



Phylogenetic reassessment of the *Chaetomium globosum* species complex

X.W. Wang¹, L. Lombard², J.Z. Groenewald², J. Li¹, S.I.R. Videira², R.A. Samson²,
X.Z. Liu^{1*}, P.W. Crous^{2,3,4*}

Key words

DNA barcode
epitypification
multi-gene phylogeny
species complex
systematics

Abstract *Chaetomium globosum*, the type species of the genus, is ubiquitous, occurring on a wide variety of substrates, in air and in marine environments. This species is recognised as a cellulolytic and/or endophytic fungus. It is also known as a source of secondary metabolites with various biological activities, having great potential in the agricultural, medicinal and industrial fields. On the negative side, *C. globosum* has been reported as an air contaminant causing adverse health effects and as causal agent of human fungal infections. However, the taxonomic status of *C. globosum* is still poorly understood. The contemporary species concept for this fungus includes a broadly defined morphological diversity as well as a large number of synonymies with limited phylogenetic evidence. The aim of this study is, therefore, to resolve the phylogenetic limits of *C. globosum* s.str. and related species. Screening of isolates in the collections of the CBS-KNAW Fungal Biodiversity Centre (The Netherlands) and the China General Microbiological Culture Collection Centre (China) resulted in recognising 80 representative isolates of the *C. globosum* species complex. Thirty-six species are identified based on phylogenetic inference of six loci, supported by typical morphological characters, mainly ascospore shape. Of these, 12 species are newly described here. Additionally, *C. cruentum*, *C. mollipilium*, *C. rectum*, *C. subterraneum* and two varieties of *C. globosum* are synonymised under *C. globosum* s.str., and six species are resurrected, i.e. *C. angustispirale*, *C. coarctatum*, *C. cochliodes*, *C. olivaceum*, *C. spiculipilium* and *C. subglobosum*. *Chaetomium ascotrichoides* is segregated from *C. madrasense* and the genus name *Chaetomidium* is rejected. Five species, including *C. globosum* s.str., are typified here to stabilise their taxonomic status. A further evaluation of the six loci used in this study as potential barcodes indicated that the 28S large subunit (LSU) nrDNA and the internal transcribed spacer regions and intervening 5.8S nrRNA (ITS) gene regions were unreliable to resolve species, whereas β -tubulin (*tub2*) and RNA polymerase II second largest subunit (*rpb2*) showed the greatest promise as DNA barcodes for differentiating *Chaetomium* species. This study provides a starting point to establish a more robust classification system for *Chaetomium* and for the *Chaetomiaceae*.

Article info Received: 8 April 2015; Accepted: 24 June 2015; Published: 25 September 2015.

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 ascomatal hairs (Corda 1840, Fries 1849, Zopf 1881, Chivers 1915, Skolko & Groves 1953, Udagawa 1960, Ames 1963, Seth 1970). The discovery of cylindrical asci 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 ascomatal 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; asci evanescent, clavate or slightly fusiform; ascospores limoniform, bilaterally-flattened, 9–12 × 8–10 × 6–8 μ m (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

¹ State Key Laboratory of Mycology, Institute of Microbiology, Chinese Academy of Sciences, No. 3, 1st Beichen West Road, Chaoyang District, Beijing 100101, China; corresponding author e-mail: liuxz@im.ac.cn.

² CBS-KNAW Fungal Biodiversity Centre, Uppsalalaan 8, 3584 CT Utrecht, The Netherlands; corresponding author e-mail: p.crous@cbs.knaw.nl.

³ Department of Microbiology and Plant Pathology, Forestry and Agricultural Biotechnology Institute (FABI), University of Pretoria, Pretoria 0002, South Africa.

⁴ Microbiology, Department of Biology, Utrecht University, Padualaan 8, 3584 CH Utrecht, The Netherlands.

Table 1 Details of isolates and their sequences employed in this study. The newly generated sequences in this study are shown in **bold**.

Species	Isolate code ^{a,b}	Country	Substrate / Locality	MGTe (°C)	GenBank accession numbers					
					LSU	ITS	tub2	tef1	rpb1	rpb2
<i>Chaetomium afropliosum</i>	CBS 145.38 (T)	–	–	–	KT214605	KT214574	KT214751	KT214713	KT214639	KT214675
<i>C. angustispirale</i>	CBS 137.58 (T)	Russia	<i>Fraxinus</i> sp., Tellerman forest, Baleshev region	33	JN209862	JN209862	JN256141	KF001734	KF001779	KF001824
<i>C. ascotrichoides</i>	CBS 113.83 (T)	Argentina	<i>Gossypium humitectum</i>	38–39	KC109752	KC109752	KC109770	KF001742	KF001787	KF001832
	CBS 110.83 (T of <i>C. gibberosporum</i>)	Israel	Soil	38–39	KC109753	KC109753	KC109771	KF001743	KF001788	KF001833
	CGMCC 3.11378	China	Soil, Yuli county, Korla region, Xinjiang	38–39	JN209900	JN209900	JN256174	KF001746	KF001791	KF001836
	CGMCC 3.11392	China	Sheep wool, Aksu region, Xinjiang	38–39	JN209903	JN209903	JN256176	KF001744	KF001789	KF001834
	CGMCC 3.12884	China	Sheep dung, Aksu region, Xinjiang	38–39	JN209904	JN209904	JN256177	KF001745	KF001790	KF001835
<i>C. capillare</i>	CBS 128489 (T)	USA	Animal hair, California	–	KT214614	KT214583	KT214760	KT214724	KT214650	KT214686
<i>C. cenicicola</i>	CBS 128492 (T)	USA	Neck of <i>Homo sapiens</i> , Texas	–	KT214592	KT214558	KT214735	KT214697	KT214623	KT214662
<i>C. citrinum</i>	CBS 693.82 (T)	Japan	Rice field soil, Tochigi	–	KT214617	KT214587	KT214764	KT214730	KT214656	KT214691
<i>C. coarctatum</i>	MUCL 18697 = CBS 162.62 (T)	Russia	Seed of <i>Cappanula medium</i> , St. Petersburg	38	JN209863	JN209863	JN256142	KF001712	KF001757	KF001802
	CGMCC 3.14293	China	Unknown animal dung, Huairou, Beijing	37–38	JN209923	JN209923	JN256193	KF001713	KF001758	KF001803
	CGMCC 3.14299	China	Dead stem of unknown plant, Xiangshan Park, Beijing	37–38	JN209924	JN209924	JN256194	KF001714	KF001759	KF001804
<i>C. cochliodes</i>	CBS 155.52 (epiT)	USA	Animal dung	38	KC109754	KC109754	KC109772	KF001721	KF001766	KF001811
	CGMCC 3.9440	China	Tube of <i>Panax notoginseng</i> , Wenshan, Yunnan Province	38	JN209866	JN209866	JN256145	KF001724	KF001769	KF001814
<i>C. contigiosum</i>	CGMCC 3.9471	China	Rhizospheres of <i>Panax notoginseng</i> , Wenshan, Yunnan Province	38	JN209868	JN209868	JN256147	KF001723	KF001768	KF001813
	CGMCC 3.14296	China	Discarded cloth, Ulanqab City, Inner Mongolia	38	JN209865	JN209865	JN256144	KF001722	KF001767	KF001812
	CBS 128494 (T)	USA	Comea of <i>Homo sapiens</i> , North East	–	KT214589	KT214555	KT214732	KT214694	KT214620	KT214659
<i>C. cucumericola</i>	CBS 378.71 (T)	Turkey	–, Izmir	–	KT214610	KT214579	KT214756	KT214718	KT214644	KT214680
	IRAN 1642C = CBS 126777	Iran	Petiole of <i>Cucumis sativus</i> , Hashtgerd, Alborz Province	–	HM365247	HM365247	KT214757	KT214719	KT214645	KT214681
<i>C. elatum</i>	CBS 910.70 (T of <i>C. ramipilosum</i>)	Germany	Leaves and dead stems of <i>Ammophila arenaria</i> , Helgoland	35–36	KC109757	KC109757	KC109775	KF001731	KF001776	KF001821
	CBS 374.66 (T of <i>C. virgicephalum</i>)	USA	Decomposing leaf, Aptos, California	35–36	KC109758	KC109758	KC109776	KF001730	KF001775	KF001820
<i>C. firmi</i>	DSM 62108 = CBS 139034 (epiT)	Germany	Soil	–	KT214593	KT214559	KT214736	KT214698	KT214624	KT214663
	CBS 153.77	Japan	–	–	KT214594	KT214561	KT214738	KT214700	KT214626	KT214664
	CBS 168.71	Canada	Decaying hay, Nashville, Ontario	–	FJ666358	KT214560	KT214737	KT214699	KT214625	FJ666389
	CBS 108.83 (T)	India	Green leaf of <i>Triticum aestivum</i>	40–41	KC109750	KC109750	KC109768	KF001735	KF001780	KF001825
<i>C. globosporum</i>	CBS 160.62 (neoT)	Germany	Compost	–	KT214596	KT214565	KT214742	KT214704	KT214630	KT214666
	CBS 105.40	Netherlands	Mouldy book, Amsterdam	–	KT214597	KT214566	KT214743	KT214705	KT214631	KT214667
	CBS 132.30 (T of <i>C. subterraneum</i>)	USA	Clay soil, Illinois	37–38	KC109755	KC109755	KC109773	KF001702	KF001747	KF001792
	CBS 147.60 (T of <i>C. mollipillium</i>)	USA	Raincoat, Jeffersonville, Indiana	38	JN209909	JN209909	JN256179	KF001703	KF001748	KF001793
	CBS 148.51	USA	Stored cotton, Washington DC	37–38	GU563363	GU563374	JF772459	KC485028	KC485058	KF001801
	CBS 164.62 (T of <i>C. rectum</i>)	Poland	–, Bydgoszcz Botanic garden	38	JN209920	JN209920	JN256190	KF001706	KF001751	KF001796
	CBS 371.66 (T of <i>C. cruentum</i>)	USA	Paper, Fort Belvoir, Virginia	37	JN209871	JN209871	JN256148	KF001705	KF001750	KF001795
	CGMCC 3.9994	China	Finger nail of <i>Homo sapiens</i> , Beijing	38	JN209894	JN209894	JN256168	KF001708	KF001753	KF001798
	MUCL 39526 (T of <i>C. globosum</i> var. <i>flavoviride</i>)	Hungary	Dead stem of <i>Juncus</i> sp.	37–38	JN209875	JN209875	JN256152	KF001710	KF001755	KF001800
	MUCL 39527 (T of <i>C. globosum</i> var. <i>griseum</i>)	Hungary	Dead stem of <i>Juncus</i> sp.	37–38	JN209899	JN209899	JN256173	KF001709	KF001754	KF001799
<i>C. graminiforme</i>	CBS 506.84 (T)	Canada	<i>Acer</i> sp., Muskoka District, Ontario	–	KT214615	KT214584	KT214761	KT214725	KT214651	KT214687
	IRAN 1064C = CBS 126780 (T)	Iran	Leaf of <i>Triticum aestivum</i> , Naghadeh, West Azerbaijan Province	–	HM365253	HM365253	HM365273	KT214692	KT214618	KT214657
<i>C. grande</i>	CGMCC 3.9414 = CBS 119758	China	Desert soil, Bayingolin, Xinjiang Autonomous Region	38	KC109749	KC109749	KC109767	KF001736	KF001781	KF001826
	IRAN 1208C = CBS 126781	Iran	Straw of <i>Triticum aestivum</i> , Bileasavar, Ardabil Province	–	KT214588	KT214554	KT214731	KT214693	KT214619	KT214658
<i>C. interruptum</i>	IRAN 1278C = CBS 126660 (T)	Iran	Seed of <i>Triticum aestivum</i> , Hadishahr, East Azerbaijan Province	–	HM365246	HM365246	KT214741	KT214703	KT214629	KT214665
<i>C. macrasense</i>	CBS 315.74 (T)	India	Rhizosphere of <i>Pennisetum typhoides</i> , Tamil Nadu, Madras	38	KC109751	KC109751	KC109769	KF001741	KF001786	KF001831

<i>C. megalocarpum</i>	MUCL 9589 = CBS 149.59 (epiT) CBS 778.71 CGMCC 3.3595 CGMCC 3.9443	Greece India China China	Leaf of <i>Ficus carica</i> Humus-rich soil Horse dung, Yinchuan Province, Ningxia City Soil, Shanhaiguan, Hebei Province	40 40 40 40	KC109744 KC109747 KC109746 KC109748	KC109744 KC109747 KC109746 KC109748	KC109762 KC109765 KC109764 KC109766	KF001738 KF001737 KF001740 KF001739	KF001783 KF001782 KF001785 KF001829
<i>C. novozelandicum</i>	CBS 124555 (T) CBS 124556 CBS 128484	New Zealand New Zealand USA	Dead decaying twig, Otaki Dead decaying twig, Otaki Scalp of <i>Homo sapiens</i> , California	– – –	KT214607 KT214608 KT214609	KT214576 KT214577 KT214578	KT214753 KT214754 KT214755	KT214715 KT214716 KT214717	KT214641 KT214642 KT214643
<i>C. nozdrenkoeae</i>	CBS 163.62 (T) CBS 809.68	Russia Germany	Soil, Novosibirsk region Greenhouse soil, Giessen	– –	KT214590 KT214591	KT214556 KT214557	KT214733 KT214734	KT214695 KT214696	KT214660 KT214661
<i>C. olivaceum</i>	CBS 418.80A CGMCC 3.9465 CGMCC 3.12883	India China China	Nilgai dung, Delhi Soil, Changchun, Jilin Province Carnel dung, Aksu region, Xinjiang	38 38 37	JN209914 JN209913 JN209911	JN209914 JN209913 JN209911	JN256184 JN256183 JN256181	KF001716 KF001715 KF001717	KF001806 KF001805 KF001807
<i>C. pilosum</i>	CBS 335.67 (T)	Australia	Grain of <i>Triticum aestivum</i> , Perth, Western Australia	–	FJ666356	KT214586	KT214763	KT214729	KT214655 FJ666387
<i>C. pseudocochliodes</i>	CGMCC 3.9441 (T) CGMCC 3.9469	China China	Roots of <i>Panax notoginseng</i> , Wenshan, Yunnan Province Rhizosphere of <i>Panax notoginseng</i> , Wenshan, Yunnan Province	38 37–38	JN209925 JN209926	JN209925 JN209926	JN256195 JN256196	KF001726 KF001725	KF001816 KF001815
<i>C. pseudoglobosum</i>	CBS 574.71 (T)	–	–	–	KT214604	KT214573	KT214750	KT214712	KT214638 KT214668
<i>C. rectangularare</i>	IRAN 1641C = CBS 126778 (T) CGMCC 3.9409 IRAN 855C = CBS 126658	Iran China Iran	Leaf of <i>Hordeum vulgare</i> , Salmas, West Azerbaijan Province Animal dung, Kanas Lake, Xinjiang Stem of <i>Hordeum vulgare</i> , Shabestar, East Azerbaijan Province	35 –	JN209873 HM365240	JN209873 HM365240	JN256150 HM365286	KF001732 KT214727	KF001822 KT214689
<i>C. spiculipilum</i>	CBS 373.66 (T)	USA	Decaying vegetable debris, California	34–35	KC109756	KC109756	KC109774	KF001719	KF001809
<i>C. spirochaete</i>	CBS 730.84 (epiT) CBS 165.52	USA –	Animal dung, Great Smokey Mountains, Tennessee Animal dung	38 –	JN209921 KT214616	JN209921 KT214585	JN256191 KT214762	KF001729 KT214728	KF001819 KT214690
<i>C. subaffine</i>	CBS 637.91 (T) CGMCC 3.14297	USSR China	Cereal Unknown plant stem, Xingtai, Hebei Province	39 39	JN209929 JN209928	JN209929 JN209928	JN256199 JN256198	KF001727 KF001728	KF001817 KF001818
<i>C. subfimeii</i>	CBS 370.66 (T, T of <i>Chaetomidium subfimeii</i>) CBS 169.71	Wales USA	Paper and vegetable material, Cardiff Soil, Kern County, California	– –	FJ666354 FJ666357	KT214562 KT214563	KT214739 KT214740	KT214701 KT214702	FJ666385 FJ666388
<i>C. subglobosum</i>	MUCL 18694 = CBS 149.60 (T) CBS 483.73	Russian Turkey	Dead herbaceous stem, St. Petersburg <i>Eriobotrya japonica</i> , Izmir	38 –	JN209930 KT214612	JN209930 KT214581	JN256200 KT214758	KF001718 KT214722	KF001808 KT214684
<i>C. telluricola</i>	CBS 151.59 (T)	United Kingdom	Soil, Suffolk, Lakenheath Warren	–	KT214613	KT214582	KT214759	KT214723	KT214685
<i>C. tenue</i>	CBS 139.38 (T) CBS 138.38 CBS 140.38 CBS 142.38 CBS 143.38	– – – – –	– – – – –	– – – – –	KT214599 KT214600 KT214601 KT214602 KT214603	KT214568 KT214569 KT214570 KT214571 KT214572	KT214745 KT214746 KT214747 KT214748 KT214749	KT214707 KT214708 KT214709 KT214710 KT214711	KT214669 KT214670 KT214671 KT214672 KT214673
<i>C. umbonatum</i>	CBS 293.83 (T)	Canada	Soil, Nova Scotia	–	KT214606	KT214575	KT214752	KT214714	KT214640 KT214682
<i>C. undulatum</i>	IRAN 857C = CBS 126775 (T) IRAN 1071C = CBS 126776	Iran Iran	Leaf of <i>Hordeum vulgare</i> , Bonab, East Azerbaijan Province Leaf of <i>Triticum aestivum</i> , Miandoab, West Azerbaijan Province	– –	HM365251 HM365250	HM365251 HM365250	HM365279 HM365278	KT214720 KT214721	KT214646 KT214683
<i>C. unguicula</i>	CBS 128446 (T)	USA	Nail of <i>Homo sapiens</i> , Los Angeles	–	KT214598	KT214567	KT214744	KT214706	KT214688
<i>Achaetomium strumarium</i>	CBS 333.67 (T)	India	Soil, Lucknow	–	AY681170	AY681204	AY681238	KC503252	KC503254

^a 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; MUCL: Mycothèque de l'Université Catholique de Louvain, Belgium. Additional culture collection numbers are available where applicable under the species notes in the Taxonomy section.

^b T: ex-type strain; epiT: ex-epitype strain; neoT: ex-neotype strain.

^c 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. cruentum*, *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, Stchigel 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 *Lasiosphaeriaceae*, 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 *Chaetomium* and *Chaetomidium* species. Both the 28S large subunit (LSU) nrDNA and β -tubulin (*tub2*) sequence data also did not support the segregation of *Chaetomidium* from *Chaetomium*.

Despite the inconsistency and contradiction in delimitation of *C. globosum*, it is, undoubtedly, one of the most important *Chaetomium* species due to its various positive and negative impacts on humans and the environment. *Chaetomium globosum* sensu Von Arx is reported to be cosmopolitan, and occurs in a great variety of environments which include soil, dung, a wide variety of plant materials and other cellulose-rich substrates, as well as in air and marine environments (Ames 1963, Carter 1982, Kopytina 2005, Momesso et al. 2008, Kharwar et al. 2011, Yamada et al. 2012). This species is also well known for its cellulolytic ability, having potential use in biodegradation of waste plant material and other industrial applications (Umikalsom et al. 1998, El-Gindy et al. 2003, Ahammed et al. 2008, Prokhorov & Linnik 2011, Longoni et al. 2012, Singh et al. 2013, Sharma et al. 2014). In order to adapt to diverse environments, *C. globosum* is capable of producing various enzymes and secondary metabolites, displaying a wide range of biological activities. These include antifungal, antibacterial, antioxidant, anti-inflammatory and anticancer activities that are of potential use in the agricultural, medicinal and industrial fields (Udagawa et al. 1979, Sekita et al. 1981, Park et al. 2005, Ding et al. 2006, Kim & Hwang 2007, Ge et al. 2008, Momesso et al. 2008, Phonkerd et al. 2008, Kaewchai et al. 2009, Zhang et al. 2010, 2012, 2013, Kharwar et al. 2011, Yamada et al. 2012, Kumar et al. 2013, Shanthiyaa et al. 2013, Awad et al. 2014, Yan et al. 2014). As a common contaminant in indoor environments, *C. globosum* has been recognised as a health hazard mainly due to the production of mycotoxins, microbial volatile organic compounds and airborne fungal fragments or ascospores that, when inhaled, may contribute to the development of symptoms of rhinitis, asthma and other health problems (Gonianakis et

al. 2005, Vesper et al. 2007, Apetrei et al. 2009, Polizzi et al. 2009, Ayanbimpe et al. 2010, Mason et al. 2010, Andersen et al. 2011, Miller & McMullin 2014). *Chaetomium globosum* has also been reported to infect humans, and is most commonly associated with onychomycosis, a disease with increasing incidence reports worldwide over recent decades (Hoppin et al. 1983, Naidu et al. 1991, Stiller et al. 1992, Yeghen et al. 1996, Lesire et al. 1999, Aspiroz et al. 2007, Latha et al. 2010, Tullio et al. 2010, Hubka et al. 2011, Hwang et al. 2012, Lagacé & Cellier 2012, Kim et al. 2013).

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.TM 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 region; gRPB1-A & fRPB1-C (Matheny et al. 2002) for partial fragments of the largest subunit of the RNA polymerase II (*rpb1*) gene; RPB2AM-1bf & RPB2AM-7R (Miller & Huhndorf 2005) for partial fragments of the *rpb2* gene region. The PCR mixtures (12.5 μ L) contained 10–20 ng of genomic DNA, 1 \times GoTaq[®] Flexi buffer (Promega, Madison, WI, USA), 1 mM MgCl₂ (2.5 mM for *rpb2*), 40 μ M dNTPs (60 μ M for *rpb2*), 0.2 μ M of each primer (0.12 μ M 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 \times); 94 °C/45 s, 58 °C/45 s, 72 °C/2 min (5 \times); 94 °C/45 s, 56 °C/45 s, 72 °C/2 min (35 \times) 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

Prism® 3730xl Genetic Analyzer (Applied Biosystems). Consensus sequences were determined using MEGA v. 6 (Tamura et al. 2013). Novel sequences generated in this study were deposited in GenBank (<http://www.ncbi.nlm.nih.gov>, Table 1).

In addition to the sequences generated in this study, other sequences from previous studies (Greif et al. 2009, Asgari & Zare 2011) were retrieved from GenBank. The sequence datasets were initially aligned using MAFFT v. 7 (Kato & Standley 2013), and were manually optimised using BioEdit v. 5.0.9 (Hall 1999). Congruency of the six loci was tested using the 70 % reciprocal bootstrap criterion (Mason-Gamer & Kellog 1996) as described by Gueidan et al. (2007) and Lombard et al. (2010).

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. Tree bisection-reconnection was used, with the branch swapping option set on 'best trees only', with all characters weighted equally and alignment gaps treated as fifth character state. The tree length (TL), consistency index (CI), retention index (RI) and rescaled consistence index (RC) were calculated for the MP phylogenies and the bootstrap analysis (Hillis & Bull 1993) was based on 1 000 replications. The ML analysis was performed using RAxML-VI-HPC v. 7.0.3 (Stamatakis 2006) on the CIPRES Science Gateway (<https://www.phylo.org>) with nonparametric bootstrapping using 1 000 replicates. Trees were viewed in FigTree v. 1.1.2 (Rambaut 2009). The alignment and derived trees were deposited in TreeBASE (submission ID 17816; <http://treebase.org/treebase-web/home.html>).

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 $x = \frac{\sum(f.b)}{\sum(f)}$, 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 cornmeal 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. angustispirale*, 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.

Fifty-four isolates representing 17 species were compared for their maximum growth temperatures (MGT) using the methods presented in Wang et al. (2014). Taxonomic information and nomenclature for new species were deposited in MycoBank (www.MycoBank.org; Crous et al. 2004).

RESULTS

Phylogeny

The phylogenetic analyses included 80 ingroup taxa, with *Achaetomium strumarium* (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 = 53; 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

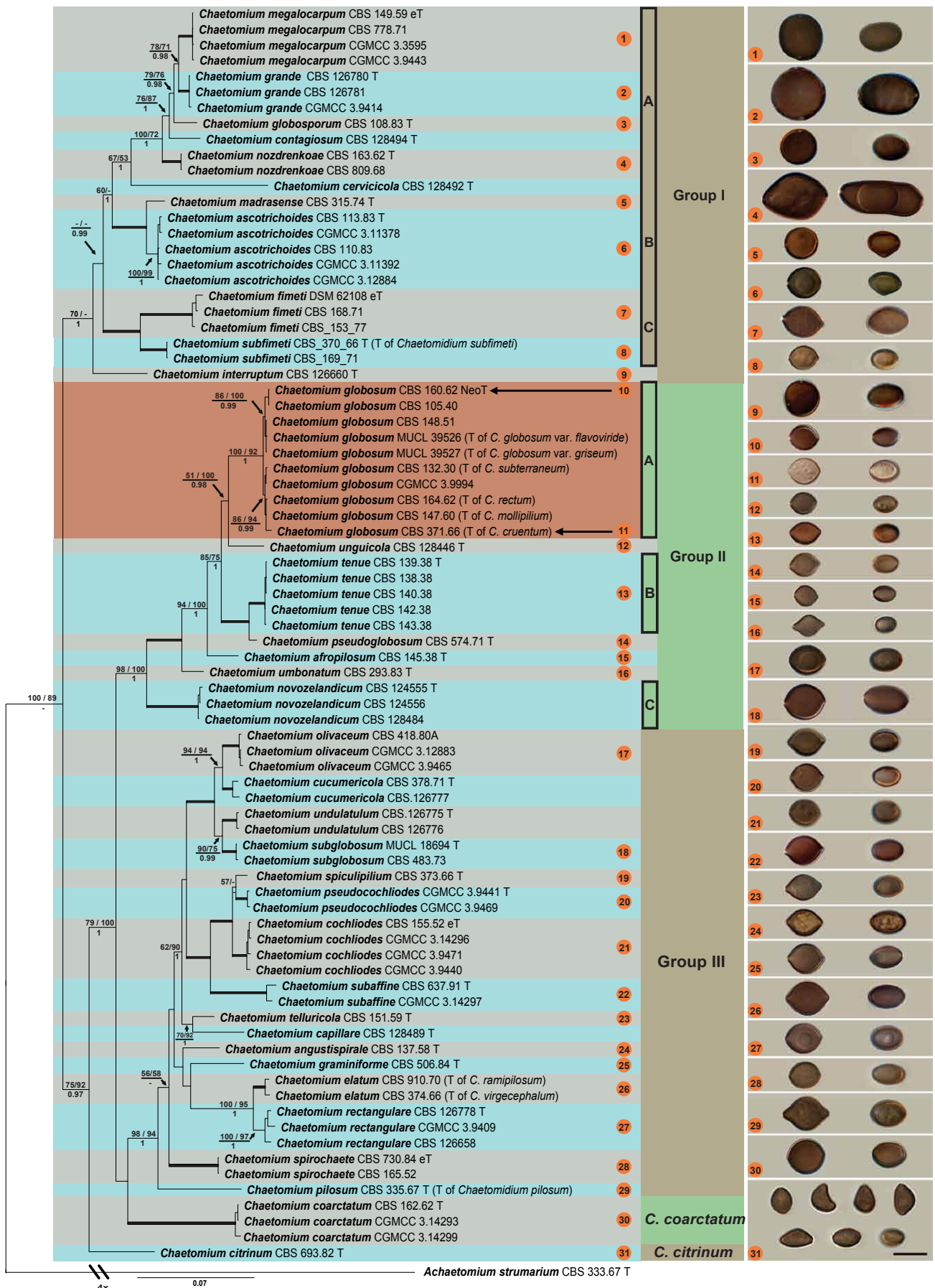


Fig. 1 Consensus phylogram resulting from a Bayesian analysis of the concatenated *rbp2*, *tub2*, *tef1*, *rbp1*, ITS and LSU gene region alignment, with the confidence values of bootstrap (BS) proportions from the MP analysis (before the backslash), the ML analysis (after the backslash) above branches, 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 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.

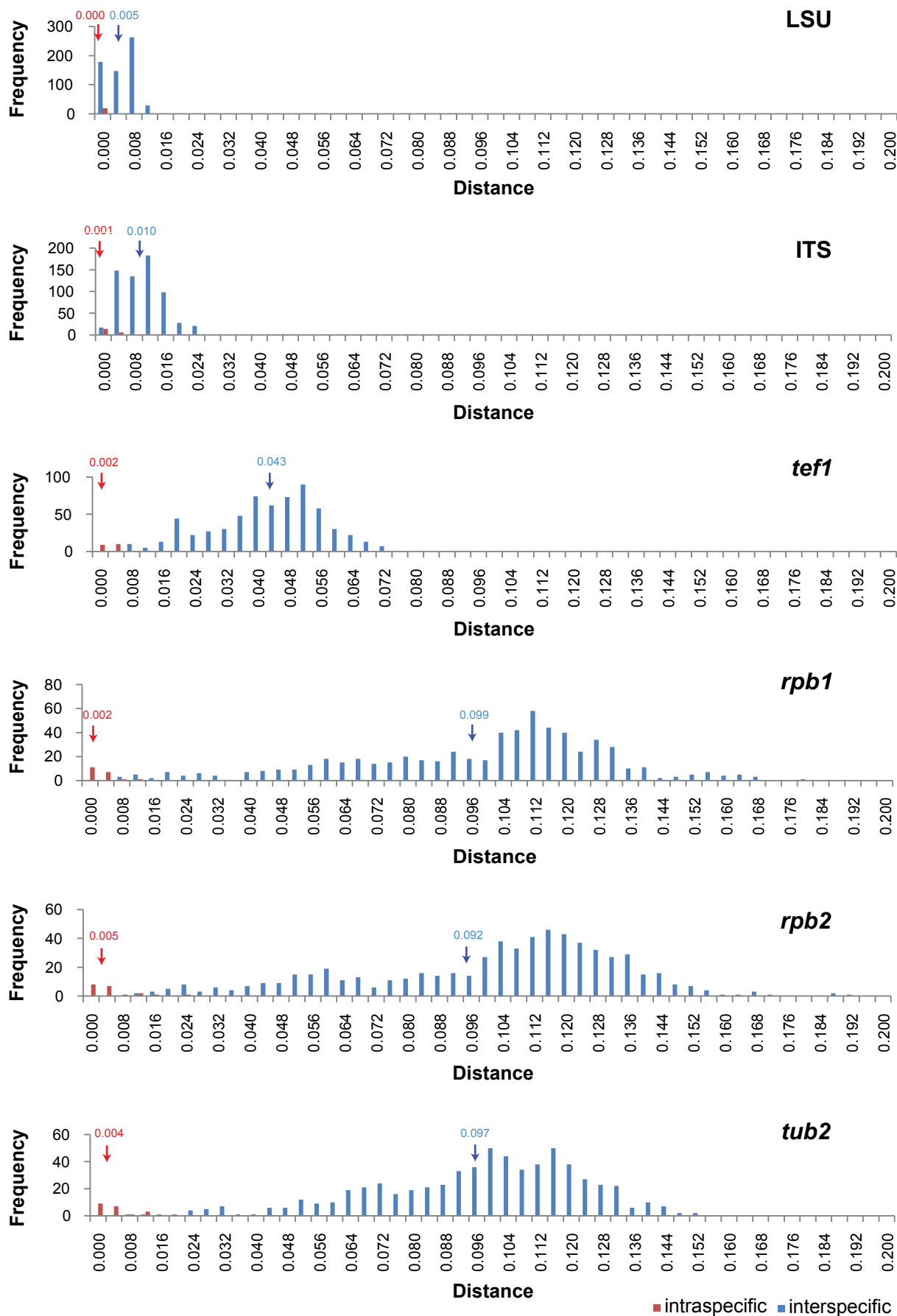


Fig. 2 The frequency distribution graphs of the Kimura-2-parameter distances (barcoding gaps) for the six individual loci. The blue arrow indicates the average interspecific distance and the red arrow indicates the average intraspecific distance with corresponding mean values above both arrows.

