

## *Phaeoacremonium* gen. nov. associated with wilt and decline diseases of woody hosts and human infections

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**Abstract:** A new hyphomycete genus, *Phaeoacremonium*, is proposed for five new species, *P. aleophilum*, *P. angustius*, *P. chlamydosporum*, *P. inflatipes*, *P. rubrigenum*, and the type species, *P. parasiticum*, which was formerly accommodated in *Phialophora*. Morphologically, the genus is intermediate between *Acremonium* and *Phialophora*. It is distinguished from *Phialophora* by its aculeate conidiogenous cells and inconspicuous collarettes, and from *Acremonium* by its pigmented vegetative hyphae and conidiophores. Because species of *Phaeoacremonium* have been associated with human infections and disease symptoms of several woody hosts, this new genus is considered to represent an ecologically important group of fungi.

**Key Words:** hyphomycetes, medical mycology, *Phialophora*, systematics

### INTRODUCTION

Grape diseases named Esca, apoplexy or Black Measles, with an extensive range of symptoms, have been described to occur in Italy (e.g. Baldacci et al., 1962), France (Viala, 1926; Dubos and Larignon, 1988), and California (Chiarappa, 1959). From grapevines (*Vitis vinifera* L.) showing these symptoms, similar fungi have been isolated including *Stereum hirsutum* (Willd.) Pers., *Phellinus igniarius* (L.: Fr.) Quél. and

a number of *Cephalosporium*-like fungi (Dubos and Larignon, 1988).

Since 1940 a slow die-back disease has been encountered sporadically in grapevines growing in the Cape Province of South Africa. Symptoms include unequal to stunted growth, eventually leading to die-back. The organism most commonly associated with these rootstocks has been identified as *Phialophora parasitica* Ajello et al. (Ferreira et al., 1994). In inoculation experiments on vine rootstocks, *P. parasitica* causes a plugging of the xylem vessels, similar to that observed under field conditions (Ferreira et al., 1994).

*Phialophora parasitica* was originally isolated from a subcutaneous infection of a human patient who had undergone a kidney transplant (Ajello et al., 1974). However, Hawksworth et al. (1976) noted that this fungus had earlier been associated with disease conditions on various woody hosts. They also reported that the decline of oaks in Texas, originally attributed to a *Cephalosporium* species (Halliwell, 1966), was in fact caused by *P. parasitica*. *Phialophora parasitica* has also been associated with various disease conditions of a *Nectandra* sp. in Costa Rica, *Phoenix dactylifera* L. in Iraq, *Prunus armeniaca* L. in Tunisia (Hawksworth et al., 1976), a *Cupressus* sp., *Aquilaria agalocha* Roxb. (Hawksworth and Gibson, 1976) and olive trees (*Olea europaea* L.) (Thanassouloupoulos and Thanassouloupoulos, 1984). A similar fungus (*Cephalosporium* sp.) has also been obtained from grapevines (Chiarappa, 1959). Hawksworth et al. (1976) re-examined the strain CBS 239.74, received from Chiarappa, and concluded that this fungus could represent a new species. They based this conclusion on the fact that the conidiophore stipes were darker and more sharply differentiated from the paler phialides than those of *P. parasitica*. The conidia were also smaller,  $2.0\text{--}5.0 \times 0.7\text{--}2.5 \mu\text{m}$ , and mostly straight, whereas those of *P. parasitica* were larger,  $2.5\text{--}6.0\text{--}8.0 \times 1.0\text{--}2.0\text{--}4.0 \mu\text{m}$ , and more allantoid. These authors refrained from describing it as a new taxon owing to the lack of sufficient strains for detailed study.

The genera *Acremonium* Link:Fr. and *Phialophora* Medlar are generally considered to be heterogeneous (Schol-Schwarz, 1970; Gams, 1971; Cole and Kendrick, 1973). The structures used to discriminate spe-

cies in these complexes are poorly differentiated. For this reason, and due to a general lack of cultures of many of the species, there has been a tendency to assign intermediate strains to either one or the other of these generic aggregates. Schol-Schwarz (1970) included several species with curved conidia in *Phialophora*, most of which apparently will have to be excluded. Species with strongly curved, sickle-shaped conidia and thin, fast-growing colonies are distinctive and characteristic of anamorphs of *Gaeumannomyces* Arx & D.L. Olivier. For this group, which also includes *Cephalosporium maydis* Samra et al., no generic name is yet available. Less curved, allantoid conidia are described for the "*Phialophora lagerbergii* group".

The strains presently available for the *P. lagerbergii* group in the CBS collection have been reexamined. Only the ex type strains, CBS 266.33 of *P. lagerbergii* (Melin & Nannf.) Conant, and CBS 294.39 of *P. repens* (R.W. Davidson) Conant, can be recognized as representing these species. Both are similar to each other, having rather broadly spreading colonies with a brown center and broad hyaline margin; partly brown, incrusting vegetative hyphae, up to 5–6  $\mu\text{m}$  wide; and rather fine, sub-hyaline, ampulliform phialides that are often aggregated in dense clusters. Conidia are tiny, normally not exceeding  $5 \times 1 \mu\text{m}$  (at least when grown on oatmeal agar for not more than 2 wk). These species seem to take a rather isolated position in *Phialophora*; they can be easily distinguished from the "*P. parasitica* group" by their rather short and ampulliform phialides. The only remaining species with conspicuous ampulliform phialides and allantoid conidia that really fits in *Phialophora* is *P. botuliformis* G.T. Cole & W.B. Kendr., which has clustered, lageniform phialides with very pronounced collarettes and conidia,  $2.5\text{--}7.0 \times 1.0\text{--}2.0 \mu\text{m}$  (Cole and Kendrick, 1973).

*Phialophora bubakii* (Laxa) Schol-Schwarz was also described as having partly allantoid conidia. This species deviates from others in *Phialophora* not only by lacking a prominent collarette but, particularly, by acropleurogenous branching of the pigmented conidiophores. Slightly curved, allantoid conidia are also described for the anamorphs of *Ascocoryne* J.W. Groves & D.E. Wilson, for which the most adequate genus is *Coryne* Gray, with several other synonyms (Groves and Wilson, 1967; Roll-Hansen and Roll-Hansen, 1979). These fungi are characterized by slimy colonies, often with some purple pigmentation and a tendency to form gelatinous conidiomata in old colonies; the hyaline phialides lack any trace of a light-microscopically visible collarette. Another group of species with slimy, generally nonpigmented or only partially pigmented colonies (sometimes with brown chlamydospores), comprise the anamorphs of

