

THE HYPHOMYCETE GENUS ENGYODONTIUM
A LINK BETWEEN VERTICILLIUM AND APHANOCLADIUM

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Sporotrichum araneorum Cavara is redescribed from living cultures and found to have two kinds of conidiogenesis: phialidic and polyblastic. The latter type which is most conspicuous in this fungus, fits the genus *Engyodontium* de Hoog. This genus is considered to be a link between *Verticillium* and *Aphanocladium* and its generic diagnosis is extended to include both progressive and retrogressive formation of new conidiiferous pegs. *Sporothrix (Tritirachium) rectidentatum* (Matsushima) de Hoog and *Cephalosporium araneorum* Petch, in which some polyblastic conidiogenous cells with narrow denticles were also found, are transferred to *Engyodontium*. For the latter species the new name *E. arachnophilum* is proposed. The genus now comprises six species, including *E. geniculatum*, sp. nov. In addition, *Acremonium obclavatum* W. Gams is described as a new species for isolates that match the description formerly given by Gams for *Verticillium tenuipes*.

De Hoog (1972) distinguished the genera *Tritirachium* Limber and *Acrodontium* de Hoog because they have cicatrized and denticulate conidiogenous rachids, respectively, and differ in pigmentation. This distinction was not recognized in some subsequent publications (Matsushima, 1975), but we still believe that it is useful and reflects natural affinities. The fungus described as *Tritirachium rectidentatum* Matsushima (1975) does not belong to either genus. It has hyaline conidiophores and the blastoconidia are usually formed on perpendicular denticles in a retrogressive order; it was tentatively classified in *Sporothrix* by de Hoog (1978). Its carbohydrate composition was found recently to deviate from that of other *Sporothrix* species by having glucose, mannose and galactose as major compounds in combination with a low chitin level (Weijman & de Hoog, 1984).

Recently several araneogenous isolates similar to *T. rectidentatum* came to our notice. This taxon also forms lateral blastoconidia retrogressively on perpendicular denticles. Part of the conidiogenous cells is definitely phialidic (matching *Verticillium* sect. *Prostrata* W. Gams); the first-formed phialoconidium is generally falcate and the 1–3 subsequent phialoconidia are ellipsoidal, similar to the lateral blastoconidia which arise soon afterwards. Often only one terminal conidium is formed which is ellipsoidal.

Dr D. W. Minter (CMI, Kew) kindly supplied a specimen (IMI 246085) tentatively identified as *Sporothrix rectidentata*, which formed scattered conidia on long, thin den-

ticles. The sequence of conidiation could not be established. This specimen seems to link *T. rectidentatum* with *Rhinotrichum parvisporum* Petch, the type of the genus *Engyodontium* de Hoog (1978). The order of conidium production in this species could not be elucidated with certainty, but it appeared to be progressive. *Tritirachium album* Limber with sympodial, progressive conidiogenesis and conidia borne on distinct denticles, was also classified in this genus by de Hoog (1978).

It is now clear that the sequence of conidiogenesis does not allow a fundamental distinction that would justify generic segregation in this group. The above species are inter-related and, like *Verticillium* sect. *Prostrata*, seem to represent anamorphs of the Clavicipitales, while the major part of *Sporothrix* is connected with the Ophiostomatales. We prefer, therefore, to classify these species in *Engyodontium*, irrespective of the retrogressive or progressive sequence of conidiogenesis. Some affinity may exist between *Engyodontium*, *Aphanocladium* W. Gams (1971) and *Pleurodesmospora* Samson & al. (1980). In *Pleurodesmospora* the conidia are produced in basipetal chains from numerous lateral and terminal denticles, whilst *Aphanocladium* is characterized by solitary conidia, produced either by flask-shaped phialides or denticulate structures which may be interpreted as reduced phialides. These latter structures also occur in species of *Engyodontium*, but there the true phialides are *Verticillium*-like (awl-shaped to subulate). Hence *Engyodontium* shows features which link the anamorph genera *Verticillium* and *Aphanocladium*.

In most species of *Engyodontium* the supporting hyphae tend to shrivel rapidly, leaving a very thin, cobweb-like net with conidia.

KEY TO THE SPECIES

- 1a. Conidiiferous rachids with denticles concentrated in the apical region 2
- b. Conidiiferous rachids with widely scattered denticles 3
- 2a. Rachids straight with very thin, c. 1 μm long denticles; conidiophore branching irregular or verticillate 1. *E. parvisporum*
- b. Rachids geniculate with regularly spaced, butt-shaped denticles; conidiophore branching strictly verticillate 2. *E. album*
- 3a. Conidiiferous denticles on long, geniculate rachids 4
- b. Conidiiferous denticles on straight conidiogenous cells 5
- 4a. Conidia slightly curved, 2.8–3.7 \times 0.8–1.0 μm 5. *E. arachnophilum*
- b. Conidia straight, ellipsoidal to obovate, 2.5–3.0 \times 1.2–1.5 μm 6. *E. geniculatum*
- 5a. Terminal conidia phialidic, in groups of 1–5, often slightly curved to falcate 4. *E. aranearum*
- b. Terminal conidia always formed singly, straight 6
- 6a. Conidia arising from thorn-like, tapering protrusions; conidiophores profusely branched at obtuse or right angles 7. *E. sp.*
- b. Conidia arising from short, narrowly cylindrical denticles; conidiogenous cells in scanty whorls 3. *E. rectidentatum*

1. *Engyodontium parvisporum* (Petch) de Hoog — Fig. 1a

The species was described by Petch (1931) and De Hoog (1978) from a dried collection (K) from arthropod remains collected in Sri Lanka. It is possible that the extremely thin denticles may appear somewhat wider in fresh collections.

