PERSOONIA
Published by Rijksherbarium / Hortus Botanicus, Leiden
Volume 15, Part 4, pp. 405–430 (1994)

ULTRASTRUCTURE OF THE ASCUS APICAL APPARATUS IN LEOTIA LUBRICA AND SOME GEOGLOSSACEAE (LEOTIALES, ASCOMYCOTINA)

GERARD J.M. VERKLEY

Rijksherbarium / Hortus Botanicus, P.O. Box 9514, 2300 RA Leiden, The Netherlands

The ultrastructure of the apical apparatus and lateral ascus wall is compared in *Leotia lubrica* and five species currently placed in the Geoglossaceae. The lateral ascus wall consists of two layers, of which the inner one increases in thickness in the apical apparatus. Considerable differences in substructure of both layers are described. On the basis of general morphology of the apical apparatus, structure and PA-TCH-SP reactivity of the apical thickening and annulus, and occurrence of an annular protrusion four main categories are distinguished. A reactive annulus is demonstrated in the apical apparatus of all species, including *L. lubrica*.

The species studied are arranged as follows: Category 1a. *Geoglossum nigritum* and *G. cookeianum*; 1b. *Trichoglossum hirsutum*; 2. *Leotia lubrica*; 3. *Microglossum viride*; 4. *Mitrula paludosa*. Most fundamental is considered the position of the annulus in the apical thickening, either fully (category 1) or partly (2–4) occupying the apical thickening, either associated with an annular protrusion (3, 4) or not (1, 2). The data on the ultrastructure of the ascus apical apparatus and lateral wall, and mode of dehiscence indicate that *L. lubrica* takes an isolated position, distant from the other Leotioideae (including Ombrophiloideae) and the Geoglossaceae. *Geoglossum*, *Trichoglossum*, and *Microglossum* can best be maintained as separate genera in the family Geoglossaceae. The ultrastructural data of *M. paludosa* indicate closer affinity with Sclerotiniaceae than with Geoglossaceae.

INTRODUCTION

The family Geoglossaceae Corda accommodates some of the largest and most conspicuous forms of the inoperculate discomycetes (Leotiales S. Carp.). It has been the subject of several monographical studies and most of its representatives are relatively well-known (Durand, 1908, 1921; Imai, 1941, 1955, 1956; Nannfeldt, 1942; Mains, 1954, 1955; Eckblad, 1963). Before the fundamental significance of the structure of the ascus apical apparatus became fully appreciated, clavate and capitate inoperculate discomycetes were treated as close relatives of operculate discomycetes like *Helvella* s.l. (Rehm, 1896).

The macromorphology of the ascocarp has always been a character of major importance to the taxonomy of the Geoglossaceae. But other characters were investigated more closely by workers like Corner (1930), who compared the ontogeny and microanatomy of stipitate, clavate, and capitate (pileate) ascocarps. Imai (1941) emphasized the shape of spores and the fleshy vs. gelatinous consistency of ascocarps. The Leotioideae, erected by Imai for *Leotia* Pers. and *Neocudoniella* Imai, were transferred to the Helotiaceae by Korf (1958). He did so on the ground of similarities in anatomy and gelatinization of excipulum to certain Ombrophiloideae, particularly *Neobulgaria* Petr. Later on, Korf (1973) merged the Ombrophiloideae into the Leotioideae. Maas Geesteranus (1964) emphasized the taxonomic importance of the structure of the stipe and the transitional region of stipe and hymenium. Under the influence of these and other relevant studies, most of the capitate genera were transferred from the Geoglossaceae to the Leotiaceae Corda (Helotiaceae sensu auct.) or Sclerotiniaceae Whetz. But many problems concerning the delimitation of genera, the position of the transferred genera, and the boundary between the Geoglossaceae on the one hand and the Leotiaceae and Sclerotiniaceae on the other remained unsolved (Benkert, 1983).

The structure of the ascus, another important source for informative characters, has hardly been exploited. In particular the ultrastructure of the apical apparatus may contribute to solving some of these problems. This study aims to determine how the ultrastructural characters of the present Geoglossaceae relate to those of *Leotia lubrica* (Scop.) Pers. and other Leotiaceae (Verkley, 1992, 1993b) and Sclerotiniaceae (Verkley, 1993a). Because the study mainly focuses on the relationships within the large family Leotiaceae, the number of taxa had to remain limited.

Most of these taxa have been the subject of earlier ultrastructural studies (Bellemère, 1975, 1977; Bellemère et al., 1987; Honegger, 1983). But, as explained in previous reports, the results are difficult to compare with those on Leotiaceae and Sclerotiniaceae obtained by Verkley (1992, 1993a, 1993b), and some important data are not yet clarified. For example, Bellemère (1977) and Honegger (1983) studied the apical apparatus in *Leotia lubrica*, but it remained unclear whether it contains an annulus like the apical apparatus in most other Leotiaceae. Bellemère (1977) and Bellemère et al. (1987) also studied the apical apparatus in selected Geoglossaceae, *Geoglossum* spec., *Microglossum viride* (Pers.) Gillet, *Spathularia flavida* Pers.: Fr., *Mitrula paludosa* Fr., and in *Heyderia abietis* (Fr.) Link, now residing in the Leotiaceae.

New and additional data are presented on ascus wall ultrastructure in *Leotia lubrica*, *Geoglossum nigritum* Cooke, *G. cookeianum* Nannf., *Trichoglossum hirsutum* (Pers.) Boud., *Microglossum viride*, and *Mitrula paludosa*. *Trichoglossum hirsutum* (Pers.) Boud. is investigated in this way for the first time. The implications of the data for the taxonomy of these fungi are discussed.

MATERIALS AND METHODS

Fresh material was collected in the field. Specimens were fixed and embedded in Epon as described earlier by Verkley (1992, 1993a). Ultrathin sections were cut using a diamond knife. Sections were either treated for PA-TCH-SP as described earlier (Verkley, 1992), or contrasted with uranyl acetate and lead citrate. Preparations were examined using a Philips EM 300 or Jeol JM 1010 electron microscope at 60 kV.

In the following list details are given about the origin of the collections, deposited in Leiden (L).

Geoglossum nigritum Cooke. Eiland van Rolfers, Amsterdamse Waterleidingduinen, prov. Noord-Holland, the Netherlands, in grassland, Oct. 1992, *G. Verkley 153*; Ruiterplaat, Noord-Beveland, prov. Zeeland, the Netherlands, Oct. 1992, *G. Verkley 141*.

Geoglossum cookeianum Nannf. Ruiterplaat, Noord-Beveland, prov. Zeeland, the Netherlands, in grassland with moss, Oct. 1992, *G. Verkley 140*.

Trichoglossum hirsutum (Pers.) Boud. Eiland van Rolfers, Amsterdamse Waterleidingduinen, prov. Noord-Holland, the Netherlands, in grassland, Oct. 1992, *G. Verkley 152*.

Leotia lubrica (Scop.) Pers. Fôret de St. Prix, Morvan, dép. de Côte d'Or, France, on the ground in mixed forest, Oct. 1990, *J. van Brummelen 7974*.

Microglossum viride (Pers.) Gillet. Payolle, dép. Hautes Pyrénées, France, on the ground amongst mosses, Oct. 1991, *J. van Brummelen 8020*.

Mitrula paludosa Fr. Roode Beek, Vlodrop, prov. Limburg, the Netherlands, on plant debris in running water, May 1990, *H. Huyser s.n.*; Smuddebos, Losser, prov. Overijssel, the Netherlands, June 1990, *F. Ligtenberg s.n.*

A detailed clarification of the terms used for wall structure and stages in ascus development including the corresponding terms used by Bellemère (1977) and Bellemère et al. (1987) has been given elsewhere (Verkley, 1992).

The circumscription of the apical chamber is extended as follows.

Apical chamber: amount of epiplasm enclosed to a variable extent by an annular protrusion, or enclosed by the most protruding part of an apical thickening which is fully occupied by an annulus (e.g. Fig. 4).

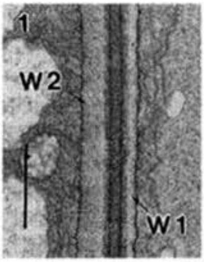
RESULTS

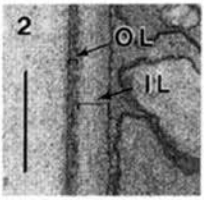
For reasons mentioned in earlier work (Verkley, 1992, 1993a, 1993b) the PA-TCH-SP technique was preferred over conventional staining of ultrathin sections for the study of wall substructure. The contrast obtained with this technique is based on the presence in the walls of PAS-positive (periodic acid-Schiff) polysaccharides. Free, vicinal hydroxyl groups of these polysaccharides are oxidized to aldehyde groups by PA. The addition of TCH to these aldehydes and the subsequent reduction of SP by thiocarbohydrazones results in a fine deposit of metallic silver on the thin sections, referred to as 'PAS-reactivity', or, simply, 'reactivity' in this paper. Since most cytoplasmic structures are insufficiently contrasted by this technique, post-staining with uranyl and lead salts was applied for closer study (Figs. 17, 18). Series of longitudinal median sections of young, immature, mature, and dehisced asci were studied. The lateral ascus wall, the apical apparatus, and some special features of the epiplasm are described.

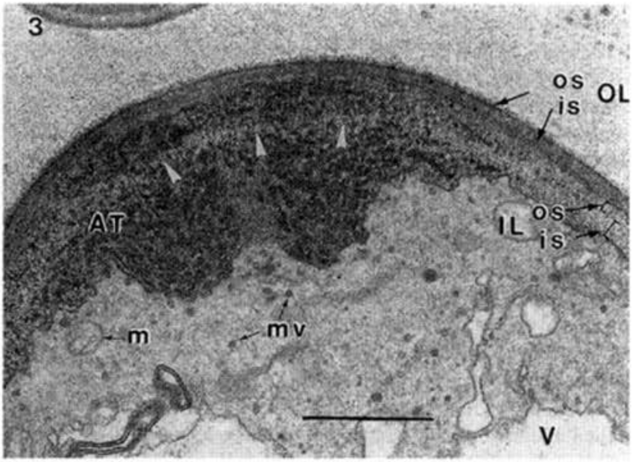
GENERAL OBSERVATIONS

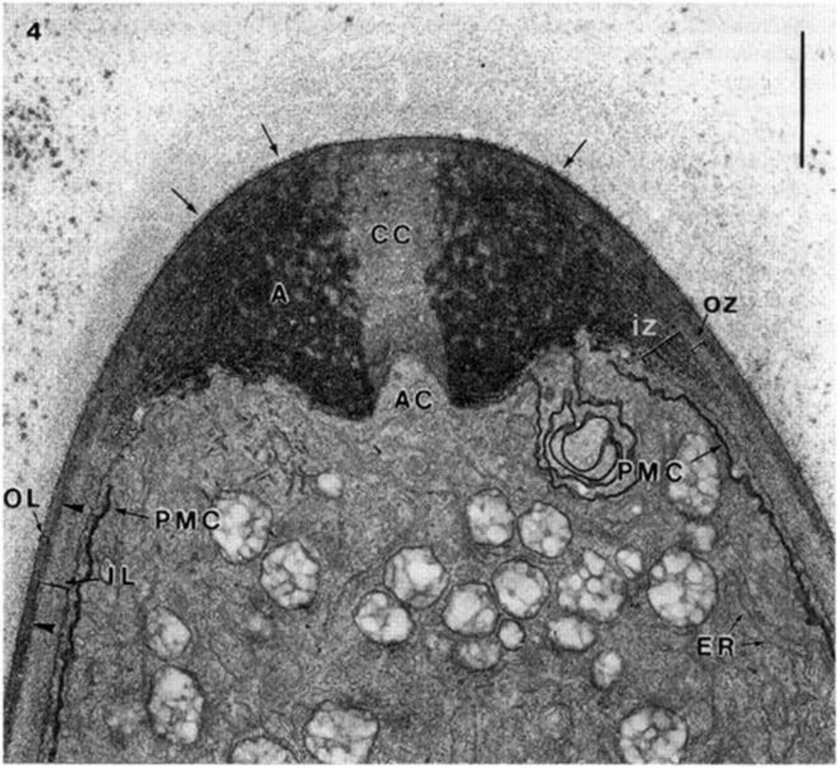
In the young, elongating ascus initial the apical cytoplasm contains a spherical area (circular in thin section) of microvesicles, surrounded by an area with a variable number of larger apical vesicles. During apex formation, when the apical apparatus is formed (Verkley, 1992), a large concentration of microvesicles containing reactive material is found in the cytoplasm in the direct vicinity of the apical wall (mv, Fig. 3).

The species studied all develop two layers in their ascus walls, of which the inner one increases in thickness at the apex. But the substructure and reactivity can differ considerably between species.


1
W2
W1


2
OL
IL


3
os
is
OL
AT
IL
os
is
m
mv
V


4
CC
A
IZ
OZ
AC
PMC
OL
PMC
IL
ER

SPECIFIC DESCRIPTIONS

Geoglossum nigritum — Figs. 1–6, 38

Lateral ascus wall – The ascus gradually tapers over a relatively extensive area in the upper part, and is characterized by a rounded apex. The outer layer, 90–110 nm thick, consists of a very thin, strongly reactive outer stratum and a much thicker, moderately to strongly reactive inner stratum (Figs. 2–4). Towards its inner side this stratum is locally delimited by a discontinuous line of more reactive material in cross section (arrowheads, Fig. 4). Over long distances of the ascus the outer stratum is closely associated with strongly reactive extra-mural material, which, especially over the apical apparatus, extends in bristle-like fibrils from the surface of the wall (arrows, Fig. 4). It represents a very thin layer, even at the apex. The diffuse, granular cap-like layer that covers this material over the upper part of most asci is also found over the ends of paraphyses. In between the hymenial and subhymenial elements a diffuse granulo-fibrillar matrix occurs, containing patches of more concentrated, granular reactive material.

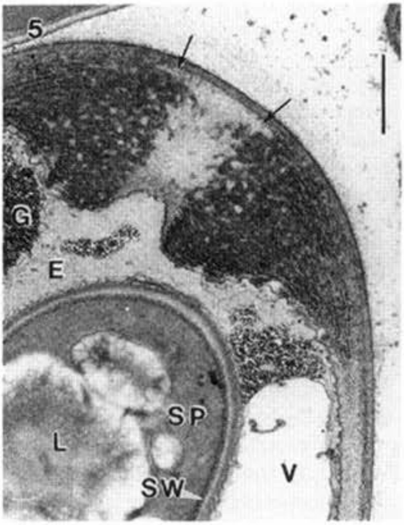
In the young elongating ascus, before the start of apex formation, the outer layer is fully developed, both in reactivity and thickness (W1, Fig. 1). During the following phase of apex formation, when elongation caused by growth is minimized, the inner layer is thickened considerably (W2, Fig. 1). By the time the apex formation is fully completed and a continuous peripheral membrane cylinder (PMC, Fig. 4) is found over an extensive area near the plasma membrane, the inner layer reaches its maximum thickness of about 320–360 nm. The inner layer shows two strata (Figs. 2–4), of which the inner one is the more reactive.

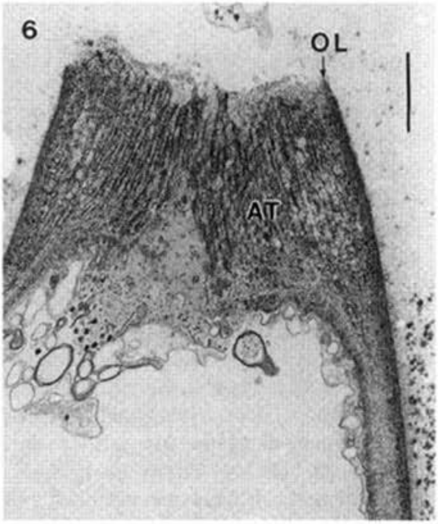
Young ascus – The inner layer increases gradually in thickness over a relatively small area in the apical apparatus. Throughout the inner layer in the apical thickening strongly reactive material is found which constitutes a broad annulus. This annulus completely occupies the apical thickening. The reactivity pattern gradually changes towards the central cylinder (Fig. 4). In the part of the apical thickening most distant from the central cylinder discontinuous layers of strongly reactive material are oriented parallel to the inner face of the wall in a moderately reactive matrix (Fig. 4). Towards the central cylinder this layered pattern is transformed into a pattern in which the strongly reactive material is found in

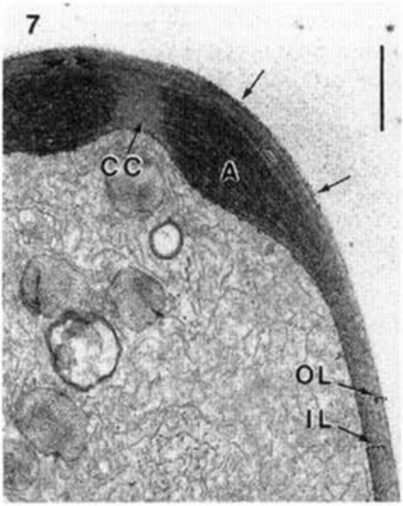
---

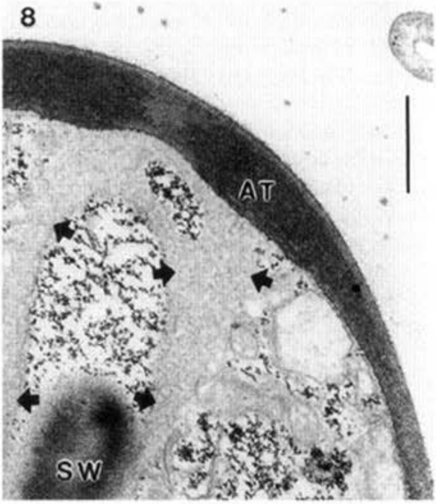
Abbreviations used in Figures 1–42. **A**, annulus; **AC**, apical chamber; **af**, apical funnel; **AP**, annular protrusion; **AS**, ascospore; **AT**, apical thickening; **AW**, ascus wall; **CC**, central cylinder; **E**, epiplasm; **ER**, endoplasmatic reticulum; **G**, glycogen; **IL**, inner layer; **im**, investing membrane; **is**, inner stratum; **iz**, inner zone; **L**, lipid body; **M**, gelatinous matrix; **m**, mitochondrion; **ms**, middle stratum; **mv**, microvesicles; **N**, nucleus; **OL**, outer layer; **os**, outer stratum; **oz**, outer zone; **Pa**, paraphysis; **PMC**, periferal membrane cylinder; **SP**, sporoplasm; **SW**, ascospore wall; **tr**, tractus; **V**, vacuole. **Ws**, wall of seta.

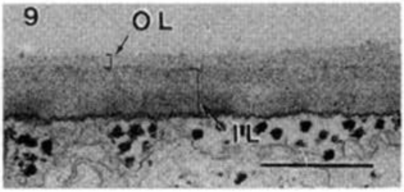
Figs. 1–4. *Geoglossum nigritum*, electron micrographs of longitudinal median sections of ascus lateral walls and apices, treated with PA-TCH-SP (bar represents 1 μm). – 1. Lateral ascus wall of young, elongating ascus (before apex formation, W1) and neighbouring young ascus during apex formation (W2); 2. lateral ascus wall of young ascus after apex maturation has been completed; 3. young ascus, advanced stage of apex formation; 4. young ascus, apex formation completed.

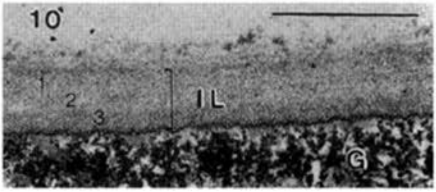

5
G
E
SP
L
SW
V


6
OL
AT


7
CC
A
OL
IL


8
AT
SW


9
OL
IL


10
1
2
3
IL
G

patches. These patches are most concentrated in the part of the apical thickening that protrudes the deepest into the ascoplasm. This part is not an annular protrusion (Verkley, 1992), since the whole area of strongly reactive material is interpreted as the annulus. This changing pattern is so gradual that an annular and a non-annular region in the apical thickening cannot be distinguished. In mounts of material treated with Melzer's or Lugol's iodine solution (IKI) the whole apical thickening appears blue under the light microscope. The inner zone of the apical thickening, i.e. the part that is continuous with the inner stratum of the inner layer in the lateral wall (iz, Fig. 4), is conspicuous in the transitional region between subapical wall and apical thickening. In this region this zone contains strongly reactive material, while the outer zone (oz, Fig. 4), which is continuous with the outer stratum of the outer layer, does not. Such zonal differentiation is not observed further upwards within the inner layer material.

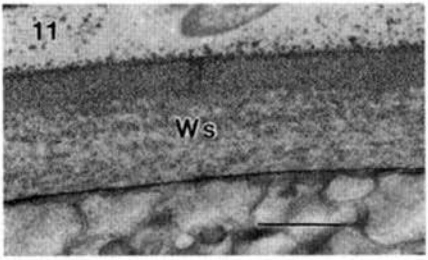
The central cylinder is moderately reactive, but may contain a variable amount of small patches of less reactive material. The boundary between inner and outer layer is particularly conspicuous here (Fig. 4). The invagination of the ascoplasm into the central cylinder represents an apical chamber (for adapted definition see 'materials and methods').

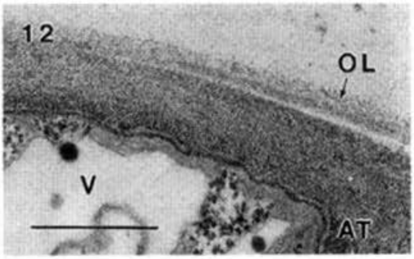
During apex formation there is still a single pattern of randomly distributed patches of strongly reactive material throughout the apical thickening. Only in asci at this stage a conspicuous zone of decreased reactivity is observed throughout the apical apparatus that is being formed (white arrowheads, Fig. 3). It appears to be in exact continuity with the inner stratum of the inner layer in the lateral wall, although it is somewhat thinner. This zone corresponds with the non-blueing zone which can be readily observed when living asci at this stage of development are treated with Lugol's iodine solution and studied with light microscopy (in *G. nigritum* and *G. cookeianum*). In the later stages of development this zone is not observed with TEM or LM.

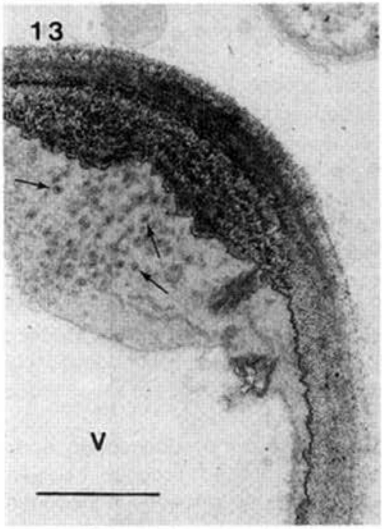
Immature ascus – At first little change is observed. In some asci the reactivity in the upper part of the inner layer material of the central cylinder tends to decrease. Later on, particularly during formation of the secondary ascospore wall, the reactivity of the central cylinder decreases markedly, but not in the lower part delimiting the apical chamber or in the outer layer. The decrease in reactivity is also observed in a small zone in the upper region of the apical thickening that delimits the central cylinder (arrows, Fig. 5). It seems to be in continuity with the outer zone of the apical thickening mentioned earlier. The reactivity pattern of the apical thickening shows no further significant change. No erosion of the outer layer is observed.

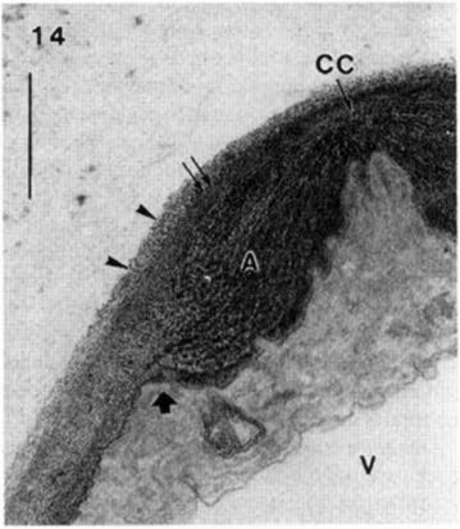
Mature ascus – The apical apparatus is considerably compressed. No further change is observed.

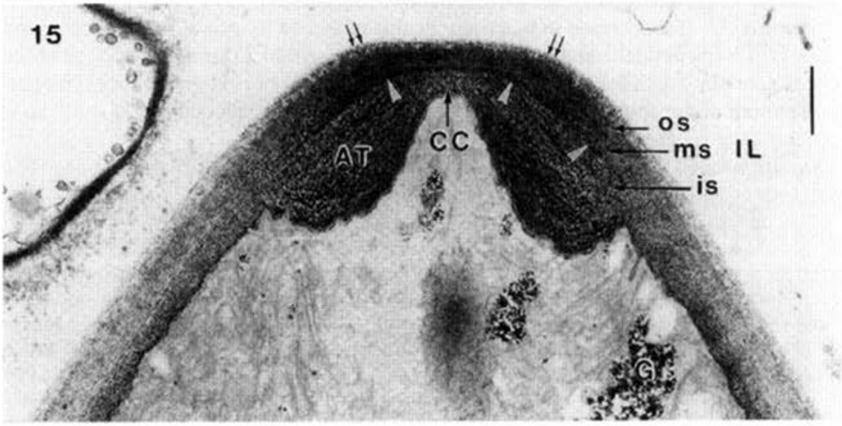
Figs. 5–10. Electron micrographs of longitudinal median sections of ascus apices and lateral ascus walls, treated with PA-TCH-SP (bar represents 1 µm). – 5, 6. *Geoglossum nigritum*. 5. Immature ascus, advanced stage; 6. dehisced ascus. – 7, 8. *Geoglossum cookeianum*. 7. Young ascus, before ascospore delimitation; 8. immature ascus, advanced stage; the wall of the uppermost ascospore (SW) has been grazed; bold arrows indicate boundaries of a strand in the epiplasm (see specific description for details). – 9, 10. *Trichoglossum hirsutum*. 9. Immature ascus, lateral wall, showing intact outer layer; 10. idem, showing disintegrated outer layer.


11
Ws


12
OL
V
AT


13
V


14
CC
A
V


15
AT
CC
os
ms
is
IL
G

Dehisced ascus – After dehiscence the apical thickening is everted over about a right angle. It appears as a rule that some remnants of the central cylinder remain attached to the wall (Fig. 6).

Geoglossum cookeianum — Figs. 7, 8

Lateral ascus wall – The ascus apex shows a shape similar to that in *G. nigritum*. The outer layer, 70–90 nm thick, consists of a very thin, strongly reactive outer stratum and a much thicker, less reactive inner stratum. The inner layer, 200–230 nm thick, also consists of two strata, of which the inner one is the more reactive (Fig. 7). Some reactive material is closely associated with the outer face of the apical wall (arrows, Fig. 7). The extra-mural matrix is similar to the one in *G. nigritum*.

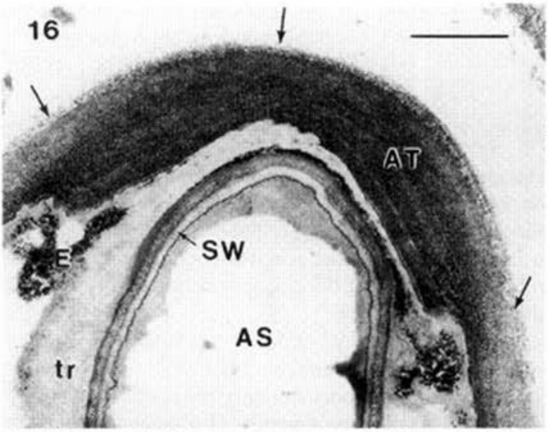
Young ascus – The inner layer increases gradually in thickness at the apex over a relatively small area (Fig. 7). In the apical thickening throughout the inner layer numerous layers of strongly reactive material occur within a moderately reactive matrix. These layers are oriented parallel to the wall surfaces. This reactive material, which constitutes a broad annulus, occurs in a single pattern. When treated with Melzer's or Lugol's iodine solution it appears blue under the light microscope. Randomly distributed patches of strongly reactive material are sometimes found throughout the annulus. The part of the apical thickening directly surrounding the central cylinder protrudes into the ascoplasm less profoundly than in *G. nigritum*. There is no annular protrusion, and the invagination of the inner face of the wall at the central cylinder represents a weakly developed apical chamber (Verkley, 1992). In the inner zone of the apical thickening, which is continuous with the inner stratum of the inner layer in the lateral wall, the reactive annular material occurs further downwards than in the outer zone. The central cylinder is moderately reactive.

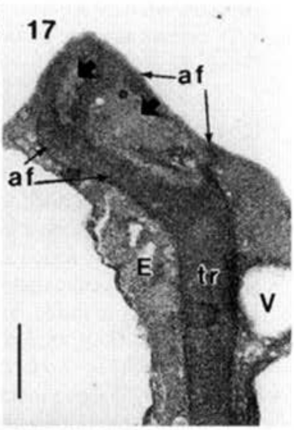
Immature and mature ascus – Upon ripening of the ascus the apical apparatus is increasingly compressed (Fig. 8). No further change is observed.

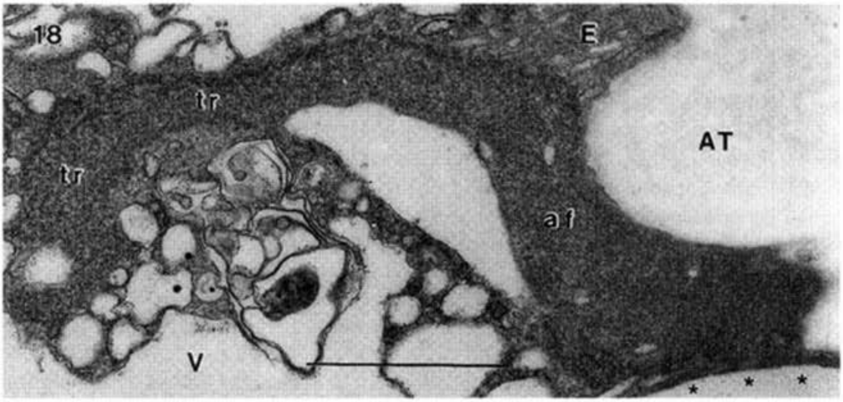
In some asci, a strand was observed filled with moderately reactive tubular to granular material (e.g. the one indicated by bold arrows in Fig. 8). It is a continuous and branched strand from the inner face of the apical wall down to at least the second ascospore from the top. Over a relatively large area it is in close contact with the investing membrane, which separates the spore wall from the epiplasm. It seems to correspond to the refractive strand sometimes observed in water mounts with light microscopy. This strand, which seems to connect the apical apparatus and the upper one or two spores, is observed in mature or advanced immature asci only. The use of cotton blue in lactic acid or iodine solutions does not enhance its rather inconspicuous appearance.

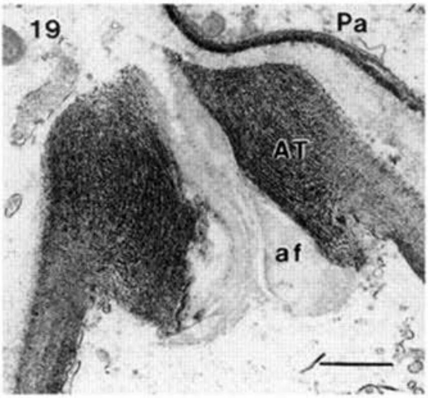
Dehisced ascus – After dehiscence the apical thickening is everted over about a right angle.

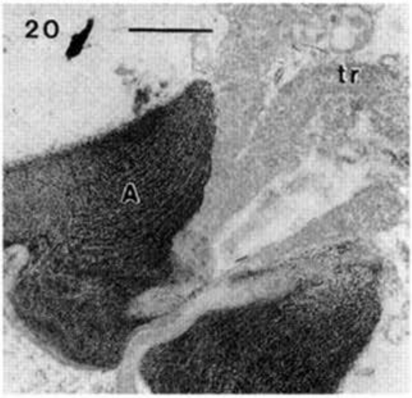
Figs. 11–15. *Trichoglossum hirsutum*, electron micrographs of longitudinal sections of setal wall (Fig. 11), ascus apices and subapical wall, treated with PA-TCH-SP (bar represents 1 µm). – 11. Lateral wall of a seta in the hymenium (Ws); 12. immature ascus, advanced stage, outer layer coming loose from subapical and apical wall; 13. young ascus, early stage of apex formation, the central cylinder has not been grazed; 14. young ascus, semi-median section (central cylinder has not been grazed fully), apex formation completed; 15. immature ascus, middle stage, median section.


16
AT
SW
E
AS
tr


17
af
af
E
tr
V


18
E
tr
tr
AT
af
V
* * *


19
Pa
AT
af


20
A
tr

Trichoglossum hirsutum — Figs. 9–20, 39

Lateral ascus wall – The ascus gradually tapers over a relatively extensive area in its upper part, and is characterized by a rounded to slightly flattened apex. The ascus wall consists of two layers. The outer layer, 160–200 nm thick, consists of a homogeneous, moderately to weakly reactive granular matrix (Fig. 9), reminding of a gelatinous matrix (semi-gelatinous). In general, the reactivity of this layer decreases during the development of the ascus. In large areas along the lateral wall it may disintegrate (Fig. 10) or, in the subapical region, come loose from the inner layer (Fig. 12). At the base of the ascus the outer stratum of the inner layer shows an increased reactivity, contrasting with the weakly reactive outer layer here, which does not participate in the basal septum of the ascus. Thus, it can be ascertained that the interpretation of the boundary of both layers in the lateral and apical wall is correct. In its more disintegrated form the outer layer misleadingly resembles an extra-mural gelatinous layer.

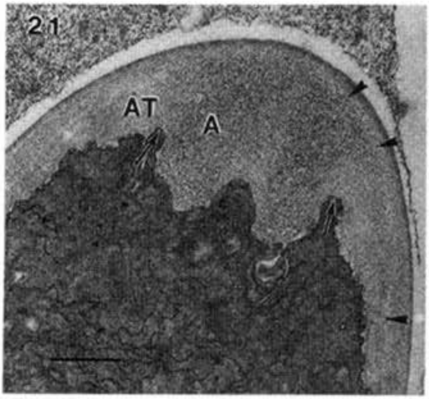
The inner layer, 650–750 nm thick, seems to consist of three strata, of which the middle one is the weakest, and the inner one usually the most reactive (Figs. 9, 10). A diffuse, fibrillar to fibrillo-granular matrix occurs between the elements of the hymenium and subhymenium. Throughout, small patch-like concentrations of reactive material are observed. These patches are contrasted significantly by uranyl acetate and lead citrate, especially when compared with the walls.

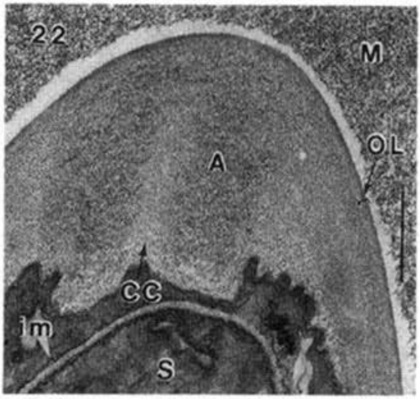
Young ascus – The young elongating ascus shows a rounded apex. The shape of the apex changes into the one described above when the ascus has reached about 90% of its ultimate length at maturity, and apex formation is started. During apex formation, numerous microvesicles containing strongly reactive material are observed in the ascoplasm near the apex (arrows, Fig. 13).

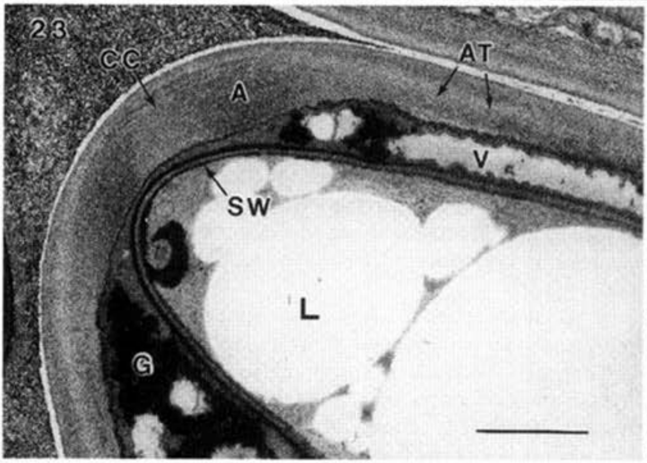
The inner layer in the apical apparatus firstly increases abruptly in thickness (bold arrow, Fig. 14), and then narrows again gradually towards the central cylinder. In all strata of the inner layer the matrix reaches its maximum reactivity in the apical apparatus (Fig. 14). The outer stratum is homogeneously and strongly reactive in the apical region and shows no layered pattern of reactivity (double arrows, Fig. 14; see also os, Fig. 15). The matrix of the middle stratum is less reactive. The inner boundary of the middle stratum is clearly delimited by a continuous thin layer of strongly reactive material in the inner stratum (white arrowheads, Fig. 15). The middle stratum may contain some discontinuous layers of strongly reactive material. But most of this material, which constitutes a broad annulus, is confined to the inner stratum of the inner layer. In this stratum the layered pattern of strongly reactive material is found throughout, and, especially towards the inner face of the wall, this pattern becomes more profound as the layers become thicker

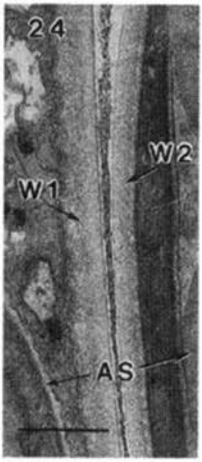
---

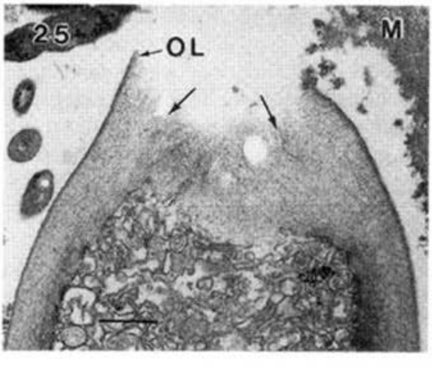
Figs. 16–20. *Trichoglossum hirsutum*, electron micrographs of longitudinal sections of ascus apices, treated with PA-TCH-SP or post-stained with uranyl acetate and lead citrate (U/L) (bar represents 1 µm). – 16. Immature ascus, advanced stage, semi-median section (central cylinder has not been grazed); 17. mature ascus, showing apical funnel (af) and tractus (tr, U/L); due to very low contrast the ascus wall is not visible in this micrograph; 18. mature ascus; asterisks indicate the position of the ascospore during fixation; afterwards, this spore has considerably shrunken during dehydration (U/L); 19. dehisced ascus, showing remains of apical funnel (af); 20. idem, also showing remains of tractus (tr) outside ascostome.

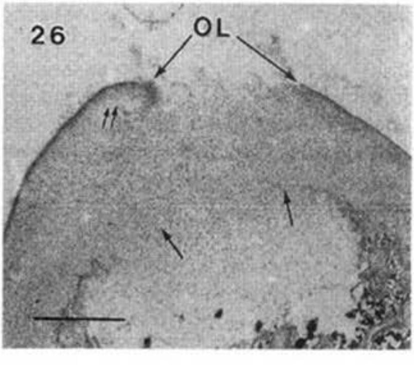

21
AT
A


22
M
A
OL
CC
im
S


23
CC
A
AT
V
SW
L
G


24
W2
W1
AS


25
OL
M


26
OL

and continuous over longer distances (Fig. 14). The annulus thus fully occupies the apical thickening, and there is no annular protrusion.

The central cylinder is a narrow structure, and is thinner than the lateral wall. Its reactivity pattern is much like the one found in the apical thickening. But in the inner stratum of the inner layer the strongly reactive material seems less densely arranged than in the apical thickening.

The material of the outer layer in the subapical and apical parts differs from that in the lateral part of the wall. It mainly consists of reactive fibrils oriented perpendicularly to the outer face of the inner layer (arrowheads, Fig. 14). Overall reactivity of this layer increases in the apical apparatus.

Immature and mature ascus – The outer layer becomes thinner over the apical apparatus as the spores mature (double arrows, Fig. 15). Only a diffuse layer of remnants of the outer layer is observed in advanced immature asci (arrows, Fig. 16). The outer face of the inner layer often appears disintegrated also. During secondary ascospore wall formation the apical apparatus becomes increasingly compressed, while the reactivity pattern of distinct, rough layers changes into a pattern of much finer layers. The apical thickening thus appears more homogeneously reactive and the strata less evident (Fig. 16).

During the formation of the primary ascospore wall numerous mitochondria, arrays of endoplasmatic reticulum and glycogen particles are observed in the epiplasm. From the beginning of secondary ascospore wall formation onwards, the organelles rapidly disintegrate and the number of glycogen particles decreases. The epiplasm becomes increasingly vacuolated, and a single, broad plasma strand, or a few of these, can be observed pending from the apical apparatus downwards (Figs. 16, 17), then branching again and making contact with the spores.

With light microscopy the epiplasma strands are also readily visible in water mounts of living or rehydrated herbarium material. The core of the epiplasma strands is highly light-refractive and stains very deep blue when cotton blue (0.2%) in lactic acid is added to the mounts. Thus, in the apical region a funnel-like structure is evident, which broadens towards the inner face of the apical wall and encloses one large or a few smaller circular areas which stain much less intensely. Further downwards it becomes a tractus, which branches to reach the surface of the spores.

With electron microscopy a tractus is demonstrated in the epiplasmic strands, consisting of relatively electron dense material in sections contrasted with uranyl acetate and lead citrate, most likely structural proteins (Figs. 17, 18). Its upper part, indicated as 'apical funnel' (af), is in close association with the inner face of the extremely electron-transparent apical thickening and central cylinder. The apical funnel includes one or a few areas of non membrane-bound epiplasm (bold arrows, Fig. 17). This epiplasm does not differ from that surrounding the tractus and apical funnel. In mature asci, the most apical spore presses against the funnel. Areas of close contact with the tractus are located at the proxi-

Figs. 21–26. *Leotia lubrica*, electron micrographs of longitudinal median sections of ascus lateral walls and apices, treated with PA-TCH-SP (bar represents 1 µm). – 21. Young ascus, shortly before ascospore delimitation; 22. immature ascus, early stage; 23. immature ascus, advanced stage; 24. lateral wall of the early immature ascus shown in Fig. 22 (W1) and a neighbouring, mature ascus (W2); 25. dehisced ascus, outer layer torn at the ascan length axis; 26. idem, but outer layer torn next to the ascan length axis.

mal end or somewhere at the lateral wall of the ascospores, and this appears not to be dependent on the position of the spore within the ascus.

Dehisced ascus – After dehiscence the apical thickening (annulus) is only slightly everted, as it is already at a small angle to the ascan length axis before dehiscence (Figs. 19, 20). The ascus opens at the central cylinder. Remnants of the apical funnel are found still attached to the inner face of the apical thickening, and also remnants of the tractus (tr, Fig. 20), which protrude through the opening. This can also be seen with light microscopy.

