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REVISION OF THE GENUS PHIALOPHORA (MONILIALES)

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(With twelve Text-figures)

The hyphomycetous genus *Phialophora* is revised. It is characterized by flask-shaped phialides with a collarette and one-celled slimy conidia. This characterization excludes species which form blastospores on sympodulae besides phialospores, and which have been revised as species of the genus *Rhinocladiella* in a previous paper.

The genus *Margarinomyces*, on the contrary, is considered to be a synonym of *Phialophora*. With this emendation there remain now twelve species or species groups which are redescribed. The necessary new combinations are proposed.

Introduction

Phialophora verrucosa n. gen. n. sp. was created by Medlar in 1915a for a previously unknown pathogenic fungus isolated from the first reported case of Chromoblastomycosis or Dermatitis verrucosa, a human skin disease. As is made clear by Medlar in his paper describing the new genus and new species and in a second paper (Medlar, 1915b) giving more details of the morphology of the fungus, the name, taxonomic position, and determinative characteristics of this new fungus were the result of suggestions and work by the eminent mycologist Professor R. Thaxter. Despite this Medlar is obviously the authority for the genus *Phialophora* rather than Thaxter as has been assumed by some authors.

The genus *Phialophora* comprises a large number of frequently ill defined species which represent conidial states of Helotiales (e.g. *Pyrenopeziza*, *Mollisia*, *Ascocoryne*) or Sphaeriales (e.g. *Coniochaeta*, *Gaeumannomyces*). These species occur commonly on decaying wood (causing blue discolorations and soft rot), in soil, water etc., also on food (apples, butter, margarine), and as causal agents of chromoblastomycosis and other skin infections. The genus shows strong variability in hyphal pigmentation and conidiophore structures. One-celled slimy conidia are formed on typically flask-shaped phialides with a collarette. The genus is delimited from

† Dr. M. Beatrice Schol-Schwarz died on July 27, 1969, after a long illness. She participated actively in this work which was completed only two weeks before her death.

Rhinocladiella by the absence of sympodulae and blastospores. The genus *Margarinomyces* is considered to be synonymous with *Phialophora*, because in old cultures collarettes are visible on the phialides similar to those in typical *Phialophora* species.

Medlar (1915a) described *P. verrucosa* with two types of conidial formation as follows: "The type found in cultures where conditions are most favourable for luxuriant growth, is semi-endogenous in character .... The second type of conidial formation is found in tissues and in the depths of certain media, such as hydrocele agar. Here the conidia are formed as budding processes from single sclerotic cells, from the individual cells of sclerotia and from the end of short terminal and lateral branchlets. They may be single or in chains of two to six. The structure is similar to that of the conidia formed on the aerial hyphae, but the form is distinctly more ovoid." The first type of spores is obviously the phialospore. Medlar called them semi-endogenous presumably because they develop inside an open collarette. The "second type of conidial formation," illustrated in Medlar's more detailed study (1915b), apparently refers to moniliform thickened hyphae which do not normally separate into individual conidia.

Numerous species of *Phialophora* have now been described. The genus comprises dematioid and hyaline fungi occurring in diseased human or animal tissues, as parasites or saprophytes in plant material and in soil.

The aim of the present investigation was a rearrangement of the species described by van Beyma thoe Kingma (1943). It started with an exhaustive study of the authentic strains maintained at the CBS and was supplemented by numerous recent isolates. The present paper provides a base for the distinction of numerous new species, awaiting to be described.

In certain instances species delimitation was found to be very difficult because of great variability and insufficient morphological differentiation of the conidial states. This is particularly the case in groups of species with closely related perfect states. As a consequence the indiscriminate term 'species group' is used to comprise such complexes of similar forms.

One of the most difficult groups is the *Phialophora hoffmannii* group. It is treated here only cursorily because a re-evaluation of species will be possible only after a thorough revision of the perfect states. Not described is the complex of *Phialophora radicicola* Cain (1952) and the conidial state of *Gaeumannomyces graminis* (Sacc.) v. Arx & Olivier (*Ophiobolus graminis* Sacc.). Although identification of this complex is not difficult the affinity or identity, which was claimed by Lemaire & Ponchet (1963), of the forms within it also requires further study of perfect states.

Some very recent reports on *Phialophora* species (Hennebert, 1968; Gams & Domsch, 1969) have not been duplicated here. Other recent publications seem to deal rather with *Rhinocladiella* than with *Phialophora* species in the stricter sense.

Phialophora cultures grow well on the usual culture media. In the present study they were grown on 2 % malt extract agar, asparagine-yeast-agar (glucose 20.0 g, asparagine 1.5 g, K_2HPO_4 1.0 g, $MgSO_4 . 7H_2O$ 0.5 g, $FeCl_3$ 0.1 g, yeast extract 1.0 g per litre), upon which medium the colour is usually lighter, and on oatmeal

agar with lupin stems. Capitalized colour names in the text refer to Ridgway (1912) with Roman figures indicating the plates.

PHIALOPHORA Medlar

Phialophora Medlar *in* Mycologia **7**: 202. 1915. — Type species: *P. verrucosa* Medlar, *op. cit.*

Cadophora Lagerb. & Melin *apud* Lagerb. & al. *in* Svenska Skogsvårdsfören. Tidskr. **25**: 263. 1927. — Type species: *C. fastigiata* Lagerb. & Melin, *op. cit.*, ≡ *Phialophora fastigiata* (Lagerb. & Melin) Conant *in* Mycologia **29**: 598. 1937.

Margarinomyces Laxa *in* Zentbl. Bakt. ParasitKde (Abt. II) **81**: 392. 1930. — Type species: *M. bubaki* Laxa, *op. cit.* ≡ *Phialophora bubakii* (Laxa) comb. nov.

Lecythophora Nannf. *apud* Melin & Nannf. *in* Svenska Skogsvårdsfören. Tidskr. **32**: 435. 1934. — Type species: *L. lignicola* Nannf., *op. cit.* ≡ *Phialophora lignicola* (Nannf.) Goidanich *apud* Goidanich & al. *in* Ente nazionale per la Cellulosa e per la Carta, Roma 112. 1938.

The mycelium is hyaline or pink to olivaceous black, with septate hyphae which sometimes have characteristic irregular warty wall thickenings (Fig. 3v, 6c, u etc.). Thick-walled inflated cells may develop acrogenously or intercalarily. Phialides vary from thread- or tube-like to ampulliform, they open with a distinct cup- or beaker-shaped collarette. Phialides develop either terminally or laterally on the hyphae, or on sympodially branched conidiophores, in which case they may form complicated penicillate brushes. The phialides are usually separated from the parent hyphae by septa. Sometimes they may be reduced to a mere collarette protruding from a hypha or a chlamydospore without a septum, so-called pleurophialides (von Arx & Gams, 1967). Occasionally phialides bear more than one collarette. Proliferation of the phialides through the apex is also rather common.

The first developed conidium is a blastospore. After it is detached, pieces of the torn cell-wall remain behind. Depending on the size of the spore, these wall-structures are of different shape, varying from an inconspicuous collarette to a distinct cup, sometimes with flaring margin (Fig. 11). The succeeding conidia develop endogenously and are pushed out through the open cup, cohering in a mucous ball at the top of the phialide.

The process of spore development has been studied by means of microkinematography by Cole & Kendrick (1969). The conidia are one-celled and variable in shape, ranging from globose to ovoid or cylindrical and are sometimes even curved. Variation often occurs in the same strain according to age and culture medium. Some species form distinctly dimorphic conidia but conidia of variable shape also occur in many other species. Cultures with predominantly cylindrical conidia may have some globular or ovoid conidia and cultures with predominantly globular or ovoid conidia may have some cylindrical conidia.

Branching of the conidiophores and size and shape of the collarette are also very variable, depending on the medium, age, and amount of illumination of the culture. This variability led in the past to description of an exaggerated number of species. On the other hand certain minor differences of constant occurrence can be found which have frequently been neglected in the past and yet may be of taxonomic importance. Types of conidiophores other than those described, such as sympodulae or annellophores, are absent in *Phialophora*; otherwise a fungus with such pleomorphic conidium formation would be regarded as *Rhinocladiella* (Schol-Schwarz, 1968).

COMMENT ON THE SYNONYMY.

1927: Lagerberg & Melin (apud Lagerberg, Lundberg & Melin) established the genus *Cadophora* with the type species *C. fastigiata.*

1930: Laxa created the genus *Margarinomyces* with the type species *M. bubaki*, a dark olivaceous fungus, isolated from margarine. Laxa did not recognize, that with age the tips of the phialides transform into open collarettes which sometimes have inconspicuously flaring ends forming a small cup. These characters seem sufficient to transfer this species to *Phialophora* and to abandon the genus *Margarinomyces*, in spite of van Beyma's (1943) opinion to the contrary. According to him the spore development in *Margarinomyces* is "basipetal" as in *Penicillium*, i.e. exogenous, but is "endogenous" in *Phialophora.* This distinction cannot be retained since in the type species of *Margarinomyces* open cups at the end of the phialides have been demonstrated, just as in *Phialophora.* The same is true for the other species described in *Margarinomyces.*

1934: Nannfeldt (*apud* Melin & Nannfeldt) created the genus *Lecythophora* with the type species *L. lignicola*, for a dematioid fungus occurring in Sweden in wood pulp and water. The conidiophores are swollen structures developing laterally or terminally on the hyphae. They end in an inconspicuous open tip, from which small ellipsoidal conidia are abstricted in rapid sequence. Nannfeldt regarded these sporogenous cells as highly reduced phialides and the conidia as phialospores. However he did not observe, that the tips may transform into real cups liberating the endogenous spores.

1937: van Beyma, after examining Nannfeldt's fungus at the CBS, observed the short open neck of the swollen conidiophores and transferred the fungus to *Cadophora.*

1937: In the same year Conant published the synonymy of *Cadophora* and *Phialophora* and transferred the type species *C. fastigiata* to *Phialophora.*

1938: Goidanich (*apud* Goidanich & *al.*) transferred Nannfeldt's *Lecythophora lignicola* once again, this time to *Phialophora.*

1944: Emmons (*apud* Binford & *al.*) emended the genus *Phialophora* after examining the strain CBS 273.37, called *Phialophora verrucosa.* This strain sometimes produced acropleurogenous conidia, as was first observed by Carrión (1940), who for that reason, transferred it to the genus *Fonsecaea.* Emmons, disagreeing with Carrión, preferred to emend the genus *Phialophora*, so that fungi with "acrogenous, pleurogenous or acropleurogenous production of brown one-celled conidia born laterally on tuberculate processes of vegetative hyphae, or, more commonly, on lateral or terminal conidiophores and frequently catenate in short chains" could be included. The present author (Schol-Schwarz, 1968) could not retain this emendation: strains with this type of lateral conidia were assembled in the genus *Rhinocladiella* Nannf. which has priority over *Fonsecaea* Carrión; the strain CBS 273.37 was regarded as representing *Rhinocladiella pedrosoi* (Brumpt) Schol-Schwarz.

KEY TO THE SPECIES

1a. At least some conidia globose or subglobose 2
1b. Globose or subglobose conidia absent, conidia ovoid, ellipsoidal, cylindrical or curved 4
2a. Colonies white, conidia 2–4.5 × 2.3–3.5 μ . . . . . *P. alba*, p. 64
2b. Colonies darkly pigmented 3
3a. Phialides flask-shaped with distinct collarette, conidia regularly globose to guttuliform, 1.5–2.5 μ . . . . . *P. cyclaminis*, p. 69
3b. Phialides flask-shaped with wide collarette with flaring margin. Conidia dimorphic; globose brown and ellipsoidal to cylindrical hyaline . . . . . *P. richardsiae*, p. 87
3c. Phialides with swollen base and long slender neck, collarette indistinct. Conidia globose to ovoid, 1.5 × 1.5 to 2 × 3 μ, on aging transformed into chlamydospores with verrucose walls . . . . . *P. atrovirens*, p. 65
4a. Conidia narrow oblong, typically curved 5
4b. Conidia broader, usually straight, or only partly curved 8
5a. Colonies thin, fast growing. Conidia strongly curved, sickle-shaped *P. radicicola* Cain and conidial *Gaeumannomyces graminis* (Sacc.) v. Arx & Olivier
5b. Colonies more compact, slow growing. Conidia only slightly curved, not sickle-shaped *P. lagerbergii* group, 6
6a. Colonies cream-coloured and frequently with a brownish to violet discoloration of the agar . . . . . *Ascocoryne sarcoides* stat. conid., p. 83
6b. Colonies darker-coloured and without any discoloration of the agar 7
7a. Phialides with very long, slender, beaker-shaped collarette . . . *P. lagerbergii*, p. 81
7b. Phialides with distinct but shorter collarette . . . . . *P. repens*, p. 82
8a. Colonies with pure grey tinges. Conidiophores strongly branched with the slender phialides forming compact clusters around the hyphae . . . . *P. cinerescens*, p. 67
8b. Colonies of other colours. Conidiophores and phialides not forming compact clusters 9
9a. Collarette forming a distinct oblong cup, darker than the rest of the phialide *P. verrucosa*, p. 90
9b. Collarette less pronounced, not darker than the rest of the phialide 10
10a. Conidia clearly dimorphic: ovoid and cylindrical or sometimes curved. Moniliform hyphae typically present 11
10b. Conidia more uniform in shape 12
11a. Collarette always distinct . . . . . *P. lignicola*, p. 84
11b. Collarette rather inconspicuous at first but becoming more obvious on older phialides *P. bubakii*, p. 65
12a. Cultures dark olivaceous, dry, cottony, velvety, with hyphal strands. Phialides with coarse wall and distinct collarette (at least in age) . . . . *P. fastigiata* group, 13
12b. Cultures in various colours, cream, pink, olivaceous or black, frequently wet yeast-like or with hyphal strands. Phialides rather inconspicuous 17
13a. Hyphae greenish, usually with smooth thin walls. Collarette distinct only in old cultures *P. malorum*, p. 75
13b. Hyphae brownish, usually with irregularly thickened walls. Collarette always distinct 14
14a. Phialides small, 4–6 × 1.5–2.2 μ, and straight . . *Mollisia cinerella* stat. conid., p. 75
14b. Phialides larger and asymmetrically swollen 15
15a. Chains of moniliform chlamydospores present in old cultures *Pyrenopeziza laricina* f. *microsperma* stat. conid., p. 74
15b. Chains of moniliform chlamydospores absent 16
16a. Conidia subglobose to ovoid, 3–7.5 × 2–3 μ . . . . . *P. fastigiata*, p. 71

16b. Conidia narrowly ovoid, 2.5–4 × 1.5–2 μ . . . . . *P. melinii*, p. 74
17a. Aleuriospores present, borne on distinct sporophores, dark-coloured, obovate with pointed base and easily detached. Young colonies with dark colours *P. mustea*, p. 86
17b. Aleuriospores absent, chlamydospores, if present, not formed on differentiated sporophores. Young colonies often with light colours (if chlamydospores are present, see *Ph. fasciculata* and *Ph. mutabilis* in this group) . . . . . *P. hoffmannii*-group, p. 79

1. PHIALOPHORA ALBA Beyma—Fig. 1

Phialophora alba Beyma *in* Antonie van Leeuwenhoek **9**: 56. 1943.

