

Chaetomidium heterotrichum from Venezuela, with a key to species and cladistic analysis of the genus *Chaetomidium*

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A species of the genus *Chaetomidium* was isolated from fallen leaves of an unknown tree during a mycofloral survey of materials from the 'Gran Sabana' region in Southeastern Venezuela. The species was identified as *C. heterotrichum*. Identification was based on the perithecium lacking a neck and ostiole, the peridium being composed of textura angularis cells, the perithecium being covered with hairs and setae at the apex, and by 4-spored asci containing uniporate ascospores. The anamorph was intermediate between *Chalara* and *Acremonium* sect. *Chaetomioides*. This is the first report of this species in Venezuela and only the second time *C. heterotrichum* has been found. An illustrated description of *C. heterotrichum* and a key to eight recognized species of *Chaetomidium*, based on morphological characters in the literature, are provided. The results of a cladistic analysis of 12 available morphological characters of the genus revealed two main groups, each based on the two characters 'ascospore shape' and 'peridial wall type'. The ascomatal hairs had little influence on the species grouping. With the exception of *C. heterotrichum*, the remaining species of *Chaetomidium* were monophyletically supported in 73% of the bootstrap replicates. *Chaetomidium heterotrichum* was the basal ingroup taxon and formed a sister group to the other species in the genus.

Key Words—*Chaetomidium*; *Chaetomidium heterotrichum*; cladistic analysis; systematics; taxonomy.

The taxonomy of the genus *Chaetomidium* (Zopf) Sacc. is controversial and its position is uncertain (Mukerji and Saxena, 1974). It has been classified in three different families: Melanosporaceae (Dennis, 1981), Thielaviaceae (Arx et al., 1988), and Chaetomiaceae (Arx et al., 1984; Eriksson and Hawksworth, 1993).

Malloch and Cain (1973) did not recognize any significant morphological differences between *Chaetomidium* and *Thielavia* and placed the former genus under *Thielavia*. Nevertheless, the validity of *Chaetomidium* has been widely recognized (Lodha, 1974, 1978; Meyer, 1983; Arx et al., 1988; Cano et al., 1993).

A lack of agreement exists concerning the concept of the genus *Chaetomidium*. In the majority of the descriptions (Arx, 1975; Arx et al., 1984, 1988), *Chaetomidium* is restricted to species with uniporate ascospores. However, Lodha (1974) placed in *Chaetomidium* species with either one or two germ pores, but later he included species with only two germ pores (Lodha, 1978).

The species *Chaetomidium heterotrichum* R. J. Meyer is easily recognized because of its setae, four-spored asci, and phialidic anamorph. It was described for the first time from red oak bark in Georgia, USA (Meyer, 1983). Until now this species was known by a single isolate.

The aim of this paper is to clarify the status of *Chaetomidium* species, provide an illustrated description of *C. heterotrichum*, found for the first time in Venezuela, along with an updated key to species, and to develop a

cladistic analysis of the genus.

Materials and Methods

Chaetomidium heterotrichum was isolated by surface sterilizing with 95% ethanol and plating small fragments of leaves on rose bengal (RB) medium. The resulting mycelial growth was then transferred to corn-meal agar (CMA) and incubated at room temperature (24°C). This medium was used for culture growth and description of the species. Measurements of 25 perithecia, hairs, setae, asci, ascospores, conidia and conidiophores were made from material mounted in water. In order to obtain additional information about the peridial layers of the ascocarp, the fungus was killed and fixed in formalin-propionic acid-ethanol 70%, embedded in paraplast, and sectioned with a microtome.

A key to *Chaetomidium* species was developed based upon published morphological descriptions, as well as our own observations in the case of *C. heterotrichum*.

Maximum parsimony analysis of a morphological data set (Tables 1, 2) was performed using the program PAUP version 3.1 (Swofford, 1993). The morphological characters were scored from published information. Heuristic searches were performed by stepwise addition of the taxa, under the option 'random addition of 10 replicates'. In this method, a pseudorandom number generator is used to permute the taxa (Swofford, 1993). Taxonomic characters and character-states used are listed in Table 1.

