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CONIDIOGENESIS AND CONIDIAL SEPTATION AS DIFFERENTIATING CRITERIA BETWEEN PHOMA AND ASCOCHYTA

G. H. Boerema & G. J. Bollen

Plantenziektenkundige Dienst, Wageningen and
Laboratorium voor Fytopathologie van de Landbouwhogeschool, Wageningen

(With 6 Text-figures, 1 Table and Plates 19–29)

New definitions of the form-genera *Phoma* Sacc. and *Ascochyta* Lib., based on developmental criteria, are presented.

Phoma species show phialidic ontogeny. The first conidium is produced within a papillate protrusion of the undifferentiated parent cell; after a conidium secedes the basal part of the papilla remains as a collarette on the conidiogenous cell which may show two or three layers corresponding with the layers of the original papilla. The conidia secede by a three-layered septum and are in principle one-celled, although secondary septation may occur, especially in vivo (0–95%). In vitro under normal laboratory conditions the majority of conidia however always remain one-celled. The pycnidia are usually glabrous but also may be hairy or setose.

Ascochyta species show annellidic ontogeny. The conidia arise as relatively thin-walled protrusions from undifferentiated parent cells. The secession of successive conidial primordia by a three-layered septum however may occur at approximately the same level, resulting in an increasing collar of periclinal annellations, which under the light microscope looks like the collarette of a phialide. After or incidentally also before secession the conidia become two- (or more-) celled by invaginations of a newly produced inner wall layer (distoseptation). In this genus therefore conidial septation is an essential part of the conidium completion, which explains that in vivo as well as in vitro the conidia are always mainly two- (or more-) celled. The pycnidia are glabrous or sometimes hairy.

These new generic concepts imply that most of the species usually placed in *Ascochyta* viz. those in *Ascochyta* sect. *Phyllostictoides* Zherbele, belong to *Phoma* as are many species at present placed in *Phyllosticta*, *Diplodina* and *Pyrenochaeta*. *Pyrenochaeta mali* Smith is shown to be identical with *Phoma herbarum*. For *Pyrenochaeta acicola* (Lév.) Sacc. the new name *Phoma leveillei* is introduced.

INTRODUCTION

In the Saccardoan system of classification of *Phoma*-like pycnidial fungi considerable emphasis was placed on the substratum and the presence or absence of septa in the conidia. In general *Phoma* was used for species with one-celled hyaline conidia

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growing on stems and twigs of vascular plants, and *Phyllosticta* for similar fungi on leaves. Species with two-celled hyaline conidia occurring on stems and twigs were placed in *Diplodina*, whereas similar states growing on leaves were included in *Ascochyta*. Of course many *Phoma*-like fungi occur as well on leaves as on stems or twigs and besides in many cases both one-celled and two-celled conidia are found in one pycnidium. This chaotic situation has lead to various *Phoma*-like fungi having synonyms in all four genera (compare van der Aa & van Kesteren, 1971, and Boerema & Dorenbosch, 1973).

With the necessary revision of this unreal classification the first principle has to be that in accordance with the International Code of Botanical Nomenclature, genera are characterized by their type-species. Recent studies of the relevant type-species have opened startling new perspectives.

The lectotype-species of *Phyllosticta* Pers. ex Desm. (1847; nom. cons.), *P. cruenta* (Kunze ex Fr.) Kickx causes leafspots of *Polygonatum* spp. and has recently been studied in detail by van der Aa (1973) and Punithalingam (1974). It represents a separate group of pycnidial fungi formerly commonly known under the name *Phyllostictina* Sydow and characterized by relatively large conidia with an apical appendage. This means that species of *Phyllosticta* sensu stricto are quite different from *Phoma* species. Van der Aa (l.c.) distinguished 46 species of *Phyllosticta* of which 12 are now known to belong to the Ascomycetous genus *Guignardia* Viala & Ravaz. He showed that the ascigerous state of *Phyllosticta cruenta* is *Guignardia reticulata* (DC. ex Fr.) van der Aa. Most *Phyllosticta* species also produce a spermatial state which is classified in *Leptodothiorella* Höhnel.

According to Boerema (1970a) the type-species of *Diplodina* Westend. (1857), *D. salicis* Westend., represents the conidial state of *Cryptodiaporthe salicella* (Fr.) Petr., the causal fungus of branch canker of willow. This conidial state also formed the basis of *Discella* Berkeley & Broome (1850), which therefore has priority. Its type-species, *Discella salicis* (Westend.) Boerema is characterized by excipuliform (cup-shaped, dish-shaped) fruit-bodies with fusoid two-celled conidia. This means that *Diplodina* Westend., as a later synonym of *Discella* Berk. & Br., is not available for *Phoma*-like fungi. According to von Arx (1970) there are about 10 species of *Discella*, all representing conidial states of *Cryptodiaporthe* Petrak.

The characteristics of the lectotype-species of *Phoma* Sacc. (1880; nom. cons.), the ubiquitous saprophyte *P. herbarum* Westend., and the selected type species of *Ascochyta* Lib. (1830), the well-known pea-parasite *A. pisi* Lib., have been comparatively studied by Brewer & Boerema (1965) with the aid of the electron microscope. Both species have similar pycnidia but show substantial differences in conidiogenesis.

In mature pycnidia of *Phoma herbarum* and other typical *Phoma* species (cf. Boerema & Dorenbosch, 1973) conidia arise successively as 'buds' on somewhat cuspidate but otherwise undifferentiated cells lining the pycnidial cavity. The 'bud' of the first conidium originates from a papillate extension; successively produced basipetal conidia arise as 'buds' from the conidiogenous locus which is then surrounded by a distinct collarette. With this kind of conidiogenesis — characterized by Boerema

(1965) as a 'monopolar repetitive budding process' — the wall of the conidial primordia almost immediately attains its final thickness. The differentiation of the conidial wall is associated with abundant production of mucilaginous material. Independently of conidiogenesis in some conidia, septation may occur as an annular ingrowth from the lateral wall. In *P. herbarum* septate conidia are infrequent, but with other *Phoma* species in vivo a high percentage of the conidia may become two-celled.

In *Ascochyta pisi* the conidia are also formed in basipetal succession on undifferentiated inner cells of the pycnidial wall. In this case, however, the first conidium as well as successive conidia arise as long, extremely thin-walled protrusions at the apex of the parent cell. The secession of each successive conidium occurs usually at a somewhat higher level than the previous conidium, leaving the top of the parent cell with a series of scars (wall ridges) corresponding with the number of conidia that have seceded. After detachment, or incidentally also before secession, against the innerside of the initial conidial wall a new wall-layer arises, simultaneously dividing the conidia into two (or more) cells. This 'distoseptation'-process (term coined by Luttrell, 1963) is associated with the production of mucilaginous material.

These differences in conidiogenesis between *Phoma* and *Ascochyta*, however, are very difficult to observe with the light microscope. Especially since further study has shown that in *Ascochyta* spp. successive conidia may also secede at approximately the same level as the first conidium, which then results in an increasing collar of wall material, under optical microscopy similar to the collarette of *Phoma* spp. The differences in septation are also very difficult to observe with a light microscope. However the fact that septation in *Phoma* is a secondary process whereas in *Ascochyta* the septation of the conidia is an essential part of the 'finishing' (completion) of conidial-development offers a simple method for distinguishing species of both genera (Boerema, 1970b). It appeared that *Phoma* species, the pycnidia of which in vivo may contain a variable percentage of septate conidia ('pseudo-Ascochytas'), in agar-cultures under normal laboratory conditions always produce mainly one-celled conidia. To induce formation of conidia with more than one cell special 'experimental conditions' depending on the species involved, are needed. True *Ascochyta* species, however, always produce mainly two- (or more-) celled conidia in vitro. Cultural studies by Zherbele (1971),[1] have shown that the number of true Ascochytas is relatively small. They are true parasites and confined to few plant families.

In summary it can be said that recent studies of type-species showed that

i. only a small number of the more than 2000 described Phyllostictas are genuine species of *Phyllosticta* Pers. ex Desm.,
ii. a small number of the about 1300 described Ascochytas and Diplodinas concern true species of *Ascochyta* Lib.,

[1] Zherbele (l.c.) classes the species with mostly two-celled conidia in *Ascochyta* 'section *Stagonosporoides*'. The species producing in culture mainly one-celled conidia are placed in *Ascochyta* 'section *Phyllostictoides*'.

iii. most of the more than 5000 species described in *Phoma*, *Phyllosticta*, *Ascochyta* and *Diplodina* refer to species of *Phoma* Sacc.

Many *Phoma* species are plurivorous, which means that the number of species of this form-genus is much smaller than is suggested by the numerous descriptions in the literature. Only cultural studies in comparison with characteristics in vivo can solve the immense problem of synonymy and nomenclature of *Phoma* species.

The present study is a continuation and an elaboration of earlier work by Brewer & Boerema (1965). Their observations are checked and emended on the basis of electron micrographs of seven species of *Phoma* and three species of *Ascochyta*. Special study is made of the mechanism of conidial secession and septation in both genera and the development of the first conidium in *Phoma* spp. Observations on the germination of conidia are also included. In three schemes a survey is given of the processes of conidiogenesis, septation and germination in both genera.

In the discussion the characteristics of conidial development in both genera are further analysed, compared with electron microscopy observations in other fungi, and defined in accordance with modern terminology of conidial ontogeny as approved by the 'First international specialists workshop-conference on criteria and terminology in the classification of Fungi imperfecti' (Kendrick, 1971).

Finally redefinitions are given of the genera *Phoma* Sacc. and *Ascochyta* Lib.

MATERIALS AND METHODS

Specimens used.

The *Phoma*-type of conidial development was studied on the type-species of *Phoma* and six other form-species. Two represent conidial states of *Didymella* species and one concerns the conidial state of a *Leptosphaeria* species.

In cultures on agar media at 20–22 °C the mature pycnidia contain only or mainly one-celled conidia; however in other conditions and especially in vivo the mature pycnidia of some of these form-species may contain a variable percentage of two-celled, or even three-celled conidia.

1. *Phoma herbarum* Westend. At the 8th International Botanical Congress at Paris (1954) this species was selected as the type-species of the form-genus *Phoma* Sacc. (see Boerema 1964, 1970b). It is a ubiquitous saprophyte with usually only one-celled conidia. The pycnidia used in this study were taken from agar-cultures of an isolate made from bathroom paintwork (dried culture: L 972.109–054).

2. *Phoma chrysanthemi* Vogl., the conidial state of *Didymella chrysanthemi* (Tassi) Garibaldi & Gullino (1971). This fungus is known as the cause of (flower) ray blight of *Chrysanthemum morifolium* cultivars, though the stems and leaves of the plants may also be attacked. A large percentage of the conidia may become two-celled (synonym: *Ascochyta chrysanthemi* F. L. Stevens), depending among others on the temperature (Blakeman & Hadley, 1968). The pycnidia used were taken from agar-cultures of isolates obtained from stems of chrysanthemums (CBS 376.67 and CBS 729.74).

3. *Phoma complanata* (Tode ex Fr.) Desm., a very common species on Umbelliferae (see Grove, 1935) producing usually only one-celled conidia. It is the type-species of *Sclerophomella* von Höhnel (1918). The pycnidia studied were obtained from agar-cultures of the fungus obtained from stems of *Angelica archangelica* (CBS 633.68).

4. *Phoma exigua* Desm. (var. *exigua*), the most frequent *Phoma* species on herbaceous plants. As a weak or wound parasite it is often associated with distinct disease symptoms such as leaf spots, fruit spots, lesions on stems and roots, damping-off, and dieback, see Boerema & Höweler (1967) and Boerema & Dorenbosch (1973). In vivo a large percentage of the conidia may become two-celled (synonym e.g.: *Ascochyta phaseolorum* Sacc., cf. Boerema, 1972), but in vitro most conidia remain one-celled. Conidiogenesis was studied in pycnidia from a potato-stem (*Solanum tuberosum*) and an agar-culture obtained from fruit rot of tomato (*Lycopersicum esculentum*) respectively (L 972.109–045 and dried culture L 970.35–200).

5. **Phoma leveillei** nom. nov.,[2] well known as *Pyrenochaeta acicola* (Lév.) Sacc., a common saprophytic soil-fungus characterized by the occurrence of setae on the pycnidia, see Dorenbosch (1970). The conidia are usually one-celled and are produced on undifferentiated parent cells and not on elongated septate conidiophores as in true species of *Pyrenochaeta* De Not. (see the monographic study of this form-genus by Schneider, 1975). The pycnidia used were taken from agar-cultures of an isolate obtained from soil (CBS 536.66).

6. *Phoma lingam* (Tode ex Schw.) Desm. the conidial state of *Leptosphaeria maculans* Desm.) Ces. & De Not., a well-known seed-borne parasite of *Brassica* species, especially turnip, swede, broccoli and cabbage. The disease is known as dryrot and canker or black leg, but the fungus also causes leaf spots. The conidial state occurs in different phenotypes (Boerema & van Kesteren, 1964): pycnidia with common pseudo-parenchymatous wall structure (type I) and thick-walled pycnidia with a typical pseudo-sclerenchymatous structure (type II) similar to that of the pseudothecia of the perfect state. Pycnidial states with this character may be placed in a separate form-genus *Plenodomus* Preuss (1851), of which *P. lingam* represents the type-species (Boerema & van Kesteren, 1964). However, the fact that conidiogenesis in *P. lingam* without doubt is '*Phoma*-like', militates in favour of a classification under *Phoma* as already adopted by von Arx (1970): '*Phoma* section *Plenodomus*'. The conidia of *P. lingam* are usually one-celled. The pycnidia used in this study (type I) were taken from agar-cultures of an isolate made from stems of swede (CBS 532.66).

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[2] Based on *Vermicularia acicola* Léveillé *in* Annls Sci. nat. (Bot.) III **9**: 259. 1848; neotype: dried culture of CBS 260.65 (Dorenbosch, 1970). A new combination with this basionym would result in a later homonym of *Phoma acicola* (Lév.) Sacc. ≡ *Sphaeropsis acicola* Lév., a different fungus.

Various otherwise typical *Phoma*-species occasionally produce pycnidia with 'setae', which may be sparse or numerous, stiff or rather hyphal-like and either short or relatively long. In our opinion this feature has to be considered only as a species-character. Smith (1963) has even described a strain of *Phoma herbarum*, obtained from spots on apples, producing setose pycnidia under the name *Pyrenochaeta mali* Smith (cf. the type-culture of *P. mali*, CBS 567.63; see also Schneider, 1975).

7. *Phoma lycopersici* Cooke, the conidial state of *Didymella lycopersici* Kleb., a well known parasite of tomato plants (*Lycopersicum esculentum*). The disease is known as stem rot (canker), although the fungus can also cause fruit rot and leaf infections. Besides one-celled conidia, two-celled ones can also occur in mature pycnidia, especially in vivo (synonym: *Ascochyta lycopersici* Brun.), see Boerema & Dorenbosch (1973). The pycnidia studied were obtained from tomato-stems and agar-cultures of the fungus (CBS 735.74).

The *Ascochyta*-type of spore development was studied on the type-species of *Ascochyta* and two other form-species of which one represents the conidial state of a *Mycosphaerella* sp.

1. *Ascochyta pisi* Lib., the lectotype-species of the form-genus *Ascochyta* Lib. (Diedicke, 1912, Clements & Shear, 1931; Sprague & Johnson, 1950; von Arx, 1970). A specialized seed-borne parasite of the pea (*Pisum sativum*). The disease is known as leaf and pod spot. It produces mainly two-, and occasionally three- or even four-celled conidia in vivo as well as in vitro, see Boerema & Dorenbosch (1973). The pycnidia studied were obtained from infected pea seeds (L 972.109–071).

2. *Ascochyta fabae* Speg., a seed-borne parasite of the broad bean (*Vicia faba*), which incidentally may occur on other Leguminosae. The disease is known as leaf spot, though the pods may also be attacked. It produces mainly two-, and occasionally three- or even four-celled conidia in vivo and in vitro, see Boerema & Dorenbosch (1973). The pycnidia studied were taken from agar-cultures of an isolate from infected pods of broad bean (CBS 649.71).

3. *Ascochyta pinodes* L. K. Jones, the conidial state of *Mycosphaerella pinodes* (Berk. & Blox.) Vestergr. This seed-borne parasite is known as the cause of foot rot and leaf and pod spot of pea (*Pisum sativum*), but is also recorded from other plants. In vivo and in vitro the conidia are mainly two-celled (sometimes three- or even four-celled), see Punithalingam & Holliday (1972c). The pycnidia used in this study were taken from agar cultures made of an isolate from infected pea-pods (dried culture: L 974.306–481).

Methods.

Pycnidia were obtained from agar plates (cherry agar, pH 4.0, and oatmeal agar, pH 6.4) exposed to near ultra-violet light, and also from diseased plant material.

To allow penetration of fixatives in most cases the pycnidia needed to be crushed on the substrate. Removal of conidia from the pycnidial fragments by the fixative was prevented by carefully covering the crushed pycnidia with a layer of water agar prior to fixation. The agar blocks (c. 2 mm^3) containing crushed pycnidia were fixed. Fixation was carried out by one of the following schedules:

1. Prefixation with 6% glutaraldehyde, buffered with Sörensen's solution (pH 7.0) for 2 hrs. at room temperature. The small pieces were then transferred to fresh buffer and rinsed, followed by postfixation in 1% OsO_4 buffered with Sörensen's solution (pH 7.0) or with veronal acetate (pH 7.4) for 4–5 hrs. at room temperature. This

schedule was used for specimens shown in the micrographs of Pls. 19A, B; 20B–D; 21A; 22D, F; 23C; 24C, D; 25C, D; 26A–E; 27A–E; 28C, D and 29A–C.

2. Prefixation with unbuffered 2% $KMnO_4$ for a period varying for the different specimens from 5 to 30 min. at room temperature. The fixed material was rinsed in fresh veronal acetate buffer (pH 7.4), followed by fixation with OsO_4 as indicated for (1). This schedule was used for specimens shown in the micrographs of Pls. 19C–E; 20A; 21D, E; 22A–C, E; 23A, B, D; 24A, B; 25A, B; 26D and 28A, B.

3. Fixation in unbuffered 2% $KMnO_4$ for 60 min. at 4 °C. The specimens were rinsed in several changes of distilled water, followed by staining in 0.5% uranyl acetate for 4 hrs. at room temperature. This schedule was used for specimens of *P. lycopersici* shown in the micrographs of Pls. 20E; 21B and C.

The application of different fixatives may explain why in the micrographs conidial walls and septa are sometimes electron-transparant and structureless and in other cases rather electron-dense with contrasting structure. For the same reason membranes and mucilaginous substances can clearly be discerned in some micrographs but not in others.

Following fixation, specimens were washed in buffer solutions, dehydrated in graded series of ethanol and embedded in 2:3 styrene butyl methacrylate at 60 °C, except for some specimens of *Phoma chrysanthemi* and *P. lycopersici* where epoxy resin was used.

Sections were cut with glass and diamond knives and examined in a Philips EM 100 and EM 300 electron microscope.

Germinated conidia were obtained by placing inverted plugs taken from agar plates with sporulating colonies onto the moist surface of water agar plates. After incubation for 16 hrs. at 18 °C germ tubes had been formed. Then the inverted plugs were removed and the plate was flooded with warm malt agar (c. 45 °C).

The difference in colour between malt agar and water agar facilitates the localization of the level at which germinated conidia were present. Small agar blocks (c. 2 mm^3) with germinated conidia were trimmed and fixed as indicated above.

ABBREVIATIONS USED IN FIGURES AND PLATES. — col, collarette. — cs, cloudy substance. — fr, basal frill. — gt, germ-tube. — il, inner layer of wall. — m, plasma membrane. — mcl, mucilage. — ml, middle layer of wall. — ol, outer layer of wall. — p, pore. — pl, plug. — pw, primary wall. — s, mucilaginous sheath. — sp, septal-plate. — srp, separation-plate. — sw, secondary wall. — ts, triangular space. — Wb, Woronin body. — wc^1, wc^2, etc., walls of successive conidia. — wr^1, wr^2, etc., annellations of successively seceded conidia.

RESULTS

The Phoma-type of conidial development.

In mature pycnidia conidia are produced by small parent cells which are usually indistinguishable from the inner cells of the pycnidial wall but for a single apical aperture. Each parent cell can produce a whole series of conidia (compare Pl. 19A);

under unfavourable conditions conidiogenesis may stop, but start again when conditions change. Finally the parent cells collapse and are replaced by new ones (compare Ciccarone & Russo, 1969).

The development of the first conidium by a parent cell is initiated by a papillate pronounced thickening of the wall at the top of the cell (Pls. 19B, C; 20A; Fig. 1A; see also Sutton & Sandhu, 1969 fig. 11, and Ciccarone & Russo, l.c. fig. 6). Within the papilla wall three layers can be distinguished, an outer almost electron transparent layer (ol) which is continuous with the wall of the parent cell, a thick, relatively electron dense middle layer (ml) which in cross section appears to be falcate, and an electron transparent inner layer (il). The plasma membrane adjoining the inner layer always shows a corrugation which is apparently associated with a concentration of elements of the endoplasmatic reticulum (compare Pl. 19D, E and Brewer & Boerema, 1965). Subsequently the papilla bulges outwards forming a bud-like protrusion (Pl. 19D, E; Fig. 1B). The outer layer (ol) sooner or later for the most part dissolves into mucilage (Pls. 19E; 20A; Fig. 1B). In some species, e.g. *Phoma exigua*, the middle layer (ml) becomes more prominent at the outset (Pl. 19E; Fig. 1B) and appears as if it will develop into the conidium wall (compare Brewer & Boerema, l.c.). The wall of the first conidium primordium (wc^1) however arises from the inner layer (il). The middle layer (ml) may have a function as an 'opener' of the conidiogenous locus of the parent cell. Like the outer layer it finally dissolves into mucilage. In some species it remains at first recognizable as a sheath surrounding the first conidium (Pl. 20A; Fig. 1C–a). In other species it seems to dissolve synchronously with the upper part of the outer layer or even earlier (Fig. 1C–b; compare Ciccarone & Russo, l.c. fig. 7). The process of wall differentiation — modification from homogenous wall substance into different outer, middle, and inner wall layers — is associated with increasing production of an electron transparent cloudy substance (cs) (Pl. 20A; Figs. 1, 2).

Conidium secession proceeds very rapidly; it looks often if the conidia are 'pinched off' (Pl. 20A, compare Brewer & Boerema, l.c.), especially because the cytoplasma of the parent cell may contract immediately after secession. However, from numerous micrographs (e.g. Pl. 20B–D) it is evident that secession is initiated by centripetal development of a very thin electron-transparent layer (Fig. 2E, F). Separation

Fig. 1. *Phoma* spp. Diagrammatic representation of our electron microscopy interpretation of the formation of the first enteroblastic phialidic conidium (A→D).

The wall of the first conidium (wc^1) arises within the inner layer (il) of the papillate thickening of the wall at the top of the parent cell (A) (m= plasma membrane). The differentiation of the conidial wall in the following bud-stage (B, C) is associated with the production of a mucilaginous cloudy substance (cs). The middle layer (ml) of the papilla seems to function as an 'opener' of the conidiogenous locus; later on it dissolves into mucilage and forms the outer layer of the mucilaginous sheath (s) around the first conidium (D). The upper part of the outer layer of the papilla (ol) sooner or later disintegrates completely (C-a, C-b). After secession of the first conidium (D) the basal part of the original papilla-wall remains as a collarette (col); sometimes the different layers of the papilla (ol, ml, il) are still recognizable in the collarette (wc^2= wall second conidial initial).

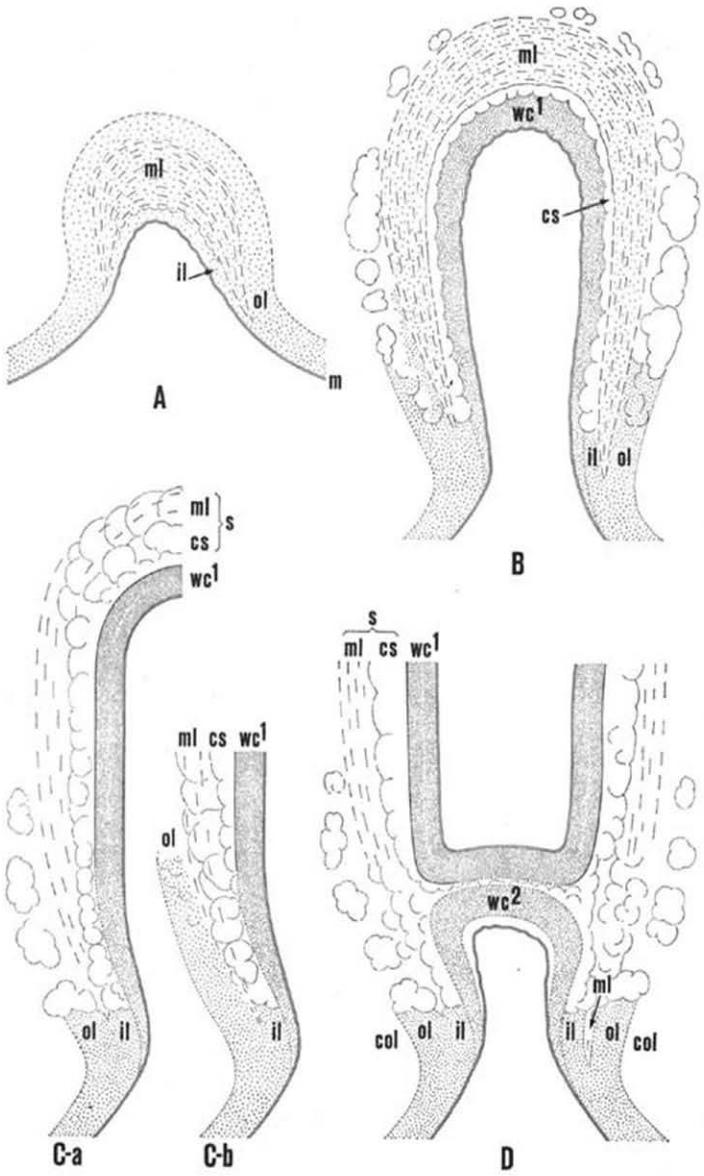
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Fig. 1

apparently occurs along this layer, indicated as separation-plate (srp). Almost simultaneously the basal wall of the conidium is produced, whereas the top of the parent cell also becomes closed by wall substance (Pls. 20E; 21A–C; Fig. 2F). The flattened wall at the base of the conidium always runs parallel to the thin separation-plate. This may also be the case with the wall material covering the parent cell (compare Pl. 21A, D; Fig. 1D), but — as already noted — often the cytoplasm of the parent cell contracts and the closing wall material is produced somewhat lower leaving sometimes plasma rests in the disorganized area between conidium and parent cell (Pls. 20E; 21B, C; Fig. 2F). At secession the separation-plate (srp) and the connecting periclinal wall areas disintegrate to mucilage (Pl. 21D; Figs. 1D, 2G), covering the next primordium (mcl).

The secession of the first conidium leaves the parent cell with a distinct collarette consisting of the undissolved basal parts of the papilla wall. Sometimes the different layers of the original papilla can also be recognized in the collarette (compare Pls. 20E; 21B, E and Figs. 1D, 2G). The collarette surrounds the fixed conidiogenous locus from which the second and subsequent conidia arise (Pl. 19A).

Apart from the papilla the development of subsequently produced conidia is the same as for the first conidium. They arise as outgrowths of the wall closing the parent cell after secession of the preceding conidium (Fig. 1D→Fig. 2E–G). The primordia are covered by some mucilaginous material (mcl, see above) whereas differentiation of the conidial wall is again associated with the production of a cloudy mucilaginous substance (cs).

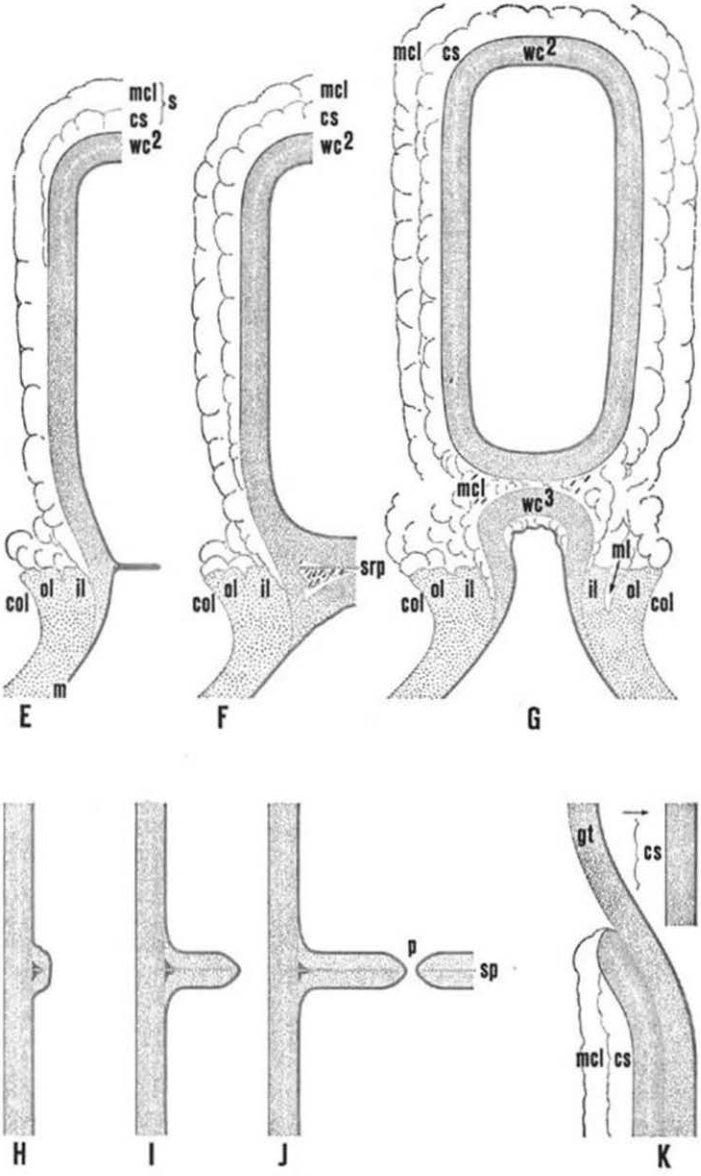
It should be noted that the conidial wall in this conidiogenous process almost immediately attains its final thickness (see e.g. Pl. 20A) and that the abundant mucilaginous mass surrounding the mature conidia apparently originates partly from dissolved wall material (papilla wall or separation-plate with connecting peri-

Fig. 2. *Phoma* spp. Diagrammatic representation of our electron microscopy interpretation of (i) second and successive enteroblastic phialidic conidial development (E→G), (ii) frequently occurring secondary septation of the conidia (H→J), and (iii) conidial germination (K).

The second and successive conidia (wc², wc³ etc.) arise as buds from the conidiogenous locus which is surrounded by a collarette (col), being the remnants of the papilla originally enclosing the first conidial primordium (ol, ml, il, see Fig. 1). Differentiation of the conidial wall is associated with production of a mucilaginous cloudy substance (cs). The conidia secede by separation of a three-layered septum. The initial separation-plate (srp) and the periclinal wall parts disintegrate into mucilage (mcl) which then covers the next primordium and will form the outer layer of the mucilaginous sheath (s) of the next conidium (m= plasma membrane).

Secondary septation of the conidia (H→J) occurs as an annular ingrowth from the lateral wall leaving a pore (p) in the centre. The septa consist of a middle lamella, the septal-plate (sp), at both sides covered with wall layers which for some distance are 'attached' to the lateral conidium wall.

Germination of the conidia (K) is initiated by a swelling. Then at the innerside a new layer can be distinguished which emerges through the ruptured wall of the conidium. Differentiation of the wall of the germ-tube (gt) is associated with the production of a mucilaginous cloudy substance (cs).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K

Fig. 2

clinal wall parts) and partly from a substance produced during conidial wall differentiation (cs).

In many *Phoma* species some conidia may become two celled. This occurs especially in vivo. The septation process proceeds rapidly, so only a few micrographs of the first stages of this process have been obtained (Pl. 22A–D). It appeared that septation occurs as an annular ingrowth from the lateral wall, which apparently from the start attains the thickness of the final septum. The process seems to be initiated by the formation of a very thin highly electron-transparent layer — the septal-plate (sp) — arising more or less perpendicularly from the lateral wall (Pl. 22B–D, F; Fig. 2H, I). Coincidently at both sides of the septal-plate electron-dense wall layers occur. In vertical section they appear decurrent with the periclinal wall to which they are 'attached' with decreasing thickness for some distance (Pl. 22E). Between the decurrent edges of these layers, the periclinal wall and septal-plate triangular 'spaces' (ts) occur, which differ in electron-density (usually more electron-dense: Pl. 22F). In the centre of the septum a pore remains (p; in most sections of course missed) (Fig. 2J) and it is associated with Woronin bodies (Wb) and membrane bounded plugs (pl) (Pl. 23A, C). Incidentally also a microporus has been observed in the septum (Pl. 23B). It should be noted that apart from the area near the septum, the wall of a septate conidium is apparently not thicker than that of a non-septate conidium.

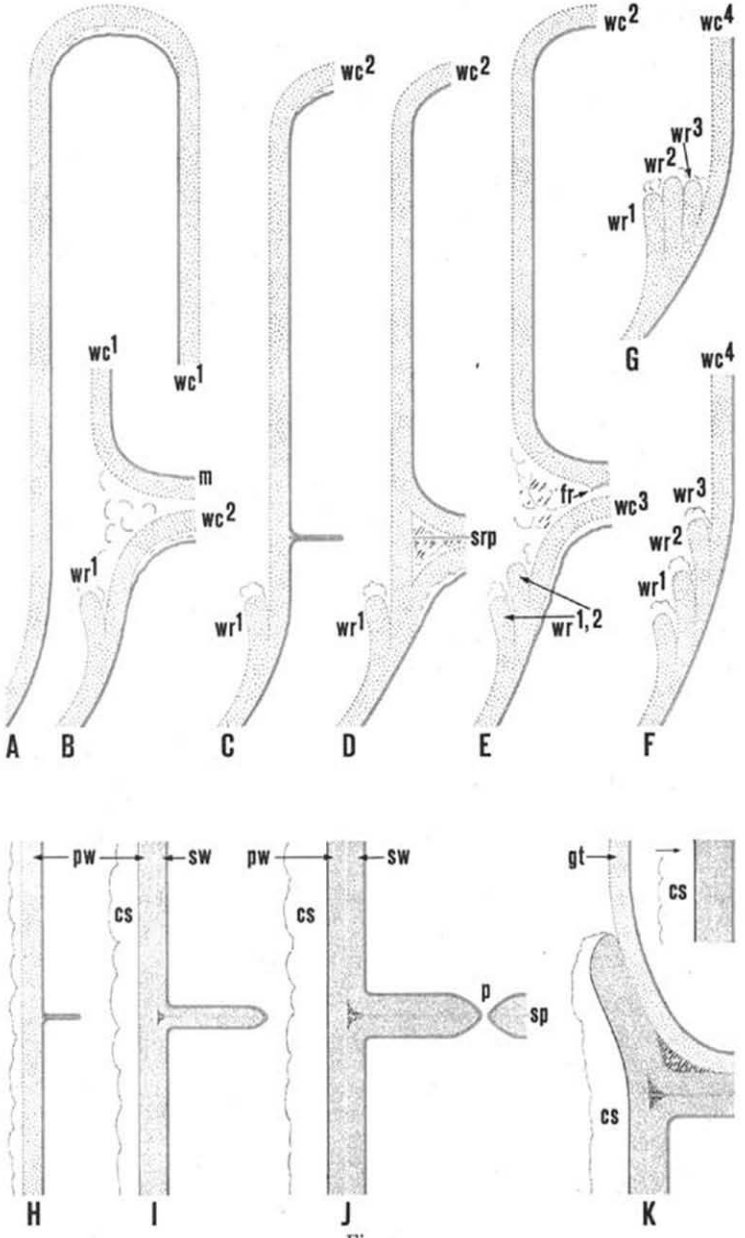
With germination (Pl. 23A, D; Fig. 2K) the conidia swell and a new electron-transparent layer can be distinguished inside the conidial wall and is continuous with the germ-tube which emerges through the ruptured outer wall of the conidium.

Fig. 3. *Ascochyta* spp. Diagrammatic representation of our electron microscopy interpretation of (*i*) annellidic conidial formation (A→G), (*ii*) distoseptation of the conidia (H→J), and (*iii*) conidial germination (K).

The first conidium arises as a long thin-walled protrusion (wc^1) at the top of the parent cell (A). When the first conidium secedes, the parent cell remains with a scar or annellation (wr^1) and the formation of the next conidium (wc^2) starts as a percurrent proliferation (B) (m = plasma membrane). The conidial secession (C→D: secession of second conidium) takes place by a three-layered septum and is initiated by the development of a thin separation-plate (srp). Transverse splitting along the separation-plate and circumscissile rupture (schizolytic) of the outer wall release the conidium. A part of the separation plate may be attached to the seceded conidium (E: fr = basal frill). The secession of each successive conidium may occur at some higher level (F), but also at approximately the same level (G) which then results in a gradually thickening collar, the annellated collar (wr^{1-3} = annellations of successively seceded conidia; wc^4 = wall of fourth conidium).

The septation of the conidia (H→J) occurs by invagination of a secondary developing inner wall (sw; pw = primary wall): distoseptation. The invagination is initiated by the development of a septal-plate (sp). In the centre of the septum remains a pore (p). The process of distoseptation is associated with an abundant production of a mucilaginous cloudy substance (cs). (compare Fig. 4).

With germination (K) the conidia swell and a new layer can be distinguished inside the conidial wall which is continuous with the germ-tube (gt) which emerges through the ruptured wall of the conidium. The wall of the germ-tube thickens secondarily (probably distoseptation).


wc2
wc4
wr3
wr2
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G
wc1
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m
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srp
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wr3
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A
B
C
D
E
F
pw
sw
cs
pw
sw
cs
p
sp
gt
cs
cs
H
I
J
K

Fig. 3

The Ascochyta-type of conidial development.

Conidia arise in succession on small undifferentiated parent cells of the meristematic tissue lining the pycnidial cavity. Under unfavourable conditions conidiogenesis may stop but start again when conditions are improved. New parent cells may replace old exhausted ones which then collapse.

The conidial initials are more or less oblong and have in comparison with mature septate conidia a thin wall (see e.g. Pls. 24A, B; 25A, B). They arise apparently simply as outgrowths of the wall at the apices of the parent cells (Pl. 24C, D; Fig. 3A, C). As in *Phoma* spp. the growing activity is associated with a corrugation of the plasma membrane and a concentration of endoplasmatic reticulum.

When the thin-walled protrusion has attained the (variable) dimension of a mature conidium the process of secession starts (Pl. 25A–D; Fig. 3C, D). This proceeds rapidly, which has made it very difficult to get pictures of the first stages. Nevertheless it was established that as in *Phoma*, three centripetally developing layers are involved: the basal conidial wall, the separation-plate (srp) and the wall closing the top of the parent cell. The initial separation-plate is very thin and highly electron-transparent just as the septal-plate (see below); it is only discernible in few micrographs (Pl. 26A, B). The basal conidial wall and the wall closing the parent cell often develop both close to and parallel with the separation-plate. Sometimes, however, the cytoplasma of the parent cell contracts and the wall closing the parent cell is partly or completely produced at some distance from the basal conidial wall; in the disorganized area between both walls then plasma rests may occur (Pl. 25C; Fig. 3D). Separation apparently takes place along the separation-plate (Pl. 25D); the periclinal walls rupture and the parent cell remains with a broken periclinal wall (wr) and a thin closing wall protruding from the inside of the periclinal wall (Fig. 3B, E). Incidentally the detached conidia show a basal frill (Pl. 25B: fr) which seems to be part of the separation-plate (compare Fig. 3E). The apical region of the closing wall of the parent cell will form the next primordium (Fig. 3E). The secession of each successive conidium may occur at a higher level than the previous conidium. This is usually the case with *Ascochyta pisi*. The top of the parent cell then becomes encircled with a series of wall ridges corresponding with the number of conidia that have seceded (Pls. 24A, B; 25A, B; Fig. 3F). Successive conidia, however, may also secede at approximately the same level as the first conidium. This is commonly the

Fig. 4. Line drawings of conidia and conidiogenous cells (phialides) of *Phoma* spp. as seen with the light microscope. — A. *Phoma herbarum* (after Sutton, 1964 figs. 4A, B, as *P. herbarum* var. *lactaria* Sutton, see Boerema, 1970b). — B. *Phoma exigua* (after Boerema & Höweler, 1967 figs. 3, 4). — C. *Phoma cucurbitacearum* (Fr.) Sacc. (after Punithalingam & Holliday, 1972a figs. C, D, as conidial state of *Didymella bryoniae* (Auersw.) Rehm, see Boerema & van Kesteren, 1972). — D. *Phoma tracheiphila* (Petri) Kantschaveli & Gikachvili (after Punithalingam & Holliday, 1973b fig. C, as *Deuterophoma tracheiphila* Petri, see Ciccarone, 1971). — E. *Phoma terrestris* Hansen (after Punithalingam & Holliday, 1973a fig. C, as *Pyrenochaeta terrestris* (Hansen) Gorenz & al., see Schneider, 1974). Note that the septate conidia in *Phoma* spp. (in vivo 0–95%) under optical microscopy cannot be distinguished from *Ascochyta*-conidia.

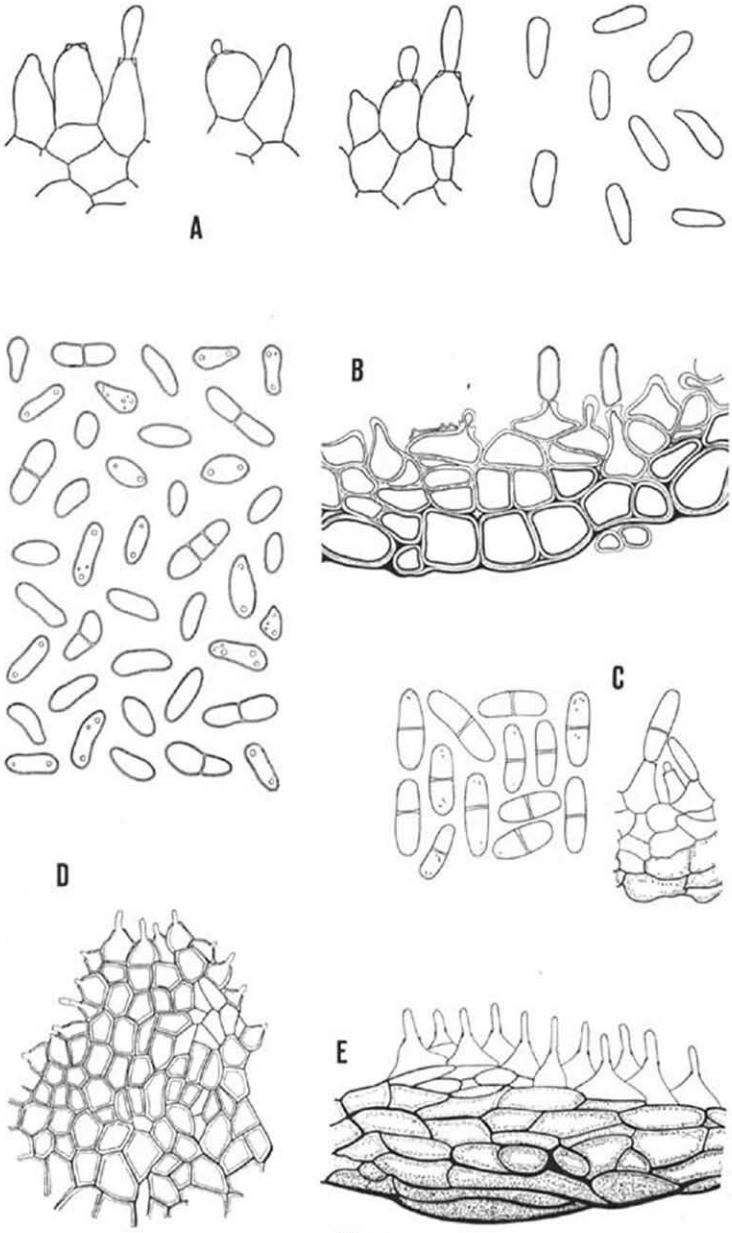

Fig. 4

case with *Ascochyta pinodes*. The top of the parent cell then shows a collar of periclinal wall ridges (Pl. 26C; Fig. 3G).

Immediately after detachment the conidia gradually become thick-walled and septate by the production of a new distinct inner wall (secondary wall: sw), see Fig. 3H–J. This process of wall-thickening and septation is associated with the production of a light cloudy substance (cs) representing the slime surrounding mature conidia (Pl. 26D, E). Most conidia form one septum but two or even three septa may be produced as well. Septation is initiated by centripetal development of a thin highly electron transparent layer, the septal-plate (sp). The development of this septal-plate occurs synchronously with the thickening of the new inner wall, which also covers the septal-plate (Pls. 27A–E; 28A, B; Fig. 3H–J). Between the outer wall, new inner wall and septal-plate, triangular 'spaces' (ts) occur which appear to be mostly electron-dense (e.g. Pl. 28C). In the centre of the septum there remains a pore (p) usually associated with Woronin bodies (Wb) and membrane-bounded electron-opaque plugs (pl) (Pls. 27E; 28D; Fig. 3J). Sometimes the septal-plate shows an undulation which then becomes levelled by the inner wall (Plate 26D; see also Brewer & Boerema, l.c. Pl. 4). Generally the production of the new inner wall and the septa starts immediately after secession; but occasionally this process occurs before secession of the conidium.

The plasma membrane of mature septate conidia sometimes shows typical invaginations (Pl. 29B, C).

Note that the mucilaginous mass surrounding the mature conidia is produced with the process of wall-thickening and septation and not during conidiogenesis.

Germination of the conidia (Pl. 29A; Fig. 3K) is initiated by a swelling of the conidial cells. Then at the innerside a new thin electron-transparent layer can be distinguished. The original wall apparently ruptures by protrusion of the new wall layer.

DISCUSSION

In addition to the electron microscopy observations by Brewer & Boerema (l.c.) this study has provided more information on conidiogenesis and secession, septation and germination of conidia in *Phoma* and *Ascochyta* species. The formation of the first conidium differs essentially in both genera, as does septation of the conidia. The

Fig. 5. Line drawings of conidia and conidiogenous cells (annellides) of *Ascochyta* spp. as seen with the light microscope. — A. Conidia of various graminicolous species (after Sprague & Johnson, 1950 fig. 1). — B. Conidiogenous cells in *Ascochyta pisi* (after Punithalingam & Holliday, 1972b figs. B, C). — C. Conidiogenous cells of *Ascochyta pinodes* (after Punithalingam & Holliday 1972c fig. E, as conidial state of *Mycosphaerella pinodes*). Note that under optical microscopy the annellides of *Ascochyta* show much resemblance with the phialides of *Phoma* (compare Fig. 4).

