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ULTRASTRUCTURE OF THE ASCOSPORE WALL IN PEZIZALES (ASCOMYCETES)—IV

Morchellaceae, Helvellaceae, Rhizinaceae, Thelebolaceae, and Sarcoscyphaceae. General discussion

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(With Plates 1–12, two Tables, and one Text-figure)

The development of wall layers and ornamentation of ascospores, plus specialized plasmic structures, are studied with the electron microscope in members of the Morchellaceae, Helvellaceae, Rhizinaceae, Thelebolaceae, and Sarcoscyphaceae; additional results in the Pyronemataceae are given. The findings are compared with those of former studies (Merkus, 1973, 1974, 1975). A general discussion on the origin and development of the different structures concludes the series. A classification based upon species representing typical developments of all the species of the four studies is made.

INTRODUCTION

Following former publications on the subject (Merkus, 1973, 1974, 1975) this electron microscopy study completes the series of papers on the ultrastructure of the ascospore wall in Pezizales. The present paper includes the results in species belonging to the Morchellaceae, Helvellaceae, Rhizinaceae, Thelebolaceae, and Sarcoscyphaceae. It also gives additional results in the Pyronemataceae sensu Eckblad, including those in *Pyronema omphalodes*, *Coprobia granulata*, *Geopyxis carbonaria*, *Mycolachnea hemisphaerica*, and *Octospora musci-muralis*.

In general, Eckblad's classification of the taxa (1968) has been followed. *Thecotheus* spec. (an eight-spored, ornamented species) and *Iodophanus carneus* are provisionally classified in the Thelebolaceae; e.g. Eckblad placed *Iodophanus* in the Pyronemataceae. According to Eckblad a member of the Otideaceae, *Geopyxis carbonaria*, is transferred provisionally to the Pyronemataceae sensu Eckblad.

The paper concludes with a general discussion on the subject.

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REVIEW OF EARLIER WORK

Only a few of the species studied by Le Gal (1947) could be examined under the electron microscope. Le Gal's light microscopy of these species is briefly reviewed. Some of the names she used (see footnotes) have been changed in accordance with the 'International Code of Botanical Nomenclature'.

Rhizina undulata Fr. per Pers.[1] and the related *Discina perlata* (Fr. per Fr.) Fr. develop a simple spore ornamentation that is formed between the primary wall and its covering layers. The ornamentation consists of callose and pectine and is of sporal origin. The primary wall is covered by an "assise sous-périsporique" and a "pellicule membranaire". The "assise sous-périsporique" is formed before the ornamentation develops. The "pellicule membranaire" is termed "coque interpérisporique", as it is formed at the same time as the ornamentation and is penetrated by the substance of ornamentation; the "coque interpérisporique" and the substance of the ornamentation both grow into one, the 'coque interpérisporique' also consisting of callose and pectine. During the development of the ornamentation a "périspore" is present on the outside of the ascospores; this "périspore" remains.

Helvella atra Holmskj. per Fr.[2], *Helvella elastica* Bull. per St.-Am.[3], *Helvella acetabulum* (L. per St.-Am.) Quél.[4], *Helvella macropus* (Pers. per S. F. Gray) P. Karst.[5] and some related species, all members of the Helvelleae of Le Gal (1947: 284), which are now placed in *Helvella* L. per St.-Am., normally develop smooth ascospores. But in a few cases the species show an ornamentation on the ascospores, consisting of coarse folds or of connected or isolated warts. According to Le Gal this ornamentation is false and formed by a substance situated in a "couche sous-épisporique", which deforms the epispore locally.

Unfortunately, no material of the species of the Sarcoscyphaceae studied by Le Gal was available. Instead *Sarcoscypha coccinea* (Scop. per S. F. Gray) Lamb. and *Desmazierella acicola* Lib., which also belong to this important taxon, could be studied. Le Gal's descriptions of the ornamentation patterns of the species involved resemble those of *Rhizina undulata* and *Discina perlata*. The "périspore" is permanent in all species; the ornamentation, which does not contain callose and pectine, penetrates its covering layers in *Cookeina sulcipes* (Berk.) O. K., *Cookeina tricholoma* (Mont.) O. K. and *Cookeina insititia* (Berk. & Curt.) O. K., and remains within these layers in *Aurophora dochmia* (Berk. & Curt. apud Berk.) Rifai[6], *Phillipsia domingensis* Berk., *Plectania campylospora* (Berk.) Nannf. apud Korf[7], and *Plectania platensis* (Speg.) Rifai[8].

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[1] *Rhizina inflata* Schaeff. per P. Karst.
[2] *Leptopodia atra* (Fr. ex König) Boud.
[3] *Leptopodia elastica* (Bull.) Boud.
[4] *Helvella sulcata* Afz.
[5] *Macropodia macropus* (Pers.) Fckl.
[6] *Phillipsia dochmia* (Berk. & Curt. apud Berk.) Seaver.
[7] *Sarcosoma sarasini* (P. Henn.) Boud.
[8] *Urnula platensis* Speg.

MATERIALS AND METHODS

Fresh material was collected in the Netherlands, Belgium, Turkey, Papua New Guinea, Indonesia, Kenya, Uganda, and Canada; some species were provided in pure culture by the Centraalbureau voor Schimmelcultures, Baarn, The Netherlands. The following list gives more details about the specimens and their origins: '*Ascophanus*' *coemansii* Boud. (a species of *Coprotus*) — *van Brummelen*, culture on cow dung, 21.VI.1973 (L); — *Piepenbroek*, on cow dung, near Welsum, Olst, Overijsel, The Netherlands; *Ascozonus woolhopensis* (Berk. & Br.) Boud. — *van Brummelen*, several cultures isolated from rat dung, on oatmeal agar enriched with horse dung decoction, Ekeren, Belgium (L); *Coprobia granulata* (Bull. per Mérat) Boud. — *van Brummelen 3562*, culture on cow dung, Hollandse Rading, Maartensdijk, Utrecht, The Netherlands (L); — *van Brummelen*, culture on cow dung, Bathmen, Overijsel, The Netherlands, 6. VIII. 1973 (L); *Desmazierella acicola* Lib. — *J. Daams*, on fallen needles of *Pinus*, "Spanderswoud", Hilversum, North Holland, The Netherlands, 11.V.1973; *Geopyxis carbonaria* (Alb. & Schw. per Pers.) Sacc. — *van Brummelen & Piepenbroek 4082*, on burnt soil, 't Joppe, Gorssel, Gelderland, The Netherlands, 6.VIII.1973 (L); — *Piepenbroek 783*, on burnt soil, 't Joppe, Gorssel, Gelderland, The Netherlands (L); *Gyromitra esculenta* (Pers. per Krombh.) Fr. — *Tjallingii & van Brummelen*, among rubbish in a garden, Wageningen, Gelderland, The Netherlands, 2.IV.1974 (L); *Helvella crispa* Scop. per Fr. — *van Brummelen 4075*, under *Pinus*, Bergen, North Holland, The Netherlands, 3.XI.1973 (L); — *van Brummelen 4506*, under deciduous trees beside a road, Diepenveen, Overijsel, The Netherlands, 15.VII.1974 (L); *Octospora musci-muralis* Graddon — *Piepenbroek 720*, among mosses on an old wall in a garden, between Deventer and Twello, Voorst, Gelderland, The Netherlands, 12.XI.1973 (L); *Iodophanus carneus* (Pers. per Pers.) Korf apud Kimbr. & Korf — *van Brummelen*, culture on sheep dung, Elspeet, Gelderland, The Netherlands, 7.XI.1972 (L); — *van Brummelen*, culture, Vogelenzang, North Holland, The Netherlands (L); — *Prof. Necat*, culture on oatmeal agar enriched with horse dung decoction, Kaskaloglu, Bornova, Izmir, Turkey; *Lasiobolus monascus* Kimbr. — *van Brummelen 3563*, several cultures isolated from porcupine dung, on oatmeal agar enriched with horse dung decoction, Mt. Suckling, Papua New Guinea, 6.IX.1972 (L); *Lasiobolus pilosus* (Fr.) Sacc. — *van Brummelen*, culture on sheep dung, Elspeet, Gelderland, The Netherlands, 7.XI.1972 (L); — *van Brummelen 4077*, culture on horse dung, Overveen, Bloemendaal, North Holland, The Netherlands, 14.V.1973 (L); — *van Brummelen*, culture on hartebeest (=*Alcelaphus caama*) dung, zoological garden, Amsterdam, North Holland, The Netherlands (L); *Morchella esculenta* L. per St.-Am. — *C. Bas 6003*, on sandy soil, Meyendel, Wassenaar, South Holland, The Netherlands, 16.IV.1974 (L); — *C. Bas*, on sandy soil-peaty soil, under *Populus* and *Crataegus*, Voorschoten, South Holland, The Netherlands, 22. IV.1975 (L);

Mycolachnea hemisphaerica (Wigg. per S. F. Gray) Maire — *Piepenbroek 769*, on sandy soil, Epserbos, Epse, Gelderland, The Netherlands, 21.VII.1974 (L); *Pyronema omphalodes* (Bull.) per St.-Am.) Fckl. — *van Brummelen 4081*, on burnt soil, 't Joppe, Gorssel, Gelderland, The Netherlands, 6.VIII.1973 (L); — CBS 373.62, several cultures on cornmeal agar (L); *Rhizina undulata* Fr. per Pers. — *van Brummelen 4076*, on burnt soil, 't Joppe, Gorssel, Gelderland, The Netherlands, 6.VIII.1973 (L); — *Piepenbroek 761*, on burnt soil, "de Poll" between Wilp and Voorst, Gelderland, The Netherlands, 20.VII.1974 (L); *Sarcoscypha coccinea* (Scop. per S. F. Gray) Lamb. — of unknown (probably Central European) origin (comm. Mr. G. D. Swanenburg de Veye), 8.III.1974 (L); *Thecotheus* spec. — culture on rhinoceros dung, P. Pentjang, W. Java, Indonesia, 28.X.1972 (L); *Thelebolus crustaceus* (Fckl.) — CBS 713.69, culture isolated from carnivore dung, on oatmeal agar enriched with horse dung decoction, *R. F. Cain & al.*, Mt. Speke, Ruvenzori Mts, Uganda, 23.VII.1969 (L); *Thelebolus stercoreus* Tode per Steudel — CBS 717.69, culture isolated from deer dung, on oatmeal agar enriched with horse dung decoction, *D. Malloch*, Simcoe Co., Ontario, Canada, 13.V.1968 (L).

As not all field collections contained ripening apothecia some specimen were kept moist in conditioned growth chambers, in alternating light and darkness; *Lasiobolus pilosus*, *Iodophanus carneus*, and *Thecotheus* spec. on their own substrate for a few days at 12 °C; *Lasiobolus monascus*, *Ascozonus woolhopensis* and another strain of *Iodophanus carneus* on oatmeal agar enriched with horse dung decoction for a few days or more at 12 °C. Of the strains received from the Centraalbureau voor Schimmelcultures, *Thelebolus stercoreus* and *T. crustaceus* were grown on oatmeal agar with horse dung decoction; *T. crustaceus* also on cornmeal agar; for at least 14 days at 12 °C, in alternating light and darkness. *Pyronema omphalodes* was cultured on cornmeal agar for 5–7 days at 23 °C, in constant light with an intermittent ultraviolet period of eight hours after two days.

A suitable procedure for fixation based on previous experiments was chosen: 1–1.5% $KMnO_4$ for 30 minutes at room temperature or 1–3.25% glutaraldehyde for 3–4 hours at 4 °C as primary fixatives, both followed by postfixation with 1% OsO_4 for 60 minutes at 4 °C; generally the lowest possible percentages were applied. At the beginning of this study the apothecia were fixed only in 1–1.5% $KMnO_4$ for 60–150 minutes at room temperature; rarely, they were fixed only in 1% OsO_4 for 60 minutes at 4 °C.

For further treatment the standard methods described in the previous papers were applied, including the occasional use of the Spurr embedding medium. All sections were cut with a diamond knife.

OBSERVATIONS

MORCHELLACEAE

MORCHELLA ESCULENTA—Pls. 1A–D; 2A, B

Fixatives: $KMnO_4$-OsO_4, glutaraldehyde-$KMnO_4$ and glutaraldehyde-OsO_4.

The apical parts of the asci are filled with compact masses of glycogen that enclose small parts of membranous material; just beneath the glycogen numerous vacuoles with contents that resemble glycogen occur. After glutaraldehyde-$KMnO_4$-fixation the glycogenic contents of the vacuoles are floccose or more granular and regularly spread over the vacuoles, in a few cases partly clustered to larger electron-dense globules. After $KMnO_4$-OsO_4 or glutaraldehyde-OsO_4-fixation the vacuoles are rather empty and only a thin layer of tiny glycogenic globules is found against the tonoplast (Pl. 1A).

The basal parts of the asci are also filled with large compact concentrations of glycogen and with vacuoles like those found in the apices.

In the one-eight-nuclear stages the subapical parts of the asci contain normal ascoplasm in which the nuclei and the tubular and vesicular elements of the endoplasmic reticulum as well as larger vesicles that show low electron density and may originate from the endoplasmic reticulum itself, scattered glycogen, plus small vacuoles of the same type as described above; apart from scattered glycogen larger accumulations also exist (Pl. 1A, B). Globular structures, which are generally electron-transparent after the three types of fixation, are also found (Pl. 1A–D). Some of them are scattered over this part of the ascoplasm but the greater part of them are concentrated in groups, almost all around the glycogen. They sometimes have a moderately electron-dense or completely electron-dense aspect after the two fixations with $KMnO_4$ (Pl. 1D).

Electron-dense and irregularly shaped membranous structures may occur in the larger vesicles with poor electron density and, more abundantly, in the smaller vacuoles, where they seem to arise from invaginating membranes; they are also found in the glycogen (Pl. 1A, B).

At later stages of development eight ascospores are delimited around the nuclei in the subapical ascoplasm. They soon have a regular, ellipsoid shape and the sporoplasm contains all the ascoplasmic elements present in this part of the ascus; they are plurinucleate and in each nucleus a nucleolus can be distinguished. The remaining epiplasm abounds in globular structures. Delimitation of small ascoplasmic fragments without nuclei also occurs.

The primary wall ($KMnO_4$-OsO_4 300–450 nm, glutaraldehyde-$KMnO_4$ 250–350 nm, and glutaraldehyde-OsO_4 about 250 nm thick) is normal in appearance and shows practically no internal differentiation (Pl. 1C).

The development of the secondary wall starts during a more extensive vacuolization

and/or glycogen formation in the epiplasm; the secondary wall material is fairly electron-dense and slightly floccose (Pl. 1C, D). As it proceeds further the endospore ($KMnO_4$-OsO_4 300–400 nm, glutaraldehyde-OsO_4 about 250 nm thick) and the epispore ($KMnO_4$-OsO_4 50–55 nm, glutaraldehyde-OsO_4 about 40 nm thick) differentiate in the primary wall. The endospore may show a more electron-dense layer in the inner parts, while the epispore consists of two electron-dense layers between which an electron-transparent layer is found (Pls. 1D; 2A, B).

The latest stages of development available in the material show a loss of epiplasmic structures; most of the globular structures have also shriveled and disappeared; those remaining cluster around the two poles of the ascospores (Pl. 2B). The secondary wall has also disappeared and left a fairly electron-transparent and vaguely structured layer around the epispore (Pl. 2B). The sporoplasm has increased in electron density and contains a few small oil drops; the epiplasm consists of glycogen and empty vacuoles.

HELVELLACEAE AND RHIZINACEAE

HELVELLA CRISPA—Pls. 2C–F; 3A, B
RHIZINA UNDULATA, GYROMITRA ESCULENTA, AND G. INFULA—Pls. 3C–G; 4A–D

Fixatives: $KMnO_4$-OsO_4 for all four species, glutaraldehyde-OsO_4 for *Helvella crispa* only.

Like in *Morchella esculenta*, vacuoles and glycogen are found in the apical parts of the asci of all these species. In *H. crispa*, *G. esculenta*, and *G. infula* the glycogen exist as compact masses in the apices, but in *R. undulata* only a small amount of glycogen is found as a thin layer or, even more, as a cap just inside the ascus wall at the apex (Pl. 2C). Vacuoles with what seem to be glycogenic contents become abundant towards the subapical parts of the asci of *H. crispa*, *G. esculenta*, and *G. infula*, with the normal ascoplasm extending in its central parts, while in *R. undulata* only a few vacuoles develop that are more randomly distributed over the ascoplasm of the apical parts.

Small to large vacuoles, varying from electron-transparent to almost entirely filled with glycogen, and masses of glycogen fill the basal parts of the asci.

In all the species the subapical parts of the asci are very much like those in *M. esculenta* in the one-eight-nucleated stages. Present are the nuclei, the tubular and vesicular elements of the endoplasmic reticulum, larger and almost electron-transparent vesicles probably originating from them, small vacuoles with traces of glycogen, and scattered or more clustered glycogen. Furthermore, scattered globular structures, which are electron-transparent to more moderately electron-dense after both types of fixation, occur all over the subapical ascoplasm in all four species but they abound in the lowermost and, even more, in the uppermost part in *H. crispa* and *R. undulata* (Pl. 2C).

The smaller vacuoles contain the same electron-dense and irregularly shaped membranous structures as in *M. esculenta*.

Later stages of development show the formation of ascospores in the subapical ascoplasm. As a result of the capricious course of the delimiting membranes the ascospores are at first very irregular. They obtain their eventual shape only when the primary spore wall is complete, so that the primary wall material must have great plasticity at these stages. The sporoplasm has a regular appearance and does not yet contain many globular structures. As in *M. esculenta*, delimitation of small parts of ascoplasm without nuclei is not infrequently found in all four species.

The primary wall is homogeneous and electron-transparent (*H. crispa:* $KMnO_4$-OsO_4 75–150 nm thick; *R. undulata:* 250–400 nm thick; *G. esculenta:* 250–450 nm thick). A notable variation in thickness arises during its development, and even formation of secondary wall material may start while primary wall development is still going on.

Secondary wall formation in *H. crispa* is regular but not extensive. The secondary wall material is fairly electron-dense and homogeneous at all stages after $KMnO_4$-OsO_4-fixation (Pls. 2D; 3A), more floccose after glutaraldehyde-OsO_4-fixation. It disappears when the ascospores mature and an endospore and epispore have developed in the primary wall; remnants of the investing membrane persist for some time (Pl. 3A, B). The endospore ($KMnO_4$-OsO_4 75–100 nm thick) does not have any internal structure; the epispore ($KMnO_4$-OsO_4 30–60 nm thick) shows the basic pattern of two electron-dense layers separated by an electron-transparent layer in which a thin, extra electron-dense layer can sometimes be distinguished (Pl. 3B).

During the ascospore development in *H. crispa*, the globular structures in the epiplasm and sporoplasm grow out distintly to large oil drops; a variable but generally large number of new and smaller oil drops seem to be added also, finally occupying the greater part of the epiplasm and sporoplasm (e.g. Pl. 2D, E). In the remaining part of the epiplasm, glycogen and vacuoles with floccose contents predominate.

A remarkable differentiation in the primary wall distinguishes *H. crispa* both from all species previously described (Merkus, 1973, 1974, 1975) and also from all those to be discussed in this study. As Le Gal (1947) already observed with the light microscope, the primary wall material grows out locally and forms thickenings on the outside that seem to be permanent. The outgrowths (young ascospores: $KMnO_4$-OsO_4 20–50 nm thick; mature ascospores: glutaraldehyde-OsO_4 about 85 nm thick) occur in both the inner and outer parts of the primary wall and are fairly electron-dense after both fixations (Pl. 2E, F).

As in *H. crispa*, secondary wall formation in *R. undulata* regularly passes off; it is far more extensive at the two poles of the ascospores, the secondary wall material is permanent. Differentiation of the primary wall into an endospore and an epispore follows the normal pattern. In the main the epispore (30–40 nm thick) has the same structure as that in *H. crispa*; the outer electron-dense layer becomes somewhat thicker in the latest stages (Pl. 3F, G) and internal striation can be seen in the intermediate electron-transparent layer (Pl. 3F). The endospore (200–300 nm thick) does

not remain homogeneous like in *H. crispa* but differentiates further in its outer parts, where two fairly electron-dense layers join the epispore; its remaining inner parts remain homogeneous and electron-transparent (Pl. 3F, G).

The secondary wall material of *R. undulata* is homogeneous and fairly electron-dense in its first stages of development but it soon becomes more electron-dense. At first some dots (Pl. 3C) and very thin layers (Pl. 3D) appear at a slight distance from the epispore. These soon form a continuous layer (Pl. 3F) which increases in thickness particularly near the two poles of the ascospores (Pl. 3G). The compact ornamentation that is finally formed at the two poles of the ascospores varies in thickness from 1200 nm up to 3000 nm and forms rounded spines or more cup-shaped projections, one at each pole, containing some large ellipsoid holes up to 700×300 nm in section (Pl. 3E). At the sides of the spores a smooth layer of secondary wall material of about 100 nm thick is present (Pl. 3F).

In *R. undulata* the globular structures in the epiplasm do not enlarge as much as in *H. crispa*, so that the epiplasm remains more intact, particularly in the layer just inside the ascus wall. The epiplasm develops glycogen and larger vacuoles with floccose contents. The sporoplasm increases in electron density and each spore generally develops two large oil drops, together with a number of smaller ones.

The development of the ascospores in *G. esculenta* and *G. infula* could not be studied extensively since only the younger stages of *G. esculenta* were present while the final stages of *G. infula* were absent. But some points should be mentioned. The differentiation of the primary wall into an endospore (*G. infula* 200–250 nm thick) and an epispore (*G. infula* 30–40 nm thick) and the formation of a secondary wall is regular in both species (Pl. 4A–D). The epispore of *G. infula* markedly resembles that of *H. crispa* and particularly that of *R. undulata*; the endospore of *G. infula* is like that in *R. undulata*, it shows differentiation in the outer parts, and even the inner parts are no longer homogeneous (Pl. 4D). The secondary wall material of *G. infula* condenses as floccose electron-dense material on the epispore but it is doubtful whether it persists (Pl. 4C, D); the mature ascospores are smooth. Both in the epiplasm and sporoplasm of the two species the oil drops increase in number and size; in the epiplasm the amount of glycogen increases and also occurs against the ascus wall in compact masses.

THELEBOLACEAE

"ASCOPHANUS" COEMANSII, THELEBOLUS CRUSTACEUS AND T. STERCOREUS—Pl. 5A–G

Fixatives: $KMnO_4$-OsO_4 for all three species, for *T. crustaceus* and *T. stercoreus* also glutaraldehyde-OsO_4. The apothecia of *T. stercoreus* are uniascal but each ascus is multispored; those of *A. coemansii* and *T. crustaceus* multiascal and all asci are multispored. As for the development of the ascospores in the ascoplasm, it is apparently rather simple in all three species.

Both fixatives show that the primary wall is homogeneously electron-transparent before further differentiation, sometimes with a slight increase in electron density in the inner parts; in *A. coemansii* it is 350–550 nm thick, in *T. crustaceus* 250–450 nm thick, and in *T. stercoreus* 300–550 nm thick after $KMnO_4$-OsO_4-fixation (Pl. 4E). It gives rise to an epispore and endospore that remain simple through all stages of development, each having the same appearance after the two different fixations.

The epispore is about 10 nm thick in all three species and seems to consist of only one electron-dense layer; this is homogeneous. Pictures of *T. crustaceus* and *A. coemansii* however suggest that the fairly electron-transparent layer just inside the electron-dense layer also belongs to the epispore. Nevertheless it is believed that this layer belongs to the endospore. The endospore is fairly electron-transparent, also without much internal differentiation; in *A. coemansii* 450–750 nm thick; in *T. crustaceus* 400–600 nm thick ($KMnO_4$-OsO_4 and glutaraldehyde-OsO_4); in *T. stercoreus* 300–550 nm ($KMnO_4$-OsO_4) and 200–350 nm (glutaraldehyde-OsO_4) thick. In *T. stercoreus* some concentration of spore wall material is present in the middle layers of the endospore while, as mentioned above, in *T. crustaceus* and *A. coemansii* endospore material seems to separate from the inner layers and join the epispore (Pls. 4F; 5A, C–G. Pl. 5F, G from *A. coemansii* are not representative of this development but added only for the epiplasmic structures).

The secondary wall starts to develop during primary wall differentiation. It is found all around the ascospores but it remains restricted to a thin layer (Pls. 4E, F; 5A). After $KMnO_4$-OsO_4-fixation the secondary wall material is fairly electron-dense and homogeneous, after glutaraldehyde-OsO_4 more floccose. It condenses on the epispore at later stages of development, where it forms a smooth and homogeneously electron-dense layer about 40 nm thick (Pl. 5C–G).

The epiplasm is fairly normal in appearance. Apart from large quantities of glycogen with scattered organels it has developed a few globular structures (electron-dense after $KMnO_4$-OsO_4-fixation; fairly electron-dense after glutaraldehyde-OsO_4-fixation), and small and electron-transparent vacuoles that do not seem to fuse at older stages. In *A. coemansii* and *T. stercoreus* the glycogen disappears as the ascospores mature; in *T. crustaceus* its electron density increases and clusters appear on the secondary wall. Furthermore, peculiar structures are found in the epiplasm of *A. coemansii* and *T. stercoreus*. In *A. coemansii* they are formed by clews of electron-dense material that probably arises from epiplasmic membranes (Pl. 5F); they show further growth during ascal development but fade into large masses of fairly electron-dense material as the ascospores mature (Pl. 5G). In *T. stercoreus* the structures are formed by large globules that occur particularly along the ascus wall and that evidently consist of a network of plaited units, each unit about 35 nm thick and made up of one broad and electron-transparent layer with a thin and electron-dense layer in the middle and bounded by electron-dense layers at both sides; loose units are possibly found in the epiplasm; the globules seem to be membrane-bounded (Pls. 4F; 5A, B). The sporoplasm is normal and contains some small vacuoles.

As the ascospores mature all the organels in the epiplasm disappear but the in-

vesting membrane is still present in the latest stages. The sporoplasm becomes electron-dense but does not develop any oil drops. The mature spores are smooth; it is not known whether the secondary wall material disappears; it could persist as an extra, smooth layer on the primary wall.

ASCOZONUS WOOLHOPENSIS—Pl. 6A–C

Fixatives: $KMnO_4$ and glutaraldehyde-OsO_4. The apothecia are multiascal and each ascus is multispored.

The development of the ascospores is as simple as it is in "*Ascophanus*" *coemansii*, *Thelebolus crustaceus*, and *T. stercoreus*. With both fixatives a homogeneous, electron-transparent and 150–250 nm thick primary wall is visible. It differentiates into a simple epispore, about 10 nm thick and consisting of a single electron-dense layer, and an endospore, which is 150–250 nm thick and increases in electron density but does not show any further differentiation (Pl. 6A–C).

Like in the three preceding species the secondary wall develops all around the ascospores but it may show a further increase in thickness (Pl. 6A). The secondary wall material is rather floccose after both fixations and does not condense; it disappears when the ascospores mature (Pl. 6B, C). The investing membrane remains present in the latest stages of development.

The development of the epiplasm could not be studied thoroughly. It contains the usual organels and much glycogen is present. Typical circular membranous units are found at some distance from the investing membrane; their origin remains unknown (Pl. 6B). Connections between the secondary wall and the epiplasm have been found in some instances along the investing membrane.

In the latest stages of development the sporoplasm has increased in electron density but neither oil drops nor vacuoles have developed. The epiplasm has lost its original structure and become vague and empty; some vacuoles are found after glutaraldehyde-OsO_4-fixation. The mature ascospores are smooth.

LASIOBOLUS PILOSUS—Pls. 6D–I; 7A, B

Fixatives: $KMnO_4$-OsO_4 and glutaraldehyde-OsO_4, the latter particularly for the older stages of development. The species has the habitual eight-spored asci, in multiascal apothecia. The youngest stages present show the beginning of secondary wall formation.

The primary wall is homogeneously electron-transparent and 600–1000 nm thick ($KMnO_4$-OsO_4). The secondary wall has started to form around the primary wall; its contents are homogeneous and fairly electron-transparent. The epiplasm is normal in appearance and shows the development of small vacuoles with somewhat floccose contents and of glycogen. Globular structures that are electron-dense after $KMnO_4$-OsO_4-fixation are also present and seem to be scattered over both the epiplasm and sporoplasm; their formation could not be studied.

In the next stages of development the secondary wall grows further into the epiplasm and increases in electron density. Endoplasmic reticulum clusters along the investing membrane and contact places between the epiplasm and the secondary wall material as well as complete invaginations from the epiplasm into the secondary wall arise in large quantities on the investing membrane; some of the invaginations enclose part of electron-dense globular structures (Pl. 6D, G). Simultaneously with the intensification of these phenomena the amount of glycogen in the epiplasm increases and the vacuoles fuse, the primary wall differentiates into an epispore and endospore and the secondary wall material condenses on the primary wall as granular material regardless of the fixatives (Pl. 6D–G).

The differentiation of the primary wall is regular and, in contrast to the preceding species of the Thelebolaceae, complex. The epispore is about 45 nm thick after $KMnO_4$-OsO_4-fixation and shows the usual pattern of two electron-dense layers, separated by an intermediate and fairly electron-transparent layer (Pl. 6E) that soon presents fine striation at later stages (Pl. 6F, H, I). After the same fixation the endospore is 500–1000 nm thick and starts to form an electron-transparent layer just beneath the epispore (Pl. 6D, E). At later stages of development this electron-transparent endospore layer is separated further from the inner and fairly electron-dense parts of the endospore by the formation of a thick, electron-dense layer which is sometimes coarsely striate, while on its outer side a fairly electron-dense and finely striated layer that probably results from endospore material develops (Pl. 6F–I).

As already mentioned, the contents of the secondary wall start to condense as granular material but in the latest stages of development they form a compact electron-dense layer on the epispore (Pl. 7A, B). It is not certain whether this layer persists or disappears with the remaining epiplasm as the ascospores mature. The mature ascospores are smooth; the sporoplasm is electron-dense, without any oil drops.

LASIOBOLUS MONASCUS—Pl. 7C–G

Fixative: $KMnO_4$-OsO_4. Like in *Thelebolus stercoreus* the apothecia contain one ascus and each ascus is multispored.

Only a few pictures of the advanced stages of development are available which show that secondary wall formation extends largely into the epiplasm (Pl. 7C–E), so that the remaining epiplasmic membranes are pressed together. Glycogen is found near the ascus wall. The secondary wall material is fairly electron-transparent and floccose and disappears in the final stages, as does the epiplasmic material (Pl. 7C–G).

Furthermore, the development of the epispore and endospore in the primary wall is difficult to trace. Comparing the pictures with those of *Lasiobolus pilosus*, it seems that also here a layer differentiates between the epispore and the endospore; the origin of the layer seems to be found in the outermost endospore layer (Pl. 7E, F).

An increase in electron density in the outer part of the endospore also occurs (Pl. 7F, G). The sporoplasm becomes electron-dense when the ascospores mature and it develops some small vacuoles but no oil drops. The mature ascospores are smooth (Pl. 7G).

IODOPHANUS CARNEUS—Pls. 7H, I; 8A, B

Fixative: $KMnO_4$-OsO_4. The apothecia are multiascal; each ascus had eight ascospores.

In the uninuclear asci small vacuoles with somewhat floccose contents are present in those parts of the ascoplasm that border the central ascoplasm containing the nucleus. The remaining apical and basal parts of the asci are completely filled with glycogen; only the uppermost parts of the asci still contain some normal ascoplasm. Small electron-dense globular structures are scattered over the ascoplasm around the nucleus. During meiosis and mitosis and the first stages of ascospore development the glycogen in the epiplasm increases in amount and appears partly as membrane-bounded globules of varying sizes and electron density, particularly around the ascospores. At the same time the vacuoles increase in number and size (Pl. 7H).

Later stages reveal the development of the ascospore walls. The primary wall is homogeneous and electron-transparent and 400–800 nm thick. It differentiates into an epispore and an endospore that both remain fairly simple. The epispore is 35–50 nm thick and reveals the usual pattern of two electron-dense layers separated by an electron-transparent layer; only the outer layer thickens somewhat more at later stages. The endospore is 300–900 nm thick and remains fairly electron-transparent; some slight increase in electron density becomes visible in its outer parts and at about 100–150 nm from the sporoplasmalemma a thin electron-dense layer arises (Pls. 7I; 8A).

Even before differentiation begins in the primary wall the investing membrane separates almost entirely from it. The secondary wall formed between the primary wall and the investing membrane consists of fairly electron-dense material that shows a close resemblance with the surrounding glycogen. Contact places along the investing membrane between the secondary wall and the epiplasm have been found; the investing membrane runs rather irregularly (Pl. 7I).

The secondary wall material starts to condense as a thin electron-dense layer on the primary wall (Pl. 7I). While the primary wall is differentiating the secondary wall is condensed further and transformed into an ornamentation that consists of warts (Pl. 8A, B). The warts vary in height from 150–600 nm and are spread irregularly over the ascospore surface; they are connected by a smooth layer that is about 30 nm thick (Pl. 8B). During the formation of the ascospore walls the glycogen in the epiplasm becomes more floccose and vacuoles with the same electron-dense coarse-floccose contents develop in between; they seem to be in contact with the glycogen and fill the basal parts of the asci completely.

When the ascospores mature, the epiplasm slowly disappears and the investing membrane is no longer recognizable; the remnants of the secondary wall material that have not condensed remain longest. The sporoplasm of the mature spores has increased in electron density and developed some small vacuoles.

THECOTHEUS SPEC.—Pl. 8C–G

Fixative: $KMnO_4$. As in *Lasiobolus pilosus* and *Iodophanus carneus* the apothecia are multiascal and each ascus has eight ascospores.

The young ascoplasm is regular. At the uni-nuclear stage a large vacuole with somewhat floccose contents occurs in the basal parts of the asci, while the apical parts of the asci contain large masses of glycogen. A few electron-dense globular structures are scattered over the ascoplasm. Once meiosis and mitosis have occurred and the formation of ascospore walls has started the amount of glycogen in the epiplasm increases further, particularly along the ascus wall, and vacuolization in the epiplasm begins; the vacuoles have the same flocosse contents as those in the basal parts of the asci.

The primary wall is about 500 nm thick at the two poles of the ascospores, elsewhere about 1000 nm thick. It is homogeneously electron-transparent at first but soon after its formation electron density increases in the inner parts (Pl. 8C); its differentiation products are the epispore (60–65 nm thick) and the endospore (at the two poles of the ascospores about 500 nm thick, elsewhere about 1000 nm thick). The epispore probably consists of a single fairly electron-dense layer when it has just been formed; at later stages an outer layer with an increased electron density differentiates. The endospore is fairly electron-dense and only its outermost part remains electron-transparent for any length of time; at the latest stages of development a rather diffuse electron-dense layer differentiates in the outermost part (Pl. 8D, F).

Before differentiation in the primary wall starts, the secondary wall develops; it is found all around the ascospore, particularly at the two poles. The investing membrane runs irregularly and shows connections between the secondary wall and the surrounding epiplasm. The secondary wall material is fairly electron-dense and floccose; it contains inclusions from the epiplasm (Pl. 8C).

During differentiation in the primary wall the secondary wall material increases in electron density and condenses (Pl. 8D). The condensation process starts throughout the secondary wall but soon concentrates on the epispore; in this way globular structures granular in appearance arise at regular intervals along the ascospore, giving ornamentation patterns of flat warts (about 200–300 nm high) (Pl. 8E, F). At the two poles of the ascospores the condensation process lags, leaving huge "blisters" which finally disappear when the ascospores mature but which create bowl-shaped ornamentation, also granular in appearance, at both poles (about 800–900 nm high) (Pl. 8E, G). During secondary wall development and formation of the ornamentation patterns the vacuoles in the epiplasm increase considerably in number and size and finally fuse to form one large vacuole. The glycogen also increases and fills up the remaining epiplasm.

At the oldest stages present in the material the sporoplasm has greatly increased in electron density and developed some small vacuoles; no oil drops are found. The epiplasm has disintegrated but the investing membrane is still present. Not all secondary wall material has condensed; its fate remains unknown.

PYRONEMATACEAE

PYRONEMA OMPHALODES—Pl. 9A–G

Fixatives: $KMnO_4$-OsO_4 and glutaraldehyde-OsO_4; the following description applies only to the $KMnO_4$-OsO_4-fixation.

Though the ascoplasm does not contain any unusual structures, it has a peculiar development in the uni-nuclear stage and in the first stages of meiosis and mitosis. In the basal parts of the asci large vacuoles with floccose electron-dense contents develop close to the nuclear material. In the apical parts of the asci the endoplasmic reticulum changes; its membranes cluster and increase in electron density, like in *Otidea bufonia* (Merkus, 1975), but they do not widen so far or form complete vesicles. In *Pyronema omphalodes*, the membranes become fairly vague locally, creating large and fairly electron-dense blurs in the ascoplasm. The same occurs with the mitochondrial membranes. Very probably the formation of electron-dense globular structures, present in these parts of the asci, is associated with the changes in membrane structure (Pl. 9A).

The young ascospores develop regularly; the primary wall ($KMnO_4$-OsO_4 250–400 nm thick) is homogeneous and electron-transparent at the younger stages of development (Pl. 9B). It increases in electron density at later stages, when a secondary wall is formed (Pl. 9C). Along the investing membrane a local and incidental attachment of secondary wall material to the primary wall is found while the latter is still developing. Both at the same time and in succeeding stages small vacuoles with floccose electron-dense material arise in the epiplasm; tubular and vesicular elements of the endoplasmic reticulum abound (Pl. 9B, C).

During the development of the secondary wall the primary wall increases in electron density and differentiates into an epispore ($KMnO_4$-OsO_4 35–50 nm, glutaraldehyde-OsO_4 35–40 nm thick) and an endospore ($KMnO_4$-OsO_4 250–450 but in extreme cases to 2000 nm thick, glutaraldehyde-OsO_4 150-250 nm thick); during this differentiation radial striation in the endospore is apparent. In the epispore an outer electron-dense layer becomes visible at first; further development reveals an inner electron-dense layer. While additional differentiation takes place the endospore becomes homogeneous (Pl. 9E, F). The secondary wall may vary in thickness along the ascospore surface. The secondary wall material is fairly electron-dense and seems to be in contact with the epiplasmic vacuoles that have meanwhile increased in volume and fused to surround the ascospores completely (Pl. 9E, F),

thereby also running out into the apical and basal parts of the asci. The remaining epiplasm around the vacuoles still contains some of the original organels, including the electron-dense globules, but for the most part it has been replaced by glycogen, particularly along the ascus wall.

At later stages the epiplasmic changes in the apical part of the asci are complete. Glycogen with scattered vesicular and membranous structures fill most of these parts of the asci; in the uppermost parts a great deal of endoplasmic reticulum occurs as tubules and vesicles and, close to the glycogen, forms clusters of typical membranous structures and electron-dense globular structures (Pl. 9D, probably also representing the "tractus" or "funiculus" described by Chadefaud (1960)). The basal parts of the asci are filled with glycogen.

By the latest stages of development the endospore has differentiated into an inner electron-transparent and an outer electron-dense part; in the latter a further striation, which joins that in the epispore, is visible (Pl. 9G). The secondary wall material disappears completely; only the investing membrane may remain for some time, together with the remnants of the epiplasm; the mature spores are smooth. The sporoplasm has increased in electron density and developed small vacuoles that are usually arranged in groups at the two poles of the oval ascospores together with electron-dense granules that line the tonoplast; no oil drops are found (Pl. 9G).

COPROBIA GRANULATA—Pl. 10A–E

Fixative: $KMnO_4$-OsO_4.

The young ascoplasm is normal in appearance. Like in *Pyronema omphalodes*, a large vacuole with floccose electron-dense contents is present at the uninuclear stage in the basal parts of the asci, and electron-dense globular structures are found scattered in the ascoplasm; their development however could not be studied. When meiosis and mitosis start vacuoles also develop near the apical parts of the asci, while in the uppermost parts typical membranous endoplasmic reticulum appears. Further stages reveal the development of the ascospores.

The primary wall is homogeneous and electron-transparent; it varies in thickness from 400 to 550 nm (but extreme values of 1000 nm are also found). When its internal differentiation starts, the inner part increases in electron density and at the boundary between the inner and more exterior parts a fairly electron-dense and somewhat radial striation becomes visible (Pl. 10A). In succeeding stages an endospore (250–500 nm, in extreme cases up to 1000 nm thick) and epispore (35–50 nm thick) arise. The inner endospore starts to take over the internal differentiation of the primary wall but this differentiation disappears at later stages and the endospore parts become more homogeneous. A thin layer in the outer endospore develops its own internal structure that immediately joins the striation arising in the inner electron-dense layer of the epispore. The outer electron-dense layer of the epispore is conspicuous and becomes rather broad at later stages. In the final stages the fairly electron-dense intermediate epispore layer has a fine radial striation that seems to continue into the inner epispore layer (Pl. 10B–E).

During the differentiation of the primary wall, changes in the epiplasm and the secondary wall take place. The secondary wall starts to develop at various places on the ascospore surface, and small vacuoles with floccose electron-dense contents that arise in the epiplasm along the ascospores fuse to form larger vacuoles in between. At first the secondary wall material consists of fairly electron-dense floccose material but when the secondary wall spreads all over the ascospore surface it encloses more homogeneous material, with vesicles and vacuoles that are clearly derived from the surrounding epiplasm (Pl. 10A). Later on it increases further in electron density, condenses internally and, together with the vacuolar material that has now fused to one large vacuole, grows so much that it fills nearly the whole ascus, leaving only a small strip of normal ascoplasm just inside the ascoplasmalemma. Here a few scattered electron-dense globular structures are still present. The contents of the vacuole have almost disappeared. Apart from some glycogen in the remaining epiplasm no further glycogen seems to be formed in the asci. In the meantime the sporoplasm has increased in electron density.

The internal condensation of the secondary wall material starts early. During differentiation of the primary wall a very thin layer of electron-dense material is formed in several places on the ascospore surface at a distance of about 30–50 nm from the primary wall. Once the layer encloses the whole ascospore more electron-dense material is apposed at regular intervals along the spore surface (Pl. 10A). Finally this results in a condensation pattern that includes globular structures at the two poles of the ascospores and more flattened structures along the sides of the spores, most of them with further internal striation of alternating electron-dense and fairly electron-dense layers (each about 15–20 nm thick) and all connected by an electron-dense layer about 15–20 nm thick (Pl. 10 B–E).

The latest stages present in the material still show the intact secondary wall with its internal condensation pattern. Since the mature ascospores are smooth it is however very probable that both will disappear when the ascospores have matured.

GEOPÝXIS CARBONARIA—Pl. 10F–K

Fixative: $KMnO_4$-OsO_4.

Like in *Coprobia granulata*, the young ascoplasm resembles that in *Pyronema omphalodes* in that in the uninuclear stage one large vacuole with floccose electron-dense contents develops in the basal parts of the asci, and electron-dense globular structures are found scattered in the ascoplasm. The presence of smaller vacuoles near the apical parts of the asci during meiosis and mitosis and of an increased amount of endoplasmic reticulum in the uppermost parts at this stage also agree with the pictures of *C. granulata*. Further stages of development reflect the differences between the three species.

From the very first stages of formation the primary wall (150–200 nm thick) has somewhat radial striation that persists in the endospore, where it differentiates in the primary wall material. Separation of the investing membrane from the primary wall

starts regularly over the complete ascospore surface but secondary wall formation becomes conspicuous at only a few places on the ascospore surface; the secondary wall material is fairly electron-dense and homogeneous at these stages. In the epiplasm endoplasmic reticulum occurs around the developing secondary wall but no contact points between the secondary wall material and the surrounding epiplasm have been found (Pl. 10F).

Like in *P. omphalodes*, at later stages the epiplasm is filled with glycogen and vacuoles with some floccose contents; for the most part the glycogen fills the apical and basal parts of the asci and is present in a continuous layer inside the ascoplasmalemma; the vacuolar material fuses to one large vacuole that completely surrounds the ascospores and extends in the apical and basal parts of the asci. The same stages of development reveal a maximum of secondary wall material, now floccose, along the whole ascospore surface.

The sporoplasm increases slightly in electron density at the first stages of development and develops a large amount of membranous material that clusters mostly at one of the poles of the ascospores; electron-dense globular structures are also found. At later stages some small vacuoles are formed and the increase in electron density becomes complete; no oil drops are present.

During the plasmic developments and the formation of secondary wall material the primary wall differentiates into an endospore (200–400 nm thick) and an epispore (30–45 nm thick). The endospore develops a further radial striation of fairly electron-dense material; in the outermost part it develops a homogeneous and fairly electron-dense layer in which extra striation becomes apparent in the latest stages. Further differentiation of the epispore reveals two electron-dense layers, separated by an electron-transparent layer; in the two electron-dense layers dense striation is sometimes visible in the latest stages (Pl. 10G–K).

Finally the secondary wall material partly condenses on the epispore as a homogeneous and compact, rather smooth electron-dense 50–100 nm thick layer (Pl. 10G–K). It is not certain whether this layer remains, to form the outermost part of the mature ascospores, or disappears, together with the remnants of the epiplasm and the rest of the secondary wall material; the mature ascospores are smooth.

MYCOLACHNEA HEMISPHAERICA—Pl. 11A–E

Fixative: $KMnO_4$-OsO_4. The youngest stages available show the development of the ascospores.

The already formed primary wall is homogeneous and electron-transparent and 550–850 nm thick. Secondary wall formation starts soon afterwards. The investing membrane shows an irregular course and in some places may extend widely in the epiplasm. Connections between the secondary wall and the epiplasm, and membranous inclusions in the secondary wall are found. The epiplasm itself is rather vague and has no glycogen and few peculiarly globular structures; the sporoplasm is of normal appearance and fairly electron-dense. The secondary wall material is

fairly electron-transparent and somewhat floccose. It increases in electron density and condenses near the primary wall at the same time that the differentiation of the epispore and endospore in the primary wall starts. At first the epispore is fairly electron-dense and homogeneous, while the endospore does not change during differentiation from the primary wall (Pl. 11A).

In a succeeding stage of development the amount of condensed secondary wall material on the epispore increases to a rather smooth layer, in which globular structures with increased electron density are present. The development intensifies at further stages and gives rise to spiny elements of ornamentation consisting of clustered and electron-dense, globular structures of different sizes (Pl. 11B–E). Meanwhile the development in the primary wall has continued and a typical triple epispore and a further differentiated endospore have been formed. The epispore is 30–40 nm thick and may show extra striation in its intermediate, electron-transparent layer. The outer electron-dense layer has increased in thickness. The endospore is 500–800 nm thick, finally consisting of at least four layers that show increased electron density towards the outside of the ascospores (Pl. 11B–E).

In the mature asci glycogen is formed as a continuous layer along the inner side of the ascus wall. The original epiplasm has disappeared; remnants of the investing membrane are still apparent; no vacuoles have developed. The sporoplasm is electron-dense and contains a few large oil drops.

OCTOSPORA MUSCI-MURALIS—Pl. 11F–H

Fixative: $KMnO_4$-OsO_4.

Like in *Mycolachnea hemisphaerica*, young ascospores have already developed and at this stage some resemblance between the two species can be noted. The primary wall is homogeneously electron-transparent and 200–400 nm thick. Secondary wall formation starts along the complete spore surface but may extend here and there in the epiplasm; the secondary wall material is fairly electron-transparent and homogeneous (Pl. 11F). Inclusions from the epiplasm in the secondary wall have been found. The sporoplasm is normal; apart from many small electron-transparent vacuoles it contains oil drops that soon grow and fuse to form one or (mostly) two large oil drops; an increase in electron density is found. The epiplasm could not be adequately fixed but more glycogen develops than in *Mycolachnea hemispaerica*.

Subsequently the primary wall differentiates into an epispore and an endospore. The epispore (35–50 nm thick) has the usual structure; both electron-dense layers and the intermediate less electron-dense layer are finely striate; the outer layer further increases in thickness. At first the endospore (150–350 nm thick) is homogeneous and electron-transparent, possibly with a slight increase in electron density in the middle layer. At later stages the outer parts increase in electron density and form complete extra layers that join the epispore, while the inner parts decrease in electron density (Pl. 11F–H). All secondary wall material finally disappears, as do the remnants of the epiplasm. The mature ascospores are smooth (Pl. 11H).

SARCOSCYPHACEAE

SARCOSCYPHA COCCINEA—Pl. 12A–D

Fixative: $KMnO_4$-OsO_4. S. coccinea has long asci with eight ascospores in a single row.

Young stages of development show the asci in the one-eight-nuclear stages. The ascoplasm in the apical parts of the asci is homogeneous and fairly electron-dense, with small spots of electron-transparent material, possibly glycogen, and with thin membranous structures and tiny vesicles. The subapical and medial parts of the ascoplasm contain an extensive amount of endoplasmic reticulum that closely resembles that in *Pyronema omphalodes* and *Otidae bufonia* (Merkus, 1975). The membranes of the endoplasmic reticulum may form electron-dense blurs in the ascoplasm; they may also widen locally and form extra vacuoles with electron-dense vesicles and membranous structures of varying sizes; an increase in electron density in the membranes also seems to exist (Pl. 12A).

In subsequent stages of development the ascospores are delimited and the primary and secondary walls are formed. The basal parts of the asci develop faster than the apical parts. The epiplasm in the apical parts of the asci is still intact; it contains the usual organels and small amounts of glycogen; the structures described earlier have disappeared. The apical ascospores lie close to one another and are irregular in form; they have not yet acquired their ultimate shape, though their primary walls are almost complete. The same phenomenon was also seen in *Helvella crispa*, *Rhizina undulata* and *Gyromitra esculenta*. Here in *S. coccinea* the primary wall is also of unequal thickness along the ascospores. The sporoplasm contains some glycogen and a few small oil drops. The epiplasm in the basal parts of the asci consists of diffuse glycogen with remnants of membranes. The basal ascospores are spaced out and become ellipsoid to oblong with truncate poles; their primary walls are complete. They contain one or two oil drops of moderate size, together with some glycogen. The secondary walls have extended widely along the poles of the basal ascospores.

Electron-dense globular structures are present in the upper parts of the asci but in the lower parts they are less electron-dense to electron-transparent, particularly in the later stages. Like in *Pyronema omphalodes* and in the *Otidea* species studied they probably arise on the endoplasmic reticulum.

In later stages the development is more homogeneous throughout the ascus; the following descriptions apply to these stages. The primary wall of the ascospores is homogeneous and electron-transparent; along the lateral sides of the spores it is up to 800 nm thick (Pl. 12B). It develops an epispore and an endospore. The epispore (35–40 nm thick) differentiates into two electron-dense layers with an electron-transparent intermediate layer; the outer layer increases further in thickness, while the intermediate and inner layer are slightly striate in the latest stages (Pl. 12D). At first the endospore is homogeneous and electron-transparent; at the poles of the ascospores it sometimes develops fairly electron-dense material internally; this contains fibrous structures.

Subsequently the endospore is differentiated into a fairly electron-dense outer part (350–450 nm thick) and a lighter inner part (200 nm thick). The change from the outer to the inner part is abrupt but wall material may also become condensed in the latest stages. Just in the middle of the truncated poles of the ascospores the outermost part of the electron-dense outer endospore often increases in thickness, forming a less electron-dense knob that is covered completely by the epispore. In the innermost part of the electron-dense outer endospore this knob is bounded by a newly formed "epispore". Where the knob is formed, the complete endospore may reach a thickness of 1200 nm (Pl. 12C, D).

During fixation in $KMnO_4$-OsO_4 the outer and the inner layer of the endospore easily split at the sides of the ascospores and particularly in both polar rims of each spore, so that the complete endospore measures from 700–1000 nm at the sides of the spores to extreme widths near the polar rims. Splitting is also found just inside the epispore.

Secondary wall formation starts during primary wall differentiation; the investing membrane detaches from the primary wall; secondary wall material, which is homogeneous and fairly electron-dense, is formed in the intermediate space. It is found all over the ascospore surface but in particular at the truncate poles of each ascospore, where the secondary walls of adjacent spores may finally meet and join.

In the latest stages of development all secondary wall material mixes with the epiplasm; this has also changed and now contains much glycogen and only a few organels. Remnants of the investing membrane persist for some time. The sporoplasm is normal and apart from small vacuoles contains a large number of oil drops, the larger ones in two groups at both poles of the ascospores, the smaller ones in a thick layer against the spore wall. No ornamentation is formed; the mature ascospores are smooth.

DESMAZIERELLA ACICOLA—Pl. 12E–G

Fixatives: $KMnO_4$-OsO_4 and glutaraldehyde-OsO_4. Only a few apothecia could be sectioned.

Asci are found that show the same differences between the apical and basal parts during ascospore development as in *Sarcoscypha coccinea*, though not to the same extent. The apical parts of the asci have an intact epiplasm; the primary walls of the ascospores, which are in a single row close to one another and do not yet have their ultimate shape, are still developing. The basal parts of the asci have an epiplasm consisting almost entirely of diffuse glycogen; the secondary walls of the oval ascospores, which are spaced out, are also still developing. Globular structures and glycogen are present throughout the asci, both in the epiplasm and sporoplasm. The globular structures occur particularly around the ascospores in the epiplasm; they are electron-dense to electron-transparent after $KMnO_4$-OsO_4-fixation, electron-transparent only after glutaraldehyde-OsO_4-fixation. Like in *S. coccinea* later stages of development show a more homogeneous pattern in the apical and basal parts of the asci.

The primary wall of the ascospores is homogeneous and electron-transparent; after $KMnO_4$-OsO_4-fixation 400–600 nm thick along the whole circumference of a spore (Pl. 12E). It develops into an epispore ($KMnO_4$-OsO_4 35–40 nm, glutaraldehyde-OsO_4 40 nm thick) and an endospore ($KMnO_4$-OsO_4 700–1000 nm, glutaraldehyde-OsO_4 about 600 nm thick) that closely resemble that in *S. coccinea*. After $KMnO_4$-OsO_4-fixation the epispore shows the same differentiation into two electron-dense layers separated by an intermediate electron-transparent layer, with the outer layer still increasing slightly in thickness. After glutaraldehyde-OsO_4-fixation (which was not applied to *S. coccinea*) the epispore consists of an electron-dense inner layer and a fairly electron-transparent outer layer in which denser striation can be discovered. At first the endospore is homogeneous and electron-transparent in both types of fixatives but it soon differentiates. After $KMnO_4$-OsO_4-fixation the same electron-dense outer part as in *S. coccinea* and the same electron-transparent inner part become apparent. After glutaraldehyde-OsO_4-fixation the endospore is delimited by a fairly electron-dense layer against the plasmalemma, from where radial striation runs to the outer surface of the ascospores (Pl. 12F, G).

The secondary wall material is deposited between the primary wall and the investing membrane (Pl. 12E). After $KMnO_4$-OsO_4-fixation it is homogeneous and fairly electron-transparent and, at later stages of development, slightly concentrated as electron-dense material on the epispore. After glutaraldehyde-OsO_4-fixation (which was applied to later stages of development only) it becomes fibrous-floccose throughout the secondary wall. It is not possible to say whether the secondary wall develops around the entire ascospore wall or only at the two poles of the ascospores as in S. coccinea; its fate is also unknown (Pl. 12F, G).

In the later stages of development the epiplasm loses its organels. The globular structures remain longest and are clustered along the borders of the secondary wall; finally they also disappear. The sporoplasm then contains small vacuoles and many smaller and larger oil drops. The mature ascospores are smooth.

DISCUSSION

From the assembled results of this study and a comparison of them with those of previous studies (Merkus, 1973, 1974, 1975) it may be concluded that throughout the Pezizales the ultrastructure and development of the ascospores show considerable agreement.

The general ascal ultrastructure is the same for all species and corresponds with the usual descriptions such as those in the summaries of Hawker (1965) and Bracker (1967). I have already discussed the basic plasmic organels in detail (Merkus, 1973) but unusual individual structures need further comment.

The occurrence of globular structures (indicated as GS on the Plates) was reported in a great many species belonging to the genera *Otidea* and *Peziza* as well as in the single species *Pulparia persoonii* (Merkus, 1975). They have been found in all the

species discussed in the present study and judging by earlier results they may also occur in other species. Being less relevant they have not been mentioned elsewhere (Merkus, 1973, 1974). Their appearance depends on the species and on the fixative applied, differing particularly after $KMnO_4$-OsO_4 and glutaraldehyde-$KMnO_4$. Intermediate forms are not frequently found; they could depend on the stage of development.

As stressed earlier (Merkus, 1975), the origin of the globular structures is not clear. Evidence that the electron-dense globular structures found after the $KMnO_4$-OsO_4-fixative are derived directly from endoplasmic reticulum has been discovered in *Otidea bufonia*, *Pyronema omphalodes*, and *Sarcoscypha coccinea*, which may represent simpler forms of ascoplasmic development. The presence of additional, more electron-transparent globular structures in *Sarcoscypha coccinea*, and particularly the more complicated ascoplasm in *Gyromitra esculenta*, *G. infula*, *Helvella crispa*, *Morchella esculenta*, *Peziza ammophila*, *P. badia*, *P. michelii*, *P. plebeia*, *P. praetervisa*, *P. succosa*, *P. succosella*, *P. vesiculosa*, and *Rhizina undulata*, with the occurrence of either electron-dense or less electron-dense to electron-transparent products after use of the $KMnO_4$-OsO_4 and glutaraldehyde-$KMnO_4$-fixatives, however, suggests that the development of the globular structures is more complicated and that other organels, like endoplasmic vesicles and membranous structures, or glycogen (indicated on the Plates as EV, MS, and G or Gr, respectively) could be involved.

All the globular structures are formed in an early stage of development, before or during meiosis and mitosis, particularly in the more apical parts of the asci; in the genera *Peziza* and *Pulparia* formation in the more basal parts of the asci is also extensive. When the ascospores are delimited in the ascoplasm, the globular structures seem to spread at random over the epiplasm and sporoplasm; formation in the epiplasm could continue for some time, so that here their number possibly increases. The role of the globular structures has been discussed (Merkus, 1975). The electron-dense globular structures are the same as the "corpuscules métachromatiques" of Guilliermond (1904, 1910, 1920) or "globules métachromatiques" of Le Gal (1947).