Cultures on 2 % malt agar reach a diameter of 9 cm after three weeks. The fungus develops a wet, white, thin but tough layer of submerged mycelium with hyphal strands in the centre. The reverse of the colony is Pale Olive Buff (XL). Sporulation is good.

The hyphae, usually 2–3 μ, are sometimes 5–7 μ wide and irregular in outline, with inflated cells, but without a thickened wall (Fig. 1a).

The phialides, 10–15 × 3–4 μ, are flask-shaped, single or branched and sometimes grouped in *Penicillium*-like brushes. Exceptionally a terminal phialide occurs. The collarette has no conspicuous margin (Fig. 1c–e).

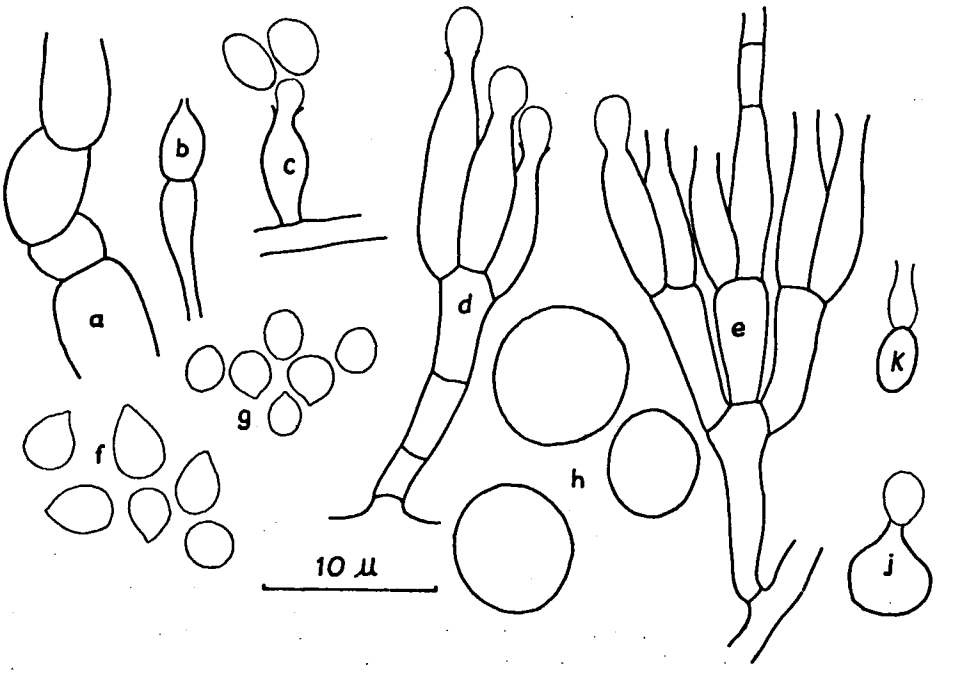

Fig. 1. *Phialophora alba*. Type culture CBS 112.43. — a. Hypha with inflated cells. — b–e. Terminal, lateral, branched and bush-like phialides. — f–h. Conidia of different age. — j. Sporulating chlamydospore. — k. Phialide developed from chlamydospore.

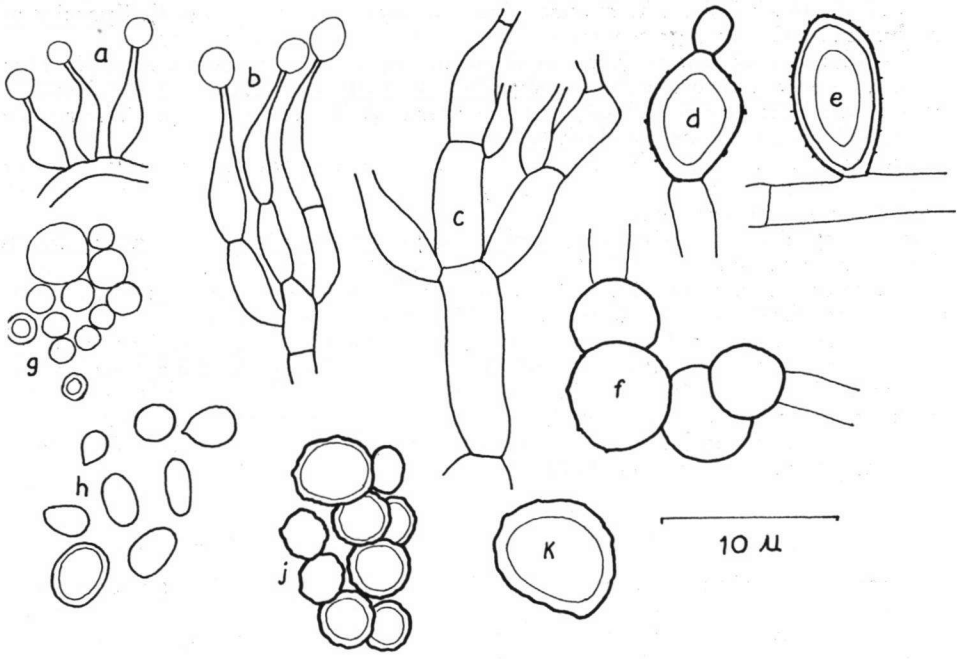

Fig. 2. *Phialophora atrovirens*. Type culture CBS 272.34. — a, b. Young phialides, single and in group. — c. Old phialides with open tips. — d–f. Terminal, lateral, and intercalary thick-walled, verrucose cells. — g. Young spore ball with spores of different size. — h. Globose and guttuliform conidia, partly changing into chlamydospores. — j. Ball of chlamydospores. — k. Single verrucose chlamydospore.

The conidia are hyaline, globose to subglobose, 2.3–4.5 × 2.3–3.5 µ. With age they may enlarge to 6–9 µ and remain hyaline, without a thickened wall. Sometimes they develop a collarette directly or they grow out into a phialide (Fig. 1j, k). No perfect state is known.

The description is based on the type strain CBS 112.43, isolated by Henriette Koning from heart-wood of *Fagus sylvatica* in the Netherlands.

Recently a strain CBS 740.68 was obtained from G. H. Bollen, Wageningen, isolated from glass-house soil, Zwijndrecht, Netherlands. According to him, the fungus is one of the first recolonizers of steamed soil in glass-houses.

2. **Phialophora atrovirens** (Beyma) Schol-Schwarz, *comb. nov.*—Fig. 2

Margarinomyces atrovirens Beyma *in* Zentbl. Bakt. ParasitKde (Abt. II) **91**: 348. 1935 (basionym).

Colonies on 2 % malt agar reach a diameter of 5.7 cm in 18 days at 25°C. They show a wet centre of 3.5 cm in diam. with a margin of 1 cm with aerial mycelium,

Olivaceous Black (LI). The reverse of the colony is Sooty Black (LI). Sporulation is abundant. Colonies grown under day light show concentric rings.

Colonies on asparagine-yeast agar attain 5.7 cm in 18 days at 25°C. They have a velvety appearance, changing from Benzo Brown (XLV) in the furrowed centre, via Hair Brown (XLVI) to Castor Gray (LII) at the margin. The reverse of the colony is Olivaceous Black (LI).

The hyphae are 3–5 μ broad, septate, with irregular wall-thickenings, wavy in outline. The hyphae develop intercalary, terminal or lateral, brown, inflated cells with a thick verrucose wall.

In young cultures the phialides, single or in groups on conidiophores, are relatively slender and gracefully tapering towards the tip with a slight inflation in the middle and a constriction at the base. They measure 7–15 × 1.5–2.5 μ. In old cultures complicated brushes of phialides with wide open tips are present.

The conidia are globose, droplet-like, exceptionally ovoid, hyaline, with an oildrop, usually measuring 1.5, but up to 2–3 μ, in diameter. With age they increase in size to 6–8 × 5 μ, and develop into chlamydospores, becoming brown with a thick, more or less verrucose wall, sometimes cohering together in a ball.

The description is based on the type strain CBS 272.34, isolated from black spots in margarine in the Netherlands.

3. **Phialophora bubakii** (Laxa) Schol-Schwarz, *comb. nov.*—Fig. 3

Margarinomyces bubaki Laxa *in* Zentbl. Bakt. ParasitKde (Abt. II) **81**: 392–396. 1930 (basionym).

Cadophora obscura Nannf. *in* Svenska Skogsvårdsfören. Tidskr. **32**: 418. 1934. — *Phialophora obscura* (Nannf.) Conant *in* Mycologia **29**: 598. 1937.

Colonies on 2 % malt agar reach a diameter of 6.5 cm after 18 days at 25° C. The growth is velvety, 0.3 cm high, with faint concentric rings, Dark Grayish Olive (XLVI), synnematous in the centre, merging via a 0.5 cm broad Deep Slate Olive (XLVI) velvety zone into a 0.1 cm broad hyaline margin. The reverse of the colony is Dull Greenish Black (XLVII) with a hyaline margin. Sporulation is abundant.

The hyphae soon become dark olivaceous; they are sometimes wavy, of varying width, mostly 3–5 μ, rarely up to 12 μ broad. When young, they are filled with dense protoplasm, with age they show irregular wall-thickenings and are sometimes verruculose. Moniliform hyphae (Fig. 3a) as well as hyphal strands are common.

EXPLANATION OF FIGURE 3

Fig. 3. *Phialophora bubakii.*

a–t. Type culture CBS 198.30. — a–e, h. Various phialides; b, h. Showing the characteristic branching. — f. Verrucose hypha. — g. Hypha with irregular wall-thickening. — j. Verrucose chlamydospore. — m. Lateral and k. terminal chlamydospore. — n. Young ovoid and r. old conidia. — q. Young curved and p. old conidia. — s. Group of rather old conidia. — t. Sclerotium.

u–x. Type culture of *Cadophora obscura*, CBS 269.33. — u. Single phialide. — v. Branched old conidiophore with one phialide proliferating and with irregularly thickened wall, a ball of chlamydospores still adhering to a phialide. — w. Conidia developed into chlamydospores. — x. Proliferating phialide.

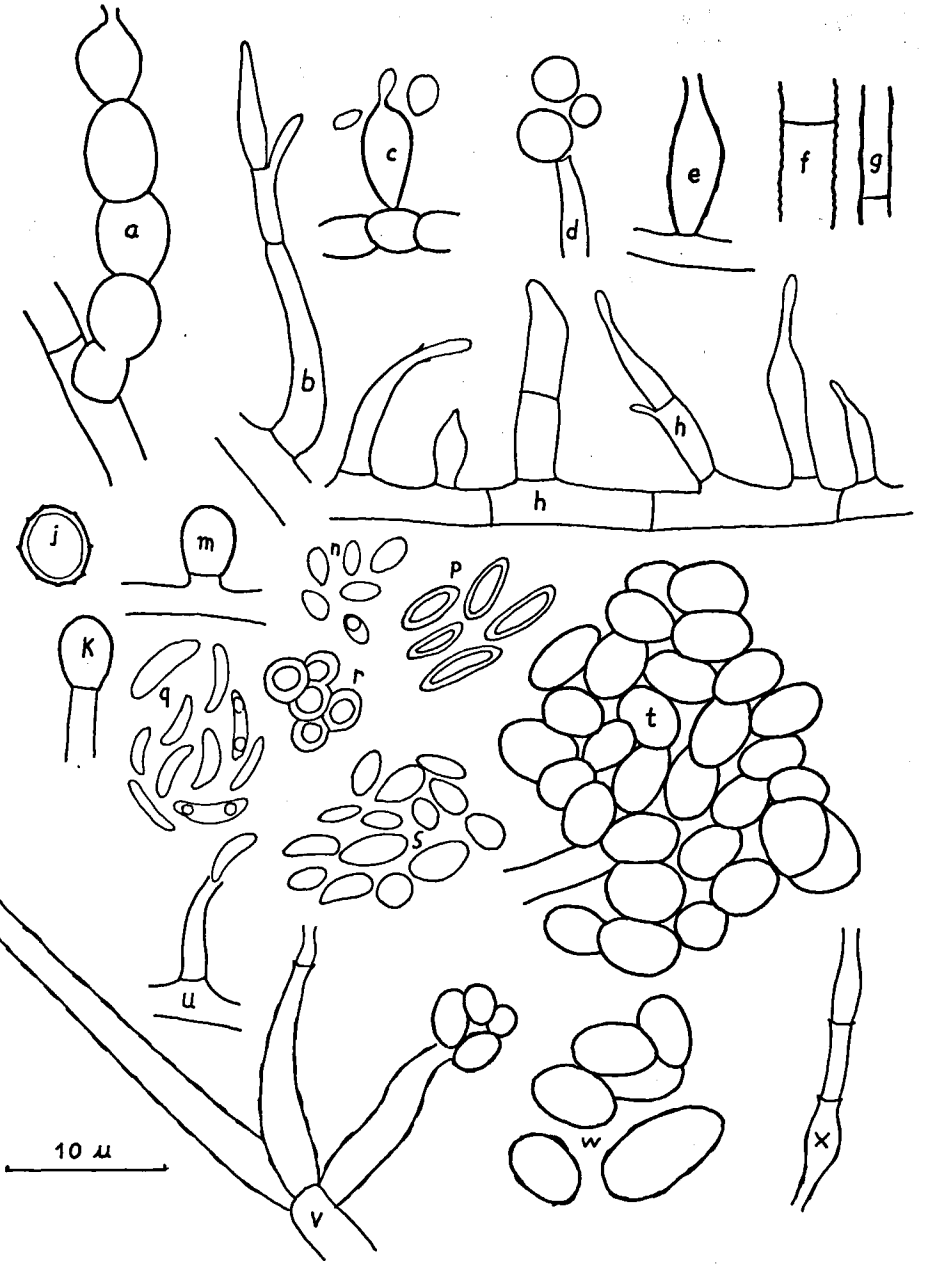

Fig. 3

Chlamydospores develop laterally or terminally on the hyphae (Fig. 3k, m). Sometimes they grow out into sclerotia, up to 80 μ in diameter (Fig. 3t).