Leotia lubrica — Figs. 21–26, 40

Lateral ascus wall – The ascus tapers gradually over a relatively extensive area, and is characterized by a rounded apex. The thickness of the two layers of the ascus wall depends strongly on the stage of development. Mature asci are on average 30% longer than early immature asci when fixed, and about as long as the paraphyses. In mature asci the wall is on average 40% thinner than in early immature asci. Apex formation is started when the asci have reached about 50–60% of their ultimate length at maturity, as could be determined in 1 µm sections of embedded material.

The thickness of the outer layer varies considerably, from 50 up to 80 nm, depending on the stage of development (Fig. 24). The outer layer consists of a very thin, moderately to strongly reactive outer stratum, and a thicker, rather variably reactive inner stratum. The inner layer varies in thickness from 170 up to 300 nm, depending on the stage. The reactivity in the inner layer is even more variable than in the outer one and the results are therefore inconclusive as far as the internal stratification of the inner layer in the lateral wall is concerned. There seems to be an inner zone of increased reactivity, at least in the apical thickening.

A dense, strongly reactive, extra-mural matrix occurs up to the tips of immature asci. This strongly gelatinous substance appears to consist of an even denser granular matrix than the ascus wall inner layer. Mature asci may, in the fixed state, protrude beyond the irregular edge of the gelatinous matrix.

Young ascus – The inner layer thickens at first gradually over a relatively extensive area in the apical apparatus. Then, it increases in thickness more abruptly, forming a fierce protrusion of the wall in the annular region of the apical thickening at this stage (arrows, Fig. 21). The annulus consists of concentrations of reactive material that seem to form a striated pattern within a moderately reactive, granular matrix (Fig. 21). The annular region does not occupy the whole apical thickening, and it is restricted to the inner zone of the thickening (arrowheads, Fig. 21). With light microscopy no blueing is observed with iodine solutions. The central cylinder is moderately reactive in PA-TCH-SP. The outer layer is considerably thinner over the annulus and central cylinder, but in the young and following stages no significant erosion occurs.

Immature ascus – At first little change is observed (Fig. 22). But during secondary ascospore wall formation, the apical thickening is considerably compressed leaving at best an inconspicuous protrusion of the wall into the ascoplasm in the annular region (Fig. 23). The reactive material in the annulus becomes more distinctly arranged in layers.

Mature ascus – The apical apparatus is further compressed and it becomes evident that there is no persistent annular protrusion or apical chamber. The annular reactivity decreases, apparently only shortly before dehiscence. Neither with LM nor with TEM level strand-like structures were observed.

Dehisced ascus – After dehiscence the apical thickening shows only little remnants of annular material. The angle of eversion is variable. The inner layer disintegrates rapidly due to excessive swelling (arrows, Figs. 25, 26), while the outer layer keeps its integrity. Over an area of variable extent the inner layer may become loosened from the outer layer (double arrows, Fig. 26). The opening is usually located at the central cylinder (Fig. 25), but in some asci it seems to be located at least partly in the annular region as well, thus next to the ascan length axis (Fig. 26).

Microglossum viride — Figs. 27–31, 41

Lateral ascus wall – The ascus is characterized by a rounded apex. Over the central cylinder a more or less distinct, rounded protuberance is observed (between bold arrows, Fig. 28). The outer layer, 50–70 nm thick, consists of a strongly reactive outer stratum and a considerably less reactive inner stratum (Fig. 27). The inner layer, 175–200 nm thick, consists of two strata, of which the inner one is more reactive than the outer one. In the outer stratum, however, the reactivity increases from the inner boundary outwards, the outermost part being more reactive than the inner stratum of the outer layer, especially in the subapical region of the wall (Fig. 28).

A diffuse to moderately dense matrix of reactive fibrillar material occurs between the elements of the hymenium, and nearly reaches the tips of mature asci.

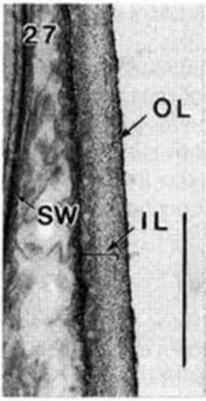
In the collection used for TEM, blueing of the apical apparatus by Melzer's reagent is quite variable, both in the non turgescent, fresh and rehydrated state. The upper part of the annulus blues weakly or not at all, irrespective of the stage of development. The lower part blues weakly in relatively mature and more strongly in young asci.

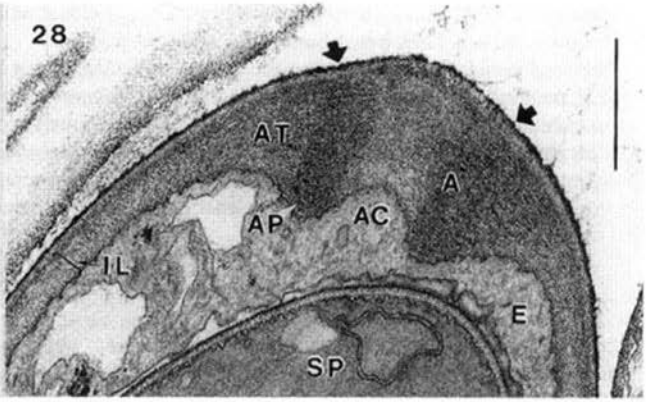
Young ascus – Not observed with TEM.

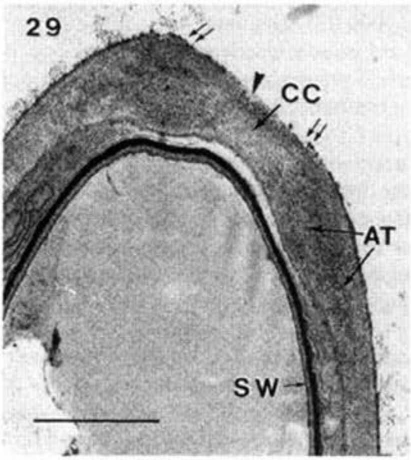
Immature ascus – The inner layer of the ascus wall increases gradually in thickness over a relatively small area in the apical apparatus (Fig. 28). The apical thickening consists of a moderately reactive, granular matrix. It is not fully occupied by the annulus, which consists of roughly granular, strongly reactive material. This material is arranged in a finely striated pattern to a greater or lesser degree. It is often the most concentrated in a narrow region directly surrounding the central cylinder and in the part of the apical thickening that is most protruding into the epiplasm. The latter part is interpreted as an annular protrusion, because the annulus is narrowing into it (Fig. 28). There is an apical chamber. The central cylinder consists of a moderately reactive, granular matrix.

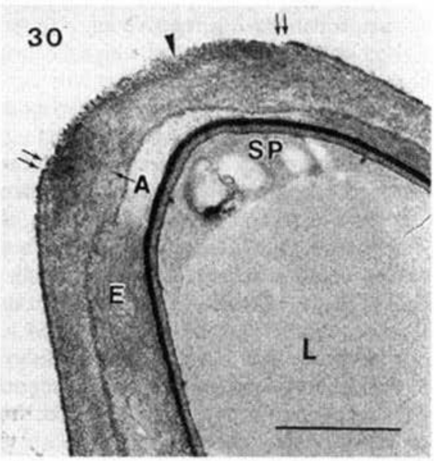
The outer layer is present over the apical apparatus. In the protuberance above the central cylinder (between the bold arrows in Fig. 28), this layer is not more developed or differentiated in structure or reactivity than elsewhere in the apical apparatus. No special structural feature is observed in the inner layer which could be related to this protuberance. In advanced immature asci the apical apparatus is increasingly compressed, and in some of them the outer layer is already partly eroded over the central cylinder and annulus.

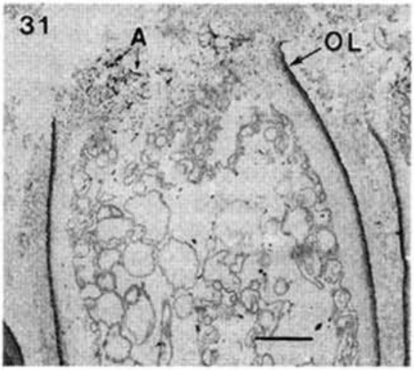
Mature ascus – The outer layer is eroded over the annulus and central cylinder (double arrows, Figs. 29, 30). The apical end of the uppermost ascospore is positioned against the central cylinder, which is bulging out. The annular protrusion, not a rigid but a flexible structure, can still be observed at this stage. It is more or less pushed aside and the

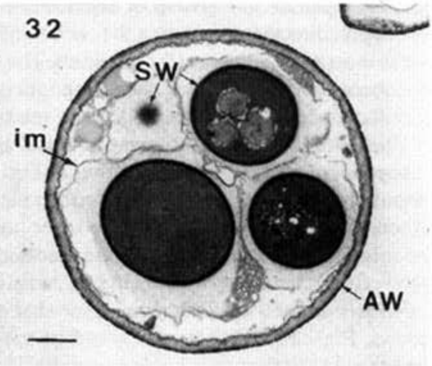

27
OL
SW
IL


28
AT
A
AP
AC
IL
E
SP


29
CC
AT
SW


30
SP
A
E
L


31
A
OL


32
SW
im
AW

apical thickening as a whole is stretched. A further erosion of the exposed part of the inner layer seems to occur (arrowhead, Figs. 29, 30). The reactivity in the lower part of the annulus decreases.

Neither with light microscopy nor with electron microscopy strand-like structures were observed.

Dehisced ascus – After dehiscence the annulus is everted over about a right angle (Fig. 31).

Mitrula paludosa — Figs. 32–37, 42

Lateral ascus wall – The ascus tapers gradually over a relatively extensive area in the upper part, and is characterized by a rounded to truncate-rounded apex. The outer layer, 55–60 nm thick, consists of a strongly reactive outer stratum and a less reactive inner stratum. The inner layer, 145–165 nm thick, shows no stratification (Figs. 32, 33). Only in the subapical wall the reactivity of the inner layer increases, which makes it difficult to observe the boundary line of the two layers. The thickness of the wall decreases to a greater or lesser degree in the subapical region (Figs. 34, 35).

Reactive, fibrillo-granular material covers the apices of most asci. It is found to be continuous with similar material, which covers the ends of paraphyses throughout the hymenium. Further downwards between the elements of the hymenium a similar, but much more diffuse matrix is observed.

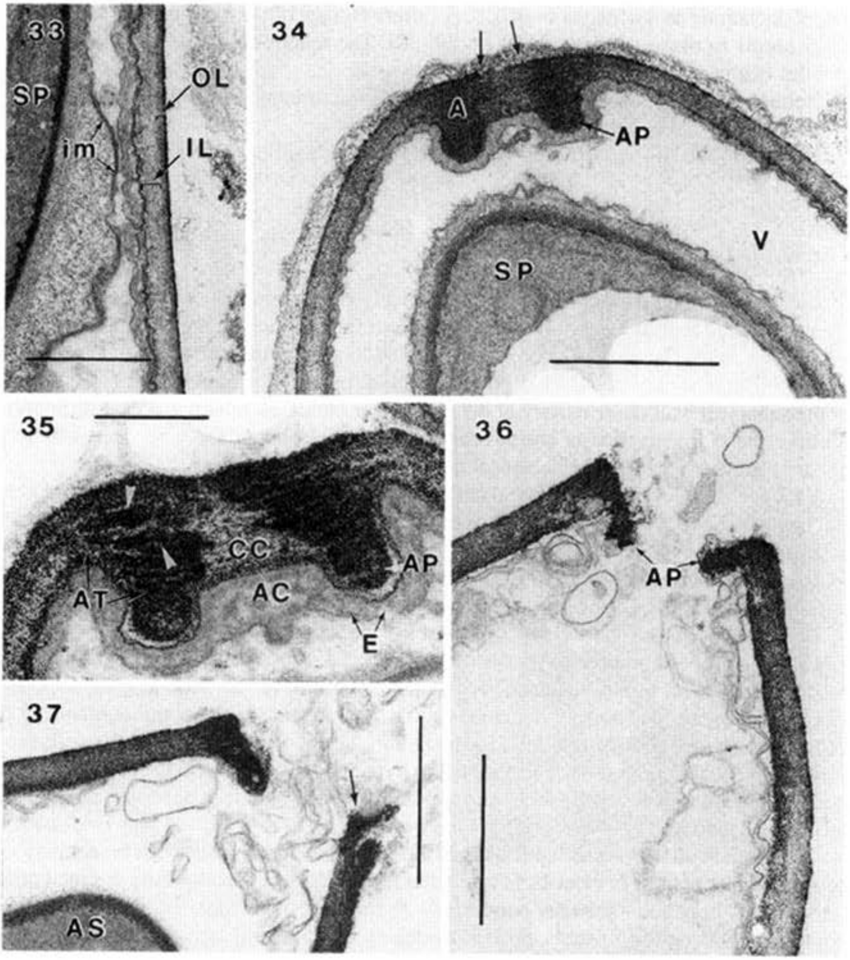
Young ascus – Not observed.

Immature ascus – The inner layer increases in thickness abruptly in the relatively small apical apparatus. An important part of the apical thickening consists of a well-developed annular protrusion, which surrounds an apical chamber. Here, the annulus consists mainly of a homogeneous, strongly reactive matrix. More upwards the annulus broadens to occupy the larger part of the apical thickening. There, it usually consists of densely packed layers of strongly reactive material in a moderately reactive matrix (white arrowheads, Fig. 35). However, in some asci a homogeneous pattern is observed throughout the annular region.

The central cylinder is much thicker than the lateral wall and consists of a moderately reactive granular matrix. In most asci the annular protrusion takes an abaxially oriented position, that is, in median sections pointing away from the axis (Figs. 34, 35), rather than pointing downwards or towards the axis, as observed in Sclerotiniaceae (Verkley, 1993a). In some asci, the outer layer is partly eroded over the central cylinder (arrows, Fig. 34).

Mature ascus – No significant change is observed. The annular protrusion is obviously a persistent and rigid structure. No strand-like structures were observed, neither with LM nor with TEM.

Figs. 27–32. Electron micrographs of longitudinal median sections of ascus lateral walls and apices, and transverse section (Fig. 32), treated with PA-TCH-SP (bar represents 1 µm). – 27–31. *Microglossum viride*. 27. Lateral ascus wall of an advanced immature ascus; 28. immature ascus, early stage; 29. mature ascus, advanced stage; 30. idem; 31. dehisced ascus, rather deteriorated; a strong reduction of reactivity of the inner layer as shown here is typical for somewhat older, dehisced or severely damaged asci of any species. – 32. *Mitrula paludosa*, transverse section of mature ascus.



Figs. 33–37. *Mitrula paludosa*, electron micrographs of longitudinal median sections of ascus lateral wall and apices, treated with PA-TCH-SP (bar represents 1 µm, except in Fig. 35, bar equals 0.5 µm). – 33. Immature ascus, advanced stage, showing lateral ascus wall and ascospore; 34. immature ascus, advanced stage; 35. idem; 36. dehisced ascus; 37. idem, showing a partly damaged annular protrusion (arrow).

Dehisced ascus – After dehiscence the annulus is everted over an angle of about 45–60°. The annular protrusion is normally still intact (Fig. 36), but in a minority of the asci observed it is damaged to a lesser or greater degree (arrow, Fig. 37), or even partly detached from the rest of the apical thickening. No remnants of the central cylinder are found.

DISCUSSION

As in previous studies on Leotiales (Verkley, 1992, 1993a, 1993b) the lateral ascus wall is basically two-layered in the species studied at present.

The organization of the apical cytoplasm of young, elongating asci agrees with that observed in Sclerotiniaceae and most Leotiaceae studied (Verkley, 1993a, 1993b). After the apical apparatus has been formed, from ascospore delimitation onwards, a further increase in length during maturation of the ascus is observed in material processed for TEM. In the Sclerotiniaceae (Verkley, 1993a) an increase of approximately 5 to 20% was measured between young and mature asci in fixed and embedded material, depending on the species. The 30% increase observed in the asci of *L. lubrica* thus seems comparatively high. The amount of decrease in thickness of the lateral wall, which is observed at the same time, was not found before. The variability in reactivity, the lack of internal stratification and especially the extreme swelling occurring after dehiscence are indications for a highly gelatinous inner layer in this species. *Mitrula paludosa* also shows a non-stratified inner layer, but this one is very thin. It needs to be stated here, that these percentages of length increase are less important than the increase exhibited by turgescent, living asci. Shrinkage caused by loss of turgor and dehydration during processing is relatively strong and may be dependent on structure and composition of the wall.

The apical apparatus

Diagrammatic schemes of the apical apparatus and subapical wall are given in Figs. 38–42. In the left half of each scheme relative reactivity in PA-TCH-SP is depicted, while in the right half interpretation of the wall stratification and range of the annular region is shown. The general shape of the apex of fixed asci does not as a rule differ significantly from that observed in living asci with light microscopy.

On the basis of the general morphology of the apical apparatus, the structure of the annulus, and the presence of an annular protrusion four categories can be outlined. The most important characters of these categories are summarized below.

1. Apical thickening fully occupied by a (partly or throughout) distinctly layered reactive annulus, no annular protrusion:

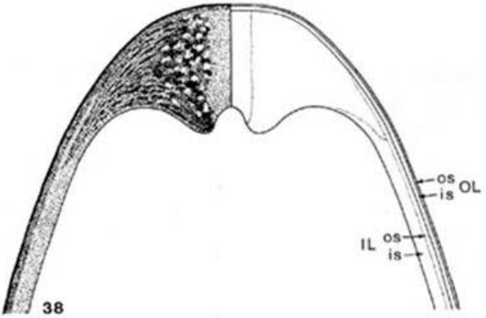
a. The thickest part of the apical thickening directly surrounding the central cylinder (proximal), and enclosing an apical chamber, outer layer consisting of two strata: *Geoglossum nigritum* (Fig. 38) and *G. cookeianum*.

b. The thickest part of the apical thickening distant from the narrow and relatively thin central cylinder (distal), outer layer semi-gelatinous, without internal stratification: *Trichoglossum hirsutum* (Fig. 39).

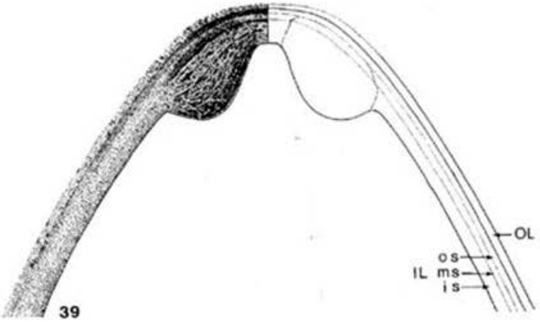
2. Apical thickening extending far downwards, only the larger part of the well-developed upper region of the thickening occupied by a broad, diffusely layered reactive annulus, no persistent annular protrusion: *Leotia lubrica* (Fig. 40).

3. Apical thickening well-developed and not fully occupied by a relatively broad, homogeneously and finely layered reactive annulus, which narrows into a flexible annular protrusion: *Microglossum viride* (Fig. 41).

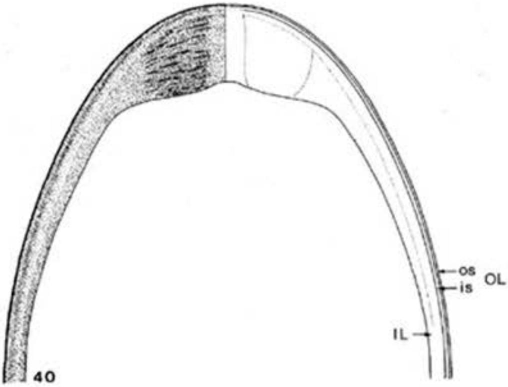
4. Apical thickening mainly consisting of a strongly developed, rigid annular protrusion, the subapical wall thinner just under the apical apparatus, and annular reactivity usually differentiated: *Mitrula paludosa* (Fig. 42).



38

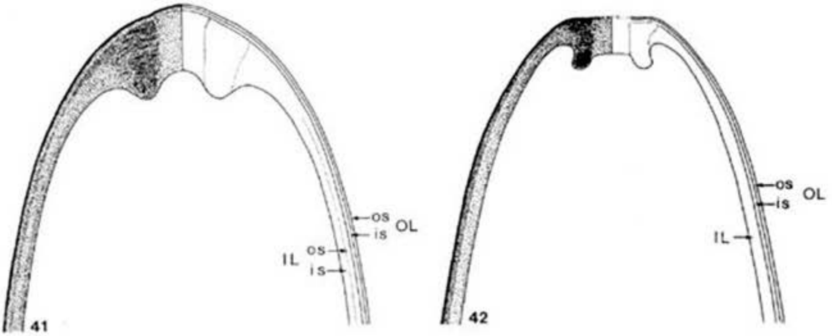


39



40

Figs. 38–40. Diagrammatic schemes of ascus apical apparatus and subapical wall, showing relative PA-TCH-SP reactivity in the left half, and interpretation of layers and strata, and range of the annular region in the right half of each scheme. – 38. *Geoglossum nigritum*, young ascus. – 39. *Trichoglossum hirsutum*, young ascus. – 40. *Leotia lubrica*, immature ascus.



Figs. 41, 42. Diagrammatic schemes of ascus apical apparatus and subapical wall. – 41. *Microglossum viride*, immature ascus. – 42. *Mitrula paludosa*, immature ascus.

The changes in apical wall structure and reactivity during the ripening of the ascus, which were indicated as 'apex maturation' (Verkley, 1992), seem to be of little diagnostic value for the group of species under study. The most important changes are summarized in Table I. Little change in reactivity occurs and there are no distinctive patterns to be recognized, as in 19 species of the Hymenoscyphoideae (Leotiaceae, Verkley 1993b). On the other hand, in most of the studied species of Ombrophiloideae (Verkley, 1992) and Sclerotiniaceae the apex maturation pattern has a diagnostic value (Verkley, 1993a).

Geoglossum

There are some differences between *G. nigritum* and *G. cookeianum* in the shape of the apical thickening, reactivity pattern of the annulus, and apex maturation (Table I). They confirm the separation at the level of the species, which is mainly based on morphology of the paraphyses. *Thuemenidium* Kuntze, which differs mainly by its colourless ascospores, may be closely related to *Geoglossum* (Eckblad, 1963; Benkert, 1983), but its apical apparatus has not been investigated with TEM.

The ultrastructure of the apical apparatus was studied by Bellemère (1975, 1977) in a '*Geoglossum* sp.', and referred to the 'type *Pezicula*'. This type is characterized by a well-developed c-layer (= outer stratum of the inner layer?), a thinner d-layer, shown in scheme Fig. 1A (Bellemère, 1977), but described as 'epaisse' in the text, and a distinctly layered, strongly reactive annulus occupying a rather narrow part of the apical thickening, in contrast to the electron micrograph Fig. 1B (Bellemère, 1977), where it occupies the whole apical thickening. However, the present results show that the inner stratum is thicker than the outer one in the inner layer of the lateral wall and in the apical thickening of *G. nigritum* and *G. cookeianum*. The proportions of the annulus seem to be comparable to those in *Pezicula*, as is the presence of a thin extramural layer of perpendicularly oriented, reactive material, indicated as 'fine periascus' by Bellemère (1977).

Table I. Survey of the main changes in reactivity related to apex maturation of the species studied, and erosion of the outer layer over the apical apparatus.

Species	Changes in reactivity		Erosion
	apical thickening or annulus	central cylinder	OL
Geoglossum nigritum	decrease in upper, narrow region	decrease	o. s. only
Geoglossum cookeianum	none	none	no
Trichoglossum hirsutum	none	none	yes
Leotia lubrica	annulus, decrease (at mature stage)	none	no
Microglossum viride	annulus, decrease in lower part	none	yes
Mitrula paludosa .	none	none	yes/no

Bellemère presented two electron micrographs of dehisced asci in a *Geoglossum* sp., which seem to agree with the present results. He did, however, not give an image or detailed description of the dehisced ascus of *Pezicula*. As described by Ingold (1971), in *Geoglossum* each spore may stopper the ascus for a relatively long period of time prior to discharge. During passage of the spores the eversion may exceed an angle of 90°, as can be observed in asci shooting spores. After fixation some asci were found with an ascospore partly sticking out of the ascostome, much like in Bellemère's micrographs (1977, fig. 1D, E).

Beckett et al. (1974) found a similar way of discharge in *Lophodermella sulcigena* (Rostr.) Höhn. The apical apparatus of this inoperculate species seems to show resemblance in general morphology to that in *Geoglossum cookeianum*, rather than to that in *Hypoderma rubi* (Pers.) DC. ex Chev. (Bellemère, 1977).

Trichoglossum

The separation at the generic level of the setose from the other geoglossoid forms with brown-walled spores is supported by the differences in general morphology of the apical apparatus and structure of the lateral ascus wall. Nevertheless, *Geoglossum* and *Trichoglossum* form a separate group, which differs from other clavate and pileate forms in structure of the ascus apical apparatus and mode of dehiscence. The semi-gelatinous type of outer layer has not been encountered earlier in Leotiales. The lateral wall is comparatively thick, which may be related to the fact that the outer layer tends to disintegrate and weakens during ascus development.

Dehiscence occurs in the same way as in *Geoglossum* (Ingold, 1971). The apical thickening is able to make close contact over a large area with the wall of the spore that is temporarily stoppering the ascostome. This would prevent leakage of fluid and enable the ascus to restore the necessary pressure level after every discharge except the last one.

For the first time the presence of a tractus and apical funnel is recorded at the LM and EM-level in a species of the Leotiales. As pointed out by Beckett (1981), the strand-like structure may disintegrate during chemical fixation. This seems to have occurred in the material of *Geoglossum cookeianum* used for the present study. But it must be stated that the presence of a tractus was not observed beyond doubt with light microscopy in *G. cookeianum*. The fact that a tractus is found in reasonable shape in *T. hirsutum*, a species with thick ascus walls, is probably due to the firmness of the structure. Chadefaud (1944) reported a tractus in *L. lubrica*, but evidence for its presence has neither been obtained at LM nor at EM-level.

Possibly homologous structures have been recorded in Sphaeriales and Pezizales, e.g. recently in certain freeze-substituted and chemically fixed species of *Scutellinia* (Cooke) Lamb. (van Brummelen, 1993), and in freeze-substituted *Thelebolus crustaceus* (Fuckel) Kimbr. (Czymmek & Klomparens, 1992).

The tractus actually connects the uppermost spore to the apical wall, and the spores to each other. It thus effectively ensures a smooth dehiscence in *T. hirsutum*. While it is discharged, each spore pulls its successor into the ascostome, and a new pressure built-up is ensured. There is, however, also some negative effect to be expected as some energy must be spent to break the tractus-spore connection.

Leotia

The general morphology of the apical apparatus, the structure of the annulus and the lateral wall, and the mode of dehiscence suggest an isolated position of *Leotia* within the Leotiales. *Cudonia* Fr. and *Spathularia* Pers., although not staining blue with iodine in the apical apparatus, do not seem to be closely related to *Leotia*. A cladistic analysis of sequences of 18S rDNA placed *Cudonia confusa* Bres. and *Spathularia flavida* in one sister group of *Leotia lubrica* (Landvik et al., 1993).

Spathularia flavida was studied by Bellemère (1977), who referred it to his 'type *Hypoderma*'(based on *H. rubi*). The genera in the Leotioideae sensu Korf (1973) that have been studied so far, *Bulgaria* Fr., *Ombrophila* Fr., *Neobulgaria* Petr. (Verkley, 1992), and *Ascocoryne* J.W. Groves & D.E. Wils. (Bellemère, 1977) do not show affinity to *Leotia* in the characters investigated. In the Leotiaceae the characters of excipular anatomy and gelatinous consistency of the ascocarp correlate meagrely with those of the structure of the ascus wall and apical apparatus.

The present results on the ultrastructure of the apical apparatus in *L. lubrica* differ considerably from those obtained by Bellemère (1977). Firstly, a reactive annulus is demonstrated. Bellemère reported on some fibrillar structures within the 'pendentif' at the moment of dehiscence, but found no annular PA-TCH-SP reactivity. Secondly, the most protruding part of the apical thickening ('pendentif') appears well-developed ('bien développé') at the young and early immature stages, but is not persistent in the mature stage (while the annulus is still very distinct), which is considered relevant, but this was not mentioned by Bellemère. Thirdly, no internal stratification is observed in the lateral wall, while in Bellemère's interpretation a d-layer was found, which is thicker than the c-layer in the lateral wall, and which is the only one increasing in thickness. Fourthly, the present results show that the apical thickening extends much further downwards than reported by Bellemère. Honegger (1983) also investigated the ascus apex of *L. lubrica*, but used a different fixation (acroleïn-glutaraldehyde) and did not apply the PA-TCH-SP technique.

The present results agree with the observations of dehisced asci by Bellemère (1977) and Honegger ('onset of dehiscence', 1983). Chadefaud (LM, 1944) used the term 'hémioperculé' for *L. lubrica*, putting emphasis on the observations that opening of the ascus wall occurs occasionally next to the ascus length axis in such a way, that it resembles the dehisced state of an operculate ascus. This variable way of dehiscence in *L. lubrica* is, however, merely the result of the diffuse structure of the annulus.

Microglossum

Bellemère et al. (1987) reported the presence in the apical apparatus of two separate rings ('anneau inférieur' and 'anneau supérieur'), differing in reactivity pattern. They placed *Microglossum* in the 'type *Pezicula*' of Bellemère (1977), close to *Geoglossum*. The present results show a change in level rather than in pattern of annular reactivity, and such a gradual change that there is no reason to designate two annuli in the apical apparatus of *M. viride*. The intensity of blueing with iodine of the annulus correlates positively with this level in reactivity. The upper part of the annulus blues much weaker than the lower part.

Unfortunately, detailed information on the way the spores are discharged is not available. At this point it is difficult to place *Microglossum*, but its position in the Geoglossaceae is not an unacceptable one. Benkert (1983) stated that many characters would support a fusion of *Geoglossum* and *Microglossum* (and *Thuemenidium*), but the ultrastructural data clearly oppose to this. The main difference between *Microglossum* and *Geoglossum* is that in the former the annulus occupies a restricted area of the apical thickening, reaching the inner boundary of the wall only in the annular protrusion. In this respect, and in the structure of the outer layer *Microglossum* also differs from *Bulgaria* (Verkley, 1992). Baral (1987) designated *Microglossum* and *Mitrula paludosa* to his apex 'typ *Bulgaria*' (LM). Although the annular protrusion is flexible and appears compressed in the mature stage, it remains a true protrusion, in contrast of that in *L. lubrica*. It is, however, different in structure from that found in *M. paludosa*.

Mitrula

Bellemère (1977) regarded the apex of *Mitrula paludosa* as a variety of his 'type *Bulgaria*'. There is certainly a resemblance at the LM-level (Baral, 1987). But in contrast to that in *Bulgaria* (Verkley, 1992), the dehisced ascus shows a limited, but distinct eversion of the very compact annular protrusion. Moreover, electron microscopy made it clear that the outer layer lacks any perpendicularly oriented constituents, and the annulus does not occupy the apical thickening completely, although close observation is necessary in the weakly developed distal part of the apical thickening. Only the thinning of the subapical wall reminds of *Bulgaria inquinans*

Well-developed annular protrusions like the one found in *M. paludosa*, occur frequently in the family Sclerotiniaceae (Schoknecht, 1975; Bellemère, 1977; Verkley, 1993a). Perhaps the genera which develop similar ascocarps, like *Mitrulinia* Spoon. or *Scleromitrula* Imai are related to *M. paludosa*. Their species have ascus apices which blue only indistinctly or not at all with iodine, at least in herbarium material (Spooner, 1987), which is uncommon in the family. This does not necessarily mean that the structure of the apical apparatus is essentially different. Investigations of this structure in *Mitrulinia* and *Scleromitrula* could provide useful information.

CONCLUSIONS

The ultrastructural data on the apical apparatus and lateral ascus wall suggest that:

(1) *Leotia lubrica* takes an isolated position, rather distant from other Leotioideae sensu Korf (1973, including Ombrophiloideae, Leotiaceae) and the Geoglossaceae investigated;

(2) *Geoglossum*, *Microglossum*, and *Trichoglossum* should be maintained as separate genera of the family Geoglossaceae;

(3) *Mitrula paludosa* is more closely related to members of the Sclerotiniaceae than to members of the Geoglossaceae.

ACKNOWLEDGEMENTS

The author is greatly indebted to Dr. J. van Brummelen for his most stimulating and supportive attention throughout this study. Dr. T. Boekhout, Dr. G.M. Lokhorst and Prof. Dr. C. Kalkman are gratefully acknowledged for critically reading the manuscript, and W. Star for giving technical advice. The author wishes to thank also those who have assisted in providing fungal material: F. Ligtenberg, L.M. Jalink, M.M. Nauta, and E.C. Vellinga.

REFERENCES

Baral, H.O. 1987. Der Apikalapparat der Helotiales. Eine lichtmikroskopische studie über Arten mit Amyloidring. Z. Mykol. 53: 119–135.

Beckett, A. 1981. The ascus with an apical pore: development, composition and function. In: D.R. Reynolds (eds.), Ascomycete Systematics. The Luttrellian Concept. New York.

Beckett, A., Heath, I.B. & McLaughin, D.J. 1974. An atlas of fungal ultrastructure. London.

Bellemère, A. 1975. Étude ultrastructural des asques: la paroi, l'appareil apical, la paroi des ascospores chez des Discomycètes inoperculés et des Hystériales. Physiol. végét. 13: 393–406.

Bellemère, A. 1977. L'appareil apical de l'asque chez quelques discomycètes: Étude ultrastructurale comparative. Rev. Mycol. 41: 233–264.

Bellemère, A., Janex-Favre, M.C. & Parguey-Leduc, A. 1987. Marius Chadefaud et les asques: données inédites. Études ultrastructurales complémentaires. Bull. Soc. bot. Fr. 134, Lettres bot. 3: 217–246.

Benkert, D. 1983. Bemerkenswerte Ascomyceten der DDR. VI. Die weißsporigen Geoglossaceen. Gleditschia 10: 141–172.

Brummelen, J. van. 1993. Ultrastructure of the ascus and the ascospore wall in Scutellinia (Pezizales, Ascomycotina). Persoonia 15: 129–148.

Chadefaud, M. 1944. Études d'asques IV: L'asque hémioperculé de Leotia lubrica. Rev. Mycol. 9: 3–13.

Corner, E.J.H. 1930. Studies in the morphology of Discomycetes III. The Clavulae. Trans. Br. mycol. Soc. 15: 107–120.

Czymmek, K.J. & Klomparens, K.L. 1992. The ultrastructure of ascosporogenesis in freeze-substituted Thelebolus crustaceus: enveloping membrane system and ascospore initial development. Can. J. Bot. 70: 1669–1683.

Durand, E.J. 1908. The Geoglossaceae of North America. Ann. myc. 6: 387–477.

Durand, E.J. 1921. New or noteworthy Geoglossaceae. Mycologia 13: 184–187.

Eckblad, F.E. 1963. Contributions to the Geoglossaceae of Norway. Nytt Mag. Bot. 10: 137–158.

Honegger, R. 1983. The ascus apex in lichenized fungi IV. Baeomyces and Icmadophila in comparison with Cladonia (Lecanorales) and the non-lichenized Leotia (Helotiales). Lichenologist 15: 57–71.

Imai, S. 1941. Geoglossaceae Japoniae. J. Fac. Agric., Hokkaido Univ. 45: 155–264.

Imai, S. 1955. Contributiones ad studia monographica Geoglossacearum. II. Sci. Rep. Yokohama Nat. Univ. Sec. II, 4: 1–11.

Imai, S. 1956. Contributiones ad studia monographica Geoglossacearum. III. Studia classificationis phylogenicarum. Sci. Rep. Yokohama Nat. Univ. Sec. II, 5: 1–8.

Ingold, C.T. 1971. Fungal spores. Their liberation and dispersal. Oxford, U.K.

Korf, R.P. 1958. Japanese discomycete notes I–VIII. Sci. Rep. Yokohama Nat. Univ. Sec. II, 7: 7–35.

Korf, R.P. 1973. Discomycetes and Tuberales. In: G.C. Ainsworth, F.K. Sparrow & A.S. Sussman (eds.), The fungi, an advanced treatise 4A: 249–319.

Landvik, S., Eriksson, O.E., Gargas, A. & Gustafsson, P. 1993. Relationships of the genus Neolecta (Neolectales ordo nov., Ascomycotina) inferred from 18S rDNA sequences. Syst. Ascom. 11: 107–118.

Maas Geesteranus, R.A. 1964. On some white-spored Geoglossaceae. Persoonia 2: 81–96.

Mains, E.B. 1954. North American species of Geoglossum and Trichoglossum. Mycologia 46: 586–631.

Mains, E.B. 1955. North-American hyaline-spored species of the Geoglossaceae. Mycologia 47: 846–877.

Nannfeldt, J.A. 1942. The Geoglossaceae of Sweden (with regard also to the surrounding countries). Ark. Bot. 30 (4): 1–67.

Rehm, H. 1887–1896. Die Pilze Deutschlands, Oesterreichs und der Schweiz. III. Abteilung: Ascomyceten. Hysteriaceen und Discomyceten. Rabenh. Krypt.-Fl. Pilze 3: 1–1275.

Schoknecht, J.D. 1975. Structure of the ascus apex and ascospore dispersal mechanisms in Sclerotinia tuberosa. Trans. Br. mycol. Soc. 64: 358–362.

Spooner, B.M. 1987. Helotiales of Australasia: Geoglossaceae, Orbiliaceae, Sclerotiniaceae, Hyaloscyphaceae. Bibl. Mycol. 116: 1–711.

Verkley, G.J.M. 1992. Ultrastructure of the apical apparatus of asci in Ombrophila violacea, Neobulgaria pura and Bulgaria inquinans (Leotiales). Persoonia 15: 3–22.

Verkley, G.J.M. 1993a. Ultrastructure of the ascus apical apparatus in ten species of Sclerotiniaceae. Mycol. Res. 97: 179–194.

Verkley, G.J.M. 1993b. Ultrastructure of the ascus apical apparatus in Hymenoscyphus and other genera of the Hymenoscyphoideae (Leotiales, Ascomycotina). Persoonia 15: 303–340.

PERSOONIA
Published by Rijksherbarium / Hortus Botanicus, Leiden
Volume 15, Part 4, pp. 431–487 (1994)

CONTRIBUTIONS TOWARDS A MONOGRAPH OF PHOMA (COELOMYCETES) – III

1. Section Plenodomus: Taxa often with a Leptosphaeria teleomorph

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

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

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

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

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

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

---

[1] Karel Doormanstraat 4^5, NL-2041 HD Zandvoort, The Netherlands.

[2] Plant Protection Service, P.O. Box 9102, NL-6700 HC Wageningen, The Netherlands.

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

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

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

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

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

There does appear to be some host specialization in *Phoma* sect. *Plenodomus,* although most species are known only from dead tissue (necrophytic). This specialization and the adaptation of the scleroplectenchymatous pycnidia to low or high temperatures may explain the difficulty in getting some members of this section to grow in vitro under normal laboratory conditions. They do not grow well and do not produce pycnidia readily, often losing their ability to produce pycnidia quickly. This has a bearing on the process of the identification as discussed in the explanatory note of the key to the species and varieties.

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

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

MATERIAL AND METHODS

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

KEY TO THE SPECIES AND THE VARIETIES[3]

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

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

---

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

1a. Scleroplectenchymatous pycnidia (II) on dead stems (occasionally on roots) of herbaceous plants 2

b. Scleroplectenchymatous pycnidia (II) on dead bark or wood (occasionally petioles) of deciduous trees and shrubs 24

2a. Pycnidia-II variable in size, relatively large, often exceeding 500 µm diam.; sometimes only pycnosclerotia (III) 3

b. Pycnidia-II usually not exceeding 500 µm diam. 5

3a. All scleroplectenchyma cells in mature pycnidia having about the same wall-thickness; pycnidia-II mostly 600–700 µm diam., with convex base of elongated cells and a long broad cylindrical neck up to 700 µm, usually with a somewhat swollen top; conidia mostly 4–5 × 1.5–2 mm; on dead stems of *Mercurialis perennis* (Euphorbiaceae); specific necrophyte .... 1. *P. macrocapsa*

[Also produces pycnidia-II in vitro, but usually with less pronounced neck.]

b. Scleroplectenchyma cells with an exceptionally thickened wall and a very small lumen (like stone cells); in addition to pycnidia-II, scleroplectenchymatous pycnosclerotia (III) frequently occur 4

4a. Conidia small, usually not exceeding 4.5 µm in length, mostly 3.5–4.5 × 1–1.5 µm; pycnidia-II mostly 300–700 µm diam., not or only slightly papillate, with narrow pore or opened by rupture; sometimes only pycnosclerotia (III); on dead stems and roots of cultivated *Brassica* spp. (Cruciferae); serious cosmopolitan pathogen
2. *P. lingam*, teleomorph *L. maculans*

[Produces only pycnidia-I in association with disease symptoms, on seed, and in vitro.]

b. Conidia up to 6 µm in length, mostly 4.5–6 × 1.5–2.5 µm; pycnidia-II mostly 350–800 µm diam., usually with long thin tubular necks of various lengths, up to 800 µm; sometimes only pycnosclerotia (III); on roots and occasionally on stems of various herbaceous plants; low temperature pathogen (especially known from the arctic regions of Eurasia and North America) .... 3. *P. sclerotioides*

[Produces also pynidia-II and pycnosclerotia (III) in vitro.]

5a. Pycnidial base convex with conspicuous diverging rows of elongated cells 16

b. Pycnidial base less thickened, cells at base similar to scleroplectenchyma cells of side walls 6

6a. Pycnidia-II globose-papillate 7

b. Pycnidia-II with pronounced necks 13

7a. Conidia very small, mostly 2–3 × 0.5–1 µm; pycnidia-II variable, relatively large with slightly papillate pore, often aggregated or irregular with the appearance of being multilocular; on dead stems of various herbaceous plants; plurivorous necrophyte (only known from mountainous regions in SW Asia) .... 4. *P. astragalina*

[Scleroplectenchyma not so conspicuous as in most other species of the section; isolates on OA at room temperature remain sterile.]

b. Conidia larger, length mostly between 3–9 µm 8

8a. Conidia often > 5 µm in length 9

b. Conidia usually < 5 µm in length 11

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

b. Pycnidia usually solitary 10

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

b. Conidia variable, mostly 5–9 × 1.5–3 µm; pycnidia-II usually non-papillate with narrow pore; dead stems of *Helianthus annuus* (Compositae); specific cosmopolitan pathogen . . . . 7. *P. macdonaldii*, teleomorph *L. lindquistii*
[In association with disease symptoms produces only pycnidia-I; in vitro pycnidia I→II.]

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

b. Pycnidia glabrous 12

12a. Pycnidia-II subglobose-conical with broad base and usually slightly papillate pore, mostly 150–250 µm diam., conidia mostly 4 × 1.5 µm; dead stems of Cruciferae, especially *Berteroa incana*; necrophyte . . . . 9. *P. conferta*, teleomorph *L. conferta*
[In vitro also produces pycnidia-II, but more irregular in shape.]

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

13a. Neck up to 500 µm long, pilose; conidia mostly 4–5.5 × 1.5–2.5 µm; on dead stems of Labiatae, especially *Leonura cardiaca* and *Ballota nigra*; necrophyte
11. *P. leonuri*, teleomorph *L. slovacica*
[In vitro produces pycnidia-II with very long pilose necks.]

