

Redefining *Humicola sensu stricto* and related genera in the Chaetomiaceae

X.W. Wang^{1,2,3}, F.Y. Yang^{2*}, M. Meijer³, B. Kraak³, B.D. Sun⁴, Y.L. Jiang⁵, Y.M. Wu⁶, F.Y. Bai¹, K.A. Seifert⁷, P.W. Crous^{3,8,9}, R.A. Samson³, and J. Houbraken^{3*}

¹State Key Laboratory of Mycology, Institute of Microbiology, Chinese Academy of Sciences, No. 3, 1st Beichen West Road, Chaoyang District, Beijing 100101, China; ²Grassland Institute, College of Animal Science & Technology, China Agricultural University, No. 2 Yuanmingyuan West Road, Haidian District, Beijing 100193, China; ³Westerdijk Fungal Biodiversity Institute, Uppsalalaan 8, 3584 CT Utrecht, The Netherlands; ⁴China General Microbiological Culture Collection Centre, Institute of Microbiology, Chinese Academy of Sciences, Beijing 100101, China; ⁵Department of Plant Pathology, Guizhou University, Guiyang 550025, China; ⁶Department of Plant Pathology, Shandong Agricultural University, Taian 271018, China; ⁷Ottawa Research and Development Centre, Biodiversity (Mycology and Microbiology), Agriculture and Agri-Food Canada, 960 Carling Avenue, Ottawa, Ontario K1A 0C6, Canada; ⁸Department of Microbiology and Plant Pathology, Forestry and Agricultural Biotechnology Institute (FABI), University of Pretoria, Pretoria 0002, South Africa; ⁹Microbiology, Department of Biology, Utrecht University, Padualaan 8, 3584 CH Utrecht, The Netherlands

*Correspondence: J. Houbraken, j.houbraken@westerdijkinstituut.nl; F.Y. Yang, yfuyu@126.com

Abstract: The traditional concept of the genus *Humicola* includes species that produce pigmented, thick-walled and single-celled spores laterally or terminally on hyphae or minimally differentiated conidiophores. More than 50 species have been described in the genus. Species commonly occur in soil, indoor environments, and compost habitats. The taxonomy of *Humicola* and morphologically similar genera is poorly understood in modern terms. Based on a four-locus phylogeny, the morphological concept of *Humicola* proved to be polyphyletic. The type of *Humicola*, *H. fuscoatra*, belongs to the Chaetomiaceae. In the Chaetomiaceae, species producing humicola-like thick-walled spores are distributed among four lineages: *Humicola sensu stricto*, *Mycothermus*, *Staphylotrichum*, and *Trichocladium*. In our revised concept of *Humicola*, asexual and sexually reproducing species both occur. The re-defined *Humicola* contains 24 species (seven new and thirteen new combinations), which are described and illustrated in this study. The species in this genus produce conidia that are lateral, intercalary or terminal on/in hyphae, and conidiophores are not formed or are minimally developed (micronematous). The ascospores of sexual *Humicola* species are limoniform to quadrangular in face view and bilaterally flattened with one apical germ pore. Seven species are accepted in *Staphylotrichum* (four new species, one new combination). Thick-walled conidia of *Staphylotrichum* species usually arise either from hyphae (micronematous) or from apically branched, seta-like conidiophores (macronematous). The sexual morph represented by *Staphylotrichum longicolleum* (= *Chaetomium longicolleum*) produces ascospores with long necks composed of a fused basal part of the terminal hairs, and ascospores that are broad limoniform to nearly globose, bilaterally flattened, with an apical germ pore. The *Trichocladium* lineage has a high morphological diversity in both asexual and sexual structures. Phylogenetic analysis revealed four subclades in this lineage. However, these subclades are genetically closely related, and no distinctive phenotypic characters are linked to any of them. Fourteen species are accepted in *Trichocladium*, including one new species, twelve new combinations. The type species of *Gilmaniella*, *G. humicola*, belongs to the polyphyletic family Lasiosphaeriaceae (Sordariales), but *G. macrospora* phylogenetically belongs to *Trichocladium*. The thermophilic genus *Mycothermus* and the type species *My. thermophilum* are validated, and one new *Mycothermus* species is described. Phylogenetic analyses show that *Remersonia*, another thermophilic genus, is sister to *Mycothermus* and two species are known, including one new species. *Thermomyces verrucosus* produces humicola-like conidia and is transferred to *Botryotrichum* based on phylogenetic affinities. This study is a first attempt to establish an inclusive modern classification of *Humicola* and humicola-like genera of the Chaetomiaceae. More research is needed to determine the phylogenetic relationships of "humicola"-like species outside the Chaetomiaceae.

Key words: *Humicola*, *Mycothermus*, Phylogeny, *Remersonia*, Sexual morphs, *Staphylotrichum*, *Trichocladium*, 43 Taxonomic novelties.

Taxonomic novelties: **new genus:** *Mycothermus* D.O. Natvig et al. ex X. Wei Wang, Houbraken & D. O. Natvig; **New species:** *Humicola atrobrunnea* X. Wei Wang, Houbraken, Y.L. Jiang & T.Y. Zhang, *Humicola christensenii* X. Wei Wang & Houbraken, *Humicola degenerans* X. Wei Wang & Houbraken, *Humicola leptodermospora* X. Wei Wang & Houbraken, *Humicola mutabilis* X. Wei Wang & Houbraken, *Humicola pulvericola* X. Wei Wang, Houbraken & Seifert, *Humicola quadrangulata* X. Wei Wang & Houbraken, *Mycothermus thermophiloides* X. Wei Wang & Houbraken, *Remersonia tenuis* X. Wei Wang, Houbraken & Seifert, *Staphylotrichum acaciicola* X. Wei Wang & Houbraken, *Staphylotrichum brevistipitatum* X. Wei Wang & Houbraken, *Staphylotrichum microascosporum* X. Wei Wang & Houbraken, *Staphylotrichum tortipilum* X. Wei Wang & Houbraken, *Trichocladium amorphum* X. Wei Wang & Houbraken; **New combinations:** *Botryotrichum verrucosum* (Pugh, Blakeman & Morgan-Jones) X. Wei Wang & Houbraken, *Humicola ampullifera* (X. Wei Wang) X. Wei Wang & Houbraken, *Humicola cuyabensis* (Decock & Hennebert) X. Wei Wang & Houbraken, *Humicola distorta* (L.M. Ames) X. Wei Wang & Houbraken, *Humicola floriformis* (Gené & Guarro) X. Wei Wang & Houbraken, *Humicola homopilata* (Omvik) X. Wei Wang & Houbraken, *Humicola malaysiensis* (D. Hawksw.) X. Wei Wang & Houbraken, *Humicola pinnata* (L.M. Ames) X. Wei Wang & Houbraken, *Humicola seminuda* (L.M. Ames) X. Wei Wang & Houbraken, *Humicola semispiralis* (Udagawa and Cain) X. Wei Wang & Houbraken, *Humicola sphaeralis* (Chivers) X. Wei Wang & Houbraken, *Humicola subspiralis* (Chivers) X. Wei Wang & Houbraken, *Humicola udagawae* (Sergejeva ex Udagawa) X. Wei Wang & Houbraken, *Humicola walleffii* (J.A. Mey. & Lanneau) X. Wei Wang & Houbraken, *Mycothermus thermophilus* (Cooney & R. Emers.) X. Wei Wang, Houbraken & D. O. Natvig, *Staphylotrichum longicolleum* (Krziemien. & Badura) X. Wei Wang & Houbraken, *Trichocladium acropullum* (X. Wei Wang) X. Wei Wang & Houbraken, *Trichocladium antarcticum* (Stchigel & Guarro) X. Wei Wang & Houbraken, *Trichocladium arxii* (Benny) X. Wei Wang & Houbraken, *Trichocladium crispatum* (Fuckel) X. Wei Wang & Houbraken, *Trichocladium griseum* (Traen) X. Wei Wang & Houbraken, *Trichocladium heterothallicum* (Yu Zhang & L. Cai) X. Wei Wang & Houbraken, *Trichocladium jilongense* (Y.M. Wu & T.Y. Zhang) X. Wei Wang & Houbraken, *Trichocladium nigrospermum* (Schwein.) X. Wei Wang & Houbraken, *Trichocladium seminis-citrulli* (Sergejeva) X. Wei Wang & Houbraken, *Trichocladium uniseriatum* (Yu Zhang & L. Cai) X. Wei Wang & Houbraken; **Nomen novum:** *Trichocladium beniowskiae* (M.D. Mehrotra) X. Wei Wang & Houbraken, *Trichocladium gilmaniellae* (Moustafa) X. Wei Wang & Houbraken.

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INTRODUCTION

Identification and classification of morphologically little-differentiated hyphomycetes have always been challenging. Species producing chlamydo-spores or similar propagules offer few morphological characters to guide taxonomists. The traditional Saccardoan approach to delimiting genera by the pigmentation and septation of spores and the cells that produce them, and the further refinements offered by studies of conidium ontogeny (including conidial secession) and cultural characteristics, provide additional information. The occurrence of synanamorphs or sexual stages also offers clues.

Phylogenetic studies using DNA provide clarity about relationships and give clues as to what phenotypic characters might be phylogenetically informative, facilitating the integration of morphologically depauperate hyphomycetes among more differentiated, often teleomorph-based taxa. Based on SSU and ITS sequence data, Hambleton *et al.* (2005) attempted to correlate differences in the details of conidium development with phylogenetic relationships among species with chlamydo-spores or aleurioconidia. Their definitions for chlamydo-spores and aleurioconidia were based on those from the first Kananaskis conference (Kendrick 1971). Chlamydo-spores were defined as “thick-walled, thallic, terminal or intercalary spores” formed on vegetative mycelium which “are not dispersed and do not secede until the adjacent hyphal cells dissolve away”, and hence are functionally a kind of “resting spores”. Aleurioconidia were defined as solitary, holothallic or monoblastic conidia produced on somewhat differentiated conidiophores or from conidiogenous cells, which are propagules and can be dispersed. Two relatively large hyphomycete genera that are central to the question of the integration of such fungi into fungal taxonomy are *Humicola* and *Trichocladium*. The spores produced by the species of these genera challenge the definitions separating the terms conidium, aleurioconidium, and chlamydo-spore, in part because there are so many intermediate forms. In this paper, we use these terms fairly loosely, with conidium used for lateral or terminal propagules that seem likely to secede and be dispersed, and chlamydo-spores for intercalary spores that seem likely to remain in the substrate and not be dispersed, i.e., resting spores. In these fungi, the occurrence of spore release by rhexolytic secession, necessary for strict use of the term aleurioconidium, is inconsistent and can be difficult to observe; for that reason, we do not use this term in the descriptions in this paper.

The hyphomycete genus *Humicola* was introduced by Traaen (1914) for two species, *H. fuscoatra* (the type) and *H. grisea*. Both species produce thick-walled, pigmented and usually single-celled spores. These spores are formed laterally or terminally on hyphae or minimally differentiated conidiophores. Although, in earlier studies, they have been called chlamydo-spores (Traaen 1914, de Bertoldi 1976) or aleurioconidia (Hambleton *et al.* 2005), based on the definitions discussed above, we call these propagules conidia. This basic morphology, a round spore in a hypha or on a stalk, is about as simple a sporulating morphology can be. Up to now, more than 50 species were described in *Humicola* (e.g. Nicoli & Russo 1974, de Bertoldi 1976, Jiang *et al.* 2016, Wang *et al.* 2016a,b), but the genus has never been comprehensively revised, nor has a thorough phylogenetic analysis been undertaken.

Trichocladium (Harz 1871) is a phragmoconidial counterpart of *Humicola*, differentiated by the production of darkly pigmented,

septate conidia. As reviewed by Goh & Hyde (1999), it includes 18 species that, despite their simple morphology, encompass a significant heterogeneity in conidial shape, pigmentation, and development. Hambleton *et al.* (2005) were surprised that the ITS sequences of *H. grisea* and the type species of *Trichocladium*, *T. asperum*, were identical, suggesting that the two species at least belong to the same genus. Some of the species of both genera also produce an inconspicuous acremonium-like synanamorph (Gams 1971), and the conidia may also have pale or thin-walled pore-like areas that might represent germ pores (Hambleton *et al.* 2005).

Both *Humicola* and *Trichocladium* have been associated with *Chaetomiaceae* (Seifert *et al.* 2011). As defined by its type species, *Humicola* is commonly considered an asexual genus in the *Chaetomiaceae* (Gams 1971, Kirk *et al.* 2008). However, there is evidence of a close relationship between asexual *Humicola* species and ascoma-producing species in the *Chaetomiaceae* (Zhang *et al.* 2017b). Several species within *Chaetomiaceae* produce humicola-like conidia together with ascomata and ascospores (von Arx *et al.* 1986, Decock & Hennebert 1997, Wang & Zheng 2005a,b). Among those, three species were classified in the genus *Farrowia*: *F. longicollea* (type species = *Chaetomium longicolleum*), *F. seminuda* (= *Chaetomium seminudum*) and *F. malaysiensis* (= *Chaetomium malaysiense*). *Farrowia* was characterized by ascomata with synchronously produced terminal hairs arising from elongated cells that fused to form a “distinct neck-like structure” below the perithecial apex (Hawksworth 1975). However, *Farrowia* was not accepted in subsequent monographs (Carter 1982, von Arx *et al.* 1986), although Untereiner *et al.* (2001) accepted the genus on the basis of the phylogenetic analysis of LSU sequences. In that study, the three *Farrowia* species clustered closely with *C. homopilatum*, *C. floriforme*, and *C. sphaerale*, which produce a humicola-like morph and ascomata lacking conspicuous necks. Detailed multi-locus molecular studies on the relationship and taxonomy of species producing chaetomium-like ascomata and/or humicola-like asexual structures are lacking.

Other species with similar thick-walled conidia, classified in various hyphomycete genera, have a similar ecology and may also be associated with *Chaetomiaceae*. A few genera with more developed conidiophores, but similar conidia and conidiogenesis to *Humicola*, are also relevant to the phylogenetic reevaluation of asexual members of *Chaetomiaceae* presented in this paper. *Botryotrichum*, with its setose, macronematous conidiophores bearing clusters of thick-walled conidia, has long been associated with *Chaetomium*, following the association of the type species *B. piluliferum* with its sexual state (Daniels 1961). Two other genera were not previously associated with *Chaetomium* sexual states but were revealed to partly belong to *Chaetomiaceae* by our phylogenetic studies. *Gilmaniella* was separated from *Humicola* and *Botryotrichum* by its branched conidiophores and the conidia with a conspicuous germ pore (Barron 1964). The conidiophores of *Staphylotrichum* species are also similar to those of *Botryotrichum* but do not terminate in setae (Nonaka *et al.* 2012).

Just because a species is morphologically simple, it does not mean it is biologically or economically unimportant. Most *Humicola* species are isolated from soil, while some are from compost, rotting plant materials, indoor environments or even fur of cats (Cooney & Emerson 1964, Tiscornia *et al.* 2009, Betancourt *et al.* 2013, Wang *et al.* 2016b). Some *Humicola*

species have potential as bio-organic fertilisers or as biological control organisms of plant diseases, such as Verticillium wilt of cotton and Phytophthora blight of pepper (Ko *et al.* 2011, Lang *et al.* 2012, Yang *et al.* 2014a,b). The invalidly named thermophilic species *Mycothermus thermophilus* (\equiv *Scytalidium thermophilum* = *Humicola insolens*) attracts considerable attention for its remarkable ability to produce thermostable enzymes used to decompose polymeric carbohydrates (Salles *et al.* 2005, Ghatora *et al.* 2006, Du *et al.* 2013, Souza *et al.* 2013, Yang *et al.* 2014a,b, Xia *et al.* 2015). This fungus also contributes to mushroom production by promoting the growth of *Agaricus bisporus* mycelium (Straatsma & Samson 1993). Some species are reported to have a negative effect on human health (Betancourt *et al.* 2013, Mejia *et al.* 2014). *Humicola* species can cause allergic reactions, and in two reports *Humicola* species are mentioned as the causal agent of peritonitis (Wang *et al.* 2011, Ogawa *et al.* 2002, Kita *et al.* 2003, Burns *et al.* 2015).

Earlier research started the reevaluation of *Humicola*- and *Trichocladium*-like species that are not associated with *Chaetomiaceae*. Table 2 in Hambleton *et al.* (2005) summarized the phylogenetic relationships, conidial characters, and synanymorphs of several chlamydo-spore or "aleurioconidial" genera associated with *Hypocreales*, *Pezizales*, and *Eurotiales*. They described the new genus *Leohumicola* in the order *Leotiomyces*, which exhibits an intermediate morphology between *Humicola* and *Trichocladium*, with lateral or terminal conidia with a dark brown terminal cell and a paler basal cell. One species of *Trichocladium*, *T. opacum*, was transferred to a new genus *Pleotrichocladium* in the *Melanommataceae* (*Pleosporales*) based on the phylogenetic analyses of SSU, LSU and ITS sequences (Hernández-Restrepo *et al.* 2017). These preliminary steps indicate that the classification of species and genera with humicola-like or trichocladium-like conidia needs a complete taxonomic update.

In this study, the generic delimitation of *Chaetomiaceae* members that produce humicola- or trichocladium-like asexual spores was re-evaluated using a four-locus phylogeny and morphological data. The phylogenetic relationships of *Humicola*, the core group of *Trichocladium*, and related genera are clarified, and the species in these genera are (re-)described and illustrated.

MATERIALS AND METHODS

Isolates

Strains producing humicola- or trichocladium-like thick-walled spores were obtained from 1) the CBS culture collection housed at the Westerdijk Fungal Biodiversity Institute, Utrecht, the Netherlands, 2) the China General Microbiological Culture Collection Centre, Institute of Microbiology, Beijing, China (CGMCC) and 3) the Herbarium of Shandong Agricultural University, Plant Pathology (HSAUP), Shandong, China. Some strains were isolated from house dust by dilution to extinction, as described by Visagie *et al.* (2014). Furthermore, a preliminary phylogenetic analysis was made based on LSU sequences from previous studies (Wang *et al.* 2016a,b) combined with sequences from the in-house database of the Westerdijk Institute. Additional strains were selected based on the results of this analysis. All the isolates used in this study are listed in Table 1, except for those selected from Wang *et al.* (2016b).

