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## KEY TO NINE UBIQUITOUS SOIL-BORNE PHOMA-LIKE FUNGI

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(With six Plates)

The differentiating characteristics on agar-media, of *Pyrenochaeta acicola*, *Phoma chrysanthemicola*, *P. eupyrena*, *P. fimeti*, *P. glomerata*, *P. herbarum*, *P. medicaginis* var. *pinodella*, and *P. prunicola* are discussed and illustrated. In a supplementary note the nomenclature of *Pyrenochaeta acicola*, *Phoma chrysanthemicola*, *P. eupyrena*, and *P. fimeti* is recorded.

In the course of time various *Phoma*-like fungi have been received which had more or less frequently been isolated from soil in Germany and the Netherlands. Several of these isolates proved to be identical with species regularly isolated in our mycological diagnostic work on diseased and dying-off plants. In this paper the diagnostic characters of nine of these ubiquitous *Phoma*-like fungi—generally necrotrophic or perthotrophic—are compared and tabulated to provide a usable identification method for them.

It should be realized that *Phoma*-like fungi of this kind cannot be differentiated and identified in culture by a few special characteristics only since none of the morphological and physiological characters is truly specific. For example a typical feature of the common saprophyte *Phoma herbarum* Westend. is produced by a reddish pigment, the colour changing to blue when NaOH is added, but the same kind of pigment occurs in various other *Phoma* species. In many species the spore dimensions, although an important differential character, are about the same size. Some of the typical features appear to be unstable while others become evident only after a long period of growth. Furthermore the conditions of growth on the agar-media greatly influence the morphological and physiological characters of the fungi.

From the above it may be gathered that Table 1, far from being a definitive key, is merely a comparative survey. This table is only usable by applying the same methods we employed, and by consulting the additional notes on the species listed. These notes include references to the literature, which gives detailed morphological descriptions, generally together with discussions on the nomenclature. The nomenclature of four species, *Pyrenochaeta acicola*, *Phoma chrysanthemicola*, *P. eupyrena*, and *P. fimeti* is treated in a supplementary note at the end of this paper.

### Methods

The fungi are compared in plate cultures on oatmeal-agar (abbreviated OA) and malt-agar (MA), prepared after the formulae given by Ainsworth (1961: 241, 242). OA is used because it stimulates the production of pycnidia and pycnidiospores; MA stimulates the mycelial growth, the production of chlamydospores, and crystal-formation.

The plates are inoculated in the centre by a punched-out piece of agar with pycnidia and placed in a dark incubator at 20–22° C for one week. The diameter of the colonies is subsequently measured and the cultures are exposed (not uncovered) to artificial daylight in order to stimulate sporulation and possibly pigment-production. It should be noted that the pigment may take a few days to several weeks to form, depending on the species and, more particularly, the strain involved. The development of dictyochlamydospores often takes quite some time as well. The best impression of the general habitus can be obtained at an early stage of growth. At that time the character of the margin of the colony is clearly determinable and the colours of the mycelium are fresh and differentiated into delicate shades.

The spore dimensions given are always taken from colonies on OA; on MA the spores are usually swollen (and therefore broader) and more guttulate.

A useful diagnostic test is the addition of a drop of concentrated alkali, e.g. NaOH-N. In *Phoma exigua* this causes the oxidation of a metabolite 'E', resulting in the successive production of characteristic bluish-green and red pigments (see Boerema & Höweler, 1967). Although the other species remain unaltered, it may be pointed out that a similar oxidation-reaction is known to occur in *Phoma*-like fungi not discussed in the present paper. The bluish-green discoloration after the addition of a drop of NaOH usually occurs within a few minutes, but it may take longer. The production of metabolite 'E' is stimulated by light, so that the NaOH-test is best examined after the plates have been exposed to daylight for several days. In order to examine whether the pigment changes colour in alkaline condition or not, a drop of NaOH-N is also added to cultures of species which produce pigment naturally; see under *Phoma chrysanthemicola*, *P. fimeti*, and *P. herbarum*.

### Discussion of the species

*Pyrenochaeta acicola* (Lév.) Sacc. in *Sylloge Fung.* 3: 220. 1884.—See remarks on nomenclature at the end of this paper. — Pl. 3 figs. 1, 2; Pl. 5 figs. 3, 4. Cultural description.—Gams & Domsch in *Nova Hedwigia* 18: 17. 1969.

The colonies of *P. acicola* are grey to dull 'Cladosporium-green' in appearance. Some strains show a lilac-rose discoloration of the medium below and around the colony. This discoloration may be quite conspicuous, but as it occurs only occasionally it is not mentioned in the table. The lilac-rose pigment does not change colour on application of NaOH.

A characteristic feature is the occurrence of setae on the pycnidia (Pl. 5 figs. 3, 4).

These vary from few to many, from stiff to rather hypha-like, and from short to relatively long.

Some strains produce broad spores with many guttules; other strains have narrow spores, usually with two guttules (see Table 1).

This common soil-fungus (compare Gams & Domsch, 1969a) has also been found on, and isolated from, leaves and seedlings of *Pinus* species, wood of *Ribes* and *Populus* species, and stem bases of *Callistephus* and *Campanula* species. It appears to be capable of destroying wood (Haider & Domsch, 1969: 341).

*Phoma chrysanthemicola* Hollós in *Annl. hist.-nat. Mus. natn. hung.* 5: 456. 1907.—See nomenclatural remarks at the end of this paper. — Pl. 1 fig. 1; Pl. 3 figs. 3, 4; Pl. 6 figs. 1, 2.

Cultural descriptions and illustrations.—Kemp in *Can. J. Pl. Sci.* 38: 469, figs. 1D (pycnidia), 2A (growth rate of colonies). 1958; Hawkins, Wiggell & Wilcox in *Pl. Path.* 12: 21, pl. 1 (pycnidia). 1963.

The colonies of *P. chrysanthemicola* are evenly pale to dark grey, but in other respects they may vary a great deal. Some isolates produce abundant aerial mycelia which are dense or loose, while in others the mycelia are much less conspicuous. Most isolates grow rather slowly.

The characteristic orange-red discoloration of the agar-media (Pl. 1 fig. 1) appears in closed or interrupted concentric zones. Addition of NaOH causes the red colour to fade. Incidentally the medium may show locally a yellow discoloration.

An important diagnostic character is the occurrence of dark brown to black structures that look like pseudosclerotial masses and consist of chlamydospores (Pl. 6 figs. 1, 2 and Table 1). These structures, very irregular in shape and size, may be present in abundance in the aerial mycelium. Unfortunately, however, they are not produced by all strains (see also the remarks on nomenclature at the end of this paper).

The pycnidia of the present fungus sometimes fuse to form large irregular fructifications with many ostioles.


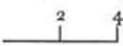







This fungus is repeatedly isolated from soil and is well known as the causal organism of a root-rot of florists' chrysanthemums (epidemiology recently studied by Peeraly & Colhoun, 1969; see also the remarks on nomenclature at the end of this paper). In the Netherlands the fungus has also been isolated from *Chrysanthemum leucanthemum*, *Achillea millefolium*, and other wild plants, which makes its isolation from soil comprehensible. The fungus appears to be capable of destroying wood (Haider & Domsch, 1969: 341).

*Phoma eupyrena* Sacc. in *Michelia* 1 (5): 525. 1879.—See nomenclatural remarks at the end of this paper. — Pl. 4 figs. 1, 2; Pl. 6. fig. 3.

Cultural descriptions and illustrations.—Dennis in *Trans. Br. mycol. Soc.* 29: 30, 31 ('Group VII'), pl. 2 fig. 1 (culture on MA). 1946; Kranz in *Sydowia* 16: 15, 16. 1963.

The colonies of *P. eupyrena* are characterized by a dense mycelial growth, which is dark green at first but soon turns black.

A useful specific character is the production of typical small chlamydospores,

	Macroscopic characters		
	Metabolites	Special growth features	Diameter of colony in cm after culture in the dark at 20–22° C for one week on MA and OA (— = variation)
<i>Pyrenochaeta acicola</i>		Setae on pycnidia (Pl. 5 figs. 3, 4)	
<i>Phoma chrysanthemicola</i>	Orange-red pigment: production stimulated by daylight (Pl. 1 fig. 1)		
<i>Phoma eupyrena</i>			
<i>Phoma exigua</i>	Substance 'E' (see Boerema & Höweler, 1967): demonstrable by addition of NaOH: bluish-green pigment → red pigment (Pl. 1 fig. 2)	Margin of colony irregularly scalloped or lobed (Pl. 4 figs 3, 4)	
<i>Phoma fimeti</i>	Yellow pigment on OA (Pl. 1 fig. 3)		
<i>Phoma glomerata</i>			
<i>Phoma herbarum</i>	Red pigment: production stimulated by daylight: with addition of NaOH staining violet-blue (Pl. 1 figs. 4, 5)		
<i>Phoma medicaginis</i> var. <i>pinodella</i>	Production of crystals on MA (Pl. 5 figs. 1, 2)		
<i>Phoma prunicola</i>			

1. A diagram of a 2-celled spore indicates the frequent occurrence of 1- (or pluri-) septate spores. In the other species septate spores may occur, but only incidentally.

## Microscopic characters

Shape and structures of spores and relative size-ratio ( $\epsilon. \times 1250$ ) on OA	Dimensions of 1-celled spores on OA	Shape and structure of chlamydo spores ( $\epsilon. \times 250$ )
	$3-7 \times 1-3 \mu$	
	$3.5-6.5 \times 1.5-2.5 \mu$	 (see Pl. 6 figs. 1, 2)
	$3.5-6 \times 1.5-3 \mu$	 (see Pl. 6 fig. 3)
	$3.5-10 \times 2-3.5 \mu$	
	$2.5-5 \times 1.5-3 \mu$	
	$4-8.5 \times 2-3.5 \mu$	 (see Pl. 6 fig. 5)
	$3.5-8 \times 1.5-3 \mu$	
	$4-9 \times 2-4 \mu$	 (see Pl. 6 fig. 4)
	$4-8 \times 2-3.5 \mu$	 (see Pl. 6 fig. 6)

2. Unusually small and large spore dimensions have not been taken into account.



originating singly or in chains (Pl. 6 fig. 3 and Table 1). These chlamydo-spores are usually present in abundance, but their production may take more than a week. In many aspects they resemble those of *Verticillium nigrescens*, also a soil-borne fungus.

This species proves to be one of the most common soil-inhabiting members of the genus *Phoma* (compare Gams & Domsch, 1967: 140; Domsch & al., 1968: 141; and Gams & Domsch, 1969b). It is known especially as a secondary un-harmful organism on potato tubers (Malcolmson, 1958; Boerema & van Kesteren, 1962), but it has also been repeatedly isolated from the underground parts of all kinds of other plants.

*Phoma exigua* Desm. in *Annls Sci. nat. (Bot.)* III, **11**: 282, 283. 1849.—Pl. 1 fig. 2; Pl. 4 figs. 3, 4.

Synonyms: *Phoma solanicola* Prill. & Delacr., *Phyllosticta decidua* Ell. & Kell.; for further synonyms, see Boerema & Höweler (1967) and Boerema (1970).

Cultural descriptions and illustrations.—Dennis in *Trans. Br. mycol. Soc.* **29**: 21–26 ('Group II'), table 3 (range of spore dimensions), pl. 1 figs. 4–6 (cultures on MA). 1946; Boerema & Höweler in *Persoonia* **5**: 15–25, table 1 (diagnostic criteria), figs. 1–4 (shape and size of pycnidia and spores), pl. 3 figs. 1–4 (cultures on MA and cherry-agar), pl. 4 figs. 1–7 (colour plate of characteristic oxidation-reaction). 1967.

A characteristic feature of the colonies of *P. exigua* is the irregularly scalloped or lobed margin, see Pl. 4 figs. 3, 4. This feature, however, is not always seen as clearly as it appears in these photographs. The colonies are extremely variable as to habitus and growth rate. Generally they are flat and dense, white to black, with various greenish and grey tinges. Light coloured colonies often grow fast, producing abundant pycnidia. Predominantly dark colonies usually grow relatively slowly, producing much aerial mycelium and barely sporulating pycnidia. Whitish or greyish aerial mycelium often occurs locally in loose tufts, consisting mostly of broadly swollen hyphae.

A workable diagnostic criterium is the bluish-green discoloration of the agar-media on application of a drop of NaOH (oxidation-reaction of metabolite 'E', see under 'Methods'). This blue-green colour (pigment  $\alpha$ ) gradually passes into brown-red (pigment  $\beta$ ), see Pl. 1 fig. 2. Some strains show a very conspicuous blue-green spot when treated with a drop of NaOH, while others show only a pale green ring.

This soil-borne fungus is the most frequent *Phoma* species on herbaceous plants (see Boerema & Höweler, 1967). As a weak or wound parasite it has often been associated with such distinct disease symptoms as leafspots, fruitspots, lesions on stems and roots, damping-off, and dieback. It has further been shown to have an inhibitory effect on the root development of some plants (see Domsch & Gams, 1968a: 67).

*Phoma fimeti* Brun. in *Bull. Soc. bot. Fr.* **36** (=II, **11**): 338. 1889.—See remarks on nomenclature at the end of this paper. — Pl. 1 fig. 3; Pl. 2 figs. 1, 2; Pl. 5 figs. 5, 6.

Cultural characters.—Not described previously.

Colonies of *P. fimeti* show a loose vividly green mycelial growth on OA; on MA the growth is denser and the colour ashen. All the isolates tested prove to be very uniform in habitus.

A specific character is the yellow discoloration of the OA-medium (Pl. 1 fig. 3), occurring in dark as well as in daylight cultures. All the isolates tested showed the presence of this pigment. In several colonies it takes some time to appear, often more than a week, but in the end it is always very conspicuous. The yellow colour does not change on application of a drop of NaOH.

The pycnidia always possess conspicuous circular ostioles, see Pl. 5 figs. 5, 6.

This soil-fungus, originally described from dung of sheep, has also been isolated from paint, wood, and dead tissue of various plant species.

*Phoma glomerata* (Corda) Wollenw. & Hochapf. in Z. ParasitKde 8: 592. 1936.—Pl. 2 figs. 5, 6; Pl. 6 fig. 5.

Synonyms: *Peyronellaea glomerata* (Corda) Goid. ex Togl., *Phoma alternariaceum* Brooks & Searle, *Phoma fumaginoides* Peyron., *Phoma saprophytica* Eveleigh; for further synonyms, see Boerema & al. (1965, 1968).

Cultural descriptions and illustrations.—Boerema, Dorenbosch & van Kesteren in Persoonia 4: 52–59, fig. 2 (pycnidiospores and dictyochlamydospores), pls. 1 (dictyochlamydospores), 2 (cultures on OA and cherry agar). 1965; Morgan-Jones in C.M.I. Descr. path. Fungi Bact. No. 134 (pycnidia, pycnidiospores, dictyochlamydospores, mycelium). 1967.

The colonies of *P. glomerata* are generally characterized by the production of abundant pycnidia and little aerial mycelium (which causes it to resemble *Phoma herbarum*, see below); however, sectors with dense woolly mycelia may also occur. The colours of the colony vary from dull dark yellow-green to various shades of grey. On application of NaOH the medium discolours to tea-brown and even more so on MA.

The typical character of this species is the occurrence of *Alternaria*-like chains of dictyochlamydospores (see Pl. 6 fig. 5 and Table 1), but these often occur only after a long period of growth. Old colonies may look black on account of the development of these dictyochlamydospores in the aerial mycelia.

This fungus is one of the few *Phoma*-species mentioned by name in studies on soil-fungi; this should be ascribed to its typical diagnostic features (dictyochlamydospores) rather than to the frequency of its occurrence in soil. The fungus is ubiquitous on a wide variety of substrates and has been found in association with dead diseased material of all kinds of plants as well as with a number of mycotic diseases of man (Boerema & al., 1965). Usually it is a secondary invader.

*Phoma herbarum* Westend. in Bull. Acad. r. Belg. Cl. Sci. 19 (3): 118. 1852.—Pl. 1 figs. 4, 5; Pl. 2 figs. 3, 4.

Synonyms: *Phoma oleracea* Sacc., *Phoma pigmentivora* Masee, *Phoma hibernica* Grimes & al., *Phoma violacea* (Bertel) Eveleigh; for further synonyms, see Boerema (1964, 1970).

Cultural descriptions and illustrations.—Dennis in Trans. Br. mycol. Soc. 29: 33–35 ('Group X'), pl. 2, figs. 3, 10 (cultures on MA). 1946; Eveleigh in Trans. Br. mycol. Soc. 44: 578–582. 1961; Boerema in Persoonia 3: 9–16, pl. 1 figs. 5–6

(cultures on MA and Ashby-agar), pl. 2 figs. 1-6 (pycnidial primordia, pycnidiospores). 1964.

The colonies of *P. herbarum* are generally characterized by the production of abundant pycnidia and sparse mycelia (pycnidial-type), see Pl. 1 fig. 5; however, strains which produce more aerial mycelium also occur, usually in sectors (mycelial-type), see Pl. 1 fig. 4. Strains of the pycnidial-type may be mistaken for *Phoma glomerata* (see above), but *P. herbarum* never produces (dictyo-)chlamydo-spores. The colours of the colonies vary between grey and green. A notable feature of the numerous isolates tested is the uniform rate of growth.

A typical character is the production of a reddish pigment (Pl. 1 figs. 4, 5). Of the numerous isolates tested, only two failed to produce any pigment. It is especially strains of the mycelium-type that are inclined to be strongly pigmented so that application of NaOH makes the change from red to blue very conspicuous. In very old colonies the red pigment changes from red to blue by itself. The addition of NaOH has no effect on uncoloured isolates.

The fungus is a ubiquitous typically saprophytic organism, occurring on a very wide variety of industrial products like butter, paint, cement, rubber, etc. (see Boerema, 1964). In many studies on soil-fungi it is reported as a typical soil-borne *Phoma* species, usually under the name *P. hibernica*. Its frequent occurrence on dead seed coats has led to confusion with seed-borne pathogens.

*Phoma medicaginis* Malbr. & Roum. var. *pinodella* (L. K. Jones) Boerema *apud* Boerema, Dorenbosch & Leffring in Neth. J. Pl. Path. 71: 88. 1965.—Pl. 4 figs. 5, 6; Pl. 5 figs. 1, 2; Pl. 6 fig. 4.

Synonyms: *Ascochyta pinodella* L. K. Jones, *Phoma trifolii* E. M. Johnson & Valleau. Cultural descriptions and illustrations.—L. K. Jones in Bull. N.Y. St. agric. Exp. Stn 547: table 2 (range of spore dimensions), pl. 1 (colour plate of culture on OA). 1927; Wehlburg, Onderz. Erwtentanthracose (Thesis, Baarn) 12, fig. 2a (shape and size of pycnidia and spores), pl. 3 (culture on OA). 1932; Boerema, Dorenbosch & Leffring in Neth. J. Pl. Path. 71: 83, fig. 2 (cultures on cherry-agar, crystals). 1965.

The colonies of *P. medicaginis* var. *pinodella* are flat, with mycelial colours varying from light grey to black. Pycnidia usually develop in radial rows, but they may also be found scattered throughout the colony.

A characteristic feature is the occurrence of crystals on MA, see Pl. 5 figs. 1, 2; the production of these varies according to the different strains; the crystals are often found only after some weeks of growth. In isolates with abundant crystal production they occur not only on MA, but also on OA.

A typical and stable character is the production of chlamydo-spores, see Pl. 6 fig. 4. These are usually found in abundance in the dark sectors of the colony after one week of growth.

The fungus is seed- and soil-borne and well known as a weak parasite of pea (footrot and leafspots) and red clover (black stem), see Boerema & *al.* (1965b). Further it often occurs on other Leguminosae, and has been isolated from the plants of other families as well. It has been shown to have a specific inhibitory action on *Pythium ultimum* (Domsch & Gams, 1968b: 170).

*Phoma prunicola* (Opiz) Wollenw. & Hochapf. in Z. ParasitKde 8: 595. 1936.—Pl. 3 figs. 5, 6; Pl. 6 fig. 6.

Synonyms: *Peyronellaea prunicola* (Opiz) Goid., *Phyllosticta pyrina* Sacc., *Peyronellaea nicotiae* Leduc; for further synonyms, see Boerema & al. (1965a, 1968).

Cultural descriptions and illustrations.—Boerema & Dorenbosch in Versl. Meded. plziektenk. Dienst 142 (Jaarb. 1964): 144–148, fig. 7 (pycnidia, pycnidiospores, chlamydospores, and dictyochlamydospores), fig. 8 (cultures on OA). 1965; Boerema, Dorenbosch & van Kesteren in Persoonia 4: 59–63, fig. 3 (pycnidia, pycnidiospores, chlamydospores and dictyochlamydospores), pl. 3 (chlamydospores, dictyochlamydospores, and cultures on OA and cherry-agar). 1965; Morgan-Jones in C.M.I. Descr. path. Fungi Bact. No. 135 (pycnidia, pycnidiospores, chlamydospores, dictyochlamydospores, mycelium). 1967.

The colonies of *P. prunicola* are generally characterized by the occurrence of different sectors, some with an abundance of pycnidia, others with much aerial mycelium. The colours of the colonies vary from green, white, and grey to black.

A typical and stable character is the production of single chlamydospores, usually produced in chains. They are initially light brown and darken gradually. Dictyochlamydospores are not always produced but they are usually present in fresh isolates. They generally arise as separate terminal spores on mycelial branches, more or less *Stemphylium*-like in shape. Sometimes they also occur in chains together with single chlamydospores.

This soil-borne fungus has been found on all kinds of dead and diseased plant material (Boerema & al., 1965a, 1968) and is known especially in association with leafspots on apple (Boerema & Dorenbosch, 1965), pear and species of *Prunus*. It is considered to be a secondary invader.

### Remarks on nomenclature

*Pyrenochaeta acicola* (Lév.) Sacc. in Sylloge Fung. 3: 220. 1884. — *Vermicularia acicola* Lév. in Annls Sci. nat. (Bot.) III, 9: 259. 1848. — Neotype: dried culture of CBS 260.65 (det. G. L. Hennebert), isolate ('C124') from soil (wheat field) made by W. Gams, Kiel-Kitzeberg, Aug. 1962 (compare Gams & Domsch, 1969a: 17); herbarium 'Centraalbureau voor Schimmelcultures', Baarn (CBS).

Synonym: *Pyrenochaeta spinaciae* Verona & Negru in Mycopath. Mycol. appl. 30: 310. 1966. — Type: Herb. Negru (CL).

The type material of *Pyrenochaeta acicola* described from fallen needles of *Pinus silvestris* in the Vosges does not appear to have been preserved. Its identity with the fungus treated in this paper is in accordance with the interpretation of *P. acicola* as given by Gams & Domsch (1969a: 17), and is based on comparison with an old living specimen named *P. acicola* in the culture collection of the 'Centraalbureau voor Schimmelcultures', CBS 260.38. The latter was isolated by ten Houten (1939: 28) from Dutch seedlings of *Pinus nigra* var. *austriaca* and morphologically agrees very well with the original, albeit vague, description of *Pyrenochaeta* (*Vermicularia*) *acicola*. In order to consolidate this concept a dried culture of a fresh isolate

of the fungus, showing all its typical characteristics, is here formally designated as neotype.

Because of the characteristic setae this *Phoma*-like fungus is maintained in the form-genus *Pyrenochaeta*. In my opinion, however, the status of *Pyrenochaeta* with respect to *Phoma* is still dubious. The spore-forming process in many species of *Pyrenochaeta*, including *P. acicola*, is in complete agreement with that in *Phoma*, even though it is true that several species sometimes show branched conidiophores. In any case the occurrence of setae is not a stable criterion, since various *Phoma*-like fungi occasionally produce setose pycnidia.

Finally it should be noted that an isolate made from original herbarium material of *Pyrenochaeta spinaciae* (seeds of spinach obtained from Prof. A. Negru) proved to be indistinguishable from *P. acicola* as interpreted in this paper.

*Phoma chrysanthemicola* Hollós in Annl. hist.-nat. Mus. natn. hung. 5: 456. 1907. — Neotype: dried culture of CBS 522.66, isolate ('1315') from stem of *Chrysanthemum morifolium* made by H. J. Wilcox, Nat. Agric. Advis. Service Kent, 1963 (compare Hawkins & al., 1963); herbarium 'Centraalbureau voor Schimmelcultures', Baarn (CBS).

*Phoma chrysanthemicola* was described from decorticated dry stems of cultivated *Chrysanthemum indicum* (= *C. morifolium*) at Kecskemét in Hungary. The original material appears to have been destroyed during the Second World War (information Museum of Natural History, Budapest). In our opinion, however, there is no doubt but that the characteristics as described for the pycnidia and pycnidiospores of *P. chrysanthemicola* justify the use of this name for the soil-borne fungus commonly occurring in association with the root- and stem-rot of florists' chrysanthemums (see Kemp, 1958; Hawkins & al., 1963; and Peerally & Colhoun, 1969). This interpretation also conforms with Srivastava's concept (1953); he examined the fungus in India on several varieties of chrysanthemum seedlings imported from the Netherlands.

It should be remarked that Kemp (l.c.), Hawkins & al. (l.c.), and Peerally & Colhoun (l.c.), in their extensive studies on the root- and stemrot disease of chrysanthemums, hesitated about adopting the name *P. chrysanthemicola*, since on the preserved plant material with *P. chrysanthemicola* studied by Srivastava (l.c.), Kemp (l.c.) failed to find the characteristic pseudosclerotial masses (see Table 1 and Pl. 6 figs. 1, 2). Our comparative study of numerous isolates of the fungus, however, revealed that some strains do and others do not produce these pseudosclerotial masses. Moreover in our opinion it is difficult to establish the occurrence of these masses in vitro. Since, furthermore Srivastava's fungus occurred on plant material from the Netherlands we are sure that Srivastava as well as Kemp, Hawkins & al., and Peerally & Colhoun were dealing with the same fungus, agreeing with *P. chrysanthemicola*. To fix the species, a typical dried culture of the fungus (with pseudosclerotial masses) is selected as neotype.

*Phoma eupyrena* Sacc. in *Michelia* 1 (5): 525, 1879; in *Sylloge Fung.* 3: 127, 1884. — Holotype: on stems of *Solanum tuberosum*, coll. by P. Brunaud, near Saintes (Charente-Inférieure), no date; Herb. Saccardo '39' (PAD).

In the literature dealing with species of *Phoma* in association with potatoes the name *Phoma eupyrena* is generally used with the emendation 'as interpreted by Wollenweber' or 'sensu Wollenweber', see Dennis (1946), Malcolmson (1958), Boerema & van Kesteren (1962), and Kranz (1963). This means that the authors did not answer the question as to whether the typical, chlamydospores-producing *Phoma* isolated by Wollenweber (1920) from potato tubers (spore dimensions usually  $3.4-5.1 \times 1.7-2.6 \mu$ ) is really identical with Saccardo's fungus (spore dimensions given as  $4 \times 1.5 \mu$ ). Malcolmson's (1958) doubts about this were even strengthened by the absence of any chlamydospores in a specimen on *Solanum dulcamara* in Saccardo's herbarium (PAD). However this specimen, labelled "*P. eupyrena* f. *dulcamaræ*" and collected in 1889 by C. E. Fairman in the U. S. A., does not represent the type. It is indeed quite different from the chlamydospores-producing *Phoma*, but it agrees in every detail with a fungus isolated by Kranz (1963: 14, 15) from dried material of *Solanum dulcamara* (spores  $4.7-6.3 \times 1.7-2.6 \mu$ , 1-celled, 1%–3% being 2-celled).

The holotype of *P. eupyrena* Sacc. is still in existence, and its characteristics accord very well with Wollenweber's interpretation. It possesses only 1-celled spores,  $3.4-5.1 \times 1.7-2.6 \mu$ , while chlamydospores also occur in association with the pycnidia! Therefore since Wollenweber's interpretation of *P. eupyrena* is in agreement with Saccardo's type the indication 'sensu Wollenweber' is superfluous.

*Phoma fimeti* Brun. in *Bull. Soc. bot. Fr.* 36 (= II, 11): 338, 1889. — Neotype: dried culture of CBS 170.70, isolate from soil (glasshouse) made by M. A. de Waard, Zwijndrecht, Dec. 1966; herbarium 'Centraalbureau voor Schimmelcultures', Baarn (CBS).

This fungus was originally described from dung of sheep at Fouras near Saintes in France, but the original material was not preserved. The description of the characteristics of pycnidia and pycnidiospores fully agrees with that of the soil-borne fungus treated in this paper under the name *P. fimeti*; it is well known that most coprophilous fungi commonly occur in soil. None of the other 'old' *Phoma* species described show so much similarity with the fungus treated in this paper.

To consolidate this concept of *P. fimeti* a dried culture of a typical soil-isolate of the fungus is designated as neotype.

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## EXPLANATION OF PLATES 1-6

## PLATE 1

Fig. 1. *Phoma chrysanthemicola*. Photograph made with side-light, showing locally a dense greyish mycelial mat, and red discoloration of the medium (OA) below the colony.

Fig. 2. *Phoma exigua*. Demonstration of the characteristic oxidation-reaction after addition of drops of NaOH: at first the appearance of a conspicuous bluish-green spot ( $\alpha$ -pigment), which gradually enlarges and then turns red ( $\beta$ -pigment).

Fig. 3. *Phoma fimeti*. Photograph made with transmitted light, showing the medium (OA) below the greenish colony discoloured yellow.

Figs. 4, 5. *Phoma herbarum*. — Fig. 4. Strain of the mycelial-type, showing different sectors and locally very intense red discoloration of the medium (OA). — Fig. 5. Strain of the pycnidial-type, showing that the reddish discoloured medium below the colony turned blue after addition of a drop of NaOH.

## PLATE 2

- Figs. 1, 2. *Phoma fimeti*. Twenty-days-old plate cultures. — 1. on OA. — 2. on MA.
- Figs. 3, 4. *Phoma herbarum*. Ten-days-old plate cultures. — 3. on OA. — 4. on MA.
- Figs. 5, 6. *Phoma glomerata*. Ten-days-old plate cultures. — 5. on OA. — 6. on MA.

## PLATE 3

- Figs. 1, 2. *Pyrenochaeta acicola*. Twenty-days-old plate cultures. — 1. on OA. — 2. on MA.
- Figs. 3, 4. *Phoma chrysanthemicola*. Twenty-days-old plate cultures. — 3. on OA. — 4. on MA.
- Figs. 5, 6. *Phoma prunicola*. Ten-days-old plate cultures. — 5. on OA. — 6. on MA.



## PLATE 4

- Figs. 1, 2. *Phoma eupyrena*. Ten-days-old plate cultures. — 1. on OA. — 2. on MA.  
Figs. 3, 4. *Phoma exigua*. — 3. Ten-days-old plate culture on OA. — 4. Twenty-days-old plate culture on MA.  
Figs. 5, 6. *Phoma medicaginis* var. *pinodella*. Ten-days-old cultures. — 5. on OA. — 6. on MA.

## PLATE 5

- Figs. 1, 2. *Phoma medicaginis* var. *pinodella*. Plate cultures on MA, photographed from below to show the characteristic crystal figures produced in the agar.  
Figs. 3, 4. *Pyrenochaeta acicola*. Pycnidia with setae,  $\times 88$ .  
Figs. 5, 6. *Phoma fimeti*. Pycnidia,  $\times 88$ .

## PLATE 6

- Figs. 1, 2. *Phoma chrysanthemicola*. Pseudosclerotial masses, consisting of chlamydo-spores,  $\times 200$ .  
Fig. 3. *Phoma eupyrena*. Chlamydo-spores,  $\times 140$ .  
Fig. 4. *Phoma medicaginis* var. *pinodella*. Chlamydo-spores,  $\times 140$ .  
Fig. 5. *Phoma glomerata*. Dictyochlamydo-spores of two strains,  $\times 140$ .  
Fig. 6. *Phoma prunicola*. Chlamydo-spores and dictyochlamydo-spores,  $\times 140$ .

## ADDITIONAL NOTES ON PHOMA HERBARUM

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The sporogenesis of *Phoma herbarum* Westend., and *Phoma* species in general, is discussed. Additional data are given on the synonymy of *P. herbarum* and the status of its various infraspecific taxa is revised. Most of the 'varieties' and 'forms' appear to belong to the ubiquitous species *Phoma exigua*. *Phoma macdonaldii* is proposed as a new species and *Stagonospora samarorum* (Desm.) as a new combination.

In a preceding paper (Boerema, 1964) the diagnostic characteristics of the ubiquitous saprophyte *Phoma herbarum* Westend., type species of the form-genus *Phoma* Sacc., were amply discussed and provisional data were given on the synonymy of the fungus. The present paper presents a description of the sporogenesis of *P. herbarum*, based upon recent electron-microscopic observations on the spore development in this and other species of *Phoma*. The differences from the spore development of *Ascochyta pisi* Lib., type species of the form-genus *Ascochyta* Lib., are also discussed. Further information is supplied on the synonymy of the species, including confusing misinterpretations and misidentifications. Finally the identity of the numerous formae and varieties of *P. herbarum* is discussed in alphabetical order.

The names of authors are abbreviated first in accordance with Grummann's "Autorenliste" (1963: 59-74), and further with Ainsworth's list (1961: 37-41). Herbaria and culture collections are coded according to Lanjouw & Stafleu (1959) and the list of abbreviations in the catalogue of the American Type Culture Collection (Ed. 8, 1968). Titles of journals are abbreviated in accordance with the "World List of Scientific Periodicals", 1963-1965.

### The spore-forming process

Recent electron-microscopic observations on the spore development and spore secession in *Phoma herbarum* and other *Phoma*-like fungi have furnished more precise information on the essential features of the sporogenesis in the form-genus *Phoma* (see also Boerema, 1965).

The first spores in a pycnidium make their appearance as soon as a cavity in the pycnidium-primordium develops. Electron-microscopic observations lend strength to the hypothesis that these first spores in the pycnidium are formed by budding or cleavage of the cytoplasm of the original central cells (Boerema, 1964: fig. 4; Boerema, 1965: fig. 31; compare also Madelin, 1966: fig. 6).

In mature pycnidia the spores arise successively at the top of somewhat cuspidate but otherwise undifferentiated cells lining the central pycnidial cavity (Sutton, 1964; Boerema, 1964). The first spore begins as a papilla arising from a broad base, secondarily acquiring the shape of a bud. The progressive thickening of the top of the parent cell as successive spores are formed and secede ('collarete', see below) leads to the subsequent development of spores as buds (Brewer & Boerema, 1965: fig. 1, pls. 1-3; Boerema, 1965: figs. 1-27; Sutton & Sandhu, 1969: figs. 11-19). This kind of sporogenesis can be characterized as a 'monopolar repetitive budding process' (Boerema, 1965). The spore wall develops as a distinct layer within the papillate or bud-like initial, whose own primary wall is continuous with that of the parent cell (Brewer & Boerema, 1965: fig. 1A, pls. 1-3; Sutton & Sandhu, 1969: figs. 11-13). Concurrently with the differentiation of the spore wall the separation of the spore cytoplasm from that of the parent cell starts with the centripetal development of a wall-layer at the base of the spore, combined with the development of a wall-layer closing the parent cell (Brewer & Boerema, 1965: fig. 1D-E, pl. 2; Sutton & Sandhu, 1969: figs. 15-19). Disintegration of the continuous periclinal wall material completes the secession of the spore (Brewer & Boerema, 1965: fig. 1F; Sutton & Sandhu, 1969: fig. 18). Remnants of the periclinal layer remain on the parent cell, contributing to the 'collarete' at the top of it. With each new spore secession this collarete becomes wider, with an increasing series of wall remnants ('ridges' or 'annellations'; Boerema, 1965: figs. 15-27; Sutton & Sandhu, figs. 14-15). The processes of differentiation of the spore wall, development of the two separating transverse wall-layers, and the disintegration of the periclinal wall material are associated with an abundant production of mucilaginous substances (Brewer & Boerema, 1965: pls. 2, 3).

In our opinion it is not expedient to fit this spore-forming process into one of the modes of sporogenesis distinguished by Hughes (1953), Tubaki (1958), and others (compare Madelin, 1966) in their scheme for the conidial ontogeny in Hyphomycetes, their classifications being based primarily on observations with the light microscope only. To do so at present would only cause confusion because of possibly differing interpretations ['blastospores' (compare Madelin 1966: fig. 6), 'acrophialospores' (Sutton, 1964), 'porospores' (Boerema, 1964; compare also Campbell, 1968), 'annellospores', "where the points at which conidia secede are at approximately the same level" (Sutton & Sandhu, 1969)].

Sutton & Sandhu (1969) are of the opinion that the spore development in the type species of *Ascochyta*, *A. pisi* (see Brewer & Boerema, 1965), is probably identical with that of *Phoma*. In *A. pisi* and other related species of *Ascochyta* the separation of the spores indeed takes place by the development of two transverse walls and 'rupture' of the connecting wall parts, also leaving a 'collarete' with ridges or annellations on the wall at the top of the parent cell (Brewer & Boerema, 1965 figs. 3D-E, pl. 5). However, it is characteristic of *A. pisi* for the spore-initial to be extremely thin-walled while the separating transverse walls are developing (Brewer & Boerema, 1965: pls. 5, 6). Against the innerside of the initial spore wall

a new wall-layer arises secondarily, simultaneously dividing the spores into two or more cells, 'distoseptation' (Brewer & Boerema, 1965: fig. 4, pl. 7). The septation of the spores in the species of *Ascochyta*, therefore, is an essential part of the 'finishing' (completion) of the spore-development. If *Phoma* species show septate spores (which happens very seldom with *P. herbarum*), this septation process, 'euseptation', occurs independently of the sporogenesis and completion of the spore wall (Brewer & Boerema, 1965). This may explain why genuine *Ascochyta* species also in vitro produce mainly 2- or more-celled spores, whereas pseudoforms—that is to say *Phoma* species, whose pycnidia in vivo may contain a variable percentage of septate spores—produce in culture mainly 1-celled spores. This offers a very simple method for distinguishing species of *Phoma*—including 'pseudo-*Ascochyta*'—from true *Ascochyta* species in culture.

In this paper electron-micrographs are intentionally omitted, as these will be published later. The above is therefore restricted to references to the electron-microscopy studies by Brewer & Boerema (1965) and Sutton & Sandhu (1969).

### Synonymy

Previously (Boerema, 1964) much attention was paid to the synonymy of *P. herbarum*. Since then many new data have accumulated. In the following all the synonyms known at present are listed with reference to type material and to host or substratum.

#### PHOMA HERBARUM Westend.

*Phoma herbarum* Westend. in Bull. Acad. r. Belg. Cl. Sci. **19** (3): 118. 1852. — Lectotype: Herb. crypt. Belg., Ed. Beyaert-Feys, Fasc. 20, No. 965. 1854, on *Onobrychis viciifolia*, type locality, date and collector not known (Herb. Westendorp & Wallays, BR), see Persoonia **3**: 10, 12, pl. 1, figs. 1, 2. 1964.

*Phoma exigua* var. ('b') *minor* Desm. in Anns Sci. nat. (Bot.) III, **11**: 283. 1849; Pl. crypt. N. France, Ed. 1, Fasc. 38, No. 1869b. 1849. — *Phoma exigua* var. *ranuncolorum* Desm. ex Sacc. in Sylloge Fung. **3**: 134. 1884 (name change). — Lectotype: on *Ranunculus bulbosus*, Parc de Lébissey, July 1847, Roberge (Herb. Desmazières, PC), see Persoonia **5**: 23, pl. 1-below. 1967 and the discussion below.

*Phoma charticola* Speg. in An. Soc. cient. argent. **10**: 153, 154. 1880. — Type: not known to be in existence, on remnants of paper in a forest, type locality: Recoleta, Argentina, see discussion below.

*Phoma urticae* Schulzer & Sacc. in Hedwigia **23**: 91. 1884; in Sylloge Fung. **3**: 140. 1884. — *Leptophoma urticae* (Schulzer & Sacc.) Höhn. in Hedwigia **59**: 262. 1918 (misapplied). — Type: not known to be in existence, on *Urtica dioica*, type locality: Vinkovce (manuscr. Schulzer von Müggenburg, Schwämme Pilze Ung. Slav. 700. 1869); for specimens examined, see Persoonia **3**: 12, 13. 1964.

*Phoma oleracea* Sacc. in Michelia **2** (1): 91. 1880; in Revue mycol. **3**/No. 9: 36. 1881; in Sylloge Fung. **3**: 135. 1884. — Type: not known to be in existence, on *Brassica oleracea*, type locality: Quevilly near Rouen, for discussion of interpretation, see Persoonia **3**: 13, 14. 1964.

*Phoma oleracea* var. *dipsaci* Sacc. in *Michelia* 2 (2): 337. 1881; in *Sylloge Fung.* 3: 135. 1884. — Holotype: on *Dipsacus sylvestris*, Rouen, no date, Malbranche (Herb. Saccardo '109' pro parte, PAD), see discussion below.

*Phoma oleracea* var. *helianthi-tuberosi* Sacc. in *Michelia* 2 (2): 337. 1881; in *Sylloge Fung.* 3: 135. 1884. — Holotype: on *Helianthus tuberosus*, Quevilly near Rouen, no date, Letendre (Herb. Saccardo '1311', PAD), see discussion below.

*Phoma oleracea* var. *scrophulariae* Sacc. in *Michelia* 2 (2): 337. 1881; in *Sylloge Fung.* 3: 135. 1884. — Holotype: on *Scrophularia nodosa*, type locality and date not known, Roumeuguère (Herb. Saccardo '276', PAD), see discussion below.

*Phoma oleracea* var. *urticae* Sacc. in *Michelia* 2 (2): 337. 1881; in *Sylloge Fung.* 3: 135. 1884. — Holotype: on *Urtica urens*, type locality and date not known, Roumeuguère (Herb. Saccardo '321', PAD), see discussion below.

*Phoma herbarum* var. *erysimi* Roum. in *Revue mycol.* 3 / No. 9: 30. 1881 ("crysimi"; nomen nudum). — Isotype: Roum., Fungi gall. exs., Cent. 11, No. 1011. 1881, on *Erysimum vulgare*, Toulouse, autumn, date and collector not known (Herb. Roumeuguère, PC), see discussion below.

*Phoma herbarum* var. *sambuci* Roum. in *Revue mycol.* 3 / No. 9: 30. 1881 (nomen nudum). — Isotype: Roum., Fungi gall. exs., Cent. 11, No. 1014. 1881 ("f. sambuci"), on *Sambucus nigra*, Toulouse, autumn, no date, Roumeuguère (Herb. Roumeuguère, PC), see discussion below.

*Phoma herbarum* f. *chenopodii-albi* Roum. in *Revue mycol.* 5: 28. 1883 (nomen nudum). — Isotype: Roum., Fungi gall. exs., Cent. 25, No. 2484. 1883, on *Chenopodium album*, Quevilly near Rouen, spring 1882, Letendre (FH), see discussion below.

*Phoma herbarum* var. *tetragoniae* Sacc. & Berl. in *Revue mycol.* 8: 35. 1886; in *Sylloge Fung.* 10: 180. 1892 (in both cases "*Phoma herbarum* \**Ph. Tetragoniae*"). — Holotype: on *Tetragonia expansa*, Algeria, no date, Trabut (Herb. Saccardo '68', PAD), see discussion below.

*Aposphaeria violacea* Bertel in *Öst. bot. Z.* 54: 205, 233, 288. 1904. — *Phoma violacea* (Bertel) Eveleigh in *Trans. Br. mycol. Soc.* 44: 577. 1961. — Neotype: on white paint, Kew, 1911, Massee (= type specimen of *Phoma pigmentivora*, K), see *Trans. Br. mycol. Soc.* 44: 577. 1961, *Persoonia* 3: 14. 1964, and discussion below.

*Phoma oleracea* f. *bryoniae* Sacc. in *Annls mycol.* 7: 435. 1909. — Holotype: on *Bryonia alba*, Tamsel, Brandenburg, May 1909, Vogel (Herb. Saccardo '73', PAD); isotype: Syd., *Mycoth. germ.*, Fasc. 17, No. 809. 1909 (M, PAD); see discussion below.

*Phoma pigmentivora* Massee in *Bull. misc. Inf. R. bot. Gdns Kew* 8: 326. 1911. — Holotype: on white paint, Kew, 1911, Massee (K), see under *Aposphaeria violacea*.

*Phyllosticta ruscigena* Sacc. in *Nuovo G. bot. ital.* II, 22: 45. 1915. — Holotype: on *Ruscus hypophyllum*, Ta Braxia, Malta, Dec. 1913, Caruana-Gatto (Herb. Saccardo '369', PAD), see discussion below.

*Phoma herbarum* f. *humuli* Gonz.-Frag. in *Trab. Mus. nac. Cienc. nat., Madr., Ser. bot.* 12: 30. 1917. — Holotype: on *Humulus lupulus*, Bot. Garden, Madrid, Aug. 1916, Caballero (MA-2084), see discussion below.

*Phoma herbarum* f. *minor* Unamuno in *An. Jard. bot. Madr.* 2 ('1941'): 56. 1942. — Holotype: non-existent (information Dr. E. Paunero, MA), on *Digitalis obscura*, type locality: Hoz de Beteta, see discussion below.

*Phoma herbarum* var. *lactaria* Sutton in *Trans. Br. mycol. Soc.* 47: 501. 1964. — Holotype: on rubber tubing of milking machine, Leicester, Derbyshire, no date, Pyman (IMI-104608); see discussion below.

*Phoma hibernica* Grimes, O'Connor & Cummins in *Trans. Br. mycol. Soc.* 17: 99-101. 1932. — Type: dried culture from cream, Cork, no date, Grimes (K), see *Persoonia* 3: 14, 15. 1964 and discussion below.

*Phoma lignicola* Rennerfelt in *Svenska SkogsvFör. Tidskr.* 35: 60. 1937. — Type: culture from woodpulp, Sofiehem, April 1937, Rennerfelt (CBS-276. 37), see *Persoonia* 3: 15. 1964.

The oldest known name for the ubiquitous saprophytic species *Phoma herbarum* seems to be *Phoma exigua* var. *minor*. The handwritten annotations accompanying the lectotype material of this infraspecific taxon (see Boerema & Höweler, 1967: pl. 1-below) suggest that the fungus is a specific parasite of *Ranunculus* species. Its microscopical characters (spores  $3.4-5.1 \times 1.7-3.4 \mu$ , usually  $4.8 \times 2.6 \mu$ ), however accord reasonably well with those of the saprophytic *P. herbarum*, whereas no similar pycnidial parasite is known from *Ranunculus* species. Its identity with *P. herbarum* also agrees with Desmazières' view; he was of the opinion that it represents only a small-spored variant of a ubiquitous fungus; compare Boerema & Höweler (1967), who also provided documentation on other specimens of *P. exigua* var. *minor*. Although *P. exigua* var. *minor* antedates *P. herbarum*, the epithet '*minor*' cannot have priority (Edinburgh-code: Art. 60) because of its being a varietal epithet.

Nearly all the specimens preserved in Saccardo's herbarium under the name *Phoma herbarum* and generally filed as forms or varieties appear to belong to fungi quite different from *P. herbarum* s.s.; see the following chapter. As previously (Boerema, 1964: 13) noted, the explanation is that Saccardo's idea of the spore dimensions of *P. herbarum* differs from the present concept of this fungus as based on the characteristics of the lectotype at Brussels. '*Phoma herbarum* \**Ph. Tetragoniae*' is the only variety described by Saccardo & Berlese that can be considered to be a true synonym of *P. herbarum* s.s. The holotype of this infraspecific taxon, consisting of six stem pieces and with the same annotations on the label as those cited in the protologue, shows numerous pycnidia, whose characteristics agree completely with those of *P. herbarum*. In the index of *Sylloge Fung.* 10 it is cited as 'var.', in *Sylloge Fung.* 13 as 'subsp.' and on the label of the type as 'f.'.

*Phoma herbarum* var. *erysimi* Roum., var. *sambuci* Roum., and f. *chenopodii-albi* Roum. are nomina nuda, as the names were published without descriptions. The isotypes, consisting of various stem parts with numerous pycnidia, reveal morphological characters identical with those of *P. herbarum* s.s. on stems and twigs. Apparently Roumeguère as well found them morphologically identical with *P. herbarum* s.s., so that the names are of value only in so far as they record the hosts.

The identity of *Phoma herbarum* f. *humuli* Gonz.-Frag. with *P. herbarum* s.s. was established by examining the holotype, which is composed of various stem pieces with many pycnidia. Gonzáles Frago noted that it differs from the 'tipo', i.e. *P. herbarum* f. *humuli* Sacc., in its spore dimensions. He did not know, however, that the form described by Saccardo actually represents a different fungus, namely the ubiquitous weak- and wound-parasitic *Phoma exigua* Desm. The latter is very probably identical with the '*Phoma herbarum*' in south- and mid-England observed in association with a wilting of hop bines (Wormald, 1939: 261); it is dealt with in the next chapter under f. *humuli* Sacc.

The original material of *Phoma herbarum* f. *minor*, described by Unamuno from dead stems of *Digitalis obscura* in Spain, has not been preserved. The identity of this '*minor*' form with *P. herbarum* s.s. is based on its spore dimensions,  $4-5.5 \times 2.5 \mu$ , which agree completely with the usual spore size of *P. herbarum*.

*Phoma herbarum* var. *lactaria*, recently described by Sutton from the rubber parts of a milking machine, was studied in vitro (culture made from a dried culture of the type). It shows the characteristics, including pigment formation, typical of the numerous isolates of *P. herbarum* that were examined. Sutton compared the characteristics of his isolate with those of the lectotype of *P. herbarum*, but it should be pointed out that this lectotype cannot possibly cover the variability of the characteristics in vitro.

The type of *Phoma oleracea* Sacc., collected by Letendre at Quevilly (near Rouen) on *Brassica oleracea*, has not been found in Saccardo's herbarium. The identity of *P. oleracea* with *P. herbarum* and the confusion in literature between it and *Phoma* (*Plenodomus*) *lingam* Todé ex Fr. has already been amply discussed (Boerema, 1964: 13, 14). Since type specimens of the infraspecific taxa of *P. oleracea* are represented in Saccardo's herbarium it was possible to check their identity with *P. herbarum*.

The original specimen (three stem pieces) on which Saccardo based the variety *Phoma oleracea* var. *dipsaci* ("sperm.  $5 \times 1\frac{1}{2}$ ") also contains the type of *P. herbarum* f. *dipsaci* ("sperm.  $8-9 \times 3-4$ "), which appears to be identical with *Phoma exigua* (see next chapter), while the characteristics of the small-spored *P. oleracea* var. *dipsaci* agree fairly well with *P. herbarum* s.s. The saprophyte *P. herbarum* is often found on dead plant material in association with weak-parasitic or true parasitic pycnidial fungi (cf. Boerema, 1964: 13).

The type material of *Phoma oleracea* var. *helianthi-tuberosi*—previously (Boerema, 1964) listed as a synonym on account of its spore dimensions ( $5 \times 2 \mu$ )—consists of three stem pieces bearing, among other things, a pycnidial fungus agreeing completely with *P. herbarum* (spore dimensions  $5-5.5 \times 2-2.5 \mu$ ). It should be noted that McDonald (1964) applied the name *P. oleracea* var. *helianthi-tuberosi* to the pycnidial stage of the causal organism of a disease of the commercial sunflower, *Helianthus annuus*, known as 'black stem'. Recently Frezzi (1968) pointed out that this stage belongs to a species of *Leptosphaeria*, viz. *L. lindquistii* Frezzi. Through the kind cooperation of Dr. McDonald we were in a position to study a typical isolate of this 'black stem' fungus. The microscopic characteristics of its pycnidia appear to be very different from those of both *P. herbarum* and the type specimen of *P. oleracea* var. *helianthi-tuberosi*. Its growth-characters in vitro show some similarity with those of *Phoma* (*Plenodomus*) *lingam*, which also belongs to a *Leptosphaeria*, viz. *L. maculans* (Desm.) Ces. & DNot. (see Boerema & van Kesteren, 1964). McDonald's interpretation of *P. oleracea* var. *helianthi-tuberosi*, therefore, seems to us unacceptable.<sup>1</sup>

<sup>1</sup> As no older name appears to be available for the pycnidial state of *Leptosphaeria lindquistii*, I propose to name it after Dr. W. C. McDonald, who was the first to study the 'black stem' parasite of sunflowers. The Latin diagnosis is a translation of McDonald's characterization of the pycnidial stage (compare also Frezzi, 1964):

***Phoma macdonaldii* Boerema, spec. nov.**

Pycnidiis subglobosis, leniter papillatis, brunneis pallidis, nigrescentibus,  $155-308 \mu$  diam.

The type material of *Phoma oleracea* var. *scrophulariae* (a single stem piece glued to a sheet of paper) appears to contain two *Phoma*-like fungi. One of these has spore dimensions different from those given in the diagnosis of var. *scrophulariae*; it has not been more closely investigated and is not dealt with here. The other, on which the diagnosis appears to have been founded, proved to have the characteristics typical of *P. herbarum*; its spore-description had already led me to make this assumption (Boerema, 1964: 10, 14). It should be noted that *P. oleracea* var. *scrophulariae* differs from the fungus-isolate described by Dennis (1946: 35, 36) as '*P. oleracea* var. *scrophulariae*' (*Phoma*-'Group XII'), which does not agree with *P. herbarum*.

The holotype of *Phoma oleracea* var. *urticae*—on the grounds of the spore dimensions previously listed as a synonym of *P. herbarum* (Boerema, 1964: 10, 14)—consists of a single stem piece (glued to a sheet of paper) bearing a pycnidial fungus whose characteristics fully confirm its identity with *P. herbarum*. Not only the spore characters but also the shape and structure of the pycnidia are in full agreement with it. *Phoma herbarum*, it may be recalled, is repeatedly found on stems of nettle, the paratype having been collected on *Urtica dioica* as well (BR; Boerema, 1964: 12; Sutton, 1964: 501); see also Dennis (1946: 34), who described an isolate of *P. herbarum* from nettle under its synonym *Phoma urticae* (Boerema 1964: 13).

The type of *Phoma oleracea* f. *bryoniae* now preserved in Saccardo's herbarium (PAD) was collected in 1909 by P. Vogel. Duplicates were later distributed by Sydow. The type and two copies of these duplicates were studied. They are composed of various stem pieces bearing numerous pycnidia with 1-celled spores identical in shape and size with those of *P. herbarum* on herbaceous stems, leading to the conclusion that *P. oleracea* f. *bryoniae* is another synonym of *P. herbarum*. Later Petrak distributed exsiccata of *Phoma oleracea* collected on *Bryonia alba* (Petr., Mycoth. gen. No. 376; leg. P. Vogel, May 1920). Examination of a copy received on loan from the 'Staatsherbarium' at München (M) shows this fungus to be a different species, viz. the ubiquitous *Phoma exigua*.

The synonyms *Aposphaeria violacea* (= *Phoma violacea*), *Phoma pigmentivora*, and *P. hibernica* listed above have already been amply discussed (Boerema, 1964: 14, 15). At that time, however, no attention was paid to the paper by Mrs. Nicot-Toulouse (1952) in which she had concluded that *A. violacea*, which occurs on paint, is a species different from the ubiquitous *P. hibernica* (= *P. herbarum*).

The differential character was assumed to lie in the pycnidia, which in *A. violacea*

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Sporulis hyalinis, continuis, reniformibus vel oblongis, utrinque obtusis, 4.3-7.2 × 1.4-2.9  $\mu$ . In foliis, caulibus, petiolis et capitulis *Helianthi annui*, Manitoba.

A dried culture on a sterile lemon leaf made in 1964 by Dr. McDonald and deposited in the Herbarium of the Department of Botany, University of Manitoba, Winnipeg (WIN) is indicated as the type of *Phoma macdonaldii*. A culture of the type is deposited in the 'Centraal-bureau voor Schimmelcultures' (CBS-381.67) at Baarn.



are said to be produced on the surface of the medium, whereas those in *P. hibernica* develop immersed. In order to check this we compared different agar-plate cultures of three typical *Phoma*-isolates from paint with those of three strains of *P. herbarum* isolated from dead plant material, see table I.

TABLE I

COMPARISON OF THE POSITION OF THE PYCNIDIA OF *Phoma herbarum* GROWN ON DIFFERENT AGAR-MEDIA (RECIPES AINSWORTH, 1961: 241, 242) SHOWING THREE ISOLATES FROM PAINT AND THREE ISOLATES FROM DEAD PLANT MATERIAL.

sup. = superficial  
● = many pycnidia

er. = erumpent  
○ = some pycnidia

imm. = immersed  
● and ○ = pycnidia often situated at the bottom of the dish

Isolates	Malt agar			Oatmeal agar			Potato glucose agar		
	sup.	er.	imm.	sup.	er.	imm.	sup.	er.	imm.
CMI-90179 bathroom paintwork		●	●	●	●	●	●	●	●
ATCC-12569 white lead paint	●	●		○	●		●	○	
PD-62/139 bathroom paintwork	○	●		●	●	○	●	●	
PD-58/158 leaf <i>Euonymus</i> sp.	●	●		●	○	○	●	○	
PD-61/125 seed coat flax	○	●			●		●	●	
PD-61/645 leaf <i>Alliaria</i> sp.	●	●		●	●	○	●	●	

The position of the pycnidia on the various agar media appears to vary a great deal. None of the isolates tested produced superficial pycnidia only; a number of them were always 'erumpent' (Ainsworth, 1961: 143) or even completely immersed in the medium. In cultures of three of the isolates deeply immersed pycnidia also occurred, often at the bottom of the dish. A very striking example was one of the paint-isolates (CMI-90179). This demonstrated the reverse of Mrs. Nicot-Toulouse's findings and shows that it is impossible to separate the two kinds of isolates according to the relative positions of the pycnidia. The possibility of making such a differen-

tiation is also denied by the behaviour of cultures of *P. herbarum* which, when isolated from plants and transferred to paint, produce symptoms similar to those of the original paint strains (Boerema, 1964).

The description of *Phoma charticola*, found in "charta stercorata putrescente" would seem to suggest *P. herbarum* which is known to grow well on decaying paper. The original material of *P. charticola* is not preserved.

*Phyllosticta ruscigena* was described from small circular dark-rimmed spots on the cladodia of *Ruscus hypophyllum* and *R. aculeatus*. In addition to an examination of the characters of a living culture (CBS-212.57) made by Bertini (1957) from similar spots on the cladodia of *Ruscus hypoglossum* a study of the characteristics of the holotype revealed the identity of *P. ruscigena* with *P. herbarum*. In both cases the fungus occurred on the spots together with typical *Ruscus*-fungi, like *Phyllosticta hypoglossi* (Mont.) Allesch. ("hippoglossi") = *Phyllostictina hypoglossi* (Mont.) Petr. & H. Syd. (type material; compare Petrak & Sydow, 1927: 203) and *Leptosphaeria rusci* (Wallr.) Sacc. with its conidial state *Coniothyrium ruscicola* (Dur. & Mont.) Sacc. (type material and the material studied by Bertini, l.c.; compare Curzi & Barbaini, 1927: 179; Müller & Tomáševič, 1957<sup>2</sup>; and Lacoste, 1965). It is evident that the dark-rimmed spots described are not caused by *P. herbarum*, which is only a secondary invader.

#### Identity of the forms and varieties described

The information newly obtained on the characters of *Phoma herbarum* makes it desirable to reconsider the status of its various forms and varieties. In agreement with Westendorp's concept of *P. herbarum* as a necrotrophic species ("sur les tiges mortes d'un grand nombre de plantes herbacées"), all these infraspecific taxa are also found on dead plant material, especially herbaceous stems. Since *Phoma exigua* is the pycnidial fungus most frequently met with on herbaceous plants (compare Boerema & Höweler, 1967), many of the forms and varieties assigned to *P. herbarum* prove to belong to *P. exigua*.

They are treated here in alphabetical order.

*absinthii*. — *P. herbarum* f. *absinthii* Sacc. in *Michelia* 1 (5): 523. 1879; in *Sylloge Fung.* 3: 133. 1884. — Holotype: Quevilly near Rouen, no date, Letendre (Herb. Saccardo '746', PAD). — Host: *Artemisia absinthium*.

The holotype is a single stem piece which, to judge from the annotations on the label and from its origin, was clearly used by the author for the description of

<sup>2</sup> These authors, referring to a study by Brefeld & von Tavel (1891) on *Leptosphaeria rusci*, erroneously cite *Phyllosticta ruscicola* Dur. & Mont. [= *Coniothyrium ruscicola* (Dur. & Mont.) Sacc.] as '*Phyllosticta ruscigena* Dur. & Mont.', which would suggest the existence of an earlier homonym of *P. ruscigena* Sacc.

the spores of this infraspecific taxon.<sup>3</sup> It contains many pycnidia with hyaline 1- and 2-celled spores. It agrees with the characteristics of *Phoma exigua* as isolated in the Netherlands from all kinds of Compositae (cf. Boerema & Höweler, 1967: Table II).