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

14a. Conidia usually exceeding 5 µm in length, mostly 5–6 × 1.5–2 µm; on dead stems of *Achillea* species (Compositae); specific(?) necrophyte (so far only known from southern Europe) . . . . 12. *P. congesta*, teleomorph *L. congesta*
[In vitro also produces pycnidia-II, usually with semi-pilose neck.]

b. Conidia usually not exceeding 5 µm in length 15

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

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

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

b. Conidia usually larger 19

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

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

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

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

19a. Conidia aseptate 20

b. Conidia occasionally also 1-septate 23

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

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

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

b. Conidia eguttulate or inconspicuously biguttulate 22

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

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

23a. Pycnidia-II with flattened base and long neck, usually at one side 20b
b. Pycnidia-II with irregular base and short papillate neck 22a
24a. Pycnidia-II mostly < 250 µm in diam. 25
b. Pycnidia-II commonly > 250 µm in diam. 26

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

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

26a. Pycnidia-II mostly 250–350 µm diam. 27
b. Pycnidia-II larger, often 400–500 µm diam. 28

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

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

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

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

[Isolates on OA at room temperature remained sterile.]

Note

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

POSSIBILITIES OF IDENTIFICATION IN VITRO

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

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

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

FUNGUS–HOST INDEX

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

A. on **herbaceous plants**

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

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

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

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

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

FUNGUS-HOST INDEX

A. on **herbaceous plants**

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

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

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

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

DESCRIPTIVE PART

Section Plenodomus (1–26)

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

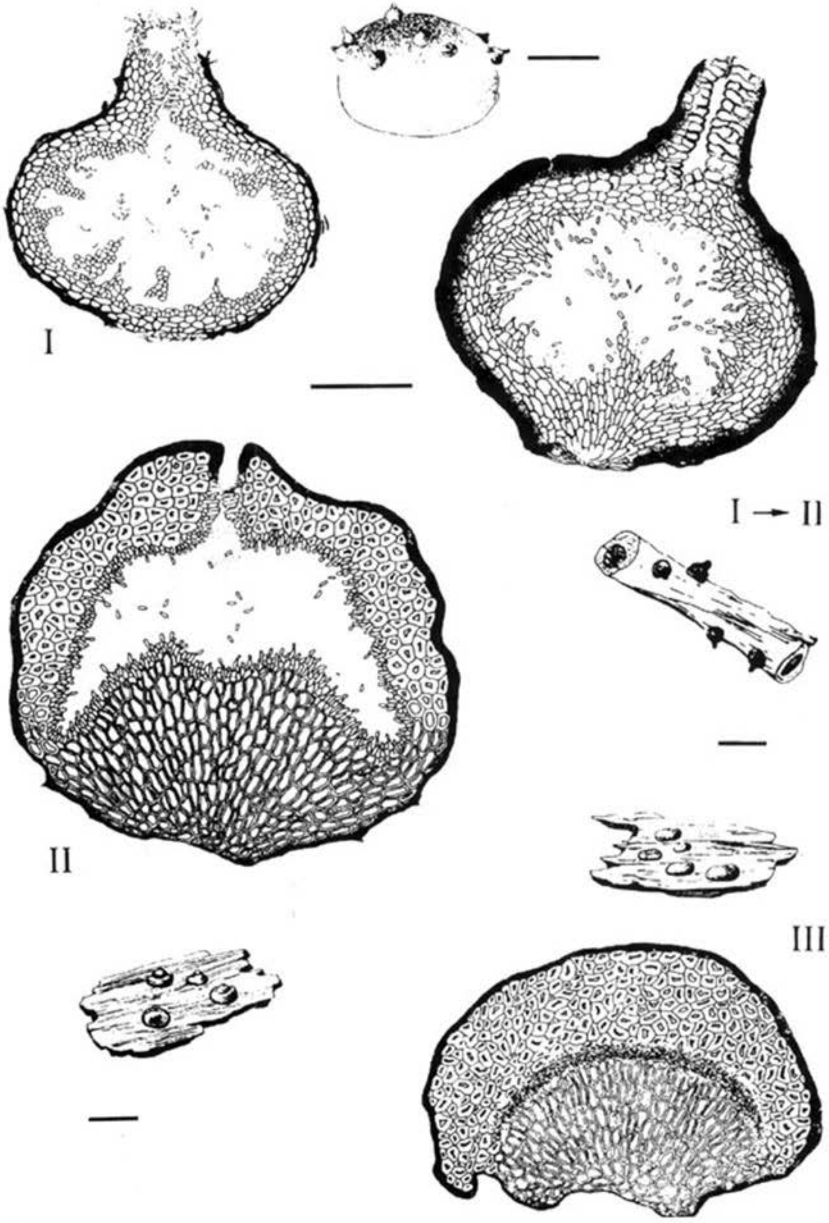
Phoma macrocapsa Trail, Scott. Nat. 8 [II, 2] (1886) 237. — *Plenodomus macrocapsa* (Trail) Rupprecht, Sydowia 13 (1959) 20–21.

Description in vivo (*Mercurialis perennis*)

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

Description in vitro

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


I
I → II
II
III

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

Representative culture. CBS 640.93.

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

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

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

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

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

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

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

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

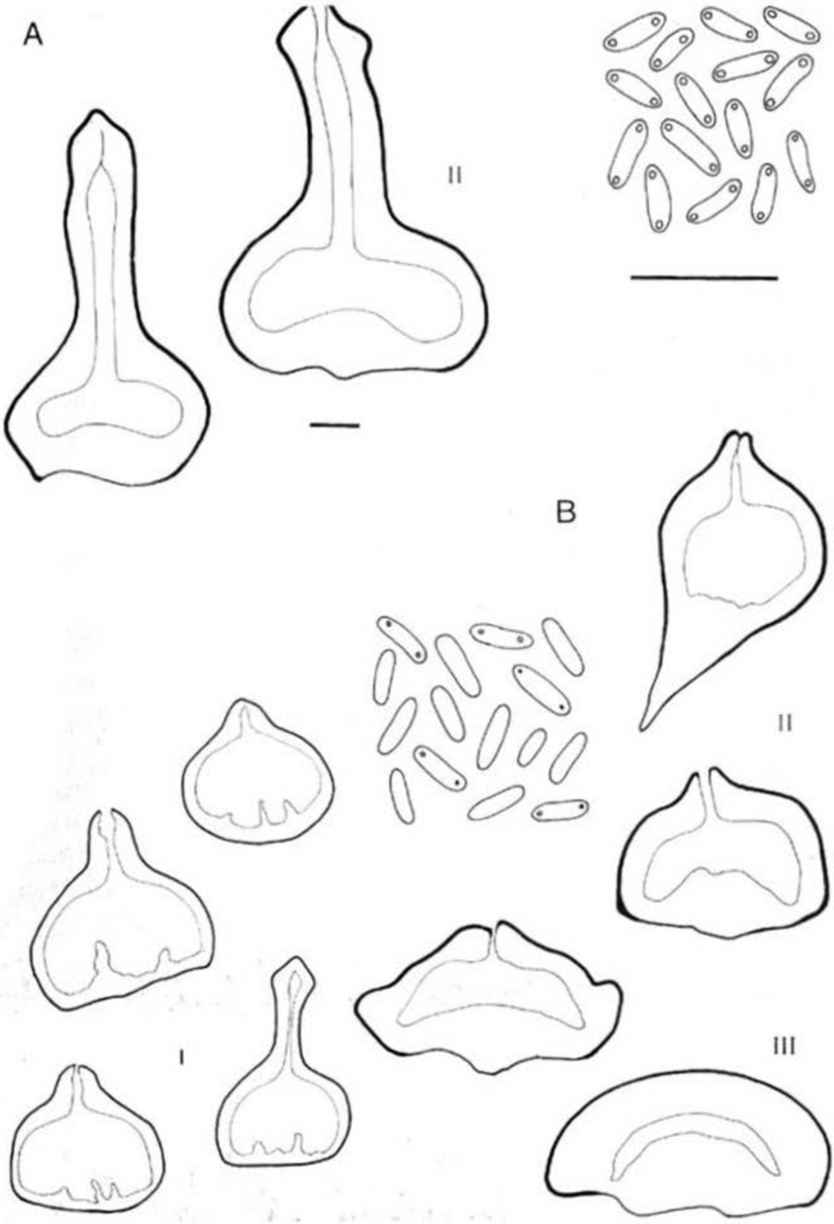
Phoma napobrassicae Rostrup, Tidsskr. Landøkon. 11 (1892) 330. — *Phoma lingam* var. *napobrassicae* (Rostrup) Grove, Br. Coelomycetes 1 (1935) 70.

Selected literature. Boerema & van Kesteren (1964).

Description in vivo (especially *Brassica* spp.)

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

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


A
II
B
II
I
III

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

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

Description in vitro

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

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

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

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

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

---

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

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

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

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

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

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

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

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

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

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

Description in vivo (especially on *Melilotus alba*)

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

Description in vitro

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

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

Representative culture. CBS 144.84.

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

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

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

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

Selected literature. Boerema & van Kesteren (1981).

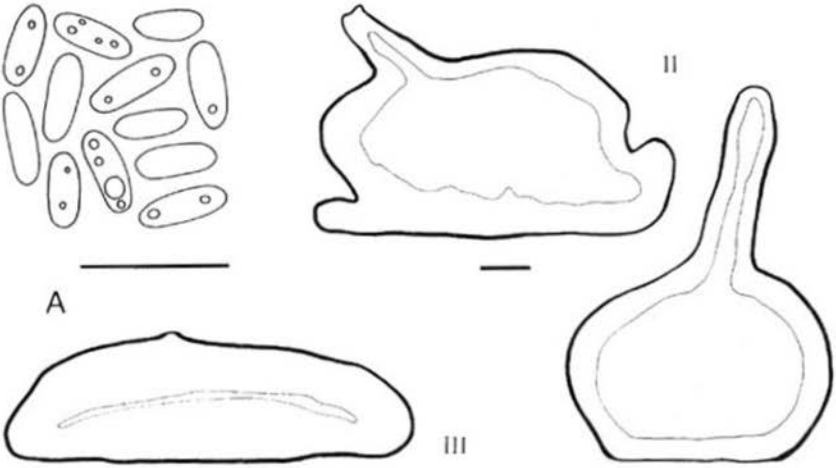
Description in vivo (especially on *Astragalus* spp.)

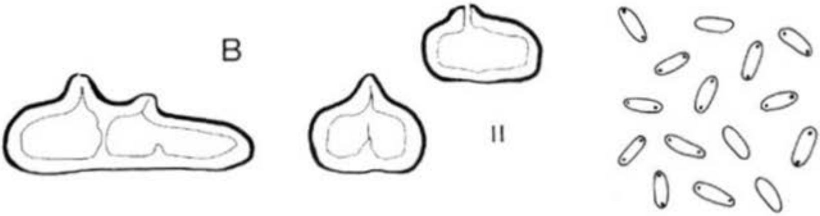
Only pycnidia-II (mostly on dead stems, scattered or in groups, subepidermal or subcortical), but scleroplectenchyma not as conspicuous as in most other species of the section, 150–300 µm diam., extremely variable, sometimes mainly depressed globose to ellipsoidal, but also more irregular in shape and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

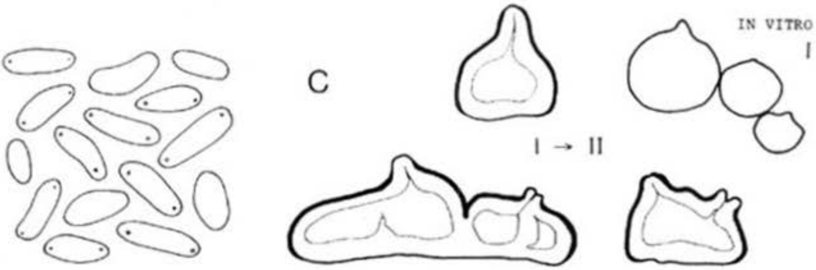
Description in vitro

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

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


II
A
III


B
II


IN VITRO
I
C
I → II

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

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

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

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

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

Description in vivo (especially *Eupatorium cannabinum*)

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

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

Description in vitro

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

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

Representative culture. CBS 121.89.

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

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

Possible teleomorph: *Leptosphaeria affinis* P. Karsten.

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

Description in vivo (*Rhinanthus* spp.)

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

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

Description in vitro

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

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

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

Teleomorph: *Leptosphaeria lindquistii* Frezzi.

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

Description in vivo (*Helianthus annuus*)

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

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

Description in vitro

OA: growth-rate 25–45 mm, aerial mycelium cottony, mostly whitish, greyish or greenish-olivaceous; reverse olivaceous greenish-yellow or glaucous tinged, often with white granular or flaky crystals. Old colonies may show a pink or red discolouration of agar becoming purplish or blue with a drop of NaOH (the presence of anthraquinone cynodontin has been demonstrated together with some unknown yellow pigments). Usually abundant production of subglobose, non-papillate pycnidia, I→II. Conidia highly variable, as in vivo.

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

Representative culture. CBS 386.80.

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

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

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

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

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

Description in vivo (*Gentiana* spp.)

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

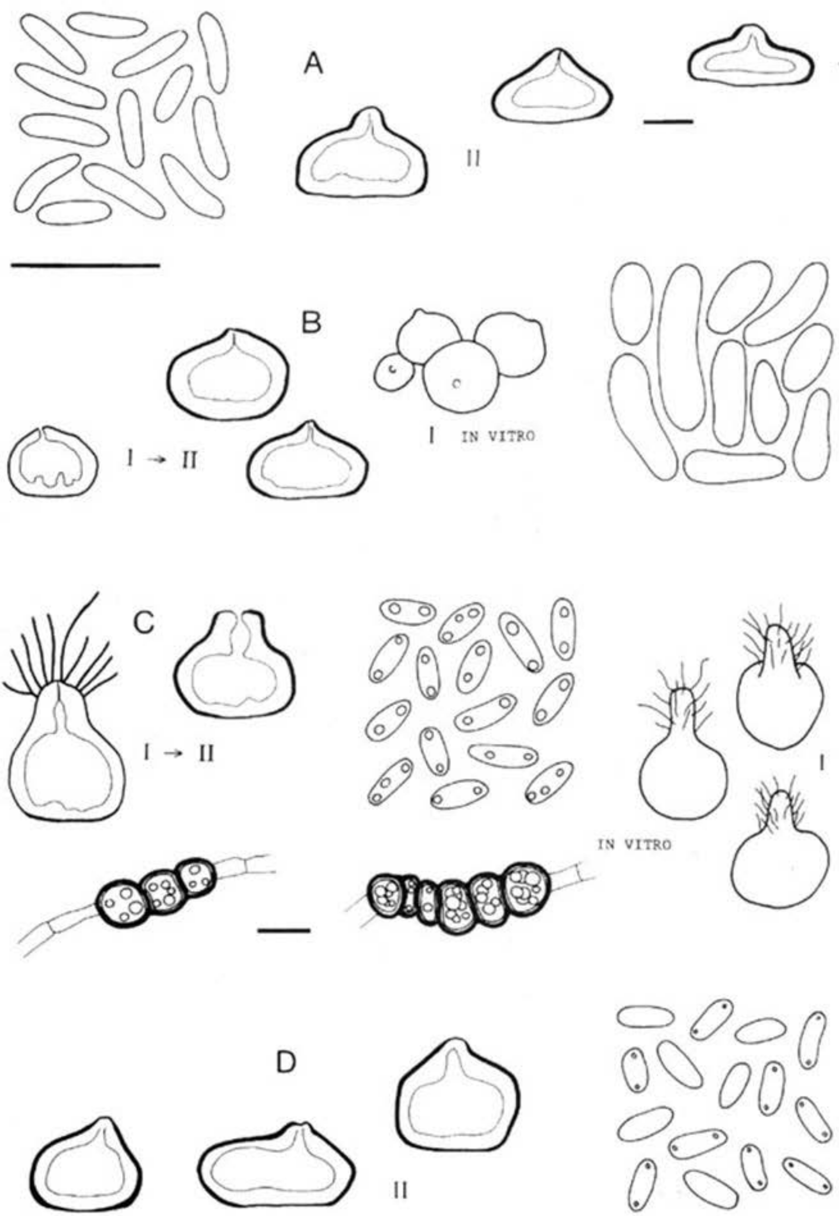
Description in vitro

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

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

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

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


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

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

Representative cultures. CBS 270.92, CBS 269.92.

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

Teleomorph: *Leptosphaeria conferta* Niessl ex Sacc.

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

Description in vivo (especially *Berteroa incana*)

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

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

Description in vitro

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

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

---

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

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

Representative culture. CBS 375.64.

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

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

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

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

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

Selected literature. Boerema & van Kesteren (1981).

Description in vivo (*Melampyrum* spp.)

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

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

Description in vitro

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

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

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

11. **Phoma leonuri** Let. — Fig. 5B

Teleomorph: *Leptosphaeria slovacica* Picb.

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

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

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

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

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

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

Description in vivo (especially *Leonurus cardiaca*)

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

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

Description in vitro

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

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

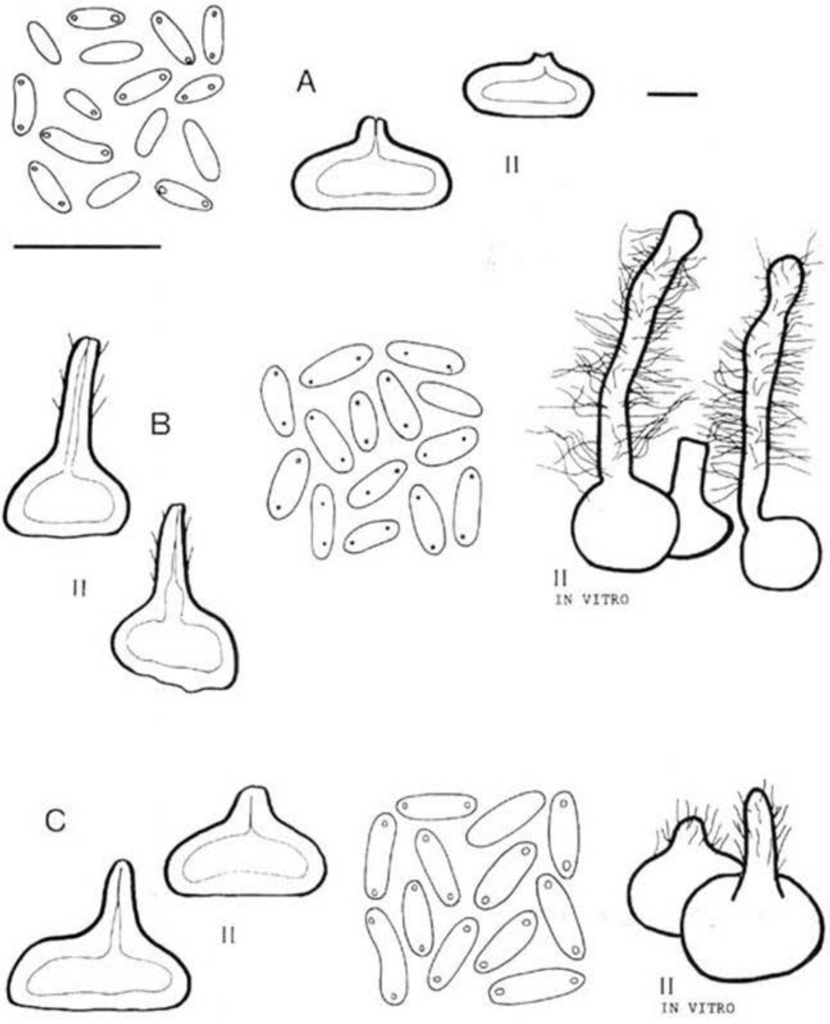


Fig. 5. A. *Phoma petrakii*. Pycnidia-II depressed globose with flattened base and distinctly papillate, usually with a dark-lined tube-shaped pore. — B. *Phoma leonuri*. Characterized by pycnidia-II with conspicuous long cylindrical necks; in vivo semi-pilose but in vitro explicitly pilose. — C. *Phoma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

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

Representative culture. CBS 389.80.

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

Teleomorph: *Leptosphaeria congesta* Lucas.

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

Selected literature. Lucas (1963).

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

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

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

Description in vitro

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

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

Dried culture. L 993.373.042.

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

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

Selected literature. Boerema & Loerakker (1985).

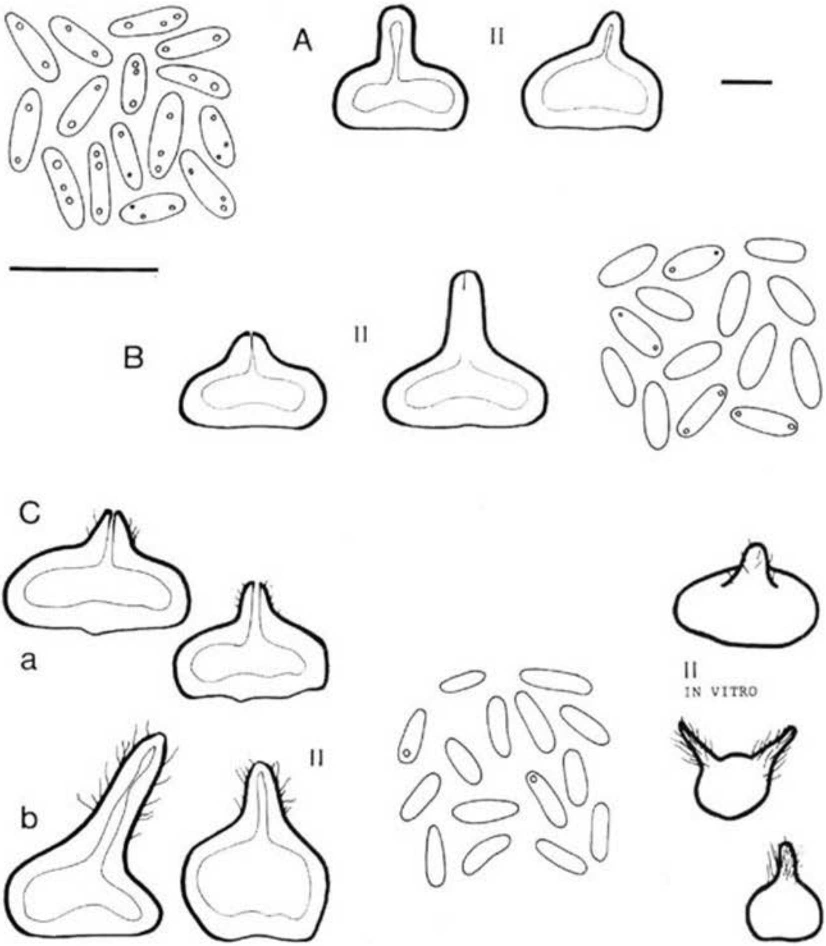


Fig. 6. A. *Phoma veronicicola*. Produces only pycnidia-II with a pronounced neck, which usually remains closed for some time; in vitro, neck sometimes pilose. Conidia 2–4 guttulate. — B. *Phoma longirostrata*. Pycnidia-II with conspicuous cylindrical poroid neck of various length. Conidia eguttulate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

Description in vivo (*Veronica* spp.)

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

Description in vitro

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

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

Representative culture. CBS 145.84.

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

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

Description in vivo (especially *Aconitum* spp.)

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

Description in vitro

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

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

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

Dried culture. L 993.373.103.

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

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

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

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

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

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

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

Description in vivo (*Urtica dioica*)

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

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

Description in vitro

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

Ecology and distribution. Very common in Europe on dead stems of nettle, especially *Urtica dioica* (anamorph and teleomorph). Reports from North America refer to different *Urtica* spp. (teleomorph). The fungus is occasionally recorded in Europe on herbaceous plants of other genera (see also below under f. sp. *phlogis*). Since 1976 the anamorph of *Leptosphaeria doliolum* s.s. on *Urtica* spp. has been known as *Phoma hoehnelii* var. *urticae,* but the present Code has made it possible to reinstate the old species name *Phoma acuta,* see Boerema & Gams (1994). However, it should be noted that *P. acuta* and its synonyms *Leptophoma acuta* and *Plenodomus acutus* have previously been used for different anamorphs in the section *Plenodomus,* compare Boerema & van Kesteren (1981, tab. 1). It has also been stated in literature that *P. acuta* as described above is the anamorph of *Leptosphaeria acuta* (Fuckel) P. Karsten, whose pseudothecia frequently occur at the base of dead stems of nettle. The pycnidia of *L. acuta, Phoma piskorzii* (no. 17) usually develop inside hollow stems and contain significantly longer conidia.

Representative culture. CBS 505.75.

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

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

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

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

Representative culture. CBS 155.94.

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

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

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

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

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

Selected literature. Boerema (1976).

Description in vivo (especially *Angelica sylvestris*)

Pycnidia-II only (on dead stems, scattered or in rows, first subepidermal, later superficial), mostly (150–)200–400(–600) µm diam., resembling those of the type subspecies *P. acuta* subsp. *acuta,* but generally more depressed globose with a rather sharply delimited poroid papilla or neck of variable length; the tube-shaped pore is usually dark-lined. Exudate also cream or whitish. Conidia similar to those of var. *acuta*, (3–)3.5–5(–5.5) × 1–1.5(–2) µm, subcylindrical and usually eguttulate.

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

Description in vitro

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

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

Representative culture. CBS 617.75.

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

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

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

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

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

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

Teleomorph: *Leptosphaeria submaculans* Holm.

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

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

Selected literature. Boerema (1981).

Description in vivo (especially *Sisymbrium* spp.)

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

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

Description in vitro

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

Ecology and distribution. In Europe on various Cruciferae (especially *Sisymbrium* spp.) and occasionally on non-cruciferous plants. It may be associated with disease symptoms resembling the well-known Dry Rot and Canker disease of brassicas caused by *Phoma lingam* (no. 2), teleomorph *Leptosphaeria maculans*. It can likewise be transmitted by seed and may very probably occur in North America [compare Petrie & Vanterpool, 1965, '*Sisymbrium*-strain' of *P. lingam*]. Both fungi are without doubt closely related, but their teleomorphs can be easily differentiated [e.g. *L. submaculans* has a short broad neck and ascospores with a short swollen third cell], although their type-I pycnidia and conidia are similar. The scleroplectenchymatous pycnidia-II of *P. sublingam* are distinguished by being smaller with a strongly papillate neck. The teleomorph has often been erroneously identified in the past as *Leptosphaeria conferta* (anamorph *Phoma conferta*, no. 9), which is also common on Cruciferae.

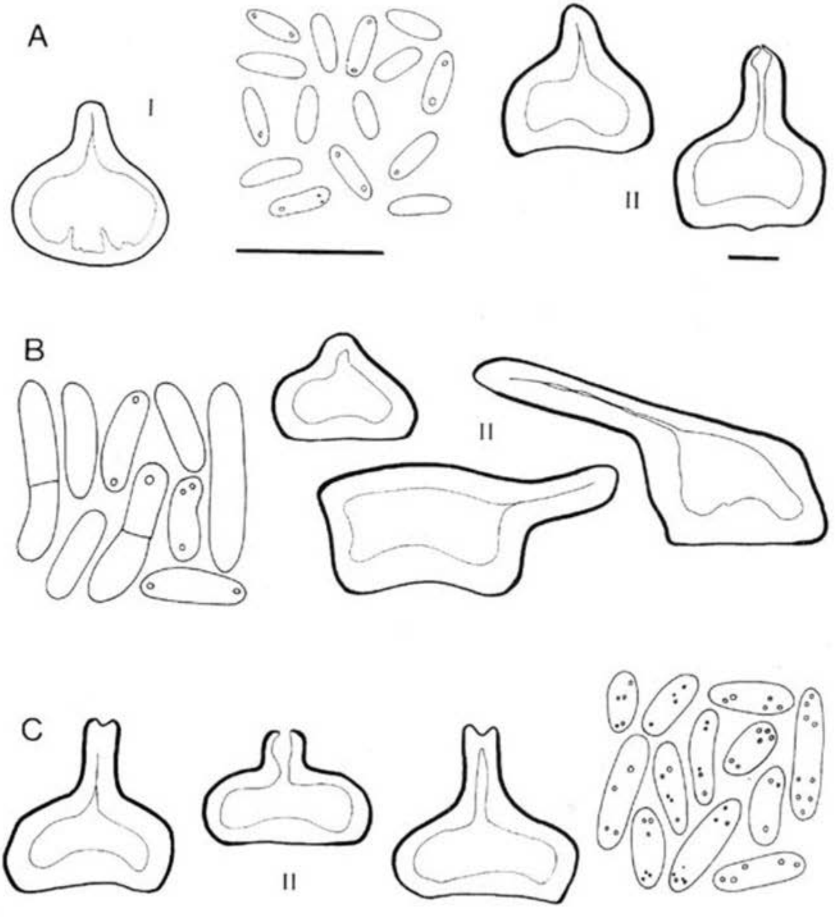


Fig. 7. A. *Phoma sublingam*. Pycnidia-I subglobose with broad base and distinct papillate neck, are found in association with disease symptoms. Pycnidia-II, depressed globose to subglobose with flattened base and a pronounced neck, occur on dead stems. — B. *Phoma piskorzii*. Pycnidia-II variable in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

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

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

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

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

Description in vivo (*Urtica dioica*)

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

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

Description in vitro

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

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

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

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

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

Phoma sydowii Boerema, van Kesteren & Loerakker, Trans. Br. mycol. Soc. 77 (1981) 71. — *Sphaeronaema senecionis* H. Sydow & P. Sydow, Annls mycol. 3 (1905) 185; not *Phoma senecionis* P. Sydow, Beibl. Hedwigia 38 (1899) 136 [belongs to sect. *Phoma*, treated in Contributions I–2; de Gruyter et al., 1993]. — *Plenodomus senecionis* (Sydow) Bubák, Annls mycol. 13 (1915) 29. — *Plenodomus senecionis* (Sydow) Petrak, Annls mycol. 19 (1921) 192.

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

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

Description in vivo (*Senecio* spp.)

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

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

Description in vitro

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

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

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

Representative culture. CBS 385.80.

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

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

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

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

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

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

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

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

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

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

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

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

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

Selected literature. Boerema (1976).

Description in vivo (especially *Foeniculum vulgare*)

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

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

Description in vitro

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

MA: rather slow growing, 10–20 mm].

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

Representative culture. CBS 616.75.

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

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

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

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

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

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

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

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

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

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

Description in vivo (especially *Pedicularis* spp.)

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

Description in vitro

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

---

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

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

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

Representative culture. CBS 390.80.

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

Hyphomycetous-anamorph: *Phialophora* sp.

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

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

Description in vivo (especially *Citrus limonia*)

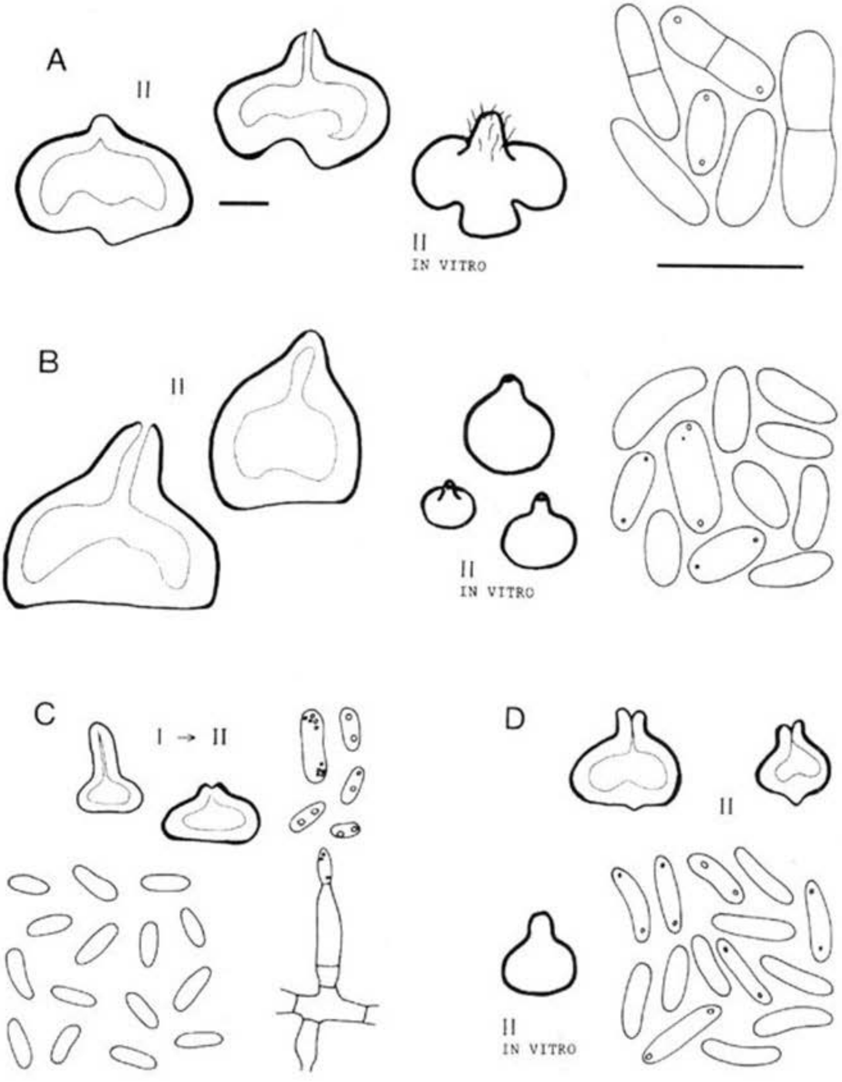
Pycnidia-I→II (on twigs and branches and around leaf scars, at first covered by the epidermis) mostly 60–135 mm diam., subglobose, at maturity always with a distinct cylindrical neck, 45–70 µm diam. and up to 250 µm in length (these necks are easily removed with the epidermis, leaving behind widely and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

Description in vitro

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

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

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


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

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

Representative culture. CBS 551.93.

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

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

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

Description in vivo (*Malus pumila*)

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

Description in vitro

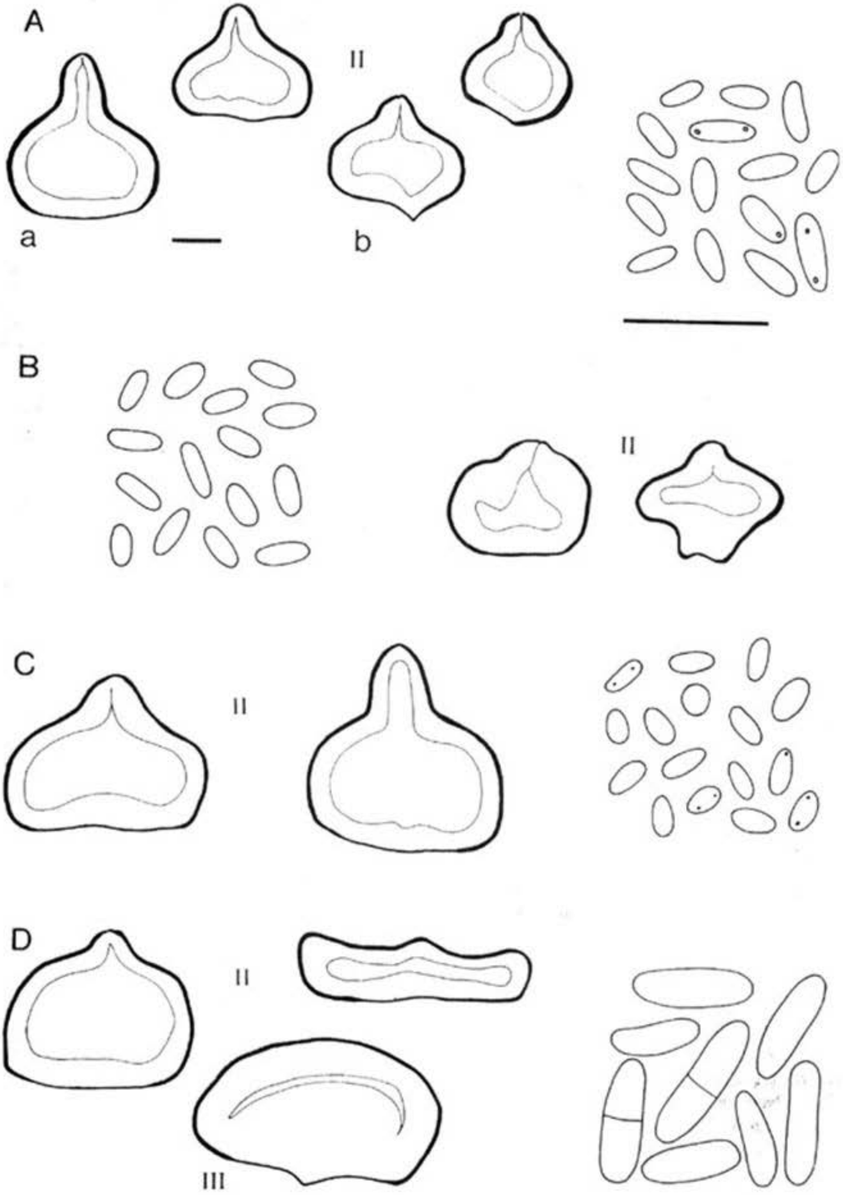
OA: slow-growing, growth-rate c. 15 mm; aerial mycelium either felted fluffy-cottony or very scant, at least in zones, colony and reverse becoming yellow, citrine, amber or dark olivaceous due to diffusible pigment(s), which become reddish (quickly fading) on application of a drop of NaOH. Rubiginous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

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

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

Representative culture. CBS 141.84.

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


A
II
a
b
B
II
C
II
D
II
III

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

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

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

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

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

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

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

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

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

Selected literature. Boerema & Loerakker (1985).

Description in vivo

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

Description in vitro

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

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

Representative culture. CBS 142.84.

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

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

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

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

Selected literature. Boerema & Loerakker (1985).

Description in vivo

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

Description in vitro

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

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

Representative culture. CBS 143.84.

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

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

Description in vivo (Salix alba)

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

Description in vitro

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

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

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

Representative culture. CBS 139.78.

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

Phoma rubefaciens Togliani, Annali Sper. agr. II, 7 (1953) 1626.

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

Description in vivo (especially *Malus* spp.)

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

Description in vitro

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

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

Representative culture. CBS 387.80.

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

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

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

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

Plenodomus helicis Curzi & Barbaini, Atti Ist. bot. Univ. [Lab. crittogam.] Pavia III, 3 (1927) 173.

Selected literature. Boerema & van Kesteren (1981).

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

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

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

Description in vitro

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

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

Addendum (27–31)

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

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

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

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

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

Description in vivo (*Saccharum officinale*)

Pycnidia (subepidermal within ring spots on leaves, usually solitary), 65–135 µm diam., subglobose-papillate, thin-walled; they often occur in association with the pseudothecia of the fungus. Exudate pale brown. Conidia 9–15 × 2–4 µm, ellipsoidal-subfusoid, provided with 2–several small guttules.

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

Description in vitro

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

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

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

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

Synanamorph: *Stagonospora meliloti* (Lasch) Petrak.

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

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

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

Description in vivo (especially *Melilotus alba*)

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

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

Description in vitro

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

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

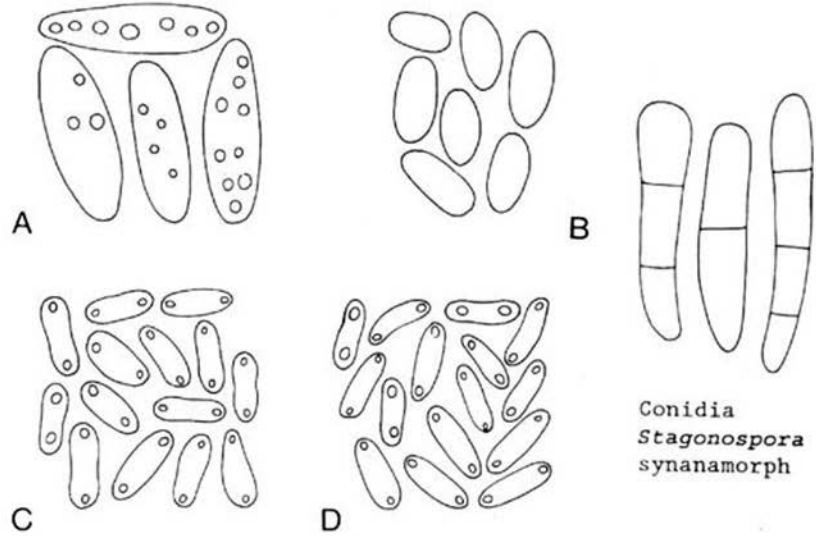


Fig. 10. Conidia of four species treated in the Addendum. — A. *Phoma annullata*. — B. *P. meliloti* and *Stagonospora*-synanamorph. — C. *P. rostrupii*. — D. *P. sanguinolenta*. — Bar = 10 µm.

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

Representative dried culture. SHEFF 2050.

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

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

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

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

Description in vivo (especially *Daucus carota*)

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

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

Description in vitro

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

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

Representative dried cultures. SHEFF 2009, SHEFF 2163.

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

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

Teleomorph: *Leptosphaeria purpurea* Rehm.

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

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

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

Description in vivo (especially *Cirsium* spp.)

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

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

Description in vitro

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

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

Representative dried cultures. SHEFF 1928, SHEFF 1929.

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

Hyphomycetous-anamorph: *Phialophora* sp.

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

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

Description in vivo (esp. *Chrysanthemum morifolium*)

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

Description in vitro

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

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

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

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

ACKNOWLEDGEMENTS

We wish to thank the Curators and Staff of the Institutes and Herbaria at Baarn, Beltsville, Budapest, Kew, Lisbon, Maracay, Munich, Padova, Paris, Sheffield, Uppsala, Vienna and Zurich. Technical assistance in the early stages was supplied by Maria M.J. Dorenbosch, Frieda van Dreven and Annelies E.F. Link. Maria E.C. Hamers helped greatly in the preparation of the manuscript. Thanks are also due to Dr. W. Gams for the Latin translations.

REFERENCES

Aa, H.A. van der, M.E. Noordeloos & J. de Gruyter. 1990. Species concepts in some larger genera of the Coelomycetes. Stud. Mycol. 32: 3–19.

Baker, K.F., L.H. Davis, S. Wilhelm & W.C. Snyder. 1985. An aggressive vascular-inhabiting Phoma (Phoma tracheiphila f. sp. chrysanthemi nov. f. sp.) weakly pathogenic to chrysanthemum. Can. J. Bot. 63: 1730–1735.

Boerema, G.H. 1976. The Phoma species studied in culture by Dr. R.W.G. Dennis. Trans. Brit. mycol. Soc. 67: 289–319.

Boerema, G.H. 1981. Mycologisch-taxonomisch onderzoek. Phoma- en Leptosphaeria-soorten bij cruciferen. Versl. Meded. Plziektenk. Dienst Wageningen 157 (Jaarb. 1980): 21–24.

Boerema, G.H. 1982. Mycologisch-taxonomisch onderzoek. Phoma-soorten van de sectie Plenodomus. Versl. Meded. Plziektenk. Dienst Wageningen 158 (Jaarb. 1981): 28–30.

Boerema, G.H. 1993. Contributions towards a monograph of Phoma (Coelomycetes)–II. Section Peyronellaea. Persoonia 15 (2): 197–221.

Boerema, G. H. & W. Gams. 1994. What is Sphaeria acuta Hoffm.: Fr.? Mycotaxon (in manuscript).

