma cells throughout. Exudate white to very pale yellow (ivory). Conidia (4–)5–6(–7) × 1.5–2 µm, oblong-ellipsoidal to subcylindrical, mostly inconspicuously biguttulate.

Pseudothecia (also on dead stems) 380–400 µm diam., globose with conical neck. Wall scleroplectenchymatous. Asci 92–120 × 12–14 µm, 8-spored, biseriate in the upper part, uniseriate below. Ascospores 24–32 × 7–8 µm, rhomboid-fusiform, 3-septate, yellowish-pale brown (for detailed description see Lucas, 1963).

Description in vitro

OA: growth-rate c. 25 mm, regular, cream-yellowish (straw-luteous), translucent; aerial mycelium very tenuous, greenish olivaceous [on MA with short coralloid hyphal branches]; reverse yellowish with broad colourless margin. Abundant production of pycnidia-II, solitary or confluent, mostly (220–)240–480(–550) µm diam., resembling those in vivo, but with a semi-pilose beak which may grow out into a long neck (up to 500 µm) [on MA often with several necks]. Conidia similar to those in vivo, but occasionally up to 8 µm long. Cultures of this fungus did not survive lyophilization.

Ecology and distribution. Most specimens are found in southern Europe (Italy, Portugal) on dead stems of different *Achillea* spp. (*A. ageratum, A. millefolium* and *A. macrophylla*). The teleomorph was first described on stems of *Erigeron canadensis*; therefore the fungus may also occur on other members of the Compositae.

Dried culture. L 993.373.042.

13. **Phoma veronicicola** Boerema & Loerakker — Fig. 6A

Phoma veronicicola Boerema & Loerakker, Trans. Br. mycol. Soc. 84 (1985) 297. — *Sphaeronaema veronicae* Hollós, Annls hist.-nat. Mus. natn. hung. 4 (1906) 341; not *Phoma veronicae* Roumeguère, Revue mycol. 6 (1884) 160.

Selected literature. Boerema & Loerakker (1985).

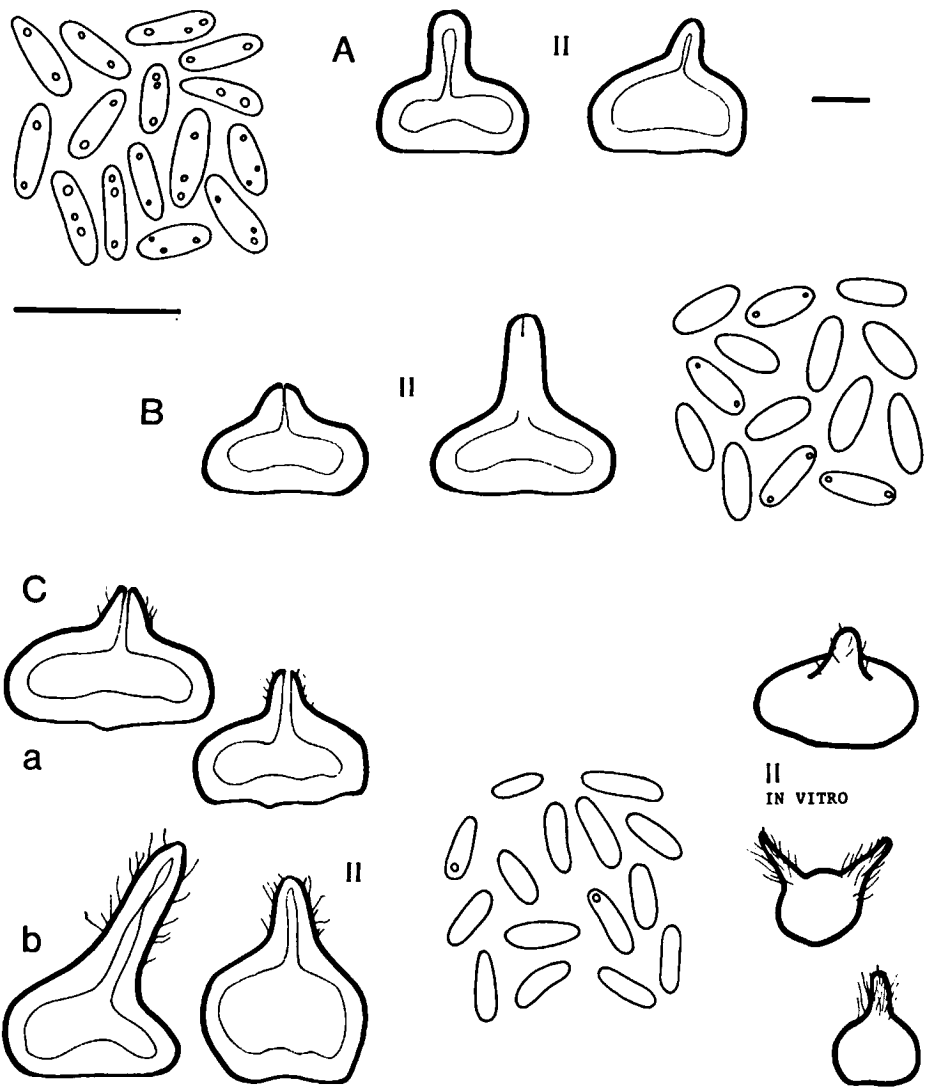


Fig. 6. A. *Phoma veronicicola*. Produces only pycnidia-II with a pronounced neck, which usually remains closed for some time; in vitro, neck sometimes pilose. Conidia 2–4 guttulate. — B. *Phoma longirostrata*. Pycnidia-II with conspicuous cylindrical poroid neck of various length. Conidia eguttulate or with 2 inconspicuous small guttules. — C. Subspecies of *Phoma acuta*. Pycnidia-II with rather sharply delimitated poroid papillae or necks of variable length. Above (a) subsp. *errabunda*, pycnidia with flattened base. At bottom (b) subsp. *acuta*, pycnidia more globose and less depressed, mostly with a long neck; in vitro (right) the pycnidia of this nettle fungus usually remain very small with pilose neck(s).

Description in vivo (*Veronica* spp.)

Pycnidia-II only (on dead stems, gregarious, subepidermal or superficial), usually 200–350 µm diam., depressed globose with a flattened base and cylindrical neck, mostly 150–200 µm long, which remains closed for some time. Initially walls uniform in thickness, later strongly thickened at the flattened base and near the tube-shaped pore; the polygonal scleroplectenchyma cells have different dimensions and may have a somewhat parallel arrangement in the basal thickening. Exudate white-yellowish. Conidia ellipsoidal to subcylindrical, (3.5–)4–5(–6) × (1–)1.5–2 µm, with 2–several more or less polar guttules.

Description in vitro

OA: growth-rate 17–23 mm diam., ochraceous, greenish olivaceous or greenish grey; aerial mycelium tenuous or rather compact, cottony or somewhat felted; reverse colourless or yellowish red, but always with a broad amber or green zone. Yellow pigment localized in cell walls, hardly diffusing into medium [no reaction with addition of a drop of NaOH]. Abundant production of pycnidia-II on and in the agar, with more or less cylindrical necks as in vivo, sometimes pilose; agar close to submerged pycnidia rusty-brown. Conidia similar to those in vivo.

Ecology and distribution. Common in Europe on dead stems of wild and cultivated perennial species of *Veronica.* Regarded as a necrophyte, but possibly weakly pathogenic. It should be noted that in mountainous regions of Europe the plurivorous *Phoma pedicularis* Fuckel (no. 20) has also been recorded on *Veronica* spp.

Representative culture. CBS 145.84.

14. **Phoma longirostrata** Bubák — Fig. 6B

Phoma longirostrata Bubák, Bull. Herb. Boissier II, 6 (1906) 476 [holotype BPI].

Description in vivo (especially *Aconitum* spp.)

Pycnidia-II only (on dead stems, scattered or in groups, subepidermal or superficial), mostly 250–450 µm diam., depressed subglobose with flattened base, with a distinct cylindrical neck of variable length (55–200 µm), occasionally confluent and with 2–several necks. The wall has a somewhat convex thickening at the base, but about the same polygonal scleroplectenchyma cells throughout. Exudate whitish or yellow. Conidia mostly 3–4(–4.5) × 1–1.5(–2) µm, oblong ovoid or ellipsoidal, eguttulate or with 2 small inconspicuous polar guttules.

Description in vitro

OA: growth-date 30–35 mm diam., regular, translucent, somewhat zonate, advanced zone faintly raised; aerial mycelium cottony but tenuous, olivaceous grey; reverse hardly coloured, zonate. Pycnidia sparse, covered by dense aerial mycelium, solitary or confluent, up to 800 µm diam., pale coloured with 1 to several dark short or long cylindrical necks. The cultures soon became stale and did not survive the lyophilization.

Ecology and distribution. In southern Europe (Montenegro, Italy) occasionally on dead stems of Ranunculaceae (*Aconitum* and *Ranunculus* spp.). It should be noted that the plurivorous *Phoma doliolum* (no. 19; teleomorph *Leptosphaeria conoidea* de Not.)

has been recorded more frequently on *Aconitum* spp. in Europe, see also Holm (1957) and Shoemaker (1984). The conidia of *P. doliolum* are significant larger than those of *P. longirostrata.*

Dried culture. L 993.373.103.

15a. **Phoma acuta** (Hoffm.: Fr.) Fuckel subsp. **acuta** — Fig. 6C-b

Teleomorph: *Leptosphaeria doliolum* (Pers.: Fr.) Ces. & de Not. subsp. *doliolum.*

Phoma acuta (Hoffm.: Fr.) Fuckel, Jb. nassau. Ver. Naturk. 23–24 (= Symb. mycol.) (1870 ['1869 und 1870']) 125 [as '*acutum* †'; see Boerema & Gams (1994)], subsp. *acuta* [autonym versus subsp. *errabunda* no. 15b, but already created in 1884 by the differentiation of *P. acuta* subsp. *amplior* Sacc. & Roum. = *P. doliolum* P. Karsten, no. 19]. — *Sphaeria acuta* Hoffmann, Veget. crypt. 1 (1787) 22: Fries, Syst. mycol. 2 (2) (1823) 507 [lectotype Sclerom. Suec. Fasc. 4, No. 118. UPS]. — *Leptophoma acuta* (Hoffm.: Fr.) Höhnel, Sber. Akad. Wiss. Wien [Math.-naturw. Kl. Abt. I] 124 (1915) 71–75 [as '(Fuck.)']. — *Plenodomus acutus* (Hoffm.: Fr.) Bubák, Annls mycol. 13 (1915) 29 [as '(Fuck.)']. — *Plenodomus acutus* (Hoffm.: Fr.) Petrak, Annls mycol. 19 (1921) 192 [as '(Fuck.)'].