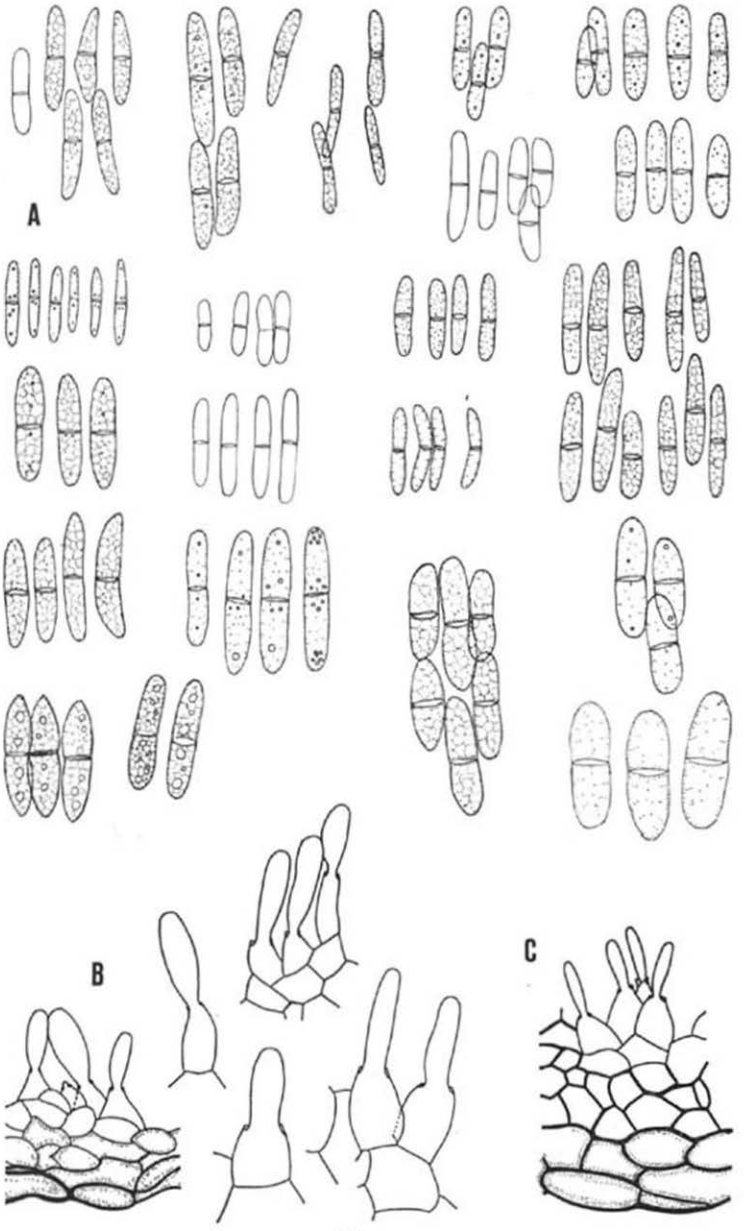

Fig. 5

processes of conidial secession and germination however show much resemblance. In Text-figures 1, 2 and 3 we have tried to reflect the differences and similarities.

First we emphasize that in both genera the conidia secede by septation. For *Ascochyta pisi* this was already established by Brewer & Boerema (l.c.) but in the case of *Phoma* spp. they referred to 'conidia which apparently become pinched off'. Conidial secession in species of both genera can now be characterized as separation by a three-layered septum ('double septum', sensu Kendrick, 1971): two layers of wall material with a very thin abscission layer, separation-plate (srp), between them (Pls. 20E; 21A-C; 26A, B). The abscission layer appears to break down (by autolysis?) and allows the conidium to separate from the parent cell (Pls. 21D; 25D). In *Ascochyta*, remnants of the separation-plate may remain attached to the detached conidium (basal frill, fr: Pl. 25B; Fig. 3E).[3] Conidial secession by a three-layered septum seems to be exclusive in Deuteromycotina and has been shown with the electron microscope for various types of conidial ontogeny (cf. Sutton, 1971; Hammill, 1974).

That the septa in conidia of *Phoma* and *Ascochyta* spp. also consist of two wall-layers with a very thin layer, the septal-plate (sp), between them (Pls. 22F; 28C) is also in accordance with electron microscopy observations of septa in other fungi (see e.g. Bracker & Butler, 1963; Brenner & Carroll, 1968; Kreger-van Rij & Veenhuis, 1971; Littlefield & Bracker, 1971, and Reisinger, 1970). The septal pores of *Phoma* and *Ascochyta* spp. that are associated with Woronin bodies and membrane-bounded electron-opaque plugs (Pls. 23C; 28D), can be characterized as of the Ascomycete-type (see e.g. Bracker, 1967). The incidental observation of a kind of micropore in a conidial septum of *Phoma exigua* (Pl. 23B) is remarkable, because micropores or plasmodesmata are only known from a few fungi in septa that are lacking a central pore (cf. Bracker, l.c.).

Conidial development in both *Phoma* and *Ascochyta* can be characterized as forms of blastic conidial ontogeny (Kendrick, 1971): the conidia differentiate from a part of the parent cell — conidiogenous locus — and there is a marked

[3] From electron microscopy studies of other fungi it is known that the separation-plate does not always disintegrate. In *Doratomyces nanus* it remains a part of the truncate base of the detached conidium (Hammill, 1972a); in *Endomycopsis platypodis* it remains attached to the parent cell (Kreger-van Rij & Veenhuis, 1969).

Fig. 6. Line drawings of conidia and conidiogenous cells of some 'problematic species' (see text Addendum) as seen with the light microscope. — A. *Ascochyta nigripycnidiicola*. Large two- and more-celled conidia as occurring in pycnidia in vivo and in vitro, and one-celled microconidia as produced in other pycnidia also in vivo as well as in vitro. — B. *Phoma oleracea* var. *solidaginis*. 'Mixture' of large two-celled conidia and one-celled microconidia as occurring in pycnidia in vitro. — C. *Ascochyta bohemica*. Large two-celled conidia as produced en masse in vivo together with some one-celled microconidia. The mature two-celled conidia easily break into two parts. In vitro only microconidia are formed which then sometimes arise from elongated cells which look like undetached macroconidia. The parent cells producing microconidia have an obvious collarette in contrast with those producing macroconidia.

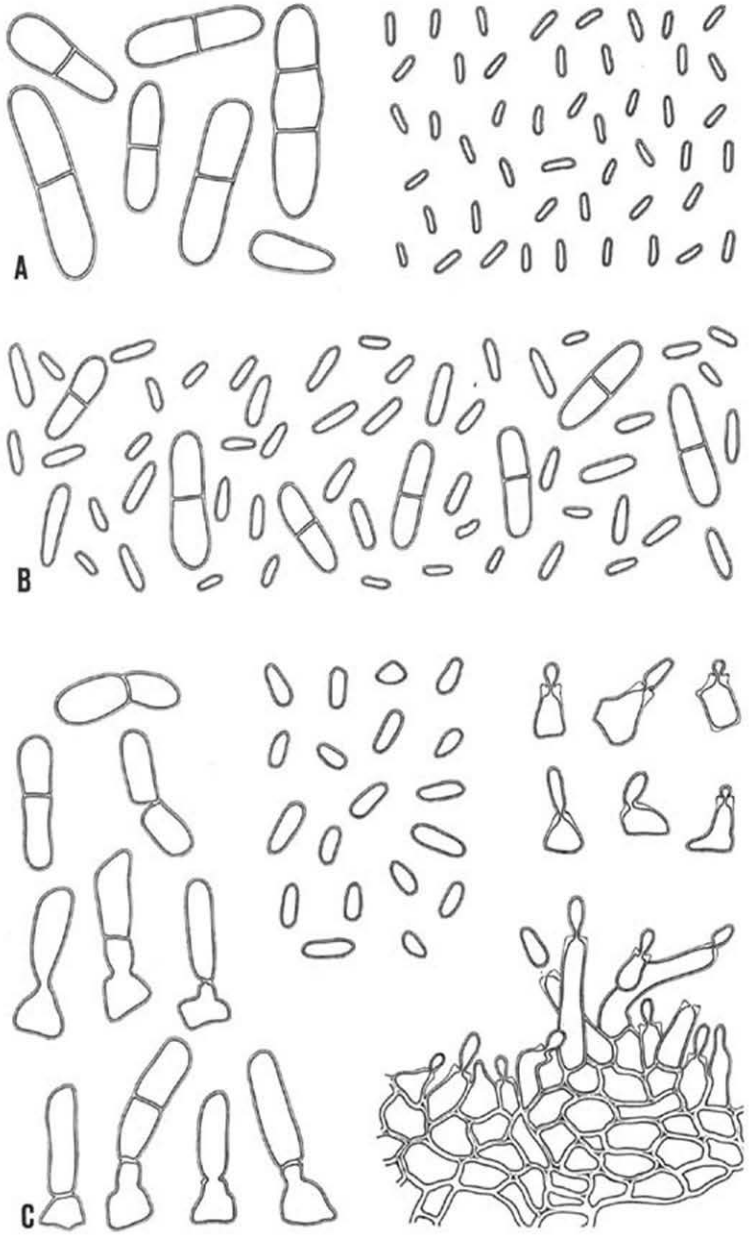

Fig. 6

enlargement of recognizable conidial initial before the initial is delimitated by a three-layered septum.

The conidia of *Phoma* spp. can further be regarded as enteroblastic (Kendrick, l.c.) because the outer layers of the wall at the apex of the parent cell are not involved in the formation of the conidial wall (Pls. 19A, E; 20A; 21E; Figs. 1, 2E–G; see also Sutton, 1971). Conidiogenous cells which produce enteroblastic conidia in basipetal succession (youngest at the base of the chain, the oldest at the tip) from a fixed conidiogenous locus are termed p h i a l i d e s (Kendrick, l.c.). A typical feature of phialides is the c o l l a r e t t e representing remnants of the wall layers originally enclosing the first conidium (compare Fig. 1A–D). On account of the conspicuous collarette the parent cells in *Phoma* spp. have already been interpreted as phialides (Sutton, 1964, Ciccarone & Russo, 1969). Boerema (1965) and Sutton & Sandhu (1969) however had raised doubts concerning this interpretation. They thought that the two or three periclinal layers that are sometimes visible with the electron microscope in the collarettes of *Phoma* spp. (compare Pl. 21B, E) represented wall ridges of detached conidia ('annellations'). The conidiogenous cells in *Phoma* then should not have a fixed meristem producing more than one conidium from it, but instead — as is the case with annellides (see below under *Ascochyta*) — various growing points each producing one conidium. The present study however has shown that the two or three layers or ridges sometimes occurring in *Phoma*-collarettes correspond with the different layers of the original papilla (ol, ml, il) enclosing the first conidium. The successively seceding conidia at the most add some mucilage to the collarette (Pl. 21D; Fig. 2G) but no real scars or annellations. Therefore conidiogenesis in *Phoma* spp. can be characterized as enteroblastic and phialidic, comparable with the enteroblastic phialidic ontogeny in some hyphomycetes as e.g. *Neuropora crassa* (Lowry & al., 1967; Subramanian, 1971: 'type 1'). A typical feature of enteroblastic phialidic ontogeny in *Phoma* spp. is that it starts with the development of a thick-walled papilla with a conspicuous usually more or less electron-dense middle layer (ml) which seems to function as 'opener' of the fixed conidiogenous locus. An additional characteristic is that the differentiation of the conidial wall to its final structure is associated with production of mucilage (cs) which together with dissolved wall material resulting from the liberation of the first conidium and secession of successive conidia, forms the abundant mucilaginous mass surrounding the conidia in *Phoma* spp. In many aspects conidiogenesis in *Phoma* spp. agrees with conidial development in the acervular fungus *Colletotrichum coccodes* (=*C. atramentarium*) as shown in the electron microscopy study by Griffiths & Campbell (1972).

For diagnostic purposes conidial development in *Phoma* spp. was described as 'monopolar repetitive budding' (Boerema, 1965), because under optical microscopy the conidia seemed to arise in succession as buds from the conidiogenous locus with often only a small cytoplasmic channel between bud and parent cell (comp. Pls. 19A; 21E). Originally 'budding' has been considered as secession without septal formation but recent electron microscopy studies have shown that buds in fungi secede by septation also (for references see Sutton, 1971 and Donk, 1973).

For *Ascochyta* spp. the formation of the first conidium by a parent cell can be described as holoblastic (Kendrick, 1971) because the whole (thin) wall at the apex of the parent cell is apparently involved in formation of the conidium wall (Pl. 25B; Fig. 3A). Holoblastic conidial development in basipetal sequence should be typical for annellides, i.e. (Kendrick, l.c.) conidiogenous cells which produce a single conidium from the apex (conidiogenous locus) of each of a succession of very short percurrent vegetative proliferations involving the basal part of the septum remaining after secession of the previous conidium (percurrent indicates a mode of vegetative proliferation in which each successive apex arises through the previous apex). From Pl. 24A–D and Pl. 25A, B, however, it cannot merely be concluded that in *Ascochyta* the conidia formed after the first one by a parent cell are truly holoblastic. In a critical discussion on the distinction between phialides and annellides Hammill (1974) also pointed out that for a number of other fungi in which conidiogenesis is considered to be typically annellidic, the conidia are 'clearly not holoblastic, at least not after the formation of the first conidium in the basipetal sequence'

Characteristic for annellides is the presence of narrow bands of wall material encircling the periclinal wall near the apex of the conidiogenous cell; these annellations are the vegetative portions of the proliferations left behind after each conidium has seceded. In contrast with the fixed meristem of phialides (see above under *Phoma*), annellides thus have various growing points at each of which one conidium is produced. With reference to the conidial ontogeny described and illustrated by Brewer & Boerema (l.c.) for *Ascochyta pisi* (compare Pls. 24A, B; 25A, B), Madelin (1966) has already interpreted the conidiogenous cells of *Ascochyta* as true annellides. As a result of our further observations we agree with this interpretation (Fig. 3). It must be noted however that the micrographs obtained from *A. fabae* and *A. pinodes* (Pls. 25C, D; 26A, C) have indicated that in *Ascochyta* spp. the conidia can originate and secede at approximately the same level as, or possibly even at a lower level than the previous conidium. The result is then not a series of annellations one above another as shown in the micrographs of *A. pisi* (Pls. 24A; 25A; cf. Fig. 3E, F), but an annellate collar composed of a number of periclinal layers corresponding with the number of conidia produced (Pl. 26C and Fig. 3G). Similar observations are made by Sutton & Sandhu (1969) on the conidiogenous cells in the acervuli of a *Cryptosporiopsis* sp.: 'annellides with successive conidium secession below, at, or above the level on which the first conidium seceded'. See also the electron microscopy study of the annellides in the acervular fungus *Steganosporium pyriforme* by Hammill (1972b). The annellate collars in *Ascochyta* spp. show much resemblance with the phialidic collarettes in *Phoma* spp., even with the electron microscope (compare Pl. 21B, C with Pl. 26A, B); under optical microscopy they cannot be distinguished at all.

Table I presents a comparison of characteristics of conidiogenous cells of *Phoma* and *Ascochyta* with those of phialides and annellides, as defined by Kendrick (1971).

The diagnostic most typical characters of conidial formation in *Ascochyta* species is the septation of the conidia as an essential part of the completion of conidium

TABLE I.—A comparison of characteristics of conidiogenous cells of *Phoma* and *Ascochyta* with those of phialides and annellides as defined by Kendrick (1971).

	phialidic sensu Kendrick	annellidic sensu Kendrick	conidiogenesis in *Phoma*	conidiogenesis in *Ascochyta*
first conidium				
enteroblastic	+		+	
holoblastic		+		+
successive conidia				
enteroblastic	+		+	?
holoblastic		+		
conidial wall 'formed de novo'	+			
conidial wall involves distal layer of separation-septum		+	+	+
conidiogenous cell				
with collarette	+		+	
with annellations or annellate collar		+		+
conidiogenous locus				
fixed, more conidia are formed at the same locus	+		+	
each conidium is formed at a new locus		+		+

development (Pls. 27, 28; Fig. 3H–J). It usually takes place just after secession of the conidium but it may also occur before the conidium has seceded. This septation process in *Ascochyta* spp. agrees with the septation of conidia in some dematiaceous hyphomycetes; compare the detailed electron microscopy study by Campbell (1969) on *Alternaria brassicicola*. For this kind of septation Brewer & Boerema used the term distoseptation (=pseudoseptation sensu Ellis pro parte), employed by Luttrell (1963) in his taxonomic study of *Drechslera* ('*Helminthosporium*'). Luttrell's study was based on optical microscopy and emphasizes the double walled structure of distoseptate conidia as appeared from crushed conidia: 'extruding hyaline cells from ruptured (dark) epispore'. Campbell (1970) considered the essential criterion of distoseptation to be the ability of distoseptate conidia to break up in their constituent cells. He interpreted that the conidia of the albino-type of *Alternaria brassicicola* were distoseptate, but not the wild-types of this fungus, because: 'they maintain their integrity as multicelled spores, even though each cell is surrounded by its own wall'. The essential character of distoseptate conidia however is that septation results from invagination of the secondary developing inner wall: 'Invaginations of the inner wall divide the protoplast into a series of cells resembling peas in a pod' (Luttrell, l.c.). See also the study of the ultrastructure of conidiogenesis in *Drechslera sorokiniana* by Cole (1973, fig. 27d, p. 634): 'a new wall layer ... developed by apposition adjacent to the thin plasma membrane ... thickens and is continuous with

septa traversing the conidia'. The invagination of the inner wall is apparently initiated by the development of the septal-plate arising perpendicularly from the outer wall (Fig. 3C). How far in mature distoseptate conidia the outer wall can be separated by pressure from the inner wall depends on differences in structure of both wall layers and is in fact not essential for the distoseptation process. In *Ascochyta pisi*, Brewer & Boerema (l.c.) incidentally could separate both layers by pressure.

The division of the conidia of *Ascochyta* spp. into two (or more) cells is on account of the distoseptation for this genus as typical as the multicellular characters of the conidia in hyphomycete genera such as *Drechslera* and *Alternaria*. The distoseptation process fully explains that true *Ascochyta* species always in vivo as well as in vitro produce mainly septate conidia (Zherbele, 1971: '*Ascochyta* sect. *Stagonosporoides*'). Just like the number of septa in conidia of *Drechslera* and *Alternaria* species show a certain variability, in *Ascochyta* spp. not all mature conidia are two-celled; one-celled and three- (or even four-) celled conidia occasionally occur.

The septation in conidia of *Phoma* spp. Pls. 22, 23A–C; Fig. 2H–J) is a secondary process which only occurs under special conditions, among others in conditions promoting germination (Pl. 23A). It thus occurs independently of conidiogenesis. Brewer & Boerema (l.c.) called this kind of septation 'euseptation', a term introduced by Luttrell (l.c.) for conidial-septation in dematiaceous hyphomycetes such as *Sporidesmium* and *Nakataea* (= *Vakrabeeja*) spp. Septal formation in the conidia of these hyphomycetes however has not been studied by electron microscopy, so we cannot judge at present if it agrees with out observations on conidial septation in *Phoma* spp. It is conspicuous that the secondary developing septa in *Phoma*-conidia apparently almost from the start attain their final thickness. In *Phoma chrysanthemi* septal formation is associated with only a partial thickening of the lateral wall at both sides of the septum (zone of attachment; Pl. 22E). This agrees with the general impression that septate conidia in *Phoma* spp. do not have thicker walls than one-celled conidia. Nevertheless it may be possible that in certain species the thickening of the lateral wall is not restricted to the 'zone of attachment' but includes the whole inside of the conidial wall. Schmid & Liese (1970) in their electron microscopy study of hyphae of the basidiomycete *Armillaria mellea* have observed two types of septa. Firstly, septa of which the wall layers at both sides of the septal-plate are continuous with the inner layers of the lateral wall and secondly, septa which, as in *Phoma chrysanthemi*, show only a restricted zone of attachment to the lateral wall. They called the latter type pseudosepta! Therefore, it seems to us inopportune to describe secondary septation of *Phoma*-conidia as euseptation. In this area many more comparative ultrastructural studies are urgently needed.

Under conditions favouring germination in the swollen conidia of *Phoma* as well as of *Ascochyta* species the initial wall of the germ-tube becomes discernable as a new layer at the innerside of the conidial wall (Pls. 23D; 29A; Figs. 2K, 3K). In *Phoma* the wall of the germ-tube seems to attain at once 'hyphal-thickness'. Optical microscopy has shown that septation of the germ-hypha occurs soon after emergence but without visible wall-thickening. At later stages the wall appears to be defined

more sharply and to be surrounded by a diffuse mucilaginous sheath (comparable with the slime surrounding conidia?; see Fig. 2K and the study of the ultrastructure of germinating conidia of *Botrytis cinerea* by Hawker & Hendy, 1963). In *Ascochyta* species the wall of the germ-tube is relatively thin. Light microscopy observations suggest that the wall of the germ-hypha thickens during septation that occurs quickly, which process can then be characterized as distoseptation.

EMENDED DEFINITIONS OF PHOMA AND ASCOCHYTA

The differences in conidial ontogeny and septation of typical *Phoma* and *Ascochyta* species and the results of cultural studies of both kind of pycnidial fungi (e.g. Zherbele, 1971 and Boerema & Dorenbosch, 1973) make it now possible to redefine both genera.

PHOMA

Phoma Sacc. *in* Michelia **2**(1): 4. 1880 (as *Phoma* 'Fr. em.'; nomen genericum conservandum, 8th Int. Bot. Congr., Paris 1954). — Lectotype-species (8th Int. Bot. Congr., Paris 1954): *Phoma herbarum* Westend. *in* Bull. Acad. r. Belg. Cl. Sci. **19**(3): 118. 1852; lectotype (Boerema, 1964) in herbarium Westendorp & Wallays (BR): exs. Herb. crypt. Belg., Ed. Beyaert-Feys, Fasc. **20**, No. 965, 1854, on stems of *Onobrychis viciifolia*.

Ascochyta sect. *Phyllostictoides* Zherbele *in* Trudy vses. Inst. Zashch. Rast. **29**: 20. 1971. For other synonyms, see von Arx (1970).

Pycnidia mostly glabrous but sometimes hairy or setose especially towards the ostiole, usually globose-subglobose or globose-ampulliform to obpyriform but also more irregular in shape, separated or in small groups, usually sub-epidermal then erumpent with mostly one, but sometimes more, distinct, impressed but more often papillate openings (ostiole or porus); wall pseudoparenchymatous or prosenchymatous, sometimes pseudosclerenchymatous, the outer cells mostly dark and thick-walled, the inner cells hyaline and more or less isodiametric, giving rise to conidiogenous cells.

Conidiogenous cells usually indistinguishable from the inner cells of the pycnidial wall but for a single aperture.

Under light microscopy the conidiogenesis may be characterized as monopolar repetitive 'budding'. The 'bud' of the first conidium arises from a papillate extension; subsequently conidia arise as 'buds' in basipetal succession from the apex of the conidiogenous cell surrounded by a distinct collarette.

Under electron microscopy the conidiogenous cells appear to be phialides producing, from a fixed conidiogenous locus, enteroblastic conidia which secede by a three-layered septum. The first conidial initial is produced within the inner layer of the papillate thickening of the wall at the apex of the conidiogenous cell (Fig. 1A, B). The upper part of the papilla wall sooner or later dissolves, but its basal part remains as a conspicuous collarette (Fig. 1C, D). The walls of successively produced conidia arise from the fixed meristem as outgrowths of the basal layer of the three-layered septum remaining after secession of the previous conidium (Fig. 2E–G). Differentiation of the conidial wall is associated with abundant production of mucilage.

Conidia hyaline or sometimes slightly coloured (yellow to pale brown), globose, obovoidal, ellipsoidal or clavate, mostly once or twice as long as wide, generally measuring between (2)2.5–10(12) × (0.5)1–3.5(5) μm. Conidia one-celled, but secondary septation may occur resulting in two- (or even more-) celled conidia (Fig. 2H–J); the percentage of septate conidia depends on the environmental conditions and may vary between 0–95% (in vivo).

Many species of *Phoma* are morphologically similar and besides, many of these species are exceedingly variable as regards size, form and structure of pycnidia and conidia. The existing Saccardoan classification of these fungi is mainly based on substrate-criteria and ignores the existence of numerous unspecialized species with wide host ranges, parasites as well as weak parasites and saprophytes (compare Boerema, 1969). The only way to reach a practical and useful classification of *Phoma* species has proved to be the study of the characteristics in vitro (see e.g. van der Aa & van Kesteren, 1971; Boerema, 1964, 1965, 1967a, 1967b, 1969, 1970b, 1972; Boerema & Dorenbosch, 1968, 1970, 1973; Boerema, Dorenbosch & van Kesteren 1965, 1968, 1971, 1973; Boerema, Dorenbosch & Leffring 1965; Boerema & Höweler, 1967; Boerema & de Jong, 1968; Dorenbosch, 1970; Dorenbosch & Boerema, 1973; Dorenbosch & Höweler, 1968; van Kesteren, 1972; Maas, 1965; Zherbele, 1971). A real and practical differentiation then appears to be possible when the morphological characteristics are combined with growth characteristics in culture including the general growth habit, rate of growth, pigment production, crystal formation, etc., in addition to the structure of the mycelium and of any chlamydospores. Classification based on study in vitro also solves the problem of differentiating *Phoma* species producing septate conidia in vivo (pseudo-Ascochytas) from true *Ascochyta* species. Under normal laboratory technique of culturing fungi on standardized agar media in petri dishes and tubes, conidial septation of *Phoma* species is always restricted (0–10%), whereas true *Ascochyta* species produce mainly septate (distoseptate) conidia (compare Boerema & Dorenbosch, 1973; Zherbele, 1971). *Phoma* species with hairy or setose pycnidia are readily distinguished from *Pyrenochaeta* by the shape of the conidiogenous cells. True species of *Pyrenochaeta* De Not. (Schneider, 1975) have elongated, septate conidiophores with lateral phialidic apertures below the septum delimiting each cell (acropleurogenous conidiophores). The pycnidia of the type-species of *Phoma*, *P. herbarum*, have a predetermined opening or ostiole; that means that structural provisions for the production of the opening are apparently already present in the pycnidial primordia (Boerema, 1964). This is the case with most typical species of *Phoma*. In certain species, however, pycnidia remain closed for an extended period; the opening then appears almost at the end of the growing process: porus instead of an ostiole. This occurs in e.g. *Phoma lingam* (Boerema & van Kesteren, 1964) and other *Phoma*-states of *Leptosphaeria* spp. (*Phoma* section *Plenodomus*, compare von Arx, 1970).

Different types of *Phoma*-parent cells and conidial shape are shown in Fig. 4 taken from Boerema & Höweler (1967), Punithalingam & Holliday (1972a, 1973a, b) and Sutton (1964).

ASCOCHYTA

Ascochyta Lib. *in* Pl. crypt. Ard., Fasc. **1**: 8. 1830; *in* Mém. Soc. Sci. Agric. Lille 1829–1830: 175. 1831 (as '*Ascoxyta*'; see discussion by Sprague & Johnson, 1950). Lectotype-species (cf. Diedicke, 1912: 139; Clements & Shear, 1931: 363; Sprague & Johnson, 1950: 529; von Arx, 1970: 135): *Ascochyta pisi* Lib. *in* Pl. crypt. Ard., Fasc. **1**, No. 59. 1830 (as '*Ascoxyta Pisi*'); holotype in herbarium Libert (BR): on pods of *Pisum sativum* (as '*Ascospora Pisi* N').

Ascochyta sect. *Stagonosporoides* Zherbele *in* Trudy vses. Inst. Zashch. Rast. **29**: 20. 1971.

Pycnidia usually glabrous but sometimes hairy, mostly globose-subglobose or ampulliform to mammiform, sometimes more irregular in shape, separated or in small groups, usually subepidermal then erumpent with usually one, but sometimes more openings (pores) which may be simple, impressed, slightly protruding or papillate; wall mostly relatively thin, usually pseudoparenchymatic, the outer cells darker and more thick-walled than the hyaline inner cells.

Conidiogenous cells not distinctly differentiated from the inner cells, but recognizable by the cuspidate or somewhat elongated apex.

Under optical microscopy the conidia arise in basipetal succession as thin-walled protrusions at the apices of the conidiogenous cells. A kind of collar may be present or not evident at all.

Under electron microscopy the conidiogenous cells appear to be annellides producing from successively developing conidiogenous loci, thin-walled conidia seceding by a three-layered septum. The wall of the first conidium arises as an outgrowth of the thin wall at the apex of the conidiogenous cell (Fig. 3A). The walls of successive conidia arise from the apical part of very short percurrent proliferations of the conidiogenous cell involving the basal layer of the three-layered septum remaining after secession of the previous conidium (Fig. 3B–E). Percurrent growth however not only occurs at increasingly higher levels resulting in a series of annellations one above another encircling the apex of the conidiogenous cell (Fig. 3F), but also at approximately the same level and then appears like a collar of periclinal annellations, the annellate collar (Fig. 3G). Conidiogenesis proceeds without evident production of mucilage.

Conidia, hyaline or sometimes slightly coloured (yellow to pale brown), usually cylindrical to ellipsoidal or cymbiform, mostly twice or three times as long as wide, generally measuring between (5)8–25(29) × (2)2.5–6(8) μm. Conidia after secession often one-celled but then soon becoming two- or occasionally three- or even four-celled.

Under electron microscopy the crosswall formation is characterized as distoseptation: production of a new inner conidial wall layer which concurrently by invagination divides the conidia in two or more cells; the invagination is initiated by the development of a septal-plate (Fig. 3H–J). This distoseptation process is associated with abundant production of mucilage.

Most species of *Ascochyta*, if not all, are typical parasites with restricted host ranges. According to Zherbele (1971) they occur especially on the Campanulaceae, Chenopodiaceae, Gramineae, Leguminosae, Solanaceae and Umbelliferae. Some of them have one specific host but then incidentally also may occur on related species of the same genus. They are in form, structure and size of pycnidia and conidia relatively stable and therefore usually easy to differentiate. Study in vitro is nevertheless also essential for identification of *Ascochyta* species, because the cultural characteristics (e.g. pigment production, occurrence of chlamydospores etc.) are often even more

specific than the purely morphological characters. Study in vitro is further necessary to distinguish *Ascochyta* species with annellate collars from 'pseudo-Ascochytas' i.e. *Phoma* species producing in vivo many conidia with septa (see above). On account of the distoseptation process, the mature conidia of true *Ascochyta* species are always, in vivo as well as in vitro, two- or more-celled, whereas *Phoma* species in culture produce mainly one-celled conidia. The openings in the pycnidia of *Ascochyta pisi* and other typical species of *Ascochyta* apparently occur towards the end of the growing process and are interpreted as a porus instead of an ostole. However it does not appear opportune to include this character as a generic criterion (see above under *Phoma*; compare also von Arx, 1973).

For the various types of conidial shape in *Ascochyta* spp., and the conidiogenous cells as seen under optical microscopy see Fig. 5 taken from the study of graminicolous species by Sprague & Johnson (1950) and the descriptions of *Ascochyta pisi* and *Mycosphaerella pinodes* by Punithalingam & Holliday (1972b, c).

ADDENDUM

Phoma- and Ascochyta-like fungi the position of which needs further study.

Most pycnidial fungi with one- or/and two-celled hyaline conidia can by study in culture easily be classified into the form-genera *Phoma* or *Ascochyta* as defined above. The observation that true Ascochytas have usually larger conidia than pseudoforms of *Phoma*, facilitates prognostication of the genus for the species producing many two-celled conidia in vivo. However as already noted by Zherbele (1971) a small number of species remain difficult to classify because they show 'mixed' or intermediate characteristics. This may be illustrated with three examples:

1. In eastern Europe *Ascochyta nigripycnidiicola* Ondřej (1968) causes spots on leaves and stems of vetches, *Vicia* spp. In the spots pycnidia are produced with extremely large two- or more-celled conidia, 20–45 × 7–12 μm. On the leaves sometimes pycnidia also occur with one-celled microconidia, 5–8 × 1.5–2 μm. In culture the fungus produces at first pycnidia with two-celled conidia, 35–62 × 10–15 μm, thus even larger than those in vivo. Later on, however, only pycnidia with microconidia, 5–12(15) × 1.5–3(3.5) μm, are formed in vitro (Ondřej, 1970). See Fig. 6A. Although the fungus probably also has a perfect state (Ondřej, 1968) the microconidia are not spermatia, but true conidia as appeared from inoculation experiments. Similar observations were made by Ondřej (1970) on *Ascochyta viciae* Lib., a parasite of *Vicia sepium*.

Does this species form pycnidia with phialides like *Phoma* and pycnidia with annellides like *Ascochyta*?

2. On last-year stems of goldenrod, *Solidago* spp., a species described by Saccardo (1884) as *Phoma oleracea* var. *solidaginis* (type in PAD) can be found. On the stems the pycnidia contain only one-celled conidia, (4)5–6(7) × 1.5–2 μm. In culture, however, apart from one-celled conidia, (2.5)3.5–7.5(8.5) × 1.5–2.5(3.5) μm, often also some

large two-celled conidia are produced in the same pycnidium, measuring (14.5) 15.5–22(24) × 4–6(7) μm. See fig. 6B.

Does this mean that phialides and annellides can be formed in one pycnidium?

3. A well-known leafspot-disease of *Campanula* spp. is caused by a fungus described as *Ascochyta bohemica* Kab. & Bubák (cf. Sauthoff, 1962). On the spots, which may also occur on stems and flowers, the pycnidia at maturity contain mainly large, two-celled conidia, (11)13–23 × (3.5)4–6 μm. Together with these conidia also some one-celled microconidia, 4–6 × 1–2 μm can be found. In culture the pycnidia usually contain only microconidia, (2.5)3.5–6(8.5) × 1.5–2(2.5) μm. Sometimes however in the same pycnidium at maturity some large, two-celled conidia are produced with dimensions similar to those in vivo. In contrast with the parent cells of the two-celled macroconidia, the parent cells producing the microconidia always show an obvious collarette. In vitro the microconidia are sometimes produced on elongated cells which look like macroconidia that have not seceded. The mature two-celled macroconidia easily break into two parts (Brewer & Boerema, 1965), which is never observed for distoseptate *Ascochyta*-conidia. See Fig. 6C.

Can parent cells of this fungus produce phialidic conidia as well as annellidic conidia? Moreover are the annellidic conidia not distoseptate?

The occurrence of aberrant forms is a common phenomenon in nature. It often reveals a stumbling-block for taxonomists. Even with the most 'natural systems' at one's disposal problematic species may remain. Using the new definitions of *Phoma* and *Ascochyta* the number of problematic species has been shown to be few (Zherbele, 1971). Electron microscopy studies of conidial ontogeny and septation in the deviating species is not only necessary for classification of these species but it may also lead to a deeper understanding of the process of conidial formation in this kind of fungi (relation between phialides and annellides) and its relevance for taxonomy.

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EXPLANATION OF PLATES 19–29

PLATE 19

Fig. A. Conidial development in *Phoma leveillei*; the conidia produced in basipetal succession arise as buds from the conidiogenous locus surrounded by a collarette (col) at the top of the parent cells.

Figs. B-E. Parent cells of *Phoma* spp. producing their first conidium. — B. *P. herbarum*. — C. *P. lingam*. — D, E. *P. exigua*. Papillate pronounced thickening of the wall at the top of the parent cells, gradually developing into a bud-like protrusion. The wall of the first conidium (wc1) arises within the electron-transparent inner layer (il) of the thickened wall. The more or less electron-dense middle layer (ml) seems to function as 'opener' of the conidiogenous locus. The outer electron-transparent layer (ol) in fig. E is already partly dissolved.

PLATE 20

Fig. A. Micrograph showing three parent cells of *Phoma exigua* in different developmental stages of the first conidium (the 'free' conidia originate from parent cells not visible in this section). The dark middle layer (ml) of the papillate stage is in the process of conidial secession still visible as the outer layer of the mucilaginous sheath around the conidia. The electron-transparent outer layer (ol) of the papilla is in the process of conidial secession, for the most part dissolved to a series of mucilaginous 'drops'. The differentiation of the conidial wall (developed within the original electron-transparent inner layer of the papilla, see Pl. 19 fig. E) is associated with the production of an electron-transparent cloudy substance (cs). This is also present around the free conidia. So far the free conidia are not first conidia, the outer layer of the mucilaginous sheath of these conidia represents dissolved wall material resulting from the process of secession of the previous conidium (compare Text-figs. 1D and 2E-G). The precise way in which the conidia become detached from the parent cells cannot be seen in this micrograph.

Figs. B-E. Micrographs of *Phoma* spp. showing the development of the initial electron-transparent separation-plate (srp) immediately followed by the formation of the basal conidial wall and a wall closing the parent cell (compare Text-fig. 2E-G; col=collarette being the basal part of the original three-layered papilla wall: ol, ml, il). — B. *P. leveillei*. — C. *P. complanata*. — D, E. *P. lycopersici*.

PLATE 21

Figs. A–C. Stages just before conidial secession in *Phoma* spp. — A. *P. herbarum*. — B, C. *P. lycopersici*. In secession three layers are involved: the basal conidial wall, the separation-plate (srp) and the wall closing the parent cell. In the collarette (col) the layers of the original papilla (ol, ml, il) sometimes can still be distinguished (e.g. in fig. B).

Fig. D. Final stage of conidial secession in *Phoma exigua*, showing the disintegration of the separation-plate and the original periclinal wall parts into mucilage.

Fig. E. *Phoma lingam*; characteristic picture of conidiogenesis in *Phoma* spp. Conidial initial arising as a bud from the conidiogenous locus which is surrounded by a distinct collarette (col), being the basal part of the original three-layered papilla-wall (ol, ml, il), compare Pl. 19 fig. C.

PLATE 22

Figs. A–F. Development of septa in conidia of *Phoma* spp. From the start three layers can be distinguished: a thin electron transparent septal-plate (sp) at both sides covered with a thicker wall layer making round edges with the lateral wall to which they are 'attached'

with decreasing thickness for some distance. Near the lateral wall at both sides of the septal-plate triangular 'spaces' (ts) occur (mostly electron-dense). Note that the developing septa apparently almost immediately attain their final thickness. — A. *P. exigua*. — B, D, E. *P. chrysanthemi*. — C, F. *P. lycopersici*.

PLATE 23

Fig. A. Conidia of *Phoma chrysanthemi* obtained from a suspension in water which encourages septation and germination. Note the closed pori in the septa with associated electron-dense membrane-bounded plugs.

Fig. B. Septum in a conidium of *Phoma exigua*, apparently perforated by a microporus (plasmodesmium).

Fig. C. Septal pore in meristematic pycnidial tissue of *Phoma exigua* showing the clumped or stocked membrane profiles (pl) similar to those usually associated with pores in septa of *Phoma*-conidia. Note also the Woronin-bodies (Wb) near the porus.

Fig. D. Germinating conidium of *Phoma lycopersici*: at the innerside of the original conidial wall a new layer can be distinguished which is continuous with the germ-tube. Note the ruptured conidial wall at both sides of the germ-tube.

PLATE 24

Figs. A–D. Different stages of conidial development in *Ascochyta* spp. — A, B. *A. pisi*. — C, D. *A. pinodes*. The conidial initials are, in comparison with the mature (=septate) conidia, extremely thin-walled. All parent cells show at the base of the conidial initials wall-ridges (wr) meaning that each cell has already produced conidia before (wr^1=wall-ridge first conidium etc.; wc^2=wall second conidium; the first conidium arises apparently simply as an outgrowth of the thin-walled apex of the parent cell, see Pl. 25 fig. B). Note that the cloudy electron transparent substance (cs; = slime) surrounding the mature (septate) conidia in figs. A, B does not occur around the initials.

PLATE 25

Figs. A-D. Micrographs showing various stages of conidial secession in *Ascochyta* spp. — A, B. *A. pisi*. — C, D. *A. pinodes*. With secession in fact three wall-layers are involved; the basal conidial wall, the wall closing the parent cell and a very thin electron transparent layer, the separation-plate (srp in fig. C; compare Pl. 26 figs. A, B) along which separation takes place. Note the different wall ridges at the base of the conidial initials (wr^1=wall ridge first conidium, etc.; wc^1=wall first conidium, etc.). The large detached conidium in fig. B shows a basal frill (fr), probably remnants of the separation-plate.

PLATE 26

Figs. A, B. Stages just before conidial secession in *Ascochyta fabae* showing three layers: basal conidial wall, the very thin electron-transparent separation-plate (srp) and the wall closing the parent cell. Note the similarity between separation-plate and septal-plate (sp) as shown in figs. D, E.

Fig. C. Collar of parent cell in *A. pinodes*: different layers (wr) corresponding with the number of conidia produced (14?); wc, wall of probably the 15th conidium formed by the parent cell.

Figs. D, E. Mature conidia of *Ascochyta* spp. showing that the septum consists of three layers: a thin electron-transparent septal-plate (sp) at both sides with a wall-layer making round edges with the lateral wall. Note that the septal-plate may be undulated. — D. *A. pisi*. — E. *A. fabae*.

PLATE 27

Figs. A–E. Various stages of septation in conidia of *Ascochyta pisi*. Centripetal development of a thin electron-transparent septal-plate (sp) concurrently with the production of a new inner conidial wall-layer which gradually increases in thickness (compare Text. fig. 3 H–J). In the centre of the septum a pore remains, usually associated with Woronin bodies (Wb) and membrane-bounded electron-dense plugs (pl).

PLATE 28

Figs. A, B. Septal formation in *Ascochyta fabae* (compare Plate 27).

Figs. C, D. Septa in mature conidia of *Ascochyta pinodes*. Three layers: the thin electron-transparent septal-plate (sp) at both sides covered with a wall-layer continuous with the inner part of the lateral wall. At the points of attachment electron-dense triangular spaces (ts) occur. Fig. D shows a pore with electron-opaque plug (pl) and two Woronin bodies (Wb).

PLATE 29

Fig. A. Micrograph showing a germinating septate conidium of *Ascochyta fabae*. The wall of one cell is just ruptured by protrusion of the wall of the germ-tube (compare Text-fig. 3 K; the septal-plate is not visible in this micrograph).

Figs. B, C. Invagination of the plasma membrane in septate conidia of *Ascochyta* spp. — B. *A. pisi*. — C. *A. pinodes*.

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OBSERVATIONS SUR QUELQUES CHAMPIGNONS HYDNOÏDES DE L'AFRIQUE

R. A. Maas Geesteranus
Rijksherbarium, Leiden

Paule Lanquetin
Université Claude Bernard, Laboratoire de Mycologie, Villeurbanne

(Avec 7 figures dans le texte et planche 30)

Parmi les champignons hydnoïdes, plutôt rares en Afrique, les auteurs signalent la présence de *Gloeodontia discolor*, *Flavodon flavus*, *Steccherícium seriatum* et révèlent l'existence de 5 *Steccherinum* nouveaux: *S. confragosum*, *S. labeosum*, *S. russum*, *S. scalare*, *S. scruposum* auxquels s'ajoutent 3 espèces provisoirement décrites et intégrées dans une Clé des *Steccherinum* africains. Pour 7 des 11 espèces hydnoïdes signalées, la description est accompagnée de l'étude des mycéliums.

Cet ensemble particulier est fort peu cité dans la littérature des champignons africains. Sans doute, faudrait-il considérer les Hydnés, notamment dimitiques, comme très rares sur ce continent. S'il est impossible de l'affirmer tant que certaines régions africaines resteront inexplorées, il nous semble cependant assez significatif que plusieurs mycologues contemporains aient fait séparément cette même remarque. Ainsi, l'un de nous (M.G.) n'a pas rencontré un seul champignon hydnoïde durant ses excursions mycologiques au Kenya et en Afrique du Sud, de fin avril à fin décembre 1949. L. Ryvarden (communication personnelle) observe que les champignons hydnoïdes sont rares dans les régions qu'il a visitées. A. David, restée un mois au Gabon (station de Makoku), n'a rencontré que 3 espèces. J. Boidin, qui, à deux reprises (1965–1967), séjourna plusieurs semaines en République centrafricaine (station de la Maboké), n'a trouvé que 4 espèces appartenant à ce groupe parmi plus de 600 récoltes de Théléphoracées. Enfin, G. Gilles, qui explore depuis plusieurs années les forêts du Gabon et celles de Côte d'Ivoire, n'a jusqu'ici découvert qu'une espèce au Gabon et 3 en Côte d'Ivoire.

L'ensemble des récoltes effectuées par ces différents mycologues ne représente donc qu'un petit nombre d'espèces. Pour en faire l'étude, nous avons eu le plaisir de pouvoir réunir les collections de ces chercheurs, aussi nous remercions vivement M. J. Boidin (Lyon), Mme A. David (Lyon) et M. G. Gilles (Abidjan), qui ont mis leurs récoltes à notre disposition et se sont astreints, lors de celles-ci, à nous (P. L.) envoyer les sporées aseptiques indispensables pour faire l'étude des mycéliums. Nous adressons également nos remerciements à M. L. Ryvarden (Oslo) pour l'envoi d'une collection de *Sarcodon* et d'un *Steccherinum*, ainsi qu'à Messieurs les Directeurs de l'herbier de Genève (G), Hamburg (HBG), Kew (K) et Oslo (O) pour le prêt d'exsiccata qui nous ont été très utiles.

AURISCALPIACEAE

GLOEODONTIA DISCOLOR (Berk. & Curt.) Boid.[1]

Gloeodontia discolor (Berk. & Curt.) Boid. *in* Cah. Maboké **4**: 22, fig. 1 A–E. 1966.

CÔTE D'IVOIRE: Abidjan, Forêt du Téké, 8 avril 1973, *G. Gilles 202* (LY 7125 et L).

Cette récolte est la seconde effectuée en Afrique. La position taxinomique de ce genre a été discutée par Boidin (1966: 22) qui estime que «Sa place semble beaucoup plus naturelle dans les Auriscalpiaceae».

L'étude des mycéliums a été publiée par ce même auteur (1966: 19). Signalons seulement que:

(i) Cette deuxième récolte LY 7125 est interfertile avec la première (LY 5559) trouvée en République centrafricaine et avec un spécimen, originaire de Louisiane (LY 5831) que nous devons à l'amabilité du Dr. A. L. Welden.

(ii) La bipolarité établie en 1966, sur LY 5559, avec quelques réserves dûes à la non-diploïdisation des haplontes compatibles, est aujourd'hui confirmée par la bipolarité de LY 7125 (sur 17 monospermes) et celle de LY 5831 (sur 25 monospermes). Dans l'étude de ces 2 polarités, nous avons pu en effet observer la diploïdisation lente mais totale des haplontes compatibles. Remarquons cependant que toutes les autres Auriscalpiaceae étudiées se sont toujours révélées tétrapolaires.