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 *Chaetomidium*, 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 novel 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.

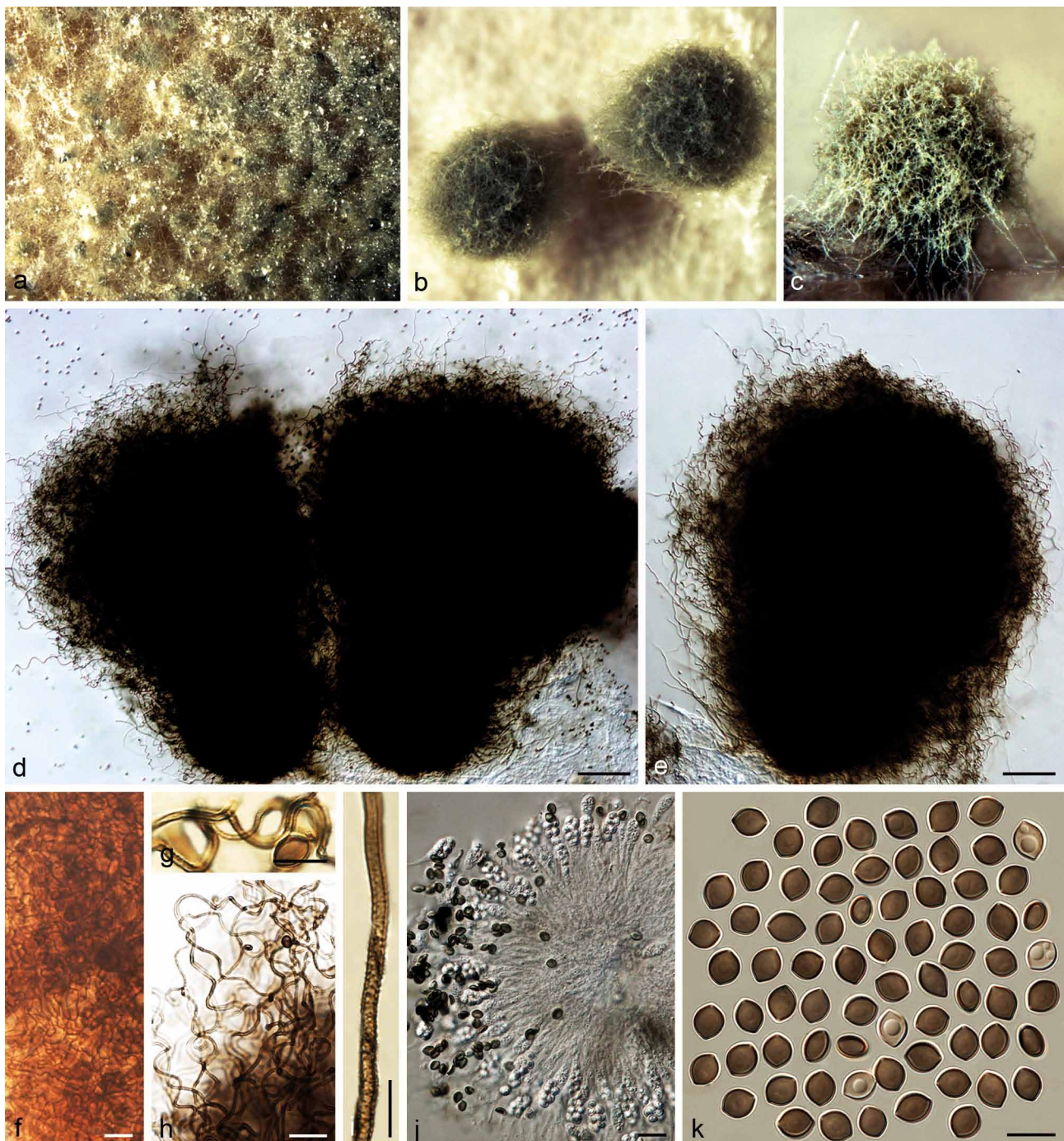


Fig. 3 *Chaetomidium afropilosum* (CBS 145.38, ex-type culture). a. Part of the colony on OA; b. ascomata on OA, top view; c. ascoma on OA, side view; d, e. ascomata mounted in lactic acid; f. structure of ascomatal wall in surface view; g, h. upper part of terminal ascomatal hairs; i. basal part of a terminal ascomatal hair; j. asci; k. ascospores. — Scale bars: d, e = 100 μ m; h, j = 20 μ m; f, g, i, k = 10 μ m.

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, *rpb2* 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 *Chaetomidium* 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. interruptum*, 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 citrine 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 hypha-like or amorphous cells, *textura intricata* or *textura epidermoidea* in surface view. *Terminal hairs* abundant, forming a dense, nearly globose head covering the ostiole, verrucose, olivaceous brown, fading towards the tips, undulate or slightly coiled, erect or flexuous at lower part, 3–4.5 µm near the base, tapering towards the tips. *Lateral hairs* similar to terminal hairs, but more flexuous. *Asci* fasciculate, clavate or slightly fusiform, spore-bearing part 18–24 × 9–11.5 µm, stalks 15–24 µm long, with eight biseriate ascospores, evanescent. *Ascospores* olivaceous brown when mature, limoniform, biapiculate, bilaterally flattened, (6.5–)7–8 × (5–)5.5–6(–6.5) × 4–5 µm, with an apical germ pore. *Asexual morph* absent.

Culture characteristics — Colonies on OA with sparse white aerial hyphae, sometimes forming thick white hyphae in the centre, producing apricot to orange exudates diffusing into the medium; reverse fulvous to sienna.

Material examined. UNKNOWN, substrate and collection details unknown, isolated and deposited in CBS by R.H. Tschudy in June 1938 (holotype CBS H-22192, culture ex-type CBS 145.38 = DAOM 19448).

Notes — Phylogenetic inference shows that *C. afropilosum* forms a unique lineage in Group II (Fig. 1), closely related to *C. globosum* s.str., *C. unguicola*, *C. tenue*, *C. pseudoglobosum* and *C. umbonatum*. *Chaetomium afropilosum* can be distinguished by its distinct ascomatal hair structure and by its smaller ascospores compared to those of *C. globosum* s.str. (8.5–10.5 × 7–8 × 5.5–6.5 µm), *C. unguicola* (7.5–9 × 6.5–7 × 4.5–5.5 µm), *C. tenue* (7.5–10 × 6–7 × 4.5–5.5 µm), *C. pseudoglobosum* (9–10 × 6.5–7.5 × 5–6 µm) and *C. umbonatum* (8–11 × 5.5–7 × 4–5 µm). This species has the smallest ascospores of all known species in the *C. globosum* species complex.

Chaetomium angustispirale Sergeeva, Not. Syst. sect. Crypt. Inst. Bot. Acad. Sci. U.S.S.R. 11: 115. 1956. — Fig. 4

Ascomata superficial, ostiolate, dark olivaceous in reflected light owing to ascomatal hairs, ellipsoid to subglobose, 270–400 µm high, 220–380 µm diam. *Ascomatal wall* brown, composed of irregular or angular cells, *textura angularis* in surface view. *Terminal hairs* brown, verrucose, partly long and thick, 5–7 µm diam near the base, erect, often circinate or coiled in the upper part, sometimes branched; partly short and thin, 3–5 µm diam near the base with relatively long coils in the upper part, often branched. *Lateral hairs* hypha-like, erect or flexuous, tapering towards the tips. *Asci* fasciculate, clavate or fusiform, spore-bearing part 28–35 × 11–19 µm, stalks 26–48 µm long, with eight biseriate ascospores, evanescent. *Ascospores* olivaceous brown when mature, limoniform, usually slightly umbonate at both ends, bilaterally flattened, (9–)9.5–11.5(–12) × (7.5–)8–9 × (5.5–)6–7 µm, with an apical germ pore. *Asexual morph* acremonium-like. *Conidiophores* discrete and simple; conidigenous cells phialidic, hyaline. *Conidia* formed in basipetal succession, aseptate, smooth, hyaline, ovate or ellipsoid, usually with truncated base and rounded apex, (2.5–)3–4.5 × 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

= *Chaetomium gibberosporum* Dreyfuss ex Sedlar et al., Arch. Mikrobiol. 92: 105. 1973 (nom. inval., Art. 38).

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 hypha-like or amorphous cells, *textura intricata* or *textura epidermoidea* in surface view. *Terminal hairs* finely verrucose, relatively sparse, brown, flexuous, undulate, sometimes simply branched, 2.5–3.5 µm near the base, hairs around ostiole often relatively short, flexuous or geniculate, constricted at septa, irregularly branched in the upper part. *Lateral hairs* hypha-like, flexuous, tapering towards the tips. *Asci* fasciculate, fusiform or clavate, spore-bearing part 30–45 × 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) × (8–)8.5–9.5(–10) × (6–)6.5–7(–7.5) µm, with an apical germ pore. *Asexual morph* absent.

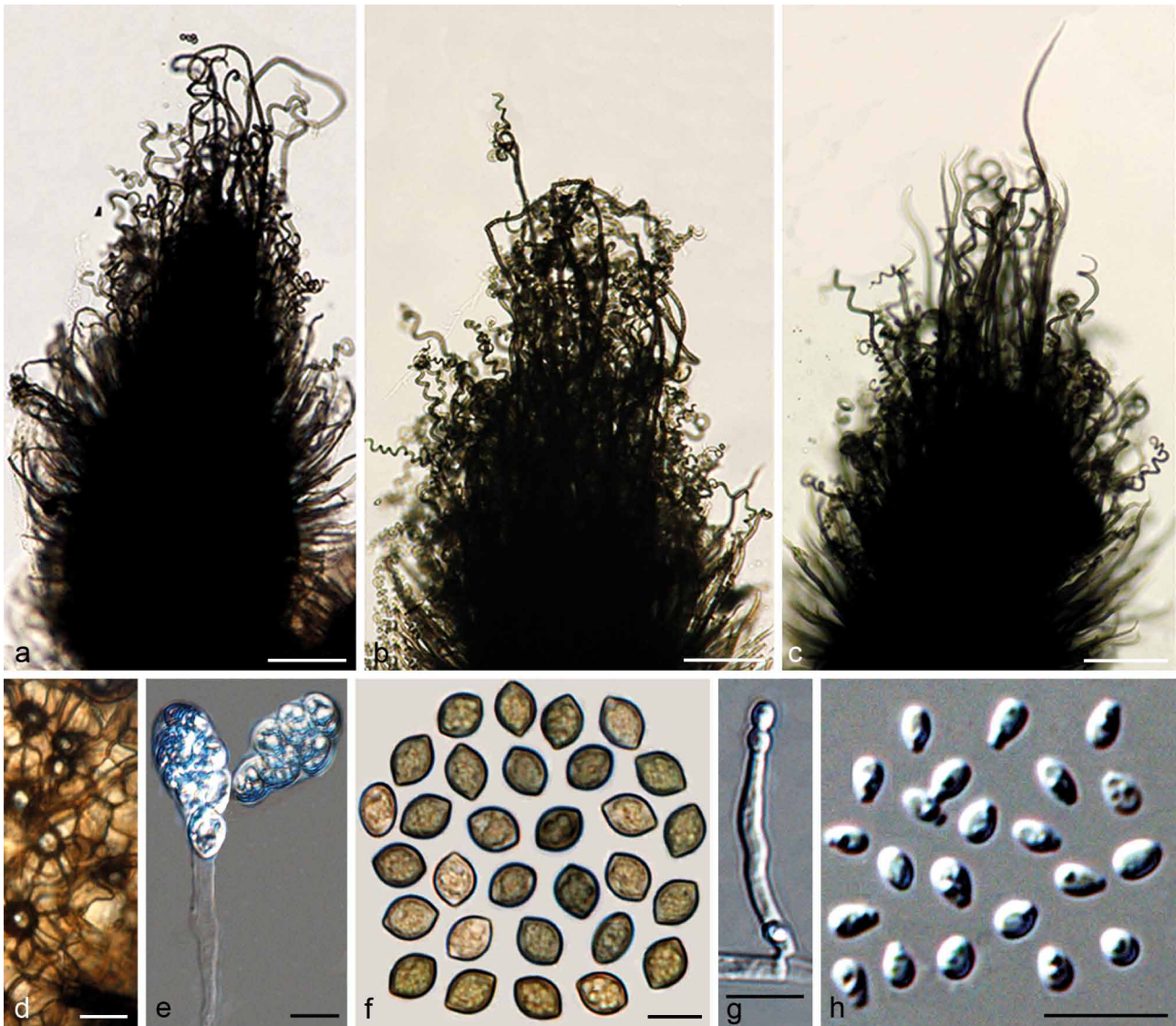


Fig. 4 *Chaetomium angustispirale* (CBS 137.58, ex-type culture). a–c. Ascomata mounted in lactic acid; d. structure of ascomatal wall in surface view; e. asci; f. ascospores; g, h. asexual morph: g. conidiophore; h. conidia. — Scale bars: a–c = 100 μ m; d–h = 10 μ m.

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

Materials examined. ARGENTINA, from *Gossypium humitectum*, Jan. 1983, B.O. Calviello (culture ex-type CBS 113.83 = IMI 182725). — CHINA, Xinjiang, Yuli County, Korla region, from soil, June 2007, F.-J. Liu, CGMCC 3.11378; Asku region, from sheep dung, June 2007, F.-J. Liu, CGMCC 3.12884; from sheep wool, June 2007, F.-J. Liu, CGMCC 3.11392. — ISRAEL, M. Dreyfuss, deposited in CBS by O. Petrini, Jan. 1983 (isotype of *C. gibberosporum* CBS H-6870, ex-isotype culture of *C. gibberosporum* CBS 110.83 = ETH 7714).

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 μ m) than those of *C. madrasense* (7.5–8.5 μ m). 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 \times 8.5–9.5 \times 6.5–7 μ m) are wider than those of *C. globosum* (8.5–10.5 \times 7–8 \times 5.5–6.5 μ m) and narrower than those of *C. coarctatum* (10–11 \times 9–10 \times 6.5–7.5 μ m).

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), 69(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), 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

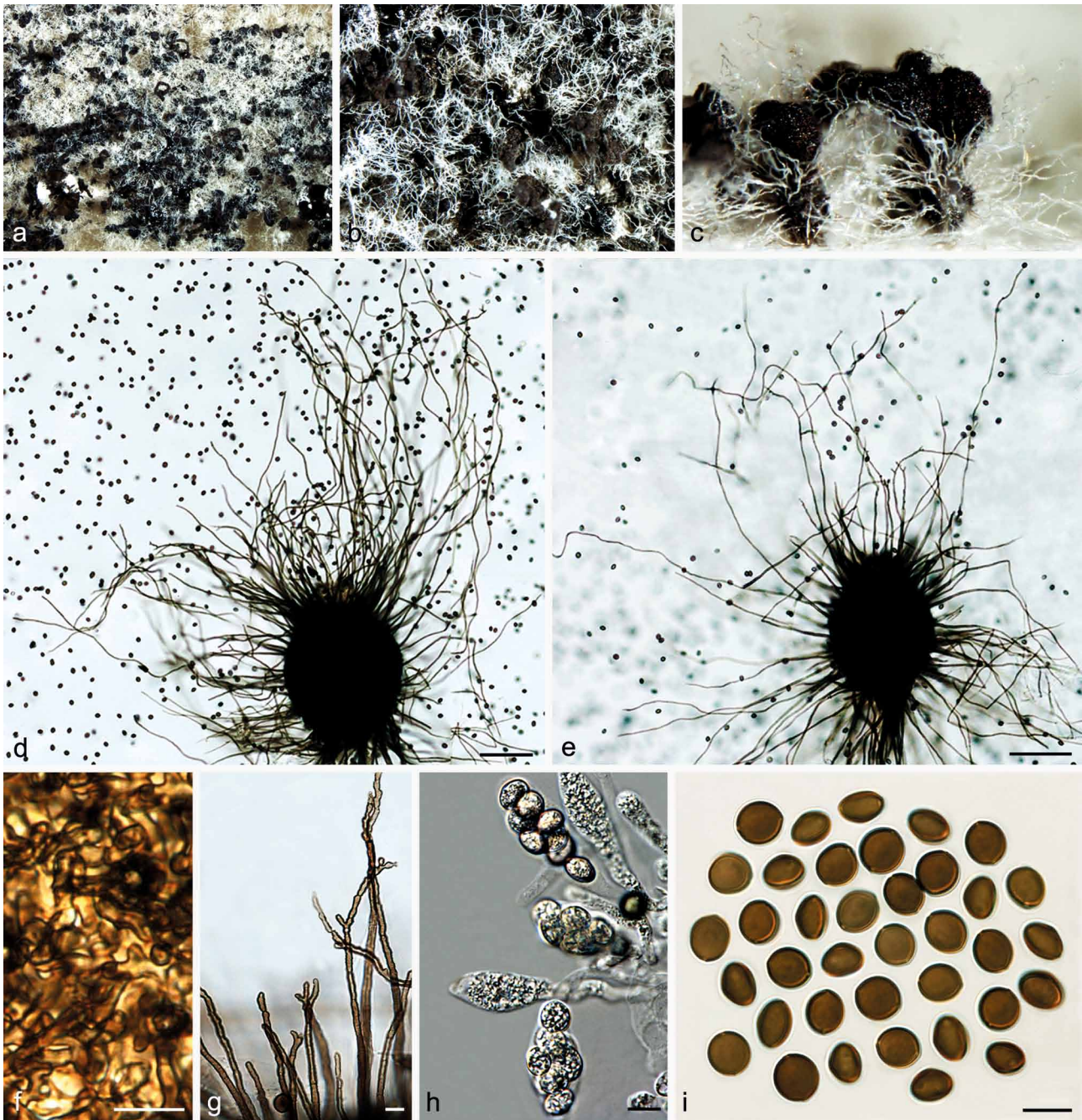


Fig. 5 *Chaetomium ascotrichoides* (CBS 113.83, ex-type culture). a. Part of the colony on OA; b. ascomata on OA, top view; c. ascomata and masses of ascospores on OA, side view; d, e. ascomata mounted in lactic acid; f. structure of ascumatal wall in surface view; g. terminal ascumatal hairs around the ostiole; h. asci; i. ascospores. — Scale bars: d, e = 100 µm; f–i = 10 µm.

601(C); *tcf1* 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), 535(T), 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 floccose 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 cervicola 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 cervicola* forms a unique lineage 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),

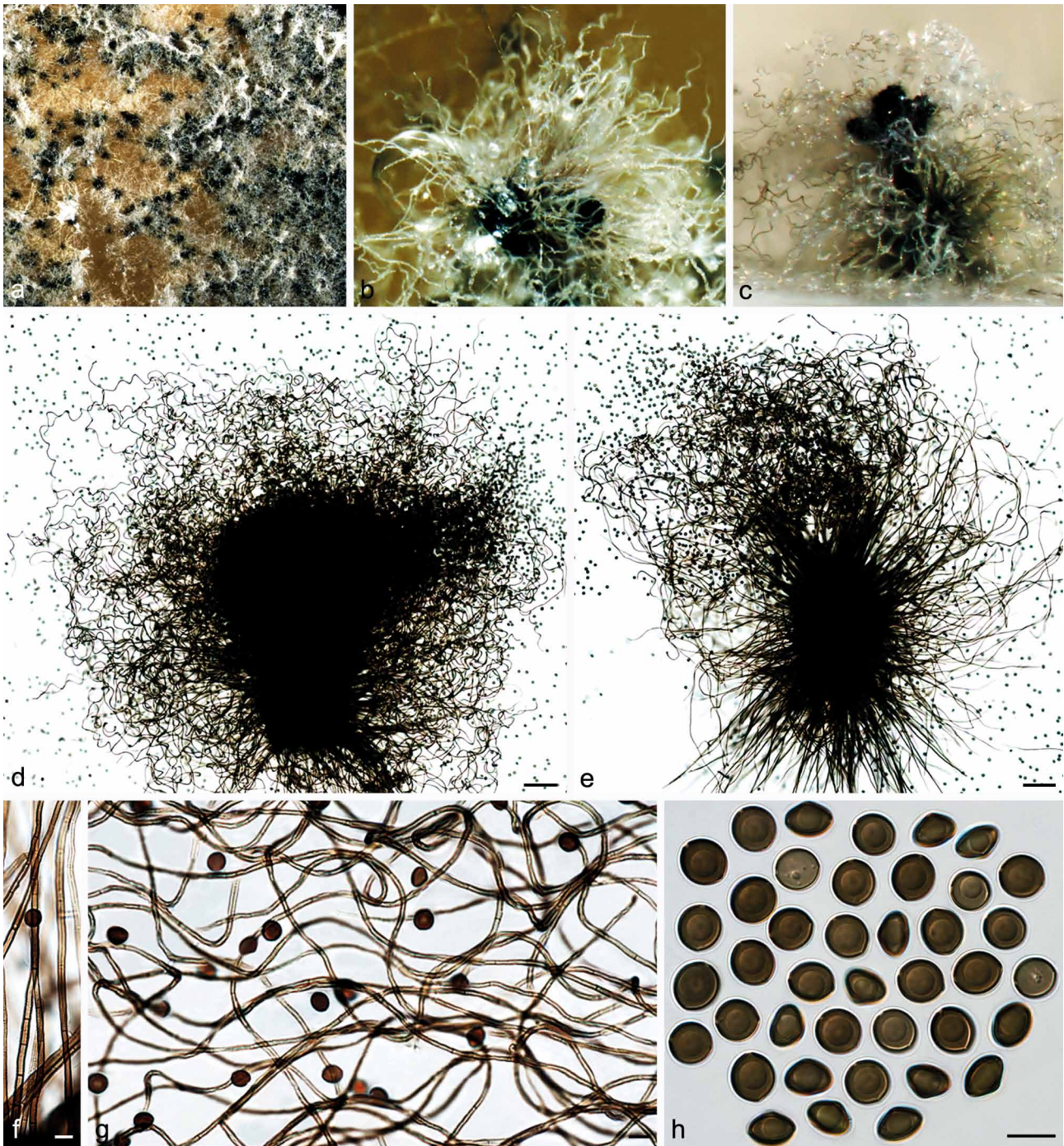


Fig. 6 *Chaetomium ascotrichoides* (CBS 110.83, ex-type of *C. gibberosporum*). a. Part of the colony on OA; b. ascoma on OA, top view; c. ascoma and mass of ascospores on OA, side view; d, e. ascomata mounted in lactic acid; f. basal part of terminal ascomatal hairs; g. upper part of terminal ascomatal hairs; h. ascospores. — Scale bars: d, e = 100 μ m; f–h = 10 μ m.

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); *tef1* 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 floccose aerial hyphae, and without coloured exudates; reverse uncoloured.

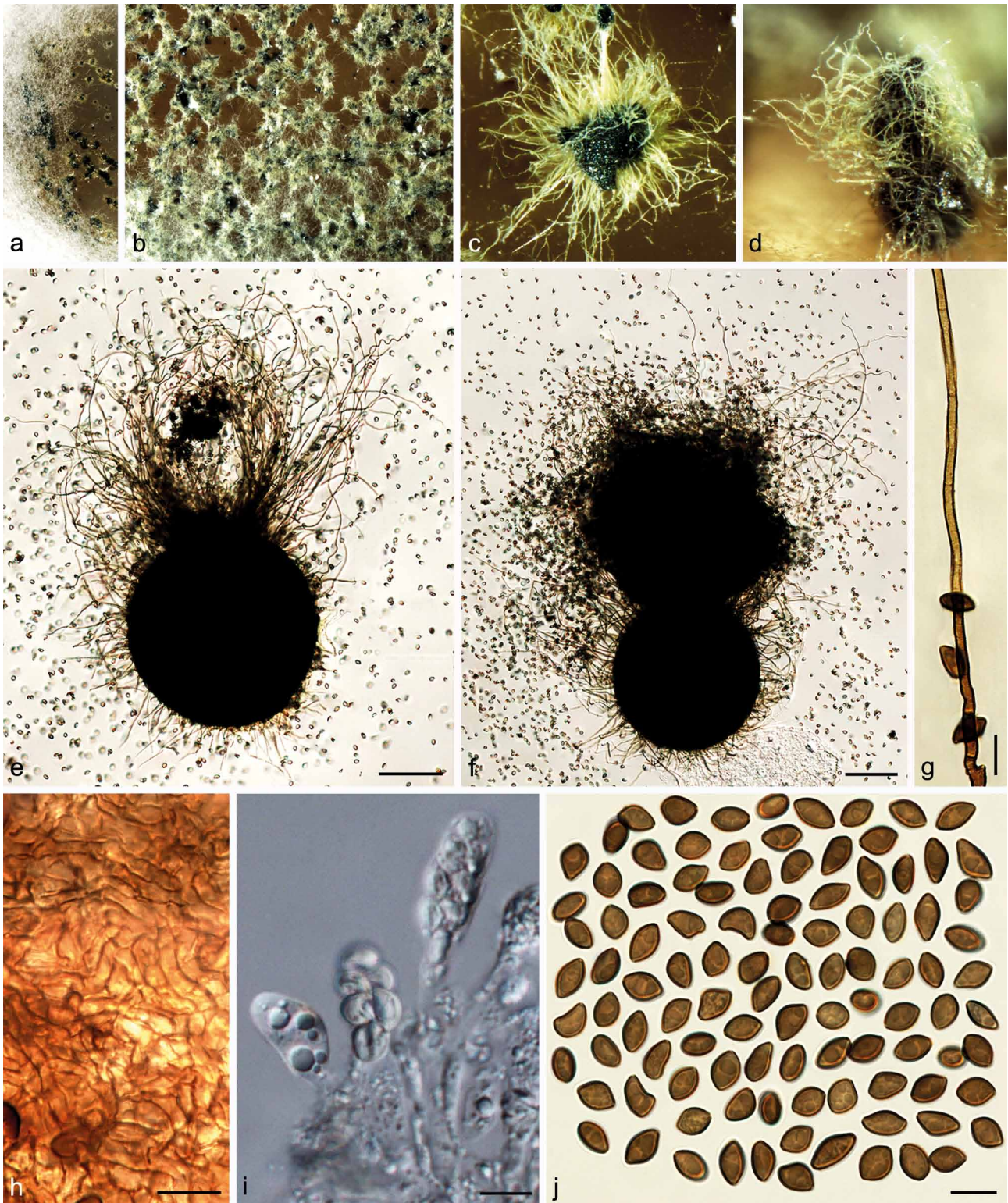


Fig. 7 *Chaetomium citrinum* (CBS 693.82, ex-type culture). a, b. Part of the colony on OA; c. ascoma and mass of ascospores on OA, top view; d. ascoma and mass of ascospores on OA, side view; e, f. ascomata mounted in lactic acid; g. terminal ascomatal hair; h. structure of ascomatal wall in surface view; i. asci; j. ascospores. — Scale bars: e, f = 100 µm; g–j = 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 biseriata ascospores, evanescent. Ascospores pale brown when mature, irregularly fusiform, limoniform, ovate, lunate or triangular, bilaterally flattened, (7–)8–10(–12) \times (4–)5–6(–7) \times 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).

Chaetomium coarctatum Sergeeva, Not. Syst. sect. Crypt. Inst. Bot. Acad. Sci. U.S.S.R. 14: 146. 1961. — Fig. 8

Ascomata superficial, ostiolate, pale grey to olivaceous buff in reflected light owing to ascumal hairs, obovate 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 \times 14–20 μm , stalks 30–53 μm long, with eight biseriata ascospores, evanescent. *Ascospores* olivaceous brown when mature, broad limoniform to nearly globose, biapiculate, bilaterally flattened, (9.5–)10–11(–11.5) \times 9–10(–10.5) \times 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.