Strigula urticae Bonorden, Bot. Ztg 11 (1853) 292. — *Clisosporium urticae* (Bonorden) Bonorden, Abh. naturforsch. Ges. Halle 8 (1869) 140.

Phoma herbarum var. *urticae* Roumeguère, Fungi gall. exs. Cent. 11 (1881) No. 1017; Revue mycol. 3 (1881) 30 [nomen nudum].

Phoma hoehnelii var. *urticae* Boerema & van Kesteren in Boerema, Trans. Br. mycol. Soc. 67 (1976) 229.

Selected literature. Boerema (1976), Boerema & Gams (1994).

Description in vivo (Urtica dioica)

Pycnidia-II only (on dead stems, usually in short rows, subepidermal or superficial), subglobose with flattened base and usually a pronounced neck, up to 400 µm long. The neck is mostly somewhat 'hairy' (semi-pilose) and thin-walled. Scleroplectenchyma is especially conspicuous at the 'shoulder' near the neck. At the base of mature pycnidia there is a convex thickening consisting of diverging rows of elongated cells. Exudate cream or whitish. Conidia relatively small, (3–)3.5–5(–5.5) × 1.5(–2) µm, subcylindrical, usually eguttulate.

Pseudothecia (also on dead stems) 300–450 µm diam., subglobose with flattened base and a short conical neck. Wall scleroplectenchymatous. Asci mostly 120–160 × 6–8 µm, 8-spored, biseriate. Ascospores (20–)24–30(–35) × 4–5(–5.5) µm [Q (length/width ratio) = 5–5.5], narrowly fusiform-ellipsoidal, 3-septate with acute end cells, brownish-guttulate, echinulate [see Note].

Description in vitro

OA: growth-rate 25–35 mm, aerial mycelium cottony or somewhat felted, olivaceous grey; reverse sometimes with yellowish-brown tinges. Often a pinkish discolouration of the agar in old cultures and slow development of pycnidia-II on and in the agar. They are small in comparison with those in vivo, mostly 80–200 µm diam., subglobose with 1 or more pilose necks. Conidia as in vivo. Transfers of this fungus soon become sterile.

Ecology and distribution. Very common in Europe on dead stems of nettle, especially *Urtica dioica* (anamorph and teleomorph). Reports from North America refer to different *Urtica* spp. (teleomorph). The fungus is occasionally recorded in Europe on herbaceous plants of other genera (see also below under f. sp. *phlogis*). Since 1976 the anamorph

of *Leptosphaeria doliolum* s.s. on *Urtica* spp. has been known as *Phoma hoehnelii* var. *urticae,* but the present Code has made it possible to reinstate the old species name *Phoma acuta,* see Boerema & Gams (1994). However, it should be noted that *P. acuta* and its synonyms *Leptophoma acuta* and *Plenodomus acutus* have previously been used for different anamorphs in the section *Plenodomus,* compare Boerema & van Kesteren (1981, tab. 1). It has also been stated in literature that *P. acuta* as described above is the anamorph of *Leptosphaeria acuta* (Fuckel) P. Karsten, whose pseudothecia frequently occur at the base of dead stems of nettle. The pycnidia of *L. acuta, Phoma piskorzii* (no. 17) usually develop inside hollow stems and contain significantly longer conidia.

Representative culture. CBS 505.75.

Note. It should be noted that the description of *L. doliolum* by Shoemaker (1984) [Q = 5–5.5] embraces the teleomorph of this nettle fungus, *L. doliolum* subsp. *doliolum,* as well as the plurivorous *L. doliolum* subsp. *errabunda,* the teleomorph of *P. acuta* subsp. *errabunda,* no. 15b.

f. sp. **phlogis** [(Roum.) Boerema, de Gruyter & van Kesteren, *comb. nov.*]

Phoma phlogis Roumeguère, Revue mycol. 6 (1884) 160 [basionym].
Sphaeronaema pirottae Ferraris, Malpighia 16 (1902) 23 [as '*Sphaeronema*'].

Ecology and distribution. In Europe (France, Great Britain, Italy, Russia, the Netherlands) frequently found on phlox (the annual *Phlox drummondii* and hybrids of the perennial *Phlox paniculata*). Indistinguishable from the anamorph on nettle, but never associated with the teleomorph. Recorded as pathogenic: Stem Lesions. Dieback.

Representative culture. CBS 155.94.

15b. **Phoma acuta** subsp. **errabunda** (Desm.) Boerema, de Gruyter & van Kesteren, *comb. nov.* — Fig. 6C-a

Teleomorph: *Leptosphaeria doliolum* subsp. *errabunda* Boerema, de Gruyter & van Kesteren, see Note below.

Phoma errabunda Desmazières, Annls Sci. nat. (Bot.) III, 11 (1849) 282 [basionym; syntypes Pl. cryptog. France (ed. 1) Fasc. 38 (1849) No. 1870 and Pl. cryptog. France (ed. 2) Fasc. 30 (1849) No. 147, PC].

Leptophoma doliolum Höhnel, Sber. Akad. Wiss. Wien [Math.-naturw. Kl., Abt. I] 124 (1915) 75. — *Plenodomus doliolum* (Höhnel) Höhnel, Ber. dt. bot. Ges. 36 (1918) 139. — *Plenodomus doliolum* (Höhnel) Petrak, Annls mycol. 21 (1923) 125. — *Phoma hoehnelii* van Kesteren, Neth. J. Pl. Path. 78 (1972) 116 [as nom. nov. to avoid homonymy with *Phoma doliolum* P. Karsten, Meddn Soc. Fauna Flora fenn. 16 (1888) 9–10, see no. 19].

Phoma oleracea var. *heraclei-lanati* Saccardo, Nuovo Giorn. Bot. Ital. II, 27 (1920) 81 [cf. holotype, PAD].

Selected literature. Boerema (1976).

Description in vivo (especially *Angelica sylvestris*)

Pycnidia-II only (on dead stems, scattered or in rows, first subepidermal, later superficial), mostly (150–)200–400(–600) µm diam., resembling those of the type subspecies *P. acuta* subsp. *acuta,* but generally more depressed globose with a rather sharply delimited poroid papilla or neck of variable length; the tube-shaped pore is usually dark-lined. Exu-

date also cream or whitish. Conidia similar to those of var. *acuta*, (3–)3.5–5(–5.5) × 1–1.5(–2) µm, subcylindrical and usually eguttulate.

Pseudothecia (also on dead stems) up to 600 µm diam., generally more depressed globose and more flattened than those of the type subsp. *doliolum*. Asci in average 120–140 × 6–7 µm. Ascospores mostly (18–)20–22(–25) × (3–)3.5–4(–5) µm, i.e. usually shorter and thinner than those of subsp. *doliolum*, but similar Q = 5–5.5 [compare Note].

Description in vitro

OA: growth-rate about the same as that of subsp. *acuta*. The cultural characters are also nearly similar, but the pycnidial development on and in the agar is always much more abundant. The dimensions of the pycnidia-II are the same as those in vivo. Conidia also as in vivo.

Ecology and distribution. A widely distributed plurivorous necrophyte in Europe and North America (*errabunda* = wandering about). The fungus is especially common on dead stems of Compositae and Umbelliferae. In North America the teleomorph is most frequently recorded on *Solidago* spp. (Comp.), in Europe the most common host of the fungus is apparently *Angelica sylvestris* (Umb.). Since the early 1970's the anamorph is usually listed as *Phoma hoehnelii* var. *hoehnelii*, based on *Leptophoma* (or *Plenodomus*) *doliolum* Höhnel. As noted under the type-subspecies (no. 15a), the present Code has made it possible to reinstate the old name *Phoma acuta* (Hoffm.: Fr.) Fuckel for the anamorph of *Leptosphaeria doliolum* sensu stricto on *Urtica* spp. The above proposed new combination for the anamorph of the plurivorous subspecies of this fungus is based on a recent comparative study of the syntypes of *Phoma errabunda* with preserved anamorphic specimens used in the cultural studies by Dennis (1946) and Boerema (1976). The latter paper includes a table on the sources of the European isolates. The teleomorph of the fungus was until recently arranged under *Leptosphaeria doliolum* var. *conoidea* (de Not.) Sacc., but now recognized as a separate species: *Leptosphaeria conoidea* (de Not.) Sacc., (anam. *Phoma doliolum*, no. 19), see Note. Both plurivorous fungi display about the same diversity in host range and may represent originally European and American counterparts.

Representative culture. CBS 617.75.

Note. The classification of the teleomorph of *P. acuta* subsp. *errabunda* as a separate subspecies of *Leptosphaeria doliolum* (Pers.: Fr.) Ces. & de Not. is based on a recent Canadian study of herbarium material (Shoemaker, 1984) and the cultural studies made earlier in England and at our laboratory (Lucas & Webster, 1967; Boerema, 1976).

Leptosphaeria doliolum subsp. ***errabunda*** Boerema, de Gruyter & van Kesteren, *subsp. nov.*

Ascosporae subsp. *doliolum* similes (utrinque acutatae, relatio longitudo: latitudo 5–5.5) sed minores, (18–)20–22(–25) × (3–)3.5–4(–5) µm. Holotypus in culmis emortuis *Angelicae sylvestris*, Powerscourt Estate, Co. Wicklow, Eire, lectus a J. Webster Sept. 1957, herb., SHEFF 2040.

This new subspecies is characterized by ascospores resembling those of *Leptosphaeria doliolum* s.s. [see above under no. 15a sub *P. acuta* subsp. *acuta*] in having acute end cells and a length-width ratio of about 5–5.5, but differing by relatively smaller dimensions, mostly (18–)20–22(–25) × (3–)3.5–4(–5) µm (in the type subspecies usually

(20–)24–30(–35) × 4–5(–5.5) µm). The conidia of the anamorphs of both subspecies of *L. doliolum* are similar and significantly smaller than those of the anamorph of *Leptosphaeria conoidea* [see no. 19 sub *Phoma doliolum*]. The ascospores of *L. conoidea* have obtuse ends and are broader than those of both subspecies of *L. doliolum*; length-width ratio about 4.

16. **Phoma sublingam** Boerema — Fig. 7A

Teleomorph: *Leptosphaeria submaculans* Holm.

Phoma sublingam Boerema, Versl. Meded. plziektenk. Dienst Wageningen 157 (Jaarb. 1980) (1981) 24. — *Plenodomus lunariae* H. Sydow & P. Sydow, Annls mycol. 22 (1924) 264; not *Phoma lunariae* Moesz, Magy. bot. Lap. 25 (1926) 36 [= *Phoma doliolum* P. Karsten, no. 19].

