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

Pyronemataceae sensu Eckblad

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(With Plates 1–14)

The development of wall layers and ornamentation of ascospores is studied with the electron microscope in members of the Pyronemataceae. In all the species primary and secondary walls are formed successively. The primary wall appears to differentiate into two layers, an inner endospore and an outer epispore. The secondary wall is homogeneous in appearance and by redistribution and differentiation gives rise to patterns of ornamentation, which in *Lamprospora crec'hqueraultii* alone show an internal structure. The epiplasm appears to be involved in the formation of the secondary wall.

INTRODUCTION

In classifying the Pezizales the ornamentation patterns of ascospores have often been used as a character for determining species and genera. In particular Le Gal's light microscopy (1947, 1949) has been of importance to this subject; her detailed and extensive study of the structure and development of the ornamentation patterns of the ascospores of the Pezizales is of great value.

An earlier study of mine (Merkus, 1973) summarized both Le Gal's work and the more recent electron microscopy of others. The discrepancies between Le Gal's observations and the results so far obtained by electron microscopy were pointed out and the importance of new studies was emphasized. My own study started with the ornamentation patterns of the ascospores of *Ascodesmis microscopica* (Crouan) Seaver and *A. nigricans* van Tiegh. It confirmed my conjecture that fewer complications in the development of ascospore ornamentation are present than Le Gal thought likely. The differences she reported in the development of the two species were not found either. My results at that time indicated that further studies on this subject were necessary.

The present paper makes it possible to present new information on the development of the ornamentation patterns of the ascospores of the Pezizales. The species studied belong to the Pyronemataceae sensu Eckblad (1968), which are practically identical with the Humariaceae of Le Gal (1947: 285). *Boudiera*, according to Eck-

blad a member of the Ascobolaceae, is added because the development of its spore ornamentation is similar to that of the other species.

REVIEW OF EARLIER WORK

Le Gal's light microscopy of the ornamentation patterns of the ascospores of the Pyronemataceae is reviewed in order to facilitate the present interpretation of it. Where necessary the names used by Le Gal (see footnotes) have been changed according to the rules of the international code of botanical nomenclature (Stafleu *& al.*, 1972).

According to Le Gal the species belonging to this family may vary widely in their mode of development of spore ornamentation. In all her species a primary wall, on which ornamentation arises, is present; the ornamentation consists of callose and pectine formations and is of sporal origin.

In *Trichophaea paludosa* (Boud.) Boud. the ornamentation is very simple and arises directly on the primary wall, extra wall layers not forming. In the other species the development of ornamentation is more complicated, their primary wall being covered by an "assise sous-périsporique" and a "pellicule membranaire". The "assise sous-périsporique" is formed before ornamentation develops. The "pellicule membranaire" is termed "tunique externe de l'assise" if it is formed before ornamentation develops and the substance of the ornamentation does not penetrate it. The "pellicule membranaire" is termed "coque interpérisporique" if it is formed at the same time as the ornamentation and the substance of the ornamentation does penetrate it; the "coque interpérisporique" and the substance of the ornamentation both grow into one, the "coque interpérisporique" also consisting of callose and pectine.

The genera *Lamprospora* and *Boudiera* are very much alike; both develop simple ornamentation. In *Lamprospora ascoboloides* Seaver, *L. areolata* Seaver, *L. crouani* (Cooke) Seaver,[1] *L. dictydiola* Boud., *L. polytrichi* (Schum. per Fr.) Le Gal, *Boudiera areolata* Cooke & Phill. apud Cooke, and *B. echinulata* Seaver the ornamentation is formed between the primary wall and its covering layers; *Lamprospora crec'hqueraultii* (Crouan) Boud. differs, the substance of the ornamentation penetrating the covering layers of the primary wall and the ornamentation developing on the "coque interpérisporique".

Scutellinia asperior (Nyl.) Dennis[2] and nearly all the other species of the genus *Scutellinia* develop simple ornamentation that penetrates the covering layers of the primary wall and develops on the "coque interpérisporique". During the development of the ornamentation a "périspore" is present on the outside of the spores but in a later stage it disappears.

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[1] *Lamprospora miniata* (Crouan) Boud.
[2] *Ciliaria asperior* (Nyl.) Boud.

Melastiza chateri (W. G. Smith) Boud.,[3] *Aleuria aurantia* (Pers. per Hook.) Fckl.,[4] *Scutellinia pseudotrechispora* (Schroet.) Le Gal,[5] *Melastiza chateri* (W. G. Smith) Boud. sensu Grelet,[6] and *Aleuria bicucullata* (Boud.) Boud.[7] develop complex ornamentation. Apart from the "assise sous-périsporique" and the "pellicule membranaire" a "périspore" as well as "masses globuleuses" are present; the ornamentation is formed on the "coque interpérisporique". In the first three species the "masses globuleuses" are epiplasmic in origin, while in a later stage they disappear; in the other two species they are of sporal origin and disappear only in *Aleuria bicucullata*. In a later stage the "périspore" disappears in all these species.

In recent light microscopy of the spore ornamentation in *Boudiera echinulata* Seaver, Dissing (1974) described the presence of a hyaline layer around the spores during spore development, which ought to have disappeared when the spores have matured.

In electron microscopy of *Pyronema domesticum* (Sow. per S. F. Gray) Sacc., Reeves (1967) described the first stages of spore development. As wall layers he found an endospore that becomes surrounded by a smooth electron-transparent spore matrix.

MATERIALS AND METHODS

The material of the species in the present study was collected in the Netherlands and in Switzerland; the following list gives some details about the specimens and their localities: *Aleuria aurantia* (Pers. per Hook.) Fckl. — *Piepenbroek 721*, on soil, Wilp, Gelderland, The Netherlands, 11.XI.1973 (L); *Anthracobia melaloma* (Alb. & Schw. per Pers.) Boud.; *Boudiera echinulata* Seaver — *Piepenbroek 665*, in foot-print of horse on soil, Duursche Waarden between Olst and Wijhe, Overijsel, The Netherlands, 23.IX.1973 (L); *Cheilymenia pulcherrima* (Crouan) Boud. — *Bas*, on cow dung, "Het Oerd", Ameland, Friesland, The Netherlands, 27.X.1973 (L); *Lamprospora crec'hqueraultii* (Crouan) Boud. — *Piepenbroek 559*, on soil, "'t Woold", Winterswijk, Gelderland, The Netherlands, 17.VI.1973 (L); *L. dictydiola* Boud. — *van Brummelen 4105*, on burnt ground among mosses, "de Bannink", Colmschate, Overijsel, The Netherlands, 12.VI.1973 (L); *Melastiza chateri* (W. G. Smith) Boud. — *Piepenbroek 722*, on sandy soil, Wilp, Gelderland, The Netherlands, 11.XI.1973 (L); "*Neotiella*" *ithacaensis* (Rehm) Schweers[8] — *van Brummelen & Piepenbroek 4101*, on clay soil, Wilp, Gelderland, The Netherlands, 3.VI.1973 (L); *Scutellinia armatospora* Denison — *Piepenbroek 575a*, on damp soil, Duursche Waarden between Olst and Wijhe, Overijsel, The Netherlands, 19.VIII. 1973 (L); *S. scutellata* (L. per St-Amans) Lamb. —

[3] *Melastiza miniata* (Fckl.) Boud.
[4] *Peziza aurantia* Pers. per Hook.
[5] *Ciliaria pseudotrechispora* (Schroet.) Boud.
[6] Le Gal 1947: 206
[7] *Peziza bicucullata* Boud.
[8] correct name not available

van Brummelen 4070, on burnt wood, Nederhorst den Berg, North-Holland, The Netherlands, 12.V.1973 (L); *van Brummelen 4006*, on dead wood, Axalp, Tiefental near Brienz, alt. 1150 m, Switzerland, 9.IX.1972 (L); *Sepultaria arenosa* (Fckl.) Rehm — *Daams & van Brummelen 4071*, on sandy soil, Nederhorst den Berg, North-Holland, The Netherlands, 12.V.1973 (L); *S. tenuis* (Fckl.) Boud. — *Piepenbroek 620*, on damp soil, Hengforder Waarden, Olst, Overijsel, The Netherlands, 9.IX.1973 (L); *Trichophaea abundans* (P. Karst.) Boud. — *van Brummelen 4106*, on burnt ground, Twello, Gelderland, The Netherlands, 12.VI.1973 (L); and *T. woolhopeia* (Cooke & Phill. apud Cooke) Boud. — *Piepenbroek 564c*, on sandy soil amongst mosses, "Frieswijk", Diepenveen, Overijsel, The Netherlands, 5.VIII.1973 (L).

The apothecia were collected on their substratum in the field. In the laboratory they were taken from the substratum and placed in the fixative. Several types of fixative were applied.

Apothecia were fixed for 30 minutes at room temperature in 1.5% $KMnO_4$ in distilled water, to which one drop of Invadine (Geigy) was added; after several washings in pure distilled water it was postfixed for 60 minutes at room temperature in 1% OsO_4 in cacodylate buffer. Other material was fixed for 3 or 4 hours at 4 °C in 3–3.25% glutaraldehyde in cacodylate buffer; after several washings in pure cacodylate buffer it was postfixed for 60 or 90 minutes at 4 °C in 1% OsO_4. Moreover some material was fixed for several days at 20 °C in 3% glutaraldehyde and 3% acrolein in cacodylate buffer; after several washings in pure cacodylate buffer it was postfixed for 60 minutes at room temperature in 1% OsO_4.

The $KMnO_4$-OsO_4-fixed material was washed in pure cacodylate buffer and dehydrated at room temperature in ethanol, as was the glutaraldehyde-acrolein-OsO_4-fixed material. The glutaraldehyde-OsO_4-fixed material was washed at 4 °C in pure cacodylate buffer, then dehydrated at 4 °C in ethanol. During dehydration the material was stained in 1% uranyl acetate in 30%, 50%, 70%, and 96% ethanol in distilled water or in the 70% and 96% solution or in the 96% solution only. In a few instances staining occurred in a series of dehydration steps, each consisting of a mixture of 1% uranyl acetate in 96% ethanol and a corresponding amount of distilled water.

The material was then transferred at room temperature to the usual Epon embedding medium (Luft, 1961), via 100% ethanol, propylene oxide, and mixtures of propylene oxide and Epon.

The Epon components were used at a rate of 6.1 g Epikote 812, 1.9 g dodecenylsuccinic anhydride, 3.3 g methylnadic anhydride, and 0.15 g 2, 4, 6-tri(dimethylaminomethyl)phenol.

Sections were cut with a glass knife or a Du Pont diamond knife on an LKB Ultrotome III, occasionally stained with various combinations of uranyl acetate (Glauert, 1967) and Reynolds' lead citrate (1963), and examined with a Philips EM 300 electron microscope.

OBSERVATIONS

The ultrastructure of these species accords fairly closely with the ultrastructure of *Ascodesmis microscopica* and *A. nigricans*. A general description will therefore be given first. This is followed by the characteristics of each species separately.

Like with *Ascodesmis microscopica* and *A. nigricans*, in the species in this study the development of the ascospores starts by a delimitation of the spores in the ascoplasm. When delimitation has been completed the two delimiting unit membranes surround sporoplasm in the middle of which a nucleus is situated. The remaining part of the ascoplasm is called the epiplasm.

At these very early stages of spore development epiplasm and sporoplasm are not essentially different from each other. Because of their common origin they have the same electron density and contain the same type of organels, like in *Ascodesmis microscopica* and *A. nigricans*. The form and structure of the organels also answer to the description of these two species. Not until the spores have evolved do the epiplasm and the sporoplasm develop an appearance characteristic of each of them.

In all the species studied here a first spore wall develops between the two delimiting unit membranes. The mode of development and the general structure of the first spore wall is the same as that described for *Ascodesmis microscopica* and *A. nigricans*. Like in those species this wall, here also called primary wall, consists of homogeneous electron-transparent material; it varies from 200–1400 nm in thickness. At a later stage two layers are present, an outer epispore and an inner endospore. In *Ascodesmis microscopica* and *A. nigricans* these two layers developed through redistribution of the primary wall material. This may also occur in the species studied here, but since the origin of the two layers could not be easily traced, I do not wish to state this without comment.

The epispore is 30–100 nm thick and at first consists of only one fairly electron-dense layer. In a later stage three layers are often found. In material fixed in permanganate-OsO_4 the outer and inner layers are electron-dense, while the middle layer is electron-transparent; the outer layer may further increase in thickness. In material fixed in glutaraldehyde-acrolein-OsO_4 or in glutaraldehyde-OsO_4 the outer and inner layers are only fairly electron-transparent, while the middle layer is electron-dense. In a few cases only two layers are found; the outer layer then seems to correspond with the afore-mentioned outer layer. Ultimately with all three fixatives still finer striation, which may alter this original pattern considerably, often becomes visible in all the layers.

The endospore varies in thickness from 150–2000 nm and has the same structure with all the fixatives. In the younger stages it is electron-transparent. Unlike the endospore in *Ascodesmis microscopica* and *A. nigricans*, in the present species the structure may vary in the later stages; its outer part often increases in electron density, sometimes developing a layered structure that joins with the epispore.

Like in *Ascodesmis microscopica* and *A. nigricans*, the inner delimiting unit membrane becomes the sporoplasmalemma and the outer delimiting unit membrane the investing membrane.

After formation of the primary wall new wall material is deposited between the primary wall and the investing membrane. In this way a second spore wall is formed. This occurs in the species that develop ornamented spores as well as in those that develop smooth spores. The very first stages in the development of this spore wall are the same as in *Ascodesmis microscopica* and *A. nigricans*. Like in those species the investing membrane separates from the primary wall and the resulting space fills up with new wall material. In the older stages however all these species show their own characteristic development, which will be described in detail for each of them. The second spore wall will be called secondary wall, as in the two species of *Ascodesmis*.

As the primary and secondary walls evolve, the epiplasm and the sporoplasm each develops its own characteristic appearance. The structural changes in the epiplasm are complete. Almost all the organels disappear, the endoplasmic reticulum probably remaining longest; in the later stages of development the organels are often found in a thin layer just inside the ascoplasmalemma. The structure of the remaining epiplasm varies according to the species; when the spores finally mature almost all the epiplasm in the upper part of the ascus disintegrates. The appearance of the sporoplasm scarcely changes, except for a general increase in electron density; in nearly all the species oil drops develop.

ALEURIA AURANTIA

Fixatives: glutaraldehyde-acrolein-OsO_4, glutaraldehyde-OsO_4, and permanganate-OsO_4. Incipient spores have been seen from the moment at which formation of the primary wall takes place.

After use of the two second fixatives the appearance of the epiplasm and the sporoplasm is in line with the general description. After use of the glutaraldehyde-acrolein-OsO_4-fixative however it is different; because of the irregular and freakish aspect of all the membranes and the presence of extensive clusters of membranes both look rather chaotic. These clusters occur along the ascus wall, where the membranes mostly run parallel to the wall and join with lomasomes; more centrally in the ascoplasm and in the sporoplasm the clusters consist of more or less regularly arranged concentric membranes, which may be associated with electron-transparent vesicles and electron-dense granules. Another frequent phenomenon after use of this fixative is bulbing of the nucleus in the sporoplasm. The bulbs are often associated with sporoplasmic membranes that occur close to the nuclear membrane.

The first structural changes in the epiplasm are found during the formation of the primary wall. In this stage the epiplasmic vacuoles increase in size and number; after fixing in permanganate-OsO_4 they contain some flocky material. The sporoplasm becomes more electron-dense but maintains its original structure. The primary wall develops regularly, becoming 300–400 nm thick.

Deposition of secondary wall material occurs regularly along the whole primary wall, but separation of the investing membrane is more conspicuous at some places

than at others. After use of the two aldehyde-OsO_4-fixatives the investing membrane runs irregularly, after fixing in permanganate-OsO_4 straighter; this difference is found in all the stages of spore development. The secondary wall material is fairly electron-dense; in the permanganate-OsO_4-fixed material it is homogeneous, in the aldehyde-OsO_4-fixed material perhaps slightly more granular (Pl. 1A, B).

When the secondary wall has joined together around the whole primary wall and widens, the structural changes in the plasm increase. The sporoplasm becomes far more electron-dense and develops two oil droplets. The epiplasm undergoes extensive vacuolation whereby the organels originally present as well as the contents of the vacuoles disappear. In the glutaraldehyde-OsO_4-fixed material the remaining epiplasm between the vacuoles is quite normal in appearance; in the permanganate-OsO_4-fixed material it seems to have about the same structure as the secondary wall, whereby it sometimes appears like more or less globularly separated parts (Pl. 1B).

The epispore and the endospore develop regularly. The epispore forms the usual complex of layers of alternating electron density, 30–50 nm thick. The distribution of electron-dense and electron-transparent material in the endospore, which is 250–350 nm thick, is less regular but fairly constant in appearance; it is especially visible after use of the aldehyde-OsO_4-fixatives (Pl. 1C, D).

During the development of the epispore and the endospore the secondary wall increases in thickness and its appearance varies according to the fixatives used. In the permanganate-OsO_4-fixed material the secondary wall material at first becomes slightly more electron-dense; the increase in electron density then occurs in special areas that are often found in the form of bands along the outer border of the secondary wall, or spread more granularly (Pl. 1B, C). In the aldehyde-OsO_4-fixed material electron-dense globules arise throughout the secondary wall; these globules expand and the intermediate material also becomes more electron-dense and granular (Pl. 1D).

During the last stages of the maturation of the spores the secondary wall material, which has further increased in electron density, appears to concentrate on the epispore, where ornamentation is formed. Meanwhile the epiplasm loses its structure completely and disappears (Pl. 1D). The ornamentation consists of a high and coarse reticulum of crests and ridges about 1000 nm thick and connected by a smooth layer about 100 nm thick covering the epispore in the meshes of the net.

ANTHRACOBIA MELALOMA

Fixative: glutaraldehyde-OsO_4. The youngest stages present show fairly advanced spore development. Not only have an epispore and an endospore developed but a secondary wall is also present.

Epiplasm, sporoplasm, and endospore are regular in appearance; the sporoplasm is more electron-dense than the epiplasm, where vacuolation has started. The epispore shows a striated structure parallel to the spore surface and striation perpendicu-

lar to it. The secondary wall has electron-dense and somewhat granular contents; the bounding investing membrane runs slightly undulating (Pl. 2A).

In a following stage the vacuolation in the epiplasm continues. The striated structure in the epispore parallel to the spore surface becomes clearly visible but the striation perpendicular to it has disappeared; the epispore is 60–80 nm thick. The endospore (300–400 nm thick) now shows a differentiated pattern of varying electron density, with largely dominant electron-dense material perpendicular to the epispore; an electron-dense layer in the innermost part of the endospore may be present, too (Pl. 2C, D). The secondary wall has also developed further and the granular contents appear to increase in electron density at several places on the epispore. In this way one or more big electron-dense mass develops on each spore (Pl. 2A).

By the latest stages of spore development the epiplasm has almost totally disappeared, while the sporoplasm has become almost electron-dense and developed several oil drops. The electron-dense masses in the secondary wall have loosened from the epispore and, together with the rest of the secondary wall, appear to be lost in the remnants of the epiplasm (Pl. 2C). No ornamentation is formed; the mature spores are smooth.

BOUDIERA ECHINULATA

Fixative: permanganate-OsO_4. The aspect of the primary wall and the sporoplasm agrees with the general description; the primary wall measures 600–1000 nm; in the sporoplasm small areas with electron-dense granular material are present.

By an early stage of spore development the structural changes have already made great progress in the epiplasm. Where the development of the secondary wall has not yet started, nearly all the organels have disappeared; those remaining are mostly found close to the ascoplasmalemma, where the epiplasm now consists of a broad layer of electron-dense granular material. More centrally in the ascus the epiplasm looks rather empty, except for numerous globules that vary in size and consist of the same granular material as that in the outer layer of the epiplasm; areas with electron-dense flocky material are also found (Pl. 3A).

The development of the secondary wall starts with the separation of the investing membrane from the primary wall. This separation occurs along the whole spore but tends to become fairly conspicuous in some places. In this stage the same flocky material and the same globular structures as in the epiplasm are present in the secondary wall. The globular structures are often seen in association with the investing membrane (Pl. 3A, B).

When the secondary wall develops further it increases in size and remains freakish in outline; it no longer contains the globular structures but consists of the flocky material only. *The epiplasm does not change its appearance; in the* sporoplasm several oil drops develop and the electron density increases (Pl. 3B).

During the development of the secondary wall an epispore and an endospore

evolve; the epispore varies in thickness from 30–45 nm, the endospore from 600–2000 nm. As the result of a vaguely layered structure sometimes present in the outer part of the endospore, the epispore and the endospore are not clearly separated from each other (Pl. 3C, D).

When the spores mature the flocky material in the secondary wall appears to concentrate on the epispore, where ornamentation is formed (Pl. 3B, C, D). The epiplasm disintegrates completely, as does the rest of the secondary wall. The ornamentation is spinose; the spines vary in height from 250–4000 nm; they are mostly regular in form but sometimes also conical or pin-shaped, or even with a split top (Pl. 3C). A rather smooth layer of about 100 nm thick covers the epispore between the spines (Pl. 3D).

CHEILYMENIA PULCHERRIMA

Fixative: permanganate-OsO_4. In the youngest stages an incipient formation of the secondary wall is present.

Both the primary wall and the sporoplasm are normal in appearance, agreeing with the general description; the primary wall is 500–700 nm thick. By an early stage of development the structural changes in the epiplasm have made great progress, like in *Boudiera echinulata*; it contains only a few organels and consists mainly of fairly electron-dense flocky material. Separation of the investing membrane has occurred along the whole primary wall; the secondary wall varies considerably in thickness and consists of the same flocky material as that in the epiplasm. The investing membrane runs straight but is often interrupted; the free endings then spread locally into the epiplasm, so that the secondary wall and the epiplasm merge into each other (Pl. 4A).

In a somewhat later stage of spore development the appearance of the primary wall and the sporoplasm has scarcely changed; the sporoplasm increases in electron density but no oil droplets are formed. The alterations in the appearance of the secondary wall and the epiplasm are more striking. The secondary wall has widened and increased in electron density; it has also become homogeneous and now contains epiplasmic inclusions. In the epiplasm the flocky material has become more homogeneous and vacuoles with flocky contents have developed. The investing membrane is no longer interrupted as it was before but now shows numerous associations with the epiplasm; the epiplasmic material seems to concentrate into globules that are incorporated in the secondary wall; numerous small vesicular and membranous structures are also found close to the secondary wall (Pl. 4B, C, D).

In a following stage an epispore (40–60 nm thick) and an endospore (600–2500 nm thick) develop (Pl. 4B, D) and at various places on the epispore diffuse and electron-dense, vaguely layered spots are found. Both the secondary wall and the homogeneous material in the epiplasm sometimes still increase in electron density; the associations of the investing membrane with the epiplasm seem to disappear, as do

the vacuoles in the epiplasm. On the epispore a thin electron-dense layer of about 50 nm develops; although nearly everywhere on the spores this layer is smooth, here and there very tiny warts may be present (Pl. 4B, D).

Still later stages were not present in the material so that ornamentation on the mature spores could not be demonstrated; in the literature the mature spores are described as smooth.

LAMPROSPORA DICTYDIOLA

Fixative: permanganate-OsO_4. In this material the spores could be examined in a very early stage of development when the primary wall had not yet reached its ultimate thickness of 200–350 nm. In this stage the epiplasm and the sporoplasm still have the same aspect, which does not differ very much from the general description; both contain areas with electron-dense granules.

When the primary wall is completed the development of the secondary wall starts. Separation of the investing membrane from the primary wall occurs fairly regularly along the whole surface of the spore; the investing membrane runs straight but is often difficult to distinguish. The secondary wall has rather electron-dense homogeneous contents and finally reaches an average thickness of 500 nm (Pl. 5A, B).

During the development of the secondary wall an epispore of 30–40 nm thick and an endospore of 150–300 nm thick are formed (Pl. 5A, B, C) and changes in the epiplasm and the sporoplasm occur. In the epiplasm the areas with electron-dense material at first seem to enlarge (Pl. 5A) but in a somewhat later stage only less electron-dense flocky material is found; close to the investing membrane it seems to be packed into globules of varying size. The electron density of this flocky material and the globules in the epiplasm corresponds with the electron density of the secondary wall material (Pl. 5B, C). In a somewhat later stage vacuolation starts in the epiplasm, whereby nearly all the other organels disappear; the vacuoles contain some flocky material (Pl. 5B, C). Further changes occur in the sporoplasm, where the electron density increases and one large oil drop is formed.

Simultaneously with the continuous changes in the epiplasm and the sporoplasm the appearance of the secondary wall alters further. On the epispore a diffuse layer with increased electron density is formed (Pl. 5C). Locally just after its formation, this layer may show very fine striation running parallel to the spore surface; in a later stage it becomes more homogeneous and about 15 nm thick. In the originally striated parts flattened globules about 50–150 nm across showing the same increased electron density and homogeneous appearance develop. The globules are distributed regularly over the spore surface and grow to rounded spines and ridges of max. 200 nm (Pl. 5D); these finally form reticulate ornamentation on the epispore. The epispore now measures 50–70 nm in thickness (Pl. 5D). Together with the epiplasm the rest of the secondary wall decreases and seems to disappear.

LAMPROSPORA CREC'HQUERAULTII

Fixatives: permanganate-OsO_4 and glutaraldehyde-OsO_4. This species closely resembles *L. dictydiola* in the stages where the primary wall (800–1100 nm thick), the epispore (60–80 nm thick), and the endospore (500–1000 nm thick) develop and the first formations of the secondary wall are found.

During the further development of the secondary wall the appearance of the epiplasm remains the same as in *L. dictydiola*. In the sporoplasm the only difference between the two species is that here instead of one large oil drop several smaller drops develop.

A marked difference between this species and *L. dictydiola* is found in the further development of the secondary wall. At first the secondary wall of this species may widen to 2500 nm (Pl. 6A). In a later stage a number of globules with a granular structure and about 300–500 nm across arise distributed regularly on the epispore (Pl. 6B). The secondary wall material then seems to shape into packets of striated structures. At first these structures are found only around the globules but in a later stage they are evident throughout the secondary wall; they start by running in all directions (Pl. 6C), then seem to pile up and finally unite into large spines of 500–3500 nm, which form complete ornamentation on the epispore (Pl. 6D). Together with the epiplasm the rest of the secondary wall disappears.

MELASTIZA CHATERI

Fixatives: permanganate-OsO_4 and glutaraldehyde-OsO_4. In the youngest stages an incipient formation of the secondary wall is found.

The structures of the primary wall (300–700 nm thick), the sporoplasm, and the epiplasm largely agree with the general description; in the sporoplasm the electron density has increased, in the epiplasm the endoplasmic reticulum is fairly abundant and in the permanganate-OsO_4-fixed material areas with electron-dense granules are found.

In the permanganate-OsO_4-fixed material vacuolation in the epiplasm is found in a somewhat later stage; the vacuoles are completely filled up with slightly electron-dense flocky material, which however disappears in the later stages. In the remaining epiplasm most of the other organels disappear and fairly electron-dense homogeneous areas are found; the granular areas increase in size (Pl. 7B, C, D). In the glutaraldehyde-OsO_4-fixed material vacuolation in the epiplasm has often started in a somewhat earlier stage of development and the vacuoles look empty. The aspect of the remaining epiplasm continues to be normal (Pl. 7A).

The epiplasmic vacuoles are all about the same size and occur against the spores. Separation of the investing membrane has started along the whole spore, but the secondary wall develops particularly between the vacuoles. The investing membrane runs straight; the secondary wall has a fairly electron-dense homogeneous structure.

Together with the development of the secondary wall an epispore (40–60 nm thick) and an endospore (300–600 nm thick) are formed. In the sporoplasm the electron density increases further in this stage and several oil drops develop (Pl. 7C, D).

In later stages the contents of the secondary wall increase in electron density locally and become fairly granular (Pl. 7B, C), ultimately forming reticulate ornamentation 700–1000 nm thick. At the two poles of the spores an apiculus of about 2000 nm may be found and in the meshes of the net the epispore is covered by a thin layer about 50 nm thick (Pl. 7D). The rest of the secondary wall disappears, as does the epiplasm.

"NEOTIELLA" ITHACAENSIS

Fixative: permanganate-OsO_4. The primary wall (300–900 nm thick) as well as the epiplasm and the sporoplasm are regular in appearance and agree with the general description; in the epiplasm small areas with electron-dense granules are present; in the sporoplasm the electron density has slightly increased.

When the secondary wall develops, separation of the investing membrane from the primary wall occurs over nearly the whole spore but locally it is very conspicuous; the investing membrane runs somewhat irregularly. The secondary wall then increases in thickness and its outline becomes undulating; its contents are homogeneous and rather electron-dense. At the same time the appearance of the epiplasm and the sporoplasm changes. In the epiplasm vacuoles with flocky contents develop; the areas with electron-dense granules enlarge but most of the organels originally present remain; in a later stage the epiplasm also contains areas with less electron-dense homogeneous material. In the sporoplasm the electron density increases and several oil drops develop (Pl. 8A, B, C).

During the development of an epispore (30–50 nm thick) and an endospore (300–500 nm thick) (Pl. 8B, C, D) a thin electron-dense layer arises about 40 nm from the epispore and at the same time large diffuse areas with increased electron density are found throughout the secondary wall (Pl. 8C). In the following stage almost globular structures, measuring about 400 nm across and sometimes looking a bit granular, and two or three extra electron-dense layers, which mostly appear to run through the globular structures, develop on the epispore (Pl. 8D). The epiplasm and the rest of the secondary wall seem to disappear. Still later stages could not be studied; it is known from the literature that the mature spores have warty ornamentation.

SCUTELLINIA ARMATOSPORA

Fixatives: permanganate-OsO_4 and glutaraldehyde-OsO_4. In the youngest stages discernible the development of the secondary wall has already started.

The primary wall (450–850 nm thick), the epiplasm, and the sporoplasm have a normal aspect. Separation of the investing membrane has occurred along the whole primary wall; the investing membrane itself mostly runs slightly undulating. The secondary wall material is homogeneous and rather electron-dense.

In the following stage of development the secondary wall at first increases only in thickness, then important changes are found. In the permanganate-OsO_4-fixed material the investing membrane is interrupted; this was also found in *Cheilymenia pulcherrima* and will be described for *Scutellinia scutellata*, *Sepultaria arenosa*, *S. tenuis*, and *Trichophaea woolhopeia*. Like in these species, the free endings of the investing membrane spread into the epiplasm, so that the secondary wall and the epiplasm merge into each other (Pl. 9A). It is not yet clear whether this phenomenon also occurs in glutaraldehyde-OsO_4-fixed material. In the epiplasm the existing organels slowly disappear and vacuolation starts. In the permanganate-OsO_4-fixed material the vacuoles remain rather small and contain flocky material; the rest of the epiplasm becomes homogeneous and fairly electron-dense; in the glutaraldehyde-OsO_4-fixed material the vacuoles may enlarge considerably and look empty, while the rest of the epiplasm looks somewhat granular. The secondary wall itself remains homogeneous and fairly electron-dense; both fixatives show the presence of epiplasmic membranous fragments and vesicles, but after fixing in permanganate-OsO_4 small electron-dense spots that seem to consist of a compact mass of membranes also occur (Pl. 9A). In the sporoplasm the electron density increases and several oil drops are formed.

In the following stage an epispore (70–80 nm thick) and an endospore (550–800 nm thick) develop (Pl. 9B, C, D, E). At the same time an increase in electron density, giving the secondary wall a somewhat more granular look, is found particularly near the epispore, on which electron-dense warts and spines arise (Pl. 9B, C, D).

When the spores mature the epiplasm disappears almost completely, just as the rest of the secondary wall appears to do. The mature spores have warty-spinose ornamentation; the warts and rounded spines are about 500–2000 nm high and may have grown together or else be connected by a continuous layer of 20–50 nm thick and covering the epispore in between completely.

SCUTELLINIA SCUTELLATA

Fixatives: permanganate-OsO_4 and glutaraldehyde-acrolein-OsO_4. The first stages of development of the spores are exactly the same as in *S. armatospora*; the primary wall measures 600–850 nm, the epispore 90–100 nm, and the endospore 500–2000 nm. The glutaraldehyde-acrolein-OsO_4-fixative gives this species a somewhat different look, like in *Aleuria aurantia*; in the epiplasm as well as in the sporoplasm the same irregular and freakish aspect of the membranes and the same clusters of membranes are found.

Differences between the two species of *Scutellinia* occur only in the last stages of development of the secondary wall (Pl. 10A, B, C, D). In the mature spores of *S.*

scutellata the distribution of electron-dense material results in ornamentation of small warts of about 200–300 nm; these may fuse, to some extent forming an irregular network; all over the epispore a thin layer of about 10 nm appears to be present in the meshes of the net. The epiplasm and the rest of the secondary wall disappear, like in *S. armatospora*.

SEPULTARIA ARENOSA

Fixatives: permanganate-OsO_4 and glutaraldehyde-OsO_4. The structures of the primary wall (250–600 nm thick), the sporoplasm, and the epiplasm do not differ from the general description; in the epiplasm and the sporoplasm small areas with electron-dense granules are found after fixing in permanganate-OsO_4.

In the following stage the investing membrane separates along the whole primary wall and a secondary wall with fairly electron-dense contents develops. In the glutaraldehyde-OsO_4-fixed material the investing membrane may run somewhat irregularly; the secondary wall material has a flocky-granular appearance; locally small homogeneously structured globules and parts of layers are then found on the primary wall (Pl. 11B). Where the investing membrane runs less irregularly the secondary wall material is more homogeneous and forms a more continuous layer on the primary wall. In a few rare cases the secondary wall thickens considerably and very large homogeneous electron-dense masses are found on the primary wall (Pl. 11B). In the permanganate-OsO_4-fixed material the investing membrane runs straight; the secondary wall material has a homogeneous aspect and shows many thickenings in which the same electron-dense spots as in *Scutellinia armatospora* and *S. scutellata* are found; further the same interruptions in the investing membrane as described earlier also occur. The electron-dense masses on the primary wall are not present (Pl. 11A).

In the epiplasm most of the organels disappear and vacuolation starts; the vacuoles remain very small and in the permanganate-OsO_4-fixed material they have flocky contents. After use of the glutaraldehyde-OsO_4-fixative the remaining part of the epiplasm obtains the same appearance as the secondary wall. After use of the permanganate-OsO_4-fixative the areas with electron-dense material in the epiplasm enlarge and large areas with the same homogeneous aspect as in the secondary wall are also present (Pl. 11C, D).

By this advanced state of spore development the sporoplasm has increased in electron density; per spore one large oil drop, occasionally accompanied by several smaller drops, is found. Simultaneously an epispore (30–40 nm thick) and an endospore (200–300 nm thick) have evolved. At first the endospore shows a rather broad electron-dense outer part; the electron-dense material then occurs for the most part as a fairly thin and sometimes interrupted layer in the innermore parts (Pls. 11C, D; 12A, B, C).

During maturation of the spores both the epiplasm and the complete secondary wall disappear; the mature spores are smooth.

SEPULTARIA TENUIS

Fixatives: permanganate-OsO_4 and glutaraldehyde-OsO_4. The development of the spores is very much the same as in *S. arenosa*. The structures of the primary wall (200–500 nm thick), the sporoplasm, and the epiplasm agree with the general description. When the secondary wall develops, the investing membrane separates along the whole primary wall. In the glutaraldehyde-OsO_4-fixed material the investing membrane may run a bit irregularly, in which case the secondary wall material is also flocky-granular in appearance; in a later stage an increase in electron density is found especially in the middle of the secondary wall. Like in *S. arenosa*, in a few rare cases the secondary wall thickens considerably and the same large homogeneously structured masses are then present on the primary wall. The permanganate-OsO_4-fixed material has the same appearance as in *S. arenosa*.

During the further development of the spores this species closely resembles *S. arenosa* (Pl. 12D, E), though the sporoplasm develops several smaller oil drops instead of one large drop. Like in *S. arenosa* both the epiplasm and the complete secondary wall disappear when the spores mature; the mature spores are smooth.

TRICHOPHAEA ABUNDANS

Fixatives: permanganate-OsO_4 and glutaraldehyde-OsO_4. The youngest stages present show an incipient formation of the secondary wall.

The structures of the primary wall (400–500 nm thick), the epiplasm, and the sporoplasm do not differ from the general description; in the epiplasm small areas with electron-dense material are found after fixing in permanganate-OsO_4. The investing membrane, which runs fairly straight, has separated from the primary wall at some places and the secondary wall formed locally in this way consists of homogeneous and rather electron-dense material. In the following stages this process of secondary wall formation proceeds along the whole primary wall (Pl. 13A).

At the same time an epispore (35–45 nm thick) and an endospore (350–450 nm thick) develop and changes in the epiplasm and the sporoplasm take place. In the epiplasm some larger vacuoles, which in the permanganate-OsO_4-fixed material have flocky contents, arise and the organels slowly disappear. In the glutaraldehyde-OsO_4-fixed material the remaining epiplasm is normal in appearance; in the permanganate-OsO_4-fixed material the electron-dense granules remain present and larger homogeneous and rather electron-dense areas are also found. In the sporoplasm the electron density increases and two oil drops develop. In the inner part of the secondary wall itself the electron density increases and a continuous electron-dense layer with a wavy outline is finally formed on the epispore (Pl. 13B, C, D).

In the mature spores the epiplasm has disintegrated completely and disappeared, together with the rest of the secondary wall; meanwhile warty ornamentation, which covers the epispore completely and varies in thickness from 50–200 nm, has developed

TRICHOPHAEA WOOLHOPEIA

Fixatives: permanganate-OsO_4 and glutaraldehyde-OsO_4. The glutaraldehyde-OsO_4-fixed material could be studied only in the latest stages of spore development.

This species at first develops the same as *T. abundans*; the primary wall is 650–1400 nm thick. At a later stage however important differences between the two species occur. The secondary wall material appears more flocky and contains the same electron-dense spots as were found in *Scutellinia armatospora*, *S. scutellata*, *Sepultaria arenosa*, and *S. tenuis*; besides epiplasmic membranous fragments, which were also present in the two species of *Scutellinia*, and the interruptions of the investing membrane described above occur (Pl. 14A, B, C). In the sporoplasm the electron density increases and one or two oil drops develop; occasionally several smaller drops are also present.

In this stage an epispore (35–40 nm thick) and an endospore (450–650 nm thick) develop (Pl. 14B, C, D). The endospore at first has a broad and electron-dense outer part, in which striation may be distinguished. In the following stage additional wall material is formed between the sporoplasmalemma and the endospore; it is electron-dense and appears to occur as a continuous layer or as globular and lens-shaped structures; it does not distort the epispore and the endospore (Pl. 14D). The occurrence of this additional wall material is very uncommon and is only found in *Trichophaea woolhopeia*.

No further changes take place until the spores mature and the epiplasm and the secondary wall disappear; the mature spores are smooth.

DISCUSSION

Like in my earlier study of *Ascodesmis microscopica* and *A. nigricans* (Merkus, 1973), the usual methods of preparing material for electron microscopy led to confirmation of the general ultrastructure given thus far for the Ascomycetes (o.a. Hawker, 1965; Bracker, 1967). Different and too aggressive fixatives may have been the cause of the deviations from it found in *Aleuria aurantia* and *Scutellinia scutellata*.

For *Ascodesmis microscopica* and *A. nigricans* the generally accepted hypothesis about the first stages of spore development could be confirmed; in my investigations the delimitation of the spores in the ascoplasm by two unit membranes and the formation of spore walls between these two unit membranes is also found in the species belonging to the Pyronemataceae. Therefore I repeat my theory that this may be seen as a very common process that possibly occurs in all Ascomycetes.

The successive formation of primary and secondary walls has been described for *Ascodesmis microscopica* and *A. nigricans*, the two wall layers are evidently different in structure. In the Pyronemataceae the two different stages in the formation of wall layers are again found. The aspect of the first wall does not differ essentially from that of the primary wall in the two species of *Ascodesmis* so that this first wall is here

also called primary wall. Though the second wall is quite different in appearance from the secondary wall in *Ascodesmis microscopica* and *A. nigricans*, it is also called secondary wall because it has exactly the same position as in the two species of *Ascodesmis* and also develops after the primary wall has been completely formed.

In my discussion on the origin of the spore walls I supposed that lomasomes do not play an important role in the formation of the primary wall in *Ascodesmis microscopica* and *A. nigricans*; this also appears to hold for the Pyronemataceae, where it seems improbable that lomasomes play an important role in the formation of both primary and secondary walls. Special activity of the sporoplasm during the formation of the secondary wall could not be found either. Again, no evidence has been obtained for Le Gal's assumption that the secondary wall is of sporal origin. On the contrary, the present study shows that emphasis should be laid on the possibility that the epiplasm plays an important role in the formation of the secondary wall. This I also emphasized with the two species of *Ascodesmis*, whereby I suggested that, according to the results obtained thus far "the way in which the epiplasm is involved possibly determines the appearance of the secondary wall".

My results on the Pyronemataceae warrant confirmation of this last statement. When spore development starts, the epiplasm has a common structure; this structure and the changes it undergoes as soon as a secondary wall begins to form differ in aspect according to the fixative applied. With both fixatives most of the organels disappear and associations of the epiplasm with the secondary wall are found. After fixing in permanganate-OsO_4 however vacuolation of the epiplasm is not so frequent or so extensive as after fixing in glutaraldehyde-OsO_4, while the epiplasm sometimes also contains electron-dense granules. These granules either remain present during the development of the spores, sometimes even increasing in number, or else they have disappeared beforehand; sometimes they are present in the sporoplasm and may be compared with the glycogen granules in *Ascodesmis microscopica* and *A. nigricans*. Together with less electron-dense homogeneous or flocky material, which often arises in the epiplasm during the development of the spores and is possibly related to the granules, they may finally form the ground mass of the epiplasm. Between the vacuoles the epiplasm often develops the same appearance as the secondary wall, especially after use of the permanganate-OsO_4-fixative; it is therefore not improbable that the epiplasm and the secondary wall both contain identical substances.

In its first stages of development the secondary wall material has the same appearance throughout the entire secondary wall. In later stages however important changes that completely alter the appearance of the secondary wall occur; in nearly all the species of the Pyronemataceae studied a local increase or decrease of the electron density of the secondary wall is found, so that it seems as though the secondary wall material condenses at certain places. A continuing increase in the amount of secondary wall material during this condensation process should not be excluded. The starting-point, the further course of the condensation process, and the ultimate ornamentation pattern on the epispore that finally results from the condensed material

differ from species to species but they are all quite regular and characteristic for each species separately.

At those places where the electron density of the secondary wall decreases the secondary wall material finally disappears completely; it is not yet clear whether it all joins the condensed areas or that part of it disintegrates. Like in the study of *Ascodesmis microscopica* and *A. nigricans* it is also uncertain whether the investing membrane remains present or disappears.

All the species with ornamented spores, viz. *Aleuria aurantia*, *Boudiera echinulata*, *Cheilymenia pulcherrima*, *Lamprospora dictydiola*, *L. crec'hqueraultii*, *Melastiza chateri*, "*Neotiella*" *ithacaensis*, *Scutellinia armatospora*, *S. scutellata*, and *Trichophaea abundans* develop their ornamentation in this way. In *Lamprospora crec'hqueraultii* the ornamentation shows a very peculiar internal structure that arises in an originally homogeneous secondary wall. In the other species the ornamentation does not show any special internal structure, although it sometimes has a somewhat granular appearance.

Apart from the species with ornamented spores several species with smooth spores have been studied. Although in these species the development of the spores is not essentially different, the smooth spores may arise in different ways. In *Anthracobia melaloma*, *Sepultaria arenosa*, and *S. tenuis* an incipient condensation disappears in a later stage, so that smooth spores rather than ornamented spores develop; it is striking that in these species the condensation may be fairly extensive but it is then restricted to one or a few spots on the epispore. In *Trichophaea woolhopeia* no condensation at all is found, there the secondary wall material in its original form disappears.

In comparing the development of the ornamentation patterns in *Ascodesmis microscopica* and *A. nigricans* and in the species that belong to the Pyronemataceae it should be stressed that in *A. microscopica* and *A. nigricans* the secondary wall builds up the ornamentation patterns in a final form immediately after it is formed; the ornamentation patterns in the Pyronemataceae however arise only through redistribution of already present secondary wall material.

In a certain stage of spore development all the species in this study show an epispore that consists of a fairly constant pattern of layers of alternating electron density. If however in a later stage extra layers arise between the existing layers, each species develops a more characteristic epispore. This was also found in *Ascodesmis microscopica* and *A. nigricans*.