DNA isolation, sequencing and phylogeny

Genomic DNA was extracted from fungal mycelium grown on oatmeal agar (OA) using the DNeasy[®] UltraClean[®] Microbial Kit (Qiagen, Germany) following the manufacturer's instructions. The following primers were used for PCR amplification: *rpb2*-5F2 (Sung *et al.* 2007) & *rpb2*AM-7R (Miller & Huhndorf 2005) for the second largest subunit of DNA-directed RNA polymerase II (*rpb2*) gene region; ITS5 (White *et al.* 1990) & NL4 (O'Donnell 1993) for the internal transcribed spacer regions (ITS), including 5.8S nrRNA gene region and the D1/D2 domains of the 28S nrDNA (LSU); T1 (O'Donnell & Cigelnik 1997) & TUB4Rd (Groenewald *et al.* 2013) for the partial beta-tubulin (*tub2*) gene region. To study the phylogenetic relationships of the *Remersonia* species, a larger fragment of the beta-tubulin (*tub2*) gene region was amplified using the primers pairs TUB2Fd & TUB3Rd (Groenewald *et al.* 2013) and TUB4Fd & TUB2Rd (Groenewald *et al.* 2013). The PCR conditions were the same as those described by Wang *et al.* (2016a,b). Each of the amplicons was sequenced in both directions using the PCR primers and the BigDye Terminator v. 3.1 Cycle Sequencing Kit (Applied Biosystems, Foster City, CA, USA) following the manufacturer's instructions. Sequencing was performed with an ABI PRISM 3730XL DNA Analyzer (Applied Biosystems, CA, USA). Consensus sequences for each locus were assembled using MEGA v. 6 (Tamura *et al.* 2013). Novel sequences generated in this study were deposited in ENA (European Nucleotide Archive, <http://www.ebi.ac.uk/ena>, Table 1).

Sequences of representative species belonging to the *Chaetomiaceae* were obtained from Wang *et al.* (2016b), the reference *rpb2* sequences of non-chaetomiaceae species in the *Sordariales* were from Miller & Huhndorf (2005). Phylogenetic analyses were based on Bayesian inference (BI), Maximum Likelihood (ML) and Maximum Parsimony (MP) as described previously (Wang *et al.* 2016a). For BI, the best evolutionary model for each locus was determined using MrModeltest v. 2.0 (Nylander 2004). Obtained trees were viewed in FigTree v. 1.1.2 (Rambaut 2009) and subsequently visually prepared and edited in Adobe[®] Illustrator[®] CS6.

Morphology

Colony morphology was examined on four different media: OA, cornmeal agar (CMA), malt extract agar (MEA) and potato carrot agar (PCA). Media were prepared as described by Crous *et al.* (2009). Cultures were inoculated in a three-point fashion and incubated in the dark at 25 °C, or 37 °C for thermophilic isolates. Colony diameters were measured after 7 d. Colony photos were taken when mature reproductive structures appeared, and the colony colour was described according to the mycological colour charts of Rayner (1970). Microscopic observations were performed using the methodology described previously (Wang *et al.* 2016a). Morphological descriptions are mainly based on cultures grown on OA. For the measurements of bilaterally flattened ascospores, the size was reported as "length" × "width in front view" × "width in lateral view". To study the asexual spore development, slides were prepared using the inclined coverslip method (Kawato & Shinobu 1959, revised in Nugent *et al.* 2006). In short, two sterilized coverslips were placed under a 45° angle in the agar medium. Subsequently, inoculations were made, and after growth, the coverslip was mounted on a microscope glass

Table 1. Details of strains included in this study.

Species	Culture accession number	Previous name	Origin	ENA accession numbers		
				ITS & LSU	<i>rpb2</i>	<i>tub2</i>
<i>Botryotrichum verrucosum</i>	CBS 116.64 ^T	<i>Thermomyces verrucosus</i>	Salt-marsh soil, mature dunes, UK	LT993567	LT993486	LT993648
<i>Humicola ampulliiella</i>	CBS 116735 ^T	<i>Chaetomium ampulliiellum</i>	Discarded sock, China	LT993568	LT993487	LT993649
	CBS 116736		Soil, China	LT993569	LT993488	LT993650
<i>H. atrobrunnea</i> ¹	HSAUPII ₀₅ -1004 ^T		Soil, China, Guizhou	LT993570	LT993489	LT993651
<i>H. christensenii</i>	CBS 127760 ^T		Soil, USA, Minnesota	LT993571	LT993490	LT993652
	CGMCC 3.08497		Substrate unknown, China	LT993572	LT993491	LT993653
<i>H. cuyabenoensis</i>	CBS 398.97 ^T	<i>Chaetomium cuyabenoensis</i>	Rain forest, Ecuador	LT993573	LT993492	LT993654
<i>H. degenerans</i>	CBS 232.65 ^T		Soil under mixed forest, Canada, Ontario	LT993574	LT993493	LT993655
	CBS 780.71		Termite mound, Angola	LT993575	LT993494	LT993656
	CBS 127324		Soil, USA	LT993576	LT993495	LT993657
<i>H. distorta</i>	CBS 417.66 ^T	<i>Chaetomium distortum</i>	<i>Populus tremuloides</i> dead leaf, USA, Iowa	LT993577	LT993496	LT993658
<i>H. floriformis</i>	CBS 815.97 ^T	<i>Chaetomium floriforme</i>	Fallen leaves, Thailand, Sukhothai	LT993578	LT993497	LT993659
<i>H. fuscoatra</i>	CBS 118.14 ^T		Soil, Norway	LT993579	LT993498	LT993660
	CGMCC 3.13428		Soil, China, Tibet	LT993580	LT993499	LT993661
<i>H. fuscogrisea</i>	CGMCC 3.13790 ^T		Soil, China, Shennongjia	LT993581	LT993500	LT993662
<i>H. homopilata</i>	CBS 157.55 ^T	<i>Chaetomium homopilatum</i>	Filter paper in soil, Norway	LT993582	LT993501	LT993663
	CBS 338.68		Unknown substrate, unknown country	LT993583	LT993502	LT993664
<i>H. leptodermospora</i>	CBS 120095 ^T		Forestal soil, Brazil	LT993584	LT993503	LT993665
<i>H. malaysiensis</i>	CBS 399.97	<i>Chaetomium malaysiense</i>	<i>Elaeis guineensi</i> , Mylaysia, Selangor	LT993586	LT993505	LT993667
	CBS 760.83		Soil, Ivory Coast, Kaprémé	LT993587	LT993506	LT993668
	CBS 167.61		Soil, Japan	LT993585	LT993504	LT993666
<i>H. mutabilis</i>	CBS 779.71 ^T		Soil, Israel	LT993588	LT993507	LT993669
<i>H. olivacea</i>	CBS 142031 ^T		Dust, USA	LT993589	LT993508	LT993670
<i>H. pinnata</i>	CBS 467.66 ^T	<i>Chaetomium pinnatum</i>	Dead wood, USA, Coronado National Forest	LT993590	LT993509	LT993671
<i>H. pulvericola</i>	CBS 144165 ^T		Dust, Mexico	LT993591	LT993510	LT993672
	CBS 144166		Dust, South Africa	LT993592	LT993511	LT993673
<i>H. quadrangulata</i>	CBS 111771 ^T		Soil, Brazil	LT993593	LT993512	LT993674
<i>H. seminuda</i>	CBS 368.84 ^{eT}	<i>Chaetomium seminudum</i>	Soil, Canada, Ontario	LT993594	LT993513	LT993675
	CBS 153.59		Leaf fragment in soil, China, Lushan	LT993595	LT993514	LT993676
	CBS 549.69		Soil under <i>Thuja occidentalis</i> , Canada, Ontario	LT993596	LT993515	LT993677
<i>H. semispiralis</i>	CBS 723.97 ^{eT}	<i>Chaetomium semispirale</i>	Paper, Canada, Toronto	LT993597	LT993516	LT993678
<i>H. sphaeralis</i>	CBS 985.87 ^{eT}	<i>Chaetomium sphaerale</i>	Soil, France	LT993598	LT993517	LT993679
<i>H. subspiralis</i>	CBS 148.58	<i>Chaetomium subspirale</i>	Leaf fragments in soil, China	LT993599	LT993518	LT993680
	CBS 119768		Soil, China	LT993600	LT993519	LT993681
<i>H. udagawae</i>	CBS 337.68 ^T	<i>Chaetomium udagawae</i>	Unknown substrate, unknown country	LT993601	LT993520	LT993682
<i>H. wallefii</i>	CBS 147.67 ^T	<i>Chaetomium wallefii</i>	Soil, Zaire	LT993602	LT993521	LT993683
<i>Mycothermus thermophiloides</i>	CBS 183.81 ^T		Soil, USA, Indiana	LT993603	LT993522	LT993684
<i>M. thermophilum</i>	CBS 625.91 ^T	<i>Humicola instens</i> <i>Humicola grisea</i> var <i>thermoides</i>	Chicken nest straw, USA, Nevada	LT993604	LT993523	LT993685
	CBS 626.91		Rotting guayule shrub, USA, California	LT993605	LT993524	LT993686
	CBS 627.91		Dung of elephant, USA, California	LT993606	LT993525	LT993687
	CBS 226.63		Mushroom compost, Switzerland	LT993607	LT993526	LT993688
	CBS 392.69		Unknown substrate, USA, California	LT993608	LT993527	LT993689
<i>Remersonia tenuis</i>	CBS 784.85 ^T		Dung of horse, India	LT993609	LT993528	LT993690
<i>R. thermophila</i>	CBS 643.91		Compost, Netherlands	LT993610	LT993529	LT993691
	CBS 645.91		Compost, Netherlands	LT993611	LT993530	LT993692
	CBS 540.69		Mushroom compost, Switzerland	LT993612	LT993531	LT993693
<i>Staphylotrichum acaciicola</i>	CBS 281.65 ^T		Acacia karroo leaf litter, South Africa	LT993613	LT993532	LT993694
	CBS 554.89		Rain forest soil, Brazil	LT993614	LT993533	LT993695
	CBS 127289		Soil, USA	LT993615	LT993534	LT993696

Table 1. (Continued).

Species	Culture accession number	Previous name	Origin	ENA accession numbers		
				ITS & LSU	<i>rpb2</i>	<i>tub2</i>
<i>S. boninense</i>	CBS 112059		Twig, Brazil	LT993616	LT993535	LT993697
	CBS 112543		Leaf litter, Brazil	LT993617	LT993536	LT993698
<i>S. brevistipitatum</i>	CBS 294.55		Soil, Zaire	LT993618	LT993537	LT993699
	CBS 408.67 ^T		<i>Eucalyptus</i> leaf litter, South Africa	LT993619	LT993538	LT993700
<i>S. coccosporum</i>	CBS 364.58 ^T		Soil, Zaire	LT993620	LT993539	LT993701
<i>S. longicolleum</i>	CBS 119.57	<i>Chaetomium longicolleum</i>	Soil, Madagascar	LT993621	LT993540	LT993702
	CBS 562.80		Woodland soil, Jamaica	LT993622	LT993541	LT993703
	CBS 100950		Leaf litter, Venezuela	LT993623	LT993542	LT993704
<i>S. microascosporum</i>	CBS 184.79 ^T		Soil from Mangifera orchard, Sudan	LT993624	LT993543	LT993705
<i>S. tortipilum</i>	CBS 103.79 ^T		Dung of pine vole, USA, North Carolina	LT993625	LT993544	LT993706
<i>Trichocladium acropullum</i>	CBS 114580 ^T	<i>Chaetomium acropullum</i>	Soil, China	LT993626	LT993545	LT993707
	CBS 126783		Leaf of <i>Hordeum vulgare</i> , Iran	LT993627	LT993546	LT993708
<i>T. amorphum</i>	CBS 127763 ^T		Greenhouse Soil, USA	LT993628	LT993547	LT993709
<i>T. antarcticum</i>	CBS 135876	<i>Thielavia antarctica</i>	<i>Usnea</i> cf. <i>aurantio-atra</i> , Antarctica	LT993630	LT993549	LT993711
	CBS 123565 ^T		<i>Usnea</i> cf. <i>aurantio-atra</i> , Antarctica	LT993629	LT993548	LT993710
<i>T. arxii</i>	CBS 104.79 ^T	<i>Chaetomidium arxii</i>	Dung of kangaroo-rat, USA, California	LT993631	LT993550	LT993712
<i>T. asperum</i>	CBS 903.85 ^{eT}		Acidic soil, Germany	LT993632	LT993551	LT993713
	CBS 140.21		Unknown substrate, Netherlands	LT993633	LT993552	LT993714
	CBS 157.22		Unknown substrate, unknown country	LT993634	LT993553	LT993715
<i>T. beniowskiae</i>	CBS 757.74 ^T	<i>Beniowskia macrospora</i>	Grass, India	LT993635	LT993554	LT993716
<i>T. crispatum</i>	CBS 149.58	<i>Chaetomium crispatum</i>	Estuarine sediment, Germany	LT993636	LT993555	LT993717
	CBS 693.71		Agricultural soil, Netherlands	LT993637	LT993556	LT993718
<i>T. gilmaniellae</i>	CBS 388.75 ^T	<i>Gilmaniella macrospora</i>	Salt-marsh soil, Kuwait	LT993638	LT993557	LT993719
<i>T. griseum</i>	CBS 119.14 NeoT	<i>Humicola grisea</i> var <i>grisea</i>	Soil, Norway	LT993639	LT993558	LT993720
	CBS 217.34		Unknown substrate, Germany	LT993640	LT993559	LT993721
	CGMCC 3.13888		Soil, China, Jilin	LT993641	LT993560	LT993722
<i>T. jilongensis</i>	HSAUPI07 1485 ^T	<i>Humicola jilongense</i>	Mountain soil, China, Tibet	LT993642	LT993561	LT993723
	CBS 195.87		Field soil, Germany	LT993643	LT993562	LT993724
<i>T. nigrosperrum</i>	CBS 103.36	<i>Monodictys nigrosperra</i>	Meal, Netherlands	LT993644	LT993563	LT993725
<i>T. seminis-citrulli</i>	CBS 143.58 ^T	<i>Chaetomium seminis-citrulli</i>	Dung of fox, Turkmenistan	LT993645	LT993564	LT993726
	CBS 637.83		Dung of goat, Israel	LT993646	LT993565	LT993727
<i>Trichocladium</i> sp.	CBS 351.77	<i>Chaetomium tetrasporum</i>	Wheat field soil, Germany	LT993647	LT993566	LT993728

Remarks: T and eT denote ex-type and ex-epitype cultures, respectively.

¹ The new species described in this study are highlighted in bold.

with lactic acid. Alternatively, slides were made using transparent adhesive tape (Titan Ultra Clear Tape, Conglom Inc., Toronto, Canada) (Bensch *et al.* 2010).

RESULTS

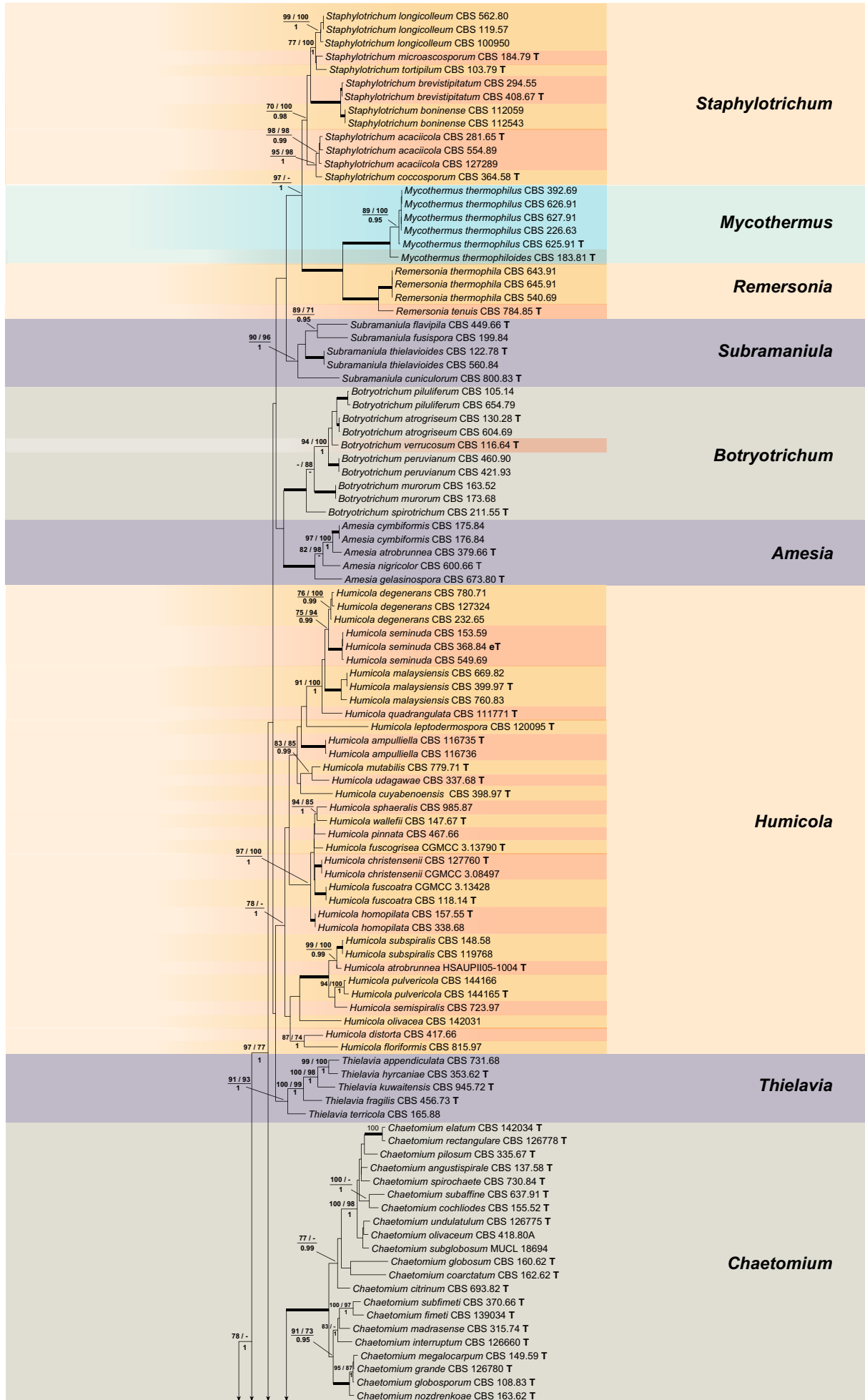
Phylogeny

Delimitation of Chaetomiaceae

A phylogram based on *rpb2* sequence data was constructed to delimit the *Chaetomiaceae* and to show the relationship of the species and genera investigated in this study (Fig. 1). Our *rpb2* sequences were combined with available sequence data generated from (reference) strains belonging to the *Chaetomiaceae*, *Lasiosphaeriaceae* and *Sordariaceae* in the *Sordariales*.

In total, 207 isolates representing 155 taxa were studied, including 91 strains of 13 other *Chaetomiaceae* genera (Wang *et al.* 2016b). *Microascus trigonosporus* CBS 218.31 (*Microascales*) was selected as an outgroup. The alignment consisted

of 901 characters including gaps. Of these, 345 characters were constant, 506 characters were parsimony-informative, and 50 characters were parsimony-uninformative. For the Bayesian inference, the GTR+I+G model was selected based on the results of the MrModel Test. Species producing humicola-like or trichocladium-like conidia fell into four clades: the *Humicola* lineage (ML-BS = 78 %; MP-BS < 70 %; PP = 1.00), the *Mycothermus* lineage (ML-BS = 100 %; MP-BS = 100 %; PP = 1.00), the *Staphylotrichum* lineage (ML-BS = 70 %; MP-BS = 100 %; PP = 0.98) and the *Trichocladium* lineage (ML-BS 97 %; MP-BS = 100 %; PP = 1.00). The *Remersonia* lineage (ML-BS 100 %; MP-BS = 100 %; PP = 1.00) forms a sister to the *Mycothermus* lineage (ML-BS 100 %; MP-BS = 100 %; PP = 1.00) and this lineage includes species that produce conidia on synnemata rather than on hyphae or hypha-like conidiophores like those in the other four lineages. *Thermomyces verrucosus* clustered within the genus *Botryotrichum*. *Gilmaniella humicola*, the type species of this genus, falls in one of the clades in the polyphyletic *Lasiosphaeriaceae*. However, CBS 388.75, the type of *Gilmaniella macrospora*, belongs to the *Trichocladium* lineage.