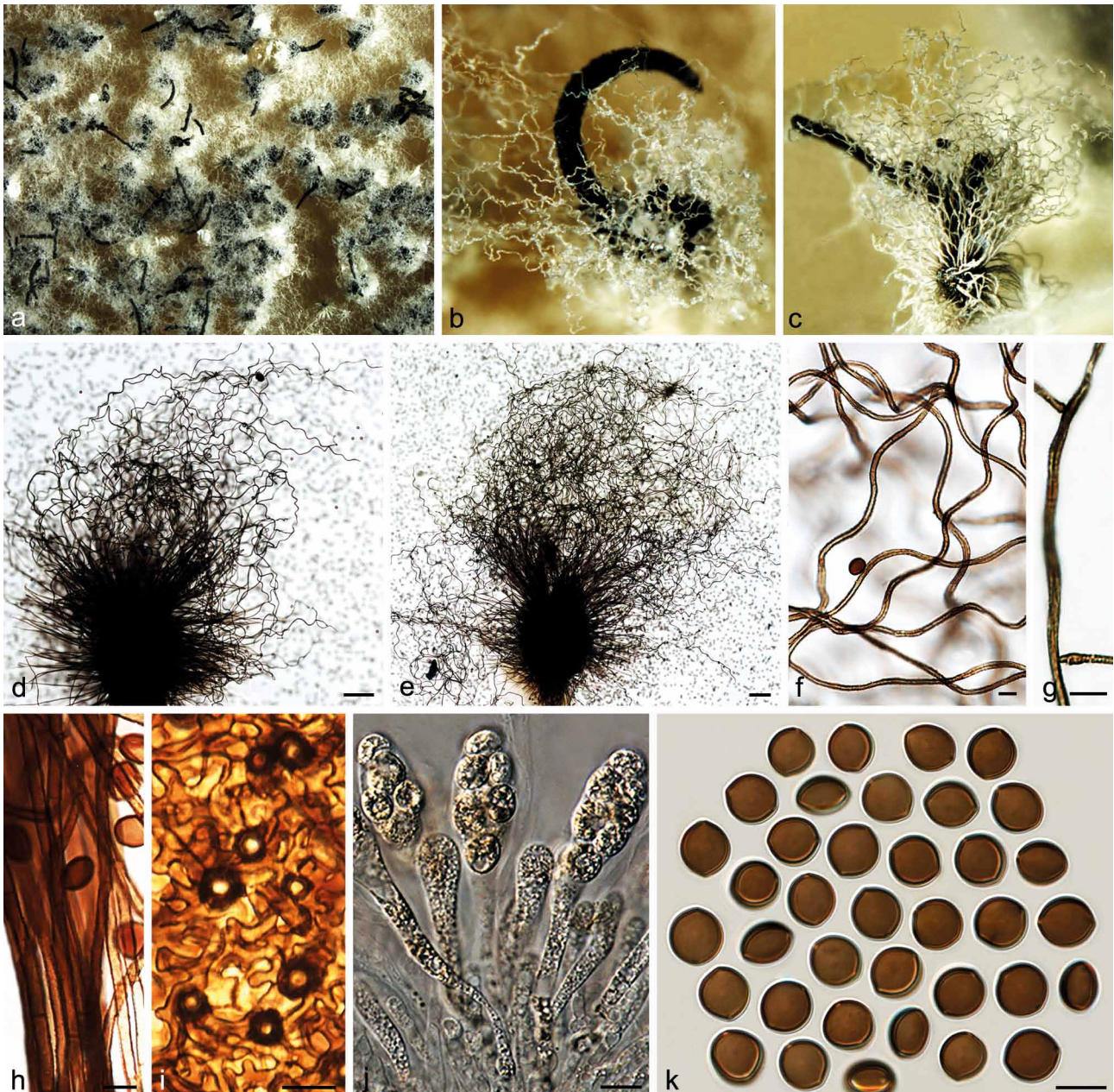


Fig. 8 *Chaetomium coarctatum* (CBS 162.62, ex-type culture). a. Part of the colony on OA; b. ascoma and mass of ascospores on OA, top view; c. ascoma and mass of ascospores on OA, side view; d, e. ascomata mounted in lactic acid; f. upper part of terminal ascumal hairs; g. branched middle part of a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

Materials examined. CHINA, Beijing, Huairou District, from animal dung, Aug. 2009, *J. Li*, CGMCC 3.14293; Xiangshan Park, from unknown plant stem, Aug. 2009, *J. Li*, CGMCC 3.14299. – RUSSIA, St. Petersburg, from seed of *Campanula medium*, collector and collection date unknown, isolated by *K.S. Sergejeva*, deposited in CBS by *K.S. Sergejeva*, Feb. 1962 (culture ex-type CBS 162.62 = ATCC 14530 = IMI 090491 = MUCL 18697 = VKM F-1946).

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 ($10\text{--}11 \times 9\text{--}10 \times 6.5\text{--}7.5 \mu\text{m}$ vs $8.5\text{--}10.5 \times 7\text{--}8 \times 5.5\text{--}6.5 \mu\text{m}$). 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.

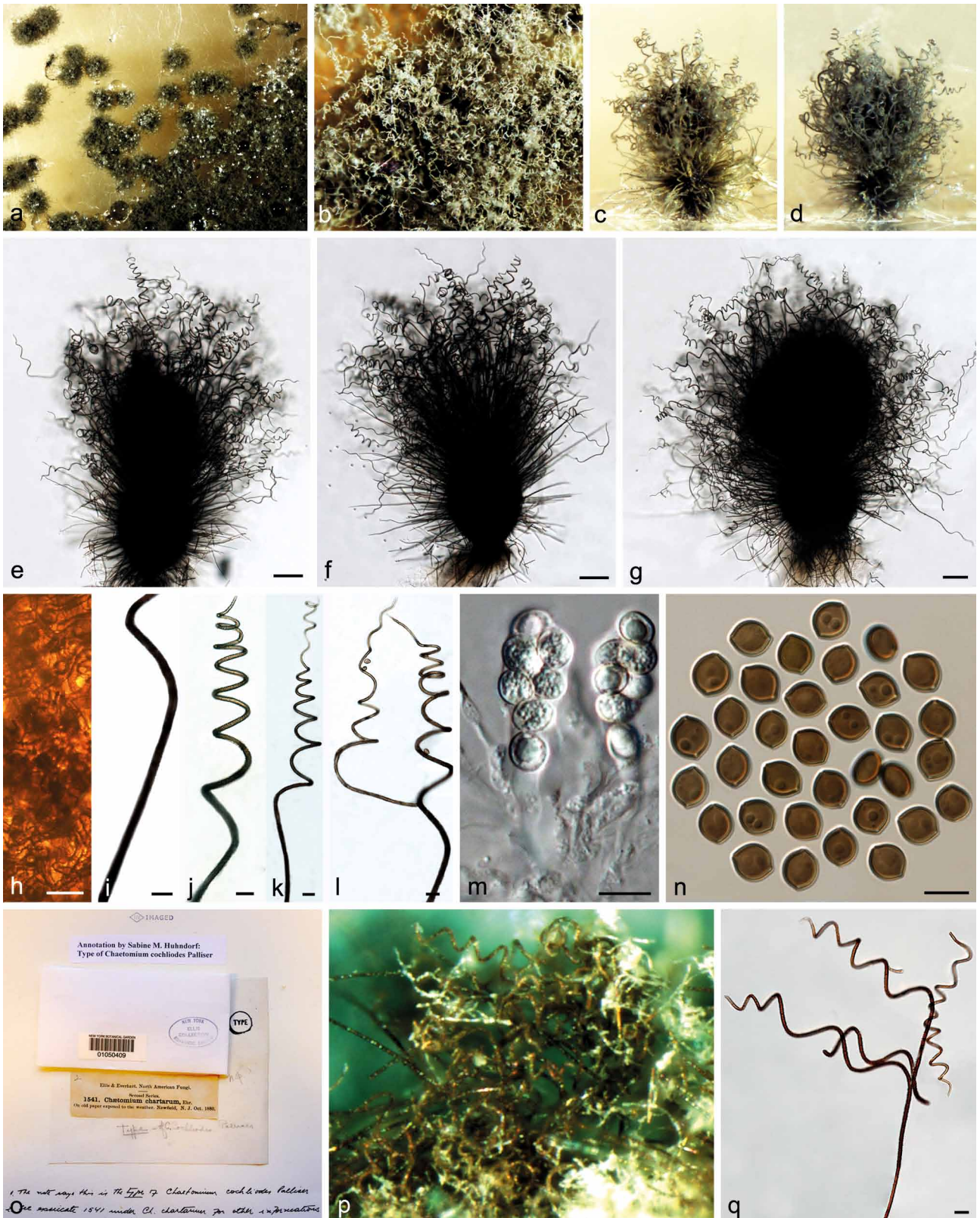


Fig. 9 *Chaetomium cochliodes* (CBS 155.52, ex-epitype culture). a. Part of the colony on OA; b. ascomata on OA, top view; c, d. ascomata on OA, side view; e–g. ascomata mounted in lactic acid; h. structure of ascomatal wall in surface view; i. basal part of a terminal ascomatal hair; j–l. upper parts of terminal ascomatal hairs; m. asci; n. ascospores; o. holotype sheet of *C. cochliodes* in New York Botanical Garden (Specimen ID 01050405); p, q. ascumatal 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 subglobose, 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. *Asci* fasciculate, fusiform 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.

Materials examined. CHINA, Yunnan Province, Wenshan County, from tuber of *Panax notoginseng*, 10 Apr. 2003, X.-Z Liu, CGMCC 3.9440; from rhizosphere of *Panax notoginseng*, 10 Apr. 2003, X.-Z Liu, CGMCC 3.9471; Inner Mongolia Autonomous Region, Huade County, from discarded cloth, Aug. 2009, J. Li, CGMCC 3.14296. — USA, Newfield, New Jersey, on old paper exposed to the weather, Oct. 1880 (Ellis & Everhart, North American Fungi 1541) (holotype New York Botanical Garden Specimen ID 01050405); from animal dung, isolated and deposited in CBS by L.M. Ames, Apr. 1952 (epitype designated here HMAS 244354, MBT201721, culture ex-epitype CBS 155.52).

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. spiculipilium* (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. globosporum* and can be distinguished based on the following fixed unique SNPs: *rpb2* positions 9(G), 45(A), 123(C), 233(A), 265(T), 333(T), 374(G) and 570(C); *tub2* 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); *rpb1* 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); *tub2* 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); *rpb1* 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.

Materials examined. IRAN, Alborz Province, Hashtgerd, isolated from petiole of *Cucumis sativus*, 22 Oct. 2005, B. Asgari, CBS 126777 = IRAN 1642C. — TURKEY, Izmir, substrate unknown, deposited in CBS by G. Turhan, Apr. 1971 (holotype CBS H-22190, culture ex-type CBS 378.71).

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

= *Chaetomium virgecephalum* Ames, A monograph of the *Chaetomiaceae*: 43. 1963.

= *Chaetomium ramipilosum* Schaumann, Arch. Mikrobiol. 91: 98. 1973.

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* fasciculate, 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 solitarily 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.

Materials examined. GERMANY, Helgoland, isolated from *Ammophila arenaria*, isolated and deposited in CBS by K. Schaumann, Nov. 1970 (culture ex-type of *C. ramipilosum* CBS 910.70). — USA, California, Aptos, from decomposing leaf, collection date unknown, H.K. Seth, deposited in CBS by H.K. Seth, Apr. 1966 (culture ex-isotype of *C. virgecephalum* CBS 374.66).

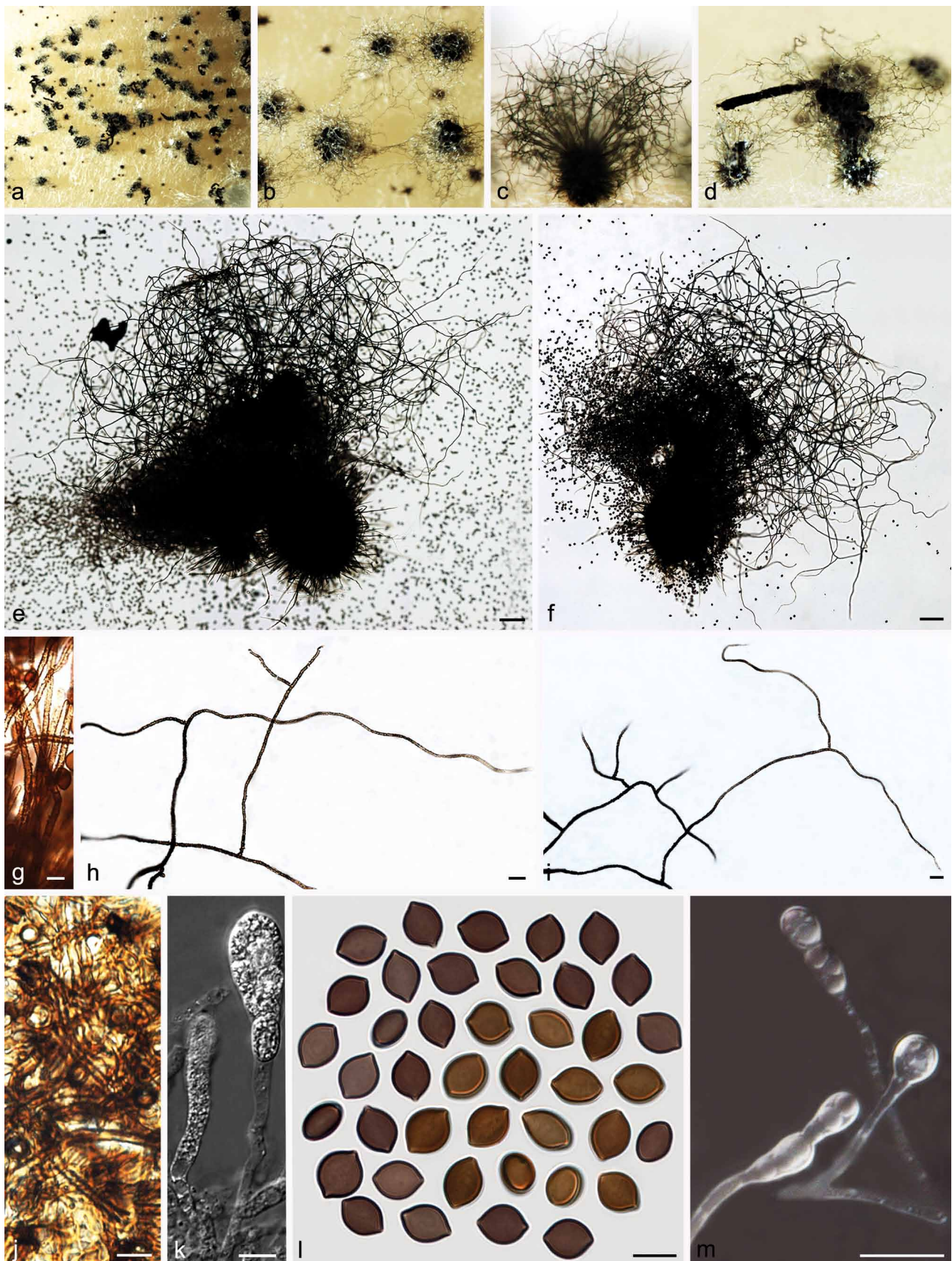


Fig. 10 *Chaetomium elatum* (CBS 910.70, ex-type culture of *C. ramipilosum*). a. Part of the colony on OA; b. ascomata and masses of ascospores on OA, top view; c, d. ascomata and masses of ascospores on OA, side view; e, f. ascomata mounted in lactic acid; g. basal parts of terminal ascumatal hairs; h, i. upper parts of terminal ascumatal hairs; j. structure of ascumatal wall in surface view; k. asci; l. ascospores; m. asexual morph (conidiophores and conidia). — Scale bars: e, f = 100 μ m; g, j–m = 10 μ m; h, i = 20 μ m.

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*

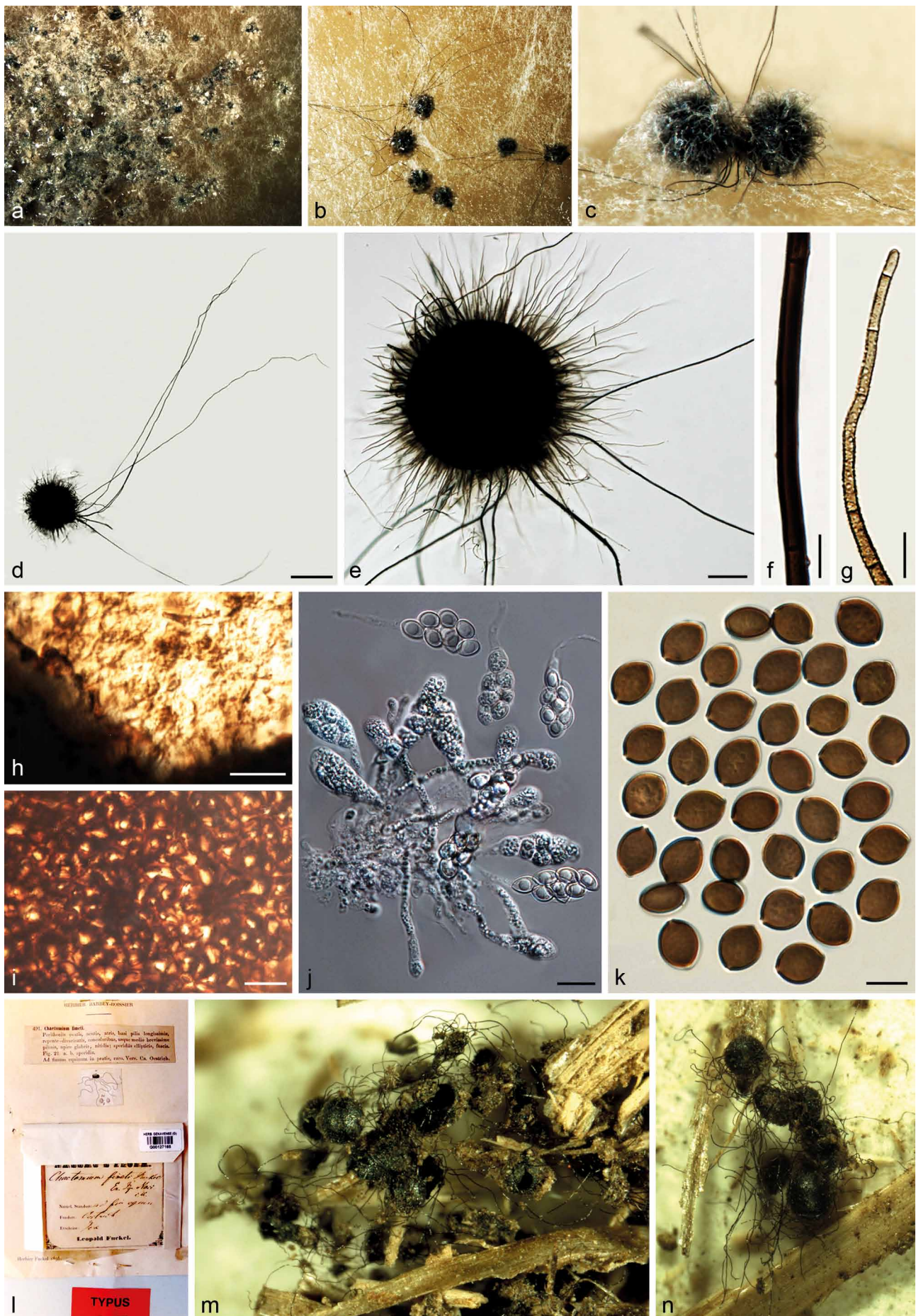


Fig. 11 *Chaetomium fimeti* (CBS 153.77). a. Part of the colony on OA; b. ascomata on OA, top view; c. ascomata on OA, side view; d, e. ascomata mounted in lactic acid; f. part of terminal ascomatal hair, longer type; g. terminal ascomatal hair, shorter type; h. inner layer structure of ascomatal wall in surface view; i. external layer structure of ascomatal wall in surface view; j. asci; k. ascospores; l. holotype sheet of *C. 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, Zentraleinrichtung 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

= *Chaetomidium fimeti* (Fuckel) Sacc., Syll. Fung. 1: 39. 1882.

= *Thielavia fimeti* (Fuckel) Malloch & Cain, Mycologia 65: 1064. 1973.

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 oblate, 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. *Asci* fasciculate, fusiform or clavate, with eight biseri-ate ascospores, spore-bearing part 30–50 × 14.5–19 µm, stalks 23–46 µm long, evanescent. *Ascospores* olivaceous brown to brown when mature, limoniform, bilaterally flattened, (11–)11.5–13.5(–16) × 9–10.5(–11) × (6–)7–8(–8.5) µm, with an apical germ pore. *Asexual morph* absent.

Culture characteristics — Colonies on OA with abundant, olivaceous buff aerial hyphae, producing ochreous to pale amber exudates diffusing into the medium; reverse cinnamon.

Materials examined. CANADA, Ontario, Nashville, from decaying hay, isolated by F.R. Cain, May 1957, deposited in CBS by D.W. Malloch, Jan. 1971, CBS 168.71 = ATCC 22330 = IMI 153720 = TRTC 33005 (sterile). — GERMANY, isolated from soil, collection date unknown, *Bredemeier* (epitype CBS H-22198, MBT201724, culture ex-epitype DSM 62108 = CBS 139034); Oestrich, from horse dung (Hebier Fuckel 1894, holotype G00127165 from HERB. GENAVENSE (G: Conservatoire et Jardin botaniques de la Ville de Genève, Switzerland). — JAPAN, substrate unknown, collector and collection date unknown, deposited in CBS by K. Furuya, Feb. 1977, CBS 153.77 = NHL 2713 = SANK 21476.

Notes — Zopf (1881) split the genus *Chaetomium* into two subgenera: *Euchaetomium* with ostiolate ascomata and *Chaetomidium* with non-ostiolate ascomata. Saccardo (1882) subsequently elevated the subgenus *Chaetomidium* to generic level with *Chaetomidium fimeti* (= *Chaetomium fimeti*) as type species. The genus *Chaetomidium* was rejected by Winter (1885), Chivers (1915) and Ainsworth (1961), but was accepted by Bainier (1910). Ainsworth (1971) re-introduced this genus based on the study of Seth (1967) and following this, Malloch & Cain (1973) treated *Chaetomidium* as a synonym of *Thielavia*, which Von Arx (1975) later distinguished from *Thielavia*. Greif et al. (2009) revealed the polyphyly of the genus *Chaetomidium* using LSU, *tub2* and *rpb2* sequence data, and suggested that this genus be restricted to two species, the type *C. fimeti* and its close relative, *C. subfimeti*. Phylogenetic inference in this study strongly supports *C. fimeti* and *C. subfimeti* as sister lineages (Group IC, Fig 1) within the *C. globosum* complex, consistent with the *rpb2* analysis of Greif et al. (2009). Thus, *Chaetomium fimeti* represents the correct species name, and the genus *Chaetomidium* is considered as a synonym of *Chaetomium*.

Chaetomium globosporum Rikhy & Mukerji, Kavaka 1: 38. 1973. — Fig. 12

Ascomata superficial, ostiolate, usually covered by aerial hyphae, yellow-amber to olivaceous in reflected light owing to ascomatal hairs, soon becoming dark brown to black due to ascospore mass on ascomata, ovate, 350–510 µm high, 210–350 µm diam. *Ascomatal wall* brown, composed of irregular or hypha-like cells, *textura epidermoidea* in surface view. *Terminal hairs* relatively sparse, finely punctate to verrucose, brown, flexuous, occasionally branched or geniculate, 2.5–4.5 µm near the base and tapering towards the tips. *Lateral hairs* similar. *Asci* fasciculate, clavate or slightly fusiform, with eight biseri-ate ascospores, spore-bearing part 24–43 × 16–24 µm, stalks 11–26 µm long, evanescent. *Ascospores* dark brown when mature, globose to subglobose, non-apiculate, bilaterally flattened, (10–)10.5–12(–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.

Material examined. INDIA, isolated from green leaf of *Triticum aestivum*, deposited in CBS by J.N. Kapoor, Jan. 1983 (culture ex-type CBS 108.83 = ITCC 1835).

Notes — Only the ex-type strain is known for this species. *Chaetomium globosporum* is closely related to *C. megalocarpum* and *C. grande* (Group IA, Fig 1). This species is easily distinguished by its smaller and more regular, oblate 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

= *Chaetomium globosum* var. *flavoviride* E.K. Novák, Ann. Univ. Sci. Budapest. Rolando Eotvos, Sect. Biol. 8: 207. 1966.

= *Chaetomium globosum* var. *griseum* E.K. Novák, Ann. Univ. Sci. Budapest. Rolando Eotvos, Sect. Biol. 8: 207. 1966.

= *Chaetomium mollipilium* Ames, Mycologia 42: 642. 1950.

= *Chaetomium rectum* Sergeeva, Not. Syst. sect. Crypt. Inst. Bot. Acad. Sci. U.S.S.R. 14: 143. 1961.

= *Chaetomium subterraneum* Swift & Povah, Mycologia 21: 210. 1929.

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. *Asci* fasciculate, fusiform or clavate, spore-bearing part 30–40 × 12–17 µm, stalks 15–25 µm long, with eight biseri-ate 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.

Materials examined. CHINA, Beijing, Peking University Third Hospital, isolated from finger nail of *Homo sapiens*, collection date unknown, D.-M. Li, CGMCC 3.9994. — GERMANY, from compost, isolated and deposited in CBS by A. von Klopotek, Apr. 1962, (neotype designated here: CBS H-22185, MBT201725, culture ex-neotype CBS 160.62). — HUNGARY, from dead stems

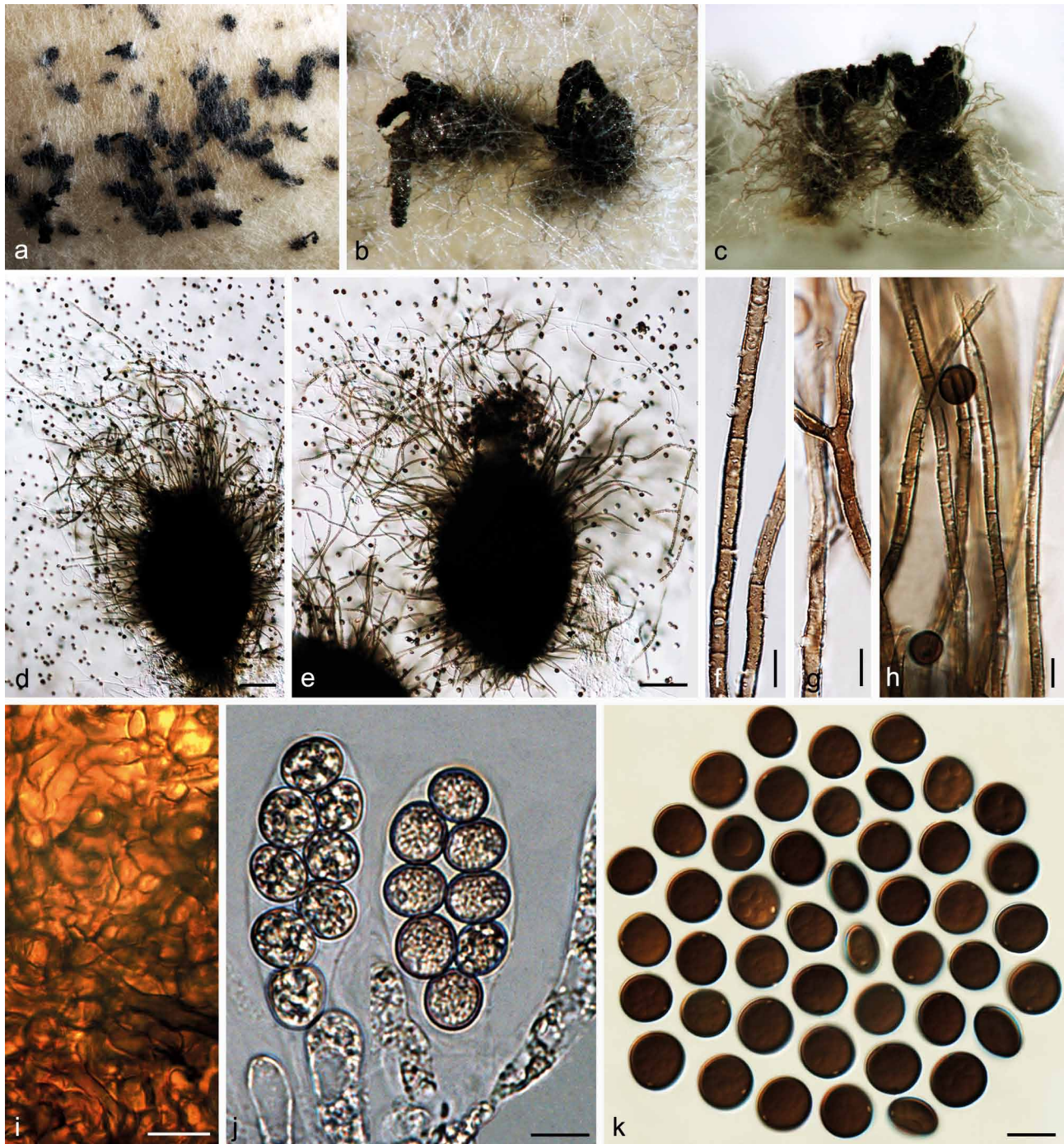


Fig. 12 *Chaetomium globosporum* (CBS 108.83, ex-type culture). a. Part of the colony on OA; b. ascomata and masses of ascospores on OA, top view; c. ascomata and masses of ascospores on OA, side view; d, e. ascomata mounted in lactic acid; f. basal parts of terminal ascumatal hairs; g. branched upper part of a terminal ascumatal hair; h. unbranched upper parts of terminal ascumatal hairs; i. structure of ascumatal wall in surface view; j. asci; k. ascospores. — Scale bars: d, e = 100 μ m; f–k = 10 μ m.

of *Juncus* sp., 1966, E. Novak, MUCL 39526 (culture ex-type of *C. globosum* var. *flavoviride*); from dead stem of *Juncus* sp., 1966, E. Novak, MUCL 39527 (culture ex-type of *C. globosum* var. *griseum*). — NETHERLANDS, Bibliotheek van het Koloniaal Instituut, Amsterdam, isolated from mouldy book, collector and collection date unknown, isolated by F.H. van Beyma, CBS 105.40. — POLAND, Bydgoszcz Botanic Garden, collector and collection date unknown, isolated by K.S. Sergejeva, 1961 (culture ex-type of *C. rectum* CBS 164.62 = ATCC 14529 = IMI 090488 = MUCL 18692 = VKM F-1949). — USA, Illinois, isolated from clay soil at 120 cm depth, collector and collection date unknown, isolated and deposited in CBS by B.B. Kanouse, July 1930 (culture ex-type of *C. subterraneum* CBS 132.30); Jeffersonville, Indiana, isolated from a Japanese raincoat, collector and collection date unknown, isolated by G.W. Martin (culture ex-type of *C. mollipilium* CBS 147.60 = ATCC 11209 = IFO 9108 = MUCL 9596 = QM 1007 = QM 1107); Washington DC, isolated from stored cotton, isolated by H. Hunfield, 1933, CBS 148.51 = ATCC 6205 = CBS 161.52 = CEB 1218.1 = CEB 1218.2 = CECT 2701 = DSM 1962 = IFO

6347 = IHEM 3826 = IMI 045550 = MUCL 1984 = NRRL 1870 = QM 459 = UPSC 3159 = USDA 1042.4 = VTT D-81079.