*a c h i l l e a e*. — *P. herbarum* f. *achilleae* Thüm. in *Fungi austr.*, Cent. 9, No. 883. 1874 (nomen nudum). — Lectotype: (*Fungi austr.* No. 883) Krems, 1871, von Thümen (W). — Host: *Achillea millefolium*.

The label accompanying the exsiccata only gives information on the provenance of the material, but it lacks a description.

The lectotype in Vienna contains only scolecosporous pycnidia, the microscopical characters of which agree with those of *Rhabdospora pleosporoides* (Sacc.) Sacc., a species occurring on dead stems of all kinds of plants, among others *Achillea millefolium* (see Jørstad, 1965: 78, 79). Allescher (1899: 329) also noted that the copy (B?) he saw contains a species of *Rhabdospora*.

The copy at Torino (TO), on the other hand, appears to contain a species of *Diplodia* which cannot be further identified.

*a n e t h i*. — [*P. herbarum* var. *anethi* Westend. apud Thüm. in *Fungi austr.*, Cent. 10, No. 982. 1874 (nomen nudum). —] *Phoma anethicola* Allesch. in *Rab. KryptogFlora*, Pilze 6: 265. 1898 ("1901"). — Lectotype: (*Fungi austr.* No. 982) Teplitz, 1872, von Thümen (Herb. Winter, B); isotype (Herb. Saccardo, PAD). — Host: *Anethum graveolens*.

The exsiccata of *P. herbarum* var. *anethi* distributed by von Thümen lacked a diagnosis, but Allescher, using the copy in Winter's herbarium (five stem pieces) and raising the variety to specific level, gave a short description.

This copy, which we designate as lectotype (one selected stem piece), contains numerous typical thick-walled pycnidia of *Phoma complanata* (Tode ex Fr.) Desm. which is a ubiquitous species on Umbelliferae, compare Grove (1935: 59, 60). For a description in vitro, see Dennis (1946: 31, 32). The isotype in the herbarium of Saccardo, consisting of four stem pieces, contains the same fungus.

<sup>3</sup> The original specimens of the various forms and varieties of *P. herbarum* described by Saccardo are generally accompanied by annotations on the spore dimensions and/or by drawings of the spores and provided with numbers, as sometimes noted in Michelia.

The manner in which the material was packed or glued to a piece of paper, the kind of paper used, and the handwriting often made it possible also to check whether the identity of the collectors corresponds with those noted by Saccardo in Michelia for the various forms of *P. herbarum* [indicated by capital letters, explained in Michelia 1 (5): 500. 1879 and 2 (1): 39. 1880].

*ansoniae-salicifoliae*. — *P. herbarum* f. *ansoniae-salicifoliae* Berl. & Roum. in *Revue mycol.* 9: 178 ("162"). 1887 (nomen nudum). — Isotype: Roum., *Fungi sel. exs.*, Cent. 43, No. 4218. 1887, Bot. Garden, Coimbra, autumn 1885, Moller (FH). — Host: *Ansonia salicifolia*.

This form was introduced without a description. The isotype in FH consists of two stem pieces and contains many small pycnidia with irregular fusoid spores, usually somewhat curved and attenuate at one end. Most of these spores are 1-celled,  $5.5-10 \times 2-3 \mu$ , but several larger ones,  $17-25 \times 2.5-3.5 \mu$ , show 1-3 septa. Spores of this kind are characteristic of a saprophytic species, first described as *Phoma samarorum* Desm. [in *Pl. crypt.* N. France, Ed. 1, Fasc. 7, No. 349. 1828; matrix: key-fruits (samarae) of *Fraxinus excelsior*; Holotype: Herb. Desmazières, PC]. For illustration of the spores, see Wollenweber & Hochapfel (1936: 604), who considered the species to belong to the genus *Septoria*, *S. samarorum* (Desm.) Wollenw. & Hochapf. ("*S. samarorum*"). As it is neither a *Phoma* nor a true *Septoria* species we assign it provisionally to the form-genus *Stagonospora* (Sacc.) Sacc., although we fully realize that this genus is urgently in need of a revision: ***Stagonospora samarorum*** (Desm.) Boerema, *comb. nov.* (basonym, *Phoma samarorum* Desm., l.c.). In vitro this slow-growing fungus is characterized by a yellow-brownish to greenish discoloration of the agar media, while the mycelial mat may also show yellow-greenish tinges. The isolates studied were obtained from soil and necrotic tissue of species of *Aubrietia*, *Delphinium*, *Hedera*, *Lavas*, *Sambucus*, *Tradescantia*, *Urtica*, and *Viburnum*.

*antherici*. — *P. herbarum* f. *antherici* Hollós in *Annls hist.-nat. Mus. natn. hung.* 8: 3. 1910. — Type: non-existent (information Museum of Natural History at Budapest); Type locality: Nagy-Körös. — Host: *Anthericum liliago*.

The description is in accordance with the characteristics of *Phoma exigua* on material of *Anthericum liliago* from the Netherlands (tested by isolation).

*anthirrhini*. — *P. herbarum* f. *anthirrhini* Sacc. in *Michelia* 2 (2): 337. 1881; in *Sylloge Fung.* 3: 133. 1884. — Type: Alençon, Orne, no date, Gillet (Herb. Saccardo '7', PAD). — Host: *Anthirrhinum majus*.

The holotype comprises three stem pieces and contains numerous pycnidia which agree with those of *Phoma exigua*. The latter was also isolated from dead stems of *Anthirrhinum majus* in the Netherlands.

*aristolochiae-siphonis*. — *P. herbarum* f. *aristolochiae-siphonis* Sacc. in *Michelia* 2 (2): 337. 1881; in *Sylloge Fung.* 3: 133. 1884. — Holotype: Dép. de l'Eure, no date, Malbranche (Herb. Saccardo '89', PAD). — Host: *Aristolochia durior* (= *A. siphon*).

The holotype, composed of three stem pieces, contains many pycnidia which correspond fully with those of *Phoma exigua* on indigenous material of *Aristolochia durior* (tested by isolation).

*artemisiae-campestris*. — *P. herbarum* f. *artemisiae-campestris* Thüm. in *Fungi austr.*, Cent. 7, No. 700. 1873 (nomen nudum); ex Allescher in Rab. *KryptogFlora*, Pilze 6: 329. 1899 ("1901", "f. *Artemisiae* Thüm."). — Isotype: (*Fungi austr.* No. 700) Krems, 1871, von Thümen (W). — Host: *Artemisia campestris*.

The exsiccata of this form are not accompanied by a diagnosis, but Allescher subsequently gave a description of the spores of the isotype (B?) he has seen. The isotype we examined (W) contains a *Phomopsis* species with only  $\alpha$ -spores ( $6.8-12.5 \times 2.5-3.5 \mu$ ). Possibly it represents the conidial stage of the '*Artemisia*-hostform' of *Diaporthe arctii* (Lasch) Nitschke, see Wehmeyer (1933: 26, 27).

*blattariae*. — *P. herbarum* f. *blattariae* Sacc. in *Michelia* 2 (1): 93. 1880; in *Sylloge Fung.* 3: 133. 1884. — Type: not known to be in existence; type locality: Quevilly near Rouen. — Host: *Verbascum blattaria*.

In Saccardo's herbarium no material of this form was found. It may be inferred from Sydow's 'Index universalis' to the 'Sylloge Fung.' (Sydow, 1898) that the host was *Verbascum blattaria*. The description reads: "sperm.  $10-12 \times 4$ , rectiuscula 2-4-guttulata; perithecia globoso-depressa 90-100 micr. d.," which does not correspond with the characteristics of any ubiquitous *Phoma*-like fungus known to us. Perhaps it is a fungus specific of *Verbascum blattaria* and related species, but thus far we have failed to find or isolate such a fungus.

*brassicae*. — *P. herbarum* f. *brassicae* Sacc. in *Sylloge Fung.* 3: 133. 1884. — Type: not known to be in existence; type locality not known. — Host: *Brassica* sp.

Material of this form is not present in Saccardo's herbarium. According to Boerema & Höweler (1967) *P. herbarum* f. *brassicae* may be considered to be a synonym of *Phoma exigua*. The latter frequently occurs on the dead stems of various species of *Brassica*, where it is sometimes confused with the cabbage parasite *Phoma lingam*, also known as *Plenodomus lingam*, see Maas (1965: 116).

*calystegiae*. — *P. herbarum* f. *calystegiae* Sacc. in *Michelia* 2 (1): 93. 1880; in *Sylloge Fung.* 3: 133. 1884. — Holotype: Rouen, no date, Malbranche (Herb. Saccardo '64', "f. *convolvuli*", PAD). — Host: *Calystegia sepium* (*Convolvulus sepium*).

The holotype contains four stem pieces bearing many pycnidia. Their charac-

teristics accord with those of *Phoma exigua*, which in the Netherlands is also found on other Convolvulaceae (tested by isolation).

*cannabis*. — *P. herbarum* f. *cannabis* Allesch. in Rab. KryptogFlora, Pilze 6: 330. 1899 ("1901"). — *Plenodomus cannabis* (Allesch.) Moesz & Smarods apud Moesz in Bot. Közl. 38: 70. 1941. — Holotype: Altenmarkt in Oberbayern, Aug. 1882, Allescher (Herb. Allescher, Forstbot. Inst. München<sup>4</sup>). — Host: *Cannabis sativa*.

The holotype material contains many stem pieces with numerous pycnidia, the latter being similar to those of *Phoma exigua* on material of *Cannabis sativa* occurring in the Netherlands (tested by isolation).

*capparidis*. — *P. herbarum* f. *capparidis* Sacc. in *Michelia* 2 (1): 93. 1880; in *Sylloge Fung.* 3: 133. 1884. — Lectotype: Roum., Fungi gall. exs., Cent. 3, No. 280. 1879 ("*Pleospora capparidis* Spegaz."), near Toulouse, winter 1878, collector not known (FH). — Host: *Capparis spinosa*.

The specimen on which Saccardo based the description of *P. herbarum* f. *capparidis* is not present in his herbarium. Boerema & al. (1968) pointed out that the copy of Fungi gall. exs. No. 280 in the Farlow Herbarium (two stem pieces) contains a pycnidial fungus identical with that described by Saccardo. This specimen is therefore indicated as lectotype. According to its microscopical characteristics *P. herbarum* f. *capparidis* appears to be conspecific with ubiquitous *Phoma prunicola* (Opiz) Wollenw. & Hochapf. (cf. Boerema & al., 1968). For a description of that species in vitro, see Boerema & al. (1965a) and Morgan-Jones (1967b).

*catalpae-capsularum*. — *P. herbarum* f. *catalpae-capsularum* Sacc. in *Michelia* 2 (1): 93. 1880; in *Sylloge Fung.* 3: 133. 1884. — Holotype: Quevilly near Rouen, no date, Letendre (Herb. Saccardo '819', PAD). — Host: *Catalpa* sp.

The type-material of this form consists of a part of the capsule of a species of *Catalpa* that bears many pycnidia. As established by Boerema & Dorenbosch (1970) the characteristics of these pycnidia agree with those of *Phoma macrostomum* Mont., a species frequently occurring on the necrotic tissue of all kinds of trees and shrubs. For a description of *P. macrostomum* in vitro, see also Boerema & Dorenbosch (1965) under the synonym *P. limitata* (Peck) Boerema.

*chenopodii-albi*. — *P. herbarum* f. *chenopodii-albi* Roum. in *Revue mycol.* 5: 28. 1883 (nomen nudum). — Isotype: Roum., Fungi gall. exs., Cent. 25,

<sup>4</sup> Not listed by Lanjouw & Stafleu (1959); address: Amalienstrasse 52, München.

No. 2484. 1883, Quevilly near Rouen, autumn 1882, Letendre (FH). — Host: *Chenopodium album*.

This agrees with *Phoma herbarum* s.s., see this paper under 'Synonymy'.

*chrysanthemii-corymbosi*. — *P. herbarum* f. *chrysanthemii-corymbosi* Allesch. in Rab. KryptogFlora, Pilze 6: 330. 1899 ("1901"). — *Peyronellaea herbarum* f. *chrysanthemii-corymbosi* (Allesch.) Goid. in Atti Accad. naz. Lincei R. VIII, 1: 455. 1946 (not validly published). — Holotype: Angerlohe-Allach near München, April 1882, Allescher (Herb. Allescher, Forstbot. Inst. München<sup>5</sup>). — Host: *Chrysanthemum corymbosum*.

This form was listed as a synonym of *Phoma glomerata* (Corda) Wollenw. & Hochapf. by Wollenweber & Hochapfel (1936: 592). The characteristics of the type material of f. *chrysanthemii-corymbosi* agree with this interpretation. This type is composed of various stem pieces and contains, apart from other fungi, pycnidia associated with multicellular chlamydospore structures similar to those of *P. glomerata* in vivo. The shape and dimensions of its spores (mostly:  $6.8 \times 3.4 \mu$ ) are also in accordance with those of *P. glomerata*. For the cultural characteristics of this fungus of world-wide distribution, see Boerema & al. (1965a) and Morgan-Jones (1967a).

*dahliae*. — *P. herbarum* f. *dahliae* Sacc. in Michelia 2 (1): 93. 1880; in Sylloge Fung. 3: 133. 1884. — Holotype: Quevilly near Rouen, no date, Letendre (Herb. Saccardo '726', PAD). — Host: *Dahlia* sp.

The holotype consists of three stem pieces and contains many pycnidia showing the same characteristics as those of *Phoma exigua*, which in the Netherlands is also repeatedly isolated from dead stems of dahlias; besides it is often associated with a black dry rot of dahlia-tubers.

*datiscae-cannabinae*. — *P. herbarum* f. *datiscae-cannabinae* Berl. & Roum. in Revue mycol. 9: 178 ("162"). 1887 (nomen nudum). — Isotype: Roum., Fungi sel. exs., Cent. 43, No. 4217. 1887, Bot. Garden, Coimbra, autumn, no date, Moller (FH). — Host: *Datisca cannabina*.

This form was published without a description. The material of the isotype examined consists of two stem fragments, bearing a pycnidial fungus which corresponds well with *Phoma exigua*.

<sup>5</sup> See note 4 on p. 27.

*daturae*. — *P. herbarum* var. *daturae* Poteb. in *Annls mycol.* 5: 14. 1907. — Lectotype: Charkow, no date, Potebnia (Herb. Saccardo, Mycoth. Sacc. No. 221, PAD). — Host: *Datura stramonium*.

Probably the exsiccatum examined, a split stem piece with many pycnidia, represents the specimen used by Potebnia for the description of *P. herbarum* var. *daturae*, although this could not be proved. As it was definitely studied by the author in the period that the name of this taxon was published, it is here designated lectotype. The characteristics of this pycnidial fungus agree with those of *P. exigua* on material of *Datura stramonium* from the Netherlands (tested by isolation).

*dianthi*. — *P. herbarum* f. *dianthi* Gonz.-Frag. in *Boln R. Soc. esp. Hist. nat.* 18: 373. 1918. — Holotype: Robledo de Chavela, Madrid, Oct. 1916, Vicioso & Planas (MA-2897). — Host: *Dianthus lusitanicus*.

The holotype, made up of various stem pieces, contains numerous pycnidia with spatulate or ellipsoid, septate spores, similar to those of *Ascochyta dianthi* (Alb. & Schw. ex Fr.) Lib., a species frequently occurring on living or fading leaves of *Dianthus* and other Caryophyllaceae; compare Grove (1935: 298). In vivo it is somewhat similar to *Stagonospora samarorum*, see under *P. herbarum* f. *ansoniae-salicifoliae*.

*dianthi-caryophylli*. — *P. herbarum* var. *dianthi-caryophylli* D. Sacc. in *Mycoth. ital.* No. 1686. 1913 (nomen nudum). — Isotype: (Mycoth. ital. No. 1686) Selva, Treviso, Oct. 1904, collector not mentioned (PAD). — Host: *Dianthus caryophyllus*.

The label accompanying the exsiccatum of this variety gives only information on the source of the material but no description.

The isotype in Saccardo's herbarium, one small stem fragment, contains the same pycnidial fungus as the holotype of *P. herbarum* f. *dianthi* (which see), i.e. *Ascochyta dianthi*.

*dipsaci*. — *P. herbarum* f. *dipsaci* Sacc. in *Michelia* 2 (2): 337. 1881; in *Sylloge Fung.* 3: 133. 1884. — Holotype: Rouen, no date, Malbranche (Herb. Saccardo '109' pro parte, PAD). — Host: *Dipsacus sylvestris*.

The material numbered '109' in Saccardo's herbarium, consisting of three stem pieces, contains two different pycnidial fungi representing the types of *P. herbarum* f. *dipsaci* ("sperm. 8-9 × 3-4") and *P. oleracea* var. *dipsaci* ("sperm. 5 × 1½"). The characteristics of the large-spored fungus accord completely with those of *Phoma exigua* on indigenous material of *Dipsacus sylvestris* (tested by isolation). The small-spored fungus agrees with *Phoma herbarum* s.s.; see this paper under 'Synonymy'.



*dulcamaricola*. — *P. herbarum* var. *dulcamaricola* Bubák in Bot. Közl. **1915**: 63. 1915. — Type: not known to be in existence; type locality: Srablje-Jezero, Zabljak, Montenegro. — Host: *Solanum dulcamara*.

Boerema & Höweler (1967) listed this variety as a synonym of *Phoma exigua*. This interpretation is supported by the characteristics of a specimen named *P. herbarum* var. *dulcamaricola* in Sydow's *Mycotheca germanica* (No. 2734, Lichtenrade near Berlin, May 1918, BPI). *P. exigua* is also repeatedly isolated from material of *Solanum dulcamara* in the Netherlands.

*dysoxyli*. — *P. herbarum* var. *dysoxyli* Sacc. in Atti Accad. scient. veneto-trent.-istriana III, **10**: 71. 1919 ("Disoxyli"); in Sylloge Fung. **25**: 117. 1931. — Holotype: Los Baños, Philippines, Sept. 1913, Baker (Herb. Saccardo '1713', PAD). — Host: *Dysoxylum decandrum*.

The holotype, composed of many stem pieces, contains numerous pycnidia of a *Phomopsis* species with  $\alpha$ -spores only (produced on inconspicuous filiform conidio-phores).

Another specimen of *P. herbarum* var. *dysoxyli* in Saccardo's herbarium, also numbered '1713' and from the same locality and date, but collected by Raimundo (see Saccardo, 1914: 306), contains the same species of *Phomopsis*.

*erysimi*. — *P. herbarum* var. *erysimi* Roum. in Revue mycol. **3**/No. 9: 30. 1881 ("erysimi"; nomen nudum). — Isotype: Roum., Fungi gall. exs., Cent. 11, No. 1011. 1881, near Toulouse, autumn, date and collector not known (PC). — Host: *Erysimum vulgare*.

Appears to be identical with *Phoma herbarum* s.s.; see this paper under 'Synonymy'.

*eupatorii-sessilifolii*. — *P. herbarum* *eupatorii-sessilifolii* Berl. & Roum. in Revue mycol. **9**: 178 ("162"). 1887 (nomen nudum). — Isotype: Roum., Fungi sel. exs., Cent. 43, No. 4219, Bot. garden, Coimbra, autumn 1886, Moller (FH). — Host: *Eupatorium sessilifolium*.

This form was introduced without a description. Examination of one of the isotypes, which contains two stem pieces, showed numerous pycnidia with 1- and 2-celled spores similar to those of *Phoma exigua* on other Compositae.

*euphorbiae-guyoniana*. — *P. herbarum* var. *euphorbiae-guyoniana* Pat., Cat. rais. Pl. cell. Tun. 116. 1897. — Holotype: Tozeur, Tunis, Jan. 1893, Patouillard ("Phoma Euphorbiae Guyoniana", PC). — Host: *Euphorbia guyoniana*.

Boerema & al. (1968) have pointed out that this variety is identical with the ubiquitous fungus *Phoma glomerata*. *P. glomerata* is characterized by the production of multicellular chlamydospore structures; these have also been found in the holotype (one stem piece) of var. *euphorbiae-guyoniana*. For a description of *P. glomerata* in vitro, see Boerema & al. (1965a) and Morgan-Jones (1967a).

*euphrasiae*. — *P. herbarum* f. *euphrasiae* Sacc. in *Sylloge Fung.* 3: 133. 1884. — Type: not known to be in existence; type locality unknown. — Host: *Euphrasia* sp.

No material of this form is present in Saccardo's herbarium. The spore dimensions given by the author (" $6-7 \times 2\frac{1}{2}-3$ ") agree with the average spore size of *Phoma exigua* on indigenous material of *Euphrasia officinalis* and other species of *Euphrasia*. It should be noted that *P. exigua* on *E. officinalis* is also capable of producing pycnidia with much larger spores, a high percentage of which then prove to be 2-celled, see under *P. herbarum* f. *euphrasiae* Bres.

*euphrasiae*. — *P. herbarum* f. *euphrasiae* Bres. apud Bres. & Sacc. in *Malpighia* 11: 305. 1897. — Holotype: Riva-Valsesia, 1891, Caresti (Herb. Carestia, Mic. Alp. penn. No. 689, TO). — Host: *Euphrasia officinalis*.

The holotype is made up of several stem pieces with seed capsules and contains many pycnidia with relatively large spores ( $6-11 \times 3-4 \mu$ ) which are mostly 2-celled. Cultures made from pycnidia with similarly large 2-celled spores found on indigenous material of *Euphrasia officinalis* always showed the fungus to be *Phoma exigua*.

On the same host this fungus can also produce pycnidia with much smaller 1-celled spores; see under *P. herbarum* f. *euphrasiae* Sacc. This is a striking example of the extremely large variability in spore dimensions of *P. exigua* in vivo.

*foeniculi*. — *P. herbarum* f. *foeniculi* Sacc. in *Michelia* 2 (1): 93. 1880; in *Sylloge Fung.* 3: 133. 1884. — Holotype: Roum., Fungi gall. exs., Cent. 2, No. 117. 1879 ("*Diplodia perpusilla* Desm."), Perpignan, winter 1877, collector not known (Herb. Saccardo, PAD). — Host: *Foeniculum vulgare* (= *Anethum foeniculum*).

The specimen of Roum., Fungi gall. exs. No. 117, on which Saccardo based this form includes three short stem fragments with *Diplodia*-pycnidia and one longer stem piece with *Phoma*-pycnidia. The spore size of the latter varies between  $6.8-13.6 \times 3.4 \mu$  and  $5.1-7.6 \times 3.4 \mu$  (Saccardo gives  $6-7 \times 3.5-4 \mu$ ). Isolates from similar large- and small-spored *Phoma*-pycnidia on *Foeniculum vulgare* from the Netherlands always revealed typical cultures of *Phoma exigua*.

*galiorum*. — *P. herbarum* f. *galiorum* Sacc. in *Michelia* 1 (5): 523. 1879; in *Sylloge Fung.* 3: 133. 1884. — Holotype: Quevilly near Rouen, no date, Letendre (Herb. Saccardo '687', PAD). — Host: *Galium* sp.

The holotype, consisting of one stem piece, contains many pycnidia of a *Phomopsis* species with only  $\alpha$ -spores. This is in accordance with the drawing on the label showing biguttulate fusoid spores with filiform sporophores. Possibly the material represents the conidial stage of the '*Galium*-hostform' of *Diaporthe arctii*, see Wehmeyer (1933: 32).

*glycyrrhizae*. — *P. herbarum* f. *glycyrrhizae* Hollós in *Annls hist.-nat. Mus. natn. hung.* 5: 457. 1907. — Type: non-existent (information Museum of Natural History in Budapest); type locality: near Kecskemét. — Host: *Glycyrrhiza echinata*.

The description suggests a *Phomopsis* with  $\alpha$ -spores only. Possibly it is the conidial stage of *Diaporthe eres* Nitschke, a polyphagous species occurring among others on the Leguminosae related to *Glycyrrhiza*.

*helianthella*. — *P. herbarum* var. *helianthella* Sacc. in *Nuovo G. bot. ital.* II, 27: 81. 1920. — Holotype: Sheridan, Wyoming, June 1917, Simmons (Herb. Saccardo "No. 10730 ex herb. James R. Weir", PAD). — Host: *Helianthus* sp.

The holotype material of *P. herbarum* var. *helianthella* consists of various split stem pieces with very different pycnidial fungi. The fungus, the spore-dimensions of which correspond with the description ("8-9  $\times$  4.7-6"), looks like a true *Ascochyta* species: spores after detachment 1-celled, later generally 2-celled (see this paper under 'The spore-forming process'). Probably it is identical with what used to be known as *Diplodina helianthi* Fautr., *Diplodina* sensu Sacc. being the same as *Ascochyta* (compare Grove, 1935: 335). In our opinion, however, additional study of the fungus in vitro is necessary before its status can be decided on.

*helichrysi*. — *P. herbarum* f. *helichrysi* Sacc. in *Sylloge Fung.* 3: 133. 1884. — Type: not known to be in existence; type locality: not known. — Host: *Helichrysum* sp.

Material of this form is not present in Saccardo's herbarium. The spore dimensions ("6-7  $\times$  2½-3") given by the author agree with the usual spore size of *Phoma exigua* frequently found on species of *Helichrysum* from the Netherlands.

*humuli*. — *P. herbarum* f. *humuli* Sacc. in *Michelia* 2 (1): 92. 1880; in *Sylloge Fung.* 3: 133. 1884. — Lectotype: Quevilly near Rouen, no date, Letendre (Herb. Saccardo '806', PAD). — Host: *Humulus lupulus*.

In Saccardo's herbarium only the exsiccatum here designated as lectotype contains *Phoma-pycnidia*; the other specimens represent a species of *Phomopsis*. On the label of the lectotype, which is made up of three stem pieces, the spore dimensions are noted as "6-3"; we measured  $5.9-6.8 \times 2.5-3.4 \mu$ , while the diagnosis mentions "6-7  $\times$  2½-3". Judging by the handwriting and the kind of wrapping paper used the selected specimen was collected by Letendre, whom Saccardo also mentioned as the collector of one of the original specimens of *f. humuli*.

Microscopically the fungus shows the same characteristics as *Phoma exigua* on material of hop from the Netherlands (identity tested by isolation). *P. exigua* is often associated with die-back symptoms and is very probably identical with '*Phoma herbarum*' mentioned by Wormald (1939: 261) as the causal organism of the wilting of hop bines occasionally observed in south- and mid-England. With this '*Phoma-wilt*' the upper parts of the bines die back, showing brown streaks and grey areas on which the *Phoma-pycnidia* appear. Its usual spore sizes are given as  $6 \times 3 \mu$  (Wormald, l.c.), while the entire range of the spore dimensions is actually  $4.5-9 \times 2-4 \mu$  (Wormald, 1928: 85; Salmon & Ware, 1936: 19). On the one side these measurements accord with the spore characters of the selected type of *P. herbarum f. humuli* Sacc. (see above); on the other they agree with the usual spore sizes and entire range of spore dimensions of *P. exigua* (Boerema & Höweler, 1967: tab. I). Dr. P. W. Talboys of the East Malling Research Station kindly informed us that the material studied by Wormald & al. has not been preserved, while the disease is "an exceedingly uncommon one and has not been seen for many years." Consequently comparison with old or fresh material of the '*Phoma-wilt*' of hop is not possible.

*h u m u l i*. — *P. herbarum f. humuli* Gonz.-Frag. in Trab. Mus. nac. Cienc. nat., Madr., Ser. bot. 12: 30. 1917. — Holotype: Bot. Garden, Madrid, Aug. 1916, Caballero (MA-2084). — Host: *Humulus lupulus*.

Agrees with *Phoma herbarum* s.s.; see this paper under 'Synonymy'.

*h y o s c y a m i*. — *P. herbarum f. hyoscyami* Sacc. in Sylloge Fung. 3: 133. 1884. — Type: not known to be in existence; type locality unknown. — Host: *Hyoscyamus* sp.

According to Boerema & Höweler (1967) identical with *Phoma exigua*.

*i p o m o e a e*. — *P. herbarum f. ipomoeae* Gonz.-Frag. in Trab. Mus. nac. Cienc. nat., Madr., Ser. bot. 10: 123. 1916. — Type apparently not preserved; type locality: near Hispalis, Sevilla, Spain. — Host: *Ipomoea coccinea*.

González Frago's herbarium contains one collection named '*P. herbarum f. ypomoeae* Trav.' (MA-1269), but this is apparently not the specimen mentioned in

the original diagnosis. Furthermore, in this material, made up of three stem pieces, no pycnidia are to be found. The description, however, clearly points to a *Phomopsis* species; this was also suggested by the author ("Probabiliter ad gen. *Phomopsis* spectat"). Probably it is the conidial stage of *Diaporthe arctii*, compare Wehmeyer (1933: 48).

**lactaria.** — *P. herbarum* var. *lactaria* Sutton in Trans. Br. mycol. Soc. 47: 501. 1964. — Holotype: Leicester, Derbyshire, no date, Pyman (IMI-104608). — Substratum: rubber tubing of milking machine.

Appears to be indistinguishable from *Phoma herbarum* s.s.; see this paper under 'Synonymy'.

**lactucae.** — *P. herbarum* f. *lactucae* Sacc. in Michelia 1 (5): 523. 1879 (nomen nudum); ex Sacc. in Sylloge Fung. 3: 133. 1884. — Holotype: near Alençon, Orne, no date, Gillet (Herb. Saccardo '13', PAD). — Host: *Lactuca sativa*.

The holotype material, composed of two stem pieces, contains many pycnidia agreeing completely with those of *Phoma exigua*. In the Netherlands *Phoma exigua* is also often isolated from lettuce (compare Boerema & Höweler, 1967: Table II), on which it usually occurs in association with symptoms of footrot.

**lappae.** — *P. herbarum* var. *lappae* P. Karst. in Meddn Soc. Fauna Flora fenn. 11: 141. 1884. — Holotype: Helsingfors, no date, Karsten (Herb. Karsten, H). — Host: *Arctium* (= *Lappa*) sp.

The holotype, which contains several stem pieces, shows many pycnidia agreeing with those of *Phoma exigua* on species of *Arctium* from the Netherlands (tested by isolation).

**lapsanae.** — *P. herbarum* f. *lapsanae* Roum. in Revue mycol. 15: 22. 1893 ("f. *laptanae*"). — Isotype: Roum., Fungi sel. exs., Cent. 63, No. 6261. 1893, Broglie, 1892, Niel (FH). — Host: *Lapsana communis*.

This form has been introduced with the annotation "spores plus petites que celles du *Phoma Lactucae*," which can be regarded as a description. The isotype examined, which shows stem pieces with seed capsules, contains many immature perithecia and small pycnidia with bacilliform spores. Therefore *P. herbarum* f. *lapsanae* probably represents the spermatogonial stage of an Ascomycete and may be a species of *Asteromella*.

**lepidii.** — *P. herbarum* f. *lepidii* D. Sacc. in Mycoth. ital. No. 941. 1902 (nomen

nudum). — Isotype: (Mycoth. ital. No. 941), Rome, Gianicolo, Febr. 1902, collector not known (PAD). — Host: *Lepidium graminifolium*.

The label of the exsiccatum gives information on the source of the material but no description; hence it is a nomen nudum. The isotype examined, containing one stem piece, bears many pycnidia of a *Phomopsis* species with only  $\alpha$ -spores (6.8–8.5  $\times$  c. 3.5  $\mu$ ). Possibly it represents the conidial stage of *Diaporthe eres*, a polyphagous species occurring among others on Cruciferae.

*lilacis*. — *P. herbarum* f. *lilacis* Sacc. in *Michelia* 2 (1): 93. 1880; in *Sylogae Fung.* 3: 133. 1884. — Type: not known to be in existence; type locality: Dép. de l'Eure. — Host: *Syringa* (= *Lilac*) sp.

The material on which Saccardo based this form was collected by Malbranche, but was not found in Saccardo's herbarium (PAD). Boerema & Dorenbosch (1970) listed this form in the synonymy of the ubiquitous species *Phoma macrostomum*. In the Netherlands *P. macrostomum* is repeatedly isolated from dead branches of *Syringa*. For a description of this fungus in vitro, see also Boerema & Dorenbosch (1965).

*loti-cretici*. — *P. herbarum* var. *loti-cretici* Nannizzi in *Atti Accad. Fisiocr. Siena* X, 2: 11. 1927. — Holotype: Taranto, island of S. Nicolicchio, Aug. 1926, Nannizzi (SIENA). — Host: *Lotus creticus*.

The holotype material, consisting of several stem pieces with leaf fragments, contains a fungus whose characteristics agree completely with those of *Phoma loticola* Died., described from dead stems of *Lotus corniculatus*. *Phoma loticola* has also been found in the Netherlands on various species of *Lotus*, and proves to be a species in its own right.

*lycopi*. — *P. herbarum* f. *lycopi* Hollós in *Annls hist.-nat. Mus. natn. hung.* 5: 457. 1907. — Type: non-existent (information Museum of Natural History in Budapest); type locality: near Kecskemét. — Host: *Lycopus exaltatus*.

The description suggests a *Phomopsis* species with  $\alpha$ -spores only. Possibly it is the conidial stage of *Diaporthe arctii*, which is also reported from other Labiatae, mostly under the synonym *Diaporthe tulasnei* Nitschke; compare Oudemans (1919–24) and Wehmeyer (1933: 23).

*marrubii*. — *P. herbarum* f. *marrubii* Sacc. in *Michelia* 1 (5): 523. 1879; in *Sylogae Fung.* 3: 133. 1884. — Holotype: near Alençon, Orne, no date, Gillet (Herb. Saccardo '10', PAD). — Host: *Marrubium* sp.

The holotype comprises a single stem piece bearing numerous pycnidia, the characteristics of which agree well with those of *Phoma exigua*. In the Netherlands *Phoma exigua* is also found on Labiatae.

*medicaginea*. — *P. herbarum* f. *medicaginis* Sacc. in *Michelia* 2 (1): 93. 1880. — *P. herbarum* f. *medicaginea* Sacc. in *Sylloge Fung.* 3: 133. 1884. (name change). — Holotype: Quevilly near Rouen, no date, Letendre (Herb. Saccardo '790', PAD). — Host: *Medicago* sp.

The holotype consists of four stem fragments bearing many pycnidia that agree with those of *Phoma exigua* on species of *Medicago* in the Netherlands (compare Boerema & Höweler, 1967: Table II).

*medicaginis*. — See under *medicaginea* and *medicaginum*.

*medicaginum*. — *P. herbarum* f. *medicaginum* Westend. in *Fungi europ. exs./Klotzschii* Herb. mycol. cont. (Ed. Rab.), Cent. 5, No. 455b. 1862 (nomen nudum); ex Fuck. in *Jb. Nassau. Ver. Naturk.* 23-24: 134. 1870 ("1869"; "f. *medicaginis*"); listed by Saccardo in *Sylloge Fung.* 3: 133. 1884 as "f. *medicaginis* Fuck.". — Isotype: (*Fungi europ.* No. 455b) near Termonde, no date, Westendorp (B, BR, M). — Host: *Medicago sativa*.

The distributed copies of *Fungi europ.* No. 455b are not accompanied by a diagnosis, but Fuckel validated the name of this infraspecific taxon by giving a description of the spores. Moreover Fuckel distributed specimens of the fungus in his *Fungi rhen.*, Fasc. 6, No. 580. 1863 (BR, FR). It is an independent species, well known as the causal organism of the 'black stem' of lucerne. Boerema & al. (1965b) pointed out that the correct name on the specific level is *Phoma medicaginis* Malbr. & Roum. (compared with the isotype of *Fungi gall. exs.*, Cent. 37, No. 3675. 1886, BR). For a description of the characteristics of this fungus, see also Rössner (1968).

*melampyri*. — *P. herbarum* f. *melampyri* Westend. in *Herb. crypt.* (Ed. Beyaert), Fasc. 23, No. 1133. 1857 ("a *Melampyri*", nomen nudum). — Isotype: (*Herb. crypt.* No. 1133) near Namur, no date, Belynyck (Herb. Westendorp & Wallays, BR; Herb. Verplancke, BR; Herb. Saccardo, PAD). — Host: *Melampyrum sylvaticum*.

The label of the exsiccatum of *P. herbarum* a *melampyri* distributed by Westendorp refers to the original description of *P. herbarum* ('Nouv. not. . . .', no. 51'), which lists *Melampyrum* as second host, but fails to give any differential criterion. The exsiccatum of *P. herbarum* f. *melampyri* Westend., distributed in 1862 by Rabenhorst

(Fungi europ. exs./Klotzschii Herb. mycol. cont., Cent. 5, No. 455a. 1862, BR, M), and collected by Westendorp near Termonde, also lacks a description. All the specimens examined possess numerous pycnidia agreeing morphologically with those of the holotype of *Phoma silvatica* Sacc. (PAD). In some cases they are associated with perithecia of *Didymella winteriana* (Sacc.) Petr. (Munk 1957: 337). Petrak (1922) suggested that *D. winteriana* represents the perfect stage of *P. silvatica*.

*mercurialis*. — *P. herbarum* f. *mercurialis* Sacc. in *Michelia* 2 (2): 337. 1881; in *Sylloge Fung.* 3: 133. 1884. — Holotype: Dép. de l'Eure, no date, Malbranche (Herb. Saccardo '132', PAD). — Host: *Mercurialis annua*.

The holotype (four stem pieces) contains numerous pycnidia which are in agreement with those of *Phoma exigua* on material of *Mercurialis annua* in the Netherlands (tested by isolation).

*minor*. — *P. herbarum* f. *minor* Unamuno in *An. Jard. bot. Madr.* 2: 56. 1942. — Type: non-existent (information Dr. E. Paunero, MA); type locality: Hoz de Beteta. — Host: *Digitalis obscura*.

According to the description this should be identical with *Phoma herbarum* s.s., see this paper under 'Synonymy'.

*nesliae*. — *P. herbarum* f. *nesliae* Thüm. in *Fungi austr.*, Cent. 12, No. 1161. 1874 (nomen nudum). — *P. oleracea* f. *nesliae* (Thüm.) ex Allesch. in *Rab. Kryptog-Flora, Pilze* 6: 274. 1898 ("1901"; "f. *Nesleae*"). — Lectotype: (Fungi austr. No. 1161) Brück, 1872, von Thümen (Herb. Saccardo, PAD). — Host: *Neslia paniculata*.

The exsiccata of *P. herbarum* f. *nesliae* distributed by von Thümen are not provided with a diagnosis, but Allescher, in transferring the form to *P. oleracea*, gave a good description based on a copy of *Fungi austr.* No. 1161 (B?). This description agrees completely with the characteristics of the material in Saccardo's herbarium selected as lectotype; this material is made up of four stem pieces. It proved to be a typical *Asteromella* species (small pycnidia with bacilliform spores, 4.2–5.1 × 0.8–1.7 μ), to be found on stems, capsules, and leaves of all kinds of Cruciferae. Probably it represents the spermatogonial stage of *Mycosphaerella cruciferarum* (Fr.) Lindau; compare Winter (1885: 378).

*nicotiana*e. — *P. herbarum* f. *nicotiana*e Roum. in *Revue mycol.* 19: 152. 1897. — Isotype: *Fungi sel. exs.*, Cent. 72. No. 7160. 1897, locality not known, May 1896, Fautrey (FH). — Host: *Nicotiana tabacum*.



The isotype material examined consists of two stem fragments and contains numerous pycnidia with 1- and 2-celled spores agreeing with those of *Phoma exigua* on *Nicotiana tabacum* in the Netherlands (tested by isolation). The characteristics of the pycnidia and spores given in the diagnosis of this form are also in accordance with those of *P. exigua*.

*parietariae*. — *P. herbarum* f. *parietariae* Brunaud in Bull. Soc. bot. Fr. **36** (=II, **11**): 338. 1889. — Type: not known to be in existence; type locality: Pons. — Host: *Parietaria officinalis*.

Judging from the description it is tenable to conclude that this form is identical with *Phoma exigua*, which in the Netherlands is also known to occur on *Parietaria officinalis*.

*phlei*. — *P. herbarum* f. *phlei* Sacc. in Michelia **2** (1): 93. 1880; in Sylloge Fung. **3**: 133. 1884 ("Phlai"). — Type: not known to be in existence; type locality: Saintes. — Host: *Phleum* sp.

The material on which Saccardo based this form was collected by Brunaud, but it is missing in Saccardo's herbarium.

The description, however, is in accordance with the characteristics of a saprophyte known to occur on all kinds of grasses, viz. *Neophoma graminella* (Sacc.) Petrak & Sydow (1927) = *Macrophoma graminella* (Sacc.) Berl. & Vogl., compare Dennis (1964: 124) and Dennis & Gray (1954).

*phytolaccae*. — *P. herbarum* f. *phytolaccae* Sacc. in Michelia **2** (1): 93. 1880; in Sylloge Fung. **3**: 133. 1884. — Holotype: Roum., Fungi gall. exs., Cent. 3, No. 230. 1879 ("Septoria phlyctaenoides B & C."), near Perpignan, winter 1878, collector not known (Herb. Saccardo, PAD). — Host: *Phytolacca decandra*.

Saccardo based this form on material made up of three stem pieces. It shows many pycnidia with 1- and 2-celled spores. The characteristics of this fungus agree fairly well with those of *Phoma exigua*.

*rubi*. — *P. herbarum* f. *rubi* Sacc. in Michelia **2** (1): 93. 1880; in Sylloge Fung. **3**: 133. 1884. — Holotype: Quevilly near Rouen, no date, Letendre (Herb. Saccardo '480', PAD). — Host: *Rubus idaeus*.

The holotype of *P. herbarum* f. *rubi*, consisting of two stem pieces, shows many pycnidia which correspond completely with indigenous material of *Phoma macrostomum* on *Rubus idaeus* (tested by isolation, see Boerema & Dorenbosch, 1970: table I). In association with the raspberry cane midge (*Thomasiniana theobaldi* Barnes) this

fungus may cause severe damage in raspberry (compare Labruyère & Engels, 1963: 250). For a description of *P. macrostomum* in vitro, see also Boerema & Dorenbosch (1965) under the synonym *P. limitata* (Peck) Boerema.

*salicariae* e. — *P. herbarum* f. *salicariae* Sacc. in *Michelia* 2 (1): 93. 1880; in *Sylloge Fung.* 3: 133. 1884. — Holotype: Quevilly near Rouen, no date, Letendre (Herb. Saccardo '889', PAD). — Host: *Lythrum salicaria*.

The holotype shows three stem pieces bearing many pycnidia with irregular fusoid-oblong 1- and more-celled spores similar to those of the ubiquitous saprophyte *Stagonospora samarorum*. See the discussion under *P. herbarum* f. *ansoniae-salicifoliae*.

*sambuci*. — *P. herbarum* var. *sambuci* Roum. in *Revue mycol.* 3/No. 9: 30. 1881 (nomen nudum). — Isotype: Roum., Fungi gall. exs., Cent. 11, No. 1014. 1881 ("f. *sambuci*"), Toulouse, autumn, no date, Roumeguère (Herb. Roumeguère, PC). — Host: *Sambucus nigra*.

This agrees with *Phoma herbarum* s.s.; see this paper under 'Synonymy'.

*sambuci-nigrae* e. — *P. herbarum* f. *sambuci-nigrae* Sacc. in *Michelia* 2 (2): 337. 1881; in *Sylloge Fung.* 3: 133. 1884. — Holotype: type locality and date not known, Roumeguère (Herb. Saccardo '359', PAD). — Host: *Sambucus nigra*.

The holotype material consists of a single split stem piece with numerous pycnidia similar to those of *Phoma exigua*. Boerema & Höweler (1967) regarded this taxon as a specialized pathogenic fungus and raised it to varietal rank, *P. exigua* var. *sambuci-nigrae* (Sacc.) Boerema & Höweler. It causes characteristic leaf spots and shoot dieback.

Vörös (1959), when discussing a *Phoma* found on dead branches of *Sambucus nigra* near Budapest, inadvertently used the combination *Phoma exigua* var. *sambuci-nigrae*. His sentence runs as follows: "Es ist sehr wahrscheinlich, dass dieser Pilz [that is, the fungus found by him], und das sehr nahestehende *Phoma exigua* Desm. "var. *sambuci-nigrae*" (Konidien 6-8 × 3-3.5 μ) mit *Phoma herbarum* West. identisch sind." Judging by the spore size mentioned by Vörös as compared with those of *P. exigua* (Saccardo: "5-7 μ longis") and *P. herbarum* (Saccardo: "6-11 × 3-4 μ"), it is clear that he must have interchanged the specific epithets '*exigua*' and '*herbarum*'. Moreover by his use of quotation marks Vörös indicated that he did not definitely accept the variety *sambuci-nigrae*.

*sarothamni*. — *P. herbarum* f. *sarothamni* Gonz.-Frag. in *Trab. Mus. nac. Cienc. nat., Madr. Ser. bot.* 10: 123. 1916. — Holotype: near Alcolea del Rio, Sevilla, Jan. 1914, Gonzáles Fragoso (MA-820). — Host: *Sarothamnus eriocarpius*.

The holotype shows many pycnidia on a single stem piece which are at first mouthless but later open with an irregularly ruptured aperture. The spores are oblong-ellipsoid,  $8(-8.5)-10(-10.5) \times 3(-3.5)-4(-4.5) \mu$ , provided with a conspicuous hilum, and subhyaline to yellow or olive-brownish. These characteristics accord quite well with those of the form-genus *Cleistophoma* erected by Petrak & Sydow (1927: 294). The infra-specific taxon f. *sarothamni* differs from the type species of *Cleistophoma* only in having smaller spores with a relatively thick wall.

*schoberiae*. — *P. herbarum* f. *schoberiae* Sacc. in *Michelia* 2 (1): 93. 1880; in *Sylloge Fung.* 3: 133. 1884. — Type: not known to be in existence; type locality: Straits of Dover. — Host: *Suaeda* sp. (= *Schoberia* sp.).

Saccardo based this form on material collected by Gaudefroy, but apparently he failed to preserve specimens for his herbarium (PAD).

Boerema & Höweler (1967) listed *P. herbarum* f. *schoberiae* as a synonym of *Phoma exigua*. In the original diagnosis the spores are described as being "curvulae," as in fact is often the case in *P. exigua*.

*scrophulariae*. — *P. herbarum* f. *scrophulariae* D. Sacc. in *Mycoth. ital.* No. 1527. 1905 (nomen nudum). — Isotype: (*Mycoth. ital.* No. 1527) Tagliacozzo, Aquila, April 1904, collector not known (Herb. Saccardo, PAD). — Host: *Scrophularia* sp.

The exsiccata of this form were distributed with a label giving information on the source of the material but no description. The isotype material examined consists of various stem fragments bearing numerous small, black, and apparently mouthless pycnidia,  $50-75 \mu$  diam., situated among subepidermal fibrils of brown hyphae. Spores very few, irregular in shape, continuous,  $5-10.2 \times 3.4 \mu$ . Except for the relatively large spore-size these characteristics fit the description of *Asteroma scrophulariae* Brunaud very well.

*scrophulariae*. — *P. herbarum* f. *scrophulariae* Roum. in *Revue mycol.* 3 / No. 9: 31. 1881 (nomen nudum). — Isotype: Roum., *Fungi sel. exs.*, Cent. 12, No. 1110, Luchon, Haute-Garonne, Febr. 1880. Roumeguère (Herb. Roumeguère, PC). — Host: *Scrophularia nodosa*.

The exsiccata of this form were distributed without a diagnosis; apparently Roumeguère considered this infra-specific taxon to be morphologically identical with *Phoma herbarum* s.s. The material examined, consisting of one stem piece, shows no trace of *Phoma*-pycnidia, so that its identity remains obscure.

*sempervivi-tectorum*. — *P. herbarum* f. *sempervivi-tectorum* Berl. &

Roum. in *Revue mycol.* **9**: 178 ("162"). 1887 (nomen nudum). — Isotype: Roum., *Fungi sel. exs.*, Cent. 43, No. 4216, Coimbra, winter 1876, Moller (FH). — Host: *Sempervivum tectorum*.

Like forma *scrophulariae* Roum. this form was introduced without a diagnosis. Examination of the two stem pieces constituting the isotype revealed a pycnidial fungus with 1-celled and some 2-celled spores similar to those of *Phoma exigua* as found on *Sempervivum tectorum* in the Netherlands (tested by isolation).

sii. — *P. herbarum* var. *sii* Hollós in *Annls hist.-nat. Mus. natn. hung.* **4**: 340. 1906. — Type: non-existent (information Museum Natural History in Budapest); type locality: near Nagy-Körös. — Host: *Sium latifolium*.

The description suggests a *Phomopsis* species with  $\alpha$ -spores only. Possibly it is the conidial stage of the 'Umbelliferae-hostform' of *Diaporthe arctii* (Wehmeyer, 1933: 41, 42).

solani-nigricantis. — *P. herbarum* f. *solani-nigricantis* Berl. & Roum. in *Revue mycol.* **9**: 178 ("162"). 1887 (nomen nudum). — Isotype: Roum., *Fungi sel. exs.*, Cent. 43, No. 4221. 1887, near Coimbra, winter, no date, Moller (FH). — Host: *Solanum nigrum*.

This form was not validly published, as it lacks a diagnosis. The syntype examined comprises various stem pieces bearing numerous pycnidia with 1- and 2-celled spores such as are known to occur in *Phoma exigua* growing on *Solanum nigrum* in the Netherlands (tested by isolation).

solidaginis. — *P. herbarum* f. *solidaginis* Sacc. in *Michelia* **2** (2): 337. 1881; in *Sylloge Fung.* **3**: 133. 1884. — Holotype: Aclon, May 1880, Malbranche (Herb. Saccardo '95', PAD). — Host: *Solidago* sp.

The holotype, consisting of two stem pieces, shows fructifications of various fungi, including two different *Phoma* species. The spore dimensions of one of these accord well with Saccardo's description, and its characteristics also agree with those of *Phoma exigua* on indigenous species of *Solidago* (tested by isolation).

stramonii. — *P. herbarum* f. *stramonii* Thüm. in *Mycoth. univ.*, Cent. 7, No. 677. 1877. ("strammonii", nomen nudum). — Isotype: (Mycoth. univ. No. 677) Bayreuth, 1876, von Thümen (Herb. Saccardo, PAD). — Host: *Datura stramonium*.

The label with which the exsiccata were distributed gives information on the source of the material but lacks a description. The isotype examined is made up

of three stem pieces containing numerous pycnidia which are identical with those of *Phoma exigua* on material of *Datura stramonium* occurring in the Netherlands (tested by isolation).

*stramonii*. — *P. herbarum* f. *stramonii* Roum. in *Revue mycol.* 1: 56. 1879 (nomen nudum). — Isotype: Roum., *Fungi gall. exs.*, Cent. 3, No. 212, near Toulouse, autumn 1878, collector not known (Herb. Roumeguère, PC). — Host: *Datura stramonium*.

The name of this form, like that of the preceding forma *stramonii* Thüm., was not validly published, as it lacks a diagnosis; apparently Roumeguère considered the form to be morphologically the same as *Phoma herbarum* s.s. The single stem piece of the material examined is devoid of *Phoma*-pycnidia, so that its identity cannot be ascertained.

*tageticola*. — *Sphaeria tageticola* Schw. in *Trans. Am. phil. Soc.* II, 4: 222. 1832 ("1834"; = *Synopsis Fung. Am. bor.*). — *P. herbarum* var. *tageticola* (Schw.) Starb. in *Bih. K. Svenska VetenskAkad. Handl.* 19 (Afd. 3, 2): 52. 1894. — Holotype: Bethlehem, no date, Schweinitz (Herb. Schweinitz, Collins collection No. 360, PH); isotype: Herb. Fries (UPS). — Host: *Tagetes* sp.

The holotype material consists of two stem pieces in an envelope while three more stem pieces are separately mounted on a piece of paper (compare Arthur & Bisby, 1918: 178–182). A duplicate of the type is to be found in Fries' herbarium (UPS) and consists of five stem pieces. Starbäck had used this material when he proposed the recombination *P. herbarum* var. *tageticola*. All these specimens agree in that they bear many pycnidia all of whose characters correspond with those of *Phoma exigua* occurring on species of *Tagetes* in the Netherlands (tested by isolation).

*tetragoniae*. — *P. herbarum* var. *tetragoniae* Sacc. & Berl. in *Revue mycol.* 8: 35. 1886; in *Sylloge Fung.* 10: 180. 1892 ("*Phoma herbarum* \**Ph. Tetragoniae*"). — Neotype: Algeria, no date, Trabut (Herb. Saccardo '68', PAD). — Host: *Tetragonia expansa*.

This agrees with *Phoma herbarum* s.s.; see this paper under 'Synonymy'.

*thulensis*. — *P. herbarum* var. *thulensis* P. Karst. in *Hedwigia* 23: 39. 1884. — Neotype: Green Harbour,† Sept. 1869, collector not mentioned (Herb. Karsten, H). — Host: *Pedicularis hirsuta*.

The type material of *P. herbarum* var. *thulensis*, collected in August 1868 by Th.

Fries, has apparently not been preserved. Consequently the only specimen of this variety in Karsten's herbarium is indicated as neotype. It consists of a few small stem pieces bearing some pycnidia with 1- and 2-celled spores similar to those of *Phoma exigua*. The latter is frequently found on various Scrophulariaceae in the Netherlands (tested by isolation).

*tulostomatis*. — *P. herbarum* var. *tulostomatis* Pat., Cat. rais. Pl. cell. Tun. 116. 1897. — Holotype: Fedjedj, Febr. 1892, Patouillard ("*Phoma Tulostomatis*", FH). — Host: *Tulostoma volvulatum* (Homobasidiomycetidae).

Boerema & al. (1968) pointed out that this variety agrees with *Phoma prunicola*, a dictyochlamydo-spores-producing fungus. This is one of the most common soil-borne *Phoma* species (Dorenbosch, 1970), so that its occurrence on another terrestrial fungus is not surprising. For a description of this species in vitro see Boerema & al. (1965a) and Morgan-Jones (1967b).

*urticae*. — *P. herbarum* f. *urticae* Sacc. in *Michelia* 1 (5): 523. 1879; in *Sylloge Fung.* 3: 133. 1884. — Holotype: Quevilly near Rouen, no date, Letendre (Herb. Saccardo '139', PAD). — Host: *Urtica* sp.

The holotype consists of part of the stem of a species of *Urtica* with several pycnidia which are identical with those of *Phoma exigua* on indigenous material of *Urtica* (tested by isolation).

*urticae*. — *P. herbarum* var. *urticae* Roum. in *Revue mycol.* 3/No. 9: 30. 1881 (nomen nudum). — Isotype: Roum., Fungi gall. exs., Cent. 11, No. 1017. 1881, near Toulouse, winter 1879, Roumeguère (Herb. Roumeguère, PC). — Host: *Urtica dioica*.

Roumeguère distributed this 'variety' of *Phoma herbarum* without a description, so that it may be inferred that he considered it morphologically identical with *P. herbarum*.

The isotype examined, consisting of one stem piece, reveals the characteristic small-spored, beaked pycnidia of *Phoma acuta* (Hoffm. ex Fr.) Fuck. = *Plenodomus acutus* (Hoffm. ex Fr.) Bubák (spore dimensions  $4.2-6.8 \times 1.7-2.5 \mu$ ), the conidial state of *Leptosphaeria acuta* (Fuck.) P. Karst. For a discussion of the characteristics of *P. acuta*, see von Höhnelt (1918: 138) and Petrak (1921: 192).

*valerianae*. — *P. herbarum* f. *valerianae* Sacc. in *Michelia* 2 (2): 337. 1881; in *Sylloge Fung.* 3: 133. 1884. — Holotype: Rouen, no date, Malbranche (Herb. Saccardo '92', PAD). — Host: *Valeriana* sp.

The holotype material, two stem pieces glued to a sheet of paper, bears numerous pycnidia of a *Phoma* species with 1-celled spores, mostly  $4.5\text{--}5.5 \times 1.5\text{--}2.5 \mu$ . Careful comparison shows that it fully corresponds with a seed-borne pathogen of Valerianaceae, recently described as *Phoma valerianellae* Gindrat, Semecnik & Bolay (1967) and subsequently under the same name by Boerema & de Jong (1968).<sup>6</sup>

In Saccardo's diagnosis the spore dimensions of *P. herbarum* f. *valerianae* were given as  $6 \times 3.5 \mu$ , which is larger than the spores actually turn out to be and this explains Boerema & de Jong's failure to recognize f. *valerianae* as a synonym of their species.

*verbasci*. — *P. herbarum* f. *verbasci* Gonz.-Frag. in Trab. Mus. nac. Cienc. nat., Madr., Ser. bot. 7: 38. 1914. — Type: non-existent (information Dr. E. Paunero, MA); type locality: Estación Alp. de Biol., Mont. Guadarrama. — Host: *Verbascum thapsi*.

The material in the fungus collection of Gonzáles Fragoso (MA-558), named *P. herbarum* f. *verbasci* and indicated as "cotypo; prope Est. Alp. de Biol. ubi collegit 14-VIII-1914," contains only a species of *Coniothyrium* with brown, relatively large spores ( $10.2\text{--}13.6 \times 5.1\text{--}6.8 \mu$ ). This cannot be the fungus described by Gonzáles Fragoso, who stated that the spores were hyaline,  $7\text{--}9 \times 3\text{--}3.5 \mu$ . The description of forma *verbasci* on the other hand, suggests that the ubiquitous species *Phoma exigua* is involved which, in the Netherlands, is found on all kinds of Scrophulariaceae.

*verbenae*. — *P. herbarum* f. *verbenae* Sacc. in Michelia 1 (5): 523. 1879 (nomen nudum); ex Sacc. in Sylloge Fung. 3: 133. 1884. — Holotype: Alençon, no date, Gillet (Herb. Saccardo '41', PAD). — Host: *Verbena* sp.

The holotype represented by four stem fragments appears to contain many pycnidia of a characteristic *Phomopsis*-stage with  $\alpha$ - and  $\beta$ -spores. The dimensions of the  $\alpha$ -spores ( $6.8\text{--}8.5 \times 2.5\text{--}3.4 \mu$ ) agree very well with those listed for *P. herbarum*

<sup>6</sup> Gindrat (Gindrat & al., 1967) misused the information he had received from Dr. R. Schneider (Berlin) and Dr. J. A. von Arx (Baarn) by publishing the manuscript-name *Phoma valerianellae* for a species which Boerema & de Jong had discovered to be undescribed. When Boerema & de Jong subsequently published the name *Phoma valerianellae* Boerema & de Jong (1968) it was a homonymous synonym of *P. valerianellae* Gindrat & al.

Gindrat, in a "Mise au point" (1968) apologized for what had happened. He tried to make rectification by declaring that "la désignation taxonomique correcte de ce champignon est: *Phoma valerianellae* Boerema & de Jong." But as to this statement it may be observed that (i) down to the final letter Gindrat's publication is in accordance with the relevant Articles of the Code, and (ii) the binomial *Phoma valerianellae* is indissolubly connected with the author names Gindrat, Semecnik & Bolay. The statement quoted above is an example of the erroneous application of the word 'taxonomic' where 'nomenclatural' is meant.

f. *verbenae* in 'Sylloge Fung.' (6-7 × 2.5-3 μ). Probably this form is the conidial stage of *Diaporthe verbenae* Tassi which, according to Wehmeyer (1933: 330), may be the same as *D. arctii*.

*verbenae-paniculatae*. — *P. herbarum* f. *verbenae-paniculatae* Berl. & Roum. in *Revue mycol.* 9: 178 ("162"). 1887 (nomen nudum). — Isotype: Roum., *Fungi scl. exs.*, Cent. 43, No. 4220. 1887, Bot. Garden, Coimbra, autumn 1886, Moller (FH). — Host: *Verbena paniculata*.

This form was introduced without a diagnosis. The isotype examined, consisting of two stem pieces, shows a pycnidial fungus with 1- and 2-celled spores similar to those in *Phoma exigua* on species of *Verbena* in the Netherlands (tested by isolation).

*vincae*. — *P. herbarum* f. *vincae* Brunaud in *Act. Soc. linn. Bordeaux* 40 (= IV, 10): 75. 1886. — Type: not known to be in existence; type locality: Saintes. — Host: *Vinca major*.

The spore dimensions given for this form, 6-8 × 2.5-3 μ, correspond in all respects with those of *Phoma exigua* on species of *Vinca* in the Netherlands. *P. exigua* is commonly associated with leaf spots and shoot dieback of these hosts, see Jansen (1965).

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ON PHOMA MACROSTOMUM MONT.,  
A UBIQUITOUS SPECIES ON WOODY PLANTS

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(With five Text-figures)

The synonymy, characteristics, and habitat of *Phoma macrostomum* are discussed. In vitro two varieties can be distinguished: variety *macrostomum* with reddish pigmented hyphae and variety *incolorata* (Horn) comb. nov. with colourless hyphae.

The comparative study of *Phoma*-isolates obtained in our diagnostic work on diseased plants has led to the recognition of various 'polyphagous' *Phoma* species; compare Boerema (1964, 1970), Boerema & al. (1965, 1968), Boerema & Höweler (1967), and Dorenbosch (1970). In this paper the synonymy, diagnostic characters, and habitat of a *Phoma* species occurring frequently on necrotic tissue of all kinds of trees and shrubs are treated.