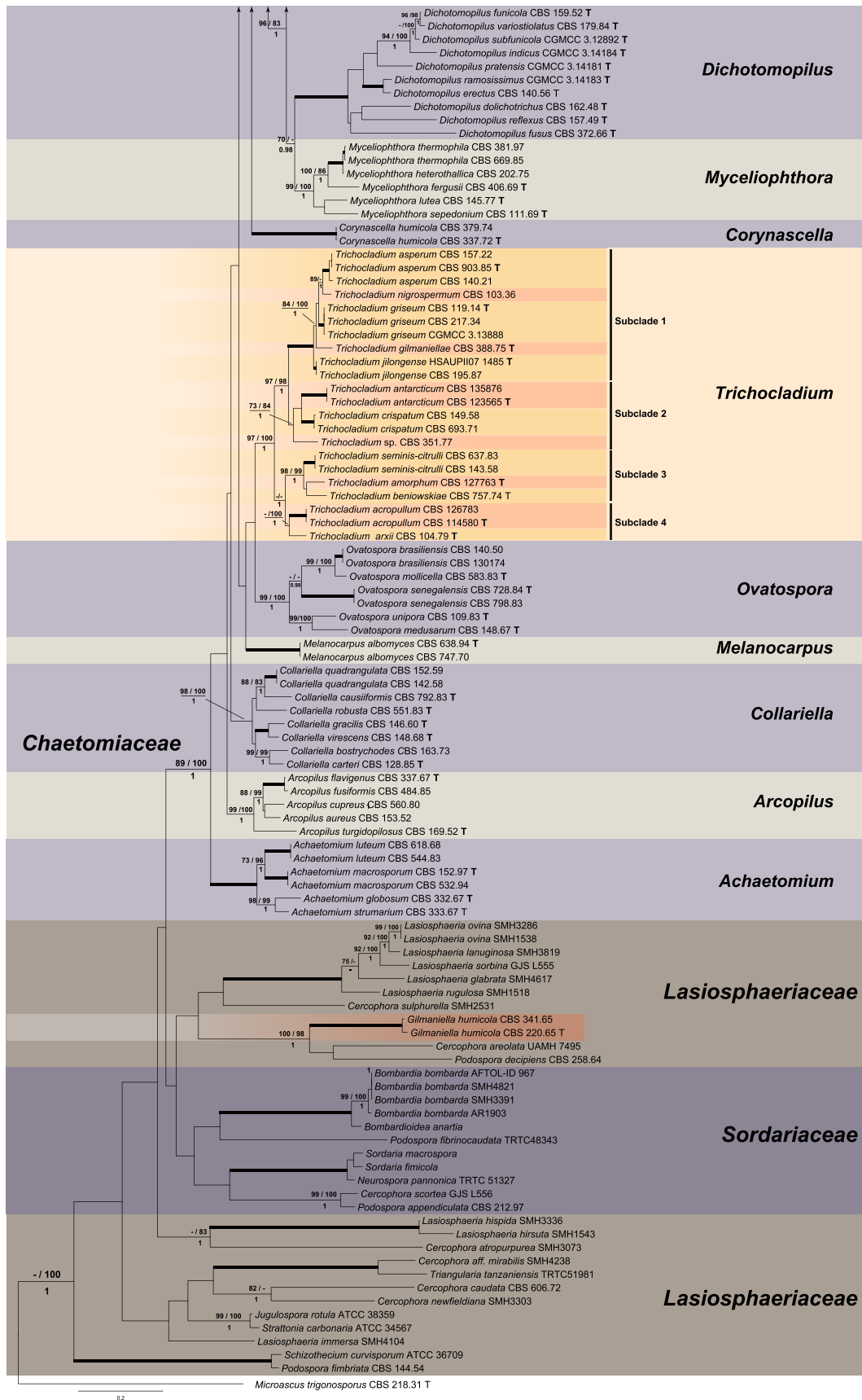


Fig. 1. (Continued).

Fig. 1. Phylogenetic tree inferred from a Maximum-Likelihood analysis of the *rpb2* gene region alignment. The confidence values are indicated at the notes: bootstrap proportions from the ML analysis (before the backslash), the MP analysis (after the backslash) above branches, and the posterior probabilities from the Bayesian analysis below branches. The “-” means lacking statistical support (<70 % for bootstrap proportions from ML or MP analyses; <0.95 for posterior probabilities from Bayesian analyses). The branches with full statistical support (ML-BS = 100 %; MP-BS = 100 %; PP = 1.0) are highlighted by thickened branches. Genus and species clades are discriminated with boxes of different colours. The scale bar shows the expected number of changes per site. The tree is rooted with *Microascus trigonosporus* strain CBS 218.31.

Four-locus phylogeny

The concatenated alignment included 173 isolates representing 125 taxa, including 91 representatives of 13 other genera in the family. The alignment contained 3264 characters (including gaps) and is composed of four partitions: 864 characters for *rpb2*, 1125 characters for *tub2*, 701 characters for ITS and 574 characters for the D1/D2 regions of LSU. Of them, 1215 characters were constant, 1584 were parsimony-informative, and 465 were parsimony-uninformative. For the Bayesian inference, the GTR+I+G model was selected as optimal for all four partitions based on the results of the MrModel Test. All of the five lineages recognised in the *rpb2* alignment were supported with robust support: the *Humicola* lineage (ML-BS = 82 %, MP-BS = 100 %, PP = 0.95), the *Mycothermus* lineage (ML-BS = 100 %, MP-BS = 100 %, PP = 1.00), the *Remersonia* lineage (ML-BS = 99 %, MP-BS = 100 %, PP = 1.00), the *Staphylotrichum* lineage (ML-BS = 98 %, MP-BS = 100 %, PP = 0.99) and the *Trichocladium* lineage (ML-BS = 99 %, MP-BS = 100 %, PP = 0.96) (Fig. 2). The *rpb2* and the concatenated phylogenetic analyses recognised the species inside in the five target lineages with robust statistical support (> 70 % BS, > 0.95 PP). Twenty-three species clades were recognised in the *Humicola* lineage, including the type species *Humicola fuscoatra*. In the *Trichocladium* lineage, thirteen species clades were recognised. Among the species recognised on the traditional morphology-based concept of *Trichocladium*, only the type species *T. asperum* is retained here in this *Trichocladium* lineage. Seven clades are present in the *Staphylotrichum* lineage. The known species *S. coccosporum*, *S. boninense*, the sexually reproducing species *S. longicolleum* (= *Chaetomium longicolleum*) and four new species belong to this lineage. The type species and a potentially novel taxon were distinguished in both the *Mycothermus* lineage and the *Remersonia* lineage.

Mycothermus and *Remersonia* (*tub2* phylogeny)

Remersonia was originally proposed as a monotypic genus. In our *rpb2* phylogeny and four-locus phylogeny, two distinctive taxa were identified. The (ex)-type material of *R. thermophila* is no longer available for this study, and in order to compare and combine our sequence data with that of Natvig et al. (2015), another longer fragment of *tub2* region needed to be analysed. Five *Remersonia* sequences and twelve *Mycothermus* sequences were included in the alignment, and the length of the data set was 1815 characters including gaps. Of these characters, 1303 were constant, 349 were parsimony-informative, and 163 were parsimony-uninformative. For the Bayesian inference, the HKY+G model was selected based from the results of the MrModel Test. Similar to the four-locus phylogeny, the *tub2* analysis revealed the presence of two distinct clades in the *Remersonia* lineage and two distinctive clades in the *Mycothermus* lineage (Fig. 3). The isolates CBS 784.85 and CBS 183.81 were confirmed to be potentially new taxa.

TAXONOMY

The three mesophilic genera *Humicola sensu stricto*, *Staphylotrichum* and *Trichocladium* are re-defined, and the thermophilic genus *Mycothermus* is validated below. In addition, the morphological diversity of the thermophilic genus *Remersonia* is presented, and *Thermomyces verrucosus* is combined in

Botryotrichum. Forty-six species are (re-)described and illustrated, including 14 new species and 28 new combinations (incl. two new names).

Botryotrichum verrucosum (Pugh, Blakeman & Morgan-Jones) X. Wei Wang & Houbraken, **comb. nov.** MycoBank MB824410. Fig. 4.

Basionym: *Thermomyces verrucosus* Pugh, Blakeman & Morgan-Jones, Trans. Brit. Mycol. Soc. 47: 116. 1964.

Micromorphology: Somatic hyphae hyaline, 1.5–4.5 µm wide. Conidiophores producing laterally from hyphae, unbranched, occasionally branched once, cylindrical, hyaline to slightly pigmented, septate, often conspicuously thickened and pigmented at septa, 4–45(–65) × 2.5–4 µm. Conidiogenous cells subhyaline to pale brown, cylindrical or slightly swollen as doliiform, holothallic. Conidia solitary, olivaceous brown, globose to subglobose, conspicuously warted, (12.5–)14–15.5(–17) µm.

Culture characteristics: Colonies on OA 28–32 mm diam after 7 d at 25 °C; edge entire; hyaline, obverse white because of aerial hyphae, fuscous black near the edge when old; reverse uncoloured. Colonies on CMA 30–36 mm diam after 7 d at 25 °C; edge entire; obverse white because of aerial hyphae; reverse uncoloured. Colonies on MEA 17–23 mm diam after 7 d at 25 °C, edge entire; texture floccose because of aerial hyphae; obverse white with mouse grey centre and edge; reverse dark mouse grey. Colonies on PCA 24–30 mm diam after 7 d at 25 °C; edge entire; obverse white because of hyaline aerial hyphae; reverse uncoloured.

Material examined: England, Lincolnshire, isolated from salt-marsh soil of mature dunes, Jan 1962, G. Morgan-Jones, ex-type culture CBS 116.64 = ATCC 22222 = IMI 096466ii = MUCL 30565 = VKM F-3568.

Notes: This species was originally classified in *Thermomyces* (Pugh et al. 1964). *Thermomyces verrucosus* is a mesophile, and earlier studies show that this species belongs to the *Chaetomiaceae* (Mouchacca 1997, Houbraken et al. 2014), but the exact taxonomic position within the family remained unknown. Our phylogenetic analyses (Figs 1, 2) indicated that *Th. verrucosus* resides in a clade with *Botryotrichum piluliferum*, *B. atrogriseum* and *B. peruvianum*. It lacks the branched conidiophores and sterile setae typically observed in *B. piluliferum* or *B. peruvianum*.

Humicola Traaen, Nytt Mag. Naturvidensk. 52: 31. 1914. MycoBank MB8566.

Type species: *Humicola fuscoatra* Traaen.

Asexual morphs producing conidia arising laterally, intercalary or terminally from hyphae without differentiated conidiophores, sometimes together with acronium-like conidiophores, occasionally only acronium-like conidiophores present. *Ascomata* absent or present, when present superficial, or covered by aerial hyphae, ostiolate. *Terminal hairs* seta-like, flexuous, undulate, coiled or arcuate with apices incurved to coiled. *Asci* clavate, with 8 biseriate or irregularly arranged ascospores, evanescent before ascospores become mature. *Ascospores* limoniform to quadrangular, bilaterally flattened, with an apical germ pore.

Notes: *Humicola* is re-defined and re-established here centred around species phylogenetically allied with the type species, *H. fuscoatra*. Fifteen *Humicola* species produce ascomata together with asexual morphs. Of the eight species that now only

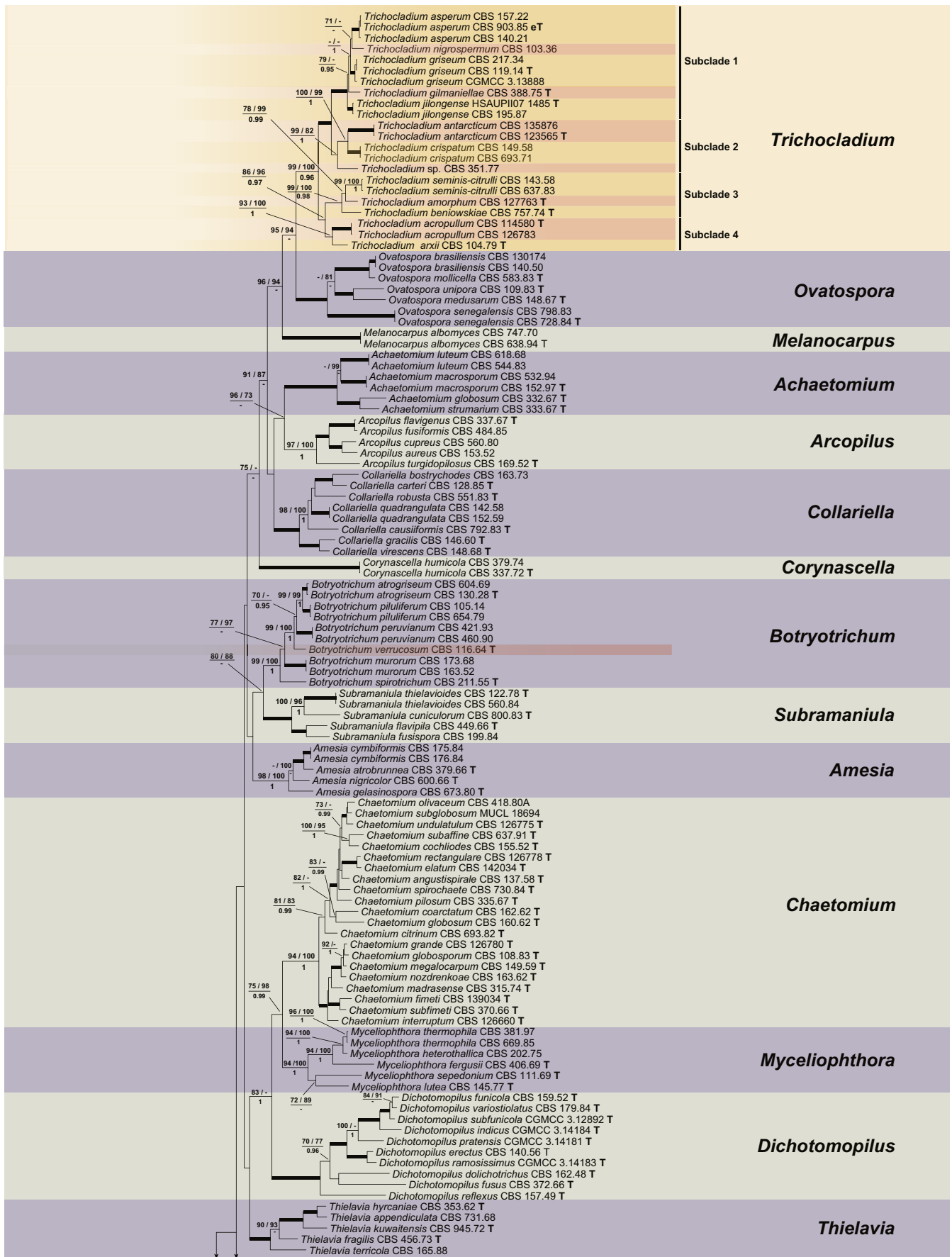


Fig. 2. Phylogenetic tree resulting from a Maximum-Likelihood analysis of the concatenated *rpb2*, *tub2*, ITS and LSU gene region alignment, with the confidence values indicated at the nodes same to the *rpb2* phylogenetic tree (Fig. 1). The “-” means lacking statistical support (<70 % for bootstrap proportions from ML or MP analyses; <0.95 for posterior probabilities from Bayesian analyses). The branches with full statistical support (MP-BS = 100 %; ML-BS = 100 %; PP = 1.0) are highlighted by thickened branches. Genus and species clades are discriminated with boxes of different colours. The scale bar shows the expected number of changes per site. The tree is rooted with *Microascus trigonosporus* strain CBS 218.31.

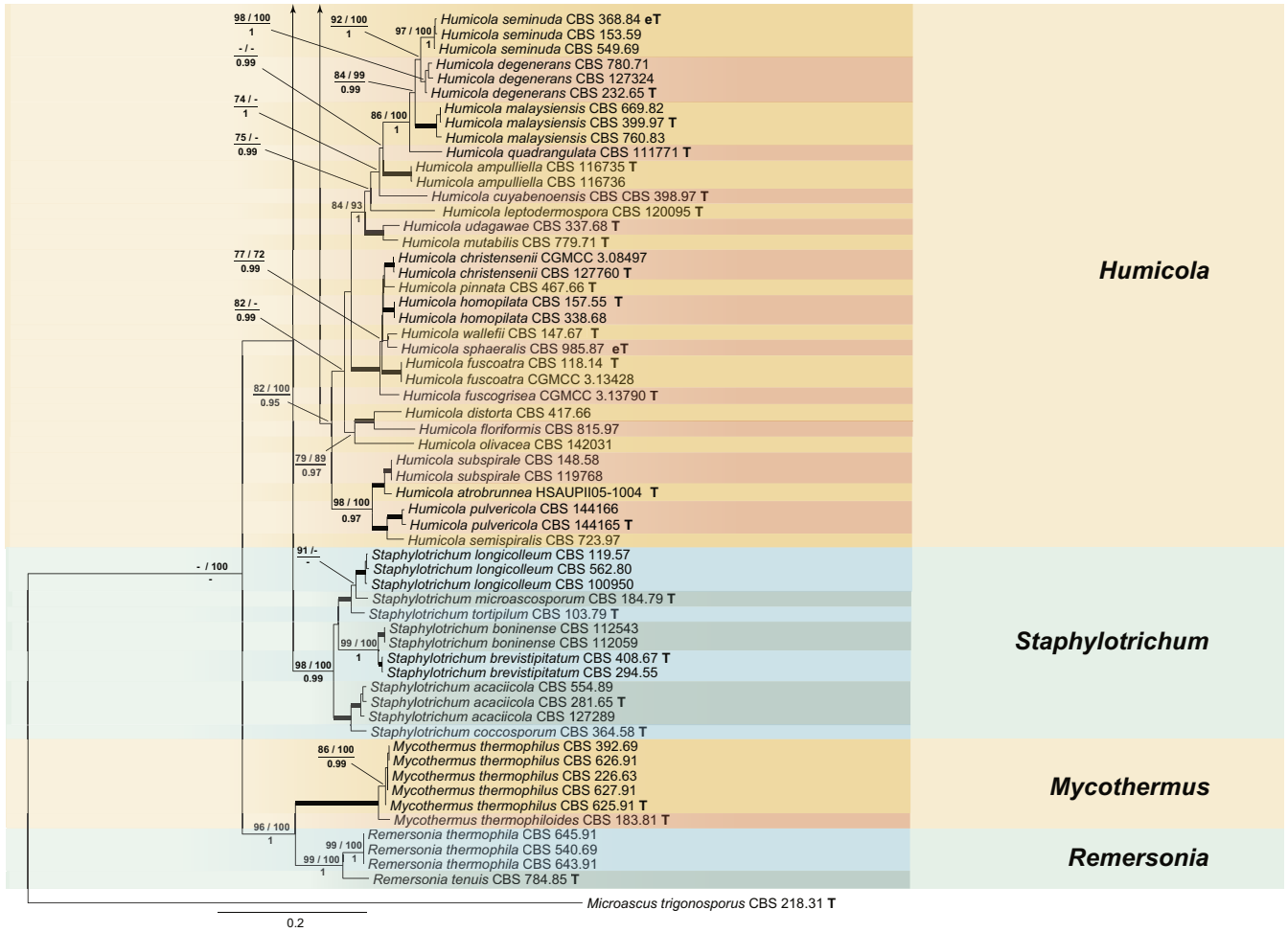


Fig. 2. (Continued).