In some species with a more complex ascoplasm, viz. *Gyromitra esculenta*, *G. infula*, *Helvella crispa*, *Morchella esculenta*, *Peziza badia*, *P. michelii*, *P. plebeia*, *P. succosa*, *P. succosella*, and *Rhizina undulata*, the globular structures grow out to true oil bodies that persist for some time in the epiplasm during ascospore development and that are permanently present in the sporoplasm, where they fuse to form larger oil drops. The ascoplasm of *Peziza trachycarpa* could not be studied adequately but apparently its further development proceeds in the same way. In *Desmazierella acicola* and *Gyromitra esculenta*, where the ascoplasm is less complex, this is also found. When present in the other species, the globular structures do not enlarge further but maintain their original form; they shrivel and disappear in the epiplasm but remain in the sporoplasm.

Independent development also causes oil drops to arise in the sporoplasm of a large number of the species, viz. *Aleuria aurantia*, *Anthracobia melaloma*, *Boudiera echinulata*, *Octospora musci-muralis*, *Lamprospora crec'hqueraultii*, *L. dictydiola*, *Melastiza*

chateri, *Mycolachnea hemisphaerica*, *Neotiella ithacaensis (Rehm) Schweers sensu Schweers*[9], *Otidea alutacea*, *O. bufonia*, *O. onotica*, *Peziza ammophila*, *P. badiofusca*, *P. emileia*, *P. petersii*, *P. praetervisa*, *P. trachycarpa*, *Pulparia persoonii*, *Pustularia cupularis*, *Scutellinia armatospora*, *S. scutellata*, *Sepultaria arenosa*, *S. tenuis*, *Trichophaea abundans*, and *T. woolhopeia*. Oil drops in the sporoplasm have not been found in *Ascodesmis microscopica*, *A. nigricans*, "*Ascophanus*" *coemansii*, *Ascozonus woolhopensis*, *Cheilymenia pulcherrima*, *Coprobia granulata*, *Iodophanus carneus*, *Geopyxis carbonaria*, *Lasiobolus monascus*, *L. pilosus*, *Peziza vesiculosa*, *Pyronema omphalodes*, *Sowerbyella radiculata*, *Thecotheus spec.*, *Thelebolus crustaceus*, and *T. stercoreus*.

Special plasmic structures other than those discussed above have been found in "*Ascophanus*" *coemansii*, *Ascozonus woolhopensis*, and *Thelebolus stercoreus*. The function of these structures could not be determined; those in "*Ascophanus*" *coemansii* are probably identical with the reticulate structures Boudier (1869) described for this species, and, together with those in *Ascozonus woolhopensis*, could result from endoplasmic reticulum.

For *Ascobolus furfuraceus* Pers. per Hook.[10] Wells (1972) mentioned the occurrence of numerous lipid globules on the surface of the perispore sac (=secondary wall) and in the sporoplasm during the latter stages of ascospore development; at maturity these disappear from the margin of the perispore sac. They may be identical with the electron-transparent globular structures of other species.

Glycogen is formed in a large number of the species. Its varying appearance and its role as a supplier of food were discussed earlier (Merkus, 1975); it will be mentioned later in relation to the development of secondary wall material.

Ascospore development follows a common line in the Pezizales (Delay, 1966; Carroll, 1966, 1967, 1969; Schrantz, 1966, 1970; Wells, 1972; Merkus, 1973, 1974, 1975); details of this line have been discussed (Merkus, 1973, 1974, 1975). The main points are the following.

All the ascospores in a single ascus are formed simultaneously through delimitation by an outer and inner delimiting unit membrane; in nearly all species they also develop simultaneously in later stages of wall formation. By contrast the ascospores of *Sarcoscypha coccinea* and *Desmazierella acicola* develop more rapidly in the basal parts of the asci than in the apical parts, as does the remaining epiplasm in these species.

Though interesting, the origin of the two delimiting membranes is not under discussion here. When the ascospore walls arise between them, the inner membrane becomes the sporoplasmalemma, which is permanent and may have a function in primary wall development. The outer membrane becomes the investing membrane, which may play a role in both primary and secondary wall formation; by the time the ascospores are mature it may have disappeared or else remain as an adhesive film on the outside of the ascospores when they leave the ascus.

The primary wall is formed first; it is homogeneous and electron-transparent.

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[9] Khare (1975), who studied the type of *Humaria ithacaensis* Rehm, found that the name was missapplied by Schweers. For Schweers' fungus a correct name is not yet available.

[10] *Ascobolus stercorarius* (Bull. per St. Amans) Schroet.

In most of the species the ascospores are rounded off before the primary wall is formed but in *Desmazierella acicola*, *Gyromitra esculenta*, *G. infula*, *Helvella crispa*, *Rhizina undulata*, and *Sarcoscypha coccinea* the ascospores round off during primary wall development. The thickness of the primary wall not only varies according to the species; it also depends on the treatment, the fixatives with glutaraldehyde giving either no swelling or at least less swelling than the fixatives with $KMnO_4$, which might produce abnormal results. Conclusions based on thickness are therefore unreliable. In *Helvella crispa* the primary wall grows out internally and forms thickenings; these were also observed by Le Gal (1947).

The secondary wall is formed next. In a few rare instances secondary wall formation was found to start on a limited scale before primary wall formation was finished. In general however secondary wall formation is found as a separate process that starts when the primary wall is complete. The secondary wall is layed down between the primary wall and the investing membrane. The formation may start immediately all over the ascospore surface, or at first more locally, either remaining so or only at later stages spreading out. In *Ascodesmis microscopica* and *A. nigricans* the secondary wall is internally differentiated; in all other species the $KMnO_4$-OsO_4-fixative gives the secondary wall material a fairly homogeneous aspect, while the glutaraldehyde-OsO_4-fixative makes it look more flocky; it is always more electron-dense than the primary wall material. To judge from their structural similarities it is highly probable that parts of the epiplasm are incorporated in the secondary wall and make up its ground substance; glycogen or derivations of it are possibly involved; the investing membrane may play an active role in the process. Though the presence of an investing membrane is not mentioned by Bellemere & Melendez-Howell (1976), these authors stress the active role of the epiplasm during the formation of the material of ornamentation. It is most unlikely that the sporoplasm has a function in secondary wall formation as was supposed by Le Gal (1947), Moore (1963, 1965), Reeves (1967), and Lynn & Magee (1970). The apposition of extra wall material on the inner side of the primary wall is very unusual and found only in *Trichophaea woolhopeia*. Secondary wall formation remains rather limited in "*Ascophanus*" *coemansii*, *Ascozonus woolhopensis*, *Thelebolus crustaceus*, and *T. stercoreus*.

All the species have a secondary wall outside the primary wall and its fate determines the ultimate aspect of the ascospores. Different groups of development can be distinguished (see also Fig. 1).

1. Without further changes all secondary wall material loses its original structure and disappears in: *Ascozonus woolhopensis*, *Helvella crispa*, *Octospora musci-muralis*, *Lasiobolus monascus*, *Morchella esculenta*, *Pyronema omphalodes*, *Sarcoscypha coccinea*, and *Trichophaea woolhopeia*.

2. Secondary wall material condenses at random for a short time and finally all of it disappears in: *Anthracobia melaloma*, *Pustularia cupularis*, *Sepultaria arenosa*, and *S. tenuis*.

3. Secondary wall material condenses to form a complete ornamentation pattern on the epispore but finally all of it disappears in: *Coprobia granulata.*

4. Secondary wall material condenses to form a permanent smooth and uniform layer on the epispore in: "*Ascophanus*" *coemansii*, *Geopyxis carbonaria*, *Lasiobolus pilosis*, *Otidea alutacea*, *O. bufonia*, *O. onotica*, *Peziza ammophila*, *P. vesiculosa*, *Thelebolus crustaceus*, and *T. stercoreus*.

5. Secondary wall material condenses to form a permanent ornamentation on the epispore in: *Aleuria aurantia*, *Boudiera echinulata*, *Cheilymenia pulcherrima*, *Iodophanus carneus*, *Lamprospora crec'hqueraulti*, *L. dictydiola*, *Melastiza chateri*, *Mycolachnea hemisphaerica*, "*Neotiella ithacaensis*", *Peziza badia*, *P. badiofusca*, *P. emileia*, *P. michelii*, *P. petersii*, *P. plebeia*, *P. praetervisa*, *P. succosa*, *P. succosella*, *P. trachycarpa*, *Pulparia persoonii*, *Rhizina undulata*, *Scutellinia armatospora*, *S. scutellata*, *Sowerbyella radiculata*, *Thecotheus* spec., and *Trichophaea abundans*.

6. Secondary wall material is penetrated by pigment granules (Wells, 1972, for *Ascobolus furfuraceus* or a violet pigment (Carroll, 1969, for *Saccobolus glaber* (Pers. per Pers.) Lamb.[11]) from the surrounding vacuoles, which finally condense on the epispore and possibly from the ultimate ornamentation in: *Ascobolus furfuraceus* and *Saccobolus glaber*.

7. Secondary wall material immediately constitutes the ornamentation patterns in: *Ascodesmis microscopica* and *A. nigricans*.

Because the series of pictures is incomplete not all species can be placed definitively in any of these groups. *Desmazierella aciocla*, *Gyromitra esculenta*, and *G. infula* belong to group 2 or 4; the position of *Otidea alutacea*, *O. bufonia*, *O. onotica*, and *Lasiobolus pilosus* in group 4 is also uncertain, the species might be transferred to group 2.

Internal differentiation of the ornamentation is found in *Ascodesmis microscopica*, *A. nigricans*, and *Lamprospora crec'hqueraultii*, and possibly also in *Sowerbyella radiculata*. Slight striation of the innermost parts of the ornamentation is found in "*Neotiella ithacaensis*". The different structures in the ornamentation of most of the *Peziza* species and of *Pulparia persoonii* is difficult to interpret and may be present only temporarily.

The formation of the epispore and the endospore is a special problem and opinions about it differ (Merkus, 1973, 1974). Though it is not recognizable in all species, it is most likely that the primary wall differentiates into an outer epispore and an inner endospore through the redistribution of primary wall material (in this my conclusion agrees with that of Delay, 1966). The redistribution of endospore material in *Sarcoscypha coccinea*, which leads to the formation of a "second epispore' inside the

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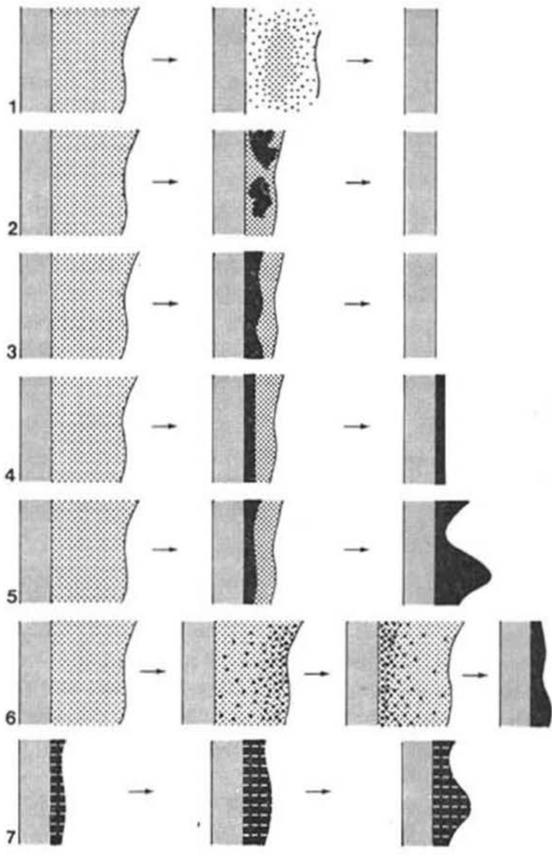
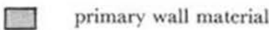
[11] *Saccobolus kervernii* (Crouan) Boud.





primary wall material

secondary wall material (undifferentiated)

secondary wall material (condensed)

secondary wall material immediately constituting the ornamentation

material precipitated from the surrounding epiplasm

Fig. 1. Diagrammatic schemes of different groups of secondary wall development. The numbers refer to the different units.

endospore, strongly supports this view. After $KMnO_4$-OsO_4-fixation the epispore in most species shows a basic patern that consists of two electron-dense layers, separated by a less electron-dense to electron-transparent intermediate layer. In a few species the epispore is simpler and seems to consist of only one electron-dense layer ("*Ascophanus*" *coemansii*, *Ascozonus woolhopensis*, *Thelebolus crustaceus*, and *T. stercoreus*), sometimes with an increase in electron density in the outer parts (*Thecotheus* spec.). Glutaraldehyde-OsO_4 may give different appearances, often with layers on the outside that are less electron-dense. Further differentiation in the epispore and endospore leading to the formation of fine or coarse striation has been found in many species. Most of the striation is fine and found in the epispore, parallel to the ascospore surface. In a number of species it is also present in the outer parts of the endospore; in that case it largely inhibits delimitation of both layers; for this there are various explanations. A general increase in electron density and coarse striation in the endospore, perpendicular to the ascospore surface, is sometimes found, particularly after glutaraldehyde-OsO_4-fixation.

Referring to the ultrastructure and the development of ascospores different types can be distinguished. The distinction is based mainly on the data resulting from $KMnO_4$-OsO_4-fixation, as only part of the species were also fixed in the glutaraldehyde-OsO_4-fixative. The *Ascobolus furfuraceus* type is based on data published by Delay (1966), Carroll (1966, 1967, 1969) and Wells (1972). De Bary "bubbles", which were described in ascospores by Dodge (1957), Kimbrough (1966), and Kimbrough & Korf (1967) could not be found after fixation.

The following types can be distinguished.—

I. *Sarcoscypha coccinea* type.

Basal parts of asci in a state of development during ascospore formation more advanced than in apical parts; ascospores acquire their ultimate shape during primary wall development; tendency to complex ascoplasm with electron-dense and electron-transparent globules, and intermediate forms; oil drops in sporoplasm derived from the electron-transparent globules; epispore without much further differentiation; endospore with marked differentiation into an electron-dense outer part that passes abruptly into an electron-transparent inner part; formation of a "second epispore" in the endospore at the apices of ascospores (not found in *Desmazierella acicola*); for secondary wall material groups 1 and 2 or 4.

Desmazierella acicola and *Sarcoscypha coccinea*.

II. *Morchella esculenta* type.

Complex ascoplasm with electron-transparent and electron-dense globules, and intermediate forms; oil drops in sporoplasm derived from the electron-transparent globules; epispore and endospore without much further differentiation; for secondary wall material group 1.

Morchella esculenta.

III. *Helvella crispa* type.
Ascospores acquire their ultimate shape during primary wall development; complex ascoplasm with electron-transparent and more electron dense globules, oil drops in sporoplasm derived from the electron-transparent globules; occasional formation of extra wall layers in primary wall; epispore and endospore without much further differentiation; for secondary wall material group 1.
Helvella crispa.

IV. *Rhizina undulata* type.
Ascospores acquire their ultimate shape during primary wall development; complex ascoplasm with electron-transparent and more electron-dense globules; oil drops in sporoplasm derived from the electron-transparent globules; epispore without much further differentiation; endospore with (slight) increases in electron density in the outermost parts; for secondary wall material groups 2 or 4 and 5.
Gyromitra esculenta, G. infula, and *Rhizina undulata.*

V. *Otidea bufonia* type.
Tendency to complex ascoplasm with electron-dense globules; independent development of oil drops in sporoplasm; further differentiation in epispore and endospore; for secondary wall material possibly group 4.
Otidea alutacea, O. bufonia, and *O. onotica.*

VI. *Peziza vesiculosa* type.
Complex ascoplasm with electron-dense and more electron-transparent globules; no oil drops in sporoplasm; epispore without much further differentiation; endospore with some fine striation in the outermost parts; for secondary wall material group 4.
Peziza vesiculosa.

VII. *Peziza praetervisa* type.
Complex ascoplasm with electron-dense globules; independent development of oil drops in sporoplasm; epispore without much further differentiation; endospore with some fine striation in the outermost parts; for secondary wall material groups 4 and 5.
Pezia ammophila and *P. praetervisa.*

VIII. *Peziza succosa* type.
Complex ascoplasm with electron-transparent globules, *Peziza trachycarpa* also with more electron-dense globules; oil drops in sporoplasm derived from the electron-transparent globules; epispore and endospore without much further differentiation; for secondary wall material group 5.
Peziza badia, P. michelii, P. plebeia, P. succosa, and *P. succosella; P. trachycarpa* possibly also belongs to this group but the ascoplasm could not be adequately studied.

IX. *Pyronema omphalodes* type.
Tendency to complex ascoplasm with electron-dense globules; generally much glycogen in the epiplasm; no oil drops in sporoplasm, epispore occasionally with

fine striation; endospore with a fairly broad electron-dense layer in the outermost parts; for secondary wall material group 1.

Pyronema omphalodes.

X. *Lamprospora dictydiola* type.

Normal ascoplasm with electron-dense globules; with or without independent development of oil drops in sporoplasm; generally much glycogen in the epiplasm, epispore occasionally with fine striation; endospore with a thin to broader electron-dense layer in the outermost parts; for secondary wall material groups 1, 3, 4 and 5.

Aleuria aurantia, Boudiera echinulata, Cheilymenia pulcherrima, Coprobia granulata, Geopyxis carbonaria, Octospora musci-muralis, Iodophanus carneus, Lamprospora crec'hqueraultii, and *L. dictydiola.*

XI. *Scutellinia armatospora* type.

Normal ascoplasm with a few or more numerous electron-dense globules; independent development of oil drops in sporoplasm; epispore with further differentiation; endospore with striation in the outermost parts; for secondary wall material groups 2 and 5.

Anthracobia melaloma, Melastiza chateri, "Neotiella ithacaensis", Scutellinia armatospora, and *S. scutellata.*

XII. *Sepultaria arenosa* type.

Normal ascoplasm with a few electron-dense globules; independent development of oil drops in sproroplasm; epispore with fine striation; endospore with an outer electron-dense and an inner electron-transparent part, also with clustered material in between; for secondary wall material groups 1, 2, and 5.

Mycolachnea hemisphaerica, Pustularia cupularis, Sepultaria arenosa, S. tenuis, Trichophaea abundans, and *T. woolhopeia.*

XIII. *Lasiobolus pilosus* type.

Normal ascoplasm with electron-dense globules; no oil drops in sporoplasm; epispore with further differentiation; endospore without much further differentiation; for secondary wall material groups 1 and, possibly 4.

Lasiobolus monascus and *L. pilosus.*

XIV. *Thecotheus* spec. type.

Normal ascoplasm with a few electron-dense globules; no oil drops in sporoplasm; simple epispore; endospore with slight increases in electron density in the outermost parts; for secondary wall material group 5.

Thecotheus spec.

XV. *Thelebolus stercoreus* type.

Normal ascoplasm with a few electron-dense globules; no oil drops in sporoplasm; simple epispore; endospore mostly with some fine striation in the outermost parts; for secondary wall material group 4; secondary wall formation strongly limited.

"Ascophanus" coemansii, Thelebolus crustaceus, and *T. stercoreus.*

Table I

Characteristics of the different types

type	ascoplasm	globules	oil drops	epispore	endospore	group of sec. wall formation
I[12] [13]	→ complex	ed., et., int.	← et. glob.	not. diff.	diff. in ed. outer and et. inner part	1, 2 or 4
II	complex	ed., et., int.	← et. glob.	not diff.	not diff.	1
III[13]	complex	ed., et.	← et. glob.	not diff.	not. diff.	1
IV[13]	complex	ed., et.	← et. glob.	not diff.	ed. in outermost parts	2 or 4, 5
V	→ complex	ed.	indep. dev.	diff.	diff.	?4
VI	complex	ed., et.	not present	not diff.	some striation in outermost parts	4
VII	complex	ed.	indep. dev.	not diff.	some striation in outermost parts	4, 5
VIII	complex	et. (+ed.)	← et. glob.	not diff.	not diff.	5
IX	→ complex	ed.	not present	diff. including fine striation	broad ed. layer in outermost parts	1
X	normal	ed.	not present or indep. dev.	diff. including fine striation	thin-broader ed. layer in outermost parts	1, 3, 4, 5

XI	normal	ed.	indep. dev.	diff.	striation in outermost parts	2, 5
XII	normal	ed.	indep. dev.	diff. including fine striation	diff. in ed. and et. inner part	1, 2, 5
XIII	normal	ed.	not present	diff.	not diff.	1, ?4
XIV	normal	ed.	not present	simple	ed. in outermost parts	5
XV	normal	ed.	not present	simple	some striation in outermost parts	4
XVI	normal	ed.	not present	simple	not diff.	1
XVII	normal	lipoid glob.	not present	diff. including fine striation	not diff.	6
XVIII	normal	ed.	not present	diff.	not diff.	7

Abbreviations: diff., differentiation; ed., electron-dense; et., electron-transparent; glob., globules; indep. dev., independent development; int., intermediate; →, tendency to; ←, derived from.

[12] Basal parts of asci in a state of development during ascopore formation more advanced than in apical parts; "second epispore" in endospore.

[13] Ascospores acquire their ultimate shape during primary wall development.

XVI. *Ascozonus woolhopensis* type.
Normal ascoplasm with a few electron-dense globules; no oil drops in sporoplasm; simple epispore; endospore without further differentiation; for secondary wall material group 1; secondary wall formation rather limited.
Ascozonus woolhopensis.

XVII. *Ascobolus furfuraceus* type.
Normal ascoplasm, in *Ascobolus furfuraceus* with lipid globules; no oil drops in sporoplasm; epispore with fine striation; endospore without further differentiation; for secondary wall material group 6.
Ascobolus immersus Pers. per Pers., *A. furfuraceus*, and *Saccobolus glaber*.

XVIII. *Ascodesmis microscopica* type.
Normal ascoplasm with a few electron-dense globules; no oil drops in sporoplasm; epispore with further differentiation; endospore without further differentiation; for secondary material group 7.
Ascodesmis microscopica and *A. nigricans*.

The different types, based only on the findings of this study, call for further remarks. The eighteen types can be grouped into six units (see Tables I and II). Though the characteristics of each unit can overlap and some are present in more than two of them, each unit clearly represents related types. While in the first two units the complex ascoplasm, or at least a tendency to one, is found, the other four units have normal ascoplasm, while the tendency to a complex ascoplasm is found in only one type (IX).

TABLE II

DISTRIBUTION OF TYPES OVER THE UNITS

first unit	second unit	third unit	fourth unit	fifth unit	sixth unit
type I–IV	type V–VIII	type IX–XIII	type XIV–XVI	type XVII	type XVIII

In the first unit the characteristic development of the asci in type I distinguishes this type from all the others; the differentiation of a "second epispore" in the endospore, which has not been found in the other species, supports this view. Type III and type IV come close to type I, as all three have in common that the ascospores have

their ultimate shape only during primary wall development; this pleads for great plasticity of the primary wall material at these stages. Regarding the other characteristics, type II is the most closely united with the three types in the first unit. In the second unit types VI and VII closely resemble each other, while type VIII comes closer to the types of the first unit. Apart from the normal ascoplasm in most of the species the third unit represents species which have in particular more differentiation in both epispore and endospore. Types IX–XII closely resemble each other and their distinction is based on the different types of endospores: type XIII lacks differentiation in the endospore and is possibly related to the fourth unit. The types of the fourth unit are similarly in having a simple epispore but otherwise also closely agree. The types of the fifth and sixth unit have been kept apart because of the characteristic development of the secondary walls, which differ completely from those of the other types.

As regards the distribution of the different species over the types, *Pustularia cupularis* is placed within the *Sepultaria arenosa* type, which represents species of the Pyronemataceae sensu Eckblad; though some characteristics agree, a closer resemblance to species of *Otidea* (a. o. mentioned by Le Gal, 1947; Dennis, 1968; Eckblad, 1968) was not revealed. Berthet (1964) also mentioned the relationship between the genera *Pustularia* and *Sepultaria*; his view is based on cytochemical reactions of the nuclei. *Iodophanus carneus* and *Boudiera echinulata*, both with amyloid ascus walls, are placed within the *Lamprospora dictydiola* type, which further contains species of the Pyronemataceae. The relationship between *Iodophanus carneus* and other members of the Pyronemataceae was given earlier by Eckblad (1968) but the relationship between *Boudiera echinulata* and species of *Ascodesmis* that he mentioned (Ascodesmidoideae; Eckblad, 1968) could not be confirmed. *Thecotheus* spec., which also has amyloid ascus walls and which was placed in the Thelebolaceae by Eckblad (1968) is a separate type that nonetheless closely resembles the types representing other Thelebolaceae. *Sowerbyella radiculata* and *Pulparia persoonii* have not been classified in the types because they are not well enough known.

In *Ascodesmis microscopica* and *A. nigricans* the term secondary wall is appropriate for the second wall as it forms a permanent and rigid ornamentation on the epispore. In all other species the term might be open to question since the second wall is a temporary and transient formation that constitutes the materials for permanent extra wall layers, smooth or forming an ornamentation and arising outside on the epispore. But despite their differences in appearances and the fate of the material of the second wall in the species, in all cases it is desirable to use the term secondary wall together with the term primary wall since the walls represent stages in development and are more natural than the complex terminology of the wall layers in Le Gal's work, not to mention the confusing use of names like endospore, epispore, and perispore by others. By using the terms primary and secondary wall for the two wall layers that are formed in succession the term endospore and epispore are reserved for the further internal differentiation products of the primary wall.

Finally it is worth while to compare Le Gal's observations (1947, 1949) and ours.

The "false ornamentation" that she describes for *Helvella crispa* probably represents the formation of extra wall material in the primary wall, which is found in this species. But about the development of ornamentation our views probably do not agree. As pointed out earlier (Merkus, 1974), no evidence has been obtained for a "complex" development of ornamentation involving "masses globuleuses". Nor can it be decided precisely what structure corresponds to the "assise sous-périsporique" or to the "périspore". In view of Le Gal's drawings it is most probable that where she found no "périspore" the secondary wall corresponds to the "assise sous-périsporique", and that where she describes a "périspore" the secondary wall corresponds to it. In the first case the investing membrane corresponds to the "pellicule membranaire", which never arises simultaneously with the ornamentation, as a "coque interpérisporique" but which is always present before ornamentation, as a "tunique externe". In the latter case the "assise sous-périsporique" must be seen either as the outermost part of the primary wall, which is also supposed by Bellemere & Melendez-Howell (1976), or as the innermost part of the secondary wall; a layer that might represent the investing membrane is then absent. Cytochemistry of the substance of ornamentation constituting the secondary wall was not carried out but might reveal more about the exact nature of the secondary wall material; Le Gal's premise that the ornamentation is mostly formed of callose and pectine could therefore not be confirmed. As stressed earlier, there is no evidence for sporal origin of the secondary wall material, as was supposed by Le Gal; in fact, all pictures produce evidence in support of the theory that it is epiplasmic in origin.

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Explanation of Plates 1–12

Abbreviations used in Plates. — AW. ascus wall; CM, condensed material; E, epiplasm; En, endospore; Ep, epispore; EV, endoplasmic vesicle; G, glycogen; GS, globular structure; IAM, inner ascospore-delimiting membrane; IM, investing membrane; MS, membranous structure; OAM, outer ascospore-delimiting membrane; N, nucleus; PI, plasmic inclusions; PW, primary wall; S, sporoplasm; SW, secondary wall; T, tonoplast; Va, vacuole.

Plate 1

Figs. A–D. *Morchella esculenta*, stained with uranyl acetate and lead citrate: Fig. A. ascoplasm during meiosis, fixed in 1% glutaraldehyde and 1% $KMnO_4$, ×4,600; Fig. B. id. detail of basal part of ascus, ×14,900; Fig. C. ascospore development, beginning of secondary wall formation, fixed in 1% $KMnO_4$ and 1% OsO_4, ×18,200; Fig. D. id. secondary wall formation and development of epispore and endospore.

Plate 2

Figs. A, B. *Morchella esculenta*, advanced states in ascospore development, fixed in 1.5% $KMnO_4$ and 1% OsO_4 and stained with uranyl acetate and lead citrate, ×18,200.

Figs. C–F. *Helvella crispa*: Fig. C. ascoplasm, upper part of ascus before meiosis and mitosis, fixed in 1.5% $KMnO_4$ and 1% OsO_4 and stained with lead citrate, ×4,600; Fig. D. ascospore development, beginning of secondary wall formation, fixed in 1.5% $KMnO_4$ and 1% OsO_4 and stained with uranyl acetate and lead citrate, ×23,100; Fig. E. id. detail of primary wall, ×36,300; Fig. F. id. fixed in 3.25% glutaraldehyde and 1% OsO_4.

Plate 3

Figs. A, B. *Helvella crispa*, ascospore development, fixed in 1.5% $KMnO_4$ and 1% OsO_4, ×23,100: Fig. A. secondary wall formation and development of epispore and endospore, stained with uranyl acetate and lead citrate; Fig. B. advanced state in ascospore development, stained with lead citrate.

Figs. C–G. *Rhizina undulata*, ascospore development, fixed in 1.5% $KMnO_4$ and 1% OsO_4: Fig. C. secondary wall formation and development of epispore and endospore, condensation of secondary wall material, stained with uranyl acetate and lead citrate, ×29,700; Fig. D. id.; Fig. E. advanced state in development of ornamentation at one of two poles of ascospore, stained with uranyl acetate and leád citrate, ×14,900; Fig. F. id. along ascospore, ×43,300; Fig. G. id. stained with lead citrate.

Plate 4

Fig. A. *Gyromitra esculenta*, ascospore development, secondary wall formation and development of epispore and endospore, fixed in 1.5% $KMnO_4$ and 1% OsO_4 and stained with uranyl acetate and lead citrate, ×29,700.

Figs. B, D. *Gyromitra infula*, ascospore development, fixed in 1.5% $KMnO_4$ and 1% OsO_4 and stained with uranyl acetate and lead citrate: Fig. B. young ascospore after formation of primary wall, ×23,100; Fig. C. secondary wall formation and development of epispore and endospore, condensation of secondary wall material, ×29,700; Fig. D. id. advanced state in ascospore development.

Figs. E, F. *Thelebolus stercoreus*, ascospore development, ×29,700: Fig. E. beginning of secondary wall formation, fixed in 1.5% $KMnO_4$ and 1% OsO_4 and stained with lead citrate; Fig. F. secondary wall formation and epiplasm with particular structures, fixed in 1.5% glutaraldehyde and 1% OsO_4 and stained with uranyl acetate and lead citrate.

PLATE 9

Figs. A–G. *Pyronema omphalodes*, fixed in 1.5% $KMnO_4$ and 1% OsO_4 and stained with uranyl acetate and lead citrate: Fig. A. ascoplasm, upper part of ascus before meiosis and mitosis, ×8,100; Fig. B. ascospore development, beginning of secondary wall formation, ×29,700; Fig. C. id. more advanced secondary wall formation, ×23,100; Fig. D. epiplasm, upper part of ascus during ascospore development, ×8,100; Fig. E. ascospore development, development of epispore and endospore, ×23,100; Fig. F. id ×29,700; Fig. G. advanced state in ascospore development; ×29,700.

PLATE 10

Figs. A–E. *Coprobia granulata*, ascospore development, stained with uranyl acetate and lead citrate: Fig. A. secondary wall formation and condensation of secondary wall material, fixed; in 1.5% $KMnO_4$, ×29,700; Fig. B. id. with development of epispore and endospore, ×46,200; Fig. C. id. fixed in 1.5% $KMnO_4$ and 1% OsO_4; Fig. D, E. advanced states in ascospore development, fixed in 1.5% $KMnO_4$, ×46,200.

Figs. F–K. *Geopyxis carbonaria*, ascospore development: Fig. F. beginning of secondary wall formation, fixed in 1% $KMnO_4$ and 1% OsO_4 and stained with uranyl acetate and lead citrate, ×23,100; Fig. G. development of epispore and endospore and condensation of secondary wall material, fixed in 1.5% $KMnO_4$ and 1% OsO_4 and stained with uranyl acetate and lead citrate, ×36,300; Fig. H. id. fixed in 1% $KMnO_4$ and 1% OsO_4; Fig. I. id. fixed in 1.5% $KMnO_4$ and 1% OsO_4; Fig. K. id. advanced state in ascospore development, stained with lead citrate.

PLATE 11

Figs. A–E. *Mycolachnea hemisphaerica*, ascospore development, fixed in 1% $KMnO_4$ and 1% OsO_4: Fig. A. secondary wall formation and development of epispore and endospore, stained with uranyl acetate and lead citrate, ×18,200; Fig. B. further states in condensation of secondary wall material and in differentiation of primary wall, stained with uranyl acetate and lead citrate; ×23,100; Fig. C. id. ×46,200; Fig. D. id. ×18,200; Fig. E. advanced state in development of ornamentation, stained with uranyl acetate and lead citrate, ×14,900.

Figs. F–H. *Octospora musci-muralis*, ascospore development, fixed in 1.5% $KMnO_4$ and 1% OsO_4: Fig. F. secondary wall formation and development of epispore and endospore, stained with uranyl acetate and lead citrate, ×29,700; Fig. G. id. detail of epispore and endospore, ×46,200; Fig. H. id. advanced state in ascospore development, stained with lead citrate.

PLATE 12

Figs. A–D. *Sarcoscypha coccinea*, fixed in 1.5% $KMnO_4$ and 1% OsO_4: Fig. A. ascoplasm, upper part of ascus before meiosis and mitoses, stained with uranyl acetate and lead citrate, ×8,100; Fig. B. ascospore development, secondary wall formation at one of two poles of ascospore, stained with uranyl acetate and lead citrate, × 12,600; Fig. C. advanced state in ascospore development, with epispore and endospore and further differentiation in endospore at one of two poles of ascospore, ×29,700; Fig. D. id. along ascospore, stained with lead citrate.

Figs. E–G. *Desmazierella acicola*, ascospore development: Fig. E. beginning of secondary wall formation fixed in 1.5% $KMnO_4$ and 1% OsO_4 and stained with uranyl acetate and lead citrate, ×23,100; Fig. F. id. advanced state in ascospore development, with epispore and endospore, stained with lead citrate; Fig. G. advancea state in ascospore development, with condensation of secondary wall material, fixed in 3.25% glutaraldehyde and 1% OsO_4 and stained with uranyl acetate and lead citrate, ×29,700.

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ZUR MORPHOLOGIE VON SACCOBLASTIA PINICOLA UND S. SEBACEA

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c/o Rijksherbarium, Leiden

(Mit 3 Abbildungen)

Die Gattung *Saccoblastia* wird hier aufgefasst im Sinne Donks (1966). Die einzige europäische Art, *S. farinacea* (*S. pinicola*), unterscheidet sich von *Helicogloea lagerheimii* (*S. sebacea*) durch den corticioiden, nicht-wachsartigen Fruchtkörper und den subapikalen Ursprung der Epibasidie an der primordialen Hyphe.

Möller errichtete 1985 die Gattung *Saccoblastia* mit zwei Arten, *S. ovispora* und *S. sphaerospora*, die er in der Umgebung von Blumenau (Brasilien) gefunden hatte. Die Gattung ist charakterisiert durch einen sackartigen Appendix, der offensichtlich als Probasidie fungiert und seitlich an der basidientragenden Hyphe inseriert ist. Möller stellte die Gattung zu den 'Auriculariaceen', genauer zu den 'Stypinelleen', auf Grund der Beobachtung, daß unterhalb der terminal gebildeten Basidie ein Seitenzweig entsteht, der diese übergipfelt und seinerseits wiederum eine Basidie bildet. Die erste und am ausführlichsten beschriebene Art Möllers, *S. ovispora*, wurde allgemein als Typusart akzeptiert. Die Interpretation dieser (und auch der zweiten Art) gestaltet sich etwas schwierig, da keine Typusaufsammlung erhalten ist. Wir sind daher auf den Protolog in Möllers Beschreibung angewiesen (l.c.: 16): "Sie bildet einen dünnen, fast durchsichtigen lockeren weissen Ueberzug, der in ganz unregelmässiger Umgrenzung mehrere Centimeter in jeder Richtung sich ausdehnte. Bei sehr feuchtem Wetter sieht dieser Ueberzug fast schleimig aus, da das Gewirr der Fäden Wasser zwischen sich festhält, bei trocknerem Wetter dagegen bemerkt man nur einen lockeren Hyphenfilz, der bei vollständigem Trocknen zur Unsichtbarkeit zusammenfällt."

Dieser Protolog macht eine eindeutige Gattungsdefinition schwierig. Bourdot & Galzin (1928), die diese Gattung erstmals für Europa nachwiesen, schufen für die beiden von ihnen aufgestellten Arten (*S. pinicola* und *S. sebacea*) zwei Untergattungen, nämlich *Saccoblastia* subgen. *Saccoblastia* für *S. pinicola* und *Saccoblastia* subgen. *Saccogloea* Bourd & Galz. für *S. sebacea*. Die erste Untergattung ist durch ein 'réceptacle floconneux hypochnoide', die zweite durch ein 'réceptacle gélatineux muqueux' charakterisiert. Ihrer Auffassung nach gehört also wesentlich zur Gattungsumschreibung von *Saccoblastia* sensu stricto der flockig-hypochnoide Fruchtkörper.

Im Gegensatz hierzu steht die Auffassung von Baker (1936). In ihrer ausgezeichnet

illustrierten Dissertation legt sie besonderen Nachdruck auf den Teil des Protologs, der die wachsartig-gallertige Konsistenz des Fruchtkörpers hervorhebt: "Bei sehr feuchtem Wetter sieht dieser Ueberzug fast schleimig aus, ... [ein] lockerer Hyphenfilz, der bei vollständigem Trocknen zur Unsichtbarkeit zusammenfällt.' (Möller, l.c.) Sie identifiziert in der Folge *Saccoblastia ovispora* Möller mit *Helicogloea lagerheimi* Pat., der Typusart der 1892 von Patouillard aufgestellten Gattung *Helicogloea*.

Donk (1958, 1966) folgt Bourdot & Galzin in der Auffassung, daß die Typusart von *Saccoblastia* ein flockig-hypochnoides Aussehen hat. Für ihn sind *Saccoblastia* und *Helicogloea* zwei verschiedene Gattungen, die zwar weitgehend übereinstimmende mikroskopische Merkmale haben, aber durch die Konsistenz des Fruchtkörpers deutlich getrennt sind. Er zitiert eine Aussage von Baker (1946: 630), die ebenfalls diese Unterschiede betont, aber sie nicht für eine Gliederung in Gattungen verwendet: "The genus falls naturally into two lines depending upon the character of the fructification, which may be of the mucous-gelatinous ("tow-like") type, or the distinctly floccose (hypochnoid) type."

Eine Art Kompromiß schließt Lowy (1971), indem er *Saccoblastia* als Subgenus akzeptiert ('stat. nov.'). Er beschreibt die Fruchtkörper als flockig und gibt für die Hyphen Schnallen an. Unglücklicherweise trifft dies gerade nicht zu für die von ihm zitierte Typusart *S. ovispora*, sondern nur für die zweite Art Möllers, *S. sphaerospora*.

Die Frage bleibt offen, ob die Verschiedenheiten in der Konsistenz der Fruchtkörper und einige weitere, im folgenden zu besprechenden mikroskopischen Unterschiede eine Trennung in zwei sicherlich nahe verwandte Gattungen erlauben. Vorläufig jedenfalls folgen wir der Abgrenzung, die Donk (1966) gegeben hat und akzeptieren die Gattung *Saccoblastia*.

Ein Aufenthalt in Paris am Naturhistorischen Museum ergab die Möglichkeit, das gesamte Material von *Saccoblastia* im Herbar Bourdot zu untersuchen. Hauptsächlich ging es uns hierbei um *S. pinicola*. Zwar sind auch einige Fundorte aus Österreich (Höhnel, Litschauer) sowie aus Dänemark (Christiansen) zusammen mit Beschreibungen publiziert worden, die Hauptmenge des Materials aber befindet sich in Paris. Interessant war die Frage, ob die Bildung der Basidie, wie sie bei *S. pinicola* zu beobachten ist, Unterschiede gegenüber den Arten mit wachsartigem Fruchtkörper zeigt. Ferner war zu untersuchen, ob die Probasidie immer als ein lateraler Sack erhalten bleibt, oder ob die Probasidien sich auch aufrichten und schließlich direkt zu Basidien entwickeln können, wie es Bourdot & Galzin (1928: 4) angeben: "Les espèces francaises de *Saccoblastia* ne présentent pas toujours nettement le caractère générique: si le contenu de certaines probasides paraît bien être une réserve utilisée pour la formation de la baside, il semble que dans bien des cas, c'est la probaside elle-même qui se redresse et se transforme directement en baside. Du moins, la section montre souvent tous les états intermédiaires entre la probaside en sac pendant et la baside arquée ou dressée."

Die Untersuchung erfolgte in verdünnter Kalilauge, wobei die Schnitte gequetscht werden mußten, um die mikroskopischen Einzelheiten besser wahrnehmen zu können. Hierbei brachen regelmäßig die großen Basidien von den sie tragenden

Hyphen ab; gleichzeitig waren zahlreiche der sackartigen Appendices frei in der Flüssigkeit und die genaue Art der Verbindung Appendix-Basidie war lange Zeit nicht deutlich. Die größeren Appendices hatten etwa die Gestalt unreifer Basidien, so daß der Schluß nahelag, daß sie sich eventuell zu Basidien weiterentwickeln könnten. Dagegen sprach, daß, entgegen den Beobachtungen von Bourdot & Galzin, keinerlei Entwicklungsübergänge zwischen den Appendices und den Basidien gefunden werden konnten. Der wahre Sachverhalt konnte erst ermittelt werden, nachdem bevorzugt die Stellen der Fruchtkörper untersucht wurden, die noch nicht zu viele kollabierte Hyphen und Basidien enthielten.

Es ergab sich, daß immer ein sackartiger Appendix unterschiedlicher Größe gebildet wird, der sich nie zu einer Basidie weiterentwickelt. Der Appendix wird unmittelbar über der zuletzt geformten Schnalle gebildet, die Hype wächst zunächst nur wenig in der ursprünglichen Richtung weiter. Nachdem der Appendix eine gewisse Größe erreicht hat, wächst die Hyphe (die primordiale Zelle in der Terminologie von Baker) weiter und stellt schließlich das Wachstum ein. Das Plasma zieht sich aus dem apikalen Teil zurück, dieser wird leer und durch ein bis drei sekundäre Querwände abgegrenzt. Subapikal, das heißt direkt unterhalb der leeren Endzelle(n) bildet sich ein Seitenzweig, der zur endgültigen Basidie (in der Terminologie Bakers der Epibasidie) heranwächst. Die Epibasidie kann ziemlich dicht oberhalb der Probasidie (*c.* 20 μm) wachsen, sie kann aber auch bis zu 100 μm von der Probasidie entfernt sein. Da die Hyphen im hymenialen Bereich dünnwandig sind, bleiben die Verbindungshyphen (=die primordialen Zellen) nur bei sehr schonendem Quetschen erhalten. Erschwerend kommt hinzu, daß die Probasidie und auch die Verbindungshyphe weitgehend leer von Plasma sind, wenn die Epibasidie voll ausgebildet ist; in solchen Fällen erwies sich die Untersuchung mit Phasenkontrastoptik als nützlich.

Saccoblastia pinicola Bourd. & Galz. hat nun *Saccoblastia farinacea* (Höhn.) Donk zu heißen. Von Höhnel (1907) beschrieb seine Art zwei Jahre vor Bourdot & Galzin unter dem Namen *Helicobasidium farinaceum*. Er sah wohl die typischen Auriculariaceen-Basidien, war aber nicht in der Lage, die Probasidien zu beobachten. In Bourdot & Galzin wird diese Art noch unter den ihnen unbekannten Taxa genannt.

SACCOBLASTIA FARINACEA (Höhn.) Donk—Fig. 1, 2

Helicobasidium farinaceum Höhn. *in* Sber. K. Akad. Wiss. Wien (Math.-nat. Kl., Abt. I) **116**: 84. 1907. — *Helicogloea farinacea* (Höhn.) D. P. Rog apud G. W. Mart *in* Univ. Iowa Stud. at Hist. **18** (3): 66. 1944. — *Saccoblastia farinacea* (Höhn.) Donk *in* Persoonia **4**: 217. 1966.

Saccoblastia pinicola Bourd. & Galz. *in* Bull. trim. Soc. mycol. Fr. **25**: 16. 1909. — *Helicogloea pinicola* (Bourd. & Galz.) Baker *in* Ann. Missouri bot. Gdn. **23**: 89. 1936.

Saccoblastia pinicola var. *defossa* Bourd. & Galz., Hym. France 4. 1928.

Saccoblastia pinicola forma *alniviridis* Bourd. *in* Bull. trim. Soc. mycol. Fr. **48**: 204. 1932.

Basidiocarp einjährig, ausgebreitet, resupinat, bis *circa* 2 cm lang, *circa* 100–500 μm dick, von hypochnoider bis membranöser Konsistenz, dem Substrat anliegend, in kleinen Stücken ablösbar; mit homogenem Kontext; die Oberfläche des Hymeniums

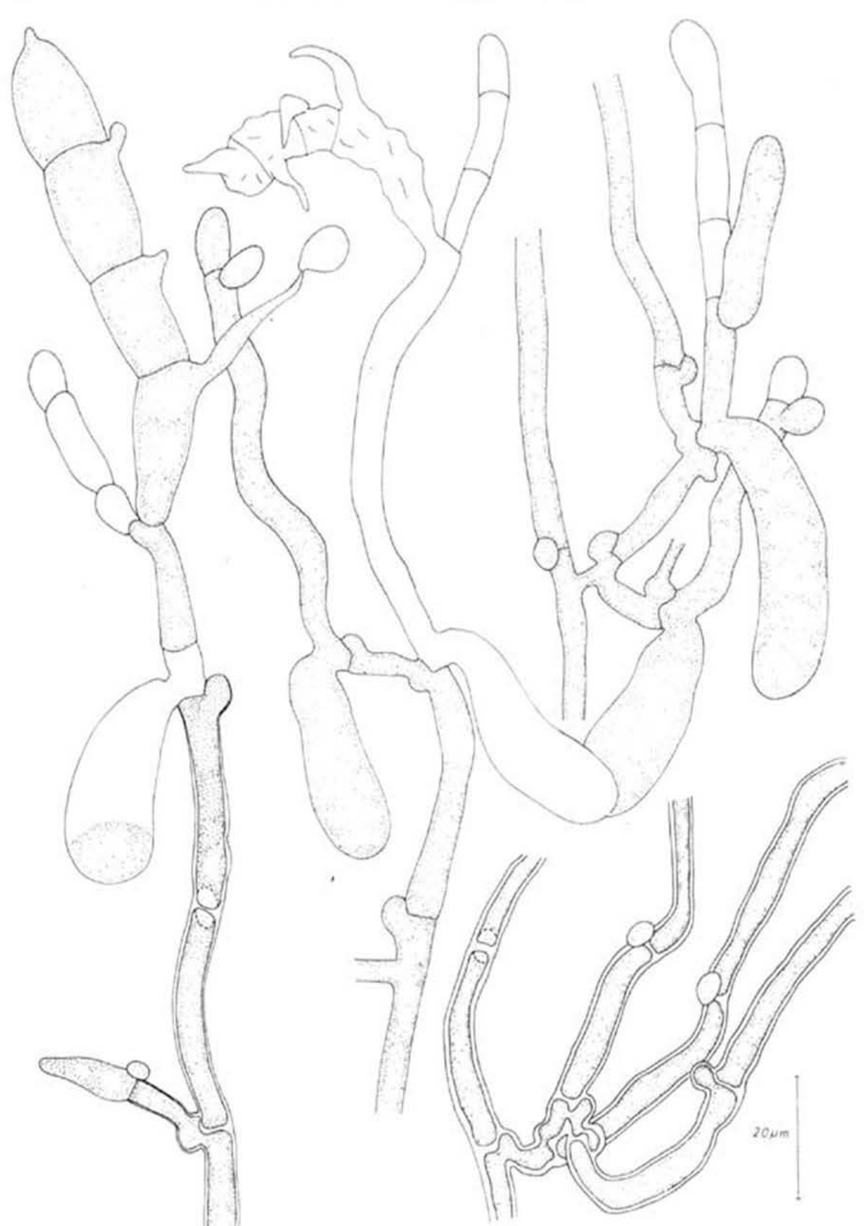

Abb. 1. *Saccoblastia farinacea*, *Bourdot 29636*.

cremefarben oder gelblich-ocker, im trockenen Zustand nicht rissig; der Rand weißlich bis cremefarben, deutlich fimbriate, Rhizomorphe fehlen. Hyphensystem monomitisch. Hyphen hyalin, cylindrisch, in Subhymenium und Trama locker angeordnet, 3–5 µm im Durchmesser, mit glatter Oberfläche, Schnallen praktisch immer vorhanden (daneben einige sekundäre Querwände ohne Schnallen). Cystiden fehlen. An der Seite einer kurzen, primordialen Hyphe bildet sich ein sackförmiges Probasidium, in dem die Kernverschmelzung stattfindet. Später wächst die primordiale Hyphe weiter aus, der apikale Teil stellt nach einer Weile das Wachstum ein und ein subapikaler Seitenzweig der primordialen Hyphe entwickelt sich zur Epibasidie. Die Probasidie mißt 30–60 × 10–15 µm, die Epibasidie 70–140 × 8–12 µm. Die Epibasidie teilt sich durch meist drei Querwände in vier Zellen, an deren apikalem Teil ein 2–3 µm dickes Sterigma hervorwächst, das meistens ungeteilt, gelegentlich aber an der Spitze auch geteilt sein kann. Die Sporen sind hyalin, breit ellipsoidisch, 11–17 × 8–12 µm, dünnwandig, mit glatter Oberfläche, nicht amyloid, dextrinoid oder cyanophil. Keimung durch Keimschläuche oder, meistens durch Bildung von Sekundärsporen an *circa* 10–15 × 3 µm großen "Sterigmata"; die Sekundärsporen sind anscheinend immer etwas kleiner als die Primärsporen, sie messen nur *circa* 10–12 × 8–10 µm.

Als Substrat wird durch Bourdot & Galzin hauptsächlich die Rinde von *Pinus* angegeben, der Pilz scheint aber ebenso häufig auf Ästen von Laubbäumen zu wachsen.

Beschreibungen der Art wurden publiziert an Hand von Material aus Frankreich (Bourdot & Galzin, 1909, 1928), Österreich (von Höhnel, 1907), Dänemark (Christiansen, 1959), Estland (Raitviir, 1967), U.S.A. und Canada (Martin, 1944, 1952).

UNTERSUCHTES MATERIAL AUS FRANKREICH (alles in PC).—DEPT. AVEYRON: (ohne Fundort) *Galzin 11425 (20558)*. — Causse Noir: 'env. 22.2.1908', *Galzin 2810 (Bourdot 5663)* (Lectotypus von *Saccoblastia pinicola* Bourd. & Galz.); *Galzin 3767 (Bourdot 6369)*; *Galzin 5681 (Bourdot 20554, 20555)*. — Causse Noir, sous Longuières, *Galzin 9084 (Bourdot 39184)*. — Causse Noir, Valat Nègre: *Galzin 4144 (Bourdot 6424)*; *Galzin 5681 (Bourdot 20556)*; *Galzin 21024 (Bourdot 18601)*; *Galzin 21025 (Bourdot 18602)*. — Causse Noir, Carbassas: *Galzin 17670 (Bourdot 15304)*; *Galzin 19896 (Bourdot 20559)*. — Montclarat: *Galzin 21885 (Bourdot 19163)*; *Galzin 23749–50 (Bourdot 24152)*; *Galzin 23751–52 (Bourdot 24153)*; *Galzin 23751 (Bourdot 24154)*; *Galzin 23753 (Bourdot 24156)*; *Galzin 24602 (Bourdot 26863)*; *Galzin 24604 (Bourdot 26865)*; *Galzin 25527 (Bourdot 29633)*; *Galzin 25530 (Bourdot 29636)*.

DEPT. HAUTE-SAVOIE, La Clusaz, (ohne Datum), *Crozals 43 (Bourdot 41386)* (Lectotypus von *Saccoblastia pinicola* forma *alniviridis* Bourd.)

DEPT. VAR., 'Env. de Toulon', 25.1.1926, *Crozals 62 (Bourdot 40325*, sub '*Saccoblastia defossa*') (Lectotypus von *Saccoblastia pinicola* var. *defossa* Bourd. & Galz.).

Auch *Saccoblastia sebacea* Bourd. & Galz. muß nun anders heißen. Nach Baker (1936, 1946) ist diese Art identisch mit *Helicogloea lagerheimii* Pat., der Typusart der Gattung *Helicogloea*. Dies bedeutet, daß wir es hier mit einer weit verbreiteten Art zu tun haben, die sowohl aus Europa als auch aus Nord- und Südamerika bekannt ist. Der Fruchtkörper ist gelatinös im frischen, wachsartig im trockenen Zustand. Die Entwicklung der Epibasidien ist nach unseren Untersuchungen an französischem Material genau so, wie sie Baker an nordamerikanischen Proben festgestellt hat.

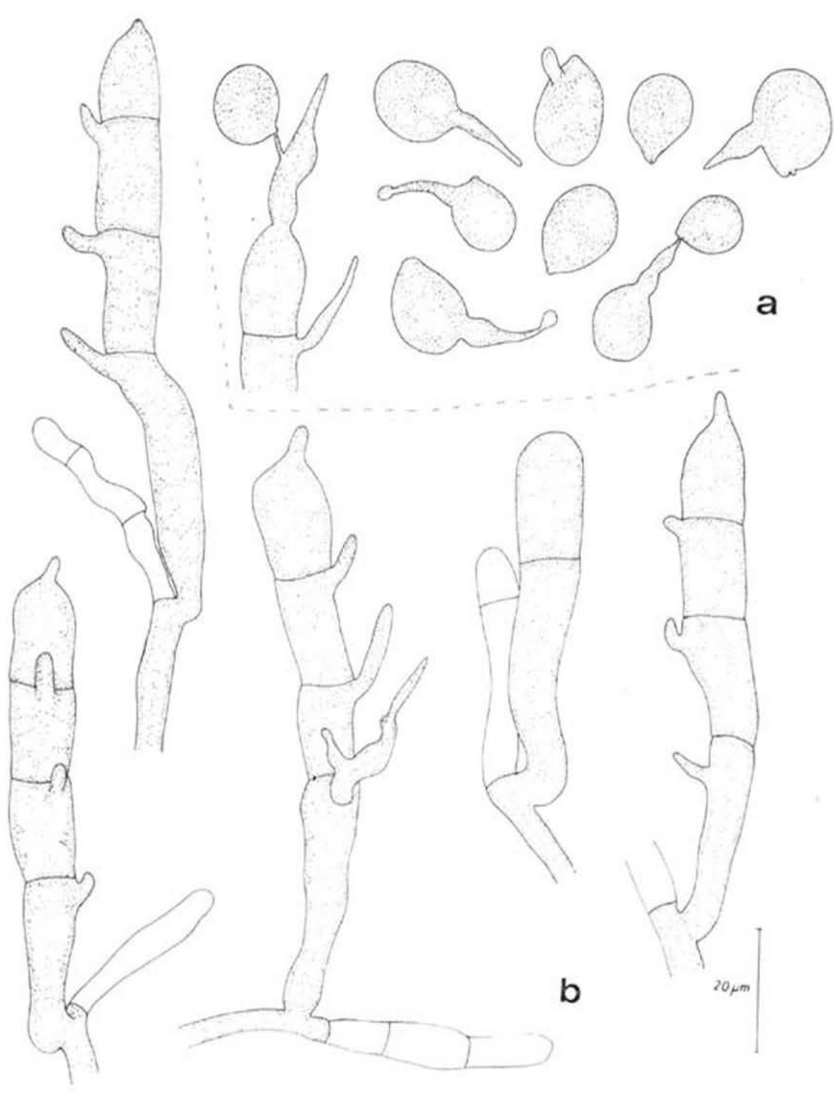

Abb. 2. *Saccoblastia farinacea*. — a. Sporen, *Bourdot 15304*. — b. Basidien, *Bourdot 29636*.

Nach der Bildung der Probasidie wächst die 'primordiale Zelle' weiter, und aus ihrer Spitze kommt die Epibasidie hervor.

Die Gattung *Helicogloea* Pat. (1892) blieb bis zur grundlegenden Arbeit von Baker (1936) unbeachtet. Dies lag daran, daß Patouillard die charakteristischen Probasidien nicht beschrieben hatte und daher die Abgrenzung von der etwas früher beschriebenen Gattung *Platygloea* Schroet. (1888) zweifelhaft war. Denn das Merkmal, worauf Patouillard (1900: 13) das Hauptaugenmerk lenkte, ist für die Typusart seiner Gattung nicht besonders charakteristisch: "Très proche de *Platygloea*, il en diffère par sa trame dont la consistance est celle d'un *Exidia* gonflé par l'eau et par ses basides à la fin flexueuses ou courbées."

HELICOGLOEA LAGERHEIMII Pat.—Fig. 3

Helicogloea lagerheimii Pat. apud Pat. & Lagerh. *in* Bull. trim. Soc. mycol. Fr. **8**: 121. 1892. — *Platygloea lagerheimii* (Pat. apud Pat. & Lagerh.) Sacc. & Syd., *in* Syll. Fung. **14**: 247. 1899.

Helicobasidium inconspicuum Höhn. *in* Sber. K. Akad. Wiss. Wien, Math.-nat. Kl., Abt. I, **117**, 1021. 1908.

Saccoblastia sebacea Bourd. & Galz. *in* Bull. trim. Soc. mycol. Fr. **25**: 15. 1909.

Saccoblastia sebacea var. *pruinosa* Bourd. & Galz., Hym. France 5. 1928.

Saccoblastia sebacea var. *typica* Bourd. & Galz. l.c.: 5.

Saccoblastia sebacea var. *vulgaris* Bourd. & Galz. l.c.: 5.