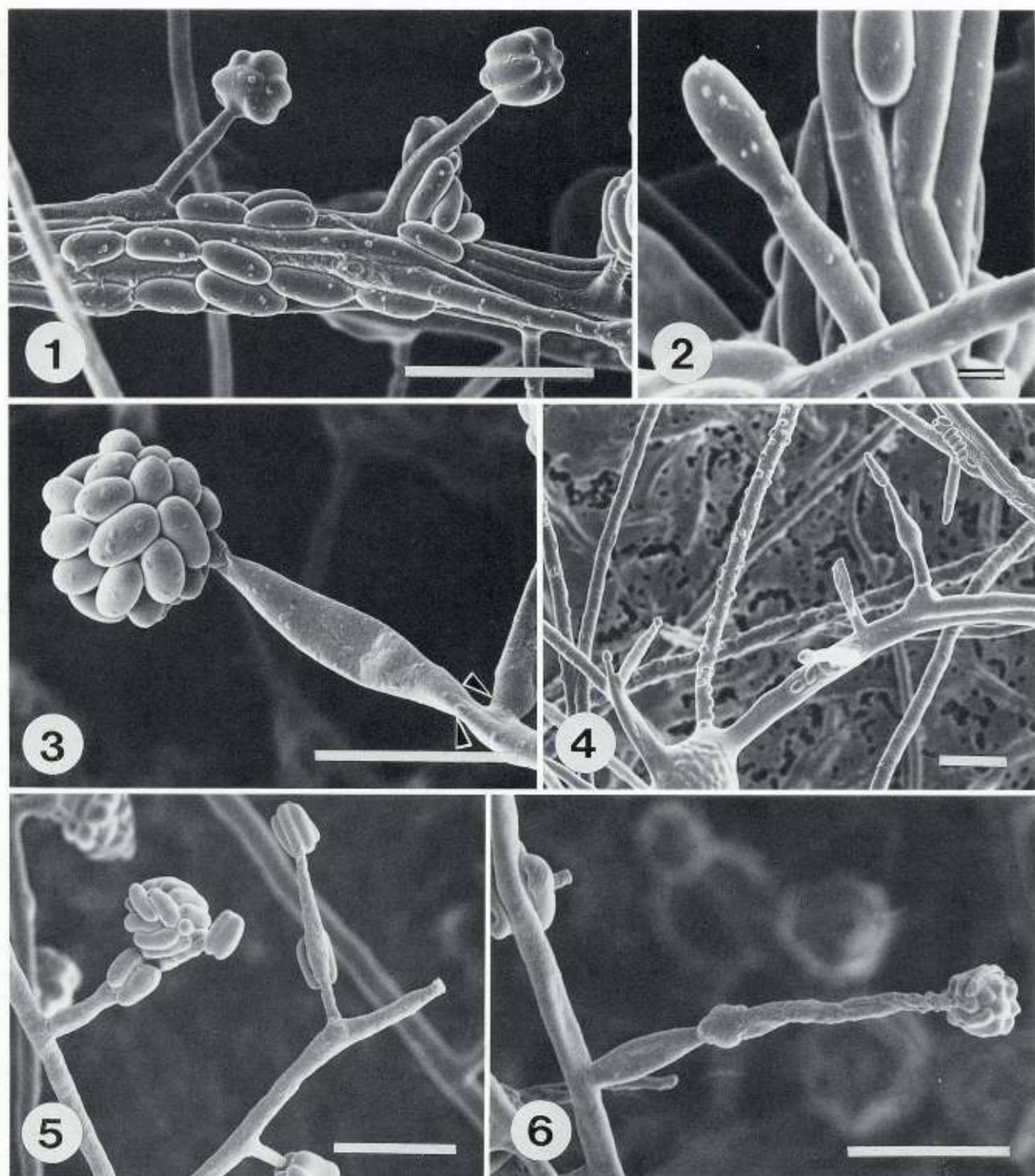
*Coniochaeta* (Sacc.) Cooke, for which the genus *Lecythophora* Nannf. has been reintroduced by Gams and McGinnis (1983). These fungi are characterized by the predominant occurrence of intercalary phialides (adelophialides of Gams, 1971).

In a step towards establishing clearer generic boundaries, Gams and McGinnis (1983) erected the genus *Phialemonium* W. Gams & McGinnis to accommodate another group of fungi intermediate between *Acremonium* and *Phialophora*. *Phialemonium* is characterized by having hyaline conidiogenous structures, and prominent, slender, lateral conidiiferous pegs (if discrete phialides are present they are slender near the base and slightly inflated near the middle). Furthermore, its very narrow vegetative hyphae (0.5  $\mu\text{m}$  in width) also distinguishes *Phialemonium* from the otherwise similar *Lecythophora*.

There is an increasing amount of evidence, based on molecular data, that the type species of *Phialophora*, *P. verrucosa* Medlar, has affinities to the Herpotrichiellaceae (Masclaux et al., 1995), a family of loculoascomycetes (Untereiner et al., 1995). This group of species differs widely from the *P. parasitica* group by having very darkly pigmented hyphae and conidiophores, and slower growing colonies. Moreover, there is no indication whatsoever of any relationship of the *P. parasitica* group with the Herpotrichiellaceae.

As more isolates of *P. parasitica* and similar fungi accumulated, it became obvious that they form a cluster of related and morphologically well-defined species that cannot be adequately accommodated in *Phialophora*. Although they are dematiaceous, such as is true of *Phialophora*, their phialides are aculeate and the collarettes tend to be inconspicuous and not flaring, not really resembling *Phialophora* (FIGS. 1–6). Conidiophore stipes and part of the vegetative hyphae are obviously pigmented, unlike those of *Acremonium*. Furthermore, in an analysis of restriction fragment length polymorphism and sequence data of rDNA from various strains identified as *P. parasitica*, Yan et al. (1995) showed that this species represents a heterogeneous assortment of taxa, which is not related to other species classified in *Phialophora*. The aim of this study was, therefore, to clarify the taxonomic position of strains determined as *P. parasitica* that are associated with human infections and disease symptoms on a diversity of woody substrates.

After more than 30 years of collecting strains of these fungi at CBS, we are now in the position to describe a new genus for these fungi which, besides the type species, comprises five new species. It is worth noting that strains of four of these have been isolated from grapevine. Their causal effects in connection with Esca disease, singly and in association



FIGS. 1-6. Conidiogenous cells and conidia of *Phaeoacremonium* spp. 1, 2. Hyphal strands and conidia of *P. parasiticum* (CBS 860.73). 3. Constricted conidiogenous cells (arrows) of *P. inflatipes* (CBS 391.71). 4. Swollen conidiogenous cell, tuberculate hyphae and small conidia of *P. chlamydosporum*. 5, 6 (CBS 229.95). Polyphialide and proliferating phialide of *P. angustius* (CBS 249.95). Scale bar = 1  $\mu$ m in FIG. 2, and 10  $\mu$ m elsewhere.

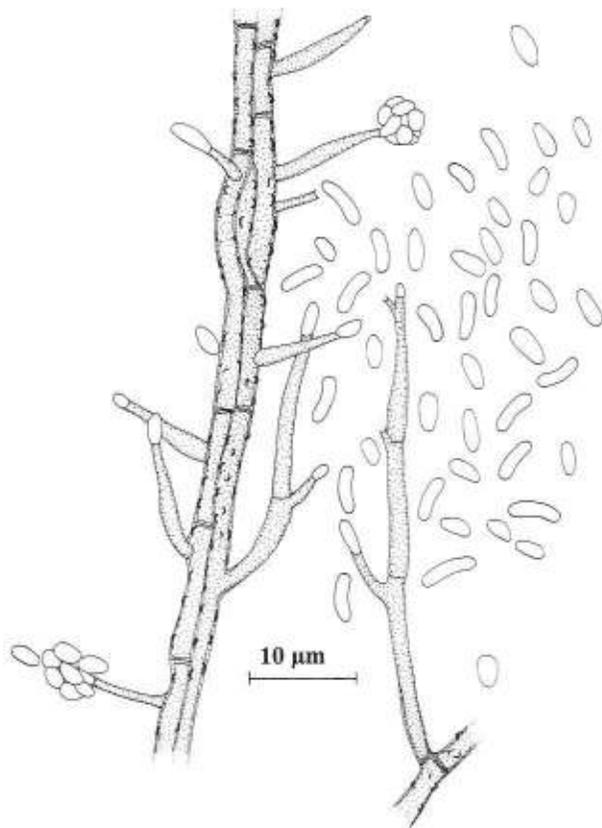


FIG. 7. Conidia, conidiophores and conidiogenous cells of *P. aleophilum* (CBS 246.91).

with *Phellinus igniarius*, will require further study. Three species have been isolated from medical material. However, two of these have also been isolated from plants, and it does not seem that there is any specialization for human pathogenicity.

#### MATERIALS AND METHODS

Single-conidial cultures derived from the ex type strains of *P. parasitica*, along with several other unidentified strains were plated onto malt extract agar (MEA; 20 g Oxoid malt extract, 15 g Difco agar, 1000 mL H<sub>2</sub>O). Cultures were incubated at 25 C under near-ultraviolet light to promote sporulation. Conidia often became 2-guttulate, bacilliform, elongated and abnormal with age. Such old and mature conidia were excluded from measurements. Fifty examples of each structure were measured, the 95% interval determined, and extremes given in parentheses.

