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STUDIES IN COPRINUS III – COPRINUS SECTION VELIFORMES
Subdivision and revision of subsection Nivei emend.

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Coprinus section *Veliformes* is defined and delimited to comprise four subsections: subsection *Micacei*, subsection *Domestici*, subsection *Nivei*, and subsection *Narcotici*, subsection nov. A key to the subsections is given. Subsection *Nivei* is emended, including also most taxa of subsection *Flocculosi* Citerin. A key is given to all species known from the Netherlands, or to be expected in the Netherlands on account of records from neighbouring countries. Three new species are described, viz. *Coprinus nemoralis*, *C. idae* and *C. pseudoniveus*. A neotype has been selected for *Coprinus poliomallus* Romagn. The following species are fully described: *C. bellulus*, *C. candidatus*, *C. cardiasporus*, *C. coniophorus*, *C. cordisporus*, *C. cortinatus*, *C. cothurnatus*, *C. ephemeroides*, *C. idae*, *C. iocularis*, *C. nemoralis*, *C. niveus*, *C. pachyspermus*, *C. patouillardii*, *C. pseudoniveus*, *C. pilosotomentosus*, *C. poliomallus*, *C. pseudocortinatus*, *C. ramosocystidiatus* and *C. utrifer*.

After the first modern revision of the genus *Coprinus* by J. Lange (1915) the genus has received considerable attention in Europe in the past decades (Bender & Enderle, 1988; Citerin, 1992; Dissing & Lundqvist, 1992; Enderle & Bender, 1990; Enderle, Krieglsteiner & Bender, 1986; Krieglsteiner, Bender & Enderle, 1982; Kühner & Romagnesi, 1953; Moser, 1983; Orton & Watling, 1979; Petersen & Vesterholt, 1990). These publications provide keys and descriptions of numerous species, and form the base of the revision of *Coprinus* in the Netherlands by the first author. Many new data were gathered by him, a number of new species described, and nomenclatural and/or taxonomic confusions solved (Uljé, 1988, 1990; Uljé & Bas, 1991).

MATERIAL AND METHODS

The present paper is based on extensive studies by the first author on material collected in the Netherlands by himself and several members of the Netherlands' Mycological Society in the Netherlands, supplemented by numerous collections from the Herbarium at Leiden. Selected material from abroad has been studied to supplement the data gathered on the material of the Netherlands. Type-studies have been undertaken of *C. bellulus*, *C. candidatus*, *C. cardiasporus*, *C. idae*, *C. iocularis*, *C. luteocephalus*, *C. nemoralis*, *C. pachyspermus*, *C. patouillardii* var. *lipophilus and C. pseudoniveus*.

For methods used for the examination of macroscopical and microscopical data, see Uljé & Bas (1991: 276).

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PRESENTATION

All collections are deposited in the Rijksherbarium, Leiden (L) unless otherwise indicated. Collections indicated by the name of the collector (Uljé), but without collection number refer to material that has been observed but not conserved.

The information on the distribution in the Netherlands is based on the first author's observations and not necessarily reflected in the number of collections studied.

The enlargements of the drawings are × 2000 for the spores, × 800 for the other microscopical characters and × 1 for the basidiocarps, unless otherwise indicated.

Synonyms are in general given only when generally accepted. For practical reasons we have refrained from studying other synonyms and their types.

In the descriptions, reference is made to the colour codes of Munsell (1975) and Kornerup & Wanscher (1978), respectively indicated as Mu. and K. & W. Other abbreviations used are:

av. = average
B = breadth of the spores in front view
bas. = basidia
c. = circa
cau. = caulocystidia
ch. = cheilocystidia
diam. = diameter
L (relating to the lamellae) = number of lamellae reaching stipe
L (relating to spores) = length
l = number of short lamellae (not reaching stipe)
l.c. = loco citato
pl. = pleurocystidia
pp. = pileipellis
Q = length divided by breadth
sp. = spores
ve. = veil
W = width of the spores in side view

The terminology applied in this paper is in accordance with the glossary in Flora agaricina neerlandica, vol. 1 (Vellinga, 1988).

A notation like [80/4/2] means: 80 spores from 4 specimens from 2 collections were measured. Spore measurements are based on samples of 20 spores.

The sizes of the spores as given in the key and the descriptions relate to L × B or L × B × W. Although in literature on agarics Q generally relates to the length and the width of the spores in side view (L : W), in this publication Q relates to the length and the breadth of the spores in front view (L : B). The reason for this is that in *Coprinus* the breadth of the spores varies much more strongly than the width, because a number of species have spores that are to some degree dorsiventrally flattened. This makes a Q value relating length to breadth a taxonomically very useful character. The given width of the spores is usually based upon less numerous observations in lentiform spores than length and breadth, as this character is very difficult to observe. Only extreme values are given.

The measurements of the cystidia, when lageniform, give the length, the width of the basal part, followed by the width of the neck.

INFRAGENERIC DELIMITATION OF COPRINUS WITH REGARD TO SECTION VELIFORMES

J. Lange (1915, 1939) demonstrated the importance of the pileipellis and veil for the classification and subdivision of the genus *Coprinus*. He divided the genus into groups without giving them taxonomic status: *Comati*, for those species with filamentous veil forming felt or squamules on the young pileus, subdivided into the *Annulati* for species

with a ring, and *Exannulati* for those without a ring; *Nudi*, for those without a veil, subdivided into the *Glabri*, for species with a glabrous pileus, and *Setulosi*, for those with setules in the pileipellis, and a third group, *Farinosi*, for all taxa with a veil consisting of rounded elements. The latter is subdivided into two subgroups, viz. *Annulati* (stipe with ring; only one species: *C. ephemeroides*), and *Exannulati* (stipe without ring). The *Exannulati* comprises the group *Micacei* with only *C. micaceus*, and the *Vestiti*, which includes all taxa with powdery/mealy veil, i.e. both the species with smooth velar elements (*C. cordisporus*, *C. cortinatus*, and *C. niveus*) and the group of *C. narcoticus/stercoreus*, characterized by velar elements densely beset with small warts. Lange also included in the *Vestiti* taxa with setules, by the present authors placed in section *Pseudocoprinus*, subsection *Setulosi* (Uljé & Bas, 1991).

Kühner & Romagnesi (1953) accepted Lange's concept of the *Vestiti*. They distinguish within the *Vestiti* the group of *Coprinus niveus*, with six species and two varieties belonging to subsection *Nivei*, viz. *C. bulbillosus*, *C. coniophorus*, *C. cortinatus*, *C. niveus*, *C. patouillardii*, *C. patouillardii* var. *isabellinus*, *C. patouillardii* var. *lipophilus* and *C. poliomallus*. *Coprinus patouillardii* var. *lipophilus* is considered by us as a synonym of *C. patouillardii* and *C. patouillardii* var. *isabellinus* as being the same as *C. cordisporus* (see descriptive part); *C. ephemeroides* is treated by Kühner & Romagnesi as *C. bulbillosus* Pat. The rest of the *Vestiti* s. Kühner & Romagnesi consists of *Coprinus stercorarius* and related taxa.

Orton & Watling (1979) delimitated *Coprinus* to three sections: *Coprinus* (with filamentous veil), *Micaceus* (veil at least in part consisting of globose elements) and *Pseudocoprinus* (pileus without veil or with setules). Section *Micaceus* in their sense is subdivided into a number of stirpes. The species of the '*niveus*'-group as presented in the present paper, are accommodated in Stirps *Flocculosus* (except for *C. flocculosus* which to our opinion belongs to subsection *Domestici* conform Kühner & Romagnesi, 1953); Stirps *Cortinatus* (except *C. filiformis*, probably a synonym of *C. cortinatus* and *C. luteocephalus* that has a filamentous veil, and therefore belongs to another section) and stirps *Niveus* (except for *C. latisporus* that is not accepted as a good species; see descriptive part with *C. niveus*). Orton & Watling (l.c.) have eight species that we accept in subsection *Nivei*, viz.: *C. cordisporus*, *C. cortinatus*, *C. cothurnatus*, *C. ephemeroides*, *C. niveus*, *C. pachyspermus*, *C. patouillardii* and *C. poliomallus*. The group of *Coprinus narcoticus* is accommodated by Orton & Watling (l.c.) in stirps *Narcoticus*.

Citerin (1992) proposed a new infrageneric classification of *Coprinus*. He distinguished three subgenera: *Coprinus*, *Micaceus* en *Pseudocoprinus*, in about the same concept as the sections in Orton & Watling (1979). Within subgenus *Micacei*, five sections are recognized: section *Veliformes* (type: *C. stercoreus*); section *Domestici* (type: *C. domesticus*; section *Micacei* (type: *C. micaceus*); and section *Farinosi* 'Lange' (type: not indicated). Section *Farinosi* is subdivided into subsection *Nivei* Citerin (type: *C. niveus*) and subsection *Flocculosi* (type: *C. flocculosus*).

Although Moser (1983) keys out the groups with smooth velar elements as well as those with warty elements as clearly different groups, he uses the name *Vestiti* for both. He distinguished altogether 7 taxa in the '*niveus*'-group: *C. coniophorus*, *C. cortinatus*, *C. cothurnatus*, *C. ephemeroides*, *C. niveus*, *C. patouillardii* and *C. poliomallus*.

Patrick (1977) split *Coprinus* up into 12 sections. The taxa with globose velar elements are accommodated in section *Veliformes* Fr. ex Cooke emend. Patrick (type: *Coprinus ster-*

coreus Fr.), *Micacei* (Fr.) Penn. (type: *C. micaceus* (Bull.: Fr.) Fr.), and section *Domestici* (Singer) Patrick (type: *C. domesticus* (Bolt.: Fr.) S.F. Gray). In the concept of Patrick, the '*niveus*'-group would be part of section *Veliformes*, together with the '*stercoreus/narcoticus*'-group.

Singer (1975, 1986) distinguished four sections in *Coprinus*: section *Coprinus*, section *Micacei*, section *Cyclodei*, and section *Hemerobii*. Section *Cyclodei* is based on the group *Vestiti* sensu J. Lange, and comprises also here both the '*niveus*'- and '*stercoreus/narcoticus*'-groups.

Petersen & Vesterholt (1990) divided *Coprinus* into five groups, without taxonomic rank (A–F). Group F comprises the whole of section *Veliformes* in our sense (including the '*niveus*'-group: *C. cortinatus, C. ephemeroides, C. latisporus, C. niveus, C. patouillardii* en *C. poliomallus*).

Dissing & Lundqvist (1992) have five sections: *Coprinus, Setulosi, Vestiti, Micacei* and *Hemerobii*. Section *Vestiti* is also in this work treated in the sense of J. Lange (1915) and Kühner & Romagnesi (1953), comprising both the '*niveus*'- and '*narcoticus/stercorius*'-groups.

Reijnders (1979) has given a comprehensive survey of the developmental anatomy of *Coprinus*. He studied 27 species, which represent a good sample of the variation found in the genus with respect to pileipellis structure and development of the veil. Reijnders attempted to make a phylogenetic tree. The species round *Coprinus niveus* and *C. narcoticus* are considered to be most primitive. The pileipellis in these species is not very much differentiated and has a thick layer of spherocysts over the pileus. In *Coprinus patouillardii* and *C. cortinatus* a differentiation of the pileipellis has taken place into an epithelium, covered by spherocysts. The species round *Coprinus micaceus* and *C. domesticus* are different from the '*niveus*'-group, as, according to Reijnders (l.c.) the pileipellis is distinctly differentiated into a palisadodermium. The veil consists of both spherocysts and elongate, filamentous elements. This supported Singer (1986) who ranged the group of *Coprinus niveus* and *C. narcoticus* in section *Cyclodei*, and the group of *C. micaceus* in the separate section *Micacei*.

The present authors consider structure of the pileipellis and development of the veil to be important characters for the infrageneric delimitation as well, and accept the classification in sections proposed by Orton & Watling (1979). Within section *Veliformes*, the taxa in the group of *C. niveus/cortinatus* are considered significantly different from those in the '*narcoticus*'-group, and therefore warranting separation on subsectional level. The differences found in structure of pileipellis and veil are even greater than those between the '*micaceus*'- and '*domesticus*'-groups. On account of the structure of the veil, four subsections are accepted within section *Veliformes*: subsection *Micacei* (Fr.) stat. nov. (basionym: *Coprinus* 'group' *Micacei* Fr., Epicr.: 1838, 247); subsection *Domestici* Sing., subsection *Nivei* Citerin 1992 emend. and subsection *Narcotici* Uljé & Noordel., subsection nov. (see below).

Subsection *Nivei* Citerin is emended here by including most of the species of subsection *Flocculosi* Citerin, except for *Coprinus flocculosus*, the type-species of the subsection, and *C. luteocephalus*. *Coprinus utrifer* is also included here in subsection *Nivei*, although the veil consists not only of globose elements, but also of hypha-like structures. Because of this mixed nature of the veil, many authors placed *C. utrifer* in other sections. Kühner

& Romagnesi (1953) place it in section *Impexi*, Orton & Watling (1979) in a stirps of its own, stirps *Utrifer* in section *Coprinus*; Moser (1983) in section *Coprinus*, and Citerin (1992) in subgenus *Coprinus* section *Picaceus*. But the present authors prefer to place it in subsection *Nivei* because of the great similarity with the structure of the veil of *Coprinus niveus*.

KEY TO THE SECTIONS AND SUBSECTIONS

1a. Pileus without veil, smooth or with setules and/or setae .... sect. *Pseudocoprinus*
b. Pileus with veil, without setules 2
2a. Veil consisting of elongate elements only ..... sect. *Coprinus*
b. Veil at least partly consisting of (sub)globose elements (sect. *Veliformes*) 3
3a. Fruit-bodies medium-sized, somewhat fleshy; stipe 3–10 mm thick; pileus usually brown, never pure white; veil present in form of scattered, granulose floccules or small flocculose scales, often (partly) thick-walled and brown-pigmented under microscope; pileus conical or campanulate, long closed, only tardily expanding, never applanate when old, not grooved, without veil at margin when young 4
b. Fruit-bodies small, very thin-fleshed; stipe 0.5–3 mm thick; pileus white to grey; veil mealy-powdery, entirely covering the pileus, at centre often woolly-floccose, white, sometimes pale pinkish brown, yellowish or grey, thin-walled, not pigmented or rarely thick-walled, pale yellow-brown in centre of pileus; pileus expanding to become applanate, usually radially grooved and splitting, when young covered in woolly veil at margin 5
4a. Veil present in scattered, granulose flocks which soon disappear, microscopically existing of a layer of globose, thin-walled cells, slightly colouring pink or lilaceous in KOH or ammonia ..... subsect. *Micacei*
b. Veil breaking up in small, more persistent flocculose scales, microscopically existing of chains of fusiform, ellipsoid to globose, in part usually thick-walled cells not colouring in KOH or ammonia ..... subsect. *Domestici*
5a. Elements of veil with persistent, nipple-shaped warts that do not dissolve in HCl; spores usually with distinct, rarely indistinct or lacking episporium ..... subsect. *Narcotici*
b. Elements of veil smooth or with crystals that easily dissolve in HCl; spores without episporium ..... subsect. *Nivei*

DESCRIPTIVE PART

Coprinus section **Veliformes** (Fr.) Penn. in Kauffm.

Basidiocarps very small to medium-sized; expanded pileus 0.1–50 mm. Pileus with veil made up of – at least in part – (sub)globose cells mixed or not with elongate, hyphal elements. Pileipellis made up of radial chains of (sub)globose or fusiform cells, often covered by a very thin layer of narrow hyphae. Stipe smooth and/or covered with very small velar flocks or – in some species – covered with lageniform or (sub)globose caulocystidia.

Subsection **Narcotici** Uljé & Noordel., *subsect. nov.*

Species ad sectionem Veliformes pertinentes; velum verrucis in HCl persistentibus praeditum; sporae frequenter cum episporio distincto. Species typica: *Coprinus narcoticus* (Batsch: Fr.) Fr.

Elements of veil with persistent, nipple-shaped warts that do not dissolve in HCl; spores usually with distinct, rarely indistinct or lacking episporium. Type species: *Coprinus narcoticus* (Batsch: Fr.) Fr.

Selected literature. Kits van Waveren, Persoonia 5 (1968) 131–176; Orton & Watling, Br. Fung. Fl. 2 (1979) 69–81.

Subsection **Nivei** Citerin emend. Uljé & Noordel.

Type species: *Coprinus niveus* (Pers.: Fr.) Fr.

General characteristics

Basidiocarps white, cream-coloured, pinkish cream or grey with mealy-powdery veil, usually forming a cortina at margin of the pileus in young specimens; veil smooth or covered with crystals or granules that dissolve in HCl; spores without episporium; smell indistinct.

Macroscopical characters

The species in section *Nivei* can be recognized by the mealy-powdery veil that covers the entire pileus in young specimens, and can easily be removed. Expanded pilei are always distinctly grooved up to centre, while the veil remains visible between the grooves, unless washed off by rain. This is in contrast with the species in subsections *Micacei* and *Domestici* which also have a veil consisting of globose elements, but there the veil breaks apart in small floccose squamules, showing the pileal surface beneath, which is never distinctly grooved, and usually of a brown colour. The veil in most species of subsection *Nivei* is white, often tinged cream-coloured or ochraceous at centre, or even more intensely coloured in dry conditions. The pileus is white with a few exceptions: in *Coprinus poliomallus* the pilei are pale grey to mouse-grey in primordia, then paler coloured; *C. coniophorus* is very dark grey, often with a weak green tinge in primordia, and stays dark at centre in mature specimens, while the marginal zone becomes white. *Coprinus patouillardii*, *C. cordisporus* and *C. cardiasporus* are pale pinkish brown in young stadia, retaining this colour at centre of the pileus when mature. *Coprinus ephemeroides* is pinkish brown, cream-coloured or yellowish in a young stage.

Size of fruit-bodies may vary strongly from one collection to another, especially in species growing on dung. *Coprinus niveus* for example, usually is a medium-sized species with closed pilei up to 25 × 15 mm, but there are collections with very minute basidiocarps, only a few mm that are in all respects completely similar, except may be in slightly smaller spores.

Lamellae are free, except in *C. coniophorus*, which has narrowly adnate lamellae, and usually narrower than 5 mm. The colour is white in young specimens, becoming grey to (pinkish) brown or black. The number of lamellae reaching the stipe varies from 6 to 38, the lamellulae range from 0 to 5.

The stipe varies from 10–130 mm in length and 0.1–5 mm in width, is usually white and covered with floccose veil which becomes denser towards base. In the group of *Copri-*

nus patouillardii the veil often forms a small volva-like structure just above the base of the stipe.

Spore-prints are not easy to obtain, if not impossible in the very small taxa, and therefore not taken into consideration in the present revision. Probably the colour of the spore-print is more or less similar in all taxa.

Microscopical characters

Spores vary from ellipsoid, rounded-angular, limoniform, cordiform, amygdaliform or weakly hexagonal in outline; *Coprinus iocularis* has spores with two blunt knobs at each side. Size varies very much from one species to another, ranging from 6–8 µm long in some species to 13–19 µm in *C. niveus*. Also within one species the variability in size of the spores may be considerable. Especially dung-inhabiting species show great differences (see discussion following the description of *Coprinus niveus*). Within one species the size of the spores also may vary considerable per collection.

Basidia are 2-spored in *Coprinus bellulus, C. pachyspermus*, and sometimes also in *C. cordisporus*; all other taxa have 4-spored basidia. The number of sterile elements around the basidia (pseudoparaphyses) ranges from 3–7(–8).

Pleurocystidia, if present, are vesiculose, utriform, broadly cylindrical, ellipsoid or subglobose.

Cheilocystidia vary from vesiculose, utriform, clavate to ellipsoid or globose. Some taxa have lageniform cheilocystidia mixed with other types. Cheilocystidia are absent in *Coprinus cortinatus* and *C. bellulus*, but in these taxa elements of the veil may adhere to the lamellar edge, and cause confusion.

Pileipellis made up of ventricose, ellipsoid, subglobose or fusiform elements (Figs. 1b, 11), covered with a suprapellis of up to 7 µm wide hyphae, consisting of oblong to ventricose elements.

Veil covering the pileipellis at centre of pileus consists of (sub)globose elements which are usually about 50 µm in diam. In *Coprinus niveus, C. pachyspermus*, and *C. cothurnatus* the elements may reach 80(–100) µm diam. In these taxa, as well as in *C. pseudoniveus* and *C. utrifer*, these elements often have scattered, coarsely warty protuberances. The surface of the velar elements may be smooth or covered in granules or crystals that easily dissolve in HCl. The velar elements are connected with branched hyphae which are smooth in the complex of *Coprinus cortinatus* or diverticulate in the group of *C. niveus*. Towards the margin of the pileus and on the surface of the stipe the velar elements are more hypha-like.

Clamp-connections may be present or absent. In the complex of *Coprinus niveus* clamps are not easy to find or not always present. This is reflected in the literature on the group. In his first, unofficially published revision on this group, Uljé (1990) recorded clamp-connections for *Coprinus niveus, C. cothurnatus, C. pachyspermus*, and *C. pseudoniveus*. Orton & Watling (1979) indicated the presence of clamps only for *Coprinus niveus* and stated that clamps were either not studied, or not found in all other taxa. Enderle, Krieglsteiner, and Bender (1986) do not mention clamp-connections at all in their description of *Coprinus niveus*, but in the accompanying figures a clamp is clearly indicated at the base of a cheilocystidium. Sometimes the hyphae elements slightly to distinctly overlap at the septa, giving the impression of a clamp-connection. We call this pseudo-clamps.

KEY TO THE SPECIESOF COPRINUS SUBSECTION NIVEI IN EUROPE

1a. Av. length of spores > 12 µm 2
b. Av. length of spores < 12 µm 4
2a. Basidia 4-spored; pileus white at first 3
b. Basidia 2-spored; pileus grey or cream-grey, sometimes white at first
4. *C. pachyspermus*
3a. Spores 12–19 × 11–15.5 µm; spores ± limoniform; pleurocystidia present
1. *C. niveus*
b. Spores 10–15 × 6.5–8.5 µm; spores ± 6-angular (hexagonal); pleurocystidia absent or very sparse . . . . . 3. *C. cothurnatus*
4a. Spores oval or ellipsoid, sometimes slightly cylindrical. 5
b. Spores differently shaped. 15
5a. Basidia 4-spored. 6
b. Basidia 2-spored . . . . . 11. *C. bellulus*
6a. Cystidia present 7
b. Cystidia absent . . . . . 10. *C. cortinatus*
7a. Both cheilo- and pleurocystidia present 8
b. Only cheilocystidia present 13
8a. Pileus very small, expanded < 6 mm; average length of spores < 9 µm. 9
b. Pileus larger, 5–25 mm when expanded or av. length of spores > 9 µm. 11
9a. In lawns, terrestrial, not on dung, young pileus white; spores 7–9.5 × 5–6.5 µm
8. *C. idae*
b. On dung; pileus grey or white and then breadth of spores < 5 µm. 10
10a. Young pileus grey; spores 7.5–9.5 × 5–6 µm . . . . . 6. *C. poliomallus*
b. Young pileus white; spores 6–7.5(–8) × 3.5–4.5(–5) µm . 7. *C. pseudocortinatus*
11a. Expanded pileus up to 25 mm; average length of spores < 9 µm; on dung
5. *C. utrifer*
b. Expanded pileus 5–12 mm; average length of spores > 9 µm 12
12a. On grasses. Cheilocystidia 20–45 × 8–13 µm . . . . . 17. *C. pilosotomentosus*
b. On wood. Cheilocystidia 50–80 × 20–35 µm . . . . . 20. *C. nemoralis*
13a. Cheilocystidia utriform . . . . . 9. *C. candidatus*
b. Cheilocystidia (sub)globose or ellipsoid 14
14a. Caulocystidia present, with finger-like diverculations at apex; cheilocystidia (sub)globose to ellipsoid, partly also diverculate . . . . . 18. *C. ramosocystidiatus*
b. Caulocystidia absent, cheilocystidia without diverticulations in apical part: see discussion under *C. cortinatus*.
15a. Spores with rounded angles (4–5-angular), 8–10.5 × 8–10 µm; pleurocystidia present 16
b. Spores differently shaped; breadth of spores < 8 µm or spores limoniform; pleurocystidia present or absent 18
16a. Ring present . . . . . 15. *C. ephemeroides*
b Ring absent 17
17a. Cheilocystidia in part lageniform. On dung . . . . . 12. *C. cordisporus*
b. No lageniform cheilocystidia present. On vegetable debris . . . . 13. *C. patouillardii*

18a. Pleurocystidia present 19
b. Pleurocystidia absent 20
19a. Breadth of spores 5–6 µm, heart- or pear-shaped . . . . . 14. *C. cardiasporus*
b. Breadth of spores 7.5–11.5 µm, limoniform . . . . . 2. *C. pseudoniveus*
20a. Veil white, often cream-coloured or slightly ochraceous at centre of pileus; spores ± 6-angular in frontal view, c. 5–6 µm broad; with two bumps at each side 16. *C. iocularis*
b. Veil at centre of pileus dark grey, usually with greenish hue; spores narrowly ovoid or amygdaliform, c. 4–5 µm broad . . . . . 19. *C. coniophorus*

1. **Coprinus niveus** (Pers.: Fr.) Fr. — Figs. 1a, 1b

Agaricus niveus Pers., Syn. meth. Fung. (1801) 400. — *Agaricus niveus* Pers: Fr., Syst., mycol. 1 (1821) 311. — *Coprinus niveus* (Pers.: Fr.) Fr., Epicr. (1838) 246.
Coprinus latisporus P.D. Orton, Notes R. bot. Gdn Edinb. 32 (1972) 140.
Selected literature. Enderle, Krieglsteiner & Bender, Z. Mykol. 52 (1986) 121.
Selected icon. R. Fillion, *Coprinus niveus*. Bull. Féd. mycol. Dauphiné-Savoie 122 (1991) 9. — M. Tabarés, Bolets de Catalunya V (1986) pl. 215.

Closed pileus ellipsoid, cylindrical-ellipsoid or subglobose, up to 25 mm high and 15 mm wide, completely covered with white, powdery veil, centre of pileus often cream-coloured to pale ochraceous; veil at margin, particularly in early stages, somewhat more hairy-floccose; expanded pileus up to 40 mm wide, conical or convex, finally applanate with slightly deflexed margin. Lamellae, L = 24–38, l = 1–3(–5), free, white at first, then grey to black. Stipe up to 100 × 4 mm, attenuate upwards, white, towards base up to 6 mm wide, and often brownish with white velar flocks. Smell absent. Spore print very dark chocolate brown, almost black.

Spores [180,9,7] 12.2–19.0 × 10.8–15.6 × 7.5–9 µm, Q = 1.05–1.40, av. Q = 1.10–1.30, av. L = 14.5–17.3, av. B = 11.9–13.9 µm, lentiform, limoniform in frontal view, ellipsoid in side view, dark red-brown, with central to slightly eccentric germ pore. Basidia 25–40 × 12–16 µm, 4-spored, surrounded by 5–7(–8) pseudoparaphyses. Pleurocystidia 50–150 × 25–60 µm, vesiculose, ellipsoid, or subcylindric. Cheilocystidia 30–80 × 15–50 µm, similar to pleurocystidia. Veil made up of up to 100 µm wide, (sub)globose elements. Clamp-connections sparse, probably just pseudoclamps.

Habitat & distribution. Solitary or a few together. On dung of horse and cow. Rather common.

Collections examined. NETHERLANDS: prov. Utrecht, Bunnik, 12 Oct. 1947, *O.F. Uffelie*; prov. Zuid-Holland, Oegstgeest, Poelgeest, 22 Aug. 1944, *R.A. Maas Geesteranus 3055*; 7 Sept. 1944, *A.C. Perdeck*; Leiden, 6 July 1959, *C. Bas 1731*; Grevelingen, 17 Nov. 1977, *C. Bas 7291*; Wassenaar, Meijendel, 28 Sept. 1991, *C.B. Uljé 1183*. — SWITZERLAND: canton Graubünden, Silvaplana, 25 Aug. 1976, *C. Bas 7016*.

Coprinus niveus can be easily recognized by the very large spores which are limoniform in frontal view and ellipsoid in side-view, borne on 4-spored basidia. Generally, *Coprinus niveus* has medium-sized basidiocarps, but in collection *Uljé 1183* they are only a few mm. In this collection the spores are also somewhat smaller than in normal *C. niveus*, viz. 12.2–16.0 × 10.8–13.0 µm, Q = 1.15–1.40, av. Q = 1.25, av. L = 14.6, av. B = 12.0 µm. In the description given above, these measurements are included.

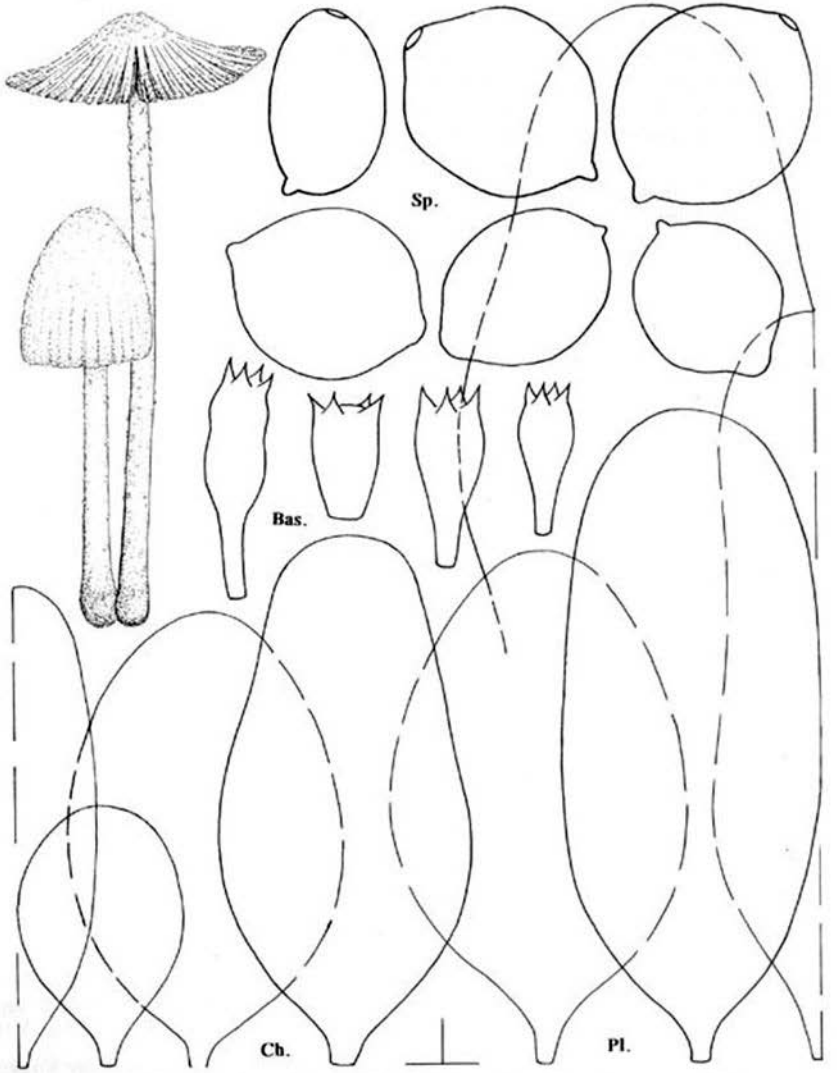

Fig. 1a. *Coprinus niveus* (Pers.: Fr.) Fr. All figures from *Maas Geesteranus 3055*.

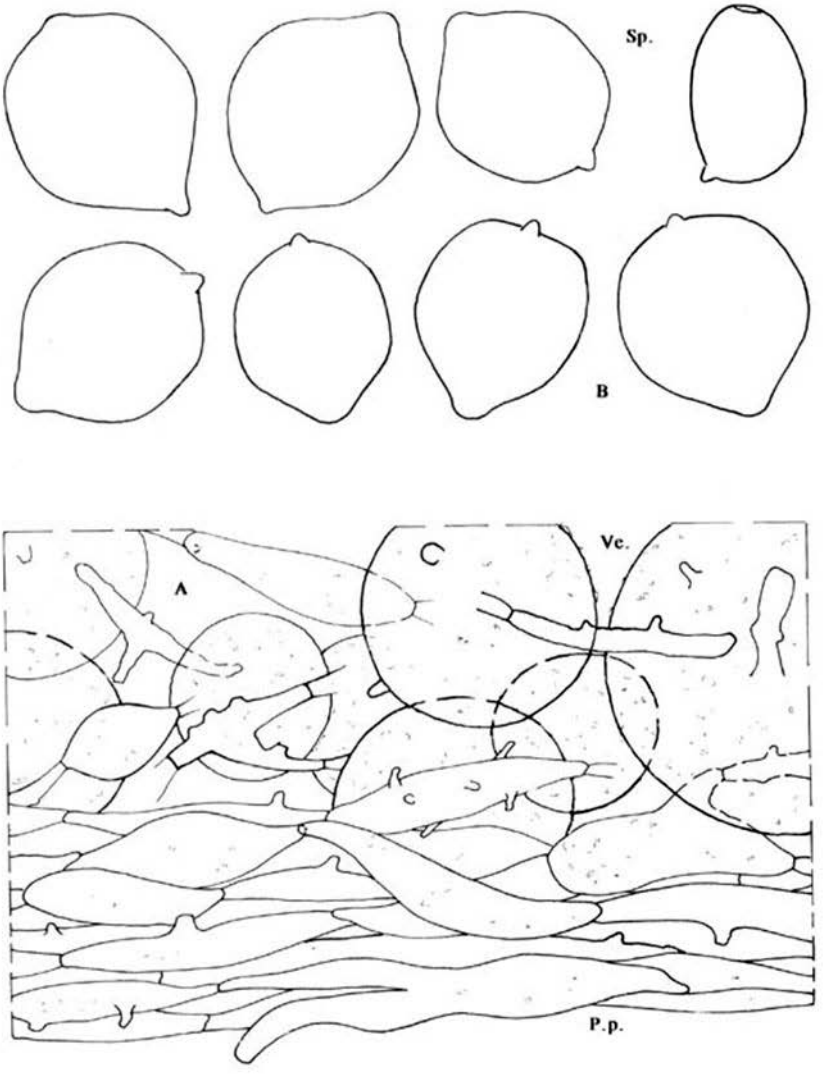

Fig. 1b. A. Pileipellis in the '*niveus*'-complex' (of *Coprinus cothurnatus* Godey, from *Uljé 1005*); B. spores of *Coprinus latisporus* (from type).

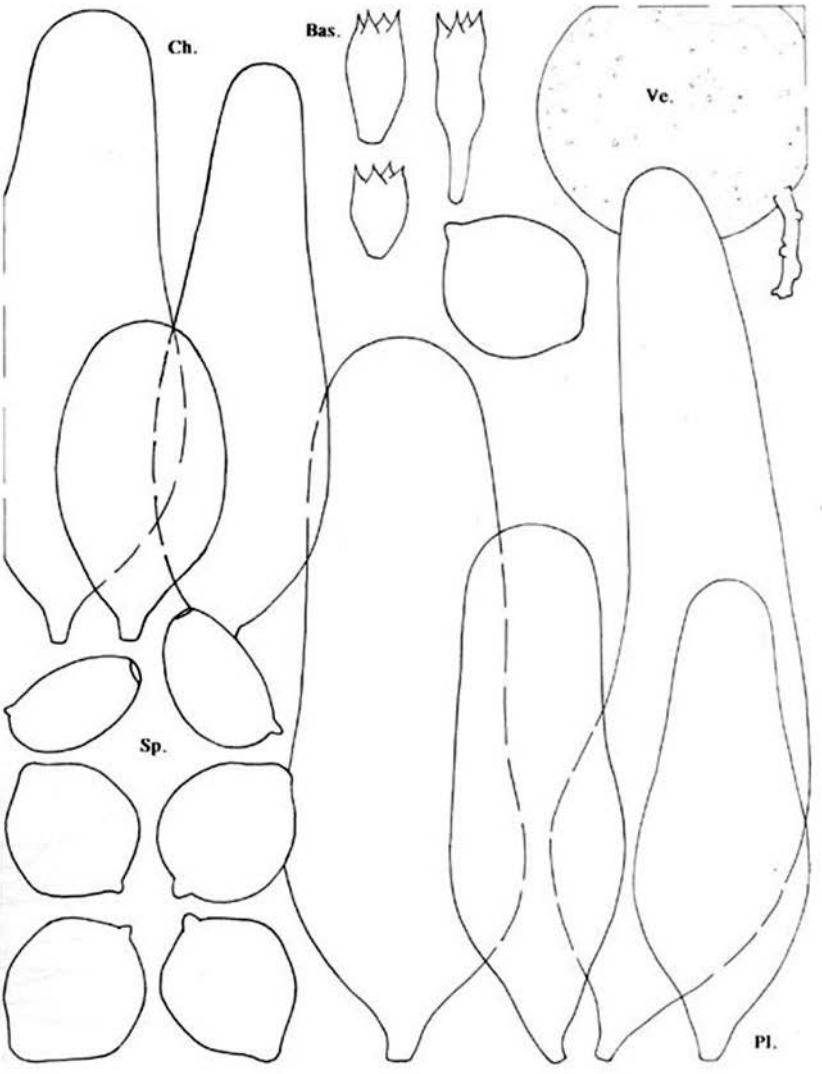

Fig. 2. *Coprinus pseudoniveus* Bender & Uljé. All figures from coll. *Veldre*.

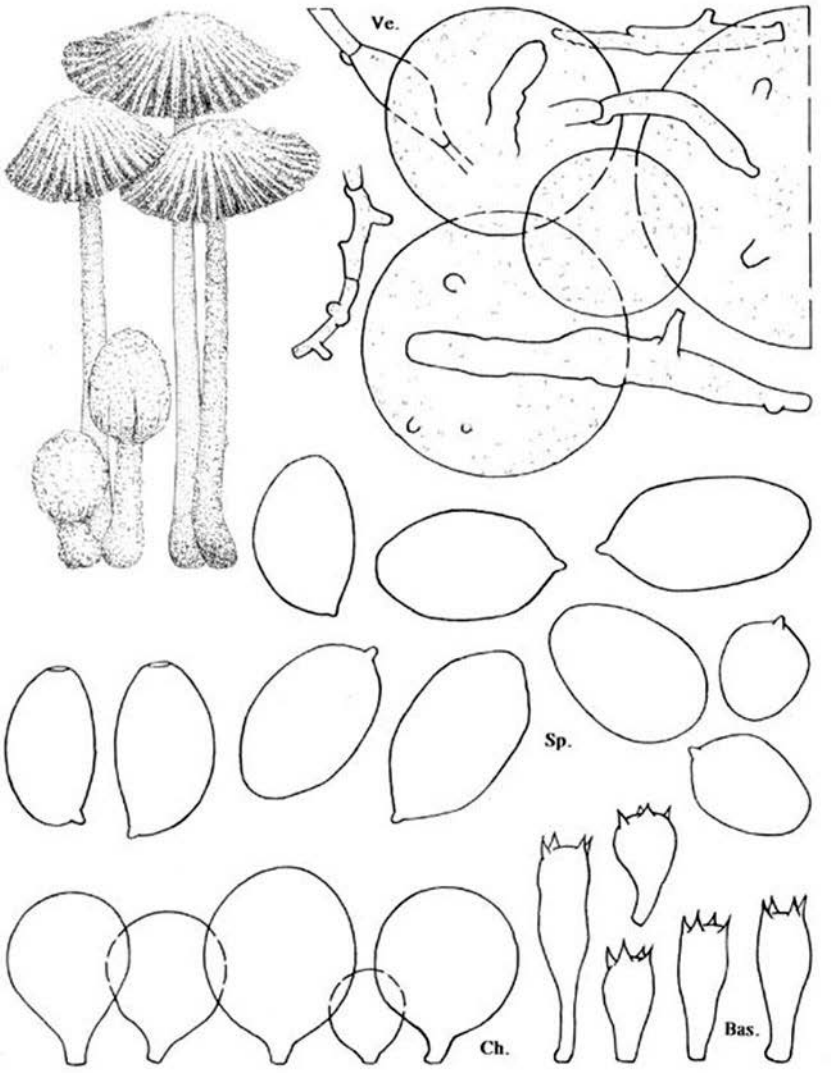

Fig. 3. *Coprinus cothurnatus* Godey apud Gillet. All figures from *Uljé 1005*.

Coprinus latisporus was characterized by Orton (1972: 160) in the original description as follows: "It could be mistaken for a small *C. niveus*, but differs from that species in its differently shaped spores, which are less elongate in side-view and more rounded and less regular in face-view, and the smaller fruit-body with less copious veil." He also depicted a small specimen. The type material consists of one, small, probably still very young basidiocarp with spores 13.0–15.4 × 11.2–14.5 µm, which appear for the greater part immature and very pale to dark brown; truly ripe, i.e. black, spores have not been found. The difference in shape, as noted by Orton, was not found (Fig. 1b) but only a slight difference in length, which can be explained by the still immature state. Furthermore, small specimens of *Coprinus niveus* may occur, as pointed out above, and the difference in veil covering does not appear to be a significant difference to us. It is likely that Orton described a small, still immature specimen of *C. niveus*, and we therefore prefer to consider *C. latisporus* a synonym.

2. **Coprinus pseudoniveus** Bender & Uljé, *spec. nov.* — Fig. 2

Pileus primo ellipsoideus, demum cylindrico-ellipsoideus, 12–20 mm altus, 6–12 mm latus, dein explanatus, 20–40 mm latus, primo pruinosus ad marginem flocculosus cum velo albido-cinerascente. Lamellae liberae, L = 22–36, l = 1–3(–5), ex albo cinerascentes vel nigricantes. Stipes usque ad 50–120 × 3–5 mm, versus basim incrassatus, albidus vel cinereus, albido floccosus. Sporae [60,3,3] 9.2–12.3 × 7.5–11.3 × 6.2–7.8 µm, Q = 1.05–1.35, in antice limoniformes, facie ellipsoideae, rufo-brunneae, poro germinativo centrico vel excentrico instructae. Basidia 15–40 × 9–13 µm, tetrasporigera. Pseudoparaphyses 4–6(–7). Pleurocystidia 75–180 × 25–50 µm, utriformia, vesiculosa vel subcylindracea. Cheilocystidia 40–65 × 20–27 µm, utriformia, vesiculosa, ellipsoidea vel subcylindracea. Velum e elementis (sub)globosis, glabris, usque ad 75 µm diam. constans. Fibulae absentes vel inconstantes vel pseudofibulae. In stercore vaccino vel sarmenta.

Holotypus: Netherlands, prov. Utrecht: Baarn, 6 Febr. 1973, *J. Daams 73-26* (L).

Closed pileus ellipsoid, then cylindrical ellipsoid, 12–20 mm high and 6–12 mm wide, completely covered with white, later greyish, powdery veil; veil at margin, particularly in early stages somewhat more hairy-floccose; expanded pileus 20–40 mm wide, at first conical, later expanded, undulated with split, reflexed margin. Lamellae, L = 22–36, l = 1–3(–5), free, white at first then grey to black with pale edge. Stipe up to 50–120 × 3–5 mm, attenuate upwards, white to greyish, with white velar flocks, at base somewhat swollen, densely white flocculose. Smell somewhat yeast-like (coll. *Bender*); of coconut, cinnamon, fruit-drop, holy grass, *Anthoxanthum odoratum* (coll. *Veldre*). Spore print black with violet hue.

Spores [60,3,3] 9.2–12.3 × 7.5–11.3 × 6.2–7.8 µm, Q = 1.05–1.35, av. Q = 1.15–1.20; av. L = 10.6–11.5, av. B = 8.8–9.9 µm, limoniform in frontal view, ellipsoid in side view, dark red-brown, with central to slightly eccentric germ pore. Basidia 15–40 × 9–13 µm, 4-spored, surrounded by 4–6(–7) pseudoparaphyses. Pleurocystidia 75–180 × 25–50 µm, utriform, vesiculose or subcylindric. Cheilocystidia 40–65 × 20–27 µm, utriform, vesiculose, ellipsoid or subcylindric. Veil made up of up to 75 µm wide, (sub)-globose elements. Clamp-connections sparse, difficult to find. Probably just pseudoclamps.

Habitat & distribution. Solitary or a few together. On cow-dung and compost heaps. Rare in the Netherlands.

Collections examined. NETHERLANDS: prov. Utrecht, Baarn, 6 Febr. 1973, *J. Daams 73-26 (holotype; L).* — AUSTRIA: Klopeiner See, 2 Sept. 1985, *H. Bender* (Herb. Bender). — ESTONIA: Valgamaa, Piiri, 5 Sept. 1985, *S. Veldre.*

The macroscopical description of *Coprinus pseudoniveus* is based upon the collection of Bender. Both this collection and that of Veldre, had a striking smell according to their collectors, although their descriptions of this smell are rather different. *Coprinus* species with a striking smell are rare, except for the taxa in subsection *Narcotici*. *Coprinus pseudoniveus*, however, belongs to the *C. niveus* complex, because of the limoniform spores and structure of the veil. It has distinctly smaller spores and narrower cystidia than *C. niveus*. *Coprinus cothurnatus* has narrower, more hexagonal spores, and is usually devoid of pleurocystidia; *C. pachyspermus* has 2-spored basidia.

3. **Coprinus cothurnatus** Godey apud Gillet — Fig. 3

Coprinus cothurnatus Godey apud Gillet, Hyménomycètes Fr. (1874) 605.
Selected literature. G.J. Krieglsteiner, H. Bender & M. Enderle, Studies zur Gattung Coprinus I, Z. Mykol. 48 (1982) 77.
Selected icon. B. Cetto, I funghi dal vero, Part 5 (ed. 2) (1989) no. 1719.

Closed pileus ellipsoid, cylindrical ellipsoid or subglobose, up to 20 mm high and 13 mm wide, completely covered with white, powdery veil; veil at margin, particularly in early stages somewhat more hairy-floccose; expanded pileus up to 35 mm wide, conical or convex, finally applanate with reflexed margin. Lamellae, L = 22–30, l = 0–3, free to narrowly adnate, white at first, then grey to black. Stipe up to 100 × 3–5 mm, slightly attenuate upwards, white, flocculose from veil; at base up to 6 mm wide, often brownish, with white velar flocks. Smell absent. Spore print black with violet hue.

Spores [40,2,2] 9.6–15.4 × 6.5–8.7 × 7–7.5 µm, Q = 1.45–1.80, av. Q = 1.50–1.55, av. L = 11.9–12.3, av. B = 7.8 µm, more or less 6-angular in frontal view, ellipsoid in side view, dark red-brown, with central to slightly eccentric germ pore. Basidia 18–50 × 9–13 µm, 4-spored, surrounded by 3–5 pseudoparaphyses. Pleurocystidia sparse or absent, 50–150 × 25–60 µm, vesiculose, ellipsoid or subcylindric. Cheilocystidia 30–80 × 15–50 µm, similar to pleurocystidia. Veil made up of up to 100 µm wide, (sub)globose elements. Clamp-connections sparse, probably just pseudoclamps.

Habitat & distribution. Solitary or a few together. On dung of horse and cow. Rather common.

Collections examined. NETHERLANDS: prov. Zuid-Holland, Hazerswoude, 31 Oct. 1988, *C.B. Uljé 1005*; prov. Zeeland, Goes, 25 Sept. 1987, *W.D.J. Kuijs.*

Coprinus cothurnatus occupies an isolated position in subsection *Nivei*, because of the hexagonal spores which are also distinctly narrower than in the other species of this complex.

In collection *C.B. Uljé 1005* a few 1-, 2- and 3-spored basidia have been found.

4. **Coprinus pachyspermus** P.D. Orton — Fig. 4

Coprinus pachyspermus P.D. Orton, Notes R. bot. Gdn Edinb. 32 (1972) 144.
Selected literature. Orton & Watling, Coprinaceae, part. 1, *Coprinus*. Brit. Fung. Fl. 2 (1979) 65.

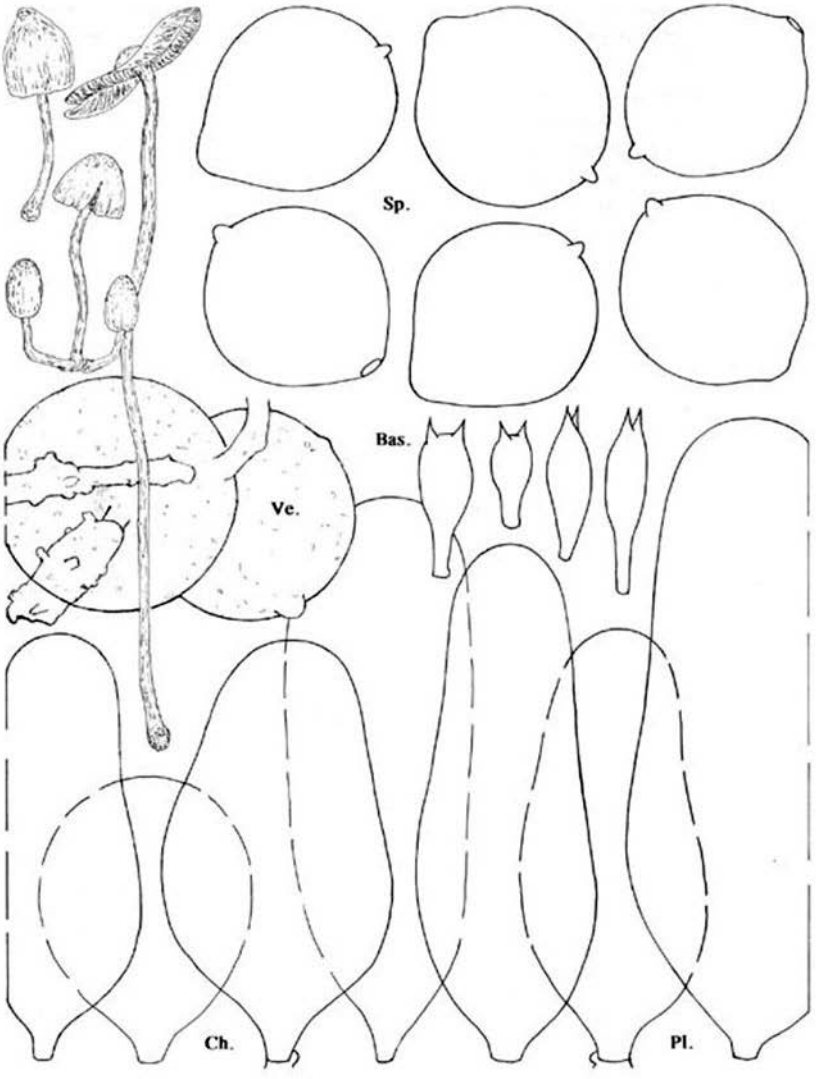

Fig. 4. *Coprinus pachyspermus* P.D. Orton. All figures from *Orton 3555* (type).

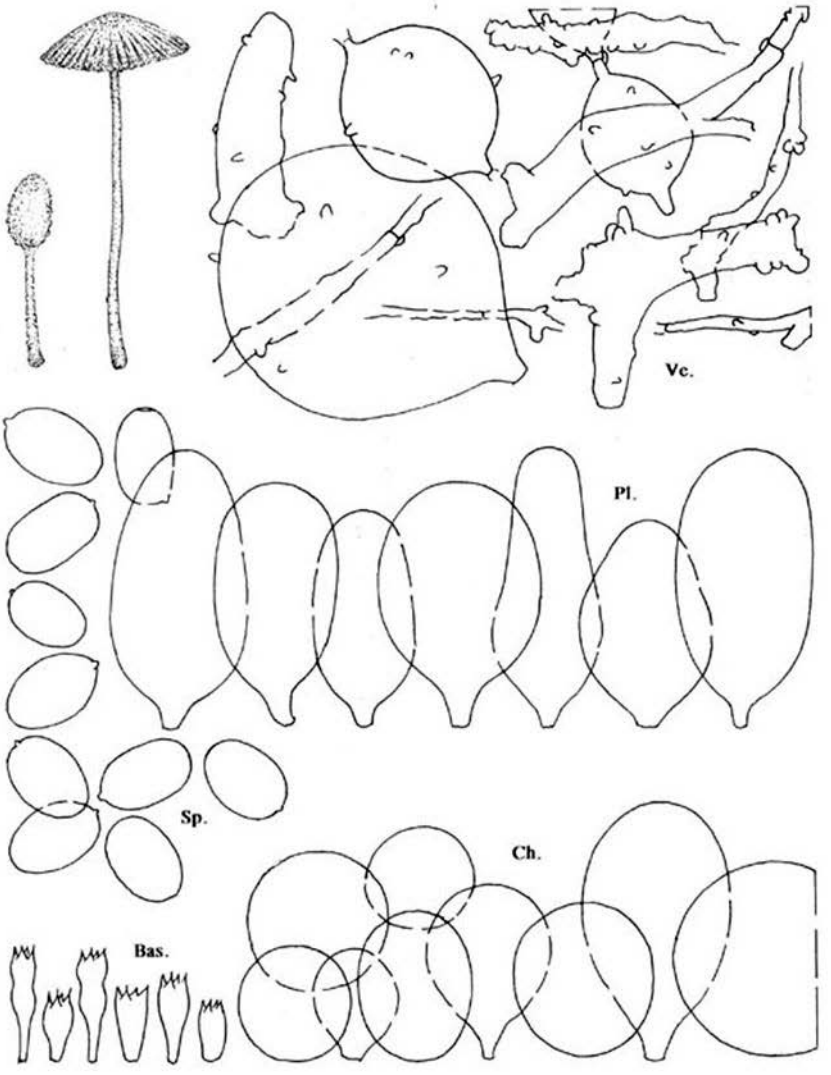

Fig. 5. *Coprinus utrifer* [Joss. ex] Watl. All figures from coll. *Veldre*.