Boerema, G.H. & H.A. van Kesteren. 1964. The nomenclature of two fungi parasitizing Brassica. Persoonia 3 (1): 17–28.

Boerema, G.H. & H.A. van Kesteren. 1981. Nomenclatural notes on some species of Phoma sect. Plenodomus. Persoonia 11 (3): 317–331.

Boerema, G.H., H.A. van Kesteren & W.M. Loerakker. 1981. Notes on Phoma. Trans. Brit. mycol. Soc. 77: 61–74.

Boerema, G.H., H.A. van Kesteren & W.M. Loerakker. 1984. Vermeldenswaardige schimmelaantastingen in de periode 1980–1984. A. Aantastingen door schimmels die in Nederland niet bekend waren. Gewasbescherming 15 (6): 163–177.

Boerema, G.H. & W.M. Loerakker. 1981. Phoma piskorzii (Petrak) comb. nov., the anamorph of Leptosphaeria acuta (Fuckel) P. Karst. Persoonia 11 (3): 311–315.

Boerema, G.H. & W.M. Loerakker. 1985. Notes on Phoma 2. Trans. Brit. mycol. Soc. 84: 289–302.

Boerema, G.H., R. Pieters & M.E.C. Hamers. 1993. Check-list for scientific names of common parasitic fungi. Supplement Series 2c, d (additions and corrections): Fungi on field crops: pulse (legumes), forage crops (herbage legumes), vegetables and cruciferous crops. Netherlands Journal of Plant Pathology 99, Supplement 1: 1–32 [the complete series 'Check-list for scientific names of common parasitic fungi' compiled by G.H. Boerema and Coworkers is in 1993 reprinted with a cumulative index. Libri Botanici 10. IHW-Verlag, Eching, D].

Ciccarone, A. & M. Russo. 1969. First contribution to the systemics and morphology of the causal agent of the 'mal secco' disease of citrus (Deuterophoma tracheiphila Petri). Proceedings of the International Citrus Symposium 1, 3: 1239–1249 (Ed. H.P. Chapman).

CMI. 1968. Plant Host-Pathogen Index to volumes 1–40 (1922–1961) Review of applied Mycology.

Dennis, R.W.G. 1946. Notes on some British fungi ascribed to Phoma and related genera. Trans. Brit. mycol. Soc. 29: 11–12.

Diedicke, H. 1912. Die Abteilung Hyalodidymae der Sphaerioideen. Annls mycol. 10: 135–152.

Frezzi, M.J. 1968. Leptosphaeria lindquistii n. sp., forma sexuel de Phoma oleracea var. helianthi-tuberosi Sacc., hongo causal de la 'Mancha negra del tallo' del girasol (Helianthus annuus L.) en Argentina. Revista Investigaciones agropecuaria Buenos Aires 5: 73–80.

Goidanich, G., G. Ruggieri & A. Gagnotto. 1948. Presenza di una terza forma di moltiplicazione agamica in Deuterophoma tracheiphila Petri. Annali delle Sperimentazione agraria II [N.S.], 2: 671–675.

Graniti, A. 1955. Morfologia di Deuterophoma tracheiphila Petri e considerazioni sul genere Deuterophoma Petri. Bollettino delle sedute dell'Accademia Gioenia di Scienze naturali in Catania IV, 3 (3): 1–18.

Grove, W.B. 1935. British stem- and leaf fungi (Coelomycetes) vol. 1, Sphaeropsidales. Cambridge Univ. Press.

Gruyter, J. de & M.E. Noordeloos. 1992. Contributions towards a monograph of Phoma (Coelomycetes) – I. 1. Section Phoma: Taxa with very small conidia in vitro. Persoonia 15 (1): 71–92.

Gruyter, J. de, M.E. Noordeloos & G.H. Boerema. 1993. Contributions towards a monograph of Phoma (Coelomycetes) – I. 2. Section Phoma: Additional taxa with very small conidia and taxa with conidia up to 7 µm long. Persoonia 15 (3): 369–400.

Höhnel, F. von. 1915. Fragmente zur Mykologie (XVII. Mitteilung, Nr. 876 bis 943). Sitzungsberichte der Akademie der Wissenschaften Wien (Mathematisch-naturwissenschaftlichen Klasse, Abteilung I) 124: 49–159.

Höhnel, F. von. 1918. Fungi imperfecti. Beiträge zur Kenntniss derselben. Hedwigia 59: 236–284.

Holm, L. 1957. Études taxonomiques sur les Pléosporacées. Symbolae botanicae upsaliensis 14 (3): 5–188.

Hudson, H.J. 1960. Pyrenomycetes of sugar cane and other grasses in Jamaica. I. Conidia of Apiospora camptospora and Leptosphaeria sacchari. Trans. Brit. mycol. Soc. 43: 607–616.

Jones, F.R. & J.L. Weimer. 1938. Stagonospora leaf spot and root rot of forage legumes. J. agric. Res. 57: 791–812.

Lacoste, L. 1965. Biologie naturelle et culturale du genre Leptosphaeria Cesati et de Notaris. Déterminisme de la reproduction sexuelle. Thèse Toulouse.

Leuchtmann, A. 1984. Über Phaeosphaeria Miyake und andere bitunicate Ascomyceten mit mehrfach querseptierten Ascosporen. Sydowia 37: 75–194.

Lucas, M.T. 1963. Culture studies on Portuguese species of Leptosphaeria I. Trans. Brit. mycol. Soc. 46: 361–376.

Lucas, M.T. & J. Webster. 1967. Conidial states of British species of Leptosphaeria. Trans. Brit. mycol. Soc. 50: 85–121.

Marić, A. & R. Schneider. 1979. Die Schwarzfleckenkrankheit der Sonnenblume in Jugoslawien und ihr Erreger Phoma macdonaldii Boerema. Phytopathol. Z. 94: 226–233.

Mel'nik, V.A. 1977. Opredelitel' gribov roda Ascochyta Lib. Akademiya Nauk SSSR, Leningrad.

Ndimande, B. 1976. Studies on Phoma lingam (Tode ex Fr.) Desm. and the dry rot on soil seed rape, Brassica napus (L.) var. oleifera Metzger. Thesis Agricultural College Uppsala.

Petri, L. 1929. Sulla posizione sistematica del fungo parassita delle piante di limone affette da «mal del secco». Boll. Staz. Patol. veg. Roma II, 9 (4): 393–396.

Petrie, G.A. & T.C. Vanterpool. 1965. Diseases of rape and cruciferous weeds in Saskatchewan in 1965. Can. Pl. Dis. Surv. 45: 111–112.

Pons, N. 1990. Estudio taxonomico de especies de Phoma y Phyllosticta sobre cana de azucar (Saccharum sp.). Fitopatologia Venezolana 3: 34–43.

Preuss, G.T. 1851. Uebersicht untersuchter Pilze, besonders aus der Umgegend von Hoyerswerda. Linnaea 24 [= Beiträge der Pflanzenkunde 8]: 99–153.

Robertson, N.F. 1967. A slow-wilt of pyrethrums (Chrysanthemum coccineum Willd.) caused by a species of Cephalosporium. Pl. Path. 16: 31–36.

Schwarz, M.B. 1922. Das Zweigsterben der Ulmen, Trauerweiden und Pfirsichbäume. Mededelingen uit het phytopathologisch Laboratorium Willie Commelin Scholten 5: 1–73.

Shoemaker, R.A. 1984. Canadian and some extralimital Leptosphaeria species. Can. J. Bot. 62: 2688–2729.

Shoemaker, R.A. & C.E. Babcock. 1989. Phaeosphaeria. Can. J. Bot. 67: 1500–1599.

Shoemaker, R.A., C.E. Babcock & J.A.G. Irwin. 1991. Massarina walkeri n. sp., the teleomorph of Acrocalymma medicaginis from Medicago sativa contrasted with Leptosphaeria pratensis, L. weimeri n. sp. and L. viridella. Can. J. Bot. 69: 569–573.

Sivanesan, A. 1984. The bitunicate Ascomycetes and their anamorphs. J. Cramer, Vaduz.

Smith, H.C. & B.C. Sutton. 1964. Leptosphaeria maculans, the ascogenous state of Phoma lingam. Trans. Brit. mycol. Soc. 47: 159–165.

Smith, J.D. 1987. Winter-hardiness and overwintering diseases of amenity turfgrasses with special reference to the Canadian prairies. Techn. Bull. Res. Branch Agric. Canada 1987–12.

Tramier, R. & S. Mercier. 1963. Sur la présence en France d'une maladie du citronnier le mal secco Deuterophoma tracheiphila Petri. Revue de Pathologie végétale et d'Entomologie agricole de France 42: 211–216.

Trotter, A. 1972. Supplementum universale Sylloge fungorum. Pars XI Syll. fung. 26. [Johnson Repr. Co., New York; revised by E.K. Cash.]

PERSOONIA
Published by Rijksherbarium / Hortus Botanicus, Leiden
Volume 15, Part 4, pp. 489–524 (1994)

TAXONOMICAL NOTES ON MACROFUNGI IN ROADSIDE VERGES PLANTED WITH TREES IN DRENTHE (THE NETHERLANDS) – I

PETER-JAN KEIZER & EEF ARNOLDS[1]

Biological Station, Wijster (Drenthe), The Netherlands

In this study descriptions, drawings and observations are presented of rare, critical or less well-known macromycetes that were encountered during mycocoenological investigations carried out in roadside verges planted with *Quercus robur* L. (53 plots) or *Fagus sylvatica* L. (23 plots). In this first part, special attention is paid to the genus *Cortinarius* S.F. Gray emend. Fr.

During the years 1986, 1987 and 1988, mycocoenological research has been carried out in 76 plots, situated in roadside verges planted with *Quercus robur* L. (53 plots) or *Fagus sylvatica* L. (23 plots), further referred to as *Quercus* or *Fagus*. The plots varied with respect to exposition, age of trees, vegetation type and vegetation management. Most of the plots were situated in the province of Drenthe, and a few in an adjacent region in the province of Friesland, all in the phytogeographical Drenthian District (Weeda, 1983), in the northern part of the Netherlands (Table I). The area of research lies 10–20 m above sea-level and consists of weakly undulating glacial cover sands. A layer of boulder clay is often present at variable depths. However, in the roadside verge verges the soil horizons are always mixed up to a depth of 0.5–1 m, due to the road construction and maintenance works.

The herb layer in the plots belongs to different grassland communities. Productivity and species composition vary with the exposition and nutrient availability from poor grassland with a relatively high moss cover (Thero-Airion and Lolio-Cynosuretum, Westhoff & Den Held, 1969) to highly productive, dense, grass-dominated communities (Agropyro-Rumicion crispi). The vegetation is rather sparse to almost absent in some dark, shady plots along roads in woods. The management of the vegetation in roadside verges outside forests consists mostly of mowing without removal of the hay two (or more) times a year, sometimes of mowing with subsequent removal of the hay. Shaded roadside verges (in woods) are only incidentally managed. In addition the top soil and vegetation are removed in many places with intervals of c. 5–10 years for reasons of traffic safety and road surface maintenance (to prevent water stagnating on and along the road).

A description of the plant communities, soil parameters and the results of the mycocoenological research will be published elsewhere (Keizer, 1994a, 1994b).

---

[1] Comm. no. 445 of the Biological Station, Centre of Soil Ecology, Wijster, The Netherlands.

Table I. List of plots.

Survey of the plots where the described species originate. All plots are situated in the province Drenthe, the Netherlands, except the plots F15 and Q5, which lie in the province Friesland.
F = roadside verge planted with Beech; Q = roadside verge planted with Common Oaks; Age = age of trees (in 1988); Exp. means exposition of the plot: + = in open landscape, ± = half shady, – = shady; Pav. refers to the pavement of the roads: A = asphalt, B = bricks, N = no pavement.

Plot	Municipality	Near village	Coordinates on the topographic map	Local name	Age of trees	Exp.	Pav.	Description of the vegetation
F11	Peize	Altena	227,3–571,6	Lieverseweg	58	+	B	poor grassland
F12	Rolde	Deurze	237,5–556,7	Rolder Hoofdweg	78	+	A	mod. poor grassl.
F13	Beilen	Wijster	232,2–537,1	Bruntingerweg	37	+	A	mod. poor grassl.
F14	Beilen	Bruntinge	234,7–536,5	Hamweg	37	+	A	poor grassland
F15	Ooststellingwerf	Wateren	219,7–548,2	Bosweg	51	+	A	poor grassland
F16	Diever	Wateren	217,4–546,3	Oude Willem	51	+	A	mod. poor grassl.
F17	Anloo	Annen	244,7–563,7	Anlooerweg	54	+	A	poor grassland
F21	Vries	Rhee	234,4–561,4	N 870	66	+	A	mod. rich grassl.
F22	Sleen	't Haantje	252,6–537,5	Slenerweg	63	+	A	mod. rich grassl.
F23	Anloo	Annen	244,8–563,7	Eexterweg	61	+	A	rich grassland
F24	Peize	Peize	229,5–573,5	Zuurse weg	57	+	B	mod. rich grassl.
F25	Odoorn	Klijndijk	253,1–539,1	Odoornerzijtak	41	+	A	rich grassland
F31	Havelte	Havelte	211,7–531,2	Linthorst-Homanlaan	140	–	B	poor woodland
F32	Diever	Diever	217,9–542,1	Bosweg	55	–	B	poor woodland
F33	Gasselte	Gieten	246,3–555,5	Houtvester Jansenweg	66	–	A	± absent
F34	Anloo	Eext	245,6–561,6	Annerweg	81	–	A	poor woodland
F35	Eelde	Eelde	235,7–572,5	Hooghullen	70	–	A	rich woodland
F36	Odoorn	Klijndijk	253,4–539,3	Odoornerzijtak	41	–	A	rich woodland
F40	Ruinen	Hoogeveen	228,6–529,7	Spaarbankbos	44	–	N	poor woodland
F41	Gasselte	Gieten	245,3–557,6	Gieterveld	69	–	N	poor woodland
F42	Havelte	Havelte	211,7–531,2		72	–	N	± absent
F43	Eelde	Eelde	245,2–557,4	Hooghullen	82	–	N	mod. rich woodl.
F44	Roden	Roden	225,1–571,1	Mensingebosch	81	–	N	± absent
Q1	Sleen	Schoonoord	247,8–541,2	Oranjekanaal Z.Z.	100	+	A	poor grassland
Q2	Westerbork	Zwiggelte	235,5–545,0	Oranjekanaal N.Z.	100	+	A	poor grassland
Q3	Westerbork	Zwiggelte	236,2–545,0	Oranjekanaal Z.Z.	100	+	A	poor grassland
Q4	Anloo	Gieten	243,5–557,2	Gieterstraat	110	+	A	poor grassland
Q5	Ooststellingwerf	Wateren	219,7–548,0	Oude Willem	55	+	A	poor grassland
Q6	Vledder	Frederiksoord	209,0–540,1	Vledderweg	91	+	A	poor grassland
Q11	Assen	Deurze	236,9–556,6	Rolder Hoofdweg	113	+	A	poor grassland
Q12	Diever	Wateren	215,4–547,2	Waterenweg	130	+	B	mod. poor grassl.
Q13	Roden	Foxwolde	226,3–574,7	Roderwolderweg	114	+	B	mod. poor grassl.
Q14	Vledder	Vledder	209,9–541,1	Vledderweg	91	+	A	poor grassland

Plot	Municipality	Near village	Coordinates on the topographic map	Local name	Age of trees	Exp.	Pav.	Description of the vegetation
Q21	Assen	Deurze	236,6 – 556,6	Rolder Hoofdweg	113	+	A	rich grassland
Q22	Westerbork	Westerbork	236,5 – 541,5	Zwiggelterstraat	98	+	A	mod. rich grassl.
Q23	Ruinen	Pesse	225,3 – 532,2	Eursinge	112	+	A	rich grassland
Q24	Ruinen	Kraloo	225,5 – 533,8	Kralooerweg	70	+	A	rich grassland
Q26	Sleen	't Haantje	252,5 – 537,5	Oranjekanaal Z.Z.	116	+	A	rich grassland
Q31	Beilen	Ter Horst	230,9 – 540,1	Ter Horst	41	+	B	poor grassland
Q32	Odoorn	Odoornerveen	251,9 – 538,5	Odoornerzijtak	68	+	A	poor grassland
Q33	Beilen	Drijber	234,0 – 534,5	De Hullen	25	+	A	mod. poor grassl.
Q34	Odoorn	't Haantje	252,6 – 537,5	Oranjekanaal N.Z.	26	+	N	mod. poor grassl.
Q35	Peize	Altena	227,8 – 572,6	Hooghaar	47	+	B	poor grassland
Q36	Beilen	Klatering	232,9 – 543,5	Klatering	15	+	A	mod. poor grassl.
Q37	Beilen	Klatering	233,0 – 543,5	Klatering	15	+	A	mod. poor grassl.
Q38	Diever	Dieverbrug	218,6 – 540,6	Dieverbrug	10	+	A	poor grassland
Q39	Beilen	Beilen	234,6 – 544,0	Eursing	12	+	A	mod. rich grassl.
Q41	Beilen	Wijster	231,6 – 538,8	Beilerweg	48	+	A	mod. poor grassl.
Q42	Odoorn	Odoornerveen	248,8 – 540,8	Oranjekanaal N.Z.	32	+	A	mod. poor grassl.
Q43	Beilen	Wijster	230,5 – 537,6	Looveen	32	+	N	poor grassland
Q44	Beilen	Hooghalen	232,6 – 548,2	Stationsstraat	34	+	A	mod. poor grassl.
Q45	Beilen	Wijster	231,3 – 537,1	Boerkoelweg	35	+	B	mod. rich grassl.
Q46	Beilen	Wijster	231,8 – 536,9	Marsweg	35	+	B	mod. rich grassl.
Q51	Zweeloo	Witteveen	241,5 – 536,0	Bosweg	48	+	B	mod. poor grassl.
Q52	Odoorn	Odoornerveen	251,5 – 538,9	Torenweg	23	+	A	rich grassland
Q53	Sleen	Noordsleen	249,9 – 534,8	Middelesweg	28	+	A	rich grassland
Q54	Dwingeloo	Dwingeloo	222,3 – 538,1	Lheeweg	15	+	A	rich grassland
Q61	Zweeloo	Schoonoord	246,3 – 540,2	Oranjekanaal Z.Z.	116	–	B	rich grassland
Q62	Dwingeloo	Lheebroek	226,5 – 539,8	Lheebroek	76	–	B	mod. poor grassl.
Q63	Havelte	Havelte	210,9 – 531,3	Busselterweg	146	–	B	rich grassland
Q64	Havelte	Havelte	212,1 – 531,6	Overcingelaan	85	–	B	rich grassland
Q65	Anloo	Gieten	243,9 – 557,4	Gieterstraat	110	–	A	mod. poor grassl.
Q71	Zweeloo	Schoonoord	245,9 – 540,0	Oranjekanaal N.Z.	116	–	A	rich grassland
Q72	Westerbork	Zwiggelte	236,8 – 545,0	Oranjekanaal N.Z.	100	–	A	mod. poor grassl.
Q73	Havelte	Havelte	210,6 – 531,3	Busselterweg	125	–	B	mod. rich grassl.
Q74	Roden	Alteveer	225,3 – 570,3	Melkweg	106	–	A	mod. poor grassl.
Q81	Ruinen	Pesse	224,9 – 532,1	Leeuwte	110	–	A	ruderal
Q82	Assen	Assen	235,4 – 556,9	Steendijk	110	–	B	mod. rich grassl.
Q83	Roden	Roden	225,6 – 571,6	Mensingeweg	97	–	A	mod. rich woodl.
Q84	Anloo	Gieten	243,6 – 557,3	Gieterstraat	100	–	A	poor woodland
Q85	Havelte	Havelte	212,1 – 531,3	Van Helomaweg	140	–	A	rich grassland
Q87	Havelte	Havelte	212,1 – 530,8	Boskampsbrugweg	143	–	B	mod. rich woodl.
Q88	Ruinen	Rheebruggen	216,9 – 553,2	Rheebruggen	114	–	B	mod. poor woodl.
Q92	Havelte	Havelte	211,6 – 530,0		144	–	N	poor woodland
Q93	Ruinen	Hoogeveen	228,6 – 529,9	Spaarbankbos	105	–	N	poor woodland
Q94	Roden	Roden	225,4 – 571,5	Mensingebosch	102	–	N	poor woodland

The fungi dealt with in this study comprise the Macrofungi. Groups with relatively small or hidden fruit-bodies (e.g. the majority of the Helotiales, resupinate Aphyllophorales) have been omitted because a complete inventory would require a much more time consuming search strategy. The following groups have been included: Basidiomycetes: Agaricales; Gasteromycetes; non-resupinate Aphyllophorales and Heterobasidiomycetes. Ascomycetes: Clavicipitales: *Cordyceps*; Elaphomycetales: *Elaphomyces*; Helotiales: *Geoglossum*, *Leotia*; Pezizales: *Helvellaceae*, *Pezizaceae*, *Tuberaceae*; Deuteromycetes: *Paecilomyces*.

The nomenclature of the Basidiomycetes is mainly after Kreisel (1987) or Arnolds (1984) if species are not mentioned in the former work. The nomenclature of the smooth spored species of the genus *Inocybe* is after Kuyper (1986) and of the genus *Psathyrella* after Kits van Waveren (1985). Ascomycetes are after Cannon et al. (1985) and Deuteromycetes after Arnolds (l.c.).

Full understanding of mycocoenological studies is often hampered by the absence or incompleteness of descriptions of critical taxa. Therefore, descriptions and/or critical notes are given in this paper of rare and critical taxa and of collections, which disagreed with descriptions in literature. This criterion has been taken in a rather broad sense. The reason for this is in the first place to provide a reference for some names used in the mycocoenological work and secondly to present the rate of disagreement with the current literature of some names that were accepted.

In the descriptions the following abbreviations of colour-codes have been used: Expo for Cailleux & Taylor (1958), K. & W. for Kornerup & Wanscher (1978) and Mu for Munsell Color Company (1954).

In the microscopic descriptions Q indicates the length/width ratio of the spores and av. Q the average of Q usually based on 10 spores per collection. In the figures the habit sketches are 0.8 × the natural size; in the microscopic drawings the bar always represents 10 µm. All collections mentioned below are made in the selected plots and deposited in the herbarium of the Biological Station in Wijster (WBS), part of the Agricultural University Wageningen. For each collection the plot number is given, where it originates. This refers to Table I, where the exact place and some brief ecological notes of the plots are listed.

ACKNOWLEDGEMENTS

We are greatly indebted to Dr. Th.W. Kuyper, Dr. M.E. Noordeloos, Prof. Dr. R.A.A. Oldeman and Dr. A.J. Termorshuizen for their critical comments on earlier versions of this paper. Dr. E. Kits van Waveren is thanked for his valuable advices concerning *Psathyrella rhombispora* Keizer & Arnolds.

I. AGARICALES

Clitocybe albofragrans (Harm.) Kuyp.

Pileus 25 mm, expanded, with centre depressed and margin involute, not hygrophanous, white, slightly pruinose; surface somewhat cracked with pale brownish cracks, margin not striate. Lamellae narrow, c. 2.5 mm broad, crowded, very shortly decurrent, light pinkish, with slightly crenulate, concolorous edge. Stipe 32 × 2 mm, cylindrical, pale beige with white fibrillum, therefore white-silky shining. Flesh in pileus and stipe pale brown, white on drying. Smell strong, anise-like.

Spores 4.6–5.5(–6.1) × 2.8–3.2(–3.7) µm, ellipsoid, thin-walled, smooth, in exsiccata often in tetrads.

Habitat. Between grass in roadside verge planted with *Quercus robur*.

Collections examined. Plot Q51, 31 Aug. 1987, *Keizer 87063*; Plot Q31, 17 Oct. 1988, *Keizer 88115.*

This species is little-known, and apparently often overlooked. It is well-characterized by the combination of a white, non-hygrophanous pileus and anise-like smell. It differs from pale forms of *C. odora* in smaller basidiocarps and smaller spores. According to Kuyper (1981) it is not uncommon in the Netherlands.

Clitocybe marginella Harm.

Pileus 27–34 mm, expanded with somewhat depressed centre, when moist at centre orange-brown (K. & W. 5C5 but more greyish), towards the margin orange-beige (5C4), at extreme margin even paler; centre contrastingly darker than the remaining parts of the pileus; margin translucently striate up to 1/3 of the radius, on drying very pale beige. Lamellae crowded, shortly decurrent, pale pinkish-beige-whitish with concolorous edge. Stipe up to 25 × 3.5 mm, cylindrical, somewhat flexuose, concolorous with centre of pileus, glabrous. Smell sweetish anise-like.

Spores 4.6–5.5 × (2.8–)2.9–3.7 µm, shortly ellipsoid.

Habitat. Terrestrial on dead organic matter in a roadside verges planted with *Quercus* on nutrient-poor sandy soil.

Collection examined. Plot Q3, 21 Dec. 1988, *Keizer 88342.*

Clitocybe marginella is related to both *C. agrestis* and *C. diatreta*. According to Kuyper (1982) the former has a more uniformly coloured pale pileus and the latter differs in a darker orange-brown cap, which is not translucently striate, and in pink lamellae.

Conocybe pygmaeoaffinis (Fr.) Kühner — Fig. 1

Pileus 20 mm, plano-convex with rather prominent umbo, hygrophanous, when moist rusty brown (Expo between F52 and F54), translucently striate up to 0.5 of the radius, on drying ochraceous yellow-brown (D68). Lamellae c. 3 mm broad, rather crowded, concolourous with cap (F54) or slightly paler, edge white-flocculose. Stipe 43 × 1.3 mm, cylindrical, at base somewhat swollen, ochraceous yellow-brown, covered with yellowish brown, shiny fibrillum, near apex powdered-flocculose (caulocystidia), darkening on handling. Context in pileus and stipe concolorous with pileus, in base of stipe dark red-brown (J42). Smell and taste not recorded.

Spores 8.5–9.1 × 4.6–5.2 µm, Q = 1.7–1.9, av. Q = 1.80, narrowly ellipsoid, ochraceous yellow-brown in NH_4OH, with distinct germ-pore. Cheilocystidia 30–40 × 7–9 µm, narrowly lageniform or narrowly fusiform.

Habitat. Terrestrial in roadside verges planted with *Quercus* on nutrient-poor sandy soil.

Collection examined. Plot Q81, 19 Sept. 1988, *Keizer 88315.*

This collection differs from the description by Watling (1982) of *C. pygmaeoaffinis* by the more slender habit, the slightly narrower spores (Watling: 8.5–10 × 5–5.5 µm), and the narrowly fusiform cheilocystidia, not gradually tapering from a broad base. Spore size and shape of cheilocystidia are in better agreement with Maire's descriptions (in Kühner, 1935: 135, 8–9 × 4.5–5.5 µm). *Conocybe striaepes* (Cooke) Lundell differs in smaller spores (7–8 × 4–4.5 µm) and lanceolate cheilocystida.

Coprinus sclerocystidiosus M. Lange & A.H. Smith — Fig. 2

Pileus 20 mm, expanded, red-brown, covered with short hairs (setae), especially near the margin, partly withered. Lamellae black, for the greater part withered. Stipe 40 × 15 mm, cylindrical, somewhat swollen near the base, pale yellowish-hyaline, covered with small hairs, base somewhat tomentose.

Spores 12.5–15.0 × 7.3–8.5 µm, Q = 1.6–1.9, av. Q = 1.77, ellipsoid, with excentric germ-pore, dark brown in NH_4OH. Pileocystidia narrowly lageniform, thick-walled, 65–88 × 7.5–10.0 µm.

Habitat. On organic debris in a roadside verge planted with *Fagus* on nutrient-poor sandy soil.

Collection examined: Plot F32, 18 Sept. 1988, *Keizer 88063*.

Mr. C.B. Uljé kindly identified this collection. *Coprinus sclerocystidiosus* is a rare species in the Netherlands.

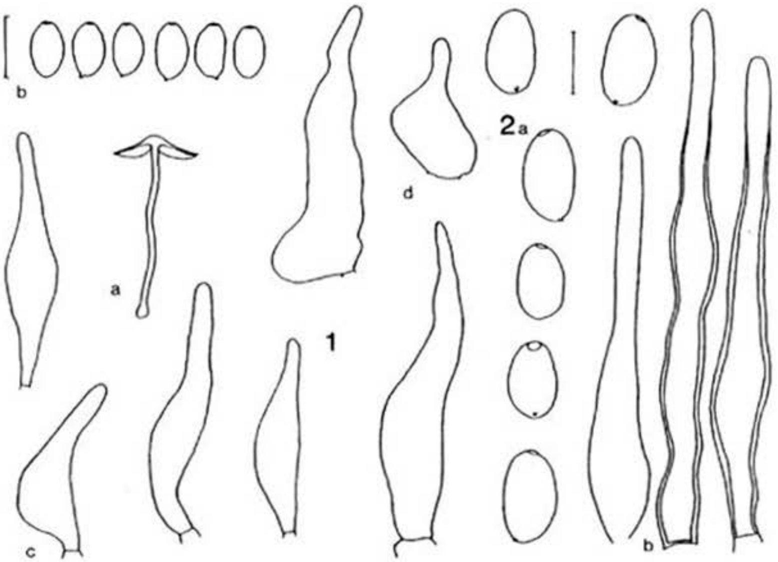


Fig. 1. *Conocybe pygmaeoaffinis*. a. habit; b. spores; c. cheilocystidia; d. caulocystidia (*88315*). — Fig. 2. *Coprinus sclerocystidiosus*. a. spores; b. pileocystidia (*88063*). — Bar represents 10 µm.

Coprinus subimpatiens M. Lange & A.H. Smith — Fig. 3

Pileus when young 3–4 × 6 mm, ovoid, soon expanding, 10–20 mm broad, broadly campanulate, with margin occasionally splitting radially, often soon desintegrating (within half a day after collecting), greyish brown (Expo C63), chestnut-brown or ochrish brown (H42, H43, F43) in centre; covered with small setae. Lamellae narrow, c. 1.5 mm broad, moderately crowded, at first pale grey-brown, then dark grey-brown, with white-flocculose edge, soon brownish black and desintegrating. Stipe 25–50 × 1.5–3 mm, cylindrical or slightly broader towards the base, white-hyaline or pale cream coloured, in one collection (*Keizer 87234*) pink (B32) at apex and greyish pink near base (C10), pruinose. Smell and taste unknown.

Spores (9.0–)9.5–15.0 × (5.9–)6.0–7.5(–7.7) µm, Q = 1.4–1.9 and av. Q = 1.53–1.71, not or hardly lentiform, smooth, with excentric germ-pore, dark purplish under microscope. Cheilocystidia of two types: vesiculose or ovoid, 35–65 × 25 µm, and lageniform, 30–40 × 10 µm. Pleurocystidia vesiculose, 40–50 × 30–35 µm.

Habitat. Terrestrial in roadside verges planted with *Fagus* or *Quercus* on nutrient-poor sandy soil.

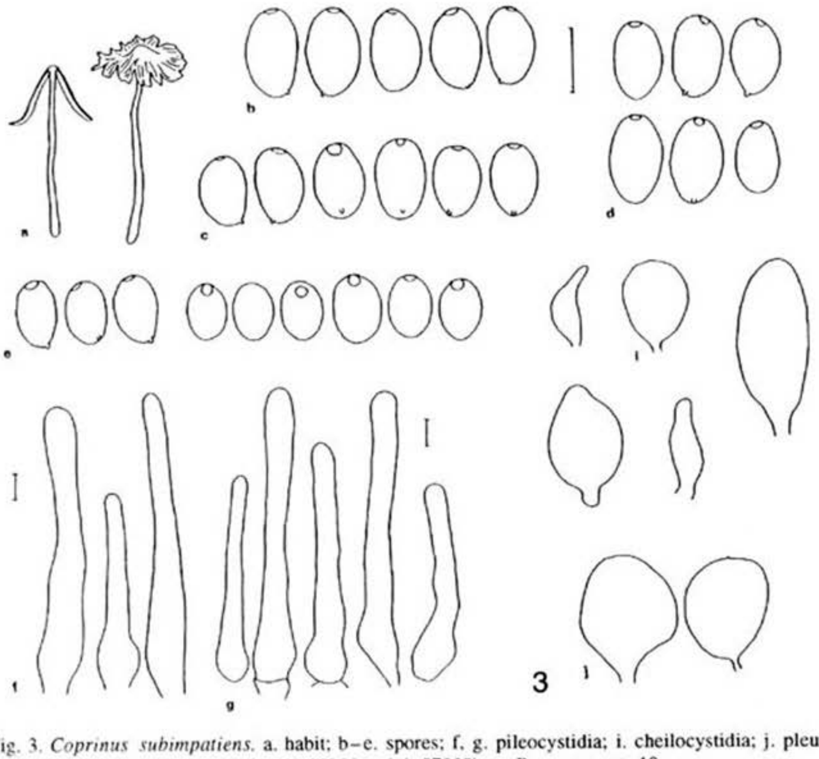


Fig. 3. *Coprinus subimpatiens*. a. habit; b–e. spores; f, g. pileocystidia; i. cheilocystidia; j. pleurocystidia (a, d, g. *88234*; b. 88319; c, f. *88231*; e, i, j. *87038*). — Bar represents 10 µm.

Collections examined. Plot F21, 30 Oct. 1986, *Keizer 86187*; Plot F32, 1 Sept. 1987, *Keizer 87038*; Plot Q22, 13 Oct. 1987, *Keizer 87234*; Anloo, Anderen, 29 July 1988, *Keizer 88045*; Plot F22, 17 Sept. 1988, *Keizer 88154*; Plot F43, 6 Oct. 1988, *Keizer 88231*; Plot F22, 16 Nov. 1988, *Keizer 88319*.

The material is heterogeneous with respect to spore size: collection *87234* has small, slightly lentiform spores, 8.6–10.8 × 5.8–8.0 µm, Q = 1.4–1.5 in front- and av. Q = 1.6–1.7 in side-view. The remaining collections are more homogeneous with respect to spore size: 11–13 × 6.5–7.7 µm. Cheilo- and pleurocystidia could exclusively be studied in immature carpophores, which were only present in collection *87234*. Because the characters of the pleuro- and cheilocystidia could not be studied in other collections, the spore size had to be used to identify this species of the *C. hiascens* group. All species except *C. subimpatiens* have narrower spores (Orton & Watling, 1979; Uljé, 1989). Collection *87234* is deviating by the pink colour in the stipe and in having smaller spores than the remaining collections. Yet, it is assigned to *C. subimpatiens*, which is confirmed by Mr. C.B. Uljé.

Coprinus xantholepis P.D. Orton

Pileus ovoid when young, c. 3 × 4 mm, white to cream-coloured, translucently striate, covered with a thick veil consisting of orange-brown scales, giving the pileus an orange-brown spotted appearance. Lamellae when young white, with age purplish-black and deliquescent. Stipe white, in maturity c. 25 × 1 mm, at base somewhat enlarged and with a zone of veil remnants. Smell and taste unknown.

Spores 6.0–6.8(–7.2) × 4.5–5.5 × 5.3–6.0 µm, lentiform, in front view broadly ellipsoid to subglobose (Q = 1.0–1.3, av. Q = 1.16), in side view ellipsoid (Q = 1.2–1.4, av. Q = 1.30), with central germ-pore. Hyphae of veil irregularly diverticulate, 3–5 µm thick, with walls of 1 µm thick, under microscope ochre-brown.

Habitat. On dead grass remains in a roadside verge planted with *Quercus* on nutrient-poor sandy soil.

Collection examined. Plot Q54, 1 Sept. 1987, *Keizer 87062*.

Our material fits well with the original description of *Coprinus xantholepis* by Orton (1972: 150) except for the slightly larger spores in front-view. It was not recorded before from the Netherlands (Arnolds, 1984).

Cortinarius Fr.

In the Netherlands few taxonomical studies are carried out concerning this genus and modern descriptions are scanty. Moreover, most of the species are critical in some respect. Therefore we have included descriptions of most species observed in this genus.

Cortinarius anomalus (Fr.: Fr.) Fr.

Pileus 32–42 mm, expanded, with broad, indistinct umbo, hygrophanous, when moist pale red-brown (Expo D56) at centre, towards the margin brownish grey (D52), on drying paler, beige, surface covered with white, shiny fibrils (silky). Lamellae up to

6 mm broad, moderately crowded, adnate, emarginate, ventricose, pale brown ('caramel-coloured') with violaceous tinge, with concolorous edge. Stipe 40–50 × 6–8 mm, cylindrical, thickened at base (up to 13 mm), hollow, beige, greyish at apex, covered with white fibrillum, with rather inconspicuous, pale yellow velar zones in lower part of stipe and remains of cortina, brown by adhering spores. Context white in pileus with a grey zone near the lamellae; beige in stipe. Smell none or faintly fungoid.

Spores 7.2–8.0 × 6.0–6.7 µm, broad ellipsoid to subglobose, Q = 1.2, coarsely verrucose with small roundish or irregular warts. Cystidia absent.

Habitat. Terrestrial in a roadside verge planted with *Fagus* on nutrient-poor sandy soil, but outside the plots in a wide variety of other habitats.

Collection examined. Plot F44, 10 Oct. 1988, *Keizer 88066.*

In old state *Cortinarius anomalus* resembles *C. valgus* which lacks, however, any violet coloration and differs in spore form.

Cortinarius balteatoalbus R. Henry — Fig. 4

Pileus 50–85 mm, expanded, with somewhat depressed or umbonate centre, tobacco-brown (Expo D54, E54) or somewhat paler, at margin concolorous, with innate, darker fibrils, in young stage viscid, later dry but with adhering leaves etc. Lamellae up to 8 mm broad, crowded, adnate, emarginate, not ventricose, when young rather pale brown, later cinnamon-brown, with paler, sometimes serrulate edge (edge sometimes with clumps of spores like in some *Hebeloma* species). Stipe 40–65 × 7–13 mm, cylindrical with slightly swollen base, usually solid, pale brownish or beige, covered with pale fibrillum and appressed brown fibrils in lower 2/3 part, with some thin velar remains and near the base with one more conspicuous belt of veil. Smell weak, fruity or sweetish. Context in pileus and stipe whitish with faint brown or pink hue. Chemical spot tests of pileus: KOH 5% pale brown with yellow margin; NH_4OH 10% bright yellow; in context of stipe KOH and NH_4OH yellow.

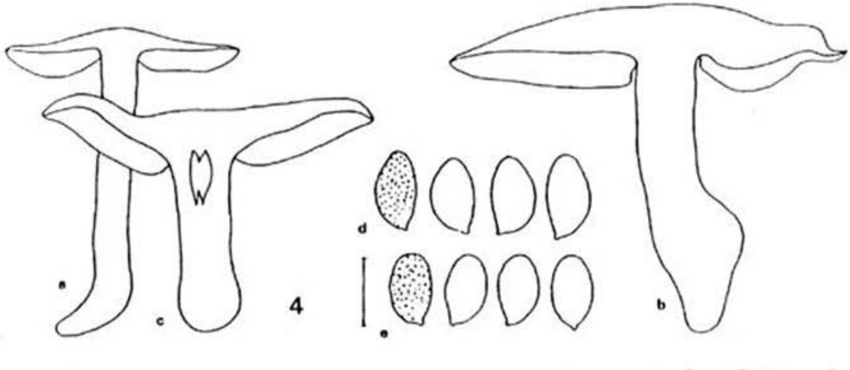


Fig. 4. *Cortinarius balteatoalbus.* a–c. habit; d, e. spores (a, d. *87284*; b. *88127*, c. *87138*). — Bar represents 10 µm.

Spores (9.0–)10.0–12.0(–12.4) × (5.3–)6.0–6.5(–6.8) µm, ellipsoid or subamygdaliform, Q = 1.5–2.2, av. Q = 1.80, ornamented with fine roundish, oval or irregular warts, the area just above the hilar appendix mostly smooth. No cheilocystidia observed.

Habitat. Terrestrial in a roadside verge planted with old *Quercus* on nutrient-poor sandy soil.

Collections examined. Plot Q2, 15 Sept. 1987, *Keizer 87138*; 13 Oct. 1988, *Keizer 88127*.

The size of the spores and the absence of cheilocystidia point towards *C. balteatoalbus*. The collection differs from the original description by Henry (1958) in slightly smaller basidiocarps and less involute margin of the pileus.

Cortinarius casimiri (Velen.) Huijsman — Fig. 5

Pileus 7–42 mm, narrowly campanulate, then plano-convex with distinct umbo; hygrophanous, when moist dark brown or dark red-brown (Expo J42, J12 (in centre), E-F22, H63-64), slightly or not translucently striate, on drying grey-brown to dark grey-brown (D-E62, E43, F62), covered with white, fibrillose scales or fibres, giving the surface a delicate, silvery appearance, stronger so towards the margin. Lamellae up to 6 mm broad, subdistant to distant, adnate, sometimes broadly adnate, emarginate, pale brown ('café-au-lait') when young, without pink or violet colours, later rusty brown, with paler edge. Stipe 20–60 × 2–6 mm, cylindrical or sometimes broader towards the base, solid or fistulose, pinkish brown to pale lilac brown, covered with white, silky, shining fibrillum, giving the stipe a pale pinkish appearance; a white annular zone and a few white floccose remnants of the veil may be present but these disappear with age. Context when moist in pileus dark brown and in the stipe pinkish brown, on drying in pileus pale beige and in the stipe pale pinkish. Smell usually indistinct, in one case earth-like and in one case sweetish.

Spores (9.7–)10.5–12.6(–13.2) × (5.0–)6.0–7.0(–7.4) µm, Q = 1.5–2.1, av. Q = 1.56–2.07, ovoid, base of spore remarkably rounded (in one case spores tapering towards the base), with ornamentation of fine punctiform or slightly irregular warts. Brown basidia present. Cystidia absent.

Habitat. In roadside verges planted with *Quercus* or *Fagus*, with poor grassy vegetation on sandy soil.

Collections examined. Plot Q32, 18 Sept. 1986, *Keizer 86148*; Plot Q2, 28 Oct. 1986, *Keizer 86178*; 18 Nov. 1986, *Keizer 86249*; 19 Aug. 1987, *Keizer 87106*; 15 Oct. 1987, *Keizer 87242*; 13 Oct. 1988, *Keizer 88130*; 15 Sept. 1988, *Keizer 88138*; Plot Q83, 24 Oct. 1986, *Keizer 86181*; 24 Aug. 1987, *Keizer 87131*; 22 Sept. 1987, *Keizer 87193*; *Keizer 87200*; 10 Oct. 1988, *Keizer 88087*; *Keizer 88280*. Plot F34, 19 Nov. 1986, *Keizer 86256a*; Plot F35, 6 Oct. 1988, *Keizer 88101*.

This species is characterized by the combination of the dark brown pileus, pink to pale lilac tinge at the stipe and especially by the large spores. The collections are in good agreement with the descriptions by Velenovský (1921: 464) and Huijsman (1955: 20). We consider *Cortinarius subsertipes* Romagn. a synonym, although Moser (1983a) placed that species in the group of *Telamonia* with a violet stipe apex and *C. casimiri* in the group without violet colours. However, Moser (l.c.) described the stipe in the latter species as: "Stiel-Spitze blaß lila ..." .