Sphaeronaema senecionis f. *sisymbrii* Krieger, Fungi sax. Fasc. 47 (1915) No. 2332 [as '*Sphaeronema*'] [nomen nudum].

Selected literature. Boerema (1981).

Description in vivo (especially *Sisymbrium* spp.)

Pycnidia-I (lesions on stems and leaves, usually solitary, subepidermal and arranged in rows) mostly 200–250 µm diam. (resembling very much those of *Phoma lingam* (no. 2), the anamorph of *Leptosphaeria maculans*), usually subglobose with a broad base and a distinct papillate neck. Exudate whitish-pink. Conidia (3.5–)4–4.5(–5) × 1–1.5(–2) µm, ellipsoidal to subcylindrical, usually with 1–2 small guttules. Pycnidia-II (on last year's dead stems) mostly 200–300 µm diam., i.e. usually smaller than those of *P. lingam*, depressed globose to subglobose with a pronounced neck; wall explicitly scleroplectenchymatous, the flattened base more or less thickened by diverging rows of elongated cells. Conidia as in pycnidia-I.

Pseudothecia (also on dead stems) usually 200–400 µm diam., depressed globose with short broad conical neck [more distinct than in *L. maculans*]. Wall scleroplectenchymatous. Asci 110–120 × 16–18 µm, 8-spored, irregularly quadriseriate. Ascospores 54–70 × 6–7 µm, narrowly fusiform, 5-septate with the third cell broader but shorter than all others [in *L. maculans* central cells are of equal length], yellowish-brown with guttules (for recent detailed description see Shoemaker, 1984). [Often old pycnidia of type I occur in association with pseudothecia; true scleroplectenchymatous pycnidia usually develop only at the end of the next season.]

Description in vitro

OA: slow-growing, growth-rate c. 25 mm, aerial mycelium greyish with yellowish brown tinges. Variable production of pycnidia-I on and in the agar. Conidia as in vivo.

Ecology and distribution. In Europe on various Cruciferae (especially *Sisymbrium* spp.) and occasionally on non-cruciferous plants. It may be associated with disease symptoms resembling the well-known Dry Rot and Canker disease of brassicas caused by *Phoma lingam* (no. 2), teleomorph *Leptosphaeria maculans*. It can likewise be transmitted by seed and may very probably occur in North America [compare Petrie & Vanterpool, 1965, '*Sisymbrium*-strain' of *P. lingam*]. Both fungi are without doubt closely related, but their teleomorphs can be easily differentiated [e.g. *L. submaculans* has a short broad

neck and ascospores with a short swollen third cell], although their type-I pycnidia and conidia are similar. The scleroplectenchymatous pycnidia-II of *P. sublingam* are distinguished by being smaller with a strongly papillate neck. The teleomorph has often been erroneously identified in the past as *Leptosphaeria conferta* (anamorph *Phoma conferta*, no. 9), which is also common on Cruciferae.

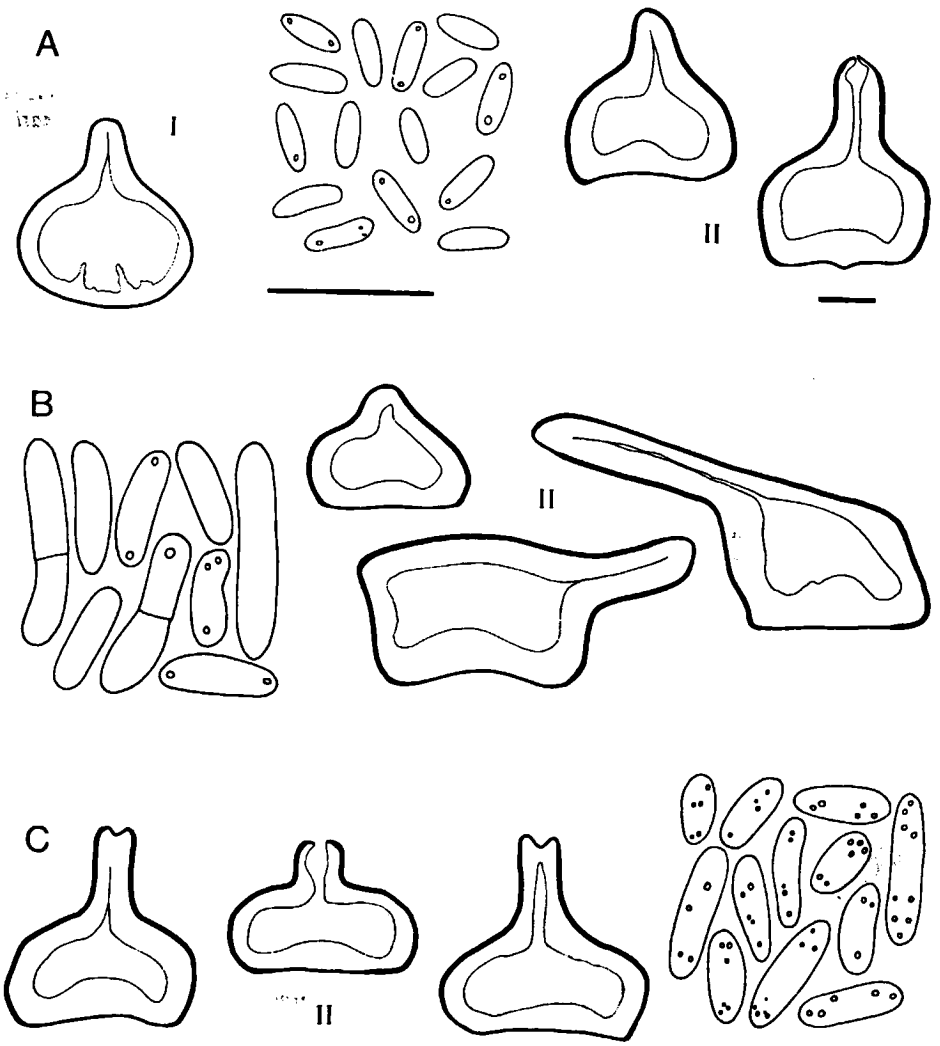


Fig. 7. A. *Phoma sublingam*. Pycnidia-I subglobose with broad base and distinct papillate neck, are found in association with disease symptoms. Pycnidia-II, depressed globose to subglobose with flattened base and a pronounced neck, occur on dead stems. — B. *Phoma piskorzii*. Pycnidia-II variable in shape, with flattened base, often subglobose-papillate, but also with a long neck, usually developing at the side. Conidia relatively large, occasionally 1-septate. — C. *Phoma sydowii*. Pycnidia-II depressed globose with flattened base and pronounced cylindrical neck with tube-shaped pore. Conidia variable and usually pluriguttulate.

17. **Phoma piskorzii** (Petrak) Boerema & Loerakker — Fig. 7B

Teleomorph: *Leptosphaeria acuta* (Fuckel) P. Karsten.

Phoma piskorzii (Petrak) Boerema & Loerakker, Persoonia 11 (3) (1981) 315. — *Diploplenodomus piskorzii* Petrak, Annls mycol. 21 (1923) 123–124[–125].

Selected literature. Boerema & Loerakker (1981), Boerema & Gams (1994).

Description in vivo (*Urtica dioica*)

Pycnidia-II only, (on the base of dead stems, especially inside stem cavity, usually solitary), 250–500 µm diam., variable in shape, mostly depressed subglobose with flattened base, usually papillate but also with a long poroid neck up to 500 µm, usually developing at one side; occasionally opened by rupture. Wall made up of polygonal scleroplectenchyma cells of variable size; usually a conspicuous convex wall-thickening at the base with diverging rows of more or less elongated cells. Conidia, usually (6–)8–10(–12) × 2–2.5(–3) µm, but occasionally also longer up to 16 µm, oblong ellipsoidal to subcylindrical, mostly continuous but occasionally two-celled with an indistinct septum, often with 1–2 guttules.

Pseudothecia (also on the base of dead stems, on outer surface) up to 500 µm diam. with a prominent truncate-conical neck and almost flattened base. Wall scleroplectenchymatous. Asci 120–150 × 7–12 µm, 8-spored, biseriate above, 12-seriate below. Ascospores 37–45(–53) × 5–7 µm, narrowly fusiform, (5–)8–13-septate [in North American collections often 7-septate], pale yellow with guttules [for recent detailed description see Shoemaker, 1984].

Description in vitro

OA: cultures at room temperature produced only sterile mycelium; the fungus requires low temperature and special nutrition for fructification, see Lacoste (1965).

Ecology and distribution. In Europe the anamorph is common at the base of dead stems of nettles, particularly *Urtica dioica,* in spring. At first the pycnidia usually develop inside the hollow stems, which explains why they have often been overlooked. The fungus is probably widespread on nettles in the whole of Eurasia. The teleomorph is also recorded in temperate North America; exact records from other continents are still wanted.

Note. In older literature the anamorph of *Leptosphaeria acuta* is sometimes referred to as '*Phoma acuta*', '*Leptophoma acuta*', or '*Plenodomus acutus*'. These names, however, refer in fact to the anamorph of *Leptosphaeria doliolum* subsp. *doliolum,* correct citation *Phoma acuta* (Hoffm.: Fr.) Fuckel subsp. *acuta* (see discussion under no. 15a). The pycnidia of the latter may be present abundantly on dead stems of nettles, occasionally together with the pseudothecia of *L. acuta*. The conidia of *Phoma acuta* are significantly shorter than those of *P. piskorzii.*

18. **Phoma sydowii** Boerema et al. — Fig. 7C

Possible teleomorph: *Leptosphaeria senecionis* (Fuckel) Winter.

Phoma sydowii Boerema, van Kesteren & Loerakker, Trans. Br. mycol. Soc. 77 (1981) 71. — *Sphaeronaema senecionis* H. Sydow & P. Sydow, Annls mycol. 3 (1905) 185; not *Phoma senecionis* P. Sydow, Beibl. Hedwigia 38 (1899) 136 [belongs to sect. *Phoma,* treated in Contributions I–2; de Gruyter et al.,

1993]. — *Plenodomus senecionis* (Sydow) Bubák, Annls mycol. 13 (1915) 29. — *Plenodomus senecionis* (Sydow) Petrak, Annls mycol. 19 (1921) 192.

Plenodomus rostratus Petrak, Annls mycol. 21 (1923) 199–200; not *Phoma rostrata* O'Gara, Mycologia 7 (1915) 41.

Selected literature. Boerema, van Kesteren & Loerakker (1981).

Description in vivo (*Senecio* spp.)