Basidiocarp einjährig, resupinat, ausgebreitet, mehrere cm lang, bis zu 600 µm dick im frischen und 100–300 µm dick im trockenen Zustand, frisch weich-gelatinös, trocken wachsartig, dem Substrat fest anliegend, mit homogenem Kontext; die Oberfläche des Hymeniums ist im jungen Zustand rötlich-braun und wird später grau-braun bis schwärzlich, ist jedoch oft weißlich bereift, alte Fruchtkörper sind oft stark rissig; der Rand ist undeutlich, verlaufend. Hyphensystem monomitisch. Hyphen hyalin, zylindrisch bis etwas torulös, in Subhymenium und Trama kompakt angeordnet, 3–6 µm in Durchmesser, die Wände der tramalen Hyphen bis zu 1,2 µm dick; Oberfläche glatt, Schnallen immer fehlend. Cystiden nicht ausgebildet. Im Verlauf der Basidienontogenie wird zunächst ein sackförmiges Probasidium angelegt (10–30×8–12 µm). Aus der primordialen Hyphe wächst an ihrem apicalen Ende die Epibasidie hervor (50–80×5–8 µm), die bisweilen leicht gekrümmt und im reifen Zustand 3–4-zellig ist; Sterigmen *circa* 2,5 µm dick. Sporen ellipsoidisch, in Seitenansicht zylindrisch und leicht gekrümmt, 8–15×5–8 µm, dünnwandig, mit glatter Oberfläche, nicht amyloid, dextrinoid oder cyanophil, an *circa* 10 µm langen "Sterigmen" Sekundärsporen bildend.

Das Substrat scheint nicht besonders spezifisch zu sein Die Art wurde angegeben für Frankreich (Bourd. & Galz., 1909, 1928), Österreich (von Höhnel, 1908), England (Wakef. & Pears., 1923), Dänemark (Christ., 1959), U.S.A. und Kanada (Rogers, 1933; Baker, 1936; Olive, 1948; Martin, 1952), Hawaii (Martin, 1952), Tahiti (Olive, 1958), Brasilien, Ekuador und Kolumbien (Baker, 1946), Panama (Lowy, 1972) und Neu-Seeland (McNabb, 1964).

UNTERSUCHTES MATERIAL AUS FRANKREICH (alles in PC; ohne weitere Angabe wurde das Material im Herbar Bourdot unter dem Namen *Saccoblastia sebacea* vorgefunden).—D e p t.

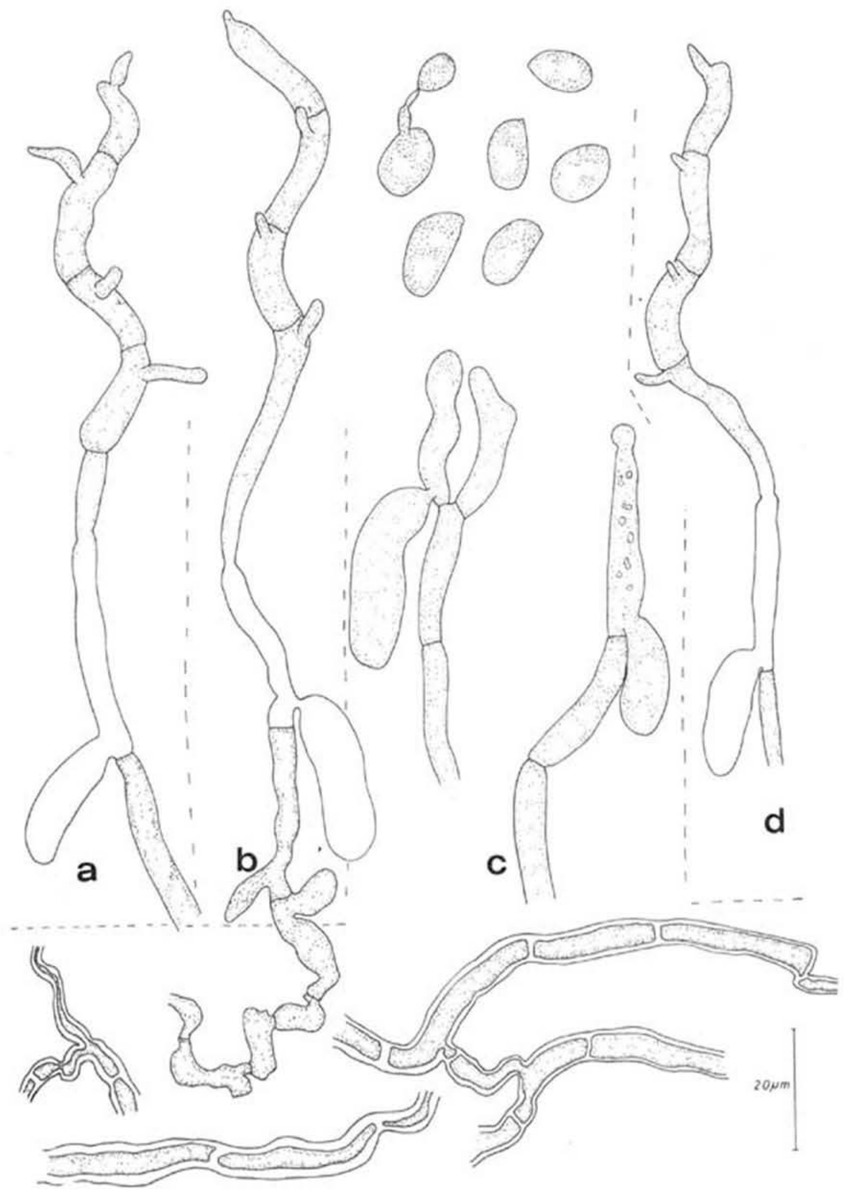

Abb. 3. *Helicogloea lagerheimii*. — a. Basidie, *Bourdot 23303*. — b, d. Basidie, *Bourdot 15979*. — c. Sporen, junge Basidie, basale Hyphen, *Bourdot 23304*.

AVEYRON: Barthe, 13.11.1913, *Galzin 14270* (sub *S. pruinosa*; *Bordot 12350*). — Carmassol, près St. Sernin: *Galzin s. n. (Bourdot 5749)*; *Galzin 3895 (Bourdot 23305)*. — Causse Noir: 9.12.1910, *Galzin 7868 (Bourdot 6710)* (Lectotypus von *Saccoblastia sebacea* var. *pinastri* Bourd. & Galz.); *Galzin 7896 (Bourdot 7612)*; *Galzin 7961 (Bourdot 23288)*; *Galzin 10085 (Bourdot 23289)*; *Galzin 14606 (Bourdot 23333*, "bon pour l'étude!"); *Galzin 16632 (Bourdot 23297)*; *Galzin 16638 (Bourdot 23296)*; *Galzin 16605 (Bourdot 23302)*; *Galzin 23088 (Bourdot 23316)*; *Galzin 23717 (Bourdot 24120)*; *Galzin 23718 (Bourdot 24121)*. — Causse Noir, Bépaume: *Galzin 14368 (Bourdot 23291)*; *Galzin 14764 (Bourdot 23293)*; *Galzin 14800 (Bourdot 12411)*, *Galzin 14825 (Bourdot 23294)*. — Causse Noir, Carbassa: *Galzin 14411 (Bourdot 23308)*; *Galzin 18899 (Bourdot 15979)*. — Evès, Galzin 16447 *(Bourdot 23301)*. — Forques, *Galzin 17454 (Bourdot 14515)*. — Fortune, *Galzin 17210 (Bourdot 23335)*. — Frégère, *Galzin 18828 (Bourdot 15419)*. — l'Hospitalet, *Galzin 21132 (Bourdot s. n.)*. — La Coste, *Galzin 10928 (Bourdot 23307)*. — Le Rec, *Galzin 11982 (Bourdot 23290)*. — Loubotis: *Galzin 16933 (Bourdot 23298)*; *Galzin 13790* (sub *S. pruinosa*; *Bourdot 12152*); *Galzin 13816* (sub *S. pruinosa*; *Bourdot 12151*); *Galzin 13817* (sub *S. pruinosa*; *Bourdot 12153*); *Galzin 14003* (sub *S. pruinosa*; *Bourdot 12349*); *Galzin 14247* (sub *S. pruinosa*; *Bourdot 12351*). — Mas de Stic., près St. Sernin, *Galzin 3951 (Bourdot 6017)*. — Mendive, *Galzin 16804 (Bourdot 23304)*. — Mendive, sur Erable, 30.11.1913, *Galzin 14749* (sub *S. pruinosa*; *Bourdot 12347*) (Lectotypus von *Saccoblastia sebacea* var. *pruinosa* Bourd. & Galz.); *Galzin 14750* (sub *S. pruinosa*; *Bourdot 12348*); *Galzin 19067* (sub *S. pruinosa*; *Bourdot 15991*). — Violette, près St. Sernin, *Galzin 4334 (Bourdot 6508)*.

DEPT. TARN: Caussanel, près S. Sernin, *Galzin 4316 (Bourdot 23306)*. — Casourgues, *Galzin 19561 (Bourdot 23310)*.

DEPT. GARD: St. Guirol *Galzin 5815 (Bourdot 23287)*.

DEPT. ALLIER: St. Priest: *Bourdot 5750*; *Bourdot 42262*. — St. Priest Bûcher de Virlobier: *Bourdot 5750*; *Bourdot 5882*. — St. Priest, Lavat., *Bourdot 39135*.

DEPT. ORNE, Forêt, de Bellême, –.10.1925, *E. Gilbert 1513* ("*Saccoblastia sebacea β vulgaris*"; *Bourdot 39816*) (Lectotypus von *Saccoblastia sebacea* var. *vulgaris* Bourd. & Galz.).

Summary

The genus *Saccoblastia* is here accepted in the sense of Donk (1966). The only European species, *S. farinacea* (=*S. pinicola*) differs from *Helicogloea lagerheimii* (=*S. sebacea*) in its corticioid, non-waxy basidiocarps and the subapical origin of the epibasidia from the primordial hyphae.

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A CONTRIBUTION TOWARDS A REVISION OF THE GENUS TULASNELLA *

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(With eleven Text-figures)

Redescriptions of nine species of *Tulasnella* are given, all based on the specimens of the Bourdot herbarium in Paris.

Although a revision of the Tulasnellaceae by Rogers (1932, 1933) and an important article by Olive (1957) have been published, there remain some problems with the specific delimitation, at least with regard to the European species. Therefore a revision of the material deposited in European herbaria has been started some time ago, with the intention to include later the extra-European species. Donk (1966) recognized thirty species for Europe, eleven of which were described by Bourdot & Galzin (1924). Since the Bourdot collection is especially rich in Tulasnellas it seemed to be particularly important to go through the whole collection (*Tulasnella*, inclusive of *Gloeotulasnella*) in order to get a better understanding of the morphological variation of the species. A part of the work could be done during a stay in Paris, while the rest of the collection will be studied at Leiden.

In order to facilitate the identification, redescriptions of some of the species are given together with the necessary figures of the microscopical characters. One great difficulty remains: the key to the species of *Tulasnella*, as given by Bourdot & Galzin (1928), does only work if one knows the colour of the fresh basidiocarp of the membranaceous species (whitish or reddish); dried specimens of this group are all whitish or cream-coloured. There seems to be no difference in the microstructure between some pairs of species (one being whitish, the other reddish when fresh). For the moment we incline to treat them as synonyms.

TULASNELLA ALBIDA Bourd. & Galz.—Fig. 1

Tulasnella albida Bourd. & Galz., Hym. de France: 59. 1928.

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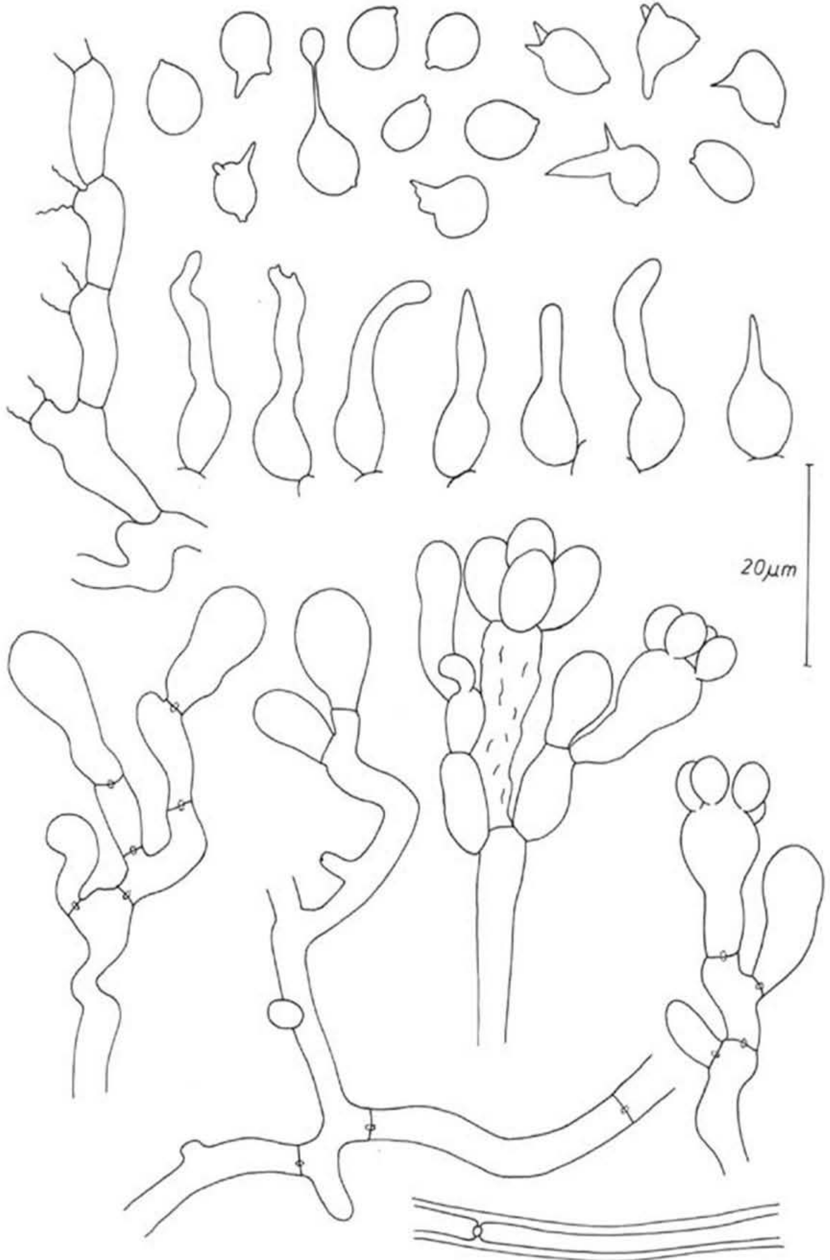


Fig. 1. *Tulasnella albida, Bourdot 6496.*

Basidiocarp resupinate, effused, several cm large, 20–60 μm thick, invisible to the naked eye when dry, ceraceous, adnate, homogeneous, hymenial surface whitish to pale greyish and pruinose when dry, even, in dry condition not cracked; margin indistinct, thinning out. Hyphae hyaline, cylindrical or slightly inflated, loosely arranged in subhymenium and trama, branching from all parts of the hyphae, 2–5.5 μm in diameter and thin-walled (0.2 μm) in the subhymenium, 2–4.5 μm in diameter and thin-walled to slightly thick-walled (up to 0.6 μm) in the trama, with smooth surface, clamps lacking, dolipore distinct, contents homogeneous. Cystidia or gloeocystidia lacking. Basidia hyaline, stalked-clavate when mature, clavate when young, 15–22 × 6.5–8 μm, thin-walled, smooth, a basal clamp lacking, contents homogeneous; with four ellipsoid to clavate epibasidia (7–9.5 × 4.8–5.3 μm) on top of which one cylindrical, mostly unbranched, flexuous sterigma (*c.* 12–15 × 1.8 μm). Spores hyaline, subglobose to broadly ellipsoid, with small apiculus, 6.5–7.5 (–9) × 4.2–5.2 μm, thin-walled, smooth, not amyloid; germination with 1–3(–4) more or less subulate outgrowths up to 7 × 1.5 μm. — Saprophytic on wood of angiosperms (*Quercus*).

MATERIAL STUDIED.—FRANCE: '*Tulasnella albida* mihi', Allier, près de Mazeau, sur bois de chêne très pourri dans un fossé, 18.7.1909, *Bourdot 6496* (lectotype, PC); Aveyron, St. Estève, 23.7.1909, *Galzin 4321* (*Bourdot 8744*) (PC).

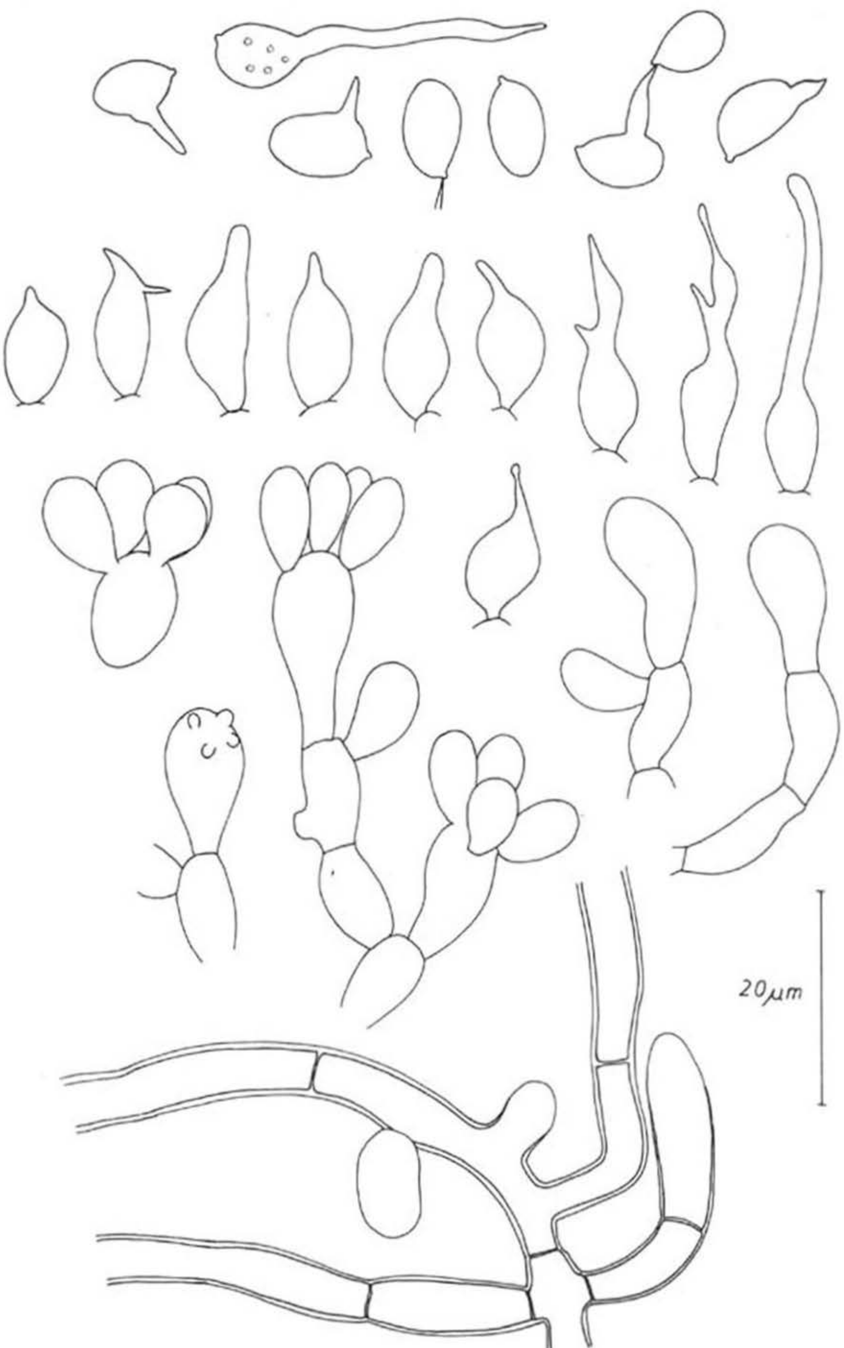
TULASNELLA ALBOLILACEA Bourd. & Galz.—Fig. 2

Tulasnella albolilacea Bourd. & Galz. *in* Bull trim. Soc. mycol. Fr. **39**: 264. 1924.

Basidiocarp resupinate, effused, several cm large, *c.* 50–80 μm thick, well visible, corticioid, consistency firm-membranaceous to somewhat ceraceous, adnate; hymenial surface whitish, even, not cracked when dry; margin indeterminate, thinning-out; rhizomorphs or hyphal strands lacking. Hyphae hyaline, cylindrical or slightly inflated, loosely arranged in subhymenium and trama, branching from all parts of the hyphae, 1.5–6 μm in diameter and thin-walled (*c.* 0.2 μm) in the subhymenium, 3.5–6 μm and thin- to thick-walled (up to 0.8 μm) in the trama, with smooth surface, clamps lacking, contents homogeneous. Cystidia or gloeocystidia lacking. Basidia hyaline, broadly clavate when mature, clavate when young, 11–17 × 7.5–8.5 μm, thin-walled, smooth, a basal clamp lacking, contents homogeneous, with four clavate to ellipsoid epibasidia (*c.* 12 × 6 μm), rather abruptly narrowed to a subulate or cylindrical, simple or branched sterigma (6–18 × 1.5–2.5 μm). Spores hyaline, ellipsoid, with distinct apiculus, 8–9 × 5–5.5(–6) μm, not glued together, smooth; germinating at first by forming subulate 'sterigmata' *c.* 6–9 μm long, later with cylindrical germ-tubus *c.* 2 μm in diameter. — Saprophytic on wood of angiosperms (*Quercus*).

MATERIAL STUDIED.—FRANCE: *Tulasnella albo-lilacea* nob', Aveyron, Boutaran, –.11. 1917, *Galzin 23485* (*Bourdot 23559*) (lectotye, PC); —.12.1917, *Galzin 32486* (*Bourdot* 23560) (PC).

This species is according to Bourdot & Galzin pale reddish when fresh. For Rogers (1933) it is identical with *Tulasnella violacea*, but this is not accepted by Donk (1966).


20 µm

TULASNELLA ARANEOSA Bourd. & Galz.—Fig. 3

Tulasnella araneosa Bourd. & Galz. *in* Bull. trim. Soc. mycol. Fr. **39**: 265. 1924.

Basidiocarp resupinate, effused, a few cm large, *c.* 50 µm thick, ceraceous, adnate, homogeneous; hymenial surface hyaline, even, not cracked when dry; margin hyaline, indistinct, rhizomorphs and hyphal strands lacking. Hyphae hyaline, cylindrical, loosely arranged in subhymenium and trama, 2–3 µm in diameter and thin-walled to slightly thick-walled in the subhymenium, 2–4 µm in diameter and slightly thick-walled up to 0.8 µm in the trama, surface smooth, clamps lacking, contents homogeneous. Cystidia and gloeocystidia lacking. Basidia hyaline, clavate when mature, 11–15×6–8 µm, thin-walled, smooth, a basal clamp lacking, contents homogeneous; with four broadly ellipsoid epibasidia (*c.* 6–9×4.5–5.5 µm), rather abruptly narrowed to form subulate, sometimes bifurcate sterigmata (7–13×1–1.5 µm). Spores hyaline, ellipsoid to slightly allantoid, with rather large apiculus, 5.9–7.5×3.7–4.5 µm, thin-walled, smooth, not amyloid.

MATERIAL STUDIED.—FRANCE: '*Tulasnella araneosa* Nob'. Aveyron, Pojade, sur Cérisier, 22.10.1914, *Galzin 16477* (*Bourdot 14281 bis*) (lectotype, PC); Aveyron, Loubotis, 22.10.1914, *Galzin 16435* (*Bourdot 42731*); Aveyron, Estic, 10.11.1914, *Galzin 16565* (*Bourdot 14280*) (PC); 5.5.1915, *Galzin 17462* (*Bourdot 14919*) (PC); Aveyron, Violette, —.7.1915, *Galzin s.n.* (*Bourdot 18335*).

All specimens in Bourdot's herbarium show arachnoid small patches on the substrate. The hyphae of these patches probably do not belong to this species, of which the basidiocarp is distinctly ceraceous and invisible when dry. Among the specimens, some show subglobose to broadly ellipsoid spores and could be identified as Tulasnella albida.

TULASNELLA BRINKMANNII Bres.—Fig. 4

Tulasnella brinkmannii Bres. *in* Annls mycol. **18**: 50. 1920.

Basidiocarp resupinate, effused, several cm large, *c.* 100 µm thick, membranaceous, adnate, separable in small pieces, homogeneous; hymenial surface cream-coloured, even, not cracked when dry; margin concolorous or whitish, thinning out, rhizomorphs or hyphal strands lacking. Hyphae hyaline, cylindrical, with distinct doliporus, loosely arranged in subhymenium and trama, branching from all parts of the hyphae, 4–6 µm and thin-walled in subhymenium and trama, with smooth surface, clamps lacking, contents homogeneous or often strongly guttulate. Cystidia lacking. Basidia hyaline, clavate when mature, 16–22×8–10 µm, thin-walled, smooth, a basal clamp lacking, contents homogeneous or slightly guttulate; with four ellipsoid epibasidia (*c.* 12–13×5–6 µm) rather abruptly narrowed to single or sometimes bifurcate sterigmata (4–9×0.5–1 µm). Spores hyaline, narrowly ellipsoid to slightly allantoid, with small apiculus, 12–14×3.7–5.2 µm, thin-walled, smooth, contents homogeneous or slightly guttulate, not amyloid.

MATERIAL STUDIED.—GERMANY: '*Tulasnella Brinkmannii* Bres. n. sp., e violaceo rosea. Ad *Alnus*, Brinkmann, spec. orig.!' (*Bourdot 7701*) (PC).

EXPLANATION OF FIGURE 2

Fig. 2. *Tulasnella albolilacea, Bourdot 23559.*

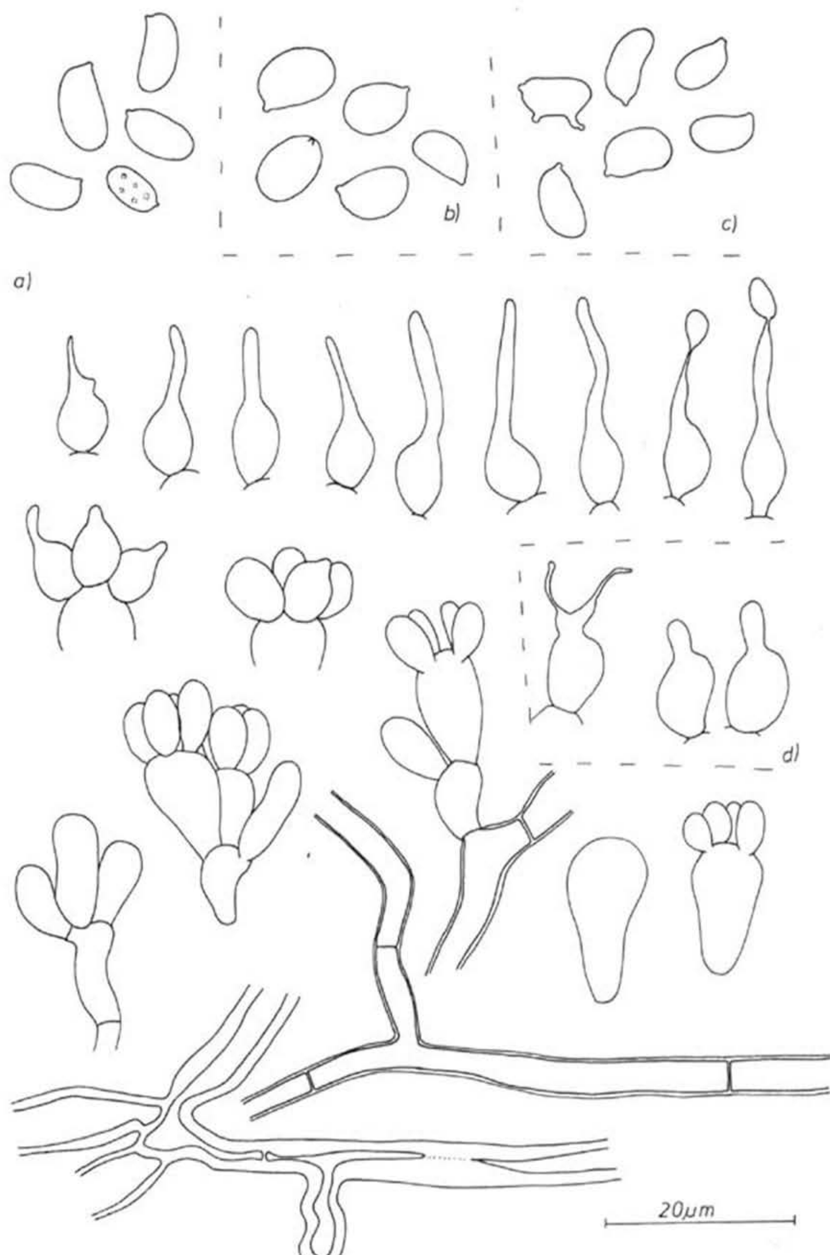


Fig. 3. *Tulasnella araneosa*. — a. lectotype (spores, epibasidia, basidia, basal hyphae). — — b. *Bourdot 14280* (spores). — c. *Bourdot 42731* (spores). — d. *Bourdot 17417* (epibasidia).

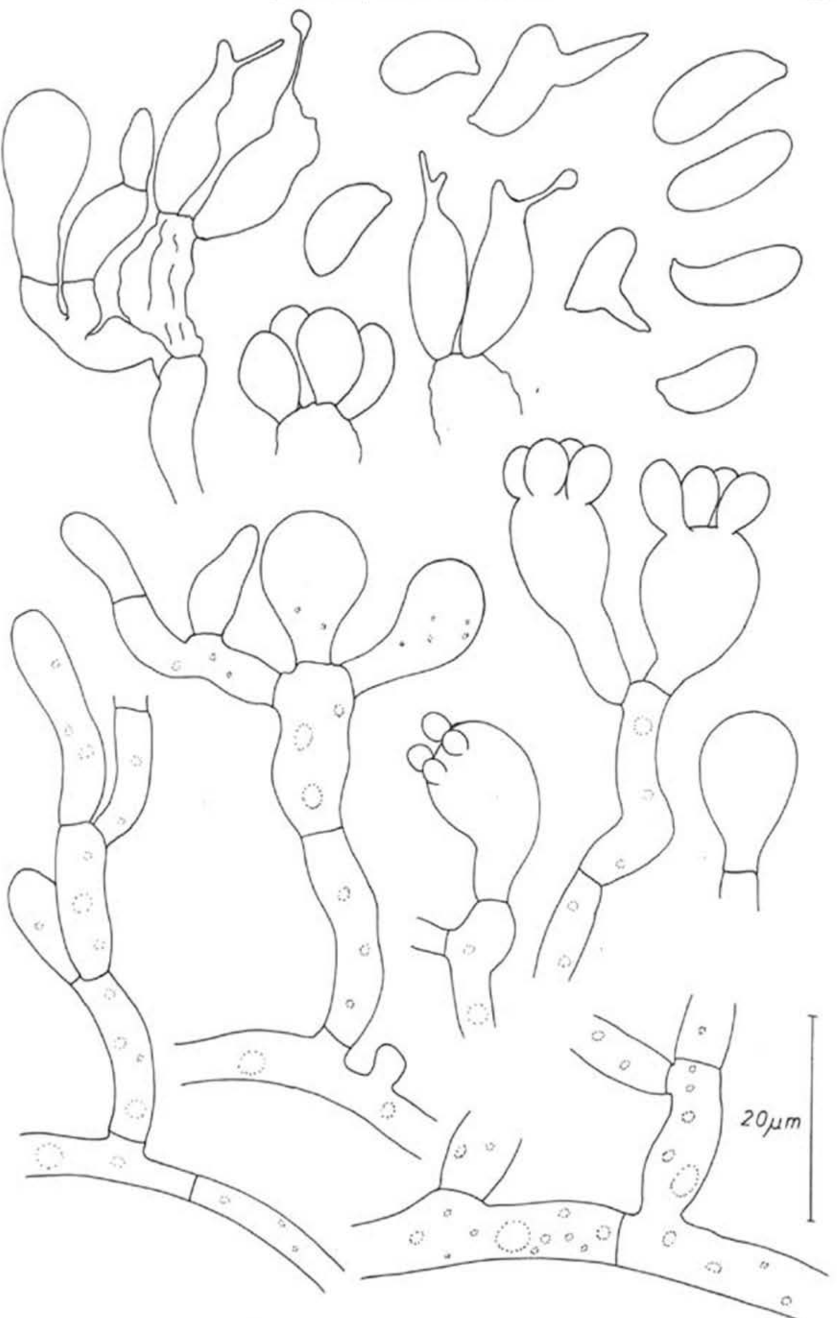
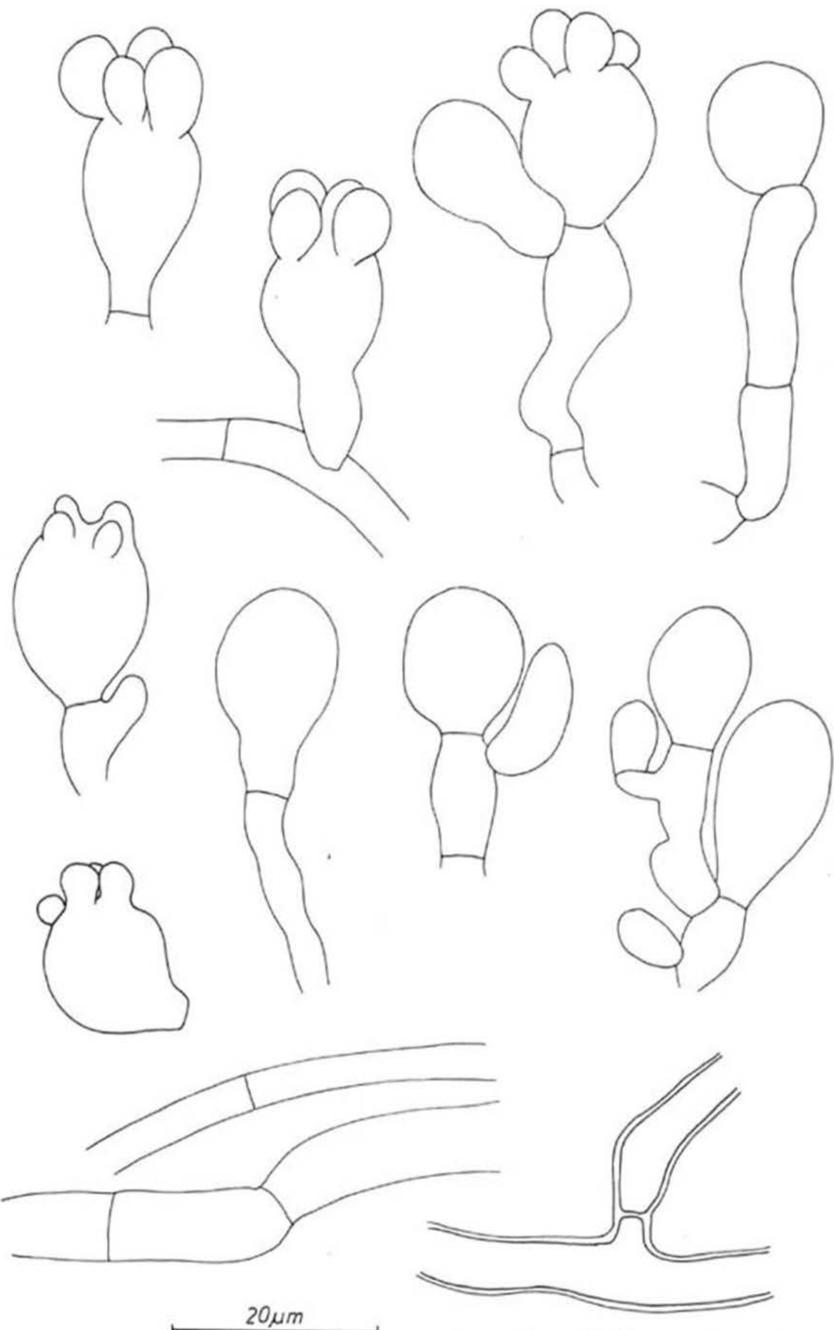


Fig. 4. *Tulasnella brinkmannii*, holotype.


20µm

According to Rogers (1933) this is identical with *Tulasnella violacea* (J.-Ols. apud Bref.) Juel.

TULASNELLA CALOSPORA (Boud.) Juel—Fig. 5, 6

Tulasnella calospora (Boud.) Juel *in* Bih. K. svenska Vet-Akad. Handl. (III) **23**[12]: 23. 1897.

Basidiocarp resupinate, effused, several cm large, *c.* 50–100 μm thick, firm-membranaceous to slightly ceraceous, adnate, separable in small pieces, contents homogeneous; hymenial surface whitish to cream-coloured, even, not cracked when dry; margin whitish, indistinct, thinning out, rhizomorphs or hyphal strands lacking. Hyphae hyaline, cylindrical, loosely arranged in subhymenium and trama, branching from all parts of the hyphae, 3–6 μm in diameter, thin-walled in the subhymenium, thin-walled to somewhat thick-walled in the trama, with smooth surface, clamps lacking, contents homogeneous. Cystidia lacking, Basidia hyaline, clavate when mature, sometimes stalked, broadly ellipsoid when young, 14–20–27 × 10–13 μm, thin-walled, smooth, a basal clamp lacking, contents homogeneous; with four broadly ellipsoid epibasidia (*c.* 12–13 × 8–9 μm), rather abruptly narrowed to subulate, sometimes branched sterigmata (up to 11 × 3.5 μm). Spores hyaline, long-sinuous, with small apiculus, 19–24 × 4.4–5.3 μm, thin-walled, smooth, contents homogeneous, not amyloid.

Material studied.—France: 'Corticium (Prototremella) calospora Boud., ad telas putridos, St. Denis, dedit D. Hétier' (in herb. Boudier – PC, sub Prototremella, holotype) (part of type in herb. Bourdot 7338 – PC).

According to the specimens studied, Tulasnella calospora f. media Bourd. & Galz. is identical with Sebacina calospora Bourd. & Galz.

TULASNELLA EICHLERIANA Bres.—Fig. 7

Tulasnella eichleriana Bres. *in* Annls mycol. **1**: 113. 1903.

Basidiocarp resupinate, effused, several cm large, *c.* 50–100 μm thick, firm-membranaceous to slightly ceraceous, adnate, separable in small pieces, context homogeneous; hymenial surface cream-coloured to pale greyish, even, not cracked when dry; margin concolorous or paler, thinning out, rhizomorphs or hyphal strands lacking. Hyphae hyaline, cylindrical or somewhat torulose in the subhymenium, with distinct dolipore, loosely arranged, branching from all parts of the hyphae, 2–5 μm in diameter, thin-walled, smooth, clamps lacking, contents homogeneous. Cystidia lacking. Basidia hyaline, clavate when mature, 7–10 × 4.5–5.5 μm, thin-walled, smooth, a basal clamp lacking, contents homogeneous; with four broadly ellipsoid epibasidia (*c.* 6–7.5 × 4.5–5 μm), rather abruptly narrowed to flexuous-cylindrical or subulate sterigmata (*c.* 3.5–4 × 2–2.5 μm). Spores hyaline, broadly ellipsoid, with small apiculus, 3.5–4.5 × 3–4 μm, thin-walled, smooth, contents homogeneous, not amyloid; forming secondary spores.

MATERIAL STUDIED.—FRANCE: Aveyron, Barthe, 10.11.1914, *Galzin 16529* (*Bourdot 35630*) (PC); Allier, Forêt de Dreuille, 1.8.1908, *Bourdot 5919* (PC).

EXPLANATION OF FIGURE 5

Fig. 5. *Tulasnella calospora*, holotype.

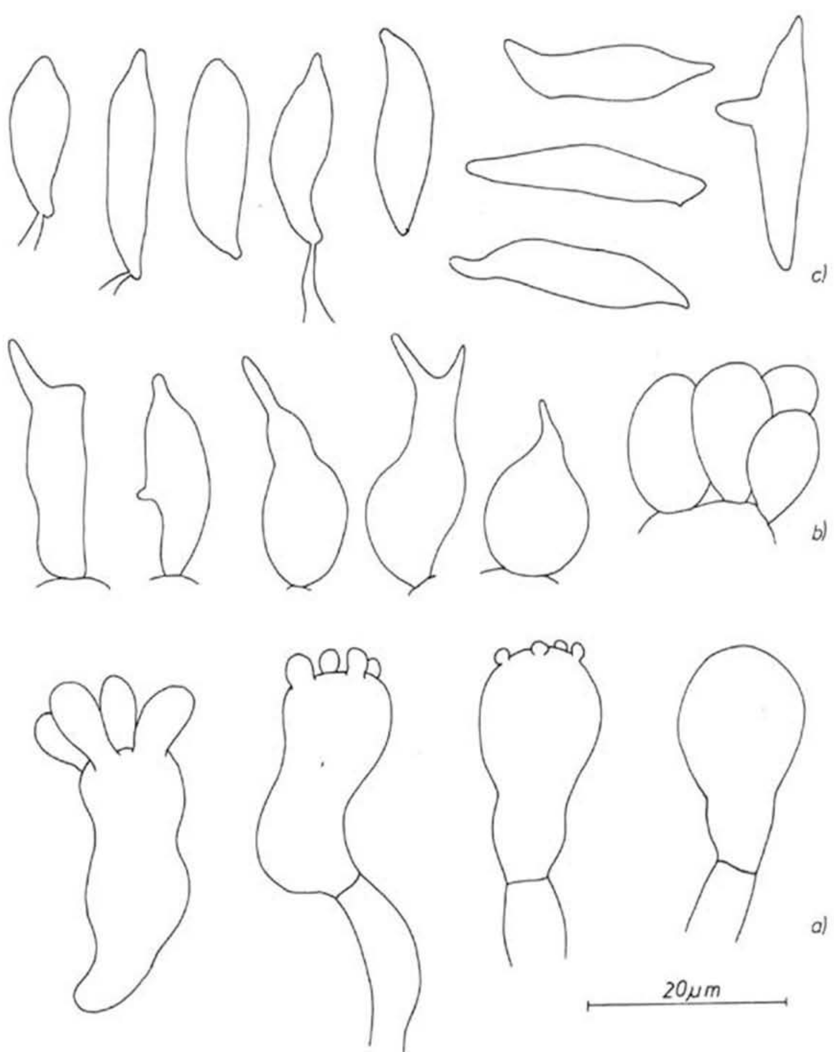


Fig. 6. *Tulasnella calospora*, holotype. — a. basidia. — b. epibasidia. — c. spores.

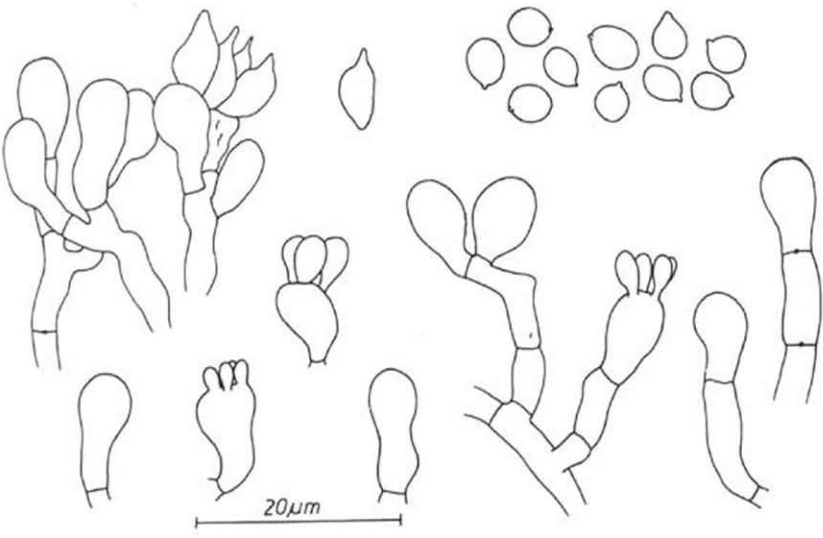


Fig. 7. *Tulasnella eichleriana*, *Bourdot 5919*.

This species shows a reddish basidiocarp when fresh. It has often been regarded as a synonym of *Tulasnella violea* (Quél.) Bourd. & Galz. but can be separated by its rather small spores. The delimitation of *T. violea* itself is an unsolved question. There are forms (taxa?) with globose or ellipsoid spores and also some forms with medium-sized spores, situated exactly between *T. violea* and *T. eichleriana*.

TULASNELLA FUSCOVIOLACEA Bres.—Fig. 8, 9

Tulasnella fuscoviolacea Bres., Fungi trident. **2**: 98. 1900.

Basidiocarp resupinate, effused, several cm large, *c.* 50–100 µm thick, membranaceous, adnate, separable in small pieces, context homogeneous; hymenial surface cream-coloured, even, not cracked when dry; margin whitish, thinning-out, rhizomorphs or hyphal strands lacking. Hyphae hyaline, cylindrical, with distinct dolipore, loosely arranged, 3–4.5 µm in diameter, thin-walled, smooth, clamps lacking, contents homogeneous. Cystidia lacking. Basidia hyaline, clavate when mature, 9.5–15 × 7.5–9 µm, thin-walled, smooth, a basal clamp lacking, contents homogeneous; with four clavate epibasidia (*c.* 10–12 × 4.5–5 µm), rather abruptly narrowed to flexuous-cylindrical sterigmata (*c.* 6 × 1.5 µm). Spores hyaline, slightly allantoid, with small apiculus, 8–12.5 × 3.7–4.5 µm, thin-walled, smooth, contents homogeneous, not amyloid; germination by means of secondary spores.

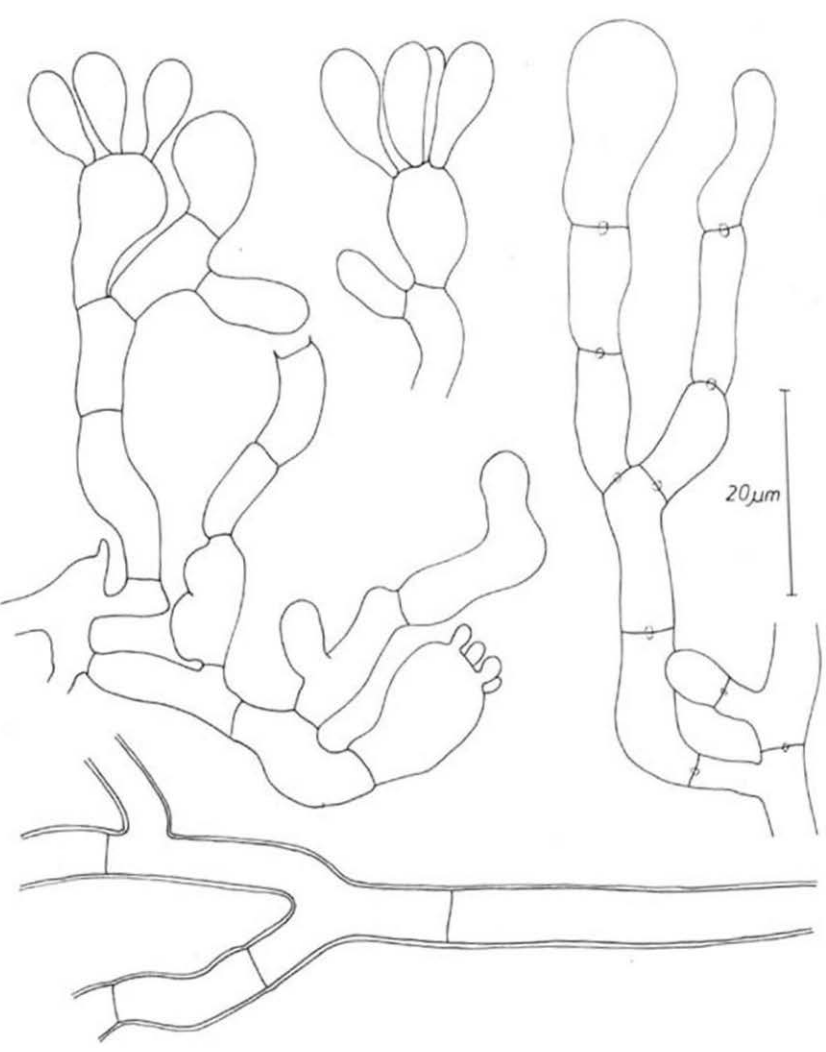


Fig. 8. *Tulasnella fuscoviolacea*, *Bourdot 25030*.

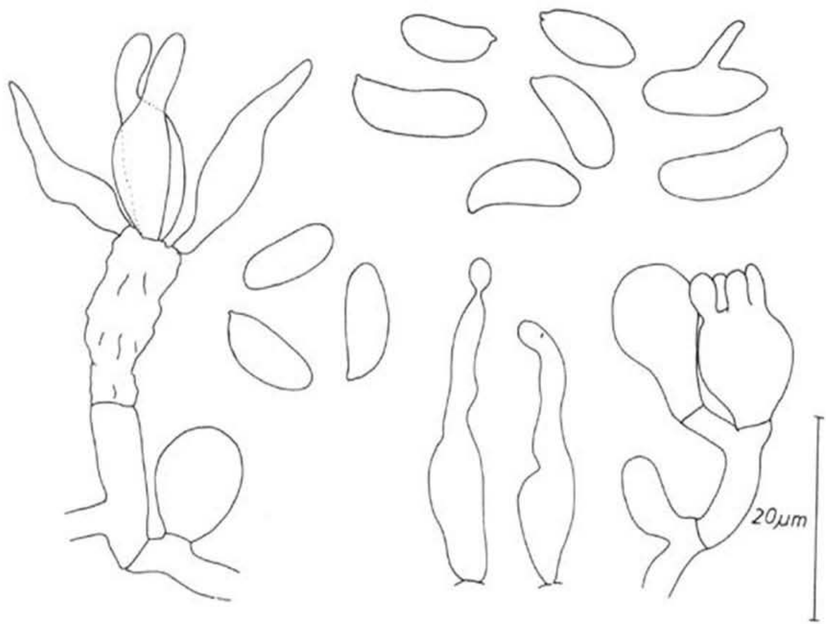


Fig. 9. *Tulasnella fuscoviolacea*. — a. *Bourdot 25030* (basidia, epibasidia, spores). — b. *Bourdot 3512* (spores above).

MATERIAL STUDIED.—FRANCE: Belfort, —.9.1918, *E. Gilbert 200* (*Bourdot 25030* — PC); Vosges, 25.4.1904, *Galzin s.n.* (*Bourdot 3512*–PC).

TULASNELLA OBSCURA Bourd. & Galz.—Fig. 10

Tulasnella obscura Bourd. & Galz. *in* Bull. trim. Soc. mycol. Fr. **39**: 265. 1924.

Basidiocarp resupinate, effused, a few cm large, *c.* 50–100 µm thick, ceraceous, adnate, not easily separable, context homogeneous; hymenial surface hyaline to brownish or blackish, even, not cracked when dry; margin concolorous, indistinct, thinning-out, rhizomorphs or hyphal strands lacking. Hyphae hyaline, cylindrical or torulose in the subhymenium, compactly arranged, 2–3 µm in diameter, thin-walled, smooth, clamps lacking, contents homogeneous. Cystidia lacking. Basidia hyaline, clavate when mature, flexuous-cylindrical to narrowly clavate when young, 10–12.5 × 5–6.5 µm, thin-walled, smooth, a basal clamp lacking, contents homogeneous; with four flexuous-subulate epibasidia (12–16 × 2.5–3 µm). Spores hyaline, broadly ellipsoid, with distinct apiculus, 3.7–5.2 × 3–4.2 µm, thin-walled, smooth, contents homogeneous, not amyloid; germination by means of secondary spores, the 'sterigmata' subulate, *c.* 6 × 1.5 µm.

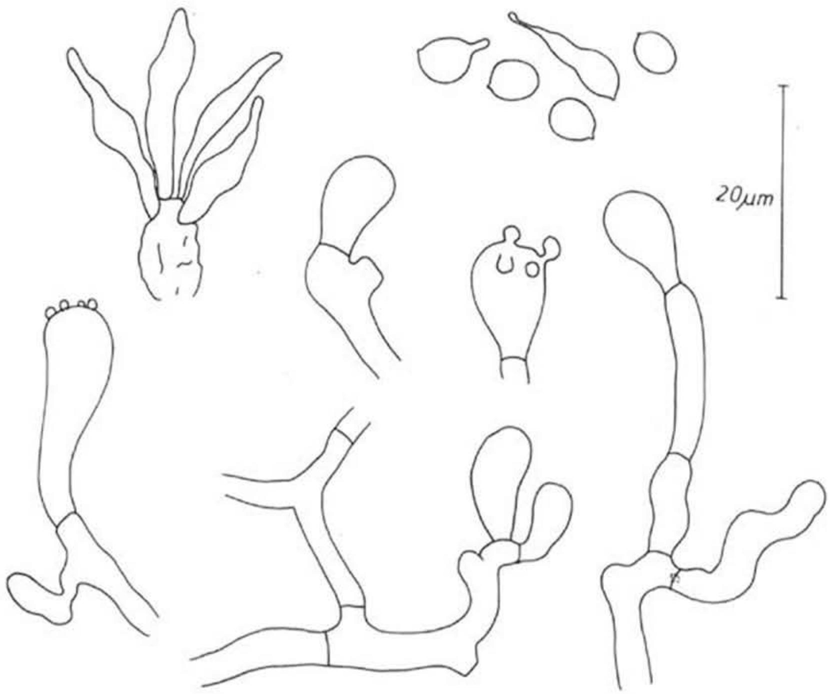


Fig. 10. *Tulasnella obscura, Bourdot 17376.*

MATERIAL STUDIED.—FRANCE: '*Tulasnella obscura*, sur noyer, Aveyron, Le Rec, 25.7.1914, *Galzin 15813*' (*Bourdot 17375*) (lectotype, PC) Aveyron, 26.12.1915, *Galzin 19123* (*Bourdot 17376*) (PC).

TULASNELLA PRUINOSA Bourd. & Galz.—Fig. 11

Tulasnella pruinosa Bourd. & Galz. *in* Bull. trim. Soc. mycol. Fr. **39**: 264. 1924.

Basidiocarp resupinate, effused, several cm large, *c.* 20–50 µm thick, visible to the naked eye, ceraceous, adnate, context homogeneous; hymenial surface pale greyish, pruinose, even, not cracked when dry; margin concolorous, indistinct, thinning out, rhizomorphs or hyphal strand lacking. Hyphae hyaline, flexuous-cylindrical, loosely arranged throughout, branching from all parts of the hyphae, 2–4 µm in diameter, thin-walled, smooth, clamps lacking, contents homogeneous. Cystidia lacking. Basidia hyaline, clavate when mature, ellipsoid when young, 9–12 × 6–7 µm, thin-walled, smooth, a basal clamp lacking, contents homogeneous; with four more or less ellipsoid, guttulate epibasidia, rather abruptly narrowed to

the subulate sterigmata (*c.* 5–6 × 1–1.5 μm). Spores hyaline, ellipsoid, some slightly curved, with distinct apiculus, 6–7.5 × 3.3–3.7 μm, thin-walled, smooth, contents slightly guttulate, not amyloid; germination by repetition, sterigma-like outgrowth *c.* 3.5 × 0.7 μm

MATERIAL STUDIED.—FRANCE: '*Tulasnella pruinosa*, sur châtaignier, Aveyron, Clavelau (St. Sernin), 19.3.1912, *Galzin 11012*' (*Bourdot 8745*) (lectotype, PC); Aveyron, Bois Dufabre 20.4.1912, *Galzin 11292* (*Bourdot 8750*); Aveyron, Violette, 25.7.1914, *Galzin 15859* (*Bourdot 35620*); Aveyron, les Vives, 24.4.1912, *Galzin 11163* (*Bourdot 14073*).

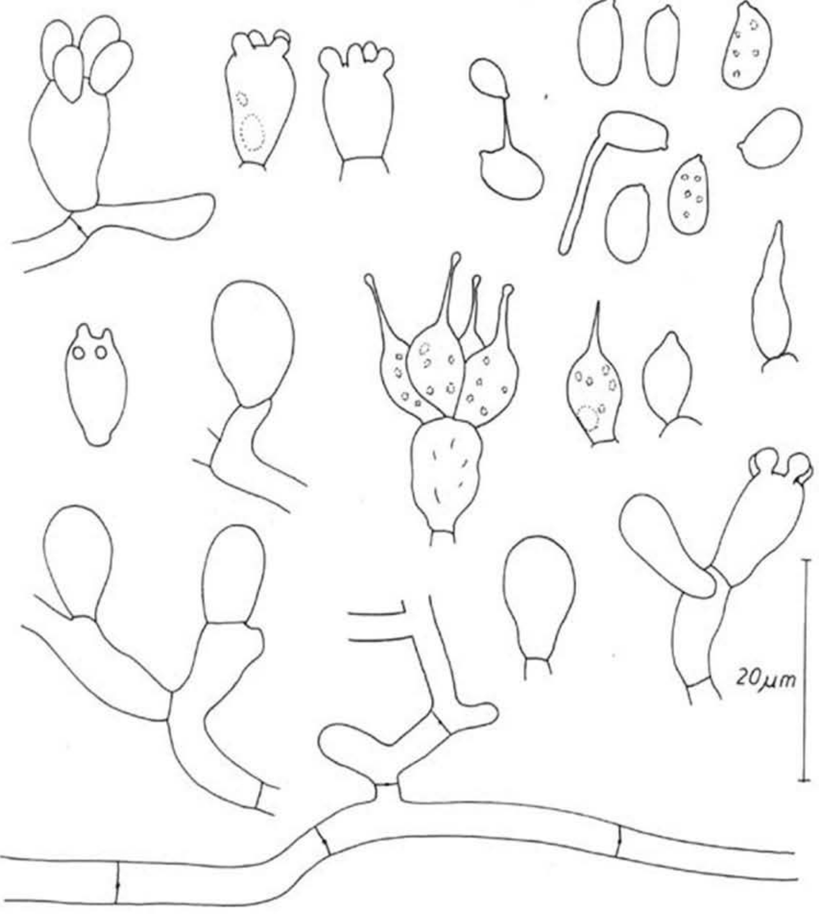


Fig. 11. *Tulasnella pruinosa*, *Bourdot 8745*.

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RECHERCHES SUR LE DÉVELOPPEMENT ET L'HISTOGENÈSE DANS LES ASTÉROSPORALES

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(With Plates 13–17)

Cette étude est dediée à Monsieur H. Romagnesi, en hommage respectueux pour sa grande monographie sur les Russules et à cause de tout l'intérêt que cet éminent observateur a toujours porté aux données ontogéniques.