Both in *Ascodesmis microscopica* and *A. nigricans* and in the species in this study the endospore starts as a homogeneous electron-transparent layer. In later stages of spore development it may become internally structured, in contrast to the endospore in the two species of *Ascodesmis* that remains homogeneous; this internal structure is especially apparent in the aldehyde-OsO_4-fixed material. The outer part of the endospore often becomes fairly electron-dense, perhaps with a layered structure joining the epispore.

For *Ascodesmis microscopica* and *A. nigricans* it appeared as though the epispore and the endospore both developed in the primary wall by a redistribution and differentiation of the primary wall material itself. Since my findings were not conclusive however

I do not wish to state this without further comment for the species belonging to the Pyronemataceae. In discussing the origin of the epispore and the endospore, it is evident that the endospore must consist of primary wall material. On the other hand the epispore may have developed from either primary wall material, secondary wall material, or primary and secondary wall material. The fact that there is a strong similarity in structure between the epispore of the present species and the epispore of *Ascodesmis microscopica* and *A. nigricans*, that the boundary between the epispore and the endospore is often not distinct but gradual, and that the secondary wall material is totally different in appearance from the epispore (only the layered structure of the innermost part of the secondary wall in "*Neotiella*" *ithacaensis* disagrees) and the endospore however confirms my theory that in the species belonging to the Pyronemataceae both the epispore and the endospore also differentiate within the primary wall.

The variation in thickness of the primary wall, the epispore, and the endospore must for a large part be ascribed to the possibility of swelling during fixation; as was also found in *Ascodesmis microscopica* and *A. nigricans* the glutaraldehyde-OsO_4-fixative gives low and fairly constant values, while the permanganate-OsO_4-fixative gives high and variable values.

Like for *Ascodesmis microscopica* and *A. nigricans*, the results of the present study do not entirely accord with Le Gal's observations (1947, 1949). In all the species the wall layers and membranes involved in the development of ornamentation have the same position, in contrast to Le Gal's descriptions of the occurrence of ornamentation on the inner or outer side of the "assise sous-périsporique" and the "pellicule membranaire". If the "pellicule membranaire" is described as "tunique externe de l'assise" the secondary wall may possibly be compared with the "assise sous-périsporique" and the investing membrane with the "pellicule membranaire". On the other hand if the "pellicule membranaire" is described as "coque interpérisporique" it should be compared with the innermost layer of the ornamentation but a layer comparable with the "assise sous-périsporique" is then absent; in that case the secondary wall should be seen as the "périspore". No evidence has been obtained for the presence of "masses globuleuses" or for sporal origin of the substance of the ornamentation constituting the secondary wall. The hyaline layer Dissing (1974) described for *Boudiera echinulata* and the spore matrix Reeves (1967) indicated for *Pyronema domesticum* are probably identical with the secondary wall.

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Explanation of Plates 1–14

ABBREVIATIONS USED IN PLATES. — AW, ascus wall; CM, condensed material; E, epiplasm; En, endospore; Ep, epispore; Gr, granules; IM, investing membrane; PI, plasmatic includings; PW, primary wall; S, sporoplasm; SW, secondary wall; T, tonoplast; Va, vacuole.

Plate 1

Figs. A–D. *Aleuria aurantia*, spore development: Fig. A. beginning of secondary wall formation, fixed in 3% glutaraldehyde and 1% OsO_4 and stained with lead citrate, × 33,300; Fig. B. condensation of secondary wall material, fixed in 1.5% $KMnO_4$ and 1% OsO_4 and stained with lead citrate, × 30,900; Fig. C. id. also showing development of the epispore and the endospore, × 23,800; Fig. D. id. fixed in 3% glutaraldehyde and 1% OsO_4 and stained with uranyl acetate and lead citrate.

PLATE 2

Figs. A–D. *Anthracobia melaloma*, spore development, fixed in 3.25% glutaraldehyde and 1% OsO_4 and stained with uranyl acetate and lead citrate: Fig. A. condensation of secondary wall material, × 36,300; Fig. B. development of the epispore and the endospore, × 47,800; Fig. C. id. × 23,100; Fig. D. id. detail of the epispore and the endospore, × 36,300.

PLATE 3

Figs. A–D. *Boudiera echinulata*, spore development, fixed in 1.5% $KMnO_4$ and 1% OsO_4: Fig. A. development of the secondary wall, stained with lead citrate, × 11,700; Fig. B. condensation of secondary wall material, stained with lead citrate, × 10,100; Fig. C. id. also showing development of the epispore and the endospore, stained with uranyl acetate and lead citrate; Fig. D. id. detail of the epispore and the endospore, × 39,700.

PLATE 4

Figs. A–D. *Cheilymenia pulcherrima*, spore development, fixed in 1.5% $KMnO_4$ and 1% OsO_4 and stained with uranyl acetate and lead citrate: Fig. A. beginning of secondary wall formation, × 22,000; Fig. B. condensation of secondary wall material and development of the epispore and the endospore, × 22,000; Fig. C. detail of the epiplasm and the secondary wall, × 22,000; Fig. D. condensation of secondary wall material and development of the epispore and the endospore, × 13,400.

PLATE 5

Figs. A–D. *Lamprospora dictydiola*, spore development, fixed in 1.5 % $KMnO_4$ and 1% OsO_4: Fig. A. development of the secondary wall, the epispore, and the endospore, stained with uranyl acetate and lead citrate, × 17,100; Fig. B. id. stained with lead citrate, × 31,200; Fig. C. condensation of secondary wall material, stained with lead citrate, × 25,500; Fig. D. id. stained with uranyl acetate and lead citrate, × 31,200.

PLATE 6

Figs. A–D. *Lamprospora crec'hqueraultii*, spore development, stained with lead citrate: Fig. A. development of the secondary wall, the epispore, and the endospore, fixed in 1.5% $KMnO_4$ and 1% OsO_4, × 14,500; Fig. B. condensation of secondary wall material, fixed in 1.5% $KMnO_4$ and 1% OsO_4, × 26,300; Fig. C. id. also showing the internal structure in the secondary wall, × 23,100; Fig. D. id. fixed in 3.25% glutaraldehyde and 1% OsO_4.

PLATE 7

Figs. A–D. *Melastiza chateri*, spore development, stained with uranyl acetate and lead citrate: Fig. A. development of the secondary wall, fixed in 3% glutaraldehyde and 1% OsO_4, × 31,200; Fig. B. condensation of secondary wall material, fixed in 1.5% $KMnO_4$ and 1% OsO_4, × 25,500; Fig. C. id. also showing development of the epispore and the endospore, × 23,200; Fig. D. id. × 14,300.

PLATE 8

Figs. A–D. "*Neotiella*" *ithacaensis*, spore development, fixed in 1.5% $KMnO_4$ and 1% OsO_4: Fig. A. development of the secondary wall, stained with lead citrate, × 39,700; Fig. B. id. also showing development of the epispore and the endospore, stained with uranyl acetate and lead citrate, × 24,800; Fig. C. condensation of secondary wall material, stained with uranyl acetate and lead citrate, × 27,300; Fig. D. id. × 55,700.

PLATE 9

Figs. A–E. *Scutellinia armatospora*, spore development, stained with uranyl acetate and lead citrate: Fig. A. development of the secondary wall, fixed in 1.5% $KMnO_4$ and 1% OsO_4, × 25,500; Fig. B. id. also showing condensation of secondary wall material and development of the epispore and the endospore, × 22,000; Fig. C. id. fixed in 3.25% glutaraldehyde and 1% OsO_4, × 26,900; Fig. D. id. × 17,100; Fig. E. detail of the epispore, fixed in 1.5% $KMnO_4$ and 1% OsO_4, × 65,800.

PLATE 10

Figs. A–E. *Scutellinia scutellata*, spore development: Fig. A. condensation of secondary wall material, fixed in 1.5% $KMnO_4$ and 1% OsO_4 and stained with uranyl acetate and lead citrate, × 29,800; Fig. B. id. fixed in 3.25% glutaraldehyde and 1% OsO_4 and stained with lead citrate; Figs. C, D. subsequent stages in the development of the epispore and the secondary wall, fixed in 1.5% $KMnO_4$ and 1% OsO_4 and stained with uranyl acetate and lead citrate, × 52,000; Fig. E. id. fixed in 3.25% glutaraldehyde and 1% OsO_4 and stained with lead citrate.

PLATE 11

Figs. A–D. *Sepultaria arenosa*, spore development: Fig. A. beginning of secondary wall formation, fixed in 1.5% $KMnO_4$ and 1% OsO_4 and stained with lead citrate, × 22,000; Fig. B. condensation of secondary wall material, fixed in 3.25% glutaraldehyde and 1% OsO_4 and stained with uranyl acetate and lead citrate, × 30,500; Fig. C. development of the epispore and the endospore, fixed in 1.5% $KMnO_4$ and 1% OsO_4 and stained with uranyl acetate and lead citrate, × 26,900; Fig. D. id. × 17,100.

PLATE 12

Figs. A–C. *Sepultaria arenosa*, subsequent stages in the development of the epispore and the endospore, fixed in 1.5% $KMnO_4$ and 1% OsO_4: Fig. A. stained with lead citrate, × 70,000; Fig. B. stained with uranyl acetate and lead citrate, × 70,000; Fig. C. id. × 70,000.

Figs. D, E. *Sepultaria tenuis*, spore development, stained with uranyl acetate and lead citrate: Fig. D. development of the secondary wall, the epispore, and the endospore, fixed in 1.5% $KMnO_4$ and 1% OsO_4, × 18,000; Fig. E. detail of the epispore and the endospore, fixed in 3.25% glutaraldehyde and 1% OsO_4, × 63,800.

PLATE 13

Figs. A–D. *Trichophaea abundans*, spore development: Fig. A. development of the secondary wall, fixed in 1.5% $KMnO_4$ and 1% OsO_4 and stained with lead citrate, × 36,100; Fig. B. condensation of secondary wall material and development of the epispore and the endospore, fixed in 1.5% $KMnO_4$ and 1% OsO_4 and stained with uranyl acetate and lead citrate, × 28,300; Fig. C. id.; Fig. D. id. fixed in 3.25% glutaraldehyde and 1% OsO_4, × 37,800.

PLATE 14

Figs. A–D. *Trichophaea woolhopeia*, spore development: Fig. A. development of the secondary wall, fixed in 1.5% $KMnO_4$ and 1% OsO_4 and stained with lead citrate, × 15,600; Fig. B. id. also showing development of the epispore and the endospore, stained with uranyl acetate and lead citrate, × 19,900; Fig. C. id. not stained, × 29,700; Fig. D. detail of the epispore and the endospore, fixed in 3.25% glutaraldehyde and 1% OsO_4 and stained with uranyl acetate and lead citrate, × 45,000.

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LIGHT AND ELECTRON MICROSCOPIC STUDIES OF THE ASCUS TOP IN ASCOZONUS WOOLHOPENSIS

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(With Plates 15–18 and two Text-figures)

The structure of the top of the ascus in live *Ascozonus woolhopensis* has been studied by phase-contrast and interference-contrast microscopy, and by ordinary light microscopy after glutaraldehyde-OsO_4-fixation. New information was obtained from stained 0.5 μm-sections of asci embedded in epoxy resin. Electron micrographs have been made of median sections of asci that were first fixed in 1.5% sodium permanganate and postfixed with osmium tetroxide.

Light and electron microscopy have given concordant information on the organization of the top of the ascus in *Ascozonus*. In the ascoplasma no structures of an apical apparatus have been found. After meiosis the wall of the ascus consists of a broad, electron-transparent inner layer and a thin, electron-dense outer layer. The structure of the ring and the conical top of the ascus wall becomes more complicated. At the time of ascospore discharge the thick inner layer locally disintegrates in the apex just under a more resistant apical disk in the outer layer.

In the taxonomy of the Ascomycetes the organization of the ascus, especially the structure of the ascus wall and the ascus top, have proven to be of great importance (Boudier, 1879; Chadefaud, 1942, 1973; Luttrell, 1951). Even within the Pezizales the characters of the ascus play a major role in the distinction of families and genera.

The asci of Pezizales were considered to be of the 'unitunicate' type (Luttrell, 1951). Investigations in the last decennium have demonstrated, however, that in several species of Pezizales the walls of the mature asci consist of two layers (Gäumann, 1964; Delay, 1966, Kimbrough, 1966; van Brummelen, 1967; Schrantz, 1970). In general these two layers closely adhere and can not be separated. Only where the ascus is fractured or damaged sometimes a thin, more brittle, firm outer layer and a thicker, soft, inner layer are recognizable in the ascus wall. A relatively high grade of independence of both layers can still be found in some species of *Thelebolus* Tode.

The ascus dehiscence in most Pezizales occurs by means of the rupture of an apical operculum. The presence or absence of an operculum in the top of the ascus is used since Boudier (1879) as the main character to subdivide the unitunicate Discomycetes into two groups: the operculate Discomycetes (or Pezizales) and the inoperculate Discomycetes (or Helotiales).

In a few genera of Ascomycetes, usually incorporated in the Pezizales, an operculum is lacking and different structures exist in the top of the ascus. Such a deviating type of ascus dehiscence is found in the genus *Ascozonus* (Renny) E. C. Hansen. The special position in the Pezizales and the ease to grow its species in culture made *Ascozonus* an attractive object for this study.

Ascozonus is characterized by asci opening by a transversal slit down to a conspicuous subapical ring, giving the ascus top a bilabiate appearance. The first species of *Ascozonus* was described more than a century ago by the Crouan brothers under the name *Ascobolus leveillei* Crouan (Crouan & Crouan 1867, 57, pl. suppl.). Boudier (1869) described *Peziza cunicularia* Boud., which might be conspecific with the species of the Crouans. He noted that the ring in the ascus wall is not identical with the opercular commissure of the typical operculum but constitutes a small ridge at the inner side of the wall.

Several other species of this genus were described by Renny (1872, 1873, 1874) in *Ascobolus* section *Ascozonus* Renny. He also gave a description 'of the formation of the zonal stripe upon the ascus'. The accompanying illustrations of asci, however, strongly suggest images observable during plasmolysis of the ascoplasm.

More recently Kimbrough (1966) in a study of selected genera of the 'Pseudoascoboleae' paid special attention to the light microscopic structure of asci. In *Ascozonus* he described a three-layered ascus wall. The outermost layer appears as a thin hyaline membrane. The second or middle layer stains differentially in Congo red and shows an abrupt thickening near the apex of the ascus, which forms the prominent ring. This middle layer of the wall continues beyond the ring almost to the tip, there leaving an opening 10–12 μm wide. The inner layer, finally, stains in acid fuchsin but not in Congo red, and extends to the full length of the ascus. At the tip this layer bulges through the opening of the middle layer and forms the nippled end. In later studies Kimbrough (1970, 115; 1972, 398) described the ascus wall as two-layered and the ring as part of the outer layer.

MATERIALS AND METHODS

In the present study a strain of *Ascozonus woolhopensis* (Berk. & Br. apud Renny) E. C. Hansen was used. This fungus was isolated from rat dung obtained from the border of Schelde river near Antwerp, Belgium. Oatmeal agar enriched with horse dung decoct was used for the production of apothecia. Since *Ascozonus*-species prove to be psychrophilic in their phase of fructification, the strain was cultured at 12 °C. Periods of 8 hours of light with an illumination intensity of about 5000 lux were alternated with periods of 16 hours of darkness. After 7 days apothecia with mature asci had developed. From the 5th day on small pieces of agar with ripening apothecia were fixed for purposes of light and electron microscopy.

Living isolated asci or bundles of gently squashed asci were observed in a drop of water or in a weakly hypotonic solution of glucose in distilled water. The slides were

examined with Zernike's phase-contrast and Zeiss Nomarski's interference-contrast optics. Within a few minutes the protoplasts of asci became disturbed and observations had to be continued with a new slide of freshly prepared asci.

For light microscopy asci were stained with a wide variety of dyes of which Congo red, acid fuchsin, trypan blue, methyl blue, and methylene blue gave satisfactory results.

Sections of material embedded in epoxy resin, cut with glass knives to a thickness of 0.5 μm, proved to be of great value for observations with the light microscope. This material was fixed in glutaraldehyde and osmium tetroxide, and subsequently embedded according to the methods described below for electron microscopy. Among the methods available for staining sections of this kind, those based upon the use of methylviolet, methylene blue, and toluidine blue proved to be useful. Especially 0.1–1.0% toluidine blue in an 1% aqueous solution of sodium tetraborate (borax) (Trump & *al.*, 1961) produced a clear differentiation of the components of the walls, displaying blue orthochromasia, violet β-metachromasia, and red or pink γ-metachromasia.

For electron microscopy, small blocks of agar with ripening apothecia on their upper surface were cut from the plates and excess agar was trimmed off.

One part of this material was fixed for 2 hours in about 5 ml of 1–1.5% $KMnO_4$ in distilled water, to which 1 drop of Invadine (Geigy) was added in order to reduce the surface tension of the fixing liquid. Another part of the material was fixed for 4 hours in 3–6.5% glutaraldehyde buffered at pH 7.2 with 0.2 M cacodylate at 4 °C. The latter material was post-fixed for 1 hour in 1% buffered OsO_4 at 4 °C. Fixed material was either dehydrated in an aceton series and embedded in Vestopal, or dehydrated in an ethanol series and embedded in Epon 812 (Luft, 1961).

During fixation and impregnation, the material was evacuated several times to draw all the air from the tissues. During dehydration the material was stained for 5 minutes in a solution of 1% uranyl acetate. Longitudinal median sections of asci in different stages were cut with glass knives on an LKB Ultrotome III, occasionally stained on the grids with various combinations of Reynolds' lead citrate, uranyl acetate, and barium permanganate.

As asci are relatively large objects, single-hole grids were used to collect the sections for electron microscopy.

A Philips EM 300 electron microscope was used for the electron micrographs.

Measurements taken from electron micrographs are indicated in nanometers.

Results

Observations with the light microscope

Very young asci are broadly clavate with a broad base and a rounded top. The wall is of uniform thickness. After meiosis the shape of the asci becomes more slender-

clavate with a flattened top. In *A. woolhopensis* usually 64 navicular ascospores are formed. During the ripening of the ascospores the top of the ascus becomes conical in shape, while its volume increases considerably. A short distance under the tip a light-refractive thickening in the shape of a ring is formed on the inner side of the ascus wall. At this time two layers can be distinguished in the lateral and the apical regions of the ascus wall: a thin rather rigid outer layer which stains red with Congo red and bluish violet with toluidine blue, and a thicker rather soft inner layer not tinted in Congo red and staining reddish violet with toluidine blue. The inner layer also shows affinity to methyl blue, trypan blue, and acid fuchsin.

The differentiation of the subapical ring is initiated shortly after meiosis in the ascus. The first indication of the ring is visible as a slight thickening of the wall of the truncate young asci, and is well observed in longitudinal, 0.5 μm thick sections. The

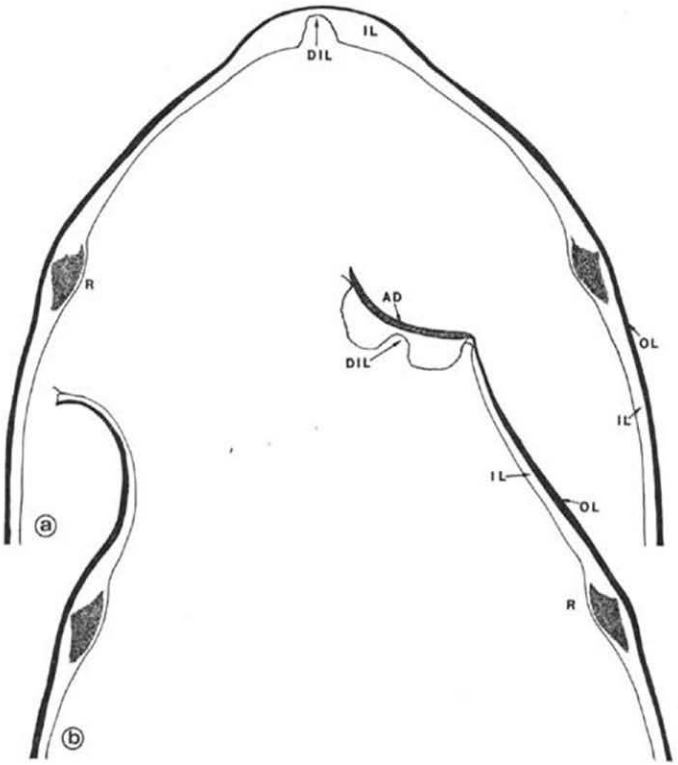

Fig. 1. *Ascozonus woolhopensis*, diagrammatic sections of ascus tops, as seen with light microscopy. — a. Almost mature ascus. — b. Ascus after spore discharge. — For abbreviations used see p. 31.

body of the young ring is about semicircular in section and stains differentially blue with toluidine blue (Pl. 15C, D).

During the formation of the ring changes take place in the top of the ascus, whereas the lateral ascus wall under the ring remains almost unchanged. In a mature ascus the ring has a thickness of 1.3–1.5 μm and reaches a diameter of 13–17 μm. The zone which stains blue with toluidine blue becomes more or less triangular in section and is free from the outer layer of the ascus wall.

In the conical top, the outer wall becomes increasingly thinner towards the tip, except for a small apical disk up to 0.3 μm thick and about 2–3 μm across. This disk is rather rigid and stains intensely in most of the stains used (Pl. 15A, B). The inner layer on the other hand thickens towards the tip, reaching a thickness of up to 1.8 μm. Shortly before ascospore discharge the central part of the inner layer breaks down locally just underneath the apical disk, thus seriously weakening the wall in the tip (Pl. 15E, F). Soon the outer layer ruptures just at the margin of the apical disk. From this slightly excentric spot extending down to the ring there appears a fissure splitting the ascus top into two halves. The mass of 64 ascospores are forcibly discharged through this tear in a single jet.

In a mature apothecium often collapsed empty asci can be found which clearly show the apical disk, sometimes even with the remnants of the inner wall layer adhering to it (Pl. 15A, G–K).

Investigations with phase-contrast and interference-contrast optics made it clear that the asci of *Ascozonus* are devoid of a 'tractus', an 'entonnoir', and a 'chambre oculaire' as described by Chadefaud (1942, 1960, 1973) for other genera.

No part of the wall stains with iodine-containing reagents.

Electron microscopy

Of the different methods of fixation and embedding used in this study, the $KMnO_4$-OsO_4-fixation followed by Epon-embedding proved to be most suited to produce images with sufficient contrast in the walls of asci. If not stated otherwise, the observations are based on such material.

The walls of the croziers and the young asci up to the moment meiosis begins are of rather uniform thickness (approximately 210 to 250 nm) and do not show a layered structure (Pl. 16A, C). After meiosis the lateral as well as the apical regions of the ascus wall become stratified by differentiation inside the wall. Then the ascus wall is composed of an inner, thick, electron-transparent layer and an outer, thin, electron-dense layer. In the lateral region of the ascus wall the inner layer reaches a thickness of approximately 440 to 540 nm and the outer layer 140 to 240 nm (Pl. 16B, D, Pl. 17B–D).

During differentiation of the ring, no structures in the ascoplasm can be observed that indicate an increased activity at this place. Adjacent to the inner side of the ascus wall the plasma membrane or the ascoplasmalemma is visible. Especially in the top of the ascus the shape of this membrane is often denticulate or irregular

(Pls. 17B, D, 18A, B). In the last phase of ripening of the ascospores the epiplasm disappears almost completely from the sporogenous part of the ascus. In well-fixed material the plasma membrane remains visible till ascospore discharge. Even in asci that have just released their spores, remnants of the plasma membrane are often found (Pls. 17A, 18C, D).

From its beginning the ring is manifest as an rather electron-transparent thickening on the inside of the ascus wall. During the maturation of the ascus, changes take place in its top. The ring reaches a thickness of 1000 to 1300 nm. On its innermost side a more electron-dense layer 50 to 70 nm thick can be distinguished. This layer cannot be followed in the ascus wall above and below the ring (Pl. 18A). In the ring an electron-transparent central part is found which is not very sharply delimited. The electron-dense outer layer of the ascus wall is seen to remain at some distance of the ring proper and can be followed right to the top as an undeflected zone. In the ring this layer measures about 130 nm, in the top it decreases to less than 80 nm. The electron-transparent inner wall layer measures 270 to 390 nm just above the ring and thickens towards the tip where it may reach a thickness of more than 1800 nm (Pls. 17B–D, 18A, B). In some preparations, with favourable staining, a weak stratification with 3 or 4 strata becomes visible in the thickest part. At maturity the central part of this layer breaks down locally, thus weakening the tip (Pl. 17B).

From the ring upwards in the outer half of the wall an electron-dense zone is seen underneath the outer layer. This middle layer is only found in the top of the ascus,

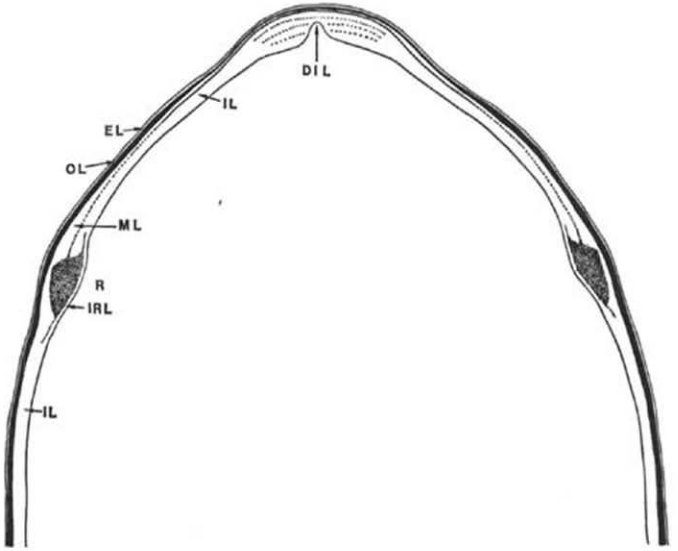

Fig. 2. *Ascozonus woolhopensis*, diagrammatic section of an almost mature ascus top, as seen with electron microscopy. — For abbreviations used see p. 31.

tapering from a thickness of 200 to 240 nm just above the ring to about 60 nm at the apex. The delimitation of the middle layer from the outer layer diminishes gradually (Pl. 17B–C).

In the central part of the extreme tip of the ascus, as part of the outer, and probably also middle, layer a disk-shaped zone, 2100 to 3030 nm across, appears. This apical disk is evident only in median sections of emptied asci as a 110 to 270 nm thick, electron-transparent structure. The fracture in the ascus top initiating the spore discharge usually arises exactly at the margin of this apical disk (Pls. 17A, 18C, D).

In sufficiently contrasted sections an electron-transparent layer with a thickness of 50 to 130 nm is frequently found completely surrounding the young and the ripening asci. This extra-ascan layer becomes evident by the staining of the surrounding hymenial mucus (Pls. 16A, D, 17B–D, 18A, B, D).

Discussion

Although no extensive cultural experiments have been carried out, our experience with cultures of *Ascozonus woolhopensis* and some other members of this genus clearly indicates that species of *Ascozonus* are psychrophilic in the phase of fructification. Fruit-bodies are produced abundantly at temperatures from 4° to 12 °C. At higher temperatures fructification is far less or absent. This may explain the fact that these fungi are only found in winter. The same phenomenon has been described by Wicklow & Malloch (1971) in the genus *Thelebolus* Tode (incl. *Rhyparobius* Boud.) and by Bergman & Shanor (1957) in *Streptotheca psychrophila* Bergm. apud Bergm. & Shanor, which is a representative of *Thelebolus* (cf. Kimbrough & Korf, 1967).

Comparison of the results of light and electron microscopy gives concordant data (Figs. 1 and 2). Using both methods, a layered lateral region of the ascus wall is observed which becomes more complex in the ring and the top. It is here that electron microscopy reveals more details. On the other hand, in young and mature asci the apical disk is only visible after staining with light microscopy.

The ring is not homogeneous and does not originate as a part of the outer layer of the ascus wall, as stated by Kimbrough (1970, 1972). It is differentiated within the ascus wall free from the outer layer, which can be followed through the region of the ring without interruption. The inner layer of the ascus wall is not continuous at the level of the ring. The structure of this layer is locally changed during the development of the ring.

Also the assumption of Vuillemin (1887) that the ring is a simple jellification of the ascus wall cannot be maintained.

The apical disk in the wall of the ascus has not been noticed by Kimbrough, but it is certainly identical with the very small operculum described by Vuillemin. At the moment of ascospore discharge, both in *Ascozonus woolhopensis* and in other species of this genus, the ascus wall is disrupted at the margin of the apical disk, immediately followed by bilabiate splitting of the wall in the ascus top. In no case a mechanism of

spore discharge was observed like described by Vuillemin for a 32-spored species of *Ascozonus*[1] in which the apical disk functions as a very small operculum, disclosing a narrow aperture through which the ascospores are projected one by one.

In the terminology of Chadefaud (1942, 1969, 1973) the inner layer of the ascus wall is called endoascus, the outer layer exoascus, while the thin extra-ascal layer surrounding the ascus is probably identical with his ectoascus. What Chadefaud calls "film interne de l'endoascus" is probably the same as the plasma membrane of the epiplasm.

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[1] Described as *Streptotheca boudieri* Vuill.

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EXPLANATION OF PLATES 15–18

ABBREVIATIONS USED IN PLATES AND TEXT-FIGURES. — AD, apical disk; AW, ascus wall; DIL, desintegration of inner layer of the ascus wall; E, epiplasm; EL, extra-ascan layer; ER, endoplasmatic reticulum; G, glycogen; IL, inner layer of the ascus wall; IRL, inner electron-dense layer of the ring; M, mitochondrion; ML, middle layer of the ascus top; N, nucleus; OL, outer layer of the ascus wall; P, paraphysis; PM, plasma membrane; R, ring; S, ascospore; SP, sporoplasma.

PLATE 15

Figs. A–K. *Ascozonus woolhopensis*, photomicrographs of asci (Figs. A, B. from squash-mounts; Figs. C–K. semi-thin median sections of asci fixed in glutaraldehyde and OsO_4 and embedded in Epon): Fig. A. empty ascus stained with Congo red; Fig. B. top of a mature ascus filled with spores, stained with Congo red; Fig. C. distal portion of ascus shortly before sporogenesis, stained with toluidine blue; Fig. D. id. stained with methyl violet; Figs. E, F. distal portion of almost mature asci, showing desintegration of the inner layer of the ascus wall in the tip, stained with methylene blue; Figs. G, J, K. apices of collapsed asci showing the apical disk, stained with toluidine blue; Fig. H. id. stained with methylene blue.

The scale markers in Plate 15 equal aproximately 10 μm.

PLATE 16

Figs. A–D. *Ascozonus woolhopensis*, electron micrographs of developing asci: Fig. A. median section of distal portion of a diploid ascus showing an undifferentiated ascus wall, fixed in 1.5% $KMnO_4$ and stained with uranyl acetate, lead citrate, and barium permanganate; Fig. B. longitudinal section of the distal portion of an ascus at an early multi-nucleate stage with initial development of the ring, fixed in 6.5% glutaraldehyde and 1% OsO_4 and stained with uranyl acetate; Fig. C. transverse section of the lateral wall of a diploid ascus, fixed in 1.5% $KMnO_4$ and stained with uranyl acetate; Fig. D. median section of the distal portion of an ascus shortly before ascospore-delimitation, showing incipient differentiation of ascus wall, fixed in 1.5% $KMnO_4$ and stained with uranyl acetate.

The scale marker equals approximately 1 μm.

PLATE 17

Figs. A–D. *Ascozonus woolhopensis*, electron micrographs of ripening and collapsed asci: Fig. A. median section through extreme apex of a collapsed ascus, showing 'lid' with apical disk, fixed in 1.5% $KMnO_4$ and stained with uranyl acetate, lead citrate and barium permanganate; Fig. B. median section of apical portion of an almost mature ascus, fixed in 1.5% $KMnO_4$ and stained with uranyl acetate; Fig. C. id. fixed in 1.5% $KMnO_4$, embedded in Vestopal, and stained with uranyl acetate and lead citrate; Fig. D. median section of apex of ripening ascus, fixed in 1.5% $KMnO_4$ and stained with uranyl acetate, lead citrate, and barium permanganate.

The scale marker equals approximately 1 μm.

PLATE 18

Figs. A–D. *Ascozonus woolhopensis*, electron micrographs of ripening and collapsed asci (all fixed in 1.5% $KMnO_4$, embedded in Epon, and stained with uranyl acetate, lead citrate, and barium permanganate): Fig. A. transverse section of ascus wall near the ring in a ripening ascus; Fig. B. median section of ascus wall in the extreme tip of a ripening ascus; Figs. C, D. median sections through extreme apices of collapsed asci.

The scale marker equals approximately 1 μm.

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CHECK LIST OF EUROPEAN HYMENOMYCETOUS HETEROBASIDIAE

Supplement and corrections

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This continuation of the "Check list of European hymenomycetous Heterobasidiae" (published in Persoonia **4**: 145–335. 1966) contains supplementary matter as well as corrections. — *Ypsilonidium* (Donk) Donk is published as a new genus. Two new specific combinations are made with this generic name. — *Muribasidiospora* Rajendren is at least tentatively reduced to *Exobasidium*. — Following Parmasto, *Exobasidiellum* Donk is removed from the Tulasnellales.

This supplement is composed along the same lines as the "Check list of European hymenomycetous Heterobasidiae" (Donk, *1966*); the reader is referred to the Chapter "Method of presentation" for details (*1966*: 147–150). I want to stipulate once more that I do not regard the Dacrymycetales and Exobasidiales as belonging to the true Heterobasidiae. These orders were included because they have often been placed among the Heterobasidiae. Moreover, the Exobasidiales in the present sense are doubtfully homogeneous.

Specific epithets of species treated before are not printed in bold face or (in case of synonyms), not spaced, as are the specific epithets of new entries.

The original 'Check list' is referred to as 'Ch. 1.'.

Supplement and corrections

Special literature.—Raitviir, *1967a* & *1969*, *1967c*, *1968*; Warcup & Talbot, *1967*.

AURICULARIINEAE

AURICULARIA Bull. per Mérat

Special literature.—Govi, *1968*; Lowy, *1951*.

mesenterica (Dicks. per S. F. Gray) Pers.

Auricularia tremelloides Bull. — *Thelephora* (Bull.) per St-Am. 1821; Laterr. 1821.

Merulius violaceus Thore apud Pers. 1825: 21 (France), not ~ Pers. 1797 (d.n.), not ~ Fr. 1818 (d.n.), not ~ (O. F. Müll. per Fr.) Secr. 1833; fide Fr. 1838: 555. — ≡ *Cantharellus thorei* Duby 1830: Fr. 1832 Ind.: 68, 118.

EOCRONARTIUM Atk.

SPECIAL LITERATURE.—Pilát, *1959*.

muscicola (Pers. per Fr.) Fitzp.
Clavaria falcatispora Velen. — Velen. 1947: *pl. 2 f. 20*.

HELICOBASIDIUM Pat.

SPECIAL LITERATURE.—Patouillard, *1886*.

brebissonii (Desm.) Donk. — McNabb 1966 (NZB 4): 533 *f. 1a, b*.
Helicobasidium purpureum Pat. — Pat. 1886 (BbF 33): 336 (var. *barlae* Pat.).
Hypochnus violaceus Erikss. — ≡ *Corticium eriksonii* Maubl. 1926: 144.

HIRNEOLA Fr.

1848 (nom. cons.), not ~ Fr. 1825 ('Stereaceae') (nom. rej.)
Laschia Fr. 1830: Fr. 1832 (nom. rej.), not ~ Jungh. 1838.

SPECIAL LITERATURE.—Møller, *1961*; Sappin-Trouffy, *1896*.

auricula-judae (Bull. per St-Am.) Berk. — Møll. 1961 (Fr. 6): 384 *f. 1, pl. 5* (*Auricularia*); D. Reid 1970 (TBS 55): 440 [var. *lactea* (Quél.) D. Reid].

PHLEOGENA Link

Martindalia Sacc. & Ell. apud Sacc. & Berl. 1885 (AIv VI 3): 726. — Monotype: *Martindalia spironema* Sacc. & Ell. apud Sacc. & Berl.

SPECIAL LITERATURE.—Barr & Bigelow, *1968*; Pilát, *1956*; Tallasch & Jahn, *1970*.

faginea (Fr. per Fr.) Link.
Martindalia spironema Sacc. & Ell. apud Sacc. & Berl. 1885 (AIv VI 3): 726 *pl. 11 f. 31* (U.S.A., New Jersey); fide Barr & Bigelow 1968 (M 60): 456–457.

TREMELLINEAE

SPECIAL LITERATURE.—Reid, *1970*.

APORPIUM Bond. & Sing. ex Sing.

SPECIAL LITERATURE.—Aoshima & *al.*, *1962*.

BASIDIODENDRON J. Rick

cinereum (Bres.) Luck. — McNabb 1966 (NZB 4): 540 *f. 10–r* (*Sebacina*); D. Reid 1970 (TBS 55): 433 *fs. 2d–f* (*Basidiodendron*).

BOURDOTIA (Bres.) Trott.

galzini (Bres.) Trott. — *Tremella* E. Krause 1933; *Elvelus* E. Krause 1934 (generic name n.v.p.).

EICHLERIELLA Bres.

Eichleriella Raitv. 1967: 64 / 1969: 50 ("Bres."; lacking Latin description), not ∽ Bres. 1903. — [≡ *Eichleriella* Bres. sensu Raitv. ll. cc., exclusive of type]. — Only species: *Eichleriella spinulosa* (B. & C. apud Berk.) Burt sensu Raitv. [= *E. deglubens* (B. & Br.) D. Reid].

deglubens (B. & Br.) D. Reid 1970. — D. Reid 1970 (TBS 55): 436, note
leucophaea Bres. — Malenç. 1968 (CbB 7): 710.

EXIDIA Fr.

Tremella S. F. Gray 1821: 593 ("Dillenius"), not ∽ L. 1753 (d.n.; 'Nostocaceae heterocysteae'), not ∽ Pers. per St-Am. 1821: Fr. 1822 (Tremellaceae). — Monotype: *Tremella recisa* Ditm. per S. F. Gray.

albida (Huds. per Hook.) Bref. (**142**). — *Elvelus* E. Krause 1934 (generic name n.v.p.). — D. Reid 1969 (RM 33): 353 *tpl. 8 f. 19?*
Tremella thuretiana Lév. — D. Reid 1970 (TBS 55): 418 *fs. 1f–h* (*Exidia*).

cinnamomescens Raitv. — *Myxarium* Raitv. 1967 (incomplete ref.: n.v.p.). — Raitv. 1967: 65 *f. 54* / 1969: 51 *f. 54* (*Myxarium*). — The basidia were too insufficiently described to be recognized with certainty as being myxaroid sphaeropedunculate [cf. Donk 1966 (Pe 4): 232].

compacta Lowy 1956 (Louisiana, U.S.A.). — Lowy 1956 (Ll 18): 164 *tpl. 4 fs. 1, 2, tpl. 5*; Raitv. 1967: 67 / 1969: 53, recorded from U.S.S.R., Armenia.

glandulosa (Bull. per St-Am.) Fr. — *Tremella* Bull. per St-Am. 1821; Laterr. 1821.
Tremella papillata Kunze. — *Elvelus* E. Krause 1934 (generic name n.v.p.).
Exidia truncata Fr. — *Elvelus* E. Krause 1934 (generic name n.v.p.).

pithya (A. & S.) per Fr. — *Tremella* E. Krause 1932 ("*pitya*"); *Elvelus* E. Krause 1934 ("*pitya*") (generic name n.v.p.).

plana (Wigg. per Schleich.) Donk
Exidia plicata Kl. — *Elvelus* E. Krause 1934 (generic name n.v.p.).

recisa (Ditm. per S. F. Gray) Fr. — *Elvelus* E. Krause 1934 (generic name n.v.p.). — Nannf. & Du R. 1952: *textplate f. 175.*
Tremella sagarum Retz. — *Elvelus* E. Krause 1934 (generic name n.v.p.).

repanda Fr. — *Elvelus* E. Krause 1934 (generic name n.v.p.).

saccharina (A. & S.) per Fr. — *Elvelus* E. Krause 1934 (generic name n.v.p.).

HETEROCHAETE Pat. apud Pat. & Lag.

Hirneolina (Pat.) Bres. apud Sacc. & D. Sacc. 1905; fide Wells 1969 (M 61): 80 = *Heterochaete* emend. Bodm. 1952.

HETEROCHAETELLA (Bourd.) Bourd. & G.

brachyspora Luck. — D. Reid 1970 (TBS 55): 439 *fs. 5d–e.*

dubia (Bourd. & G.) Bourd. & G. — D. Reid 1970 (TBS 55): 437 *fs. 5a–c* ("*Heterochaete*" [= *Heterochaetella*]).

MYXARIUM Wallr.

hyalinum (Pers.) Donk (**143**).

Myxarium nucleatum Wallr. — D. Reid 1970 (TBS 55): 421 *fs. 1a, b.*

M.—*Tremella nucleata* Schw. sensu Berk. — McNabb 1966 (NZB 4): 535 *fs. 1c–e*, spores 10–13.5 (—17.5) × 4–5.8 μ.

laccatum (Bourd. & G.) D. Reid 1970 [transferred from *Sebacina*, Ch. 1. p. 177]. — D. Reid 1970 (TBS 55): 428 *fs. 3e, f.*

Sebacina mesomorpha Bourd. & G. — *Tremella* E. Krause 1932; *Elvelus* E. Krause 1934 (generic name n.v.p.). — [See further under *Sebacina laccata*, Ch. 1. p. 177].

subhyalinum (A. Pears.) D. Reid 1970. — *Sebacina* A. Pears. 1928 (England). — A. Pears. 1928 (TBS 13): 70, 71 *f. 3* (*Sebacina*); D. Reid 1970 (TBS 55): 426 *fs. 4f–i* (*Myxarium*).

Sebacina sublilacina G. W. Mart. (U.S.A., Iowa); fide D. Reid 1970 (TBS 55): 426. — *Myxarium* Raitv. 1967: 66 / 1969: 52 (incomplete ref.: n.v.p.) — [See further under *Sebacina*, Ch. 1., p. 178].

M.—*Sebacina fugacissima* Bourd. & G. sensu G. W. Mart. — [See further under *Sebacina subhyalina*, Ch. 1., p. 178].

PROTODONTIA Höhn.

SPECIAL LITERATURE.—Pilát, *1958.*

piceicola (Kühner ex Bourd.) G. W. Mart. — Nannf. & Du R. 1952: *text-plate f. 173* (*Protohydnum*).

PSEUDOHYDNUM P. Karst.

1868, not ∽ J. Rick 1904.

SEBACINA Tul.

calcea (Pers. per St-Am.) Bres. — *Thelephora* Pers. per St-Am. 1821; Laterr. 1821; *Stereum* E. Krause 1928.

Sebacina letendreana Pat. — *Sebacina* Pat.; Cost. & Duf. 1891: 207 ("*Letendrea*"); *Tremella* E. Krause 1930 ("*Letendrea*"), misapplied; 1932; *Elvelus* E. Krause 1934

(generic name n.v.p.). — Sensu E. Krause → *Tremella epigala* E. Krause, see "List of omitted names".

calospora (Bourd. & G.) Bourd. & G. — D. Reid 1970 (TBS 55): 432 *fs. 1c–e.*

crozalsii Bourd. & G. — Malenç. 1968 (CbB 7): 707, note.

effusa (Bref. ex Sacc.) Pat. — D. Reid 1970 (TBS 55): 429 *fs. 3a–d* (*Exidiopsis*).

Sebacina quercina (Vuill.) ex Maire. — *Tremella* E. Krause 1930, not ~ Pollini per Pollini 1824; *Elvelus* E. Krause 1934 (generic name n.v.p.).

epigaea (B. & Br.) Neuh. — McNabb 1966 (NZB 4): 538.

Exidiopsis glaira (Lloyd) Wells.

Sebacina opalea Bourd. & G. — D. Reid 1970 (TBS 55): 431 *fs. 2g–l* (*Exidiopsis*).

incrustans (Pers. per Fr.) Tul.