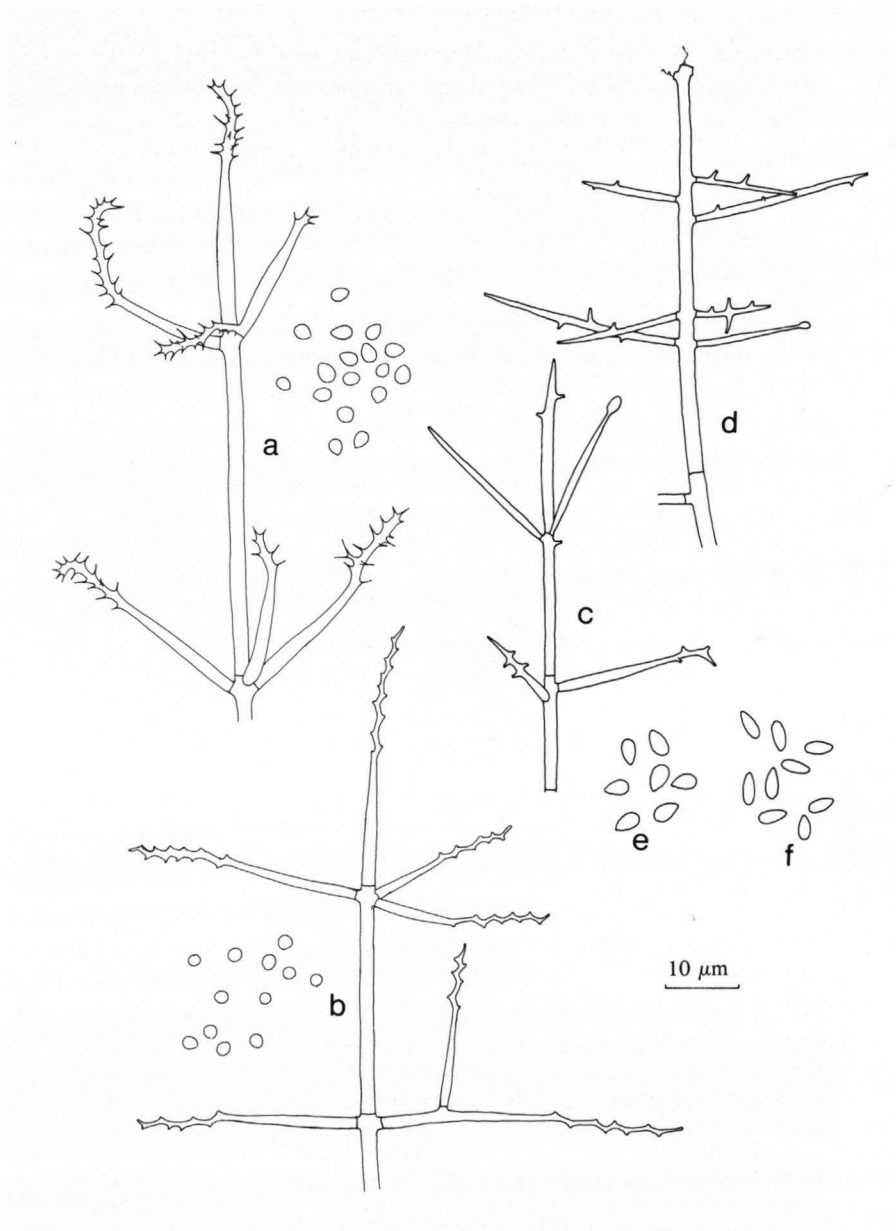


Fig. 1. a. *Engyodontium parvisporum*, specimen Petch R-400 (herb. K.). — b. *E. album*, CBS 348.55, 2-week-old culture on MEA. — c-f. *E. rectidentatum*; c, e. IMI 223175, holotype specimen, d, f. IMI 215001, dried specimen.

2. *Engyodontium album* (Limber) de Hoog—Fig. 1b

The fertile structures are usually strictly verticillate, though in CBS 504.83, received from Prof. H. Seeliger and isolated as a probable contaminant from human brain abscess, no distinguishable main branches were present.

Descriptions and illustrations of the species were given by Limber (1940), De Hoog (1972) and Matsushima (1975). Judging from the diagnoses, *Tritirachium fungicola* Shvartsman & al. (1973) and *Sporotrichum gorlenkoanum* Kuritzina & Sizova (1967) are identical. Unfortunately no type material of either species was available for study.