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*.

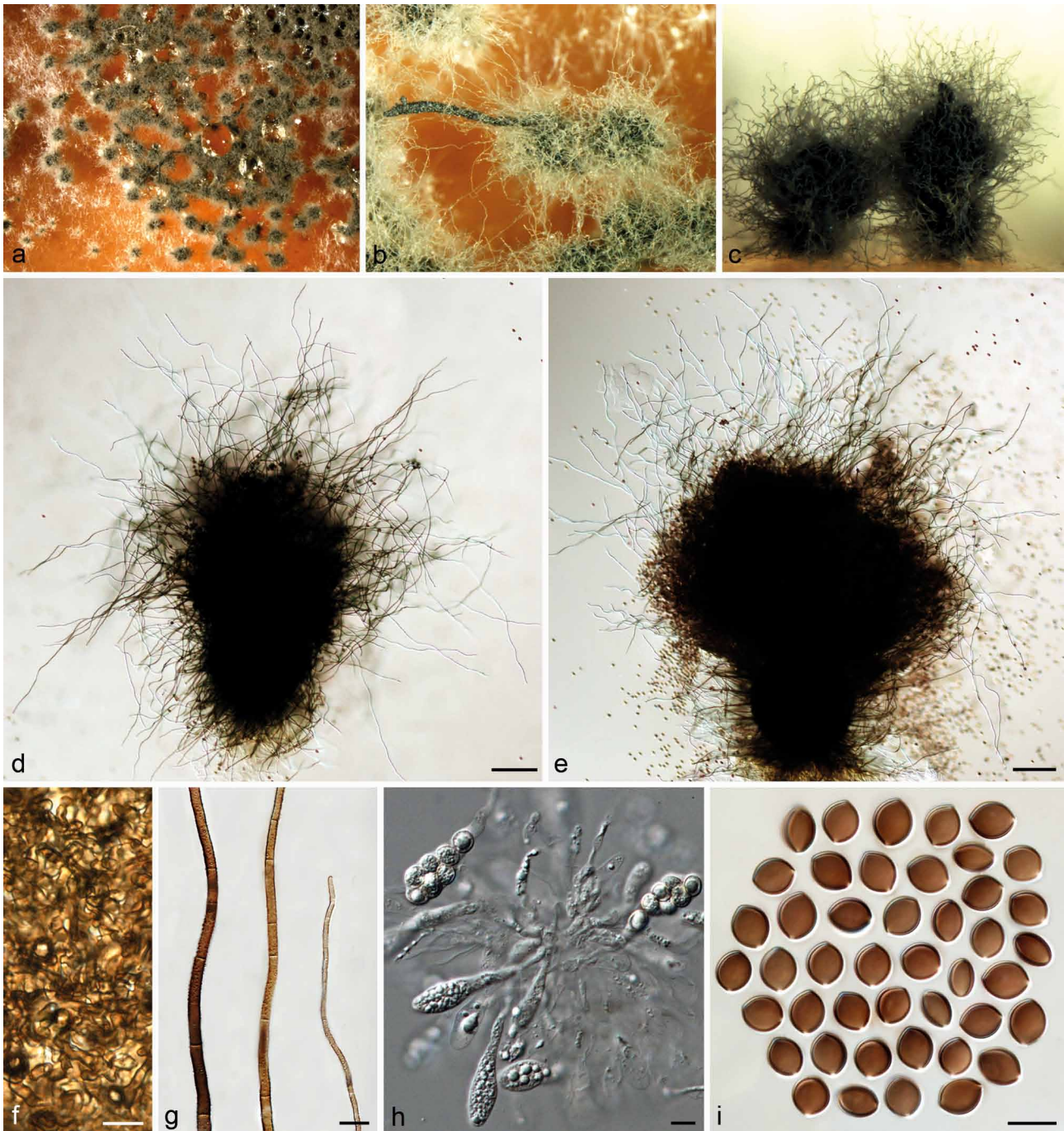


Fig. 13 Typical morphology of *Chaetomium globosum* sensu stricto-1 (CBS 160.62, ex-neotype culture). a. Part of the colony on OA; b. ascomata and masses of ascospores on OA, top view; c. ascomata on OA, side view; d, e. ascomata mounted in lactic acid; f. structure of ascomatal wall in surface view; g. terminal ascomatal hairs (from left to right: lower part, middle part and upper part); h. asci; i. ascospores. — Scale bars: d, e = 100 μ m; f–i = 10 μ m.

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 \times 7.5–8.5 \times 5.5–6 μ m) and CBS 147.60 (9–10.5 \times 7.5–8.5 \times 5–6 μ m) resemble those of *C. globosum* s.str. (8.5–10.5 \times 7–8 \times 5.5–6.5 μ m). 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 μ m diam near the base) than those of typical *C. globosum* (3–5 μ m 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-

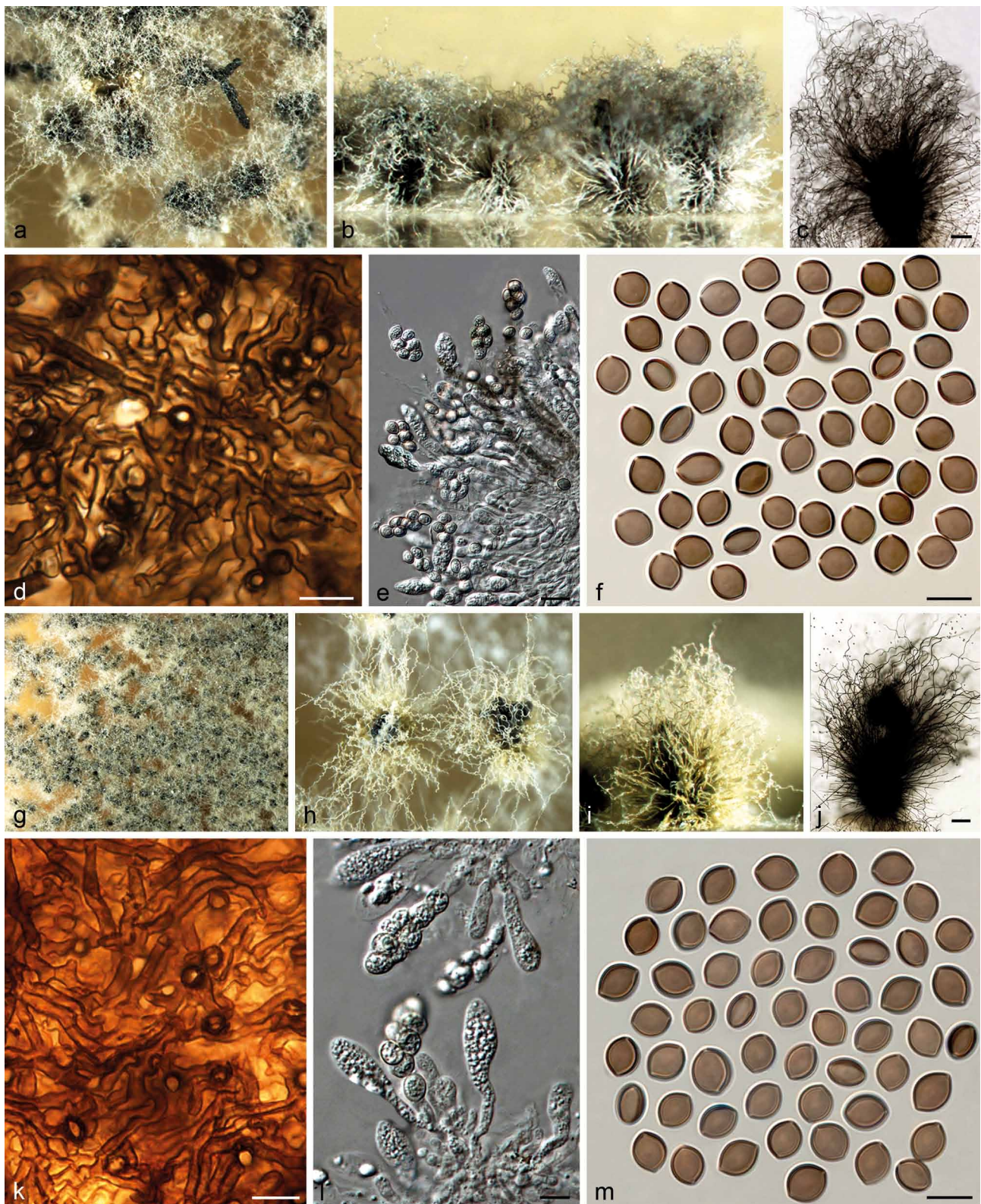


Fig. 14 Typical morphology of *Chaetomium globosum* sensu stricto-2. a–f. MUCL 39526 (ex-type of *C. globosum* var. *flavoviride*): a. Ascomata and masses of ascospores on OA, top view; b. ascomata on OA, side view; c. ascoma mounted in lactic acid; d. structure of ascomatal wall in surface view; e. 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 μ m; d, f, k–m = 10 μ m; e = 20 μ m.

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.

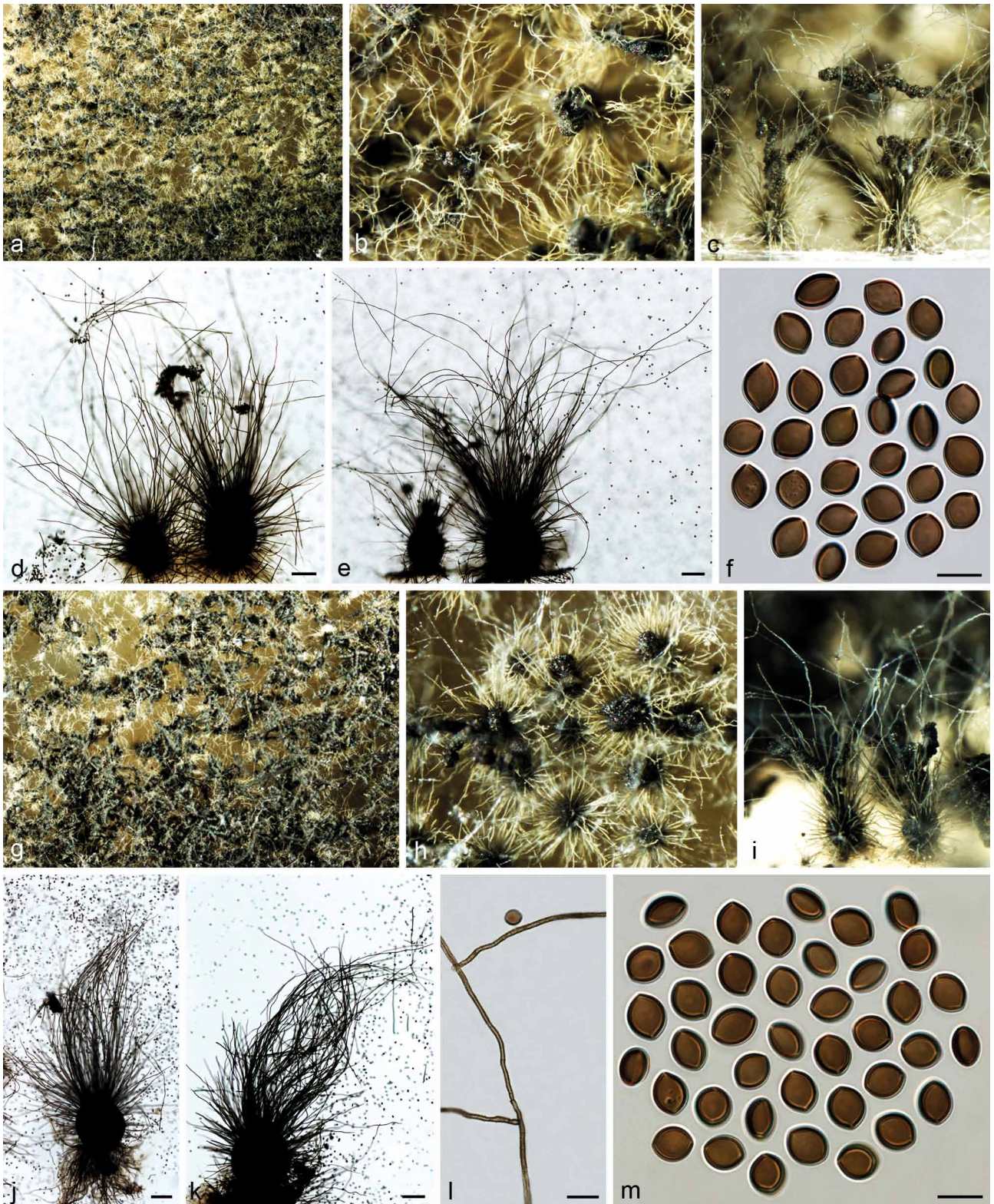


Fig. 15 Variation of *Chaetomium globosum*. a–f. CBS 164.62 (ex-type of *C. rectum*): a. Part of the colony on OA; b. ascomata and masses of ascospores on OA, top view; c. ascomata and masses of ascospores on OA, side view; d, e. ascomata mounted in lactic acid; f. ascospores. – g–m. CBS 147.60 (ex-type of *C. mollipilium*): g. part of the colony on OA; h. ascomata and masses of ascospores on OA, top view; i. ascomata and masses of ascospores on OA, side view; j, k. ascomata mounted in lactic acid; l. simply-branched ascomatal hairs; m. ascospores. — Scale bars: d, e, j, k = 100 µm; l = 20 µm; f, m = 10 µm.

***Chaetomium globosum* morphological form ‘*cruentum*’ — Fig. 16**

Ascomata superficial, ostiolate, globose, ellipsoid, ovate or obovate, 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, $9.5\text{--}11\text{--}(11.5) \times 7.5\text{--}8.5\text{--}(9) \times (6\text{--})6.5\text{--}7$ µm, with an apical germ pore. *Asexual morph* absent.

Culture characteristics — Colonies on OA without aerial hyphae, and producing yellow to yellowish amber exudates

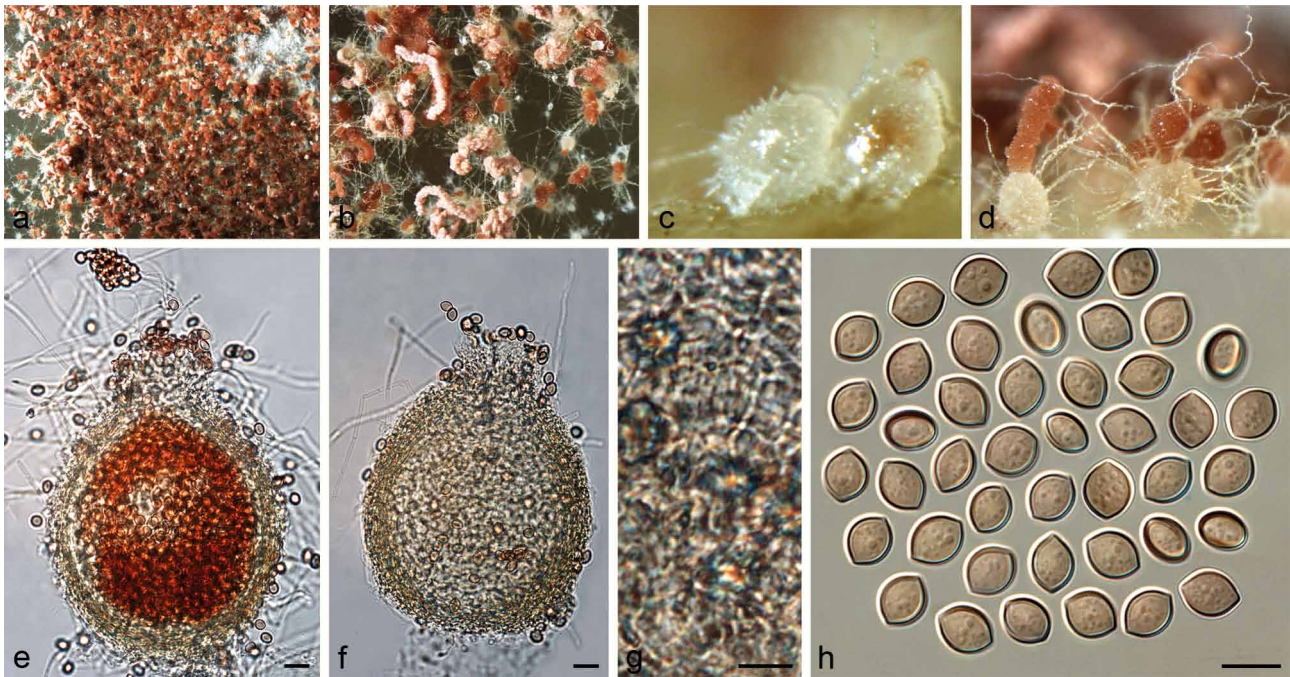


Fig. 16 *Chaetomium globosum* morphological form 'cruentum' (CBS 371.66, ex-type of *C. cruentum*). a. Part of the colony on OA; b. ascomata and masses of ascospores on OA, top view; c. young ascomata on OA; d. mature ascomata and masses of ascospores on OA, side view; e. ascoma full of ascospores; f. ascoma from which ascospores have been discharged; g. structure of ascomal wall in surface view; h. ascospores. — Scale bars: e, f = 20 μ m; g, h = 10 μ m.

diffusing into the medium; reverse uncoloured, but ochreous or fulvous under ascomata.

Materials examined. UK, isolated from rabbit dung, collector and collection date unknown, isolated by *H.K. Seth*, deposited in CBS by *H.K. Seth*, Oct. 1968 (culture ex-type of *Lophotrichus incarnatus* CBS 730.68 = ATCC 18597 = IMI 135564). — UNKNOWN, substrate and collection details unknown, isolated and deposited in CBS by *L.M. Ames*, June 1958, CBS 145.58. — USA, Fort Belvoir, Virginia, from paper, collection date unknown, isolated by *L.M. Ames*, deposited in CBS by *H.K. Seth*, Apr. 1966 (isotype of *C. cruentum* CBS H-6860, culture ex-isotype CBS 371.66).

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

Etymology. Refers to the grass-like ascomatal hairs formed by this fungus.

Ascomata superficial, ostiolate, luteous to amber or citrine in reflected light owing to ascomatal hairs, becoming dark due to ascospore masses on the top, ellipsoid, subglobose or ovate, 200–320 μ m high, 170–260 μ m diam. **Ascomatal wall** brown, composed of hypha-like or amorphous cells, *textura epidermoidea* or *textura intricata*. **Terminal hairs** sparse, olivaceous brown and fading towards the tips, punctate, erect or flexuous, sometimes simply branched, 3.5–4.5 μ m diam near the base, tapering towards almost pointed tips. **Lateral hairs** similar. **Asci** fasciculate, fusiform or clavate, spore-bearing part 25.5–40 \times 12.5–16 μ m, stalks 14.5–29 μ m long, with eight biserial ascospores, evanescent. **Ascospores** olivaceous brown when mature, limoniform, bilaterally flattened, (9.5–)10–11.5(–12) \times 9–10 \times (5.5–)6–7 μ m, 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 usually uncoloured, but dark grey-olivaceous under ascomata.

Material examined. CANADA, Muskoka District, Ontario, from *Acer* sp., 1967, *D. Malloch*, isolated and deposited in CBS by *J.C. Krug* (holotype CBS H-22193, culture ex-type CBS 506.84 = TRTC 47862).

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 \times 8–9 \times 6–7 μ m) compared to those of *C. globosum* morphological form 'rectum' (9–10.5 \times 7.5–8.5 \times 5–6 μ m). 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*.

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, olivaceous in reflected light owing to ascomatal hairs, subglobose or ovate, 270–380 μ m high, 190–310 μ m diam. **Ascomatal wall** brown, composed of amorphous cells, *textura epidermoidea* in surface view. **Terminal hairs** finely punctate to verrucose, brown at the base, fading towards the tips, flexuous to undulate, sometimes branched, 3–4.5 μ m near the base, tapering towards the tips. **Lateral hairs** similar. **Asci** fasciculate, fusiform or clavate, with eight biserial or irregularly-arranged ascospores, spore-bearing part 51–66 \times 22.5–28.5 μ m, stalks 20.5–38 μ m long, evanescent. **Ascospores** dark brown when mature, ellipsoid to subglobose, usually irregular, bilaterally flattened, (17–)18–20.5(–22.5) \times (14.5–)16–18(–19) \times (11–)12–13.5(–14) μ m, with two apical or subapical germ pores. **Asexual morph** absent.

Culture characteristics — Colonies on OA with abundant white aerial hyphae, usually without exudates; reverse cinnamon to fulvous.

Materials examined. CHINA, Xinjiang Autonomous Region, Bayinguoleng, isolated from desert soil, June 2012, *X.-W. Wang*, CBS 119758 = CGMCC 3.9414. — 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

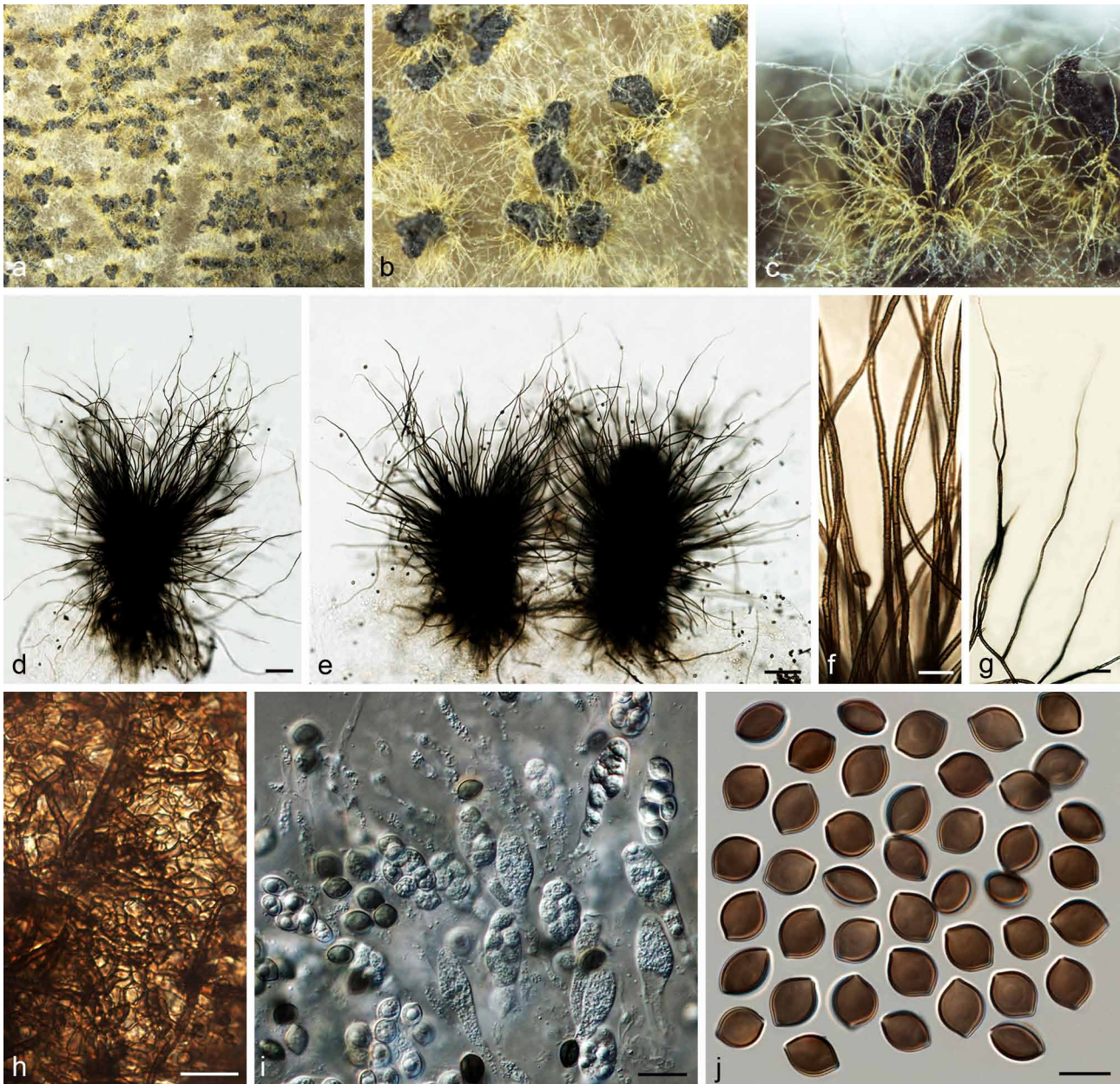


Fig. 17 *Chaetomium graminiforme* (CBS 506.84, ex-type culture). a. Part of the colony on OA; b. ascomata and masses of ascospores on OA, top view; c. ascomata and masses of ascospores on OA, side view; d, e. ascomata mounted in lactic acid; f. basal parts of terminal ascumatal hairs; g. upper parts of terminal ascumatal hairs; h. structure of ascumatal wall in surface view; i. asci; j. ascospores. — Scale bars: d, e = 100 μ m; f–i = 20 μ m; j = 10 μ m.

June 2005, *B. Asgari* (holotype IRAN 14608F, culture ex-type CBS 126780 = IRAN 1064C).

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 μ m) compared to those of *C. megalocarpum* (13–15 \times 11.5–14 \times 8.5–10 μ m) and *C. globosporum* (10.5–12 μ m diam, 7.5–8.5 μ m 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 ascumatal hairs, ovate or ellipsoid, 230–360 μ m high, 170–240 μ m diam. **Ascumatal 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 μ m diam near the base, tapering towards the tips. **Lateral hairs** similar. **Asci** fasciculate, clavate or fusi-form, with eight biseriolate or irregularly arranged ascospores, spore-bearing part 30–41 \times 14–28 μ m, stalks 15–29 μ m long, evanescent. **Ascospores** dark brown when mature, globose to subglobose, non-apiculate, bilaterally flattened, (10–)11–12 μ m diam, (7.5–)8–9 μ m 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.

Material examined. IRAN, East Azerbaijan province, Hadishahr, isolated from seed of *Triticum aestivum*, 24 June 2005, *B. Asgari* (holotype IRAN 14607F, culture ex-type CBS 126660 = IRAN 1278C).



Fig. 18 *Chaetomium grande* (CGMCC 3.9414). a. Part of the colony on OA; b. ascomata on OA, top view; c. ascoma and mass of ascospores on OA, side view; d, e. ascomata mounted in lactic acid; f. basal parts of terminal ascomatal hairs; g. upper part of a terminal ascomatal hair; h. structure of ascomatal wall in surface view; i, j. asci; k. ascospores. — Scale bars: d, e = 100 μ m; f–h, j, k = 10 μ m; i = 20 μ m.

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 \times 170–240 μ m) with abundant, smooth and undulate ascomatal hairs distinguish *C. interruptum* from *C. globosporum*, which produce larger ascomata (350–510 \times 210–350 μ m) 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 μ m high, 140–260 μ m 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 μ m near the base. *Lateral hairs* similar. *Asci* fasciculate, fusi-form or clavate, spore-bearing part 28–38 \times 13–20 μ m, stalks 16–30 μ m long, with eight biserial 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

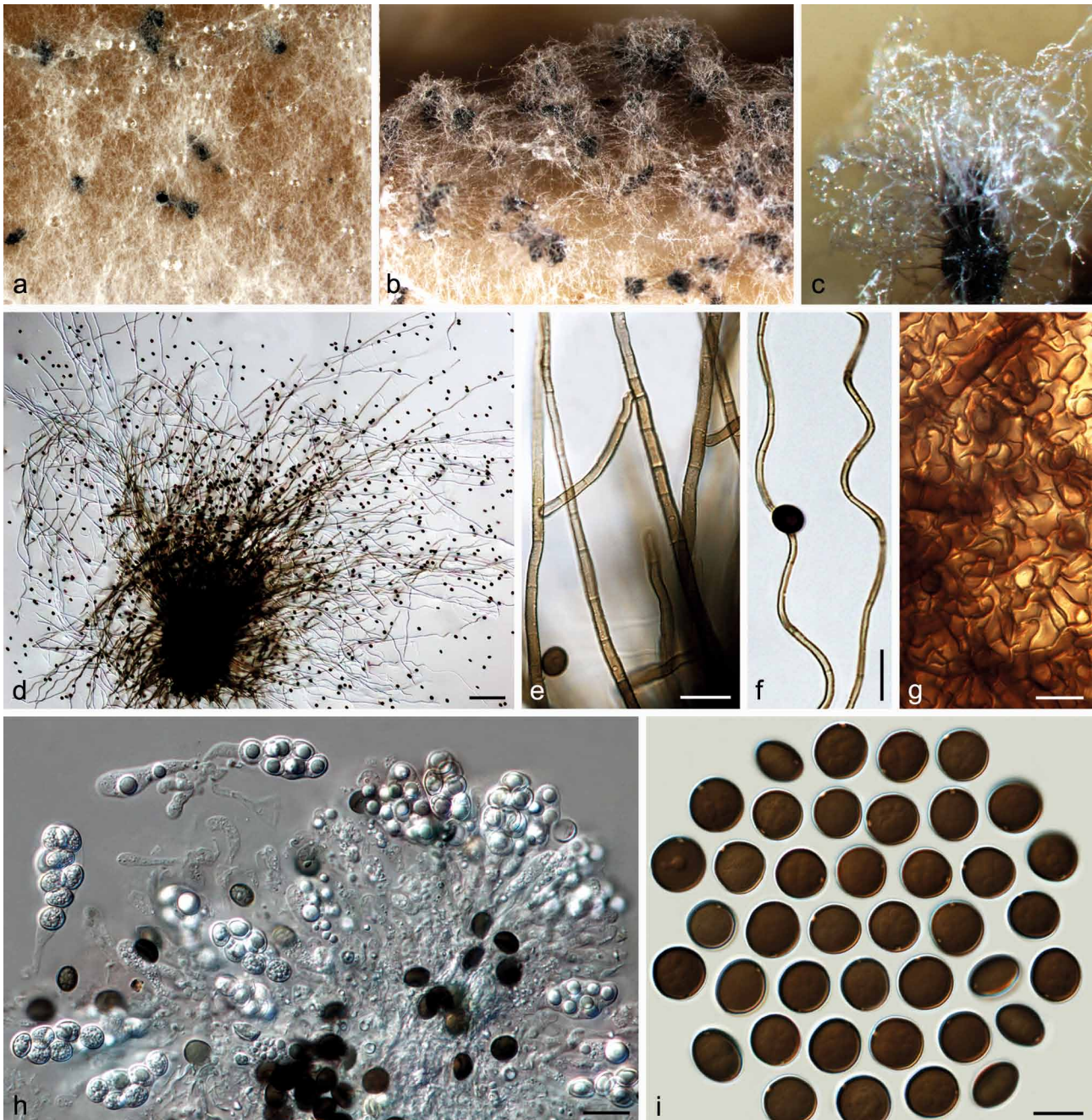


Fig. 19 *Chaetomium interruptum* (CBS 126000, ex-type culture). a. Part of the colony on OA; b. ascomata on OA, top view; c. ascoma on OA, side view; d. ascoma mounted in lactic acid; e. basal parts of terminal ascomatal hairs; f. upper parts of terminal ascomatal hairs; g. structure of ascomatal wall in surface view; h. asci; i. ascospores. — Scale bars: d = 100 μm ; e, f, h = 20 μm ; g, i = 10 μm .

bulge, 10–11(–11.5) \times (8–)9–10 \times 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.