The phialides, up to 40 μ long, are of variable shape. They develop terminally or laterally on the hyphae. They are simple or in groups supported by a conidiophore, slender or swollen. When young they end in a sharp point, with age a rather indistinct collarette becomes visible. Side branches are common (Fig. 3b, h); in some strains proliferation occurs (Fig. 3v, x).

The conidia are dimorphic, hyaline to subhyaline, with one or two oildrops. In young cultures allantoid conidia (1.5–) 3–5 (–7.5) × 0.75–3 μ prevail (Fig. 3q). In older cultures ovoid conidia, 1.5–4 × 1–2 μ, are common (Fig. 3n), however both types occur in every culture. With age the ovoid spores develop into brown chlamydospores, 4.5–6.5 × 4–5 μ, sometimes with an irregularly thickened wall (Fig. 3j, v, w). Exceptionally old allantoid spores with thickened walls occur (Fig. 3p). No perfect state is known.

Description based upon the type strain CBS 198.30.

HABITAT: In margarine, forming dark greenish spots, Czechoslovakia, Austria, the Netherlands, and other European countries. From fresh water and from pulp of *Populus tremula* in Sweden.

MATERIAL EXAMINED.

a. Herbarium material.

1. Type material of *Cadophora obscura* consisting of 3 slides: 217:28a, 242:42, 1203:5, marked by E. Melin "Västerbotten, Umeå, Sofiehems Trämassefabrik, fresh water, det. J. A. Nannfeldt, Holotypus" (UPS).

2. N. F. Conant's dried culture 334, from Nannfeldt via CBS, isolated from fresh water in Sofiehem, Sweden. Authentic material of *Cadophora obscura* (FH).

b. Living strains.

CBS 198.30, type culture of *Margarinomyces bubaki*;

CBS 269.33, authentic culture of *Cadophora obscura*, strain 389:11, obtained from E. Melin.

CBS 221.37, isolated from margarine from Vienna, by A. Knetemann, Rotterdam.

Strains CBS 835.69 (1040), 836.69 (1107), 837.69 (1133), and 838.69 (1135), all isolated from margarine or butter and sent by A. Knetemann via Unilever Laboratory, Rotterdam.

CBS 834.69 (H 36-6), isolated from pulp of *Populus tremula*, by T. Nilsson, Sweden, 1968.

Cultures of CBS 198.30, type of *Margarinomyces bubaki*, and CBS 269.33, type of *Cadophora obscura*, are strikingly similar in colour and appearance, when grown on various media. Microscopically there are differences but none are worthy of specific rank. In CBS 198.30 the hyphae are up to 12 μ broad and the conidiophores are typically branched (Fig. 3 b, h). The hyphae in CBS 269.33 reach only a width of 5 μ, and proliferation of phialides is rather common. In some other strains proliferation also occurs. van Beyma (1943) described a strain from butter sent to the CBS by A. Knetemann as *Phialophora obscura*. This culture was lost in 1961, but the still existing drawings agree with those of *Phialophora bubakii*.

4. PHIALOPHORA CINERESCENS (Wollenw.) Beyma—Fig. 4

Verticillium cinerescens Wollenw. *in* Arb. biol. Reichsanst. Berlin-Dahlem **17**: 296. 1930. — *Phialophora cinerescens* (Wollenw.) Beyma *in* Antonie van Leeuwenhoek **9**: 59. 1943.

Colonies on 2 % malt extract agar reach a diameter of 7 cm in 30 days at room temperature. The growth is woolly, zonate, Light Mineral Gray (XLVII) in the centre, merging via Smoke Gray (XLVI) and Deep Slate Olive (XLVII) into a 0.7 cm broad hyaline margin of appressed mycelium. The reverse of the colony shows in a radial direction passing from the centre to the margin Smoke Gray (XLVI), Dull Greenish Black (2) (XLVII) and hyaline zones. Sporulation is good.

The hyphae are septate, 1–3 μ wide; on aging they frequently develop irregularly swollen cells, covered with flat warts, and up to 5 μ wide (Fig. 4e). Hyphal strands occur.

The phialides are flask-shaped, mostly with the broadest part somewhat above the middle. Characteristically they are arranged in densely verticillate bushes in clusters on very short conidiophores (for this reason the fungus was originally placed in the genus *Verticillium*). Exceptionally phialides occur singly on the hyphae. The phialides end in a very short but distinct collarette with a minute flaring margin, both collarette and margin being somewhat darker than the phialide itself.

The conidia when young are hyaline to subhyaline, more or less ellipsoidal but slightly apiculate at the basal end, with a thin wall and two—sometimes only one—oildrops, measuring 3–6 × 1.5–2 μ, although there is actually considerable variation in size and also in shape. In older cultures the conidia are darker, covered with a thicker wall, and more regular, measuring 4–6 × 2.5–3 μ. Very rarely curved spores are present (Fig. 4b).

The description is based mainly on the type strain, CBS 276.29.

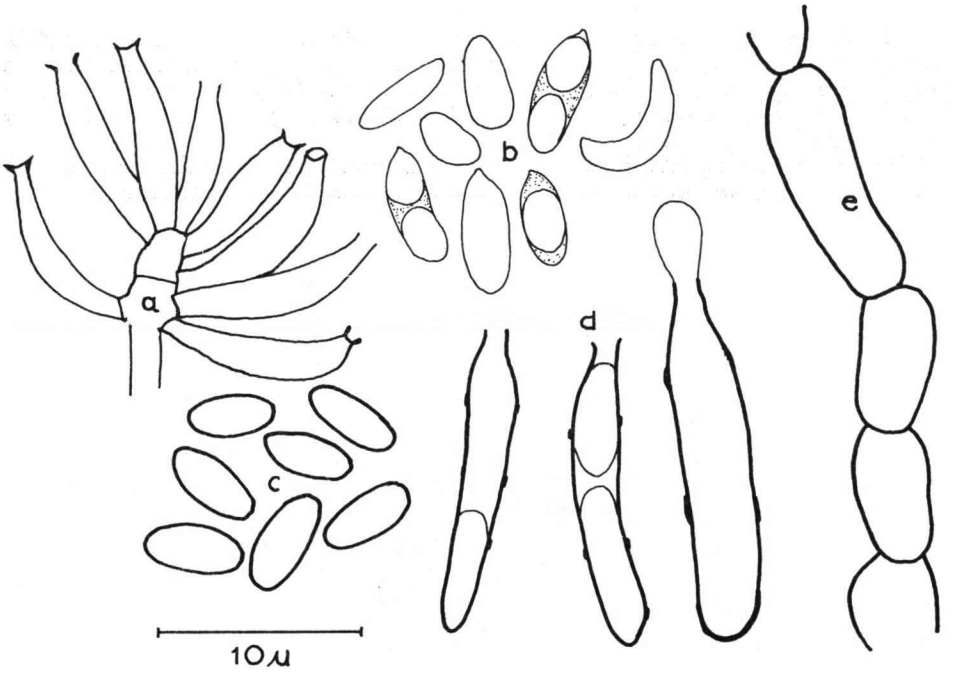

Fig. 4. *Phialophora cinerescens*. Type culture, CBS 276.29. — a. Bush of phialides. — b. Young conidia (one of them curved). — c. Old conidia with a distinct wall. — d. Chlamydospores directly transformed into phialides. — e. Inflated cells.

MATERIAL EXAMINED (living strains).

CBS 276.29, type culture, isolated from wilting *Dianthus caryophyllus*, in Geisenheim, Germany, sent as *Verticillium cinerescens* by H. W. Wollenweber in 1929.

CBS 280.35, isolated from wilting *Dianthus caryophyllus* in England, sent by G. M. Wickens, 1935.

CBS 418.50, isolated from wilting *Dianthus caryophyllus* in the Netherlands, sent by G. Brink in 1949.

CBS 209.57, isolated from wilting *Dianthus caryophyllus* in the U.S.A., sent by I. Isaac under No. 11157 in 1957.

The species is a common parasite of *Dianthus caryophyllus*; it grows through the xylem vessels of the host and causes wilt. It is of economic importance in the Netherlands, Germany, England, and Denmark. The results of extensive studies of the disease have been published by Wickens (1935), Hellmers (1958), and Hantschke (1961). In the Netherlands the disease and its control have been studied by Roodenburg (1945) and Noordam (1948).

5. PHIALOPHORA CYCLAMINIS Beyma—Fig. 5

Phialophora cyclaminis Beyma *in* Antonie van Leeuwenhoek **8**: 115. 1942.

Colonies on 2 % malt agar attain a diameter of 8.5 cm after 3 weeks at 25° C. The growth is woolly, sometimes feathery towards the margin, with faint concentric rings and a slight central elevation, Dark Mouse Gray (LI); the margin is 2 mm broad, more or less submerged, Blackish Mouse Gray (LI). Reverse of the colony Iron Gray (LI). Sporulation is good.

The hyphae are septate, brown, up to 4–5 μ broad, exceptionally covered with wall thickenings, without inflated, thick-walled cells. No hyphal strands.

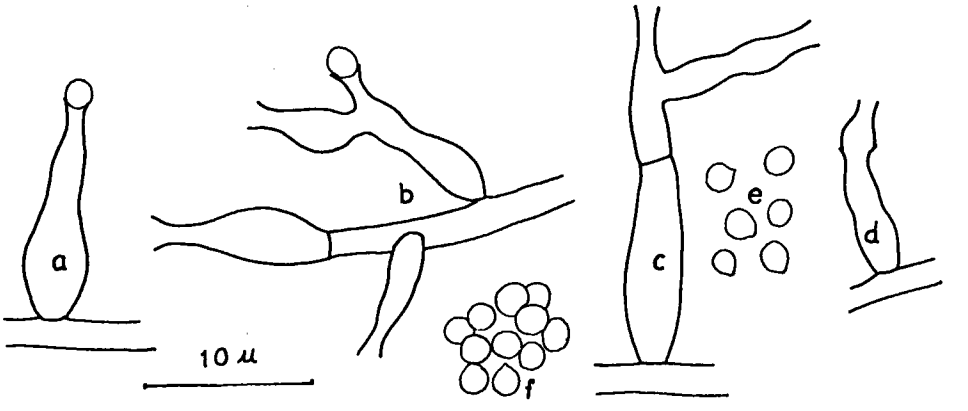

Fig. 5. *Phialophora cyclaminis*. — a, b, d–f. Type culture CBS 166.42, c. CBS 608.69. — a–d. Phialides, simple and with furcation and proliferation. — e. Conidia. — f. Conidia in a cluster.

The phialides, usually 15–25 μ but up to 45 μ long, develop laterally or terminally on the hyphae. They are mostly simple, but furcation and proliferation are common. They have a narrow base, followed by a slight inflation and a constriction in the middle of the phialide. The collarette is distinct.

The conidia, 1.5–2.5 μ in diameter, are hyaline, thin-walled and sometimes with an oildrop. They are globose or slightly guttuliform and cohere at the top of the phialide.

The description is based mainly on the type culture CBS 166.42 which was isolated from leaves of *Cyclamen persicum* in Aalsmeer, Netherlands, 1942.

MATERIAL EXAMINED.

CBS 166.42, type culture, isolated from *Cyclamen persicum*, Aalsmeer, 1942, by J. W. M. Roodenburg.

CBS 608.69, isolated from water in an aquarium, sent by A. J. van der Plaats-Niterink, Utrecht, 1963.

CBS 245.69 isolated from wood, sent as strain 64 by G. Giordano, Firenze, 1969.

6. PHIALOPHORA FASTIGIATA group

Colonies grow rather slowly. The group is characterized by greyish mycelium with a tinge of brown, cottony or velvety in appearance, with hyphal strands. The conidiophores are strongly verticillately branched; the phialides are sturdy, rather short and open with a distinct broad cup without a flaring margin. The conidia have a distinct wall, with age they are often transformed into chlamydospores; characteristic flat wall thickenings are frequently present in vegetative hyphae and sporulating structures.

Species described in this group are:

6 (1). PHIALOPHORA FASTIGIATA (Lagerb. & Melin) Conant—Fig. 6a–j

Cadophora fastigiata Lagerb. & Melin *in* Svenska Skogsvårdsfören. Tidskr. **25**: 263. 1927. — *Phialophora fastigiata* (Lagerb. & Melin) Conant *in* Mycologia **29**: 598. 1937.

Colonies on 2 % malt agar reach a diameter of 4.5 cm after 13 days at 25 °C. The growth is velvety, Olive Brown (XL), with a 0.4 cm broad margin of appressed hyaline mycelium. In older cultures concentric rings develop. The reverse of the colony is Dark Olive (XL). Sporulation is abundant.

