Phylogenetic reassessment of the Chaetomium globosum species complex

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INTRODUCTION

The genus Chaetomium was established by Kunze (Kunze & Schmidt 1817), based on C. globosum. Due to the poorly-informative original description, C. globosum has been re-defined on several occasions, and many similar species have been subsequently described, mainly based on the morphology of ascocarp hairs (Corda 1840, Fries 1849, Zopf 1881, Chivers 1915, Skolko & Groves 1953, Udagawa 1960, Ames 1963, Seth 1970). The discovery of cylindrical ascii by Fuckel (1869) and ascospore germ pores by Zopf (1881), however, provided better insights into the morphological definition of the genus Chaetomium. On the other hand, the taxonomic value of ascocarp hair characteristics has been considered unreliable by several authors (Tschudy 1937, Hawksworth & Wells 1973, Dreyfuss 1976, Von Arx et al. 1984). Sörgel (1960) and Dreyfuss (1976) suggested the combined morphological traits of ascospores, asci and surface structure of the ascomatal wall for the classification of Chaetomium. Millner (1977) and Millner et al. (1977) attempted to classify Chaetomium species using features of ascospore germ pores and the growth responses of species to different temperatures. Based on a limited sampling, Dreyfuss (1976) divided the genus Chaetomium into 10 species groups. In a detailed comparative study of the C. globosum group, he noticed continuous variation in ascomatal hair morphology of C. globosum, and hence emphasised ascospore morphology for species delimitation. The monographic studies by Von Arx et al. (1984, 1986), which form the basis of contemporary classification of the genus Chaetomium, summarised the previous studies and placed emphasis on the morphology of asci, ascospores, the germ pores on ascospores, and the structure of the ascomatal wall, but paid less attention to the morphology of ascomatal hairs. Based on this classification, C. globosum was characterised by globose, ovate or obovate ostiolate ascomata; ascomatal wall of textura intricata; ascomatal hairs erect, flexuous or coiled; ascus evanescent, clavate or slightly fusiform; ascospores limoniform, bilaterally-flattened, 9–12 × 8–10 × 6–8 μm (length × width × thickness) in size, with an apical germ pore. Twenty-eight species were reduced to synonymy under C. globosum, and two additional species were tentatively maintained: C. cruentum as an albino form of C. globosum, and C. spirochaete slightly deviating from C. globosum by more regularly coiled and thicker ascomatal hairs. Several species, including C. elatum and C. subaffine, were also considered as close relatives of C. globosum. The
## Table 1
Details of isolates and their sequences employed in this study. The newly generated sequences in this study are shown in **bold.**

<table>
<thead>
<tr>
<th>Species</th>
<th>Isolate code</th>
<th>Country</th>
<th>Substrate / Locality</th>
<th>MGT* (°C)</th>
<th>GenBank accession numbers</th>
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<td>Decaying hay, Nashville, Ontario</td>
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<td>Mouldy book, Amsterdam</td>
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<td>Raincoat, Jeffersonville, Indiana</td>
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<td>Paper, Fort Belvoir, Washington DC</td>
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<td>Acor sp., Muskoka District, Ontario</td>
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C. megacarpum  = CBS 149.59 (epiT)  
Greece  
Leaf of Ficus carica  
40  
KC109744  
KC109744  
KC109762  
K001738  
K001783  
K001828

C. megalocarpum  
India  
Humus-rich soil  
40  
KC109747  
KC109747  
KC109765  
K001737  
K001782  
K001827

C. novae-landiae  
CBS 124555 (T)  
New Zealand  
Dead decaying twig, Otaki  
–  
K124607  
K124657  
K124753  
K124715  
K124641  
K124677

C. ozrenkoae  
CBS 163.62 (T)  
Russia  
Soil, Novosibirsk region  
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K124590  
K124656  
K124733  
K124695  
K124621  
K124660

C. olivaceum  
CBS 418.80A  
India  
Nilgai dung, Delhi  
38  
JN209914  
JN209914  
JN256184  
K001716  
K001761  
K001806

C. pilosum  
CBS 124556  
New Zealand  
Dead decaying twig, Otaki  
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K124608  
K124657  
K124754  
K124716  
K124642  
K124678

C. spiculipilium  
CBS 373.66 (T)  
USA  
Decaying vegetable debris, California  
34–35  
KC109756  
KC109756  
KC109774  
K001719  
K001764  
K001809

C. spirochaete  
CBS 730.84 (epiT)  
USA  
Animal dung, Great Smoky Mountains, Tennessee  
38  
JN209921  
JN209921  
JN256191  
K001729  
K001774  
K001819

C. subaffine  
CBS 637.91 (T)  
USSR  
Cereal  
35  
JN209873  
JN209873  
JN256150  
K001725  
K001770  
K001815

C. subfimeti  
CBS 370.66 (T, T of Chaetomium subfimeti)  
Wales  
Paper and vegetable material, Cadiff  
–  
FJ663584  
FJ124652  
FJ664187

C. subglobosum  
MUC 16994 = CBS 149.60 (T)  
Russia  
Dead herbaceous stem, St. Petersburg  
38  
JN209930  
JN209930  
JN256200  
K001718  
K001763  
K001808

C. telluricola  
CBS 151.59 (T)  
Turkey  
Eriobotrya japonica, Iemiri  
37–38  
K124612  
K124651  
K124758  
K124722  
K124648  
K124684

C. tenue  
CBS 139.38 (T)  
–  
–  
–  
K124600  
K124657  
K124746  
K124708  
K124634  
K124670

C. umbonatum  
CBS 293.83 (T)  
Canada  
Soil, Nova Scotia  
38  
K124606  
K124657  
K124752  
K124714  
K124640  
K124676

C. unguicola  
CBS 124557 (T)  
Iran  
Leaf of Hordeum vulgare, Bonab, East Azerbaijan Province  
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HM365251  
HM365251  
HM365279  
K124620  
K124646  
K124682

C. unguicola  
CBS 124558 (T)  
Iran  
Leaf of Triticum aestivum, Miandoab, West Azerbaijan Province  
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HM365250  
HM365250  
HM365278  
K124621  
K124647  
K124683

Achaetomium strumarium  
CBS 333.67 (T)  
India  
Soil, Lucknow  
–  
AY861170  
AY861204  
AY861233  
K003252  
K003253  
K003254

\* CBS: CBS-KNAW Fungal Diversity Centre, Utrecht, The Netherlands; CGMCC: China General Microbiological Culture Collection Centre in the Institute of Microbiology, Beijing, China; DSM: Deutsche Sammlung von Mikroorganismen und Zellkulturen GmbH, Braunschweig, Germany; IRAN: Iranian Research Institute of Plant Protection, Tehran, Iran; MUC: Mycothèque de l'Université Catholique de Louvain, Belgium. Additional culture collection numbers are available where applicable under the species notes in the Taxonomy section.

\* T: ex-type strain; epiT: ex-epitype strain; neoT: ex-neotype strain.

\* Maximum Growth Temperature.
definition of C. globosum sensu Von Arx, however, was considered by subsequent researchers as being too broad (Seth et al. 1987, Asgari & Zare 2011, Doveri 2013).

Based on a three-gene phylogeny, which mainly included Iranian isolates, Asgari & Zare (2011) recognised five species groups within the genus Chaetomium. Eleven species were included in their C. globosum group, constituting C. coarctatum, C. cruentatum, C. elatum, C. globosum, C. madrasense, C. megalocarpum, C. subaffine and four newly described species. The sequence data, however, only included three isolates of C. globosum sensu Von Arx and failed to clarify the species concept of C. globosum.

As the non-ostiolate counterpart genus of Chaetomium, Chaetomidium is characterised by cleistothecial ascomata bearing usually long and flexuous ascomatal hairs, and ellipsoidal to limoniform, single-celled ascospores with a single apical germ pore. This genus currently includes 12 species (Von Arx 1975, Stichsig et al. 2004, Greif & Currah 2007). Recently, a phylogenetic analysis including nine Chaetomidium species using sequence data of three gene regions revealed that the studied species were scattered throughout the Chaetomiaceae and Lasiosphaeraceae, indicating that Chaetomidium is polyphyletic (Greif et al. 2009). As Chd. fimeti, the type species of Chaetomidium, and Chd. subfimeti, formed a strongly supported clade in all three analyses, it was suggested that Chaetomidium should be restricted to Chd. fimeti and Chd. subfimeti. However, the phylogenetic placement of Chaetomidium sensu Greif et al. (2009) was inconsistent in the three gene regions analysed. Analysis of the RNA polymerase II second largest subunit (rpb2) revealed a highly supported clade that included Chaetomidium sensu Greif et al. (2009), Chd. pilosum, C. elatum and C. globosum, forming a sister clade to the clade which included both Chaetomidium and Chaetomium species. Both the 28S large subunit (LSU) nrDNA and β-tubulin (tub2) sequence data also did not support the segregation of Chaetomidium from Chaetomium.


Clarification of the species concepts of C. globosum and allied taxa is of indispensable importance not only for taxonomy of the genus, but also to obtain a better understanding of the economical importance of the species. Therefore, the aim of the present study is to resolve the species concept of C. globosum s.str. and its relationship with allied species using phylogenetic inference based on six loci in combination with morphological features.

MATERIALS AND METHODS

Isolates

The Chaetomium isolates used in this study are housed in the collections of the CBS-KNAW Fungal Biodiversity Centre, Utrecht, The Netherlands (CBS), and the China General Microbiological Culture Collection Centre, Institute of Microbiology, Beijing, China (CGMCC). Overall, 800 strains assigned to Chaetomium species were screened for strains belonging to the C. globosum species complex. Based on a preliminary phylogenetic analysis (data not shown) of the rpb2 and tub2 gene regions, 80 representative strains were selected for further study (Table 1).

DNA phylogeny

Genomic DNA was extracted from mycelium harvested from cultures grown on 2 % (w/v) malt extract agar (MEA) for 7–14 d at room temperature using the E.Z.N.A.™ HP Fungal DNA Kit (Omega Bio-Tek, Norcross, GA), or the CTAB extraction method (Damm et al. 2008) with minor modification: after adding the CTAB extraction buffer, samples were subjected to three cycles of freezing in liquid nitrogen and thawing in a water bath, instead of incubating at 100 °C for 3 min. The primers used for PCR-amplification and sequencing included ITS5 & ITS4 for the internal transcribed spacer regions and intervening 5.8S nrRNA gene region (ITS; White et al. 1990); NL1 & NL4 for the D1/D2 domains of the 28S nrRNA gene region (LSU; O'Donnell 1993); T1 (O'Donnell & Cigelnik 1997) & T222 (Glass & Donaldson 1995) for the partial tub2 gene region; EF1-983F & EF1-2218R (S. Rehner, AFTOL, http://aftol.org/) for the partial translation elongation factor 1-α (tef1) gene sequence; gRPB1-A & fRPB1-C (Matheny et al. 2002) for partial fragments of the largest subunit of the RNA polymerase II (rpb1) gene; RPB2AM1-bf & RPB2AM1-Tr (Miller & Huhndorf 2005) for partial fragments of the rpb2 gene region. The PCR mixtures (12.5 μL) contained 10–20 ng of genomic DNA, 1× GoTaq® Flexi buffer (Promega, Madison, WI, USA), 1 mM MgCl₂ (2.5 mM for rpb2), 0.2 mM of each primer (0.12 μM for rpb2) and 0.5 Unit GoTaq® Flexi DNA polymerase (Promega, Madison, WI, USA). The PCR conditions for ITS, LSU, rpb1, tef1 and tub2 were the same as those described by Wang et al. (2014). The cycle conditions for amplification of the partial rpb2 gene included cycles of 94 °C/3 min (initial denaturation); 94 °C/45 s, 60 °C/45 s, 72 °C/2 min (5×); 94 °C/45 s, 58 °C/45 s, 72 °C/2 min (5×); 94 °C/45 s, 56 °C/45 s, 72 °C/2 min (35×) and 72 °C/8 min (final extension). The PCR products were purified and sequenced in both directions using the BigDye® Terminator v. 3.1 Cycle Sequencing Kit (Applied Biosystems Life Technologies, Carlsbad, CA, USA) and an ABI
Phylogenetic analyses of individual gene alignments and the concatenated six-locus dataset were based on Bayesian inference (BI), Maximum Likelihood (ML) and Maximum Parsimony (MP) analyses. For BI, the best evolutionary model for each partition was determined using MrModeltest v. 2 (Nylander 2004) and incorporated into the analyses. A Markov Chain Monte Carlo (MCMC) algorithm was used to generate phylogenetic trees using MrBayes v. 3.2.1 (Ronquist & Huelsenbeck 2003) under optimal criteria for each locus. The MCMC analysis continued until the average standard deviation of split frequencies came below 0.01 with trees saved every 1 000 generations. The first 25 % of saved trees were discarded as the ‘burn-in’ phase and posterior probabilities (PP) were determined from the remaining trees. The MP analysis was performed using PAUP v. 4.0b10 (Phylogenetic Analysis Using Parsimony; Swofford 2003). Phylogenetic relationships were estimated by heuristic searches with 1 000 random addition sequences.

Kimura-2-parameter values

To evaluate the efficiency of each gene region for species delimitation, individual alignments of each locus were analysed using MEGA v. 6 (Tamura et al. 2013), generating both inter- and intraspecific distance matrices using the Kimura-2-parameter model, with substitutions including transitions and transversions. Uniform rates among sites were used and gaps were completely deleted. The obtained distance values were exported in a Microsoft Excel workbook format and then sorted into frequency distribution bins (from distance 0–0.2 with intervals of 0.008 between bins). The frequency distribution mean was calculated according to the formula \( M = \sum f.b / \sum f \), in which \( f \) is the frequency and \( b \) is the bin. The distance between the mean of the inter- and intraspecific distance distributions represents the barcoding gap (Fig. 2).

Morphology

All the representative isolates were inoculated onto 3 % oatmeal (w/v) agar (OA; Crous et al. 2009), and incubated in the dark at 25 °C until the ascomata matured. Isolates that appeared to be sterile, were also inoculated onto commeal agar (CMA), MEA, as well as water agar (WA) and OA supplemented with sterile filter paper strips, barley leaves or elm stems. Cultures were incubated at room temperature (fluctuating from day to night), 25 °C or 28 °C in the dark or under continued UV-light in order to induce sporulation. Colonies and ascomata were observed using a Nikon SMZ 1500 dissecting-microscope and colony colours were determined using the colour charts of Rayner (1970). Microscopic features were studied using a Nikon Eclipse 80i compound microscope equipped with differential interference contrast (DIC) illumination. Shear’s mounting medium was used to observe the asci from young or newly-matured ascomata. Microscopic features of ascomata, ascomatal hairs and ascospores were determined in lactic acid with the exception of the ascospores of C. angustissipale, which were studied in water. Lactic acid mounts were gently heated to remove air bubbles and prevent ascospore shrinkage. At least 30 measurements were made for all morphologically informative features. The ascospore measurements include the extreme values given in parentheses and, in between, the 95 % confidence interval of 30 individual measurements, for the three dimensions of length, width and thickness.