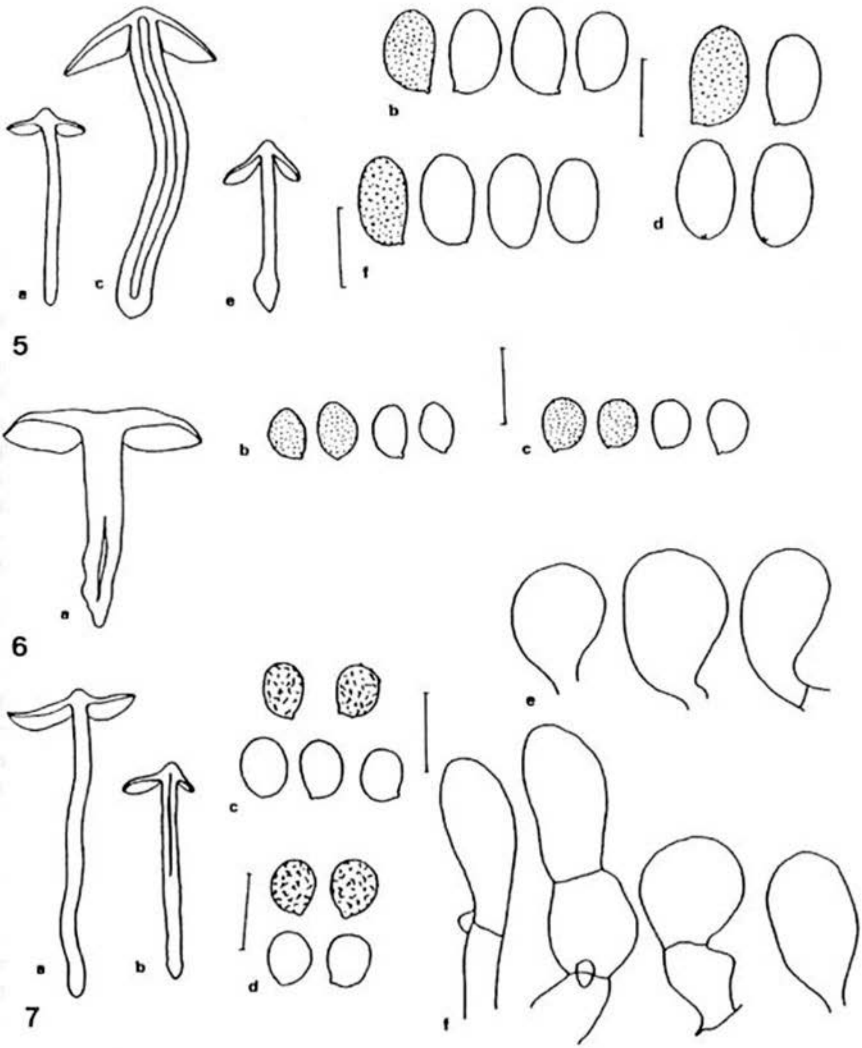


Fig. 5. *Cortinarius casimiri*. a, c, e. habit; b, d, f. spores (a, b. *87193*; c, d. *87200*; e, f. *87290*). — Fig. 6. *Cortinarius causticus*. a. habit; b, c. spores (a, b. *88124*; c. *88103*). — Fig. 7. *Cortinarius comptulus*. a, b. habit; c, d. spores; e, f. sterile cells in lamella edge (a, c, e. *88249*; b, d, f. *87348*). — Bar represents 10 µm.

Cortinarius causticus Fr. — Fig. 6

Pileus 17–70 mm diam., plano-convex without umbo, when moist whitish with pink-brown tinge (Expo B63, B64), in old specimens warm brown (more or less like *C. obtusus*), translucently striate, paler on drying, viscid. Lamellae up to 6 mm broad, moderately crowded, emarginate-adnate, pale ochre-brown, then more rusty brown, with paler edge. Stipe 40–45 × 3–7 mm, cylindrical, somewhat tapering towards the base, white, pale ochraceous-yellow with age, with brownish (due to spores) cortina-zone, viscid when moist. Smell sweetish or strongly fungoid; taste of pileipellis very bitter, in the other parts strongly fungoid.

Spores (6.2–)6.4–7.3(–7.9) × (3.9–)4.0–5.4(–5.5) µm, Q = 1.3–1.7 and av. Q = 1.35–1.58; pale yellowish brown under microscope, minutely punctate.

Habitat. Terrestrial in roadside verges planted with *Fagus* or *Quercus* on nutrient-poor sandy soil.

Collections examined. Plot F24, 7 Oct. 1988, *Keizer 88103*; 8 Sept. 1988, *Keizer 88348*; Plot Q2, 14 Oct. 1988, *Keizer 88124*.

The three collections studied show some differences: the fruit-bodies of collections *88103* and *88348* are small: pileus 17–22 mm broad and stipe c. 40 × 3 mm, pale ochre-yellow (old specimens) and with sweetish smell. In the other collection (*88124*) the fruit-bodies are larger: pileus 40–70 mm broad, stipe 45 × 7 mm, white and the smell is strongly fungoid. The spores of the collections *88124* and *88348* are narrower (4.0–4.8(–5.0) µm) than in collection *88103* (4.8–5.5 µm). The small variant was collected under *Fagus*, the other under *Quercus*. Kühner & Romagnesi (1953: 253) and Moser (1983: 392) described *C. causticus* with pileus 30–60 mm wide and with considerably narrower spores, 6–9 × 3–4 µm. The spore size reported by Konrad & Maublanc (1932: 137, 6.5–8 × 4–4.5 µm) agrees with the small-spored specimen, described above. In spite of the observed differences, the three collections are called *C. causticus* because of the distinctive bitter taste being present only in the pileipellis. This species is accepted here in this broad sense because the observed differences between the three collections did not correlate whith each other.

Cortinarius comptulus Mos. — Fig. 7

Pileus 15–28 mm, campanulate wnen young, soon expanding, with umbo, hygrophanous, when moist red-brown (colours like *C. hemitrichus*), only short-translucently striate, on drying paler, beginning around the centre (colours like *C. striaepilus*), surface covered with numerous white, hairy-fibrillose scales, densely fibrillose towards the margin, producing a dirty-white zone of about 3 mm broad. Lamellae up to 3 mm broad, moderately distant, adnate, emarginate, weakly ventricose, when young pale brown, later darker brown, with white-flocculose edge. Stipe 40–60 × 3 mm, cylindrical, flesh-coloured brown, towards the base of the stipe dark brown, covered with shiny white fibrillum, total impression pale brown, with some white floccose velar remnants. Context in apex of stipe greyish, downwards brown dark brown. Smell indistinct.

Spores (6.4–)6.5–7.2(–7.5) × (4.5–)4.8–5.5(–5.6) µm, Q = 1.2–1.4(–1.5), av. Q = 1.35, broadly ellipsoid with ornamentation consisting of rather coarse, roundish to elongate or irregular warts, somewhat stronger towards the apex, brown under microscope. Edge of the lamellae with hyaline, vesiculose sterile cells originating from the trama.

Habitat. Terrestrial in roadside verges planted with *Quercus robur* on nutrient-poor sandy soil.

Collections examined. Plot Q2, 15 Sept. 1987, *Keizer 87348*; Plot Q74, 10 Oct. 1988, *Keizer 88249*.

Cortinarius comptulus is in macroscopic characters almost identical with *C. hemitrichus*, but readily distinguished by the smaller spores.

Cortinarius erythrinus (Fr.) Fr. — Fig. 8

Pileus 9–45 mm, conical, then expanding with more or less prominent umbo; hygrophanous, when moist very dark brown with purplish hue (Expo J62, H42, J10), towards the margin slightly paler due to greyish, silky remnants of veil, on drying greyish brown (E52, E52/54, F21, F41) with centre much darker (J21, H61), not translucently striate. Lamellae up to 8 mm broad, moderately crowded to subdistant, emarginate-adnate, in old specimens ventricose, when young brownish, later rusty brown, with concolorous or slightly paler edge. Stipe 20–40 × 2–7 mm, cylindrical, stuffed, greyish lilac or pink-lilac (C41, C21, B21), with shiny fibrillum and often ± halfway a concolorous velar zone. Context in pileus greyish beige, in stipe pink-lilac-brownish, somewhat browner than surface of stipe. Smell indistinct.

Spores (7.0–)7.2–8.0(–8.3) × (5.0–)5.2–5.8(–6.0) µm, ellipsoid, Q = 1.3–1.6, av. Q = 1.38–1.50, strongly ornamented with coarse, irregular, elongate warts, coarser towards the apex. Cystidia not observed.

Habitat. Terrestrial in roadside verges planted with *Fagus* or *Quercus* on nutrient-poor sandy soil.

Collections examined. Plot F17, 19 Nov. 1986; *Keizer 86248*; Plot F24, 10 Nov. 1986, *Keizer 86235*; Plot Q1, 18 Sept. 1986, *Keizer 86152*; Plot Q2, 15 Sept. 1988, *Keizer 88140*; Plot Q31, 20 Oct. 1986, *Keizer 86176*; Plot Q31, 19 Aug. 1987, *Keizer 87075*; Plot Q32, 18 Sept. 1986, *Keizer 86153*; 5 Nov. 1986, *Keizer 86237*; 18 Aug. 1987, *Keizer 87096*.

All well-developed carpophores of this species had clearly visible, pinkish velar zones on the stipe, although Moser (1978) states that the stipe is mostly glabrous, with grey-brown veil present only in one (unnamed) variety. In the field this species is easily recognisable by the very dark cap (when moist) and the pink-lilac stipe with concolorous context. Microscopically, the relatively small spores with strong ornamentation are characteristic.

The species presented here is *Cortinarius erythrinus* (Fr.) Fr. sensu Ricken (1915), Lange (1935) and Bohus (1979; as *C. erythrinus* var. *russulaesporus* Bohus.). Lange (l.c.) described the spores as "pale and smooth" which indicates that he probably has studied deviating or unripe specimens. The macroscopic description and the plate agree well with this species. *Cortinarius erythrinus* sensu Henry and Favre possibly represents another taxon with narrower spores (7.5–9 × 4–5.5 µm, Kühner & Romagnesi, 1953: 305). Although *C. erythrinus* is stated to be a vernal species (Ricken, 1915; Kühner & Romagnesi (1953), the species is during this study only encountered in the autumn and not in other periods.

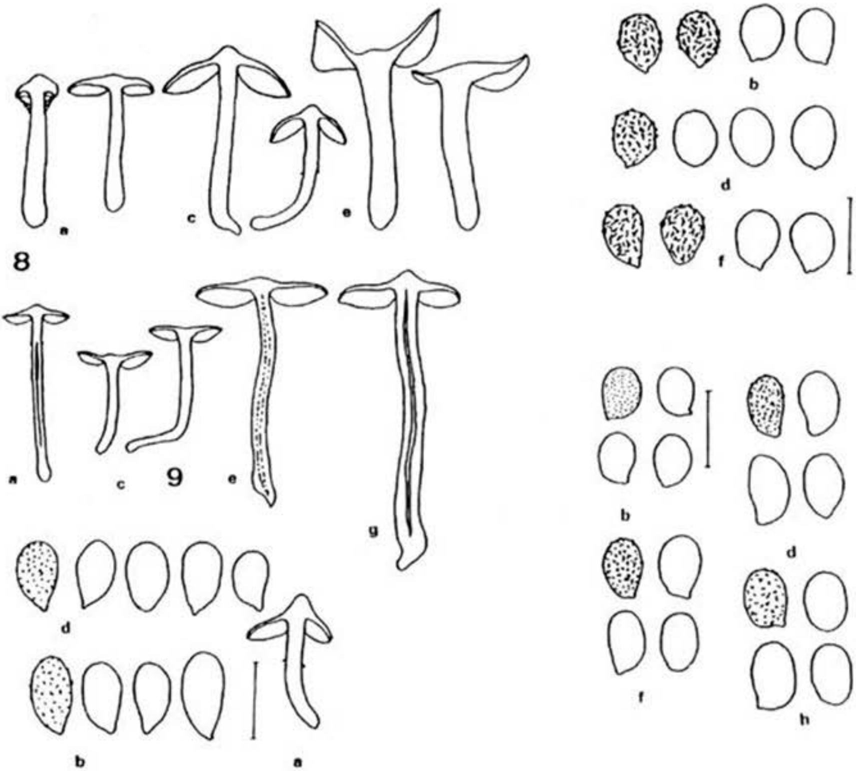


Fig. 8. *Cortinarius erythrinus.* a, c, e. habit; b, d, f. spores (a, b. *86152*; c, d. *88140*; e, f. *86237*). — Fig. 9. *Cortinarius flexipes.* a, c, e, g. habit; b, d, f, h. spores (a, b. *86184*; c, d. *87295*; e, f. *87165*; g, h. *88121*). — Bar represents 10 µm.

Cortinarius flexipes (Pers.: Fr.) Fr. sensu Kühner (1961) — Fig. 9

Pileus 12–35 mm, when young conical or convex, soon expanding, often with well-developed umbo, hygrophanous, when moist dark reddish grey-brown (Expo D34, E34, F23, F43, F52, H42, H52, J21, J42), towards the margin slightly paler (C43, E52, J22, H43), translucently striate up to 1/3 of the radius, on drying slightly paler, more greyish red-brown (E43, E54, somewhat paler than H42), with darker centre, when young covered by sparse, thin, white fibrils, soon disappearing and then ± shiny, at margin frequently covered by concentrically arranged pink-greyish velar remnants. Lamellae up to 3–4.5 mm broad, moderately crowded, in old specimens somewhat ventricose, when young pink (e.g. D42), soon only pink on the edge, finally entirely pale brown to rusty brown. Stipe 20–60 × 2–4 mm, cylindrical, sometimes with swollen base, usually becoming fistulose, pink-brown, covered by white or violaceous white fibrillum, general impression pale pink (A41), veil usually present in form of a white annuliform zone and scattered flocks that disappear with age.

Spores (6.7–)7.0–9.2(–10.0) × (4.4–)4.6–5.2(–5.5) µm, Q = 1.3–1.8, av. Q = 1.41–1.82, ellipsoid to oblong with small to coarse warts, often coarser towards the apex. Basidia with brown content present. Cystidia absent.

Habitat. Terrestrial in the grassy vegetation in roadside verges planted with *Fagus* or *Quercus*.

Collections examined. Plot F24, 24 Aug. 1987, *Keizer 87084*; Plot F34, 30 Oct. 1986, *Keizer 86186*; 28 Oct. 1988, *Keizer 88284*; Plot F43, 7 Oct. 1988, *Keizer 88102*; Plot Q1, 5 Nov. 1986, *Keizer 86236*; 18 Aug. 1987, *Keizer 87082*; Plot Q2, 13 Oct. 1988, *Keizer 88253*; 14 Oct. 1988, *Keizer 88121*; *Keizer 88240*; Plot Q32, 17 Sept. 1987, *Keizer 87165*; 13 Oct. 1987, *Keizer 87295*; Plot Q83, 24 Oct. 1986, *Keizer 86184*; 10 Oct. 1988, *Keizer 88279*; Plot Q84, 30 Oct. 1986, *Keizer 86182*.

This species is above all characterized by the pale pinkish (and not violaceous) colour of the stipe and the arrangement of the velum on the cap (only visible in material in good condition). The dark greyish red-brown colour of the cap is also distinctive. Macroscopically it is very similar to *Cortinarius casimiri*, which differs in the larger spores. The mere presence of violaceous colours in the young carpophore (in the lamellae and/or in the apex of the stipe) is considered the most important distinguishing character in this group of *Telamonia*. A closely related species with violaceous colours is *C. sertipes* Kühn. 1955 (syn.: *C. flexipes* forma *sertipes* Kühn. 1961, *C. contrarius* Geesink 1976). The species without violaceous but with (pale) pink colour in the stipe is referred to as *C. flexipes*.

Cortinarius decipiens (Pers.: Fr.) Fr. is very close, but may differ in a less-developed veil and lack of a pink tinge in the young lamellae (Persoon, 1801: 298; Fries, 1821: 236). However, *C. decipiens* sensu J. Lange (1938: 47; pl. 103D) is in our opinion identical with *C. flexipes*.

On the other hand, the description by Jansen (1984: 80) of *C. decipiens* refers to *C. casimiri*.

Cortinarius fusisporus Kühn. — Fig. 11

Pileus 12–13 mm, expanded with incurved margin, hygrophanous, when moist brown to yellowish brown (Expo E64), at centre darker, margin paler and somewhat fibrillose, on drying paler brownish. Lamellae moderately crowded, adnexed, emarginate, pale brown ('caramel-coloured') with paler edge. Stipe cylindrical, brown with yellow-brown fibrillum, in lower half with a few dirty white velar remains. Smell indistinct.

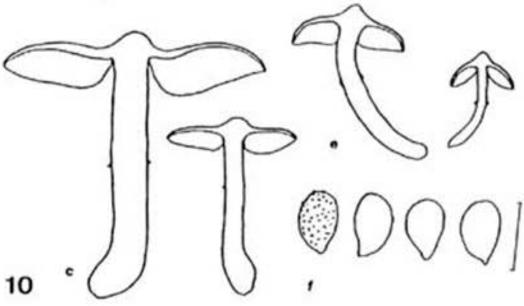
Spores (9.2–)9.5–11.5(–11.6) × 4.4–5.0(–5.1) µm, Q = 1.9–2.6, av. Q = 2.21, subcylindrical-fusiform, ornamentation consisting of fine punctiform warts. Cystidia absent.

Habitat. Terrestrial in roadside verge planted with *Quercus robur*.

Collection examined. Odoorn, Odoornerveen, 31 Oct. 1989, *Keizer 89104*.

The long and narrow spores are distinctive for this species, but *Cortinarius semivestitus* Mos. seems to be very close to *C. fusisporus*, if not identical. *C. semivestitus* has yellowish brown velar remnants on the stipe; these are dirty white in *C. fusisporus*. *Cortinarius incisus* Pers.: Fr. sensu Moser (1983b) is considered a synonym of *C. fusisporus*.

10



11

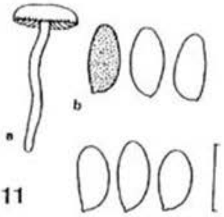


Fig. 10. *Cortinarius helveolus*. a, c, e. habit; b, d, f. spores (a, b. *87308*; c, d. *87207*; e, f. *88146*). — Fig. 11. *Cortinarius fusisporus*. a. habit; b. spores (*89104*). — Bar represents 10 µm.

Cortinarius helveolus (Bull.) Fr. — Fig. 10

Synonym: *Cortinarius basililaceus* Pearson ex P.D. Orton.

Pileus 15–60 mm, campanulate or conical, then plano-convex, with prominent, acute umbo, hygrophanous, when moist ochraceous yellow-brown or warm orange-brown (Expo E56, E58 (mostly), F54), in centre more intensely coloured, the margin slightly paler due to the presence of thin, silky fibrils, not or slightly and shortly translucently striate, on drying pale ochre-brown to yellow-brown or straw-coloured (B66, C58, C66, D58, E56), in centre more intensely brown (C58, D58, E56). Lamellae up to 10 mm broad, very distant (6–9 per 10 mm at margin of pileus), often interveined, thickish, adnate, emarginate, distinctly ventricose, when young violet in most cases, soon fading to pale brown ('caramel-brown'), finally (purplish-)rusty brown, with concolorous or paler edge. Stipe 20–70 × 2–8 mm, cylindrical or slightly enlarged at the base, fistulose or stuffed, ground colour like moist pileus, covered by shiny, pale brown fibrils, causing a somewhat paler appearance, in young specimens with violet apex and base, fading with age, approximately halfway the stipe with a distinct, yellowish white, almost membranaceous annulus, downwards with some additional velar zones or flocci. Context in pileus concolorous with surface, in stipe violaceous in top and base of young specimens, later ochre-brown. Smell weak or distinct, musty or sweetish.

Spores (8.2–)8.8–10.2(–11.3) × (4.5–)4.7–5.6(–6.5) µm, Q = 1.6–2.1 and av. Q = 1.64–1.92, oblong, often tapering towards the base, with small, subglobose or oval warts, stronger developed towards the apex. Basidia with brown or golden-brown content present; brown extracellular pigment present in the hymenophoral trama. No sterile cells have been found in the hymenium.

Habitat. In poor, grassy vegetation of roadside verges planted with *Fagus* or *Quercus*. Often on moist places.

Collections examined. Plot F24, 3 Nov. 1987, *Keizer 87254*; Plot Q2, 15 Oct. 1987, *Keizer 87277*; 15 Sept. 1988, *Keizer 88146*; Plot Q74, 23 July 1988, *Keizer 88038*; 10 Oct. 1988, *Keizer 88199*; Plot Q82, 1 Oct. 1987, *Keizer 87207*.

The rather robust habit, the distant lamellae and the warm (yellowish) brown colours indicate that this species is related to *Cortinarius hinnuleus* Fr. Some characters separate it clearly from *C. hinnuleus*, viz. the prominent, almost pointed umbo, the (often) violaceous colours of the young lamellae and stipe, the warm, more yellowish brown colour of the pileus and the persistent, almost membranaceous annular zone on the stipe. Microscopically, the spores are slightly longer, more slender and often tapering towards the base.

The descriptions of '*C. helveolus* Fr. ss. Bresadola' by Kühner & Romagnesi (1953: 301) and Moser (1978: 408) differ in a number of characters from the material presented here, especially in the lack of violet colours. Nevertheless, we consider these interpretations as probably conspecific with our material, on account of the well-developed annulus and distant lamellae. Both descriptions refer to plate 653 by Bresadola (1929) (although Kühner & Romagnesi (1953) expressed their doubt with a question mark), which does neither show the bright yellow-brown pileus, nor any violaceous hue in lamellae or stipe.

Cortinarius quadricolor Fries (1874: 378) is rather similar, but the stipe of that species was described as violaceous white without brown colours. Of this species no recent records seem to exist.

The picture of *Cortinarius hinnuleus* by Phillips (1981: 138) is a misapplication of *C. helveolus*.

Orton (1984) presented *Cortinarius basililaceus* Pearson ex P.D. Orton, which was said to differ from *C. helveolus* Fr. by the non-coniferous habitat, the smell (not inodorous), yellowish veil, striate pileus, more slender stature and more elongate spores and from *C. helveolus* sensu Kühner & Romagnesi (1953) by the presence of violet colours. Except for the veil (*zona annulari ferrugineo-marginata*) Fries (1874) did not mention these characters and the violet colour in the young lamellae and near the base of the stipe of *C. basililaceus* was described as very variable. It is concluded that the description of *C. basililaceus* agrees with the description of *C. helveolus* Fr. and the interpretations of Kühner & Romagnesi (l.c.) and Moser (1978). Consequently, *C. basililaceus* is considered as a synonym of *C. helveolus*. Moreover, it seems unlikely that this species, which apparently is wide spread in at least the UK and the Netherlands, would not have been noticed before the forties of this century.

Cortinarius hinnuleus Fr. — Fig. 12

Pileus 20–65 mm, when young convex, later expanding, usually with broad and blunt umbo, finally applanate to concave and then umbo not conspicuous, hygrophanous, when moist warm ochre-brown to red-brown (Expo H42, H43, D54, D64, E52, E54, E56, E58, F54, H52, H64, J34), with usually more intensely coloured centre (e.g. H52, H64, F52, H32), often paler and more greyish at margin due to a fibrillose layer, not translucently striate, often with a pattern of radial dark streaks, on drying ochre-brown, greyish ochre-brown or straw-coloured (B64, B72, C56, C63, C64, D56, D66, E58, E66, E68, F48). Lamellae up to 10–14 mm broad, distant, sometimes veined on the sides and interveined, in old specimens strongly ventricose, rather narrowly adnate, first pale brown, older darker brown because of ripening of the spores, with whitish edge, especially when young, without violet or pink colours. Stipe 35–70 × 4–14 mm, cylindrical, tapering towards the

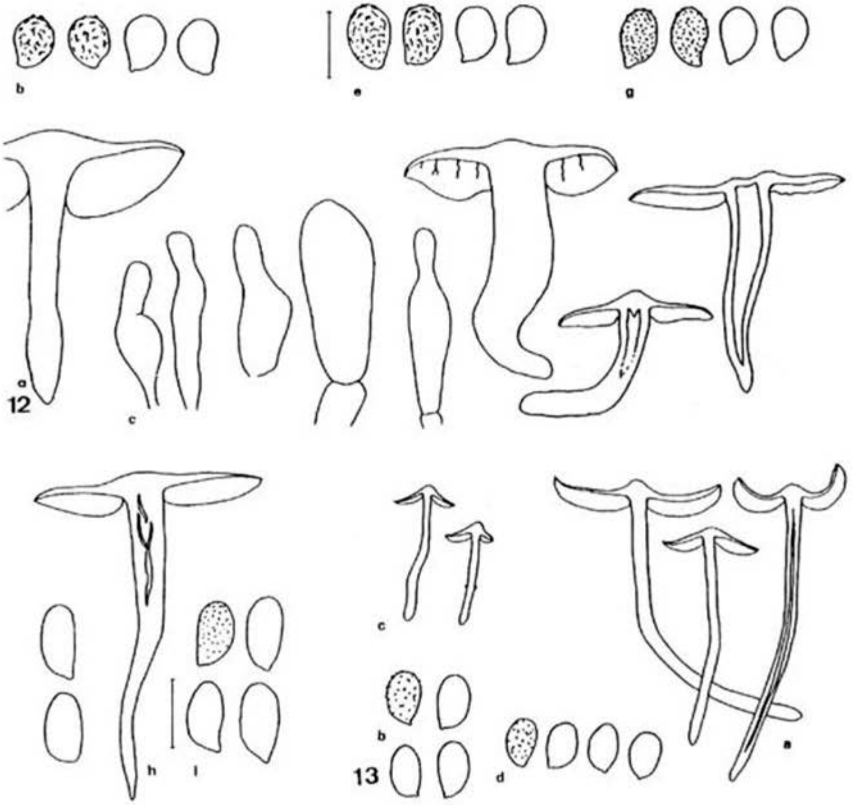


Fig. 12 a–g. *Cortinarius hinnuleus*. a. habit; b. spores; c. sterile cells in lamella edge (*87143*); d, f. habit; e, g. spores. — Fig. 12 h, i. *C. hinnuleus* var. *griseascens*. h. habit; i. spores (d, e. *87312*; f, g. *88126*; h, i. *86238*). — Fig. 13. *Cortinarius lanatus*. a, c. habit; b, d. spores (a, b. *88195*; c, d. *87051*). — Bar represents 10 µm.

base or basal part somewhat enlarged, fistulose or solid, brown, concolorous with moist pileus, covered by shiny, pale brown fibrillum, giving the stipe a pale brown appearance, darker brown towards the base, with one or several white, annuliform velar zones which may fade with age, basal part often white tomentose ('sock'). Context in stipe concolorous with surface of pileus, on drying cork-coloured, finally dark brown in basal part of the stipe. Smell distinctly musty, dusty or sweetish, but sometimes indistinct.

Spores (6.6–)7.0–9.0(–9.8) × (4.9–)5.1–6.1(–6.5) µm, Q = 1.3–1.8, av. Q = 1.40–1.60, ellipsoid to oblong, with oval to irregular, moderately coarse warts; ornamentation stronger developed at the apex of the spore. In one collection sterile cells were present at the edge of the lamellae (Fig. 12c.). Brown basidia present.

Habitat. Terrestrial in the poor, grassy vegetation of roadside verges planted with *Fagus* or *Quercus*.

Collections examined. Plot F35, 6 Oct. 1988, *Keizer 88092*; Plot Q2, 28 Oct. 1986, *Keizer 86179*; 18 Nov. 1986, *Keizer 86247*; 15 Sept. 1987, *Keizer 87143*; 15 Oct. 1987, *Keizer 87339*; 15 Oct. 1988, *Keizer 88136*; Plot Q6, 8 Nov. 1987, *Keizer 87312*; *Keizer 87316*; Plot Q32, 14 Oct. 1987, *Keizer 87236*; Plot Q83, 1 Oct. 1986, *Keizer 86176*; Odoorn, Odoornerveen, 13 Oct. 1987, *Keizer 87294*; 22 Sept. 1988, *Keizer 88126*.

Cortinarius hinnuleus is known as a variable species (e.g. Dähncke & Dähncke, 1979), which is confirmed by our observations. In the present concept variants with a slender fusiform stipe have been united with variants with a thick-set to (slightly) bulbous stipe. Small and slender forms may be confused with *C. striaepilus* but the lamellae of the latter are more crowded and the pileus is usually translucently striate. In one collection (*87143*) sterile cells were observed at the edge of the lamellae. These seem to originate from the lamellar trama and are therefore not true cheilocystidia. As this collection fits otherwise well into the adopted concept of *C. hinnuleus*, no taxonomic importance has been assigned to this character. This feature can be found occasionally among other species of *Cortinarius* as well and may be explained by the observation that the edge of the lamellae is the last part becoming fertile, and some basidia may fail to ripen. A closely related taxon is *C. helveolus* (see there).

Cortinarius lanatus (Mos.) Mos. — Fig. 13

Pileus 7–38 mm, when young campanulate or conical, then expanding usually with a prominent umbo, hygrophanous, with centre of pileus drying first in an irregular pattern, when moist warm red-brown to dark red-brown (Expo H44, H42, H52, H43, J22, F52, F62), translucently striate up to 1/3 of the radius, at margin yellowish due to presence of a fibrillose layer, on drying ochre-brown, straw-coloured (C56, D56, C63, E56, C66), with small, yellow-brown, fibrillose hairy scales. Lamellae up to 4 mm broad, moderately crowded to subdistant, emarginate-adnate, somewhat ventricose, when young pale brown, later rusty brown, with concolorous edge. Stipe 13–70 × 2–4(–5) mm, cylindrical, narrowly fistulose, ground colour rather dark brown, darker towards the base, covered by yellow-brown to straw-coloured, shining fibrils and with a woolly, brown annular zone, downwards with several more brownish floccose velar remains. Context in all parts rusty brown, black-brown in base of stipe. Smell weak, fungoid or sweetish.

Spores (6.2–)6.9–8.3(–8.8) × (4.2–)4.4–5.0 µm, Q = (1.4–)1.5–1.9, av. Q = 1.56–1.67, ellipsoid, pale yellowish brown under microscope, minutely punctate, somewhat stronger so towards the apex. Cystidia absent.

Habitat. Terrestrial in roadside verges planted with *Quercus* or *Fagus*.

Collections examined. Plot F34, 10 Nov. 1987, *Keizer 87325*; Plot F43, 7 Oct. 1988, *Keizer 88073*; Plot Q65, 24 Sept. 1988, *Keizer 88266*; Plot Q82, 4 Sept. 1987, *Keizer 87051*; Plot Q93, 30 Oct. 1987, *Keizer 87302*; 21 Sept. 1988, *Keizer 88056*; Odoorn, Odoornerveen, 18 Nov. 1987, *Keizer 87297*; 1 Nov. 1988, *Keizer 88195*.

Among the small *Telamonia* species with brown veil and squamulose pileus three names come into consideration for our taxon, viz. *Cortinarius psammocephalus* Fr., *C. strobilaceus* Mos. and *C. lanatus* (Mos.) Mos. Moser (1978) quoted the plate of

C. psammocephalus by Lange (1935: 99F) under *C. strobilaceus* and apparently considered these names as synonyms. This plate shows a more squamulose pileus than our collections, and Lange observed larger spores. The description of *C. lanatus* ("pileus brown, scaly") by Moser (1978) fits better than that of *C. strobilaceus* ("pileus … grey-fibrillose or fine scaly") although the differences are small. Therefore the former name has been chosen.

Cortinarius psammocephalus, a closely related species, occurs in the Netherlands along lanes on clay mainly along the river Rhine and its affluents. This species differs in having more prominently developed squarrulose scales on the pileus, more abundant remains of the veil on the stipe and a slightly less slender habit. The question whether *C. psammocephalus* and *C. strobilaceus* are synonyms remains to be solved.

Cortinarius paleaceus (Fr. in Weinm.) Fr. — Fig. 14

Pileus 8–22 mm, campanulate, later expanded, usually with well developed umbo but umbo sometimes almost absent, hygrophanous, when moist dark red-brown (Expo J32, E62, F62), towards the margin more greyish due to fibrillose veil remains, on drying pale pinkish brown, greyish beige (B61, D63), darker brown (E52) at centre, whitish-fibrillose margin, covered with white hairy scales, which may disappear with age. Lamellae up to 3 mm broad, moderately crowded but sometimes more distant, emarginate-adnate, when young pale brown without lilac colours, later rusty brown, with concolorous edge. Stipe 15–40 × 1–3 mm, cylindrical, sometimes attenuate at the base, middle brown, covered with dirty-white or pale brownish, shiny fibrils, giving a shiny pale brown appearance, in one collection with weak lilac hue, usually with a white annular zone and several floccose veil remains below, which may disappear with age. Context in pileus and stipe pale beige when dry, reddish brown when wet. Smell usually distinct like crushed leaves of *Pelargonium zonale* (L.) Ait., sometimes more like the lemon-smell of *P. radens* H.E. Moore.

Spores (7.0–)7.5–8.7(–9.5) × (4.5–)5.0–5.7(–5.9) µm, Q = 1.4–1.9, av. Q = 1.48–1.86, ellipsoid, with small punctiform warts or with stronger developed and elongate to irregular warts, usually stronger at the apex of the spore, under the microscope brown to rather dark brown. No cystidia observed.

Habitat. Terrestrial in roadside verges planted with *Quercus* or *Fagus* on nutrient-poor soil.

Collections examined. Plot F34, 19 Nov. 1986, *Keizer 86256b*; Plot Q2, 28 Oct. 1986, *Keizer 86183*; 15 Sept. 1987, *Keizer 87152*; 15 Oct. 1987, *Keizer 87293*; *Keizer 87306*; Plot Q33, 30 Oct. 1987, *Keizer 87314*; Plot Q74, 22 Sept. 1987, *Keizer 87178*; Plot Q82, 4 Sept. 1987, *Keizer 87098*; Plot Q83, 22 Sept. 1987, *Keizer 87194*; Odoorn, Odoornerveen, 13 Oct. 1987, *Keizer 87331*.

A description of this species is given to enable a comparison with the closely related *C. paleiferus*.

Cortinarius paleiferus Svrček — Fig. 18

Pileus 20–30 mm, convex, without umbo, hygrophanous, when moist reddish brown (Expo F44-F46), towards the margin more grey due to a fibrillose layer of dirty-white veil

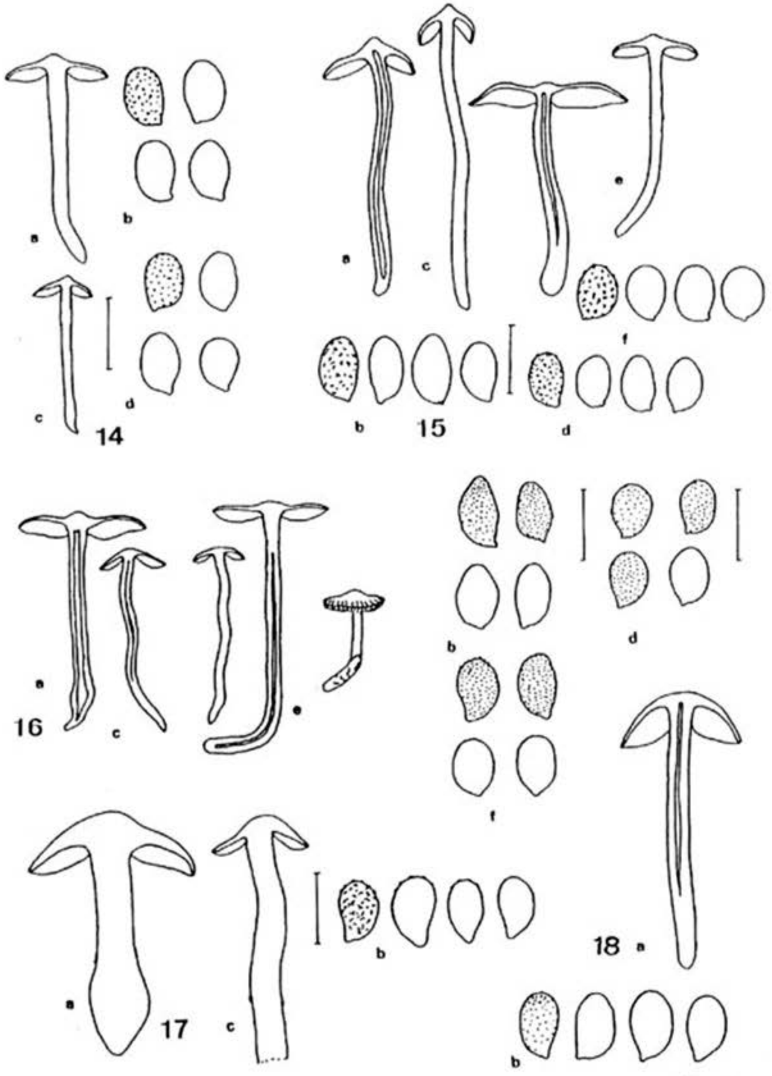


Fig. 14. *Cortinarius paleaceus*. a, c. habit; b, d. spores (a, b. *87306*; c, d. *87194*). — Fig. 15. *Cortinarius parvannulatus*. a, c, e. habit; b, d, f. spores (a, b. *87197*; c, d. *87239*; e, f. *88131*). — Fig. 16. *Cortinarius striaepilus*. a, c, e. habit; b, d, f. spores (a, b. *87168*; c, d. *88142*; e, f. *87252*). — Fig. 17. *Cortinarius privignus*. a, c. habit; b. spores (a, b. *86147*; c. *86151*). — Fig. 18. *Cortinarius paleiferus*. a. habit; b. spores (*86246*). — Bar represents 10 µm.

remains; on drying pinkish grey-brown (E22), pale greyish towards the margin, covered with white hairy scales. Lamellae up to 5 mm broad, distant, emarginate-adnate, somewhat ventricose, sinuose and venose, rusty brown with violet hue, with concolorous edge. Stipe 55–60 × 6 mm, cylindrical, fistulose, concolorous with pileus, but with violet apex, covered with white shiny fibrils, in addition with some white velar remains, violaceously tomentose at base (K. & W. 18D4). Context in stipe and pileus slightly darker coloured than surface, with smell like *Pelargonium zonale*.

Spores (8.2–)8.3–9.0(–9.2) × (5.2–)5.4–5.6(–6.0) µm, Q = 1.5–1.9, av. Q = 1.58–1.85, ellipsoid to oblong, faintly verrucose, rather dark brown under microscope. No cys-tidia observed.

Habitat. Terrestrial in roadside verges planted with *Quercus* or *Fagus* on nutrient-poor soil.

Collections examined. Plot F17, 19 Nov. 1986, *Keizer 86246*; Plot Q31, 17 Oct. 1988, *Keizer 88214*; Odoorn, Odoornerveen, 1 Nov. 1988, *Keizer 88184*.

Cortinarius paleiferus is distinct from the related *C. paleaceus* because of the violaceous young lamellae, apex and basal tomentum of the stipe and the distant lamellae. Jansen (1984) considered these names as synonyms. However, in the present material a satisfactory distinction could be made between the two species. If old material is studied the violaceous coulors may disappear and then the distinction between the species becomes difficult. Yet, future research on more extensive material might prove that the species are identical.

Cortinarius parvannulatus Kühner — Fig. 15

Pileus 10–35 mm, campanulate, then expanding, mostly with obvious umbo, when moist warm brown to chestnut-brown (K. & W. 6E7, 6E8, Expo between F34-36 and E58), somewhat darker at centre, in one case more ochre-brown (between D54 and D56), translucently striate, covered with small whitish hairs, towards the margin with whitish fibrillose veil, on drying yellowish brown (C56, C63). Lamellae up to 4–5 mm broad, moderately crowded to subdistant, emarginate-adnate, not ventricose, when young pale ('caramel'-)brown, often with pink-lilac hue, later darker rusty brown, edge concolorous or slightly paler. Stipe 25–65 × 1.5–3.5 mm, cylindrical, usually fistulose, flesh-coloured brown, covered with pale yellow-brown, shiny fibrils, (e.g. D58, C61), giving the stipe a pale yellowish brown appearance, apex lilac, fading with age, not or hardly darker towards the base, often with a conspicuous, white annular zone, and additional white floccose veil remnants may be present in the lower part of the stipe. Context in pileus and stipe concolorous with surface to slightly darker, in base of stipe dark brown. Smell of cedar-wood or as *Camarophyllus russocoriaceus* but weaker.

Spores (7.0–)7.5–9.0(–11.9) × (4.3–)4.8–5.3(–5.5) µm, Q = 1.5–2.0(–2.1), av. Q = 1.60–1.73, ellipsoid to oblong, ornamentation consisting of moderately coarse, roundish, elongate or irregular warts, slightly stronger at the apex of the spore. No cystidia observed.

Habitat. Terrestrial in roadside verges planted with *Fagus* or *Quercus*.

Collections examined. Plot F33, 24 Sept. 1988, *Keizer 88273*; Plot Q2, 15 Oct. 1987, *Keizer 87239*; Plot Q31, 28 Oct. 1987, *Keizer 87267*; Odoorn, Odoornerveen, 3 Oct. 1989, *Keizer 89036*.

Collection *Keizer 88131*, 13 Oct. 1988, Plot Q2, which agrees macroscopically with the above description, differs in the size and shape of the spores (6.8–)6.9–7.5(–7.9) × 5.1–5.6(–5.7) with Q = 1.3–1.5 and av. Q = 1.36, and in the ornamentation consisting of coarser warts.

Cortinarius cedriolens (Mos.) Mos. with the same smell, is said to differ by the absence of an annular veil-zone (but velar zones often present (Moser, 1978)) and absence of violaceous tinges in the top of the stipe. Both characters can vary considerably in subgenus *Telamonia*. Therefore, Lindström & Brandrud (1987: 9), Grünert (1989: 141) and Brandrud et al. (1990) consider these taxa as synonyms, with which view we agree.

Cortinarius privignus Fr. sensu lato — Fig. 17

Pileus 21–36 mm, convex, later plano-convex with rather weak, obtuse, broad umbo, hygrophanous, when moist warm orange-brown (Expo E58) with paler margin, not translucently striate, on drying ochre-brown (D68); margin white-silky fibrillose by remains of white veil. Lamellae up to 4 mm broad, moderately distant, not or slightly ventricose, narrowly and somewhat emarginate-adnate, rather pale brown, with white edge, without a trace of violet. Stipe 25–50 × 5–8 mm, cylindrical with clavate base, up to 13 mm broad, stuffed, pale brown, covered by white-silky fibrils, causing a pale beige appearance with white annuliform veil remnants in lower half of stipe. Smell none; taste not known.

Spores 7.5–8.5(–10.0) × 5.0–5.5(–6.0) µm, Q = 1.4–1.7(–1.8), av. Q = 1.60–1.64, ± amygdaliform, with rather coarse, elongate or irregular warts, more prominent towards the apex. Brown basidia present. No cystidia observed.

Habitat. Terrestrial in roadside verges planted with *Quercus* on nutrient-poor soil.

Collections examined. Plot Q2, 15 Sept. 1988, *Keizer 88134*; Plot Q32, 18 Sept. 1986, *Keizer 86147*; *Keizer 86151*.