The hyphae are 3–4 μ in diameter, with age they show the characteristic wall thickenings which also occur in the sporulating structures (Fig. 6c). Thick-walled cells up to 8 μ in diam. are common. The mycelium tends to develop hyphal strands and tufts in petri dish cultures.

The phialides occur singly, laterally or terminally on the hyphae, or in verticillate clusters (Fig. 6f). They can reach up to 30 μ in length but more often they are short, up to 12 μ, and asymmetrically swollen at the lower end. They open with a distinct cup without a flaring margin. Proliferation occurs (Fig. 6a, d, f, h).

The conidia are globose, subglobose, lacrymoid or ovoid, mostly straight but sometimes curved, varying from 3–6(–7.5) × 2–3 μ. When young they are hyaline and thin-walled, with age they become subhyaline or greyish and develop a thicker wall. In old cultures they develop into chlamydospores which are spherical or

ellipsoidal, sometimes apiculate, up to 7 μ in diameter and often attached in a ball at the tip of the phialide (Fig. 6d, e, g).

The description is based on the dried type specimen and numerous living strains listed below.

HABITAT: On pine and spruce timber in Sweden and on various substrates in other countries.

MATERIAL EXAMINED.

a. Herbarium material.

Two slides, 151.3a from ground woodpulp and 143:14/137 from white water, both from Värmland (UPS).

Dried culture 331 of N. F. Conant, from ground wood pulp, sent by J. A. Nannfeldt to the CBS (FH).

b. Living strains.

CBS 226.30, from blueing *Pinus strobus*, East Canada, sent by C. W. Fritz in 1930 as No. I b.

CBS 307.49, from blueing *Pinus*, sent by S. O. Pehrson, Sweden, in 1949.

CBS 611.69 (1038/2) from *Picea abies*, CBS 612.69 (1136/4) and CBS 618.69 (1005/6) from *Populus tremula*, CBS 613.69 (1094/3) and CBS 614.69 (1094/2) from *Pinus sylvestris*, CBS 617.69 (BII 15) from *Fagus*, sent by F. Mangenot, Nancy, France, 1963.

CBS 682.69 = strain WS-B from rotting wood of *Fagus sylvatica*, sent by W. Liese, München, 1962.

CBS 863.69 (M.K. 9) and CBS 864.69 (M.K. 52) from wood, sent by W. Kerner, Berlin, 1967.

CBS 865.69 (27) and CBS 867.69 (10c) from blueing wood of *Pinus sylvestris* sent by A. E. Graentz, München, 1964.

CBS 866.69 = PD 64/121, from *Cyclamen* tuber, sent by G. H. Boerema, Wageningen 1964.

CBS 868.69 (T 18) soft rot fungus from *Pinus sylvestris*, sent by U. Cederkreutz, Helsinki, 1966.

CBS 869.69 = G.L.H. 6856, from wood of *Picea excelsa*, sent by G. L. Hennebert, Louvain, 1965.

CBS 870.69 = strain C from *Asparagus officinalis*, sent by P. van Maris, Venlo, 1959.

EXPLANATION OF FIGURE 6

Fig. 6. *Phialophora fastigiata* group

a–j. *Cadophora fastigiata*, N. F. Conant's dried culture 331 (FH). — a, f. Phialides. — b. Conidia. — c. Irregularly thickened wall of a hypha. — d. Proliferating phialide with ball of conidia developed into chlamydospores. — e. Chlamydospores with wall thickenings. — g. Chlamydospores.

h–j. CBS 609.69. — h. Proliferation of phialides. — j. Bush of phialides with long beakers, containing frequently two conidia.

k–p. *Cadophora melinii*, paratype (UPS). — m. Bush of phialides. — k, o. Conidia of various shape. — p. Chain of thick-walled cells. — n. Chlamydospores sporulating like phialides.

q–t. *Pyrenopeziza laricina* f. *microsperma*, CBS 568.63. — q. Chain of chlamydospores. — r. Conidia. — s. Curved conidia in a young culture. — t. Phialides.

u–w. *Mollisia cinerella*, CBS 312.61. — u. Bush of phialides. — v. Conidia. — w. Phialide with a ball of chlamydospores, from an old culture.

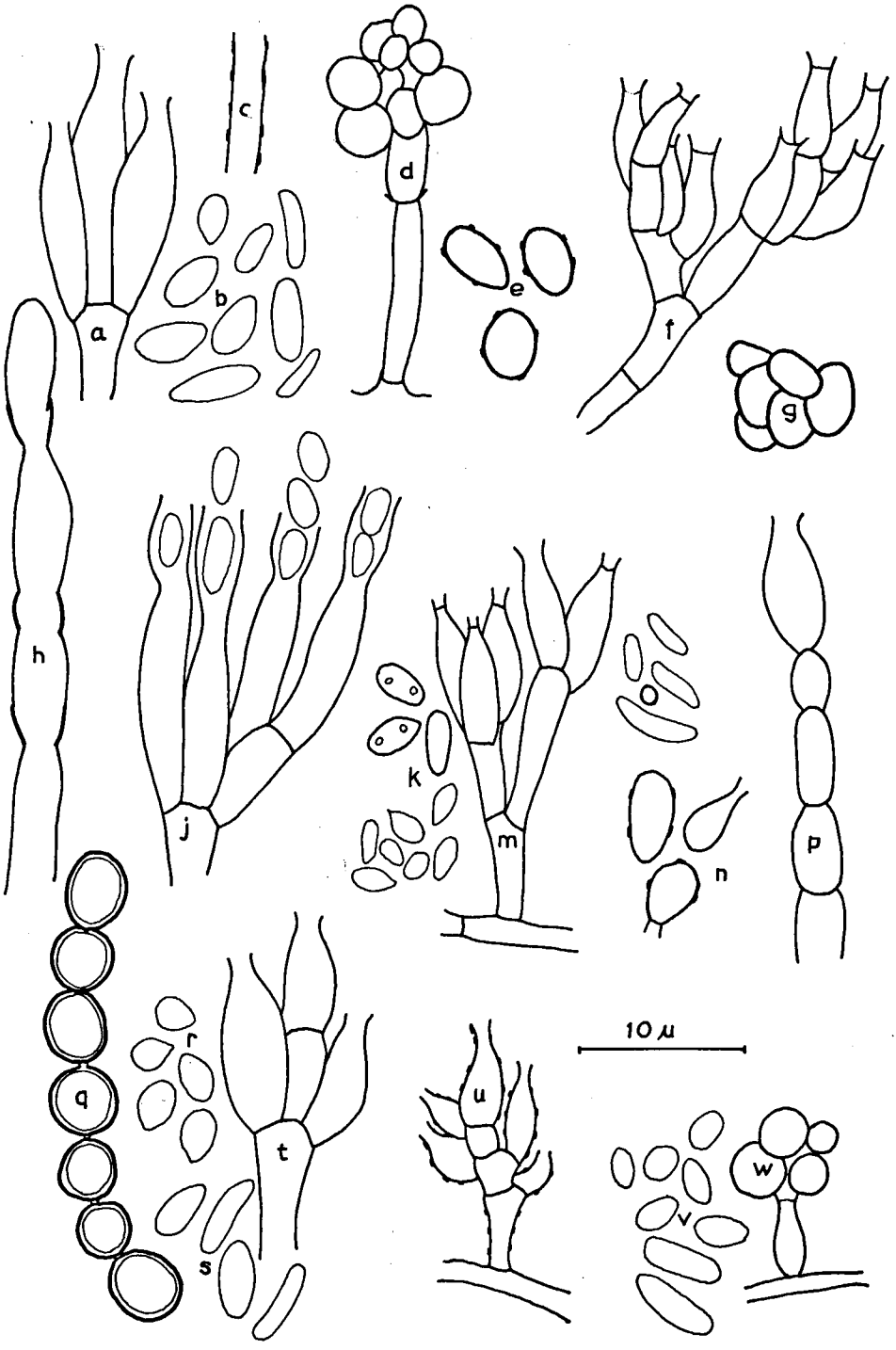

Fig. 6

Strain PD 9-263 from dying *Rubus idaeus*, sent by G. H. Boerema, Wageningen, 1960.
Strain 29a, laboratory contamination, sent by V. Tchernoff, Baarn, 1960.
Strain C, from oak wood of a ship, that had been lying on the bottom of the Baltic since the 17th century, sent by H. Kiessling, Stockholm, 1963.
Strain PD 63/103 from dead pear twigs, sent by G. H. Boerema, 1963.
Somewhat different:
CBS 609.69 = DAOM 33739, from rotting wood of *Betula lutea*, New Brunswick, sent by S. J. Hughes, 1966.

6 (2). PHIALOPHORA MELINII (Nannf.) Conant—Fig. 6k–p

Cadophora melinii Nannf. *in* Svenska Skogsvårdsfören. Tidskr. **32**: 417. 1934. — *Phialophora melinii* (Nannf.) Conant *in* Mycologia **29**: 598. 1936.

This species differs from *Phialophora fastigiata* only by the prevalently ovoid spores, which are also mostly somewhat smaller than in *P. fastigiata*, measuring 5–4 × 1.5–2 μ, although in young cultures slightly curved conidia, up to 6 × 2 μ, occur as well. With age the spores develop into chlamydospores up to 6 μ in diam.
The description is based on the type culture CBS 268.33.
HABITAT: In woodpulp in Sweden.

MATERIAL EXAMINED.

a. Herbarium material.

4 slides, marked "Paratypus", all from isolates of Melin in Sabrå Parish, Ulfviks Trämasse-fabrik, 211:2, 236:1b, 242:22 from ground wood pulp, 236.42 from the air (UPS).
Culture marked "authentic", N. F. Conant 329, from ground wood pulp in Sweden, from J. A. Nannfeldt to CBS, with photograph; slide marked "Paratypus" from strain isolated by E. Melin from ground wood pulp, Ulfviks Trämasse-Fabrik, Sweden (FH).

b. Living strains.

CBS 268.33 = IMI 59,445, type culture, sent by E. Melin in 1933.
CBS 848.69 = G.L.H. 7515-E isolated from wood chip of *Fagus sylvatica*, Heikendorf, Kr. Plön, by G. L. Hennebert, July 1965.
CBS 849.69 = G.L.H. 7560, isolated from *Picea*-wood, Hann. Münden, sent by H. Zycha, as Ka 13, July 1965.

6 (3). PYRENOPEZIZA LARICINA Rehm f. MICROSPERMA Le Gal & Mangenot, stat. con.—Fig. 6q–t

Pyrenopeziza laricina Rehm f. *microsperma* Le Gal & Mangenot, stat. con. *in* Revue Mycol. **26**: 266–270. 1961.

In the hyphae the characteristic wall thickenings are obvious.
The phialides are sturdy; they develop in loosely forked groups or in compact verticillate clusters. Exceptionally a sessile collarette occurs on the hyphae. Proliferation occurs.
The conidia are thin-walled and very variable, mostly ovoid, 2.5–4 × 2–2.5 μ,

but also cylindrical, sometimes slightly curved, up to 5 × 3 μ. With age they develop into globose chlamydospores, up to 4–5 μ in diam. Characteristic moniliform chains of globose to subglobose chlamydospores, up to 5 × 4 μ, occur in old cultures.

Material examined.
CBS 568.63, isolated from *Abies* trunk, near Fraize (Vosges), sent by F. Mangenot in 1963.

6(4). MOLLISIA CINERELLA Sacc. stat. con., Le Gal & Mangenot — Fig. 6 u–w

Mollisia cinerella Sacc. stat. con., Le Gal & Mangenot *in* Revue Mycol. **26**: 265. 1961.

Characteristic wall thickenings of the hyphae and irregular thick-walled cells, up to 8 μ broad, are common.

The phialides are symmetrically swollen and not as broad as in *Pyrenopeziza laricina* f. *microsperma*. The author could not, however, observe the flat broad collarette as shown in Mangenot's drawings. The phialides develop singly, in loosely forked arrangements or in complicated verticillate bushes. Proliferation occurs. Sometimes a sessile collarette on a hypha was observed.

The conidia have a distinct wall. Very variable in shape and size they are generally globose to ovoid, 2.5–4.5 × 2–2.5 μ, but straight, cylindrical spores, up to 6 × 2–3 μ, are also common. In old cultures conidia develop into globose thick-walled chlamydospores and adhere in balls at the collarette of the phialides.

MATERIAL EXAMINED.
CBS 312.61, isolated from *Fagus* wood, Génicourt (Meuse), sent by F. Mangenot in 1961.

The last two mentioned species represent only examples of conidial states of the large and closely related genera *Mollisia* and *Pyrenopeziza* of the Helotiales which are still too little investigated and known in pure culture. Although the differences between the four *Phialophora* states of this group so far mentioned, are slight, it seemed preferable to leave the species apart instead of considering the conidial state of *Mollisia cinerella* identical with *Phialophora melinii*, as was done by Le Gal & Mangenot (1961). Of the four species described above *Phialophora melinii* seems to be the one with the smallest conidia.

CBS 609.69 (DAOM 33739) was illustrated by Hughes (1953); it is characterized by very long beaker-shaped collarettes which contain usually two oval spores, 4.5–5 × 1.5–3 μ. The densely branched sturdy phialides are similar to those of *P. fastigiata*, to which it must be closely related.

6 (5). PHIALOPHORA MALORUM (Kidd & Beaumont) McColloch—Fig. 7

Sporotrichum malorum Kidd & Beaumont *in* Trans. Br. mycol. Soc. **10**: 111. 1924. — *Phialophora malorum* (Kidd & Beaumont) McColloch *in* Mycologia **36**: 589. 1944.