RESULTS

Phylogeny

The phylogenetic analyses included 80 ingroup taxa, with Achaeto- etomium strumarum (CBS 333.67, ex-type) as outgroup. No topological conflicts were observed when the 70 % bootstrap reciprocal tree topologies of the analysed loci were compared, except for the ITS and LSU which failed to resolve most of the phylogenetic species recovered by the remaining four protein-coding gene regions. However, all six loci were combined following the argument of Cunningham (1997) that combining incongruent partitions could increase phylogenetic accuracy. The combined alignment consisted of 4 128 characters including alignment gaps. Of these, 2 671 characters were constant, 359 parsimony-uninformative and 1 098 parsimony-informative. For the Bayesian inference, a GTR+I+G model was selected for ITS, rpb1, rpb2 and tef1, and a HKY+I+G model for LSU and tub2. A total of 2 332 trees were generated during the Bayesian inference from which 582 trees were discarded as the ‘burn-in phase’ and posterior probabilities (PP) were calculated from the remaining 1 750 trees. Both the BI consensus tree and PP confirmed the tree topologies and bootstrap support (BS) values obtained with the ML and MP analyses. The MP analysis resulted in four equally most parsimonious trees (TL = 3 616; CI = 0.554; RI = 0.866; RC = 0.480). The BI consensus tree is presented here (Fig. 1) with the relevant BS values of the MP and ML analyses shown at the nodes.

The phylogenetic tree (Fig. 1) resolved 36 well-supported clades representing possible cryptic species within the C. globosum species complex (MP-BS = 100; ML-BS = 89; PP < 0.9). The species complex was divided into two main clades, which was further divided into three groups (Fig. 1. Groups I – III). The first main clade represented Group I (MP-BS = 70; ML-BS = < 50; PP = 1.0), with C. interruptum forming a basal sister lineage to the remaining members of this group. The other taxa in Group I were further divided into three well-supported subclades (A – C). The largest of these (Group IA; MP-BS = 67; ML-BS = 89; PP = 1.0) included six well-supported lineages, two of which (CBS 128492 and CBS 128494) represent possible novel taxa. The second subclade (Group IB; MP-BS = 100; ML-BS = 100; PP = 1.0) includes C. ascotrichoides (ex-type culture CBS 113.83) forming a clade (MP-BS = 100; ML-BS = 99; PP = 1.0) separate from the ex-type culture of C. madrasense (CBS 87X.W. Wang et al.: Phylogeny of Chaetomium globosum complex
Fig. 1  Consensus phylogram resulting from a Bayesian analysis of the concatenated rpb2, tub2, tef1, rpb1, ITS and LSU gene region alignment, with the confidence values of bootstrap (BS) proportions from the MP analysis (before the backslash), the ML analysis (after the backslash) above branches, and the posterior probabilities (PP) from the Bayesian analysis below branches. The '-' indicates lacking statistical support (< 50 % for ML-BS and MP-BS analyses; < 0.90 for PP from Bayesian analyses). The branches with full statistical support (MP-BS = 100 %; ML-BS = 100 %; PP = 1.0) are highlighted with thickened posterior probabilities (PP) from the Bayesian analysis below branches. The '-' indicates lacking statistical support (< 50 % for ML-BS and MP-BS analyses; confidence values of bootstrap (BS) proportions from the MP analysis (before the backslash), the ML analysis (after the backslash) above branches, and the posterior probabilities (PP) from the Bayesian analysis below branches. The tree is rooted to Achaetomium strumarium. Each species clade is discriminated with boxes in a different colour. Ascospores of all sporulating species treated in this study are illustrated at the right side of tree (scale bar = 10 μm; ascospores face view on the left and side view on the right, except for C. citrinum in the last line). The ascospores are correlated with each corresponding species using the same numbers in orange circles.
Fig. 2  The frequency distribution graphs of the Kimura-2-parameter distances (barcoding gaps) for the six individual loci. The blue arrow indicates the average interspecific distance and the red arrow indicates the average intraspecific distance with corresponding mean values above both arrows.
315.74) in the same subclade. The third subclade (Group IC; MP-BS = 100; ML-BS = 100; PP = 1.0) includes *Chaetomidium* (*Chd.*) *fimeti* (ex-epitype culture DSM 62108), the type species of the genus, and *Chd.* *subfimeti* (ex-type culture CBS 370.66). The second main clade (including Group II and III; MP-BS = 75; ML-BS = 92; PP = 0.97) includes *C. citrinum* (ex-type culture CBS 693.82), as a basal lineage to the clade. The remaining taxa (MP-BS = 79; ML-BS = 100; PP = 1.0) are divided into three monophyletic subclades. The first subclade (Group II; MP-BS = 98; ML-BS = 100; PP = 1.0) includes several single-isolate lineages (CBS 128446, CBS 574.71 and CBS 145.38, respectively) as possible novel taxa, and the ex-type culture (CBS 293.83) of *C. umbonatum*. Representative strains of *C. globosum* s.str., the type species of the genus *Chaetomium*, clustered together in a well-supported clade (Group IIA; MP-BS = 100; ML-BS = 92; PP = 1.0). The remaining isolates clustered in two well-supported clades (Group IIB and IIC; both with MP-BS = 100; ML-BS = 100; PP = 1.0; containing CBS 139.38 and CBS 124555, respectively), each clade representing possible phylogenetic species.

The second subclade (Group III; MP-BS = 98; ML-BS = 94; PP = 1.0) includes 16 well-supported phylogenetic species, from which six isolates (CBS 373.66, CBS 151.59, CBS 128489, CBS 137.58, CBS 506.84 and CBS 335.67) represent unique single-isolate lineages. Of these, three strains (CBS 151.59, CBS 506.84 and CBS 128489) are possible novel phylogenetic species. These single-isolate lineages also include the ex-type culture of *Chd. pilosum* (CBS 335.67), for which a new combination is required. Two clades in Group III, one represented by CBS 378.71 (MP-BS = 100; ML-BS = 100; PP = 1.0), and the other by CG-MCC 3.9441 (MP-BS = 100; ML-BS = 100; PP = 1.0) are also possible novel phylogenetic species.

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**Fig. 3** *Chaetomium afropilosum* (CBS 145.38, ex-type culture). a. Part of the colony on OA; b. ascomata on OA, top view; c. ascoma on OA, side view; d, e. ascomata mounted in lactic acid; f. structure of ascomatal wall in surface view; g, h. upper part of terminal ascomatal hairs; i. basal part of a terminal ascomatal hair; j. asci; k. ascospores. — Scale bars: d, e = 100 μm; h, j = 20 μm; f, g, i, k = 10 μm.
Kimura-2-parameter values
The individual loci showed varying degrees of overlap in their K2P distribution graphs (Fig. 2). In these datasets, tub2 showed the best barcode gap distance between the inter- and intraspecific distances, followed by rpb1, rpb2 and tef1, respectively. Of the latter three loci, rpb1 was chosen over rpb1 due to ease of amplification across the Chaetomiaceae.

Taxonomy
The phylogenetic inference resulted in the recognition of 36 species within the C. globosum species complex. Of these, 12 species are described as novel species. The genus Chaetomium is synonymised under Chaetomium since the type species, Chd. fimeti, was shown to belong to Chaetomium based on our phylogenetic analyses. Therefore, new combinations are provided here for Chd. fimeti, Chd. pilosum and Chd. subfimeti in the genus Chaetomium. Several isolates (CBS 119758 of C. grande, CBS 126660 of C. internatum, CBS 108.83 of C. globosporum and CBS 483.73 of C. subglobosum) only produced viable ascomata on OA supplemented with sterile elm stems. Six phylogenetic species failed to produce any viable ascomata containing ascospores under all conditions tested in our study, five of which represent novel taxa and C. undulatum. These five novel taxa are described here based on sequence data only, following the approach of Gomes et al. (2013) for Diaporthe. Furthermore, 23 existing species are re-described based on their morphology on OA.

Chaetomium afropilosum X. Wei Wang, Crous & L. Lombard, sp. nov. — MycoBank MB812942; Fig. 3
Etymology. Refers to the ‘afro’-like appearance of the ascomatal hairs.

Ascomata superficial, often covered by sparse aerial hyphae, ostiolate, pale cinere to grey-olivaceous in reflected light owing to ascomatal hairs, globose or ovate, 210–360 μm high, 180–310 μm diam. Ascomatal wall brown, composed of hyphalike or amorphous cells, textura intricata or textura epidermoidea in surface view. Terminal hairs abundant, forming a dense, nearly globose head covering the ostiule, verrucose, olivaceous brown, fading towards the tips, undulate or slightly coiled, erect or flexuose at lower part, 3–4.5 μm near the base, tapering towards the tips. Lateral hairs similar to terminal hairs, but more flexuose. Ascii fasciculate, clavate or slightly fusiform, spore-bearing part 18–24 μm x 9–11.5 μm, stalks 15–24 μm long, with eight biseriate ascospores, evanescent. Ascospores olivaceous brown when mature, limoniform, usually slightly umbonate at both ends, bilaterally flattened, (9.5–)11.5–(12) μm x (7.5–)8–9 μm x (5.5–)6–7 μm, with an apical germ pore. Asexual morph acromion-like, Conidiophores discrete and simple; conidigenous cells phialidic, hyaline. Conidia formed in basipetal succession, aseptate, smooth, hyaline, ovate or ellipsoid, usually with truncate base and rounded apex. (2.5–)3–4.5 μm x 2–3 μm.

Culture characteristics — Colonies on OA with greyish white to white aerial hyphae, often producing olivaceous exudates diffusing into the medium; reverse olivaceous to cinnamon.

Material examined. RUSSIA, Baleshev region, Tellerman Forest, from Fraxinus sp., 1956, K.S. Sergejeva (culture ex-type CBS 137.58 = IMI 074952 = VKM F-1942).

Notes — Chaetomium angustispirale is only known from its ex-type culture (CBS 137.58), and it was difficult to induce sporulation. Ascomata were only obtained by growing the isolate on OA supplemented with sterile elm stem pieces at the beginning of this study, and ascospores were studied using water as mounting medium. All attempts to induce sporulation again, for better morphological data, failed. Ames (1963) provided a description of C. angustispirale and noted the two types of terminal hairs as mentioned above, but did not mention its asexual morph. Von Arx et al. (1986) suggested this species to be a heterothallic relative of C. globosum, but at the same time listed it in the synonyms of C. globosum. The phylogeny suggests that this species is in Group III (Fig. 1), relatively distant from C. globosum s.str. (Group IIA).

Chaetomium ascotrichoides Calviello, Revista Mus. Argent. Cien. Nat. B. Aires, Bot. 3: 372. 1972. — Fig. 5, 6

Ascomata, superficial, ostiolate, pale olivaceous buff, or occasionally rosy buff in reflected light owing to ascomatal hairs, later becoming black due to ascospore masses on ascomata, ellipsoid, ovate or obovate, 170–290 μm high, 130–250 μm diam. Ascomatal wall brown, composed of hyphalike or amorphous cells, textura intricata or textura epidermoidea in surface view. Terminal hairs finely verrucose, relatively sparse, brown, flexuose, undulate, sometimes simply branched, 2.5–3.5 μm near the base, hairs around ostiule often relatively short, flexuose or geniculate, constricted at septa, irregularly branched in the upper part. Lateral hairs hypha-like, flexuose, tapering towards the tips. Ascii fasciculate, fusiform or clavate, spore-bearing part 30–45 μm x 11–19 μm, stalks 18–35 μm long, with eight biseriate ascospores, evanescent. Ascospores olivaceous brown when mature, broad limoniform, slightly apiculate at both ends, bilaterally flattened, usually triangle-shaped in side view due to a lateral bulge, (8.5–)9.5–10.5(–11) μm x (8–)8.5–9.5(–10) x (6–)6.5–7(–7.5) μm, with an apical germ pore. Asexual morph absent.
Culture characteristics — Colonies on OA with sparse, white aerial hyphae, and without coloured exudates; reverse uncoloured.


Notes — *Chaetomium ascotrichoides* is morphologically similar to *C. madrasense*, and was treated as a synonym of the latter by Von Arx et al. (1986). This species can be distinguished by flexuous or irregularly branched ascomatal hairs compared to the coiled hairs of *C. madrasense* and narrower ascospores in lateral view (6.5–7 μm) than those of *C. madrasense* (7.5–8.5 μm). Isolate CBS 110.83 was originally attributed to *C. gibberosporum* without description, rendering this species name invalid under the International Code of Nomenclature for algae, fungi and plants (ICN; Art. 38; McNeill et al. 2012). Although isolate CBS 110.83 has relatively numerous and undulate to slightly coiled ascomatal hairs (Fig. 6), the presence of branched ascomatal hairs and narrow ascospores indicate that it must be conspecific with CBS 113.83, the ex-type culture of *C. ascotrichoides*, as was shown by phylogenetic inference (Group IB, Fig. 1). Several Chinese isolates of *C. ascotrichoides* possess only a few ascospores with a lateral bulge and, therefore, may be confused with *C. globosum* or *C. coarctatum*. However, the ascospores of *C. ascotrichoides* (9.5–10.5 × 8.5–9.5 × 6.5–7 μm) are wider than those of *C. globosum* (8.5–10.5 × 7–8 × 5.5–6.5 μm) and narrower than those of *C. coarctatum* (10–11 × 9–10 × 6.5–7.5 μm).

*Chaetomium capillare* X. Wei Wang, Crous & L. Lombard, sp. nov. — MycoBank MB812975

Etymology. Refers to animal hair from which this fungus was first collected.

Cultures sterile. *Chaetomium capillare* forms a unique lineage in Group III (Fig. 1), sister to *C. telluricola*. This species differs from the closest phylogenetic lineage, *C. telluricola*, by several fixed unique single nucleotide polymorphisms (SNP) in the six loci used in this study: *rpb2* positions 21(A), 60(C), 120(G), 132(A), 147(G), 165(T), 177(T), 195(C), 198(T), 222(T), 227(T), 228(G), 240(T), 246(T), 249(C), 265(C), 273(A), 282(C), 291(C), 294(T), 300(G), 324(C), 333(A), 351(A), 373(C), 405(C), 409(A), 411(G), 420(C), 428(T), 477(T), 513(T), 546(T) and 582(T); *tub2* positions 9(T), 12(G), 14(A), 15(G), 16(C), 28(T), 71(C), 90(indel), 97(T), 127(indel), 228(C), 264(T), 265(T), 331(C), 337(T), 360(G), 368(A), 370(indel), 371(indel), 372(indel), 373(indel), 405(G), 561(A), 571(G), 577(A), 593(A) and 594(T)
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601(C); tef1 positions 33(C), 216(C), 363(C), 399(C), 411(C), 459(G), 501(T), 683(G), 846(T), 909(T); rpb1 positions 107(G), 122(indel), 160(C), 202(C), 286(C), 292(T), 319(T), 331(C), 343(G), 370(C), 388(C), 436(T), 442(T), 455(A), 505(A), 544(T), 574(A), 592(C), 610(G), 628(C), 631(C), 676(T), 697(C), 706(T) and 709(T); ITS positions 31(C), 81(C), 89(A), 105(T), 162(A); LSU position 441(A).

Culture characteristics — Colonies on OA with white floc-

cose aerial hyphae, and without coloured exudates; reverse uncoloured.

Material examined. USA, California, isolated from animal hair, collection
date unknown, deposited in CBS by D.A. Sutton, 29 Sept. 2010 (holotype
CBS H-22187, culture ex-type CBS 128489 = UTHSC 03-1339 = dH 21593).

Notes — All attempts to induce sporulation on OA failed,
even with the addition of sterile elm twig pieces. Phylogenetic
inference and SNP analysis indicate that this isolate belongs to
Group III, and it forms a sister lineage to C. telluricola (Fig. 1),
representing a novel phylogenetic species, introduced here
as C. capillare.

Chaetomium cervicicola X. Wei Wang, Crous & L. Lombard,
sp. nov. — MycoBank MB812976

Etymology. Refers to the neck of Homo sapiens, from which this fungus
was isolated.