3. *Engyodontium rectidentatum* (Matsushima), *comb. nov.*—Fig. 1c–f

Tritirachium rectidentatum Matsushima, Ic. Microf. Matsushima lect.: 160. 1975 (basionym). — *Sporothrix rectidentata* (Matsushima) de Hoog, in *Persoonia* 10: 64. 1978.
Acrodontium album Kushwaha & Agrawal in *Mykosen* 20: 97. 1976.

Colonies reaching 15–16 mm diam. in 6 days on 2% malt extract agar at approx. 20°C, white, cottony, reverse uncoloured. Odour none. Vegetative hyphae 1.2–2.5 µm wide. Conidiogenous cells arising in whorls from prostrate aerial hyphae, 18–35 × 0.8–1.2 µm, consistently polyblastic, bearing thin, perpendicular denticles, 0.5–1.5 µm long, scattered along the upper half. Conidia ovoid to fusiform, with apiculate base, hyaline, smooth-walled, 3.2–9 × 1.0–1.5 µm. Chlamydospores absent.

Material examined. — Living cultures: CBS 206.74 = IMI 179090, ex air over sugar-cane field, Gorakhpur, India, received from Kamal. — CBS 641.74, ex buried keratinous material, India, received from S. C. Agrawal. — CBS 247.82 = IMI 215001, isolated by S. K. Shrivastava, Gyanpur, India, July 1977.

Herbarium specimens: IMI 223175 = MFC 1439 (slide), type of *T. rectidentatum*, ex forest soil, Yaku Island, Kogashima, Japan, July 1971. — IMI 179837, type of *A. album*, ex soil of teak forest, R. K. S. Kushwaha, Dec. 1973. — IMI 114485, ex soil, India, received from M. N. Gupta (CMI).

The conidial dimensions are somewhat variable, e.g. CBS 641.74 has longer conidia (4.0–9.0 µm) than CBS 206.74 (3.2–4.5 µm), but in both they are significantly shorter than in *E. araneorum* and never curved. *Engyodontium rectidentatum* is found mainly in soil, while *E. araneorum* seems to be restricted to spiders.

The dried specimen IMI 215001 has no verticillate conidiophores; the conidiogenous cells are formed as orthotropic needles on mature conidiophores. Subcultures of this isolate, however, are indistinguishable from the other isolates of *E. rectidentatum*.

4. *Engyodontium araneorum* (Cavara), *comb. nov.*—Fig. 2–3

Sporotrichum araneorum Cavara, Fungi Longob. exsicc. 5: fasc. 240. 1895 (basionym). — *Acremonium tenuipes* Petch in *Trans. Br. mycol. Soc.* 21: 64. 1937 [non *Acremonium araneorum* Petch 1931]. — *Verticillium tenuipes* (Petch) W. Gams, *Cephalosporium*-art. *Schimmelp.*: 176. 1971.

? *Cephalosporium falcatum* Petch in *Trans. Br. mycol. Soc.* 11: 259. 1926 = *Verticillium falcatum* (Petch) W. Gams, *Cephalosporium*-art. *Schimmelp.*: 187. 1971.

Colonies reaching 10 mm diam. in 10 days in 2% malt extract agar at 20°C, white, cottony; reverse uncoloured. Odour none. Vegetative hyphae 1.5–2.0 µm wide. Conidio-