The species under consideration here is named *Cortinarius privignus*. In literature (Kühner & Romagnesi (1953), Moser (1978)) several similar taxa have been distinguished (*C. privignofulvus* R. Henry, *C. privignus* Fr., *C. privignorum* R. Henry, *C. privignoides* R. Henry, *C. pseudoprivignus* R. Henry) based on (slight) differences in colour of and degree of hygrophaneity of the pileus, and the shape of the stipe. The characters mentioned appear to be gradual and since representatives of this group seem to be rare in the Netherlands, critical comparison and evaluation of the given differences could not be made. However, to our opinion the distinction of so many taxa based upon these characters, does not seem justified. The ornamentation of the spores in our collections differs from that given by Marchand (1983: 152), where punctiform warts are shown.

Cortinarius rigens (Pers.: Fr.) Fr. — Fig. 19

Pileus 44–60 mm, plano-convex or applanate, without or with low umbo and with somewhat involute margin; hygrophanous, when moist wood-coloured brown to grey-brown (Expo B-E54) or (orange-red-)brown (E46-E58), margin not translucently striate, on drying straw-coloured ochraceous yellow-brown (B56, C64), at centre darker (C56); surface radially silky or slightly fibrillose, towards the margin with white velar fibrils.

Lamellae up to 8 mm broad, somewhat crowded to somewhat distant, not ventricose, crenulate, emarginate-adnate, rusty brown, with paler, yellow-brown edge. Stipe 78–80 × 9–16 mm, cylindrical or irregularly inflated, gradually tapering into pointed, rooting base; hollow or solid, pale ochre-beige mixed with white, covered with white fibrillum and a few indistinct fibrillose remnants of the veil, on drying white or whitish. Smell distinct, like jodoform.

Spores (6.5–)7.0–8.7(–9.0) × (4.2–)4.9–5.6(–5.9) µm, Q = (1.4–)1.5–1.6(–1.7), av. Q = 1.53–1.61; ellipsoid, ornamentation verrucose with punctiform, sometimes elongate or irregular warts, ornamentation often stronger towards the apex of the spore.

Habitat. Terrestrial in roadside verges planted with *Quercus* on nutrient-poor soil.

Collections examined. Plot Q2, 15 Sept. 1988, *Keizer 88139*; Odoorn, Odoornerveen, 18 Nov. 1987, *Keizer 87291*; 9 Nov. 1989, *Keizer 89113*.

Cortinarius rigens as depicted by Lange (1938: 100C) with stipe 4–9 mm broad fits these collections well, but is somewhat different from the description by Moser (1978) with a stipe only 3–5 mm broad. Nevertheless, Moser quoted Lange's plate for his *C. rigens*. Persoon (1801: 288) originally described *Agaricus rigens* with a stipe 6.3–8.5 mm thick. He did not mention any characteristic smell. Two species are related to *C. rigens*, viz. *C. velenovskyi* R. Henry and *C. duracinus* Fr. The former is smaller and darker and the latter is more robust and inodorous according to Ricken (1915), Konrad & Maublanc (1924–1937), Bresadola (1927–1933), Marchand (1983) and Moser (1978). However, Bon (1988) reported a iodoform-like smell but a stipe 15 mm broad for *C. duracinus*, so that the identity of his plate remains uncertain.

Cortinarius striaepilus J. Favre — Fig. 16

Pileus 7–25(–40) mm, convex or conical, rather soon expanding, mostly umbonate with inconspicuous and blunt to prominent, almost papilla-like umbo, hygrophanous, when moist dark reddish brown or dark yellowish brown (Expo F44, H44, H43, E54, H52, F54, F46), towards the margin paler by fibrillose covering, translucently striate up to 1/3 to 1/2 radius, sometimes more, on drying pale yellowish brown or straw-coloured (C63, C64, C62, B56 (darker), between E56 and E63, C56), slightly more reddish brown (E56) at centre, when young covered with very thin pale-whitish hairy remains of velum, disappearing with age, margin split and fringed in old specimens. Lamellae (L = 20–30), up to 3–6 mm broad, more or less distant (8–10 per 10 mm at cap margin), in old specimens ventricose, emarginate, first pale brown, ('caramel-coloured'), later more rusty brown with pale edge, sometimes edge with a very faint and soon disappearing pink flush. Stipe (20–)30–50 × 1.5–3 mm, cylindrical or sometimes slightly swollen at the base, hollow; apex very pale, almost hyaline, towards base darker brown, more or less concolorous with pileus, with shiny pale brown to whitish fibrillum, in addition with an annuliform velar zone and some floccose veil-remnants, base frequently white-tomentose. Flesh in drying pileus and upper part of stipe pale cork-coloured, in lower part of stem dark brown. Smell none or weakly fungoid, in one collection *Pelargonium*-like.

Spores (6.2–)7.0–9.0(–11.0) × 4.5–5.5 µm, Q = 1.3–1.9, av. Q = 1.45–1.75, ellipsoid or ellipsoid-oblong, with small round or elongate warts, often slightly stronger warty at the apex. Basidia present with brown content. No cystidia observed.

Habitat. In roadside verges planted with *Fagus* or *Quercus* on nutrient-poor sandy soil, especially on the steep side of ditches.

Collections examined. Plot F24, 10 Nov. 1986, *Keizer 86226*; *Keizer 86229*; 7 Oct. 1988, *Keizer 88090*; Plot F33, 1 Oct. 1987, *Keizer 87201*; Plot F34, 30 Oct. 1986, *Keizer 86180*; *Keizer 86185*; 19 Nov. 1986, *Keizer 86243*; *Keizer 86255*; 10 Nov. 1987, *Keizer 87329*; 28 Sept. 1988, *Keizer 88236*; Plot F35, 22 Sept. 1987, *Keizer 87199*; Plot F41, 15 Sept. 1986, *Keizer 86143*; 10 Nov. 1987, *Keizer 87323*; Plot Q1, 6 Oct. 1986, *Keizer 86170*; 3 Oct. 1988, *Keizer 88074*; Plot Q2, 18 Nov. 1986, *Keizer 86253*; 19 Aug. 1987, *Keizer 87121*; 15 Sept. 1987, *Keizer 87148*; 15 Oct. 1987, *Keizer 87240*; 15 Sept. 1988, *Keizer 88142*; Plot Q13, 22 Sept. 1987, *Keizer 87184*; 3 Nov. 1987, *Keizer 87263*; Plot Q35, 6 Oct. 1988, *Keizer 88091*; Plot Q81, 3 Nov. 1986, *Keizer 86242*; Plot Q82, 24 Sept. 1988, *Keizer 88083*; Plot Q83, 1 Oct. 1986, *Keizer 86175*; 10 Nov. 1986, *Keizer 86224*; 24 Aug. 1987, *Keizer 87068*; 4 Nov. 1987, *Keizer 87252*; 8 Sept. 1988, *Keizer 88161*; *Keizer 88174; Keizer 88317; Keizer 88354*; Plot Q84, 19 Nov. 1986, *Keizer 86252*; Plot Q93, 29 Sept. 1986, *Keizer 86177*; Odoorn, Odoornerveen, 17 Sept. 1987, *Keizer 87168*; 22 Sept. 1988; *Keizer 88267; Keizer 88112.*

Cortinarius striaepilus is conceived here in a rather wide sense with 1) colours varying from warm dark red-brown to dark yellowish brown, 2) small to medium-sized sporocarps and 3) spores with av. Q = 1.45 to 1.75. All three characters are intergrading. The colour of the pileus depends on the thickness of the pale fibrillose layer, which is subject to individual variation and which tends to wear off with age. The habit of the carpophores ranges from slender to rather thick-set with rounded or umbonate cap and with base of stipe enlarged or not, but this character varies independently from the other characters studied. The spore shape varies from rather broadly ellipsoid to oblong-ellipsoid (Fig. 19 b, d). All intermediate shapes do exist (Fig. 19 f), and spore shape does not not correlate with other characters. The smell is usually insignificant but in some specimens of one collection it was obviously *Pelargonium*-like (as in *C. paleaceus*). The other characters and the fact that in the same group many odourless sporocarps were present are indicative of *C. striaepilus*.

Cortinarius striaepilus J. Favre has been considered the correct name for this taxon. The description and plates match fairly well the material collected during this study. Minor differences are 1) the lamellae which were described by Favre (1948: 119) as "rather crowded", whilst the lamellae of our collections are subdistant, 2) the stipe which is frequently hollow and (slightly) swollen towards the base, unlike the specimens depicted by Favre, and 3) Favre (l.c.) described the habitat as wet coniferous forest.

A species that comes close to *C. striaepilus* with respect to habit and which is known to many authors is *C. incisus* (Pers.) Fr.; Moser (1978); Kühner & Romagnesi (1953); Bresadola (1930); Michael-Hennig-Kreisel (1985). This species differs from the present material by the not translucently striate and more fibrillose pileus and by the stipe which is not darkening towards the base. In the original description by Persoon (1801: 310) no reference was made to a striation of the pileus in *Agaricus incisus*. It was described as a small species with a squamulose pileus and was considered by Persoon (l.c.) closely related to *A. psammocephalus* Bull. Consequently, this name will not be used for the present taxon. However, it remains unlikely that such a common species was not described earlier than 1948.

The plate of '*C. incisus* forma' by Lange (1938: 99C) lacks the darkening stipe, but the pileus is of the right colour and distinctly striate. Consequently, this plate probably represents *C. striaepilus*.

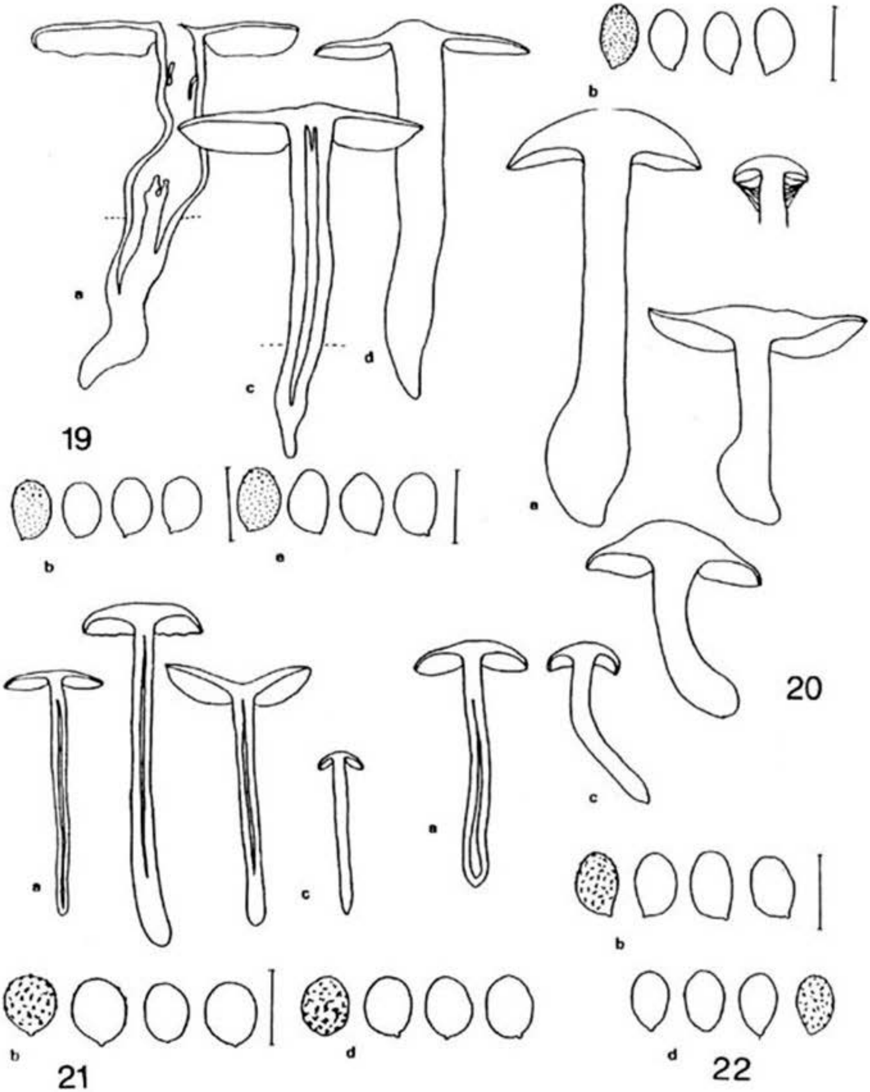


Fig. 19. *Cortinarius rigens*. a, c, d. habit; b, e. spores (a–c. *87291*; d, e. *88139*). — Fig. 20. *Cortinarius subbalaustinus*. a, c. habit; b. spores (a, b. *87183*; c. *88094*). — Fig. 21. *Cortinarius tabularis*. a, c. habit; b, d. spores (a, b. *88192*; c, d. *88135*). — Fig. 22. *Cortinarius valgus*. a, c. habit; b, d. spores (a, b. *88235*; c, d. *87241*). — Bar represents 10 µm.

Cortinarius incisus Pers.: Fr. sensu Moser (1983b) deviates from previous concepts of this species by the long and narrow spores. This taxon is considered by us as identical with *C. fusisporus* Kühner.

Cortinarius helobius Romagn. is similar, but differs by the complete absence of veil on the stipe and its occurrence in marshy habitats.

Cortinarius striaepilus, although listed as very rare in the Netherlands (Arnolds, 1984), is a rather common species in the studied plots. It has probably frequently been overlooked or confused with other similar taxa.

Cortinarius subbalaustinus R. Henry — Fig. 20

Pileus 15–45 mm, convex, then expanded, umbo low and broad or absent, strongly hygrophanous, when moist warm orange- or red-brown (Expo F46), not translucently striate, on drying pale orange-brown (D48) to almost straw-coloured (Expo C56, B56), margin covered by a 2 mm broad, pale, fibrillose layer. Lamellae up to 6 mm broad, moderately crowded, not ventricose, emarginate-adnate, when young pale brown (C64), soon rusty brown, edge paler. Stipe 35–80 × 6–10 mm, cylindrical with bulbous base, up to 17 mm wide, pale brown, covered by thick, cream-coloured fibrillum, thus appearance of stipe pale beige and shiny, over the lower half some white, floccose veil remnants, bulb white-tomentose, entire stipe darkening with age. Context in pileus when moist beige, on drying white, in stipe when moist with darker and paler parts. Smell indistinct.

Spores (8.0–)8.2–9.0(–9.6) × (4.5–)4.9–5.0(–5.4) µm, Q = 1.6–1.9, av. Q = 1.75, oblong, with ornamentation of fine, punctiform warts, stronger at the apex. Cystidia absent.

Habitat. Terrestrial in a roadside verge planted with *Quercus robur* on nutrient-poor sandy soil.

Collections examined. Plot Q35, 22 Sept. 1987, *Keizer 87183*; 3 Nov. 1987, *Keizer 87247*; 7 Oct. 1988, *Keizer 88094*.

Cortinarius tabularis (Bull.) Fr. — Fig. 21

Pileus 9–40 mm, convex, soon plano-convex, finally centre somewhat depressed, hardly hygrophanous, when moist greyish or ochraceous red-brown (Expo D54, D56, E56, E58), towards margin more greyish (D52), due to greyish fibrillose veil remnants, in the smallest specimen the margin weakly translucently striate, surface somewhat micaceous, not viscid. Lamellae up to 4 mm broad, moderately crowded, emarginate-adnate, pale ('caramel'-) or ochre-brown, later rusty brown, with serrulate edge, sometimes paler than the sides. Stipe 33–70 × 2.5–6(–9) mm, cylindrical or enlarged at the base, very pale greyish white, covered by white fibrillum and in the lower 2/3 of the stipe with pale beige or cream-coloured zones of veil, therefore general appearance white. Context when moist in pileus watery grey, in stipe pale brown; on drying in pileus white, in stipe very pale beige. Smell indistinct.

Spores (7.2–)7.5–8.6(–8.8) × (4.9–)5.6–6.5(–6.8) µm, Q = 1.2–1.4, av. Q = 1.31, broadly ellipsoid to ellipsoid; ornamentation consisting of rather coarse, round or irregular warts. Cystidia not observed.

Habitat. Terrestrial in a roadside verge planted with old *Quercus robur*, in the presence of low, mown *Betula* spec., on nutrient-poor sandy soil.

Collections examined. Plot Q2, 15 Sept. 1988, *Keizer 88135*; 13 Oct. 1988, *Keizer 88192*.

Cortinarius tabularis is a rarely reported species (Arnolds, 1984) and close to *C. anomalus*, mainly differing by the lack of violaceous lamellae in young specimens. However, according to Lange (1938: 31) intermediate forms occur and are even more common than typical carpophores. This is not confirmed by our observations. *Cortinarius tabularis* and *C. decoloratus* are very similar and Geesink (1972) therefore suggested that they should be considered as synonyms. The two species are said to differ in the surface of the pileus which is dry in the former and viscid in the latter species (Moser, 1978). Whether this difference warrants a distinction on specific level cannot be decided here. The specimens found during this study had dry pilei and are therefore named *C. tabularis*.

Cortinarius umbrinolens P.D. Orton — Fig. 23

Misapplied name: *Cortinarius rigidus* (Scop. Fr.) ss. J. Lange

Pileus 12–36 mm, campanulate, then expanding with distinct umbo, hygrophanous, when moist dark brown, dark grey-brown or dark reddish brown (Expo H42, J42, H52, H64, F62), on drying pallescent to grey-brown (F62, E54), covered with scattered, small, silky hairs, more densely so towards the margin, disappearing with age. Lamellae up to 7 mm broad, distant, emarginately adnate, when young pale brown, soon dark rusty brown, with pale brown or whitish edge (but no cheilocystidia present). Stipe 30–70 × 3–7 mm, cylindrical or sometimes slightly swollen at the base, fistulose or solid, rather dark brown (as surface of pileus), covered with beige or whitish, shiny fibrillum giving the stipe a pale brown, shiny appearance, when old without fibrils and therefore darker, usually with a dirty white annular zone and some floccose veil remains. Context in pileus pale brown or cork-coloured; in stipe brown to rather dark brown, in base black-brown. Smell usually strong, dusty, like *Cystoderma amianthinum*.

Spores 6.8–10.5(–10.8) × (4.0–)4.5–6.0 µm, Q = 1.4–1.9(–2.0), av. Q = 1.51–1.74, ellipsoid, ornamentation moderately verrucose. Cystidia absent.

Habitat. Terrestrial in roadside verges planted with *Quercus robur* on nutrient-poor sandy soil.

Collections examined. Plot Q1, 3 Oct. 1988, *Keizer 88093*; Plot Q43, 11 Oct. 1988, *Keizer 88202*; Plot Q45, 21 Sept. 1988, *Keizer 88169*.

The collections can be divided into two groups concerning spore size: collection *88169* with spores (8.8–)9.2–10.5(–10.8) × (5.0–)5.3–6.0 µm, Q = 1.7–1.9(–2.0); collections *88093* and *88202* with spores 6.8–8.0 × (4.0–)4.5–5.0(–5.5) µm, Q = 1.4–1.8. The small-spored variant has spores with coarser and more irregular warts. These microscopic differences do not correlate with variation in macroscopic characters. Several other studied collections from the herbarium at Wijster (WAG-W) appeared to have intermediate spores sizes. Therefore *C. umbrinolens* is accepted here as a separate species with an unusually big variation in spore size.

Cortinarius valgus Fr. — Fig. 22

Pileus 15–24 mm, convex to plano-convex, not or weakly hygrophanous, at centre reddish brown (Expo F52), towards the margin paler, greyish red-brown (D52, D54), surface with white shiny fibrils and with radially oriented, very thin, dark brown fibrillose covering, at extreme margin greyish by velar covering. Lamellae up to 3–4 mm broad, moderately crowded to subdistant, rather narrow, emarginate, at first loam-coloured grey-brown with violaceous tinge, later rusty brown with paler edge. Stipe 33–45 × 4–5 mm, cylindrical or slightly broadened towards the base, hollow with age, pale beige-brown, paler than pileus, indistinct violaceous greyish colour sometimes present at apex, covered with pale beige fibrillum, and in the lower half some dirty-whitish velar zones. Context in pileus cork-coloured, in the apex of the stipe greyish or greyish with lilac flush; downwards pale brown, slightly darkening towards the base. Smell absent or slightly raphanoid when cut.

Spores 7.2–8.8(–9.0) × 4.8–5.6(–5.7) µm, Q = 1.4–1.6, av. Q = 1.49–1.52, ellipsoid to oblong, with rather fine verrucose ornamentation. Cystidia absent.

Habitat. Terrestrial in roadside verges planted with *Quercus* or *Fagus* on nutrient-poor sandy soil.

Collections examined. Plot Q2, 15 Oct. 1987, *Keizer 87241*; 14 Oct. 1988, *Keizer 88225*.

Our description agrees well with the description in Moser & Keller-Dilitz (1983). However, in the present material no cheilocystidia were found, although Moser (l.c.) mentions them as "often frequent". The spore size is rather variable, although the two collections studied come from the same place: in collection *87241*: 7.2–7.7(–7.8) × 4.8–5.0 µm, av. Q = 1.49 and in collection *88225*: 8.0–8.8(–9.0) × (5.3–)5.4–5.6(–5.7) µm, av. Q = 1.52. These values fall within the variation reported by Moser (1983: 350) and Moser & Keller-Dilitz (1983: 45). The species was also observed in a roadside verge outside the studied plots on nutrient-poor sandy soil with *Fagus* and there the carpophores were considerably larger: pileus 20–50 mm and stipe 50–70 × 3–8 mm.

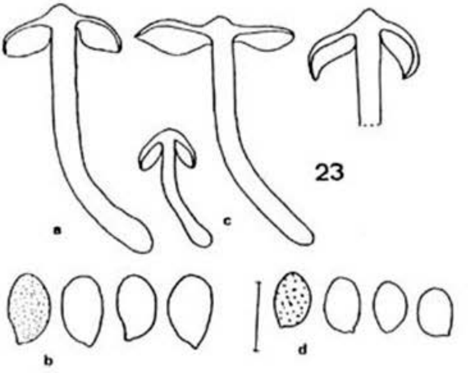
Cortinarius valgus is a little-known species and has probably often been overlooked. It was not recorded before from the Netherlands (Arnolds, 1984; Arnolds et al., 1989) but has been found several times since.

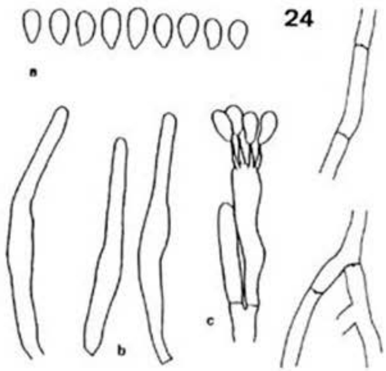
Cortinarius velenovskyi R. Henry — Fig. 26

Pileus 11–45 mm, convex, then plano-convex, usually without, but sometimes with indistinct low umbo, with margin often incurved, hygrophanous, when moist dark red-brown or chestnut-brown (Expo F-H52, H42, H34-36, F23, F48), towards the margin sometimes somewhat paler (E44-46), only short translucently striate, up to 1/4 of the radius, on drying ochraceous yellow-brown, orange yellow-brown (Expo E58, D56, F42), paler towards the margin (C66, D56, C58-68), surface with greyish bloom caused by a fine white fibrillose layer which fades with age but remains visible for a long time especially at the margin; pattern of drying irregularly centripetal, i.e. margin dries first. Lamellae up to 6 mm broad, subdistant, emarginate, at first pale brown ('café-au-lait') with yellowish edge, when older rusty brown and ventricose. Stipe 20–60 × 4–9 mm, cylindrical, often tapering towards the base and rooting, the root sometimes short and indistinct, solid or fistulose, when moist pale beige (Expo A62), covered with white fibrillum, on drying white; few white, soon disappearing veil remains may be present. Context in pileus pale brownish, in stipe beige, paler towards the base. Smell usually iodoform-like but sometimes with rancid or cedar wood component.

Spores (7.0–)7.5–9.0(–9.7) × (4.2–)4.8–5.5(–6.0) µm, Q = 1.4–1.8(–1.9), av. Q = 1.47–1.76, ellipsoid, ornamentation finely verrucose with mostly punctiform warts; no cystidia observed; few brown basidia present; trama with brown incrusting pigment.

Habitat. Terrestrial in roadside verges planted with *Fagus* or *Quercus* on nutrient-poor sandy soil.





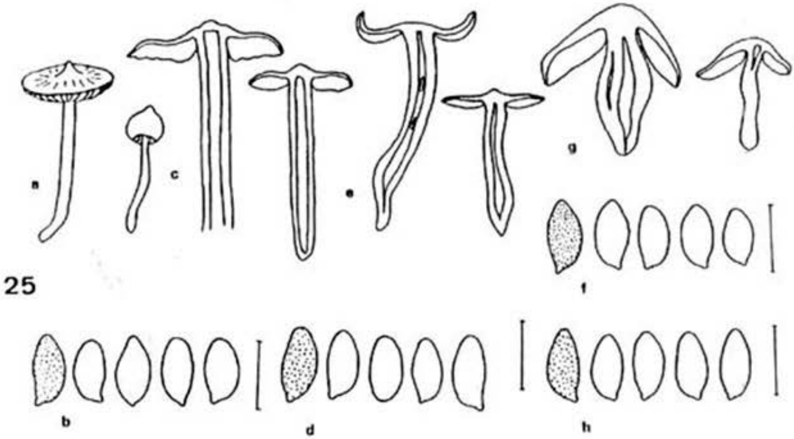


Fig. 23. *Cortinarius umbrinolens* a, c. habit; b, d. spores (a, b. *88169*; c, d. *88203*). — Fig. 24. *Cyphellostereum laeve*. a. spores; b. cystidia; c. basidium; d. hyphae (*87303*). — Fig. 25. *Cortinarius violilamellatus*. a, c, e, g. habit; b, d, f, h. spores (a, b. *88080*; c, d. *87233*; e, f. *87179*; g, h. *86225*). — Bar represents 10 µm.

Collections examined. Plot F34, 28 Sept. 1988, *Keizer 88123*; 28 Oct. 1988, *Keizer 88188*; Plot Q82, 24 Sept. 1988, *Keizer 88084*; Odoorn, Odoornerveen, 18 Nov. 1987, *Keizer 87256; Keizer 87296*; 22 Sept. 1988, *Keizer 88100; Keizer 88113*; 1 Nov. 1988, *Keizer 88182*.

Cortinarius velenovskyi differs from *C. rigens* and *C. obtusus* (both with iodoform-like smell) in the relatively dark colours and grey-fibrillose layer on the pileus. In addition, *C. obtusus* has a striate cap when moist. *Cortinarius velenovskyi* is a little-known species, not reported before from the Netherlands (Arnolds, 1984; Arnolds et al., 1989).

Cortinarius velenovskyi was described two times by Henry (1940, 1967). The first description refers directly to the description by Velenovský (1921) of *C. obtusus*. The second description is an extension of the first, but differs in the description of the smell, which is 'weak' in the first and "of cedar-wood, like that of *Camarophyllus russocoriaceus* (Berk. & Miller) Lange", sometimes mixed with iodoform or radish, in the second description. The plate of *C. velenovskyi* in the publication of 1967 shows rather pale (dried out?) specimens. In our opinion the two descriptions do not differ substantially and therefore we do not agree with Gaugé (1974, 1977) who created a new name (*C. fragrantior* Gaugé) for the species described by Henry (1967).

The specimens studied here deviate from the description by Henry (1967) in having a smell which is predominantly iodoform-like, without other components.

Cortinarius violilamellatus Pearson ex P.D. Orton — Fig. 25

Carpophores often (sub)cespitose, growing in clusters of (1–)3–10. Pileus 13–35 mm, campanulate, soon expanding with broad to pointed umbo, hygrophanous, when moist dark reddish grey-brown or red-brown (Expo H22-J22(-J26), H52, H12, F52), centre slightly darker, margin translucently striate, when dry wood- to straw-coloured, ochraceous yellow-brown (C63-C64, B56, somewhat yellower than E46), paler towards the margin, surface slightly innately fibrillose, especially so at the margin, sometimes with sparse whitish hairy scales, more distinct towards the margin. Lamellae 3–6 mm broad, distant, sometimes irregularly veined, emarginate, not or slightly ventricose, at first pinkish violet or purplish, with edge remaining violet for some time, later entirely rusty brown with paler edge. Stipe 35–60 × (2–)3–6 mm, cylindrical, sometimes slightly enlarged and tapering towards the base, hollow, concolorous with pileus, but appearance somewhat paler due to shiny pale brown fibrillum, darker to the base, the apex sometimes showing a violet hue, with whitish floccose velar remnants in lower half. Context in pileus coloured like surface, in the stipe yellowish brown, downwards dark brown. Smell distinct, as *Pelargonium zonale* or *Cortinarius paleaceus*.

Spores (8.0–)8.9–10.3(–11.0) × (4.0–)4.3–5.0(–5.1) µm, Q = (1.8–)1.9–2.3 (–2.5), av. Q = 1.85–2.44, narrowly amygdaliform or slightly fusiform, frequently with small depression just above the hilar appendix, minutely punctate or verruculose. No cystidia observed. Basidia with brown content present; brown extracellular pigment present in the hymenophoral trama.

Habitat. Terrestrial in the grassy vegetation of roadside verges planted with *Fagus* or *Quercus* on nutrient-poor sandy soil.

Collections examined. Plot F24, 10 Nov. 1986, *Keizer 86228*; 7 Oct. 1988, *Keizer 88095*; Plot F34, 19 Nov. 1986, *Keizer 86254*; 1 Oct. 1987, *Keizer 87289*; 28 Oct. 1988, *Keizer 88286*; Plot Q32, 18 Sept. 1986, *Keizer 86149*; Plot Q35, 10 Nov. 1986, *Keizer 86225*; 22 Sept. 1987, *Keizer 87189; Keizer*

87197; 3 Nov. 1987, *Keizer 87260*; 7 Oct. 1988, *Keizer 88080*; Odoorn, Odoornerveen, 13 Oct. 1987, *Keizer 87233; Keizer 87311*; 19 Nov. 1987, *Keizer 87304*; Assen, Kloosterveen, 13 Oct. 1988, *Keizer 88335* (leg. E. Arnolds).

The combination of *Pelargonium*-like smell, violaceous colours in the young lamellae, rather small size, sparse whitish velar remnants on the cap and especially the more or less fusiform spores are characteristic for this species. Besides, the (sub)cespitose growth of the carpophores in open grassy vegetation on nutrient-poor sandy soil seems to be characteristic as well.

Cortinarius violilamellatus clearly differs from *C. sertipes* and *C. pulchripes* in much narrower spores and the *Pelargonium*-like smell. *Cortinarius fusisporus* Kühner may be related but the smell is absent, the veil is dirty whitish and the spores are longer with av. Q = 2.1-2.5 while most spores have av. Q = 2.3. Moser (1983) mentions three species with Pelargonium-smell, viz. *C. paleaceus*, *C. paleiferus* and *C. rigidus* Fr. ss. Kühn. & Romagn. The first species has more abundant white hairy scales on the pileus and no violaceous colours in the lamellae when young which are also morer crowded. The second has more distant (Marchand, 1983) and violaceous lamellae when young like in the present species, but the spores are broader and the pileus is covered with white hairy scales. *Cortinarius rigidus* ss. Kühn. & Romagn. has crowded lamellae without violaceous colours and smaller spores (7.2–9.5 × 4.2–5.7 µm).

Orton (1984) described *C. violilamellatus* as occurring in coniferous forests. In our opinion, no taxonomic value can be ascribed to ecological preferences. The morphological characters of the specimens found during this study fit sufficiently well the description in Orton (l.c).

Cyphellostereum laeve (Fr.: Fr.) D. Reid — Fig. 24

Fruit-body c. 5–10 mm long, irregularly ear-shaped, outer surface whitish, inner surface (hymenium) cream-coloured, dorsally attached to bryophytes: *Dicranella heteromalla*, *Isopterygium elegans*, *Mnium hornum*.

Spores (4.0–)4.5–5.2(–6.2) × (1.8–)2.0–2.5(–2.7) µm, Q = (1.8–)2.0–2.7, av. Q = 2.27, pip-shaped, often in tetrads. Cystidia 30–40 × 3.5 µm, narrowly fusiform with blunt apex, thin-walled, hyaline. Basidia 4-spored. Hyphae 2–2.5 µm broad, septa without clamp-connections.

Habitat. Terrestrial in roadside verges planted with *Fagus* or *Quercus* on nutrient-poor sandy soil.

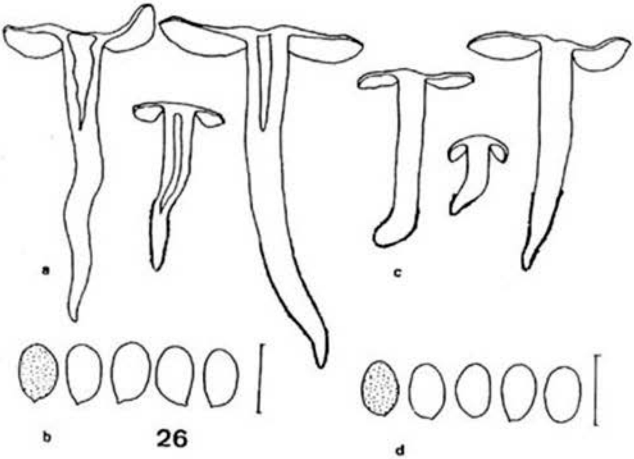
Collection examined. Plot Q93, 21 Sept. 1987, *Keizer 87303*.

Macroscopically this species is rather similar to *Mniopetalum globisporum*, which differs among other things in the globose spores.

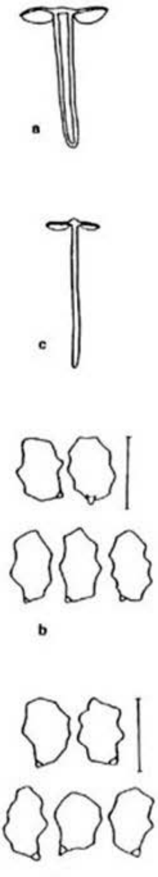
Cyphellostereum laeve has been recorded only a few times in the Netherlands (Arnolds, 1984).

Entoloma lividoalbum (Kühn. & Romagn.) Kubička — Fig. 27

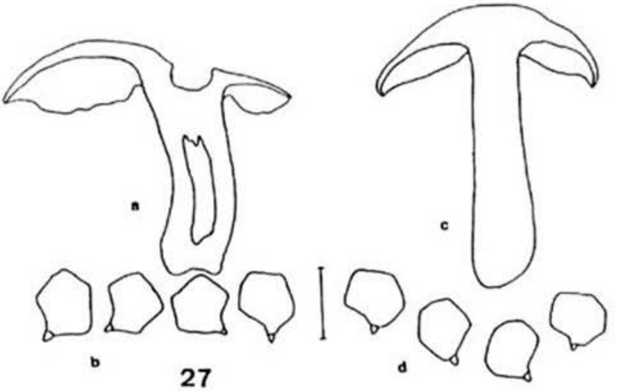
Pileus 45–65 mm, convex to plano-convex without prominent umbo; hygrophanous, when moist yellowish grey-brown (Expo E64) or more greyish brown, shortly translucently striate (c. 5 mm), on drying paler (C72-74). Lamellae distant, moderately to strongly ventricose, crenulate, pink, with concolorous edge. Stipe 40–55 × 10–15 mm, cylindrical or slightly broader towards the base, yellowish white to white, silvery white striate. Context in all parts greyish white. Smell indistinct; taste somewhat farinaceous with bitter after-taste.



26



28



27

Fig. 26. *Cortinarius velenovskyi*. a, c. habit; b, d. spores (a, b. *88182*; c, d. *88100*). — Fig. 27. *Entoloma lividoalbum*. a, c. habit; b, d. spores (a, b. *88088*; c, d. *87164*). — Fig. 28. *Entoloma undulatosporum*. a, c. habit; b, d. spores (a, b. *87011*; c, d. *87177*). — Bar represents 10 µm.

Spores (7.5–)8.0–9.0 × 6.5–8.0 µm, isodiametrical to slightly oblong, Q = (0.9–) 1.1–1.3, av. Q = 1.17–1.23, mostly 5-angled. No cystidia observed. Pigment in pileipellis light greyish brown, diffuse, intracellular; clamp-connections present.

Habitat. Terrestrial in roadside verges planted with *Quercus* on nutrient-poor sandy soil.

Collections examined. Plot Q82, 24 Sept. 1988, *Keizer 88088*; Odoorn, Odoornerveen, 17 Sept. 1987, *Keizer 87164*.

Entoloma lividoalbum is very rare in the Netherlands. It was reported by Noordeloos (1988: 102) from two localities only. Our collections differ in slightly narrower spores.

Entoloma undulatosporum Arnolds & Noordel. — Fig. 28

Pileus 9–19 mm, plano-convex with weak or small, pointed umbo, hygrophanous, when moist dark grey-brown (Expo E41, F41), translucently striate, on drying somewhat paler, then silvery silky shining, sometimes radially splitting. Lamellae up to 3.5 mm broad, distant, ventricose, dark grey-brown like pileus or slightly paler (between D61 and D63), with paler edge, crenulate. Stipe 25–32 × 1–4 mm, cylindrical, grey-brown, at apex paler and with minuscule white squamules, downwards glabrous or somewhat silver-white, striate, fistulose or solid. Smell absent or weakly farinaceous.

Spores (8.0–)8.2–10.0(–10.5) × 5.0–6.5(–7.0) µm, 6–8 angled in side-view, Q = 1.3–1.7(–2.0), av. Q = 1.43–1.61. Basidia 4–(2-)spored. Cheilocystidia absent. Pigment in pileipellis diffuse, intracellular. Clamp-connections present.

Habitat. Terrestrial in roadside verges planted with old *Quercus* on nutrient-poor sandy soil.

Collections examined. Plot Q74, 22 Sept. 1987, *Keizer 87177*; Plot Q83, 29 June 1987, *Keizer 87011*; 8 Sept. 21988, *Keizer 88318*.

The described collections differ in some respects from the description by Noordeloos (1988), viz. in the silvery striate stipe and relatively narrow spores. The undulate outline of the spores is regarded as distinctive for this species.

REFERENCES

Arnolds, E. 1984. Standaardlijst van Nederlandse macrofungi. Coolia 26 (suppl.): 1–362.

Arnolds, E., E. Jansen, P.J. Keizer, & M. Veerkamp. 1989. Standaardlijst van de Nederlandse Macrofungi, suppl. 1. Arnhem.

Bohus, G. 1979. Interessante Cortinarius-Arten aus dem Karpaten-Becken (Agaricales, Cortinariaceae), III. Ann. Hist.-nat. Mus. Nat. Hung. 71: 65–72.

Bon, M. 1988. Pareys Buch der Pilze. Hamburg, Berlin.

Brandrud, T.E., H. Lindström, H. Marklund, J. Melot & S. Muskos. 1990. Cortinarius Flora Photographica. Vol. 1. Cortinarius HB. Sweden.

Bresadola, J. 1927–1933. Iconographica mycologica 1–26. Milano.

Cailleux, A. & G. Taylor. 1958. Code Expolaire. Paris.

Cannon, P.C., D.L. Hawksworth & M.A. Sherwood-Pike. 1985. The British Ascomycotina – an annotated checklist. Kew.

Dähncke, R.M. & S.M. Dähncke. 1979. 700 Pilze in Farbfotos. Stuttgart.

Favre, J. 1960. Catalogue descriptif des champignons supérieurs de la zone subalpine du parc National Suisse. Ergebn. wiss. Unters. schweiz. Nat. Parks 6 (N.F.) 42: 321–610. Liestal.

Fries, E. 1821. Systema Mycologicum. Vol. 1. Lundae.

Fries, E. 1874. Hymenomycetes Europaei. Upsaliae.

Gaugé, G. 1974. Revision des Cortinaires: II. Doc. Myc. 15: 43–50.

Gaugé, G. 1977. Cortinarius fragrantior Gaugé nom. nov. Doc. Myc. 27–28: 54.

Geesink, J. 1972. Vier jaar mycologische observaties op brandplekken. Coolia 15 (5): 118–132.

Geesink, J. 1976. Cortinarius contrarius, a new species identical with C. sertipes Kühn. sensu Svrček. Persoonia 8 (4): 443–446.

Grünert, H. 1989. Seltene und bemerkenswerte Pilzfunde unter Weide (Salix sp.) von der östlichen Uferzone des Ammersees in Bayern. Beitr. Kenntn. Pilze Mitteleur. 5: 141–154.

Henry, R. 1940. Suite à l'étude du genre Hydrocybe. Bull. Soc. mycol. Fr. 56: 85–119.

Henry, R. 1958. Suite à l'étude des Cortinaires. Bull. Soc. mycol. Fr. 74: 249–361.

Henry, R. 1967. Étude provisoire du genre Hydrocybe: Hydrocybes a pied attenué à la base. Bull. Soc. mycol. Fr. 83: 989–1046.

Huijsman, H.S.C. 1955. Observations on Agarics. Fungus 25: 18–43.

Jansen, A.E. 1984. Vegetation and macrofungi of acid oakwoods in the north-east of the Netherlands. Wageningen.

Keizer, P.J. 1994a. Mycocoenology of roadside verges planted with common oaks (Quercus robur L.) in Drente, the Netherlands. Nova Hedwigia. In press.

Keizer, P.J. 1994b. Mycocoenology of roadside verges planted with beech trees (Fagus sylvatica L.) in Drente, the Netherlands. Phytocoenologia. In press.

Kits van Waveren, E. 1985. The Dutch, French and British species of Psathyrella. Persoonia Suppl. 2: 1–300.

Konrad, P. & A. Maublanc. 1924–36 [1937]. Icones selectae fungorum, Vol. 1–5. Paris.

Kornerup, A. & J.H. Wanscher. 1978. Methuen Handbook of Colour. 3rd. ed.

Kreisel, H. 1987. Pilzflora der Deutschen Demokratischen Republik. Jena.

Kühner, R. 1935. Le genre Galera. Encyclopédie Mycologique 7. Paris.

Kühner, R. 1961. Notes descriptives sur les agarics de France. I. Cortinarius. Bull. mens. linn. Lyon 30: 50–65.

Kühner, R. & H. Romagnesi. 1953. Flore analytique des champignons supérieurs. Paris.

Kuyper, Th.W. 1981. Aantekeningen over Clitocybe 2. "Lepista" albofragrans. Coolia 24: 68–71.

Kuyper, Th.W. 1986. A revision of the genus Inocybe in Europe. Persoonia Suppl. 3: 1–247.

Lange, J.E. 1935–1940. Flora Agaricina Danica. Vol. 1–5. Copenhagen.

Lindström, H. & T.E. Brandrud. 1987. Notes on some Cortinarius subgenus Telamonia species collected at the Cortinarius foray, Frederikstad 1986. Agarica 8 (16): 7–12.

Marchand, A. 1971–86. Champignons du nord et du midi. Tomes 1–9. Perpignan.

Michael-Hennig-Kreisel. 1960–1988. Handbuch für Pilzfreunde I–VI. Jena.

Moser, M. 1978. Die Röhrlinge und Blätterpilze. Kleine Kryptogamenflora IIb/2. 4. Auflage. Stuttgart-New York.

Moser, M. 1983a. Die Röhrlinge und Blätterpilze. Kleine Kryptogamenflora IIb/2. 5. Auflage. Stuttgart-New York.