Table 1. Taxonomic characters of *Chaetomidium* used in the cladistic analysis.

1. Ascoma diam: 211.6–299.5 μm =0, 123.5–211.5 μm =1, 299.6–387.5 μm =2;
2. Ascum hairs: of 2 types=0, of 1 type=1, of 3 types=2;
3. Hairs with circinate tips: absent=0, present=1;
4. Hair width (mean), at the base: 1.0–3.4 μm =0, 3.5–6.9 μm =1, 7.0–12.0=2;
5. Ascum wall: not cephalothecoid=0, cephalothecoid=1;
6. Ascus width (mean): 9.8–13.4 μm =0, 13.5–16.9 μm =1, 17.0–20.5 μm =2;
7. Ascospore shape: broadly ellipsoid or obovate=0, limoniform=1;
8. Ascospore shape in cross-section: round=0, flattened on one side=1, bilaterally flattened=2;
9. Ascospore length (mean): 6.5–9.3 μm =0, 9.4–12.0 μm =1, 12.1–14.9 μm =2;
10. Ascospore width (mean): 5.0–7.3 μm =0, 7.4–9.6 μm =1, 9.7–12.0 μm =2;
11. Ascospore (length/width) ratio: 1.5–1.7=0, 1.2–1.4=1;
12. Anamorph: unknown or absent=0, present (phialoconidia or aleurioconidia)=1.

Bootstrapping was performed to estimate the support of the branches. Character polarity was obtained using *Emilmuelleria spirotricha* (R. K. Benj.) Arx as the outgroup. Characters were weighted equally. Plesiomorphies in the outgroup were coded as 0 within the ingroup, and apomorphies were coded as 1 or 1–2, with missing data being identified by "?". The characters were unordered, and among them, seven were multistate (Table 2). The tree was rooted by making the ingroup monophyletic. Non-informative characters and autapomorphies, such as the presence of 4-spored asci and thick-walled setae, only found in the species *C. heterotrichum*, were not included in the analysis.

Results

Taxonomy

Chaetomidium heterotrichum R. J. Meyer, *Mycologia* 75: 1064–1069. 1983. Figs. 1–12

Anamorph: Intermediate between *Chalara* and *Acremonium* sect. *Chaetomioides*.

Colonies on CMA slow-growing, with a colony diam of 3.5 cm after 10 d. Mycelial hyphae hyaline, (2.2–) 4 (–5.5) μm in diam. Ascocarp initials as coiled hyphal branches (Fig. 1). Ascum a non-ostiolate perithecium, brown-colored at maturity, superficial or occasionally immersed, globose to subglobose, (137–)168–172 (–223) \times (124.5–)160–175.5 (–219) μm , 167.5 \times 170 μm on average (Figs. 2, 3). Perithecial wall composed of 2 layers when viewed in cross-section: an outer, dark-brown layer with flattened cells, and an inner, pale-brown layer with inflated cells (Fig. 4). In surface view,

Table 2. Data matrix for the cladistic analysis of *Chaetomidium*.

Taxa	Characters											
	1	2	3	4	5	6	7	8	9	10	11	12
<i>Emilmuelleria spirotricha</i>	0	0	0	0	0	0	0	0	0	0	0	0
<i>Chaetomidium pilosum</i>	1	1	0	0	0	1	1	2	2	1	0	0
<i>C. trichorobustum</i>	0	2	1	2	0	?	1	2	2	2	1	0
<i>C. arxii</i>	1	1	0	1	1	2	0	0	2	2	1	0
<i>C. subfimetii</i>	0	0	0	1	0	?	1	2	0	0	1	0
<i>C. heterotrichum</i>	0	1	0	0	0	0	0	0	0	0	1	1
<i>C. khodense</i>	0	1	0	1	1	1	0	1	1	0	0	0
<i>C. fimeti</i>	2	0	0	1	0	1	1	2	2	2	1	0
<i>C. cephalothecoides</i>	1	1	1	1	1	2	0	0	2	1	0	1