Pycnidia-II only (on dead stems, generally scattered, subepidermal, later superficial), mostly 300–450 µm diam., depressed globose, with flattened base and pronounced cylindrical neck of variable length and with a tube-shaped pore, neck usually 150–200 µm but also longer up to 600 µm. Wall explicitly scleroplectenchymatous with a flat, or somewhat convex thickening at the base consisting of diverging rows of elongated cells. Exudate pink-whitish. Conidia (4–)5–8(–8.5) × (1.5–)2–2.5 µm, irregular, oblong-ellipsoidal to subcylindrical, conspicuously variable in length, with 2–several small, more or less polar guttules.

[Pseudothecia (dead stems) 300–350 µm diam., globose with a flattened base and a short truncate-conical neck. Wall scleroplectenchymatous. Asci 80–90 × 11–12 µm, 8-spored, biseriate. Ascospores 24–30 × 6.5–7.5 µm, broadly fusiform, 3-septate, yellowish brown with guttules (for this supposed teleomorph see Holm, 1957; North American collections differ by broader asci, shorter and broader ascospores without guttules)].

Description in vitro

OA: growth-rate 10–28 mm diam., tomentose, translucent, zonated, green, greenish yellow with colourless submerged margin; reverse green, yellowish green or bluish green, sometimes with amber or straw zones. Mostly abundant production of pycnidia; they have about the same dimensions as those in vivo and usually also a conspicuous cylindrical neck (often blackened around the pore). Conidia variable as in vivo, usually with numerous small guttules.

MA: very slow-growing, c. 1–3 mm diam.

Ecology and distribution. Common in Europe on dead stems of wild, perennial species of *Senecio,* but also recorded on other Compositae. Often accompanied with pseudothecia of the above teleomorph, but a single identity must still be proved by cultural experiments. In the past *P. sydowii* was erroneously considered to be conspecific with the nettle fungus *Phoma acuta* subsp. *acuta* (no. 15a; teleomorph *Leptosphaeria doliolum* subsp. *doliolum*). The latter produces significantly smaller conidia.

Representative culture. CBS 385.80.

19. **Phoma doliolum** P. Karsten — Fig. 8A

Teleomorph: *Leptosphaeria conoidea* (de Not.) Sacc.

Phoma doliolum P. Karsten, Meddn Soc. Fauna Flora fenn. 16 (1888) 9–10.

Phoma acuta subsp. *amplior* Saccardo & Roumeguère, Revue mycol. 6 (1884) 30; Sylloge Fung. 3 (1884) 133–134 [in both cases as '*Phoma acuta - Ph. amplior*']. — *Phoma hoehnelii* subsp. *amplior* (Sacc. & Roum.) Boerema & van Kesteren in Boerema, Trans. Br. mycol. Soc. 67 (1976) 299.

Plenodomus microsporus Berlese, Bull. Soc. mycol. Fr. 5 (2) (1889) 55–56. — *Diplodomus microsporus* (Berl.) Höhnel, Hedwigia 59 (1918) 250.

Phoma lampsana P. Karsten, Acta Soc. Fauna Flora fenn. 27 (1905) 7.

Diploplenodomus malvae Diedicke, Annls mycol. 10 (1912) 140 [nomen nudum] ex Diedicke, Krypt.-Fl. Mark. Brandenb. 9, Pilze 7 (1912) 415.

Plenodomus labiatarum Petrak, Annls mycol. 21 (1923) 237[–238].

Phoma seseli Hollós, Annls hist.-nat. Mus. natn. hung. 4 (1906) 340.

Plenodomus aconiti Petrak, Annls mycol. 20 (1922) 151.

Phoma lunariae Moesz, Magy. bot. Lap. 25 (1926) 36.

Phoma origani Markova-Letova, Bolez. Rast. 16 (1927) 194. [– *Plenodomus origani* (Mark.-Let.) Petrak in herb. Petrak, ETH-Z, comb. prov., not published].

Plenodomus vincetoxici Petrak, Kryptog. Forsch., Bayer. bot. Ges. Erforsch. heim. Flora 2 (2) (1931) 187–188.

Selected literature. Boerema (1976).

Description in vivo (especially *Foeniculum vulgare*)

Pycnidia-II only (on dead stems, scattered or in groups, first subepidermal, later becoming superficial), relatively large (250–)300–500(–800) × 150–250(–300) µm, depressed globose, usually with irregular deformed flattened base and a short papillate neck with tube-shaped pore. Wall explicitly scleroplectenchymatous with a convex or irregular thickening at the base and more or less parallel cell-structure; sometimes also irregular outgrowths from the sidewalls, sometimes making the pycnidial cavity appears multilocular. Exudate cream or dirty white. Conidia extremely variable in size, often (4–)5–7 × 2–2.5(–3) µm, but also much larger: (7–)8–12 × 2–3 µm and then often 1-septate, ellipsoidal to subcylindrical, eguttulate or with 2 small polar guttules.

Pseudothecia (also on dead stems) up to 500 µm diam., depressed globose with flattened base and short conical neck. Wall scleroplectenchymatous. Asci 75–135 × 7–8 mm, i.e. variable in length and relatively broad, 8-spored, uniseriate. Ascospores (18–)20–23(–25) × 5–6.5(–7) µm [generally broader than those of *L. doliolum,* Q = 4], broadly ellipsoidal, 3-septate with obtuse rather than acute end cells, yellowish-brown with 1 guttule per cell, echinulate (for recent detailed description see Shoemaker, 1984).

Description in vitro

OA: growth-rate 30–40 mm, aerial mycelium cottony or somewhat felted, olivaceous-greyish, reverse with buff, salmon or ochraceous discolouration of the agar. Abundant production of relatively large pycnidia on and in the agar, resembling those in vivo. Conidia usually 4–6(–7.5) × 1.5–2.5(–3) µm.

MA: rather slow growing, 10–20 mm].

Ecology and distribution. A plurivorous necrophyte, widespread in Europe and North America, and especially common on dead stems of Compositae or Umbelliferae. Many records in Canada (teleomorph) refer to *Solidago* spp. (Compositae) and in Europe the most common hosts (anamorph and teleomorph) are *Angelica* and *Foeniculum* spp. (Umbelliferae). The wide host range is similar to that of the plurivorous *Phoma acuta* subsp. *errabunda,* no. 15b, teleomorph *Leptosphaeria doliolum* subsp. *errabunda.* As also noted under no. 15b it is possible that both fungi represent originally European and American counterparts. In an earlier paper with a table on sources of European isolates (Boerema, 1976) the present fungus was listed as *Leptosphaeria doliolum* subsp. *pinguicula* Sacc. [the anamorph as *Phoma hoehnelii* subsp. *amplior*], but taking account of the specific characteristics of conidia as well as ascospores [see Note and Shoemaker, 1984] it has now been raised to a separate species.

Representative culture. CBS 616.75.

Note. The ascospore dimensions given by Boerema (1976) for *L. doliolum* subsp. *pinguicula* are the same as those of *L. conoidea*; those given for *L. doliolum* subsp. *conoidea* referred to the present *L. doliolum* subsp. *errabunda*. The name of the anamorph of *L. conoidea* indicates that originally it was thought that it belonged to *L. doliolum*.

20. **Phoma pedicularis** Fuckel — Fig. 8B

Phoma pedicularis Fuckel in Von Heuglin, Reisen Nordpolarmeer III Beitr. Fauna Fl. Geol. (1874) 318–319 [as '*pedicularidis*']; not *Phoma pedicularis* Wehmeyer, Mycologia 38 (1946) 319. — *Diplodina pedicularis* (Fuckel) Lind, Rep. scient. Results Norw. Exped. Novaya Zemlya 1, 19 (1924) 21 [as '*pedicularidis*'; misapplied]. — *Ascochyta pedicularis* (Fuckel) von Arx, Proc. K. ned. Akad. Wet. C 66 (1963) 180 [as '*pedicularidis*'; misapplied].

Phoma lingam f. *linariae* Saccardo & Paoli in Sacc., Mém. Soc. r. Bot. Belg. [Supplement to Bull. Soc. r. Bot. Belg.] 28 (1889) 96–97 ['Myc. Sibir.', reprint: 20–21] [author-citation cf. Sacc., Sylloge Fung. 10 (1892) 175].

Sphaeronaema gentianae Moesz, Bot. Közl. 14 (1915) 152 [as '*Sphaeronema*']. — *Plenodomus gentianae* (Moesz) Petrak, Annls mycol. 23 (1925) 54.

Phoma prominens Bresadola, Studi trent. Cl. II Sci. nat. econ. 7 (1926) 67. — *Plenodomus prominens* (Bres.) Petrak ex Von Arx, Sydowia 4 (1950) 390.

Plenodomus karii Petrak, Annls mycol. 14 (1936) 453–455.[4]

Plenodomus sphaerosporus Petrak, Annln naturh. Mus. Wien 52 (1942) 384–385.

Plenodomus helveticus Petrak, Sydowia 2 (1948) 239–240. — *Phoma acuta* f. *gentianae* Roumeguère, Fungi gall. exs. Fasc. 11 (1881), No. 1009; Revue mycol. 3 (1881) 30 [nomen nudum].

Selected literature. Boerema, van Kesteren & Loerakker (1981).

Description in vivo (especially *Pedicularis* spp.)

Pycnidia-I→II (on dead stems, leaves and seed capsules, scattered or densely crowded, subepidermal or superficial) initially 200–300 µm diam., subglobose-papillate, irregular cellular protrusions into the pycnidial cavity; gradually becoming larger, more conoid with flattened base, 300–600 µm, with conspicuous dark beak-like elongated papillate neck (under snow cover necks can be up to 150 µm long), wall then explicitly scleroplectenchymatous with a more or less convex thickening consisting of diverging rows of elongated cells at the base; occasionally confluent and with 2 or more necks. Exudate whitish to pale ochraceous or primrose. Conidia vary markedly in size and shape; two types may be present: 4–8(–8.5) × 2–3 µm, oblong to ellipsoidal, subcylindrical or allantoid, and 4–6 × (2–)2.5–4(–4.5) µm, oval ovoid or nearly sphaerical; usually eguttulate, occasionally with 1–2 minute guttules.