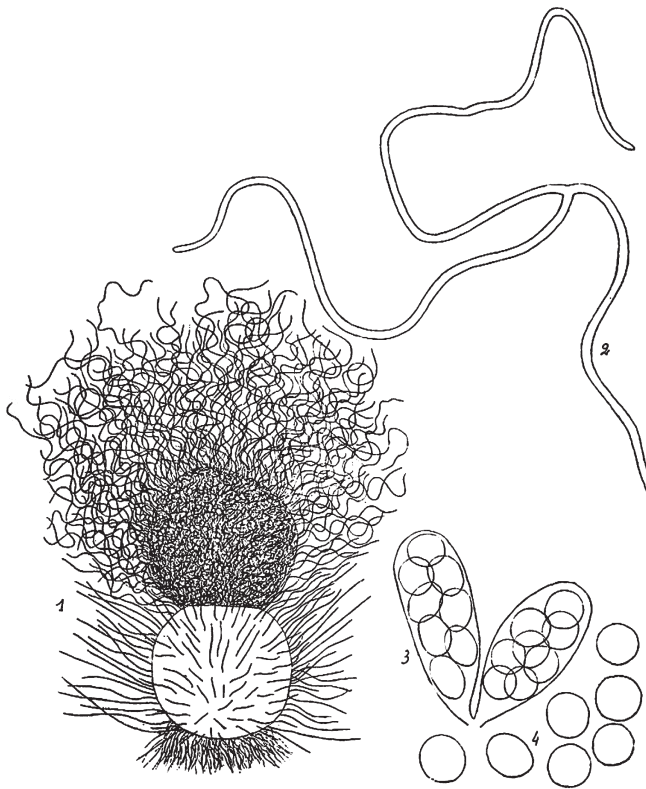
Material examined. INDIA, Madras, Tamil Nadu, from rhizosphere of *Pennisetum typhoides*, collection date unknown, K. Natarajan, isolated by K. Natarajan, 1966 (isotype CBS H-6877, culture ex-isotype CBS 315.74).

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 to undulate, sometimes branched, 3–5 μm near the base, tapering towards the tips. **Lateral hairs** similar. **Asci** fasciculate, fusiform or clavate, with eight biseriate or irregularly arranged ascospores, spore-bearing part 30.5–50.5 \times 15–24 μm , stalks 14–30.5 μm long, evanescent. **Ascospores** dark brown when



G. BAINIER ad nat. del.

Chaetomium megalocarpum sp. nov. (fig. 1-4).

Fig. 20 *Chaetomium megalocarpum*. Illustrated by Bainier (1910, Bull. Soc. Mycol. Fr. 25: PL XVI, f. 1-4), selected as a lectotype in this study.

mature, ellipsoid to subglobose, usually irregular, bilaterally flattened, (12–)13–15(–17) × (10–)11.5–14 × (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 fulvous 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 (epitype designated here CBS H-22186, MBT201728, culture ex-epitype CBS 149.59 = IMI 075851 = MUCL 9589). — INDIA, Yusmarg, 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 × 11.5–14 × 8.5–10 µm vs 18–20.5 × 16–18 × 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 novozelandicum X. Wei Wang, Crous & L. Lombard, sp. nov. — MycoBank MB812980

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

Cultures sterile. *Chaetomium novozelandicum* 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), 69(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); *tub2* 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), 570(G), 579(G), 656(T) and 707(T); *tef1* 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 724(C); ITS positions 142(C) and 452(C).

Culture 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, culture ex-isotype CBS 124555); same collection details, CBS 124556. — USA, California, isolated from scalp of *Homo sapiens*, deposited in CBS by D.A. Sutton, 29 Sept. 2010, CBS 128484 = UTHSC 08-1518 = dH 21631.

Notes — Both phylogenetic inference and SNP analysis indicate that *C. novozelandicum* 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.

Chaetomium nozdrenkoae Sergeeva, Not. Syst. sect. Crypt. Inst. Bot. Acad. Sci. U.S.S.R. 14: 140. 1961. — Fig. 23

Ascomata superficial or covered by aerial hyphae, ostiolate, umber 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 apices, 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 biserially or irregularly-arranged ascospores, occasionally with eight ascospores uniseriately arranged in a nearly cylindrical ascus, spore-bearing part 53–93 × 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) × (11–)11.5–15(–17) × (9–)10–11.5(–12.5) µm, usually with two, three or occasionally four apical, subapical or lateral germ pores. *Asexual morph* absent.

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

Materials examined. GERMANY, Giessen, isolated from greenhouse soil, collector and collection date unknown, isolated by D. Bredemeier, 1967, CBS 809.68 = IMI 180408. — RUSSIA, Novosibirsk region, isolated from virgin soil, collector and collection date unknown, isolated by K.S. Sergejeva, 1961 (culture ex-type CBS 163.62 = ATCC 14528 = IMI 090490 = IMI 090490ii = MUCL 18703 = VKM F-1953).

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.

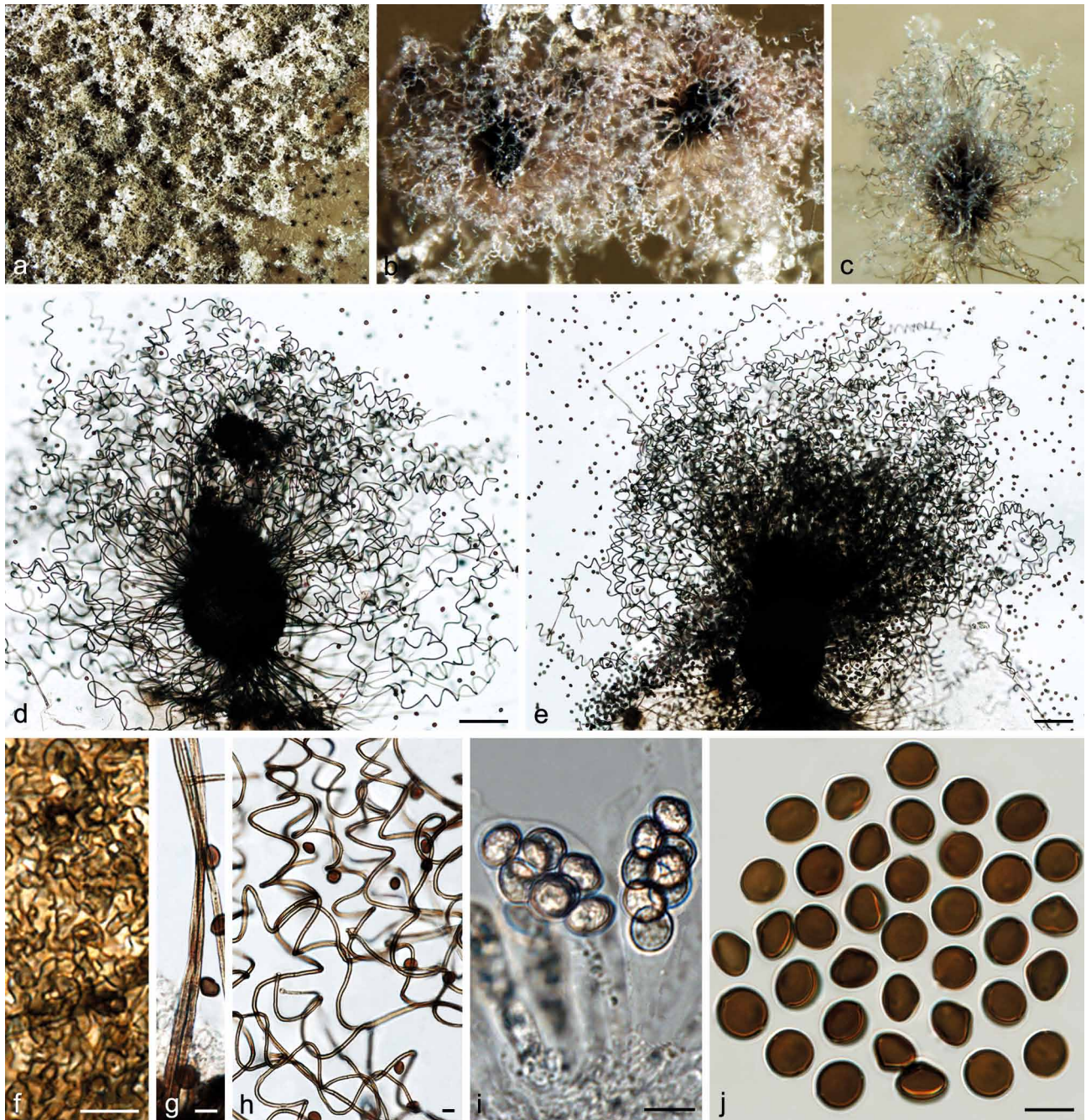


Fig. 21 *Chaetomium madrasense* (CBS 315.74, ex-type culture). a. Part of the colony on OA; b. ascomata and masses of ascospores on OA, top view; c. ascoma on OA, side view; d, e. ascomata mounted in lactic acid; f. structure of ascomatal wall in surface view; g. basal parts of terminal ascomatal hairs; h. upper parts of terminal ascomatal hairs; i. asci; j. ascospores. — Scale bars: d, e = 100 μ m; f–j = 10 μ m.

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 μ m high, 200–360 μ m 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 μ m near the base, tapering towards the tips. **Lateral hairs** similar. **Asci** fasciculate, clavate or slightly fusiform, with eight biserial ascospores, spore-bearing part 34–41 \times 13–20 μ m, stalks 26–45 μ m long, evanescent. **Ascospores** olivaceous brown when mature, limoniform to broad limoniform, usually biapiculate, bilaterally flattened, (10–)11–12(–12.5) \times 8–9 \times 6–7 μ m, 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.

Materials examined. CHINA, Aksu region, Xinjiang, from camel dung, Mar. 2009, F.-J. Liu, CGMCC 3.12883; Jilin Province, Changchun, from soil, Aug. 2002, X.-W. Wang, CGMCC 3.9465. — INDIA, Delhi, from nilgai (*Boselaphus tragocamelus*) dung, 28 Apr. 1977, K.G. Mukerji, isolated by J.A. von Arx, CBS 418.80A.

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 \times 9–10 \times 6–7 μ m) than those of *C. globosum* (8.5–10.5 \times 7–8 \times 5.5–6.5 μ m). Phylogenetic inference indicated that *C. olivaceum* is in Group III (Fig. 1), closely related to *C. cucumericola* (sterile species), *C. undulatum* and *C. subglosum*. *Chaetomium undulatum* (Asgari & Zare 2011) can be distinguished from *C. olivaceum* by smaller ascomata (230–280 μ m high, 185–250 μ m diam),

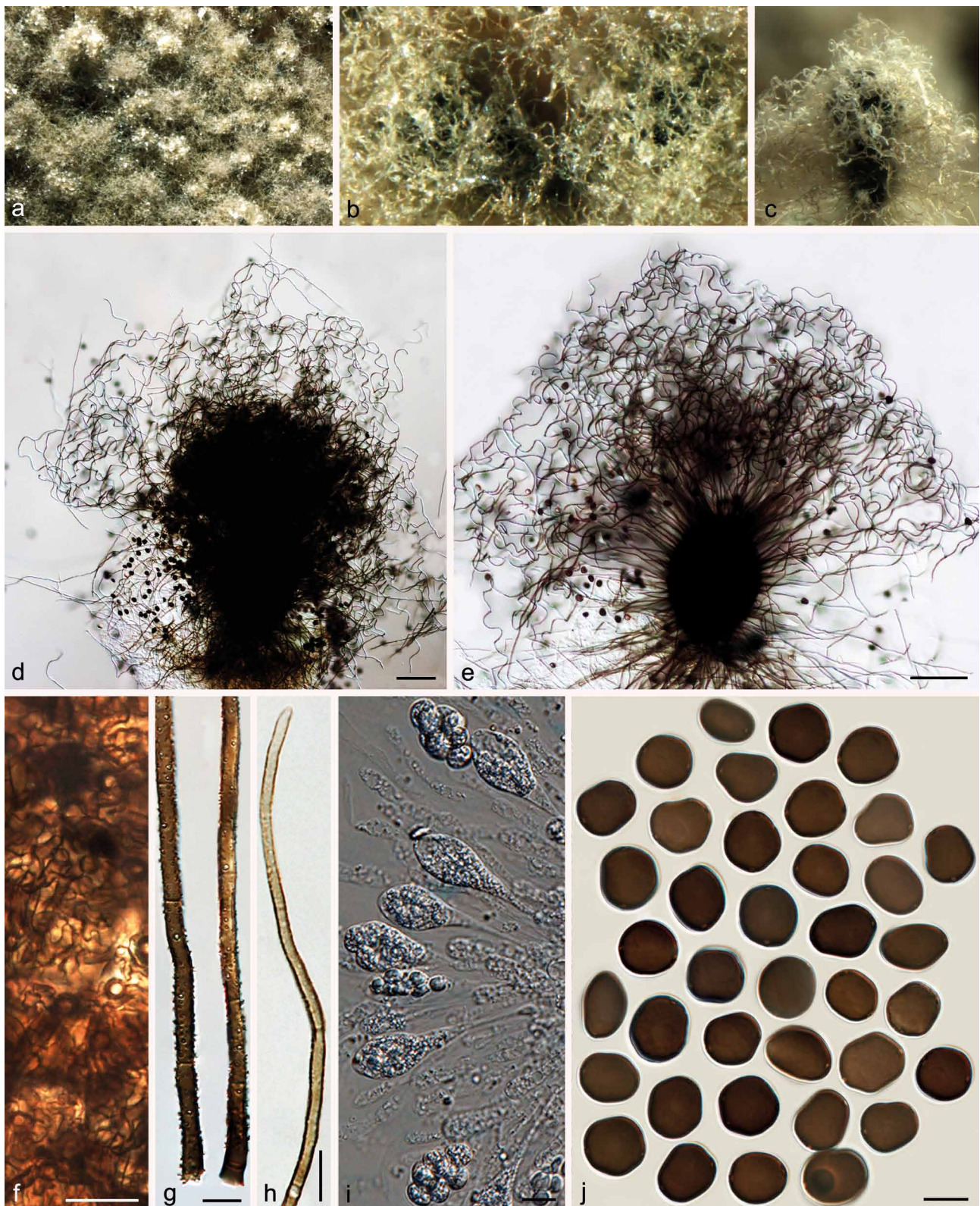


Fig. 22 *Chaetomium megalocarpum* (CBS 149.59, ex-epitype culture). a. Part of the colony on OA; b. ascomata on OA, top view; c. ascoma and mass of ascospores on OA, side view; d, e. ascomata mounted in lactic acid; f. structure of ascomatal wall in surface view; g. basal parts of terminal ascomatal hairs; h. upper part of a terminal ascomatal hair; i. asci; j. ascospores. — Scale bars: d, e = 100 μ m; f–h = 20 μ m; i, j = 10 μ m.

longer ascospores (12–13.5 \times 8–10 \times 6–7.5 μ m) and more undulate ascomatal hairs. *Chaetomium subglobosum* is also distinct from *C. olivaceum* in having larger ascospores (12–13.5 \times 10.5–12 \times 7–8.5 μ m). 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 & Sipton) X. Wei Wang & Crous, *comb. nov.* — MycoBank MB812981; Fig. 25

Basionym. *Thielavia pilosa* C. Booth & Sipton, *Trans. Brit. Mycol. Soc.* 49: 665. 1966.

\equiv *Chaetomidium pilosum* (C. Booth & Sipton) Arx, *Stud. Mycol.* 8: 16. 1975.

Ascomata superficial, or covered by aerial hyphae, non-ostio-late, black in reflected light due to the dark ascomatal wall,

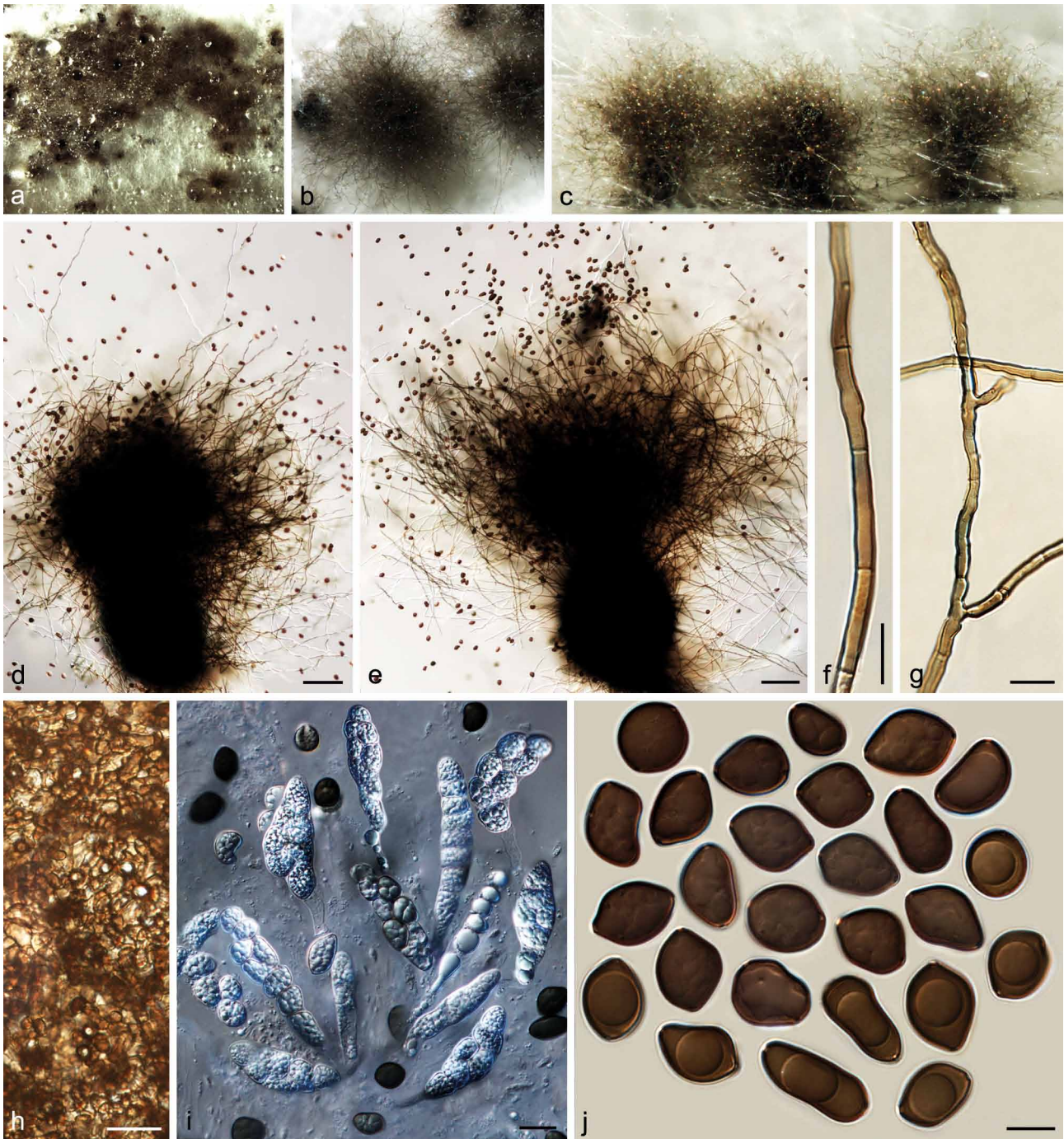


Fig. 23 *Chaetomium nozdrenkoae* (CBS 163.62, ex-isotype culture). a. Part of the colony on OA; b. ascomata on OA, top view; c. ascomata on OA, side view; d, e. ascomata mounted in lactic acid; f. terminal ascomatal hair; g. branched terminal ascomatal hair; h. structure of ascomatal wall in surface view; i. asci; j. ascospores. — Scale bars: d, e = 100 µm; f, g, j = 10 µm; h, i = 20 µm.

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 biserial or irregularly arranged ascospores, spore-bearing part 22–38 × 12.5–18 µm, stalks 10–24 µm long, evanescent. *Ascospores* 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*.

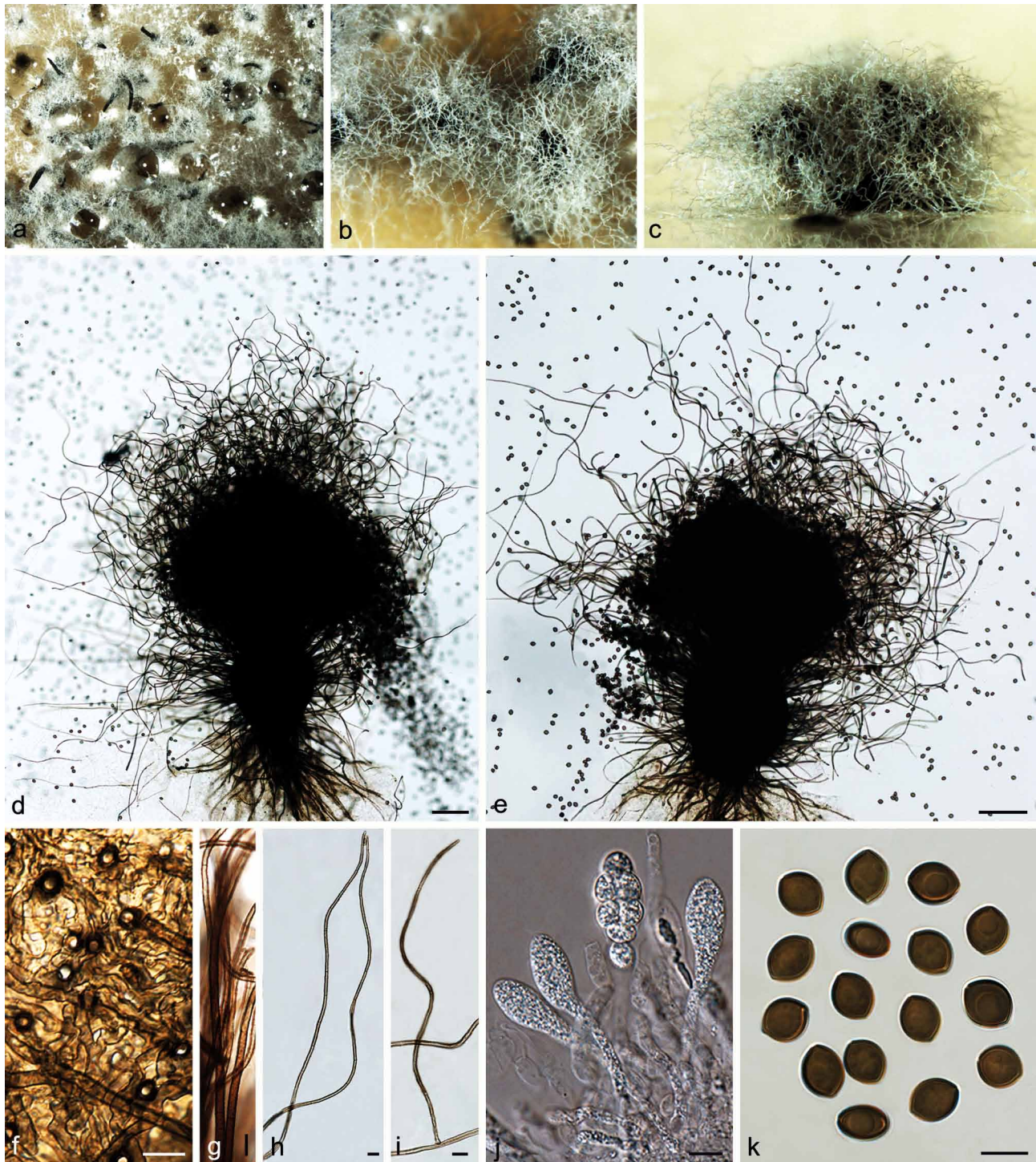


Fig. 24 *Chaetomium olivaceum* (CBS 418.80A). a. Part of the colony on OA; b. ascomata on OA, top view; c. ascomata on OA, side view; d, e. ascomata mounted in lactic acid; f. structure of ascomatal wall in surface view; g. basal parts of terminal ascomatal hairs; h, i. upper parts of terminal ascomatal hairs; j. asci; k. ascospores. — Scale bars: d, e = 100 μ m; f–k = 10 μ m.

Ascomata superficial, ostiolate, citrine green to citrine in reflected light owing to ascomatal hairs, ellipsoid, ovate or subglobose, 270–425 μ m high, 190–370 μ m 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 μ m 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 μ m near the base, flexuous. *Lateral hairs* hypha-like, flexuous, tapering towards tips. *Asci* fasciculate, elongated clavate, spore-bearing part 24–37 \times 7–14 μ m, stalks 17–42 μ m long, with eight bise-

riate ascospores, evanescent. *Ascospores* olivaceous brown or brown when mature, limoniform, biapiculate, slightly umbonate at both ends, bilaterally flattened, (9–)9.5–11(–11.5) \times (7–)7.5–8.5(–9) \times 5.5–6.5(–7) μ m, 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.

Materials examined. CHINA, Yunnan Province, Wenshan County, from fibrous root of *Panax notoginseng*, 10 Apr. 2003, X.-Z. Liu (holotype HMAS 244435, isotype CBS H-22197, culture ex-type CGMCC 3.9441); from the rhizosphere of *P. notoginseng*, 13 Apr. 2003, X.-Z. Liu, CGMCC 3.9469.

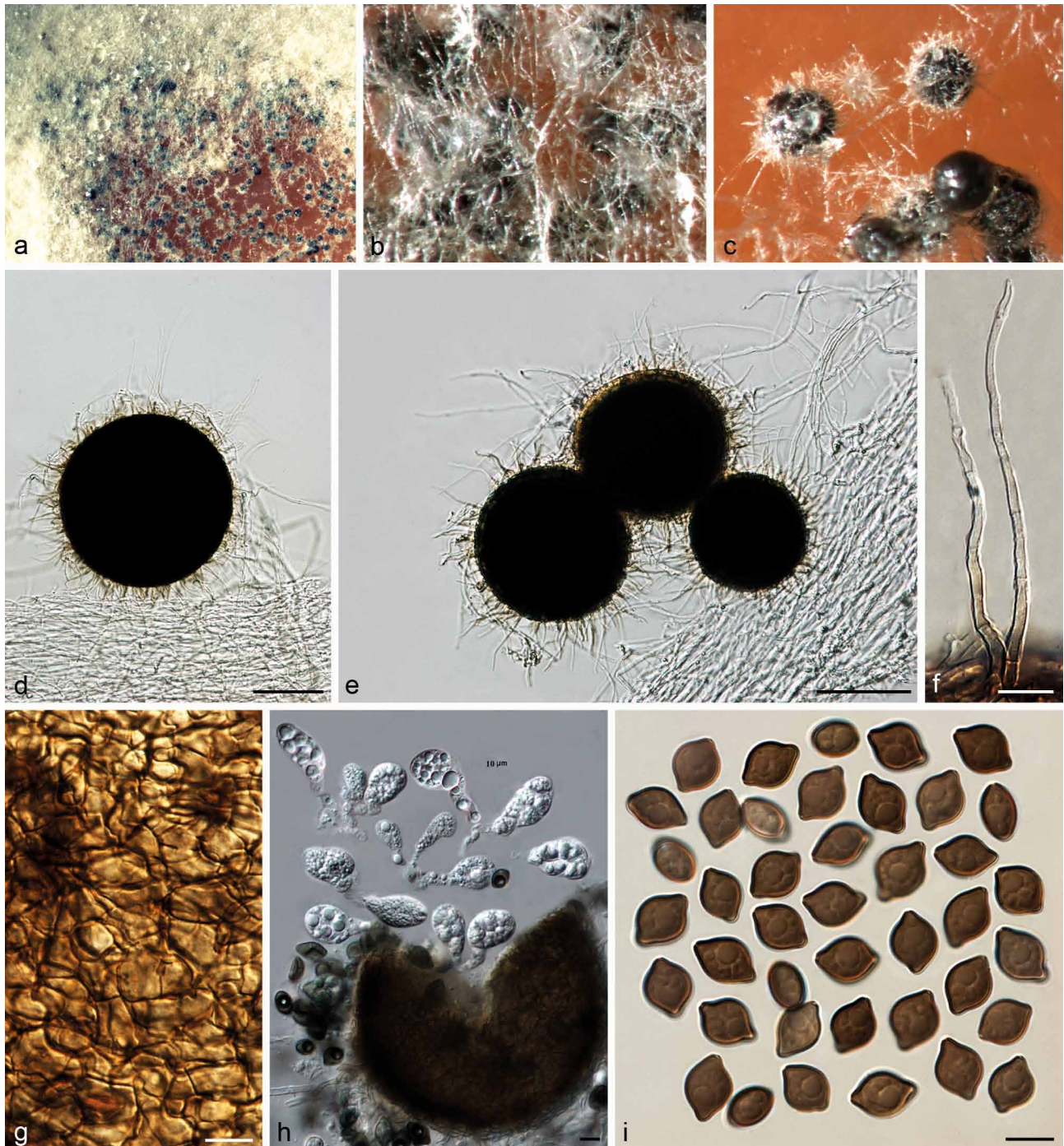


Fig. 25 *Chaetomium pilosum* (CBS 335.62, ex-epitype culture). a. Part of the colony on OA; b. ascomata covered by hyphae on OA, top view; c. exposed ascomata on OA, top view; d, e. ascomata mounted in lactic acid; f. ascomatal hairs; g. structure of ascomatal wall in surface view; h. asci; i. ascospores. — Scale bars: d, e = 100 μm ; f–i = 10 μm .