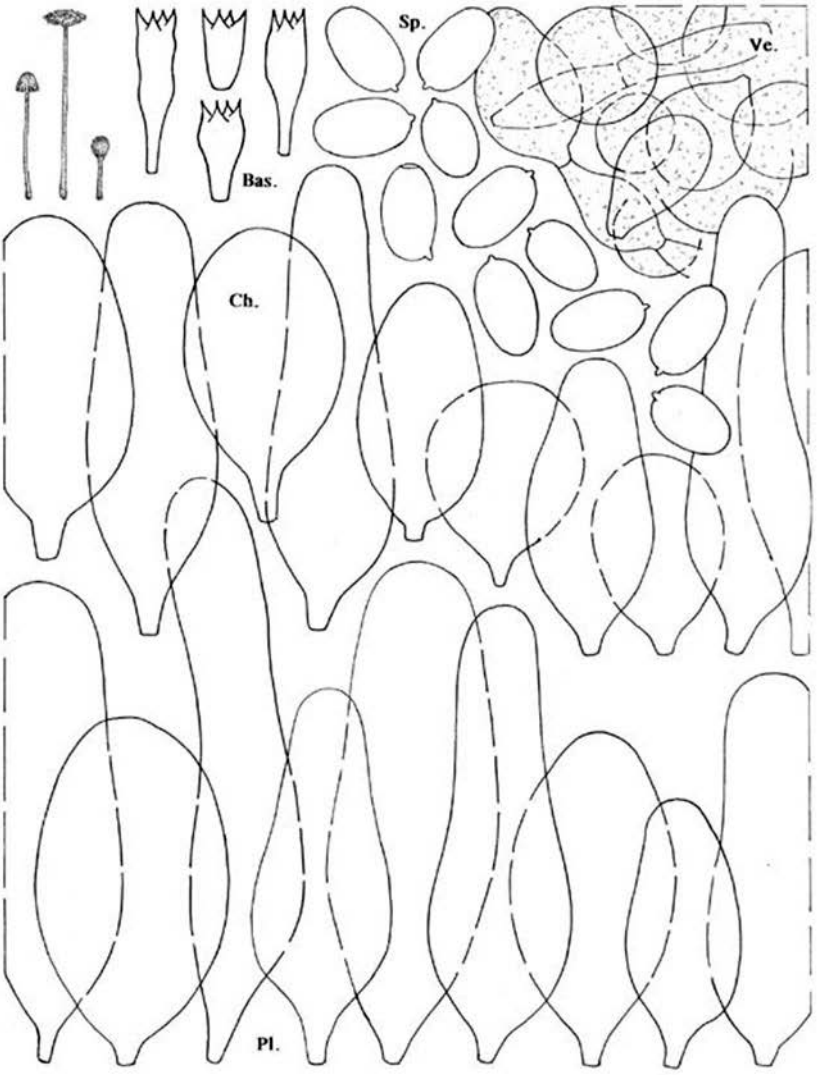

Fig. 6. *Coprinus poliomallus* Romagn. All figures from neotype (*Uljé 1181*).

Closed pileus subglobose to ellipsoid, up to 30 mm high and 18 mm wide, completely covered with grey or creamy-grey, powdery, mealy-floccose, often somewhat pointed veil, at centre of pileus sometimes rather dark sepia-brown at the tips of the scales; expanded pileus up to 40 mm wide, conical or convex, finally applanate with slightly deflexed margin. Lamellae, L = 24–38, l = 1–3(–5), free, white at first then grey to black. Stipe up to 110 × 4 mm, attenuate upwards, whitish; at base up to 6 mm wide, often brownish, with white velar flocks. Smell absent. Spore print fuscous black.

Spores [20,1,1] 13.4–16.7 × 12.7–15.4 × c. 8.5–10 µm, Q = 1.05–1.20, av. Q = 1.10, av. L = 15.1, av. B = 13.7 µm, lentiform, limoniform in frontal view, ellipsoid in side view, dark red-brown, with slightly to strongly eccentric germ pore. Basidia 18–38 × 9–13 µm, 2-spored, surrounded by 4–6 pseudoparaphyses. Pleurocystidia 80–160 × 30–60 µm, vesiculose, utriform, ellipsoid or subcylindric. Cheilocystidia 30–90 × 20–50 µm, similar to pleurocystidia. Veil made up of up to 90 µm wide, (sub)globose elements. Clamp-connections sparse, probably just pseudoclamps.

Habitat & distribution. Solitary or a few together. On old cow dung. Known only from the type locality.

Collection examined. UNITED KINGDOM: Inverness-shire, Nettle Bridge, 28 Aug. 1969, *Orton 3555* (holotype, E).

The macroscopical description is based on the original diagnosis by Orton (l.c.); the microscopical data are based on our study of the holotype.

According to the description by Orton (1972), *Coprinus pachyspermus* can be readily recognised by the 2-spored basidia and the large lentiform spores. Although the pileus is described as grey or cream grey (Orton, l.c.; Orton & Watling, 1979), Orton & Watling in their key (1979: 16) characterized the species as 'white or grey to clay-buff scaly.' If the species exists also truly white, the only difference between *C. pachyspermus* and *C. niveus* is in the 2-spored basidia.

Orton (l.c.) did not mention the clamp-connections. We found some in the type material, but like in the other species in the *'C. niveus'*-complex, they are difficult to find and not abundant.

5. **Coprinus utrifer** [Joss. ex] Watl. — Fig. 5

Coprinus utrifer Joss., Bull. Soc. mycol. Fr. 64 (1948) 26 (invalid, no Latin description). — *Coprinus utrifer* Joss. ex Watl., Notes R. bot. Gdn Edinb. 31 (1972) 362.

Closed pileus ellipsoid or cylindrical ellipsoid, up to 13 mm high and 3–8 mm wide, completely covered with creamy-white, later pale greyish-ochre, powdery veil (according to the description of Watling (l.c.) the pileus is covered throughout with pale grey scurfy sheath-like veil with a faint flush of ochraceous; finally the pileus is evenly sepia with remnants of the veil in irregular patches flushed with ochraceous); veil at margin, particularly in early stages somewhat more hairy-floccose; expanded pileus 10–25 mm wide, first conical or campanulate, later applanate with reflexed margin. Lamellae free, white at first then grey (violaceous grey according to Watling) then black with pale edge. Stipe up to 50 × 1–2 mm, attenuate upwards, white to greyish, with small velar flocks, at base somewhat swollen, white hairy-flocculose. Smell absent. Spore print violaceous black.

Spores [20,1,1] 6.0–7.7 × 4.2–5.0 × 4.1–4.5 µm, Q = 1.35–1.70, av. Q = 1.50; av. L = 7.0, av. B = 4.7 µm, cylindrical-ellipsoid in frontal view, ellipsoid in side-view, red-brown, with central, truncate germ pore, difficult to see. Basidia 10–22 × 6–8 µm, 4-spored, surrounded by 3–5 pseudoparaphyses. Pleurocystidia 30–55 × 15–35 µm, ellipsoid, utriform, vesiculose or subcylindric. Cheilocystidia 20–50 × 15–35 µm, ellipsoid or (sub)globose. Veil made up of (sub)globose elements, 25–60 µm in diam., mixed with fusiform or elongate, 2–15 µm wide elements. Clamp-connections present.

Habitat & distribution. Solitary or a few together. On dung of sheep, cow and horse. Not known from the Netherlands.

Collection examined. ESTONIA: 19 July 1988, on horse dung, *S. Veldre.*

Coprinus utrifer is microscopically easy to identify by its small subcylindrical spores. Some measurements in literature appear to be slightly different: spores (Watling: 7.5–8.5 [–9.0] × 4.5–5.5 µm; Josserand: 7.8–8.8 × 4.6–5.3[–5.5] µm); pleurocystidia (Watling: 40–100 × 17–23 µm; Josserand: 60–100 × 20–30 µm), cheilocystidia (Watling: 25–40 × 25–35 µm; Josserand (15–)25–40 × 10–20 µm), but we think the Estonian collection studied fits well in the concept of *Coprinus utrifer*.

The species is included here in section *Nivei* because of the very similar veil, that is made up of (sub)globose and elongate elements. The relatively strongly diverculate elements also resembles the veil found in other groups of *Coprinus* which is the reason that *C. utrifer* is placed in different sections by various authors. Kühner & Romagnesi (1953) place it in section *Impexi*, Moser (1983) in section *Coprinus* and Citerin (1992) in section *Picaceus* (see also the paragraph on infrageneric classification).

6. **Coprinus poliomallus** Romagn. — Fig. 6

Coprinus poliomallus Romagn., Rev. mycol. 10 (1945) 89.

Selected literature. M. Enderle & H. Bender, Studien zur Gattung Coprinus V, Z. Mykol. 56 (1990) 32.

Closed pileus ellipsoid to cylindrical-ellipsoid, up to 5 × 3 mm, expanding up to 7 mm broad, in buds dark grey or mouse-grey, becoming paler with age, entirely powdery but at margin somewhat hairy-floccose. Lamellae, L = 8–16, l = 0–1, free, rather distant, first white but soon grey to spotted blackish. Stipe up to 20 × 0.5 mm, vitreous, subbulbous at base. Smell absent.

Spores [140,7,6] 6.3–10.3 × 3.8–6.2 µm, Q = 1.34–1.95, av. Q = 1.55–1.80, av. L = 7.4–9.3, av. B = 4.5–5.7 µm, cylindrico-ellipsoid, ellipsoid or ovoid, red-brown under microscope, with central, 1.3 µm wide germ pore. Basidia 12–28 × 7–9 µm, 4-spored, surrounded by (3–)4–5(–6) pseudoparaphyses. Pleurocystidia 50–120 × 21–38 µm, ellipsoid, utriform or subcylindrical. Cheilocystidia 40–90 × 18–32 µm, similar to pleurocystidia. Pileipellis consisting of roundish elements covered by narrow hyphae, passing upwards into velar tissue. Velar elements (sub)globose to ellipsoid, up to 50 µm wide, connected by 10–75 µm long and 3–7 µm wide, cylindrical, sometimes fusiform hyphae, hyaline, greyish in part, thin-walled, granular. Velum at margin of pileus and on stipe made up of cylindrical to fusiform or clavate elements for the most part. Clamp-connections absent.

Habitat & distribution. Solitary or in groups; on pure dung, especially of cow.

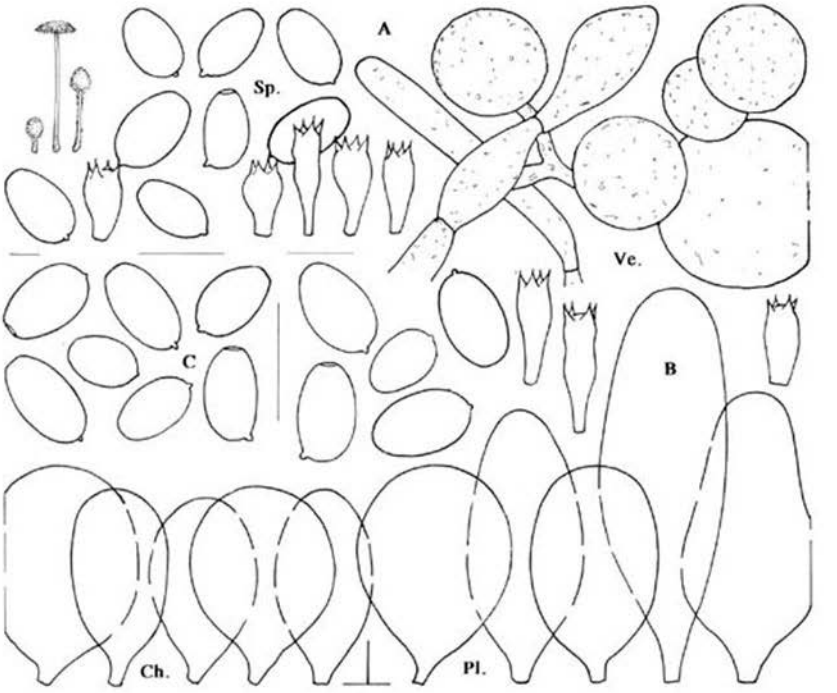

Fig. 7. *Coprinus pseudocortinatus* Locq. A. Veil, spores and basidia from *Vellinga*, 1 June 1986; B. spores, basidia and cystidia from *Uljé*, 22 Jan. 1990; C. spores from *Uljé 1051*.

Collections examined. NETHERLANDS: prov. Utrecht, Huizen, 29 Nov. 1986, *C.B. Uljé 823*; prov. Noord-Holland, Landsmeer, 26 Sept. 1992, *C.B. Uljé 1229*; prov. Zuid-Holland, Hazerswoude, Spookverlaat, 1 Nov. 1989, *C.B. Uljé 1055*; ibid. 12 Sept. 1990, *C.B. Uljé 1129*; Wassenaar, 28 Sept. 1991, *C.B. Uljé 1181* (neotype). — GERMANY: St. Märgen, 6 Sept. 1987, *H. Bender*.

The type of *C. poliomallus* is lost (H. Romagnesi pers. comm.) Therefore, collection *Uljé 1181* is selected here as neotype.

Coprinus coniophorus, the only other species in subsection *Nivei* with greyish veil, differs from *C. poliomallus* by the larger basidiocarps, amygdaliform spores, gregarious growth, and the habitat, being on and round rotten wood.

7. **Coprinus pseudocortinatus** Locq. — Fig. 7

Coprinus pseudocortinatus Locq., Bull. Soc. myc. Fr. 63 (1947) 81 (invalid, no Latin description).

Closed pileus globose, subglobose to ellipsoid, 0.3–4 mm high, 0.2–2.5 mm wide, completely covered with white, powdery veil; veil at margin, particularly in early stages, somewhat more hairy-floccose; expanded pileus 1–7 mm wide, convex, later applanate,

finally with slightly deflexed margin, veil on pileus becoming grey with age. Lamellae, L = 6–12, l = 0–1, free, white at first then greyish to grey with blackish spots. Stipe up to 20 × 0.1–0.7 mm, whitish, vitreous, at base up to 1 mm wide, often brownish, with white velar flocks. Smell absent.

Spores [120,6,5] 5.6–7.7 × 3.5–4.7 µm; Q = 1.50–2.00, av. Q = 1.65–1.70; av. L = 6.5–6.6, av. B = 3.9–4.0 µm, ellipsoid or ovoid, with central germ pore, red-brown. Basidia 9–30 × 6–8.5 µm, 4-spored, surrounded by (3–)4–6 pseudoparaphyses. Pleurocystidia 50–90 × 20–40 µm, utriform, a few subcylindric or ellipsoid. Cheilocystidia 30–50 × 15–30 µm, subglobose, ellipsoid, utriform or subcylindric. Velar elements up to 55 µm wide, globose. Clamp-connections absent.

Habitat & distribution. Solitary, in small groups on dung. Rather rare.

Collections examined. NETHERLANDS: prov. Utrecht, Huizen, 29 Nov. 1986, *C.B. Uljé*; prov. Noord-Holland, Vogelenzang, 1 June 1986, *E.C. Vellinga*; prov. Zuid-Holland, Leiden, 12 Sept. 1985, *C.B. Uljé*; Hazerswoude, Spookverlaat, 1 Nov. 1989, 5 Nov. 1989, *C.B. Uljé 1051*; 22 Jan. 1990, *C.B. Uljé*.

Because of the small size of the basidiocarps, a number of collections of *C. pseudocortinatus* could not be preserved after examination, but the observations on these finds are taken into consideration while preparing the description given above.

We have not been able to locate original material of *Coprinus pseudocortinatus*. It would have been a good opportunity here to validate Locquin's species by publishing a Latin diagnosis and designing a holotype. Unfortunately we have no good, rich collection for such a purpose.

Other small and rather similar species are *C. poliomallus* and *C. idae*. The former has dark mouse-grey basidiocarps when young, and the latter is terrestrial and has broader, differently shaped spores.

8. **Coprinus idae** Uljé, *spec. nov.* — Fig. 8

Pileus primo conicus demum plano-convexus vel applanatus, usque ad 8 mm latus, albo-pruinosus, demum cinerascens. Lamellae liberae, distantes (L = 11–18, l = 0–1), ex albo cinerascentes vel nigricantes. Stipes usque ad 35 × 0.2–1 mm, basi subbulbosus, albidus, hyalinus, flocci albi velii. Sporae 6.7–9.7 × 4.7–6.8 µm, Q = 1.5–1.6, late ellipsoideae vel ovaliformes, pallide rubro-brunneae, cum poro germinativo centrico. Basidia 16–28 × 6.5–8 µm, tetrasporigera. Pseudoparaphyses 4–5. Pleurocystidia 25–55 × 14–28 µm, (sub)globosa, ellipsdoidea, utriformia vel vesiculosa. Cheilocystidia similia, 25–50 × 16–28 µm. Velum mixtum, e elementis globosis, glabris, ad 50 × 38 µm vel elementis diverticulatis constans. Fibulae absentes. Ad terram inter gramina.

Typus: Netherlands, Alphen a/d Rijn, near Zegersplas, 5.V.1988, *C.B. Uljé 908* (L).

Etymology: named after the author's wife.

Closed pileus up to 3.5 × 2.5 mm, in most cases somewhat smaller, first conical then plano-convex, finally applanate and then up to 8 mm wide, completely white-powdery, soon becoming greyish. Lamellae, L = 11–18, l = 0–1, free, white at first then grey to blackish spotted. Stipe up to 35 × 0.2–1 mm, with subbulbous base, whitish-hyaline, covered with white velar flocculi. Smell absent.

Spores [120,6,3] 6.7–9.7 × 4.7–6.8 µm, Q = 1.30–1.75, av. Q = 1.50–1.55, av. L = 8.0–8.8 µm, av. B = 5.1–5.9 µm, broadly ellipsoid to oval, rather pale red-brown, with central germ pore. Basidia 16–28 × 6.5–8 µm, 4-spored, surrounded by 4–5 pseudoparaphyses. Pleurocystidia 25–55 × 14–28 µm, (sub)globose, ellipsoid, utriform or

vesiculose. Cheilocystidia 25–50 × 16–28 µm, similar to pleurocystidia. Veil on pileus consisting of smooth or somewhat granular globose and 12–42 µm wide elements and ellipsoid to oval elements, up to 50 × 38 µm, mixed with frequently branching, colourless, thin-walled hyphae with processes. Clamp-connections absent.

Habitat & distribution. Terrestrial in lawn, solitary or a few together. Very rare, known only from type-locality.

Collections examined. NETHERLANDS: prov. Zuid-Holland, Alphen a/d Rijn, near Zegerplas, 5 June 1988, *C.B. Uljé 908*, 11 July 1988, *C.B. Uljé*; same locality, 11 June 1990, *C.B. Uljé 1070* (holotype; L).

Coprinus idae is a very small, white species like *C. pseudocortinatus*. The latter has narrower, differently shaped spores, larger pleurocystidia, and grows on pure dung.

9. **Coprinus candidatus** Uljé — Fig. 9

Coprinus candidatus Uljé, Persoonia 13 (1988) 483.

Pileus ovoid to subglobose and up to 8 × 6 mm when still closed, expanding up to 16(–20) mm, white to cream, becoming sordid with age, entirely powdery but at margin somewhat hairy-floccose. Lamellae, L = 21–28, l = 0–3, free, first white but soon grey to spotted blackish, with white edge. Stipe c. 50 × 1.5 mm, attenuate upwards subbulbous at base, white-flocculose. Smell absent.

Spores [140,7,4] 7.3–11.5 × 4.6–6.0 µm, Q = 1.60–2.05, av. Q = 1.70–1.90, av. L = 8.6–10.9, av. B = 5.0–5.8 µm, cylindrico-ellipsoid, but somewhat conical towards apiculus, red-brown under microscope, with central, up to 2 µm wide germ pore. Basidia 15–35 × 7–10 µm, 4-spored, surrounded by 3–5 pseudoparaphyses. Cheilocystidia up to 40(–50) µm long, with 7–15(–25) µm wide ventricose part and 4–10(–15) µm wide neck, utriform to more rarely lageniform or vesiculose, with more or less cylindrical neck and rounded apex. Pleurocystidia absent. Veil made up of colourless to slightly yellowish, smooth to granular, up to 50 µm wide, globose elements. Clamp-connections present.

Habitat & distribution. Terrestrial on bare soil, sometimes on or against fallen branchlets. Not common.

Collections examined. NETHERLANDS: prov. Utrecht, Breukelen, estate 'Over-Holland', 19 Sept. 1986, *C.B. Uljé 807*; prov. Noord-Holland, Amsterdam, Amsterdamse Bos, 2 Sept. 1986, *C.B. Uljé 812* (holotype; L); ditto, 20 Sept. 1987, *C.B. Uljé 852*; prov. Zuid-Holland, Leiden, 26 March 1985, *C.B. Uljé 486*.

Among the species of the *C. cortinatus*-group, *C. candidatus* is easily recognized by its utriform cheilocystidia and by its usually cylindrico-ellipsoid spores.

10. **Coprinus cortinatus** J. Lange — Fig. 10

Coprinus cortinatus J. Lange, Dansk bot. Ark. 2 (3) (1915) 45.

Misapplied name. Coprinus filiformis s. H. Bender & M. Enderle, Z. Mykol. 54 (1988) 49.

Selected literature. H. Bender & M. Enderle, Studien zur Gattung Coprinus IV, Z. Mykol. 54 (1988) 49 (as *C. filiformis*); C.B. Uljé & C. Bas, Four new species from the Netherlands, Persoonia 13 (1988) 479.

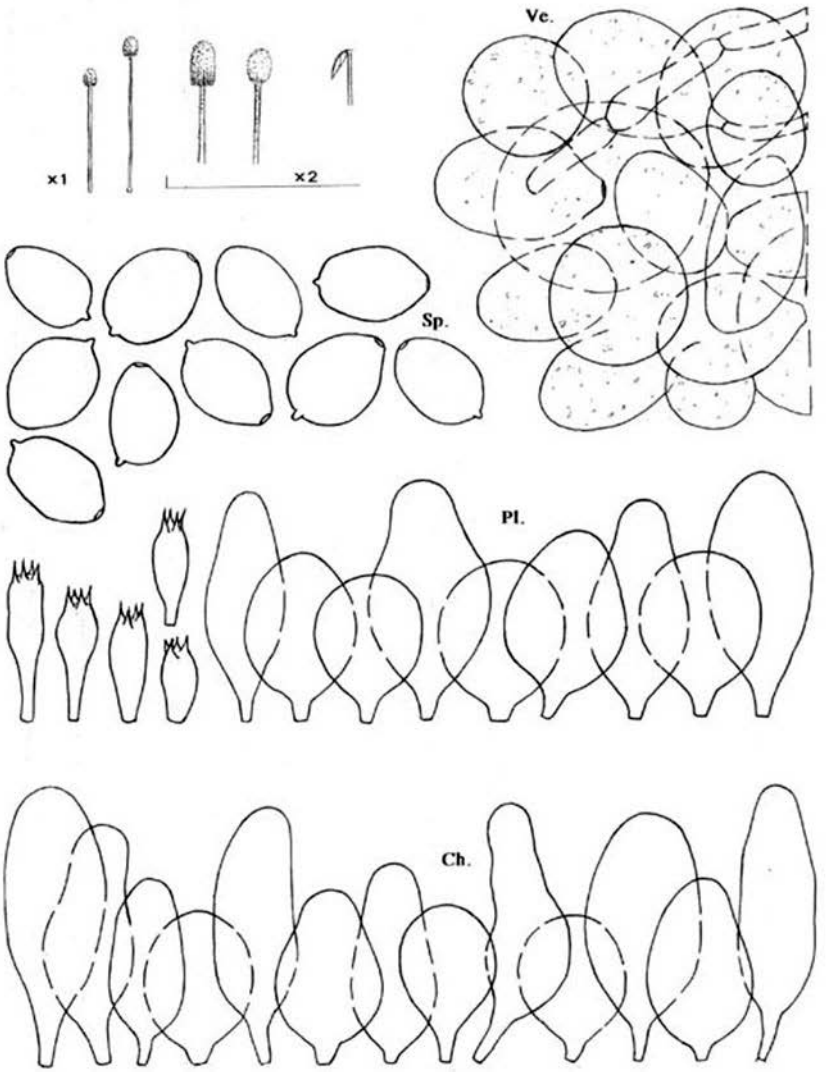

Fig. 8. *Coprinus idae* Uljé. All figures from *Uljé 908* (type).

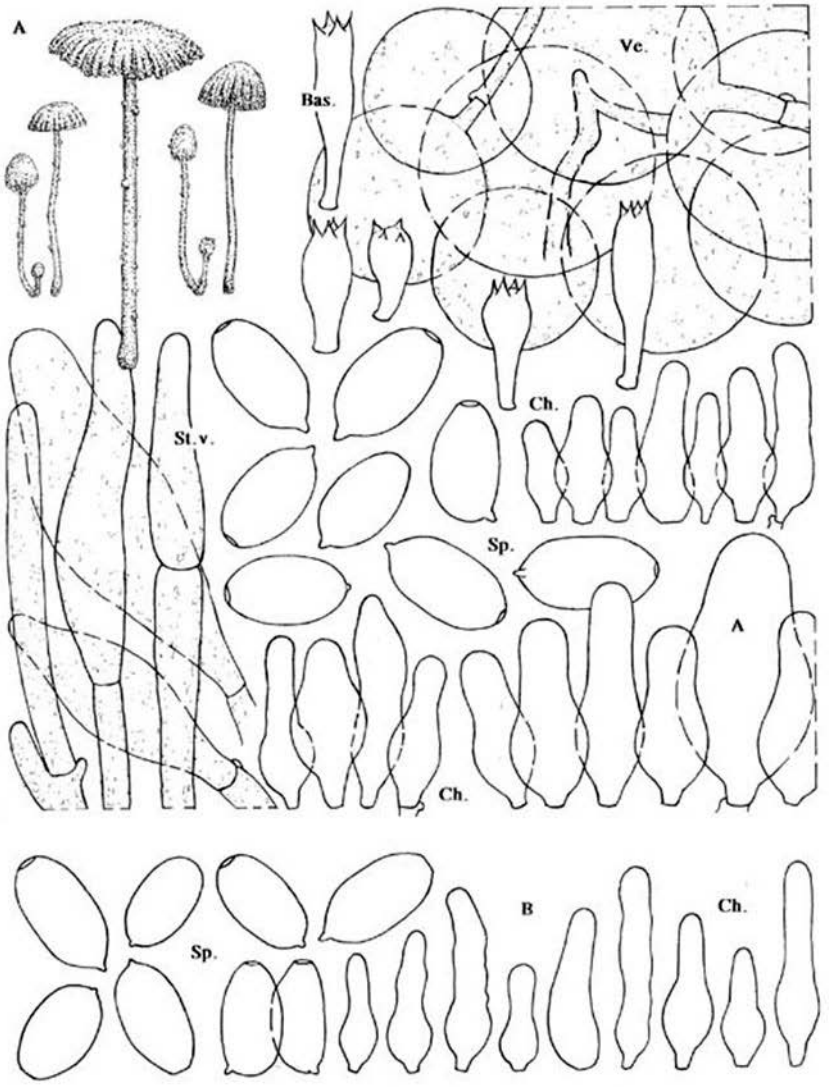

Fig. 9. *Coprinus candidatus* Uljé. All figures from *Uljé 812* (type).

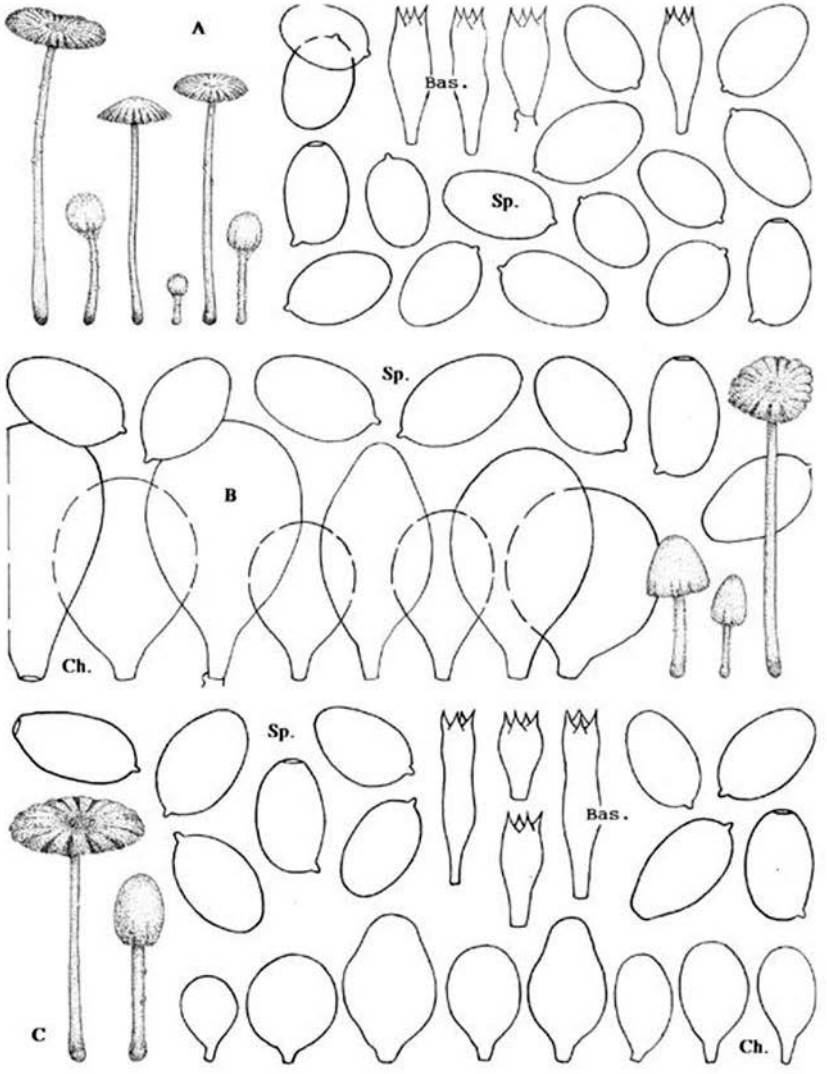

Fig. 10. *Coprinus cortinatus* J. Lange. A. from *Uljé 41/86*; B. from *Uljé 1177*; C. from *Uljé 65*.

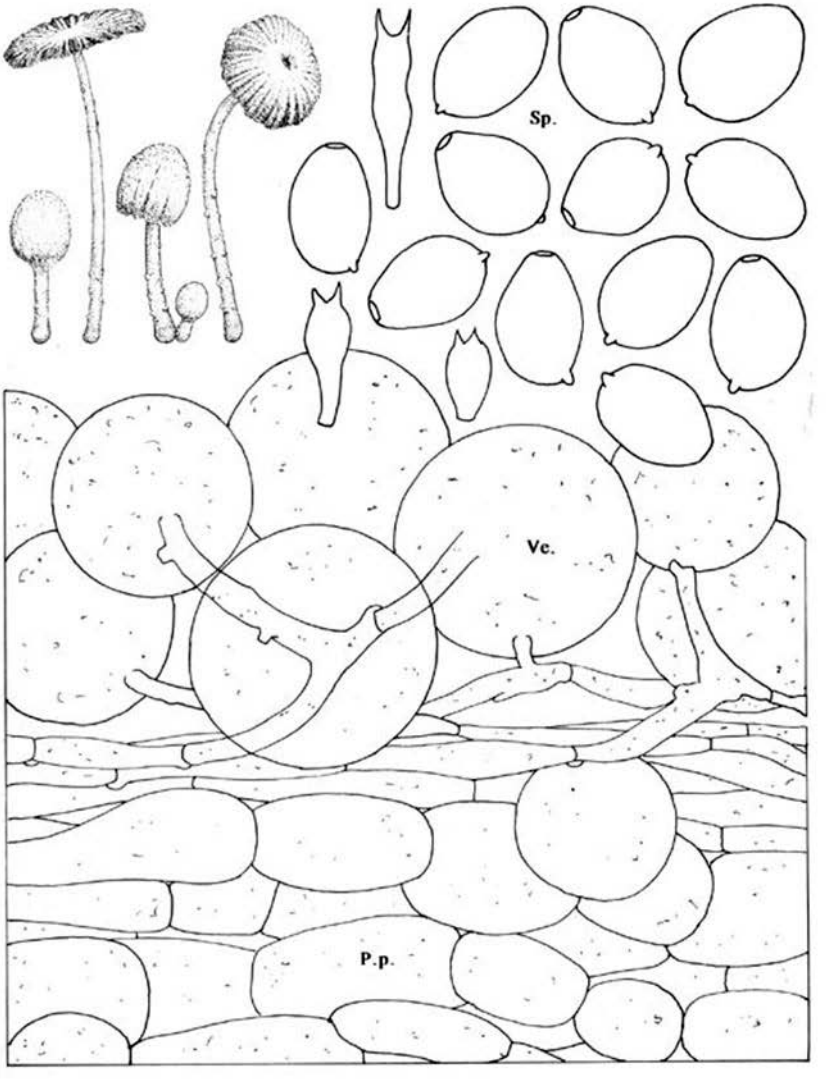

Fig. 11. *Coprinus bellulus* Uljé. All figures from *Uljé 777* (type).

Closed pileus globose, subglobose to ellipsoid, up to 6 mm high and 5 mm wide, completely covered with powdery white veil, often cream to pale ochraceous at centre; veil at margin, particularly in early stages, somewhat more hairy-floccose; expanded pileus up to 15 mm wide, convex or flat, finally lamellae with slightly deflexed margin; veil greying with age. Lamellae, L = 18–24, l = 1–3, free, up to 2 mm wide, white at first, then greyish to grey with blackish spots. Stipe up to 40 × 0.5–1 mm, attenuate upwards, at base up to 1.5 mm wide, white, somewhat hyaline; at base up to 3.5 mm wide, often brownish, with white velar flocks. Smell absent. Spore print dark chocolate brown (Munsell 5 YR 2/1).

Spores [180,9,9] 6.2–9.7 × 4.3–6.0, Q = 1.30–1.70, av. Q = 1.45–1.55, av. L = 7.9–8.4, av. B = 5.1–5.4 µm, ellipsoid, sometimes slightly amygdaliform, dark red-brown, with central germ pore. Basidia 15–26 × 7–8 µm, 4-spored, surrounded by 3–5 pseudoparaphyses. Cheilo- and pleurocystidia absent but here and there sterile elements (probably somewhat enlarged basidioles) projecting from lamellae and sometimes velar remnants sticking to lamellar edge. Veil made up of colourless to slightly yellowish, smooth to granular, up to 50 µm wide, globose elements, mixed with some hypha-like elements. Clamp-connections present.

Habitat & distribution. Solitary or in small groups; on bare soil or in grassy-mossy places, in most cases under shrubs or trees. Not rare in the Netherlands.

Collections examined. DENMARK: (exact locality unknown), 20 Jan. 1939, *J.E. Lange 1903* (C). — NETHERLANDS: prov. Gelderland, Bergh, 2 Aug. 1952, *H.S.C. Huijsman*; prov. Utrecht, Breukelen, estate 'OverHolland', 27 Aug. 1986, *C.B. Uljé 22/86*; Haarzuilens, 8 Aug. 1987, *C.B. Uljé*; prov. Noord-Holland, Amsterdam, 10 Dec. 1958, *E. Kits van Waveren*; prov. Zuid-Holland, Leiden, Leidse Hout, 29 Sept. 1986, *C.B. Uljé 41/86*, 10 Sept. 1986, *C.B. Uljé 30/86*; Leiden, Nov. 1983, *C.B. Uljé*, 19 Oct. 1985, *C.B. Uljé 65/85*.

The present concept agrees well with that of J. Lange (1915), who does not mention hymenial cystidia. However, we collected several taxa very close to *Coprinus cortinatus* in the present sense, but with distinct, broadly clavate to ellipsoid cheilocystidia. For example we have a number of terrestrial collections with cheilocystidia up to 30 × 18 µm (*C.B. Uljé 65*, *C.B. Uljé*, 4 Sept. 1986, *C.B. Uljé 982* en *C.B. Uljé 1177*; with cheilocystidia resp. 15–30 × 11–16, 21–30 × 10–14, 11–27 × 7–12 en 20–32 × 13–18 µm) and collections from dung with larger cheilocystidia, up to 50 × 25(–35) µm (*Bender*, 3 Aug. 1983, *Bender*, 23 June 1985, *C.B. Uljé 1001*; with cheilocystidia resp. 20–52 × 15–38 µm, 20–33 × 12–25 µm and 20–40 × 15–35 µm). Intermediates, however, seem to exist, as two collections not growing on dung (*C.B. Uljé 991* on wood and *C.B. Uljé 48/86* on soil) have large cheilocystidia similar to the collections mentioned above from dung (cheilocystidia 26–37 × 22–30 µm and 30–50 × 19–29 µm). Finally there is one collection (*C.B. Uljé*, 17 Aug. 1985, Huys ten Donk) with large, utriform cheilocystidia and differently shaped spores, that is undoubtedly related to *Coprinus cortinatus*. An observation on two collections from dung with very small basidiocarps (< 2 mm) revealed smaller spores (5–7 × 4–5 µm and 5–6 × 3.7–4.5 µm), but the material has not been preserved. It will be clear that more studies need to be undertaken in the complex of *Coprinus cortinatus*. We therefore refrain from describing the taxa with cheilocystidia in detail and await more information.

Bender & Enderle (1988: 49) described what they considered to be *Coprinus filiformis* B. & Br., which should differ from *C. cortinatus* in the structure of the veil, consisting of two types of elements. Besides the normal globose elements, also hypha-like elements are said to be present, whereas *C. cortinatus* in their conception is said to have only globose velar elements. Our observations revealed that in all species of section *Nivei* both types of elements can be found, especially near the margin of the pileus. This is also the case in our conception of *Coprinus cortinatus*. *Coprinus filiformis* in its original concept of Berkeley & Broome is a very small mushroom with a pileus only 1 mm high when still closed. As no original material seems to exist, nor collections that fit with *C. filiformis*, we consider it a nomen dubium. Compare also Uljé (1988).

11. **Coprinus bellulus** Uljé — Fig. 11

Coprinus bellulus Uljé, Persoonia 13 (1988) 481.
Selected icon. M. Enderle & H. Bender, Studien zur Gattung Coprinus V, Z. Mykol. 56 (1990) 24.

Closed pileus globose, subglobose to ellipsoid, up to 12 mm high and 9 mm wide, completely covered with powdery white veil, but very young buds and centre of pileus of more advanced stages often cream to pale ochraceous (Mu. 10 YR 8/3); veil at margin, particularly in early stages, somewhat more hairy-floccose; expanded pileus up to 25(–5) mm wide, convex or flat with slightly deflexed margin, rarely completely expanded; veil with age greying. Lamellae, L = 20–36, l = 1–3, free, up to 2 mm wide, white at first, then greyish to grey with blackish spots. Stipe up to 80 × 2.5 mm, attenuate upwards, at apex up to 1.5 mm wide, white but at apex often somewhat hyaline and brownish towards subbulbous, up to 3.5 mm wide base, with white velar flocks. Smell absent. Spore print dark chocolate brown (Mu. 5 YR 2/1).

Spores [160,8,8] 7.3–10.6 × 5.8–8.0 × 5.0–7.1 µm, Q = 1.20–1.65, av. Q = 1.40–1.50, L = 9.6–9.9, B = 6.6–7.1 µm, in face view broadly ellipsoid, sometimes with slightly flattened side, but often somewhat irregularly shaped, dark red-brown, with central germ pore and somewhat attenuate apex. Basidia 15–32 × 7–9 µm, 2-spored, surrounded by 3–5 pseudoparaphyses. Cheilo- and pleurocystidia absent but here and there sterile elements (probably somewhat enlarged basidioles) projecting from lamellae and sometimes velar remnants sticking to lamellar edge. Velar elements up to 50 µm in diam., (sub)globose. Clamp-connections present.

Habitat & distribution. Mostly in small groups, more rarely in bundles of up to 40 specimens, but sometimes also solitary. On bare soil or at grassy-mossy places, usually under shrubs or trees, but also in lawns. Not rare in the Netherlands.

Collections examined. NETHERLANDS: prov. Flevoland, Oostelijk Flevoland, Bremerbergbos, 4 Oct. 1986, *G. Tjallingii-Beukers* (herb. Tjallingii); prov. Zuid-Holland, Alphen a/d Rijn, 26 June 1984, *C.B. Uljé 320*, 1 Aug. 1985, *C.B. Uljé 530* & 11 Sept. 1987, *C.B. Uljé 827*; Leiden, 28 Aug 1986, *C.B. Uljé 648* & 31 May 1987, *C.B. Uljé 849*; Ter Aar, Langeraar, 10 Nov, 1983, *C.B. Uljé 308* & 16 Oct. 1986, *C.B. Uljé 777* (holotype; L)

Coprinus bellulus is easily distinguished from the other members of the *C. cortinatus*-group by the 2-spored basidia, lacking pleuro- and cheilocystidia, and the somewhat irregular, broadly ellipsoid spores.

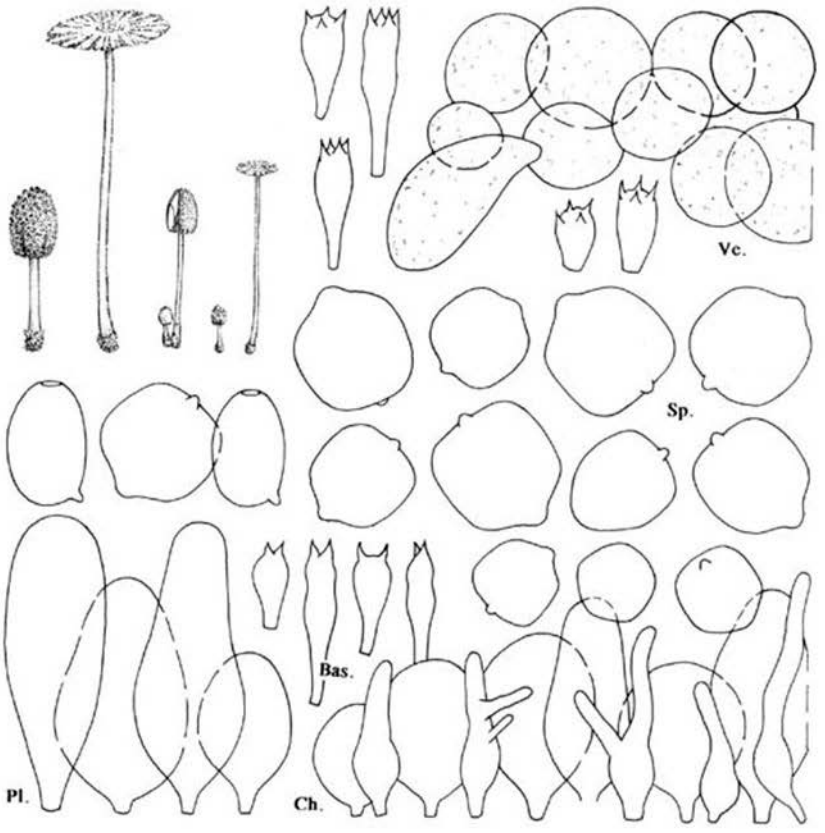

Fig. 12. *Coprinus cordisporus* Gibbs. All figures from *Uljé 915*.

12. **Coprinus cordisporus** Gibbs — Fig. 12

Coprinus cordisporus Gibbs, The Naturalist (1908) 100.

Coprinus patouillardii ssp. *isabellinus* Locq., Bull. Soc. mycol. Fr. 63 (1947) 83 (invalid, no Latin description).

Selected literature. M. Enderle, G.J. Krieglsteiner & H. Bender, Studien zur Gattung Coprinus, Z. Mykol. 52 (1986) 124 (as *C. patouillardii*).

Closed pileus globose, subglobose, ellipsoid or cylindrical ellipsoid, up to 12 mm high and 8 mm wide, completely covered with powdery, pale pinkish brown veil (Mu. 7.5 YR 5/4, K. & W. 6C4 at centre) which forms small conical flocks at centre of pileus; at margin, particularly in early stages, with somewhat more hairy-floccose veil; expanded pileus up to 25 mm wide, conical or convex, later applanate. Lamellae, L = 18–24, l = 0–3,

free, up to 1.5 mm wide, white at first, then greyish to black. Stipe up to 60 × 0.5–1.5 mm, white, somewhat hyaline, at base clavate, up to 2.5 mm wide, often brownish, with white velar flocks, often building a small, volva-like, erect collar. Smell absent.

Spores [240,12,12] 7.3–11.6 × 6.5–10.1 µm; Q = 0.95–1.25, av. Q = 1.05–1.20; av. L = 7.9–10.2, av. B = 7.1–9.4 µm, rectangular lemon-shaped, lentiform, dark red-brown, with central germ pore. Basidia 12–32 × 7–10 µm, 4-spored (sometimes 2-spored and than spore-size about equal to that of the 4-spored collections), surrounded by (3–) 4–6 pseudoparaphyses. Pleurocystidia 40–80 × 16–28 µm, utriform, subglobose to ellipsoid or subcylindric. Cheilocystidia 20–50 × 17–32 µm, utriform, subglobose to ellipsoid or subcylindric, mixed with lageniform ones (20–50 × 8–12 × 3–5 µm). Veil made up of (sub)globose to ellipsoid elements, smooth to granular, up to 50 µm wide. Clamp-connections absent.

Habitat & distribution. Solitary or in small groups; on dung of several kinds of animals. Rather common in the Netherlands.

Collections examined. NETHERLANDS: prov. Utrecht, 's-Graveland, 14 June 1971, *J. Daams 71-140*; Hilversum, 24 Oct. 1970, *J. Daams 70-84*; Kortenhoef, 10 Oct. 1968, *J. Daams 48-5*; Naarden, 24 April 1956, *C. Bas 1002*; prov. Limburg, Roermond, 23 July 1948, *C.Ph. Verschueren*; prov. Noord-Holland, Vogelenzang, 12 May 1986, *E.C. Vellinga* (coll. *C.B. Uljé 915*); prov. Zuid-Holland, Hazerswoude, Spookverlaat, 31 Oct. 1988, *C.B. Uljé 1004*; prov. Zeeland, Terneuzen, 9 Apr. 1981, *A. de Meijer 242*; Walcheren, Oranjezon, 15 Nov. 1936, *H.S.C. Huijsman 1299*; Oostburg, 24 July 1983, *A. de Meijer 685*. — AUSTRIA: Kastelruht, 7 Oct. 1988, *H. Bender* (herb. Bender). — NORWAY: Svalbard, 13 Aug. 1985, *Jalink 1299* (herb. Jalink).

The most distinctive character of *Coprinus cordisporus* is the presence of lageniform cheilocystidia.

Coprinus cordisporus is very similar to *C. patouillardii*. Many authors consider them to be synonyms (Kühner & Romagnesi, 1953; Enderle, Krieglsteiner & Bender, 1986). Orton & Watling (1979) differentiate *Coprinus cordisporus* from *C. patouillardii* on habitat (pure, relatively fresh dung), smaller sized fruit-bodies (pileus 5–10 mm), smaller spores, and presence of pleurocystidia. *C. patouillardii* has a larger pileus (10–20 mm), and grows on kitchen refuse, silage, straw and soil mixed with old dung. Arnolds (1982) accepted the taxa on account of presence or absence of pleurocystidia, but expressed his doubt as to the validity of these concepts. Citerin (1992) also accepted two taxa, based on presence or absence of pleurocystidia and a difference in width of the spores. To the present authors the differences indicated above are not strong enough to warrant a distinction on specific level between *Coprinus cordisporus* and *C. patouillardii*. Size of the fruit-bodies and spores is rather variable in this complex. In material from both taxa pleurocystidia have been found. The only difference found in microscopy, is the presence of lageniform cheilocystidia in *Coprinus cordisporus*. Following Kuyper (1988) the difference between the two taxa would best be recognized on varietal level. However, considering also the genetic studies by Kemp (1980), who showed that within this complex several incompatible taxa exist, we decided for the time being to maintain the two taxa awaiting more information.

Coprinus patouillardii ssp. *isabellinus* Locq. differs only by the smaller basidiocarps and smaller spores. In all other microscopical characters it is similar to *C. cordisporus*, especially by the presence of lageniform cheilocystidia. Therefore, we consider it a synonym of *Coprinus cordisporus* rather than a subspecies of *C. patouillardii*.

Coprinus cordisporus is also very similar to *C. cardiasporus*, and somewhat less to *C. ephemeroides*. It differs from both by the lageniform cheilocystidia. *Coprinus ephemeroides* has a small annulus, its size is somewhat smaller, and the pileus is more yellowish. *C. cardiasporus* has heart-shaped spores.

The lageniform cheilocystidia of *Coprinus cordisporus* are sometimes branched at apex, which was clearly visible in coll. *Jalink 1299* and *Bender*, 7 Oct. 1988. Also on the stipe similar caulocystidia have been found, mixed with globose velar elements.

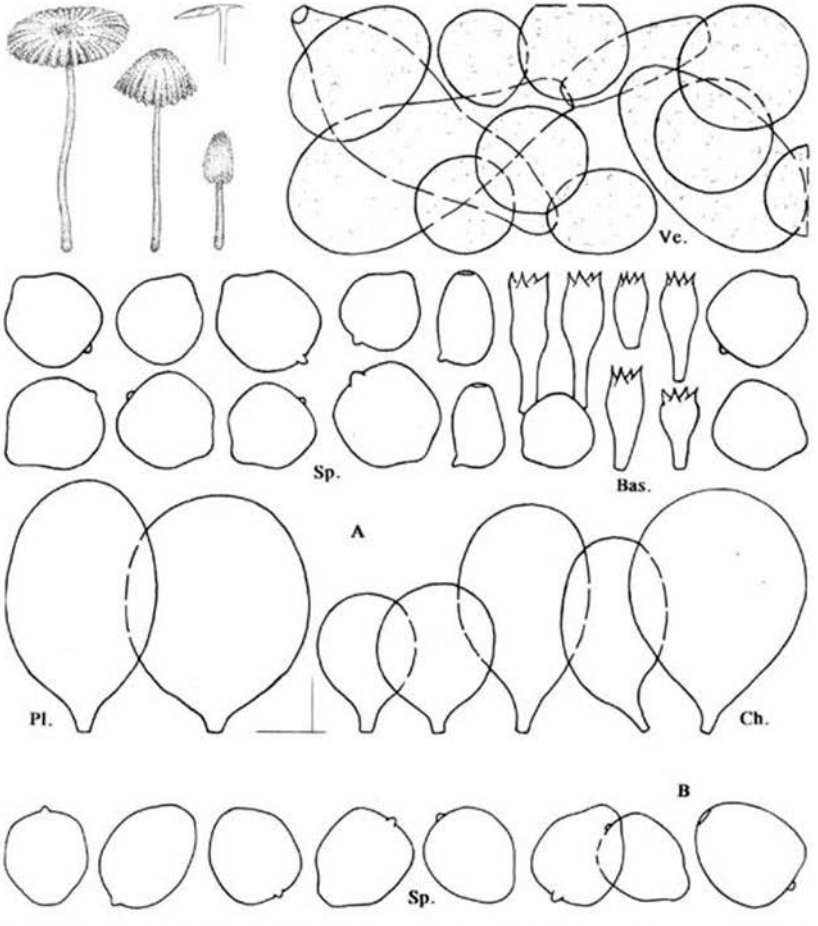

Fig. 13. A. *Coprinus patouillardii* Quél. All figures from *Uljé 1098*. — B. *Coprinus patouillardii* var. *lipophilus* Romagn., spores from type.

13. **Coprinus patouillardii** Quél. — Fig. 13

Coprinus patouillardii Quél., Tab. Anal. Fung. 1 (1884) 107. — *Coprinus patouillardii* var. *lipophilus* Heim & Romagn., Bull. Soc. mycol. Fr. 50 (1934) 187.

Closed pileus globose, subglobose, ellipsoid or cylindrical ellipsoid, up to 5(–8) mm high and 4 mm wide, completely covered with powdery, pale pinkish brown veil (Mu. 7.5 YR 5/4, K. & W. 6C4 at centre), producing small conical flocks at centre of pileus; veil at margin, particularly in early stages, somewhat more hairy-floccose; expanded pileus up to 15(–22) mm wide, conical or convex, later flat. Lamellae, L = 16–22, l = 0–3, free, up to 1.5 mm wide, white at first, then greyish to black. Stipe up to 50 × 0.5–1 mm, white, somewhat hyaline. Base of stipe clavate, up to 1.5 mm wide, often brownish, with white velar flocks, often forming a small erect collar. Smell absent.

Spores [80,3,3] 6.0–8.9 × 5.8–7.8 µm, Q = 1.00–1.35, av. Q = 1.05–1.20, av. L = 7.4–8.0, av. B = 6.6–7.0 µm, rectangular lemon-shaped, lentiform, dark red-brown, with central germ pore. Basidia 15–30 × 7–8 µm, 4-spored, surrounded by 3–6 pseudoparaphyses. Pleurocystidia 30–50 × 35–40 µm, subglobose to ellipsoid. Cheilocystidia 20–45 × 15–35 µm, globose, subglobose to ellipsoid. Pileipellis made up of (sub)globose to ellipsoid elements, smooth to granular, up to 50 µm wide. Clamp-connections absent.

Habitat & distribution. Solitary or in small groups on compost heaps. Rather rare in the Netherlands.

Collections examined. NETHERLANDS: prov. Zuid-Holland, Alphen a/d Rijn, 15 Sept. 1990, *C.B. Uljé 1098*, 19 Oct. 1990, *C.B. Uljé 1106*. FRANCE: Yerres (S.-et-O.), Aug. 1932, *H. Romagnesi* (type *C. patouillardii* var. *lipophilus*).

The collections studied fit the original description very well. The original *Coprinus patouillardii* also grew on vegetable refuse (on dregs from decaying grapes). A macroscopically and microscopically very similar taxon from dung is described as *C. cordisporus* Gibbs in this paper. See the discussion under that species.

The type material of *C. patouillardii* var. *lipophilus* Heim & Romagn. (1934: 187) proved to be very poor. It is nothing but a black mass, in which it was impossible to tell the lamellae apart. The shape and size of the spores of that material (Fig. 13B) fit very well with that of *C. patouillardii*, however. The differences indicated by Heim & Romagnesi, viz. the larger, convex pileus, the floccose volva-like veil at base of the stipe, also fits well into the variability of *C. patouillardii*. The habitat, greasy soil, does not seem to be of great importance. Therefore, we think it is not different from the type-variety of the species.

14. **Coprinus cardiasporus** Bender — Fig. 14

Coprinus cardiasporus Bender in Enderle, Krieglsteiner & Bender, Z. Mykol. 52 (1986) 102.

Closed pileus ellipsoid or cylindrical ellipsoid, up to 7 mm high and 4 mm wide, completely covered with powdery, white, cream-coloured or pale pinkish ochre veil, at centre of pileus somewhat granular flocculose; expanded pileus up to 10 mm wide, conical or convex, later applanate. Lamellae, L = 18–25, l = 0–3, free or narrowly adnate, c. 1 mm wide, white at first then greyish to black. Stipe up to 35 × 0.5–1 mm, white, somewhat hyaline, minutely floccose, at base clavate, up to 1.5 mm wide, often pale brownish, felty. Smell absent.