Description in vitro

OA: growth-rate 15–21 mm diam.; aerial mycelium tenuous, translucent, fluffy or downy, whitish grey or olivaceous, often with grey to dark olivaceous felted or compact cottony sectors; reverse pale ochraceous, but below the felted sectors, dark olivaceous, bordered by a narrow white zone [pigment quickly fading in daylight and not reacting to a drop of NaOH]. In fresh isolates usually abundant production of globose papillate pycnidia, I→II (i.e. initially thin-walled but gradually becoming scleroplectenchymatous),

[4] This species was formerly placed in synonymy with *P. sclerotioides* (no. 3), but additional study of the type specimen (W) convinced us that it belongs to *P. pedicularis* (pycnidia with broad conical neck and convex basal thickening with diverging rows of elongated cells).

very small, 100–200 µm diam., in comparison with the pycnidia in vivo. Conidia of two types as in vivo (Q = 3–4 and Q = 1.9–2.6), but less variable and always produced in the same pycnidium.

Ecology and distribution. In Eurasian regions with prolonged snow cover this species is frequently found on dead stems, leaves and seed capsules of various herbaceous plants. Typically it is a plurivorous fungus with an arctic-alpine distribution, but it has also been recorded in the desert areas of Central Siberia. Most records refer to last year's stems of Scrophulariaceae (especially *Pedicularis* and *Veronica* spp.) and Gentianaceae (various *Gentiana* spp.). *Phoma pedicularis* has been confused with *Ascochyta pedicularis* (Rostrup) von Arx, which has much larger two-celled conidia (Mel'nik, 1977).

Representative culture. CBS 390.80.

21. **Phoma tracheiphila** (Petri) Kant. & Gik. — Fig. 8C

Hyphomycetous-anamorph: *Phialophora* sp.

Phoma tracheiphila (Petri) Kantschaveli & Gikachvili, Tr. Inst. Zashch. Rast, Tiflis 5 (1948) 20. — *Deuterophoma tracheiphila* Petri, Boll. R. Staz. Petol. veg. Roma II, 9 (4) (1929) 396. — *Bakerophoma tracheiphila* (Petri) Ciferri, Atti Ist. bot. Univ. Pavia V, 5 (1946) 307.

Selected literature. Graniti (1955), Ciccarone & Russo (1969).

Description in vivo (especially *Citrus limonia*)

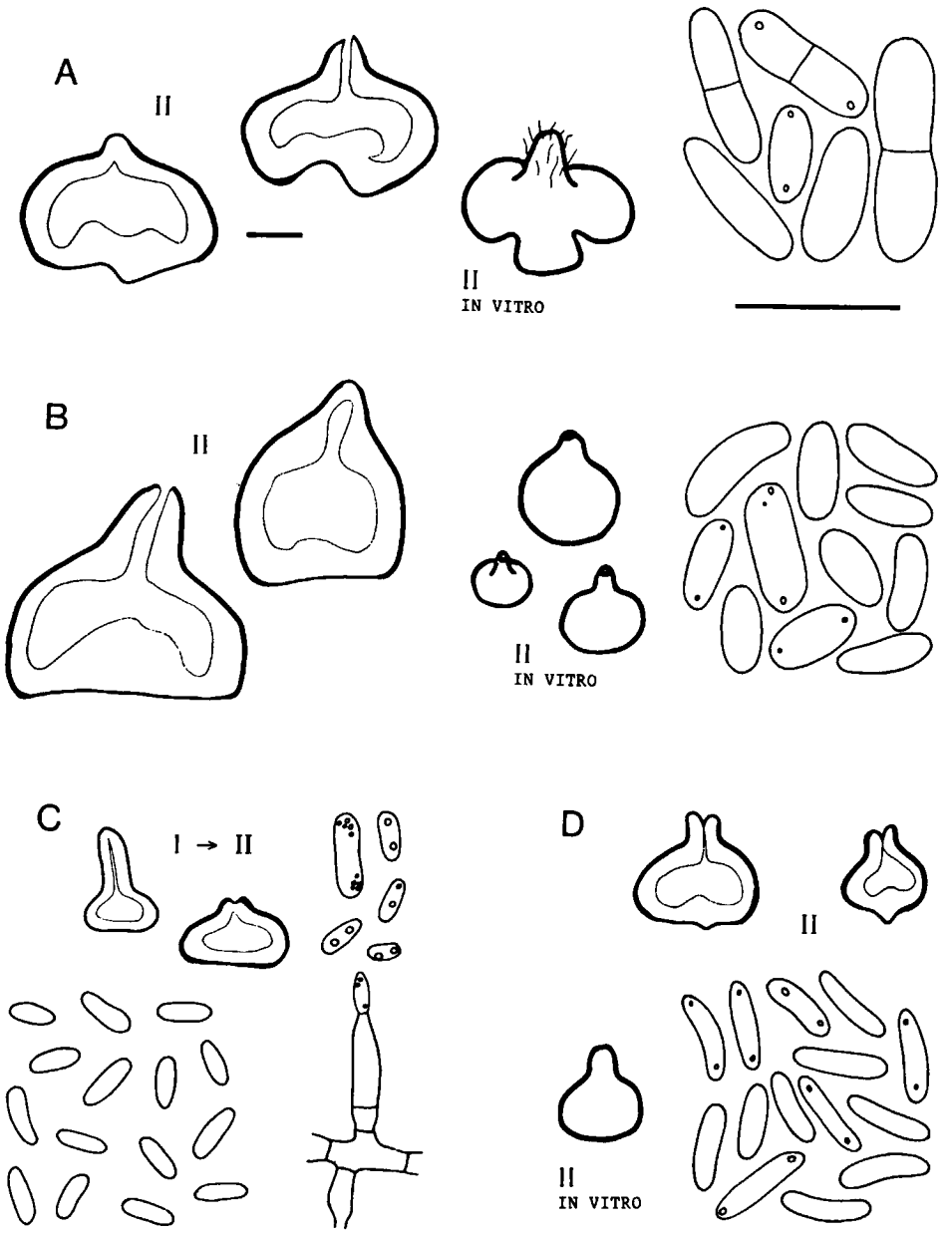
Pycnidia-I→II (on twigs and branches and around leaf scars, at first covered by the epidermis) mostly 60–135 mm diam., subglobose, at maturity always with a distinct cylindrical neck, 45–70 µm diam. and up to 250 µm in length (these necks are easily removed with the epidermis, leaving behind widely and irregularly opened pycnidial bodies). Wall of mature pycnidia consists of randomly arranged polygonal scleroplectenchyma cells and is about the same thickness throughout. Conidia 2–3(–3.5) × 1–1.5 µm, subcylindrical, straight or slightly curved, eguttulate or biguttulate.

Description in vitro

OA: fresh isolates grow well, growth-rate 25–30 mm, colonies flat with little aerial mycelium; pigmentation of mycelial mat and medium variable, depending on strain and ranging from pale pink and bright orange to dark olive brown. On application of NaOH the reddish pigments turn blue (the presence of helminthosporin and cynodontin have been demonstrated). Production of pycnidia is scarce; these often remain incomplete, thin-walled (I) and open irregularly at maturity.

Hyphal conidia are usually produced in abundance, arising from papillate or flask-shaped conidiogenous cells formed on the aerial mycelium (representing the *Phialophora*-anamorph). The hyphal conidia are variable in shape and size, depending on strain, often 2–2.5 × 1–1.5, but also larger, 3–8 × 1.5–3 µm, usually with 2–several polar guttules.

Ecology and distribution. Well-known in the Mediterranean and Black Sea areas as vascular pathogen of lemons and other *Citrus* spp.: Mal Secco Disease. The typical symptoms consist of red discoloured strands in the xylem of stems, veinal chlorosis, wilt and shedding of leaves and ultimately dieback of twigs and branches. Infection occurs through


A
II
II
IN VITRO
B
II
II
IN VITRO
C
I → II
D
II
II
IN VITRO

stomata and wounds. The production of pycnidia is fluctuating and often rare. An ashy appearance on the stem indicates the presence of pycnidia beneath the epidermis.

Representative culture. CBS 551.93.

Note. A similar *Phoma* inhabiting the vascular system with a *Phialophora*-synanamorph is known on pyrethrum (Robertson, 1967) and chrysanthemum (Baker et al., 1985: '*Phoma tracheiphila* f. sp. *chrysanthemi*'). At present there are no data on production of scleroplectenchyma by that pathogen, so it cannot be included in section *Plenodomus,* but the fungus is described in the Addendum to this paper as *Phoma vasinfecta,* no. 31.

22. **Phoma coonsii** Boerema & Loerakker — Fig. 8D

Phoma coonsii Boerema & Loerakker, Trans. Br. mycol. Soc. 84 (1985) 289[–290].
Selected literature. Boerema & Loerakker (1985).

Description in vivo (*Malus pumila*)

Pycnidia-II only (immersed in bark and on wood, usually densely grouped), 100–150 (–250) µm diam., subglobose with a flattened or somewhat pointed base and a dark papillate pore, often with a protruding lip. The wall of a mature pycnidium has randomly arranged polygonal scleroplectenchyma cells and is about the same thickness throughout, but may have some invaginations. Pycnidial primordia (protopycnidia) are completely filled with diverging rows of somewhat elongated cells. Conidial exudate dirty white. Conidia 4.5–6.5 × 1–2 µm, (sub)cylindrical, often slightly curved, eguttulate and biguttulate.