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 \times 10–14 μm , stalks 17–36 μm long, with eight biseri-ate ascospores, evanescent. **Ascospores** olivaceous brown when mature, limoniform, bilaterally flattened, 9–10(–10.5) \times (6–)6.5–7.5(–8) \times 5–6(–6.5) μm , with an apical germ pore. **Asexual morph** absent.

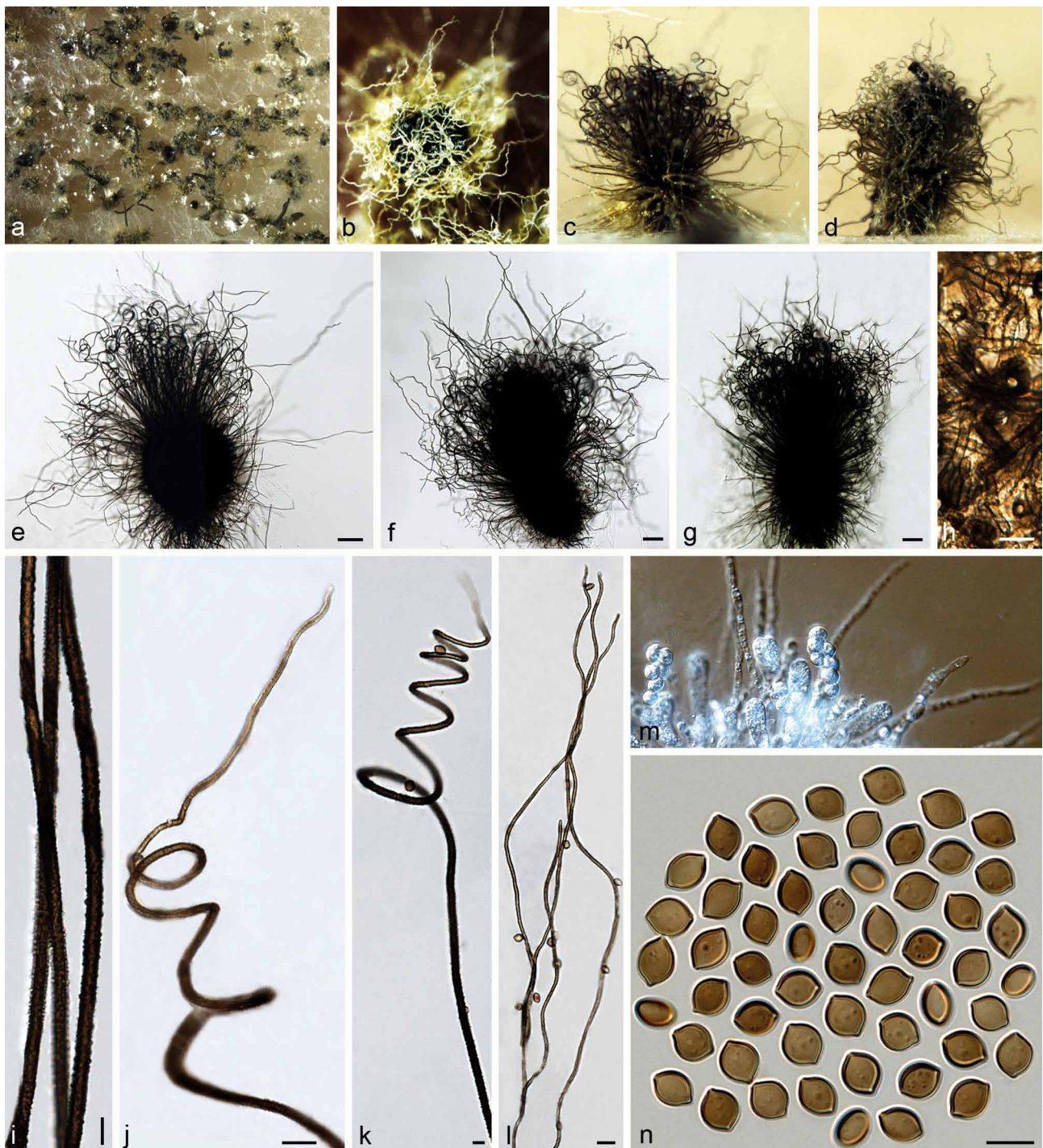


Fig. 26 *Chaetomium pseudocochliodes* (CGMCC 3.9441, ex-type culture). a. Part of the colony on OA; b. ascoma and mass of ascospores on OA, top view; c, d. ascomata on OA, side view; e–g. ascomata mounted in lactic acid; h. structure of ascomatal wall in surface view; i, j, k. upper parts of terminal ascomatal hairs of type I; l. terminal ascomatal hairs of type II; m. asci; n. ascospores. — Scale bars: e–g = 100 μ m; h, i, k, m, n = 10 μ m; j, l = 20 μ m.

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 ascomata.

Material examined. UNKNOWN, substrate and collection details unknown, deposited in CBS by J.E. Wright, Sept. 1971 (holotype CBS H-10083, culture ex-type CBS 574.71).

Notes — Phylogenetic inference in this study showed that *C. pseudoglobosum* is in Group II, closely related to *C. tenue* (Group IIB, Fig 1). The latter species produces smaller ascospores (9–10 \times 6.5–7.5 \times 5–6 μ m vs 8.5–9.5 \times 6–7 \times 5–5.5 μ m) 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 \times 5.5–6 \times 4–5 μ m).

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 μ m high, 215–380 μ m 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 μ m diam near the base,

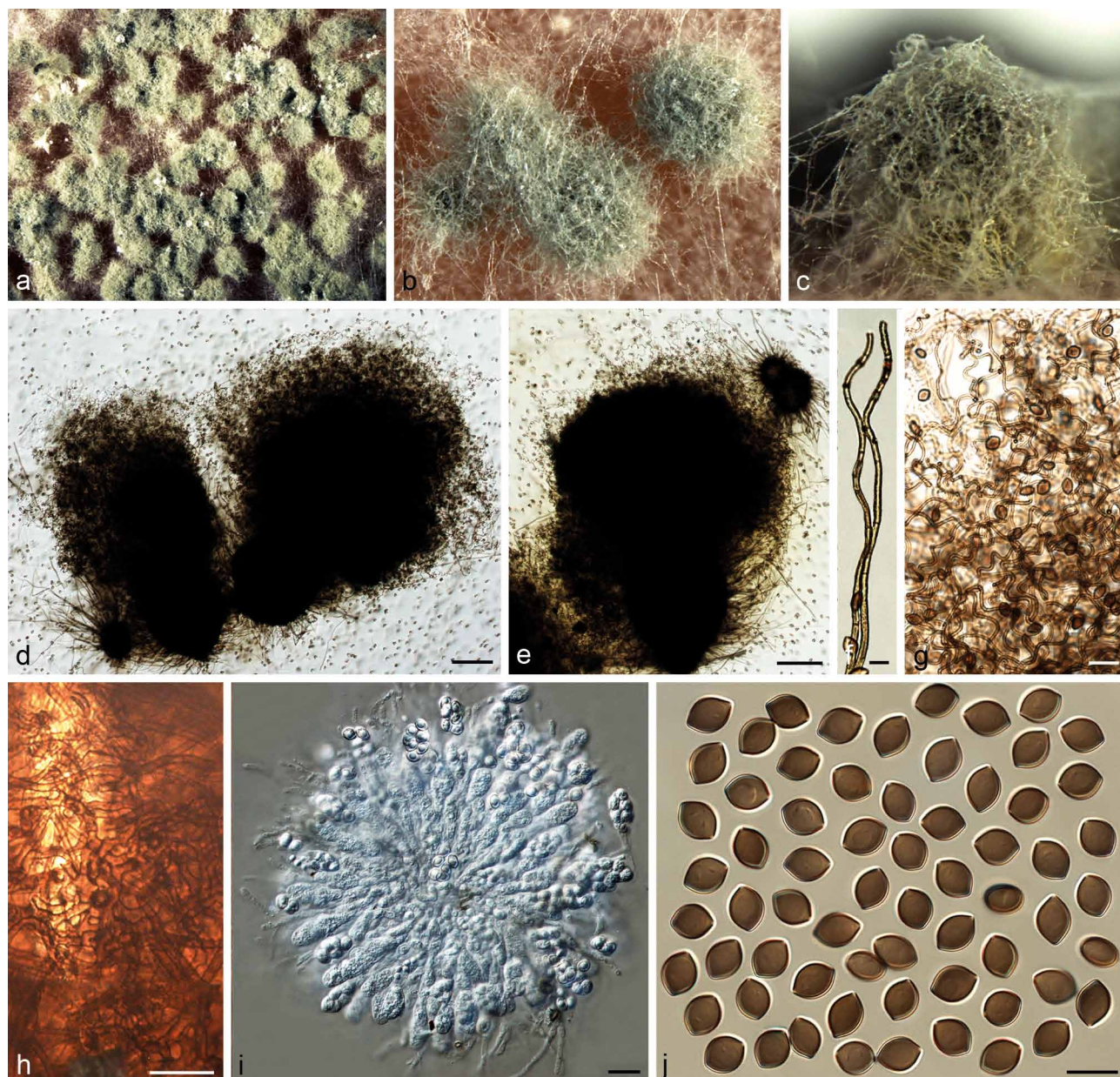


Fig. 27 *Chaetomium pseudoglobosum* (CBS 574.71, ex-type culture). a. Part of the colony on OA; b. ascomata on OA, top view; c. ascoma on OA, side view; d, e. ascomata mounted in lactic acid; f. basal parts of terminal ascomatal hairs; g. upper parts of terminal ascomatal hairs; h. structure of ascomatal wall in surface view; i. asci; j. ascospores. — Scale bars: d, e = 100 μ m; f, j = 10 μ m; g–i = 20 μ m.

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 \times 11–16 μ m, stalks 23–37 μ m long, with eight biseriate ascospores, evanescent. *Ascospores* olivaceous brown when mature, limoniform, biapiculate, bilaterally flattened, (9–)10–11(–12) \times 7–9 \times 6–7.5(–8) μ m, with an apical germ pore. *Asexual morph* acremonium-like. *Conidiophores* formed laterally from aerial hyphae, simple, 13–29 μ m long, 2–4.5 μ m 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) \times 2–3 μ m.

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

Materials examined. CHINA, Xinjiang Autonomous Region, Kanas Lake, from animal dung, June 2003, X.-W. Wang, CGMCC 3.9409. — IRAN, West Azerbaijan Province, Salmas, from leaf of *Hordeum vulgare*, 22 June 2005, B. As-

gari (holotype IRAN 14606F, culture ex-type CBS 126778 = IRAN 1641C); East Azerbaijan Province, Shabestar, from stem of *Hordeum vulgare*, 22 May 2005, B. Asgari, CBS 126658 = IRAN 855C. — UK, from decaying hard wood, collection details unknown, CGMCC 3.5617.

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.

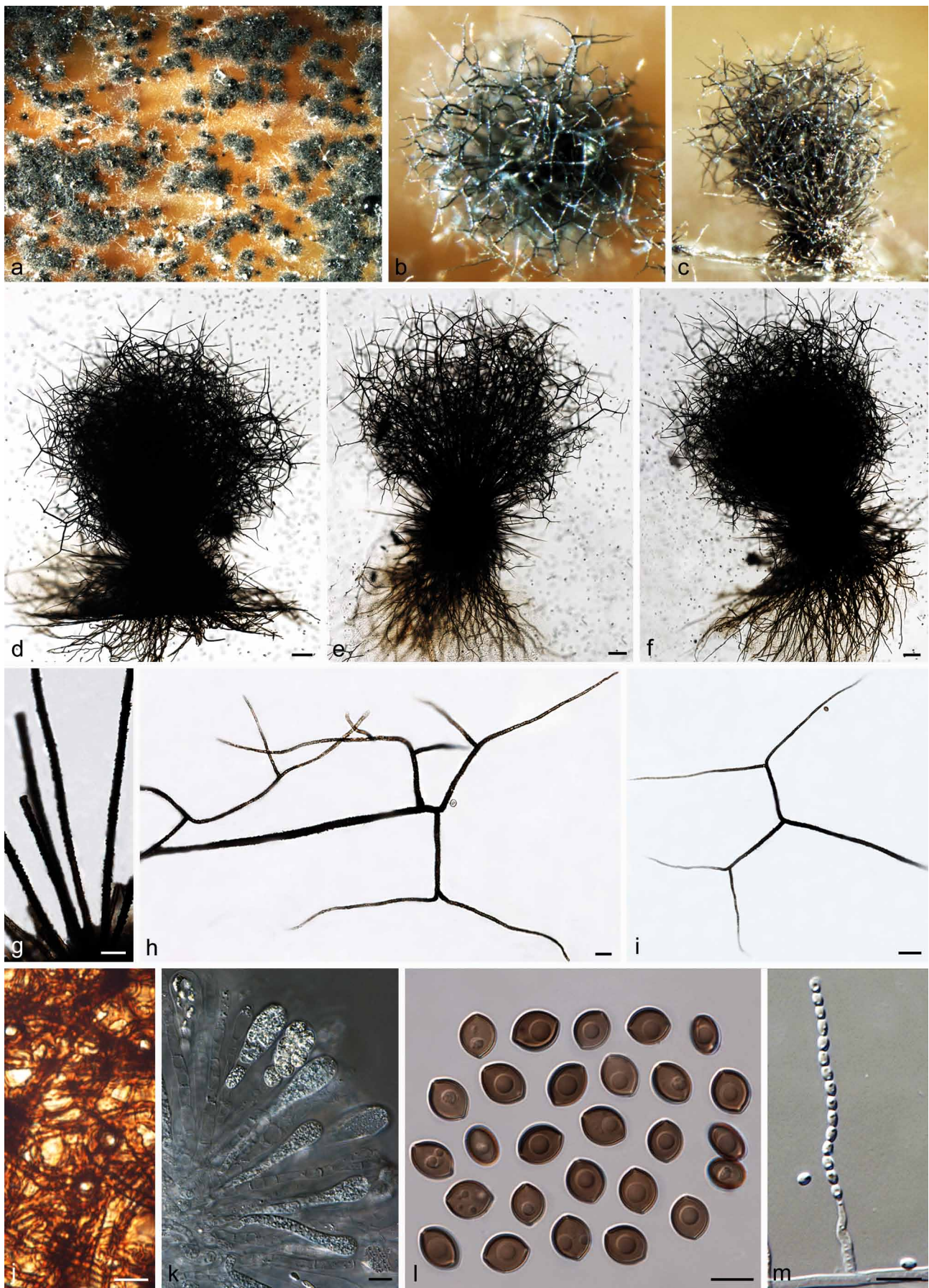


Fig. 28 *Chaetomium rectangulare* (CBS 126658). a. Part of the colony on OA; b. ascoma on OA, top view; c. ascoma on OA, side view; d–f. ascomata mounted in lactic acid; g. basal parts of terminal ascomatal hairs; h, i. upper parts of terminal ascomatal hairs; j. structure of ascomatal wall in surface view; k. asci; l. ascospores; m. asexual morph (conidiophore and conidia). — Scale bars: d–f = 100 μ m; g–i = 20 μ m; j–m = 10 μ m.

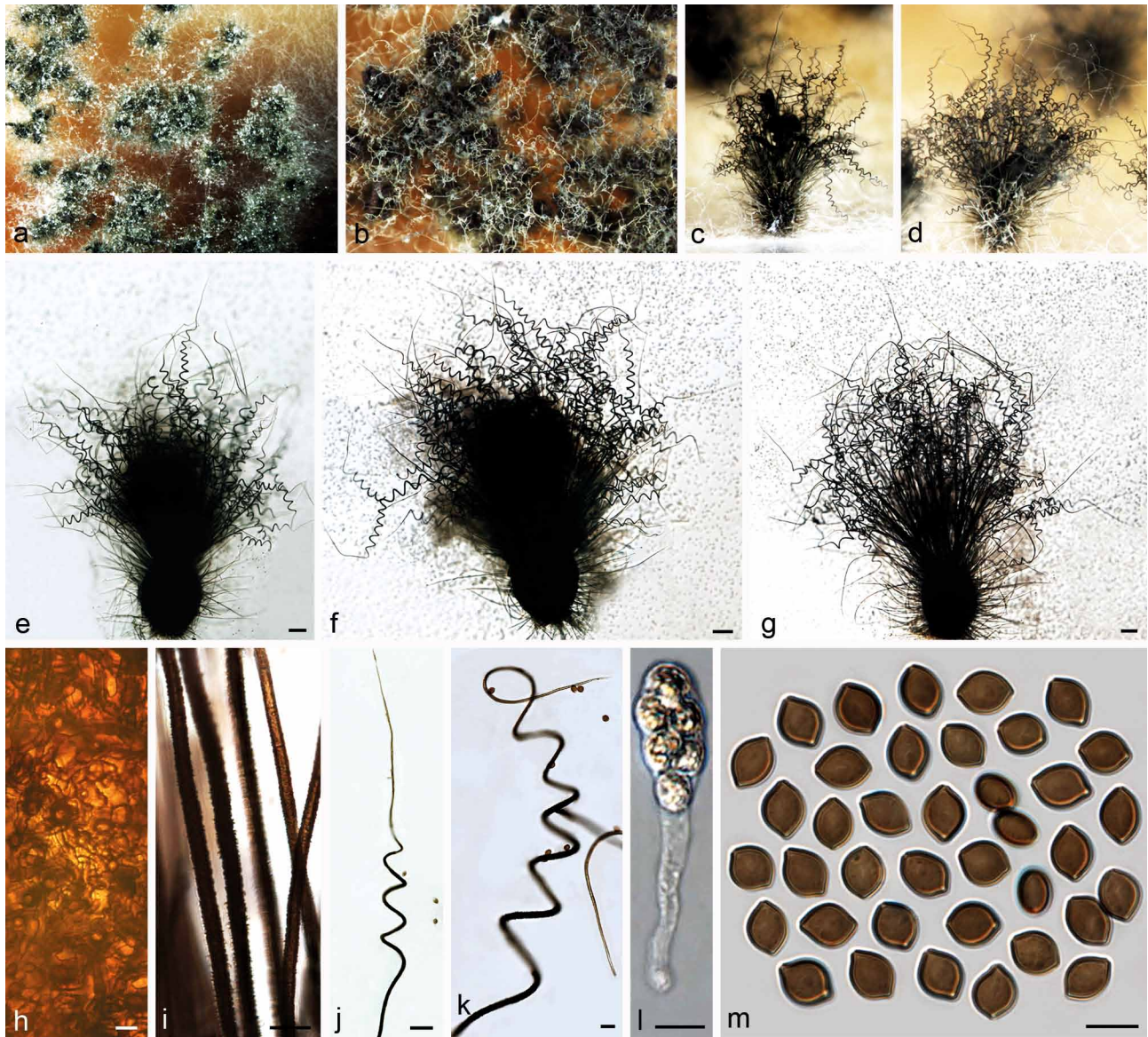


Fig. 29 *Chaetomium spiculipilium* (CBS 373.66, ex-type culture). a. Part of the colony on OA; b. ascomata on OA, top view; c, d. ascomata on OA, side view; e–g. ascomata mounted in lactic acid; h. structure of ascomatal wall in surface view; i. basal parts of terminal ascum hairs; j, k. upper parts of terminal ascum hairs; l. ascus; m. ascospores. — Scale bars: e–g = 100 μ m; h, k–m = 10 μ m; i = 20 μ m; j = 50 μ m.

***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 μ m high, 300–385 μ m 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 μ m 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 \times 13–16.5 μ m, stalks 27–43 μ m long, with eight biserial ascospores, evanescent. *Ascospores* olivaceous brown when mature, limoniform, usually biapiculate, occasionally umbonate at one or both ends, bilaterally flattened, (9–)10–13(–15) \times (7–)7.5–9(–10) \times 5.5–6.5(–7) μ m, 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 μ m diam near the base) with a conspicuous seta-like extension at the tip, compared to those of *C. cochliodes* (3.5–6 μ m near the base), *C. pseudocochliodes* (4–6 μ m near the base for regularly coiled hairs) and *C. spirochaete* (3–4.5 μ m near the base). The ascospores of *C. spiculipilium* (10–13 \times 7.5–9 \times 5.5–6.5 μ m) are also slightly larger than those of *C. cochliodes* (9–10 \times 7.5–8.5 \times 5–6 μ m) and *C. pseudocochliodes* (9.5–11 \times 7.5–8.5 \times 5.5–6.5 μ m).



Fig. 30 *Chaetomium spirochaete* (CBS 370.84, ex-epitype culture). a. Part of the colony on OA; b, c. ascomata on OA, top view; d. ascusa on OA, side view; e–g. ascomata mounted in lactic acid; h. structure of ascomatal wall in surface view; i. basal parts of terminal ascumal hairs; j, k. upper parts of terminal ascumal hairs; l. asci; m. ascospores; n. holotype sheet of *C. spirochaete* in New York Botanical Garden (Specimen ID 01050443); o, p. ascumal hairs from holotype specimen. — Scale bars: e–g = 100 µm; h, l, m = 10 µm; i–k, p = 20 µm.

Chaetomium spirochaete Palliser, N. Amer. Fl. 3: 61. 1910. — Fig. 30

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 epidermoidea* or *textura intricata* in surface view. *Terminal hairs*

verrucose, brown, 3–4.5 µm near the base, equally diametered 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 L.M. Ames, deposited in CBS by J.C. Krug, Nov. 1984 (epitype designated here HMAS 244438, MBT201732, culture ex-epitype CBS 730.84 = IMI 287303 = QM 6702).

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* (Chivers 1915, Ames 1963) and later re-introduced by Dreyfuss (1976). Von Arx et al. (1986) 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 thicker 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 III, distant from *C. globosum* (Group IIA, Fig 1). *Chaetomium spirochaete* has regularly coiled ascomatal hairs, resembling those of *C. cochliodes*, *C. pseudocochliodes* and *C. spiculipilium*. Among them, *C. spiculipilium* has slightly larger ascospores, while the ascospores of the three remaining species are similar. However, *C. spirochaete* can be distinguished 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).

Chaetomium subaffine Sergeeva, Not. Syst. sect. Crypt. Inst. Bot. Acad. Sci. U.S.S.R. 14: 148. 1961. — Fig. 31

Ascomata usually covered by thick aerial hyphae, ostiolate, olivaceous or umber to dark-brick in reflected light owing to ascomatal hairs, obovate or ovate, 220–410 µm high, 180–340 µm diam. **Ascomatal wall** brown, composed of hypha-like cells, *textura intricata* in surface view. **Terminal hairs** verrucose, brown, erect to flexuous or slightly undulate, usually unbranched, 3.5–5 µm near the base, tapering towards the tips. **Lateral hairs** similar. **Asci** fasciculate, clavate or slightly fusiform, with eight biserial ascospores, spore-bearing part 29–46 × 12–18 µm, stalks 32–58 µm long, evanescent. **Ascospores** brown when mature, limoniform, usually biapiculate, bilaterally flattened, (10.5–)11.5–13.5(–14) × 8.5–10(–10.5) × (6–)6.5–7.5(–8) µm, with an apical germ pore. **Asexual morph** acremonium-like. **Conidiophores** discrete, simple; conidogenous cells phialidic, hyaline. **Conidia** formed in basipetal succession, aseptate, smooth, hyaline, ovate or spherical, usually attenuated into a narrowly truncate base, (3–)3.5–5 × 2–3 µm.

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

Materials examined. CHINA, Beijing, from animal dung, Aug. 2009, J. Li, CGMCC 3.14293; Hebei Province, Xingtai, from unknown plant stem, Aug. 2009, J. Li, CGMCC 3.14297. — NETHERLANDS, Zwolle, from finger skin of *Homo sapiens*, collector and collection date unknown, deposited in CBS by Bact. Lab. Zwolle, Jan. 1976, CBS 111.76. — USSR, from cereal, collector and collection date unknown, deposited in CBS by K.S. Sergejeva, Nov. 1991 (culture ex-type CBS 637.91 = ATCC 14531 = IMI 90489).

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

Basionym. *Chaetomidium subfimetii* Seth, Trans. Brit. Mycol. Soc. 50: 46. 1967.

≡ *Thielavia subfimetii* (Seth) Malloch & Cain, Mycologia 65: 1070. 1973.

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. **Asci** fasciculate, clavate or slightly fusiform, with eight biserial 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 *Chaetomidium subfimetii* CBS H-6839, culture ex-isotype of *Chaetomidium subfimetii* 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 subfimetii* formed a sister lineage to *C. fimeti* (Group IC, Fig 1) as was supported by our morphological observations. *Chaetomium subfimetii* can be distinguished by producing smaller ascomata (170–360 µm diam vs 320–500 µm diam) and ascospores (8.5–9.5 × 7–7.5 × 5.5–6 µm vs 11.5–13.5 × 9–10.5 × 7–8 µm) than those of *C. fimeti*.



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 μ m; g–l = 10 μ m.

Chaetomium subglobosum Sergeeva, Not. Syst. sect. Crypt. Inst. Bot. Acad. Sci. U.S.S.R. 13: 172. 1960. — Fig. 33

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 μ m

high, 265–355 μ m 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

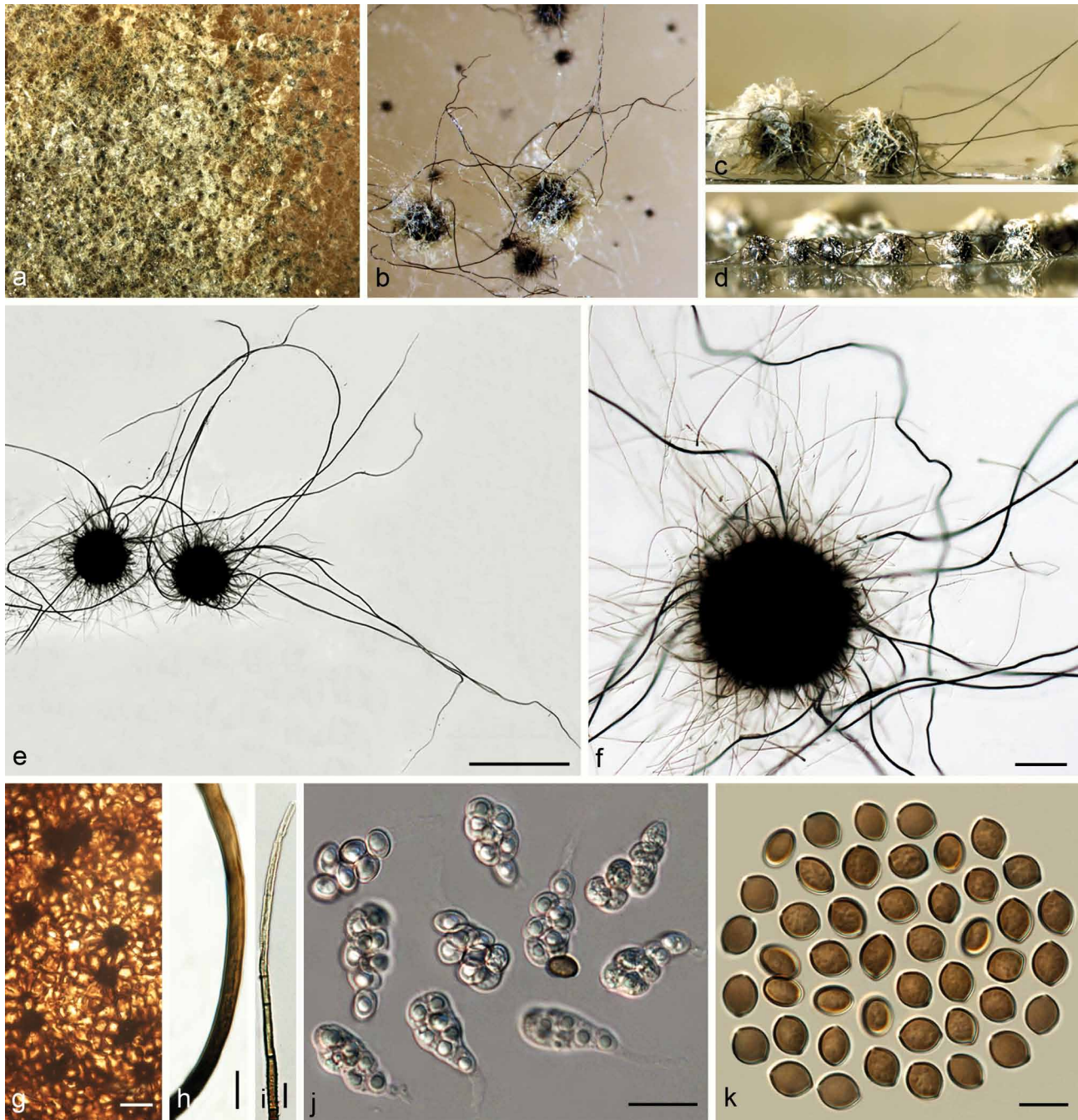


Fig. 32 *Chaetomium subfimetii* (CBS 370.66, ex-type culture). a. Part of the colony on OA; b. ascomata on OA, top view; c, d. ascomata on OA, side view; e, f. ascomata mounted in lactic acid; g. structure of ascomatal wall in surface view; h. basal part of a terminal ascomatal hair; i. upper part of a terminal ascomatal hair; j. asci; k. ascospores. — Scale bars: e = 500 μ m; f = 100 μ m; g–i, k = 10 μ m; j = 20 μ m.

punctate to verrucose, brown, fading towards the tips, flexuous, sometimes branched, 3–5.5 μ m near the base, tapering towards the tips. *Lateral hairs* similar. *Asci* fasciculate, clavate or slightly fusiform, with eight biserial or irregularly-arranged ascospores, spore-bearing part 32.5–45 \times 13.5–18 μ m, stalks 25.5–36.5 μ m long, evanescent. *Ascospores* olivaceous brown when mature, limoniform to broad limoniform, usually biapiculate, bilaterally flattened, (11–)12–13.5(–14) \times (10–)10.5–12(–13.5) \times 7–8.5(–9) μ m, with an apical germ pore. *Asexual morph* absent.