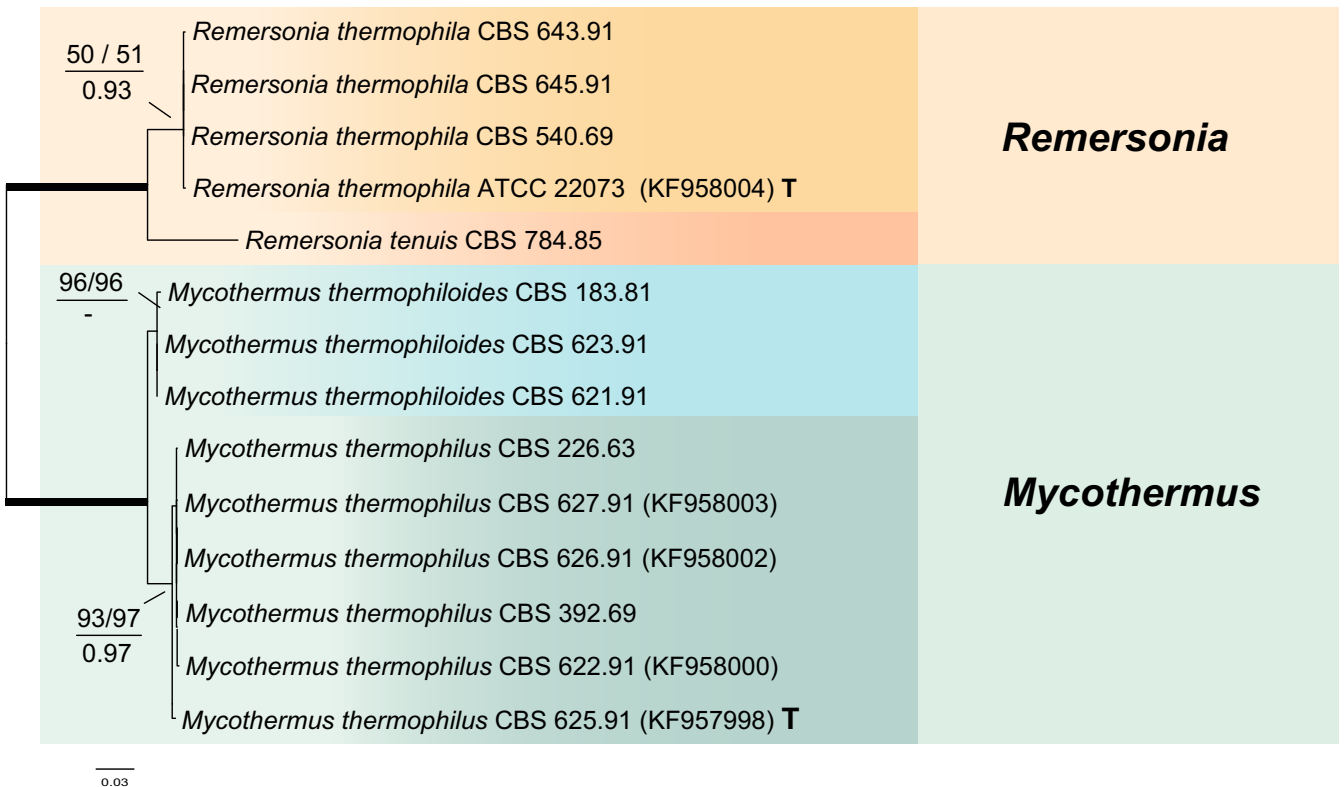


Fig. 3. An unrooted phylogenetic tree from ML analysis for the identification of species in *Remersonia* and *Mycothermus* based on the longer *tub2* alignment. The confidence values are indicated at the notes same to Fig. 1. The scale bar shows the expected number of changes per site.

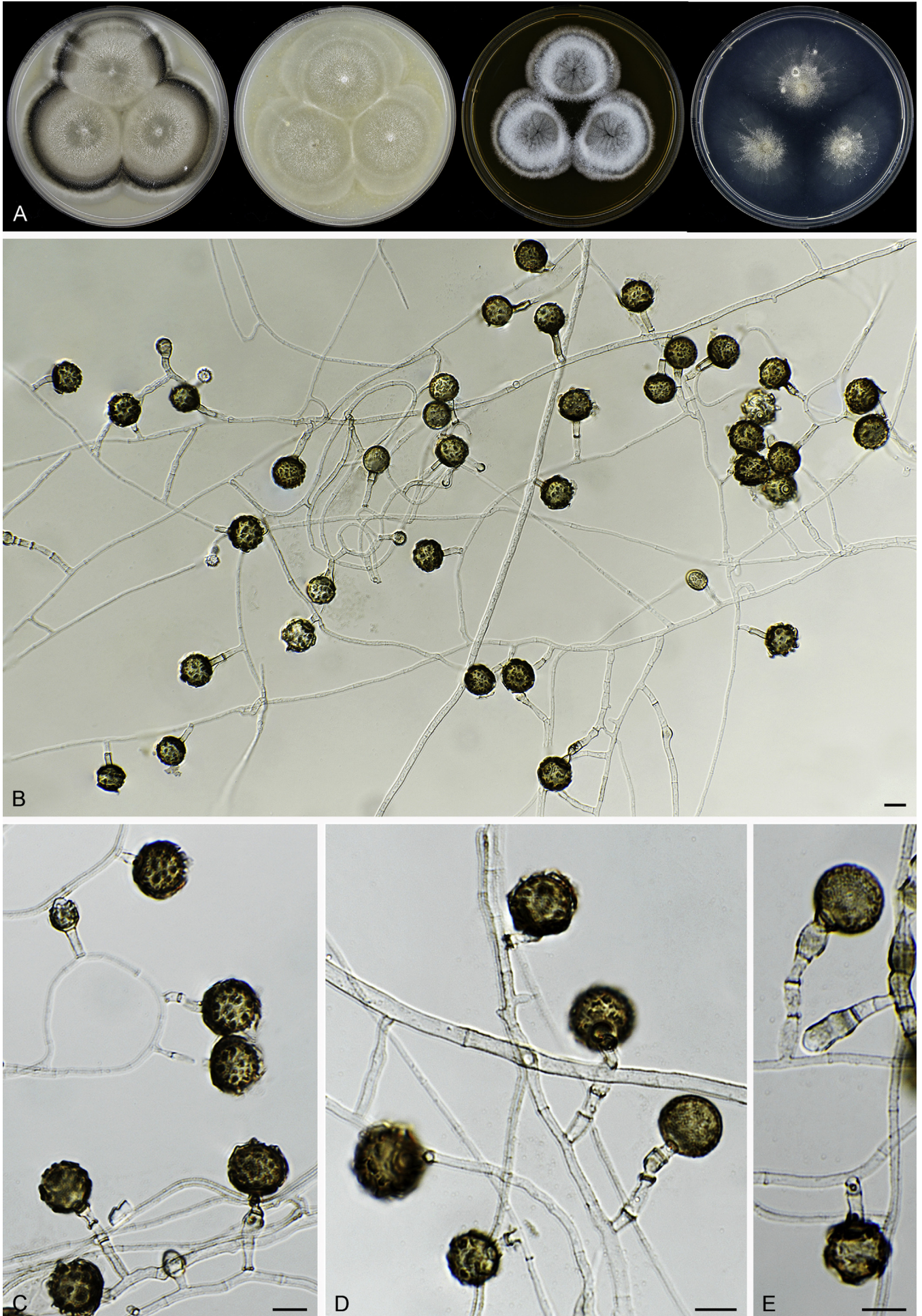


Fig. 4. *Botryotrichum verrucosum* (CBS 116.64, ex-type culture). **A.** Colonies from left to right on OA, CMA, MEA and PCA after 3 wk incubation. **B–E.** Hyphae, conidiophores and conidia. Scale bars = 10 μ m.

exhibit an asexual morph in culture, three originally were deposited in the CBS collection under their sexual morph name: CBS 815.97 (ex-type of *Humicola floriformis*, deposited as *Chaetomium floriforme*), CBS 120095 (as *Chaetomium longicolleum*) and CBS 147.67 (ex-type of *H. wallefii*, as *Ch. wallefii*). *Humicola sensu stricto* is characterised by the presence of conidia on hyphae without differentiation of conidiophores, and the co-occurrence of an acremonium-like morph in some species. Ascospores, if present, are limoniform to quadrangular and bilaterally flattened with an apical germ pore.

Humicola ampulliella (X. Wei Wang) X. Wei Wang & Houbraken, **comb. nov.** MycoBank MB824419. Fig. 5.

Basionym: *Chaetomium ampullillum* X. Wei Wang, Nova Hedwigia 81: 248. 2005.

Micromorphology: *Ascomata* superficial, ostiolate, leaden black with pale luteous to amber hairs in reflected light, elongate obpyriform, obclavate or ampulliform below, apically attenuated to an elongate conical or short cylindrical neck, 160–260 µm high, 65–130 µm diam at the widest part, with the neck part about 40–120 µm long, 29–45 µm wide in the middle portion. *Ascomatal wall* brown, composed of angular and irregular cells, or elongated to cylindrical cells in the neck part in surface view. *Terminal hairs* arising from the extension of the adjacent ostiolar cells, seta-like and delicate, smooth, tapering and fading to hyaline towards the tips, 1.5–3 µm diam near the base, usually surrounded by several closely septate, long, thick and seta-like hairs which are 3.5–6 µm diam near the base. *Lateral hairs* similar to thick terminal ones, tapering and fading towards the tips. *Asci* narrowly clavate to cylindrical, with spore-bearing part 22.5–34.5 × 6–9.5 µm and stalks about 7–21.5 µm long, with 8 biseriate or uniseriate ascospores, evanescent. *Ascospores* rust brown when mature, limoniform, prominently umbonate at both ends, bilaterally flattened, (6.5–)7–8.5(–9.5) × 5.5–6.5(–7.5) × 3.5–4.5 µm, with an apical germ pore. *Conidia* usually oblate, ellipsoidal or subglobose, sometimes obovoid to pyriform, arising laterally or terminally from the hyaline aerial hyphae, solitary, sometimes two cells in chains or several in clusters, fawn, (7–)8–12(–14) × (6–)7–9(–9.5) µm.

Culture characteristics: Colonies on OA 33–39 mm diam after 7 d at 25 °C; edge entire or slightly crenate; obverse showing leaden black mature ascomata mixed with young ascomata covered by pale luteous to amber ascomata hairs, and sparse white aerial hypha; soluble pigment absent; reverse uncoloured. Colonies on CMA similar to those on OA, 31–37 mm diam after 7 d at 25 °C. Colonies on MEA 29–35 mm diam after 7 d at 25 °C; edge entire, obverse showing a thin layer of white aerial mycelium mixed with sparse ascomata; reverse saffron to ochreous. Colonies on PCA 27–33 mm diam after 7 d at 25 °C, edge entire; translucent; aerial hyphae absent; soluble pigment absent; reverse uncoloured.

Material examined: China, Fujian province, Wuyi Mountain, isolated from a discarded sock, Aug 2003, X. W. Wang, ex-type culture CBS 116735 = CGMCC 3.6696; Hunan province, Changsha, isolated from soil under a tree, X. W. Wang, Jun 2003, culture CBS 116736 = CGMCC 3.6697.

Notes: This species can easily be distinguished from other species by the production of delicate ostiolar hairs, narrowly clavate to cylindrical asci, limoniform ascospores that are prominently umbonate at both ends and oblate to ellipsoidal conidia.

Humicola atrobrunnea X. Wei Wang, Houbraken, Y.L. Jiang & T.Y. Zhang, **sp. nov.** MycoBank MB824420. Fig. 6.

Etymology: The epithet refers to the dark brown conidia of this species.

Micromorphology: *Somatic hyphae* hyaline, 1–4.5 µm wide. *Conidia* produced laterally on the side of vegetative hyphae, occasionally terminally on the short branches of hyphae, single-celled, olivaceous with dark brown thick wall, solitary, sometimes 2–3 in chain or several in cluster, smooth, globose, subglobose to oblate, occasionally obovoid or pyriform, (7–)8–11(–13.5) µm high, (7–)8–10(–10.5) µm wide.

Culture characteristics: Colonies on OA 30–36 mm diam after 7 d at 25 °C; edge entire; aerial hyphae thin, obverse white, becoming olivaceous along the edge because of the formation of conidia; reverse uncoloured. Colonies on CMA 28–34 mm diam after 7 d at 25 °C; morphology similar to those on OA. Colonies on MEA 29–35 mm diam after 7 d at 25 °C; edge entire or slightly lobate, obverse white; texture floccose because of the hyaline aerial hyphae; reverse uncoloured. Colonies on PCA 29–35 mm diam after 7 d at 25 °C; edge entire; aerial hyphae sparse or absent, obverse olivaceous around the centre; reverse olivaceous around the centre.

Material examined: China, Guizhou, isolated from garden soil, 2004, Y.L. Jiang (**holotype** CBS H-23481, culture ex-type HSAUPL05-1004 = CBS 114167).

Notes: This species is morphologically similar to *H. fuscoatra*, but can be distinguished by its more thick-walled and darker conidia.

Humicola christensenii X. Wei Wang & Houbraken, **sp. nov.** MycoBank MB824422. Fig. 7.

Etymology: Named in memory of Dr Martha Christensen, who isolated the ex-type culture of this species.

Micromorphology: *Ascomata* superficial, ostiolate, leaden black with honey hairs in reflected light, ovoid, obpyriform or obclavate below, apically attenuated to an elongate conical or short cylindrical neck, 160–240 µm high, 105–150 µm diam at the widest part, with the neck part about 30–50 µm long, 32–42 µm wide in the middle. *Ascomatal wall* brown, composed of angular and irregular cells in surface view. *Terminal hairs* arising around ostiolar pore, erect in the lower part, smooth to slightly punctulate, closely septate, 3–5 µm diam near the base, flexuous, undulate or slightly and loosely coiled in the upper part, often constricted at septa, tapering and fading towards the tips. *Lateral hairs* seta-like, closely septate. *Asci* clavate, with spore-bearing part 18–32 × (7–)8–11 µm and stalks about 7–15 µm long, with 8 biseriate or irregularly arranged ascospores, evanescent. *Ascospores* rust brown when mature, limoniform, umbonate at both ends, bilaterally flattened, 6.5–7.5(–8) × 5.5–6 × 3.5–4.5 µm, with an apical germ pore. *Conidia* subglobose to oblate, sometimes obovoid, arising laterally, intercalary or terminally from the hyaline aerial hyphae, solitary, sometimes two cells in chains, fawn, 5.5–9 µm diam.

Culture characteristics: Colonies on OA 30–36 mm diam after 7 d at 25 °C; edge entire or slightly crenate; obverse showing a thick layer of irregularly distributed white aerial mycelium covering ascomata; soluble pigment olivaceous; reverse olivaceous to brown vinaceous. Colonies on CMA similar to those on OA, 30–36 mm diam after 7 d at 25 °C. Colonies on MEA 33–39 mm diam after 7 d at 25 °C; edge entire; obverse showing a relatively thin layer of white aerial mycelium; sporulation

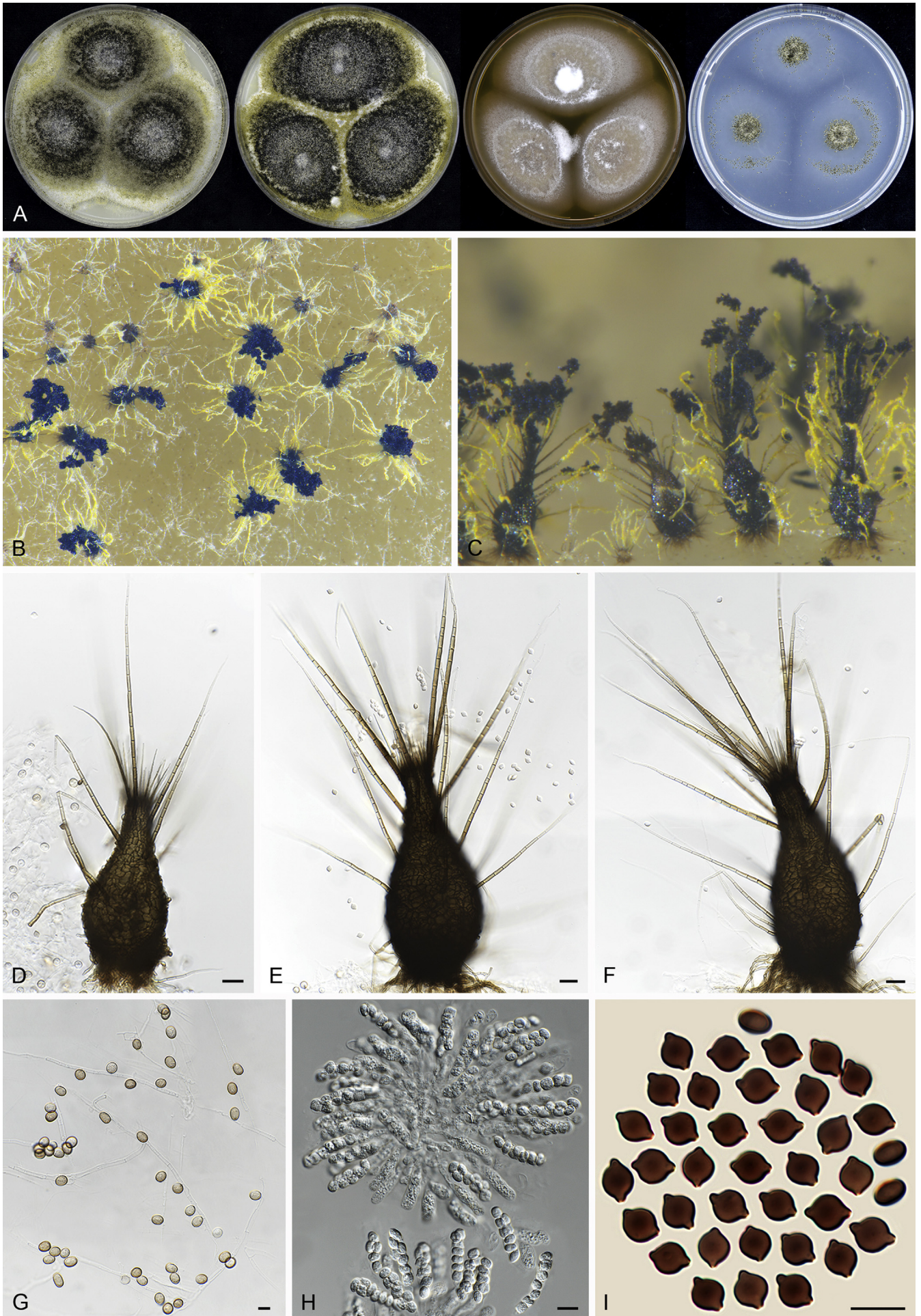


Fig. 5. *Humicola ampullifera* (CBS 116735, ex-type culture). **A.** Colonies from left to right on OA, CMA, MEA and PCA after 4 wk incubation. **B.** Mature ascomata on OA, top view. **C.** Mature ascomata on OA, side view. **D–F.** Ascomata mounted in lactic acid. **G.** Hyphae and conidia. **H.** Asci. **I.** Ascospores. Scale bars: D–F = 20 µm; G–I = 10 µm.