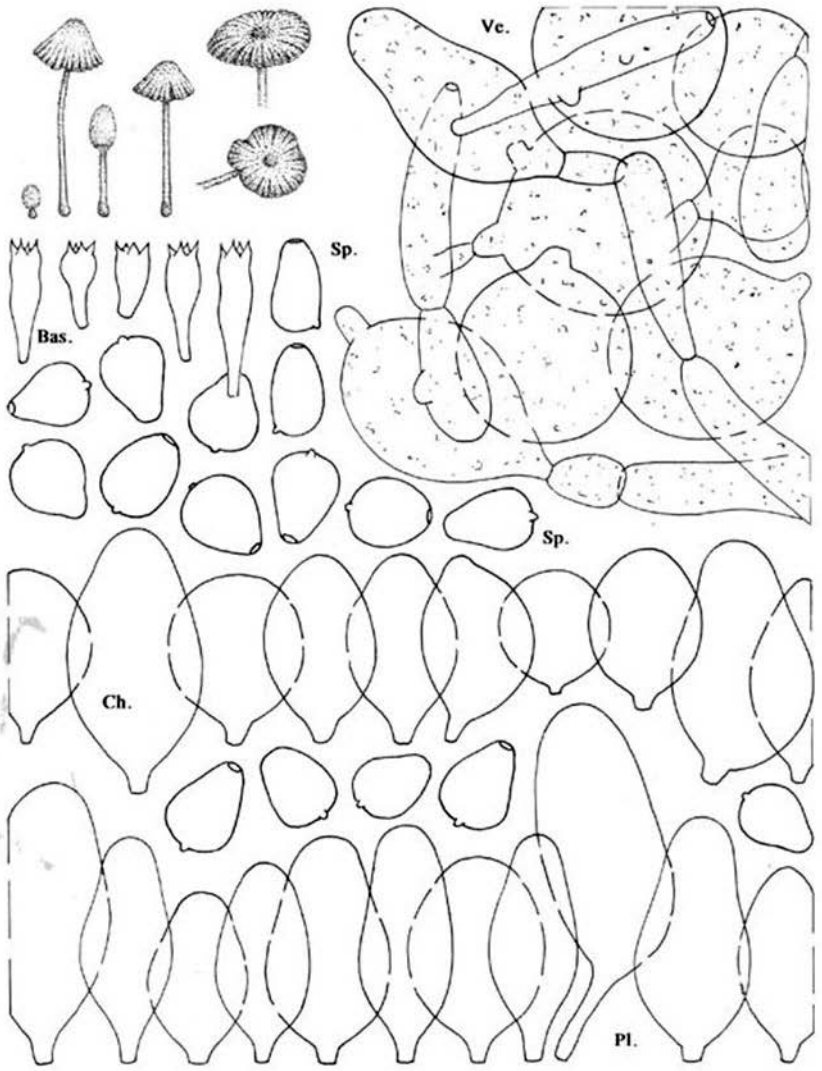

Fig. 14. *Coprinus cardiasporus* Bender. All figures from type.

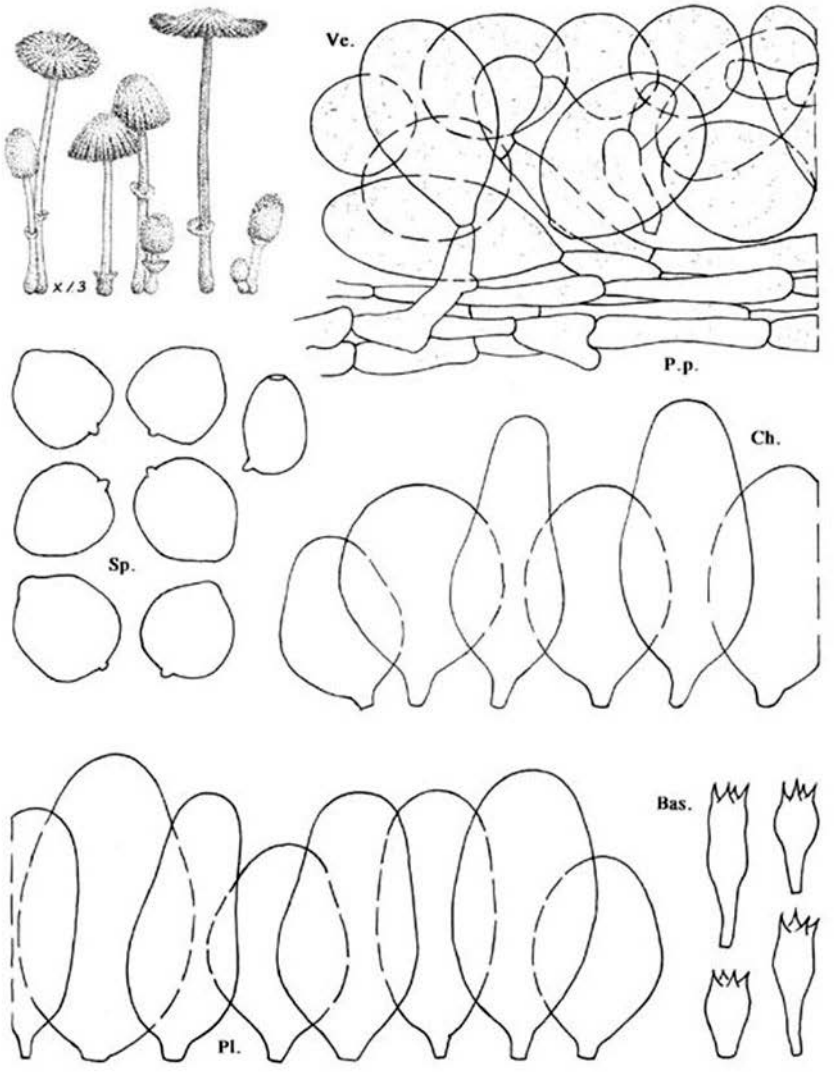

Fig. 15. *Coprinus ephemeroides* (DC.: Fr.) Fr. All figures from *Uljé 1007*.

Spores [80,4,3] 5.5–8.5 × 4.8–6.5 × 3.7–4.5 µm, Q = 1.00–1.40, av. Q = 1.10–1.20, av. L = 6.1–7.3, av. B = 5.3–5.5 µm, cordiform, lentiform, red-brown, with central germ pore. Basidia 12–28 × 7–8 µm, 4-spored, surrounded by 3–6 pseudoparaphyses. Pleurocystidia 30–55 × 15–26 µm, vesiculose, utriform or ellipsoid. Cheilocystidia 25–50 × 15–30 µm, subglobose, ellipsoid or utriform. Veil made up of (sub)globose to ellipsoid elements, smooth to granular, up to 50 µm wide. Clamp-connections absent.

Habitat & distribution. Solitary or in small groups; on compost heaps and horse-dung mixed with soil and wood-chips. Very rare in the Netherlands.

Collections examined. NETHERLANDS: prov. Zuid-Holland, Alphen a/d Rijn, 16 Sept. 1990, *C.B. Uljé 1100*; ditto 27 Nov. 1990, *C.B. Uljé 1112*. — GERMANY: Mönchengladbach, 27 June 1985, *H. Bender* (part of holotype; herb. Bender).

The collection from Germany studied is part of the holotype. *Coprinus cardiasporus* is very close to *C. patouillardii* Quél. It differs by having spores that are narrowing towards the germ pore, whereas the spores are rounded angular in *C. patouillardii*.

According to Bender (1986), *Coprinus cardiasporus* has clamped hyphae in the mycelium; we failed to demonstrate them in our study of part of the holotype.

15. **Coprinus ephemeroides** (DC.: Fr.) Fr. — Fig. 15

Agaricus ephemeroides DC. in DC. & Lam., Fl. franç. 2 (1805) 145. — *Agaricus ephemeroides* DC.: Fr., Syst. mycol. 1 (1821) 313. — *Coprinus ephemeroides* (DC.: Fr.) Fr., Epicr. (1838) 250.

Agaricus hendersonii Berk. apud Hooker, Engl. Fl. 5 (1836) 122. — *Coprinus hendersonii* (Berk.) Fr., Epicr. (1838) 250.

Coprinus bulbillosus Pat., Tab. anal. Fung. 2 (1889) 60.

Closed pileus subglobose, ellipsoid, cylindrical ellipsoid or ovoid, up to 5(–7) mm high and 3 mm wide, completely covered with powdery, pale pinkish brown or yellowish veil, forming small conical flocks at centre of pileus; expanded pileus up to 10(–13) mm wide, conical or convex, later applanate. Lamellae, L = 14–23, l = 0–3, free, white at first, then greyish to black. Stipe up to 50 × 0.5–1 mm, white, somewhat hyaline; at base clavate, up to 1.5 mm wide, with yellowish or pale brown velar flocks, forming a small erect collar when very young, later forming the ring about halfway the stipe or lower. Smell absent.

Spores [60,3,3] 5.8–9.2 × 5.4–8.0 × 4.4–4.9 µm, Q = 0.95–1.20, av. Q = 1.05–1.15, av. L = 6.7–8.6, av. B = 6.3–7.6 µm, rectangular lemon-shaped, lentiform, dark red-brown, with central germ pore. Basidia 13–28 × 7–9 µm, 4-spored, surrounded by (3–)4–7(–8) pseudoparaphyses. Pleurocystidia 30–60 × 20–35 µm, vesiculose, utriform, ellipsoid, cylindrical ellipsoid. Cheilocystidia 20–60 × 15–35 µm, utriform, vesiculose, (sub)globose or ellipsoid. Veil made up of (sub)globose to ellipsoid elements, smooth to granular, up to 50 µm wide. Clamp-connections absent.

Habitat & distribution. Solitary or in small groups; on dung, especially from horse. Rather common in the Netherlands.

Collections examined. NETHERLANDS: prov. Noord-Holland, Vogelenzang, 1 June 1986, *E.C. Vellinga*; prov. Zuid-Holland, Hazerswoude, 1 Nov. 1988, *C.B. Uljé 1007*; Wassenaar, Meijendel, 28 Sept. 1991, *C.B. Uljé 1182*.

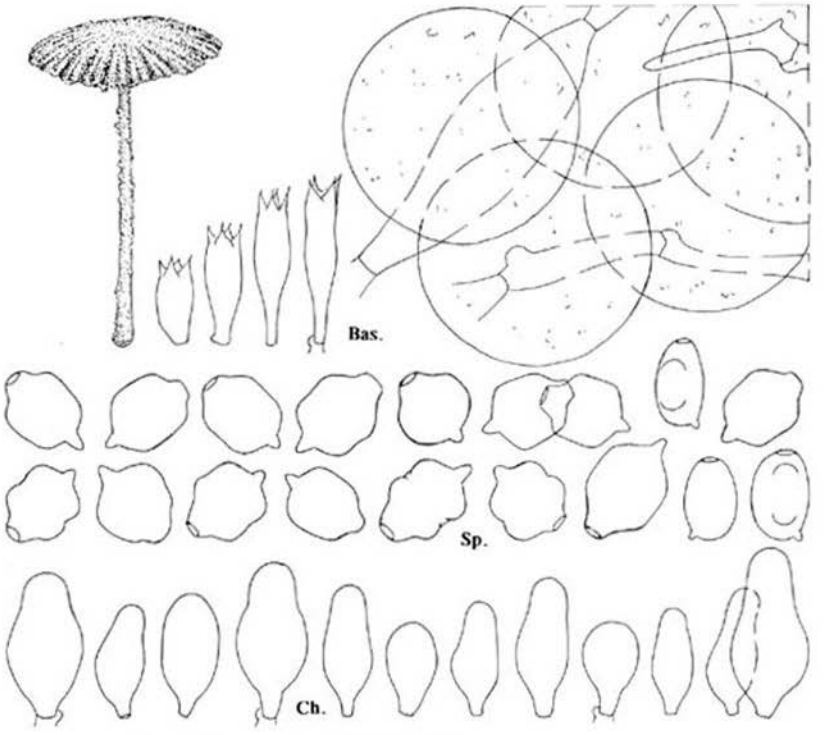

Fig. 16. *Coprinus iocularis* Uljé. All figures from *Uljé 851* (type).

Coprinus ephemeroides is a species close to *C. patouillardii* and *C. cordisporus*. It differs by having a small annulus and by the colour of the pileus which usually is more yellowish.

The sparse lageniform cheilocystidia, similar to those found in *Coprinus cordisporus* were also noted in *C. ephemeroides* (coll. *C.B. Uljé 1182*).

Orton & Watling (1979: 68) mentioned a somewhat similar 2-spored taxon. On account of the larger spores and the larger and greyer fruit-bodies they think the difference warrants separation as a distinct species.

16. **Coprinus iocularis** Uljé — Fig. 16

Coprinus iocularis Uljé, Persoonia 13 (1988) 485.

Pileus 27 mm wide, plano-convex, completely white-powdery. Lamellae L = c. 26, l = 1–3, free, first white, then grey to blackish spotted. Stipe 45 × 1.5 mm, with subbulbous base, whitish-hyaline, covered with white velar flocculi. Smell absent.

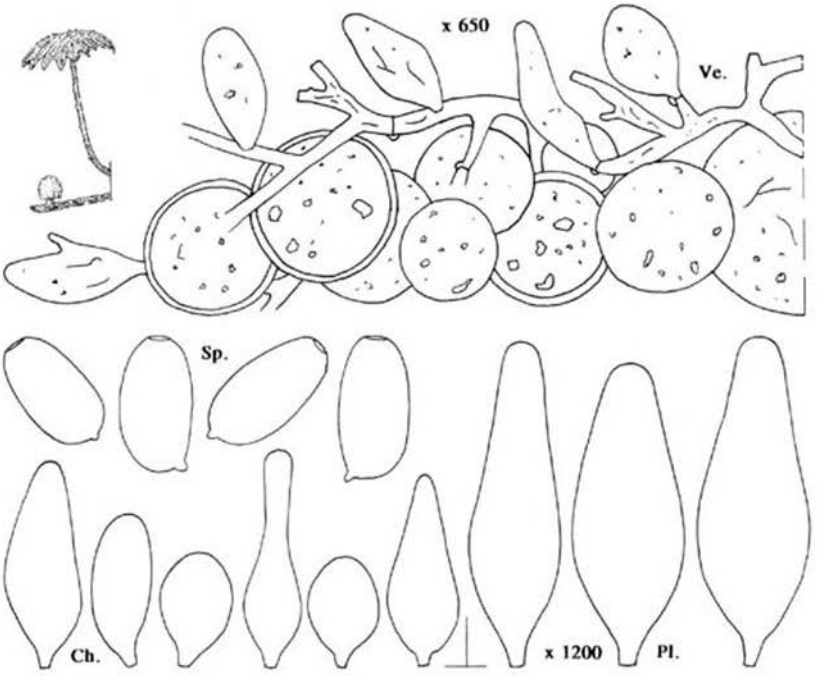

Fig. 17. *Coprinus pilosotomentosus* Bender. Figures based on original description.

Spores [60,2,2] 5.9–8.3 × 4.8–5.9 × 4.0–4.3 µm, Q = 1.05–1.45, av. Q = 1.25, av. L = 6.7–6.8 µm, av. B = 5.3–5.4 µm, in face view more or less hexagonal but frequently with two rounded lateral nodules at each side because of slightly depressed lateral faces, red-brown, with central germ pore. Basidia 13–32 × 6–8 µm, 4-spored, surrounded by 3–5 pseudoparaphyses. Cheilocystidia 20–35 × 8.5–15.5 µm, mostly utriform; neck 6–9.5 µm wide. Pleurocystidia absent. Veil on pileus consisting of up to 50 µm wide, smooth or somewhat granular globose elements mixed with frequently branching, colourless, thin-walled hyphae with processes. Clamp-connections present.

Habitat & distribution. Terrestrial on lawn. Very rare.

Collections examined. NETHERLANDS: prov. Zuid-Holland, Alphen a/d Rijn, near Zegerplas, 23 Aug. 1987, *C.B. Uljé 851* (holotype; L); Boskoop, Voshol, 15 Sept. 1989, *C.B. Uljé 1029*.

Coprinus iocularis can be recognized immediately by the characteristic shape of its spores. In face view the spores are more or less hexagonal (because of the two rounded lateral nodules at each side), in side view elliptical.

17. **Coprinus pilosotomentosus** Bender — Fig. 17

Coprinus pilosotomentosus Bender in Enderle & Bender, Z. Mykol. 56 (1990) 31.

Characteristics

Closed pileus globose, subglobose to ellipsoid or oval, up to 8 mm high and 4 mm wide, at first white to grey or pale brownish with powdery white veil beneath a cortina-like covering; expanded pileus 5–12 mm, then margin conspicuously split in the shape of a star and centre of pileus pale grey-brown; lamellae free, somewhat distant, white to blackish; stipe 20–50 × 0.5–1.2 mm, hollow, equal or attenuate upwards, when young covered with white velar flocks, at base more dense and forming a volva-like ring zone; smell absent.

Spores (8–)9–11.5 × 6–7(–7.5) µm, in side view somewhat cylindrical, oval or ellipsoid in frontal view, with central germ pore, dark red-brown; basidia 4-spored; cheilocystidia 18–45 × 8–13 µm, variable in shape: (sub)globose, ellipsoid, elongate-ellipsoid, utriform or (mostly) lageniform; pleurocystidia up to 60 µm in length, ellipsoid or utriform; pileipellis made up of ventricose, ellipsoid and subglobose elements covered by about 7 µm wide hyphae consisting of oblong-ventricose elements and these passing upwards into thin-walled colourless to slightly yellowish, smooth to granular, up to 45(–55) µm wide, globose velar elements, mixed with elongate elements; clamp-connections present.

Habitat & distribution. Gregarious. On dying grass (stems of *Festuca*). Known only from the type locality.

The description and illustration given here are based on the original description by Enderle & Bender (l.c.).

The most important differentiating characters of *Coprinus pilosotomentosus* are the dominantly lageniform cheilocystidia, presence of pleurocystidia and occurrence on grasses. Apart from some dung-inhabiting species, the only species in this subsection with pleurocystidia is *Coprinus idae*. This species differs in the shape of its cheilocystidia which are globose to utriform, the smaller, differently shaped spores, and smaller fruit-bodies.

Enderle & Bender (l.c.) do not indicate in which (sub)section their species should be placed. On account of the structure of the veil, we place it in subsection *Nivei*.

18. **Coprinus ramosocystidiatus** Bender — Fig. 18

Coprinus ramosocystidiatus Bender in Enderle & Bender, Z. Mykol. 56 (1990) 35.

Characteristics

Closed pileus 4 mm high and 3 mm broad, oval to ellipsoid then conical to convex, finally flat with upturned split margin, pale grey-brown with yellow-orange centre of pileus; with granular-powdery veil; expanded pileus 4–8 mm, slowly wilting; lamellae narrowly adnate, whitish to blackish; stipe 12–18 × 0.4–0.8 mm, hollow, equal, when young pruinose, base with white velar flocks; smell absent.

Spores 7.5–11.5 × 6–7.5 × (5–)5.5–6.5 µm, very variable in size (see discussion below), oval or ellipsoid in frontal view, the broader ones sometimes a little angular, ellipsoid to slightly amygdaliform in side view, with small central germ pore, c. 1.2 µm in diam.; basidia 4-spored; cheilocystidia (sub)globose, ellipsoid to ovoid, 10–21 in length

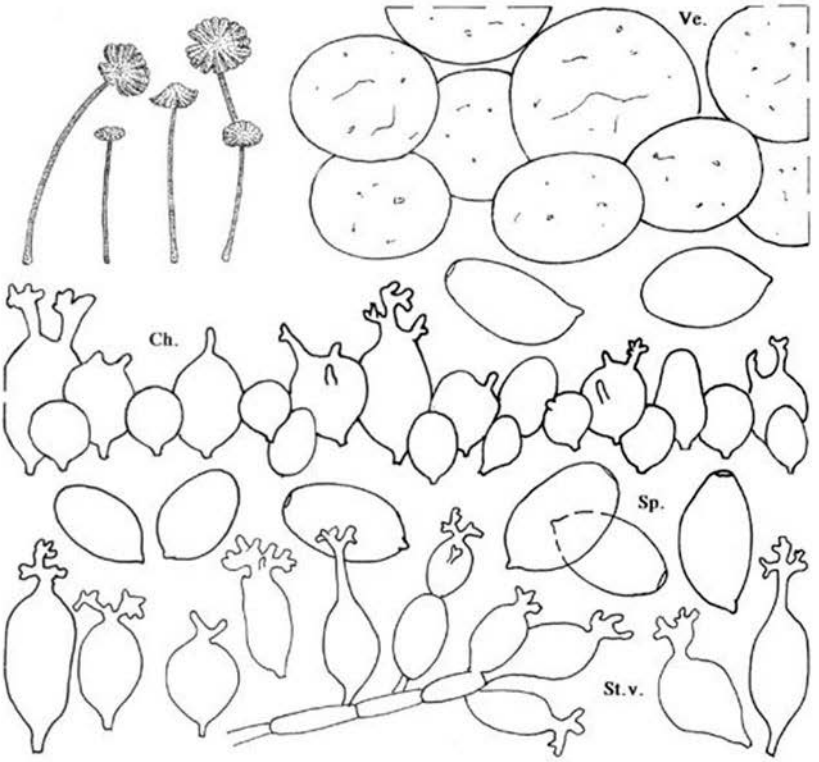

Fig. 18. *Coprinus ramosocystidiatus* Bender. Figures based on original description.

or with diverticulations and then up to 30 µm in length; pleurocystidia absent; pileipellis made up of slightly thick-walled, ventricose, ellipsoid and subglobose elements, 10–21 (–29) µm wide. Clamp-connections not found.

Habitat & distribution. Solitary or in small groups; on soil, among grasses and herbs. Known only from the type locality.

The description and illustration given here is based on the original publication of Bender (l.c.).

Coprinus ramosocystidiatus can be easily identified by the diverticulate cheilocystidia. The only other species known in subsection *Nivei* with such cystidia, is *C. cordisporus* which has completely differently shaped spores. From the type-locality several collections were gathered. Spore-size appears to be very variable: collection 7 Aug. 1987: (8.5–)10–11.5 × 6–7 × (5–)5.5–6 µm; collection 15 Aug. 1987 (holotype): 7.5–8.5 × 6–7 × 5.5–6 µm; collection 20 Aug. 1987: 9–10.5 × 6.5–7.5 × 5.5–6.5 µm.

Although Enderle & Bender (l.c.) placed *C. ramosocystidiatus* in the *'micaceus'*-group, we place it in subsection *Nivei*, on account of the mealy-powdery aspect of the veil, which can be easily seen in the coloured photograph that was published in the original publication. It is possible that the caulocystidia described by Bender actually represent remnants of the veil, adhering to the stipe surface. In the illustration (Bender, l.c.), these 'caulocystidia' were erroneously named 'pleurocystidia.'

19. **Coprinus coniophorus** Romagn. — Fig. 19

Coprinus coniophorus Romagn., Rev. Mycol. 6 (1941) 126.

Closed pileus globose, subglobose or ellipsoid, up to 7 mm high and 5 mm wide, completely covered with powdery, dark grey-brown veil (Mu. 10 YR 3–5/2, 7.5 YR 6–7/4), often with olive-green hue (Mu. 5 Y 3/1–2, 2.5 Y 5/4, 5 Y 5/3), forming small granular flocks at centre of pileus; veil at margin quickly disappearing, showing the white pileal surface; expanded pileus up to 12(–15) mm wide, conical or convex, later applanate. Lamellae, L = 14–24, l = 0–3, narrowly adnate, white at first then greyish to black. Stipe up to 30 × 0.5–1 mm, white, somewhat hyaline, at base clavate, up to 1.5 mm wide, often with brownish velar flocks. Smell absent.

Spores [140,7,6] 6.3–8.9 × 3.8–5.2 µm, Q = 1.45–2.10, av. Q = 1.70–1.85, av. L = 7.3–7.9, av. B = 4.0–4.6 µm, amygdaliform or ovoid, with central germ pore, red-brown. Basidia 13–30 × 6–8 µm, 4-spored, surrounded by 4–5 pseudoparaphyses. Pleurocystidia absent. Cheilocystidia 10–28 × 8–15 µm, variably shaped, narrowly clavate, clavate, ellipsoid, broadly utriform or subglobose, sometimes with median constriction. Veil made up of (sub)globose to ellipsoid or fusiform elements, smooth to (usually) strongly granular, up to 50 µm wide. Clamp-connections present.

Habitat & distribution. Gregarious, on and around stumps of deciduous trees. Rare in the Netherlands.

Collections examined. NETHERLANDS: prov. Noord-Holland, Amsterdam, Amsterdamse Bos, 17 Sept. 1986, *C.B. Uljé 32/86*; Amsterdam, Vliegenbos, 17 Sept. 1991, *R. Chrispijn* (*C.B. Uljé 1179*); prov. Utrecht, Breukelen, Sterreschans, 16 June 1992, *C.B. Uljé 1221, 1222, 1223, 1224.*

Coprinus coniophorus is very easy to identify, but the caespitose growth and shape of the basidiocarps (similar to *Coprinus disseminatus*) cause it to be easily overlooked. When in the field a group of *'Coprinus disseminatus'* is encountered with rather whitish basidiocarps, it is worthwhile to have a closer look, as it may well turn out to be *Coprinus coniophorus*. Contrary to *Coprinus disseminatus*, the primordia are not cream-coloured but dark grey. Later, when the pileus is expanding, the white colour of the pileus becomes visible as the veil disappears. As pointed out in the description, young specimens of *Coprinus coniophorus* may have a weak olivaceous tint, which is visible only under certain circumstances. Microscopically the shape of the cheilocystidia and size and shape of the spores are important diagnostic features. Sometimes the spores are ovoid for the most part, but usually they are distinctly amygdaliform, protruding to the germ-pore. Cheilocystidia are not always easy to find, sometimes sparse, but anyway characteristically shaped.

Coprinus poliomallus, another small mouse-grey species grows on dung, solitary or in small groups. It has always elliptical or ovate spores and distinct pleurocystidia.

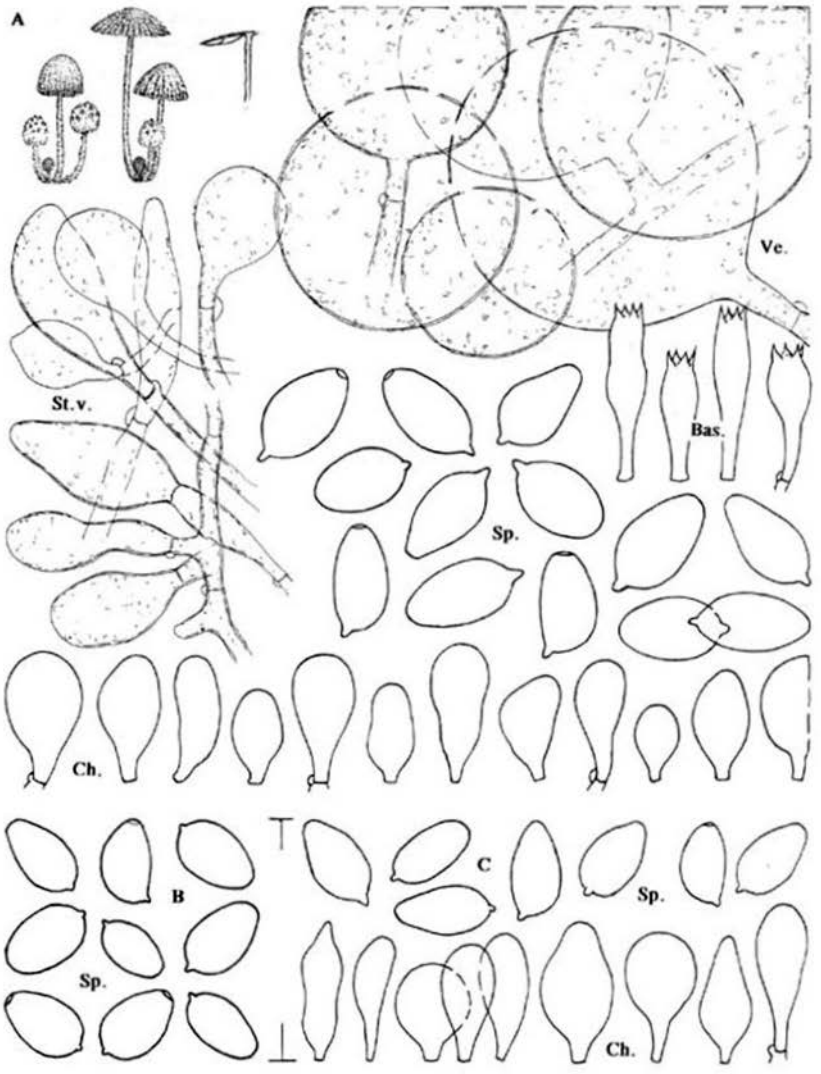

Fig. 19. *Coprinus coniophorus* Romagn. All figures from *Uljé 32/86*.

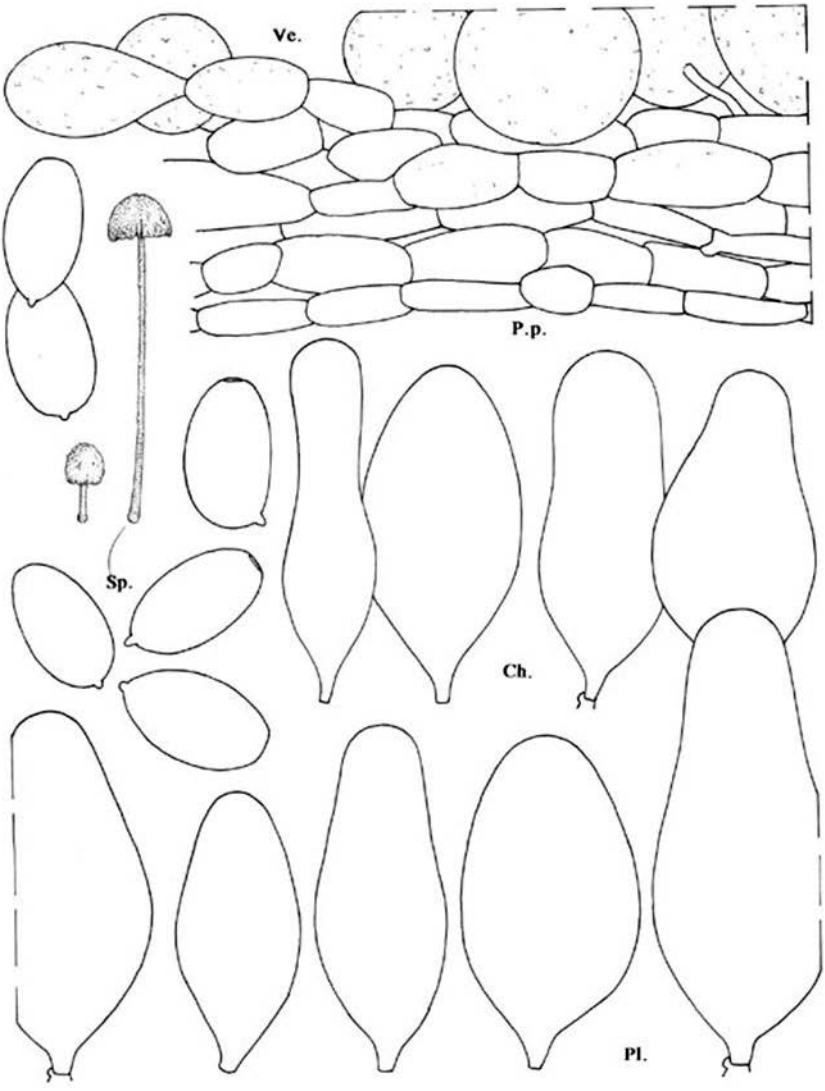

Fig. 20. *Coprinus nemoralis* Bender. All figures from holotype (coll. *Bender*, 16 June 1984).

20. **Coprinus nemoralis** Bender, *spec. nov.* — Fig. 20

Pileus primo ovatus, subglobosus vel ellipsoideus, usque ad 6 mm altus, usque ad 4 mm latus, toto pruinosus velo albo, centro cremeo vel ochraceo, dein explanatus ad 10 mm latus, convexus vel applanatus margine deflexus. Lamellae, L = c. 18, l = 1–3, liberae, ex albo-cinerascentes vel nigricantes. Stipes usque ad 50 × 0.5–1 mm, aequalis, albidus, juventute flocculosus, demum vitreus, versus basim incrassatus usque ad 1.5 mm, frequenter albo-flocculosus. Odore nullo.

Sporae 10–11.5 × 6.5–7.0 × 5.8–6.5 µm, Q = 1.45–1.90, in antice ovatae, ellipsoideae vel cylindraceo-ellipsoideae, in facie ellipsoideae vel amygdaliformes rubro-brunneae, cum poro germinativo centrico instructae. Basidia 15–36 × 7–9 µm, tetrasporigera. Pseudoparaphyses 3–5. Pleurocystidia vesiculosa, utriformia, ellipsoidea vel subcylindracea, interdum medio constricta. Cheilocystidia nulla. Velum e elementis globosis, usque ad 50 µm in diam., glabris vel granulosis constans. Fibulae presentes. Ad lignum putridum.

Holotypus: Germany, Mönchengladbach, Volksgarten (MTB 4804), 16 June 1984, *H. Bender* (L).

Closed pileus oval, subglobose to ellipsoid, up to 6 mm high and 4 mm wide, completely covered with powdery white veil, often cream to pale ochraceous at centre; expanded pileus up to 10 mm wide, convex or flat, finally with slightly deflexed margin; veil greying with age. Lamellae, L = c. 18, l = 1–3, free, white at first, then greyish to grey, finally black. Stipe up to 50 × 0.5–1 mm, equal, white, when young somewhat floccose, slightly hyaline; at base up to 1.5 mm wide, often with white velar flocks. Smell indistinctive.

Spores 10–11.5 × 6.5–7.0 × 5.8–6.5 µm (according to Uljé: sp. 9.7–12.3 × 5.7–6.8 µm, Q = 1.45–1.90, av. Q = 1.70, av. L = 10.9, av. B = 6.4 µm), oval, ellipsoid or cylindrico-ellipsoid in frontal view, ellipsoid, sometimes slightly amygdaliform in face view, red-brown in water, with central germ pore. Basidia 15–36 × 7–9 µm, 4-spored, surrounded by 3–5 pseudoparaphyses. Pleurocystidia vesiculose, utriform, ellipsoid or subcylindric, some with median constriction. Veil made up of colourless to slightly yellowish, smooth to granular, up to 50 µm wide, globose elements. Clamp-connections present.

Habitat & distribution. Solitary or in small groups; on branches and other pieces of wood. Known only from type locality.

Collection examined. GERMANY: Mönchengladbach, Volksgarten (MTB 4804), 16 June 1984, *H. Bender* (holotype; L).

Coprinus nemoralis differs from other species having ellipsoid spores and pleurocystidia in its larger spores and cystidia and its growth on woody debris. *C. pilosotomentosus* has spores similar to those of *C. nemoralis*, but that species grows on grasses and the cystidia are much smaller.

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Sincere thanks are due to Mr. H. Bender, Mönchengladbach, Germany and Mr. S. Veldre, Estonia for the loan and gift of valuable material for this study. Many members of the Netherlands' Mycological Society supplied us with interesting material. The Director of the Royal Botanic Gardens, Edinburgh, is thanked for the loan of type-material. Dr. R.A. Maas Geesteranus and Dr. Th.W. Kuyper critically reviewed and improved the text of this paper, for which we are very grateful.

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ULTRASTRUCTURE OF THE ASCUS APICAL APPARATUS IN HYMENOSCYPHUS AND OTHER GENERA OF THE HYMENOSCYPHOIDEAE (LEOTIALES, ASCOMYCOTINA)

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The ultrastructure of the ascus apical apparatus is compared in 19 species of the Hymenoscyphoideae, currently placed in seven genera. The ascus wall consists of an outer layer of two strata, and an inner layer of also two, and in one species of three strata. At the apex only the inner layer increases in thickness. On the basis of the general morphology and PA-TCH-SP reactivity pattern of the apex five main groups are recognized. A further division into subgroups is also outlined. The most important diagnostic features used in the analysis are the relative development and the reactivity pattern of the apical thickening, the occurrence of an annular protrusion, the structure and the reactivity pattern of the annulus, and the apex maturation pattern. In addition to the electron micrographs diagrammatic schemes are given to illustrate the author's interpretation.

The species studied are thus arranged as follows: Group 1a. *Hymenoscyphus caudatus*, *H. fructigenus*, *H. salicellus*, *H. salicinus*, and *Bisporella pallescens*; 1b. *H. imberbis* and *Phaeohelotium subcarneum*; 1c. *H. consobrinus*, *H. repandus*, and *Crocicreas pallidum*; 1d. *Discinella boudieri*; Group 2a. *H. herbarum*; 2b. *Pezizella gemmarum*; 2c. *Chlorociboria aeruginascens* and *Pezizella alniella*; 2d. *Crocicreas cyathoideum* [var. *cyathoideum*]; Group 3. *Bisporella sulfurina*; Group 4. *Cudoniella clavus* var. *grandis*; Group 5. *Cudoniella acicularis*.

Most fundamental are considered firstly the position of the annulus in the apical thickening, either partly (groups 1, 2, 4, 5) or fully (3) occupying the thickening, either associated (2, 4, 5) or not associated with an annular protrusion (1), and secondly the dehiscence mechanism, either an eversion of the annulus over an angle of about 90° (1, 2, 3?, 4) or a two-step mechanism (5) previously undescribed in Leotiales. The absence of an amyloid reaction in the apex, which is a diagnostic feature in *Cudoniella acicularis* and *C. clavus* var. *grandis*, is based on two fundamentally different structures in these species. The apex in the last mentioned fungus closely resembles that in *Ombrophila violacea*, while the apex in *C. acicularis* is unique in general morphology and dehiscence mechanism.

The ultrastructural data of the apical apparatus are found to correlate with characters of excipulum anatomy, especially in the genera *Hymenoscyphus* and *Bisporella*. Their importance in segregating more natural genera from large ill-defined genera like *Hymenoscyphus* or *Pezizella* is discussed.

INTRODUCTION

The structure of the ascus is of paramount importance in the classification of the higher taxa in the Ascomycotina (Boudier, 1879, 1907; Nannfeldt, 1932; Korf, 1973; Eriksson & Hawksworth, 1987, 1988). In contrast, its influence at lower taxonomic levels is lim-

ited. Several students of ascomycetes have emphasized the possible significance of the structure of the ascus for the delimitation of families and genera (Luttrell, 1951; Chadefaud, 1973; Beckett, 1981). The light optical studies on ascus structure in the Leotiales S. Carp. were valuable as far as they were focussed on structures with dimensions well above the limit of the resolving power of the light microscope. For the study of structures in the ascus with dimensions close to or under this limit, such as the basal septum and the apical apparatus, only the transmission electron microscope offers the appropriate resolving power. As yet this instrument has been used by few taxonomists to study a limited number of species of the Leotiales (Schoknecht, 1975; Bellemère, 1975, 1977; Benny et al., 1978; Bellemère et al., 1987; Verkley, 1992, 1993).

Monographers of Leotiales are still faced with a scarcity of distinctive characters useful to define generic concepts. Especially for the circumscription of genera in the family Leotiaceae Corda they have to depend largely on characters most of which also occur outside the group of species to be considered. Some genera are ill-defined and an extremely large number of species has been referred to them over the years. *Hymenoscyphus* S.F. Gray and *Pezizella* Fuckel thus became classical examples of a 'waste-basket genus' (Korf, 1973).

The genus *Hymenoscyphus* as interpreted by most authors for many years (Dennis, 1964, 1978; Dumont, 1981) and most recently by Lizoñ (1992), shows considerable variation in the anatomy of the ectal excipulum and in ascospore characters, e.g. shape and presence of 'cilia'. Efforts to separate from the large genus *Hymenoscyphus* a number of new genera were not successful (Dennis, 1956, 1964; Dumont, 1981). Several species of *Bisporella* Sacc., *Pezizella*, and *Phaeohelotium* Kanouse have been considered more closely related to, or congeneric with, certain species of *Hymenoscyphus* (Baral & Krieglsteiner, 1985). Baral & Krieglsteiner (1985) have proposed major systematic changes under the influence of their light microscopic observations of the ascus apex. For reasons mentioned above this is a less fortunate approach. It illustrates the great need for additional characters that are less variable at the genus level and of a comparatively conservative evolutionary nature. Ultrastructural studies of the apical apparatus may provide a complex of such characters. The present investigation of eight species of *Hymenoscyphus* is an effort to determine the variation of this character complex, firstly within a group of species considered structurally more similar to the type species, *H. fructigenus* (Bull.: Fr.) S.F. Gray, than others, and secondly between this group and structurally different species currently referred to this genus.

The variation in ultrastructure of the ascus wall and the apical apparatus in other genera of the Hymenoscyphoideae sensu Korf (1973) is also practically unknown. Therefore, the ultrastructure of the ascus apical apparatus of 11 selected species from the genera *Bisporella*, *Cudoniella* Sacc., *Chlorociboria* Seaver ex Ramamurthi et al. emend. Dixon, *Discinella* Boud., *Crocicreas* Fr., and *Pezizella* were studied. The data are compared with those obtained in earlier studies on Sclerotiniaceae and Ombrophiloideae sensu Dennis (Verkley, 1992, 1993). They are discussed in relation to other characters like those pertaining to the structure of the excipulum and the ascospores.

MATERIALS AND METHODS

Fresh material was collected in the field. Parts of fruit-bodies were fixed for 3 hours using 1% glutaraldehyde in 0.1 M cacodylate buffer (pH 7.2) at 4°C. After washing in buffer the material was postfixed for 1 hour using 1% osmium tetroxide in cacodylate buffer at room temperature. During dehydration the material was stained with 1% uranyl acetate dissolved in 30, 50, 70, and 96% ethanol in water (5 minutes for each grade). Then the material was embedded in Epon 3/7. Ultrathin sections were cut using a diamond knife on a Reichert Jung Ultracut E ultratome.

Sections were picked up on 200 mesh gold grids and treated for periodic acid-thiocarbohydrazide-silver proteinate (PA-TCH-SP) as described by Verkley (1992) and modified from Thiéry (1967).

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).

Bisporella pallescens (Pers.) S. Carp. & Korf. 'Oud Poelgeest', Oegstgeest, prov. Zuid-Holland, the Netherlands, on shredded wood, May 1992, *G. Verkley 126*.

Bisporella sulfurina (Quél.) S. Carp. Windesheim, Zwolle, prov. Overijssel, the Netherlands, on wood, Oct. 1990, *Piepenbroek 1834*; Oostvaardersplassen, Lelystad, prov. Flevoland, the Netherlands, on dead stems of *Epilobium*, July 1991, *G. Verkley 87*.

Chlorociboria aeruginascens (Nyl.) Kanouse ex Ramamurthi et al., Fôret de Citeaux, Bagnot, dép. Côte d'Or, France, on dead wood, Oct. 1990, *J. van Brummelen 7957*.

Crocicreas cyathoideum (Bull.: Fr.) S. Carp. [var. *cyathoideum*]. Windesheim, Zwolle, prov. Overijssel, the Netherlands, on dead stems of Umbelliferae, May 1990, *Piepenbroek 1760*; Oranjepolder, Voorschoten, prov. Zuid-Holland, the Netherlands, on dead stems of *Urtica*, Apr. 1992, *G. Verkley 123*.

Crocicreas pallidum (Velen.) S. Carp. Oranjepolder, Voorschoten, prov. Zuid-Holland, the Netherlands, on fallen petioles of *Fraxinus* and *Acer*, Oct. 1991, *G. Verkley 96*.

Cudoniella acicularis (Bull.: Fr.) J. Schroet. Finnån river, east of Femsjö, Smölland, Sweden, on soil and plant debris, Aug. 1989, *J. van Brummelen 7885*.

Cudoniella clavus (Alb. & Schw.: Fr.) Dennis var. *grandis* (Boud.) Dennis, Roode Beek, Vlodrop, prov. Limburg, the Netherlands, on dead wood, May 1990, *H. Huijser s.n.*

Discinella boudieri (Quél.) Boud. Fôret de St. Prix, Arnay-le-Duc, dép. Côte d'Or, France, on soil, Oct. 1990, *H. Marxmüller (J. van Brummelen 7975)*.

Hymenoscyphus caudatus (P. Karst.) Dennis. Oranjepolder, Voorschoten, prov. Zuid-Holland, the Netherlands, on dead herbaceous stems and fallen petioles of *Fraxinus*, July 1991, *G. Verkley 95*.

Hymenoscyphus consobrinus (Boud.) Hengstmengel. Hengforder Waarden, Olst, prov. Overijssel, the Netherlands, on dead herbaceous stems, June 1990, *Piepenbroek 1770*; Windesheim, Zwolle, prov. Overijssel, the Netherlands, on dead herbaceous stems, July 1990, *Piepenbroek 1790*.

Hymenoscyphus fructigenus (Bull.: Fr.) S.F. Gray. 'Oud Poelgeest', Oegstgeest, prov. Zuid-Holland, the Netherlands, on fallen acorns of *Quercus*, Sept. 1992, *G. Verkley 132*.

Hymenoscyphus herbarum (Pers.: Fr.) Dennis. Goudplaat, Wissenkerke, prov. Zeeland, the Netherlands, on dead stems of *Urtica*, Oct. 1992, *G. Verkley 139*.

Hymenoscyphus imberbis (Bull.: Fr.) Dennis. Oranjepolder, Voorschoten, prov. Zuid-Holland, the Netherlands, on fallen branches of *Salix*, Oct. 1991, *G. Verkley 97*.

Hymenoscyphus repandus (Phill.) Dennis. Groot Berkheide, Wassenaar, prov. Zuid-Holland, the Netherlands, on dead stems of *Epilobium*, May 1990, *G. Verkley s.n.*

Hymenoscyphus salicellus (Fr.) Dennis. Hengforder Waarden, Olst, prov. Overijssel, the Netherlands, on dead branches of *Salix*, June 1990, *Piepenbroek 1766* and *1769*; Windesheim, Zwolle, prov. Overijssel, the Netherlands, on dead branches of *Salix*, July 1990, *Piepenbroek 1791*.

Hymenoscyphus salicinus (Pers.: Fr.) Kuntze. Harderbos, Zeewolde, prov. Flevoland, the Netherlands, on dead wood, May 1990, *F. Ligtenberg s.n.*; Windesheim, Zwolle, prov. Overijssel, the Netherlands, on fallen branches of *Salix*, Oct. 1990, *Piepenbroek 1827*.

Pezizella alniella (Nyl.) Dennis. St. Jansberg, Mook en Middelaar, prov. Limburg, the Netherlands, on fallen female catkins of *Alnus*, March 1992, *G. Verkley 100*.

Pezizella gemmarum (Boud.) Dennis. Bos van Bosman, Leiden, prov. Zuid-Holland, the Netherlands, on fallen budscales of *Populus*, April 1992, *G. Verkley 120* and *124*.

Phaeohelotium subcarneum (Schum.) Dennis. Fôret de St. Léger, dép. Côte d'Or, France, on wood, Oct. 1990, *J. van Brummelen 7963*.

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

RESULTS

The extracellular matrix is not noticeably contrasted during the uranyl staining as presently applied. In agreement with earlier work (Verkley, 1992, 1993) the term reactivity is therefore used as an equivalent of electron density in the walls. In the ascoplasm uranyl, osmium and silver deposition determine the electron density. Series of longitudinal median sections of young, immature, mature and dehisced asci were studied. The lateral ascus wall and the apical apparatus are described.

(text continued on page 319)

Abbreviations used in figures 1–77. **A**, annulus; **AC**, apical chamber; **AP**, annular protrusion; **AS**, ascospore; **AT**, apical thickening; **av**, apical vesicle; **AW**, ascus wall; **CC**, central cylinder; **E**, epiplasm; **ER**, endoplasmatic reticulum; **G**, glycogen; **IL**, inner layer; **im**, investing membrane; **is**, inner stratum; **L**, lipid body; **M**, gelatinous matrix; **m**, mitochondrion; **mf**, 'myelin figure'; **ms**, middle stratum; **mv**, microvesicles; **N**, nucleus; **OL**, outer layer; **os**, outer stratum; **P**, periascus; **Pa**, paraphysis; **pw**, primary ascospore wall; **SP**, sporoplasm; **SW**, ascospore wall; **sw**, secondary ascospore wall; **ts**, tubular system; **V**, vacuole.

LEGENDS TO FIGURES 1–61:

Figs. 1–6. Longitudinal median sections of ascus apices treated with PA-TCH-SP (bar equals 1 μm). – 1. *Discinella boudieri*. Young elongating ascus. – 2. *Cudoniella acicularis*. Young elongating ascus with rounded apex. – 3–5. *Bisporella pallescens*. 3. Young ascus; 4. mature ascus; 5. dehisced ascus. – 6. *Bisporella sulfurina*. Young ascus.

Figs. 7–12. Longitudinal median sections of ascus apices treated with PA-TCH-SP (bar equals 1 μm). – 7–9. *Bisporella sulfurina*. 7. Immature ascus; 8. mature ascus; 9. dehisced ascus. – 10–12. *Chlorociboria aeruginascens*. 10. Young ascus; 11. immature ascus; 12. mature ascus.

Figs. 13–17. Longitudinal median sections of ascus apices treated with PA-TCH-SP (bar equals 1 μm). – 13–15. *Crocicreas cyathoideum*. 13. Young ascus; 14. immature ascus, advanced stage; 15. dehisced ascus. – 16, 17. *Crocicreas pallidum*. 16. Young ascus; 17. mature ascus.

Figs. 18–24. *Cudoniella acicularis*. Longitudinal median sections of ascus apices treated with PA-TCH-SP (bar equals 1 μm). 18. Young elongating ascus, with conical apex; 19. immature ascus, early stage (primary ascospore wall development); 20. immature ascus, advanced stage (secondary ascospore wall development); 21. mature ascus; 22. idem; 23. dehisced ascus; 24. idem.

Figs. 25–30. Longitudinal median sections of ascus apices and lateral ascus wall (Fig. 30) treated with PA-TCH-SP (bar equals 1 μm). – 25, 26. *Cudoniella clavus* var. *grandis*. 25. Young ascus; 26. immature ascus, advanced stage. – 27–29. *Discinella boudieri*. 27. Immature ascus, early stage (ascospores have just been delimited); 28. immature ascus, advanced stage; 29. dehisced ascus. – 30. *Hymenoscyphus caudatus*. Lateral ascus wall in immature ascus.

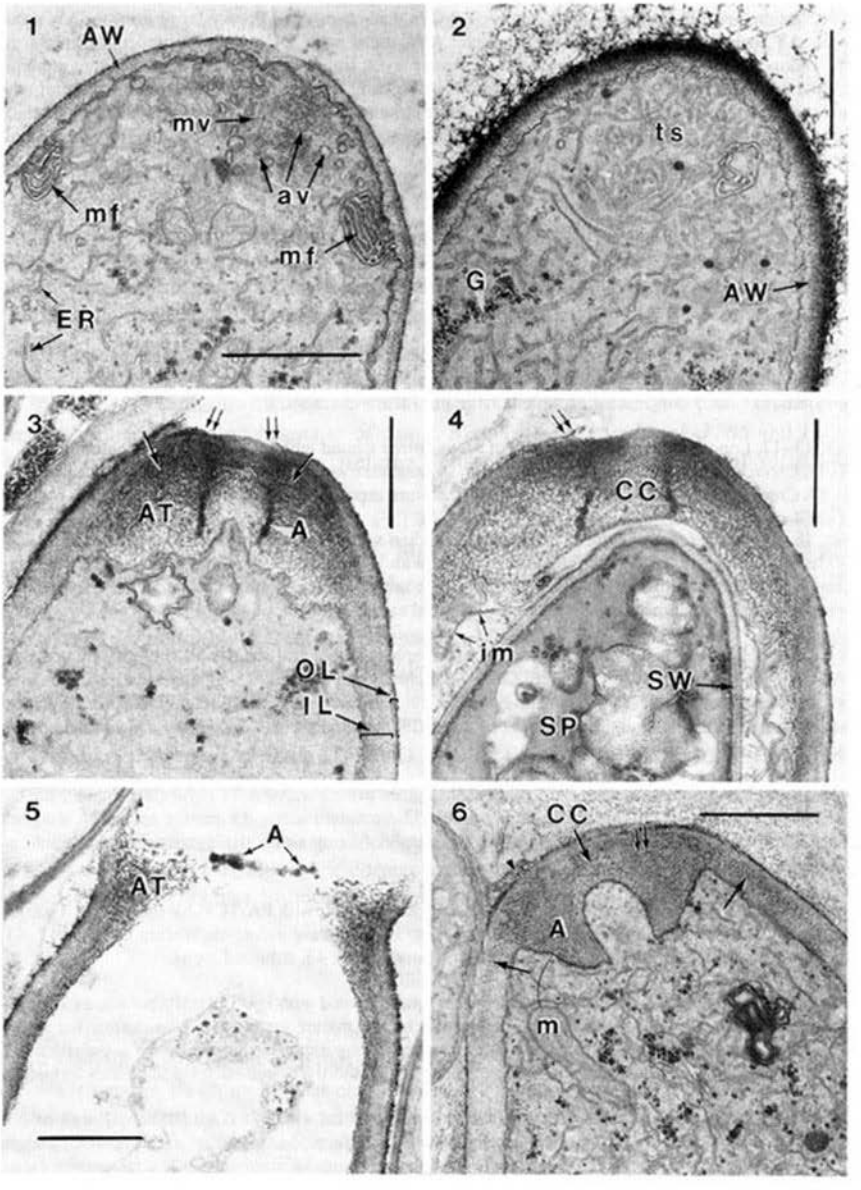
Figs. 31–37. Longitudinal median sections of ascus apices treated with PA-TCH-SP (bar equals 1 μm). – 31–35. *Hymenoscyphus caudatus*. 31. Young ascus; 32. immature ascus; 33. mature ascus; 34. dehisced ascus; 35. idem. – 36, 37. *Hymenoscyphus fructigenus*. 36. Young ascus, during ascospore delimitation; 37. dehisced ascus.

Figs. 38–43. Longitudinal median sections of ascus apices treated with PA-TCH-SP (bar equals 1 μm). – 38–40. *Hymenoscyphus salicellus*. 38. Young ascus; 39. immature ascus; 40. mature ascus. – 41–43. *Hymenoscyphus salicinus*. 41. Young ascus; 42. immature ascus; 43. dehisced ascus.

Figs. 44–49. Longitudinal median sections of ascus apices treated with PA-TCH-SP (bar equals 1 μm). – 44, 45. *Hymenoscyphus consobrinus*. 44. Immature ascus; 45. mature ascus. – 46. *Hymenoscyphus repandus*. Immature ascus. – 47, 48. *Hymenoscyphus imberbis*. Young ascus, during ascospore delimitation; 48. mature ascus. – 49. *Hymenoscyphus herbarum*. Young ascus, shortly before completion of apex formation.

Figs. 50–55. Longitudinal median sections of ascus apices treated with PA-TCH-SP (bar equals 1 μm). – 50–52. *Hymenoscyphus herbarum*. 50. Immature ascus, early stage; 51. immature ascus, advanced stage; 52. dehisced ascus. – 53–55. *Pezizella alniella*. 53. Young ascus; 54. immature ascus; 55. mature ascus.