Cultures sterile. Chaetomium cervicicola forms a unique line-
age in Group IA (Fig. 1), sister to a clade, which includes the
five species, C. megalocarpum, C. grande, C. globosporum,
C. contagiosum and C. nozdrenkoae. This species differs from
the latter species by several unique fixed SNPs for the six loci
used in this study: rpb2 positions 36(T), 42(T), 45(C), 64(C),
66(G), 69(C), 72(T), 108(C), 135(G), 138(A), 147(A), 153(T),
180(A), 184(A), 207(A), 210(C), 213(A), 222(G), 231(A), 264(T),
267(A), 285(C), 300(C), 339(A), 345(C), 349(C), 350(A), 360(T),
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366(A), 367(C), 368(A), 378(T), 387(T), 429(C), 435(G), 447(C), 450(G), 456(T), 468(T), 504(A), 525(A), 537(G), 555(G), 579(G) and 582(G); tub2 positions 22(C), 29(indel), 39(indel), 40(indel), 41(indel), 66(C), 72(A), 73(A), 76(T), 79(indel), 80(indel), 81(indel), 82(indel), 94(G), 103(T), 146(G), 147(A), 152(A), 153(G), 156(G), 161(A), 164(A), 167(indel), 172(G), 173(T), 178(C), 183(T), 226(T), 233(C), 250(T), 251(C), 264(G), 269(C), 278(C), 279(A), 321(C), 322(indel), 323(indel), 324(indel), 325(indel), 326(indel), 327(indel), 336(A), 440(A), 450(T), 456(C), 465(T), 477(T), 494(C), 560(T), 563(C), 568(indel), 573(indel), 577(G), 589(T), 594(A), 595(A) and 604(A); tef7 positions 18(C), 24(T), 78(T), 129(T), 255(C), 333(T), 376(T), 387(T), 459(T), 627(C), 636(T), 675(C), 679(T), 687(G), 864(C), 918(C) and 927(G); rpb1 positions 65(A), 83(A), 85(T), 94(G), 107(A), 108(C), 125(G), 127(indel), 131(A), 137(G), 138(A), 139(G), 229(T), 234(A), 235(C), 251(T), 252(G), 253(G), 256(G), 262(T), 271(G), 272(A), 273(A), 278(G), 286(G), 288(C), 289(C), 290(G), 291(G), 292(A), 294(G), 295(G), 296(A), 297(C), 298(C), 300(T), 301(C), 303(A), 310(G), 337(T), 412(G), 472(C), 475(C), 490(C), 493(T), 535(A), 587(C), 613(T), 634(T), 670(C), 685(C), 691(G), 715(T), 718(T) and 724(C); ITS positions 105(C), 146(C), 452(C), 483(G), 489(G), 491(indel), 504(indel), 505(indel), 506(indel), 507(indel); LSU positions 403(G), 411(A), 424(T), 433(C), 477(G), 517(C), 520(C), 521(G) and 522(C).

Culture characteristics — Colonies on OA with white flocose aerial hyphae, and without coloured exudates; reverse uncoloured.

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**Fig. 6** Chaetomium ascotrichoides (CBS 110.83, ex-type of C. gibberosporum). a. Part of the colony on OA; b. ascoma on OA, top view; c. ascoma and mass of ascospores on OA, side view; d, e. ascomata mounted in lactic acid; f. basal part of terminal ascomatal hairs; g. upper part of terminal ascomatal hairs; h. ascospores. — Scale bars: d, e = 100 μm; f–h = 10 μm.
Material examined. USA, Texas, isolated from neck of Homo sapiens, deposited in CBS by D.A. Sutton, 29 Sept. 2010 (holotype CBS H-22188, culture ex-type CBS 128492 = UTHSC 07-3593 = dH 21625).

Notes — All attempts to induce sporulation of this isolate during this study failed, even with the addition of sterile elm twig pieces. Phylogenetic inference indicates that this species forms a basal branch in Group IA (Fig. 1), and represents a novel phylogenetic species, which is further supported by SNP analysis.

Chaetomium citrinum Udagawa & T. Muroi, Trans. Mycol. Soc. Japan 22: 15. 1981. — Fig. 7

Ascomata covered by thick aerial hyphae or exposed, ostiolate, citrine-green to pale amber in reflected light owing to ascomatal hairs, globose, 200–380 μm diam. Ascomatal wall brown, composed of hypha-like cells, textura intricata in surface view. Terminal hairs finely punctate to verrucose, pale brown, hypha-like, flexuous or undulate, sometimes geniculate, 3–5 μm near the base. Lateral hairs similar to terminal hairs, but shorter. Asci fasciculate, clavate to fusiform, spore-bearing part 13.5–28 ×
6.5–13 μm, stalks 10–40 μm long, with eight biseriate ascospores, evanescent. Ascospores pale brown when mature, irregularly fusiform, limoniform, ovate, lunate or triangular, bilaterally flattened, (7–)8–10(–12) × (4–)5–6(–7) × 4–5(–5.5) μm, with an apical germ pore. Asexual morph absent.

Culture characteristics — Colonies on OA with profuse, floccose, white aerial hyphae often covering ascomata, producing ochreous to luteous exudates diffusing into the medium; reverse cinnamon to fulvous.

Material examined. Japan, Tochigi, Nasu-gun, Nishinasuno-machi, from rice-field soil, collector and collection date unknown, isolated by S. Udagawa, 23 Apr. 1978 (culture ex-type CBS 693.82 = NHL 2873).

Notes — *Chaetomium citrinum* is only known from its ex-type strain. It is characterised by irregular and relatively small ascospores. Von Arx et al. (1986) suggested that this species is closely related to *C. globosum* and allied species, especially *C. madrasense*. Phylogenetic analysis indicates *C. citrinum* to be a distinct species basal to Group III (Fig. 1).


Ascomata superficial, ostiolate, pale grey to olivaceous buff in reflected light owing to ascomatal hairs, obvate to subglobose, 260–420 μm high, 190–330 μm diam. Ascomatal wall brown, composed of amorphous or hypha-like cells, textura epidermoidea or textura intricata in surface view. Terminal hairs verrucose, brown, undulate or slightly coiled, sometimes branched, 3–4 μm near the base and tapering. Lateral hairs erect or flexuous, tapering towards the tips. Asci fasciculate, fusiform or clavate, spore-bearing part 28–43 × 14–20 μm, stalks 30–53 μm long, with eight biseriate ascospores, evanescent. Ascospores olivaceous brown when mature, broad limoniform to nearly globose, biapiculate, bilaterally flattened, (9.5–)10–11(–11.5) × 9–10(–10.5) × 6.5–7.5(–8) μm, with an apical germ pore. Asexual morph absent.

Culture characteristics — Colonies on OA with sparse white aerial hyphae and pale orange to slightly dark brick exudates diffusing into the medium; reverse fulvous to sienna.

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**Fig. 8** *Chaetomium coarctatum* (CBS 162.62, ex-type culture). a. Part of the colony on OA; b. ascoma and mass of ascospores on OA, top view; c. ascoma and mass of ascospores on OA, side view; d. e. ascomata mounted in lactic acid; f. upper part of terminal ascomatal hairs; g. branched middle part of a terminal ascomatal hair; h. basal part of terminal ascomatal hair; i. structure of ascomatal wall in surface view; j. ascii; k. ascospores. — Scale bars: d, e = 100 μm; f–k = 10 μm.

Notes — Von Arx et al. (1986) treated *C. coarctatum* as a synonym of *C. globosum*. However, *C. coarctatum* has broader limoniform to nearly globose and larger ascospores (10–11 × 9–10 × 6.5–7.5 μm vs 8.5–10.5 × 7–8 × 5.5–6.5 μm). Phylogenetic inference indicated that *C. coarctatum* has a basal position to the second main clade and is sister to Group III (Fig. 1), but its closest relatives remain unclear.

**Fig. 9** Chaetomium cochliodes (CBS 155.62, ex-epitype culture). a. Part of the colony on OA; b. ascomata on OA, top view; c, d. ascomata on OA, side view; e–g. ascomata mounted in lactic acid; h. structure of ascomatal wall in surface view; i. basal part of a terminal ascomatal hair; j–l. upper parts of terminal ascomatal hairs; m. asci; n. ascospores; o. holotype sheet of *C. cochliodes* in New York Botanical Garden (Specimen ID 01050405); p, q. ascomatal hairs of holotype specimen. — Scale bars: e–g = 100 μm; h–l, q = 20 μm; m, n = 10 μm.
**Chaetomium cochliodes** Palliser, N. Amer. Fl. 3: 61. 1910. — Fig. 9

Ascomata superficial, ostiolate, greenish olivaceous in reflected light owing to ascomatal hairs, ellipsoid or subglobulous, 270–450 μm high, 165–380 μm diam. Ascomatal wall brown, composed of hypha-like cells, textura intricata in surface view. Terminal hairs verrucose, dark brown, erect in the lower part, 3.5–6 μm near the base, tapering and fading towards the tips, spirally coiled in the upper part, with coils regularly tapering in diameter to appear as an elongated cone, occasionally with coiled branches. Lateral hairs brown, flexuous, undulate or coiled, tapering and fading towards the tips. Ascii fusiform, fuscous or clavate, spore-bearing part 23–32 × 13–15 μm, stalks 28–46 μm long, with eight biseriate ascospores, evanescent. Ascospores olivaceous brown when mature, limoniform, usually biapiculate at both ends, bilaterally flattened, (8–)9–10(–11) × (7–)7.5–8.5 × 5–6(–6.5) μm, with an apical germ pore. Asexual morph absent.

Culture characteristics — Colonies on OA without aerial hyphae, usually without coloured exudates, but occasionally producing yellowish ochreous exudates diffusing into the medium; reverse uncoloured, but grey olivaceous under ascomata.


Notes — The epitype of *C. cochliodes* designated here is morphologically similar to that of the holotype, particularly in morphology of the ascospores and ascomatal hairs, and originates from the same country as the type locality. *Chaetomium cochliodes* was once treated as a synonym of *C. globosum* (von Arx et al. 1986). Here, *C. cochliodes* is re-introduced based on phylogenetic inference supported by morphological characters. Phylogenetic inference indicates that *C. cochliodes* clusters in Group III, closely related to *C. pseudocochliodes* and *C. spiculilium* (Fig. 1). *Chaetomium cochliodes* can be distinguished from these species by distinctive coiled ascomatal hairs.

**Chaetomium contagiosum** X. Wei Wang, Crous & L. Lombard, *sp. nov.* — MycoBank MB812977

Etymology. Refers to the ability of this fungus to infect the cornea of Homo sapiens.

Culture sterile. **Chaetomium contagiosum** forms a unique lineage (Group IA, Fig. 1) closely related to *C. megalocarpum, C. grande* and *C. globosum* and can be distinguished based on the following unique fixed SNPs: *rpb2* positions 9(G), 45(A), 123(C), 233(A), 265(T), 333(T), 374(G) and 570(C); *ubt2* positions 12(G), 16(indel), 99(G), 277(T), 327(T), 351(T), 410(A), 472(indel), 572(G), 585(G), 594(C) and 623(C); *tef1* positions 291(G), 325(A), 326(C), 332(C), 343(T), 344(C), 487(A), 633(T), 654(T), 683(C), 738(C), 747(T) and 837(C); *rbp1* positions 214(A), 220(T), 234(T), 247(C), 274(G), 288(T), 324(T), 325(G), 388(C), 427(A), 455(T), 601(T), 658(G) and 721(C).

Culture characteristics — Colonies on OA with white floccose aerial hyphae, and without coloured exudates; reverse uncoloured.

Material examined. USA, North East, isolated from cornea of Homo sapiens, deposited in CBS by D.A. Sutton, 29 Sept. 2010 (holotype CBS H-22189, culture ex-type CBS 128494 = UTHSC 10-726 = dh 21640).

Notes — Phylogenetic inference and SNP analysis indicate that this species is a novel phylogenetic species in Group IA (Fig. 1). All attempts to induce sporulation on OA failed, even with the addition of sterile elm twig pieces.

**Chaetomium cucumericola** X. Wei Wang, Crous & L. Lombard, *sp. nov.* — MycoBank MB812978

Etymology. Refers to the plant host *Cucumis sativus*, from which this fungus was isolated.

Cultures sterile. **Chaetomium cucumericola** forms a unique lineage in Group III (Fig. 1), sister to *C. olivaceum* and is distinguished from the latter by fixed unique SNPs in four loci: *rpb2* positions 48(C), 132(A), 156(C), 195(G), 203(G), 306(G), 432(A) and 507(C); *ubt2* positions 71(G), 217(A), 237(C), 338(G), 363(C), 378(A), 467(G), 560(indel), 570(A), 591(A) and 604(G); *tef1* positions 33(T), 283(A), 347(G), 453(C) and 681(T); *rbp1* positions 148(C), 169(T), 190(A), 253(A), 303(C), 307(T), 337(T), 376(T), 394(T), 397(A), 487(C), 538(C), 619(T) and 688(C).

Culture characteristics — Colonies on OA with white floccose aerial hyphae, and without coloured exudates; reverse uncoloured.


Notes — Phylogenetic inference and SNP analysis indicated that both representative isolates of *C. contagiosum* form a lineage in Group III, sister to *C. olivaceum* (Fig. 1). All attempts to induce sporulation on OA failed, even with the addition of sterile elm twig pieces.

**Chaetomium elatum** Kunze, Deutsche Schwämme 8: 3. No. 184. 1818. — Fig. 10


Ascomata superficial, ostiolate, greenish olivaceous in reflected light owing to ascomatal hairs, globose or obovate, 230–400 μm high, 175–365 μm diam. Ascomatal wall brown, composed of hypha-like or amorphous cells, textura intricata or textura epidermoidea in surface view. Terminal hairs verrucose or warty, brown, tapering and fading towards the tips, erect or flexuous in the lower part, 2.5–4.5 μm diam near the base, repeatedly and dichotomously branched at right to nearly straight angles in the upper part, with relatively flexible, flexuous or undulate terminal branches. Lateral hairs brown, flexuous, tapering towards the tips. Asci fusiform, clavate, spore-bearing part 36–49 × 13.5–16 μm, stalks 24–55 μm long, with eight biseriate ascospores, evanescent. Ascospores brown when mature, limoniform, biapiculate or umbonate, bilaterally flattened, (11–)12–13(–14) × 9–10.5(–11) × (6–)7–8(–9) μm, with an apical germ pore. Asexual morph acremonium-like. Conidiophores formed laterally from aerial hyphae, simple, 6–18 μm long, 1.5–2.2 μm diam at the base. Conidia formed solitary or in chains, hyaline, aseptate, smooth, globose, ellipsoidal or ovate, often with a truncated base and a rounded apex, 4.5–6.5(–7) × (3.5–)4–6 μm.

Culture characteristics — Colonies on OA with sparse aerial hyphae, and without coloured exudates; reverse uncoloured.

Notes — Dreyfuss (1976) restricted *C. elatum* to heterothallic isolates with acremonium-like asexual morphs, and classified homothallic isolates, mostly without asexual morphs, as *C. virgecephalum*. Von Arx et al. (1986) reduced *C. virgecephalum* to synonymy with *C. elatum*, meaning that the species *C. elatum* was expanded to include both heterothallic and homothallic isolates. The phylogenetic inference in this study supports the classification of Von Arx et al. (1986). The holotype of *C. elatum*
Fig. 11  Chaetomium fimeti (CBS 153.77). a. Part of the colony on OA; b. ascomata on OA, top view; c. ascomata on OA, side view; d, e. ascomata mounted in lactic acid; f. part of terminal ascomatal hair, longer type; g. terminal ascomatal hair, shorter type; h. inner layer structure of ascomatal wall in surface view; i. external layer structure of ascomatal wall in surface view; j. asci; k. ascospores; l. holotype sheet of Chaetomium fimeti in HERB. GENAVENSE (G00127165 in Switzerland); m, n. ascomata of holotype specimen. — Scale bars: d = 500 μm; e = 100 μm; f–i, k = 10 μm; j = 20 μm.
was originally collected in Germany, and all attempts to locate the holotype of *C. elatum* from B (Botanischer Garten und Botanisches Museum Berlin-Dahlem, Zentralinstitut der Freien Universität Berlin) were unsuccessful as a fire in 1943 destroyed parts of the ascomycete collection. Typification of this species awaits recollection from the type locality.