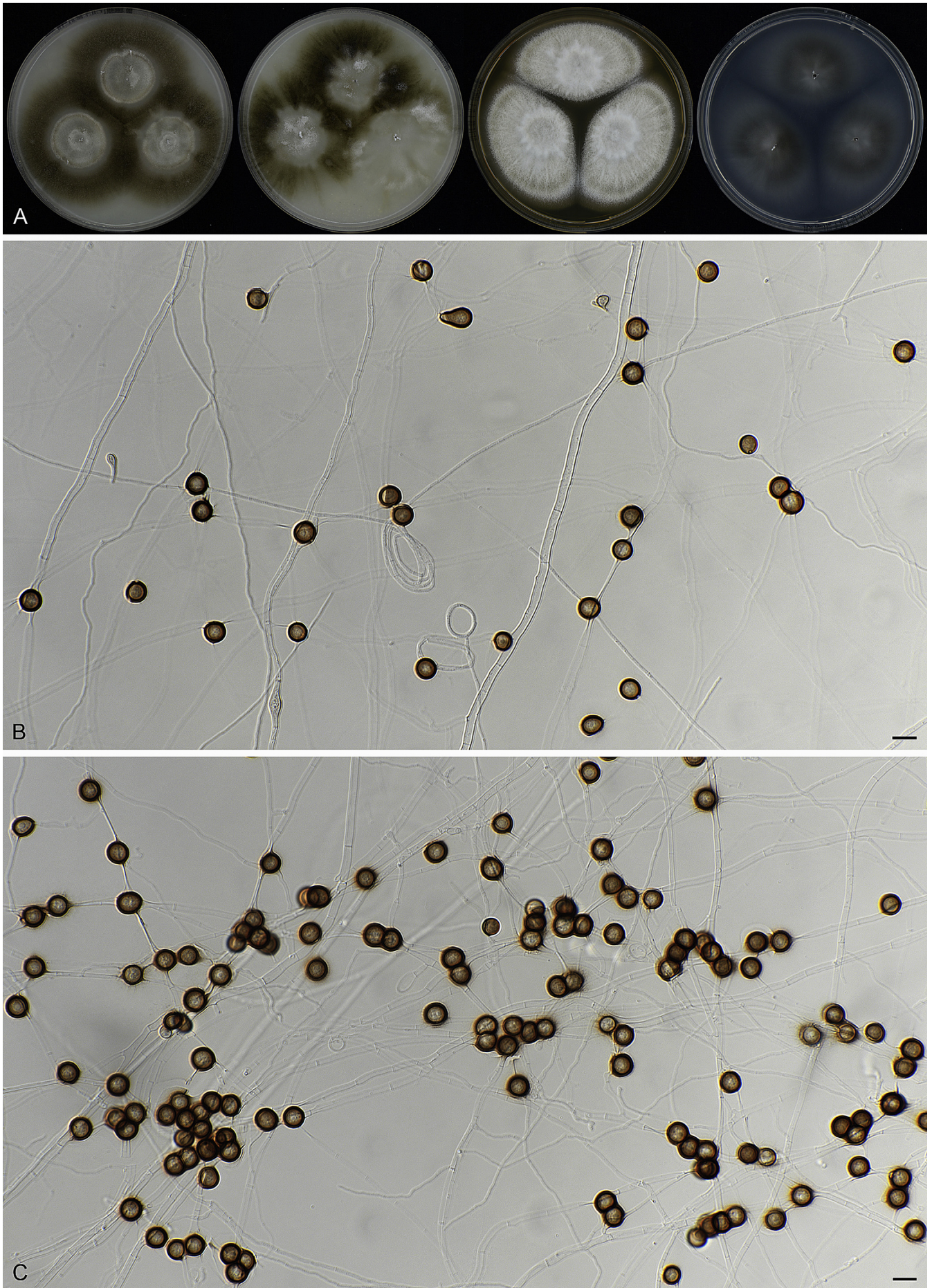


Fig. 6. *Hemicola atrobrunnea* (HSAUPI₀₅₋₁₀₀₄, ex-type culture). **A.** Colonies from left to right on OA, CMA, MEA and PCA after 1 wk incubation. **B–C.** Hyphae and conidia. Scale bars = 10 μ m.

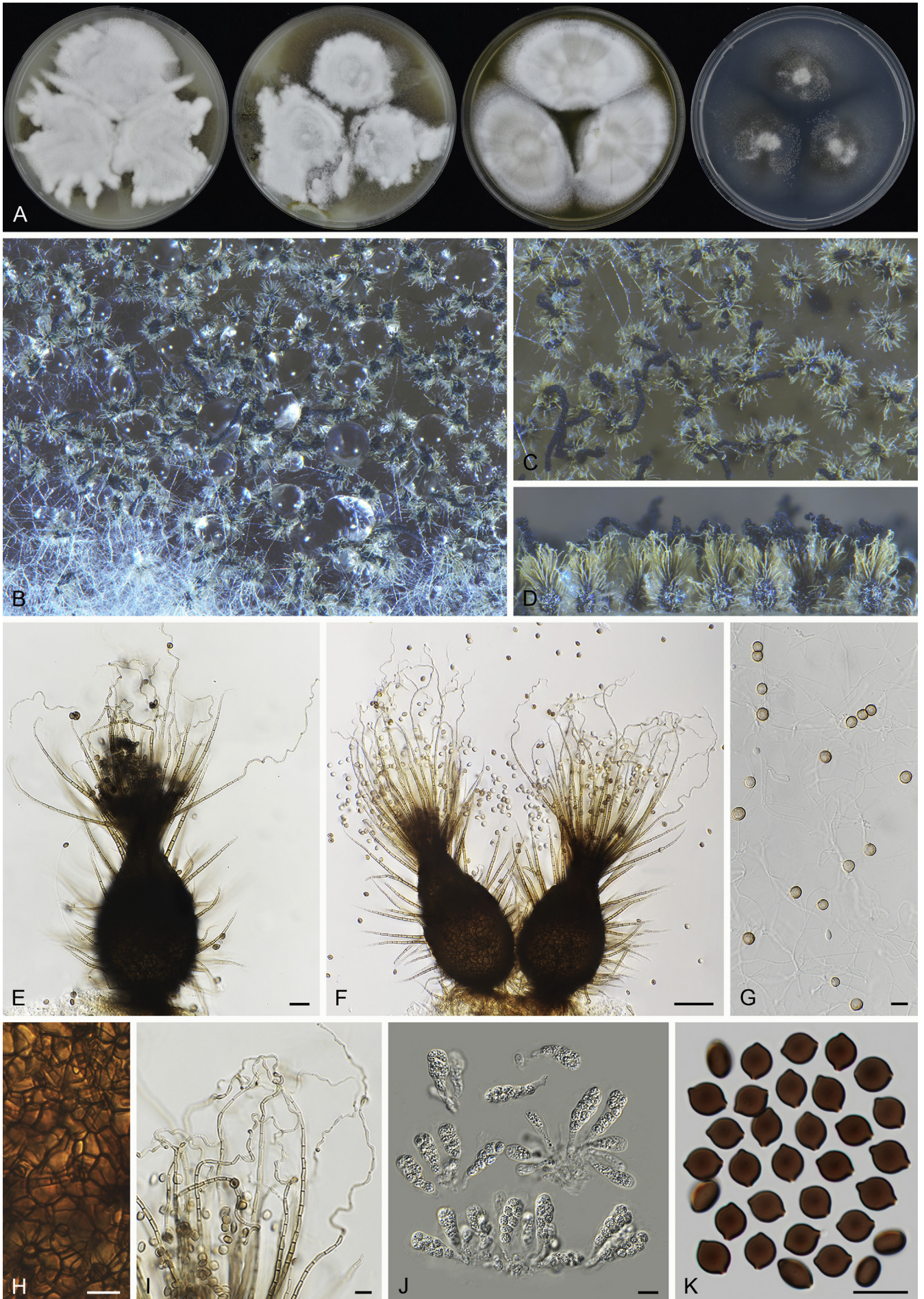


Fig. 7. *Humicola christensenii* (CBS 117760, ex-type culture). **A.** Colonies from left to right on OA, CMA, MEA and PCA after 5 wk incubation. **B.** Part of the colony on OA. **C.** Mature ascomata on OA, top view. **D.** Mature ascomata on OA, side view. **E–F.** Ascomata mounted in lactic acid. **G.** Hyphae and conidia. **H.** Structure of ascomatal wall in surface view. **I.** Terminal ascomatal hairs. **J.** Asci. **K.** Ascospores. Scale bars: E = 20 μ m; F = 50 μ m; G–K = 10 μ m.

absent; reverse cinnamon to fuscous black. Colonies on PCA 26–32 mm diam after 7 d at 25 °C; edge entire; obverse showing sparse aerial hyphae; translucent; soluble pigment absent; reverse uncoloured.

Material examined: USA, Minnesota, isolated from soil, unknown date, M. Christensen (**holotype** CBS H-23482, culture ex-type CBS 127760 = RMF 9051).

Notes: *Humicola christensenii* can be distinguished from *Humicola homopilata* (= *Chaetomium homopilatum*) by the production of terminal hairs that are undulate or loosely coiled in the upper part, and by smaller ascospores (6.5–7.5 × 5.5–6 × 3.5–4.5 µm vs 8–9 × 6–7 × 4–5.5 µm).

Humicola cuyabenoensis (Decock & Hennebert) X. Wei Wang & Houbraken, **comb. nov.** MycoBank MB824423. Fig. 8.

Basionym: *Chaetomium cuyabenoensis* Decock & Hennebert, *Mycol. Res.* 101: 309. 1997.

Synonym: *Farrowia cuyabenoensis* (Decock & Hennebert) D. Hawksw., *Syst. Ascomycetum* 16: 52. 1998.

Micromorphology: *Ascomata* superficial, ostiolate, leaden black in reflected light, elongate obpyriform, obclavate or ampulliform below, apically attenuated to a cylindrical, thread-like neck with a truncate apex, (550–)1 000–1 500(–2 400) µm high, 55–100 µm diam at the widest part, with the neck part usually (760–)950–1 360(–2 300) µm long, 20–27.5 µm wide. *Ascomatal wall* brown, composed of angular cells or elongated to cylindrical cells at the neck part in surface view. *Terminal hairs* arising from the extension of the adjacent ostiolar cells with pointed tips and forming a fimbriate apex of ascoma, smooth, 1.5–3.5 µm diam near the base, less than 80 µm long. *Lateral hairs* sparse, scattered on the whole ascoma including the side of the neck, seta-like, tapering and fading towards the tips. *Asci* narrowly clavate to clavate, occasionally cylindrical, with spore-bearing part 17–29 × 5–9.5 µm and stalks 7–17 µm long, with 8 biserial ascospores, evanescent. *Ascospores* olivaceous brown when mature, broad limoniform, umbonate at both ends, bilaterally flattened, 6–7 × 5.5–6.5 × 3.5–4.5 µm, with an apical germ pore. *Conidia* globose or subglobose, sometimes piriform or clavate, usually 6.5–10.5 µm diam.

Culture characteristics: Colonies on OA 26–32 mm diam after 7 d at 25 °C; edge entire; aerial hyphae very sparse or absent; soluble pigment amber or absent; reverse partly amber. Colonies on CMA similar to those on OA, 22–28 mm diam after 7 d at 25 °C. Colonies on MEA 25–31 mm diam after 7 d at 25 °C; edge entire; obverse fulvous, with a thin layer of grey-white aerial mycelium; reverse fulvous to orange or sienna. Colony on PCA 21–27 mm diam after 7 d at 25 °C; edge entire; aerial mycelium absent; soluble pigment absent; reverse uncoloured.

Material examined: Ecuador, Sucumbios province, Reserva de Producción Faunística Cuyabeno, isolated from rainforest, unknown date, C. Decock, ex-type culture CBS 398.97 = MUCL 38838.

Notes: This species is distinct from the other *Humicola* species by the production of ascomata with long, cylindrical necks sparsely covered by lateral hairs and the short terminal hairs on the fimbriate apex of the ascomata. Furthermore, the ascospores are prominently umbonate at both ends.

Humicola degenerans X. Wei Wang & Houbraken, **sp. nov.** MycoBank MB824424. Figs 9, 10.

Etymology: The epithet refers to the degenerated terminal ascomatal hairs which are sparsely produced or even absent.

Micromorphology: *Ascomata* superficial to immersed in the medium, solitary to aggregated, ovoid to obpyriform, with a short conical ostiolar beak, 58–145 µm high, 35–80 µm diam. *Ascomatal wall* brown, *textura angularis* with the beak part composed of vertically arranged rectangle cells; amorphous and deliquescent cells surrounding the ostiolar opening in surface view. *Terminal hairs* sparse, 1.5–3 µm diam near the base, or absent. *Lateral hairs* sparse, seta-like, tapering and fading towards the tips. *Asci* clavate, with spore-bearing part 22–28 × 10–16 µm and stalks 4–11 µm long, with 8 irregularly arranged ascospores, evanescent. *Ascospores* olivaceous brown when mature, limoniform, bilaterally flattened, apiculate to umbonate at both ends, 9–10(–10.5) × 7–8 × 5–6.5 µm, with an apical germ pore. *Conidia* globose to subglobose, subhyaline to pale olivaceous, lateral, or terminal on the hyphae or short branches of hyphae, solitary, 7–10.5 µm diam.

Culture characteristics: Colonies on OA 35–41 mm diam after 7 d at 25 °C; edge entire; obverse greenish black because of a great number of ascospores released and gathered on the top of each of the ascomata; aerial hyphae absent; soluble pigment honey to ochreous; reverse uncoloured or olivaceous grey because of a number of ascomata immersed into the medium. Colonies on CMA similar to those on OA, 37–43 mm diam after 7 d at 25 °C. Colonies on MEA 33–39 mm diam after 7 d at 25 °C; edge entire; obverse mouse grey with white floccose aerial hyphae near the central area; reverse sienna caused by soluble pigment diffusing into the medium. Colonies on PCA 32–38 mm diam after 7 d at 25 °C; edge entire; aerial hyphae absent, soluble pigment absent, reverse uncoloured.

Material examined: Angola, Rio Chipin vila Rob. Williase, isolated from a termite mound, unknown date, E. Müller, culture CBS 780.71. Canada, Ontario; Guelph, isolated from soil under mixed forest, Aug 1964, G.L. Barron (**holotype** CBS H-23483, culture ex-type CBS 232.65 = IMI 109880 = OAC 10275). USA, Kansas, isolated from soil, unknown date and collector, culture CBS 127324.

Notes: This species is similar to *Humicola seminuda* and can be distinguished by the apical structures of ascomata, which are usually hyaline with rare terminal hairs. The morphology of CBS 780.71 (Fig. 10) differs from the type (Fig. 9): the ascomata are smaller (55–95 µm vs 110–145 µm high, 35–60 µm vs 45–80 µm diam), aggregated and often immersed or sub-immersed in the medium, with transparent ascomatal wall and only a few asci inside. Based on phylogenetic data, both strains are identified as *Humicola degenerans*.

Humicola distorta (L.M. Ames) X. Wei Wang & Houbraken, **comb. nov.** MycoBank MB824427. Fig. 11.

Basionym: *Chaetomium distortum* L.M. Ames, *Monograph Chaetomiaceae*: 21. 1963.

Micromorphology: *Ascomata* superficial, ostiolate, citrine or greenish olivaceous in reflected light because of ascomatal hairs, subglobose or ovate, 100–150 µm high, (60–)75–120 µm diam. *Ascomatal wall* brown, *textura angularis* in surface view. *Terminal hairs* straight or arcuate, apically incurved, circinate to coiled, slightly verrucose, brown, closely septate, 2–3.5 µm diam near the base. *Lateral hairs* flexuous or recurved. *Asci* clavate, with spore-bearing portion 20–25 × 8.5–10.5 µm and stalks 7–12 µm long, with 8 irregularly arranged ascospores, evanescent. *Ascospores* olivaceous brown when mature, limoniform, biapiculate or umbonate at both ends, bilaterally flattened, (6–)6.5–7.5(–8) × 5–6(–6.5) × 3.5–4.5 µm, with an apical germ pore. *Conidia* globose to oblate, sometimes obovoid or pyriform,

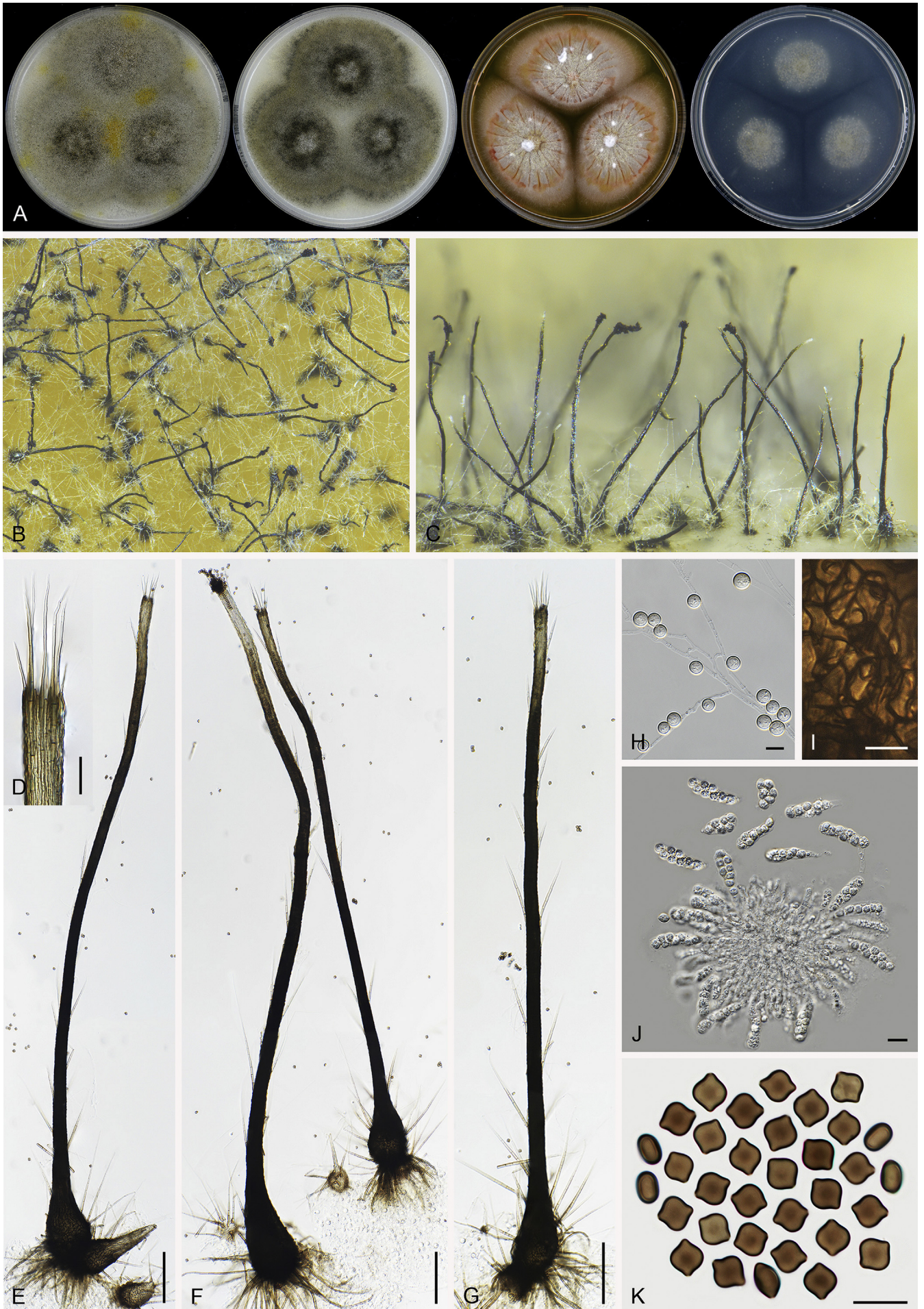


Fig. 8. *Humicola cuyabenoensis* (CBS 398.97, ex-type culture). **A.** Colonies from left to right on OA, CMA, MEA and PCA after 4 wk incubation. **B.** Mature ascomata on OA, top view. **C.** Mature ascomata on OA, side view. **D.** Apical structure of the ascoma. **E–G.** Ascomata mounted in lactic acid. **H.** Hyphae and conidia. **I.** Structure of ascomatal wall in surface view. **J.** Asci. **K.** Ascospores. Scale bars: D = 20 μ m ; E–G = 100 μ m ; H–K = 10 μ m.