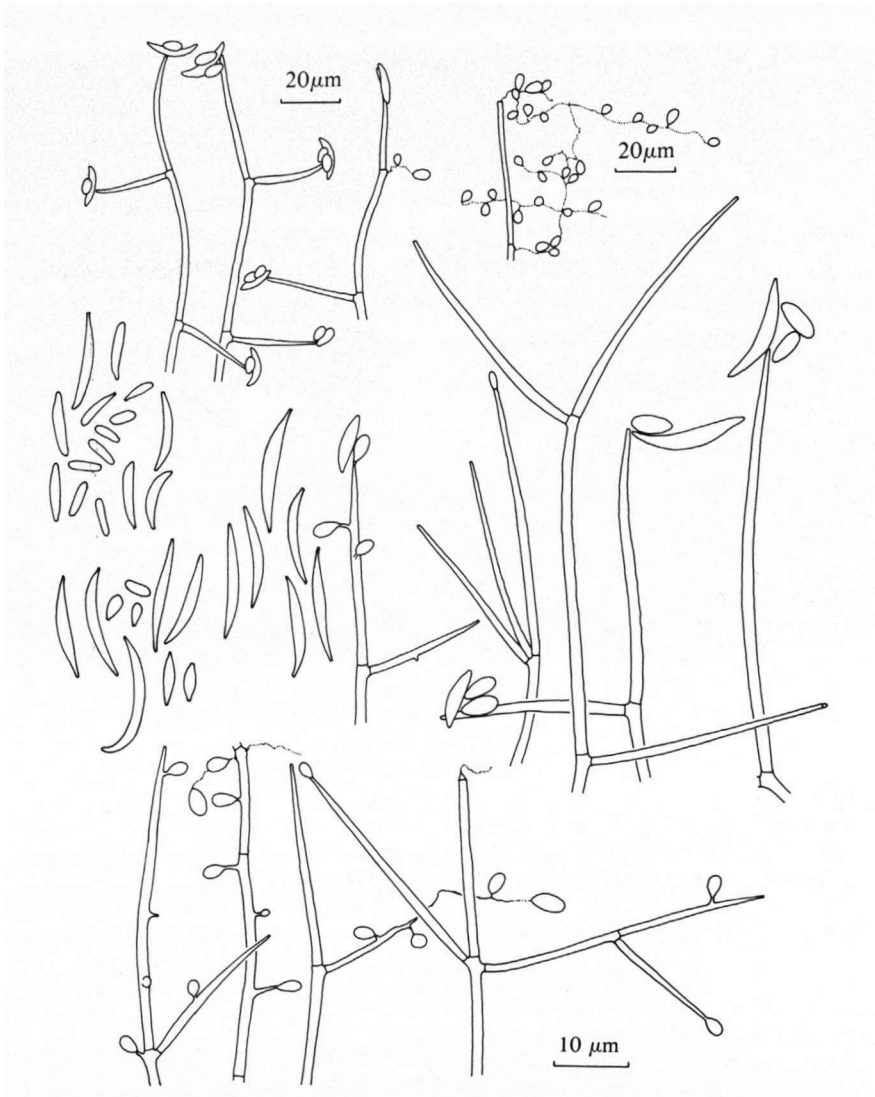


Fig. 2. *Engyodontium araneorum*, CBS 241.81, on various media. Note phialidic development in young cells and blastic conidiation in older cells.

genous cells arising singly or in scanty whorls from the aerial hyphae, $20-35(-40) \times 1.2-1.5 \mu\text{m}$. Conidiogenesis of two kinds: (a) polyblastic with several short, cylindrical, perpendicular denticles ($0.5-1.0 \mu\text{m}$ long), scattered along the upper half, producing ovoid to almost ellipsoidal, straight conidia, $3.0-5.5(-6.5) \times 1.0-1.5 \mu\text{m}$; (b) phialidic, with few conidia usually transversely attached to the tip of the conidiogenous cells; primary conidia fusiform to falcate, rarely becoming 2-celled, $8-17 \times 1.5-1.8 \mu\text{m}$, sub-

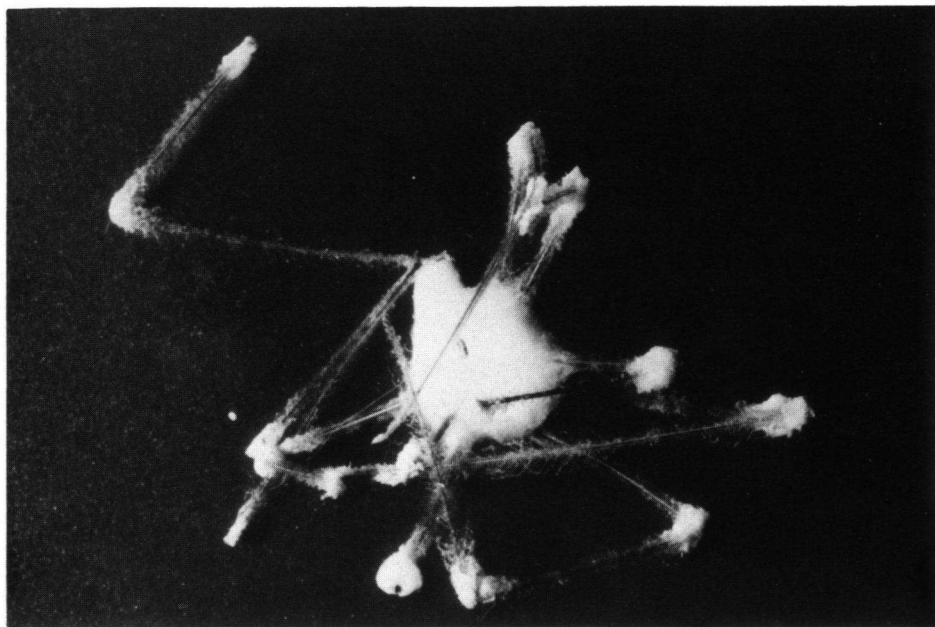


Fig. 3. Unidentified Opilionid spider (CBS 003321), showing colonies of *Engyodontium aranearum*, on legs and body ($\times 2.5$).

sequent ones usually shorter. In some rare cases both conditions occur together on one conidiogenous cells. Chlamydo-spores absent.

The species attacks spiders, mainly Opilionids, in moist localities all over the world and forms whitish powdery cushions, particularly on the joints of the legs.

Material examined. — Herbarium specimens: *Sporotrichum aranearum*, Fungi Longob. exsicc. 240 (isotype in B). — *Acremonium tenuipes* on spiders (Opilionids) in a greenhouse, Cambridge, Mass., *W. G. Farlow*, Jan. 1890 (two specimens annotated by Petch in FH). — *Cephalosporium falcatum*. on a fly attached to the lower surface of a leaf, Hakgala, Sri Lanka, *T. Petch*, March 1922 (holotype in K). — CBS 003320, on Opilionid, Lisse, Netherlands, *M. Elders*, 19 Feb. 1980. — CBS 003321, on Opilionid, Leiden, Netherlands, *C. Bas*, March 1981.