**Chaetomium fimeti** Fuckel, Enum. Fung. Nass., Ser. 1: 491. 1861. — Fig. 11


**Ascomata** superficial, non-ostiolate, dark brown to black, with numerous short, olivaceous buff to honey ascomatal hairs, and sparse, long and black hairs in reflected light, spherical or obolate. 320–500 μm diam. **Ascomata walls** composed of two layers, easily separating from each other: the external wall thick, dark brown, composed of thick-walled, angular or irregular cells, *textura angularis* in surface view; the inner layer thin, luteous to pale brown, composed of amorphous cells, *textura epidermoidea* in surface view. **Ascomatal hairs** of two types: shorter type covering the whole ascomata, punctate to verrucose, dark brown at the lower part, fading to greyish yellow-green or pale greyish sepia at the tips, 3–4.5 μm near the base, 30–580 μm long; longer type arising from the bases of the ascomata, smooth, dark brown, 4–8.5 μm near the base, 500–4 200 μm long. **Ascii** fasciculate, fusiform or clavate, with eight biseriate ascospores, spore-bearing part 24–43 × 16–24 μm, stalks 11–26 μm long, evanescent. **Ascospores** brown to brown when mature, limoniform, bilaterally flattened, (10–)11.5–12(–12.5) μm diam, (7–)7.5–8.5(–9) μm wide in lateral view, with one or two germ pores. **Asexual morph** absent.

**Culture characteristics** — Colonies on OA with white or pale grey aerial hyphae, producing pale ochreous exudates diffusing into the medium; reverse ochreous to fulvous.


**Notes** — Only the ex-type strain is known for this species. *Chaetomium globosum* is closely related to *C. megalocarpum* and *C. grande* (Group IA, Fig 1). This species is easily distinguished by its smaller and more regular, obolate ascospores (10.5–12 × 7.5–8.5 μm) compared to those of *C. megalocarpum* (13–15 × 11.5–14 × 8.5–10 μm) and *C. grande* (18–20.5 × 16–18 × 12–13.5 μm).

**Chaetomium globosum** Kunze, Mykol. Hefte 1: 16. 1817. — Fig. 13–15


**Ascomata** superficial, ostiolate, greenish olivaceous or slightly dark olivaceous buff to grey in reflected light owing to ascomatal hairs, globose, ellipsoid, ovate or obovate, 160–300 μm high, 135–250 μm diam. **Ascomatal wall** brown, composed of hypha-like or amorphous cells, *textura intricata* in surface view. **Terminal hairs** abundant, finely verrucose, brown, tapering and fading towards the tips, 3–5 μm diam near the base, flexuous, undulate to loosely coiled with erect or flexuous lower part, usually unbranched. **Lateral hairs** brown, flexuous, fading and tapering towards the tips. **Ascii** fasciculate, fusiform or clavate, spore-bearing part 30–40 × 12–17 μm, stalks 15–25 μm long, with eight biseriate ascospores, evanescent. **Ascospores** olivaceous brown when mature, limoniform, usually biapiculate, bilaterally flattened, (8–)8.5–10.5(–11) × 7–8(–8.5) × 5.5–6.5(–7) μm, with an apical germ pore. **Asexual state** absent.

**Culture characteristics** — Colonies on OA without aerial hyphae or with sparse white aerial hyphae in the centre, producing luteous to orange exudates diffusing into the medium; reverse fulvous to umber, but darker under ascomata.


Notes — Chaetomium globosum, the type species of the genus Chaetomium, was described based on an isolate collected from the stem of Dianthus carthusianorum in Leipzig, Germany. Our attempt to locate the holotype of C. globosum housed in B (Botanischer Garten und Botanisches Museum Berlin-Dahlem, Zentraleinrichtung der Freien Universität Berlin) was unsuccessful because the ascomycete collection was partly destroyed by a fire in 1943. Therefore, a dried culture, CBS H-22185 from the isolate CBS 160.62, that was collected in Germany from the same locality as the holotype, is designated here as neotype of C. globosum.

![Fig. 12 Chaetomium globosporum (CBS 108.83, ex-type culture). a. Part of the colony on OA; b. ascomata and masses of ascospores on OA, top view; c. ascomata and masses of ascospores on OA, side view; d. e. ascomata mounted in lactic acid; f. basal parts of terminal ascomatal hairs; g. branched upper part of a terminal ascomatal hair; h. unbranched upper parts of terminal ascomatal hairs; i. structure of ascomatal wall in surface view; j. asc; k. asco- spores. — Scale bars: d, e = 100 μm; f–k = 10 μm.](image)
The description provided above represents the typical characteristics of *C. globosum* s.str., in which the morphological diversity was captured to some extent, especially in ascomatal hairs and exudate colours. For example, CBS 160.62 (the ex-neotype culture) and CBS 105.40 exhibit greenish olivaceous ascomatal hairs with flexuous to slightly undulate upper part and orange exudates diffusing into the medium (Fig. 13); while CBS 145.51 and MUCL 39526 exhibit slightly dark olivaceous buff to grey ascomatal hairs with undulate to loosely coiled upper part and luteous exudates diffusing into the medium (Fig. 14).

Ames (1950) characterised *C. mollipilium* by its sparse and often branched ascomatal hairs at wide angles, but did not include *C. rectum* in his monograph. Von Arx et al. (1986) later reduced both species to synonymy under *C. globosum*. However, the ex-type cultures of *C. rectum* (CBS 164.62; Fig. 15a–f) and *C. mollipilium* (CBS 147.60; Fig. 15g–m) are distinguished from one another as well as from other typical isolates of *C. globosum* s.str. based on the six-locus phylogeny generated in this study (Group IIA, Fig. 1). Also, the average ascospore dimensions of both CBS 164.62 (9–10.5 × 7.5–8.5 × 5.5–6 μm) and CBS 147.60 (9–10.5 × 7.5–8.5 × 5–6 μm) resemble those of *C. globosum* s.str. (8.5–10.5 × 7–8 × 5.5–6.5 μm). Both species are, therefore, reduced to synonyms of *C. globosum* s.str. However, both ex-type isolates differ from *C. globosum* s.str. based on their ascomatal hair morphology: sparse, erect to flexuous terminal hairs, often branching at wide or narrow angles, and also thinner (2.5–3.5 μm diam near the base) than those of typical *C. globosum* (3–5 μm diam near the base).

Von Arx et al. (1986) regarded *C. cruentum* as an albino form of *C. globosum*, which possesses ascospores characteristic of *C. globosum* s.str., but paler and slightly larger. The other morphological structures of *C. cruentum* also present an albi-
nistic or degenerated morphology when compared to the typical C. globosum s.str. isolates, which make it look conspicuously different from typical C. globosum. Asgari & Zare (2011) indicated that C. cruentum and C. globosum (CBS 148.51) clustered together with high bootstrap support in a phylogenetic inference of the combined ITS, LSU and tub2 gene regions. This result was also supported in the present study (Group IIA, Fig. 1).

As there is no evidence available based on the analyses of six loci to distinguish the morphological species C. cruentum from C. globosum s.str., this taxon is reduced to synonymy under C. globosum s.str. The morphological variation ascribed to ‘cruentum’, however, is described below to present its conspicuous differences from the typical morphology observed among isolates of C. globosum s.str. Future studies of the genome may reveal the genetic mechanism linked to this variation.

Fig. 14 Typical morphology of Chaetomium globosum sensu stricto-2. a–f. MUCL 39526 (ex-type of C. globosum var. flavoviride): a. Ascomata and masses of ascospores on OA, top view; b. ascomata on OA, side view; c. ascoma mounted in lactic acid; d. structure of ascomatal wall in surface view; e. asci; f. ascospores. – g–m. CBS 148.51 (authentic isolate of C. globosum): g. part of the colony on OA; h. ascomata and masses of ascospores on OA, top view; i. ascoma on OA, side view; j. ascoma mounted in lactic acid; k. structure of ascomatal wall in surface view; l. asci; m. ascospores. — Scale bars: c, j = 100 μm; d, f, k–m = 10 μm; e = 20 μm.
**Chaetomium globosum morphological form ‘cruentum’** — 
**Fig. 16**

Ascomata superficial, ostiolate, globose, ellipsoid, ovate or ob-ovate, 210–300 μm high, 145–220 μm diam, hyaline when young, then saffron in reflected light owing to ascospore masses. Ascospore masses on the top of ascomata, rust when fresh, then slightly pale scarlet to salmon in reflected light when becoming dry. Ascomatal wall translucent, composed of amorphous or angular cells, textura epidermoidea or textura angularis in surface view. Ascomatal hairs sparse, hyaline, flexuous and delicate. Asci disappearing quickly. Ascospores pale cinnamon when mature, limoniform, usually biapiculate, bilaterally flattened, 9.5–11(–11.5) × 7.5–8.5(–9) × (6–)6.5–7 μm, with an apical germ pore. Asexual morph absent.

Culture characteristics — Colonies on OA without aerial hyphae, and producing yellow to yellowish amber exudates...
Chaetomium globosum — MycoBank MB812979; Fig. 17

Chaetomium graminiforme X. Wei Wang, Crous & L. Lombard, sp. nov. — MycoBank MB812979; Fig. 17

Chaetomium grande Asgari & Zare, Mycologia 103: 874. 2011. — Fig. 18

Description & Illustration — Based on the culture on MEA, CMA and PCA supplemented with cellulose; also see Asgari & Zare (2011).

Ascomata superficial, ostiolate, luteous to amber or citrine in reflected light owing to ascomatal hairs, becoming dark due to ascosporic masses on the top, ellipsoid, subglobose or ovate, 200–320 μm high, 170–260 μm diam. Ascomatal wall brown, composed of hypha-like or amorphous cells, textura epidermoidea or textura intricata. Terminal hairs sparse, olivaceous brown and fading towards almost pointed tips. Lateral hairs similar. Asci fasciculate, fusiform or clavate, spore-bearing part 25.5–40 × 12.5–16 μm, stalks 14.5–29 μm long, with eight biseriate ascospores, evanescent. Ascospores olivaceous brown when mature, limoniform, bilaterally flattened, (17–)18–(20.5–)22.5 μm, stalks 20.5–38 μm long, evanescent. Ascospores dark brown when mature, ellipsoid to subglobose, usually irregular, bilaterally flattened, (7.5–)9–(10–11.5 × (6–7) × 9–10 μm), with an apical germ pore. Asexual morph absent.

Culture characteristics — Colonies on OA usually without aerial hyphae and coloured exudates diffusing into the medium; reverse uncoloured, but dark grey-olivaceous under ascomata.


Notes — The ascomata of C. graminiforme appears similar to the ‘rectum’-like variation of C. globosum by having sparse, erect to flexuous ascomatal hairs, but can be distinguished by larger ascospores (10–11.5 × 8–9 × 6–7 μm) compared to those of C. globosum morphological form ‘rectum’ (9–10.5 × 7.5–8.5 × 5–6 μm). Phylogenetic inference showed that C. graminiforme is distantly related to C. globosum (Group IIA, Fig 1), and clusters with C. elatum and C. rectangular. However, the relationship of C. graminiforme to C. elatum and C. rectangular is not supported (Group III, Fig. 1), and the ascomatal hair morphology of this species is also different from those of C. elatum and C. rectangular.

Materials examined. CHINA, Xinjiang Autonomous Region, Bayingoleng, isolated from desert soil, June 2012, X.-W. Wang, CBS 119758 = CGMCC 2.9414. – IRAN, Ardabil Province, Bilesavar, isolated from straw of Triticum aestivum, 21 June 2005, B. Asgari, CBS 126781 = IRAN 1208C; West Azerbaijan province, Naghadeh, isolated from leaf of Triticum aestivum, 23
Notes — The description provided here is based on isolate CBS 119758 as the other isolates of this species, including the ex-type culture, are sterile. *Chaetomium grande* is closely related to *C. megalocarpum* and *C. globosporum* (Group IA, Fig 1). These three species all produce globose or subglobose ascospores without apiculate or umbonate ends, and usually with two germ pores. *Chaetomium grande* is easily distinguished by its much larger ascospores (18–20.5 \( \times \) 16–18 \( \times \) 12–13.5 μm) compared to those of *C. megalocarpum* (13–15 \( \times \) 11.5–14 \( \times \) 8.5–10 μm) and *C. globosporum* (10.5–12 μm diam, 7.5–8.5 μm wide in lateral view).

*Chaetomium interruptum* Asgari & Zare, Mycologia 103: 874. 2011. — Fig. 19

Description & Illustration — Based on the culture on MEA and CMA or PCA supplemented with cellulose; also see Asgari & Zare (2011).

Ascomata superficial, ostiolate, often covered by aerial hyphae, olivaceous or pale umber in reflected light owing to ascomatal hairs, ovate or ellipsoid, 230–360 μm high, 170–240 μm diam. Ascomatal wall brown, composed of amorphous cells, textura epidermoidea in surface view. Terminal hairs smooth or finely verrucose, brown, flexuous, undulate, sometimes simply branched, 3–4.5 μm diam near the base, tapering towards the tips. Lateral hairs similar. Asci fasciculate, clavate or fusiform, with eight biseriate or irregularly arranged ascospores, spore-bearing part 30–41 × 14–28 μm, stalks 15–29 μm long, evanescent. Ascospores dark brown when mature, globose to subglobose, non-apiculate, bilaterally flattened, (10–)11–12 μm diam, (7.5–)8–9 μm wide from lateral view, with one or two germ pores. Asexual morph absent.

Culture characteristics — Colonies on OA with white, sparse to floccose aerial hyphae, producing cinnamon to fulvous exudates diffusing into the medium; reverse olivaceous.

Chaetomium interruptum is morphologically similar to *C. globosporum*. Asgari & Zare (2011) indicated that the ascospores of *C. interruptum* only have one indistinct, apical or slightly subapical germ pore. Our observations showed that the ascospores of *C. interruptum* frequently have two germ pores, which are conspicuous and often subapical or lateral. The smaller ascomata (230–360 × 170–240 μm) with abundant, smooth and undulate ascomatal hairs distinguish *C. interruptum* from *C. globosporum*, which produce larger ascomata (350–510 × 210–350 μm) with sparse, verrucose and flexuous ascomatal hairs. Phylogenetic inference also showed that *C. interruptum* takes a basal position to Group I (Fig. 1), and is distant from *C. globosporum*.

**Notes** — *Chaetomium interruptum* is morphologically similar to *C. globosporum*. Asgari & Zare (2011) indicated that the ascospores of *C. interruptum* only have one indistinct, apical or slightly subapical germ pore. Our observations showed that the ascospores of *C. interruptum* frequently have two germ pores, which are conspicuous and often subapical or lateral. The smaller ascomata (230–360 × 170–240 μm) with abundant, smooth and undulate ascomatal hairs distinguish *C. interruptum* from *C. globosporum*, which produce larger ascomata (350–510 × 210–350 μm) with sparse, verrucose and flexuous ascomatal hairs. Phylogenetic inference also showed that *C. interruptum* takes a basal position to Group I (Fig. 1), and is distant from *C. globosporum*.