HERICIACEAE

STECCHERICIUM SERIATUM (Lloyd) Maas G.—Pl. 30 fig. 1, 2

Steccherícium seriatum (Lloyd) Maas G. *in* Proc. K. Ned. Akad. Wet. (C) **69**: 325, fig. 15–19. 1966.

CÔTE D'IVOIRE: Abidjan, Forêt du Banco, 9 déc. 1972, *G. Gilles 162* (LY 7077 et L).

Cette espèce a déjà été signalée en Afrique (Maas Geesteranus, 1967: 84), d'une station située environ 3000 kms à l'est d'Abidjan et, sous le synonyme *S. fistulatum*, d'une autre station encore plus éloignée, Mpanga (Uganda).

Etude des mycéliums.

GERMINATIONS.—Elles apparaissent 15 à 20 jours après la dispersion des spores.

[1] Pour les références et les synonymies, le lecteur de l'article se reportera à Maas Geesteranus (1974).

MONOSPERMES.—Ils sont formés d'hyphes sans boucles aux articles uninucléés. On observe les mêmes éléments: chlamydospores et gloeocystides, que dans le polysperme. Dans plusieurs cultures monospermes nous avons observé une abondante sporée blanche produite par des fructifications parthénogénétiques non bouclées, présentant des basides le plus souvent bisporiques mais parfois à un seul stérigmate. Des tests d'interfertilité ont été effectués entre les haplontes africains LY 7077 et ceux d'une récolte américaine, LY 6968, faite par Mme A. David lors d'un séjour à la Guadeloupe. Tous les résultats enregistrés sont positifs et vont la plupart du temps, jusqu'à l'apparition de fructifications bouclées montrant des basides tétrasporiques et projetant des spores blanches, uninucléées. C'est, après *Laxitextum bicolor* (Boidin, 1958), le deuxième exemple de parthénogénèse bisporique expérimentale.

Polarité (LY 6968): Après plusieurs échecs sur milieu de Hagem, la tétrapolarité de cette espèce a pu être établie sur milieu de Nobles.

A_1B_1: 1–2
A_1B_2: 6–7–8
A_2B_2: 5–10–11
A_2B_1: 3–4–9

Dans toutes les confrontations compatibles, des fructifications apparaissent d'abord sur la ligne de contact, puis envahissent toute la culture dont le couvercle se couvre d'une abondante sporée blanche. Malgré une croissance difficile, la formation aisée des fructifications dans cette espèce aurait facilité l'étude de la polarité si, près de la moitié des confrontations incompatibles ne portaient pas également des fructifications produisant de même une abondante sporée blanche. Il s'agit alors de fructifications parthénogénétiques, dépourvues de boucles et portant des basides à 2 (ou 1 seul) stérigmates.

POLYSPERME (LY 7077, LY 6968).—Pl. 30 fig. 1, 2.

Croissance: Extrêmement lente (10–13mm à 6 semaines).

Aspect: La marge est irrégulière, submergée; le mycélium aérien, peu abondant, duveteux, blanc, formé des petits amas feutrés puis granuleux. Plus ou moins abondants, ils peuvent parfois gagner toute la culture (sauf la marge) qui se couvre ensuite d'une multitude de petits aiguillons blanchâtres, fins et courts (fructification). Revers: milieu inchangé. Odeur: aromatique légère distincte de celle des *Steccherinum*.

Microscopie: Mycélium aérien: Les hyphes, × 1,5–4 μm, régulières, à paroi distincte et contenu homogène, sont à boucles constantes. Les chlamydospores, souvent terminales, subsphériques (5–7 × 6–8 μm) et à paroi épaissie, sont très nombreuses. On observe aussi des gloeocystides peu différenciées: ce sont des articles terminaux longs (70–150 × 4 μm) dont le contenu très réfringent apparaît plus ou moins solidifié. Souvent le mycélium aérien produit des fructifications bouclées dont les basides (12–15(–40) × 4 μm au sommet et seulement 2–2,5 μm à la base) possèdent 4 stérigmates fins portant des spores petites, finement ornées. Les gloeocystides longues et étroites ont, comme celles du mycélium, un contenu qui ne réagit pas dans les sulfo-aldéhydes.

Il est à noter que le mycélium aérien, originellement à boucles constantes, tend très rapidement à perdre ses boucles. Celles-ci sont toujours observées au voisinage des fructifications, tandis que le mycélium situé à quelque distance de la zone fructifiée en est totalement dépourvu. Ceci, ajouté à une croissance extrêmement lente, explique les difficultés rencontrées, au début, dans l'établissement de la polarité de cette espèce.

Mycélium submergé: Hyphes régulières × 2–3 μm, à boucles constantes ou sur de grandes plages totalement dépourvues de boucles et alors uninucléées.

Cytologie: Articles binucléés.

Oxydases[2]: ac. gallique: +++,o gaïacol: +++,o
p. crésol: — tyrosine: —,o

CODE.[3]—2a-3c-15-34-36-38-47-48-53-58-60-61.

POLYPORACEAE

FLAVODON FLAVUS (Kl.) Ryv.

Flavodon flavus (Kl.) Ryv. *in* Norw. J. Bot. **20**: 3. 1973.

TANZANIA: Amani, juillet—novembre 1903, *F. Eichelbaum* 77 (HBG); Usambara, juillet 1890, *C. Holst 3132* et juin 1893, *C. Holst 2357* (HBG).

RÉPUBLIQUE CENTRAFRICAINE: La Maboké, sur arbre tombé, à distance du sol, 12 mai 1965, *J. Boidin* (LY5401 et L); id°, sur bois très dur au sol (LY 5402, LY 5408 et L); M'Balé, sur *Chrysophyllum perpulchrum* (Sapotacée) mort debout, 21 sept. 1967, *J. Boidin* (LY 5988); La Maboké, sur *Coffea robusta*, 23 sept. 1967, *J. Boidin* (LY 6003, LY 6004).

GABON: Makoku, sur poteau dressé, 4 juillet 1970, *Mme A. David* (LY AD 1004).

ZAIRE: Katanga, Kipopo, sur branche morte, 14 oct. 1971, *D. Thoen* (LY 6724).

Eichelbaum (1907: 49) indiquait qu'il avait récolté la forme *natalensis* de l'*Irpex flavus*, ommettant d'ailleurs d'en donner une description. Nous n'avons pas vu cette collection, qui se trouve probablement à Amani; nous ne croyons cependant pas qu'elle soit notablement différente de la forme typique de *F. flavus*, elle même assez variable.

Etude des mycéliums.

Banerjee & Purkayastha (1957) signalent l'absence de boucles et la similitude des caractères macro- et microscopiques des cultures monospermes et polyspermes.

Manjusri Sen (1973: 285, pl. 2) donne une étude détaillée des mycéliums, à laquelle nous ajouterons seulement quelques compléments concernant la cytologie.

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[2] Pour les techniques employées et l'expression de ces résultats voir Boidin (1958).

[3] Selon Nobles (1965) complété par Boidin (1966).

GERMINATIONS (LY 5402).—En moins de 24 heures, les spores binucléées émettent par 1 ou 2 extrémités, des filaments formés d'articles à 4–10 noyaux, sauf le terminal qui en contient 10 à 16.

MONOSPERMES.—Les hyphes sans boucles sont cénocytiques et identiques à celles du polysperme.

POLYSPERMES (LY 5402–5408).—Les hyphes sont constituées d'articles contenant 4 à 10 noyaux, sauf le terminal qui possède 8 à 20 noyaux.

STECCHERINACEAE

STECCHERINUM S. F. Gray

CLÉ DES ESPÈCES TROUVÉES EN AFRIQUE
(basée sur des caractères observés à l'état sec)

1. Aiguillons de couleur peu foncée.
   2. Chapeau (ou partie réfléchie) à zones concentriques, parfois peu nombreuses, mais toujours bien individualisées.
      3. Chair du chapeau brun rougeâtre ou brun cannelle, du moins en arrière; spores de 2–2,5 µm de large.
         4. Cystides d'origine tramale. Chapeau laineux-tomenteux, gibbeux ou muni de tubercules vers la base . . . . . *S. scruposum*, p. 161
         4. Cystides de deux sortes. Chapeau subtomenteux, à surface affaissée vers la base *S. proximum*, p. 156
      3. Chair du chapeau pâle, tout au plus d'un jaune brunâtre en arrière.
         5. Spores (3,1–)3,4–4,5(–4,7) µm de long.
            6. Chapeau à marge épaisse; spores 1,3–1,8 µm de large; cystides glabres *S. labeosum*, p. 154
            6. Chapeau à marge ténue; spores (1,6–)1,8–2,5(–2,7) µm de large; cystides incrustées . . . . . *S. ochraceum*, p. 155
         5. Spores 2,5–3,1 µm de long.
            7. Cystides d'origine tramale . . . . . *S. scalare*, p. 160
            7. Cystides de deux sortes . . . . . *S. confragosum*, p. 149
   2. Chapeau dépourvu de zones concentriques, ou basidiome étalé.
      8. Spores 4–4,6 µm de long . . . . . *S. russum*, p. 159
      8. Spores 2,6–3,2 µm de long . . . . . *S. exiguum*, p. 153
1. Aiguillons d'une couleur rouge brun assez foncé, soit glabres, soit recouverts d'une pruine blanchâtre ou bleuâtre; spores 2,7–3,6 × 1,3–1,8 µm; cystides de deux sortes (voir Maas Geesteranus, 1974: 508) . . . . . *S. ethiopicum*.

Steccherinum confragosum Maas G. & Lanq., *spec. nov.*[4]—Pl. 30 fig. 3

Basidiomata pileata, imbricata. Pileus usque ad 37 mm antice productus, 55 mm latus, basi attenuata, flabelliformis, plano-convexus; postice (partem basalem versus) colliculosus confragosusque, tomentosus, sordide ochraceus; ceterum planiusculus, leviter radialiter sub-

[4] Etymologie: *confragosus*, bosselé.

rugulosus, glabrescens, ochraceo-fulvus vel spadiceus, zonis concentricis obscurioribus (umbrinis) munitus; margine acutus, zonis concentricis obsolete depressis praeditus, tomentosus, sordide luteo-albidus. Aculei usque ad 2 mm longi, 0,1–0,3 mm lati, conferti, subulati, teretes vel applanati, recti vel curvati, simplices vel connati, argillacei vel gilvi, pruinosi, apicibus integris. Caro usque ad 2 mm crassa, coriacea vel lignea, pallida, postice isabellina, e hyphis generatoriis skeletalibusque formata. Hyphae generatoriae 2,5–3,5 μm latae, aegre sub oculos cadentes, haud inflatae, tenuiter tunicatae, ramosae, septatae, fibulis instructae. Hyphae skeletales 2,5–6 μm latae, crasse tunicatae. Basidia collapsa. Sporae 2,7–3,1 × 1,3–1,5 μm, ellipsoideae, laeves, hyalinae, apiculo minuto obliquo praeditae. Cystidia diversi generis; altera usque ad 5,5 μm lata, aculeorum partem distalem versus inventa, hypharum skeletalium apices formantia, sparsa, immersa vel parum prominentia, haud incrustata, crasse tunicata, cylindracea vel subfusiformia, apice plus minusve deflexa, obtusa; altera 9–13,5 × 2,5–5,5 μm, aculeorum partes medias basalesque versus inventa, subhymenialia, numerosissima, plus minusve prominentia, haud incrustata, crasse tunicata, clavata vel fusiformia vel cylindracea, apice attenuata haud tamen acuta.

Holotypus: Gabon, km 20 Libreville, Forêt de la Mondah, sur tronc abattu très pourri, 22 janv. 1972, *G. Gilles 80* (LY 6731; pars in L).

Basidiome à chapeaux superposés. Chapeau atteignant 37 mm de diamètre et 55 mm de large, attaché par une base atténuée, flabelliforme, plan-convexe, muni en arrière de plusieurs petites bosses, tomenteux, ocracé sale (vers 10 YR 7/6);[5] ailleurs plus ou moins plan, faiblement ruguleux radialement, glabrescent, ocracé-brun ou châtain (7,5 YR entre 6/6 et 5/4), à zones concentriques d'une couleur plus sombre (7,5 YR entre 4/4 et 3/2); marge mince, tomenteuse, d'un blanc jaunâtre sale (± 10 YR 8/3), montrant également quelques zones concentriques qui sont obscurément déprimées. Face adhyméniale finement tomenteuse-porée, blanchâtre. Aiguillons atteignant jusqu'à 2 mm de long, 0,1–0,3 mm de large, serrés, subulés, cylindriques ou comprimés, droits ou courbes, simples ou connés, alutacés, pruineux, entiers au sommet. Chair du chapeau jusqu'à 2 mm d'épaisseur, coriace ou ligneuse, pâle, jaune brunâtre en arrière.

Contexte dimitique, constitué d'hyphes génératrices et squelettiques. Hyphes génératrices larges de 2,5–3,5 μm, difficiles à découvrir (à cause de l'état assez mauvais du champignon d'une part, et de la prédominance des hyphes squelettiques d'autre part), non renflées, à paroi mince, ramifiées, cloisonnées, bouclées. Hyphes squelettiques larges de 2,5–6 μm, à paroi épaisse. Trame des aiguillons semblable. Basides collapsées. Spores 2,7–3.1 × 1,3–1,5 μm, ellipsoïdes, lisses, incolores, à apicule petit et oblique. Cystides de deux sortes: (a) les unes jusqu'à 5,5 μm de diamètre, se trouvant vers le sommet des aiguillons et constituant les terminaisons des hyphes squelettiques, éparses, incluses ou peu émergentes, dépourvues de cristaux, à paroi épaisse, cylindriques ou légèrement fusiformes, plus ou moins incurvées au sommet et obtuses; (b) les autres 9–13,5 × 2,5–5,5 μm, se trouvant dans les parties médianes et basales des aiguillons, d'origine subhyméniale, abondantes, plus ou moins émergentes, glabres, à paroi épaisse, claviformes, fusiformes ou cylindriques, atténuées vers le sommet qui cependant n'est jamais aigu.

GABON: km 20 Libreville, Forêt de la Mondah, sur tronc abattu très pourri, 22 janv. 1972, *G. Gilles 80* (Holotype, LY 6731; en partie à L).

CÔTE D'IVOIRE: Abidjan, Forêt du Banco, 5 juin 1972, *G. Gilles 32*, sur bois mort, (LY 6847 et L); Abidjan, Forêt du Téké, 19 mars 1973, *G. Gilles 188* (LY 7110 et L).

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[5] Nous avons utilisé les codes de la Munsell Color Company, Baltimore U.S.A., notamment le «Munsell Soil Color Charts» (1954).

OBSERVATIONS.—Pour les 3 récoltes, nous disposons de quelques notes prises à l'état frais, par le récolteur:

LY 6731—Imbriqué. Face stérile: très pâle à la marge, presque blanche, puis zonée obscurément, beige rosé pâle, 7,5 YR 8/2 sur 5–6 mm de large, puis brun ombre 5 YR 4/3 avec fines zones peu nettes. Face fertile: blanche à la marge sur 1 mm, passant ensuite progressivement à 7,5 YR 8/2, puis à beige rosé 7,5 YR 7/2, et atteignant presque 7,5 YR 6/2 (light drab R.) près du support. Aiguillons serrés (4 à 6 au mm), blanchâtres puis brunissant un peu vers le support.

LY 6847—Flabelliforme, dimidié, peu distinctement zoné. Face stérile: bordure blanche large de 5 mm, tranchant nettement sur le reste, brun rougeâtre, ombre, 5 YR 4/4, parfois plus pâle. Face fertile: bordure 10 YR 8/1, 8/2, blanche, à l'extrême marge sur 1 mm, puis brunissant jusqu'à havane, 7,5 YR 5/4. Aiguillons petits, denses, blanchâtres à brun suivant l'âge, cylindriques ou aplatis.

LY 7110—Dimidié, jusqu'à 7×4 cm, mince et souple. Face stérile: 5 YR 6/4 (fawn R.) sur les deux tiers, puis nettement plus foncée, brun 5 YR 5/4 (mikado brown R.) dans le tiers situé vers le stipe. Le spécimen montre de nombreuses zones fines et pâlit beaucoup en séchant. Apparence poudreuse sous une loupe ordinaire. A la loupe binoculaire, on observe un feutre très dense et très court. Face fertile: aiguillons très denses, très fins, très aigus et relativement longs; de même couleur que la face stérile, mais ici les couleurs persistent à l'état sec. A la marge, zone plus jaune, isabelle, 7,5 YR 7/6, large de 5 mm. L'extrême marge est blanchâtre, 7,5 YR 8/2, à aiguillons nuls ou atrophiés.

Nous connaissons plusieurs espèces dont les cystides sont de deux sortes, à savoir *Steccherinum ethiopicum* Maas G., *S. rawakense* (Pers. apud Gaud.) Banker, *S. reniforme* (Berk. & Curt.) Banker et *S. subrawakense* Murrill (voir Maas Geesteranus, 1974). Le premier s'écarte de *S. confragosum* par un ensemble de caractères non reliés: le chapeau est (1) en grande partie unicolore, étant à peu près dépourvu de zones concentriques d'une couleur plus foncée, (2) dépourvu de tout relief; (3) les aiguillons sont plus longs; (4) les cystides subhyméniales sont pour la plupart remplies d'une matière oléagineuse et munies d'une paroi mince. A cause de ses gloeocystides, *S. rawakense* s'éloigne catégoriquement de cette espèce. *Steccherinum reniforme* a les spores un peu plus larges, 1,6–1,8 (–2,3) μm, les cystides subhyméniales à paroi épaisse et à sommet aigu, tandis que les aiguillons sont finement pubescents ou pulvérulents et d'une couleur différente. La dernière espèce *S. subrawakense*, qui, elle aussi, est caractérisée par des pustules en forme de coupole vers la base du chapeau, se sépare toutefois de *S. confragosum* par (1) le manque de zones concentriques plus obscures, (2) les aiguillons qui sont sensiblement plus longs et presque hirsutes, (3) les cystides d'origine tramale qui sont incrustées, et enfin (4) les cystides subhyméniales, dont la plupart ont une paroi mince.

En étudiant les caractères microscopiques d'un jeune basidiome apparu dans une culture de LY 6731, nous avons observé que les cystides du type (a) possèdent au sommet une substance cristalline bien visible. Il semble que ces cristaux disparaissent avec l'âge, ce qui expliquerait que les cystides du spécimen type soient actuellement trouvées glabres.

Etude des mycéliums.

GERMINATIONS.—Elles sont obtenues au bout de 4 jours. Le filament, issu de la spore uninucléée, est constitué d'articles uninucléés.

MONOSPERMES.—Formés d'hyphes sans boucles aux articles uninucléés, ils présentent aussi des fibres à paroi épaisse. Une trentaine de tests d'interfertilité, effectués entre les monospermes LY 6731, LY 6847 et LY 7110, ont tous donné des résultats positifs et malgré une diploïdisation très lente, des fructifications sont apparues à la périphérie de certaines cultures âgées de 10 semaines.

Polarité: Les haplontes LY 6731 ont permis d'établir la tétrapolarité de cette espèce.

A_1B_1: 1–7
A_1B_2: 3–4–9
A_2B_2: 2–6–10
A_2B_1: 5–8

à une seule exception près: 6×9, les confrontations de monospermes ayant le facteur «B» commun et le facteur «A» différent, n'ont pas montré de fausses boucles ni de crochets.

POLYSPERME (LY 6731, LY 6847, LY 7110).—Pl. 30 fig. 3.

Croissance: Lente (boîte couverte en 6 semaines).

Aspect: La marge irrégulière, un peu arborescente est submergée. Le mycélium presqu'entièrement submergé montre une disposition rayonnante nervurée. Quelques nervures principales sont soulignées par de très fines granulations blanchâtres ou par quelques petits amas feutrés blancs de mycélium dense devenant beige (10 YR 7/3) avec l'âge. Ces derniers, que l'on observe également à la périphérie de la culture, sont parfois porteurs d'une fructification (5 YR 6/3 à 5/3) à aiguillons d'abord alutacés (10 YR 8/4) ensuite cannelle (7,5 YR 6/4 à 5/4), qui atteignent 3 à 4,5 mm de long et sont coniques ou quelquefois soudés, formant alors des crêtes (plates, courbées ou en S). Revers: milieu inchangé (LY 6731, LY 6847) ou légère teinte caramel pâle (LY 7110). Odeur: nette, un peu miellée et caractéristique de la plupart des cultures de *Steccherinum*.

Microscopie: Mycélium aérien: Les hyphes, peu régulières, ×(1,5–)2–4(–5) µm, à boucles constantes, à paroi ferme ou nettement épaisse (× 1 µm) ont un contenu très homogène. Sur les plus larges (5 µm), les cloisons de retrait sont fréquentes. A coté de fibres étroites, × 1,5–2(–2,5) µm on observe des cystides peu différenciées): ce sont des articles terminaux, bouclés, à paroi épaisse atteignant 1–1,25 µm, et dont le sommet est couvert par un capuchon de cristaux biréfringents.

Pour les 3 récoltes, des fructifications en culture ont été obtenues. Les aiguillons mesurent 2–4(–5 mm) de long, leur trame est constituée d'hyphes squelettiques × 3,5 µm, à paroi épaisse 1,2–1,5 µm et d'hyphes génératrices × 2,5–3,5 µm, à paroi mince, bouclées. L'hyménium présente:

(i) Des basides (9–12 × 4 µm) à 4 stérigmates de 2,5 µm de long, produisant des petites spores, 2,5–3×1,5 µm, lisses, blanchâtres.

(ii) Des cystides étroites (20–40 × 3–4,5 µm) à paroi épaisse (1 µm), souvent coiffées au sommet par un capuchon de cristaux qui se dissout dans KOH/phloxine au bout d'un certain temps. Ces petites cystides prennent naissance sur une hyphe génératrice.

(iii) Des éléments, à paroi mince et contenu homogène, plus larges que les précédents (25–)33–55(–60) × 5–7(–10) µm, ayant leur origine dans le sous-hyménium.

Mycélium submergé: Les hyphes, × 1–3(–5) µm sont irrégulières, à boucles constantes, à paroi mince ou un peu épaissie.

Remarque: Après un an de stokage à 15°, la culture LY 6731 ne montre plus aucune boucle et ses hyphes sont formées d'articles uninucléés. Le polysperme LY 6847, observé à six mois possède un mycélium superficiel, bouclé mais le mycélium submergé est déjà totalement dépourvu de boucles. Le polysperme LY 7110, encore très jeune est totalement bouclé.

Cytologie: Articles binucléés.

Oxydases: ac. gallique: ++++,o gaïacol: ++++,o
p.- crésol: – tyrosine: +, tr.

CODE.—2a–(2b)–3c–8–9–12–14–32–36–38–46–48–53–60–61.

STECCHERINUM EXIGUUM, *nom. provis.*—Pl. 30 fig. 4

Basidiome étalé-réfléchi, 25 × 30 mm de diamètre, apparemment attaché par le dos à la face inférieure d'une branche tombée et par conséquent presque discoïde. Face abhyméniale finement veloutée, crème. Face adhyméniale subtomenteuse, un peu luisante, blanchâtre. Aiguillons d'environ 2 mm de long sur 0,1–0,2 mm de large, assez espacés, subulés, cylindriques ou un peu comprimés, droits, simples, incarnat-jaunâtre, pruineux, à sommet entier ou incisé. Chair du chapeau ne dépassant pas 1 mm d'épaisseur, coriace, pâle.

Contexte dimitique, constitué d'hyphes génératrices et squelettiques. Hyphes génératrices larges de 2,7–3,6 µm, non renflées, à paroi mince, ramifiées, cloisonnées, bouclées. Hyphes squelettiques larges de 3,6–7 µm, à paroi épaisse. Trame des aiguillons semblable. Basides collapsées. Spores 2,6–3,2 × 1,4–1,7 µm, ellipsoïdes, lisses, incolores, à apicule petit et oblique. Cystides 3,5–5,5 µm de diamètre, d'origine tramale, éparses, incluses ou émergentes, à paroi modérément épaisse et glabre.

GABON: Makoku, juillet 1970, *Mme A. David* (LY 6546, en partie à L).

Le matériel cité est d'un aspect assez banal, faisant même penser macroscopiquement à *S. ochraceum* (qui cependant s'en sépare nettement), sans caractères microscopiques particulièrement notables. C'est pourquoi nous pensons vain de nous efforcer à l'heure actuelle de décrire ce champignon comme une espèce nouvelle, d'autant qu'il n'existe qu'un unique échantillon, probablement pas complètement adulte, dont la variation nous est inconnue.

Etude des mycéliums.

Les spores sont uninucléées et le comportement nucléaire des mycéliums est «normal».[6] L'espèce est hétérothalle. Effectuées entre cultures monospermes, des

[6] Pour la terminologie concernant les caractères des mycéliums voir Boidin (1964).

confrontations avec *Steccherinum proximum* (LY 5955, LY 5977) et avec les *S.* du groupe *ochraceum* africains (LY 5598, LY 6547) et européens, ont toutes donné des résultats négatifs.

FOLYSPERME. (LY 6546).—Pl. 30 fig. 4.

Croissance: Très lente (50 à 70 mm en 6 semaines).

Aspect: La marge est irrégulière, submergée. En arrière, le mycélium aérien est pratiquement nul, la culture translucide, glabre, blanc-jaunatre est totalement immergée et présente par transparence sur fond sombre, un aspect arborescent. Dans la partie agée, on observe la seule petite plage un peu ceracée de mycélium superficiel blanc, feutré, mat, à finement poudreux (jeune fructification). La bouture et ses abords se teintent légèrement de «ferrugineus Sacc.», 5 YR 6/8. Revers: inchangé. Odeur aromatique nette.

Microscopie: Mycélium aérien: Les hyphes × 1.75–4 µm, peu régulières, à paroi mince, ou nettement épaissie, sont à boucles constantes. On observe des fibres, × 2 µm, à paroi épaisse (0,75 µm).

La fructification montre des basides tétrasporiques bouclées qui produisent des petites spores 3 × 1,8 µm; des éléments, 60 × 3–3,5 µm, à paroi épaisse (sauf au sommet) prenant naissance sur une hyphe mince bouclée, rarement incrustés; enfin des éléments plus larges, × 8–11 µm, à paroi mince, également bouclés à la base.

Mycélium submergé: Les hyphes identiques à celles du mycélium superficiel sont à boucles constantes.

Remarque: Trois mois après cette étude, le mycélium superficiel est toujours bouclé, mais le mycélium submergé a déjà perdu ses boucles. L'année suivante la culture est totalement dépourvue de boucles et ses hyphes sont formées d'articles uninucléés.

Cytologie: Articles binuclées.

Oxydases: ac. gallique: ++++,0 gaïacol: ++++,0
p.- crésol: – tyrosine: ++, tr.

CODE.—2-3c-8-9-14-32-36-38-47-48-53-58-61.

Steccherinum labeosum Maas G. & Lanq., *spec. nov.*[7]—Fig. 1,2

Basidioma effuso-reflexum, interdum subimbricatum. Pars reflexa 10–15 mm antice producta, 10–20 mm lata, parte effusa multo angustior, conchata, deflexa, tenuissime concentrice sulcata, zonis sparsis angustis obscurioribusque (badiis) munita, margine minute velutina, retrorsum subtomentosa vel glabrescens, ochraceo-fulva, margine obtusa, concolore. Pars effusa bene substrato allevanda. Aculei usque ad 3 mm longi, 0,1–0,3 mm lati, conferti, subulati, teretes vel compressi, recti vel curvati, simplices vel connati, ochraceo-brunnei, albido-pruinosi subtiliterque puberuli, apicibus integris vel incisis. Caro usque ad 1 mm crassa, coriacea, parte pileata concolor, e hyphis generatoriis skeletalibusque formata. Hyphae generatoriae 1,8–3,6 µm latae, haud inflatae, tenuiter tunicatae, ramosae, septatae, fibulatae. Hyphae skeletales 2,2–6,3 µm latae, crasse tunicatae vel fere solidae. Basidia 7–9 × 2,7–3,6 µm, tantum immatura visa, clavata, fibulata. Sporae 3,4–3,6 × 1,3–1,8 µm, graciliter ellipsoideae,

[7] Etymologie: *labeosus*, à lèvres épaisses (allusion à la marge du chapeau).

rectae vel leviter curvatae, adaxialiter applanatae, laeves, hyalinae, apiculo minuto obliquo praeditae. Cystidia 3,5–5,5 μm lata, in aculeorum parte media reperta, hypharum skeletalium apices geniculatos formantia (an etiam subhymenialia?), interdum e ramo orta, numerosa sed parum prominentia et glabra, ideo inconspicua, crasse tunicata, clavata vel cylindracea vel subfusiformia, apice obtusa.

Holotypus: «[Kenia] Nairobi, Ngong Forest, 24.5.[19]29, *J. M. Macdonald*» (K, fragmentum in L).

Basidiomes étalés-réfléchis, parfois un peu imbriqués. Partie réfléchie 10–15 mm de diamètre, 10–20 mm de large, plus étroite que la partie étalée, conchoïde, rabattue en dessous, munie de dépressions concentriques peu profondes et de quelques zones étroites plus obscures (baies), finement veloutée à la marge, subtomenteuse ou devenant glabre en arrière, ocracé fauvâtre (± entre 7.5 YR 8/6 et 10 YR 8/6), à marge épaisse et concolore. Partie étalée aisément séparable du support. Face adhyméniale subtomenteuse ou glabre, jaunâtre. Aiguillons atteignant jusqu'à 3 mm de long, 0,1–0,3 mm de large, serrés, subulés, cylindriques ou aplatis, droits ou courbes, simples ou connés, d'un ocracé brunâtre, couverts d'une pruine blanchâtre et finement pubérulents, entiers ou incisés au sommet. Chair de la partie réfléchie jusqu'à 1 mm, coriace, de même couleur que la surface réfléchie.

Contexte dimitique, constitué d'hyphes génératrices et squelettiques. Hyphes génératrices larges de 1,8–3,6 μm, non renflées, à paroi mince, ramifiées, cloisonnées, bouclées. Hyphes squelettiques larges de 2,2–6,3 μm, à paroi épaisse et parfois lumen subnul. Trame des aiguillons semblable. Basides 7–9 × 2,7–3,6 μm, vues seulement immatures, claviformes, bouclées à la base. Spores 3,4–3,6 × 1,3–1,8 μm, étroitement ellipsoïdes, droites ou faiblement incurvées, aplaties à la face interne, lisses, incolores, à apicule petit et oblique. Cystides 3,5–5,5 μm de diamètre, se trouvant dans la partie médiane des aiguillons, consistant en des terminaisons des hyphes squelettiques géniculées et pas rarement ramifiées (il n'est pas impossible qu'il y ait aussi, ça et là, quelques cystides d'origine subhyméniale), nombreuses, peu émergentes et glabres, passant de ce fait aisément inaperçues, à paroi épaisse, de forme variable (claviformes, cylindriques ou plus ou moins en forme de fuseau), arrondies au sommet.

Holotype: «[Kenia] Nairobi, Ngong Forest, 24.5.[19]29, *J. M. Macdonald*» (K; fragment à L).

Cette espèce ressemble remarquablement à *S. gilvum* Maas G. (Maas Geesteranus, 1974: 512) par le même aspect, des couleurs similaires et presque les mêmes spores grèles. *S. gilvum* cependant se distingue par les aiguillons qui sont d'une couleur plus foncée (brun-rouge), par les spores qui sont un peu plus longues (3,6–4,2 μm) et enfin par les cystides qui sont répandues sur toute la longueur des aiguillons, bien émergentes et fortement incrustées.

Du matériel assez morcelé se trouve dans l'herbier de G, récolté par la même personne et au même endroit, mais se distinguant du type par le support qui est un morceau d'écorce d'aspect différent.

STECCHERINUM OCHRACEUM (Pers. apud Gmel. ex Fr.) S. F. Gray

Hydnum ochraceum Pers. *apud* Gmel., Syst. Nat. **2**: 1440. 1792; *ex* Fr., Syst. mycol. **1**: 414. 1821. — *Steccherinum ochraceum* (Pers. apud Gmel. ex Fr.) S. F. Gray, Nat. Arrang. Br. Pl. **1**: 651. 1821.

Pour la synonymie complète, voir Maas Geesteranus, 1974: 517.

GABON: Makoku, juillet 1970, *Mme A. David* (LY 6547).
RÉPUBLIQUE CENTRAFRICAINE: Bomango, 1 avril 1965, *J. Boidin*, sur bois (LY 5598, en partie à L).
TANZANIA: «Mt. Kilimanjaro, east of Lemosho Glades, 1970, *L. Ryvarden 5138*» (O; en partie à L).
OBSERVATIONS.—Pour LY 5598, quelques observations sur le frais ont été notées par le récolteur: «étalé, confluent, se détache en entier comme une peau coriace. Marge blanche, non adhérente, villeuse. Ailleurs il est chamois clair, jaune de Naples R., 2,5 Y 8/6 et surtout alutacé, 10 YR 8/6 mais plus vif. Sa couleur avec l'âge, va localement jusqu'à bai, 2,5 YR 4/5». L'étude qui suit concerne exclusivement cette récolte.

Macroscopiquement et microscopiquement les collections africaines citées correspondent tout à fait à ce qu'on considère comme *Steccherinum ochraceum* en Europe. Pourtant il serait plus prudent de parler ici provisoirement du groupe *ochraceum*, groupe difficile où des collections semblables morphologiquement se montrent interstériles.

Etude des mycéliums.

SPORES.—Uninucléées

MONOSPERMES.—Ils sont constitués d'hyphes sans boucles aux articles uninuclées. Tous les tests d'interfertilité pratiqués avec les représentants européens du groupe *Steccherinum ochraceum* ont donné des résultats négatifs.

POLYSPERME.—

Croissance: Rapide (boîte couverte en 3 semaines).

Aspect: Marge rhizoïde. Le mycélium submergé, blanc, a une structure un peu rayonnante, la surface du milieu reste brillante car elle est à peine couverte par des fibrilles rayonnantes, appliquées. Revers inchangé. Odeur nulle sur milieu de Nobles tandis que sur milieu de Hagem, les cultures sentent nettement la rose.

Microscopie: Mycélium aérien: Les hyphes grêles, × 2–3 μm, régulières, bouclées, sont parfois engainées de gros cristaux. A la surface du milieu des hyphes plus larges ×4–5–7 μm ont des cloisons régulières ou au contraire plus rapprochées avec un léger étranglement à leur niveau. On observe des fibres très nettes, bouclées à la base, × 1,8–2–2,4 μm et parfois ramifiées. L'artcile qui les porte peut être à paroi épaisse lui aussi. Ces fibres ont tendance à porter sur leur parcours d'abondants cristaux très biréfringents formant presqu'une gaine.

Mycélium submergé: Les hyphes bouclées grêles, × 2–2,5 (–3,5) μm, présentent quelques renflements flasques.

Cytologie: Articles binucléés.

Oxydases: ac. gallique: ++++,0 gaïacol: +++++,0
p. crésol: –, précipité blanc tyrosine: –, traces à 1 cm (coloration diffuse orangée)

CODE.—2a–3c–8–9–32–36–38–43–53–58–61.

STECCHERINUM PROXIMUM, *nom. provis.*—Pl. 30 fig. 5

Basidiome étalé-réfléchi ou à chapeau saillant d'un disque fermement attaché au support. Partie réfléchie (ou chapeau) 18–25 mm de diamètre, zonée concentrique-

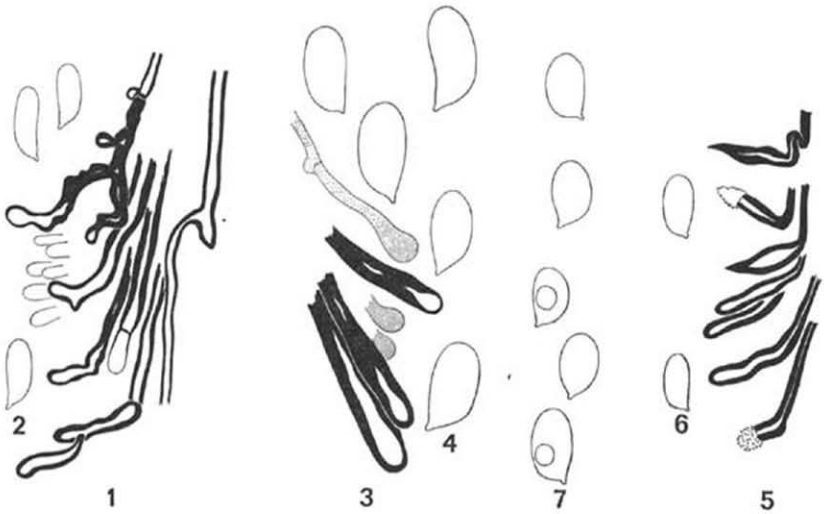

Fig. 1, 2. *Steccherinum labeosum*. — 1. Hyphes squelettiques de la région subhyméniale et quelques cystides ramifiées. — 2. Trois spores.

Fig. 3, 4. *Steccherinum russum*. — 3. Cystides et quelques hyphes à sommet renflé. — 4. Cinq spores.

Fig. 5, 6. *Steccherinum scalare*. — 5. Cystides. — 6. Deux spores.

Fig. 7. *Steccherinum scruposum*, cinq spores.

(Eléments hyméniaux, ×700; spores, ×2800.)

ment de plusieurs lignes très peu déprimées, subtomenteuse et jaunâtre sale à la marge, à surface affaissée en arrière et un peu luisante, d'un brun jaunâtre assez variable (par exemple 7,5 YR 7/4–6/4, ou 5 YR 6/4–5/6) avec quelques zones plus foncées. Face adhyméniale subtomenteuse-porée, un peu luisante, plus claire que la face supérieure (abhyméniale). Aiguillons d'environ 1×0,1—0,2 mm, assez serrés, subulés, cylindriques ou aplatis, droits, simples ou connés, beiges, finement pubérulents, entiers ou incisés au sommet. Chair du chapeau jusqu'à 1 mm de diamètre, coriace assez pliable, brun cannelle.

Contexte dimitique, constitué d'hyphes génératrices et squelettiques. Hyphes génératrices larges de 2,7–3,6 µm, non renflées, à paroi mince, ramifiées, cloisonnées. Hyphes squelettiques larges de 2,7–5,4 µm, à paroi épaisse. Trame des aiguillons semblable. Basides collapsées [(12–)14–17(–18)×(3–)4 µm dans un basidiome en culture]. Spores 3–3,5×2–2,4 µm, ellipsoïdes, lisses, incolores, à apicule petit et oblique. Cystides de deux sortes: (a) les unes jusqu'à 4,5 µm de diamètre, se trouvant dans la partie médiane des aiguillons, d'origine tramale, éparses, plus ou moins émergentes, glabres ou un peu incrustées, à paroi assez mince, cylindriques ou plus ou moins fusiformes, arrondies au sommet; (b) les autres 9–25×3,5–4,5 µm, se trouvant vers la base des aiguillons, d'origine subhyméniale, émergentes, glabres ou incrustées, à paroi épaisse et parfois lumen subnul, le plus souvent fusiformes, à sommet attenué ou aigu.

RÉPUBLIQUE CENTRAFRICAINE: La Maboké, 20 sept. 1967, *J. Boidin*, sur branche de *Polyalthia* sp. (LY 5955, en partie à L); M'Balé, 21 sept. 1967, *J. Boidin*, sur branche (LY 5977).

OBSERVATIONS.—Notes prises à l'état frais par le récolteur: LY 5955 — En petits disques résupinés, ou dimidié, ou étalé dimidié, ou parfois substipité. Face supérieure zonée, finement tomenteuse, 5 YR 4 à 5/4 et 4 à 5/6, bai ferrugineux; tomentum aéré, plus clair par zone avec l'âge, vers isabelle, 7,5 YR 7/4; marge assez large, pâle, 7,5 YR 8/3. Hyménium blanc, lisse à la marge, puis tuberculeux, enfin portant des aiguillons obtus, serrés, assez régulièrement disposés mais souvent aplatis ou même cunéiformes; la teinte moyenne beige, 10 YR 7/3, atteint cannelle 7,5 YR 6/4.

LY 5977—Sur un large coussinet mycélien brun, 5 YR 4/6 à 7,5 YR 4/6, à marge blanche, (14 mm de diamètre), stipe court, glabrescent, cannelle, 7,5 YR 6/6, puis étalé en demi disque à face supérieure glabre, bai ferrugineux 5 YR 4/6, parfois chocolat, 5 YR 3/3, à marge pâle. Face hyméniale à marge lisse blanche, à aiguillons régulièrement serrés mais souvent aplatis ou cunéiformes, beiges, 10 YR 7/3 à 6,5/3.

Bien que les deux collections citées montrent quelques différences entre elles, nous croyons que celles-ci ne dépassent pas la variabilité spécifique. En tout cas, cette variabilité est inférieure à celle exposée par LY 5955, où certains aiguillons sont absolument dépourvus de cystides quelconques, tandis que d'autres du même basidiome, en montrent beaucoup. Il s'agit vraiment d'une disposition embarrassante.

L'identification des deux collections pose également un problème difficile. Parmi les espèces connues jusqu'alors, LY 5955 et LY 5977 évoquent *Steccherinum reniforme*, dont l'aire de répartition est principalement sudaméricaine. Cependant plusieurs caractères s'opposent à une telle identification: (1) l'inconstance ou même l'absence des cystides, (2) la largeur comparative des spores, (3) le nombre des guttules dans les spores sur le vif: le plus souvent 2 dans les collections africaines, 1 dans une collection sudaméricaine (la seule collection dont nous possédons une description sur le frais). Mais ces objections n'ont peut-être pas l'importance que nous leur attachons, et c'est évidemment les tests d'interfertilité qui nous fourniront la réponse. Malheureusement nous n'avons pas pu obtenir une culture ou un spécimen frais du vrai *Steccherinum reniforme* de l'Amérique du Sud et les tests d'interfertilité souhaités restent à faire.

Eichelbaum (1907: 49) signalait la découverte d'*Hydnum glabrescens* Berk. & Rav. apud Berk. aux environs d'Amani (Usambara, Tanzania). Etant donné le fait que ce nom est un synonyme de *Steccherinum reniforme*, il n'est pas impossible que la récolte d'Amani se réfère précisément à *S. proximum*.

Etude des mycéliums.

GERMINATIONS.—Les spores uninucléées germent au bout de 3 ou 4 jours. Les filaments issus de la spore sont régulièrement uninucléés.

MONOSPERMES.—Ils sont formés d'hyphes, sans boucles, dont les articles sont uninucléés. Les confrontations effectuées entre les haplontes LY 5955 et LY 5977 ont toujours donné des résultats positifs qui permettent d'affirmer l'identité des 2 récoltes malgré les petites différences notées dans l'étude des carpophores.

Polarité: La tétrapolarité de l'espèce est établie avec les monospermes LY 5977.

A_1B_1: 1•-3-7-8-11
A_1B_2: 10•-14-15-
A_2B_2: 2-4•-5-6-9-12-18-19-20
A_2B_1: 13-16-17

Dans la lecture de ce tableau, nous n'avons pas observé de fausses boucles. A noter que la confrontation «8×10», montrait à 2 mois un mycélium binucléé bouclé jusqu'aux extrémités des haplontes, tandis que deux mois plus tard, le mycélium de cette même culture se révélait totalement dépourvu de boucles. Mais nous avons constaté déjà plusieurs fois cette tendance des cultures de *Steccherinum* à retourner rapidement à l'état haploïde. Ainsi, le polysperme bouclé LY 5977, du mois de septembre, était, au mois de janvier suivant, totalement constitué d'hyphes sans boucles, aux articles uninucléés. Par contre, le polysperme LY 5955, qui fructifie régulièrement lors des repiquages, est toujours bouclé après 7 ans de culture.

POLYSPERME (LY 5955).—Pl. 30, fig. 5.

Croissance: Très lente (50 mm en 6 semaines).

Aspect: La marge est irrégulière, appliquée et buissonnante. Nettement en arrière, le mycélium aérien peu abondant est formé de granules juxtaposés. Légèrement teintés, épars ou en plages denses, ils donnent à la culture un aspect granuleux: il s'agit d'une jeune fructification. Revers: inchangé. Odeur nette (de *Steccherinum* en culture).

Microscopie: Mycélium aérien: Les hyphes, × 1.5–3(–4) µm, peu régulières, sont bouclées, à paroi mince ou épaisse et portent des amas de cristaux. Quelques hyphes ont des articles renflés, × 6–10 µm. On observe de rares fibres, × 2 µm, (elles sont plus abondantes sur Hagem). Le mycélium aérien produit des fructifications brunâtres (5 YR 6/2—6/3 à 5/4), à aiguillons tendres, montrant dans l'axe des fibres (× 3 µm) à paroi épaisse (1 µm) et des hyphes hyalines, × 2–4 µm, bouclées, très irrégulières avec des renflements. A coté des basides, (12–)14–18(–22) × (3–)4 µm, on observe dans l'hyménium de nombreux éléments à paroi mince, portant un chapeau ou un manchon de cristaux et d'autres d'origine sous-hyméniale: les uns, assez rares, mais localement nombreux, à paroi épaisse, encapuchonnés de cristaux (50–55×5 µm), les autres, assez nombreux et facilement observables, à paroi mince et contenu suboléifère (35–60 × 5–8 µm), ne réagissant pas dans les sulfoaldéhydes. Tous ces éléments prennent naissance sur une hyphe bouclée.

Mycélium submergé: Les hyphes, × 1,5–4 µm, sont à boucles constantes, à paroi mince ou localement épaissie. Certaines présentent d'abondantes cloisons de retrait.

Cytologie: Articles binucléés.

Oxydases: ac. gallique: +++,o gaïcaol: +++,o
p- crésol: M tyrosine: (+), o

CODE.—2a–(2b)–3c–8–9–12–14–15–32–36–38–47–48–53–60–61.

Steccherinum russum Maas G. & Lanq., *spec. nov.*[8]—Fig. 3, 4

Basidioma effusum, aliquot cm diam., incarnatum, passim sulphureum, margine sericeum, albidum, male allevandum. Aculei usque ad 1,5 mm longi, 0,1–0,2 mm lati, subdistantes, subulati, tereti, recti, simplices vel connati, basi incarnati vel fere hysgini, apicem versus

[8] Etymologie: *russus*, roux.

luteo-albidi, pulverulenti vel puberuli, apicibus integris. Subiculum pertenue, albidum vel sulphureum, e hyphis generatoriis skeletalibusque formatum. Hyphae generatoriae 2,2–3,6 μm latae, haud inflatae, tenuiter tunicatae vel parietibus modice incrassatis instructae, ramosae, septatae, fibulatae. Hyphae skeletales 3,6–8 μm latae, crasse tunicatae vel solidae. Basidia collapsa, cellulis subhymenialibus elongatis materia oleaginosa lutea repletis apiceque inflatis immixta. Sporae 4–4,6 × 2,2–2,6 μm, ellipsoideae, adaxialiter applanatae vel curvatulae, laeves, hyalinae, apiculo obliquo praeditae. Cystidia 4,5–8 μm lata, e trama orta, numerosa, immersa vel parum prominentia, incrustata, crasse tunicata vel solida, cylindracea, apice obtusa.