Description in vitro

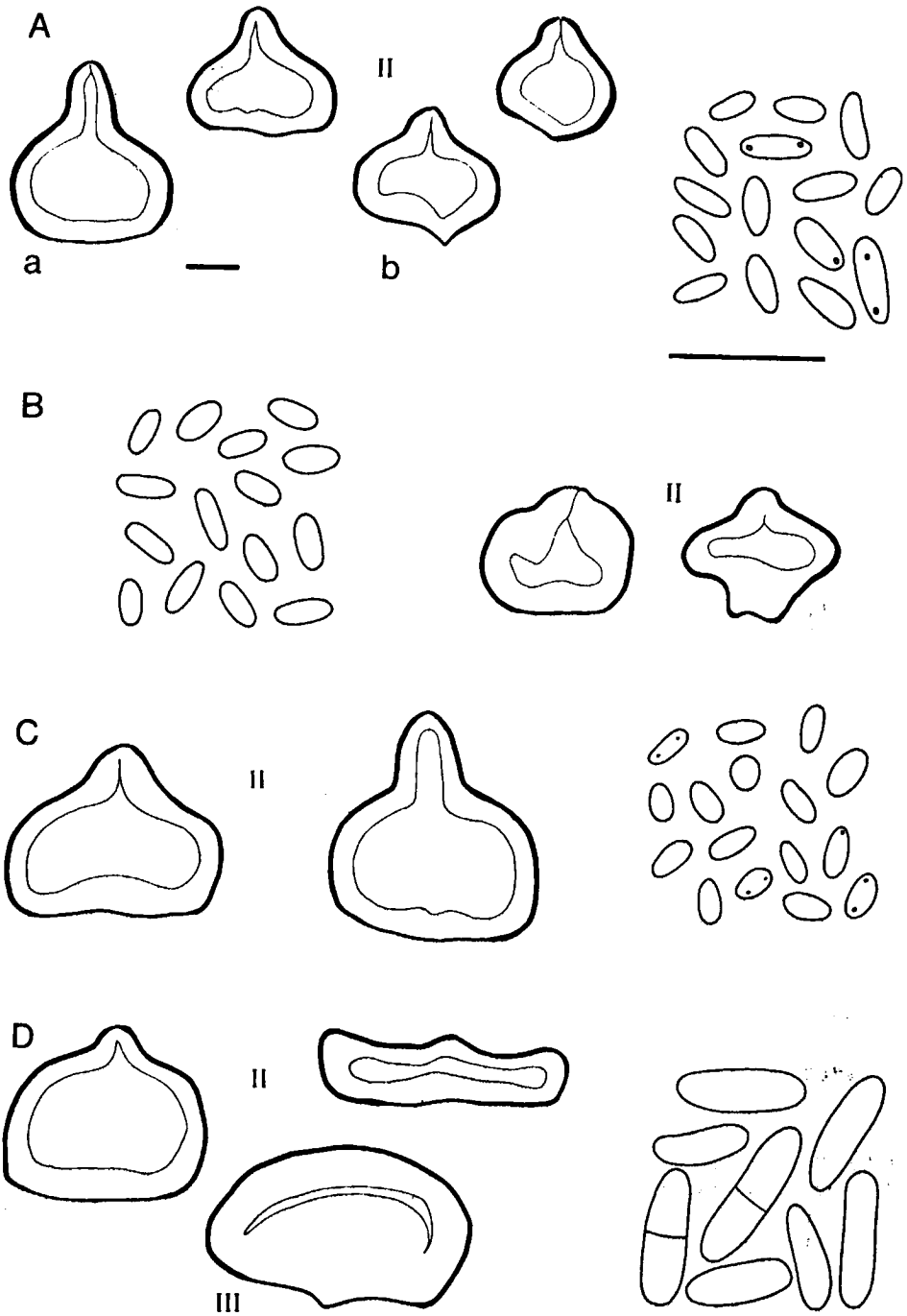
OA: slow-growing, growth-rate c. 15 mm; aerial mycelium either felted fluffy-cottony or very scant, at least in zones, colony and reverse becoming yellow, citrine, amber or dark olivaceous due to diffusible pigment(s), which become reddish (quickly fading) on application of a drop of NaOH. Rubiginous verrucose granules, up to 15 µm diam., are produced in old colonies. Pycnidia often develop only after 1 or even 2 months. Conidia as in vivo.

MA: very slow-growing with an odour of lovage or liquorice.

Ecology and distribution. On bark and wood of apple, *Malus pumila,* in North America (United States) and Japan. Reputed to be pathogenic, Bark Canker, but probably only an opportunistic parasite.

Representative culture. CBS 141.84.

Fig. 8. A. *Phoma doliolum.* Pycnidia-II depressed globose, usually with irregular deformed flattened base and short papillate neck. Conidia variable in dimension, the larger ones often 1-septate. — B. *Phoma pedicularis.* Pycnidia-I→II, initially small subglobose-papillate, finally relatively large, conoid with flattened base and conspicuous beak-like elongated neck. Conidia vary markedly in shape and dimensions. In vitro the pycnidia remain subglobose-papillate and small. — C. *Phoma tracheiphila.* This pathogen of citrus trees is characterized by very small pycnidia-I→II, subglobose with a gradually developing cylindrical neck. In vitro conidia may arise from free conidiogenous cells on the mycelium (*Phialophora*-synanamorph). — D. *Phoma coonsii.* Pycnidia-II relatively small, subglobose with a flattened or somewhat pointed base and broad papillate pore, often with a protruding lip.


A
II
a
b
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II
III

23a. **Phoma enteroleuca** Sacc. var. **enteroleuca** — Fig. 9A

Phoma enteroleuca Saccardo, Michelia 1 (4) (1878) 358, var. *enteroleuca*. — *Phomopsis enteroleuca* (Sacc.) Wollenw. & Hochapf., Z. ParasitKde 8 (1936) 571 [misapplied].

Phoma armeniacae Thümen, Mitt. forstl. VersWes. Ost. 11 (1888) 3.

Phoma malvacei Brunaud, Bull. Soc. Sci. nat. Ouest Fr. 3 (1893) 218.

Phoma berberidella Saccardo & P. Sydow, Sylloge Fung. 14 (1899) 867. — *Phoma berberidicola* Brunaud, Act. Soc. Linn. Bordeaux (1898) 12 [cf. fresh isol.]; not *Phoma berberidicola* Vestergren, Öfvers. Vetens.-Akad. Forh. (1897) 38.

Phoma macra P. Sydow, Beibl. Hedwigia 38 (1899) 136.

Phoma cornicola D. Saccardo in Saccardo & P. Sydow, Sylloge Fung. 16 (1902) 856; not *Phoma cornicola* Oudemans, Ned. kruidk. Archf III, 2 (1) (1900) 234.

Phyllosticta catalpicola Oudemans, Ned. kruidk. Archf III, 2 (4) (1903) 890; not *Phyllosticta catalpicola* (Schw.) Ellis & Everhart, N. Am. Pyren. (1892) 747.

'Plenodomus chondrillae' sensu Batista & Vital, Annais Soc. Biol. Pernamb. 15 (1957) 419 [misapplied; Plen. chondrillae Died. = *Phoma agnita* Gonz.-Frag., no. 5].

Selected literature. Boerema & Loerakker (1985).

Description in vivo

Pycnidia-I→II (superficial on dead branchlets, cankers, leaf scars, etc.; usually densely crowded), mostly 250–400 µm diam., globose-papillate, initially thin-walled (I) but gradually becoming scleroplectenchymatous (II). Wall of mature pycnidia often with irregular invaginations at the base and at the sides; consisting of polygonal scleroplectenchyma cells of variable size, usually in more or less parallel rows at the base. Exudate pink. Conidia relatively small, 3–4(–4.5) × 1–2 µm, ellipsoidal or ovoid, mostly eguttulate.

Description in vitro

OA: growth-rate 36–43 mm, pale olivaceous grey, greenish glaucous to greenish yellow; aerial mycelium tenuous, twined or tufted with red, needle-shaped crystals; reverse yellowish (buff, straw or amber), locally red discolouration (purplish-blue with addition of a drop of NaOH), due to diffusible pigments, partly fluorescent under UV. Pycnidia-I→II scattered on and in the agar, globose, becoming papillate as in vivo. Conidia resembling those in vivo.

Ecology and distribution. Recorded from bark, wood and fruits of various deciduous trees and shrubs in Europe (France, Germany, Italy, the Netherlands) and North America (United States). Opportunistic parasite. This fungus is sometimes confused with *Phoma fimeti* Brun. (sect. *Phoma*, described in Contributions I–1, de Gruyter & Noordeloos, 1992; easily distinguished by a broader conidium frequently with a large guttule).

Representative culture. CBS 142.84.

Fig. 9. A. Varieties of *Phoma enteroleuca*. Pycnidia-I→II, globose-papillate with flattened or somewhat pointed base; var. *enteroleuca* (a) produces slightly larger pycnidia than var. *influorescens* (b). — B. *Phoma intricans*. Characterized by very thick-walled pycnidia-II, subglobose or irregular in shape with narrow pore and flattened, often somewhat elongated base. — C. *Phoma rubefaciens*. Pycnidia initially thin-walled, I→II, relatively large, globose-papillate or with a short cylindrical neck. — D. *Phoma pezizoides*. Produces relatively large pycnidia-II and pycnosclerotia-III. Pycnidia usually globose-papillate with flattened base; at length they often collapse and become discoid or pezizoid. Conidia very variable and occasionally 1-septate.

23b. **Phoma enteroleuca** var. **influorescens** Boerema & Loerakker — Fig. 9A

Phoma enteroleuca var. *influorescens* Boerema & Loerakker, Trans. Br. mycol. Soc. 84 (1985) 290 [as '*inflorescens*'].

Phyllosticta tweediana Penzig & Saccardo in Penzig, Atti r. Ist. ven. Sci. VI, 2 ['Funghi Mortola'] (1884) 647 [holotype PAD; cf. morphology and dimensions rather var. *influorescens* than var. *enteroleuca*].

Selected literature. Boerema & Loerakker (1985).

Description in vivo

Pycnidia-I→II (superficial in groups on dead branchlets etc.) resembling those of the type variety, also globose-papillate, but generally somewhat smaller, mostly 150–350 µm in diameter, and conidial exudate colourless, not pink. Conidia similar to those of var. *enteroleuca*, but often somewhat larger, 3–4(–5) × (1–)1.5–2 µm, and acute at one end.

Description in vitro

OA: slower growing than var. *enteroleuca*, growth-rate 21–27 mm; more (greenish-) yellow and aerial mycelium not tufted but plumose (red crystals absent); reverse also yellowish (mostly with a distinct citrine zone), but not fluorescent; red pigment may also be produced (purplish-blue with a drop of NaOH). Pycnidia in zones on and in the agar, globose-papillate as in vivo. Conidia as in vivo.

Ecology and distribution. On various trees and shrubs in Europe and North America, as with the type-variety, but apparently much less common. Opportunistic parasite.

Representative culture. CBS 143.84.

24. **Phoma intricans** Schwarz — Fig. 9B

Phoma intricans Schwarz, Meded. phytopath. Lab. Willie Commelin Scholten 5 (1922) [42–]44.

Description in vivo (*Salix alba*)

Pycnidia-II only (immersed in bark and on wood, usually densely crowded), 250–350 µm diam., mostly subglobose-papillate with flattened, often somewhat elongated base, sometimes without any definite shape, but always with one narrow pore. The walls of mature pycnidia usually have many invaginations and consist of polygonal scleroplectenchyma cells of quite different sizes. Extensive wall-thickenings at the base of the pycnidial cavities have a diverging parallel structure. Exudate pink-violet. Conidia 2.5–3.5 (–4) × 1–1.5(–2) µm, ovoid to ellipsoidal, eguttulate.

Description in vitro

OA: growth-rate 50–57 mm, regular, aerial mycelium scarce, velvety or fluffy, olivaceous grey with sectoring hyphal and pycnidial zones; reverse olivaceous and greenish-black with pale red (coral) margin. With addition of a drop of NaOH the reddish pigment turns blue. The pycnidia are always scleroplectenchymatous (II), globose-papillate and relatively small, 150–250 µm diam., in comparison with those in vivo.