outer perithecial wall brown, composed of pseudoparenchymatous cells, textura epidermoidea (Fig. 5). Perithecia covered by hairs and thick-walled setae. Hairs of one type, septate and unbranched, straight or flexuous, terminating in round or slightly hooked tips, slightly roughened, pale brown, (53–)100.5–101.5 (–144) \times 2–3 (–4.5) μm at the base, 101 \times 2.5 μm on average (Fig. 6). Setae aseptate, thick-walled, especially at the apex, brown and shading to pale brown at the tips, tapering to narrow ends, smooth, (53–)69.5–80.5 (–120) \times (9–) 12.9–13 (–22) μm at the base, 75 \times 13 μm on average (Fig. 7). Mature ascospores brown, one-celled, broadly ellipsoid, and truncate at one end in face view, round in cross-section, 6–7.5 (–9) \times 4.5–5.5 (–6.5) μm , 6.8 \times 5 μm on average, smooth, with a prominent basal germ pore (Fig. 8). Asci unitunicate, (22.5–) 27 (–33.5) \times (8–) 10.3–10.7 (–13) μm , 27 \times 10.5 μm on average, formed in a basal layer, clavate with long stalks or occasionally short-stalked, mostly four-spored, occasionally five or six-spored (Fig. 9), with walls evanescent at maturity.

Anamorph phialidic; conidia one-celled, hyaline, produced in heads, obovoid with a truncate base, 2.7–3.7 (–4) \times 1.7–2.1 (–2.2) μm , 3.2 \times 1.9 μm on average, smooth, and produced endogenously. Phialides hyaline, tubular to flask-shaped, (4.5–) 6.9–7.6 (–9.9) \times 2.5–3.2 (–3.6) μm , 7.3 \times 2.9 μm on average, wider at the base and tapering to cylindrical tips; collarete cylindrical and hyaline (Figs. 10–12).