The names of authors are abbreviated in accordance with Grumann's "Autorenliste" (1963: 59-74), and with Ainsworth's list (1961: 37-41). Herbaria and culture collections are coded according to Lanjouw & Stafleu (1959) and the list of abbreviations in the catalogue of the American Type Culture Collection (Ed. 8, 1968). Titles of journals are abbreviated in accordance with the "World List of Scientific Periodicals", 1963-1965.

PHOMA MACROSTOMUM MONT. var. MACROSTOMUM

*Phoma macrostomum* Mont. in *Anns Sci. nat. (Bot.)* III, 11: 52. 1849. — Lectotype: isotype, Salon, 1849, Castagne (Herb. Roussel, PC).

*Phoma phyllostictoides* Desm. in *Pl. crypt. France* II [ed. 3] Fasc. 14, No. 694. 1859.

*Phoma herbarum* f. *catalpae-capsularum* Sacc. in *Michelia* 2 (1): 93. 1880; in *Sylloge Fung.* 3: 133. 1884.

*Phoma herbarum* f. *lilacis* Sacc. in *Michelia* 2 (1): 93. 1880; in *Sylloge Fung.* 3: 133. 1884.

*Phoma herbarum* f. *rubi* Sacc. in *Michelia* 2 (1): 93. 1880; in *Sylloge Fung.* 3: 133. 1884.

*Phoma pomi* Schulzer & Sacc. ["*Phoma (Aposphaeria?) pomi*"] in *Hedwigia* 23: 109. 1884; not *Phoma pomi* Pass. in *Atti Accad. naz. Lincei R. (Cl. Sci. fis. mat. nat.)* 4 (2): 96. 1888 (see Brooks & Black in *Phytopathology* 2: 63-72. 1912). — *Aposphaeria pomi* (Schulzer & Sacc.) Sacc. in *Sylloge Fung.* 3: 177. 1884.

*Phoma mororum* Sacc. in *Boll. mens. Bachicolt.* II, 2: 53-56. 1884; in *Sylloge Fung.* 3: 95. 1884.

*Phoma cicatricum* Pass. in *Atti Accad. naz. Lincei R. (Cl. Sci. fis. mat. nat.)* 4 (2): 96. 1888.

*Aposphaeria caricae* Pass. ("*Aposphaeria*") in Atti Accad. naz. Lincei Rc. (Cl. Sci. fis. mat. nat.) 4 (2): 99. 1888.

*Phyllosticta saxifragae* Brunaud in Anns Soc. Sci. nat. Charente-Infér. 1889: 53. 1889 (or 1890?, not seen).

*Phoma friesii* Brunaud in Bull. Soc. bot. Fr. 36 (= II, 11): 337. 1889.

*Phyllosticta mali* Prill. & Delacr. in Bull. Soc. mycol. Fr. 6: 181. 1890; not *Phyllosticta mali* Briard, Fl. cryptog. Aube & Suppl. cat. Troyes 79. 1888 [= *Asteromella mali* (Briard) Boerema; see Boerema & Dorenbosch, 1965].

*Phyllosticta limitata* Peck in Rep. N.Y. St. Mus. nat. Hist. 50: 115. 1897. — *Phoma limitata* (Peck) Boerema apud Boerema & Dorenbosch in Versl. Meded. plziektenk. Dienst 142 (Jaarb. 1964): 138. 1965.

*Phyllosticta robinicola* Hollós ("*P. robiniaeicola*") in Anns hist.-nat. Mus. natn. hung. 8: 2. 1910.

*Phyllosticta taxi* Hollós in Anns hist.-nat. Mus. natn. hung. 8: 3. 1910.

*Polyopeus purpureus* var. *verus* Horne in J. Bot., Lond. 58: 240. 1920.

#### MISAPPLICATIONS.—

*Phoma mori* Mont. [*Aposphaeria mori* (Mont.) Sacc.] sensu Wollenw. & Hochapf. in Z. ParasitKde 8: 583. 1936, and *Aposphaeria pezizoides* Ell. & Ev., *Phoma morearum* Brunaud, *Phoma salicina* Westend., *Phoma euonymella* Brunaud, *Phoma cinerascens* Sacc. sensu Wollenw. & Hochapf. in Z. ParasitKde 8: 583. 1936 (as syn. of "*P. mori*").

*Phoma elliptica* Fuck. ("*P. ellipticum*"; name change of *Hysterium samarae* Fr.) sensu Wollenw. & Hochapf. in Z. ParasitKde 8: 586. 1936, and *Phoma platanoidis* Cooke sensu Wollenw. & Hochapf. in Z. ParasitKde 8: 586. 1936 (as syn. of "*P. ellipticum*").

*Phoma exigua* Desm. sensu Brook in N.Z. J agric. Res. 11: 242. 1968.

DESCRIPTIONS & ILLUSTRATIONS IN VITRO.—Horne in J. Bot., Lond. 58: 240, 241. 1920 (*Polyopeus purpureus* var. *verus*); Wollenweber & Hochapfel in Z. ParasitKde 8: 583–586, fig. 10. 1936 ("*Phoma mori*", misapplied); in Z. ParasitKde 8: 586–587, fig. 11. 1936 ("*Phoma ellipticum*", misapplied); Boerema & Dorenbosch in Versl. Meded. plziektenk. Dienst 142 (Jaarb. 1964): 138–142, figs. 2, 3. 1965 (*Phoma limitata*).

DIAGNOSTIC CHARACTERS IN VIVO.—Pycnidia (Fig. 1) immersed to superficial, ferruginous to black, spherical-oval, 80–260  $\mu$  diam., with one distinct ostiole 10–30  $\mu$  in diam. Pycnidiospores (Fig. 2) hyaline, ellipsoid or oval, usually 1-celled, occasionally 2-celled, 4.2–8.5  $\times$  2.1–3.8  $\mu$  (av. 6.3  $\times$  3.1  $\mu$ ).

DIAGNOSTIC CHARACTERS IN VITRO.—Pycnidia (Fig. 3) superficial or immersed in agar, ferruginous to black, spherical to subpyriform (pitcher-shaped), or irregular, sometimes with one or more neck-like outgrowths, size variable, mostly 100–230  $\mu$  (80–300  $\mu$ ); ostioles 20–45  $\mu$  diam. Pycnidiospores (Fig. 4) hyaline, generally ellipsoid to reniform-oblong; 1-celled, 5–8  $\times$  2–4  $\mu$  (av. 6.5–2.6  $\mu$ ) or 2-(occasionally 3- or 4-) celled, 8.5–14  $\times$  3–4  $\mu$ . The spore exudate is usually tinged pink. In old cultures the pycnidia may also contain swollen brown coloured spores (Fig. 5), nearly twice the size of the hyaline pycnidiospores.

The hyphae have red to violet pigment in the plasma and the guttules, rendering the fungus characteristically dull red-violet in culture.

HABITAT.—Ubiquitous on necrotic tissue of various parts of all kinds of woody plants; also incidental on herbaceous plants (see Table I). Very often associated with spots on leaves and fruits of apple. The fungus behaves like a weak parasite or wound parasite.

## SPECIMENS EXAMINED.—

EXSICCATA: *Phoma macrostomum*, lectotype (Herb. Roussel, PC); *Phoma phyllostictoides*, isotype (Herb. Desmazières, PC); *Phoma herbarum* f. *catalpae-capsularum*, holotype (Herb. Saccardo, PAD); *Phoma herbarum* f. *rubi*, holotype (Herb. Saccardo, PAD); *Phyllosticta mali* Prill. & Delacr., holotype (Herb. Delacroix, VER<sup>1</sup>).

CULTURES: *Phyllosticta limitata*, from leaf spots of apple, USA, isolated by Whetzel (CBS 115.12); "*Phoma ellipticum*" (misapplied), (Nr. 4992) from stem of *Rosa multiflora* 'Cathayensis', Germany, isolated by Wollenweber (CBS 297.36); "*Phoma exigua*" (misapplied), (Nr. 68109) from pre-harvest lenticel spot of apple, New Zealand, isolated by Brook (1968); and numerous Dutch isolates from all kinds of trees and shrubs (Table I), e.g. from apple branches (*Phoma limitata*, ATCC 16583, CBS 529.66 and CMI 118.020) and branch of elm (*Phoma limitata*, CBS 371.61).

Although the fungus frequently produces septate spores, especially in vitro, its sporogenesis places it in the form-genus *Phoma* Sacc., see Boerema (1965).

Its oldest known name, *Phoma macrostomum*, refers to the characteristic, usually wide, ostiole of the fungus; compare Boerema & Dorenbosch (1965). The original material of *P. macrostomum* in Herb. Roussel (PC), selected here as lectotype, consists of four pieces of *Hedera helix* stem with numerous pycnidia, each containing ellipsoid spores typical of the fungus growing in vivo (see 'Diagnostic characters' above). The microscopical characteristics of the type material have further been compared with Dutch material of the fungus on ivy; cultures from these were also studied (Table I).

The fungus appears to have been described in vitro for the first time by Horne (1920) as *Polyopeus purpureus* var. *verus*, type of the form-genus *Polyopeus*. The epithet 'purpureus' refers to the characteristic rose-purple colour of the mycelium in culture. Three other 'varieties' of *Polyopeus purpureus* distinguished by Horne did not show this pigmentation; they belong to *Phoma macrostomum* var. *incololata*, discussed below. Both Horne and Kidd & Beaumont (1924) frequently isolated *Polyopeus purpureus* var. *verus* from "spotted" fruits of various commercial apple varieties. This type of injury caused by the fungus ('latent parasite', cf. Bondoux, 1967) is still well known; compare Boerema & Dorenbosch (1965), van Kesteren (1966), van der Scheer (1969), and Brook (1968, under the misapplied name *Phoma exigua*). The criterion of Horne's genus *Polyopeus* differentiating it from *Phoma* was thought to be the development of one or more tubular neck-like outgrowths on the pycnidia, which is common in cultures of *Phoma macrostomum* (see 'Diagnostic characters'); however, various *Phoma* species may occasionally show such (multi)rostrate pycnidia in vitro. Therefore we agree with Grove (1935: 162) that it is unreal and undesirable to base a separate genus on the occurrence of rostrate pycnidia.

The widespread occurrence of the fungus on various parts of all kinds of trees and shrubs was first recognized by Wollenweber & Hochapfel (1936). Because of small differences in the sizes of the spores and pycnidia in culture—which is a matter

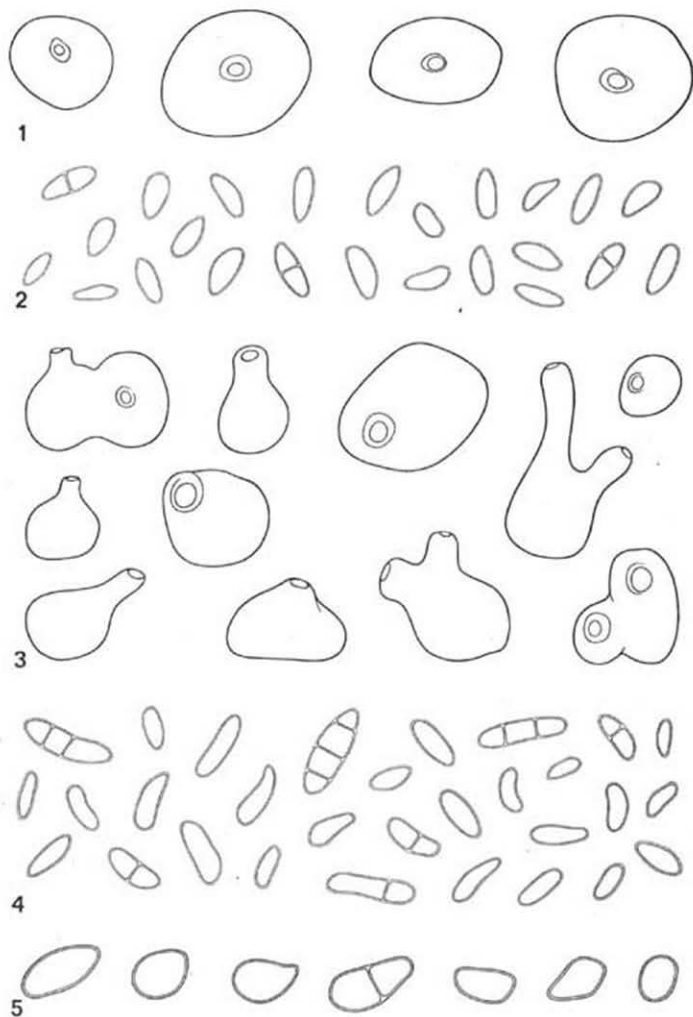
<sup>1</sup> Station centrale de Pathologie Végétale, Versailles; not listed by Lanjou & Staffeu (1959).

TABLE I

HOSTPLANTS FROM WHICH PHOMA MACROSTOMUM HAS BEEN ISOLATED

Aceraceae	4	Hamamelidaceae	1	Rosaceae (cont.)	
<i>Acer</i> (2 + 1 <sup>+</sup> )		<i>Hamamelis</i> (1)		<i>Prunus</i> (15)	
<i>Anthurium</i> (1)		Hippocastanaceae	1	<i>Pyrus</i> (27 + 2 <sup>+</sup> )	
Apocynaceae	1	<i>Aesculus</i> (1)		<i>Rosa</i> (8)	
<i>Vinca</i> (1)		Iridaceae	1	<i>Rubus</i> (2)	
Araliaceae	2	<i>Freesia</i> (1)		<i>Sorbus</i> (4)	
<i>Hedera</i> (2)		Juglandaceae	4	<i>Stranvaesia</i> (1 + 1 <sup>+</sup> )	
Berberidaceae	3	<i>Juglans</i> (4)		Salicaceae	6
<i>Berberis</i> (2)		Liliaceae	2	<i>Populus</i> (2)	
<i>Mahonia</i> (1)		<i>Convallaria</i> (1 <sup>+</sup> )		<i>Salix</i> (4)	
Bignoniaceae	2	<i>Tulipa</i> (1)		Saxifragaceae	14
<i>Catalpa</i> (2)		Magnoliaceae	4	<i>Hydrangea</i> (5)	
Caprifoliaceae	13	<i>Magnolia</i> (4)		<i>Philadelphus</i> (2)	
<i>Viburnum</i> (8)		Moraceae	2	<i>Ribes</i> (7)	
<i>Sambucus</i> (5)		<i>Morus</i> (2)		Scrophulariaceae	2
Chenopodiaceae	2	Oleaceae	21	<i>Antirrhinum</i> (1)	
<i>Beta</i> (1)		<i>Forsythia</i> (2)		<i>Scrophularia</i> (1 <sup>+</sup> )	
<i>Chenopodium</i> (1)		<i>Fraxinus</i> (12)		Solanaceae	5
Compositae	6	<i>Ligustrum</i> (1)		<i>Lycium</i> (3)	
<i>Achillea</i> (1)		<i>Syringa</i> (6)		<i>Solanum</i> (2)	
<i>Chrysanthemum</i> (2)		Orchidaceae	1	Taxaceae	1
<i>Galinsoga</i> (1)		<i>Pterocaulis</i> (1)		<i>Taxus</i> (1)	
<i>Lactuca</i> (1)		Papaveraceae	1	Thymelaeaceae	1
<i>Solidago</i> (1)		<i>Dicentra</i> (1)		<i>Daphne</i> (1)	
Cornaceae	2	Papilionaceae	6	Tiliaceae	1
<i>Cornus</i> (2)		<i>Colutea</i> (1)		<i>Tilia</i> (1)	
Corylaceae	2	<i>Laburnum</i> (1)		Ulmaceae	2
<i>Alnus</i> (1)		<i>Robinia</i> (3)		<i>Ulmus</i> (2)	
<i>Corylus</i> (1)		<i>Trifolium</i> (1)		Umbelliferae	5
Cucurbitaceae	1	Platanaceae	1	<i>Apium</i> (2)	
<i>Cucumis</i> (1)		<i>Platanus</i> (1)		<i>Heracleum</i> (1)	
Cupressaceae	1	Rosaceae	149	<i>Sium</i> (1 + 1 <sup>+</sup> )	
<i>Chamaecyparis</i> (1)		<i>Cotoneaster</i> (3)		Urticaceae	2
Elaeagnaceae	1	<i>Crataegus</i> (4)		<i>Urtica</i> (2)	
<i>Elaeagnus</i> (1)		<i>Exochorda</i> (1)		Vitaceae	2
Ericaceae	3	<i>Fragaria</i> (3)		<i>Vitis</i> (2)	
<i>Rhododendron</i> (3)		<i>Malus</i> (73 + 3 <sup>+</sup> )			
Guttiferae	2	<i>Mespilus</i> (1)			
<i>Hypericum</i> (2)		<i>Physocarpus</i> (1)			

The ciphers in the table refer to the number of isolates made of *Phoma macrostomum* (+ denotes var. *incolorata*). In the period 1961-1969, 280 isolates were made from diseased or dead plant material distributed over 39 families and 73 genera of Phanerogams. These isolates were obtained from stems (144), leaves (59), roots (6), and seeds or fruits (71).



Figs. 1-5. *Phoma macrostomum* s. l. — 1. Pycnidia in vivo. — 2. Pycnidiospores in vivo. — 3. Pycnidia in vitro. — 4. Pycnidiospores in vitro. — 5. Swollen dark coloured spores from old pycnidia in vitro.



of phenotypes—they differentiated this pigmented fungus into two "species," which they described under the names "*Phoma mori*" and "*Phoma ellipticum*." Both names were misapplied, as already noted by Boerema & Dorenbosch (1965). *Phoma (Aposphaeria) mori* proves to be the *Phomopsis*-state of *Diaporthe sociabilis* Nitschke, see von Höhnel (1910: 660) and Wehmeyer (1933: 119). According to Fuckel, *Fungi rhen. Suppl. Fasc. 7, No. 2128* (1868) at M and G, *Phoma elliptica* ("ellipticum"; = *Hysterium samarae*) is probably a species of *Dothichiza (Sclerophoma)*; compare Petrak, 1923: 266, 267) and is in any case quite different from *P. macrostomum*. (No original material of *Hysterium samarae* has been preserved.)

Various other names listed by Wollenweber & Hochapfel as synonyms of "*P. mori*" and "*P. ellipticum*" are also misapplied. *Phoma morearum* [= *Phomopsis morearum* (Brunaud) Curzi & Barbaini] probably represents, like *Phoma mori*, the conidial state of *Diaporthe sociabilis*. *Phoma salicina*, on account of its recorded similarity with *Phoma malvacearum* Westend. (Westendorp, 1857: 564), is undoubtedly also a *Phomopsis* species (compare Grove, 1935: 103, 201, 223); probably it refers to the conidial state of *Diaporthe eres* Nitschke, see Wehmeyer (1933: 88, 89). *Phoma euonymella*, according to its description (Brunaud, 1889), is also a *Phomopsis* species and probably also belongs to the ubiquitous ascomycete *Diaporthe eres* (compare Wehmeyer, 1933: 76). The same is true of *Phoma cinerascens* [= *Phomopsis cinerascens* (Sacc.) Trav.] (see Saccardo, 1914: 306; Wehmeyer, 1933: 77; Grove, 1935: 186, 187) and *Phoma platanoidis* [= *Phomopsis platanoidis* (Cooke) Died.] (see Grove, 1935: 166; Wehmeyer, 1933: 64). According to the type specimen in FH and copies of N. Am. Fungi No. 3158 (1894) at FH, L, and PAD, *Aposphaeria pezizoides* is a species of *Plenodomus*, identical with *Plenodomus salicum* (Sacc.) Diedicke (1911: 140).

Apart from *Polyopeus purpureus* var. *verus* discussed above, Wollenweber & Hochapfel (l.c.) further mention as synonyms: *Aposphaeria caricae*, *Phoma cicatricum*, *Phoma mororum*, and *Phyllosticta saxifragae*. Original material of these four species is not known to be in existence (not in PARMA, PAD, or PC), but the diagnoses accord well with the characteristics of *Phoma macrostomum* in vivo. Considering that Wollenweber & Hochapfel's interpretation was based on isolates from the hosts mentioned in the diagnoses of these species (*Ficus*, *Morus*, and *Saxifraga* species) we accept their interpretation.

The name *Phoma (Aposphaeria) pomi*, enumerated in our list of synonyms, has also been adopted from Wollenweber & Hochapfel's study. They listed this species in the synonymy of "*Phoma striaeformis*," a misapplied name for the non-pigmented variety of *Phoma macrostomum* dealt with on p. 55. Original material of *P. pomi* is not known to be in existence (not in PAD), but its original diagnosis corresponds with the characteristics of *P. macrostomum* in vivo. However we cannot agree with Wollenweber & Hochapfel's arrangement of this species under the non-pigmented variety. Only a study of cultures makes it possible to differentiate the pigmented and non-pigmented forms. Moreover, in our experience the pigmented variety is by far the most frequently isolated form of *P. macrostomum* (see Table I).

The identification of *Phoma phyllostictoides* with *P. macrostomum* is based on the study of isotype-material (see 'Specimens examined') collected on legumes of *Colutea*

*arborescens*; it proved to contain many pycnidia typical of *P. macrostomum*. We isolated the fungus ourselves from the same substratum (Table I).

The holotype material of *Phoma herbarum* f. *catalpae-capsularum* and *P. herbarum* f. *rubi* (see 'Specimens examined') also showed numerous pycnidia characteristic of *P. macrostomum*. They were compared with similar Dutch material of *P. macrostomum* from *Catalpa* and *Rubus* (tested by isolation; Table I). The material on which Saccardo based *P. herbarum* f. *lilacis* (from *Lilac* = *Syringa*) was not present in Saccardo's herbarium (PAD). The description of the spores, however, points to *P. macrostomum*, which we have repeatedly isolated from dead branches of *Syringa* spp. (Table I).

The synonymy of *Phoma friesii*, *Phyllosticta robinicola* ("robiniaeicola") and *Phyllosticta taxi* with *Phoma macrostomum* is also based on comparison of their diagnoses with the characteristics of *P. macrostomum* on the same hosts (*Ligustrum*, *Robinia* and *Taxus* species; compare Table I). The original material on which Brunaud based the description of *Phoma friesii* has not been preserved, while the type material of *Phyllosticta robinicola* and *P. taxi* described by Hollós was lost during the Second World War (information Museum of Natural History in Budapest).

The synonyms *Phyllosticta mali* and *Phyllosticta (Phoma) limitata* described from leaf spots of apple have been discussed extensively by Boerema & Dorenbosch (1965). The holotype-material of *Phyllosticta mali* was examined (Boerema & Dorenbosch, l.c. Fig. 1); of *Phyllosticta (Phoma) limitata* a typical American isolate was studied (see 'Specimens examined'). For the phytopathological literature on *P. macrostomum* in association with leaf spots of apple we also refer to Boerema & Dorenbosch, l.c.

Finally we note that because of its occurrence on apple leaves the fungus has often been confused with *Phoma prunicola* (Opiz) Wollenw. & Hochapf., see Boerema & al. (1965, 1968) and Morgan-Jones (1967). Recently Brook (1968) confused the fungus with *Phoma exigua* Desm., which is quite different, see Boerema & Høweler (1967).

***Phoma macrostomum* var. *incolorata*** (Horne) Boerema & Dorenb., *comb. nov.*

*Polyopeus purpureus* var. *incoloratus* Horne in J. Bot., Lond. 58: 240. 1920 (basionym).

*Polyopeus purpureus* var. *latirostratus* Horne in J. Bot., Lond. 58: 240. 1920.

*Polyopeus purpureus* var. *nigrirostratus* Horne in J. Bot., Lond. 58: 240. 1920.

MISAPPLICATIONS.—

*Phoma striaeformis* Dur. & Mont. *sensu* Wollenw. & Hochapf. in Z. ParasitKde 8: 587. 1936, and *Phoma petiolorum* Desm., *Phoma petiolorum* f. *juglandis* Brunaud, *Phoma depressa* Berk. & Br., *Phoma planiuscula* Sacc., *Cytispora abnormis* Berk. & Curt. [*Phoma abnormis* (Berk. & Curt.) Sacc.], *Phoma siliquastris* Sacc., *Phoma pomi* Schulzer & Sacc. [*Aposphaeria pomi* (Schulzer & Sacc.) Sacc.], *Phoma mespili* Oudem., *Phoma bismarckii* Kidd & Beaum. *sensu* Wollenw. & Hochapf. in Z. ParasitKde 8: 587. 1936 (as syn. of "*P. striaeformis*").

*Phoma aceris-negundinis* Arcangeli *sensu* Wollenw. & Hochapf. in Z. ParasitKde 8: 590. 1936, and *Phoma fraxinifoliae* Allesch. *sensu* Wollenw. & Hochapf. in Z. ParasitKde 8: 590. 1936 (as syn. of "*P. aceris-negundinis*").

DESCRIPTIONS & ILLUSTRATIONS IN VITRO.—Horne in J. Bot., Lond. 58: 240, 241. 1920 (*Polyopeus purpureus* var. *incoloratus*, *P. purpureus* var. *latirostratus*, *P. purpureus* var. *nigrirostratus*); Wollenweber & Hochapfel in Z. ParasitKde 8: 587–590, fig. 12. 1936 (“*Phoma striaeformis*”, misapplied) in Z. ParasitKde 8: 590–591, fig. 13. 1936 (“*Phoma aceris-negundinis*”, misapplied).

DIAGNOSTIC CHARACTERS.—Morphologically similar to variety *macrostomum*, but in vitro easily distinguished by the absence of reddish pigment in the hyphae.

HABITAT.—This variety occurs in the same habitats as *P. macrostomum* var. *macrostomum*, i.e. it is found especially on necrotic tissue of woody plants, such as stems, leaves, and fruits. However it appears to be less widely distributed than *P. macrostomum* var. *macrostomum*.

SPECIMENS EXAMINED.—

Cultures: “*Phoma striaeformis*” (misapplied), (Nr. 3197) from twig of *Robinia pseudoacacia*, Germany, isolated by Wollenweber (CBS 300.36); and from bud of apple, Switzerland, isolated by Geigy (CBS 369.52); and various isolates of *Phoma macrostomum* var. *incolorata* from different trees and shrubs in the Netherlands (Table I).

Because this fungus can be distinguished from *P. macrostomum* var. *macrostomum* only by the absence of red-violet pigment in the hyphae, we think it in accordance with the purpose of the artificial system of the Deuteromycetes to consider it merely a variety of *P. macrostomum* (compare Boerema & Höweler, 1967).

Three strains (phenotypes) of this non-pigmented variety of *Phoma macrostomum* appear to have been described from England by Horne (1920) as successively *Polyopeus purpureus* var. *incoloratus* (with narrow rostra), *P. purpureus* var. *latirostratus* (with wide rostra) and *P. purpureus* var. *nigrirostratus* (with black rostra). The new combination *Phoma macrostomum* var. *incolorata* has been based on the first mentioned infraspecific taxon. Horne's isolates were made from “spotted” apples; it should be noted, however, that the pigmented *Polyopeus purpureus* var. *verus* (= *Phoma macrostomum* var. *macrostomum*) occurs much more frequently in association with “spotted” apples in England than the non-pigmented strains (cf. Kidd & Beaumont, 1924: 105).

Wollenweber & Hochapfel (1936) also studied some isolates of this colourless variety of *Phoma macrostomum*. On account of small differences in the sizes of the pycnidia—which are conditioned phenotypically—they distinguished two “species,” described under the misapplied names “*Phoma striaeformis*” and “*Phoma aceris-negundinis*.” Examination of a specimen of *Phoma striaeformis*, issued by Desmazières [Pl. crypt. France II (ed. 3) Fasc. 2, No. 59 (1853) in PC] showed that this name refers to a species of *Phomopsis* [*P. striaeformis* (Dur. & Mont.) Grove (1917: 65)], which is probably identical with the conidial state of *Diaporthe eres* Nitschke; compare Wehmeyer (1933: 82) and Grove (1935: 215). According to the isotypes Erb. crittog. ital. II No. 1379 (PAV and PISA), *Phoma aceris-negundinis* is also a

*Phomopsis* species, similar to *Phomopsis pustulata* (Sacc.) Died., the conidial state of *Diaporthe pustulata* (Desm.) Sacc., see Wehmeyer (1933: 153-155) and Grove (1935: 166, 167).

Various other names listed by Wollenweber & Hochapfel as synonyms of "*P. striaeformis*" likewise appear to refer to *Phomopsis* species: *Phoma petiolorum* [= *Phomopsis petiolorum* (Desm.) Grove (1917: 60)], represents the conidial state of *Diaporthe oncostoma* (Duby) Fuck., see Wehmeyer (1933: 143). According to the type and two other specimens in FH, *Cytospora* (*Phoma*) *abnormis* is also identical with the *Phomopsis*-state of *Diaporthe oncostoma*. *Phoma petiolorum* f. *juglandis*, judging by the description of the fruitbodies (Brunaud, 1889), is also a species of *Phomopsis*. It probably is the conidial state of the ubiquitous species *Diaporthe eres*; compare Hamond (1931: 146) and Wehmeyer (1933: 89). The same is true of *Phoma mespili*, the type of which is preserved at L. *Phoma siliquastris* is probably the *Phomopsis*-state of *Diaporthe medusaea* Nitschke; compare Saccardo (1884: 68) and Wehmeyer (1933: 101 et seq.). Finally *Phoma depressa* [= *Fusicoccum depressum* (Berk. & Br.) Grove (1935: 254)] and *Phoma planiuscula* [= *Phomopsis planiuscula* (Sacc.) Sacc. (1915: 135)] refer to a *Phomopsis* species similar to the conidial state of *Diaporthe perijuncta* Niessl; compare Wehmeyer (1933: 117, 118) and Grove (1935: 254).

*Phoma bismarckii*, also listed by Wollenweber & Hochapfel as a synonym of "*P. striaeformis*," was described by Kidd(-Owen) & Beaumont (1924: 104) as being quite different from *Polyopeus purpureus* = *Phoma macrostomum*. The description points to *Phoma prunicola* (Opiz) Wollenw. & Hochapf., often found in association with apples; see Wollenweber & Hochapfel (1936: 595-597) and Boerema & al. (1965).

The characteristics of *Phoma* (*Aposphaeria*) *pomi* agree closely with those of *P. macrostomum*. Whether it belongs to the colourless variety of this fungus, as suggested by Wollenweber & Hochapfel (as syn. of "*P. striaeformis*"), however, is uncertain and can be decided only from data on the growth in vitro. Therefore *P. pomi* is taken as a synonym of the much more widely distributed *P. macrostomum* var. *macrostomum*.

Finally, according to its original diagnosis *Phoma fraxinifolii*, mentioned by Wollenweber & Hochapfel as synonym of "*P. aceris-negundinis*," is a pycnidial fungus with true sporophores, so that it cannot belong to *P. macrostomum*.

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## REVISION OF THE GENUS PHIALOPHORA (MONILIALES)

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(With twelve Text-figures)

The hyphomycetous genus *Phialophora* is revised. It is characterized by flask-shaped phialides with a collarete and one-celled slimy conidia. This characterization excludes species which form blastospores on sympodulae besides phialospores, and which have been revised as species of the genus *Rhinocladiella* in a previous paper.

The genus *Margarinomyces*, on the contrary, is considered to be a synonym of *Phialophora*. With this emendation there remain now twelve species or species groups which are redescribed. The necessary new combinations are proposed.

### Introduction

*Phialophora verrucosa* n. gen. n. sp. was created by Medlar in 1915a for a previously unknown pathogenic fungus isolated from the first reported case of Chromoblastomycosis or Dermatitits verrucosa, a human skin disease. As is made clear by Medlar in his paper describing the new genus and new species and in a second paper (Medlar, 1915b) giving more details of the morphology of the fungus, the name, taxonomic position, and determinative characteristics of this new fungus were the result of suggestions and work by the eminent mycologist Professor R. Thaxter. Despite this Medlar is obviously the authority for the genus *Phialophora* rather than Thaxter as has been assumed by some authors.

The genus *Phialophora* comprises a large number of frequently ill defined species which represent conidial states of Helotiales (e.g. *Pyrenopeziza*, *Mollisia*, *Ascocoryne*) or Sphaeriales (e.g. *Coniochaeta*, *Gaeumannomyces*). These species occur commonly on decaying wood (causing blue discolorations and soft rot), in soil, water etc., also on food (apples, butter, margarine), and as causal agents of chromoblastomycosis and other skin infections. The genus shows strong variability in hyphal pigmentation and conidiophore structures. One-celled slimy conidia are formed on typically flask-shaped phialides with a collarete. The genus is delimited from

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† Dr. M. Beatrice Schol-Schwarz died on July 27, 1969, after a long illness. She participated actively in this work which was completed only two weeks before her death.

*Rhinocladiella* by the absence of sympodulae and blastospores. The genus *Margarinomyces* is considered to be synonymous with *Phialophora*, because in old cultures collarettes are visible on the phialides similar to those in typical *Phialophora* species.

Medlar (1915a) described *P. verrucosa* with two types of conidial formation as follows: "The type found in cultures where conditions are most favourable for luxuriant growth, is semi-endogenous in character . . . The second type of conidial formation is found in tissues and in the depths of certain media, such as hydrocele agar. Here the conidia are formed as budding processes from single sclerotic cells, from the individual cells of sclerotia and from the end of short terminal and lateral branchlets. They may be single or in chains of two to six. The structure is similar to that of the conidia formed on the aerial hyphae, but the form is distinctly more ovoid." The first type of spores is obviously the phialospore. Medlar called them semi-endogenous presumably because they develop inside an open collarette. The "second type of conidial formation," illustrated in Medlar's more detailed study (1915b), apparently refers to moniliform thickened hyphae which do not normally separate into individual conidia.

Numerous species of *Phialophora* have now been described. The genus comprises dematioid and hyaline fungi occurring in diseased human or animal tissues, as parasites or saprophytes in plant material and in soil.

The aim of the present investigation was a rearrangement of the species described by van Beyma thoe Kingma (1943). It started with an exhaustive study of the authentic strains maintained at the CBS and was supplemented by numerous recent isolates. The present paper provides a base for the distinction of numerous new species, awaiting to be described.

In certain instances species delimitation was found to be very difficult because of great variability and insufficient morphological differentiation of the conidial states. This is particularly the case in groups of species with closely related perfect states. As a consequence the indiscriminate term 'species group' is used to comprise such complexes of similar forms.

One of the most difficult groups is the *Phialophora hoffmannii* group. It is treated here only cursorily because a re-evaluation of species will be possible only after a thorough revision of the perfect states. Not described is the complex of *Phialophora radicolica* Cain (1952) and the conidial state of *Gaeumannomyces graminis* (Sacc.) v. Arx & Olivier (*Ophiobolus graminis* Sacc.). Although identification of this complex is not difficult the affinity or identity, which was claimed by Lemaire & Ponchet (1963), of the forms within it also requires further study of perfect states.

Some very recent reports on *Phialophora* species (Hennebert, 1968; Gams & Domsch, 1969) have not been duplicated here. Other recent publications seem to deal rather with *Rhinocladiella* than with *Phialophora* species in the stricter sense.

*Phialophora* cultures grow well on the usual culture media. In the present study they were grown on 2% malt extract agar, asparagine-yeast-agar (glucose 20.0 g, asparagine 1.5 g,  $K_2HPO_4$  1.0 g,  $MgSO_4 \cdot 7H_2O$  0.5 g,  $FeCl_3$  0.1 g, yeast extract 1.0 g per litre), upon which medium the colour is usually lighter, and on oatmeal

agar with lupin stems. Capitalized colour names in the text refer to Ridgway (1912) with Roman figures indicating the plates.

#### PHIALOPHORA Medlar

*Phialophora* Medlar in *Mycologia* 7: 202. 1915. — Type species: *P. verrucosa* Medlar, *op. cit.*  
*Cadophora* Lagerb. & Melin *apud* Lagerb. & al. in Svenska Skogsvårdsfören. Tidskr. 25: 263. 1927. — Type species: *C. fastigiata* Lagerb. & Melin, *op. cit.*, ≡ *Phialophora fastigiata* (Lagerb. & Melin) Conant in *Mycologia* 29: 598. 1937.

*Margarinomyces* Laxa in *Zentbl. Bakt. ParasitKde* (Abt. II) 81: 392. 1930. — Type species: *M. bubaki* Laxa, *op. cit.* ≡ *Phialophora bubakii* (Laxa) comb. nov.

*Lecythophora* Nannf. *apud* Melin & Nannf. in Svenska Skogsvårdsfören. Tidskr. 32: 435. 1934. — Type species: *L. lignicola* Nannf., *op. cit.* ≡ *Phialophora lignicola* (Nannf.) Goidanich *apud* Goidanich & al. in *Ente nazionale per la Cellulosa e per la Carta*, Roma 112. 1938.

The mycelium is hyaline or pink to olivaceous black, with septate hyphae which sometimes have characteristic irregular warty wall thickenings (Fig. 3v, 6c, u etc.). Thick-walled inflated cells may develop arogenously or intercalarily. Phialides vary from thread- or tube-like to ampulliform, they open with a distinct cup- or beaker-shaped collarette. Phialides develop either terminally or laterally on the hyphae, or on sympodially branched conidiophores, in which case they may form complicated penicillate brushes. The phialides are usually separated from the parent hyphae by septa. Sometimes they may be reduced to a mere collarette protruding from a hypha or a chlamydospore without a septum, so-called pleurophialides (von Arx & Gams, 1967). Occasionally phialides bear more than one collarette. Proliferation of the phialides through the apex is also rather common.

The first developed conidium is a blastospore. After it is detached, pieces of the torn cell-wall remain behind. Depending on the size of the spore, these wall-structures are of different shape, varying from an inconspicuous collarette to a distinct cup, sometimes with flaring margin (Fig. 11). The succeeding conidia develop endogenously and are pushed out through the open cup, cohering in a mucous ball at the top of the phialide.

The process of spore development has been studied by means of microkinematography by Cole & Kendrick (1969). The conidia are one-celled and variable in shape, ranging from globose to ovoid or cylindrical and are sometimes even curved. Variation often occurs in the same strain according to age and culture medium. Some species form distinctly dimorphic conidia but conidia of variable shape also occur in many other species. Cultures with predominantly cylindrical conidia may have some globular or ovoid conidia and cultures with predominantly globular or ovoid conidia may have some cylindrical conidia.

Branching of the conidiophores and size and shape of the collarette are also very variable, depending on the medium, age, and amount of illumination of the culture. This variability led in the past to description of an exaggerated number of species. On the other hand certain minor differences of constant occurrence can be found which have frequently been neglected in the past and yet may be of taxonomic importance. Types of conidiophores other than those described, such as sympodulae or annellophores, are absent in *Phialophora*; otherwise a fungus with such pleomorphic conidium formation would be regarded as *Rhinochlaetia* (Schol-Schwarz, 1968).



## COMMENT ON THE SYNONYMY.

1927: Lagerberg & Melin (*apud* Lagerberg, Lundberg & Melin) established the genus *Cadophora* with the type species *C. fastigiata*.

1930: Laxa created the genus *Margarinomyces* with the type species *M. bubaki*, a dark olivaceous fungus, isolated from margarine. Laxa did not recognize, that with age the tips of the phialides transform into open collarettes which sometimes have inconspicuously flaring ends forming a small cup. These characters seem sufficient to transfer this species to *Phialophora* and to abandon the genus *Margarinomyces*, in spite of van Beyma's (1943) opinion to the contrary. According to him the spore development in *Margarinomyces* is "basipetal" as in *Penicillium*, i.e. exogenous, but is "endogenous" in *Phialophora*. This distinction cannot be retained since in the type species of *Margarinomyces* open cups at the end of the phialides have been demonstrated, just as in *Phialophora*. The same is true for the other species described in *Margarinomyces*.

1934: Nannfeldt (*apud* Melin & Nannfeldt) created the genus *Lecytophora* with the type species *L. lignicola*, for a dematioid fungus occurring in Sweden in wood pulp and water. The conidiophores are swollen structures developing laterally or terminally on the hyphae. They end in an inconspicuous open tip, from which small ellipsoidal conidia are abstricted in rapid sequence. Nannfeldt regarded these sporogenous cells as highly reduced phialides and the conidia as phialospores. However he did not observe, that the tips may transform into real cups liberating the endogenous spores.

1937: van Beyma, after examining Nannfeldt's fungus at the CBS, observed the short open neck of the swollen conidiophores and transferred the fungus to *Cadophora*.

1937: In the same year Conant published the synonymy of *Cadophora* and *Phialophora* and transferred the type species *C. fastigiata* to *Phialophora*.

1938: Goidanich (*apud* Goidanich & *al.*) transferred Nannfeldt's *Lecytophora lignicola* once again, this time to *Phialophora*.

1944: Emmons (*apud* Binford & *al.*) emended the genus *Phialophora* after examining the strain CBS 273.37, called *Phialophora verrucosa*. This strain sometimes produced acropleurogenous conidia, as was first observed by Carrión (1940), who for that reason, transferred it to the genus *Fonsecaea*. Emmons, disagreeing with Carrión, preferred to emend the genus *Phialophora*, so that fungi with "acrogenous, pleurogenous or acropleurogenous production of brown one-celled conidia born laterally on tuberculate processes of vegetative hyphae, or, more commonly, on lateral or terminal conidiophores and frequently catenate in short chains" could be included. The present author (Schol-Schwarz, 1968) could not retain this emendation: strains with this type of lateral conidia were assembled in the genus *Rhinocladiella* Nannf. which has priority over *Fonsecaea* Carrión; the strain CBS 273.37 was regarded as representing *Rhinocladiella pedrosoi* (Brumpt) Schol-Schwarz.

## KEY TO THE SPECIES

- 1a. At least some conidia globose or subglobose . . . . . 2  
 1b. Globose or subglobose conidia absent, conidia ovoid, ellipsoidal, cylindrical or curved . . . . . 4  
 2a. Colonies white, conidia  $2-4.5 \times 2.3-3.5 \mu$  . . . . . *P. alba*, p. 64  
 2b. Colonies darkly pigmented . . . . . 3  
 3a. Phialides flask-shaped with distinct collarette, conidia regularly globose to guttuliform,  $1.5-2.5 \mu$  . . . . . *P. cyclaminis*, p. 69  
 3b. Phialides flask-shaped with wide collarette with flaring margin. Conidia dimorphic; globose brown and ellipsoidal to cylindrical hyaline . . . . . *P. richardsiae*, p. 87  
 3c. Phialides with swollen base and long slender neck, collarette indistinct. Conidia globose to ovoid,  $1.5 \times 1.5$  to  $2 \times 3 \mu$ , on aging transformed into chlamydo-spores with verrucose walls . . . . . *P. atrovirens*, p. 65  
 4a. Conidia narrow oblong, typically curved . . . . . 5  
 4b. Conidia broader, usually straight, or only partly curved . . . . . 8  
 5a. Colonies thin, fast growing. Conidia strongly curved, sickle-shaped  
     *P. radicolica* Cain  
     and conidial *Gaeumannomyces graminis* (Sacc.) v. Arx & Olivier  
 5b. Colonies more compact, slow growing. Conidia only slightly curved, not sickle-shaped  
     *P. lagerbergii* group, 6  
 6a. Colonies cream-coloured and frequently with a brownish to violet discoloration of the agar . . . . . *Ascocoryne sarcoides* stat. conid., p. 83  
 6b. Colonies darker-coloured and without any discoloration of the agar . . . . . 7  
 7a. Phialides with very long, slender, beaker-shaped collarette . . . . . *P. lagerbergii*, p. 81  
 7b. Phialides with distinct but shorter collarette . . . . . *P. repens*, p. 82  
 8a. Colonies with pure grey tinges. Conidiophores strongly branched with the slender phialides forming compact clusters around the hyphae . . . . . *P. cinerescens*, p. 67  
 8b. Colonies of other colours. Conidiophores and phialides not forming compact clusters . . . . . 9  
 9a. Collarette forming a distinct oblong cup, darker than the rest of the phialide  
     *P. verrucosa*, p. 90  
 9b. Collarette less pronounced, not darker than the rest of the phialide . . . . . 10  
 10a. Conidia clearly dimorphic: ovoid and cylindrical or sometimes curved. Moniliform hyphae typically present . . . . . 11  
 10b. Conidia more uniform in shape . . . . . 12  
 11a. Collarette always distinct . . . . . *P. lignicola*, p. 84  
 11b. Collarette rather inconspicuous at first but becoming more obvious on older phialides  
     *P. bubakii*, p. 65  
 12a. Cultures dark olivaceous, dry, cottony, velvety, with hyphal strands. Phialides with coarse wall and distinct collarette (at least in age) . . . . . *P. fastigiata* group, 13  
 12b. Cultures in various colours, cream, pink, olivaceous or black, frequently wet yeast-like or with hyphal strands. Phialides rather inconspicuous . . . . . 17  
 13a. Hyphae greenish, usually with smooth thin walls. Collarette distinct only in old cultures  
     *P. malorum*, p. 75  
 13b. Hyphae brownish, usually with irregularly thickened walls. Collarette always distinct . . . . . 14  
 14a. Phialides small,  $4-6 \times 1.5-2.2 \mu$ , and straight . . . . . *Mollisia cinerella* stat. conid., p. 75  
 14b. Phialides larger and asymmetrically swollen . . . . . 15  
 15a. Chains of moniliform chlamydo-spores present in old cultures  
     *Pyrenopeziza larinina* f. *microsperma* stat. conid., p. 74  
 15b. Chains of moniliform chlamydo-spores absent . . . . . 16  
 16a. Conidia subglobose to ovoid,  $3-7.5 \times 2-3 \mu$  . . . . . *P. fastigiata*, p. 71

- 16b. Conidia narrowly ovoid,  $2.5-4 \times 1.5-2 \mu$  . . . . . *P. melinii*, p. 74  
 17a. Aleuriospores present, borne on distinct sporophores, dark-coloured, obovate with pointed base and easily detached. Young colonies with dark colours *P. mustea*, p. 86  
 17b. Aleuriospores absent, chlamydospores, if present, not formed on differentiated sporophores. Young colonies often with light colours (if chlamydospores are present, see *Ph. fasciculata* and *Ph. mutabilis* in this group) . . . . . *P. hoffmannii*-group, p. 79

I. PHIALOPHORA ALBA Beyma—Fig. 1

*Phialophora alba* Beyma in Antonie van Leeuwenhoek 9: 56. 1943.

Cultures on 2% malt agar reach a diameter of 9 cm after three weeks. The fungus develops a wet, white, thin but tough layer of submerged mycelium with hyphal strands in the centre. The reverse of the colony is Pale Olive Buff (XL). Sporulation is good.

The hyphae, usually  $2-3 \mu$ , are sometimes  $5-7 \mu$  wide and irregular in outline, with inflated cells, but without a thickened wall (Fig. 1a).

The phialides,  $10-15 \times 3-4 \mu$ , are flask-shaped, single or branched and sometimes grouped in *Penicillium*-like brushes. Exceptionally a terminal phialide occurs. The collarete has no conspicuous margin (Fig. 1c-e).

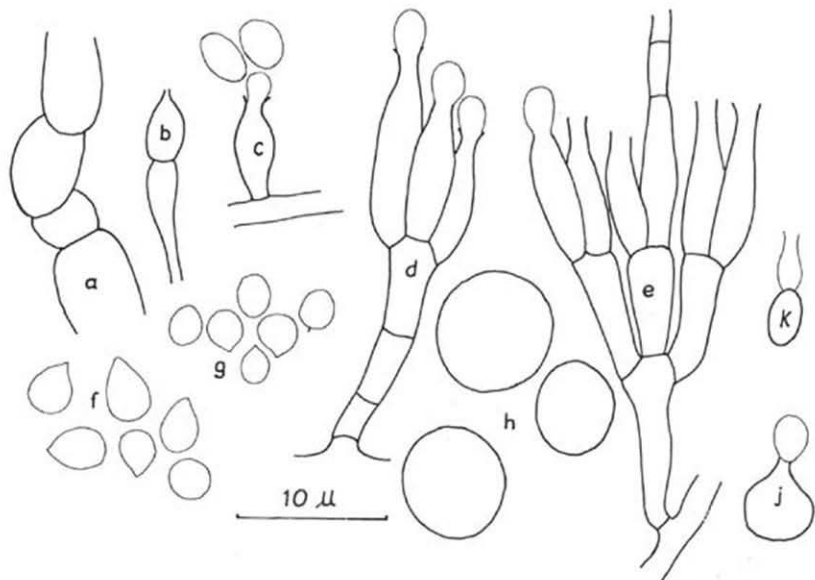


Fig. 1. *Phialophora alba*. Type culture CBS 112.43. — a. Hypha with inflated cells. — b-c. Terminal, lateral, branched and bush-like phialides. — d. Hypha with phialides. — e. Bush-like phialide. — f-h. Conidia of different age. — i. Cluster of conidia. — j. Sporulating chlamydospore. — k. Phialide developed from chlamydospore.

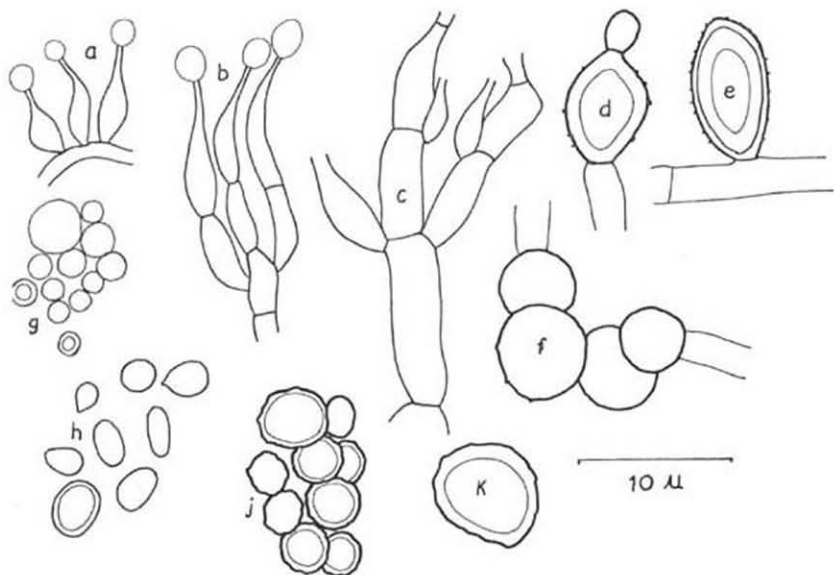


Fig. 2. *Phialophora atrovirens*. Type culture CBS 272.34. — a, b. Young phialides, single and in group. — c. Old phialides with open tips. — d-f. Terminal, lateral, and intercalary thick-walled, verrucose cells. — g. Young spore ball with spores of different size. — h. Globose and guttuliform conidia, partly changing into chlamydo spores. — j. Ball of chlamydo spores. — k. Single verrucose chlamydo spore.

The conidia are hyaline, globose to subglobose,  $2.3-4.5 \times 2.3-3.5 \mu$ . With age they may enlarge to  $6-9 \mu$  and remain hyaline, without a thickened wall. Sometimes they develop a collarette directly or they grow out into a phialide (Fig. 1j, k). No perfect state is known.

The description is based on the type strain CBS 112.43, isolated by Henriette Koning from heart-wood of *Fagus sylvatica* in the Netherlands.

Recently a strain CBS 740.68 was obtained from G. H. Bollen, Wageningen, isolated from glass-house soil, Zwijndrecht, Netherlands. According to him, the fungus is one of the first recolonizers of steamed soil in glass-houses.

## 2. *Phialophora atrovirens* (Beyma) Schol-Schwarz, *comb. nov.*—Fig. 2

*Margarinomyces atrovirens* Beyma in Zentbl. Bakt. ParasitKde (Abt. II) 91: 348. 1935 (basionym).

Colonies on 2% malt agar reach a diameter of 5.7 cm in 18 days at 25°C. They show a wet centre of 3.5 cm in diam. with a margin of 1 cm with aerial mycelium,

Olivaceous Black (LI). The reverse of the colony is Sooty Black (LI). Sporulation is abundant. Colonies grown under day light show concentric rings.

Colonies on asparagine-yeast agar attain 5.7 cm in 18 days at 25°C. They have a velvety appearance, changing from Benzo Brown (XLV) in the furrowed centre, via Hair Brown (XLVI) to Castor Gray (LII) at the margin. The reverse of the colony is Olivaceous Black (LI).

The hyphae are 3–5  $\mu$  broad, septate, with irregular wall-thickenings, wavy in outline. The hyphae develop intercalary, terminal or lateral, brown, inflated cells with a thick verrucose wall.

In young cultures the phialides, single or in groups on conidiophores, are relatively slender and gracefully tapering towards the tip with a slight inflation in the middle and a constriction at the base. They measure 7–15  $\times$  1.5–2.5  $\mu$ . In old cultures complicated brushes of phialides with wide open tips are present.

The conidia are globose, droplet-like, exceptionally ovoid, hyaline, with an oil drop, usually measuring 1.5, but up to 2–3  $\mu$ , in diameter. With age they increase in size to 6–8  $\times$  5  $\mu$ , and develop into chlamydo spores, becoming brown with a thick, more or less verrucose wall, sometimes cohering together in a ball.

The description is based on the type strain CBS 272.34, isolated from black spots in margarine in the Netherlands.

### 3. *Phialophora bubakii* (Laxa) Schol-Schwarz, *comb. nov.*—Fig. 3

*Margarinomyces bubaki* Laxa in Zentbl. Bakt. ParasitKde (Abt. II) 81: 392–396. 1930 (basionym).

*Cadophora obscura* Nannf. in Svenska Skogsvårdsfören. Tidskr. 32: 418. 1934. — *Phialophora obscura* (Nannf.) Conant in Mycologia 29: 598. 1937.

Colonies on 2% malt agar reach a diameter of 6.5 cm after 18 days at 25°C. The growth is velvety, 0.3 cm high, with faint concentric rings, Dark Grayish Olive (XLVI), synnematous in the centre, merging via a 0.5 cm broad Deep Slate Olive (XLVI) velvety zone into a 0.1 cm broad hyaline margin. The reverse of the colony is Dull Greenish Black (XLVII) with a hyaline margin. Sporulation is abundant.

The hyphae soon become dark olivaceous; they are sometimes wavy, of varying width, mostly 3–5  $\mu$ , rarely up to 12  $\mu$  broad. When young, they are filled with dense protoplasm, with age they show irregular wall-thickenings and are sometimes verruculose. Moniliform hyphae (Fig. 3a) as well as hyphal strands are common.

#### EXPLANATION OF FIGURE 3

Fig. 3. *Phialophora bubakii*.

a–t. Type culture CBS 198.30. — a–c, h. Various phialides; b, h. Showing the characteristic branching. — f. Verrucose hypha. — g. Hypha with irregular wall-thickening. — j. Verrucose chlamydo spore. — m. Lateral and k. terminal chlamydo spore. — n. Young ovoid and r. old conidia. — q. Young curved and p. old conidia. — s. Group of rather old conidia. — t. Sclerotium.

u–x. Type culture of *Cadophora obscura*, CBS 269.33. — u. Single phialide. — v. Branched old conidiophore with one phialide proliferating and with irregularly thickened wall, a ball of chlamydo spores still adhering to a phialide. — w. Conidia developed into chlamydo spores. — x. Proliferating phialide.

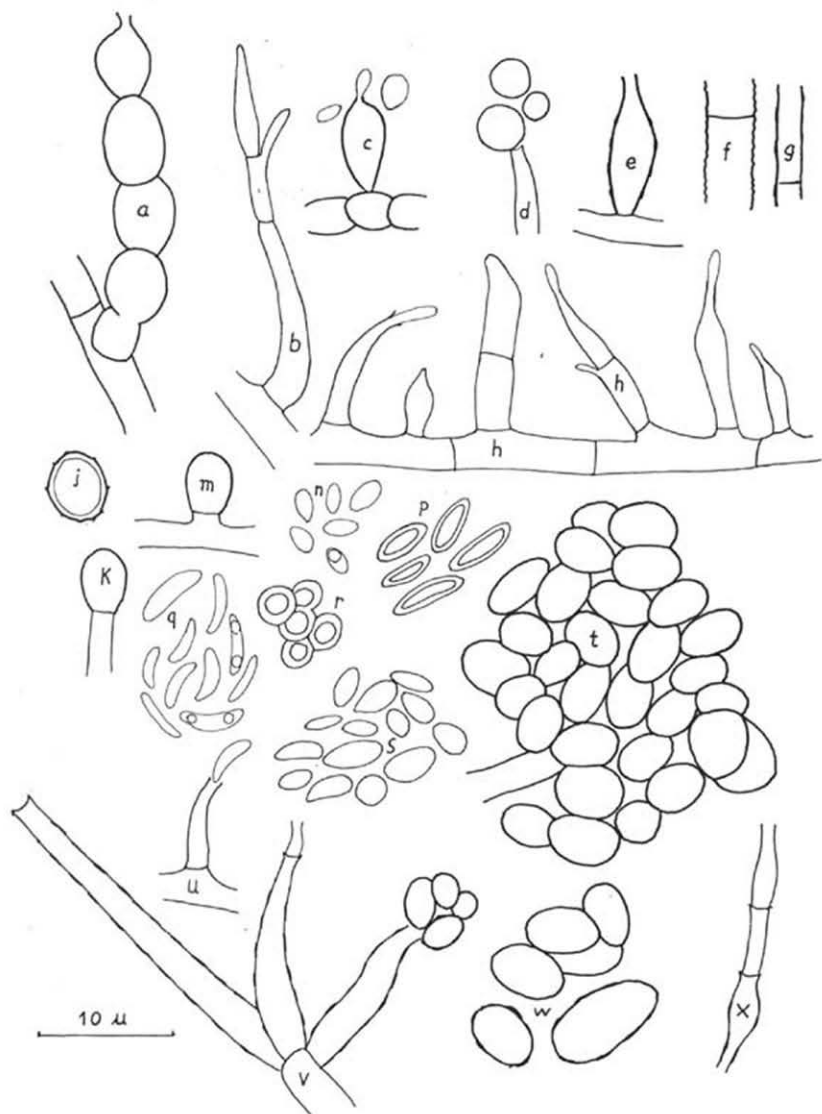


Fig. 3

Chlamydo-spores develop laterally or terminally on the hyphae (Fig. 3k, m). Sometimes they grow out into sclerotia, up to 80  $\mu$  in diameter (Fig. 3t).

The phialides, up to 40  $\mu$  long, are of variable shape. They develop terminally or laterally on the hyphae. They are simple or in groups supported by a conidiophore, slender or swollen. When young they end in a sharp point, with age a rather indistinct collarete becomes visible. Side branches are common (Fig. 3b, h); in some strains proliferation occurs (Fig. 3v, x).

The conidia are dimorphic, hyaline to subhyaline, with one or two oildrops. In young cultures allantoid conidia (1.5–) 3–5 (–7.5)  $\times$  0.75–3  $\mu$  prevail (Fig. 3q). In older cultures ovoid conidia, 1.5–4  $\times$  1–2  $\mu$ , are common (Fig. 3n), however both types occur in every culture. With age the ovoid spores develop into brown chlamydo-spores, 4.5–6.5  $\times$  4–5  $\mu$ , sometimes with an irregularly thickened wall (Fig. 3j, v, w). Exceptionally old allantoid spores with thickened walls occur (Fig. 3p). No perfect state is known.

Description based upon the type strain CBS 198.30.

HABITAT: In margarine, forming dark greenish spots, Czechoslovakia, Austria, the Netherlands, and other European countries. From fresh water and from pulp of *Populus tremula* in Sweden.

#### MATERIAL EXAMINED.

##### a. Herbarium material.

1. Type material of *Cadophora obscura* consisting of 3 slides: 217:28a, 242:42, 1203:5, marked by E. Melin "Västerbotten, Umeå, Sofiehems Trämassefabrik, fresh water, det. J. A. Nannfeldt, Holotypus" (UPS).

2. N. F. Conant's dried culture 334, from Nannfeldt via CBS, isolated from fresh water in Sofiehem, Sweden. Authentic material of *Cadophora obscura* (FH).

##### b. Living strains.

CBS 198.30, type culture of *Margarinomyces bubaki*;

CBS 269.33, authentic culture of *Cadophora obscura*, strain 389:11, obtained from E. Melin.

CBS 221.37, isolated from margarine from Vienna, by A. Knetemann, Rotterdam.

Strains CBS 835.69 (1040), 836.69 (1107), 837.69 (1133), and 838.69 (1135), all isolated from margarine or butter and sent by A. Knetemann via Unilever Laboratory, Rotterdam.

CBS 834.69 (H 36-6), isolated from pulp of *Populus tremula*, by T. Nilsson, Sweden, 1968.