Figs. 56–61. Longitudinal median sections of ascus apices treated with PA-TCH-SP (bar equals 1 μm). – 56–58. *Pezizella gemmarum*. 56. Young ascus; 57. mature ascus; 58. dehisced ascus. – 59–61. *Phaeohelotium subcarneum*. 59. Immature ascus, early stage; 60. mature ascus; 61. dehisced ascus.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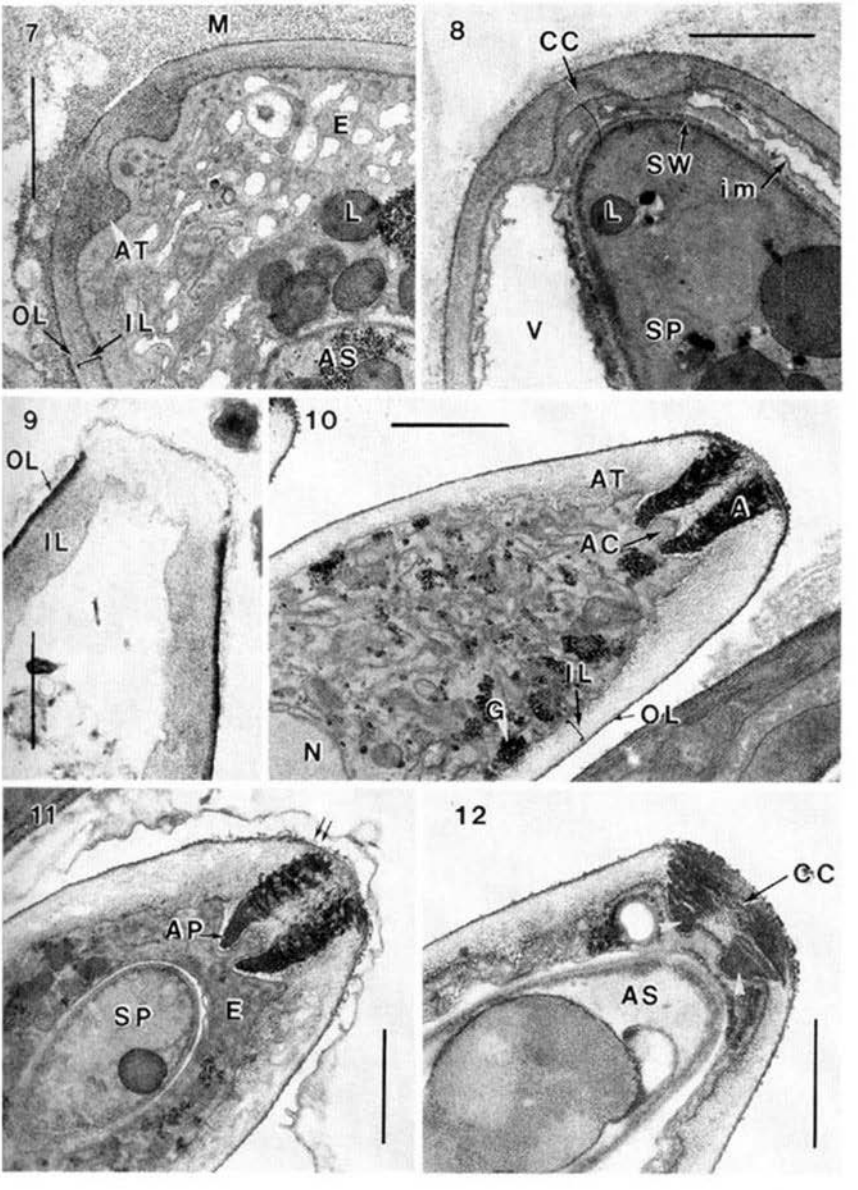
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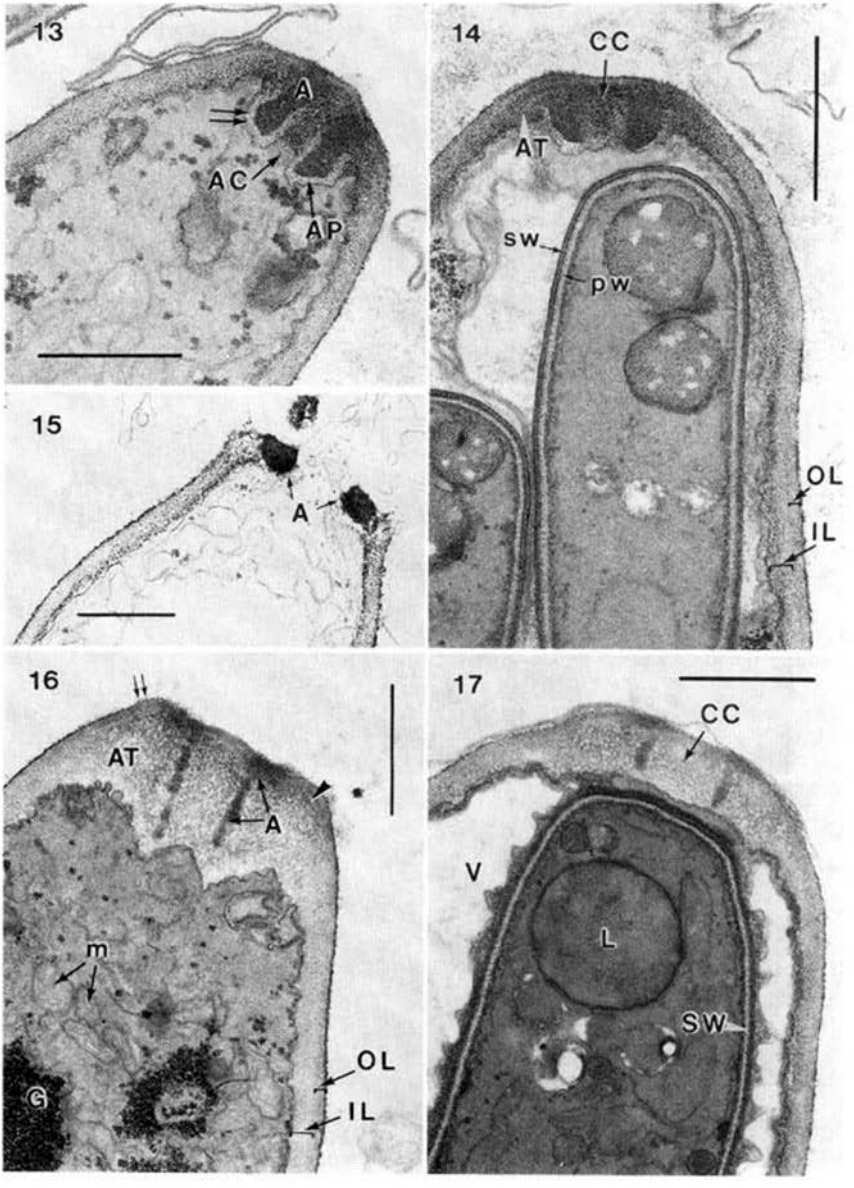
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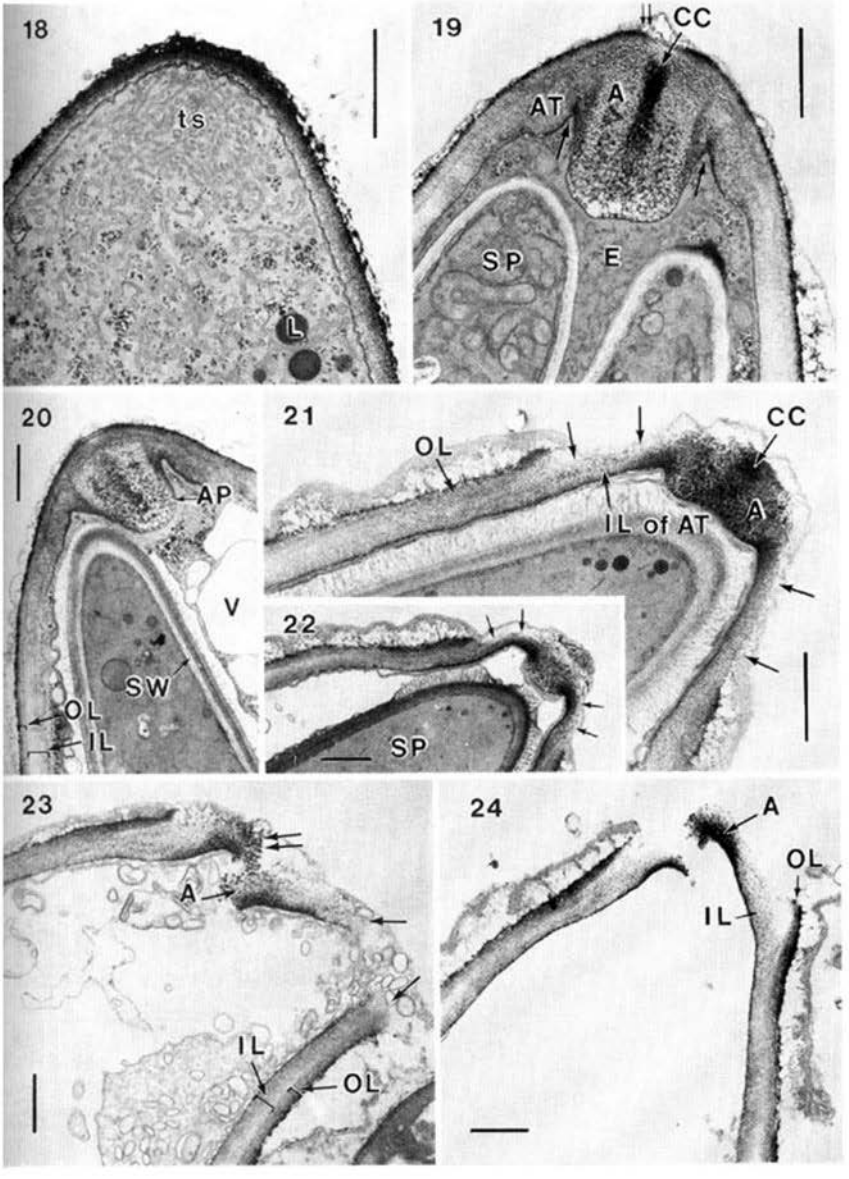
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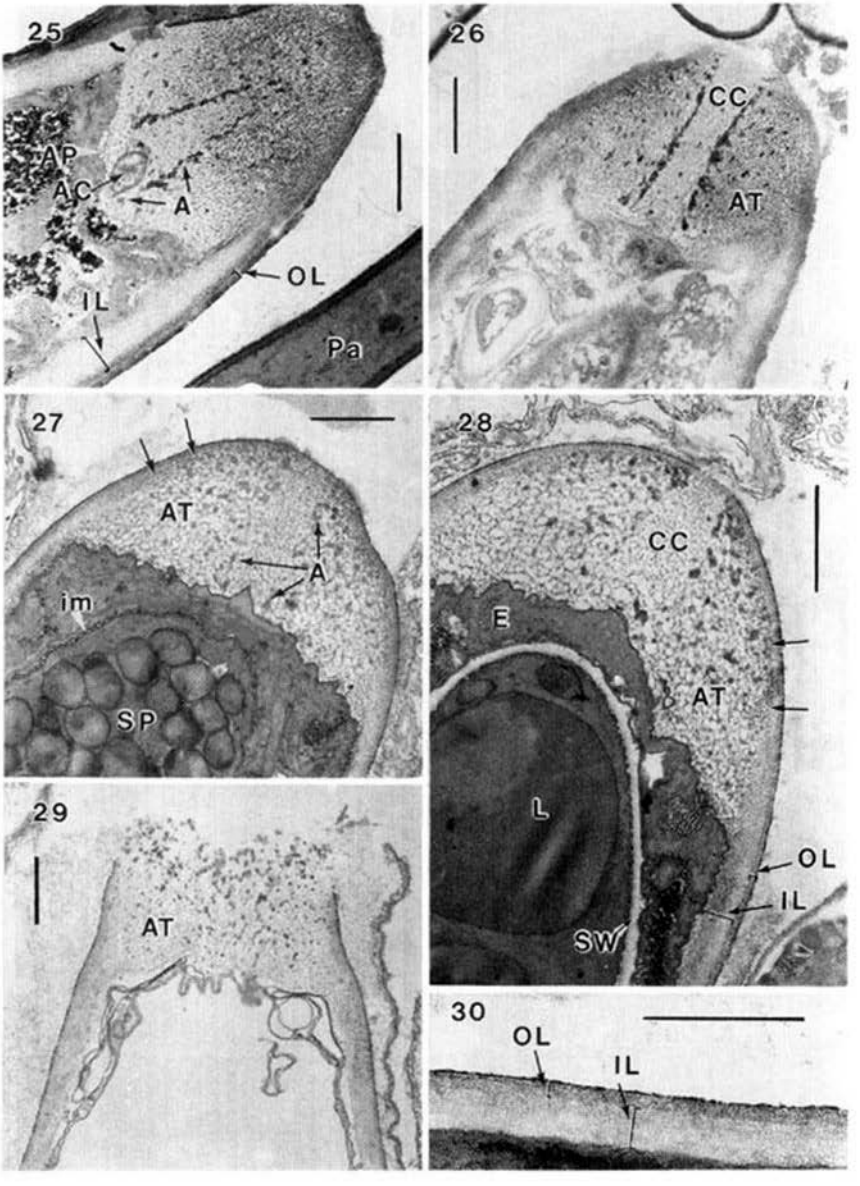
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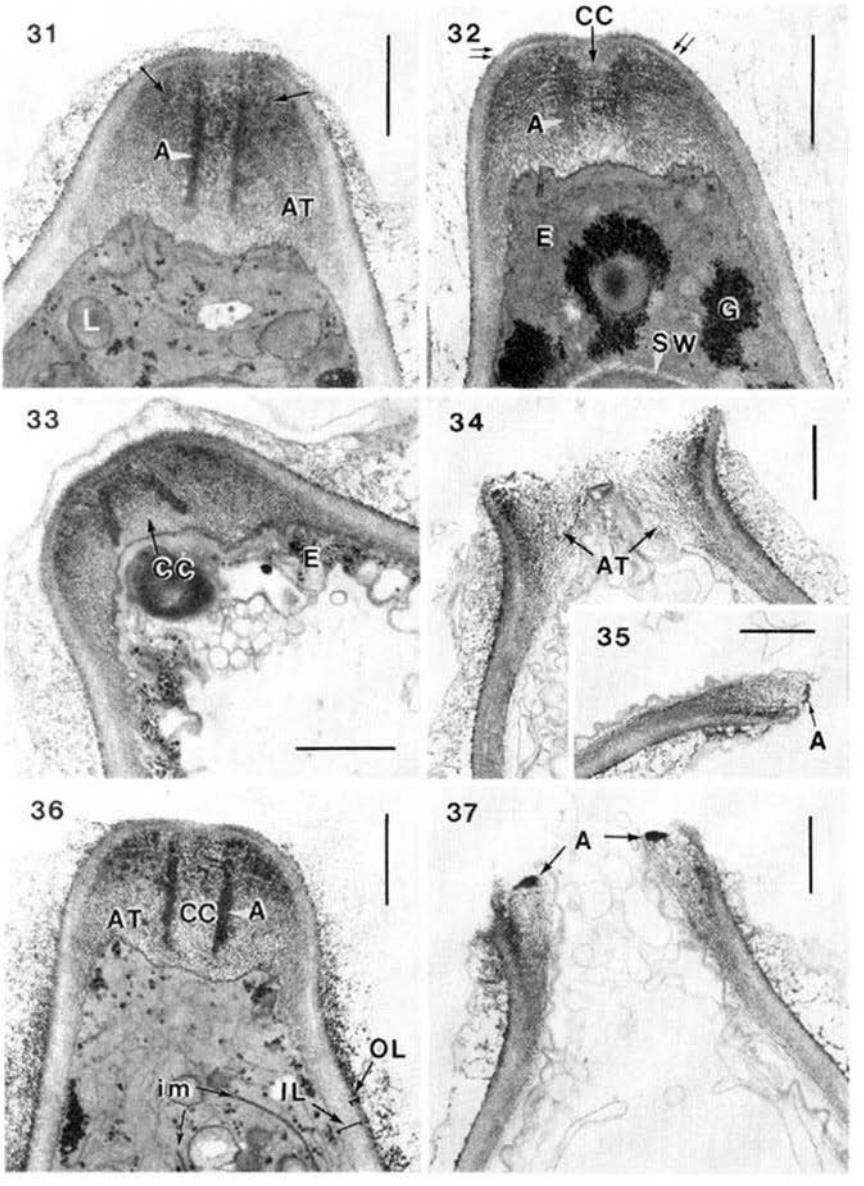
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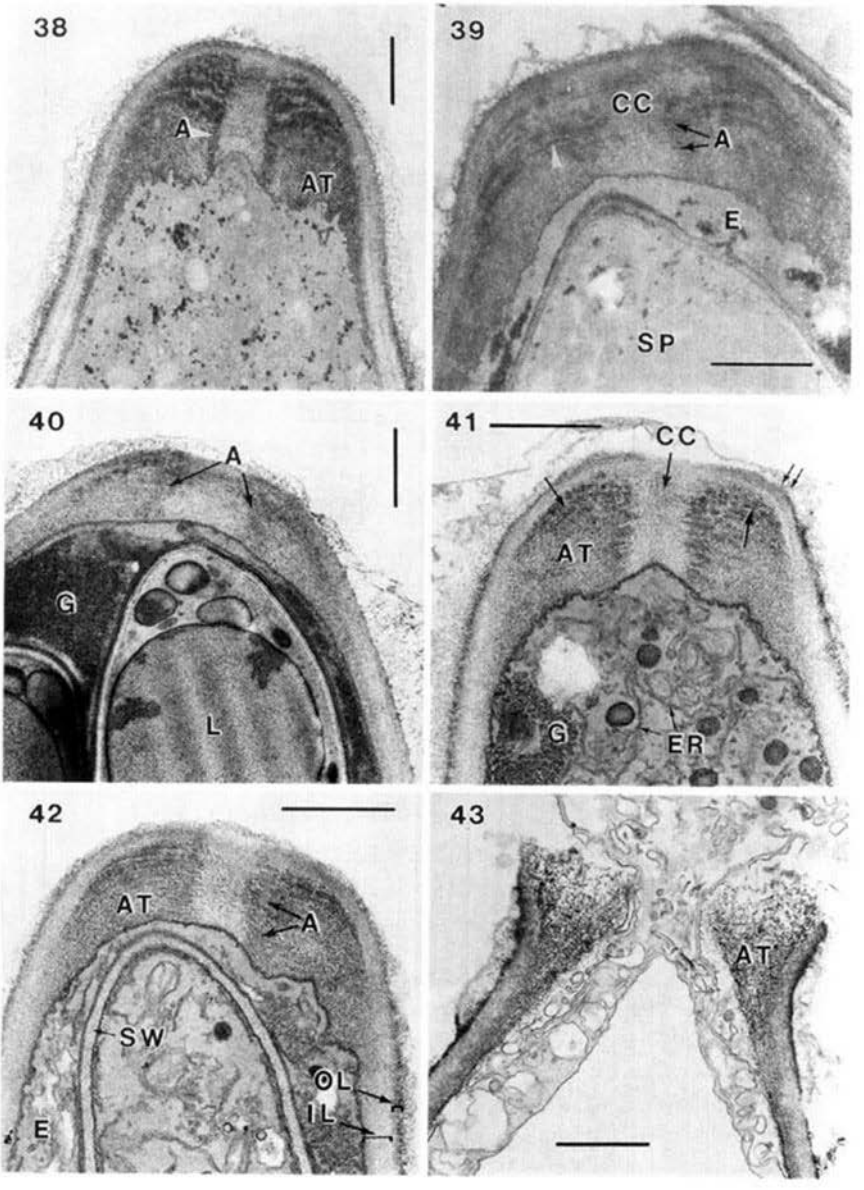
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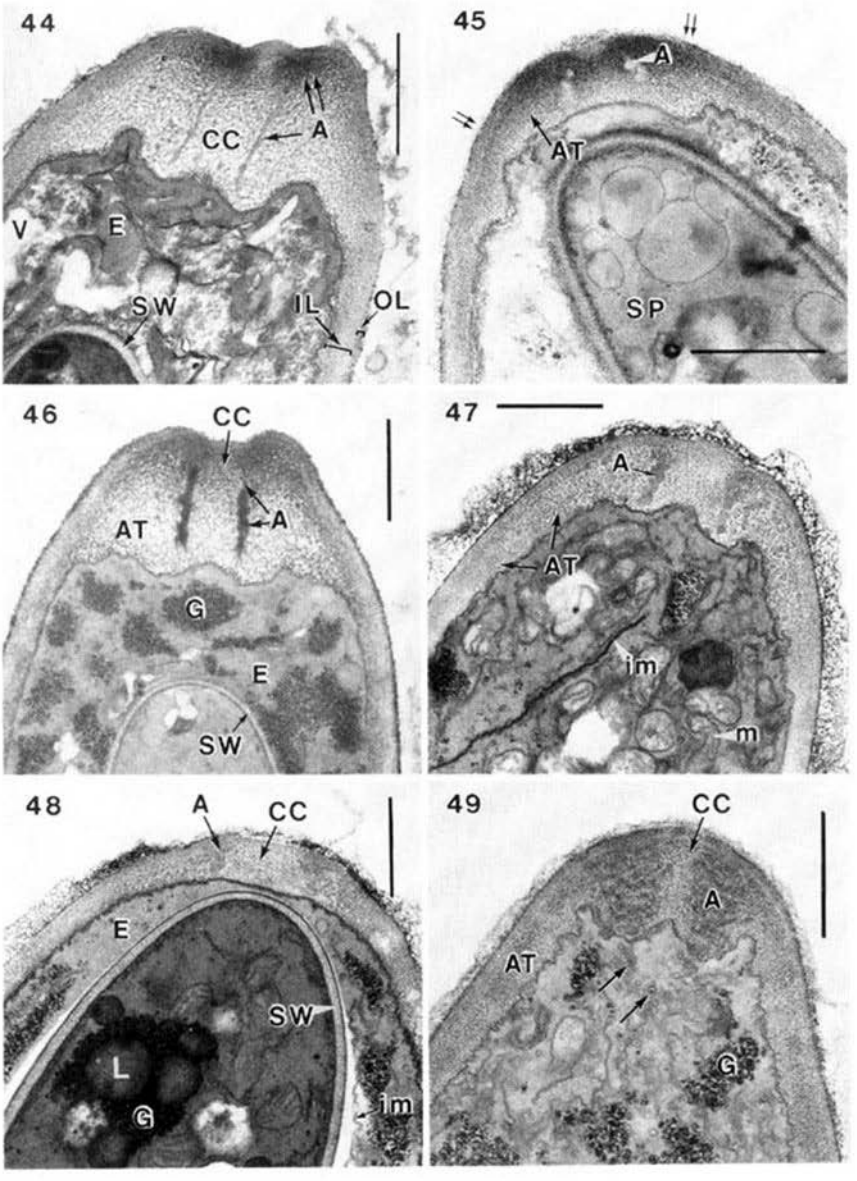
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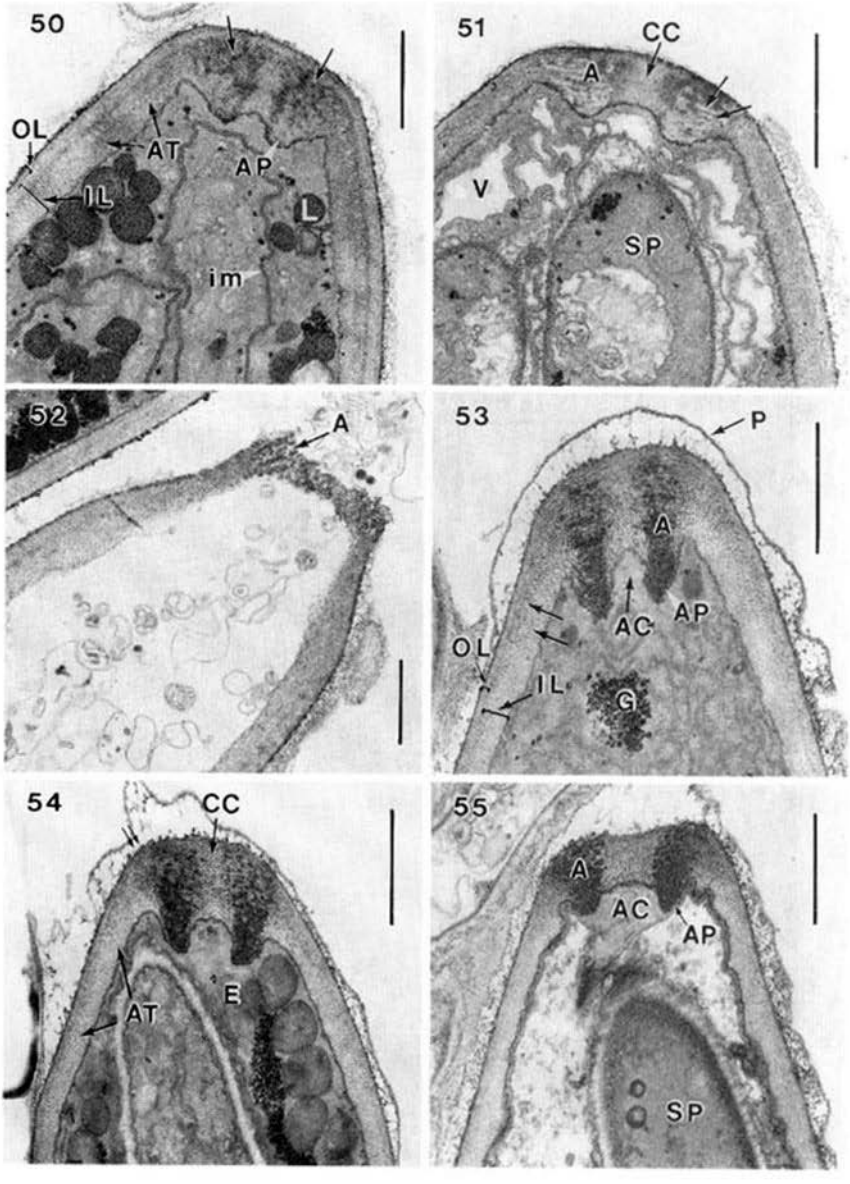
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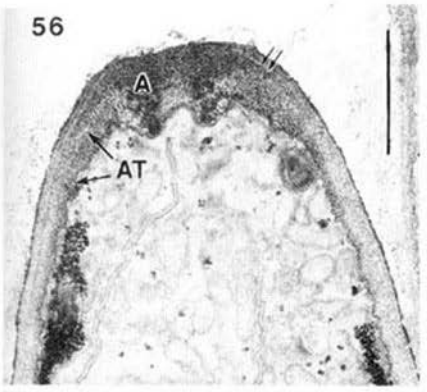
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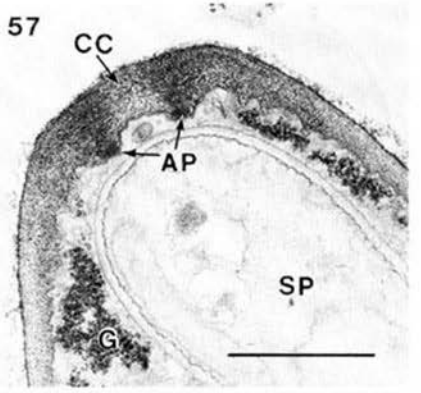
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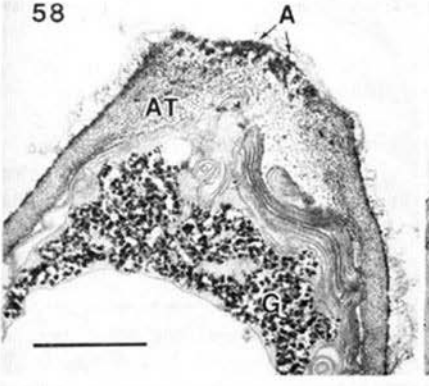
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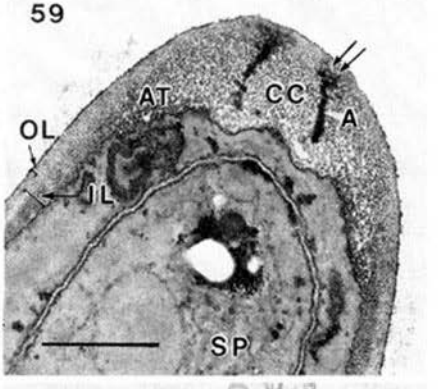
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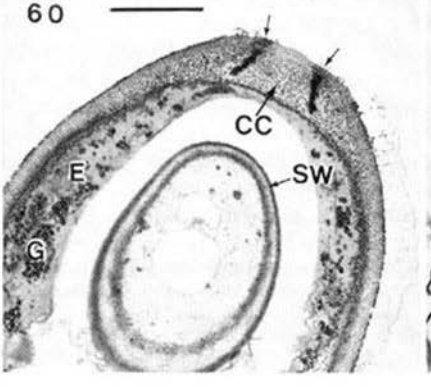
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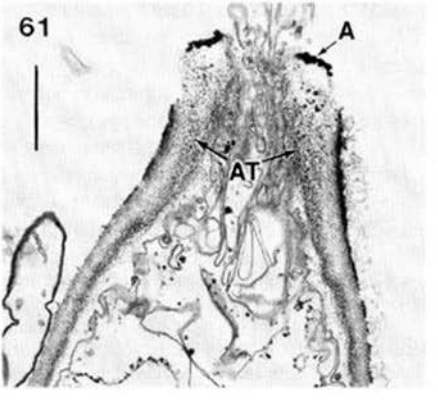
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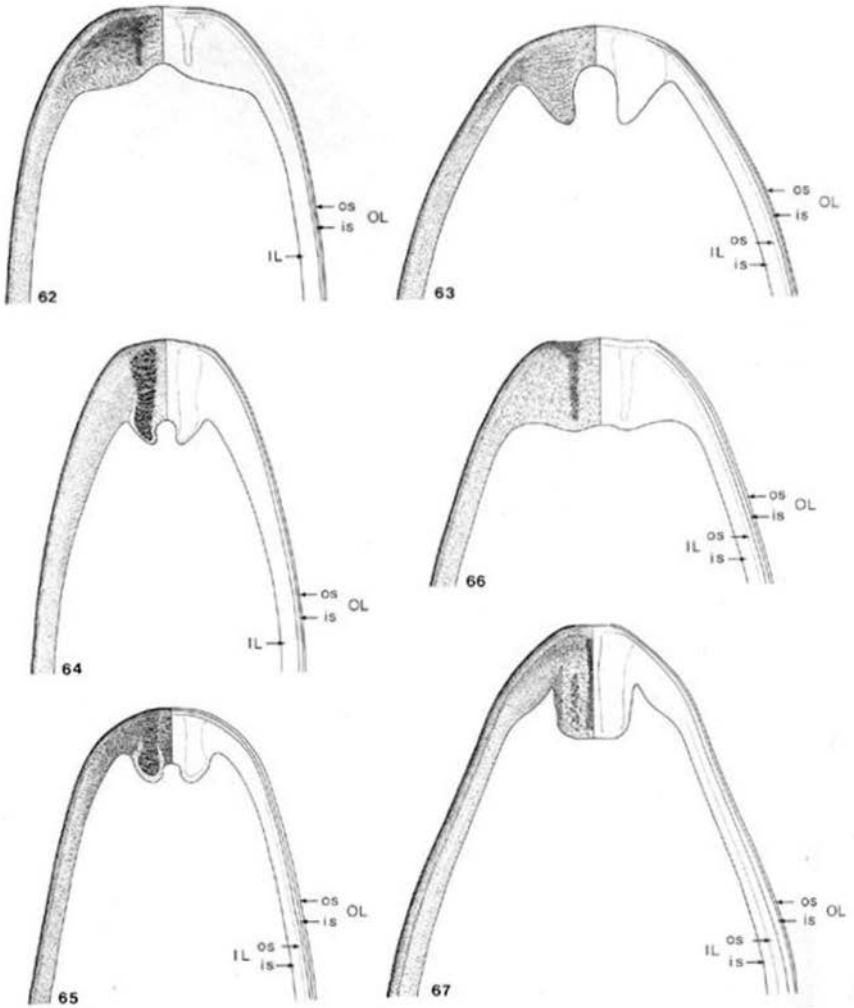
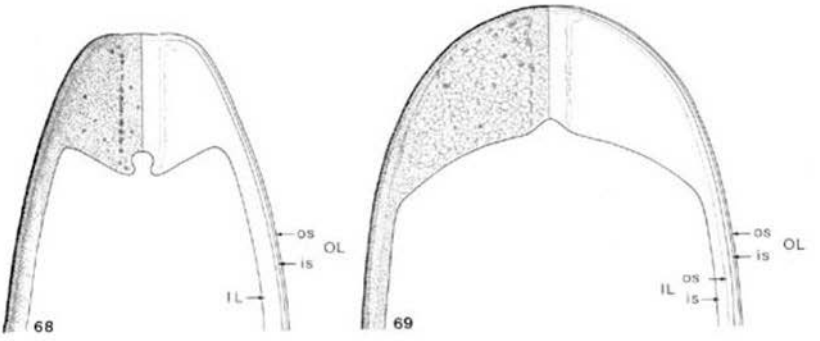


Figs. 62–67. Diagrammatic schemes of median images of the ascus apical apparatus and subapical wall, showing relative PA-TCH-SP reactivity on the left half, and corresponding interpretation of layers, strata and annular region on the right half of each scheme. – 62. *Bisporella pallescens*. Young ascus. – 63. *Bisporella sulfurina*. Young ascus. – 64. *Chlorociboria aeruginascens*. Young ascus. – 65. *Crocicreas cyathoideum*. Young ascus. – 66. *Crocicreas pallidum*. Young ascus. – 67. *Cudoniella acicularis*. Young ascus.



Figs. 68, 69. Diagrammatic schemes of ascus apical apparatus and subapical wall. – 68. *Cudoniella clavus* var. *grandis*. Young ascus. – 69. *Discinella boudieri*. Young ascus.

GENERAL OBSERVATIONS

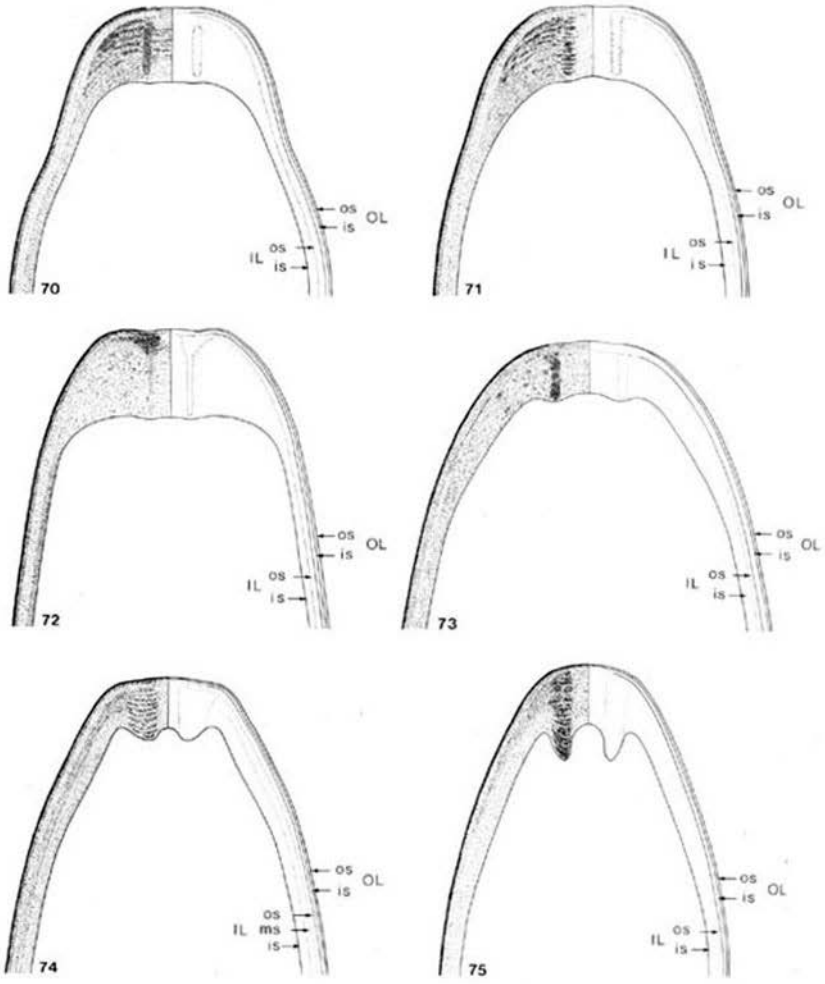
In the species studied it is exceptional to encounter all four stages of ascus development in a single ascoma. For example, in a single apothecium some advanced immature and many mature and dehisced asci of a first 'wave' are encountered together with many young, still elongating asci of a second 'wave'. A certain stage can therefore be missing in some of the species studied.

All species develop an ascus wall with two layers, of which only the inner one increases in thickness at the apex. In dehisced asci the outer layer of the wall remains intact much longer than the inner layer which tends to disintegrate soon after dehiscence.

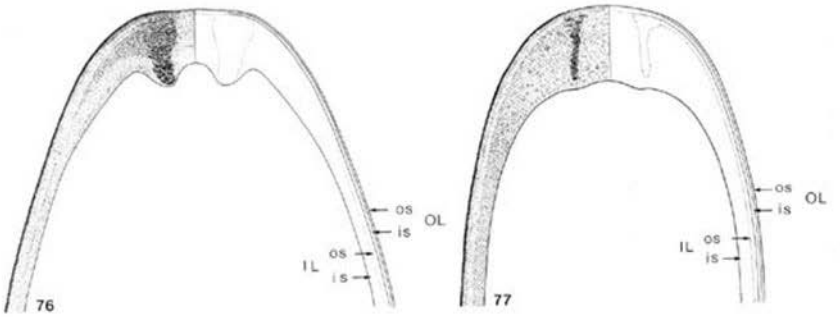
A cap-like layer of reactive material over the apical and subapical wall ('periascus') is found in the majority of asci studied in the species *Cudoniella acicularis*, some species of *Hymenoscyphus* (*H. imberbis*, *H. fructigenus*, *H. salicinus*, *H. salicellus*), *Pezizella alniella* and *Bisporella sulfurina*. In these species this material is clearly associated with the apical wall and is not part of the reactive layer that covers the hymenium as a whole and is observed in other species too. Both types of layers appear to be dislocated quite easily and it is sometimes difficult to discriminate between them or to determine their origin. Deeper within the hymenium between asci and paraphyses a strongly reactive matrix is found in *Pezizella alniella*, *P. gemmarum*, *Discinella boudieri*, *Crocicreas cyathoideum*, *Cudoniella acicularis*, *Chlorociboria aeruginascens*, *Bisporella pallescens*, and *B. sulfurina*.

The young, rapidly elongating ascus initial shows a rounded apex, with in the apical ascoplasm a circular area containing numerous predominantly small vesicles ('microvesicles', Fig. 1), surrounded by an area with predominantly larger vesicles ('apical vesicles', Fig. 1). After the ascus has reached about 80% of its ultimate length at maturity (measured in 1 µm sections of fixed material), apex formation starts and the apical apparatus is formed.

Cudoniella acicularis differs in these respects from the other species. Firstly, when the young elongating ascus has reached 50–60 % of its ultimate length, its apex changes shape from rounded to conical. Secondly, the ascoplasm in both rounded and conical



Figs. 70–75. Diagrammatic schemes of ascus apical apparatus and subapical wall. – 70. *Hymenoscyphus caudatus*. Immature ascus. – 71. *Hymenoscyphus salicinus*. Young ascus. – 72. *Hymenoscyphus consobrinus*. Immature ascus. – 73. *Hymenoscyphus imberbis*. Young ascus. – 74. *Hymenoscyphus herbarum*. Young ascus. – 75. *Pezizella alniella*. Young ascus.



Figs. 76, 77. Diagrammatic schemes of ascus apical apparatus and subapical wall. – 76. *Pezizella gemmarum*. Young ascus. – 77. *Phaeohelotium subcarneum*. Immature ascus.

apices is largely filled with an extensive system of branched tubular elements, and shows few if any vesicles (Figs. 2, 18). Apex formation starts when the ascus has reached 80–90 % of its ultimate length.

In all species studied ascospore delimitation starts after the apical apparatus has been fully formed.

SPECIFIC DESCRIPTIONS

Bisporella pallescens — Figs. 3–5, 62

The ascus apex is rounded to truncate-rounded. In the lateral ascus wall two layers are observed. The outer layer, 50–80 nm thick, consists of a strongly reactive outer stratum and a less reactive inner stratum. The reactivity of the inner stratum may be stronger over the apical apparatus (Figs. 3, 4). The inner layer, 230–260 nm thick, seems also to consist of two strata since the inner half of this layer frequently shows a stronger reactivity, but this is not always the case.

Young ascus – The apical apparatus is formed by an increase in thickness of the inner layer which is at first gradual, and then more abruptly towards the tip. The apical thickening shows an inner zone which seems continuous with the possible inner stratum of the inner layer. In this zone discontinuous layers containing strongly reactive material are oriented parallel to the outer face of the wall (single arrows, Fig. 3). Inwards these layers become less densely arranged and then gradually replaced by a network of reactive microfibrils. In the central cylinder a similar pattern is found with an overall decrease in reactivity towards the ascan length axis. The narrow annulus consists of a homogeneous matrix of strongly reactive material. In the upper part this material seems to change gradually into the strongly reactive layers mentioned above. Some of the asci show wall material below the annulus protruding into the ascoplasm. But this protrusion of material is never closely associated with the annular material nor is it observed in later stages. So, strictly there is

no annular protrusion. The annulus is restricted to the inner zone of the apical thickening. In most asci the outer stratum of the outer layer is largely eroded over the central cylinder (double arrows, Fig. 3).

Immature and mature ascus – Upon ripening the apical apparatus appears increasingly compressed (Fig. 4). The inner stratum of the outer layer increases in reactivity and its boundary line with the upper part of the annular region becomes less distinct. The outer stratum is partly eroded over the apical thickening as well (double arrows, Fig. 4).

Dehisced ascus – The annulus seems to be everted over about a right angle. The annular material of the lower part is often found disconnected from the rest of the apical thickening (Fig. 5). The material of the central cylinder has disappeared.

Bisporella sulfurina — Figs. 6–9, 63

The ascus apex is conical. The lateral ascus wall consists of two layers. The outer layer, 50–60 nm thick, is composed of a strongly reactive outer stratum and a less, but variably reactive inner stratum. The inner layer, 250–280 nm thick, consists of two strata also showing a variable reactivity (Figs. 6, 7). The hymenium is covered by a strongly reactive, gelatinous layer.

Young ascus – The apical apparatus is formed by an abrupt increase in thickness of the inner layer. The whole of the apical thickening seems occupied by a broad annulus, so, strictly there is no annular protrusion. Within the inner stratum of the inner layer in the subapical region of the lateral wall a zone of increased reactivity is conspicuous (single arrows, Fig. 6). The annulus is composed of a very fine, layered pattern of reactive microfibrils which are oriented parallel to the inner face of the wall (double arrows, Fig. 6). The central cylinder shows a granular, moderate reactivity. The outer layers outer stratum is usually already partly eroded over the central cylinder and annulus at this stage (arrowhead, Fig. 6).

Immature ascus – The apex appears to be flattened, and often a circular depression in the outer face is seen over the annulus (Fig. 7). Towards the end of this stage the apical thickening becomes more compressed and the annular reactivity decreases in most cases, of which in some already markedly.

Mature ascus – In most asci the annular reactivity decreases. No further change is observed (Fig. 8).

Dehisced ascus – In most asci the apical thickening is severely damaged after dehiscence and few remnants of the annular material are found (Fig. 9).

Chlorociboria aeruginascens — Figs. 10–12, 64

The ascus apex is narrowly conical and often flattened at its tip. The lateral ascus wall consists of two layers. The outer layer, 40–55 nm thick, contains a highly reactive outer stratum and a less but variably reactive inner stratum (Fig. 10). In the inner layer, 195–210 nm thick, no conspicuous stratification is observed, but there is a gradual increase in reactivity inwards.

Young ascus – The apical apparatus is characterized by a gradual increase in thickness of the inner layer over a relatively extensive area, a well-developed annulus and annular

protrusion enclosing an apical chamber (Fig. 10). Also in the apical thickening the inner layer shows a gradual increase in reactivity inwards. The annulus consists of densely packed, discontinuous layers of strongly reactive material. The upper part of the annulus is broader (Fig. 10). The central cylinder shows a fine granular reactivity. In most asci the outer layer is present over the apex.

Immature and mature ascus – In most asci the upper part of the central cylinder is somewhat stronger reactive. The annular material in the protrusion now forms a homogeneous, strongly reactive mass (arrowheads, Fig. 12). The apparatus is considerably compressed and the layered aspect of the material in the upper part of the annulus becomes more distinct (Fig. 12). The outer stratum of the outer layer is eroded over most of the apical apparatus (double arrows, Fig. 11).

Dehisced ascus – Not observed.

Crocicreas cyathoideum — Figs. 13–15, 65

The ascus apex is rounded to conical-rounded. The lateral ascus wall consists of two layers. In the outer layer, 45–65 nm thick, a strongly reactive outer stratum and a less reactive inner stratum are found. The inner layer, 120–130 nm thick, seems to consist of two strata. The inner stratum is variably reactive and usually only conspicuously stronger reactive than the outer stratum in the advanced immature and mature ascus (Fig. 14).

Young ascus – The apparatus is formed by an at first gradual increase in thickness of the inner layer towards the apex, followed by a fierce increase in the annular protrusion. It is characterized by an apical thickening and central cylinder which both mainly consist of a matrix of strongly reactive material densely packed in layers. In the broad annulus this material is the most densely packed (Fig. 13). The lower part of this annulus is outlined by an area of weakly reactive material (double arrows, Fig. 13), while its upper part is often difficult to distinguish from the neighbouring parts of the central cylinder and apical thickening. The well-developed annular protrusion encloses an apical chamber. The outer layer is still present over the apex.

Immature and mature ascus – At first no change is observed. But after the formation of the secondary ascospore wall has started (Fig. 14), the apparatus becomes more compressed and the strongly reactive material of the annulus gets a more homogeneous, amorphous appearance. In most asci reactivity increases in the central cylinder and upper part of the apical thickening. At maturity a further compression of the apparatus is observed and the apical chamber seems to disappear almost completely.

Dehisced ascus – After dehiscence the annulus still appears as a massive ring, that has now been everted over about a right angle. No remnants of the central cylinder remain attached to the annulus (Fig. 15).

Crocicreas pallidum — Figs. 16, 17, 66

The ascus apex is truncate-rounded. In the lateral wall two layers are observed. The outer layer, 55–80 nm thick, consists of a strongly reactive outer stratum and a less reactive inner stratum. The inner layer, 170–195 nm thick, is composed of two strata, of which the inner one is the most reactive (Figs. 16, 17).

Young ascus – The apical thickening is formed by a gradual increase in thickness of the inner layer (Fig. 16). The annulus is composed of densely packed reactive material. It is narrow in the inner zone of the apical thickening (i.e. the part that is continuous with the inner layer's inner stratum in the lateral wall). In Fig. 16 the outer boundary of this zone is indicated by the arrowhead. The upper part of the annulus, which partly consists of outer layer material also, is broader. In most of the central cylinder the matrix is similar to that in the apical thickening, except for the part formed by the outer layer's inner stratum. Occasionally material protruding into the ascus cytoplasm was observed (Fig. 16). Since such material never contained reactive annular material and was not observed in later stages of ascus development, it cannot be considered an annular protrusion. The outer layer's outer stratum is usually eroded over the central cylinder and partly over the apical thickening as well (double arrows, Fig. 16).

Immature and mature ascus – The apparatus is more compressed on further ripening and there is clearly no annular protrusion (Fig. 17).

Dehisced ascus – After dehiscence the annulus is everted over about a right angle. The inner layer of the ascus wall disintegrates rapidly after dehiscence, while the outer layer is more persistent.

Cudoniella acicularis — Figs. 2, 18–24, 67

The ascus apex is conical. The lateral ascus wall consists of two layers. The outer layer, 150–170 nm thick, consists of a strongly reactive outer stratum and a much thicker, less reactive inner stratum (Figs. 20, 23). The inner layer, 320–370 nm thick, also consists of two strata, of which the inner one is the more reactive. The thickness of the outer layer decreases towards the ascus top.

Young and immature ascus – Before apex formation begins the conical apex contains an extensive tubular system (Fig. 18; see also general observations and Fig. 2). The apical thickening consists of two parts which are separated by a circular constriction in the wall (single arrows, Fig. 19). The subapical (distal) part is characterized by a gradual thickening of the inner layer. The apical (proximal) part is characterized by a fierce thickening of the inner layer, and since it is almost completely filled with annular material it can be considered an annular protrusion. There is no apical chamber, and even a depression at the inner face of the wall in the centre of this part of the apical thickening is normally absent. Thus, the narrow central cylinder and the annular protrusion form a complex. Most of the apical thickening consists of a moderately reactive matrix (Fig. 19).

The uppermost part of the annulus contains fine reactive fibrils oriented more or less in layers parallel to the outer face of wall, while the lower part contains randomly distributed patches of strongly reactive material concentrated in the core. The narrow central cylinder contains strongly reactive material, except for the uppermost part where reactivity is low. The outer layer is usually partly eroded over the central cylinder and annulus in the early immature ascus (double arrows, Fig. 19).

In most late immature asci the complex of the annular protrusion and central cylinder is pushed aside by the uppermost ascospore (Fig. 20).

Mature ascus – The uppermost ascospore presses the complex of the annular protrusion and central cylinder out of the outer layer, stretching the inner layer material in the

subapical thickening. The expanded inner layer now shows a thickness about equal to that in the lateral wall (arrows, Figs. 21, 22).

Dehisced ascus – Three different dehiscence events are recorded. Firstly, in the majority of the asci observed, the expanded inner layer is partly torn (single arrows, Fig. 23). The complex is pushed aside but remains attached to the rest of the wall. Disintegration of the central cylinder seems to occur soon after dehiscence (double arrows, Fig. 23). Secondly, in some asci the opening is formed somewhere through the complex of annular protrusion and central cylinder (not necessarily through the central cylinder), without a distinct eversion of the annular remnants (Fig. 24). Thirdly, in some asci the complex is completely torn off by a circular tearing of the expanded inner layer.

Cudoniella clavus var. **grandis** — Figs. 25, 26, 68

The apex is truncate-rounded. The lateral ascus wall consists of two layers. The inner layer, 100–130 nm thick, consists of a strongly reactive outer stratum and a less reactive inner stratum. The inner layer, 260–330 nm thick, seems to consist of only a single stratum (Fig. 25). An outer zone of inwards rapidly decreasing reactivity is found, but it varies in thickness and its boundary is unclear. Further downwards an inner zone of somewhat stronger reactivity is observed.

Young ascus – The apical thickening is formed by an abrupt increase in thickness of the inner layer (Fig. 25). Its matrix mainly consists of a fine network of reactive microfibrils. The matrix of the central cylinder is similar in structure. The narrow, discontinuous annulus consists of patches of strongly reactive material. Similar patches are also found scattered throughout the rest of the apical thickening and central cylinder (Fig. 25). There is a distinct annular protrusion surrounding an apical chamber. The reactivity of the outer layer's inner stratum increases over the central cylinder and annulus. The outer stratum is eroded over the central cylinder.

Immature and mature ascus – Usually the outer layer is eroded over most of the apical apparatus. No further change is observed (Fig. 26).

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

Discinella boudieri — Figs. 27–29, 69

The ascus apex is rounded. The lateral ascus wall consists of two layers. The outer layer, 85–100 nm thick, contains a thin, strongly reactive outer stratum and a less reactive inner stratum (Fig. 28). This inner stratum is much thinner in the apical region. The inner layer, 170–225 nm thick, seems to consist of two strata, of which the inner one is more reactive than the outer one (Fig. 28).

Young and immature ascus – The inner layer thickens rather abruptly towards the apex. A thin zone of reactive material is found in the apical region at the boundary of the inner layer's outer and inner stratum (arrows, Figs. 27, 28). In the transitional region from the lateral wall to the apical thickening the matrix is converted from a fine granular reactivity into a regular network of reactive microfibrils (Figs. 27, 28). The apical thickening appears to be swollen, since its inner boundary with the ascoplasm is rather irregular. Patches of concentrated reactivity are found throughout the apical thickening. In the uppermost part

of the apical thickening and near the boundary line with the central cylinder these patches occur more frequently and constitute a diffuse, discontinuous annulus (Fig. 27). A similar but denser network of reactive microfibrils occurs in the central cylinder. Here the patches of concentrated reactivity are only occasionally observed. There is no protrusion associated with the annulus. The outer layer still fully covers the apex in most asci observed. At the advanced immature stage the apical apparatus is more compressed, but no changes are observed in reactivity (Fig. 28). In some asci the outer stratum is eroded over the central cylinder.

Mature ascus – Not observed.

Dehisced ascus – After dehiscence the apparatus is everted over an angle of about 60–90° (Fig. 29).

Hymenoscyphus caudatus — Figs. 30–35, 70

The ascus apex is rounded at the tip and especially characterized by becoming rapidly broader in the subapical region, a feature also observable with the light microscope. In the lateral ascus wall two layers are observed. The outer layer, about 65–80 nm thick, consists of a strongly reactive outer stratum and a less reactive inner stratum (Fig. 30). The inner layer, 190–220 nm thick, consists of at least two strata, of which the inner one is usually the more reactive (Figs. 30, 33).

Young ascus – The inner layer forms the apical apparatus as it gradually thickens towards the tip (Fig. 31). The central cylinder and the inner zone of the apical thickening, which is continuous with the inner stratum of the inner layer in the lateral wall, show a granular matrix of moderately reactive material, in which patches of more reactive material are found, especially in the uppermost part (arrows, Fig. 31). The upper part of the central cylinder and the adjacent part of the inner stratum of the outer layer show the same fine granular matrix. The narrow annulus consists of densely packed, strongly reactive material and does not reach into the uppermost part of the apical thickening. There is no annular protrusion (Fig. 31).

Immature ascus – In the apical thickening and central cylinder (except the lower part) the patches of strongly reactive material appear to become more orderly arranged in layers oriented more or less parallel to the outer face of the wall (Fig. 32). The annular material remains homogeneously distributed. The outer layer is partly absent over the central cylinder in most asci (double arrows, Fig. 32).

Mature ascus – Overall reactivity decreases in most of the apparatus, except for the annulus (Fig. 33).

Dehisced ascus – After dehiscence the annulus is everted over about a right angle. It is usually found intact (Fig. 35), but in some asci it seems to have been disrupted during dehiscence (Fig. 34).

Hymenoscyphus fructigenus — Figs. 36, 37

The general shape of the ascus apex is the same as observed in *H. caudatus*. In the lateral wall two layers are observed. The outer layer, 70–90 nm thick, consists of a strongly reactive outer stratum covering a less reactive inner stratum. In the inner layer, 200–230

nm thick, two strata are observed in the lateral wall. The inner stratum is usually considerably more reactive than the outer one. In the subapical region however, especially in the young ascus, the reactivity of this inner stratum may vary considerably (Fig. 36).

The apical apparatus agrees with that of *H. caudatus* in structure and reactivity before and after dehiscence (Figs. 36, 37). Here also, the annulus forms a homogeneous mass of strongly reactive material throughout ascus development.

Hymenoscyphus salicellus — Figs. 38–40

The ascus apex shows a shape similar to that in *H. caudatus*. The stratification of the lateral wall largely resembles that described for *H. caudatus*.

The structure of the apical apparatus also resembles that of *H. caudatus*. However, in the late immature and mature ascus the annulus shows a pattern of thin, strongly reactive layers, which are continuous with the layers found in the rest of the apical thickening (arrowhead, Fig. 39), and in the central cylinder as well, but to a lesser degree than in *H. caudatus* (Figs. 38–40). The mode of dehiscence also agrees with that in *H. caudatus*.