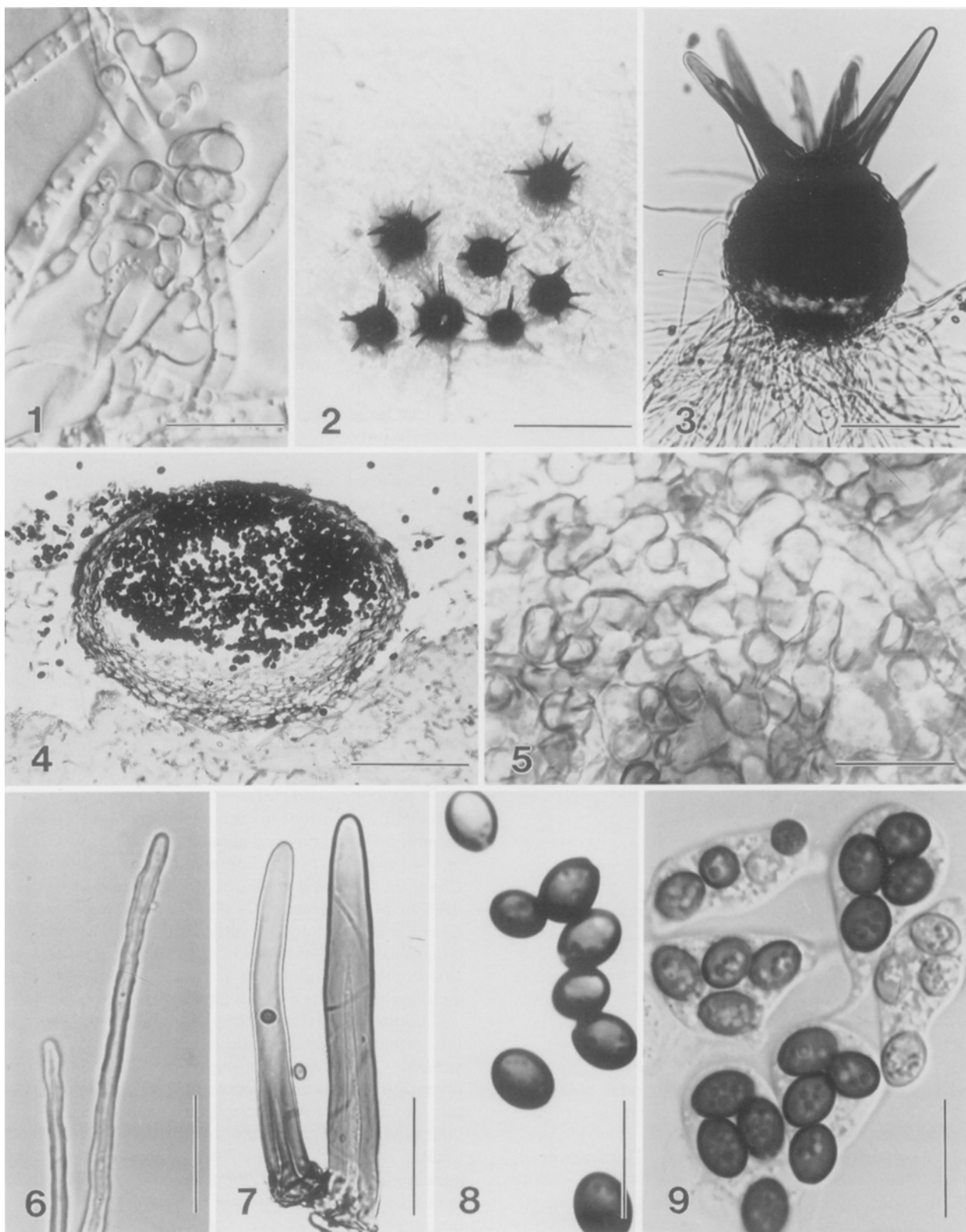
Habitat: On fallen leaves of an unknown tree, Gran Sabana, Bolivar, Venezuela.

Specimen examined: RTH 2561, a culture isolated from fallen leaves of an unknown tree, Gran Sabana, Bolivar, Venezuela, 24 April 1994, collected by R. T. Hanlin.

Cladistic analysis

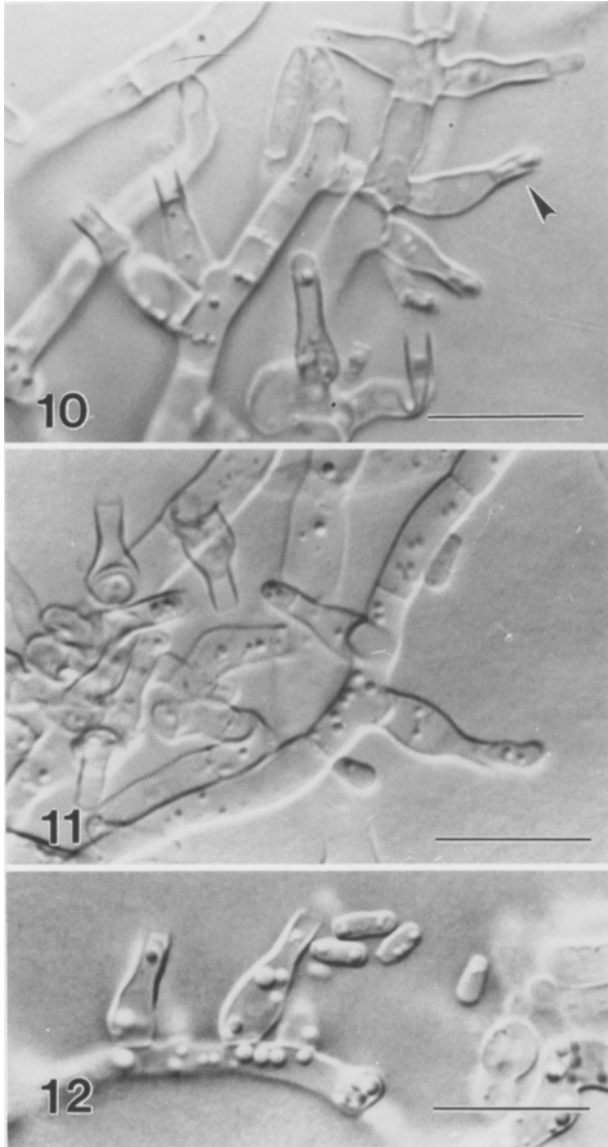
A preliminary cladistic analysis based on 12 morphological characters was undertaken in order to investigate the relationships among eight species of *Chaetomidium*, using *E. spirotricha* as the outgroup. Since only one outgroup taxon was used, numerical assessment of the monophyly of all eight species of *Chaetomidium* was not ascertainable.