Thelephora sebacea Pers. — *Sebacina* Maire apud Maire & Pol. 1940.

laccata Bourd. & G. — Transfer to *Myxarium q.v.*

letendrea, see *Sebacina letendreana* under *S. calcea.*

molybdea McGuire. — D. Reid 1970 (TBS 55): 431, in obs. & as syn. of *Exidiopsis opalea* → [*Sebacina*] *Exidiopsis glaira* [Ch. 1., p. 175].

mucedinea Pat. apud Pat. & Lag. 1895 (Ecuador). — *Thelephora* Sacc. 1899; *Sebacina* Pat. 1900 ("*mucedina*"); *Exidiopsis* Wells 1957. — G. W. Mart. 1944 (Ll 7): 68 *f. 4*; (*Sebacina*); Wells 1957 (Ll 20): 46 *f. 1* (*Exidiopsis*); L. Olive 1958 (BTC 85): 23 (*Sebacina*); Wells 1960 (M 51): 560; 1961 (M 53): 346 (*Exidiopsis*); McNabb 1966 (NZB 4): 541 *fs. 2a–d* (*Sebacina*); reported from Armenia and Azerbaydjan by Raitv. 1967: 52 / 1969: 40 (*Exidiopsis*).

podlachica Bres. — *Myxarium* Raitv. 1967: 66 / 1969: 52 (incomplete ref.: n.v.p.). — D. Reid 1970 (TBS 55): 426, in obs.

Sebacina subhyalina A. Pears. — Transfer to *Myxarium q.v.* as a distinct species.

sublilacina G. W. Mart. — Transfer to *Myxarium q.v.* as a syn. of *M. subhyalinum.*

vermifera Oberw. — Warc. & Talb. 1967 (NPh 66): 638 *f. 7*, no clamps (same species ?).

SIROBASIDIUM Lag. & Pat.

SPECIAL LITERATURE.—Ramakrishnan & Subramanian, *1951.*

TREMELLA Pers. per St-Am.

SPECIAL LITERATURE.—Bandoni, *1965*; Jahn, *1969*; Pilát, *1928*; Slodki, *1966*; Slodki & *al.*, *1966*; Torkelsen, *1968.*

Elvelus E. Krause 1934 M.B.: 109 (nom. nud.: n.v.p.) (**144**). — Lectotype: *Helvella mesenterica* Schaeff.

aurantia Schw. 1822: Fr. 1822 (U.S.A., North Carolina). — *Dacrymyces* Farl. 1883, misapplied; *Guepiniopsis* Pat. 1893, misapplied; *Dacryopsis* Lloyd 1920 (error for *Dacrymyces*: n.v.p.), excl. of type; *Naematelia* Burt 1921, misapplied. — Sensu Bandoni 1961 (AMN 66): 326 *f. 4*; ? Raitv. 1967: 74 / 1969: 57, record for

Armenia, descr. poor. — Sensu Fr. 1828 (nomen) & Weinm. 1836 = *Tremella elegans* (nom. dub.) [Ch. 1., p. 312], fide Fr. 1874: 691; sensu Farl. → *Dacrymyces palmatus*; sensu Lloyd 1908 (LMW 3, O.S.): 11 *f. 225* (*Tremella*) = *Tremella tremelloides* (Berk.) Mass. (extra-European).

encephala Pers. per Pers. — *Elvelus* E. Krause 1934 (generic name n.v.p.). — Tork. 1968 (NyM 15): 228 *fs. 1h, 3, 4, 6.*

exigua Desm.

Tremella genistae Lib. ex Roum. — *Elvelus* E. Krause 1934 (generic name n.v.p.).

foliacea (Pers. per S. F. Gray) Pers. — Tork. 1968 (NyM 15): 232 *fs. 1i, 8, 10.*

Tremella undulata Hoffm. — *Tremella* Hoffm. per Pollini 1824, Zant. 1824.

frondosa Fr. — *Elvelus* E. Krause 1934 (generic name n.v.p.).

globospora D. Reid 1970 (England). — D. Reid 1970 (TBS 55): 414 *fs. 4j, k.*

? *Sebacina globospora* Whelden, 1935 (Rh 37): 126 *pl. 331* (U.S.A., Kentucky); fide G. W. Mart. 1944 (SIa 183): 54 = *Tremella tubercularia* [sensu Bourd. & L. Maire], but cf. Donk 1966 (Pe 4): 254 and D. Reid 1970 (TBS 55): 415.

M.—*Tremella tubercularia* Berk. sensu Bourd. & L. Maire 1920. — [See further under this name in Ch. 1., p. 183].

indecorata Sommerf. — Elvelus E. Krause 1934 (generic name n.v.p.). — Tork. 1968 (NyB 15): 229 *fs. 1g, 5, 7.*

mycophaga G. W. Mart. — Tork. 1968 (NyM 15): 226 *f. 1a.*

obscura (L. Olive) M. P. Christ. — Tork. 1968 (NyM 15): 232 *f. 1j.*

polyporina D. Reid 1970 (England). — D. Reid 1970 (TBS 55): 416 *fs. 1i–k.*

simplex Jack. & Mart. apud G. W. Mart. — Tork. 1968 (NyM 15): 226 *fs. 1b, c, 2.*

tuberculata Berk. — Transfer to "List of omitted species" *q.v.* — Sensu Bourd. & L. Maire → *Tremella globospora.*

virescens (Schum. per Fr.) Bref. — *Elvelus* E. Krause 1934 (generic name n.v.p.).

Incertae sedis: 'Microtremella'

fusispora Bourd. & G. — *Sebacina* Raitv. 1967 (incomplete ref.: n.v.p.); 1968, misapplied ? — Identification doubtful: Raitv. 1967: 60 f. 49 / 1969: 46 *f. 49*; 1968 (TÜT 211): 96 *f. 2* (*Sebacina*).

TREMELLODENDROPSIS (Corner) D. A. Crawf.

SPECIAL LITERATURE.—Corner, *1966.*

TREMISCUS (Pers.) Lév.

SPECIAL LITERATURE.—Noguti, *1934*; Pilát, *1930.*

helvelloides (DC. per Pers.) Donk. — *Tremella* DC. per Pers. 1822, not ~ (Schw.) Lloyd 1919 (n.v.p.).

Tremella rufa Jacq. per Pers. — Noguti 1934 (JJB 10): 120 *fs. 1–3* (*Gyrocephalus*).

M.—*Craterellus cochleatus* Fr. sensu Strauss 1853 (StP Hfte 33–34): 7 *pl. 4* (**146**).

TULASNELLACEAE

SPECIAL LITERATURE.—Warcup & Talbot, *1967*.

CERATOBASIDIUM D. P. Rog. (**147**)

SPECIAL LITERATURE.—Castellani, *1936*; Hussain & McKeen, *1963*; Parmeter, Whitney, & Platt, *1967*.

Ceratobasidium **sp.** — Parmeter *& al.* 1967 (Ph 57): 220 *fs. 3, 5 at bottom, 6 at bottom* (**147**).

Rhizoctonia fraxini E. Cast. [Ch. 1., p. 189]; fide Parmeter *& al.* 1967 (Ph 57): 221, "mycelium binucleate and resembles *Ceratobasidium* sp".

Rhizoctonia pini-insignis E. Cast. [Ch. 1., p. 189]; fide Parmeter *& al.* 1967 (Ph 57): 221, "mycelium binucleate and resembles *Ceratobasidium* sp".

Rhizoctonia callae E. Cast. [Ch. 1. p. 189]; fide Parmeter *& al.* 1967 (Ph 57): 221, "mycelium binucleate and resembles *Ceratobasidium* sp".

Rhizoctonia munerati E. Cast. 1936 (NGi II 43): 563 *f. 1, pl. 7* (Italy) (lacking Latin descr.: n.v.p.) (nom. anam.); fide Parmeter *& al.* 1967 (Ph 57): 221, "mycelium binucleate and resembles *Ceratobasidium* sp".

Rhizoctonia endophytica Saks. & Vaar. 1960 (CJB 38): 936 *fs. 1–3, 16, 17* (Canada, Saskatchewan) (nom. anam.); fide Parmeter *& al.* 1967 (Ph 57): 222, "mycelium binucleate and resembles *Ceratobasidium* sp".

Rhizoctonia fragariae Hussain & McKeen 1963 (Ph 53): 533 *fs. 1–6* (Canada, Ontario) (nom. anam.); fide Parmeter *& al.* 1967 (Ph 57): 221, "mycelium binucleate and resembles *Ceratobasidium* sp".

Ceratobasidium **sp.** (Scotland). — Warc. & Talb. 1967 (NPh 66): 635 *f. 3*.

EXOBASIDIELLUM Donk

Transfer to Exobasidiales.

OLIVEONIA Donk

atrata (Bres.) Talbot.

? *Hypochnus subviolaceus* Peck 1894 (RNS 47): 151 (Canada); cf. M. Lars. 1966 (M 58): 603. — M. Lars. 1966 (M 58): 601 *f. 2* (*Hypochnus*).

THANATEPHORUS Donk (**148**)

SPECIAL LITERATURE. — Bracker & Butler, *1963*, *1964*; Dodman *& al.*, *1968*; Flentje, Dodman, & Kerr, *1963*; Flentje, Stretton, & McKenzie, *1967*; Hauerslev *1969*; Nakai *& al.*, *1968*; Parmeter, Sherwood, & Platt, *1969*; Parmeter, Whitney & Platt, *1967*; Shatla & Sinclair, *1966*; Tu *& al.*, *1969*; Whitney & Parmeter, *1963*

cucumeris (Frank) Donk. — Warc. & Talb. 1967 (NPh 66): 632, notes (*Thanatephorus*); Parmeter & *al.* 1967 (Ph 57): 220 *fs. 1, 2; & 5 at top, 6 at top* (basidia), cult. char.; Hauersl. *1969* (*Thanatephorus*).

orchidicola Warc. & Talb. 1966 (England). — Warc. & Talb. 1966 (TBS 49): 432 *f. 2*; 1967 (NPh 66): 633.

praticola (Kotila) Talbot; fide Talbot apud Parmeter & *al.* 1967 (Ph 57): 219 = *Thanatephorus cucumeris*.

sterigmaticus (Bourd.) Talbot. — Transfer to *Ypsilonidium q.v.*

Nomina anamorphosium

Rhizoctonia callae E. Cast. — Transfer to *Ceratobasidium* sp. Parmeter & *al.*

Rhizoctonia fraxini E. Cast. — Transfer to *Ceratobasidium* sp. Parmeter & *al.*

Rhizoctonia pini-insignis E. Cast. — Transfer to *Ceratobasidium* sp. Parmeter & *al.*

Rhizoctonia repens N. Bern. (**148**).

TULASNELLA J. Schroet.

allantospora Wak. & Pears. — Warc. & Talb. 1971 (NPh 70): 36 *f. 1*.

calospora (Boud.) Juel. — Warc. & Talb. 1967 (NPh 66): 635 *f. 4* (**148**).

violea (Quél.) Bourd. & G. — Warc. & Talb. 1971 (NPh 70): 37 *f. 2*, spores too small ?, 4.5–6.5 × 4–5.5 µm.

YPSILONIDIUM (Donk) Donk (**149**)

sterigmaticum (Bourd.) Donk. — Donk 1972 (PNA 75): 371 (**149**). — Warc. & Talb. 1967 (NPh 66): 633 *f. 1* (*Thanatephorus*). — Transferred from *Thanatephorus*, Ch. 1., p. 188.

langlei-regis (D. Reid) Donk. — Donk 1972 (PNA 75): 371 (**149**). — *Thanatephorus* D. Reid 1969. — D. Reid 1969 (TBS 52): 22 *fs. 3a, b* (*Thanatephorus*).

DACRYMYCETALES

SPECIAL LITERATURE.—Donk, 1964 (correction).

CALOCERA (Fr.) Fr.

furcata (Fr.) Fr. — D. Reid 1969 (RM 33): 346 *tpl. 8 fs. 18a–c*.

viscosa (Pers. per Fr.) Fr. — *Corallium* Hahn 1883.

DACRYMYCES Nees per Fr.

chrysocomus (Bull. per St-Am.) L. Tul. — Malenç. 1968 (CbB 7): 711 *f. 3*.

enatus (B. & C. apud Berk.) Mass.

Dacrymyces deliquescens var. *castaneus* Bourd. & G. (France). — Malenç. 1968 (CbB 7): 712.

estonicus Raitv. — D. Reid 1969 (RM 33): 350 *tpl. 7 fs. 22a–c.*

Ditiola nuda B. & Br. — Cf. McNabb 1966 (NZJ 4): 554.

Ditiola fagi Oud. — Cf. McNabb 1966 (NZB 4): 553.

Ditiola ulicis Plowr. — Cf. McNabb 1966 (NZB 4): 554.

tortus (Willd.) per Fr.

Dacrymyces punctiformis Neuh. — Nannf. & Du R. 1952: 226 *textplate f. 174.*

DITIOLA Fr.

SPECIAL LITERATURE.—McNabb, *1966.*

radicata (A. & S.) per Fr. — McNabb 1966 (NZB 4): 548 (**150**).

GUEPINIOPSIS Pat.

1883. — Published again as "Gen. nov." by Pat. 1885 (JMi 9): 120 with "Ex. *Guepiniopsis tortus* (Willd.), sp. nov. (*Guepinia*, de By)".

buccina (Pers. per Pers.) L. Kenn. — Delete '*Guepinia* Sacc. 1873' as a recombination under this name. Add as a synonym:

Guepinia b u c c i n a Sacc. 1873 (Italy). — Sacc. 1873 (ASv 2): 108 *pl. 8 fs. 1–6.*

EXOBASIDIALES

Muribasidiosporaceae Kamat & Rajendren apud Rajendren 1970 (M 61): 1159.
Dicellomycetaceae Parmasto 1968 (EAT 17): 226.

SPECIAL LITERATURE.—Norberg, *1968*; Parmasto, *1968*; Raitviir, *1967*; Rajendren, *1968, 1970a, 1970b.*

DICELLOMYCES L. Olive

1945 [1956 (Re 4): 115]. — Holotype: *Dicellomyces gloeosporus* L. Olive.

SPECIAL LITERATURE.—Olive, *1945*; Parmasto, *1968.*

scirpi Raitv. apud Parm. 1968 (Estonia). — Parm. 1968 (EAT 17): 223 *f. 1.*

EXOBASIDIELLUM Donk

culmigenum Webster & Reid apud D. Reid 1969. — D. Reid 1969 (TBS 52): 20 *f. 2.*
graminicola (Bres.) Donk [Ch. 1., p. 186]. — Parm. 1968 (EAT 17): 224 *f. 2.*

EXOBASIDIUM Woronin

≡ *Exobasidiotus* E. Krause 1934 M.B.: 109.
Muribasidiospora Kamat & Rajendren apud Rajendren 1968 (Myp 36): 219. — Holotype: *Muribasidiospora indica* Kamat & Rajendren apud Rajendren (**151**).

SPECIAL LITERATURE.—Norberg, *1968*; Pilát, *1936* (n.v.); Raitviir, *1967b.*

On Ericaceae

arctostaphyli Harkn. 1884 (BCA 1): 30 (U.S.A., California). — Linder 1947: 272, in obs., *f. 5f–h* (*Exobasidium*); Savile 1959 (CJB 37): 649 *f. 2* (*E. vaccinii* var.). — This European record is based on Liro, Mycoth. fennica No. 624.

discoideum J. B. Ell. — Siemaszko 1915 (MMR 1[3]): 30 *f. 10*, no descr.

rhododendri (Fuck.) Cramer apud Geyler.

Exobasidium rhododendri Quél. — Pat. 1886 (BbF 33): 336 ("Doass." in litt.).

vaccinii (Fuck.) Woronin. — *Exobasidiotus* E. Krause 1934.

On other families

citri Siemaszko. — Transfer to "List of omitted names", *q.v.*

Notes

TREMELLINEAE

Exidia

(**142**). Reid [1970 (TBS 55): 420] rejected the name *Exidia albida* [Ch. 1., pp. 166, 223] in favour of *E. thuretiana* mainly because Hudson's original description was thought to be insufficient for certain recognition or even based on something different. This exchange of names would upset the use of the often accepted name *E. albida*, although the name *E. thuretiana* is also in use. After a renewed study of Hudson's description I am now inclined to agree with Reid that it is far from certain that Hudson described *E. thuretiana*, although I am not yet completely convinced. Moreover, *E. albida* has been applied in different senses and *E. thuretiana* has not. The use of *E. thuretiana* appears preferable.

Myxarium

(**143**). Reid [1970 (TBS 55): 423] believed that Donk [Ch. 1., pp. 171, 234] "has upset the nomenclature by resurrecting an old epithet of Persoon which is tied to an inadequate diagnosis". This in connection with my use of the name *Myxarium hyalinum* instead of *M. nucleatum* Wallr. I gave my reasons for so doing. First, I followed the interpretation accepted by Bourdot & Galzin and Neuhoff; secondly, the same description scorned by Reid was considered to be just sufficient. I see no reason to change my mind. The fact that Wallroth mentioned the nuclei is of course undeniable, but the species often does not form them, and this seems to have been the case with Persoon's fungus.

Tremella

(**144**). Krause (1934 M.B.: 109) published "*Elvelus*" as a nomen nudum. He gave no reference or description and merely added "Tremelleae aut"., and invalid refer-

ence to an unspecified group above the rank of a genus. He included not only *Tremella* but all Tremellineae. In order to be able to place the name in synonymy *Helvella mesenterica* Schaeff. is herewith selected as 'type'. The genus is not to be identified with *Elvela* L. (1753: 1180, devalidated name) per St-Am. (1821: 537, "*Helvella*"), the well-known genus of Pezizales (Ascomycetes).

(**145**). The record of *Tremella aurantia* from Armenia by Raitviir requires some scepticism. His description is brief and does not mention a whitish and firm core at the inside of the fruitbody. Such a core is characteristic of species formerly referred to the genus *Naematelia*, which appeared to be based on a species of *Tremella* parasitizing a species of *Stereum*. Raitviir does mention this connection in a somewhat tentative manner: 'together with *Stereum hirsutum* Fr. and probably parasitizing it' (translated). Confusion with *T. mesenterica* seems not altogether impossible.

Specific delimitations between these parasitizing tremellas are apparently not too well settled. For this reason it was tentatively suggested [cf. Ch. 1., p. 244] to restrict *T. encephala* to material growing on coniferous wood and consistently parasitizing *Stereum sanguinolentum*. Raitviir recorded *T. aurantia* from wood of deciduous trees and as growing together with *Stereum hirsutum*. Apart from certain collections on hardwoods (deciduous trees) that were tentatively referred to *T. encephala* by American authors (for instance, *Naematelia cerebriformis* J. B. Ell. apud Peck on *Carpinus*, by Bandoni [1961 (AMN 66): 323]) North American collections on hardwood have been often referred to *Naematelia quercina* Coker = *Tremella tremelloides* (Berk.) Mass. = *Tremella aurantia* Schw. "in the sense of various authors" (inclusive of Lloyd). According to Bandoni [1966 (AMN 66): 325–326] the true *T. aurantia* is different from *T. tremelloides*.

Tremiscus

(**146**). The identity of what Fries (1838: 534) described as *Craterellus cochleatus* is unknown (cf. also Corner 1966: 92). The plate published by Strauss was commented upon by Fries (1863 M. 2: 341) thus: "Icon eximia, at color magis, quam in meo, roseus". I have little doubt that Strauss depicted *Tremiscus helvelloides*, but I still find it difficult to recognize this fungus from Fries's original description.

TULASNELLACEAE

Ceratobasidium

(**147**). The number of species of *Ceratobasidium* is rapidly increasing in connection with strains isolated from orchids and the study of previously described *Rhizoctonia* isolates. These rhizoctonias fall apart into two groups, one with hyphal cells with only a single dikaryon (*Ceratobasidium*) and one with coenocytic cells apparently containing several dikaryons (*Thanatephorus*). Parmeter & *al.* (1967) con-

centrated all strains of *Ceratobasidium* into a single species, their "*Ceratobasidium* sp". which may not be homogeneous. Warcup & Talbot (1967, 1971) obtained no less than five species from orchids of which *C. cornigerum* and C. sp. were represented by isolates from Scotland.

Thanatephorus

(**148**). *Rhizoctonia repens* has been repeatedly isolated from orchids. Warcup & Talbot [1967 (NPh 66): 636, 640] referred some of the more recent isolates placed under this name to *Tulasnella calospora*. They also remarked that the moniliform blastospores of their interpretation of *Sebacina vermifera* Oberw. are similar in form and size to those of *Rhizoctonia repens*.

Ypsilonidium

(**149**). *Ypsilonidium* Donk 1972 (PNA 75): 371.

Ypsilonidium sterigmaticum (Bourd.) Donk was placed by Donk [1958 (Fu 28): 21] in *Uthatobasidium* but with some hesitation which will explain why he placed it in a special section of that genus and did not make a new combination. Talbot [1965 (Pe 3): 390] transferred it to *Thanatephorus*. I am not sure that this is a better disposition. It is as yet not known whether the hyphal cells are coenocytic as they are in the typical species of *Thanatephorus*, or dikaryotic as in the species of *Ceratobasidium* investigated in this respect. *Thanatephorus* comprizes species that may act as typical parasites and regularly form *Rhizoctonia* stages. *Ypsilonidium sterigmaticus* is saprobic and lacks a *Rhizoctonia* state.

Another fungus has been described with similar basidia and sterigmata, also lacking a *Rhizoctonia* state, and doubtfully an active parasite. This second species, *Ypsilonidium langlei-regis* (D. Reid) Donk differs in its closed, palisadic hymenium which reminded me of *Corticium terrigenum*. However, Talbot [1965 (Pe 4): 401 *f. 19*] found that its spores were not repetitive; they also become septate and the basidia are 3–4-spored with relatively much less strongly developed sterigmata. Both Reid and Talbot (*apud* Reid) believed the species closely related to *Corticium sterigmaticum*. I now agree with them that this is the more likely relationship of *Ypsilonidium langlei-regis* and that the structure of the fruitbody is merely of a more strongly developed and condensed structure than in *Corticium sterigmaticum*. The two species seem worthy of generic separation from both *Uthatobasidium* and *Thanatephorus*. However, further investigation is much desired.

DACRYMYCETALES

Ditiola

(**150**). McNabb [1966 (NZJ 4): 550] included *Coryne gyrocephala* B. & C. and its synonyms as a distinct variety in *Ditiola radicata*. All his records of the latter are

from Europe while those of the former are from North America. For the time being I treat the two taxa here as if they were distinct species. For *Coryne gyrocephala*, see "List of omitted names".

EXOBASIDIALES

Exobasidium

(**151**). The genus *Muribasidiospora* (Rajendren, *1968*) was primarily based on an Indian species, *M. indica* Kamat & Rajendren *apud* Rajendren, growing on *Rhus mysorensis* (Anacardiaceae). It produces basidiospores that become muriformly septate; the basidia protrude in fascicles through stomata of the host. Two other species that had been referred to *Exobasidium* and produce muriformly septate spores were also included in the new genus. One of these species is *E. hesperidum* Maire on *Rhus oxyacantha* (Anacardiaceae) described from Morocco. Like *M. indica* it forms tufts of basidia protruding from stomata; the fascicles finally destruct the epidermis and become confluent into patches. The other species is *E. celtidis* T. & K. Ramakr. which grows in India on *Celtis tetrandra* (Ulmaceae); it forms hymenia at the underside of leaves. Both these species were included in *Muribasidiospora* but this assumption of relationship appears ill-founded as far as *E. celtidis* is concerned.

Later Rajendren (*1970a*) published a special family (Muribasidiosporaceae) for his genus after he had obtained the fungus in culture (*1970b*) and found its growth radically different from the usual yeast colonies developing in cultures of other species of *Exobasidium* (such as parasitize Ericaceae). I am convinced that the mycelial state described by him must be a contamination; there is little doubt that it belongs to that ubiquistous 'black mould' and imperfect fungus *Aureobasidium pullulans* (Bary) Arnaud. On my request Dr. J. A. von Arx kindly wrote me that in his opinion the figures indicate in every respect this fungus. There is no reason to assume that Rajendren established the true connection between this imperfect fungus and a basidiferous state.

Rajendren (*1968*: 221) also thought that after the exclusion of the muriformly spored species *Exobasidium* became a genus with transversally septate spores and inciting hypertrophy in their hosts. He is wrong on both counts because even if confining the genus to species on Ericaceae some of them are not known to form septa and several do not cause hypertrophy. As long as *Exobasidium* is maintained in a wide sense including also species growing on hosts belonging to various other families than Ericaceae, I cannot find sufficient arguments not to reduce *Muribasidiospora* to *Exobasidium*. That *Muribasidiospora* should not cause galls is certainly not true for *E. hesperidum*, of which Maire [1917 (BfA 1),: 183] wrote, "Il y a donc là de véritables cécidies".

List of omitted names

albida, *Tuberculariа*, Berk.; ≡ *Tremella tuberculariа* Berk. [Ch. 1., p. 183]; ≡ *Endostilbum albidum* (Berk.) D. Reid 1970 (TBS 55): 413, an imperfect state, and the correct name for *E. cerasi* (Bourd. & G.) Malenç. [Ch. 1., p. 308]. — Sensu Bourd. & L. Maire → *Tremella globospora* D. Reid.

aurantiaca, *Dacrymycetella*, D. Reid 1969 (RM 33): 347 *tpl. 8 fs. 21a–c* (France, Corsica). — An imperfect fungus considered by the author to be a state of some species of *Dacrymyces*.

brunnea, *Dacryomitra*, G. W. Mart. 1934 (M 26): 263 *pl. 31 fs. 11–14* (Canada, Ontario). — L. Kenn. 1964 (M 56): 302 and McNabb 1966 (NZB 4): 550, 551 referred this to *Ditiola radicata* var. *gyrocephala* (= *Coryne* [*Ditiola*] *gyrocephala*, see this list), cf. also (**150**).

caesia, *Sebacina*, (Pers.) Tul. [Ch. 1., p. 307]; *Tremella* E. Krause 1930, misapplied; *Elvelus* E. Krause 1934 (generic name n.v.p.), misapplied.

camelliae, *Exobasidium*, Shirai [Ch. 1., p. 307]. — D. Reid 1969 (TBS 52): 19 *f. 1a–d*, *pl. 3 f. 2*.

candidus, *Tremellodon*, (Schmidt per Fr.) Quél. 1888; *Hydnum* Schmidt 1817 (MH 1): 89 (Germany) (d.n.) per Fr. 1821, not ~ Willd. 1788 (d.n.); *Sarcodon* Quél. 1886; *Malacodon* Bataille 1924. — Nomen dubium.

cerasi, *Sirobasidium*, Bourd. & G. [Ch. 1., p. 308] = *Endostilbum albidum*, see this list.

citri, *Exobasidium*, Siemaszko 1915 (MMR 1[3]): 30 *fs. 5–9* (U.S.S.R., Caucasia). — I saw the original publication and recognized *Aureobasidium pullulans* (Bary) Arnaud from it. This determination was confirmed by Dr. J. A. von Arx, Baarn.

clavariaeformis, *Tremella*, Wulf. 1788 [Ch. 1., p. 309]; *Tremella* Arth. 1901.

culmigena, *Dacryopsis*, (Mont. & Fr. apud Mont.) Höhn. 1909; *Pistillaria* Mont. & Fr. apud Mont. 1836 (ASn II 5): 337 *pl. 12 f. 1* (France); *Clavaria* P. Karst. 1881; *Typhula* J. Schroet. 1888; *Dacryopsella* Höhn. 1915. — A species of Clavariaceae, cf. Donk 1933: 96; Corner 1950: 479.

Epidochiopsis P. Karst. [Ch. 1.,'p. 313]; 1892 (BFi 51): 499 ("n. sl.").

epigala, *Tremella*, E. Krause 1932 B.r.: 146 (Germany); *Elvelus* E. Krause 1934 (generic name n.v.p.); [≡ *Tremella letendreana* (Pat.) E. Krause sensu E. Krause 1930 B.r.: 104 ("Letendrea")]. — Nomen dubium. — The specific epithet has no connection with that of *Sebacina* '*epigaea*'.

esculenta, *Tremella*, Rox. Clem. 1864: 63 (Spain). — Nomen nudum.

fuciformis, *Tremella*, Berk. [Ch. 1., p. 315]. — McNabb 1966 (NZB 4): 536 *f. 1f, g*, New Zealand. — Special literature: Pilát, *1928*.

gyrocephala, *Coryne*, B. & C. 1849 (HJB 1): 239, Berk. 1873 (G 2): 20 (U.S.A., South Carolina); *Dacryopsis* Mass. 1891; *Dacryomitra* Pat. 1900; *Ditiola radicata* var. L. Kenn. 1964. — Referred to *Ditiola radicata* as a var. by L. Kenn. and McNabb 1966 (NZB 4): 550 f. 1b (with descr.) but cf. (**150**).

japonicum, *Exobasidium*, Shirai [Ch. 1., p. 318]; *Exobasidiotus* E. Krause 1934 ("Ulbrich").

juniperina, *Tremella*, L. 1753 [Ch. 1., p. 318]; *Tremella* Arth. 1901.
mespili, *Tremella*, Arth. 1901 [Ch. 1., p. 321] (nom. nud.).
penicillata, *Tremella*, Arth. 1901 [Ch. 1., p. 325] (nom. nud.).
pezizoides, *Tubercularia*, Schum. in herb. (Denmark). — Rostr. 1885 (OdF 1884[3]): 150 studied Schumacher's specimen of which he wrote: "Expl. i Samlingen tilhøre *Dacrymyces chrysocomus* (Bull.), og er irst nok den samme som i Enum. p. 416 er beskreven under Navn af *Peziza subplana*".
rolleyi, *Exidia*, L. Olive 1958 (BTC 85): 95 (Society Is.) — Cited with doubt as a syn. of *Sebacina* [*Tremella*] *fusispora* by Raitv. 1968 (TÜT 211): 96, an unlikely guess.
rosea, *Tremella*, E. Krause 1930 B.r.: 104 (Germany), not ~ (Schreb.) Plan. 1788 (d.n.), not ~ Höhn. 1903; *Elvelus* E. Krause 1934 (generic name n.v.p.). — Nomen dubium.
sabinae, *Tremella*, Dicks. 1785 [Ch. 1., p. 328]; *Tremella* Arth. 1901.
sanguinea, *Tulasnella*, (Fr.) E. Krause 1934 ≡ *Peniophora* [*Phanerochaete*] *sanguinea* (Fr.) Höhn. & L. — 'Corticiaceae'.
spathularia, *Dacryopinax*, (Schw.: Fr.) G. W. Mart. [Ch. l., p. 329]. — The syns. of this species (an alien in Europe) are fully listed by McNabb 1965 (NZB 3): 63. — Special literature: Goldstrohm & Lilly, *1965*; Vall & Lilly, *1968*.
squamosa, *Tremella*, Schum. [Ch. 1., p. 330]. — Rostr. 1885 (OdF 1884[3]): 157 studied Schumacher's specimen and concluded that it was without doubt a conidial form (unknown until then) of *Onygena equina* (Willd.) per S. F. Gray. [?]
stipitata, *Tremella*, Peck 1875 (RNS 27): 100 *pl. 2 fs. 22, 23* (U.S.A., New York), not ~ Willd. 1787 (d.n.), not ~ Bosc per Schw. 1822; *Dacryomitra* Burt 1921. — Referred by L. Kenn. 1959 (M 50): 893 to *Dacryopinax spathularia* (as a "phase"), but McNabb made it a syn. of *Ditiola radicata* var. *gyrocephala* = *Coryne* [*Ditiola*] *gyrocephala* (see this list), cf. also (**150**).
tubercularia, *Tremella*, Berk. → *Tubercularia albida*, see this list.
tuberculariodes, *Ditiola*, Lib. "Herb. n. 470" (Belgium) (n.v.p.); *Ciliciopodium* (Lib.) ex Sacc. 1881 F.d.: *f. 755*. — Fide Booth 1959 (MPa 73): 32 = *Nectria aurantiaca* (Tul.) Jacz., stat. imp. — Deuteromycetes.
uvida, *Thelephora viscosa* var. Fr. 1828 E. 1: 218 (Sweden); *Tremella* E. Krause 1930, misapplied; *Elvelus* E. Krause 1934 (generic name n.v.p.), misapplied; = *Phlebia livida* (Pers. per Fr.) Bres. (Corticiaceae).
violacea, *Tremella*, Pers. — *Dacrymyces* "*violascens* C.D" [= *D. violacea* sensu Tul.; Cost. & Duf.] of E. Krause 1925 (ANM 78): 135, 1928 B.r.: 59 is fide E. Krause 1930 B.r. 105, "zu streichen; vgl. . . . *Stereum* [*Gloeocystidiellum*] *lividocaeruleum*. Die übrigen Exemplare waren Konidienträger von *Coryne purpurea* Fuckel".
violascens → *violacea*, *Tremella*, Pers.

Explanation of strongly reduced bibliographic references

(**ANM**), Arch. Freunde NatGes. Mecklenb. — (**ASv**), Atti Soc. ven.-trent. Sci. nat. (**BfA**), Bull. Stn Rech. for. N. Afr.

(**CbB**), Collnea bot., Barcinone — Corner **1966**, Monogr. cantharelloid Fungi. — Cost. & Duf. **1891**, Nouv. Fl. Champ.

Ell. & Ev. **N.A.F.**, N. Am. Fungi [exs.] II

S. F. Gray **1821**, Nat. Arr. Br. Pl. 1

(**JJB**), J. Japan. Bot. — (**JMi**), J. Microgr.

E. Krause **B.r.**, Basidiom. rostock.; **M.B.**, Mecklenb. Basid.

(**LMW**), Lloyd, Mycol. Writ.

Maubl. **1926**, Maladies paras., 3e Ed. (Delacr. & Maubl., Maladies Pl. cult.).

Nannf. & Du R. **1952**, Vilda Växt. Norden, Uppl. 2. — (**NPh**), New Phytol. — (**NyM**), Nytt Mag. Bot.

(**OdF**), Overs. K. danske Vidensk. Selsk. Forh.

Raitv. **1967**, Opred. geterob. Grib. / 1969, Key Heterobas. USSR [English translation]. — (**Rh**), Rhodora. — Rox. Clem. **1864**, Plantas Titáguas **in** Revta Progr. Ci. exact. fis. nat. **14** [Reprint cited; ed. Colm.; "Rojas"]

Sacc., **F.d.**, Fungi ital. autogr. delin.

Velen. **1947**, Novit. mycol. nov.

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NOTES ON THE CYANOPHILY OF SPORES, WITH A DISCUSSION OF THE GENUS LEUCOGYROPHANA (CORTICIACEAE)

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The genus *Leucogyrophana* Pouz. has been placed in the Coniophoraceae by some authors on account of the cyanophilous spores, by which character the Coniophoraceae are said to differ from the Corticiaceae. Contrary to this opinion it is shown that not all the species of the Coniophoraceae exhibit cyanophily. Moreover the same spore reaction has been observed in a rather large number of species of the Corticiaceae. This means that 'cyanophily' is not a conclusive key character for a distinction between the two families mentioned. It is proposed to maintain *Leucogyrophana* in the Corticiaceae. A key to the accepted species of this genus is presented.

In 1958, Pouzar created a monotypic genus for *Merulius molluscus* Fr., viz. *Leucogyrophana*. This genus was said to be closely related to *Serpula* (Pers.) S. F. Gray, a genus of the Coniophoraceae. "Both genera have in common before all the brown colouration of the spore wall in Melzer's reagent and a very intensive blue colouration of endospore in cresyl blue". (p. 31). The name strongly suggests a *Serpula* (syn.: *Gyrophana* Pat.), but "...the difference between these two genera is in colour of the spores which is brown in *Serpula* and hyaline in *Leucogyrophana*". (p. 36). By now this genus comprises six species, in at least one of which the spore wall shows no affinity to cotton blue. After having studied some species of *Leucogyrophana* and of the Coniophoraceae I have my doubts about the value of the character "spore-wall stained in cotton blue", regarding the systematics at family level.

The first to introduce the use of cotton blue in the microscopy of the hymenomycetes were Nannfeldt & Eriksson (1953) who while studying *Coniophora ochroleuca* Bres. were "...surprised to find that the spores ... stained an intense blue colour". This prompted them to examine further species of the genera *Jaapia*, *Coniophora*, and *Serpula*, after which they were satisfied that "... the expected reaction was obtained". After discussing the possible relationships of the genus *Jaapia* Bres. the authors declared that "... all these facts show that *Jaapia* is a true member of the Coniophoraceae, and the structure of the spore-wall (esp. its stain reactions) not only serves as a most useful diagnostic character but affords, in our opinion, convincing proof that the family is a most natural one".

It is necessary here to mention that the authors not only noticed a staining of the spore-wall but were able to demonstrate "... that the stain had been absorbed by the inner layer of the spore-wall, while the thinner outer layer had remained per-

fectly hyaline". This phenomenon mostly in connection with additional characters has been adopted by other mycologists to define the Coniophoraceae. Thus one reads in Donk (1964: 255): "Spore-wall rather thick, presumably always double. . ., both layers smooth, the inner strongly absorbing Cotton Blue (cyanophilous)".

So far the application of this character offers no problems. Difficulties arise when an author ascribes to or removes from the Coniophoraceae a species or genus solely on account of the spores becoming stained in cotton blue or not. This was the very reason why Pouzar (1958) and Donk (1964) attributed *Leucogyrophana* to the Coniophoraceae, which was not accepted by Parmasto (1968) who placed the genus in the Corticiaceae (Athelioideae) as did Eriksson (1958) and Christiansen (1960) with the type species of *Leucogyrophana*, *Merulius molluscus* Fr.

The purpose of my observations recorded below was to (re)study the behaviour in cotton blue of the spores of a number of species of the Coniophoraceae and the Corticiaceae and thus to gain a better insight in the taxonomic value of this behaviour.

Methods and terminology

I used a solution of cotton blue (Baumwollblau - Chroma/Germany) in lactophenol. It is often necessary to boil the material for several seconds in order to accelerate the absorption of the dye. If the cyanophily of the spore-wall is not strong, empty spores have to be examined.

In this connection some remarks on the terminology are necessary. The dyes cotton blue and cresyl blue have been used by agaricologists since Kühner introduced the latter in his study of *Marasmius* (1933) without creating a new name for the reaction. Later on the term "metachromatic" has been adopted for a spore-wall staining red in the blue solution of cresyl blue whereas — more rarely — "orthochromatic" is spoken of when the spore-wall becomes blue-coloured, but the term metachromatic is also used to indicate a blue colouration of gloeocystidia by several blue dyes. Not seldom authors speak simply of a "cresyl blue reaction". A new term has been introduced by Kotlaba & Pouzar (1964: 131): "We propose the term 'cyanophily' for the staining of the spore-wall, or its ornamentation, and the hyphal wall in Cotton Blue and 'acyanophily' when they do not stain, as a precise term is desirable for describing this reaction".

Mention should be made of a note by Eriksson & Ryvarden (1973) that the spores of *Amphinema byssoides* (Fr.) J. Erikss. stained in cotton blue are ". . . ± red in phase contrast". This, however, is nearly always the case with spores that have taken up a blue stain as well as in all other stained parts of the basidiocarp such as hyphae, basidia, cystidia which have been broken in small fragments or which are strongly curved (thus the red colour is well visible in sterigmata e.g.). This means that the colour change from blue to red visible in phase contrast in blue-stained objects is of no taxonomic importance.

In my opinion the expression 'cyanophilous reaction' is not a very felicitous one, but I am using it for want of better.

SPECIAL PART

I first studied some species of the Coniophoraceae to become more acquainted with a well-established cyanophilous reaction, and obtained the following results.

The spores of *Coniophora arida* (Fr.) Karst. are distinctly cyanophilous. Normally the inner wall is strongly stained, suffused with a slight purple tint, whereas the outer wall becomes only slightly bluish. The capacity to become stained seems to be independent of time (collected between 1915 and 1965) and state of preservation.

MATERIAL STUDIED (all collected in the Netherlands)[1].—1915 (L 959.313–269), 1952 (L 952.287–905), 1957 (L 956.312–066), 1958 (L 958.284–013), 1965 (L 966.116–036).

Coniophorella olivacea (Pers.) Karst. has also cyanophilous spores; but here particularly the outer layer of the spore-wall stains, whereas the inner layer shows a less intense colour.

MATERIAL STUDIED.—Mycotheca Estonica 15 (*Parmasto* 1956; L); Kryptogamae exsiccatae, Wien, 1601 (*v. Höhnel*; L).

Jaapia ochroleuca (Bres. apud Brinkm.) Nannf. & J. Erikss. shows also cyanophilous spore-walls; a distinction between the two layers is not always easy to detect.

MATERIAL STUDIED.—Type, *Brinkmann* 1897 (S); Brinkmann, Westf. Pilze 28 (*Brinkmann* 1899; L).

Serpula himantioides (Fr.) Boud.: The spores of all the specimens I studied were not cyanophilous; only the young spores with almost hyaline walls showed a reaction to cotton blue, whereas the older spores with brown walls remained unstained. After several weeks and once more boiling of the spore-suspension in cotton blue solution, some spores acquired a greenish-olivaceous colour, owing to the addition of a blue stain to the yellowish-brown colour already present in the spores. No strong affinity to cotton blue could be demonstrated in this species. Nevertheless it may be possible — by repeated heating or treating with chemicals — to force the spores to take up a greater amount of the cotton blue stain, but this was not the aim of the present study. In any case it is clear that after the 'normal' process, that is treating the spores with a cotton blue solution and boiling for several seconds, this species is not cyanophilous.

MATERIAL STUDIED.—Netherlands, 1958 (L 958.319–091), 1959 (L 955.283–158), 1960 (L 960.262–506), 1965 (L 966.116–035), 1968 (L 968.101–006); England, 1954 (L 943.250–136); Parmasto, Mycotheca Estonica 16, 1956 (L).

From these results it is clear that the character "the inner layer of the spore-wall strongly absorbing cotton blue" does not apply to all typical species of the Coniophoraceae. First of all, after the normal treatment the colour reaction cannot be

[1] In order to save space, most collections are referred to by their collecting date and admission number.

obtained in all species; secondly, it is not always especially the inner layer that stains: sometimes it is not possible (with a light microscope) to distinguish between the two layers, in other cases the outer layer seems to have a stronger affinity to cotton blue than the inner layer.

Even if the cyanophilous reaction cannot always be obtained within the Coniophoraceae it would nevertheless be a useful character if it were restricted to this family. It is, however, also a main character of the Gomphaceae. Fortunately, this creates no great problems since in this family the spores show a distinct cyanophilous ornamentation and, in addition, never have such thickened walls as is the case in typical species of the Coniophoraceae. Also in the polypores and in the Agaricales there are some genera with cyanophilous spores, but as these can be easily distinguished by means of other characters, no difficulties arise here either. Furthermore it was found that in some unnamed specimens of *Tomentella* the young spores are distinctly cyanophilous. The main problem, however, remains how to distinguish the Corticiaceae from the Coniophoraceae. Nannfeldt & Eriksson (1953: 178) stated that ". . . . several other aphyllophorous species with ± thick-walled spores were tested in the same way but reacted negatively". Since they did not state which species they examined, the uncertainty remains whether among the material investigated there were any Corticiaceae. Pouzar (1958) mentioned one corticiaceous species with cyanophilous spores, viz. *Merulius molluscus* Fr., which he placed in the separate genus *Leucogyrophana* that according to him belonged to the Coniophoraceae. Kotlaba & Pouzar (1964: 137) said that ". . . no species of the Corticiaceae are known to have cyanophilous spores, except for some species of the genus *Hypochnicium*". In a footnote, (1964: 134) they mentioned *Peniophora mollis* (Fr.) Bourd. & Galz. as having amyloid as well as cyanophilous spores. Maas Geesteranus (1971), who warns with reason of overestimating this colour reaction, found ". . . a very marked cyanophily . . ." in *Cristella fastidiosa* (Pers. per Fr.) Brinkm. My own studies show that cyanophily is present in some other genera of Corticiaceae, too.

In *Piloderma* Jülich, a genus segregated from *Athelia*, the two common species *P. bicolor* (Peck) Jülich and *P. byssinum* (Karst.) Jülich have been studied. In both species the spore-wall reveals a cyanophilous reaction. Since the spores are slightly yellowish one may philosophize about a possible relationship with the Coniophoraceae. Against this view speak the much smaller spores and the lack of clamps.

MATERIAL STUDIED.—*Piloderma bicolor* (spores of all specimens studied are cyanophilous), Austria, 1968 (Herb. Jülich 1299b); Denmark, 1964 (L 964.281–460); France, 1952 (Herb. Donk 11173).

Piloderma byssinum (cyanophily sometimes rather weak), Sweden, 1932 (Herb. Donk nos. 3577, 3580), 1962 (Herb. J. Eriksson 10454); France, 1909 (Herb. Donk 1172); Austria, 1968 (Herb. Jülich 1247).

In the genus *Byssocorticium* Bond. & Sing. the spores of most species are slightly thick-walled and of an olivaceous to grey-bluish colour. This means that cyanophily

is not always easily detectable. Nevertheless the spores of *B. atrovirens* (Fr.) Bond. & Sing. are distinctly cyanophilous while those of *B. pulchrum* (Lund.) Christ. are only slightly so.