Hymenoscyphus salicinus — Figs. 41–43, 71

The ascus apex is rounded to truncate-rounded. In the lateral wall two layers are observed. The outer layer, 65–85 nm thick, consists of two strata, a strongly reactive outer stratum and a weaker reactive inner stratum. The inner layer, 190–230 nm thick, seems to consist of two strata which both vary in reactivity (Figs. 41, 42).

Young ascus – The inner layer forms the apical apparatus by thickening gradually towards the apex (Fig. 41). The inner zone of the apical thickening consists of a moderately reactive granular matrix. In its upper part patches of strongly reactive material occur which seem to be arranged in layers (single arrows, Fig. 41). The annulus consists of strongly reactive, fine granular material densely arranged in layers. The granular matrix in the central cylinder is less reactive than the one in the inner zone of the apical thickening and does not contain concentrations of strongly reactive material. The inner face of the wall in the central cylinder usually delimits a conical invagination of the wall, but there is no annular protrusion, and therefore no apical chamber. The outer stratum of the outer layer is eroded over most of the apical apparatus at this stage (double arrows, Fig. 41).

Immature and mature ascus – The arrangement in layers of the strongly reactive material in the inner zone of the apical thickening becomes more distinct (Fig. 42). At maturity the apical apparatus is considerably compressed.

Dehisced ascus – After dehiscence the annulus seems to have been everted over about a right angle, but it is usually difficult to trace the remnants of this structure (Fig. 43).

Hymenoscyphus consobrinus — Figs. 44, 45, 72

The ascus is rounded to truncate-rounded. The lateral ascus wall consists of two layers. The outer layer, about 50–60 nm thick, consists of a strongly reactive outer stratum and a less reactive inner stratum. The inner layer, about 180–200 nm thick, also consists of two strata, of which the inner one is the more reactive and shows a rough granular appearance (Fig. 44).

Young ascus – Not observed.

Immature ascus – The inner layer forms the apical apparatus as it gradually increases in thickness towards the apex (Fig. 44). The annulus consists of two structurally different parts. The upper part is relatively broad and contains reactive microfibrils which are densely arranged parallel to the outer face of the wall (double arrows, Fig. 44). The lower part consists of a narrow ring with a homogeneous matrix of fine, granular material. Both parts consist of inner layer material and the lower and most of the upper part of the annulus are embedded in the inner zone of the apical thickening (i.e. the part that is continuous with the inner stratum of the inner layer) (Fig. 44). In the central cylinder and the inner zone of the apical thickening a network of reactive microfibrils occurs which gradually becomes denser from the inner face of the wall outwards. In one of the collections the reactive material was more arranged in layers here. In the uppermost part of the central cylinder there is a small area showing a weaker reactivity. The protrusion of wall material observed below the annulus at this stage is not found in the mature ascus. The outer stratum of the outer layer is eroded over most of the apex.

Mature ascus – No marked change is observed. The apical thickening is considerably compressed. The reactivity in the upper part of the annulus and surrounding material increases in some asci (Fig. 45). The outer stratum of the outer layer is further eroded over the apex (double arrows, Fig. 45).

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

Hymenoscyphus repandus — Fig. 46

The ascus apex is rounded to truncate-rounded. The apical apparatus closely resembles that of *H. consobrinus*, both in structure and reactivity pattern. The lower part of the annulus is generally more reactive, and the reactive material of the outer part of the apical thickening and central cylinder is always arranged in layers (Fig. 46). After dehiscence the annulus is everted over an angle of about 90°.

Hymenoscyphus imberbis — Figs. 47, 48, 73

The apex is rounded to truncate-rounded. The lateral ascus wall consists of two layers. The outer layer, 55–70 nm thick, is composed of a variably reactive inner stratum covered by a more reactive outer stratum. The inner layer, 180–210 nm thick, is composed of two strata, of which the inner one is usually somewhat more reactive (Fig. 48).

Young ascus – The apical apparatus is characterized by a gradual increase in thickness of the inner layer towards the apex over a relatively extended area (Fig. 47). In most asci the wall material protrudes weakly into the ascoplasm in the annular region. The annulus contains a fine and dense granular reactivity, and tends to be somewhat broader and more diffuse in the upper part. Also throughout the rest of the apical thickening patches of relatively stronger reactivity are found. In most asci the outer stratum of the outer layer is absent over the central cylinder and annulus.

Immature and mature ascus – During the formation of the secondary ascospore wall the apical apparatus becomes more compressed and the annulus is clearly not associated with any form of protrusion (Fig. 48).

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

Hymenoscyphus herbarum — Figs. 49–52, 74

The ascus apex is conical to conical-rounded. The lateral ascus wall consists of two layers. The outer layer, 65–80 nm thick, consists of a strongly reactive outer stratum and a less reactive inner stratum. The inner layer, 235–260 nm thick, consists of three strata that are best visible at the early and mid-immature stages (from spore delimitation untill beginning of secondary spore wall formation, Fig. 50), when each stratum is delimited by a thin line of strongly reactive material. The middle stratum is usually the more reactive. In the lateral wall of the mature ascus these lines are absent and especially the boundary between the outer stratum of the inner layer and the inner stratum of the outer layer is difficult to indicate.

Young ascus – Vesicles containing reactive material are found near the plasma membrane at the apex during apex formation (arrows, Fig. 49). The inner layer forms the apical apparatus. The apical thickening shows a poorly developed lower part, while its upper part is well-developed and is almost completely occupied by the annulus. The latter part, which can also be considered an annular protrusion, encloses an apical chamber (Fig. 49). In the annulus layers of strongly reactive material are arranged parallel to the inner face of the wall. The annulus is restricted to the part of the apical thickening that is continuous with the middle and inner stratum of the inner layer in the lateral wall. The central cylinder is moderately reactive. The outer layer is still present over the apparatus at this stage (Fig. 49).

Immature and mature ascus – At the early (Fig. 50) and mid-immature stage the fierce layers of strongly reactive material in the annulus are replaced by a pattern of fine microfibrils intermingled with patches of relatively stronger reactivity (arrows, Fig. 50) that are most concentrated in the upper and inner part of the annulus. In the central cylinder the reactivity of the material along the boundary with the annulus increases in some asci. At the advanced immature (Fig. 51) and mature stage this was the case in all asci studied. At this stage most of the annular material looses its reactivity. This material appears in distinct layers within a now strongly reactive matrix (arrows, Fig. 51). The boundary with the outer layer's inner stratum becomes less evident due to a local increase in reactivity in this stratum.

In the mature ascus the outer stratum of the outer layer is eroded over the central cylinder. The lower part of the apical thickening becomes strongly compressed.

Dehisced ascus – After dehiscence the annulus is everted over an angle of about 90° (Fig. 52).

Pezizella alniella — Figs. 53–55, 75

The apex is conical. The lateral ascus wall consists of two layers. The outer layer, 40–55 nm thick, consists of a strongly reactive outer stratum and a less reactive inner stratum. The inner layer, 155–170 nm thick, consists of two strata, of which the inner one is the more reactive, but the reactivity of both strata tends to vary more in the subapical region (Fig. 53).

Young ascus – The inner layer at first gradually increases in thickness over an extended area, and then abruptly forms a distinct annular protrusion which encloses an apical chamber (Fig. 53). In the part of the apical thickening that is continuous with the inner

layer two zones can be observed, a strongly reactive outer zone and a less reactive inner zone (arrows, Fig. 53). The thickness of the outer zone gradually decreases downwards. It is difficult to verify the continuity of these zones with the strata found in the inner layer of the lateral wall. The annulus contains numerous layers of strongly reactive material. In the lower part of this annulus these layers are more closely arranged. The central cylinder shows a granular pattern of reactivity, resembling that observed in most of the apical thickening. The outer layer is present over the apex in most asci.

Immature ascus – No marked change is observed. The outer stratum of the outer layer is eroded over most of the apical apparatus (double arrows, Fig. 54).

Mature ascus – The apparatus is considerably compressed (Fig. 55). A circular depression in the wall surface is evident over the central cylinder in most asci.

Dehisced ascus – Not observed.

Pezizella gemmarum — Figs. 56–58, 76

The ascus apex is conical-rounded to rounded and slightly flattened at its tip. In the lateral wall two layers are observed. The outer layer, 45–65 nm thick, consists of a strongly reactive outer stratum and an inner stratum of variable reactivity. However, at the apex there is little difference between both strata. The inner layer, 135–155 nm thick, is homogeneously reactive throughout, but in the subapical part of the wall a line of stronger reactivity seems to reveal two strata (Fig. 56).

Young, immature and mature ascus – The inner layer increases in thickness gradually, thus forming a well-developed apical thickening (Figs. 56, 57). The annulus consists of patches of strongly reactive material in the annular protrusion. Upwards it becomes much broader and contains material of equal reactivity which is packed in densely spaced layers (Fig. 57). There the annulus merges with the strongly reactive middle zone of the apical thickening (double arrows, Fig. 56). The innermost part of the apical thickening frequently shows a zone of stronger reactivity. The upper half of the central cylinder is more reactive than the lower half. During the maturation of the ascus no significant change occurs.

Dehisced ascus – After dehiscence the annulus is everted over an angle of about 90° (Fig. 58).

Phaeohelotium subcarneum — Figs. 59–61, 77

The ascus apex is rounded. The lateral ascus wall consists of two layers. The outer layer, 65–90 nm thick, consists of a strongly reactive outer stratum and a less reactive inner stratum (Fig. 59). The inner layer, 155–170 nm thick, also consists of two strata, of which the inner one is the more reactive (Figs. 59, 60).

Young ascus – Not observed.

Immature ascus – The inner layer thickens gradually towards the apex over a relatively extended area. The inner zone of the apical thickening and the broad central cylinder consist of a matrix of rough granular material. The outer zone of the apical thickening (continuous with the outer stratum of the inner layer) and the inner stratum of the outer layer show a much finer matrix (Fig. 59). The lower two third part of the annulus is narrow

and consists mainly of a homogeneous, strongly reactive matrix. Approximately the upper one third part of the annulus is broader and consists of scattered patches of similar material (double arrows, Fig. 59). Such patches are found in small numbers in the rest of the apical thickening as well. The protrusion of some wall material just below, but never closely associated with, the annulus is only encountered in asci at this stage and not in mature asci. The outer stratum of the outer layer is eroded over most of the central cylinder and annulus (Fig. 59).

Mature ascus – The apical apparatus is considerably compressed (Fig. 60). The outer stratum of the outer layer is further eroded over the apical thickening. The reactivity in the inner stratum of the outer layer has increased over the annular region (arrows, Fig. 60).

Dehisced ascus – After dehiscence the annulus is everted over an angle of about 90°, and although it is often disconnected from the other material of the apical thickening, the structure itself is still intact (Fig. 61).

DISCUSSION

The lateral ascus wall

The two-layered substructure of the lateral ascus wall found in the Hymenoscyphoideae agrees with the one described in several other Leotiales (Corlett & Elliott, 1974; Benny et al., 1978; Verkley, 1992, 1993), Sphaeriales and other pyrenomycetes (Griffiths, 1971; Beckett & Crawford, 1973), and many Pezizales (van Brummelen, 1978). Bellemère (1975, 1977) was the first to study the ascus ultrastructure in the Leotiales in a systematic way using the PA-TCH-SP method of Thiéry (1967). He distinguished four layers in the lateral wall. The outer two, a and b, that were assumed to correspond to the 'exoascus' of Chadefaud (1973), probably correspond to the outer and inner stratum respectively of the outer layer as observed in this study and others (Verkley, 1992, 1993). Whether the layers c and d of Bellemère ('endoascus' of Chadefaud) correspond to the two strata of the inner layer as observed in most species studied presently is more difficult to say. An inner layer with three strata is observed in *Hymenoscyphus herbarum*. Some species of the Sclerotiniaceae also have an inner layer with three strata (Verkley, 1993).

The elongating ascus

The organization of the apical cytoplasm in the elongating ascus initial of all species, except *Cudoniella acicularis*, agrees with that observed earlier in ten species of the Sclerotiniaceae (Verkley, 1993). Therefore, the organization of the apical ascoplasm appears in general to be the same as in the vegetative hyphae of the Ascomycotina (Grove & Bracker, 1970). The occurrence of a tubular system in the apical ascoplasm of *C. acicularis* is taxonomically interesting because characters pertaining to systems of cytoplasmic organelles involved in growth and development would not be expected to vary even within the higher taxa of the fungi. The tubular structures are most likely part of the Golgi system, which normally is less well-preserved in chemically fixed material of fungi (Hoch, 1986).

The apical apparatus

Diagrammatic schemes of the apical apparatus and the subapical wall are depicted in Figs. 62–77. The left half of each scheme shows the relative reactivity in PA-TCH-SP and the right half the interpreted stratification of the wall. The ascus apices of *Hymeno-*

scyphus fructigenus and *H. salicellus* resemble the apex of *H. caudatus* (Fig. 70) and the apex of *H. repandus* resembles that in *H. consobrinus* (Fig. 72). The apices of these species are therefore not illustrated. The general shape of the apex as described here in the fixed material generally agrees with the shape of the ascus apex observed in light microscopy. This is not always the case when dried material is rehydrated and observed with the light microscope.

During maturation of the ascus little change is observed in the structure and reactivity pattern of the apical apparatus in most species, especially when compared with those reported in ten species of the Sclerotiniaceae by Verkley (1993). The apex maturation pattern of *Hymenoscyphus herbarum* is characterized by a significant change in the reactivity pattern of the annulus. It may be indicated as an 'inversion pattern' since the annulus reactivity type changes from 'positive' to 'negative'. In *Lanzia luteo-virescens* (Rob.) Dumont & Korf and *Ciboria conformata* (P. Karst.) Svrček of the Sclerotiniaceae this occurs the other way round (Verkley, 1993). In *Bisporella sulfurina* the annular reactivity decreases markedly. In the other species studied presently only small local changes occur in reactivity in addition to a general compression of the apparatus as a whole as maturation progresses. Therefore only one stage is presented in the diagrammatic schemes.

On the basis of the general morphology of the apical apparatus and reactivity pattern of the annulus five main groups can be distinguished. The main characters of these groups and the species referred to them are given below. For group 1 and 2 subgroups of species are outlined as well.

1. Apical thickening without an annular protrusion; reactivity of the annulus in a continuous or discontinuous homogeneous matrix, or in layers; apex rounded to truncate-rounded:

a. Concentration of strongly reactive material in the apical thickening arranged in layers at some stage of apex maturation; annulus continuous and homogeneous: *Bisporella pallescens* (Fig. 62), *Hymenoscyphus caudatus* (Fig. 70), *H. fructigenus*, *H. salicellus*, *H. salicinus* (Fig. 71).

b. Apical thickening extending relatively far downwards, with patches of strongly reactive material; annulus continuous and homogeneous: *Hymenoscyphus imberbis* (Fig. 73), *Phaeohelotium subcarneum* (Fig. 77).

c. Apical thickening without concentrated reactivity; annulus continuous, often with two distinctive parts: *Crocicreas pallidum* (Fig. 66), *Hymenoscyphus consobrinus* (Fig. 72), *H. repandus*.

d. Apical thickening with patches of strongly reactive material; annulus discontinuous: *Discinella boudieri* (Fig. 69).

2. Apical thickening with a well-developed annular protrusion and increasing gradually in thickness over an extended part of the subapical wall; reactivity of the annulus in conspicuous layers; apex conical to conical-rounded:

a. Inner layer in apical thickening with distinct statification at some stage of ascus development; annulus relatively broad, showing 'inversion pattern': *Hymenoscyphus herbarum* (Fig. 74).

b. Inner layer in apical thickening with a strongly reactive zone extending from the upper annular region downwards; annulus relatively broad, no 'inversion pattern': *Pezizella gemmarum* (Fig. 76).

c. Inner layer in apical thickening homogeneously reactive; annulus relatively narrow: *Chlorociboria aeruginascens* (Fig. 64), *Pezizella alniella* (Fig. 75).

d. Apical thickening relatively weakly developed (except for the annular protrusion), and homogeneous strongly reactive as the central cylinder; annulus particularly well-developed in lower part: *Crocicreas cyathoideum* (Fig. 65).

3. Apical thickening fully occupied by an annulus with a reactivity in fine layers (no annular protrusion by definition of Verkley, 1992); apex conical; apex maturation pattern characterized by a marked decrease in annular reactivity: *Bisporella sulfurina* (Fig. 63).

4. Apical thickening increasing in thickness abruptly, with an annular protrusion; annulus narrow and discontinuous; apex truncate to truncate-rounded: *Cudoniella clavus* var. *grandis* (Fig. 68).

5. Apical thickening constricted around a well-developed complex of annular protrusion and central cylinder, central cylinder extremely narrow; apex conical: *Cudoniella acicularis* (Fig. 67).

The taxonomic implications of these results will be discussed more deeply below in 'remarks on taxonomy'.

The dehiscence mechanism

The dehiscence mechanism of the species in groups 1, 2 (not observed in *Chlorociboria aeruginascens* and *Pezizella alniella*), and 4 is in agreement with the mechanism found in the family Sclerotiniaceae (Schoknecht, 1975; Bellemère, 1975, 1977; Corlett & Elliott, 1974; Verkley, 1993) and several Leotiaceae (Bellemère 1977; Verkley, 1992). Here, after dehiscence, the annulus is found everted over an angle of about 90°. Usually, the inner side of the annulus is damaged to a lesser or greater degree and no material of the central cylinder is observed associated with the annulus after dehiscence in most species. In the species of Leotiales studied thus far no preformed weakened region in the central cylinder or any (other) indication for active wall decomposition by lysis prior to dehiscence has been found.

Although there is a difference in structure, the central cylinder and annulus form a continuous part of the apical wall. From the structural point of view, terms used in TEM studies like 'pore' (Beckett, 1981), 'pore-plug', or 'plug' (Corlett & Elliott, 1974) are not accurate for Leotiales. The term 'plug', for example, seems to suggest that the central cylinder is segregated from the annulus as a unity during the opening, but this is not the only possible way to be considered. The cylinder may well be internally disrupted during opening, and/or tearing of the annulus may occur to a lesser or greater degree.

What seems to happen next is that the uppermost ascospore everts the annulus on passing through the initially very small opening, stretching the annulus, with the hydrostatic pressure inside the ascus as the driving force. After the tension in the annulus has been relieved, a considerable disintegration of this structure is evident in the ascus after dehiscence. If there were any remnants of the central cylinder attached to the annulus as it is stretched, these are not likely to be found again after dehiscence. After having been everted, the annulus seems to be prevented from returning to its position prior to dehiscence by the swollen wall material of the apical thickening.

The dehiscence mechanism in *Bisporella sulfurina* (group 3) is unknown. The annulus, which in fact is the apical thickening, may be insufficiently preserved during fixation

procedures, or more likely, so severely disrupted during the dehiscence event that it is impossible to determine what happens. Also at the light microscopical level the observations give little information on these very small ascus apices.

In *Cudoniella acicularis* dehiscence occurs in two steps. In the first step the inner layer of the subapical thickening is stretched beyond the erosion rim of the outer layer probably as a result of the increasing internal pressure. The intact outer layer could be expected to prevent this expansion, considering its quite unusual thickness, on average two to three times the thickness of the outer layer in most of the other species. Although such an erosion is common among many other Leotiales and Sclerotiniaceae in particular, an expansion or stretching of the exposed part of inner layer in the apical thickening was never observed in any stage of ascus development in these taxa (Verkley, 1992, 1993). It seems that the expansion in *C. acicularis* is somehow related to a feature of this particular part of the apical thickening, but its ultrastructure is not different from other parts. There are no indications for a physical separation of the outer and inner layer in the sense of a movement of the one along the other. The expansion differs therefore fundamentally from the expansion of the 'endotunica' observed during the dehiscence in bitunicate Ascomycetes (Eriksson, 1981), of which the expansion is also limited in the species of the 'semifissitunicate' type.

In the second step of dehiscence in *C. acicularis* the wall is partly torn normally somewhere in the expansion region next to the complex of annular protrusion and central cylinder. Only rarely this event appears to result in the complete segregation of the complex from the wall. In the rare cases the wall is torn somewhere within this complex no distinct eversion of the annular remnants is observed (occurring in 'semifissitunicate' and 'rostrate' types, Eriksson, 1981). The place in the wall where the opening is started to be formed seems to be determined by the position of the uppermost spore prior to dehiscence. As the internal pressure builds up this spore is pressed against the wall in most cases next to the complex, because there is no apical chamber or depression in the inner face of this complex into which the spore could easily be fixed.

This two step mechanism was also observed in another collection studied alive with the light microscope and can therefore not be an artefact of fixation. In mounts of rehydrated material it is more difficult to observe the undisturbed step-one stage and that is perhaps why this unusual mechanism of dehiscence has not been reported earlier for this rather common species. From the variation in the second step it can be speculated that this species is on the way of developing an apomorphous dehiscence mechanism, new for the order. The similarity in the dehiscence mechanism with some bitunicate ascomycetes is probably based on homoplasy, not on homology.

Remarks on taxonomy

Bisporella

Bisporella pallescens and *B. sulfurina* show fundamental differences in the general morphology of their ascus apices. The apex of *B. pallescens* strongly resembles those in species of *Hymenoscyphus* like *H. fructigenus* and *H. caudatus*. The apex in *B. sulfurina* is unlike any of the apices observed in the other species presently studied, but does have

certain characters in common with the ascus apex of *Bulgaria inquinans* (Pers.) Fr. of the Ombrophiloideae sensu Dennis (Verkley, 1992). As in the latter species, the apical thickening in *B. sulfurina* is fully occupied by a broad annulus and a zone of higher reactivity extends downwards into the subapical wall (indicated for *B. inquinans* as 'strate annellogène' by Chadefaud, 1973). But the apex maturation pattern is different and the typical structure of the outer layer of the ascus wall described for *Bulgaria* is not observed in *Bisporella sulfurina* (Verkley, 1992). The ultrastructure of the apical apparatus in *B. citrina* (Batsch.) Korf & S. Carp. seems to differ from those of both *B. pallescens* and *B. sulfurina* (Bellemère et al., 1987). Bellemère et al. state that the apex is similar to the one in *Neobulgaria* Petrak, but this seems insufficiently founded.

The genus *Bisporella*, typified by *B. pallescens*, is predominantly defined by the anatomy of the outer tissue of the receptacle (Korf & Carpenter, 1974). There is, however, a difference in anatomy between *B. pallescens* and *B. sulfurina* which seems to correlate with the differences in ultrastructure of the apices in these species. In *B. pallescens* the hyphae in the well-defined ectal excipulum have thick gelatinized walls which are not clearly delimited from the surrounding gelatinous matrix of reactive polysaccharides (TEM observations) and form a textura oblita. The hyphae in the medullary excipulum are not embedded in such a matrix and form a textura intricata. In *B. sulfurina* the excipular hyphae have thinner walls of which the outer face is more clearly delimited from the surrounding gelatinous matrix. They form a single tissue of textura oblita-intricata throughout the receptacle, except for a zone directly below the hymenium (Baral & Krieglsteiner, 1985; own observations).

Crocicreas

Carpenter (1981) monographed *Crocicreas* and defined it in a broad sense. He already noticed the occurrence of two types of ascus apices in the genus, one he called the 'papillate apex' and the other the 'rounded to subtruncate apex'. The first exhibits two thick blue lines in optical cross-section after treatment with Melzer's reagent. It is found in e.g. *C. cyathoideum* and in *C. gramineum*, the type species of *Crocicreas*. The second type shows two thin blue lines at best and, according to Carpenter (1981), sometimes none at all. It is found in e.g. *C. pallidum* and *C. coronatum*, the lectotype species of *Cyathicula* De Not. In *C. pallidum* the lower part of the reactive annulus now observed in TEM corresponds to the thin blue lines observed in light microscopy, while in *C. cyathoideum* rather the whole reactive annulus observed in TEM corresponds to the region blueing in Melzer's. Although he considers characters of hymenial elements, e.g. ascospore size, shape, and septation in general of a more conservative evolutionary nature, Carpenter (1981) does not mention the possible significance of the ascus apical structures. On the characters size and number of teeth on the apothecial margin he comments that these show a considerable intraspecific variation in some species and can in general be considered less conservative. That is why Dennis (1978) and Carpenter (1981) both consider the species with even margins formerly referred to *Phialea* (Fr. ex Pers.) Gill. (Dennis, 1956), but with structurally similar excipulum as the species with dentate margins formerly referred to *Cyathicula*, as congeneric. The occurrence of gel between the characteristic widely spaced hyphae in the ectal excipulum is given the most weight by Carpenter (1981), and he directs the genus to the Ombrophiloideae. He rejects a placement in the Leotioideae or

Hymenoscyphoideae (Korf, 1973), because he does not consider *Leotia* Pers.: Fr. or *Hymenoscyphus* closely related. Yet it appears that it is mainly the occurrence of a gelatinous matrix which presently separates *B. pallescens* and certain species with a 'rounded to subtruncate apex' of *Crocicreas* from *Hymenoscyphus*. Furthermore, there is no evidence in the ultrastructural data to support the hypothesis that *Crocicreas* (including the species with a 'papillate' apex presently investigated, *C. cyathoideum*) is more closely related to the Ombrophiloideae (Verkley, 1992) than to certain genera of the Hymenoscyphoideae. Gelatinization of walls and gel in the extra-mural compartments can occur in various degrees, and even some species of *Hymenoscyphus* have extra-mural fibrillous polysaccharides in the ectal excipulum, but in smaller amounts which can only be demonstrated at the ultrastructural level using PA-TCH-SP (own observations).

From the present data concerning the ultrastructure of the apex it can be concluded 1) that there are probably two distinct groups of species in *Crocicreas*, 2) that both groups show more similarity to other species in the Hymenoscyphoideae than to the species of Ombrophiloideae investigated, and 3) that the group represented by *C. pallidum*, and most probably also by *C. coronatum*, is particularly close to *Hymenoscyphus consobrinus* and some allied species of *Hymenoscyphus*.

Chlorociboria

The apical apparatus of *Chlorociboria aeruginascens* agrees well with that of *Chlorociboria aeruginosa* (Pers.: Fr.) Seaver ex Ramamurthi et al. described by Bellemère (1975). Furthermore, it shows interesting similarities in both general morphology and reactivity pattern with the apices in certain species of the Sclerotiniaceae, especially *Poculum petiolorum* (Rob. ex Desm.) Dumont & Korf, but less so with the species of *Ciboria* Fuckel (Verkley, 1993). The apex maturation pattern observed in *P. petiolorum* is not found in *C. aeruginascens*. The species referred to *Chlorociboria* have long been considered closely related to *Ciboria* Fuckel and thus been treated as members of either the Helotiaceae (Rehm, 1896, in 'Ciborieae'; Nannfeldt, 1932, who was uncertain about the position at the subfamily level) or the Sclerotiniaceae later on (Ramamurthi et al., 1957; Korf, 1959; White, 1941). Dixon (1975) concluded in his monograph on *Chlorociboria* that the genus belongs in the family Leotiaceae, tribe Leotieae. If *Chlorociboria* is to be kept in the family Leotiaceae, the genus is most likely one of the closest related to the family Sclerotiniaceae.

Cudoniella

The general morphology of the apical apparatus and the dehiscence mechanism in *Cudoniella acicularis* are unlike any of those reported in other Leotiales untill now. In comparison with other Leotiaceae, the morphology of the apical apparatus appears apomorphic, i.e. is more likely to be interpreted as a derived, more specialized form than a primitive form. It is assumed that the central cylinder has been reduced and has lost its function. The apical apparatus in *C. clavus* var. *grandis* is remarkably similar in general morphology to the apparatus in *Ombrophila violacea* Fr. (Verkley, 1992), even more so than *Neobulgaria pura* (Fr.) Petrak. The more diffuse annulus in *C. clavus*, especially in the annular protrusion, may explain why in contrast to *O. violacea* no blueing by Melzer's reagent is observed under the light microscope. The present results demonstrate that the genus *Cudoniella* in its current interpretation is very artificial.

It appears that the light microscopic comparative study of 'inamyloid' ascus apices is of little value from the morphological taxonomic point of view, because it leads to erroneous interpretations.

Discinella

In respect of its apical apparatus *Discinella boudieri* seems most closely allied to the species of *Hymenoscyphus* outlined in 'group 1', *B. pallescens* and *Phaeohelotium subcarneum*. *Discinella boudieri* is the type species of a well-established genus which is characterized by an ascus apex blueing weakly in iodine and a preference for terrestrial substrates (Dennis, 1978). The present ultrastructural data support the view of most authors that the genus belongs in the subfamily Hymenoscyphoideae (Korf, 1973) next to *Hymenoscyphus* (Korf, 1973; Dennis, 1956, 1978).

Hymenoscyphus and *Phaeohelotium*

Hymenoscyphus caudatus, *H. fructigenus* (the type species of *Hymenoscyphus*), and *H. salicellus* agree largely in the ultrastructure of the apical apparatus. They are examples of a group of species in *Hymenoscyphus* that can be characterized by an ectal excipulum of textura porrecta to textura prismatica, fairly specialized ascospores often with tapered distal and 'hooked' proximal ends, with relatively few but large oil-droplets at maturity and with at least in some spores distal and/or proximal 'cilia'. *Hymenoscyphus scutula* (Pers.: Fr.) Phill. is another example of this group, which seems to agree with the one indicated by Dumont (1981) as 'the *H. caudatus* group'. *Hymenoscyphus salicinus*, which shows a similar excipular anatomy but different ascospores, may be closely related considering its apical ultrastructure.

Hymenoscyphus consobrinus and *H. repandus* seem to represent another group of species with an excipular anatomy similar to that in the first group, but with simple, always aciliate, ellipsoid to fusoid ascospores (Dennis, 1978; Lizoñ, 1992; own observations). Their apices strongly resemble the apex in *Crocicreas pallidum*.

Hymenoscyphus imberbis can be an example of a third group of species in *Hymenoscyphus* developing light-coloured, sessile to short-stalked apothecia with an ectal excipulum of textura globulosa to textura angularis and again simple, aciliate ascospores. This group agrees with 'the *H. epiphyllus* group' as outlined by Dumont (1981). The anatomy of the excipulum in *H. imberbis* is virtually the same as in *Phaeohelotium subcarneum*, and correlates with the resemblance in apical ultrastructure of both species. The only distinct difference concerns the central cylinder, which is broader in *P. subcarneum*, and was noticed by Dennis (1978) as 'broad pore'. Baral & Krieglsteiner (1985) also drew attention to the similarity of these two species in particular. They treated *Phaeohelotium* species in *Hymenoscyphus*, but Lizoñ (1992) proposed to keep *Phaeohelotium* for the brown-spored species (*H. subcarneus* (Sacc.) Kuntze being a different species according to Lizoñ).

Hymenoscyphus herbarum differs strongly in its apical ultrastructure from the other species of *Hymenoscyphus* studied as yet, showing resemblance with *Pezizella gemmarum*. The ectal excipulum consists of rectangular cells at a low angle to the surface, the outer hyphae ending in short, smooth-walled, clavate to cylindrical hair-like protuberances. The ascus apex blues intensely in iodine and especially in the upper annular region more than in most other species of *Hymenoscyphus*. Emphasizing the importance of these characters, Baral & Krieglsteiner (1985) reestablished the genus *Calycina* Nees ex S.F.

Gray to accommodate *H. herbarum* [Arendholz (1989) remained doubtful about the identity of Persoon's collections of *Peziza herbarum* Pers. at L.] and several other species they considered congeneric, such as *Pezizella gemmarum* and *P. alniella*. They referred *Calycina* to the Hyaloscyphaceae. Lizoñ (1992) still considers *Peziza herbarum* a species of *Hymenoscyphus*.

From the present data, however, it seems that Baral & Krieglsteiner assembled a still rather diverse group of species doubtfully related to the family Hyaloscyphaceae. There is now sufficient evidence both at LM and TEM level to reject the hypothesis that *H. herbarum* and *H. fructigenus* are congeneric, and it is therefore proposed to accept the recombination of *H. herbarum* to *Calycina* Nees ex S.F. Gray. *Calycina*, considered in a more restricted sense than proposed by Baral & Krieglsteiner (1985), can at present best be placed in the family Leotiaceae, for still very little is known about the ultrastructure of the ascus in Hyaloscyphaceae.

Pezizella

The two species of the very large genus *Pezizella* that have been studied ultrastructurally, show a considerable difference in the structure of the apical apparatus. *Helotium gemmarum* Boud. was recombined to *Pezizella gemmarum* by Dennis (1956), although the distinct incrustration on the hair-like protruberances of the ectal excipulum is not characteristic of *Pezizella* in the view of Dennis (1978). Whether *P. gemmarum* is congeneric with *H. herbarum* can best be assessed when the ultrastructure of the apical apparatus of more species will be studied.

The close resemblance of the apices in *P. alniella* and *Chlorociboria aeruginascens* is rather unexpected. It seems reasonable to reject the suggestion of Carpenter (1981, following Müller) that *P. alniella* belongs in *Hymenoscyphus*.

CONCLUSIONS

In the limited selection of 19 species of the Leotiaceae already a large heterogeneity is recorded in the structure of the ascus apical apparatus, especially when compared with the variation in this structure recorded in ten species of the Sclerotiniaceae (Verkley, 1993).

The characters attributed to the ascus apical apparatus show little variation within groups of species already considered more closely related on the basis of apothecial structure and ascospore characters, such as the type species *Hymenoscyphus fructigenus* and allied species. They may facilitate the arrangement of more natural genera, especially for those ascomycetes with few other distinctive characters.

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MYCENA ACROCEPHALA
A new member of section Adonideae from Sikkim

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Mycena acrocephala is described as a new species, based on copious material collected in Sikkim. Its characters are compared with those of *Agaricus flavominiatus* Berk.

The subject of the following note is a species collected in Sikkim under No. 165 and recorded as *Mycena flavominiata* (Berk.) Sacc. (Horak, 1980: 107).

Through an unfortunate coincidence, the part of the type material of *Agaricus flavominiatus* originally sent for investigation to the second author turned out to be so poor that it was of little help. It was mainly on account of the occurrence in the same region where the type had been found (Sikkim) and Berkeley's macroscopic description that No. 165 was believed to represent Berkeley's species.

Another part of the type, sent to the first author of the present note, gave very different results and led to the conviction that No. 165 is a new species.

Mycena acrocephala Maas G. & Horak, *nov. spec.* — Figs. 1–6

Basidiomata sparsa. Pileus 5–12 mm latus, conicus, acuto-umbonatus, haud sulcatus, margine translucente striatus, glaber, siccus, cinnabarinus. Caro tenuis, odore saporeque indistinctis. Lamellae 14–15 stipitem attingentes, molles, adscendentes, c. 0.5 mm latae, adnexae vel subemarginatae, albidae, rubro-tinctae, margine concolore. Stipes 25–40 × 0.5–1 mm, cavus, aequalis, cylindraceus, flexuosus, levis, apice subfloccosus, deorsum glaber, siccus, albidus vel pallide flavus, basi fibrillis crassis albisque munitus.

Basidia 28–34 × 6.5–8 µm, clavata, 2-spora, efibulata, sterigmatibus 4.5–5.5 µm longis praedita. Sporae 9–10.7 × 4.5–5.3 µm, inaequilateriter ellipsoideae, leves, inamyloideae. Cheilocystidia 32–55 × 6.5–10 × 2 µm, fusiformia, lageniformia, efibulata, levia. Pleurocystidia similia. Trama lamellarum iodi ope haud vinescens. Hyphae pileipellis 2–4.5 µm latae, efibulatae, leves. Hyphae stipitis corticales 1.8–2.5 µm latae, efibulatae, leves; caulocystidia 45–65 × 7–11 µm, cylindracea vel subclavata, efibulata, haud numerosa.

Lignicola.

Holotypus: No. 165 (ZT); isotypus: No. 980.41-111 (L).

Etymology: ακρος = pointed; κεφαλη = head; referring to the strikingly pointed umbo.

Basidiomata scattered. Pileus 5–12 mm across, conical, with a small acute umbo, smooth, translucent-striate towards the margin, glabrous, dry, coral red to vermilion, pallescent with age. Flesh thin. Odour and taste indistinctive. Lamellae 14–15 reaching the stipe, tender, ascending, c. 0.5 mm broad, adnexed to submarginate, whitish with vermilion tint, with straight to somewhat convex, concolorous edge. Stipe 25–40 × 0.5–1 mm, hollow, equal, terete, flexuous, smooth, apically minutely floccose, glabrous farther below, dry, whitish to pale yellow, the base covered with coarse, white fibrils.

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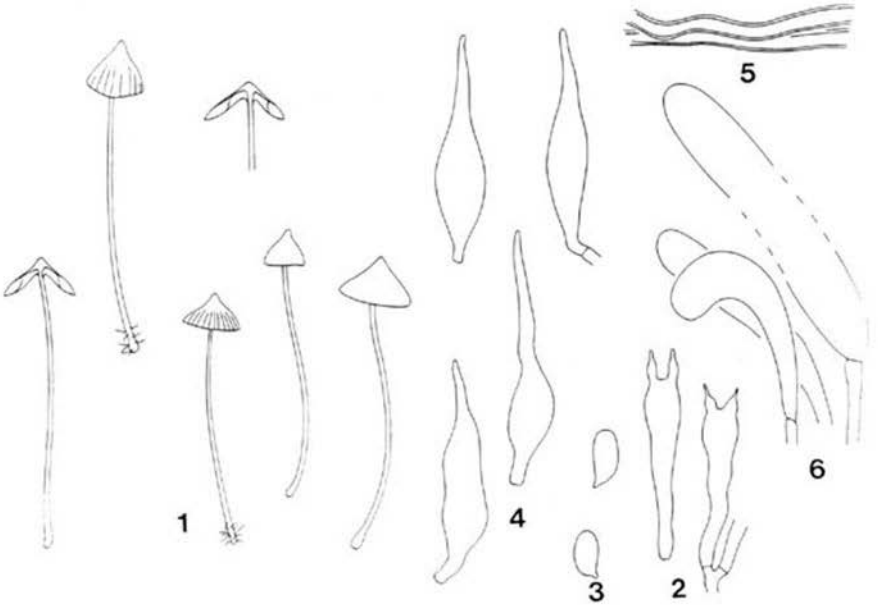

Figs. 1–6. *Mycena acrocephala* (holotype). 1. Habitus of some basidiomata; 2. basidia; 3. spores; 4. cheilocystidia; 5. hyphae of the pileipellis; 6. caulocystidia. — Fig. 1 (Horak) × 1; Figs. 2–6 (Maas Geesteranus) × 700.

Basidia 28–34 × 6.5–8 µm, slender-clavate, 2-spored, clampless, with plump sterigmata 4.5–5.5 µm long. Spores 9–10.7 × 4.5–5.3 µm, pip-shaped, almost cylindrical, smooth, non-amyloid. Cheilocystidia 32–55 × 6.5–10 × 2 µm, occurring mixed with basidia, fusiform, lageniform, clampless, smooth. Pleurocystidia similar, not numerous. Lamellar trama non-vinescent in Melzer's reagent. Hyphae of the pileipellis 2–4.5 µm wide, clampless, smooth, apparently agglutinated but not visibly gelatinized, somewhat thick-walled. Hyphae of the cortical layer of the stipe 1.8–2.5 µm wide, clampless, smooth, the caulocystidia 45–65 × 7–11 µm, cylindrical to subclavate, occurring scattered or in bunches, clampless, straight to more or less curved, not numerous.

On rotten branches and twigs in forests (*Pinus, Quercus*).

Holotype: Sikkim, Upper Rangit, Bakhim, 2600 m, 11 Nov. 1979, *E. Horak No. 165* (ZT); isotype: No. 980.41-111 (L).

There is no doubt that *Mycena acrocephala* belongs to the section *Adonideae* (Fr.) Quélet but in one respect it differs from all Northern Hemisphere members of this section: the hyphae of the pileipellis are slightly thick-walled and smooth. It comes near *Mycena adonis* (Bull.: Fr.) S.F. Gray which is often 2-spored in Europe, but the latter has a broadly rounded pileus and narrower spores.

Another *Mycena* species from Sikkim characterized by the vermilion colour of its pileus is *Agaricus flavominiatus* Berk. (1852: 103). This species has been shown to be the same as *Mycena acicula* (Schaeff.: Fr.) Kummer (Maas Geesteranus, 1982: 531). The following table is given to facilitate comparison.

Table 1. Comparison of some characters of *Agaricus flavominiatus*, *Mycena acicula* and *M. acrocephala*.

	A. flavominiatus	*M. acicula*	*M. acrocephala*
hyphae pileipellis smooth	–	–	+
hyphae stipe cortex smooth	–	–	+
cheilocystidia little protruding	+	+	–
cheilocystidia apically obtuse	+	+	–
basidia 4-spored	+	+	–
umbo of pileus acute	–	–	+
pileus with some yellow tints, either apically or marginally	+	+	–
stipe bright yellow to orange-yellow	+	+	–

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AMANITA GRALLIPES, A NEW SPECIES IN AMANITA SUBSECTION VITTADINIAE FROM SOUTHERN BRAZIL

C. BAS[1] & A.A.R. DE MEIJER[2]

Amanita grallipes, a new species from the State of Paraná in southern Brazil, belonging to *Amanita* sect. *Lepidella* subsect. *Vittadiniae*, is extensively described and illustrated. It is well-characterized by a long, slightly rooting stipe with a non-bulbous base and scattered remnants of the universal veil, a dark brown pileus with dark brown warts, lamellae turning maize yellow, ellipsoid spores shorter than 9.5 µm and the presence of clamp-connections.

In large areas of South America the genus *Amanita* is poorly represented. After six years of collecting in the Brazilian State of Paraná and bringing together material of more than 1000 species of macromycetes, the second author for the first time found a probably indigenous species of *Amanita*, presented here under the name *Amanita grallipes*, spec. nov.

Amanita grallipes belongs to the rapidly expanding subsection *Vittadiniae* of which many species are almost certainly non-ecto-mycorrhizal, as they are able to grow in fields, pampas, prairies, meadows and lawns without any tree or shrub in the surroundings. In the case of the present species, little can be said about this important ecological aspect, as its type-locality is a mixed forest in which *Araucaria augustifolia* is present. This tree, however, probably has endotrophic and no ectotrophic mycorrhiza (Harley & Smith, 1983: 19).

The abbreviation K. & W. refers to Kornerup & Wanscher (1978). The notation [30/2/1] stands for '30 spores measured from 2 basidiocarps belonging to one collection'.

Amanita grallipes Bas & A. de Meijer, *spec. nov.* — Figs. 1–6

? *Amanita spissa* var. *laeta* Rick, Brotéria 5 (1906) 25.

Pileus 22–90 mm latus, initio hemisphaericus vel convexus, demum plano-convexus vel planus, exumbonatus, brunneus, fibrillosus, siccus, margine appendiculatus, verrucis sparsis, conicis, adnatis, concoloribus ornatus. Lamellae liberae, confertae, usque ad 11 mm latae, ex albo flavescentes. Stipes 70–120 × 6–18 mm, subfusiformis, solidus, radicans, sub annulo squamis floccosis, erectis vel adpressis, pallide flavobrunneis munitus. Annulus fugax, coacto-membranaceus, albus, margine verrucis brunneis praeditus. Caro albo, inodora, mitis.

Sporae 7.5–9.6 × 5.6–6.9 µm, amyloideae. Fragmenta volvae cellulis elongatis, catenulatis composita. Fibulae frequentes.

Typus: '*A.A.R. de Meijer 2078*, 31 Dec. 1991, Brazil, Paraná, Curitiba, Parque Barigui, L'.

Etymology: grallae = stilts; pes = foot.

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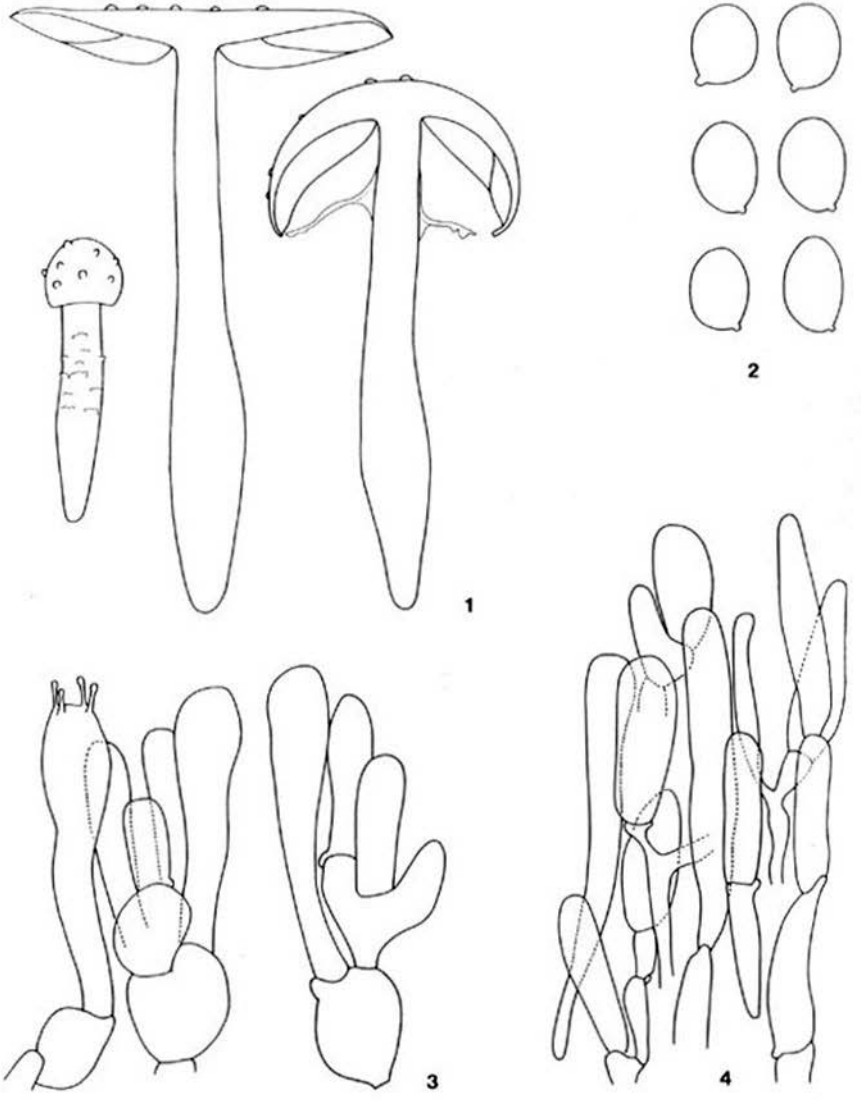


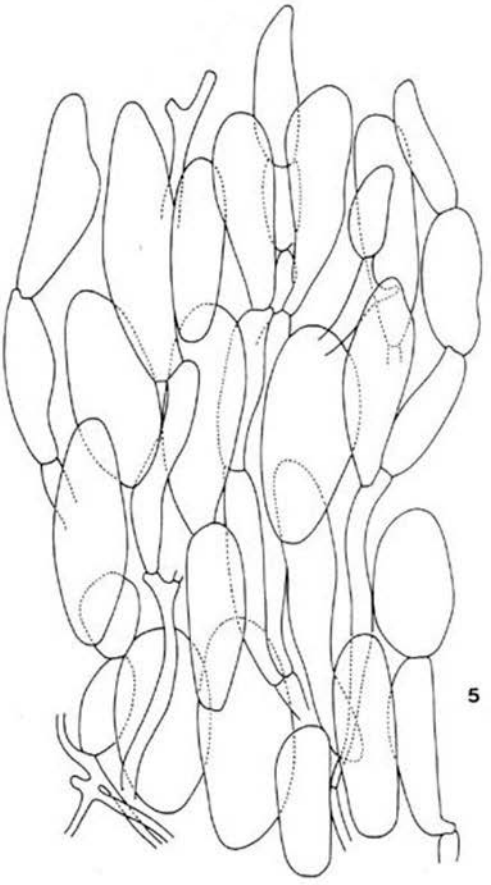
Figs. 1–4. *Amanita grallipes*. 1. Basidiocarps, × 0.5; 2. spores, × 1500; 3. basidia and subhymenial cells, × 1000; 4. volval tissue on stipe, × 500 (all from type).

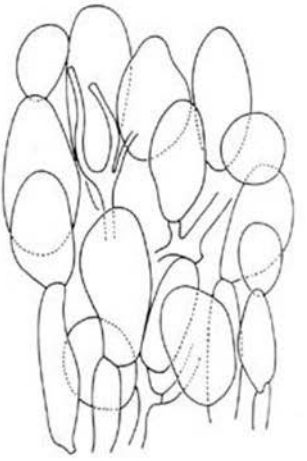
Basidiocarps large and slender, solitary to subgregarious. Pileus 22–90 mm in diam., from hemispherical or conico-convex to plano-convex or flat without umbo, with smooth margin appendiculate when young, uniformly dark brown to somewhat paler greyish brown (K. & W. 6E5 to 5D4), dry, with scattered, concolorous, adnate, pyramidal warts, fleshy (context up to 10 mm thick near centre and up to 6 mm thick above midpoint of lamellae). Lamellae free, very crowded, fairly broad (up to 11 mm), first pure white, then cream (4A2), finally yellow (3.5A5) to golden yellow (K. & W. 4A6), with concolorous, even edge; lamellulae attenuate. Stipe 70–120 mm long, 10–18 mm wide at broadest part just above the soil, 6–11 mm wide at narrowest part, with lower 20–45 mm tapering downwards and rooting, solid, white, at first annulate but soon exannulate, below annulus covered with small, erect to appressed, pale yellowish brown, floccose volval scales, dry. Annulus apical, pendulous, rather thick felted-membranous, fugacious, white and smooth below and above, at margin with brown pyramidal warts similar to those on pileus. Context white, unchanging except for a slight yellowing in base of stipe after bruising, inodorous; taste mild. Spore print pure white when fresh.

Spores [50/4/2] (7.2–)7.5–9.6 × 5.6–6.9(–7.5) µm, Q = (1.15–)1.2–1.5(–1.6), average Q = 1.25–1.4, broadly ellipsoid to ellipsoid, thin-walled, smooth, amyloid, with small, abrupt apiculus, usually with granular contents and/or one or a few large oil-drops. Basidia 37–51 × 8.3–9.9 µm, 4-spored, with distinct clamp-connection. Marginal tissue, only present in very early stages, consisting of early disintegrating strands of colourless, thin-walled, 1–3 µm wide hyphae parallel to edge of lamellae. Hymenophoral trama bilateral, with narrow, 20–30 µm wide central plate of 2.5–7 µm wide, parallel hyphae, flanked by 30–40 µm wide zones of diverging hyphae and up to 20 µm wide, diverging, inflated elements, and 30–35 µm wide subhymenial zones of mostly ellipsoid to ovoid or irregularly shaped inflated cells, 10–30 × 9.5–19 µm, in rows perpendicular to hymenium. Pileipellis a rather indistinct, non-gelatinized layer of mainly radial, 5–10 µm wide hyphae gradually passing into trama of pileus. Volval tissue directly overlaying the pileipellis consisting of repent to ascending short rows of elongate-fusiform, elongate-subclavate, and subcylindrical cells, 57–240 × 22–57 µm, with brown vacuolar pigment (dissolving in NH_4OH) and sparsely branching, 5–14 µm wide hyphae; volval warts on pileus made up of sparse, 2–8 µm wide, branching hyphae and dominant, erect chains of inflated, thin- to slightly thick-walled, slenderly to broadly fusiform, clavate, and oblong cells, 45–135 × 15–45 µm, with intracellular brown pigment, but inflated cells shorter to almost globose, 25–85 × 20–40 µm, and paler in apex of warts. Context of stipe acrophysalidic with remarkably wide, thin- to slightly thick-walled acrophysalides, 165–380 × 25–85 µm; refractive vascular hyphae present but scarce. Scales on stipe made up of parallel rows of mainly cylindrical to subfusiform or oblong, almost colourless cells, 110–240 × 14–25(–32) µm. Clamp-connections abundant in all parts.

Habitat & distribution. Found twice at the type-locality and once at a second locality in southern Brazil, in mixed ombrophilous forest with or without *Araucaria angustifolia*, at c. 900 m altitude.

Collections examined. BRAZIL: Paraná, Curitiba, 'Parque Barigui', 31 Dec. 1991, *A.A.R. de Meijer 2078* (holotype, L); Curitiba, Parque Barreirinha, 13 March 1992, *A.A.R. de Meijer 2179* (L).





Figs. 5–6. *Amanita grallipes*. 5. Volval tissue in centre of wart on pileus; 6. volval tissue in apex of wart on pileus (both from type; × 500).

Amanita grallipes is a typical member of *Amanita* sect. *Lepidella* subsect. *Vittadiniae*. With Bas (1969: 347) it keys out in stirps *Vittadinii* because of its clamp-connections, broadly ellipsoid to ellipsoid spores and remnants of the volva evenly distributed over the part of the stipe below the annulus. Within stirps *Vittadinii*, as presented by Bas (l.c.), *A. grallipes* belongs to a group of species with spores shorter than 9.5 µm, consisting of one North American species, *A. silvifuga* Bas, and four South American species, viz.

A. bubalina Bas, *A. lilloi* Sing. & Digilio, *A. singeri* Bas and *A. boliviana* (nom. prov.). None of these five species, however, combines a uniformly dark brown pileus with distinctly yellowing gills. *Amanita silvifuga* from Texas comes very close microscopically to *A. grallipes* but has a paler pileus (white to pale ochraceous) with at first brown but later concolorous warts, no conspicuously yellowing lamellae, a non-rooting stipe, and a bitter taste.

The present species also cannot be named with the keys to South American Amanitas given by Garrido & Bresinsky (1985: 530) and to Colombian Amanitas by Tulloss et al. (1992). Two recently described members of subsect. *Vittadiniae* from Idaho (Miller et al., 1990), viz. *A. armillariiformis* Trueblood & Jenkins and *A. malheurensis* Trueblood et al., have pale pilei and spores longer than 10 µm.

Amanita ingrata, described by Pegler (1983: 293) from Martinique, with a paler brown pileus and deep cream-coloured lamellae, has a nauseous smell, larger spores (8–11.5 × 6.5–8.5 µm) and clampless basidia.

In the key to the species of subsect. *Vittadiniae* at present known from the United States, constructed by Tulloss (in msc.), *A. grallipes* belongs to a group of small-spored species (spores < 9.5 µm) consisting of *A. praegraveolens* (Murrill) Sing., *A. silvifuga,* and *A. thiersii* Bas, but all three have whitish or paler pilei. Moreover, *A. praegraveolens* has globose to broadly ellipsoid spores (Q = 1.0–1.3) and a nauseous smell and *A. thiersii* (sub)globose spores, no clamp-connections, and a bitter taste. *Amanita silvifuga* has already been discussed above.

Among the distinctly coloured species in Tulloss' key, only *A. pruittii* Tulloss & Lindgren (Tulloss, in msc.) from western Oregon has microscopical characters more or less similar to those of *A. grallipes* and a dark universal veil. But it has somewhat longer and distinctly wider spores (8–12 × 7–9 µm), the volval remnants on the pileus more grey-brown to grey, and a thick to very thick stipe (its thickness often one quarter to one third, sometimes even approaching one half of its length).