Cultures of CBS 198.30, type of *Margarinomyces bubaki*, and CBS 269.33, type of *Cadophora obscura*, are strikingly similar in colour and appearance, when grown on various media. Microscopically there are differences but none are worthy of specific rank. In CBS 198.30 the hyphae are up to 12  $\mu$  broad and the conidiophores are typically branched (Fig. 3 b, h). The hyphae in CBS 269.33 reach only a width of 5  $\mu$ , and proliferation of phialides is rather common. In some other strains proliferation also occurs. van Beyma (1943) described a strain from butter sent to the CBS by A. Knetemann as *Phialophora obscura*. This culture was lost in 1961, but the still existing drawings agree with those of *Phialophora bubakii*.

#### 4. PHIALOPHORA CINERESCENS (Wollenw.) Beyma—Fig. 4

*Verticillium cinerescens* Wollenw. in Arb. biol. Reichsanst. Berlin-Dahlem 17: 296. 1930. — *Phialophora cinerescens* (Wollenw.) Beyma in Antonie van Leeuwenhoek 9: 59. 1943.

Colonies on 2% malt extract agar reach a diameter of 7 cm in 30 days at room temperature. The growth is woolly, zonate, Light Mineral Gray (XLVII) in the centre, merging via Smoke Gray (XLVI) and Deep Slate Olive (XLVII) into a 0.7 cm broad hyaline margin of appressed mycelium. The reverse of the colony shows in a radial direction passing from the centre to the margin Smoke Gray (XLVI), Dull Greenish Black (2) (XLVII) and hyaline zones. Sporulation is good.

The hyphae are septate, 1–3  $\mu$  wide; on aging they frequently develop irregularly swollen cells, covered with flat warts, and up to 5  $\mu$  wide (Fig. 4c). Hyphal strands occur.

The phialides are flask-shaped, mostly with the broadest part somewhat above the middle. Characteristically they are arranged in densely verticillate bushes in clusters on very short conidiophores (for this reason the fungus was originally placed in the genus *Verticillium*). Exceptionally phialides occur singly on the hyphae. The phialides end in a very short but distinct collarette with a minute flaring margin, both collarette and margin being somewhat darker than the phialide itself.

The conidia when young are hyaline to subhyaline, more or less ellipsoidal but slightly apiculate at the basal end, with a thin wall and two—sometimes only one—oil drops, measuring 3–6  $\times$  1.5–2  $\mu$ , although there is actually considerable variation in size and also in shape. In older cultures the conidia are darker, covered with a thicker wall, and more regular, measuring 4–6  $\times$  2.5–3  $\mu$ . Very rarely curved spores are present (Fig. 4b).

The description is based mainly on the type strain, CBS 276.29.

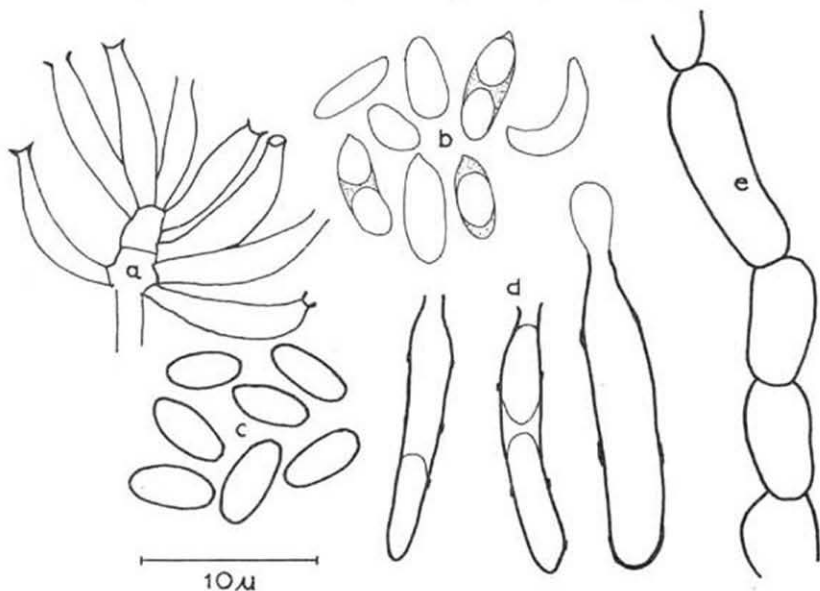


Fig. 4. *Phialophora cinerescens*. Type culture, CBS 276.29. — a. Bush of phialides. — b. Young conidia (one of them curved). — c. Old conidia with a distinct wall. — d. Chlamydo-spores directly transformed into phialides. — e. Inflated cells.



## MATERIAL EXAMINED (living strains).

CBS 276.29, type culture, isolated from wilting *Dianthus caryophyllus*, in Geisenheim, Germany, sent as *Verticillium cinerescens* by H. W. Wollenweber in 1929.

CBS 280.35, isolated from wilting *Dianthus caryophyllus* in England, sent by G. M. Wickens, 1935.

CBS 418.50, isolated from wilting *Dianthus caryophyllus* in the Netherlands, sent by G. Brink in 1949.

CBS 209.57, isolated from wilting *Dianthus caryophyllus* in the U.S.A., sent by I. Isaac under No. 11157 in 1957.

The species is a common parasite of *Dianthus caryophyllus*; it grows through the xylem vessels of the host and causes wilt. It is of economic importance in the Netherlands, Germany, England, and Denmark. The results of extensive studies of the disease have been published by Wickens (1935), Hellmers (1958), and Hantschke (1961). In the Netherlands the disease and its control have been studied by Roodenburg (1945) and Noordam (1948).

## 5. PHIALOPHORA CYCLAMINIS Beyma—Fig. 5

*Phialophora cyclaminis* Beyma in Antonie van Leeuwenhoek 8: 115, 1942.

Colonies on 2% malt agar attain a diameter of 8.5 cm after 3 weeks at 25° C. The growth is woolly, sometimes feathery towards the margin, with faint concentric rings and a slight central elevation, Dark Mouse Gray (LI); the margin is 2 mm broad, more or less submerged, Blackish Mouse Gray (LI). Reverse of the colony Iron Gray (LI). Sporulation is good.

The hyphae are septate, brown, up to 4–5  $\mu$  broad, exceptionally covered with wall thickenings, without inflated, thick-walled cells. No hyphal strands.

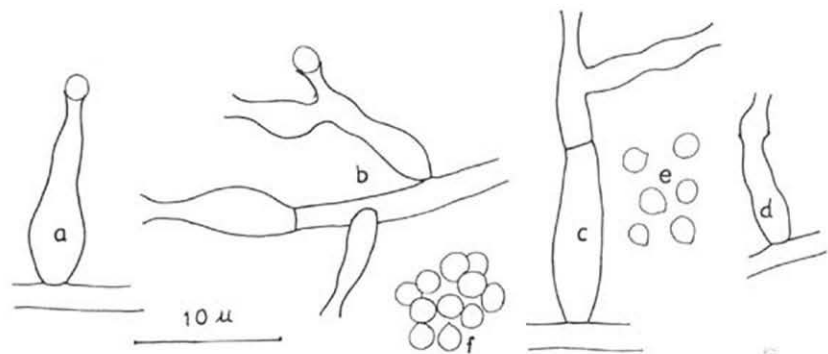


Fig. 5. *Phialophora cyclaminis*. — a, b, d–f. Type culture CBS 166.42, c. CBS 608.69. — a–d. Phialides, simple and with furcation and proliferation. — e. Conidia. — f. Conidia in a cluster.

The phialides, usually 15–25  $\mu$  but up to 45  $\mu$  long, develop laterally or terminally on the hyphae. They are mostly simple, but furcation and proliferation are common. They have a narrow base, followed by a slight inflation and a constriction in the middle of the phialide. The collarette is distinct.

The conidia, 1.5–2.5  $\mu$  in diameter, are hyaline, thin-walled and sometimes with an oil drop. They are globose or slightly guttuliform and cohere at the top of the phialide.

The description is based mainly on the type culture CBS 166.42 which was isolated from leaves of *Cyclamen persicum* in Aalsmeer, Netherlands, 1942.

#### MATERIAL EXAMINED.

CBS 166.42, type culture, isolated from *Cyclamen persicum*, Aalsmeer, 1942, by J. W. M. Roodenburg.

CBS 608.69, isolated from water in an aquarium, sent by A. J. van der Plaats-Niterink, Utrecht, 1963.

CBS 245.69 isolated from wood, sent as strain 64 by G. Giordano, Firenze, 1969.

### 6. PHIALOPHORA FASTIGIATA group

Colonies grow rather slowly. The group is characterized by greyish mycelium with a tinge of brown, cottony or velvety in appearance, with hyphal strands. The conidiophores are strongly verticillately branched; the phialides are sturdy, rather short and open with a distinct broad cup without a flaring margin. The conidia have a distinct wall, with age they are often transformed into chlamydo-spores; characteristic flat wall thickenings are frequently present in vegetative hyphae and sporulating structures.

Species described in this group are:

#### 6 (1). PHIALOPHORA FASTIGIATA (Lagerb. & Melin) Conant—Fig. 6a–j

*Cadophora fastigiata* Lagerb. & Melin in Svenska Skogsvårdsfören. Tidskr. 25: 263. 1927. — *Phialophora fastigiata* (Lagerb. & Melin) Conant in Mycologia 29: 598. 1937.

Colonies on 2% malt agar reach a diameter of 4.5 cm after 13 days at 25 °C. The growth is velvety, Olive Brown (XL), with a 0.4 cm broad margin of appressed hyaline mycelium. In older cultures concentric rings develop. The reverse of the colony is Dark Olive (XL). Sporulation is abundant.

The hyphae are 3–4  $\mu$  in diameter, with age they show the characteristic wall thickenings which also occur in the sporulating structures (Fig. 6c). Thick-walled cells up to 8  $\mu$  in diam. are common. The mycelium tends to develop hyphal strands and tufts in petri dish cultures.

The phialides occur singly, laterally or terminally on the hyphae, or in verticillate clusters (Fig. 6f). They can reach up to 30  $\mu$  in length but more often they are short, up to 12  $\mu$ , and asymmetrically swollen at the lower end. They open with a distinct cup without a flaring margin. Proliferation occurs (Fig. 6a, d, f, h).

The conidia are globose, subglobose, lacrymoid or ovoid, mostly straight but sometimes curved, varying from 3–6(–7.5)  $\times$  2–3  $\mu$ . When young they are hyaline and thin-walled, with age they become subhyaline or greyish and develop a thicker wall. In old cultures they develop into chlamydo-spores which are spherical or

ellipsoidal, sometimes apiculate, up to  $7\ \mu$  in diameter and often attached in a ball at the tip of the phialide (Fig. 6d, e, g).

The description is based on the dried type specimen and numerous living strains listed below.

**HABITAT:** On pine and spruce timber in Sweden and on various substrates in other countries.

#### MATERIAL EXAMINED.

##### a. Herbarium material.

Two slides, 151.3a from ground woodpulp and 143:14/137 from white water, both from Värmland (UPS).

Dried culture 331 of N. F. Conant, from ground wood pulp, sent by J. A. Nannfeldt to the CBS (FH).

##### b. Living strains.

CBS 226.30, from blueing *Pinus strobus*, East Canada, sent by C. W. Fritz in 1930 as No. I b.

CBS 307.49, from blueing *Pinus*, sent by S. O. Pehrson, Sweden, in 1949.

CBS 611.69 (1038/2) from *Picea abies*, CBS 612.69 (1136/4) and CBS 618.69 (1005/6) from *Populus tremula*, CBS 613.69 (1094/3) and CBS 614.69 (1094/2) from *Pinus sylvestris*, CBS 617.69 (BII 15) from *Fagus*, sent by F. Mangelot, Nancy, France, 1963.

CBS 682.69 = strain WS-B from rotting wood of *Fagus sylvatica*, sent by W. Liese, München, 1962.

CBS 863.69 (M.K. 9) and CBS 864.69 (M.K. 52) from wood, sent by W. Kerner, Berlin, 1967.

CBS 865.69 (27) and CBS 867.69 (10c) from blueing wood of *Pinus sylvestris* sent by A. E. Graentz, München, 1964.

CBS 866.69 = PD 64/121, from *Cyclamen* tuber, sent by G. H. Boerema, Wageningen 1964.

CBS 868.69 (T 18) soft rot fungus from *Pinus sylvestris*, sent by U. Cederkreutz, Helsinki, 1966.

CBS 869.69 = G.L.H. 6856, from wood of *Picea excelsa*, sent by G. L. Hennebert, Louvain, 1965.

CBS 870.69 = strain C from *Asparagus officinalis*, sent by P. van Maris, Venlo, 1959.

#### EXPLANATION OF FIGURE 6

##### Fig. 6. *Phialophora fastigiata* group

a-j. *Cadophora fastigiata*, N. F. Conant's dried culture 331 (FH). — a, f. Phialides. — b. Conidia. — c. Irregularly thickened wall of a hypha. — d. Proliferating phialide with ball of conidia developed into chlamydo-spores. — e. Chlamydo-spores with wall thickenings. — g. Chlamydo-spores.

h-j. CBS 609.69. — h. Proliferation of phialides. — j. Bush of phialides with long beakers, containing frequently two conidia.

k-p. *Cadophora melinii*, paratype (UPS). — m. Bush of phialides. — k, o. Conidia of various shape. — p. Chain of thick-walled cells. — n. Chlamydo-spores sporulating like phialides.

q-t. *Pyrenopeziza laricina* f. *microsperma*, CBS 568.63. — q. Chain of chlamydo-spores. — r. Conidia. — s. Curved conidia in a young culture. — t. Phialides.

u-w. *Mollisia cinerella*, CBS 312.61. — u. Bush of phialides. — v. Conidia. — w. Phialide with a ball of chlamydo-spores, from an old culture.

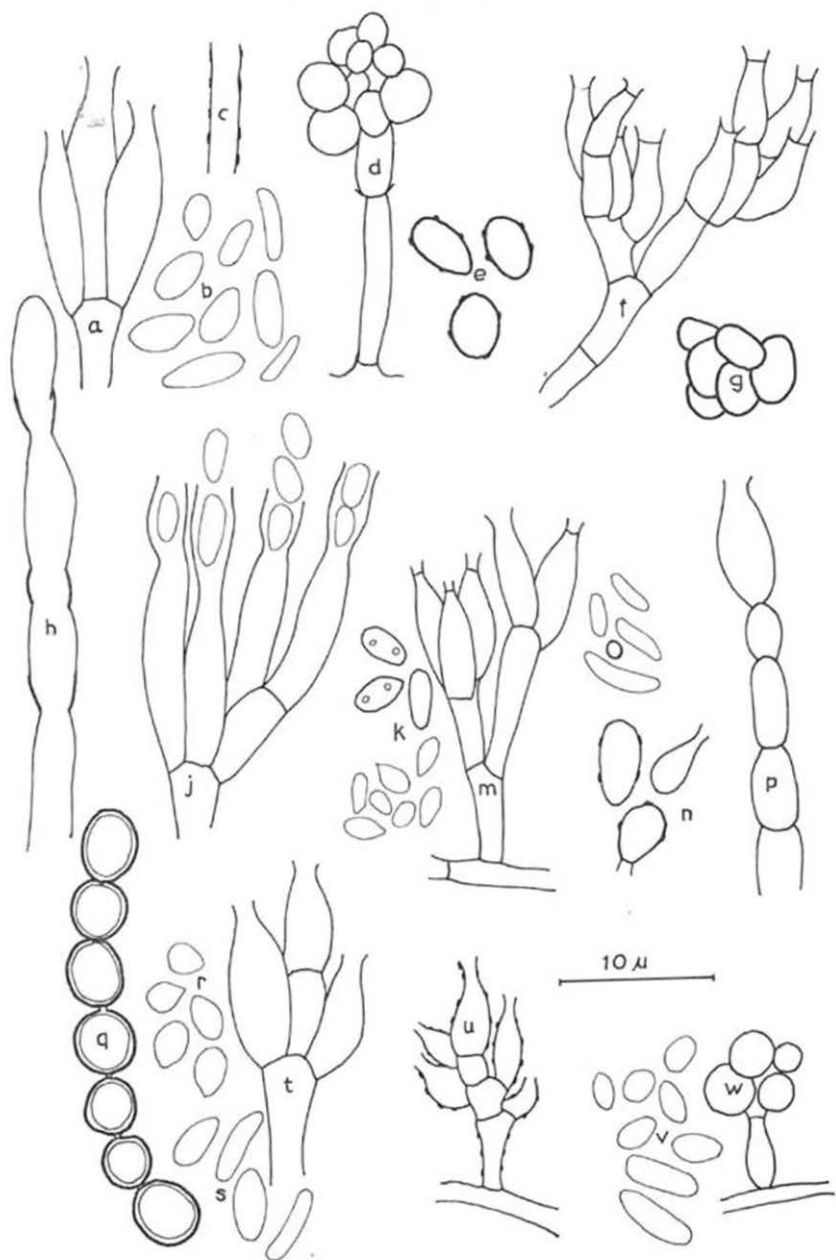


Fig. 6

Strain PD 9-263 from dying *Rubus idaeus*, sent by G. H. Boerema, Wageningen, 1960.

Strain 29a, laboratory contamination, sent by V. Tchernoff, Baarn, 1960.

Strain C, from oak wood of a ship, that had been lying on the bottom of the Baltic since the 17th century, sent by H. Kiessling, Stockholm, 1963.

Strain PD 63/103 from dead pear twigs, sent by G. H. Boerema, 1963.

Somewhat different:

CBS 609.69 = DAOM 33739, from rotting wood of *Betula lutea*, New Brunswick, sent by S. J. Hughes, 1966.

6 (2). PHIALOPHORA MELINII (Nannf.) Conant—Fig. 6k-p

*Cadophora melinii* Nannf. in Svenska Skogsvårdsfören. Tidskr. 32: 417. 1934. — *Phialophora melinii* (Nannf.) Conant in Mycologia 29: 598. 1936.

This species differs from *Phialophora fastigiata* only by the prevalently ovoid spores, which are also mostly somewhat smaller than in *P. fastigiata*, measuring  $5-4 \times 1.5-2 \mu$ , although in young cultures slightly curved conidia, up to  $6 \times 2 \mu$ , occur as well. With age the spores develop into chlamydo-spores up to  $6 \mu$  in diam.

The description is based on the type culture CBS 268.33.

HABITAT: In woodpulp in Sweden.

MATERIAL EXAMINED.

a. Herbarium material.

4 slides, marked "Paratypus", all from isolates of Melin in Sabrå Parish, Ulfviks Trämasse-fabrik, 211:2, 236:1b, 242:22 from ground wood pulp, 236.42 from the air (UPS).

Culture marked "authentic", N. F. Conant 329, from ground wood pulp in Sweden, from J. A. Nannfeldt to CBS, with photograph; slide marked "Paratypus" from strain isolated by E. Melin from ground wood pulp, Ulfviks Trämasse-Fabrik, Sweden (FH).

b. Living strains.

CBS 268.33 = IMI 59,445, type culture, sent by E. Melin in 1933.

CBS 848.69 = G.L.H. 7515-E isolated from wood chip of *Fagus sylvatica*, Heikendorfer, Kr. Plön, by G. L. Heinebert, July 1965.

CBS 849.69 = G.L.H. 7560, isolated from *Picea*-wood, Hann. Münden, sent by H. Zycha, as Ka 13, July 1965.

6 (3). PYRENOPEZIZA LARICINA Rehm

f. MICROSPERMA Le Gal & Mangenot, stat. con.—Fig. 6q-t

*Pyrenopeziza laricina* Rehm f. *microsperma* Le Gal & Mangenot, stat. con. in Revue Mycol. 26: 266-270. 1961.

In the hyphae the characteristic wall thickenings are obvious.

The phialides are sturdy; they develop in loosely forked groups or in compact verticillate clusters. Exceptionally a sessile collarete occurs on the hyphae. Proliferation occurs.

The conidia are thin-walled and very variable, mostly ovoid,  $2.5-4 \times 2-2.5 \mu$ ,

but also cylindrical, sometimes slightly curved, up to  $5 \times 3 \mu$ . With age they develop into globose chlamydo-spores, up to  $4-5 \mu$  in diam. Characteristic moniliform chains of globose to subglobose chlamydo-spores, up to  $5 \times 4 \mu$ , occur in old cultures.

Material examined.

CBS 568.63, isolated from *Abies* trunk, near Fraize (Vosges), sent by F. Mangenot in 1963.

6(4). MOLLISIA CINERELLA Sacc.

stat. con., Le Gal & Mangenot—Fig. 6 u-w

*Mollisia cinerella* Sacc. stat. con., Le Gal & Mangenot in *Revue Mycol.* 26: 265. 1961.

Characteristic wall thickenings of the hyphae and irregular thick-walled cells, up to  $8 \mu$  broad, are common.

The phialides are symmetrically swollen and not as broad as in *Pyrenopeziza laricina* f. *microsperma*. The author could not, however, observe the flat broad collarette as shown in Mangenot's drawings. The phialides develop singly, in loosely forked arrangements or in complicated verticillate bushes. Proliferation occurs. Sometimes a sessile collarette on a hypha was observed.

The conidia have a distinct wall. Very variable in shape and size they are generally globose to ovoid,  $2.5-4.5 \times 2-2.5 \mu$ , but straight, cylindrical spores, up to  $6 \times 2-3 \mu$ , are also common. In old cultures conidia develop into globose thick-walled chlamydo-spores and adhere in balls at the collarette of the phialides.

MATERIAL EXAMINED.

CBS 312.61, isolated from *Fagus* wood, Génicourt (Meuse), sent by F. Mangenot in 1961.

The last two mentioned species represent only examples of conidial states of the large and closely related genera *Mollisia* and *Pyrenopeziza* of the Helotiales which are still too little investigated and known in pure culture. Although the differences between the four *Phialophora* states of this group so far mentioned, are slight, it seemed preferable to leave the species apart instead of considering the conidial state of *Mollisia cinerella* identical with *Phialophora melinii*, as was done by Le Gal & Mangenot (1961). Of the four species described above *Phialophora melinii* seems to be the one with the smallest conidia.

CBS 609.69 (DAOM 33739) was illustrated by Hughes (1953); it is characterized by very long beaker-shaped collarettes which contain usually two oval spores,  $4.5-5 \times 1.5-3 \mu$ . The densely branched sturdy phialides are similar to those of *P. fastigiata*, to which it must be closely related.

6 (5). PHIALOPHORA MALORUM (Kidd & Beaumont) McColloch—Fig. 7

*Sporotrichum malorum* Kidd & Beaumont in *Trans. Br. mycol. Soc.* 10: 111. 1924. — *Phialophora malorum* (Kidd & Beaumont) McColloch in *Mycologia* 36: 589. 1944.

*Torula heteroderæ* Korab in *Ukrain. Res. Inst. Sugar Ind. Kiev* 6 (16): 29-67. 1929. — *Cadophora heteroderæ* (Korab) Beyma in *Zentbl. Bakt. ParasitKde (Abt. II)* 96: 428. 1937. — *Phialophora heteroderæ* (Korab) Beyma in *Antonie van Leeuwenhoek* 9: 61. 1943.

*Sporotrichum carpogenum* Ruchle in *Phytopathology* 21: 1144. 1931.

*Phialophora luteo-olivacea* ("lutea-olivacea") Beyma in *Antonie van Leeuwenhoek* 6: 280. 1940.

*Phialophora atra* Beyma in *Antonie van Leeuwenhoek* 8: 113. 1942.

*Phialophora goidanichii* Delitala in *Ann. sperim. Agrar. Roma, N.S.* 6: 254. 1952.

#### MISAPPLICATION.

*Trichosporium populneum* Lamb. & Fautr. *apud* Fautr. & Lamb. in *Revue Mycol.* 18: 145. 1896.

Colonies on 2% malt agar attain a diameter of 7 cm after 24 days at 25° C. The growth is wet with some fascicles in the centre. In transmitted light a radial darker striation is visible. The colour is Deep Slate Olive (XLVII), the margin of 0.5 cm of appressed mycelium is colourless. The reverse of the colony is Deep Slate Green (XLVII). Sporulation is abundant.

The hyphae are 1.5–3  $\mu$  broad, without wall-thickenings. Chains of irregular thick-walled cells, up to 5  $\mu$  broad, are common in old cultures.

The phialides are generally gracefully tapering, but in old cultures stalks with sturdy verticillate phialides are observed (Fig. 7 b, e, f).

The conidia are very variable with or without a distinct wall. Predominantly they are ellipsoidal and slightly apiculate, with two oildrops, 4.5–7  $\times$  2.5–3  $\mu$ , but cylindrical, somewhat curved, spores can also occur.

HABITAT: In waste water in Sweden and from different other substrata, e.g. soil, fruits, nematode cysts, amphibians, in Europe and the U.S.A.

The description is based mainly on CBS 141.41 type of *P. luteo-olivacea*.

#### MATERIAL EXAMINED.

##### Living strains.

##### a. Isolates from rotting apples:

CBS 266.31, sent by F. D. Heald, and

CBS 260.32, isolated by G. H. Ruchle, sent by F. D. Heald, under the name *Sporotrichum carpogenum*, both from U.S.A.

CBS 357.51, type of *Phialophora goidanichii* Delitala, sent by G. Goidanich, Italy, 1951.

CBS 355.59, No. 10-1, sent by E. Olthoff, Wageningen, 1959.

4 strains, numbered 10-5, 43-1, 43-2, and 43-7, sent by E. Olthoff, Wageningen, 1959.

##### b. Other origin.

CBS 259.32, from cysts of *Heterodera schachtii* in Bohemia, sent by J. Rozsypal as *Torula heteroderae*, 1932.

CBS 141.41, type of *Phialophora luteo-olivacea*, from sewage of "Schleifery Byske", Sweden, sent by S. Foghammer in 1939.

#### EXPLANATION OF FIGURE 7

Fig. 7. *Phialophora fastigiata* group: *Phialophora malorum*. a–g. Type strain of *Phialophora luteo-olivacea*, CBS 141.41. — a, c. Conidia in a young culture, d. in an old culture. — b, e. Phialides in a young culture, f. in an old culture. — g. Chain of thick-walled cells.

h–m. Type strain of *Phialophora atra*, CBS 165.42. — h. Conidia and chlamydospores of different age and shape. — j. Young phialides. — k. Chlamydospore developing a phialide. — m. Old phialides.

n–q. Authentic strain of *Phialophora heteroderae*, CBS 259.32. — n–p. Phialides. — q. Conidia.

r–t. Type strain of *Phialophora goidanichii*, CBS 357.51. — r, t. Phialides, s. Conidia.

u–w. Authentic strain of *Phialophora malorum*, CBS 266.31. — u, w. Phialides. — v. Conidia.

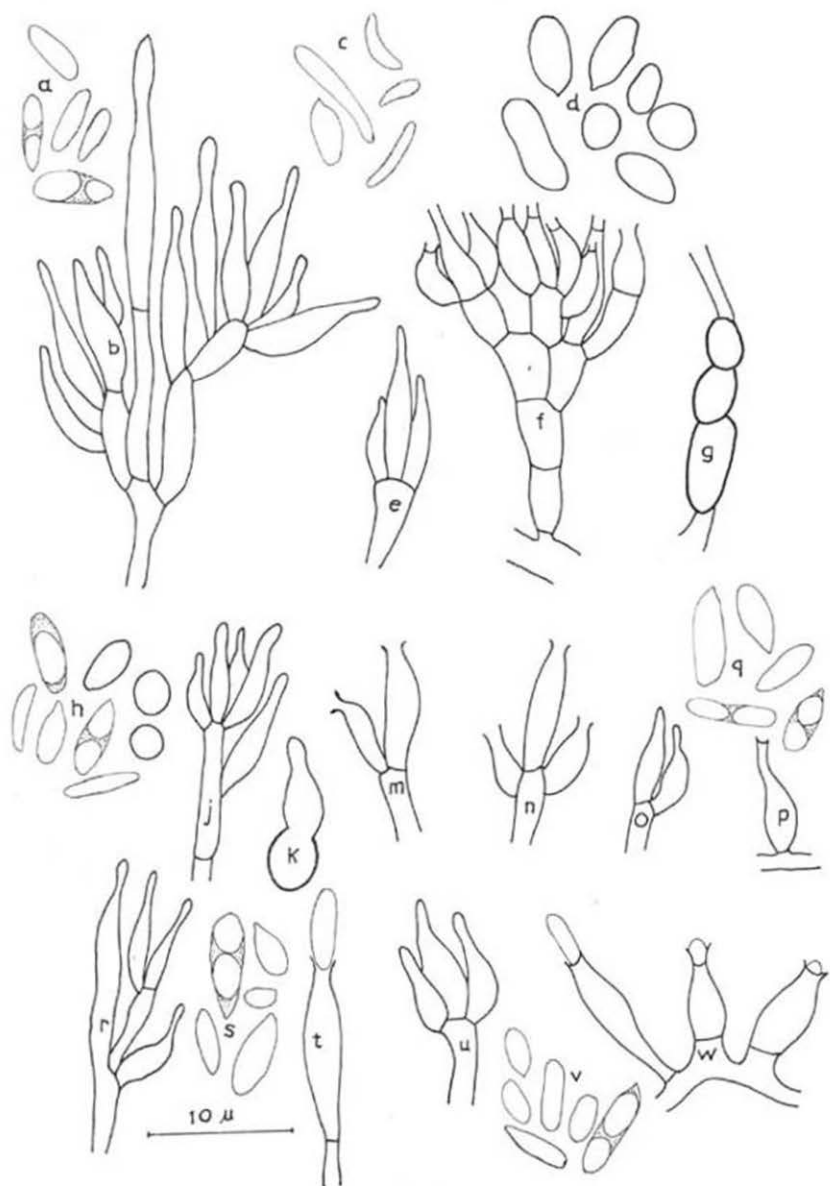


Fig. 7



CBS 165.42, type of *Phialophora atra*, isolated from an Axolotl, sent by S. A. de Lange, Amsterdam, 1942.

CBS 208.57, from human bronchial excrete, sent by G. Cochet, Belgium, 1957.

CBS 245.60, from air, sent by L. Tybring, Denmark, 1959, as No. 1376.

CBS 850.69 (C 386), CBS 851.69 (C 542), CBS 852.69 (C 570) and CBS 853.69 (C 574), from agricultural soil, sent by K. W. Gams, Kiel-Kitzeberg, 1963.

CBS 854.69 (162) from polyvinylacetate and CBS 855.69 (189) from tricresylphosphate, sent by H. J. Hueck, Delft, 1963.

CBS 856.69 (1213/2/2) and CBS 857.69 (1208/3) from *Picea abies*, sent by F. Roll-Hansen, Norway, 1963.

CBS 858.69 from polyvinylchloride tubing, sent by H. Kühlwein, Karlsruhe.

CBS 859.69 (102d) from stalactite in Lehman Cave, U.S.A., sent by F. W. Went, 1968.

CBS 860.69 = PD 67/890 from crocus bulbs, sent by G. H. Boerema, Wageningen, 1968.

*Phialophora malorum* is a common fungus in water and soil, where it may attack cysts of nematodes; it also grows on apples, where it causes rotting spots. The characters of *P. fastigiata* and *P. malorum* are compared in the following table:

TABLE 1 — COMPARISON OF PHIALOPHORA FASTIGIATA AND P. MALORUM

<i>Phialophora fastigiata</i>	<i>Phialophora malorum</i>
Hyphal strands present	Hyphal strands present
Hyphae brownish	Hyphae greenish
Wall-thickenings common	Wall-thickenings generally absent
Phialides sturdy, with very distinct collarettes	Phialides when young, gracefully bent, with age the collarettes become visible
Conidia very variable but mostly ovoid, with age developing into chlamydo-spores	Conidia very variable, but mostly ellipsoidal and slightly apiculate, with oildrops

Transitional strains between the two species occur commonly. *P. malorum* is distinct from the former species by a narrower opening of the phialide apex and by conidia with a thinner wall and slight apiculation, with less tendency towards transformation into chlamydo-spores.

The variability of the species led to the erection of three species causing apple rots: *Sporotrichum malorum* by Kidd & Beaumont (1924), *Sporotrichum carpogenum* by Ruehle (1931), and *Phialophora goidanichii* by Delitala (1952).

Isolates from cysts of *Heterodera schachtii* made by Rozsypal were identified by Jaczewski in a letter to Rozsypal as *Torula heteroderae* Korab. A culture sent by Rozsypal to the CBS under this name and preserved as CBS 259.32 was first re-identified by van Beyma as *Trichosporium populneum* (Rozsypal, 1934). In 1937 van Beyma recognized it as different from other isolates considered as *Trichosporium populneum* and made the new combination *Cadophora heteroderae* (Jacz.) Beyma for Rozsypal's fungus. The correct author's citation for *Cadophora heteroderae* is (Korab) Beyma, but the correct name reads *Phialophora heteroderae* (Korab) Beyma.

*Trichosporium populneum* Lamb. & Fautr. is *Spadicoides atrum* (Corda) Hughes according to the type specimen (Hughes, 1958).

#### 7. PHIALOPHORA HOFFMANNII group

Colonies often wet, yeast-like, phialides on hyphae or on hyphal strands, short, stout, swollen, bottle-shaped or of varying wavy forms, with the apical opening becoming wider at a late state.

The group can be subdivided into:—

- a. strains with pale, cream-coloured cultures, and
- b. strains with pink cultures, sometimes darkening with age.

Under certain conditions of light and temperature some strains of the first group develop apothecia of Discomycetes, others form a pycnidial or sporodochial state, often containing branched conidiophores with an open tip. These strains could not be identified with any known genera, they require a special study.

In the second group dark spots of hyphal aggregates, sometimes covered with setae, develop readily; they are interpreted as perithecium initials. Some fresh isolates develop mature perithecia belonging to the genus *Coniochaeta*. A suitable technique for inducing perithecia is cultivation on 2% malt extract agar (with 0.2–0.5% yeast extract), or cornmeal or oatmeal agar, sometimes with addition of lupin stems, for two weeks at 25° C, then exposure to black light (12 hrs per day) for two weeks or more at the same temperature, and finally for 1–2 weeks at 5° C. The perfect states so far observed differ only slightly from each other and are connected by intermediate forms. This feature reflects the slight, but constant differences in the conidial states.

It is doubtful whether a specific distinction on the basis of the knowledge of the conidial state alone will ever be possible.

*Phialophora luteo-viridis* appears to be constantly connected with dark-spored *Coniochaeta* species, such as *C. velutina* (Fuck.) Munk. Rogers (1965) described the conidial state of *C. ligniaria* (Grev.) Massee which belongs to pink strains of the *P. hoffmannii*-group. Udagawa and Takada (1967) described the conidial state of *C. tetraspora* Cain which belongs to the same group. Another example is *Coniochaeta* spec., cf. *Rosellinia xyloxylopora* Cooke & Ellis (Munk, 1957).

Representative strains of this group were described under the following names (arranged according to intergrading cultural characters, from pure pink to dark olivaceous, almost black, and with chlamyospores):

#### 7 (1). *Phialophora hoffmannii* (Beyma) Schol-Schwarz, *comb. nov.*

*Margarinomyces hoffmannii* Beyma in Zentbl. Bakt. ParasitKde (Abt. II) 99: 386. 1939 (basionym).

*Phialophora aurantiaca* Beyma in Antonie van Leeuwenhoek 6: 277. 1940.

Colonies permanently light coloured. At most the reverse reaches Antique Brown (III) in the centre. Type culture CBS 245.38, isolated from butter in Switzerland by D. Hoffmann.

van Beyma (1943) declared *P. aurantiaca* and *Margarinomyces hoffmannii* as identical, but he did not decide as to the synonymy of the genera. Instead, he incorrectly dropped the earlier name *M. hoffmannii*.

7 (2). **Phialophora decumbens** (Beyma) Schol-Schwarz, *comb. nov.*

*Margarinomyces decumbens* Beyma in Antonie van Leeuwenhoek 8: 111. 1942 (basionym).

Mycelium light pink in young cultures, becoming somewhat darker with age. Type culture CBS 153.42, isolated from strawberries.

7 (3). **Phialophora fasciculata** (Beyma) Schol-Schwarz, *comb. nov.*

*Margarinomyces fasciculatus* Beyma in Zentbl. Bakt. ParasitKde (Abt. II) 99: 384. 1939 (basionym).

Colonies strongly fasciculate, predominantly light coloured, the reverse in the centre reaching Warm Sepia (XXIX). Type culture CBS 205.38, isolated from butter in Switzerland by D. Hoffmann.

7 (4). **Phialophora luteo-viridis** (Beyma) Schol-Schwarz, *comb. nov.*

*Margarinomyces luteo-viridis* Beyma in Zentbl. Bakt. ParasitKde (Abt. II) 99: 381. 1939 (basionym).

Mycelium dark olivaceous but also with yellow and dark orange tinges. Type culture CBS 206.38, isolated from butter in Switzerland by D. Hoffmann.

7 (5). **Phialophora mutabilis** (Beyma) Schol-Schwarz, *comb. nov.*

*Margarinomyces mutabilis* Beyma in Antonie van Leeuwenhoek 10: 48. 1944/45 (basionym).

Cultures have pink mycelium initially and darken with age by the formation of irregularly shaped, terminal or intercalary chlamydospores. The terminal chlamydospores are attached on a broad base.

Chlamydospores may produce conidia directly through collarettes or give rise to phialides. Conidium formation through short collarettes from intercalary hyphal cells is common. With age the phialospores become dark like chlamydospores. The species is known from soil and water. Type culture CBS 157.44, isolated by S. Windisch from river water.

The different species were originally all based on single isolates, except for *P. hoffmannii*. None of the original strains developed perithecia. In recent years the CBS has received for identification a large number of strains belonging to this

group. It has not been possible to identify them with one of the known pink species because of small but rather constant differences. Amongst both the pink and the dark coloured cultures some human and animal pathogenic strains have been found.

### 8. PHIALOPHORA LAGERBERGII group

Colonies grow easily on various media.

Conidiophores consist of one or two stalk cells with repeatedly verticillate clusters of phialides, forming an obconical brush.

Phialides strongly swollen, terminating in distinct and usually long beaker-shaped collarettes without flaring margins.

The conidia are hyaline, slender, generally somewhat curved, and measure  $3-8 \times 1.5-2 \mu$ .

#### 8 (1). PHIALOPHORA LAGERBERGII (Melin & Nannf.) Conant Fig. 8 a-c, j-o

*Cadophora lagerbergii* Melin & Nannf. in Svenska Skogsvårdsfören. Tidskr. 32: 415. 1934. —  
*Phialophora lagerbergii* (Melin & Nannf.) Conant in Mycologia 29: 598. 1937.

Colonies on 2% malt agar attain a diameter of 9 cm after 12 days at 25° C. The growth is woolly and the colour from the centre to a radius of 2 cm Dark Olive (XL), then for a 1.5 cm wide zone Brownish Olive (XXX), for a 0.75 cm zone Ochraceous Tawny (XV), finally with a 0.25 cm wide flat margin. The reverse of the colony is Cinnamom Drab (XLVI). Sporulation is abundant.

The septate hyphae are brown, usually 2-3  $\mu$  wide, and develop characteristic thickenings of the wall with age. Sometimes they are swollen or moniliform with a thickened wall and up to 5-6  $\mu$  wide (Fig. 8o). Hyphal strands are common. Sometimes the hyphal tips are swollen. These swellings may develop into phialides.

The phialides in young cultures are simple, slender and gracefully tapering, sometimes with a septum. In older cultures stout bushes of *Penicillium*-like, branched, inflated phialides, 3-4  $\mu$  wide, develop laterally on solid stalks on the hyphae (Fig. 8 b). These bushes are characteristic of the species. The phialides are 15-25  $\mu$  long, they have an extremely long narrow collarette, up to  $7 \times 2 \mu$ , without a flaring margin. Sometimes proliferation occurs (Fig. 8m).

The conidia are hyaline and predominantly allantoid,  $3-4.5 (-6) \times 1-1.5 \mu$ . Very occasionally ovoid conidia and globose chlamydo-spores, 5  $\mu$  in diameter, occur in old cultures. No perfect state is known.

The description is based on the type strain of the species, CBS 266.33.

HABITAT: on wood of *Pinus sylvestris* in Sweden.

#### MATERIAL EXAMINED.

##### a) Herbarium material.

Paratypus of *Cadophora lagerbergii*, isolated by E. Melin from wood of pine in Uppland, Ed Parish, Bisslinge (UPS).

Authentic material of *Cadophora lagerbergii*, isolated from wood of *Pinus sylvestris* in Sweden. Culture from Nannfeldt, via CBS sent to N. F. Conant with his number 332 (FH).

## b) Living strain.

CBS 266.33, originally isolated by E. Melin = N. F. Conant's strain 332.

Spore development in this species has been studied by Cole & Kendrick (1969).

## 8 (2). PHIALOPHORA REPENS (Davidson) Conant—Fig. 8g, h

*Cadophora repens* Davidson in J. agric. Res. 50: 803. 1935. — *Phialophora repens* (Davidson) Conant in Mycologia 29: 598. 1937.

The most striking difference with *P. lagerbergii* is the absence of the long narrow beaker-shaped extension of the collarettes in the phialides. In *P. repens* the collarette

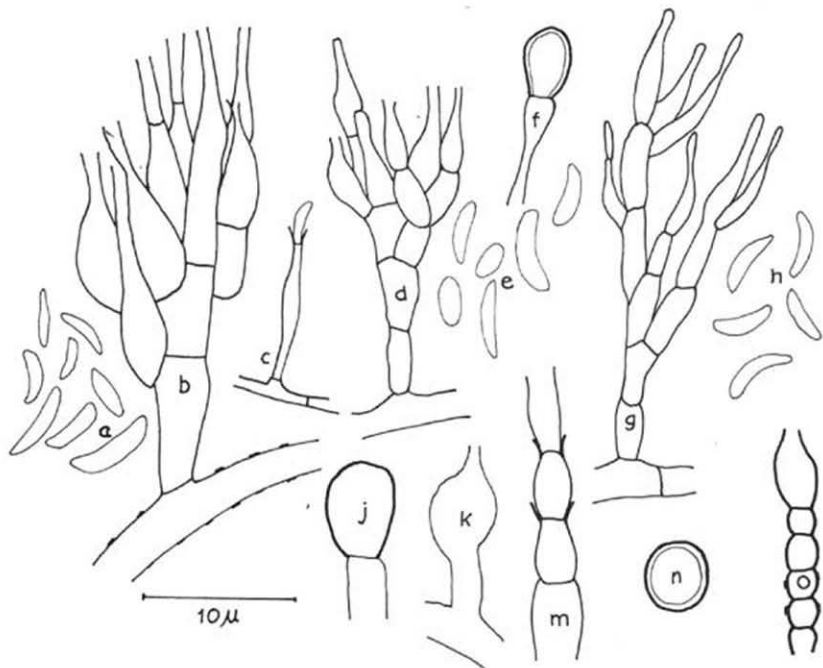


Fig. 8. *Phialophora lagerbergii* group

a-c, j-o. Type culture of *P. lagerbergii*, CBS 266.33. — a. Conidia. — b. Bush of phialides. — c, k, o. Simple phialides. — j. Terminal chlamydospore. — m. Proliferating terminal phialide. — n. Chlamydospore.

g, h. Type culture of *P. repens*, CBS 294.39. — g. Bush of phialides. — h. Conidia.

d-f. *Phialophora* state of *Ascocoryne sarcoides*, CBS 364.61. — d. Bush of phialides. — e. Conidia. — f. Terminal chlamydospore.

is distinct, but short. The conidia measure  $3-7 \times 1-1.5 \mu$ . The growth is powdery and more rapid than in *P. lagerbergii*. No perfect state is known.

The description is based on the type culture CBS 294.39.

HABITAT: in wood of *Pinus sylvestris*, U.S.A.

#### MATERIAL EXAMINED.

Authentic material of *Cadophora repens*, isolated from wood = Conant's strain 338 (FH).

Living strain.

CBS 294.39, type culture of *Cadophora repens*, sent by R. W. Davidson to the CBS in 1939; morphologically identical with the material in FH.

#### 8 (3). ASCOGORYNE SARCOIDES (Jacq. ex S. F. Gray) Groves & Wilson Fig. 8d-f

*Ascogoryne sarcoides* (Jacq. ex S. F. Gray) Groves & Wilson in *Taxon* 16: 35. 1967.

1. stat. con.: *Phialophora* spec.

2. stat. con. with sporodochia: *Coryne dubia* Pers. ex S. F. Gray.

The CBS maintains 7 strains under the name *Coryne sarcoides* (Jacq. ex Fr.) Tul. These have a cream-coloured mycelium and most of them when grown on oatmeal or malt extract agars, produce a brownish to violet pigment which diffuses into the agar. Some of the strains do not produce sporodochia any longer or have never produced them but each strain develops a conidial apparatus that is verticillately branched and very similar to that of *Phialophora lagerbergii* and *P. repens*. The conidia are curved and measure up to  $5 \times 1.5 \mu$ .

Description based on CBS 364.61 and several other strains.

#### MATERIAL EXAMINED.

Living strains.

CBS 153.31, sent by W. Loos, Germany, in 1931.

CBS 155.35, sent by T. Lagerberg, Sweden, under No. 25:3 from coniferous tree, identified by F. H. van Beyma, 1935.

CBS 170.56, from *Nothofagus*, Dovey Forest, No. 14.5.13, and CBS 171.56, from *Pinus*, Kielder Forest, No. 16.5.137, both sent by S. Batko, Surrey, in 1956.

CBS 192.62, ascospore isolate from P. Berthet, Lyon, sent by J. Boidin, 1962.

CBS 364.61, sent by W. R. Day, Oxford, as No. 4505, isolated from rotting wood of Norway spruce (*Picea excelsa*), identified first as *P. repens*.

CBS 407.69 = strain 1675, isolated by H. A. van der Aa, from rotting wood, Baarn, 1969.

The position of CBS 237.53, representing *Margarinomyces microsperma* (Corda) Mangelot (*in Revue gén. Bot.* 59: 20. 1952, and based on *Ceratocladium microspermum* Corda, *Prachtflora* 41, pl. 20. 1839) remains uncertain because of atypical behaviour and poor sporulation of Mangelot's strain.

*Ceratocladium microspermum* Corda is an entirely different fungus. It has been redescribed by Hughes (1951).

On the basis of their conidial apparatus and characteristically curved spores, these three species are closely related but not identical. A perfect state is known only in one of them, but most probably the two others also belong to closely related genera.

9. *PHIALOPHORA LIGNICOLA* (Nannf. apud Melin & Nannf.)

Goidanich apud Goidanich & al.—Fig. 9

*Lecythophora lignicola* Nannf. apud Melin & Nannf. in Svenska Skogsvårdsfören. Tidskr. 32: 432. 1934. — *Cadophora lignicola* (Nannf. apud Melin & Nannf.) Beyma in Zentbl. Bakt. Parasitkde (Abt. II) 96: 427. 1937. — *Phialophora lignicola* (Nannf. apud Melin & Nannf.) Goidanich apud Goidanich & al., Ricerche sulle alterazioni . . . Roma 112. 1938.

Colonies on 2% malt agar reach a diameter of 4.6 cm after 16 days at 25° C. The centre, somewhat elevated and tufted up to 0.5 cm high, is Deep Grayish Olive (XLVI), surrounded by flat Chaetura Black (XLVI) mycelium which extends into a 0.7 cm broad, light-coloured margin which becomes pink in the light; the aerial mycelium is Tilleul Buff (XL) near the margin and merges into a zone of appressed Vinaceous Buff (XL) mycelium. The reverse of the colony is Olivaceous Black (LI) with a Vinaceous Buff (XL) margin. Sporulation is abundant. On potato dextrose agar a yellow pigment is developed.

The hyphae are 1.5–3  $\mu$  wide, often aggregated in strands, they readily develop moniliform, occasionally branched, chains of inflated cells, 4–8  $\mu$  wide, sometimes with thickened verrucose walls (Fig. 9a, p, m). Terminal and lateral chlamydospores which become brown with age, are common (Fig. 9c, y). The fungus is easily recognized by its moniliform hyphae which resemble those in *P. verrucosa*.

The phialides, up to 20  $\mu$  long, are variable in shape, mostly short and strongly inflated but occasionally long and slender. Sometimes they are reduced to collarettes on the hyphae. The collarettes are distinct. The phialides occur singly in lateral or terminal positions, or in groups on conidiophores, exceptionally forming bushes. They become brown with age. Terminal phialides occur also on moniliform hyphae. Proliferation occurs (Fig. 9v).

The conidia are hyaline to subhyaline, dimorphic and variable in shape and size. In young cultures cylindrical or curved spores, 5–8  $\times$  1.5–3  $\mu$ , are rather common (Fig. 9s), with age ovoid conidia, sometimes slightly apiculate, 3–4.5  $\times$  1.5–2  $\mu$ , prevail. These may develop into globose chlamydospores, 5–6.5  $\times$  3.5–4.5  $\mu$  (Fig. 9g). The description is based on the lectotype culture, CBS 267.33.

In 3 months old cultures, sclerotia, possibly representing initials of fruiting bodies, were observed (Fig. 9d).

HABITAT: In ground wood-pulp, bluing wood, "white water" from paper mills, fresh water, and in sewage, Sweden.

MATERIAL EXAMINED.

a. Herbarium material.

*Lecythophora lignicola* Nannf., 4 slides and one dried culture, each labelled "Paratypus, isolated by E. Melin", viz. 130:1 Västmanland, white water, 130:12 Norrbotten, Luleå, Trämassefabrik, 159:6 Hälsingland, 160:44 Ångermanland, white water, culture from Västerbotten, Sofiehems Trämassefabrik, white water (all UPS).

*Lecythophora lignicola* Nannf., 5 slides, each labelled "Paratypus, isolated by E.

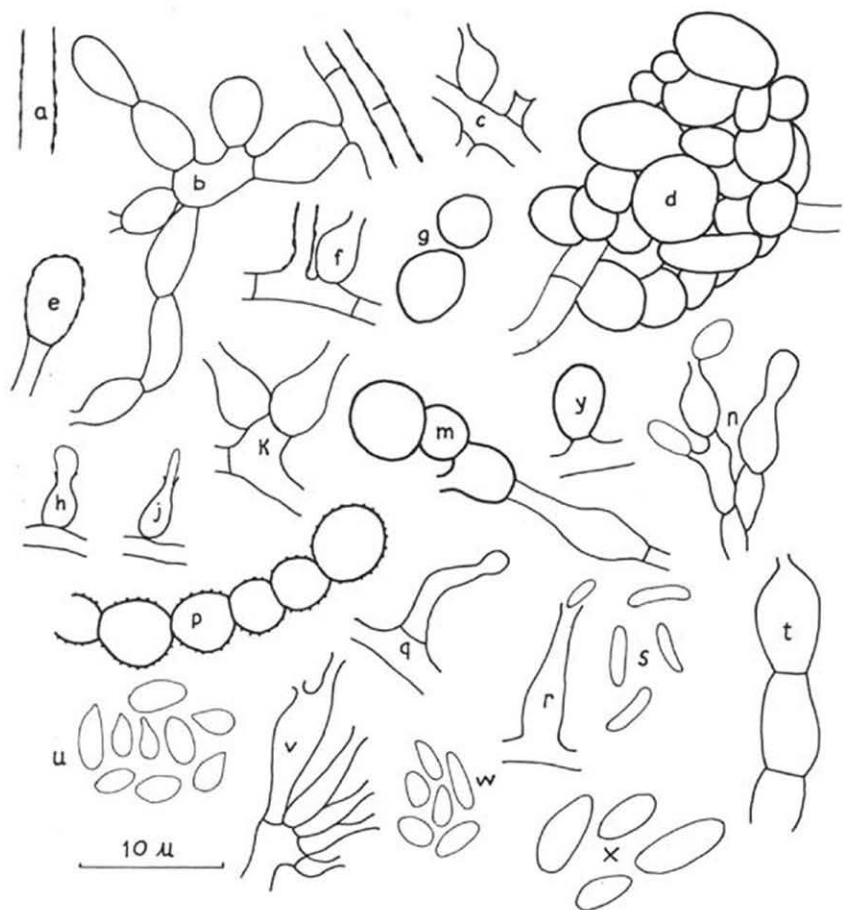


Fig. 9. *Phialophora lignicola*. b-d, f, u, v. type culture, CBS 267.33; e, g, k, m. from paratype material (UPS and FH); a, h, j, y. CBS 308.49. — a. Hypha with typical thickening of the wall. — b. Branched moniliform hyphae with terminal collarettes. — c. Lateral phialide and a mere collarette. — d. Sclerotium. — e. Terminal chlamydospore with irregularly thickened wall. — f. Hypha with thickened wall. — g. Chlamydospores. — h, j. Lateral phialides, one producing a globose, the other a cylindrical conidium. — k. Branched phialide. — m. Thick-walled cells, one with a collarette. — n. Branched phialide. — p. Moniliform hypha with roughened wall. — q, r. Single phialides. — s. Group of long, slightly curved conidia. — t. Terminal phialide. — u. Group of young conidia. — v. Branched phialides with a proliferation. — w, x. Groups of conidia. — y. Lateral chlamydospore.



Melin", viz. 130:1, 160:8, 160:24, Västmanland, white water, 134:27 Hälsingland, 152:13 Jämtland, white water (all FH).

b) Living strains.

CBS 267.33, lectotype culture of *Lecytophora lignicola* Nannf., sent to the CBS by E. Melin in 1933.

CBS 308.49, isolated from blucing wood, sent by S. O. Pehrson, Stockholm, in 1949.

10. PHIALOPHORA MUSTEA Neergaard—Fig. 10

*Phialophora mustea* Neergaard in Zentbl. Bakt. ParasitKde (Abt. II) 104: 407. 1942.

Colonies on 2% malt extract agar attain a diameter of 7.3 cm after three weeks at 25° C. From the centre to a radius of 2 cm, the growth is woolly. Smoke Gray to Dark Grayish Olive (XLVI) in colour, surrounded by a 1.6 cm wide wet ring, Olivaceous Black (1) (XLVI), with faintly radiating mycelium and indistinct concentric rings; the margin of appressed mycelium is 0.5 cm wide, Pale Smoke Gray (XLVI). The reverse of the colony is Olivaceous Black (XLVI) at the centre, merging into Dark Grayish Olive (XLVI) and Pale Smoke Gray (XLVI) at the margin. Sporulation is abundant.

The septate hyphae are 2–4  $\mu$  wide, at first hyaline, soon becoming dark; they may develop hyphal strands and contain numerous oildrops.

The phialides, 10  $\times$  2–3  $\mu$ , are borne singly or in bushes, rarely they are in a terminal position. Generally they taper gradually towards the tip; sometimes they are short and swollen, up to 6  $\mu$  broad. In young cultures collarettes are indistinct, in old ones they are clearly visible (Fig. 10a–d).

The phialospores are hyaline, cylindrical, ellipsoidal, 3–8  $\times$  1.5–2.5  $\mu$ , often with one or two, exceptionally three, oildrops. With age the conidia increase in diameter up to 4  $\mu$ , and develop into dark chlamydospores with a thick wall, covered with the characteristic irregular thickenings.

The species is characterized by its aleuriospores, 4.5–7.5  $\times$  4–6  $\mu$ . They develop singly on short, slender or sometimes broader protuberances, or on sporophores—without a basal septum—which are swollen in the middle and taper towards a sharp point. The aleuriospores are very regular in shape, ovoid with the basal end sharply pointed, to globose and are easily detached. Because of the regularity of the spores and the differentiated sporophores the designation as aleuriospores is preferable to chlamydospores which occur in other species but not in *P. mustea*, where the aleuriospores are never in an intercalary position.

HABITAT: Apple must, in which it develops a white mycelium and causes dark discoloration of the sap; Denmark.

The description is based on the strain CBS 142.41.

MATERIAL EXAMINED.

CBS 142.41, authentic strain from apple must, sent by C. A. Jörgensen, Denmark, 1941, to P. Neergaard and to the CBS.

Strain 18, from fruit juice, sent by H. Lüthi, Wädenswil, Switzerland, 1951.

*Phialophora mustea* can easily be confused with *Ph. mutabilis*, but it has dark mycelium without a tinge of pink and without any intercalary chlamydospores. The aleurio-

spores are very regular and develop singly on sporophores which end in a sharp point. With age phialospores develop into chlamydo-spores up to  $4 \mu$  broad. The species is known only from fruit juices.

11. PHIALOSPORIA RICHARDSIAE (Nannf. apud Melin & Nannf.)  
Conant—Fig. 11

*Cadophora richardsiae* Nannf. apud Melin & Nannf. in Svenska Skogsvårdsfören. Tidskr. 32: 421. 1934. — *Phialophora richardsiae* (Nannf. apud Melin & Nannf.) Conant in Mycologia 29: 598. 1937.

*Cadophora brunnescens* Davidson in J. agric. Res. 50: 803. 1935. — *Phialophora brunnescens* (Davidson) Conant in Mycologia 29: 598. 1937.

*Phialophora caliciformis* G. Smith in Trans. Br. mycol. Soc. 45: 391. 1962.

Colonies on 2% malt agar attain a diameter of 5.7 cm after 3 weeks at  $25^{\circ}$  C. In the central area growth is flat and Olive Brown (XL), outside this there is a 0.2 cm broad ring of vertically directed hyphal strands, Buffy Brown (XL) in colour, surrounded by a velvety margin with faint Brownish Olive (XXX) rings. The reverse is Fuscous Black (XLVI). A brownish pigment diffuses into the malt agar. Sporulation is abundant. When exposed to day-light for several weeks, various strains may show a tinge of pink.

The mycelium, at first hyaline, becomes light brown in three days and then dark brown; aerial mycelium is erect, tufted, and also dark brown; the hyphae are septate,  $2.5-4 \mu$  in diameter, and usually aggregated in strands. The walls of hyphae and conidiophores are often irregularly thickened.

The phialides are very numerous, sturdy, arising perpendicular on hyphal

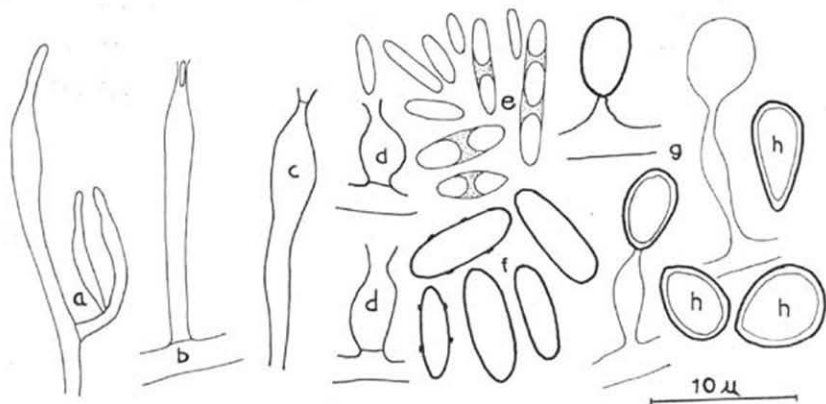


Fig. 10. *Phialophora mustea*. Type culture, CBS 142.41. — a-d. Phialides, a. branched, b. single in young culture, c. in terminal position, d. broad forms. — e, f. Phialospores in young and old cultures respectively, the latter developing into chlamydo-spores. — g. Sporophores bearing aleuriospores. — h. Aleuriospores.

strands as well as on individual hyphae; they are 10–35  $\mu$  long, 2.5–4  $\mu$  broad at the base, tapering to 1.2–2  $\mu$  at the top, and end in a light brown, sometimes somewhat darker, cup-shaped collarette with flaring margin, 1  $\mu$  deep and up to 5  $\mu$  broad. The longer conidiophores have, besides the usual septum at the base, one or two more septa and are often branched. Proliferation is common.

The conidia are typically dimorphic. Hyaline, cylindrical, sometimes allantoid, spores, 3–8  $\times$  1.5–3  $\mu$ , occur predominantly in young cultures. Globose or lacrymoid, subhyaline, conidia, 3–3.5  $\mu$  in diameter, with a distinct wall and darkening with age, are more prevalent in older cultures. However, both types occur in every culture and may even develop in the same spore-ball (Fig. 11d). The species can be easily recognized by the sturdy phialides with the broad, shallow cups with flaring margins and by the dimorphic conidia. Optimum temperature is 25–30° C. No perfect state is known.

Description is based on the strain CBS 295.39.

НАВИТАТ: on wood and ground wood pulp, in sewage and soil, in North America, Europe, Africa, Asia. The fungus has also been isolated once from plastic material in the open air in Africa (Nicot, 1966), from a prostate gland in the Netherlands (G. A. de Vries, pers. commun.), and from a subcutaneous cystic granuloma in New York by Schwartz & Emmons (1968).

#### MATERIAL EXAMINED.

##### a. Herbarium material.

Paratype material of *Cadophora richardsiae*: Slide 194:3, labelled "Paratypus of *Cadophora richardsiae*, isolated from ground wood pulp, North America, culture 82219-2, received from Miss Richards."

Two slides 194:4, 272:4, from culture 6723-1 from Miss Richards, same origin, labelled "paratypus" (UPS).

Two slides 229a and 237:21a, isolated by E. Melin, 1932, from ground wood pulp in Västerbotten, Umeå, Sofiehems Trämässfabrik, "paratypus", all det. by J. A. Nannfeldt (UPS).