One most parsimonious tree (Fig. 13) was generated by analysis of the data matrix (Table 2). The cladogram



Figs. 1-9. *Chaetomidium heterotrichum*.

1. Coiled ascocarp initials. 2. Setose perithecia on agar. 3. A mature perithecium with setae at the apex. 4. Section through a perithecium showing the wall in cross-section. 5. Outer perithecial wall, textura epidermoidea in surface view. 6. Perithecial hair tips. 7. Thick-walled setae. 8. Mature ascospores with depressed germ pore. 9. Young and mature four-spored asci with long stalks. Scale bars: Fig. 1 = 11 μm , Fig. 2 = 143 μm , Fig. 3 = 63 μm , Fig. 4 = 95 μm , Fig. 5 = 48 μm , Fig. 6 = 8 μm , Fig. 7 = 28 μm , Fig. 8 = 12 μm , Fig. 9 = 7.7 μm .



Figs. 10–12. Conidial state of *Chaetomidium heterotrichum*. 10. Cluster of tubular to flask-shaped phialides with collarette (arrow). 11. Conidia produced endogenously. 12. Close-up of a phialide and obovoid conidia with a truncate base. Scale bars: Fig. 10 = 6.5 μm , Fig. 11 = 11.5 μm , Fig. 12 = 11.5 μm .

was 29 steps long and had a consistency index of 0.65, a retention index of 0.61, and a homoplasy index of 0.35. The bootstrap values are given in Fig. 13.

Two distinct groups were obtained. The first one included *Chaetomidium trichorobustum* Seth, *C. fimeti* (Fuckel) Sacc., *C. subfimeti* Seth, and *C. pilosum* (C. Booth et Shipton) Arx. This group was supported by the synapomorphies 'ascospore shape limoniform', and 'ascospore bilaterally flattened'. The species *C. trichorobustum* and *C. fimeti* appear to be more closely related to each other than to any other taxa in this group.

The second group was formed by *C. arxii* Benny, *C. cephalothecoides* (Malloch et Benny) Arx, and *C.*

rhodense Cano, Guarro et El Shafie. This group was supported by the synapomorphy 'peridium cephalothecoid'.

The groupings *C. trichorobustum* - *C. fimeti* and *C. arxii* - *C. cephalothecoides* were monophyletic in only 46% and 74% of the bootstrap replicates, respectively. The basal species of the ingroup, *C. heterotrichum*, formed alone a sister group to the rest of the *Chaetomidium* species. Excluding *C. heterotrichum*, the other *Chaetomidium* species appear to be monophyletic and are supported by 73% of the bootstrap replicates.

Discussion

Chaetomidium heterotrichum is mainly characterized by ascomata covered with hairs and few setae at the apex, 4-spored asci, and a phialidic anamorph. The characteristics of the anamorph do not fit those of any other conidial fungus and it may represent a new genus, intermediate between *Acremonium* sect. *Chaetomioides* and *Chalara*.