Chez *Lactarius* aussi bien que chez quelques espèces de *Russula* du moins, les pelotes de sphérocystes sont précédées de la formation de rosettes primaires, qui vues en coupes transversales se montrent composées d'un cercle de petites sphérocystes autour d'une hyphe centrale.

Les complexes de sphérocystes dans la trame des carpophores de *Russula* sont généralement plus larges: ils englobent plusieurs rosettes primaires. Les complexes de sphérocystes dans les Lactaires se groupent généralement autour de l'axe du carpophore, du moins dans le stipe.

L'hyphe centrale ou axile d'une rosette primaire qui n'est pas un laticifère, est susceptible d'exercer une influence inductrice sur les hyphes environnantes qui détermine leur croissance et la formation d'une chaîne de petites sphérocystes.

Des complexes de sphérocystes se présentent également dans le pied rudimentaire d'une espèce d'*Arcangeliella* et d'une espèce d'*Elasmomyces*, une hyphe inductrice paraît être présente aussi dans ce cas.

Il est probable que les structures particulières que l'on rencontre dans la trame des Astérosporales et que l'on a dénommées rosettes (primaires), se rattachent à certains caractères généraux du tissu de bulbes qui se pésentent chez un grand nombre d'Agaricales.

Le tissu emmêlé dans lequel naissent les complexes de sphérocystes, remplit une très grande partie des primordiums des Astérosporales, à l'encontre de la situation chez les Agaricales où un tissu emmêlé (caractéristique du bulbe) se localise souvent à la base du pied, surtout dans les stades plus avancés.

Une grande partie au moins des cystides chez les Russules sont homologues aux poils: une des fonctions de ces éléments est la protection des primordiums contre le dessèchement dans les jeunes stades.

INTRODUCTION

La présente publication traite en premier lieu de la genèse des îlots de sphérocystes dans la chair des Lactaires et des Russules, bien connus de tous ceux qui s'occupent de ces genres. Notre attention a été dirigée fortuitement sur ce phénomène qui n'a toujours pas été étudié d'une manière intégrale. Lorsque nous eûmes observé le

groupement des sphérocystes en forme de rosette autour d'une hyphe centrale dans une coupe transversale du stipe de jeunes carpophores d'un Lactaire, nous ne réussîmes pas à retrouver la même disposition dans la chair des Russules. Dans la trame de celles-ci, les sphérocystes sont généralement agglomérées en groupes plus étendus dans lesquels les rosettes ne se dessinent plus distinctement: disposition qui suggère la conclusion que les rosettes y font défaut. Ce n'était qu'après une étude prolongée des coupes que nous nous sommes aperçu qu'elles s'y présentent quand même, mais seulement dans de jeunes stades et par endroits. La répartition et la genèse des rosettes (comme vues en coupes transversales) dans la chair des Astérosporales qui ont été traitées dans les manuels mycologiques relatifs aux laticifères (de Bary, 1884; Fayod, 1889; Lohwag, 1941; etc.), seront donc notre point de départ.

La découverte des laticifères dans les champignons remonte à Schultz 1823 — ce même auteur est censé avoir observé pour la première fois les rosettes (1839) — mais c'est Corda (1839: tab. 3, tab. 4, tab. 7 fig. 106, tab. 10 fig. 139) qui les a représentées exactement dans ses Icones fungorum. Il nomme la plante dans laquelle il a étudié ces structures: *Agaricus (Russula) foetens* var. *lactiflua*, et c'est à cause de cette nomenclature que l'on se trouve dans l'incertitude quant à la vraie nature de cette espèce: s'agit-il d'une Russule ou quand même d'un Lactaire? *Russula foetens* var. *lactiflua* n'est pas reconnu ailleurs et on ne peut admettre qu'il y ait des specimens de *Russula foetens* Fr. qui émettent du lait. De l'autre côté, la figure 139 évoque plutôt le tissu d'une Russule que d'un Lactaire: les îlots de sphérocystes se composent de plusieurs rangées. Quoi qu'il en soit, il est assez improbable que les auteurs suivants aient observé les rosettes de sphérocystes avec leurs hyphes axiles dans la chair des Russules, bien qu'ils aient supposé tous leur présence chez les dernières, analogue à leur disposition dans les Lactaires. Néanmoins, de nos jours, Lenz (1971: pl. IV fig. 28) les a reproduites, mais sans hyphe axile.

De nombreux auteurs se sont occupés de la nature de cette hyphe axile; c'est seulement Hoffmann (1861: Tafel 2) qui a nié son existence, en y admettant simplement un méat intercellulaire. Il y a en effet des coupes transversales qui renferment des rosettes où cette hyphe axilé fait défaut dans les Lactaires (par exemple *Lactarius deliciosus* (L. ex Fr.) S. F. Gray), comme l'a remarqué Oehm (1931), mais dans la plupart des cas, elle est présente et se dessine nettement. Selon Weiss, on peut même trouver deux ou trois fragments de ces hyphes au centre des rosettes, au lieu d'une. Schultz et Corda étaient déjà les premiers qui y vissent un laticifère, après eux Istvanffi (1896), Rouge (1907) et Oehm (1931), se sont prononcés dans le même sens, tandis que de Bary (1884) et Weiss (1885) décrivent l'hyphe centrale des rosettes comme une hyphe protenchymatique ordinaire. Pour en faire la détermination, on s'est servi de divers colorants ou de réactifs (acide sulfurique); cependant, sous ce rapport, ceux-ci sont suje's à caution. Fayod (1889) qui avait fait la distinction entre laticifères et hyphes oléifères, pensait que l'hyphe axile se rangeait dans la dernière catégorie. (Cf. aussi Lohwag, 1941: 384, 387; Lentz, 1954: 146; Reijnders, 1963: 273–274).

Oehm (l.c.) qui avait donc opté pour la nature laticifère de l'hyphe centrale, a

également remarqué que cette dernière manquait dans environ un tiers des coupes de rosettes chez le *Lactarius deliciosus*. Lohwag a avancé l'idée que quand les rosettes sont une fois présentes, les laticifères poussent accidentellement dans le canal central.

Tandis que le désaccord régnait donc sur la nature de l'hyphe axile, les auteurs ont tous admis que les sphérocystes sont issus d'hyphes filamenteuses ordinaires, donc protenchymatiques. Rouge (l.c.) a même figuré exactement les hyphes hélicoïdales autour d'une hyphe centrale (dite laticifère) avec les sphérocystes naissantes.

Voilà donc un bref résumé de ce qui était connu de ces remarquables structures dans la chair des Astérosporales. Nous nous proposons de décrire la genèse des rosettes d'une manière plus détaillée et dès leur origine, ce qui nous permettra de comparer aussi leur situation chez les Russules et les Lactaires. En plus de ces observations sur les rosettes et leur hyphe axile, nous fixerons notre attention sur les autres structures de ces primordiums curieux qui dévient considérablement de ceux des vrais Agaricales.

La recherche des primordiums des espèces du genre *Russula* est difficile. On est forcé de les découvrir dans le sol, faute de cultures qui fructifient. Mais, en règle générale, leur croissance dans le sol paraît être très lente, en d'autres termes ils restent cachés pendant une période relativement longue et quand les jeunes carpophores se montrent en sortant du sol, les primordiums avoisinants ont disparu. En outre, les Russules ne poussent pas en groupes serrés dans la plupart des cas; quoique le nombre d'exemplaires d'un mycélium puisse être grand, ces champignons sont souvent assez éloignés les uns des autres (comme par exemple les bolets). Les espèces dont nous avons réussi à récolter tout de même des primordiums sont: *Russula anthracina* Romagnesi, *R. ochroleuca* Fr. et *R. fragilis* Pers. ex Fr.; ce sont des espèces appartenant à des groupes très différents (selon la classification de Romagnesi, au sous-genre des *Compactae*, aux *Ingratae* et aux *Piperinae*; selon Singer (1975) aux *Compactae*, aux *Ingratae* et à *Russula*). À part ces trois espèces, nous serons à même de décrire quelques particularités structurales des primordiums d'une espèce d'*Arcangeliella* et d'une espèce d'*Elasmomyces*, grâce à une petite série de coupes que nos amis viennois, M. et Mme Mader, nous ont envoyée. La comparaison de la trame de ces espèces hypogées avec celle des Russules, s'avérera extrêmement utile.

Le nombre des publications qui s'occupent du développement des Lactaires et des Russules est encore très restreint, à l'exception des études susmentionnées sur les rosettes et leur hyphe centrale (Reijnders, 1963: 142, tableau synoptique). Heim (1937) a fait quelques observations sur le développement d'un Lactaire et de deux Russules annelées de la flore malgache, surtout au point de vue de l'origine de l'anneau. Kühner (1926: 225) a examiné quelques stades très jeunes de *Lactarius rufus* (Scop. ex Fr.) Fr. mais, pas plus que ses prédécesseurs, il n'a pas réussi à élucider la vraie nature de l'hyphe axile des rosettes, ce qu'il reconnaît lui-même (l.c.: 39). Enfin, nous avons décrit l'ontogénie de quelques structures de *Russula emetica* (Schaeff. ex Fr.) S. F. Gray et de *Russula olivacea* (Schaeff. ex Secr.) Fr. (Reijnders, 1963) et la naissance des îlots de sphérocystes, mais les hyphes axiles qui se manifestent quand même chez les Russules, ont échappé à notre perception; nous en traiterons la cause dans les pages suivantes.

Nous étions donc bien surpris en découvrant que ces rosettes se trouvent généralement à la base de l'évolution de ces pelotes de sphérocystes dans les Astérosporales, les Russules y comprises.

DESCRIPTION DES DÉVELOPPEMENTS

LACTARIUS MAMMOSUS (Fr.) Fr.

(1) Le premier stade que nous avons examiné, se compose d'un petit pédicule élancé (longueur 1575 μm, largeur à la base 530 μm, largeur en haut 380 μm), qui ne montre pas encore de trace du développement du chapeau, sauf la présence d'hyphes palissadiques à la surface, tout en haut (sur une distance de 130 μm). On remarquera la différence de la figure avec celle des primordiums des Russules. Dans la partie centrale de la moitié inférieure, on observe déjà des chaînes doubles de sphérocystes avec leurs hyphes axiles; la bande corticale qui est privée de ces cellules élargies, a déjà une largeur d'environ 110 μm. On y trouve des hyphes très minces en direction longitudinale (diamètre 1,5–2 μm) et des laticifères (d'une largeur de 5–10 μm) qui accusent généralement la même orientation. Le tissu entre les pelotes de sphérocystes se compose d'hyphes emmêlées (diamètre 3–5 μm, leur largeur diminue vers le haut). Les complexes de sphérocystes sont plus larges à mesure qu'ils se trouvent plus bas; il en est de même pour le diamètre (jusqu'à environ 40 μm) des sphérocystes qui sont généralement un peu étirées dans le sens transversal. Les complexes de sphérocystes se développent évidemment à partir de la base, donc de bas en haut. Les hyphes axiles sont presque toujours fortement colorées, ce qui prouve qu'elles sont encore jeunes; elles ont une direction strictement longitudinale (comme les laticifères sous l'écorce, mais pas dans la partie centrale) et se montrent souvent sur un long espace dans la coupe. Plus en haut, où les sphérocystes sont petites ou manquent encore, les hyphes axiles sont tout de même présentes; elles se dessinent comme des lignes foncées, parfois presque parallèles et pas très distantes les unes des autres. Le diamètre de ces hyphes (2–5 μm) est bien inférieur à celui des laticifères (5–10 μm): nous les avons photographiées ensemble (Pl. 13A) dans la partie inférieure du pédicule, colorées selon le triple procédé de Flemming (pour les colorants voir: Discussion). Une autre différence notable avec les laticifères est que les hyphes axiles sont cloisonnées, voire multicloisonnées. Nous insérons également une photographie de la partie supérieure du pédicule où l'on voit naître les sphérocystes (encore minuscules) autour des hyphes axiles; plusieurs d'entre elles sont encore dépourvues de ces chaînes (Pl. 13B).

(2) Le deuxième stade est celui de la Planche 13C (longueur 2,2 mm, diamètre un peu au-dessus de la marge saillante 844 μm). On remarquera que les rangées de sphérocystes qui se prolongent dans la partie piléique, sont groupées autour de l'axe du primordium et qu'elles occupent la majeure partie de la trame. Mais dans une zone sous-corticale du pied et une couche un peu plus large sous la surface piléique,

elles manquent, ainsi que dans la marge piléique. Celle-ci se compose d'hyphes parallèles protenchymatiques qui sont dirigées vers le bas et convergent un peu. Les hyphes palissadiques de l'hyménium sont décurrentes sur le stipe; il y a probablement des cystides. Outre les laticifères qui s'étendent en sens longitudinal sous l'écorce du pied, on en trouve des fragments répandus dans la trame centrale; il leur manque une direction déterminée.

Dans les rangées de sphérocystes, qui sont dans la plupart des cas doubles (l'une à côté de l'autre), on observe par-ci par-là des hyphes axiles, susceptibles de se trouver sur un large espace dans la coupe; dans la plupart des cas, elles sont déjà vides et beaucoup plus minces que les laticifères. Dans la partie piléique les doubles rangées de sphérocystes sont plus jeunes, ce qui explique pourquoi on y trouve plus d'hyphes axiles intactes que dans le pied où les hyphes centrales sont déjà plus ou moins détériorées. Pas de piléipellis.

(3) La Planche 13D représente une coupe transversale de la partie supérieure d'un pied (diamètre 725 μm). L'attention portera sur les îlots de sphérocystes qui sont groupés autour de l'axe. La Planche 13E représente sous un grossissement plus fort cette configuration. Cette coupe transversale permet de constater qu'un ensemble de sphérocystes (qui, à la coupe longitudinale, se présente comme un corps oblong ou même étiré), consiste généralement en une rosette ou, tout au plus, en deux ou trois rosettes réunies. Entre les groupes de sphérocystes serpentent des fascicules minces d'hyphes protenchymatiques. On observera que presque chaque rosette est munie d'une hyphe axile mince, se dessinant comme un petit cercle ou point foncé. Le volume de ces groupes se limite fréquemment à une seule rosette, s'augmentant parfois de cellules disposées en forme de spirale autour de l'hyphe axile. Il arrive que, dans ces coupes, celle-ci ne soit pas coupée exactement en sens transversal et qu'elle soit probablement entraînée par le couteau, de sorte qu'un véritable fragment d'hyphe est visible dans la coupe. Parfois ce sont les extrémités supérieures de ces hyphes qu'on observe ainsi; nous avons photographié de tels fragments qui sont toujours minces et un peu en massue sur la Planche 14A (observez la flèche). Quelques rosettes primaires avec un cercle de cellules à dimensions plus réduites autour d'une hyphe centrale, se trouvent parmi les ensembles plus étendus de sphérocystes, surtout au pourtour de ce dernier.

La coupe longitudinale du premier stade et cette coupe transversale permettent de reconnaître des hyphes axiles qui traversent le tissu en sens longitudinal (dans le stipe) sans être accompagnées de rangées de sphérocystes. La coupe transversale montre dans le tissu, entre les rosettes et le contour du stipe, des petits ronds de teinte plus foncée; dans la coupe longitudinale, les hyphes axiles isolées se dessinent comme des lignes également plus colorées (Pl. 13B). Il s'ensuit de ces observations que les hyphes axiles (qui, d'après leur fonction s'appellent aussi "hyphes inductrices") n'exercent cette influence que par endroits (voir Discussion).

La question de la nature de cette hyphe centrale a été discutée par les auteurs plus anciens et ils ont émis des opinions très différentes sous ce rapport (voir: Introduction et Discussion).

RUSSULA ANTHRACINA Romagn.

Les jeunes primordiums des Russules accusent tous à peu près la même forme trapue, à pied court et à partie latérale du chapeau se manifestant dès un jeune stade. Nous avons renoncé à les figurer encore et toujours et nous allons entamer tout de suite les détails. Ces détails sont: la genèse des groupes de sphérocystes, celle du piléipellis et de l'hyménophore.

(1) Quant à la première, les rosettes primaires se montrent déjà dans un stade très jeune (longueur env. 1,4 mm, diamètre de la partie piléique également 1,4 mm) dans le stipe aussi bien que dans le chapeau dont la trame est presque complètement occupée par ces structures, sauf à l'extrême bord où les hyphes sont emmêlées ou parallèles. Mais dans la partie supérieure du pied, il existe une zone où les rosettes sont absentes. Ce primordium est gymnocarpe, la marge piléique est hérissée de longs poils. Le piléipellis se compose d'éléments dressés, agglutinés les uns aux autres et dont les extrémités sont libres, elles se recourbent et s'appliquent contre la face supérieure du chapeau (Pl. 14B). Les hyphes palissadiques de l'hyménophore naissent dans l'angle entre la face inférieure du chapeau et du pied.

(2) Dans un stade un peu plus avancé (longueur et largeur 2,4 mm), nous avons trouvé des îlots de sphérocystes assez étendus dans le pied et dans la trame piléique auprès de l'axe; dans les parties latérales de la trame se présentaient de nombreuses rosettes primaires, mais d'un diamètre beaucoup plus réduit que celui des groupes axiaux. Par-ci par-là, nous avons rencontré des hyphes centrales des rosettes qui s'étendaient sur un large espace dans la coupe. L'hyménium sans basides mûres est décurrent sur le pied; il y a déjà des cystides proéminentes qui paraissent être septées. Le subhyménium naît sous les palissades, ses sphérocystes sont encore petites (diamètre 3–4 μm) par comparaison aux sphérocystes des îlots dont le diamètre est déjà de 25 μm, mais les sphérocystes des rosettes primaires en voie de formation, sont également menues.

(3) Nous passons à un stade plus développé, un jeune champignon pour ainsi dire (diamètre du chapeau 5,6 mm, longueur 6,3 mm). La répartition des îlots plus grands de sphérocystes et des rosettes est identique à celle du stade précédent; les sphérocystes manquent dans la partie recourbée du chapeau à partir du niveau de la face inférieure de celui-ci, la trame dans cette partie est emmêlée (pas d'hyphes parallèles). Il y a déjà des plis lamellaires (pas très hauts encore) qui accusent la même structure que celle de *Russula emetica* (Reijnders, 1963: 41, pl. 8 figs. 1–3). Le médiostrate s'édifie d'hyphes parallèles à cellules assez courtes, le subhyménium celluleux est déjà large et les fentes interlamellaires sont complètement bourrées de cystides assez grandes et en majeure partie cloisonnées. Les rosettes manquent encore dans la trame de ces lames; ce n'est que plus tard qu'elles s'y manifesteront également. Le piléipellis est maintenant gélifié à un haut degré, la contenance des hyphes ne se dessine que par des stries minces traversant la masse de mucus et qui sont rarement élargies en forme de massue.

(4) Une coupe tangentielle du chapeau d'un stade encore plus avancé (Pl. 14D,

épaisseur sans lames 2,3 mm, hauteur des lames env. 0,6 mm) nous a permis de faire les observations suivantes. La chair piléique est entièrement criblée de groupes de sphérocystes qui sont séparées les unes des autres par de minces faisceaux d'hyphes sans direction prévalente. C'est seulement dans une mince zone au-dessus des lames que les sphérocystes manquent partiellement, car elles descendent déjà dans leur trame. Dans la plupart des cas, les sphérocystes sont rangées en forme de simples rosettes autour d'une hyphe centrale, surtout dans la zone inférieure du chapeau. Le subhyménium est bien développé et large, avec des cellules d'un diamètre beaucoup plus réduit que celles des sphérocystes des rosettes, lesquelles ont évidemment une tout autre origine. Le subhyménium est traversé de cystides qui sont donc très longues, ou bien il s'agit ici de laticifères qui se terminent en une cystide (Pl. 14E). C'est probablement à cause du fait que les laticifères ne se distinguent guère des autres hyphes par suite d'une coloration peu favorable, que nous n'étions pas à même de dépister exactement les rapports entre les laticifères et les autres éléments de cette espèce. La trame des lames se compose d'abord d'hyphes approximativement parallèles, mais plus tard, des sphérocystes, partiellement arrangées en rosettes primaires, s'y manifestent à partir du niveau supérieur (Pl. 15A).

Le piléipellis gélifié est relativement épais (env. 164 μm), ses hyphes sont plutôt emmêlées; nous n'avons pas remarqué de dermatocystides, quoique le volume des hyphes gélifiées puisse s'élargir un peu; les laticifères manquent dans la couche sousjacente (subpellis) (Pl. 14C).

RUSSULA OCHROLEUCA (Pers. ex Secr.) Fr.

(1) Un primordium très jeune (Pl. 15B, longueur 788 μm, largeur au niveau du rebord 441 μm paraît être édifié à l'aide d'hyphes parfaitement emmêlées, d'une dimension très variable. Parmi les hyphes grêles (diamètre 2–3 μm), on en trouve de plus larges (diamètre 5 μm) et le nombre d'extrémités arrondies et libre s'avère être élevé (diamétre 5–8 μm). Le primordium est enveloppé de poils perpendiculaires à la surface sur le pied et rayonnants sur le chapeau. Particulièrement à la marge piléique, ils sont d'une longueur considérable. On observe des laticifères dans la chair et surtout sous le pourtour du chapeau, leur diamètre s'élève jusqu'à env. 11 μm, leur contenance est un peu métachromatique. Il n'y a pas de piléipellis différencié.

(2) Tandis que la partie piléique s'agrandit, le stipe reste court, de sorte que le primordium prend une forme trapue et robuste (longueur 1,2 mm, largeur environ 1 mm, pas figuré). Les hyphes parallèles ne se montrent qu'à l'extrême marge du piléus. Les extrémités libres et arrondies des hyphes sont répandues dans toute la trame. Dans le stipe, nous remarquons une partie subcorticale avec des hyphes grêles qui fixent davantage l'hématoxyline et une partie centrale, laquelle se compose d'hyphes densément entrelacées (diamètre 3–5 μm), sans méats, qui serpentent, et accusent déjà partout une tendance hélicoïde autour des pelotes de petites sphéro-

cystes; ces parties sont traversées de faisceaux horizontaux. La découverte de rosettes y est un peu difficile, peut-être à cause de la direction longitudinale de la coupe. Par contre, nous avons découvert de telles structures dans la partie supérieure de la trame piléique, sous la surface. Elles sont encore très petites, évidemment dans une phase initiale. Le tissu à spirales nombreuses se continue un peu au-dessus du niveau des lames, mais la plus grande partie de la trame piléique se compose d'hyphes intriquées en tous sens. Les hyphes palissadiques de l'hyménophore commencent à se développer dans l'angle entre le pied et la face inférieure du pileus.

(3) Dans un stade bien plus avancé qui représente déjà un petit champignon (longueur env. 7 mm, largeur du pileus 6,7 mm), on retrouve les mêmes détails structuraux. Les complexes de sphérocystes occupent tout le pied, sauf une zone subcorticale assez épaisse et le centre de la trame piléique, à l'exception d'une zone sous la surface supérieure et la marge recourbée dont la partie inférieure, à partir du niveau des lames, est édifiée d'hyphes parallèles que l'on ne trouve nulle part dans les autres tissus de ces espèces classées autrefois dans les Agaricales, mais bien différentes des autres champignons qui constituent cet ordre (Pl. 15C). Nous avons photographié les pelotes de sphérocystes et des hyphes qui se joignent à elles (tout en accusant souvent une tendance spiroïdale), avec les faisceaux d'hyphes entre elles qui rélèvent le même phénomène quant à leur croissance dans des coupes transversales (Pl. 15D). Les rosettes primaires y sont évidentes, mais les pelotes ont souvent englobé plus d'une rosette par l'activité des hyphes qui les entourent et qui déposent toujours de nouvelles cellules en chaînes hélicoïdes. Dans les parties latérales du chapeau, mais surtout dans la zone subpelliculaire, on rencontre davantage d'îlots moins étendus à une rosette, mais le plus souvent il y a du moins quelques cellules complémentaires, disposées au pourtour d'elles. En examinant attentivement les coupes, on découvre par-ci par-là des hyphes axiles des rosettes qui ont été saisies dans le sens de leur longueur, surtout dans les coupes longitudinales des primordiums. Sur la photographie (Pl. 16A) nous en voyons deux, l'une fortement colorée, probablement à cause d'une contenance protoplasmique abondante, l'autre déjà vide et partiellement détériorée. Ces fragments d'hyphes axiles ont été découverts dans une coupe du troisième stade. Les rosettes manquent également dans une mince couche entre la partie centrale de la trame piléique et les lames. Celles-ci sont caractérisées par un mince médiostrate à hyphes parallèles et un subhyménium large, à cellules d'un petit diamètre, plein de granules fortement colorées qui sont partiellement des noyaux et partiellement des dolipores volumineux. Les lames sont gaînées d'un revêtement ininterrompu de grosses cystides dont les extrémités ne se touchent pourtant pas partout dans les fentes interlamellaires (cf. les autres Russules). L'hyménium n'est pas décurrent sur le pied, mais celui-ci est entièrement revêtu de poils qui accusent seulement parfois la forme d'une cystide en haut du stipe sous le chapeau. Le piléipellis est de nature simple chèz cette espèce, se composant d'éléments dressés, bien serrés, mais cette couche est surmontée de poils métachromatiques lâches dont le contenu paraît avoir disparu (Pl. 16B).

RUSSULA FRAGILIS (Pers. ex Fr.) Fr.

Étant donné que les particularités du développement de cette espèce et de la précédente se ressemblent beaucoup, nous renonçons a décrire le développement de *Russula fragilis* en présentant des stades successifs comme nous le faisons d'habitude. Nous rencontrons par exemple chez les deux espèces la même figure trapue du jeune primordium et la même organisation générale des tissus. Les pelotes de sphérocystes se rangent auprès de l'axe dans le pied aussi bien que dans le jeune chapeau, plus tard elles apparaissent aussi dans les parties latérales de celui-ci. La forme des complexes n'est pas étirée, ni en sens longitudinal comme chez les Lactaires, mais ils sont globuleux, ellipsoïdaux ou oblongs. Nous les avons photographiés (Pl. 16C) pour démontrer que leur genèse se produit de la même manière que chez les autres Russules: d'abord il se forme une rosette primaire, de dimensions peu étendues en tous sens, mais qui peuvent être étirées le long de l'hyphe axile (Pl. 16D), ensuite les faisceaux d'hyphes protenchymatiques environnants déposent de nouvelles cellules contre les rosettes en forme de chaînes spiralées, l'agglomération s'accroît de plus en plus par l'activité de nouvelles hyphes qui s'infléchissent, tandis que leurs extrémités percent le corps cellulaire. Finalement naissent des ensembles de cellules qui ont assimilé plusieurs rosettes. Quand le nombre des pelotes est grand, leur croissance diminue, probablement sous une influence inhibitoire mutuelle des complexes.

L'hyménophore a la structure usuelle des Russules. Nous n'avons pu observer un sub-hyménium celluleux précoce, de sorte que le médiostrate est probablement large chez les jeunes. Les fentes interlamellaires sont étroites et les faces des lames contiguës strictement parallèles. Les fentes sont comblées de cystides volumineuses (Pl. 16E, détail d'un chapeau d'une largeur d'environ 4 mm).

Nous tenons à fixer l'attention sur le développement des cystides chez les Russules, question d'une grande importance sans aucun doute, que nous nous proposons de discuter ici et encore plus loin. En voici la description. Un primordium dont le chapeau a environ 1,6 mm de large, est entièrement enveloppé d'éléments dressés; sur le pied, ce sont des caulocystides en grande partie subcylindriques et cloisonnées (Pl. 16F, par exemple 25,5 × 5 μm), parfois subulées ou avec l'extrémité en collier de perles; sur le chapeau il y a des pilocystides obtuses en forme de cigare, également cloisonnées (Pl. 17A, 35–50 × 6,5 μm); à la marge piléique se trouvent des poils allongés qui représentent simplement l'extrémité d'hyphes parallèles de cette partie (144 × 3–4 μm), et dans l'hyménium on trouve des cheilo- et pleurocystides similaires, obtuses, relativement larges et uniloculaires.

Nous avons photographié la marge piléique et la face inférieure d'un piléus de 2,1 mm de large (Pl. 17B), afin de représenter un ensemble de ces structures superficielles: les poils de la marge, 55×2 μm, les cheilocystides environ 32–48 × 6,5 μm, sans cloisons et obtuses et les caulocystides jusqu'à 48 × 5 μm, fusiformes, subulées, parfois à extrémité en collier de perles et multicloisonnées. Le passage de ces dernières aux cystides hyméniales est assez abrupt, mais dans la zone circumpédiculaire qui touche aux lames, on peut trouver les deux espèces de cystides mêlées.

Finalement, nous avons photographié les poils de la marge piléique du stade plus âgé (diamètre du piléus 4 mm, Pl. 17C), parce que ces poils sont susceptibles d'accuser quelques caractéristiques de cystides: ils sont devenus plus larges, multicloisonnés et ont une extrémité obtuse ou en collier de perles. Il est donc impossible de bien établir les différences entre les pilocystides et ces poils. À la suite de comparaisons analogues, H. Romagnesi (1967: 57) arrive à conclure "Aussi peut-on supposer que la dermatocystide ne serait en somme qu'un poil, analogue à ceux du chevelu fondamental, mais ayant évolué vers une fonction secrétrice". Nous croyons que nos observations ontogéniques soutiennent vigoureusement cette conclusion qui s'applique également aux caulocystides et probablement aussi aux cystides hyméniales.

Lorsque les primordiums sont encore très petits, on voit déjà apparaître entre les pilocystides de fines lignes fortement colorées qui s'élèvent environ jusqu'à la surface du chapeau, tandis que plusieurs cystides dépassent cette face. Elles représentent le contenu protoplasmique des poils pelliculaires (que Romagnesi appelle cuticulaires), dont les parois sont déjà en voie de gélification. Nous avons photographié les deux composantes du piléipellis d'un stade un peu plus avancé (Pl. 17D).

Nulle part, nous ne sommes parvenus à déceler des connexions entre cystides et laticifères chez cette espèce. Quant aux cystides hyméniales, on peut admettre qu'elles n'existent pas et leur absence apparente dans le piléipellis et le cortex du pied peut être attribuée à deux causes: elles y font réellement défaut ou bien la coloration à l'hématoxyline ne permet pas de les dépister. Quoique les cystides elles-mêmes aient évidemment un contenu métachromatique (plus gris que le reste de la coupe), on n'observe pas non plus de laticifères dans la trame des primordiums: leur différenciation morphologique (par exemple la largeur) semble donc être peu notable.

On peut donc conclure que les rapports des cystides et des poils chez cette espèce sont assez compliqués; pour une comparaison plus détaillée avec les autres espèces étudiées, nous renvoyons à la discussion.

ARCANGELIELLA species.

Le développement d'*Arcangeliella stephensii* (Berk. & Br.) Zeller & Dodge = *Octaviania stephensii* (Berk. & Br.) Tul., a été étudié par Fischer (1925; voir Reijnders, 1963: 210–213). Ce Gastéromycète curieux qui, cependant, occupe certainement une place parmi les Astérosporales (Malençon, 1931) commence par être gymnocarpe, le primordium ressemble beaucoup aux jeunes stades de *Russula* et, quoique le stipe reste court, il est bien développé au début, Dans un très jeune stade déjà, la partie latérale du chapeau s'est infléchie et la marge piléique touche à la base du stipe. À la face inférieure du chapeau, pavée d'hyphes palissadiques, se forment des plis qui, en s'anastomosant, feront naître les logettes de la gléba.

Nous devons quelques belles coupes de jeunes primordiums d'une espèce voisine à nos amis M. et Mme Mader de Vienne. Il n'y a qu'un aspect de ce développement

sur lequel nous voulons fixer l'attention: c'est la présence de pelotes de sphérocystes dans le pied et, à un degré moindre, dans la couche supérieure de la trame du piléus. Dès le stade où la largeur est de 1,6 mm et la hauteur de 1,2 mm par exemple (la largeur dépasse la hauteur comme chez beaucoup de primordiums de *Russula*), et avec un stipe de 630 × 500 µm, elles sont présentes dans un tissu emmêlé à hyphes relativement larges (par exemple 5 µm à la base du pied) et à nombreuses extrémités libres (diamètre environ 6,5 µm). La tendance spiralée des hyphes autour de ces îlots de cellules rondes est évidente, mais ces ensembles de petites figures circulaires (auxquelles s'ajoutent les inévitables coupes transversales d'hyphes), sont bien plus courts que chez les Lactaires et même les Russules: pour autant que les coupes bimensionales permettent d'en juger, on dirait qu'ils sont souvent globuleux. Nous ne sommes pas à même de déterminer s'il existe dans tous les cas une hyphe centrale (à fonction inductrice; néanmoins nous avons pu observer une telle hyphe une fois); les pelotes sont plus irrégulières que chez les Lactaires et, dans une certaine mesure, elles sont analogues à de telles agglomérations dans les bulbes des Agaricales en général, auxquelles nous vouerons un autre article. De telles configurations se présentent également dans la couche souscorticale de la trame piléique (mais elles ne sont pas très nettes dans la partie centrale de celle-ci qui consiste en des hyphes lâches, emmêlées), mais là, elles sont beaucoup plus petites. Il est possible que ce tissu extérieur provienne de celui du bulbe primordial, tandis que le tissu intermédiaire (donc des parties centrale et latérale du chapeau) est né par l'activité secondaire de la marge piléique. Les laticifères abondent dans ce tissu.

Nous avons photographié deux de ces pelotes d'un stade plus développé (diamètre 5 mm, hauteur 4 mm, largeur du stipe, déjà très rudimentaire, 950 µm). Un de ces ensembles montre clairement une extrémité libre autour de laquelle se groupent des cellules, l'autre présente la tendance hélicoïde et une chaîne de petites cellules.

Grâce à l'obligeance de M. Mader nous venons de recevoir encore une série de coupes d'*Elasmomyces krjukowensis* Buchh. (= *Macowanites krjukowensis* (Buchh.) Sing. & Smith) qui nous a mis à même de constater que les rapports structuraux relatifs aux complexes de sphérocystes égalent ceux d'*Arcangeliella*. Ces complexes sont encore plus nets chez l'*Elasmomyces* car les sphérocystes sont plus grandes. Ils se montrent dans le stipe, la columella et la partie extérieure de la trame piléique dont la couche extérieure deviendra le péridium, mais ils manquent dans la trame des cloisons de la gléba (formation secondaire). Dans ce cas aussi nous avons pu observer une fois une hyphe axile, de sorte qu'on peut admettre que celle-ci se présente chez ces genres gastéroïdes des Astérosporales de façon plus générale.

DISCUSSION

LA NATURE DE L'HYPHE AXILE.—Nos connaissances actuelles de la structure de la trame de *Lactarius* reposent sur des études anciennes que nous avons énumérées dans l'Introduction. Les observations concernent toute une série d'espèces dont le

Lactarius deliciosus a été étudié le plus souvent. On a été intrigué par la structure curieuse des rosettes et on a essayé de déterminé la vraie nature de l'hyphe axile lorsqu'on avait appris sa présence générale. Nous croyons inutile de mentionner une à une toutes les opinions des chercheurs (cf. aussi l'aperçu de cette littérature chez Lohwag, 1941: 384–388; Reijnders, 1963: 273–274); il suffit de relever les conclusions de Oehm (1931) qui a examiné cette question en dernier lieu. Oehm a observé que l'hyphe axile manquait au centre d'un tiers des rosettes et il a conclu, à la suite de l'application de colorants, qu'elle représente un laticifère chez le *Lactarius deliciosus*. Déjà en vertu de considérations purement morphologiques, nous ne pouvons pas nous rallier à ces conclusions de Oehm. Les hyphes axiles ne sont certainement pas des laticifères chez le *Lactarius mammosus* et elles sont censées avoir une toute autre function. Quoique la largeur des hyphes soit en général un critère peu favorable à la détermination de leur vraie nature, les laticifères sont en moyenne tellement plus larges que les hyphes axiles, que l'on les distingue facilement dans la coupe, même quand ces dernières ne sont pas encore entourées de sphérocystes. Certes, le nombre de laticifères minces est aussi élevé dans les coupes et des cas de doute sont possibles. Alors, on se rendra compte de la deuxième grande différence entre ces éléments. Les hyphes axiles sont cloisonnées et la distance des cloisons n'est pas toujours grande. En général, les auteurs sont d'accord sur l'absence des cloisons dans les laticifères, ou bien on y a rencontré des septums quand ils sont jeunes, mais ceux-ci disparaissent plus tard, du moins en partie, de sorte que les septums intacts sont toujours bien éloignés les uns des autres. Troisièmement: les hyphes axiles se dégradent déjà bientôt, de sorte que l'on rencontre dans les coupes de jeunes primordiums de telles hyphes centrales qui sont vides et qui se fragmentent bientôt. Nous avons vu plus d'hyphes axiles peu colorées et fragmentées que de telles hyphes de teinte foncée et bien intactes; ces dernières se présentent principalement dans les stades initiaux, tel le premier stade de *Lactarius mammosus*. Les laticifères, par contre, restent, s'élargissent encore et sont caractérisés par un contenu dense, bien colorable.

Ces trois critères sont assez convaincants à nos yeux pour établir des différences fondamentales entre laticifères et hyphes centrales; par surcroît, nous avons essayé, quelques colorants pour voir s'il est possible de produire par cette voie une différenciation déterminante entre ces éléments. Il va de soi que nos coupes sont peu appropriées à cette fin, car les solvents comme l'éthanol, le xylène, etc. ont enlevé beaucoup de substances qui peuvent être cruciales à ce point de vue. Aussi n'avons-nous pas réussi à obtenir un résultat satisfaisant. Les coupes qui étaient colorées à la safraninevert rapide montraient effectivement une différenciation. Il y avait dans les coupes des hyphes vasiformes qui avaient pris une teinte rouge, tandis que les autres éléments étaient bleu-vert. Ce n'étaient pas les fragments des vaisseaux les plus larges qui se dessinaient de cette manière; ils étaient bleu-vert comme l'autre tissu, mais dans ces fragments se trouvaient par-ci par-là des taches rouges: les laticifères les plus larges n'accusaient cette couleur que par endroits. Il y avait également des fragments d'hyphes axiles qui étaient teintés de rouge; il faut donc constater le même comportement envers ces colorants de ces dernières et des vaisseaux minces. Mais la

plupart des hyphes axiles étaient déjà vides, donc un peu colorées en bleu. Environ le même phénomène se produisait avec la méthode de Mallory (orange G, bleu d'aniline, fuchsine acide), tandis que la méthode de Flemming (triple coloration: safranine, violet de gentiane, orange G) nous procurait des coupes très belles et bien colorées, mais d'une teinte uniforme. Probablement, la très forte capacité colorante du violet de gentiane en était la cause. Le bleu de crésyl, colorant métachromatique, ne donnait pas non plus de résultats remarquables. Les coupes qui avaient pris une teinte bleu foncé renfermaient des laticifères qui avaient absorbé beaucoup de colorant et qui, observés dans l'ammoniaque et à la lumière du jour, accusaient une teinte rouge foncé peu constante.

Les différences susmentionnées des deux premières colorations entre les tubes plus minces qui prennent davantage une couleur rouge que les vaisseaux plus larges, pourraient se rapporter à la différence entre hyphes oléifères et laticifères que l'on distingue après Fayod (voir aussi Lenz, 1954). Romagnesi (1967) signale la présence des deux espèces d'hyphes dans la chair des Russules, mais il ne se sert pas du terme hyphe oléifère. Si une telle coloration était déterminative (mais nous croyons qu'il n'en est pas ainsi), elle pourrait désigner une certaine affinité entre les hyphes oléifères et les hyphes axiles des pelotes de sphérocystes.

Il vaut mieux considérer la fonction des hyphes axiles au lieu de tirer de telles conclusions qui sont sujettes à caution. Car tout le processus de la naissance des sphéroscystes par l'activité d'hyphes se tournant autour de l'hyphe axile, suggère la conclusion que cette dernière exerce une influence inductrice, propice à une répartition favorable des groupes de sphérocystes. À l'heure actuelle, cette manière de voir s'impose, mais les auteurs précédents ne connaissaient pas encore l'importance énorme de ce principe en embryologie. Nous proposons donc de nommer les hyphes axiles: hyphes inductrices.

L'absence de l'hyphe centrale dans un tiers des rosettes chez les carpophores adultes de *Lactarius deliciosus* s'explique par la dégradation rapide des hyphes inductrices quand elles se sont acquittées de leur tâche. Weiss (1885) et Oehm (1931) ont également observé plus d'un petit cercle au centre des rosettes; ils les attribuent à des ramifications des hyphes axiles. Nous n'avons pas observé plus d'une hyphe centrale dans les rosettes de *Lactarius mammosus*, ce qui ne veut pas dire qu'elles n'existent pas chez les autres espèces.

LACTARIUS ET RUSSULA.—Les Lactaires présentent donc un système inducteur d'hyphes minces qui, dans les très jeunes stades, sont orientées en sens longitudinal et qui sont probablement issues d'hyphes ordinaires protenchymatiques (mais l'examen de cette origine est extrêmement difficile dans les coupes microtomiques). Autour de ces hyphes naissent les sphérocystes au bout d'hyphes hélicoïdes qui accusent généralement dans le pied une direction transversale. Ainsi se forment ces complexes de sphérocystes qui sont étirés, du moins dans le stipe. Nous avons appelé rosette primaire l'ensemble d'une hyphe inductrice avec un cercle de sphérocystes autour d'elle. Le nombre des rosettes primaires réunies dans les complexes est

toujours réduit; dans la plupart des cas, ils ne se composent que d'une rosette primaire.

Dans l'introduction, nous avons touché à la question de l'absence apparente des rosettes primaires dans la chair des Russules. On doute parfois des anciennes observations, mais il est possible que Schultz (1822) les ait vues. Dans la trame des Russules adultes, on trouve des amas de sphérocystes (presque toute la chair en est remplie) avec quelques faisceaux d'hyphes protenchymatiques qui restent. Néanmoins, il est possible de les dépister dans les coupes de jeunes stades, comme nous l'avons montré. Au début, elles sont également étirées en sens longitudinal ou dans le chapeau en sens radial. Mais les faisceaux d'hyphes qui tournoient à leur périphérie déposent les sphérocystes de manière à englober plusieurs rosettes primaires dans un complexe. Les complexes de sphérocystes sont donc plus irréguliers chez les Russules et plus larges que chez les Lactaires, et plus tard, quand les hyphes inductrices se sont désagrégées, on n'observe plus la structure typique des rosettes; donc les sphérocystes font simplement partie d'un ensemble plus étendu.

Il est à noter que nous avons trouvé des îlots de sphérocystes dans le pied rudimentaire de l'*Arcangeliella* et de l'*Elasmomyces*, membres gastéroïdes des Astérosporales. Il y a des structures qui évoquent celle des rosettes primaires, la présence d'une hyphe axile a été observée également chez ces espèces; mais la structure des groupements de sphérocystes chez l'*Arcangeliella* species paraît être plus simple, en évoquant davantage celle de pelotes comparables dans les bulbes d'Agaricales vrais (voir aussi Phylogénie à la suite de la Discussion).

LE PILÉIPELLIS ET LES CYSTIDES.—Romagnesi se sert des termes cutis, subcutis et épicutis. Selon lui, le cutis peut se composer d'hyphes emmêlées (*Russula foetens*), dans d'autres cas le cutis est constitué par des hyphes à peu près parallèles ou tout au plus faiblement emmêlées. L'épicutis est généralement caractérisé par des hyphes dressées; il représente la partie la plus intéressante et renferme les éléments qui ont été décrits par Romagnesi d'une manière très détaillée au profit de la taxinomie. Comme nous avions adopté la nomenclature de Lohwag (Reijnders, 1963: 25), nous parlons de cortex, cutis et derme dans un sens restreint. Le cutis est toujours un revêtement à hyphes couchées parallèles à la surface, le derme à hyphes redressées. C'est pourquoi, nous préférons désigner les tissus que Romagnesi a appelés subcutis, cutis et épicutis par les noms: subpellis, piléipellis et épipellis, selon une suggestion de C. Bas qui a proposé le terme piléipellis pour l'ensemble des revêtements qui se restreignent au chapeau, donc non pas pour les voiles.

Russula anthracina a un piléipellis complètement gélifié dans les stades un peu plus avancés; cette couche est née d'hyphes approximativement dressées, mais non pas strictement parallèles, qui se collent les unes aux autres (Pl. 14B). Quelques extrémités de ces hyphes se recourbent et s'appliquent contre la gelée. Plus tard, les hyphes dans celle-ci sont franchement emmêlées (Pl. 14C). Romagnesi appelle cette couche l'épicutis, mais alors le cutis manque, car en-dessous on ne trouve que des hyphes banales, intriquées, qui ne se distinguent point de celles de la trame entre les îlots de sphérocystes. Il n'y a guère de pilocystides.

Russula ochroleuca montre dans un stade très jeune de longe poils autour de tout le primordium; parmi les poils du stipe on observe des éléments qui accusent la forme d'une caulocystide. À la base de ces poils métachromatiques, à pigment incrustant, se développent sur le chapeau des hyphes très minces, également dressées (cf. l'espèce de *Russula* qui suit); ce sont les éléments qui se gélifient après. Nous n'avons pu observer d'"hypoderme de sphérocystes" (Romagnesi, 1967: 380).

Dans les pages précédentes, nous avons amplement décrit les cystides de *Russula fragilis:* les caulocystides cloisonnées et souvent pointues, les cheilo- et pleurocystides en forme de cigare sans cloisons et les pilocystides également obtuses, mais multi-cloisonnées. Le piléipellis s'achève un peu plus tard par le développement d'éléments minces également dressées en grande partie, et qui commencent d'emblée à se gélifier. Ce sont donc les poils "cuticulaires ou épicuticulaires" de Romagnesi, mais au début ils ne s'élèvent pas jusqu'au niveau des extrémités des cystides.

On trouve à peu près les mêmes particularités chez *Russula emetica* (Schaeff. ex Fr.) S. F. Gray dont nous avons publié quelques structures du développement dans notre livre de 1963 (Reijnders, 1963: 40–42, pl. 7 et 8). Par conséquent, les trois types de cystides et les longs poils de la marge piléique se présentent également chez cette espèce. Les pilocystides sont très grandes; en dessous on observe des poils d'abord en massue; leur gélification semble être plus tardive.

Russula olivacea (Schaeff. ex Secr.) Fr. est d'emblée également recouverte d'un chevelu, mais sans cystides. Les poils accusent des formes très variées, surtout sur le chapeau: ils sont relativement longs et plusieurs d'entre eux ont des articles élargis; ils sont par exemple ampullacés, mais parfois aussi en massue par un article terminal gonflé. À la marge piléique, les poils sont élancés.

Avant de tirer une conclusion générale sur une fonction éventuelle des cystides chez les Russules, nous rappelons un phénomène qui se présente probablement chez la plupart des espèces de ce genre, sinon chez toutes, c'est que les fentes inter-lamellaires, dites vallécules, sont d'abord parfaitement bourrées de cystides dont les extrémités se touchent les unes les autres. Nous avons représenté ces structures chez *Russula emetica* dans notre livre de 1963 (pl. 8 figs. 1 et 2) et pour *Russula fragilis* dans le présent article (Pl. 16E). En les comparant à la situation des pilocystides chez *Russula fragilis* (Pl. 17A), où celles-ci se serrent également de manière à former une couverture unie, on est forcé d'admettre que les cystides, comme les poils de ces revêtements, servent à diminuer l'évaporation. Quand on considère toutes les formes passagères entre poils et cystides, cette conclusion s'impose encore davantage. La sécheresse affecte en premier lieu les revêtements des primordiums qui présentent souvent des détériorations dues à cette cause. Ceci ne veut pas dire que cette adaptation pendant l'état primordial constitue la seule fonction des cystides (cf. aussi Reijnders, 1963: 292). Nous sommes donc d'accord avec Romagnesi (1967: 57): lorsqu'il compare les "dermatocystides" et les "poils": il attribue aux premières une fonction sécrétrice, mais celle-ci n'a pas été prouvée à l'exception d'autres encore et ceci regarde également les cystides hyméniales.

Résumant, nous concluons: Les primordiums de beaucoup d'espèces de Russules

sont enveloppés d'emblée par un chevelu dans lequel peuvent se présenter des éléments accusant la forme de cystides et qui peut se gélifier localement. Le piléipellis montre souvent une différenciation de ces éléments: les cystides apparaissent d'abord de manière à constituer une couche unie, de petits poils dont les parois se gélifient naissent bientôt au niveau de la base des cystides.

PHYLOGÉNIE.—Le *Lactarius mammosus* dispose donc dans ses carpophores d'un système d'hyphes susceptibles d'exercer une influence inductrice en faveur de la naissance de complexes de sphérocystes: des cellules qui se gonflent beaucoup et qui constituent finalement la majeure partie de la trame. On peut admettre que tous les Lactaires sont pourvus de telles hyphes, comme toutes les espèces de *Russula*. En étudiant plusieurs parties des coupes de primordiums, on remarque que les hyphes inductrices ne sont pas accompagnées partout de chaînes de sphérocystes. Il faut donc qu'il y ait d'autres facteurs qui déterminent la naissance des sphérocystes. Nous les rencontrons chez les Lactaires, près de l'axe du primordium, mais non pas dans les tissus périphériques et ceux-ci en sont également dépourvus chez les Russules. La formation des pelotes de sphérocystes commence pour les deux genres à la base du pied et au centre de la trame piléique, de sorte que la succession de ce processus est basifuge et centrifuge. On en trouve les premières traces au centre du pied en bas et au milieu de la trame piléique. Il est probable que les pelotes de sphérocystes enraient la croissance d'autres masses avoisinantes, en d'autres termes qu'elles exercent une influence inhibitoire les unes sur les autres. En vertu de telles considérations, l'influence inductrice locale devient plausible.

Une autre caractéristique des primordiums des Astérosporales, est que la plus grande partie de leur trame est remplie d'hyphes emmêlées en tous sens; on ne trouve les hyphes fasciculées et parallèles qu'à l'extrême marge du chapeau et sur la face inférieure de celui-ci pour constituer la trame des lames. Par lesdits tissus, ces primordiums ont plutôt l'air d'un bulbe sorti de la terre. Nous avons déjà relevé que les complexes de sphérocystes se trouvent également dans le stipe rudimentaire de l'*Arcangeliella* et d'*Elasmomyces*, comme probablement dans la columella, mais qu'ils sont là moins étendus, parfois un peu irréguliers et parfois sans hyphe axile décelable. Une étude provisoire de bulbes d'Agaricales, nous a révélé l'existence d'une série de structures susceptibles d'éclaircir les rapports tels qu'on les trouve chez les Astérosporales. Des grumelots d'éléments courts, formés d'hyphes densément intriquées, d'hyphes enroulées, accusant une croissance hélicoïdale, de multiples extrémités libres de ramifications des hyphes; on retrouve ces structures dans les bulbes d'espèces du genre *Agaricus* par exemple, mais plutôt isolées et non pas réunies en cet ensemble caractéristique de la trame des Astérosporales: les îlots de sphérocystes nés de rosettes primaires.

Ensuite, on est porté à des comparaisons encore plus audacieuses avec une trame également déviante de celle des autres Agaricales, celle des Amanitacées. Mais nous renonçons à entamer ces questions ici; nous nous réservons de les traiter dans un article suivant sur la structure des bulbes en général.

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Summary

In *Lactarius*, as well as in at least some species of *Russula*, the development of clumps of spherocysts, occurring in the trama of the carpophores is initiated by the formation of structures which, as seen in section, resemble rosettes. These consist of a central hypha sheathed with small spherocysts.
The clumps of spherocysts in *Russula* are in general much larger, and usually more primary rosettes are involved. This condition contrasts with the narrow complexes in *Lactarius* which are drawn out longitudinally and generally arranged round the axis of the primordium, at least in the stipe.
The central hypha is believed to induce locally the formation of chains of spherocysts by exerting directional influence upon the surrounding protenchymatic hyphae while stimulating them to produce cells. After this action the central hypha soon disintegrates.
Clumps of spherocysts occur also in the rudimentary stipe of *Arcangeliella* and in *Elasmomyces*; it is probable that here, too, a certain hypha is responsible for their formation.
The complicated construction of the trama of the Asterosporales may correspond with some structures generally present in the bulbs of Agaricales consisting of knots of much entangled hyphae with short cells, curving and winding hyphae and many free ends of hyphal ramifications.
In the primordia of Asterosporales a considerable portion of the trama consists of a similar intricate and polymorphous tissue, parallel hyphae being found only at the extreme margin of the pileus and in the trama of the gills.
The majority of the cystidia of *Russula* is homologous to hairs, one of the functions of these elements being the protection of the primordium against exsiccation.

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LÉGENDE DES PLANCHES 13–17

PLANCHE 13

Figs. A–E. *Lactarius mammosus*. — Fig. A. Chaînes de sphérocystes avec les hyphes axiles (a) et laticifères (l) dans l'écorce de la partie inférieure du stipe d'un jeune primordium × 250. — Fig. B. Hyphes axiles (a) avec sphérocystes naissantes et laticifères (l) dans la partie supérieure du stipe du même primordium × 250. — Fig. C. Coupe longitudinale d'un jeune primordium × 25. — Fig. D. Coupe transversale d'un stipe d'un jeune primordium × 62,5. — Fig. E. Partie centrale du stipe du même primordium × 250.

PLANCHE 14

Fig. A. *Lactarius mammosus*. Rosette avec l'extrémité d'une hyphe axile (a) dans une coupe transversale du même primordium × 250.

Figs. B–E. *Russula anthracina*. — Fig. B. Piléipellis d'un jeune stade × 250. — Fig. C. Piléipellis d'un stade avancé × 160. — Fig. D. Coupe tangentielle du chapeau d'un stade avancé × 25. — Fig. E. Partie inférieure de la trame piléique avec une cystide (c) traversant le subhymenium × 160.

PLANCHE 15

Fig. A. *Russula anthracina* Rosettes primaires (r) descendant dans la trame des lames × 250.
Figs. B–D. *Russula ochroleuca.* — Fig. B. Marge piléique et trame d'un très jeune stade × 250. — Fig. C. Partie latérale du chapeau d'un stade relativement avancé × 25. — Fig. D. Pelotes de sphérocystes dans la trame × 250.

PLANCHE 16

Figs. A, B. *Russula ochroleuca.* — Fig. A. Hyphes inductrices au centre de chaînes de sphérocystes dans la partie supérieure de la trame piléique d'un stade avancé × 250. — Fig. B. Piléipellis × 500.
Figs. C–F. *Russula fragilis.* — Fig. C. Rosettes primaires et agglomérations de sphérocystes × 250. — Fig. D. Hyphe axile dans la trame piléique × 250. — Fig. E. Lames et cystides d'un primordium dont le chapeau a une largeur de 4 mm × 250. — Fig. F. Caulocystides d'un primordium × 500.

PLANCHE 17

Figs. A–D. *Russula fragilis.* — Fig. A. Pilocystides d'un primordium × 500. — Fig. B. Poils (a) de la marge piléique, cheilocystides (b) et caulocystides (c) d'un primordium dont le chapeau a une largeur de 2,1 mm × 250. — Fig. C. Poils de la marge d'un piléus qui a une largeur de 4 mm × 500. — Fig. D. Piléipellis d'un stade relativement avancé × 500.
Figs. E, F. *Arcangeliella* spec. — Fig. E. Pelotes de cellules courtes dans le tissu du pied × 416. — Fig. F. Pelote de sphérocystes montrant la tendance spiralée × 600.

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SOME OOMYCETES AND ZYGOMYCETES WITH ASEXUAL ECHINULATE REPRODUCTIVE STRUCTURES

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(With Plate 18 and two Text-figures)

Fungi producing ornamented asexual structures and belonging to the Oomycetes (*Trachysphaera*) or Zygomycetes (*Azygozygum*, *Mortierella*) are described. They were studied by light and scanning electron microscopy while also mating experiments and carbohydrate analyses were performed. *Azygozygum chlamydosporum* is closely related to *Mortierella indohii* and therefore *Azygozygum* is considered to be a synonym of *Mortierella*. *Mortierella echinosphaera spec. nov.* is also closely related, but no zygotes are known, only ornamented chlamydospores have been observed. Absence of glucuronic acid and fucose and a low glucosamine content in *Trachysphaera fructigena* show that it belongs to the Oomycetes.

Introduction

A number of Oomycetes and Zygomycetes produce ornamented reproductive structures. In the Oomycetes these structures are generally the sexual state of the fungus, the oogonia; ornamented asexual structures (conidia, chlamydospores) only have been observed in the genus *Trachysphaera* Tabor & Bunting. In the Zygomycetes ornamented chlamydospores (stylospores) are known in the genera *Azygozygum* Chesters and *Mortierella* Coemans. Because the cell wall composition of Oomycetes differs greatly from that of Zygomycetes, cell wall analysis should yield definite taxonomic information.

Tabor & Bunting (1923) described a disease of cocoa and coffee fruit, reminescent of that caused by *Phytophthora faberi* Maubl. The causal agent, *Trachysphaera fructigena*, is characterized by oogonia and amphigynous antheridia, indicating that is is related to *Phytophthora*. *Trachysphaera fructigena* also produces numerous spiny 'conidia' originating from branched stalks which form several vesicles. These vesicles give rise to short projections which may bear either conidia or extend to form another vesicle. Zoosporangia and zoospores are unknown. Tabor & Bunting noticed that when the sex organs are absent, the species may be mistaken for *Muratella* (=*Cunninghamella*).

Azygozygum chlamydosporum Chesters is characterized by the absence of sporangia and the presence of zygospores and spiny chlamydospores, the latter being intercalary

or terminal on erect stalks. Chesters (1933) recognized the affinity with *Mortierella* because the chlamydospores resemble those of *Mortierella polycephala* Coemans. Hesseltine & Ellis (1973) placed the genus provisionally in the Mucoraceae, but also mentioned the Endogonaceae as a possible alternative.

In *Mortierella* similar chlamydospores are known. They have often been confused with one-spored sporangioles, which are borne on sporangiophores with swollen bases, gradually tapering toward the apex (Gams, 1963). Chlamydospores, when terminal, are formed on hyphae of equal diameter over their entire lenght. *Mortierella indohii* Chien is described (Chien *& al.*, 1974) as a species lacking sporangia. In other respects *M. indohii* also closely resembles *Azygozygum chlamydosporum*, but it was placed in *Mortierella* because of the invested zygospores.