*Cadophora richardsiae*, photograph and dried culture, isolated from wood pulp, via CBS to N. F. Conant (No. 330), authentic material (FH).

*Cadophora brunnescens*, type material consisting of 2 dried cultures and a photograph from N. F. Conant (No. 377) (FH).

##### b. Living strains.

CBS 270.33, authentic strain No. 389:12 from E. Melin, sent in 1933, as *C. richardsiae*.

CBS 295.39, type of *Cadophora brunnescens*, sent by R. W. Davidson in 1939, No. 59048, from pine lumber, Louisiana, isolated 1931.

CBS 310.49, isolated from wax by M. D. Horst, identified by A. L. van Beverwijk.

CBS 302.62 = IMI 89387, type of *Phialophora caliciformis*, sent by G. Smith, 1962, isolated March, 1954, by W. P. K. Findlay, from African Mahogany (*Khaya* sp.) at the Forest Products Research Laboratory, Princes Risborough.

CBS 271.66, obtained from G. A. de Vries, 1966, isolated from a prostate gland from a patient in the Netherlands.

CBS 573.67, sent by J. Nicot, 1967, isolated by P. Fusey, 1964, from plastic material in the Central African Republic.

CBS 841.69 and CBS 842.69 isolated by A. L. van Beverwijk as contaminants of the laboratory, Baarn.

CBS 843.69 (1573), CBS 844.69 (1551), CBS 845.69 (490), CBS 846.69 (3880),

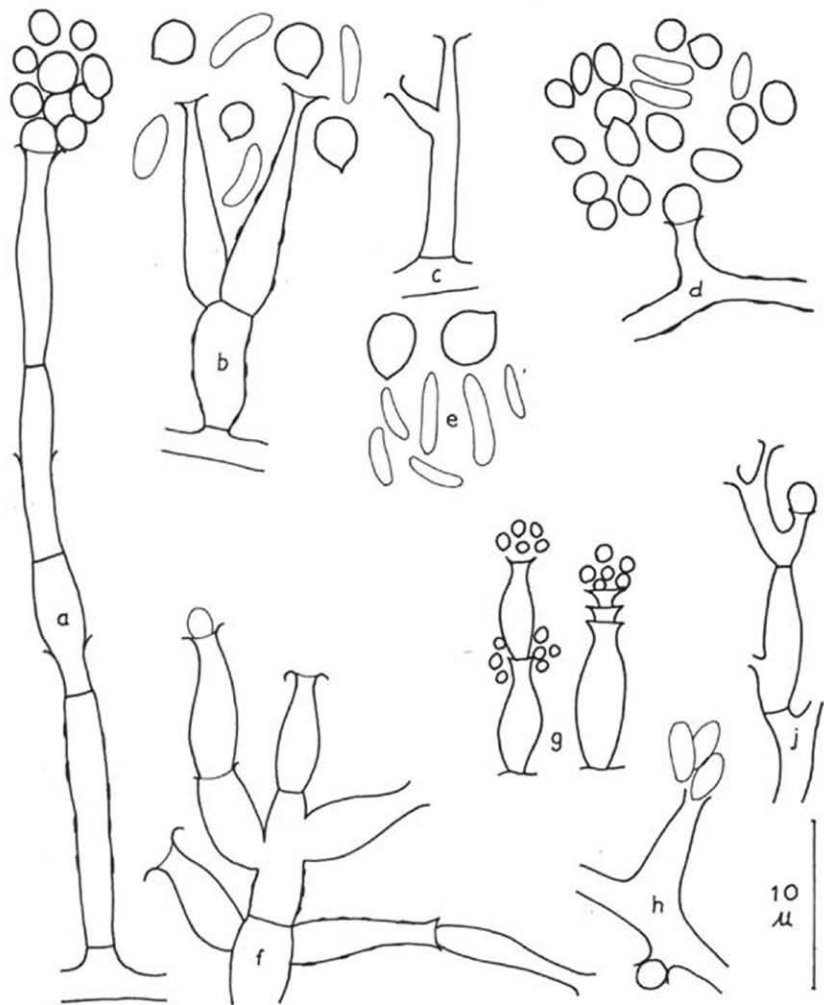


Fig. 11. *Phialophora richardsiae*. a, d, h. CBS 841.69; b, e. Conant's dried culture 337 (FH) as *Cadophora brunnescens*; c, f. Conant's dried culture 330 (FH) as *Cadophora richardsiae*. — a. multiple proliferation, the basal part with irregularly thickened wall. — b, c. furcate phialide and spores in various shapes and sizes. — d. spore-mass with dimorphic spores. — e. subglobose pigmented and cylindrical hyaline conidia. — f. branched conidiophores with proliferations. — g. schematic figure showing what may happen when secondary phialides become shorter (after G. L. Hennebert). — h. short phialides on the same hyphae producing long oval as well as globose conidia. — j. laterally proliferating phialides.

CBS 847.69 (3627), sent by W. B. Cooke via G. L. Hennebert, from waste stabilization ponds and sewage in Ohio.

In the diagnosis of this fungus Nannfeldt (1934) mentioned only subglobose conidia with a distinct brown wall. Davidson (1935) wrote in his diagnosis of *Cadophora brunnescens*: "Conidia hyaline and ovoid or cylindrical at first, 1.2  $\mu$  to 3  $\mu$  by 3  $\mu$  to 8  $\mu$ , later globose and light brown, 1.5  $\mu$  to 3  $\mu$  in diameter." In a letter to van Beyma in 1939, he suggested the synonymy of *Phialophora brunnescens* with *P. richardsiae* and this was later confirmed by van Beyma (1943).

Smith (1962) described a new species, *Phialophora caliciformis*, mentioning only the brown, globose or subglobose conidia. The type culture of this, IMI 89387 = CBS 302.62, turned out, however, to be identical with *P. richardsiae*, as Nicot (1966) mentioned in her publication.

In the strain CBS 573.67 Nicot (1967) described the formation of successive collarettes at the top of a phialide. She explained this phenomenon as a minute lengthening of the cup but it may be explained more correctly as a very reduced proliferation of the phialide (Fig. 11g).

In this particular strain the globose spores may become verruculose with age.

#### 12. PHIALOPHORA VERRUCOSA Medlar—Fig. 12

*Phialophora verrucosa* Medlar in *Mycologia* 7: 203. 1915.

*Cadophora americana* Nannf. apud Melin & Nannf. in Svenska Skogsvårdsfören. Tidskr. 32: 412. 1934. — *Phialophora americana* (Nannf. apud Melin & Nannf.) Hughes in Can. J. Bot. 36: 795. 1958 (synonymy according to Conant, 1937).

Colonies on 2% malt agar reach a diameter of 6–7 cm in 4 weeks at 25° C. They are woolly, Dark Mouse Gray (LI) to Deep Olive Gray (LI). At the periphery of the colony the mycelium grows submerged over a zone 2–3 mm broad and has a darker tinge, Iron Gray (LI) to Olivaceous Black (3) (LI).

Colonies on asparagine-yeast agar at 25° C grow somewhat faster, reaching 8 cm in diameter in 4 weeks. They are woolly and Hair Brown (XLVI). The submerged margin is irregular, 1–3 mm broad and Dark Grayish Olive (XLVI). Optimum temperature 25–30° C.

Hyphae are septate, up to 5  $\mu$  wide, sometimes aggregated in strands, and sometimes moniliform because of inflated, thick-walled cells, up to 10–15  $\mu$  long (Fig. 12r).

Phialides, up to 30  $\mu$  long, develop terminally or laterally on the hyphae. They are slender or more often bottle-shaped, single or branched and then sometimes forming bushes. They end in a very distinct cup-shaped collarette with flaring margin obviously darker than the rest of the phialide, and up to 3.5  $\mu$  in diameter and 4.5  $\mu$  in depth. Proliferation occurs (Fig. 12 a, g, n).

Conidia are hyaline, 3–5  $\times$  2–3  $\mu$ , variable in shape and size, ovoid or cylindrical or exceptionally allantoid (occurring in Conant's exsiccate), cohering in a mucous ball at the top of the phialide, becoming darker with age and growing into large, more or less globose, thick-walled spores, with a brown wall, 5–7(–10–15)  $\times$  3–6  $\mu$  (Fig. 12b, f). These may develop a cup or a muzzle-like protuberance from which

secondary conidia are pushed out (Fig. 12c-e). Anastomoses occur. No perfect state is known.

Description based mainly on CBS 281.35.

HABITAT: in human skin lesions, pathogenic for man and mice; in wood pulp and soil.

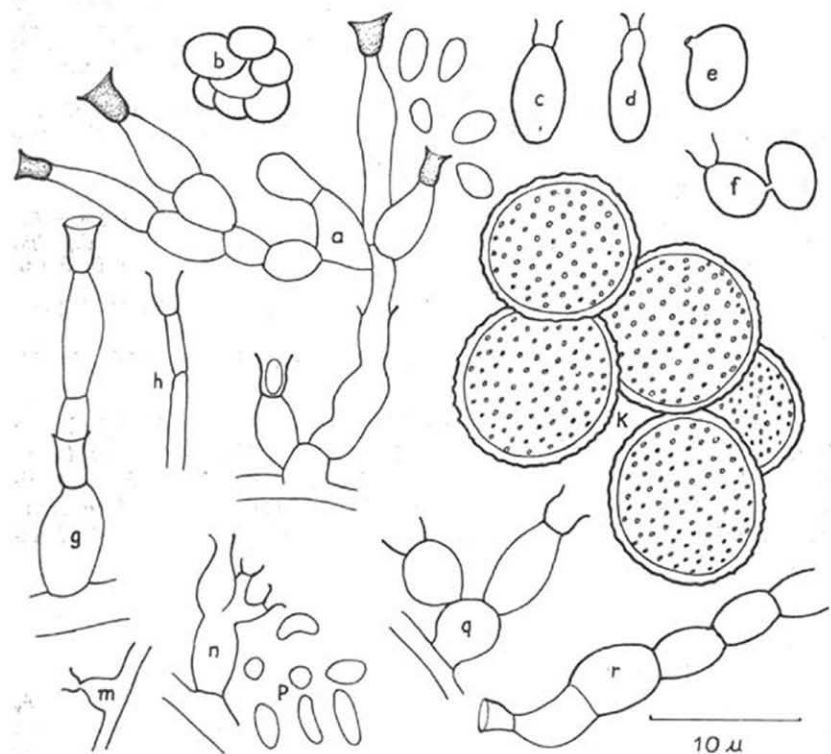


Fig. 12. *Phialophora verrucosa*. a-c, e, g. CBS 281.35; d, f, h, m, n, p. dried culture of Conant 204 (FH); k, q, r. *P. verrucosa*, type material (FH). — a. Proliferating conidiophore with conidia. — b. Globular mass of chlamydo-spores. — c, d. Chlamydo-spores with a collarette and developing into a phialide. — e. Chlamydo-spore with muzzle-like protuberance. — f. Anastomosis of chlamydo-spores. — g. Proliferating phialide. — h. Thread-like phialide. — k. Chlamydo-spores. — m. Lateral phialide. — n. Proliferating phialide. — p. Conidia of various shape. — q. Branched conidiophore. — r. Moniliform hypha with terminal phialide.

## MATERIAL EXAMINED.

## a. Herbarium material.

Type material of *Phialophora verrucosa* Medlar, consisting of a photograph and a dried culture on agar, both labelled "*Phialophora verrucosa* Thaxter, type"; photograph and dried culture on agar labelled "*Phialophora verrucosa* Thaxter: Texan case, N. F. Conant, culture No. 204"; photograph labelled "*Phialophora verrucosa* Thaxter, Uruguay case, N. F. Conant, culture No. 283" (FH).

Type material of *Cadophora americana* Nannfeldt, 2 slides: 194:2, 339:2 both labelled "Miss Richards' cult. 6320-2, typus" (UPS). 6320-2 was isolated by Audrey Richards and sent to Nannfeldt who described it. Melin sent this strain to the CBS in 1933 where it has been preserved as "strain Melin" under the original name; in 1937, according to Conant, the name was changed into *Phialophora verrucosa*. The strain became contaminated and was lost in 1959.

The same isolate is also preserved as dried culture on agar labelled "*Cadophora americana* Nannfeldt, N. F. Conant cult. 333, culture from Audrey Richards, to Nannf. to Centraalbureau, from paper pulp, Wisconsin" (FH).

## b. Living strains.

CBS 281.35 = ATCC 4806 = IMI 21.191 original strain Weidman No. 2261, isolate from "verrucous dermatosis of the legs" and described by Wilson & al., 1933.

CBS 400.67, sent by A. Ch. Batista in 1967, isolated from soil, Recife, Brasil.

CBS 738.67 = L.C. 971 = strain Langeron.

CBS 839.69 (P 152-8) isolated from birch-wood, sent in 1968 by Th. Nilsson, Stockholm.

CBS 840.69 (501) isolated from decaying lumber and sent in 1967 by A. Salonen, Helsinki.

In some cultures structures covered with setae developed which might be the beginning of fruit-bodies but these never became ripe. Ajello & Runyon (1953) have described similar structures, interpreted by them as probably abortive perithecia, in an isolate of this species. Extensive physiological studies of this fungus were published by Carrión & Silva (1947) with special reference to its medical importance.

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## CLADOBOTRYUM-KONIDIENFORMEN VON HYPOMYCES-ARTEN

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(Mit 6 Abbildungen)

Die Gattung *Cladobotryum* Nees per Steudel wird charakterisiert durch meist verticillat verzweigte Konidienträger mit Phialiden, trockene einzellige bis mehrzellige Konidien in Köpfchen oder unregelmässigen Ketten und mehrzellige Chlamyosporen oder Sklerotien. Acht Arten werden besprochen. Bei vier Arten ist die zugehörige *Hypomyces*-Art bekannt, bei einer wird sie vermutet. Bei *Hypomyces rosellus* und *H. odoratus* wurden durch Kreuzen kompatibler Stämme in Reinkultur Perithezien erhalten. Die konidienbildenden Zellen werden bei allen Arten als Phialiden betrachtet, auch wenn sich die meristematische Zone über der Scheitel hinaus verlängert und mit einer sekundären Wand umgibt.

### Einleitung

Die auffallenden und verbreiteten *Hypomyces*-Konidienformen wurden meist (zuletzt durch Arnold, 1969) aufgrund der Konidienseptierung in verschiedenen Gattungen untergebracht. Hughes (1958) vereinigte eine Reihe von Arten in der Gattung *Cladobotryum*. Da diese Gattung noch nicht genau charakterisiert ist und die verwendeten Epitheta z.T. wenig bekannt sind, ergab sich die Aufgabe, die Arten ausführlich zu beschreiben und die oft komplizierte Nomenklatur zu dokumentieren.

In der Gattung *Hypomyces* wurde ursprünglich eine grössere Artenzahl fungicoler Sphaeriales beschrieben. Wollenweber (1913) charakterisierte die Gattung durch das Merkmal der Chlamyosporen und erweiterte sie um die perfekten Formen von *Martiella*-Fusarien. Eine natürliche Einheit lässt sich vor allem durch die charakteristische Scheitelverdickung der Asci und die biapiculaten 2-zelligen Ascosporen umgrenzen (Petch, 1938; Müller & von Arx, 1962).

Zahlreiche frische Aufsammlungen wurden im Herbst und Winter 1968 für Reinkulturen verwendet. Sporenmessungen wurden in Milchsäurepräparaten vorgenommen. Es sind jedoch noch nicht von allen *Hypomyces*-Arten Reinkulturen verfügbar.

### CLADOBOTRYUM Nees per Steud.

*Cladobotryum* Nees, Syst. Pilze Schwämme 55. 1816; per Steud., Nomencl. bot. 118. 1824. — Lectotypus: *Cladobotryum varium* Nees per Steud.

*Botrytis* trib. *Corymbosi* Fr., Syst. Orb. veg. 183. 1825.

*Diplocladium* Bon., Handb. allg. Mykol. 98. 1851.

*Didymoelidium* Sacc. in Sylloge 4: 186. 1886.

FALSCH ANGEWENDET: *Dactylium* Nees sensu Sacc. in *Michelia* 2: 20. 1880; in *Sylloge* 4: 188. 1886.

Hypohomyceten mit raschwüchsigen Kolonien, zartwandigen, hyalinen, breiten Hyphen (meist über  $4 \mu$  im Durchm.), meist wirtelig verzweigten, hyalinen Konidienträgern mit pfriemlichen, am Oberende breit abgestutzten Phialiden. Phialosporen  $\pm$  zylindrisch, mit breiter oft seitlich verschobener Ansatzfläche, dünn- und glattwandig, hyalin, ein-, zwei- oder mehrzellig; in trockenen strahligen Köpfchen oder unregelmässigen Ketten vereinigt. Mehrzellig: Chlamydo­sporen regelmässig vorhanden, hyalin oder hellbraun, terminal an kurzen Seitenästen oder interkalär, gelegentlich auch sklerotiumartig, dickwandig, glattwandig oder warzig.

Hauptfruchtform, soweit bekannt, *Hypomyces* (Fr.) Tul. (1860: 11).

Im Dezember desselben Jahres 1824 wurde die Gattung *Cladobotryum* auch durch Brogniart genannt. Bei der Validierung der Gattung durch Steudel (1824: 118) wurden 3 Arten angeführt: *C. agaricinum* (Link) Nees, *C. macrosporum* (Link per Pers.) Schmaltz und *C. varium* Nees. Davon übernahm Fries (1832: 414) *Dactylium varium* und *D. macrosporum*, während er *Botrytis agaricina* mit *D. dendroides* zusammenlegte. Von den beiden gleichrangigen Arten wählte Hughes (1958) *C. varium* ( $\equiv$  *C. variospermum*) als Lectotypus. Da bei *C. macrosporum* die Gattungszugehörigkeit noch teilweise umstritten ist, erscheint die Wahl von *C. varium* als die zweckmässigste. Clements & Shear (1931) nannten *C. thuenenii* Sacc. als Typus in Anlehnung an Saccardo (1880: 18). Das Material dieser viel jüngeren Art (in PAD) erwies sich bei Nachprüfung als eine *Athelia*-Art.

#### SCHLÜSSEL FÜR DIE BESPROCHENEN ARTEN

- A. Konidien ein- bis zweizellig, in strahligen Köpfchen.
1. Phialiden ohne sekundäre apikale Verzweigung.
    - a. Konidien subglobos bis ovoid, Chlamydo­sporen hyalin oder hellbraun. *C. verticillatum*
    - b. Konidien birnförmig oder keulig, Chlamydo­sporen braun und grobwarzig. *C. apiculatum*
  2. Phialiden mit apikaler Verzweigung ohne Querwandbildung . . . . . *C. spec.*
- B. Konidien regelmässig zweizellig, in unregelmässigen Ketten.
1. Reichliche Konidienbildung, normalerweise keine Perithezien in Reinkultur. *C. varium*
  2. In Reinkultur dominieren Perithezien . . . . . *Hypomyces trichothecioides*
- C. Konidien zwei- bis mehrzellig, in unregelmässigen Köpfchen.
1. Konidien 7–12  $\mu$  breit.
    - a. Phialiden endigen sehr breit abgestutzt, ohne sekundäre Verlängerung. *C. mycophilum*
    - b. Phialiden verlängern sich sekundär im Laufe der Konidienentwicklung. *C. dendroides*
  2. Konidien 6–7  $\mu$  breit . . . . . *C. leptosporum*

## CLADOBOTRYUM VERTICILLATUM (Link per S. F. Gray) Hughes—Abb. 1

*Acremonium verticillatum* Link in Mag. Ges. naturf. Freunde, Berlin 3: 15. 1809; per S. F. Gray, Nat. Arrang. Br. Pl. 1: 550. Sept. 1821. — *Mycogone verticillata* (Link per S. F. Gray) Spreng., Linn. Syst. Veg., Ed. 16, 4: 555. 1827. — *Cladobotryum verticillatum* (Link per S. F. Gray) Hughes in Can. J. Bot. 36: 750. 1958.

*Botrytis agaricina* Link in Mag. Ges. naturf. Freunde, Berlin 3: 15. 1809; apud Ditmar in Sturm, Deutschl. Fl., Heft 4: 103, Taf. 51. 1817; per Pers., Mycol. europ. 1: 34. 1822. — *Verticillium agaricinum* (Link per Pers.) Corda, Icon. Fung. 2: 15. 1838.

*Sporotrichum agaricinum* Link in Jb. Gewächskde 1: 170. 1818; per Link, Linn. Spec. Pl., Ed. 4, 6 (1): 7. 1824. — *Monosporium agaricinum* (Link per Link) Bon., Handb. allg. Mykol. 95, Fig. 112. 1851 (Synonymie fide icon. bei Bonorden).

*Verticillium lactarii* Peck in Rep. N.Y. St. Mus. nat. Hist. 35: 140. 1882 (fide diagn.).

Auf Malzagar in 3 Tagen bei 20° C 24 mm im Durchm., weiss, bald stark wollig werdend. Sporulation beginnt nach 4 Tagen. Luftmycel dicht, bis 25 mm hoch. Unterseite crème-beige, Konidienmassen weiss, besonders am Rand der Kultur. Konidienträger entstehen an Luftthyphen, wiederholt wirtelig verzweigt, ca. 6,5 µ breit. Phialiden pfriemlich, mit abgestutztem oberem Ende. Konidien einzeln oder in Köpfchen, subglobos-länglich birnförmig, mit deutlicher basaler, manchmal seitlich verschobener Ansatzfläche, einzellig, selten 2-zellig, 11,5–24 × 9–12 µ. Trotz der variablen Form sind die Konidien in einem Köpfchen im allgemeinen von einheitlicher Gestalt. Chlamydosporen zahlreich, endständig oder interkalär, mehrzellig, an den Septen eingeschnürt, dickwandig, glatt, hyalin bis hellbraun.

## UNTERSUCHTES MATERIAL.

## a. Herbariummaterial.

*Acremonium verticillatum* Link auf Kiefernborke, Rostock, und III 429 Herb. Ehrenberg, beide mit Links Handschrift; *Sporotrichum agaricinum* Link, auf Hutpilzen (unkenntlich), in Herb. B.

## b. Lebende Kulturen.

CBS 823.69, von *Lactarius blennius* (Fr. per Fr.) Fr., Vogelbos bei Utrecht, Okt. 1968.

CBS 822.69, von *Lactarius mitissimus* (Fr.) Fr., Texel, Okt. 1968.

Zahlreiche weitere Isolate von *Lactarius rufus* (Scop. per Fr.) Fr. u. a. *Lactarius* spp., *Russula fragilis* (Pers. per Fr.) Fr., *R. ochroleuca* (Pers. per Secr.) Fr. u. a. *Russula* spp. in der Provinz Utrecht, sowie von *Boletus edulis* Bull. per Fr. bei Apeldoorn, Aug. 1968.

Von *Botrytis agaricina* war kein Material auffindbar, jedoch ist Ditmars Zeichnung sehr treffend für den hier beschriebenen Pilz. Diese Art wurde jedoch durch Fries (1832) u. a. Autoren in Synonymie gestellt mit *Dactylium dendroides*.

**Cladobotryum apiculatum** (Tubaki) W. Gams & Hoozem.,  
comb. nov.—Abb. 2

*Cylindrophora apiculata* Tubaki in Nagaoa 5: 16. 1955 (Basionym).

CHLAMYDOSPORENFORM: *Blastotrichum puccinioides* Preuss.

*Blastotrichum puccinioides* Preuss in Sturm, Deutschl. Fl., Heft 25–26: 21, Taf. 11. 1848; in Linnaea 24: 113. 1851. — *Mycogone puccinioides* (Preuss) Sacc. in Sylloge 4: 184. 1886.

Kulturen auf Malzagar raschwüchsig, dünn wattig, anfangs weiss, später in manchen Stämmen durch reichliche Chlamydosporenbildung braun werdend. Konidienträger meist mit einfachen, selten 2 gegenüberstehenden Seitenästen, 1,5–3,5  $\mu$  breit, ca. 200  $\mu$  lang. Konidien einzeln oder in kleinen strahligen Gruppen, von unregelmässiger birnförmiger bis keuliger bis zylindrischer Form, mit zugespitzter, zuletzt abgestutzter Basis, meist einzellig, selten 2-zellig, 16–34  $\times$  4,5–7,5  $\mu$ . Chlamydosporen mehrzellig, interkalär oder häufiger an kurzen Seitenästen, braun, grob warzig, dickwandig, von unregelmässiger Form und Grösse.

#### UNTERSUCHTES MATERIAL.

a. Typenmaterial von *Blastotrichum puccinioides*, Mycel auf einer Glasplatte, in Herb. Preuss (B).

b. Typenkultur von *Cylindrophora apiculata*, CBS 174.56, isoliert von *Amanita pantherina* (DC. per Fr.) Secr., leg. Y. Kobayasi, Japan.

c. CBS 828.69 = PC 1896, isoliert von *Russula coerulea* [Pers.] Fr., durch J. Nicot, Okt. 1967.

CBS 827.69 = PC 1891, isoliert von *Lactarius* spec. durch G. Arnold, Weimar, 1962.

CBS 829.69 = J. N. 10.24, isoliert von *Russula sardonia* Fr. em. Rom. durch J. Nicot, Okt. 1966.

Der Stamm CBS 828.69 produziert die meisten Chlamydosporen, während bei den anderen untersuchten Kulturen das weisse Mycel, teilweise mit Phialosporenbildung, überwiegt.

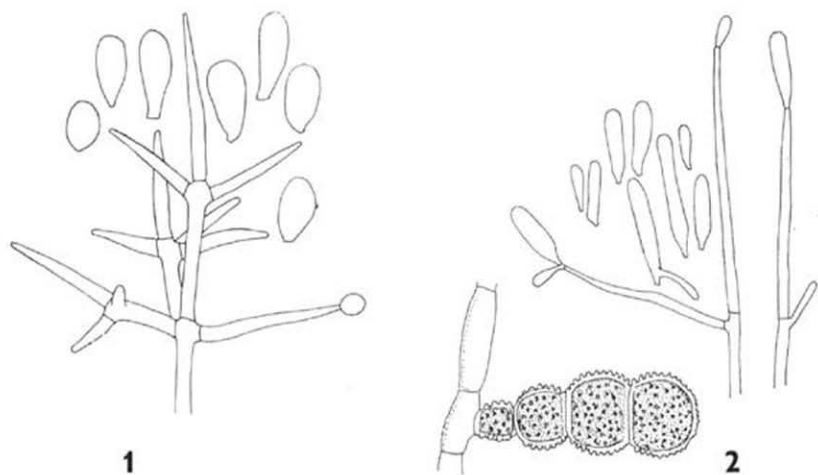


Abb. 1. *Cladobotryum verticillatum*. Konidienträger und Konidien (500: 1).

Abb. 2. *Cladobotryum apiculatum*. Konidienträger, Konidien (ein Konidium mit Keimschlauch) und Chlamydo-spore (500: 1).

*Cladobotryum apiculatum* ist vermutlich die Konidienform von *Hypomyces ochraceus* (Pers. per Schw.) Tul. (syn. *H. armeniacus* Tul.). Die Zusammenhänge sind jedoch durch die häufige Verwechslung der Phialosporenform mit *C. verticillatum* (seit Tulasne, 1865) unsicher. Die Unterschiede in der Konidien- und Chlamydosporenform wurden von Tubaki (1955), Nicot (1966) und Arnold (1969) deutlich herausgearbeitet. Frisches Perithezienmaterial stand nicht zur Verfügung. Kreuzungsversuche in dieser und der vorigen Art blieben erfolglos.

Die Gattung *Blastotrichum* Corda (Typenart: *B. confervoides*; Typenmaterial in PR nicht erhalten) dürfte mit *Monacrosporium* Oudem. verwandt sein. *Blastotrichum puccinioides* ist ausdrücklich für die Chlamydosporenform aufgestellt, obwohl im Typenmaterial auch Phialosporen zu finden sind. Für die Phialidenform ist offenbar die von Tubaki (1955) beschriebene *Cylindrophora apiculata* der älteste Name. Die Identität der Gattung *Cylindrophora* Bon. ist im übrigen zweifelhaft.

CLADOBOTRYUM spec.—Abb. 3

Eine weitere mit *Cladobotryum apiculatum* ähnliche Art wurde zweimal isoliert. Sie ist besonders auffallend durch apikale Verzweigung der Phialiden ohne Querwandbildung (Schizophialiden). Kulturen grauweiss, flockig-wattig. Konidien-

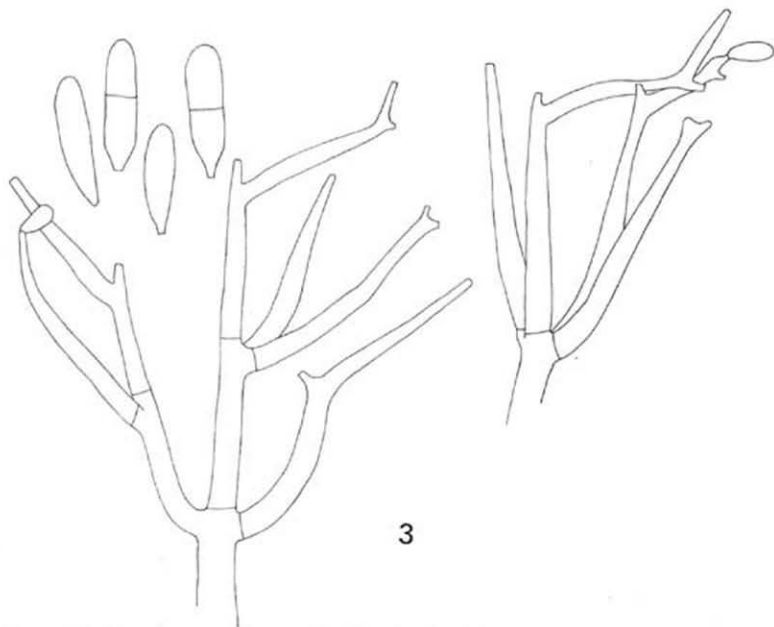


Abb. 3. *Cladobotryum* spec., Stamm CBS 831.69, Konidienträger und Konidien (1000: 1).

träger wiederholt wirtelig verzweigt. Unter der Spitze der Phialiden entsteht nach der Bildung der ersten Konidiengruppe oft ein etwas längerer Seitenzweig, der ebenfalls Phialosporen entlässt. Dieser Vorgang kann sich mehrmals wiederholen. Konidien keulig mit deutlich apikulater Basis, ein- oder meist zweizellig ( $13-16-23$  ( $-27$ )  $\times$   $3-6,5$   $\mu$ ). Chlamydosporen endständig oder interkalär, dickwandig, glatt, mehrzellig, hyalin.

#### UNTERSUCHTE KULTUREN.

CBS 830.69, isoliert von *Hirneola auricula-judae* (Bull. per St-Amans) Berk.

CBS 831.69, isoliert von *Bjerkandera adusta* (Willd. per Fr.) Karst., beide in den Dünen bei Vogelzang, Z.-Holland, November 1968.

#### HYPOMYCES AURANTIUS (Pers. per S. F. Gray) Tul.

*Sphaeria aurantia* Pers., Icon. Descr. Fung. min. cogn. 2: 45, Taf. 11 Fig. 4, 5. 1800; per S. F. Gray, Nat. Arrang. Brit. Pl. 1: 526. Sept. 1821 («*aurantiaca*»); Fr., Syst. mycol. 2: 440. 1823. — *Nectria aurantia* (Pers. per S. F. Gray) Fr., Summa Veg. Scand. 388. 1849. — *Hypomyces aurantius* (Pers. per S. F. Gray) Tul., Sel. Fung. Carpol. 3: 43. 1865.

*Sphaeria aurea* Grev., Scott. crypt. Fl. Taf. 47. 1823.

*Nectria cesatii* Mont. in Anns Sci. nat. (Bot.), IV, 8: 308. 1857. — *Hypomyces cesatii* (Mont.) Tul., Sel. Fung. Carpol. 3: 40. 1865.

KONIDIENFORM: *Cladobotryum varium* Nees per Duby.

*Cladobotryum varium* Nees, Syst. Pilze Schwämme 56, Taf. 4 Fig. 54. 1816. — *Botrytis varia* Nees per Duby, Bot. gall. 2: 919. 1830. — *Dactylium varium* (Nees per Duby) Fr., Syst. mycol. 3: 414. 1832.

*Botrytis variasperma* Link in Mag. Ges. naturf. Freunde, Berlin 7: 36. 1816; per Pers., Mycol. europ. 1: 35. 1822. — *Cladobotryum variospermum* (Link per Pers.) Hughes in Can. J. Bot. 36: 750. 1958.

? *Alytsporium roseum* Ehrenb., Sylvae mycol. berol. 11. 1818 (fide Fries, 1832; Typus nicht erhalten).

? *Sporotrichum cylindrosporium* Link, Linn. Spec. Pl., Ed. 4, 6 (1): 14. 1824 (fide Fries, 1832; Typus nicht erhalten).

*Diplocladium minus* Bon., Handb. allg. Mykol. 98, Fig. 119. 1851 («*minor*», fide icon.).

*Cladotrichum ternatum* Bon., Handb. allg. Mykol. 78, Fig. 84. 1851 (fide icon.). — *Didymocladium ternatum* (Bon.) Sacc. in Sylloge 4: 187. 1886.

*Dactylium rennyi* Berk. & Br. in Ann. Mag. nat. Hist., IV, 11: 346. 1873 (fide Massee, vgl. Petch, 1941). — *Diplocladium rennyi* (Berk. & Br.) Sacc. in Sylloge 4: 177. 1886.

*Dactylium melleum* Berk. & Br. in Ann. Mag. nat. Hist., IV, 11: 345, Pl. 8 Fig. 6. 1873; in Grevillea 2: 138. 1874 (fide Petch, 1941). — *Diplocladium melleum* (Berk. & Br.) Sacc. in Sylloge 4: 177. 1886.

*Diplocladium penicillioides* Sacc. in Sylloge 4: 177. 1886 (fide Petch, 1941; Typus nicht erhalten).

Kolonien auf Malzagar in 3 Tagen 10 mm im Durchm., später stark wattig und 10–15 mm hoch, weiss. Unterseite zitronengelb; Konidienmassen weiss staubig. Konidienträger aufrecht, aus Lufthyphen entspringend, 4–7  $\mu$  breit, verticillat verzweigt. Phialiden 27–50  $\times$  3–4,5  $\mu$ . Konidien in unregelmässigen Ketten zusammengehalten, ovoid, regelmässig 2-zellig (selten einzellig), meist mit breiter, oft etwas schiefer, basaler Ansatzfläche, 10,5–16  $\times$  5–7  $\mu$ . Chlamydosporen in oder wenig über dem Agar gebildet, interkalär oder an kurzen Trägern, hell bis ockerbraun, ein- bis mehrzellig, dickwandig, glatt, von unregelmässiger Form, Einzelzellen

15–19  $\mu$  breit. Auf dem natürlichen Substrat wurden häufig orangegelbe Perithezien beobachtet. Ascosporen 2-zellig, fein warzig, 23–26  $\times$  3,7–4  $\mu$ . Die perfekte Form wurde von Nicot & Parguey (1963) nach etwa 3-monatiger Inkubation auch in Reinkulturen erhalten.

#### UNTERSUCHTES MATERIAL.

##### a. Herbariummaterial.

*Nectria cesatii* Mont., 3 Kollektionen (PC).

«*Botrytis variosperma* Nees ab Esenbeck» sowie eine weitere Kollektion von «*Cladobotryum variosperrum* Lk. (*Botrytis*)» auf *Thelephora*, beide mit Links Handschrift (B).

«*Diplocladium minus* in *Stereo hirsuto*, leg. Brunaud», scr. Saccardo (PAD).

##### b. Lebende Kulturen.

CBS 184.65, *Cladobotryum variosperrum*, von Walderdt, North Bay, Ontario, 1965, G. L. Barron.

Zahlreiche eigene Isolate von Perithezien und Konidienkollektionen auf *Trametes versicolor* (L. per Fr.) Pilát, *Armillaria mellea* (Vahl per Fr.) Kummer, *Bjerkandera adusta* (Willd. per Fr.) Karst., *Polyporus melanopus* Sw. per Fr. (leg. J. A. von Arx, Aug. 1965) in der Prov. Utrecht; auf *Polyporus picipes* Fr. bei Dorst, N.-Brabant; auf *Polyporus squamosus* Huds. per Fr. im Kr. Schleswig; auf *Polyporus varius* Pers. per Fr., Hunosø, Møn, Dänemark.

Wie Hughes (1958) feststellte, sind *C. varium* und *Botrytis variosperrum* obligat synonym, da Link (1816: 36) deutlich schreibt: «misit Nees» und auch Nees (1816: 56) sich auf seine Korrespondenz mit Link beruft. Von Nees sind 2 verschiedene Kollektionen erhalten: a) in Herb. Berlin gut erkennbares Material, das den hier beschriebenen Pilz zeigt, b) in Herb. Leiden unter 910.263–233 spärliches Material mit 4-zelligen Konidien, 29–33  $\times$  10–13  $\mu$ , die mit denen von *C. dendroides* übereinstimmen. Das mit Link ausgetauschte Material ist zweifellos als Typus zu betrachten. Nach der Wahl von Fries (1832) hat der Art-Name *varium* zu gelten.

#### HYPOMYCES TRICHOHEGIOIDES Tubaki

*Hypomyces trichothecioides* Tubaki in Nagaoa 7: 31, Fig. 2. 1960.

Diese Art besitzt im Gegensatz zu *H. aurantius* viel zartere Konidienträger. Perithezien dominieren in Reinkultur. Die Morphologie wurde von Hanlin (1964) nochmals ausführlich beschrieben. Tubaki (l. c.) bezeichnete die Konidienform als *Trichothecium*. Die Konidienträger sind bei der Typenkultur (CBS 274.61) jedoch wirtelig verzweigt und die Phialiden verändern nicht ihre Länge mit fortschreitender Konidienbildung. Die Konidienform passt also auch sehr gut in die Gattung *Cladobotryum*.

#### HYPOMYCES ODORATUS Arnold—Abb. 4

*Hypomyces odoratus* Arnold in Česká Mykol. 18: 144, Fig. 1–8. 1964.



KONIDIENFORM: *Cladobotryum mycophilum* (Oudem.) W. Gams & Hoozem., *comb. nov.*  
*Dactylum mycophilum* Oudem. in Arch. néerl. Sci. 2: 42. 1867 (Basionym).  
 ? *Diplocladium majus* Bon., Handb. allg. Mykol. 98, Fig. 168. 1851 («major»)  
*Diplocladium elegans* Bain. & Sart. in Annls mycol. 11: 359, Taf. 19. 1913.  
 «*Cladobotryum* State of *Hypomyces roseus*» Barron, Genera Hyphomyc. Soil 128, Fig. 54B.  
 1968.

Kolonien auf Malzagar in 3 Tagen bei 20° C 21 mm im Durchmesser, anfangs grauweiss, bald gelblich, von der Mitte aus rotviolett, teilweise ockergelb. Luftmycel bis 5 mm hoch. Sporulation beginnt nach 4 Tagen, an der Peripherie am stärksten. In der Koloniemitte zahlreiche dunkelrote Sklerotien von unregelmässiger Form. Starker kampherartiger Geruch. Konidienträger aufrecht aus dem Luftmycel entspringend, wirtelig verzweigt. Phialiden schwach verjüngt mit sehr breitem Scheitel. Sie werden einzeln gebildet in basipetaler Abfolge, ohne dass sich das Ende der Phialiden verändert, und lagern sich in unregelmässigen Gruppen zusammen. Konidien ein- bis dreizellig, meist zweizellig, zylindrisch, mit sehr breiter basaler Anheftungsfläche,  $(15-20-28(-32) \times (7,5-8,5-12 \mu$ . Auf natürlichen Substraten wurden ausschliesslich ein- bis zweizellige Konidien gefunden,  $22-25 \times 10,5-11,5 \mu$ , also wesentlich grösser als bei *C. varium*. Ausser unregelmässig verdickten, stark verzweigten Zellkomplexen (Sklerotiuminitialen) werden keine Chlamydosporen gebildet.

Durch Kreuzung kompatibler Stämme wurden auf Malzagar (optimal bei 25° C) nach ca. 3 Wochen reife Perithezien erhalten. Perithezien birnförmig, hell orange bis bräunlich, mit der Basis im Agar eingesenkt, meist in Gruppen stehend,  $335-500 (-540) \times 200-275 \mu$ . Ascosporen meist 2-zellig, am Septum etwas eingeschnürt, warzig, mit 2 stachelförmigen Fortsätzen,  $18-24 \times 4,5-6 \mu$ . Die Perithezienform ist offenbar nur aus Reinkulturen bekannt.

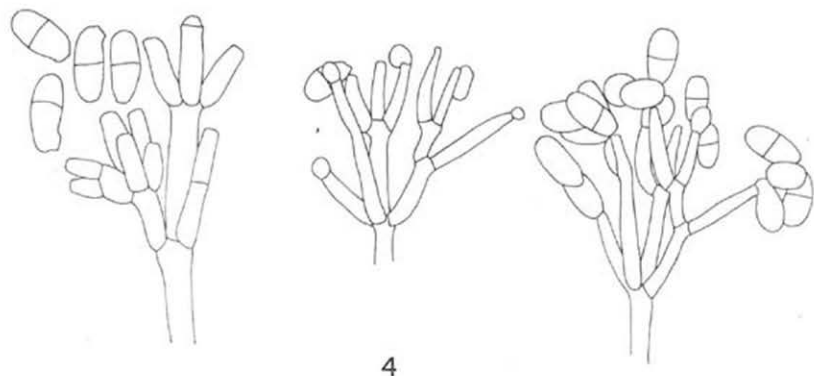


Abb. 4. *Cladobotryum mycophilum*. Konidienträger und Konidien. Mitte und rechts 2 Entwicklungsstadien desselben Trägers in Deckglaskultur (500: 1).

## UNTERSUCHTES MATERIAL.

## a. Herbariummaterial.

«*Diplocladium majus* sopra un' Agaricina prope Tregnago» scr. Saccardo (PAD).

## b. Lebende Kulturen.

Zahlreiche eigene Isolate von sehr verschiedenen Wirtsarten:

CBS 764.68, von *Camarophyllus niveus* (Scop. per Fr.) Wünsche, Vogelbos bei Utrecht, Okt. 1968, ist kompatibel mit CBS 818.69, von *Armillaria mellea*, Texel, Okt. 1968, und CBS 819.69, von *Lactarius mitissimus* (Fr.) Fr. vom selben Fundort. Ferner von *Agaricus xanthoderma* Gen., *Cortinarius mucosus* (Bull. per Fr.) Fr., *Entoloma clypeatum* (L. per Fr.) Kummer, und *Calocybe gambosa* (Fr.) Donk (CBS 820.69) aus der Prov. Utrecht. Weitere Wirtsarten bei Arnold (1964).

Die Peritheciumformen von *Hypomyces odoratus* und *H. rosellus* sind kaum zu unterscheiden, die Konidienträger und Konidien dagegen sehr gut; Sklerotien kommen nur bei *H. odoratus* vor. Von den verschiedenen für die Konidienform verwendeten Namen sind keine Typenkollektionen erhalten. Für *Diplocladium majus* werden die Sporen durch Bonorden (1851) als schwärzlich beschrieben, die Abbildung stimmt im übrigen gut mit dem vorliegenden Pilz überein. Oudemans (1919) betrachtete sein *Dactylium mycophilum* als synonym mit dieser Art, was auf der Beschreibung hyaliner Konidien bei Saccardo (1886: 177) beruhen kann, die tatsächlich mit der Konidienform von *H. odoratus* völlig übereinstimmt. Diese Auffassung Saccardos wird auch durch sein Herbariummaterial belegt. Im übrigen hat die Abbildung von Oudemans grössere Ähnlichkeit mit dem oben beschriebenen *Cladobotryum spec.* Fuckel (1870) unterschied die Arten *Hypomyces rosellus* und *H. roseus* und deren Konidienformen. Die ursprüngliche Identität von *H. roseus* ist jedoch unsicher. Von der bei Fuckel für *H. roseus* genannten Konidienform *Botrytis carnea* Schum. ist in Kopenhagen kein Herbariummaterial erhalten. *Hypomyces roseus* wurde von Plowright (1882) mit *H. rosellus* vereinigt. Die ausführliche Erstbeschreibung von *Diplocladium elegans* lässt über die Identität dieses Pilzes mit *C. mycophilum* keinen Zweifel aufkommen.

## HYPOMYCES ROSELLUS (Alb. &amp; Schw. per Fr.) Tul.—Abb. 5

*Sphaeria rosella* Alb. & Schw., Consp. Fung. 35, Taf. 7 Fig. 5. 1805; per Fr., Syst. mycol. 2: 441. 1823. — *Nectria rosella* (Alb. & Schw. per Fr.) Fr., Summa Veg. Scand. 388. 1849. — *Nectria albertinii* Berk. & Br. in Ann. Mag. nat. Hist., III, 7: 452. 1862 (Namensveränderung wegen Unklarheit in der Auffassung von *Sphaeria rosella*). — *Hypomyces rosellus* (Alb. & Schw. per Fr.) Tul. in Annls Sci. nat. (Bot.) IV, 13: 12. 1860; Sel. Fung. Carpol. 2: 276. 1863; 3: 45. 1865.

? *Sphaeria rosea* Pers., Syn. Fung. 18. 1801; per Fr., Syst. mycol. 2: 338. 1823. — *Hypocrea rosea* (Pers. per Fr.) Ces. & De Not. in Comment. crittog. ital. No. 4: 193. 1863. — *Nectria rosea* (Pers. per Fr.) Fuck., Fungi rhen., No. 2049. 1867. — *Hypomyces roseus* (Pers. per Fr.) Fuck. in Jb. Nassau. Ver. Naturk. 23-24 (= Symb. mycol.): 182. 1870 [«1869»]; Sacc. in Sylloge 2: 469. 1883.

KONIDIENFORM: *Cladobotryum denroides* (Bull. per Mérat) W. Gams & Hoozem., comb. nov.

[*Mucor* (ohne Epitheton) Bull., Herb. Fr., Taf. 504, Fig. 9. 1790. —] *Mucor dendroides* Bull., Hist. Champ. Fr. 105. 1791 (Basionym). — *Botrytis dendroides* Bull. per Mérat, Nouv. Fl. Envir. Paris, Ed. 2, 1: 14. 1821. — *Dactylium dendroides* (Bull. per Mérat) Fr., Syst. mycol. 3: 414. 1832.

*Botrytis macrospora* Link in Mag. Ges. naturf. Freunde, Berlin 3: 15. 1809; per Pers., Mycol. europ. 1: 33. 1822. — *Cladobotryum macrosporum* (Link per Pers.) Schmalz in Flora, Jena 6: 569. 1823; Chevall., Fl. gén. Envir. Paris 1: 61. 1826. — *Dactylium macrosporum* (Link per Pers.) Fr., Syst. mycol. 3: 414. 1832.

? *Sporotrichum boletorum* Ehrenb., Sylvae mycol. berol. 10, 22. 1818; per Steud., Nomencl. bot. 401. 1824 (Synonymie fide Fries, 1832. Typenmaterial nicht erhalten). — *Dactylium boletorum* (Ehrenb. per Steud.) Sacc. in Sylloge 4: 190. 1886.

*Cladobotryum ternatum* Corda, Icon. Fung. 1: 21, Taf. 6 Fig. 277. 1837.

*Cladobotryum ternatum* Corda var. *binatum* Preuss in Linnæa 24: 124. 1851. — *Cladobotryum binatum* (Preuss) Sacc. in Sylloge 4: 160. 1886.

? *Trichothecium candidum* (Link) Bon., Handb. allg. Mykol. 99, Fig. 167. 1851 (fide icon.); non *Trichothecium candidum* Wallr., Fl. cryptog. Germ. 2: 285. 1833.

? *Trichothecium agaricinum* Bon., Handb. allg. Mykol. 99, Fig. 114. 1851 (fide icon.). — *Dactylium agaricinum* (Bon.) Sacc. in Sylloge 4: 189. 1886.

? *Helminthophora tenera* Bon., Handb. allg. Mykol. 93, Fig. 137. 1851 (fide icon.).

*Cladobotryum terrigenum* Karst. in Meddn Soc. Fauna Fl. fenn. 16: 35. 1888.

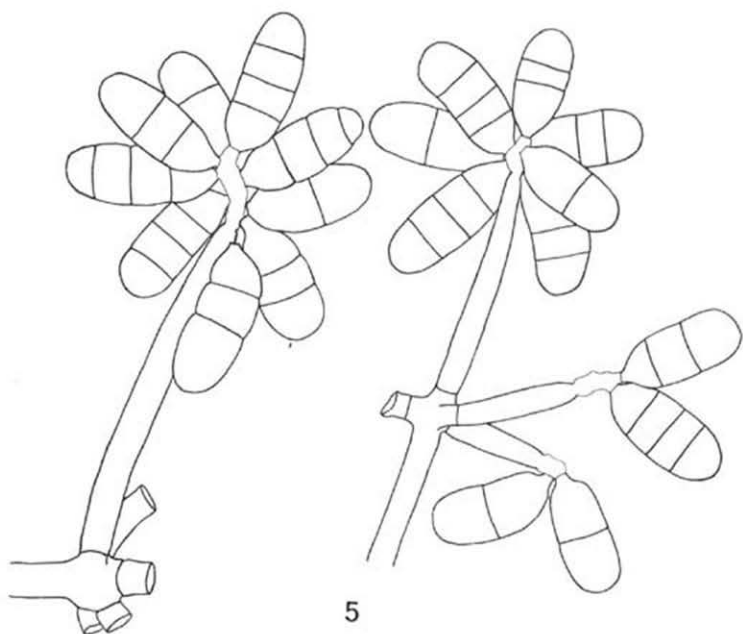


Abb. 5. *Cladobotryum dendroides*. Konidienträger und Konidien in alter eintrocknender Kultur (1000: 1).

Kulturen auf Malzagar erreichen bei 20° C in 3 Tagen einen Durchmesser von 32 mm; Sporulation beginnt nach 4 Tagen in dem weissen Luftmycel. Der Agar wird weinrot bis violett oder gelbbraun verfärbt. Gelbfärbung weist nach Zycha (1935) auf niedrige pH-Werte. Konidienmassen weiss. Konidienträger aufrecht, wiederholt wirtelig verzweigt. Phialiden pfriemlich mit breitem Scheitel. Bei jedem neu gebildeten Konidium wird ein Teil des meristematischen Plasmas ausgestossen, wodurch die zuerst gebildeten Konidien in eine seitliche Stellung gedrängt werden (Abb. 5). In dem verlängerten Stück der Phialide ist die Wand dünner als im unteren Teil. Konidien zylindrisch, mit meist drei, seltener einem Septum; manchmal an den Septen eingeschnürt, mit basaler oft etwas seitlich verschobener Ansatzfläche, (19-)24-28 × 7-10,5  $\mu$ . Chlamydo-sporen mehrzellig, braun, dickwandig, glatt, von unregelmässiger Form und Grösse, an kurzen lateralen Aesten im Luftmycel oder Agar gebildet. Sklerotien fehlen.

Wie bereits Zycha (1935) feststellte, ist die Art heterothallich. Durch Kreuzen kompatibler Stämme wurden regelmässig Peritheccien erhalten. Peritheccien hellbraun oder weinrot, 560-625 × 215-315  $\mu$ . Asci lang zylindrisch mit kurzem Stiel, 115-130 × 6-7  $\mu$ . Ascosporen ein-, meist zweizellig, grob warzig, beidseits mit stachelförmigem Fortsatz, 25-27 × 4,8-6,5  $\mu$ . Ausführliche Beschreibung bei Zycha (1935).

#### UNTERSUCHTES MATERIAL:

##### a. Herbarmaterial:

*Sphaeria rosella* A.S. in Herb. Persoon (L) unter 910.269-423 und PH unter 1495-350. "An diversa a *Sph. rosea*?" scr. Schweinitz. Beide Kollektionen nicht mehr bestimmbar.

*Sphaeria rosea* Pers. in Herb. Persoon (L) unter 910.269-433, nicht mehr bestimmbar.

*Nectria rosea* (Pers.) Fuckel in Fungi rhenani No. 2049 (früher GRO, jetzt L).

*Botrytis macrospora*, Typenmaterial von Link (B).

*Cladobotryum ternatum* Corda, Typenmaterial auf morschem Holz in Herb. Corda (PR) unter No. 155417.

"*Cladobotryum* ? *binatum* auf *Agaricus glaucopus*" Herb. Preuss (B).

*Cladobotryum terrigenum* Karst., auf Bodenprobe, 1866, Herb. P. A. Karsten (H).

##### b. Lebende Kulturen:

Verschiedene Isolate von *Armillaria mellea*, Drunensche Duinen, N.-Brabant (CBS 816.69 und CBS 817.69), bei Tilburg und Groeneveld bei Baarn. Isolat 1111 von *Russula mustelina* Fr. bei Innsbruck, Okt. 1965. CBS 817.69 war mit CBS 816.69 und anderen Stämmen kompatibel.

Zur Unterscheidung von *Hypomyces odoratus* vgl. das bei dieser Art Gesagte. Hughes (1958) zitierte die Art als *Cladobotryum macrosporum* (Link) Chevall. Das Epitheton *dendroides* hat jedoch Priorität durch frühere Validierung; es ist ausserdem viel bekannter. Obwohl von *Mucor dendroides* kein Material verfügbar ist, besteht über die Identität dieser Art in der Literatur kein Zweifel. In den Kollektionen von *Botrytis macrospora* und *Cladobotryum ternatum* ist die sekundäre Verlängerung der Phialiden noch deutlich zu erkennen. *Trichothecium candidum* (Link) Bon. basiert vermutlich auf *Sporotrichum candidum* Link (1809: 13) dessen Typenkollektion (B) nicht mehr bestimmbar ist.

**Cladobotryum leptosporum** (Sacc.) W. Gams, *comb. nov.*—Abb. 6

*Dactylium dendroides* \**leptosporum* Sacc. in *Michelia* 2: 576. 1882 (Basionym). — *Dactylium leptosporum* (Sacc.) Lentz in *Mycopath. Mycol. appl.* 32: 14, Fig. 1 B, 6 A-D. 1967.

In dem ursprünglichen Material sind nur spärliche Konidien erkennbar,  $20-23 \times 6-7 \mu$ , (nach der Beschreibung  $22 \times 8 \mu$ ), 4-zellig.

Ein damit übereinstimmender Stamm ist als CBS 821.69 verfügbar. Die Konidienmasse stimmen genau mit dem Typenmaterial überein, jedoch wachsen die Kulturen sehr langsam (5–6 mm Durchmesser in 3 Tagen), sind erst weisslich, später gelbgrün, dünn wattig, unregelmässig gezont, und die Sporulation setzt spät ein. Konidienträger von Lufthyphen aufsteigend, zart, mehrfach wirtelig verzweigt. Phialiden bei mehrfacher Konidienbildung nicht verlängert. Konidien  $16-23 \times 5,5-6,5 \mu$ , meist 4-, seltener 2-zellig, in sternförmigen Gruppen. Die Konidien lösen sich oft kaum von den Phialiden; sie können auch durchwachsen und neuerlich Phialiden bilden.

## UNTERSUCHTES MATERIAL:

a. Typenkollektion von Saccardo auf morscher Borke, Newfield, N. J. (Ellis No. 3575) in PAD.

b. CBS 821.69, isoliert von *Stereum* spec., Forst Eckholt, Kr. Segeberg, Apr. 1965.

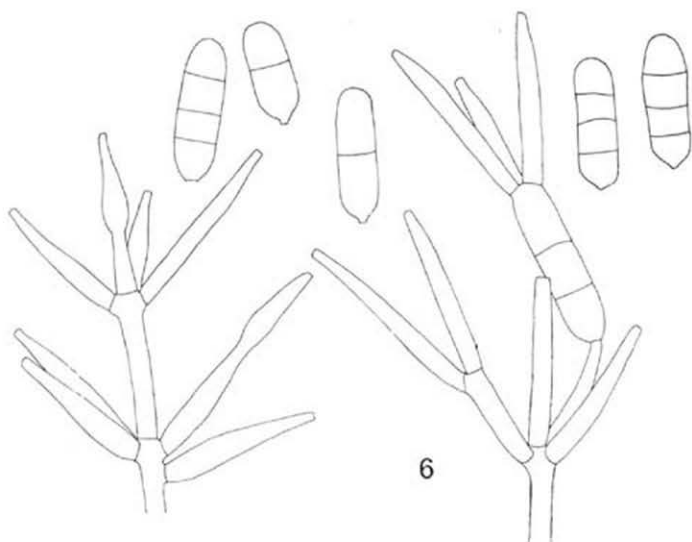
Die Kultur CBS 821.69 ist durch langsames Wachstum und fehlende Chlamydosporen nicht typisch für die Gattung *Cladobotryum*. Mit 4-zelligen strahlig angeordneten Konidien lässt sie sich jedoch auch nicht in *Verticillium* unterbringen.

Lentz (1967) beschreibt als *Dactylium leptosporum* eine Kollektion mit weissen Konidienmassen, wirtelig verzweigten Konidienträgern und apikal nicht verlängerten Phialiden. Die Konidien sollen  $22-27 \times 7,5-8(-10) \mu$  messen. Dieses Material, F.P. 110463, stammt von einer *Tomentella* sp. auf *Acer negundo* L., Catfish Point, Mississippi. Lentz (1967) erwähnt eine weitere Kollektion, TRTC 32281 im Herbarium in Toronto auf *Corticium radiosum* Fr. und *Peniophora subulata* Bourd. & Galz., bei der sich auch der Phialidenscheitel verlängert wie bei *C. dendroides*. Die für dieses Material angegebenen Sporenmasse fallen durchaus in den Variationsbereich dieser Art.

## Diskussion

Soweit bekannt, gehören die hier beschriebenen Konidienformen zu nahe verwandten *Hypomyces*-Arten. Die Verwandtschaft der Konidienformen untereinander wird erst bei Untersuchung der Konidienbildung deutlich. Die Natur der sporogenen Zellen wurde auf verschiedene Weise interpretiert, insbesondere bei *Cladobotryum dendroides* durch Barron (1968) und bei *C. apiculatum* durch Tubaki (1958).

Tubaki (1958) verglich die Konidienbildung von *C. apiculatum* mit der von *Trichothecium roseum* (Pers.) Link ex S. F. Gray. Diese Art besitzt Meristem-Arthrosporen; wie Kendrick & Cole (1969) deutlich zeigten, wird im Laufe der Sporulation der Konidienträger fortschreitend verkürzt. Ausserdem sind bei *Trichothecium* die



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Abb. 6. *Cladobotryum leptosporum*, Stamm CBS 821.69. Konidienträger und Konidien. Eine Phialospore ist durchwachsen mit neuerlicher Phialidenbildung. Rechts oben 2 Konidien aus dem Typenmaterial in PAD (1000: 1).

Konidienträger unverzweigt. Diese beiden Merkmale treffen bei den *Cladobotryum*-Arten nicht zu, wie in Deckglaskulturen einwandfrei festgestellt werden konnte.

Die Verlängerung der Phialiden bei *C. dendroides*, die schon durch Tulasne (1865, Tafel 5) deutlich abgebildet wurde, widerspricht allen für Phialidenpilze aufgestellten Regeln. Hughes (1958) reihte diese Art bereits als *Cladobotryum macrosporum* ein, Barron (1968) stellte sie jedoch nach sorgfältiger Beobachtung wieder als *Dactylium* in eine eigene Gattung. Wie dieser Autor deutlich zeigt, besitzt der verlängerte apikale Teil der Phialiden eine eigenartige Struktur, die weder mit der Verlängerung der Konidienträger bei Sympodulae noch mit Annelophoren direkt vergleichbar ist. Typische Sympodulae bilden durch Ausstülpung der primären Wand der sporogenen Zelle Blastosporen, die meist durch Zwischenräume voneinander getrennt sind. Bei Annelophoren entwickeln sich die Konidien immer in axialer Richtung und sitzen mit breiter Basis auf der sporogenen Zelle. Im Gegensatz dazu werden bei *Cladobotryum dendroides* die breiten Anheftungsflächen der älteren Konidien unregelmässig nach allen Seiten verdrängt. Es bleibt eine scharfe Grenze des ursprünglichen Phialidenscheitels bestehen, während sich bei fortschreitender Konidienbildung die sporogene Zelle unter Ausbildung einer unregelmässigen dünneren sekundären Wand verlängert. Cole & Kendrick (1969) definieren nach Untersuchung einer verschiedenartigen Auswahl von Hyphomyceten Phialiden

folgendermassen: «A phialide is a sporogenous cell which produces conidia (phialospores) in a basipetal succession from a fixed meristem whose position may vary in different fungi from the apex of the cell to deep within the body of the cell. The first formed phialospore ruptures the outer, or primary, wall of the phialide apex, and subsequent conidia are extruded through this 'open end'. Each conidium is clad in a 'secondary wall' especially laid down during its differentiation . . .». Der Scheitel der Phialidenwand ist durch die einmalige Ruptur eindeutig festgelegt, während das endogene Meristem (das chromophile Plasma) bei jedem neu zu bildenden Konidium aufs neue vorgeschoben wird. Die Besonderheit von *Cladobotryum dendroides* besteht darin, dass sich das Meristem schrittweise über den Rand der Phialidenwand emporschiebt. Nach allen übrigen Merkmalen lässt sich die konidienbildende Zelle trotzdem als Phialide bezeichnen. Die Konidienbildung ähnelt der von *Cacumisporium capitulatum* (Corda) Hughes, die von Goos (1969) ausführlich beschrieben, jedoch nicht als Phialidenbildung betrachtet wurde.