Holotypus: «Tanzania, Arusha Prov., Ngurdoto National Park, Lake Kusare, 3° 13′ S. 36° 53′ E, 16 Jan. 1970, *L. Ryvarden 5237*» (O, pars in L).

Basidiome étalé, atteignant quelques centimètres de diamètre. Marge soyeuse, blanchâtre, à peine séparable du support. Face adhyméniale tomenteuse, incarnat, çà et là de couleur sulfurine. Aiguillons atteignant jusqu' à 1,5 mm de long, 0,1–0,2 mm de large, assez espacés, subulés, cylindriques, droits, simples ou connés, incarnat assez foncé à la base, plus pâles et d'un jaune blanchâtre vers le sommet (la couleur qui en résulte s'approche de 7.5 YR 7/6), pulvérulents ou pubérulents, entiers au sommet. Subiculum très mince, blanchâtre ou sulfurin.

Contexte dimitique, constitué d'hyphes génératrices et squelettiques. Hyphes génératrices larges de 2,2–3,6 μm, non renflées, à paroi mince à assez épaisse, ramifiées, cloisonnées, bouclées. Hyphes squelettiques larges de 3,6–8 μm, à paroi épaisse et parfois lumen subnul. Trame des aiguillons semblable. Basides collapsées. Spores 4–4,6 × 2,2–2,6 μm, ellipsoïdes, aplaties à la face interne ou un peu incurvées, lisses, incolores, à apicule oblique. Entre les basides on trouve des cellules difficiles à suivre, mais évidemment d'origine subhyméniale, allongées, remplies de matière oléagineuse jaune, à sommet renflé en ballon. Cystides 4,5–8 μm de diamètre, constituant les terminaisons des hyphes squelettiques, nombreuses, incluses ou peu émergentes, incrustées, à paroi épaisse ou lumen subnul, cylindriques, obtuses au sommet.

Holotype: «Tanzania, Arusha Prov., Ngurdoto National Park, Lake Kusare, 3° 13′ S. 36° 53′ E, 16 Jan. 1970, *L. Ryvarden 5237*» (O; en partie à L).

Il n'existe aucune autre espèce de *Steccherinum* dont la chair montre une couleur sulfurine. Malheureusement l'assez mauvais état du type nous a empêché d'observer la localisation de cette couleur. Les parois des hyphes génératrices montrent, à vrai dire, un reflet jaunâtre, mais la vraie matière colorante se trouve ailleurs. Plongé dans une solution alcaline un petit morceau du subiculum dégage un nuage dans le liquide.

L'espèce est en outre caractérisée par la présence dans l'hyménium de cellules à sommet renflé.

Steccherinum scalare Maas G. & Lanq., *spec. nov.*[9]—Fig. 5, 6

Basidioma pileatum. Pilei scalarum more superpositi, 8–12 mm antice producti, 10–17 mm lati, a tergo coaliti, lateraliter concrescentes, patentes, conchati, retrorsum contracti, prorsum undulati, tomentosi vel puberuli, sordide ochracei vel ochracco-brunnei, compluribus zonis

[9] Etymologie: *scalaris*, appartenant à un escalier (allusion aux chapeaux superposés ressemblant aux marches d'un escalier).

concentricis obscurioribus (fulvis, badiis vel fuligineis) glabrescentibusque variegati, margine acutiusculi. Aculei usque ad 1 mm longi, 0,1–0,3 mm lati, conferti, subulati, teretes vel compressi, recti, simplices vel connati, ochraceo-brunnei vel brunneo-incarnati, albido-pruinosi subtiliterque puberuli, apicibus integris vel incisis. Caro usque ad 1 mm crassa, coriacea, sordide ochracea, e hyphis generatoriis skeletalibusque formata. Hyphae generatoriae 1,8–3,6 μm latae, haud inflatae, tenuiter tunicatae, ramosae, septatae, fibulis munitae. Hyphae skeletales 3,5–5,4 μm latae, crasse tunicatae. Hyphae skeletales in aculeorum contextu similes sed plerumque fere solidae. Basidia collapsa. Sporae 2,5–3,1 × 1,5–1,8 μm, ellipsoideae, adaxialiter applanatae, laeves, hyalinae, apiculo minuto obliquo praeditae. Cystidia 2,5–4,5 μm lata, passim vel aculeorum partem apicalem versus reperta, hypharum skeletalium apices geniculatos formantia (an etiam subhymenialia?), numerosa vel pauca, vulgo prominentia atque apice incrustata, crasse tunicata vel interdum solida, fusiformia, apice obtusa vel acuta.

Holotypus: «British Cameroons [est Nigeria], District Buea, to Musaka Camp, May 1929, *T. D. M[aitland]* 76, 4500′, on erect decayed tree trunk» (K, fragmentum in L).

Basidiome à chapeaux superposés. Chapeaux 8–12 mm de diamètre et 10–17 mm de large, coalisés en arrière, concrescents latéralement, écartés, conchoïdes, rétrécis en arrière, ondulés en avant, tomenteux ou pubérulents, ocracé sale (entre 10 YR 8/3 et 2.5 YR 8/4) à ocracé fauvâtre (±7.5 YR 6/6), munis de plusieurs zones concentriques plus foncées et glabrescentes (fauves, baies ou fuligineuses), à marge assez aigue. Face adhyméniale subtomenteuse, jaunâtre. Aiguillons atteignant jusqu'à 1 mm de long, 0,1–0,3 mm de large, serrés, subulés, cylindriques ou aplatis, droits, simples ou connés, d'un ocracé brunâtre ou brun incarnat, couverts d'une pruine blanchâtre et finement pubérulents, entiers ou incisés au sommet. Chair jusqu'à 1 mm, coriace, ocracé sale.

Contexte dimitique, constitué d'hyphes génératrices et squelettiques. Hyphes génératrices larges de 1,8–3,6 μm, non renflées, à paroi mince, ramifiées, cloisonnées, bouclées. Hyphes squelettiques larges de 3,5–5,4 μm, à paroi épaisse. Trame des aiguillons semblable, les hyphes squelettiques le plus souvent à lumen subnul. Basides collapsées. Spores 2,5–3,1 × 1,5–1,8 μm, ellipsoïdes, aplaties à la face interne, lisses, incolores, à apicule petit et oblique. Cystides 2,5–4,5 μm de diamètre, se trouvant un peu partout ou plus spécialement vers la région apicale des aiguillons, formant des terminaisons géniculées des hyphes squelettiques (ou peut-être aussi d'origine subhyméniale?), nombreuses ou non, ordinairement émergentes et capitées par des incrustations, à paroi épaisse ou lumen subnul, fusiformes, obtuses ou aigues au sommet.

Holotype: «British Cameroons [maintenant Nigeria], District Buea, to Musaka Camp, May 1929, *T. D. M[aitland]* 76, 4500′, on erect decayed tree trunk» (K; fragment à L).

A vrai dire *S. scalare* ne ressemble à aucune autre espèce du genre, bien qu'il soit difficile de signaler un seul caractère saillant. C'est plutôt par son ensemble de caractères (chapeaux superposés, l'absence de sillons concentriques, ondulation de la marge, exiguïté des spores, forme des cystides) que cette espèce se distingue.

Steccherinum scruposum Maas G. & Lanq., *spec. nov.*[10]—Fig. 7 et Pl. 30 fig. 6

Basidioma effuso-reflexum. Pars reflexa sicut pileata, 15 mm antice producta, 30 mm lata, semicircularis, plana; basi tuberculis sparsis munita vel colliculosa, alibi radiato-rugosa, lanoso-tomentosa, crustulina, zonis concentricis hinnuleis praedita, margine acuta. Aculei

[10] Etymologie: *scruposus*, raboteux.

usque ad 1 mm longi, 0,1–0,2 mm lati, conferti, subulati, applanati, recti, simplices vel connati, fulvi, albopruinosi, apicibus integris vel incisis. Caro usque ad 1 mm crassa, coriacea, pallida, postice cinnamomea, e hyphis generatoriis skeletalibusque formata. Hyphae generatoriae 2,5–3,6 µm latae, haud inflatae, tenuiter tunicatae, ramosae, septatae, fibulatae. Hyphae skeletales 2,5–6 µm latae, crasse tunicatae. Basidia collapsa. Sporae 2,8–3,6 × 2–2,5 µm, ellipsoideae, adaxialiter applanatae, laeves, hyalinae, apiculo minuto obliquo praeditae. Cystidia collapsa, vix observata, nec vero non e aculeorum trama orta.

Holotypus: Gabon, Makoku, juillet 1970, *Mme A. David* (LY 6499; pars in L).

Basidiome étalé-réfléchi, mais la partie réfléchie se présentant tout à fait comme un chapeau dimidié. Chapeau 15 mm de diamètre et 30 mm de large, demi-circulaire, aplani, muni à la base de tubercules épars ou gibbeux, ailleurs radié-rugueux, laineux-tomenteux, ocracé-brun (± entre 7.5 YR 6/6 et 10 YR 7/6), à zones concentriques fauves (± 7.5 YR 5/6), à marge aigue. Face adhyméniale finement tomenteuse-porée, ocracé sale. Aiguillons jusqu'à 1 mm de long, 0,1–0,2 mm de large, serrés, subulés, aplatis, droits, simples ou connés, fauves, couverts d'une pruine blanchâtre, entiers ou incisés au sommet. Chair du chapeau jusqu'à 1 mm, coriace, pâle, brun rougeâtre en arrière.

Contexte dimitique, constitué d'hyphes génératrices et squelettiques. Hyphes génératrices larges de 2,5–3,6 µm, non renflées, à paroi mince, ramifiées, cloisonnées, bouclées. Hyphes squelettiques larges de 2,5–6 µm, à paroi épaisse. Trame des aiguillons semblable. Basides collapsées. Spores (prises d'une sporée) 2,8–3,6 × 2–2,5 µm, ellipsoïdes, aplaties à la face interne, lisses, incolores, à apicule petit et oblique. Cystides difficiles à observer, collapsées, en tout cas d'origine tramale.

Holotype: Gabon, Makoku, juillet 1970, *Mme A. David* (LY 6499; en partie à L).

Bien que le type ne comporte qu'un seul spécimen, qui du reste est en assez mauvais état, puisque l'hyménium et même les cystides sont collapsés, il est évident qu'il s'agit ici d'une espèce nouvelle.

En vertu de la gibbosité à la base du chapeau on pourrait penser à *S. confragosum* et *S. subrawakense*, mais ceux-ci montrent un chapeau d'aspect différent (plus uni et moins velu), leurs cystides sont de deux sortes, et les spores sont un peu plus étroites.

La couleur cannelle de la chair vers la base du chapeau évoque *S. reniforme*, une espèce jusqu'alors connue de l'aire sudaméricaine, à chapeau glabrescent, aux aiguillons d'aspect un peu plus «velu», à cystides de deux (ou trois) sortes.

Il est toujours possible que certaines cystides du *S. scruposum* soient des gloeocystides. Dans ce cas une comparaison s'impose avec *S. rawakense*, mais les différences ne laissent aucun doute: son chapeau est glabrescent, la chair est d'une couleur différente et plus pâle, les spores sont bien plus étroites.

Etude des mycéliums.

Comme les espèces précédentes, le mycélium de *S. scruposum* a un comportement nucléaire «normal». Sur 30 germinations prélevées 2 jours après la dispersion, 23 seulement se développent et 8 d'entre elles se révèlent bouclées au premier examen. Deux des monospermes vérifiés sans boucles ont produit par la suite des fructifications bouclées et des spores. Les appariements tentés à plusieurs reprises n'ont donné que de très rares résultats positifs qui ne permettent pas de préciser la thallie de l'espèce.

POLYSPERME (LY 6499).—Pl. 30 fig. 6.

Croissance: Très lente (70 mm en 6 semaines).

Aspect: La marge est irrégulière, appliquée, arborescente. Toute la culture a une structure arborescente d'autant plus nette que le mycélium aérien blanc, généralement subnul, devient plus dense au niveau des ramifications principales qui, de ce fait, se trouvent soulignées. Dans la région voisine de la bouture, on observe une fructification beige foncé, vers 10 YR 7/3, 5, portant des aiguillons et produisant une sporée dans le couvercle de la boîte de Pétri. Revers: inchangé. Odeur aromatique faible (plus nette sur milieu de Hagem), c'est celle des *Steccherinum* en culture.

Microscopie: Mycélium aérien: Il est caractérisé par l'abondance des cristaux. Les hyphes, $\times 1{,}5$–$4{,}5(-5{,}5)$ μm, très irrégulières, à paroi mince et contenu homogène, sont bouclées à toutes les cloisons. On observe aussi quelques fibres à paroi épaisse congophile.

Sur la bouture il fait place à une fructification à aiguillons montrant dans leurs axes, des fibres $\times 2$–3 μm à paroi épaisse atteignant 1 μm. Dans l'hyménium, à côté des cystides non incrustées, nous avons observé des basides tétrasporiques bouclées, $\times 3{,}75$ μm (au sommet) produisant des petites spores ellipsoïdes $3{,}5$–4×2–$2{,}5$ μm.

Mycélium submergé: A boucles constantes, à paroi distincte ou légèrement épaissie, les hyphes axiales, $\times 3{,}5$–$4(-5)$ μm, de même que les rameaux, $\times 1{,}5$–$2{,}5$ μm sont très irrégulières. Leur parcours et leur diamètre sont très fantaisistes. Elles présentent quelques vésicules flasques et de nombreuses cloisons de retrait.

Cytologie: Articles binucléés.

Oxydases: ac. gallique: +++++, o — gaïacol: +++++, o
p.-crésol: — — tyrosine: —, 3 à 5 mm

Remarque: A l'âge de 2 ans, la culture polysperme a totalement perdu ses boucles, le mycélium aérien, comme le mycélium submergé est alors constitué d'hyphes aux articles régulièrement uninucléés.

CODE.—2a–3c–8–14–32–36–38–47–48–53–58–61.

NOTE

L'espèce du *Steccherinum* indéterminable provenant du District des Lacs Edouard et Kivu (Maas Geesteranus, 1967: 106) a été étudiée de nouveau et comparée avec celles que nous connaissons à l'heure actuelle. L'échantillon se distingue de toutes les autres espèces mais l'absence de spores nous empêche d'en offrir une description.

THELEPHORACEAE

SARCODON cf. QUIETUS Maas G.

Sarcodon quietus Maas G. *in* Bull. Jard. bot. natn. Belg. **37**: 95. 1967.

RHODESIE DU NORD: «Southern Prov., Mulanje Distr., Mulanje Mts., Lichenya Plateau, 9–10 March 1973, *L. Ryvarden 11343*, 1800–2000 m alt.» (L).

L'identité du spécimen étudié est loin d'être sûre. Pour autant qu'on puisse savoir, il est clair que ce matériel n'appartient pas à *Sarcodon procerus* Maas G. (Maas Geesteranus, 1967:93). Ceci laisserait *S. quietus* Maas G. comme la seule possibilité s'il n'y avait pas les divergences suivantes: (1) le centre du chapeau de cette récente collection semblait dépourvu de squamules, (2) le stipe était noté de même couleur que le chapeau: olive sale, et (3) les spores sont plus grandes, 9–9,8 × 6,3–6,7 μm. De plus le récolteur était incapable de dire la couleur du contexte et s'il avait viré au noir après exposition à l'air. Les caractères, énumérés ci-dessus le rapporterait plutôt à *S. atro-viridis* (Morgan) Banker (ce qui serait une découverte étonnante), mais pour conclure il faut attendre de nouvelles récoltes accompagnées de croquis en couleur ou de diapositives.

SUMMARY

In this paper some further African localities are recorded for *Gloeodontia discolor*, *Flavodon flavus*, and *Steccherícium seriatum*. In the genus *Steccherinum* five new species are described (*S. confragosum*, *S. labeosum*, *S. russum*, *S. scalare*, and *S. scruposum*), while three more are provisionally recognized, one of which being an unnamed member of the *S. ochraceum* group. A key to all species of *Steccherinum* thus far known from Africa is provided. For a number of the species their cultural and mycelial characteristics are given.

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LÉGENDE DE LA PLANCHE 30

Fig. 1–6. Cultures sur milieu de Nobles. — 1 et 2. *Steccherinum seriatum* (LY 6968). La photo d'une culture âgée de 6 semaines ne présentant aucun intérêt, nous préférons illustrer l'aspect, très caractéristique, observé à un stade plus avancé (3 mois). — 3. *Steccherinum confragosum* (LY 6731). — 4. *Steccherinum exiguum* (LY 6546). — 5. *Steccherinum proximum* (LY 5955). — 6. *Steccherinum scruposum* (LY 6499).

Les numéros 3 à 6 montrent l'aspect des cultures âgées de six semaines.

CORRECTIONS

Some bad errors crept into my work 'Die terrestrischen Stachelpilze Europas' and I am indebted to Dr. V. Demoulin, Liège, for having rapped my knuckles.

Sarcodon regalis Maas G. *in* Verh. K. Ned. Akad. Wet., Afd. Natuurk., Tweede reeks **65**: 106. 1975. — The Latin description remains unaltered. Collection *Maas Geesteranus 15291* (L) is here formally indicated as lectotype.

Sarcodon cyrneus Maas G. *in* Verh. K. Ned. Akad. Wet., Afd. Natuurk., Tweede reeks **65**: 109. 1975. — The Latin description remains unaltered. Collection *Demoulin 4608* (LG; part in L) is here formally indicated as lectotype.

Finally, Dr. Demoulin pointed out that the holotype of *Hydnellum coalitum* Maas G. should be designated V. Demoulin (LG); the isotype in L is duplicate No. 106. The fungus collections in LG receive no serial number.

R. A. MAAS GEESTERANUS

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FARROWIA, A NEW GENUS IN THE CHAETOMIACEAE

D. L. HAWKSWORTH

Commonwealth Mycological Institute, Kew

(With four Text-figures and one Table)

The new genus *Farrowia* D. Hawksw. is described to accommodate *Chaetomium longicolleum* Krzem. & Badura and *C. longirostre* (Farrow) L. Ames, species formerly incorrectly referred to *Chaetoceratostoma* Turc. & Maffei. These two species are united under the name *F. longicollea* (Krzem. & Badura) D. Hawksw. *comb. nov.*, the type species of *Farrowia*. The genus is also considered to include two further species, *F. malaysiensis* D. Hawksw. *sp. nov.* and *F. seminuda* (L. Ames) D. Hawksw. *comb. nov.* (syn. *Chaetomium seminudum* L. Ames). The separation of the genus from *Chaetomium* Kunze ex Fr. and *Scopinella* Lév. is discussed and conidial states reported in the family Chaetomiaceae Wint. reviewed. A key to the species of the Chaetomiaceae with *Botryotrichum*-like aleuriospores is included. The name *B. piluliferum* Sacc. & Marchal may refer to conidial states of several members of the Chaetomiaceae in addition to *C. piluliferum* J. Daniels.

In the course of studies in the family Chaetomiaceae Wint. (Ascomycotina—Pyrenomycetes — Sphaeriales) it has become increasingly clear that within the genus *Chaetomium* Kunze ex Fr. *C. longirostre* (Farrow) L. Ames and some allied taxa merit recognition as a distinct genus. The generic name *Chaetoceratostoma* Turc. & Maffei has been adopted for this group by several authors (Farrow, 1955; Badura, 1964; Dennis, 1970; Hawksworth, 1971, Hawksworth & Wells, 1973), but a closer examination of the type species of *Chaetoceratostoma*, *C. hispidum* Turc. & Maffei, has recently shown that this taxon is conspecific with *Scopinella barbata* (Pers. ex Gray) Lév. ex Sacc. (Hawksworth, 1975). *S. barbata*, the only species of the monotypic genus *Scopinella* Lév., differs from *Chaetomium longirostre* in so many characters that the taxa cannot be regarded as congeneric (Table I).

No detailed account of the segregate from *Chaetomium* including *C. longirostre* has previously been published. In this paper the new genus *Farrowia* D. Hawksw. is proposed to accommodate this group of *Chaetomium*-like fungi.

Apart from *C. hispidum* referred to above and taxa treated in detail elsewhere in this paper, only one other taxon has been referred to *Chaetoceratostoma*, viz. *C. graphioides* (Sacc.) C. Booth & Dennis, which proves to be a synonym of *Phaeostoma vitis* (Fuckel) Arx & E. Müll. (Hawksworth, 1975).

TAXONOMY

The characters distinguishing *Farrowia* from *Chaetomium* and *Scopinella* are indicated in Table I. Of these it was the formation of a distinctive long neck which led Farrow

TABLE 1

SYNOPSIS OF CHARACTERS SEPARATING CHAETOMIUM, FARROWIA AND SCOPINELLA

	PERITHECIA	ASCI AND ASCOSPORES	CULTURES AND CONIDIAL STATE
CHAETOMIUM (180+spp.)	Subglobose to vasiform, with lateral and terminal hairs which may be variously branched or contorted; terminal hairs not arising synchronously from adjacent elongated cells at the apex of the perithecia, not fused or adhering to form a neck; hairs with slight rugose (few spp.) to coarse (most spp.) ornamentation (× 10,000); pedestal-like rhizoidal base usually absent.	Asci clavate or cylindrical, deliquescing before the ascospores mature; ascospores varying in shape, not usually 1-guttulate, not ornamented.	Most species known in culture; cultures not usually producing reddish pigments in the medium (c. 3 spp.); conidial state absent in most species, *Acremonium* (3+spp.), *Botryotrichum* (8-9 spp.) or *Scopulariopsis* (1 sp.).
FARROWIA (3 spp.)	Subglobose, with lateral and terminal hairs which are straight and unbranched; terminal hairs arising synchronously from adjacent elongated cells at the apex of the perithecia, fused below to form a distinct neck-like structure which may be rudimentary; hairs ± smooth (× 10,000); pedestal-like rhizoidal base usually present.	Asci clavate, deliquescing before the ascospores mature; ascospores lemoniform, biapiculate with a subapical germ pore, usually 1-guttulate; not ornamented.	Only known in culture; cultures often forming reddish pigments in the medium in the presence of contaminants; conidial state *Botryotrichum* (all species).
SCOPINELLA (1 sp.)	Subglobose, with lateral and terminal hairs which are both straight, unbranched, and fused in groups; terminal hairs arising synchronously from adjacent elongated cells at the apex of the perithecia, fused below to form a distinct neck-like structure, fused above the neck to varying extents; hairs smooth (× 10,000); pedestal-like rhizoidal base absent.	Asci clavate, deliquescing after the ascospores mature; ascospores quadrangular, not guttulate; with a broad Z-shaped deeply pigmented band.	Not known in culture; conidial state (if any) unknown.

(1955) to describe his *Chaetoceratostoma longirostre* in a genus other than *Chaetomium*. A few species of *Chaetomium* have perithecia which become somewhat elongated, vasiform or cone-like above but where this does occur the apical region always appears to be composed of cells similar to those making up the rest of the peridium and not elongated cells which give rise to the neck-like structures in *Farrowia*. Within *Farrowia* the neck may be extremely tall or reduced to a few short elongated cells representing a rudimentary neck in *F. seminuda*. The lateral and terminal hairs in *F. longicollea* are completely smooth when examined by scanning electron microscopy (Hawksworth & Wells, 1973) and this is also true for *F. malaysiensis*. Hawksworth & Wells detected some slight rugose ornamentation in *F. seminuda* and this is sometimes visible towards the bases of the lateral hairs even by light microscopy. Of the other 91 species of *Chaetomium* studied by these authors, only five (*C. atrobrunneum* L. Ames, *C. erectum* Skolko & Groves, *C. fusisporale* Rai & Mukerji, *C. indicum* Corda and *C. reflexum* Skolko & Groves) had a similar type of ornamentation on their hairs to that seen in *F. seminuda*. Interestingly all these five species belong to a group of *Chaetomium* species with stiff, usually dichotomously branched, terminal hairs which lack all other features separating *Farrowia* from *Chaetomium*.

The method of attachment of perithecia to the substrate is a somewhat overlooked character in the Chaetomiaceae. In *Chaetomium* the perithecia are attached by hyaline to pale brown hyphae which ramify and spread prostrately along or penetrate the substrate to varying degrees. When grown in culture these hyphae, which I will refer to as 'rhizoidal', are sometimes concentrated below the perithecia but within the agar. In *Farrowia*, in contrast, the rhizoidal hyphae usually form a distinct, compact, pedestal-like tuft which supports the perithecium above the surface of the substrate. It is possible that some taxa in *Chaetomium* may have a pedestal-like tuft as in *Farrowia* to judge from published illustrations of various species but in all those I have so far been able to examine this proves not to be the case.

The ascospores of *Farrowia* are remarkably similar in shape, apical apparatus and in often having a single massive round guttule. I have not seen exactly comparable guttulate ascospores in any *Chaetomium* species; where guttules occur in *Chaetomium* ascospores there tend to be several small guttules rather than a single massive round one or an almost quadrangular one (*C. bostrychodes* Zopf). A study by transmission electron microscopy might conceivably reveal some differences in internal structure between ascospores of *Chaetomium* and *Farrowia*.

A consideration of any conidial states and resting spores has also been a very much neglected character in the Chaetomiaceae. Ames (1963) provided measurements and illustrations of aleuriospores he noted (frequently incorrectly applying the term 'chlamydospores' to them) but in the more recent publication of Seth (1972) even these were omitted from the descriptions of species. The majority of *Chaetomium* species do not appear to have any conidial state at all but in *Farrowia* all three species have a *Botryotrichum*-like aleuriospore state. Conidia referrable to *Botryotrichum* Sacc. & Marchal are known to me in *Chaetomium* from *C. brevipilium* L. Ames, *C. homopilatum* Omvik and *C. piluliferum* J. Daniels. In addition, to judge from published descriptions,

Botryotrichum-like aleuriospores also occur in *C. distortum* L. Ames, *C. pinnatum* L. Ames, *C. pulchellum* L. Ames, *C. semispirale* Udagawa & Cain, some strains of *C. bostrychodes* Zopf (Calviello, 1971), and possibly also in *C. silvaticum* var. *variabile* Kiril. The only other conidial states (apart from true chlamydospores or other resting structures) reported in *Chaetomium* are of *Scopulariopsis* Bain. in *C. trigonosporum* (Marchal) Chiv. (Corlett, 1966) and of *Acremonium* Link ex Fr.-like states in *C. elatum* Kunze ex Fr. (Moreau & Moreau, 1954; Domsch & Gams, 1970), *C. globosum* Kunze ex Fr. (Zopf, 1881), *C. piluliferum* J. Daniels (Daniels, 1961) and possibly a few other species. In *Thielavia* Zopf (sensu Malloch & Cain, 1973), a cleistocarpic genus of the Chaetomiaceae, conidial states referrable to *Botryotrichum* (*T. cephalothecoides* Malloch & Benny), *Chrysosporium* Corda (*T. novoguineensis* Udagawa & Horie and *T. sepedonium* Emmons; see Udagawa & Horie, 1972), *Sporotrichum* Link ex Fr. (*T. thermophila* Fergus & Sinden), possibly *Acremonium* (*T. terrestris* (Apinis) Malloch & Cain) and of uncertain position (*T. pallidospora* Pidopl. & al.) occur. As in *Chaetomium*, however, most *Thielavia* species do not appear to produce any conidial state.

Perfect states for *Botryotrichum*-like aleuriospores are unknown outside the genera *Chaetomium*, *Farrowia* and *Thielavia*. Apart from some variations in size and pigmentation, both features perhaps related to cultural conditions, the aleuriospores are remarkably similar, so much so that in the absence of perithecia it seems to be impossible at the present time to determine to which perfect state such imperfect isolates belong. The name *C. piluliferum* J. Daniels was introduced by Daniels (1961) as that for the perfect state of *B. piluliferum* Sacc. & Marchal, but in my view conidial states referrable to *B. piluliferum* should not be assigned to this *Chaetomium* in the absence of the perfect state. The 'setae' characteristic of *B. piluliferum* are perhaps merely mycelial hairs which arise just prior to the initiation of perithecia in *Chaetomium* and *Farrowia*. A key to the taxa reported as having *Botryotrichum*-like aleuriospores is included below (p. 171); details of aleuriospores are omitted from this for the reasons indicated above.

The occurrence of an imperfect state in all species of *Farrowia* is of interest as this is the first genus of the Chaetomiaceae to be recognised in which all species have an imperfect state referable to a single imperfect state genus. All species of *Ascotricha* Berk. have conidial states belonging to *Dicyma* Boul., but that genus is more appropriately placed in either the Coniochaetaceae Malloch & Cain or the Xylariaceae Tul. (Hawksworth & Wells, 1973).

The affinity of *Farrowia* to the Chaetomiaceae is also supported by the production of *Thielavia*-like cleistothecia in mutants from one strain of *F. longicollea* (p. 177). This is the first time an ostiolate species in this family appears to have been reported as producing non-ostiolate ascocarps in culture. This phenomenon is well known in some other pyrenomycete families, however, and this subject has recently been reviewed by von Arx (1973). The genera *Thielavia* (incl. *Chaetomidium* (Zopf) Sacc.) and *Corynascus* Arx may be interpreted as cleistocarpic counterparts of *Chaetomium* (and ? *Farrowia*) and *Achaetomiella* Arx, respectively.

The characters of the *Farrowia* species treated here are of interest in other respects as well. The nature of the structures at the apices of the perithecia in *F. malaysiensis* and *F. seminuda* resemble growth stages through which *F. longicollea* passes (Doguet, 1955a; Cooke, 1973). These characters are maintained in culture, however, and it appears almost as if development becomes arrested at different stages in the three species—indicating genotypic differences. The ascospores in *F. longicollea* tend to be very slightly larger than those in *F. malaysiensis* and *F. seminuda*, these latter having ascospores almost identical in size. The geographical distribution of soil fungi is generally accorded little taxonomic weight but this may perhaps to a large extent arise from inadequate study of soil mycofloras throughout the world. Bartoli (1972) drew attention to the fact that *F. longicollea* had been obtained almost exclusively from tropical soils and this is largely borne out by my own studies (Fig. 1). *F. malaysiensis* is currently known only from three independently made isolations from Malaysia — it will be of interest to see if it is in fact so restricted geographically as studies of soil fungi in other parts of the world proceed. *F. longicollea* is unknown from Malaysia, in contrast, and it might be tempting to speculate that geographical isolation had played some role in its speciation. *F. seminuda* perhaps tends to prefer slightly cooler soils, predominates in North America, and is unknown from India and Central and South America. Doguet (1959) found that the ascospores of *F. longicollea* were tolerant of high temperatures and it would appear that an investigation of the temperature requirements of other species in the genus might yield interesting information.

Chemotaxonomy is almost unknown in pyrenomycetes. Both *F. longicollea* and *F. malaysiensis* produce a reddish-purple pigment in the presence of contaminant organisms which appears to be due to a lack of the enzyme saccharase (Doguet, 1955b; see p. 178). Reddish pigments are formed by several *Chaetomium* species in pure culture (in the absence of contaminants) but whether the compounds involved are the same as those in *Farrowia* is uncertain — in neither case is their structure known. The shades of colour produced, however, suggest that the compounds involved may well be different and so there may also be chemotaxonomic differences between these two genera.

KEY TO THE PERFECT STATES OF MEMBERS OF THE CHAETOMIACEAE WITH BOTRYOTRICHUM-LIKE ALEURIOSPORES

1a. Ascocarps cleistothecia; peridium cephalothecoid; ascospores 12–15.5 × 8–10.5 μm; aleuriospores 8–25 μm diam. . . . . *Thielavia cephalothecoides* Malloch & Benny
b. Ascocarps perithecia; peridium not cephalothecoid 2
2a. Perithecia with distinct necks over 80 μm tall formed from synchronously arising fused terminal hairs; hairs not ornamented; perithecia with a distinct pedestal-like tuft of rhizoidal hyphae; cultures producing reddish pigments in the presence of contaminant organisms 3
b. Perithecia without distinct necks over 80 μm tall formed from synchronously arising fused terminal hairs 4

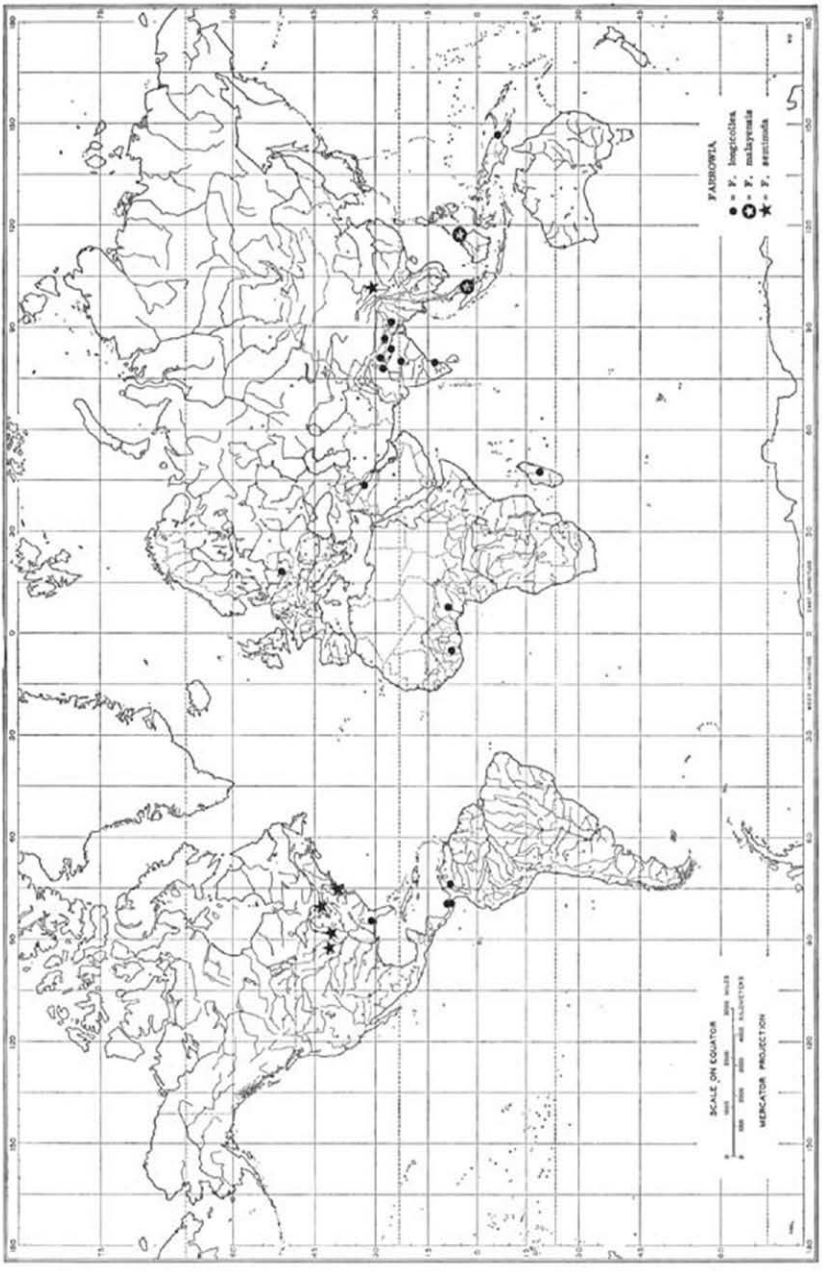
FABROMYIA
● = F. longicollata
○ = F. malayensis
★ = F. sessilanda
SCALE ON EQUATOR
MERCATOR PROJECTION

Fig. 1

3a. Terminal hairs (including fused portion) 850–2500 μm tall when mature; ascospores 8–12 × 8–10 μm. . . . . *Farrowia longicollea* (Krzem. & Badura) D. Hawksw., p. 174
b. Terminal hairs (including fused portion) 275–350(–400) μm tall when mature; ascospores 7–9(–10) × 7–8 μm. . . . . *Farrowia malaysiensis* D. Hawksw., p. 178
4a. Apex of perithecium composed of elongated cells forming a distinct but rudimentary neck; perithecia with a distinct pedestal-like tuft of rhizoidal hyphae; hairs not or scarcely ornamented; ascospores 7.5–9(–10) × 7–8.5 μm *Farrowia seminuda* (L. Ames) D. Hawksw., p. 182
b. Apex of perithecium not composed of elongated cells forming a rudimentary neck; perithecia lacking a distinct pedestal-like tuft of rhizoidal hyphae; hairs usually distinctly coarsely ornamented 5
5a. Terminal hairs flexuose, irregularly to dichotomously branched, not coiled; ascospores 6–7 × 4.5–6 μm [material not seen] . . . . . *Chaetomium pinnatum* L. Ames
b. Terminal hairs not as above 6
6a. Terminal hairs spirally or circinately coiled at least at the apices 7
b. Terminal hairs not distinctly spirally or circinately coiled 9
7a. Terminal hairs geniculately branched with circinately coiled apices; ascospores 6–8 × 4–6 μm [material not seen] . . . . . *Chaetomium distortum* L. Ames
b. Terminal hairs spirally coiled above 8
8a. Terminal hairs often branched, heads readily becoming detached; ascospores with quadrangular guttules, 5.5–8 × 5.5–6.5 μm . . . . . *Chaetomium bostrychodes* Zopf
b. Terminal hairs unbranched, heads not becoming detached; ascospores not guttulate, (4.5–)6–8 × 3.5–5 μm [aleuriospores not seen in isotype although reported by Ames (1963)] . . . . . *Chaetomium pulchellum* L. Ames
9a. Perithecia elongate to vasiform 10
b. Perithecia subglobose to ovoid. 11
10a. Terminal hairs forming a dense apical tuft, straight to somewhat recurved; ascospores ellipsoid, 7–8 × 6.5–8 μm . . . . . *Chaetomium brevipilium* L. Ames
b. Terminal hairs sparse, not forming a dense tuft; ascospores biumbonate, 7–9 × 5–7 μm [conidial state possibly not *Botryotrichum*; material not seen] *Chaetomium silvaticum* var. *variabile* Kiril.
11a. Ascospores 13–16 × 8.5–10.5 μm . . . . . *Chaetomium piluliferum* J. Daniels
b. Ascospores less than 12 μm long 12
12a. Terminal hairs straight, rigid, sparse; ascospores 5.5–7 × 4.5–6 μm *Chaetomium homopilatum* Omvik
b. Terminal hairs flexuous to undulate, abundant; ascospores 7–9.5 × 6.5–7.5 μm [material not seen] . . . . . *Chaetomium semispirale* Udagawa & Cain

Farrowia D. Hawksw., *gen. nov.*

Genus Pyrenomycetum (Sphaeriales, Chaetomiaceae). Perithecia dispersa, singularia, infra subglobosa ad obpyriformia, brunnea ad nigra; muris compositis e 2–3 stratis cellularum atrobrunnearum, polyedricarum sed elongatarum ad apicem; affixa ad substratum hyphis basi peritheciorum exorientibus, plerumque formantibus caespitem pedicello-similem; pila lateralia singularia, brunnea, recta, non ramosa, muris levibus instructa; pila terminalia

Fig. 1. The known world distribution of *Farrowia* species; records of *F. longicollea* from Iraq, Ivory Cost and Nigeria have not been accurately localized and dots have been placed centrally in those countries; literature records of *F. seminuda* from Angola and Israel are omitted as in need of confirmation. (Base map copyright The University of Chicago Press; for *F. malayensis* read *F. malaysiensis*.)

simul cellulis contiguis apice peritheciorum exorientia, infra fasceatim connata itaque collum formantia, supra secreta (sed in una specie rudimentalia), brunnea, recta, non ramosa, muris levibus praedita.

Asci exorientes in fasciculis basi cavositatis peritheciorum, clavati, unitunicati, deliquescentes ante sporarum maturitatem, octospori. Paraphyses desunt. Ascosporae irregulariter in asco dispositae, in cirrhum accumulatae demissae, late ellipsoideae, biapiculatae, cum uno poro subapicali germinativo, brunneae ad atrobrunneae, simplices, plerumque 1-guttulatae.

Aleurisporae ad *Botryotrichum* pertinentes, exorientes e hyphis hyalinis et prostratis, plerumque copiosae.

Culturae contaminatae centro plerumque pigmentum rubro-purpurascentem producentes.

SPECIES HOLOTYPICA: *Farrowia longicollea* (Krzem. & Badura) D. Hawksw. (syn. *Chaetomium longicolleum* Krzem. & Badura, *Chaetoceratostoma longirostre* Farrow).

Genus of Pyrenomycetes (Sphaeriales, Chaetomiaceae). Perithecia scattered, single, subglobose to obpyriform below, brown to black; peridium composed of 2–3 layers of cells, cells dark brown, polyhedral but becoming elongate towards the apex of the perithecium; attached to the substrate by hyphae originating from the base of the perithecium, often producing a pedestal-like tuft; lateral hairs arising singly, brown, straight, unbranched, smooth-walled (× 10,000); terminal hairs arising simultaneously from adjacent cells at the apex of the perithecium, fused and producing a distinct neck below but separating and single above (but in one species rudimentary), brown, straight, unbranched, smooth-walled (× 10,000).

Asci arising in a fascicle at the base of the perithecial cavity, clavate, unitunicate, deliquescing before the ascospores mature, eight-spored. Paraphyses absent. Ascospores irregularly arranged in the asci, discharged in a cirrhus through the neck formed by the terminal hairs, broadly ellipsoid, biapiculate, with a single subapical germ pore, brown to dark brown, simple, often 1-guttulate.

Aleuriospores belonging to the genus *Botryotrichum*, arising from hyaline, prostrate hyphae, often abundant.

Contaminated cultures often producing a reddish-purple pigment in the medium.

ETYMOLOGY.—Named after W. M. Farrow, the first author to recognise that the type species of the genus should be placed in a genus other than *Chaetomium*.

HOLOTYPE SPECIES.—*Farrowia longicollea* (Krzem. & Badura) D. Hawksw. (syn. *Chaetomium longicolleum* Krzem. & Badura, *Chaetoceratostoma longirostre* Farrow).

The genus is known to comprise three species and has representatives in Africa, Asia, Europe and Central, North and South America (Fig. 1). A key to the species is included in that to the perfect states of members of the Chaetomiaceae with *Botryotrichum*-like aleuriospores presented above (pp. 171–173). The characters separating the genus from *Chaetomium* and *Scopinella* are summarised in Table I and discussed in more detail on pp. 169–171.

Farrowia longicollea (Krzem. & Badura) D. Hawksw., *comb. nov.*—Fig. 2

Chaetomium longicolleum Krzem. & Badura *in* Acta Soc. Bot. Poloniae **23**: 748. 1954 (basionym). — *Chaetoceratostoma longicolleum* (Krzem. & Badura) Badura *in* Allionia **9**: 181. 1964. —

Fig. 2. *Farrowia longicollea*. — a. Perithecia. — b. Portion of the lower part of the "neck" region. — c. Origin of a lateral hair. — d. Rhizoidal hyphae. — e. Aleuriospores. — f. Ascospores. (From the holotype of *Chaetoceratostoma longirostre*, IA.)

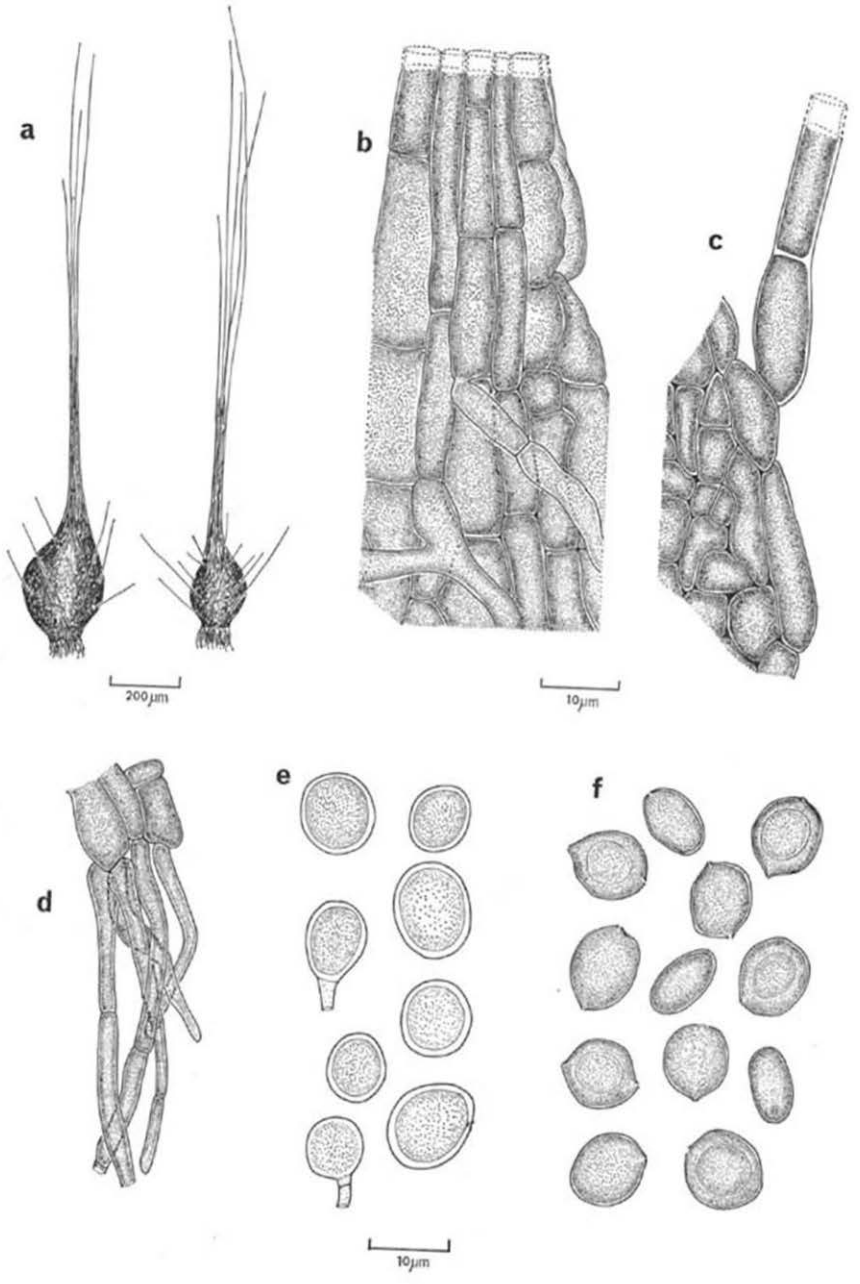

Fig. 2

Lectotype: Poland, Kieleckin Province [Kielce], Miechów, isol. ex soil from coniferous forest, 1947, *H. Krzemieniewska & L. Badura* (BPI-A 121, slide).