Chaetomidium sensu Arx (1975) and Arx et al. (1988) is delimited by species with thick-walled and dark, non-ostiolate ascomata, covered with hairs, and ascospores with an apical germ pore. It resembles *Thielavia* in centrum structure and in the absence of an ostiole (Lodha, 1978; Dennis, 1981). However, in *Thielavia*, ascomatal hairs and setae are absent (Arx, 1975). In *Melanocarpus*, a related genus with one germ pore, short setae or undifferentiated hyphae can be produced in non-ostiolate ascomata (Guarro et al., 1996). *Melanocarpus* can be differentiated from *Chaetomidium* by its *Chrysonilia*-like anamorph (Arx, 1981).

Malloch and Cain (1973) had a broader concept of the genus *Thielavia*, which included *Chaetomidium*. They did not consider the vestiture of the ascocarp as a sufficiently important taxonomic character to support the separation of these two genera. However, Arx (1975) and Arx et al. (1988) defended the maintenance of *Chaetomidium* as a separate genus, as the non-ostiolate relative of *Chaetomium*. The authors suggested that *Chaetomium* should be restricted to species with ostiolate ascomata and thinner ascomatal wall, while *Chaetomidium* should be limited to species with non-ostiolate ascomata and with a thicker ascomatal wall.

Lodha (1978) had a different concept of *Chaetomidium*, retaining in this genus species with biporate ascospores. *Thielavia* was suggested for species with uniporate ascospores. Based on this taxonomic character, he transferred the species *Chaetomidium ellipticum* Lodha, with one germ pore, to *Thielavia elliptica* (Lodha) Lodha; and the species *Thielavia ovalispora* Lodha, *T. sepedonium* Emmons, *T. setosa* Dade, and *T. thermophila* Fergus et Sinden, with two germ pores, to *Chaetomidium ovalisporum* (Lodha) Lodha, *C. sepedonium* (Emmons) Lodha, *C. setosum* (Dade) Lodha, and *C. thermophilum* (Fergus et Sinden) Lodha, respectively.

Arx et al. (1988) accepted as *Chaetomidium* only species with one germ pore, excluding those species with two germ pores. They recognized the biporate species (sensu Lodha) *C. sepedonium*, *C. setosum*, and *C.*

thermophilum as *Corynascus sepedonium* (Emmons) Arx, *C. setosus* (Dade) Arx, and *C. thermophilus* (Fergus et Sinden) Klopotek, respectively. *Corynascus* is delimited by species possessing two germ pores and forming a *Chrysosporium* conidial state.

Chaetomidium spirotrichum (R. K. Benj.) Malloch et Cain (*Thielavia spirotricha* (R. K. Benj.) Malloch et Cain sensu Malloch and Cain, 1973), cited by Arx (1975) in his previous revision of the genus, is now recognized as *E. spirotricha* (Arx, 1985).

Two other species, *Chaetomidium hyalotrichum* Taparia et Lodha, described by Taparia and Lodha (1974), with hyaline peridial hairs and unequal-sided ascospores, and *C. ovalisporum* (Lodha, 1978), with an almost glabrous ascocarp, globose to broadly clavate asci, and two large germ pores, have not been accepted or mentioned in any recent revision or key to the genus.

Arx et al. (1988) revised the genus and reported *Chaetomidium* with eight-spored asci, not mentioning the four-spored asci produced by *C. heterotrichum*. This character was used initially in our key to separate *C. heterotrichum* from other species in the genus, which are eight-spored. The type of peridial hairs, shape and size of ascospores, and the peridial wall type (cephalothecoid in *C. arxii*, *C. cephalothecoides*, and *C. khodense*) were additional taxonomic characters for the development of the key.

Although the minimum ascospore size recorded by Meyer (1983) is smaller than in our material, our size range falls within the measurements given by Meyer. An important feature not mentioned in his descriptions was the presence of slightly hooked ascomatal hair tips in addition to round tips.

A cladistic analysis of the eight recognized species of *Chaetomidium* was undertaken to determine the relationships and monophyly of the genus. In general, parsimony analysis reflects the traditional or taxonomic relationships that were used to construct the key.