Die Verlängerung und Verzweigung der Phialiden bei *Cladobotryum spec.* stellt einen Sonderfall der von Cole & Kendrick (1969) definierten Polyphialiden dar. Im Gegensatz zur typischen Ausbildung (z.B. bei *Codinaea*) bildet die Phialide im obersten Teil deutliche Seitenäste; diese sind an Grösse der ursprünglichen Phialide untergeordnet, im Gegensatz zu anderen Proliferationsformen, die terminal (häufig bei *Chloridium*, *Phialophora* u.a.) oder lateral (z.B. bei *Capnophialophora*) sein können. Diese apikale Aufspaltung der Phialiden in einige kurze, einander übergipfelnde Seitenäste ohne Querwandbildung ist eine artspezifische Erscheinung, die auch bei einigen *Acremonium*-Arten vorkommt. Deshalb wird dafür hier die Bezeichnung Schizophialide vorgeschlagen.

Die von Lentz (1966) vorgeschlagene Konservierung der Gattung *Dactylium* sensu Saccardo gegen *Dactylium* Nees (? = *Dactylaria* Sacc.) wurde inzwischen abgewiesen (Donk, 1968); sie ist überflüssig, wenn die Art *dendroides* in *Cladobotryum* untergebracht wird.

*Cladobotryum* zeigt die meiste Ähnlichkeit mit der Gattung *Verticillium* Nees, deren Hauptfruchtformen, soweit bekannt, in die Gattung *Nectria* gehören. Ausserdem wachsen bei den Arten dieser Gattung die Kolonien wesentlich langsamer, der Phialidenscheitel ist stärker zugespitzt, und die Konidien sind in schleimigen Köpfchen oder in Ketten vereinigt, meist kleiner und haben eine weniger deutlich abgestutzte Basis.

Bei pleomorpher Konidienbildung ist die Phialidenform im allgemeinen massgeblicher für die Beurteilung der natürlichen Verwandtschaft als die Chlamydo-sporenform, wenngleich diese manchmal auffallender ist. In den hier beschriebenen Arten (Ausnahme *C. apiculatum*) ist die Phialosporenform stärker ausgeprägt als die Chlamydo-sporenform. Einige weitere verwandte Pilze sind jedoch unter dem Namen der Chlamydo-sporenform beschrieben worden, z.B. als *Sepedonium*, *Leiosepium*, *Mycogone* und *Stephanoma*. Andere *Hypomyces*-Arten (z.B. *H. lateritius* Tul.) sind vor allem durch die Peritheciumform bekannt und besitzen nur sehr unscheinbare *Acremonium*-ähnliche Phialiden.

Wir danken Herrn Dr. J. A. von Arx herzlich für viele Anregungen bei dieser Arbeit, Herrn Dr. M. A. Donk für seine unschätzbare Hilfe bei der Dokumentation alter Literatur und Beratung in nomenklatorischen Fragen sowie Fr. A. J. Rademaker für die Reinzeichnung der Abbildungen.

### Summary

The genus *Cladobotryum* Nees is characterized by mostly verticillately branched conidiophores with phialides, dry, one-celled or pluricellular conidia in heads or irregular chains, and pluricellular chlamydo-spores or sclerotia. Eight species are considered. In four of them the corresponding *Hypomyces* state is known, in one species it is conjectured. In cultures of *Hypomyces rosellus* and *H. odoratus* perithecia were obtained after mating of compatible strains. The conidium-forming cells are interpreted as phialides in all species, even if the meristematic zone extends beyond the apex and surrounds itself with a secondary wall.

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## SOIL FUNGI FROM NORTH-EAST AND NORTH BRAZIL—VIII

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(With Plate 7 and two Text-figures)

*Hesseltinella*, a new genus of the Thamnidaceae is described with a single species, *H. vesiculosa*, isolated from Brazilian soil. Main characters of the new genus are branchlets, radiating from swellings of the sporangiophore and terminating in secondary swellings bearing single sporangia.

Further Mucorales isolated for the first time from Brazilian soils are: *Absidia pseudocylindrospora*, *A. cylindrospora*, *A. corymbifera*, *A. cuneospora*, *A. blakesleeana*, *Choanephora circinans*, *C. infundibulifera*, *Cunninghamella elegans* (syn.: *C. batistae* Upadhyay & Ramos), *G. phaeospora*, and *Mortierella hyalina*.

In continuation of the previous studies on soil fungi from the North-east and North of Brazil a new genus, *Hesseltinella*, is erected to accommodate a new species. The genus and its type species, *H. vesiculosa* Upadhyay, are described, and some interesting Mucorales isolated for the first time from Brazilian soils are mentioned. Methods and materials used are those described in the first paper of this series (Warcup, 1950; Batista & Upadhyay, 1965).

### ***Hesseltinella*** Upadhyay, *gen. nov.*

Hyphae hyalinae vel subhyalinae; sporangiophora erecta, simplicia vel aetate ramosa, una vel compluribus intumescentiis apicalibus vel intercalaribus vel lateralibus praedita, e quibus ramuli secundarii undique radiantes oriuntur; ramuli secundarii vesiculis egrediuntur e quibus sporangia singula pediculo portata oriuntur; sporangia globosa, pariete spinulis radiantibus oblecto, multas sporas hyalinas levesque ferentia. Sporangia collumellata absunt.

Ad Mucorales, Thamnidaceas spectat.

Species typica: *H. vesiculosa* Upadhyay.

Hyphae hyaline or subhyaline, branched; sporangiophores erect, simple or branched when old, with 1 or a small number of apical, lateral or intercalary swellings. Secondary branches radiating from these swellings bearing apically a secondary swelling; sporangia borne singly on a short apical stalk arising from the secondary swelling, globose, with spiny wall, containing a large number of one-celled, hyaline, smooth sporangiospores; columellate sporangia absent.

Type species: *H. vesiculosa* Upadhyay.

### ***Hesseltinella vesiculosa*** Upadhyay, *sp. nov.*—Fig. 1, Pl. 7, figs. 1-3

Coloniae tarde crescunt, 5-6 cm in diam. 8 diebus 25° C; primum albae vel subochraceae, deinde media colonia olivaceo-brunneae vel obscure griseae, margine subochraceo; reverso

pallide olivaceo vel olivaceo. Stolones hyalini, leves vel rugulosi, 2.5–7  $\mu$  in diam.; rhizoidea parca vel nulla; sporangiophora hyphis submersis vel stolonibus assurgentia, simplicia vel ramosa vel aetate dichotoma, levia vel rugulosa, nonnumquam sub intumescentiis septata, longitudine variabili, 5–21  $\mu$  in diam. (plerumque 9–12  $\mu$ ); una vel complures intumescitiae terminales, intercalares vel laterales; ramuli ex intumescentiis radiantes fere simplices, 10.5–50  $\times$  2.5–4.5  $\mu$ , raro ramosi et longiores, 3–7  $\mu$  in diam., hyalini, leves; vesiculae terminales hemisphaericae vel urniformes, leves, 6–11  $\mu$  in diam., pediculum 2–4.5  $\mu$  longitudine ferunt qui sporangiola procreat; sporangiola globosa, hyalina vel luteola vel brunnea, 9–27  $\mu$  in diam., maturitate disjuncta et deliquescentia, pariete perlucido, spinis tenuibus, ad 12  $\mu$  longis obtecto; sporangiosporae oblongae, fusiformes, lunatae vel reniformes, tenues, leves, hyalinae, 3.5–10  $\times$  1.5–3.5  $\mu$  (plerumque 6–7  $\mu$ ) longae. Chlamydosporae absunt, zygosporae ignotae.

Typus CBS 197.68 (in herb. et coll.), isolatus e solo arenoso oryzae cultae, Maranhão, Brasilia, Oct. 1967.

Colonies on synthetic mucor-agar slow-growing, attaining a diam. of 5–6 cm in 8 days at 25° C, at first white to ochre-white, later on becoming Olive-Gray to Pale Smoke-Gray to Pale Olive-Buff<sup>1</sup> in the centre, and white or ochre-white at the margin; colony centre often depressed or even moist in appearance; colony reverse Pale-Olive to Olive-Buff or Deep Olive-Buff after 30 days, sometimes radially wrinkled; odour none; stolons hyaline, smooth to slightly roughened, sometimes septate; 2.5–7  $\mu$  in diam.; rhizoids poorly developed or absent; sporangiophores usually arising from substrate mycelium, sometimes from stolons, hyaline, smooth or slightly roughened, sometimes septate below the swellings, erect, with 1 or a small number of terminal, lateral, and intercalary swellings, terminating in a short blunt process projecting beyond the terminal swelling, simple or racemously branched or even dichotomously when old, 5–21  $\mu$  in diam. (typically 9–12  $\mu$ ); secondary branches radiating from the primary swelling of the sporangiophore,



Fig. 1. *Hesseltnella vesiculosa*, sporangiospores.

usually simple, 10.5–50  $\times$  2.5–4.5  $\mu$ , occasionally branched and much longer, 3–7  $\mu$  in diam., hyaline, smooth, terminating into small secondary swellings which are hemispherical to urn-shaped, smooth-walled, hyaline, 6–11  $\mu$  in diam., apically bearing a single sporangiole on a short stalk; stalks 2–4.5  $\mu$  in length; sporangiola globose, hyaline to yellow-tinted or brown, 9–27  $\mu$  in diam., easily detached, persisting for a long time, deliquescing or breaking with considerable pressure when ripe, multispored; sporangiolar wall transparent, covered with up to 12  $\mu$  long slender spines; sporangiospores lunate, fusiform, oblong to reniform, thin-walled, hyaline, smooth, 3.5–10  $\times$  1.5–3.5  $\mu$  (typically 6–7  $\mu$  in length); columellate sporangia, chlamydosporae, and zygosporae absent.

<sup>1</sup> Capitalized colour names refer to Ridgway (1912).

Isolated from soil of paddy fields in the states of Maranhão and Pernambuco (at Recife), October, 1967. Cultures are kept in the Mycotheca of IMUFPe, Recife, Brazil, the Commonwealth Mycological Institute, Kew, England, the Centraalbureau voor Schimmelcultures (CBS 197.68, type), Baarn, The Netherlands, and the N.R.R.L., Peoria, Illinois, U.S.A.

This fungus grows on a variety of media such as potato-dextrose-agar (PDA), synthetic-mucor-agar (SMA), carrot-agar (CA), Sabouraud-agar, malt-agar (MA), and hay-agar (HA), and the resulting colonies may display minor variations in growth-rate and fertility. On Czapek's agar, its growth is poor but sporulation is good. The fungus shows optimum growth at 28° C. But it also grows at a minimum temperature of 15° C and a maximum of 37° C.

The following observations were made on the morphological development of the sporangiophores, swellings, branches, and sporangia. In young culture the sporangiophore usually forms a terminal swelling and terminates in a short sterile process (Pl. 7 figs. 1-3). From this swelling, branches, referred to as secondary branches in the above description, radiate, terminating again in an apical swelling, referred to as secondary swelling, which bears terminally a single sporangiole on a short stalk. However, the sporangiophore gradually forms a small number of lateral and intercalary swellings when older. The secondary branches radiating from these swellings may be simple or branched.

The present fungus is a typical member of the Thamnidiaceae and appears to be related to genera such as *Helicostylum* Corda (Corda, 1840; Lythgoe, 1958), *Cokeromyces* Shanor (Shanor & al., 1950), and *Radiomyces* Embree (Embree, 1959). The genus *Helicostylum* differs by columellate terminal sporangia, and sporangia borne directly at the apex of circinate branches instead of on secondary swellings. In *Cokeromyces*, the sporangia are also borne directly on recurved secondary stalks. *Radiomyces* is closely related to the present fungus, the main difference being that the secondary swellings bear several sporangia.

*ABSIDIA PSEUDOCYLINDROSPORA* Hesseltine & Ellis—Fig. 2

*Absidia pseudocylindrospora* Hesseltine & Ellis in *Mycologia* 53: 406. 1961.

More than 21 isolates from soils of paddy and sugar-cane fields in the states of Pernambuco, Paraíba, and Maranhão are in good agreement with cultural and morphological characters of *Absidia pseudocylindrospora*. In addition to the features of this species, as described by Hesseltine & Ellis (1961), the Brazilian strains commonly possess the following characters: (i) formation of swellings in the sporangiophores, (ii) branched sporangiophores sometimes arising from an apical swelling, (iii) occasional presence of subglobose or globose sporangiospores. However, most of the microscopic and cultural characters of our isolates are like those of *A. pseudocylindrospora* and they form zygospores with an opposite strain of that species (Hesseltine & Ellis, 1964); hence we refer our fungus to it.

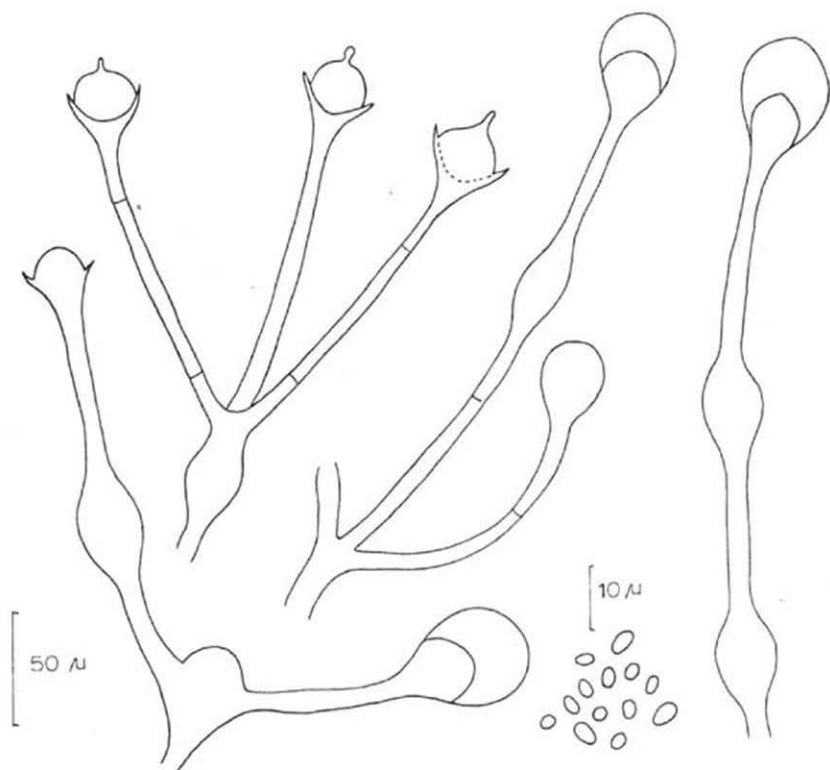


Fig. 2. *Absidia pseudocylindrospora*; branched and unbranched sporangiophores with swellings and sporangiospores.

Cultures are deposited in the Mycotheca of IMUFPe, Recife, the Centraalbureau voor Schimmelcultures, Baarn (CBS 480.66), the Commonwealth Mycological Institute, Kew, and the N.R.R.L., Peoria.

This species had not yet been isolated outside the U.S.A. and Mexico (Hesseltine & Ellis, 1964).

#### ABSIDIA CYLINDROSPORA Hagem

*Absidia cylindrospora* Hagem in Skr. VidenskSelsk. Christiania, Mat.-natv. Kl. No. 7: 45. 1908.

*Absidia cylindrospora* was isolated as one of the most common species of the genus from soil in various states of the North-east and North of Brazil. It had been isolated from garden soil at Niteroi, state of Guanabara (Hesseltine & Ellis, 1964) but was as yet unknown from the North-east and North of Brazil.

ABSIDIA CORYMBIFERA (Cohn) Sacc. & Trotter

*Absidia corymbifera* (Cohn) Sacc. & Trotter, Syll. Fung. 21: 825. 1912.

More than 170 isolates from sandy soils are in good agreement with *Absidia corymbifera* in cultural and morphological characters, as described by Ellis & Hesseltine (1966). This species has a world-wide distribution but remained to be reported from the North-east and North of Brazil.

ABSIDIA CUNEOSPORA Orr & Plunkett

*Absidia cuneospora* Orr & Plunkett in Mycologia 51: 203. 1959.

This species was twice isolated from soils of paddy field and forest in the state of Maranhão, April, 1966. It had been reported only from soil in the western part of the United States of America so far.

ABSIDIA BLAKESLEEANA Lendner

*Absidia blakesleeana* Lendner in Bull. Soc. bot. Genève, II, 15: 148. 1923.

Two isolates, one from sandy soil in the state of Maranhão and another from chicken dung collected from the poultry of the Veterinary Department of the Rural Federal University of Pernambuco, agree in their cultural and morphological characters with *A. blakesleeana* according to the description given by Hesseltine & Ellis (1966).

CHOANEPHORA CIRCINANS (Naganishi & Kawakami) Hesseltine & Benjamin

*Choanephora circinans* (Naganishi & Kawakami) Hesseltine & Benjamin in Mycologia 49: 723. 1957.

Isolated from soils of paddy and sugar-cane cultivation in the states of Paraíba and Pernambuco. This is the first record of the species from Brazil.

CHOANEPHORA INFUNDIBULIFERA (Currey) Sacc.

*Choanephora infundibulifera* (Currey) Sacc., Syll. Fung. 9: 339. 1891.

This species was frequently isolated from various garden and forest soils in the state of Pernambuco.

## CUNNINGHAMELLA ELEGANS Lendner

*Cunninghamella elegans* Lendner in Bull. Herb. Boissier 7: 250. 1907.

This fungus was commonly isolated from sandy soils of forest and paddy fields in the states of Paraíba, Rio Grande do Norte, and Maranhão. All strains produced predominantly spherical to subspherical spores and unbranched or poorly branched conidiophores and therefore it was supposed to be a new species, deposited in C.B.S., Baarn, (CBS 481.66) as *Cunninghamella batistae* Upadhyay & Ramos (Samson, 1969). However, matings with *C. elegans* revealed its identity. This species was reported from soil at Recife, Pernambuco, by the present author (1967), but remained to be reported from the above states.

## CUNNINGHAMELLA PHAEOSPORA Boedijn

*Cunninghamella phaeospora* Boedijn in Sydowia 12: 348. 1958.

Isolated from soils at Recife (Pernambuco), Natal (Rio Grande do Norte) and in the state of Maranhão. After its isolation in Indonesia it had been only found in India (Rai & al., 1968), according to Samson (1969).

## MORTIERELLA HYALINA (Harz) W. Gams

*Mortierella hyalina* (Harz) W. Gams in Nova Hedwigia 18: 13. 1969.

It was twice isolated from soil at Garanhuns (Pernambuco) where the temperature remains rather low (approximately 15° C) during the months of June and July and these isolations were obtained in June, 1966. This is the first record of the species not only for Brazil but also for Latin America.

## ACKNOWLEDGMENTS

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## EXPLANATION OF PLATE 7

Figs. 1-3. *Hesseltinella vesiculosa*. — 1, 2. Typical sporangiophores with secondary branches radiating from primary swelling. — 3. Sporangiophore with a terminal and a lateral swelling. (All figs., 640 ×.)



## THE GENUS CONOCYBE SUBGEN. PHOLIOTINA

### I. The European annulate species

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(With 54 Text-figures)

Sixty-five collections, comprising all known European annulate species of *Conocybe*, subgenus *Phliotina*, were examined, including the type specimens of *C. vexans* P. D. Orton and *C. percincta* P. D. Orton. In accordance with Orton, it is argued that Ricken, Kühner, and several other authors reversed the original conception of *C. blattaria* and *C. togularis*, as used by Fries, but that the specific epithet 'togularis' should be replaced by 'arrhenii'. *Conocybe aporos* and *C. arrhenii* var. *hadrocystis* are described as a new species and a new variety respectively. It is argued that *C. vexans* is conspecific with *C. blattaria*, and *C. percincta* with *C. teneroides*. Singer's observation—hitherto the only one of its kind—that 2-spored basidia may occur in *C. filaris* was confirmed and such basidia were also found in one collection of *C. arrhenii*. The taxonomic significance of several macroscopic and microscopic characters, often used for the distinction of the species are both scrutinized and criticized and often found to be very little or none. A key to the annulate species of the subgenus *Phliotina*, chiefly based on the characters of spores and cheilocystidia, is given.

The incentive to making an exhaustive study of the European annulate species of *Conocybe*, subgenus *Phliotina*, was our private herbarium containing twenty-three personal finds of these species by the end of 1968. To these could be added eight collections from the Rijksherbarium at Leiden, twenty-four from the Herbarium, Royal Botanic Garden, Edinburgh, five from the herbarium of Mr. P. B. Jansen, Breda, and three finds from Mr. J. Daams, Oud-Loosdrecht, altogether sixty-three collections. All our own collections are deposited in the Rijksherbarium, including the type specimens of *C. aporos* and *C. arrhenii* var. *hadrocystis*. We were also able to study the type specimens of *C. vexans* P. D. Orton and *C. percincta* P. D. Orton. Apart from two of our own collections of *C. blattaria*, one of *C. arrhenii* and one of *C. filaris*, the twenty-four collections from the Herbarium at Edinburgh and the two type specimens aforementioned, all of which were found in the British Isles, only Dutch material was studied. In consecutive papers, Dr. R. Watling, Edinburgh, will deal with the exannulate species and the section *Intermediae* of the genus *Conocybe* and some extra-European annulate species of *Conocybe*.

For the benefit of the reader, a list is given of the European annulate species of this subgenus as we know them now, together with a list of the corresponding

names, used by Kühner in his monograph 'Le Genre Galera' (1935); and a list of names as given in the 'New Check List of British Agarics and Boleti' (Dennis, Orton & Hora, 1960).

Kühner	New Check List	Kits van Waveren
1. <i>C. blattaria</i> f. <i>typica</i> <i>C. blattaria</i> f. <i>dentata</i>	<i>C. togularis</i> non sensu Kühn.	<i>C. arrhenii</i> var. <i>arrhenii</i> <i>C. arrhenii</i> var. <i>arrhenii</i> <i>C. arrhenii</i> var. <i>hadrocystis</i>
2.		<i>C. aporos</i>
3.		<i>C. blattaria</i>
4. <i>C. togularis</i>	<i>C. vexans</i>	<i>C. teneroides</i>
5. <i>C. teneroides</i>	<i>C. percincta</i> , <i>C. blattaria</i>	<i>C. filaris</i>
6. <i>C. filaris</i>	<i>C. filaris</i>	

For the descriptions of the colours of the cap, stem, gills, and flesh and also of the spores, mounted in water (under oil immersion and with rather strongly lit field of view), we used the American Munsell Soil Color Charts (abbreviated in the text to M.) and the code, designating its colours. For the methods by which we studied and depicted spores, basidia, cheilocystidia, and the cells of the cuticle of the cap and made sporograms, basidiograms, and cheilocystidiograms, one is referred to a previous paper (Kits van Waveren, 1968: 132). Spore sizes were based on samples from the gills as in the majority of cases no spore-prints were available. Great care was taken to measure only ripe, i.e. dark coloured, spores.

The herbaria to which reference is made are abbreviated as usual (Lanjouw & Stafleu, 1959).

We wish to thank very much the Director of the Rijksherbarium, Leiden (L) for the hospitality received in his institute, the Director of The Herbarium, Royal Botanic Gardens, Kew (K) for lending the type specimens of *C. vexans* and *C. percincta*, and especially Dr. R. Watling for sending us the twenty-four specimens of the Herbarium of the Royal Botanic Garden, Edinburgh (E), for his comments on and corrections of the manuscript, and for our unique collaboration in dealing with the taxonomy of *Conocybe*, in which we both are so very much interested. We are greatly indebted to Dr. F. Kotlaba for translating some of Velenovský's descriptions and to Mr. G. A. Rasch for translating Singer's paper of 1950, published in Russian. Finally we wish to express our profound gratitude to Drs. M. A. Donk, R. A. Maas Geesteranus, C. Bas and J. van Brummelen for their very great help and their interest taken in our mycological activities.

#### CONOCYBE subgen. PHOLIOTINA (Fayod) Kühn.

*Conocybe* subgen. *Pholiotina* (Fayod) Kühn., Le Genre Galera 44, 139. 1935.

Cap 4–40 mm diameter, conical to conico-campanulate, then convex to applanate, often subumbonate, striate but never radially-sulcate, surface smooth, infrequently rugulose, hygrophanous, reddish-brown to dark brown and paler shades of brown. Velum parziale either forming a conspicuous ring with striate-plicate upper surface

(annulate species) or white denticles along the margin of the cap (ex-annulate species), but in the former group the veil sometimes forms denticles instead of a ring. Gills ochre-brown, ventricose, narrowly adnexed, edge white. Stem 20–70 × 1–6 mm, cylindrical or slightly thickened towards the base, pale yellowish-brown at the pruinose apex, increasingly brown towards the dark fuliginous brown base, colours partly masked by the whitish fibrillose-striate superficial layer. Spore-print deep rust-brown, ochre-brown. Cuticle of the cap hymeniform (hymeniderm). Spores ellipsoid to slightly amygdaliform with flattened adaxial face, yellow with just a trace of red when mounted in water, often with a germ-pore. Basidia as a rule 4-, but sometimes 2-spored. Cheilocystidia always present, cylindrical, sublageniform, lageniform, clavate, utriform, only in section *Intermediae* (to be described by Dr. R. Watling) more or less lecythiform. Pleurocystidia always absent.

### **Conocybe versus Pholiotina**

According to Fayod (1889: 357) who erected *Conocybe* and *Pholiotina* as two separate genera, the species of *Pholiotina* have (1) a "voile général fibreux, formant l'épicutis; double et annuliforme sur le stipe," (2) the "subhyménium et hyménopodium denses et à éléments filiformes fins, peu distincts," (3) "cellules hyménales allongées, claviformes," (4) "cystides allongés, cylindracés." The species of *Conocybe* have a "subhyménium très développé" and "cellules hyménales courtes, sub-cylindriques," neither a veil nor cystidia being mentioned in the definition of *Conocybe*.

However, from the investigations of Kühner (1949: 275) and Reynders (1963: 347) we know that *C. pubescens* and *C. antipus* are paravelangiocarpic in that they show traces of a lipsanenenchyma, i.e. a velum parziale (*C. hebelomatooides* was found to be gymnangiocarpic). Watling (*apud* Reynders, 1963: 347; doctorate thesis Edinburgh 1964, unpublished; and personal communication) found traces of a veil in several species of *Conocybe*, for instance *C. farinacea* (Watling, 1964: 309), *C. tenera*, *C. subovalis*, *C. coprophila*, *C. appendiculata*. In *Conocybe* therefore traces of a veil are also encountered outside *Pholiotina*.

Kühner (1935: 18) very carefully studied the hymenophoral trama in species of both *Conocybe* and *Pholiotina*. He indeed found that in *Pholiotina* the mediostratum is broad, consisting of inflated cells, and lined on both sides with filiform hyphae (the hymenopodium), separating the mediostratum from the subhymenium, whereas in *Conocybe* the subhymenium is so strongly developed that the hymenopodia from both sides almost touch each other, the mediostratum being almost obliterated. But he also noticed that the latter structure often could be found only in the small gills or near the edge of the large gills and that in several species of *Conocybe* at the base of the larger gills the hymenophoral pattern was similar to that in species of *Pholiotina*: broad mediostratum with widely separated hymenopodia, only narrowing near the edge of the gill, the hymenopodia touching (Kühner, 1935: 11, fig. 3; 19, fig. 5; and 20, fig. 6). He therefore considered the assumed structural differences between the two genera only to be "une différence de degré" as indeed they are.

Watling (personal communication) confirmed this in *C. pubescens*, *C. farinacea*, *C. subpubescens*, *C. tenera*, and *C. subovalis*.

Kühner's observations are in full agreement with the concept of the thickening hymenium in which the cells of the subhymenium during the process of producing the hymenial elements increase in number and size; this would imply that locally the stage of maturity in the gills decides the thickness of the subhymenium (Donk, 1957: 3 and personal communication). Kühner also very carefully measured and compared the sizes of spores and basidia in species of both *Conocybe* and *Pholiotina* and found the differences too small to serve the purpose of maintaining *Pholiotina* as a genus separate from *Conocybe*.

Singer (1949: 482; 1962: 521), later followed by Moser (1967: 225), is the only author to adopt Fayod's separation of *Conocybe* and *Pholiotina*, which he, however, based exclusively on the alleged difference in the structure of the hymenophoral trama.<sup>1</sup> Discarding Fayod's original definition this resulted with Singer in (1) the inclusion in *Pholiotina* of the species of section *Piliferae* of *Conocybe*, which lack a veil but possess pileocystidia, structures which are absent in the majority of species of *Pholiotina*; (2) the inclusion of the species of section *Intermediae*, which have lecythiform cheilo- and caulocystidia, while Fayod's concept of *Pholiotina* implies that this "genus" should only comprise species with "cystides allongés, cylindracés"; (3) the exclusion of some species of *Conocybe* which possess traces of an annulus.

In agreement with Watling (1965: 289-323) it was therefore decided not to maintain *Pholiotina* as an independent genus as Singer and his school did, but to subordinate it in *Conocybe* as a subgenus. This view was also recently expressed by Romagnesi (1968: 365).

### Discussion of macroscopic characters

Caps, when young, moist, and fresh, very often are decidedly dark reddish-brown (M. 5 YR 3/3, 3/4, 4/3), but, being hygrophanous, the reddish colour very soon disappears, making way for some shade of brown (M. 7.5 YR 4/4, 5/6, 6/6), finally, when the process of drying out is complete, of pale brown (M. 10 YR 5/6, 6/6, 7/6 or even 7/4). Remoistening of the cap, for instance by putting the stem in water, never brings back the reddish colour but does bring back some of the brown colour but in all *Conocybe* species never quite the original shade of brown. This process of drying out and remoistening is bound to happen also while the carpophores are still in the field. The rapid loss of the red colour is particularly deceiving and one feels that quite a few descriptions in the literature must have been based on

<sup>1</sup> "In *Conocybe* the hymenophoral trama is reduced to a very thin mediostrium of a few filamentous hyphae which are flanked by the enormously developed hymenopodium, consisting of voluminous elements, the hymenopodia of both sides of the mediostrium almost touching each other," whereas in *Pholiotina* "the mediostrium is more developed and the hymenopodium less developed" (Singer, l.c.).

specimens in which the process of drying out was already well on its way. For instance the colour of the caps of the eight specimens of *Agaricus togularis* var. *filaris*, depicted by Fries (1884: pl. 104, fig. 4) on which J. E. Lange (1938: 63) based his description of *Pholiotia filaris*, and also of the caps of the specimens depicted by Lange himself (1938: pl. 106 C, C 1) is obviously too pale (M. 10 YR 7/4 and only near the margin  $\pm 7.5$  YR 7/6 on Fries's plate;  $\pm 7.5$  YR 7/6 on Lange's plate, which does show, however, a trace of reddish in the centre of the caps). Accordingly the caps on both Fries' and Lange's plates are hardly striate. Caps may be dark warm brown and seem quite moist, when nevertheless they are already well on their way of drying out.

Moist caps of all species of the subgenus *Pholiotina* may be striate well beyond halfway to the centre, sometimes even up to  $2/3$ – $3/4$  of the radius, even in *C. arrhenii* ("*blattaria*"), which in the literature is reputed to be somewhat less striate than the other species of *Pholiotina*. The extent to which the caps are striate, however, varies a great deal within one and the same species and depends largely on the degree of drying out, in the process of which the striation becomes less and less, finally to disappear. The degree of striation therefore cannot have any taxonomic significance, neither can it serve as a key character.

Kühner, however, did use the striation of the cap in his key to the subgenus *Pholiotina* (1935: 44): in item 5 the choice is between either "chapeau longuement et fortement strié" plus the striking pale colour of the cap (= *C. appendiculata*), or "chapeau plus fortement coloré" (degree of striation not mentioned). In the full description of *C. appendiculata*, it is then stated that the caps are "d'abord à peine striolé mais devenant vite nettement ou même fortement strié, souvent jusqu'au delà de la moitié rayon," so the striae may even reach beyond halfway to the centre of the cap. In the description of *C. blattaria* f. *exannulata*, the first species of the alternative choice, however, it is stated that the cap is "nettement strié, soit au bord seulement, soit jusqu'à la moitié du rayon piléique ou même au delà" and the cap of yet another of the alternative choices, the annulate *C. filaris*, is "assez longuement strié."

Particularly in *C. filaris*, the surface of the cap is sometimes definitely veined, rugulose, and this character led to the description of a new species by Peck (1898: 102), *C. rugosa*, and of a new variety by Singer (1950: 429), *C. filaris* var. *rugosa*. In both cases one no doubt is dealing with specimens of *C. filaris*, having a conspicuously veined surface of the cap. Our own material contains several collections of *C. filaris* in which the surface of the cap of some specimens was distinctly rugulose when fresh, while it was quite smooth in others. Although this phenomenon is more frequent in *C. filaris*, we also noticed it in specimens of *C. arrhenii*, *C. arrhenii* var. *hadrocystis*, and *C. aporos*.

The velum parziale causes the species of the *Pholiotina* group to be either annulate or exannulate, the margin of the cap then carrying a number of small white denticles, the remnants of the veil. But the dividing line between the two groups is by no means sharp. Kühner (1935: 150) described of *C. arrhenii* ("*blattaria*") a "forma

*dentata*," which neither macroscopically nor microscopically differed in any way from "forma typica" except for the veil, which in the former had failed to form a ring around the stem and instead had remained as denticles all along the margin of the cap. The inner surface (facing the stem) of the denticles was striate like the upper surface of the ring in "forma typica," thus proving the common origin of both ring and denticles. Kühner also noticed that on rare occasions in his "forma *dentata*," as might be expected, small remnants of a ring could still be found in spite of the presence of the denticles.

In our own material two out of the three specimens of our find of *C. arrhenii* of 28 Sept. 1968, representing Kühner's *C. "blattaria" f. dentata*, had, apart from distinct denticles along the margin of the cap, also remnants of a ring on the stem. Of our find of *C. arrhenii* of 11 Oct. 1969, consisting of fourteen specimens, one specimen did not show a ring but did show right in the centre of the cap quite a number of white velar fibres, also halfway down the centre a conspicuous circle of isolated patches of velar remnants and finally very close to the margin of the cap a few remnants of the veil. A few specimens of the same lot had a conspicuous be it sometimes rather small ring and besides a fairly large number of white velar flocci on the surface of the cap close to and along the entire margin of the cap and sometimes also higher up till even close to the centre.

On the other hand three out of the four specimens of our find of *C. brunnea* (lecythiform cystidia!) of 10 Sept. 1968 near Tomich (Scotland) had the white velar denticles along the margin of the cap, typical of this species, while the fourth specimen had quite a large ring and hardly any of these denticles. In this respect the twelve specimens of our find of *C. brunnea* of 19 Oct. 1969 in Ommen, were even more striking in that only one showed the denticles, two only a very conspicuous and distinctly striate-plicate ring and eleven neither denticles nor a ring! Kühner (1935: 146) stated that with some species of *Pholiotina*—his examples are *C. arrhenii* ("*blattaria*"), *C. brunnea*, and *C. appendiculata*—in some specimens the veil may remain attached to the margin of the cap, while in others it stays on the stem as a ring. Mr. P. B. Jansen, who for many years has been collecting the annulate *C. aporos* in the South of the Netherlands, reported that "in unfavourable weather conditions, slow growth, specimens of this species may show no ring, but instead an appendiculate veil along the margin of the cap."

One of our own collections, totalling ten specimens, found on 2 June 1962, which at the time had been described in detail, had remained unidentified until—while studying the subgenus *Pholiotina* recently—it became clear that they must be a "dentate" form of *C. aporos*. Next it was discovered that the forty specimens in the Rijksherbarium (No. 1281) found by Dr. J. van Brummelen on 22 April 1961 and at the time identified as *C. exannulata*, fully fulfilled all requirements for the identification as *C. aporos*, but that, when they were collected, none of them carried a ring, while most of them showed distinct remnants of the veil along the margin of the cap.

It is clear that under certain conditions (weather, velocity of growth or expansion of the cap, firmness by which the veil is attached to either the stem or the cap),

the veil, instead of remaining attached to the stem, forming a ring, may stick to the cap, breaking up into a number of denticles along its margin (*C. brunnea*, *C. arrhenii*, *C. aporos*) and vice versa (Kühner: *C. appendiculata*). Consequently we believe this phenomenon neither warrants distinguishing a "forma *dentata*" of the species involved, nor a "forma *annulata*" of *C. appendiculata*. We have therefore not recognized Kühner's f. *dentata* of *C. "blattaria"*.

Great emphasis, however, must be put on the existence of these 'dentate' forms as in the field 'dentate' specimens may very easily be taken for some member of the exannulate group. A very careful study and particularly microscopical examination is needed to arrive at the proper identification.

In item 3 of his key (1960: 192) to the annulate species of *Conocybe*, Orton puts some emphasis on the appearance of the surface of the stem below the annulus. It is described as "not conspicuously floccose-scaly at first" in *C. blattaria* (= *C. teneroides*) as opposed to "whitish or yellowish floccose-scaly at first" for both species of item 4, *C. vexans* (= *C. blattaria*) and *C. percincta* (= *C. teneroides*). In the description of the microscopical characters to follow hereafter, it will be outlined that the superficial layer of the stem below the ring of all species of *Pholiotina* consists of colourless hyphae, of which many terminate in a chain of some 3 to 6 short and broader cells and that very often these chains lump together, forming clusters of often quite considerable size. The extent to which they lump together greatly varies, most likely with age and external conditions and these chains and their conglomerations were found in all species. It is clear that these clusters are responsible for the floccose-scaly appearance of the stems, often mentioned in descriptions in the literature. This appearance, although not always present, was often noticed by us too and in our opinion this floccose-scaliness can be of no taxonomic significance. All that may be stated is that the stems of *C. blattaria* and *C. teneroides* as a rule are more finely, silky striate than those of the other species.

With regard to the smell, it should be mentioned that specimens of *C. aporos* (and according to the excellent naturalist Mr. P. B. Jansen, particularly the young specimens) often have a very distinct smell of pelargonium, especially on bruising. Kühner (1935) reported an "odeur forte acide" in specimens of *C. arrhenii* ("*blattaria*") found early in the year (February, March, and May) so that these may well have been specimens of *C. aporos*, although shape of cystidia and absence of germ-pore were not mentioned.<sup>2</sup>

### Discussion of microscopic characters

The microscopic characters have been admirably studied and described by Kühner (1935), who besides made a special study of the cuticle and flesh of the

<sup>2</sup> The one and only specimen of *C. appendiculata* var. *macrospora* we ever found had an acid, pelargonium-like smell and Kühner reported an "odeur acide nette" for *C. appendiculata* and even an "odeur fortement acide" for *C. appendiculata* var. *macrospora*.

cap and the trama of the gills, so that the reader is referred to his excellent treatise on these structures.

The cuticle of the cap might be called a palisadoderm, the cells constituting the cuticle being arranged in a palisade-like manner. Their shape and size vary considerably, besides they originate from different levels in the hypoderm, but their apices all lie more or less in one plane. They consist of a stalk and a vesiculose, more or less globose, thin-walled apex. A great many of the stalks are thick-walled and brown, the thicker the wall the browner the colour, but many stalks are thin-walled and colourless; small incrustations are rarely found at the base of the stalks.

At one time during our investigations, we believed that these cells might furnish differential characters between some of the species (in our two collections of *C. blattaria* and one of *C. teneroides*, for instance, the stalks were strikingly short and rarely slightly thickened and brown), but for the moment we prefer ignoring these possible differences as, because of the very great variability of these cells, a larger number of collections of each of the species would have to be available for examination. The age of the specimens largely seems to be responsible for these differences, the size of the cells and particularly the colour and thickness of the walls of their stalks seeming to increase with age.

Following Kühner's advice (1935: 27) we searched the surface of the stems of the annulate species of the subgenus *Pholiotina* below the level of the ring for caulocystidia, but never found any. The superficial whitish fibrillose layer of the stems at that level consists of a dense and chiefly longitudinal network of colourless hyphae,  $c.$  1.6–8  $\mu$  thick. Many of these are seen to terminate in a chain of some 3 to 6 short (often very short) and broad cells (up to  $c.$  12.8  $\mu$ ) of which the terminal cell is broadest, obtuse, and sometimes forked or irregularly shaped or carrying 1 or 2 broad and blunt protuberances. Small and large clusters of these terminal hyphal chains are very frequent and no doubt cause the floccose-scaliness of the stems. There is no sharp dividing line between the colourless hyphae of this network and the thin superficial, very pale brown hyphae of the actual flesh of the stem, the latter becoming increasingly broader, (up to 24  $\mu$ ) and browner towards the centre of the stem. The hyphae of the superficial network and particularly those of the terminal chains, carry great numbers of clamps.

The spores are ellipsoid, slightly amygdaliform and yellow (M. 2.5 Y 7/6; 5 Y 7/6, 8/6) with just a trace of red in water, but in *C. blattaria* and *C. teneroides* the yellow colour is slightly darker (M. 2.5 Y 8/8), probably because their spores are larger and their walls thicker (germ-pore conspicuous!). The apiculus is small but distinct and all spores except those of *C. aporos* have a germ-pore, which is very inconspicuous in *C. arrhenii* ("subporé") and quite distinct, even large, in *C. blattaria* and *C. teneroides*.

The basidia are practically always 4-spored, but in *C. teneroides* 2-spored and we were able to confirm Singer's observation (the only one we found in the literature) that in *C. filaris* 2-spored basidia may occur adjacent to 4-spored. We also found 2-spored adjacent to a majority of 4-spored basidia in one collection of *C. arrhenii* of which the spores were slightly larger than usual.



The shape of the cheilocystidia is considered to be highly specific for each of the annulate species of the subgenus *Pholiotina* and therefore has been used by both Kühner—who depicted these cells for every single species—and us as a major key character for the delimitation of the species. These cells are very firmly fixed to the subhymenium and consequently very difficult to isolate with the object of making them visible over their full length. For *C. arrhenii* (“*blattaria*”) Kühner (1935: 152) even contented himself by depicting only the top half of a bunch of seven cheilocystidia and only one at full length. The cystidia are colourless, their walls are of normal thickness, and rarely are some of the apices covered with a thin layer of mucus.

### Habitat, frequency

The species of the annulate group of the subgenus *Pholiotina* prefer a rather rich, clayey soil and as a result are usually found along roadsides, in gardens, parks, in grass and particularly in orchards and in or near greenhouses. Except for *C. aporos*, which only grows in the spring, all species grow in the summer and autumn, even as late as November and December if the weather is favourable. They grow either solitary or in small groups (3–6 specimens) but *C. arrhenii*, *C. aporos*, and *C. filaris* have been found growing more or less gregariously and Mr. P. B. Jansen even reported having found *C. aporos* “by the hundred.”

The annulate species of the subgenus *Pholiotina* are considered to be rare; Kühner & Romagnesi (1953: 343) called all species of this subgenus “rare” or “assez rare” and Kühner (1935) only had 15 finds of the annulate group at his disposal. In the Netherlands *C. arrhenii*, *C. aporos*, and *C. filaris* are uncommon, *C. arrhenii* var. *hadrocystis* has been found twice, *C. teneroides* only once, while *C. blattaria* has not yet been recorded.

### Nomenclatural discussion

#### I. *Agaricus togularis* Bull. ex Fr. 1821, an *Agrocybe*.

In 1821 Fries (1821: 241) described *Agaricus togularis* and this name next appeared in all his subsequent publications (1828: 38; 1838: 161; 1857: 306; 1874: 216; 1884: 2. pl. 104 fig. 4) in which he consistently referred to Bulliard's species of that name (1809: 639) and to his Plate 595 fig. 2. Before embarking on Fries' concept of *A. togularis*, we must therefore first concentrate on the species Bulliard had in mind when he described *A. togularis*.

According to Bulliard's description, the cap of *A. togularis* is 30–50 mm broad and the largest specimen depicted on his plate even measures 60 mm (stem 80 × 4 mm and × 6 mm at the base); the cap of the one but largest specimen of his plate measures 41 mm, its stem measures 55 × 4.5 mm and × 7 mm at the base. The shape of the cap is described as “arrondie,” then “semiorbiculaire,” finally “aplatis,”

the colour as "bistre-jaune-paille," the colour of the gills as white at first, soon "bistre-paille-cendré," but Bulliard's plate shows sordid brown gills (M. 5 YR 5/4; 7.5 YR 5/4). The stem is also "jaune-paille-cendré," it carries a fugacious ring which is not stated as being striate above, while the specimens depicted on Bulliard's plate do not show any striation either.

From the above it is clear that Bulliard's description and plate of *A. togularis* pertain to an *Agrocybe* (most likely *A. praecox*). Quélet (1888: 96) was of the same opinion; he put a question-mark behind his citation of Bulliard's plate as synonym of *Hylophila togularis*, while later (1894: 485) he wrote that "*A. togularis* Bull. pl. 595 fig. 2 paraît être la même espèce que *praecox* Pers., nom qui ne peut pas être identifié avec *Arrhenii* Fries." Singer (1950: 431) also considered Bulliard's *A. togularis* to be an *Agrocybe*.<sup>3</sup>

Our reasoning that Bulliard's *A. togularis* must have been an *Agrocybe* tells even more with the descriptions Fries (1821: 241; 1828: 38; 1838: 161; 1857: 306) gave of *Agaricus togularis*. With Fries the mature cap even measures 75 mm ("3 unc."), the cap is fleshy ("carnoso"), pale brown (1821: "subargillaceo, pallescens"; 1828, 1838, and 1857: "humidus dilute ferrugineus l. ferrugineo-lividus, siccus expallens argillaceus"), the margin is not or only a little striate (1828: "in vivo striatus"; 1838: "subexstrio"; 1857: "udi striatus"), the stems are robust and thick (1821, 1828, 1857: "3 unc. × 2-3 lin. et ultra" = 75 × 4.6-6.9 mm and more and in 1838 Fries even mentions a thickness of "5 lin." = 11.5 mm); in none of the descriptions is the ring called striate, whereas this striation is characteristic of all annulate species of *Conocybe*! The colour of the gills is called "pallide, dein dilute cinnamomeae" in 1821, "pallide, demum aquose ferrugineae" in 1828, "ex argillaceo ferrugineis" in 1838, and "pallide, dein aquose-ferrugineae" in 1857. It is quite clear that Fries' descriptions mentioned above also pertain to an *Agrocybe*, most likely *A. praecox*.

From Fries' comments, following his descriptions of 1821, 1828, 1838, and 1857, it is clear that he himself must have sensed that this species was, what we now call, an *Agrocybe*. Already in 1821 he stated that *Agaricus togularis* is perhaps a variety of *A. praecox* and in 1838 that Bulliard's species (diameter of cap 30-50 mm!) stands between *A. arrhenii* and *A. togularis*. In 1874, in his description of *A. ombrophilus*, he linked yet another species of the present-day genus *Agrocybe* with *Agaricus togularis* by declaring that species to be synonymous with *A. togularis*, as described by him in 1821. He repeated this in his comment on the picture of *A. ombrophilus* in his *Icones* (1884: 2. pl. 103), where he said that *A. togularis*, as described by him in the 'Epicrisis' (1838: 161) was synonymous with *A. ombrophilus*. Fries therefore must

<sup>3</sup> Bulliard himself referred to several earlier publications and, although these do not in the least influence the identifications of Bulliard's species, they may be briefly enumerated just for the sake of completeness: Battara's species (1755: 30. pl. 1 B) is unidentifiable; *Agaricus cereolus* Schaeffer (1762: pl. 51) represents *Agrocybe praecox* (colour of gills!); *Agaricus candicans* Schaeffer (1800: pl. 217) is almost certainly a *Stropharia* (blackish-brown gills!) and Bolton's (1788: 10) plate might pertain to *Psathyrella hydrophila*.

have had severe doubts about the identity of his *A. togularis*. This is stressed by J. E. Lange (1938: 63), who wrote: "The synonymy is made still more confused by the alterations made by Fries himself, who in 'Monographia' (while calling *P. togularis*, *P. arrhenii*) used the name *P. togularis* for the species which in 'Hymenomyces' he calls *P. ombrophila*."

In the 19th century the use of the name *A. togularis*, given by Bulliard and by Fries in his earlier works for a species which undoubtedly was an *Agrocybe*, was wide-spread, while sometimes more confusing data were even added.

*Agaricus togularis* as described by Persoon (1801: 262) with reference to Bulliard's plate, had a cap measuring 50–75 mm and the stem measured 50–75 × 4.3–6.9 mm. With Secretan (1833: 83) the cap of *A. togularis* measured 50 mm, it was "fauve-nankin, revêtu d'un soyeux blanc," the flesh was 7 mm thick, the stem 62.5 × 10.3 mm and Secretan referred to Bulliard's plate. With Kickx (1864: 163), who referred to Bulliard's plate the cap of *A. togularis* was 40–50 mm broad and "jaune-argileux pâle." In Kummer's (1871: 85) key to the species of *Pholiota*, *P. togularis* follows immediately after *P. praecox*, of which it must have been just a form; later (1882: 83) it was made to follow immediately after *P. dura*.

The size, habitus, and colour of the specimens, depicted by Gillet (1876: 435, pl. 530) and named *Pholiota togularis*, strongly suggest that these must have been *A. praecox*; Gillet referred to Bulliard's plate but in the text Fries is mentioned as the author and in the index (1876: 788) *A. arrhenii* as being conspecific with *A. togularis*. *Pholiota togularis* as described by Quélet (1872: 125) is no doubt an *Agrocybe* (diameter of cap 90 mm) and so is probably *Pholiota togularis* as described by Saccardo (1916: 678) (stem 80–100 × 6 mm or more) as he referred to Quélet's description of 1872 and Bulliard's plate (on the other hand he also quotes Fries' Plate 104 fig. 4 of 1884, depicting *Conocybe filaris* and Cooke's Plate 350/379 of 1884–1886, depicting *C. blattaria*!).

Karsten (1879: 293) described *Pholiota togularis* as a very large species (diameter of cap 30–90 mm, stem 120 × 2–9 mm) with rust-brown gills. He referred on the one hand to Bulliard's plate, but on the other hand also to Fries' Icones, 1884: pl. 104 fig. 4 (= *Conocybe filaris*), to *A. arrhenii* Fr. (1838: 161), and to *A. mesodactylus* Berk. & Br. (1848: 261, pl. 9 fig. 1). Earlier he had given a description in Latin (1876: 114) of *A. togularis*, which is a true copy of Fries' description of that species of 1874, to which Karsten refers, as also to *A. arrhenii* Fr. (1838: 161). Needless to say the two descriptions do not tally. From Britzelmayr's (1883: 151) descriptions of *A. togularis* it is not clear to which species they pertain, very likely *Agrocybe praecox* as Britzelmayr later (1893: 9) described two forms, one of which he considered to be intermediate between *Pholiota togularis* and *P. erebia*, the other between *P. togularis* and *P. ombrophila*. It is impossible to identify the species described by Britzelmayr (1894: 252; reprint: 164) as *A. blattarius* as a *Conocybe*, as the surface of the cap is called "kurz faserschuppig."

The species described by W. G. Smith (1908: 123) as *Togaria togularis* also must have been an *Agrocybe* (cap 56 mm, "pallid ochraceous, mild sienna or umber," stem 78 × 4.7 mm).

II. *Agaricus arrhenii* Fr. 1838 and *A. togularis* sensu Fr. 1874.

*Agaricus arrhenii* was first described by Fries in the 'Epicrisis' (1838: 161) and again and in greater detail in the 'Monographia' (1857: 307), where, while citing his description of 1838, he distinguished three forms:

Form A was rather large but slender ("major at gracilis"), the stem measured 75-100 × 4.6 mm and was "fibrilloso-striatus," at the apex "lutescens," farther down "fuscescens," and it carried midway a large ring of which it was not stated whether it was striate or not; the cap measured 37.5 mm ("1½ unc."), it was "pallide ochraceo," not striate ("exstrius"); the gills did not turn brown ("lutescentes, demum pallide ferrugineae nec umquam fuscescentes").

Form B was more slender, the stem thinner and often "flexuoso" and of this form, of which no sizes were given, it was stated that it corresponded exactly ("haec forma quae exacte") with *A. mesodactylus* Berk. & Br. (diameter of cap 40 mm, stem 60 × 3 mm, slightly waving, and carrying midway a conspicuously striate ring).

Form C was called very small, "pusillus," but nevertheless the stem measured 25 (or even slightly longer) × 2.3 mm and the cap 25 mm. Fries believed these three forms to lie on a continuum and to be merely forms of one and the same species. From his description it is indeed clear that the difference in size is the only real difference.

It is most remarkable that in Fries' 'Hymenomycetes' the name *A. arrhenii* was withdrawn, having made way for *A. togularis*, of which accordingly *A. arrhenii* was cited as a synonym. It is equally remarkable to see that the description of this *A. togularis* differs on five points from all Fries' previous descriptions of *A. togularis*: in the 1874 description (1) no sizes of cap and stem are given, (2) the cap is still called "carnoso," but for the first time also "tenui," (3) the colour of the cap is not called "dilute ferrugineus," but "pallide ochraceus," (4) the colour of the gills is not "aquose ferrugineus" any more but "lutescentibus," and (5) although Fries still refers to Bulliard's Plate 595 fig. 2, he mentions for the first time *A. arrhenii* from 'Epicrisis' (1838: 161) and *A. mesodactylus* Berk. & Br. (1848: 261, pl. 9 fig. 1) as synonyms.

Obviously Fries changed his ideas about the identity of *A. togularis*, while stating that the many specimens, collected by him, had taught him, what he had already suspected earlier to be true that the fungus, described as *A. togularis*, belonged to *A. arrhenii*. Linking his description of *A. arrhenii* of 1857 with that of *A. togularis* of 1874 and choosing the latter name for the specific epithet, Fries stated that *A. togularis* is a very variable species with a variable habitus ("Proteus statura admodum varius"). Not too much significance should be attached (like many authors, however, did) to the fact that Fries never mentioned the striation of the ring in either *A. togularis* or *A. blattarius*. He must either have overlooked this character or failed to include it in his descriptions. His artist, however, painted this striation very clearly (1884: pl. 104 fig. 4) and after all Fries declared his form B

of *A. arrhenii* to be exactly the same as Berkeley & Broome's *A. mesodactylus* and their figure shows a conspicuously striate ring!

It is the unexpected use of an older name for a different and younger taxon (a clear case of a name being misapplied) that created a confusion which has lasted to the present day. Only very few authors mentioned *A. arrhenii* while discussing the nomenclature of *Pholiota* or *Conocybe togularis* or *blattaria* and even then only casually (Quélet, J. E. Lange, Kühner, Singer, Orton) and very few authors mentioned *A. arrhenii* in giving the synonymy of *Conocybe* "*togularis*" or "*blattaria*" as the case may be. This confusion is very well reflected in the works of Quélet. This author (1872: 125) described *Pholiota togularis*, which must have been an *Agrocybe* (diameter of cap 90 mm and gills "rouillés pâles"), like Quélet himself stated later (1894: 485). In his 'Additions aux Agaricinées' (1872: 248) Quélet described a *Pholiota arrhenii*, saying that this species should be inserted immediately after *P. togularis*, described earlier (1872: 125). Still later, in his 'Supplément' (1872: 319) he added *P. blattaria*, saying that that species should follow immediately after *P. arrhenii*. To Quélet these three species therefore must have seemed closely related. In the 'Flore mycologique' (1888: 96) we find a description of *Hylophila* (*Cyclopus*) *ombrophilus*, a typical *Agrocybe*-species. Accepting the lectotypification by Donk (1962: 79) *Cyclopus* (Quélet) Barbier 1907 is a typonym of *Agrocybe* Fayod. The description of *Hylophila togularis* in the 'Flore mycologique' is quite different from the one of 1872 and turns out to correspond very well with the description Quélet gave of *P. arrhenii* in 1872. The latter name has disappeared from the 'Flore mycologique', obviously having made way for *Hylophila togularis*, of which indeed *A. arrhenii* is said to be a synonym (only the spores are much too large, 14  $\mu$ ).

In conclusion, in 1874 Fries described a taxon, which he called *A. togularis*, but in all his earlier publications this name had pertained to some species of *Agrocybe*. In 1874 Fries declared *A. togularis* to be identical with *A. arrhenii*, a species, which he had already described in 1838 and he withdrew the latter name in favour of the former. He stressed the point that *A. togularis* is a very variable species and this had led him earlier even to distinguish three forms of *A. arrhenii*. This fungus because of its structural characters has been transferred to the genus *Conocybe*, its correct name now should be *Conocybe arrhenii*.

### III. *Agaricus blattarius* Fr.

In contrast to *Agaricus arrhenii* Fries never made alterations of any importance in his descriptions of *Agaricus blattarius* (1821: 246; 1828: 29; 1838: 162; 1857: 308; 1874: 216). From these it is clear that *A. blattarius* is a smaller and more slender species: "Est Galera optime annulata" (Fries 1857: 308). Later Quélet called this species "un Galera muni d'un anneau" and this comparison has been made by other authors as well (for instance, W. G. Smith, 1908: 123).

With Fries (1821: 246) the cap is "parvus" and "subcarnosus," later he called

it "pusillus" and "carnosulo" and of a darker colour than *A. arrhenii* ("ferrugineo, disco subumbonato obscuriore laevi"), the margin is always called "striato." The stem is 12.5–25 × 2.3 mm ("½–1 unc. × 1 lin.") and in all his descriptions the surface of the stem is described as "sericeus" (as against "fibrillosus-striatulus" in *A. arrhenii*) and the gills as "aqueose cinnamomeus" ("lutescentibus" in *A. arrhenii*). In 1821 and 1857 Fries described the upper surface of the ring as "laevis" but in 1838 and 1874 no description of this surface was given (in 'Elenchus' this species is merely mentioned, no description being given).

Fries referred to the descriptions of this species by Duby (1830: 812), Secretan (1833: 86), and Weinmann (1836: 203) and these descriptions fully correspond with the one by Fries. But he only referred to a single illustration, Plate 525 fig. 2 of Bulliard, which represents *A. pygmaeus* Bull. Of this figure Fries said in 'Elenchus' that the species depicted, so perfectly corresponded with his *A. blattarius* that he considered Bulliard's species to be a non-annulate form of his *A. blattarius*! In 1874, however, he was somewhat more reluctant with regard to this statement and he then merely said that the habitus of his *A. blattarius* was almost the same as that of *A. pygmaeus*. Weinmann on the contrary believed that Bulliard's fungus did not correspond very well with *A. blattarius*, chiefly because the latter is annulate. Bulliard's illustration depicts fourteen specimens, all growing on a piece of wood and obviously representing specimens of *Psathyrella pygmaea* (Bull. ex Fr.) Singer. Both Fries (1828) and Weinmann (1836) in this connection mentioned the picture of *A. unicolor* (Fl. dan., pl. 1071), depicting an annulate agaric, which may well have been *Galerina marginata* (Fr.) Kühn. or might represent *A. blattarius* Fr.

*Agaricus blattarius* therefore is an annulate *Conocybe* with the facies of a *Galerina*, it is smaller and more slender than *A. arrhenii*, it has a rather conico-campanulate, brown to yellowish-ochre, striate cap, the surface of the stem is rather silky-striate, and the stem carries a conspicuous ring of which the upper surface is striate-plicate (see figures of *P. blattaria*, Harper, 1912: 1011, pl. 59 and of *P. togularis*, Ricken, 1912: pl. 56 fig. 5; Bresadola, 1930: pl. 687; Kühner, 1935: 161).

#### IV. 'Togularis' versus 'blattarius' in the literature.

Since Ricken (1912: 199) used the epithet 'togularis' for the species, which Fries named 'blattaria' and vice versa, a number of authors followed his example (Overholts, 1924: 265, and 1927: 113; Bresadola, 1930: pl. 687 and 688; Kühner, 1935: 165; Kühner & Romagnesi, 1953: 343; Moser, 1967: 230; Singer, 1950: 427). But already earlier Cooke (1884–1886: pl. 350/379) had depicted Fries' *A. blattarius* as *A. togularis* Bull. and subsequently (1889–1891: pl. 1172 B / 1173 B) Fries' *A. togularis* as *A. blattarius* Fr. Cooke's description (1890: 373) of *C. arrhenii* (*A. "blattarius"*) and that (1886: 141) of *C. blattaria* (*A. "togularis"*), however, are far from clear and both descriptions show a good deal of resemblance. But the Plates 1172 B / 1173 B and 350/379 no doubt do represent *C. arrhenii* and *C. blattaria* respectively. Ricken's descriptions are much clearer and this is probably why the reversal of the

epithets is put down to him and not to Cooke. Curiously enough Cooke's plates and descriptions are not mentioned by Orton.