MA: slow-growing, growth-rate 30–45 mm, aerial mycelium compact, cottony, greenish olivaceous with reddish tinge caused by orange needle-like crystals on the hyphae; reverse olivaceous black, becoming yellowish milky in the centre.

Ecology and distribution. Very common in Europe on varieties and hybrids of *Salix alba*. Reported to be pathogenic: Bark Canker, but probably only an opportunistic parasite. The fungus is also incidental occurring on deciduous trees of other genera.

Representative culture. CBS 139.78.

25. **Phoma rubefaciens** Togl. — Fig. 9C

Phoma rubefaciens Togliani, Annali Sper. agr. II, 7 (1953) 1626.
Selected literature. Boerema, van Kesteren & Loerakker (1981).

Description in vivo (especially *Malus* spp.)

Pycnidia-I→II (subepidermal in centre of red fruit spots, immersed and inconspicuous in wood and bark), (350–)400–500 µm, globose-papillate or with a short cylindrical neck. Wall of mature pycnidia shows randomly arranged polygonal scleroplectenchyma cells. Conidiogenous cells well-differentiated, cone-shaped. Exudate whitish. Conidia (3.5–)4–5 × 2–2.5(–3) µm, ovoid-oval to subcylindrical, eguttulate or with 1–2 minute guttules.

Description in vitro

OA: growth-rate 10–17 mm, aerial mycelium sparse or velvety-cottony, greyish or greenish, abundant production of pycnidia in concentric rings on the agar, thin-walled or scleroplectenchymatous, I→II, covered by dark hyphae; reverse of colony yellow-red or greenish-yellow with yellow margin [chemical analysis revealed the anthraquinone cynodontin and a yellow pigment with a chrysophenol-like UV-visible spectrum].

Ecology and distribution. Isolated from bark and wood of various deciduous trees in Europe. The fungus has been recorded in association with red skin necroses on apple, but is probably only an opportunistic pathogen.

Representative culture. CBS 387.80.

26. **Phoma pezizoides** (Ell. & Ev.) Boerema & v. Kest. — Fig. 9D

Phoma pezizoides (Ell. & Ev.) Boerema & van Kesteren, Persoonia 11 (3) (1981) 322. — *Aposphaeria pezizoides* Ellis & Everhart, Proc. Acad. nat. Sci. Philad. (1894) 358. — *Coniothyrium pezizoides* (Ell. & Ev.) O. Kuntze, Revis. Gen. Pl. 3 (3) (1898) 459.

Aposphaeria salicum Saccardo, Mycoth. germ. [Ed. H. & P. Sydow] Fasc. 2 (1903) No. 89; Annls mycol. 1 (1903) 537–538. — *Plenodomus salicum* (Sacc.) Diedicke, Annls mycol. 9 (1911) 140.

Phoma wallneriana Allescher, Rabenh. Krypt.-Flora [ed. 2], Pilze 6 [Lief. 61] (1898 [vol. dated '1901']) 175. — *Plenodomus wallneriana* (Allescher) Bubák, Annls mycol. 13 (1915) 30.

Plenodomus helicis Curzi & Barbaini, Atti Ist. bot. Univ. [Lab. crittogam.] Pavia III, 3 (1927) 173.
Selected literature. Boerema & van Kesteren (1981).

Description in vivo (esp. *Salix* spp.)

Pycnidia-II only (especially on decorticated branches, often in rows), mostly 250–500 µm diam., but also larger, up to 1000 µm diam., usually globose-papillate with flattened base; at length the pycnidia often collapse and become discoid or pezizoid. The wall consists of polygonal scleroplectenchyma cells; with a more or less parallel arrangement in the thickened, somewhat convex base. Protopycnidia are completely filled with such polygonal cells; the proliferating layer develops initially in a cap-shaped pattern. Exudate whitish. Sometimes the pycnidial primordia remain closed and sterile: forming pycnosclerotia

(III). Conidia vary markedly in dimensions and shape: 4.5–6(–7.5) × 2–3 µm, ovoid-oval, and/or 6–10 × 2–3 µm, ellipsoidal to subcylindrical; in both types mostly biguttulate. Occasionally two-celled conidia also occur, 8–10 × 2–3 µm.

Description in vitro

OA: cultures at room temperature produced only sterile mycelium. The fungus apparently needs special conditions for fructification.

Ecology and distribution. In Europe (Austria, Germany, Italy) and North America (USA) on dead branches, twigs and petioles of various trees and shrubs, especially near river banks. The fungus probably originates from Central Europe. Sometimes the pycnidia contain only the short conidial type, in other specimens conidia are of the longer type. Various collections, however, bear pycnidia with both types, see Boerema & van Kesteren (1981). The pycnidia of *P. pezizoides* superficially resemble the scleroplectenchymatous pycnidia-II of *Phoma lingam* (no. 2; teleomorph *Leptosphaeria maculans*) on dead cabbage stems. This explains the statement in old literature that the latter also occurs on wet, old wood.

Addendum (27–31)

In the literature on cultural studies of species of *Leptosphaeria* sensu lato there are various *Phoma*-like anamorphs, which apparently do not produce scleroplectenchymatous pycnidia and therefore do not fit into the section *Plenodomus*. Some of these *Leptosphaeria* spp., however, do produce scleroplectenchyma in their pseudothecia. Species of *Leptosphaeria* s.l. with only pseudoparenchymatous pseudothecia (commonly occurring on grass-like monocotyledons), are at present placed in a separate genus, *Phaeosphaeria* Miyake, whereas their *Phoma*-like anamorphs have been characterized as '*Aposphaeria*-like' or as 'microconidial forms associated with *Stagonospora*', see e.g. Leuchtmann (1984). We have not yet a definite opinion on the classification of all these pseudoparenchymatous *Phoma*-like anamorphs. Most of them do not have a specific name, but four anamorphs which do, are discussed briefly below (nos 27–30). See Sivanesan (1984) for the characteristics of the other *Phoma*-like anamorphs of *Leptosphaeria* s.l. Finally, a vascular pathogen of *Chrysanthemum* spp. with a *Phialophora*-synanamorph like *P. tracheiphila* (no. 21), but having only 'common' pseudoparenchymatous pycnidia, has been described and documented under no. 31.

27. **Phoma annullata** Pons — Fig. 10A

Teleomorph: *Leptosphaeria sacchari* van Breda (*Phaeosphaeria* cf. Shoemaker & Babcock, 1989).

Phoma annullata Pons, Fitopatol. Venez. 3 (2) (1990) 38–39. — *Phyllosticta saccharicola* P. Hennings, Ann. Mus. Congo Bot. 5 (2) (1907/1908) 100; not *Phoma saccharicola* Ahmad, Biologia, Lahore 6 (2) (1960) 131 [= *Phoma sorghina* (Sacc.) Boerema et al., sect. *Peyronellaea*, described in Contributions II; Boerema, 1993].

Selected literature. Hudson (1960), Pons (1990).

Description in vivo (Saccharum officinale)

Pycnidia (subepidermal within ring spots on leaves, usually solitary), 65–135 µm diam., subglobose-papillate, thin-walled; they often occur in association with the pseudo-

thecia of the fungus. Exudate pale brown. Conidia 9–15 × 2–4 µm, ellipsoidal-subfusoid, provided with 2–several small guttules.

Pseudothecia (also subepidermal in the ring spots) mostly 110–140 µm diam., globose-papillate. Wall pseudoparenchymatous. Asci mostly 60–72 × 9–13 µm. Ascospores 21–25 × 4.5–6 µm, ellipsoidal, 3-septate, second cell from the apex enlarged, each cell with a single large guttule (for detailed description see Hudson, 1960).

Description in vitro

OA: slow-growing white colonies, which soon turn pink to umber with sparse aerial mycelium. Pycnidia may be produced all over the surface, as single or multilocular structures, 180–350 µm diam., i.e. larger than on the host. Conidia similar to those in vivo.

Ecology and distribution. In Africa, Asia and South America well-known as pathogen of sugar-cane leaves: Ring Spot. Usually of little economic importance.

Representative specimens. VIA 5645 (holotype, B), VIA 4866.

28. **Phoma meliloti** Allescher — Fig. 10B

Synanamorph: *Stagonospora meliloti* (Lasch) Petrak.

Teleomorph: *Leptosphaeria weimeri* Shoemaker et al. (formerly confused with *L. pratensis* Sacc. & Briard and *L. viridella* (Peck) Sacc.).

Phoma meliloti Allescher, Ber. bot. Ver. Landshut 12 (1892) 19 [holotype in herb. Allescher (M) showed that conidia were considerably broader than stated in description].

Selected literature. Jones & Weimer (1938), Lucas & Webster (1967), Shoemaker, Babcock & Irwin (1991).

Description in vivo (especially *Melilotus alba*)

Pycnidia (immersed in lesions on stems and leaves, usually solitary) mostly 150–200 µm diam., subglobose with a distinct neck of variable length, usually narrower at the base than at the apex, thin-walled. They may contain conidia of the *Phoma*-type or conidia of the *Stagonospora*-type. *Phoma*-conidia 4–6 × 2–3 µm, oblong-ellipsoidal without guttules; *Stagonospora*-conidia 8–20 × 2.5–3 µm, truncate at the base, tapering to the rounded apex, 1–3-septate, eguttulate.

Pseudothecia (subepidermal on last year's dead stems) mostly 250–350 µm diam., depressed globose with flattened base and conical neck composed of scleroplectenchyma cells. Asci mostly 70–80(–100) × 10–11 µm, 8-spored, overlapping biseriate. Ascospores 20–24 × 5–6 µm, fusoid, 3-septate, second cell from the apex enlarged, with or without small guttules (for detailed description see Shoemaker, Babcock & Irwin, 1991).

Description in vitro

OA: rapidly growing, producing a dark green mycelium with patches of white and orange aerial hyphae; reverse dark green with orange margin. Pycnidia were found within 3 months, usually as composed structures, more or less globose or irregular in shape; incidentally conidia of both types were produced in the same pycnidium.