Living cultures: CBS 658.80, ex spider, isolated by *G. J. Samuels* (G. J. S. 80–101), Auckland, New Zealand. — CBS 241.81, ex spider, isolated by *G. Zimmermann*, Darmstadt, FRG, 1981.

When both phialidic and polyblastic conidiogenesis were observed in one culture, repeated attempts were made to purify the fungus. Conidia of both types consistently developed from single-conidium isolates of either type of conidia. The proportion of each type was influenced, however, by the medium: on 2% MEA the phialidic type developed, on potato-carrot agar and SEA the polyblastic type was more abundant. The polyblastic conidiophores collapse very rapidly and more readily than in *E. rectidentatum* when exposed.

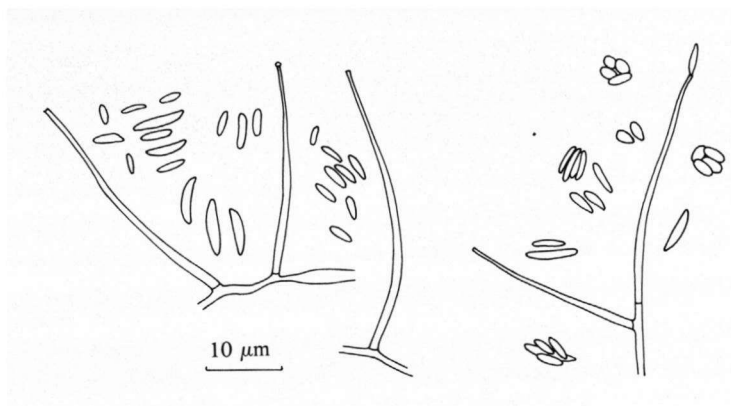


Fig. 4. *Cephalosporium falcatum*. Type specimen (herb. K).

Engyodontium araneorum can be confused with *Verticillium psalliotae* Treschow, which also has falcate, larger ($6-9 \times 1.5-1.8 \mu\text{m}$), primary, and ellipsoid-fusiform, smaller, secondary conidia, but both types are formed always terminally on phialides. Colonies of this fungus usually become reddish in reverse, a phenomenon never observed in *E. araneorum*. *Verticillium psalliotae* is a ubiquitous fungus and sometimes occurs as a mycoparasite or on insects but is not known from spiders. Another similar fungus is *E. arachnophilum* (see below) which has smaller, falcate conidia, $2.8-3.7 \times 0.8-1.0 \mu\text{m}$.

When Gams (1971) examined Cavara's specimen of *Sporotrichum araneorum*, he was unaware of the *rectidentatum*-type of conidiogenous cells and overlooked the lateral denticles. From the illustration accompanying the specimen, it is evident that Cavara (1895) also ignored these structures as did Petch (1937). Upon re-examination of the same slides, a few lateral denticles were seen. Petch (1937) mentioned two specimens of *A. tenuipes* preserved at FH. These were also examined in the present study and found to be *E. araneorum*. His other specimens preserved at K, however, represent different species (Gams, 1971). Polyblastic conidiogenesis was illustrated for *S. araneorum* by Nannizzi (1934).

On a slide prepared from the type specimen of *C. falcatum* Petch (in K, Fig. 4), Gams (1971) found oval or slightly curved conidia which were not sufficiently distinctive of the species and he suggested that another collection in Petch's herbarium ('*Cephalosporium longisporum*, Explor. Puerto Rico No. 725') might be used as neotype of *C. falcatum*. The conidia in that specimen were, however, significantly broader ($10.2-11.8 \times 2.6-3.0 \mu\text{m}$) than in Petch's diagnosis ($10-13 \times 1.5-2.0 \mu\text{m}$). A new species may eventually have to be described for this fungus when more material becomes available. Renewed study of the type specimen of *C. falcatum* has revealed some more conidia which fit the original diagnosis and a few solitary, non-denticulate phialides. The conidia agree with the phialidic conidia described for *C. falcatum*, but the synonymy with *E. araneorum* cannot be proved. The unnamed *Verticillium* sp. described by Sartory & al. (1931) from spiders 'in association with a *Sporotrichum*' may have been this species as well.

