## FARROWIA, A NEW GENUS IN THE CHAETOMIACEAE

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#### (With four Text-figures and one Table)

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

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

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

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

#### TAXONOMY

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

	SYNOPSIS OF CHARACTERS S	EPARATING CHAETOMIUM, FARROWIA AND	Scopinella
	Perithecia	Asci and ascospores	CULTURES AND CONIDIAL STATE
CHAETOMIUM (180+spp.)	Subglobose to vasiform, with lateral and terminal hairs which may be variously branched or contorted; terminal hairs not arising synchronously from adjacent elongated cells at the apex of the peri- thecia, not fused or adhering to form a neck; hairs with slight rugose (few spp.) to coarse (most spp.) ornamentation $(\times 10,000)$ ; pedestal-like rhizoidal base	Asci clavate or cylindrical, deliquescing before the ascospores mature; ascospores varying in shape, not usually 1-guttulate, not ornamented.	Most species known in culture; cultures not usually producing reddish pigments in the medium (c. 3 spp.); conidial state absent in most species, Acremonium (3+spp.), Botryotrichum (8-9 spp.) or Scopulariopsis (1 sp.).
FARROWIA (3 spp.)	Subglobose, with lateral and terminal hairs which are straight and unbran- ched; terminal hairs arising synchronous- ly from adjacent elongated cells at the apex of the perithecia, fused below to form a distinct neck-like structure which may be rudimentary; hairs $\pm$ smooth (X 10,000); pedestal-like rhizoidal base usually present.	Asci clavate, deliquescing before the ascospores mature; ascospores lemoni- form, biapiculate with a subapical germ pore, usually 1-guttulate; not ornamen- ted.	Only known in culture; cultures often forming reddish pigments in the medium in the presence of contaminants; coni- dial state Botryotrichum (all species).
scopinella (I sp.)	Subglobose, with lateral and terminal hairs which are both straight, unbran- ched, and fused in groups; terminal hairs arising synchronously from adja- cent elongated cells at the apex of the perithecia, fused below to form a distinct neck-like structure, fused above the neck to varying extents; hairs smooth $(\times 10,000)$ ; pedestal-like rhizoi- dal base absent.	Asci clavate, deliquescing after the ascospores mature; ascospores quadran- gular, not guttulate; with a broad Z- shaped deeply pigmented band.	Not known in culture; conidial state (if any) unknown.

TABLE I

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

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

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

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

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

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

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

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

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

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

# Key to the perfect states of members of the Chaetomiaceae with Botryotrichum-like Aleuriospores

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



Fig. I

3a.	Terminal hairs (including fused portion) 850–2500 $\mu$ m tall when mature; ascospores
	8-12×8-10 µm Farrowia longicollea (Krzem. & Badura) D. Hawksw., p. 174
b.	Terminal hairs (including fused portion) $275-350(-400) \mu m$ tall when mature; as-
	cospores $7-9(-10) \times 7-8 \mu m.$ Farrowia malaysiensis D. Hawksw., p. 178
4a.	Apex of perithecium composed of elongated cells forming a distinct but rudimentary
-	neck; perithecia with a distinct pedestal-like tuft of rhizoidal hyphae; hairs not or
	scarcely ornamented; as cospores 7.5–9(-10) $\times$ 7–8.5 $\mu$ m
	Farrowia seminuda (L. Ames) D. Hawksw., p. 182
b.	Apex of perithecium not composed of elongated cells forming a rudimentary neck;
	perithecia lacking a distinct pedestal-like tuft of rhizoidal hyphae; hairs usually distinctly
	coarsely ornamented
5a.	Terminal hairs flexuose, irregularly to dichotomously branched, not coiled; ascospores
5	6-7×4.5-6 µm [material not seen] Chaetomium pinnatum L. Ames
b.	Terminal hairs not as above
6a.	Terminal hairs spirally or circinately coiled at least at the apices
b.	Terminal hairs not distinctly spirally or circinately coiled
7a.	Terminal hairs geniculately branched with circinately coiled apices; as cospores $6-8\times$
	4-6 µm [material not seen]
b.	Terminal hairs spirally coiled above
8a.	Terminal hairs often branched, heads readily becoming detached; ascospores with
	quadrangular guttules, 5,5-8 × 5,5-6,5 µm
b.	Terminal hairs unbranched, heads not becoming detached; ascospores not guttulate.
	$(4.5-)6-8 \times 3.5-5 \mu m$ [aleuriospores not seen in isotype although reported by Ames
	(1063)]
oa.	Perithecia elongate to vasiform
Ъ.	Perithecia subglobose to ovoid
10a.	Terminal hairs forming a dense apical tuft, straight to somewhat recurved; ascospores
	ellipsoid, 7–8×6.5–8 µm
b.	Terminal hairs sparse, not forming a dense tuft; as cospores biumbonate, $7-9 \times 5-7 \mu m$
	[conidial state possibly not <i>Botryotrichum</i> : material not seen]
	Chaetomium silvaticum var. variabile Kiril.
11a.	As cospores $13-16 \times 8.5-10.5 \ \mu\text{m}$
b.	Ascospores less than $12 \ \mu m \log 12 \ \dots \ $
12a.	Terminal hairs straight, rigid, sparse: ascospores $5.5-7 \times 4.5-6 \mu m$
	Chaetomium homobilatum Omvik
b.	Terminal hairs flexuous to undulate, abundant; ascospores $7-0.5 \times 6.5-7.5 \mu m$ [material
	not seen] Chaetomium semispirale Udagawa & Cain