Moser, M. 1983b. Notizen zu einiger Cortinarien aus der Untergattung Telamonia. Mycol. Helvetica 1: 1–16.

Moser, M. & H. Keller-Dilitz. 1983. Cortinarius raphanoides and related species. Cryptog., Mycol., Tome 4: 41–50.

Munsell Color Company. 1954. Munsell soil color charts. Baltimore.

Noordeloos, M.E. 1988. Entolomataceae Kotl. & P. In: C. Bas et al. (eds.), Flora agaricina neerlandica 1: 77–177. Rotterdam, Brookfield.

Orton, P.D. 1972. Notes on British Agarics Notes R. Bot. Gdn. Edinb. IV: 135–150.

Orton, P.D. 1984. Notes on British Agarics: VIII. Notes R. Bot. Gdn. Edinb. 41 (3): 565–624.

Orton, P.D. & R. Watling. 1979. Coprinaceae. Part 1: Coprinus. British Fungus Flora, Agarics and Boleti 2: 1–149.

Persoon, C.H. 1801. Synopsis methodica Fungorum. Gottingae.
Phillips, R. 1981. Paddestoelen en Schimmels van West-Europa. Utrecht, Antwerpen.
Ricken, A. 1915. Die Blätterpilze (Agaricaceae). Vol. 1–2. Leipzig.
Uljé, C. 1989. Coprinus Subsectie Setulosi J.E. Lange (1915). Alphen aan de Rijn.
Velenovský, J. 1920–1922. Ceské houby. Prague.
Watling, R. 1982. Bolbitiaceae: Agrocybe, Bolbitius & Conocybe. British Fungus Flora, Agarics and Boleti, vol. 3.
Weeda, E. 1983. In: Heukels/Van der Meijden, Flora van Nederland: 12–18. Groningen.
Westhoff, V. & A.J. den Held. 1969. Plantengemeenschappen in Nederland. Zutphen.

PERSOONIA
Published by Rijksherbarium / Hortus Botanicus, Leiden
Volume 15, Part 4, pp. 525–529 (1994)

BIOCONCENTRATION OF MANGANESE AND IRON IN PANAEOLOIDEAE SING.

T. STIJVE & C. BLAKE

Nestec Ltd, Nestlé Research Centre, Vers-chez-les-Blanc, CH-1000 Lausanne 26, Switzerland

According to literature, the manganese content of most basidiomycetes fluctuates between 10 and 60 mg/kg, whereas the iron levels range from 100–500 mg/kg (both expressed on dry weight). The present authors report that bioconcentration of manganese is a distinguishing feature of the Panaeoloideae, as demonstrated by the analysis of 44 collections representing 15 taxons. Carpophores generally contain between 250 and 2500 mg/kg on dry weight, and, with the notable exception of *Panaeolus semiovatus, P. antillarum* and *P. phalaenarum*, their iron content is 2 to 3 times lower. This phenomenon was not observed in members of related genera such as *Psathyrella* and *Coprinus*.

Manganese is an essential element for both plants and animals. It is a component of important cellular enzymes such as decarboxylase, arginase and possibly others involved in nucleic acid metabolism (Reilly, 1991).

Generally, higher fungi do not seem to have a requirement for manganese that would necessitate the uptake of high levels. Indeed, the manganese content of most basidiomycetes fluctuates between 10 and 60 mg/kg on dry weight, whereas iron concentrations range from 100–500 mg/kg (Schmitt et al., 1977). These levels are well below the average concentrations measured in soils which are 1000 mg/kg for manganese, and even 15000 mg/kg for iron (Reilly, 1991).

Schmitt et al. (1977) analysed 262 samples of higher fungi for both metals, and observed higher than average contents in Tremellales and Auriculariales, although iron always predominated. Among the gasteromycetes the same authors reported unusually high manganese levels in a number of Phallaceae. In some of these fungi the proportion Fe : Mn was well below 1.

Tyler (1980) subjected 130 species of basidiomycetes to analysis for several elements, and found a median value of 19 mg/kg for manganese. However, he observed bioconcentration in two unrelated species, namely *Panaeolus campanulatus* (1140 mg/kg) and *Polyporus hirsutus* (735 mg/kg). Vetter (1989) analysed 80 species and reported mean values of 28 mg/kg for manganese and 305 mg/kg for iron.

So far, *Panaeolus campanulatus* is the only gilled fungus reported to have an unusually high manganese content, but this seems to be an isolated observation pertaining to only one collection (Tyler, 1980). Since *Panaeolus* species have already been analysed for various metabolites in this laboratory (Stijve et al., 1984; Stijve, 1985, 1987), it was decided to use the remaining collections for an investigation of their manganese and iron content.

For a better appreciation of the findings the investigation was extended to other dark brown and black spored Agarics, such as Strophariaceae, Coprinaceae, Agaricaceae and Bolbitiaceae. The results of the analyses are reported and discussed in this paper.

METHODS

Most species analysed were collected in Switzerland during 1983–1990. Some *Panaeolus* were obtained from Germany, the Netherlands, France, Hawaii, Brazil and Australia. The collections were either freezedried or dehydrated at 55°C in an airstream. Subsequently, the material was ground to fine powder and stored in glass jars at 10°C until analysed.

Samples were hydrolysed for 30 minutes with hot 6N hydrochloric acid (Simpson & Blay, 1966). After filtration of the extracts, manganese and iron were determined with an ARL model 3410 sequential inductively coupled plasma atomic emission spectrometer, using respectively 257.61 nm and 259.94 nm as emission lines (Gouvielos, 1989).

RESULTS AND DISCUSSION

The manganese and iron contents measured in 15 Panaeoloideae (44 collections) are listed in Table I. In most collections manganese uptake is very marked, and most often the ratio Fe : Mn is well below 1, which has not yet been observed in gilled fungi from other genera.

Uptake of both metals can even be so tremendously high that it interferes with the normal physiology of the carpophores: at one time, we collected a number of *Panaeolus sphinctrinus* growing beneath freshly planted shrubs that had received an ample supply of fertiliser supplemented with trace elements. The carpophores had an unusually light brown colour, and their gills were remarkably clear, indicating absence of spores. These sterile fruit-bodies loaded with 0.55 percent manganese and 0.2 percent iron did not contain any urea, a metabolite associated with sporulation, but had a remarkably high serotonin content (Stijve, 1987). Both urea and serotonin can be considered final metabolites in biochemical detoxification processes used to neutralise ammonia from the substrates (Iwanoff, 1924; Grosse, 1982).

The enzymes involved in the conversion of ammonia to urea apparently do not need much manganese for their activation, but it is not unthinkable that those governing the biosynthesis of serotonin need the metal. It is interesting to note that representatives of the related genera *Coprinus* and *Psathyrella* contain neither serotonin (Stijve, 1987), nor high levels of manganese (Table II).

As a matter of fact, in all dark spored agarics analysed, the iron content predominated well over that of manganese. Indeed, these more or less distantly related fungi had concentrations of both metals comparable to those reported for other Agaricales (Schmitt et al., 1977; Vetter, 1989).

Among the Panaeoloideae analysed so far, *P. semiovatus, P. antillarum* and *P. phalaenarum* – which are considered as a separate tribe called *Anellaria* by some authors (Karsten, 1879; Hora, 1957) – have manganese contents well below those of iron. This can probably be explained by the low levels of manganese in horse dung, their particular substrate. Horse dung contains about 10 times less of both manganese and iron than the average soil. The ratio Fe : Mn fluctuates between 12 and 25. Hence it is not impossible that the low amounts in the three *Anellaria* species still represent a bioconcentration phenomenon.

Large fluctuations in the concentrations of both metals were observed in *P. cyanescens* and *P. subbalteatus*. Sometimes high manganese uptake was noted, whereas in other col-

Table I. Manganese and iron levels in Panaeoloideae Sing.

Species	N	Manganese	Iron	Ratio Fe : Mn (mean)
Panaeolina foenisecii (Pers.: Fr.) Maire	6	239–471 (388)	93–374 (235)	0.60
Panaeolopsis nirimbii Watling & Young	1	560	265	0.47
Panaeolus bernicii Young, sp. nov.	1	992	102	0.10
P. fimicola (Pers.: Fr.) Quél.	1	800	464	0.58
P. clelandii Gerhardt	1	75	152	2.03
P. ater (J. Lange) Kühn. & Romagn.	1	637	187	0.29
P. olivaceus Moell.	2	587–1290	176–198	0.20
P. acuminatus (Schaeff.: ex Secr.) Quél. s. str.	2	2071–2125	651–671	0.32
P. subbalteatus (Berk. & Br. Sacc.)	6	130–557 (273)	318–956 (595)	2.18
P. campanulatus (Bull.: Fr.) Quél.	3	867–1076 (950)	208–392 (296)	0.31
P. sphinctrinus (Fr.) Quél.	4	545–912 (747)	140–379 (229)	0.31
P. sphinctrinus, sterile carpophores	1	5500!	1970!	0.36
P. semiovatus (Sow.: Fr.) Pears & Dennis	6	30–59 (38)	109–287 (214)	5.6
P. phalaenarum (Bull.: Fr.) Mos.	2	24–41	104–229	5.1
P. antillarum (Fr.) Dennis	3	15–69 (35)	102–159 (132)	3.8
P. (Copelandia) cyanescens (Berk. & Br.) Sacc.	4	126–2320 (779)	271–883 (644)	0.83

All concentrations in mg/kg on dry matter. Mean values in brackets.

lections iron clearly predominated. Here again, the explanation can be sought in the different substrates: *P. cyanescens* mostly grows on cow dung, but its mycelium probably extends to the underlying manganese-rich soil. The *P. subbalteatus* material analysed represented collections from manured lawns, horse dung, rotten straw and a mixture of these substrates. Apparently, manganese was readily available to the single collection of lignicolous *P. bernicii*. According to Young (1989) this taxon is found on nearly decomposed wood.

The new, yet unpublished taxon *P. clelandii* (Gerhardt, pers. comm.) was formerly considered an Australian variety of *P. fimicola*, but there are microscopic differences (Gerhardt, 1991). Moreover, the manganese and iron levels for single collections are totally different, and *P. clelandii* was found to contain psilocybin, baeocystin and tryptamine, which were not detected in European collections of *P. fimicola* (Stijve, 1991).

Table II. Manganese and iron levels in some dark brown and black spored agarics (other than *Panaeolus*).

Genus	Number of species	Manganese	Iron	Ratio Fe : Mn (mean)
		in mg/kg dry weight		
Agrocybe	4	27–45 (35)	349–430 (387)	11.1
Coprinus	5	6–37 (19)	92–310 (209)	11.0
Psathyrella	6	6–53 (28)	64–566 (221)	7.9
Psilocybe	6	28–74 (42)	280–680 (420)	10
Agaricus	10	20–46 (30)	120–338 (168)	5.6

Average values in brackets.

CONCLUSION

A better insight in the uptake of both manganese and iron can undoubtedly be obtained by pure culture studies. Meanwhile, the results reported in this paper strongly suggest that manganese uptake is a distinguishing feature of the Panaeoloideae, just as is their ability to biosynthesize serotonin (Stijve, 1987).

ACKNOWLEDGEMENTS

The authors thank Dr. E. Gerhardt of the Botanical Institute of the Berlin University for his help in the determination of various *Panaeolus* collections. John Allen (Hawaii, USA), Erich Jahn (Bad Schwartau, Germany), André de Meijer (Curitiba, Brazil), Georges Scheibler (Le Locle, Switzerland), Anke Schmitt (Lübeck, Germany), and Anthony Young (Blackbutt, Australia) are thanked for generously supplying samples of fungi. The skill of Marija Basic and Bernadette Hug in performing the ICP analysis, and Karima Ziaoullah's help in preparing the manuscript are gratefully acknowledged.

REFERENCES

Gerhardt, E. 1991. Personal communication, 27.8.1991.

Gouvielos, L. 1989. Manganese determination by atomic emission spectroscopy with inductively coupled plasma. Internal report T-AQ 1989/18. Quality Assurance Department, Nestec Ltd, Avenue Nestlé 55, 1800 Vevey, Switzerland.

Grosse, W. 1982. Function of serotonin in seeds of walnuts. Phytochemistry 21 (4): 819–822.

Hora, F.B. 1957. The genus Panaeolus in Britain. The Naturalist: 77–87.

Iwanoff, N. 1924. Über die Ursache des verschiedenen Harnstoffgehaltes in Pilzen. Biochem. Z. 154: 391–398.

Karsten, P.A. 1879. Hymenomycetes. Hattsv. Bidr. Finl. Nat. Folk. 32: 517–520.

Reilly, C. 1991. Metal Contamination of Food, 2nd Edition, Elsevier Applied Science. London and New York.

Schmitt, J.A., H.U. Meisch & W. Reinle. 1977. Schwermetalle in höheren Pilzen, II, Mangan und Eisen. Z. Naturforsch. 32c: 712–723.

Simpson, G.R. & R.A. Blay. 1966. Rapid method for the determination of the metals copper, zinc, tin, iron and calcium in foodstuffs by Atomic Absorption Spectroscopy. Food Trade Review 8: 35–37.

Stijve, T. 1985. Een chemische verkenning van het geslacht Panaeolus. Coolia 28 (4): 81–89.

Stijve, T. 1987. Vorkommen von Serotonin, Psilocybin und Harnstoff in Panaeoloideae. Beitr. Kenntn. der Pilze Mitteleur. III: 229–234.

Stijve, T. 1991. Unpublished data.

Stijve, T., C. Hischenhuber & D. Ashley. 1984. Occurrence of 5-hydroxylated indole derivatives in Panaeolina foenisecii (Fr.) Kühner from various origin. Z. Mykol. 50: 361–368.

Tyler, G. 1980. Metals in sporophores of Basidiomycetes. Trans. Br. mycol. Soc. 74: 41–49.

Vetter, J. 1989. Prüfung des Mineralstoffgehaltes von höheren Pilzen. Int. J. Mycol. Lichenol. 4 (1: 2): 107–135.

Young, A.M. 1989. The Panaeoloideae (Fungi, Basidiomycetes) of Australia. Aust. Syst. Bot. 2: 75–97.

PERSOONIA
Published by Rijksherbarium / Hortus Botanicus, Leiden
Volume 15, Part 4, pp. 531–535 (1994)

TWO NEW MYCENAS OF SECTION FRAGILIPEDES FROM SOUTHERN NORWAY.

A. ARONSEN

Torødveien 54, N-3135 Torød, Norway

Mycena austera and *Mycena parca*, belonging to section *Fragilipedes*, are proposed as new species. *Mycena austera* is identified mainly by the 4-spored basidia, the absence of clamp connections, the dark pileus, and the nitrous odour. The species is compared with *M. leptocephala* and *M. deceptor*. *Mycena parca* is compared with *M. leptocephala* from which it differs mainly on account of the absence of nitrous odour, and differently shaped cheilocystidia and terminal cells of the cortical layer of the stipe.

Section *Fragilipedes* (Fr.) Quél. is the largest section in *Mycena*, and in spite of the impressive work by Maas Geesteranus (1988) there still seem to occur undiscovered species. *Mycena austera* and *M. parca*, found in the County of Vestfold in southern Norway, do not match any of the species described so far.

Mycena austera Aronsen, *spec. nov.* — Figs. 1–7

Pileus usque ad 20 mm latus, vulgo umbonatus, obscure griseus. Caro odore nitroso. Lamellae 26–30 stipitem attingentes, adscendentes, grisae. Stipes –50 × 3 mm, glaber, griseolus. Basidia 29–35 × 8–9 µm, clavata, 4-sporigera. Sporae 9.3–11(–12.5) × 5.1–6.5 µm, amyloideae. Cheilocystidia 50–103 × 13–24 × 3.5–6.5 µm, fusiformia. Pleurocystidia similia. Trama lamellarum Melzeri reagente vinescens. Hyphae pileipellis 2.7–6.3 µm latae, diverticulatae, subgelatinosae, cellulae terminales varieformes. Hyphae stipitipellis 1.8–2.5 µm latae, leves vel diverticulatae, haud gelatinosae, caulocystidia 2.5–10 µm latae, crasse diverticulata.

Fibulae desunt.

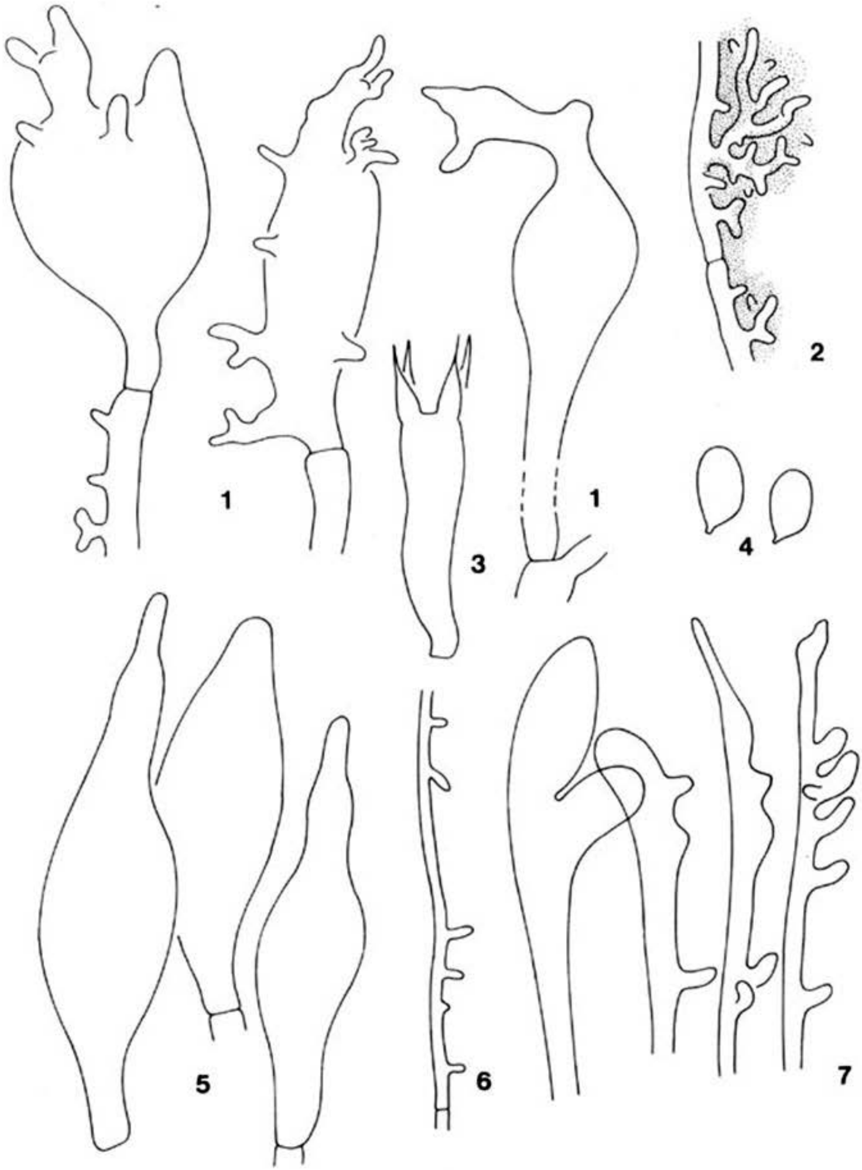
Terricola. Basidiomata gregaria vel caespitosa.

Holotypus: Norway: Vestfold, Nøtterøy, Torød, 5 Nov. 1991. Leg. A. Aronsen A 17/91 (O).

Etymology: Austerus, dark.

Basidiomata gregarious to cespitose. Pileus up to 20 mm across, conical to convex, flattening with age, mostly with a prominent umbo, translucent-striate, sulcate, hygrophanous, fairly dark grey with a darker, greyish brown to almost black centre, the margin paler to whitish. Odour nitrous. Taste not recorded. Lamellae 26–30 reaching the stipe, ascending, narrowly adnate, with or without a short decurrent tooth, 1 mm broad (dry), somewhat intervenose with age, grey to dark grey, the edge convex, paler. Stipe up to 50 × 3 mm, straight to somewhat curved, terete, hollow, glabrous (at least in older specimens), pale grey at the apex, darker greyish downwards, paler than the pileus, the base densely covered with long, coarse, flexuous, whitish fibrils.

Basidia 29–35 × 8–9 µm, clavate, 4-spored, clampless, with plump sterigmata 9–12 µm long. Spores 9.3–11.0(–12.5) × 5.1–6.5 µm, pip-shaped, smooth, amyloid. Cheilo-



Figs. 1–7. *Mycena austera* (holotype). 1. Terminal elements of pileipellis; 2. hypha of pileipellis; 3. basidium; 4. spores; 5. cheilocystidia; 6. hyphae of stipe surface; 7. caulocystidia. Bar = 10 µm.

cystidia 50–103 × 13–24 × 3.5–6.5 µm, occurring mixed with basidia, fusiform, clampless, smooth. Pleurocystidia numerous, similar.

Lamellar trama brownish vinescent in Melzer's reagent. Hyphae of the pileipellis 2.7–6.3 µm wide, clampless, covered with simple to very much branched excrescences 2.5–22.5 × 2 µm which tend to become covered with gelatinous matter; terminal cells 45–70 × 12.5–24 µm, variously shaped, subcylindrical, fusiform, clavate, frequently covered with coarse excrescences 4.5–11 × 2.5 µm. Hyphae of the cortical layer of the stipe 1.8–2.5 µm wide, clampless, smooth to sparsely covered with simple, cylindrical excrescences 1.8–4.5 × 1.8–2.5 µm; terminal cells (caulocystidia) 2.5–10 µm wide, with few to fairly numerous, coarse excrescences.

Growing terrestrial among grass and fallen leaves under *Salix*.

Material examined: Norway: Vestfold, Nøtterøy, Torød, 4 Nov. 1991 (A 16b/91), 5 Nov. 1991 (A 17/91) (holotype) (O).

Following the key to sect. *Fragilipedes* (Maas Geesteranus, 1988), *M. austera* comes close to *M. deceptor* Maas G., but there are several differences. In the former species the pileus is dark grey and centrally almost black, 26–30 lamellae reach the stipe, and the smell is nitrous. In *M. deceptor* the pileus is pale vinaceous brown, dingy brown or greyish brown, 14–22 lamellae reach the stipe, and the smell is indistinctive. In addition *M. deceptor* has a smaller pileus (4–8 mm), whitish lamellae and a narrow stipe (0.5–0.75 mm wide). Microscopically there seems to be little to separate the two species, but in *M. austera* the hyphae of the pileipellis are gelatinizing while they are not in *M. deceptor*. The conspicuous, variously shaped terminal cells of the pileipellis in *M. austera* may also be a decisive difference.

Macroscopically the material was first mistaken for *M. leptocephala* (Pers.: Fr.) Gillet, but it can be told apart from that species on account of the absence of clamp connections, the cheilocystidia occurring mixed with the basidia, the conspicuous terminal cells of the pileipellis, and the differently shaped caulocystidia. (4-spored *M. leptocephala* may also very rarely occur devoid of clamps (Maas Geesteranus,1991: 548).)

The presence or absence of clamps is generally a very reliable character in *Mycena*, but there are a few exceptions (Aronsen, in prep.). Taking into account the remote possibility that the species described here would be found in a form possessing clamps too, there is still no other species known to fit the description.

Mycena parca Aronsen, *spec. nov.* — Figs. 8–12

Basidiomata gregaria. Pileus 7–15 mm latus, parabolicus, primo pruinosus, glabrescens, translucente striatus, sulcatus, griseus. Odor indistinctus. Sapor ignotus. Lamellae 17–22 stipitem attingentes, adscendentes, dente anguste adnatae, griseae, margine albae. Stipes –60 × 1.5 mm, procerus, cylindraceus, cavus, glaber, apice pallide griseus, infra griseobrunneus, basi fibrillis longis, crassis, flexuosis albidisque munitus. Basidia c. 27 × 7 µm, clavata, 4-sporigera, fibulata. Sporae 7.0–9.0 × 4.5–6.0 µm, leves, amyloideae. Cheilocystidia 38–68 × 9–16 × 2.5–5 µm, lageniformia, fibulata, levia. Pleurocystidia simila, haud numerosa. Trama lamellarum iodi ope brunneo-vinescens. Hyphae pileipellis 2.7–4.5 µm latae, fibulatae, surculis 4.5–18 × 1.8–2.2 µm, cylindraceis, curvatis vel flexuosis praeditae. Hyphae stipitis corticales 1.6–3.5 µm latae, fibulatae, leves, cellulae terminales haud numerosae, 45–65 × 5.5–7 µm, clavatae.

Inter aciculas *Juniperi communis*.

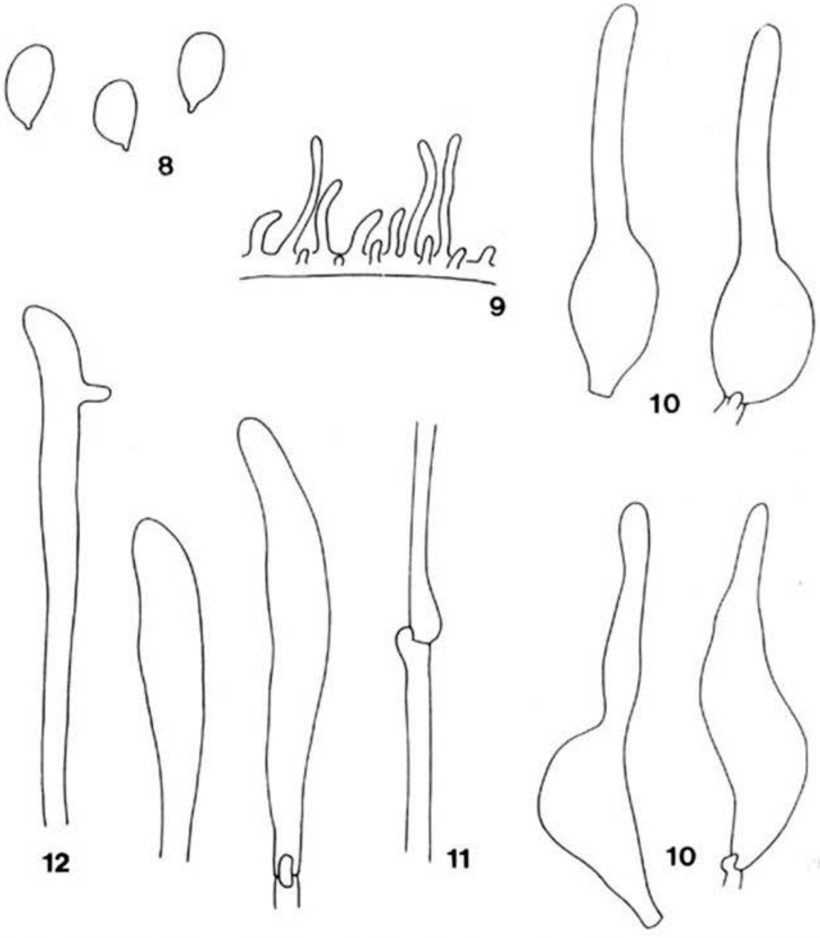
Holotypus: Norway: Vestfold, Tjøme, Moutmarka, 30 Aug. 1992.

Leg. A. Aronsen (A 16/92) (O); isotypus, No. 998.279-774 (L).

Etymology: Parcus, stingy, referring to the avarice of the fungus to form caulocystidia.

Basidiomata gregarious. Pileus 7–15 mm across, parabolical, at first pruinose, glabrescent, translucent-striate, sulcate, grey. Odour not distinct. Taste not recorded. Lamellae 17–22 reaching the stipe, ascending, narrowly adnate with a short tooth, grey with white edge. Stipe up to 60 × 1.5 mm, straight, terete, hollow, glabrous, apically pale grey, grey-brown below, the base covered with long, coarse, flexuous, whitish fibrils.

Basidia c. 27 × 7 µm, clavate, 4-spored, clamped, with sterigmata c. 7 µm long. Spores 7.0–9.0 × 4.5–6.0 µm, pip-shaped, smooth, amyloid. Cheilocystidia 38–68 × 9–16 × 2.5–5 µm, forming a sterile band, lageniform, clamped, smooth. Pleurocystidia similar, not numerous. Lamellar trama brownish vinescent in Melzer's reagent. Hyphae of the



Figs. 8–12. *Mycena parca* (holotype). 8. Spores; 9. hyphae of pileipellis; 10. cheilocystidia; 11. hypha of stipe surface; 12. caulocystidia. Bar = 10 µm

pileipellis 2.7–4.5 µm wide, clamped, but clamps hard to find, not very densely covered with cylindrical, curved to flexuous excrescences 4.5–18 × 1.8–2.2 µm. Hyphae of the cortical layer of the stipe 1.6–3.5 µm wide, clamped, smooth, terminal cells scarce, 45–65 × 5.5–7 µm, clavate.

Collected among needles under *Juniperus communis*.

Holotype: Norway, Vestfold, Tjøme, Moutmarka, 30 Aug. 1992. Leg. A. Aronsen (A 16/92) (O).

The species keys out near *M. fragillima, M. subexcisa, M. subcana,* and *M. leptocephala* (Maas Geesteranus, 1988: 48), of which *M. leptocephala* seems to be the closest. There are, however, several deviating features. *Mycena leptocephala* is usually nitrous-smelling, with the lamellae rather darker grey, and the pileus often more brownish grey. The cheilocystidia in *M. parca* are predominantly lageniform, the hyphae of the pileipellis are generally unbranched, and with no tendency to gelatinize, and the end cells of the cortical layer of the stipe are scarce and fairly narrow. The cheilocystidia in *M. leptocephala* are variously shaped, but rarely lageniform, the hyphae of the pileipellis are often branched, and with a tendency to become somewhat gelatinized, and the end cells of the cortical layer of the stipe are much more numerous and more inflated.

ACKNOWLEDGEMENTS

I would like to express my sincere thanks to Dr. R.A. Maas Geesteranus, Leiden, who through the years always has encouraged and inspired my *Mycena* studies. He has been very helpful with the Latin diagnosis, and he has also provided the microscopical figures.

I am also grateful to Dr. K. Høiland, Oslo for reading an early draft of the manuscript.

REFERENCES

Maas Geesteranus, R.A. 1988. Conspectus of the Mycenas of the Northern Hemisphere – 9. Section Fragilipedes, species A–G. Proc. Kon. Ned. Akad. Wetensch. (Ser. C) 91: 43–83.

Maas Geesteranus, R.A. 1991. Studies in Mycenas. Additions and Corrections. Proc. Kon. Ned. Akad. Wetensch. 94: 377–403.

PERSOONIA
Published by Rijksherbarium / Hortus Botanicus, Leiden
Volume 15, Part 4, pp. 537–540 (1994)

LEPIOTA CINGULUM SPEC. NOV. A NEW SPECIES IN SECTION STENOSPORAE

P.H. KELDERMAN

'Paddestoelenstudiegroep Limburg, Natuurhistorisch Genootschap in Limburg', Herkenbroekerweg 23,
6301 EG Valkenburg a/d Geul, The Netherlands

Lepiota cingulum, belonging to *Lepiota* section *Stenosporae*, is described as new, characterized by medium-sized basidiocarps with distinct dark brown zones on stipe, macroscopically resembling *L. cortinarius* J. Lange. Microscopically *L. cingulum* is characterized by spurred spores 7.5–10.0 × 3.7–4.3 µm, mostly clavate cheilocystidia and a pileus covering made up of long non-septate elements with brown membranal pigment.

Lepiota cingulum Kelderman, *spec. nov.* — Fig. 1

Selected literature. Kelderman, Coolia 31 (1988) 89–91, fig. 1 (as *Lepiota* spec.).

Pileus 20–75 mm, convexus et late umbonatus, dein plano-convexus, tomentoso-pubescens, squamulis concentricis in zonis, aquilus, badius vel medio-fuscus. Lamellae liberae, albae vel cremeae. Stipes 35–70 × 5–8(–10) mm, cylindraceus, cremeus, basi clavato vel subbulboso, squamulis in cingulis superiore vel inferiore, aquilus ad rutilo-fuscum, pugnans cum caro. Velum partiale cortinoideum, album. Odor ei tuberorum *Solani tuberosi* et ei *Lepiotae cristatae* affinis.

Sporae 7.5–10.0 × 3.7–4.3 µm, calcarigerae. Cheilocystidia 22–38 × 7–13 µm, diversiformes, clavatae, fusiformes, subcylindraceae, subutriformesque. Cellulae squamularum pilei erectae, 140–350(–400) × 9–20(–23) µm, elongatae, cylindraceae, tenue fusiformes, pigmento membranae brunneo. Fibulae numerosae.

In fusis lapidibus excisis e metallis et in silvis frondosis ubero luteo, autumno.

Typus: 'Netherlands, prov. Limburg, Kerkrade, 8.IX.1980, J. Conen (*P.H. Kelderman 887*, holotype, L, isotype in herbarium Kelderman)'.

Pileus 20–75 mm in diameter and 10–30 mm high, hemispherical to campanulate when young, then convex with broad umbo, plano-convex to often applanate with umbonate centre, sometimes even plano-concave with undulating margin, in early stage uniformly finely tomentose-pubescent, often with reticulate design from centre towards margin, when older at centre minutely squamulose and around centre flocculose in concentric zones, dark brown, maroon, towards margin rather ruddy-brown to medium brown, sometimes cinnamon-coloured; underlying context, when exposed, at first white creamish, then beige and when damaged ruddy-pink; margin remaining inflexed for a long time and hung with white cortinoid remains of velum partiale, often with a dark brown rim above this zone originating from velum universale. Lamellae, L = 48–60, l = 1–3, rather crowded, free, particularly when old with a minute tooth attached to a narrow collarium-like zone, occasionally furcate, subventricose to ventricose, 4–8 mm broad, at first whitish cream, then beige, when older somewhat brownish maculate, in young basidiocarps usually with a greenish tinge, with edge irregularly undulating and strongly to weakly fimbriate, paler than sides. Stipe 35–70 × 5–8(–10) mm, cylindrical, often curved, usually subclavate to

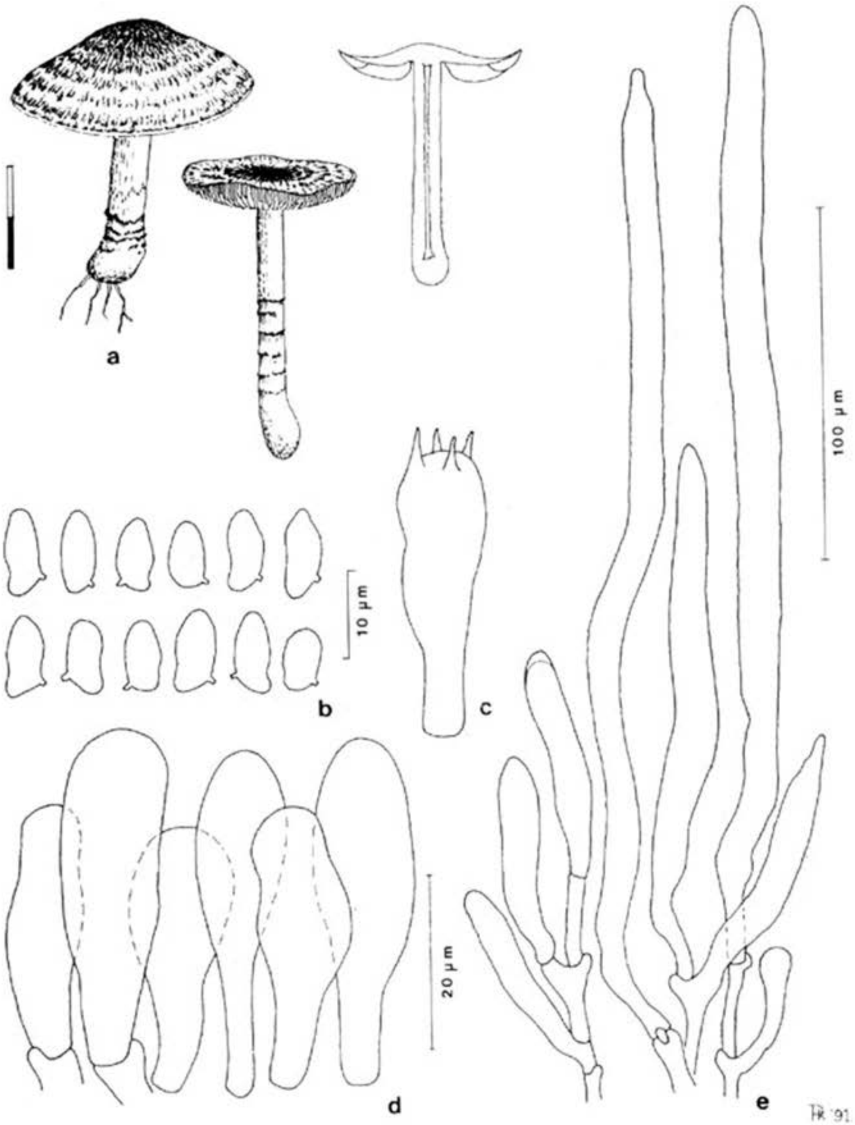


Fig. 1. *Lepiota cingulum*. a. Basidiocarps; b. spores; c. basidium; d. cheilocystidia; e. elements of pileus covering. All figures from holotype.

subbulbose at base (up to 9–11 mm broad), and often somewhat truncate at base, fistulose with age, cream-coloured and fibrillose with verrucose-flocculose dark brown to ruddy-brown velar zones over whole length except at utmost apex or only in lower part, strongly contrasting with the cream to beige, sometimes somewhat ruddy-pink background, with distinct white rhizomorphs at base. Context in pileus and stipe white to cream, in cortex of stipe in young basidiocarps sometimes with green tinge, and eventually slightly yellowish-ruddy. Smell variable, weak and resembling that of potatoes, *Lilium bulbiferum* or when older slightly of *L. cristata*. Taste slightly farinaceous. Spore print colour white.

Spores [205/14/14] in side view (7.0–)7.5–10.0(–10.5) × (3.5–)3.7–4.3(–4.5) µm, av.l. × av.w. = 8.5–9.0 × 3.8–4.1 µm, Q = (1.9–)2.0–2.6(–2.9), av.Q = 2.1–2.3, projectile-shaped to cylindrical, with obtuse to rather acute apex, with distinct eccentric hilar appendage, dextrinoid. Basidia 22–35(–40) × (6.5–)7.5–10.0(–11.5) µm, clavate, often slightly widened at middle, 4-spored, rarely 2-spored and then spores up to 11–12 (–13) µm long; sterigmata up to 5 µm long. Cheilocystidia numerous, (17–)22–38(–45) × (6–)7–13(–15) µm, clavate, fusiform, cylindrical to subutriform, hyaline, with up to 0.8 µm thick wall. Pleurocystidia absent. Hymenophoral trama (45–)55–90(–100) µm wide, regular to subregular, consisting of irregular cylindrical to inflated elements, with a gradual transition into a pseudoparenchymatic subhymenium. Pileus covering an irregular trichoderm made up of long cylindrical, elongated fusiform elements (100–)140–350 (–400) × (8–)9–20(–23) µm, tapering towards apex, sometimes with subcapitate apex or with papilla, with up to 2 µm thick wall at apex, with subhymeniform basal layer with short elements, 38–100 × 8–15 µm, clavate, cylindrical to subfusiform. Pigment brown and membranal. Pileitrama made up of cylindrical, inflated and fusiform, often branched elements, 90–140 × 2–20(–25) µm. Stipitipellis consisting of cylindrical 1.5–6(–8) µm wide hyphae. Stipititrama made up of parallel, cylindrical to slightly inflated and sometimes furcate hyphae, 2–15(–20) µm broad. Elements of velum partiale 2–7 µm broad, hyaline. Stipe covering very similar to pileus covering, but elements rather stockier and broader, (60–)100–300 × 10–23(–28) µm, not seldom with septum at base. Clamp connections present in all parts of basidiocarp.

Habitat & distribution. Until recently this taxon had been found exclusively at the coal-mine dumps in southern Limburg, the Netherlands. The taxon is now also reported in frondose woods on clayey soils near Amsterdam (Amsterdamse Bos) and at Nijenrode (prov. Utrecht). On the rock dumps the species fructifies solitarily or subgregariously at the base of slopes exposed to the north and to the north-west, in loose debris mixed with particles of compost with a pH of 4.5, under *Populus* spec., *Carpinus betulus, Fagus silvatica, Robinia pseudoacacia, Salix* spec., and *Betula* spec., with *Athyrium filix-femina* and *Rubus* spec. among others. August–October.

Collections examined. NETHERLANDS: prov. Limburg, Brunssum, coal-mine dump 'Hendrik', 29.X. 1981, *P.H. Kelderman 1508*, and 30.X.1982, *P.H. Kelderman 1599*; Kerkrade, coal-mine dump 'Laura-Julia', 8.IX.1980, J. Conen, coll. *P.H. Kelderman 887* (holotype, L), 13.IX.1980, *P.H. Kelderman 882*, 20.IX.1980, *P.H. Kelderman 887b*, 27.IX.1980, *P.H. Kelderman 875*, 18.X.1980, *P.H. Kelderman 888*, 18.VIII.1981, *P.H. Kelderman 1500*, 28.VIII.1981, *P.H. Kelderman 899*, 8.IX.1982, *P.H. Kelderman 1531*, 11.IX.1982, *P.H. Kelderman 1582*, 25.IX.1982, *P.H. Kelderman 1529*, 21.IX.1990, *P.H. Kelderman 2056*, and 6.X.1990, *P.H. Kelderman 2002*; Valkenburg, Biebosch, 5.IX.1992, *P.H. Kelderman 2231* (all collections in herbarium Kelderman, except holotype).

This taxon was first found on 8 September 1980 by Mr J. Conen from Heerlen on a coal-mine dump at Kerkrade. Afterwards this taxon has appeared regularly every year and rather abundantly at this locality. Subsequent finds were also made on another dumping-ground, viz. that of the former 'Hendrik' coal-pit at Brunssum.

This taxon is not conformable to any species from *Lepiota* sect. *Stenosporae*. Macroscopically, due to its robust and fleshy characteristics, it somewhat resembles *L. cortinarius* J. Lange, but it lacks the typical bulbous base of the stipe. Microscopically the pileus covering does not differ much either, as to shape and size, from *L. cortinarius*. But the spores are distinctly different: projectile-shaped to mostly triangular in side view in *L. cingulum*, and more or less cylindrical in *L. cortinarius* (see also Kelderman, 1988, and Vellinga, 1992). The spores of *L. cingulum* show a distinct depression on the abaxial side, whereas spores of *L. cortinarius* are more or less straight on that side.

Spore sizes agree with those of *L. tomentella* J. Lange to some extent, but otherwise the two taxa are entirely different, in macroscopical and microscopical characteristics (see for a description of *L. tomentella* Vellinga & Huijser, 1993). It is distinguished from other more or less brownish species in the section, *L. boudieri* Bres. or *L. castanea* Quél., by the differences in pileus covering. In *L. boudieri* the elements are articulate and provided with intracellular pigment; in *L. castanea* the elements are septate, with membranal pigment.

Exceptionally long cheilocystidia (up to 80 µm) have been found once in one basidiocarp of a collection from Nijenrode (pers. comm. H.A. Huijser). These sizes are not representative of the taxon.

ACKNOWLEDGEMENTS

My particular gratitude goes to Mr J.C. Leeuwenburgh for the English text and to Else C. Vellinga for scrutinizing an earlier draft of this paper.