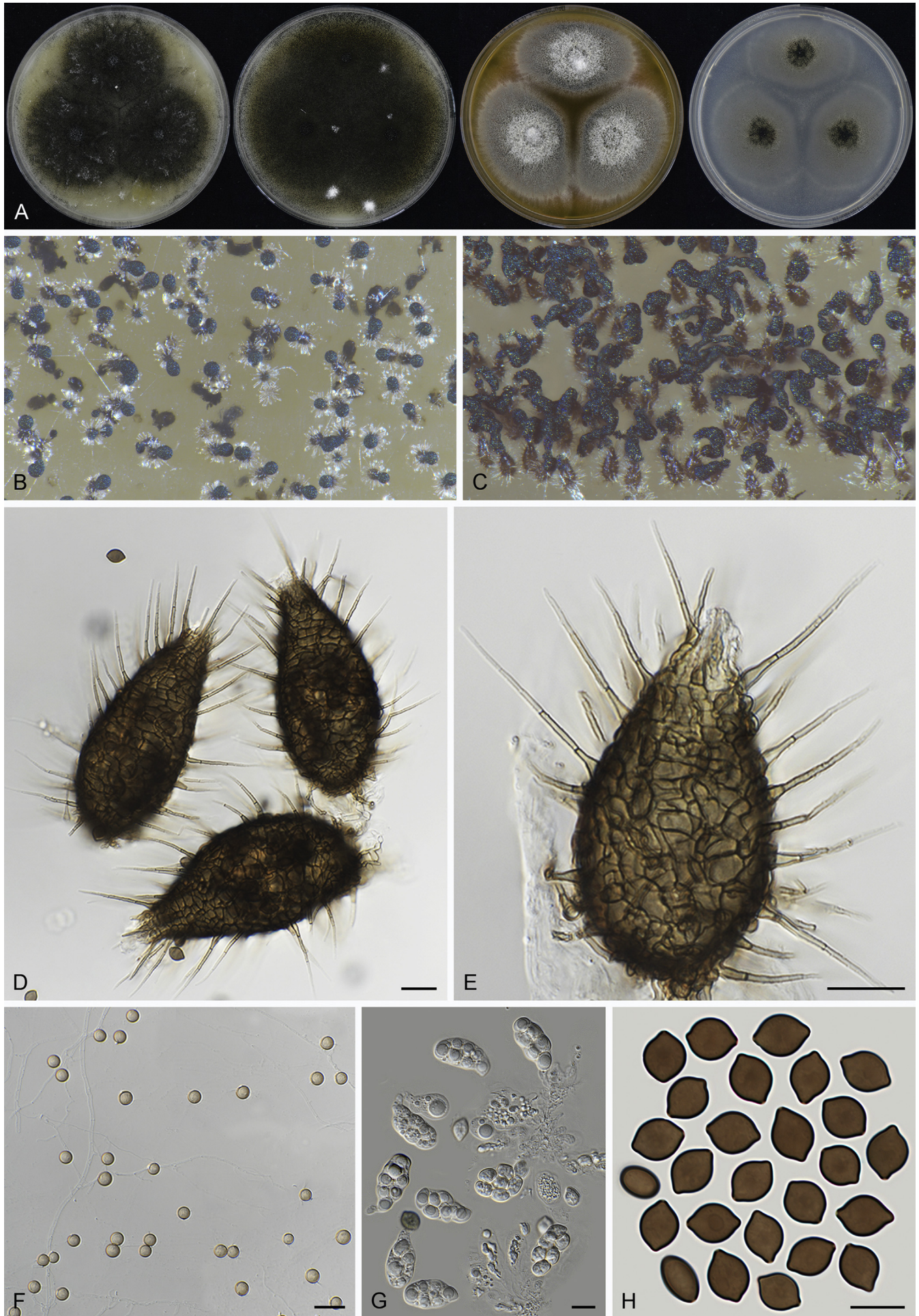


Fig. 9. *Humicola degenerans* (CBS 232.65, ex-type culture). **A.** Colonies from left to right on OA, CMA, MEA and PCA after 2 wk incubation. **B.** Mature ascomata on OA, top view. **C.** Mature ascomata on OA, side view. **D–E.** Ascomata mounted in lactic acid. **F.** Hyphae and conidia. **G.** Asci. **H.** Ascospores. Scale bars: D–F = 20 μm ; G–H = 10 μm .

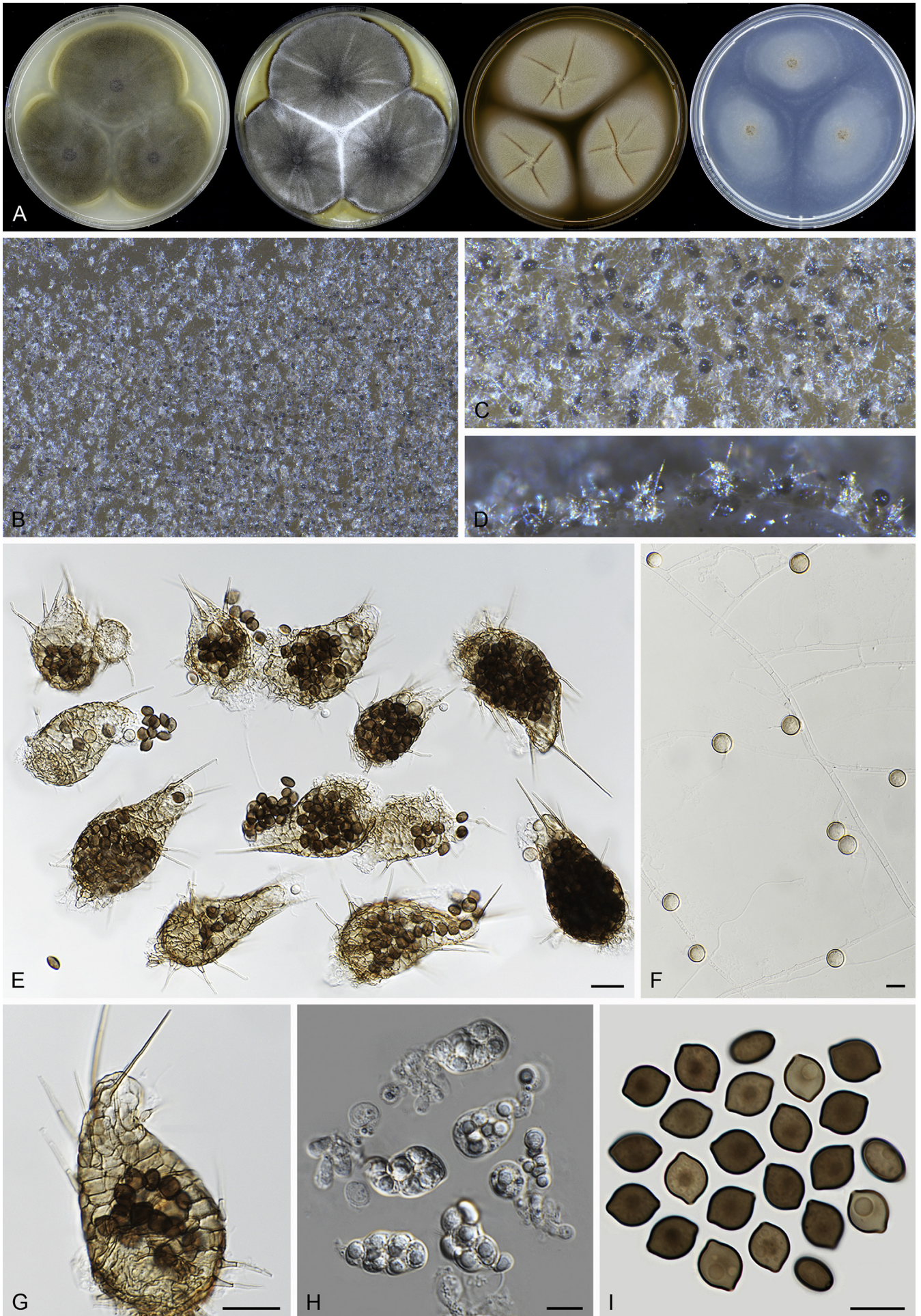


Fig. 10. Morphological variety of *Humicola degenerans* (CBS 780.71). **A.** Colonies from left to right on OA, CMA, MEA and PCA after 4 wk incubation. **B.** Part of the colony. **C.** Mature ascomata on OA, top view. **D.** Mature ascomata on OA, side view. **E.** Ascomata mounted in lactic acid. **F.** Hyphae and conidia. **G.** An ascoma showing structures of the apex and ascomatal wall in surface view. **H.** Asci. **I.** Ascospores. Scale bars: E, G = 20 μm ; F, H, I = 10 μm .

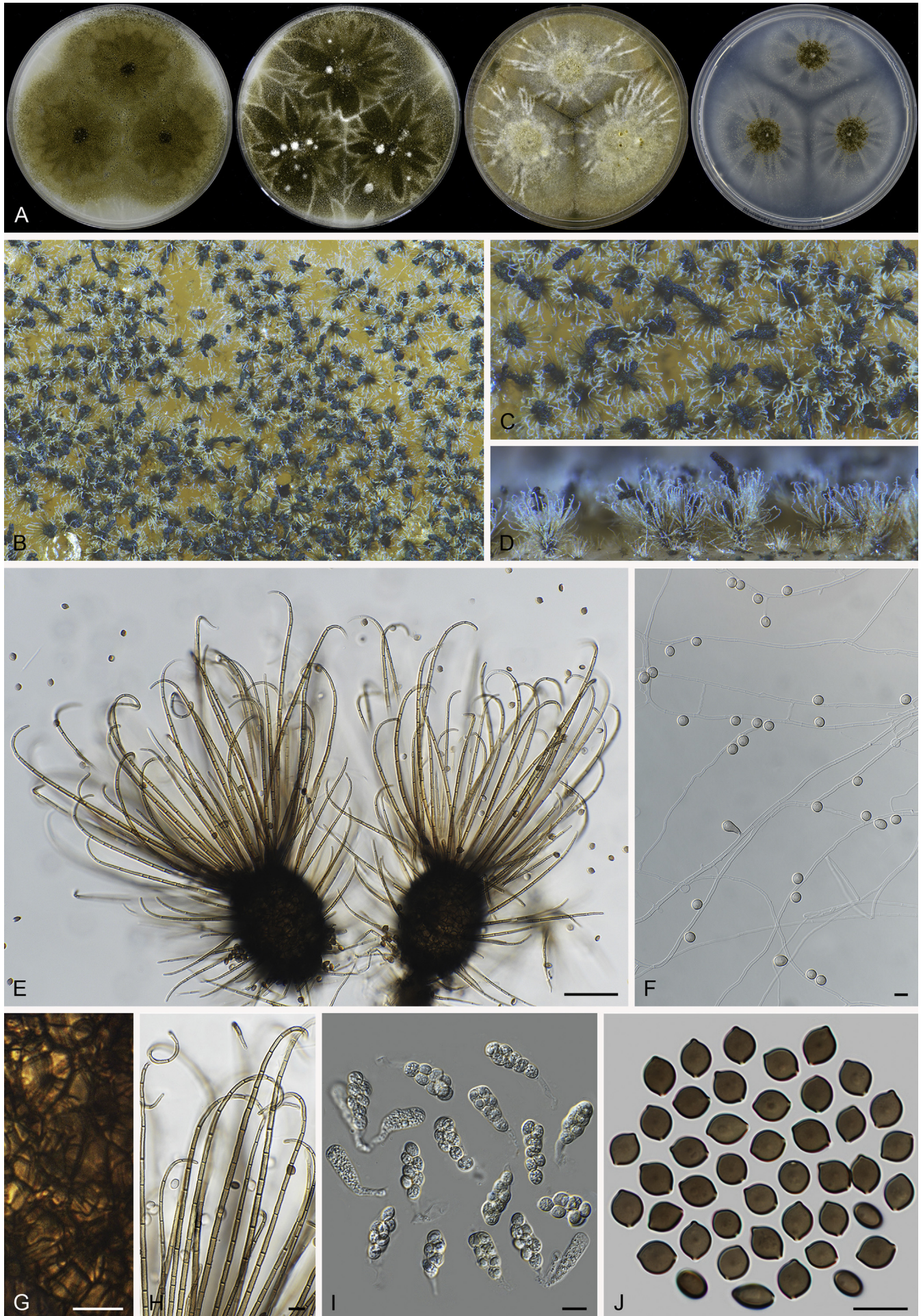


Fig. 11. *Humicola distorta* (CBS 417.66, ex-type culture). **A.** Colonies from left to right on OA, CMA, MEA and PCA after 2 wk incubation. **B.** Part of the colony. **C.** Mature ascomata on OA, top view. **D.** Mature ascomata on OA, side view. **E.** Ascomata mounted in lactic acid. **F.** Hyphae and conidia. **G.** Structure of ascomatal wall in surface view. **H.** Terminal ascomatal hairs. **I.** Asci. **J.** Ascospores. Scale bars: E = 50 μ m; F–J = 10 μ m.

hyaline or subhyaline, produced laterally, or terminally on the hyphae or short branches of hyphae, solitary, 6.5–14.5 µm high, 7–9 µm diam.

Culture characteristics: Colonies on OA 26–32 mm diam after 7 d at 25 °C; edge entire; obverse citrine to greenish olivaceous or grey olivaceous because of ascospore masses; aerial hyphae absent, soluble pigment absent; reverse olivaceous buff. Colonies on CMA similar to those on OA, 27–33 mm diam after 7 d at 25 °C. Colonies on MEA 22–28 mm diam after 7 d at 25 °C; edge entire, obverse honey to olivaceous buff because of slowly developing young ascomata mixed with white aerial mycelium; soluble pigment absent; reverse ochreous, fawn to olivaceous. Colony on PCA 26–32 mm diam after 7 d at 25 °C; edge entire; aerial hyphae absent, soluble pigment absent; reverse uncoloured.

Material examined: USA, Iowa, isolated from a dead leaf of *Populus tremuloides*, unknown date, G.W. Martin, ex-type culture CBS 417.66.

Notes: This species produces ascomatal hairs that are similar to those of some species of *Arcopilus*. *Arcopilus* species do not produce an asexual morph, and their ascospores are usually more or less inequilateral. If they are limoniform, then they have germ pores at both ends (*H. distorta* produces ascospores with one apical germ pore).

Humicola floriformis (Gené & Guarro) X. Wei Wang & Houbraken, **comb. nov.** MycoBank MB824429. [Fig. 12.](#)

Basionym: *Chaetomium floriforme* Gené & Guarro, Mycol. Res. 100: 1005. 1996.

Micromorphology: *Somatic hyphae* hyaline, 1.2–4.5 µm wide. *Conidia* numerous, produced laterally on the hyphae, sometimes terminally on the short branches of hyphae, smooth, single-celled, olivaceous brown to brown, globose, subglobose, obovoid or pyriform, solitary, often densely in bunch around the hyphae, (6–)7.5–9.5(–12) µm high, (4.5–)6–8(–9) µm wide. *Acremonium-like conidiophores* arising laterally from hyphae, hyaline, phialidic, unbranched, 5.5–23 µm long, 1.5–3.5 µm wide near the base. *Acremonium-like conidia* formed basipetally in chains, aseptate, obovoid, ellipsoidal, with a truncated base and a rounded apex, 2.5–3.5 × 1–2 µm. *Sexual morph fide Gené & Guarro (1996):* *Ascomata* discrete, superficial, metallic or pale grey in reflected light, obovate, ostiolate, 230–320 × 190–260 µm; *Ascomatal wall* dark brown, *textura angularis* in surface view, partly covered by brown and interwoven hyphae. *Ascomatal hairs*, unbranched, brown, thick-walled, gradually tapering and paling to a rounded tip, regularly septate, prominently constricted at the septa, appearing articulate and readily breaking into cylindrical segments of variable length. *Terminal hairs* numerous, incurved and forming a dense tuft around the ostiole, with the upper part undulate to loosely coiled, nearly smooth toward the base and finely verrucose toward the tip, 4–7 µm diam near the base, up to 400 µm long. Lateral hairs straight or undulate, finely verrucose, constricted at the septa, gradually tapering and paling to a rounded tip, up to 250 µm long. *Asci* numerous, clavate, stalked, 8-spored, evanescent, 30–45 × 8.5–11 µm. *Ascospores* broadly limoniform to nearly spherical, laterally flattened, slightly biapiculate, hyaline and not dextrinoid when young, pale grey at maturity, dark grey in mass, smooth- and rather thick-walled, 7–8.5 × 6–7 × 5–6 µm, with an apical or slightly subapical germ pore.