Radial growth of species in culture was determined on MEA plates after 8 d in the dark as previously explained by Crous and Wingfield (1994). Cardinal temperatures for growth were determined on MEA plates at 5–35 C at 5 C intervals with three replicate plates per temperature interval. Colony color (rated from in-

verted plates) was determined after 8 d at 25 C in the dark using the color designations of Rayner (1970).

Scanning electron microscopy (SEM) was used to observe differences in phialide morphology. Specimens were flash frozen (–212 C) in liquid nitrogen under vacuum for cryo-SEM, transferred to the preparation chamber, and then to the SEM chamber where the frozen samples were sublimated (–80 C) to remove ice particles. Samples were sputter coated with gold palladium in the preparation chamber for 75 s under 1.2 KV at –170 C. Specimens were viewed under 5 KV at –188 C with a Jeol JSM 6100 scanning electron microscope.

#### TAXONOMY

**Phaeoacremonium** W. Gams, Crous et M. J. Wingf., gen. nov.

Genus hyphomycetum, positione intermedia inter *Acremonium* et *Phialophoram*. Coloniae plerumque griseo-olivaceae, viridi-brunneae vel ochraceae, raro rubescentes, fere lente crescentes, paulo mycelio aereo griseo vel brunneo. Hyphae ramosae, septatae, singulae vel fasciculatae, plus minusve verruculosae, dilute brunneae, in parte conidiogena pallidiores vel hyalinae. Chlamydo-sporae absentes vel praesentes. Conidiophora ex hyphis aeriis vel submersis oriunda, erecta, simplicia vel racemosa, subcylindrica, plus minusve brunnea, sursum pallidiora, nonnumquam verruculosa in parte inferiore, recta vel modice flexuosa, 1–7-septata, longitudine variabilia, 2–4 μm lata. Cellulae conidiogenaes terminales vel laterales, plerumque monophialidicae, raro in coloniis vetustis percurrenter proliferantes; phialides subcylindricae vel elongato-ampulliformes, collari terminali anguste infundibuliformi praeditae. Phialides minores intercalares hyalinae saepe ex hyphis vegetativis oriundae. Conidia in capitulis mucidis aggregata, hyalina vel subhyalina, aseptata, levia, oblonge ellipsoidea vel cylindrica, sed saepe allantoidalia. Teleomorphosis ignota.

Species typica *Phaeoacremonium parasiticum* (Ajello, Georg et C.J.K. Wang) W. Gams, Crous et M.J. Wingf.

A hyphomycete genus morphologically intermediate between *Acremonium* and *Phialophora*. Colonies on MEA (reverse) usually buff to grey-olivaceous, green-brown or honey, rarely red in color, moderately spreading, with some grey to brown aerial mycelium. Mycelium consisting of branched, septate hyphae; hyphae simple, or occurring in strands, smooth or verruculose to tuberculate, medium brown, becoming lighter brown to hyaline towards the conidiogenous region. Chlamydospores absent or present. Conidiophores macronematous and micronematous, arising

from aerial or submerged hyphae, erect, simple or racemously branched, subcylindrical, medium brown, becoming lighter toward the tip, sometimes tuberculate to verruculose in the lower part, straight or slightly flexuous, 1–7-septate, variable in length, 2–4  $\mu\text{m}$  wide. *Conidiogenous cells* terminal or lateral, typically monophialidic but also polyphialidic; in old cultures sometimes proliferating percurrently; phialides subcylindrical or elongate-ampulliform, with a terminal, narrowly funnel-shaped collarette. Micronematous conidiophores common, as lateral, unpigmented phialidic necks (adelophialides in Gams,

1971) arising along vegetative hyphae. *Conidia* becoming aggregated into round, slimy heads at the apices of conidiogenous cells, hyaline to sub-hyaline, aseptate, smooth-walled, oblong-ellipsoidal to obovate or cylindrical, but most typically allantoid. *Teleomorph* unknown, but some globose, firm brown structures observed in mature cultures of *P. parasiticum*. *Synanamorph* rare, but a *Phoma*-like state has been induced for isolates of *P. chlamyosporum* on a medium containing autoclaved tea leaves.

Type species: *Phaeoacremonium parasiticum* (Ajello, Georg & C.J.K. Wang) W. Gams, Crous & M.J. Wingf.

KEY TO HYPHOMYCETE GENERA WITH WET PHIALOCONIDIA, SIMILAR TO *PHAEOACREMONIUM*  
(GENERA WITH VERTICILLATE-PENICILLATE CONIDIOPHORES EXCLUDED)

1. Discrete phialides usually absent, conidiogenesis through lateral necks arising from undifferentiated hyphae ..... 2
1. Discrete erect phialides present in varying proportions (observe undisturbed colony directly in petri dish) ..... 3
  2. Vegetative hyphae 1.0  $\mu\text{m}$  or more wide; phialidic opening 1.2  $\mu\text{m}$  or wider, periclinal thickening usually recognizable under a light microscope ..... *Lecythophora*
  2. Vegetative hyphae often less than 1.0  $\mu\text{m}$  wide; short, erect phialides sometimes present which are narrow near the base and widest near the middle; opening 1.0  $\mu\text{m}$  or less in width, periclinal thickening not recognizable under a light microscope ..... *Phialemonium*
3. Colonies white, very slow-growing (< 1 cm diam in 2 wk), more or less sparingly and tardily sporulating; conidiophores never branched, consisting of aculeate phialides which often lack a basal septum ... *Neotyphodium* (anam. of *Epichloë*)
3. Colonies white or variously pigmented, faster growing, more abundantly sporulating; phialides usually delimited by a basal septum, but reduced intercalary phialidic necks may also occur ..... 4
  4. Colonies (apart from sometimes dark sclerotia) pink, moist; conidiophores unbranched; phialides with a more or less thickened wall in the lower part, sometimes swollen above and ending with an aculeate thin-walled portion ..... *Monocillium*
  4. Colonies pink or differently colored; conidiophores unbranched or branched, but then mostly in the lower part; phialide wall not markedly thickened in the lower part ..... 5
5. Vegetative hyphae and conidiophores consistently hyaline or in pale colors (at most brightly olivaceous-green, but not olivaceous-brown to black); conidia hyaline (or with dark superficial pigment incrustation), smooth or roughened .. 6
5. Vegetative hyphae and conidiophores with brown to olivaceous pigmentation; conidia smooth ..... 7
  6. Conidia adhering in slimy heads or chains, but in the latter case lacking an apical apiculation; phialides broadest near base ..... *Acronium*
  6. Conidia adhering in regular chains, with apiculation at both ends; phialides narrowed near base ..... *Sagenomella*
7. Colonies slow-growing (< 1.8 cm diam in 2 wk), with olivaceous-brown pigmentation throughout; young colonies sometimes yeast-like; conidiogenesis annellidic (seen under SEM), but under the light microscope often appearing phialidic; conidia also slightly pigmented and showing a basal apiculation ..... *Exophiala*
7. Colonies mostly faster growing, not or less conspicuously pigmented throughout; conidiogenesis phialidic ..... 8
  8. Conidial wall brown throughout; phialide collarette not pronounced ..... *Pseudogliomastix*
  8. Conidial wall hyaline or slightly pigmented, but then collarette conspicuous ..... 9
9. Conidiophores simple or branched, mostly pigmented, particularly the basal cells; phialides aculeate, with a narrow collarette; conidia generally allantoid, at least partly, and hyaline ..... *Phaeoacremonium*
9. Conidiophores simple or branched to penicillate, hyaline to pigmented; phialides more or less swollen, flask-shaped, with a flaring collarette; conidia variously shaped, but only rarely allantoid, hyaline or pigmented ..... *Phialophora*