Ecology and distribution. In Australia, Europe and North America on various Leguminosae, e.g. *Medicago, Melilotus, Trifolium* and *Ulex* spp. Causes Leaf Spot, Stem

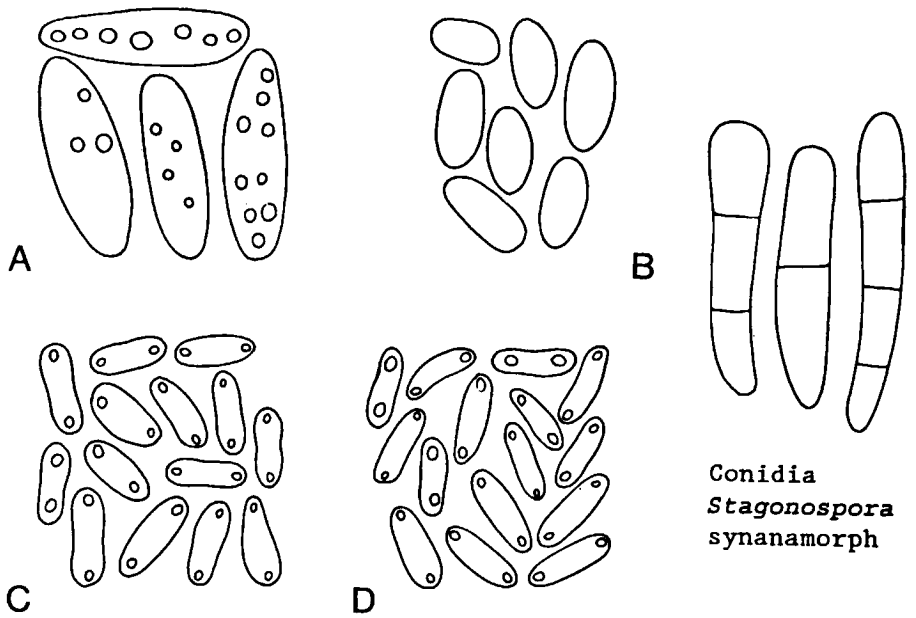

Fig. 10. Conidia of four species treated in the Addendum. — A. *Phoma annullata*. — B. *P. meliloti* and *Stagonospora*-synanamorph. — C. *P. rostrupii*. — D. *P. sanguinolenta*. — Bar = 10 µm.

Canker and Root Rot of forage legumes. Low temperatures (± 8°C) induce the development of the *Phoma*-anamorph, higher temperatures the *Stagonospora*-anamorph.

Representative dried culture. SHEFF 2050.

29. **Phoma rostrupii** Sacc. — Fig. 10C

Teleomorph: *Leptosphaeria libanotis* (Fuckel) Niessl [also quoted as '*libanotidis*' and as '(Fuckel) Sacc.'].

Phoma rostrupii Saccardo, Sylloge Fung. 11 (1895) 490. — *Phoma sanguinolenta* Rostrup, Tidsskr. Landøkon. 5 (7) (1888) 384; not *Phoma sanguinolenta* Grove, J. Bot., Lond. 23 (1885) 162 [see no. 30 below].

Selected literature. Grove (1935), Lucas & Webster (1967), CMI (1968: 611, 668), Sivanesan (1984).

Description in vivo (especially *Daucus carota*)

Pycnidia (on stems and inflorescences, lesions on roots; usually densely grouped), subglobose apparently always thin-walled, exudate bright-red. Conidia (4–)5–6(–6.5) × 1.5–2.5 µm, oblong ellipsoidal or dumbbell-shaped, biguttulate.

Pseudothecia (on dead stems) mostly 360–415 µm diam., globose or conical globose with flattened base. Wall scleroplectenchymatous. Asci 100–125 × 8–10(–11) µm, 8-spored, uniseriate. Ascospores mostly 18–20 × 5.5–7 µm, ellipsoidal, 3-septate, second cell from the apex enlarged, eguttulate (for detailed description see Holm, 1957).

Description in vitro

OA: rapidly growing, forming an olive-green mycelial mat with copious yellowish cream surface hyphae; reverse dark yellow to brown. Usually abundant production of thin-walled pycnidia up to 320 µm diam., subglobose or depressed globose. Conidia similar to those in vivo.

Ecology and distribution. In Europe the teleomorph has been recorded on stems and roots of various Umbelliferae, especially *Angelica sylvestris.* In northern Europe *P. rostrupii* was known in the past as a serious pathogen of carrots: *Phoma* Root Rot, Carrot Phomosis, Dieback of seedlings.

Representative dried cultures. SHEFF 2009, SHEFF 2163.

Note. The teleomorph *L. libanotis* is a characteristic representative of the scleroplectenchymatous 'Group *doliolum*' of the genus *Leptosphaeria.* However, so far only thin-walled pseudoparenchymatous pycnidia of *P. rostrupii* are known. It should also be noted that recent East European records of *P. rostrupii* on carrots refer to two entirely different species of *Phoma,* viz. *P. exigua* Desm. var. *exigua* [sect. *Phyllostictoides,* see van der Aa et al. (1990)] and *P. complanata* (Tode: Fr.) Desm. [sect. *Sclerophomella,* see de Gruyter & Noordeloos (1992: 89)].

30. **Phoma sanguinolenta** Grove — Fig. 10D

Teleomorph: *Leptosphaeria purpurea* Rehm.

Phoma sanguinolenta Grove, J. Bot., Lond. 23 (1885) 162; not *Phoma sanguinolenta* Rostrup, Tidsskr. Landøkon. 5 (7) (1888) 384 [≡ *Phoma rostrupii* Sacc., see no. 29 above].

Phoma rubella Grove, J. Bot., Lond. 23 (1885 [June]) 162; not *Phoma rubella* Cooke, Grevillea 14 (1885 [Sept.]) 3 [≡ *Phoma porphyrogona* Cooke]. — *Phoma grovei* Berlese & Voglino, Sylloge Fung. 10 (1892) 168 [superfluous new name]. [*P. rubella* and *P. sanguinolenta* were simultaneously published by Grove; when these two taxa are united, the resulting species must be called *P. sanguinolenta,* because that name was chosen by Lucas & Webster (1967), see Art. 57.2.]

Selected literature. Grove (1935), Lucas & Webster (1967), Sivanesan (1984).

Description in vivo (especially *Cirsium* spp.)

Pycnidia (at the base of rotting stems, loosely gregarious) 280–400 µm diam., subglobose-papillate, thin-walled, surrounded by purplish hyphae. Conidia 4–5.5 × 1.5–2.5 µm, oblong-ellipsoidal, biguttulate.

Pseudothecia (subepidermal on dead stems) mostly 250–350 µm diam., globose to depressed globose with flattened base and truncate-conical neck composed of red polygonal cells. Wall ascocarp scleroplectenchymatous. Asci 55–95 × 8–11 µm, 8-spored, overlapping biseriate to tetraseriate. Ascospores (22–)27–31(–35) × 4.5–5.5 µm, narrowly fusiform, 3-septate, central cells slightly shorter than end cells, distinctly guttulate (for recent detailed description see Shoemaker, 1984).

Description in vitro

OA: rapidly growing; producing a pale olive-green mycelial mat with patches of whitish aerial hyphae, reverse with a purple discolouration of the agar. Pycnidia discovered in culture resembling those in vivo, thin-walled 280–400 µm diam., depressed globose. Conidia similar to those in vivo.

Ecology and distribution. Common in Europe and North America (Canada) in reddened or purple coloured patches on dead stems of various composites. Occasionally recorded on other families.

Representative dried cultures. SHEFF 1928, SHEFF 1929.

31. **Phoma vasinfecta** Boerema, de Gruyter & van Kesteren *spec. nov.*

Hyphomycetous-anamorph: *Phialophora* sp.

Diagnosis coloniae in agaro PDA dicto cultae traducta e Robertson (1967): Pycnidia superficialia, 53–162 µm diam., subglobosa, saepe modice rostrata, operculo late evoluto, tenuitunicata, cellulae exteriores fuscae et fere magnae. Conidia bacilliformia vel modice curvata, 1.95–3.25 × 0.65–1.3 µm. Conidia paulo maiora, 1.95–5.2 × 0.65–2.6 µm, ex hyphis vegetativis ipsis oriunda, cellulis conidiogenis 7.2–28.6 × 1.8–3.6 µm. Holotypus exsiccatus IMI 128761, isolatus e fasciculis vascularibus discoloratis in caule floriali pyrethri, *Chrysanthemi coccinei*, Chatteris, Cambridgeshire in Anglia.

Phoma tracheiphila f. sp. *chrysanthemi* Baker, Davis, Wilhelm & W.C. Snyder, Can. J. Bot. 63 (1985) 1733.

Description in vivo (esp. *Chrysanthemum morifolium*)

Pycnidia (subepidermal in linear rows on stem bases, sometimes in cankers and on leaf scars) mostly 75–150 µm, light brown to black, solitary, rarely in groups, subglobose-obpyriform or irregular, usually with a short neck (up to 40 µm). Wall consists of a rind of large black thick-walled cells enclosing several layers of hyaline cells. Conidiogenous cells globose or bottle-shaped. Exudate milky cream. Conidia oblong, straight or curved, mostly 2.5–4 × 1–1.5 µm.

Description in vitro

Growth-rate rather variable, depending on strain and agar medium (on PDA c. 25–35 mm), sparse yellow-green aerial mycelium, colony margin irregular and whitish, compact, pigmentation variable depending on strain, whitish pink becoming reddish brown grey, or greenish grey becoming dark grey green to black; reverse also variable in colours, ranging from distinctly pink or purple-reddish brown to dark greenish grey or almost black. On application of a drop of NaOH the reddish diffusible pigments turn blue. Pycnidia produced sparsely, superficially on the agar, similar to those in vivo, with a late developing opening (pore) at the top of the short neck. Conidia usually somewhat smaller than those in vivo (see Latin description).

Hyphal conidia arising from free conidiogenous cells on the aerial mycelium (representing the *Phialophora*-anamorph) are variable in size, mostly 2–5.5 × 1–2(–2.5) µm.

Ecology and distribution. The present concept of this pathogen of the vascular system of *Chrysanthemum* spp. (Slow Wilt, Phoma Decline Disease) includes records from Europe, North America and Australia. Baker et al. (1985) treated it merely as a specialized pathogenic form of *Phoma tracheiphila* (no. 21), the cause of 'Mal Secco Disease' of citrus trees in the Mediterranean and Black Sea areas. However, there are sufficient reasons for differentiating both pathogens at the species level. Apart from their quite different hosts and ecology, there are also obvious differences in pycnidial morphology. The pycnidia of *P. vasinfecta* are only slightly beaked and do not consist of scleroplectenchyma. The pycnidial conidia in vivo are usually larger than those of the citrus pathogen.

The *Phialophora*-synanamorph of *P. vasinfecta* is indistinguishable from *Phialophora chrysanthemi* (Zachos et al.) W. Gams. The latter hyphomycete may be considered to be a synanamorph of *P. vasinfecta,* but can also exist separately and independently [compare the analogue of *Epicoccum nigrum* L. and *Phoma epicoccina* Punith. et al., discussed in Contributions II, Boerema, 1993].

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