Among some recently described species from South Africa (Reid & Eicker, 1991), *A. foetidissima* Reid & Eicker is microscopically rather similar to *A. grallipes,* but has a paler pileus (buff to yellowish ochre), lamellae not turning deep yellow, and a nauseous smell. The same authors (l.c.) redescribed *A. pleropus* (Kalchbr. & MacOwan) Reid, another brownish species with clamp-connections, ellipsoid spores and clamped basidia in subsect. *Vittadiniae,* but with large spores (10–14 × 7–9.5 µm).

It is possible that *A. grallipes* represents the taxon described under the name *A. spissa* var. *laeta* by Rick (1906: 25) from Rio Grande do Sul in southern Brazil. Singer (1953) studied Rick's types, but did not report on that taxon, which probably means that its type does not exist. Ricks protologue reads as follows (translated): "138. *Amanita spissa* var. *laeta* Rick. Pileus and scales are isabella-grey; the stipe widens upwards, has no bulb, and is from below upwards covered with concentric scales; the lamellae are deep yellow."

Taking into consideration the lack of a type collection, hence the lacking information on microscopical characters, the poor protologue, and the colour described for the pileus (isabella-grey instead of dark brown), we prefer to describe a new species with extensive notes and illustrations, based on a well-dried type collection, rather than raising Rick's var. *laeta* to the rank of species and applying its name to the present collection.

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NOTULAE AD FLORAM AGARICINAM NEERLANDICAM – XXII
New taxa in Marasmiellus

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Two new taxa in *Marasmiellus* are described from the Netherlands, viz. *M. lateralis* Bas & Noordel., a pleurotoid species in sect. *Marasmiellus*, found on a decaying stump of *Pseudotsuga menziesii*, and *M. trabutii* var. *longisporus* Bas & Noordel. in sect. *Tricolores* from leaf-sheaths of *Ammophila arenaria*.

Marasmiellus lateralis Bas & Noordel., *spec. nov.* — Figs. 1–6

Basidiomata gregaria, pleurotoidea, 3–8 mm lata; pileus albus, haud hygrophanus, nec striatus, omnino pruinosus vel subtomentosus; lamellae subventricosae, albae; stipes nullus vel valde reductus, albus, pruinosus.

Sporae 5.5–7.0 × 2.5–3.0 µm, Q = 2.2–2.5, basidia 4-sporigera; cheilocystidia 24–52 × 2–5 µm, lageniformia vel filiformia; pileipellis trichoderma ex cellulis coralloideis constans pigmentum nullum; fibulae abundantes.

Ad lignum putridum *Pseudotsugae menziesii*.

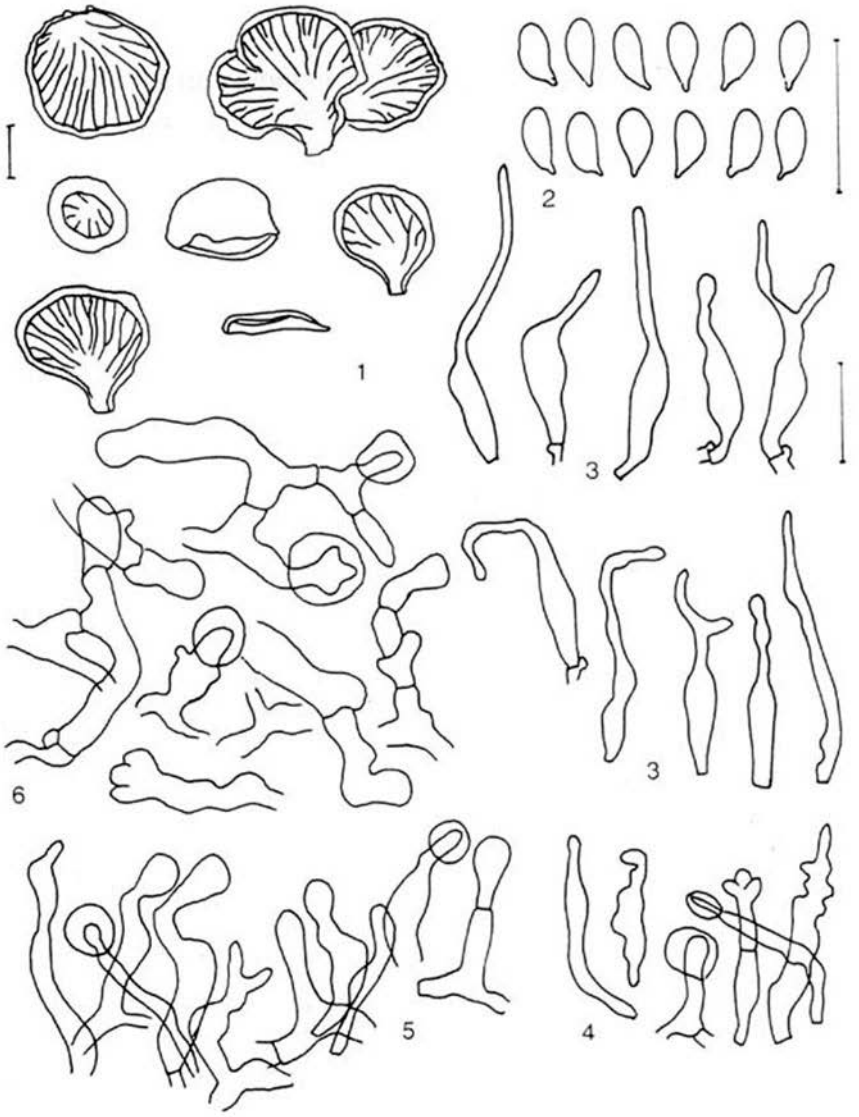
Holotypus: *M.T. Veerkamp s.n.*, 31.X.1988, Apeldoorn, prov. Gelderland, Netherlands (L).

Basidiocarps gregarious, 3–8 mm broad, cupulate when young, then pleurotoid with flabelliform to spathulate or circular shape, with strongly involute margin, not hygrophanous, not translucently striate, white, opaque, entirely pruinose to subtomentose (lens). Lamellae, L = 8–12, l = 0–5, well-developed, subventricose, white with concolorous, entire edge. Stipe lacking or rudimentary in young stages only, white, pruinose. Context thin, white. Smell none. Taste not tried.

Spores 5.5–7.0 × 2.5–3.0 µm, Q = 2.2–2.5(–2.9), average Q = 2.3, oblong to subcylindrical or narrowly clavate, attenuated towards base, with pronounced hilar appendage. Basidia 20–25 × 4.5–6 µm, 4-spored, clamped. Subhymenium densely ramose, made up of very narrow, branched hyphae. Lamella edge heterogeneous. Cheilocystidia abundant, but always mixed with basidia, 24–52 × 2–5 µm, versiform, lageniform with short to long, 1–3 µm wide neck, or filiform to more or less coralloid especially towards margin of pileus, thin-walled. Hymenophoral trama subregular, made up of 1.5–6.5 µm wide, somewhat inflated hyphae with thin or slightly thickened, refringent walls. Pileipellis a trichoderm of irregular, coralloid elements, 2–8 µm wide, with irregular, often lobed or subcapitate to vesiculose apex, sometimes with hyaline, apical slimecap. Clamp-connections abundant.

Habitat. On decaying stump of *Pseudotsuga menziesii*.

Collections examined. NETHERLANDS: prov. Gelderland, Apeldoorn, Uchelen, forest reserve 'Het Leeste', 31 Oct. 1988, *M.T. Veerkamp s.n.* (holotype, L); same locality, 20 Oct. 1989, *M.T. Veerkamp s.n.* (L).



Figs. 1–6. *Marasmiellus lateralis*. 1. Basidiocarps; 2. spores; 3. cheilocystidia (middle of edge); 4. cheilocystidia (near margin of pileus); 5. pileipellis in radial view; 6. pileipellis in scalp. — Scale bar with basidiocarps 1 mm, with microscopic characteristics 10 μm.

Thus far *Marasmiellus lateralis* is the only European representative of the genus with a sessile, pleurotoid basidiocarp. In the monograph of Singer (1973) it keys out in sect. *Marasmiellus* on account of the pleurotoid habit and lack of a distinct gelatinized zone in the pileitrama. The oblong spores and pigmentless basidiocarps places our species in subsect. *Inodermini*. The practically absent stipe leaves only three Central and South American species that are similar to our species.

Marasmiellus gossypinulus Sing. is very close, but differs by a lobate pileus, broader spores (6.0–8.3 × 3.0–5.0 µm, Q = 1.7–2.0), and very inconspicuous, scattered, basidiomorphous, or rarely diverticulate cheilocystidia. It grows on wood in Argentina and Chile.

Marasmiellus concolor (Berk. & Curt.) Sing. has very similar spores (5.0–7.0 × 2.5–3.3 µm), but lacks cheilocystidia and has a strongly developed *Rameales*-structure in the pileipellis. It is known only from the type-locality in tropical forest in Cuba, growing on dicotyledonous wood. Pegler (1983) studied the same collection, with the following data: spores 6.5–7.5 × 3.7–4.5 µm, Q = 1.7, and lamella edge sterile with cheilocystidia 15–22 × 4–5 µm, clavate to ventricose, irregularly nodulose-diverticulate at apex.

Marasmiellus microscopicus (Speg.) Sing. described from Paraguay, has smaller, ellipsoid spores (4.8–5.5 × 3.5 µm), relatively broad, crowded lamellae, glabrous pileus, and cheilocystidia are absent.

Marasmiellus trabutii var. **longisporus** Bas & Noordel., *var. nov.* — Figs. 7–10

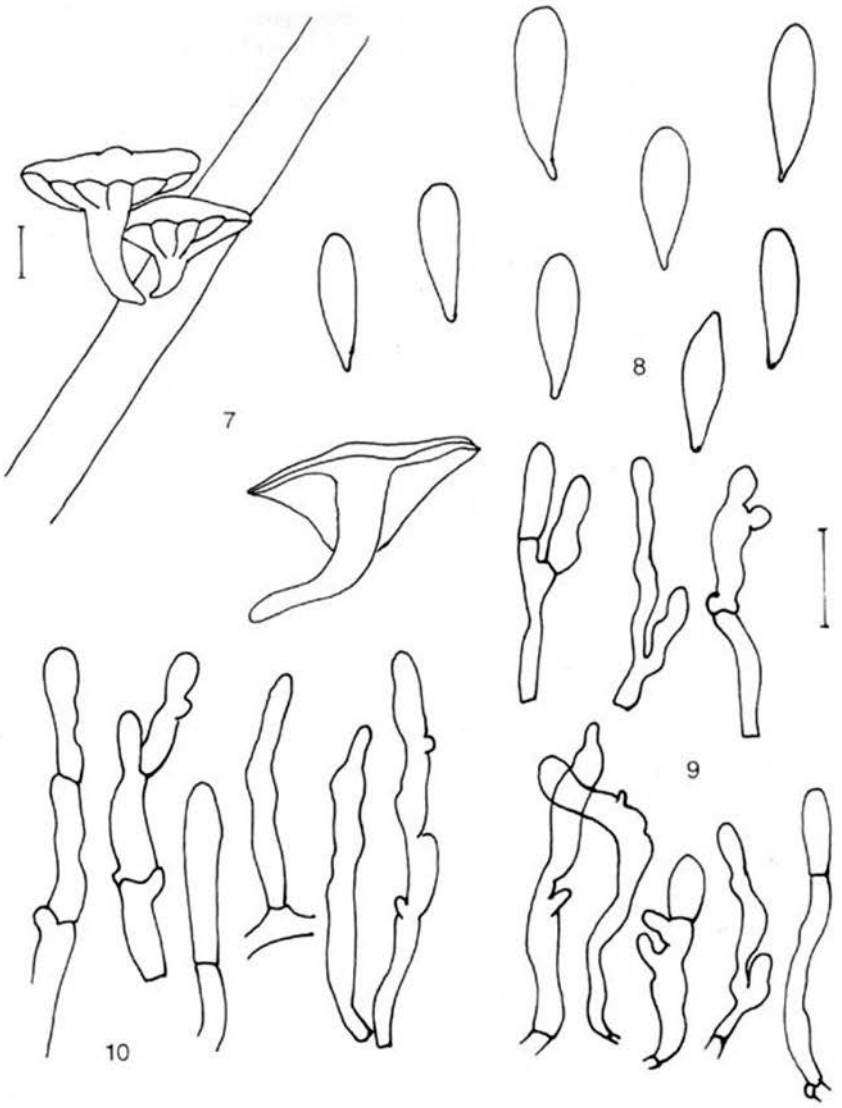
A varietate typica differt sporis longioribus (15.0–24.5 × 4.5–7.0 µm, Q = 2.6–6.4) et ad folia *Ammophilae arenariae* crescens.

Holotypus: *E.J. Weeda s.n.*, 26.X.1988, Zandvoort, Netherlands (L).

Pileus 8–14 mm, plano-convex at first, soon becoming somewhat irregularly flattened with small umbo, not hygrophanous, not translucently striate, pale isabella, white towards margin, very minutely pale brown squamulose under lens, somewhat lubricious when moist. Lamellae, L = 15–17, l = 1–3, entire lamellae sometimes forked and somewhat undulating, lamellulae strongly anastomosing, broadly adnate to subdecurrent, rather broadly triangular, up to 3.5 mm broad, very pale isabella with concolorous, entire or subpruinose (lens) edge. Stipe 4–8 × 1–1.5 mm, rather strongly tapering downwards, curved, whitish at apex, bluish grey in the middle, dark grey-brown below, sparsely minutely pruinose to subpubescent (lens) on fibrillose background, concolorous, tomentose at base. Smell indistinct. Taste unknown.

Spores 15.0–24.5 × 4.5–7.0 µm, Q = 2.6–6.4, average Q = 3.5, fusiform, clavate or cylindrical. Basidia 4-spored, clamped. Lamella edge sterile. Cheilocystidia 30–70 × 4–8 µm, subcylindrical to irregularly flexuose with undulating outline, thin-walled, clamped. Hymenophoral trama irregular, gelatinized, made up of undulating, subcylindrical hyphae, 2–11 µm wide. Pileipellis a cutis with distinct *Rameales*-structure. Subpellis and pileitrama distinctly gelatinized, subregular, made up of cylindrical to inflated hyphae, 3–15 µm wide, with encrusted walls in subpellis. Caulocystidia abundant, irregularly flexuose to coralloid, 15–70 × 3–8 µm. Clamp-connections abundant.

On dead leaf-sheaths of *Ammophila arenaria* (L.) Link in primary coastal dunes.



Figs. 7–10. *Marasmiellus trabutii* var. *longisporus*. 7. Basidiocarps; 8. spores; 9. cheilocystidia; 10. caulocystidia. — Scale bar with basidiocarps 1 mm, with microscopic characteristics 10 µm.

Collections examined. NETHERLANDS: prov. Noord-Holland, Zandvoort, 26 Oct. 1988, *E.J. Weeda s.n.* (holotype, L).

Macroscopically the collection described above is perfectly similar to *Marasmiellus trabutii* var. *trabutii*, as described by Noordeloos (1975) and Honrubia (1984). The only difference microscopically is formed by the very long spores, which, nevertheless, are also born on 4-spored basidia. Also the habitat is different, as in western Europe, *M. trabutii* var. *trabutii* is only found on *Juncus maritimus* in western Europe. Therefore it was decided to describe the present collection as a taxon in its own right on the level of variety.

ACKNOWLEDGEMENTS

The authors are very grateful to Mirjam Veerkamp and Eddy Weeda for putting material of respectively *M. lateralis* and *M. trabutii* var. *longisporus* at our disposal.

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SOME NEW SPECIES OF COPRINUS FROM THE NETHERLANDS

C.B. ULJÉ[1] & C. BAS[2]

Four new species of *Coprinus* are illustrated and described as *C. calosporus* and *C. ochraceolanatus* in sect. *Coprinus* subsect. *Lanatuli* (Fr.) Sing. and *C. goudensis* and *C. piepenbroekii* in sect. *Coprinus* subsect. *Alachuani* Sing. (= *Impexi* s. Kühn. & Rom., 1953).

At the base of the stem of a Yucca, growing in a flowerpot in a room of the Rijksherbarium at Leiden, a number of basidiocarps of a species of *Coprinus* were found by H. Kruijer, bryologist at the Rijksherbarium. Macroscopically they resembled *C. lagopus*, but microscopical examination showed that the spores were conspicuously nodulose and had a different shape. As in literature no suitable name could be found, the concerning taxon is newly described here as *C. calosporus*.

Coprinus ochraceolanatus is another new species in subsect. *Lanatuli*, distinguishing itself in the field by its rather deep ochraceous yellow veil. Kemp (1975a: 382 and 1975b: 62) has shown by means of oidial homing that there is another good reason to consider this fungus (then provisionally named *C. ochraceovelatus*) as a species in its own right in the *C. lagopus*-group.

A recent collection of a *Coprinus* growing on a stump of *Fraxinus* near Gouda turned out to represent an undescribed species in subsect. *Alachuani* and is named *C. goudensis*.

Among the unnamed collections of *Coprinus* in the Rijksherbarium, Leiden, a second new species in the same subsection, collected almost 20 years ago by Mr. J.H. and Mrs. G. Pie-penbroek, has been discovered. It is named after its collectors: *C. piepenbroekii*. Although the single collection available of this species consists of no more than 3 young basidiocarps, it was decided to publish it as new, because of its outstanding characters.

In the following descriptions the colour code of Munsell Soil Color Charts (abbreviated Mu.) is used to designate colours. Other abbreviations in text and drawings are:

av. – average
B – breadth of spores in frontal view
Bas. – basidia
Ch. – cheilocystidia
diam. – diameter
L (relating to lamellae) – number of lamellae reaching stipe
L (relating to spores) – length
l – number of lamellulae between two lamellae
Pl. – pleurocystidia
P.p. – pileipellis
Q – length divided by breadth
s. – sensu
Sp. – spores
St.v. – veil from stipe
Ve. – veil from centre of pileus

The notation [60,2,1] stands for '60 spores from 2 basidiocarps from 1 collection measured'. All collections Uljé in herb. Uljé (L); other collections examined have been deposited in the Rijksherbarium, Leiden.

The enlargements of the drawings are: × 2000 for the spores, × 800 for the other microscopical characters, and × 1 for the basidiocarps, unless indicated otherwise.

1) Van Dijkstraat 21, 2405 XE Alphen a/d Rijn, The Netherlands.
2) Rijksherbarium / Hortus Botanicus, P.O. Box 9514, 2300 RA Leiden, The Netherlands.

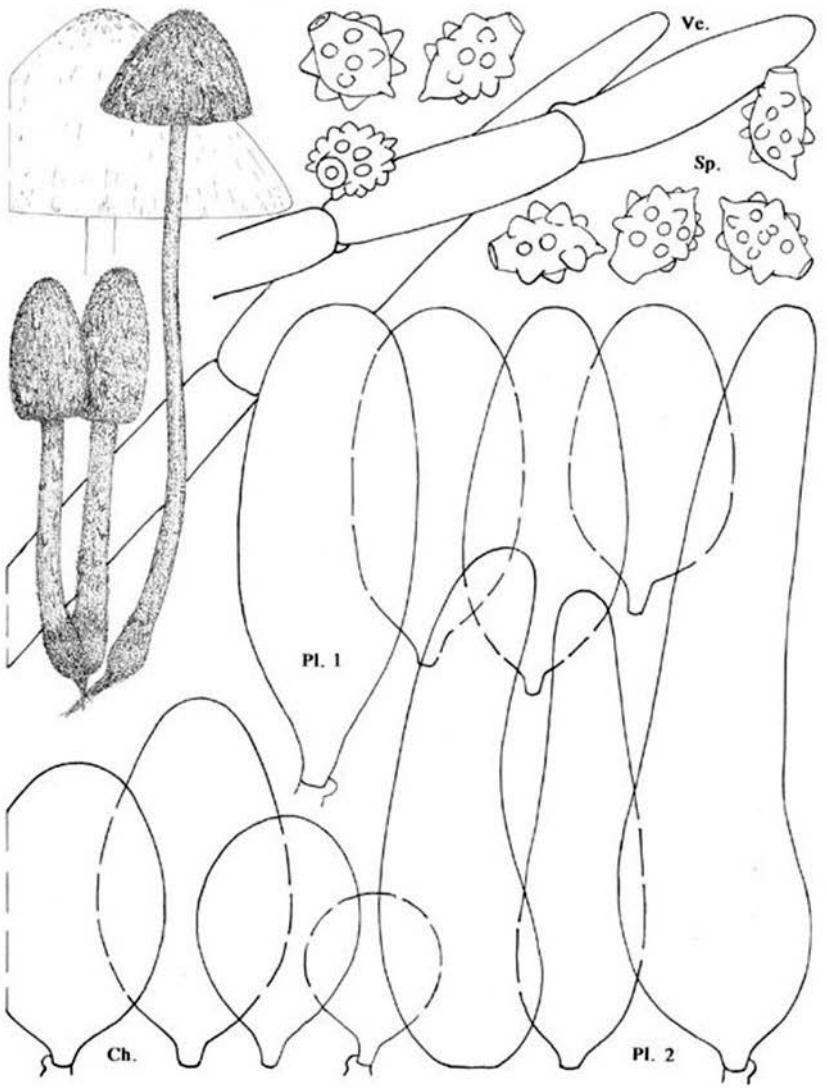

Fig. 1. *Coprinus calosporus*. Pl. 1 from young basidiocarp; Pl. 2 from older one. All figures from *Uljé 1131* (isotype).

Coprinus calosporus Bas & Uljé, *spec. nov.* — Fig. 1

Pileus ad c. 30 mm latus, initio albus, mox cinerascens vel cinereo-brunnescens, velo fibrilloso vel floccoso, primo albo, postea pallide griseo vel pallide griseo-brunneo obtectus. Lamellae liberae, subconfertae, initio albae, mox griseo-brunneae vel nigrae. Stipes 50–100 × 2–4 mm, sursum subattenuatus, basi clavatus vel subbulbosus, pseudorhiza brevi, attenuata praeditus, cavus, albidus, fibrilloso-floccosus.

Sporae 7.3–9.8 × 4.6–5.8 µm, rubro-brunneae, apice late truncatae, poro germinativo, angusto, centrali instructae, c. 16–24 nodulis conicis, magnis ornatae. Basidia tetraspora. Pleurocystidia 30–150 × 20–40 µm, elongato-ellipsoidea vel oblonga vel sublageniformia. Cheilocystidia 30–70 × 20–35 µm, ellipsoidea vel oblonga. Pileipellis ex hyphis repentibus, 4–22 µm latus, constans. Velum cellulis cylindricis vel subinflatis, catenulatis, 30–150 × 5–25 µm metientibus. Fibulae adsunt.

Typus: 'Netherlands, prov. Zuid-Holland, Leiden, 18.IV.1991, *C. Bas 8795* (L).'

Pileus when still closed up to 29 × 12 mm, ellipsoid, cylindrico-ellipsoid, often somewhat conical, white in very young stage, soon becoming greyish or grey-brown, underneath veil somewhat darker (Mu. 10 YR 5/4), darkest at centre, expanding to conical, then via convex to applanate, finally plano-concave with reflexed margin, up to c. 30 mm in diam. when mature. Veil in primordia smooth, mat, pure white, later pale grey to pale grey-brown (10 YR 7/3), covering entire pileus, soon radially splitting into hairy to fibrillose, often pointed and adpressed or – especially at centre – recurving flocks. Lamellae, L = 32–46, l = 1–3(–5), free, narrow, rather crowded, first white, soon greyish brown to blackish. Stipe 50–100 × 2–4 mm, whitish, somewhat tapering upwards, up to 5 mm wide at clavate to slightly bulbous base, with short and narrow pseudorhiza, hollow, hairy-flocculose over entire surface but particularly densely so at lower part, becoming glabrous with age. Spore print not available.

Spores [60,2,1] 7.3–9.8 × 4.6–5.8 µm (L × B, without ornamentation), av. L = 8.0–8.4, av. B = 5.0–5.4 µm, Q = 1.35–1.75, av. Q = 1.60, red-brown under microscope, amygdaliform, often with attenuate base and with broadly truncate, somewhat nozzle-shaped apex, covered with c. 16–24 large, short, broad, rounded-conical nodules, with central germ pore, seemingly c. 3 µm wide, but because of thick wall actual pore c. 1.3 µm wide. Basidia 13–24 × 6–8 µm, 4-spored. Pseudoparaphyses (3–)4–5(–6) around each basidium. Pleurocystidia 30–150 × 20–40 µm, elongate-ellipsoid to oblong to rather broadly sublageniform. Cheilocystidia 30–70(–90) × 20–35 µm, ellipsoid to oblong, sometimes slightly vesiculose. Pileipellis consisting of radial, repent, 4–22 µm wide hyphae. Veil made up of elongate, sausage-like elements, 30–150(–250) × (3–)5–25(–40) µm, often somewhat inflated, usually constricted at septa. Clamp-connections present.

Habitat. Fasciculate against stem of *Yucca* in flowerpot. Indoors.

Collections examined. NETHERLANDS: prov. Zuid-Holland, Leiden, Rijksherbarium, 18 April 1991, *C. Bas 8795a* (holotype), *C.B. Uljé 1131* (isotype); 30 April 1991, *C. Bas 8795b.*

Macroscopically it is not possible to distinguish *C. calosporus* from other members of subsect. *Lanatuli*. One look at the spores under the microscope, however, is sufficient to establish its identity. Their ornamentation of large, rounded-conical nodules and their very broadly truncate, somewhat elongate apex make them highly characteristic.

We know only one other species of *Coprinus* with nodulose spores, viz. *C. iocularis* Uljé (Uljé, 1988: 485), but that belongs to subsect. *Nivei* and consequently looks very much different. Moreover, the spores of that species have only four, much weaker developed nodules which render the spores in frontal view more or less hexagonal.

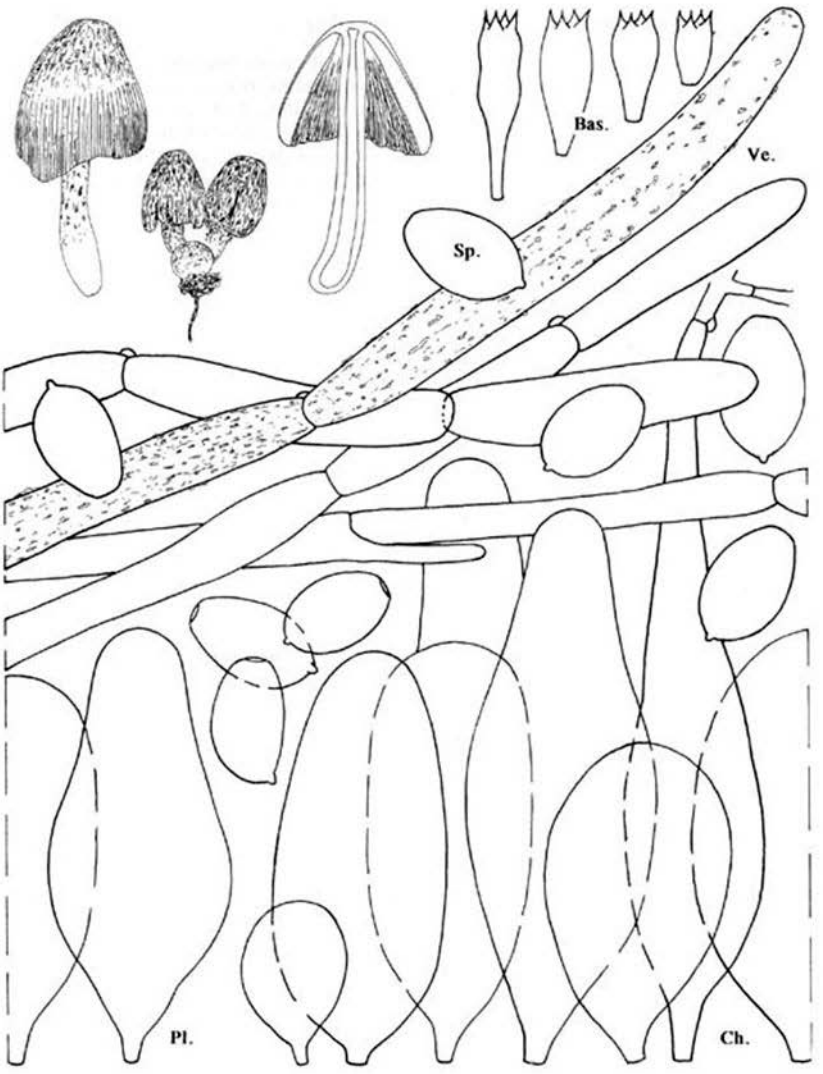

Fig. 2a. *Coprinus ochraceolanatus*. All figures from *Bas 5813* (type).

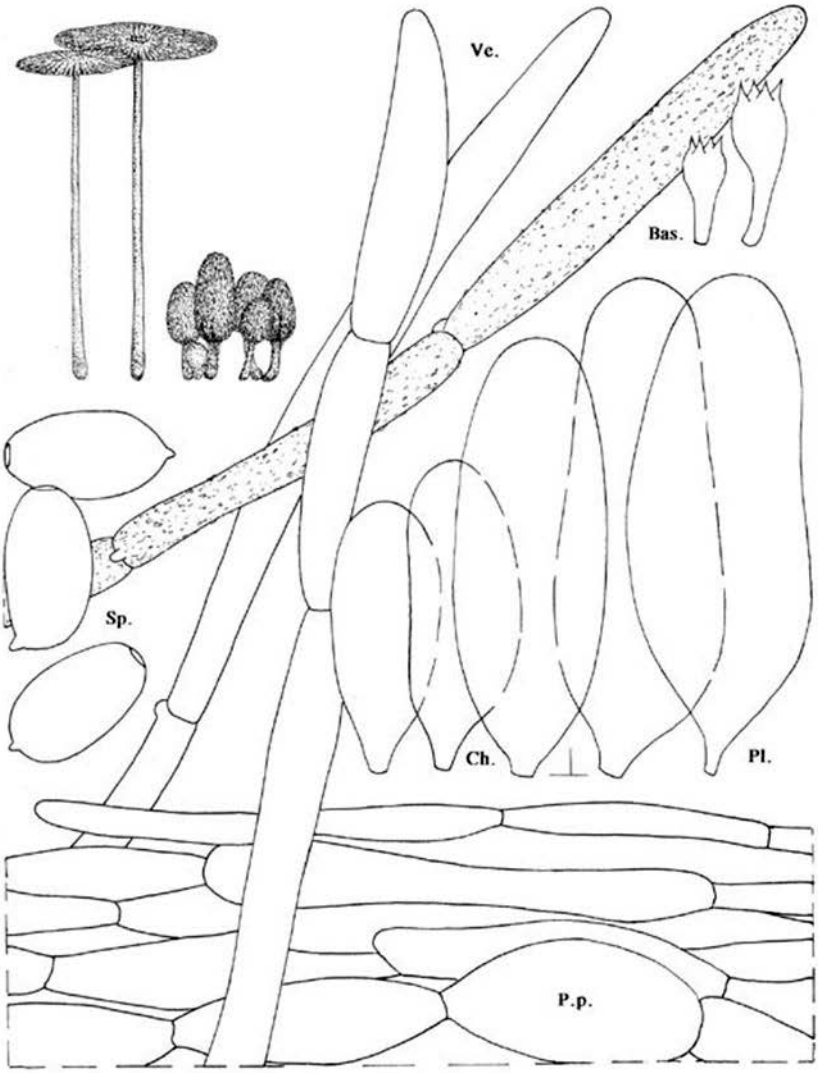

Fig 2b. *Coprinus ochraceolanatus*. All figures from *Uljé 1062*.

Coprinus ochraceolanatus Bas, *spec. nov.* — Figs. 2a, 2b

Pileus ad c. 50 mm latus, pallide griseus vel griseo-brunneus, velo adpresso, fibrilloso-squamoso, ochraceo ornatus. Lamellae liberae, confertae, purpureo-brunneae vel obscure griseo-purpureo-brunneae. Stipes ad 80 × 5.5 mm, sursum attenuatus, interdum pseudorhiza brevi praeditus, (sub)fasciculatus, griseo-albidus, dense ochraceo-fibrillosus, interdum basi ochraceo-squamulosus.

Sporae 8.3–13.4 × 5.7–7.3 µm, rubro-brunneae, ellipsoideae vel ovoideae, poro germinativo centrali instructae. Basidia tetraspora. Pleurocystidia 50–140 × 20–50 µm, elongato-ellipsoidea, vesiculosa, cylindrica vel late fusiformia. Cheilocystidia 30–120 × 15–50 µm, primo subglobosa, postea ellipsoidea, oblonga, clavata vel cylindrica. Pileipellis ex hyphis repentibus 8–26 µm latis constans. Velum cellulis cylindricis vel subfusiformibus, flavo-incrustatis, 45–200 × 7–20 µm metientibus. Fibulae adsunt.

Typus: 'Netherlands, prov. Zuid-Holland, Voorschoten, 31.V.1972, *C. Bas 5813* (L).'

Pileus just before expanding up to 30 × 20 mm, ovoid, sometimes with truncate apex and irregular somewhat lobed margin, rather pale grey (Mu. 5 Y 6/1) at margin to somewhat darker (5 Y 5/1) near apex, but slightly more brownish although not as brown as 2.5 Y 6/2 to 5/2 in *Bas 5813*, rather more brown (7.5 YR 3/2 to 10 YR 4/3) in *Uljé 1062*, deeply and densely sulcate at margin, sulcate-striate near centre, with appressed (but in young buds suberect), long, thin, fibrillose, ochraceous to salmon-ochraceous (10 YR 7/4 to 7/6) velar scales condensed to a thin, felted, salmon-ochraceous patch at centre; margin of cap in early stages loosing contact with stem; pileus up to c. 50 mm when expanded. Lamellae, L = 36–41, l = 1–3(–5), crowded, free, rather narrow (up to 4 mm wide), already in young buds fairly dark chocolate-brown (7.5 YR 3/2), finally dark greyish purple-brown (5 YR 2/2) with thin, pale ochraceous, subflocculose edge; pleurocystidia visible with handlens. Stipe up to 80 × 5.5 mm, tapering upwards, hollow, subfasciculate to fasciculate, in some specimens with thin, up to 12 mm long pseudorhiza, slightly greyed whitish, densely fibrillose, with ochraceous tinge because of rather deeply ochraceous-yellow superficial fibrils (under lens), especially near base sometimes with a few incomplete, pale ochraceous, floccose girdles or many small, similarly coloured scales. Context ± chocolate-brown in centre of cap, slightly more greyish purple-brown in base of stipe and paler along cavity of stipe; rest pale. Smell indistinct, weakly fungoid. Taste subraphanoid with somewhat bitterish, unpleased aftertaste. Spore print not available.

Spores [100,5,3] 8.3–13.4 × 5.7–7.3 µm (L × B), av. L = 9.4–12.3, av. B = 6.1–6.8 µm, Q = 1.45–2.10, av. Q = 1.55–1.85, red-brown under microscope (not as blackish brown as in *C. lagopus*), ellipsoid to ovoid; germ pore central, 1.5–1.8 µm wide. Basidia 15–38 × 8–11 µm, 4-spored. Pseudoparaphyses 3–5(–6) around each basidium. Pleurocystidia 50–140 × 20–50 µm, elongate-ellipsoid, subglobose, cylindrical or broadly fusiform. Cheilocystidia 30–120 × 15–50 µm, in very young pileus subglobose or vesiculose, later rather more elongate or ellipsoid, clavate, oblong, vesiculose or cylindrical. Pileipellis consisting of repent, radial chains of ± cylindrical to inflated, 8–26 µm wide cells. Veil made up of parallel, yellowish, granular-incrusted hyphae of 45–200 × 7–20 µm large, often somewhat fusiform elements, not or only slightly constricted at septa. Incrustations on velar hyphae persistent in HCl 10% and alcohol, loosening in KOH and NH_4OH and dissolving in Melzer's reagent. Clamp-connections present.

Habitat. Fasciculate on old mud taken out of ditch one year earlier, in old deciduous forest on sandy clay with much humus and forest litter; gregarious on wood-chips; near old stump of tree.

Collections examined. NETHERLANDS: prov. Utrecht, Maarseveen, Zuidplas, 15 May 1982, *C.B. Uljé 313*; prov. Zuid-Holland, Voorschoten, 'Ter Wadding', 31 May 1972, *C. Bas 5813* (holotype, L); Ter Aar, 'de Put', 9 May 1990, *C.B. Uljé 1062*.

Coprinus ochraceolanatus is rather close to *C. lagopus*, but differs in having more slender and densely incrusted velar cells (up to 20 µm wide), whereas *C. lagopus* has smooth velar cells which are much more inflated (up to 40 µm wide). Macroscopically the colour of the veil of *C. ochraceolanatus* is yellowish ochre, in *C. lagopus* whitish or greyish, more rarely pale yellow but then the hyphal walls are not incrusted.

The length of the spores of *C. ochraceolanatus* shows a great deal of variation. In *Bas 5813* the spores measure 8.3–11.8 × 5.8–6.8 µm, with a quotient of 1.45–1.90. The other collections examined have spores with a length up to c. 13 µm, whereas the breadth of the spores is very constant in all collections. Consequently the L/B-quotient is 1.50–2.10. Such a difference in size of the spores is not unusual in *Coprinus* and therefore we accept the collections with spores up to 13 µm long as to belong to *C. ochraceolanatus* also, because they share with the type-collection the yellow, granular-incrusted, 7–20 µm wide hyphae of the universal veil.

Kemp (1975a: 382; 1975b: 62) introduced the reactions of monokaryotic hyphae to oidia in cultures as a way of testing the degree of relationship among species of *Coprinus* sect. *Lanatuli*.

Three interspecific reactions are possible: 1. hyphal tips of one species do not curve to grow towards oidia of another species ('no homing'); 2. hyphal tips of one species curve to grow towards oidia of another species ('homing'); 3. hyphal tips of one species grow towards oidia of another species and fuse with these, but the fusion is lethal ('homing and lethal'). Kemp considers case 3 as indicating the highest degree of relationship and case 1 as the lowest.

Coprinus ochraceolanatus (in Kemp's papers provisionally called *C. ochraceovelatus*, 1975a: 380) was tested in this respect against nine other species of sect. *Lanatuli*. In none of the tests with *C. ochraceolanatus* homing plus a lethal reaction occurred. In fact in most tests there was no homing at all. In three cases there was homing of hyphae towards conidia of *C. ochraceolanatus*, viz. with *C. cinereus*, *C. macrocephalus*, and *C. radiatus*, but in the reciprocal tests hyphae of *C. ochraceolanatus* showed no homing to conidia of any of the species involved.

Thus Kemp's tests strongly support the taxonomic value of *C. ochraceolanatus* as a species.

Coprinus goudensis Uljé, *spec. nov.* — Fig. 3

Pileus 10–20 mm latus, albus vel griseolus, centro griseo-brunneus, velo albo, fibrilloso-flocculoso vel fibrilloso-squamuloso obtectus. Lamellae liberae, subdistantes, primo albae vel griseo-brunneae, postea nigrae. Stipes 20–40 × 1–1.5 mm, deorsum subincrassatus, basi interdum subbulbosus, albo-fibrilloso-flocculosus.

Sporae 7.0–9.8 × 4.6–6.0 µm, ovoideae, ellipsoideae vel subamygdaliformes, pallide griseo-rubro-brunneae, poro germinativo centrali instructae. Basidia tetraspora. Pleurocystidia 60–100 × 35–50 µm, ellipsoidea vel late cylindrica, raro subglobosa vel obovoidea. Cheilocystidia 30–80 × 20–50 µm, (sub)-globosa, ellipsoidea vel obovoidea, raro late utriformia vel cylindrica. Pileipellis ex hyphis repentibus, 3–18 µm latis constans. Hyphae veli ramosae, tenui-tunicatae, 3–10 µm latae, raro ad 15 µm latae et disperse diverticulatae; diverticula 8–15 × 1–4 µm, cylindrica, apice rotundata. Fibulae adsunt.

Typus: 'Netherlands, prov. Zuid-Holland, Reeuwijk near Gouda, 14.XI.1991, *C.B. Uljé 1217* (L).'

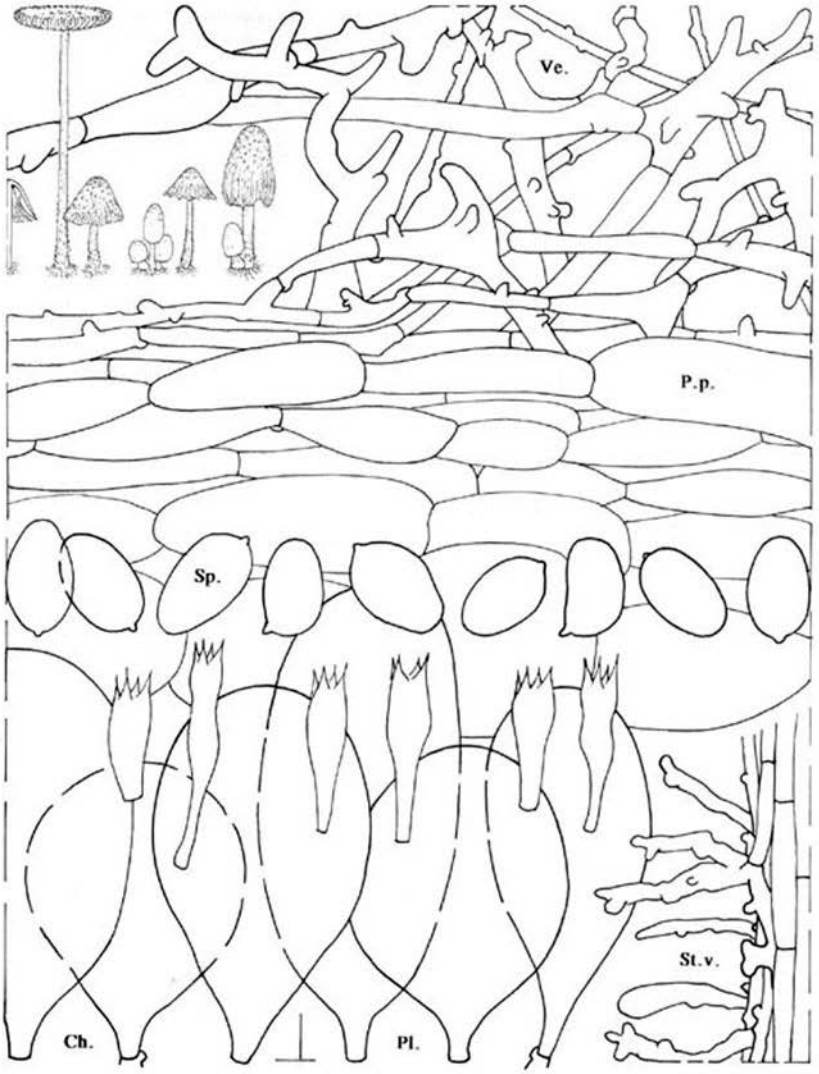

Fig. 3. *Coprinus goudensis*. All figures from type.

Pileus up to 12 × 9 mm when still closed, first ellipsoid to ovoid, then conical, finally flattened with reflexed margin, 10–20 mm wide when expanded, covered with white veil and this unbroken when young but soon radially splitting up in hairy-flocculose scales, with surface white to greyish under veil, dark grey-brown at centre when fresh, paler when drying. Lamellae, L = 23–26, l = 0–3, free, subventricose, moderately distant, white to greyish brown, finally black. Stipe 20–40 × 1–1.5 mm, hollow, whitish, slightly thickening towards equal to subbulbous base, white hairy-flocculose all over but more densely so at base than at apex.

Spores [60,2,2] 7.0–9.8 × 4.6–6.0 µm, av. L = 8.4–8.8, av. B = 5.0–5.1, Q = 1.50–1.90, av. Q = 1.65–1.70, ovoid, ellipsoid or slightly amygdaliform, rather pale greyish red-brown; germ pore central, c. 1.3 µm wide. Basidia 18–40 × 7–9 µm, 4-spored. Pseudoparaphyses (3–)4–5(–6) around each basidium. Pleurocystidia 60–100 × 35–50 µm, ellipsoid to broadly cylindrical, more rarely subglobose or obovoid. Cheilocystidia 30–80 × 20–50 µm, globose, subglobose, ellipsoid or obovoid, seldom broadly utriform or subcylindrical. Pileipellis consisting of repent, 3–18 µm wide hyphae consisting of cylindrical or somewhat inflated elements, constricted at septa. Elements of suprapellis in part diverticulate. Veil on pileus consisting of branched, hyaline, thin-walled, 3–10 µm wide, sometimes up to 15 µm wide hyphae locally with cylindrical or upwards tapering diverticulations with rounded apex, up to 8(–15) µm in length and 1–4 µm wide. Clamp-connections present.

Habitat. On the side of a stump of *Acer pseudoplanatus* in a maple plantation.

Collections examined. NETHERLANDS: prov. Zuid-Holland, Reeuwijk near Gouda, Reeuwijker Hout, 20 Oct. 1991, *C.B. Uljé 1213*; 14 Nov. 1991, *C.B. Uljé 1217* (holotype, L).

Because of the branched, diverticulate veil *C. goudensis* belongs to the subsect. *Alachuani* Sing. (= *Impexi* s. Kühn. & Rom., 1953). In this section, six species have been compared with the present species, viz. *C. suburticicola* Pilát & Svrček (1967: 140), *C. urticicola* (Berk. & Br.) Buller s. Redhead & Traquair (1981: 388), the tropical species *C. neotropicus* Redhead & Traquair (1981: 394), *C. luteocephalus* Watling (1972: 359), *C. xenobius* P.D. Orton (1976: 148), and *C. stanglianus* Enderle et al. (1988: 62). *Coprinus urticicola* differs in much smaller basidiocarps, smaller spores (5.5–8 × 4–5.5 µm according to Pilát & Svrček, 5.5–8 × 3.9–5.1 µm acc. to Redhead & Traquair) and its habitat on grasses. *Coprinus suburticicola* deviates in the same features except the size of the spores (7–9 × 5–6 µm). After an examination of the type Redhead & Traquair (1981: 390) stated that although many of its spores are larger than in typical *C. urticicola*, the spore size ranges overlap too much to maintain *C. suburticicola* as a separate species. *Coprinus neotropicus* is a tropical species with much smaller and much broader spores. *Coprinus luteocephalus* has yellow veil, larger spores and grows on dung; the last two characters also apply to *C. xenobius*. *Coprinus stanglianus* has much larger spores and basidiocarps and grows on the soil, among grasses.

Coprinus piepenbroekii Uljé & Bas, *spec. nov.* — Fig. 4

Pileus 10–20 mm latus, centro mox obscure brunneus, velo ochraceo vel viridi-ochraceo, fibrilloso vel fibrilloso-squamuloso obtectus. Lamellae liberae, subdistantes, primo albidae vel griseo-brunneae, postea nigrae. Stipes 20–40 × 1–2 mm, deorsum subincrassatus, basi subbulbosus, albidus.

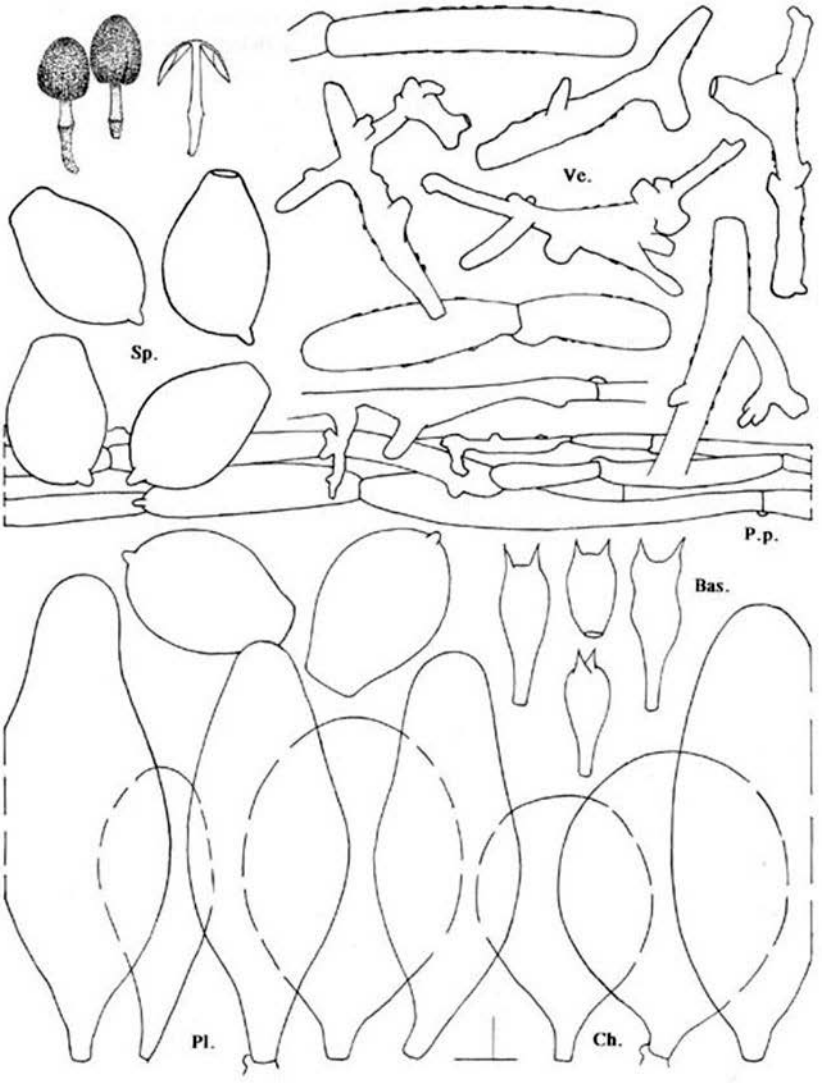

Fig. 4. *Coprinus piepenbroekii*. All figures from type.

Sporae 11.9–15.3 × 7.7–10.5 µm, amygdaliformes, apice truncatae, obscure rubro-brunneae, poro germinativo centrali instructae. Basidia bispora. Pleurocystidia 55–90 × 22–40 µm, subglobosa, vesiculosa, ellipsoidea vel utriformia. Cheilocystidia 40–85 × 25–45 µm, (sub)globosa vel ellipsoidea, interdum oblonga. Pileipellis ex hyphis repentibus, 2–15 µm latus, cylindricis vel inflatis constans. Hyphae veli ramosae, tenui-tunicatae, 3–9 µm, interdum ad 12 µm latae, disperse diverticulatae; diverticula ad 15 µm longa, 1–4 µm lata, apice rotundata. Fibulae adsunt.

Typus: 'Netherlands, prov. Gelderland, Wilp, 22.VII.1974, *J.H. & G. Piepenbroek 787* (L).'

Pileus up to 10 × 7 mm when still closed, first ellipsoid to ovoid, then conical, finally flattened with reflexed margin, 10–20 mm wide when expanded, soon dark brown at centre, covered with ochraceous veil often with greenish hue and outside centre splitting up into small flocculose scales. Lamellae free, white to greyish brown, finally black. Stipe 20–40 × 1–2 mm, whitish, hollow, slightly thickening towards subbulbose base.

Spores [60,3,1] 11.9–15.3 × 7.7–10.5 µm, av. L = 12.7–13.8, av. B = 8.4–9.4 µm; Q = 1.30–1.60, av. Q = 1.45–1.50, amygdaliform, dark red-brown, with central, c. 2.5 µm wide germ pore. Basidia 15–32 × 9–12 µm, 2-spored. Pseudoparaphyses 4–6 around each basidium. Pleurocystidia 55–90 × 22–40 µm, subglobose, ellipsoid, vesiculose or utriform. Cheilocystidia 40–85 × 25–45 µm, (sub)globose or ellipsoid, sometimes elongate. Pileipellis consisting of repent hyphae made up of cylindrical to somewhat inflated, 2–15 µm wide elements. Elements of suprapellis in part diverticulate. Veil on pileus consisting of branched, hyaline, non-incrusted, thin-walled hyphae, 3–9 µm wide, but sometimes up to 12 µm wide in places with cylindrical diverticulations with rounded apex, up to 15 µm in length and 1–4 µm wide. Clamp-connections present.

Habitat. Gregarious on burnt ground.

Collection examined. NETHERLANDS: prov. Gelderland, Wilp, Wilpse Dijk, 22 July 1974, *J.H. & G. Piepenbroek 787* (holotype, L).

The macroscopical description is derived from the dried material and a colour slide; no descriptive notes are available. There only was a note that the veil had a distinct greenish tinge. Microscopically the green pigmentation could not been found in the elements of the veil.

Coprinus piepenbroekii is easily recognized by its microscopical features: large, amygdaliform spores in combination with diverticulate elements of the veil and two-spored basidia.

ACKNOWLEDGEMENTS

We are very grateful to Mr. H. Kruijer for bringing to our attention the growth of *C. calosporus* in one of his flowerpots.

Many thanks are due to Mr. J.H. & Mrs. G. Piepenbroek for the hundreds of excellent collections sent to the Rijksherbarium over a long period of years, among which again a new species has been discovered which we gladly name after them.

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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

J. DE GRUYTER[1], M.E. NOORDELOOS[2] & G.H. BOEREMA[3]

Twenty-seven taxa in section *Phoma* with conidia not exceeding 7 µm in length are keyed out and described on account of their characteristics in vitro. Four new species are introduced: *Phoma aurea* de Gruyter, Noordel. & Boerema, *Phoma crystallifer* de Gruyter, Noordel. & Boerema, *Phoma flavescens* de Gruyter, Noordel. & Boerema and *Phoma subherbarum* de Gruyter, Noordel. & Boerema. As new names are proposed *Phoma chenopodiicola* de Gruyter, Noordel. & Boerema, *Phoma pereupyrena* de Gruyter, Noordel. & Boerema and *Phoma selaginellicola* de Gruyter, Noordel. & Boerema. New combinations of species originally classified in *Phyllosticta* Auct. include: *Phoma ajacis* (Thümen) v.d. Aa & Boerema, *Phoma arachidis-hypogaeae* (Vasant Rao) v.d. Aa & Boerema, *Phoma haematocycla* (Berk.) v.d. Aa & Boerema, *Phoma piperis* (Tassi) v.d. Aa & Boerema and *Phoma poolensis* var. *verbascicola* (Ell. & Kellerm.) v.d. Aa & Boerema. Host-fungus and fungus-host indices are provided, and short comments on the ecology and distribution of the taxa are given.