**Chaetomium madrasense** Natarajan, Proc. Indian Acad. Sci., B. 74: 255. 1971. — Fig. 21

Ascomata superficial, ostiolate, olivaceous buff or rosy buff, occasionally salmon in reflected light owing to ascomatal hairs, ellipsoid, ovate or obovate, 130–300 μm high, 140–260 μm diam. Ascomatal wall brown, composed of amorphous or hypha-like cells, *textura epidermoidea* or *textura intricata* in surface view. Terminal hairs relatively abundant, brown, finely verrucose, coiled or undulate, occasionally with simple branches, 2.5–4.5 μm near the base. Lateral hairs similar. Asci fasciculate, fusiform or clavate, spore-bearing part 28–38 × 13–20 μm, stalks 16–30 μm long, with eight biseriate ascospores, evanescent. Ascospores olivaceous brown when mature, broad limoniform, often slightly apiculate at both ends, bilaterally flattened, triangle-shaped in lateral view due to a conspicuous lateral.
bulge, 10–11(–11.5) × (8–)9–10 × 7.5–8.5(–9) μm, with an apical germ pore. Asexual morph absent.

Culture characteristics — Colonies on OA with sparse, white aerial hyphae, usually without exudates; reverse uncoloured, but usually black under ascomata.

Material examined. India, Madras, Tamil Nadu, from rhizosphere of Pennisetum typhoides, collection date unknown, K. Natarajan, isolated by K. Natarajan, 1966 (isotype CBS H-6877, culture ex-isotype CBS 315.74).

Notes — Von Arx et al. (1986) reduced C. ascotrichoides and C. gibberosporum to synonymy under C. madrasense, both having ascospores with a lateral bulge. Phylogenetic inference in this study distinguished C. madrasense from C. ascotrichoides (and C. gibberosporum) that was shown to be conspecific with C. ascotrichoides; Group IB, Fig 1). Chaetomium madrasense is, therefore, restricted here to the ex-type strain. This species can be distinguished by its coiled ascomatal hairs and more protruding lateral bulges of ascospores that appear wider than those of C. ascotrichoides (7.5–8.5 μm vs 6.5–7 μm).

Chaetomium megalocarpum Bainier, Bull. Soc. Mycol. France 25: 202. 1910. — Fig. 22

Ascomata superficial, ostiolate, honey to fawn in reflected light owing to ascomatal hairs, subglobose or ovate, 200–260 μm high, 148–220 μm diam. Ascomatal wall brown, composed of hypha-like or amorphous cells, textura epidermoidea or textura intricata in surface view. Terminal hairs punctate or finely verrucose, dark brown at the base, fading towards the tips, flexuous to undulate, sometimes branched, 3–5 μm near the base, tapering towards the tips. Lateral hairs similar. Ascii fasciculate, fusiform or clavate, with eight biseriate or irregularly arranged ascospores, spore-bearing part 30.5–50.5 × 15–24 μm, stalks 14–30.5 μm long, evanescent. Ascospores dark brown when

Fig. 19 Chaetomium interruptum (CBS 126000, ex-type culture). a. Part of the colony on OA; b. ascomata on OA, top view; c. ascoma on OA, side view; d. ascoma mounted in lactic acid; e. basal parts of terminal ascomatal hairs; f. upper parts of terminal ascomatal hairs; g. structure of ascomatal wall in surface view; h. asci; i. ascospores. — Scale bars: d = 100 μm; e, f, h = 20 μm; g, i = 10 μm.
Cultures sterile. Chaetomium novozeelandicum forms a unique lineage (Group IIc, Fig. 1), basal to the C. globosum clade. This species differs by fixed unique SNPs in five loci: rpb2 positions 3(C), 9(C), 12(C), 24(A), 39(C), 51(A), 60(T), 68(T), 99(C), 124(T), 138(A), 177(G), 186(C), 220(A), 300(C), 306(A), 312(A), 372(G), 376(T), 393(T), 420(C), 450(A), 525(T), 570(T), 573(C), 579(G), 582(G) and 597(T); tuf2 positions 12(C), 28(G), 97(T), 102(indel), 109(A), 142(indel), 143(indel), 144(indel), 168(C), 235(G), 236(G), 278(C), 319(T), 322(indel), 343(T), 368(A), 375(T), 378(A), 387(C), 447(indel), 459(C), 509(T), 507(G), 579(G), 656(T) and 707(T); teff positions 262(A), 284(T), 396(C), 465(C), 519(T), 683(C), 744(C), 762(T), 816(C) and 870(C); rpb1 positions 44(T), 59(C), 110(indel), 111(indel), 117(G), 163(C), 166(A), 175(G), 211(C), 256(C), 268(C), 272(A), 316(C), 364(T), 418(T), 427(G), 455(A), 457(C), 463(T), 487(C), 523(C), 535(T), 556(T), 580(G), 592(A), 613(C), 676(C), 685(T), 721(G) and 742(C); ITS positions 142(C) and 452(C).

Cultura characteristics — Colonies on OA with white, floccose aerial hyphae, without coloured exudates; reverse uncoloured.

**Materials examined.** NEW ZEALAND, town of Otaki on west coast, isolated from dead unidentified, decaying twig in a compost pile, collection date unknown, D.P. Mahoney (holotype AEB 1071, isotype CBS H-22191; same collection details, CBS 124555). — USA, California, isolated from scalp of Homo sapiens, deposited in CBS by D.A. Sutton, 29 Sept. 2010, CBS 128484 = UTHSC 09-1518 = dH 21631.

Notes — Both phylogenetic inference and SNP analysis indicate that C. novozeelandicum represents a novel phylogenetic species basal to Group II (Group IIC, Fig. 1). All attempts to induce sporulation on OA failed, even with the addition of sterile elm twig pieces.


Ascomata superficial or covered by aerial hyphae, ostiolate, umbor or olivaceous to dark brick in reflected light owing to ascomatal hairs, subglobose to obovate, 280–520 μm high, 230–405 μm diam. Ascomatal wall brown, composed of amorphous cells, textura epidermoidea in surface view. Terminal hairs abundant, smooth, olivaceous brown, paler at the apexes, hypha-like, flexuous, often branched, sometimes geniculate, 3–4.5 μm diam near the base. Lateral hairs similar. Asci fasciculate, fusiform or elongate clavate, with eight biseriate or irregularly-arranged ascospores, occasionally with eight ascospores uniseriately arranged in a nearly cylindrical ascus, spore-bearing part 53–93 x 13–24 μm, stalks 15–36 μm long, evanescent. Ascospores olivaceous brown when mature, irregularly limoniform to fusiform or ovate, bilaterally flattened, (12.5–)15–22(–26) x (11–)11.5–15(–17) x (9–)10–11.5(–12.5) μm, usually with two or three or occasionally four apical, subapical or lateral germ pores. Asexual morph absent.

Cultura characteristics — Colonies on OA with abundant floccose, white to pale grey aerial hyphae, usually without exudates diffusing into medium; reverse uncoloured.


Notes — Chaetomium nozdrenkoae forms a unique lineage in Group IA (Fig. 1), sister to a clade including three species: C. grande, C. megalocarpum and C. globosporum. However, the latter species are distinguished from C. nozdrenkoae by having more regular, mostly globose to subglobose ascospores. All these taxa differ in their ascospores dimensions.

**Chaetomium megalocarpum** X. Wei Wang, Crous & L. Lombard, *sp. nov.* — MycoBank MB812980

_Etymology._ Refers to the country New Zealand, where this fungus was first collected.

_mature, ellipsoid to subglobose, usually irregular, bilaterally flattened, (12–)13–15(–17) x (10–)11.5–14 x (7.5–)8.5–10(–10.5) μm, with two apical, subapical or lateral germ pores. Asexual morph absent._

_Culture characteristics — Colonies on OA lacking aerial hyphae, producing pale orange exudates diffusing into the medium; reverse fuscous to black under ascomata._

_Materials examined._ CHINA, Yinchuan Province, Ningxia City, isolated from horse dung, other collection information unknown, culture CGMCC 3.3595; Shanhaiguan, isolated from soil, other collection information unknown, culture CGMCC 3.9443. — FRANCE, lectotype of _C. megalocarpum_, designated here (MBT201727; Bull. Soc. Mycol. France 25: PL XVI, f. 1–4, 1910, drawn by G. Bainier based on the ex-type strain isolated from rotten paper, reproduced here as Fig. 20 after excluding the illustration of _C. indicum_ (f. 5–14)). — GREECE, near the border to Yugoslavia, isolated from leaf of _Ficus carica_, collector and collection date unknown, isolated by G. Sörgel, 22 Nov. 1958 (epitotype designated here CBS H-22186, MBT201728, culture ex-epitope CBS 149.59 = IMI 075851 = MUCL 9589). — INDIA, Yusrarg, Drug Tolan, isolated from humus-rich soil, collection date unknown, E. Müller, CBS 778.71 = ETH 1924.

_Notes — Chaetomium megalocarpum_ is differentiated from the closest species, _C. grande_, by possessing smaller ascospores (13–15 x 11.5–14 x 8.5–10 μm vs 18–20.5 x 16–18 x 12–13.5 μm). Phylogenetic inference showed that _C. megalocarpum_ and _C. grande_ form sister lineages in Group IA (Fig. 1), and are closely related to _C. globosporum_ which produces the smallest, globose ascospores (10.5–12 μm diam, 7.5–8.5 μm wide in lateral view)._
**Chaetomium olivaceum** Cooke & Ellis, Grevillea 6: 96. 1878.

— Fig. 24

Ascomata superficial, ostiolate, pale olivaceous buff in reflected light owing to ascomatal hairs, subglobose to obovate, 260–440 μm high, 200–360 μm diam. Ascomatal wall brown, composed of hypha-like or amorphous cells, textura intricata or textura epidermoidea in surface view. Terminal hairs abundant, finely verrucose, brown, paler towards the apices, undulate or flexuous, occasionally branched, 2.5–4.5 μm near the base, tapering towards the tips. Lateral hairs similar. Asci fasciculate, clavate or slightly fusiform, with eight biseriate ascospores, spore-bearing part 34–41 × 13–20 μm, stalks 26–45 μm long, evanescent. Ascospores olivaceous brown when mature, limoniform to broad limoniform, usually biapiculate, bilaterally flattened, (10–)11–12(–12.5) × 8–9 × 6–7 μm, with an apical germ pore. Asexual morph absent.

Culture characteristics — Colonies on OA with sparse white aerial hyphae, producing pale fawn exudates diffusing into the medium; reverse olivaceous, but black under ascomata.


Notes — *Chaetomium olivaceum* was reduced to synonymy under *C. globosum* by Von Arx et al. (1986). This species can be distinguished by larger ascospores (11–12 × 9–10 × 6–7 μm) than those of *C. globosum* (8.5–10.5 × 7–8 × 5.5–6.5 μm). Phylogenetic inference indicated that *C. olivaceum* is in Group III (Fig. 1), closely related to *C. cucumericola* (sterile species), *C. undulatum* and *C. subglobosum*. *Chaetomium undulatum* (Asgari & Zare 2011) can be distinguished from *C. olivaceum* by smaller ascomata (230–280 μm high, 185–250 μm diam),
longer ascospores (12–13.5 × 8–10 × 6–7.5 μm) and more undulate ascomatal hairs. Chaetomium subglobosum is also distinct from C. olivaceum in having larger ascospores (12–13.5 × 10.5–12 × 7–8.5 μm). The holotype of C. olivaceum was originally collected in Newfield (New Jersey, USA). No ex-type culture or isolate from the type locality is presently available. Therefore, typification of this species awaits recollection from the type locality.

Chaetomium pilosum (C. Booth & Shipton) X. Wei Wang & Crous, comb. nov. — MycoBank MB812981; Fig. 25


Ascomata superficial, or covered by aerial hyphae, non-ostiolate, black in reflected light due to the dark ascomatal wall,
spherical or oblate, pilose, 120–265 μm diam. **Ascomatal wall** brown, composed of angular cells, **textura angularis** in surface view. **Ascomatal hairs** covering the whole ascoma, hypha-like, smooth or finely verrucose, pale ochreous at the base, fading to hyaline in the upper part, 2.5–4 μm near the base, less than 120 μm long. **Asci** fasciculate, clavate to obovate, with eight biseriate or irregularly arranged ascospores, spore-bearing part 22–38 × 12.5–18 μm, stalks 10–24 μm long, evanescent. **Asco- spores** olivaceous brown to brown when mature, limoniform, umbonate at both ends, bilaterally flattened, (11–)12–14.5(–16) × 9–10(–11) × (6–)7–8 μm, with an apical germ pore. **Asexual morph** absent.

**Culture characteristics** — Colonies on OA with white to pale grey aerial hyphae, usually producing apricot to orange exudates diffusing into the medium; reverse ochreous to apricot.

**Material examined**. AUSTRALIA, Western Australia, Perth, isolated from grain of *Triticum aestivum*, collector and collection date unknown, isolated by W.A. Shipton, 1965 (isotype of *Thielavia pilosa* CBS H-6838, culture ex-isotype of *Thielavia pilosa* CBS 335.67 = IMI 113231 = VKM F-1851).

Notes — Only the ex-isotype strain is available for this species. *Chaetomium pilosum* forms a unique lineage basal to Group III, distant from two other species in the *C. globosum* complex, which have non-ostiolate ascomata, *C. fimeti* and *C. subfimeti* (Group I, Fig. 1). This species is easily distinguished by its non-ostiolate ascomata covered with hyaline hairs and distinctly umbonate ascospores.

**Chaetomium pseudocochliodes** X. Wei Wang, X.Z. Liu & Crous, sp. nov. — MycoBank MB812982; Fig. 26

**Etymology**. Refers to the morphological similarity to *C. cochliodes.*
Ascomata superficial, ostiolate, citrine green to citrine in reflected light owing to ascomatal hairs, ellipsoid, ovate or subglobose, 270–425 μm high, 190–370 μm diam. Ascomatal wall brown, composed of hypha-like cells, textura intricata in surface view. Terminal hairs brown, tapering, partly type I: dark, verrucose, thick and erect in the lower part, 4–6 μm near the base, tapering and fading towards the tips, circinate (often on young ascomata) or spirally coiled in the upper part, with coils often tapering or in irregular form, sometimes with a short flexuous hypha-like extension at the tip, occasionally branched; partly type II: pale brown, finely verrucose, thinner, 3–4 μm near the base, flexuous. Lateral hairs hypha-like, flexuous, tapering towards tips. Asci fasciculate, elongated clavate, spore-bearing part 24–37 × 7–14 μm, stalks 17–42 μm long, with eight biseriate ascospores, evanescent. Ascospores olivaceous brown or brown when mature, limoniform, biapiculate, slightly umbo-nate at both ends, bilaterally flattened, (9–)9.5–11(–11.5) × (7–)7.5–8.5(–9) × 5.5–6.5(–7) μm, with an apical germ pore. Asexual morph absent.

Culture characteristics — Colonies on OA with sparse white aerial hyphae or in the centre of colonies with thick, felt-like hyphae, producing luteous to rust exudates diffusing into the medium; reverse fulvous to sienna, black under ascomata.