# Farrowia D. Hawksw., gen. nov.

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

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

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

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

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

Culturae contaminatae centro plerumque pigmentum rubro-purpurascentem producentes. SPECIES HOLOTYPICA: Farrowia longicollea (Krzem. & Badura) D. Hawksw. (syn. Chaetomium longicolleum Krzem. & Badura, Chaetoceratostoma longirostre Farrow).

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

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

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

Contaminated cultures often producing a reddish-purple pigment in the medium. ETYMOLOGY.—Named after W. M. Farrow, the first author to recognise that the type species of the genus should be placed in a genus other than *Chaetomium*.

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

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

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

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

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



Fig. 2

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

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

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

Asci arising in a basal fascicle within the perithecial cavity, apparently not accompanied by lateral or hymenial paraphyses, unitunicate, clavate, short-stalked, thin-walled, deliquescing before the ascospores mature,  $(25-)40-60 \times 10-20 \,\mu\text{m}$ , 8-spored. Ascospores irregularly arranged in the asci, accumulating in a cirrhus and discharged, often in  $\pm$  parallel rows, through the neck-like fused portion of the terminal hairs, hyaline at first but becoming brown to dark brown when mature, subglobose to ellipsoid, usually distinctly 1-guttulate, simple, smooth-walled, biapiculate with a distinct often subapical germ-pore at one end,  $8-12\times8-10\,\mu\text{m}$  in surface view,  $6-7\,\mu\text{m}$  wide in lateral view.

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

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

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

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

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

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

OTHER SPECIMENS EXAMINED.—COLOMBIA: near El Banco, c. 160 miles south of Barranquilla, 1965, leg. Oxford Labs. (Chicago, Illinois), isol. ex plant debris on surface of soil-water culture, 3 Sept. 1966, E. E. Davis (ATCC 16509, IMI 186019).

INDIA: Varanasi, Banaras Hindu University, comm. 31 Jan. 1967, Singh & Pande 5 (IMI 137386); Aurangabad, Marathwade University, comm. 6 Febr. 1969, L. V. Gangawane 2 (IMI 137648); Jabalpur, isol. ex grassland soil, comm. 22 Sept. 1971, P. D. Agrawal 93 (IMI 160309); sine loc., isol. ex soil, comm. 12 April 1972, V. Nair 8k (IMI 165736k); Agra College, isol. ex soil, comm. 7 April 1974, M. N. Gupta 20 (IMI 185148), 33 (IMI 185159).

IRAQ: Bakoba Nursery, isol. ex soil, comm. 25 May 1968, M. Majeed 6 (IMI 133629). NIGERIA: Samaru, Institute of Agricultural Research, isol. ex Arachis hypogaea fruits, comm. 6 Jan. 1966, D. McDonald 807 (IMI 116862).