KEY TO THE SPECIES OF *PHAEOACREMONIUM*

1. Chlamydo-spores present; colonies grey-olivaceous to olivaceous-black; conidiogenous cells pale green-brown, often supported by much darker cells, 8.0–55.0  $\times$  1.5–4.0  $\mu\text{m}$ ; conidia oblong-ellipsoidal to obovate, permanently straight, subhyaline (1.5–)3.0–4.0(–4.5)  $\times$  1.0–1.5(–2.0)  $\mu\text{m}$ ; temperature optimum 25 C ..... 3. *P. chlamyosporum*

1. Chlamydo-spores absent; conidia broader and at least partially allantoid ..... 2
  2. Colonies buff to grey-olivaceous; hyphae with warts up to 3  $\mu\text{m}$ ; phialides regularly aculeate, generally straight; conidia ellipsoidal, often allantoid, (2.0–)3.0–4.0(–6.0)  $\times$  (1.0–)1.5–2.0  $\mu\text{m}$ ; temperature optimum 25 C ..... 5. *P. parasiticum*
  2. Colonies usually of other color; hyphae less coarsely tuberculate ..... 3

3. Phialides mostly with basal constriction; temperature optimum 30 C ..... 4
3. Phialides mostly without basal constriction; temperature optimum below or above 30 C ..... 5
4. Colonies becoming vinaceous in reverse; conidia oblong-ellipsoidal to allantoid, 3.0–4.0(–6.0) × (1.0–)1.5–2.0 μm ..... 6. *P. rubrigenum*
4. Colonies consistently smoke-grey to honey in reverse; conidia conspicuously allantoid, 3.0–5.0(–7.0) × (1.0–)1.5–2.0(–2.5) μm ..... 4. *P. inflatipes*
5. Optimum growth at 25 C (no growth at 35 C), cultures brownish; conidia mostly subcylindrical, straight to allantoid, (3.5–)4.5–6.0(–8.0) × (1.0–)1.5–2.0 μm ..... 2. *P. angustius*
5. Optimum growth at 35 C, cultures honey colored; conidia oblong-ellipsoidal to allantoid, (2.5–)3.0–4.5(–6.0) × 1.5–2.5(–3.0) μm ..... 1. *P. aleophilum*

1. **Phaeoacremonium aleophilum** W. Gams, Crous, M.J. Wingf. et L. Mugnai, sp. nov. FIG. 7

Hyphae ramosae, septatae, singulae vel ad decenas fasciculatae, plus minusve verruculosae, dilute brunneae, parietibus et septis paulo obscurioribus, in parte conidiogena pallidiores, 1.5–3 μm latae. Chlamydosporae absentes. Conidiophora ex hyphis aeriis vel submersis oriunda, erecta, simplicia, saepe tantum phialides hyphis insidentes, raro 1–2-septata, subcylindrica, dilute brunnea, sursum pallidiora, levia vel verruculosa, recta vel paulo curvata, 4–40 μm longa, 2–3 μm lata. Cellulae conidiogena terminales vel laterales, subcylindricae vel anguste ellipsoideales, leves vel verruculosae, subhyalinae, 3–21 μm longae, e 1.0–2.5 μm prope basim ad 1.0–1.5 μm sursum angustatae, collari inconspicuo 0.5–1.0 μm longo praeditae. Conidia in capitulis mucidis aggregata, hyalina, non septata, oblongo-ellipsoidea vel allantoidea, 2-guttulata, (2.5–)3.0–4.5(–6.0) × 1.5–2.5(–3.0) μm. Coloniae in agar maltoso deorsum ochraceae, ad 4 mm radio post 8 dies 35 C. Temperatura optima crescentiae 35 C.

**HOLOTYPE.** YUGOSLAVIA. On roots and stems of *Vitis vinifera*, 1990, *M. Muntanaola-Cvetković* (CBS 246.91 dried specimen, cultures ex type CBS 246.91, CMW 2031, STE-U 776, dried ISOTYPE lodged at PREM).

**Etymology.** The specific epithet refers to the ability to grow at high temperatures.

**Mycelium** consisting of branched, septate hyphae; hyphae occurring singly or in strands of up to 10, tuberculate (warts to 1 μm) to verruculose, light brown, walls and septa slightly darker, becoming lighter toward the conidiogenous region, 1.5–3.0 μm diam. *Chlamydosporae* absent. *Conidiophores* mostly micronematous, arising from aerial or submerged hyphae, erect, simple, frequently reduced to conidiogenous cells, rarely 1–2-septate, subcylindrical, light brown, becoming lighter towards the tip, smooth to verruculose, straight to gently curved, 4–40 μm tall, 2–3 μm wide. *Conidiogenous cells* terminal or lateral, mostly monophialidic, subcylindrical to narrowly ellipsoidal, smooth to verruculose, subhyaline, 3–21 μm long, 1.0–2.5 μm wide at the base, 1.0–1.5 μm wide at the apex, with a terminal, inconspicuous, almost

convergent collarette, 0.5–1.0 μm long, 1.0 μm wide. *Conidia* becoming aggregated into round, slimy heads at the apices of conidiogenous cells, hyaline, oblong-ellipsoidal to allantoid, becoming 2-guttulate with age, (2.5–)3.0–4.5(–6.0) × 1.5–2.5(–3.0) μm.

**Cultural characteristics.** Colonies on MEA (reverse) honey (21<sup>b</sup>), reaching a radius of 4 mm at 35 C in the dark after 8 d. Cardinal temperatures for growth 10 C (min.), 35 C (opt.), above 35 C (max.).

**Substrate.** *Vitis vinifera*.

**Distribution.** Italy, Yugoslavia.

**Additional culture examined.** ITALY. On stems and roots of *Vitis vinifera*, 1994, *L. Mugnai* (CBS 631.94, Ist. Patol. Foreste No. 69–257).

**Notes.** *Phaeoacremonium aleophilum* is readily distinguished from *P. parasiticum* and *P. inflatipes* by its culture characteristics, conidial dimensions and smaller conidiophores that are not racemosely branched. Isolate CBS 631.94 agrees with the ex type strain in having very pale brown hyphae and phialides, conidia of similar dimensions [3.0–4.5(–7.0) × 1.5–2.0(–2.5) μm], and an optimal growth rate at 35 C of 8–13 mm diam after 8 d.

2. **Phaeoacremonium angustius** W. Gams, Crous et M.J. Wingf., sp. nov. FIGS. 5, 6, 8, 9

Hyphae ramosae, septatae, singulae vel ad decenas fasciculatae, plus minusve verruculosae, dilute brunneae, parietibus et septis paulo obscurioribus, in parte conidiogena pallidiores, 1.5–3.0 μm latae. Chlamydosporae absentes. Conidiophora ex hyphis aeriis vel submersis oriunda, erecta, simplicia vel in parte inferiore racemosa, subcylindrica, dilute brunnea, sursum pallidiora, plus minusve verruculosa, recta vel flexuosa, 0–5-septata, longitudine variabilia (10–90 μm), 2–4 μm lata, haud constricta ad septa. Cellulae conidiogena terminales vel laterales, verruculosae vel leves, dilute brunneae vel hyalinae, subcylindrica, 8–25 μm longae, ex 1.5–2.5 μm prope basim sursum ad 1.0–1.5 μm angustatae, collari terminali anguste infundibuliformi, 1–3 μm longo praeditae. Conidia in capitulis mucidis aggregata, hyalina, non septata, dimorphica: seu subcylindrica, recta vel allantoidea, ad 8 μm longa, seu breviora, ellipsoidea, (3.5–)4.5–6.0(–8.0) × (1.0–)1.5–2.0 μm. Coloniae in agar maltoso deorsum ochraceae vel isabellinae, ad 8 mm radio post 8 dies 25 C. Temperatura optima crescentiae 25 C.

**HOLOTYPE.** UNITED STATES. CALIFORNIA: Salinas, on stems and roots of *Vitis vinifera*, Aug. 1992, *Ph. Larignon* (CBS 249.95 dried specimen and ex type culture, dried ISOTYPE lodged at PREM).