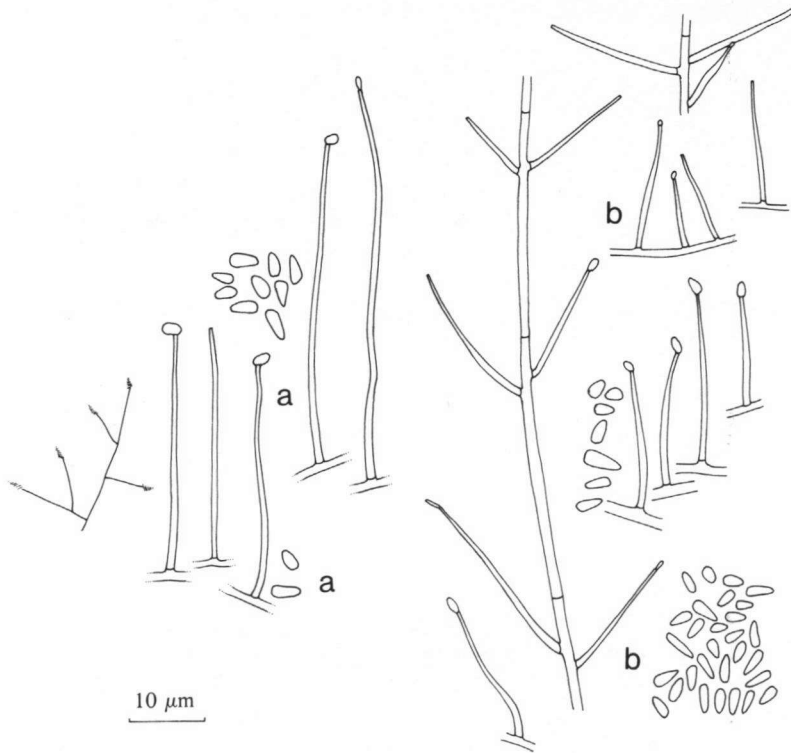


Fig. 5. *Acremonium obclavatum*. — a. CBS 311.74, 2-week-old culture on MEA. — b. CBS 510.82.

Strains which produce only *V. tenuipes*-type phialides (Gams, 1971), with no evidence of polyblastic conidiogenous cells, are considered better accommodated in the anamorph genus *Acremonium* and the following new species is proposed:

4a. *Acremonium obclavatum* W. Gams, *sp. nov.* — Fig. 5

Coloniae post 10 dies 18–26 mm diam. 25°C, albae, lanosae, margine fimbriata circumdatae. Hyphae vegetativae 0.5–1.5 µm latae. Hyphae aerae plus minusve prostratae, numquam fasciculatae. Phialides orthotropicae singulae, numquam verticillatae, plerumque ex hyphis aeriis profundis oriundae; phialides (15–)30–52 µm longae, e 0.8–1.2 µm prope basim ad 0.5 µm sursum attenuatae. Conidia oblique expulsa, apice latiore collari affixa, catenis imbricatis irregularibus cohaerentia; conidia obclavata ad fere ellipsoidea, 2.0–4.5 × 1.0–2.0 µm. Chlamydo sporae absentes.

Typus CBS 311.74 (isotypus IMI 185383), vivus et exsiccatus, isolatus ex aere, prope Gorakhpur in India, a Kamal, 1974.

Colonies on 2% MEA reaching 18–26 mm diam. in 10 days at 25°C, white, cottony, about 3 mm deep, with fimbriate margin. Reverse either remaining white or later becoming greenish (particularly at higher temperature) or pale reddish in some strains. Vegetative hyphae 0.5–1.5 µm wide. Aerial hyphae more or less prostrate, never fasciculate.

Orthotropic phialides generally arising singly (never in whorls) in the deeper layers of the aerial hyphae, occasionally also from submerged hyphae; phialides (15–)30–52 μm long, 0.8–1.2 μm wide at the base, tapering to about 0.5 μm at the tip. Conidia extruded obliquely from the phialide tip, attached at the broader end, forming short imbricate chains, obclavate to almost ellipsoidal, 2.0–4.5 \times 1.0–2.0 μm . Chlamydospores absent. Prismatic crystals commonly present in the medium.

Equally good growth occurring at 34°C, no growth occurring at 37°C.

Material examined. — Living cultures: CBS 311.74 = IMI 185383, from air above a sugar-cane field in Gorakhpur, India, received from Kamal; CBS 250.76, from soil in Saugar, India, S. C. Agrawal. — CBS 586.81, from tannin-bearing barks and tan liquors in Madras, India, C. K. Rao. — CBS 510.82 from rust pustules on *Arachis hypogaea*, Madras, India, B. P. R. Vittal.

The four isolates from India fit in *Acremonium* sect. *Albo-lanosa* Morgan-Jones & W. Gams (1982) by forming exclusively solitary phialides. Contrary to the opinion expressed in that paper (p. 313), the senior author feels, that fungi with just a few verticillate conidiophores should be left in *Verticillium* sect. *Prostrata*, and that sect. *Albo-lanosa* of *Acremonium* should be reserved for fungi with exclusively solitary phialides. The present species is quite distinct with its obclavate conidia arranged in imbricate chains.

5. *Engyodontium arachnophilum* Evans & Samson, *nom. nov.* — Fig. 6

Cephalosporium aranearum Petch in Trans. Br. mycol. Soc. 16: 226. 1931 (basionym, non *Engyodontium aranearum* (Cavara) W. Gams & al.). — *Verticillium aranearum* (Petch) W. Gams, *Cephalosporium*-art. Schimmelp.: 186. 1971.

Teleomorph: *Torribiella alba* Petch in Trans. Br. mycol. Soc. 16: 226. 1931.

Spider hosts covered by white to yellow mycelium, often extending around the host onto the leaf surface, or occurring on old synnemata of *Gibellula*. Vegetative hyphae hyaline, smooth-walled, 1.2–2.0 μm wide. Conidiogenous cells single or two–three in a whorl, mostly phialidic, but also polyblastic, occasionally formed on the same conidiophore. Phialides awl-shaped, straight or slightly bent, 12–30 μm long, with a base 1.0–1.5 μm wide (for a more detailed description of these phialides see Gams, 1971). Polyblastic cells with a straight or slightly bent base, 1.0–1.5 μm wide, and a thin (0.4–0.7 μm) rachis, covered with 1–8 conspicuous denticles, 1.0–4.5 \times 0.4–0.6 μm . Conidia fusiform, slightly curved, mostly with rounded ends, 2.8–3.7 \times 0.8–1.0 μm . Chlamydospores not observed.