Torula heteroderae Korab *in* Ukrain. Res. Inst. Sugar Ind. Kiev **6** (16): 29–67. 1929. — *Cadophora heteroderae* (Korab) Beyma *in* Zentbl. Bakt. ParasitKde (Abt. II) **96**: 428. 1937. — *Phialophora heteroderae* (Korab) Beyma *in* Antonie van Leeuwenhoek **9**: 61. 1943.

Sporotrichum carpogenum Ruehle *in* Phytopathology **21**: 1144. 1931.
Phialophora luteo-olivacea ("*lutea-olivacea*") Beyma *in* Antonie van Leeuwenhoek **6**: 280. 1940.
Phialophora atra Beyma *in* Antonie van Leeuwenhoek **8**: 113. 1942.
Phialophora goidanichii Delitala *in* Ann. sperim. Agrar. Roma, N.S. **6**: 254. 1952.

MISAPPLICATION.
Trichosporium populneum Lamb. & Fautr. *apud* Fautr. & Lamb. *in* Revue Mycol. **18**: 145. 1896.

Colonies on 2 % malt agar attain a diameter of 7 cm after 24 days at 25° C. The growth is wet with some fascicles in the centre. In transmitted light a radial darker striation is visible. The colour is Deep Slate Olive (XLVII), the margin of 0.5 cm of appressed mycelium is colourless. The reverse of the colony is Deep Slate Green (XLVII). Sporulation is abundant.

The hyphae are 1.5–3 μ broad, without wall-thickenings. Chains of irregular thick-walled cells, up to 5 μ broad, are common in old cultures.

The phialides are generally gracefully tapering, but in old cultures stalks with sturdy verticillate phialides are observed (Fig. 7 b, e, f).

The conidia are very variable with or without a distinct wall. Predominantly they are ellipsoidal and slightly apiculate, with two oildrops, 4.5–7 × 2.5–3 μ, but cylindrical, somewhat curved, spores can also occur.

HABITAT: In waste water in Sweden and from different other substrata, e.g. soil, fruits, nematode cysts, amphibians, in Europe and the U.S.A.

The description is based mainly on CBS 141.41 type of *P. luteo-olivacea*.

MATERIAL EXAMINED.

Living strains.

a. Isolates from rotting apples:

CBS 266.31, sent by F. D. Heald, and

CBS 260.32, isolated by G. H. Ruehle, sent by F. D. Heald, under the name *Sporotrichum carpogenum*, both from U.S.A.

CBS 357.51, type of *Phialophora goidanichii* Delitala, sent by G. Goidanich, Italy, 1951.

CBS 355.59, No. 10-1, sent by E. Olthoff, Wageningen, 1959.

4 strains, numbered 10-5, 43-1, 43-2, and 43-7, sent by E. Olthoff, Wageningen, 1959.

b. Other origin.

CBS 259.32, from cysts of Heterodera schachtii in Bohemia, sent by J. Rozsypal as *Torula heteroderae*, 1932.

CBS 141.41, type of *Phialophora luteo-olivacea*, from sewage of "Schleifery Byske", Sweden, sent by S. Foghammer in 1939.

EXPLANATION OF FIGURE 7

Fig. 7. *Phialophora fastigiata* group: *Phialophora malorum*. a–g. Type strain of *Phialophora luteo-olivacea*, CBS 141.41. — a, c. Conidia in a young culture, d. in an old culture. — b, e. Phialides in a young culture, f. in an old culture. — g. Chain of thick-walled cells.

h–m. Type strain of *Phialophora atra*, CBS 165.42. — h. Conidia and chlamydospores of different age and shape. — j. Young phialides. — k. Chlamydospore developing a phialide. — m. Old phialides.

n–q. Authentic strain of *Phialophora heteroderae*, CBS 259.32. — n–p. Phialides. — q. Conidia.

r–t. Type strain of *Phialophora goidanichii*, CBS 357.51. — r, t. Phialides, s. Conidia.

u–w. Authentic strain of *Phialophora malorum*, CBS 266.31. — u, w. Phialides. — v. Conidia.

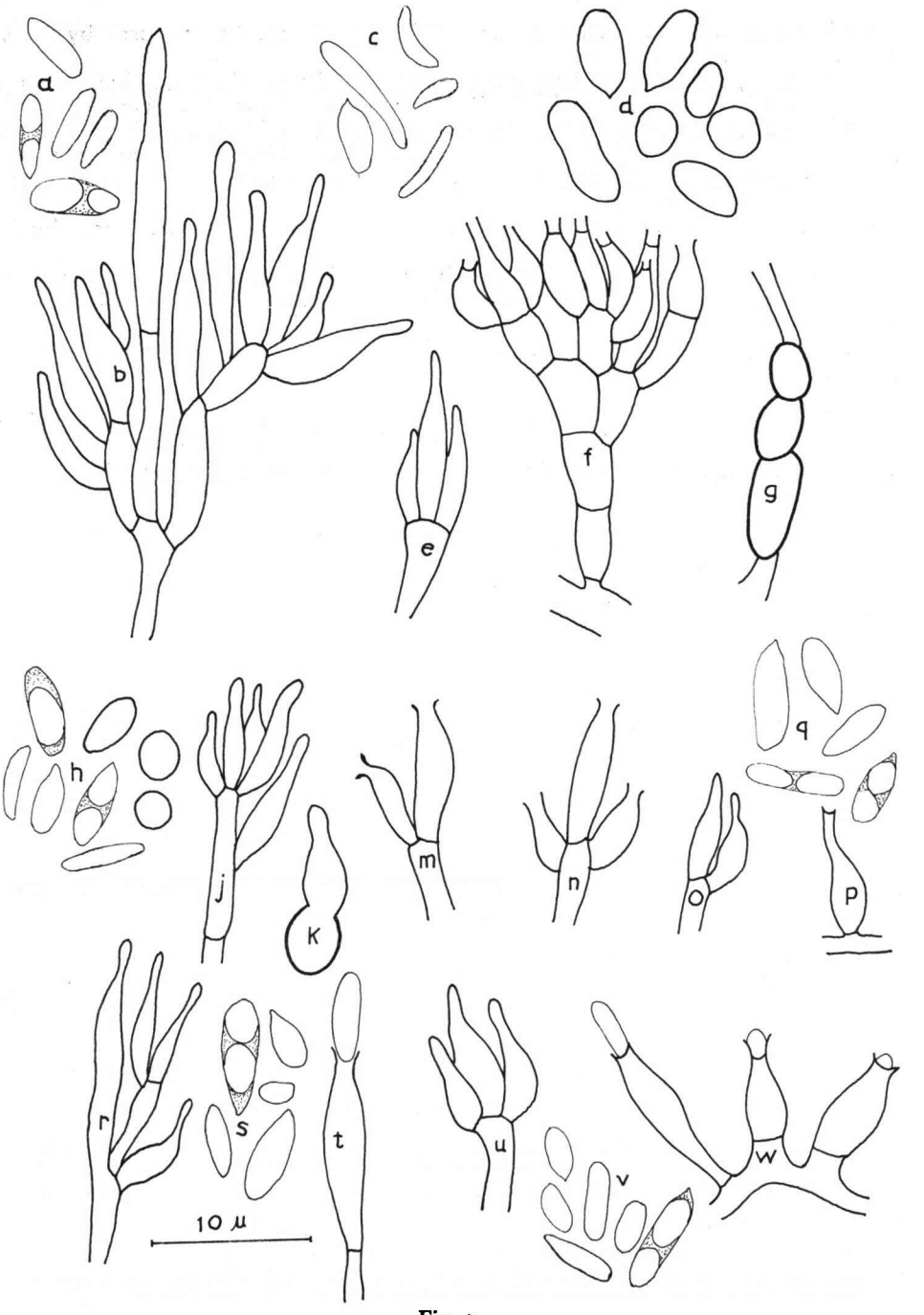

Fig. 7

CBS 165.42, type of *Phialophora atra*, isolated from an Axolotl, sent by S. A. de Lange, Amsterdam, 1942.

CBS 208.57, from human bronchial excrete, sent by G. Cochet, Belgium, 1957.

CBS 245.60, from air, sent by L. Tybring, Denmark, 1959, as No. 1376.

CBS 850.69 (C 386), CBS 851.69 (C 542), CBS 852.69 (C 570) and CBS 853.69 (C 574), from agricultural soil, sent by K. W. Gams, Kiel-Kitzeberg, 1963.

CBS 854.69 (162) from polyvinylacetate and CBS 855.69 (189) from tricresylphosphate, sent by H. J. Hueck, Delft, 1963.

CBS 856.69 (1213/2/2) and CBS 857.69 (1208/3) from *Picea abies*, sent by F. Roll-Hansen, Norway, 1963.

CBS 858.69 from polyvinylchloride tubing, sent by H. Kühlwein, Karlsruhe.

CBS 859.69 (102d) from stalactite in Lehman Cave, U.S.A., sent by F. W. Went, 1968.

CBS 860.69 = PD 67/890 from crocus bulbs, sent by G. H. Boerema, Wageningen, 1968.

Phialophora malorum is a common fungus in water and soil, where it may attack cysts of nematodes; it also grows on apples, where it causes rotting spots. The characters of *P. fastigiata* and *P. malorum* are compared in the following table:

TABLE 1 — COMPARISON OF PHIALOPHORA FASTIGIATA AND P. MALORUM

Phialophora fastigiata	*Phialophora malorum*
Hyphal strands present	Hyphal strands present
Hyphae brownish	Hyphae greenish
Wall-thickenings common	Wall-thickenings generally absent
Phialides sturdy, with very distinct collarettes	Phialides when young, gracefully bent, with age the collarettes become visible
Conidia very variable but mostly ovoid, with age developing into chlamydospores	Conidia very variable, but mostly ellipsoidal and slightly apiculate, with oildrops

Transitional strains between the two species occur commonly. *P. malorum* is distinct from the former species by a narrower opening of the phialide apex and by conidia with a thinner wall and slight apiculation, with less tendency towards transformation into chlamydospores.

The variability of the species led to the erection of three species causing apple rots: *Sporotrichum malorum* by Kidd & Beaumont (1924), *Sporotrichum carpogenum* by Ruehle (1931), and *Phialophora goidanichii* by Delitala (1952).

Isolates from cysts of Heterodera schachtii made by Rozsypal were identified by Jaczewski in a letter to Rozsypal as *Torula heteroderae* Korab. A culture sent by Rozsypal to the CBS under this name and preserved as CBS 259.32 was first reidentified by van Beyma as *Trichosporium populneum* (Rozsypal, 1934). In 1937 van Beyma recognized it as different from other isolates considered as *Trichosporium populneum* and made the new combination *Cadophora heteroderae* (Jacz.) Beyma for Rozsypal's fungus. The correct author's citation for *Cadophora heteroderae* is (Korab) Beyma, but the correct name reads *Phialophora heteroderae* (Korab) Beyma.

Trichosporium populneum Lamb. & Fautr. is *Spadicoides atrum* (Corda) Hughes according to the type specimen (Hughes, 1958).

7. PHIALOPHORA HOFFMANNII group

Colonies often wet, yeast-like, phialides on hyphae or on hyphal strands, short, stout, swollen, bottle-shaped or of varying wavy forms, with the apical opening becoming wider at a late state.

The group can be subdivided into:—

a. strains with pale, cream-coloured cultures, and

b. strains with pink cultures, sometimes darkening with age.

Under certain conditions of light and temperature some strains of the first group develop apothecia of Discomycetes, others form a pycnidial or sporodochial state, often containing branched conidiophores with an open tip. These strains could not be identified with any known genera, they require a special study.

In the second group dark spots of hyphal aggregates, sometimes covered with setae, develop readily; they are interpreted as perithecium initials. Some fresh isolates develop mature perithecia belonging to the genus *Coniochaeta*. A suitable technique for inducing perithecia is cultivation on 2 % malt extract agar (with 0.2–0.5 % yeast extract), or cornmeal or oatmeal agar, sometimes with addition of lupin stems, for two weeks at 25° C, then exposure to black light (12 hrs per day) for two weeks or more at the same temperature, and finally for 1–2 weeks at 5° C. The perfect states so far observed differ only slightly from each other and are connected by intermediate forms. This feature reflects the slight, but constant differences in the conidial states.

It is doubtful whether a specific distinction on the basis of the knowledge of the conidial state alone will ever be possible.

Phialophora luteo-viridis appears to be constantly connected with dark-spored *Coniochaeta* species, such as *C. velutina* (Fuck.) Munk. Rogers (1965) described the conidial state of *C. ligniaria* (Grev.) Massee which belongs to pink strains of the *P. hoffmannii*-group. Udagawa and Takada (1967) described the conidial state of *C. tetraspora* Cain which belongs to the same group. Another example is *Coniochaeta* spec., cf. *Rosellinia xylarispora* Cooke & Ellis (Munk, 1957).

Representative strains of this group were described under the following names (arranged according to intergrading cultural characters, from pure pink to dark olivaceous, almost black, and with chlamydospores):

7 (1). **Phialophora hoffmannii** (Beyma) Schol-Schwarz, *comb. nov.*

Margarinomyces hoffmannii Beyma *in* Zentbl. Bakt. ParasitKde (Abt. II) **99**: 386. 1939 (basionym).

Phialophora aurantiaca Beyma *in* Antonie van Leeuwenhoek **6**: 277. 1940.

Colonies permanently light coloured. At most the reverse reaches Antique Brown (III) in the centre. Type culture CBS 245.38, isolated from butter in Switzerland by D. Hoffmann.

van Beyma (1943) declared *P. aurantiaca* and *Margarinomyces hoffmannii* as identical, but he did not decide as to the synonymy of the genera. Instead, he incorrectly dropped the earlier name *M. hoffmannii*.

7 (2). **Phialophora decumbens** (Beyma) Schol-Schwarz, *comb. nov.*

Margarinomyces decumbens Beyma *in* Antonie van Leeuwenhoek **8**: 111. 1942 (basionym).

Mycelium light pink in young cultures, becoming somewhat darker with age. Type culture CBS 153.42, isolated from strawberries.