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

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

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

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

# Farrowia malaysiensis D. Hawksw., sp. nov.-Fig. 3

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

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

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



Fig. 3.

Aleuriosporae ad *Botryotrichum* pertinentes, hyphis hyalinis et prostratis exorientes, globosae vel subglobosae, muris crassis munitae, hyalinae, praecipue  $5-15 \mu m$  diam., plerumque sparsae.

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

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

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

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

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

times with a slightly flattened base, mainly  $5-15\,\mu$ m diam. Cultures growing fairly rapidly on most media (MA, PCA, PDA, TWA, etc.), usually attaining 4.5-5.5 cm diam. in eight weeks at room temperature; aerial mycelium when present, flocculose, white to pale orange, composed of hyaline hyphae mainly  $1-4\,\mu$ m diam; sectoring not seen; in the presence of contaminant organisms a characteristic reddish-purple pigment is produced which diffuses into the agar and is readily visible in reverse; reverse otherwise  $\pm$  uncoloured.

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

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

ETYMOLOGY.—Malaysiensis, from Malaysia.

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

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

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

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

### Farrowia seminuda (L. Ames) D. Hawksw., comb. nov.-Fig. 4.

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

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

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

Aleuriospores almost always present and abundant, *Botryotrichum*-like; conidiophores arising from hyaline, sparsely septate hyphae mainly  $1.5-3 \mu m$  diam. spreading prostrately around the perithecia; conidiogenous cells integrated, terminal, determinate, monoblastic, cylindrical; conidia (aleuriospores) arising singly at the apices of the conidiogenous cells, hyaline or with a slight fuscous-brown tinge, simple, very thick-walled, smooth-walled, sometimes slightly flattened at the base, mainly  $7-10 \,\mu\text{m}$  diam.

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

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

Етумоlogy.—From Latin semi-, half, and nudus, naked.

ILLUSTRATIONS.—Ames in Mycologia 41: 643 figs. 23–29. 1949; Ames, Monogr. Chaet. pl. 24 Figs. 13–19. 1963; Mazzucchetti, Gen. Chaetom.: 323 pl. 24 Fig. 13–19. 1965; Seth in Beih. Nova Hedwigia 37: fig. 51. 1972; Skolko & Groves in Can. J. Bot. 31: pl. 2 figs. 1–4, pl. 13 fig 10. 1953. DISTRIBUTION.—I have examined material from Canada (Ontario), China (prov.

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

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

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

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

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

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





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

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

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

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#### References

- AGNIHOTHRUDU, V. (1958). Chaetoceratostoma from the rhizosphere of some plants in South India. In Sci. Cult. 23: 555-556.
- AMES, L. M. (1949). New cellulose destroying fungi isolated from military material and equipment. In Mycologia 41: 637-648.
- ---- (1963). A Monograph of the Chaetomiaceae. U.S. Army Research and Development series No. 2, Washington D.C.
- ARX, J. A. VON (1973). Ostiolate and non-ostiolate Pyrenomycetes. In Proc. K. Ned. Akad. Wet. (C) 76: 289-296.
- BADURA, L. (1964). Fungulli nuovi, rari o critici isolati dal suola sotto i Faggi dell' Orto Botanica di Torino. In Allionia 9: 175-185.
- BARTOLI, A. (1972). Chaetoceratostoma longirostre Farrow in Ivory Coast soils. In Annali Bot. 31: 41-44.
- CALVIELLO, B. (1971). Estudio de las especies Argentinas del genero Chaetomium. In Revta Mus. argent. Cienc. nat. Bernardino Rivadavia, Bot. 3: 337-369.
- COOKE, J. C. (1973). Perithecium development of Chaetomium longirostre. In Can. J. Bot. 50: 2271-2274.
- CORLETT, M. (1966). Perithecium development in Chaetomium trigonosporum. In Can. J. Bot. 44: 155-162.
- DANIELS, J. (1961) Chaetomium piluliferum sp. nov., the perfect state of Botryotrichum piluliferum. In Trans. Br. mycol. Soc. 44: 79–86.