Chaetoceratostoma longirostre Farrow *in* Mycologia **47**: 418. 1955. — *Chaetomium longirostre* (Farrow) L. Ames, Monogr. Chaetom.: 29. 1963. — Holotype: Panamá Canal Zone, Barro Colorado Island, Rio Sardinilla, isol. ex soil, summer 1952, *G. W. Martin 8875* (IA). — Isotypes: ATCC 16959, BPI-A 122, CBS 155.55, DAOM 41854, IMI 184923, UCSW.

Perithecia superficial, scattered, arising singly, subglobose to obpyriform below, 135–200(–270) × 70–120 μm, dark brown to black, often somewhat shiny; peridium mainly 2–3 layers of cells thick, cells brown to dark brown, polyhedral, mainly 5–15 μm diam. except near the neck where they become elongated; pale brown ± vertically orientated rhizoidal hyphae arising from the base of the perithecium, forming a compact pedestal-like tuft usually 40–70 μm tall, hyphae rather thin-walled, undulate to contorted, mainly 2–4 μm diam.; lateral hairs arising singly from the peridium, brown, not fused in groups, straight, septate, unbranched, smooth-walled, mainly (150–)200–600(–650) μm tall, basal cell swollen and 5–8 μm diam., tapering above and 3–5 μm diam. for most of their length; terminal hairs arising synchronously from adjacent elongated ± rectangular cells at the apex of the perithecium, brown, straight, septate, unbranched, smooth-walled, 850–2500 μm tall, singly mainly 6–10 μm diam. at the base, tapering above and 3–5 μm diam. for most of their length, fused together for one third to one half of their length to form a tapering beak-like neck 35–55 μm diam. at the base and through the channel of which the ascospores are discharged; a few secondary 'supporting hyphae' may arise from peridial cells near the base of the neck.

Asci arising in a basal fascicle within the perithecial cavity, apparently not accompanied by lateral or hymenial paraphyses, unitunicate, clavate, short-stalked, thin-walled, deliquescing before the ascospores mature, (25–)40–60 × 10–20 μm, 8-spored. Ascospores irregularly arranged in the asci, accumulating in a cirrhus and discharged, often in ± parallel rows, through the neck-like fused portion of the terminal hairs, hyaline at first but becoming brown to dark brown when mature, subglobose to ellipsoid, usually distinctly 1-guttulate, simple, smooth-walled, bi-apiculate with a distinct often subapical germ-pore at one end, 8–12 × 8–10 μm in surface view, 6–7 μm wide in lateral view.

Aleuriospores almost always present, often abundant, *Botryotrichum*-like; conidiophores arising from hyaline, sparsely septate hyphae mainly 1–2.5 μm diam. spreading prostrately around the perithecia; conidiogenous cells integrated, terminal, determinate, monoblastic, cylindrical; conidia (aleuriospores) arising singly at the apices of the conidiogenous cells, usually hyaline but occassionally with a slight brownish tinge, simple, very thick-walled, smooth-walled, globose, sometimes with a somewhat flattened base, mainly 7–12(–15) μm diam.

Cultures growing fairly rapidly on most media (MA, OMA, PCA, PDA, TWA, etc.), usually attaining 4–5 cm diam. in eight weeks at room temperature; aerial mycelium, when present, flocculose, white to pale orange, composed of hyaline hyphae mainly 1–3.5 μm diam.; sectoring occuring in some strains, sectors sometimes producing non, or aberrant, ascocarps (cleistothecia 70–150 μm diam. with hairs to 150 μm long and 2.5–4(–8) μm diam. at the base, ascospores thin-walled and failing to mature) and sometimes no aleuriospores; in the presence of contaminant organisms a characteristic reddish-purple pigment is produced which diffuses into the agar and is readily visible in reverse; reverse otherwise ± uncoloured.

SUBSTRATE.—Known only from material in culture isolated from soils of various types, plant debris and fruits of *Arachis hypogaea*. Also reported by Agnihothrudu (1958) from the rhizospheres of *Camellia sinensis*, *Monochoria vaginalis* var. *plantaginea* and *Polygonum glabrum*.

ETYMOLOGY.—From Latin *longus*, long, and *collum*, neck.

ILLUSTRATIONS.—Agnihothrudu *in* Sci. Cult. **23**: 748 figs. A–E. 1958; Ames, Monogr. Chaet. pl. 24 figs. 1–2. 1963; Bartoli *in* Annali Bot. **31**: 45–47 figs. 1–10. 1972; Benedeck *in* Mycopath. Mycol. appl. **14**, Icon. mycol. pl. C 40 fig. 2 a–e. 1961; Cooke *in* Can. J. Bot. **50**: 1272–1273 pl. I figs. 1–15, II figs. 16–26. 1973; Doguet *in* Revue Mycol. **20** (Suppl. colon. 2): 135–141 figs. 1 a–l, 2 a–j, 3 a–h. 1955; Farrow *in* Mycologia **47**: 417–418 figs. 1–5. 1955; Hawksworth & Wells *in* Mycol. Pap. **134**: pl. 7 figs. C–D. 1973; Krzemieniewska & Badura *in* Acta Soc. Bot. Poloniae **23**: 780 pl. 2 figs. 2–4. 1954; Mazzucchetti, Gen. Chaetom.: 323 pl. 24 figs. 1–12. 1965; Seth *in* Beih. Nova Hedwigia **37**: fig. 37 a–d. 1972; Udagawa, Furuya & Horie *in* Bull. natn. Sci. Mus., Tokyo **16**: 511 fig. 14 a–f. 1973.

DISTRIBUTION.—I have examined material from Colombia, India, Iraq, Nigeria, Panamá and Poland. In addition there are reliable reports from the Ivory Coast (Bartoli, 1972), Madagascar (Doguet, 1955a, 1955b, 1959), New Guinea (Udagawa & al., 1973) and the U.S.A. (Georgia; Cooke, 1973). *Farrowia longicollea* appears to be not uncommon in India, from which country it was first reported by Agnihothrudu (1958) on the basis of three collections, and Farrow (1955) indicated that it was 'isolated frequently' in Panamá. The paper of Harvey & al. (1969) utilised isotype material derived from Ames (via H. K. Seth) and the source of that employed by Sedlar & al. (1973) is uncertain.

OTHER SPECIMENS EXAMINED.—COLOMBIA: near El Banco, c. 160 miles south of Barranquilla, 1965, leg. *Oxford Labs. (Chicago, Illinois)*, isol. ex plant debris on surface of soil-water culture, 3 Sept. 1966, *E. E. Davis* (ATCC 16509, IMI 186019). INDIA: Varanasi, Banaras Hindu University, comm. 31 Jan. 1967, *Singh & Pande 5* (IMI 137386); Aurangabad, Marathwade University, comm. 6 Febr. 1969, *L. V. Gangawane 2* (IMI 137648); Jabalpur, isol. ex grassland soil, comm. 22 Sept. 1971, *P. D. Agrawal 93* (IMI 160309); sine loc., isol. ex soil, comm. 12 April 1972, *V. Nair 8k* (IMI 165736*k*); Agra College, isol. ex soil, comm. 7 April 1974, *M. N. Gupta 20* (IMI 185148), *33* (IMI 185159). IRAQ: Bakoba Nursery, isol. ex soil, comm. 25 May 1968, *M. Majeed 6* (IMI 133629). NIGERIA: Samaru, Institute of Agricultural Research, isol. ex *Arachis hypogaea* fruits, comm. 6 Jan. 1966, *D. McDonald 807* (IMI 116862).

Doguet (1955a), Ames (1963) and Mazzucchetti (1965) endeavoured to separate *Chaetomium longicolleum* from *C. longirostre* on the basis of the latter having a longer neck and narrower spore-channel. This character varies considerably within single isolates, however, and material conforming to the lectotype of *C. longicolleum* occurs within isotype cultures of *C. longirostre*. Apart from in this feature, the perithecia of *F. longicollea* are very constant in their characters. The amount of aerial mycelium produced in culture varies according to the medium, more being formed on nutrient-rich than on nutrient-poor media. Of particular interest is the sectoring produced by one isolate (IMI 186019 = ATCC 16509) in which cleistothecia are produced. These cleistothecia, described above, arise in sectors lacking aleuriospores, have hairs distributed over their surface and fail to form ascospores. These were obtained from single-ascospore isolates from perithecia several times but perithecia were not produced by cleistothecial isolates or in subcultures prepared from them.

Although Farrow (1955) did not mention any aleuriospores in his original description of *Chaetoceratostoma longirostre*, these are in fact present in both the holotype collection and isotype cultures.

Farrowia longicollea has been the subject of detailed ontogenetic investigations by Doguet (1955a) and Cooke (1973). Doguet's studies showed a *Chaetomium*-like rather than a *Melanospora*-like pattern of development with perithecia originating from stalked ascogonial coils which become enveloped in hyphae growing up from the base of the stalk with the perithecial cavity forming by the deliquescence of pseudoparenchymatous cells. Periphyses occur in the upper portion of the perithecial cavity at first but appear to be lost as maturation proceeds. Cooke's investigations confirm Doguet's interpretation in all important respects but Cooke did not find any mycelial hairs although these are not uncommonly encountered in young cultures and have been figured by Doguet (1955a) and Bartoli (1972); Bartoli terms these 'setulae'. Cooke's opinion that the presence of mycelial hairs might afford a useful specific criterion in the *Chaetomiae* does not therefore appear to be well founded in at least this case.

Doguet (1955b) carried out some detailed studies on the production of the reddish-purple pigment in this species. Although the chemical nature of the compound concerned remains unknown, it is only produced in the presence of contaminant bacteria or fungi with saccharase enzymes which, on saccharose-rich media, permit *F. longicollea* to produce this pigment. Doguet suggested that this species might serve as a valuable indicator for saccharase within other organisms.

The reaction of the spores of this species to high temperatures has also been investigated by Doguet (1959) who found a few spores could survive a treatment of 61°C. Harvey & al. (1969), investigating spore liberation, found that most spores were liberated only under moist conditions, and Sedlar & al. (1973) confirmed that the species was homothallic, as reported by Doguet (1955a), on the basis of single-ascospore cultures.

Farrowia malaysiensis D. Hawksw., *sp. nov.*—Fig. 3

Perithecia superficialia, dispersa, infra subglobosa ad obpyriformia, 125–180 × 70–120 µm, atrobrunnea ad nigra, plerumque nifida; muris compositis e 2–3 stratis cellularum atrobrunnearum, polyedricarum, praecipue 6–14 µm diam. sed elongatarum ad apicem; affixa ad substratum hyphis brunneis, 2–5 µm diam., formantibus caespitem pedicellio usque 25–50 µm alto similem; pila lateralia singularia, brunnea, recta, non ramosa, muris levibus instructa, praecipue 50–150 µm longa; pila terminalia simul cellulis contiguis apice peritheciorum exorientia, 275–350(–400) µm longa, infra fasceatim connata itaque collum 25–40 µm latum formantia, supra secreta, brunnea, recta, non ramosa, muris levibus praedita.

Asci exorientes in fasciculis basi cavositatis peritheciorum, clavati, unitunicati, deliquescentes ante sporarum maturitatem, 20–35 × 8–16 µm, octospori. Paraphyses desunt. Ascosporae irregulariter in asco dispositae, in cirrhum accumulatae per collem demissae, late ellipsoideae, biapiculatae, cum uno poro subapicali germinativo, brunneae ad atrobrunneae, simplices, plerumque 1-guttulatae, 7–9(–10) × 7–8 µm, 4–6 µm latae aspectu laterali.

Fig. 3. *Farrowia malaysiensis*. — a. Perithecium. — b. Upper portion of the "neck" region. — c. Origin of a lateral hair. — d. Rhizoidal hyphae. — e. Asci in various stages of maturation. — f. Aleuriospores. — g. Ascospores. (From the holotype, IMI 183184.)

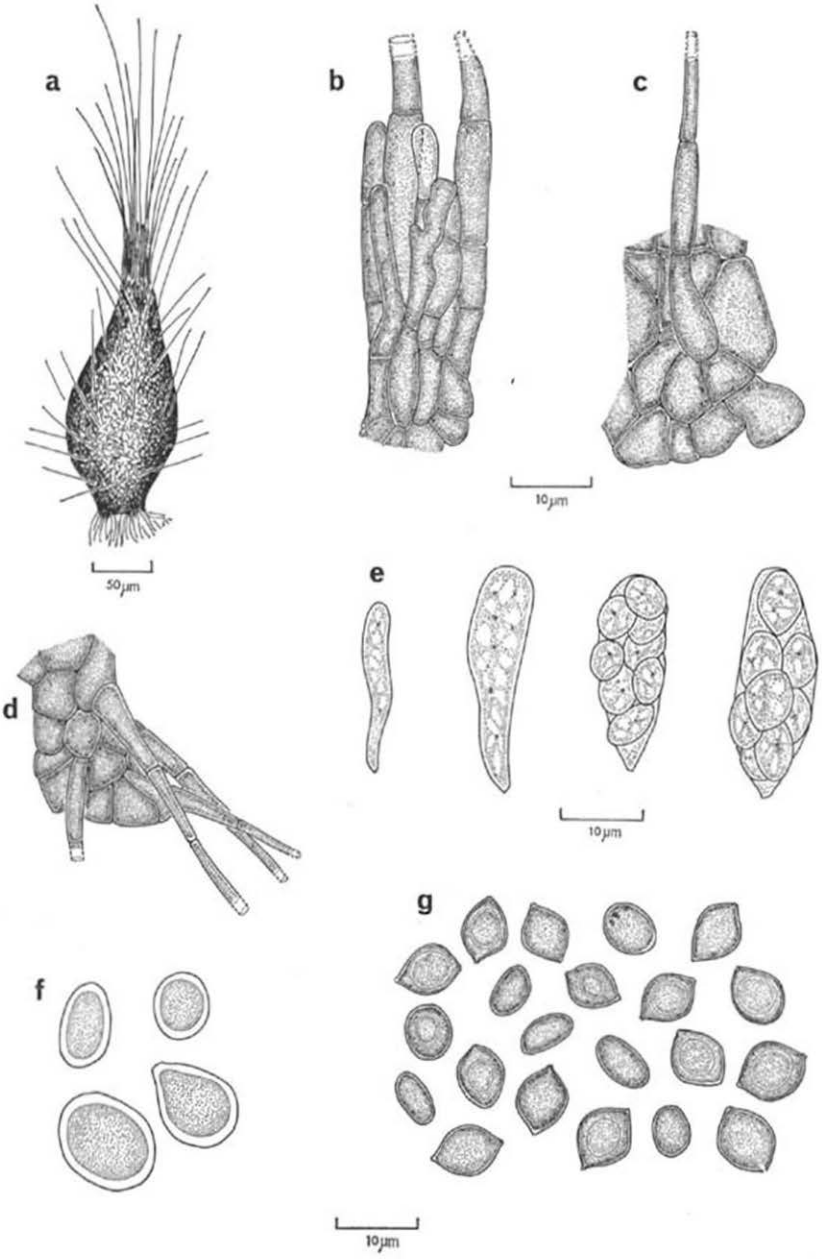

Fig. 3.

Aleuriosporae ad *Botryotrichum* pertinentes, hyphis hyalinis et prostratis exorientes, globosae vel subglobosae, muris crassis munitae, hyalinae, praecipue 5–15 μm diam., plerumque sparsae.

Culturae ad 4.5–5.5 cm diam. post 8 hebdomades, mycelium aerium floccosum, albidum ad pallide aurantiacum vel plusminusve absens; culturae contaminatae centro pigmentum rubro-purpurascentem plerumque producentes.

HOLOTYPUS: Malaysia occidentalis, Malaya, Selangor, Malaysian Agricultural Research and Development Institute, isol. ex *Elaeis guineensis*, comm. 19. iii. 1974, *Tai Luang Huan K* (IMI 183184).

Perithecia superficial, scattered, arising singly, subglobose to obpyriform below, 125–180 × 70–120 μm, dark brown to black, often somewhat shiny; peridium mainly 2–3 layers of cells thick, cells brown to dark brown, polyhedral, mainly 6–14 μm diam. except near the neck where they become elongated; pale brown to brown ± vertically orientated entwined rhizoidal hyphae arising from the base of the perithecium, forming a compact pedestal-like tuft usually 25–50 μm tall, hyphae rather thin walled, mainly 2–5 μm diam.; lateral hairs arising singly from the peridium, brown, not fused in groups, straight, septate, unbranched, smooth-walled, 50–150 μm tall, basal cell swollen and 5–6 μm diam., tapering above and 2–3.5 μm diam. for most of their length; terminal hairs arising synchronously from adjacent elongated ± rectangular cells at the apex of the perithecium, brown, straight, septate, unbranched, smooth-walled, 275–350(–400) μm tall, singly mainly 5–7 μm diam. at the base, tapering above and 2–4 μm diam. for most of their length, fused together for one third to one half of their length to form a tapering beak-like neck 25–40 μm diam. at the base and through the channel of which the ascospores are discharged; secondary 'supporting hyphae' arising from peridial cells near the base of the neck absent or poorly developed.

Asci arising in a basal fascicle within the perithecial cavity, apparently not accompanied by lateral or hymenial paraphyses, unitunicate, clavate, short-stalked, thin-walled, deliquescing before the ascospores mature, 20–35 × 8–16 μm, 8-spored. Ascospores irregularly arranged in the asci, accumulating in a cirrhus and discharged through the neck-like fused portion of the terminal hairs, hyaline at first but becoming brown to dark brown when mature, subglobose to ellipsoid, usually distinctly 1-guttulate, simple, smooth-walled, bi-apiculate with a distinct often subapical germ pore at one end, 7–9(–10) × 7–8 μm in surface view, 4–6 μm wide in lateral view.

Aleuriospores usually present but often rather sparse, *Botryotrichum*-like; conidiophores arising from hyaline, sparsely septate hyphae mainly 1–3 μm diam. spreading prostrately around the perithecia; conidiogenous cells integrated, terminal, determinate, monoblastic, cylindrical; conidia (aleuriospores) arising singly at the apices of the conidiogenous cells, usually hyaline, simple, very thick-walled, globose, sometimes with a slightly flattened base, mainly 5–15 μm diam.

Cultures growing fairly rapidly on most media (MA, PCA, PDA, TWA, etc.), usually attaining 4.5–5.5 cm diam. in eight weeks at room temperature; aerial mycelium when present, flocculose, white to pale orange, composed of hyaline hyphae mainly 1–4 μm diam; sectoring not seen; in the presence of contaminant organisms a characteristic reddish-purple pigment is produced which diffuses into the agar and is readily visible in reverse; reverse otherwise ± uncoloured.

HOLOTYPE.—West Malaysia, Malaya, Selangor, Malaysian Agricultural Research and Development Institute, isol. ex *Elaeis guineensis*, comm. 19 March 1974, *Tai Luang Huan K* (IMI 183184).

SUBSTRATE.—Known only from material in culture isolated from *Elaeis guineensis*, *Theobroma cacao* and *Uncaria gambir*.

ETYMOLOGY.—*Malaysiensis*, from Malaysia.

DISTRIBUTION.—Known only from East Malaysia (Sabah) and West Malaysia (Malaya).

OTHER SPECIMENS EXAMINED.—EAST MALAYSIA: Sabah (North Borneo), isol. ex *Theobroma cacao*, comm. 30 Oct. 1973, *P.S.W. Liu PP1425/60* (IMI 180057).

WEST MALAYSIA: Malaya, Kuala Lumpur, isol. ex *Uncaria gambir*, comm. 26 Dec. 1969, *Chee Keng Hoy 1162* (IMI 145691).

Farrowia malaysiensis is a distinctive species very similar to *F. longicollea* in most respects but differing in having a much shorter neck and terminal hairs and also in the ascospores being slightly smaller. It may also differ in being restricted to Malaysia (from which *F. longicollea* is unknown, although that species does occur in New Guinea) and has so far not been isolated from soil.

Farrowia seminuda (L. Ames) D. Hawksw., *comb. nov.*—Fig. 4.

Chaetomium seminudum L. Ames *in* Mycologia **41**: 642. 1949 (basionym). — Holotype: U.S.A., Iowa, Ames, Iowa State College, isol. ex vegetable detritus, *J. C. Gilman* (BPI-A 153, slide). — Isotype: DAOM 24579.

Perithecia superficial, scattered, arising singly, obpyriform, (125–)150–180(–200) × 75–100(–110) μm, yellowish brown and somewhat translucent at first, becoming darker brown when mature; peridium mainly 2–3 layers of cells thick, cells brown, polyhedral, mainly 7–15 μm diam. except near the neck where they become elongated; pale brown ± vertically orientated rhizoidal hyphae arising from the base of the perithecium, forming a short spreading to pedestal-like tuft, hyphae rather thin-walled, undulate, mainly 2–5 μm diam.; lateral hairs arising singly from the peridium, pale brown to brown, not fused in groups, straight, septate, unbranched, smooth-walled or with a slight rugose ornamentation near the base, mainly 70–100 μm tall, basal cell somewhat swollen and 5–6 μm diam., tapering above and 2–3.5 μm diam., for most of their length; terminal hairs rudimentary, arising ± synchronously from adjacent elongated ± rectangular cells at the apex of the perithecium, pale brown to brown, straight, septate, unbranched, ± smooth-walled, (some exceptionally to 75 μm tall, singly mainly 5–6 μm diam. at the base, tapering above and (1.5–) 2–3.5 μm diam. for most of their length), ± fused together below to form a short neck-like structure mainly 10–25 μm tall and 20–30 μm wide and through which the ascospores are discharged in long tendrils; secondary "supporting hyphae" absent.

Asci arising in a basal fascicle within the perithecial cavity, apparently not accompanied by lateral or hymenial paraphyses, unitunicate, clavate, short-stalked, thin-walled, deliquescing before the ascospores mature, 25–32 × 10–15 μm, 8-spored. Ascospores irregularly arranged in the asci, accumulating in a cirrhus and discharged through the short neck, hyaline at first but becoming brown to dark brown when mature, subglobose to ellipsoid, usually 1-guttulate, simple, smooth-walled, biapiculate with a distinct often subapical germ pore at one end, 7.5–9(–10) × 7–8.5 μm in surface view, 4–6 μm wide in lateral view.

Aleuriospores almost always present and abundant, *Botryotrichum*-like; conidiophores arising from hyaline, sparsely septate hyphae mainly 1.5–3 μm diam. spreading prostrately around the perithecia; conidiogenous cells integrated, terminal, determinate, monoblastic, cylindrical; conidia (aleuriospores) arising singly at the apices of the conidiogenous cells, hyaline or with a slight fuscous-brown tinge, simple,

very thick-walled, smooth-walled, sometimes slightly flattened at the base, mainly 7–10 μm diam.

Cultures growing fairly rapidly on most media (MA, PCA, PDA, TWA, etc.) usually attaining about 5.5–7 cm diam. in eight weeks at room temperature; aerial mycelium, when present, flocculose, white, composed of hyaline hyphae mainly 1–3.5 μm diam.; sectoring not seen; no reddish pigment diffusing into the agar seen; reverse ± uncoloured or with a slight orange tinge.

SUBSTRATE.—Known only from material in culture isolated from dung, soil, vegetable detritus and seeds of *Lycopersicum esculentum*.

ETYMOLOGY.—From Latin *semi-*, half, and *nudus*, naked.

ILLUSTRATIONS.—Ames *in* Mycologia **41**: 643 figs. 23–29. 1949; Ames, Monogr. Chaet. pl. 24 Figs. 13–19. 1963; Mazzucchetti, Gen. Chaetom.: 323 pl. 24 Fig. 13–19. 1965; Seth *in* Beih. Nova Hedwigia **37**: fig. 51. 1972; Skolko & Groves *in* Can. J. Bot. **31**: pl. 2 figs. 1–4, pl. 13 fig 10. 1953.

DISTRIBUTION.—I have examined material from Canada (Ontario), China (prov. Szechwan) and the U.S.A. (Iowa and Pennsylvania). There are also published reports from Illinois (Parker, 1973), Angola (Sedlar & al., 1973) and Israel (Sedlar & al., 1973); these latter two records are in need of confirmation.

OTHER SPECIMENS EXAMINED.—CANADA: Ontario, Guelph, isol. ex soil in mixed wood, Aug. 1964, *G. L. Barron* (IMI 109880, OAC 10275).

CHINA: prov. Szechwan, Lushan, isol. ex leaf fragments in soil, 1958, *G. Sörgel 8517* (IMI 75854).

U.S.A.: Pennsylvania, Philadelphia, isol. ex seeds of *Lycopersicum esculentum*, 5 July 1943, *A. J. Skolko* (DAOM 15042, IMI 44209).

This species is being included in *Farrowia* with some reservations as placing it here broadens the circumscription of the genus and accounts for most of the 'usually' phrases in the generic description. While *F. seminuda* has almost all the characters seen in the other two species they tend to be of a rather rudimentary nature. At first sight this species is very similar to some other taxa in *Chaetomium*: *C. deceptivum* Malloch & Benny (ascospores 18–23×7.5–10 μm), *C. homopilatum* Omvik (aleuriospores; ascospores 5.5–7×4.5–6 μm), *C. minutum* Krzem. & Badura (ascospores 9.5–11×7–9 μm; treated by Badura, 1964, as a synonym of *C. seminudum*), *C. parvotrichum* Mazz. (material not seen; ascospores 9.3–11.5×6–6.5 μm), *C. subterraneum* Swift & Povah (material not seen; ascospores 7–10×5–7 μm) and *C. thielavioideum* Chen (material not seen; ascospores 13–15×6–7.5 μm). All these six species appear to have distinctly ornamented hairs (in those studied), ± no terminal hairs, and pale, almost translucent peridia (as do young perithecia of *F. seminuda*). They recall the genus *Achaetomiella* Arx (i.e. *A. macrospora* (Rai & al.) Arx, *A. megaspora* (Sörgel) D. Hawksw., *A. virescens* Arx and some undescribed taxa) in many respects and are currently being investigated further to ascertain their most appropriate generic position. None of these taxa, however, have a neck like that seen in *F. seminuda* and only one (*C. homopilatum*) produces aleuriospores. That perithecial development in

Fig. 4. *Farrowia seminuda*. — a. Perithecia. — b. The "neck" region of a perithecium. — c. Rhizoidal hyphae. — d. Asci in different stages of maturation. — e. Aleuriospores. — f. Ascospores. (From IMI 44209.)

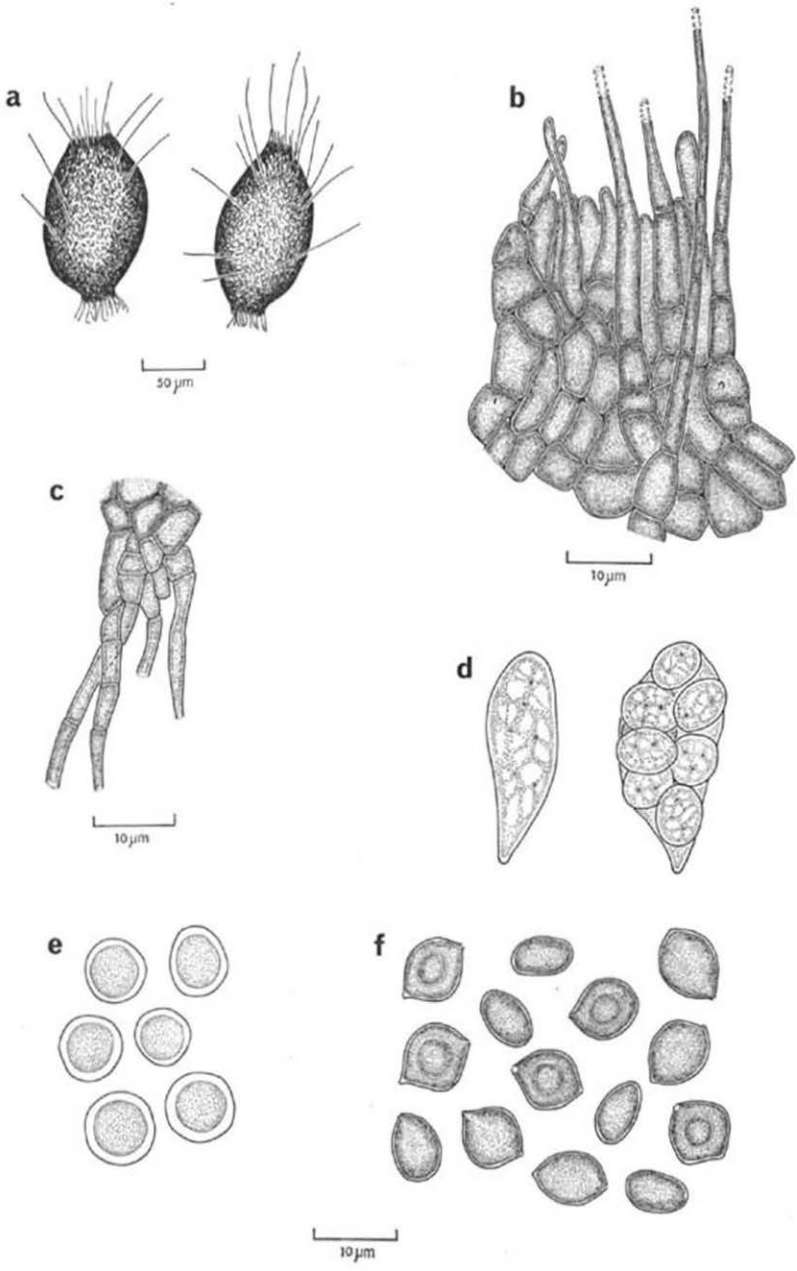

Fig. 4.

F. longicollea passes through a stage which is very like the mature perithecia of *F. seminuda* appears to add weight to its treatment in *Farrowia*, but the possibility of parallel evolution cannot be entirely ruled out.

Skolko & Groves (1953) compared the species to *C. torulosum* Bain. (a taxon with some similarities to the reportedly aleuriospore forming *C. brevipilium* L. Ames), but that species appears quite distinct from *F. seminuda* in many characters. These authors also pointed out that the measurements of the ascospores given by Ames (1949) of 9–14 × 7–8 μm were incorrect — something apparently overlooked by Seth (1972). My examination of the holotype slide shows that Skolko & Groves' conclusion was indeed correct. The holotype slide is unfortunately not in a very good condition and the description presented above is consequently based primarily on other specimens examined (including IMI 44209 compared with cultures from the type by Skolko & Groves, 1953).

This species was reported to be homothallic by Tveit (1955), who studied IMI 44209, and the same conclusion was reached by Sedlar & al. (1973) on the basis of material from Angola and Israel they considered to belong to this species.

ACKNOWLEDGEMENTS

I am very grateful to the directors and curators of the herbaria cited in the text for the loan of material in their care, and particularly to Dr. P. L. Lentz for sorting out various material from amongst Ames' collections now in BPI. Dr. R. A. Maas Geesteranus kindly checked the Latin diagnoses.

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STUDIEN AN CYSTIDEN—I

Subulicystidium Parm.

W. JÜLICH
Rijksherbarium, Leiden

(Mit den Tafeln 31–33)

Die Cystiden der Gattung *Subulicystidium* wurden mit dem Raster-Elektronenmikroskop untersucht. Dabei zeigte es sich, daß die Ornamentation, die im Lichtmikroskop aus vier Reihen von Kristallen gebildet zu werden scheint, in Wirklichkeit aus zwei Reihen bandförmiger Strukturen besteht, die quer zur Hauptachse der Cystiden angeordnet sind und deren freie Enden doppelbrechend sind. Ein Schlüssel zu den drei Arten wird gegeben, eine Neukombination wird gemacht.

Vor einiger Zeit begann ich mit Untersuchungen der Oberflächenstrukturen von Sporen, Cystiden und Haaren der Aphyllophorales, wobei besonderer Nachdruck auf die Arten der Corticiaceae und Thelephoraceae gelegt wurde. Was die Cystiden betrifft, so können bereits jetzt verschiedene Typen unterschieden werden, von denen einer, der ausschließlich von der Gattung *Subulicystidium* Parm. her bekannt ist, hier beschrieben werden soll.

Die Gattung *Subulicystidium* Parm. (Corticiaceae) ist u.a. charakterisiert durch lang-zylindrische, apikal zugespitzte Cystiden, die (bei flüchtiger Untersuchung im Lichtmikroskop) stäbchenförmige Kristalle aufweisen, die normalerweise in vier Längsreihen angeordnet zu sein scheinen. Überraschend ergaben Beobachtungen mit dem Raster-Elektronenmikroskop, daß in Wirklichkeit zwei Reihen breitbandförmiger Strukturen vorhanden sind.

Der größte Teil dieser Strukturen ist mit der Cystidenwand verwachsen; die seitlichen Enden dagegen sind frei und etwas zurückgebogen. Diese Randabschnitte sind stark lichtbrechend, sowohl im Hellfeld wie im polarisierten Licht deutlich sichtbar und haben bisher jeden Untersucher zu der vorschnellen Annahme verführt, daß vier Reihen stäbchenförmiger Kristalle vorliegen. Eine erneute lichtmikroskopische Untersuchung ergab, daß auch im Hellfeld diese Strukturen sichtbar sind, zumindest dann, wenn man weiß, wie sie auszusehen haben.

Mehrere Proben der kosmopolitisch verbreiteten Art *Subulicystidium longisporum* (Pat.) Parm. wurden im Raster-Elektronenmikroskop untersucht, alle zeigten sie im Prinzip die gleichen Oberflächenstrukturen an den Cystiden. Das Grundprinzip ist eine quer zur Hauptachse der Cystide liegende bandförmige Struktur, deren Seiten frei von der Cystidenwand abstehen. Diese seitlichen Enden sind meistens gerade und häufig etwas in Richtung der Cystidenachse verlängert; in der Mitte ist nicht selten eine flach-kreisförmige Erhebung sichtbar. In alten Fruchtkörpern oder an älteren

Cystiden sind die seitlichen Enden dieser bandförmigen Strukturen häufig abgerundet, die Bänder sind außerdem etwas dicker und weisen in der Mitte zusätzlich-konzentrische oder schneckenförmige Ablagerungen auf; auch bei diesen Cystiden sind hauptsächlich die frei abstehenden seitlichen Teile dieser Bänder im Lichtmikroskop sichtbar. Die Spitze der Cystiden weist mehrere langgestreckt-stabförmige, stark lichtbrechende Strukturen auf, die aber häufig von einer amorphen Masse überlagert sind, die in KOH schnell aufgelöst wird.

Von Bourdot & Galzin (1928) wurden mehrere Varietäten von *Peniophora longispora* (Pat.) Höhn. beschrieben, alle ausgestattet mit dem gleichen Cystidentyp, aber etwas unterschiedlichen anderen mikroskopschen Merkmalen. Einige dieser Varietäten konnten untersucht werden und erwiesen sich als identisch mit *S. longisporum* (Pat.) Parm.:

Die Taxa *Peniophora longispora* var. *clavispora* Bourd. & Galz. und var. *cylindrispora* Bourd. & Galz. wurden für Proben mit etwas abweichender Sporenform aufgestellt. Die langgestreckten, schmalen Sporen von *S. longisporum* sind aber in der Form auch innerhalb einer Probe nicht konstant, sie können zylindrisch, mit deutlich abgerundeten Enden sein (var. *obtusispora* Bourd. & Galz. in herb.), oder leicht fusiform bzw. schmal clavat, gerade oder etwas allantoid; die beiden ober erwähnten Varietäten können daher nicht akzeptiert werden. Die var. *gloeocystidiata* Bourd. & Galz. soll durch schmale Gloeocystiden ausgezeichnet sein: diese konnten in zwei authentischen Proben nicht gefunden werden, wohl aber waren unter den normalen Cystiden auch solche mit gelblichem Cytoplasma. Ich vermute, daß Bourdot & Galzin diese Cystiden gemeint haben, bin aber gleichzeitig davon überzeugt, daß es sich hierbei lediglich um alte oder sonstwie gestörte Fruchtkörper handelt. Die Fruchtkörper von *S. longisporum* sind recht variabel, normalerweise sind sie hellgrau gefärbt und sehr dünn häutchenförmig, gelegentlich können sie aber auch dicklich-hypochnoid bis membranös werden, mit hellgrauer bis leicht gelblicher Farbe (var. *lutescens* Bourd. & Galz. in herb.), oder aber das Subiculum ist stark vorherrschend mit gleichzeitig gering entwickelter Hymenialschicht (var. *mycelialis* Bourd. & Galz.); stets ist der Fruchtkörper leicht vom Substrat ablösbar. Alle genannten Varietäten können nicht als eigene Taxa anerkannt werden. Über die von J. Rick beschriebene Varietät "*macrosporus*" kann nichts mitgeteilt werden, da kein Material zur Untersuchung zur Verfügung stand.

Von besonderem Interesse ist ein imperfektes Stadium, das 1928 von Bourdot & Galzin unter dem Namen *Aegerita tortuosa* beschrieben wurde. Es handelt sich hierbei um etwa 0.1 mm große, etwa kugelige Gebilde, die nur selten gesammelt wurden, stets aber in unmittelbarer Nachbarschaft von *S. longisporum* (Pat.) Parm. Sie bestehen aus dicht verflochtenen Hyphen, die an der Oberfläche der *Aegerita* kleine keulenförmige Zellen bilden, die in der Form unreifen Basidien ähneln. Interessant und für die eindeutige Zuordnung zum perfekten Stadium von besonderer Bedeutung sind die langen Cystiden, die nach allen Seiten aus der Hyphenmasse herauswachsen; diese sind sowohl im Licht- wie im Raster-Elektronenmikroskop nicht von den Cystiden des perfekten Stadiums zu unterscheiden. Da dieser Cystidentyp einmalig

ist, kann an der Zuordnung von *Aegerita tortuosa* Bourd. & Galz. zu *S. longisporum* (Pat.) Parm. kein Zweifel bestehen.

Von *S. nikau* (G. Cunn.) Jülich wurden die Cystiden nur im Lichtmikroskop untersucht und zeigten dort die gleichen bandförmigen Strukturen wie bei *S. longisporum*. Dagegen konnte von der afrikanischen Art *S. brachysporum* (Talbot & Green) Material im Raster-Elektronenmikroskop untersucht werden. Die Cystiden dieser Art zeigen ebenfalls die gleichen Oberflächenstrukturen, wie sie offensichtlich kennzeichnend für die Gattung *Subulicystidium* sind. Die Anschwellung an der Basis der Cystiden ist nicht immer so deutlich entwickelt, kommt im übrigen aber auch gelegentlich bei *S. longisporum* vor.

Die Gattung *Subulicystidium* Parm. besteht nun aus den folgenden drei Arten, von denen *S. longisporum* (Pat.) Parm. eine kosmopolitische Verbreitung zeigt, während *S. nikau* (G. Cunn.) Jülich bisher ausschließlich von Neu-Seeland bekannt ist. Die ursprünglich aus Süd-Afrika beschriebene Art *S. brachyspora* (Talbot & Green) ist offensichtlich in Afrika weiter verbreitet, wie je eine untersuchte Probe aus Nigeria und Sierra Leone zeigte.

SUBULICYSTIDIUM LONGISPORUM (Pat.) Parm.

Hypochnus longisporus Pat. *in* J. Bot., Paris (ed. Morot) **8**: 221. 1894. — *Kneiffia longispora* (Pat.) Bres. *in* Annls mycol. **1**: 105. 1903. — *Peniophora longispora* (Pat.) Höhn. *in* Annls mycol. **3**: 325. 1905. — *Subulicystidium longisporum* (Pat.) Parm., Consp. Syst. Cortic.: 121. 1968.

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Peniophora longispora var. *cylindrospora* Bourd. & Galz. *in* Bull. trimest. Soc. mycol. Fr. **28**: 392. 1913.

Peniophora longispora var. *gloeocystidiata* Bourd. & Galz. *in* Bull. trimest. Soc. mycol. Fr. **28**: 392. 1913.

Peniophora longispora var. *lutescens* Bourd. & Galz. in herb.

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Peniophora longispora var. *obtusispora* Bourd. & Galz. in herb.

IMPERFEKTES STADIUM.—*Aegerita tortuosa* Bourd. & Galz., Hym. Fr.: 298. 1928.

SUBULICYSTIDIUM NIKAU (G. Cunn.) Jülich

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

Peniophora sororia G. Cunn. *in* Trans. R. Soc. N. Zeal. **83**: 280. 1955; non ∽ Bourd. & Galz. 1913.

Subulicystidium brachysporum (Talbot & Green) Jülich, *comb. nov.*

Peniophora longispora var. *brachyspora* Talbot & Green *apud* Talbot *in* Bothalia **7**: 148–149. 1958 (basionym).

Ein Schlüssel zu den drei Arten sei zur Erleichterung der Bestimmung gegeben:

1a. Sporen breit-ellipsoidisch, 6.5–8.5 × 3–4.5 µm. Hyphen 3–4 µm breit. Basidien 16–20 × 4–5 µm. Cystiden 60–80 × 5–7 µm. Neu-Seeland . . . . . *S. nikau* (G. Cunn.) Jülich
b. Sporen schmaler, langgestreckt ellipsoidisch oder cylindrisch 2
2a. Sporen 10–16–19 × 1.5–3 µm. Hyphen 2.5–4 µm breit. Basidien 15–25 × 4–5 µm. Cystiden 40–80 × 4–5 µm. Kosmopolitisch. . . . . *S. longisporum* (Pat.) Parm.
b. Sporen 6.5–7.5 × 2–3 µm. Hyphen 2.5–3.2 µm. Basidien 13–17 × 3–4 µm. Cystiden 40–70–80 × 3–3.5 µm. Afrika . . . . . *S. brachysporum* (Talbot & Green) Jülich

SUMMARY

The cystidia of the genus *Subulicystidium* have been studied with the scanning electron microscope. Their ornamentation consists of two rows of ribbon-shaped structures, arranged crosswise to the main axis of the cystidia. The free ends of these structures are double-refractive and have formerly been described as 'four rows of short crystals'. A key to the accepted three species is given; one new combination is proposed.

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ERKLÄRUNGEN ZU DEN TAFELN 31–33

TAFEL 31

Abb. A–E. *Subulicystidium longisporum*. — A. Übersichtsaufnahme des Hymeniums mit weit herausragenden Cystiden (× 58). — B. Cystiden im Lichtmikroskop (Hellfeld; × 2700). — C. Cystiden im Lichtmikroskop (polarisiertes Licht; × 2700). — D. Imperfektes Stadium *Aegerita tortuosa* (× 58). — E. Übersichtsaufnahme des imperfekten Stadiums (× 2). (Abb. A–C nach L 971.265–115; Abb. D–E nach *Donk 3764*, L).

TAFEL 32

Abb. A–E. *Subulicystidium longisporum*. — Cystiden des perfekten Stadiums. Abb. A, C und D zeigen die typische Ausbildung der Oberflächenstruktur, in Abb. B sind relativ junge, in Abb. E relativ alte Strukturen sichtbar. (Abb. A × 2000; Abb. B, D und E × 5000; Abb. C × 10000; alle Abb. nach *Jülich 1144*, Herb. Jülich).

TAFEL 33

Abb. A–F. *Subulicystidium longisporum*. — Cystiden des imperfekten Stadiums, *Aegerita tortuosa*. (Abb. A und B × 2050; Abb. C × 520; Abb. D × 5200; Abb. E und F × 10000; alle Abb. nach *Donk 3764*, L).

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REVISION OF MICROASCUS WITH THE DESCRIPTION OF A NEW SPECIES

J. A. VON ARX

Centraalbureau voor Schimmelcultures, Baarn

(With one Text-figure)

The genus *Microascus* is redescribed. It now comprises species with ostiolate, dark ascomata and small, asymmetrical, one-celled, smooth, yellow ascospores with a single germ pore at the base. The conidial states fit *Scopulariopsis* or *Wardomyces*. A key is given to 11 accepted species and two similar species of *Kernia* and *Chaetomium*. A fungus isolated from soil in West Africa is described as *Microascus senegalensis*. A list of 7 excluded or doubtful species is added.

The Microascaceae sensu Malloch (1970) represent a natural group of Ascomycetes related to the Ophiostomataceae and the Melanosporaceae. The family is characterized mainly by the ascospores which are small, 1-celled, smooth, dextrinoid when young, yellowish or reddish brown when ripe, and often have one or two germ pores. The ascomata are usually dark, spherical or flask-shaped and ostiolate or non-ostiolate. Malloch (1970) distinguished the genera *Kernia*, *Lophotrichus*, *Petriella*, *Petriellidium* and *Microascus*. The last-mentioned genus, however, proved to be heterogeneous, as was shown by von Arx (1973a, b). Typical *Microascus* species form ascomata with a cylindrical ostiolum, have small, short, often curved or angular ascospores with an often prominent germ pore and include a *Scopulariopsis*-conidial state. Von Arx (1973a) classified species without conidial states, such as *Microascus nidicola*, in a new genus *Pithoascus*, which also is characterized by thick-walled, inconspicuously ostiolate or non-ostiolate ascomata and by narrow ascospores in which no germ pores could be observed. The genus *Pithoascus* was described in detail by von Arx (1973b), comprising six soil-borne or entomogenous species.

The genus *Microascus* was monographed by Barron & al. (1961) and again by Morton & Smith (1963). The former authors accepted 13 species, the latter reduced this number and accepted only 10, of which, however, *M. lunasporus* and *M. pedrosoi* are doubtful.

The following concept of the genus and species is based on a study of all cultures present in the CBS-collection (see CBS, List of Cultures, 1972), supplemented with a number of strains sent by Dr. G. F. Orr (Dugway) and with some freshly isolated strains.

MICROASCUS Zukal

Microascus Zukal *in* Verh. zool.-bot. Ges. Wien **35**: 339. 1888.
Fairmania Sacc. *in* Annls mycol. **4**: 276. 1906.
Nephrospora Loubière *in* C.r. hebd. Séanc. Acad. Sci., Paris **177**: 211. 1923.
Peristomium Lechmère *in* Bull. trim. Soc. mycol. Fr. **29**: 307. 1913.

Colonies rather spreading, soon becoming brown by pigmented aerial mycelium; ascomata superficial or immersed at the base, spherical or flask-shaped, with a papilla-like or cylindrical ostiolum, brown or black, often hairy or setose, especially around the ostiolum, with a pseudoparenchymatous wall composed of 3–6 layers of isodiametric or slightly flattened, dark cells; asci numerous, clustered or catenulate, often in vertical rows, obovoid or broadly clavate, 8-spored, evanescent; ascospores asymmetrical, often reniform, heart-shaped or triangular, one-celled, smooth, dextrinoid when young, yellowish or straw coloured when mature, with a single, small, but often prominent germ pore at the base.

CONIDIAL STATE.—*Scopulariopsis* or *Wardomyces*.

TYPE SPECIES.—*M. longirostris* Zukal.

Ascospores with 2 germ pores, as indicated by Malloch (1970), could never be observed. In some species the germ pore is rather indistinct, but its position can be observed during ascospore germination; a single germ tube is formed.