7 (3). **Phialophora fasciculata** (Beyma) Schol-Schwarz, *comb. nov.*

Margarinomyces fasciculatus Beyma *in* Zentbl. Bakt. ParasitKde (Abt. II) **99**: 384. 1939 (basionym).

Colonies strongly fasciculate, predominantly light coloured, the reverse in the centre reaching Warm Sepia (XXIX). Type culture CBS 205.38, isolated from butter in Switzerland by D. Hoffmann.

7 (4). **Phialophora luteo-viridis** (Beyma) Schol-Schwarz, *comb. nov.*

Margarinomyces luteo-viridis Beyma *in* Zentbl. Bakt. ParasitKde (Abt. II) **99**: 381. 1939 (basionym).

Mycelium dark olivaceous but also with yellow and dark orange tinges. Type culture CBS 206.38, isolated from butter in Switzerland by D. Hoffmann.

7 (5). **Phialophora mutabilis** (Beyma) Schol-Schwarz, *comb. nov.*

Margarinomyces mutabilis Beyma *in* Antonie van Leeuwenhoek **10**: 48. 1944/45 (basionym).

Cultures have pink mycelium initially and darken with age by the formation of irregularly shaped, terminal or intercalary chlamydospores. The terminal chlamydospores are attached on a broad base.

Chlamydospores may produce conidia directly through collarettes or give rise to phialides. Conidium formation through short collarettes from intercalary hyphal cells is common. With age the phialospores become dark like chlamydospores. The species is known from soil and water. Type culture CBS 157.44, isolated by S. Windisch from river water.

The different species were originally all based on single isolates, except for *P. hoffmannii*. None of the original strains developed perithecia. In recent years the CBS has received for identification a large number of strains belonging to this

group. It has not been possible to identify them with one of the known pink species because of small but rather constant differences. Amongst both the pink and the dark coloured cultures some human and animal pathogenic strains have been found.

8. PHIALOPHORA LAGERBERGII group

Colonies grow easily on various media.

Conidiophores consist of one or two stalk cells with repeatedly verticillate clusters of phialides, forming an obconical brush.

Phialides strongly swollen, terminating in distinct and usually long beaker-shaped collarettes without flaring margins.

The conidia are hyaline, slender, generally somewhat curved, and measure 3–8 × 1.5–2 μ.

8 (1). PHIALOPHORA LAGERBERGII (Melin & Nannf.) Conant
Fig. 8a–c, j–o

Cadophora lagerbergii Melin & Nannf. *in* Svenska Skogsvårdsfören. Tidskr. **32**: 415. 1934. — *Phialophora lagerbergii* (Melin & Nannf.) Conant *in* Mycologia **29**: 598. 1937.

Colonies on 2 % malt agar attain a diameter of 9 cm after 12 days at 25° C. The growth is woolly and the colour from the centre to a radius of 2 cm Dark Olive (XL), then for a 1.5 cm wide zone Brownish Olive (XXX), for a 0.75 cm zone Ochraceous Tawny (XV), finally with a 0,25 cm wide flat margin. The reverse of the colony is Cinnamom Drab (XLVI). Sporulation is abundant.

The septate hyphae are brown, usually 2–3 μ wide, and develop characteristic thickenings of the wall with age. Sometimes they are swollen or moniliform with a thickened wall and up to 5–6 μ wide (Fig. 8o). Hyphal strands are common. Sometimes the hyphal tips are swollen. These swellings may develop into phialides.

The phialides in young cultures are simple, slender and gracefully tapering, sometimes with a septum. In older cultures stout bushes of *Penicillium*-like, branched, inflated phialides, 3–4 μ wide, develop laterally on solid stalks on the hyphae (Fig. 8 b). These bushes are characteristic of the species. The phialides are 15–25 μ long, they have an extremely long narrow collarette, up to 7 × 2 μ, without a flaring margin. Sometimes proliferation occurs (Fig. 8m).

The conidia are hyaline and predominantly allantoid, 3–4.5 (–6) × 1–1.5 μ. Very occasionally ovoid conidia and globose chlamydospores, 5 μ in diameter, occur in old cultures. No perfect state is known.

The description is based on the type strain of the species, CBS 266.33.

HABITAT: on wood of *Pinus sylvestris* in Sweden.

MATERIAL EXAMINED.

a) Herbarium material.

Paratypus of *Cadophora lagerbergii*, isolated by E. Melin from wood of pine in Uppland, Ed Parish, Bisslinge (UPS).

Authentic material of *Cadophora lagerbergii*, isolated from wood of *Pinus sylvestris* in Sweden. Culture from Nannfeldt, via CBS sent to N. F. Conant with his number 332 (FH).

b) Living strain.

CBS 266.33, originally isolated by E. Melin = N. F. Conant's strain 332.

Spore development in this species has been studied by Cole & Kendrick (1969).

8 (2). PHIALOPHORA REPENS (Davidson) Conant—Fig. 8g, h

Cadophora repens Davidson *in* J. agric. Res. **50**: 803. 1935. — *Phialophora repens* (Davidson) Conant *in* Mycologia **29**: 598. 1937.

The most striking difference with *P. lagerbergii* is the absence of the long narrow beaker-shaped extension of the collarettes in the phialides. In *P. repens* the collarette

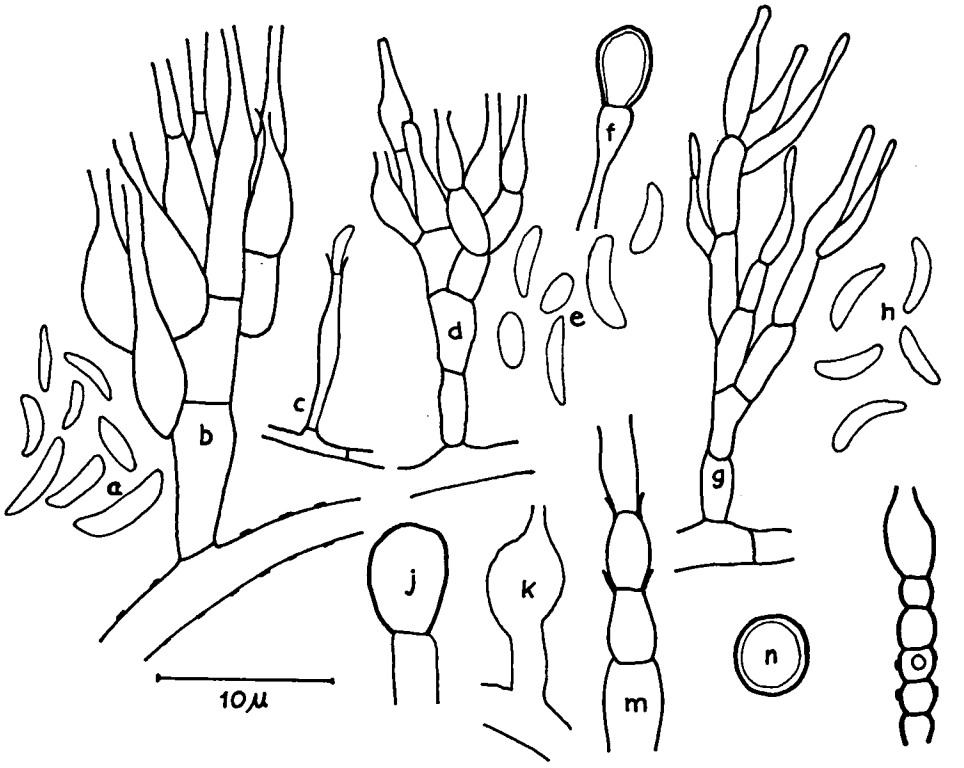

Fig. 8. *Phialophora lagerbergii* group

a–c, j–o. Type culture of *P. lagerbergii*, CBS 266.33. — a. Conidia. — b. Bush of phialides. — c, k, o. Simple phialides. — j. Terminal chlamydospore. — m. Proliferating terminal phialide. — n. Chlamydospore.

g, h. Type culture of *P. repens*, CBS 294.39. — g. Bush of phialides. — h. Conidia.

d–f. *Phialophora* state of *Ascocoryne sarcoides*, CBS 364.61. — d. Bush of phialides. — e. Conidia. — f. Terminal chlamydospore.

is distinct, but short. The conidia measure 3–7 × 1–1.5 μ. The growth is powdery and more rapid than in *P. lagerbergii*. No perfect state is known.

The description is based on the type culture CBS 294.39.

HABITAT: in wood of *Pinus sylvestris*, U.S.A.

MATERIAL EXAMINED.

Authentic material of *Cadophora repens*, isolated from wood = Conant's strain 338 (FH).

Living strain.

CBS 294.39, type culture of *Cadophora repens*, sent by R. W. Davidson to the CBS in 1939; morphologically identical with the material in FH.

8 (3). ASCOCORYNE SARCOIDES (Jacq. ex S. F. Gray) Groves & Wilson
Fig. 8d–f

Ascocoryne sarcoides (Jacq. ex S. F. Gray) Groves & Wilson *in* Taxon **16**: 35. 1967.

1. stat. con.: *Phialophora* spec.
2. stat. con. with sporodochia: *Coryne dubia* Pers. ex S. F. Gray.

The CBS maintains 7 strains under the name *Coryne sarcoides* (Jacq. ex Fr.) Tul. These have a cream-coloured mycelium and most of them when grown on oatmeal or malt extract agars, produce a brownish to violet pigment which diffuses into the agar. Some of the strains do not produce sporodochia any longer or have never produced them but each strain develops a conidial apparatus that is verticillately branched and very similar to that of *Phialophora lagerbergii* and *P. repens*. The conidia are curved and measure up to 5 × 1.5 μ.

Description based on CBS 364.61 and several other strains.

MATERIAL EXAMINED.

Living strains.

CBS 153.31, sent by W. Loos, Germany, in 1931.

CBS 155.35, sent by T. Lagerberg, Sweden, under No. 25:3 from coniferous tree, identified by F. H. van Beyma, 1935.

CBS 170.56, from *Nothofagus*, Dovey Forest, No. 14.5.13, and CBS 171.56, from *Pinus*, Kielder Forest, No. 16.5.137, both sent by S. Batko, Surrey, in 1956.

CBS 192.62, ascospore isolate from P. Berthet, Lyon, sent by J. Boidin, 1962.

CBS 364.61, sent by W. R. Day, Oxford, as No. 4505, isolated from rotting wood of Norway spruce (*Picea excelsa*), identified first as *P. repens*.

CBS 407.69 = strain 1675, isolated by H. A. van der Aa, from rotting wood, Baarn, 1969.

The position of CBS 237.53, representing *Margarinomyces microsperma* (Corda) Mangenot (*in* Revue gén. Bot. **59**: 20. 1952, and based on *Ceratocladium microspermum* Corda, Prachtflora 41, pl. 20. 1839) remains uncertain because of atypical behaviour and poor sporulation of Mangenot's strain.

Ceratocladium microspermum Corda is an entirely different fungus. It has been redescribed by Hughes (1951).

On the basis of their conidial apparatus and characteristically curved spores, these three species are closely related but not identical. A perfect state is known only in one of them, but most probably the two others also belong to closely related genera.

9. PHIALOPHORA LIGNICOLA (Nannf. apud Melin & Nannf.) Goidanich apud Goidanich & al.—Fig. 9

Lecythophora lignicola Nannf. *apud* Melin & Nannf. *in* Svenska Skogsvårdsfören. Tidskr. **32**: 432. 1934. — *Cadophora lignicola* (Nannf. apud Melin & Nannf.) Beyma *in* Zentbl. Bakt. ParasitKde (Abt. II) **96**: 427. 1937. — *Phialophora lignicola* (Nannf. apud Melin & Nannf.) Goidanich *apud* Goidanich & al., Ricerche sulle alterazioni .... Roma 112. 1938.

Colonies on 2 % malt agar reach a diameter of 4.6 cm after 16 days at 25° C. The centre, somewhat elevated and tufted up to 0.5 cm high, is Deep Grayish Olive (XLVI), surrounded by flat Chaetura Black (XLVI) mycelium which extends into a 0.7 cm broad, light-coloured margin which becomes pink in the light; the aerial mycelium is Tilleul Buff (XL) near the margin and merges into a zone of appressed Vinaceous Buff (XL) mycelium. The reverse of the colony is Olivaceous Black (LI) with a Vinaceous Buff (XL) margin. Sporulation is abundant. On potato dextrose agar a yellow pigment is developed.

The hyphae are 1.5–3 μ wide, often aggregated in strands, they readily develop moniliform, occasionally branched, chains of inflated cells, 4–8 μ wide, sometimes with thickened verrucose walls (Fig. 9a, p, m). Terminal and lateral chlamydospores which become brown with age, are common (Fig. 9e, y). The fungus is easily recognized by its moniliform hyphae which resemble those in *P. verrucosa*.

The phialides, up to 20 μ long, are variable in shape, mostly short and strongly inflated but occasionally long and slender. Sometimes they are reduced to collarettes on the hyphae. The collarettes are distinct. The phialides occur singly in lateral or terminal positions, or in groups on conidiophores, exceptionally forming bushes. They become brown with age. Terminal phialides occur also on moniliform hyphae. Proliferation occurs (Fig. 9v).

The conidia are hyaline to subhyaline, dimorphic and variable in shape and size. In young cultures cylindrical or curved spores, 5–8 × 1.5–3 μ, are rather common (Fig. 9s), with age ovoid conidia, sometimes slightly apiculate, 3–4.5 × 1.5–2 μ, prevail. These may develop into globose chlamydospores, 5–6.5 × 3.5–4.5 μ (Fig. 9g). The description is based on the lectotype culture, CBS 267.33.

In 3 months old cultures, sclerotia, possibly representing initials of fruiting bodies, were observed (Fig. 9d).

HABITAT: In ground wood-pulp, blueing wood, "white water" from paper mills, fresh water, and in sewage, Sweden.

MATERIAL EXAMINED.

a. Herbarium material.