**Etymology.** The specific epithet refers to the slender conidia.

**Mycelium** consisting of branched, septate hyphae; hyphae occurring singly or in strands of up to 10, tuberculate (warts to 0.5 μm) to verruculose, light brown, walls and septa slightly darker, becoming lighter towards the conidiogenous region, 1.5–3.0 μm diam. *Chlamydosporae* absent. *Conidiophores* mostly micronematous, arising from aerial or submerged hyphae, erect, simple or racemosely branched in the lower part, subcylindrical, light brown, becoming light-

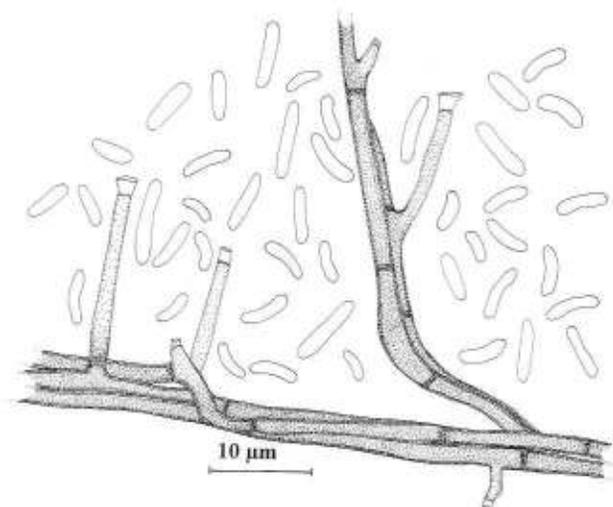


FIG. 8. Conidia, conidiophores and conidiogenous cells of *P. angustius* (CBS 249.95).

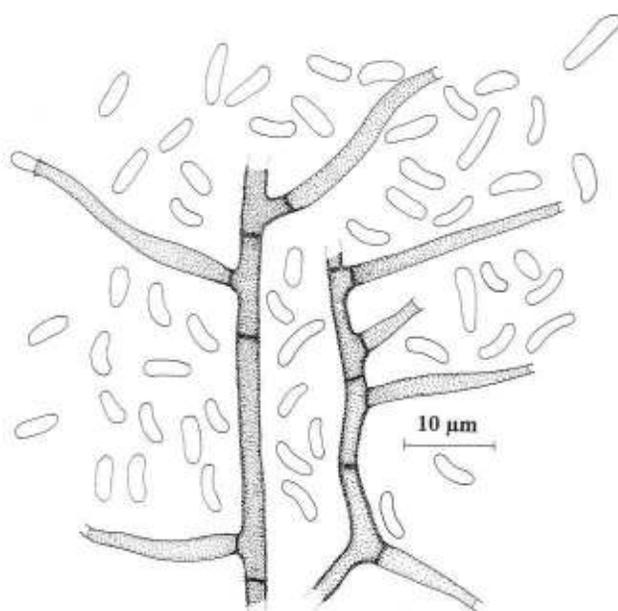


FIG. 9. Conidia, conidiophores and conidiogenous cells of *P. angustius* (CBS 777.83).

er towards the tip, tuberculate to verruculose, straight or flexuous, 0–5-septate, variable in length, 10–90  $\mu\text{m}$  tall, 2–4  $\mu\text{m}$  wide, not constricted at the septa. *Conidiogenous cells* terminal or lateral, mostly monophialidic, verruculose to smooth, pale brown to hyaline, subcylindrical, 8–25  $\mu\text{m}$  long, 1.5–2.5  $\mu\text{m}$  wide at base, 1.0–1.5  $\mu\text{m}$  wide at apex, with a terminal, narrowly funnel-shaped collarete, 1–3  $\mu\text{m}$  long, 1.5–2.0  $\mu\text{m}$  wide, slightly or not constricted at base. *Conidia* becoming aggregated into round, slimy heads at the apices of conidiogenous cells, hyaline, dimorphic, partly subcylindrical, straight to allantoid, to 8  $\mu\text{m}$  long, and partly shorter and ellipsoidal (to 6  $\mu\text{m}$  long), both types becoming 2-guttulate, (3.5–)4.5–6.0(–8.0)  $\times$  (1.0–)1.5–2.0  $\mu\text{m}$ .

*Cultural characteristics.* Colonies on MEA (reverse) honey to isabelline (19<sup>b</sup>–17<sup>i</sup>), reaching a radius of 8 mm at 25 C in the dark after 8 d. Cardinal temperatures for growth above 5 C (min.), 25 C (opt.), below 35 C (max.).

*Substrate.* *Vitis vinifera*, soil.

*Distribution.* Argentina, United States (California).

*Additional culture examined.* ARGENTINA. BUENOS AIRES: soil, A. Martínez (CBS 777.83).

*Notes.* *Phaeoacremonium angustius* is distinct from the other species of *Phaeoacremonium* in having longer, dimorphic conidia that are subcylindrical, straight to allantoid, or short and ellipsoidal. Isolate CBS 777.83 closely resembles *P. angustius* in having the same cardinal temperatures for growth, colony color, growth rate and conidium morphology. However, conidia of the latter strain are not prominently dimorphic as observed in the type, suggesting that this feature may be taxonomically equivocal.

### 3. *Phaeoacremonium chlamydosporum* W. Gams, Crous, M.J. Wingf. et L. Mugnai, sp. nov.

FIGS. 4, 10

Hyphae ramosae, septatae, singulae vel ad decenas fasciculatae, plus minusve verrucosae, viridi-brunneae, parietibus et septis paulo obscurioribus, in parte conidiogena pal-

lidiore, 2–4  $\mu\text{m}$  latae. Chlamydosporae haud copiosae, globosae vel subglobosae, plerumque singulae, raro ad quinas catenatae, olivaceae et leves vel viridi-brunneae et verrucosae, 7–15  $\times$  5–17  $\mu\text{m}$ . Conidiophora ex hyphis aeriis vel submersis oriunda, erecta, semper simplicia, cylindrica, cellula apicali elongato-ampulliformi vel lageniformi, viridi-brunnea, crassitunicata prope basim, sursum magis tenuitunicata et pallidiora, verrucosa vel levia, 1–3-septata, 12–40  $\mu\text{m}$  alta, 1.5–4.0  $\mu\text{m}$  lata. Cellulae conidiogenaes terminales, dilute viridi-brunneae, verrucosae vel leves, elongate ampulliformes vel lageniformes vel subcylindricae, 8–20  $\mu\text{m}$  longae, ex 1.5–4  $\mu\text{m}$  prope basim sursum ad 1.0–1.5  $\mu\text{m}$  angustatae, collari infundibuliformi 0.5–2.0  $\mu\text{m}$  longo praeditae. Conidia in capitulis mucidis aggregata, subhyalina, levia, non septata, oblongo-ellipsoidea vel obovata, semper recta, (1.5–)3.0–4.0(–4.5)  $\times$  1.0–1.5(–2.0)  $\mu\text{m}$ . Coloniae in agar maltoso deorsum griseo-olivaceae vel olivaceo-atrae, ad 5–6 mm radio post 8 dies 25 C. Temperatura optima crescentiae 25 C.

*HOLOTYPE.* ITALY. On stems and roots of *Vitis vinifera*, 25 Jan. 1995, L. Mugnai (CBS 229.95 dried specimen and ex type culture, dried ISOTYPE lodged at PREM).

*Etymology.* The specific epithet refers to the production of chlamydo-spores in culture.