MATERIAL STUDIED.—*B. atrovirens*, France, *L. Maire* (L 931.71–112), *Bourdot & Galzin* (L 931.71–97); England, 1961 (L 961.204–061).
B. pulchrum, Germany, Jaap, Fungi selecti exsiccati 281 (L).

Amphinema byssoides (Pers. ex Fr.) J. Erikss. has weakly cyanophilous spores.

MATERIAL STUDIED.—Netherlands, 1928 (Herb. Donk 975); Germany, 1968 (Herb. Jülich 955, 993, 1016, 1203, 2083, 2101).

Botrybasidium laeve (J. Erikss.) Parm. is a species with thin-walled spores which are weakly to distinctly cyanophilous. This reaction is naturally not as distinct as e.g. in *Piloderma* since the spore-wall is much thinner, but cyanophily (best seen in empty spores!) is definitely present. The basidia and especially the hyphae exhibit a remarkably strong cyanophily.

MATERIAL STUDIED (both specimens determined by J. Eriksson).—Germany, 1933 (Herb. Donk 8070); Netherlands, 1928 (Herb. Donk 1290).

Botryohypochnus isabellinus (Fr.) J. Erikss.: The spore-walls, spines, and basal hyphae are distinctly cyanophilous.

MATERIAL STUDIED.—England, 1959 (L 961.3–925); Germany, 1968 (Herb. Jülich 1143); France, *Bourdot* (L 931.82–28).

In the genus *Hypochnicium* two species with more or less cyanophilous spores have been studied, viz. *H. bombycinum* (Sommerf.) J. Erikss. (distinctly cyanophilous) and *H. punctulatum* (Cooke) J. Erikss. (weakly cyanophilous).

MATERIAL STUDIED.—*H. bombycinum*, Germany, Brinkmann, Westf. Pilze 11 (L); *H. punctulatum*, Netherlands, 1952 (L 951.328–008); England, 1960 (L 961.3–936); Germany, 1967 (Herb. Jülich 927).

Two specimens of *Cristella sulphurea* (Pers. ex Fr.) Donk have been studied, in both of which the spore (incl. warts) are cyanophilous. The same has been said for *Cristella fastidiosa* by Maas Geesteranus (1971). In other unnamed specimens of *Cristella* no cyanophily could be detected. According to Eriksson (1954: 191) the spores of *Cristella* "... do not stain with Cotton Blue".; unfortunately he did not mention which species he studied.

MATERIAL STUDIED.—Germany, 1967 and 1968 (Herb. Jülich 768 and 1499).

Since it was now clear that cyanophily is a character also present in genera of the Corticiaceae, I examined only three more species of *Corticium*, viz. *C. confluens* (Fr.) Fr., *C. evolvens* (Fr.) Fr., and *C. coprophilum* Wakef. The two former species have more

or less thin-walled, hyaline spores, and show a weak cyanophily. The last named species has thick-walled and strongly cyanophilous spores.

MATERIAL STUDIED.—*C. confluens*, Germany, Brinkmann, Westf. Pilze 13 (L); *C. evolvens*, Germany, 1968 (Herb. Jülich 1014); *C. coprophilum*, Netherlands, 1973 (L).

Furthermore the observation of Eriksson (1954) has to be mentioned that in *Peniophora abietis* both the outer layer of the spore wall and the aculei stain in cotton blue.

From the observations above it seems clear that cyanophily is by no means such a remarkable and conclusive feature as has been thought by some authors. At specific level it is often valuable, but for the delimitation of genera or even families it seems less suited. The transfer of *Leucogyrophana mollusca* from the Corticiaceae to the Coniophoraceae, merely because its spores are cyanophilous, is ill-founded, as several Corticiaceae have cyanophilous spores and many more species of this family probably will show the same reaction. Hence *Leucogyrophana mollusca* should remain in the Corticiaceae. This view is further supported by the observation that not all of the species of *Leucogyrophana* have cyanophilous spores:

Leucogyrophana mollusca (Fr.) Pouzar. All specimens seen have cyanophilous non amyloid spores.

MATERIAL STUDIED.—USSR, Parmasto, Corticiaceae URSS 140 (UPS); Sweden, Lundell & Nannfeldt, Fungi exs. suecici 86 (UPS); Netherlands, 1933 (Herb. Donk 5135).

Leucogyrophana mollis (Bres.) Parm. According to Kotlaba & Pouzar (1964) "... only the young spores have cyanophilous walls". I myself have not seen such young spores and observed only absolutely acyanophilous spores. Instead, I noticed that the spores are distinctly amyloid. Since within the genus *Leucogyrophana* the microscopical features do not show great diversity, this is an important distinctive character.

MATERIAL STUDIED.—Czechoslovakia, *Pouzar* 1963 (L 963.168–662); Netherlands, 1931 and 1932 (Herb. Donk 2319 and 4059); Sweden, 1932 (Herb. Donk 3731).

Leucogyrophana subtessulata (Parm.) Jülich has cyanophilous spores. Judging by the specimens seen, *Leucogyrophana cremeo-isabellina* (Litsch.) Parm. is conspecific. Both have inamyloid but cyanophilous spores of the same size, while hyphae, basidia, and rhizomorphs (which are not always present) seem to be identical.

MATERIAL STUDIED.—a) *Leucogyrophana subtessulata*, URSS, Parmasto, Corticiaceae URSS 126 (paratype, UPS). — b) *Leucogyrophana cremeo-isabellina*, Sweden: "An altem Zaunholz. Sdl. Neglinge-Skogsö, unweit Saltsjöbaden, 14.11.1906, *L. Romell*" (type; W no. 18266); Sweden: Upland, Knifsta, 13.12.1908, L. *Romell 1908* (W); URSS: Parmasto, Corticiaceae URSS 111 and 112 (UPS).

Leucogyrophana subillaqueata (Litsch.) Jülich, *comb. nov.* — Basionym: *Corticium subillaqueatum* Litsch. *in* Annls mycol. **39**: 128–129. 1941.

This species has an interesting history. Litschauer based his description on two collections made by Romell in Sweden. According to this description, the hyphae are sometimes ampulliform at the septa, and microscopical details too are similar to those of *Corticium illaqueatum* Bourd. & Galz. [now: *Ceraceomyces tessulatus* (Cooke) Jülich] except that the rhizomorphs are lacking and the spores are somewhat smaller. Oberwinkler (1965), who restudied the two specimens, found the basidia to be cylindrical-pedunculate, and consequently placed this species in his "ad interim" genus *Athelopsis* Oberw.; according to him the spores are hyaline, thin-walled and inamyloid. Parmasto (1968), validly publishing and emendating the genus *Athelopsis*, did not include this species but left it in his list of species of doubtful position. On studying the two specimens myself, I found the spores slightly yellowish, slightly thick-walled, amyloid becoming greyish, and cyanophilous. The morphology of hyphae, basidia, and spores leaves no doubt that thé place of this species is in the genus *Leucogyrophana*. The key characters are: hymenial surface even, spores amyloid and cyanophilous, thus differing from all other species of the genus *Leucogyrophana*.

MATERIAL STUDIED.—Sweden, "Stockholm, Lidingö, 29.5.1910, *L. Romell 2068* (type; M); Upl., Lohärad sn, Erken, "Bibacken", 3.11.1918, *L. Romell 4095* (UPS).

I had no occasion to study two other species described by Parmasto, viz. *Leucogyrophana pouzarii* Parm., and *L. pseudomollusca* (Parm.) Parm. According to his descriptions the spores are not amyloid but dextrinoid; he mentions no cyanophilous reaction.

KEY TO THE SPECIES OF LEUCOGYROPHANA

1a. Hymenial surface in dried specimens even, in fresh condition sometimes slightly merulioid. 2
2a. Spores amyloid.
3a. Spores not cyanophilous, (4.5–)5.5–6.5(–7.5) × 2.5–3(–4) µm.
L. mollis (Bres.) Parm.
3b. Spores cyanophilous, 4–5 × 3–4 µm. . . . . *L. subillaqueata* (Litsch.) Jülich
2b. Spores inamyloid, cyanophilous, 4–7 × 2.7–4 µm.
L. cremeo-isabellina (Litsch.) Parm.
Syn.: *L. subtessulata* (Parm.) Jülich.
1b. Hymenial surface in fresh and dried condition distinctly merulioid.
4a. Spores cyanophilous but not amyloid and not dextrinoid, 4.5–5.5(–6) × 3.3–4.3 (–4.5) µm. . . . . *L. mollusca* (Fr.) Pouzar
4b. Spores dextrinoid, not cyanophilous (?), about 6–7 × 4–5 µm.
5a. Cystidia present, 20–30 × 7–8 µm. . . . . *L. pouzarii* Parm.
5b. Cystidia lacking. . . . . *L. pseudomollusca* (Parm.) Parm.

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THE GENERA OF THE HYPHODERMOIDEAE (CORTICIACEAE)

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(With 19 Text-figures)

The type species and additional species of the genera of the Hyphodermoideae have been studied. Key-characteristics, based mainly on basidial morphology, have been elaborated for a delimitation of the genera. The new genera *Cylindrobasidium*, *Bulbillomyces*, and *Lagarobasidium* are described. Several new combinations are proposed. A key to the genera is given.

There are many examples in the Corticiaceae of species being much easier to determine than the genera to which they belong. For many of the species the delimitation is rather well known, but to gain a clear insight into the limits of a genus one has to study as many of its species as possible, thus trying to synthezise a genus-concept. Another possibility, of course, is to recur to the generic description published by the author of the genus in question, but this is where difficulties often arise. The older genera are not seldom poorly defined and also several recent genera published between 1950 and 1960, mainly by Donk and Eriksson, are not clearly delimited. Sometimes a genus which was well defined in the beginning becomes a jumble-shop through the accumulation of species of unknown affinities, and finally nobody knows how it is really to be delimited—as for instance is the case in the genera *Phlebia* Fr. emend. Donk and *Radulomyces* Christ. emend. Parm. Other genera are known which never had a good circumscription, such as *Hyphoderma* Wallr. emend. Donk and *Hyphodontia* Eriksson.

Donk (1957) opens his description of *Hyphoderma* with the sentence: "The average species may be characterized as follows". What follows is a rather elaborate characterization of the most common species which by no means covers all of the 24 species he combines under this genus; unfortunately no figures are given and nothing is said about the shape and size of the basidia.

Eriksson (1958) on the other hand gives beautiful figures of ten species of the genus *Hyphodontia*, combines 20 species of which he gives no description, while the entire diagnosis of the genus consists of barely two lines: "Genus Hymenomycetum corticioideum et hydnoideum, generi Hyphodermati affine sed differt basidiis minoribus, fructificationibus fibrosis et hyphis angustioribus". This was judged by Gilbertson (1968, published 1971) a "very brief and rather vague description". He was indeed the first to give a clear and extensive description of the genus.

Since I had and often still have serious difficulties in naming collections especially from tropical regions—and by this I mean mainly the determination of the genus to which they belong—I undertook a study of the type-species of the genera of the subfamily Hyphodermoideae, while I intend to extend this work to the Phlebioideae. As shown in the present paper I was above all interested in disclosing the differences between *Hyphoderma* and *Hyphodontia*, two rather large genera of cosmopolitan distribution, and of which, besides the type-species, I studied another ten species each.

This study was not designed to solve all the problems, because this is only possible—at the earliest—after good monographs of the larger genera have become available. But I hope to give a working basis which may be adapted to such needs as may arise. It emphasizes some points which have been overlooked or forgotten, while its main aim is to bring out the basidial morphology.

I adopted the arrangement in subfamilies as given by Parmasto (1968), and of the Hyphodermoideae I studied only the genera he listed. I fully realize that there are some genera within other subfamilies of the Corticiaceae which ultimately have to be transferred to the Hyphodermoideae, but for the moment I found it more practicable to restrict myself to this subfamily as delineated by Parmasto; however, *Odonticium* Parm. has been omitted.

Numerous observations have been made on the hyphae of the genera here treated, although surely more remains to be done. Not nearly as much is known about the basidia, however, and since I believe that their properties have to be used as the main characteristics of the Corticiaceae, description of size, shape and origin of the basidia is the main purpose of the present study. In this connection it is interesting to note for instance that for only two out of 21 species treated in his excellent work on the Swedish species of *Peniophora* sect. *Coloratae*, Eriksson (1950) gives a figure of an entire basidium from top to base, whereas in all other species only the upper part of the basidia is illustrated. I know from personal experience that in some species it is very difficult or almost impossible to get a clear view of the whole basidium, but this should not be a deterrence to try again and again (in this respect *Peniophora* surely does not seem to belong to the most difficult genera).

The genus *Radulomyces* Christ. may serve as an example of the importance to study the whole basidium. The basal parts of the basidia are conspicuously constricted, thus giving the basidium a distinctly stalked appearance. This provides an excellent basis for separating this genus from the other genera of the Hyphodermoideae.

Another interesting fact is that in *Peniophora quercina* the basal parts of the basidial walls are clearly thickened (up to 0.8 μm). Since the sterigmata are formed only at a very late stage of basidial development, unripe basidia (not seldom with secondary clamps) look very much like cystidia.

An interesting but not yet exhaustively studied feature is the difference in shape of young and adult basidia. In the Hyphodermoideae in most cases the young basidia are cylindrical or ± narrowly clavate, but in *Basidioradulum* Nobles their shape is completely different: the young basidia are broadly ellipsoidal or even pyriform, thus rather strongly differing from those of *Hyphoderma*.

I tried to establish the number of nuclei in the cells of the basidiocarp of all species treated here. Unfortunately the results where not always equally good, since the uptake of the nuclear stain (carmine, orcein, or coriphosphine) depends on the condition of the basidiocarp and the chemicals used for poisoning the fungi. In *Pulcherricium caeruleum* this study yielded the interesting observation that dendrophyses can develop into basidia, thus functioning as probasidia.

The most difficult group of the Hyphodermoideae is formed by the genera *Basidioradulum*, *Hyphoderma*, *Hyphodontia*, and *Metulodontia*, since the shape of their basidia seems to be identical. The type species of *Basidioradulum*, *B. radula*, has been transferred by Donk to *Hyphoderma*. There is, in fact, no difference between both genera as to size and shape of the mature basidia, but the hyphal texture of the subhymenium is much more dense in *Basidioradulum*, while in this genus the developing basidium passes from broadly ellipsoidal or even pyriform to suburniform.

In *Hyphoderma* itself the basidia develop from cylindrical to clavate or suburniform. It would seem that the difference in basidial ontogeny as well as in the structures of the basidiocarps (hymenial surface, hyphal texture) carry sufficient weight to maintain *Basidioradulum* as a separate, although probably small or even monotypic genus.

Metulodontia shows no difference from *Hyphoderma* as far as hyphae and basidia are concerned but differs in having thick-walled, heavily incrusted and aseptate cystidia.

The remaining genera to be discussed are *Hyphodontia* and *Hyphoderma*. It is possible to recognize a group of species with mostly grandinioid or odontoid basidiocarps, small basidia (up to about 16 μm) and spores, and narrow, often somewhat thick-walled hyphae and cystidia. These have been placed in *Hyphodontia*. There is another group of species with mostly even basidiocarps, larger basidia (approximately 20–45 μm long) and spores, wider hyphae (which are at least as thick-walled as in *Hyphodontia* but with a wider lumen) and often larger cystidia (in some species also with gloeocystidia). These species have been placed in *Hyphoderma*. Several species placed by Eriksson in *Hyphodontia*—e.g. *Corticium niveum* Bres., *Thelephora sambuci* (Pers.) ex Pers.—differ in having typical large basidia and rather thin-walled hyphae; consequently they are transferred to *Hyphoderma*.

Many species of *Hyphodontia* have the walls of the basal hyphae of the basidiocarp not much thickened so that they are reminiscent of a miniature *Hyphoderma*. This is where the two genera under discussion seem to touch, and the only clear-cut difference I can see lies in the size of the basidia. This is the reason why the separation of the two genera seems to be merely a matter of taste and convenience, although it is true that often their outward appearance is somewhat different, a smooth hymenium being a characteristic of *Hyphoderma*, a hydnoid hymenium of *Hyphodontia*. At this junction, therefore, I prefer to keep the two groups of species separated, not in the least because the union of the two rather large genera, which are likely to grow in the near future, is bound to result in an unwieldy supergenus.

At first I tried to maintain *Metulodontia* as a separate genus, which differs from *Hyphoderma* solely on account of its thick-walled, aseptate and incrusted cystidia, whereas the hyphal structure and especially the size and shape of the basidia are

identical. If such a separation is accepted, three species of *Hyphoderma* [viz. *H. mutatum* (Peck) Donk, *H. heterocystidium* (Burt) Donk, *H. populneum* (Peck) Donk] will have to be transferred to *Metulodontia* since they all have the same type of cystidia. On the other hand they exhibit in addition glococystidia which is also a feature of "true" Hyphodermas, like *H. argillaceum* (Bres.) Donk and *H. clavigerum* (Bres.) Donk.

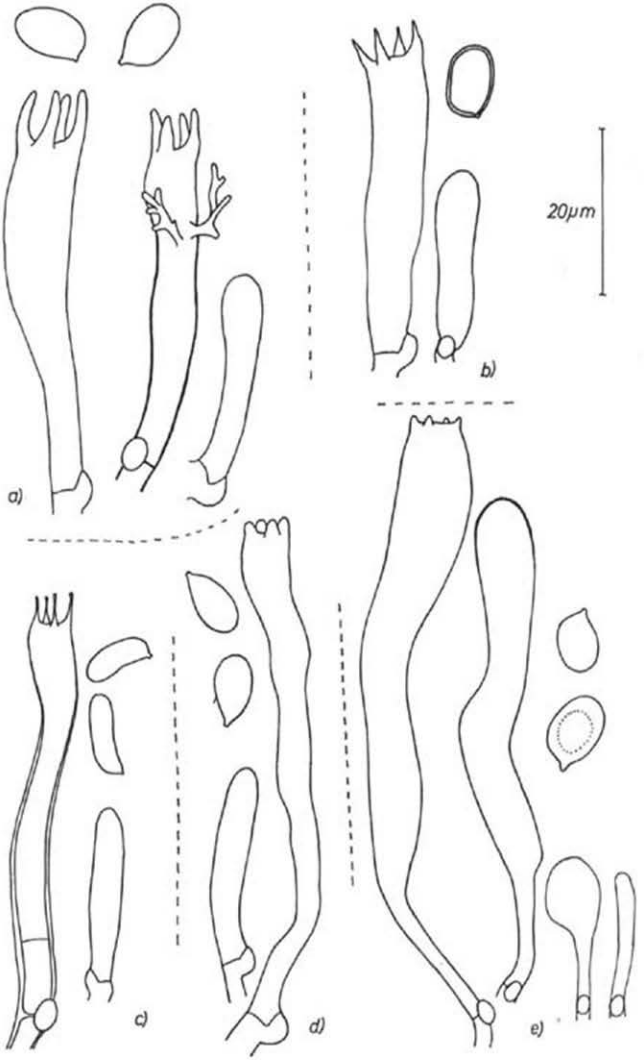

Fig. 1. Basidia: a. *Pulcherricium caeruleum*; b. *Hypochnicium bombycinum*; c. *Peniophora quercina*; d. *Cylindrobasidium evolvens*; e. *Radulomyces confluens*.

This means that the three species mentioned above are intermediate between *Hyphoderma* and *Metulodontia*. After having studied all the species enumerated above (with the exception of *H. populneum*) I see no possibility to keep *Hyphoderma* and *Metulodontia* apart on morphological grounds.

However, this disposition clashes with the findings of Boidin, Mc Keen and others who have studied the sexual behaviour of corticiaceous species. Boidin & Lanquetin (1965) found *Peniophora nivea* (Karst) Bourd. & Galz.—the type species of *Metulodontia*—to be tetrapolar, whereas all other species of *Hyphoderma* were reported by Boidin to be bipolar. In addition, McKeen found *H. heterocystidium*, *mutatum* and *populneum* to be bipolar too. It would seem to me that too much emphasis is laid upon the importance of the difference between bipolar and tetrapolar behaviour. I am not convinced that it can be used as a differential character at the generic level. The two modes of sexual behaviour occur in taxa of great morphological similarity. In a tabel given by Boidin 1964 the genera *Hyphodontia*, *Peniophora* and *Radulomyces* are indicated as being tetrapolar, while *Hyphoderma* and *Phlebia* are said to be bipolar. If the differential sexual behaviour as accepted as an infallible character, *Hyphoderma* and *Metulodontia* must be considered to be quite different genera, while many other taxonomic problems among the genera of the Corticiaceae would be solved. The disturbing fact remains, however, that as yet no good morphological characters are known to separate the two genera in question. I have no personal experience with cultures, neither did I study the sexual behaviour of Corticiaceae, but literature provides an interesting example which very suitably illustrates my point. Boidin 1971 mentioned the genus *Gloeocystidiellum* as consisting of bipolar, tetrapolar, and homothallic species. But unfortunately this example bears new problems. Boidin here came across difficulties which he tried to explain by assuming that e.g. in the homothallic species the verticillate clamps were "derived . . . by overevolution", followed by the sentence that "the verticillate clamps have not been derived but are an extravagant reinvention".

Since I am unable to reduce terms like "overevolution" and "extravagant reinvention" to a purely morphological level, I am inclined to lay the emphasis on the morphological facts rather than on interfertility tests in such cases where seemingly different results are obtained. This applies all the more since the two genera *Hyphoderma* (bipolar) and *Hyphodontia* (tetrapolar), kept so widely apart by Boidin, are surely much more closely related to each other than to any other bipolar respectively tetrapolar genus. It may even be said that the distinction between the two genera, which is based merely on different sizes of basidia, spores and hyphae, often seems to be more a matter of taste.

Key to the genera (see Figs. 1–2)

1a. Spores thick-walled (*c.* 0.4–0.8 μm), smooth or sculptured 2
1b. Spores thin-walled, smooth 4
2a. Spores distinctly thick-walled; young basidia more or less cylindrical; imperfect *Aegerita*-state absent 3

2b. Spores only slightly thick-walled; basidia 20–26–32 µm long, in young state broadly ellipsoidal; imperfect *Aegerita*-state present . . . . . *Bulbillomyces*, p. 69
3a. Basidia 30–45–60 × 5–7–9 µm; spores smooth or sculptured . . . . *Hypochnicium*, p. 81
3b. Basidia 10–18–20 × 4–6 µm; spores smooth . . . . . *Lagarobasidium*, p. 84
4a. Cystidia with bifurcate base, covered with crystals arranged in longitudinal rows; basidia exhibiting repetition (difficult to observe) . . . . . *Subulicystidium*, p. 95
4b. Cystidia lacking or different, never with bifurcate base and crystals arranged in rows; no repetitive basidia 5
5a. Dendrophyses present 6
5b. Dendrophyses absent. 7
6a. Basidiocarp bright or dull coloured, never blue; hyphal texture dense, individual hyphae difficult to observe; if dendrophyses present, then always together with gloeocystidia or thick-walled cystidia, or not covered with blue granules; dendrophyses not developing into basidia. . . . . *Peniophora* pro parte, p. 87
6b. Basidiocarp blue or greenish-blue; hyphae distinct; only dendrophyses present, some of which may develop into basidia; no glococystidia or thick-walled cystidia formed *Pulcherricium*, p. 88
7a. Basidia clavate or distinctly stalked (the basal part abruptly constricted); if irregularly cylindrical, then *c.* 40–80 µm long 8
7b. Basidia urniform or suburniform, up to 35–45 µm long 11
8a. Basidiocarp bright or dull coloured, rather compact, mostly ceraceous; hyphal texture dense, individual hyphae difficult to observe; dendrophyses, gloeocystidia or lamprocystidia (thick-walled, aseptate, heavily incrusted) present; spore-print said to be red *Peniophora*, p. 87
8b. Basidiocarp mostly cream-coloured, pellicular, membranaceous or only slightly ceraceous; hyphae distinct; cystidia and gloeocystidia present or absent; spore-print white 9
9a. Basidiocarp pellicular, with a distinct subiculum of loosely interwoven hyphae; cylindrical cystidia with septa and clamps present . . . . . *Amphinema*, p. 65
9b. Basidiocarp membranaceous, no well developed subiculum present; cystidia absent, gloeocystidia or hyphidia may be present 10
10a. Basidia stalked, up to 50–70 µm long, with abruptly constricted basal part, the early stages often like a long-stalked pleurobasidium; cystidia or gloeocystidia absent, hyphidia in some species present . . . . . *Radulomyces*, p. 92
10b. Basidia narrowly clavate, up to 80 µm long, the basal parts not abruptly constricted, the early stages distinctly and narrowly cylindrical; fusiform cystidioles present *Cylindrobasidium*, p. 72
11a. Cystidia present, aseptate, thick-walled and heavily incrusted, 7–12–18(–24) µm wide; basidia urniform or suburniform 12
11b. Cystidia lacking or present, septate or aseptate, but then not thick-walled, never heavily incrusted and only up to *c.* 7–8 µm wide; basidia suburniform 13
12a. Basidia suburniform, slightly constricted in the middle; young basidia more or less cylindrical or narrowly clavate; imperfect *Aegerita*-state absent *Hyphoderma* pro parte, p. 87
12b. Basidia urniform to suburniform, mostly strongly constricted in the middle; young basidia broadly ellipsoidal; imperfect *Aegerita*-state present. . . . . *Bulbillomyces*, p. 69
13a. Young basidial stages broadly ellipsoidal or even pyriform, adult basidia *c.* 20–30 µm long; basidiocarp raduloid . . . . . *Basidioradulum*, p. 67
13b. Young basidial stages cylindrical to narrowly clavate; basidiocarp even, grandinioid or odontioid. 14
14a. Basidia rather small, *c.* 10–16 × 3–5 µm; spores mostly less than 7 µm long (up to 8 µm) *Hyphodontia*, p. 80
14b. Basidia longer, *c.* 20–35–45 × 6–8 µm; spores mostly more than 7 µm long (up to 12–15 µm) . . . . . *Hyphoderma*, p. 78

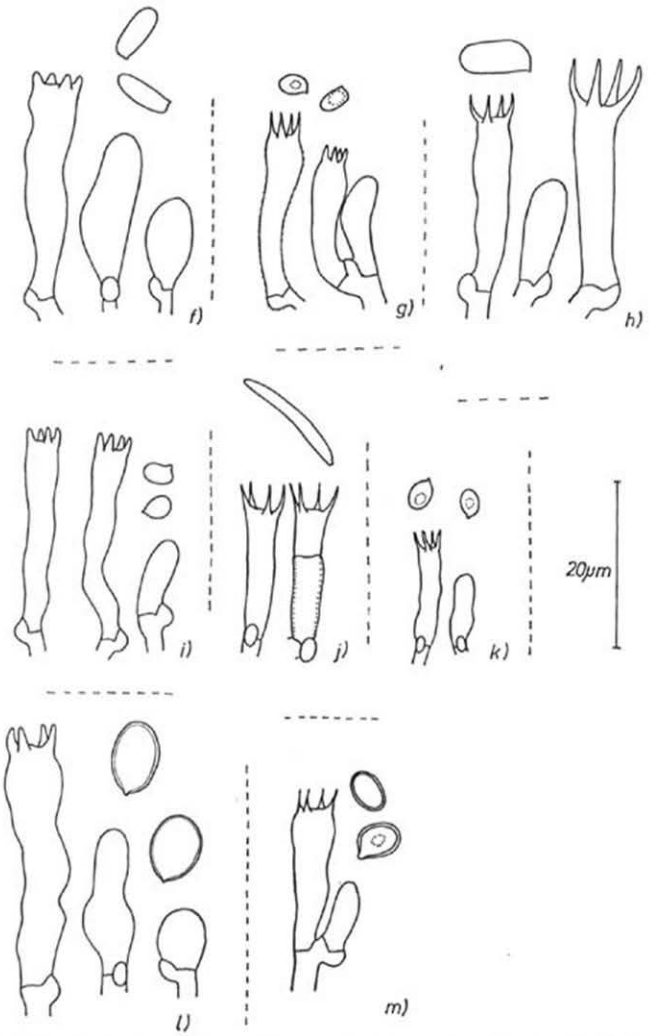

Fig. 2. Basidia: f. *Basidioradulum radula*; g. *Amphinema byssoides*; h. *Hyphoderma setigerum*; i. *Metulodontia nivea*; j. *Subulicystidium longisporum*; k. *Hyphodontia pallidula*; 1. *Bulbillomyces farinosus*; m. *Lagarobasidium pruinosum*.

AMPHINEMA P. Karst.

Amphinema P. Karst. *in* Bidr. Känn. Finl. Nat. Folk **51**: 228. 1892 (name change for *Diplonema* P. Karst. 1889, not ∽ G. Don 1837, not ∽ De Not. 1846, not ∽ Kjellmann 1855). — Type species: *Diplonema sordescens* P. Karst. = *Thelephora byssoides* Pers. ex Fr.

Basidiocarp effused, pellicular with a subiculum of loosely interwoven hyphae, rarely membranaceous and closely adnate; rhizomorphs present. Hymenial surface even, under a lens hairy owing to the far projecting cystidia. Hyphal system monomitic. Hyphae yellowish, rarely hyaline, often covered with small granules, more or less thin-walled, *c.* 2–4 μm in diameter. Cystidia hypha-like, cylindrical, nodose-septate, yellowish, rarely hyaline, densely covered with small granules, slightly thick-walled. Basidia suburniform or clavate, four-spored, clamped, *c.* 20–25 μm long. Spores hyaline, small, thin- to slightly thick-walled, often guttulate, not amyloid.

SCOPE.—One or two species of cosmopolitan distribution.

AMPHINEMA BYSSOIDES (Pers. ex Fr.) J. Erikss.—Fig. 3

Thelephora byssoides Pers. ex Fr., Syst. mycol. **1**: 452. 1821. — *Amphinema byssoides* (Pers. ex Fr.) J. Erikss. *in* Symb. bot. upsal. **16** (1): 112. 1958. — For the synonymy, see Rogers & Jackson (1943).

Basidiocarp effused, soft-membranaceous or often pellicular, loosely attached to the substrate, consisting of a rather thick subiculum of loosely interwoven hyphae supporting a thin hymenial layer; yellowish rhizomorphs often present. Hymenial surface even, more or less cream-coloured, slightly velvety owing to the projecting cystidia; often crater-like depressions can be seen on the surface: these are small patches of the basidiocarp where the basidia are lacking and the hyphae of the subiculum are visible. Hyphal system monomitic. Hyphae yellowish, cylindrical, distinct, rather thin-walled (0.2–0.3 μm), 2–3–4 μm in diameter, with clamps throughout, the surface often granulose, not cyanophilous. Cystidia hypha-like, yellowish, with clamps, slightly thick-walled (0.3–0.6 μm), 70–150 × 4–6 μm, 40–90 μm projecting, the surface mostly granulose, not cyanophilous; sometimes the cystidia develop from the clamps or more rarely apically a basidium or a cluster of basidia. Basidia cylindrical to mostly clavate, somewhat irregularly shaped, mostly smooth, but sometimes covered with small granules (like those found on hyphae and cystidia), hyaline, 20–25 × 4–5 μm, with four subulate, short sterigmata *c.* 2–3 × 0.8 μm; young basidia cylindrical. Spores hyaline, ellipsoidal, smooth, thin-walled to very slightly thick-walled (*c.* 0.3 μm), 4–4.5 × 2–2.5 μm, often 1-guttulate, with small, lateral apiculus; neither amyloid nor dextrinoid, not or only slightly cyanophilous (contrary to the statement by Eriksson & Ryvarden (1973) who found a "strong reaction to cotton blue").

CYTOLOGY.—Hyphae, cystidia and young basidial stages 2-nucleate, spores 1-nucleate.

SUBSTRATE.—Saprophytic on wood or bark of coniferous or frondose trees, on leaves, mosses, lichens, and on soil; also in mouse-holes, often met with under *Cladonia*-cushions.

MATERIAL STUDIED.—Germany: West-Berlin, Grunewald, 2.12.1967, *W. Jülich 955*; West-Berlin, Langes Luch, 14.2.1968, *W. Jülich 993*; Hessen, Weiszenborn, Graburg, 24.9.1968, *W. Jülich 2083*; Hessen, Albungen, Bilstein, 26.9.1968, *W. Jülich 2101*; Bayern, Füssen, 20.4.1968, *W. Jülich 1016*; Bayerischer Wald, Preying, 17.7.1968, *W. Jülich 1203*.

Austria: Hohentauern, 29.7.1968, *W. Jülich 1156*; Kärnten, Windisch Bleiberg, 17.9.1968, *W. Jülich 1409*; Kärnten, Göltschach südl. Klagenfurt, 16.9.1968, *W. Jülich 1246*; Kärnten, Gotschuchen, 18.9.1968, *W. Jülich 1459* (all specimens in Herb. Jülich).

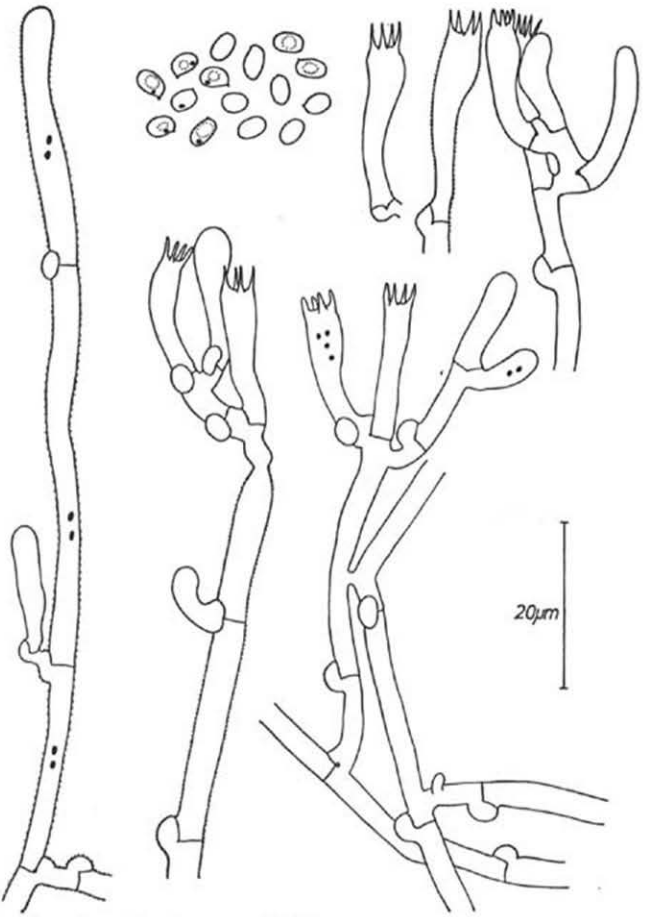

Fig. 3. *Amphinema byssoides*, Germany, *Jülich 955*.

Normally there is no difficulty in recognizing this yellowish coloured species even macroscopically, but there are some colour-variations: I collected two specimens with pure white basidiocarps, hyphae and rhizomorphs, (*W. Jülich 1409, 2101*) which are microscopically absolutely identical with the normal yellow forms.

BASIDIORADULUM Nobles

Basidioradulum Nobles *in* Mycologia **59**: 192. 1967. — Type species: *Hydnum radula* Fr.

Basidiocarp effused, resupinate or effuso-reflexed, membranaceous or with a ceraceous hymenial layer. Hymenial surface raduloid. Hyphal system monomitic. Hyphae hyaline, the basal ones more or less loosely arranged, the hymenial layer

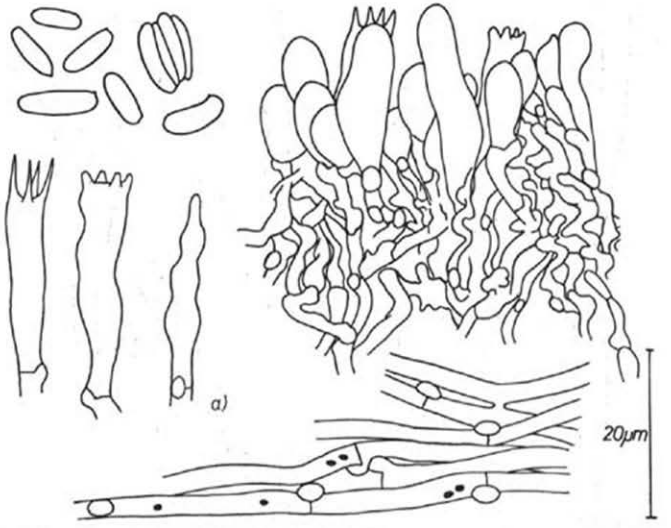

Fig. 4. *Basidioradulum radula*, Netherlands, *Maas Geesteranus 11785*. — a. Moniliform hypha

compact; thin-walled, clamped. Cystidioles present. Basidia when mature subumiform and constricted in the middle, the young stages broadly ellipsoidal or pyriform; with clamps at the base. Spores hyaline, thin-walled, cylindrical, non-amyloid.

SCOPE.—Only a few species or perhaps monotypic.

BASIDIORADULUM RADULA (Fr. ex Fr.) Nobles—Fig. 4

Hydnum radula Fr. ex Fr., Syst. mycol. **1**: 422. 1821. — *Basidioradulum radula* (Fr. ex Fr.) Nobles *in* Mycologia **59**: 192. 1967. — For the synonymy, see Nobles (1967).

Basidiocarp orbicular, later confluent, effused, up to several decimetres long in one direction, thick-membranaceous; margin adnate or reflexed, rhizomorphs lacking. Hymenial surface at first even, but soon covered with teeth of variable shape, from cylindrical or conical to plate-like, the tip in younger stages fertile, after rapid growth often sterile, scattered over the whole surface or slightly fasciculate; cream-coloured, the margin lighter. Hyphal system monomitic. Hyphae hyaline, rather thin-walled (0.2–0.4 µm), 2–3.5–5 µm in diameter, with clamps at all septa, the basal ones distinct and straight, the subhymenial ones often tortuous-torulose and indistinct. Cystidia and gloeocystidia lacking but moniliform cystidioles (35–60 × 5–7 µm) sometimes present. Basidia at first broadly ellipsoidal, later irregularly cylindrical to narrowly clavate, 22–30 × 4.6-6 µm, clamped at the base, with four subulate sterigmata *c.* 4–5 × 0.8–1 µm. Spores hyaline, cylindrical, often slightly curved, 7–10–11 × 2.3–3 µm, with small apiculus; neither amyloid nor dextrinoid or cyanophilous.

CYTOLOGY.—Hyphae 2-nucleate; I was unable to see nuclei in the basidia and the spores.

SUBSTRATE.—On bark of frondose trees (*Populus*, *Betula*, *Carpinus*, *Salix*, *Acer*, *Philadelphus*).

MATERIAL STUDIED.—Netherlands: Voorne, Oostvoorne, 6.10.1956, *R. A. Maas Geesteranus 11785* (L); Voorne, Rockanje, Quackjeswater, 6.5.1956, *R. A. Maas Geesteranus 11540* (L); Rijssen, Rijsserberg, 11.9.1955, *R. A. Maas Geesteranus 10664* (L); Wassenaar, Meyendel, Kijfhoek, 16.10.1954, *R. A. Maas Geesteranus 10170* (L); St. Pietersberg, Oosthelling, 17.10.1952, *R. A. Maas Geesteranus 9201* (L); Wassenaar, Meyendel, Bierlap, 30.10.1952, *C. Bas & R. A. Maas Geesteranus 9272* (L).
Germany: Lengerich, .12.1898, *W. Brinkmann* in Brinkmann, Westf. Pilze 85 (L).
England: Stockgrove Woods, Heath and Reach, near Rushmere Lodge, 14.5.1955, *D. A. Reid* (L 943.250–050).
Sweden: Gästrikland, Gävle, 18.4.1965, *J. A. Nannfeldt 19375* (L).
Finland: Elimäki, Mustiala, 29.6.1963, *O. von Schulmann* (L 962.271–112).

Bulbillomyces Jülich, *gen. nov.*

Carposoma resupinatum, membranaceum, adnatum, margo indistincta. Hymenium laeve, griseum vel cremeum. Systema hypharum monomiticum. Hyphae hyalinae, distinctae vel indistinctae, ± tenuitunicatae, fibulatae. Cystidia crasse tunicata, incrustata, fibulata. Basidia urniformia vel suburniformia, *c.* 20–30 µm longa, tetraspora, fibulata. Sporae hyalinae, tenui- vel incrassate tunicatae, inamyloideae. — Status imperfectus adest (*Aegerita*), cellis terminalibus ± clavatis, fibulatis. Typus: *Kneiffia farinosa* Bres. 1903.

Basidiocarp effused, adnate, membranaceous, margin indistinct. Hymenial surface even, greyish to ochraceous. Hyphal system monomitic. Hyphae hyaline, distinct or soon collapsed, rather thin-walled, with clamps, guttulate. Thick-walled cystidia present, incrusted, clamped. Basidia urniform or suburniform, *c.* 20–30 µm long, with four sterigmata and a clamp at the base. Spores hyaline, smooth, thin- or somewhat thick-walled, not amyloid. — Imperfect state present (*Aegerita*); its terminal cells more or less clavate and clamped.

The genus differs from other genera of the Hyphodermoideae in having urniform or strongly constricted suburniform basidia, thick-walled and incrusted cystidia (this is also the case in *Metulodontia*), and an imperfect *Aegerita*-state.

Bulbillomyces farinosus (Bres.) Jülich, *comb. nov.*—Figs. 5, 6

Kneiffia farinosa Bres. *in* Ann. mycol. **1**: 105. 1903 (basionym).
Peniophora farinosa (Bres.) Höhn. & Litsch. *in* Sber. Akad. Wiss. Wien **117**: 1095. 1908. — *Metulodontia farinosa* (Bres.) Parm., Consp. Syst. Cortic. 118. 1968.
Thelephora lactea Fr. *sensu* Fuckel *in* Jb. nassau. Ver. Naturk. **27–28**: 8. 1873 (misapplied).
Peniophora aegerita Höhn. & Litsch. *in* Sber. Akad. Wiss. Wien **116**: 810. 1907. — *Kneiffia aegerita* (Höhn. & Litsch.) Lindau, Krypt.-Fl. f. Anf. **1**: 13. 1911.
Peniophora candida Lyman *in* Proc. Boston Soc. nat. Hist. **33**: 168. 1907. — *Kneiffia candida* (Lyman) Herter, Krypt.-Fl. Mark Brandenb. **6**: 109. 1910.
Imperfect state: *Aegerita candida* Pers. ex Fr. 1821.

Basidiocarp effused, at first very thin and closely adnate, later more or less soft-membranaceous; margin indistinct, rhizomorphs lacking. Hymenial surface even, at first light greyish, later ochraceous, under a lens hispid owing to the long projecting cystidia. Hyphal system monomitic. Hyphae hyaline, thin- to slightly thick-walled

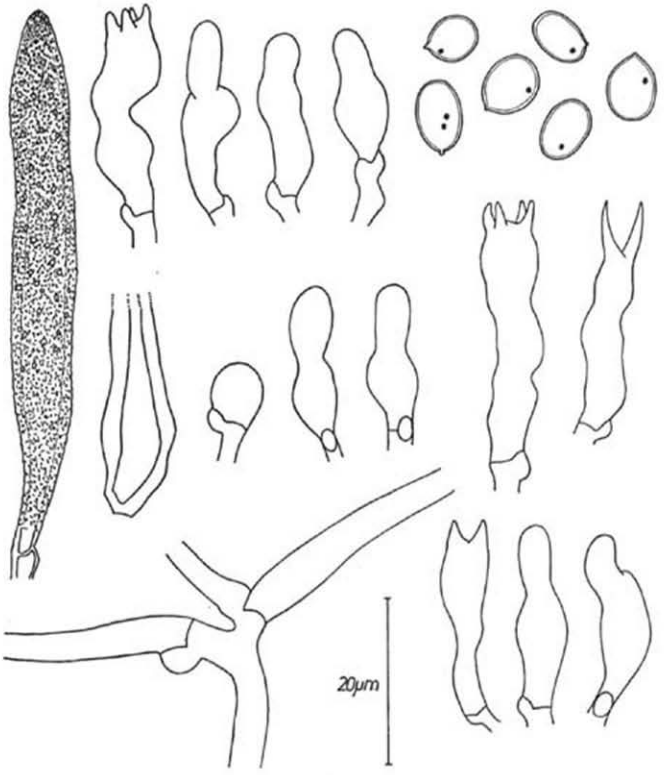

Fig. 5. *Bulbillomyces farinosus* (perfect state), Netherlands, *Maas Geesteranus 12911*.