The carbohydrate composition of cell walls is a useful criterion for distinguishing larger groups of fungi and can be of importance when the available morphological characters are insufficient. Bartnicki-Garcia (1968, 1970) distinguished eight groups within the fungi, based on overall cell wall composition. *Pythium* and related genera were included in the cellulose-glucan group (Oomycetes), whereas *Mortierella* was placed in the chitosan-chitin group (Mucorales). In addition to glucans, chitosan and chitin, other cell wall carbohydrates may serve as indicators for subdividing fungal taxa. Intact cell analysis, applied to this study, is an abbreviated procedure allowing the prediction of qualitative differences in cell wall composition. This approach has been successfully applied to taxonomic problems with bacteria (Jantzen *& al.*, 1972; Lechevalier & Lechevalier, 1970) and to fungi of the *Ceratocystis-Ophiostoma* group (Weijman & de Hoog, 1975).

Methods

All strains were grown on cornmeal, 2% malt, soil-extract and potato-carrot agars. In some cases a sucrose-nitrate medium was used (Chesters, 1933). Mating experiments were carried out on 'Bambix' agar which is analogous to Kuhlman's (1972) 'Pablum' agar (Bambix is a commercial baby food, produced by Nutricia, Zoetermeer, The Netherlands), consisting of 12.5 gr Bambix, 15 gr agar and 1 liter distilled water; inocula were placed about 0.5–1 cm apart in Petri dishes and incubated at 15 or 20°C.

For scanning electron microscopy (SEM) chlamydospores were transferred to squares of double-sided adhesive tape, attached to specimen stubs and air-dried for 24 hours. In other cases small pieces of agar containing mycelium with chlamydospores were fixed in osmium tetroxide, washed in distilled water, dehydrated in an alcohol-series, passed through an amylacetate-series, dried in a Polaron critical point drying apparatus under CO_2 and attached to specimen stubs. The specimens were coated with gold in a sputter coater for two minutes at 1.2 kV. Preparations were examined with a Cambridge Stereoscan microscope at an accelarating voltage of 15 kV.

For carbohydrate analysis the strains were grown on glucose (2%)-peptone (1%)-yeast extract (0.5%) medium in conical flasks for ten days at 25°C on a rotary shaker, operated at 100 rpm. Carbohydrates released from intact cells by acid hydrolysis were analysed by gas-liquid chromatography (GLC) as their trimethylsilyl ethers as described by Weijman & de Hoog (1975).

Hexosamines were estimated quantitatively by a modification of the Elson-Morgan method, as described by Gatt & Berman (1966), using glucosamine-HCl as a standard. Prior to the analysis samples were hydrolyzed with 2N HCl under N_2 for 12 h. at 110°C. Measurements were taken with a recording Perkin-Elmer 402 UV-visible spectrophotometer using glass cuvettes.

MATERIAL EXAMINED

Mortierella chlamydospora (Chesters) Plaats-Niterink: CBS 120.34, type strain, *C. G. C. Chesters*, from *Antirrhinum majus* roots, England. — CBS 529.75, I. Blok, from *Saintpaulia* roots, The Netherlands.

Mortierella echinosphaera Plaats-Niterink: CBS 574.75, *J. H. van Emden*, from soil, The Netherlands. — CBS 575.75, type strain, *A. J. van der Plaats-Niterink*, from *Begonia* roots, The Netherlands. — CBS 576.75, *P. S. W. Liu*, from *Citrus mitis*, Malaysia.

Mortierella indohii Chien: CBS 720.71 (—), type strain, *C, Y. Chien*, from animal dung, U.S.A. — CBS 655.70 (—), CBS 666.70 (—), *J. H. van Emden*, from soil, The Netherlands, — CBS 219.72 (—), *J. W. Veenbaas-Rijks*, from soil, The Netherlands. — CBS 220.72 (—), *L. H. Kaastra-Höweler*, from greenhouse soil, The Netherlands. — CBS 331.74 (—), *C. L. de Graaff*, from wheat roots, The Netherlands. — CBS 460.75 (+), *C. Y. Chien*, from animal dung, U.S.A. — CBS 528.75 (—), *W. F. O. Marasas*, from begasse, S. Africa.

Mortierella polycephala Coemans: CBS 649.68, *C. W. Hesseltine*.

Pythium oligandrum Drechsler: CBS 382.34, *C. G. C. Chesters*, from *Viola* spec. roots, England.

Pythium spinosum Sawada: CBS 290.31, *S. F. Ashby*, from *Carica papaya*, S. Africa.

Trachysphaera fructigena Tabor & Bunting: CBS 315.31, type strain, *R. Bunting*, from *Theobroma cacao*, Goldcoast.

RESULTS AND DISCUSSION OF THE CHEMICAL STUDY

The carbohydrate analysis of intact cells of *Trachysphaera* reveals, as in *Pythium spinosum* and *P. oligandrum*, a low hexosamine content and the absence of glucuronic acid and fucose (Table 1; Fig. 1a, 1b). If intact cell samples differ considerably in hexosamine content, this difference would be even more pronounced between purified cell-wall samples. On the other hand, if fucose and glucoronic acid are absent in the intact cells, they may be excluded as important cell wall components. Hexosamine detected in oomycetous fungi is probably not released from chitin (Sietsma & *al.*, 1969), although the absence of chitin in Oomycetes has not been conclusively demonstrated in intact cells (Lin & Aronson, 1970).

The following strains (studied only by GLC) yielded the same sugar pattern as the *Mortierella* strains listed in Table 1: *M. indohii* CBS 665.70, CBS 666.70, CBS 219.72,

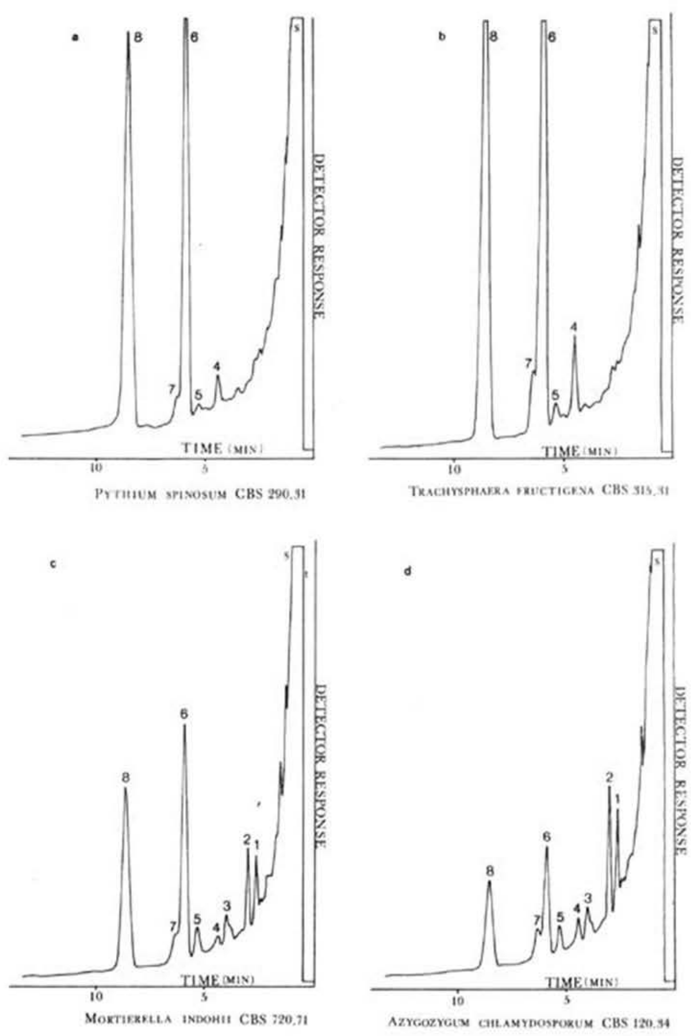

Fig. 1. — Gas chromatograms of carbohydrates (TMS derivatives) released from intact fungal cells by acid hydrolysis. Column temperature: 180°C. Liquid phase: 3% OV–1 coated on Chromosorb W(HP).

S: solvent peak. 1: α-fucose; 2: β-fucose; 3: glucuronolacton; 4: α-mannose; 5: α-galactose; 6: α-glucose; 7: β-mannose and β-galactose; 8: β-glucose.

Table 1. Distribution of hexosamine, fucose and glucuronic acid in some species of *Pythium*, *Trachysphaera*, and *Mortierella*.

strain		hexosamine (%)[1]	fucose[2]	glucuronic acid[2]
Pythium spinosum	CBS 290.31	0.5	—	—
Pythium oligandrum	CBS 382.34	1.0	—	—
Trachysphaera fructigena	CBS 315.31	0.5	—	—
Mortierella chlamydospora	CBS 120.34	6.0	+	+
	CBS 529.75	6.0	+	+
Mortierella indohii	CBS 720.71	5.0	+	+
	CBS 528.75	6.5	+	+

CBS 220.72, *M. echinosphaera* CBS 574.75, CBS 575.75, and *M. polycephala* CBS 649.68. Figures 1c and 1d show characteristic patterns.

Fucose and glucuronic acid polymers are among the common polysaccharides in Zygomycetes (Gooday, 1973). The presence of these components could be demonstrated in all *Mortierella* species studied, but it is not possible to further subdivide these strains on the basis of the chemical data, the gas chromatograms being almost identical. The hexosamine detected in hydrolysates of intact Zygomycete cells is probably derived from chitosan and chitin (Kreger, 1954; Bartnicki-Garcia, 1968).

DESCRIPTIONS AND TAXONOMIC CONCLUSIONS

(1) TRACHYSPHAERA FRUCTIGENA Tabor & Bunting.—Plate 18c

Colonies on cornmeal and soil-extract-agars submerged with some scanty aerial mycelium bearing clusters of conidia. Hyphae thin-walled, up to 6 μm wide. Oogonia subglobose or pyriform, 25–32 × 24–28 μm, with irregular sac-like outgrowths, varying from short blunt projections to long finger-like processes which may be curved or forked. Antheridia amphigynous, 11–15 × 11–16 μm. Oospores globose, aplerotic, 21–27 μm in diameter, wall 3–4 μm thick. Conidiophores simple or branched, bearing a terminal vesicle or complex of vesicles from which projections arise, reaching up to 30 μm and bearing conidia. Conidia hyaline to yellowish, globose, (24–)32–43(–50) μm in diameter, wall 3–4 μm thick, covered with conical spines up to 3 μm long with blunt, elongated and sometimes slightly curved tips. Daily growth rate: 10 mm at 25 °C.

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[1] Average on the basis of intact cell dry weight.
[2] Determined by GLC. Glucuronic acid was analyzed in the lactone form.

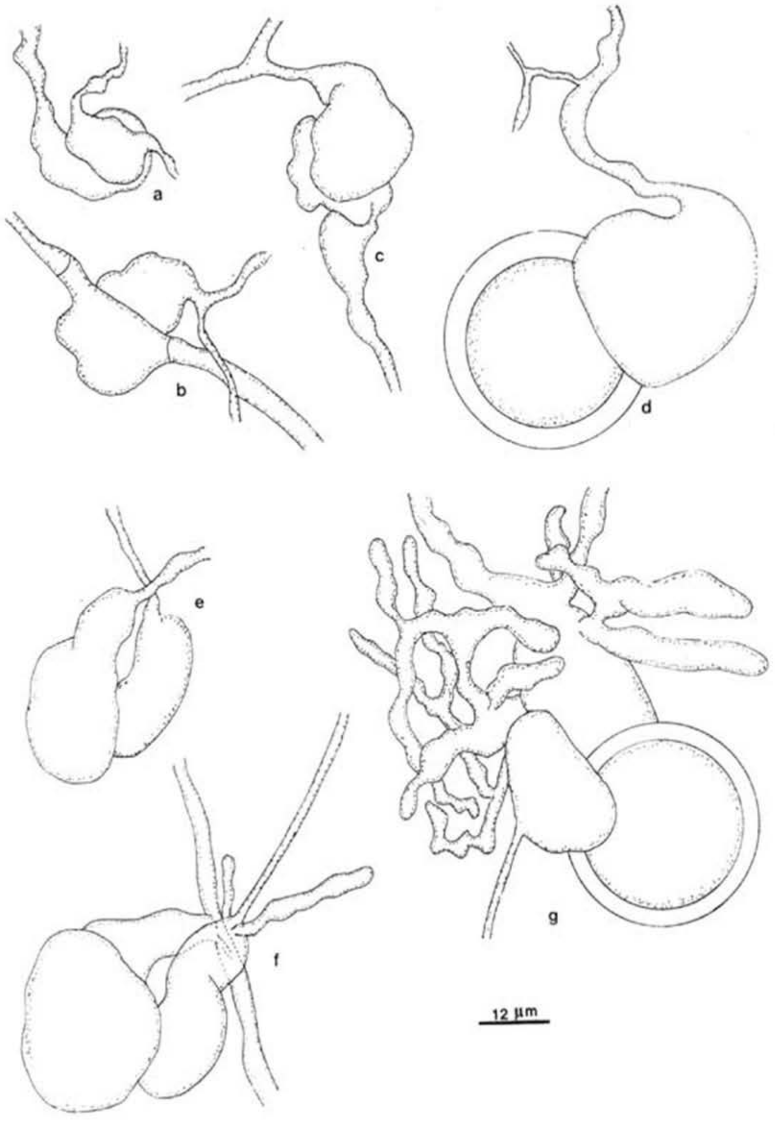

Fig. 2. — Various stages in the development of zygospores. — a–d. *Mortierella chlamydospora*. — e–g. *M. indohii*.

(2) **Mortierella chlamydospora** (Chesters) Plaats-Niterink *comb. nov.*
Plate 18 b, Fig. 2a–d

Azygozygum chlamydosporum Chesters *in* Trans. Br. mycol. Soc. **18**: 213, 1933 (basionym).

Colonies on cornmeal agar form a low white aerial mycelium; on soil extract agar only scanty aerial mycelium develops. No or indistinct *Mortierella*-like odour. Hyphae 1–4 μm wide. Sporangia unknown. Chlamydospores terminal and intercalary in the aerial and submerged mycelium on 2–4 μm wide stalks. Chlamydospores globose or elongated when intercalary, with a varying number of spines or sometimes smooth when submerged, (12–)15–26(–28) μm in diameter, wall 1.2 μm thick. Spines cylindrical, about 1 μm wide and up to 4 μm long, with a blunt tip which may be curved. On sucrose-nitrate medium at 20 °C zygospores are formed after one week in single cultures of all strains examined. When mature they are naked, thick-walled, 25–50 μm in diameter, with one inflated suspensor, 25–40 μm in diameter, the other suspensor having disappeared. The initial stage consists of two approaching swollen hyphal tips which later fuse. One suspensor swells until it is nearly the same size as the zygospore which becomes thick-walled. The other suspensor is caducous. In rare cases both zygospore and large suspensor become thick-walled and the thick seperating wall between both cells may be partially or completely absorbed as illustrated by Chesters (1933). Daily growth rate: 9 mm at 25 °C.

(3) **Mortierella echinosphaera** Plaats-Niterink *spec. nov.*—Plate 18 c–d

Coloniae tenues, interdum chlamydosporis farinosae. Mycelium aerium sparsum, albidum. Odor distinctus abest. Hyphae hyalinae, 1–5(–7) μm diametro. Sporangiophora absunt. Chlamydospora normaliter intercalares, interdum terminales, globosae vel elongatae, dense spinulosae, raro glabrae, crassitunicatae, (14–)17–28(–33) μm diametro. Spinulae cylindricae, ad 5 μm longae. Typus: CBS 575.75, e radicibus Begoniae, in Neerlandia.

Colonies on cornmeal agar form a low irregular aerial mycelium, sometimes powdery due to numerous chlamydospores; on soil extract agar submerged, sometimes with some scanty aerial mycelium. No characteristic odour. Hyphae 1–5(–7) μm wide. Chlamydospores usually intercalary, occasionally terminal, in aerial and submerged mycelium, globose to elongated, densely spiny or rarely smooth-walled, (14–)17–28(–33) μm in diameter, wall up to 3 μm thick. Spines cylindrical, sometimes flexuous, with a blunt tip, 1 μm wide and up to 5 μm long. Number of spines variable, all intermediates from smooth to markedly spiny chlamydospores can be found. Sporangia and zygospores unknown. Daily growth rate: 13 mm at 25 °C.

(4) Mortierella indohii Chien.—Plate 18a; Fig. 2e–g

Colonies on cornmeal agar with low cottony aerial mycelium, sometimes appearing powdery due to numerous chlamydospores; on soil extract agar aerial mycelium very scanty. Odour characteristic, garlic-like. Hyphae hyaline, 1–4 μm wide. Chlamydospores terminal or sometimes intercalary, originating both from the aerial mycelium as well as from the submerged parts, mostly on simple or sparingly branched stalks with the same diameter as the hyphae, 10–150 μm long, sometimes subterminally swollen. Chlamydospores globose, (11–)14–21(–27) μm in diameter,

occasionally subglobose, limoniform or elongated when intercalary, spiny, rarely smooth, particularly when submerged. Spines cylindrical with a blunt tip, 1 µm wide and up to 3 µm long. On 'Bambix' agar at 15 °C zygospores are formed after one week in the mating line between two compatible strains. Zygospores smooth, globose to subglobose, 24–50 µm in diameter, wall 3–6 µm thick. Suspensors unequal, the larger one developing a mass of strongly branched irregular hyphae at its base. Sporangia unknown. Daily growth rate: 8–10 mm at 25 °C.

The conidia of *Trachysphaera fructigena* show some resemblance to the spores or chlamydospores (the term 'stylospores' is confusing and should be abandoned (Gams, personal communication)) of some Mucorales (e.g. *Cunninghamella*, *Mortierella*), but the sexual state (oogonia and amphigynous antheridia) and the chemical composition are comparable to those of the Oomycetes. The absence of glucuronic acid and fucose and a low hexosamine content in *Trachysphaera fructigena* exclude the possibility of it being related to the Zygomycetes. The genus *Trachysphaera* may be considered to be closely related to *Phytophthora*.

The genus *Mortierella* is characterized by sporangia lacking a columella. Invested zygospores were discovered in the type species *M. polycephala* (Dauphin, 1908). Since 1908 numerous species have been shown to produce naked zygospores with unequal suspensors, mostly after mating (Kuhlman, 1972; Chien & *al.*, 1974). *M. chlamydospora* has typical naked zygospores, but is homothallic. In *M. polycephala* the zygospore-covering hyphae originate, according to Dauphin (1908) from both suspensors; in *M. indohii* only one of the suspensors bears some investing hyphae, so that this species is of an intermediate type. So far there is no reason to subdivide the genus *Mortierella* into one group with naked and one with invested zygospores.

Mortierella indohii, *M. echinosphaera*, and *M. chlamydospora* are distinct but closely related. *Mortierella indohii* differs from the other species by the nature of the chlamydospores which are more often terminal, smaller and more densely spiny while the spines are shorter. *Mortierella indohii* is heterothallic and has a specific aromatic odour which is less distinct or absent in the other species. The sexual state of *M. echinosphaera* is unknown, crossings between the three strains and with *M. indohii* were repeatedly negative. *Mortierella chlamydospora* and *M. echinosphaera* differ not only in their sexual behaviour but also in growth rate, which is significantly faster in *M. echinosphaera*. Like *M. indohii*, *M. chlamydospora*, and *M. echinosphaera* are placed in *Mortierella* on behalf of their zygospores (when present), their overall colony appearance and the resemblance of the chlamydospores to those of other *Mortierella* species, e.g. *M. polycephala*. There is no reason to retain the genus *Azygozygum* as it is considered to be a synonym of *Mortierella*.

Acknowledgement

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EXPLANATION OF PLATE 18

Fig. a. *Mortierella indohii*, CBS 720.71. — Fig. b. *M. chlamydospora*, CBS 529.75. — Figs. c, d. *M. echinosphaera*, CBS 575.75. — c. Young. — d. Mature. — Fig. e. *Trachysphaera fructigena*, CBS 315.31. The scale represents 5 μm.

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FRANZ PETRAK, 1886–1973

(With Plate 19)

Dr. F. Petrak passed away on October 9, 1973 in Vienna at the age of 87 years. He was born on October 9, 1886 in Mährisch-Weisskirchen, at that time a small town in the Moravian province of the Austrian Monarchy, but now belonging to the CSSR under the Czech name Hranice. A gift of some books, especially some volumes of 'Rabenhorst's Kryptogemenflora', and a small herbarium collection, stimulated Petrak's interest in mycology in 1910. He had previously been a botany student at the University of Vienna and his thesis, written under the supervision of R. von Wettstein, dealt with some species of the thistle genus *Cirsium*. During World War I he served in the Austrian army and was able to collect fungi in Galicia, Bosnia, Albania, and Macedonia. After the war he could not find a suitable appointment in Vienna or elsewhere in the remaining parts of Austria, and returned to Mährisch-Weisskirchen where he modestly started a career as a private scientist. He married in 1917 and in 1921 a son was born, the family income consisting of meagre honoraria for writings in 'Just's Botanischem Jahresbericht' and from the sale of exsiccata (e.g. Flora Bohemiae et Moraviae exsiccata).

Petrak became a well known mycologist through his numerous publications which have appeared in Hedwigia and Annales Mycologici since 1914. In 1919 the series 'Mykologische Notizen' was started; about 1000 numbers appearing filling more than 1400 pages. Petrak maintained an extensive correspondence with mycologists all over the world, especially with H. Sydow in Berlin. Large herbarium collections were sent to him and therefore he also became familiar with tropical fungi. This again resulted in publications by Petrak, with the senders of the specimens as co-authors. In 1938 he was appointed to the Botanical Department of the Museum of Natural History at Vienna. After World War II he edited Sydowia (Annales Mycologici, Series 2), of which 25 volumes have been published to date. Petrak was also given the opportunity to travel, and in 1950 he stayed at the Division of Mycology, United States Department of Agriculture, in Beltsville for nearly one year. There he identified numerous, mainly tropical, fungus collections and examined many type collections.

Franz von Höhnel, Hans Sydow, Ferdinand Theissen, and Franz Petrak by their critical studies pioneered the natural classification of the Ascomycetes and Coelomycetes. All this work was done without the aid of well equipped laboratories or libraries and without any assistance from governmental or other bodies (in fact the work was often obstructed). Petrak, in particular, encountered many set-backs during his life; he and his family often hardly keeping body and soul together. He was a self-conscious, shy, but friendly and helpful person with a warm heart. He was,

on the other hand, confident of his capacity as a taxonomist, being quickly offended and sensitive to criticism. His knowledge, not only of Micromycetes, but also of toadstools and higher plants was enormous. A small piece of dead twig, bark or rotting wood was sufficient for him to identify a host-plant and he had an amazing memory.

Franz Petrak was a corresponding member of the Mycological Society of America and of the British Mycological Society. As a student in 1947, the writer of this obituary worked for half a year under the guidance of Franz Petrak who stimulated his enthusiasm and familiarised him with mycological taxonomy.

With Petrak the mycological world has lost the last of a group of leading German-speaking taxonomists of microfungi and his author's name remains attached to a large number of fungal taxa.

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THE DISTRIBUTION PATTERN OF HIRNEOLA AURICULA-JUDAE IN THE NETHERLANDS

H. F. VAN DER LAAN

Arnhem, The Netherlands

(With three Text-figures and two Tables)

The distribution pattern of *Hirneola auricula-judae* in the Netherlands is discussed. At first this pattern was thought to be mainly determined by the average daily minimum temperatures in winter; high population densities correlating with high winter temperatures. The curve which best fits the data is so steep, that it would mean the virtual exclusion of *Hirneola auricula-judae* from regions with winter temperatures only a few degrees lower than in the Netherlands. Nevertheless the species is reported as not uncommon in the northern U.S.A. and southern Canada, as well as in Central Europe. From the literature it appears that '*H. auricula-judae*' in North America is not conspecific with the taxon so named in Europe, but specimens from Central Europe were found to be morphologically inseparable from specimens from Western Europe. Revaluation of the data on the distribution of the species in the Netherlands in relation to plant geographical districts showed that coexistent with the positive correlation of high population density with high winter temperatures is another one with alcaline soils. The corrected gradient of the correlation between population density and winter temperatures is less steep than originally calculated and consequently the relatively high population density in Central Europe is no longer inconsistent with the distribution pattern of the species in the Netherlands.

Preliminary study and first working hypothesis

A few years ago a preliminary study of the distribution of *Hirneola auricula-judae* in the Netherlands was made within the framework of the survey of the distribution of one hundred macromycetes in Europe by a committee of the European Mycological Congress (van der Laan, 1970). Purpose of the study was not only to record the distribution, but also to find the principal factors responsible for its pattern. *Hirneola auricula-judae* was chosen because it may be found all year round and can be easily identified. The results were recorded in a topographical grid of 5×5 km squares. Only collections of which specimens had been deposited in the Rijksherbarium, Leiden, were accepted as records. The majority was the result of accidental finds of numerous mycologists. They were supplemented by special searches of the author trying to fill gaps in the knowledge thus obtained. No attempt was made to search any area systematically square by square.

The preliminary results indicated that *H. auricula-judae* may be found almost anywhere in the Netherlands, but that its population density varies within wide limits. Population density in this study is measured by the number of squares in which *H. auricula-judae* has been found, expressed as a percentage of the total number

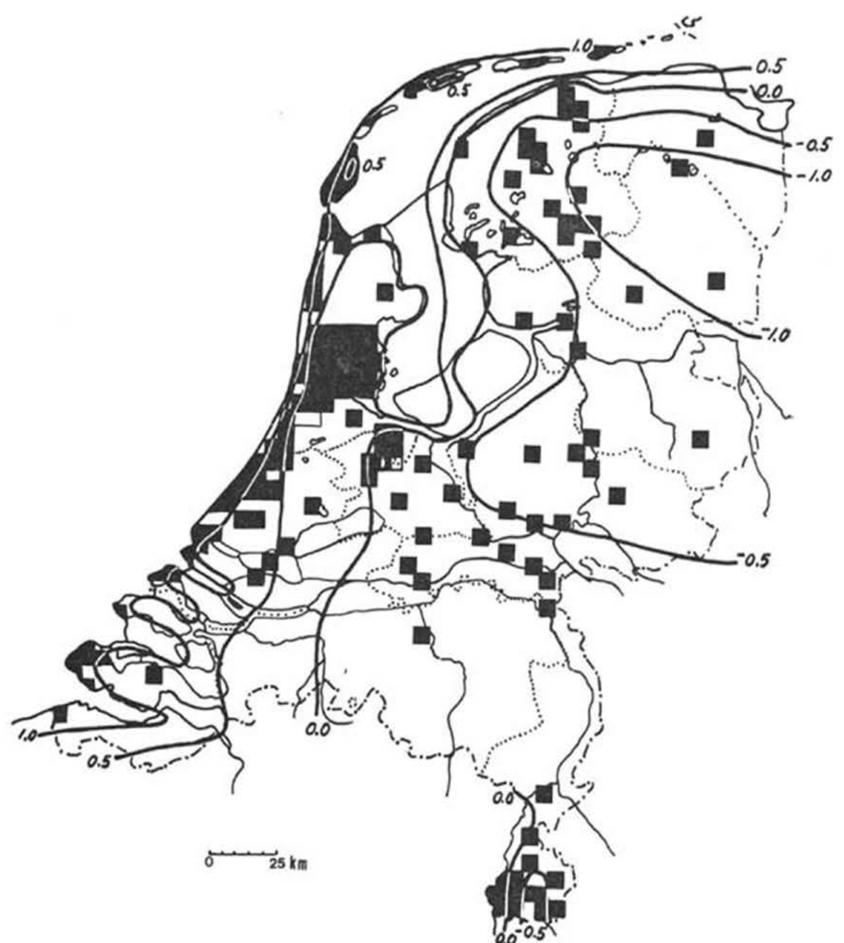

Fig. 1. Distribution of *H. auricula-judae* in the Netherlands related to division into zones of equal average daily minimum temperature in winter; black squares indicating squares of 5×5 km in which *H. auricula-judae* has been collected; fat lines indicating isotherms in °C.

of squares in a certain area. It was found to be at a maximum (of 30) along the coast. Further inland a gradual drop of the population density to less than one was found in the east and south. A notable exception was found in the extreme south-east, where the population density was almost equal to that in the coastal regions.

The preliminary study did not suggest a connection with soil conditions but, as shown later, this proved to be an erroneous conclusion. To a certain extent there seemed to be a correlation with the population density of *Sambucus nigra*, which in the Netherlands like elsewhere in Europe is the principal substrate of *H. auricula-judae*. In areas where the latter is abundant also *Sambucus nigra* is frequently found. The reverse, however, is not necessarily true.

Observations in the field showed that the fructifications are sensitive to low temperatures, especially below freezing point. As a rule the species is found only in relatively sheltered places. Experiments showed that sporulation is discontinued when the fruit-bodies are exposed to a temperature of 0 °C, but resumed when the temperature is again raised by a few degrees. However, sporulation of a (moist) specimen that had been exposed to —13 °C was not resumed after thawing.

The connection between chances of survival and occurence of low temperatures seemed to be fully confirmed by the excellent correlation which was found to exist between average daily minimum temperatures in winter (December–February) and population density of *H. auricula-judae*. The country was divided into zones between isotherms at 0.5 °C intervals, which were drawn up especially for this purpose by Dr. J. P. M. Woudenberg of the Royal Netherlands Meteorological Institute. They are based on observations at 35 weather stations during a period of 17 years (Fig. 1). They only provide a broad picture, because the number of stations is too small to allow conclusions on local conditions. The population density of each temperature zone was calculated, and the results were plotted in the manner shown in Figure 2. It was possible to draw a closely fitting exponential curve.

At the conclusion of the preliminary study it seemed to be justified to accept a working hypothesis, based on the following:

(1) Winter temperatures are the principal factor determining the distribution pattern in the Netherlands.
(2) Low temperatures correlate with low population densities.
(3) The population density gradient is very steep.

ADDITIONAL DATA CONFIRMING HYPOTHESIS

The working hypothesis seemed to be fully confirmed when in the course of the next few years the number of localities where *H. auricula-judae* had been found had increased from 80 to the present number of 175. (Figs. 1 and 2.) A reduction of the minimum temperature in winter of 1 °C corresponds with a reduction of the population density by 70%.

Again most of the finds were made by chance but an exeption must be made for

the results from the collections of Mr. J. A. Witte, who within a period of a few months succeeded in locating the species in every square from which it was not recorded before on the island of Texel and in an area of 25×25 km around his place of residence, Wormer, in the province of North Holland. These data have been included in the present work, but it should be noted that they were not obtained in the same manner as the others. For that reason, any calculation or conclusion based on all of the distribution data has been checked after excluding these 32 squares. Fortunately, their influence is rather limited, because 28 of them are situated in one temperature zone (+0.5–0) in which the population density amounts to only 8 if Mr. Witte's data are excluded, instead of the 20 shown in Figure 2.

The fact that Mr. Witte collected in the extremely mild winter of 1974–5 undoubtedly contributed to his success, for there was hardly any frost that winter. Moreover several of the preceding winters had had temperatures well above average. An important question is whether it would be possible to duplicate Mr. Witte's results in most of the other parts of the country. If so, our distribution pattern would be accidental and meaningless. The answer is that, while this may be possible in zones with a very high population density, it is extremely unlikely to happen in zones where the population density is medium or low. At about the same time when Mr. Witte made his survey, the author investigated the Achterhoek in the eastern part of the country, from where *H. auricula-judae* had not previously been reported. The search of this area produced only one locality where the species was found. *Hirneola auricula-judae* was also found several times in a region in the province of South Holland, similar to the one in which Mr. Witte had worked, but there was no indication of its simultaneous presence in every square of this area.[1]

The sensitivity of *H. auricula-judae* to low temperatures is confirmed by the results of the work of Tryel (1971: 413), who reports that the mycelium of the species is killed by exposure to a temperature of —22°C for a period of 5 weeks.

The existence of a relation between distribution and temperature conditions also follows in a general way from the data presented by Lowy (1952: 659), which show that *H. auricula-judae* is limited to a range between latitudes 22° and 55° N.

The North American form

Extrapolation of the graph shown in Figure 2 leads to the conclusion that *H. auricula-judae* should be extremely rare in regions where minimum temperatures in winter are but a few degrees below those prevailing in the eastern part of the Netherlands. Lowy's data on Europe are very scanty, but his map clearly shows that the species is found all over the U.S.A. and southern Canada, including areas that have much more severe winters than the Netherlands. In some of these areas *H. auricula-judae* is even considered to be common (Graham, 1944: 77).

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[1] Mr. Witte (personal communication, 1976) confirmed these experiences in failing to find a single specimen when searching for *H. auricula-judae* in the north-western part of the province of North Brabant, from which region the species had been reported but once.

Duncan & Macdonald (1967: 817) have shown that there are sufficient reasons to consider *H. auricula-judae* of Western Europe and the similar taxon in North America to be two 'evolutionary units' or even distinct species. In the first place there is an important difference in substrates. In the southern, midwestern and eastern states of the U.S.A. *Hirneola auricula-judae* is found on deciduous trees, but not on *Sambucus nigra* which does not exist in North America. In the northern and western states of the U.S.A. and in Canada the species is exclusively found on coniferous trees (ibid: 807). Collections from deciduous trees were found to be completely, and collections from coniferous trees virtually intersterile with collections from Western Europe, including some from Austria (ibid: 808). Spore dimensions of the North American and West European material were found to be significantly different (Table I). The authors do not mention any macroscopical characters by which the two species might be distinguished.

This is in accordance with the experience of the present author. Ten collections from coniferous trees collected by the late Dr. M. A. Donk in the U.S.A. and Canada and one from Newfoundland, obtained by courtesy of Dr. F. Tjallingii, were compared with an equal number of collections from Sambucus nigra in the Netherlands. Although one is immediately struck by the dense pilosity of the upper surface and the pronounced venulose folds of the American material, in the Netherlands' collections too one frequently finds specimens showing folds of the same height (1–3 mm) and width (1–2 mm) and having a pilose upper surface as well.

Duncan & Macdonald measured 125 spores per collection to a tenth of a μm, calculated the arithmetical mean, and determined the range of means at the 5% level of confidence. For the present study as a rule only 20 spores per collection were measured, rounded off to whole μm. Instead of calculating the arithmetical mean, the median value was determined for each collection, and for a group of collections the range of such medians. This considerably simpler method appears to give just as good results as the far more time consuming one of Duncan & Macdonald (Table I).

All specimens that had been air-dried after collecting, readily sporulated upon resuscitation under moist conditions. An exception was found with the material from North America available to the author, which probably was too old to resume sporulation, and in this the spores had to be scraped from the hymenium. In four of these collections no spores could be found at all. In the others an average of only 12 spores per collection was measured. The different conditions of the material studied, should account for the difference in length between the spores measured by Duncan & Macdonald and those measured by the present author.

The forms of *H. auricula-judae* in Western Europe and North America are so different from each other that the presence of this species in areas of North America, where winter temperatures are very much lower than in the Netherlands, does not have to be considered inconsistent with the correlation between population density and temperature established for the latter country.

Raitviir (1971: 93–94) reports that also in the extreme eastern part of Siberia *H. auricula judae* is found on deciduous and on coniferous trees. He mentions the

Table I

Spore dimensions (in μm)

Region	Substrate	Author	Length		Breadth	
			Average or Median	Range	Average or Median	Range
W. Europe	Sambucus	Duncan/Macdonald	20.2 (a)	18.2–22.2	6.6 (a)	6.0–7.2
Netherlands	Sambucus	van der Laan	20 (m)	19–21	7 (m)	7–8
N. America	coniferous	Duncan/Macdonald	15.0 (a)	13.0–17.0	5.2 (a)	4.6–5.8
N. America	coniferous	van der Laan	14 (m)	13–14(–15)	5 (m)	5–6
N. America	deciduous	Duncan/Macdonald	13.8 (a)	12.6–15.0	5.3 (a)	4.7–5.9
E. Siberia	coniferous deciduous	Raitviir		13–15		5–6
C. Europe	deciduous	Michael-Hennig		11–15		4–7
C. Europe	deciduous	Pilát		13–15		5–6
C. Europe	deciduous	Schroeter		11–15		5–7
C. Europe	deciduous	Velenovsky		12–15		
C. Europe	deciduous	van der Laan	20 (m)	19–21	7 (m)	7–(8)

a = arithmetical mean; the range is calculated on basis of the 5% level of confidence
m = median of all collections, range of medians of individual collections is indicated in the next column

conspicuous pilosity of the form growing on coniferous wood, which he named forma *abietis*. One set of spore dimensions is given (Table I), which agrees well with Duncan & Macdonald's figures for North American collections. In European Russia *H. auricula-judae* is found in the Baltic states, the Ukraine and the Caucasus on deciduous trees only, principally *Sambucus* and *Quercus* (Raitviir, 1967: 34). Unfortunately, data on spore dimensions of collections from these areas are not available. The species has not been reported from western Siberia.

Central European data

The map showing the distribution of *H. auricula-judae* in (part of) Europe, based on the survey of a committee of the European Mycological Congress (Lange, 1974: 55) reflects considerable differences in the approach of,the work by the participating countries. For that reason, a quantitative comparison of data, as attempted for the Netherlands, is out of the question.

A part of the picture seems to corroborate the working hypothesis arrived at in the Netherlands. The species is absent in Norway and Sweden, hence its northern limit is rather close to the Netherlands, as was to be expected from the steep gradient of the curve in Figure 2. The relatively high population density in England and the much lower one in Scotland, as well as the fact that in Scotland and in Denmark the species is predominantly found along the coast, are in accordance with the findings in the Netherlands. This may also apply to the relatively low population density in the northern part of West Germany and the higher one in the southern parts of that country (see also Bresinsky & Dichtel, 1971: 101).

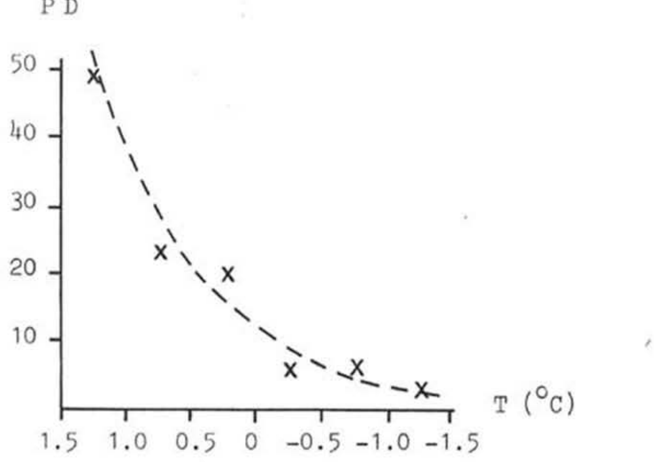

Fig. 2. Population density (PD) and average daily minimum temperature in winter (T); broken line indicating exponential curve of best fit.

The data presented for Central Europe, on the other hand, appear to be completely inconsistent with our working hypothesis. In Czechoslovakia, for instance, winter temperatures are about 5 °C below those in the Netherlands. Extrapolation of the (exponential) curve of Figure 2 gives at that temperature a population density of *H. auricula-judae* of less than one hundredth of that of the Netherlands. Application of the 'round dot mapping method' employed by Lange (1974: 12) to the finds in the Netherlands as recorded in Figure 1 results in about 50 'dots' for this country. (The European survey map shows but a fraction of this number, because it presents the distribution data as known before the present study had been started.) The surface area of Czechoslovakia is about 4 times that of the Netherlands. Therefore, by application of our working hypothesis one could expect $(4:100) \times 50 = 2$ dots in Czechoslovakia. The map shows a total of 86! The situation in East Germany is similar, and unexpectedly high population densities are also found in Hungary, Poland, and Rumania.

Could it be that *H. auricula-judae* found in Central Europe, like the one of North America, is different from the Western European form? Against this supposition is the fact that in Central Europe the species is usually found on Sambucus nigra but never on coniferous trees. On the other hand, Pilát (1957: 140) and Velenovský (1920: 794) in Czechoslovakia as well as Hennig (1960: 281) and Schroeter (1888: 386) in East Germany give spore dimensions in the range of $11-15 \times 4-7$ µm (Table I).

By courtesy of Dr. F. Kotlaba four fresh collections of *H. auricula-judae* from central Bohemia, two from southern Slovakia and three from East Germany (Baltic coast) were studied. Of six of them the substrate was *Sambucus nigra*; the others were found on *Acer* and *Morus*. Macroscopically they did not seem to be different from material found in Western Europe. Of each collection the spores of two fruit-bodies have been measured. As shown in Table I there is no difference between spore dimensions of the Western- and Central European material as far as studied by me. For the time being I am not yet prepared to incorporate into my considerations the smaller dimensions as given by Pilàt, Velenovský, Hennig, and Schroeter.

As no support has been found for the assumption that the *H. auricula-judae* from Central Europe is not conspecific with that from Western Europe, the working hypothesis had to be modified, for instance by taking into account other factors which might determine the distribution pattern.

Soil composition and distribution

An indication of where to look for other influences on the distribution pattern of *H. auricula-judae* was the fact that large differences of population density exist within the temperature zones into which the Netherlands has been divided. In some parts of the country the species has hardly been located at all, and such almost blank areas seem to range over more than one temperature zone. This is especially noticeable in the province North Brabant and the northern part of the province Limburg in the south of the country, and also in the eastern parts of the provinces Gelderland

and Overijssel in the east of the country. At first it was thought that these gaps were a consequence of lack of interest on the part of the mycologists working in those areas, but after special attention had been given to the problem it became a certainty that H. auricula-judae is extremely rare in those parts of the country.

The plant geographical districts which van Soest (1929) distinguished in the Netherlands have proved their value in the study of distribution of higher plants. It seemed worthwhile to investigate whether or not they also might throw some light on the distribution of *H. auricula-judae*. It should be understood that van Soest's division is based on the distribution pattern of several plants and plant associations as well as on soil conditions. It is only meant to give a broad picture, hence boundaries are almost straight lines. The districts are shown in Figure 3, together with the distribution data of *H. auricula-judae*. The population density of each district is shown in the second column of Table II.

The most conspicuous figures are the far above average ones of the Marl district (Krijt) in the south-east, of the Dunes district along the coast in the south-west, and of the Shallows district (Wadden) that comprises the northern part of the sand dunes on the mainland and the islands in the north. The data on the population density of the small Shallows district, however, are very much influenced by Mr. Witte's collecting. Without the latter its population density amounts to only 36. The Marl district and the Dunes district are characterized by a highly calcareous soil. In the Marl district Cretaceous rocks are close to the surface, in the Dunes district the lime content is derived from shell fragments. The Shallows district is heterogeneous, containing sand dunes with a relatively low lime content and clays that are partly calcareous.

At the other end of the scale are the Campine, the Subcentreuropean and the Guelders districts with very low population densities of *H. auricula-judae*. In all these districts acid sandy soils are abundant. The Drentian district has similar soils, but a somewhat higher population density.

Intermediate between these extremes are the small Loess district (adjacent to the Marl district, but with a less alkaline soil), and the large Haff and Fluviatile districts together covering about half of the country. Also the population density of the Haff district shown in Table II has strongly been influenced by Mr. Witte's survey which was carried out almost exclusively within this district. The population density of the Haff district drops to 9 if Mr. Witte's results are left out. Both Haff and Fluviatile districts are characterized by being largely 'man-made'. Nearly all of the former and 20% of the latter is reclaimed land, situated below sea level. The remaining 80% of the Fluviatile district would be flooded frequently if the rivers had not been embanked. Both are intensively used for agricultural purposes. Neither highly calcareous nor acid soils are found in these districts. The Haff district consists of a very heterogeneous mixture of marine clays (calcareous as well as non-calcareous) and clayey peat soils. River clays and sands with a varying lime content and calcareous marine clay constitute the Fluviatile district. Large parts of the last mentioned clay area, in the south-west of the country, were inundated at the end of World War

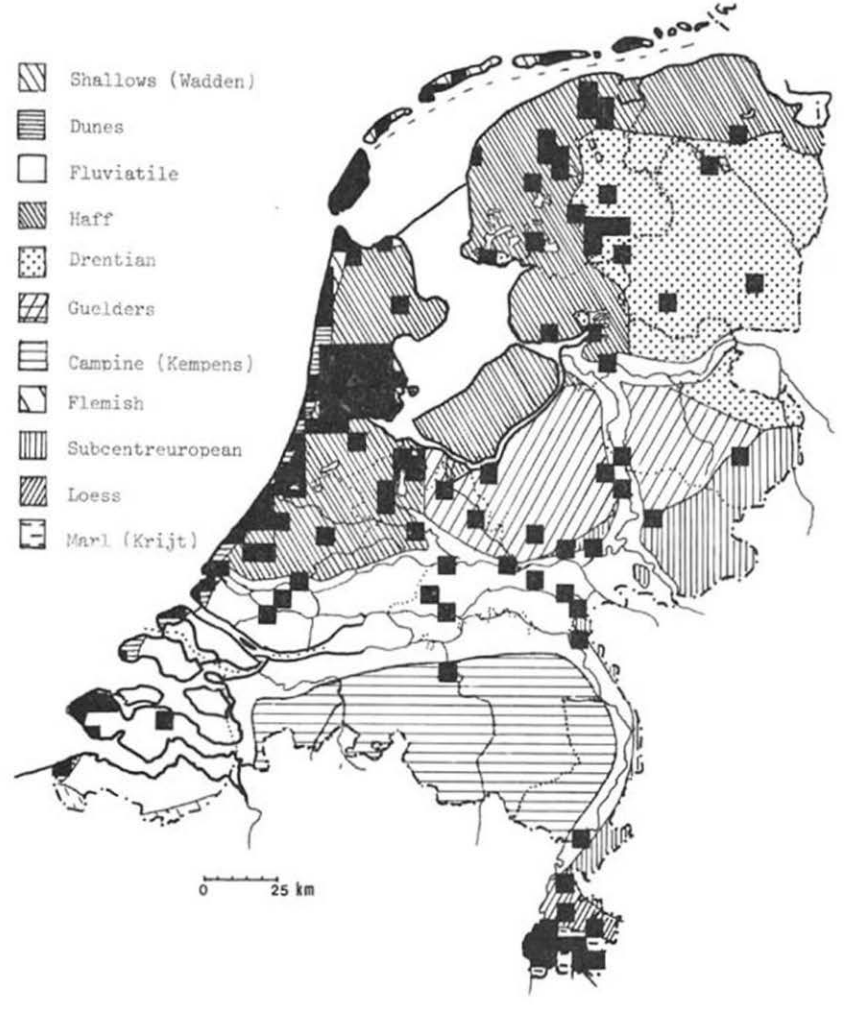

Fig. 3. Distribution of *H. auricula-judae* in the Netherlands related to division into plant geographical districts; black squares indicating squares of 5 × 5 km in which *H. auricula-judae* has been collected.

II or flooded in 1953 by salt water, which might explain the paucity of records of *H. auricula-judae* from this region. The population density in the remainder of the Fluviatile district amounts to 6.

It appears from the above that the population density of *H. auricula-judae* is considerably higher on calcareous or alkaline soils than on neutral or acid ones.

DISTRIBUTION PATTERN AS A RESULT OF SOIL CONDITIONS AND TEMPERATURE

It is difficult to differentiate between the influences of soil condition and of temperature on the distribution pattern. Most of the districts with alkaline soil are situated in the zones with high temperature and those with acid soil are found in the zones with low temperature. One may even ask whether the correlation between population density and temperature is perhaps merely accidental. Clear indication that this is not the case is found when the districts are divided into temperature zones and the population density is calculated for each zone of each district. The results are shown in Table II. To separate the influences of temperature and soil conditions the population density corresponding to temperature zones within each district has been adjusted by dividing by the overall population density for that district. The overall population density corresponding to temperature zones for the whole country, after adjustment in this manner, is shown in the last line of Table II. It is calculated by dividing the numer of squares in which *H. auricula-judae* has been found within a zone by the sum of the products of the overall population density of each district and the total number of squares of that district in that zone.[2]

It can be shown that a highly significant positive correlation exists between temperature and adjusted population density. The estimated upper tail-probability is 0.016. The latter has been found by comparing the calculated correlation coefficient with the corresponding ones when the columns of Table II are independently permutated at random (500 times).

Repetition of the calculations without making use of Mr. Witte's data yields a result which is not very different from the above.

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[2] The adjusted overall population density is calculated by the formula

$$\frac{\sum_{i=1}^{11} P_{ij}}{\sum_{i=1}^{11} PD^*_i T_{ij}} \quad \text{where } j = 1, 2, \ldots 6.$$

Here i refers to the different plant geographical districts and j refers to the different temperature zones. P_{ij} is the number of squares in which *H. auricula-judae* has been found in district i and temperature zone j. T_{ij} is the total number of squares in district i and temperature zone j. PD^*_i is the overall population density for district i, indicated in the third column of Table II.

Temperature zone (°C)	Combined			+1.0			+1.0–+0.5			+0.5–0			0—0.5			—0.5—1.0			—1.0		
Plant geographical district	T*	P*	PD*	T	P	PD	T	P	PD	T	P	PD	T	P	PD	T	P	PD	T	P	PD
Shallows-Wadden	18½	10½	57	4	4	100	13	5½	42	1½	1	67									
Dunes	26	18½	71	18½	14	76	7½	4½	60												
Fluviatile	322½	15½	5	17	2½	15	73	2	3	49½	–	–	147	8	5	36	3	8			
Haff	371	71½	19	1½	–	–	29½	15½	52	140	39½	28	133	10	8	67	6½	10			
Drents	221	12½	6				1½	1½	100	2	1	50	1	–	–	82	6	7	134½	4	3
Gelders	139½	6	4							½	–	–	38½	3½	9	100½	2½	2			
Campine-Kempens	173½	1	1							19	–	–	154½	1	1						
Flemish	5½	–	–	½	–	–	2½	–	–	2½	–	–									
Subcentreuropean	71½	2	3										16½	½	3	55	1½	3			
Loess	14½	3	21							3	–	–	10	3	30	1½	–	–			
Marl-Krijt	16	12	75							3½	3	86	6½	5½	85	6	3½	58			
Total country	1379½	152½	11	41½	20½	49	127	29	23	221½	44½	20	507	31½	6	348	23	7	134½	4	3
Adjusted overall population densities				1.24			1.32			1.32			0.74			0.77			0.53		

T = Total number of squares in area P = Number of squares in which *H. auricula-judae* has been found PD = Population density

* Refers to combined (or overall) values

Obviously it is not feasible to construct a smooth curve from a plot of the adjusted population density values against the temperatures. The densities may be compared, however, with the results found originally and shown in Figure 2, after adjusting the latter by dividing by the overall population density for the whole country. The adjusted population densities of the zones shown in the same sequence as in Table II are as follows: 4.48, 2.08, 1.82, 0.56, 0.60, 0.27. A cursory comparison of these results with those shown in the last line of Table II reveals that the gradient of the population density due to temperature conditions is now much smaller than the one arrived at before. Consequently the calculated population density of *H. auricula-judae* in Czechoslovakia, found by extrapolation of the findings in the Netherlands will now be much higher. (By a factor 10, roughly estimated.) This fact, together with the discovery of the importance of soil composition, appear to be sufficient to remove the inconsistency which seemed to exist between the distribution data published for Central Europe and the experience gained in the Netherlands.

It appears that further study may be based on a new working hypothesis, which may be worded as follows:

The distribution pattern of *Hirneola auricula-judae* in the Netherlands is mainly formed by the following factors:

(i) the availability of *Sambucus nigra*,
(ii) average daily minimum temperatures in winter, and
(iii) composition of the soil.

High temperatures and alkaline soils correlate with high population densities.

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The most important contribution to this study, however, was undoubtedly made by the numerous mycologists, most of them amateurs, who took the trouble te record (with proof!) the presence of the subject of this study. Without their spontaneous cooperation the work could not even have been started.

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SOME NEW OR NOTEWORTHY SPECIES OF MORTIERELLA

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Centraalbureau voor Schimmelcultures, Baarn

(With 22 Text-figures)

Twenty-two species of *Mortierella* are described and distributed over the sections defined by Gams (1970) which include the following new species: Section *Pusilla: M. roseo-nana;* Section *Alpina: M. globalpina* and *M. polygonia*; Section *Simplex: M. amoeboidea*; Section *Hygrophila: M. elongatula, M. kuhlmanii, M. parazychae, M. armillariicola, M. selenospora, M. basiparvispora,* and *M. clonocystis*; Section *Spinosa: M. epicladia, M. acrotona, M. cystojenkinii,* and *M. fimbricystis.*

Complete accounts on species described in *Mortierella* are given by Linnemann (*in* Zycha & Siepmann, 1970) and Mil'ko (1974). Linnemann's arrangement of sections caused many difficulties in determination and consequently Gams (1970) proposed a different arrangement of sections but had not yet given a detailed account of or a key to the species. New findings sometimes allow the recognition of long forgotten species (e.g. Gams & Hooghiemstra, 1976), but several apparently new species from different origins have accumulated during the last years in the CBS collection and are described in this communication. In addition some hitherto imperfectly delimited species and, in particular, some species recently published in Russia are redescribed from type strains and more sharply delimited.

The species are arranged in the sections defined by Gams (1970). Cultures were generally grown on 2% malt extract agar (MEA) for the assessment of the macroscopic characters and growth rate, on soil extract agar (SEA) or potato-carrot agar (PCA) for the study of the sporangiophores, and incubated at room temperature (18–22 °C) for approximately one week or longer. The sexual states were not obtained in most species; usually too few strains were available to give a chance for compatible mating, but in some cases proved compatibility led to the synonymy of some already described species. On the other hand, the absence of a mating reaction justified the separation of strains which deviate from known species in minor characters, e.g. *M. elongatula* and *M. sarnyensis* from *M. elongata*, and *M. kuhlmanii* from *M. beljakovae.* From previous work on zygospore formation (Kuhlman, 1972) it is known, that in some species zygospore production is erratic and difficult to obtain; *M. humilis* and *M. marburgensis*, however, gave interspecific zygospores (Chien *&* *al.*, 1974). A positive or negative result of mating with new isolates therefore only has limited value in delimiting species and the novelty of a species is judged rather on morphological characters of the asexual state than on mating behaviour. In so doing,

however, a considerable variability in length, width and branching intensity of the sporangiophores as well as in the size of the spores has been taken into account, whilst the type of ramification (acrotonous or basitonous), development of a columella and usually also the shape of the spores are found to be reliable criteria.

DESCRIPTIONS

Section ISABELLINA Turner

Growth restricted, compact, velvety. Sporangia often pigmented, many-spored or one-spored. Garlic-like odour never produced.

1. **Mortierella roseo-nana** W. Gams & Gleeson *spec. nov.*—Fig. 1

Coloniae lente crescunt, velutinae, dilute roseae, non olent. Sporangiophora numerosa in agaro malti ex hyphis aeriis vel submersis oriuntur, prope superficiem 2–4 ramulos verticillatos proferunt, omnino 60–130 μm longa, e 6–8 μm ad 3–4 μm angustata. Sporangia unispora, 10–16 μm diam., rubida, levia, dilapsa collare minutum relinquunt; sporae multis guttulis oleaginosis repletae. Chlamydosporae absunt.

Holotypus: CBS 473.74, isolatus e solo paupero, Parkville, ad Universitatem Melbourniensem in Australia, leg. *P. Gleeson*, Aug. 1974.

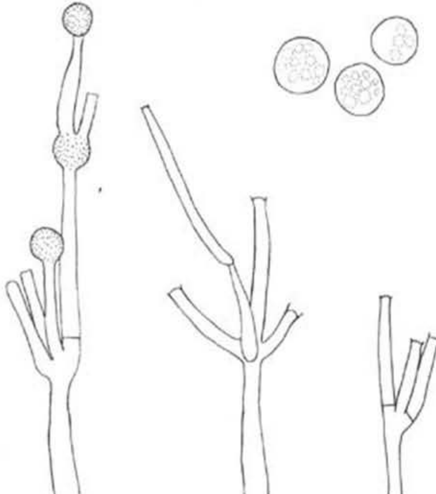

Fig. 1. *Mortierella roseo-nana*, sporangiophores (some proliferating) and one-spored sporangia ×500.

Colonies reaching 2.2–3.0 cm in diameter in six days, velvety, very pale pink due to sporangia (like *M. vinacea*); odour absent. Good sporulation up to the margin on MEA; sporangiophores arising from aerial hyphae or from the substratum, in the latter case branching near the agar surface; bearing 2–4 short, verticillate branches, total length 60 up to more than 130 μm, tapering from 6–8 μm to 3–4 μm. Sporangia one-spored, 10–16 μm in diameter, reddish, smooth-walled, on dehiscence leaving a minute collarette. Spores containing numerous oil droplets. Chlamydospores absent.
Know only from the type culture.

Mortierella roseo-nana is intermediate between *M. vinacea* Dixon-Stewart and *M. nana* Linnem. The occurrence of pigmented, one-spored sporangia is an indication that the latter species is properly classified in the section *Isabellina*.

Section ALPINA Linnem.

Sporangiophores usually less than 200 μm tall, always unbranched, often with an irregular swelling at the foot. Sporangia usually many-spored.

2. **Mortierella globalpina** W. Gams & Veenbaas-Rijks *spec. nov.*—Fig. 2

Coloniae fere lente crescunt, dense lobulatae, mycelio aerio sparso obtectae, modice olent. Sporangiophora ex hyphis aeriis oriuntur, aculeata, 45–70 μm longa, e 4–6 μm ad 1.7–3.0 μm

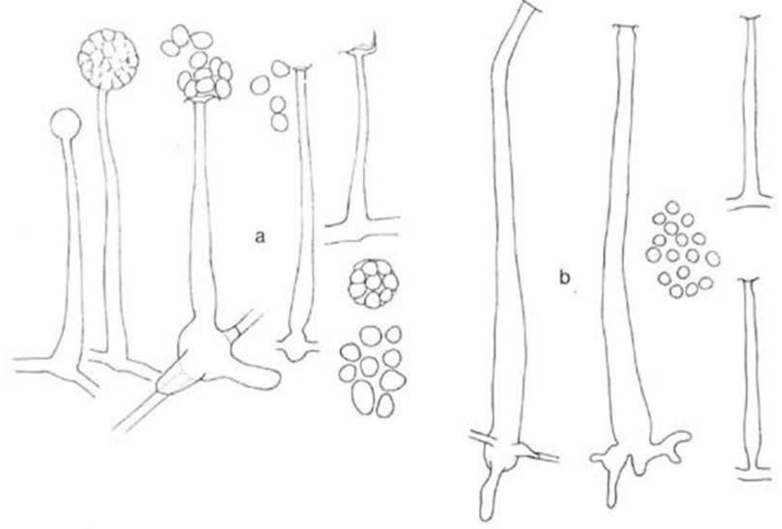

Fig. 2. *Mortierella globalpina*, sporangiophores, sporangia, and spores ×500. — a. Strain from Kiel. — b. CBS 360.70.

angustata, numquam ramosa, prope basin inflata et saepe appendiculos velut rhizoidea proferentia. Sporangia semper multispora, 8–15 μm diam., globosa et levia, dilapsa collare conspicuum relinquunt. Sporae ± globosae, leves, 2.5–4.0 μm diam. Chlamydosporae plerumque absunt.