Culture characteristics: Colonies on OA 40–46 mm diam after 7 d at 25 °C; edge entire; obverse olivaceous because of the formation of a large number of conidia; texture floccose because of a thick layer of hyaline aerial hyphae; reverse uncoloured. Colonies on CMA similar to those on OA, 40–46 mm diam after 7 d at 25 °C; aerial hyphae relatively thin. Colonies on MEA 42–48 mm diam after 7 d at 25 °C; edge entire; texture floccose because of a thick layer of hyaline aerial hyphae; reverse fawn to olivaceous. Colonies on PCA 40–46 mm diam after 7 d at 25 °C; edge entire; aerial hyphae sparse; reverse uncoloured.

Material examined: Thailand, Sukhothai, isolated from fallen leaves, 10 Aug. 1994, J. Gené, ex-type culture CBS 815.97 = MUCL 40181.

Notes: The holotype of *H. floriformis* (IMI 368520) was isolated from fallen leaves in Sukhothai (Thailand) by J. Gené on 10 Aug. 1994 and the species was described in 1996 (Gené & Guarro 1996). This isolate was deposited in MUCL by J. Gené in 1997, and subsequently sent from the MUCL to CBS. Based on the information from MUCL (locality, substrate and collector), CBS 815.97 should represent the ex-type of the species. The examined culture is degenerated and produces only the asexual morph. According to the original description, this species produces ascomata together with conidia and no acremonium-like synanamorph was described. We observed the same conidia as described in the original publication; however, acremonium-like conidiophores and conidia were also present in CBS 815.97.

Humicola fuscoatra Traaen, Nytt Mag. Naturvidensk 52: 33. 1914. MycoBank MB188714. [Fig. 13.](#)

Micromorphology: *Somatic hyphae* hyaline, 1–2.5 µm wide. *Conidia* produced laterally on the side of vegetative hyphae, occasionally terminally on the short branches of hyphae, single-celled, solitary, sometimes two in chain or a few in cluster, smooth, olivaceous brown, globose, subglobose to oblate, occasionally obovoid or pyriform, (5–)6.5–9(–12.5) µm high, (5.5–)7–9(–10.5) µm wide.

Culture characteristics: Colonies on OA 29–35 mm diam after 7 d at 25 °C, edge entire; obverse olivaceous because of the formation of a large number of conidia; aerial hyphae sparse; reverse pale olivaceous grey to olivaceous grey mainly because of the immersed conidia and smoke grey soluble pigment. Colonies on CMA similar to those on OA, 24–30 mm diam after 7 d at 25 °C; edge slightly crenate. Colonies on MEA 18–24 mm diam after 7 d at 25 °C; edge entire or slightly lobate; obverse greyish sepia to fuscous black, with a thin layer of aerial hyphae and a few (2–4) radiating furrows, reverse greyish sepia. Colonies on PCA 17–23 mm diam after 7 d at 25 °C; edge entire, aerial hyphae rare, obverse greyish sepia to olivaceous in the centre; reverse greyish sepia to olivaceous in the centre.

Material examined: China, Tibet, isolated from soil, May 2008, Y. Hao CGMCC 3.13428. Norway, isolated from soil, 1914, A.E. Traaen, ex-type culture CBS 118.14 = ATCC 22721 = MUCL 8010 = VKM F-3001.

Notes: *Humicola fuscoatra* and *H. grisea* (= *Trichocladium griseum*) are the first two species described in *Humicola* (Traaen 1914). Based on the original descriptions, *Humicola fuscoatra* produces an acremonium-like synanamorph. In this study, an acremonium-like synanamorph was observed in the culture of *H. grisea* rather than *H. fuscoatra*, indicating that production of an acremonium-like morph is a variable characteristic.

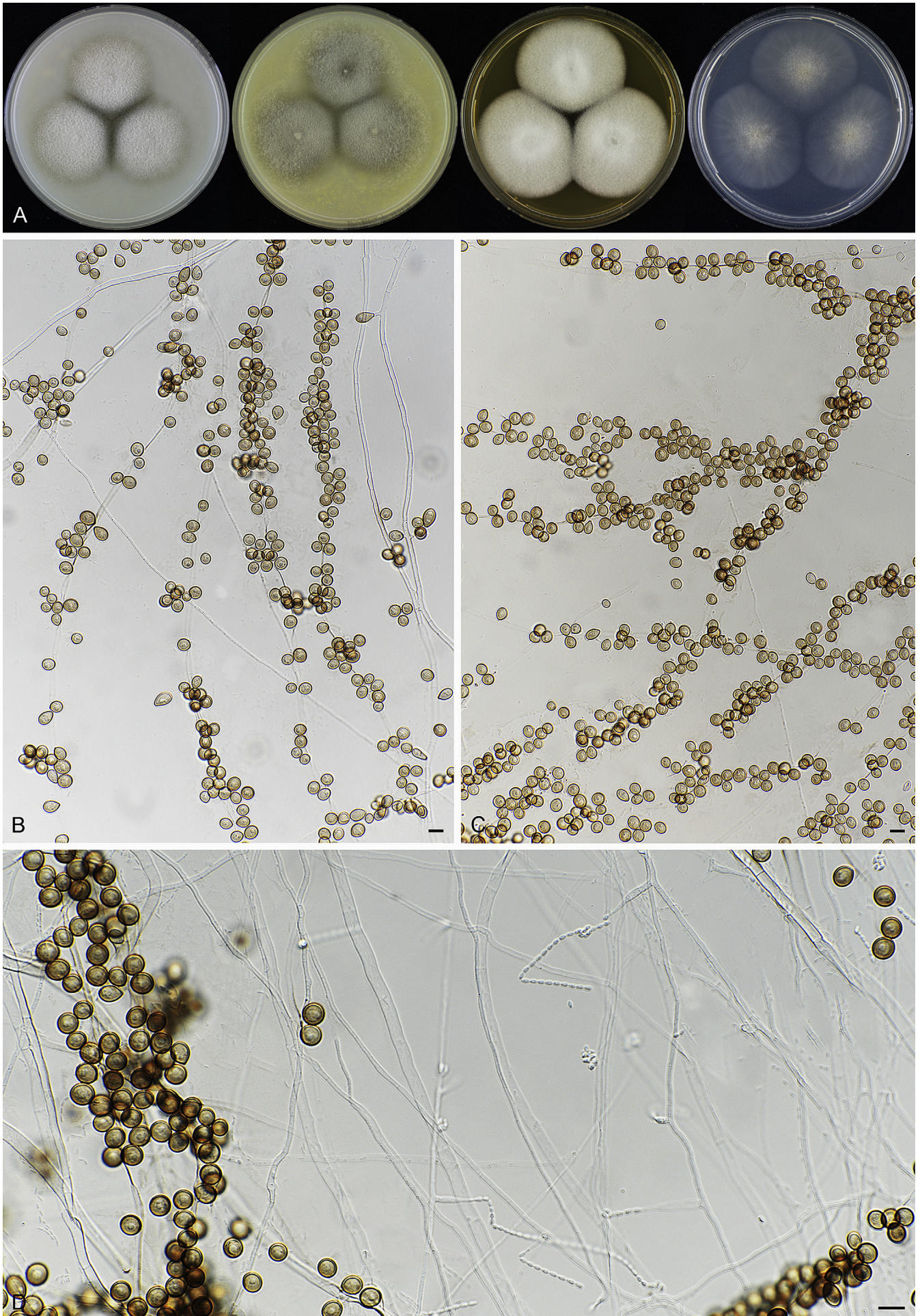


Fig. 12. *Humicola floriformis* (CBS 815.97, ex-type culture). **A.** Colonies from left to right on OA, CMA, MEA and PCA after 1 wk incubation. **B–C.** Hyphae and conidia. **D.** Hyphae, conidia and acremonium-like synanamorph. Scale bars = 10 μ m.

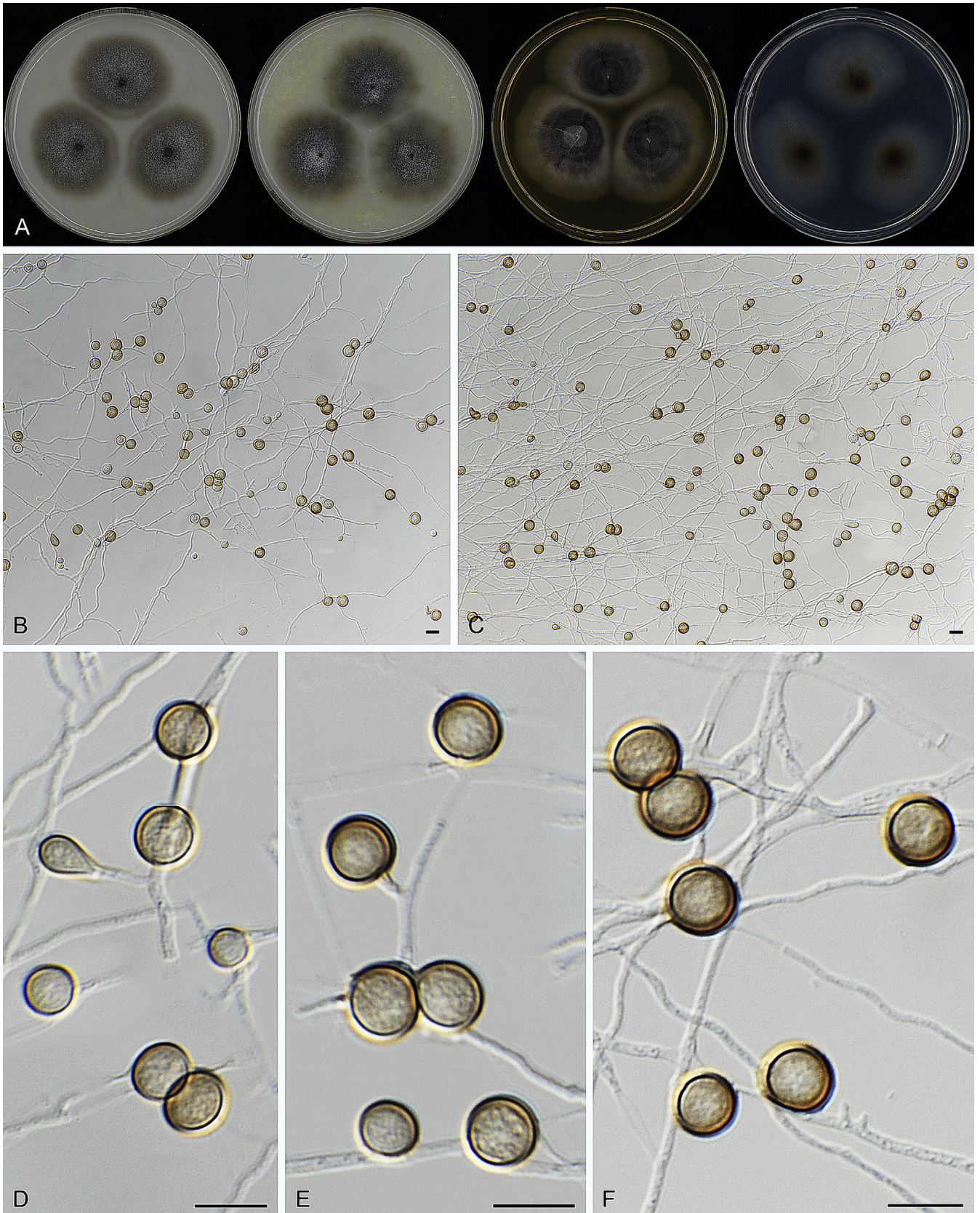


Fig. 13. *Humicola fuscoatra* (CBS 118.14, ex-type culture). **A.** Colonies from left to right on OA, CMA, MEA and PCA after 2 wk incubation. **B–F.** Hyphae and conidia. Scale bars = 10 μ m.

Humicola fuscogrisea Y.L. Jiang & T.Y. Zhang. *Mycosystema* 28: 649. 2009. MycoBank MB513355. [Fig. 14.](#)

Micromorphology: Somatic hyphae hyaline, 1–2.5 μ m wide. Conidia produced laterally on the side of vegetative hyphae,

occasionally terminally on the short branches of hyphae, single-celled, olivaceous, with dark brown thick wall, solitary, sometimes 2–3(–8) in a chain or several in a cluster, smooth, oblate to subglobose, (6–)6.5–8(–8.5) μ m high, (7–)7.5–9(–9.5) μ m wide.

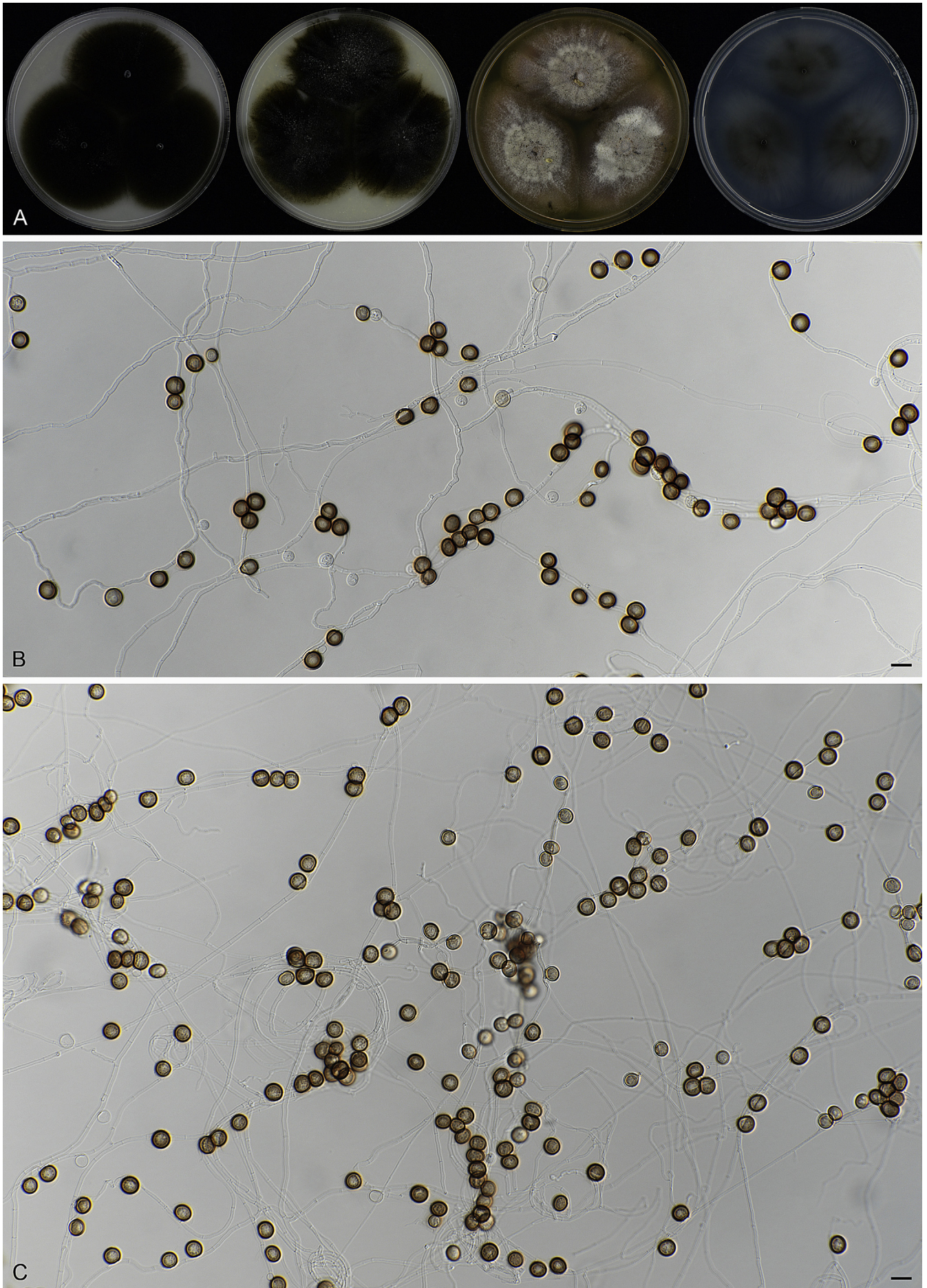


Fig. 14. *Humicola fuscogrisea* (CGMCC 3.13790, ex-type culture). A. Colonies from left to right on OA, CMA, MEA and PCA after 2 wk incubation. B–C. Hyphae and conidia. Scale bars = 10 μ m.

Culture characteristics: Colonies on OA 29–35 mm diam after 7 d at 25 °C; edge entire; obverse greenish black because of the formation of conidia; aerial hyphae absent; reverse greenish black. Colonies on CMA similar to those on OA, 31–37 mm diam after 7 d at 25 °C; edge crenate. Colonies on MEA 35–41 mm diam after 7 d at 25 °C; edge entire; about, obverse showing a relatively thin layer of white to buff aerial hyphae; reverse cinnamon. Colonies on PCA 27–33 mm diam after 7 d at 25 °C; edge entire; aerial hyphae absent, obverse olivaceous grey because of the formation of conidia; reverse olivaceous to olivaceous grey.

Material examined: China, Hubei, isolated from soil, 2000, T.Y. Zhang, ex-type culture CGMCC 3.13790.

Notes: This species is similar to *H. atrobrunnea* but can be distinguished by relatively pale, thin-walled and smaller conidia (6.5–9 µm diam vs 8–11 µm diam), and its greenish black colonies on OA and CMA.

Humicola homopilata (Omvik) X. Wei Wang & Houbraken, **comb. nov.** MycoBank MB824432. Fig. 15.

Basionym: *Chaetomium homopilatum* Omvik, Mycologia 47: 749. 1955.

Synonym: *Chaetomium amesii* Sergejeva, Nov. Syst. Plant. non vasc. P.112. 1965.

Micromorphology: *Ascomata* superficial, often covered by white aerial hyphae, with pale luteous to amber ascomata hairs in reflected light, ovoid or obpyriform, ostiolate, with a short conical or cylindrical ostiolar beak, 150–210 µm high, 110–160 µm diam. *Ascomatal wall* brown, *textura angularis* in surface view, often elongated and radially arranged around the basal cells of the lateral hairs. *Terminal hairs* seta-like, straight or slightly undulate or flexuous, usually unbranched, closely septate, slightly granulate, olivaceous brown, tapering and fading towards the tips, 3–4.5 µm diam near the base. *Lateral hairs* similar to the terminal hairs, but relatively sparse and short. *Asci* clavate, with spore-bearing part 20.5–32 × 9–13 µm and stalks 7–16 µm long, with 8 biseriolate ascospores, evanescent. *Ascospores* olivaceous brown when mature, limoniform, bilaterally flattened, umbonate at both ends, (7.5–)8–9(–9.5) × 6–7 × 4–5.5 µm, with an apical germ pore. *Conidia* globose to subglobose, occasionally obovoid or obpyriform, hyaline, pale olivaceous, lateral, or terminal on the hyphae or short branches of hyphae, occasionally intercalary, solitary, sometimes two in chains or a few in clusters, (6–)7–8.5(–10) µm long, 7– 8.5(–9) µm wide.