(*c.* 0.3–0.4 µm), easily collapsed, *c.* 3–6 µm in diameter, with clamps. Cystidia present, thick-walled (*c.* 2–3 µm), incrusted, with a basal clamp, approximately cylindrical, gradually tapering towards the obtuse apex, 50–100×8–10 µm, projecting up to 60 µm. Basidia at first subglobose to pyriform, becoming urniform, later growing out at the apical part, giving the mature basidium a suburniform appearance, 20–26–32×6–8 µm, with four (*c.* 3×1 µm) rarely two (5–6×1.6 µm) sterigmata and a basal clamp. Spores smooth, hyaline, subglobose to broadly ellipsoidal, slightly thick-walled (*c.* 0.3–0.4 µm), 6–8.5–10×5–7 µm, with small apiculus, neither amyloid nor dextrinoid, not or only very slightly cyanophilous.

Aegerita candida-state: bulbils mostly ochraceous, sometimes pure white but becoming ochraceous in the herbarium, more or less ovoid (*c.* 0.2×0.1 mm), composed of centrifugally arranged branching chains of progressively larger cells, with clamps at all septa and numerous anastomoses; the apical cells broadly clavate and often stalked (*c.* 15–23×10–13 µm), at the apex with slightly thickened walls, otherwise thin-walled; the cytoplasma immediately turns a reddish brown colour in Melzer's reagent.

SUBSTRATE.—On wood or bark of frondose trees, mostly in very wet places.

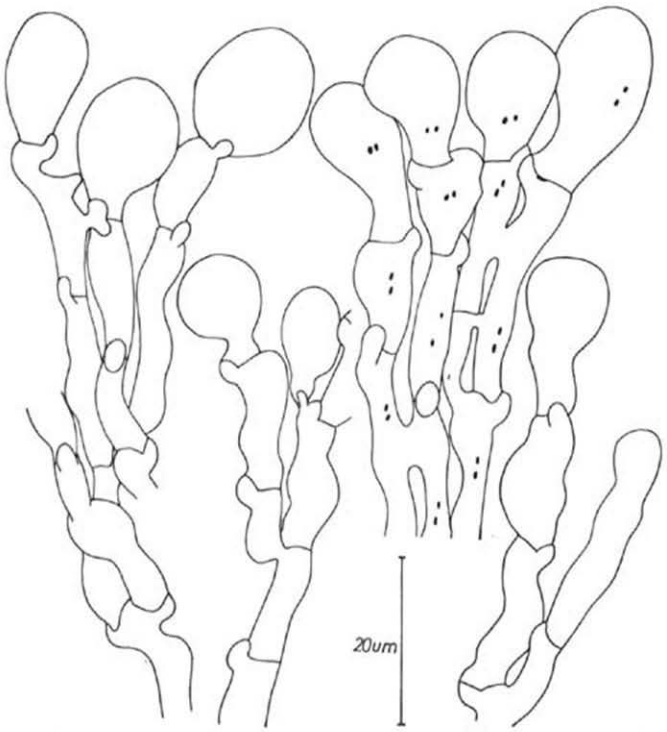

Fig. 6. *Bulbillomyces farinosus* (imperfect state), *Aegerita candida*, Netherlands, *Maas Geesteranus 12911*.

CYTOLOGY.—Spores mostly 1-nucleate, some 2-nucleate; in the Aegerita-state all the cells have constantly two nuclei.

MATERIAL STUDIED.—P o l a n d: (all under the name *Peniophora farinosa* Bres. n. sp.) (*sine loc.*), 1901, *Eichler* (S); (*sine loc.*), ad ramos deciduos, August, *Eichler 12* (S); (*sine loc.*), Auf *Ulmus*, Oktober, *Eichler 12a* (S).

G e r m a n y: West-Berlin, Spandau, Teufelsbruch, 12.11.1966, *W. Jülich 81*; 4.11.1967, *W. Jülich 873*, 887 (Herb. Jülich); Prov. Brandenburg, Triglitz in der Prignitz, 15.10.1913, *O. Jaap* in Jaap, Fung. sel. exs. 663 (L).

N e t h e r l a n d s: Groenekan, (Utr.), .11.1929, *H. Hirsch & M. A. Donk 1684* (L); 's-Gravenhage, Haagsche Bosch, 10.1930, *M. A. Donk 2172* (L); Goor-Diepenheim, 9.1929, *M. A. Donk 1935* (L); Ulvenhout, Ulvenhoutse Bos, 18.8.1959, 1.9.1959, *R. A. Maas Geesteranus 12911*, *12923* (L); Slangenburg prope Doetinchem, 10.9.1935, *W. J. Lütjeharms 2018* (L); Nuenen, Nederwetten, 24.9.1961, *R. A. Maas Geesteranus 13558* (L); Winterswijk, Walienseweg, 29.9.1956, *R. A. Maas Geesteranus 11763* (L); 's-Graveland, "Boekesteyn", 12.11.1966, *J. Daams* (L).

F r a n c e: Aveyron, Loubotis, 26.11.1913, *Galzin 14910* (L); (*sine loc.*), *L. Maire* (L).

C z e c h o s l o v a k i a: Jevany, 8.1924, *A. Pilát* (L).

The synonymy has been extensively discussed by Weresub (1961) who showed *Kneiffia farinosa* Bres. to be the oldest available name for the perfect state. In the Persoon herbarium at Leiden, one specimen is filed under the name "*Aegerita candida* P. / Specimen e Suecia missum. / Albert. et Schw. in herb. Pers." (L 910.249–1205); the bulbils are identical with the often collected imperfect state of *Kneiffia farinosa* Bres.

Cylindrobasidium Jülich, *gen. nov.*

Carposoma resupinatum vel raro resupinato-reflexum, molle, membranaceum, margo fimbriata. Hymenium laeve, cremeum. Systema hypharum monomiticum. Hyphae hyalinae vel leviter flavidae, laxe intertextae, distinctae, fibulatae. Cystidiola fusiformia adsunt. Basidia longa, plus minusve cylindracea vel paene clavata, 40–80 µm longa, tetraspora, fibulata. Sporae hyalinae, tenuitunicatae, inamyloideae. Typus: *Thelephora evolvens* Fr. ex Fr., Syst. mycol. **1**: 441. 1828.

Basidiocarp resupinate or seldom effuso-reflexed, membranaceous, with more or less fimbriate margin. Hymenial surface even, about cream-coloured. Hyphal system monomitic. Hyphae hyaline or slightly yellowish, loosely interwoven, distinct, with clamps. Fusiform cystidioles present. Basidia rather long, cylindrical to narrowly clavate, about 40–80 µm long, with clamps at the base, four-spored. Spores hyaline, thin-walled, non-amyloid.

SCOPE: One or two species.

Cylindrobasidium evolvens (Fr. ex Fr.) Jülich, *comb. nov.*—Figs. 7, 8

Thelephora evolvens Fr. ex Fr., Syst. mycol. **1**: 441. 1821 (basionym).

Thelephora cruenta Pers. ex Fr. *sensu* Fr., Syst. mycol. **1**: 444. 1821.

Corticium laeve f. *cucullatum* Bourd. & Galz., Hym. Fr.: 184. 1928. — *Corticium evolvens* f. *cucullatum* (Bourd. & Galz.) Donk *in* Meded. Ned. mycol. Ver. **18–20**: 142. 1931. — Type locality: France.

Corticium laeve f. *cystidiolatum* Bourd. & Galz. *in* Bull. Soc. mycol. Fr. **27**: 232. 1911. — Type locality: France.

Thelephora evolvens Fr., Obs. mycol. 154, pl. 4, fig. 1a, b. 1815 (devalidated name) ex Fr., Syst. mycol. **1**: 441. 1821. — *Corticium evolvens* (Fr. ex Fr.) Fr., Epicr.: 557. 1838. — *Stereum evolvens* (Fr. ex Fr.) Karst. *in* Bidr. Känn. Finl. Nat. Folk **37**: 126. 1882; *in* Medd. Soc. Fauna Fl. fenn. **9**: 52. 1882. — *Auricularia evolvens* (Fr. ex Fr.) Quél., Fl. mycol. France: 25. 1888. — *Basidioradulum evolvens* (Fr. ex Fr.) Parm., Consp. Syst. Cortic.: 112. 1968. — Neotype: "*Corticium evolvens* Fr., Lund" (Herb. E. Fries, UPS).

Corticium laeve f. *expallidum* Bres. *apud* Strass. *in* Verh. zool.-bot. Ges. Wien **52**: 430. 1902 (nom. nud.). — Type: not seen.

Corticium incarnatum var. *fallax* (Pers.) *sensu* E. P. Fries in herb. E. Fries, UPS.

Thelephora fibrosa Desm. in herb. E. Fries, UPS.

Thelephora fissilis Pers., Mycol. europ. **1**: 133. 1822. — Lectotype: "*Thelephora fissilis*. Mycol. Europ., — hirsuta (detrita?) vix" (L 910.267–465).

Thelephora flaccida Fr. in herb. E. Fries, UPS.

Thelephora flocculenta Fr., Elench. **1**: 184. 1828. — Fide Donk 1959.

Corticium laeve f. *imbricato-reflexum* Bourd. & Galz., Hym. Fr.: 184. 1928 (lacking descr.). — *Corticium evolvens* f. *imbricato-reflexum* (Bourd. & Galz.) ex Donk *in* Meded. Ned. mycol. Ver. **18–20**: 142. 1931. — Type locality: France.

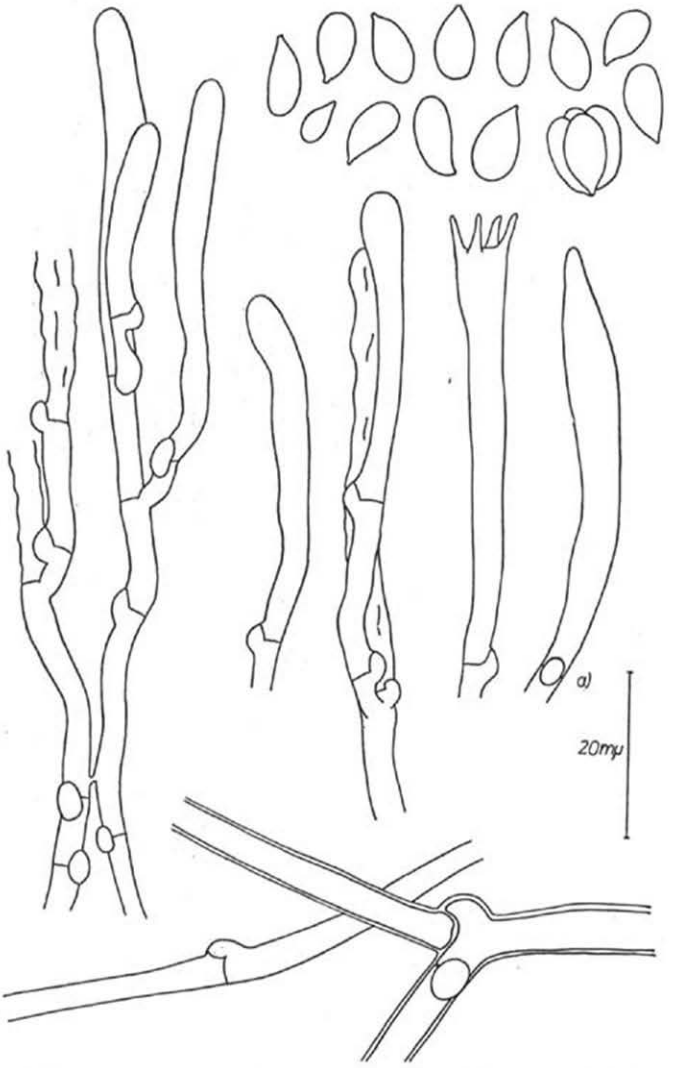

Fig. 7. *Cylindrobasidium evolvens*, Sweden, Neotypus, Herb. Fries. — a. Cystidiole.

Corticium laeve Pers. *in* Neues Mag. Bot. **1**: 110. 1794; Tent. Disp. Fung.: 30. 1797 (devalidated name). — *Thelephora laevis* Pers., Syn. Fung.: 575. 1801 (devalidated name). — *Thelephora laevis* (Pers.) ex Fr., Syst. mycol. **1**: 451. 1821; Pers., Mycol. europ. **1**: 130. 1822. — *Corticium laeve* (Pers. ex Fr.) Fr., Epicr.: 560. 1838. — *Hypochnus laevis* (Pers. ex Fr.) Bonord., Handb. Allg. Mykol.: 160. 1851. — *Stereum laevis* (Pers. ex Fr.) Karst. *in* Medd. Soc. Fauna Fl. fenn. 9: 70. 1882. — *Peniophora laevis* (Pers. ex Fr.) Burt *apud* R. Fries *in* Acta R. Sci. Soc. gothob. IV, **3**: 36. 1900 (misapplied). — *Kneiffia laevis* (Pers. ex Fr.) Bres. *in* Annls mycol. **1**: 100. 1903

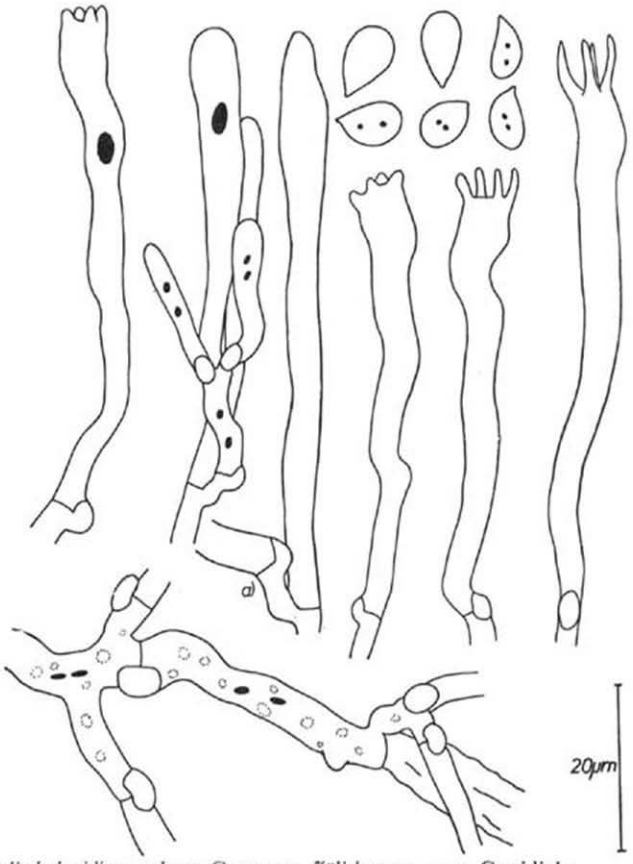

Fig. 8. *Cylindrobasidium evolvens*, Germany, *Jülich 1014*. — a. Cystidiole.

(misapplied). — Lectotype: "*Thelephora laevis*. Syn. fungorum" [scripsit Persoon] (L 910.267-619).

Thelephora laxa Pers., Mycol. europ. **1**: 143. 1822; not ~ Fr., Elench. **1**: 196. 1828. — *Corticium evolvens* subsp. *laxum* (Pers.) Fr., Epicr.: 557. 1838. — Lectotype: "*Thelephora*" [scripsit Mougeot] "*laxa*. Myc. Europ. **1**. p. 148. *Th. evolvens* var. d. Fries. Elench. fung. p. 182" [scripsit Persoon] "Ecorce de Hêtres morts au sommet de Voges" [scripsit Mougeot] (L 910.267-613).

Cladoderris minima Berk. & Br. *in* Ann. Mag. nat. Hist. V, **1**: 24. 1878. — *Stereum minimum* (Berk. & Br.) Lloyd in Mycol. Writ. **4** (Syn. stip. Ster.): 36. 1913. — Fide D. A. Reid 1962. *Stereum nodulosum* v. Post in herb. E. Fries, UPS.

Corticium laeve f. *odontioidea* W. Brinkm. *in* Bot. Z. **67** II: 229. 1909 (without separate descr.). — No specimen mentioned.

Thelephora populina Sommerf., Suppl. Florae Lapp.: 284. 1826; Fr., Elench. **1**: 183. 1828 (not definitely accepted: "...utrum varietates, an species haud dicam."); not ~ Fr., Elench. **1**: 184. 1828 ("ined.", as synonym of *Thelephora flocculenta* Fr.). — *Corticium populinum* (Sommerf.) Fr., Epicr.: 559. 1838. — Type: not seen.

Athelia salicum Pers. *sensu* Fr. 1828 et 1838.

Thelephora sarcoides Fr., Elench. **1**: 185. 1828. — *Corticium sarcoides* (Fr.) Fr., Epicr.: 558. 1838. — Terana sarcoides (Fr.) O.K., Rev. Gen. Pl. **2**: 872. 1891 ("*sarcodes*"). — *Lomatina sarcoides* (Fr.) Höhn. & Litsch. *in* Ann. mycol. **4**: 294. 1906. — *Cytidia sarcoides* (Fr.) Herter *in* KryptogFl. Brandenb. **6**: 84. 1910 (misapplied); W. B. Cooke *in* Mycologia **43**: 204. 1951 (misapplied). — Neotype: "*Corticium sarcoides* Fr., Femsjö" (Herb. E. Fries, UPS).

Aleurodiscus sendaiensis Yas. *apud* Lloyd *in* Mycol. Writ. **7**: 1162. 1922 (nom. nud.). — Fide Lemke 1964.

Basidiocarp membranaceous, at first forming rounded resupinate patches with white fimbriate margin, often with one wart in the middle, then confluent and widely effused, up to several decimeters in one direction, totally resupinate and adnate or with loosened margins or more rarely effuso-reflexed with distinct small pilei; rhizomorphs lacking. Hymenial surface even, cream coloured or ochraceous. Hyphal system monomitic. Hyphae almost hyaline, but the basal and older ones often slightly yellowish-brownish; thin- to somewhat thick-walled (up to 0.4–1.0 μm), 3–4–5 μm in diameter, with clamps, guttulate. Fusiform cystidioles present, sometimes rare, *c.* 60–80 × 6–7.5 μm, clamped. Basidia cylindrical to very narrowly clavate, not distinctly stalked, 40–60–80 × 6–7–8 μm, always clamped at the base, with four sterigmata *c.* 4–6 × 1–1.5 μm. Spores hyaline, pyriform, thin-walled, 8–10–12 × 4.3–5–6 μm, with large apiculus, often agglutinated, not amyloid or dextrinoid, in some specimens slightly cyanophilous.

CYTOLOGY.—Hyphae, young basidial stages and spores bi-nucleate.

SUBSTRATE.—On leaves, wood or bark of frondose and coniferous trees.

This is a very common and variable species. For the pileate form Fries (Obs. mycol., 1815) created the name *Thelephora evolvens* after a specimen he received from Acharius. His description runs as follows (p. 154): "197. *Thelephora evolvens*, junior subrotunda clausa, dein evolvens subcupulaeformis, extus marginaeque pallida tomentosa, disco glabro obscuriori". Plate IV, fig. 1 shows two glubular fruitbodies, the younger one *c.* 4 mm in diam. and still closed, the adult one *c.* 7–8 mm in diameter and opened with a *c.* 2–3 mm wide mouth. In 1821 (Mycol. europ. **1**) Fries repeats his first diagnosis with only slight modifications (p. 441): "*T. evolvens*, junior, subrotunda clausa, dein evoluta cupulaeformis, . . .". In 1828 (Elench. **1**) he speaks of "resupinata, submarginata", but recognizes several very variable forms: "forma, effusa excepta, nulla constans; variat a) cupularis; b) effuso-reflexa, pileata; c) minuta, immarginata, sed demum involuta; d) prorsus immarginata et effusa" (l.c.). In 1838 (Epicr.: 557) he describes the species as "molle, resupinatum, submarginatum" and mentions a cupular, an effuso-reflexed, and a resupinate form.

Several further synonyms have been given by Fries (1828) and later mycologists, but not all of them really belong to this species.

e v o l v e n s. — Under this name three specimens determined by Fries himself are present in his herbarium (UPS): a) *Corticium evolvens* Fr., Lund", consisting of several small, more or less pileate basidiocarps on bark of *Betula*, in outer appearance and substrate coming closest to the original description. Fries (1815: 155) describes substrate and collector as follows: "In ramis & truncis betulinis rarissimam & distinctissimum speciem invenit mecumque liberalissime communicavit ill. Prof. & Eques

Acharius". In his later work (Fries, 1821: 442) we only find: "Ad cortices Betulae. Aut. (v.s.)". — Since there is no indication that this is the holotype sent by Acharius, I consider this specimen the neotype of the species. — b) "*Corticium evolvens*, Upsaliae". Basidiocarp effused, resupinate, strongly cracked. — c) "*Corticium evolvens* Fr., Femsjö". Basidiocarp resupinate, adnate; on bark of a coniferous tree.

f a l l a x. — Herb. E. Fries, UPS. — "*Corticium incarnatum* v. *fallax* (P.), Upsala 1857, E. P. Fries". Basidiocarp more or less orbicular, tuberculate, confluent and resupinate.

f i b r o s u s. — A specimen filed under *Corticium evolvens* Fr. in herb. E. Fries, UPS was sent to E. Fries by Desmazières. The latter gave an extensive description of this fungus, followed by the sentences: "Cette espèce a des rapports avec le thelephora sericea. Si ce nest pas lui comme je le pense on pourroit l'appeler thel: fibrose. Votre opinion s'il vous plaît, Desmazières"

f i s s i l i s. — There are three specimens in the Persoon herbarium filed under this name, all of them are identical with *Thelephora evolvens* Fr. The first one (L 910.267-465) bears the following label in Persoon's handwriting: "*Thelephora fissilis.* — hirsuta (detrita?)". Later (because the colour of the ink is different) Persoon added to fissilis "Mycol. Europ." and to hirsuta "vix". The morphology of the basidiocarp agrees very well with his description in Mycol. europ. **1**: 133. 1822: "longitudinaliter effusa, sordide alutacea, demum in particulas basi cohaerentes fissa, papillis copiosis magnis subaequalibus". He (loc. cit.) already suggests an affinity to *Thelephora laevis*, but also to *T. incarnata*, now a *Peniophora*. The other two specimens are: "*Thelephora*" [scripsit Mougeot] "*fissilis* Mycol. Europ. **1**. p. 133. — *laevis* var?" [scripsit Persoon] "in ramulis Aceris Pseudoplatani" [scripsit Mougeot] (L 910.267-471). — "*Th. fissilis?*" [scripsit Persoon] "*Thelephora frustulata* Pers. p. 577 / celle ci me paroit se rapporter d'avantage à votre description mais qu'est le No. 193" [scripsit Mougeot] (L 910.267-464).

f l a c c i d u s. — "*Thelephora flaccida. Corticium*". Herb. E. Fries, UPS. — Basidiocarps resupinate, adnate or with loosened margins; on bark of *Betula*. The genus name *Corticium* has later been added.

l a e v i s. — In 1797 Persoon described his fungus (p. 30) as ". . .Juvenili quidem orbiculata & papilla saepe unica instructa, in adultis vero speciminibus superficies tota laevis est & papillae evanescunt". Later, in Persoon 1801, 1822, Fries 1821, 1828, 1838, 1874, the papillae are no longer mentioned.

Several specimens of *Thelephora laevis* are in the Persoon herbarium, one of them is here designated as lectotype: "*Thelephora laevis.* Syn. fungorum" scripsit Persoon (L 910.267-619); it agrees very well with the descriptions in Persoon and Fries and is well preserved. Furthermore it is the only collection collected before 1821 and 1822 and the only one which has been accepted by Persoon without adding "?", "var?" or other remarks. All other specimens have been studied with the following results:

a) "No. 13 thelephora laevis Mycolog. p. 130.? / on le trouve maintenant sur divers arbres abattus et dénudés d'écorce. il n'a pas changé de couleur par la dessication" [scripsit Desmazières] (L 910.267–621); is this species. — b) "*Theleph. laevis* ? var.? *tuberculosa*" [scripsit Persoon] (L 910.267–558); is this species.

c) "*Theleph. laevis*?" [scripsit Persoon] (L 910.267–549); has narrow, clamped hyphae; is not this species. — d) "*Thelephora laevis* Pers. p. 575" [scripsit Chaillet] "*Thelephora*" [scripsit Persoon] (L 910.267–551); is a *Peniophora* spec. — e) "*Thelephora laevis*. var.? / sed margo non villosus est. / Sylvula Vincennes / prope Parisios / Junio-Julio, 1828". [scripsit Persoon] (L 910.267–64); is not this fungus. — f) "*Thelephora? laevis*? / Prope Parisios" [scripsit Persoon] (L 910.267–63); is not this fungus.

laxus. — The lecto-type specimen (L 910.267–613) agrees, as to the morphology of the basidiocarp, perfectly with the description given by Persoon (1822: 143): ". . . orbicularis . . . . Forte nondum bene evoluta. Affinitatem habere videtur cum *Peziza amorpha*". The type locality "Hab. in summitatibus montium Vogesiorum". (Pers., loc. cit.) is identical with the habitat written by Mougeot "au sommet de voges." — Two other specimens are present in the Persoon herbarium: a)" "*Thelephora*" [scripsit Mougeot] "*mesenterica laxa* ? / an fungus bene evolutus?" [scripsit Persoon) "Je n'ai trouvé qu'un Echantillon de cette espece que je partage avec vous, voila Monsieur vous en voyez ici si peu." [scripsit Mougeot]; this specimen is *Peniophora polygonia* (Pers. per Fr.) Bourd. & Galz. — b) "*Thelephora* ? *laxa* / prope Parisios" [scripsit Persoon]; the fungus has disappeared. — According to Fries (1828, Elench. **1**: 182) *Thelephora laxa* Pers. is identical with his variety α "fide spec. Mougeot!".

nodulosus. — Herb. E. Fries, UPS. — "*Stereum* ? *nodulosum* v.P., pa Björkqvist — Entragen 9/11, 61, H. v. Post". Basidiocarp resupinate; on bark of *Betula*.

populinus. — Of this species, one specimen is present in herbarium E. Fries, UPS: "*Corticium Populi* Smrft (teste Blytt), Christiania, M. N. Blytt" scripsit Th. M. Fries; this is identical with *Thelephora evolvens* Fr. According to Bresadola (cited in J. Egeland, *in* Nytt Mag. Naturvid. **49**: 374. 1912) "Likeledes es Sommerfelts *Corticium populinum* identisk med *C. evolvens* Fr. hvilket Bresadola har fastslaat i skrivelse til mig efter undersøkelse av typer fra Sommerfelts herbarium."

salicum. — *Athelia salicum* Pers. is a true species of *Athelia*, relate to *A. epiphylla* Pers. but differs in having broader ellipsoidal spores. *Athelia salicum* Pers. *sensu* Fries is identical with *Thelephora evolvens* Fr. Fries based his opinion on a specimen he received from Chaillet with the following remark: "*Athelia salicum* N. E. J'ignore complettement la plante que Persoon me met sur le corps, je lui ai envoyé celle ci sous le nom de *Thelephora salicum*, dans sa reponce il l'appellait frustulata. si ce nest pas celle ci je ne scais ce que c'est. Chaillet" (Herb. E. Fries, UPS) (sub *Corticium evolvens*).

sarcoides. — "*Corticium sarcoides* Fr., Femsjö" Herb. E. Fries, UPS. — Basidiocarps mostly small, orbicular or tuberculate, some of them with reflexed edges; on bark of *Betula*. "*Corticium sarcoides*, Christiania, M. N. Blytt" Herb. E. Fries, UPS. — Basidiocarps resupinate, with loose margins; on bark of *Betula*.

FURTHER SPECIMENS STUDIED.—Germany: Füssen im Algau, 20.4.1968, *H. Wunder* (Herb. Jülich 1014).
Tunisia: N. of Hammamet, 9.4.1968, *W. Jülich 1012* (Herb. Jülich).
Canada: Ontario, Nashville, York Co., 30.10.1955, *R. F. Cain* (L 958.142–029).

HYPHODERMA Wallr. emend. Donk

Hyphoderma Wallr., Fl. crypt. Germ. **2**: 576. 1833; not ∽ Fr. 1849; emend. Donk *in* Fungus **27**: 13. 1957. — Type species: *Hyphoderma spiculosum* Wallr. = *Thelephora setigera* Fr.
Kneiffia Fr., Fl. scand. 340. 1835 (nom. nud.); Fr., Gen. Hym. 17. 1836; not ∽ Spach 1835. — Type species: *Thelephora setigera* Fr.
Kneiffiella Underw. *in* Bull. Torrey bot. Cl. **24**: 205. 1897; not ∽ Karst. 1889. — Isonym[1] of *Kneiffia* Fr.
Kneiffiella Henn. *in* Engl. & Prantl, Natürl. PflFam. **1**(1**): 139. 1838. — Isonym of *Kneiffia* Fr.
Neokneiffia Sacc., Tab. comp. Gen. Fung. **11**: 1898; Syll. Fung. **14**: 11. 1899. — Isonym of *Kneiffia* Fr.
Pycnodon Underw. *in* Bull Torrey bot Cl. **25**: 631. 1898. — Isonym of *Kneiffia* Fr.
Atheloderma Parm., Consp. Syst. Cortic. 73. 1968. — Type species: *Atheloderma mirabile* Parm.
Metulodontia Parm., Consp. Syst. Cortic. 117. 1968. — Type species: *Kneiffia nivea* Karst.

Basidiocarp effused, membranaceous or somewhat ceraceous, in some species pellicular. Hymenial surface mostly even, in some species grandinioid or odontioid. Hyphal system monomitic. Hyphae hyaline, thin-walled to slightly thick-walled, normally cylindrical (*c.* 3–5 μm in diameter), but in some species ampulliform (up to 10 μm in diameter), with clamps at the primary septa. Cystidia, gloeocystidia or cystidioles present in most species. Basidia when mature suburniform and constricted in the middle, when young cylindrical to narrowly clavate, *c.* 20–45 × 6–8 μm, with a basal clamp, often guttulate. Spores hyaline, thin-walled, cylindrical to ellipsoidal, normally longer than 7 μm, often guttulate, non-amyloid.
SCOPE: More than 40 species.

HYPHODERMA SETIGERUM (Fr.) Donk—Fig. 9

Thelephora setigera Fr., Elench. **1**: 208. 1828. — *Hyphoderma setigerum* (Fr.) Donk, *in* Fungus **27**: 15. 1957. — For the synonymy, see Rogers & Jackson 1943: 282–283.

Basidiocarp resupinate, membranaceous, loosely adnate, with arachnoid margin; rhizomorphs lacking. Hymenial surface even or mostly mealy-granulose to slightly odontioid, more or less cream-coloured. Hyphae hyaline, loosely interwoven, thin-walled to somewhat thick-walled (up to 1.0 μm), 3–5 μm in diameter, with clamps; in older hyphae some secondary hyphae with simple septa present. Cystidia hyaline to slightly yellowish, long, cylindrical, mostly septate, smooth or loosely covered with crystals, somewhat thick-walled (up to 1.0 μm), 100–200 × 7–10 μm, projecting about 30–80–130 μm; the primary septa have always a clamp whereas the secondary septa of the older cystidia are simple. Basidia clavate, 15–25–35 × 6–8 μm, with basal clamp; with four sterigmata *c.* 5–6 × 1.5 μm. Spores hyaline, cylindrical to slightly allantoid, thin-walled, 9–12–14 × 4–5 μm, with small lateral apiculus, neither amyloid nor dextrinoid or cyanophilous.

[1] Isonym, a name having the same basionym.

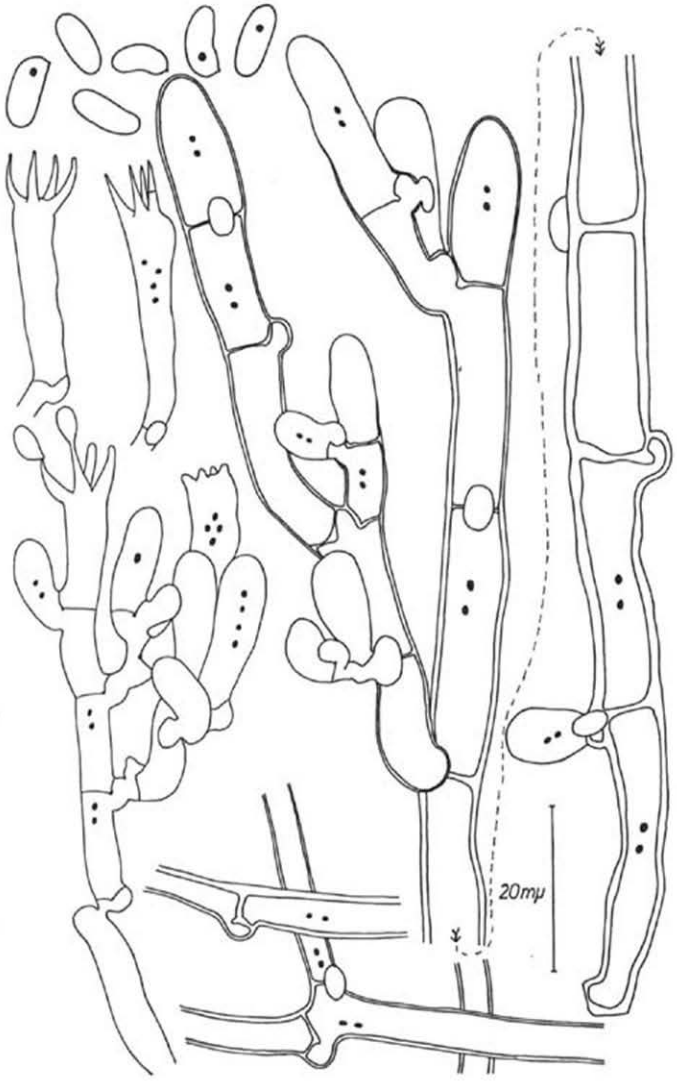

Fig. 9. *Hyphoderma setigerum*, Netherlands, Meyendel, 1973, *Jülich*.

CYTOLOGY.—Hyphal cells, young basidial stages and cystidial cells 2-nucleate, spores 1-nucleate.

SUBSTRATE.—On wood or bark of coniferous or frondose trees.

MATERIAL STUDIED.—E n g l a n d: Kings, Langley, Herts., 19.10.1953, *D. A. Reid* (L 954.017–061).

Germany: Berlin-West, 1967 and 1968, *W. Jülich 562, 614, 861, 880, 1171.* (Herb. Jülich); Hessen, Eschwege, Lotzenkopf, 25.9.1968, *W. Jülich 2046* (Herb. Jülich).
Austria: Kärnten, Viktring, 19.9.1968, *W. Jülich 1336* (Herb. Jülich).

Some species have to be transferred to *Hyphoderma*: **Hyphoderma alienum** (Parm.) Jülich, *comb. nov.* (basionym: *Basidioradulum alienum* Parm., Consp. Syst. Cortic. 204. 1968); **Hyphoderma anthracophilum** (Bourd.) Jülich, *comb. nov.* (basionym: *Corticium anthracophilum* Bourd. *in* Rev. sci. Bourbonn. **23**: 9. 1910); **Hyphoderma bresadolae** Jülich, *nom. nov.* (basionym: *Corticium niveum* Bres. *in* Annls mycol. **1**: 98. 1903, not *Hyphoderma niveum* Fuck. 1869); **Hyphoderma compta** (Jacks.) Jülich, *comb. nov.* (basionym: *Peniophora compta* Jacks. *in* Can. J. Res. **26**: 138. 1948); **Hyphoderma cremeo-album** (Höhn. & Litsch.) Jülich, *comb. nov.* (basionym: *Corticium cremeo-album* Höhn. & Litsch., Wiesner-Festschrift 63. 1908); **Hyphoderma cremeo-alutaceum** (Parm.) Jülich, *comb. nov.* (basionym: *Metulodontia cremeo-album* Parm., Consp. Syst. Cortic. 216. 1968); **Hyphoderma gemmiferum** (Bourd. & Galz.) Jülich, *comb. nov.* (basionym: *Corticium gemmiferum* Bourd. & Galz. *in* Bull. Soc. mycol. France **27**: 250. 1911); **Hyphoderma griseo-flavescens** (Litsch.) Jülich, *comb. nov.* (basionym: *Corticium griseo-flavescens* Litsch. *in* Pilát & Lindtner, Bull. Soc. sci. Skopje **18**: 178. 1938); **Hyphoderma karstenii** Jülich, *nom. nov.* (basionym: *Kneiffia nivea* Karst. *in* Hedwigia **35**: 173. 1896; not *Hyphoderma niveum* Fuck. 1869); **Hyphoderma mirabile** (Parm.) Jülich, *comb. nov.* (basionym: *Atheloderma mirabile* Parm., Consp. Syst. Cortic. 200. 1968); **Hyphoderma orientale** (Parm.) Jülich, *comb. nov.* (basionym: *Atheloderma orientale* Parm., Consp. Syst. Cortic. 202. 1968); **Hyphoderma probatum** (Jacks.) Jülich, *comb. nov.* (basionym: *Peniophora probata* Jacks. *in* Can. J. Res. **26**: 134. 1948); **Hyphoderma pruni** (Lasch) Jülich, *comb. nov.* (basionym: *Odontia pruni* Lasch *in* Rabenh., Fung. eur. exs. 1514. 1872); **Hyphoderma sambuci** (Pers. ex Pers.) Jülich, *comb. nov.* (basionym: *Thelephora sambuci* Pers. ex Pers., Mycol. europ. **1**: 152. 1822.

HYPHODONTIA J. Erikss.

Hyphodontia J. Erikss. *in* Symb. bot. upsal. **16**(1): 101. 1958. — Type species: *Peniophora pallidula* (Bres.) Bres. ex Bourd. & Galz.

Basidiocarp effused, resupinate, membranaceous, sometimes pellicular or thin-ceraceous; rhizomorphs absent. Hymenial surface rarely even, more often grandinioid or odontoid. Hyphal system monomitic (but with a tendency to dimitism). Hyphae narrow-cylindrical, thin-to somewhat thick-walled, mostly with clamps. Cystidia often present. Basidia when mature suburniform, constricted in the middle, cylindrical to narrowly clavate when young, *c.* 12–16×3–5 µm, with four (rarely two) sterigmata, mostly with a clamp at the base. Spores hyaline, thin-walled, subglobose to cylindrical or allantoid, in most species not longer than 7 µm, non-amyloid.

SCOPE.—More than 30 species.

The genus *Fibricium* J. Eriksson 1958 is very similar, differing only in the dimitic hyphal system. I studied three specimens of *Corticium rude* Karst. (ex S) which are identical with *F. greschikii* (Bres.) J. Erikss.: **Fibricium rude** (Karst.) Jülich, *comb. nov.* (basionym: *Corticium rude* Karst. *in* Bidr. Känn. Finl. Nat. Folk **37**: 143. 1882; Meddn Soc. Fauna Fl. fenn. **9**: 53. 1882 (Lat. diagn.); not ~ Pat. 1915).

HYPHODONTIA PALLIDULA (Bres.) J. Erikss.—Fig. 10

Gonatobotrys pallidula Bres. *in* Ann. mycol. **1**: 127. 1903. — *Hyphodontia pallidula* (Bres.) J. Erikss. *in* Symb. bot. upsal. **16**(1): 104. 1958. — For the synonymy, see Rogers & Jackson, 1943. — *Hyphodontia alutaria* (Burt) J. Erikss. is probably another synonym.

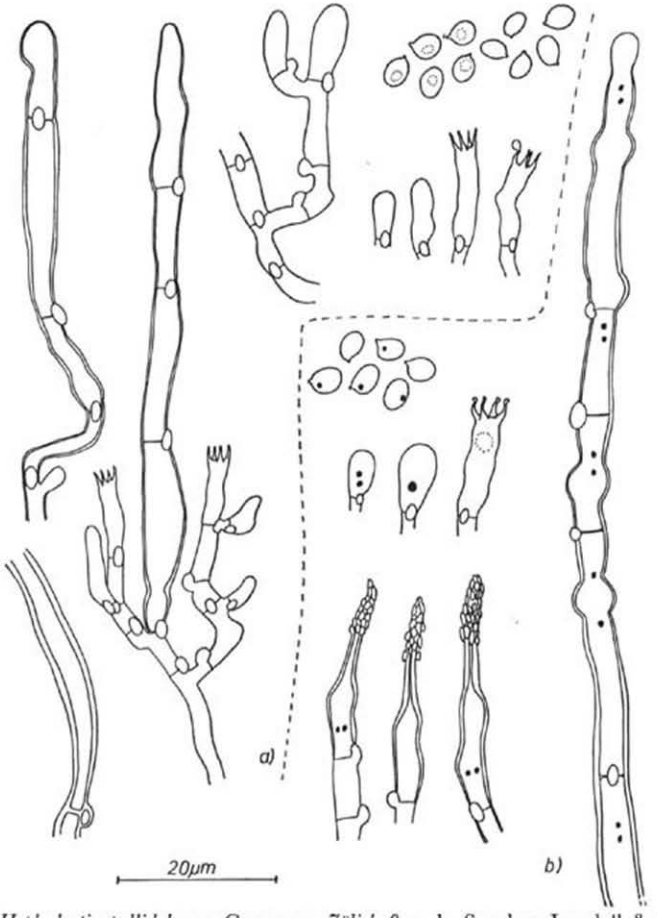

Fig. 10. *Hyphodontia pallidula*: a. Germany, *Jülich 849*; b. Sweden, Lundell & Nannfeldt, Fung. exs. suec. 572.

Basidiocarp effused, resupinate, membranaceous, thinning out towards the margin which is not definite; rhizomorphs lacking. Hymenial surface even to grandinioid, pale greyish-ochraceous. Hyphal system monomitic, but the basal hyphae often rather thick-walled. Hyphae cylindrical, hyaline to slightly yellowish (the basal ones), rather thick-walled (0.4–0.8–1.2 μm), 2.5–4 μm in diameter, with clamps, cyanophilous. Cystidia irregular-cylindrical with apical and intercalary swellings, rather thick-walled (0.4–0.8 μm) *c.* 40–90×4–7(–10) μm, up to 50 μm projecting, with clamped septa; the top of the cystidia often somewhat capitate and thin-walled, which seems to suggest that the cystidia are capable to grow out from this point, keeping pace with the thickening hymenium; distinctly cyanophilous. Lagenocystidia, i. e. short cystidia with abruptly narrowed and incrusted apical part, may be present. Basidia irregularly cylindrical with a constriction in the middle, 12–16×3.2–4.5 μm, with a basal clamp; with four subulate sterigmata curved inwards, *c.* 3×1 μm; somewhat cyanophilous; young basidia broadly cylindrical to ellipsoidal, Spores hyaline, smooth, broadly ellipsoidal, thin-walled, 3.5–4.5×2.5–3.5 μm, with distinct apiculus, often 1-guttulate, neither amyloid nor dextrinoid, not or only slightly cyanophilous.

CYTOLOGY.—Hyphae, cystidia and young basidia 2-nucleate, spores 1-nucleate.

SUBSTRATE.—On rotten wood of frondose and coniferous trees.

MATERIAL STUDIED.—Sweden: Västergötland, Östad, SO. om St. Kangekärr, 15.9.1968, *K. Hjortstam* (S); Småland, Femsjö par., the N. slope of Dullaberget, 10.8.1937, *S. Lundell* (S).

Denmark. Amager, Kongelunden, 1.10.1955, *MP. Christiansen* (L).

Germany: Niedersachsen, Harz, Achtermann, 20.10.1967, *W. Jülich 849, 897* (Herb. Jülich); Görlitz, 10.1933, *A. Pilát* (PC).

Great Britain. Cumberland, Keswick, 3.6.1962, *D. A. Reid* (L).

Canada: Little White River, Twp. 1. B., Algoma D. Ont., 14.9.1956, *R. F. Cain* (L).

HYPOCHNICIUM J. Erikss.

Hypochnicium J. Erikss. *in* Symb. bot. upsal. **16**(1): 100. 1958. — Type species: *Corticium bombycinum* (Sommerf.) Karst.

Basidiocarp resupinate, effused, membranaceous; rhizomorphs lacking. Hymenial surface even, grandinioid or odontoid. Hyphal system monomitic. Hyphae hyaline, thin-walled to somewhat thick-walled, with clamps. Gloeocystidia or cystidioles often present. Basidia clavate or suburniform when mature, almost cylindrical when young, clamped at the base with four sterigmata. Spores hyaline or slightly yellowish, distinctly thick-walled, the surface smooth or sculptured, non-amyloid.

SCOPE.—About 10 species.

HYPOCHNICIUM BOMBYCINUM (Sommerf.) J. Erikss.—Fig. 11

Thelephora bombycina Sommerf., Suppl. Fl. lapp. ed. Wahlenb. 284. 1826; Fries, Elench. **1**: 211. 1828. — *Corticium bombycinum* (Sommerf.) Karst. *in* Hedwigia **32**: 120. 1893. — *Hypochnicium bombycinum* (Sommerf.) J. Erikss. *in* Symb. bot. upsal. **16** (1): 101. 1958.