Holotypus: CBS 360.70, isolatus e solo agresti, East-Flevoland Polder in Neerlandia, *J. W. Veenbaas-Rijks*, 7 Oct. 1969.

Colonies rather slow-growing with a daily radial increment of 7–10 mm, forming a rosette of dense narrow lobes, with a moderate amount of aerial mycelium; odour weak but typical of the genus. Sporulation poor on MEA, abundant on SEA; sporangiophores arising from the aerial hyphae, awl-shaped, 45–70 μm tall, always unbranched, tapering from 4–6 μm at the base to 1.7–3.0 μm at the tip, with a typical basal swelling ('basal foot' of Linnemann) and often some rhizoid-like outgrowths. Sporangia always many-spored, 8–15 μm in diameter, globose and smooth-walled, leaving a distinct collarette on dehiscence. Spores ± globose, smooth-walled, 2.5–4.0 μm in diameter. Chlamydospores generally absent, rarely present as little differentiated intercalary structures not much wider than the original hypha.

CULTURES EXAMINED.—CBS 266.70 and 360.70 (type strain), ex agricultural soil in the East-Flevoland Polder, *J. W. Veenbaas-Rijks*, 7 Oct. 1969. Two more strains were isolated in 1964 by the author from a wheat field soil at Kiel, F. R. G., but are now lost.

Mortierella globalpina differs from *M. alpina* Peyronel not only by the globose shape of the spores but also by the absence of deciduous sporangioles which are not divided into small spores. It differs from the description of *M. antarctica* Linnem. (*in* Zycha & Siepmann, 1970) by the possession of smaller spores (*M. antarctica* is reported to have spores of 3–10 μm) and the absence of catenulate chlamydospores. Unfortunately the type strain of this species, CBS 609.70, has never shown any sporulation since it is preserved at Baarn, but still produces abundant chlamydospores. *Mortierella globalpina* may have been identified as *M. pusilla* Oudem. (e.g. Mil'ko, 1974), *M. humicola* Oudem. or *M. subtilissima* Oudem., three similar species, all inadequately described by Oudemans & Koning (1902), which are best abandoned as doubtful, since they may equally well have been quite different, and no type or other material is in existance.

3. **Mortierella polygonia** W. Gams & Veenbaas-Rijks *spec. nov.*—Fig. 3

Coloniae fere lente crescunt, vix lobulatae, mycelio aerio copioso obtectae, modice olent. Sporangiophora plerumque ex hyphis submersis oriuntur, aculeata, numquam ramosa, 40–60(–115) μm longa, e 3.5–5.0 μm ad 1.5–2.0 μm angustata, prope basin vix inflata. Sporangia 10–14 μm diam., semper multispora, dilapsa collare conspicuum relinquunt. Sporae irregulariter lobatae, 6–9 μm diam. Chlamydosporae vulgo absunt.

Holotypus CBS 685.71, isolatus e solo agresti prope Wageningen, *J. W. Veenbaas-Rijks*, 16 Apr. 1971.

Colonies rather slow-growing with a daily radial increment of approx. 5 mm, hardly lobed with much aerial mycelium; odour moderate, typical of the genus. Sporulation poor on MEA, good on SEA; sporangiophores arising mainly from the

substratum, awl-shaped, always unbranched, 40–60 μm tall in fresh isolates, 85–115 μm after several transfers, tapering from 3.5–5.0 μm to 1.5–2.0 μm at the tip, with the base hardly swollen, but in older cultures the lower part of the sporangiophores often undulate. Sporangia 10–14 μm in diameter, sometimes appearing reddish, always many-spored, leaving no columella but a distinct collarette on dehiscence. Spores irregularly lobed, with 4–5 projections in optical section and 6–9 μm in maximal diameter. Chlamydospores normally absent, but short hyphal fragments may act as such.

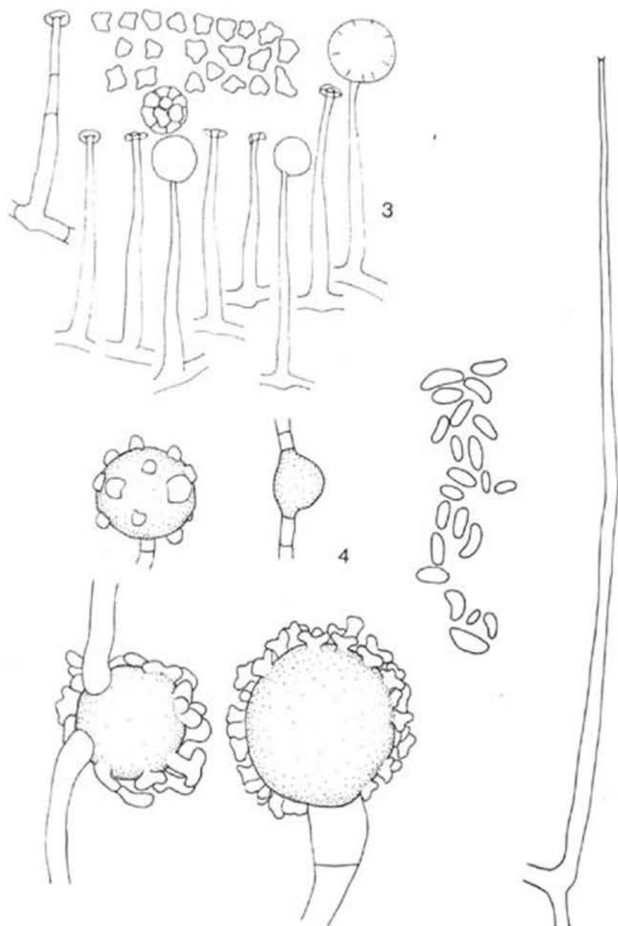

Fig. 3. *Mortierella polygonia*, sporangiophores and spores ×500.
Fig. 4. *Mortierella amoeboidea*, sporangiophore, spores, and chlamydospores ×500.

CULTURES EXAMINED.—CBS 685.71, ex agricultural soil, Wageningen, *J. W. Veenbaas-Rijks*, 16 Apr. 1971 (strain 606). Another identical strain was isolated in 1965 by the author from a wheat field soil at Kiel, F. R. G., but is now lost.

Mortierella polygonia is unique in the genus by its lobed spores, but the sporangiophores are typical of section *Alpina*.

Section SIMPLEX W. Gams

Species with constantly unbranched, but sometimes aggregated, large and wide sporangiophores. One-spored sporangioles may occur jointly with many-spored sporangia.

4. **Mortierella amoeboidea** W. Gams *spec. nov.*—Fig. 4

Coloniae fere lente crescunt, dense lobulatae, mycelio aerio parco in medio obtectae, modice olent. Sporangiophora pauca ex hyphis submersis oriuntur, 150–260 μm longa, e 5 μm ad 1.5 μm angustata, numquam ramosa. Sporangia 10–15 μm diam., multispora, dilapsa collare inconspicuum relinquunt. Sporae elongato-ellipsoideae, nonnumquam curvatae, leves, 6–11(–13) × 3.5–5.0 μm. Chlamydosporae abundantes, nonnumquam aggregatae, terminales vel laterales, dilute brunneae, 30–45 μm diam., appendicibus retusis, saepe dichotomis, 6–10 μm longis obtectae; chlamydosporae minores, leves etiam copiosae.
Holotypus: CBS 889.72, isolatus e *Chromelosporio* spec., Beller Holz, in Silva Teutoburgensi in Germania, *W. Gams*, Sept. 1972.

Colonies rather slow-growing with 5–7 mm daily radial increment, delicately and densely lobed, with some aerial mycelium in the centre; odour faint but typical. Sporulation rather poor on all media; sporangiophores arising from the substratum, 150–260 μm tall, unbranched, tapering from 5 μm to approx. 1.5 μm at the tip. Sporangia 10–15 μm in diameter many-spored, leaving an indistinct collarette after dehiscence. Spores elongate ellipsoidal, sometimes curved, smooth-walled, 6–11 (–13) × 3.5–5.0 μm. Chlamydospores abundantly produced on SEA in the agar, in terminal or lateral positions, sometimes aggregated in clusters, light brown, 30–45 μm in diameter, covered with blunt, often dichotomous appendages, 6–10 μm long; smaller, smooth-walled chlamydospores also abundant.
Known only from the type culture.

Mortierella amoeboidea differs from *M. echinosphaera* Plaats-Niterink (in van der Plaats Niterink *&* *al.*, 1976) by larger chlamydospores and the possession of unbranched sporangiophores, whilst *M. fimbricystis* W. Gams (cf. p. 138) has smaller spores and acrotonously branched sporangiophores. In both these species the chlamydospore appendages are narrower than in *M. amoeboidea* and fringe-like. The sporangiophores of *M. amoeboidea* are unusually small in the section *Simplex*.

Section HYGROPHILA Linnem. emend W. Gams (1970)

Sporangiophores tall or short, with basitonous, cymose ramification, bearing many- or few-spored sporangia.

5. MORTIERELLA ECHINULA Linnem.

in Zentbl. Bakt. ParasitKde, Abt. 2, **107**: 229. 1953.—Fig. 5

Colonies growing rather fast with a daily radial increment of 6–10 mm, hardly lobed, without aerial mycelium; odour weak, typical of the genus. Sporulation poor; sporangiophores arising from the substratum, 320– over 500 μm tall, with abundant basitonous ramification, tapering from 9–15 μm to 3–4(–5) μm at the tip. Sporangia 30–50 μm in diameter, many-spored, leaving a minute collarette on dehiscence. Spores ± globose, distinctly echinulate, 8–10(–14) μm in diameter. Chlamydospores scarcely produced on SEA, abundantly on MEA after 12 days, globose, thin-walled, 9–13 μm in diameter, filled with oil drops.

CULTURE EXAMINED.—CBS 282.71, ex soil in Iceland, comm. *E. G. Kuhlman*, 1971.

Linnemann's original isolate is lost. The present strain matches the original description fairly well in which the spores are given as 7–8 μm. *Mortierella echinula* may be confused with *M. globulifera* Rostrup (cf. Turner, 1956) which has similar spores but always unbranched sporangiophores. *Mortierella hyalina* (Harz) W. Gams (syn. *M. hygrophila* Linnem.) may also be mistaken for *M. echinula* since the spores are finely roughened (although always described as smooth!), but much less than in *M. echinula*; spores of *M. hyalina* are larger and the chlamydospores more abundant and lemon-shaped.

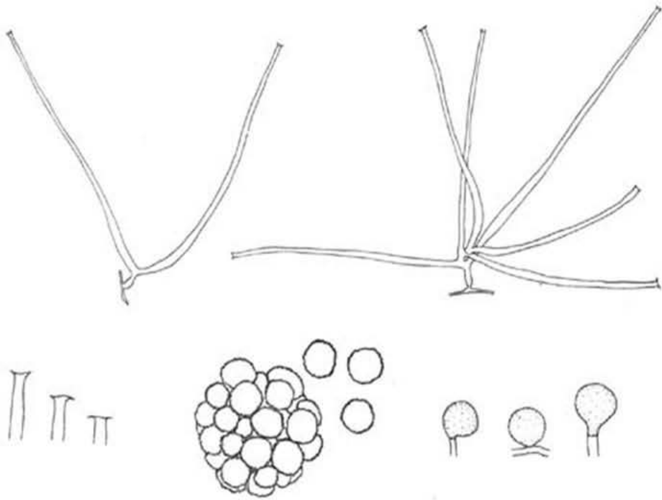

Fig. 5. *Mortierella echinula*: sporangiophores ×100; sporangiophore tips, sporangium and spores, and chlamydospores ×500.

6. MORTIERELLA cf. VERRUCOSA Linnem.

in Zentbl. Bakt. ParasitKde, Abt. 2, **107**: 229. 1953.—Fig. 6

Colonies growing moderately fast with a daily radial increment of approx. 8 mm, broadly lobed and zonate, with some aerial mycelium mainly in the centre; odour very strong and typical. Sporulation abundant on MEA and SEA; sporangiophores arising from aerial hyphae, 60–160 μm tall, with abundant basitonous ramification (habit of *M. humilis* Linnem.), tapering from 7–9 μm to 2.0–2.5 μm near the tip. Sporangia 20–30 μm in diameter, usually not containing more than 10 spores, leaving a minute columella and a collarette on dehiscence. Spores ± globose, finely echinulate, 6–12(–16) μm in diameter. Chlamydospores abundantly produced on SEA, elongate, ± lemon-shaped, 10–14 μm in diameter.

CULTURE EXAMINED.—CBS 181.73, ex *Tricholoma flavovirens* (Pers. ex Fr.) Lund., Kootwijker Zand, Netherlands, *W. Gams*, 4 Nov. 1972.

Linnemann's original strains of *M. verrucosa* from Germany and Mexico are lost. The species is described as having sporangiophores up to 260 μm tall, 3–4 μm wide

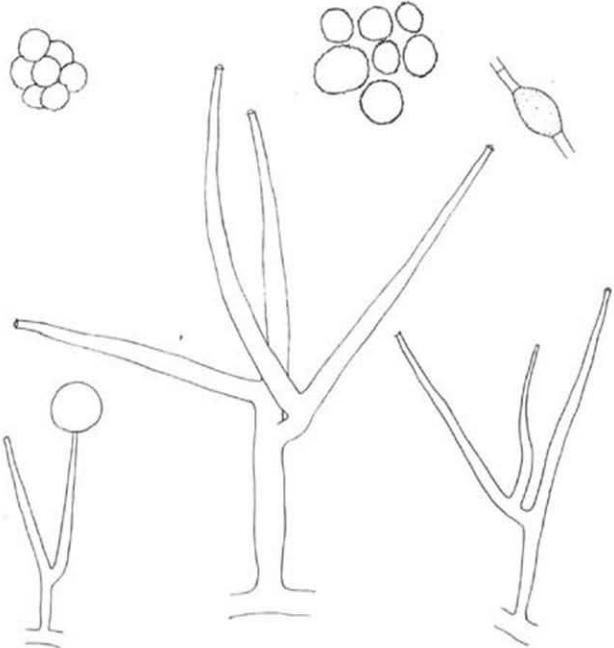

Fig. 6. *Mortierella* cf. *verrucosa*, sporangiophores, sporangium and spores, and chlamydospore ×500.

near the tip and spores of 15–20 μm diameter. The present strain is the closest to this description so far seen by the author. It is clearly distinct from *M. echinula* by shorter sporangiophores and somewhat larger spores.

7. MORTIERELLA SARNYENSIS Mil'ko
in Nov. Sist. niz. Rast. 1973: 87.—Fig. 7

Mortierella fatshederae Linnem. *in* Zycha & Siepmann, Mucorales, 205. 1970 ('1969') (nom. inval. Art. 37).

Colonies growing moderately fast with a daily increment of approx. 5 mm, densely lobed, with much aerial mycelium in the centre; odour strong and typical of the genus. Good sporulation on SEA, less on MEA; sporangiophores arising from aerial hyphae, 100–275 μm tall, many times basitonously branched, tapering from 5–7 μm to 1.5–2.5 μm near the tip. Sporangia 12–22 μm in diameter, many-spored, leaving an indistinct collarette on dehiscence. Spores ellipsoidal to cylindrical, smooth-walled, 5.5–7.0 × 3.5–4.5 μm. Chlamydospores absent.

CULTURE EXAMINED.—CBS 122.72 = BKM-F 1638, type strain, ex soil near Sarny, Ukr. S. S. R., *A. A. Mil'ko*, 1971.

Mortierella fatshederae Linnem. was not validly published nor has a strain of it been preserved; neither can the designation of an iconotypus by Linnemann (1971) be accepted as a validation. It is described as having strongly bent sporangiophores but in all other aspects it agrees with the present species. *Mortierella sarnyensis* is very close to *M. elongata* Linnem. from which it is supposed to differ by shorter spores (Mil'ko, 1974) and the absence of chlamydospores. The sporangiophores are considerably shorter. The first criterion cannot be regarded as significant because many compatible strains of *M. elongata* with equally small spores have become available. In a mating experiment with a tester pair of *M. elongata* no zygospores were obtained.

8. **Mortierella elongatula** W. Gams & Domsch *spec. nov.*—Fig. 8

Coloniae fere lente crescunt, dense et inconspicue lobulatae, in medio parco mycelio aerio obtectae, typice olent. Sporangiophora ex hyphis aeriis oriuntur, 100– >300 μm alta, raro basitone ramosa, e 4–13 μm ad 1.0–2.5 μm angustata. Sporangia 10–30 μm diam., multispora, dilapsa collare inconspicuum relinquunt. Sporae ellipsoideo-fusiformes, leves, 5.5–8.5 × 2.0–3.0 μm. Chlamydosporae copiosae, tenuitunicatae, globosae, nonnumquam paucis appendicibus papillatis praeditae, ad 40 μm diam., guttulis oleaginosis repletae.
Holotypus: CBS 488.70, isolatus e dejectis domesticis, Braunschweig in Germania, *K. H. Domsch*, 1970.

Colonies growing rather slowly, with a daily radial increment of 4–5 mm, with a delicate rosette pattern of dense lobes, in the centre with some aerial mycelium; odour typical of the genus, moderately strong. Sporulation poor on MEA, better on SEA; sporangiophores arising from aerial hyphae, 100 to more than 300 μm tall, rarely basitonously branched, tapering from 4–13 μm to 1.0–2.5 μm at the tip.

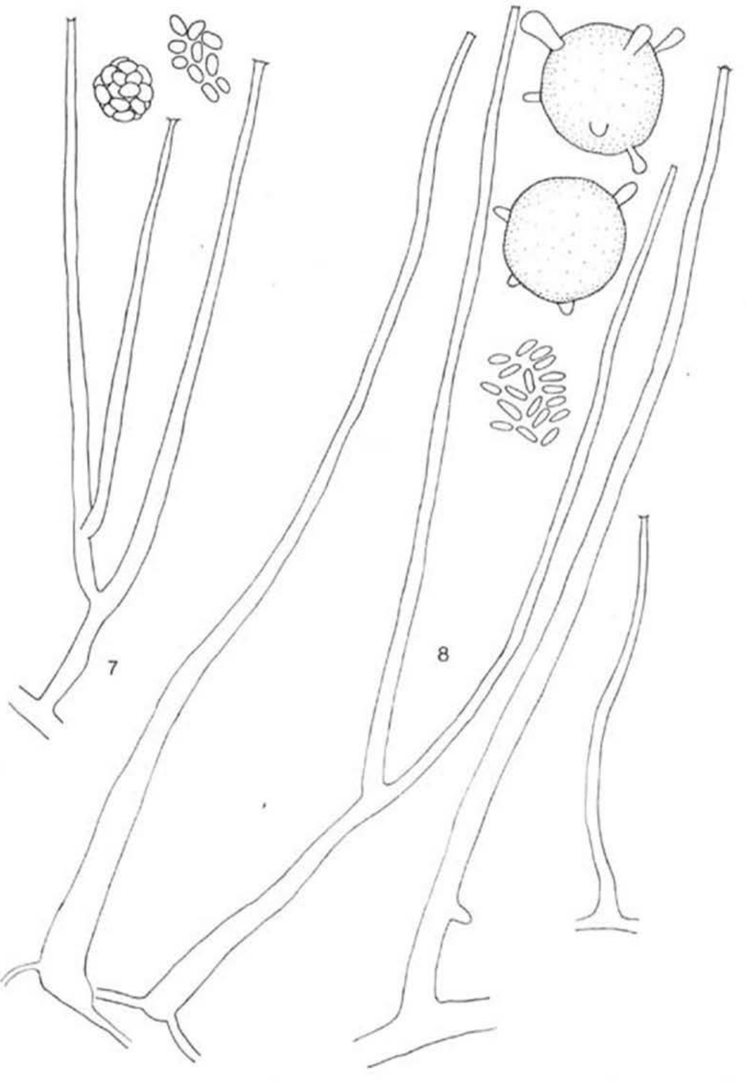

Fig. 7. *Mortierella sarnyensis*, sporangiophore, sporangium, and spores × 500.
Fig. 8. *Mortierella elongatula*, CBS 468.70, sporangiophores, spores, and chlamydospores × 500.

Sporangia 10–30 µm in diameter, many-spored, leaving an indistinct collarette on dehiscence. Spores ellipsoidal to fusiform, smooth-walled, 5.5–8.5 × 2.0–3.0 µm. Chlamydospores abundantly produced on MEA and some other media, scarcely on SEA, thin-walled, globose, up to 40 µm in diameter, sometimes with a few teat-like appendages, filled with small oil droplets.

CULTURES EXAMINED.—CBS 488.70 (D 79) and 661.70 (D 224), ex municipal wastes, Braunschweig, F. R. G., *K. H. Domsch*, 1970.

Mortierella elongatula is close to *M. elongata* Linnem. and *M. epigama* W. Gams & Domsch (Gams & *al.*, 1972). It differs from the former by more fusiform spores and the presence of larger and globose chlamydospores. The latter species has similar spores but is homothallic and produces abundant zygospores but no chlamydospores. In mating experiments with *M. elongata* no reaction was observed; therefore *M. elongatula* is regarded as a distinct species.

9. MORTIERELLA GEMMIFERA Ellis

in Trans. Br. mycol. Soc. **24**: 95. 1940.—Fig. 9

Colonies growing rather fast with a daily radial increment of 5–8 mm, broadly lobed and zonate, evenly covered with a thin cottony aerial mycelium with numerous hyphal knots. Sporulation good on SEA, somewhat less on MEA; sporangiophores arising from the substratum and from aerial hyphae, 600–700 µm tall, with frequent basitonous ramification, tapering from 10–13 µm to 2–4 µm near the tip. Sporangia 12–35 µm in diameter, leaving a minute trace of a columella and a distinct collarette on dehiscence. Spores short ellipsoidal to cylindrical, often irregularly bent, smooth-

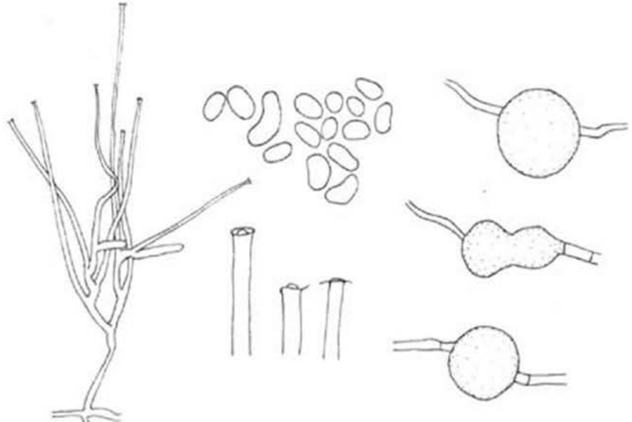

Fig. 9. *Mortierella gemmifera*, strain Kuhlman 4 II A: sporangiophore × 100; sporangiophore tips, and chlamydospores × 500.

walled, 8–12(–17) × 5–7(–9) μm. Chlamydospores abundant, globose or irregularly lemon-shaped, ochraceous, 20–25 μm in diameter (orig. description 30–50 μm). Invested zygospores, 100–150 μm in diameter, were described by Ellis (l.c.) but not observed since.

CULTURES EXAMINED.—CBS 134.45 = NCTC 6082, type strain, ex pine forest soil near Nottingham, G. B.; CBS 842.70 (strain 7353), ex forest soil, sent by Mrs. M. Turner to E. G. Kuhlman in 1970, possibly identical with CBS 134.45 but with better sporulation.

CBS 124.72, ex humus layer of an oak forest soil, Meerdink-Bos near Winterswijk, Netherlands, *B. E. Söderström*, 1971.

NRRL A-16538, ex pine roots, North Carolina, *E. G. Kuhlman* (4IIA).

After publishing *M. gemmifera*, Turner (pers. comm.) doubted the justification of the specific separation of this species. Mating experiments with a tester pair of *M. elongata* Linnem. had no results. Therefore this uncommon species is regarded as sufficiently distinct.

10. **Mortierella kuhlmanii** W. Gams *spec. nov.*—Fig. 10

Mortierella elongata Linnem. sensu Kuhlman *in* Mycologia **64**: 335. 1972.

Coloniae celeriter crescunt, modice zonatae, mycelio aerio tenui obtectae, fortiter olent. Sporangiophora numerosa ex hyphis submersis vel aeriis oriuntur, 250–500 μm alta, crebro basitone ramosa, e 12–20 μm ad 4–8(–10) μm angustata, sed in summo ad 8–14 μm inflata. Sporangia 25–30 μm diam., multispora, dilapsa columellam applanatam conspicuam relinquunt. Sporae elongato-ellipsoideae, nonnumquam curvatae, leves, 8–12(–17) × 4–5(–7) μm. Chlamydosporae abundantes, globosae, singulae, ochraceae, 9–22 μm diam. Species homothallica: zygosporae crassitunicatae, leves, 50–55 μm diam.

Holotypus: CBS 157.71, isolatus e trunco *Pini palustris*, Miley in Carolina meridionali, U.S.A., *E. G. Kuhlman*, 1971.

Colonies fast-growing with a daily radial increment of 8–9 mm, faintly zonate, covered with thin aerial mycelium; odour strong and typical of the genus. Sporulation good on MEA and SEA; sporangiophores arising from the substratum and aerial hyphae, 250–500 μm tall, with abundant basitonous ramification, tapering from 12–20 μm to 4–8(–10) μm below the tip, with a pronounced apical inflation (apophysis) of 8–14 μm in diameter and a slightly lower columella. Sporangia 25–35 μm in diameter, many-spored. Spores elongate ellipsoidal, sometimes curved, smooth-walled, 8–12(–17) × 4–5(–7) μm. Chlamydospores abundant, globose, solitary, ochraceous, 9–22 μm in diameter. Zygospore formation in the homothallic species was described by Kuhlman (1972) but could not be reproduced by the present author; zygospores smooth and thick-walled, 50–55 μm in diameter.

CULTURES EXAMINED.—CBS 157.71, type strain, ex stump of *Pinus palustris*, Miley, South Carolina; CBS 269.71 (= NRRL A-11646); CBS 270.71, ex stump of *Pinus taeda*, Patrick, South Carolina; CBS 271.71, ex seedling of *Pinus palustris*, South Carolina; all comm. E. G. Kuhlman.

Mortierella kuhlmanii differs from the similar *M. elongata* by the wide sporangiophores with an apical apophysis and the larger and globose chlamydospores. The distinction

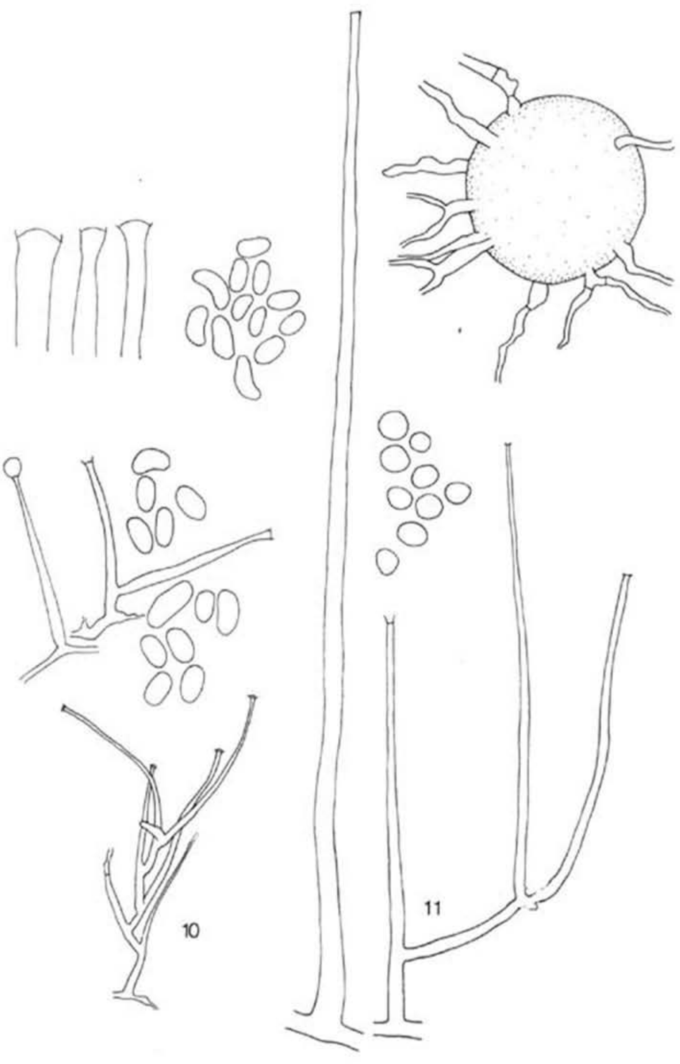

Fig. 10. *Mortierella kuhlmanii*, CBS 157.71 and 271.71: sporangiophores × 100; sporangiophore tips and spores × 500.

Fig. 11. *Mortierella sclerotiella*, sporangiophores, spores, and a chlamydospore × 500.

between these two species is also proved by the absence of any mating reaction between a tester pair of *M. elongata* and *M. kuhlmanii*. *Mortierella elongata* has smaller zygospores with a honey-comb like surface (Gams & *al.*, 1972). *Mortierella kuhlmanii* has more affinity with *M. beljakovae* Mil'ko (cf. below) because of the apophysate sporangiophores; it differs from this species by the more elongate spores, always solitary chlamydospores and the homothallic behaviour, whilst *M. beljakovae* is heterothallic (Kuhlman, 1972).

11. MORTIERELLA BELJAKOVAE Mil'ko
in Nov. Sist. niz. Rast. 1973: 85.—Fig. 12

Mortierella candelabrum Tiegh. & Le Monn. sensu Kuhlman *in* Can. J. Bot. **47**: 1721. 1969; *in* Mycologia **64**: 334. 1972.
Mortierella zychae Linnem. sensu Kuhlman *in* Mycologia **64**: 339. 1972.

Colonies fast-growing with a daily radial increment of 6–9 mm, surface even or sometimes broadly zonate and usually without aerial mycelium; odour typical of the genus but not strong (on SEA). Sporulation abundant on SEA, less on MEA; sporangiophores arising from the substratum, 150 to more than 800 μm tall, with abundant basitonous ramification, tapering from 10–15(–18) μm to 4–8 μm below the tip, with an inflation (apophysis) 7–13 μm in diameter, and a somewhat shorter columella. Sporangia 20–35 μm in diameter, many-spored. Spores short ellipsoidal to subglobose, smooth-walled, 6–9(–11) × 5–8 μm. Chlamydospores abundantly produced, solitary or often in chains or irregular clusters (reminiscent of *M. zychae* Linnem.), globose, thick-walled, ochraceous, 20–45(–60) μm in diameter. Zygospores were obtained by Kuhlman (1972) after mating between compatible strains; zygospores smooth and thick-walled, 43–56 μm in diameter.

CULTURES EXAMINED.—CBS 805.68 (2 B) and 806.68 (127), ex pine root bark, North Carolina, *E. G. Kuhlman*, 1968 (previously preserved as *M. gemmifera* Ellis).
CBS 601.68 (13 B), ex pine stump bark; CBS 267.71 (M 70), mating type A, and 268.71 (M 72), mating type B, ex *Pinus taeda* seedling, *E. G. Kuhlman*, 1971, sent as *M. zychae* Linnem.
CBS 274.71 (M 92), mating type A, CBS 275.71 (M 29, NRRL A-16539), mating type B, CBS 276.71 (M 93, NRRL A-16540), mating type A, all three ex *Pinus taeda* root, South Carolina, *E. G. Kuhlman*, 1971, sent as *M. candelabrum* Tiegh. & Le Monn.
CBS 123.72 = BKM F-1608, type strain, ex soil near Sarny, Ukr. S. S. R., *A. A. Mil'ko*, 1971.
CBS 209.72 (M 122), ex Piedmont soil, North Carolina, *C. S. Hodges*, 1971 (comm. E. G. Kuhlman).

The arrangement of the chlamydospores in chains and clusters has been observed in all strains but is not equally pronounced in all of them. The single chlamydospores are usually completely rounded off in contrast with *M. zychae* Linnem., where the chlamydospore outline merges gradually into the connecting hyphal parts. The sporangiophores of *M. zychae* are more slender than in *M. beljakovae* and do not have an apophysis. No further difference was observed between the strains originally sent as *M. candelabrum* and *M. zychae*. The species is very close to *M. kuhlmanii* W. Gams

(cf. p. 122). Gams & Domsch (1970) put forward arguments for synonymizing *M. spinosa* Linnem. with *M. candelabrum* but this suggestion was not taken over by other specialists in this genus. The original description of *M. candelabrum* (van Tieghem & Le Monnier, 1873) agrees less with *M. beljakovae* than with *M. spinosa* or *M. hyalina*

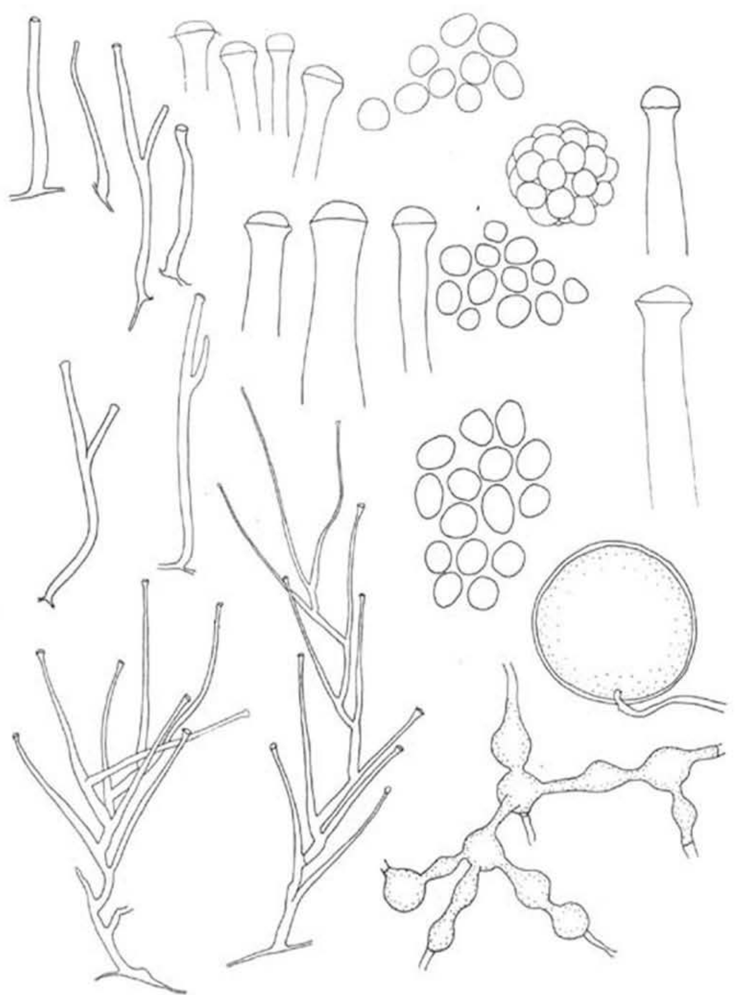

Fig. 12. *Mortierella beljakovae*: CBS 806.68, sporangiophores ×100, sporangiophore tips and spores ×500; CBS 209.72, chlamydospores ×500.

(Harz) W. Gams; moreover, *M. beljakovae* is apparently very rare or absent in central and western Europe and has probably not been available to van Tieghem & Le Monnier (1873). *Mortierella candelabrum* is best left in the status of a doubtful species, so that misunderstandings about its identity can be avoided.

12. **Mortierella parazychae** W. Gams *spec. nov.*—Fig. 13a

Coloniae fere celeriter crescunt, dense lobulatae et zonatae, mycelio aerio in medio obtectae, fortiter olent. Sporangiophora pauca ex hyphis aeriis vel submersis oriuntur, 80–250 μm alta, raro basitone ramosa, e 4–6 μm ad 2.5–3.0 μm angustata. Sporangia 12–20 μm diam., multispora, dilapsa collare inconspicuum et columellam minutissimam relinquunt. Sporae ellipsoideae ad cylindricae, leves, duplicitunicatae, 3.5–8.0 × 2.0–3.3 μm. Chlamydosporae copiosae, praecipue in mycelio aerio, dense catenulatae et acervatae, ex articulis fere globosis, 10–18 μm diam. compositae.

Holotypus: CBS 868.71, isolatus e ligno putrido *Pini sylvestris* una cum *Botryobasidio subcoronato* (Höhn. & Litsch.) Donk, Treek prope Amersfoort in Neerlandia, *J. A. Stalpers*, 1971.

Colonies growing moderately fast with a daily radial increment of 5–7 mm, densely lobed and zonate, with some aerial mycelium in the centre; odour rather strong and typical of the genus. Sporulation moderate on SEA, poor on MEA; sporangiophores arising from aerial hyphae or from the substratum, 80–250 μm tall, with infrequent basitonous ramification, tapering from 4–6 μm to 2.5–3.0 μm at the tip. Sporangia 12–20 μm in diameter, many-spored, leaving an inconspicuous collarette and a trace of a columella on dehiscence. Spores ellipsoidal to cylindrical, smooth-walled, surrounded by a thin outer wall, 3.5–8.0 × 2.0–3.3 μm. Chlamydospores abundantly produced, particularly in the aerial mycelium, in dense clusters, almost globose, gradually merging into the narrow portions, thin-walled, 10–18 μm in diameter.

Known only from the type culture.

Mortierella parazychae differs from the similar *M. zychae* Linnem. (see Fig. 13b for comparison) by smaller (*M.zychae* 8—12 × 4.5—6.0 μm), double-walled spores and also shorter, less conspicuously branched sporangiophores.

13. Mortierella sclerotiella Mil'ko
in Nov. Sist. niz. Rast. 1967: 160.—Fig. 11

Colonies growing moderately fast, with a daily radial increment of 5–6 mm, densely lobed and zonate with little aerial mycelium in the centre; odour weak but typical of the genus on SEA. Sporulation moderate on SEA; sporangiophores arising from the substratum or from aerial hyphae, 50–300 μm tall, with basitonous ramification, tapering from 5–8 μm to 2–4 μm at the tip. Sporangia 15–20 μm in diameter, few-spored, on dehiscence leaving an imperceptible collarette. Spores

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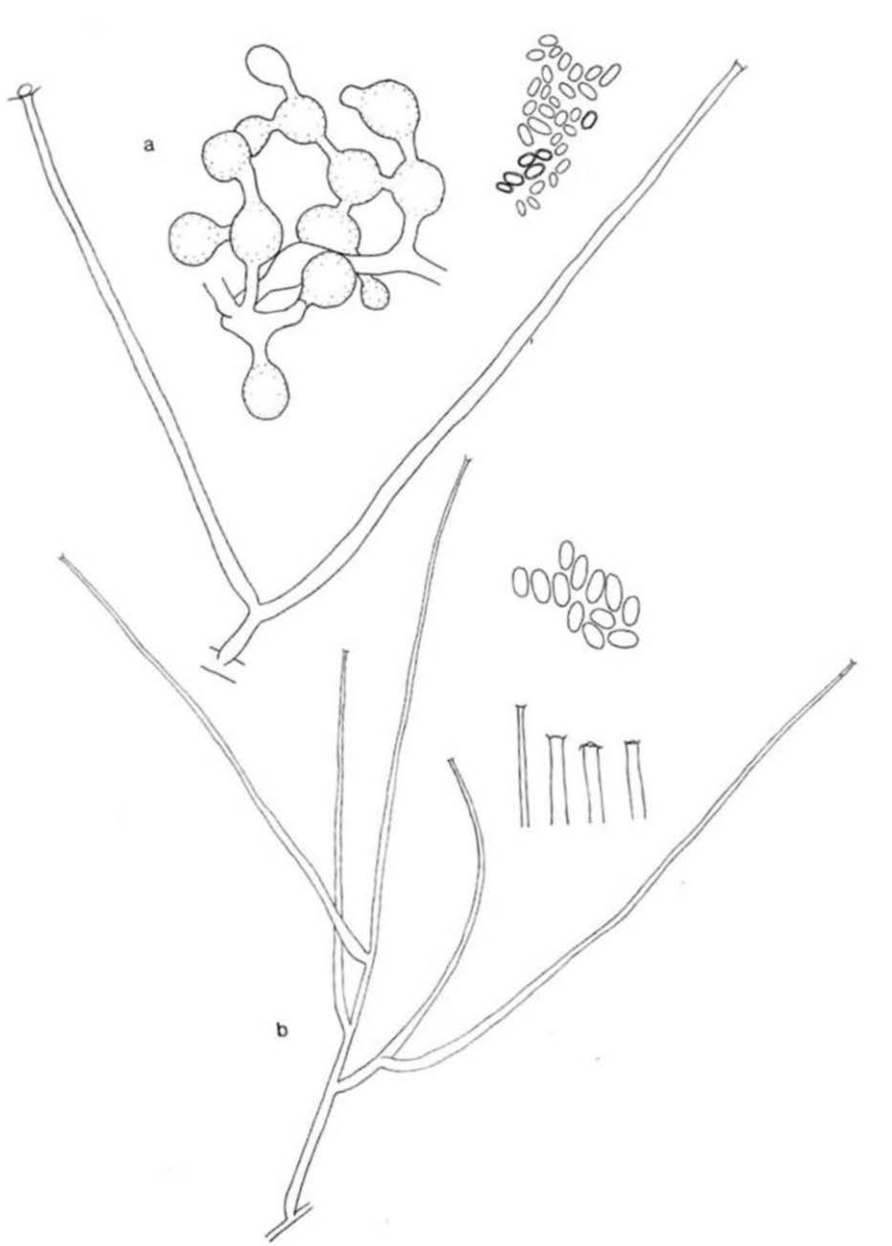
Fig. 13a. *Mortierella parazychae*, sporangiophore, spores, and cluster of chlamydospores × 500.
Fig. 13b. *Mortierella zychae*, CBS 316.52: sporangiophore × 100; sporangiophore tips and spores × 500.


a
b

short ellipsoidal to subglobose, sometimes curved, with a minute striate ornamentation (visible particularly in lactic acid mounts where the outer wall is separated from the spore content), 6–10 × 6–8 μm. Chlamydospores abundantly produced, globose, sometimes elongate, ochraceous, 40–90 μm in diameter, often giving rise to numerous shorter or longer radiating hyphae.

CULTURE EXAMINED.—CBS 529.68 = BKM-F 1909, type strain, ex mouse excrements, near Kiev, Ukr.S.S.R., *A.A. Mil'ko*, 1964.

M. sclerotiella is close to *M. gemmifera* Ellis, but differs by shorter, finely ornamented spores and the fimbriate appearance of the chlamydospores.

14. **Mortierella armillariicola** W. Gams *spec. nov.*—Fig. 14

Coloniae celeriter crescunt, in margine lobulatae, in medio mycelio aerio obtectae, vix olent. Sporangiophora ex hyphis aeriis vel submersis oriuntur, ad 1500–1700 μm alta, irregulariter basitone vel mesotone vel raro acrotone ramosa, e 18–20 μm ad 5–7 μm angustata. Sporangia 60– > 90 μm diam., multispora, dilapsa collare fere conspicuum relinquunt. Sporae irregulariter elongatae, saepe reniformes, leves, 18–26(–32) × 8–12(–17) μm. Chlamydosporae globosae, singulae, crassitunicatae, 40–60 μm diam.

Holotypus: CBS 914.73, isolatus e lamellis *Armillariae melleae* una cum *Endomycete decipiente* (Tul.) Reess, Groeneveld prope Baarn in Neerlandia, *W. Gams*, Nov. 1973.

Colonies in fresh isolates fast-growing, after some transfers slow, with a daily radial increment of 2 mm, minutely lobed at the margin, covered with some aerial mycelium in the centre; odour weak. Sporulation abundant on SEA and PCA, moderate on MEA; sporangiophores arising from aerial and submerged hyphae, with a little distinct base, up to 1500–1700 μm tall, with irregularly basitonous to mesotonous or rarely acrotonous ramification, tapering from 18–20 μm to 5–7 μm near the tip. Sporangia 60– over 90 μm in diameter, many-spored, leaving a rather conspicuous collarette but no columella on dehiscence. Spores irregularly elongate, often kidney-shaped, smooth-walled, 18–26(–32) × 8–12(–17) μm. Chlamydospores commonly produced, globose, solitary, thick-walled, 40–60 μm in diameter.

Known only from the type strain and some other isolates from the same origin and locality.

M. armillariicola is similar to *M. gemmifera* Ellis, but has much larger dimensions.

15. **Mortierella selenospora** W. Gams *spec. nov.*—Fig. 15

Coloniae celeriter crescunt, late zonatae, mycelio aerio pauco obtectae, modice olent. Sporangiophora ex hyphis submersis oriuntur, paucis rhizoideis praedita, 350–900 μm alta, basitone vel mesotone ramosa, e 7–12 μm ad 3 μm angustata. Sporangia 35–50 μm diam., multispora, dilapsa collare inconspicuum relinquunt. Sporae lunatae, pariete utrinque inspissato, leves, 15–20 × 5–9 μm. Chlamydosporae rarae, terminales, pyriformes, 15–18 μm diam.

Holotypus: CBS 811.68, isolatus e fimo culturae agaricorum, Horst/L. in Neerlandia, Sept. 1968.

Colonies fast-growing, with a daily radial increment of 7–8 mm, broadly zonate with little aerial mycelium; odour moderate but typical of the genus. Sporulation abundant on SEA, less on MEA; sporangiophores arising from the substratum with a few rhizoids, 350–900 μm tall, with basitonous to mesotonous diffuse ramification, tapering from 7–12 μm to 3 μm at the tip. Sporangia 35–50 μm in diameter, many-spored, on dehiscence leaving an inconspicuous collarette. Spores lunate (shape of

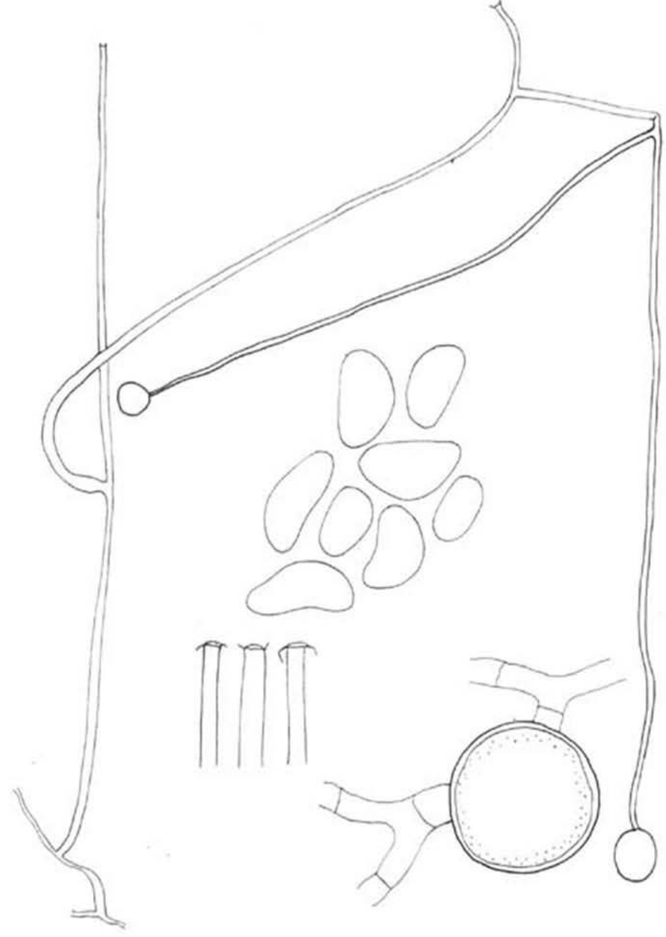


Fig. 14. *Mortierella armillariicola:* sporangiophore ×100; sporangiophore tips, spores, and chlamydospore ×500.

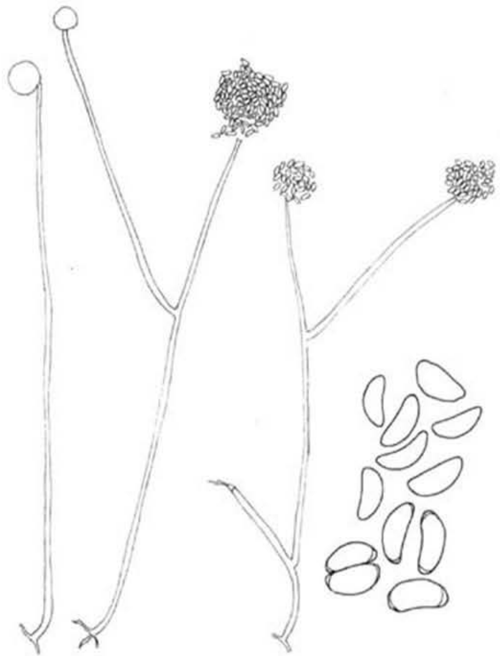


Fig. 15. *Mortierella selenospora*: sporangiophores × 100; spores × 500.

an orange slice) with a thickened wall at either end, smooth-walled, 15–20 × 5–9 μm. Chlamydospores scarcely produced, terminal, pyriform, 15–18 μm in diameter.
Known only from the type strain.

The only other species with lunate spores is *M. umbellata* Chien (1972) which has unusual acrotonously verticillate sporangiophores and smaller spores of 7–10 × 3–5 μm.

16. **Mortierella basiparvispora** W. Gams & Grinbergs *spec. nov.*—Fig. 16

Coloniae fere celeriter crescunt, dense radiatim striatae, pauco mycelio aerio in medio obtectae, modice olent. Sporangiophora numerosa ex hyphis submersis oriuntur, 250–300 μm alta, crebro basitone ramosa, e 8–13(–18) μm ad 3–7 μm angustata. Sporangia 25–50 μm diam., multispora, dilapsa collare conspicuum relinquunt. Sporae subglobosae ad globosae, leves, 3–4 μm diam. vel 5–6 × 4–5 μm. Chlamydosporae absunt.
Holotypus: CBS 518.72, isolatus e solo sub *Fitzroya cupressoide*, Cordillera Pelada prope Valdiviam Chilensem, *J. Grinbergs*, 1972.

Colonies growing moderately fast, with a daily radial increment of 4–5 mm, narrowly radially striate, with little aerial mycelium in the centre; odour faint, but typical of the genus. Sporulation moderate on MEA, very rich on SEA; sporangiophores arising from the substratum, 250–300 μm tall, with repeated basitonous ramification, tapering from 8–13(–18) μm to 3–7 μm near the tip. Sporangia 25–50 μm in diameter, many-spored, leaving a conspicuous collarette on dehiscence. Spores subglobose to globose, smooth-walled, 3–4 μm in diameter or 5–6 × 4–5 μm. Chlamydospores absent.

CULTURES EXAMINED.—CBS 517.72 (No. 21) and 518.72 (No. 108), type strain, ex soil under *Fitzroya cupressoides*, Cordillera Pelada, Valdivia, Chile, *J. Grinbergs*, 1972.

The two strains differ somewhat in spore size and shape: 518.72 has smaller and globose spores and the sporangiophores are more slender at the tip (3 μm), whilst in CBS 517.72 the spores are bigger, subglobose and the sporangiophore tips 5–7 μm wide. *Mortierella basiparvispora* can be regarded as a counterpart of *M. parvispora* Linnem. with consistently basitonous ramification and no trace of a columella; therefore it is placed in sect. *Hygrophila*.

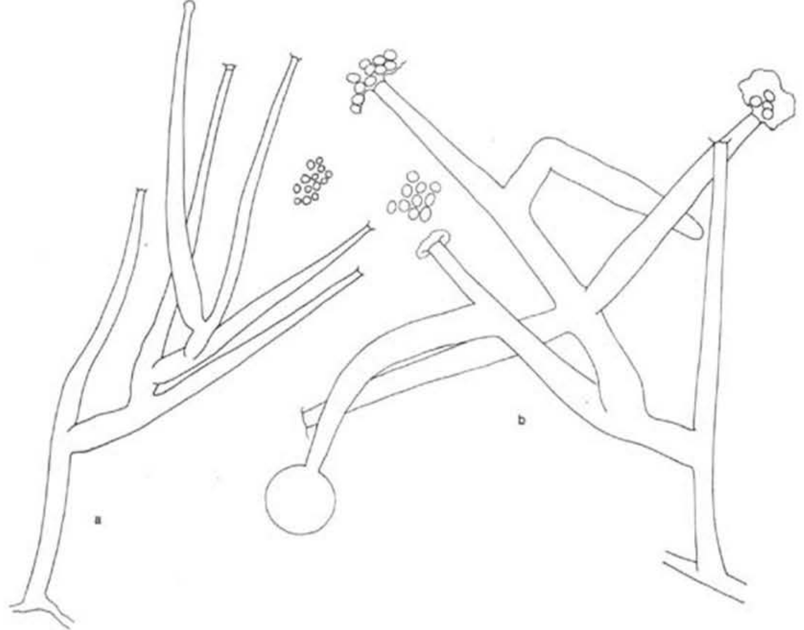


Fig. 16. *Mortierella basiparvispora*, sporangiophores and spores × 330. — a. CBS 518.72. — b. CBS 517.72.

17. **Mortierella clonocystis** W. Gams *spec. nov.*—Fig. 17

Coloniae modice celeriter crescunt, late lobatae, quoque lobo mycelio aerio obtecto, modice olent. Sporangiophora pauca plerumque ex hyphis submersis oriuntur, 85–160 μm alta, raro unum ramum mesotonum proferunt, e 2.5–3.0 μm ad 1.0 μm angustata. Sporangia 10–12 μm diam., multispora, dilapsa collare inconspicuum relinquunt. Sporae subglobosae, leves, 2.5–4.0 μm diam. Chlamydosporae aut parvae globosae, 6–10 μm diam., aut rangiformes ex hyphis ramosis inflatus submersis vel aeriis, 7–12 μm latis transformatae.

Holotypus: CBS 357.76, isolatus e solo sub *Apollonia canariensi* (Willd.) Nees in insula Gran Canaria prope Tafiram, leg. *J. A. von Arx*, Apr. 1976.

Colonies growing moderately fast with a daily radial increment of 6–8 mm, broadly lobed, with patchy floccose aerial mycelium on the lobes; odour not strong but typical of the genus. Sporulation moderate on SEA, absent on MEA. Sporangiophores mostly arising from the substratum, 85–160 μm tall, rarely bearing a mesotonously inserted lateral branch, tapering from 2.5–3.0 μm to 1.0 μm. Sporangia 10–12 μm in diameter, many-spored, on dehiscence leaving an inconspicuous collarette. Spores subglobose, smooth-walled, 2.5–4.0 μm in diameter. Chlamydospores of two types: (a) small, ± globose, 6–10 μm in diameter, and (b) consisting of submerged or aerial broadened hyphal branches, repeatedly dichotomous, 7–12 μm wide.

Known only from the type strain.

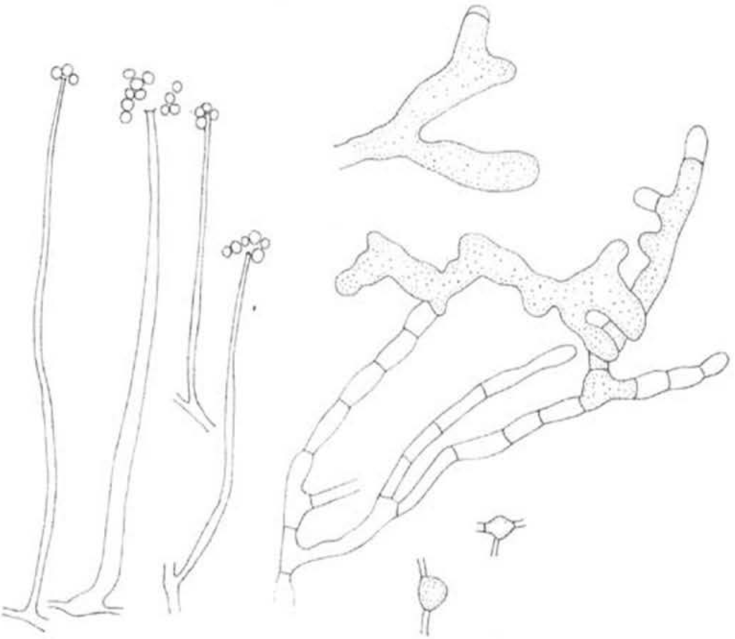


Fig. 17. *Mortierella clonocystis*, sporangiophores, spores, and two kinds of chlamydospores × 500.

Mortierella clonocystis recalls *M. globalpina*, but has longer and more slender sporangiophores with an occasional side branch. It is therefore placed in section *Hygrophila.*

SECTION SPINOSA Linnem. emend. W. Gams

Sporangiophores with a wide, often curved base, bearing mesotonous to acrotonous cymose branches. Sporangia usually with a minute columella.

18. **Mortierella epicladia** W. Gams & Emden *spec. nov.*—Fig. 18

Coloniae fere celeriter crescunt, dense lobulatae, mycelio aerio parco obtectae, modice olent. Sporangiophora ex hyphis submersis vel aeriis oriuntur, 60–160 μm alta, 1–3 ramos acrotonos proferunt, e 6–8(–9) μm ad 1.5–2.0(–3.5) μm angustata. Sporangia 12–20 μm diam., multispora, dilapsa columellam minutam et collare inconspicuum relinquunt. Sporae ± globosae, leves, 4–7(–10) μm diam. Chlamydosporae rarae, ± limoniformes, vulgo 6 μm diam.

Holotypus: CBS 355.76, isolatus e solo sub *Apollonia canariknsi* (Willd.) Nees in insula Gran Canaria prope Tafiram, leg. *J. A. von Arx*, Apr. 1976.