The study of *Phoma* species in vivo and in vitro has led to the differentiation of a number of sections within the genus, see e.g. Van der Aa, Noordeloos & de Gruyter (1990). The first paper in this series of precursors of a planned monograph of *Phoma*, Contributions I–1 (De Gruyter & Noordeloos, 1992), deals with 18 species of section *Phoma* with very small conidia in vitro, i.e. having a length usually not exceeding 5.5 µm. While working on the taxa with conidia up to 7 µm long, several species were encountered that actually belong to the group with conidia up to 5.5 µm long. These taxa have also been included in the present paper. Among the species treated in this paper, *inter alia* the type species of the genus *Phoma* is to be found, the ubiquitous saprophyte *P. herbarum* Westend. This species (Fig. 1) displays also the typical characteristics of section *Phoma*: thin-walled ostiolate pycnidia producing in vivo and in vitro only one-celled hyaline conidia. The pycnidia are mostly glabrous, but may show some hyphal outgrowths (semi-pilose). The conidiogenous cells are, in young pycnidia, more or less globose, later becoming bottle-shaped, which means a variation between ampulliform and doliiform. In old pycnidia it is often difficult to differentiate the conidiogenous cells from those of the inner pycnidial wall. *Phoma herbarum* does not form any chlamydospore, but the section also includes a number of species producing unicellular chlamydospores. Species with multicellular chlamydospores have been classified in sect. *Peyronellaea*, treated in Contributions II of this series

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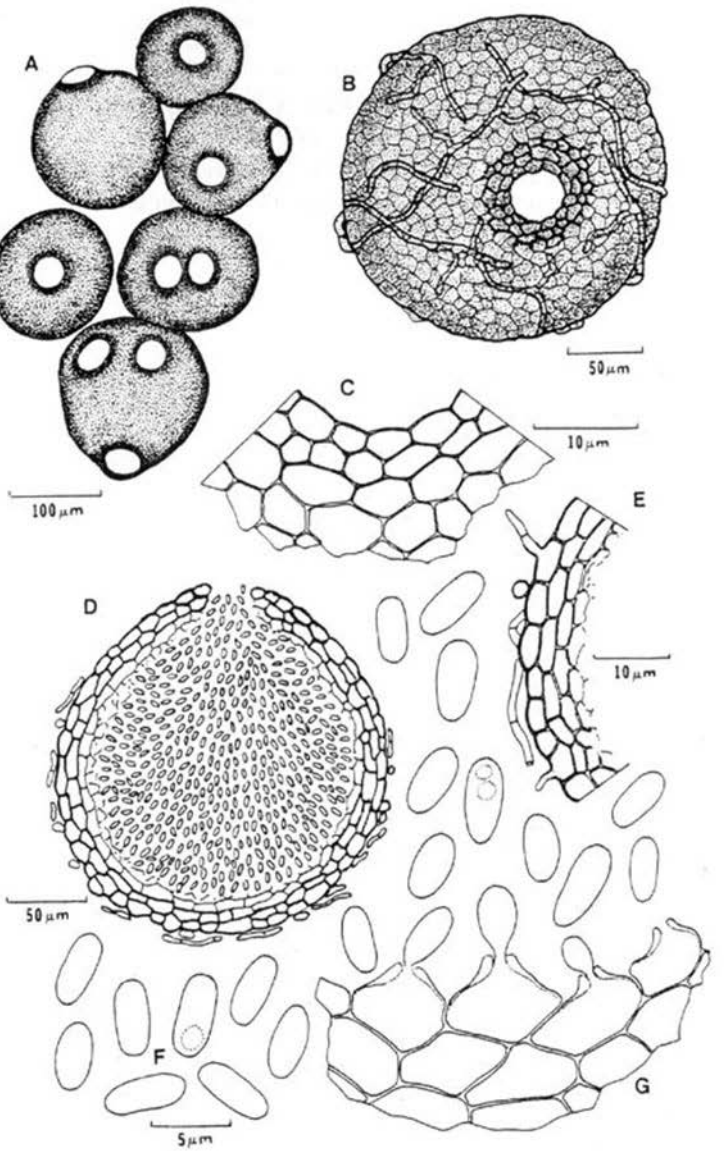


Fig. 1. *Phoma herbarum*, type species of *Phoma* sect. *Phoma*. A & B. pycnidia from 14-day-old colonies; C. surface view of pycnidial wall in vicinity of ostiole; D. vertical section of pycnidium; E. portion of pycnidial wall in section; F. conidia; G. conidiogenous cells. — Drawings after Morgan-Jones (1988a), with permission.

(Boerema, 1993). Most species of sect. *Phoma* are not associated with a teleomorph; one of the exceptions is also discussed in this paper, viz. *P. adianticola* (Young) Boerema, which in vitro may produce apart from pycnidia also pseudothecia belonging to the genus *Didymella* Sacc.

MATERIAL AND METHODS

The material and methods are the same as described in the first contribution of this series (De Gruyter & Noordeloos, 1992); some additional information is given here. The media used have the following compositions:

MA: 40 g malt extract-oxoid L39, 15 g oxoid agar no. 1, 1 l tapwater.
OA: 20 g oat-flakes, boiled in 0.5 l tapwater, filtered through cheesecloth and filled up to 1 l with tapwater, 15 g oxoid agar no. s3.
CA: 0.1 l cherry juice, 20 g oxoid agar no. 3, 0.9 l tapwater.
The petridishes used are 9 cm in diameter and 16 mm high, with ridges in the lid.
The size of the conidiogenous cells has been indicated by height × width.

KEY TO THE SPECIES TREATED IN THIS PAPER

1a. Growth-rate very slow on OA, only 14–35 mm in one week 2
b. Growth-rate at least 40 mm on OA in one week 4
2a. Colonies with distinct dull green to herbage green tinges on OA; dull green on MA and CA; pathogenic to *Lupinus* spp. (so far only known from North and South America) ..... 1. *P. lupini*
b. Colonies without green tinges, usually colourless or pale rosy-buff, ochre or buff 3
3a. Conidia in average 5.6 × 2.7 µm with two, large polar guttules (so far only known from soil in the Netherlands) ..... 2. *P. flavescens*
b. Conidia in average 4.2 × 1.6 µm; without guttules or with 1–2 inconspicuous guttules; pathogenic to *Phormium tenax* ..... 3. *P. haematocycla*
4a. NaOH reaction positive, at least on MA 5
b. NaOH reaction negative 14
5a. NaOH discolouring diffusible pigments on MA to blue-purplish, red, yellow-green, or orange-purplish 6
b. NaOH causing initially a yellow-green discolouration, gradually changing to red (E+ reaction) 9
6a. Growth-rate up to 50 mm on OA 7
b. Growth-rate 60–65 mm on OA 8
7a. MA usually staining reddish, NaOH reaction blue or purplish; pycnidia finally olivaceous black; plurivorous saprophyte (world-wide recorded) ..... 4. *P. herbarum*
b. MA staining yellow, NaOH reaction red; pycnidia honey with olivaceous tinge around ostiole; specific necrophyte of *Senecio* spp. ..... 5. *P. senecionis*
8a. MA staining scarlet, NaOH reaction yellow-green; pathogenic to *Adianthum* spp. and other Polypodiaceae ..... 6. *P. adianticola*

b. MA staining yellow, NaOH reaction orange, later purplish; specific necrophyte of *Linum* spp. ..... 7. *P. lini*

9a. Colony colourless on OA, but general impression salmon caused by abundant conidial mass exuding from pycnidia 10

b. Colony different 11

10a. Growth-rate 65–80 mm; pathogenic to *Bellis perennis* ..... 8. *P. bellidis*

b. Growth-rate 40–60 mm; specific necrophyte of *Eupatorium cannabinum* 9. *P. eupatorii*

11a. Colonies with dull green or citrine tinges on OA and MA, and coarsely floccose aerial mycelium; pathogenic to *Crinum* spp. and other Amaryllidaceae ... 10. *P. crinicola*

b. Colonies on OA almost colourless or with grey olivaceous, olivaceous grey or pale olivaceous sectors 12

12a. Colony colourless with grey olivaceous or olivaceous grey on OA, CA staining red; pathogenic to *Delphinium* spp. ..... 11. *P. ajacis*

b. Colony almost colourless on OA and CA, sometimes with (grey) olivaceous sectors 13

13a. Pycnidia after some transfers often non-ostiolate; esp. pathogenic to *Antirrhinum majus* ..... 12a. *P. poolensis* var. *poolensis*

b. Pycnidia always ostiolate; pathogenic to *Verbascum* spp. 12b. *P. poolensis* var. *verbascicola*

14a. Colonies staining agar flesh to rust coloured due to the release of a coloured pigment; plurivorous saprophyte (so far only known from North and South America) 13. *P. subherbarum*

b. Colonies without such pigment production 15

15a. Citrine green crystals formed on CA within three weeks; esp. pathogenic to *Arachis hypogaea* ..... 14. *P. arachidis-hypogaeae*

b. If crystals present, then not citrine green 16

16a. Chlamydospores present 17

b. Chlamydospores absent 20

17a. Growth-rate between 40–55 mm; pathogenic to *Acacia* spp. .... 15. *P. henningsii*

b. Growth-rate > 65 mm 18

18a. Specifically associated with *Olea europaea* (so far only known from southern Europe) ..... 16. *P. insulana*

b. Plurivorous; non-specific on various hosts (esp. known from India) 19

19a. Colonies distinctly pigmented grey olivaceous to olivaceous or olivaceous grey, reverse iron grey to leaden black; pycnidia sometimes with tubular outgrowths; conidia always with 2 distinct uniform polar guttules; plurivorous opportunistic pathogen 17. *P. pereupyrena*

b. Colonies colourless to weakly olivaceous, at least on OA and CA, on MA often more distinctly pigmented; pycnidia sometimes with long neck, conidia with 2–4 guttules; plurivorous opportunistic pathogen ..... 18. vars of *P. multirostrata*

20a. Conidia in average more than 4.5 µm long 21

b. Conidia in average less than 4.5 µm long 25

21a. Colonies with distinct grey olivaceous to olivaceous colour, plurivorous saprophyte (esp. known from southern Eurasia) ..... 19. *P. labilis*
b. Colonies colourless or with brown, buff, ochre, primrose, luteous or greenish tinges 22
22a. Crystals present especially on OA and MA; colonies colourless to buff, orange-brown on MA; specific necrophyte of Leguminosae ..... 20. *P. crystallifer*
b. Crystals absent 23
23a. Colonies with ochre, primrose or yellow tinges, especially on MA (so far only known from a dead plant in New Zealand) ..... 21. *P. aurea*
b. Colonies colourless to grey olivaceous, olivaceous grey, greenish olivaceous or citrine 24
24a. Colonies grey olivaceous to greenish olivaceous, with citrine tinges by pigmentation of the agar; plurivorous saprophyte (world-wide recorded) ..... 22. *P. nebulosa*
b. Colonies colourless to grey olivaceous or olivaceous grey, often with ochre tinges; specific necrophyte of *Chenopodium* spp. ..... 23. *P. chenopodiicola*
25a. Real chlamydospores absent, but swollen cells are present, intercalary or terminal, solitary or in short chains, 5–12 µm diam.; colony pale buff to grey olivaceous (OA); specific necrophyte of *Malus pumila* ..... 24. *P. bismarckii*
b. Swollen cells absent; colony colourless to (olivaceous) buff 26
26a. On all media fine needle-like crystals present; colony on OA colourless without aerial mycelium; pathogenic to *Piper* and *Peperomia* spp. ..... 25. *P. piperis*
b. Crystals absent; colony on OA colourless to (olivaceous) buff; with fine velvety aerial mycelium; pathogenic to *Selaginella* spp. ..... 26. *P. selaginellicola*

HOST/SUBSTRATUM–FUNGUS INDEX

Plurivorous (but sometimes with special host relation, see below): *P. bismarckii, P. herbarum, P. labilis, P. multirostrata* vars, *P. nebulosa, P. pereupyrena, P. subherbarum.*

Isolated from soil: *P. flavescens, P. herbarum, P. labilis, P. multirostrata* vars, *P. nebulosa.*

Isolated from seeds and fruits: *P. ajacis, P. bellidis, P. bismarckii, P. herbarum, P. insulana, P. lupini, P. pereupyrena, P. poolensis* vars, *P. subherbarum.*

Isolated from water: *P. lini.*

Frequently found on specific plants:

Acacia spp. (Mimosaceae) — *P. henningsii*
Amaryllidaceae (esp. *Crinum* spp.) — *P. crinicola*
Antirrhinum majus (Scrophulariaceae) — *P. poolensis* var. *poolensis*
Arachis hypogaea (Leguminosae) — *P. arachidis-hypogaeae*
Bellis perennis (Compositae) — *P. bellidis*
Chenopodium spp. (Chenopodiaceae) — *P. chenopodiicola*

Delphinium spp. (Ranunculaceae)	*P. ajacis*
Eupatorium cannabinum (Compositae)	*P. eupatorii*
Leguminosae	*P. crystallifer*
Linum spp. (Linaceae)	*P. lini*
Lupinus spp. (Leguminosae) (only America)	*P. lupini*
Malus pumila (Rosaceae)	*P. bismarckii*
Olea europaea (Oleaceae) (only southern Europe)	*P. insulana*
Phormium tenax (Liliaceae)	*P. haematocycla*
Piperaceae (*Peperomia* spp. and *Piper* spp.)	*P. piperis*
Polypodiaceae (*Adiantum, Polystichum* and *Pteris* spp.)	*P. adianticola*
Selaginella spp. (Selaginellaceae)	*P. selaginellicola*
Senecio spp. (Compositae)	*P. senecionis*
Verbascum spp. (Scrophulariaceae)	*P. poolensis* var. *verbascicola*
Zea mays (Gramineae) (only America)	*P. subherbarum*

FUNGUS–HOST INDEX

P. adianticola	Polypodiaceae (*Adiantum tenerum, Polystichum adiantiforme* and *Pteris ensiformis*)
P. ajacis	*Delphinium* spp. (Ranunculaceae)
P. arachidis-hypogaeae	*Arachis hypogaea* (Leguminosae)
P. bellidis	*Bellis perennis* (Compositae)
P. bismarckii	*Malus pumila* (Rosaceae)
P. chenopodiicola	*Chenopodium* spp., esp. *Ch. album* and *Ch. quinoa* (Chenopodiaceae)
P. crinicola	Amaryllidaceae (*Crinum* spp. and *Nerine bowdenii*)
P. crystallifer	Leguminosae
P. eupatorii	*Eupatorium cannabinum* (Compositae)
P. haematocycla	*Phormium tenax* (Liliaceae)
P. henningsii	*Acacia* spp. (Mimosaceae)
P. insulana	*Olea europaea* (Oleaceae)
P. lini	*Linum* spp. (occ. *L. usitatissimum*) (Linaceae)
P. lupini	*Lupinus* spp. (esp. *L. mutabilis*) (Leguminosae)
P. piperis	Piperaceae (*Piper* spp., esp. *P. longus* and *Peperomia* spp.)
P. poolensis var. *poolensis*	*Antirrhinum majus* (Scrophulariaceae)
P. poolensis var. *verbascicola*	*Verbascum* spp. (Scrophulariaceae)
P. selaginellicola	*Selaginella* spp., esp. *S. helvetica* (Selaginellaceae)
P. senecionis	*Senecio* spp. (Compositae)
P. subherbarum	*Solanum* spp. series *Tuberosa* (Solanaceae) and *Zea mays* (Gramineae)

DESCRIPTIVE PART

1. **Phoma lupini** Ell. & Ev. — Fig. 2

Phoma lupini Ellis & Everhart, Bull. Washburn [Coll.] Lab. nat. Hist. 1 (1884) 6; not *Phoma lupini* Buchwald in Möller, Fungi Faeröes 2 (1958) 153. — *Sphaeropsis lupini* (Ell. & Ev.) O. Kuntze, Revisio Gen. Pl. 3 (2) (1898) 526. — *Stictochorella lupini* (Ell. & Ev.) H. Sydow in H. Sydow & Petrak, Annls mycol. 22 (1924) 397; later homonym of *Stictochorella lupini* H. Sydow, see below. — *Asteromella lupini* (Ell. & Ev.) Petrak, Sydowia 9 (1955) 495.

Stictochorella lupini H. Sydow in H. Sydow & Petrak, Annls mycol. 20 (1922) 202.

Phyllosticta ferax Ellis & Everhart, Proc. Acad. Phil. (1894) 355.

Phyllosticta lupini Lee Bonar, Mycologia 20 (1928) 297 [cf. Petrak, Sydowia 10 (1956) 303].

Selected literature. Frey & Yabar (1983).

Description in vitro

OA: growth-rate 26–32 mm (14 days: 48–57 mm), regular, with floccose or finely floccose, white to grey, or some dull green aerial mycelium; colony dull green to dark herbage green; reverse dull green, with olivaceous or dark herbage green centre.

MA: growth-rate 27–32 mm (14 days: 48–60 mm), regular, with fluffy, white to dull green aerial mycelium; colony pale to dull green; reverse concentrically zonate sepia and greyish blue, outer margin hazel to buff.

CA: growth-rate 25–33 mm (14 days: 52–64 mm), regular, with floccose or finely floccose, white to olivaceous grey aerial mycelium; colony dull green; reverse dull green to olivaceous black, paler at margin.

Pycnidia 40–175 µm in diam., globose to irregular, solitary or confluent, glabrous, with 1(–3) non-papillate or slightly papillate ostioles; citrine to honey then olivaceous black; walls made up of 3–5 layers of cells, outer layers pigmented; with rosy vinaceous to pale vinaceous conidial exudate; on and in the agar, often also in aerial mycelium. Conidiogenous cells 3–8 × 3–6 µm, globose to bottle-shaped, on and in the agar, often also in aerial mycelium. Conidia 3.2–5.2(–6.4) × 1.4–2.4 µm, av. 4.0–4.4 × 1.5–1.9 µm, Q = 1.5–4.0, av. Q = 2.1–2.9; ellipsoidal without or sometimes with 1 (2) inconspicuous guttules.

Chlamydospores absent.

NaOH spot test: negative.

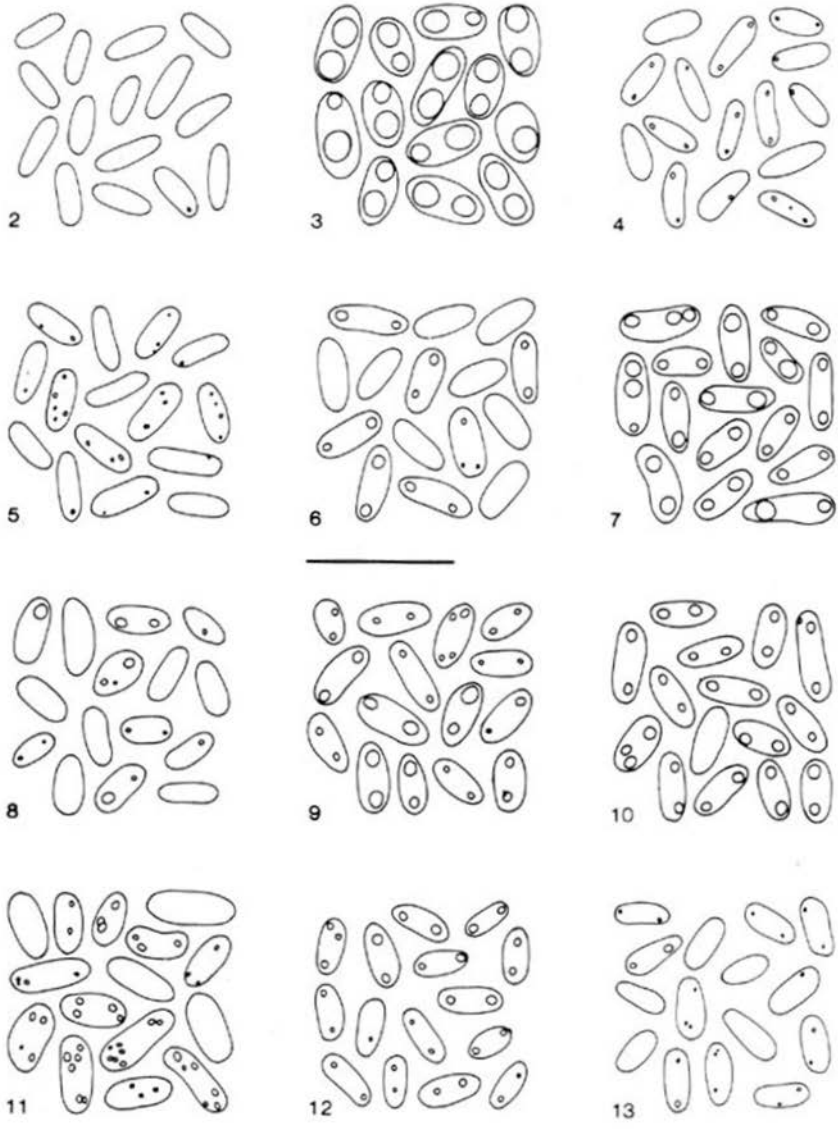
Ecology and distribution. A seed-borne pathogen known from various *Lupinus* spp. indigenous to North and South America. On account of its small conidia this pathogen has erroneously been interpreted as only a spermatial state. The fungus may infect all above ground parts of the lupines: Leaf, Stem and Pod Spot. In the Andean highlands of South America, above 3800 m, this appeared to be the most common pathogen of *Lupinus mutabilis*, an important albuminous food crop of the Indians.

Culture studied. CBS 248.92 (PD 79/141) ex *Lupinus mutabilis* (Leguminosae), Peru.

Note. In North and South America similar disease symptoms on lupines also may be caused by *Ascochyta lupini* Boerema & R. Schneider, see Boerema (1984).

2. **Phoma flavescens** de Gruyter, Noordel. & Boerema, *spec. nov.* — Fig. 3

Coloniae in agaro maltoso tarde crescentes, incoloratae, flavescentes, sine mycelio acrio, in NaOH immutabiles; pycnidia circa 140 µm in diam., solitaria vel agglutinata, glabra, haud papillata, ostiolata;



Figs. 2–13. Conidia. 2. *Phoma lupini*; 3. *P. flavescens*; 4. *P. haematocycla*; 5. *P. herbarum*; 6. *P. senecionis*; 7. *P. adianticola*; 8. *P. lini*; 9. *P. bellidis*; 10. *P. eupatorii*; 11. *P. crinicola*; 12. *P. ajacis*; 13. *P. poolensis* var. *poolensis*. — Bar = 10 µm.

conidiophora phyalidea; conidia hyalina, glabra, ellipsoidea, unicellulata, 4.2–6.8 × 2.1–3.4 µm, proprio biguttulata; chlamydosporae desunt. Typus: L 989.300-189 (siccus); CBS 178.93 (PD 82/1062) (vivus); ex soil, the Netherlands.

Description in vitro

OA: growth-rate 14–15 mm (14 days: 25 mm), regular, without aerial mycelium; colony colourless, becoming luteous in a later stage due to the production of a yellow pigment; reverse similar.

MA: growth-rate 13–14 mm (14 days: 23–26 mm), irregular with lobed outline, without aerial mycelium; colony ochraceous with white margin; reverse similar.

CA: growth-rate 10–11 mm (14 days: 21–25 mm), irregular with lobed outline, without aerial mycelium; colony ochraceous; reverse similar.

Pycnidia 20–140 µm in diam., globose, solitary or confluent, with rather indistinct non-papillate ostiole, glabrous or covered by hyphae; citrine to honey, later olivaceous to olivaceous black; walls made up of 2–4 layers of cells, outer layers pigmented; conidial exudate not observed; on and in the agar. Conidiogenous cells 4–6 × 3–6 µm, globose to bottle-shaped. Conidia 4.2–6.8 × 2.1–3.4 µm, av. 5.6 × 2.7 µm, Q = 1.5–2.7, av. Q = 2.1, ellipsoidal with 2 large polar guttules.

Chlamydospores absent.

NaOH spot test: negative.

Ecology and distribution. This species is thus far known only from an isolate of a soil-sample drawn from a potato field in the Noordoostpolder, the Netherlands. The epithet *flavescens* refers to the luteous discolouring on OA in a final stage.

Culture studied. CBS 178.93 (PD 82/1062) ex soil, the Netherlands.

3. **Phoma haematocycla** (Berk.) v.d. Aa & Boerema, *comb. nov.* — Fig. 4

Phyllosticta haematocycla Berk., Enum. Fungi. coll. Portugal by Welw. (1853) 5 [sometimes erroneously quoted with the author citation 'Berk. & Welw.'] [basionym; neotype dried culture of CBS 175.93, isolate from *Phormium tenax*, New Zealand, L 990.290-099].

Description in vitro

OA: growth-rate 24–25 mm (14 days: 33–36 mm), regular, with appressed velvety-felted, white aerial mycelium; colony colourless to rosy buff; reverse similar.

MA: growth-rate 21–22 mm (14 days: 28–29 mm), regular, with velvety to woolly, smoke grey aerial mycelium; colony buff; reverse ochraceous to fulvous.

CA: growth-rate 18–19 mm (14 days: 23–25 mm), regular, with compact velvety, white to smoke grey aerial mycelium; colony ochraceous; reverse fulvous to rust.

Pycnidia 60–130 µm in diam., globose to subglobose, solitary or confluent, glabrous, with 1(–3) papillate ostioles; olivaceous, later olivaceous black; wall made up of 2–5 layers of cells, outer layer(s) pigmented; with white to rosy buff conidial exudate; mainly on the agar. Conidiogenous cells 4–7 × 3–5 µm, globose to bottle-shaped. Conidia 3.8–4.6 × 1.4–1.8 µm, av. 4.2 × 1.6 µm, Q = 2.2–3.1, av. Q = 2.6, ellipsoidal with or without 1–2 inconspicuous polar guttules.

Chlamydospores absent, but hyphal swellings present, about 8–9 µm diam., intercalary or terminal.

NaOH spot test: negative.

Ecology and distribution. A common specific pathogen of New Zealand flax, *Phormium tenax*, causing red-encircled (*'haematocycla'*) spots on the leaves: Leaf Spot. The type material of *P. haematocycla* could not be found. To fix the identity of the species a dried culture of the isolate studied has been indicated as neotype.

Culture studied. CBS 175.93 (LEV 14846, PD 92/370) ex *Phormium tenax* (Liliaceae), New Zealand.

4. **Phoma herbarum** Westend. — Figs. 1, 5

Phoma herbarum Westendorp, Bull. Acad. r. Belg. Cl. Sci. 19 (3) (1852) 118.

Phoma leguminum Westendorp, Herb. crypt. [Ed. Beyaert & Feys] Fasc. 23 (1847) No. 1135; Bull. Acad. r. Belg. Cl. Sci. II, 11 (1861) 645 [cf. holotype, BR; as collective name often misapplied].

Phoma oleracea Saccardo, Michelia 2 (1) (1880) 91.

Phoma pigmentivora Massee, Bull. misc. Inf. R. bot. Gdns Kew 8 (1911) 326.

Phoma hibernica Grimes, O'Connor & Cummins, Trans. Br. mycol. Soc. 17 (1932) 99–101.

Phoma lignicola Rennerfelt, Svenska SkogsvFör. Tidskr. 35 (1936) 60.

Aposphaeria violacea Bertel, Öst. bot. Z. 54 (1904) 205, 233, 288. — *Phoma violacea* (Bertel) Eveleigh, Trans. Br. mycol. Soc. 44 (1961) 577.

For additional synonyms see Boerema (1970, 1976; 26 names including 14 infraspecific taxa). The history of this lectotype species of *Phoma* Sacc. is discussed by Boerema (1964) and Morgan-Jones (1988a).

Description in vitro

OA: growth-rate 38–50 mm, regular, without aerial mycelium; colony flesh-coloured with greenish tinge caused by abundant pycnidia or greenish olivaceous to olivaceous; reverse similar.

MA: growth-rate 38–41 mm; regular, with well-developed or poorly developed, fluffy to floccose, white, flesh-coloured or olivaceous grey aerial mycelium; colony reddish brown with rusty margin or greenish olivaceous with buff margin; reverse chestnut with rust-peach margin or leaden black with grey olivaceous margin.

CA: growth-rate 38–47 mm, regular, with white, felty to finely floccose aerial mycelium; colony sienna or olivaceous grey to olivaceous black with citrine margin; reverse dark vinaceous to olivaceous black with leaden grey centre.

Pycnidia 50–300 µm in diam., globose to elongate, solitary or confluent, glabrous or with short hyphal outgrowths, with usually one, sometimes papillate ostiole; honey-citrine to olivaceous, finally olivaceous black; wall consisting of 1–4(–6) layers of cells, outer layer(s) pigmented; with white to buff or rosy vinaceous conidial exudate; abundant, formed on and in the agar. Conidiogenous cells 3–6 × 3–6 µm, globose to bottle-shaped. Conidia 4.0–5.6 × 1.4–2.0 µm, av. 4.5–4.8 × 1.6–1.8 µm, Q = 2.0–3.5, av. Q = 2.6–2.9, oblong to ellipsoidal without or with inconspicuous guttules.

Chlamydospores absent.

NaOH spot test: positive: red pigment on MA changes to blue or purplish.

Ecology and distribution. This world-wide recorded fungus is unique in having a very wide substratum range. It has been isolated from dead material of all kinds of herbaceous and woody plants (esp. in spring), as well as from animal (incl. human) and inorganic material. Its common occurrence on dead seed coats explains why it often has been confused with specific seed-borne pathogens. The fungus is reported to be the causal

agent of a lethal disease of the air-bladder in salmon and trout. In man, the fungus is known from peripheral lung tissue with asthma patients. Other sources of repeated isolates are air, asbestos, butter, carpets, cement, cream, oil-paint, paper, plaster, rubber, soil, woodpulp and water.

Cultures studied. CBS 276.37 (PD 92/332) ex wood pulp, Sweden; CBS 615.75 (PD 73/665, ATCC 24909, IMI 199779) ex *Rosa* sp. (Rosaceae), the Netherlands; CBS 502.91 (PD 86/276) ex *Nerium* sp. (Apocynaceae), the Netherlands; CBS 503.91 (PD 87/499) ex *Thuja* sp. (Cupressaceae), the Netherlands.

Note. Fish-mycosis may also be caused by an undescribed species of *Phoma*, differing from *P. herbarum* by the production of unicellular chlamydospores and faster growth on OA and MA, see Hatai et al. (1986).

5. **Phoma senecionis** P. Sydow — Fig. 6

Phoma senecionis P. Sydow, Beibl. Hedwigia 38 (1899) 136.
Phyllosticta albobrunnea Bubák & Wróblewski, Hedwigia 57 (1916) 330.

Description in vitro

OA: growth-rate 47–49 mm, with sparse floccose, white aerial mycelium; colony regular, colourless; reverse similar to yellowish.

MA: growth-rate 27–30 mm, with fine compact, fluffy, white aerial mycelium; colony irregular, sienna to pale luteous, staining the agar yellow by a diffusible pigment; reverse fulvous with luteous marginal zone.

CA: growth-rate 45–47 mm, with fluffy-woolly, white aerial mycelium; colony irregular, olivaceous black with buff margin; reverse olivaceous black with hazel or honey margin.

Pycnidia 160–250 µm in diam., more or less globose, solitary or confluent, with 1 or 2 distinct ostioles, occasionally with a neck; glabrous, honey with olivaceous tinge around ostiole; wall consisting of 2–3 layers of cells, outer layer(s) pigmented; conidial exudate salmon; abundant, mainly in aerial mycelium. Micropycnidia present, 50–90 µm. Conidiogenous cells 3–8 × 3–7 µm, globose to bottle-shaped. Conidia 4.0–6.4 × 1.6–2.4 µm, av. 5.1 × 2.0 µm, Q = 1.7–3.4, av. Q = 2.6, oblong to ellipsoidal with or without 2 polar guttules.

Chlamydospores absent, but in the agar dense strands of dark-coloured, short-celled hyphae are formed.

NaOH spot test: negative on OA and CA, but yellow pigment on MA stains red.

Ecology and distribution. This fungus with yellow-brown pycnidia has been found on and isolated from dead tissue of different *Senecio* spp. It probably occurs wherever the hosts are growing. It seems to be a saprophyte or necrophyte with a specific host relation.

Culture studied. CBS 160.78 (PD 92/1533, LEV 11451) ex *Senecio jacobaea* (Compositae), New Zealand.

6. **Phoma adianticola** (Young) Boerema — Fig. 7

Teleomorph: *Didymella* sp.

Phoma adianticola (Young) Boerema, Versl. Meded. Plziektenk. Dienst Wageningen 159 (Jaarb. 1982) (1983) 25. — *Phyllosticta adianticola* Young, Mycologia 7 (1915) 144.

Description in vitro

OA: growth-rate 60–65 mm, regular, with thin, appressed-felted, white aerial mycelium or without any; colony colourless, staining the agar flesh, saffron, apricot-fulvous or ochraceous caused by the release of a diffusible pigment; pycnidia in concentric zones, sometimes together with pseudothecia; reverse staining the agar in a similar way.

MA: growth-rate 42–70 mm, regular, or with undulating margin, with very thin, velvety olivaceous grey or smoke grey aerial mycelium; colony colourless or smoke grey to olivaceous, staining the agar sienna to scarlet at centre and yellow in marginal zone by diffusible pigment; reverse similar or darker scarlet to bay or blood-colour.

CA: growth-rate 47–55 mm, regular, with velvety to finely floccose, olivaceous grey aerial mycelium; colony olivaceous, by a fulvous pigmentation of the agar; reverse similar or more umber.

Pycnidia 80–250 µm in diam., globose to subglobose to irregularly shaped, usually confluent, glabrous or with hyphal outgrowths, with 1–5 ostioles, occasionally with a short neck; citrine, later olivaceous finally olivaceous black; wall made up to 3–5 layers of cells, outer layers pigmented; conidial exudate buff, pale luteous or peach; abundant, both on and (partly) in the agar. Conidiogenous cells 4–7 × 3–6 µm, globose to bottle-shaped. Conidia 3.8–6.4 × 1.6–2.4 µm, av. 4.6–4.7 × 1.8–2.1 µm, Q = 1.8–3.5, av. Q = 2.2–2.6, ellipsoidal with usually two polar guttules.

Pseudothecia 120–180 × 150–200 µm, subglobose or pyriform. Asci 40–45 × 7–8 µm, 8-spored. Ascospores 12.0–15.5 × 3.5–5.2 µm, 2-celled, the lower cell subcylindrical with a rounded or slightly truncate base, the upper cell widest near the septum, tapering gradually to a round apex.

Chlamydospores absent.

NaOH spot test: positive, yellow-green on MA and OA.

Ecology and distribution. A pathogen of Polypodiaceae, probably widespread, distributed in (sub)tropical America. First described from *Adiantum tenerum* on the island of Porto Rico. In the Netherlands repeatedly isolated from leaves of *Polystichum adiantiforme* imported from Florida, USA and Costa Rica. Later also from diseased prothallia of *Pteris ensiformis* grown in a Dutch nursery: Leaf Spot. The teleomorph is thus far only known from occasional observations in vitro (provisional description by Van der Aa & Boerema in manuscript).

Cultures studied. CBS 187.83 (= PD 82/128) and CBS 258.92 (PD 89/1887) ex *Polystichum adiantiforme* (Polypodiaceae), Costa Rica; CBS 260.92 (PD 86/1103) ex *Pteris ensiformis* (Polypodiaceae), glasshouse, the Netherlands.

7. **Phoma lini** Pass. — Fig. 8

Phoma lini Passerini, Diagn. Funghi nuov. 4 (1890) no. 81.

Description in vitro

OA: growth-rate 63–65 mm, regular, with very scanty, colourless aerial mycelium or without any; colony colourless or very pale greenish olivaceous; reverse similar.

MA: growth-rate 67–68 mm, regular, with sparse, fluffy, grey olivaceous to olivaceous aerial mycelium; colony grey olivaceous with dull green to olivaceous with greenish olivaceous spots, staining the agar yellow due to the release of a verdigris pigment; reverse

olivaceous to grey olivaceous with verdigris and honey-isabelline patches, forming an irregular pattern of three colours.

CA: growth-rate 62 mm, regular, with fluffy, greenish olivaceous to olivaceous aerial mycelium; colony olivaceous to malachit green, marginal zone colourless; reverse remarkable in being zonate with concentric rings of purplish grey alternating with dark slate blue, greenish grey and fuscous black.

Pycnidia 60–210 µm in diam., globose to irregularly shaped, solitary or confluent, glabrous, with one ostiole, without marked neck; honey to olivaceous then olivaceous black; wall made up of 3 layers of cells, outer layers pigmented; with sienna conidial exudate; abundant, in and on the agar. Conidiogenous cells about 3–5 × 3–5 µm in diam., globose to bottle-shaped. Conidia 3.4–5.6 × 1.6–2.2 µm, av. 4.2 × 1.8 µm, Q = 1.9–2.8, av. Q = 2.4, ellipsoidal, occasionally with one or two polar guttules.

Chlamydospores absent.

NaOH spot test: positive: on MA a orange, later a purplish discolouring occur, both on the yellowish and greenish patches.

Ecology and distribution. A saprophyte in Europe frequently recorded on dead stems of *Linum* spp., but probably also occurring on other herbaceous plants. Occasional isolates of the fungus from stagnant water (the Netherlands, Yugoslavia) were associated with experiments on, or the practice of retting of flax, *Linum usitatissimum*. The fungus has been repeatedly confused with a foot rot pathogen of flax, *Phoma exigua* var. *linicola* (Naum. & Vass.) Maas (sect. *Phyllostictoides*: producing always some septate conidia), see Maas (1965).

Culture studied. CBS 253.92 (PD 70/998) ex Wisconsin tank, the Netherlands.

8. **Phoma bellidis** Neerg. — Fig. 9

Phoma bellidis Neergaard, Friesia 4 (1950) 74 [as '*Phoma (Phyllosticta)*'].

Description in vitro

OA: growth-rate 68 mm, regular, with poorly developed, felted, white aerial mycelium; colony colourless in centre with salmon shade due to pycnidial exudate; reverse similar.

MA: growth-rate 76–77 mm, regular, with finely floccose, white to pale grey aerial mycelium; colony olivaceous to pale olivaceous grey or grey olivaceous, with citrine margin; reverse leaden grey or leaden black, margin greenish olivaceous.

CA: growth-rate 78 mm, regular, with finely floccose, white or very pale olivaceous grey aerial mycelium; colony colourless to olivaceous; reverse isabelline.

Pycnidia 50–260 µm in diam., solitary or confluent, globose to irregularly composed, glabrous, with 1 to 5 ostioles, non-papillate or slightly papillate; citrine to honey, later olivaceous to olivaceous black; wall consisting of 2–3 layers of cells, outer layer(s) pigmented; with salmon to saffron conidial exudate; abundant, on or partly in the agar, rarely submerged. Conidiogenous cells 3–6 × 4–8 µm, globose to bottle-shaped. Conidia 3.8–6.4 × 1.8–2.6 µm, av. 4.9 × 2.1 µm, Q = 1.9–3.1, av. Q = 2.3, ellipsoidal with usually two, polar guttules.

Chlamydospores absent.

NaOH spot test: positive on MA: greenish then red (E+ reaction).

Ecology and distribution. This fungus has repeatedly been recorded on seed of daisy, *Bellis perennis*, from various European countries (Denmark, England, Italy, the Netherlands, Switzerland). It may cause the death of infected seeds and Damping-off of seedlings.

Culture studied. CBS 714.85 (= PD 74/265) ex *Bellis perennis* (Compositae), the Netherlands.

9. **Phoma eupatorii** Died. — Fig. 10

Phoma eupatorii Diedicke, Annls mycol. 10 (1912) 447.

Description in vitro

OA: growth-rate 50–51 mm, regular, without aerial mycelium; colony colourless, but general impression salmon caused by abundant conidial mass exuding from pycnidia; reverse similar.

MA: growth-rate 58–60 mm, somewhat irregular, with undulating margin with compact, finely floccose, white aerial mycelium; colony white to salmon, due to the aerial mycelium and exuding pycnidia; reverse ochraceous with chestnut centre, with concentric rings; agar staining ochraceous due to the release of a ochre pigment.

CA: growth-rate 43–47 mm, irregular, with undulating to crenate margin, with floccose to felted, white aerial mycelium; colony white to salmon, due to the aerial mycelium and exudating pycnidia; reverse similar.

Pycnidia 50–210 µm in diam., solitary or confluent, globose to irregularly shaped when confluent, glabrous, with one to 5 ostioles, occasionally with a short neck; honey to citrine, later olivaceous to olivaceous black; wall consisting of 3–4 layers of cells, outer layers pale coloured; abundant, covering the whole plate or in concentric rings on or partly in the agar, rarely submerged, often associated with dense, olivaceous hyphal strands. Conidiogenous cells 5–7 × 4–6 µm, bottle-shaped. Conidia 4.2–5.6 × 1.6–2.4 µm, av. 4.8 × 1.9 µm, Q = 1.9–3.1, av. Q = 2.5, ellipsoidal with two polar guttules.

Chlamydospores absent.

NaOH spot test: positive on MA: yellow-green then reddish (E+ reaction).

Ecology and distribution. This seems to be a common necrophyte of *Eupatorium cannabinum* ('Hemp Agrimony') found in different parts of Europe. The fungus frequently occurs on dead flower heads and may be seed-borne. On dead stems the pycnidia are connected by a subepidermal mycelial network, comparable with the hyphal strands in vitro.

Culture studied. CBS 123.93 (PD 77/1148) ex *Eupatorium cannabinum* (Compositae), the Netherlands.

10. **Phoma crinicola** (Siem.) Boerema — Fig. 11

Phoma crinicola (Siem.) Boerema in Boerema & Dorenbosch, Versl. Meded. Plziektenk. Dienst Wageningen 153 (Jaarb. 1978) (1979) 18. — *Phyllosticta crinicola* Siemaszko, Acta Soc. Bot. Pol. 1 (1923) 22.

Description in vitro

OA: growth-rate 65–70 mm in 5 days, regular; with coarsely floccose, dull green to olivaceous aerial mycelium; colony colourless to dull green or olivaceous; reverse similar.

MA: growth-rate 78–80 mm in 5 days, regular; with coarsely floccose, dull green aerial mycelium; colony dull green or citrine; reverse leaden grey to olivaceous black with hazel spots.

CA: growth-rate 73–75 mm in 5 days, with compact, felted-floccose, olivaceous-grey or scattered white, aerial mycelium; colony olivaceous, somewhat concentrically zoned; reverse olivaceous to olivaceous black with radial sectors.

Pycnidia 70–185 µm in diam., globose to irregular, solitary or confluent, with or without distinct ostiole, without neck, glabrous or with hyphal outgrowths; citrine to honey, later olivaceous to olivaceous black; walls made up of 2–4 layers of cells, outer layers pigmented; with white conidial exudate; abundant, on and in the agar, often also in aerial mycelium. Conidiogenous cells 4–7 × 4–7 µm, globose to bottle-shaped. Conidia 3.8–6.4 × 1.8–2.8 µm, av. 4.8 × 2.3 µm, Q = 1.7–3.1, av. Q = 2.1–2.2, ellipsoidal to cylindrical, without or with 2 or more small, usually polar guttules.

Chlamydospores absent, but clusters of short, swollen cells may be present.

NaOH spot test: positive, greenish, then red (E+ reaction).

Ecology and distribution. A pathogen of Amaryllidaceae so far only found in Europe. Originally described from a wild species of *Crinum* in Poland. In the Netherlands it is frequently isolated from the hybrid *Crinum powellii*; also from *Nerine bowdenii*: Leaf Spot, Bulb Rot.

Cultures studied. CBS 109.79 (= PD 77/747) ex *Crinum powellii* (Amaryllidaceae), the Netherlands; CBS 118.93 (PD 70/195) ex *Crinum* sp., the Netherlands.

Note. On dead leaves of *Crinum* sp. perithecia of an ascomycete were observed by Siemaszko l.c., in association with the pycnidia. He described this ascomycete as *Mycosphaerella crinicola* Siem. However, in inoculation experiments done on the Plant Protection Service, a teleomorph of *Phoma crinicola* has not been found.

11. **Phoma ajacis** (Thümen) v.d. Aa & Boerema, *comb. nov.* — Fig. 12

Phyllosticta ajacis Thümen in Bolle & Thümen, Boll. Soc. adriat. Sci. nat. 6 (1880) 329 [basionym; neotype dried culture of CBS 177.93, isolate from *Delphinium* sp., probably *D. ajacis*, L 989.300-136].

Description in vitro

OA: growth-rate 72–75 mm, regular, with well-developed or poorly developed, floccose, white to pale olivaceous grey aerial mycelium; colony colourless with grey olivaceous or olivaceous grey shade; reverse similar.

MA: growth-rate 73–77 mm, regular, with compact, woolly, white aerial mycelium; colony colourless to olivaceous grey with greenish olivaceous or citrine margin; reverse leaden black to olivaceous black with citrine margin.

CA: growth-rate 74–81 mm, regular, with compact, floccose, white aerial mycelium; colony olivaceous grey to olivaceous, staining the agar red due to the release of a pigment; reverse apricot to scarlet.

Pycnidia 130–300 µm in diam., globose, solitary or confluent, glabrous, with one or two ostioles, occasionally papillate; citrine-honey, later olivaceous to olivaceous black; walls made up of 3–5 layers of cells, outer layers pigmented; with white conidial exudate; abundant, mainly on, sometimes partly in the agar, hardly in aerial mycelium. Conidiogenous cells 4–6 × 4–6 µm, globose to bottle-shaped. Conidia 3.4–5.6 × 1.6–2.4 µm,

av. 4.2–4.7 × 1.8 µm, Q = 1.6–3.3, av. Q = 2.3–2.6, oblong to ellipsoidal with two, distinct polar guttules.

Chlamydospores absent.

NaOH spot test: positive, yellow-green or blue-green later orange finally brick (OA), or yellow-green or green with red margin (MA) (E+ reaction).

Ecology and distribution. In southern Eurasia probably a widely occurring seed-borne pathogen of annual species of *Delphinium*: Leaf Spot. The fungus also has been found in association with Stem Rot. The original material of this fungus on *Delphinium ajacis* is apparently not preserved. To fix the species a typical dried culture of the fungus has been selected as neotype.

Cultures studied. CBS 176.93 (= PD 86/547) ex *Delphinium* sp. (Ranunculaceae), the Netherlands; CBS 177.93 (= PD 90/115) ex *Delphinium* sp. (Ranunculaceae), Kenya.

Note. Similar leaf spots on *Delphinium* spp. may be caused by a large-spored *Ascochyta*-like fungus, known as *Ascochyta aquilegiae* (Rabenh.) Höhnel, compare Mel'nik (1977).

12a. **Phoma poolensis** Taub. var. **poolensis** — Fig. 13

Phoma poolensis Taubenhaus, Dis. Greenhouse Crops (1919) 203, var. *poolensis* [autonym created by the separation of the variety *verbascicola*, see below].

Phoma oleracea var. *antirrhini* Saccardo, Sylloge Fung. 3 (1884) 135 [no priority in species rank].

Phyllosticta antirrhini P. Sydow, Beibl. Hedwigia 38 (1889) 134 [sometimes wrongly quoted as '*Phoma*'].

Phoma antirrhini Dzhalagonija, Nov. Sist. Nizsh. Rost. (1965) 157.

Selected literature. Guba & Anderson (1919).

Description in vitro

OA: growth-rate 67–68 mm, regular, with appressed floccose, white aerial mycelium; colony almost colourless but with olivaceous tinge; reverse similar or greenish olivaceous.

MA: growth-rate 69–71 mm, regular, with finely woolly, white aerial mycelium; colony grey-olivaceous; reverse olivaceous black or grey olivaceous with honey marginal zone.

CA: growth-rate 74–75 mm, regular, with finely floccose, white aerial mycelium; colony colourless with olivaceous sectors; reverse grey olivaceous.

Pycnidia 60–170 µm in diam., globose to subglobose, solitary or confluent, glabrous, without visible ostiole or neck; honey to olivaceous; walls made up of 2–3 layers of cells, outer layer(s) pigmented; with buff conidial exudate. Conidiogenous cells 2–7 × 3–6 µm, globose to bottle-shaped; on and in the agar. Conidia 3.6–5.2 × 1.6–2.0 µm, av. 4.3 × 1.7 µm, Q = 2.0–3.0, av. Q = 2.5, ellipsoidal, usually with two inconspicuous polar guttules.

Chlamydospores absent.

NaOH spot test: positive on MA: yellow-green, later reddish (E+ reaction).

Ecology and distribution. A world-wide recorded pathogen of cultivated varieties of snapdragon, *Antirrhinum majus*: Leaf Spot and (Basal) Stem Rot. It is frequently encountered on seed of this host: Damping-off in seedlings; sometimes apparently quite destructive. The fungus also has been isolated from other Scrophulariaceae. Comparative inoculation experiments demonstrated the occurrence of different host forms, which may

have been promoted by the common seed transmission. Isolates from *Verbascum* spp., characterized by distinctly ostiolate pycnidia and somewhat wider range of conidial dimensions, are distinguished as a separate variety, see below.

Cultures studied. CBS 113.20 (PD 92/774) ex *Anthirrhinum majus* (Scrophulariaceae), USA; CBS 116.93 (PD 71/884) ex *Antirrhinum majus*, the Netherlands; CBS 115.93 (PD 74/206) ex *Scrophularia nodosa* (Scrophulariaceae), the Netherlands.

Note. Transfers of isolates of this fungus commonly display an abnormality which is also known of some other species of *Phoma*. Namely that the development of an ostiole fails to materialize, so that fully mature pycnidia are still non-ostiolate. For release of the conidia the pycnidial wall then has to burst open. Experiments by Rajak & Rai (1983, 1984) demonstrated that certain species of *Phoma* are predisposed to this phenomenon and also that the pH and the nutrient composition of the agar-media may influence it. The occurrence of such non-ostiolate mature pycnidia in vitro must not be confused with the fact that in some species of *Phoma* the formation of an opening in the pycnidia occurs only at the end of the pycnidial growing process (porus instead of ostiolum, e.g. a feature of section *Plenodomus*, see Boerema, Van Kesteren & Loerakker, 1981).

12b. **Phoma poolensis** var. **verbascicola** (Ell. & Kellerm.) v.d. Aa & Boerema, *comb. nov.* — Fig. 14

Phyllosticta verbascicola Ell. & Kellerm., Bull. Torrey bot. Club 11 (1884) 115 [basionym; cf. holotype NY].

Description in vitro

OA: growth-rate 62–68 mm, regular, with scanty, floccose, white aerial mycelium; colony almost colourless, sometimes with pale olivaceous sectors; reverse colourless to grey olivaceous.

MA: growth-rate 59–63 mm, regular, with rather compact, woolly to floccose, white aerial mycelium; colony colourless or grey olivaceous; reverse saffron to cinnamon with olivaceous centre or entirely olivaceous with pale luteous or honey spots near margin.

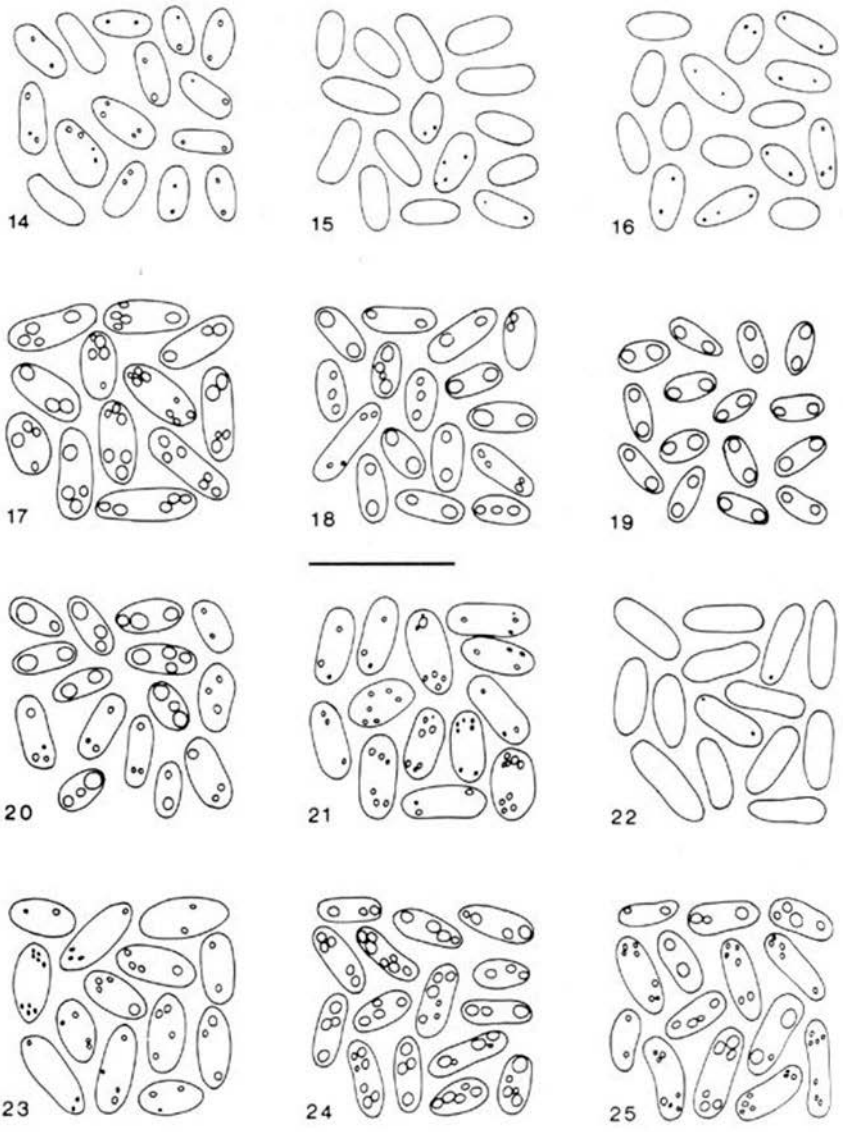
CA: growth-rate 66–72 mm, regular, with scanty, floccose, white or greyish aerial mycelium; colony colourless; reverse colourless to pale olivaceous.

Pycnidia 70–225 µm in diam., globose, solitary or more or less confluent, glabrous, with 1–2(–5) papillate ostioles; citrine to honey at first, later olivaceous to olivaceous black; walls made up of 2–3 layers of cells, outer layer(s) pigmented; with colourless or white conidial exudate; on and in the agar. Conidiogenous cells 2–6 × 4–6 µm, globose to bottle-shaped. Conidia 3.4–5.6 × 1.6–2.4 µm, av. 4.2–4.8 × 1.7–1.8 µm, Q = 1.5–3.5, av. Q = 2.4–2.8, ellipsoidal with two (or more), rather inconspicuous polar guttules.

Chlamydospores absent.

NaOH spot test: positive on MA: yellow-green, later reddish (E+ reaction).

Ecology and distribution. This characteristic variety on *Verbascum* species is probably widely distributed in Eurasia and North America. Inoculation experiments have shown that it possesses pathogenic capacities with regard to the hosts, and may cause necrotic lesions on leaves and stems and damping-off of young plants. The fungus did not cause disease symptoms on snapdragon, *Anthirrhinum majus*, the principle host of the type



Figs. 14–25. Conidia. 14. *Phoma poolensis* var. *verbascicola*; 15. *P. subherbarum*; 16. *P. arachidis-hypogaeae*; 17. *P. henningsii*; 18. *P. insulana*; 19. *P. pereupyrena*; 20. *P. multirostrata*; 21. *P. labilis*; 22. *P. crystallifer*; 23. *P. aurea*; 24. *P. nebulosa*; 25. *P. chenopodiicola*. Bar = 10 µm.

variety *P. poolensis* var. *poolensis*. In vitro it can be distinguished by the stable production of distinctly ostiolate pycnidia and the somewhat wider size range of the conidia.