Freshly isolated strains often form mainly the ascigerous state and hardly any conidia. Such strains can be recognized as *Microascus*, delimited from *Pithoascus* by the size and shape of the ascospores and by cultural characters, especially the formation of aerial mycelium. After many transfers the strains may become mainly conidial.

KEY TO THE SPECIES (derived from Barron & al., 1961)

1a. Ascospores triangular or quadrangular in planar view 2
b. Ascospores reniform, falcate or heart-shaped in planar view 5
2a. Ascospores triangular or quadrangular in planar view, often nearly square; colonies spreading, becoming dark . . . . . *M. pyramidus*, p. 193
b. Ascospores triangular in planar view; colonies rather restricted. 3
3a. Ascospores 8–12 µm long, brown. . . . . *Chaetomium trigonosporum*, p. 193
b. Ascospores shorter than 7 µm, yellow. 4
4a. Ascospores 3–5 µm in size . . . . . *M. trigonosporus*, p. 193
b. Ascospores 5–7 µm in size. . . . . *M. trigonosporus* var. *macrosporus*, p. 193
5a. Ascospores about twice as long as broad, usually planoconvex 6
b. Ascospores less than twice as long as broad, usually concavo-convex 7
6a. Ascospores 5–7 × 2.5–4 µm; conidia 3.5–5 × 2–3 µm, thin-walled . . *M. cinereus*, p. 194
b. Ascospores 7–9 × 4–4.5 µm; conidia 4.5–5.5 × 3.5–4.5 µm, rather thick-walled, brown *M. senegalensis*, p. 194
7a. Ascospores 3–4 × 2.5–3.5 µm . . . . . *M. longirostris*, p. 193
b. Ascospores 4–7 µm long 8
8a. Ascomata 500–700 µm in diameter, with an elongated beak; conidial state belonging to *Wardomyces* . . . . . *M. giganteus*, p. 193
b. Ascomata smaller; conidial state belonging to *Scopulariopsis* 9
9a. Ascomata non-ostiolate; conidia narrow, 4–12 × 2–4 µm. . . *Kernia hippocrepida*, p. 194
b. Ascomata usually ostiolate; conidia usually wider or shorter 10
10a. Conidia finely striate, 4–7 × 3–4 µm; ascospores heart-shaped in planar view, 5–7 × 5–7 µm, ascomata with an often inconspicuous ostiolum . . . . . *M. singularis*, p. 193
b. Conidia not striate; ascospores usually smaller; ascomata with a distinct ostiolum 11
11a. Colonies greyish; ascospores 4–6 × 3.5–5.5 µm; conidia broadly pyriform or nearly spherical, 3–5 µm in diameter . . . . . *M. cirrosus*, p. 193
b. Colonies usually white; conidia 6–10 µm long 12
12a. Ascomata 200–500 µm in diameter; conidia 7–10 × 2–3.5 µm . *M. albo-nigrescens*, p. 194
b. Ascomata less than 200 µm in diameter; conidia 6–8 × 5–6 µm . . *M. manginii*, p. 194

1. MICROASCUS LONGIROSTRIS Zukal

Microascus longirostris Zukal *in* Verh. zool.-bot. Ges. Wien **35**: 339. 1885.
Microascus variabilis Massee & Salmon *in* Ann. Bot. **15**: 313. 1901.
DESCRIPTIONS.—Barron & al., 1961; Udagawa, 1963; Morton & Smith, 1963; Corlett, 1963.

2. MICROASCUS GIGANTEUS Malloch

Microascus giganteus Malloch *in* Mycologia **62**: 731.1970.
DESCRIPTION.—Malloch, 1970.

3. MICROASCUS TRIGONOSPORUS Emmons & Dodge

Microascus trigonosporus Emmons & Dodge *in* Mycologia **23**: 313. 1931.
DESCRIPTIONS.—Barron & al., 1961; Udagawa, 1962; Morton & Smith, 1963; Corlett, 1963.

4. MICROASCUS TRIGONOSPORUS Emmons & Dodge var. MACROSPORUS Orr

Microascus trigonosporus Emmons & Dodge var. *macrosporus* Orr *apud* Barron & al *in* Can. J. Bot. **39**: 1617. 1961.
M. triangulisporus Orr in litt. (CBS, List of Cultures p. 152. 1972).
DESCRIPTION.—Barron & al., 1961.

5. CHAETOMIUM TRIGONOSPORUM (Marchal) Chivers

Bommerella trigonospora Marchal *in* Bull. Soc. bot. Belg. **24**: 164. 1885. — *Chaetomium trigonosporum* (Marchal) Chivers *in* Mem. Torrey bot. Club **14**: 166. 1915.
DESCRIPTION.—Udagawa, 1970.

This species is intermediate between *Microascus* and *Chaetomium*. The *Scopulariopsis* conidial state and the triangular, young dextrinoid ascospores point to *Microascus*, the fasciculate, narrowly clavate, stalked asci and the at maturity brown ascospores to *Chaetomium*. The ascomata are covered with rather numerous, dark, septate, straight, stiff setae.

6. MICROASCUS PYRAMIDUS Barron & Gilman

Microascus pyramidus Barron & Gilman *apud* Barron & al. *in* Can. J. Bot. **39**: 1618. 1961.
Microascus staurosporus Orr *in litt.* (CBS, List of Cultures, p. 152, 1972).
DESCRIPTION.—Barron & al., 1961.

7. MICROASCUS CIRROSUS Curzi

Microascus cirrosus Curzi *in* Boll. Staz. Patol. veg. Roma **10**: 302. 1910.
Microascus desmosporus sensu Morton & Smith (1963); non *Microascus desmosporus* (Lechmère) Curzi
DESCRIPTIONS.—Barron & al., 1961; Udagawa, 1962; Morton & Smith, 1963 (as *M. desmosporus*); Corlett, 1966.

8. MICROASCUS SINGULARIS (Sacc.) Malloch & Cain

Fairmania singularis Sacc. *in* Annls mycol. **4**: 276. 1906. — *Microascus singularis* (Sacc.) Malloch & Cain *in* Can. J. Bot. **49**: 859. 1971.
Microascus doguetii F. Moreau *in* Revue Mycol. **18**: 177. 1953.
DESCRIPTIONS.—Barron & al., 1961; Udagawa, 1963 (both as *M. doguetii*).

9. KERNIA HIPPOCREPIDA Malloch & Cain

Kernia hippocrepida Malloch & Cain *in* Can. J. Bot. **49**: 856. 1971.
DESCRIPTION.—Malloch & Cain, 1971.

This cleistothecial species may be close to *Microascus albo-nigrescens*. *Kernia nitida* (Sacc.) Nieuwland and other typical species of the genus *Kernia* differ by symmetrical, usually ovoid ascospores.

10. MICROASCUS MANGINII (Loubière) Curzi

Nephrospora manginii Loubière *in* C.r. hebd. Séanc. Acad. Sci., Paris, **177**: 211. 1923. — *Microascus manginii* (Loubière) Curzi *in* Boll. Staz. Patol. veg. Roma **11**: 60. 1931.
DESCRIPTIONS.—Barron & al., 1961; Udagawa, 1963; Morton & Smith, 1963.

11. MICROASCUS ALBO-NIGRESCENS (Sopp) Curzi

Acaulium albo-nigrescens Sopp *in* Skr. VidenskSelsk. Christiania, Mat.-naturv. Kl. **11**: 70. 1912. — *Microascus albo-nigrescens* (Sopp) Curzi, l.c.
DESCRIPTION.—Barron & al., 1961.

12. MICROASCUS CINEREUS (Emile-Weil & Gaudin) Curzi

Scopulariopsis cinerea Emile-Weil & Gaudin *in* Archs Méd. exp. Anat. path. Paris **28**: 452. 1919. — *Microascus cinereus* (Emile-Weil & Gaudin) Curzi *in* Boll. Staz. Patol. veg. Roma **11**: 60. 1931.
Microascus griseus Mathur & al. *in* Sydowia **16**: 47. 1962 (publ. 1963).
Microascus lunasporus Jones *in* Mycologia **28**: 503. 1936.
Microascus pedrosoi Fuentes & Wolf *in* Mycologia **48**: 63. 1956 and **48**: 446.
Microascus reniformis Orr *in litt.* (CBS, List of Cultures, p. 152, 1972).
DESCRIPTIONS.—Barron & al., 1961; Udagawa, 1962; Morton & Smith, 1963; Corlett, 1966.

The synonymy of *M. lunasporus* is based on the description, that of *M. griseus* on a study of the type strain. *M. desmosporus* is discussed under "Excluded species".

13. **Microascus senegalensis** v. Arx, *sp. nov.*—Fig. 1.

Coloniae in agaro farina maydis addita 33 °C in dies 1.5–2 mm crescunt, primum albae, deinde dilute brunneae, e hyphis 1.5–3 μm crassis, hyalinis vel dilute pigmentatis constant; ascomata aggregata vel discreta, superficialia vel parte immersa, sphaerica, nigra, 180–250 μm diam., ostiolo cylindrico, 50–80 μm longo, 40–50 μm crasso, levi praedita; paries 9–14 μm crassus e 3–4 stratis cellularum crassitunicatarum, obscure viridi-brunnearum; asci plerumque in seriebus verticalibus dispositi, ellipsoidei vel late clavati, deorsum truncati, 15–22 × 4–11 μm, evanescentes, octospori; ascosporae reniformes, primum dextrinoideae, maturitate luteolae vel stramineae, 7–9 × 4–4.5 μm, poro germinationis basilari exiguo praeditae; cellulae conidiogenae cylindricae, annellatae, 6–20 μm longae, 2–2.5 μm crassae; conidia basipetalia catenulata, obovoidea vel late clavata, basi truncata, fere levia, flavo-brunnea, 4.5–5.5 × 3.5–4 μm. Typus: CBS 277.74, isolatus e terra mangrovae, Joal in Senegal, Feb. 1974.

Colonies on cornmeal-agar at 33 °C growing daily 1.5–2 mm, at first white, later light brown, composed of 1.5–3 μm wide, hyaline or slightly pigmented hyphae; ascomata aggregated, discrete, superficial or slightly immersed at the base, spherical,

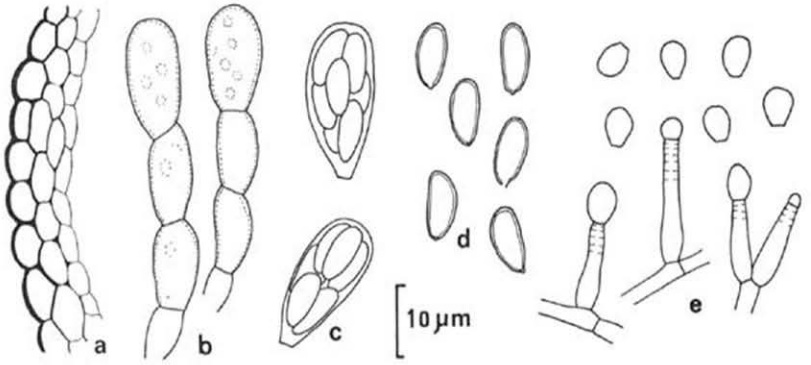

Fig. 1. *Microascus senegalensis*. — a. Part of the ascoma wall. — b. Catenulate asci. — c. Mature asci. — d. Ascospores. — e. Conidiogenous cells and conidia.

black, 180–250 µm in diameter, with a cylindrical, 50–80 µm long, 40–50 µm broad, smooth ostiolum; wall of the ascomata 9–14 µm thick, composed of 3–4 layers of thick-walled, dark greenbrown, 4–6 µm sized cells; asci usually borne in vertical rows, ellipsoidal or broadly clavate, truncate at the base, 15–22 × 4–11 µm, evanescent, 8-spored; ascospores reniform, dextrinoid when young, yellowish or straw coloured when mature, 7–9 × 4–4.5 µm, with a small, prominent germ pore at the base; conidiogenous cells usually arise solitarily on vegetative hyphae, cylindrical, elongating, with annellations, 6–20 µm long, 2–2.5 µm broad; conidia borne in basipetal succession, obovoid or broadly clavate, truncate at the base, smooth or nearly so, yellowbrown, 4.5–5.5 × 3.5–4 µm.

TYPE.—CBS 277.74, isolated from mangrove soil, Joal, Senegal, Feb. 1974.

The species is close to *Microascus cinereus*; it can be distinguished by larger ascospores with a prominent germ pore and by shorter but broader conidia. It shows its optimal development on cornmeal-agar at temperatures between 33 and 36°C, whereas *M. cinereus* usually shows optimal growth at 30°C.

EXCLUDED AND DOUBTFUL SPECIES

d e s m o s p o r u s. — *Microascus desmosporus* (Lechmère) Curzi *in* Boll. Staz. Patol. veg. Roma, N.S., **11**: 60, 1931. — *Peristomium desmosporum* Lechmère *in* Bull. trim. Soc. mycol. Fr. **29**: 309. 1913 (name based on 2 different fungi).

Lechmère (1913) distinguished 2 varieties; the type strains of both are maintained in the CBS collection. *Peristomium desmosporum* var. *oidium* (CBS 125.14) proved to belong to the *Phialophora mutabilis* (Beyma) Schol-Schwarz group. In most of the cultures only catenulate chlamydospores develop, as described by Lechmère. Phialoconidia could be observed only occasionally. *Peristomium desmosporum* var. *verticillatum* (CBS 125.14) represents the *Scopulariopsis* conidial state of *Microascus cinereus*; ascomata could not be observed.

exsertus. — *Microascus exsertus* Skou *in* Antonie van Leeuwenhoek **39**: 529. 1973. — *Pithoascus exsertus* (Skou) v. Arx *in* Persoonia **7**: 373. 1973.

This species is characterized by elongated navicular or falcate ascospores without a germ pore and by the absence of any conidial state. It differs from the other species of the genus *Pithoascus* by its irregularly spreading colonies.

intermedius. — *Microascus intermedius* Emmons & Dodge *in* Mycologia **23**: 313. 1931. — *Pithoascus intermedius* (Emmons & Dodge) v. Arx *in* Proc. K. Ned. Akad. Wet. (C) **76**: 292. 1973.

nidicola. — *Microascus nidicola* Massee & Salmon *in* Ann. Bot. **15**: 313. 1901. — *Pithoascus nidicola* (Massee & Salmon) v. Arx *in* Proc. K. Ned. Akad. Wet. (C) **76**: 292. 1973.

This species has been chosen as type of the genus *Pithoascus* v. Arx. A description is given by von Arx (1973b).

niger. — *Microascus niger* (Sopp) Curzi *in* Boll. Staz. Patol. veg. Roma **11**: 60. 1931.

This species has been discussed by Thom (1930), Curzi (1931) and Barron & al. (1961). The species name is based on *Acaulium nigrum* Sopp, which has been placed in the synonymy of *Scopulariopsis asperula* (Sacc.) Hughes by Morton & Smith (1963).

schumacheri. — *Microascus schumacheri* (Hansen) Curzi *in* Boll. Staz. Patol. veg. Roma **11**: 60. 1931. — *Pithoascus schumacheri* (Hansen) v. Arx *in* Proc. K. Ned. Akad. Wet. (C) **76**: 292. 1973.

No cultures or specimens of this species could be examined.

stysanophorus. — *Microascus stysanophorus* (Mattirolo) Barron & al. *in* Can. J. Bot. **39**: 1621. 1961. — *Melanospora stysanophora* Mattirolo *in* Nuovo G. bot. ital. **18**: 121. 1886.

Microascus stysanosporus Curzi *in* Boll. Staz. Patol. veg. Roma **11**: 60. 1931.

This species could not be studied. It has been discussed by Barron & al. (1961); its taxonomic position, however, is doubtful. The fungus discussed by Doguet (1957) as *Microascus stysanophorus* has no conidial state and may belong to *Pithoascus schumacheri* or *P. nidicola*.

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SOME NOTES ON TORULA

VASANT RAO* and G. S. DE HOOG
Centraalbureau voor Schimmelcultures, Baarn.

(With three Text-figures)

A new species of *Torula* Pers. per Fr., collected at Hyderabad, India, is described as *T. rhombica* Rao & de Hoog. It forms chains of reddish brown, regularly rhomboid conidia. A key to the accepted species of *Torula* is given. All CBS strains maintained under the name *Torula* are discussed; they can be assigned to six different genera. New combinations are proposed in *Polypaecilum* Smith and *Moniliella* Stolk & Dakin, and a new species of *Scytalidium* Pesante is described.

In the course of studies on dematiaceous Hyphomycetes, the senior author reported on a new species of *Bahusandhika* Subram. as *B. sundara* Rao & Rao (1972). Another species, resembling *Torula terrestris* Misra (1967), is described in this communication. In order to delimit the new species all strains maintained in the CBS collection under the name *Torula* were studied. As a result a key is proposed for the species of *Torula* sensu stricto (Ellis, 1971). The strains which do not fit this genus are re-classified.

Torula rhombica Rao & de Hoog, *sp. nov.*—Fig. 1

Coloniae in ligno putrido effusae, 1–3 mm diam., quasi 1 mm altae, atrobrunneae; hyphae steriles superficiales, repentes, leves, fere tenuitunicatae, subhyalinae vel pallide rubrobrunneae, 1.5–2 μm crassae, cellulis 4–6 μm longis; hyphae fertiles repentes vel adscendentes, rubrobrunneae, crassitunicatae, verrucosae, plerumque 2–3 μm crassae, septis tenuibus circa 30 μm distantibus, apicibus conidiiferis lateralibus vel terminalibus. Cellulae conidiogenae singulae vel modice acervatae, sessiles vel pedicellatae, fere crassitunicatae, verrucosae, rubrobrunneae, pyriformes, 3–6 μm longae, sursum conspicue inflatae ad 5.5 μm, unam rarius duas cicatrices conidiiferas, 1–1.5 μm diam. ferunt. Blastoconidia sicca, catenulata, plerumque 5–6-septata, fusiformia vel rhomboidalia, utrinque symmetrica, fere crassitunicata, cellulis mediis dense verrucosis, obscure rubrobrunneis, septis crassis, opacis, extus modice constrictis, 33–43 μm longa, 11–18 μm crassa in medio, 3–3.5 μm in cellulis terminalibus, dilute brunneis; conidiorum catenae simplices, nonnumquam ramosae, ad 150 μm longae.

Typus: Herb. IMI 162.901 (Herb. CBS 77), in ligno putrido, in seminario arborum Balaji, Hyderabad, Andhra Pradesh, India, Sept. 1969.

Colonies on the natural substrate effused, 1–3 mm in diameter, less than 1 mm high, blackish brown. *Sterile hyphae* superficial, creeping, smooth- and thin- or somewhat thick-walled, subhyaline to pale reddish brown, 1.5–2 μm wide, with septa at 4–6 μm distance. *Fertile hyphae* creeping or ascending, reddish brown,

* Present address: Department of Botany, Vivek Vardhini College, Hyderabad, A.P., India.

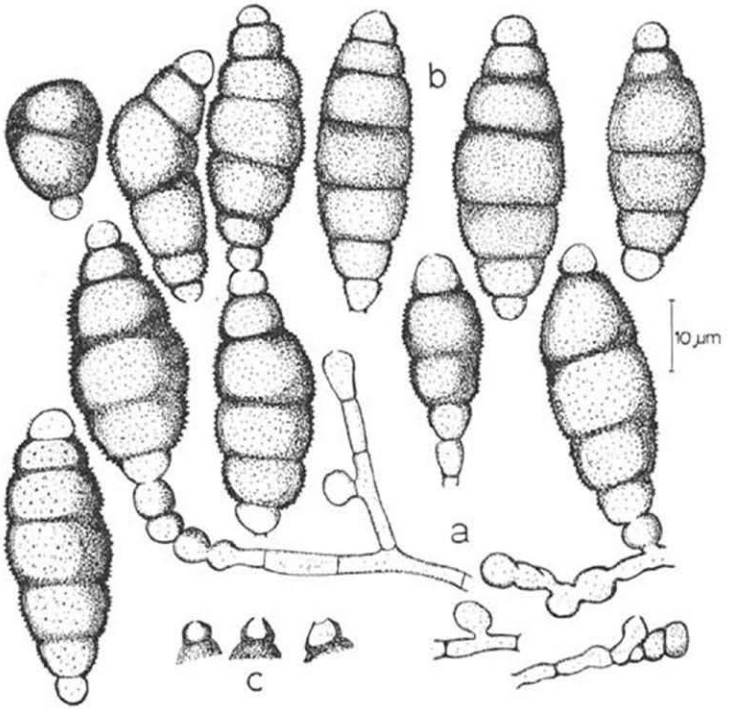

Fig. 1. *Torula rhombica*. — a. Hyphae bearing conidiogenous cells and conidia. — b. Conidia — c. Conidial tips showing apertures or scars.

thick-walled, verrucose, usually 2–3 µm wide, with thin septa about every 30 µm, in the apical region with conidiiferous structures in lateral or terminal position. *Conidiogenous cells* solitary or in small groups, sessile or supported by 1–3 short cells, rather thick-walled, verrucose, reddish brown, pear-shaped, 3–6 µm long, apically conspicuously inflated up to 5.5 µm, with one, occasionally with two thin-walled circular scars 1–1.5 µm in diameter at the tip. *Conidia* blastic, dry, catenate, usually 5- to 6-septate (number of the septa ranging from 3–7 ultimately), fusiform to rhomboidal, symmetrical, 33–43 µm long, 11–18 µm wide in the median part, 3–3.5 µm at the base and apex, somewhat constricted at the septa, basal and apical cells light brown, the latter cells moderately thick-walled, median cells densely verrucose, dark reddish brown, septa heavily pigmented to form black zones; conidial chains simple, sometimes branched, up to 150 µm long.

MATERIAL EXAMINED.—IMI 162.901 (type; isotype, slides in Herb. CBS no. 77), on decaying wood, Balaji Nursery, Hyderabad, Andhra Pradesh, India, September 1969, *V. Rao*.

In all species of the genus *Torula*, as circumscribed by Ellis (1971), series of conidial cells arise acropetally from inflated conidiogenous cells. Invariably the first cell is initially joined with its supporting cell by a narrow cytoplasmic connection, at most

1.5 μm wide, which soon becomes partitioned by a double septum. Formation of the subsequent cells can take place in two ways. Occasionally the above budding is repeated once or several times, but more often the first cell elongates from a wide, little constricted base and becomes septate after almost having attained its ultimate size (Hashmi & al., 1973). The latter type of cell formation reiterates almost indefinitely, or is interrupted at more or less regular sequences by the firstly mentioned budding. In this way the chains become articulated, the intermediate cell-rows can be regarded as phragmoconidia. Occasionally the phragmoconidia break apart into their separate cells.

The above details of morphogenesis can be used as taxonomic criteria to group the species of *Torula*. In *T. herbarum* (Pers.) Link per S. F. Gray (in L, nrs. 910.267–924, and 998.1000; CBS 379.58, and CBS 442.51, received as *T. graminis*) and *T. caligans* (Batista & Upadhyay) M. B. Ellis (CBS 576.65—type, 269.72 and 308.73), one-celled propagules are rare; if present, they arise by budding and can be regarded as ameroconidia. The phragmoconidia consist of few cells only, which are all of about the same shape and size.

Torula graminis Desm. (CBS 245.57=IMI 1.332, received as *T. herbarum*), is characterized by long, many-celled phragmoconidia, which frequently break up into their separate cells. Only a few narrow connections are found; usually they are confined to the primary cell of the chain and the basal cells of its ramifications.

In developing conidia of *Torula terrestris* Misra (1967; CBS 311.67—type, 330.67 and 902.72) and *T. ndjilensis* Kiffer (1972; CBS 543.73—type), often hardly any constriction can be observed. The phragmoconidia are well defined, with cells mutually differing considerably in shape and size, the median ones being the largest and the darkest. Occasionally the conidia are not catenate. Also *T. rhombica* can be assigned to this group. It is distinct from both species due to the regularly symmetric, fusiform to rhomboid shape of the conidia with the apical and basal cells being of the same shape and size, the dark red-brown colour of the conidia and the mycelium, and the fine, densely verrucose ornamentation of the median conidial cells.

The species hitherto accepted in *Torula* sensu stricto can be identified by the following key:

1a. Conidia many-celled, often breaking up into small fragments; conidial cells all alike *T. graminis*
b. Not combining above characters 2
2a. Conidia usually 3- to 5-celled; basal cells of conidia as dark as or darker than the median cells and of about the same width, apical cells pale or bi-coloured 3
b. Conidia usually 5- to 7-celled; basal cells of conidia conspicuously paler and/or narrower than the median cells, apical cells pale or dark 4
3a. Conidia smooth or finely verrucose; apical conidial cell usually brown with a hyaline tip *T. herbarum*
b. Conidia tuberculate; apical conidial cell entirely subhyaline . . . . . *T. caligans*
4a. Conidia fusiform to rhomboid, densely verrucose, red-brown . . . . . *T. rhombica*
b. Conidia fusiform to ellipsoidal, tuberculate, brown to olivaceous 5
5a. Conidia usually 10–12 μm wide. . . . . *T. terrestris*
b. Conidia usually 13–15 μm wide. . . . . *T. ndjilensis*

It is pertinent to record here that *T. caligans* and *T. terrestris* occasionally produced single terminal conidia, as was already noted by Misra (1967). As such these species are reminiscent of *Polyschema* Upadhyay and differ from both known species in this genus, *P. terricola* Upadhyay (1966) and *P. congolensis* Reisinger & Kiffer (1974), only by some minor morphological characters. Consequently, the synonymy of *Polyschema* and *Pithomyces* Berk. & Br., as suggested by Kendrick & Carmichael (1973) is rejected here, because of the absence of differentiated conidiogenous cells in the latter genus.

The considered strains which could not be classified in *Torula* sensu stricto are discussed below in alphabetical order.

a l l i i. — *Torula allii* (Harz) Sacc., CBS 441.51, sent by E. Baldacci under no. MMP-162.

This strain can be identified as *Humicola nigrescens* Omvik. It does not fit the original diagnosis (Harz, 1871).

b o t r y o i d e s. — *Torula botryoides* Brooks & Hansf., CBS 143.23, T, isolated from a halibut in cold storage, May 1918.

The species was well described and depicted by Brooks & Hansford (1923). In culture it appears to be indistinguishable from the type strain of *Polypaecilum capsici* (Beyma 1944) G. Smith, CBS 176.44. Consequently the species should be referred to as **Polypaecilum botryoides** (Brooks & Hansf.) Rao & de Hoog, *comb. nov.* (basionym: *Torula botryoides* Brooks & Hansf. *in* Trans. Br. mycol. Soc. **8**: 134. 1923).

d e m a t i a. — *Torula dematia* Berkhout, CBS 314.31, sent by P. Lindner; CBS 381.36 and 382.36, isolated by J. W. Jollyman from tobacco; CBS 349.33, isolated by J. J. Harris from condensed milk.

The former three strains are characterized by the presence of long, acropetal chains of pale brown, slightly thick-walled conidia, and hyaline or subhyaline arthroconidia. They are identical with *Moniliella suaveolens* (Lindner) v. Arx. CBS 349.33 has compact, olivaceous colonies, whereas the subhyaline conidia are borne in long acropetal chains, which fragment only in a very late stage. The fungus shows superficial resemblance to *Rhinocladiella compacta* (Carrión) Schol-Schwarz.

j a a p i i. — *Torula jaapii* Lindau, CBS 171.40 (=IFO 6396), isolated by G. A. Heubel from wood of *Camellia sinensis* L.

Since in young cultures of this strain the subhyaline hyphae locally fragment, and in a later stage terminal, brown, thick-walled chlamydospores are formed, it should be classified in *Scytalidium* Pesante. It cannot be identified with any of the known species in this genus; as a consequence it is described here as new. The strain does not fit the original diagnosis of *Torula jaapii* given by Lindau (1907); the type specimen (at B) could be identified with *Alysidium resinae* (Fr.) M. B. Ellis.

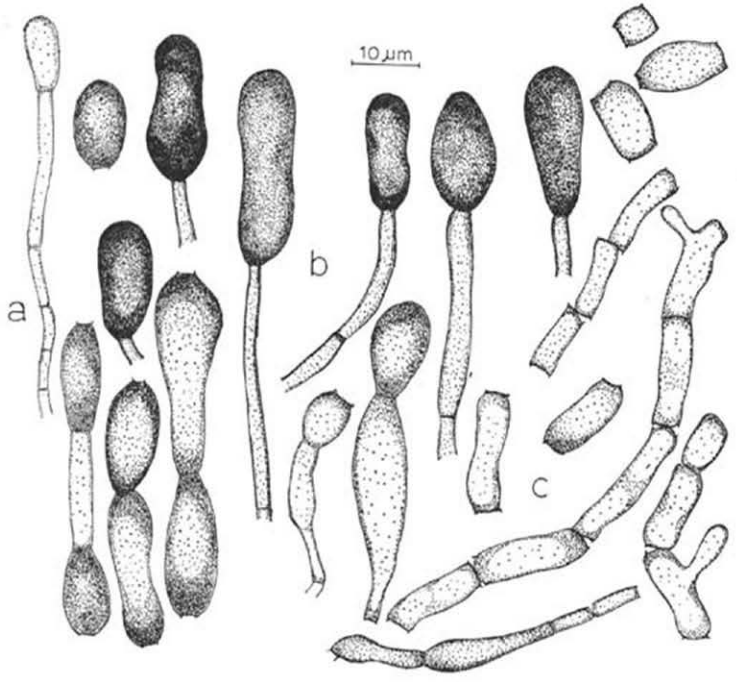

Fig. 2. *Scytalidium terminale*. — a. Fertile hypha with young chlamydospore. — b. Mature chlamydospores. — c. Arthric conidia.

Scytalidium terminale Rao & de Hoog, *sp. nov.*—Fig. 2

Coloniae in agaro farina avenae addita 20 °C ad 14 mm diam. post 10 dies, effusae, leves, primum subhyalinae, deinde obscure testaceae. Mycelium pro maxima parte submersum, hyphis levibus tenuitunicatis, hyalinis vel subhyalinis, 1.5–3.0 µm crassis. Conidia duobus modis formantur: altera arthroconidia singula vel catenulata, levia et tenuitunicata, a hyphis colore non differunt, rectangularia, plerumque 10–20 × 3–5 µm, nonnumquam modice inflata; alterae chlamydosporae terminales, nonnumquam intercalares, singulae, nonnumquam breviter catenulatae, leves, crassitunicatae, dilute vel obscure brunneae, obovoidales, ellipsoideae vel pyriformes, plerumque 15–25 × 7–9 µm.

Typus: CBS 171.40, isolatus ex ligno *Camelliae sinensis* a I. Heubel.

Colonies on oatmeal agar at 20 °C attaining a diameter of 14 mm in 10 days, effused, smooth, at first subhyaline, later becoming dark brick. *Mycelium* mainly submerged, hyphae smooth- and thin-walled, hyaline to subhyaline, 1.5–3 µm wide. *Conidia* of two types: arthric conidia singly or in chains, smooth- and thin-walled, concolorous with the hyphae, rectangular, usually 10–20 × 2–3 µm, sometimes slightly swollen; chlamydospores terminal, sometimes intercalary, single, occasionally in short chains, smooth- and thick-walled, pale to dark brown, obovoidal, ellipsoidal or pyriform, usually 15–25 × 7–9 µm.

Type: CBS 171.40.

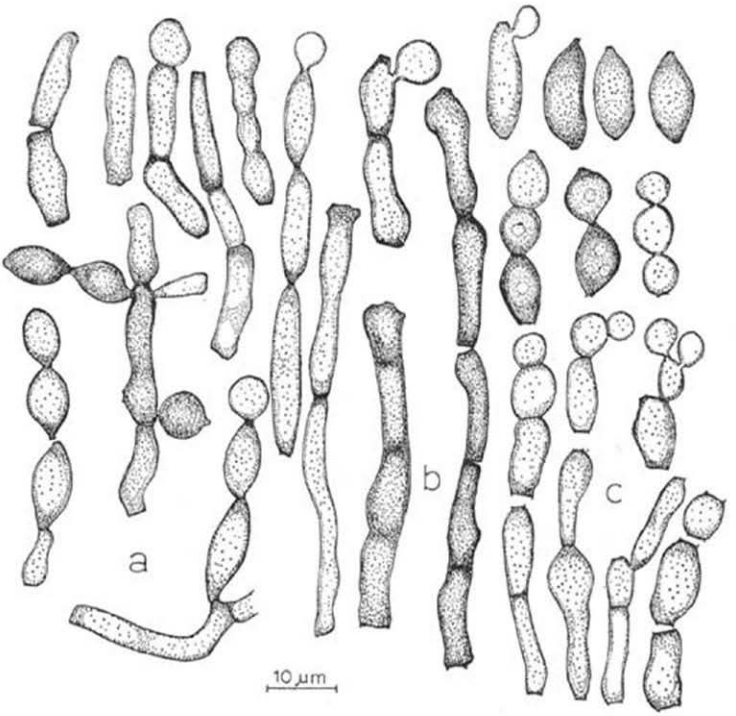

Fig. 3. *Moniliella mellis*. — a. Mature arthric and blastic conidia. — b. Fragmenting hyphae. — c. Young arthric and blastic conidia.

Scytalidium terminale can easily be recognized from other species of the genus by its characteristic terminal chlamydospores, which only rarely occur in short intercalary chains. It is reminiscent of some *Humicola* species, but differs by the presence of arthric conidia.

l i g n i p e r d u s. — *Torula ligniperda* (Wilkomm) Sacc., CBS 383.36, isolated by L. Grodsinsky from *Abies alba* Mill., Tucumán, Argentina; CBS 317.56 (=IFO 6397), isolated by S. Batko from root of *Quercus* sp.

Both strains are characterized by subhyaline hyphae with chains of intercalary, brown, thick-walled chlamydospores. They are very similar to *Humicola brevis* (Gilman & Abbott) Gilman. According to Siggers (1922), who gave a detailed description of *T. ligniperda*, probably no original material has been preserved; it is not maintained in B. Consequently the identity of this species remains doubtful.

m e l l i s. — *Torula mellis* Fabian & Quinet, CBS 350.33, T, isolated from honey.

This strain shows abundant sporulation with acropetal chains of conidia, as well as arthric conidia. It can be classified in *Moniliella* Stolk & Dakin, and should be referred to as **Moniliella mellis** (Fabian & Quinet) Rao & de Hoog, *comb. nov.* (Fig. 3) (basionym: *Torula mellis* Fabian & Quinet *in* Tech. Bull. Mich. (St. Coll.) agric. Exp. Stn **92**: 26. 1928). A detailed description is given below.

Colonies on oatmeal agar at 20°C attaining its maximum diameter of 10–15 mm in 30 days, remaining smooth, pale brown, in age becoming dark to blackish brown. *Mycelium* partly submerged, hyphae smooth- and thin-walled, hyaline to subhyaline, 2–3 μm wide, sometimes swollen up to 5 μm, at a very young stage fragmenting into separate cells. *Conidia* of two types: arthric conidia singly or in chains, smooth, at first thin-walled and subhyaline, later becoming thick-walled and light brown, 0- to 1-septate, usually rectangular, sometimes swollen or irregular, about 6–20 × 3–6 μm, the apical conidia usually give rise to several chains of blastoconidia; blastoconidia arising in terminal or sometimes lateral, simple or branched, acropetal chains, smooth- and thin- or slightly thick-walled, subhyaline to pale brown, continuous, globose, ovoidal or fusiform, intermediate conidia oblong to limoniform, with usually unpigmented scars, 5–15 × 4–6 μm, in each chain the basal conidia conspicuously longer than the apical ones.

The present species can be distinguished from *Moniliella acetoabutans* Stolk & Dakin by the presence of dark, intercalary chlamydospores. It is very similar to *M. suaveolens* (Lindner) v. Arx, but differs by its cultural characteristics, the strongly fragmenting mycelium, the pigmentation of the arthric conidia, and the shape and size of the blastic conidia. It is reminiscent of *Hormoconis resinae* (Lindau) v. Arx & de Vries, but can be recognized by the presence of arthric conidia and the absence of erect, markedly differentiated conidiophores. *Cladosporium* Link per Fr. and some closely related genera are also distinguished on the absence of arthric conidia; moreover they usually differ by having conspicuously pigmented conidial scars (von Arx, 1973).

ACKNOWLEDGEMENTS

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SOME NEW HYPHOMYCETES

G. S. DE HOOG and VASANT RAO*

Centraalbureau voor Schimmelcultures, Baarn

(With three Text-figures)

Three new Hyphomycetes are described: *Acrodontium intermissum* from Norway, *Beauveria vermiconia* from Chile, and *Periconia pseudolateralis* from India.

Acrodontium intermissum de Hoog & Rao, *sp. nov.*—Fig. 1

Coloniae in agaro farina avenacea addita 20 °C post 8 dies 1 mm diam. attingentes, post 20 dies et diutius maxime 4 mm diam., velutinae, depressae, dilute cinnamomeae, reverso dilute roseo-bubalino. Exsudatum et odor absunt. Hyphae submersae hyalinae, leves et tenuitunicatae, 1.5–2.5 μm crassae. Hyphae aeriae ochraceae, leves et modice crassitunicatae, adscendentes, diametro semper circa 2 μm, frequenter plagiotropice irregulariter verticillatae. Cellulae conidiogenae ochraceae, modice crassitunicatae, e parte basilari cylindrica, 40–60 μm longa, modice inflata ad 1.5–2.5 μm, sursum attenuata, et rachide conidiifera subhyalina, fere tenuitunicata, saepe plus quam 30 μm longa et 1.0–1.5 μm crassa, irregulariter nodosa constant; nodi denticulis conidiiferis haud numerosis, conspicuis, breviter cylindricis obtecti, 3–6 μm distantes. Conidia hyalina, levia et tenuitunicata, ellipsoidea vel oblonga, basi rotundata, 3.5–5 × 2–3 μm. Chlamydosporae absunt.

Typus: CBS 644.74, isolatus a K. Venn e terra prope Ås in Norvegia.

Colonies on oatmeal agar at 20 °C attaining a diameter of 1 mm in 8 days, reaching its maximum of 4 mm within three weeks, velvety, less than 1 mm high, pale cinnamon, reverse pale pinkish buff. Exudate and odour absent. *Submerged hyphae* hyaline, smooth- and thin-walled, 1.5–2.5 μm wide. *Aerial hyphae* ochraceous, smooth- and slightly thick-walled, ascendent, of uniform width throughout about 2 μm, without main stalk, with strong, plagiotropic, irregularly verticillate branching. *Conidiogenous cells* ochraceous, slightly thick-walled, consisting of a cylindrical basal part, 40–60 μm long, somewhat swollen near the base up to 1.5–2.5 μm, tapering very slightly towards the tip, and a subhyaline, rather thin-walled, irregularly nodose conidiiferous rachis, often exceeding 30 μm in length, 1–1.5 μm wide; nodes with a small number of conspicuous, short cylindrical conidium-bearing denticles, at intervals of 3–6 μm. *Conidia* hyaline, smooth- and thin-walled, ellipsoidal to oblong, rounded at the base, 3.5–5 × 2–3 μm. No chlamydospores observed. *Perfect state* unknown.

MATERIAL EXAMINED.—CBS 644.74, type culture, isolated by K. Venn from soil, Ås, Norway, February 1973.

* Present address: Department of Botany, Vivek Vardhini College, Hyderabad, A.P., India.

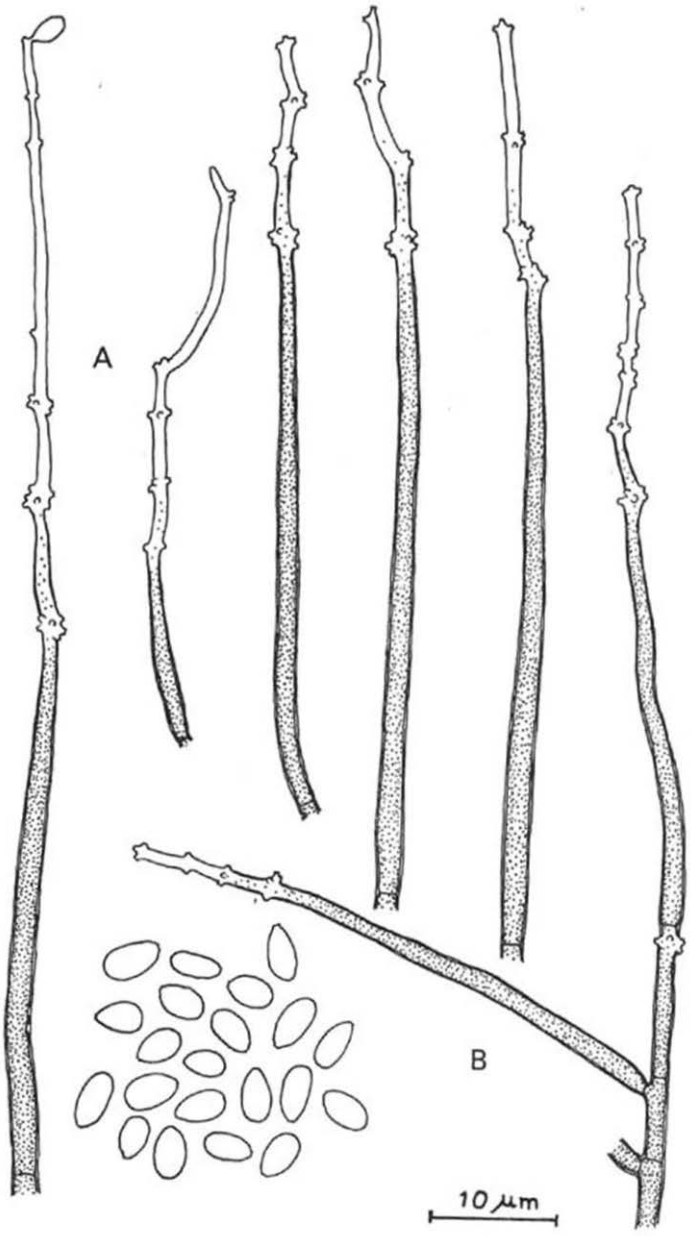

Fig. 1. *Acrodontium intermissum*. — a. Conidiogenous cells. — b. Conidia.

The present species is classified in *Acrodontium* (section *Griseum* de Hoog, 1972) because of its pigmented, slightly tapering conidiogenous cells which are constant in shape and size, and have denticulate rachids and ellipsoidal to oblong conidia. The last mentioned characters are sometimes also found in *Nodulisporium cylindroconium* de Hoog (1973), which is distinct in strictly cylindrical conidiogenous cells with equally wide rachids and flat, not prominent conidial scars. Some species of *Tritirachium* Limber are also reminiscent of *Acrodontium intermissum*, but can be distinguished by regularly flexuose conidiiferous rachids, on which the conidial scars are traced with difficulty under the light microscope. *Sporothrix* Hektoen & Perkins ex Nicot & Mariat differs e.g. by hyaline, thin-walled conidiogenous cells (although the mycelium may be dull brown or olivaceous), and spreading or smooth colonies.

Beauveria vermiconia de Hoog & Rao, *sp. nov.*—Fig. 2

Coloniae in agaro farina avenacea addita 20 °C post 8 dies 20 mm diam. attingentes, pulverulentae vel velutinae, lanuginosae ad marginem, ad 1 mm altae, modice zonatae, deinde

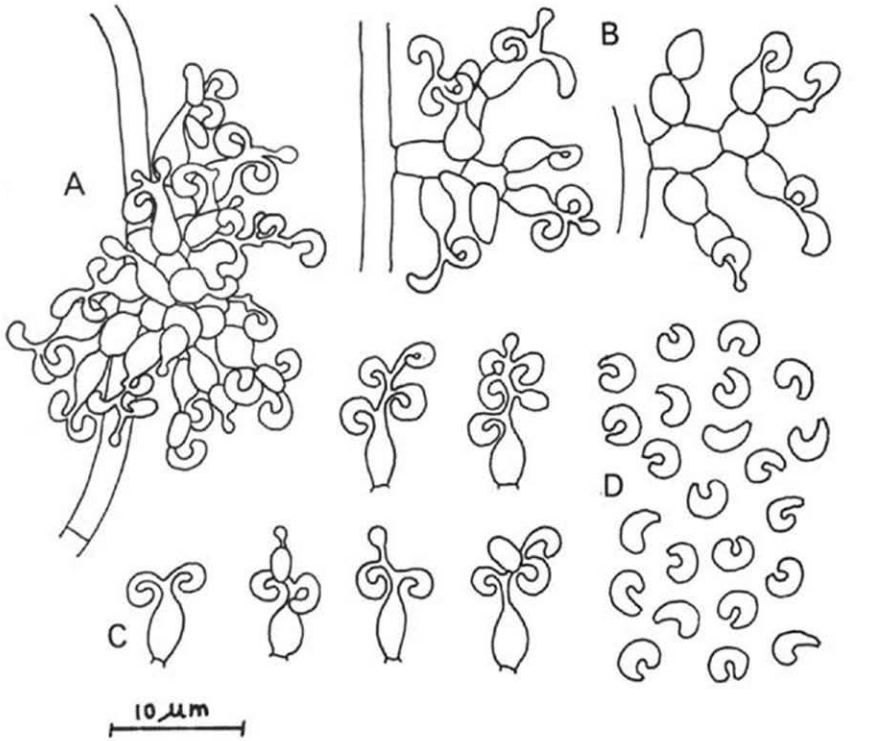

Fig. 2. *Beauveria vermiconia.* — a. Conidial apparatus. — b. Fertile branches. — c. Conidiogenous cells. — d. Conidia.

in medio dilute citrinae. Reversum primum hyalinum, deinde partim dilute roseum. Exsudatum et odor absunt. Hyphae hyalinae, leves et tenuitunicatae, 1.5–3.5 μm crassae, repentes vel adscendentes, frequenter plus minusve dichotome ramosae. Structurae conidiogenae dense aggregatae e cellulis lateralibus inflatis, plerumque 5–6 × 3–4 μm constant quae acervos cellularum secundariarum vel conidiogenarum preferunt. Cellulae conidiogenae e basi ellipsoidea vel lageniformi, plerumque 4–5 × 2–2.5 μm, et rachide tenui, ad 12 μm longa et semper 0.7–1.0 μm crassa, flexuosa, denticulis conidiiferis minutis obtecta constant; conidia sero secedunt. Conidia levia et tenuitunicata, commaeformia vel falcata, diam. arcus 2.5–3.5 μm, radius segmenti 1.0–1.5 μm. Chlamydosporae absunt.

Typus: CBS 645.74 isolatus a J. Grinbergs e cinere vulcanica, prope Valdiviam Chilensem.