Fig. 24 Chaetomium olivaceum (CBS 418.80A). a. Part of the colony on OA; b. ascomata on OA, top view; c. ascomata on OA, side view; d, e. ascomata mounted in lactic acid; f. structure of ascomatal wall in surface view; g. basal parts of terminal ascomatal hairs; h, i. upper parts of terminal ascomatal hairs; j. asci; k. ascospores. — Scale bars: d, e = 100 μm; f–k = 10 μm.
Notes — Phylogenetic inference indicated that *C. pseudo-cochliodes* belongs to Group III, closely related to *C. cochliodes* and *C. spiculipilium* (Fig. 1), which is further confirmed by morphological characters. All three species produce regularly coiled ascomatal hairs and ascospores with similar dimensions. This species can be distinguished from *C. cochliodes* and *C. spiculipilium* by its more irregular and diverse ascomatal hairs as well as ascospores that usually have more protruding ends.

**Chaetomium pseudoglobosum** X. Wei Wang, Crous & L. Lombard, *sp. nov.* — MycoBank MB812983; Fig. 27

*Etymology.* Refers to the striking resemblance to *C. globosum.*

Ascomata superficial or covered by sparse aerial hairs, ostiolate, olivaceous buff to greenish olivaceous in reflected light owing to ascomatal hairs, ovate to subglobose, 210–330 μm high, 165–315 μm diam. **Ascomatal wall** brown, composed of hypha-like cells, *textura intricata* in surface view. **Terminal hairs** abundant, forming a dense and nearly globose head over the ostiole, verrucose, olivaceous brown, fading towards the tips, loosely coiled, erect or flexuous at the lower part, 2.5–3.5 μm near the base, tapering towards the tips. **Lateral hairs** hypha-like, flexuous or slightly undulate, tapering and fading towards the tips. **Asci** fasciculate, clavate or fusiform, spore-bearing part 23–32 × 10–14 μm, stalks 17–36 μm long, with eight biseriate ascospores, evanescent. **Ascospores** olivaceous brown when mature, limoniform, bilaterally flattened, 9–10(–10.5) × (6–)6.5–7.5(–8) × 5–6(–6.5) μm, with an apical germ pore. **Asexual morph** absent.

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Fig. 25 *Chaetomium pilosum* (CBS 335.62, ex-epitype culture). a. Part of the colony on OA; b. ascomata covered by hyphae on OA, top view; c. exposed ascomata on OA, top view; d, e. ascomata mounted in lactic acid; f. ascomatal hairs; g. structure of ascomatal wall in surface view; h. asci; i. ascospores. — Scale bars: d, e = 100 μm; f–i = 10 μm.
Culture characteristics — Colonies on OA with sparse white aerial hypha, producing pale apricot to pale orange exudates diffusing into the medium; reverse usually uncoloured, but fulvous to umber under ascoma.


Notes — Phylogenetic inference in this study showed that Chaetomium pseudoglobosum is in Group II, closely related to C. tenue (Group IIB, Fig 1). The latter species produces smaller ascospores (9–10 × 6.5–7.5 × 5–6 μm vs 8.5–9.5 × 6–7 × 5–5.5 μm) and less dense ascomatal hair structures. Chaetomium pseudoglobosum forms dense ascomatal hair structures covering the ascomatal ostioles, which resemble those of C. afropilosum. However, C. afropilosum produces smaller ascospores (7–8 × 5.5–6 × 4–5 μm).

Chaetomium rectangulare Asgari & Zare, Mycologia 103: 872. 2011. — Fig. 28
Ascomata superficial, ostiolate, firmly attached to the medium by well-developed rhizoids, olivaceous grey in reflected light owing to ascomatal hairs, globose to subglobose, 300–450 μm high, 215–380 μm diam. Ascomatal wall brown, composed of hypha-like or amorphous cells, textura intricata or textura epidermoidea in surface view. Terminal hairs verrucose, dark brown, erect in the lower part, 4.5–7 μm diam near the base,
regularly and dichotomously branched at right to nearly straight angles in the upper part, with relatively erect and rigid spear-shaped branches, fading and tapering towards the tips. Lateral hairs brown, seta-like or sometimes terminally branched, tapering and fading towards the tips. Asci fasciculate, clavate, spore-bearing part 26–43 × 11–16 μm, stalks 23–37 μm long, with eight biseriate ascospores, evanescent. Ascospores olivaceous brown when mature, limoniform, biapiculate, bilaterally flattened, (9–)10–11(–12) × 7–9 × 6–7.5(–8) μm, with an apical germ pore. Asexual morph acremonium-like. Conidiophores formed laterally from aerial hyphae, simple, 13–29 μm long, 2–4.5 μm diam at the base. Conidia formed in chains, hyaline, aseptate, smooth, ovate or ellipsoidal, often with a truncated base and a rounded apex, (3–)3.5–5(–6) × 2–3 μm.

Culture characteristics — Colonies on OA without aerial hyphae, producing pale luteous to orange exudates diffusing into the medium; reverse cinnamon, but black under ascomata.


Notes — The ex-type culture (CBS 126778) of *C. rectangulare* is sterile, and therefore the description here is based on CBS 126658. *Chaetomium rectangulare* is morphologically and phylogenetically close to *C. elatum* (Group III, Fig. 1). They are both morphologically distinguished in the *C. globosum* species complex by having dichotomously branched ascomatal hairs. Asgari & Zare (2011) compared both species, and distinguished *C. elatum* from *C. rectangulare* by having flexuous, irregularly branched and narrower ascomatal hairs, wider asci and larger ascospores. Our observations confirmed that *C. rectangulare* produces smaller asci and ascospores than those of *C. elatum*. However, the ascomatal hairs of both species branch at right to nearly straight angles in the upper part. *Chaetomium rectangulare* can also be distinguished from *C. elatum* by thicker, darker and rigid terminal ascomatal hairs, and well-developed rhizoids.
Fig. 28 Chaetomium rectangulare (CBS 126658). a. Part of the colony on OA; b. ascoma on OA, top view; c. ascoma on OA, side view; d–f. ascomata mounted in lactic acid; g. basal parts of terminal ascomatal hairs; h, i. upper parts of terminal ascomatal hairs; j. structure of ascomatal wall in surface view; k. asci; l. ascospores; m. asexual morph (conidiophore and conidia). — Scale bars: d–f = 100 μm; g–i = 20 μm; j–m = 10 μm.
**Chaetomium spiculipilium** Ames, A Monograph of the Chaetomiaceae: 37. 1963. — Fig. 29

Ascomata superficial, ostiolate, citrine-green to greenish olivaceous in reflected light owing to ascomatal hairs, ellipsoid, ovate or subglobose, 370–480 μm high, 300–385 μm diam. Ascomatal wall brown, composed of amorphous or hypha-like cells, textura epidermoidea or textura intricata in surface view. Terminal hairs verrucose, dark brown, rigid, erect in the lower part, 5–8 μm diam near the base, tapering and fading towards the tips, coiled in the upper part; coils regular, sometimes slightly tapering, with a conspicuous, rigid seta-like extension at the tip, often with coiled or seta-like branches. Lateral hairs hypha-like, flexuous, fading and tapering towards the tips. Asci fasciculate, clavate, spore-bearing part 21–42 × 13–16.5 μm, stalks 27–43 μm long, with eight biseriate ascospores, evanescent. Ascospores olivaceous brown when mature, limoniform, usually biapiculate, occasionally umbonate at one or both ends, bilaterally flattened, (9–)10–13 (–15) × (7–)7.5–9 (–10) × 5.5–6.5 (–7) μm, with an apical germ pore. Asexual morph absent.

Culture characteristics — Colonies on OA with thick, white aerial hyphae only in the centre, producing luteous to orange or brick to vinaceous exudates diffusing into the medium; reverse fulvous to sienna.

Material examined. USA, California, Aptos, from decaying vegetable debris, collection date unknown, H.K. Seth, isolated by L.M. Ames (isotype CBS H-6893, culture ex-isotype CBS 373.66).

Notes — *Chaetomium spiculipilium* is closely related to *C. cochliodes*, *C. pseudocochliodes* and *C. spirochaete* by having regularly coiled ascomatal hairs. Phylogenetic inference also showed that *C. spiculipilium*, belonging to Group III, is closely related to *C. cochliodes* and *C. pseudocochliodes* (Fig. 1). *Chaetomium spiculipilium* can be distinguished by having thicker and more rigid ascomatal hairs (5–8 μm diam near the base) with a conspicuous seta-like extension at the tip, compared to those of *C. cochliodes* (3.5–6 μm near the base), *C. pseudocochliodes* (4–6 μm near the base for regularly coiled hairs) and *C. spirochaete* (3–4.5 μm near the base). The ascospores of *C. spiculipilium* (10–13 × 7.5–9 × 5.5–6.5 μm) are also slightly larger than those of *C. cochliodes* (9–10 × 7.5–8.5 × 5–6 μm) and *C. pseudocochliodes* (9.5–11 × 7.5–8.5 × 5.5–6.5 μm).
Chaetomium spirochaete Palliser, N. Amer. Fl. 3: 61. 1910. —

Ascomata superficial, ostiolate, honey to pale hazel in reflected light owing to ascomatal hairs, ellipsoid, ovate or elongate ovate, 135–230 μm high, 118–205 μm diam. Ascomatal wall brown, composed of amorphous or hypha-like cells, textura epi-dermoidea or textura intricata in surface view. Terminal hairs verrucose, brown, 3–4.5 μm near the base, equally diamerced from the base to the tip, erect in the lower part, coiled in the upper part with coils equal in diameter, sometimes with coiled branches. Lateral hairs pale brown, flexuous, tapering towards the tips. Asci fasciculate, clavate, spore-bearing part 26–43.5 × 13.5–16 μm, stalks 18–32 μm long, with eight biseriate ascospores, evanescent. Ascospores olivaceous brown when mature, limoniform, bilaterally flattened, sometimes inequilateral,
(9–)10–11(–12) × 7.5–9(–9.5) × (5.5–)6–7 μm, with an apical germ pore. Asexual morph absent.

Culture characteristics — Colonies on OA with sparse white aerial hyphae and producing yellowish ochreous exudates diffusing into the medium; reverse uncoloured, but dark olivaceous under ascomata.

Materials examined. **Unknown**, collection details unknown, from animal dung, isolated and deposited in CBS by L.M. Ames, Apr. 1952, CBS 165.52. — USA, Iowa, from cotton root, June 1890, L.H. Pammet (holotype New York Botanical Garden Specimen ID01050443), Tennessee, Great Smokey Mountains, unknown collection details, isolated by York Botanical Garden Specimen ID01050443); Tennessee, Great Smokey Mountains, unknown collection details, isolated by York Botanical Garden Specimen ID01050443). — Note: — **Notes** — The epitype of *C. spirochaete*, designated here, is morphologically similar to the holotype, particularly in morphology of ascospores and ascomatal hairs, and originates from the same locality as the type. *Chaetomium spirochaete* was synonymised under *C. spirale* in 1961 (Chivers 1915, Ames 1963) and followed this treatment and rejected the species *C. spirale* because the type had been lost and the species could not be recognised from the original description. *Chaetomium spirochaete* was considered a relative of *C. globosum* and differed from *C. globosum* in having regularly coiled, relatively dark and thick (5–6 μm) ascomatal hairs (Von Arx et al. 1986). Our observations, however, showed that the ascomatal hairs of *C. spirochaete* (3–4.5 μm near the base) are not thinner than those of *C. globosum* s.str. (3–5 μm diam near the base). *Chaetomium spirochaete* can be distinguished from *C. globosum* by regularly coiled ascomatal hairs, and slightly larger ascospores. In addition, the phylogenetic inference places *C. spirochaete* in Group IIA, distant from *Chaetomium cochliodes* and differed by the uniform diameter in both the ascomatal hairs themselves and the coils formed by the ascomatal hairs. Furthermore, the ascomatal hairs (3–4.5 μm near the base) of *C. spirochaete* are thinner than those of *C. cochliodes* (3.5–6 μm near the base), *C. pseudocochliodes* (4–6 μm near the base for regularly coiled hairs) and *C. spiculipilium* (5–8 μm diam near the base).

**Notes** — Von Arx et al. (1986) maintained *C. subaffine* as a separate species as the ascospores (11–15 × 8–11 × 7–8.5 μm) are larger than those of *C. globosum* (9–12 × 8–10 × 6–8 μm), and suggested that this species is related to *C. elaum*. Phylogenetic inference indicates that *C. subaffine* is closely related to *C. cochliodes*, *C. pseudocochliodes* and *C. spiculipilium* (Group III, Fig. 1). However, *C. subaffine* can be distinguished by having abundant white mycelia covering the ascomata, mostly straight to flexuous ascomatal hairs, and having an asexual morph. The ascospores of *C. subaffine* are also larger than those of *C. cochliodes* (9–10 × 7.5–8.5 × 5–6 μm), *C. pseudocochliodes* (9.5–11 × 7.5–8.5 × 5.5–6.5 μm) and *C. spiculipilium* (10–13 × 7.5–9 × 5.5–6.5 μm).

**Chaetomium subfimeti** (Seth) X. Wei Wang & Crous, comb. nov. — MycoBank MB812984; Fig. 32


Ascomata superficial or covered by thick aerial hyphae, non-ostiolate, fawn to black with numerous short, pale citrine ascomatal hairs, and sparse, long and black hairs in reflected light, spherical or oblate, 170–360 μm diam. Ascomatal wall brown, composed of thick-walled, angular or irregular cells, textura angularis in surface view. Ascomatal hairs of two types: shorter type covering the whole ascomata, less than 500 μm long, hypha-like, verrucose, dark brown at the lower part, fading to pale luteous-coloured at the apex, 2–3.5 μm near the base; longer type arising from the base of the ascomata, 200–3500 μm long, smooth, erect, flexuous or slightly undulate, dark brown, 3.5–5.5 μm near the base. Ascii fusiform, clavate or slightly fusiform, with eight biseriate ascospores, spore-bearing part 15–31.5 × 7.5–14 μm, stalks 7–18 μm long, evanescent. Ascospores olivaceous brown to brown when mature, limoniform, bilaterally flattened, (8–)8.5–9.5(–10) × (6.5–)7–7.5(–8) × 5.5–6(–6.5) μm, with an apical germ pore. Asexual morph absent.

Culture characteristics — Colonies on OA usually with thick, floccose to felt-like, white or pale honey aerial mycelia, sometimes covering the ascomata, producing yellowish ochreous exudates diffusing into the medium; reverse cinnamon to fulvous.

Materials examined. UK, Wales, Cardiff, isolated from paper and vegetable material, collection date unknown, isolated by H.K. Seth, 25 Dec. 1963 (isotype of *Chaetomium subfimeti* CBS H-6839, culture ex-isotype of *Chaetomium subfimeti* CBS 370.66 = ATCC 18209 = IMI 116692 = LCP 82.3317). — USA, California, Kern County, isolated from soil, collector and collection date unknown, isolated by G.F. Orr, CBS 169.71 = ATCC 22277 = IMI 153721.

Notes — *Chaetomium subfimeti* formed a sister lineage to *C. fimeti* (Group IC, Fig 1) as was supported by our morphological observations. *Chaetomium subfimeti* can be distinguished by producing smaller ascomata (170–360 μm diam vs 320–500 μm diam) and ascospores (8.5–9 × 7–7.5 × 5.5–6 μm vs 11.5–13.5 × 9–10.5 × 7–8 μm) than those of *C. fimeti*.