Material examined. — *Cephalosporium aranearum*, on spiders, Nuwara Eliya, Sri Lanka, collected by T. Petch (K, see also Gams, 1971: 186). — CBS 003337 = R.S. 0050, on spider, on cocoa leaf, Tafo, Ghana, H. C. Evans, Jan. 1972.

Petch (l.c.) and Gams (1971) had overlooked the presence of denticulate conidiogenous cells in this fungus, but in recent collections from Ghana this structure was quite evident in addition to the simple phialides characteristic of *Verticillium* sect. *Prostrata*. A renewed study of Petch's specimens (Fig. 6a) showed that polyblastic (or possibly polyphialidic) conidiogenous cells were also present in this material. Therefore we trans-

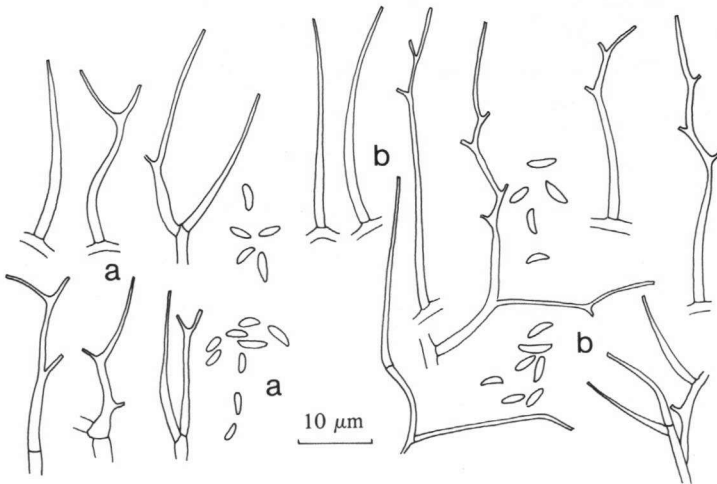


Fig. 6. *Engyodontium arachnophilum*, conidiogenous structures and conidia. — a. Petch's specimens. — b. CBS 003337.

fer this fungus to *Engyodontium*. Like *E. araneorum* it forms a link between this genus and *Verticillium* sect. *Prostrata*.

6. *Engyodontium geniculatum* Evans & Samson, *sp. nov.* — Fig. 7

Mycelium hospitem (insectum vel araneam) obtegens, album, saepe ad substratum evadens. Hyphae vegetativae hyalinae, leves, tenuitunicatae, 1.2–2.0 µm latae. Cellulae conidiogenae singulae vel verticillatae ex hyphis aeriis oriundae, 20–100 × 1.0–2.2 µm, raro phialides, saepius polyblasticae. Ambo formae nonnumquam in uno conidiophoro junctae. Cellulae conidiophorae seu phialides subulatae, sursum ad 0.5 µm angustatae, seu polyblasticae e basi recta vel curvata et rhachide angusta (0.5–0.8 µm) geniculata nonnullis denticulis conidiiferis (1.0–3.0 × 0.2–0.5 µm) praedita constantes. Conidia ellipsoidea vel obovata, levia, hyalina, 2.5–3.0 × 1.2–1.5 µm. Chlamydosporae et teleomorphosis ignotae.

Typus CBS 003323 = R.S. 0033, in Homoptero quodam (Flatidae), folio Theobromae cacaois adfixo, prope Tafo in Ghana, coll. *H. C. Evans*, 15.I.1972.

Arthropod host covered by fine, white mycelium often extending around the host onto the leaf surface. Vegetative hyphae hyaline, smooth-walled, 1.2–2.0 µm wide. Conidiogenous cells arising singly or in whorls from aerial hyphae, 20–100 × 1.0–2.2 µm, rarely phialidic, more often polyblastic. Both types sometimes occurring on the same conidiophore. Phialides awl-shaped to subulate, apically narrowing to 0.5 µm. Polyblastic conidiogenous cells with a straight, occasionally sinuous base and a thin (0.5–0.8 µm) rachis, which is covered with several to many conspicuous denticles, 1.0–3.0 × 0.2–0.5 µm, occurring in regular or irregular geniculate rachids. Conidia ellipsoidal or obovoidal, smooth-walled, hyaline, 2.5–3.0 × 1.2–1.5 µm. Chlamydospores and teleomorph not observed.