Colonies on oatmeal agar at 20 °C attaining a diameter of 20 mm in 8 days, appearing powdery to velvety, lanose near the margin, up to 1 mm high, slightly zonate, white, becoming pale citron yellow in the centre. Reverse at first uncoloured, soon locally pale pinkish. Exudate and odour absent. *Hyphae* hyaline, smooth- and thin-walled, 1.5–3.5 μm wide, creeping or ascendent, with strong, often more or less dichotomous branching. Conidial apparatus tightly clustered, consisting of groups of swollen lateral cells, mostly 5–6 × 3–4 μm, which by further branching give rise to smaller swollen cells or several conidiogenous cells in the first or second order. *Conidiogenous cells* consisting of an ellipsoidal to flask-shaped basal part, usually 4–5 × 2–2.5 μm, and a slender, up to 12 μm long and rather constantly 0.7–1 μm wide, flexuose rachis, on the edges provided with small conidium-bearing denticles; conidia remaining attached to the rachis for a long period. *Conidia* smooth- and thin-walled, comma- or sickle-shaped, 1–1.5 μm in face view, diameter in side view about 2.5 μm. No chlamydospores observed. *Perfect state* unknown.

MATERIAL EXAMINED.—CBS 849.73 and 645.74 (type culture), isolated by J. Grinbergs from volcanic ash, Valdivia, Chile.

Beauveria vermiconia is closely related to *B. bassiana* (Bals.) Vuill., but can be easily recognized by its comma-shaped conidia. It is also reminiscent of *Isaria amorpha* Höhnel (=*I. orthopterorum* Petch; de Hoog, 1972), but the species of *Isaria* (sensu v. Arx, 1970; de Hoog, 1972) are distinguished by the presence of synnemata, and by conidiogenous cells with small groups of conidium-bearing denticles, only rarely extending into a short flexuose rachis.

Periconia pseudolateralis de Hoog & Rao, *sp. nov.*—Fig. 3

Coloniae in substrato naturali effusae, atrobrunneae. Mycelium in hospite submersum, e hyphis crassitunicatis, subhyalinis vel fuscis, 3–7 μm crassis, cellulis 2–5 μm longis, dense intricatis, stromatoideis constat. Stipites solitarii vel acervati, erecti, nonnumquam curvati, 2–5-septati, simplices, raro ramulos fertiles singularum vel ternarum cellularum proferentes, leves vel verrucosi, crassitunicati, atrobrunnei, sursum pallidiores, 160–350 μm longi, ad basim 10–20 μm crassi, sursum ad 2–5 μm attenuati. Cellulae conidiogenae spirales e parte superiore stipitis oriuntur, singulae vel seriatae, ovoideae, globosae vel subglobosae vel forma variabiles, leves vel verrucosae, crassitunicatae, 5–7 μm longae, 8–11 μm crassae; cellulae conidiogenae et conidia saepe vix distinguenda. Conidia sicca, continua, in catenulis acropetalibus simplicibus vel ramosis disposita, deorsum maturantia, crassitunicata, spinis ad 1 μm longis obtecta, dilute vel fusce pigmentata, globosa vel subglobosa, 6–9 μm diam.

Typus: Herb. CBS 118, in bambusoidea putrescente, prope Srisailem, Andhra Pradesh, India, Sept. 1971.

Colonies on the natural substrate effused, blackish brown. *Mycelium* submerged in the host tissue, composed of thick-walled, subhyaline to dark brown, 3–7 μm wide hyphae, septate every 2–5 μm, tightly interwoven, forming stroma-like bodies. *Stipes* solitary or in groups, erect, occasionally curved, 2–5-septate, simple, rarely with short fertile branches of 1–3 cells, smooth or verrucose, thick-walled, blackish brown, slightly paler towards the apex, 150–350 μm long, 10–20 μm wide at the base, and 2–5 μm wide at the apex. *Conidiogenous cells* spirally arranged on the stipe in the upper two-third of the length, singly or in short series, ovoidal, globose, subglobose or irregular, smooth or verrucose, thick-walled, 5–7 μm long, 8–11 μm wide; often conidiogenous cells and conidia are not markedly different. *Conidia* dry, 1-celled, arising in acropetal, single or branched chains, maturing from apex backwards, thick-walled, spiny (spines up to 1 μm long), dark yellowish brown, globose or subglobose, 6–9 μm in diameter.

MATERIAL EXAMINED.—Herb. CBS no. 118, on decaying bamboo, Srisailem, Andhra Pradesh, India, September 1971, *Rao*.

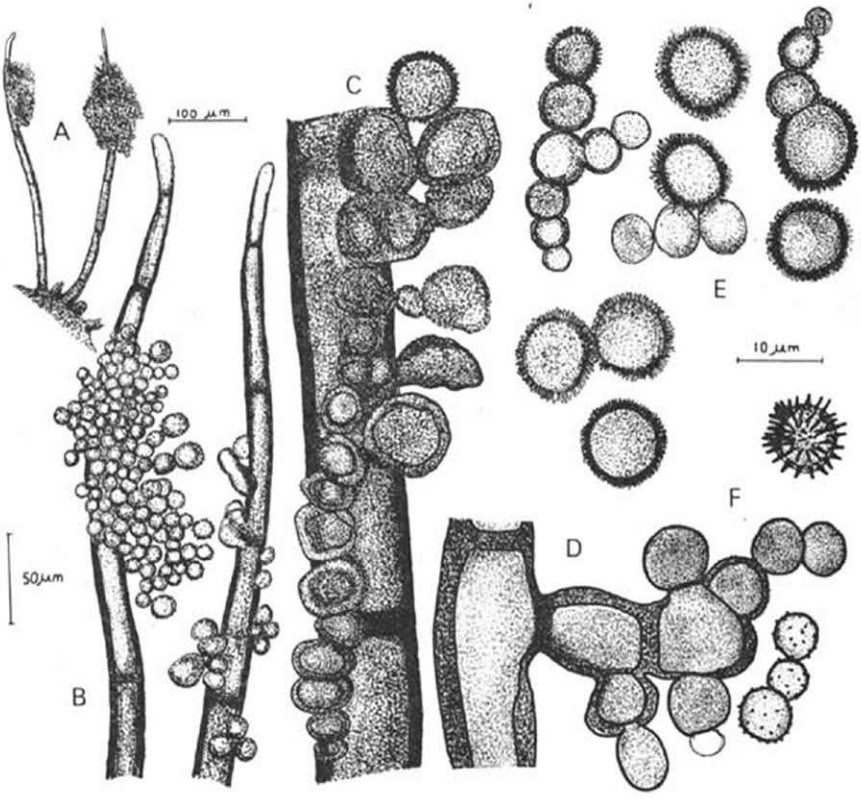

Fig. 3. *Periconia pseudolateralis*. — a. Stipes on the natural substrate. — b. Apical region of stipes. — c. Arrangement of conidiogenous cells. — d. Fertile branch. — e. Conidia in various stages of development. — f. Conidium, focussed on spines.

This species is very similar to *Periconia lateralis* Ellis & Everh. (1886; Ellis, 1971), hitherto the only known species with unilateral conidiophores having a sterile apex. In the type specimen of the latter (IMI 52,615) and other collections kept in the CMI the conidiogenous cells are intermixed with sterile branches, and the conidia are verrucose to echinulate. In *P. pseudolateralis* sterile branches are absent, the basal conidiogenous cells are arranged in more regular spiral rows and the ornamentation of the conidia is much more conspicuous.

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NOTES AND BRIEF ARTICLES

A NEW CLAVICORONA

R. A. Maas Geesteranus

Rijksherbarium, Leiden

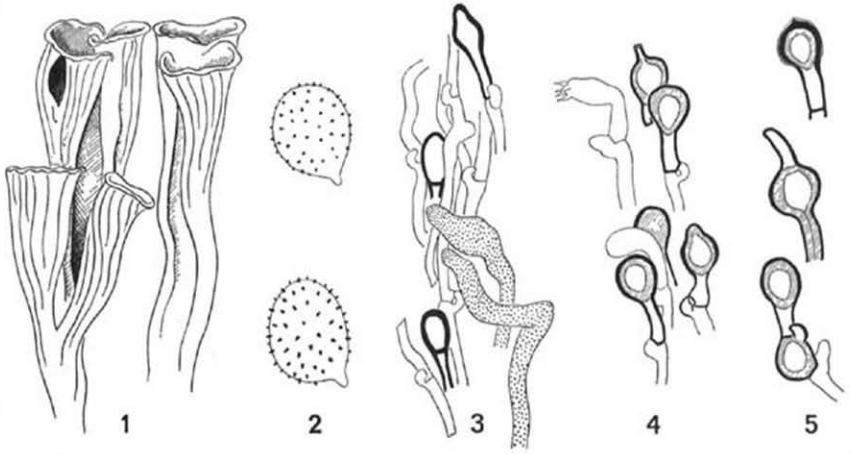
Clavicorona dryophila Maas G., *spec. nov.*

Basidiomata circa 20 mm alta, caespitosa, basi vel media altitudine ramosa. Rami 1 mm lati, sursum tubae more dilatati usque ad 2 mm, recti vel curvati, infra cylindracei, supra depressi vel infundibuliformes, interdum uno latere profunde fissi, itaque marginibus involutis vel cochleares, labro revoluto, integro vel varie inciso, intus laevi, extus costato-venosi, glabri, subnitentes, avellanei vel badii, sursum nigrescentes. Stipes vix evolutus, mycelio basali ortus. Caro albida, odore saporeque ignotis.

Hyphae 3.5–11.5 μm latae, subinflatae, parietibus tenuibus vel modice incrassatis instructae, anastomosantes, ramosae, septatae, fibulis munitae; hyphae materia oleosa replatae 2.5–6.5 μm latae. Basidia 27–32 × 5.4–6.3 μm (matura non visa), clavata, fibulata, quadrispora, sterigmatibus 3.6–4.5 μm longis. Sporae 4.3–4.9 × 3.6–4.3 μm, late ellipsoideae vel subglobosae, pariete modice incrassato praeditae, aculeis minutis sat numerosis asperulatae, hyalinae, amyloideae, apiculo obliquo instructae. Cystidia haud visa. Gloeocystidia 2.7–4.5 μm lata, apice geniculata, cylindracea vel fusiformia. Chlamydosporae usque ad 10 μm latae, ramorum parte inferiore ortae, numerosae, vulgo terminales, obclavatae vel oblageniformes, interdum papillatae, pariete valde incrassato instructae.
Holotypus: *P. Ypelaar 10*, vide infra (WBS).

Basidiomata c. 20 mm high, cespitose, branched from the base or halfway up. Branches 1 mm wide, gradually dilated to 2 mm upwards, trumpet-like, straight or curved, cylindrical below, depressed or funnel-shaped above, sometimes deeply incised on one side, hence helicoid or with involute margins, with revolute and entire or variously incised lip, smooth inside, marked with ribs or veins outside, glabrous, somewhat shiny, avellaneous to bay below, blackish brown above. Stipe hardly developed, springing from a mycelial growth immersed in the wood. Context whitish. Odour and taste unknown.

Hyphae 3.5–11.5 μm wide, somewhat inflating, thin- to moderately thick-walled (up to 1 μm), anastomosing, branched, septate, with clamp-connections. Gloeoplerous hyphae 2.5–6.5 μm wide, particularly numerous under the surface. Basidia 27–32 × 5.4–6.3 μm (not seen mature), clavate, with basal clamp, 4-spored, with 3.6–4.5 μm long sterigmata. Spores 4.3–4.9 × 3.6–4.3 μm, broadly ellipsoid to subglobose, somewhat thick-walled, fairly densely echinulate, colourless, amyloid, with oblique apiculus. Cystidia not seen. Gloeocystidia 2.7–4.5 μm wide, geniculate in the hymenial region, cylindrical to fusiform. Chlamydospores up to 10 μm wide, occurring in the surface layers of the lower part of the branches and reaching the lower limit of the hymenium, numerous, usually terminal, obclavate to oblageniform, sometimes papillate, very thick-walled.



Figs. 1–5. *Clavicorona dryophila*. — 1. Some of the branches of a basidiome. — 2. Two spores. — 3. Longitudinal section through the cortex in the lower part of a branch, showing generative and gloeoplerous hyphae, and three chlamydospores. — 4. Chlamydospores among immature basidia in the lower reaches of the hymenium. — 5. Diverse shapes of chlamydospores.
(Fig. 1, ×10; fig. 2, ×2800; figs. 3–5, ×700.)

Holotype: "Netherlands, prov. Drente, Boswachterij Dwingelo, Schurenberg, 28 Aug. 1972, *P. Ypelaar 10*, among mosses on decayed wood of *Quercus robur*" (WBS).

A note with this collection indicates the spores as 5–8 × 4–7 μm, but I have not seen them of that size. It should be pointed out, however, that the above description has been drawn up from dried material which to all appearances was not fully mature when it was collected.

Even allowing for possible changes in somewhat older material, sufficient differences can already be pointed out now to warrant separation from all other species thus far described.

The species of subgenus *Clavicorona* (see Dodd, 1972: 747) can be ruled out on account of the colour and the permanently unbranched condition of the clavula. *Clavicorona cristata* (Kauffm.) Doty and *C. divaricata* Leathers & Smith of subg. *Ramosa* Dodd differ in having elongate-ellipsoid spores. *Clavicorona candelabrum* (Massee) Corner, *C. dichotoma* Corner, and *C. turgida* (Lév.) Corner drop out since their basidia are said to be less than 20 μm long. Of the three remaining species, *C. pyxidata* (Pers. ex Fr.) Doty is excluded by its narrow spores less than 3 μm broad. *Clavicorona colensoi* (Berk. apud Hook.) Corner, if taken to be a different species from *C. piperata*, can be separated from *C. dryophila* by the following characters: the base of the basidiome is 'inserted on small, brown, hairy, effuse mycelial patch with

fibers radiating from attached stalk' (Dodd, 1972: 755), the hyphae are thin-walled, the basidia are rather short (20–25 μm long), the spores are stated to be thin-walled. In addition, it seems unlikely that a New Zealand species should turn up in Holland, without having been detected in other parts of Europe as well. *Clavicorona piperata* (Kauffm.) Leathers & Smith, finally, differs from *C. dryophila* in (i) being branched verticillately in 2–5 ranks, (ii) wider branches, (iii) hirsute stipe, (iv) thin-walled spores, and (v) occurrence on conifer logs.

From all these species, *C. dryophila* differs moreover in the possession of conspicuous chlamydospores.

Reference

Dodd, J. L. (1972). The genus *Clavicorona*. *In* Mycologia **64**: 737–773.

MELASTIZA FLAVORUBENS FOUND IN THE NETHERLANDS

R. A. Maas Geesteranus

Rijksherbarium, Leiden

Melastiza flavorubens (Rehm) Pfister & Korf apud Korf

[*Geoscypha depressa* var. *flavorubens* Rehm *in* P. Sydow, Mycoth. march., No. 884. 1885 (?), without descr., not validly publ.] — *Humaria flavorubens* Rehm *in* Rabenh., Kryptog Fl. II **1** (3): 960. 1894. — *Melastiza flavorubens* (Rehm) Pfister & Korf *apud* Korf *in* Phytologia **21**: 204. 1971.

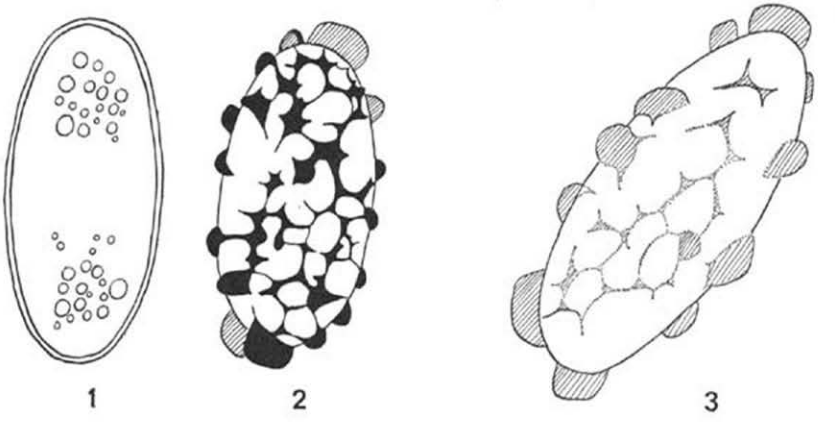
Type distribution: P. Sydow, Mycoth. march., No. 884.

Apothecia up to 7 mm across, sessile on a narrow base, cup-shaped to discoid. Disc orange-red, somewhat paler than Séguy No. 181 (equalling Methuen 7 B8). Receptacle dingy orange-yellow, marked with closely spaced darkish brown warts or short veins made up of bunches of excipular hairs. (The hairs may also be visible individually.) Excipular hairs up to 70 μm long, 8–12 μm wide, shorter towards margin, few-celled to 1-celled, with moderately thickened, yellow-brown walls, with blunt tips. Ectal excipulum of textura globuloso-angularis (cells 12–30 × 12–24 μm), towards medullary excipulum gradually passing into textura intricata-like tissue. Asci 195–225 × 10–12 μm, 8-spored, not blued by iodine. Spores 13.4–16.1 × 7.2–8 μm (probably not quite mature), obliquely 1-seriate in ascus, 1-celled, ellipsoid, with a cluster of small oil drops at each end, ornamented. Ornamentation consisting of smaller or larger blobs (the largest at the ends of the spores), which readily stain blue in Cotton Blue and which are united by a low, incomplete reticulum. Paraphyses 2–4 μm wide, septate, branched near base or simple, apices clavate, 6–8 μm wide, densely filled with orange granulations and droplets which turn green in iodine.

On damp, moss-covered sand near a pond.
Netherlands: prov. Overijsel, Deventer, De Wijtenhorst, 22 June 1969, *Mr. & Mrs. J. H. Piepenbroek* (L).

Not previously recorded from this country.

There is an annotation slip by Korf & Pfister in Herb. Stockholm indicating the following material as holotype: '16 / ? *Geoscypha depressa* (Phill.) var. *flavorubens* Rehm / Auf feuchter Erde unter Gebüsch in Grunewald / August 1885. leg. P. Sydow / (Scheibe frisch gelblich roth!)' Apparently they acted under the presumption that this material was part of Sydow's Mycotheca marchica 884, a copy of which is also present in S. This is an error. The label of this exsiccatum reads: 'Auf Erde im Thiergarten b[ei] Berlin / 7. 1885. leg. P. Sydow.' The holotype label stuck to the envelope marked No. 16 should be removed; it is No. 884 which serves as type distribution.



Figs. 1–3. *Melastiza flavorubens*. — 1, 2. A young and an almost mature spore taken from the Dutch collection. — 3. Immature spore from Stockholm copy of Mycoth. march. 884. (All figures, ×2800).

The copy of this exsiccatum at Stockholm is rather poor, containing two and a half apothecia, while the copy at Uppsala is somewhat better in having more and better preserved apothecia.[1] I used a loose fragment (probably from near the centre of an apothecium) of the Stockholm material for the following redescription.

Ectal excipulum of textura globuloso-angularis (cells 13.5–35 × 13.5–22 μm), bearing scattered excipular hairs 27–70 × 6–12 μm, with 0–3 septa, with moderately

[1] I gratefully acknowledge the loan of valuable material from the herbaria at Stockholm and Uppsala.

thickened, somewhat brownish walls, and with blunt tip. Asci 9–10 μm wide, 8-spored. Spores 16.8–19.7 × 6.3–8.1 μm (somewhat swollen from the harsh treatment they had been subjected to?), obliquely 1-seriate in ascus, 1-celled, ellipsoid, with a small oil drop at each end, with very faint ornamentation of scattered spots and few lines of incipient reticulum. Paraphyses 2.7–3.6 μm, septate, with apices 4.5–6.3 μm wide.

ON CEROCORTICIUM P. HENN., A GENUS DESCRIBED FROM JAVA

W. Jülich

Rijksherbarium, Leiden

In 1899, P. Hennings described a new genus of 'Thelephoraceae', viz. *Cerocorticium*, based on two specimens collected by E. Nyman and M. Fleischer on Java. According to him these specimens represented two different species of his new genus.

The descriptions Hennings gave of the genus and the two species are rather poor and incorrect. His diagnosis of the genus runs: 'Resupinato-effusum, subgelatinosum, sicco ceraceum. Hymenium glabrum, laeve. Basidia conferta, subclavata, 2-sterigmatibus. Sporae ellipsoideae vel ovoideae, hyalinae.' (p. 138, in reprint p. 40). In a short discussion he declared the genus to be quite different from any *Corticium* because of the permanently 2-spored basidia and distinct from *Michenera* because of the absence of paraphyses. Contrary to this, examination of the type material revealed that the basidia are always 4-spored and paraphysoid hyphae are always present! The two species *C. bogoriense* P. Henn. and *C. tjibodense* P. Henn. are conspecific and nothing else but *Corticium ceraceum* Berk. & Rav., as already mentioned by von Höhnel (1910).

At the time of Hennings and von Höhnel the genus *Cerocorticium* seemed unnecessary since there was no reason for removing the two species from the main genus *Corticium*. But nowadays this genus has been split up in a large number of smaller genera, most of which are probably good. In this series of genera *Cerocorticium* P. Henn. has a clearly delimited place. The genus is characterized by ceraceous basidiocarps, large basidia and large inamyloid spores, as well as by the presence of paraphysoid hyphae between the basidia and clamp-connections at all septa. Up to now this genus is monotypic, but several other species of uncertain affinities will probably show to have their proper place in this genus.

The question that remains is, from which name the specific epithet has to be taken: from *Corticium molle* Berk. & Curt., *C. ceraceum* Berk. & Rav., or *C. armeniacum* Sacc.

Type material of *Corticium ceraceum* Berk. & Rav. was distributed in 1855 in Ravenel, Fungi Carol. Exs. III, 29 without any description, leaving the name a *nomen nudum*. The description was not published until 1890 by Massee. In the meantime (1868)

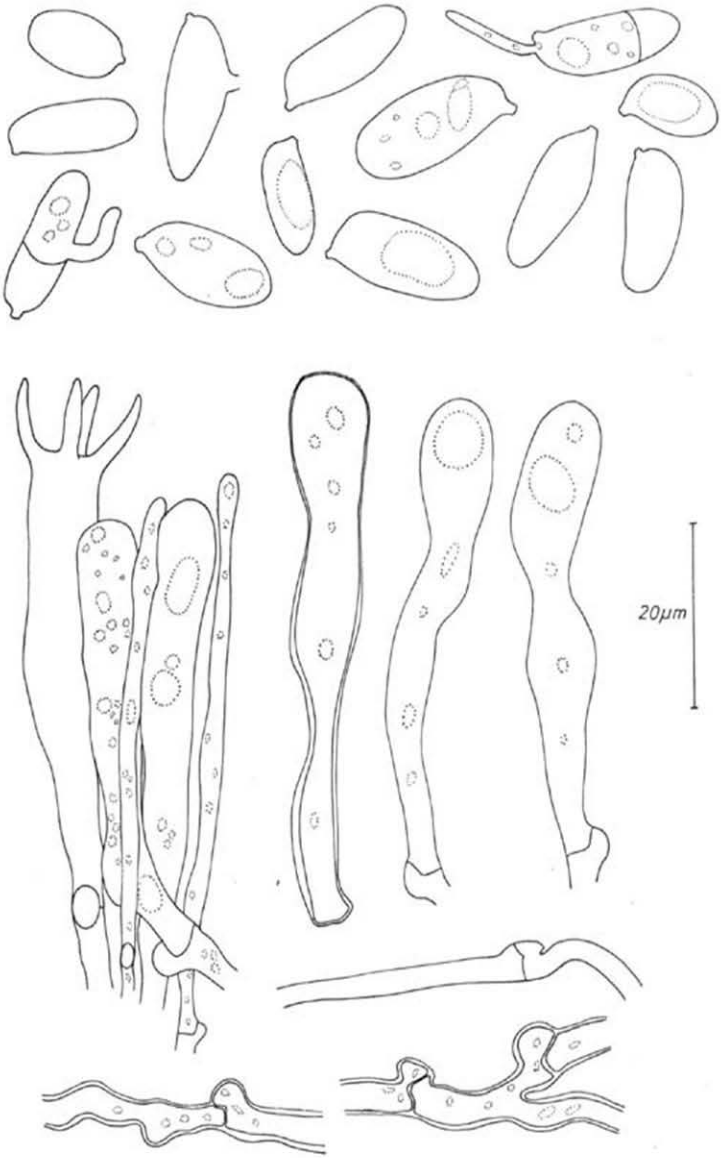


Fig. 1. *Cerocorticium molle* (Berk. & Curt.) Jülich. — Spores, paraphysoid hyphae, basidia (thin- or slightly thick-walled), and basal hyphae.
(All Figs. from A. L. Welden, L 967.254–055).

Berkeley published a new name accompanied by a description for the species in question, viz. *Corticium molle* Berk. & Curt., based on material from Cuba. Some years later he redescribed the same species under the same name (1873). In 1874 Fries, obviously without any knowledge of the species published by Berkeley, transferred *Thelephora mollis* Fr. 1821, a quite different species, to *Corticium*. When Saccardo (1888) compiled the species descriptions for Sylloge Fungorum Vol. VI, he twice found the name *Corticium molle* and proposed for the younger epithet '*molle* Berk. & Curt.' the new name *Corticium armeniacum* Sacc. It may be added that he did not accept the species '*molle* Fr.' as belonging to *Corticium*, but placed it in the genus *Hypochnus*.

Since the name *Corticium molle* Berk. & Curt. is the oldest one available for the species in question, and since *Corticium molle* (Fr.) Fr. is a later homonym, the epithet '*molle* Berk. & Curt.' is to be used in connection with *Cerocorticium*.

Cerocorticium P. Henn.

Cerocorticium P. Henn. *in* O. Warburg, Monsunia **1**: 138. 1899; *in* Engler & Prantl, Natürl. PflFam. **1**(1[xx]): 553. 1900. Type species: *Cerocorticium bogoriense* P. Henn. 1899 = *Corticium molle* Berk. & Curt. 1868.

Basidiocarp resupinate, effused, ceraceous. Hymenial surface more or less even, light coloured. Hyphal system monomitic. Hyphae hyaline, thin- or thick-walled, with clamp-connections. Paraphysoid hyphae present. Basidia large, clavate or broadly cylindrical, with a basal clamp. Spores hyaline, smooth, large, inamyloid, with a rather large apiculus, more or less thin-walled.

Scope: originally described with two species, up to now monotypic.

Cerocorticium molle (Berk. & Curt.) Jülich, *comb. nov.*

Corticium molle Berk. & Curt. *in* J. Linn. Soc. (Bot.) **10**: 336. 1868 (basionym); not ∽(Fr.) Fr. 1874.

Corticium armeniacum Sacc., Sylloge Fung. **6**: 637. 1888.

Corticium ceraceum Berk. & Rav. *apud* Massee *in* J. Linn. Soc. (Bot.) **27**: 150. 1890.

Cerocorticium bogoriense P. Henn. *in* O. Warburg, Monsunia **1**: 139 (in reprint p. 41). 1899.

Cerocorticium tjibodense P. Henn. *in* O. Warburg, Monsunia **1**: 139 (in reprint p. 41). 1899.

Corticium mauritianum Berk. in herb.

Basidiocarp resupinate, effused, adnate, hymenial part ceraceous, basal part as well as margin often more membranaceous. Hymenial surface even or slightly warted, yellowish-orange, not or only slightly cracked when dry. Hyphae hyaline, always with clamps, often with oily droplets in the cytoplasma, thin-walled and agglutinated in the hymenium, thick-walled (up to 1.3 μm) in base of context, often somewhat torulose and densely interwoven but not glued together, 2–4 μm in diameter. Paraphysoid hyphae hyaline, thin-walled, irregular-cylindrical, with some oily droplets in the cytoplasma and a basal clamp, 2–3 μm in diameter. Basidia hyaline, clavate, thin- or slightly thick-walled, with a basal clamp, 40–70 × 7–9 μm, with four large and slightly curved sterigmata 7–10 × 1.5–2.2 μm, contents of unripe basidia with some large or many small oily droplets. Spores hyaline, thin-walled,

smooth, often with oily contents, with large, conspicuous apiculus, 15–18 × 5.9–7 μm; germination mostly with one germ tube, often a secondary septum formed in spores concentrating the amount of cytoplasma.

CYTOLOGY.—Basal hyphae 2-nucleate.

REACTIONS.—No part of basidiocarp amyloid, dextrinoid or cyanophilous.

DISTRIBUTION.—Known from the southern parts of North America, Mexico, Cuba, North and South Africa, and Java.

MATERIAL STUDIED.—NORTH AMERICA, U.S.A.: Louisiana, St. Martinsville, 11 April 1898 and 14 March 1899, *A. B. Langlois* (S); Louisiana, Plaquemines par., Hebert Center, 12 March 1972, *A. L. Welden* (L); Ohio, C. G. Lloyd (S); South Carolina, *Ravenel* (=Ellis, N. Am. Fung. 607) (K, S).

CUBA: C. Wright (S). — Wright, Fung. Cub. 446 (K, S).

AFRICA: Algeria, Zambese, Torrend (S).

JAVA: without any dates, types of *Cerocorticium bogoriense* P. Henn. and *Cerocorticium tjibodense* P. Henn. (S).

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A NEW SPECIES OF CORYNESPORA

W. M. LOERAKKER

Centraalbureau voor Schimmelcultures, Baarn

In the course of investigations on fungi occurring on bark of deciduous trees, an unknown dematiaceous fungus was encountered. Because of its long, septate conidia, arising from the apex of dark conidiophores, the specimen was thought to represent an undescribed species of the genus *Corynespora* Güssow. This identification was kindly confirmed by Dr. M. B. Ellis, C. M. I., Kew.

Corynespora proliferata Loerakker, *sp. nov.*—Fig. 1

Coloniae nigrae, irregulares, effusae. Mycelium in substrato immersum, partim et superficiale, e hyphis ramosis, levibus, hyalinis, tenuitunicatis, 2.5–4 μm crassis constans. Stromata superficialia e singulis vel paucis stratis cellularum brunnearum, irregularium, 5–20 μm crassarum constantia, parietibus ad 1 μm crassis. Conidiophora singula e cellulis stromatis,

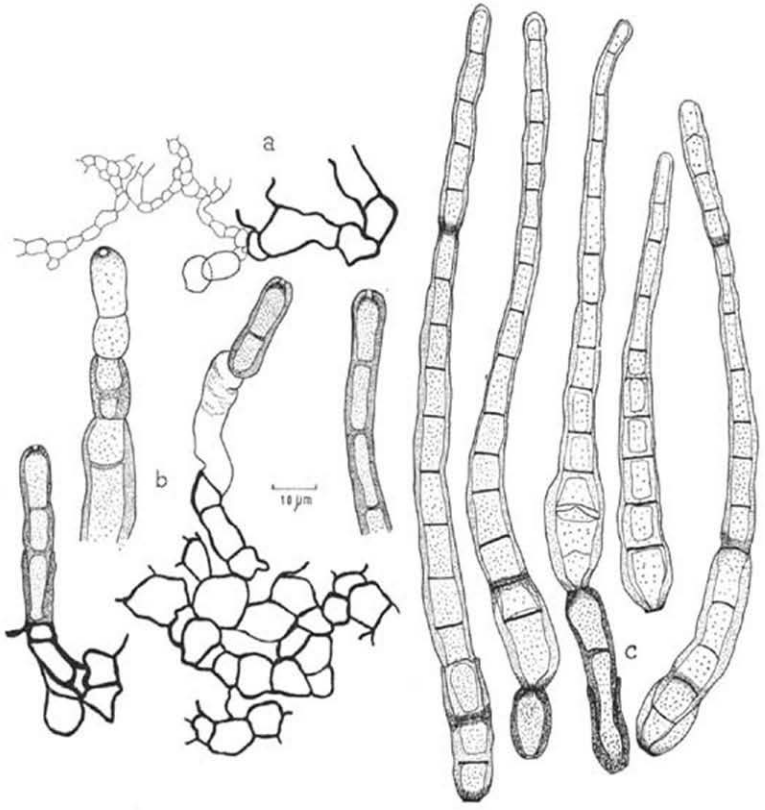

Fig. 1. *Corynespora proliferata*. — a. Mycelium. — b. Stromal cells and conidiophores. — c. Conidia.

nonnumquam et e hyphis mycelialibus oriuntur, erecta, simplicia, recta, fusca, levia et fere crassitunicata, plerumque bis vel ter septata, 30–70 µm longa, 7–8(–10) µm crassa; porus apicalis circa 1.5 µm diam., zona fuscata crassitunicata circumdatus. Conidiophora saepe percurrenter proliferant in partem secundariam uni- ad tricellularem. Conidia singula oriuntur, primum sursum hyalina et fragilia, apicem versus maturant; extensio nonnumquam interrupta et subinde continuata zonam fuscatam, constrictam relinquens. Conidia matura olivaceo-brunnea, crassitunicata, levia, recta vel modice curvata, rostrata vel obclavata, 6–19 septis praedita, 90–185 µm longa, deorsum 12–13 µm crassa, sursum 4.5 µm.

Typus in Herbario IMI 183.273 (in Herb. CBS 79) praeservatur, lectus in ligno *Fagi sylvaticae* prope Baarn.

Colonies black, irregular, effuse. *Mycelium* immersed in the substratum, occasionally superficial, composed of branched, smooth- and thin-walled hyphae consisting of

hyaline, rounded cells 3–6 × 2.5–4 μm, locally with somewhat inflated, pale brown, rather thick-walled cells. *Stromata* superficial, composed of one or few cell layers; cells brown, irregular in shape, 5–20 μm in diameter, with up to 1 μm thick walls. *Conidiophores* arising singly from cells of the stroma, occasionally directly from the mycelium, erect, simple, straight, dark brown, smooth- and rather thick-walled, (0–)2–3(–5) septate, 30–75 μm long and 7–8(–10) μm wide. Apical pore c. 1.5 μm wide, surrounded by a darker thick-walled zone. Frequently the conidiophore proliferates percurrently and gives rise to a short, 1–3-celled secondary conidiophore; rarely a tertiary conidiophore is formed. *Conidia* arising singly, when young apically with a hyaline, fragile wall, ripening from the base towards the tip. Extension growth often interrupted at irregular sequences and continued afterwards, usually leaving darker, constricted zones. Mature conidia olivaceous brown, smooth-walled, straight or slightly curved, rostrate to obclavate, with 6–19 septa, 90–185 μm long; width 12–13 μm in the broadest part, 4.5 μm near the apex and 3–4 μm at the usually truncate, darkened basal scar.

Type: IMI 183.273 (slides in herb. CBS no. 79), on wood of *Fagus sylvatica* L., Baarn.

Corynespora proliferata is closely related to *C. gigaspora* (Berk. & Br.) M. B. Ellis, which differs by conidiophores usually arising in small fascicles from a stroma, and by narrower conidia with larger basal scars. *Corynespora polyphragmia* (Sydow) M. B. Ellis is also similar, but has broader conidia and basal scars, and longer conidiophores, which mostly arise in groups and frequently show up to four percurrent proliferations. *Corynespora vismiae* M. B. Ellis can be distinguished by smaller conidia, and *C. smithii* (Berk. & Br.) M. B. Ellis by longer conidiophores, which often occur in dense tufts, and cylindrical conidia with a larger basal scar. *Corynespora cassiicola* (Berk. & Curt.) Wei possesses long conidia too, but can be recognized by the absence of any stroma. In a number of species of *Corynespora*, e.g. in *C. gigaspora*, *C. polyphragmia* and *C. vismiae*, Ellis (1957, 1961, 1963) describes similarly constricted conidia as in *C. proliferata*, but regards them as conidial chains. In *C. proliferata*, however, no fragmentation of conidia could be observed.

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MARASMIELLUS CAESPITOSUS (PAT.) SING. IN THE NETHERLANDS

M. E. Noordeloos
Rijksherbarium, Leiden

In the late summer of 1971 a tiny whitish agaric was collected by the algologists C. J. den Hartog and V. N. de Jonge on dead leaf-sheaths of *Juncus maritimus* in the salt-marshes of the Mokbaai on the island of Texel (prov. Noord-Holland). When the material arrived at the Rijksherbarium it was in a bad condition because of age and transport, and a thorough microscopical analysis was therefore difficult to make. During the three following years, however, I succeeded in collecting more material in a better state from the same locality and also from another salt-marsh on the island of Goeree (prov. Zuid-Holland) in the south-western part of the Netherlands.

The fruit-bodies of this characteristic species are marasmioid, about 1 cm high with a white or yellowish pileus, slightly decurrent, white lamellae and a pruinose, blue-grey stipe.

There are two species, both described from Tunesia, of which the descriptions more or less fit this marasmioid agaric.

First there is *Marasmius trabutii* Maire, transferred to the genus *Marasmiellus* Murrill by Singer. Maire describes this species as occurring on stems and rootlets of *Scirpus holoschoenus* var. *australis*, a sedge growing on the same type of brackish soils as *Juncus maritimus*. His description is very comprehensive and there seems to be no significant discrepancies between the type collection and the collections mentioned above.

Secondly there is *Clitocybe caespitosa* Pat., also occurring in Tunesia, collected on dead culms of the grass *Erianthus ravennae*. Singer (1946: 129) studied the type and concluded that this species had to be transferred to *Marasmiellus*. He considered Patouillard's species very closely related to *Marasmiellus tricolor* (Alb. & Schw. ex Fr.) Sing. because of the habit and the covering of the pileus and the stipe. He discovered that the spores, which according to Patouillard's description measure 9–10 × 4–5 μm, are much larger when mature, viz. 12.5–19 × 5–6.5 μm. Singer himself did not study specimens of *Marasmius trabutii* Maire, but in his opinion there is not much to distinguish *Clitocybe caespitosa* from *Marasmius trabutii*. After comparing Patouillard's description with that of Maire and with my notes on the Netherlands' collections, I see no reason not to accept Singer's view. As Patouillard's name has priority, *Marasmiellus caespitosus* is the correct name, and *Marasmiellus trabutii* a later synonym.

MARASMIELLUS CAESPITOSUS (Pat.) Sing.—Figs. 1–7

Clitocybe caespitosa Pat. *in* C.r. Congr. Socs sav. Paris, Sect. Sci.: 248. **'1908'** [1909]. — *Marasmiellus caespitosus* (Pat.) Sing. *in* Pap. Mich. Acad. Sci. **32**: 129. 1946.

Marasmius trabutii Maire *in* Bull. Soc. bot. Fr. **56**: 278–279, pl. xx, figs. 15–23. 1909. — *Marasmiellus trabutii* (Maire) Sing. *in* Lilloa **22**: 300. '1949' [1951].

Pileus (1.5–)4–8 mm broad, 1–3 mm high, conico-convex to plano-convex, older specimens often flat or slightly omphaloid, often with a distinct papilla, with incurved margin in young specimens, sometimes weakly radially striate-sulcate, glabrous, or finely powdery-pruinose (under lens), sordid white, at centre (very) pale ochraceous-yellow (3A2–3A3).[1] Lamellae (7–)10–16, unequal, with 1–2–5 lamellulae between each pair, sometimes forked or anastomosing, broadly adnate to slightly decurrent, concolorous with cap, somewhat waxy, white (remaining whitish several hours after collecting). Stipe (3–)5–8 × 0.2–0.7(–1) mm, with bulbous base 1–1.5 mm wide, whitish-cream at apex, downwards passing through yellowish-greyish or olivaceous-greyish colours (3C6–3D6) to dark blue-grey at base (22F2, 23F2), pruinose-pubescent, with whitish, towards base more closely set hairs, sometimes glabrescent with age, elastic, very narrow hollow or solid. Flesh of pileus and stipe white. Smell indistinctive, fungoid. Taste mild. Spore print whitish-cream (Romagnesi's colour chart in 'Les Russules': 1b–2a, 'blanchâtre' to 'crême-blanchâtre').

Spores (11.5–)12.6–17.5 × 5.5–7.8 μm, obovate, sometimes lacrymoid, smooth, hyaline, often with 1 or 2 guttulae and many granules, with large apiculus. Basidia 36–45 × 9–12 μm, 4-spored, clavate, with clamp; sterigmata often short with a broad base. Subhymenium composed of branching hyphae. Edge of lamellae with marginal hairs varying from simply fusiform with an abrupt conical tip to irregularly coralloid-nodulose or branched, scattered among basidia. Trama of lamellae irregular, consisting of hyphae 3–8 μm wide, more or less embedded in a gelatinous matter; trama of pileus organized in the same way. Pileipellis consisting of interwoven, mostly repent, irregularly branching, warty hyphae, with heavy incrustations. Cortex of stipe made up of dark brown hyphae 5–11 μm wide and thick-walled (–2.5 μm), in cross-section round to ovate or polygonal; free tips of surface hyphae forming simple or 2-celled, often slightly warty, hyaline hairs with brown base. Context of stipe also with thick-walled hyphae but paler brown to nearly colourless. Hyphae all non-amyloid; clamp connections abundant.

HABITAT.—Solitary or subgregarious on dead leaf-sheaths of dense clumps of *Juncus maritimus* L. in salt-marshes along the Netherlands' coast, August-September.

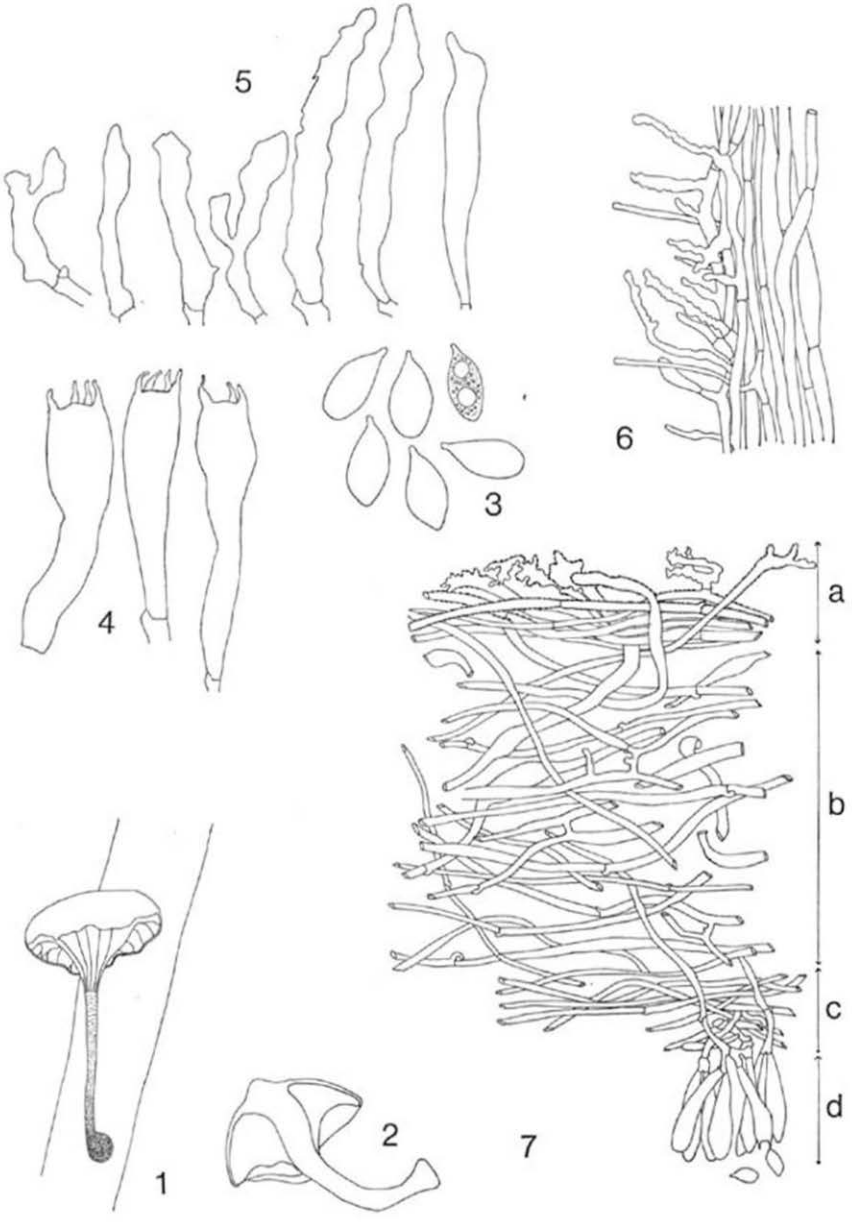
MATERIAL EXAMINED.—NETHERLANDS: prov. Noord-Holland, island of Texel, Mokbaai, 23 Aug. 1971, *C. J. den Hartog*; 11 Sept. 1971, *V. N. de Jonge*; 7 Sept. 1972, 25–26 Aug. 1973, and 22 Aug. 1974, *M. E. Noordeloos*; prov. Zuid-Holland, island Goeree, Kwade Hoek, 10 Sept. 1974, *A. E. Jansen & M. E. Noordeloos* (all coll. in L).

Marasmiellus caespitosus is quite close to *M. tricolor* (Alb. & Schw. ex Fr.) Sing. in having a whitish pileus, a bluish-grey stipe and the same type of covering of pileus and stipe; it differs in having lamellae remaining white after desiccation, much larger spores, typical marginal hairs and perhaps in the gelatinous trama of pileus and lamellae.

[1] These numbers refer to the colour code: Kornerup & Wanscher, Methuen handbook of colour, 2nd ed. London. 1967.

Figs. 1–7. *Marasmiellus caespitosus* (Pat.) Sing. — 1. Carpophore (×4). — 2. Carpophore, radial section (×4). — 3. Spores (×800). — 4. Basidia (×800). — 5. Marginal hairs (×800). — 6. Radial section of stipe, surface hyphae with hairs (×160). — 7. Radial section of pileus; a. Pileipellis, b. Trama=gelatinized zone, c. Subhymenium, d. Hymenium (×160).

(1, 2, and 7 from Mokbaai, 7 Sept. 1972; 3, 4, and 5 from Goeree, 10 Sept. 1974; 6 from Mokbaai, 25/26 Aug. 1972)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In the mycological literature I did not find records of *M. trabutii* or *M. caespitosus* from Western Europe, so perhaps the Netherlands' collections are the first. In western Europe this species is possibly restricted to *Juncus maritimus*, and since not many mycologists collect in salt-marshes, this *Marasmiellus* may not be uncommon along the European coasts where its host occurs.