Thus, since Ricken great confusion has existed about which epithet belonged to which species; the epithets 'filaris' and 'teneroides' to some extent have been involved in this controversy. Indeed J. E. Lange (1938: 63) called the nomenclature for these species "hopelessly confused."

Kühner (1935: 166) made an unsuccessful attempt to arrive at an acceptable solution, but his own wording shows that he must have been rather sceptical about whether it was correct. He followed Ricken because "l'interprétation de *togularis* par Ricken ne nous semble pas notoirement inexacte," also "l'interprétation de *blattaria* nous paraît beaucoup moins certaine!" By leaving out a number of important data his exposition is very incomplete. He failed to stress sufficiently the confusion caused by Fries' earlier descriptions of *A. togularis*, pertaining to a species of *Agrocybe* and in no less than four footnotes he brought forward arguments against his own decision. On carefully reading Kühner's exposition one really finds more arguments against Kühner's conclusion than in favour of it.

Orton attempted to solve the 'togularis-blattarius' controversy and did so, but only partly. He demonstrated that the interchange brought about by Ricken was incorrect, but in the end still did not arrive at the correct nomenclature as he overlooked a few important facts. First of all he only compared Fries' descriptions of 1821 of *A. togularis* and *A. blattarius* without dealing with the exact identity itself of these two taxa. Neither did he mention the ever returning reference by Fries to Bulliard's Plate 595 fig. 2, which—as argued above—pertains to a species of *Agrocybe*, nor the fact that *A. togularis* from Fries' earlier publications really was an *Agrocybe*. He did quote the diameter of the cap of Fries' *Agaricus togularis* as being 75 mm broad (= 3 unc.) but then ignored the fact that this size is much too large for any species of the *Pholiotina* group of *Conocybe* and accordingly is never met with in any of the descriptions of these species by post-Friesian authors. Orton also ignored the fact that—although in none of Fries' descriptions the upper surface of the ring is described as either 'laevis' or 'striatus'—Fries in his description of 1874 of *Agaricus togularis* referred to Berkeley & Broome's *A. mesodactylus*, which was depicted by these authors with a beautifully striate ring. Next, Orton made no use of Fries' important statement that his form B of *A. arrhenii* (mentioned only casually by Orton, but considered identical with *A. togularis* by Fries in 1874) corresponds exactly with *A. mesodactylus*. He further wrote that Fries "replaced the name '*togularis*' temporarily by '*arrhenii*' in his 'Monographia'," but this work contains both names, each accompanied by its own description of a fungus. Finally Orton's statement that "*C. togularis* was described as *Agaricus (Pholiotia) mesodactylus* by Berkeley & Broome" is not quite correct. It was Fries, who recognized in Berkeley & Broome's description of *A. mesodactylus* his own *A. arrhenii*, which later he called *A. togularis*.

A few more descriptions of *C. togularis* and *C. blattaria* and their interpretations may be mentioned to illustrate the existing confusion in this field.

The interpretation of Berkeley's (1866: 93-98, pl. 1, No. 1) black and white

picture (which lacks a description) of what he called *A. arrhenii* is hazardous, but favours *C. blattaria* rather than *C. arrhenii*.

Although Cooke (1877: 157) in a few short annotations mentioned *A. togularis* and said that this species was synonymous with *A. arrhenii* and *A. mesodactylus*, he also mentioned *A. mycenoides* as being related and he referred to his Plate 85 fig. 3, which depicts a species, which very much resembles *Conocybe blattaria* (this figure corresponds extremely well with Cooke's Pl. 350/379, depicting *Conocybe blattaria*, but by Cooke was called *A. togularis*).

Massee (1893: 213) gave the standard description of *Conocybe* ('*Pholiota*') *blattaria* to which he added a description of specimens seen by himself. These, indeed, must have been *Conocybe blattaria* as they "resemble a *Galera* with a ring." In the standard description, however, he referred both to *A. blattarius* Fr. (1821) and to Cooke's Pl. 1172/1173 B, which depicts *C. arrhenii*, and the spores are only  $4 \times 2 \mu$ . Vice versa in his description of *Pholiota togularis*, which probably pertains to *C. arrhenii* (spores  $8 \times 3.5 \mu$ ), Massee (l.c.: 212) referred to Bulliard's Pl. 595 fig. 2 (= *Agrocybe*), to *A. mesodactylus* (= *C. arrhenii*)—the correct figure, Pl. 9 fig. 1 is cited but the text gives the wrong number of 681 (= *A. mycenoides*) instead of 329—and finally to Cooke's Pl. 350/379 (= *C. blattaria*).

The specimens that Harper (1912: 482) described as *Pholiota togularis* were "somewhat hygrophanous" and some "more hygrophanous," the gills were "toothed decurrent," the rings "evanescent," the spores  $5 \times 8 \mu$ , but neither germ-pore nor basidia nor cystidia were mentioned. The description gives no sizes and the photograph of 7 specimens (Pl. 32, scale not mentioned but no doubt somewhat enlarged, as is clear from Overholts'—1927: pl. 15—reproduction of part of Harper's plate) shows these to have a habitus, which is unlike that of *Conocybe togularis* or *C. blattaria*, decurrent gills, and a ring, which looks more like an annuliform zone.

Judging by Velenovský's (1921: 552) description of the macroscopic characteristics of *Galera togularis*, this species represents *Conocybe blattaria*, although the size of the spores is slightly too small ( $8-10 \mu$ ). Velenovský did not state whether the spores had a germ-pore or whether the basidia were 2- or 4-spored; the cystidia were "from the ellipsoid base long sharp pointed" (translation Dr. F. Kotlaba). It is less certain whether Velenovský's (1921: 501) *Pholiota blattaria* is *Conocybe arrhenii*. The size of the spores was given as  $9-10 \mu$  (which means they are even longer than those of Velenovský's *Galera togularis*!) and it is not stated whether the spores had a germ-pore and whether the basidia were 2- or 4-spored. The marginal cells were called "big, lageniform, thin pointed" (translation Dr. F. Kotlaba).

Rea (1922: 113) described as *Pholiota togularis* very clearly *Conocybe arrhenii*, giving the correct sizes of the spores ( $7-9 \times 3-4 \mu$ ), but unfortunately he quoted Ricken's data of *Pholiota togularis* (ss. Ricken) for the other microscopical details ("flattened germ-pore, cystidia fusiform,  $25-36 \times 6-8 \mu$ "), obviously having failed to notice Ricken's switching of the epithets. Vice versa, Rea (l.c.) in his description of his *Pholiota blattaria* (spores  $8-10 \times 4-5 \mu$ ) quoted Ricken's data of *Pholiota blattaria* (ss. Ricken) for the other microscopical details ("cystidia fusiform-subulate"). Orton (1960: 191) has already drawn attention to this error.



Overholts' descriptions of *Pholiota blattaria* (1924: 265 and 1927: 113) certainly pertain to *C. arrhenii*, but considerable doubt is justified as to whether *Pholiota togularis* as described by Overholts (1924: 266 and 1927: 114) really is *C. blattaria* and not an *Agrocybe*. The colours given are not very convincing for *C. blattaria*, the diameter of the cap is too large (10–40 mm) and Bulliard's Plate 595 fig. 2 (= *Agrocybe*) and Boudier's Plate 101 (= *C. arrhenii*) were quoted. But Overholts did not mention a smell and he stated "cystidia none," no doubt meaning the absence of pleurocystidia, which disfavours the interpretation as an *Agrocybe*. He, however, also referred to the plates given by Harper (1912: 1011, pl. 59) and Cooke (1884–1886: pl. 350/379), both, particularly the latter, obviously depicting *C. blattaria*. Konrad & Maublanc (1929: pl. 69 fig. 2) interpreted Overholts' description of *Pholiota togularis* as *C. blattaria*, but their description of *C. blattaria* really pertains to *C. teneroides*, which macroscopically very closely resembles *C. blattaria*.

V. *Conocybe arrhenii*, *C. aporos*, *C. arrhenii* var. *hadrocystis*.

In the literature the descriptions of the macroscopical characters of *Conocybe arrhenii* show a fair uniformity and expose the variability of this species. Out of the only eleven descriptions, partly under the specific epithet 'togularis' (Quélet, 1888: 96; Boudier, 1906: 51; Rea, 1922: 113; Konrad & Maublanc, 1929: pl. 69 fig. 1) partly as 'blattaria' (Ricken, 1912: 199; Overholts, 1927: 113; Bresadola, 1930: pl. 688; Kühner, 1935: 150; Kühner & Romagnesi, 1953: 343; Singer, 1950: 427; and Moser, 1967: 230) in which the size of the spores is given, only five (Overholts, Kühner, Kühner & Romagnesi, Bresadola, and Singer) mentioned the number of spores per basidium (always 4) and only four the germ-pore. There is a great divergence of opinion about the latter, so that in the light of our further discussion the pore cannot serve our purpose. Overholts merely indicated the possible presence of a germ-pore by saying that the apex of the pore is "sometimes slightly truncate," Konrad & Maublanc denied the presence of a germ-pore, Kühner spoke of a "pore indiscutable mais pas toujours évident," and Singer described the pore as being narrow or broad.

But six authors mentioned the presence and shape of the cheilocystidia (not including Rea, who in his description of 'togularis'—*C. arrhenii* in the present paper—quoted Ricken's description of the marginal cells in what is *Conocybe blattaria*!). The first description is by Ricken ("spindelig, pfriemlich" for what is *Conocybe arrhenii*!). Konrad & Maublanc called the cheilocystidia "cylindriques, sinueuses." In full accordance with both descriptions Kühner (1935: 150) described these cells as "filiforme, allongé, grêle," and Singer (1950: 427) as narrow and cylindrical.

In the *C. arrhenii*-group the longest-known species, *C. arrhenii* is therefore characterized microscopically by small spores and very narrow, cylindrical, and slightly flexuous marginal cells. They are very well depicted by Kühner (1935: 150), be it

not over their full length. Kühner is the only author to mention the width of the cells at the apex: 2–4.7  $\mu$ ; moreover he added that these cells are “parfois clavulé au sommet,” but none of the eight cells he depicted show this swollen apex.

It is thus very striking that J. E. Lange (1938: 62, pl. 106 A and A 1) described marginal cells with a conspicuously swollen apex (“coarsely hairshaped, apex slightly swelled up to 7  $\mu$ ”); also his species occurred “early in the season, May–April.” Earlier Lange (1921: 7) had already given a short and incomplete description of this species. In our material we have the same species (apex of the cheilocystidia 3–7  $\mu$ , occasionally 9  $\mu$ ) and all our nine Dutch collections and five out of eight Scottish collections were found either in March, April, or May; three Scottish collections were found early in June. Moreover we found that the spores never had a germ-pore (not mentioned by Lange). This species had already been noticed earlier in our country by Dr. C. Bas, who gave it the provisional name of ‘*Conocybe vernalis*’. On account of these three striking features (swollen apex of the cheilocystidia, absence of a germ-pore, and early occurrence) it is proposed to describe this as a new species—*Conocybe aporos*.

It is quite possible that this species had already been noticed by earlier authors and most certainly by Kühner himself. Quélet (1888: 96) for instance gave two separate periods of occurrence for *Hylophila togularis*: “printemps et fin d’automne.” Of *P. togularis* (= *C. arrhenii*) Boudier (1906: 51) said it occurred “généralement printanière mais aussi en automne,” Rea (1922: 113) gave May till November as time of occurrence, Konrad & Maublanc (1929: pl. 69 fig. 1) “printemps, été, automne,” and Singer (1950: 427, as *Pholiotina blattaria*) May till October. But the latter two authors did not describe the cheilocystidia as having swollen apices.

Kühner (1935: 155) certainly must have seen this species. In his observations on a species he described as *C. blattaria* forma *exannulata*, he said having found in May [!] specimens which had remnants of the veil on the cap, spores measuring 7.2–8.7  $\times$  4.2–5  $\mu$  and having no germ-pore [!], “l’extrémité de leurs poils d’arête souvent renflée en massue ou en tête de 5–12  $\mu$  de large [!]” and an “odeur parfois forte [!]. This description fully corresponds with ours of ‘dentate’ specimens of *C. aporos*, in which the veil instead of forming a ring had remained attached to the cap.

Bresadola (1930: pl. 688) described as *Pholiotina blattaria* yet another form of *C. arrhenii*. Its cheilocystidia were “clavato-cylindraceae, subcapitatae, 35–50  $\times$  12–18  $\mu$ ,” and its time of occurrence was not the spring, but the summer, and the species was “subinodora.” We have in our material two collections answering this description, on which we based *C. arrhenii* var. *hadrocystis*.

#### VI. *Conocybe blattaria* and *C. vexans*; *Conocybe teneroides* and *C. percincta*.

For the discussion on the interpretation of Orton’s *Conocybe vexans* (1960: 197) the reader is first of all referred to chapter III, at the end of which the macroscopic

characteristics of *C. blattaria* are given. As for the microscopic characteristics, the literature contains twelve descriptions (eleven authors) in which the size of the spores of that species is given as being c.  $9-12 \times 5-6 \mu$ : Quélet (1872: 319 and 1888: 96), Schroeter (1889: 608), Ricken (1912: 199), Harper (1912: 1011), Velenovský (1921: 552), Rea (1922: 113), Bresadola (1930: pl. 687), Kühner (1935: 161), Singer (1950: 431), Kühner & Romagnesi (1953: 343), Moser (1967: 230). Only Quélet (1872: 319) first mentioned  $8 \mu$ , later (1888: 96)  $10 \mu$ ; Bresadola (1930: pl. 687) mentioned  $7.5-10 \times 5-6 \mu$  and Rea (1922: 113)  $8-10 \times 4-5 \mu$ , but with these three authors the size is always larger than that of the spores of *C. arhenii* (either described as *C. togularis* or as *C. blattaria*). Ricken (1912: 199) was the first to mention the presence of a germ-pore, which he called very conspicuous and such a germ-pore was also described by Rea, Overholts, Bresadola, Kühner, Singer, Kühner & Romagnesi. Only three authors (Kühner, Singer, and Kühner & Romagnesi) mentioned the number of spores per basidium: 4.

The first description of the cheilocystidia is by Schroeter (1889: 608) who called them "unten bauchig, oben haarförmig"; he also gave a clear description of the macroscopic characters of this fungus and mentioned the large spores. Velenovský (1921: 552) called the cheilocystidia "from ellipsoid base long sharp pointed" (translation Dr F. Kotlaba) and Kühner (1935: 162) called them "ventruées, à partie supérieure atténuée ou contractée en un bec court et obtus" (clearly depicted by Kühner).

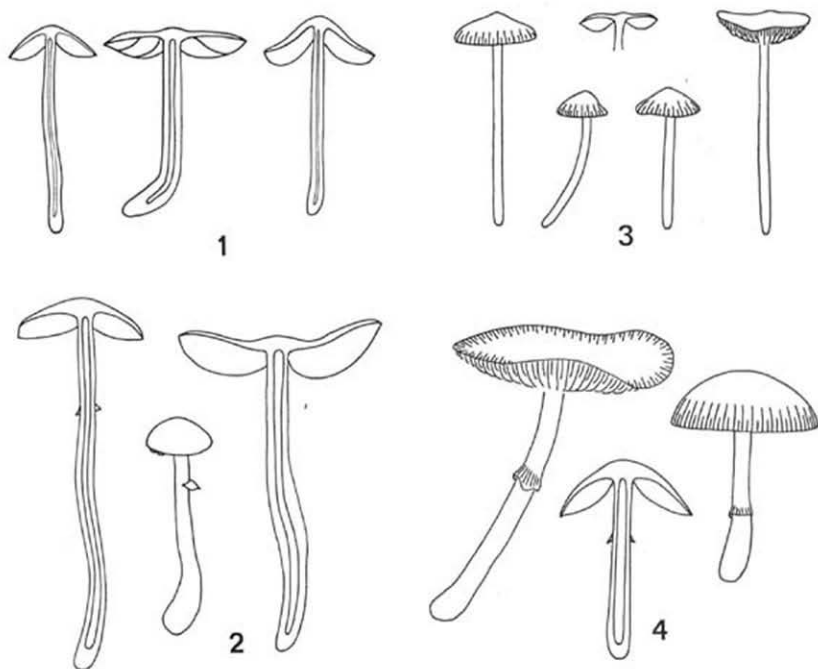
Since Fries' description of *C. blattaria* by its macroscopic characters, this taxon never caused any taxonomical problems, it was adopted by all post-Friesian authors, some of whom in the course of years added the microscopic characters (large spore-size and shape of cheilocystidia by Schroeter in 1889, large germ-pore by Ricken in 1912, basidia being 4-spored by Kühner in 1935). This is why we have rejected *Conocybe vexans* Orton, of which its author himself said, as indeed it is, that this species is identical with what Kühner had described as the 4-spored form of *C. togularis*, the latter, however, being just *Conocybe blattaria* as defined by us before.

Orton stressed in his description of *C. vexans* that the cap is "not or only slightly striate at margin only" and he believed that Ricken's *C. togularis* therefore must be his *C. vexans*, because Ricken "does not specify a striate cap and shows a strongly striate ring in his figure." Ricken, however, did call the cap striate ("durchscheinend gerieft"), and his Pl. 56, fig. 5 does show conspicuously striate caps and the rings of all annulate species of *Conocybe* are beautifully striate-plicate. Besides—as was reasoned in our chapter on morphology—the striation of the cap is of no taxonomic value.

There is one very characteristic species in the annulate group of *Pholiotina*, *Conocybe teneroides*, of which only six descriptions can be found in the literature: J. E. Lange (1921: 7, as *Pholiota teneroides*), Konrad & Maublanc (1929: pl. 69 fig. 2 as *Pholiota blattaria*, which they considered to be conspecific with *C. teneroides*), Kühner and Maire apud Kühner (1935: 162 as *C. teneroides*, but see p. 141), J. E. Lange (1938: 63,

pl. 106 B as *Pholiota teneroides*), and Singer (1950: 431 as *Pholiotina togularis* f. *bispora*, which he considered to be synonymous with *C. teneroides*). The macroscopic characters as described in each of these six descriptions resemble each other very much indeed and they can hardly be distinguished from those of *C. blattaria*. All six descriptions mention two very striking microscopic characteristics, which are quite different from those of *C. blattaria*, i.e. 2-spored basidia and strikingly variable cheilocystidia, the shape of which besides differs considerably from that in any other member of the group. Lange called these cystidia "cylindric, flask-shaped, obtuse," Konrad & Maublanc "fusiformes en forme de bouteille, à sommet obtus," Kühner "claviformes, non rétrécies en col au sommet," also "cylindraccés ou subclaviformes à sommet arrondi obtus," Maire "fusiformes," Singer "flask-shaped, cylindric, clavate."

There is another description, really the seventh in this series that is the one of *C. percincta* Orton, of which the macroscopic characteristics are identical with those described for *C. teneroides* and like *C. teneroides* it has 2-spored basidia and extremely



Figs. 1-4. *Conocybe aporos*, habit sketches. — 1. Overveen, 22 April 1961. — 2. Dorst, 2 April 1957. — 3. Santpoort, Duin en Kruidberg, 2 June 1962. — 4. Amsterdam, Amsterdamse Bos, 30 April 1965, holotype. (All figs.:  $\times 1$ .)

variable and curiously shaped cheilocystidia, which Orton has described as "obtuse, cylindrical-clavate, utriform or irregular fusiform." Except for Singer all authors gave pictures of these cystidia. The inevitable conclusion is that *C. percincta* Orton is conspecific with *C. teneroides*.

A few points, concerning Orton's description of *C. percincta*, however, need discussion.

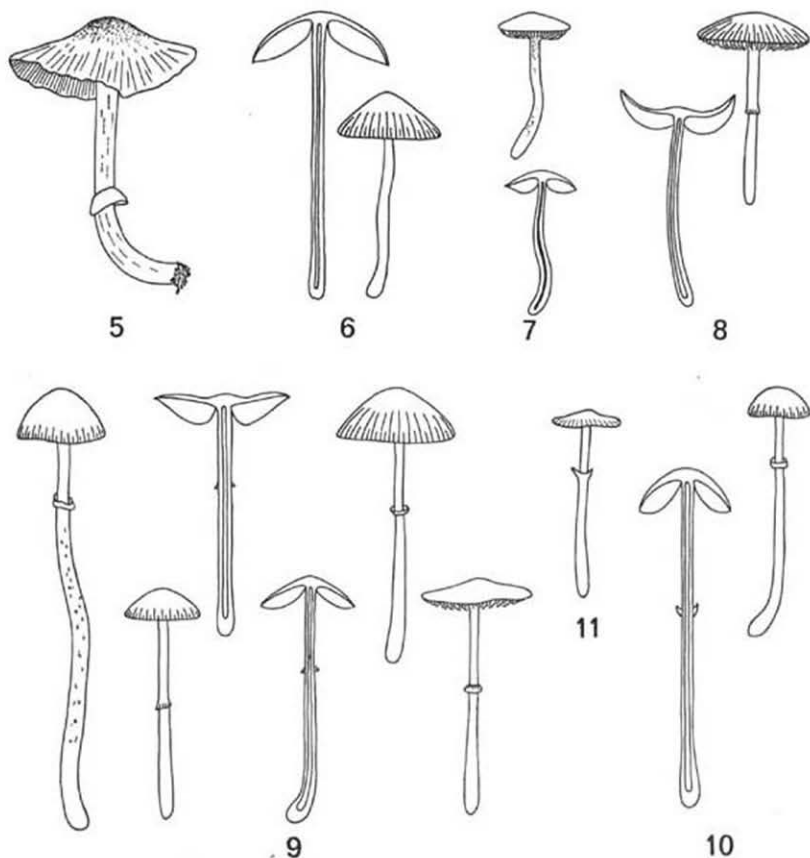
Orton concludes his description by saying that his species is "distinguished from its allies by yellowish ring, dark flesh in stem, obtuse marginal cystidia and spore size," thereby curiously enough leaving unmentioned the two major and very striking characteristics, the 2-spored basidia and curious cheilocystidia. However, in the actual description, the ring is called "pale yellowish," but in the description of *C. vexans* (= *C. blattaria*), certainly an ally and even its closest, the ring has the same colour, "pale dirty yellowish" and we found the ring in *C. blattaria* (also in *C. filaris*) whitish to even pale brown. Next, the flesh of the stems of all annulate species of the *Pholiotina* group is dark and even very dark to fuliginous brown in the lower part of the stem in mature specimen. For the spore size Orton gives  $10-12 \times 5-6 \mu$  for *C. percincta* and  $10-12 \times 6-6.5 \mu$  for *C. vexans* (= *C. blattaria*), so here there hardly is a difference either. The cystidia, indeed, are "obtuse," but their very striking and very variable shape is left unmentioned.

The size of the cap as given and depicted by Orton is rather large (12-38 mm), whereas Kühner mentions only 10-16 mm, Maire 10-12 mm and the caps of our own specimens also were small, 6-13 mm. This difference, we at first thought, might have some significance, but it has not, as Lange reported 15-20 mm and Konrad & Maublanc even 20-30 mm.

The gills in Orton's description are called crowded and, indeed, he found 34-40 large gills. But Kühner, while not actually stating anything about the gills being either crowded or not, counted only 23-28 large gills and would not have called these crowded, as even in *C. arhenii* ("*blattaria*"), where he counted 26-35 large gills, he called them "moyennement serrées." Perhaps there were so many gills in Orton's specimens because they were so large.

With regard to the striation of the cap—an unreliable character, as pointed out in the chapter on morphology—, we found that Orton in his exposition partly based some of his arguments in favour of his interpretation of *C. vexans* and *C. percincta* on some misquotations. Orton said the cap of *C. togularis* "forme tetrasporique" (= *C. blattaria*) as described by Kühner was "usually non-striate," but in fact Kühner called it "striolé" (meaning: somewhat striate). He further said, having retained the epithet 'blattaria' for what Kühner had called *C. togularis* "forme bisporique" (= *C. teneroides*) "since this is stated to have a striate cap in the description of Maire and Lange." But Lange did not mention the striation at all, neither does his picture (Pl. 106 B) show any trace of striation. Orton called the caps of *C. percincta* "not striate when moist." Judging, however, from Orton's description of the colour of the cap ("pale yellow, deeper ochre-yellow at centre, then honey or tinged date-brown,") he may well have dealt with specimens which already

were in the act of drying. It is extremely unlikely that any of the annulate species of the *Pholiotina* group should be non-striate in the moist phase. Konrad & Maublanc recorded striate caps and Kühner, very prudently, stated of the cap of *C. teneroides* "non vu strié."



Figs. 5-10. *Conocybe arrhenii* var. *arrhenii*, habit sketches. — 5. Gronsveld, Savelsbos, 26 Oct. 1958. — 6. Castricum, 28 Sept. 1968. — 7. 's-Graveland, Bockestejn, 8 Nov. 1968. — 8. 's-Graveland, Bockestejn, 8 Nov. 1968. — 9. Apeldoorn, 11 Oct. 1969. — 10. Apeldoorn, 12 Oct. 1969. (All figs.:  $\times 1$ .)

Fig. 11. *Conocybe arrhenii* var. *hadrocystis*, habit sketch. Nieuwersluis, Over-Holland, 30 Sept. 1967, holotype. ( $\times 1$ .)

In conclusion, we agree with Lange that *C. teneroides* is a species in its own right. Kühner (1935: 162) apparently favoured an intermediate point of view; it is true that technically he made the recombination *Conocybe teneroides*, but he obviously did not accept this taxon as a species, as he interpreted it as a bisporous form of *C. "togularis"* (= *C. arrhenii*). Therefore, his recombination is not valid. His figures very clearly show the difference in shape of the cheilocystidia between his 4- and 2-spored forms of this species. Kühner & Romagnesi (1935: 343) mentioned *C. teneroides* as a separate species, adding "N'est probablement que la f. bisporique du *C. togularis* (ss. Ricken) Kühn." Singer (1950: 431) regarded this species as only a 2-spored form of *C. blattaria* ("*togularis*").

Konrad & Maublanc (1929: pl. 69 fig. 2) particularly stressed the point that what they described as *P. blattaria* is synonymous with *P. teneroides* Lange and from this it should be concluded that they found its basidia to be 2-spored, although they did not specifically say so in their description. Orton, in spite of this, interpreted the species described by Konrad & Maublanc as his 4-spored *C. vexans* for the same reasons as he believed *Pholiotia togularis* as described by Ricken to be his *C. vexans*, i.e. cap not clearly striate and ring strongly striate. As we pointed out previously, both reasons are not valid, neither for *C. togularis* ss. Ricken, nor for Orton's *C. vexans*. Orton evidently overlooked the fact that Konrad & Maublanc's specimens must have been 2-spored.

*C. teneroides* must be a very rare species and one must bear in mind that each of the six authors mentioned has only seen one or two collections, calling the species "rather rare," or "assez rare." We have found it only once. It would therefore be impossible from one collection to study adequately the striking shape of the cheilocystidia and the evidently even more striking variability of this shape. Only Singer found this species more often, once in the Caucasus, once in the Altaj (Russia), also in Germany, Spain, and Australia, and he believed that this species probably occurs more often in the Soviet Union. According to Dr. Watling (personal communication) it is not uncommon in the British Isles.

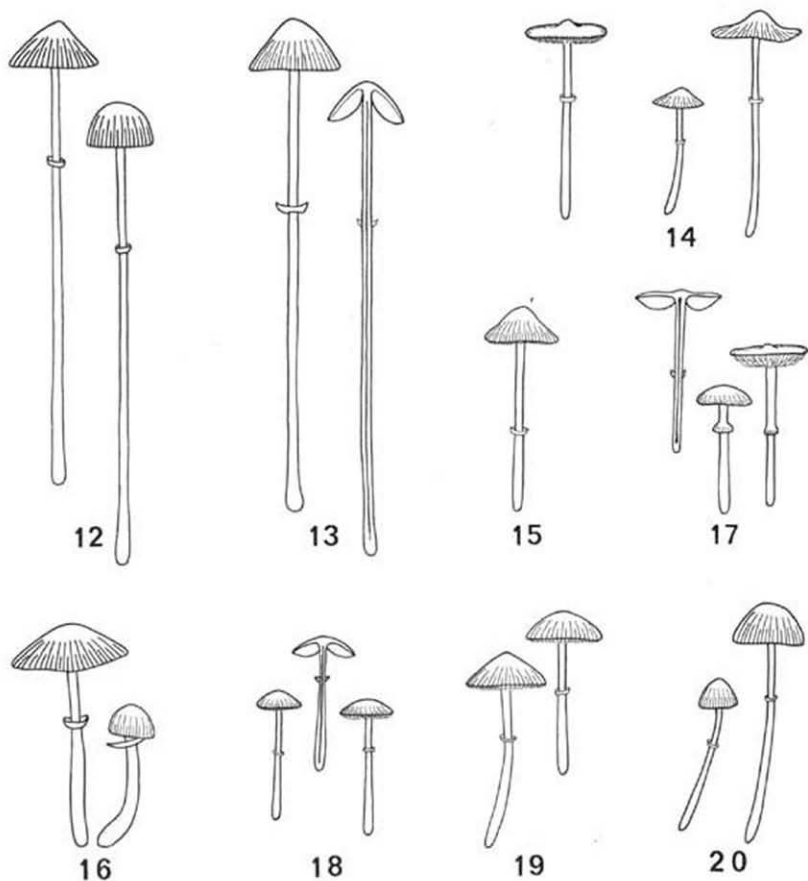
The interpretation of *C. blattaria*, mentioned by Orton (1960: 192) in his key remains obscure. Under item 3 of the key the alternative choice is between *C. blattaria* and on the other hand *C. vexans* and *C. percincta* of item 4. But the differences between the macroscopic characters figuring in both items and advocated for the specific delimitation are too unreliable and vague. The colours of the cap and stem and particularly of the cap are—as argued in the chapter on morphology—too variable to go by in *Pholiotina*; besides under item 3 they are only called "frequently paler" for *C. vexans* and *C. percincta* (item 4) as compared with *C. blattaria*. Neither the striation of the cap (hardly different for *C. blattaria* as compared with the two species of item 4) nor the floccose scaliness of the stem can be used for specific delimitation in this group of fungi, as outlined in the chapter on morphology. Neither does the ring, being "sometimes rather small or only striate where it joins the stem" in *C. blattaria* as opposed to being "well formed, often strongly striate" in the two species of item 4 furnish a distinct difference. Far more important, however,

are the microscopic characters, but close scrutiny of the key reveals that both *C. blattaria* and *C. percincta* have large spores and 2-spored basidia (curiously enough, in the key the basidia of *C. percincta* are called 2-spored or 2-3(-4)-spored, whereas in the full description of the species they are just 2-spored and the cheilocystidia of *C. blattaria* are "variable, clavate, utriform or lageniform" and of *C. percincta* "cylindric-clavate or utriform or irregular fusiform-lageniform." Orton (1960: 191) said, having "retained the epithet 'blattaria' for *C. togularis* forme bisporique Kühn. (= *Pholiota teneroides* J. Lange)." So both *C. percincta* (as argued above) and *C. blattaria* sensu Orton are conspecific with *C. teneroides*.

## KEY TO THE SPECIES

1. Velum parziale forming a distinct ring about half-way the stem or in upper half of the stem (in *C. arrhenii* var. *arrhenii* and *C. aporos* sometimes forming appendiculate denticles on margin of cap instead of a ring).
  2. Spores (9.9-)10.8-12.6 × 5.3-6.4 μ, germ-pore conspicuous.
    3. Basidia 2-spored, cheilocystidia very variable, globose, subcylindrical, clavate, obovoid, utriform (Figs. 49, 52) . . . . . *C. teneroides*
    3. Basidia 4-spored or sometimes 4- and 2-spored on same gill, cheilocystidia lageniform, obclavate or sicyoid and much more uniform.
      4. Basidia exclusively 4-spored; cheilocystidia sicyoid (neck cylindrical, distinctly delimited from ventricose cell-body) or lageniform, obclavate (neck tapering towards acute or subacute apex (Figs. 38, 41); tall species (stem 40-70 mm).  
*C. blattaria*
      4. Basidia both 2- and 4-spored and consequently spores both large (10.8-12.6 × 5.4-6.8 μ) and small (8.1-9.9 × 4.5-5.4 μ); cheilocystidia obclavate, lageniform, neck tapering towards acute or obtuse apex, not or indistinctly delimited from cell-body (Figs. 44-46); small species (stem 15-35 mm) . . . . . *C. filaris*
  2. Spores (6.8-)7.2-9.9 × 4.1-5.4 μ, germ-pore conspicuous, very small or absent.
    5. Cheilocystidia obclavate, lageniform, never capitate or subcapitate, neck tapering towards acute or subacute apex, not or indistinctly delimited from cell-body (Figs. 44-46); stem 1-1.5 mm thick, small species (cap 6-20 mm) . . . . . *C. filaris*
    5. Cheilocystidia different; stem 1.5 mm thick or thicker, larger species (cap 11-40 mm).
      6. Cheilocystidia filiform; subcylindric, lageniform, with elongated and often flexuose neck, few subcapitate (Figs. 32, 33), 22.5-50 × 2.5-7.5 × 1.5-4(-5) μ; veil usually forming a ring, sometimes only appendiculate denticles on margin of cap, Sept.-Nov. . . . . *C. arrhenii* var. *arrhenii*
      6. Cheilocystidia thicker and capitate (Figs. 30, 31, 34).
        7. Germ-pore present but small; cheilocystidia 25-50(-55) × 5-9(-10) × 5-15 μ, Sept.-Nov. . . . . *C. arrhenii* var. *hadrocystis*
        7. Germ-pore absent; cheilocystidia 22.5-60 × 4-12.5 × 3-9 μ; veil usually forming a ring, sometimes only appendiculate denticles on margin of cap; March-May . . . . . *C. aporos*
1. Velum parziale incomplete, never forming a distinct ring, but leaving remnants on lower half of stem or volva-like remnants at base of stem (hitherto not reported from Europe and only from Algiers; for description, see Kühner, 1935: 157) . . . . . *C. pezonata*





Figs. 12, 13. *Conocybe blattaria*, habit sketches. — 12. Braemar, Invercauld Estate, 28 Aug. 1961. — 13. Tomich, 17 Sept. 1968.

Figs. 14-19. *Conocybe filaris*, habit sketches. — 14. Oldenzaal, Dijkhuis, 16 Oct. 1963. — 15. 's-Graveland, Boekestejn, 3 Aug. 1968. — 16. 's-Graveland, Boekestejn, 25 Sept. 1968. — 17. 's-Graveland, Boekestejn, 3 Oct. 1968. — 18. 's-Graveland, Boekestejn, 8 Nov. 1968. — 19. Santpoort, Duin en Kruidberg, 1 Dec. 1960.

Fig. 20. *Conocybe teneroides*, habit sketch. Santpoort, Duin en Kruidberg, 1 Dec. 1960.

**Conocybe aporos** Kits van Wav., *sp. nov.*

Figs. 1-4, 21-24, 30, 31

MISAPPLIED NAME: *Pholiota togularis* (Bull. ex Fr.) Quéf. *sensu* J. E. Lange in Dansk bot. Ark. 2 (11): 7. 1921; Fl. agar. dan. 3: 63, pl. 106 fig. A, A 1. 1938.

SELECTED DESCRIPTION AND ILLUSTRATION.—J. E. Lange, Fl. agar. dan. 3: 63, pl. 106 fig. A, A 1. 1938 (*P. togularis*).

Pileus 12-40 mm latus, primo semiglobatus vel campanulatus, dein convexus vel plano-convexus vel plano-concavus, subumbonatus, striatus, centro obscure fulvus (Munsell 5 YR 3/4, 4/3, 4/4) vel fuscus (Munsell 7.5 YR 4/2), marginem versus brunneus vel ochraceo-brunneus (Munsell 7.5 YR 4/4, 5/4, 6/6), laevis vel interdum rugulosus, hygrophanus, sine velo.

Stipes 21-52 × 1.5-4 mm, cylindræus, ad basin paulo incrassatus, 4-5 mm, etiam clavatus, striatura superficiali argenteo-albella ornatus, apice pallide cinnamomeus, deorsum brunnescens, ad basin atro-fuliginæus, apice albo-pruinoseus.

Annulus sat amplus, distans medius, superne striato-plicatus.

Lamellæ 27-38, confertæ, ventricosæ, angustæ vel perangustæ adnæxæ, 3-5.5 mm latæ, obscure ochraceo-brunnæ (Munsell ± 10 YR 5/4), ad aciem flocculoso-denticulatæ, albæ.

Caro in pileo 2-3 mm crassa, obscure fulva, in stipitis parte apicali cinnamomea, deorsum brunnescens, ad basin atrobrunnea, odore nullo vel aciduloso vel *Pelargonii*.

Sporæ (7.2-8.1-9.9 × 4.5-5.4 μ, ellipsoideæ, subamygdaliformes, sub microscopio citrinæ, apiculo parvo, poro nullo. Basidia (19-)21-27.5(-30) × (5-6-7.5(-9) μ, 4-sporigera. Pleurocystidia nulla. Cheilocystidia 22.5-60 × (3-)5-10(-11) × 3-7(-9) μ, copiosa, conferta (qua de causa lamellarum acies sterilis), subcylindrica vel sublageniformia, sæpe flexuosa vel irregularia, apicibus incrassatis. Pilei cuticula e cellulis clavatis vel vesiculososis longe stipitatis sæpe ochraceis formata.

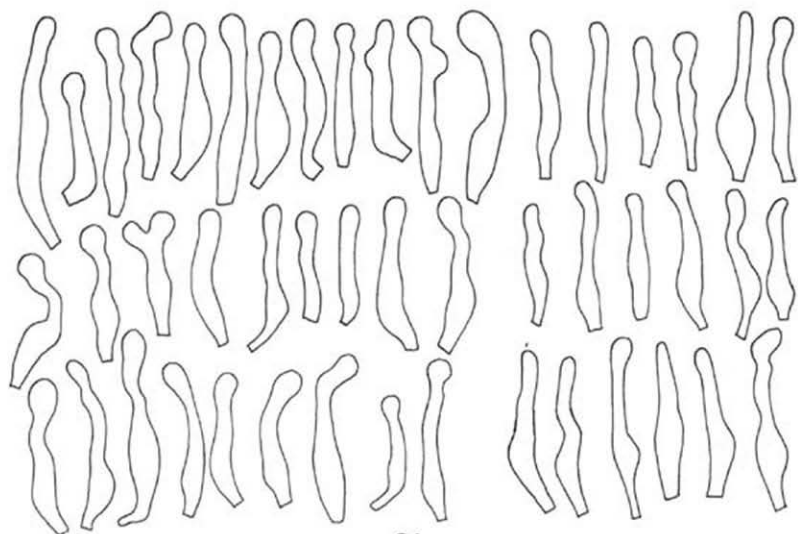
Terricola, vernalis, mensibus III-V inventa.

Typus: Amsterdam, Amsterdamse Bos, 30 Apr. 1965, *E. Kits van Waveren* (L).

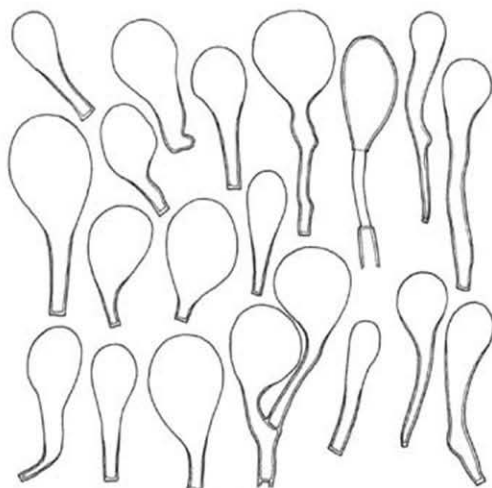
MACROSCOPIC CHARACTERS.—Cap 12-40 mm, at first semiglobate to campanulate, more rarely conico-campanulate, soon convex, then plano-convex and even plano-concave, often subumbonate, when moist striate from margin in to 1/4-2/3 of radius of cap, surface smooth but sometimes slightly rugulose, very slightly viscid when moist, the centre dark reddish-brown (M. 5 YR 3/4, 4/3, 4/4) to dark brown (M. 7.5 YR 4/2) towards the margin brown or ochre-brown (M. 7.5 YR 4/4, 5/4, 6/6); hygrophanous, leaving central half ochre-brown (M. 7.5 YR 6/6) and the peripheral half yellowish (M. 10 YR 7/6; 2.5 Y 8/4) striae disappearing. Marginal veil as a rule absent.

Stem 21-52 × 1.5-4 mm, equal, at the base slightly thickened (4-5 mm) or even clavate, hollow, non-rooting, very pale yellowish-brown at the apex, increasingly brown towards the base and dark fuliginous brown in the lower part (1/2-1/3) of the stem and particularly at the base, these colours being partly masked by a silvery-whitish, somewhat shining, fibrillose-striate layer, often disjointed below the ring and covering the entire stem, the apex over a variable distance pruinose.

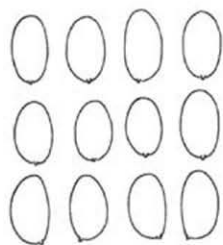
Velum partiale large, cuff-like, usually descending, about midway or even slightly lower down the stem, felt-like, white or orange-brown from spore-deposits, coarsely striate-plicate above. Occasionally the veil, instead of forming a ring, remains along the entire margin of the cap as small white denticles, either appendiculate or upturned or stuck to the surface of the cap very close to the margin.



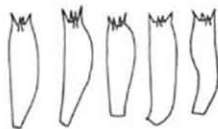
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23



24

Figs. 21-24. *Conocybe aporos* (Amsterdam, Amsterdamse Bos, 30 April 1965). — 21. Cheilocystidiogram. — 22. Cells of surface of cap. — 23. Spores. — 24. Basidia. (Figs. 21, 22, 24:  $\times 575$ ; Fig. 23:  $\times 1212$ .)

Gills crowded, numerous (L 27-38), ventricose, narrowly to very narrowly adnexed, 3-5.5 mm broad, dark ochre-brown (M.  $\pm$  10 YR 5/4), edge flocculose-denticulate, white.

Flesh in the centre of the cap rather thick, up to 2-3 mm, dark reddish-brown, dirty pale yellowish when dry, in stem pale yellowish-brown at apex, increasingly brown towards the base, very dark brown to blackish-brown at the base.

Smell sometimes none but usually, particularly after bruising and particularly in young specimens, distinctly acidulous or pelargonium-like.

MICROSCOPIC CHARACTERS.—Spores ellipsoid to slightly amygdaliform, yellow (M. 2.5 Y 7/6; 5 Y 8/6), with a trace of red in water, apiculus small, germ-pore absent, wall of normal thickness (7.2-8.1-9.9  $\times$  4.5-5.4  $\mu$ ).

Basidia 4-spored, (19-)21-27.5(-30)  $\times$  (5-)6-7.5(-9)  $\mu$ . Cheilocystidia closely packed (edge of gill sterile or with only scattered basidia), subcylindrical, sublageniform to lageniform, often irregularly shaped and/or flexuose, the apex conspicuously swollen, colourless, the wall of normal thickness, 22.5-60  $\times$  (3-)5-10(-11)  $\times$  3-7.5(-9)  $\mu$ , in between them often a small number of small spheropedunculate cells. Pleurocystidia none.

Cuticle of cap hymeniform, for full description, see p. 126.

Superficial hyphae of stem, for full description, see p. 126.

HABITAT.—On clayey or rich soil in deciduous woods (*Quercus*, *Salix*, *Populus*) and orchards, gardens, parks, along roadsides; solitary or in small groups, rarely gregariously in large groups. March to May. Uncommon.

#### COLLECTIONS EXAMINED.

##### NETHERLANDS

Noord-Holland: Amsterdam, Amsterdamse Bos, 1 May 1961, *E. Kits van Waveren* (L); 30 Apr. 1965, *E. Kits van Waveren* (type, L); Overveen, 22 Apr. 1961, *J. van Brummelen* (dentate form, L); Santpoort, Estate Duin en Kruidberg, 2 June 1962, *E. Kits van Waveren* (dentate form, L).

Noord-Brabant: Dorst, 20 Apr. 1954, 5 May 1955, 6 May 1965, 14 March 1966, *P. B. Jansen* (L); Dorst, 2 Apr. 1957, *C. Bas* (L); Baarle-Nassau, 2 May 1965, *P. B. Jansen* (L).

Limburg: 5 Apr. 1967, Eysder Bos, *P. B. Jansen* (L).

##### BRITISH ISLES

Perthshire: Loch Rannoch, 13 May 1967, *P. D. Orton* 2945 (E); Camghouran, 14 May 1967, *P. D. Orton* 2946 and 2947; 24 May 1967, *P. D. Orton* 2937 (E); Rannoch, 26 May 1967, *P. D. Orton* 2938 (E); Trinafon, 4 June 1967, *P. D. Orton* 2939 (E); Dall, 7 June 1967, *P. D. Orton* 2940 (E); Camghouran, 11 June 1967, *P. D. Orton* 2941 (E).

OBSERVATIONS.—For nomenclatural discussion, see p. 135.

The spores of this species when compared with those of *C. arrhenii*, apart from lacking a germ-pore are also very slightly larger, the difference being very small but real. This conclusion is based on the evidence of 20 measurements in each of six collections of *C. arrhenii* and each of eight collections of *C. aporos*. Accordingly, the basidia in *C. aporos* were also found to be very slightly larger. The cheilocystidia of *C. aporos* are not only capitate, but also slightly thicker than those of *C. arrhenii*.

Like in the description of *C. arrhenii*, we wish to stress the point that it is extremely misleading when the velum parziale, instead of forming a ring, fails to do so and

remains as appendiculate denticles on the margin of the cap. In attempting to identify such specimens one might very easily be led into the group of exannulate species of *Pholiotina*, some of which may have irregularly shaped and even capitate cheilocystidia. In the species of that group, however, a germ-pore is always present (except in *C. vestita*) and the species do not exclusively occur in the spring.

***Conocybe arrhenii* (Fr.) Kits van Wav., comb. nov.**

*Agaricus arrhenii* Fr., Epicr. 161. 1838 (basonym); Monogr. 307. 1857. — *Pholiota arrhenii* (Fr.) Quél. in Mém. Soc. Emul. Montbél. 2: 248. 1872.

*Agaricus mesodactylus* Berk. & Br. in Ann. Mag. nat. Hist. II 2: 261, pl. 9 fig. 1. 1848.

MISAPPLIED NAMES.

*Agaricus togularis* Bull. ex Fr. sensu Fr., Hym. europ. 216. 1874. — *Hylophila togularis* (Bull. ex Fr.) Quél., Fl. mycol. 96. 1888.

*Agaricus blattarius* Fr. sensu Cooke, Ill. Brit. Fungi, pl. 1172 B / 1173 B. 1889-1891. — *Pholiota blattaria* (Fr.) Ricken, Blätterp. 199, pl. 56 fig. 3, 1915. — *Conocybe blattaria* (Fr.) Kühn., Le Genre Galera 150. 1935.

SELECTED DESCRIPTIONS AND ILLUSTRATIONS.—Berk. & Br. in Ann. Mag. nat. Hist. II 2: 261, pl. 9 fig. 1. 1848 (*A. mesodactylus*); Cooke, Ill. Brit. Fungi: pl. 1172 B / 1173 B. 1889-1891 (*A. blattarius*); Boudier, Icon. mycol., Sér. 4, Livrais. 18: 3 pl. provis. 325. 1908 (= 1: 51; 2: pl. 101. 1904-11) (*P. togularis*); Ricken, Blätterp. 199, pl. 56 fig. 3. 1915 (*P. blattaria*); Konr. & Maubl., Icon. sel. Fung. 1: pl. 69 fig. 1. 1929 (*P. togularis*); Bresadola, Icon. mycol. 14: pl. 688. 1930 (*P. blattaria*); Kühner, Le Genre Galera 150. 1935 (*C. blattaria*).

OTHER DESCRIPTIONS.—Patouillard, Tab. anal. Fung. 4: 154, pl. 112. 1885 (*A. togularis*); Saccardo, Syll. Fung. 5: 738. 1887 (*P. togularis*); Peck in Bull. N.Y. St. Mus. 122: 145. 1908 (*P. togularis*); Rea, Brit. Basid. 113. 1922 (*P. togularis*, except description of germ-pore and cystidia, misquoted from Ricken); Overholts in N. Am. Fl. 10 (4): 265. 1924 (*P. blattaria*); Overholts in Ann. Mo. bot. Gdn 14: 113. 1927 (*P. blattaria*); Singer in Acta Inst. bot. Acad. Komar. Sci. URSS, Ser. 2 (Pl. crypt.) 6: 427. 1950 (*P. blattaria*); Kühn. & Romagn., Fl. anal. 343. 1953 (*C. blattaria*); Orton in Trans. Br. mycol. Soc. 43: 192. 1960 (*C. togularis*); Moser in Kl. Kryptfl., Ed. 3, 2 (B/2): 230. 1967 (*P. blattaria*).

MACROSCOPIC CHARACTERS.—Cap 11-30 mm, at first campanulate, soon convex and often subumbonate, rarely distinctly umbonate, finally appanate or even plano-concave with upturned margin; surface smooth, often faintly to distinctly rugulose; when entirely moist or not or only slightly striate (but sometimes striate from margin up to 1/3-1/4 of radius of cap), dark reddish-brown or purplish-brown (M. 2.5 YR 2/4; 5 YR 3/3, 3/4, 4/3), near the margin browner (M. 5 YR 4/4) and at the margin just brown (M. 7.5 YR 5/6); when only slightly less moist or when striate, centre (and striae) reddish-brown or purplish-brown and towards the margin of the cap (between the striae) yellowish-brown (M. 7.5 YR 5/6, 6/6; 10 YR 5/6) and near the margin sometimes brownish-yellow (10 YR 6/6, 7/6), the centre remaining darker (M. 10 YR 6/8, 8/8), the striae disappearing. Marginal veil as a rule absent (but see below).

Stem 17-62 × (1-)1.5-3(-4) mm, equal, often slightly and gradually thickening at the base, firm, hollow, non-rooting, covered by a thin but dense fibrillose-striate silvery whitish layer in the upper half, becoming thicker in the lower half, sometimes

even flocculose to scaly-fibrillose and usually disjointed or even partly disappearing, exposing the colour of the stem. This colour, partly masked by the whitish layer, is very pale brown (M. 10 YR 8/3) at the apex, becomes increasingly brown towards the base, dark reddish-brown to fuliginous brown in the lower  $1/4-1/3$  of the stem and blackish-brown at the base. Stem slightly to coarsely pruinose above the ring or only at the apex.

Velum parziale almost always forming a very conspicuous cuff-like ring, which is large, descending but sometimes ascending, located about midway or either higher up or even slightly lower down the stem, felt-like, whitish to cream-colour, upper surface coarsely striate-plicate and usually orange-brown because of spore-deposits. Occasionally the veil, instead of forming a ring, remains along the entire margin of the cap as small white denticles, either appendiculate or upturned or stuck to the surface of the cap very close to the margin, rarely somewhat higher up or even close to the centre of the cap.

Gills crowded (L 26-33), ventricose, narrowly and sometimes very narrowly adnexed, 2-4 mm broad, ochre- or yellowish-brown (M. 7.5 YR 5/6; 10 YR 5/4-5/6), edge flocculose-denticulate, white.

Flesh in centre of the cap 0.75-1.5 mm thick, very thin near the margin, dark reddish-brown or very dark brown (M. 5 YR 3/3, 3/4; 10 YR 3/4) in the cap, in the stem pale brown (M. 2.5 Y 8/2, 8/4) at the apex, very soon becoming darker towards the base, very dark brown to reddish-brown in the lower half and fuliginous blackish-brown at the base.

Smell none.

MICROSCOPIC CHARACTERS.—Spores ellipsoid to slightly amygdaliform, yellow (M. 2.5 Y 7/6, 8/6; 5 Y 7/6, 8/6) with a trace of red in water, apiculus small, germ-pore small and inconspicuous, (6.8-)7.2-8.1(-9)  $\times$  4.1-4.5(-5)  $\mu$ .

Basidia 4-spored, 17.5-25  $\times$  5-7.5  $\mu$ .

Cheilocystidia closely packed (edge of gill sterile or with only scattered basidia), filiform, subcylindric, sublageniform to lageniform, rarely subcapitate, often irregularly shaped and/or flexuose, colourless, wall of normal thickness, 22.5-50  $\times$  2.5-7.5(-9)  $\times$  1.5-4(-5)  $\mu$ .

Pleurocystidia none.

Cuticle of cap hymeniform (for full description, see p. 126), cells 27.5-60  $\times$  8-27.5  $\mu$ .

Superficial hyphae of stem below ring, for full description, see p. 126.

HABITAT.—On clayey or rich soil in deciduous woods (*Quercus*, *Salix*, *Populus*) and orchards, gardens, parks, along roadsides; solitary or in small groups. September to early November. Uncommon.

CONOCYBE ARRHENII var. ARRHENII—Figs. 5-10, 25-29, 32, 33

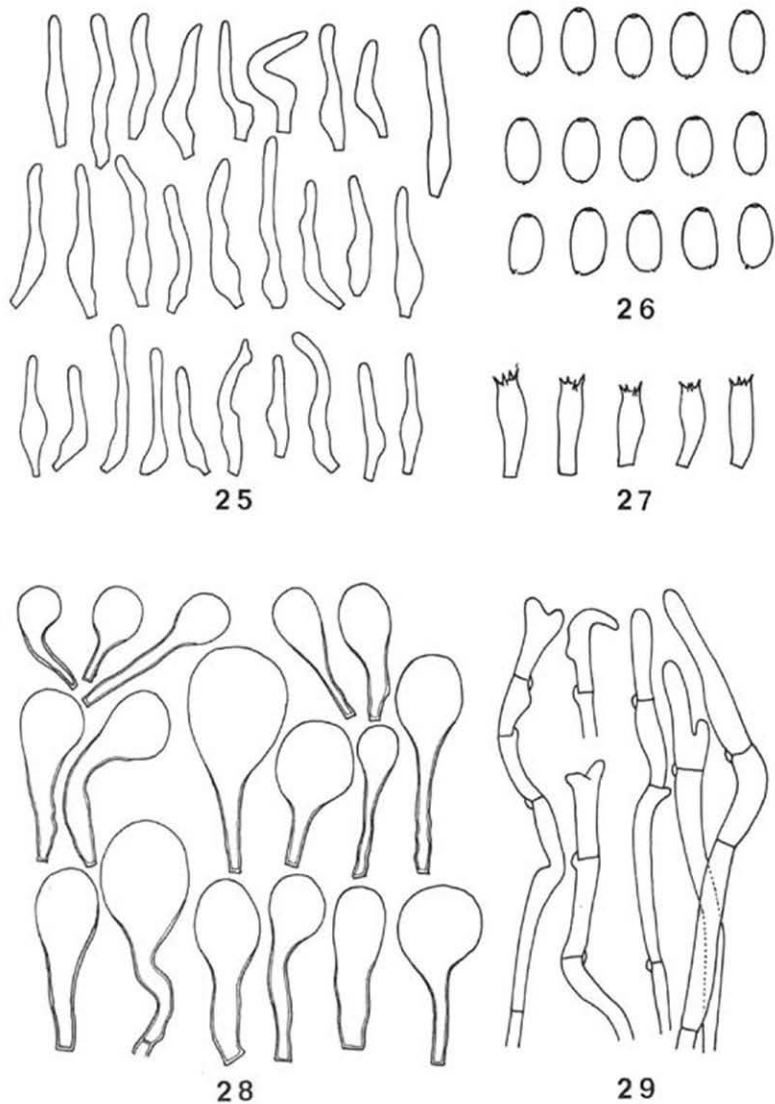
For synonymy, see p. 147.

MICROSCOPIC CHARACTERS.—Cheilocystidia filiform, subcylindric, sublageniform to lageniform, rarely subcapitate, often irregularly shaped and/or flexuose, 22.5-50  $\times$  2.5-7.5(-9)  $\times$  1.5-4(-5)  $\mu$ .

COLLECTIONS EXAMINED.

NETHERLANDS

G e l d e r l a n d: Apeldoorn, Royal Estate, 11 Oct. 1969, *E. Kits van Waveren* (L).  
N o o r d - H o l l a n d: Amsterdam, Amsterdamse Bos, 7 Nov. 1959 and 26 Oct. 1961, *E. Kits van Waveren* (L); Castricum, Dunes of County Watersupply, 28 Sept.



Figs. 25–28. *Conocybe arthenii* var. *arthenii* (Amsterdam, Amsterdamse Bos, 26 Oct. 1961). — 25. Cheilocystidiogram. — 26. Spores. — 27. Basidia. — 28. Cells of surface of cap. (Figs. 25, 27, 28:  $\times 575$ ; Fig. 26:  $\times 1212$ .)

Fig. 29. *Conocybe arthenii* var. *arthenii* (Lake Vyrnwy, 10 Sept. 1960). Hyphae of stem. ( $\times 575$ .)

1968 *E. Kits van Waveren* (dentate form, L); 's Graveland, Estate Boekesteijn, 8 Nov 1968, *E. Kits van Waveren* (both annulate and dentate forms, L).

Limburg: Gronsveld, 26 Oct. 1958, *R. A. Maas Geesteranus* (L); Mook, near Plasmolen, 23 Oct. 1964, *E. Kits van Waveren* (L).

#### BRITISH ISLES

Montgomeryshire: Lake Vyrnwy, 10 Sept. 1960, *E. Kits van Waveren* (L).

Morayshire: Darnaway, 24 Sept. 1955, *P. D. Orton* 615 (E).

CONOCYBE ARRHENII var. **hadrocystis** Kits van Wav., *nov. var.*  
Figs. 11, 34-37

MISAPPLIED NAME (but good description and illustration).

*Pholiotia blattaria* (Fr.) Quél. *sensu* Bres., *Icon. mycol.* 14: pl. 688. 1930.

A var. *arrhenii* differs cheilocystidiis latioribus, 5-9(-10)  $\mu$ , et apice distinctissime clavato-capitatis, 5-15  $\mu$ .

Typus: Nieuwersluis, Over-Holland, 30 Sept. 1967, *E. Kits van Waveren* (L).

This variety differs from the typical variety by the more irregular and very variable shape of the cheilocystidia, which besides are broader, 5-9(-10)  $\mu$ , and above all distinctly clavate-capitate, 5-15  $\mu$ . Isolated and small groups of spheropedunculate cells occur between them.

COLLECTIONS EXAMINED.

#### NETHERLANDS

Utrecht: Nieuwersluis, Estate Over-Holland, 30 Sept. 1967, *E. Kits van Waveren* (type, L).

Zuid-Holland: Rotterdam, Kralingerhout, 17 Sept. 1960, *C. Bas* (L).

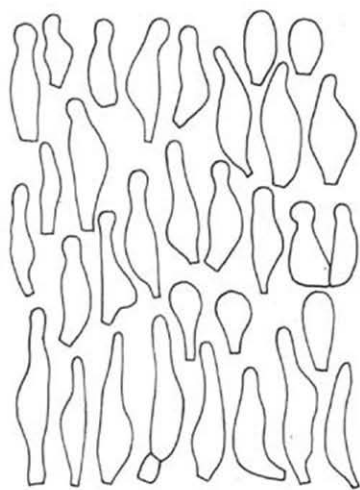
OBSERVATIONS.—For nomenclatural discussion, see p. 135.

Kühner's description (1935: 151) of the germ-pore in *C. "blattaria"* (= *C. arrhenii*) ("pore indiscutable mais pas toujours très évident") is exactly the same as that of the germ-pore in *C. "blattaria"* f. *dentata* ("pore indiscutable assez distinct, pas très évident pourtant"), but curiously enough he depicted very distinct germ-pores for *C. "blattaria"* f. *dentata* but none at all for *C. "blattaria"*.

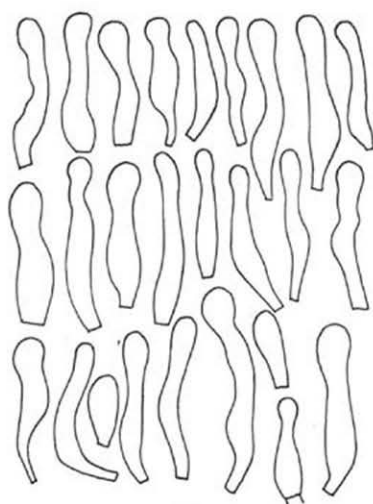
Again (see p. 124) we wish to stress the point that it is extremely misleading when the velum parziale, instead of forming a ring, fails to do so and remains as appendiculate denticles on the margin of the cap. In attempting to identify such specimens one might very easily be led into the group of exannulate species of *Pholiotina*, none of which, however, have the thin non-capitate cheilocystidia of *C. arrhenii*.