Basidiocarp effused, adnate, membranaceous, with fimbriate margin, lacking rhizomorphs. Hymenial surface even or sometimes warted, about cream-coloured.

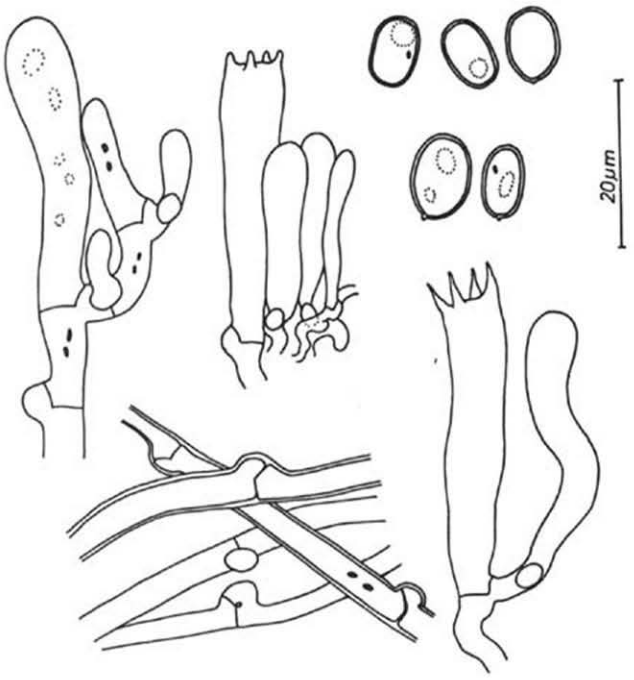

Fig. 11. *Hypochnicium bombycinum*, Norway, type.

Hyphal system monomitic. Hyphae hyaline, thin- to thick-walled (up to 0.8–1.2 µm), 3–6 µm in diameter, with clamps at the septa (rarely some secondary septa lacking clamps). Cystidia lacking, but in compact basidiocarps hyphidia may be present. Basidia large, clavate, somewhat flexuous, thin-walled to slightly thick-walled, hyaline, 30–35–45 × 7–8–9 µm, clamped at the base, containing oil-drops in the cytoplasma, with four subulate sterigmata *c.* 4–5 × 0.8–1 µm. Spores hyaline, broadly ellipsoidal, smooth, distinctly thick-walled (0.4–0.6–0.8 µm), 8–11 × 6–8 µm, with small apiculus, neither amyloid nor dextrinoid but often weakly cyanophilous, mostly with 1–2 guttules.

CYTOLOGY.—Hyphae, hyphidia and young basidial stages 2-nucleate, spores 1-nucleate.

SUBSTRATE.—On wood or bark of frondose trees.

MATERIAL STUDIED.—Norway: "Saltdalen, in cortice Alni, 10/23, *Sommerfelt*" (type, S).

Sweden: Västergötland, Östad, 10.9.1968, *K. Hjortstam* (S). Västergötland, Vänga par., 25.9.1969, *K. Hjortstam* (S).

Germany: Westfalen, Lengerich, Winter 1898/99, *W. Brinkmann* (Brinkmann, Westf. Pilze 11) (L); West-Berlin, Grunewald, 6.10.1968, *W. Jülich 1239* (Herb. Jülich); Hessen, Weißenborn, Graburg, 24.9.1968, *J. Poelt W. Jülich 2137* (Herb. Jülich).

Lagarobasidium Jülich, *gen. nov.*

Carposoma late effusum, membranaceum, albidum vel cremeum, adhaerens; rhizomorphae desunt. Hymenium laeve vel aculeis ornatum. Systema hypharum monomiticum. Hyphae distinctae, saepe incrassatae tunicatae, fibulatae, *c.* 2.5–5 μm in diam. Cystidia, gloeocystidia vel cystidiola adsunt, tenuiter vel paulum incrassatae tunicata, haud crasse incrustata. Basidia suburniformia, 10–20 μm longa, tetraspora, fibulata. Sporae laeves, ellipsoideae, hyalinae vel leviter flavidae, incrassatae tunicatae, saepe guttulatae, non amyloideae. Typus: *Odontia pruinosa* Bres.

Basidiocarp effused, membranaceous, rhizomorphs lacking. Hymenial surface even or odontioid. Hyphal system monomitic. Hyphae hyaline, almost cylindrical, thin-walled to somewhat thick-walled, *c.* 2.5–5 μm in diameter, with small clamps at the primary septa. Cystidia, gloeocystidia or cystidioles present, thin-walled to somewhat thick-walled, not heavily incrusted, with a basal clamp. Spores hyaline to very slightly yellowish, smooth, ellipsoidal, thick-walled, often guttulate, not amyloid.

SCOPE.—Three species.

Lagarobasidium pruinosum (Bres.) Jülich, *comb. nov.*—Fig. 12

Odontia pruinosa Bres. *apud* Bourd. & Galz. *in* Bull. Soc. mycol. France **30**: 265. 1914; Bres. *in* Annls. mycol. **18**: 43. 1920 (with Latin diagnosis; basionym).

Basidiocarp thin-membranaceous, somewhat pruinose, margin indistinct, rhizomorphs lacking. Hymenial surface even to grandinioid, ochraceous. Hyphae hyaline, distinct, cylindrical, 2–4 μm in diameter, slightly thick-walled (up to 0.6 μm), with clamps. Cystidia lacking. Gloeocystidia present, hyaline, clavate, thin-walled (but the base often thick-walled up to 1.5 μm), 80–110×8–10 μm, projecting up to 50 μm, with a clamp at the base. Some cystidioles present, thin-walled, subulate, *c.* 16×3 μm. Basidia suburniform, 14–18–20×4.5–6 μm, with four small subulate sterigmata *c.* 3×0.8 μm, with a clamp at the base. Spores hyaline, smooth, somewhat thick-walled (0.4–0.8 μm), subglobose to broadly ellipsoidal, 5–6×4–5 μm, with small apiculus, often guttulate, neither amyloid nor dextrinoid, only slightly cyanophilous.

MATERIAL STUDIED.—*Odontia pruinosa* Bres., Lengerich (Westfalen), *W. Brinkmann, 3310* (type, L).

Two other species have to be transferred to this genus, viz. **Lagarobasidium cymosum** (Rog. & Jacks.) Jülich, *comb. nov.* (Basionym: Peniophora cymosa Rog. & Jacks. *apud* Jackson *in* Can. J. Res. **26** (C): 133. 1948), and **Lagarobasidium nikolajevae** (Parm.) Jülich, *comb. nov.* (Basionym: *Hyphodontia nikolajevae* Parmasto, Consp. Syst. Cortic., Tartu 213. 1968).

Metulodontia Parm.

Metulodontia Parmasto, Consp. Syst. Cortic. 117. 1968 — Type species: *Peniophora nivea* (Karst.) Bourd. & Galz.

Basidiocarp resupinate, effused or effuso-reflexed, membranaceous to ceraceous; rhizomorphs present or absent. Hymenial surface even to hydnoid. Hyphal system monomitic. Hyphae hyaline, thin-walled to slightly thick-walled, with clamps.

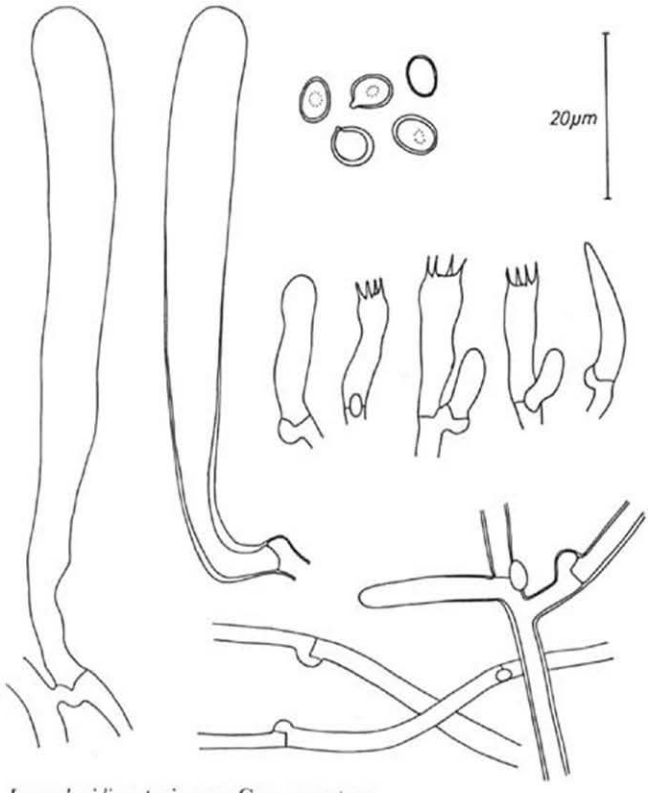

Fig. 12. *Lagarobasidium pruinosum*, Germany, type.

Cystidia present, thick-walled (but the top often thinner), aseptate, heavily incrusted, with clamps. Basidia when mature suburniform or clavate, cylindrical or narrowly clavate when young, with clamps, normally with four sterigmata, with clamps. Spores hyaline, thin-walled, non-amyloid.

As explained in the introduction, I see no reason to keep this genus apart from *Hyphoderma* since the same type of cystidia is present in both genera and no difference in basidial morphology is to be found.

To facilitate a comparison of the two genera in question, a description and figures are given of the type species of *Metulodontia*. From these it is clear, that *Metulodontia* has to be treated as a synonym of *Hyphoderma*.

Metulodontia nivea (Karst.) Parm.—Fig. 13

Kneiffia nivea Karst. *in* Hedwigia **35**: 173. 1896. — *Peniophora nivea* (Karst.) Bourd. & Galz. *in* Bull. Soc. mycol. Fr. **28**: 394. 1913. — Metulodontia nivea (Karst.) Parm., Consp. Syst. Cort. 118. 1968.

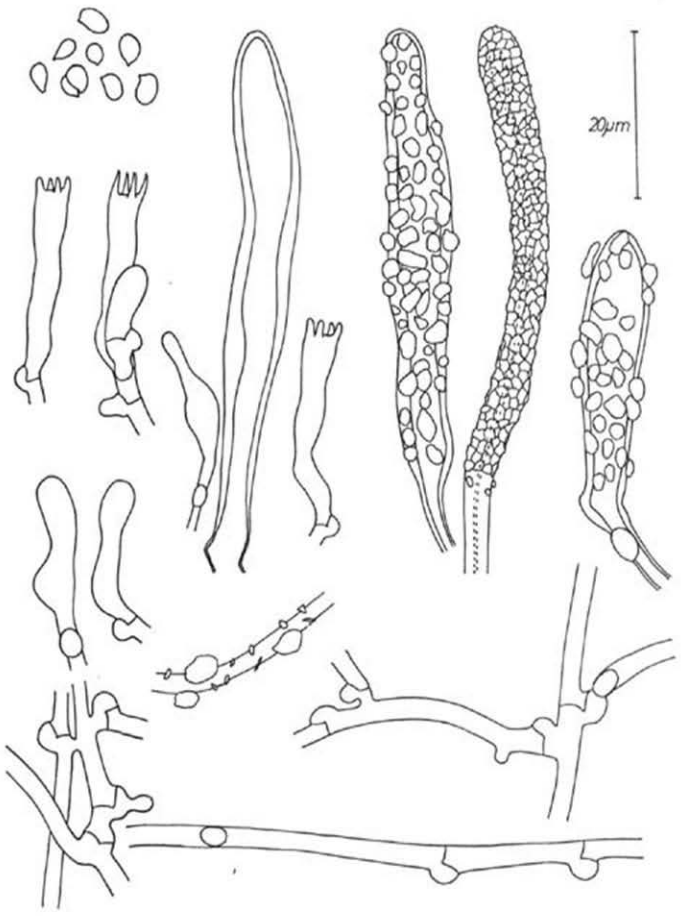

Fig. 13. *Metulodontia nivea*, France, *Galzin 7670*.

Basidiocarp effused, adnate, membranaceous; the margin slightly fimbriate; rhizomorphs present. Hymenial surface even or tuberculate, cream-coloured. Hyphal system monomitic. Hyphae loosely arranged, hyaline, distinct, rather thin-walled, 2–4 µm in diameter, with clamps at all septa; the basal hyphae straight and partly covered with small crystals, the subhymenial hyphae somewhat torulose. Cystidia abundant, clavate, moderately thick-walled (1–2 µm), heavily incrusted, immersed or projecting up to 50 µm, 20–40–100 × 5–8–12 µm. A few conical cystidioles present, *c.* 20 × 6 µm. Basidia flexuose, narrowly clavate, 18–20–25 × 4–5 µm, clamped at the base, with four subulate sterigmata *c.* 3–4 × 1 µm. Spores hyaline, smooth, more or less ellipsoidal, thin-walled, 4–6 × 2.5–3.5 µm, with small apiculus, neither amyloid nor dextrinoid or cyanophilous.

SUBSTRATE.—On wood or bark of frondose and coniferous trees.

MATERIAL STUDIED.—France: Aveyron, Loubotis, sur Cerisier, 29.11.1910, *Galzin 7670* (*Bourdot 7570*; L); Lyon, 1919, *L. Maire* (L 930.58–28).

PENIOPHORA Cooke emend. Donk

Peniophora Cooke *in* Grevillea **8**: 20. 1879; emend. Donk *in* Fungus **27**: 15. 1957 (see there for synonymy). — Type species: *Corticium quercinum* (Pers. ex Fr.) Fr.

Basidiocarp effused, resupinate, or effuso-reflexed, membranaceous or more often ceraceous. Hymenial surface even to slightly tuberculate. Hyphal system monomitic. Hyphae hyaline, mostly forming a dense layer in which individual hyphae are hardly discernible, the basal hyphae sometimes brown and distinct; thin- to thick-walled, in most species with-clamps. Cystidia in most species present, in some species gloeocystidia or dendrophyses are formed. Basidia narrowly clavate, thin-walled to somewhat thick walled, the older ones not seldom with secondary septa, in most species with clamps at the base, normally with four sterigmata. Spores hyaline, thin-walled, smooth, cylindrical or ellipsoidal, non-amyloid, said to be pale red in mass.

SCOPE.—More than 30 species.

PENIOPHORA QUERCINA (Pers. ex Fr.) Cooke—Fig. 14

Thelephora quercina Pers. ex Fr., Syst. mycol. **1**: 442. 1821. — *Peniophora quercina* (Pers. ex Fr.) Cooke *in* Grevillea **8**: 20. 1879. — For the synonymy see J. Eriksson, 1950.

Basidiocarp effused, up to 0.5 mm thick, the margin at first adnate but soon reflexed and showing a blackish underside, ceraceous; rhizomorphs lacking. Hymenial surface even, greyish-violaceous. Hyphae hyaline, only those at the extreme base being brown, forming a compact ceraceous layer, thick-walled (*c.* 0.5–2.0 μm), about 4–5 μm in diameter, with thick-walled clamps; thin secondary septa lacking clamps are often present. Cystidia hyaline, mostly thick-walled, almost conical, with heavily incrusted apical part, 40–60 × 10–15 μm, projecting about 20 μm, clamped at the base; gloeocystidia lacking. Basidia elongate-cylindrical to narrowly clavate, 30–50–64 × 5–7 μm, thin-walled at the apex, but otherwise, especially at the basal part, slightly thick-walled (*c.* 0.4–0.8 μm), with clamps at the base; sterigmata four, very slender, about 5 × 0.2–0.4 μm; in older basidia several thin secondary septa may be present; young basidial stages narrowly cylindrical. Spores hyaline, cylindrical to slightly allantoid, thin-walled, 8–11 × 3–4 μm, with small apiculus, neither amyloid nor dextrinoid or cyanophilous.

CYTOLOGY.—Hyphae and young basidial stages 2-nucleate, spores 1-nucleate; no nuclei observed in the cystidia. The nuclear division seems to take place only in fairly adult basidia with sterigmata.

MATERIAL STUDIED (Of this well known and often studied species only four collections are cited.).—Germany: West-Berlin, Tegel, Jungfernheide, 25.8.1968, *W. Jülich 1163* (Herb. Jülich).
Austria: Kärnten, Viktring, Ostseite des Opferholzes, 19.9.1968, *W. Jülich 1474* (Herb. Jülich).
Tunisia: Atlas-Mountains, 7 km south of Ain Draham, 11.4.1968, *W. Jülich 1047* (Herb. Jülich); Zaghouan, Djebel Zaghouan, 15.4.1968, *W. Jülich 1044* (Herb. Jülich).

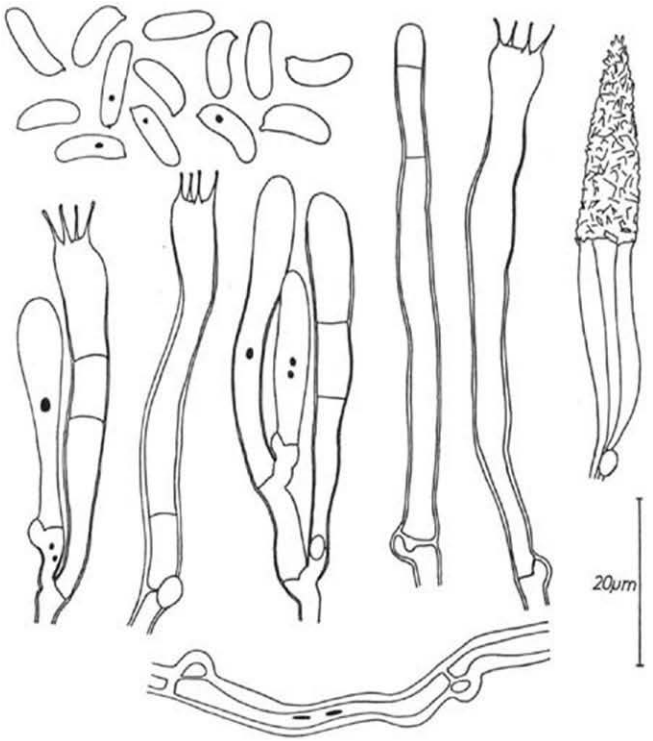

Fig. 14. *Peniophora quercina*, Austria, *Jülich 1474*.

PULCHERRICIUM Parm.

Pulcherricium Parm., Consp. Syst. Cortic. 132. 1968. — Type species: *Thelephora caerulea* Fr.

Basidiocarp effused, resupinate or effuso-reflexed, membranaceous. Hymenial surface at first blue, later bluish-greenish, smooth. Hyphal system monomitic. Hyphae bluish, distinct, somewhat thick-walled, 4–6 µm in diameter, with clamps. Cystidia and glococystidia lacking. Dendrophyses present, the appendaged covered with dark blue granules, at least some of them capable of growing out to form basidia, with a clamp at the base. Basidia clavate, hyaline or slightly bluish, with clamps at the base and four sterigmata; some basidia with lateral appendages. Spores hyaline to slightly bluish, rather thin-walled, large, non-amyloid.

SCOPE.—Monotypic.

PULCHERRICIUM CAERULEUM (Fr.) Parm.—Fig. 15, 16

Thelephora caerulea Fr., Elench. 1: 202. 1828. — *Pulcherricium caeruleum* (Fr.) Parm., Consp. Syst. Cortic. 133. 1968.

Basidiocarp membranaceous, effused, resupinate, sometimes slightly reflexed, with fimbriate and light-coloured margin; rhizomorphs lacking. Hymenial surface

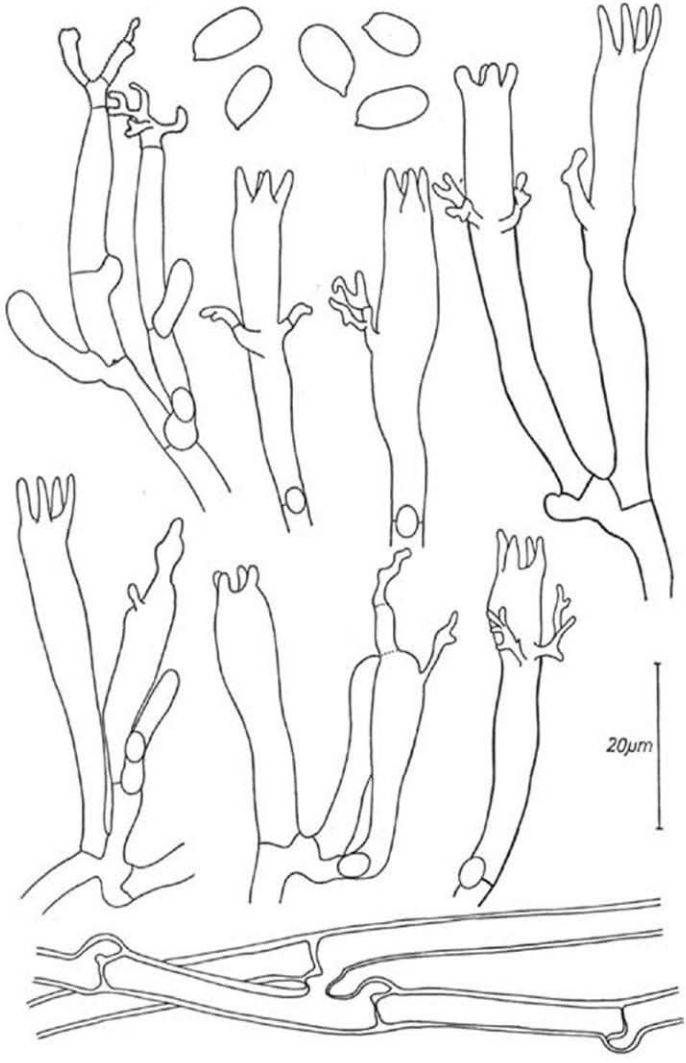

Fig. 15. *Pulcherricium caeruleum*, France, Desmazières, Fung. exs. 307.

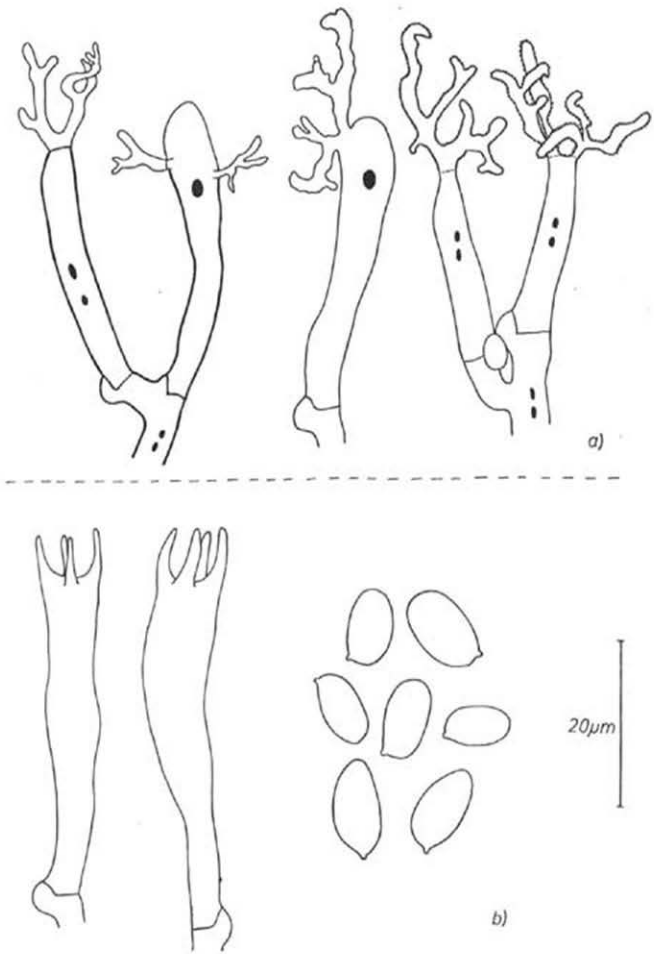

Fig. 16. *Pulcherricium caeruleum*: a. Kenya, *Maas Geesteranus 5299*; b. Germany, *Beckhaus*.

even, of a deep blue colour when immature, later becoming dirty bluish-greenish. Hyphae mostly bluish or greenish, the basal ones slightly brownish, somewhat thick-walled (*c.* 0.4–0.8 µm), 4–6 µm in diameter, always with clamps; the surface can be incrusted with a dark blue substance or is somewhat covered with small, hyaline crystals. Dendrophyses present, *c.* 20–40×4–6–8 µm, with appendages of very variable length and shape, which are often coloured with darkblue granules; clamped at the base. Basidia clavate, hyaline or slightly bluish, thin-walled or slightly thick-walled (*c.* 0.4 µm), 30–60×5.5–8 µm, with clamps at the base, with four rather large sterigmata (*c.* 6–8×2 µm), sometimes laterally with small appendages resembling those of the dendrophyses. Spores hyaline to slightly bluish, ellipsoidal, rather thin-walled, 8–10–13×5–7 µm, neither amyloid nor dextrinoid or cyanophilous.

CYTOLOGY (only studied in African material).—hyphae 2-nucleate; dendrophyses 2-nucleate but some of them with a synkaryon.

SUBSTRATE.—On wood or bark of (only?) frondose trees.

MATERIAL STUDIED.—Netherlands: 's-Gravenhage, 1888, *C. E. Destrée* (L). Germany: Westfalen, Höxter, 2.1881, *Beckhaus* (L); Lengerich, Winter 1902, *W. Brinkmann* (Brinkmann, Westf. Pilze 106; L); Prov. Brandenburg, Triglitz in der Prignitz, 30.3.1899, *O. Jaap* (Jaap, Fung. sel. exs. 23; L). Denmark: Skårup, Fünen, Nov. 1877, *E. Rostrup* (in: Thümen, Herb. myc. oeconom. 641; Thümen, Mycotheca univ. 1207; L). France: Environs de Toulouse, 6.1879, *C. Roumeguère* (Roumeguère, Fung. sel. gall. 505; L); without locality, *Léveillé* (L); Andelot, Ht. Marne, 1918, 1920, and without locality 1926, *L. Maire* (L); Aveyron, St. Priest en Murat, 6.1931, *H. Bourdot & M. A. Donk* (L). without locality, *Desmazières* (Desmazières, Fung. exs. 307; L); Corsica, *Otto* (L). Italy: Avellino, 2.1904, *A. Trotter* (D. Saccàrdo, Mycoth. ital. 1418; L). Florentia, 1.1865, *L. Caldesi* (Rabenhorst, Fung. eur. 1005; L); Longobardia, in horto botanico ticinensi, hyeme, *Cavara* (Cavara, Fung. Longobard. exs. 13; L). U.S.A.: Illinois, Metropolis, 29.10.1919, *C. J. Humphrey 9656* (L); Indiana, Athens, 10.1925, J. H. Miller (L); Alabama, Dallas Co., S. of Selma on rt. 22, 11.11. 1961, *D. E. Stone* (L). Tunisia: Zaghouan, Djebel Zaghouan, 15.4.1968, *W. Jülich 1024* (L). Kenya: Nyanza Province, Distr. of Kisumu-Londiani, Tinderet Forest Reserve, 1.7.1949, *R. A. Maas Geesteranus 5299* (L). Indonesia: Java, Tjibodas, 4.1930, *K. B. Boedijn 529* (L).

Although this is a cosmopolitan species which has been collected in America, Europe, Africa, Java, and Australia, it obviously occurs mainly in warmer subtropical and tropical regions. In Europe it has been collected fairly often in the southern countries (France, Italy), but is rather rare in Germany and Great Britain and extremely rare in Denmark and Scandinavia: for Denmark Christiansen (1960) has seen only specimens from two places — the most recent collections dating from 1882, and according to Eriksson (1958) the species in Scandinavia is "not found outside the region with the mildest winter climate".

The appendages of the dendrophyses are very variable in legth and ramification, generally being much longer and more often ramified in southern, warmer countries than farther north. The material from Germany and Denmark, e.g., shows rather short appendages on the dendrophyses, whereas the longest and best developed ones where those in the specimen from Kenya; similarly the material from Africa shows a more intense colour and a denser incrustation of hyphae and dendrophyses.

The two specimens from Tunisia and Kenya showed — as was to be expected — a dikaryon in the dendrophyses, but in the larger ones a synkaryon was formed. The nuclear fusion, which normally takes place only in basidia, indicates that in dendrophyses, too, a meiotic division of the synkaryon and spore-production may occur. Although the two specimens were collected so young as to lack basidia, some dendrophyses were observed to have a change in shape. Normally the appendages are at the apex of the cells, but some of the latter which were obviously capable to enlarge had grown out to become distinctly clavate in shape, as a result bearing the

appendages laterally. The cell-walls in the newly formed parts were seen to be thinner, almost hyaline, and not incrusted. Such dendrophyses (with their synkaryon) looked very much like clavate, immature basidia with lateral appendages.

In order to get a better impression of what happens with these dendrophyse/basidium-like cells, a well developed specimen of Desmazière's exsiccate was studied. A rather large number of basidia — with well developed sterigmata — were seen to have lateral appendages of the typical shape, although they were not as long as those in the African material. Thus it is clear that many dendrophyses are able to grow out to normal basidia. This is very interesting from a theoretical point of view. Usually cystidia, gloeocystidia, and dendrophyses are considered to be sterile elements of the hymenium, cytologically characterized by a synkaryon with permanently separated nuclei, which never fuse and eventually perish, leaving behind a dead cell. But in the case of *P. caerulea*, obviously the dendrophyses do not behave as exclusively sterile elements in that at least a number of them can develop into normal basidia. In this case the dendrophyses function as probasidia. It is probable that especially in some species of *Aleurodiscus sensu lato* the same phenomenon may occur which, as far as I know, has never been studied cytologically.

To avoid a wrong impression, it is necessary to emphasize that in a full-grown basidiocarp of *P. caerulea* most basidia develop in the normal way, arising from side-branches of the subhymenial hyphae. The indirect way via dendrophyses obviously occurs only in an early stage of hymenial development: the fungus remains sterile for a longish time, then at least some of the dendrophyses develop further into basidia and form a proper hymenium. Probably all basidia which follow originate directly from subhymenial hyphae and consequently show no appendages (like those found on the dendrophyses). It may be pointed out that, in contrast with the material of Desmazière's exsiccate, the dendrophyses in the German and Danish collections seen (which happened to be poorly developed) exhibit only rather small appendages, while the basidia seemed to be without any.

RADULOMYCES Christ.

Radulomyces Christ. *in* Dansk bot. Ark. **19**: 230. 1960. — Type species: *Thelephora confluens* Fr. ex Fr.

Basidiocarp effused, resupinate or effuso-reflexed, membranaceous or slightly ceraceous. Hymenial surface more or less cream-coloured, even to hydnoid. Hyphal system monomitic. Hyphae hyaline, rather distinct, thin-walled to slightly thick-walled, *c.* 2–5 μm in diameter, with clamps. Thick-walled cystidia lacking. Basidia elongate-clavate, distinctly stalked, when young at first cylindrical, becoming long-stalked clavate or long-stalked pleurobasidial, with clamps at the base, normally with four sterigmata and often oil drops in the cytoplasma. Spores hyaline, thin-walled to slightly thick-walled, smooth, often guttulate, large, non-amyloid.

SCOPE.—*c.* 5 species.

RADULOMYCES CONFLUENS (Fr. ex Fr.) Christ.—Fig. 17

Thelephora confluens Fr. ex Fr., Syst. mycol. **1**: 447. 1821. — *Radulomyces confluens* (Fr. ex Fr.) Christ. *in* Dansk bot. Ark. **19**: 231. 1960. — For synonymy see Rogers & Jackson, 1943.

Basidiocarp effused, at first appearing as small patches with fimbriate margin, later confluent and several cm long, membranaceous, adnate; rhizomorphs lacking. Hymenial surface even, cream-coloured or ochraceous, sometimes slightly greyish. Hyphae hyaline, thin- to slightly thick-walled (up to 0.4 μm), 2.5–4–5 μm in diameter, not or only weakly cyanophilous; cystidia lacking. Basidia elongate-clavate, distinctly stalked, thin-walled, but the walls at the top of the larger basidia (which still lack the sterigmata) distinctly thickened (up to 0.4 μm) and then often slightly cyanophilous; young basidia cylindrical, then stalked-clavate or of irregular shape; 30–50–70 × 8–9 μm, with clamps at the base, often with small oil drops, with four curved sterigmata *c.* 5 × 1.2 μm. Spores hyaline, broadly ellipsoidal, rather thin-walled, 7–10 × 6–8 μm, with rather large and distinct apiculus, not amyloid or dextrinoid, but sometimes slightly cyanophilous.

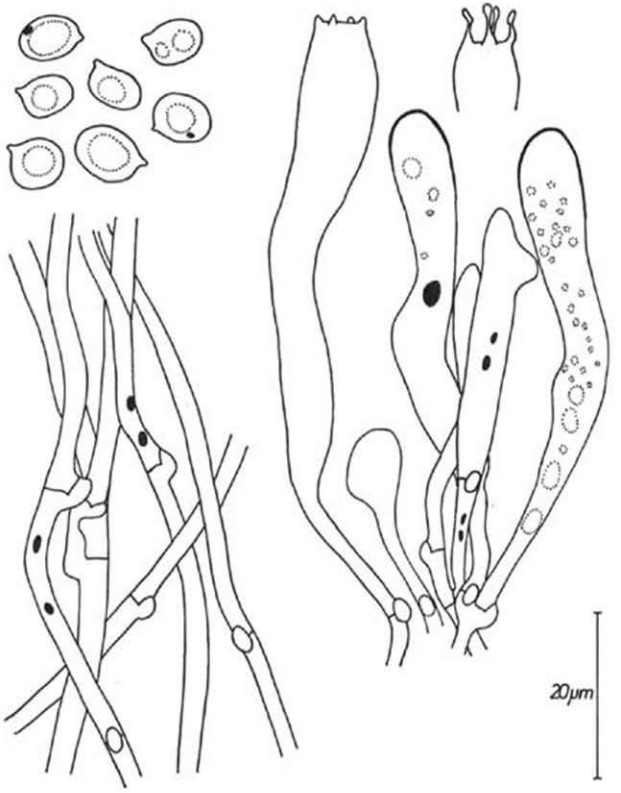

Fig. 17. *Radulomyces confluens*, Germany, *Jülich 567*.

CYTOLOGY.—Hyphae and young basidial stages 2-nucleate, spores probably 1-nucleate (this is difficult to observe because of the presence of numerous guttules of equal shape).

SUBSTRATE.—On bark and wood of frondose, rarely coniferous trees.

MATERIAL STUDIED.—S w e d e n: Lapland, Abisko, 17.7.1967, *W. Jülich* (Herb. Jülich); Västergötland, Österplana par., 11.10.1969, *K. Hjortstam* (S).

G e r m a n y: Brandenburg, Tamsel, 26.2.1915, *P. Vogel* (Sydow, Mycoth. germ. 1308; L); Lengerich, Winter 1899/1900, *W. Brinkmann* (Brinkmann, Westf. Pilze 13; L); West-Berlin, Botanischer Garten, 19.9.1967, *R. Dudat* (Herb. Jülich); West-Berlin, Forst Düppel, 25.10.1967, *W. Jülich* (Herb. Jülich).

F r a n c e: Southern France, Brive, 18.8.1967, *W. Jülich* (Herb. Jülich). "Fraize (Vosges), 24.4.1918, récolte no. 438 sur br. sapin à terre" (type of *Corticium confluens* fa. *abietis* Bourd. & L. Maire; L 931.71-13).

RADULOMYCES MOLARIS (Chaill. ex Fr.) Christ.—Fig. 18

Hydnum molare Chaill. ex Fr., Elench. **1**: 151. 1828 (*pro syn.*). — *Radulum orbiculare* var. *molaris* (Chaill. ex Fr.) Quél., Fl. mycol. Fr. 437. 1888. — *Radulomyces molaris* (Chaill. ex Fr.) Christ. *in* Dansk bot. Ark. **19**: 232. 1960.

Sistotrema rude Pers., Mycol. europ. **2**: 192. 1825.

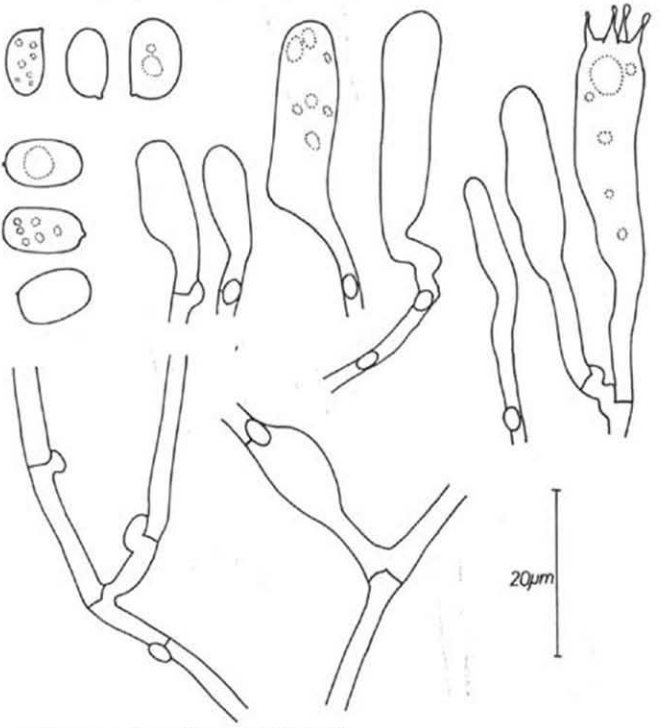

Fig. 18. *Radulomyces molaris*, France, *Jülich 560*.

Basidiocarp effused, resupinate, membranaceous, adnate; margin fimbriate; rhizomorphs lacking. Hymenial surface odontoid to hydnoid, the teeth 1–2 mm long, cream-coloured or ochraceous. Hyphae hyaline, distinct, rather thin-walled, mostly cylindrical, 1.5–3–4 μm in diameter, sometimes near the clamps swollen, up to 8–10 μm in diameter, with clamps at all septa; cystidia lacking. Basidia clavate, stalked, 35–46 × 6–8 μm, clamped at the base, often with numerous guttules in the cytoplasma, with four sterigmata *c.* 5 × 1.2 μm. Spores hyaline, broadly cylindrical to ellipsoidal, rather thin-walled, 9–11 × 5.5–7 μm, guttulate, with large apiculus, neither amyloid, dextrinoid nor cyanophilous.

CYTOLOGY.—Hyphae and young basidial stages 2-nucleate, spores probably 1-nucleate.

SUBSTRATE.—On bark of frondose trees.

MATERIAL STUDIED.—France: Pyrenees, Brive, 18.8.1967, *W. Jülich 560* (Herb. Jülich); Locality unknown (type of *Sistotrema rude* Pers.; Herb. Persoon, L 910.270–453).

SUBULICYSTIDIUM Parm.

Subulicystidium Parm., Consp. Syst. Cortic. 120. 1968. — Type species: *Hypochnus longisporus* Pat.

Basidiocarp resupinate, effused, soft-membranaceous, often very thin. Hymenial surface even, under a lens slightly hairy owing to the projecting cystidia. Hyphal system monomitic. Hyphae hyaline to slightly yellowish, thin-walled to somewhat thick-walled, always with clamps. Cystidia acuminate-cylindrical, thick-walled, with bifurcate base, covered with crystals which in polarized light seem to be short-bacilliform and arranged in 3–4 longitudinal rows, but as depicted by scanning electron microscopy they are flat-circular bodies arranged in about two rows. Basidia more or less clavate, exhibiting repetition, clamped at the base with four, rarely two sterigmata. Spores hyaline, thin-walled, long-cylindrical or ellipsoidal, non-amyloid.

SCOPE.—2–4 species.

SUBULICYSTIDIUM LONGISPORUM (Pat.) Parm.—Fig. 19

Hypochnus longisporus Pat. *in* J. Bot., Paris (ed. Morot) **8**: 221. 1894. — *Subulicystidium longisporum* (Pat.) Parm., Consp. Syst. Cortic. 121. 1968. — For the synonymy see Rogers & Jackson (1943).

Basidiocarp effused, adnate, hypochnoid or membranaceous, easily separable; rhizomorphs lacking. Hymenial surface even, whitish or light greyish-brownish (in older specimens). Hyphal system monomitic. Hyphae hyaline, thin-walled to slightly thick-walled (up to *c.* 0.8 μm), 2.5–4 μm in diameter, clamped at all septa. Cystidia abundant, cylindrical, acuminate, brittle, with thickened walls (*c.* 1–1.5 μm), bearing flat circular crystal-like bodies normally arranged in two longitudinal rows (although in phase-contrast there seems to be 3–4 rows of small, oblong crystals), 40–80 × 4–5 μm, up to 50 μm projecting, the base mostly bifurcate. Basidia cylindrical to narrowly clavate, somewhat flexuose, 18–25 × 4–6 μm, clamped at the base, with four subulate sterigmata *c.* 2–3 × 0.5 μm; in well developed specimens the basal half of most of the basidia is loosely surrounded by a wall (which may be slightly incrusted):

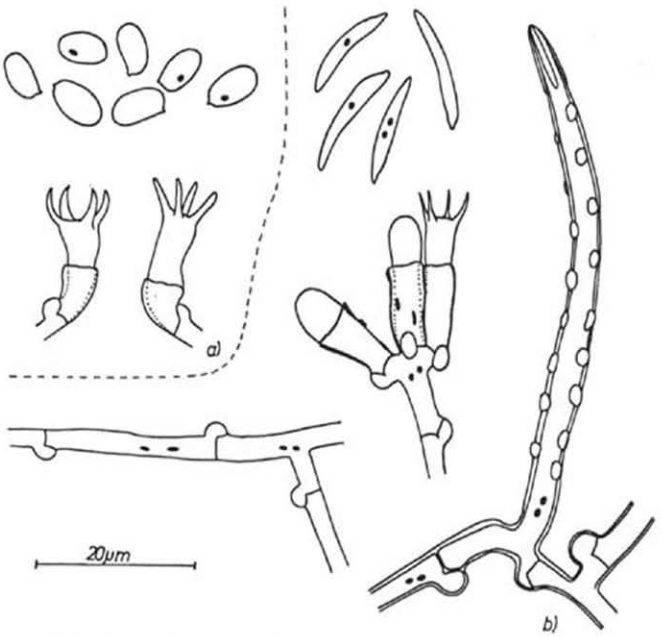

Fig. 19. a. *Subulicystidium nikau*, New Zealand, type. — b. *S. longisporum*, Germany, *Jülich 1144*.

there is strong evidence that these are the remaining walls of the former basidia, inside which a new basidium has developed (=basidial repetition: Jülich 1969). Spores hyaline, more or less cylindrical, straight or somewhat curved, slightly narrowed at both ends, thin-walled, 10–16 × 1.5–3 µm, often with several guttules, apiculus not distinctive, neither amyloid nor dextrinoid or cyanophilous.

CYTOLOGY.—Hyphae, cystidia and young basidial stages 2-nucleate, Spores 1-, rarely 2-nucleate. This has been studied in some specimens from Europe and one from Jamaica. It may be added that the two nuclei of the cystidia are either situated in the base or in the apex of the cystidia, but it is also not rare to find one nucleus in the apex and one in the base. This explains the high number of seemingly uninucleate cystidia which lack only a small part of the apex.

SUBSTRATE.—On rather rotten wood.

IMPERFECT STATE.—Small compact globules of strongly interwoven hyphal cells have been described by Bourdot & Galzin as *Aegerita tortuosa*. They are not always present but seem in fact to be connected with the perfect form.

MATERIAL STUDIED.—Netherlands: Zuid-Holland, Loosduinen, Ockenrode, 20.11.1933, *M. A. Donk 5329* (L); Boekhorst, 10.1860, *L. H. Buse* (L 910.234–290). Germany: West-Berlin, Pfaueninsel, 20.8.1968, *W. Jülich 1144* (Herb. Jülich). France: Aveyron, .8.1919, *Galzin 24864* (*Bourdot 28089*; L); Aveyron, vers la Courbe, env. de St. Sernin, 9.1907, *Galzin 2230* (Herb. Donk 2433; L). England: Surrey, Horsley, 4.8.1946, *M. A. Donk 11029* (L).

Sweden: Upland, Årby Skog near Storvreta, 14.9.1932, *M. A. Donk 5345* (L); Upland, Fundbo, 9.1932, *S. Junell* (Herb. Donk 3764; L).
U.S.A.: Michigan, St. Johns, 9.6.1932, *C. A. Brown 407* (Herb. Donk 3241; L).
Jamaica: St. Andrew Parish, St. Helen Gap to Monkey Hill, 1.9.1957, *A. L. Welden 905* (L).