*Mycelium* consisting of branched, septate hyphae occurring singly or in strands of up to 10, tuberculate (warts to 1  $\mu\text{m}$ ) to verruculose, green-brown, walls and septa darker, becoming lighter towards the conidiogenous region, 2–4  $\mu\text{m}$  diam. *Chlamydo-spores* abundant in the type strain, but sparse in others; globose to subglobose, mostly singular, rarely in chains of up to 5, olivaceous and smooth to green-brown and tuberculate, 7–15  $\mu\text{m}$  long, 5–17  $\mu\text{m}$  diam. *Conidiophores* mostly micronematous, arising from aerial or submerged hyphae, erect, simple, not racemosely branched, cylindrical with an elongate-ampulliform to lageniform api-

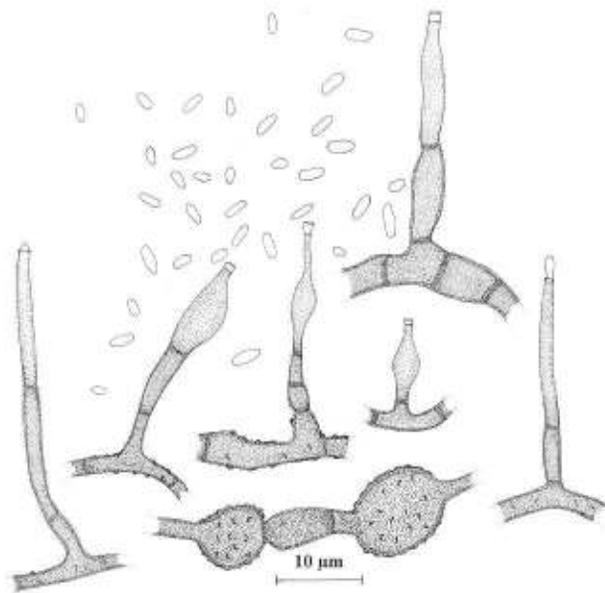


FIG. 10. Conidia, conidiophores and conidiogenous cells of *P. chlamydosporum* (CBS 229.95).

cal cell, green-brown, thick-walled at base, becoming thinner-walled and lighter green-brown towards apex, verrucose to smooth, 1-3-septate, 12-40  $\mu\text{m}$  tall, 1.5-4.0  $\mu\text{m}$  wide. *Conidiogenous cells* terminal, monopialidic, light green-brown, verrucose to smooth, elongate-ampulliform to lageniform or subcylindrical, 8-20  $\mu\text{m}$  long, 1.5-4.0  $\mu\text{m}$  wide at swollen part, 1.0-1.5  $\mu\text{m}$  wide at apex, with a terminal, funnel-shaped collarette, 0.5-2.0  $\mu\text{m}$  long and wide. *Conidia* becoming aggregated in round, slimy heads at the apices of the conidiogenous cells, subhyaline, oblong-ellipsoidal to obovate, permanently straight, (1.5-)3.0-4.0(-4.5)  $\times$  1.0-1.5(-2.0)  $\mu\text{m}$ .

*Cultural characteristics.* Colonies on MEA (reverse) grey-olivaceous to olivaceous-black (23<sup>m</sup>i-23<sup>m</sup>k), reaching a radius of 5-6 mm at 25 C in the dark after 8 d. Cardinal temperatures for growth 15 C (min.), 25 C (opt.), below 35 C (max.).

*Substrate.* *Vitis vinifera*.

*Distribution.* Italy, South Africa (Stellenbosch), United States (California).

*Additional cultures examined.* SOUTH AFRICA. CAPE PROVINCE: Stellenbosch, on stems and roots of *Vitis vinifera*, 1991, E. Venter (CMW 2255, STE-U 774); *Vitis vinifera*, 1994, S. Ferreira (STE-U 809); on stems of *V. vinifera*, 1990, M.J. Wingfield (CBS 161.90); on stems of *V. vinifera*, 1991, M.J. Wingfield (CBS 103.92-105.92). UNITED STATES. CALIFORNIA: on stems and roots of *V. vinifera*, 31 Aug. 1966, L. Chiarappa (CBS 239.74, IMI 192881).

*Notes.* This species can be easily distinguished from other species of *Phaeoacremonium* by its characteristically green-brown, frequently swollen conidiogenous cells, smaller, straight conidia, and the presence of chlamydospores.

In the Californian as well as the South African isolates, chlamydospores were observed to be more sparsely distributed, and smoother than in the ex type strain. Hyphae were frequently covered by large, globose warts, while phialides

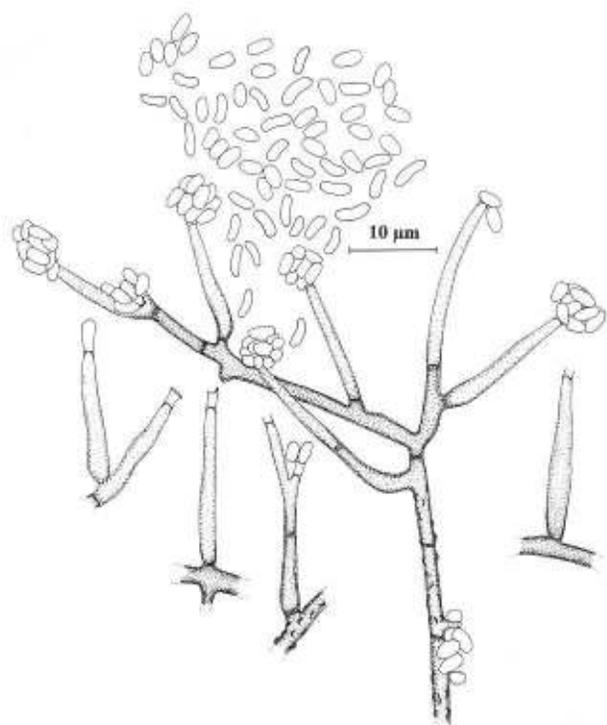


FIG. 11. Conidia, conidiophores and conidiogenous cells of *P. inflatipes* (CBS 391.71).

were mostly subcylindrical, 15.0-55.0  $\times$  2.0-2.5  $\mu\text{m}$ , situated on 1-2-septate conidiophores, 20.0-65.0  $\times$  2.0-2.5  $\mu\text{m}$ . Although these features vary from those in the type strain, all strains had similar temperature requirements for growth, characteristic olivaceous colonies, green-brown conidiophores, chlamydospores, and small, straight, oblong-ellipsoidal to obovate conidia.

#### 4. *Phaeoacremonium inflatipes* W. Gams, Crous et M.J. Wingf., sp. nov. FIGS. 3, 11

Hyphae ramosae, septatae, singulae vel ad decenas fasciculatae, plus minusve verrucosae, dilute brunneae, pallidiores in parte conidiogena, 1.5-3.0  $\mu\text{m}$  latae. Chlamydosporae absentes. Conidiophora ex hyphis aeriis vel submersis oriunda, erecta, simplicia vel racemosa in parte inferiore, subcylindrica, dilute brunnea, sursum pallidiora, verruculosa, recta vel flexuosa, 0-5-septata, longitudine variabilia (10-110  $\mu\text{m}$ ), 2-4  $\mu\text{m}$  lata, ad septa haud constricta, sed saepe ad basim inflata vel in parte inferiore cellulae proliferantis. Cellulae conidiogena terminalis vel laterales, phialidicae, verruculosae vel raro leves, dilute brunneae vel hyalinae, subcylindricae vel elongato-ampulliformes, saepe percurrenter proliferantes, 10-36  $\mu\text{m}$  longae, ex 1.5-3.5  $\mu\text{m}$  prope basim sursum ad 1.0-1.5  $\mu\text{m}$  angustata. Conidia aggregata in capitula mucida, hyalina, aseptata, oblongo-ellipsoidea vel conspicue allantoidea, 2-guttulata, 3.0-5.0(-7.0)  $\times$  (1.0-)1.5-2.0(-2.5)  $\mu\text{m}$ . Coloniae in agar maltoso griseo-ochraceae vel ochraceae, ad 13 mm radio 30 C post 8 dies. Temperatura crescentiae optima 30 C.

HOLOTYPE. UNITED STATES. TEXAS: on stems of *Quer-*

*cus virginiana* Mill., 1966, R.S. Halliwell (CBS 391.71 dried specimen, and ex type cultures CBS 391.71, IMI 192880, CMW 2027, STE-U 770, dried ISOTYPE lodged at PREM).