Colonies growing moderately fast with a daily radial increment of 6–8 mm, forming a rosette of dense lobes, with very little aerial mycelium; odour moderate but typical of the genus. Sporulation rich on SEA, less on MEA, sporangiophores arising from the substratum or aerial hyphae, 60–160 μm tall, bearing 1–3 acrotonous branches, tapering from 6–8(–9) to 1.5–2.0 (–3.5) μm at the tip. Sporangia 12–20 μm in diameter, many-spored, on dehiscence leaving a minute columella and inconspicuous collarette. Spores ± globose, smooth-walled, 4–7(–10) μm in diameter. Chlamydospores scarcely produced, ± lemon-shaped, about 6 μm in diameter.

CULTURES EXAMINED.—CBS 246.75, ex soil under *Elaeis guineensis*, Surinam, *J. H. van Emden*, 1975.

CBS 355.76 (type strain) and 356.76, ex soil, Gran Canaria, nr. Tefira, under *Apollonias canariensis*, leg. *J. A. von Arx*, Apr. 1976.

This is the only *Mortierella* species isolated during an extended study of soil fungi in a soil sample from Surinam by J. H. van Emden. *M. epicladia* is closest to *M. pulchella* Linnem., but differs by faster growth (*M. pulchella* has 4–5 mm daily radial increment), slightly bigger spores and the presence of chlamydospores. The relative length of the lateral branches is variable (cf. Fig. 18a and b) as in *M. pulchella* and cannot be regarded as being of taxonomic importance.

19. **Mortierella acrotona** W. Gams *sp. nov.*—Fig. 19

Coloniae celeriter crescunt, late zonatae, mycelio aerio tenui lanuginoso usque ad marginem obtectae, modice olent. Sporangiophora ex hyphis aeriis tarde oriuntur, 110–350 μm alta, plerumque unum (raro duos) ramulum acrotonum proferunt, e 7–12 μm ad 2–5 μm angustata. Sporangia 15–40 μm diam., 1–4-spora, dilapsa collare conspicuum infundibuliforme relinquunt. Sporae globosae, leves, duplicitunicatae, 11–24 μm, plerumque 17–20 μm diam. Chlamydosporae vulgo adsunt, fere globosae, 15–22 μm diam.

Holotypus: CBS 386.71, isolatus e solo prope Rambagh Palace Hotel, Jaipur in India, leg. *D. H. Wieringa-Brants*, Jan. 1971.

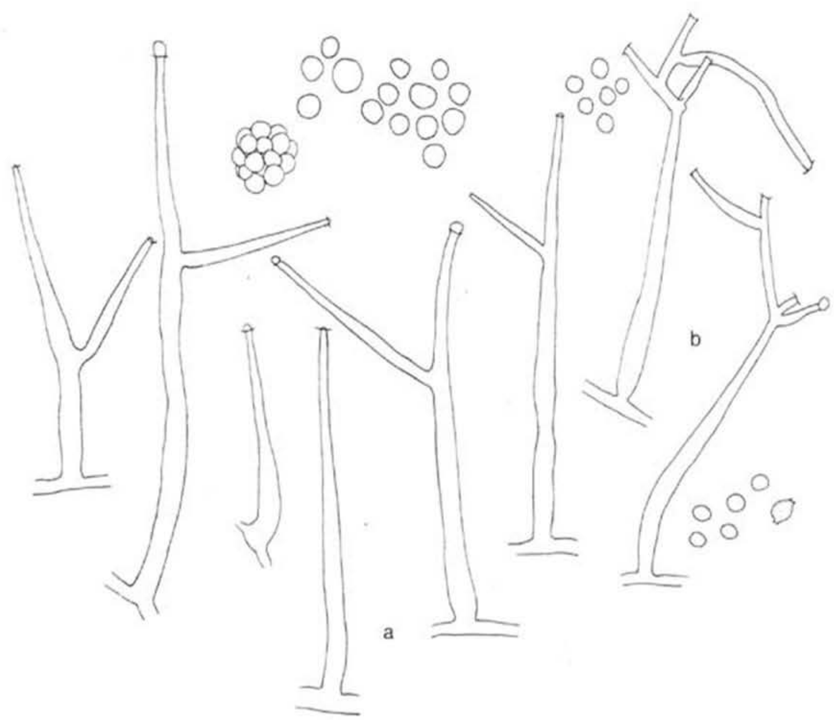


Fig. 18. *Mortierella epicladia*, sporangiophores, sporangium, spores, and chlamydospore ×500. — a. CBS 355.76. — b. CBS 246.75.

Colonies fast-growing with a daily radial increment of 9–12 mm, broadly zonate, evenly covered with a thin cottony aerial mycelium which extends to the margin; odour moderate but typical of the genus. Sporulation appearing only after 2–3 weeks on MEA and SEA; sporangiophores arising from aerial hyphae, 110–350 µm tall, bearing usually one (rarely two) acrotonous branches, tapering from 7–12 µm to 2–5 µm at the tip. Sporangia 15–40 µm in diameter, containing each 1–4 spores, on dehiscence leaving a pronounced, funnel-shaped collarette. Spores globose, smooth-walled, surrounded by a thin outer wall, 11–24 µm, mostly 17–20 µm in diameter. Chlamydospores commonly produced, globose, gradually merging into the subtending hypha, 15–22 µm in diameter.

CULTURES EXAMINED.—CBS 383.71, 385.71, 386.71 (type strain), ex soil near Rambagh Palace Hotel, Jaipur (loose light-brown soil), India, leg. *D. H. Wieringa-Brants*, Jan. 1971.

Mortierella acrotona is very distinct by its large, double-walled spores. Similar wall structures occur rarely in species of various sections, viz. in *M. angusta* (Linnem.) W. Gams, *M. parazychae* W. Gams (cf. p. 126), and *M. wolfii* Mehrotra & Baijal.

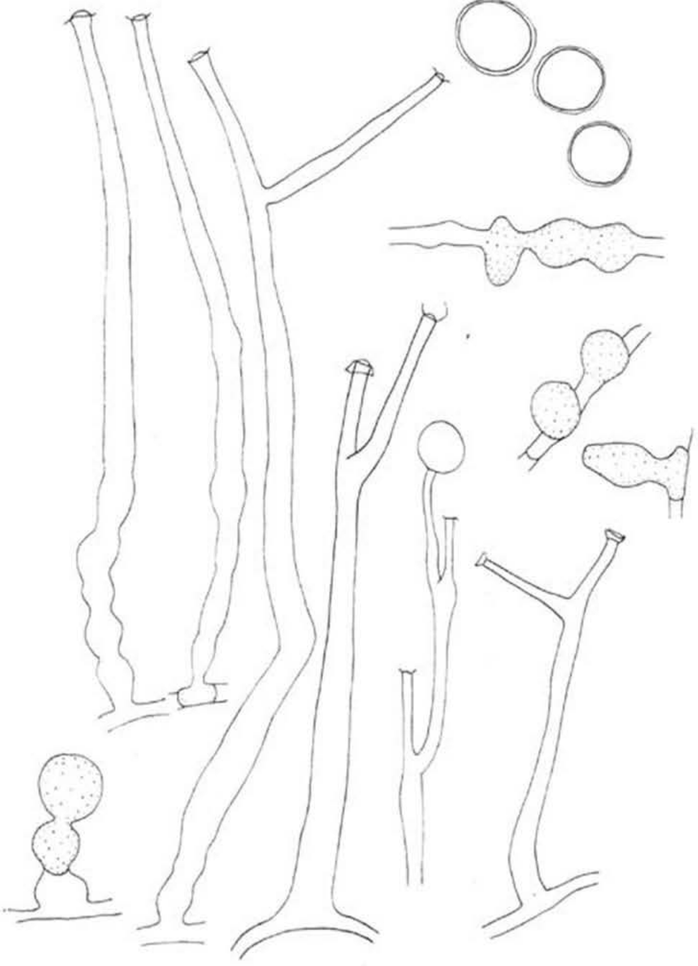


Fig. 19. *Mortierella acrotona*, CBS 386.71 and 385.17, sporangiophores, spores, and chlamydospores ×500.

20. MORTIERELLA JENKINII (A. L. Sm.) Naumov—Fig. 20

Mortierella bainieri Cost. var. *jenkinii* A. L. Sm. *in* J. Bot., Lond. **36**: 180. 1898. — *Mortierella jenkinii* (A. L. Sm.) Naumov, Opredelitel' Mukorovykh (Mucorales), Ed. 2: 97. 1935. Moskva-Leningrad.

Colonies moderately fast-growing with a daily radial increment of about 5 mm, finely radially striate, with little aerial mycelium in the centre; odour typical of the genus but not strong. Sporulation abundant on SEA and oatmeal agar, weak on MEA; sporangiophores arising mostly from aerial hyphae, sometimes from the substratum with rhizoids, 400– over 1500 μm tall, the basal part often curved and up

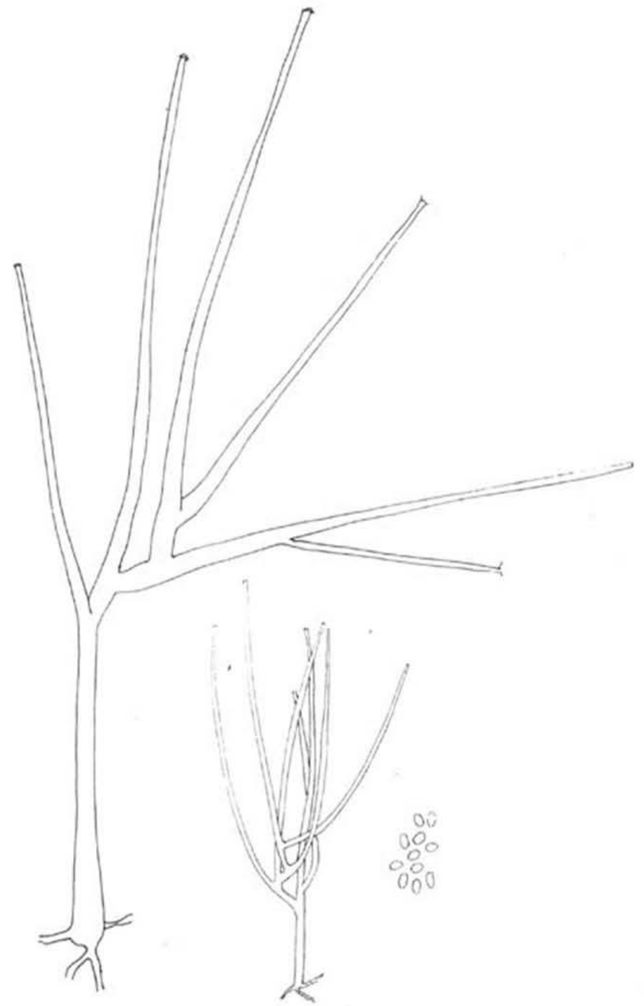


Fig. 20. *Mortierella jenkinii*, CBS 667.70: sporangiophores × 100 and × 350; spores × 500.

to 600 μm long before the numerous basitonous, mesotonous or acrotonous branches are inserted, tapering from 10–12 (to over 20) μm to 2.0–3.5 μm at the tip. Sporangia 10–60 μm in diameter, many-spored, on dehiscence leaving a minute trace of a columella and a small collarette. Spores short-ellipsoidal to cylindrical, smooth-walled, 3.5–4.0(–0.5) × 2.0–2.5 μm. Chlamydospores absent or tardily produced, lemon-shaped, 7–10 μm in diameter. Zygospores were not obtained in spite of repeated mating.

CULTURES EXAMINED.—CBS 109.68, ex *Daedalea quercina* (L. ex Fr.) Pilát, Iloo Forest, Kr. Rendsburg, F. R. G., *W. Gams*, 1965.

CBS 667.70 and 850.70, ex agricultural soil, Wageningen, *J. W. Veenbaas-Rijks*, 1970.

CBS 516.72, ex soil under *Fitzroya cupressoides*, Cordillera Pelada, Valdivia, Chile, *J. Grinbergs (No. 107)*, 1972.

CBS 188.73, ex turf layer of a golf green which has received fungicidal treatment for a long period, Nottingham, G. B., comm. J. I. Williams, 1973.

CBS 965.73 A–D and 666.75 A–D, ex forest soil under *Picea abies*, Sweden, *B. E. Söderström*.

The strains listed here are of rather constant morphology with the very variable branching pattern ranging from basitonous to acrotonous. The classification in section *Spinosa* is preferred over section *Hygrophila* because of the thick, often curved basal part of the sporangiophores and the sometimes occurring minute columella. This interpretation of *M. jenkinii* agrees perfectly with the original description and illustration, but expands the range of variability.

21. **Mortierella cystojenkinii** W. Gams & Veenbaas-Rijks *spec. nov.*—Fig. 21

Coloniae fere lente crescunt, leves, parco mycelio aerio obtectae, modice olent. Sporangiophora numerosa ex hyphis submersis vel aeriis oriuntur, 120–>200 μm alta, raro mesotone vel acrotone ramosa, e 3–8 μm ad 1.2–3.0 μm angustata. Sporangia 10–20 μm diam., multispora, dilapsa collare inconspicuum et columellam minutissimam relinquunt. Sporae ellipsoideo-cylindricae, leves, 3–4 × 1.2–2.0 μm. Chlamydosporae abundantes, globosae, crassitunicatae, dilute brunneae, 20–60 μm diam.

Holotypus: CBS 456.71, isolatus e solo agresti prope Wageningen, *J. W. Veenbaas-Rijks*, 20 Feb. 1971.

Colonies rather slow-growing, with a daily radial increment of about 5 mm, smooth, with little aerial mycelium; odour weak but typical of the genus. Sporulation abundant on MEA and SEA; sporangiophores arising from the substratum and aerial hyphae, 120 to over 200 μm tall, with infrequent mesotonous to acrotonous ramification, tapering from 3–8 μm to 1.2–3.0 μm at the tip. Sporangia 10–20 μm in diameter, many-spored, leaving an inconspicuous collarette on dehiscence and a small trace of a columella. Spores ellipsoidal-cylindrical, smooth-walled, 3–4 × 1.2–2.0 μm. Chlamydospores abundantly produced, globose, thick-walled, light brown, 20–60 μm in diameter.

CULTURES EXAMINED.—CBS 456.71, type strain, ex agricultural soil, Wageningen, *J. W. Veenbaas-Rijks*, 20 Feb. 1971. Another strain was isolated from *Betula* leaf litter, Osterau, Kr. Plön, F. R. G. in 1965, but is now lost.

Mortierella cystojenkinii differs from *M. jenkinii* not only by the presence of large, globose chlamydospores but also by smaller spores.

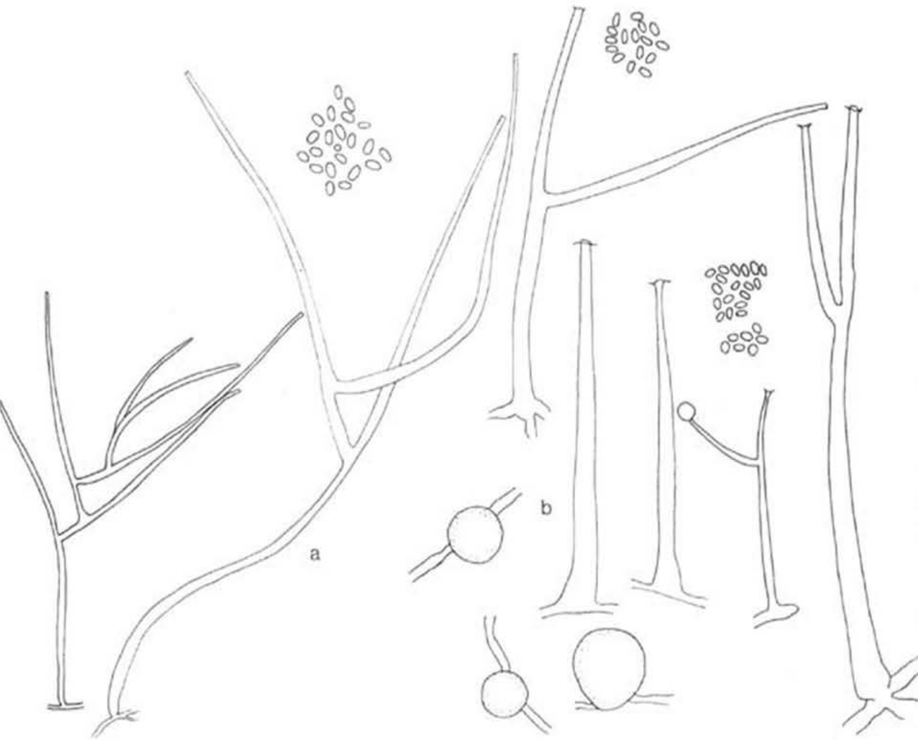


Fig. 21. *Mortierella cystojenkinii*: sporangiophore × 100; sporangiophore, spores, and chlamydospore × 500. — a. strain from *Betula* litter. — CBS 456.71.

22. **Mortierella fimbricystis** W. Gams *spec. nov.*—Fig. 22

Coloniae fere lente crescunt, inconspicue radiatim striatae, mycelio aerio absente, modice olent. Sporangiophora ex hyphis submersis, nonnumquam ad basin rhizoideis praedita, vel ex hyphis aeriis oriuntur, 140–320 μm alta, raro acrotone ramosa, e 7–13 μm ad 2–4 μm angustata. Sporangia 15–30 μm diam., multispora, dilapsa collare inconspicuum et columellam minutissimam relinquunt. Sporae ellipsoideo-cylindricae, leves, 4.0–5.5 × 2.0–3.0 μm. Chlamydosporae copiosae, praecipue in mycelio aerio, intercalares vel laterales, globosae vel elongatae, ochraceae ad aurantiacae, 28–45 μm diam., appendicibus 2–4 μm longis dense fimbriatae.

Holotypus: CBS 973.70, isolatus e pulvino musci cuiusdam, Puerto Edwards in Patagonia meridionali prope canalem navis Beagle, *F. W. Went*, 1970.

Colonies rather slow-growing with a daily radial increment of 3–5 mm, with a fine radiating structure and no aerial mycelium; odour weak but typical of the

genus. Sporulation good on MEA and SEA; sporangiophores arising from the substratum, sometimes with rhizoids, or from aerial hyphae, 140–320 μm tall, with scarce acrotonous ramification, tapering from 7–13 μm to 2–4 μm at the tip. Sporangia 15–30 μm in diameter, many-spored, leaving an inconspicuous collarette and a trace of a columella on dehiscence. Spores ellipsoidal-cylindrical, smooth-walled,

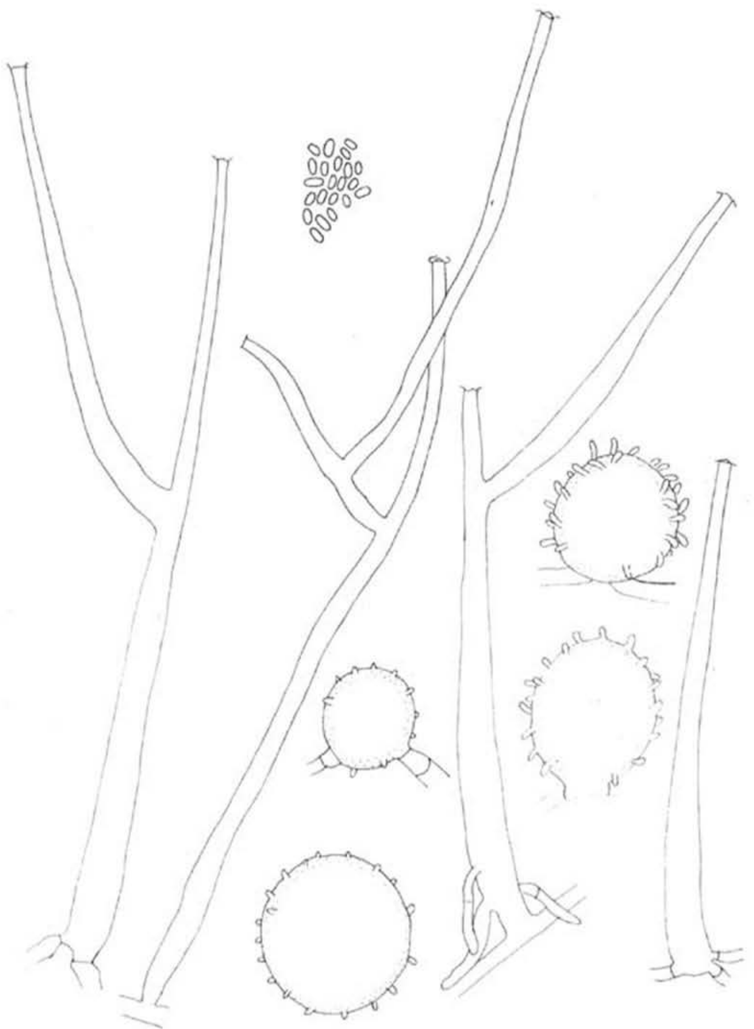


Fig. 22. *Mortierella fimbricystis*, sporangiophore, spores, and chlamydospores $\times$ 500.

4.0–5.5 × 2.0–3.0 µm. Chlamydospores abundantly produced, often in the aerial mycelium in intercalary or lateral position, globose or elongate, ochraceous to orange, 28–45 µm in diameter, densely covered with fimbriate appendages, 2–4 µm long.
Known only from the type strain.

Mortierella fimbricystis is close to *M. echinosphaera* Plaats-Niterink (van der Plaats-Niterink *& al.*, 1976) but differs by larger, somewhat pigmented chlamydospores and the presence of sporangiophores. The strain was preserved as *M. alliacea* Linnem. until recently, but differs from this species by taller and branched sporangiophores and also taller chlamydospores.

Acknowledgements

The writer thanks all the mycologists mentioned in the text who contributed isolates of *Mortierella* to this study. Miss C. A. N. van Oorschot corrected the English and Miss M. Nieuwstad inked the drawings.

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NOTES AND BRIEF ARTICLES

MORTIERELLA TURFICOLA LING YONG

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(With one Text-figure)

Several species of *Mortierella* described until 1930 are today unknown since living cultures are unavailable. The diagnoses of most of these species have been reproduced by Linnemann (in Zycha & Siepmann, 1970). but it is difficult to assess the justification of their retention. Recently Kuhlman & Hodges (1972) rediscovered *M. rostafinskii* Bref. and *M. strangulata* Tiegh., two similar but distinct species. This contribution concerns the rediscovery of another so far problematic species.

During the study of the fungal flora of the Heseper Moor near Meppen, Niedersachsen, F. R. G., *Mortierella turficola* Ling Yong (1930) was found to be the predominating *Mortierella* species. A stand of *Sphagnum recurvum* P. Beauv. with some *Eriophorum vaginatum* L. (pH *c.* 4.8) was sampled on 28 June 1976 during a very hot period. Warcup's soil plates were poured from various zones of decaying *Sphagnum* plants. *Mortierella turficola* appeared on 75% of the plates from the yellow zone at the foot of the living plants, on 85–100% of the plates from the underlaying brown zone and on 0–25% of the plates from the next, yellow zone at 8–10 cm below the surface of the living plants. *Mortierella exigua* Linnem. was once found in addition to *M. turficola*.

Mortierella turficola Ling Yong
in Revue gén. Bot. **42**: 743. 1930.—Fig. 1

Colonies on 2% MEA (pH 7) growing moderately fast, reaching 6–6.5 cm diam. in 6 days, with scanty aerial mycelium mostly present; odour weak but typical of the genus. Sporangiophores numerous, arising mostly from aerial hyphae, generally unbranched, rarely producing one basitonous lateral branch, 100–250 μm tall, at the base 6–10(–17) μm wide, tapering to 2–4 μm at the tip; some dichotomous rhizoids commonly produced near the base of the sporangiophores; tips imperceptibly widening below the sporangium. Sporangia mostly 20–32 μm in diameter, many-spored, leaving a more or less prominent, 2–5 μm high columella on dehiscence. Spores regularly globose, smoot-hwalled, 2.5–3.0(–4.5) μm in diameter. Chlamydospores absent.

Scanty immature zygospores were obtained after mutual combinations of 12 isolates on various media in only two combinations on cherry decoction agar after 6 days at 15–17.5 °C but not above; suspensors developing without initial entangling, of unequal size and shape; zygospores smooth- and thin-walled, 22–30 μm in diameter, but not developing any wall differentiation of mature zygospores.

COLONIES PRESERVED.—CBS 430.76, 431.76, 432.76, 433.76; ex decaying *Sphagnum recurvum*, Heseper Moor, Niedersachsen, F. R. G., *H. Hooghiemstra*, 28 June 1976. CBS 432.76 is compatible with 431.76 and 433.76 and is designated as neotype strain of the species.

Mortierella turficola was described by Ling Yong (1930, spelt Ling Young in the journal, Ling Yong in the reprint) as occurring in peaty soil. Wolf (1954) studying *Mortierella* species in south German peatbogs did not mention this species nor did she describe any similar species. Turner & Pugh (1961) tentatively identified some

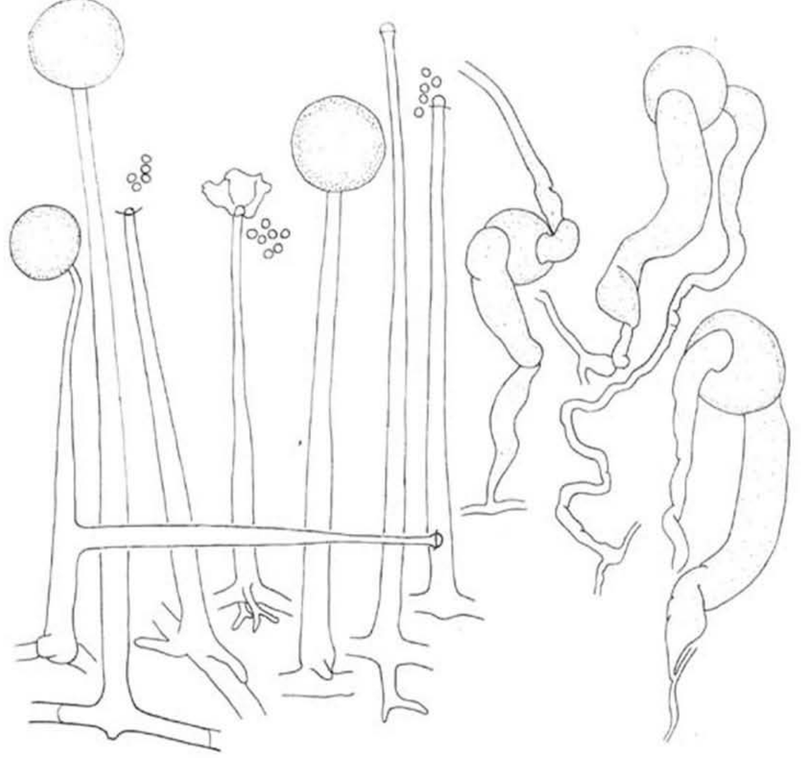

Fig. 1. *Mortierella turficola*, Sporangiophores with spores and development of zygospores ×500.

salt marsh isolates as *M. turficola*; one of their strains (CBS 898.68) bears less resemblance to *M. turficola* than the present isolates; the sporangiophores are mesotonously branched, have no columella and the spores are subglobose, up to 6 μm diam. Dickinson & Maggs (1974) mention the frequent isolation of *M. turficola* from washed leaves of *Sphagnum magellanicum* at an ombrophilous peat mire in Fozy Moss, Northumberland, G. B., down to a depth of 4 cm, but do not give further information on the fungus.

Our strains agree very well with Ling Yong's observations in the basitonous branching, length of sporangiophores, presence of a columella and the tiny globose spores. Ling Yong illustrated two branches of the sporangiophore, a number we never observed. His measurements of sporangia (10–15 μm) and spores (1.8–2.0 μm) are smaller than ours, but seem somewhat unrealistic. We therefore do not doubt that the identification is correct.

The species keys out in section *Hygrophila* according to Gams (1970) because of the basitonous ramification. The strongly developed columella is unusual in this section. It can be expected that this species has been described under other species with unbranched sporangiophores, since ramification is scarce, and a classification in section *Simplex* W. Gams would be particularly tempting. In Linnemann's keys *M. pulchella* Linnem. best fits this fungus, but the rarely observed (in our observations on SEA cultures not infrequent) acrotonous ramifications exclude a possible identity. The description of *M. pusilla* Oudem. sensu Linnemann (*in* Zycha & Siepmann, 1970) also suggests this fungus, but its original isolation from a pine-oak forest soil at Spanderswoud, Netherlands (Oudemans & Koning, 1902) makes this identity very unlikely. Samples of this soil studied recently by the senior author yielded amongst others *M. pulchella* Linnem. Several authors interpreted *M. pusilla* in the sense of *M. isabellina* Oudem., but this is contradictory to the original description of unpigmented rosette growth. This species might have been a relative of *M. alpina* Peyr., but is best left in the status of a doubtful species. *Mortierella turficola* does not have much affinity with *M. alpina*. The sporangiophores are longer and do not show the characteristic awl-shaped habit with a swollen 'basal foot' and the zygospores develop in the agar. Therefore we prefer to retain it in the section *Hygrophila* in which, to date, it is unique by its small, globose spores and the presence of a columella.

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NOTES ON MYCOACIA—I

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(With one Text-figure)

The genus *Mycoacia* Donk (1931) originally contained four species, viz. *M. fuscoatra* (Fr. ex Fr.) Donk (type), *M. uda* (Fr.) Donk, *M. stenodon* (Pers.) Donk, and *M. setosa* (Pers.) Donk. This last species, however, is the type species of *Sarcodontia* S. Schulzer 1866. Later (1952) Donk considered *M. setosa* as generically distinct. The monotypic genus *Sarcodontia* has globose to subglobose spores with thickened walls and is parasitic, while *Mycoacia* has ellipsoid to allantoid thin-walled spores and is saprophytic. When *Mycoacia* and *Sarcodontia* are considered as congeneric (e.g. Nikolajeva, 1961), *Sarcodontia* is the correct name for the genus.

Mycoacia and *Sarcodontia* are both classified in the Corticiaceae (Donk, 1964; Parmasto, 1968); they are characterized by the resupinate hydnoid ceraceous basidiocarp, the monomitic hyphal system and the smooth non-amyloid spores. The genera are closely related to *Phlebia*.

Another eight species have been added to *Mycoacia*. Four really belong there (although they cannot all be accepted as distinct species), of two species no type material is available and two are good species, but have to be excluded. These last two species are described and discussed below.

MYCOACIA DENTICULATA (Pers.) Parm.

The type specimen is *Steccherinum ochraceum* (Pers. apud Gmel. ex Fr.) S. F. Gray (Maas Geesteranus, 1974). However, Nikolajeva (1961) as well as Parmasto (1967) considered the species in the sense of Bourdot & Galzin (1928), who described a quite different species under this name. The latter should be classified in the genus *Resinicium*.

Resinicium bisporum Stalpers *spec. nov.*—Fig. 1a–e

Fructificatio resupinata, effusa, hydnoidea, membranacea vel ceracea. Aculei ad 2 mm longi. Hymenium ochraceum vel cinnamomeum. Systema hypharum dimiticum. Hyphae fibratae in parte centrale aculeorum, 2.5–4.5(–5) μm diam. Hyphae subhymeniales irregulares, fibulatae, 2–3.5(–7) μm diam., interdum subgelatinosae. Cystidiolae capitatae vel fusiformae, normaliter ad apices halonatae. Basidia subclavata, 11–17 × 3–4 μm, cum 2 sterigmatibus. Sporae hyalinae, leves, ellipsoideae vel cylindricae, 4.5–5.5(–6) × 2.2–2.8 μm, non amyloideae. Specimen typicum: *Bourdot 4277* (PC).

Basidiocarp annual, resupinate, effused, membranaceous to ceraceous, cracked when dry, densely covered with spines. Spines single, rarely concrescent at the very base, slender, acute or somewhat fimbriate at the apex, up to 2 mm long. Hymenial surface ochraceous to cinnamon. Margin paler. No reaction with KOH. Hyphal system dimitic. Skeletal hyphae in central cylinder of spines, 2.5–4.5(–5) μm in diameter, thick-walled (up to 2.2 μm), leaving a narrow or invisible lumen, which expands at the tip. Generative hyphae hyaline, thin-walled, irregular, 2–3.5(–7) μm in diameter, cells typically less than 25 μm long, sometimes gelatinized. Clamps present. Some hyphae encrusted with yellowish material. Cystidioles originating in subhymenium, hyaline, thin-walled, obtuse to capitate, rarely fusiform, 16–25 × 2.5–4 μm, typically with large yellowish oil-cap (halo) up to 9 μm in diameter. Basidia in small clusters, subclavate, 11–17 × 3–4 μm, with (1–)2 sterigmata, basally with clamps. Spores hyaline, thin-walled, smooth, narrowly ellipsoid to cylindrical, flattened at one side, 4.5–5.5(–3) × 2.2–2.8 μm, not amyloid.

MATERIAL EXAMINED.—On *Alnus*, bank of the Garnafag, between Le Mazeau and La Roche (Chappes), France, *Bourdot 4277*, 9.VIII.1905 (PC, type). — On *Alnus*, bank of the Gange, St.-Marcel, *Bourdot 4995*, 27.VIII.1907 (PC, as *Acia fuscoatra*).

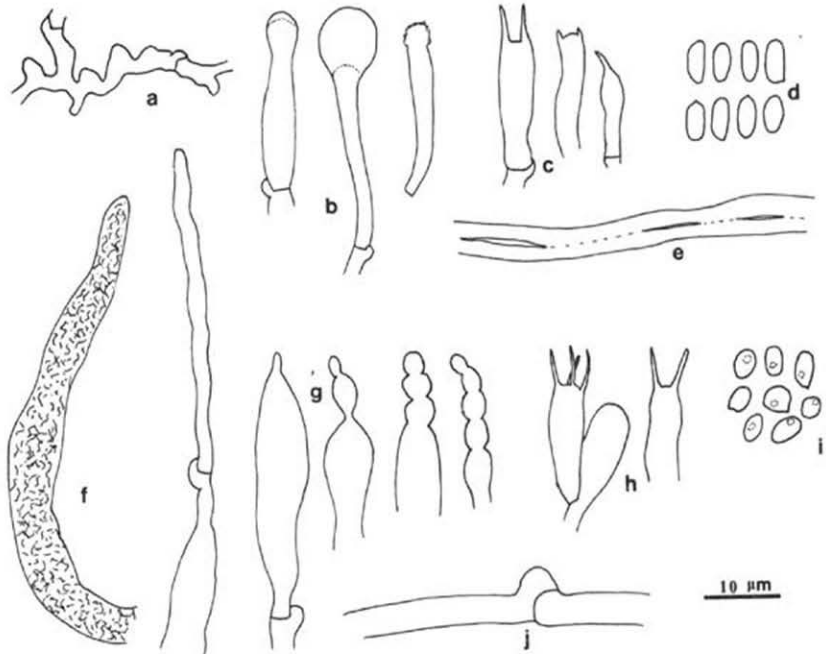

Fig. 1. a–e. *Resinicium bisporum*. — a. Irregular hypha. — b. Cystidioles. — c. Basidia. — d. Spores. — e. Skeletal hypha. — f–j. *Dentipellis isidioides*. — f. Gloeocystidium from subiculum. — g. Hymenial gloeocystidia, apical structures. — h. Basidia. — i. Spores. — j. Hypha.

The species is classified in *Resinicium* because of the typical cystidioles, which are unique in the Corticiaceae. Basidiocarp texture, basidia and spores are also concordant. It differs from all other species by the dimitic hyphal system, a fact which would in the past have been reason enough to erect a new monotypic genus. The author, however, is not so inclined, since the species is so close to *Resinicium* in other respects and since there are several precedents where genera contain monomitic and dimitic species (e.g. *Tomentella, Aleurodiscus, Coniophora*).

Within the genus *Resinicium R. chiricahuaense* Gilberts. & Budington is most closely related, but differs in the allantoid spores (4–6 × 1.5–2 μm), the generally 4-spored basidia, the monomitic hyphal system, the preference of gymnospermous wood and the distribution (only known from North America) (Gilbertson & Budington, 1970).

Dentipellis isidioides (Berk.) Stalpers *comb. nov.*—Fig. 1, f–j

Hydnum isidioides Berk. *in* Hook. J. Bot. (London) **4**: 58. 1845 (basionym). — *Sarcodontia isidioides* Reid *in* Kew Bull. 1955: 641. 1956.

Basidiocarp resupinate, effused, membranaceous, densely covered with spines. Spines single, not concrescent, slender, up to 5 mm long; apex not fimbriate, often covered with a whitish bloom, appearing farinaceous. Between the spines a whitish subiculum is visible. Hymenial surface ochraceous. Margin adnate, indistinct. Hyphal system monomitic. Hyphae hyaline, with thin or slightly thickened walls, 2–4 μm in diameter. Clamps present. Gloeocystidia thin-walled, with refractive contents, originating in the subiculum and than up to 7(–10) μm in diameter or originating in the subhymenium, 30–65 × 4–8 μm, apically abruptly narrowed and forming a tubular (1.5–2 μm wide) or moniliform outgrowth with up to eight constrictions, often somewhat projecting, sulpho-negative. Basidia in small clusters, subclavate to cylindrical, 12–18 × (3.5–)4–5 μm, with (2–)4 sterigmata. Spores hyaline, with thin to slightly thickened walls, smooth, subglobose to broadly ellipsoid, 2.5–4(–4.5) × 2–2.7(–3) μm, with small apiculus, amyloid.

MATERIAL EXAMINED. — On *Polyporus gryphaeformis*, Swan River, Australia, *Drummond 149*, Herb. Berkeley, 1879 (K, type). — On *Atherospermum* moschatum. Powelltown, Victoria, Australia, *E. W. B. Da Costa 2169*, 20.IV.1949 (K). — On *Eucalyptus regnans*, Powelltown, Victoria, Australia, C. S. I. R. O. 2572B, 18.VII.1950.

The sulpho-negative gloeocystidia, the amyloid spores, the resupinate hydnoid basidiocarp and the monomitic hyphal system give this species a place in *Dentipellis* (Hericiaceae). When Reid (1956) published the combination in *Sarcodontia*, the genus *Dentipellis* and the family of the Hericiaceae had not yet been erected. However, he indicated the relationship when he mentioned *Hydnum macrodon* Pers. ex Fr. (=*Dentipellis macrodon* (Pers. ex Fr.) Furukawa) as being closely related.

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ON THE CLAVARIOID RAMARIA STRICTA (FR.) QUÉL. IN BORNEO

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I recorded this species from Mt Kinabalu, North Borneo, in typical form and as var. *concolor* (Corner, 1970: 259). One copious collection of var. *stricta*, namely *RSNB 5742*, I distributed to several herbaria. The fruit-bodies in this case had grown in large numbers, in places almost caespitose, along a fallen rotten trunk in *Trigonobalanus*-forest at 1600 m; they were old, but not effete and in many the branches, with thickened hymenium, had sagged and become divaricate (Corner, 1970: pl. 3). The interest of the collection was clear at the time. The second collection, *RSNB 8475*, consisted of younger fruit-bodies with the characteristic fastigiate branching. Now two duplicates of the first collection, *RSNB 5742*, have been studied by Petersen (1975), who refers that at the Bureau of Plant Industry (Maryland) to *Ramaria africana* Petersen (l.c.: 110) and that at Leiden to *R. polypus* Corner (l.c.: 120). In both cases he overlooks the field-notes which I had published in 1970, and they show that, with yellow tips to the branches, vinescent tissue, and fragrance of aniseed, the collection does not belong with either of those species. When I run down the collection in Petersen's key (1975: 104), it comes to *R. stricta* var. *alba* (which it is not) or *R. stricta* var. *stricta*. It may be supposed that I had confused two or three species at the time of collection, but I clearly recall the occasion and am certain that this was not the case. In fact I do not recall any instance where two or more species of clavarioid fungi had grown intermixed. Hence I conclude that the fruit-bodies of *RSNB 5742* bore the two kinds of spore by which Petersen seeks to distinguish *R. africana* (1975: 137, fig. 10) and *R. polypus* (1975: 139, fig. 15), though he is not definite on this point, and that fruit-bodies macroscopically identical with *R. stricta* produce spores which differ from those that Petersen regards as typical (Petersen, 1967: figs. 3d, e). To me this indicates the slight variations in spore that may occur in a species of such wide distribution.

In distinguishing *R. africana*, *R. kisantuensis*, *R. molleriana*, and *R. polypus*, Petersen introduces a character which seems to me very dubious. He separates the first two because they have the slender skeletal hyphae of the mycelial subiculum or rhizomorphs also in the tissue at the base of the stem of the fruit-body, and they are absent from the base in the other two species. The state in *R. stricta* is not described by Petersen (1975) but it agrees with that of *R. molleriana* (Corner, 1950). Now the base of the stem is a transitional region from rhizomorph or subiculum to the fruit-body and it is generally impossible to decide exactly where one begins and the other stops. In the transition skeletal hyphae of the rhizomorph variously intrude into the beginning of the stem, as the carry-over of one construction to another; in old fruit-bodies the mycelial hyphae, with skeletals, may extend up, over, and into the

stem. Hence I have avoided this region for a diagnostic purpose; many collections, indeed, do not have the feature because the fruit-bodies had been torn off the wood. I note that this dimitic state is not that of *Ramaria* subgen. *Lentoramaria* ser. *Dimiticae* in which the skeletal hyphae occur throughout the fruit-body.

With regard to *R. molleriana*, which I have called *R. moelleriana* for some reason that I cannot now trace in deference to his German origin (Exell, 1944), this is a common and very variable tropical and subtropical species. The fruit-bodies vary in height and density of branching from 1–2 cm high in some collections to 11 cm in others, but they never have the yellow tips to the branches, the vinescence (or but slightly), and the odour of *R. stricta*, which I have never seen in the lowland tropics. Of *R. molleriana* I have seen hundreds of living specimens. There is certainly variation in all points, including the size and markings of the spores, but I have never satisfactorily correlated them. Hence I regard *R. africana*, *R. kisantuensis*, and *R. polypus* as, at most, states of *R. molleriana* distinguishable as given in the Supplement to my monograph (Corner, 1970). I would point out that in his copy of my description of *R. polypus*, Petersen (1975: 118) has transposed the measurements of the stem, transposed my remarks on smell and taste, omitted the colour of the spores, and referred to them as guttulate (? when dried).

With regard to the size and markings of spores, these properties are connected with the expansion of the hypha into the basidium the size of which is critical, and the extension of the basidium into the spore-circles (Corner, 1972). One result is the relation between the length and width of spores and those of the basidium, as I have illustrated in the form of sporographs and basidiographs; and in spite of the remark by Petersen (1975: 146) that 'species did not evolve to fit sporographs' I re-affirm the facts. Another result is the surmise that smooth spores are derived from the ornamented, possibly as endospores, and that, of these ornamented spores, possibly the reticulate may have been the ancestral. Thus I distinguished *Ramaria* sugen. *Lentoramaria* ser. *Retisporae* for the one species with reticulate ornamentation (Corner, 1970; 239, 256). In disregarding this, Petersen (1975: 151) fails to realise that the spore-markings of *Ramaria* in general may be the result of degeneration of the reticulum in a manner that can vary within a species, e.g. *R. zippelii* var. *cristatospora* (Corner, 1967).

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ON CORTICIUM UDICOLA BOURD.*

W. JÜLICH

Rijksherbarium, Leiden

(With two Text-figures)

One of the fungi with very variable basidia is *Corticium udicola* Bourd., showing in the same basidiocarp all stages between sessile clavate basidia, podo- and pleurobasidia. Interesting features are the large sterigmata — not often found in species of Corticiaceae — and the amyloid spores. For this species Hauerslev (1974) created the monotypic genus *Melzericium*, based on his own collection from Sweden. A stay at the Muséum National d'Histoire Naturelle in Paris gave the opportunity to study all the specimens of *Corticium udicola*. Soon it was evident that the collections contained two different but closely related species, one of which agreed very well with the descriptions given by Bourdot (1910) and Bourdot & Galzin (1928). The second species is characterized by a deviating shape of the spores which is rather unique in the Corticiaceae. The first and obviously more common species is at the same time identical with Hauerslev's specimen from Sweden. For the second species no name is available. It is, as far as I know, in France only represented by its type specimen, but is also found in North Sweden (Strid, 1975; sub *Melzericium udicola*).

Corticium udicola was one of the first species which Bourdot described. Since he was the most important promotor of our knowledge of the Corticiaceae, I find it appropriate to name the second species after him.

MELZERICIUM UDICOLA (Bourd.) Hauerslev—Fig. 1

Corticium udicola Bourd. *in* Rev. scient. Bourbonn. **23**: 10. 1910. — *Melzericium udicola* (Bourd.) Hauerslev *in* Friesia **10**: 316 1975.

Basidiocarp resupinate, effused, often only a few mm large, rarely confluent to larger patches, 50–150 μm thick, membranaceous, adnate, separable in small pieces, context homogeneous; hymenial surface cream coloured, even, not cracked when dry; margin concolorous or whitish, indeterminate, thinning out, rhizomorphs or hyphal strands lacking. Hyphae hyaline, cylindrical to torulose, loosely arranged, branching from or near the clamps, 2–4 μm in diameter, some inflated up to 6 μm,

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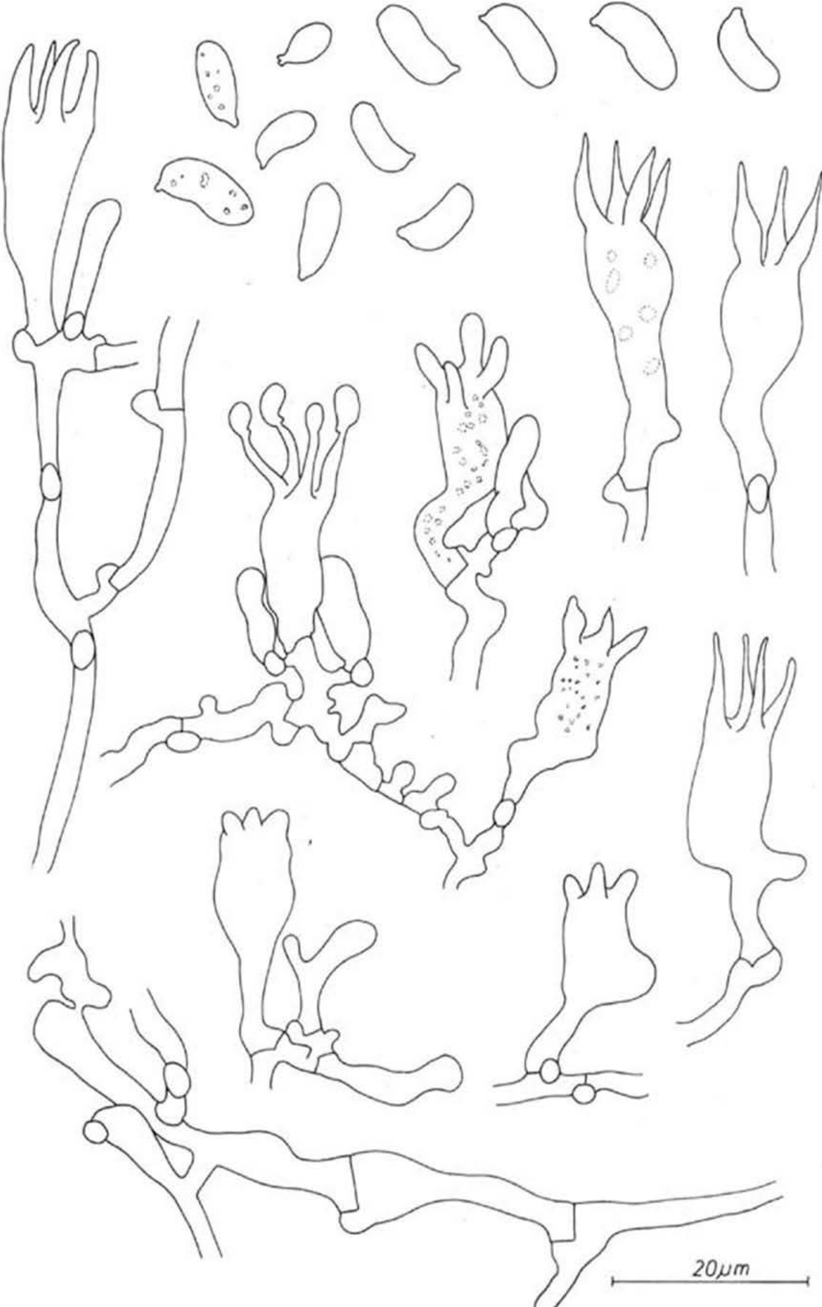

Fig. 1. *Melzericium udicola*, lectotype.

thin walled or the basal ones slightly thick-walled, with smooth surface, clamps present, contents homogeneous. Cystidia lacking. Basidia often stalked (podobasidia), some pleurobasidioid, hyaline, clavate when mature, flexuous-cylindrical when young, 20–25×6.5–7 μm, thin-walled, smooth, a basal clamp present, contents homogeneous or slightly guttulate; with four large sterigmata (8–10×1.5–2.5 μm). Spores hyaline, curved cylindrical, with distinct apiculus, 8–10×3–4 μm, thin-walled, smooth, contents homogeneous or slightly guttulate. amyloid, not dextrinoid or cyanophilous.

MATERIAL STUDIED.—FRANCE: Tarn, Marais de Frègefont, –.9.1909, *Galzin 4543 (Bourdot 6778)* (lectotype, PC); –.9.1909 *Galzin 4926 (Bourdot 69894)*; 5.9.1909, *Galzin 4528 (Bourdot 6767)* (PC); 26.9.1909, *Galzin 4839, 4890 (Bourdot 6841)* (PC); 5.9.1909, *Galzin 4544 (Bourdot 6770)*.

Melzericium bourdotii Jülich, *spec. nov.*—Fig. 2

Carposoma resupinatum, effusum, membranaceum, cremeum, adhaerens; rhizomorphae desunt; hymenium laeve. Systema hypharum monomiticum. Hyphae distinctae, plus minusve tenui-tunicatae, cylindricae vel torulosae, interdum inflatae, 2–4 μmin diam., semper fibulatae. Cystidia desunt. Basidia saepe podobasidia nonnumquam pleurobasidia, clavata, 15–20×5–6 μm, fibulata, tetraspora. Sporae hyalinae, ellipsoideae, constrictae tenui-tunicatae, amyloideae. — Typus: 'Tarn, Marais de Frègefont, sur Marsaule, 26.10.1909, *Galzin 4834 (Bourdot 6990)* (PC).

Basidiocarp resupinate, effused, often only a few mm large, rarely confluent to larger patches, 50–150 μm thick, membranaceous loosely adnate, spearable in small pieces, context homogeneous; hymenial surface cream-coloured, even, not cracked when dry; margin concolorous or whitish, indeterminate, thinning out, rhizomorphs or hyphal strands lacking. Hyphal system monomitic. Hyphae hyaline, cylindrical to somewhat torulose, some inflated, loosely arranged, branching from clamps or opposite to these, 2–4 μm in diameter, inflated up to 8 μm, thin-walled in the subhymenium, thin- to slightly thick-walled in the trama, with smooth surface, clamps present, contents homogeneous or slightly guttulate. Cystidia lacking. Basidia often stalked (podobasidia) or like pleurobasidia, hyaline, clavate when mature, flexuous-cylindrical when young, 15–20×5–6 μm, thin-walled, smooth, a basal clamp present, contents homogeneous or guttulate; with four large sterigmata *c.* 5–8×2–2.5 μm. Spores hyaline, ellipsoid, distinctly constricted in the middle (like a dumb-bell), with small apiculus, 8–10.5×4–5 μm, not glued together, thin-walled, smooth, contents homogeneous or somewhat guttulate, amyloid, not dextrinoid or cyanophilous.

DISTRIBUTION.—Known from the type-collection in France and from one specimen of North Sweden (Strid, 1975).

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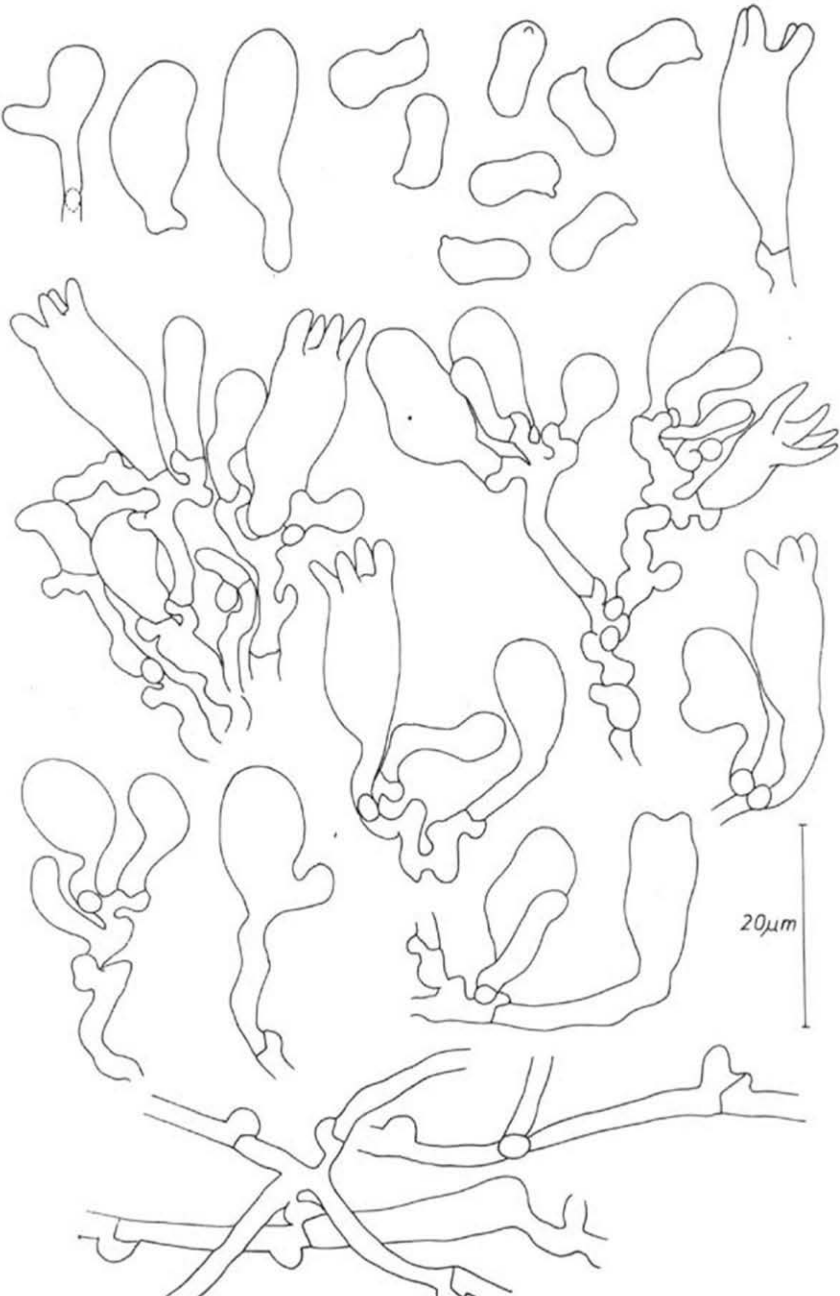

Fig. 2. *Melzericium bourdotii*, holotype.

SCHIZOPORA PHELLINOIDES IN THE NETHERLANDS

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SCHIZOPORA PHELLINOIDES (Pilát) Domanski

Poria phellinoides Pilát *in* Bull. Soc. mycol. Fr. **51**: 383. 1935. — *Poria pseudoobducens* Pilát *in* Sb. nár. Mus. Praze **9**B (2) (Bot. 1): 107 1953 — *Xylodon versiporus* (Pers.) Bond. var. *microporus* Komarova *in* Bot. Mater. Inst. spor. Rast **12**: 249. 1959. — *Schizopora phellinoides* (Pilát) Domanski *in* Acta Soc. Bot. Pol **38**: 255. 1969.

Fruit-body mainly resupinate, rarely effused-reflexed with a smooth brownish orange superior surface; on almost vertical substrates the lower surface looks like the underside of a staircase, composed of 1.5–2.5 mm wide horizontal pore areas and 4–5 mm high vertical surfaces made up of tube walls. Margin well defined. Subiculum and context soft-fibrous when fresh, hard-coriaceous after drying. Subiculum cream-coloured, up to 0.5 mm thick. Tubes 4–5 mm long, brownish orange, except for cream-coloured lower part, pores 0.1–0.2 mm diameter, averaging 5–6 per mm, rather regularly circular or slightly elongated, dissepiments 0.05–0.1 mm thick, covered with a white pruina, pore surface cream-coloured.

Hyphal system of context and subiculum monomitic. Generative hyphae flexuose, rather thick-walled, septate with clamps, frequently branched from or opposite to a clamp (like in the genus *Hyphodontia* Erikss.), 2–3 μm in diameter. The hyphae terminate sometimes in a bladder, (6–)7–8(–10) μm in diameter, generally surrounded by a 1 μm thick layer of an oily suüstance. Such bladders are also found between septa.

Hyphal systems of dissepiments dimitic. The ends of some of the generative hyphae heavily incrusted with crystals, forming club-shaped bodies of 50–75 × 8–15 μm. In the hymenium and especially on the edges of the dissepiments the hyphal ends are sparsely incrusted. Skeletal hyphae, thick-walled, 3–3.5 μm in diameter, interwoven, abundant in the dissepiments, which also contain numerous masses of crystals, with diameter up to 40 μm.

Basidia utriform, 12–18 × 4–5 μm. Spores hyaline, smooth, short-ellipsoid to subglobose, 1-guttate, 4–5 × 3–4 μm.

SPECIMEN EXAMINED.—The Netherlands, prov. Limburg, Bunde-Geulle, Bunderbos, 11 Oct. 1975, *F. Tjallingii*, on *Alnus* on highly calcareous soil.

The collection cited, consists only of a portion of a fruit-body. As a consequence the above macroscopic description is not complete.

The species is well-named, macroscopically it shows a striking resemblance to some resupinate species of *Phellinus*, microscopically it is extremely close to the common *Schizopora paradoxa*, though macroscopically the latter could hardly be more different. Domanski (1972: 144) states that it has been rather frequently observed in the U.S.S.R., but cites for Poland only two places where it has been found.