SUBULICYSTIDIUM NIKAU (Cunn.) Jülich

Peniophora nikau Cunn., Thelephoraceae Austr. New Zeal. 127. 1963. — *Subulicystidium nikau* (Cunn.) Jülich *in* Ber. dt. bot. Ges. **81**: 419. 1969.

This species is almost identical with *S. longisporum*, exhibiting repetobasidia and the same peculiar type of cystidia (also with mostly bifurcate base; not mentioned in Jülich, 1969). It differs mainly in its broadly ellipsoidal (also 1-nucleate) spores of 6.5–8.5 × 3–4.5 μm, and in having basidia of somewhat smaller dimensions.

MATERIAL STUDIED.—Type collection (K).

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NOTES ON HYGROPHORUS—I

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(With five Text-figures)

Hygrophorus (*Hygrocybe*) *helobius* Arnolds, a new species from bogs is described, and a number of new combinations are given.

From 1969 on I have studied the taxonomy and ecology of species of the Friesian genus *Hygrophorus* in the Netherlands; until 1971 as a part of my university education in biology, under the supervision of Dr. C. Bas (Rijksherbarium, Leiden). Special attention has been given to the grassland-inhabiting species of the subgenera *Cuphophyllus* (= *Camarophyllus sensu auct.*), *Hygrocybe*, and *Hygrotrama*. Many dozens of collections were made. The results of my studies, including a key and detailed descriptions of all taxa, have been published in a report in the Dutch language (Arnolds, 1974a). The most important results however will be published separately as notes in this journal. In the present notes a new species is described and some new combinations used in the above report are validated.

I am very much indebted to Dr. C. Bas for his help in preparing this paper, to Dr. R. A. Maas Geesteranus (Leiden) for correcting the Latin diagnosis, and to Mr. P. K. C. Austwick (London) for improving the English text. Thanks are also due to the Directors and Curators of the Botanical Museum, Copenhagen, and the Farlow Herbarium of Cryptogamic Botany, Cambridge, U.S.A. for kindly making available to me some important collections.

Hygrophorus helobius Arnolds, *sp. nov.*—Figs. 1–5

MISAPPLIED NAMES.—*Hygrocybe miniato-alba* (Pat.) Möller *sensu* Möller, Fungi Faeröes **1**: 154, *pl. 1 fig. c.* 1945. — *Hygrocybe mollis* (Berk. & Br.) Moser *sensu* Moser *in* Z. Pilzk. **33**: 9. 1967.

Pileus 10–25 mm latus, convexus, dein expansus vel planus, disco depressum, margine undulato-lobatus, coccineus vel miniatus, posterior aurantius vel aurantio-luteus, disco squamulis parvis pilosis miniatis vel aurantiis obtectus. Lamellae (L = 19–29, l = 1–3) adnatae vel late adnatae, ventricosae, subdistantes, vulgo primo pallidissime roseae vel salmonicolores, dein saepe cremeae. Stipes (15–)18–58 × (1.5–)1.8–3.5(–5) mm, deorsum aequalis vel attenuatus, vulgo leviter flexuosus, cavus, primo miniatus, dein aurantius vel aurantio-luteus, basi vulgo flavo-albus, siccus. Odor et sapor nulli. Sporae 7–11(–12.5) × (4–)4.5–6.5 (–7) µm, vulgo ellipsoideo-ovoideae vel -oblongae, interdum cylindricae vel pyriformes, haud

raro strangulatae. Basidia 34–45 × (6–)7.5–11(–13) µm, 4(2–)sporigera. Lamellarum acies fertilis. Lamellarum stipitisque trama subregularis, cellulis longissimis, (67–)98–670(–710) × (8.5–)9.5–34(–37) µm formata. Pileipellis trichodermiformis, hyphis ad septa strangulatis, cellulis exterioris clavatis, 6–12 µm latis. Aestate. Inter Sphagna in locis uliginosis. Holotypus: 'Zegveld, De Meye, 18 Aug. 1970, *E. Arnolds 511*' (L).

ETYMOLOGY: ἕλος, a marsh; βίος, life.

Cap 10–25 mm wide, first convex or broadly flattened conical, then expanded with depressed centre, often with wavy, lobed margin, scarlet, vermilion or orange-red at first, gradually discolouring to orange or orange-yellow, finally brownish yellow, not viscid when moist, with small concolorous or slightly paler, fibrillose-pilose scales especially at centre; margin not striate. Gills [L = 19–29, l = 1–3] moderately to broadly adnate, mostly with decurrent tooth, ventricose, thickish, rather distant, rosy white to very pale salmon pink at first, then yellowish white to pale salmon orange with pale yellowish edge.

Stem (15–)18–58 × (1.5–)1.8–3.5(–5) mm, l/b (= length-breadth ratio) (7.8–)8.3–18.0, slender, hollow, often somewhat flexuose, equal or attenuate at base, fragile, orange-red or vermilion at first, discolouring from base upwards to orange or orange-yellow, at base often yellowish white, and white tomentose, otherwise smooth and dry, sometimes at apex slightly pruinose. Flesh in cap thin, very fragile, in centre pale orange-yellow, otherwise concolorous with surface of cap and stem. Smell and taste none.

Spores [75/6/5][1] 7–11(–12.5) × (4–)4.5–6.5(–7) µm, l/b (1.3–)1.4–2.3(–2.6); very variable in a given mount, in side-view mostly ellipsoid, ellipsoid-oblong or ovoid, but sometimes pear-shaped or cylindrical, and constricted, in face-view mostly broader, ovoid or maize grain-shaped, with rather large oblique apiculus, colourless in water and bases, yellowish in Melzer's (Fig. 2). Basidia [32/5/4] 34–45 × (6–)7.5–11(–13) µm, l/b (3.2–)3.5–5.2(–5.5), rather broadly clavate, 4-spored, sometimes a few 2-spored (Fig. 3). Pleuro- and cheilocystidia absent. Trama of gill composed of parallel hyphae with very long and broad tubular cells more or less attenuate towards septa, often flexuose near ends, measuring [45/5/4] (67–)98–670(–710) × (8.5–)9.5–34 µm, l/b (4.0–)6.6–37.5, usually with scattered irregularly twisted and branched, vascular hyphae 3–5(–7) µm broad (Fig. 4). Pileipellis[2] a trichodermium, composed of repent hyphae and especially at centre erect hyphae forming small upright squamules made up of many rather short cylindrical cells more or less constricted at septa; terminal cells rounded or somewhat clavate and 6–12 µm broad. Trama of pileus consisting of somewhat interwoven radially disposed hyphae with long cylindrical cells, 8–22 µm broad. Stipitepellis[2] a poorly developed layer of repent hyphae with some scattered erect ends 4.5–8 µm broad (Fig. 5). Stipitetrama composed of parallel hyphae with very long tubular cells 11–23(–26) µm broad, and scattered vascular hyphae 2.5–6 µm broad (Fig. 5). Clamps frequent at basidia, also found in subhymenium and on hyphae of pileipellis.

HABITAT.—In the Netherlands known from several mesotrophic bog areas, among *Sphagnum* and other mosses in regularly mown reedy marshes belonging to the plant community Pallavicinio-Sphagnetum Meltzer 1945, and poor, unmanured, wet hayfields, belonging to the plant community Cirsio-Molinietum Siss. & de Vries 1942 (see Westhoff & den Held, 1969).

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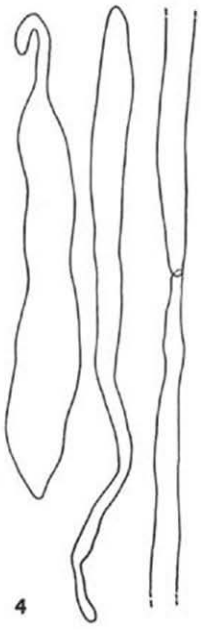
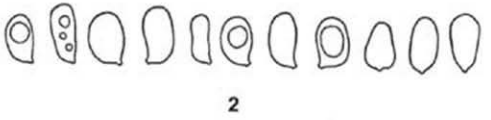
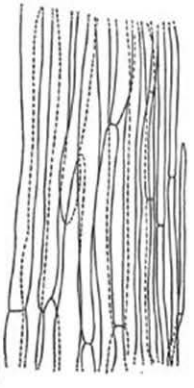
[1] Spores [75/6/5] ... means: 75 spores, taken from 6 fruitbodies belonging to 5 collections measured, ...

[2] With regard to the use of these terms, cf. Bas (1969: 327).







Figs. 1–5. *Hygrophorus helobius*. — 1. Fruit-bodies, ×1/2. — 2. Spores, ×750. — 3. Basidia, ×750. — 4. Elements of trama of gill, ×300. — 5. Longitudinal section of stipitetrama (stipitepellis to the right), ×175.

COLLECTIONS EXAMINED.—THE NETHERLANDS: prov. Overijssel, Wanneperveen, Zuideindinger Wiede, 24 June 1961, *Barkman 7541* (Wag-W); prov. Utrecht: Zegveld, De Meye, 18 Aug. 1970, *Arnolds 511* (holotype, L); prov. Zuid-Holland: Nieuwkoop, Nieuwkoopse Plassen, 27 June 1957, *Bas 1208* (L); Nieuwkoop, De Haeck, 31 Aug. 1971, *Kortselius* (Arnolds 622; L).

FAEROES: Syderö, 28 Aug. 1938, *F. H. Möller* (C); Strömö, 13 July 1938, *F. H. Möller* (C).

This species is related to *H. miniatus* (Fr.) Fr., but differs from it macroscopically by the very pale colour of the gills and the fragile context, microscopically by the very long elements in the trama of the gills [for comparison: the cells of the gills in 5 Dutch collections of *H. miniatus* measure (37–)43–124(–192) × (6.5–)8.5–19(–22.5) µm], and somewhat shorter and broader basidia [*H. miniatus*: (32–)34–53(–59) × 5.5–10(–10.5) µm, cf. Arnolds, 1974a], ecologically by the occurrence in bogs and by early fructification. In ecological respect there is more agreement with *H. coccineocrenatus* Orton (= *H. turundus sensu* Lange, Kühner & Romagnesi etc.), which fructificates also in summer among *Sphagnum*. The latter, however, has a brownish or blackish scaly cap, larger spores [according to Orton, 1960: 262, 10–13(–14) × 6–8 µm; after my own observations (8–)8.5–12.5 × (5–)5.5–7.5(–8) µm] and much shorter elements in the trama of the gills, like *H. miniatus* (see above). It is also interesting to note, that up till now *H. helobius* has been found in the Netherlands only in the western holocene part of the country in bogs, and *H. coccineocrenatus* only in the eastern pleistocene part in peatmoors and closing fens. This seems to indicate an ecological difference between these two species. Probably *H. helobius* prefers a more mesotrophic and less acid habitat than *H. coccineocrenatus* does (cf. Arnolds, 1974b).

Hygrophorus helobius has been described and figured before by Möller (1945: 154, *pl. I C*) from the Faeroes, as "*Hygrocybe miniato-alba* (Pat.) comb. n." Patouillard (1913: 213) introduced the name *Hygrophorus miniatoalbus* for a fungus, collected in Indo-China. The type, labelled "*Hygrophorus miniatoalbus* Pat., M. Demange 367, Thai Ha, Hanoi, 6–7–1909," is kept in the Farlow Herbarium. A study of this collection made it clear to me that it represents another fungus than the one described by Möller. The cap of *H. miniatoalbus* Pat. is strongly umbilicate and the gills are deeply decurrent. Some microscopic characters are different also: basidia [8/1/1] are (46–)54–66 × (8–)9.5–11(–12) µm, l/b (4.7–)5.0–6.6, that is longer and more slender than in Möller's material; the elements in the trama of the gill measure [5/1/1] 42–86 × 9–20 µm; that is much shorter than in *H. helobius*. According to my observations the dimensions of the spores are [10/1/1] 7–9.5 × 5–6 µm. I was unable to reinflate sufficiently the outermost tissue of the cap for an examination of the pileipellis. The original description says that it was "pelucheux à la loupe."

This combination of characters suggests to me a close relationship of *H. miniatoalbus* Pat. to *H. cantharellus* (Schw.) Fr. In fact I was unable to find any difference of importance between the Netherlands' collections of the latter species and Patouillard's fungus. The notes on the habitat, "au revers d'un talus" and "sur la terre," are also in agreement with the environmental conditions at most of the localities, where *H. cantharellus* has been found in the Netherlands.

Recently *H. helobius* has been described by Moser (1967: 9) under the name *Hygrocybe mollis* (Berk. & Br.) Moser. All given characters agree with those of the collections mentioned above. The true *H. mollis*, however, is another taxon in the *H. miniatus*-complex, originally described by Berkeley & Broome (1871: 10) as a variety of *H. turundus* (Fr. ex Fr.) Fr., with a golden yellow cap ("aureus") with squamules of the same colour. *Hygrophorus mollis* is very close to *H. miniatus*; the only

differences in fact are the yellow colour of young caps and the pale gills, as described by Orton (1960: 249) and Arnolds (1974a).

The following new combinations are proposed:

Hygrophorus subgenus **Hygrotrama** (Sing.) Arnolds, *comb. nov.* Basionym: *Hygrotrama* Sing. *in* Sydowia **12**: 221. "1958" [1959].

Hygrophorus subgenus **Cuphophyllus** (Donk) Arnolds, *comb. nov.* Basionym: *Hygrocybe* subgenus *Cuphophyllus* Donk *in* Beih. Nova Hedwigia **5**: 45. 1962.

Hygrophorus sect. **Coccinei** (Fayod) Arnolds, *comb. nov.* Basionym: *Hygrocybe* sect. *Coccineae* Fayod *in* Annls Sci. nat., VII **9**: 308. 1889.

Hygrophorus sect. **Insipidi** (Herink) Arnolds, *comb. nov.* Basionym: *Gliophorus* sect. *Insipidi* Herink *in* Act. Mus. Boh. sept. Liberec. **1**: 81. 1959.

Hygrophorus subsect. **Chlorophani** (Herink) Arnolds, *comb. nov.* Basionym: *Godfrinia* subsect. *Chlorophanae* Herink (sub nom. *Chlorophaninae*) *in* Act. Mus. Boh. sept. Liberec. **1**: 66. 1959.

Hygrophorus subsect. **Laeti** Arnolds, *subsect. nov.*[3] Type: *Hygrophorus laetus* (Pers. ex Fr.) Fr. Acies lamellarum gelatinosae, steriles, cheilocystidiis gracilibus confertis obtectae. Subhymenium gelatinosum.

Hygrophorus conicus var. **conicoides** (P. D. Orton) Arnolds, *comb. nov.* Basionym: *Hygrophorus conicoides* P. D. Orton *in* Trans. Brit. mycol. Soc. **43**: 262. 1960.

Hygrophorus conicus var. **conicopalustris** (Haller) Arnolds, *comb. nov.* Basionym: *Hygrophorus conico-palustris* Haller *in* Schweiz. Z. Pilzk. **31**: 141. 1953.

Hygrophorus conicus var. **olivaceoniger** (P. D. Orton) Arnolds, comb. nov. Basionym: *Hygrophorus olivaceoniger* P. D. Orton *in* Trans. Brit. mycol. Soc. **43**: 263. 1960.

Hygrophorus acutoconicus var. **cuspidatus** (Peck) Arnolds, *comb. nov.* Basionym: *Hygrophorus cuspidatus* Peck *in* Bull. Torrey bot. Club **24**: 141. 1897.

Hygrophorus miniatus var. **mollis** (Berk. & Br.) Arnolds, *comb. nov.* Basionym: *Hygrophorus turundus* var. *mollis* Berk. & Br. *in* Ann. Mag. nat. Hist. IV **7**: 425–436 (spec. no. 1279). 1871.

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THE SPECIES DIPODASCOPSIS UNINUCLEATA (BIGGS) BATRA & MILLNER

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(With three Text-figures)

Morphological and physiological properties of *Dipodascopsis uninucleata* (Biggs) Batra & Millner are described. Two varieties, var. *uninucleata* and var. *wickerhamii* nov. var. are recognized.

INTRODUCTION

Biggs (1937) gave the following description of *Dipodascus uninucleatus*:

"Colony circular pulvinate; edge wavy, surface glistening, gyrosely wrinkled; consistency butyrous; color opaque; coloration of the medium none. Hyphae branched, septate, constricted at the cross walls, 2.4–2.6 μ in diameter in young cultures, in old cultures very irregular. Asexual reproduction none. Cells consistently uninucleate. Asci elongate, multisporous, diameter 7–8 μ tapering to 4–5 μ at the tip, length extremely variable, in young cultures 90–180 μ. Spores minute ellipsoid 0.5–1.0 × 2.0–2.8 μ, liberated from the tip of the ascus by gradual extrusion".

The single strain of this species studied by Biggs had been isolated from a dead pupa of *Drosophila melanogaster*.

Dipodascus uninucleatus corresponds to the first species of the genus, *D. albidus*, in the formation of the typical elongate multispored ascus, but there are also differences between them: *D. uninucleatus* forms no arthrospores and the ascospores are very small; *D. albidus* produces arthrospores and much larger ascospores.

Batra (1959), in a study of the genus *Dipodascus*, described two strains of *D. uninucleatus*, the original one and a strain NRRL-Y-2181, and records Wickerham's finding that the second strain differs from the first one in the inability to assimilate sucrose, raffinose and inulin, and in the ability to assimilate D-arabinose and L-rhamnose.

Kreger-van Rij & Veenhuis (1974) examined the ultrastructure of *Dipodascus* species and found that the septa in *D. uninucleatus* have a simple narrow pore, whereas those of *D. aggregatus* have plasmodesmata. The spore wall in the latter species is thin at first and expands considerably later on, which is not the case in *D. uninucleatus*. The authors pointed to another important difference between *D. uninucleatus* on the one

hand and *D. albidus* and *D. aggregatus* on the other, namely the method of ascus formation. In the last two species gametangia are formed from the lateral wall of the hypha on two adjacent cells. The tips of the gametangia fuse and from the zygote a large cylindrical ascus arises "standing with two feet" on the hypha. In *D. uninucleatus* gametangia are formed at both sides of the septum between adjacent cells, and after fusion, the ascus "hangs" between the gametangiogamic cells. Apart from these differences, in *D. uninucleatus* Kreger-van Rij & Veenhuis observed a capsule on the cells and a starch reaction of the mycelium.

Batra & Millner (Batra, in the press) transferred *D. uninucleatus* to a new genus, *Dipodascopsis*, described as follows: Thin mycelium without conidia; asci formed after gametangiogamy. The gametangia arise on adjacent cells. The ascus is conical and multispored; the spores are reniform or ellipsoidal. No fermentation; nitrate is not assimilated.

In the present paper the results of the examination of three strains of *Dipodascopsis uninucleata* using the methods of "The Yeasts" (Lodder, 1970) are described. The species is subdivided into its type variety and a new variety *wickerhamii*, named after Dr. L. J. Wickerham.

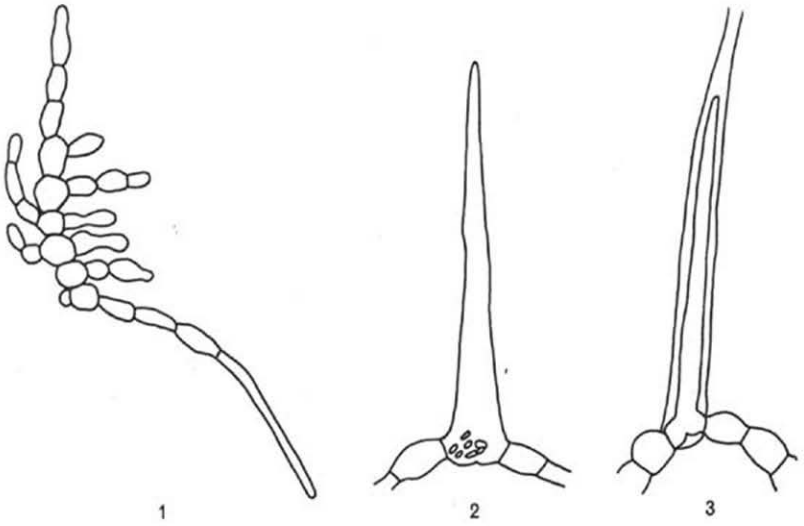
DIPODASCOPSIS UNINUCLEATA (Biggs) Batra & Millner var. UNINUCLEATA—Figs. 1–3

GROWTH IN MALT EXTRACT: After 5 days at 25 °C, a thin loose sediment is formed. After one month at room temperature, a sediment and a dull pellicle are present.

GROWTH ON MALT AGAR: Branched mycelium, often with short cells and constrictions at the septa (Fig. 1). The cells are capsulated. Old cultures give a starch reaction with iodine solution, the wall of the hyphae staining blue. Arthrospores are not formed, but the mycelium may break up between two gametangia. Side branches arise near a septum or in the middle of hyphal cells. After one month at room temperature, the culture is light brown, dull, raised, butyrous and delicately wrinkled.

FORMATION OF THE ASCUS: In two adjacent cells in a hypha cross walls are formed resulting in two new small cells, the gametangia, at both sides of the septum between the original cells. After fusion of the gametangia, a long tapered aerial ascus develops with numerous small reniform or ellipsoidal spores (Fig. 2). The spores do not stain with iodine solution. They are liberated from the tip of the ascus and initially remain clustered. New gametangia may be formed on the first gametangiogamic cells from the same site, and thus within the first ascus (Fig. 3). After fusion, a second ascus develops within the first one, often protruding through the apical pore. A third and a fourth ascus may follow. Occasionally, only one gametangium develops or the two gametangia do not fuse and grow out as septate hyphae inside the former ascus. Perforation of the ascus wall from the inside by the tip of such a hypha has been observed. The spores germinate by swelling to a sphere and then produce a tube. This may happen when the spores are still inside the ascus. Asci are formed on malt agar, glucose-yeast extract-peptone agar and, very profusely, on arbutin agar. Biggs (1937) found that fusion of gametangia from different hyphae may take place and she observed the development of asci without previous fusion of cells.

FERMENTATION: Negative.



Figs. 1–3. *Dipodascopsis uninucleata* var. *uninucleata*. — 1. Mycelium on malt agar. — 2. A long tapered ascus between two gametangiogamic cells. Only a few of the numerous ascospores are drawn in the ascus. — 3. A second ascus has developed inside the first one.

ASSIMILATION OF CARBON COMPOUNDS:

Glucose	+	D-Ribose	—
Galactose	—	L-Rhamnose	—
L-Sorbose	+	Ethanol	+
Sucrose	+	Glycerol	+ (very weak) or —
Maltose	+	Erythritol	—
Cellobiose	—	Ribitol	+
Trehalose	+	Galactitol	—
Lactose	—	D-Mannitol	—
Melibiose	+	D-Glucitol	—
Raffinose	+	α-Methyl-D-glucoside	+
Melezitose	+	Salicin	—
Inulin	+	DL-Lactic acid	—
Soluble starch	+ or —	Succinic acid	—
D-Xylose	+	Citric acid	—
L-Arabinose	+	Inositol	+
D-Arabinose	+ (weak)		

SPLITTING OF ARBUTIN: Negative.

ASSIMILATION OF POTASSIUM NITRATE: Negative.

GROWTH IN VITAMIN-FREE MEDIUM: Negative.

GROWTH ON 50% (W/W) GLUCOSE-YEAST EXTRACT AGAR: Negative.

GROWTH AT 37 °C: Positive.

CULTURES EXAMINED. — Two strains of this variety have been studied: the type strain described by Biggs (CBS 190.37), and a second strain received from Dr. C. P. Kurtzman with the number NRRL-Y-1268 and indicated as "Mrak 75-Burkholder".

DIPODASCOPSIS UNINUCLEATA
var. **wickerhamii** Kreger-van Rij, *var. nov.*

Haec varietas a varietate *uninucleata* differt: L-Rhamnosum assimilatur, at non sucrosum, raffinosum et inulinum.

This variety is similar to var. *uninucleata* with the exception of the assimilation of the following carbon compounds:

Sucrose	—	Inulin	—
Raffinose	—	L-Rhamnose	+

One strain of this variety has been studied and this is the type strain. It was received from Dr. C. P. Kurtzman with the number NRRL-Y-2181, and it had been isolated from *Drosophila* by Dr. H. J. Phaff. This strain has been deposited in the collection of the Centraalbureau voor Schimmelcultures at Baarn; dried material of it is preserved in the Rijksherbarium at Leiden (L).

DISCUSSION

Separation of *D. uninucleatus* from the genus *Dipodascus* and its inclusion in a new genus *Dipodascopsis* seem amply justified. The more important features distinguishing *Dipodascopsis uninucleata* from species of *Dipodascus* are: the absence of arthrospores, the ultrastructure of the septum and the lateral wall, the method of gametangium formation, and, in consequence, the position of the ascus, the formation of a second, third or fourth ascus within the first one, and the shape, size and ultrastructure of the ascospores. Perhaps of less importance are the presence of a capsule on the cells and the starch reaction of the mycelium.

Development of a second ascus within the first one has never before been observed in *Dipodascopsis*. It resembles the proliferation of asci in *Ascoidea* (Brefeld, 1891), but in this genus gametangiogamy is absent.

Examination of the strains of *Dipodascopsis uninucleata* with the methods used for yeasts reveals physiological differences among them. Therefore, two varieties are recognized differing in the assimilation of four carbon compounds. The auxanographic test proved to be suitable for showing these differences.