Lecythophora lignicola Nannf., 4 slides and one dried culture, each labelled "Paratypus, isolated by E. Melin", viz. 130:1 Västmanland, white water, 130:12 Norrbotten, Luleå, Trämassefabrik, 159:6 Hälsingland, 160:44 Ångermanland, white water, culture from Västerbotten, Sofiehems Trämassefabrik, white water (all UPS).

Lecythophora lignicola Nannf., 5 slides, each labelled "Paratypus, isolated by E.

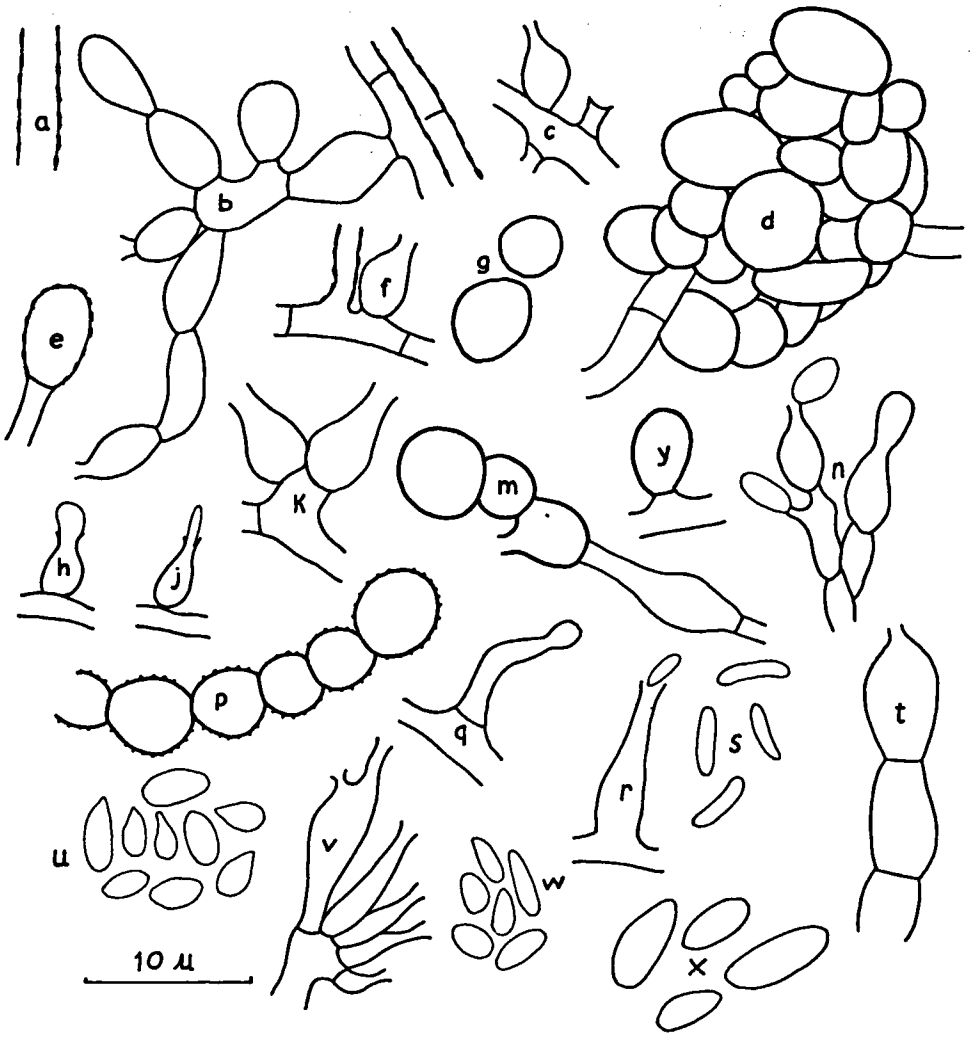

Fig. 9. *Phialophora lignicola.* b–d, f, u, v. type culture, CBS 267.33; e, g, k, m. from paratypus material (UPS and FH); a, h, j, y. CBS 308.49. — a. Hypha with typical thickening of the wall. — b. Branched moniliform hyphae with terminal collarettes. — c. Lateral phialide and a mere collarette. — d. Sclerotium. — e. Terminal chlamydospore with irregularly thickened wall. — f. Hypha with thickened wall. — g. Chlamydospores. — h, j. Lateral phialides, one producing a globose, the other a cylindrical conidium. — k. Branched phialide. — m. Thick-walled cells, one with a collarette. — n. Branched phialide. — p. Moniliform hypha with roughened wall. — q, r. Single phialides. — s. Group of long, slightly curved conidia. — t. Terminal phialide. — u. Group of young conidia. — v. Branched phialides with a proliferation. — w, x. Groups of conidia. — y. Lateral chlamydospore.

Melin", viz. 130:1, 160:8, 160:24, Västmanland, white water, 134:27 Hälsingland, 152:13 Jämtland, white water (all FH).

b) Living strains.

CBS 267.33, lectotype culture of *Lecythophora lignicola* Nannf., sent to the CBS by E. Melin in 1933.

CBS 308.49, isolated from blueing wood, sent by S. O. Pehrson, Stockholm, in 1949.

10. PHIALOPHORA MUSTEA Neergaard—Fig. 10

Phialophora mustea Neergaard *in* Zentbl. Bakt. ParasitKde (Abt. II) **104**: 407. 1942.

Colonies on 2 % malt extract agar attain a diameter of 7.3 cm after three weeks at 25° C. From the centre to a radius of 2 cm, the growth is woolly, Smoke Gray to Dark Grayish Olive (XLVI) in colour, surrounded by a 1.6 cm wide wet ring, Olivaceous Black (1) (XLVI), with faintly radiating mycelium and indistinct concentric rings; the margin of appressed mycelium is 0.5 cm wide, Pale Smoke Gray (XLVI). The reverse of the colony is Olivaceous Black (XLVI) at the centre, merging into Dark Grayish Olive (XLVI) and Pale Smoke Gray (XLVI) at the margin. Sporulation is abundant.

The septate hyphae are 2–4 μ wide, at first hyaline, soon becoming dark; they may develop hyphal strands and contain numerous oildrops.

The phialides, 10 × 2–3 μ, are borne singly or in bushes, rarely they are in a terminal position. Generally they taper gradually towards the tip; sometimes they are short and swollen, up to 6 μ broad. In young cultures collarettes are indistinct, in old ones they are clearly visible (Fig. 10a—d).

The phialospores are hyaline, cylindrical, ellipsoidal, 3–8 × 1.5–2.5 μ, often with one or two, exceptionally three, oildrops. With age the conidia increase in diameter up to 4 μ, and develop into dark chlamydospores with a thick wall, covered with the characteristic irregular thickenings.

The species is characterized by its aleuriospores, 4.5–7.5 × 4–6 μ. They develop singly on short, slender or sometimes broader protuberances, or on sporophores—without a basal septum—which are swollen in the middle and taper towards a sharp point. The aleuriospores are very regular in shape, ovoid with the basal end sharply pointed, to globose and are easily detached. Because of the regularity of the spores and the differentiated sporophores the designation as aleuriospores is preferable to chlamydospores which occur in other species but not in *P. mustea*, where the aleuriospores are never in an intercalary position.

HABITAT: Apple must, in which it develops a white mycelium and causes dark discoloration of the sap; Denmark.

The description is based on the strain CBS 142.41.

MATERIAL EXAMINED.

CBS 142.41, authentic strain from apple must, sent by C. A. Jörgensen, Denmark, 1941, to P. Neergaard and to the CBS.

Strain 18, from fruit juice, sent by H. Lüthi, Wädenswil, Switzerland, 1951.

Phialophora mustea can easily be confused with *Ph. mutabilis*, but it has dark mycelium without a tinge of pink and without any intercalary chlamydospores. The aleurio-

spores are very regular and develop singly on sporophores which end in a sharp point. With age phialospores develop into chlamydospores up to 4 μ broad. The species is known only from fruit juices.

11. PHIALOSPORA RICHARDSIAE (Nannf. apud Melin & Nannf.) Conant—Fig. 11

Cadophora richardsiae Nannf. *apud* Melin & Nannf. *in* Svenska Skogsvårdsfören. Tidskr. **32**: 421. 1934. — *Phialophora richardsiae* (Nannf. apud Melin & Nannf.) Conant *in* Mycologia **29**: 598. 1937.

Cadophora brunnescens Davidson *in* J. agric. Res. **50**: 803. 1935. — *Phialophora brunnescens* (Davidson) Conant *in* Mycologia **29**: 598. 1937.

Phialophora caliciformis G. Smith *in* Trans. Br. mycol. Soc. **45**: 391. 1962.

Colonies on 2 % malt agar attain a diameter of 5.7 cm after 3 weeks at 25° C. In the central area growth is flat and Olive Brown (XL), outside this there is a 0.2 cm broad ring of vertically directed hyphal strands, Buffy Brown (XL) in colour, surrounded by a velvety margin with faint Brownish Olive (XXX) rings. The reverse is Fuscous Black (XLVI). A brownish pigment diffuses into the malt agar. Sporulation is abundant. When exposed to day-light for several weeks, various strains may show a tinge of pink.

The mycelium, at first hyaline, becomes light brown in three days and then dark brown; aerial mycelium is erect, tufted, and also dark brown; the hyphae are septate, 2.5–4 μ in diameter, and usually aggregated in strands. The walls of hyphae and conidiophores are often irregularly thickened.

The phialides are very numerous, sturdy, arising perpendicular on hyphal

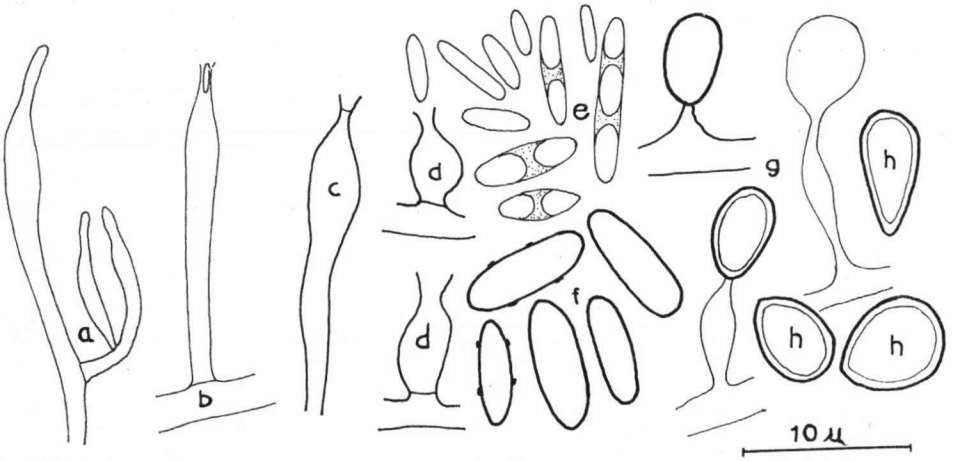

Fig. 10. *Phialophora mustea*. Type culture, CBS 142.41. — a–d. Phialides, a. branched, b. single in young culture, c. in terminal position, d. broad forms. — e, f. Phialospores in young and old cultures respectively, the latter developing into chlamydospores. — g. Sporophores bearing aleuriospores. — h. Aleuriospores.

strands as well as on individual hyphae; they are 10–35 μ long, 2.5–4 μ broad at the base, tapering to 1.2–2 μ at the top, and end in a light brown, sometimes somewhat darker, cup-shaped collarette with flaring margin, 1 μ deep and up to 5 μ broad. The longer conidiophores have, besides the usual septum at the base, one or two more septa and are often branched. Proliferation is common.

The conidia are typically dimorphic. Hyaline, cylindrical, sometimes allantoid, spores, 3–8 × 1.5–3 μ, occur predominantly in young cultures. Globose or lacrymoid, subhyaline, conidia, 3–3.5 μ in diameter, with a distinct wall and darkening with age, are more prevalent in older cultures. However, both types occur in every culture and may even develop in the same spore-ball (Fig. 11d). The species can be easily recognized by the sturdy phialides with the broad, shallow cups with flaring margins and by the dimorphic conidia. Optimum temparature is 25–30° C. No perfect state is known.

Description is based on the strain CBS 295.39.

HABITAT: on wood and ground wood pulp, in sewage and soil, in North America, Europe, Africa, Asia. The fungus has also been isolated once from plastic material in the open air in Africa (Nicot, 1966), from a prostate gland in the Netherlands (G. A. de Vries, pers. commun.), and from a subcutaneous cystic granuloma in New York by Schwartz & Emmons (1968).

MATERIAL EXAMINED.

a. Herbarium material.

Paratype material of *Cadophora richardsiae*: Slide 194:3, labelled "Paratypus of *Cadophora richardsiae*, isolated from ground wood pulp, North America, culture 82219-2, received from Miss Richards."

Two slides 194:4, 272:4, from culture 6723-1 from Miss Richards, same origin, labelled "paratypus" (UPS).

Two slides 229a and 237:21a, isolated by E. Melin, 1932, from ground wood pulp in Västerbotten, Umeå, Sofiehems Trämassefabrik, "paratypus", all det. by J. A. Nannfeldt (UPS).

Cadophora richardsiae, photograph and dried culture, isolated from wood pulp, via CBS to N. F. Conant (No. 330), authentic material (FH).

Cadophora brunnescens, type material consisting of 2 dried cultures and a photograph from N. F. Conant (No. 377) (FH).

b. Living strains.

CBS 270.33, authentic strain No. 389:12 from E. Melin, sent in 1933, as *C. richardsiae*.

CBS 295.39, type of *Cadophora brunnescens*, sent by R. W. Davidson in 1939, No. 59048, from pine lumber, Louisiana, isolated 1931.

CBS 310.49, isolated from wax by M. D. Horst, identified by A. L. van Beverwijk.