Cultures studied. CBS 114.93 (PD 74/228) ex *Verbascum* sp. (Scrophulariaceae), the Netherlands; CBS 127.93 (PD 92/347) ex *Verbascum densiflorum*, the Netherlands.

Note. Collections of this fungus on dead stems and seed capsules of *Verbascum* spp. usually have been identified as *Phoma verbascicola* (Schw.) Cooke, but the type material of the basionym of this binomial, *Sphaeria verbascicola* Schweinitz (PH, duplicate BPI), contains only immature ascomata, probably belonging to *Pleospora scrophulariae* (Desm.) Höhnel [also interpreted as referring to a species of *Mycosphaerella: M. verbascicola* (Schw.) Fairman].

13. **Phoma subherbarum** de Gruyter, Noordel. & Boerema, *spec. nov.* — Fig. 15

Coloniae in agaro maltoso celeriter crescentes, incoloratae, sine mycelio acrio, agarum rubescentes, in NaOH immutabiles; pycnidia 100–200 µm in diam., solitaria vel agglutinata, glabra, papillata, ostiolata; conidiophora phyalidea; conidia hyalina, glabra, ellipsoidea, unicellulata, 4.0–5.2(–6.4) × 1.6–2.2, eguttulata; chlamydosporae desunt. Typus: L 992.177-439 (siccus); CBS 250.92 (PD 92/371, DAOM 171914) (vivus); ex *Zea mays* (Gramineae), Canada.

Description in vitro

OA: growth-rate 78–81 mm, regular, without aerial mycelium; colony colourless with saffron-flesh and olivaceous zones; reverse similar.

MA: growth-rate 82–83 mm, regular, with appressed felted or floccose, olivaceous grey or smoke grey aerial mycelium; colony flesh to rust; reverse rust to chestnut.

CA: growth-rate 77–80 mm, regular, without or with very sparse smoke grey or olivaceous grey aerial mycelium; colony colourless to flesh, sometimes with olivaceous to greenish olivaceous spots and sectors; reverse flesh-coral with olivaceous spots, or olivaceous to olivaceous black with dull green margin.

Pycnidia 90–200 µm in diam., globose to subglobose or irregularly shaped, solitary or confluent, glabrous, or with short hyphal outgrowths, with 1(–3) papillate ostioles; sienna, later olivaceous black; wall made up of up to 3 layers of cells, outer layers dark pigmented; with white to rosy-buff conidial exudate; abundant in and on the agar; micropycnidia present, 30–70 µm in diam. Conidigenous cells 3–5 × 3–7, globose to bottle-shaped. Conidia 4.0–5.2(–6.4) × 1.6–2.2 µm, av. 4.5 × 1.8 µm, Q = 2.0–3.6, av. Q = 2.5, oblong to ellipsoidal, without guttules.

Chlamydospores absent.

NaOH spot test: negative.

Ecology and distribution. This saprophyte, resembling in many respects the ubiquitous *Phoma herbarum* Westend. (no. 4), seems to be a fungus from (South?) American origin. The isolates studied were obtained from necrotic leaves of wild potatoes (*Solanum* spp. series *Tuberosa*) in Peru (Andes, alt. 2500 m) and the surface of overwintered seeds of maize (*Zea mays*), collected in Canada (Ottawa: 'most common fungus isolated from discoloured seed').

Cultures studied. CBS 249.92 (PD 78/1088) ex *Solanum* sp. series *Tuberosa* (Solanaceae), Peru; CBS 250.92 (PD 92/371, DAOM 171914, identical with DAOM 171915 and DAOM 171916) ex *Zea mays* (Gramineae), Canada.

14. **Phoma arachidis-hypogaeae** (Vasant Rao) v.d. Aa & Boerema, *comb. nov.* — Fig. 16

Phyllosticta arachidis-hypogaeae Vasant Rao, Sydowia 16 ['1962'] (1963) 275–276 [basionym; cf. holotype AMH 134].

Selected literature. Patil (1986).

Description in vitro

OA: growth-rate 47–48 mm, regular with undulating margin, with poorly developed, flat, finely floccose, white to greenish grey aerial mycelium; colony colourless to buff with grey olivaceous centre, reverse olivaceous at centre, towards margin buff.

MA: growth-rate 46 mm, irregularly undulating, with compact, woolly-floccose, dark herbage green to greenish glaucous aerial mycelium; colony colour difficult to see caused by compact aerial mycelium, at margin citrine; reverse zonate citrine to cinnamon with olivaceous black, at centre olivaceous black.

CA: growth-rate 20–24 mm, irregular, probably inhibited by the medium, with abundant, compact, coarsely floccose, citrine-green aerial mycelium; colony olivaceous black with citrine margin; reverse citrine-green at centre, then with purplish grey concentric zone, margin buff.

Pycnidia 80–200 µm in diam., globose or bottle-shaped, solitary or in rows along hyphal strands, not confluent, glabrous, papillate, citrine-honey; then olivaceous to olivaceous black; walls made up of 3–5 layers of cells, outer layers pigmented; with whitish conidial exudate; abundant, mainly on and in the agar but also in aerial mycelium. Conidiogenous cells 3–8 × 3–7 µm, globose to bottle-shaped. Conidia 3.2–5.2 × 1.8–2.4 µm, av. 4.3 × 2.1 µm, Q = 1.6–2.7, av. Q = 2.1, oblong to ellipsoidal without or with two indistinct polar guttules.

Chlamydospores absent.

Crystals present on CA after three weeks, citrine green.

NaOH spot test: not specific, only on MA a slight reddish discolouring occurs.

Ecology and distribution. In India frequently found on living leaves of groundnut, *Arachis hypogaea*: Leaf Spot. The fungus is probably indigenous to that subcontinent. Inoculation experiments have shown that the fungus could also infect various other plants, esp. Leguminosae. Another plurivorous species of *Phoma* in India repeatedly isolated from groundnut plants is *P. multirostrata* (Mathur et al.) Dorenbosch & Boerema (no. 18).

Culture studied. CBS 125.93 (= PD 77/1029) ex *Arachis hypogaea* (Leguminosae), India.

15. **Phoma henningsii** Sacc. — Figs. 17, 29

Phoma henningsii Saccardo, Sylloge Fung. 10 (1892) 139. — *Phoma acaciae* P. Hennings, Bot. Jb. 14 (1892) 368–369; not *Phoma acaciae* Penzig & Saccardo, Atti Ist. ven. Sci. VI, 2 (1884) 650 [= Funghi Mortola n. 23].

Description in vitro

OA: growth-rate 43–44 mm, without aerial mycelium, only a short white-felted zone near margin; colony regular, colourless; reverse colourless to pale olivaceous.

MA: growth-rate 51–53 mm, with floccose, grey olivaceous aerial mycelium; colony regular, honey with olivaceous tinge; reverse isabelline with olivaceous tinge, margin honey.

CA: growth-rate 46–47 mm, with fine velvety-floccose, smoke grey aerial mycelium; colony pale olivaceous with buff margin; reverse concentrically zonate buff-olivaceous and isabelline.

Pycnidia 70–220 µm in diam., globose, solitary or confluent, with usually one, non-papillate ostiole, glabrous; honey to citrine, later olivaceous to olivaceous black; wall consisting of 2–4 layers of cells, outer layer(s) pigmented; conidial exudate salmon to pale vinaceous; abundant, in concentric rings (partly) in the agar. Conidiogenous cells 3–8 × 3–8 µm, globose to bottle-shaped. Conidia 4.8–7.4 × 2.2–3.2 µm, av. 5.9 × 2.5 µm, Q = 1.6–3.1, av. Q = 2.4, ellipsoidal, with 2 (3) large polar guttules.

Chlamydospores present, 6.0–10.0 µm in diam., olivaceous, with greenish guttules, intercalary or terminal, in chains or clusters.

NaOH spot test: negative or weakly yellow on MA, not specific.

Ecology and distribution. This fungus has been recorded in East Africa as a harmful wound parasite of *Acacia* spp. On account of its saprophytic vigour and the conidial dimensions in vivo it has been confused with *Phoma herbarum* Westend. (no. 4).

Culture studied. CBS 104.80 (PD 74/1017) ex *Acacia mearnsii* (Mimosaceae), Kenya.

16. **Phoma insulana** (Mont.) Boerema & Malathr. — Figs. 18, 30

Phoma insulana (Mont.) Boerema & Malathrakis in Boerema, Versl. Meded. Plziektenk. Dienst Wageningen 158 (Jaarb. 1981) (1982) 28. — *Phyllosticta insulana* Montagne, Annls Sci. nat. (Bot.) IV, 5 (1856) 343.

Description in vitro

OA: growth-rate 68 mm, regular, nearly without aerial mycelium; colony olivaceous with colourless concentric ring near margin; reverse olivaceous with greenish olivaceous outer margin.

MA: growth-rate 70–72 mm, regular, with downy compact grey olivaceous aerial mycelium in central part, margin without aerial mycelium; colony olivaceous with brick sectors near margin; reverse olivaceous black with brick and leaden grey sectors.

CA: growth-rate 65–66 mm, regular, with finely fluffy-floccose grey olivaceous aerial mycelium; colony olivaceous with grey olivaceous; reverse olivaceous black with olivaceous and leaden grey sectors.

Pycnidia 140–270 µm, globose, solitary or confluent, in centre confluent pycnidia up to 470 µm, glabrous, with 1–5 ostioles, non-papillate or with distinctly papillate neck; citrine to honey then olivaceous black; walls made up to 2–3 layers of cells, outer layer(s) pigmented; with white conidial exudate; scattered on or partly in the agar. Conidiogenous cells 2–8 × 4–6 µm, globose to bottle-shaped. Conidia 3.2–5.6(–6.8) × 1.6–2.4 µm, av. 4.6 × 1.8 µm, Q = 1.7-3.3, av. Q = 2.5, ellipsoidal, with 2 (3), usually polar guttules.

Chlamydospores (4.0–)5.5–10.5(–14.5) µm in diam., solitary or in chains, intercalary or terminal, olivaceous, with green guttules.

NaOH spot test: negative.

Ecology and distribution. In southern Europe this fungus in autumn commonly occurs on discolouring leaves and ripening fruits of the olive, *Olea europaea*. In Crete it appeared

to be one of the fungi involved in the natural processing of olive fruits (such fruits are greatly estimated by local people as table fruits).

Culture studied. CBS 252.92 (PD 80/1144) ex *Olea europaea* (Oleaceae), Greece.

17. **Phoma pereupyrena** de Gruyter, Noordel. & Boerema, *nom. nov.* — Figs. 19, 31

Polyopeus pomi Horne, J. Bot., Lond. 58 (1920) 240; not *Phoma pomi* Schulzer von Müggenburg & Saccardo, Hedwigia 23 (1884) 109 [= *Phoma macrostoma* Mont. var. *macrostoma*]; not *Phoma pomi* Passerini, Atti R. Accad. naz. Lincei Rc. 4 (2) (1888) 96 [= *Asteromella mali* (Briard) Boerema].

Description in vitro

OA: growth-rate 68 mm, regular, with felted to downy, olivaceous grey aerial mycelium; colony grey olivaceous to olivaceous with radiating hyphae; reverse olivaceous grey, iron grey or grey olivaceous.

MA: growth-rate 71–72 mm, regular, with abundant, woolly-floccose, olivaceous grey aerial mycelium; colony olivaceous grey to grey olivaceous; reverse leaden grey to leaden black.

CA: growth-rate 70–71 mm, regular, with floccose, olivaceous grey aerial mycelium; colony iron grey to olivaceous grey at margin, with distinct radiating mycelial strands; reverse leaden grey to leaden black, with olivaceous margin.

Pycnidia 50–210 µm in diam., globose to irregular, solitary or confluent, glabrous or semi-pilose, with 1–3 ostioles, non-papillate, slightly papillate or occasionally with long tubular outgrowths; citrine to honey, later olivaceous to olivaceous black; walls consisting of 5–8 layers of cells, outermost 2 layers with thickened, dark pigmented walls; exudate white to straw-coloured; abundantly formed on or partly in the agar. Conidiogenous cells 3–7 × 3–6 µm, globose to bottle-shaped. Conidia 3.4–5.2 × 1.6–2.0 µm, av. 4.0 × 1.7 µm, Q = 2.0–2.8, av. Q = 2.4, ellipsoidal with two polar guttules.

Chlamydospores solitary or in chains, intercalary, globose or elongate, (3.5–)6–9 (–13) µm in diam., olivaceous, with green guttules.

NaOH spot test: negative.

Ecology and distribution. In Eurasia this fungus has been isolated from above-ground parts (fruits and leaves) of quite different woody and herbaceous plants. It seems to be a plurivorous opportunistic parasite. The fungus in vitro shows much resemblance to the widely occurring soil fungus *Phoma eupyrena* Sacc. (treated in Contributions I–1), but can be recognized by its larger conidia and different cultural behaviour. Its original classification in a separate genus, *Polyopeus* Horne, is based on the fact that under certain conditions the pycnidia in culture develop several long tubular outgrowths or 'necks', compare Kidd & Beaumont (1924).

Culture studied. CBS 267.92 (PD 76/1014) ex *Coffea arabica* (Rubiaceae), India.

18. **Phoma multirostrata** (Mathur et al.) Dorenb. & Boerema var. **multirostrata** — Figs. 20, 32

Phoma multirostrata (Mathur & al.) Dorenbosch & Boerema, Mycopath. Mycol. appl. 50 (1973) 255–256, var. *multirostrata*. — *Sphaeronaema multirostratum* Mathur et al. in Mathur & Thirumalachar, Sydowia 13 (1959) 146 [as '*S. multirostrata*'].

Phoma ushtrina Rai & Misra, Curr. Sci. 50 (1981) 377.

Phoma multirostrata var. **macrospora** Boerema

Phoma multirostrata var. *macrospora* Boerema, Versl. Meded. Plziektenk. Dienst Wageningen 164 (Jaarb. 1985) (1986) 29.

Phoma multirostrata var. *macrospora* Mathur & Thirumalachar [in 1965 deposited in CBS-collection, but never published: 'collection name'].

Sphaeronaema indicum Mathur et al., Sydowia 13 (1959) 146a [as '*S. indica*'].

Phoma lucknowensis Saksena, Nand & Sarbhoy, Mycopath. Mycol. appl. 34 (1968) 93; not *Phoma lucknowensis* Agarwal & Misra, Curr. Sci. 50 (1981) 66.

Phoma terrestris Saksena, Nand & Sarbhoy, Mycopath. Mycol. appl. 29 (1966) 86 [as '*terrestre*']; not *Phoma terrestris* Hansen, Phytopathology 19 (1929) 699.

Phoma multirostrata var. **microspora** (Allescher) Boerema

Phoma multirostrata var. *microspora* (Allescher) Boerema, Versl. Meded. Plziektenk. Dienst Wageningen 164 (Jaarb. 1985) (1986) 30. — *Phoma decorticans* var. *microspora* Allescher, Rabenh. Krypt.-Flora [ed. 2], Pilze 6 [Lief. 63] (1898 [vol. dated '1901']) 284.

Phoma microspora Balasubramanian & Narayanasamy, Indian Phytopath. 33 (1980) 136; not *Phoma microspora* Saccardo apud Roumeguère, Revue Mycol. 1885 (1885) 158; not *Phoma microspora* Patouillard in Hariot, Champ. Cap Horn (1889) 196.

Phoma lucknowensis Agarwal & Misra, Curr. Sci. 50 (1981) 66 [pycnidial primordia misinterpreted as 'dictyochlamydospores']; not *Phoma lucknowensis* Saksena, Nand & Sarbhoy, Mycopath. Mycol. appl. 34 (1968) 93.

For full synonymy of this fungus see Boerema (1986). It includes 7 other combinations in *Phoma* and 6 in *Phyllosticta*. The history of the species is discussed by Morgan-Jones (1988b).

Description in vitro

OA: growth-rate 67–72 mm, regular, with poorly developed, felted, white to grey olivaceous aerial mycelium or without any; colony colourless to weak olivaceous; reverse olivaceous.

MA: growth-rate 78–82 mm, regular, with felty to floccose or woolly, pale olivaceous grey to olivaceous buff aerial mycelium; colony olivaceous to olivaceous buff, outer margin fulvous; reverse leaden grey to olivaceous black.

CA: growth-rate 76–82 mm, regular, with velvety or finely floccose to woolly, white to olivaceous grey aerial mycelium; colony colourless to hazel; reverse hazel with olivaceous at center.

Pycnidia (75–)150–300(–450) µm in diam., globose to subglobose, or irregular with much elongated neck, solitary or confluent, glabrous, with one or more ostioles; honey to citrine, later olivaceous to olivaceous black; walls made up of 2–5 layers of cells, outer layer(s) pigmented; with white to cream conidial exudate; on and in the agar. Conidiogenous cells 3–7 × 3–6 µm, globose to bottle-shaped. Conidia (2.6–) 3.2–6.0 (–7.5) × 1.4–2.4 (–3.0) µm, av. 3.9–5.5 × 1.9–2.4 µm, Q = 1.1–2.7, av. Q = 2.0–2.1, ellipsoidal with 2 or more guttules.

Chlamydospores 5–11 µm in diam., oblong to ellipsoidal, in short chains or clustered, intercalary, olivaceous with green guttules.

NaOH spot test: on MA weak brownish red, not specific.

Ecology and distribution. Most records of this variable warmth preferring or thermotolerant fungus are from India (centre of origin?), but the fungus appears to have a world-

wide distribution in subtropical regions and warm greenhouses. The type-variety refers to soil-isolates with extremely large pycnidia. Similar isolates with smaller pycnidia and variable conidial dimensions – the varieties *macrospora, microspora* and intermediate variants – have been obtained from necrotic lesions on leaves and stems of all kinds of herbaceous plants. Inoculation experiments with different isolates from plants have shown that the fungus can be characterized as a plurivorous soil-borne opportunistic plant pathogen.

Cultures studied. CBS 274.60 (IMI 81598, PD 92/1756) ex soil from poultry farm, India; CBS 368.65 (HACC 154, PD 92/1757), India; CBS 110.79 (PD 67/622) ex stem of *Cucumis sativus*, the Netherlands.

Note. The data given are from the original descriptions of the cultures studied, i.e. the type of *Phoma multirostrata* (Mathur et al.) Dorenb. & Boerema var. *multirostrata* (CBS 274.60), *Phoma multirostrata* var. *macrospora* Boerema (CBS 368.65) and *Phoma multirostrata* var. *microspora* (Allescher) Boerema (CBS 110.79), as given by Boerema (1986). These data agree with those of Morgan-Jones (1988b). However, the original isolates appear to be degenerated, because in a recent study the pycnidia and conidia remained small, and in the pycnidia of isolate CBS 110.79 no conidia were formed.

19. **Phoma labilis** Sacc. — Fig. 21

Phoma labilis Saccardo, Michelia 2 (2) (1881) 341.

Description in vitro

OA: growth-rate 62–63 mm, regular, with scanty, appressed, whitish to grey olivaceous aerial mycelium; colony grey olivaceous to olivaceous; reverse similar.

MA: growth-rate 64–66 mm, regular, with woolly-floccose grey olivaceous aerial mycelium with white sectors; colony grey olivaceous with citrine outer margin; reverse olivaceous black with leaden grey tinges.

CA: growth-rate 66–69 mm, regular, with compact, felted, white aerial mycelium; colony colourless with olivaceous sectors or entirely olivaceous; reverse luteous-amber, ochraceous with or without olivaceous sectors.

Pycnidia 70–250 µm in diam.; globose, glabrous, solitary or confluent, usually with one papillate ostiole; citrine or honey, later olivaceous to olivaceous black; walls made up of 2–4 layers, outer layers pigmented; with white to pale luteous or ochraceous conidial exudate; abundant on and in the agar. Conidiogenous cells 5–7 × 4–8 µm, globose to bottle-shaped. Conidia 4.0–6.6 × 2.0–3.0 µm, av. 5.3–5.4 × 2.4–2.5 µm, Q = 2.2–2.7, av. Q = 2.2, oblong to ellipsoidal with two (or more) polar guttules.

Chlamydospores absent.

NaOH spot test: positive: both on MA and OA a reddish brown discolouring, not specific.

Ecology and distribution. Isolates of this warmth-preferring saprophyte have been obtained from soil and various herbaceous and woody plants grown in southern Eurasia (Italy, Turkey, Israel, Kuwait, Indonesia). In the Netherlands the fungus has been recorded in glasshouses. *Phoma labilis* tends to loose the ability to produce pycnidia quite quickly (see note). Most isolates have not survived the freeze drying treatment.

Cultures studied. CBS 479.93 (PD 70/93) ex *Rosa* sp. (Rosaceae), Israel; CBS 124.93 (PD 87/269) ex *Lycopersicon esculentum* (Solanaceae), the Netherlands.

Note. The degeneration of this fungus often starts in sectors with a yellow pigmentation. Transfers from such a sterile yellow sector in CBS 479.93 once resulted in a well sporulating *Acremonium* culture, identified by Dr. W. Gams (CBS Baarn) as *A. ochraceum* W. Gams.

20. **Phoma crystallifer** de Gruyter, Noordel. & Boerema, *spec. nov.* — Fig. 22

Coloniae in agaro maltoso moderatim crescentes, bubalinae, cum mycelio acrio olivaceo-cinereo, reversus plumbeus, in NaOH immutabiles; crystalliferae, pycnidia usque ad 250 µm in diam., solitaria vel agglutinata, glabra, papillata, ostiolata; conidiophora phyalidea; conidia hyalina, glabra, ellipsoidea, uni-cellulata, 4.0–5.8 × 1.6–2.2 µm, eguttulata vel obscure guttulata; chlamydosporae desunt. Typus: L992.177-456 (siccus); CBS 193.82 (PD 80/1249) (vivus); ex *Chamaespartium* sp. (Leguminosae), Austria.

Description in vitro

OA: growth-rate 53–54 mm, regular, without or with scanty pale olivaceous grey or smoke grey aerial mycelium; colony colourless; with radially arranged rows of greyish pycnidia; reverse buff.

MA: growth-rate 26–35 mm (14 days: 39–48 mm), irregular, with woolly, olivaceous grey to grey olivaceous aerial mycelium; colony buff, with orange-brown tinges caused by abundant pycnidia; reverse between saffron and buff with darker concentric zones (sepia).

CA: growth-rate 19–23 mm (14 days: 32–35 mm), irregular, with floccose olivaceous grey or grey olivaceous aerial mycelium; colony colourless to buff with darker sepia clusters of pycnidia; reverse grey olivaceous to olivaceous black with leaden grey reflex.

Pycnidia 80–250 µm in diam., globose to subglobose, solitary or confluent, glabrous or with short hyphal outgrowths, with 1–2 papillate ostioles; honey to citrine, later olivaceous to olivaceous black; walls made up of up to 7 layers of cells, outer layers pigmented; with white conidial exudate; on and in the agar. Also micropycnidia are present, 40–60 µm in diam. Conidiogenous cells 3–7 × 3–6 µm, globose to bottle-shaped, sometimes more elongate. Conidia 4.0–5.8 × 1.6–2.2, av. 5.3 × 1.9 µm, Q = 2.4–3.4, av. Q = 2.8, oblong to ellipsoidal without or with some inconspicuous, polar guttules.

Chlamydospores absent; swollen cells, sometimes clustered, may be present.

Crystals white to pale luteus, abundant, especially on OA and MA.

NaOH spot test: negative.

Ecology and distribution. In Central Europe this species is probably a common necrophyte of Leguminosae. The name *crystallifer* indicates the formation of crystals in vitro. The crystals are not dendritic, in contrast with those of some other *Phoma* species occurring on Leguminosae (Noordeloos et al., 1993). On dead stems of the leguminous hosts, the fungus in old compilating works has been referred to as '*Phoma melaena* (Fr.) Mont. & Dur.', which was used as collective name for different *Phoma*-like species associated with 'very black patches'[1].

Culture studied. CBS 193.82 (PD 80/1249) ex *Chamaespartium* sp. (Leguminosae), Austria.

[1] The identity of the basionym *Sphaeria melaena* Fr. : Fr. is not yet fixed. Sutton (1980) listed Petrak's (1921) interpretation as *Podoplaconema melaenum* (Fr.) Petrak, referring to stromatic non-ostiolate small-spored pycnidia found on *Silene nutans* (Caryophyllaceae).

21. **Phoma aurea** de Gruyter, Noordel. & Boerema, *spec. nov.* — Fig. 23

Coloniae in agaro maltoso moderatim crescentes, ochraceae, margine luteolae, mycelio acrio albido flocculoso, in NaOH immutabiles vel ferriginascentes demum olivascentes; pycnidia circa 150 µm in diam., solitaria glabra, haud papillata, uni-ostiolata; conidiophora phyalidea; conidia hyalina, glabra, ellipsoidea, unicellulata, 4.4–6.8 × 2.2–3.2 µm, pauci-guttulata; chlamydosporae desunt. Typus: L 992.177-422 (siccus); CBS 269.93 (PD 78/1087) (vivus); ex *Medicago polymorpha* (Leguminosae), New Zealand.

Description in vitro

OA: growth-rate 46–48 mm, regular, with poorly developed, flat, pure white aerial mycelium in scattered floccules over whole dish; colony weakly olivaceous buff to greenish olivaceous; reverse similar, but with olivaceous tinge (after three weeks the colony is distinctly more pigmented to olivaceous).

MA: growth-rate 56–58 mm, regular, with very fine, compact, white aerial mycelium; colony weakly ochraceous (aureate) with primrose outer margin; reverse slightly more intensely ochraceous, at margin pale luteous.

CA: growth-rate 45–49 mm, regular, with white, powdery aerial mycelium; colony salmon with grey olivaceous tinge caused by the presence of abundant pycnidia; reverse similar, but more intense.

Pycnidia 50–150 µm in diam., globose, solitary, glabrous, with one ostiole, non-papillate or slightly papillate; citrine-honey, later olivaceous; walls made up of 3–4 layers of cells, outer layers pigmented; with whitish grey conidial exudate; abundant, mainly on and in the agar but also rarely in aerial mycelium. Conidiogenous cells 4–6 × 4–6 µm, globose to bottle-shaped. Conidia 4.4–6.8 × 2.2–3.2 µm, av. 5.5 × 2.6 µm, Q = 1.6–2.8, av. Q = 2.1, oblong to ellipsoidal, often acuminate, with 2-many, small guttules.

Chlamydospores absent.

NaOH spot test: not specific, only on OA a slight discolouring to rust, later olivaceous tints occur.

Ecology and distribution. This fungus is so far known only of an isolate from dead stems of *Medicago polymorpha* in New Zealand. It may be a common saprophyte in Australasia. The epithet *aurea* refers to golden-coloured colonies on MA.

Culture studied. CBS 269.93 (= PD 78/1087) ex *Medicago polymorpha* (Leguminosae), New Zealand.

22. **Phoma nebulosa** (Pers. : Fr.) Berk. — Fig. 24

Phoma nebulosa (Pers. : Fr.) Berkeley, Outl. Br. Fung. (1860) 314 [as *Ph. nebulosa* 'Mont.']. — *Sphaeria nebulosa* Persoon, Obs. mycol. 2 (1799) 69; Syn. meth. Fung. (1801) 31; Fries, Syst. mycol. 2 [Sect. 2] (1823) 430. — *Exormatostoma nebulosa* (Pers. : Fr.) S.F. Gray, Nat. Arr. Br. Pl. 1 (1821) 522 [as '*nebulosum*']. — *Sphaeropsis nebulosa* (Pers. : Fr.) Fries, Summ. Veg. Scand. 2 [Sectio posterior] (1849) 419.

Selected literature. Boerema (1976).

Description in vitro

OA: growth-rate 44–55 mm, regular, with rather coarsely floccose, white aerial mycelium mainly in central part, or without aerial mycelium; colony grey olivaceous at centre,

towards margin colourless to citrine, greenish olivaceous or dull green, with greyish zones with pycnidia; reverse similar.

MA: growth-rate 47–55 mm, regular, with coarsely woolly, white to citrine aerial mycelium; colony colourless to grey olivaceous zonate, with agar staining citrine due to a pigment production; reverse similar.

CA: growth-rate 48–54 mm, regular, with white floccose to fluffy aerial mycelium; colony greenish olivaceous at centre, towards margin colourless; reverse slightly more green with olivaceous black centre, also with rosy-buff tinges.

Pycnidia 100–250 µm in diam., subglobose, usually with distinct neck, especially in submerged pycnidia; solitary or confluent, glabrous, with 1 to 2 ostioles; citrine to honey, later olivaceous to olivaceous black; walls made up of 3–5 layers of cells, outer layers pigmented; with white to buff conidial exudate; abundant, mostly on, sometimes (partly) in the agar. Also micropycnidia are formed, mostly in the agar, 45–80 µm. Conidiogenous cells 5–8 × 3–6 µm, globose to bottle-shaped, often with conspicuous neck. Conidia 3.6–6.6 × 1.4–2.0, av. 4.4–5.4 × 1.7–1.8 µm, Q = 2.0–3.7, av. Q = 2.4–3.2, oblong to ellipsoidal with 2-many, usually polar-orientated guttules.

Chlamydospores absent.

Crystals: no true crystals formed, but at centre of colony agglutinated, yellow gelatinous pigment clots observed on MA.

NaOH spot test: negative.

Ecology and distribution. In Europe a common soil-borne saprophyte, isolated from dead tissue of various herbaceous and woody plants (cf. isolates from Austria, Belgium, Germany, Great Britain and the Netherlands). The fungus has also been recorded in New Zealand, North America (United States) and India. The history of this species is a concatenation of different interpretations. The present *Phoma*-concept is fixed by a lectotype in Persoon's herbarium (L 910.269-51).

Cultures studied. CBS 503.75 (IMI 194766, ATCC 32163, PD 74/4) ex *Urtica dioica* (Urticaceae), Austria; CBS 117.93 (PD 83/90) ex *Mercurialis perennans* (Euphorbiaceae), the Netherlands; CBS 112.93 (PD 90/99) ex *Acer negundo* (Aceraceae), the Netherlands; CBS 113.93 (PD 90/1312) ex *Cannabis sativa* (Cannabaceae), the Netherlands.

23. **Phoma chenopodiicola** de Gruyter, Noordel. & Boerema, *nom. nov.* — Fig. 25

Gloeosporium chenopodii P. Karsten & Hariot, J. Bot., Paris 3 (1889) 207 [cf. holotype PC]. — *Plenodomus* (= *Phoma*) *chenopodii* (P. Karsten & Har.) von Arx, Verh. Kon. Ned. Akad. Wet. (Afd. Natuurk.) reeks 2, 51 (3) [= Revis. Gloeosporium, ed. 1] (1957) 73; not *Phoma chenopodii* Ahmad, Sydowia 2 (1948) 79; not *Phoma chenopodii* Pavgi & Singh, Mycopath. Mycol. appl. 30 (1966) 265.

Description in vitro

OA: growth-rate 39–55 mm, regular, without aerial mycelium or with scanty, compact, white aerial mycelium; colony colourless to grey olivaceous or greenish olivaceous, or olivaceous grey; reverse olivaceous black with ochre margin, or grey to greenish olivaceous with vinaceous buff margin.

MA: growth-rate 39–62 mm, regular or with crenate margin, with finely floccose, whitish, olivaceous grey or grey olivaceous aerial mycelium; colony greenish olivaceous,

grey olivaceous to olivaceous grey; reverse leaden grey, olivaceous black to olivaceous buff or violaceous black, sometimes zonate, outermost margin somewhat saffron.

CA: growth-rate 38–62 mm, regular, with finely floccose, white to pale olivaceous grey to grey olivaceous aerial mycelium; colony grey olivaceous, olivaceous grey to olivaceous with colourless sectors or zones, with whitish margin; reverse fuscous black, purplish grey or olivaceous mixed with grey olivaceous, with olivaceous or ochraceous margin, sometimes rather pale: hazel with olivaceous sectors.

Pycnidia 100–250 µm in diam., more or less globose, usually confluent, glabrous, with 1 or 2 distinct ostioles, sometimes papillate or with elongate neck; olivaceous to olivaceous black; walls made up of 3–5 layers of cells, outer layers pigmented; with white to saffron conidial exudate; abundant, mainly on the agar but also (partly) submerged in the agar. Conidiogenous cells 4–8 × 4–6 µm. Conidia 4.0–6.8(–9.8) × 1.6–2.6(–4.0) µm, av. 4.8–5.5 × 2.0–2.2 µm, Q = 1.8–3.0, av. Q = 2.4–2.6, oblong to ellipsoidal with 2-many, small guttules.

Chlamydospores absent.

NaOH spot test: negative.

Ecology and distribution. In Europe a common necrophyte on *Chenopodium album*. It probably has a world-wide distribution on this host by seed transmission. In South America it is repeatedly found on a cultivated variety of the related *Chenopodium quinoa*. In vivo the pycnidia are often deeply immersed, which may explain the original classification in *Gloeosporium*. The fungus has been confused with the plurivorous *Phoma exigua* Desm. which in Europe also commonly occurs on dead stems of *C. album*. [The latter fungus may produce similar continuous conidia, but usually also 1-septate conidia occur: sect. *Phyllostictoides*, see Van der Aa et al., 1990.]

Cultures studied. CBS 128.93 (PD 79/140) ex *Chenopodium quinoa* cv. Sajana (Chenopodiacae), Peru; CBS 129.93 (PD 79/803) ex *Chenopodium quinoa* cv. Sajana, Peru; CBS 130.93 (PD 91/1314) ex *Chenopodium album*, the Netherlands.

24. **Phoma bismarckii** Kidd & Beaumont — Fig. 26

Phoma bismarckii Kidd & Beaumont, Trans. Br. mycol. Soc. 10 (1924) 104–105.

Description in vitro

OA: growth-rate 69–76 mm, regular, without or with scanty pruinose, white to grey olivaceous aerial mycelium; colony very pale buff to grey olivaceous, with grey tone caused by the presence of abundant pycnidia; reverse similar or slightly more greyish olivaceous to olivaceous.

MA: growth-rate 80–82 mm, regular, with floccose, white to grey olivaceous aerial mycelium; colony olivaceous grey to grey olivaceous; reverse leaden grey with olivaceous black sectors, margin grey olivaceous to greenish olivaceous, sometimes with distinct sectors.

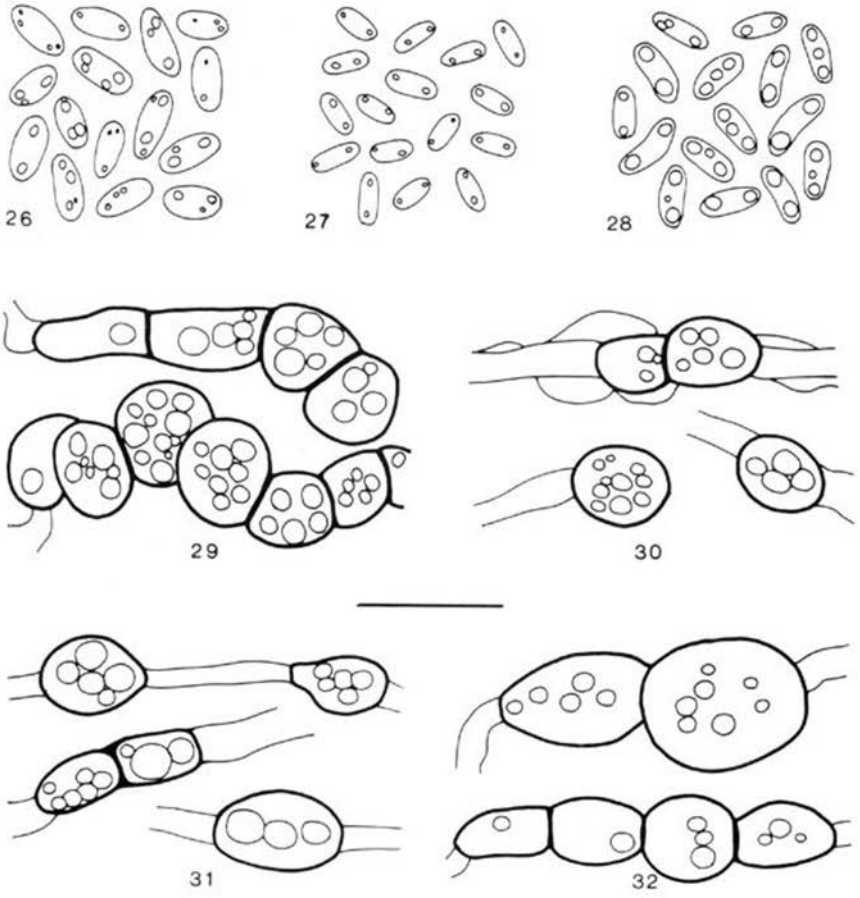
CA: growth-rate 81–83 mm, regular, with finely floccose, white to olivaceous grey aerial mycelium in sectors; colony with almost colourless to olivaceous or vinaceous buff sectors; reverse with vinaceous buff and olivaceous sectors.

Pycnidia 50–250 µm in diam., globose or irregular, solitary or confluent, glabrous or with hyphal outgrowths, with distinct ostiole, sometimes papillate; citrine to honey, later

olivaceous; walls made up of 3–5 layers of cells, outer layers pigmented; with white, pale vinaceous or buff conidial exudate; abundant, on the agar and in the aerial mycelium. Conidiogenous cells 2–7 × 4–6 µm, globose to bottle-shaped. Conidia 3.4–5.2 × 1.6–2.6 µm, av. 4.2–4.6 × 2.1–2.2 µm, Q = 1.7–2.8, av. Q = 2.0–2.1, oblong to ellipsoidal with two polar guttules.

Chlamydospores absent, but grey-olivaceous swollen cells are present, intercalary or terminal, solitary or in short chains, globose, 5–12 µm in diam.

NaOH spot test: negative, but a not specific reddish discolouring may occur.



Figs. 26–28. Conidia. 26. *Phoma bismarckii*; 27. *P. piperis*; 28. *P. selaginellicola*. — Figs 29–32. Chlamydospores. 29. *Phoma henningsii*; 30. *P. insulana*; 31. *P. pereupyrena*; 32. *P. multirostrata*. — Bar = 10 µm.

Ecology and distribution. This species has world-wide occasionally been recorded on dead branches of apple trees, *Malus pumila*. Its occurrence in association with lenticel rot of apples 'Bismarck' has led to the assumption that it was conspecific with *Phoma pomorum* Thümen (chlamydosporic sect. *Peyronellaea*, Contributions II, Boerema, 1993), but *P. bismarckii* does not produce any chlamydospore in culture. In New Zealand the fungus also has been isolated from leaf spots on *Carya pecan*, which points to a plurivorous behaviour.

Cultures studied. CBS 119.93 (PD 78/1101) ex *Malus pumila* (Rosaceae), Japan; CBS 120.93 (LEV 10607, PD 92/1720) ex *Carya pecan* (Juglandaceae), New Zealand.

Note. In North America this species has been identified as *Phoma pyrina* (Fr.) Ellis, Proc. Acad. nat. Sci. Philad. (1895) 28 [reprint p. 9] [as '(Schw.)', i.e. based on a specimen labelled *Sphaeria pyrina* Fr. in herb. Schweinitz]. However, *Sphaeria pyrina* Fr. in Kunze, Mycol. Hefte 2 (1823) 53 : Fr., Syst. mycol. 2 (2) (1823) 494 refers to a species of *Myxofusicoccum* or *Paradiscula*, see Boerema & Dorenbosch (1973: 16) and Sutton (1977: 166).

25. **Phoma piperis** (Tassi) v.d. Aa & Boerema, *comb. nov.* — Fig. 27

Phyllosticta piperis Tassi, Boll. R. Orto bot. [Boll. Lab. Orto Bot.] Siena 3 (2) (1900 ['1899']) 28 [basionym; holotype Siena].

Description in vitro

OA: growth-rate 55 mm, without well-developed aerial mycelium, only a few tufts of white mycelium; colony regular, colourless; reverse colourless to pale greyish buff.

MA: growth-rate 51–54 mm, with fine granulose smoke grey aerial mycelium; colony regular, greenish olivaceous; reverse pale olivaceous grey to olivaceous grey with grey olivaceous to buff outer margin.

CA: growth-rate 45–47 mm, with sparse pruinose, smoke-grey aerial mycelium; colony irregularly lobed, saffron-buff; reverse similar, but with sienna to umber tinge at centre.

Pycnidia 75–160 µm in diam., globose or bottle-shaped, solitary or confluent, glabrous or with hyphal outgrowths, with one or two ostioles, papillate to elongate neck; honey to citrine, later olivaceous to olivaceous black; wall consisting of 2–5 layers of cells, outer layer(s) pigmented; conidial exudate buff; abundant, mainly on, but sometimes also (partly) in the agar. Conidiogenous cells 2–5 × 3–5 µm, globose to bottle-shaped. Conidia 3.2–4.8 × 1.4–1.6 µm, av. 3.5 × 1.6 µm, Q = 2.0–3.0, av. Q = 2.2, oblong, with 2 indistinct polar guttules.

Chlamydospores absent.

On all media fine white to buff, needle-like crystals are formed.

NaOH spot test: negative.

Ecology and distribution. This fungus is described and well-known as causal organism of irregular leaf spots on shrubs of *Piper longus* (Indian long pepper) and other species of *Piper*. Members of the tropical South American genus *Peperomia*, in Europe commonly grown in glasshouses, may also be attacked by this fungus: Leaf Spot.

Culture studied. CBS 268.93 (PD 88/720) ex *Peperomia pereskiaefolia* (Piperaceae), the Netherlands.

26. **Phoma selaginellicola** de Gruyter, Noordel. & Boerema, *nom. nov.* — Fig. 28

Phyllosticta selaginellae Saccardo, Malpighia 11 (1897) 304. Holotype in Herb. Saccardo, PAD (leg. Carestia) no. 355; not *Phoma selaginellae* Cooke & Massee, Grevillea 16 (1888) 102.

Description in vitro

OA: growth-rate 48–54 mm, regular, with fine, velvety olivaceous grey aerial mycelium; colony colourless to (olivaceous) buff; reverse (olivaceous) buff with grey concentric zones to grey olivaceous.

MA: growth-rate 52 mm, regular, with fine velvety to woolly, olivaceous grey aerial mycelium; colony olivaceous grey to olivaceous black with grey olivaceous to greenish olivaceous marginal zone; reverse dark slate blue.

CA: growth-rate 44–45 mm, irregular, with crenate margin, aerial mycelium finely velvety, olivaceous grey; colony olivaceous grey to olivaceous black; reverse leaden grey to leaden black.

Pycnidia 125–330 µm in diam., globose, solitary, glabrous, with one usually non-papillate ostiole; citrine to honey, changing quickly to olivaceous black; walls made up of 3–6 layers of cells, outer layers pigmented; with straw conidial exudate; abundant, mainly on the agar, partly also in aerial mycelium. Conidiogenous cells 3–6 × 3–5 µm, globose to bottle-shaped. Conidia 3.2–4.6 × 1.4–1.6 µm, av. 4.0 × 1.6 µm, Q = 2.1–3.1, av. Q = 2.6, ellipsoidal, sometimes curved, with two or three guttules.

Chlamydospores absent.

NaOH spot test: negative.

Ecology and distribution. This seems to be an opportunistic parasite of *Selaginella* spp. In Italy the fungus is repeatedly found on wilting leaves of wild plants of *S. helvetica*. In a Dutch nursery it occurred in association with leaf necroses of a selected cultivar of the same species. The conidial size is variable in vivo and probably dependant on the age and ecological situation of the host.

Culture studied. CBS 122.93 (PD 77/1049) ex cultivar of *Selaginella helvetica* (Selaginellaceae), the Netherlands.

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Cuadernos de Trabajo de Flora Micologica Iberica.

Vol. 6 – M.T. Telleria (Ed.). *Bases corológicas de Flora Micologica Ibérica, 250–375.* (Madrid. 1993.) Pp. 180. Price: 1500 Ptas.
This is a continuation of volumes 3 and 4 of the series, treating 125 taxa of resupinate, non-poroid Aphyllophorales.

Vol. 7 – C. Lado (Ed.). *Bases corológicas de Flora Micologica Ibérica, 376–692.* (Madrid. 1993.) Pp. 305. Price: 2000 Ptas.
This volume treats 317 taxa of Myxomycetes.

K. Gessner-Ulrich. *Untersuchungen zur Expression und Funktion des linearen, mitochondrialen Plasmides pClK1 von Claviceps purpurea.* (Bibliotheca Mycologica 148, J. Cramer in der Gebrüder Borntraeger Verlagsbuchhandlung, Berlin, Stuttgart. 1992.) Pp. 83, 23 text-figs., 2 tables. Price: DM 60.-.

This thesis is a continuation of the study of a linear, mitochondrial plasmid of *Claviceps purpurea*. The molecular expression and function of this plasmid were studied. It remained difficult to identify the terminal proteins of these linear genetic elements. Experiments to transfer linear plasmids between strains of *Claviceps purpurea* and *Neurospora crassa* showed that such transfers do not occur. The author concludes that the study of the linear plasmid of *Claviceps purpurea* strongly suggests that these genetic elements are most probably of viral origin.

J. Hermanns. *Mitochondriale Genomveränderungen und Altern. Struktur und Funktion eines linaren Plasmides einer langlebige Mutante von Podospora anserina.* (Bibliotheca Mycologica 142, J. Cramer in der Gebrüder Borntraeger Verlagsbuchhandlung, Berlin, Stuttgart. 1992.) Pp. 100, 33 text-figs., 8 tables. Price: DM 60.-.

In the ascomycete *Podospora anserina* age-related modifications are genetically controlled, with a distinct role of the mitochondrial genome. In this thesis the structure and function of a linear plasmid of a long-living mutant of *P. anserina* was analysed. It was found that the longevity of the mutant is due to a delayed amplification of the plasmid DNA. This process is controlled as well by chromosomal as by extrachromosomal factors.

I. Krisai-Grailhuber. *Die Makromyceten im Raum von Wien. Ökologie und Floristik.* (Libri Botanici 6. IHW Verlag, Bert Brechtstraße 18, D-85386 Eching, Germany. 1992.) Pp. 190, 24 text-figs., 16 col. pls. Price: DM 88.-.

The author conducted a long-term mycofloristical-ecological research project in the surroundings of Vienna, Austria, from 1981 to 1987. The main object has been the ob-

servation of the fungi in 15 permanent plots in the nature reserves Lobau and Lainzer Tiergau. The present volume deals with 1241 macromycetes that have been recorded and documented during this study. The phytocoenological results will be presented in a second volume to be published later in the same series. It has been proved that the mycoflora of the surroundings of Vienna deviates from the typical Central European flora, as it contains many thermophilous elements. It therefore forms a link to the Submediterranean and East European Mycofloras. All taxa are represented with data on their ecology and distribution in the area, and critical taxa are fully described and illustrated. Also 16 species are depicted in colour. The illustrations are well-done and of good quality. The book gives good, modern descriptions of many rare and interesting taxa and is therefore highly recommended for all who are seriously interested in European macrofungi.

O. Petrini & G.A. Laursen (Eds.). *Arctic and Alpine Mycology 3–4. Proceedings of the Third and Fourth International Symposium on Arcto-Alpine Mycology.* (Bibliotheca Mycologica 150, J. Cramer in der Gebrüder Borntraeger Verlagsbuchhandlung, Berlin, Stuttgart. 1993.) Pp. 269. Price: DM 90.-.

This volume constitutes the Proceedings of the Third and Fourth International Symposium on Arctic and Alpine Mycology. It presents 21 papers largely on fungal taxonomy, but also on mycofloristics and myco-ecology of the arctic and alpine regions. One contribution deals with *Myxomycota* (slime moulds), six with *Ascomycota*, and 13 with *Basidiomycota*, while one is devoted to the study of distribution patterns of parasitic fungi in high mountains. That the arctic and alpine regions comprise still many little known fungi is demonstrated by the fact that 19 new fungal taxa are described in this volume. Keys are provided for the identification of species of *Entoloma*, *Ciliolaria*, and Xylariaceae.

J. Rammeloo & R. Walleyn. *The edible fungi of Africa south of the Sahara: a literature survey* (Scripta Botanica Belgica 5. National Botanic Garden, Domein van Bouchout, B-1860 Meise, Belgium. 1993.) Pp. 62, several text-figs. Price: Bfrs 230.- excl. postage.

This booklet gives a survey of the information on importance, nutritive content, knowledge, collecting, trade, culture, local traditions, new introductions and preparation for eating of about 300 species whose edibility has been explicitly mentioned in literature. The species are arranged in alphabetical order with references to the countries from which they have been recorded with source of literature. In some cases short comments are given. A few species are illustrated with nice-looking line drawings.

M. Rohe. *Untersuchungen zur Phylogenese linearer genetischer Elemente. Extrachromosomale DNA des Ascomyceten Morchella conica.* (Bibliotheca Mycologica 146, J. Cramer in der Gebrüder Borntraeger Verlagsbuchhandlung, Berlin, Stuttgart. 1992.) Pp. 118, 25 text-figs., many tables. Price: DM 60.-.

Plasmids are extrachromosomal genetic elements able of self replication. The first plasmids discovered were circular in structure, but recently also many plasmids of linear structure were found, especially in eucaryotes. The linear plasmids of yeasts are of a spe-

cial type and located in the cytoplasm, while those of the other fungi are of a special structure and integrated into the mitochondria. The aim of this study is to characterize more accurately the linear plasmids as a group of genetic elements.

The linear plasmid of *Morchella conica* was chosen because preliminary studies of this allowed fast DNA sequence analysis. Indications on the function and on the origin of linear plasmids were obtained from comparison of nucleotid sequences, coding capacity, and transcription analysis. The results indicate that the linear plasmids are of procaryotic origin and clearly related with linear bacteriophages. This is in agreement with the endosymbiont hypothesis about the origin of mitochondria.

S. Ryman & I. Holmåsen. *Pilze. Über 1500 Pilzarten ausführlich beschrieben und in natürlicher Umgebung fotografiert.* Aus den Schwedischen übersetzt und bearbeitet von T.R. Lohmeyer & H.-G. Unger. (Bernhard Thalacker Verlag, Braunschweig. 1992.) Pp. 718, 1100 col. pls. Price: DM 138.-.

This is the German edition of Ryman & Holmåsen's 'Svampar'. The main part of this well-printed book consists of 1100 impressive colour-photographs mostly taken by the distinguished Swedish nature photographer Ingmar Holmåsen. The translators have taken into account the Central-European ecology and distribution of the macromycetes described. They also added many new references. Data on the origin of the material pictured are replaced by the 'Red-list' categories for Germany. In the introductory part there are chapters on macromycete habitats, recent threats of the fungus-flora, and collecting of mushrooms. A key to the genera of the basidiomycetes is included. Occasionally keys to the most important species of large genera are provided in the text among the descriptions.

L. Ryvarden & R.L. Gilbertson. *European Polypores, Part 1. Abortiporus–Lindtneria.* (Fungiflora A/S, Postbox 95, Blindern, N-0314 Oslo, Norway. 1993.) Pp. 387, numerous text-figs. and distribution maps. Price: NOK 360.-.

This flora contains keys, descriptions and illustrations to all Polypores known from Europe, and will be published in two volumes. The first volume contains an introduction, definitions of macro- and micromorphological characters, a survey of the higher taxonomy of the group, and chapters on decay characteristics, pathology, culturing, sexuality, forest regions and mycogeography. Guide-lines are given as to collecting and determination. The keys are dichotomic and concise. The genera are treated in alphabetical order, and this first volume treated *Albatrellus* through *Lindtneria*. As can be expected from the authors, well known specialists in this group, the descriptions and illustrations are of high quality. The book will prove to be a valuable tool for taxonomists and forestry people.

R. Smit. *Entwicklung von Transformationssystemen für den phytopathogenen Ascomyceten Claviceps purpurea.* (Bibliotheca Mycologica 143. J. Cramer in der Gebrüder Borntraeger Verlagsbuchhandlung, Berlin, Stuttgart. 1992.) Pp. 95, 14 text-figs., 10 tables. Price: DM 60.-.

The aim of this thesis was to find the underlying conditions to apply recombinant DNA techniques for the study of phytopathological and biotechnological problems in *Claviceps*

purpurea. Because of the complicated life-cycle of this fungus, the classical methods of genetic recombination are not practicable. Several experiments with gene transfer were successful and indicated that *C. purpurea* is a promising object for the study of the alcaloid metabolism and the host-parasite interaction.

M. Walz. *Molekulare Analysen zur Expression von β-Lactam-Genen bei Acremonium chrysogenum*. (Bibliotheca Mycologica 147, J. Cramer in der Gebrüder Borntraeger Verlagsbuchhandlung, Berlin, Stuttgart. 1992.) Pp. 101, 23 text-figs., 11 tables. Price: DM 70.-.

This thesis is devoted to genetic problems concerning a better production of antibiotics in strains of *Acremonium chrysogenum*. Especially the expression of the β-lactam antibiotic biosynthetic gene is studied for this purpose with experimental techniques.

The absence of an English summary with a publication of more than local importance in an international mycological series is felt as an omission.

E. Weber. *Untersuchungen zu Fortpflanzung und Ploidie verschiedener Ascomyceten*. (Bibliotheca Mycologica 140, J. Cramer in der Gebrüder Borntraeger Verlagsbuchhandlung, Berlin, Stuttgart. 1992.) Pp. 186, 6 text-figs. Price: DM 90.-.

In the first part of this thesis the reproductive system in 15 species of Leotiales and 17 species of Pezizales was examined. Different single spore mycelia of these species were confronted in cultures and analysed. About 94% proved to be homothallic and 6% heterothallic. Interesting observations were made on the relative DNA content in the nuclei of ascogenous hyphae and of young asci during karyogamy and meiosis. In the second part of this study the relative DNA content in 566 species of Ascomycetes, mainly Leotiales (413) and Pezizales (84), was established by cytofluorometry. From this the degree of polyploidy, or 'ploidy level', was calculated. Mrs. Weber found that in the haplophase only 3% of the species of Leotiales and Pezizales are monoploid, 97% showed higher ploidy levels. The highest levels ever recorded in fungi were found in the genera *Neottiella* and *Octospora* (respectively 50 × and 18 ×). In general within otherwise closely related taxonomic groups more primitive and older species have lower ploidy levels than derived and younger ones. Great care has been taken in the collecting and identification of the many species investigated.

H. Weber (Ed.). *Allgemeine Mykologie*. (Gustav Fischer Verlag, Jena, Stuttgart. 1993.) Pp. 541, 206 text-figs., 66 tables. Price: DM 148.-.

This is a well-printed reference book pretending to give a survey of the total field of mycology. Twelve authors, active in research and education at universities and institutes in the eastern part of Germany, have contributed well-documented and up-to-date chapters on the different aspects of modern mycology. There are chapters on cytology, morphology, propagation, physiology, ecology, taxonomy, pathology, and the practical importance of fungi. This book is recommended to all interested in recent developments in mycology in its widest sense.