We once found ('s-Graveland, Estate Boekesteijn), specimens of the dentate form of *C. arrhenii*, of which the spores showed an unusual variation in size and were somewhat larger, (7.7-) 8.1-10.8  $\times$  4.5-5.4  $\mu$  in one specimen in which 2-spored basidia were definitely found and (8.1-) 9-9.9 (-10.8)  $\times$  5-5.4 (-5.9)  $\mu$  in another specimen in which in spite of a long search no 2-spored basidia were seen. The

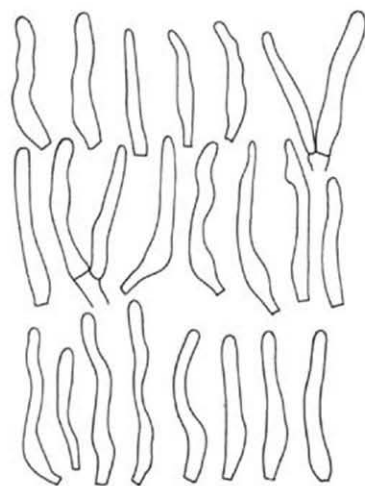




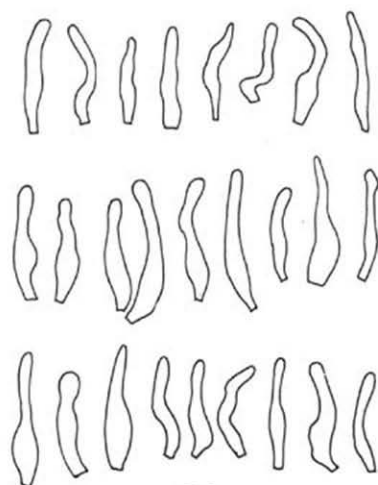
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Figs. 30, 31. *Conocybe aporos*, cheilocystidiogram. — 30. Overveen, 22 April 1961. — 31. Amsterdam, Amsterdamse Bos, 1 May 1961. (Both figs.:  $\times 575$ .)

Figs. 32, 33. *Conocybe arrhenii* var. *arrhenii*, cheilocystidiogram. — 32. Castricum, 28 Sept. 1968. — 33. Mook, 23 Oct. 1964. (Both figs.:  $\times 575$ .)

basidia in these specimens were larger than usual,  $21-38 \times 7.5-10 \mu$ . In the same area of this locality we found specimens of *C. filaris* which were 4-spored and others which had both 4-spored and 2-spored basidia and also large quantities of specimens of the common 2-spored form of *Galerina nana* (Petri) Kühn.

Unlike *C. aporos*, of which the cheilocystidia also are distinctly capitate, var. *hadrocystis* occurs in the autumn and possesses spores with a germ-pore.

CONOCYBE BLATTARIA (Fr.) Kühn.—Figs. 12, 13, 38-43

*Agaricus blattarius* Fr., Syst. mycol. 1: 246. 1821; Elench. 1: 29. 1828; Epicr. 162. 1838; Monogr. Hym. Succ. 1: 308. 1857; Hym. europ. 216. 1874. — *Pholiota blattaria* (Fr.) Quél. in Mém. Soc. Emul. Montbél. II 5: 319. 1872. — *Hylophila blattaria* (Fr.) Quél., Fl. mycol. 96. 1888. — *Togaria blattaria* (Fr.) W. G. Smith, Syn. Brit. Basid. 123. 1908. — *Conocybe blattaria* (Fr.) Kühn., Le Genre Galera 161. 1935 (misapplied).

*Conocybe vexans* P. D. Orton in Trans. Br. mycol. Soc. 38: 197. 1935.

MISAPPLIED NAMES.

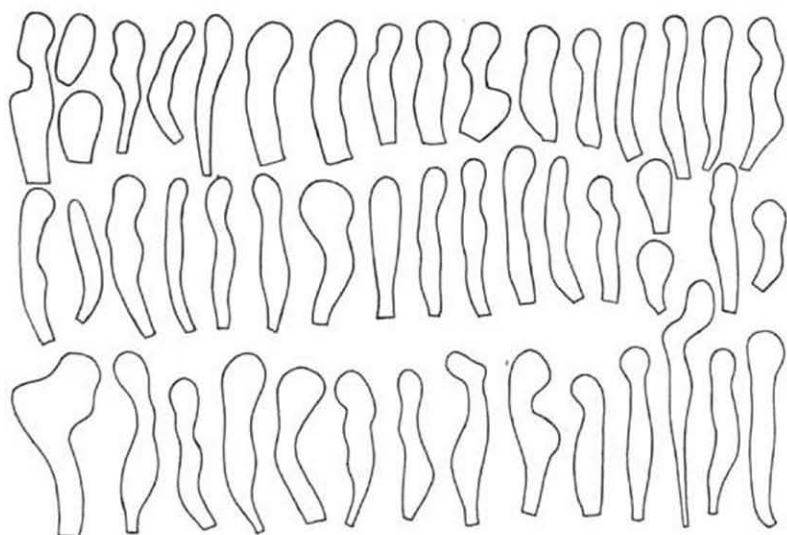
*Agaricus togularis* (Bull. ex Fr.) Fr. sensu Cooke, Ill. Brit. Fungi pl. 350/379. 1884-1886. — *Pholiota togularis* (Bull. ex Fr.) Ricken, Blätterp. 199, pl. 56 fig. 5. 1915. — *Conocybe togularis* (Bull. ex Fr.) Kühn., Le Genre Galera 161. 1935 ("Ricken").

SELECTED DESCRIPTIONS AND ILLUSTRATIONS.—Cooke, Ill. Brit. Fungi Pl. 350/379. 1884-1886 (*A. togularis*); Ricken, Blätterp. 199, pl. 56 fig. 5. 1915 (*P. togularis*); Bresadola, Icon. mycol. 14: pl. 687. 1930 (*P. togularis*); Kühner, Le Genre Galera 161. 1935 (*C. togularis*); Kühner & Romagnesi, Fl. anal. 343. 1953 (*C. togularis*).

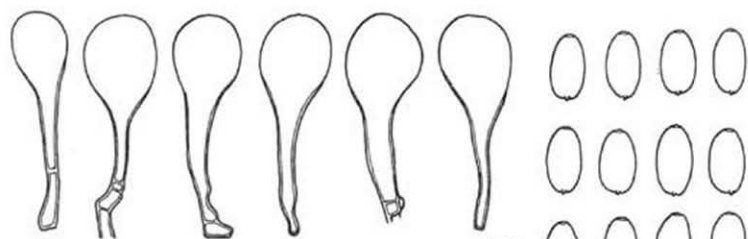
OTHER DESCRIPTIONS.—Duby, Bot. gall. 812. 1830 (*A. blattarius*); Secretan, Mycogr. suisse 86. 1833 (*A. blattarius*); Karsten in Bidr. Känn. Finl. Nat. Folk. 35: 114. 1876 and 32: 293. 1879 (*P. blattaria*); Gillet, Champ. Fr., Hymen. 433, pl. 519. 1876. (*P. blattaria*); Cooke, Handb. Brit. Fungi 141. 1886 (*A. togularis*); Saccardo, Syll. Fung. 5: 738. 1887 (*P. blattaria*); Schroeter in KryptFl. Schles. 3(1): 608. 1889 (*P. blattaria*); Masee, Brit. Fung. Fl. 2: 213. 1893 (*P. blattaria*); Harper in Trans. Wis. Acad. Sci. Arts Lett. 17(2): 1011. 1912 (*P. blattaria*); Velenovský, České Houby 552. 1921 (*Galera togularis*); Rea, Brit. Basid. 113. 1922 (*P. blattaria*), except description of cheilocystidia, misquoted from Ricken; Singer in Acta Inst. bot. Acad. Komar. Sci. URSS, Ser. 2 (Pl. crypt.) 6: 431. 1950 (*Pholiotina togularis*).

MACROSCOPIC CHARACTERS.—Cap 8-15 mm, conical, campanulate or conico-campanulate, when moist strongly striate from margin up to  $1/2-2/3$  of radius of the cap, surface smooth, the centre and striae dark ochre-brown or dark yellowish-brown (M. 10 YR 5/8), outside centre and between striae brownish-yellow or dark yellow (M. 10 YR 6/8, 7/8); hygrophanous, drying out to yellow (M. 10 YR 8/8) and even pale yellow (M. 2.5 Y 7/4), striation completely disappearing. Marginal veil absent.

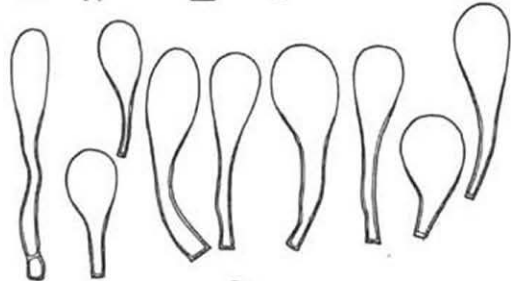
Stem 40-70  $\times$  1-1.5 mm, equal, slightly thickened near and at the base, hollow, non-rooting, at first dirty whitish and only slightly coloured towards the base, covered over its entire length by a very thin, silvery, white, silky, fine fibrillose-striate superficial layer, through which the colour of the flesh appears, later very pale yellow (M. 2.5 Y 8/4) at the apex, becoming slightly darker and browner towards the ring, pale yellowish-brown (M.  $\pm$  10 YR 7/6) just above the ring, further down yellowish-brown (M. 10 YR 5/6) to brown or bronze-brown (M.  $\pm$  7.5 YR 5/6-4/4), after removal of the superficial whitish layer fuliginous brown at the base, increasingly pruinose from ring upwards.



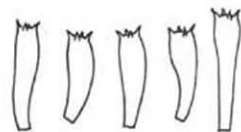
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Figs. 34-37. *Conocybe arrhenii* var. *hadrocystis* (Nieuwersluis, Over-Holland, 30 Sept. 1967, holotype). — 34. Cheilocystidiogram. — 35. Cells of surface of cap. — 36. Spores. — 37. Basidia. (Figs. 34, 35, 37:  $\times 575$ ; Fig. 36:  $\times 1212$ .)

Velum parziale always forming a conspicuous, thick (0.5–1 mm) and broad (2.5–6 mm) ring, located about  $1/4$ – $1/3$  of the total length of the stem from the apex, as a rule conspicuously standing out horizontally from the stem (not cuff-like and rather reminiscent of the ring of *Lepiota procera*), often becoming detached from the stem and then movable and easily slipping down the stem of breaking and then disappearing altogether, striate-plicate above, whitish or very pale brown (M. 10 YR 8/3), sometimes the upper surface orange-brown because of spore-deposit.

Gills fairly crowded (L 19–23) ventricose, narrowly adnexed, 2–2.5 mm broad, dirty brown (M. 10 YR 5/4) to yellowish-brown (M. 10 YR 5/6), edge flocculose-dentate, white.

Flesh in the centre of the cap 0.5–1 mm thick, very thin near the margin, dark yellowish-brown (M. 10 YR 5/8), in the stem very pale yellow at the apex, becoming pale brown near the ring and then increasingly brown towards the base, dark fuliginous brown at the base.

Smell none.

MICROSCOPIC CHARACTERS.—Spores ellipsoid to slightly amygdaliform, yellow (M. 2.5 Y 8/8) with a trace of red in water, apiculus fairly small, germ-pore large ( $1.5$ – $2 \mu$ ), ( $9.9$ – $10.8$ – $12.6 \times 5.4$ – $6.8 \mu$ ).

Basidia 4-spored,  $22.5$ – $35 \times 7.5$ – $10 \mu$ .

Cheilocystidia closely packed (edge of gill sterile), neck cylindrical and distinctly delimited from the rather large and vesiculose ( $10$ – $25 \mu$  diameter) cell-body (sicyoid), or indistinctly delimited from smaller ( $7.5$ – $14 \mu$  diameter) cell-body (lageniform), and tapering towards the acute or subacute apex, also intermediate forms; colourless; wall of normal thickness.

Pleurocystidia none.

Cuticle of cap hymeniform (for full description, see p. 126), cells  $15$ – $50 \times 7.5$ – $27.5 \mu$ .

Superficial hyphae of stem below ring, for full description, see p. 126.

HABITAT.—In deciduous woods in moss or soil, solitary or in very small groups. End of May to September. Rare.

COLLECTIONS EXAMINED.

#### BRITISH ISLES

Perthshire: Camghouran, 24 May 1967, *P. D. Orton 2949* (E); Dall, 25 May 1967, *P. D. Orton 2950*; 29 May 1967, *P. D. Orton 2951*; 7 June 1967, *P. D. Orton 2952*; 13 June 1967, *P. D. Orton 2953* (E); Camghouran, 17 July 1965, *P. D. Orton 2721*; 31 July 1965, *P. D. Orton 2722*; 26 September 1965, *P. D. Orton 2723* (E).

Aberdeenshire: Braemar, Invercauld Estate (Altdour Road), 28 August 1961, *E. Kits van Waveren* (L).

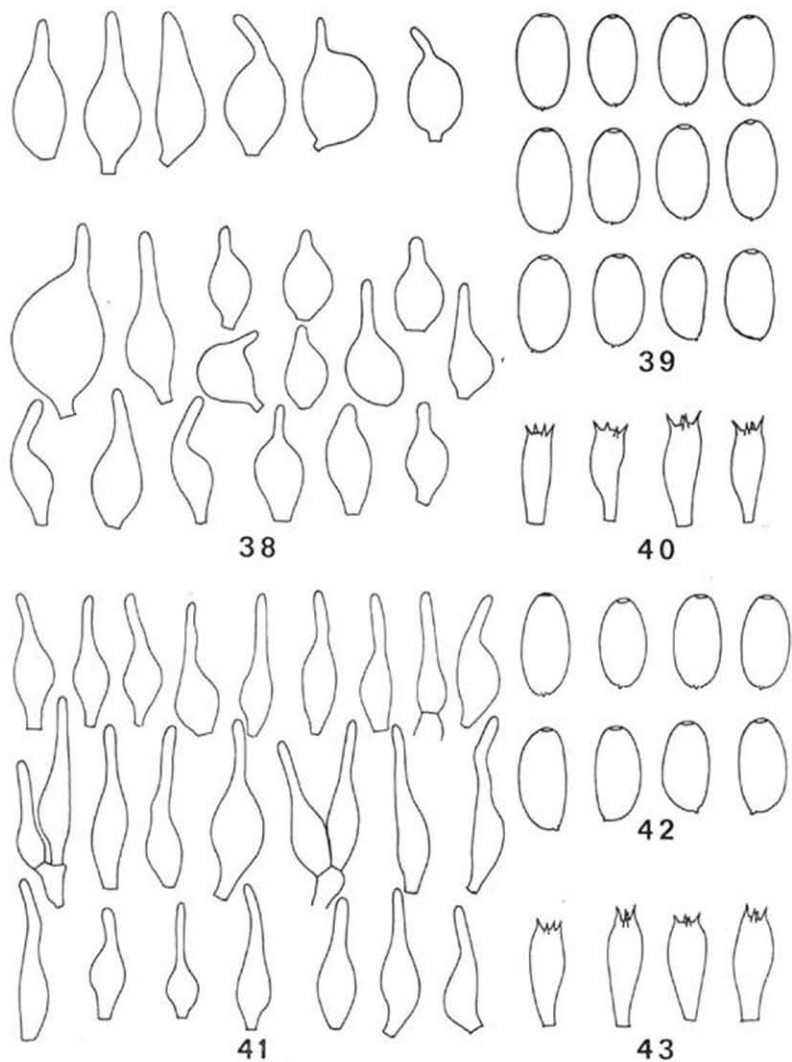
Invernesshire: Tomich, 1 September 1957, *P. D. Orton* (type specimen of *C. vexans*, K.); Guisachan, 19 September 1958, *P. D. Orton 1484* (E); Tomich, 17 September 1968, *E. Kits van Waveren* (L).

Durham: High Force Woodland, 22 September 1963, *R. Watling g. 415* (E).

OBSERVATIONS.—For nomenclatural discussion, see p. 131.

This species has not yet been recorded for the Netherlands.

*C. blattaria* being tall and slender, having a comparatively small cap and as a result having a striking habitus, very much resembles a *Galerina*; accordingly in the literature it is occasionally referred to as an "annulate *Galera*."



Figs. 38-40. *Conocybe blattaria* (Braemar, 28 Aug. 1961). — 38. Cheilocystidiogram. — 39. Spores. — 40. Basidia. (Figs. 38, 40:  $\times 575$ ; Fig. 39:  $\times 1212$ .)

Figs. 41-43. *Conocybe blattaria* (Tomich, 17 Sept. 1968). — 41. Cheilocystidiogram. — 42. Spores. — 43. Basidia. (Figs. 41, 43:  $\times 575$ ; Fig. 42:  $\times 1212$ .)

We found the walls of the stalks of the cells of the cuticle of the cap rarely and even then only very slightly thickened and coloured and the hyphae and inflated cells of the hypodermis also very little coloured and carrying comparatively few encrustations, which may well account for the cap being distinctly brighter and above all more yellow than the caps of *C. arrhenii*, *C. aporos*, and *C. filaris*.

Looking from underneath the cap into the gills of our specimens of 17 Sept. 1968, we were struck by the curious sordid yellowish-brown colour of the gills (looking at the face of the gills of some of the specimens the colour could be designated as M. 10 YR 5/4), which reminded us of the colour of the gills of *Galerina mniophila*. Orton's description of the colour of the gills of his *C. vexans*—which we consider to be conspecific with *C. blattaria*—also suggests a curious shade of brown: "clay-whitish then pale clay-ochraceous to dirty honey finally rusty-honey."

It is curious to note that Orton (1960: 197) found his *C. vexans* near Tomich (Invernesshire) on 1 Sept. 1957, where according to Dr. Watling (personal communication) it was again found on 14 Sept. 1958, while we found *C. blattaria* under trees near a farm at the far end of the same village Tomich on 17 Sept. 1968 (also near Braemar on 28 Aug. 1961).

CONOCYBE FILARIS (Fr.) Kühn.—Figs. 14–19, 44–48

*Agaricus togularis* var. *filaris* Fr., Icon. sel. 2: 2, pl. 104 fig. 4. 1884. — *Pholiota filaris* (Fr.) Peck in Bull. N.Y. St. Mus. 122: 144. 1908. — *Conocybe filaris* (Fr.) Kühn., Le Genre Galera 159. 1935. — *Pholiotina filaris* (Fr.) var. *kühneri* Sing. in Acta Inst. bot. Acad. Komar. Sci. URSS, Ser. 2 (Pl. crypt.) 6: 429. 1950 (new name).

*Galera pusilla* Qué., Enchir. 81. 1886. — *Pholiota pusilla* (Qué.) Maire apud Kühn., Le Genre Galera: 160. 1935.

*Pholiota rugosa* Peck in Rep. N.Y. St. Mus. nat. Hist. 50: 102. 1898. — *Pholiotina rugosa* (Peck) Sing. in Pap. Mich. Acad. Sci. 30: 148. 1946. — *Pholiotina filaris* var. *rugosa* (Peck) Sing. in Acta Inst. bot. Acad. Komar. Sci. URSS, Ser. 2 (Pl. crypt.) 6: 429. 1950.

*Pholiotina filaris* (Fr.) var. *ochracea* Sing. in Acta Inst. bot. Acad. Komar. Sci. URSS, Ser. 2 (Pl. crypt.) 6: 429. 1950.

SELECTED DESCRIPTIONS AND ILLUSTRATIONS.—Fries, Icon. sel. 2: 2, pl. 104 fig. 4. 1884 (*A. togularis* var. *filaris*); Kühner, Le Genre Galera 159. 1935 (*C. filaris*); J. E. Lange, Fl. agar. dan. 3: 63, pl. 106 C, C 1 (*P. filaris*); Kühn. & Romagn., Fl. anal. 343. 1953 (*C. filaris*); Overholts in Ann. Mo. Bot. Gdn 14: 115, pl. 15 upper left (*P. rugosa*).

OTHER DESCRIPTIONS.—Britz, in Ber. naturh. Ver. Augsburg 27: 151. 1883 (*A. togularis* var. *filaris*); Peck in Bull. N.Y. St. Mus. 122: 144. 1908 (*P. rugosa*); Harper in Trans. Wis. Acad. Sci. Arts Lett. 17: 482. 1912 (*P. togularis* var. *filaris* and *P. rugosa*); J. E. Lange in Dansk bot. Ark. 2 (11): 6. 1921 (*P. togularis* var. *filaris*); Overholts in N. Am. Fl. 10 (4): 265, 266. 1924 (*P. rugosa* and *P. filaris*); Overholts in Ann. Mo. bot. Gdn 14: 115, 116. 1927 (*P. rugosa* and *P. filaris*); A. H. Smith in Annls mycol. 32: 478. 1934 (*P. filaris*); Singer & Digilio in Lilloa 25: 312. 1951 (*P. filaris*); Moser in Kl. KryptogFl., Ed. 3, 2(B2): 230. 1967 (*P. filaris*).

MACROSCOPIC CHARACTERS.—Cap 6–20 mm, predominantly conical with obtuse apex or conico-campanulate, later sometimes convex or even applanate and then sometimes with distinct obtuse umbo, when moist strongly striate up to 1/3–2/3 of

radius from margin, or up to umbo, surface smooth and often distinctly and sometimes even strongly rugulose, centre and striae dark reddish-brown (M. 5 YR 3/3, 3/4) between the striae dark brown (M. 7.5 YR 4/4; 10 YR 5/8) in the area around the non-striate centre becoming brown (M. 7.5 YR 5/6) and yellowish-brown (M. 10 YR 5/6, 6/6) towards the margin, hygrophanous, the reddish colour rapidly and already in early stages making way for brown (M. 7.5 YR 4/4, 5/6) then yellowish-brown (M. 10 YR 5/6, 5/8, 6/6), finally pale brown-yellow (M. 10 YR 7/4, 7/6), the striation disappearing. Marginal veil absent.

Stem 15–35 × 0.75–1.5(–2) mm, equal, sometimes slightly thickened at the base, firm, hollow, non-rooting, pruinose over some distance at apex, fairly and sometimes very coarsely fibrillose-striate by a whitish to greyish or very pale brown layer of fibrils, often below the ring even flocculose-fibrillose or woolly-hairy or disjointed and masking the brown colour underneath; very pale yellow or brown (M. 2.5 Y 8/4, 7/4 and 10 YR 7/4, 7/6, 6/6) at the apex, increasingly brown towards the base and fuliginous to blackish-brown at the base.

Velum parziale always forming a conspicuous ring just above to just below the middle of the stem, large, ascending, horizontal or descending, often detached from the stem and then easily sliding along the stem, whitish to pale brown, felt-like, coarsely striate-plicate and often orange-brown above because of spore-deposit.

Gills ventricose, not crowded (L 13–25), adnexed (sometimes narrowly or even very narrowly), 1–2.5 mm broad, ochre-brown (M. 7.5 YR 5/6 or paler), edge flocculose-denticulate, white.

Flesh of the cap 0.5–1 mm thick in the centre, very thin near the margin, very dark brown, of the stem very pale brown at the apex, increasingly brown towards the base, fuliginous brown to blackish-brown in the lower 1/4–1/3 of the stem and almost always black at the base.

Smell none.

MICROSCOPIC CHARACTERS.—Spores ellipsoid to slightly amygdaliform, yellow (M. 2.5 Y 7/6) with a trace of red in water, apiculus small, germ-pore conspicuous (1–1.5  $\mu$ ), 8.1–9.9(–10.4) × 4.5–5.4(–5.9)  $\mu$  in 4-spored specimens and many up to 12–12.5 × 6  $\mu$  in specimens with both 4- and 2-spored basidia.

Basidia usually 4-spored but sometimes both 4- and 2-spored basidia on the same gill, 17.5–27 × 5–10  $\mu$ .

Cheilocystidia closely packed (edge of gill sterile but often with scattered basidia or very small groups of basidia), obclavate, lageniform, the majority if not all the necks indistinctly delimited from the cell-body, tapering towards the acute to obtuse apex, colourless, wall of normal thickness, 20–50 × (4)–6–11 × 1.5–2.5(–3)  $\mu$ .

Pleurocystidia none.

Cuticle of the cap hymeniform, for full description, see p. 126.

Superficial hyphae of the stem below the ring, for full description, see p. 126.

HABITAT.—In rich, clayey soil of gardens, parks particularly in and around greenhouses, along paths, in moss, also found in sawdust and compost. In small or, gregariously, in large groups, rarely solitary. Uncommon.

COLLECTIONS EXAMINED.

#### NETHERLANDS

O v e r y s e l: Ommen, Estate Ada's Hoeve, 15 Sept. 1963, *E. Kits van Waveren* (L); Oldenzaal, Estate Dykhuis, 16 Oct. 1963, *E. Kits van Waveren* (L).

U t r e c h t: Zaltbommel, 27 Oct. 1968, *M. H. J. Kortselius* (L).

N o o r d - H o l l a n d: 's-Graveland, Estate Boeckesteyn, 12 June 1967, 27 May 1968, 3 Aug. 1968, *J. Daams* (L); 's-Graveland, Estate Boeckesteyn, 25 Sept. 1968,

3 Oct. 1968, 8 Nov. 1968, *E. Kits van Waveren* (L); Santpoort, Estate Duin en Kruidberg, 1 Dec. 1960, *E. Kits van Waveren* (L).

Zuid-Holland: Leiden, Nieuweroord, 21 Aug. 1960, *R. A. Maas Geesteranus* (L).

Noord-Brabant: Breda in garden of Meerten Verhoffstraat 9, 2 Sept. 1961, *P. B. Jansen* (L).

#### BRITISH ISLES

Montgomeryshire: Lake Vyrnwy, 5 Sept. 1959, *E. Kits van Waveren* (L).

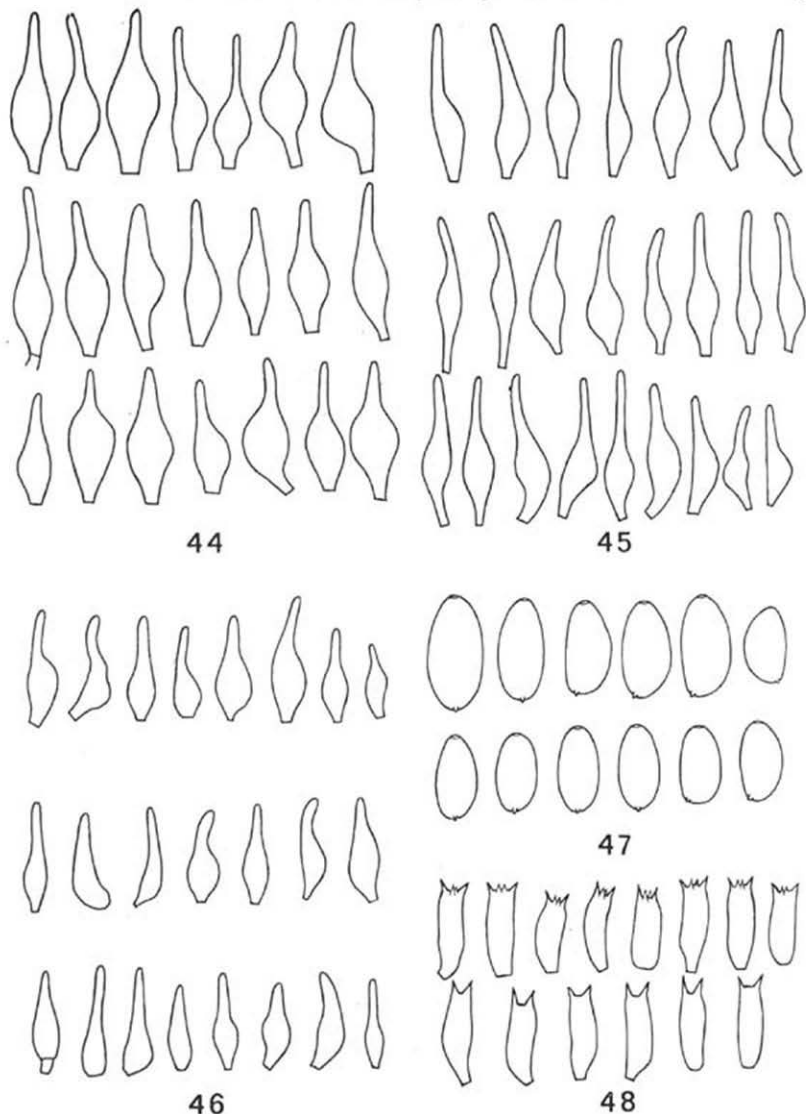
Perthshire: Loch Rannoch, 31 Oct. 1964, *P. D. Orton* 2559, 2560; 2 Nov. 1964, *P. D. Orton* 2561 (E).

OBSERVATIONS.—From Peck's descriptions (1896: 102; 1908: 144) of *Pholiota rugosa* and from the redescriptions by Overholts (1924: 265) and Singer (1946: 148) it is quite obvious that this species was based on specimens of *C. filaris* of which the surface of the cap—as so often is the case in this species—was distinctly wrinkled, all other macroscopic and microscopic characters being identical with those of *C. filaris*. Accordingly Singer & Digilio (1951: 312) stated that they wished to identify as *C. rugosa* those forms of *C. ("Phliotina") filaris* which have a rugulose cap, and as *C. filaris* those forms of *C. rugosa* (of which Singer gave a description in 1946: 148) which have a smooth cap!

Earlier Singer (1950: 429) had distinguished no less than six varieties of *Conocybe ("Phliotina") filaris*, all of which he believed to be intermediate forms between *C. filaris* and *C. arrhenii ("blattaria")*: var. *rugosa*, clearly the form of *C. filaris* with the surface of the cap wrinkled; var. *ochracea* also clearly *C. filaris* of which, however, all traces of red had disappeared from the cap (surface of cap slightly wrinkled, obtuse umbo, 2- and 4-spored basidia, etc.); var. *recedens*; var. *recedens* f. *subochracea*; var. *exannulata*, and var. *Kühneri*. Judging by Cooke & Masee's original description (apud Cooke, 1889: 25) of *Agaricus recedens*, this species is clearly not *C. filaris*, but, on account of its very long stem (75–100 × 4.6 mm) and fairly large cap (25 mm diameter), may well have been *C. blattaria* or *C. teneroides*. Singer's description looks like being merely a copy of the one by Cooke & Masee, both giving  $9 \times 5 \mu$  for the size of the spores and neither of them mentioning the cheilocystidia or the basidia as being 4- or 2-spored or both. Var. *exannulata* is quite a different species (no ring, indistinct germ-pore, cheilocystidia lageniform but also, be it less often, clavate). Var. *Kühneri* is *C. filaris* as described above and accordingly Singer considered it to be conspecific with *A. togularis* var. *filaris* and *C. filaris* as described by Kühner (1935: 159).

In trying to identify the annulate species of the *Phliotina* group from descriptions in the literature in which the microscopic characters are missing or described inadequately, one should—with regard to *C. filaris*—go by the two major macroscopic characteristics of this species, the small size (stem 15–35 mm) and the predominantly conical shape of the cap (the specimens depicted by Fries on his Pl. 104 fig. 4 also are predominantly conical). *Agaricus recedens* as described by Cooke & Masee (apud Cooke, 1889: 25) and *Galera togularis* as described by Velenovský





Figs. 44-48. *Conocybe filaris* (44: 's-Graveland, Boekestejn, 3 Oct. 1968; 45: Leiden, Nieuweroord, 21 Aug. 1960; 46: Santpoort, Duin en Kruidberg, 1 Dec. 1960; 47 & 48: Oldenzaal, Dijkhuis, 16 Oct. 1963). — 44-46. Cheilocystidiogram. — 47. Spores. — 48. Basidia, 2- and 4-spored. (Figs. 44-46, 48:  $\times 575$ ; Fig. 47:  $\times 1212$ .)

(1921: 552) in this respect cannot be regarded—as Singer (1950: 431) did—as synonyms of *C. filaris*. The stems of both species were very long and Velenovský used only the words “arch-like expanded” (translation Dr. Kotlaba) for the shape of the cap. Indeed, Watling (personal communication) who has examined the type material in Herb. Kew, stated *Agaricus recedens* is a member of the Cortinariaceae, named *Rescolea recedens* by Singer (1955: 407).

Kühner (1935: 161) concluded that *Galera pusilla* Quél. (1886: 81) only differed from *C. filaris* by its very small size (diameter of cap 4 mm) and concluded from Maire's unpublished notes that this author had also found this species “sous les cèdres de l'Atlas de Blida” and had named it *Pholiota pusilla*. On looking at Quétel's original description Kühner's conclusion certainly seems justified. Smith & Singer (1964: 296) believed *Pholiota minima* Peck (1888: 65), by that name also described by Overholts (1924: 266), to be a *Galerina*.

It was quite a surprise, when, while studying our collection of *C. filaris* of 16 Oct. 1963, large numbers of 2-spored basidia were found among the majority of 4-spored basidia, as at that time Singer's paper, the only one recording 2-spored basidia in *C. filaris*, had not yet come to our knowledge. Later we found 2-spored basidia in small numbers in the collections of 25 Sept., 3 Oct., and 8 Nov. 1968 from 's-Graveland.

*Conocybe filaris* evidently has great preference for growing in or near greenhouses. Singer (1950: 429) reported several of his varieties of *C. filaris* from greenhouses, Overholts (1924: 265), and Singer (1948: 148) reported the same for *C. rugosa*, and our own collections from 's-Graveland and Oldenzaal also were growing in or near greenhouses.

The caps of *C. filaris* dry out very rapidly, and this probably explains why many descriptions in the literature fail to mention its dark reddish-brown colour in the earliest stages (see p. 122). Coloured photographs in our collection, taken of specimens found 1 Dec. 1960, bring out this colour beautifully. The photographs reproduced by Overholts (1927: 115, pl. 15), although in black and white, are excellent and depict the typical size and shape of the carpophores very well; in the accompanying description the colour of the caps is called “yellowish-red or dark ferruginous.”

**Conocybe teneroides** (J. E. Lange) Kits van Wav., *comb. nov.*

Figs. 20, 49–54

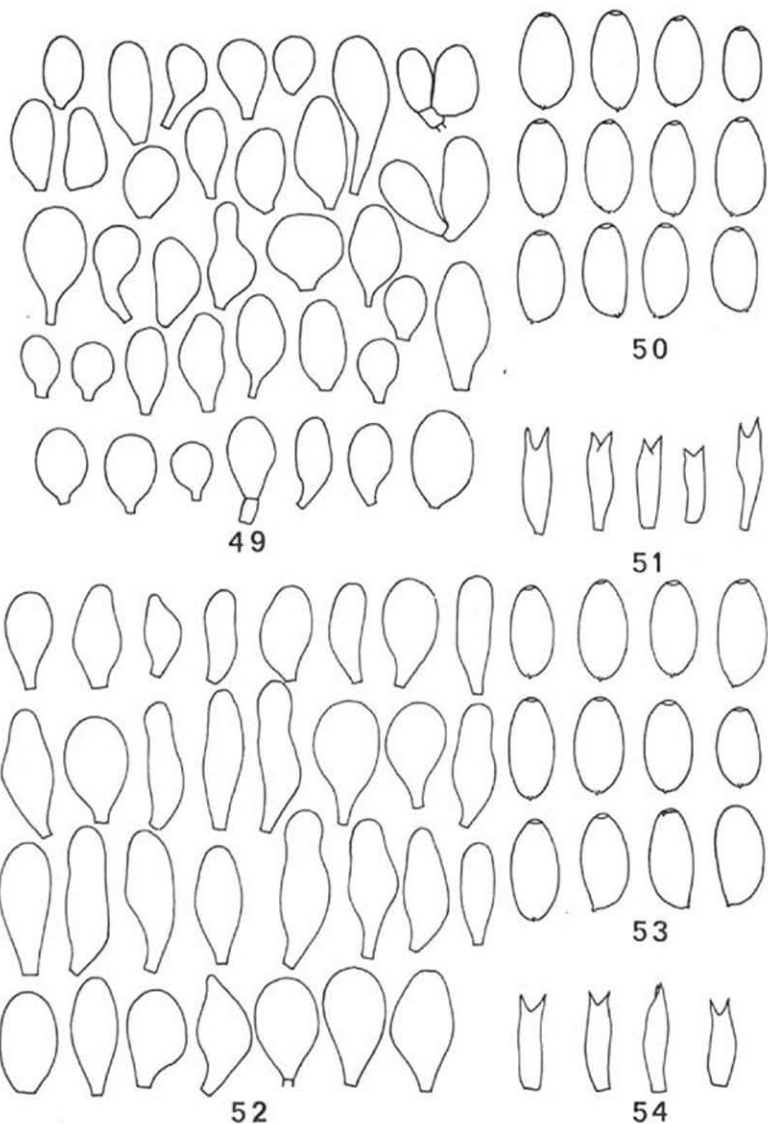
*Pholiota teneroides* J. E. Lange in Dansk bot. Ark. 2 (11): 7. 1921. — *Conocybe teneroides* (J. E. Lange) Kühn., Le Genre Galera 162. 1935 (not validly published).

*Conocybe togularis* forme bisporique, Kühn., Le Genre Galera 162. 1935.

*Conocybe percincta* P. D. Orton in Trans. Br. mycol. Soc. 43: 194. 1960.

MISAPPLIED NAMES.

*Pholiota blattaria* (Fr.) Quél. *sensu* Konr. & Maubl., Icon. sel. Fung. 1: pl. 69 fig. 2. 1929. — *Pholiotina togularis* f. *bispora* Singer in Acta Inst. bot. Acad. Nom. Komarovi Sci. URSS, Ser. 2 (Pl. crypt.) 6: 431. 1950. — *Conocybe blattaria* (Fr.) Kühn. *sensu* Orton in Trans. Br. mycol. Soc. 43: 191. 1960; Dennis, Orton & Hora in Trans. Br. mycol. Soc., Suppl. 33. 1960.



Figs. 49-51. *Conocybe teneroides* (Santpoort, Duin en Kruidberg, 1 Dec. 1960). — 49. Cheilocystidiogram. — 50. Spores. — 51. Basidia. (Figs. 49, 51:  $\times 575$ ; Fig. 50:  $\times 1212$ .)

Figs. 52-54. *Conocybe percincta* (Covenhope, 21 Nov. 1959, type). — 52. Cheilocystidiogram. — 53. Spores. — 54. Basidia. (Figs. 52, 54:  $\times 575$ ; Fig. 53:  $\times 1212$ .)

SELECTED DESCRIPTIONS AND ILLUSTRATIONS.—Konrad & Maublanc, *Icon. sel. Fung.* 1: pl. 69 fig. 2. 1929 (*P. blattaria*); J. E. Lange, *Fl. agar. dan.* 3: 63, pl. 106 B. 1938 (*P. teneroides*); Kühn., *Le Genre Galera* 162. 1935 (*P. teneroides*); Orton in *Trans. Br. mycol. Soc.* 43: 191. 1960 (*C. percincta*).

MACROSCOPIC CHARACTERS.—Cap 6–13 mm, conico-campanulate to campanulate, when moist striate from margin up to  $1/2$ – $2/3$  of radius of the cap, surface smooth, ochre-brown (M. 10 YR 5/6) to brownish-yellow (M. 10 YR 6/6), hygrophanous, drying out to yellow (M. 10 YR 7/6) and pale brownish-yellow (M. 10 YR 8/4, 8/6), striation completely disappearing. Marginal veil absent.

Stem 20–35 × 1.5–2 mm, equal, hollow, non-rooting, colour very pale yellowish at the apex, pale yellowish-brown slightly lower down, then increasingly brown and rather pinkish-brown towards the base, dark brown at the base, these colours breaking through a very thin, whitish, fine fibrillose-striate superficial layer, the apex pruinose.

Velum parziale forming a conspicuous, thick (c. 0.5–1 mm) and broad (2–5 mm) ring, located at about  $1/4$ – $1/3$  of the total length of the stem from the apex, as a rule standing out horizontally from the stem (not cuff-like and rather reminiscent of the ring of *Lepiota procera*), often becoming detached from the stem and then movable and easily slipping down the stem or breaking and then disappearing altogether, striate-plicate above, whitish.

Gills fairly crowded, (L 20–24), ventricose, narrowly adnexed, 1.5–2.5 mm broad, brownish-yellow to ochre (M. 10 YR 6/6, 5/6), edge flocculose-dentate, white.

Flesh thin, ochraceous in cap, deep honey to dark ochre over the gills; in stem horn-ochraceous at apex and, when dry, rich ochre-yellow, tinted faintly tawny; sepia brown towards base, vandyke to umber at the very base; rapidly drying out.

Smell none.

MICROSCOPIC CHARACTERS.—Spores ellipsoid to slightly amygdaliform, yellow (M. 2.5 Y 8/8) with a trace of red in water, apiculus fairly small, germ-pore large ( $1.5$ – $2 \mu$ ),  $10.8$ – $11.7 \times 5.4$ – $6.3 \mu$ .

Basidia 2-spored,  $17.5$ – $25 \times 7$ – $8 \mu$ .

Cheilocystidia closely packed (edge of gill sterile), very variable, spheropedunculate-globose, ellipsoid, cylindrical, clavate, fusiform, obovoid, utriform,  $15$ – $40 \times 9$ – $20 \mu$ , colourless, wall of normal thickness.

Pleurocystidia none.

Cuticle of cap hymeniform (for full description, see p. 126), cells  $17.5$ – $55 \times 12$ – $25 \mu$ .

Superficial hyphae of the stem below the ring, for full description, see p. 126.

HABITAT.—In moss in woods, solitary or in very small groups. Autumn. Very rare.

COLLECTIONS EXAMINED.

#### NETHERLANDS

Noord-Holland: Santpoort, Estate Duin en Kruidberg, 1 Dec. 1960, E. Kits van Waveren (L).

#### BRITISH ISLES

Surrey: Mickleham, Juniper Hall, 19 Nov. 1954, P. D. Orton 321 (E).

Perthshire: Tomich, Guisachan Forest, 1 Sept. 1957, P. D. Orton 1141 (E); Covenhope, 21 Nov. 1959, P. D. Orton (type of *C. percincta*, K.).

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## REVIEWS

E. J. H. CORNER, *A monograph of Thelephora (Basidiomycetes)*. In Beih. Nova Hedwigia 27: 110 pp., 52 figs., 6 plates. 1968. Price DM 40.—.

Referring to the author's own words (A monograph of Cantharelloid fungi, 1966: 2) one is perfectly justified in qualifying the present book as "another need . . . fulfilled."

It is a rare accomplishment for a botanist, after having spent a full life in the tropics and occupying himself there with a variety of subjects, to offer the mycological world his third monograph. The author is to be congratulated on the completion of this work.

Fifty-one species have been treated—not counting the species incertae—, nineteen of which appear to be new, not seventeen as stated on p. 2.

The chapter "Form of Fruit-body" makes illuminating reading; it has been written by a mycologist who from his wide experience as a field-botanist and his intimate knowledge as a morphologist tries to reconstruct the evolutionary trend in *Thelephora*.

Morphology plays an equally important part in the chapter in which the difference between the thelephoroid papilla and the hydroid spine is explained.

Inced by Malençon's paper on spore development in Thelephoraceae, Corner grouped some of his spore drawings according to the series he recognizes. The result, however, does not seem entirely convincing as, although some differences are apparent, similarities in the shapes of spores belonging to different series are also manifest.

Some of the descriptions are very unequal in length, compare those of *T. crustacea* and *T. ramarioides*, and of *T. arbuscula* and *T. magnifica*.

The way the collections are cited is not uniform, as for instance in *T. fuscella* and *T. gelatinoidea*, while in at least ten species collections are not mentioned at all.

Why such casualness? The author citation of *T. fuscella* should read (Ces.) Lloyd, not Lloyd; *Thelephora palmata* var. *diffusa* (Fr.) Bourd. & Galz., not Bourd. & Galz.; *Thelephora spiculosa* (Fr.) Fr., not Fr.

*Thelephora zeylanica* is a new name, not a new species.

The author regards *Hydnum nauseo-foetidum* Teng as a synonym of *Thelephora gelatinoidea*, but is he quite sure it is a *Thelephora*?

The basionym which served for Lloyd's recombination *Thelephora fuscella* is *T. multipartita* var. (not forma) *fuscella* Cesati. This variety was published in 1879 ["finita stampare il di 18 agosto 1879"], not 1878. It does not bear the number 43. Could it be that the symbol 3 has any relation with the serial number of Cesati's paper? It is number 3. Unfortunately variety *fuscella* is a nomen nudum, for, unlike varieties *soluta* and *isarioides* published on the same page, it lacks a description.

R. A. MAAS GEESTERANUS

*Mushroom Science VII*. Proceedings of the Second Scientific Symposium and the Seventh International Congress on Mushroom Science. Hamburg. 1968 (Centre for Agricultural Publishing and Documentation, Wageningen, 1969). Pp. 614, numerous text-figures and tables, 14 × 21.6 cm, sewn. Price f 50.—.

In general set-up, scope, style, and finish the present volume is identical to its predecessor. The quality of the paper used seems to be even better.



Fifty-eight papers are included, of which, to accentuate just a few, the following are of eminent importance for the mushroom grower and the taxonomist alike. M. J. Cross & L. Jacobs (*Some observations on the biology of spores of Verticillium malthousei*, pp. 239-244); D. M. Huffman (*Cytology of Collybia maculata var. scorzonera*, pp. 579-583); L. R. Kneebone (*Strain selection, development and maintenance*, pp. 531-541); R. von Sengbusch & Gerda Fritsche (*Neuester Stand der züchterischen Arbeiten an Stamm 59c*, pp. 507-513); H. O. Schwantes (*Wirkung unterschiedlicher Stickstoffkonzentrationen und -verbindungen auf Wachstum und Fruchtkörperbildung von Pilzen*, pp. 257-272); Charlotte Thielke (*Die Substruktur der Zellen im Fruchtkörper von Psalliota bispora*, pp. 23-30).

R. A. MAAS GEESTERANUS

M. J. LARSEN, *Tomentelloid fungi of North America*. In Techn. Publ. St. Univ. Coll. For., Syracuse No. 93: 157 + (i) pp. 1 (text) pl., 52 figs. 1960. Price \$ 2.00.

Students of the Thelephoraceae (in the modern sense) may congratulate themselves with the recent publication of three important studies on the tomentellas and on *Thelephora*, two related groups that at present cannot be satisfactorily separated from each other except by artificial definitions. The tomentellas of North America (almost exclusively of subboreal and temperate North America) were the subject of the above-mentioned thesis by Larsen; those of the British Isles were reviewed in a paper by E. M. Wakefield (*in Trans. Br. Mycol. Soc.* 53: 161-206). The third study I have in mind is by E. J. H. Corner, "A monograph of *Thelephora* (Basidiomycetes)", reviewed above. Among the principal characters used in both groups for describing the species are the hyphae and the spores. The problem of building up an adequate spore terminology has been differently approached by Corner and Larsen. There is still need here for unification and improvement. As to Larsen's spore terminology, more will be mentioned about it below.

Through the work of Bourdot & Galzin, Litschauer, Svrček, Christiansen, and Wakefield the number of European species of the tomentelloid fungi has been raised to a number that is perhaps slightly in excess of that described by Larsen (*viz.* 51). After Burt's treatment of "*Hypochnus*" (a very artificial genus, but mainly consisting of tomentellas) little has been done towards a better knowledge of the North American species, until the publication of Larsen's thesis which stands out as a notable achievement. Little is known about the tomentellas outside North America and western and central Europe.

Larsen distributes the species over *Pseudotomentella* Svrček (6), *Kneiffiella* P. Karst. (1), and *Tomentella* Pat. (43). The last genus includes *Caldesiella* Sacc. and, again, *Tomentellastrum* Svrček. The genus *Pseudotomentella* has been emended to contain species with basidia usually "sphaeropedunculate" when immature and spores with warts usually "dichotomously branched"; clamp-connections may be frequent in some of the species. By the revised definition the group of *Tomentella echinospora* has become displaced, a situation for which no remedy is as yet offered. As stated, *Tomentellastrum* (introduced for a group of clampless species) is retained in *Tomentella* which, under the present conditions, seems to be the most sensible solution, although it is one of the groups that in part has been placed also in *Thelephora*. The genus *Kneiffiella* received an improved definition that suggests perhaps a closer relationship with *Pseudotomentella* rather than with *Tomentella*. However, its only species has been given a new name, *K. fibrosa* (B. & C.) M. J. Lars.

No attempt was made to subdivide *Tomentella* as was done by Bourdot & Galzin. Neither did Wakefield. The lack of a well-founded subdivisional classification will be difficult to remedy; this makes the search for, and the insertion of, a species rather a cumbersome matter. This situation would suggest rather that the genus is a "homogeneous" one; yet I would not be surprised if eventually *Tomentella* would appear to consist of several "reduced" groups of different derivation within the Thelephoraceae.

Each species is fully described and accompanied by sets of figures which in most cases occupy a full page. These figures are extremely well done and merit a special word of admiration. The descriptions are fuller than is usual in connection with this group; each is followed by a short discussion of the differential characters. Following this detailed treatment of the species admitted is a chapter on "Excluded species" and another one on "Extra limital species"; the latter is of particular interest to European mycologists. All in all this monograph is indispensable to students of the tomentelloid fungi. Let us hope that when it is replaced, this will be by a monograph of all the species of the world by the same author.

If some objections have to be raised it will be in connection for instance with the terminology, in the first place of the spores. The introduction states, "Five basic types of spores are recognized here, following the definitions in Webster's Third International Dictionary (1963). They are aculeate, echinulate, aculeolate, warty, and verrucose (Plate 1, a-c)." No verbal definitions are given; apparently one is supposed to look these up in the dictionary mentioned. This is more than may be expected from the average user, especially if he is working outside the U.S.A. Why this neglect of that classic work by B. D. Jackson, "A glossary of botanic terms", or of that other one, W. T. Stearn's, "Botanical Latin"? The effect is that 'warty' and 'verrucose', which are used as having different meaning, in reality express precisely the same idea. The choice of the other three terms is also hardly fortunate.

'Sphaeropedunculate' for the young basidia of *Pseudotomentella* invokes an exaggeration of the average actual shape, usually a more or less broadly clavate body with a slender stalk.

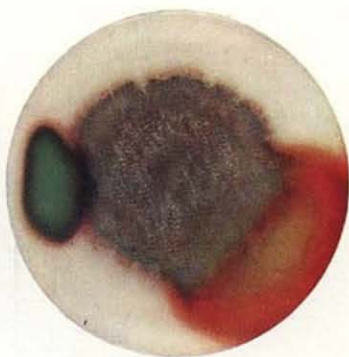
As to the references, the abbreviations of titles of serials and books are often inconsistent and not free from errors. Why "känn." (without a capital); why the use of the subtitle "Ann. Mycol. . . (series II)" for "Sydowia"? "Wein" should be "Wien"; and so on.

There are also a few nomenclatural questions that in my opinion have not been properly solved. Some of these may be discussed on another occasion in preliminary notes preceding a check list of the European resupinate Hymenomycetes by the reviewer.

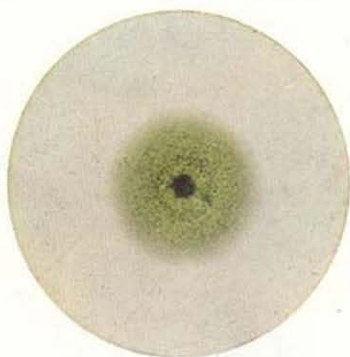
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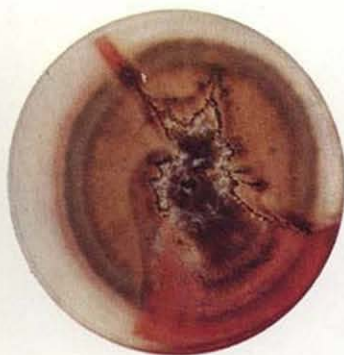
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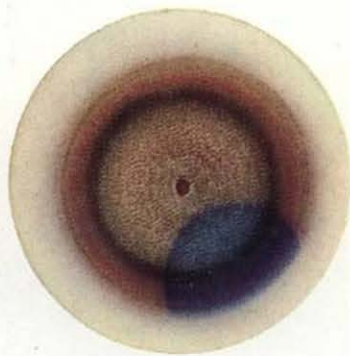
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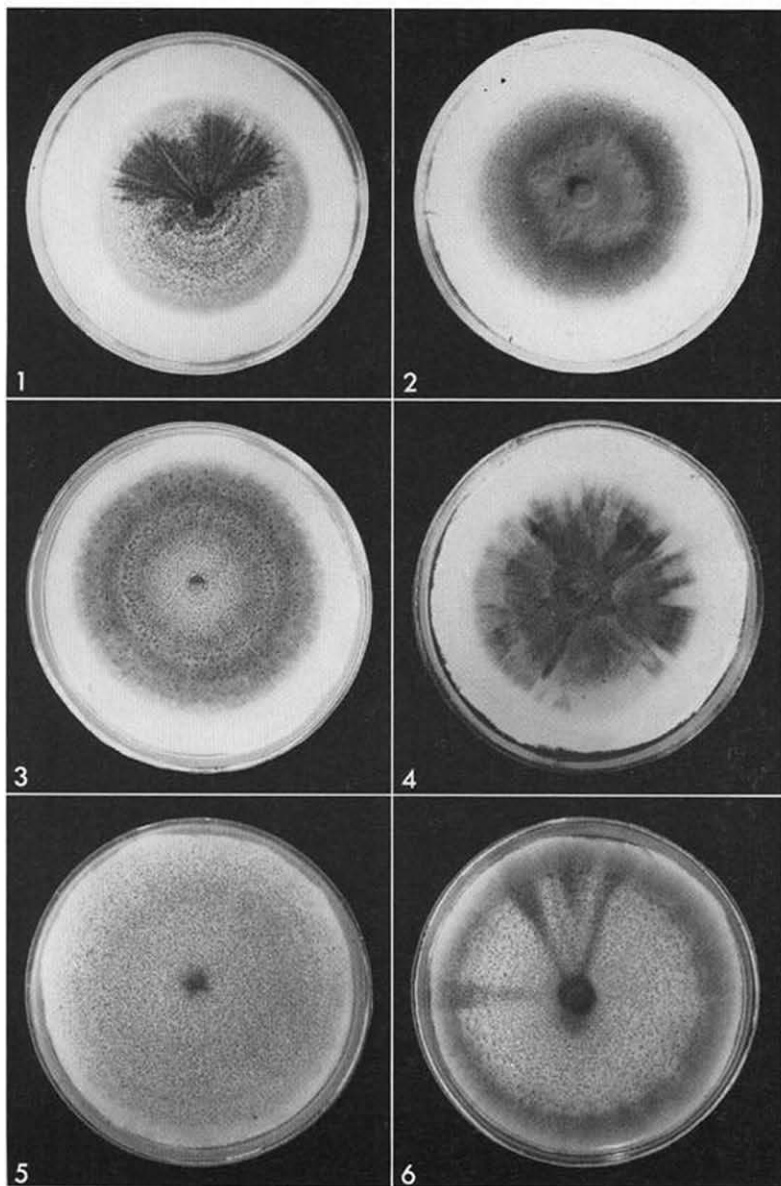
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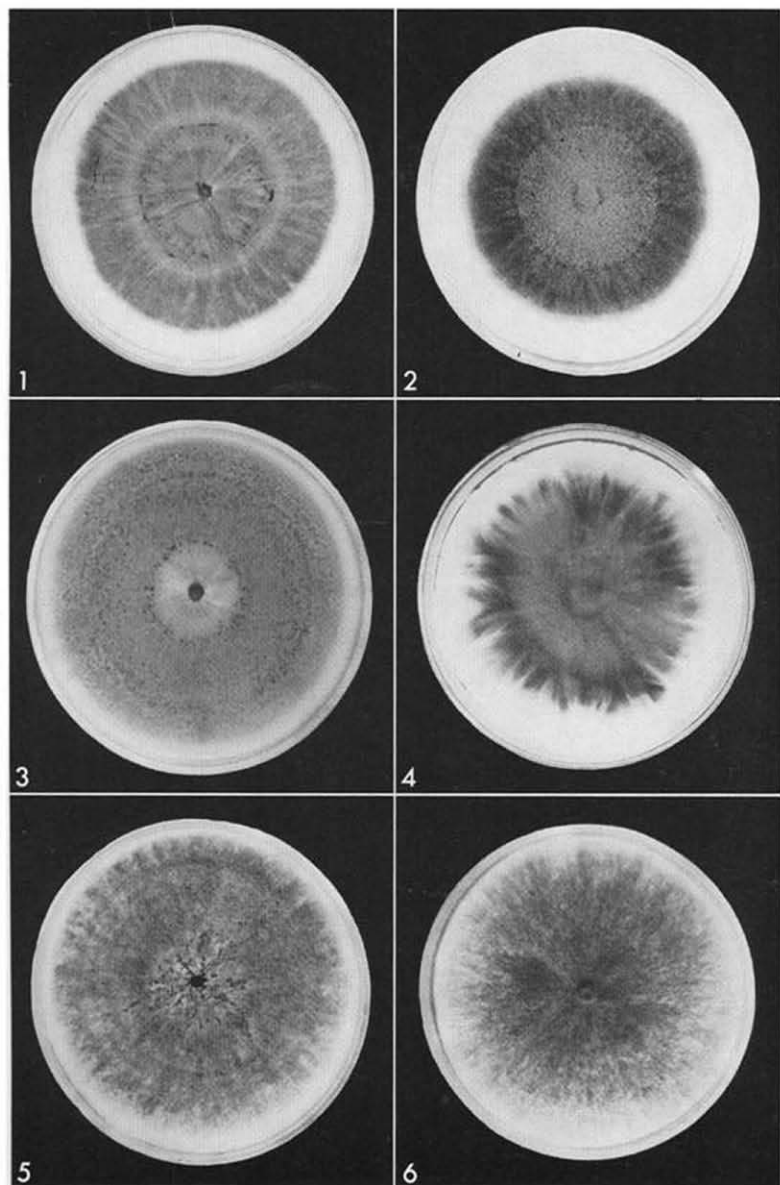


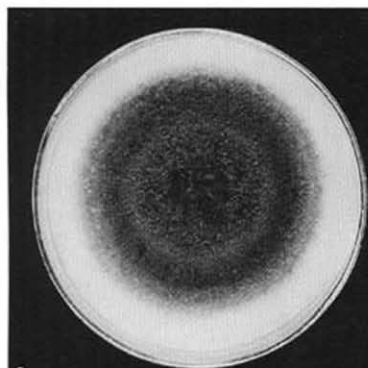
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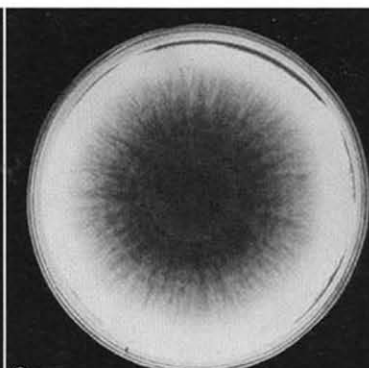
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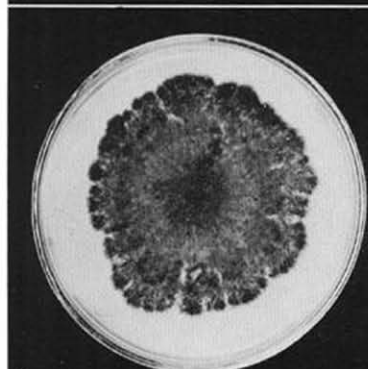




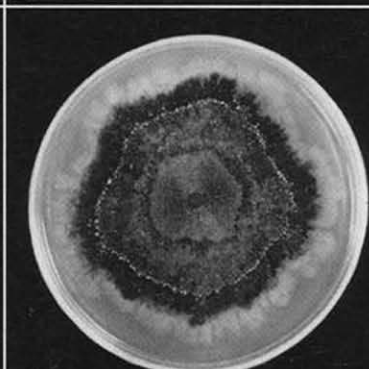
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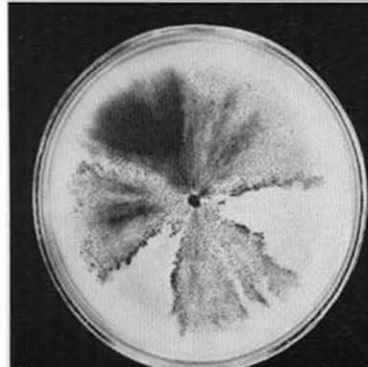
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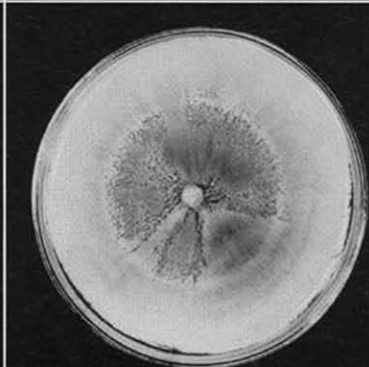
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