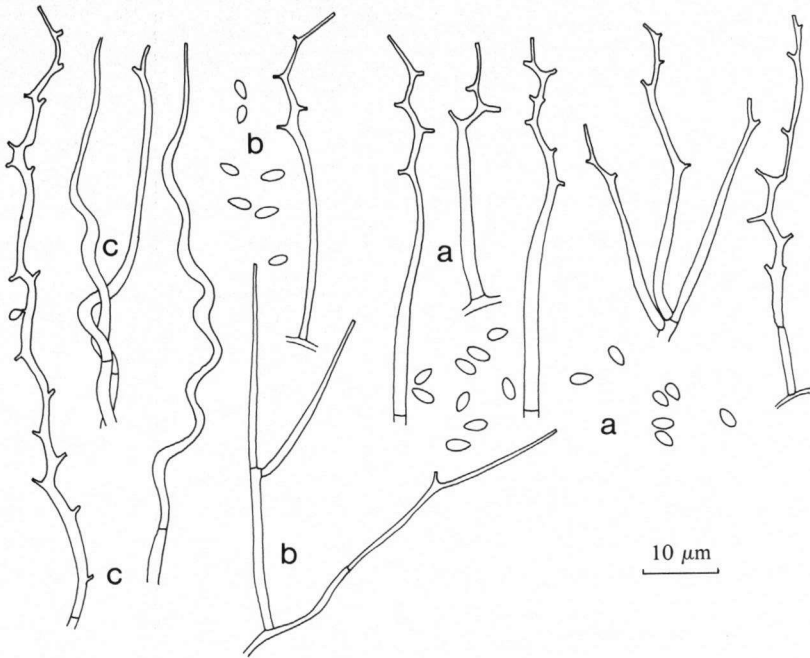


Fig. 7. *Engyodontium geniculatum*, conidiogenous structures. — a. CBS 003323. — b. CBS 003333. — c. CBS 003334.

Material examined.—Herbarium specimens (all specimens collected by *H. C. Evans* in Tafo, Ghana, on cocoa leaves): CBS 003323 (= R.S. 0033), holotype, on unidentified Flatidae (Homoptera), Jan. 1972. — CBS 003333 = R.S. 0075 and CBS 003334 = R.S. 130, both on spiders, Apr. and May 1972. — CBS 003335 = R.S. 144, on nymphs of *Steatococcus* sp. (Coccidae, Homoptera), May 1972.

Engyodontium geniculatum is known only from herbarium material collected in Ghana. It is characterized by the long polyblastic (or possibly polyphialidic) conidiogenous cells with geniculate rachids covered by numerous distinct denticles.

Acrodontium myxomyceticola Crane & Schoknecht (1982) is similar to *E. geniculatum*, but lacks the pronounced remote denticles and the rachis is less distinctly geniculate.

Engyodontium geniculatum does not appear to be host-specific since it was found on both spiders (Araneida) and insects (Homoptera). Although apparently restricted to spiders, *E. arachnophilum* occasionally occurs on hosts previously colonized by *Gibellula*. This may indicate that these species are in fact facultative or fungicolous parasites rather than true pathogens.

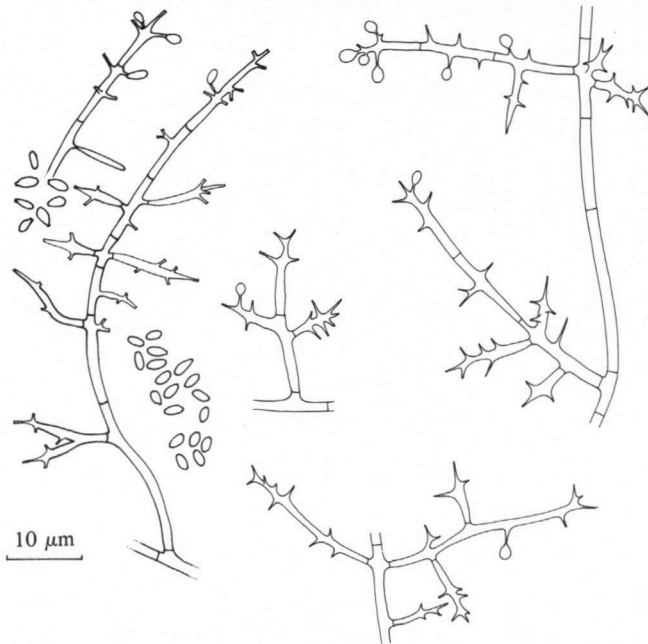


Fig. 8. *Engyodontium* sp., from slide IMI 246085.

7. *Engyodontium* sp. — Fig. 8

Conidiophores arising more or less orthotropically from undifferentiated hyphae, composed of 1–4 cells which may bear short secondary branches; conidiogenous cells $7\text{--}15 \times 1.0\text{--}1.8 \mu\text{m}$, with scattered, perpendicular, thorn-like, tapering denticles, $2.0\text{--}3.5 \mu\text{m}$ long. Conidia ellipsoidal, thin-walled, hyaline, $2.2\text{--}2.6 \times 1.5\text{--}2.2 \mu\text{m}$. Chlamydospores absent.

Material examined. — IMI 246085 (slide), ex culture isolated from thermometer, Royal Botanic Garden, Kew, England, *B. L. Brady*, Nov. 1979.

The specimen probably represents a new *Engyodontium* species characterized by short conidiogenous cells with thorn-like denticles and orthotropic branches. Since, however, only a slide is now available for study, we are reluctant to attribute a formal name. Moreover, as there are also similarities with *Myriodontium keratinophilum* Samson & Polonelli (1978), the true identity of this taxon can only be elucidated after examination of living cultures.

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