CBS 302.62 = IMI 89387, type of *Phialophora caliciformis*, sent by G. Smith, 1962, isolated March, 1954, by W. P. K. Findlay, from African Mahogany (*Khaya* sp.) at the Forest Products Research Laboratory, Princes Risborough.

CBS 271.66, obtained from G. A. de Vries, 1966, isolated from a prostate gland from a patient in the Netherlands.

CBS 573.67, sent by J. Nicot, 1967, isolated by P. Fusey, 1964, from plastic material in the Centralafrican Republic.

CBS 841.69 and CBS 842.69 isolated by A. L. van Beverwijk as contaminants of the laboratory, Baarn.

CBS 843.69 (1573), CBS 844.69 (1551), CBS 845.69 (490), CBS 846.69 (3880),

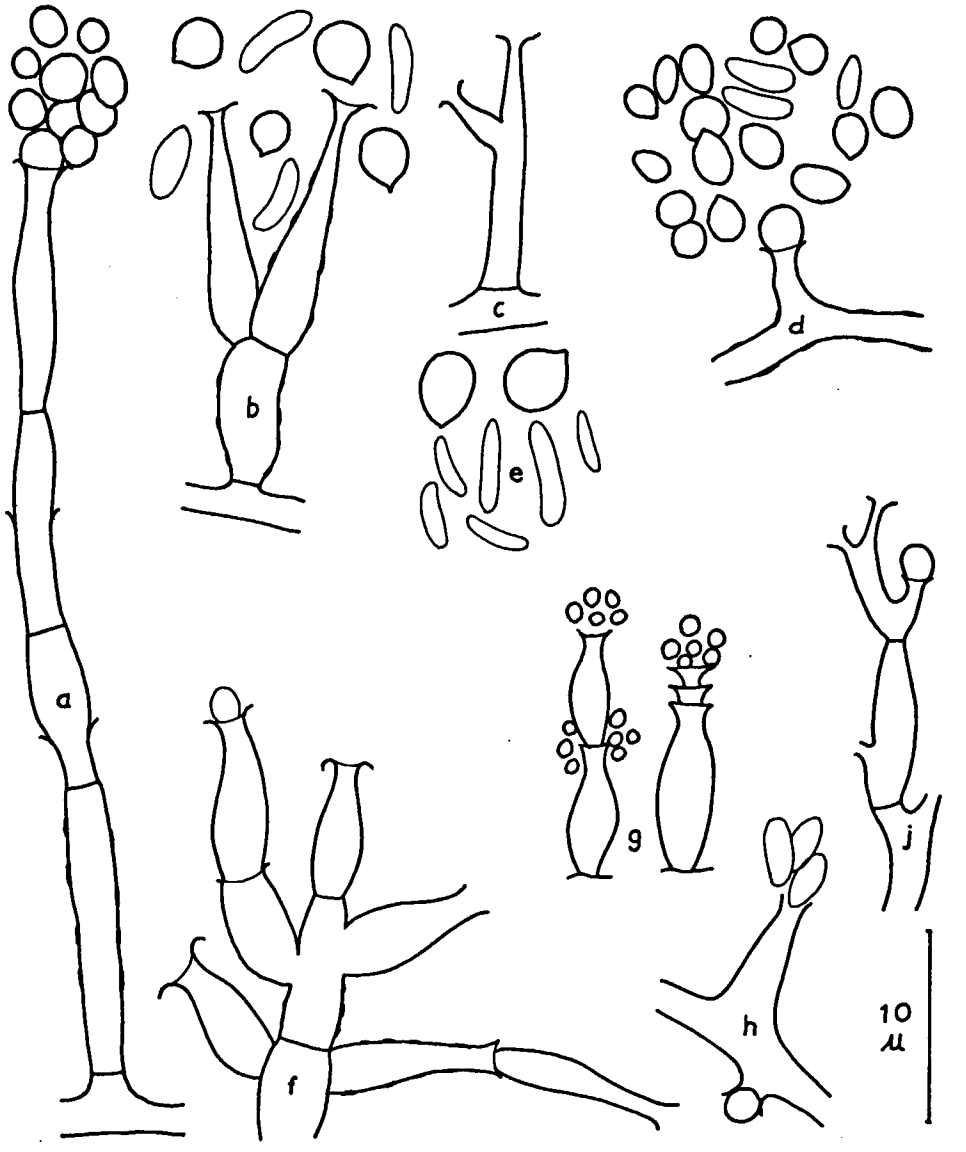

Fig. 11. *Phialophora richardsiae*. a, d, h. CBS 841.69; b, e. Conant's dried culture 337 (FH) as *Cadophora brunnescens*; c, f. Conant's dried culture 330 (FH) as *Cadophora richardsiae*. — a. multiple proliferation, the basal part with irregularly thickened wall. — b, c. furcate phialide and spores in various shapes and sizes. — d. spore-mass with dimorphic spores. — e. subglobose pigmented and cylindrical hyaline conidia. — f. branched conidiophores with proliferations. — g. schematic figure showing what may happen when secondary phialides become shorter (after G. L. Hennebert). — h. short phialides on the same hyphae producing long oval as well as globose conidia. — j. laterally proliferating phialides.

CBS 847.69 (3627), sent by W. B. Cooke via G. L. Hennebert, from waste stabilization ponds and sewage in Ohio.

In the diagnosis of this fungus Nannfeldt (1934) mentioned only subglobose conidia with a distinct brown wall. Davidson (1935) wrote in his diagnosis of *Cadophora brunnescens*: "Conidia hyaline and ovoid or cylindric at first, 1.2 μ to 3 μ by 3 μ to 8 μ, later globose and light brown, 1.5 μ to 3 μ in diameter." In a letter to van Beyma in 1939, he suggested the synonymy of *Phialophora brunnescens* with *P. richardsiae* and this was later confirmed by van Beyma (1943).

Smith (1962) described a new species, *Phialophora caliciformis*, mentioning only the brown, globose or subglobose conidia. The type culture of this, IMI 89387 = CBS 302.62, turned out, however, to be identical with *P. richardsiae*, as Nicot (1966) mentioned in her publication.

In the strain CBS 573.67 Nicot (1967) described the formation of successive collarettes at the top of a phialide. She explained this phenomenon as a minute lengthening of the cup but it may be explained more correctly as a very reduced proliferation of the phialide (Fig. 11g).

In this particular strain the globose spores may become verruculose with age.

12. PHIALOPHORA VERRUCOSA Medlar—Fig. 12

Phialophora verrucosa Medlar *in* Mycologia **7**: 203. 1915.

Cadophora americana Nannf. *apud* Melin & Nannf. *in* Svenska Skogsvårdsfören. Tidskr. **32**: 412. 1934. — *Phialophora americana* (Nannf. apud Melin & Nannf.) Hughes *in* Can. J. Bot. **36**: 795. 1958 (synonymy according to Conant, 1937).

Colonies on 2 % malt agar reach a diameter of 6–7 cm in 4 weeks at 25° C. They are woolly, Dark Mouse Gray (LI) to Deep Olive Gray (LI). At the periphery of the colony the mycelium grows submerged over a zone 2–3 mm broad and has a darker tinge, Iron Gray (LI) to Olivaceous Black (3) (LI).

Colonies on asparagine-yeast agar at 25° C grow somewhat faster, reaching 8 cm in diameter in 4 weeks. They are woolly and Hair Brown (XLVI). The submerged margin is irregular, 1–3 mm broad and Dark Grayish Olive (XLVI). Optimum temperature 25–30° C.

Hyphae are septate, up to 5 μ wide, sometimes aggregated in strands, and sometimes moniliform because of inflated, thick-walled cells, up to 10–15 μ long (Fig. 12r).

Phialides, up to 30 μ long, develop terminally or laterally on the hyphae. They are slender or more often bottle-shaped, single or branched and then sometimes forming bushes. They end in a very distinct cup-shaped collarette with flaring margin obviously darker than the rest of the phialide, and up to 3.5 μ in diameter and 4.5 μ in depth. Proliferation occurs (Fig. 12 a, g, n).

Conidia are hyaline, 3–5 × 2–3 μ, variable in shape and size, ovoid or cylindrical or exceptionally allantoid (occurring in Conant's exsiccate), cohering in a mucous ball at the top of the phialide, becoming darker with age and growing into large, more or less globose, thick-walled spores, with a brown wall, 5–7(–10–15) × 3–6 μ (Fig. 12b, f). These may develop a cup or a muzzle-like protuberance from which

secondary conidia are pushed out (Fig. 12c–e). Anastomoses occur. No perfect state is known.

Description based mainly on CBS 281.35.

HABITAT: in human skin lesions, pathogenic for man and mice; in wood pulp and soil.

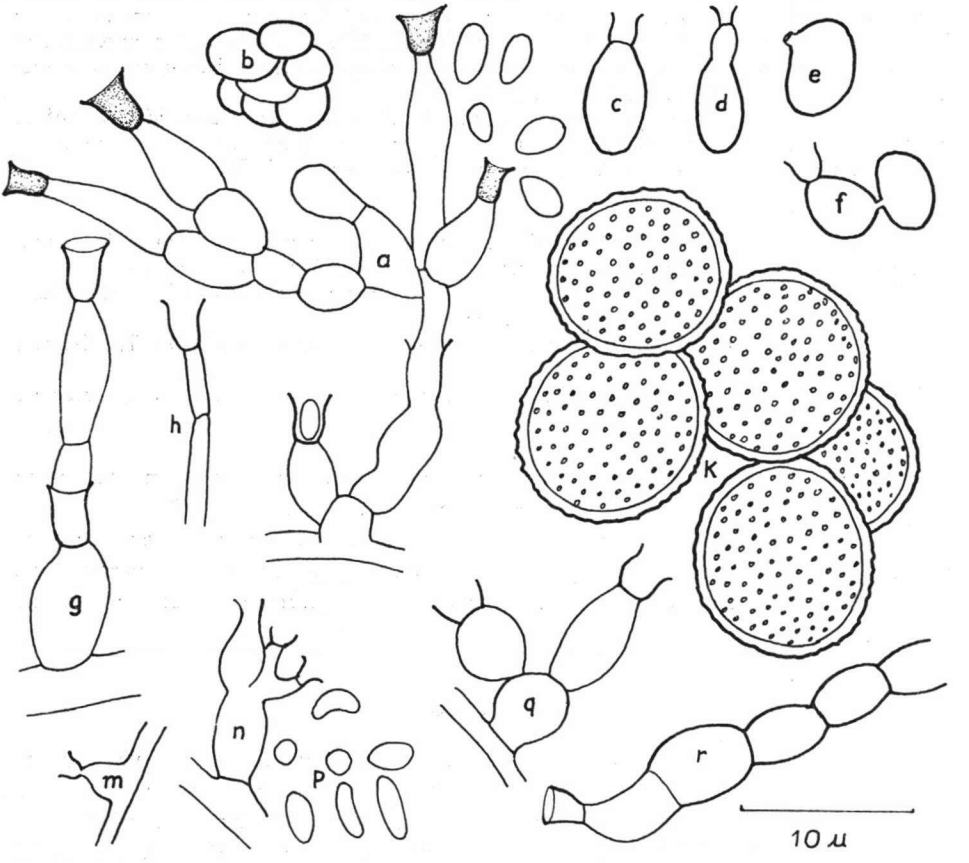

Fig. 12. *Phialophora verrucosa.* a–c, e, g. CBS 281.35; d, f, h, m, n, p. dried culture of Conant 204 (FH); k, q, r. *P. verrucosa,* type material (FH). — a. Proliferating conidiophore with conidia. — b. Globular mass of chlamydospores. — c, d. Chlamydospores with a collarette and developing into a phialide. — e. Chlamydospore with muzzle-like protuberance. — f. Anastomosis of chlamydospores. — g. Proliferating phialide. — h. Thread-like phialide. — k. Chlamydospores. — m. Lateral phialide. — n. Proliferating phialide. — p. Conidia of various shape. — q. Branched conidiophore. — r. Moniliform hypha with terminal phialide.

MATERIAL EXAMINED.

a. Herbarium material.

Type material of *Phialophora verrucosa* Medlar, consisting of a photograph and a dried culture on agar, both labelled "*Phialophora verrucosa* Thaxter, type"; photograph and dried culture on agar labelled "*Phialophora verrucosa* Thaxter: Texan case, N. F. Conant, culture No. 204"; photograph labelled "*Phialophora verrucosa* Thaxter, Uruguay case, N. F. Conant, culture No. 283" (FH).

Type material of *Cadophora americana* Nannfeldt, 2 slides: 194:2, 339:2 both labelled "Miss Richards' cult. 6320-2, typus" (UPS). 6320-2 was isolated by Audrey Richards and sent to Nannfeldt who described it. Melin sent this strain to the CBS in 1933 where it has been preserved as "strain Melin" under the original name; in 1937, according to Conant, the name was changed into *Phialophora verrucosa*. The strain became contaminated and was lost in 1959.

The same isolate is also preserved as dried culture on agar labelled "*Cadophora americana* Nannfeldt, N. F. Conant cult. 333, culture from Audrey Richards to Nannf. to Centraalbureau, from paper pulp, Wisconsin" (FH).

b. Living strains.

CBS 281.35 = ATCC 4806 = IMI 21.191 original strain Weidman No. 2261, isolate from "verrucous dermatosis of the legs" and described by Wilson & al., 1933.

CBS 400.67, sent by A. Ch. Batista in 1967, isolated from soil, Recife, Brasil.

CBS 738.67 = L.C. 971 = strain Langeron.

CBS 839.69 (P 152-8) isolated from birch-wood, sent in 1968 by Th. Nilsson, Stockholm.

CBS 840.69 (501) isolated from decaying lumber and sent in 1967 by A. Salonen, Helsinki.

In some cultures structures covered with setae developed which might be the beginning of fruit-bodies but these never became ripe. Ajello & Runyon (1953) have described similar structures, interpreted by them as probably abortive perithecia, in an isolate of this species. Extensive physiological studies of this fungus were published by Carrión & Silva (1947) with special reference to its medical importance.

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