Jahn (1971 : 64) lists four localities for Westfalen, but expects the species to be present in other parts of Germany too. He also mentions collections from Czechoslovakia and from France. Pegler (1973) does not list it for Great Britain. It had not been recorded before from The Netherlands. That so little is known about the distribution of a fungus with such a remarkable combination of characteristics, and the fact that it was first described only a little over forty years ago, based on a collection from eastern Siberia, indicates that *Schizopora phellinoides* is a rare species.

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PERSOONIA
Published by the Rijksherbarium ,Leiden
Volume 9, Part 1, p. 157 (1976)

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H. Veldkamp, *Continuous culture in microbial physiology and ecology*. (Meadowfield Press, Shildon, England, 1976.) Pp. 68, 20 Text-figs. Price: $ 8.40.

A comprehensive introduction to the technique and its possibilities for those who wish to study the interrelations between microbes (especially bacteria and yeasts) and their biotic and abiotic enviroment.

R. E. Strange, *Microbial response to mild stress*. (Meadowfield Press, Shildon, England, 1976). Pp. 83, 14 Text-figs. Price: $ 8.40.

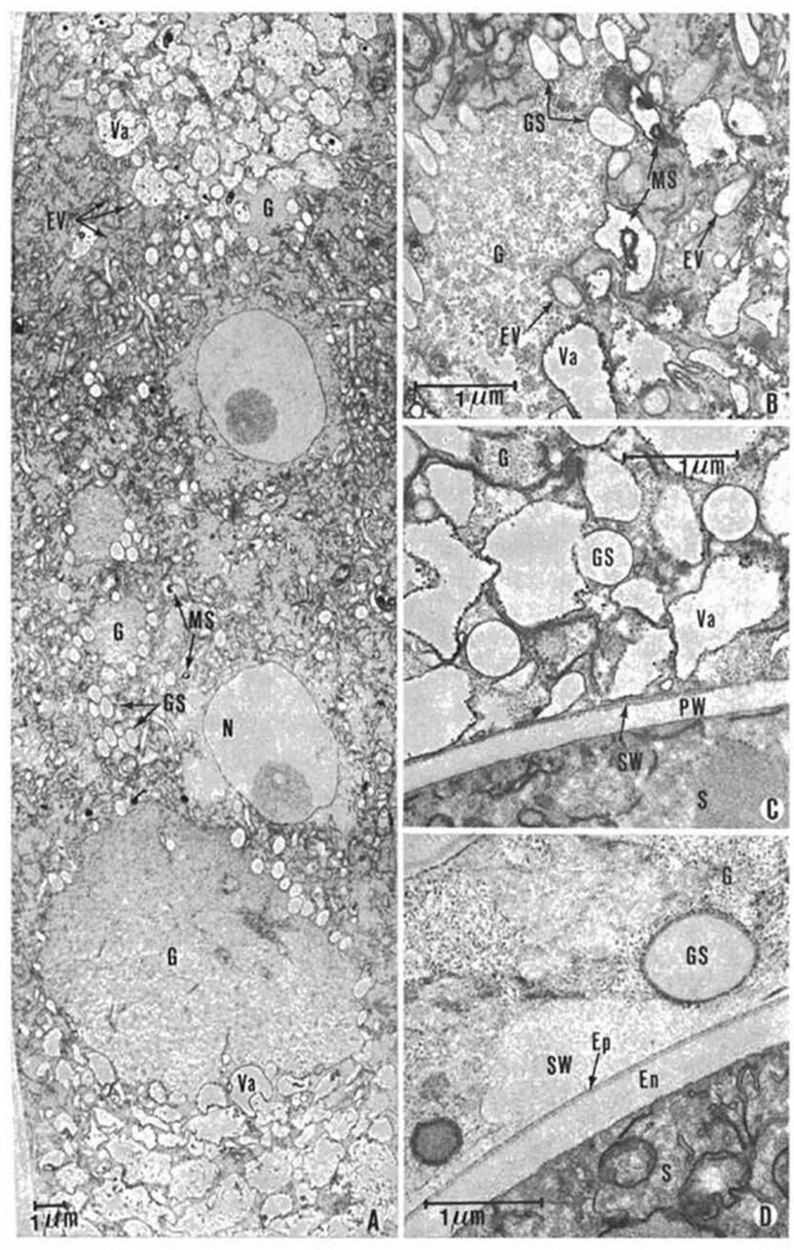
In this booklet a survey is given of the recent advances in our understanding of microbial response to conditions of mild stress The biochemical and structural changes that occur during starvation, mild heat stress, cold shock, osmotic shock, and aerosolization are briefly treated. This work is designed as an introduction to the subject for students and laboratory workers in microbiology.

J. Berthier, *Monographie des Typhula Fr., Pistillaria Fr. et genres voisins*. (Bull. Soc. Linn. Lyon **45**, Numéro spécial, Société Linnéenne de Lyon, 33 rue Bossuet, Lyon, 1976). Pp. 213, 39 Text-figs., 2 Pl. (col.). Price: 100 Frs.

In this world-wide monograph 71 species of the genera *Typhula* Fr., *Ceratellopsis* Konr. & Maubl., and *Macrotyphula* Petersen are accurately described and depicted. On plausible grounds *Pistillaria* Fr. is treated as one of the seven subgenera of *Typhula*. Special attention has been paid to anatomical characters. The determination of the species is greatly facilitated by carefully constructed keys and clear illustrations.

J. Schlittler, *Das große Buch der Pilze*. (Verlag Herder, Freiburg, Germany, 1975.) Pp. 256, Text-figs, colour-photographs (128 pp.). Price: 68 DM.

This is a new issue of the mushroom album in two volumes brought out in 1972 by the Silva Verlag, Zürich. The main attraction of this book is the splendid reproduction in natural colours after photographs of 140 species of mushrooms. A general introduction to fungology is followed by macroscopic descriptions and keys to the species treated.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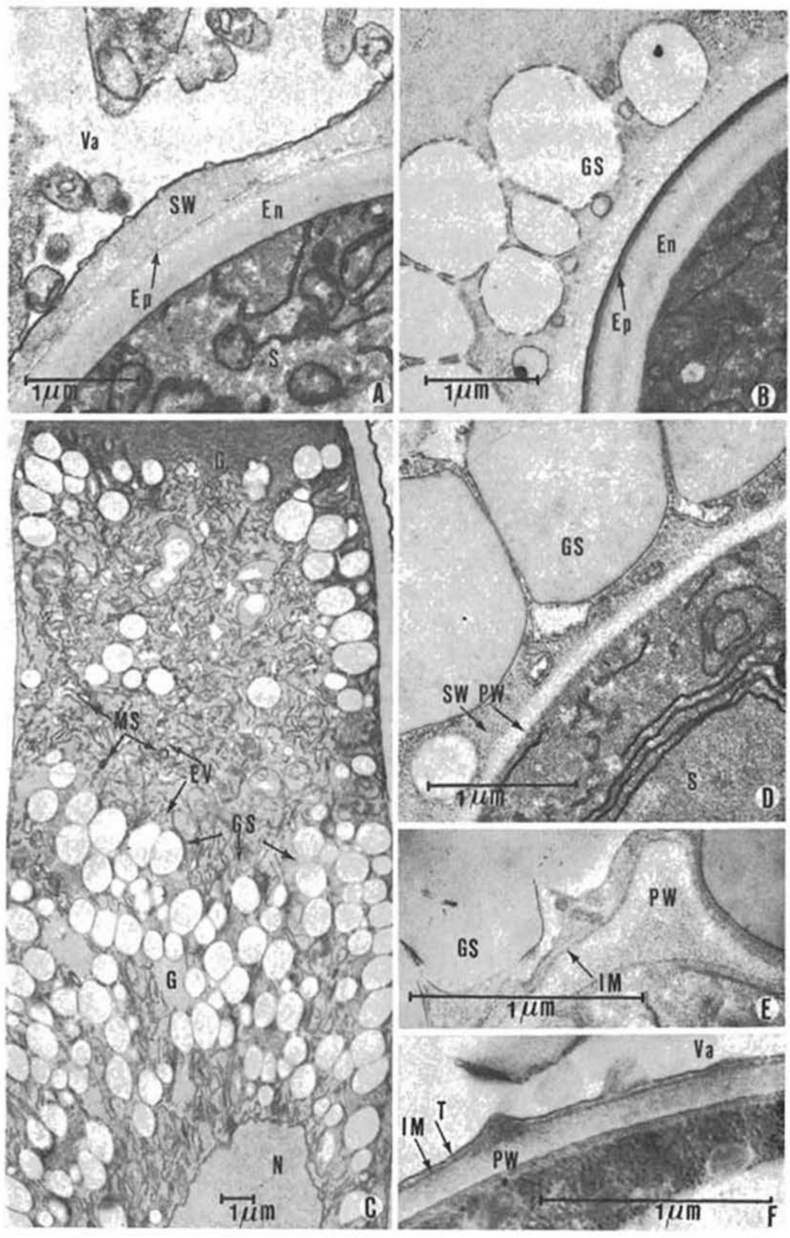
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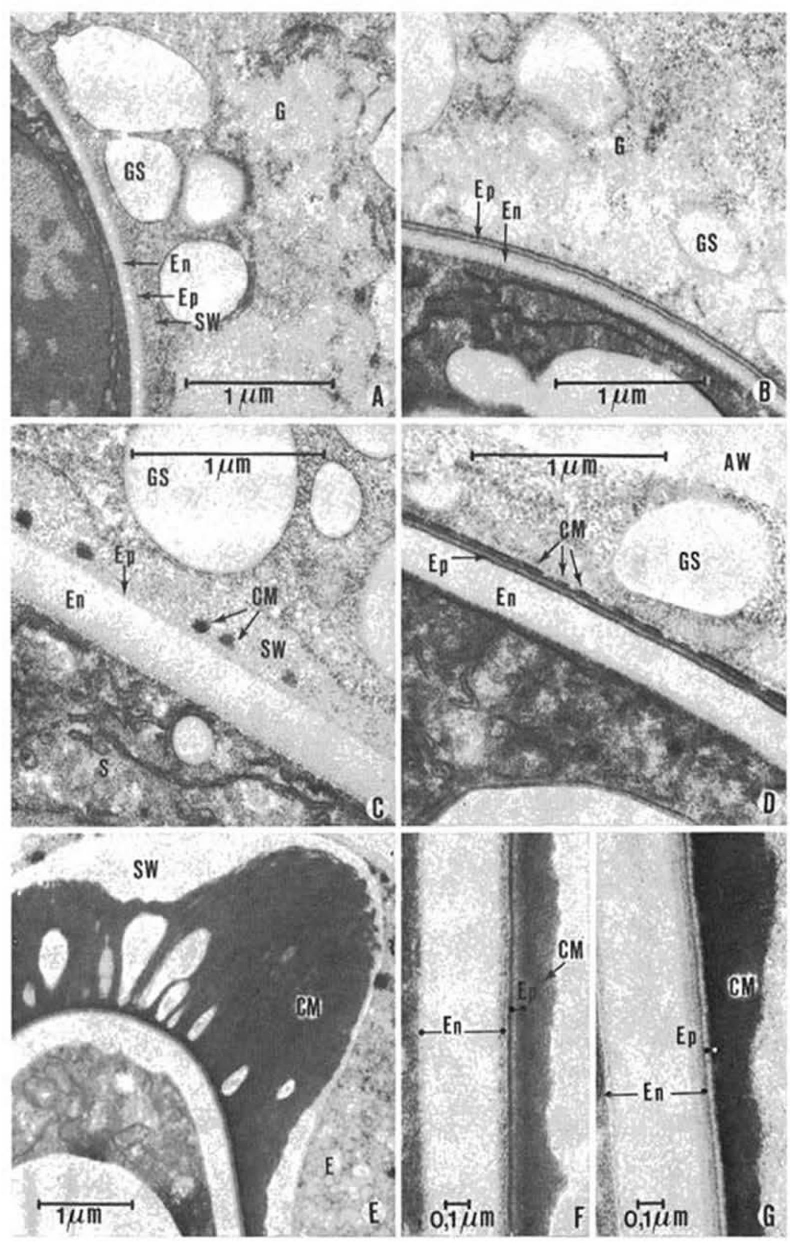
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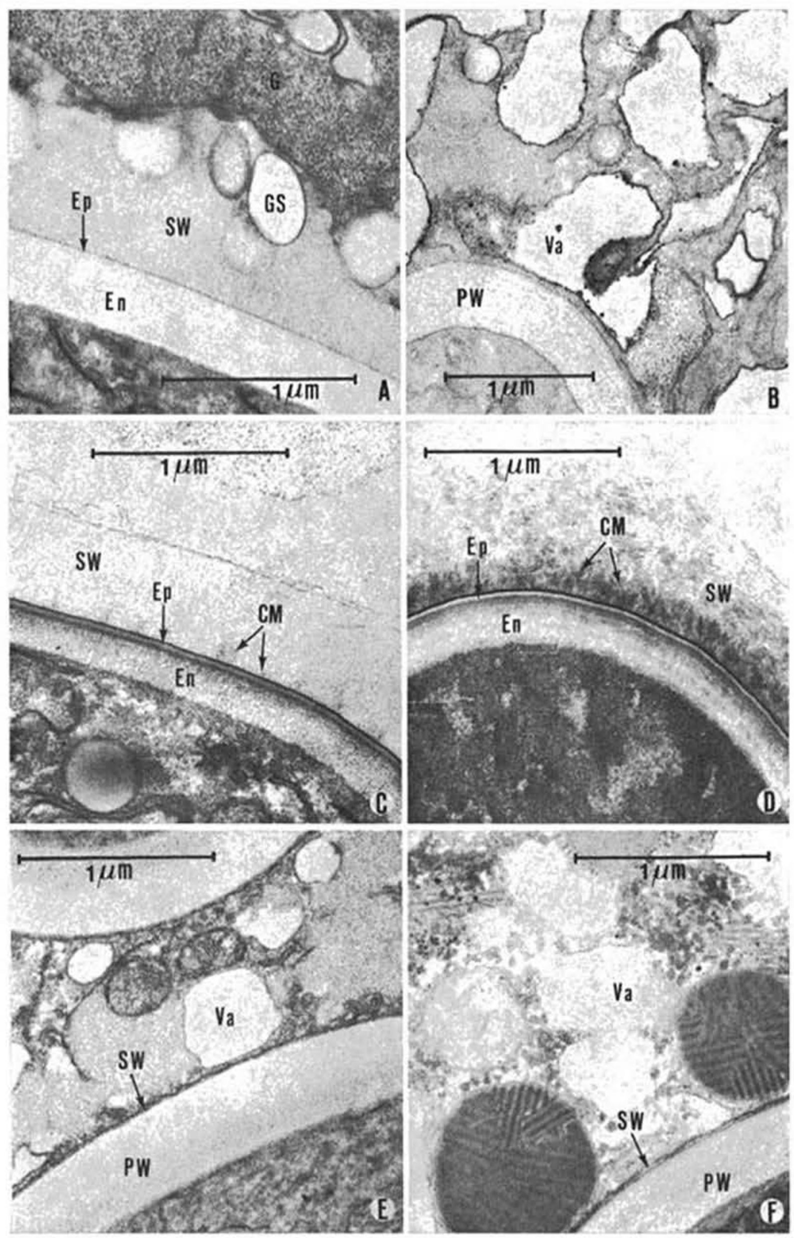

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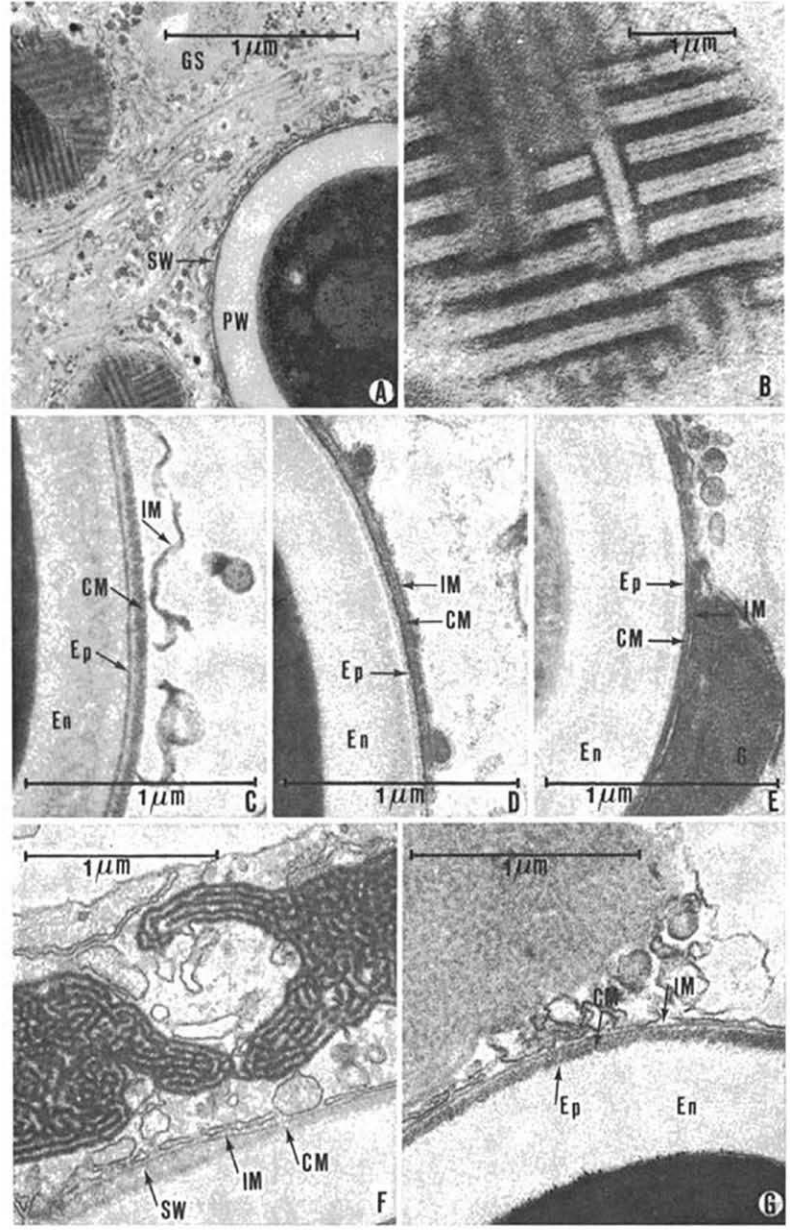
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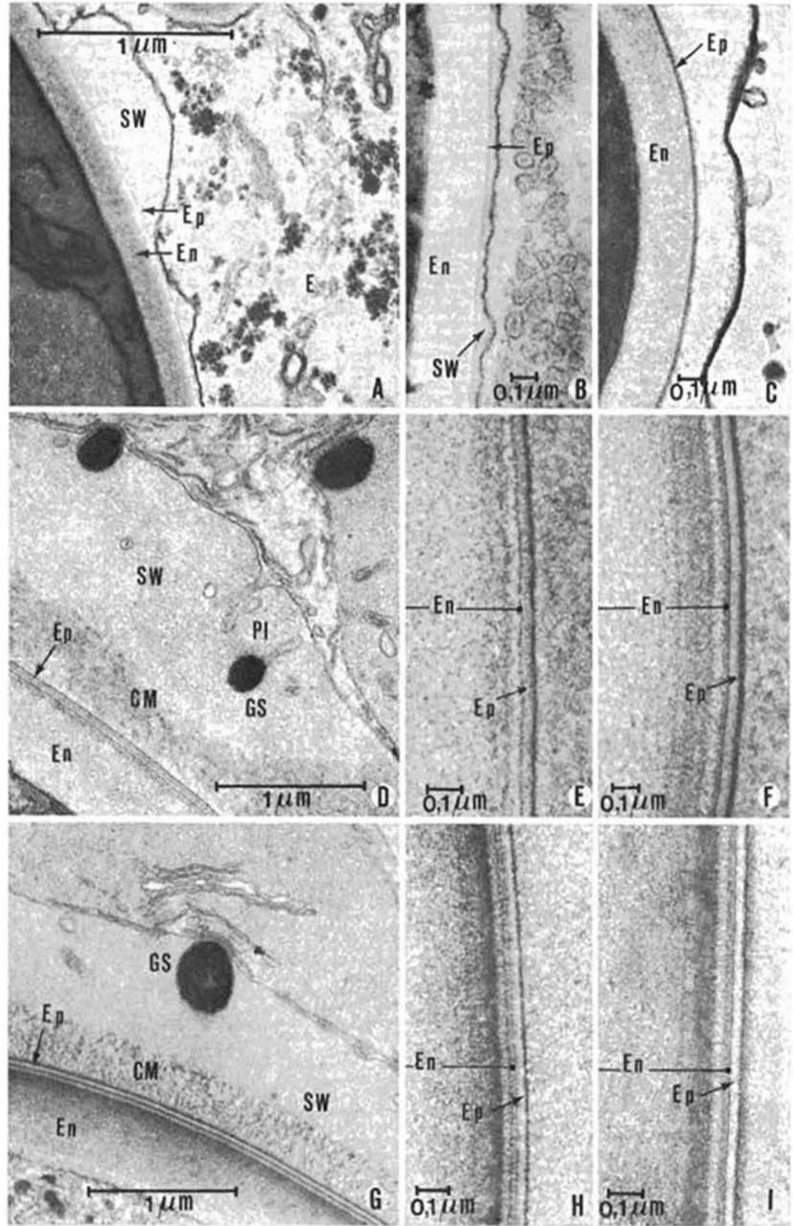
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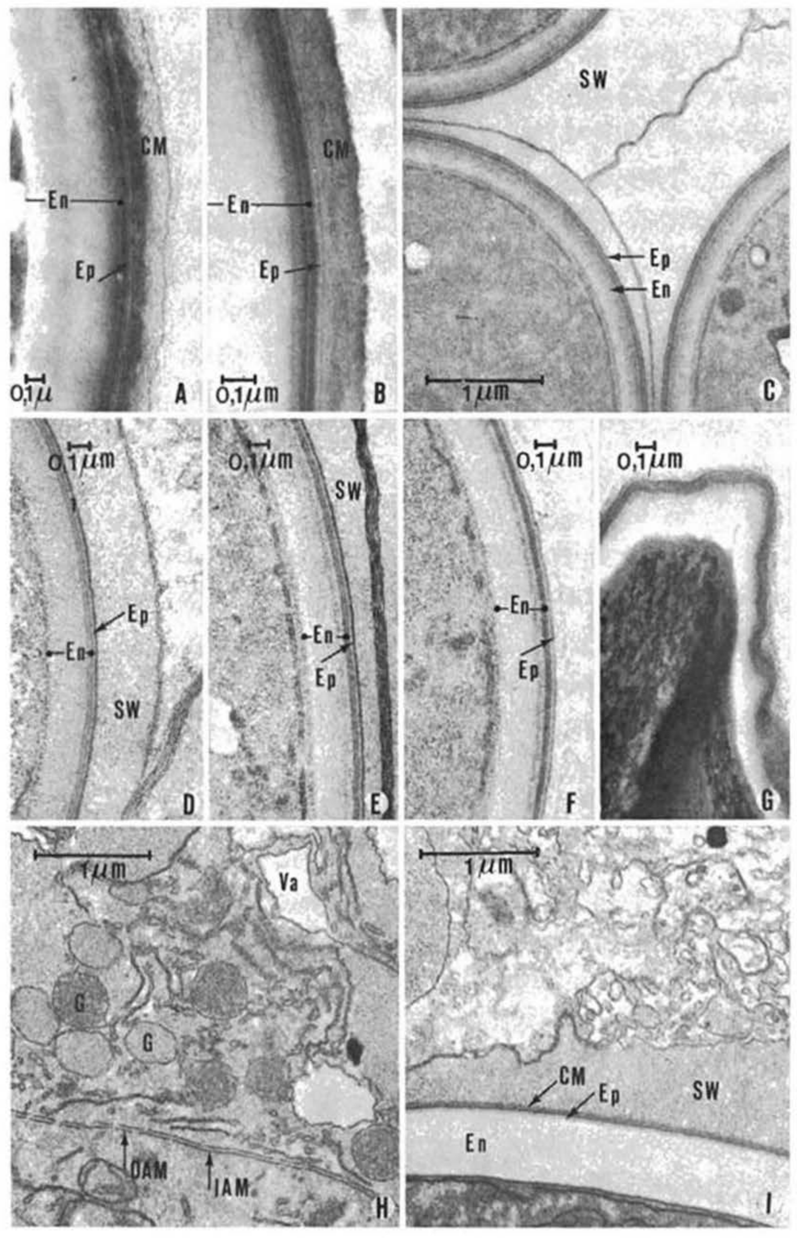
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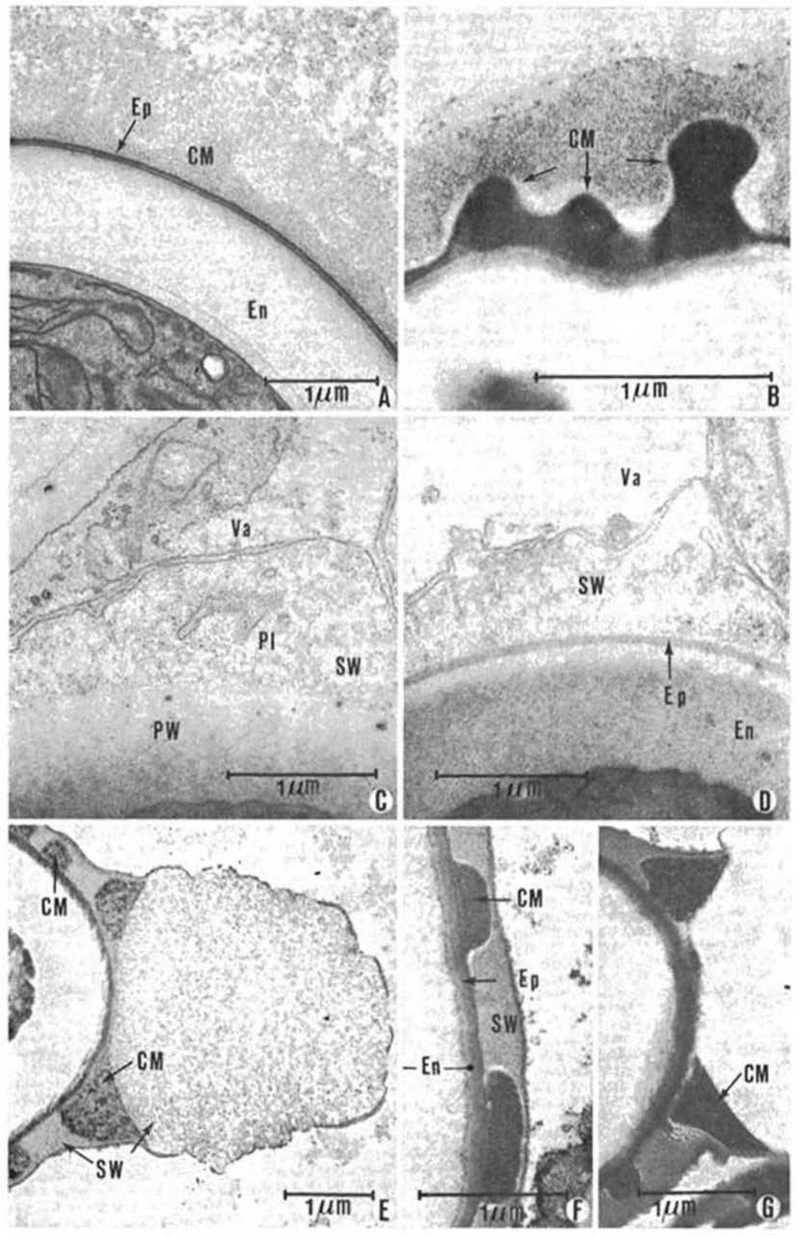
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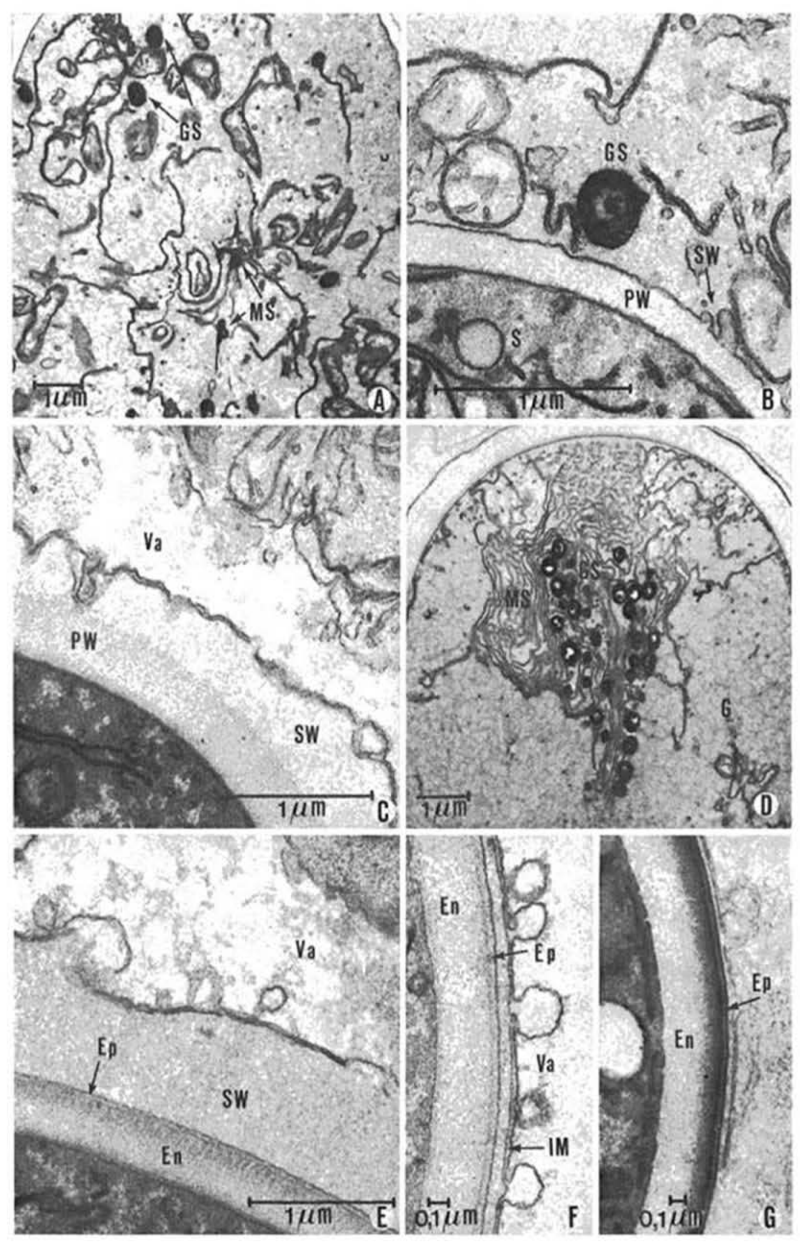
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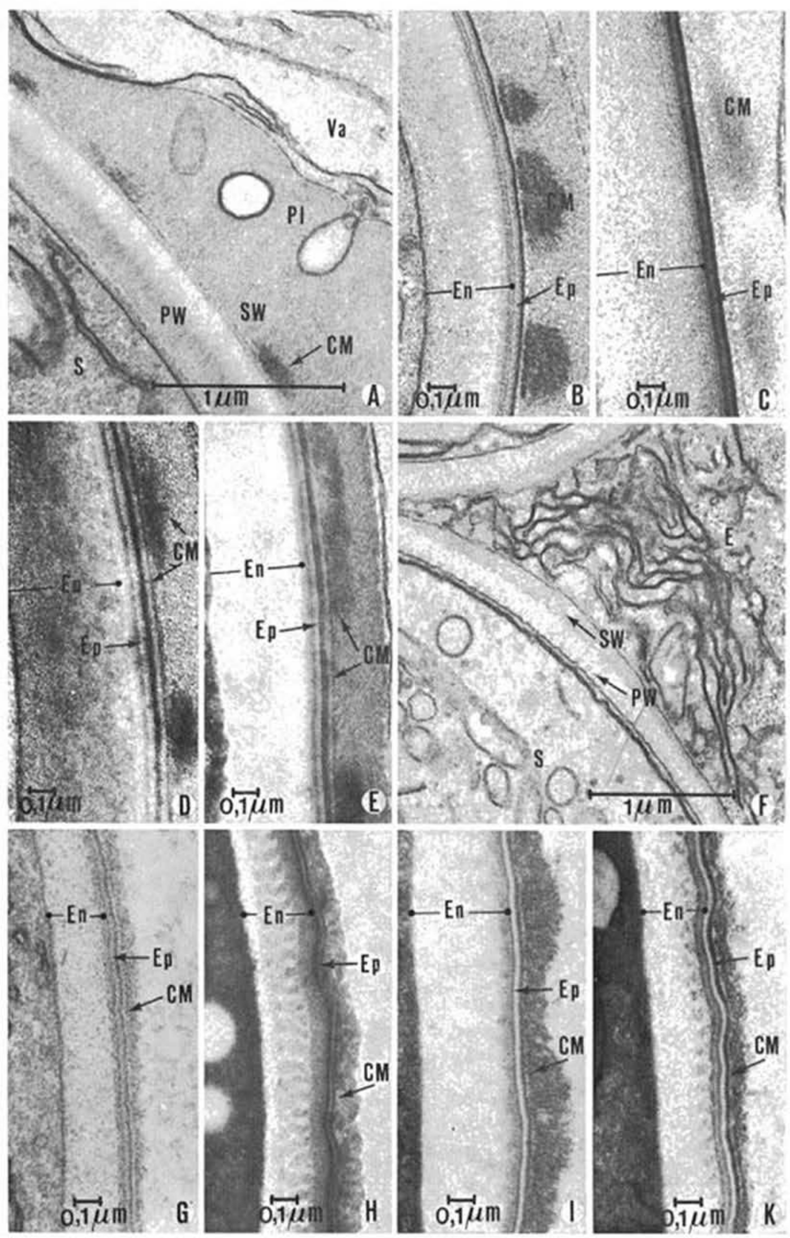

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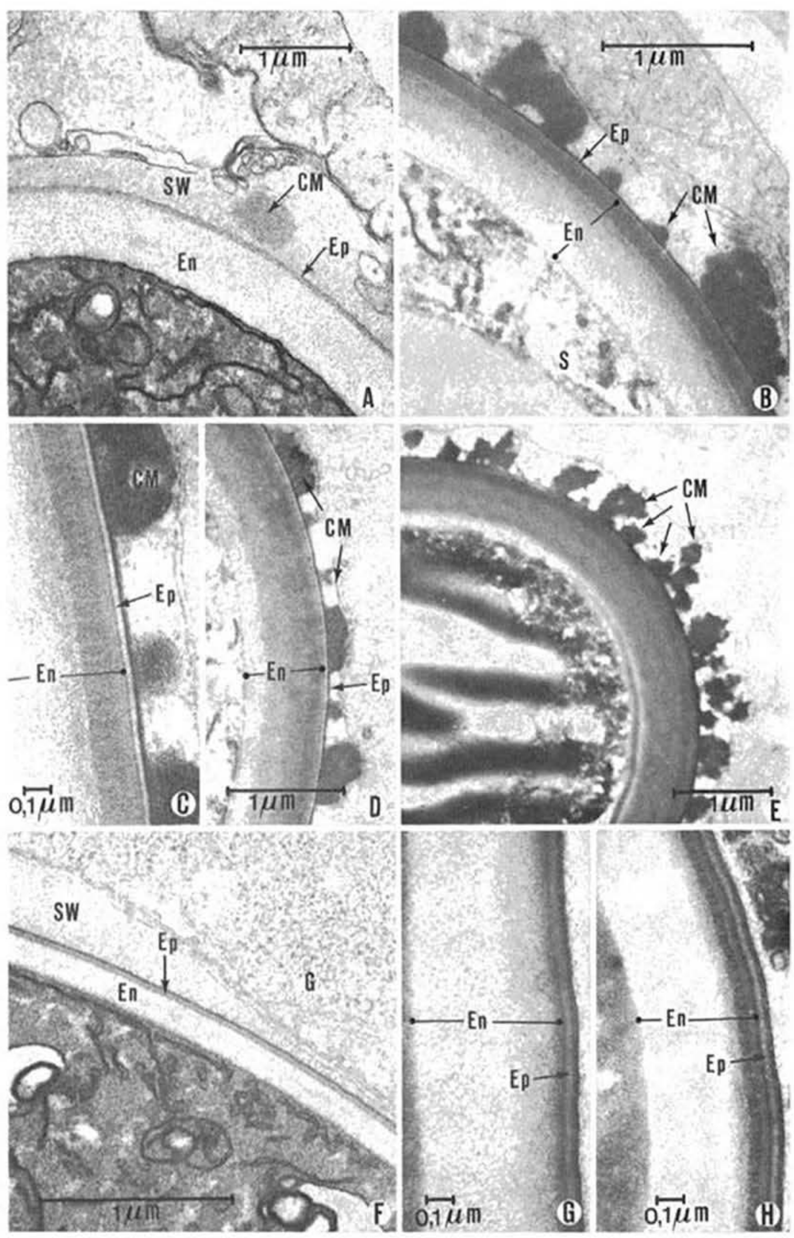
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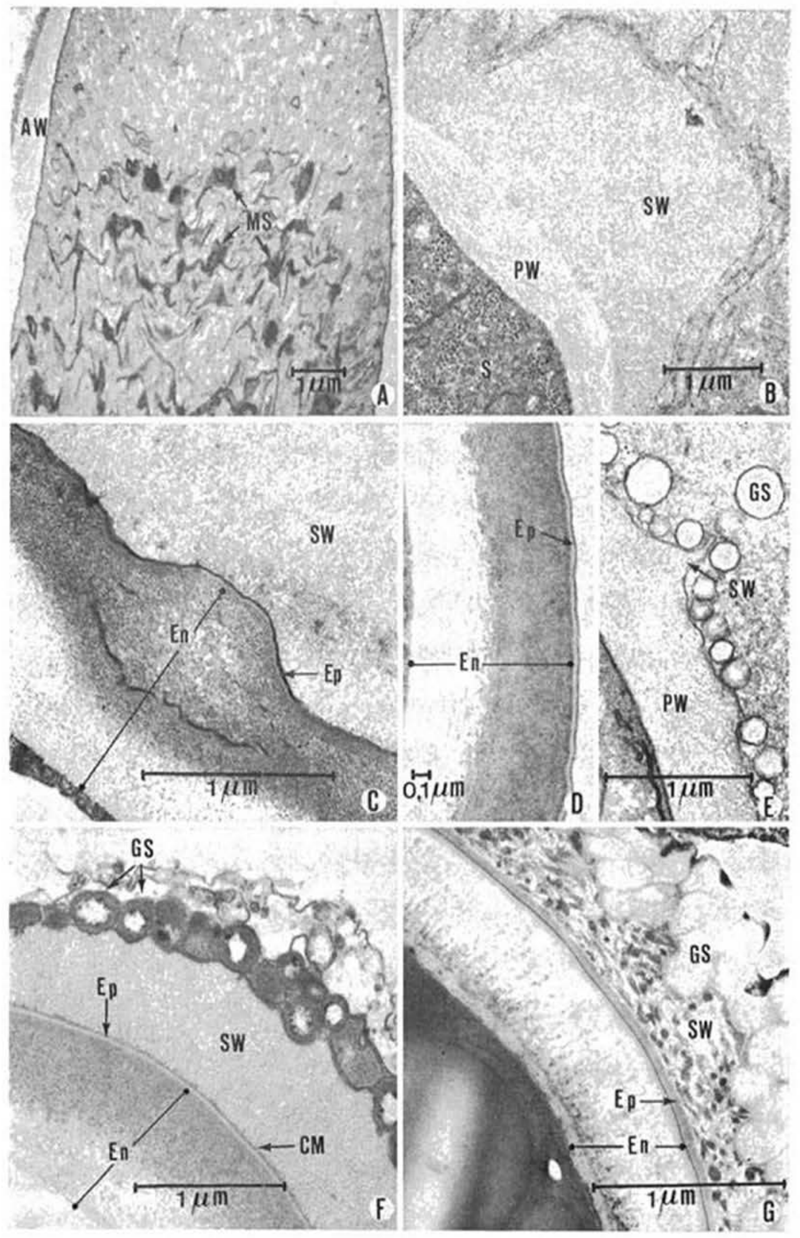
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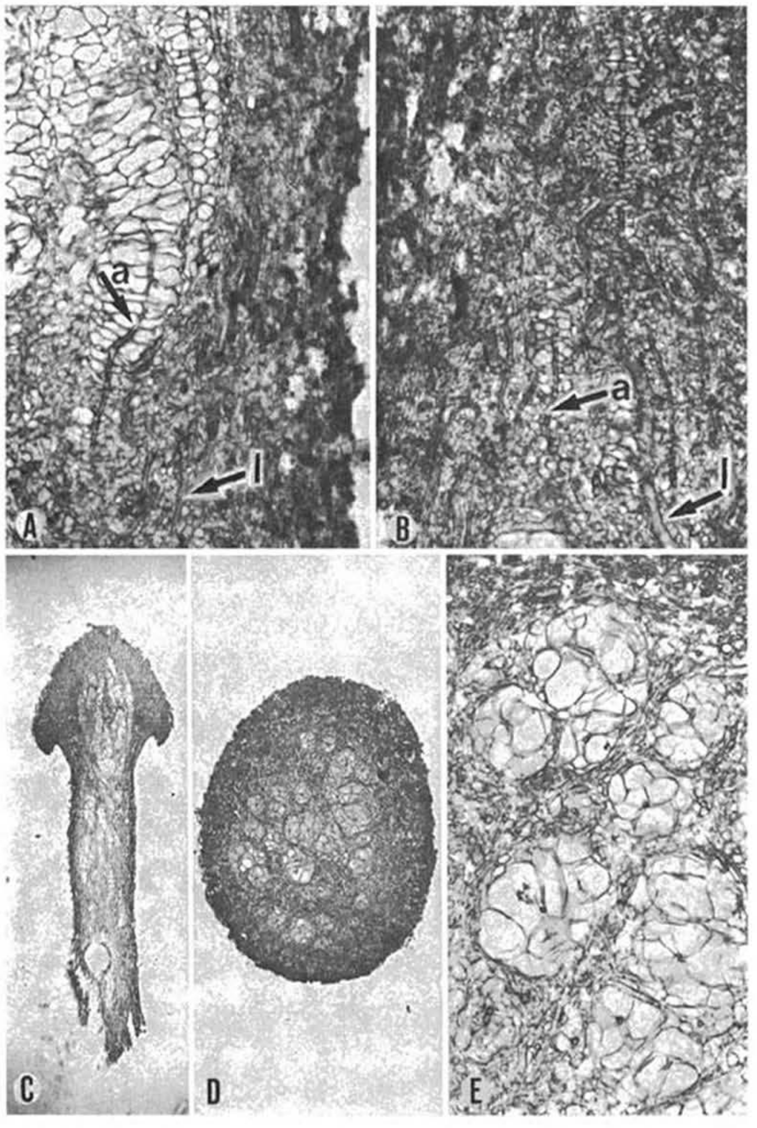
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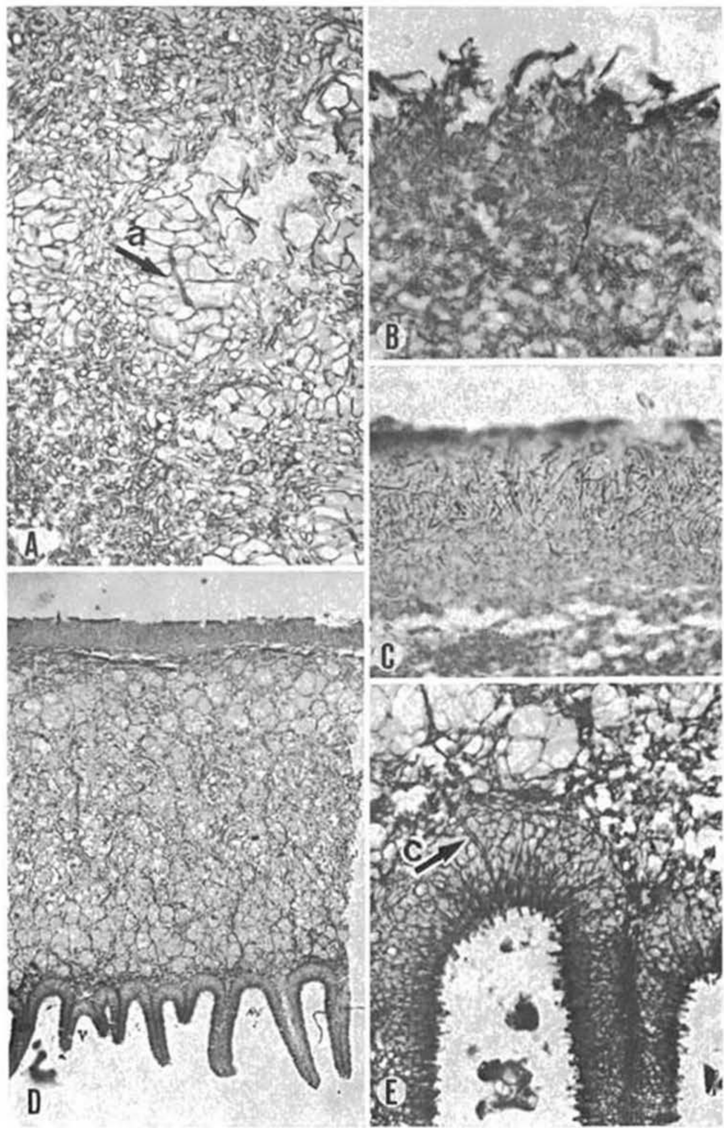
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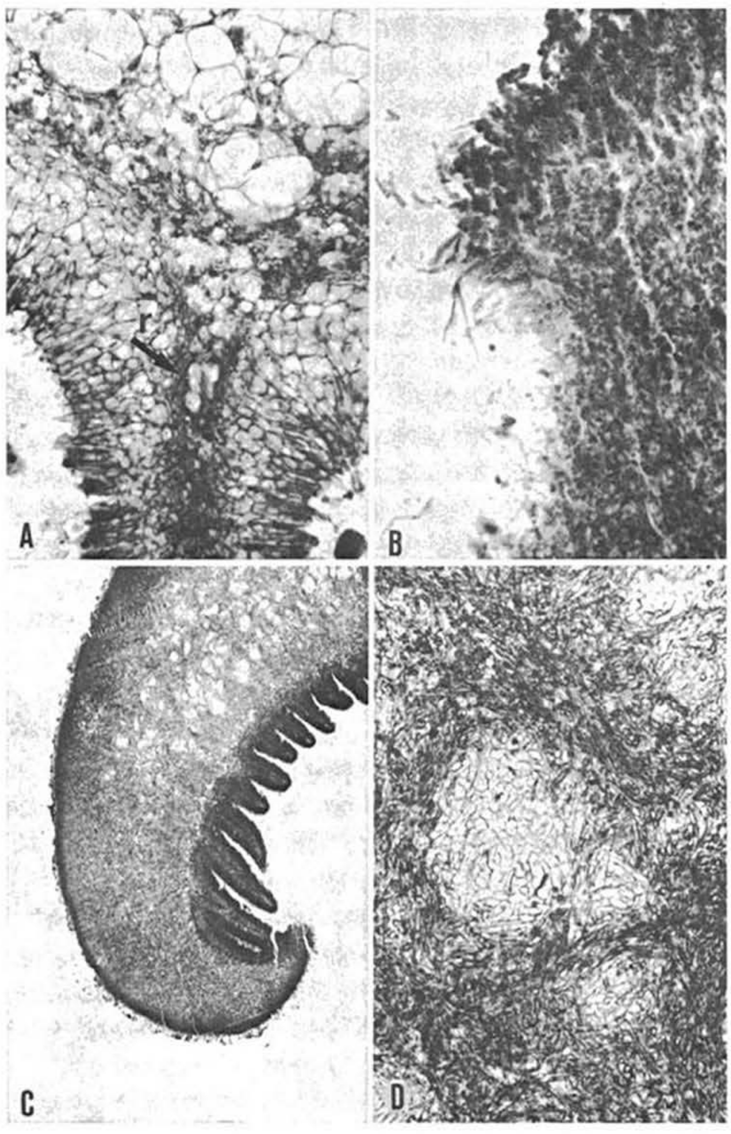
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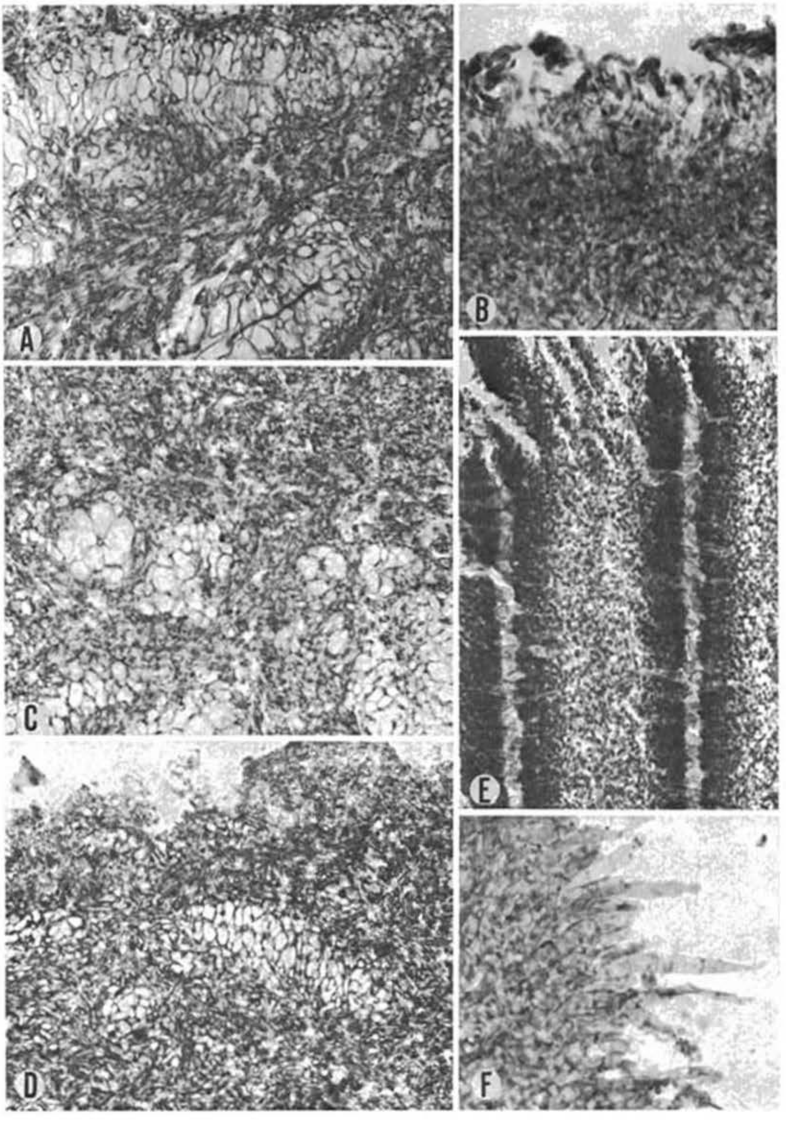
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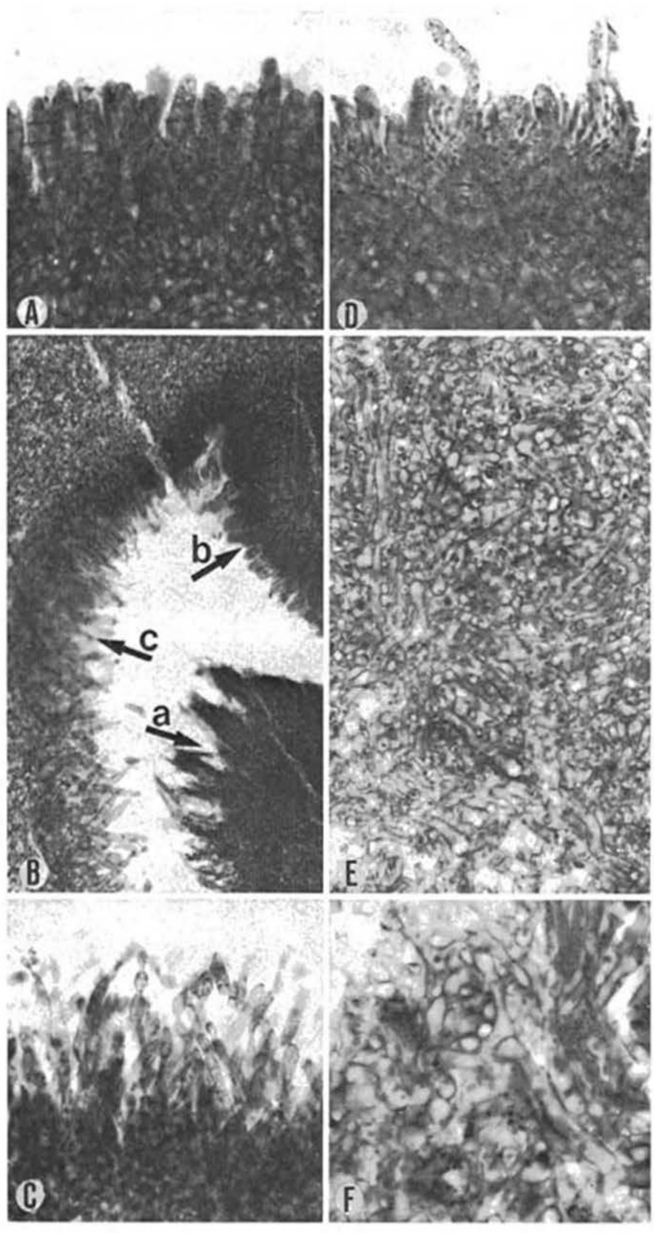
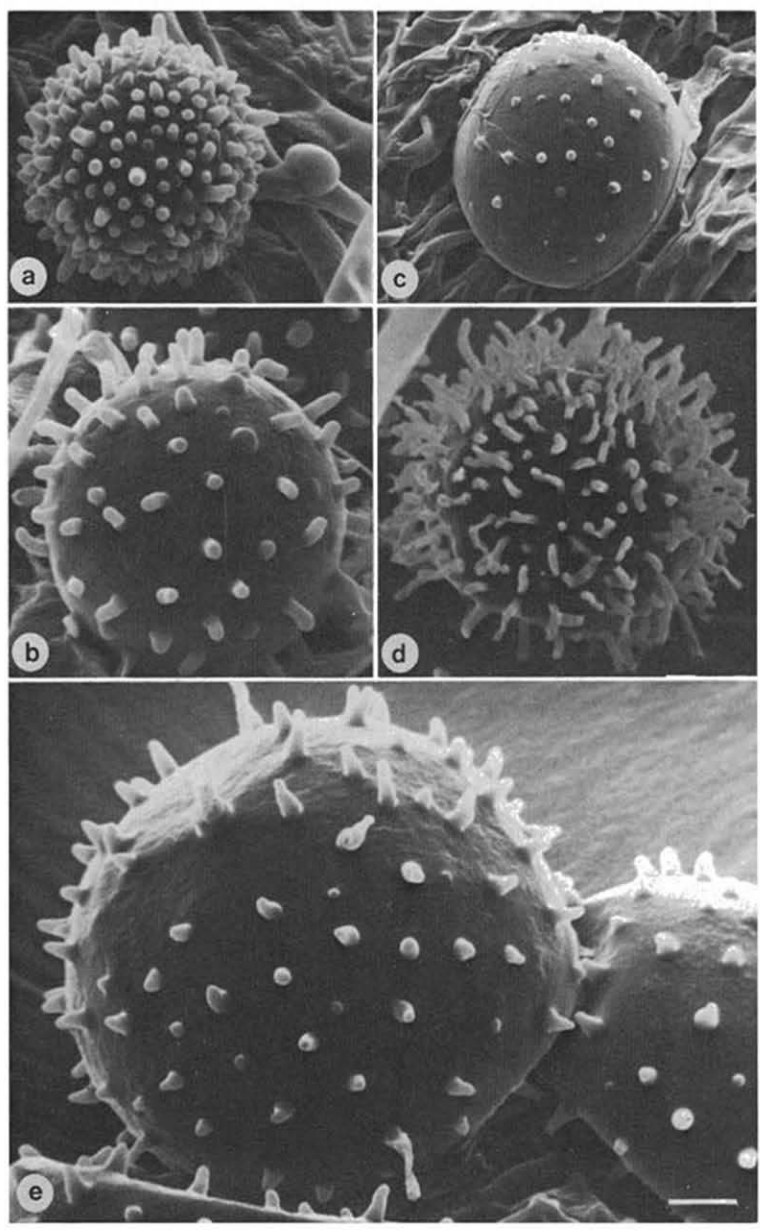

A
D
b
c
a
B
E
C
F


a
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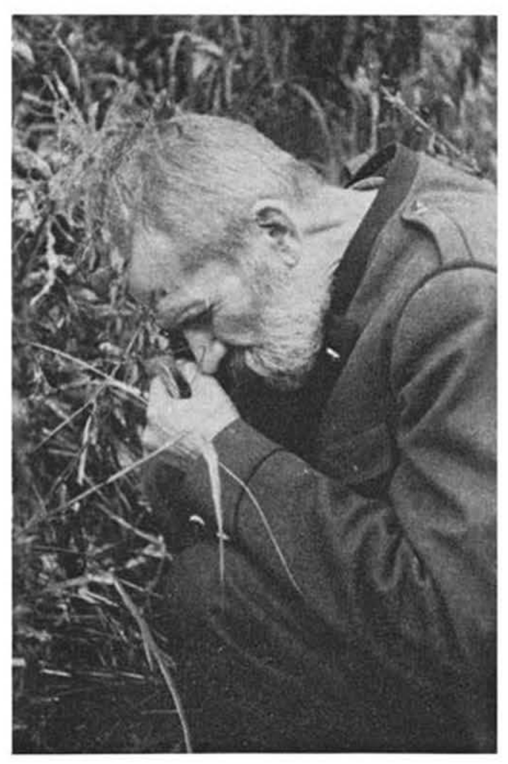
b
d
e



FRANZ PETRAK

Photograph, made in 1947 by H. Petrak (his son)