ACKNOWLEDGEMENTS

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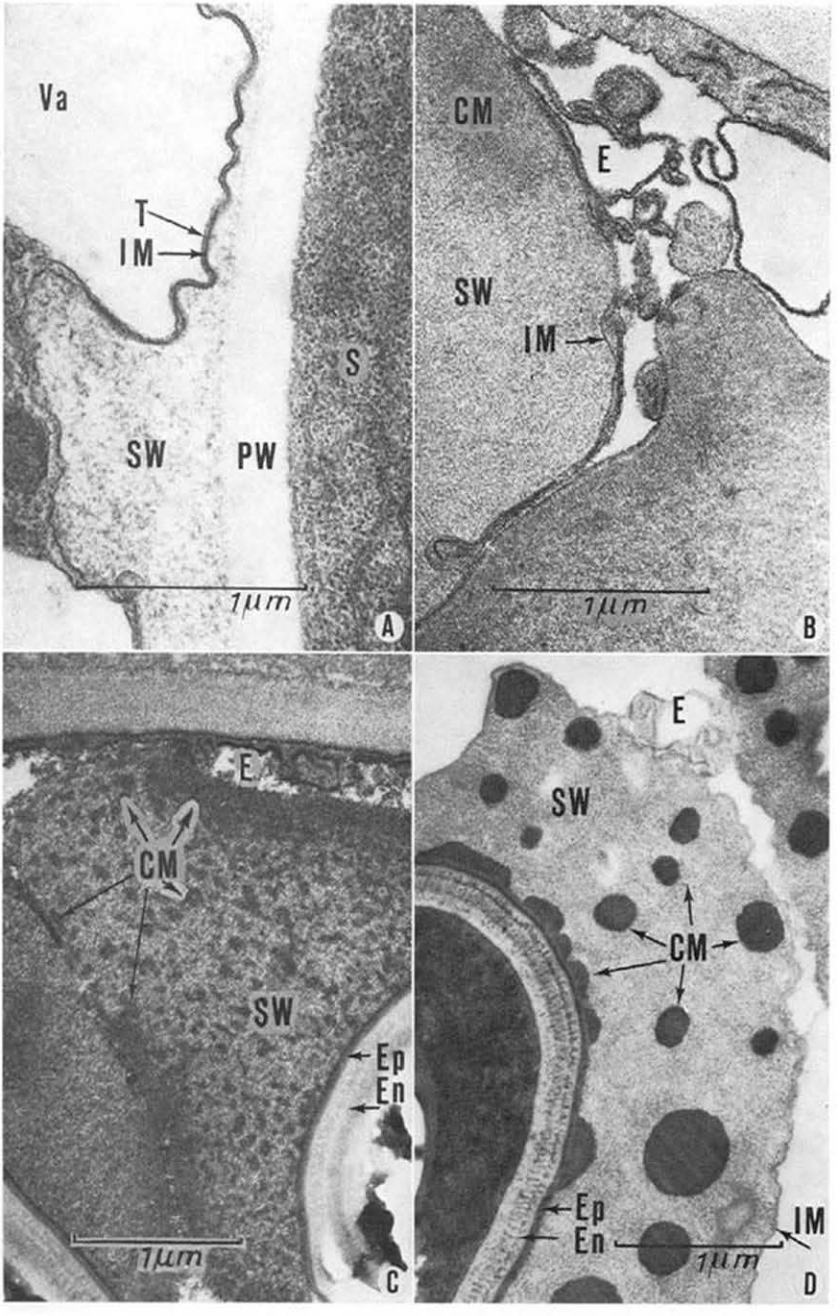
PLATES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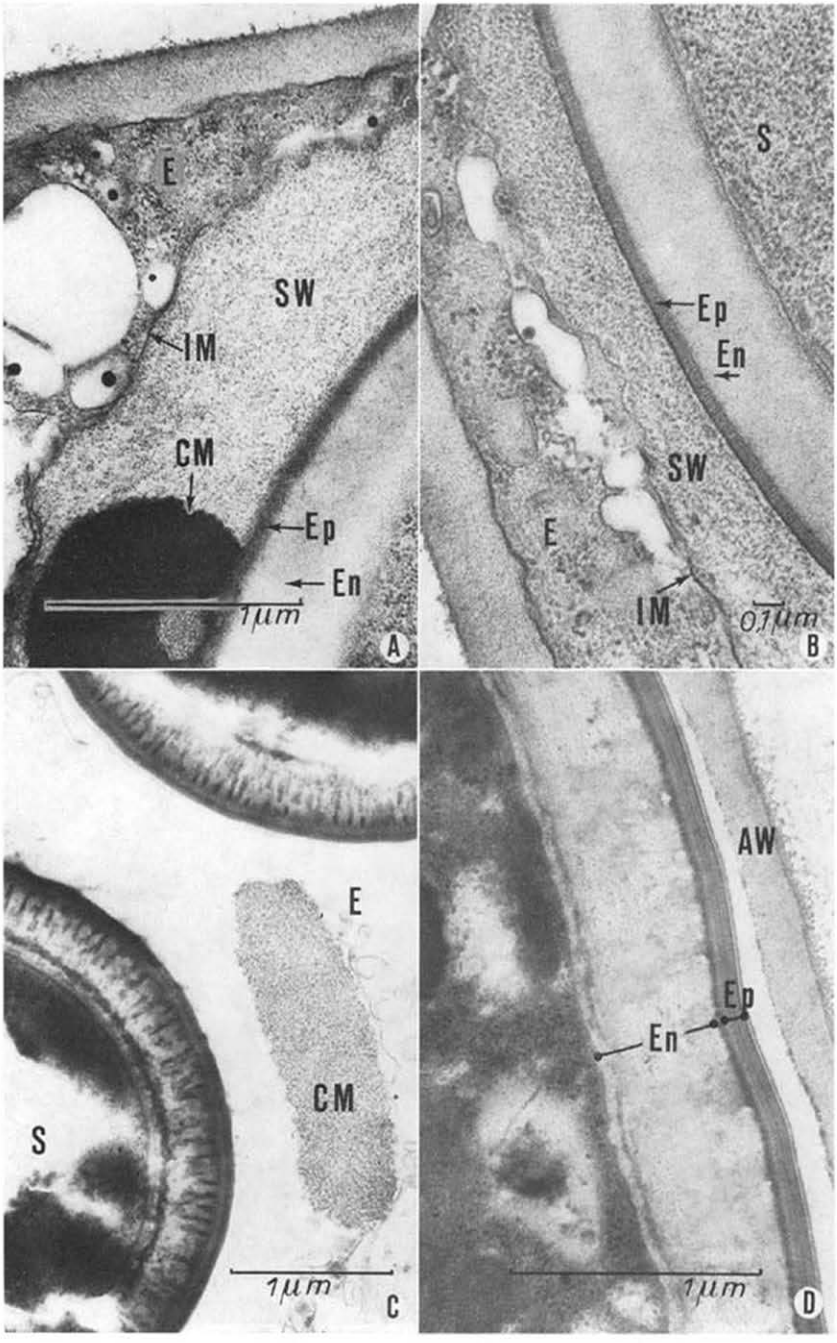
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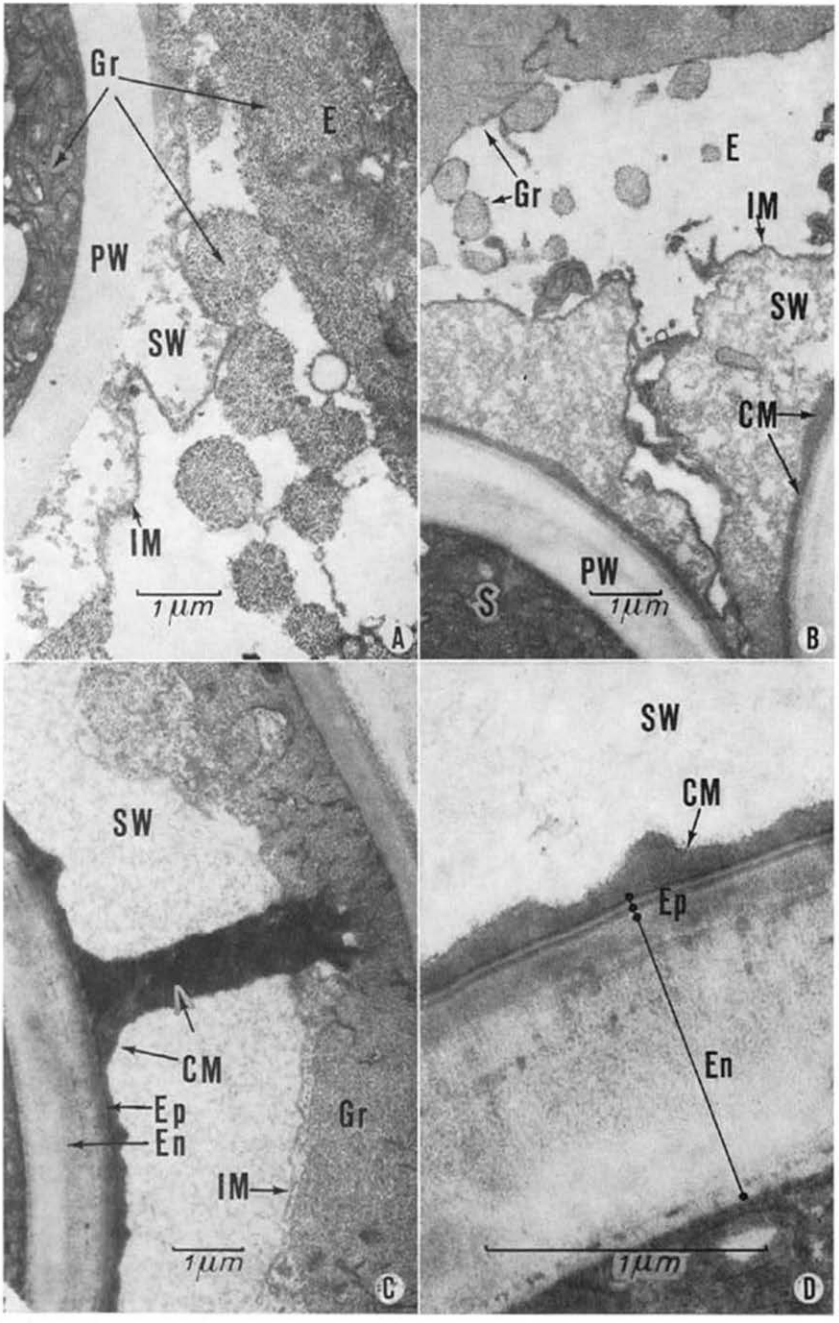
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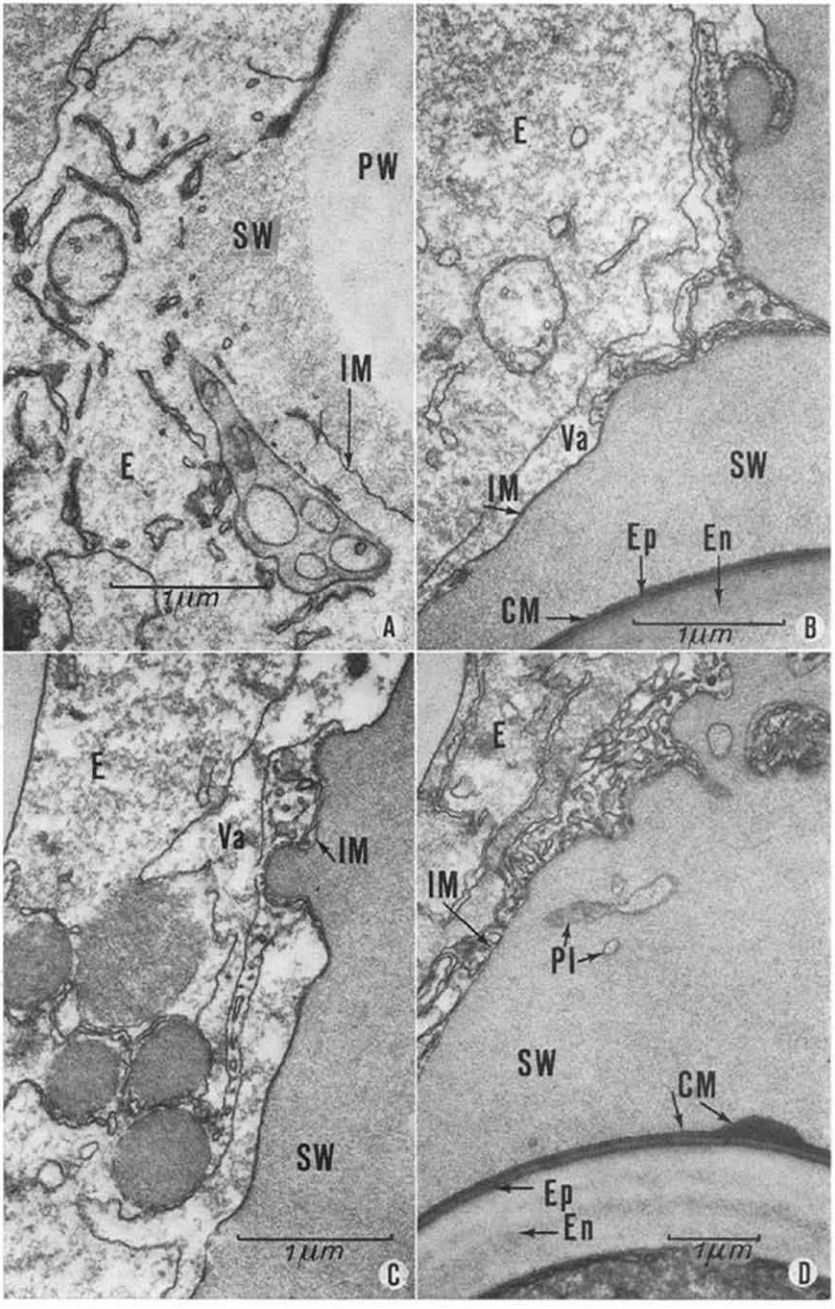
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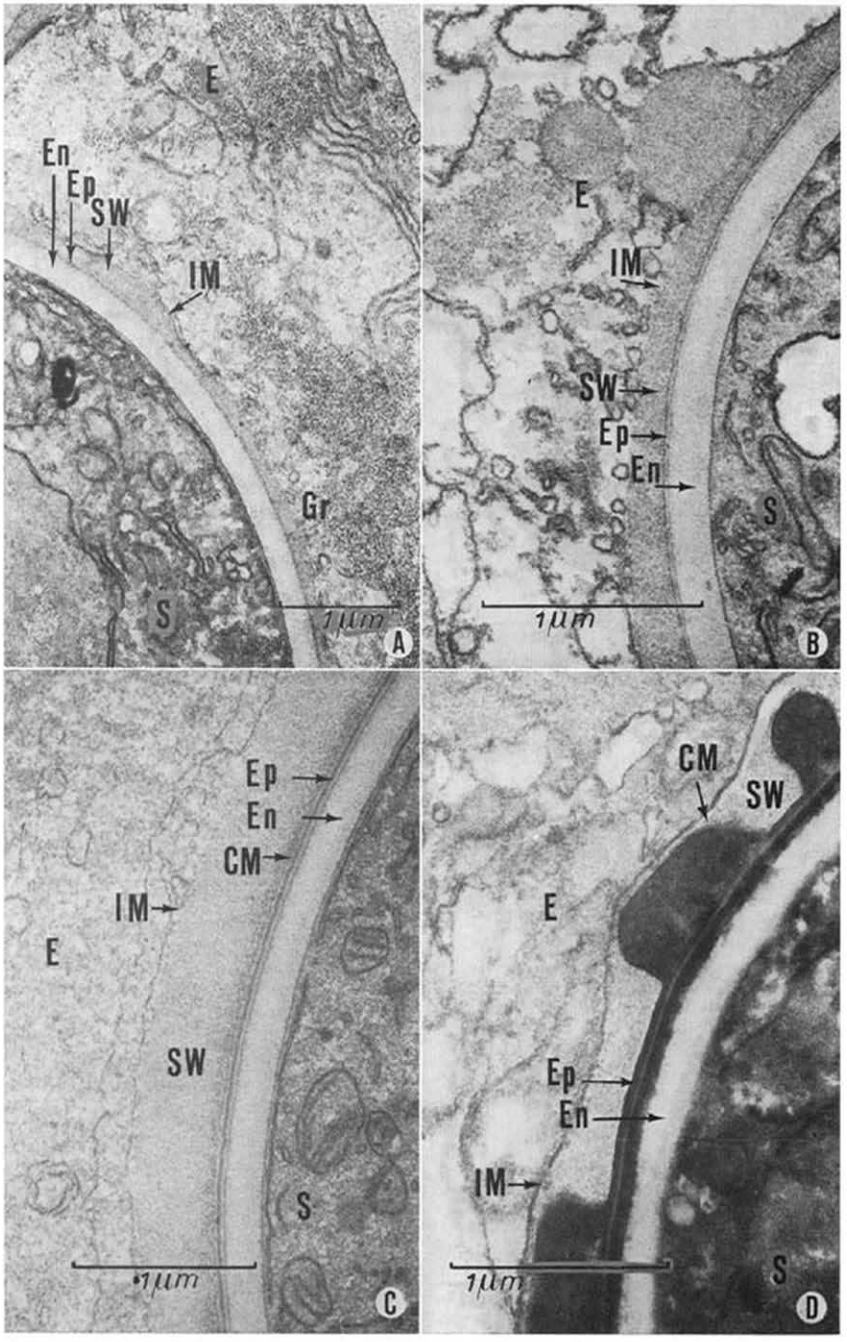
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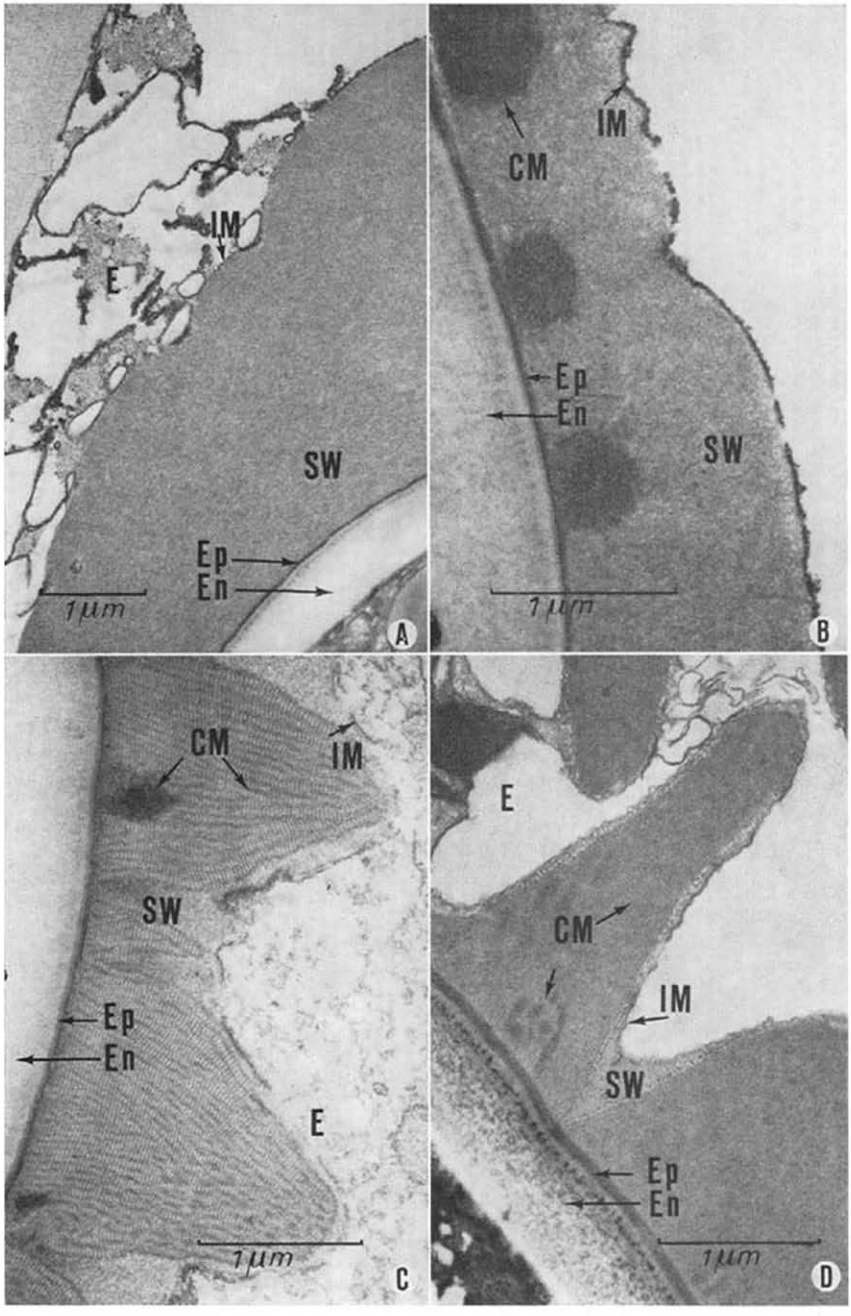
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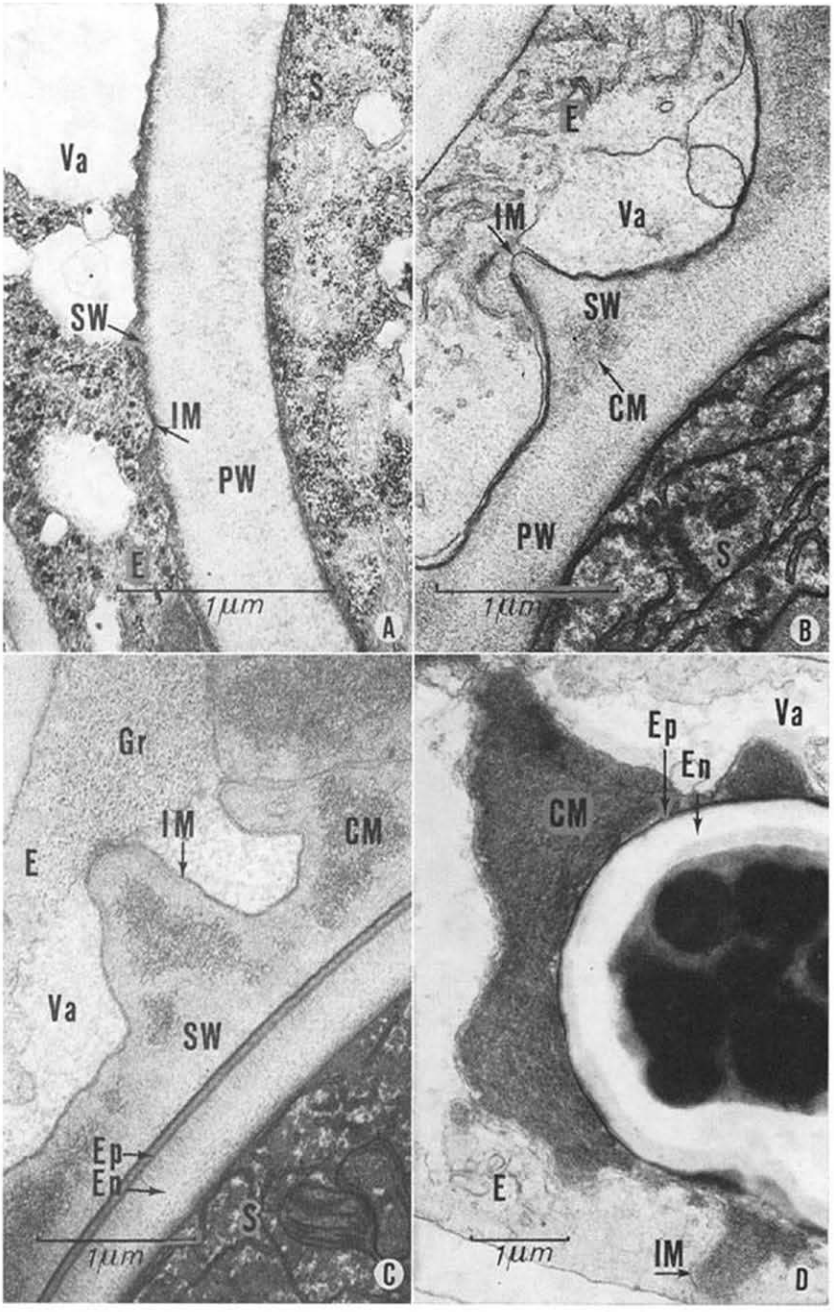
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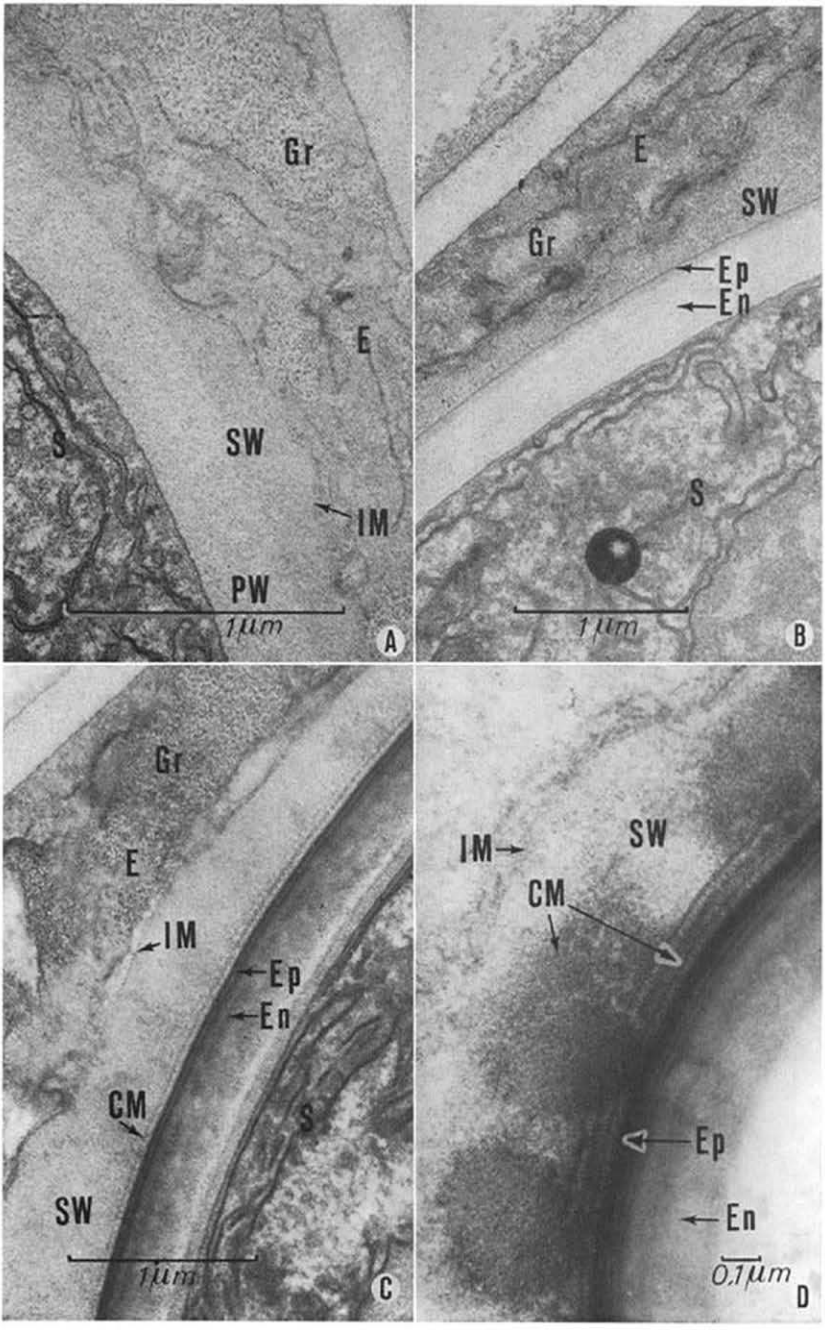
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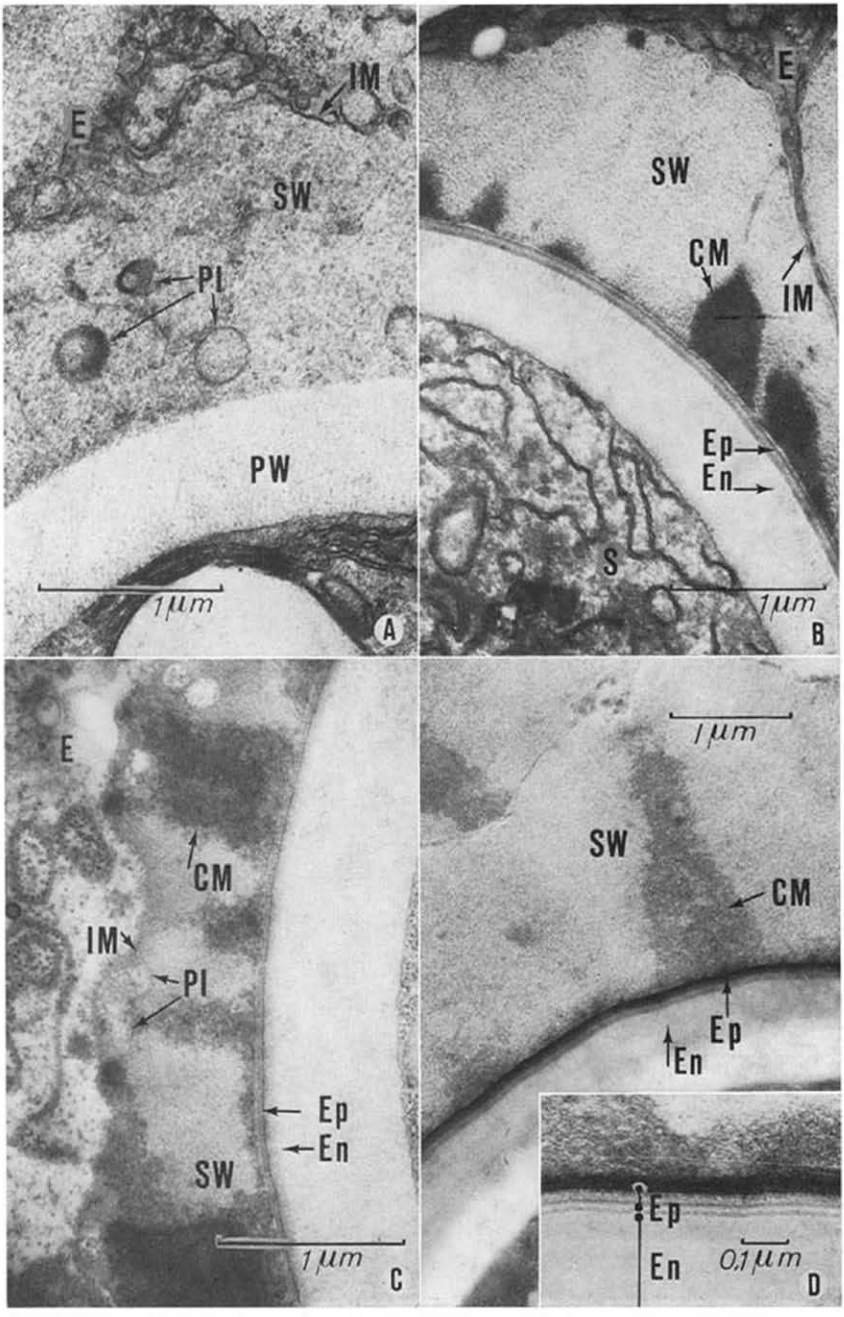
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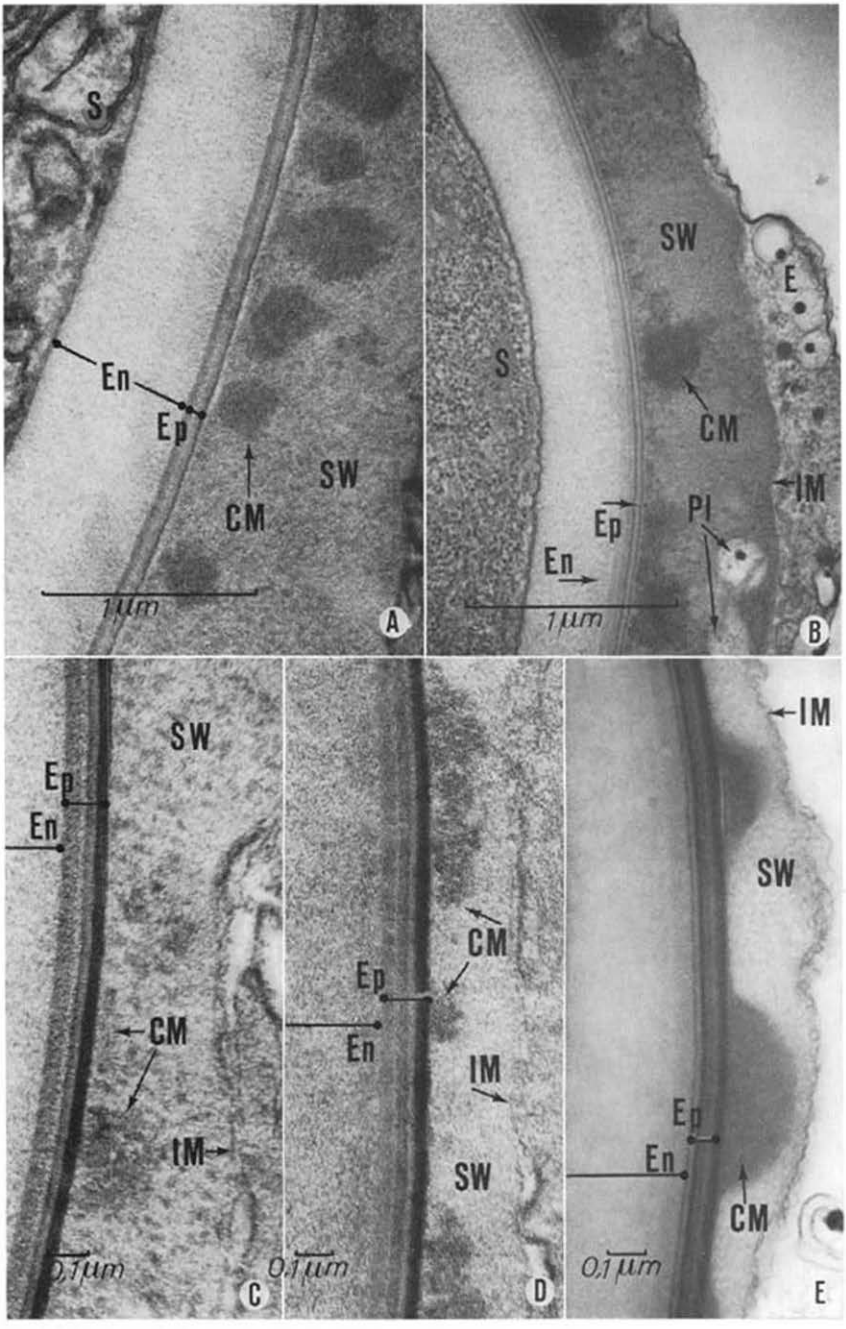
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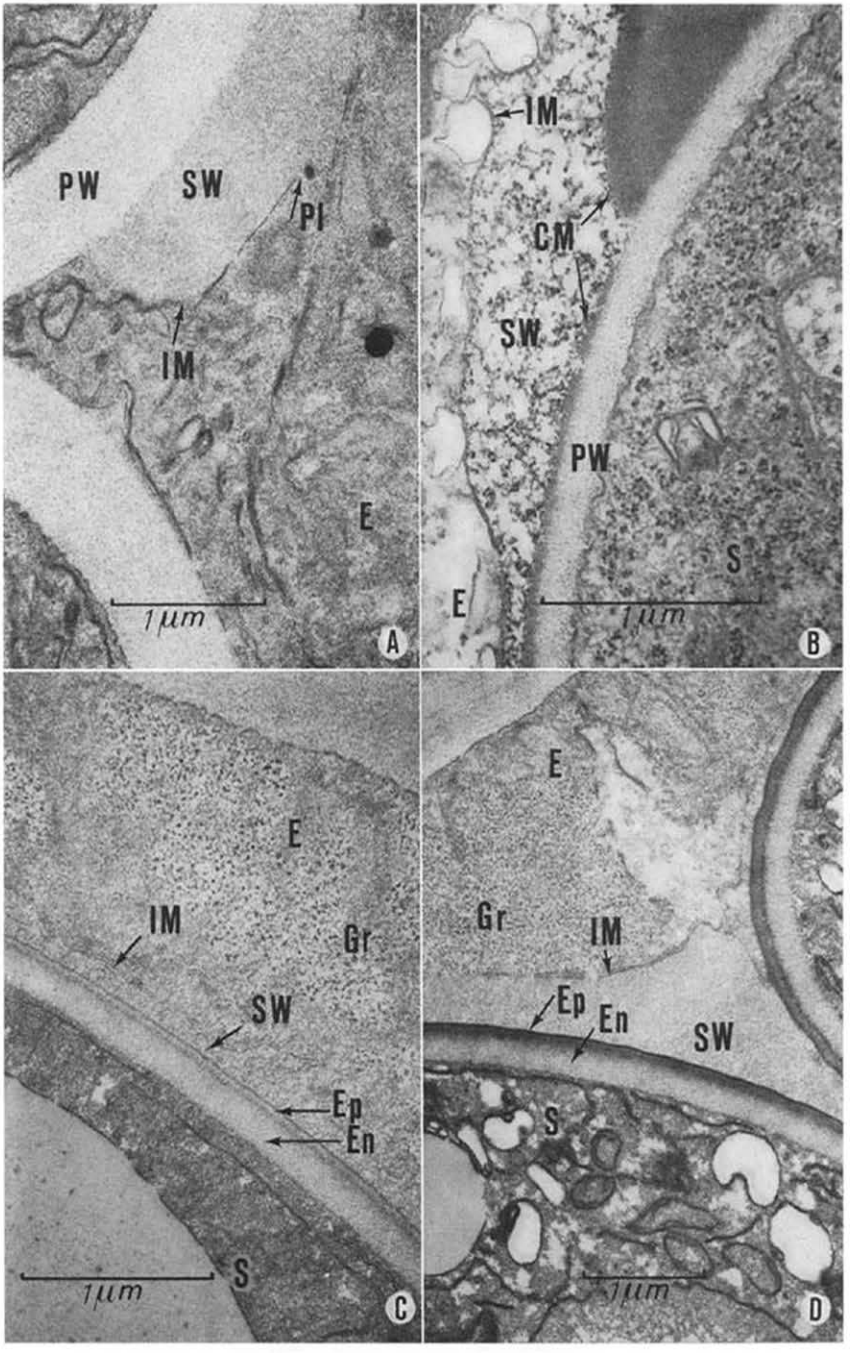
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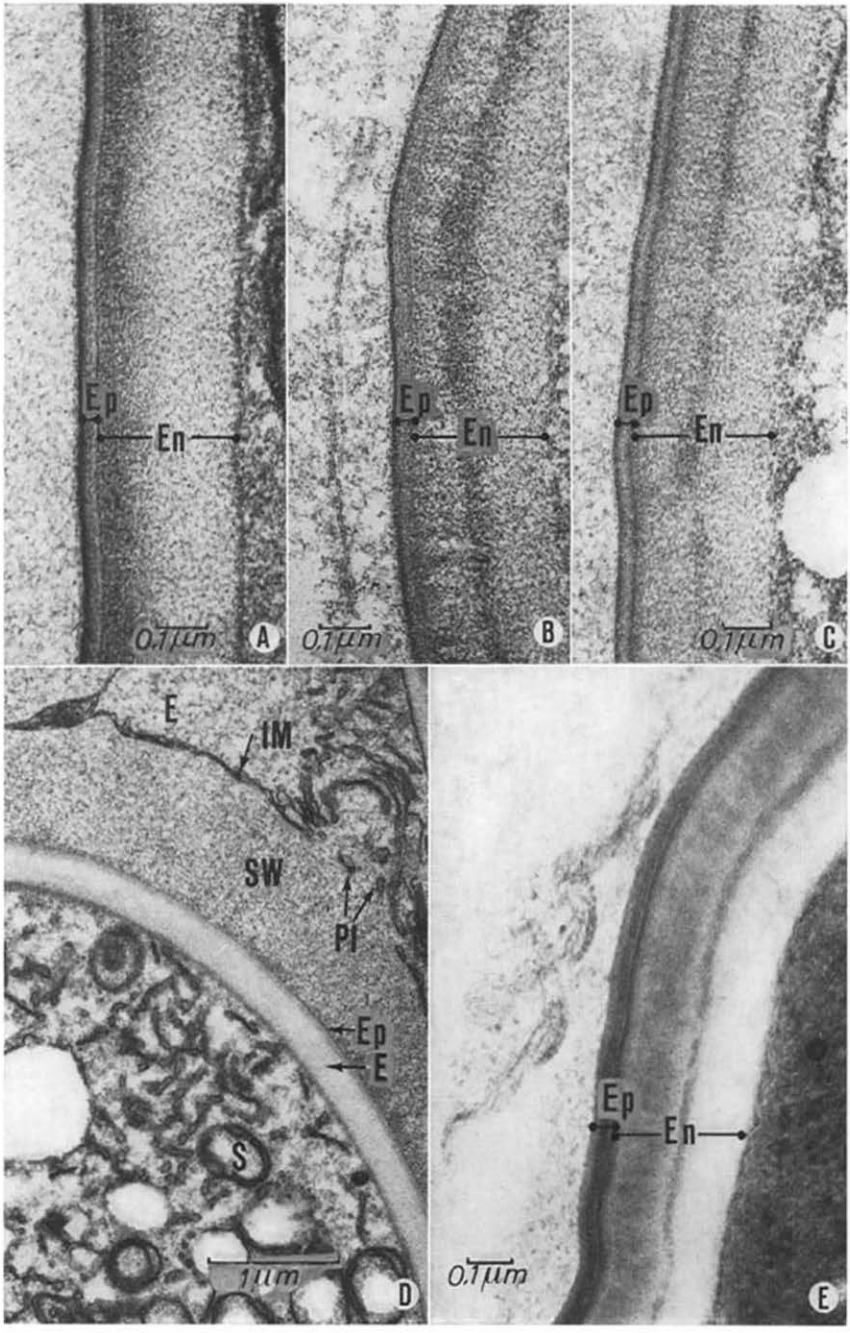
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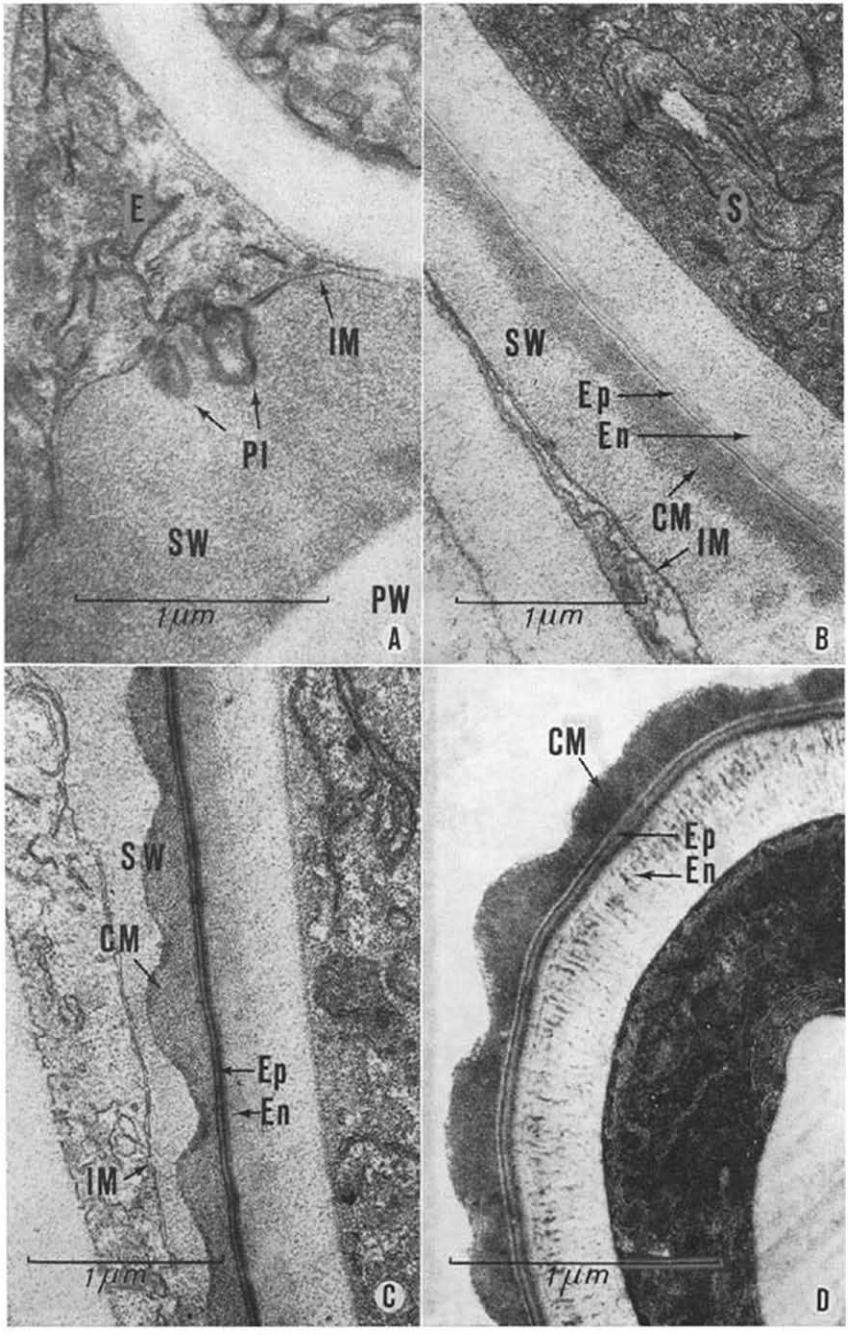
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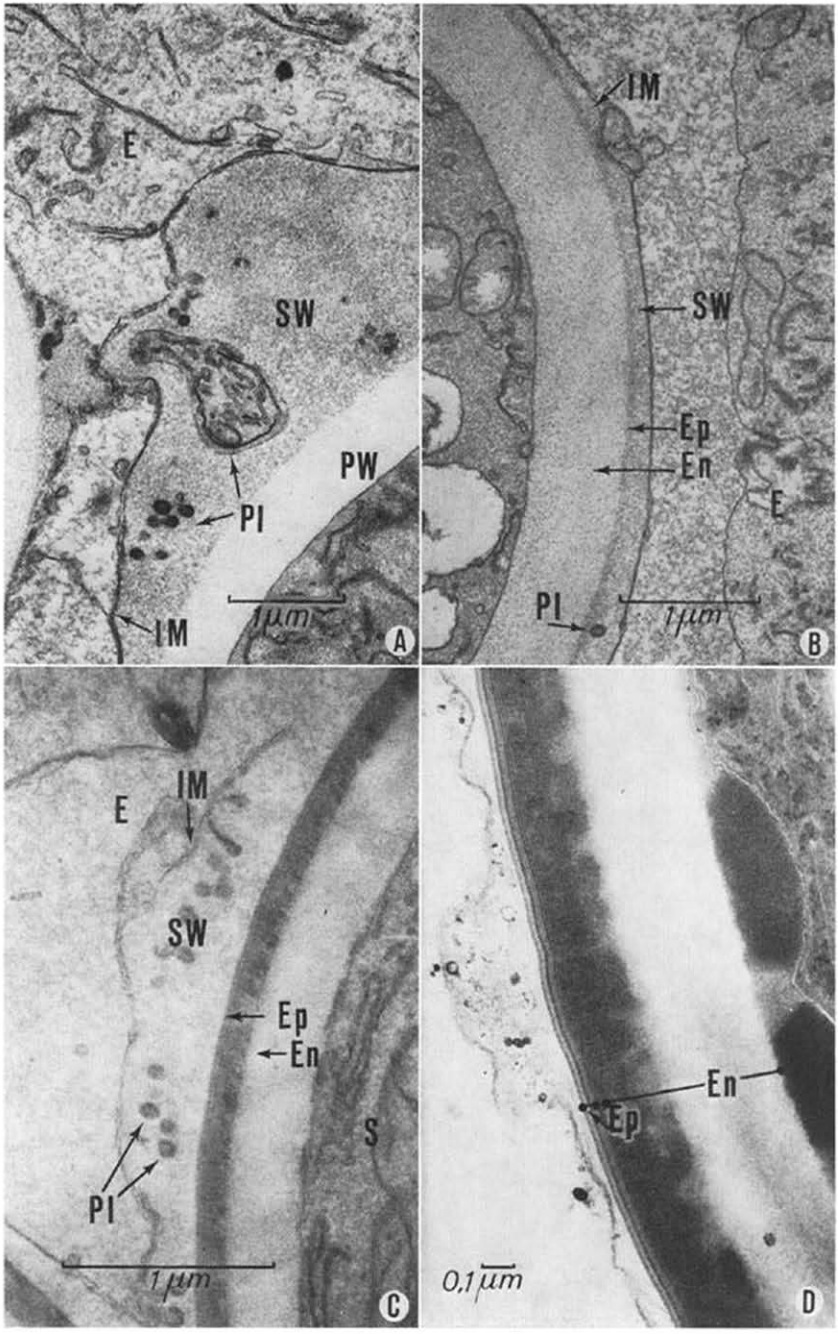
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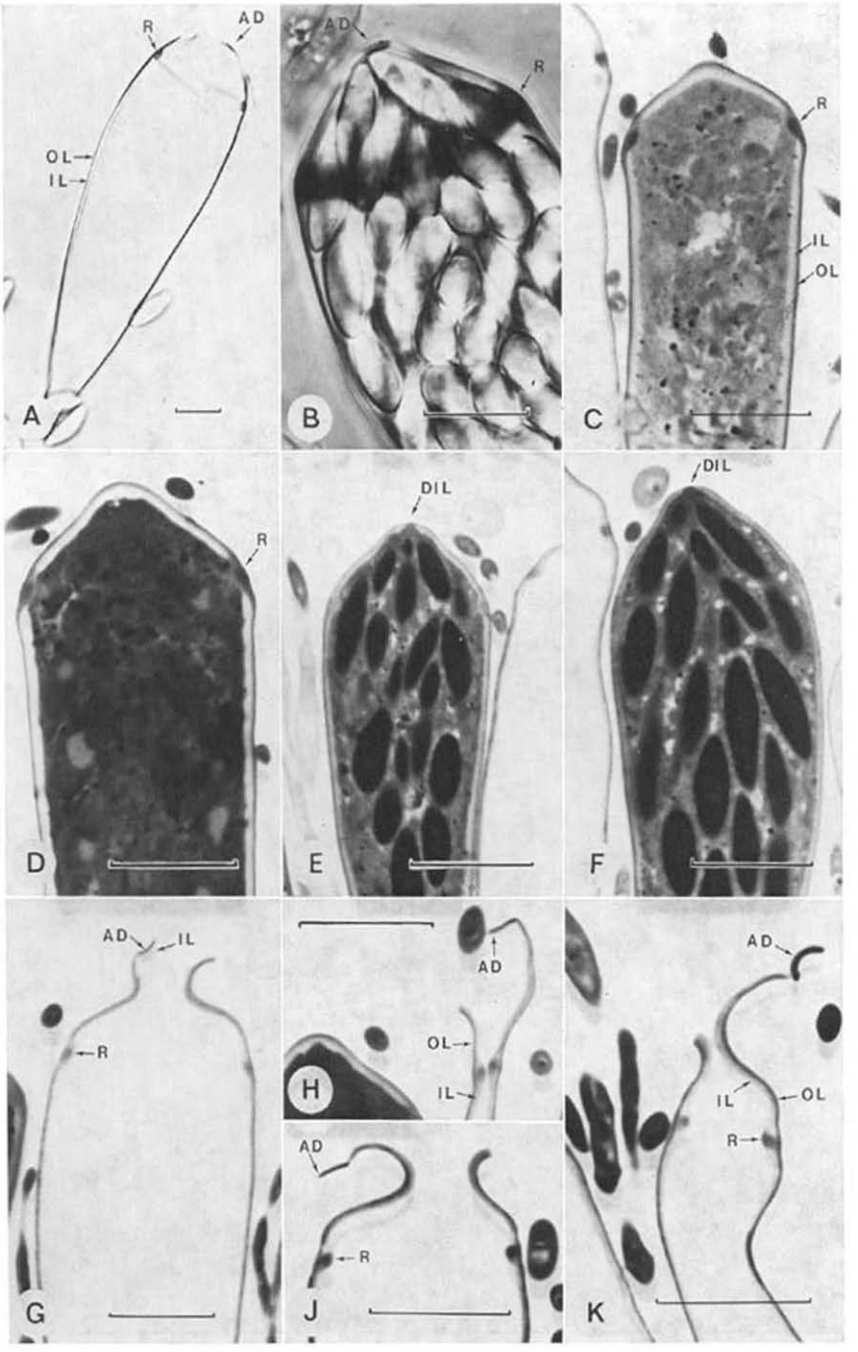
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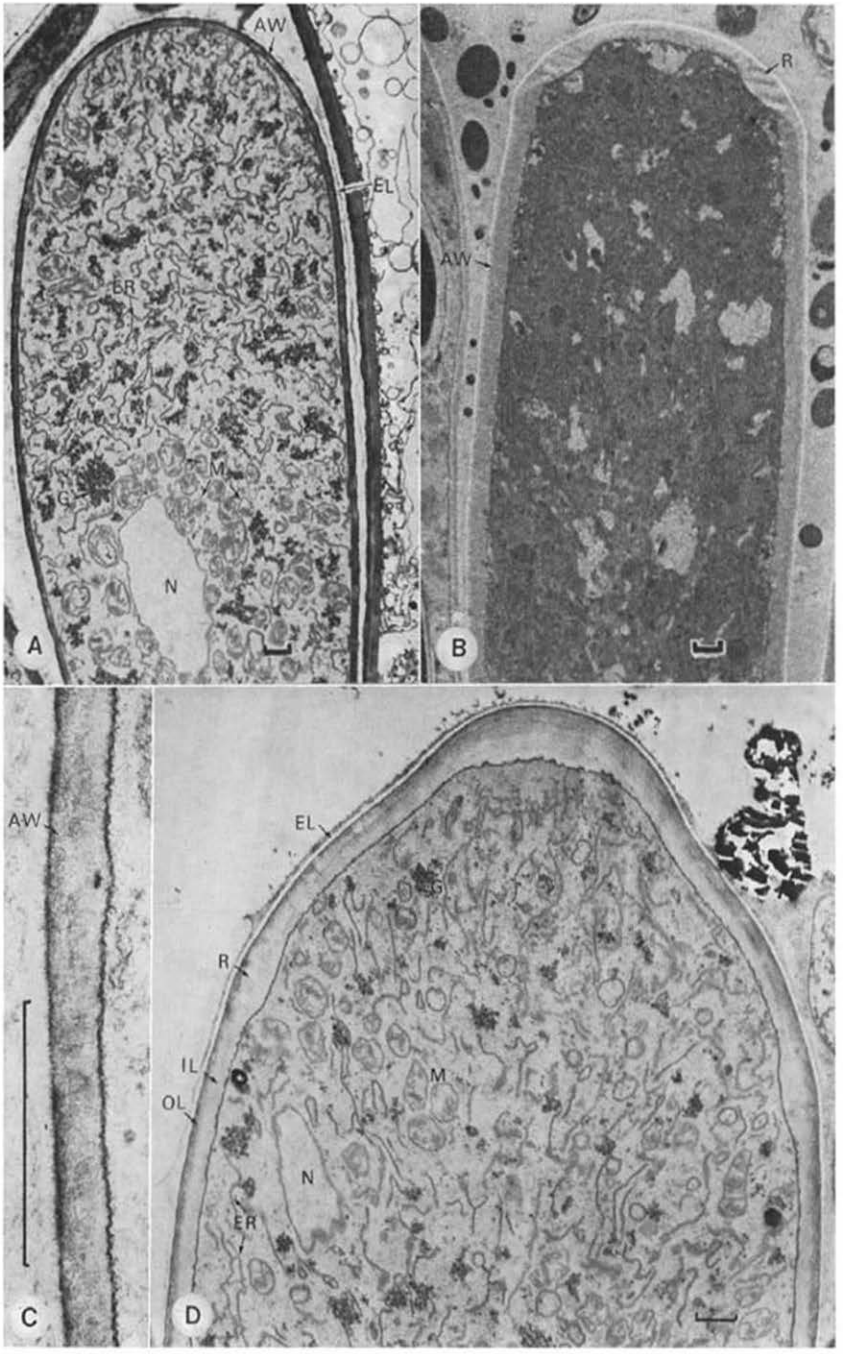
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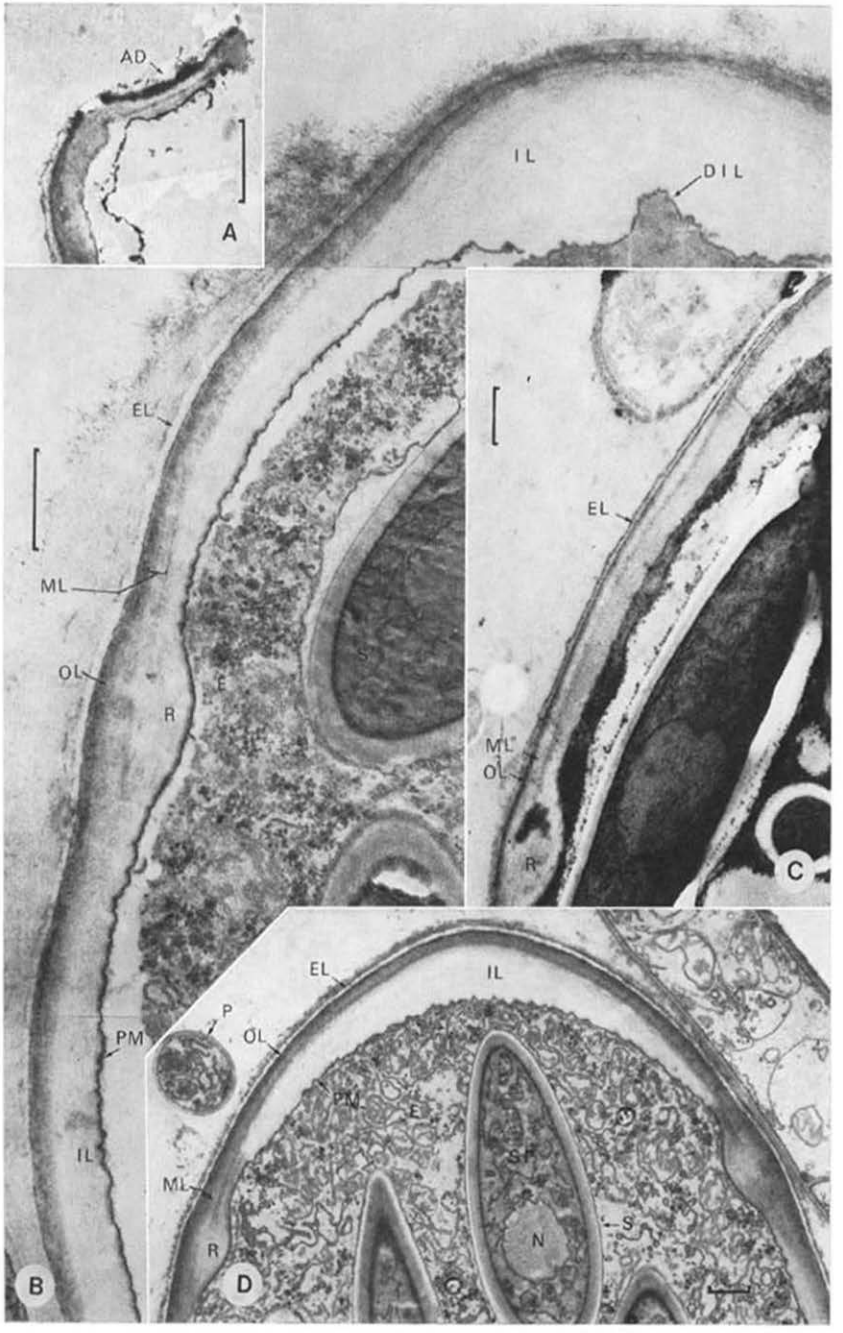
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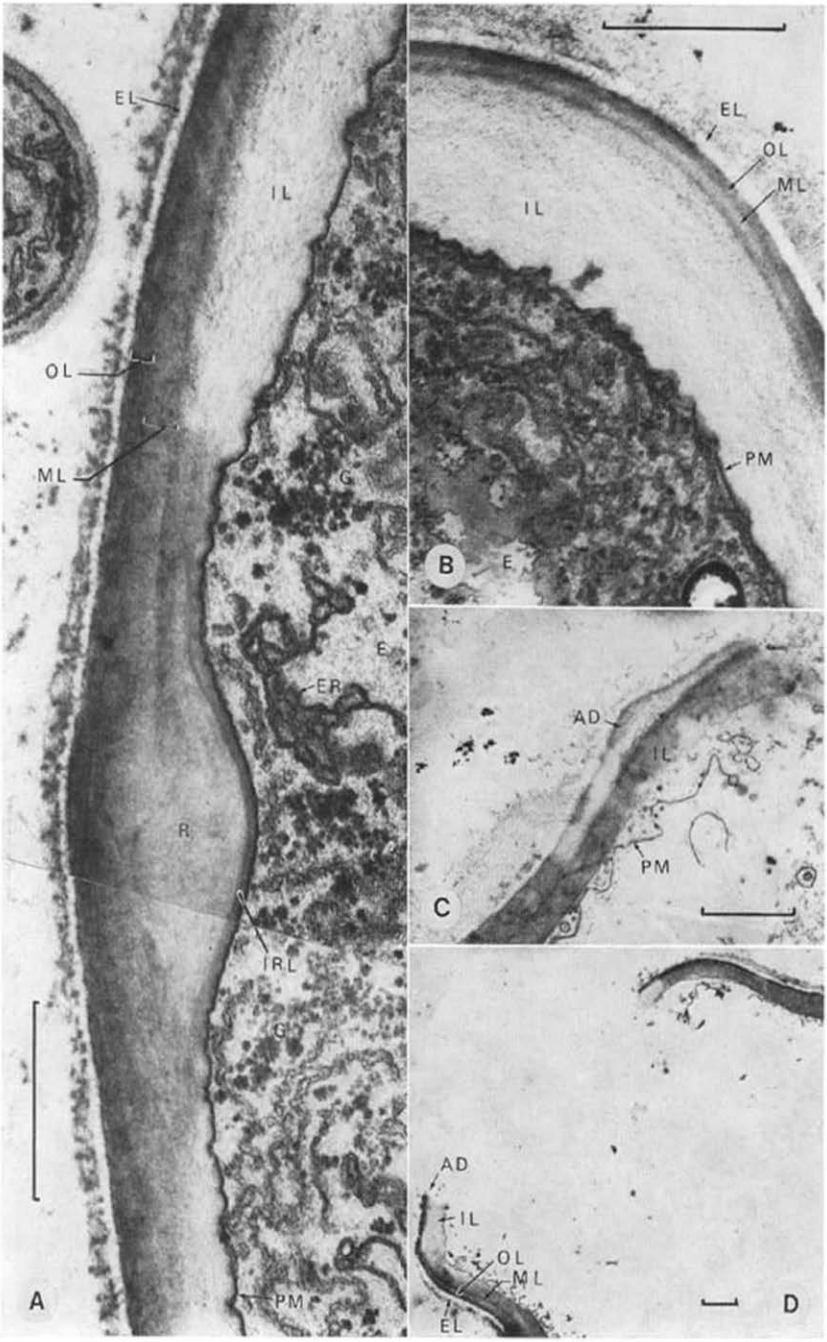
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