REFERENCES

Kelderman, P.H. 1988. Nieuwe en zeer zeldzame Lepiota-soorten III. Coolia 31: 89–93.

Vellinga, E.C. 1992. Notulae ad Floram agaricinam neerlandicam – XVIII. Some notes on Cystolepiota and Lepiota. Persoonia 14: 407–415.

Vellinga, E.C. & H.A. Huijser. 1993. Notulae ad Floram agaricinam neerlandicam – XXI. Lepiota section Stenosporae. Persoonia 15: 223–240.

PERSOONIA
Published by Rijksherbarium / Hortus Botanicus, Leiden
Volume 15, Part 4, pp. 541–544 (1994)

BOOKS RECEIVED BY THE RIJKSHERBARIUM LIBRARY

R. Agerer (Ed.). *Colour atlas of ectomycorrhizae, Issue 7.* (Einhorn Verlag, Eduard Dietenberger GmbH, Schwäbisch Gmünd. 1993.) Pp. 33, 8 col. pls. Price: DM 73.- incl. 1 binder.

The seventh issue of this loose-leaf colour atlas of ectomycorrhizae gives 8 coloured plates, of *Boletopsis leucomelaena, Gyrodon lividus, Hydnellum peckii, Phellodon niger, Piceirhiza oleiferans, Scleroderma citrinum, Suillus laricinus* and *Tricholoma acerbum*, together with half-tone photographs of anatomical features, and legends. Also in this issue, extensive additions are given to the glossary, check-lists on morphology, chemical tests, anatomy of the mantels, emanating elements, and cross sections. Keys are given for ectomycorrhizae on *Abies, Alnus, Betula, Cyclobalanopsis, Elaeocarpus, Fagus, Picea, Pinus,* and *Salix*. In an appendix a list is given of the plates that have been issued hitherto, and how to arrange them. A synoptic table makes identification of ectomycorrhizae easier. As the series progresses a new binder is necessary, and is supplied at cost with the present issue.

R.M. Dähncke. *1200 Pilze in Farbfotos.* (AT Verlag, Aarau-Stuttgart. 1993.) Pp. 1179, 1200 col. pls. Price: DM 148.-.

This is a new edition of R.M. Dähncke & S. Dähncke, 700 Pilze in Farbfotos, published in 1979. As the title suggests, the new edition is substantially enlarged with several hundreds of new photographs. Although the pictures mostly have been taken in a studio, they are generally of good quality and show very well the diagnostic features of the species involved. In comparison with the first edition of the book, many more species have been identified by specialists, which considerably increased the value of this book. Also some errors in the first edition have been corrected. The book will certainly be welcomed by professionals and amateurs, especially those that do not have the first edition.

D. Frese. *Die molekularbiologische Analyse der physiologischen Phänomene des Seneszenzsyndroms bei dem Ascomyceten Podospora anserina.* (Bibliotheca Mycologica 149, J. Cramer in der Gebrüder Borntraeger Verlagsbuchhandlung, Berlin, Stuttgart. 1993.) Pp. 117, 40 text-figs., 6 tables. Price: DM 60.-.

As an aerobic organism *Podospora anserina* produces energy by respiration with the help of cytochrome C oxidase. But if this system is inactivated an alternative respiratory system takes over. It was found during this study that, when both respiratory systems become simultaneously active, the mycelium ages quickly. If only one of the respiratory systems is blocked a long-living mycelium results. It has been suggested that as long as the cytochrome respiration is active and the alternative respiration plays only a minor role, a choice of mitochondrial DNA is available. But when the alternative respiration becomes more active simultaneously, this choice is no longer available and incompetent mitochondria are accumulated, which finally kills the mycelium.

G.J. Krieglsteiner (Ed.). *20 Jahre Arbeitsgemeinschaft Mykologie Ostwürttemberg (AMO). Beiträge zur Kenntnis der Pilze Mitteleuropas IX.* (Einhorn Verlag, Eduard Dietenberger GmbH, Schwäbisch Gmünd. 1993.) Pp. 204, 10 col. pls. Price: DM 38.-.

The present volume of this series, that is published with irregular intervals, contains 17 papers written by Central European specialists in various fields of mycology (Babos, Benkert, Bohus, Clemençon, Enderle, Frommberger, Forstinger, Gminder, Haas, Krieglsteiner, Moser, Rastetter, and Tortic). Most of the contributions are floristic or taxonomic, dealing with macromycetes. The colour plates are of good quality, and depict 48 rare and interesting species.

G.J. Krieglsteiner. *Verbreitungsatlas der Großpilze Deutschlands (West). Band 2: Slauchpilze.* (Verlag Eugen Ulmer GmbH & Co., 1993.) Pp. 596, 7 text-figs., 1987 distribution maps. Price: DM 88.-.

This is the second volume of an atlas with distribution maps of macro-fungi for West Germany. It contains the Euascomycetes with the exception of Taphrinales, Erysiphales, and marine or submerse taxa. It is a large (A4-format) volume with well-printed illustrations and 1987 maps in colour. Initially meant to cover only the distribution of Ascomycetes in Baden-Württemberg (Germany), the region was extended to the whole territory of the former Federal Republic of Germany ('Bundes Republik'). The list of Ascomycetes is based on Baral & Krieglsteiner (1985), 'Bausteine zu einer Ascomyceten-Flora der BR. Deutschland' (Z. Mykol. Beih. 6); while the nomenclature is followed after Cannon, Hawksworth & Sherwood-Pike (1985), 'The British Ascomycotina. An annotated checklist'. The observations of 500 cooperators are included. In the numbered distribution maps records after 1 May 1945 are presented; earlier records, records from literature, or records from uncertain localities are presented without number in an overall list of the species.

In the introductory part a survey is presented of the projects of mycological mapping in Europe. Despite the great care that is taken to present in a uniform way the identifications and records of so many cooperators, still a few irregularities could be observed: *Aleuria hortensis* (No. 15) is a species of *Peziza* and not of *Aleuria* Fuckel; *Coprotus aurora* (No. 0360) and *C. glaucellus* (No. 0361) are also presented as *Ascophanus aurora* (No. 106) and *A. glaucellus* (No. 108); *Rhyparobius depauperatus* (No. 1710) and *Ascophanus holmskjoldii* are undoubtedly the same as *Saccobolus depauperatus* (No. 1715) and *Thecotheus holmskjoldii* (No. 1833), respectively.

M. Moser & W. Jülich. *Farbatlas der Basidiomyceten. Colour Atlas of Basidiomycetes. Lief. 10.* (Gustav Fischer Verlag, Stuttgart & New York. 1993.) Pp. 184, 60 pls. Price: DM 92.-.

The tenth issue of this loose-leaf colour atlas contains figures in colour of *Hygrophorus, Lacrymaria, Marasmius, Mniopetalum, Mycena, Nyctalis, Panellus, Phaeocollybia, Pholiotina, Phyllotus, Pluteus, Porpoloma, Psathyrella, Resupinatus, Rickenella, Rozites, Russula, Strobilurus, Tricholomopsis,* and *Tulostoma*. The photographs are of variable quality, ranging from rather poor to fairly good.

H. Neubert, W. Nowotny & K. Baumann. *Die Myxomyceten Deutschlands und des angrenzenden Alpenraumes unter besonderer Berücksichtigung Österreichs, Band 1. Ceratiomyxales, Echinosteliales, Liceales, Trichiales.* (Karlheinz Baumann Verlag, Lindenstrasse 40, D-72810 Gomaringen, Germany. 1993.) Pp. 344, numerous col. pls., line drawings and SEM pictures. Price: DM 190.-.

The present volume is the first of a three-part Monograph of Myxomycetes in Germany and the Alps, in particular the Austrian Alps, and covers the Ceratiomyxales, Echinosteliales, Liceales and Trichiales. In the general part information is given on the life-cycle of myxomycetes, and the characters for identification, followed by chapters in ecology and distribution, methods for sampling and conservation, and an extensive glossary. The taxonomic part gives keys and descriptions of all species known from the area. The descriptions are very elaborate and extensive. The line-drawings give good, clear information on the diagnostic features, but what makes this book unique are the colour plates. These are of superb quality, highly professional, and depict all species strongly enlarged, as you may see them under a stereomicroscope. Therefore this publication is warmly recommended, not only to taxonomists, but also to teachers, who will find it most useful as an introduction in the world of myxomycetes for their students.

D.N. Pegler, L. Boddy, B. Ing & P.M. Kirk (Eds.). *Fungi of Europe: investigation, recording and mapping.* (Publications Sales, Royal Botanic Gardens, Kew, Richmond, Surrey TW9 3AE, England. 1993.) Pp. 322, numerous line illustrations. Price: £ 18.-.

This book gives the proceedings of the eleventh Congress of European Mycologists, held at the Royal Botanic Gardens, Kew, 1992. It contains twenty-three papers, written by international experts and arranged under the headings Fungal Recording & Mapping, Fungi in European Ecosystems, and Conservation of European Fungi. As such it gives the latest state of research in these fields in Europe.

D.N. Pegler, B.M. Spooner & T.W.K. Young. *British Truffles. A revision of British hypogeous fungi.* (Royal Botanic Gardens, Kew. 1993.) Pp. 216, 30 text-figs., 26 plates (of which 12 in colour). Price: £ 19.50.

This book is a full treatment of the British hypogeous fungi by three different authors. After a short introduction, T.W.K. Young treats the 'Pea Truffles' (*Zygomycotina,* Endogonales), B.M. Spooner the 'True Truffles' (*Ascomycotina,* Elaphomycetales and Pezizales), and D.N. Pegler the 'False Truffles' (*Basidiomycotina,* in six orders). The small group of the 'Anamorphic Truffles' (*Deuteromycotina*) is anonymously included. After earlier treatments by Rev. M.J. Berkeley & C.E. Broome (1846–1875), and Prof. L.E. Hawker (1954 and 1974), the study of hypogeous fungi in Britain was stimulated by the British Mycological Society by an annual 'truffle hunt'. In the present account all relevant material deposited in the herbaria of the Royal Botanic Gardens, Kew and the Royal Botanic Garden, Edinburgh is revised and included. The considerable taxonomic developments during the last decennia are also taken into account. Keys are provided for the identification of all orders, families, genera, and species included. Each species is fully described and illustrated in black-and-white line-drawings, habitus sketches in colour, and scanning electron micrographs of details and spores. An indispensable work for those who are interested in hypogeous fungi.

INDEX

New names are in **bold-face** type. Subdivisions of genera are indicated by the sign §, illustrations by an asterisk (*) added to the page number.

Agaricus § Calodontes 41, 43; § Fragilipedes 37, 39; § Hygrocyboideae 41; § Mycena 34; alcalinus 37; bicrenatus 44; colligatus 41; ephemeroides 292; epibryus 163; epipterygius 41; flavominiatus 341, 343; fuliginarius 48; galericulatus 34, 36; glauconitens 193; hendersonii 292; incisus 513; nitens 194; niveus 265; pelianthinus 41, 42; pinsitus 246; purus 44, 45; rigens 512; tintinnabulum 36
Albotricha **ammophilae 169**; 170*
Aleuria 97, 129, 147; bovina 179; umbrina 181
Alternaria 197, 203; alternata 197; chrysanthemi 197; citri 197; radicina 197; raphani 197
Amanita 345; § Lepidella 348; § Vittadiniae 345, 348, 349; armillariiformis 349; boliviana 349; bubalina 349; foetidissima 349; grallipes 345, 346*, 348*, 349; ingrata 349; lilloi 349; malheurensis 349; pleropus 349; praegraveolens 349; pruittii 349; silvifuga 348, 349; singeri 349; spissa var. laeta 345; spissa var. laeta 349; thiersii 349
Ammophila arenaria 169
Anthracobia 147
Aposphaeria brassicae 447; glomerata 203; humicola 77; pezizoides 479; putaminum 79; salicum 479
Aposphaeria violacea 378
Ascobolus crec'hqueraultii 94, 98
Ascochyta 198; aquilegia 384; clematidina 217; davidiana 217; indusiata 217; lupini 375; nobilis 90; pedicularis 472, 473; trachelospermi 204; vitalbae 217
Ascocoryne 427
Ascotremella 4
Asteromella 78; dictamni 91; lupini 375

Bakerophoma tracheiphila 473
Bisporella 304; citrina 335; pallescens 305, 307, 308*, 318*, 319, 321, 332, 334, 335; pallescens 337; sulfurina 305, 307, 308*, 398*, 318*, 319, 322, 332, 333; sulfurina 334, 335
Bulgaria 20 427, 428; inquinans 3, 4, 12*, 14*, 16, 18, 19*, 20, 335, 428 Calycella 173

Calycellina 173; **calycelloides** 171*, **172**
Calycina 337, 338
Camarophyllus russocoriaceus 510, 519
Cercospora 66, 68; abelmoschi-cannabini 68; gossypii 66; gossypina 66; hibisci 68; lhuillieri 66; malvacearum 68; malvarum 68; malvastri 68; malvicola 68; polymorpha 68; sphaeralceicola 68
Cercosporella gossypii 63
Ceuthospora astragalina 451
Cheilymenia 147
Chlorociboria 304, 336; aeruginascens 305, 307, 309*, 318*, 319, 321, 333, 336, 338
Chrysanthemi coccinei 484
Ciboria 336
Ciliaria asperior 98; hirta 129
Cladosporium anomalum 68; gossypiicola 66; gossypiicola var. minor 66; oligocarpum 66; oligocarpum var. malvacearum 66; tenuissimum 66
Clavaria obtusissima 109, 115
Clavariadelphus pistillaris 112; truncatus 113
Clisosporium urticae 464
Clitocybe agrestis 493; albofragrans 492; diatreta 493; marginella 493; odora 493
Clitopilus 241; § Pleurotelloides 241, 244; daamsii 242; fasciculatus 242, 247; giovanellae 241; hobsonii 242, 247; passeckerianus 242, 246, 247*; **paxilloides 242**, 243*, 244, 247; pinsitus 244, 246; prunulus 241, 244; quisquiliaris 242, 244; rhodophyllus 242, 245*, 246, 247; scyphoides f. reductus 242; scyphoides var. intermedius 241; scyphoides var. scyphoides 241
Collybia impudica 125
Coniothyrium eucalypti 86; glomerata 203; pezizoides 479; prunicola 205; putaminum 79
Conocybe pygmaeoaffinis 493, 494*; striaepes 494
Copelandia 120; cyanescens 117
Coprinus 117, 357, 359, 363; § Alachuani 357, 365; § Annulati 258, 259; § Comati 258; § Coprinus 259–261; § Cortinatus 259; § Cyclodei 260; § Domestici 259–262; § Exannulati 259; § Farinosi 259; § Flocculosus 259; § Fraxinus 357; § Glabri 259; § Hemerobii 260; § Impexi 261, 276, 365; § Lanatuli 357, 363; § Micacei 259, 260–262; § Micaceus 259; § **Narcotici** 260–**262**, 271; § **Nivei** 257, 259–**262**, 264, 271, 277, 295–297, 359; § Nudi 259; § Picaceus 261, 276; § Pseudocoprinus 259, 261; § Setulosi 259, 260; § Utrifer 261; § Veliformes 257, 259–261; § Vestiti 259, 260; bellulus 257, 263, 264, 283, 285; bulbillosus 259, 292; **calosporus** 357, 358*, **359**, 363; candidatus 257, 264, 279, 281*; cardiasporus 257, 262, 265, 288–290*, 292; cinereus 363; conio-

phorus 259, 262, 265, 277, 279, 298*; cordisporus 259, 262–264, 286*–289, 293; cortinatus 259, 260, 264, 279, 282, 284, 285; cothurnatus 259, 263, 264, 269*, 271; disseminatus 297; domesticus 259, 260; ephemeroides 259, 260, 262, 264, 288, 291*–293; filiformis 259, 279, 285; flocculosus 259, 260; **goudensis** 357, **363**, 364*, 365; hiascens 496; **idae** 257, 264, **278**, 279, 280*, 295; iocularis 257, 263, 265, 293, 294, 359; lagopus 357; latisporus 259, 260, 265, 267*, 270; luteocephalus 257, 259, 260, 365; macrocephalus 363; micaceus 259, 260, 297; narcoticus 259, 260, 262; **nemoralis** 257, 264, 299*, **300**; neotropicus 365; niveus 259, 260, 262–265, 266*, 267*, 270, 271, 275; **ochraceolanatus** 357, 360*, 361*, **362**, 363; ochraceovelatus 357, 363; pachyspermus 257, 259, 263, 264, 271, 272*, 275; patouillardii 259, 260, 262–264, 286, 287, 288*, 289, 292, 293; patouillardii var. isabellinus 259, 286, 287; patouillardii var. lipophilus 257, 259, 289; **piepenbroekii** 357, **365**, 366*, 367; pilosotomentosus 264, 294*, 295, 300; poliomallus 259, 260, 262, 264, 274*, 276–278, 297; pseudocortinatus 264, 277*–279; **pseudoniveus** 257, 265, 268*, **270**, 271; radiatus 363; ramosocystidiatus 264, 295, 296*, 297; sclerocystidiosus 494*; stanglianus 365; stercorarius 259; stercoreus 259, 260; subimpatiens 495*, 496; suburticicola 365; urticicola 365; utrifer 260, 263, 264, 273*, 275, 276; xantholepis 496; xenobius 365
Coprobia 147
Cordyceps 152
Cortinarius anomalus 496, 516; balteatoalbus 497*, 498; brasilaceus 504, 505; casimiri 498, 499*, 503; causticus 499*, 500; cedriolens 511; comptulus 499*–501; contrarius 503; decipiens 503; decoloratus 516; duracinus 512; erythrinus 501, 502*; erythrinus var. russulaesporus 501; flexipes 502, 503; flexipes f. sertipes 503; fragrantior 519; fusisporus 503, 504*, 515, 520; helobius 515; helveolus 504*, 505, 507; hemitrichus 500, 501; hinnuleus 505, 506*, 507; hinnuleus var. griseascens 506*; incisus 503, 513, 515; lanatus 506*–508; obtusus 519; paleaceus 508, 509*, 510, 513, 519, 520; paleiferus 508, 509*, 510, 520; parvannulatus 509*, 510; privignofulvus 511; privignoides 511; privignorum 511; privignus 509*, 511; psammocephalus 507, 508, 513; pseudoprivignus 511; quadricolor 505; rigens 511, 512, 514*, 519; rigidus 516, 520; semivestitus 503; sertipes 503, 520; striaepilus 507, 509*, 512, 513, 515; strobilaceus 507, 508; s ubbalaustinus 514*, 515; subsertipes 498; tabularis 514*–516; umbrinolens 516, 518; valgus 514*, 517; velenovskyi 512, 517, 519, 521*; violilamellatus 518*, 519, 520
Crepidotus 155; applanatus 163; bickhamensis 159, 162*, 163, 164*; carpaticus 161; cesatii 158; cesatii var. subsphaerosporus 158; epibryus 159, 163; harperi 156*, 160*, 161, 163; inhonestus 161; juniperi 159; lundellii 159, 161, 163, 164; lundellii var. subglobisporus 159; luteolus 163; pubescens 166; serbicus 155, 156*; subepibryus 156*, 157*, 158; subtilis 162*–165; subverrucisporus 156*, 158*, 159, 163, 165; velenovskyi 156*, 159; versutus 161, 162, 166*; versutus var. subglobisporus 156*, 159, 160*, 161; wakefieldiae 161, 163
Crocicreas 304, 335, 336; coronatum 335, 336; cyathoideum var. cyathoideum 305, 307, 310*, 318*, 319, 323, 333, 335, 336; gramineum 335; pallidum 305, 307, 310*, 318*, 323, 332, 335–337
Cudonia 427; confusa 427
Cudoniella 304, 336; acicularis 305, 307, 308*, 311*, 318*, 319, 324, 331, 333; acicularis 334, 336; clavus var. grandis 305, 307, 312*, 319*, 325, 333, 336
Cyathicula 335
Cyphellostereum laeve 518; laeve 520
Cystoderma amianthinum 516

Depazea brassicicola 447; prunicola 205; vagans var. brassicae 447
Dermoloma 187, 190; cuneifolium 187, 189, 191, 193, 194, 196; hygrophorus 191, 193; josserandii 187, 190, 193, 194, 196; josserandii var. josserandii 190*, 191, 192*, 193; josserandii var. **phaeopodium** 190*, 193, 194*, **195**; murinellum 194; phaeopodium 195; phaeopodium 196; pragensis 191, 193, 195; pseudocuneifolium 187, 189*, 190*, 196; pseudocuneifolium var. pragensis 191
Deuterophoma tracheiphila 473
Dictamnus albus 91
Diplodina 198; clematidina 217; pedicularis 472; vitalbae 217
Diploplenodomus malvae 471; microsporus 470; pizkorzii 469
Discinella 304, 337; boudieri 305, 307, 308*, 312*, 319*, 325, 332, 337

Entoloma 23; § Asprellum 30; § Cyanula 25; § Dysthales 123; § Entoloma 28; § Griseoru

bida 30; § Leptonia 24–26; § Parvisporae 30; § Polita 28; § Pouzarella 123; § Rhamphocystotae 26; § Trichopilus 29; § Versatilia 123; allochroum 24; conocybecystis 28, 29; dichroum 24; dysthales 123; dysthales f. acystidiosum 123; elodes 29; farinasprellum 30; fuscotomentosum 29; jubatum 29; **lactarioides 27**, 28; **leochromus 26**; lividoalbum 520, 521*, 522; longistriatum 26, 27; **mutabilipes 30**; nigroviolaceum 25; **ochromicaceum 27**; olivaceotinctum 30; **politoflavipes 29**, 30; porphyrophaeum 29; **pseudodysthales 123**, 124*; **rhynchocystidiatum 25**, 26; **roseotinctum 31**; scabrosum 25; subcorvinatum 26; turci 26; undatum 24; undulatosporum 521*, 522; **viiduense 24**, 25; **violaceozonatum 23**, 24; weholtii 30
Epicoccum 198, 209–211, 218, 220; nigrum 197, 199; nigrum 220; nigrum 485
Exormatostoma nebulosa 394

Funaria hygrometrica 251

Gaeumannomyces sp. 170*
Galactina echinospora var. autumnalis 181; echinospora 181; moravecii 184
Geoglossum 425, 426, 428, 429; cookeianum 406, 407, 410*, 411, 413, 423, 425–427; nigritum 406, 408*, 409, 410*, 411, 423, 424*–426; sp. 406, 425
Geopyxis carbonaria 251
Gloeosporium chenopodii 395

Helotium gemmarum 338
Helvella 405
Hendersonia curtisii 215
Heyderia abietis 406
Hiatula grangei 235
Humaria bovina 179; modesta 94; rubens 55, 56*, 57*, 59; rustica 59; sanguinea 55, 59
Hydropus 48; § Floccipedes 49; § Spurii 49; eburneus 34; eburneus 48*–50; porphyrodes 49; scabripes 49; taxodii 49
Hymenoscyphus 304, 336, 337; caudatus 305, 307, 312*, 320*, 326, 327, 332, 334, 337; consobrinus 306, 307, 315*, 320*, 327, 328, 332, 336, 337 epiphyllus 337; fructigenus 304, 306, 307, 313*, 319, 326, 332, 334, 337, 338; herbarum 306, 307, 315*, 320*, 329, 331, 332, 338; imberbis 306, 307, 315*, 319, 320*, 328, 332, 337; repandus 306, 307, 315*, 328, 332, 337; salicellus 306, 307, 314*, 319, 327, 332, 337; salicinus 306, 307, 314*, 319, 320*, 327, 332, 337; scutula 337
Hypholoma fasciculare 113
Hypocrea cupiliaca 151
Hypoderma rubi 426; rubi 427
Hysteronaevia **fimbriata** 172*, **173**
Laetinaevia 177
Lamprospora 96; crec'hqueraultii 93, 96, 98; crec'hqueraultii var. modesta 93, 98; exapetala 94; ovalispora 93, 94
Lanzia luteo-virescens 332
Leotia 336, 405, 427; lubrica 405–407, 416, 418, 423, 424*, 426–429
Leotiales 3
Lepiota § Stenosporae 223, 537, 540; acerina 239; boudieri 223, 237, 238*, 239, 540; castanea 237; **cingulum 537**, 538*, 540; cortinarius 540; cristata 226, 228, 230, 537; forquignonii 235; fulvella 223, 237–239; fulvella f. gracillis 237; grangei 223, 224, 231, 234–236*; grangei f. brunneoolivacea 231, 233, 234; griseovirens 223, 229, 231, 232*, 234; griseovirens subsp. obscura 224, 231; griseovirens var. griseovirens 22, 231; griseovirens var. obscura 231, 233, 234; ochraceocyanea 235; pilodes 226, 227*, 229; **poliochloodes** 226, **229**, 230*, 231, 234; pseudofelina 223, 231, 234; tomentella 223–225*, 226, 228, 229, 540
Lepteutypa hippophaes 170*
Leptophoma acuta 464, 465, 469; doliolum 465, 466
Leptosphaeria 432; acuta 436, 442, 444, 458, 465, 469; affinis 435, 442, 444, 454; agnita 435, 439, 440, 444, 453; conferta 435, 439, 441, 444, 445, 457, 468; congesta 435, 439, 444, 461; conoidea 437, 439–442, 444, 463; conoidea 466, 467, 470, 472; doliolum subsp. doliolum 436, 439, 442, 444, 458, 461, 464, 465, 466, 469, 470, 471; **doliolum** subsp. **errabunda** 436, 440–442, 444, 458, 465, **466**, 471, 472; doliolum subsp. pinguicula 471, 472; doliolum var. conoidea 466, 472; libanotis 438, 442, 444, 482, 483; lindquistii 435, 439, 440, 444, 454; maculans 434, 439, 441, 444, 447, 450, 467, 480; napi 450; pratensis 481; purpurea 438, 439, 444, 483; sacchari 438, 441, 444, 480; senecionis 436, 439, 440, 445, 469; slovacica 435, 439, 441, 444, 459; submaculans 436, 439, 441, 445, 450, 457, 458, 467; suffulta 435, 442, 444, 458; viridella 481; weimeri 438, 441, 444, 481
Lophodermella sulcigena 426

Marasmiellus 351, 353; § Inodermini 353; concolor 353; gossypinulus 353; hiemalis 47; **lateralis 351**, 352*, 353; microscopicus 353; olidus 47; **trabutii** var. **longisporus 353**, 354*; trabutii var. trabutii 355

Melastiza 97
Microglossum 428, 429; viride 406, 407, 419, 420*, 423, 425*, 426, 428
Mitrula paludosa 406, 407, 420*, 421, 422*, 423, 425*, 426, 428, 429
Mitrulinia 428
Mollisia **orcadensis 173**, 174*; **stromaticola** 174*, **175**
Mycena § Adonideae 43, 341, 342; § Calodontes 34, 41–45; § Fragilipedes 10, 33, 34, 37–39, 531, 533; § Hiemalis 34, 47; § Hygrocyboideae 41; § Marginatae 34, 42, 43; § Mycena 34, 43, 48; § Myceneae 52; § Polyadelphia 101, 102, 105, 106; § Purae 34, 44–46; § Violacellae 34, 45; **abietina** 33, **37**, 38; abramsii 38; acicula 343; **acrocephala 341**, 342*, 343; adonis 342; albiceps 106, 107; alcalina 39; alnicola 38; atrocyanea 37, 38; aurantiorubra 43; auroricolor 46; **austera 531**, 532*, 533; bathyrrhiza 33, 37, 38; cinnabarina 34, 40*, 42, 43; coalita 34, 39, 40*, 41; conocephala 50; coracina 38; culmigena 102; **dasypus 101**, 102*, 103; deceptor 533; epipterygia 41; flavominiata 341; fragillima 535; fuyoensis 43; galericulata 34, 35*, 36; gentilis 34, 45, 46; herbarum 103; juncicola 102; leptocephala 533, 535; lohwagii 103; miniata 43; minirubra 43; olida 34, 47, 48*; **parca** 531, **533**, 534*, 535; pearsonia 46; polyadelpha 106; praeclara 43; pseudo-inclinata 41; pura 43, 44; pura f. pura 44, 45; quercus-ilicis 106; riparia 106; rubiaetinctus 43; sanguinolenta 50, 51; subacicula 43; subcana 38, 535; subexcisa 535; **terena 105**, 106, 107*; tintinnabulum 34, 35*, 36; violacella 45
Mycosphaerella 66; areola 63; crinicola 383; gossypina 66; opuntiae 78; verbascicola 387
Mycovellosiella 68
Myxofusicoccum 398

Neobulgaria 4, 20, 335, 405, 427; pura 3, 4, 10*, 11*, 16, 18*–20, 336
Neocudoniella 405
Nimbomollisia eriophori 176
Niptera **ambigua** 171*, **175**

Octospora 96, 147; crec'hqueraultii 93; libussae 59, 61; rubens 55, 59, 60; rustica 55, 58*, 59, 60*, 61
Ombrophila 3, 4, 20, 427; violacea 3, 4, 7*, 8*, 16, 17*, 18, 20, 336
Omphalina campanella 50
Otidea 129, 147

Panaeolina foenisecii 527
Panaeolopsis nirimbii 527
Panaeolus 120; acuminatus 527; antillarum 526, 527; ater 527; bernicii 120, 527; campanulatus 525, 527; clelandii 527; cyanescens 117–120, 526, 527; fimicola 527; olivaceus 527; phalaenarum 526, 527; semiovatus 526, 527; sphinctrinus 526, 527; subbalteatus 526, 527
Paradiscula 398
Parastenella magnoliae 68
Peronellaea musae 209; nainensis 209; circinata 209; glomerata 203; indianensis 211; nigricans 209; stemphylioides 211
Pezicula 425, 426, 428
Peziza 179; asperior 98; asterigma 179, 180, 184; bovina 179, 180, 184; cerea 179, 180; echinospora 179, 181, 182*, 184; fimeti 180; herbarum 338; hortensis 180; modesta 94, 98; moravecii 179, 184; perdicina 179, 183*, 184; umbrina 181; vesiculosa 179, 180, 184
Pezizella 304, 338; alniella 306, 307, 316*, 319, 320*, 329, 333, 338; gemmarum 306, 307, 317*, 319, 321*, 330, 332, 337, 338
Phaeohelotium 304, 337; subcarneum 306, 307, 317*, 321*, 330, 332, 337
Phaeostagnosporopsis 217
Phallus impudicus 152
Phialea 335
Phialophora 432; chrysanthemi 485
Phoma 71, 72, 197, 198, 203, 205, 211, 215, 216, 369; § Deuterophoma 431, 432; § Didymella 371; § Diploplenodomus 431, 432; § Leptophoma 431, 432; § Peyronellaea 197, 198, 203, 369, 431; § Phoma 71, 369, 371, 431–433; § Phyllostictoides 381; § Plenodomus 385, 431–433, 438, 439; § Sclerophomella 89; acaciae 388; acuta 466, 469, 470; acuta f. ballotae 459; acuta f. gentianae 472; acuta f. petasites 453; **acuta** f. **phlogis 465**; acuta subsp. acuta 436, 439, 442, 444, 458, 461, 462*, 464–466, 469, 479; acuta subsp. amplior 470; **acuta** subsp. **errabunda** 436, 439–442, 444, 458, 462*, 464, **465**, 466, 471; adianticola 371, 374, 376*, 379; agnita 435, 439, 440, 444, 453*, 477; ajacis 372–374, 376*, 383; amaryllidis 215; americana 200, 201, 208*, 209, 210; amplior 470; anigozanthi 73, 74, 76*, 84, 221; annulata 438, 441, 444, 480, 482*; anserina 72, 74, 76*, 77; antirrhini 384; apiicola 73, 74, 76*, 83; **arachidis-hypogaeae** 372–374, 386*, **388**; armeniacae 477; astragalina 434, 440, 441, 444, 451, 453*; **aurea** 373, 386*, **394**; bellidis 372–374, 376*, 381; berberidella 477; berberidicola 477; berteroae 458; bismarckii 373,

374, 396, 397*, 398; brassicae 447; capitulum 73, 74, 76*, 79; **chenopodiicola** 373, 374, 386*, **395**; chondrillae 453; chrysanthemicola 200, 201, 218*, 219; chrysanthemicola f. chrysanthemicola 219; clematidina 200, 201, 216*, 217; complanata var. acuta 459, 483; conferta 435, 439, 441, 444, 445, 457*, 458, 468; congesta 435, 439, 444, 460*, 461; coonsii 437, 439, 443, 445, 475*; cornicola 477; costarricensis 73, 74, 76*, 80; crinicola 372–374, 376*, 382, 383; crystallifer 373, 374, 386*; curtisii 215; cyanea 199, 201, 202*, 203; cyperi 205; decorticans var. microspora 391; densiuscula 447; dianthi 451; dictamni 90; **dictamnicola** 73, 76*, **90***, 91; doliolum 437, 439, 440, 441, 442, 444, 463, 464, 466, 467, 470 **dorenboschii** 73, 76*, **83**, 84; drobnjacensis 435, 441, 444, 455, 457*; dunorum 79; enteroleuca var. enteroleuca 437, 439, 443, 445, 477*, 478 enteroleuca var. influorescens 437, 439, 443, 445, 477*, 478 epicoccina 199, 201, 218*, 220, 485; errabunda 465, 466; eucalyptica 73, 74, 76*, 86; eupatorii 372, 374, 376*, 382; eupyrena 73, 74, 76*, 88*, 390; exigua 396; exigua var. exigua 458, 483; exigua var. linicola 381; fimeti 73, 74, 76*, 82; **flavescens** 371, 373, **375**, 376*, 377; flavigena 72, 74, 76*, 78; glomerata 199, 201, 202*, 203, 205, 213, 215; grovei 483; **haematocycla** 371, 374, 376*, **377**, 378; hedericola 73, 76*, 87; henningsii 372–374, 386*, 388, 397*; herbarum 369, 370*, 371, 373, 374, 376*, 378, 379, 387, 389, 455 herbarum var. urticae 464; hibernica 378; hoehnelii 465, 466; hoehnelii subsp. amplior 470, 471; hoehnelii var. urticae 464; incompta 73, 74, 76*, 89; indianensis 211; insidiosa 211; insulana 372–374, 386*, 389, 397*; intricans 437, 439, 443, 445, 478; jolyana var. circinata 199, 201, 209; jolyana var. jolyana 199, 201, 208*, 209, 210; jolyana var. sahariensis 199, 201, 209, 210; jolyi 209; labilis 373, 386*; lampsana 470; leguminum 378; leonuri 435, 439, 441, 444, 459, 460*, 461; lignicola 378; lingam 431, 434, 439, 441, 444, 447*, 449*, 450, 467, 480; lingam f. linariae 472; lingam var. napobrassicae 447; lini 371, 373, 374, 376*, 380; longirostrata 436, 442, 444, 463, 464; lucknowensis 391; lunariae 46, 471; lupini 371, 374–376*; macdonaldii 435, 439, 440, 444, 454, 457*; macra 477; macrocapsa 434, 441, 444, 445, 449*; macrostoma var. macrostoma 390; malvacei 477; marchali 77; meliloti 438, 441, 444, 481; microspora 391; **minutispora** 72, 74, **75**, 76*, 221; multipora 73, 74, 76*, 81, 88*, 221; multirostrata 372, 373, 386*, 388, 390, 397*; multirostrata var. macrospora 391; multirostrata var. microspora 391; multirostrata var. multirostrata 390; musae 209; nainensis 209; napobrassicae 447; **narcissi** 200, 201, 214*, **215**, 217; nebulosa 373, 386*, 394; nobilis 90; oleracea 378; oleracea var. antirrhini 384; oleracea var. helianthi-tuberosi 455; oleracea var. heraclei-lanati 465; opuli 85; opunticola 72, 74, 76*, 77; origani 471; oryzae 75; ostiolata 79; ostiolata var. brunnea 79; pedicularis 437, 439–442, 444, 463, 472, 473, 475*; **pereupyrena** 372, 373, 386*, **390**, 397*; petrakii 435, 442, 444, 458, 459, 460*; pezizoides 438, 443, 445, 450, 477*, 479, 480; phlogis 465; pigmentivora 378; pimprina 200, 201, 212*, 213; **piperis** 373, 374, 397*, **398**; piskorzii 436, 442, 444, 458, 465, 468*, 469; pomi 390; pomorum 398; pomorum var. **calorpreferens** 199, 201, 205, **207**; pomorum var. pomorum 199, 201, 205, 207; poolensis 373; poolensis var. poolensis 372–374, 376*, 384, 387; poolensis var. verbascicola 372, 374, 385, 386*; porphyrogona 483; prominens 472; prunicola 205; putaminum 73, 74, 76*, 79; pyrina 398; radicicola 79; radicis-callunae 77; richardiae 213; rostrata 470; rostrupii 438, 442, 444, 482*, 483; rubefaciens 437, 439, 443, 445, 477*, 479; rubella 483; ruttneri 435, 442, 444, 454, 457*; sahariensis 210; sanguinolenta 438, 439, 444, 482*, 483; sclerotioides 434, 439, 440, 442, 444, 450, 453*, 472; selaginellae 399; **selaginellicola** 373, 374, 397*, **399**; senecionis 371, 374, 376*, 379, 469; seseli 471; sorghina 200, 201, 211, 212*, 213, 480; **subglomerata** 199, 201, **204**, 207; subherbarum 372–374, 386*, 387*; sublingam 436, 439, 441, 445, 450, 457, 458, 467, 468*; suecica 77; sydowii 436, 439, 440, 445, 468*–470; terrestris 391; tracheiphila 432, 437, 438, 443, 445, 473, 475*; tracheiphila f. chrysanthemi 475, 480, 484; trachelospermi 204; tropica 73, 74, 76*, 86; ushtrina 390; valerianae 73, 74, 76*, 81; **vasinfecta** 438, 439, 445, 475, **484**, 485; verbascicola 387; veronicae 461; veronicicola 436, 439, 442, 445, 461, 462; viburni 85; viburnicola 73, 74, 76*, 85; violacea 378; violicola 200, 201, 216*, 217; wallneriana 479; zantedeschiae 200, 201, 213, 214*

Phomopsis chondrillae 453; enteroleuca 477; sp. 90

Phyllosticta 198, 205, 211; adianticola 379; ajacis 383; albobrunnea 379; antirrhini 384; arachidis-hypogaeae 388; brassicae 447; catalpicola 477; coffeicola 80; concava 78; crinicola 382; destructiva var. hederae 87; dictamni 90; dictamnicola 91; ferax 375; gemmipara 215; haematocycla 377; hedericola 87; hymenocallidis 215; insulana 389; lupini 375; narcissi 215; opuli 85; oryzae 75; oudemansii 215; piperis 398; prunicola 205; richardiae 213, 215; selaginellae 399; sorghina 211; tweediana 478; valerianae-tripteris f. minor 81; verbascicola 385; violae 219; violae f. violae-hirtae 217; violae f. violae-sylvaticae 217

Plenodomus aconiti 471; acutus 464, 465, 469; astragalinus 451; chenopodii 395; chondrillae 453, 477; dianthi 451; doliolum 465, 466; drobnjacensis 455; gentianae 472; helicis 479; helveticus 472; karii 472; khorasanicus 451; labiatarum 471; leonuri 459; lingam 447; lunariae 467; macrocapsa 445, 446; meliloti 450; microsporus 470; niesslii 458; origani 471; prominens 472; rabenhorstii 431, 447; rostratus 470; ruttneri 454; salicum 479; sclerotioides 450; senecionis 470; sorghii 450; sphaerosporus 472; sylvaticus 458, 459; vincetoxici 471; wallneriana 479

Pleospora scrophulariae 387

Pleurotus passeckerianus 246; pinsitus 244; rhodophyllus 244, 246

Plicaria echinospora var. autumnalis 181; endocarpoides 251; perdicina 184

Poculum petiolorum 336

Polyporus hirsutus 525; pomi 390

Pouzarella foetida 123

Psathyrella 117; § Hydrophilae 249, 251; rannochii 251; **wavereniana 249**, 250*, 251

Pseudocercospora 68; abelmoschi 68; anomala 67, 68*; azanzae 68; hibiscina 68; hibiscicannabini 68; hibisci-mutabilis 68; kydiae 69

Pseudonaevia 177; **caricina** 176*, **177**

Psilocybe semilanceata 118, 120

Pyrenochaeta gentianae 455

Pyronema 147

Ramaria 63, 109, 111, 114; aurea 114; flava 114; leiospora 109, 111; obtusissima 109, 111, 114; schildii 109, 110*, 111, 112*, 114, 115; terrea 115

Ramsbottomia 93, 96; asperior 98; crec'hqueraultii 93–95*, 96*, 97*, 98*; lamprosporoidea 93; ovalispora 94

Ramularia 68; anomala 68; areola 63; gossypii 63, 64*, 66; malvae 65, 66; malvae f. malvaealceae 66; malvae-moschatae 66; malvastri 68; sidae 66, 68; sidarum 68

Rhodophyllus caliginosus 27

Schulzeria grangei 235

Scleromitrula 428

Sclerotinia 19, 20; sclerotiorum 20; tuberosa 20; sphaeriaeforme 447

Scutellinia 129, 144, 146, 147*, 427; armatospora 129, 144; patagonica 130, 131, 135, 139, 143, 145, 147; pseudotrechispora 130–133*, 137, 142, 144, 145, 147; scutellata 129–131, 141*, 144, 146, 147; trechispora 129–131, 140, 144, 145, 147; umbrorum 130, 131, 134, 138, 143, 145, 147

Septoria brassicae 447; dictamni 91

Spathularia 427; flavida 406, 427

Sphaceloma prunicola 205

Sphaeria acuta 459, 464; corniformis 150; guepini 151, 152; lingam 447; nebulosa 394; pyrina 398; tortuosa 153; verbascicola 387

Sphaeronaema gentianae 472; indicum 391; multirostratum 390; pirottae 465; sahariense 210; senecionis 469; senecionis f. sisymbrii 467; veronnicae 461

Sphaeropsis lupini 375; nebulosa 394

Sphaerospora perplexa 94, 98

Sphaerosporella perplexa 93

Stagnospora 198, 215; crini 215; melioti 481, 482*; narcissi 215

Stagonosporopsis 215; curtisii 215

Stenella kydiae 69

Stictochorella lupini 375

Strigula urticae 464

Symphiosira areola 63

Tephrocybe atrata 251

Thelebolus crustaceus 427

Thuemenidium 425, 428

Trichoglossum 426, 429; hirsutum 406, 407, 410*, 412*, 413, 414*, 415, 423, 424*, 426, 427

Tricholoma cuneifolium 187; hygrophorus 191

Xeromphalina 50–52; § Mutabilis 51; **aspera** 34, **50**, 51*, 52; disseminata 52

Xerulaceae 52

Xylaria acuta 149; aff. feejeensis 152; badia 149; bulbosa 149, 150*, 151; corniformis 149–151; cornu-damae 149; coronata 149, 152; digitata 149, 151–153; digitata var. americana 150; divisa 152; eupiliaca 151; friesii 149, 152; guepini 149, 150*, 151*, 152; guepini var. eupiliaca 150*, 151*; hypoxylon 149; longipes 16, 149; luteostromata 150; melanaxis 152; nigripes 152; polymorpha 149; scotica 150*, 151*, 152; sp. 150*; tortuosa 149, 150*, 153.