- DENNIS, R. W. G. (1970). Fungus flora of Venezuela and adjacent countries. In Kew Bull., add. ser. 3: i-xxxiv, 1-531. H.M.S.O., London.
- DOGUET, G. (1955a). Étude du développement du Chaetoceratostoma longirostre Farrow. In Revue Mycol. 20 (Suppl. colon. 2): 132-143.
- ----- (1955b). Un détecteur biologique de la saccharase: le Chaetoceratostoma longirostre Farrow. In Bull. Soc. bot. Fr. 102: 301-305.
- ---- (1959). Action de températures élevées, voisines de la température léthale, sur les spores de deux champignons. In Bull. Soc. bot. Fr. 106: 177-186.
- DOMSCH, K. H. & GAMS, W. (1970). Pilze aus Agrarböden. Gustav Fischer, Stuttgart.
- FARROW, W. M. (1955). A new species of Chaetoceratostoma. In Mycologia 47: 416-419
- HARVEY, R., HODGKISS, I. J. & LEWIS, P. N. (1969). Air-spora studies at Cardiff II. Chaetomium. In Trans. Br. mycol. Soc. 53: 269-278.
- HAWKSWORTH, D. L. (1971). A revision of the genus Ascotricha Berk. In Mycol. Pap. 126: 1-28.
- ---- (1975). Chaetoceratostoma Turc. & Maffei, a genus to be rejected. In Trans. Br. mycol. Soc. 64: 447-453.
- HAWKSWORTH, D. L. & WELLS, H. (1973). Ornamentation on the terminal hairs in Chaetomium Kunze ex Fr. and some allied genera. In Mycol. Pap. 134: 1-24.
- MALLOCH, D. & CAIN, R. F. (1973). The genus Thielavia. In Mycologia 65: 1055-1077.
- MAZZUCCHETTI, G. (1965). Il Genre Chaetomium. Laboratorio di Cartotecnica Speciale, Rome.
- MOREAU, M. & MOREAU, F. (1954). Sur le développement des périthèces du Chaetomium elatum Kunze. In Revue Mycol. 19: 167-171.
- PARKER, A. D. (1973). Coprophilous ascomycetes of Illinois. I. Pyrenomycetes. In Trans. Illinois St. Acad. Sci. 66: 94-96.
- SEDLAR, I., DREYFUSS, M. & MÜLLER, E. (1972). Kompatibilitätsverhältnisse in Chaetomium I. Vorkommen von Homo- und Heterothallie in Arten und Stämmen. In Arch. Mikrobiol. 83: 172-178.
- SEDLAR, I., MÜLLER, E. & DREYFUSS, M. (1973). Kompatibilitätsverhältnisse in Chaetomium II. Interspezifische Fertilität. In Arch. Mikrobiol. 92: 105-113.
- SETH, H. K. (1972). A monograph of the genus Chaetomium. In Beih. Nova Hedwigia 37: i-viii, 1-134.
- SKOLKO, A. J. & GROVES, J. W. (1953). Notes on seed-borne fungi VII. Chaetomium. In Can. J. Bot. 31: 779-809.
- TVEIT, M. T. (1955). Heterothallism in *Chaetomium* spp. and its relation to antibiotic producing capacity. In Acta path. microbiol. scand. 37: 429-433.
- UDAGAWA, S.-I., FURUYA, K. & HORIE, Y. (1973). Mycological reports from New Guinea and the Solomon Islands 19. Notes on some ascomycetous microfungi from soil. *In* Bull. natn. Sci. Mus., Tokyo 16: 503-520.
- UDAGAWA, S.-I. & HORIE, Y. (1972). A new species of *Thielavia* and its *Chrysosporium* conidial state. In Bull. natn. Sci. Mus., Tokyo 15: 191-196.
- ZOPF, W. (1881). Zur Entwickelungsgeschichte der Ascomyceten, Chaetomium. In Nova Acta Ksl. Leop.-Carol.-Deutsch. Akad. Naturf. **42**(5): 199–292.