**Etymology.** The specific epithet refers to the inflated phialides with basal constrictions.

**Mycelium** consisting of branched, septate hyphae that occur singly or in strands of up to 10; hyphae tuberculate (warts to 0.5  $\mu\text{m}$ ) to verruculose, light brown, walls slightly darker, becoming lighter towards the conidiogenous region, 1.5–3.0  $\mu\text{m}$  diam. *Chlamydospores* absent. *Conidiophores* mostly macronematous, arising from aerial or submerged hyphae, erect, simple or racemously branched in the lower part, subcylindrical, light brown, becoming lighter towards the tip, tuberculate to verruculose, straight or flexuous, 0–5-septate, variable in length, 10–110  $\mu\text{m}$  tall, 2–4  $\mu\text{m}$  wide, not constricted at the septa, but frequently with a slightly swollen base (if basal septum is present), or swollen at the base of old percurrently proliferating cells in the conidiophore; up to three such proliferations visible in one unbranched conidiophore. *Conidiogenous cells* terminal or lateral, mostly monophialidic, tuberculate to verruculose, rarely smooth, pale brown to hyaline, subcylindrical to elongate-ampulliform, frequently proliferating percurrently, 10–36  $\mu\text{m}$  long, 1.5–3.5  $\mu\text{m}$  wide at the base, 1.0–1.5  $\mu\text{m}$  wide at the apex, with a terminal, narrowly funnel-shaped collarette, 1–3  $\mu\text{m}$  long, 1.0–1.5  $\mu\text{m}$  wide. *Conidia* becoming aggregated into round, slimy heads at the apices of conidiogenous cells, hyaline, oblong-ellipsoidal to conspicuously allantoid, becoming 2-guttulate, 3.0–5.0(–7.0)  $\times$  (1.0–)1.5–2.0(–2.5)  $\mu\text{m}$ .

**Cultural characteristics.** Colonies on MEA (reverse) smoke-grey to honey (21" d–21" b), reaching a radius of 13 mm at 30 C in the dark after 8 d. Cardinal temperatures for growth 10 C (min.), 30 C (opt.), above 35 C (max.).

**Substrate.** Humans, *Nectandra* sp., *Quercus virginiana*, *Sorbus intermedia* Pers., *Vitis vinifera*.

**Distribution.** Costa Rica, Finland, Germany, Tahiti, United States (California, Texas), Venezuela.

**Additional cultures examined.** COSTA RICA. Turrialba, on stems and roots of a *Nectandra* sp., 7 Nov. 1974, I.A.S. Gibson (CBS 166.75, CMW 2025, IMI 190668, STE-U 771). FINLAND. University of Helsinki, human toenail, 1994 (CBS 736.94, M 547). GERMANY. Bonn, on stems and roots of *Sorbus intermedia*, K. Weise (CBS 428.95, 429.95, 444.95). TAHITI. soil, A.M. Fontana (CBS 139.69). UNITED STATES. CALIFORNIA: Sacramento River, on stems and roots of *Vitis vinifera*, 1995, Ph. Larignon (CBS 222.95); Berkeley, human synovial fluid, A.A. Padhye (CBS 408.78, CDC 78–042877). VENEZUELA. human mycetoma of foot (ATCC 32628, CBS 651.85).

**Notes.** Apart from having slightly larger conidia and different culture characteristics, phialides of *P. inflatipes* are also more prominently constricted at their bases than those of *P. parasiticum*, and hyphae generally have smaller warts (to 0.5  $\mu\text{m}$  high). These observations are also supported by the large distance (36 bp) in sequence data obtained for CBS 166.75 of *P. inflatipes* and CBS 860.73 (ATCC 26366) of *P. parasiticum* (Yan et al., 1995). An additional strain, CBS 513.82 (HD 307, from a human foot abscess in the United States), has similar morphology and temperature re-

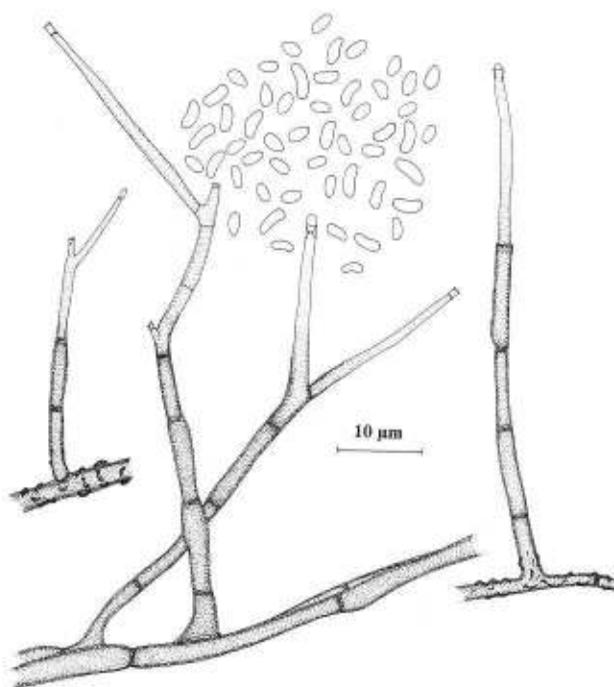


FIG. 12. Conidia, conidiophores and conidiogenous cells of *P. parasiticum* (CBS 860.73).

quirements for growth to other isolates of *C. inflatipes*. However, sequence data (Yan et al., 1995) indicate that this strain is distinct from others placed in *C. inflatipes*, and could represent another taxon. Another strain with morphology and cultural characteristics similar to *P. inflatipes* is CBS 694.88 (from a human subcutaneous cyst). This strain differs from *P. inflatipes* in possessing lightly pigmented hyphae and conidiophores that are mostly reduced to conidiogenous cells, suggesting that it may also represent an additional species.

5. *Phaeoacremonium parasiticum* (Ajello, Georg et C.J.K. Wang) W. Gams, Crous et M.J. Wingf., comb. nov.

FIGS. 1, 2, 12

= *Phialophora parasitica* Ajello, Georg et C.J.K. Wang, Mycologia 66: 493. 1974.

**Mycelium** consisting of branched, septate hyphae, that occur in strands of up to 20; hyphae tuberculate (to 3  $\mu\text{m}$ ) to verruculose, medium brown, walls and septa darker brown, becoming lighter brown to hyaline towards the conidiogenous region, 2.0–3.5  $\mu\text{m}$  diam. *Chlamydospores* absent. *Conidiophores* mostly macronematous, arising from aerial or submerged hyphae, erect, simple or racemously branched in the lower part, subcylindrical, medium brown, becoming lighter towards the tip, tuberculate to verruculose in the lower part, straight or flexuous, 1–7-septate, variable in length, 20–130  $\mu\text{m}$  tall, 2.0–3.5  $\mu\text{m}$  wide, not constricted at septa; unbranched conidiophores

sometimes slightly swollen at the base, while bases of older, percurrently proliferating cells in conidiophores are mostly swollen. *Conidiogenous cells* terminal or lateral, mostly monophialidic, frequently proliferating percurrently, tuberculate to verrucose, light brown, becoming smoother and hyaline towards the apex, subcylindrical, rarely elongate-ampulliform, generally straight, 15–35  $\mu\text{m}$  long, 2–3  $\mu\text{m}$  wide at base, 1.0–1.5  $\mu\text{m}$  wide at apex, with a terminal, narrowly funnel-shaped collarete, 0.5–2.0  $\mu\text{m}$  long, 1–2  $\mu\text{m}$  wide. *Conidia* becoming aggregated into round, slimy heads at the apices of the conidiogenous cells, hyaline, oblong-ellipsoidal to obovate or allantoid, becoming 2-guttulate with age, (2.0–)3.0–4.0(–6.0)  $\times$  (1.0–)1.5–2.0  $\mu\text{m}$ . Copious mucus produced, and the conidia remaining aggregated in masses when mounted in lactic acid (not lactophenol). Due to a hardening and discoloration of the mucous layer, conidial masses appearing olivaceous when still attached to conidiogenous cells or conidiophores.