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

Materials examined. RUSSIA, St. Petersburg, from dead herbaceous stem, in moist chamber, K.S. Sergejeva, collection date unknown, isolated and deposited in CBS by K.S. Sergejeva, June 1960 (culture ex-type CBS 149.60

= ATCC 14533 = IMI 081770 = MUCL 18694 = VKM F-1951). — TURKEY, Izmir, from *Eriobotrya japonica*, collection date unknown, isolated and deposited in CBS by E. Onogur, May 1973, CBS 483.73.

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. subglobosum* as a separate species based on morphological and molecular evidence. *Chaetomium subglobosum* can be distinguished from *C. globosum* s.str. by producing larger ascomata (300–450 \times 265–355 μ m vs 160–300 \times 135–250 μ m) and ascospores (12–13.5 \times 10.5–12 \times 7–8.5 μ m vs 8.5–10.5 \times 7–8 \times 5.5–6.5 μ m). 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).

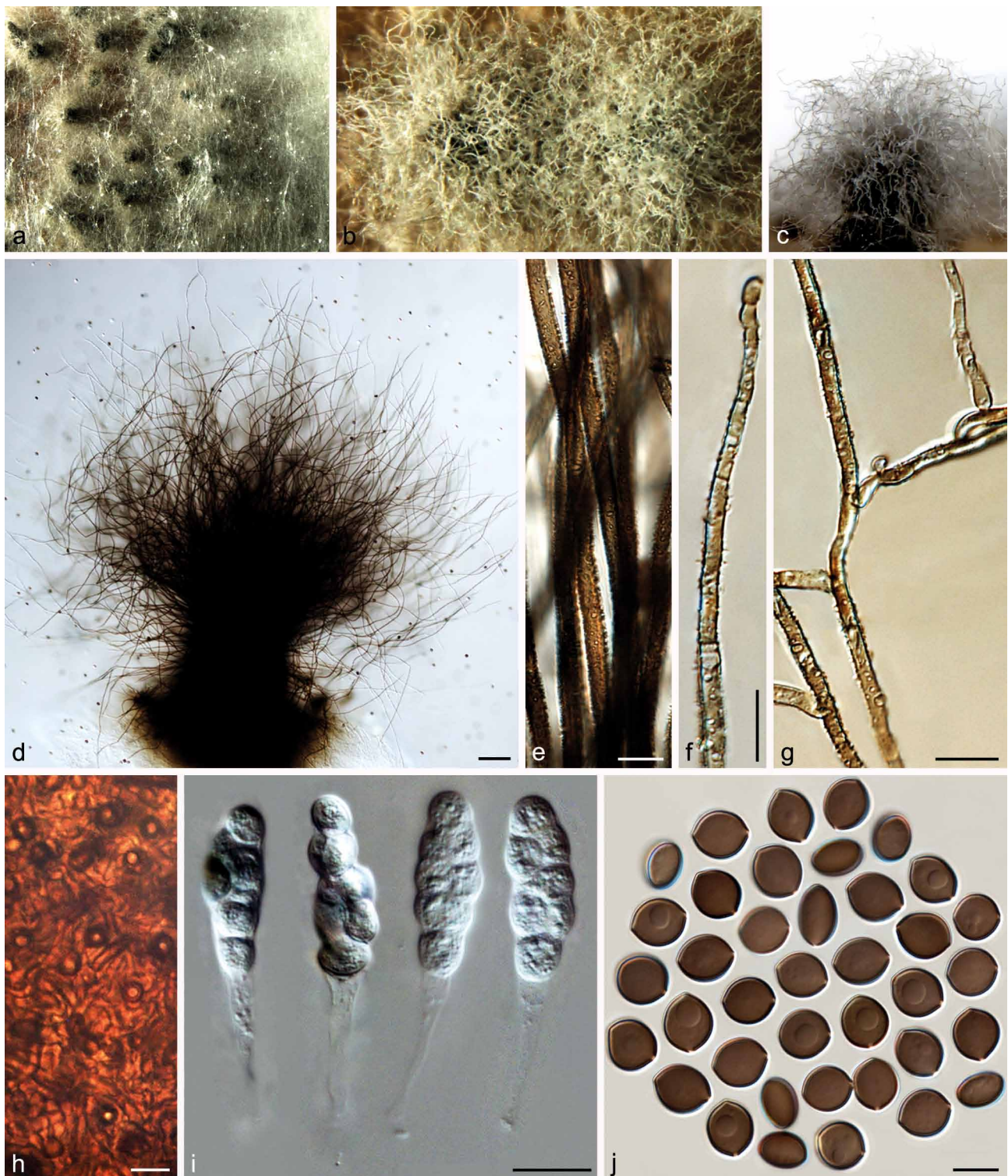


Fig. 33 *Chaetomium subglobosum* (CBS 483.73). a. Part of the colony on OA; b. ascomata on OA, top view; c. ascoma on OA, side view; d. ascoma mounted in lactic acid; e. basal parts of terminal ascomatal hairs; f. upper part of a terminal ascomatal hair; g. branched middle parts of terminal ascomatal hairs; h. structure of ascomatal wall in surface view; i. asci; j. ascospores. — Scale bars: d = 100 μ m; e–h, j = 10 μ m; i = 20 μ m.

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 μ m high, 140–300 μ m 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, oli-

vaceous brown, fading towards the tips, slightly tapering, erect or flexuous at the lower part, undulate at the upper part, 3–5 μ m 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 \times 11.5–16.5 μ m, stalks 21–37 μ m long, with eight biserial ascospores, evanescent. *Ascospores* olivaceous brown when mature, elongate limoniiform to broadly fusiform, or slightly irregular, bilaterally flattened, (9–)10–13(–15) \times (6–)7.5–8(–8.5) \times 5–6 μ m, with an apical germ pore. *Asexual morph* absent.

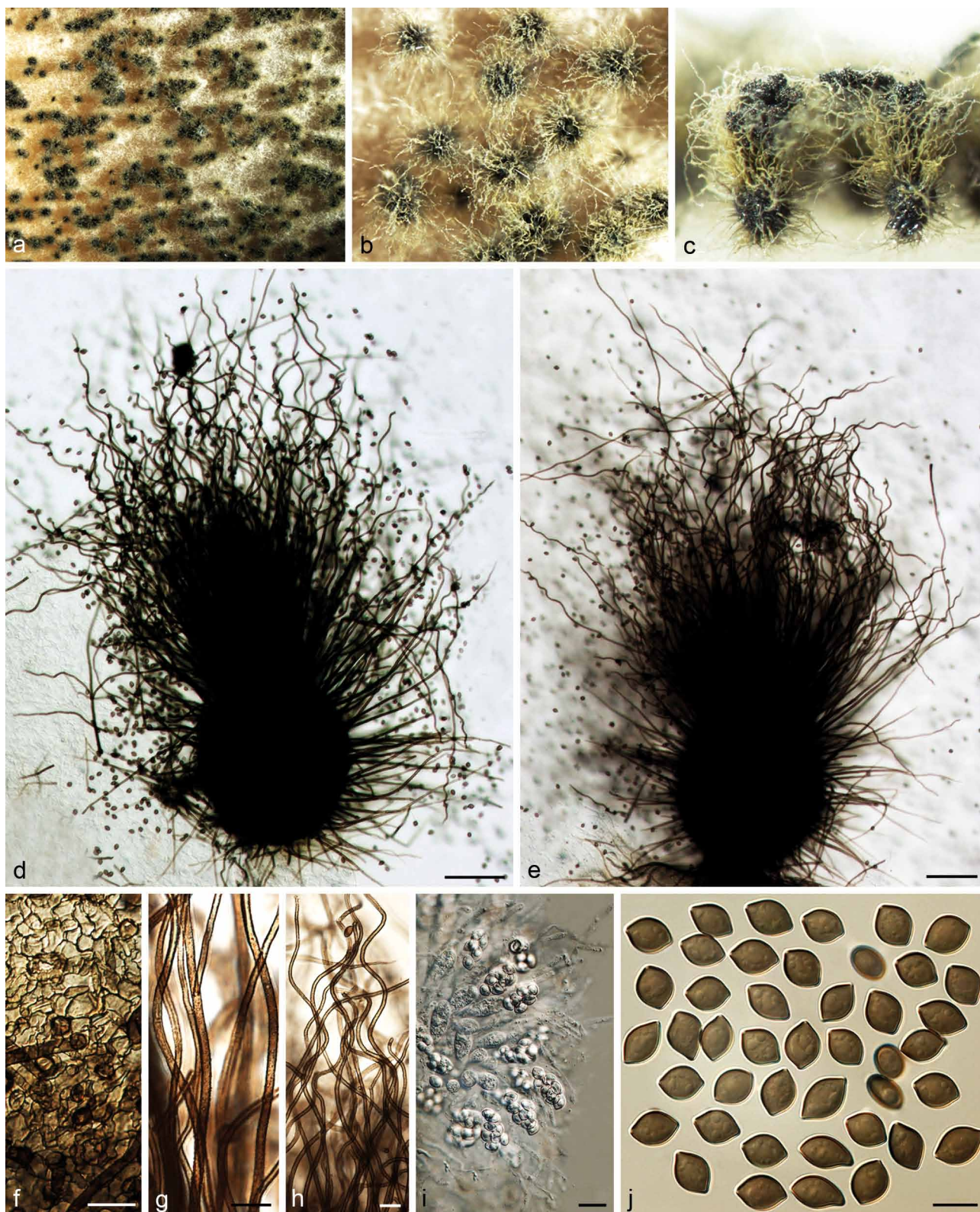


Fig. 34 *Chaetomium telluricola* (CBS 151.59, ex-type culture). a. Part of the colony on OA; b. ascomata on OA, top view; c. ascomata and masses of ascospores on OA, side view; d, e. ascomata mounted in lactic acid; f. structure of ascomatal wall in surface view; g. basal parts of terminal ascumal hairs; h. upper parts of terminal ascumal hairs; i. asci; j. ascospores. — Scale bars: d, e = 100 μ m; f, g, i = 20 μ m; h, j = 10 μ m.

Culture characteristics — Colonies on OA usually without aerial hyphae and coloured exudates; reverse uncoloured, but greenish olivaceous under ascumata.

Material examined. UK, Suffolk, Lakenheath Warren, isolated from soil, collection date unknown, *J.H. Warcup*, deposited in CBS by IMI, Apr. 1959 (holotype CBS H-676, culture ex-type CBS 151.59 = IMI 032543).

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.

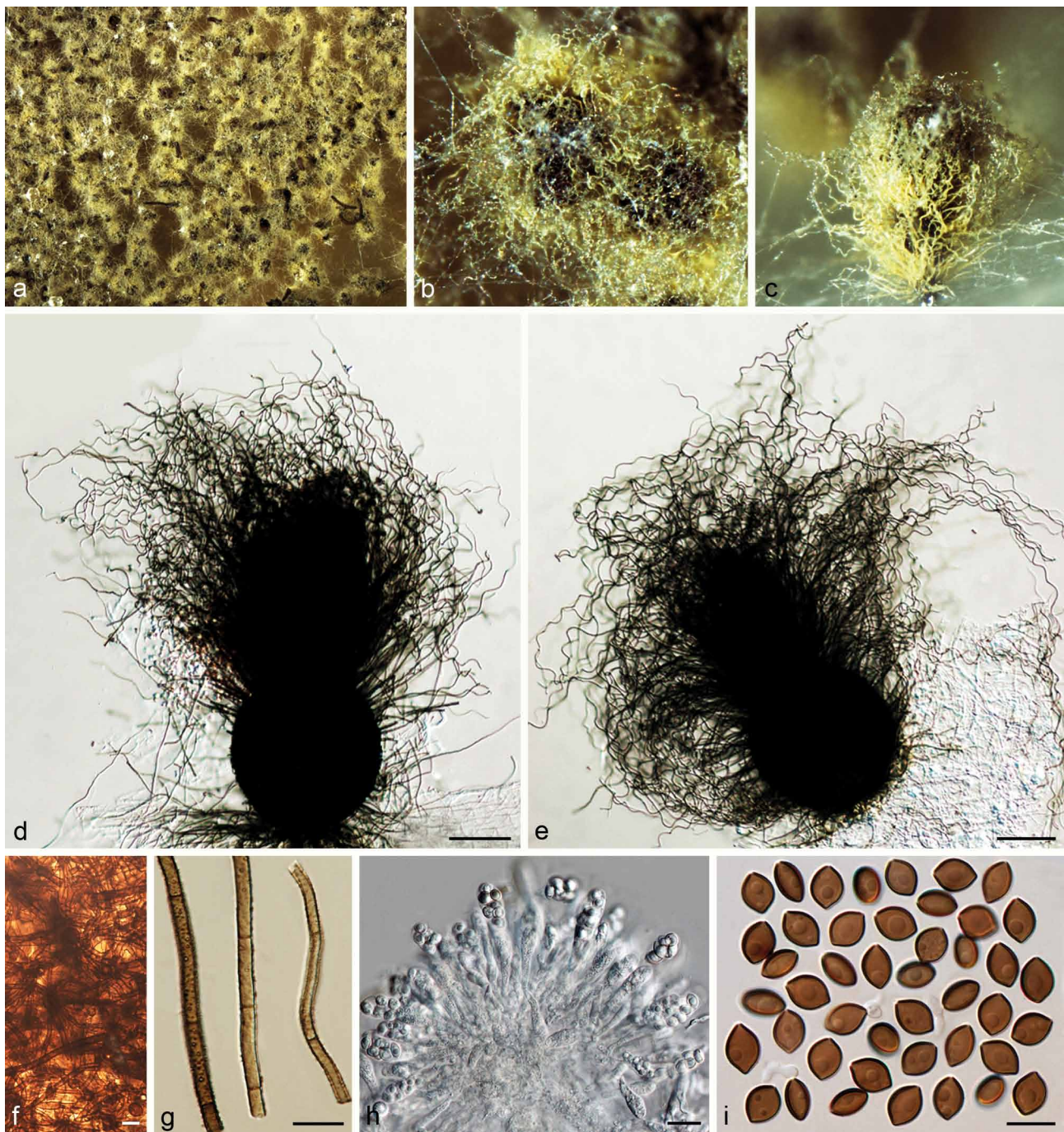


Fig. 35 *Chaetomium tenue* (CBS 139.38, ex-type culture). a. Part of the colony on OA; b. ascum on OA, top view; c. ascum on OA, side view; d, e. ascomata mounted in lactic acid; f. structure of ascomatal wall in surface view; g. terminal ascomatal hairs (from left to right: lower part, middle part and upper part); h. asci; i. ascospores. — Scale bars: d, e = 100 μ m; f, g, i = 10 μ m; h = 20 μ m.

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 μ m high, 150–300 μ m 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 μ m diam near the base, tapering towards the tips. *Lateral hairs* flexuous or similar. *Asci* fasciculate, clavate or slightly fusiform, spore-bearing part 23–33 \times 10–14 μ m, stalks 16–36 μ m long, with eight biserial ascospores, evanescent. *Ascospores* brown when mature, elongate limoniform to broadly fusiform, biapiculate, bilaterally flattened, (7.5–)8.5–9.5(–10.5) \times 6–7(–7.5) \times (4.5–)5–5.5 μ m, 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 \times 6–7 \times 5–5.5 μ m) than those of *C. pseudoglobosum* (9–10 \times 6.5–7.5 \times 5–6 μ m).

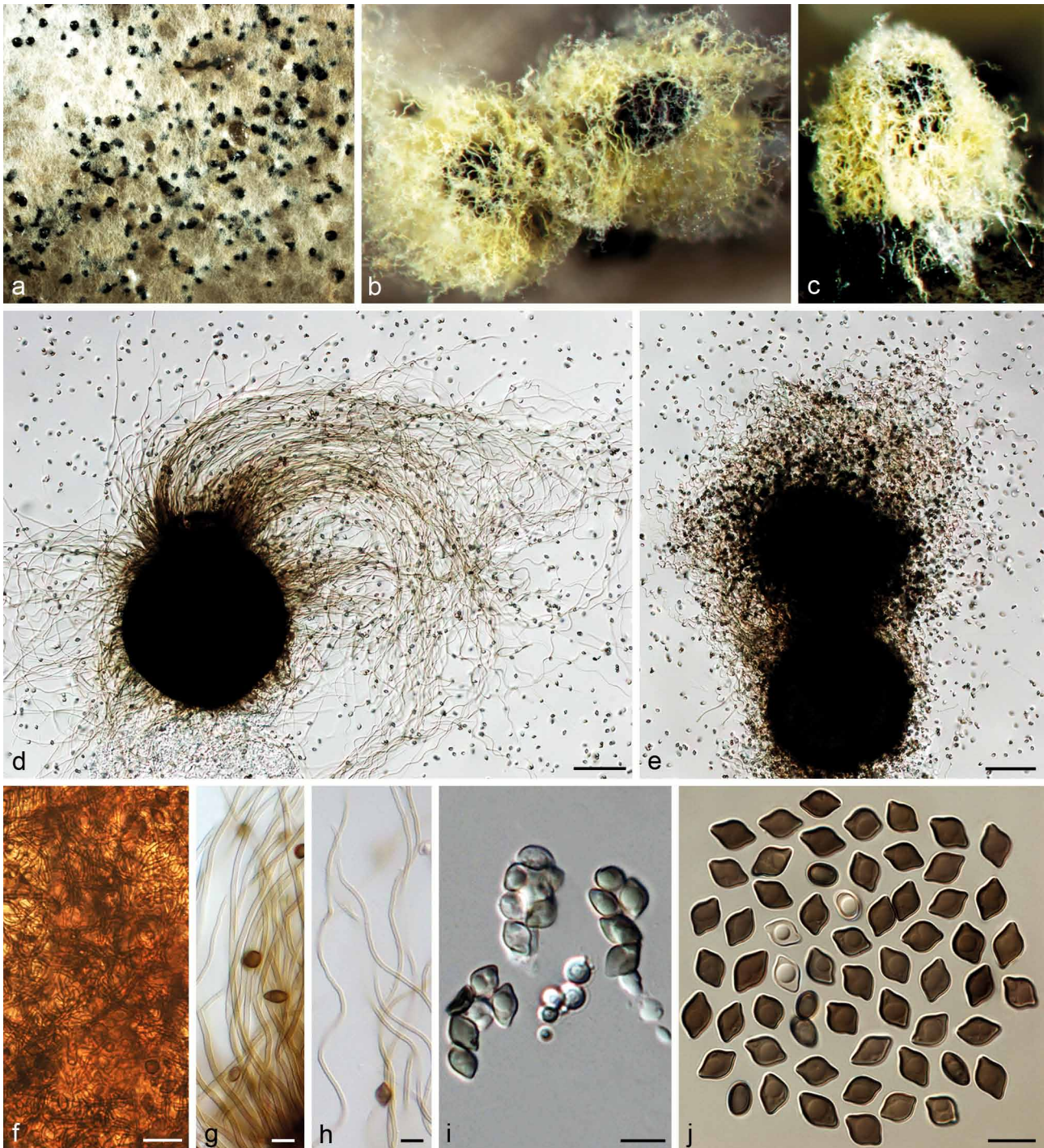


Fig. 36 *Chaetomium umbonatum* (CBS 293.83, ex-type culture). a. Part of the colony on OA; b. ascomata and masses of ascospores on OA, top view; c. ascoma on OA, side view; d, e. ascomata mounted in lactic acid; f. structure of ascomatal wall in surface view; g. basal parts of terminal ascumatal hairs; h. upper parts of terminal ascumatal hairs; i. asci; j. ascospores. — Scale bars: d, e = 100 μ m; f = 20 μ m; g–j = 10 μ m.

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 ascumatal hairs, globose or slightly ovate, 260–360 μ m high, 210–320 μ m 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 μ m 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 \times 8–12.5 μ m,

stalks 13–18 μ m long, evanescent. *Ascospores* olivaceous brown when mature, elongate limoniform, biconical, prominently umbonate at both ends, bilaterally flattened, (7.5–)8–11(–12) \times (5–)5.5–7(–7.5) \times (3.5–)4–5(–5.5) μ m, 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 28768 = IMI 138895).

Notes — *Chaetomium umbonatum* is easily recognised by its ascospores. Von Arx et al. (1986) suggested that this

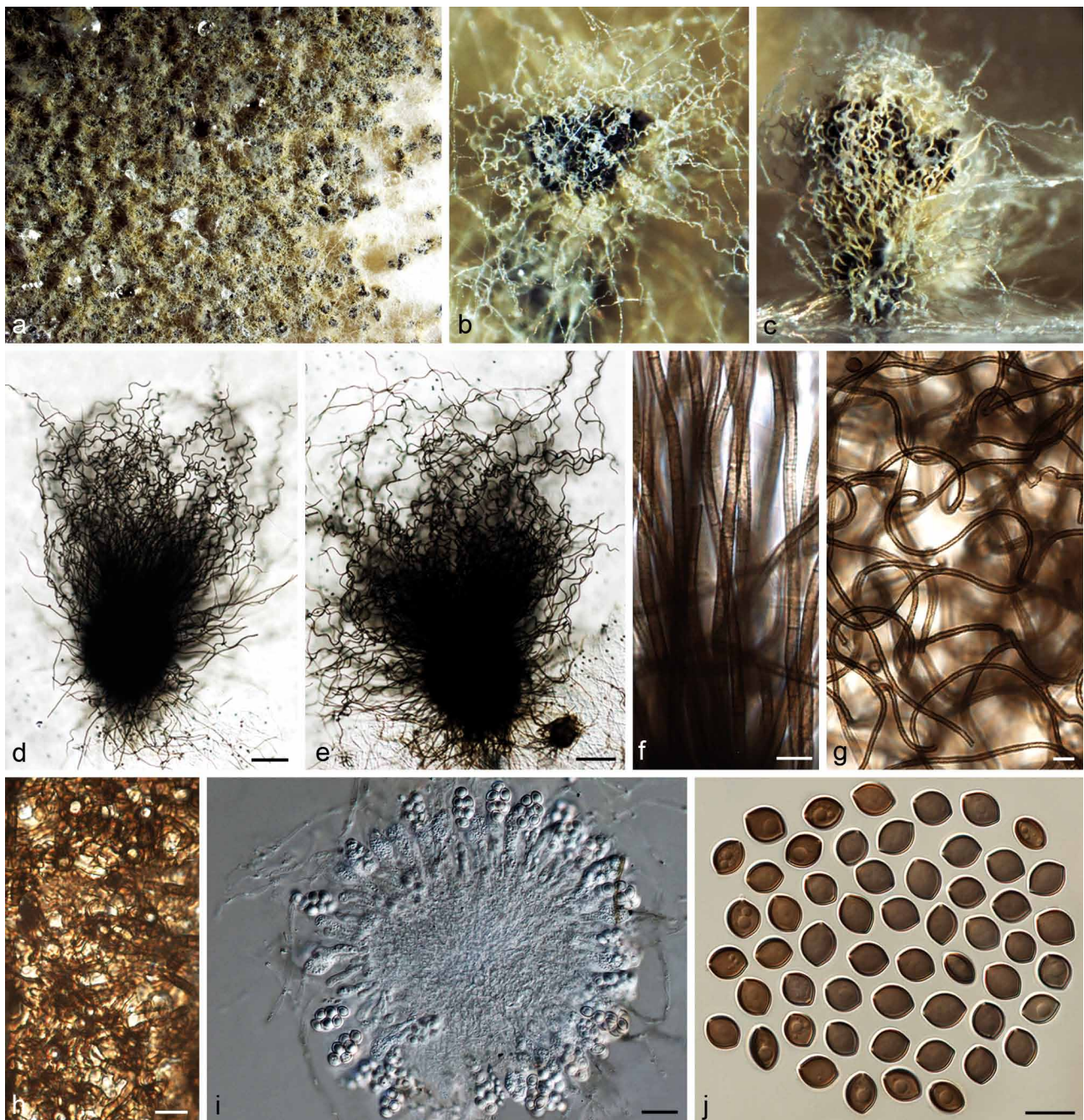


Fig. 37 *Chaetomium unguicola* (CBS 128446, ex-type culture). a. Part of the colony on OA; b. ascoma and mass of ascospores on OA, top view; c. ascoma and mass of ascospores on OA, side view; d, e. ascomata mounted in lactic acid; f. basal parts of terminal ascomatal hairs; g. upper parts of terminal ascomatal hairs; h. structure of ascumatal wall in surface view; i. asci; j. ascospores. — Scale bars: d, e = 100 μ m; f–h, j = 10 μ m; i = 20 μ m.

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 \times 5.5–6 \times 4–5 μ m) 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 \times 9–10 \times 7–8 μ m). *Chaetomium pilosum* is also phylogenetically distant from *C. umbonatum* (basal in Group III, Fig. 1).

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

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, *textura epidermoidea* or *textura intricata* in surface view. *Terminal hairs* finely verrucose, dark olivaceous, 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 \times 10–14.5 μm , stalks 11–24 μm long, evanescent. *Ascospores* olivaceous brown when mature, limoniform, bilaterally flattened, (7–)7.5–9 \times (6–)6.5–7(–7.5) \times 4.5–5.5 μm , with an apical germ pore. *Asexual morph* absent.

Culture characteristics — 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 H-22196, culture ex-type CBS 128446 = UTHSC 07-2213 = dH 21624).

Notes — *Chaetomium unguicola* 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. unguicola* can be distinguished by its smaller ascospores (7.5–9 \times 6.5–7 \times 4.5–5.5 μm vs 8.5–10.5 \times 7–8 \times 5.5–6.5 μm).

KEY TO SPECIES OF THE CHAETOMIUM GLOBOSUM COMPLEX

1. Parts of ascospores with more than one germ pore . . . 2
1. Ascospores with only one germ pore 6
2. Ascospores irregularly limoniform to fusiform in front view, 12.5–26 \times 11–17 \times 9–12.5 μm *C. nozdrenkoe*
2. Ascospores globose to subglobose in front view 3
3. Ascospores shorter than 12.5 μm , with one or two germ pores 4
3. Ascospores longer than 12 μm , with two or more germ pores 5
4. Ascomata 350–510 \times 210–350 μm , ascomatal hairs verrucose and flexuous *C. globosporum*
4. Ascomata 230–360 \times 170–240 μm , ascomatal hairs nearly smooth and undulate *C. interruptum*
5. Ascospores 12–17 \times 10–14 \times 7.5–10.5 μm *C. megalocarpum*
5. Ascospores 17–22.5 \times 14.5–19 \times 11–14 μm *C. grande*
6. Ascospores irregular fusiform, limoniform, ovate, lunate or triangular in front view, 7–12 \times 4–7 \times 4–5.5 μm *C. citrinum*
6. Ascospores typically limoniform to broad fusiform in front view 7
7. Ascomata non-ostiolate 8
7. Ascomata ostiolate 10
8. Ascomata with only short, hypha-like hairs; ascospores umbonate at both ends, 11–16 \times 9–11 \times 6–8 μm *C. pilosum*
8. Ascomata with longer and shorter types of hair; ascospores biapiculate 9
9. Ascomata 320–500 μm diam; ascospores 11–16 \times 9–11 \times 6–8.5 μm *C. fimeti*
9. Ascomata 170–360 μm diam; ascospores 8–10 \times 6.5–8 \times 5.5–6.5 μm *C. subfimeti*
10. Parts of ascospores with a lateral bulge 11
10. Ascospores without a lateral bulge 12
11. Ascospores 10–11.5 \times 8–10 \times 7.5–9 μm ; terminal ascomatal hairs coiled *C. madrasense*
11. Ascospores 8.5–11 \times 8–10 \times 6–7.5 μm ; terminal ascomatal hairs flexuous or irregularly branched *C. ascotrichoides*
12. Terminal ascomatal hairs repeatedly dichotomously branched; usually with acromonium-like asexual morphs . . . 13
12. Terminal ascomatal hairs not repeatedly dichotomously branched 14
13. Terminal hairs 4.5–7 μm diam near the base; ascospores 9–12 \times 7–9 \times 6–8 μm *C. rectangulare*
13. Terminal hairs not more than 4.5 μm diam near the base; 11–14 \times 9–11 \times 6–9 μm *C. elatum*
14. Possessing regularly coiled terminal ascomatal hairs . . . 15
14. Terminal ascomatal hairs erect, flexuous, undulate to only slightly or loosely coiled 19
15. With acromonium-like asexual morphs; parts of terminal hairs longer, 5–7 μm diam at base, parts of terminal hairs shorter, 3–5 μm diam near the base; ascospores 9–12 \times 7.5–9 \times 5.5–7 μm *C. angustispirale*
15. Asexual morph absent 16
16. Terminal ascomatal hairs nearly isodiametric from base towards tip, 3–4.5 μm diam, coiled in the upper part with coils equal in diameter; ascospores 9–12 \times 7.5–9.5 \times 5.5–7 μm *C. spirochaete*
16. Terminal ascomatal hairs tapering towards the tips . . 17
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 \times 7–10 \times 5.5–7 μm *C. spiculiplium*
17. Terminal ascomatal hairs less than 6 μm diam near the base, without a rigid seta-like tip extension; ascospores 8–11.5 \times 7–9 \times 5–7 μm 18
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 *C. cochliodes*
18. Ascospores usually umbonate; parts of the terminal hairs 4–6 μm near the base, with circinate or coiled upper part; parts 3–4 μm near the base, flexuous *C. pseudocochliodes*
19. Terminal ascomatal hairs less than 3 μm diam near the base, smooth; ascospores prominently umbonate, 7.5–12 \times 5–7.5 \times 3.5–5.5 μm *C. umbonatum*
19. Terminal ascomatal hairs more than 3 μm diam near the base, verrucose; ascospores usually biapiculate 20
20. Ascospores broad limoniform to nearly globose 21
20. Ascospores not as above 22
21. Terminal ascomatal hairs flexuous; rhizoidal structure thriving and dense; ascospores 11–14 \times 10–13.5 \times 7–9 μm *C. subglobosum*
21. Terminal ascomatal hairs undulate to slightly coiled; rhizoids sparser; ascospores 9.5–11.5 \times 9–10.5 \times 6.5–8 μm *C. coarctatum*
22. Terminal hairs forming a dense, nearly globose head covering over the ascomatal ostiole 23
22. Terminal hairs not as above 24
23. Ascospores 6.5–8 \times 5–6.5 \times 4–5 μm *C. afropilosum*
23. Ascospores 9–10.5 \times 6–8 \times 5–6.5 μm *C. pseudoglobosum*
24. Ascospores elongate limoniform to broadly fusiform . . 25
24. Ascospores typically limoniform 26
25. Ascospores 9–15 \times 6–8.5 \times 5–6 μm *C. telluricola*
25. Ascospores 7.5–10.5 \times 6–7.5 \times 4.5–5.5 μm *C. tenue*
26. Ascospores shorter than 11.5 μm and narrower than 8.5 μm in front view 27
26. Ascospores up to 12.5 μm or longer and up to 9.5 μm or wider in front view 30

27. Ascospores $7-9 \times 6-7.5 \times 4.5-5.5 \mu\text{m}$. . . *C. unguicola*
 27. Ascospores $8-11.5 \times 7-8.5 \times 5-7 \mu\text{m}$
 (*C. globosum* s.str.) 28
28. Ascomatal wall translucent; ascomatal hairs hypha-like, sparse and hyaline; ascospore mass rust to salmon in reflected light
 'cruentum' morphological form of *C. globosum* s.str.
28. Ascomatal wall and ascomatal hairs not as above; ascospore mass black in reflected light 29
29. Terminal hairs erect to flexuous, $2.5-3.5 \mu\text{m}$ diam near base 'rectum'-like *C. globosum* s.str.
29. Terminal hairs flexuous, undulate to slightly coiled, $3-5 \mu\text{m}$ diam near base *C. globosum* s.str.
30. Aerial hyphae abundant and often cover ascomata; asexual morph acremonium-like; ascomatal hairs erect to flexuous; ascospores $10.5-14 \times 8.5-10.5 \times 6-8 \mu\text{m}$ *C. subaffine*
30. Aerial hyphae sparse or lacking; asexual morph absent 31
31. Ascospores $12-13.5 \times 8-10 \times 6-7.5$; ascomatal hairs flexuous, undulate to loosely coiled *C. undulatum*
31. Ascospores shorter than $12.5 \mu\text{m}$ 32
32. Terminal hairs relatively sparse, luteous to amber or citrine in reflected light, erect or flexuous; ascospores $9.5-12 \times 9-10 \times 5.5-7 \mu\text{m}$ *C. graminiforme*
32. Terminal hairs abundant, slightly pale olivaceous buff in reflected light, undulate or flexuous; ascospores $10-12.5 \times 8-9 \times 6-7 \mu\text{m}$ *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. megalocarpum* 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 *Chaetomium* 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 *Chaetomidium* 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*, *Farrowia* 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 *Chaetomidium* 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 *Chaetomidium* 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 repre-

senting 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. *Chaetomidium fimeti*, *Chd. subfimeti* and *Chd. pilosum* were shown to belong to the *C. globosum* species complex and cluster in two different groups. *Chaetomidium triangulare* clustered outside the *Chaetomiaceae*, while the other available *Chaetomidium* 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, Stchigel & Guarro 2007).