ACKNOWLEDGEMENTS

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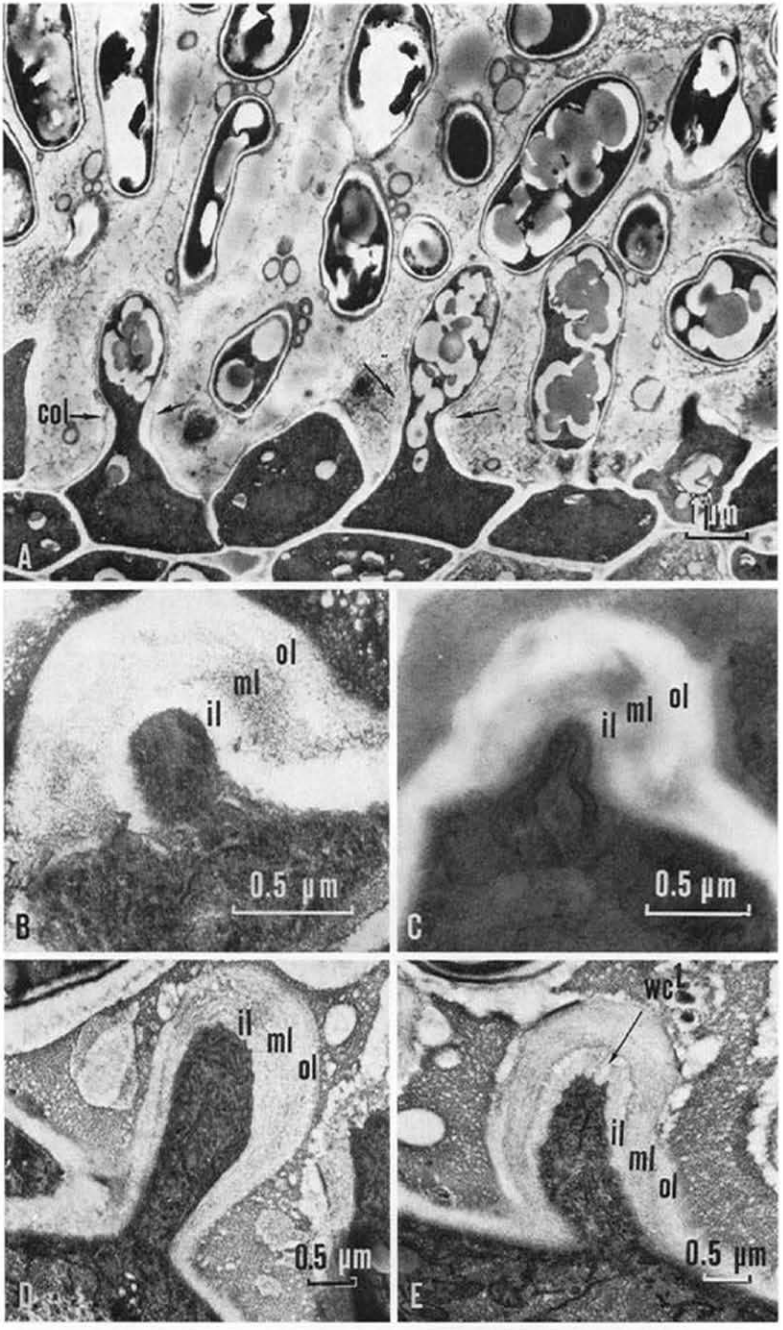
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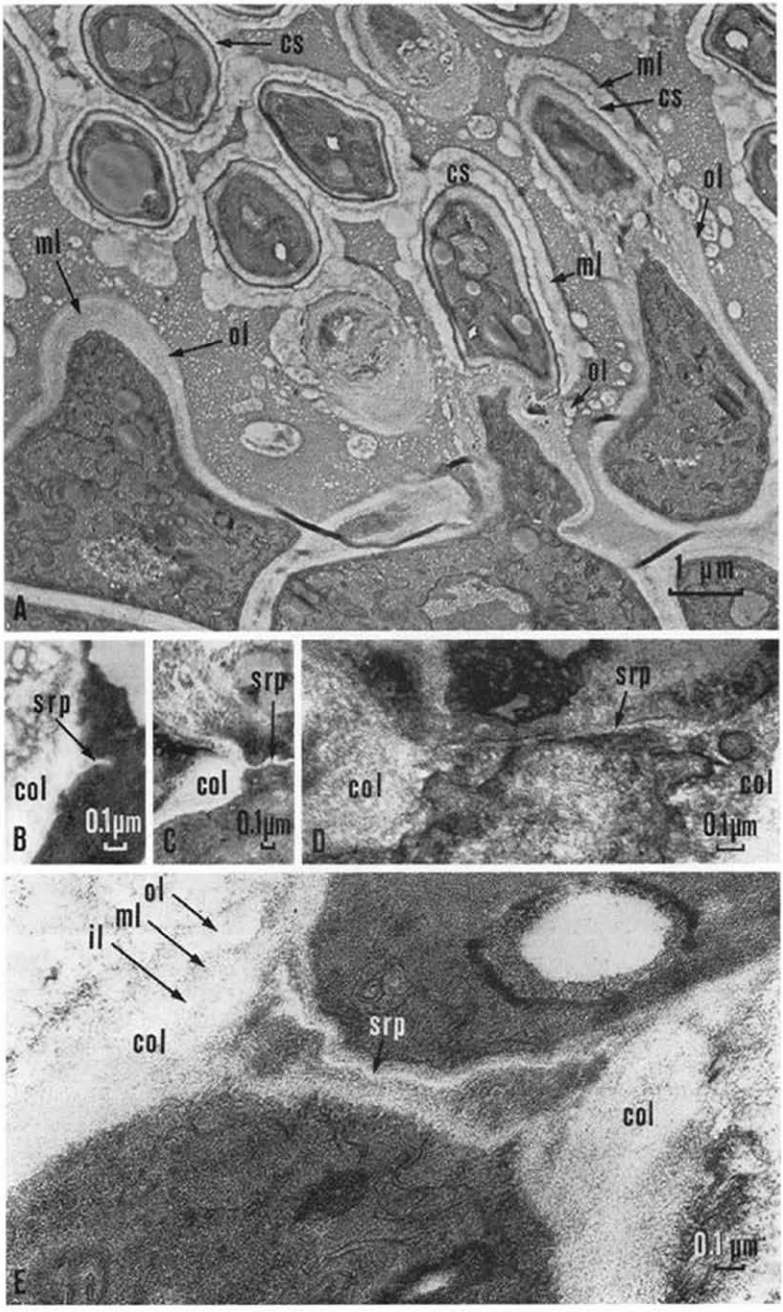
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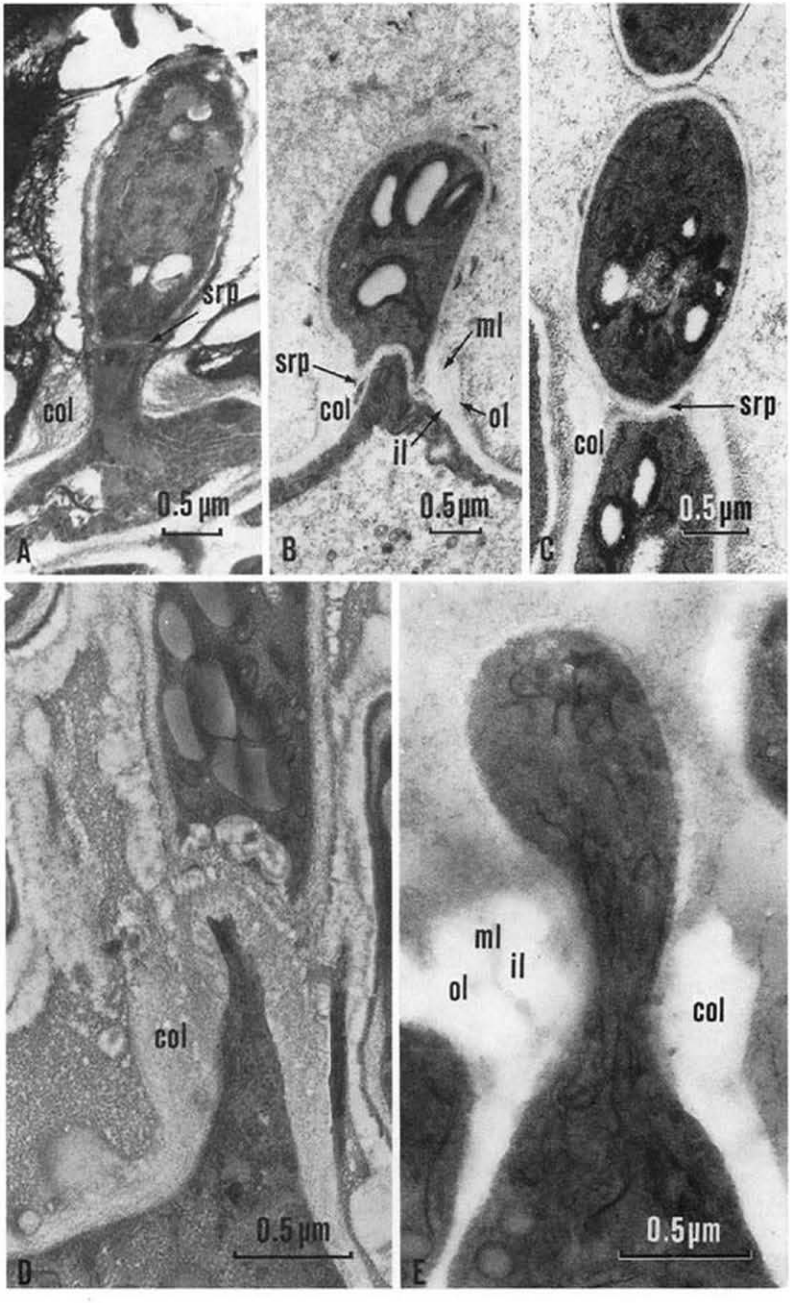
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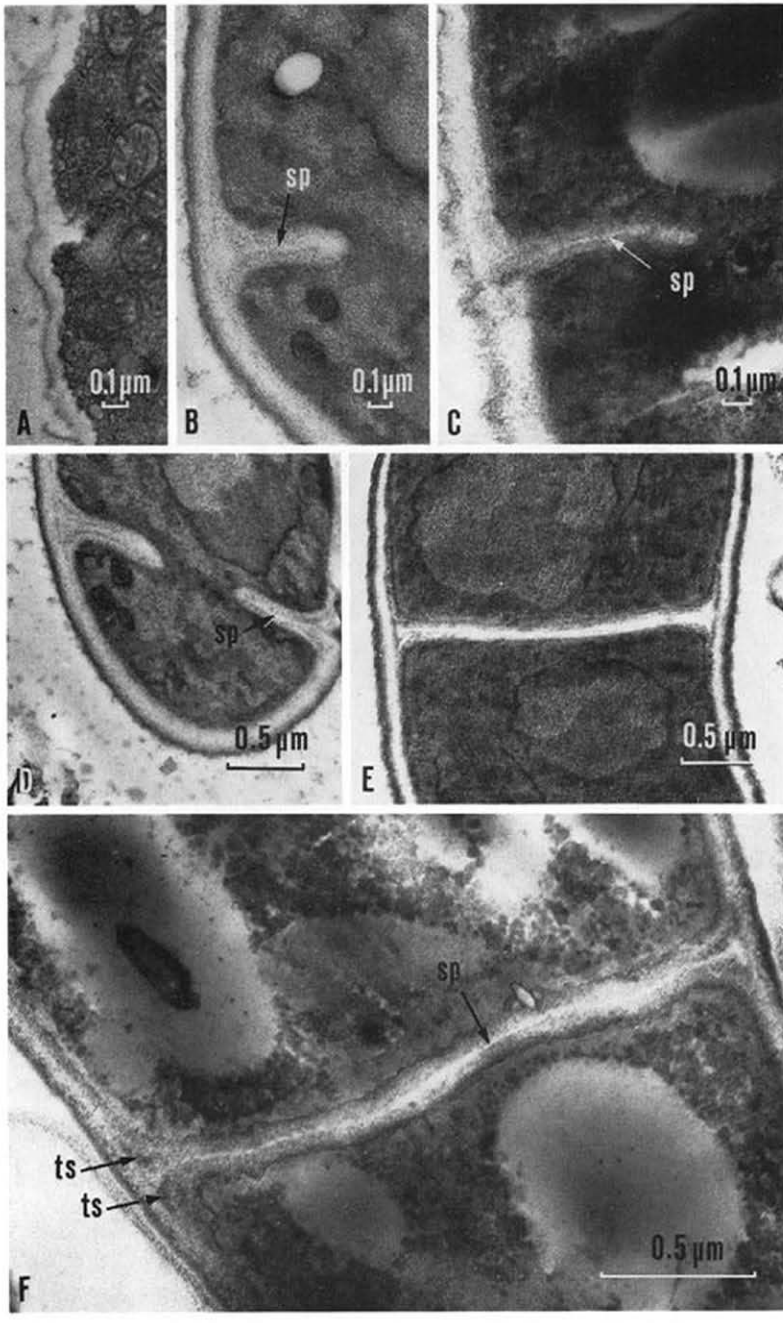
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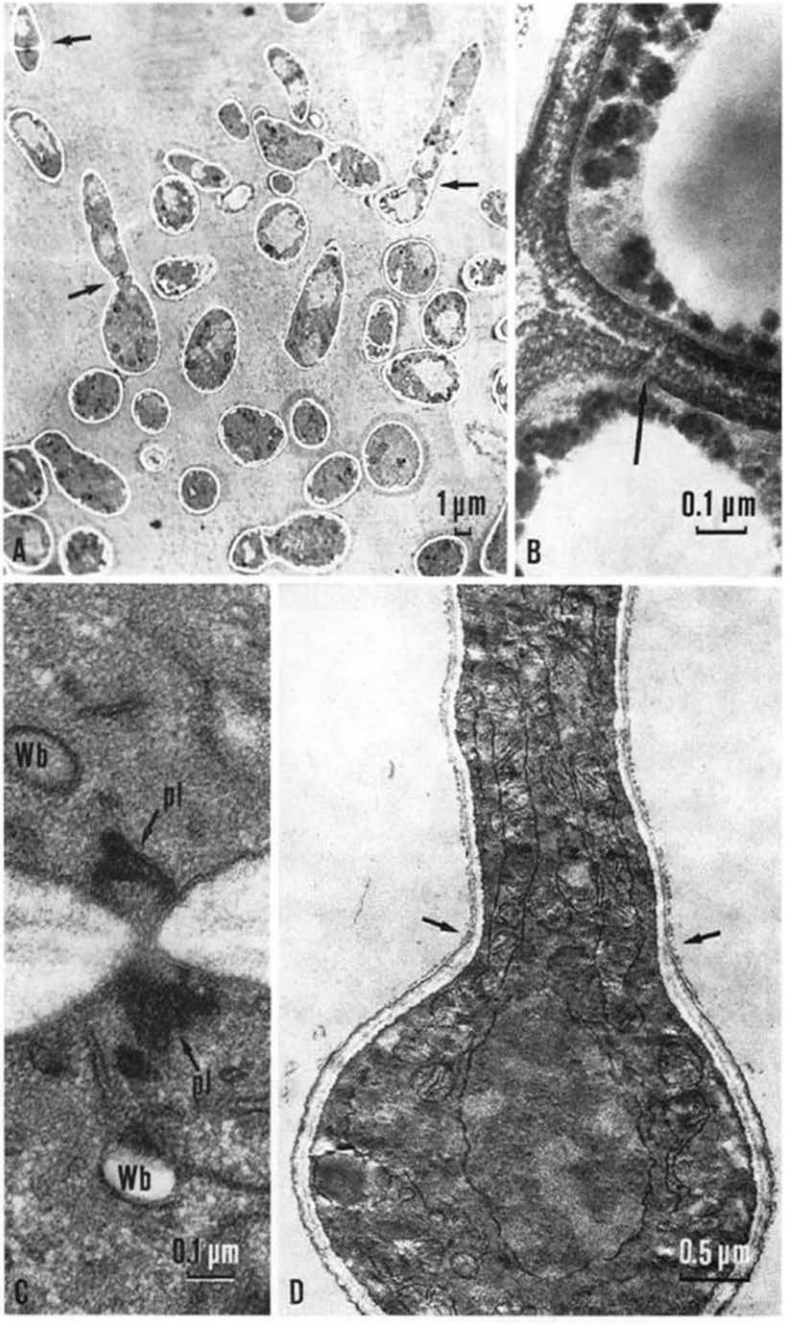
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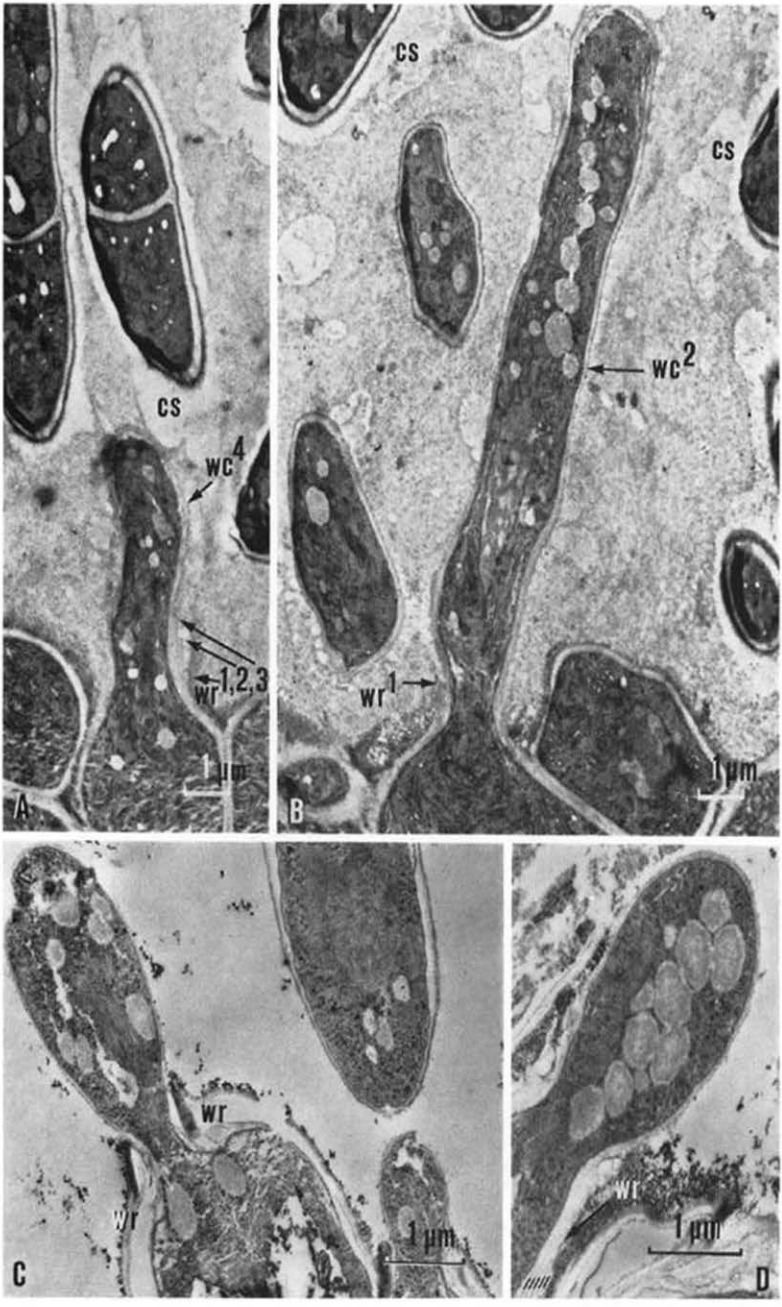
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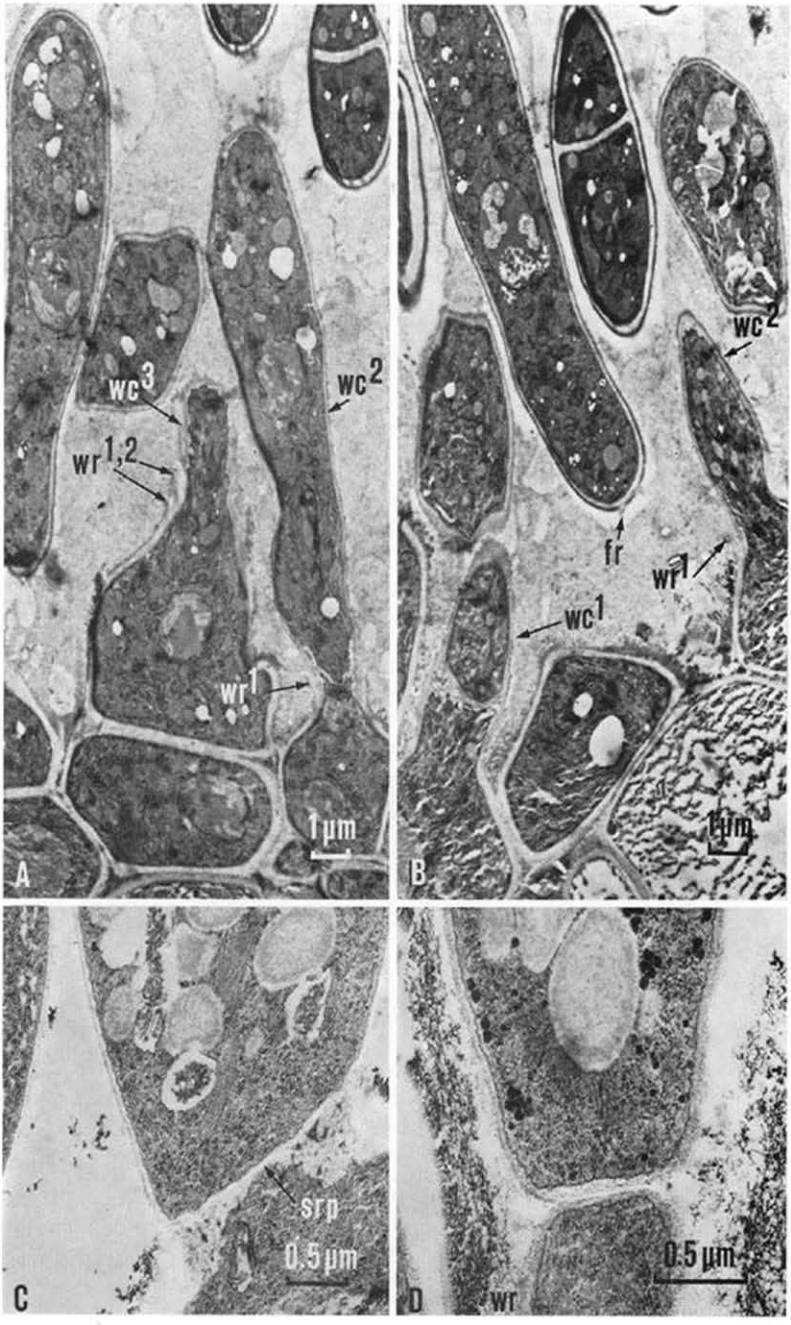
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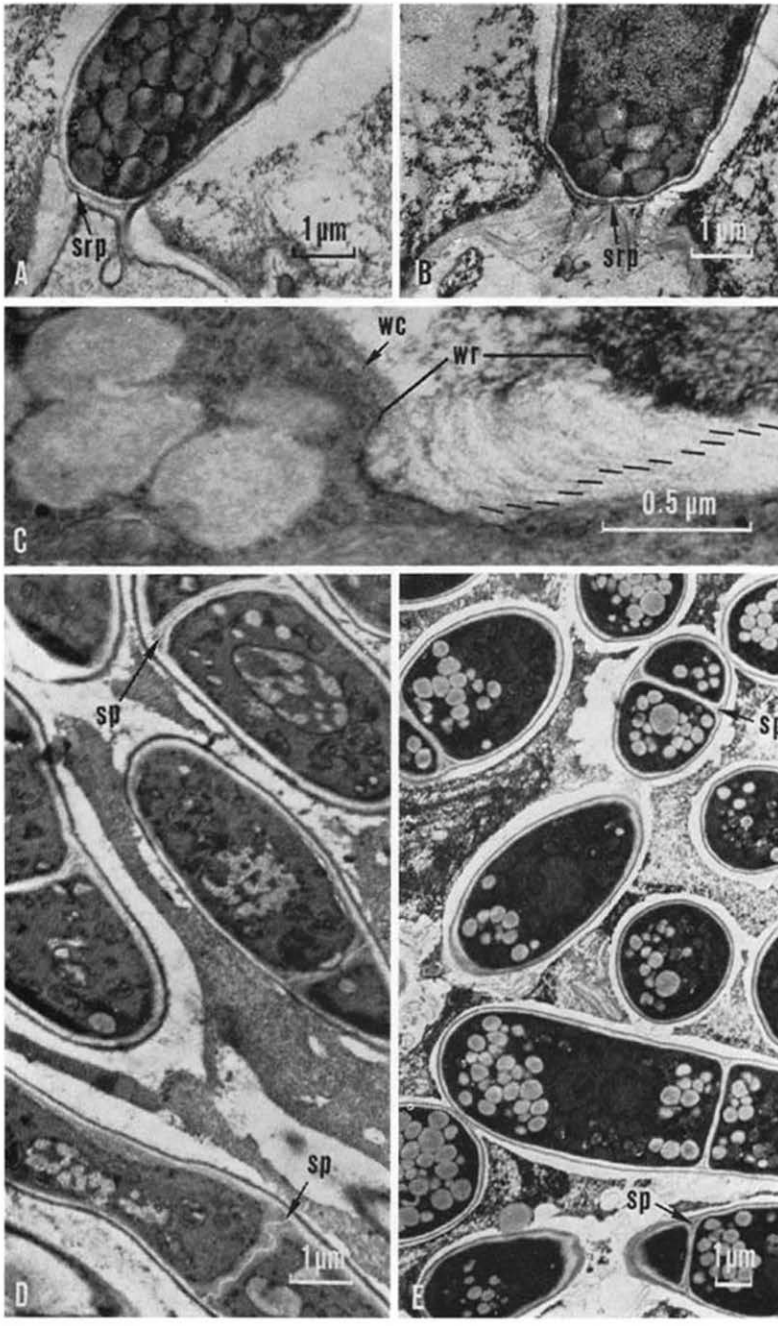
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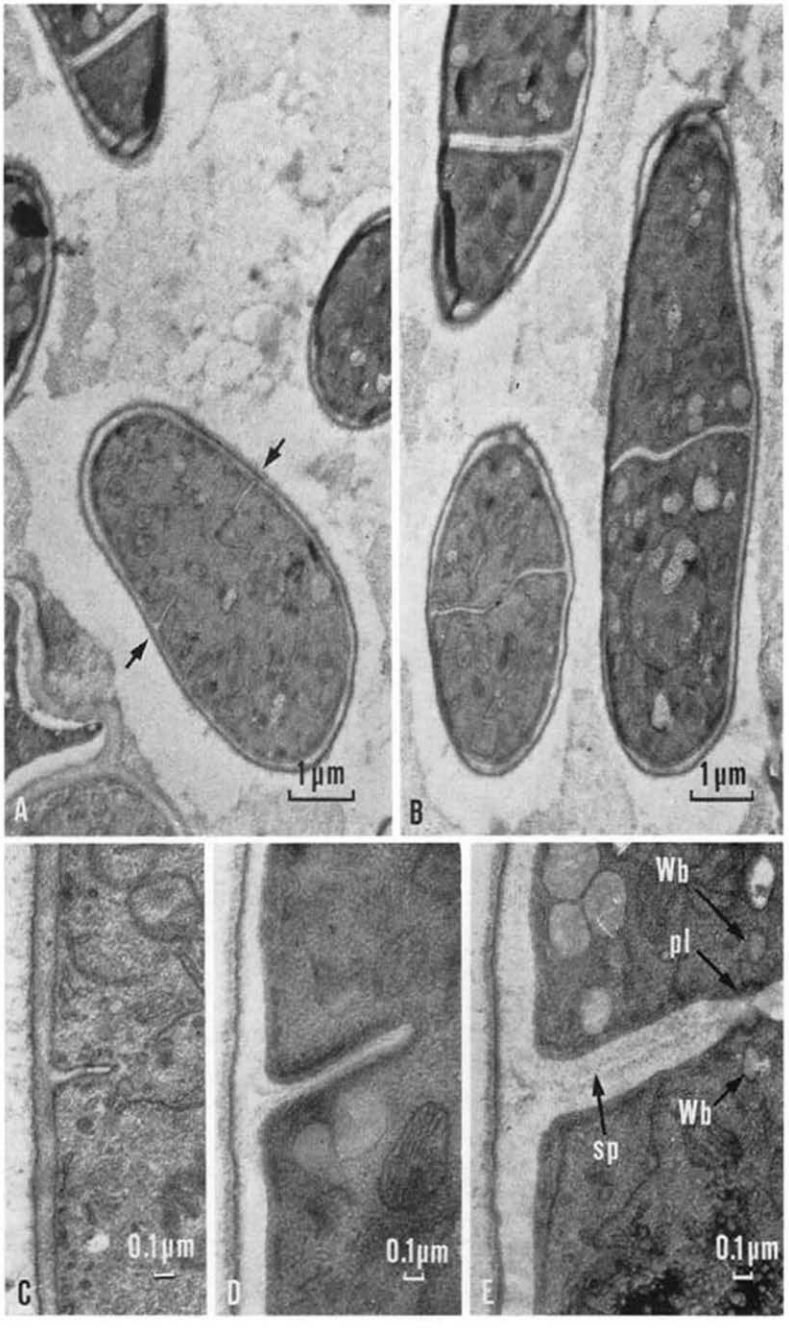
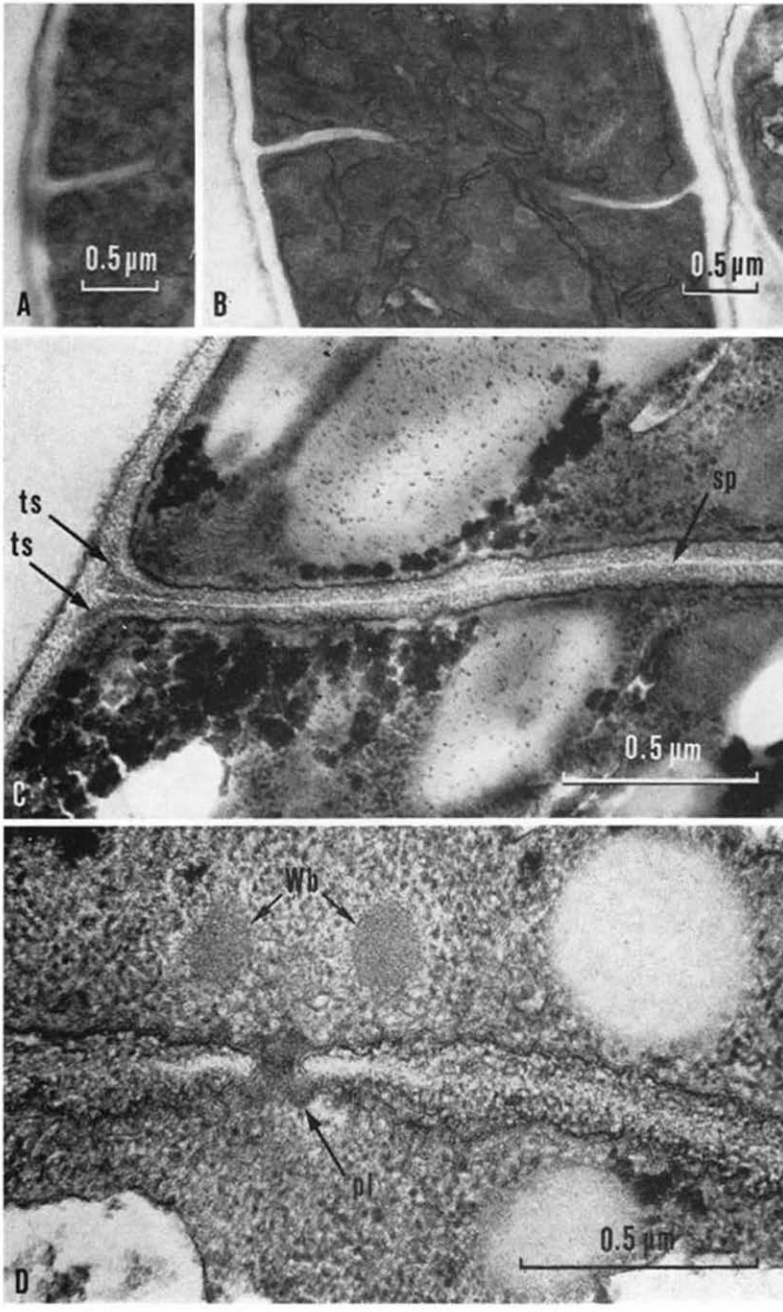
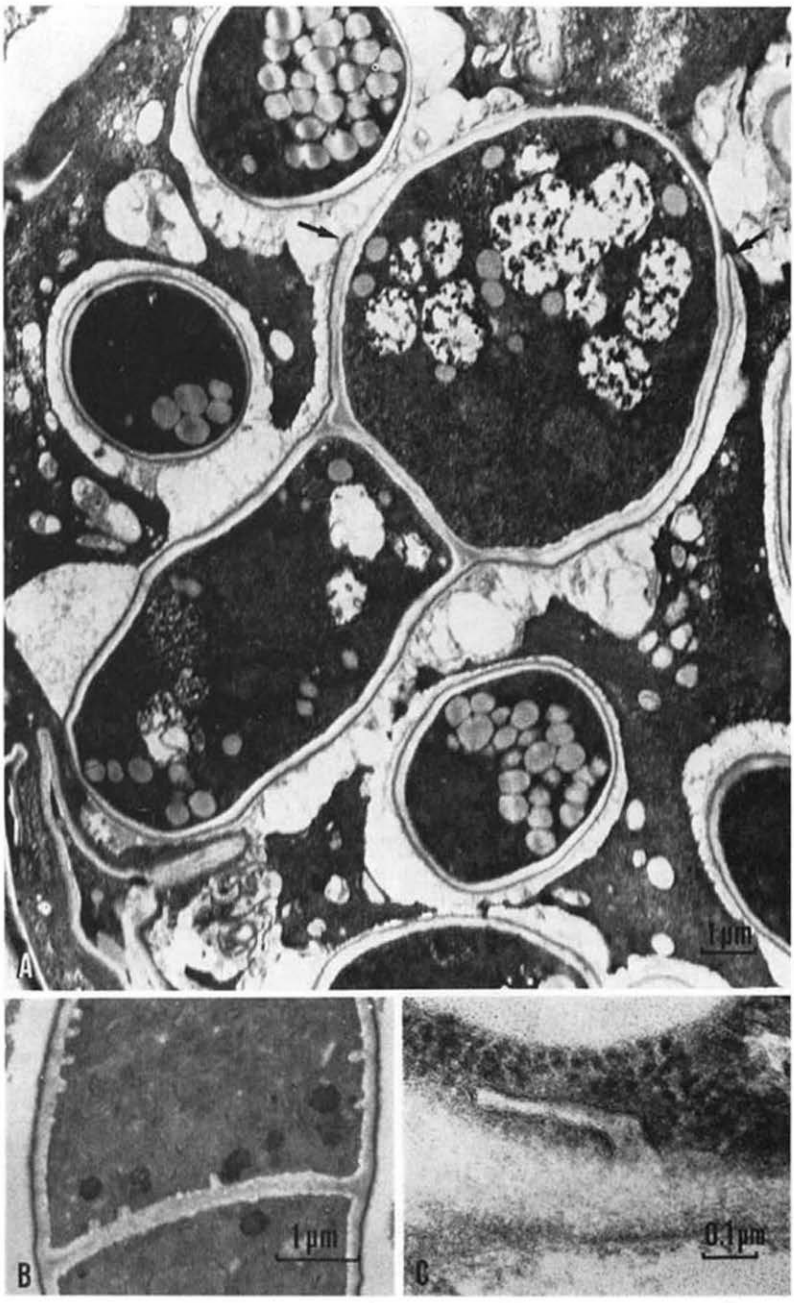
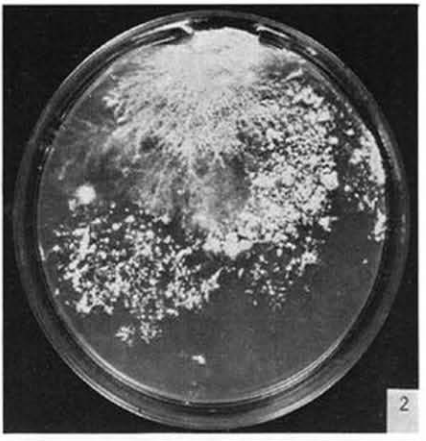
0.5 µm
D
sp
sp
1 µm
E
sp
sp
1 µm


A
1 µm
B
1 µm
C
0.1 µm
D
0.1 µm
E
Wb
pl
sp
Wb
0.1 µm


0.5 µm
A
0.5 µm
B
ts
ts
sp
0.5 µm
C
Wb
pl
0.5 µm
D


A
1 µm
B
1 µm
C
0.1 µm

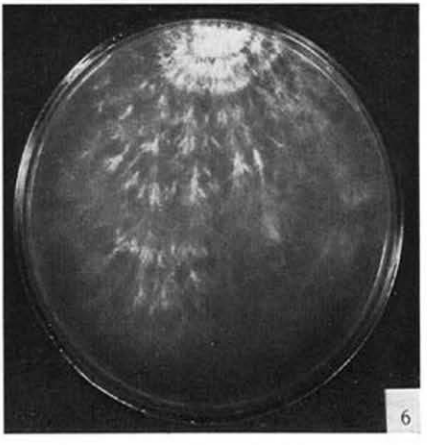

1


2


3


4


5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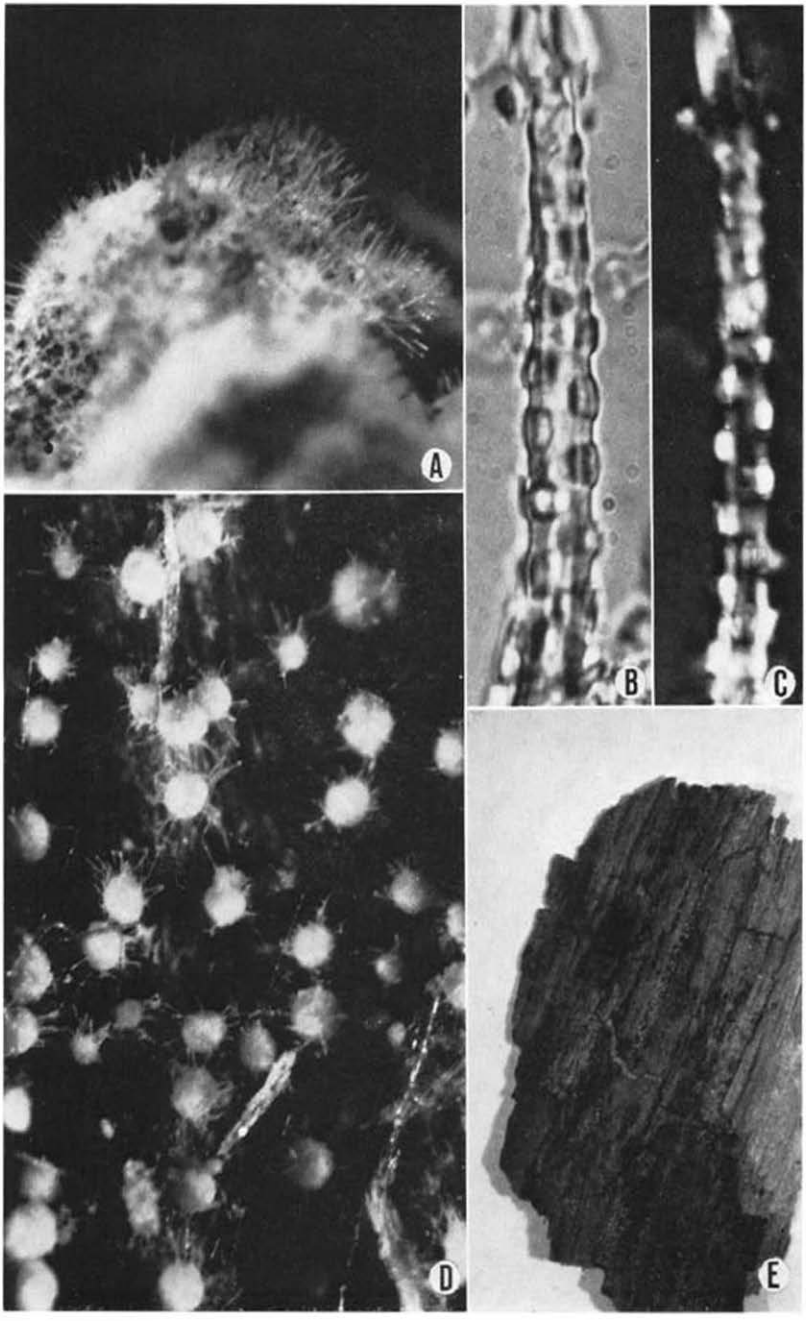
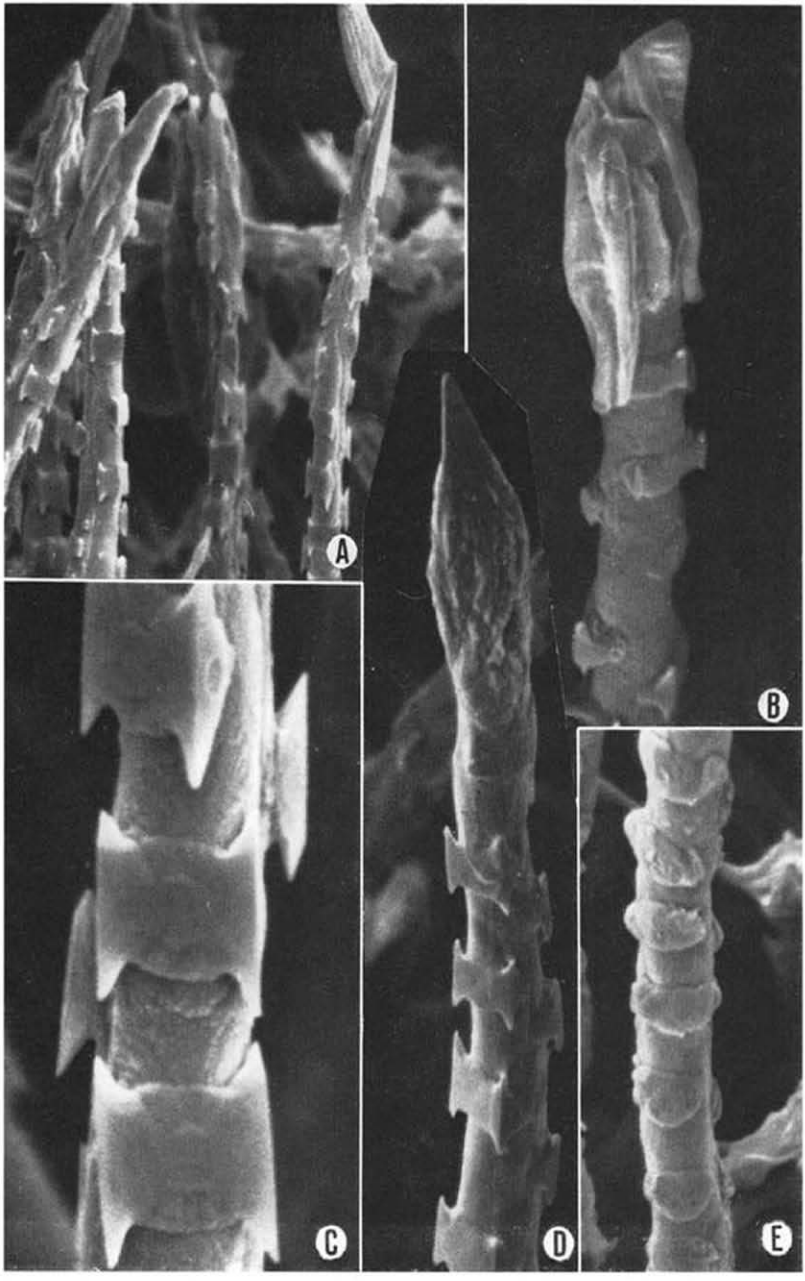
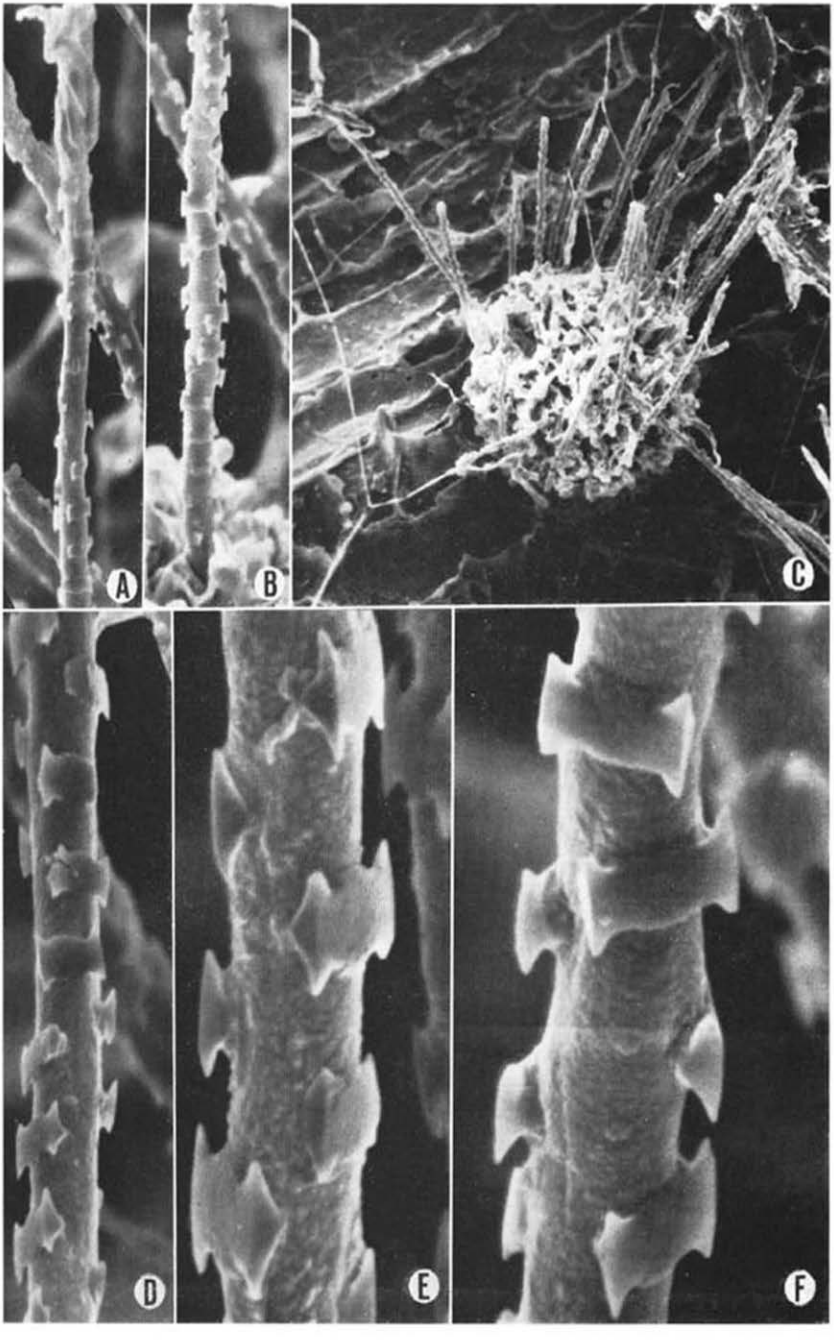

A
B
C
D
E


A
B
C
D
E


A
B
C
D
E
F