*Cultural characteristics.* Colonies on MEA (reverse) buff to grey-olivaceous or pale olivaceous-grey (19<sup>b</sup>–21<sup>m</sup>b or 21<sup>m</sup>d), reaching a radius of 4–11 mm at 25 C in the dark after 8 d. Cardinal temperatures for growth 15 C (min.), 25 C (opt.), above 35 C (max.).

*Substrate.* Humans, *Prunus armeniaca*.

*Distribution.* Tunisia, United States (California).

*Cultures examined.* UNITED STATES. CALIFORNIA: Stanford University Hospital, isol. from subcutaneous phaeohyphomycotic infection of man, 1971, *R.T. Steigbigel* (dried specimen at BPI, HOLOTYPE, cultures ex type B-1335, CBS 860.73, IMI 181115, CMW 2024, STE-U 772). TUNISIA. On stems and roots of *Prunus armeniaca*, 1973, *B. Jamoussi* (CBS 984.73, IMI 192879, CMW 2030, STE-U 773).

*Notes.* *Phaeoacremonium parasiticum* has characteristically dark hyphae with warts up to 3  $\mu\text{m}$  high. Strain CBS 984.73 was found to be the same as the ex type strain CBS 860.73, which is in agreement with the sequence data of Yan et al. (1995). Based on sequence data, CBS 514.82 (HD 875, from human synovial fluid) was also accommodated in the group characterized by *P. parasiticum* (Yan et al., 1995). However, it is different from other strains of *P. parasiticum* in having an optimum radial growth rate of 9–10 mm at 35 C after 8 d. Morphological characteristics, such as its constricted phialides with allantoid conidia, also suggest that CBS 514.82 differs from *P. parasiticum* and deserves further study.

6. *Phaeoacremonium rubrigenum* W. Gams, Crous et M.J. Wingf., sp. nov. FIG. 13

Hyphae ramosae, septatae, singulae vel ad 20 fasciculatae, verrucosae vel granulosae, plus minusve dilute brunneae,

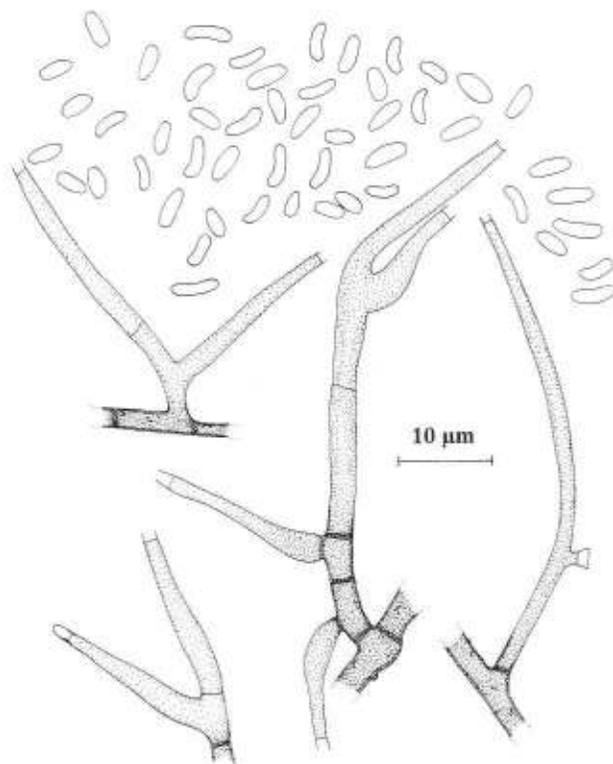


FIG. 13. Conidia and conidiogenous cells of *P. rubrigenum* (CBS 498.94).

parietes et septa paulo obscuriores, pallidiores in parte conidiogena, 1.5–3.0  $\mu\text{m}$  latae. Chlamydosporae absentes. Conidiophora ex hyphis aeriis vel submersis oriunda, erecta, simplicia vel racemosa in parte inferiore, subcylindrica, dilute brunnea, sursum pallidiora, plus minusve verrucosa, recta vel flexuosa, 0–4-septata, 30–70  $\mu\text{m}$  longa, 2–3  $\mu\text{m}$  lata, ad septa haud constricta. Cellulae conidiogenaee terminales vel laterales, plus minusve verrucosae, raro leves, dilute brunneae vel hyalinae, subcylindricae vel elongato-ampulliformes, 5–35  $\mu\text{m}$  longae, ex 1.5–3.0  $\mu\text{m}$  prope basin ad 1.0–1.5  $\mu\text{m}$  sursum angustatae, collari anguste infundibuliformi, 1–3  $\mu\text{m}$  longo praeditae. Conidia in capitulis mucidis aggregata, hyalina, nonseptata, oblongo-ellipsoidea vel allantoida, 2-guttulata, 3.0–4.0(–6.0)  $\times$  (1.0–)1.5–2.0  $\mu\text{m}$ . Coloniae in agar maltoso livido-rubrae, ad 8 mm radio post 8 dies 30 C. Temperatura optima crescentiae 30 C.

HOLOTYPE. UNITED STATES. Bethesda, National Institutes of Health, human patient with pneumonia, *K.J. Kwon-Chung* (CBS 498.94 dried specimen and ex type culture, dried ISOTYPE lodged at PREM).

*Etymology.* The specific epithet refers to the red pigmentation of the colonies.

*Mycelium* consisting of branched, septate hyphae; hyphae occurring singly or in strands of up to 20, tuberculate (to 1  $\mu\text{m}$ ) to verruculose, light to medium brown, walls and septa slightly darker, becoming lighter towards the conidiogenous region, 1.5–3.0  $\mu\text{m}$  diam. *Chlamydospores* absent. *Conidiophores* mostly micronematous, arising from aerial or submerged hyphae, erect, simple or racemously branched in the lower part, subcylindrical, light brown, becoming

lighter towards the tip, tuberculate to verruculose, straight or flexuous, 0–4-septate, 30–70  $\mu\text{m}$  tall, 2–3  $\mu\text{m}$  wide, not constricted at the septa. *Conidiogenous cells* terminal or lateral, mostly monophialidic, tuberculate to verruculose, rarely smooth, pale brown to hyaline, subcylindrical to elongate-ampulliform, 5–35  $\mu\text{m}$  long, 1.5–3.0  $\mu\text{m}$  wide at base, 1.0–1.5  $\mu\text{m}$  wide at apex, with a terminal, narrowly funnel-shaped collarette, 1–3  $\mu\text{m}$  long, 1–2  $\mu\text{m}$  wide. *Conidia* becoming aggregated into round, slimy heads at the apices of conidiogenous cells, hyaline, oblong-ellipsoidal to allantoid, becoming 2-guttulate, 3.0–4.0(–6.0)  $\times$  (1.0–)1.5–2.0  $\mu\text{m}$ .

*Cultural characteristics.* Colonies on MEA (reverse) livid red (71<sup>i</sup>), reaching a radius of 8 mm at 30 C in the dark after 8 d. Cardinal temperatures for growth 10 C (min.), 30 C (opt.), above 35 C (max.).

*Substrate.* Humans.

*Distribution.* United States.

*Notes.* Morphologically this species is similar to others in the *P. inflatipes* group, but it is easily distinguished by the vinaceous pigmentation of the colonies on agar.

Strain CBS 184.75 (=IMI 151951 from Iraq) from *Phoenix dactylifera* L., formerly identified as *P. parasitica*, appears to be distinct from the taxa discussed above in having larger conidia (3–)5–8(–10)  $\times$  1.5–2.0(–3)  $\mu\text{m}$ , and subhyaline to pale olivaceous hyphae. However, it is possible that this strain has become atypical with subculturing, as sectors of the colonies frequently appear pale brown, in contrast to the nearly hyaline hyphae in the rest of the colony. Conidiophores and conidiogenous cells are also hyaline to pale brown, suggesting that this strain is now atypical. Although the conidial dimensions support it as being distinct, we are refraining from describing this as a distinct species based on the uncertainties regarding its cultural features.

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