Only one parsimony hypothesis (Fig. 13) was suggested by the data matrix (Table 2). Two main groups were formed, based primarily on the ascospore shape and type of peridium. In spite of the usefulness of the ascomatal hairs for the identification and differentiation of the species in the key, this study suggests that the type of hair is a secondary character, having little influence in the phylogenetic grouping of the species.

The first group was formed by the species *C. trichorobustum*, *C. fimeti*, *C. subfimeti*, and *C. pilosum*, characterized by ascospores limoniform and bilaterally flattened.

Despite the similarities in the structure of the hairs of *C. fimeti* and *C. subfimeti* (Seth, 1967), these species are not sister species in the cladistic analysis. This was probably due to differences in ascospore size, smaller ($8-11 \times 6-7 \mu\text{m}$) in *C. subfimeti* and larger ($11-16 \times 8-10 \mu\text{m}$) in *C. fimeti*, as well as variation in ascomata size (Arx et al., 1988).

Chaetomidium fimeti grouped with *C. trichorobustum*. However, they were supported by a low bootstrap value of 46%. This grouping was mostly due to similarities in hair width and ascospore shape and size, even though they have different hair features. In *C. trichorobustum* they are of three kinds (one with circinate tips), short, and up to $10 \mu\text{m}$ (Seth, 1968). In *C. fimeti* the hairs are of two kinds, without circinate tips, and less than $6 \mu\text{m}$ wide (Arx, 1975).

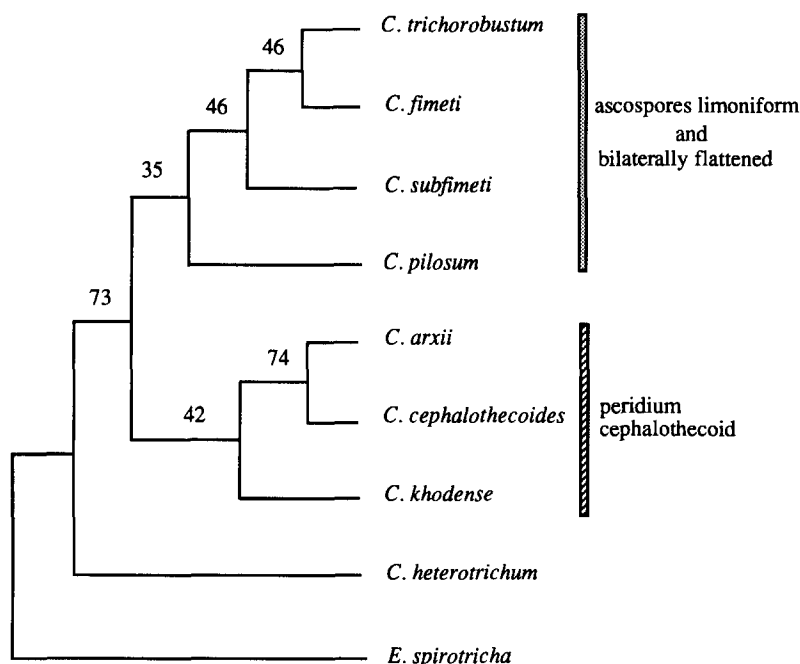


Fig. 13. The single most parsimonious tree based upon the analysis of 12 morphological characters of eight *Chaetomidium* species using *Emiliumella spirotricha* as the outgroup. Bootstrap values are given above the branches. Length=29 steps, CI=0.65, and RI=0.61.

Chaetomidium pilosum can be distinguished from *C. fimeti*, *C. subfimeti*, and *C. trichorobustum* mostly by the short and stiff hypha-like hairs (Booth and Shipton, 1966).