Ascomata superficial or covered by aerial hyphae, ostiolate, greenish olivaceous or grey-olivaceous in reflected light owing to ascomatal hairs, subglobose to oblong, 300–450 μm high, 265–355 μm diam, firmly attached to the medium by well-developed and densely-combined rhizoids forming compact structures at the base. Ascomatal wall brown, composed of hypha-like or amorphous cells, textura intricata or textura epidermoidea in surface view. Terminal hairs abundant, finely

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Fig. 31  *Chaetomium subaffine* (CBS 637.91, ex-type culture). a. Part of the colony on OA; b. ascomata entangled by hyphae on OA, top view; c, d. ascomata and masses of ascospores on OA, side view; e, f. ascomata mounted in lactic acid; g. basal parts of terminal ascomatal hairs; h. upper part of a terminal ascomatal hair; i. structure of ascomatal wall in surface view; j. asci; k. ascospores; l. asexual morph (conidiophore and conidia). — Scale bars: e, f = 100 μm; g–l = 10 μm.
punctate to verrucose, brown, fading towards the tips, flexu-ous, sometimes branched, 3–5.5 μm near the base, tapering towards the tips. Lateral hairs similar. Asci fasciculate, clavate or slightly fusiform, with eight biseriate or irregularly-arranged ascospores, spore-bearing part 32.5–45 × 13.5–18 μm, stalks 25.5–36.5 μm long, evanescent. Ascospores olivaceous brown when mature, limoniform to broad limoniform, usually biapi-culate, bilaterally flattened, (11–)12–13.5(–14) × (10–)10.5–12(–13.5) × 7–8.5(–9) μm, with an apical germ pore. Asexual morph absent.

Culture characteristics — Colonies on OA with abundant white aerial hyphae, without coloured exudates; reverse un-coloured.


Notes — The description provided here is based on the isolate CBS 483.73 since the ex-type culture (CBS 149.60) is sterile. Von Arx et al. (1986) reduced C. subglobosum to synonymy under C. globosum. However, we consider C. sub-globosum as a separate species based on morphological and molecular evidence. Chaetomium subglobosum can be distin-guished from C. globosum s.str. by producing larger ascomata (300–450 × 265–355 μm vs 160–300 × 135–250 μm) and ascospores (12–13.5 × 10.5–12 × 7–8.5 μm vs 8.5–10.5 × 7–8 × 5.5–6.5 μm). The phylogenetic inference also showed that C. subglobosum is placed in Group III (Fig. 1), distant from C. globosum s.str. (Group IIA, Fig. 1).
Chaetomium telluricola X. Wei Wang, Crous & L. Lombard, sp. nov. — MycoBank MB812985; Fig. 34

Etymology. Refers to soil, the substrate from which this fungus was isolated.

Ascomata superficial, ostiolate, amber to citrine in reflected light owing to ascomatal hairs, globose or ovate, 140–350 μm high, 140–300 μm diam. Ascomatal wall brown, composed of angular or amorphous cells, arranged in a petal form around the bases of hairs, textura angularis or textura epidermoidea in surface view. Terminal hairs relatively sparse, verrucose, olivaceous brown, fading towards the tips, slightly tapering, erect or flexuous at the lower part, undulate at the upper part, 3–5 μm near the base. Lateral hairs hypha-like, erect or flexuous, tapering towards the tips. Asci fasciculate, clavate or slightly fusiform, spore-bearing part 24–38 × 11.5–16.5 μm, stalks 21–37 μm long, with eight biseriate ascospores, evanescent. Ascospores olivaceous brown when mature, elongate limoniform to broadly fusiform, or slightly irregular, bilaterally flattened, (9–)10–13(–15) × (6–)7.5–8(–8.5) × 5–6 μm, with an apical germ pore. Asexual morph absent.

Fig. 33 Chaetomium subglobosum (CBS 483.73). a. Part of the colony on OA; b. ascomata on OA, top view; c. ascoma on OA, side view; d. ascoma mounted in lactic acid; e. basal parts of terminal ascomatal hairs; f. upper part of a terminal ascomatal hair; g. branched middle parts of terminal ascomatal hairs; h. structure of ascomatal wall in surface view; i. asci; j. ascospores. — Scale bars: d = 100 μm; e–h, j = 10 μm; i = 20 μm.
Culture characteristics — Colonies on OA usually without aerial hyphae and coloured exudates; reverse uncoloured, but greenish olivaceous under ascomata.


Notes — Chaetomium telluricola is morphologically distinct in the C. globosum species complex having elongate limoniform to broadly fusiform ascospores. Phylogenetic inference showed that C. telluricola is closely related to C. capillare in Group III (Fig. 1).

Chaetomium tenue X. Wei Wang, Crous & L. Lombard, sp. nov. — MycoBank MB812986; Fig. 35

Etymology. Refers to the relatively narrow ascospores formed by this fungus.
Ascomata superficial or covered by sparse aerial hyphae, ostiolate, olivaceous buff or greenish olivaceous, to pale amber or citrine-green in reflected light owing to ascomatal hairs, globose to subglobose, 165–330 μm high, 150–300 μm diam. Ascomatal wall dark brown, composed of hypha-like cells, textura intricata in surface view. Terminal hairs verrucose, olivaceous brown, fading towards the tips, undulate with erect or flexuous lower part, 3–4.5 μm diam near the base, tapering towards the tips. Lateral hairs flexuous or similar. Asci fasciculate, clavate or slightly fusiform, spore-bearing part 23–33 × 10–14 μm, stalks 16–36 μm long, with eight biseriate ascospores, evanescent. Ascospores brown when mature, elongate limoniform to broadly fusiform, biapiculate, bilaterally flattened, (7.5–)8.5–9.5 × 6–7 × 4.5–5.5 μm, with an apical germ pore. Asexual morph absent.

Culture characteristics — Colonies on OA with sparse to thick white aerial hyphae, usually without coloured exudates; reverse uncoloured.

Materials examined. **UNKNOWN**, no collection information, deposited in CBS by A.L. McAulay, Aug. 1938 (holotype CBS H-22195, culture ex-type CBS 139.38); other cultures with identical information, CBS 138.38, CBS 140.38, CBS 142.38, CBS 143.38.

Notes — Phylogenetic inference in this study showed that *C. tenue* is closely related to *C. pseudoglobosum* (Group IIB, Fig. 1). However, it is differentiated by having less dense, undulate ascomatal hairs and elongate limoniform to broadly fusiform ascospores, slightly narrower (8.5–9.5 × 6–7 × 5–5.5 μm) than those of *C. pseudoglobosum* (9–10 × 6.5–7.5 × 5–6 μm).
**Chaetomium umbonatum** D. Brewer, Proc. Trans. Nova Scotium Inst. Soc. 27: 59. 1974. — Fig. 36

Ascomata superficial or covered by aerial hyphae, ostiolate, sulphur-yellow to ochreous in reflected light owing to ascomatal hairs, globose or slightly ovate, 260–360 μm high, 210–320 μm diam. Ascomatal wall brown, composed of hypha-like or amorphous cells, textura intricata or textura epidermoidea. Terminal hairs hypha-like or undulate with flexuous lower part, smooth, flexible, fulvous to pale brown at the bases, fading towards the tips, 1.5–3 μm near the base, slightly tapering towards the rounded tips. Lateral hairs similar. Asci fasciculate, clavate or slightly fusiform, with eight biseriate or irregularly-arranged ascospores, spore-bearing part 22–27 × 8–12.5 μm, stalks 13–18 μm long, evanescent. Ascospores olivaceous brown when mature, elongate limoniform, biconical, prominently umbonate at both ends, bilaterally flattened, (7.5–)8–11(–12) × (5–)5.5–7(–7.5) × (3.5–)4–5(–5.5) μm, with an apical germ pore. Asexual morph absent.

Culture characteristics — Colonies on OA with white to pale grey aerial hyphae, usually not producing coloured exudates; reverse uncoloured.

Material examined. **Canada**, Nova Scotia, isolated from soil, collection date unknown, D. Brewer (isotype CBS H-6904, culture ex-isotype CBS 293.83 = ATCC 26766 = IMI 138895).

Notes — *Chaetomium umbonatum* is easily recognised by its ascospores. Von Arx et al. (1986) suggested that this
species is related to *C. globosum*, which is confirmed by the phylogenetic inference in this study. *Chaetomium umbonatum* is closely related to *C. afropilosum* in Group II (Fig. 1), which has smaller (7–8 × 5.5–6 × 4–5 μm) and biapiculate ascospores. *Chaetomium umbonatum* resembles *C. pilosum* in ascospore shape and pale ascomatal hairs, but the latter is characterised by non-ostiolate ascomata and larger ascospores (12–14.5 × 9–10 × 7–8 μm). *Chaetomium pilosum* is also phylogenetically distant from *C. umbonatum* (basal in Group III, Fig. 1).

**Chaetomium undulatulum** Asgari & Zare, *Mycologia* 103: 870. 2011

Description & Illustration — See Asgari & Zare (2011).

Materials examined. IRAN, East Azerbaijan Province, Bonab, isolated from leaf of *Hordeum vulgare*, 22 May 2005, B. Asgari (holotype IRAN 14605 F, culture ex-type CBS 126775 = IRAN 857C); West Azerbaijan Province, Miandoab, isolated from leaf of *Triticum aestivum*, 23 June 2005, B. Asgari, CBS 126776 = IRAN 1071C.

Notes — The isolates of *C. undulatulum* deposited in CBS are sterile. Phylogenetic inference in the present study indicated that *C. undulatulum* is closely related to *C. subglobosum* (Group III, Fig. 1). *Chaetomium undulatulum* can be distinguished from *C. subglobosum* by smaller ascomata (230–280 × 185–250 μm vs 300–450 × 265–355 μm) and narrower ascospores (12–13.5 × 8–10 × 6–7.5 μm vs 12–13.5 × 10.5–12 × 7–8.5 μm).

**Chaetomium unguicola** X. Wei Wang, Crous & L. Lombard, *sp. nov.* — MycoBank MB812987; Fig. 37

Etymology. Refers to a nail of *Homo sapiens*, the substrate from which this fungus was isolated.

Ascomata superficial or sometimes covered by sparse aerial hyphae, ostiolate, amber to citrine-green in reflected light owing
to ascomatal hairs, ovate or obovate to subglobose, 170–280 μm high, 150–260 μm diam. Ascomatal wall brown, composed of amorphous or hypha-like cells, texture epidermoidea or texture intricata in surface view. Terminal hairs finely verrucose, dark olive-vaceous, fading towards the tips, undulate to loosely coiled with erect or flexuous lower part, 3–4.5 μm near the base, tapering towards the tips. Lateral hairs flexuous to undulate, tapering towards the tips. Asci fasciculate, fusiform or clavate, with eight biseriate or irregularly arranged ascospores, spore-bearing part 15.5–24.5 × 10–14.5 μm, stalks 11–24 μm long, evanescent. Ascospores olive brown when mature, limoniform, bilaterally flattened, (7–)7.5–9 × (6–)6.5–7–(7.5) × 4.5–5.5 μm, with an apical germ pore. Asexual morph absent.

Character cultures — Colonies on OA with white aerial hyphae, usually not producing coloured exudates; reverse uncoloured.

Material examined. USA, Los Angeles, isolated from a nail of Homo sapiens, deposited in CBS by D.A. Sutton, 29 Sept. 2010 (holotype CBS 128446 = UTHSC 07-2213 = dH 21624).

Notes — Chaetomium unguicula forms a sister lineage to C. globosum (Group IIA, Fig. 1). This species is also morphologically close to C. globosum in ascomata and ascomatal hair morphology. However, C. unguicula can be distinguished by its smaller ascospores (7.5–9 × 6.5–7 × 4.5–5.5 μm vs. 8.5–10.5 × 7–8 × 5.5–6.5 μm).