The first main clade (Group I, Fig 1) resolved here corresponded to the *C. megalocarpum* 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. grande*, *C. megalocarpum* and *C. nozdrenkoae*) 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 coarctatum* 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. cochliodes*, *C. cryptocochliodes*, *C. spiculipilium* and *C. spirochaete*) to repeatedly dichotomously branched (*C. elatum* and *C. rectangulare*). *Chaetomium pilosum*, a species previously placed in the genus *Chaetomidium*, 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. rectangulare* and *C. subaffine*) in this complex. We can, however, define this complex with the following morphological features:

ascomata globose, ellipsoid to ovate 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 epidermoidea* in surface view; asci clavate or fusiform with eight biserial (or irregularly arranged) ascospores and evanescent; ascospores limoniform, globose to irregular, bilaterally flattened and longer than 7 μm in length; asexual morphs, if present, acromonium-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 hairs together with flexuous to undulate hairs is very common in many species (*C. globosum*, *C. graminiforme*, *C. grande*, *C. interruptum*, *C. megalocarpum*, *C. nozdrenkoae* 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. spiculipilium* 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 ascomata with walls composed of well-defined *textura angularis*, which include *C. bostrychodes*, *C. seminudum*, *C. sphaerale* and *C. subspirale* and the close relatives of each species. Details on ascomata, ascospore sizes or asexual morph will help to further distinguish these lineages from the *C. globosum* species complex (Hawksworth 1975, Von Arx et al. 1986, Untereiner et al. 2001, Wang & Zheng 2005).

Untereiner et al. (2001) used the D1/D2 regions of LSU to investigate the relationships of the genera *Chaetomium* and *Farrowia*, representing the first study using DNA sequence data for the *Chaetomiaceae*. Greif et al. (2009) later used the LSU, *tub1* and *rpb2* gene regions to re-evaluate the genus *Chaetomium*. Asgari & Zare (2011) used the ITS, partial LSU, and *tub2* gene regions to identify new *Chaetomium* species from Iran. Wang et al. (2014) provided a phylogenetic re-assessment of the *C. indicum* species complex based on DNA sequences of the ITS, partial LSU, *tub2*, *tef1* and *rpb1* gene regions. A useful DNA barcode should have a clearly defined barcode gap between inter- and intraspecific variation and a small to non-existing overlap between the inter- and intraspecific frequency distance distributions to ensure the adequate species resolution or a high probability of correct identification (Schoch et al. 2012). In the present study, similar tree topologies were produced for the four protein-coding gene regions, suggesting that the efficiency of each locus as possible secondary DNA barcode(s) for the *C. globosum* species complex could be evaluated. Using the Kimura-2-parameter analysis, the D1/D2 region of LSU showed the lowest species-level resolution. The ITS region, the standard DNA barcode marker for the Kingdom *Fungi* (Schoch et al. 2012), was also shown to be unreliable for species identification in the *C. globosum* species complex. Although all four protein-coding genes regions used in this study provided sufficient resolution for species delimitation in the *C. globosum* species complex, the *tub2* gene region provided the best species resolution, closely followed by the *rpb2*, which also amplified easier across the family than *rpb1*. Therefore, a two-marker system including the *tub2* and *rpb2* genes is suggested here as secondary DNA barcode for the *C. globosum* species complex.

Chaetomium globosum is known as one of the causal agents of human onychomycosis (Naidu et al. 1991, Stiller et al. 1992, Aspiroz et al. 2007, Latha 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, Lesire 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.

Acknowledgements We are very grateful to New York Botanical Garden Herbarium and Herbarium Genavense (Switzerland) for the loan of the holotypes, and also to Dr Cornelia Dilger-Endrulat (Herbarium Tubingense, Germany) for providing information about herbaria. We acknowledge the CBS-KNAW Fungal Collection for providing cultures, and the Alfred Sloan Foundation Programme on the Microbiology of the Built Environment for partially supporting the senior author. This work was jointly supported by the National Natural Science Foundation of China (Project No. 30570007) and the Ministry of Science and Technology of P.R. China (No. 2006FY120100).

REFERENCES

- Abbott SP, Sigler L, McAleer R, et al. 1995. Fatal cerebral mycoses caused by the ascomycete *Chaetomium strumarium*. *Journal of Clinical Microbiology* 33: 2692–2698.
- Ahmed SK, Aggarwal R, Kapoor HC. 2008. Production, partial purification and characterization of extracellular xylanase from *Chaetomium globosum*. *Journal of Plant Biochemistry & Biotechnology* 17: 95–98.
- Ainsworth GC. 1961. *Ainsworth & Bisby's Dictionary of the Fungi*, 5th ed. CAB International, Wallingford.
- Ainsworth GC. 1971. *Ainsworth & Bisby's Dictionary of the Fungi*, 6th ed. CAB International, Wallingford.
- Ames LM. 1950. New species of cellulose destroying fungi II. *Mycologia* 42: 642–645.
- Ames LM. 1963. A monograph of the *Chaetomiaceae*. U.S. Army Research and Development, Series 2.
- Anandi V, John TJ, Walter A, et al. 1989. Cerebral phaeohyphomycosis caused by *Chaetomium globosum* in a renal transplant recipient. *Journal of Clinical Microbiology* 27: 2226–2229.
- Andersen B, Frisvad JC, Søndergaard I, et al. 2011. Associations between fungal species and water-damaged building materials. *Applied and Environmental Microbiology* 77: 4180–4188.

- Apetrei IC, Draganesc GE, Popescu IT, et al. 2009. Possible cause of allergy for the librarians: books manipulation and ventilation as sources of fungus spores spreading. *Aerobiologia* 25: 159–166.
- Asgari B, Zare R. 2011. The genus *Chaetomium* in Iran, a phylogenetic study including six new species. *Mycologia* 103: 863–882.
- Aspiroz C, Gene J, Rezusta A, et al. 2007. First Spanish case of onychomycosis caused by *Chaetomium globosum*. *Medical Mycology* 45: 279–282.
- Awad NE, Kassem HA, Hamed MA, et al. 2014. Bioassays guided isolation of compounds from *Chaetomium globosum*. *Journal de Mycologie Médicale* 24: e35–e42.
- Ayanbimpe GM, Wapwera SD, Kuchin D. 2010. Indoor air mycoflora of residential dwellings in Jos metropolis. *African Health Sciences* 10: 172–176.
- Bainier G. 1910. Monographie des *Chaetomidium* et des *Chaetomium*. *Bulletin de la Société Mycologique de France* 25: 191–237.
- Barron MA, Sutton DA, Veve R, et al. 2003. Invasive mycotic infections caused by *Chaetomium perucidum*, a new agent of cerebral phaeohiphomycosis. *Journal of Clinical Microbiology* 41: 5302–5307.
- Berbee ML, Taylor JW. 1992. Convergence in ascospore discharge mechanism among Pyrenomycete fungi based on 18S ribosomal RNA gene sequence. *Molecular Phylogenetics and Evolution* 1: 59–71.
- Carter A. 1982. A taxonomic study of the ascomycete genus *Chaetomium* Kunze. PhD thesis, University of Toronto, Canada.
- Chivers AH. 1915. A monograph of the genera *Chaetomium* and *Ascotricha*. *Memoirs of the Torrey Botanical Club* 14: 155–240.
- Corda ACJ. 1840. *Icones fungorum hucusque cognitorum* 4: 1–53.
- Crous PW, Gams W, Stalpers JA, et al. 2004. MycoBank: an online initiative to launch mycology into the 21st century. *Studies in Mycology* 50: 19–22.
- Crous PW, Verkley GJM, Groenewald JZ, et al. 2009. *Fungal Biodiversity. CBS Laboratory Manual Series 1. CBS-KNAW Fungal Biodiversity Centre Utrecht, The Netherlands.*
- Cunningham CW. 1997. Can three incongruency tests predict when data should be combined? *Molecular Biology and Evolution* 14: 733–740.
- Damm U, Mostert L, Crous PW, et al. 2008. Novel Phaeoacremonium species associated with necrotic wood of Prunus trees. *Persoonia* 20: 87–102.
- De Hoog GS, Ahmed SA, Najafzadeh MJ, et al. 2013. Phylogenetic findings suggest possible new habitat and routes of infection of human eumycetoma. *PLoS Neglected Tropical Diseases* 7: e2229.
- Ding G, Song YC, Chen JR, et al. 2006. Chaetoglobosin U, a cytochalasan alkaloid from endophytic *Chaetomium globosum* IFB-E019. *Journal of Natural Products* 69: 302–304.
- Doveri F. 2013. An additional update on the genus *Chaetomium* with descriptions of two coprophilous species, new to Italy. *Mycosphere* 4: 820–846.
- Dreyfuss M. 1976. Taxonomische Untersuchungen innerhalb der Gattung *Chaetomium*. *Sydowia* 28: 50–133.
- El-Gindy AA, Saad RR, Fawzi E. 2003. Purification and some properties of exo-1,4-beta-glucanase from *Chaetomium olivaceum*. *Acta Microbiologica Polonica* 52: 35–44.
- Fries E. 1849. *Summa vegetabilium scandinaviae*. Stockholm & Leipzig.
- Fuckel I. 1869. *Symbolae mycologicae*. Wiesbaden.
- Ge HM, Zhang WY, Ding G, et al. 2008. Chaetoglobosins A and B, two unusual alkaloids from endophytic *Chaetomium globosum* culture. *Chemical Communications* 45: 5978–5980.
- Glass NL, Donaldson GC. 1995. Development of primer sets designed for use with the PCR to amplify conserved genes from filamentous ascomycetes. *Applied and Environmental Microbiology* 61: 1323–1330.
- Gomes RR, Glienke C, Videira SIR, et al. 2013. *Diaporthe*: a genus of endophytic, saprobic and plant pathogenic fungi. *Persoonia* 31: 1–41.
- Gonianakis M, Neonakis I, Darivianaki E, et al. 2005. Airborne ascomycotina on the island of Crete: Seasonal patterns based on an 8-year volumetric survey. *Aerobiologia* 21: 69–74.
- Greif MD, Currah RS. 2007. Development and dehiscence of the cephalothecoid peridium in *Aporoethelavia leptoderma* shows it belongs in *Chaetomidium*. *Mycological Research* 111: 70–77.
- Greif MD, Stichigal AM, Huhndorf SM. 2009. A re-evaluation of genus *Chaetomium* based on molecular and morphological characters. *Mycologia* 101: 554–564.
- Gueidan C, Roux C, Lutzoni F. 2007. Using multigene phylogeny analysis to assess generic delineation and character evolution in Verrucariaceae (Verrucariales, Ascomycota). *Mycological Research* 111: 1145–1168.
- Hall TA. 1999. BioEdit: a user-friendly biological sequence alignment editor and analysis program for Windows 95/98/NT. *Nucleic Acids Symposium Series* 41: 95–98.
- Hawksworth DL. 1975. *Farrowia*, a new genus in the Chaetomiaceae. *Persoonia* 8: 167–185.
- Hawksworth DL, Wells H. 1973. Ornamentation on the terminal hairs in *Chaetomium* Kunze ex Fr. and some allied genera. *Mycological Papers* 134: 1–24.
- Hillis DM, Bull JJ. 1993. An empirical test of bootstrapping as a method of assessing confidence in phylogenetic analysis. *Systematic Biology* 42: 182–192.
- Hoppin EC, McCoy EL, Rinaldi MG. 1983. Opportunistic mycotic infection caused by *Chaetomium* in a patient with acute leukemia. *Cancer* 52: 555–556.
- Hubka V, Mencl K, Skorepova M, et al. 2011. Phaeohiphomycosis and onychomycosis due to *Chaetomium* spp., including the first report of *Chaetomium brasiliense* infection. *Medical Mycology* 49: 724–733.
- Hwang SM, Suh MK, Ha GY. 2012. Onychomycosis due to nondermatophytic molds. *Annals of Dermatology* 24: 175–180.
- Kaewchai S, Soyong K, Hyde KD. 2009. Mycofungicides and fungal biofertilizers. *Fungal Diversity* 38: 25–50.
- Katoh K, Standley DM. 2013. MAFFT multiple sequence alignment software version 7: improvements in performance and usability. *Molecular Biology and Evolution* 30: 772–780.
- Kharwar RN, Mishra A, Gond SK, et al. 2011. Anticancer compounds derived from fungal endophytes: their importance and future challenges. *Natural Product Reports* 28: 1208–1228.
- Kim BS, Hwang BK. 2007. Microbial fungicides in the control of plant diseases. *Journal of Phytopathology* 155: 641–653.
- Kim DM, Lee MH, Suh MK, et al. 2013. Onychomycosis caused by *Chaetomium globosum*. *Annals of Dermatology* 25: 232–236.
- Kopytina NI. 2005. Distribution of the fungi from the genus *Chaetomium* (Ascomycota) in north-western part of the Black Sea. *Mikologiya I Fitopatologiya* 39: 12–18.
- Kumar S, Kaushik N, Proksch P. 2013. Identification of antifungal principle in the solvent extract of an endophytic fungus *Chaetomium globosum* from *Withania somnifera*. *SpringerPlus* 2: 37.
- Kunze G, Schmidt JK. 1817. *Mykologische Hefte* 1. Leipzig, Germany.
- Lagacé J, Cellier E. 2012. A case report of a mixed *Chaetomium globosum*/Trichophyton mentagrophytes onychomycosis. *Medical Mycology Case Reports* 1: 76–78.
- Latha R, Sasikala R, Muruganandam N, et al. 2010. Onychomycosis due to ascomycete *Chaetomium globosum*: A case report. *Indian Journal of Pathology and Microbiology* 53: 566–567.
- Lesire V, Hazouard E, Dequin PF, et al. 1999. Possible role of *Chaetomium globosum* in infection after autologous bone marrow transplantation. *Intensive Care Medicine* 25: 124–125.
- Lombard L, Crous PW, Wingfield BD, et al. 2010. Phylogeny and systematics of the genus *Calonectria*. *Studies in Mycology* 66: 31–69.
- Longoni P, Rodolfi M, Pantaleoni L, et al. 2012. Functional analysis of the degradation of cellulosic substrates by a *Chaetomium globosum* endophytic isolate. *Applied and Environmental Microbiology* 78: 3693–3705.
- Malloch D, Cain RF. 1973. The genus *Thielavia*. *Mycologia* 65: 1055–1077.
- Mason S, Cortes D, Horner WE. 2010. Detection of gaseous effluents and by-products of fungal growth that affect environments (RP-1243). *HVAC & R Research* 16: 109–121.
- Mason-Gamer R, Kellogg E. 1996. Testing for phylogenetic conflict among molecular datasets in the tribe Tiriceae (Graminae). *Systematic Biology* 45: 524–545.
- Matheny PB, Liu YJ, Ammirati JF, et al. 2002. Using RPB1 sequences to improve phylogenetic inference among mushrooms (Inocybe, Agaricales). *American Journal of Botany* 89: 688–698.
- McNeill J, Barrie FR, Buck WR, et al. 2012. International Code of Nomenclature for algae, fungi, and plants (Melbourne Code) adopted by the Eighteenth International Botanical Congress Melbourne, Australia, July 2011. Koeltz Scientific Books, Koenigstein.
- Miller AN, Huhndorf SM. 2005. Multi-gene phylogenies indicate ascomal wall morphology is a better predictor of phylogenetic relationships than ascospore morphology in the Sordariales (Ascomycota, Fungi). *Molecular Phylogenetics and Evolution* 35: 60–75.
- Miller JD, McMullin DR. 2014. Fungal secondary metabolites as harmful indoor air contaminants: 10 years on. *Applied Microbiology and Biotechnology* 98: 9953–9966.
- Millner PD. 1977. Radial growth responses to temperature by 58 *Chaetomium* species, and some taxonomic relationships. *Mycologia* 69: 492–502.
- Millner PD, Motta JJ, Lentz PL. 1977. Ascospores, germ pores, ultrastructure, and thermophilism of *Chaetomium*. *Mycologia* 69: 720–733.
- Momesso LD, Kawano CY, Ribeiro PH, et al. 2008. Chaetoglobosins produced by *Chaetomium globosum*, endophytic fungus found in association with *Viguiera robusta* Gardn (Asteraceae). *Química Nova* 31: 1680–1685.
- Naidu J, Singh SM, Pauranik M. 1991. Onychomycosis caused by *Chaetomium globosum* Kunze. *Mycopathologia* 113: 31–34.
- Nylander JAA. 2004. MrModeltest v. 2. Programme distributed by the author. Evolutionary Biology Centre, Uppsala University.

- O'Donnell K. 1993. Fusarium and its near relatives. In: Reynolds R, Taylor JW (eds), *The fungal holomorph: mitotic, meiotic and pleomorphic speciation in fungal systematics*: 225–233. CAB International, Wallingford.
- O'Donnell K, Cigelnik E. 1997. Two divergent intragenomic rDNA ITS2 types within a monophyletic lineage of the fungus *Fusarium* are nonorthologous. *Molecular Phylogenetics and Evolution* 7: 103–116.
- Park J-H, Choi GJ, Jang KS, et al. 2005. Antifungal activity against plant pathogenic fungi of chaetoviridins isolated from *Chaetomium globosum*. *FEMS Microbiology Letters* 252: 309–313.
- Paterson PJ, Seaton S, Yeghen T, et al. 2005. Molecular confirmation of invasive infection caused by *Chaetomium globosum*. *Journal of Clinical Pathology* 58: 334.
- Phonkerd N, Kanokmedhakul S, Kanokmedhakul K, et al. 2008. Bis-spiroazaphilones and azaphilones from the fungi *Chaetomium cochliodes* VTh01 and *C. cochliodes* CTh05. *Tetrahedron* 64: 9636–9645.
- Polizzi V, Delmulle B, Adams A, et al. 2009. JEM Spotlight: Fungi, mycotoxins and microbial volatile organic compounds in mouldy interiors from water-damaged buildings. *Journal of Environmental Monitoring* 11: 1849–1858.
- Prokhorov VP, Linnik MA. 2011. Morphological, cultural, and biodestructive peculiarities of *Chaetomium* species. *Moscow University Biological Sciences Bulletin* 66: 95–101.
- Rambaut A. 2009. FigTree v. 1.3.1. Computer program and documentation distributed by the author at <http://tree.bio.ed.ac.uk/software/>.
- Rayner RW. 1970. A mycological colour chart. CMI and British Mycological Society. Kew, Surrey, England.
- Ronquist F, Huelsenbeck JP. 2003. MrBayes 3: Bayesian phylogenetic inference under mixed models. *Bioinformatics* 19: 1572–1574.
- Saccardo PA. 1882. *Sylogae Pyrenomycetum. Sylogae Fungorum* 1: 1–768.
- Schoch CL, Seifert KA, Huhndorf S, et al. 2012. Nuclear ribosomal internal transcribed spacer (ITS) region as a universal DNA barcode marker for Fungi. *Proceedings of the National Academy of Sciences of the USA* 109: 6241–6246.
- Sekita S, Yoshihira K, Natori S, et al. 1981. Mycotoxin production by *Chaetomium* spp. and related fungi. *Canadian Journal of Microbiology* 27: 766–772.
- Seth HK. 1967. *Chaetomidium subfimetii* sp. nov. from Wales. *Transactions of the British Mycological Society* 50: 45–47.
- Seth HK. 1970. A monograph of the genus *Chaetomium*. *Beihefte zur Nova Hedwigia* 37: 1–133.
- Seth HK, Chen QT, Chen YD. 1987. A view on the retention of *Chaetomium globosum* Kze. and *C. olivaceum* Cooke & Ellis as separate species. *Acta Mycologica Sinica* 6: 82–85.
- Shanthiyaa V, Saravanakumar D, Rajendran L, et al. 2013. Use of *Chaetomium globosum* for biocontrol of potato late blight disease. *Crop Protection* 52: 33–38.
- Sharma S, Aggarwal R, Yadav A, et al. 2014. Protein mapping of *Chaetomium globosum*, a potential biological control agent through proteomics approach. *Journal of Plant Biochemistry and Biotechnology* 23: 284–292.
- Singh RK, Tiwari MK, Kim D, et al. 2013. Molecular cloning and characterization of a GH11 endoxylanase from *Chaetomium globosum*, and its use in enzymatic pretreatment of biomass. *Applied Microbiology and Biotechnology* 97: 7205–7214.
- Skolko AJ, Groves JW. 1953. Notes on seed-borne fungi VII. *Chaetomium*. *Canadian Journal of Botany* 31: 779–809.
- Sörgel G. 1960. Zum problem der trennung von arten bei pilzen, dargestellt am beispiel der ascomycetengattung *Chaetomium*. *Archives of Microbiology* 36: 51–66.
- Stamatakis A. 2006. RAxML-VI-HPC: Maximum likelihood-based phylogenetic analyses with thousands of taxa and mixed models. *Bioinformatics* 2: 2688–2690.
- Stchigel AM, Guarro J. 2007. A reassessment of cleistothecia as a taxonomic character. *Mycological Research* 111: 1100–1115.
- Stchigel AM, Guarro J, Jato V, et al. 2004. Two new species of *Chaetomidium* (Sordariales). *Studies in Mycology* 50: 215–220.
- Stillier MJ, Rosenthal S, Summerbell RC, et al. 1992. Onychomycosis of the toenails caused by *Chaetomium globosum*. *Journal of the American Academy of Dermatology* 26: 775–776.
- Sugiyama K, Sano A, Murakami M, et al. 2008. Three isolations of *Chaetomium globosum* from erythematous epilation of canine skin. *Medical Mycology* 46: 505–510.
- Suh S-O, Blackwell M. 1999. Molecular phylogeny of the cleistothecial fungi placed in Cephalothecaceae and Pseudeurotiaceae. *Mycologia* 91: 836–848.
- Swofford DL. 2003. PAUP*: Phylogenetic Analysis Using Parsimony (*and other methods), version 4. Sinauer Associates, Sunderland, Massachusetts, USA.
- Tamura K, Stecher G, Peterson D, et al. 2013. MEGA6: Molecular Evolutionary Genetics Analysis version 6.0. *Molecular Biology and Evolution* 30: 2725–2729.
- Tschudy RH. 1937. Experimental morphology of some species of *Chaetomium* I. Use of cultural reactions in determining species characteristics. *American Journal of Botany* 24: 472–480.
- Tullio V, Banche G, Allizond V, et al. 2010. Non-dermatophyte moulds as skin and nail foot mycosis agents: *Phoma* herbarum, *Chaetomium globosum* and *Microascus cinereus*. *Fungal Biology* 114: 345–349.
- Udagawa S. 1960. A taxonomic study on the Japanese species of *Chaetomium*. *The Journal of General and Applied Microbiology* 6: 223–251.
- Udagawa S, Muroi T, Kurata H, et al. 1979. The production of chaetoglobosins, sterigmatocystin, O-methylsterigmatocystin, and chaetocin by *Chaetomium* spp. and related fungi. *Canadian Journal of Microbiology* 25: 170–177.
- Umikalsom MS, Ariff AB, Hassan MA, et al. 1998. Kinetics of cellulose production by *Chaetomium globosum* at different levels of dissolved oxygen tension using oil palm empty fruit bunch fibre as substrate. *World Journal of Microbiology and Biotechnology* 14: 491–498.
- Untereiner WA, Débois V, Naveau FA. 2001. Molecular systematics of the ascomycete genus *Farrowia* (Chaetomiaceae). *Canadian Journal of Botany* 79: 321–333.
- Vesper S, McKinstry C, Ashley P, et al. 2007. Quantitative PCR analysis of moulds in the dust from homes of asthmatic children in North Carolina. *Journal of Environmental Monitoring* 9: 826–830.
- Von Arx JA. 1975. On *Thielavia* and some similar genera of ascomycetes. *Studies in Mycology* 8: 1–32.
- Von Arx JA, Dreyfuss M, Müller E. 1984. A re-evaluation of *Chaetomium* and Chaetomiaceae. *Persoonia* 12: 169–179.
- Von Arx JA, Guarro J, Figueras MJ. 1986. The Ascomycete genus *Chaetomium*. *Beihefte zur Nova Hedwigia* 84: 1–162.
- Wang XW, Wang XL, Liu FJ, et al. 2014. Phylogenetic assessment of *Chaetomium indicum* and allied species, with the introduction of three new species and epitypification of *C. funicola* and *C. indicum*. *Mycological Progress* 13: 719–732.
- Wang XW, Zheng RY. 2005. *Chaetomium ampulliforme* sp. nov. (Chaetomiaceae, Ascomycota) and similar species from China. *Nova Hedwigia* 81: 247–255.
- White TJ, Bruns T, Lee S, et al. 1990. Amplification and direct sequencing of fungal ribosomal RNA genes for phylogenetics. In: Innis MA, Gelfand DH, Sninsky JJ, et al. (eds), *PCR protocols: a guide to methods and applications*: 315–322. New York, Academic Press, Inc.
- Winter G. 1885. *Ascomyceten: Gymnoasceen und Pyrenomyceten*. Rabenhorst's Kryptogamen-Flora von Deutschland, Oesterreich und der Schweiz 1, 2.
- Yamada T, Jinno M, Kikuchi T, et al. 2012. Three new azaphilones produced by a marine fish-derived *Chaetomium globosum*. *The Journal of Antibiotics* 65: 413–417.
- Yan W, Ge HM, Wang G, et al. 2014. Pictet-Spengler reaction-based biosynthetic machinery in fungi. *Proceedings of the National Academy of Sciences of the United States of America* 111: 18138–18143.
- Yeghen YT, Fenelon L, Campbell CK, et al. 1996. *Chaetomium pneumonia* in patient with acute myeloid leukaemia. *Journal of Clinical Pathology* 49: 184–186.
- Zhang GZ, Wang FT, Qin JC, et al. 2013. Efficacy assessment of antifungal metabolites from *Chaetomium globosum* No. 05, a new biocontrol agent, against *Setosphaeria turcica*. *Biological Control* 64: 90–98.
- Zhang J, Ge HM, Jiao RH, et al. 2010. Cytotoxic chaetoglobosins from the endophyte *Chaetomium globosum*. *Planta Medica* 76: 1910–1914.
- Zhang Q, Li HQ, Zong SC, et al. 2012. Chemical and bioactive diversities of the genus *Chaetomium* secondary metabolites. *Mini Reviews in Medical Chemistry* 12: 127–148.
- Zopf W. 1881. Zur Entwicklungsgeschichte der Ascomyceten: *Chaetomium*. *Nova Acta der Kaiserlich Leopoldinisch-Carolinisch Deutschen Akademie der Naturforscher* 42: 199–292.