The second group was formed by species with a cephalothecoid peridium: *C. arxii*, *C. cephalothecoides*, and *C. khodense*. This type of peridium is characterized by plates radiating from a central meristematic region. It has been suggested that it can facilitate the breaking of the wall and the liberation of the ascospores in non-ostiole fungi (Hawksworth and Booth, 1974). *Chaetomidium arxii* and *C. cephalothecoides* are probably monophyletic and are supported by 74% of the bootstrap replicates. These species grouped with each other mostly due to the similarities in ascoma diameter, ascus diameter, ascospore shape in cross section, and ascospore length. However, they can be separated based on the different structure of the hairs. In *C. arxii* they are shorter (up to 380 μm in length) (Benny, 1980), whereas in *C. cephalothecoides* they can be up to 2 mm in length and have circinate tips (Malloch and Cain, 1973). Anamorphs are absent in *C. arxii*, but in *C. cephalothecoides*, an arthroconidial anamorph belonging to either *Botryotrichum* or *Staphylotrichum* is produced (Benny, 1980).

Chaetomidium khodense has bigger ascoma and smaller ascospore length and width than *C. arxii* and *C. cephalothecoides*. Additionally, it has ascospores flattened on one side in cross view. These differences contributed to the separation of *C. khodense* from the other

two species. *Chaetomidium cephalothecoides* differs from *C. khodense* by the thicker peridial walls and by the regularly arranged cells in the cellular plates. In *C. khodense*, they are irregularly arranged (Cano et al., 1993).

The monophyly of *Chaetomidium* was suggested by the parsimony analysis, except for *C. heterotrichum*. This species was a sister group to the other seven species and came as a basal species in the ingroup. It shared with the outgroup, *E. spirotricha*, most of the plesiomorphic characters (Table 2).

The overall relationships of *Chaetomidium* species were proposed in this paper. However, due to the low bootstrap values obtained, and the small number of characters available for the analysis, more conclusive results, with the inclusion of combined data from morphological and molecular characters, are necessary in order to elucidate relationships within the genus and with closely related genera, such as *Thielavia*, *Chaetomium*, and *Melanocarpus*.

Since *Chaetomidium* was last revised (Arx et al., 1988), a new species, *C. khodense*, has been described (Cano et al., 1993), so a provisional key with the inclusion of this species is provided.

Presently eight species of *Chaetomidium* (sensu Arx), having ascospores with only one germ pore, are accepted. They are *C. arxii*, *C. cephalothecoides*, *C. fimeti*, *C. heterotrichum*, *C. khodense*, *C. pilosum*, *C. subfimeti*, and *C. trichorobustum*.

Key to recognized species of *Chaetomidium*

- | | |
|--|----------------------------|
| 1. Asci four-spored; ascomata with thick-walled setae; anamorph phialidic | <i>C. heterotrichum</i> |
| 1. Asci eight-spored; ascomata without setae; anamorph present or absent | 2 |
| 2. Ascumatal wall cephalothecoid, with sutures; ascospores broadly ellipsoid or obovate | 3 |
| 2. Ascumatal wall not cephalothecoid; ascospores limoniform and bilaterally flattened in cross section | 5 |
| 3. Ascumatal hairs long, tips circinate; anamorphs aleurioconidia and occasionally arthroconidia | <i>C. cephalothecoides</i> |
| 3. Hairs flexous or straight, tips round or tapering; anamorph absent | 4 |
| 4. Ascospores flattened on one side in cross section, ascospore width < 7.0 μm | <i>C. khodense</i> |
| 4. Ascospores round in cross section, ascospore width > 7.0 μm | <i>C. arxii</i> |
| 5. Hairs of three types, one with circinate tips, hair width at the base > 9 μm | <i>C. trichorobustum</i> |
| 5. Hairs of one or two types, without circinate tips, hair width at the base < 9 μm | 6 |
| 6. Ascumatal hairs of one type, stiff, verruculose, and pale | <i>C. pilosum</i> |
| 6. Ascumatal hairs of two types, one long and smooth, arising from the base of the ascomata, the other short and verruculose | 7 |
| 7. Ascospores 8–11 \times 7–8 \times 6–7 μm | <i>C. subfimeti</i> |
| Ascospores 11–16 \times 10–12 \times 8–10 μm | <i>C. fimeti</i> |

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