**KEY TO SPECIES OF THE CHAETOMIUM GLOBOSUM COMPLEX**

<table>
<thead>
<tr>
<th>1. Parts of ascospores with more than one germ pore</th>
<th>2. Ascospores with only one germ pore</th>
<th>6.5–7 μm</th>
<th>6–8 μm</th>
</tr>
</thead>
<tbody>
<tr>
<td>2. Ascospores irregularly limoniform to fusiform in front view, 12.5–26 × 11–17 × 9–12.5 μm</td>
<td>C. nozdrenkoi</td>
<td>5.5–6.5 μm</td>
<td>6–8 μm</td>
</tr>
<tr>
<td>2. Ascospores globose to subglobose in front view</td>
<td>C. globosum</td>
<td>6–8.5 μm</td>
<td>6–8 μm</td>
</tr>
<tr>
<td>3. Ascospores shorter than 12.5 μm</td>
<td>C. megalocarpum</td>
<td>6–8 μm</td>
<td>C. pseudocochliodes</td>
</tr>
<tr>
<td>3. Ascospores longer than 12 μm, with two or more germ pores</td>
<td>C. interruptum</td>
<td>6–8 μm</td>
<td>C. pseudocochliodes</td>
</tr>
<tr>
<td>5. Ascospores 12–17 × 10–14 × 7.5–10.5 μm</td>
<td>C. citrinum</td>
<td>6–8 μm</td>
<td>C. pseudocochliodes</td>
</tr>
<tr>
<td>5. Ascospores 17–22.5 × 14.5–19 × 11–14 μm</td>
<td>C. grande</td>
<td>6–8 μm</td>
<td>C. pseudocochliodes</td>
</tr>
<tr>
<td>6. Ascospores irregular fusiform, limoniform, ovate, lunate or triangular in front view, 7–12–4 × 4–7 × 5.5–5 μm</td>
<td>C. cilaminum</td>
<td>6–8 μm</td>
<td>C. pseudocochliodes</td>
</tr>
<tr>
<td>6. Ascospores typically limoniform to broad fusiform in front view</td>
<td>C. citrinum</td>
<td>6–8 μm</td>
<td>C. pseudocochliodes</td>
</tr>
<tr>
<td>7. Ascomata non-oostiolate</td>
<td>8. Ascomata ostiolate</td>
<td>6–8 μm</td>
<td>C. pseudocochliodes</td>
</tr>
<tr>
<td>8. Ascomata with only short, hypha-like hairs; ascospores umbonate at both ends, 11–16 × 9–11 × 6–8 μm</td>
<td>C. pifolus</td>
<td>6–8 μm</td>
<td>C. pseudocochliodes</td>
</tr>
<tr>
<td>8. Ascomata with longer and shorter types of hair; ascospores biapiculate</td>
<td>9. Ascomata 320–500 μm diam; ascospores 11–16 × 9–11 × 6–8 μm</td>
<td>C. fimeti</td>
<td>6–8 μm</td>
</tr>
<tr>
<td>9. Ascomata 170–360 μm diam; ascospores 8–10 × 6.5–8 × 5.5–6.5 μm</td>
<td>C. subfimeti</td>
<td>6–8 μm</td>
<td>C. pseudocochliodes</td>
</tr>
<tr>
<td>10. Parts of ascomata with a lateral bulge</td>
<td>11. Ascomata without a lateral bulge</td>
<td>6–8 μm</td>
<td>C. pseudocochliodes</td>
</tr>
<tr>
<td>11. Ascomata 10–11.5 × 8–10 × 7.5–9 μm; terminal ascomatal hairs coiled</td>
<td>C. madrasense</td>
<td>6–8 μm</td>
<td>C. pseudocochliodes</td>
</tr>
<tr>
<td>12. Ascospores 8.5–11 × 8–10 × 6–7.5 μm; terminal ascometal hairs flexuous or irregularly branched</td>
<td>C. ascolirichoides</td>
<td>6–8 μm</td>
<td>C. pseudocochliodes</td>
</tr>
<tr>
<td>12. Terminal ascomatal hairs repeatedly dichotomously branched; usually with accrement-like asexual morphs</td>
<td>13. Terminal ascomatal hairs not repeatedly dichotomously branched</td>
<td>6–8 μm</td>
<td>C. pseudocochliodes</td>
</tr>
<tr>
<td>13. Terminal hairs 4.5–7 μm diam near the base; ascospores 9–12 × 7–9 × 6–8 μm</td>
<td>C. rectangulare</td>
<td>6–8 μm</td>
<td>C. pseudocochliodes</td>
</tr>
<tr>
<td>13. Terminal hairs not more than 4.5 μm diam near the base;</td>
<td>C. elatum</td>
<td>6–8 μm</td>
<td>C. pseudocochliodes</td>
</tr>
<tr>
<td>14. Possessing regularly coiled terminal ascomatal hairs</td>
<td>15. Terminal ascomatal hairs erect, flexuous, undulate to only slightly or loosely coiled</td>
<td>6–8 μm</td>
<td>C. pseudocochliodes</td>
</tr>
<tr>
<td>14. Terminal ascomatal hairs erect</td>
<td>15. With accrement-like asexual morphs; parts of terminal hairs longer, 3–5 μm diam at base, parts of terminal hairs shorter, 3–5 μm diam near the base; ascospores 9–12 × 7.5–9 × 5.5–7 μm</td>
<td>6–8 μm</td>
<td>C. pseudocochliodes</td>
</tr>
<tr>
<td>15. Asexual morph absent</td>
<td>16. Terminal ascomatal hairs nearly isodiametric from base to tip, 3–4.5 μm diam, coiled in the upper part with coils equal in diameter; ascospores 7.5–9.5 × 5.5–7 μm</td>
<td>6–8 μm</td>
<td>C. pseudocochliodes</td>
</tr>
<tr>
<td>16. Terminal ascomatal hairs tapering towards the tips</td>
<td>17. Terminal ascomatal hairs 5–8 μm diam near the base, with a rigid seta-like extension occurring at the tips of coiled hairs; ascospores 9–15 × 7–10 × 5.5–7 μm</td>
<td>6–8 μm</td>
<td>C. pseudocochliodes</td>
</tr>
<tr>
<td>17. Terminal ascomatal hairs less than 6 μm diam near the base, without a rigid seta-like tip extension; ascospores 8–11.5 × 7–9 × 5–7 μm</td>
<td>6–8 μm</td>
<td>C. pseudocochliodes</td>
<td></td>
</tr>
<tr>
<td>18. Ascospores biapiculate; the hairs terminal 3.5–6 μm near the bases and the coiled upper part appears as an elongate cone with coils tapering in diameter</td>
<td>C. cochliodes</td>
<td>6–8 μm</td>
<td>C. pseudocochliodes</td>
</tr>
<tr>
<td>18. Ascospores usually umbonate; parts of the terminal hairs 4–6 μm near the base, with cincinate or coiled upper part; parts 3–4 μm near the base, flexuous</td>
<td>20. Ascomata broad limoniform to nearly globose</td>
<td>6–8 μm</td>
<td>C. pseudocochliodes</td>
</tr>
<tr>
<td>19. Terminal ascomatal hairs less than 3 μm diam near the base, smooth; ascospores prominently umbonate, 7.5–12 × 5–7.5 × 3.5–5.5 μm</td>
<td>C. umbonatum</td>
<td>6–8 μm</td>
<td>C. pseudocochliodes</td>
</tr>
<tr>
<td>19. Terminal ascomatal hairs more than 3 μm diam near the base, verrucose; ascospores usually biapiculate</td>
<td>20. Ascomata not as above</td>
<td>6–8 μm</td>
<td>C. pseudocochliodes</td>
</tr>
<tr>
<td>20. Ascomata broad limoniform to nearly globose</td>
<td>21. Terminal ascomatal hairs flexuous; rhizoidal structure thriving and dense; ascospores 11–14 × 10–13.5 × 7–9 μm</td>
<td>6–8 μm</td>
<td>C. subtubosum</td>
</tr>
<tr>
<td>21. Terminal ascomatal hairs undulate to slightly coiled; rhizoids sparser; ascospores 9.5–11.5 × 9–10.5 × 6.5–8 μm</td>
<td>C. caaractarum</td>
<td>6–8 μm</td>
<td>C. pseudocochliodes</td>
</tr>
<tr>
<td>22. Terminal hairs forming a dense, nearly globose head covering over the ascomatal ostiole</td>
<td>23. Ascomata 6.5–8 × 5.6–5.5 × 4–5 μm</td>
<td>6–8 μm</td>
<td>C. afropilosum</td>
</tr>
<tr>
<td>22. Terminal hairs not as above</td>
<td>23. Ascomata 9–10.5 × 6–8 × 5–6.5 μm</td>
<td>6–8 μm</td>
<td>C. pseudocochliodes</td>
</tr>
<tr>
<td>24. Ascomata elongate limoniform to broadly fusiform</td>
<td>25. Ascomata typically limoniform</td>
<td>6–8 μm</td>
<td>C. pseudocochliodes</td>
</tr>
<tr>
<td>25. Ascomata 9–15 × 6–8.5 × 5–6 μm</td>
<td>C. telluricola</td>
<td>6–8 μm</td>
<td>C. pseudocochliodes</td>
</tr>
<tr>
<td>26. Ascomata shorter than 11 μm and narrower than 8.5 μm in front view</td>
<td>27. Ascomata up to 12.5 μm or longer and up to 9.5 μm or wider in front view</td>
<td>6–8 μm</td>
<td>C. pseudocochliodes</td>
</tr>
</tbody>
</table>
Ascomata: Wall translucent; ascomatal hairs hypha-like, sparse and hyaline; ascospore mass rust to salmon in reflected light. 

Ch. fimeti, and Ch. subfimeti

Aerial hyphae abundant and often cover ascomata; asexual morph acremonium-like; ascomatal hairs erect to flexuous; ascospores 10.5–14 × 8.5–10.5 × 6–8 μm. C. subaffine

Aerial hyphae sparse or lacking; asexual morph absent. 

Ascomata 12–13.5 × 8–10 × 6–7.5; ascomatal hairs flexuous, undulate to loosely coiled. C. undulatatum

Ascomata shorter than 12.5 μm. 

Terminal hairs relatively sparse, luteous to amber or citrine in reflected light, erect or flexuous; ascospores 9.5–12 × 9–10 × 5.5–7 μm. C. graminiforme

Terminal hairs abundant, slightly pale olivaceous buff in reflected light, undulate or flexuous; ascospores 10–12.5 x 8–9 × 6–7 μm. C. olivaceum

DISCUSSION

The ever-increasing realisation of the importance of C. globosum and its close relatives requires the clarification of their species concepts. The broad species concept of C. globosum sensu Von Arx has resulted in extensive arguments (Seth et al. 1987, Asgari & Zare 2011, Doveri 2013). The inconsistency in species delimitation for C. globosum sensu Von Arx has constantly limited our understanding of its metabolism, function and importance. Based on phylogenetic inference of the ITS, LSU and tub2 gene regions, Asgari & Zare (2011) proposed a C. globosum species group similar to that of Dreyfuss (1976), which grouped into three clades: the C. elatum, C. globosum and C. megasporum clades. Eleven species were included in their C. globosum species group, although only three isolates of the broad C. globosum sensu Von Arx, i.e. CBS 162.62, CBS 371.66 and CBS 148.51, were treated. These data indicated some phylogenetic relationships between C. globosum and other Chaetomiaceae species, but failed to resolve the boundaries of C. globosum sensu Von Arx and allied species. Based on phylogenetic inference of the LSU, tub2 and rpb2 gene regions, Greif et al. (2009) re-evaluated the genus Chaetomium and indicated that this genus is polyphyletic. For all three loci analysed in that study, eight of the nine examined species were interspersed among species of Chaetomium, Farlowia and Thielavia within the Chaetomiaceae, whereas Chd. triangulare fell outside the Chaetomiaceae. Greif et al. (2009) failed to resolve the phylogenetic placement of most of the Chaetomium species due to the limited sampling in the family. However, the rpb2 phylogenetic inference in that study clearly showed that Chd. fimeti, Chd. subfimeti, Chd. pilosum, C. elatum and C. globosum formed a strongly supported clade. Their molecular evidence apparently disagreed with their own suggestion to restrict Chaetomium to its type species, Chd. fimeti, and Chd. subfimeti. After a preliminary screening of the isolates preserved at CBS, and the isolates collected from diverse substrates in China, using partial rpb2 and tub2 gene sequences, 80 isolates representing the morphological diversity of C. globosum and related species were selected as representatives for further study. This revealed a much more expanded C. globosum complex than that of Dreyfuss (1976) and Asgari & Zare (2011). Thirty-six species were recognised in this complex, which grouped into two main clades representing three Groups. Chaetomium fimeti, Chd. subfimeti and Chd. pilosum were shown to belong to the C. globosum species complex and cluster in two different groups. Chaetomium triangulare clustered outside the Chaetomiaceae, while the other available Chaetomium species were interspersed throughout the Chaetomiaceae (data not shown). In addition, many studies have indicated that fungi with cleistothecial ascomata represent a heterogeneous assemblage that evolved independently on different occasions from diverse ascomycetes (Berbee & Taylor 1992, Suh & Blackwell 1999, Stichgel & Guarro 2007).

The first main clade (Group I, Fig 1) resolved here corresponded to the C. megasporum clade of Asgari & Zare (2011). This Group includes several species characterised by distinct morphological features. The four species that sporulated in culture from Group IA (C. globosporum, C. granda, C. megasporum and C. nozdenkoei) produce ascospores with more than one germ pore but vary in size and shape. Chaetomium madrasense and C. ascotrichoides (Group IB) are distinguished by broad limoniform ascospores with a lateral bulge. Group IC, which includes C. fimeti and C. subfimeti, is characterised by non-ostiolate ascomata possessing typical limoniform ascospores. Chaetomium interruptum, distinguished by its globose ascospores with one or two germ pores, forms a basal lineage to Group I. Except for those of C. fimeti and C. subfimeti, ascomatal hairs of species in Group I appeared typical ‘globosum-like’: flexuous, undulate to loosely coiled. Chaetomium citrinum, a distinct species characterised by irregular ascospores, forms a basal lineage of the second main clade (Group II & III, Fig 1) in the C. globosum species complex. Group II corresponds to the C. globosum clade of Asgari & Zare (2011), which is characterised by relatively small and typical limoniform ascospores and flexuous to undulate or slightly coiled terminal ascomatal hairs. Chaetomium coarcatum can be distinguished by relatively large and broad limoniform to nearly globose and biapiculate ascospores and forms a basal lineage to Group III. Group III corresponds to the C. elatum clade of Asgari & Zare (2011) and includes 16 species, which are characterised by larger ascospores than Group II. These species exhibit a diverse morphology of terminal ascomatal hairs ranging from flexuous or undulate (C. graminiforme, C. olivaceum, C. subaffine, C. subglobosum, C. telluricola and C. undulatum) or regularly coiled (C. cochlides, C. cryptocochlides, C. spiculiplum and C. spirochaeta) to repeatedly dichotomously branched (C. elatum and C. rectangularis). Chaetomium pilosum, a species previously placed in the genus Chaetomium, is characterised by non-ostiolate ascomata, and also forms part of Group III. The C. globosum complex is shown to be monophyletic and includes a high diversity of morphological characters in the Chaetomiaceae: ascomata are ostiolate or non-ostiolate; the morphology of the ascomatal hairs embraces nearly all types in the family, ranging from hypha-like, flexuous, undulate, coiled to simply or dichotomously branched, with verrucose to smooth surface and pale to dark in colour; ascospores can be limoniform or globose to strongly irregular with one or two (occasionally three or even four) apical, subapical or lateral germ pores. The ascospores of all species in this group are bilaterally flattened. The acremonium-like asexual morph is only known for four species (C. angustispirale, C. elatum, C. rectangularis and C. subaffine) in this complex. We can, however, define this complex with the following morphological features:
ascomata globose, ellipsoid to ovoate or obovate, ostiolate or non-ostiolate; ascomatal wall, with a few exceptions (C. angustispirale, C. fimeti and C. subfimeti), composed of textura intricata or textura epidermidea in surface view; ascii clavate or fusiform with eight biseriate (or irregularly arranged) ascospores and evanescent ascospores; ascospores limoniform, globose to irregular, bilaterally flattened and longer than 7 μm in length; asexual morphs, if present, acermonium-like.

Characteristics of ascomatal hairs were underrated by Von Arx et al. (1986) in recognition of C. globosum and close relatives. Species with erect, flexuous to undulate or even slightly (loosely and irregularly) coiled hairs are the most predominant feature in the C. globosum species complex. Among them, the occurrence of simply branched ascomatal hairs together with flexuous to undulate hairs is very common in many species (C. globosum, C. graminiforme, C. grande, C. interruptum, C. megalocarpum, C. nozdenkae and C. subglobosum). The variation of ascomatal hairs could be used to differentiate species to an extent, such as the dichotomously branched ascomatal hairs of C. elatum and C. rectangulare and regularly (spirally) coiled ascomatal hairs of C. cochliodes, C. spiculipilum and C. spirochaete. The detailed features of the ascomatal hairs, which include diameter, appearance of the coiled portions, smooth or with surface ornamentation ( verrucose, punctate or spinulose) also help to discriminate species.

There are several other lineages within the genus Chaetomium which possess limoniform and bilaterally flattened ascospores, but these taxa all produce ascoma with walls composed of well-defined textura angularis, which include C. bostrychodes, C. seminudum, C. sphaerale and C. subspirale. The detailed features of the ascomatal hairs, which include diameter, appearance of the coiled portions, smooth or with surface ornamentation ( verrucose, punctate or spinulose) also help to discriminate species.

Chaetomium globosum is known as one of the causal agents of human onychomycosis (Naidu et al. 1991, Stiller et al. 1992, Aspiropr et al. 2007, Lathe et al. 2010, Tullio et al. 2010, Hubka et al. 2011, Hwang et al. 2012, Lagacé & Cellier 2012, Kim et al. 2013) and skin infection of other animals (Sugiyama et al. 2008). However, whether this species and close relatives can cause systemic and deep infections remains controversial (Hoppin et al. 1983, Abbott et al. 1995, Yeghen et al. 1996, Li et al. 1999, Barron et al. 2003, Paterson et al. 2005, De Hoog et al. 2013). A single isolate from a clinical case of fatal brain abscess was originally identified as C. globosum (Anandi et al. 1989). Abbott et al. (1995) later re-classified this isolate as C. atrobrunneum based on morphology and ability to grow at 42 °C and suggested that infections by C. globosum are confined to cooler areas of the human body due to restricted growth at 37 °C. Growth response of a fungal species at 37 °C is used as an indicator of its potential for internal infection of humans (Abbott et al. 1995, Barron et al. 2003). In another study, Yeghen et al. (1996) reported that C. globosum caused fatal pneumonia in a patient with acute myeloid leukemia. Paterson et al. (2005) supported this diagnosis, using Southern hybridization and 18S rRNA (SSU) gene sequences. However, their data can only verify that the infection was not caused by an Aspergillus species. In this study we determined MGT for all isolates of the 17 species selected in the C. globosum species complex. Only isolates of C. globosporum, C. megalocarpum and C. subaffine can grow at 37–38 °C, whereas the growth of the other species, including C. globosum s.str., is restricted at 37–38 °C. More research, however, is required to clarify the adaptation of C. globosum and allied species to human bodies.

The present study provides both molecular and morphological knowledge for each species presently known in the C. globosum species complex, highlighting the importance of correct identification for especially medical cases. This study provides a phylogenetic backbone and framework for future studies of the genus Chaetomium. Further studies are presently underway to ascertain a definite position of the C. globosum species complex in the genus, using a wider sampling of relevant taxa.

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