Culture characteristics: Colonies on OA 42–48 mm diam after 7 d at 25 °C; edge entire; obverse white; texture floccose because of aerial hyphae; soluble pigment fuscous black; reverse olivaceous grey to iron grey. Colonies on CMA similar to those on OA, 40–46 mm diam after 7 d at 25 °C. Colonies on MEA 46–52 mm diam after 7 d at 25 °C; edge entire; texture floccose because of a thick layer of white aerial mycelium; soluble pigment dark mouse grey; reverse ochreous to fuscous black. Colony on PCA 41–47 mm diam after 7 d at 25 °C; edge entire; obverse showing white aerial mycelium in the central area; soluble pigment absent; reverse uncoloured.

Material examined: Norway, isolated from filter paper in soil, unknown date, A. Omvik, ex-type culture CBS 157.55. **Unknown country**, unknown substrate, unknown date, L.M. Ames, culture ex-isotype of *Chaetomium amesii* CBS 338.68.

Notes: Omvik (1955, Fig. 1-c) observed some tuberculate projections on the surface of the ascomatal hairs, which we did not

see in this study. Perhaps the material from which the tuberculate projections are made is soluble in lactic acid. von Arx *et al.* (1986) adopted a broad concept for *C. homopilatum* and accepted a large variability in the ascomatal hairs of this species. Our phylogenetic study did not support *C. homopilatum sensu* von Arx, and the available ex-type cultures of the synonymized species were re-examined. Several species, such as *C. distortum*, *C. pinnatum*, *C. wallefii* and *C. udagawae* are resurrected and are transferred to *Humicola* in this paper.

Humicola leptodermospora X. Wei Wang & Houbraken, **sp. nov.** MycoBank MB824435. Fig. 16.

Etymology: The epithet refers to the relatively thin-walled conidia of this fungus.

Micromorphology: *Somatic hyphae* hyaline, 1–5 µm wide. *Conidia* produced laterally or intercalary on the side of vegetative hyphae, sometimes terminally on the short hyphal branches, single-celled, hyaline when young, then pale olivaceous, solitary, smooth, subglobose, sometimes obovoid, pyriform or irregular-shaped, often wrinkled because of the relatively thin cell walls, (7–)8.5–11(–12.5) µm long, (6–)6.5–8(–8.5) µm diam.

Culture characteristics: Colonies on OA 37–43 mm diam after 7 d at 25 °C; edge entire; obverse showing white floccose aerial hyphae; reverse fawn to olivaceous black. Colonies on CMA similar to those on OA, 36–42 mm diam after 7 d at 25 °C. Colonies on MEA 37–43 mm diam after 7 d at 25 °C; edge entire or crenate; obverse showing white floccose aerial hyphae; reverse olivaceous to olivaceous black. Colony on PCA 37–43 mm diam after 7 d at 25 °C; edge entire; obverse olivaceous because of the formation of conidia; aerial mycelium sparse; reverse uncoloured.

Material examined: Brazil, Estado do Paraná, isolated from forest soil, Mar 2005, J. Guarro & A.M. Stchigel (**holotype** CBS H-23484, culture ex-type CBS 120095).

Notes: The ex-type culture of *H. leptodermospora* was deposited as *Chaetomium longicolleum* in CBS, indicating that this species is able to produce ascomata with a long neck. *Chaetomium longicolleum* (= *Staphylotrichum longicolleum*) was revealed to be the sexual morph of *Staphylotrichum* in this study. In our phylogenetic analyses (Figs 1, 2), *H. leptodermospora* belongs to *Humicola* rather than *Staphylotrichum*, implying its ascomata should not be staphylotrichum-like (see “*Staphylotrichum*” part below for details). The culture is now degenerated and only produces conidia.

Humicola malaysiensis (D. Hawksw.) X. Wei Wang & Houbraken, **comb. nov.** MycoBank MB824437. Fig. 17.

Basionym: *Farrowia malaysiensis* D. Hawksw., Persoonia 8: 178. 1975.

Synonym: *Chaetomium malaysiense* (D. Hawksw.) v. Arx, Nova Hedwigia, Beih. 84: 38. 1986.

Micromorphology: *Ascomata* superficial, ostiolate, greenish black in reflected light, elongate obpyriform, obclavate or ampulliform below, apically attenuated to an elongate conical or short cylindrical neck, 185–365 µm high, 60–90 µm diam at the widest part, with the neck part about 55–125 µm long, 15–25 µm wide in the mid. *Ascomatal wall* brown, composed of angular and irregular cells and elongated to cylindrical cells in the neck part in surface view. *Terminal hairs* arising from the extension of the adjacent ostiolar cells with round tips, smooth, partly finger-like,

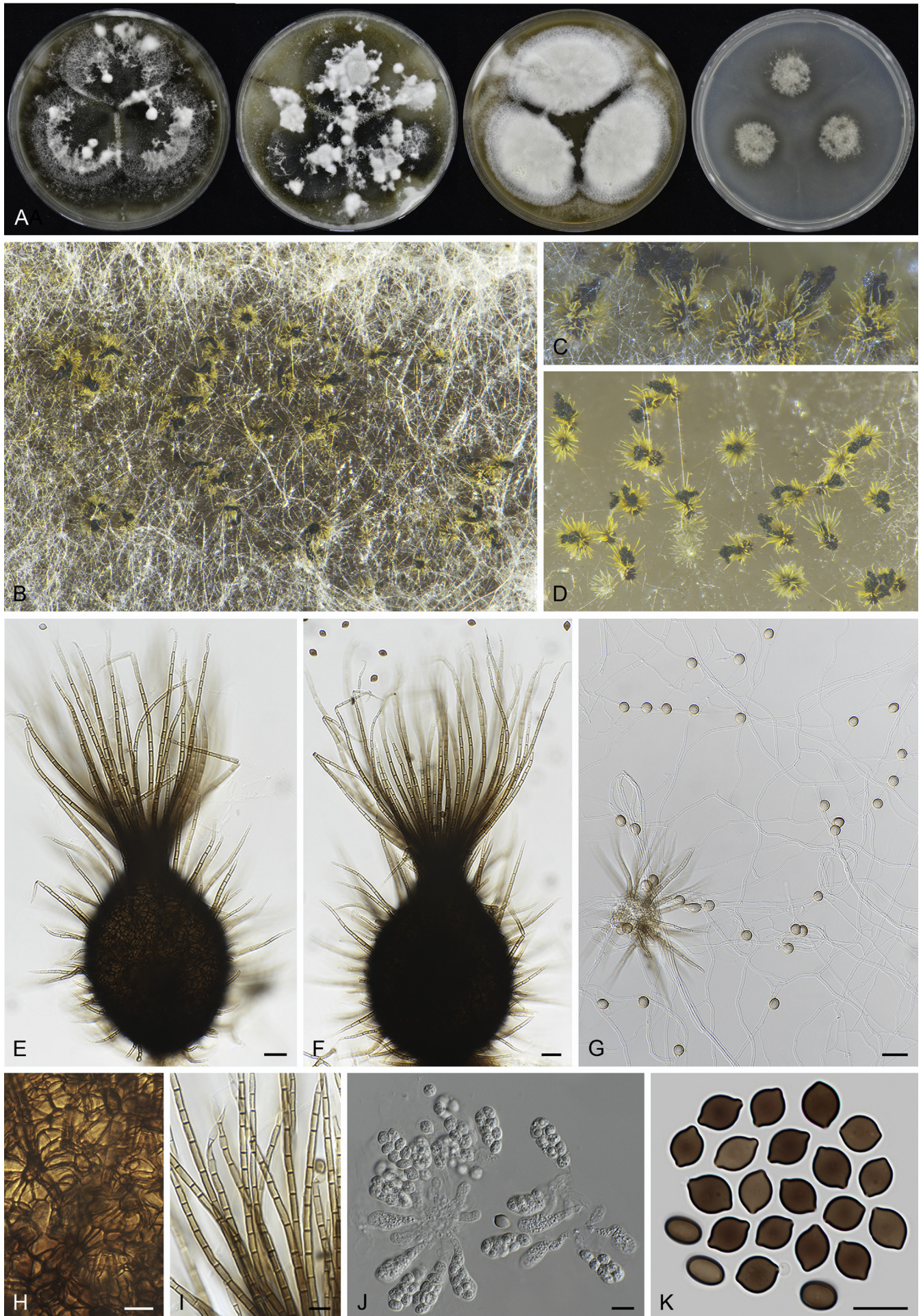


Fig. 15. *Humicola homopilata* (CBS 157.55, ex-type culture). **A.** Colonies from left to right on OA, CMA, MEA and PCA after 3 wk incubation. **B.** Part of the colony on OA. **C.** Mature ascomata on OA, side view. **D.** Mature ascomata on OA, top view. **E–F.** Ascomata mounted in lactic acid. **G.** Hyphae and conidia together with an ascogonium initial. **H.** Structure of ascomatal wall in surface view. **I.** Terminal ascomatal hairs. **J.** Asci. **K.** Ascospores. Scale bars: E–G = 20 μ m; H–K = 10 μ m.

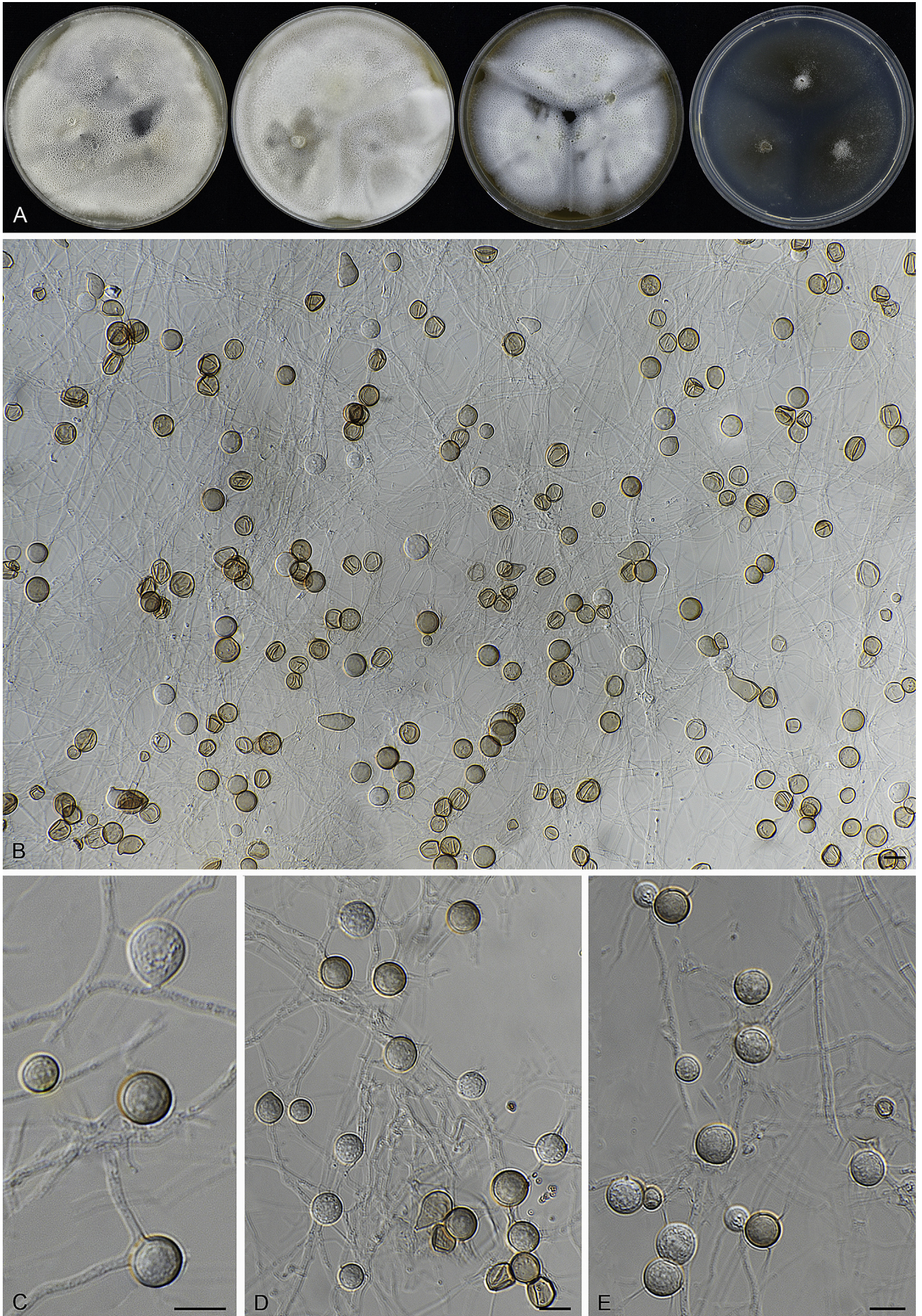


Fig. 16. *Humicola leptodermospora* (CBS 120095, ex-type culture). **A.** Colonies from left to right on OA, CMA, MEA and PCA after 3 wk incubation. **B–E.** Hyphae and conidia. Scale bars = 10 μ m.

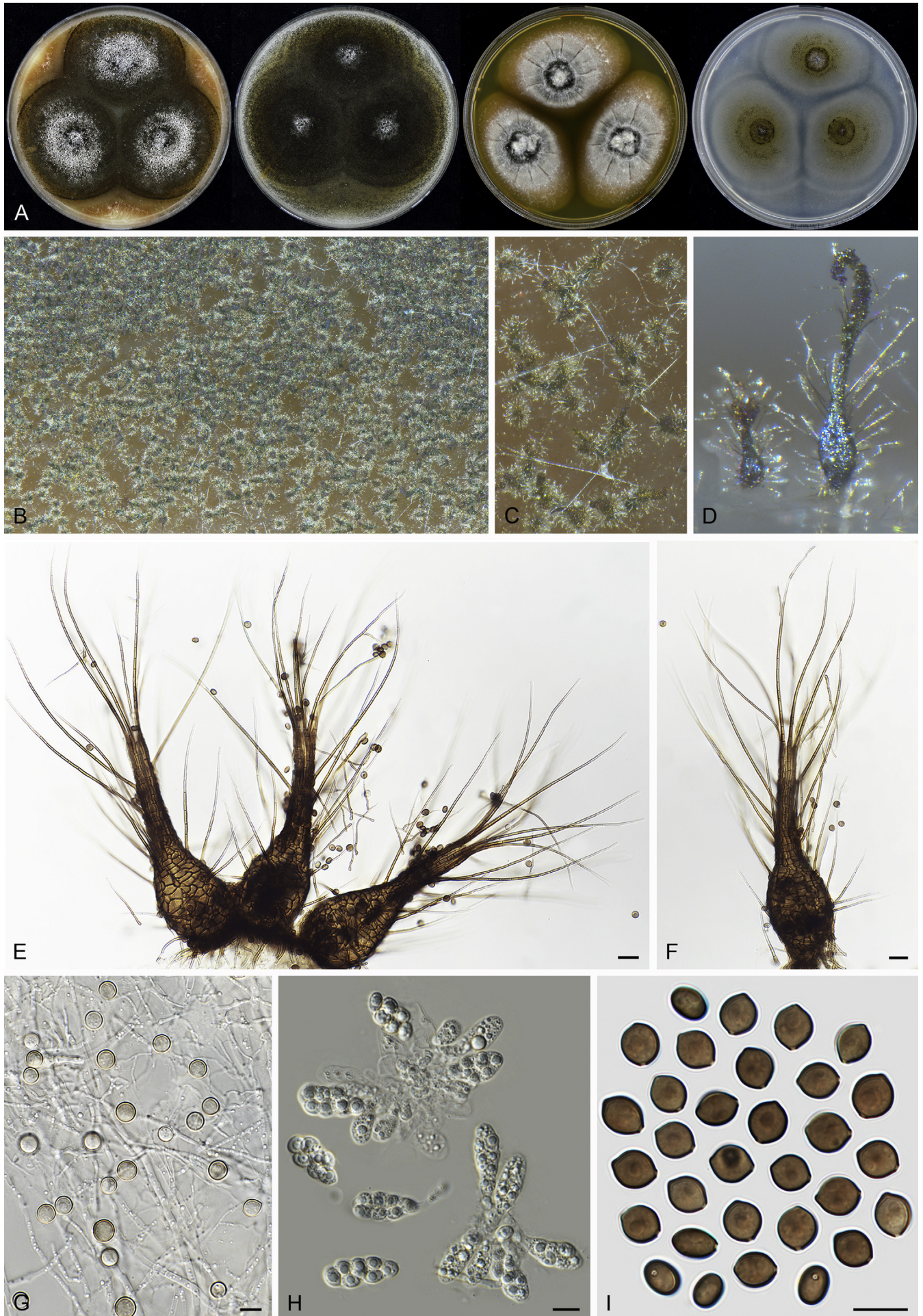


Fig. 17. *Humicola malaysiensis* (CBS 780.83). **A.** Colonies from left to right on OA, CMA, MEA and PCA after 2 wk incubation. **B.** Part of the colony. **C.** Mature ascomata on OA, top view. **D.** Mature ascomata on OA, side view. **E–F.** Ascomata mounted in lactic acid. **G.** Hyphae and conidia. **H.** Asci. **I.** Ascospores. Scale bars: E–F = 20 µm; G–I = 10 µm.

partly long and seta-like, sometimes simply branched, 3–4.5 µm diam near the base. *Lateral hairs* similar to terminal ones, scattered on the whole ascoma including the side of the neck. *Asci* narrowly clavate to clavate, occasionally cylindrical, with spore-bearing part 19–28.5 × 8.5–12 µm and stalks about 6–13.5 µm long, with 8 biseriate ascospores, evanescent. *Ascospores* olivaceous brown when mature, limoniform, biapiculate or slightly umbonate at both ends, bilaterally flattened, 7.5–9 × (6–)6.5–7.5(–8) × 5–6 µm, with an apical germ pore. *Conidia* globose or subglobose, sometimes obovoid, usually arising laterally or terminally from the aerial hyphae, hyaline to subhyaline, 7–12.5 µm diam.

Culture characteristics: Colonies on OA 43–49 mm diam after 7 d at 25 °C; edge entire; obverse violaceous grey because of the masses of ascospores, aerial hypha sparse in the central part, covering ascomata and mixed with the masses of ascospores; soluble pigment pale luteous or amber to umber, reverse cinnamon to fawn. Colonies on CMA 49–55 mm diam after 7 d at 25 °C; edge entire; white aerial hypha sparse, only in the central point; soluble pigment pale luteous to luteous; reverse grey sepia to olivaceous. Colonies on MEA 30–36 mm diam after 7 d at 25 °C; edge entire; obverse showing white aerial hyphae mixed with ascomata, with an irregular and circled furrow around the center and radiating furrows started from the circle furrow; ascomata concentrated mainly in the center; reverse umber to sienna caused by soluble pigment. Colonies on PCA 41–47 mm diam after 7 d at 25 °C; edge entire; aerial hyphae absent; soluble pigment pale luteous; reverse pale luteous or amber to hazel caused by soluble pigment.

Material examined: **Ivory Coast**, Kaprémé, isolated from soil, unknown date, M. Dreyfuss, culture CBS 760.83. **Japan**, Tanegoshima, Kagoshima, isolated from soil, Dec 1958, S. Udagawa, culture CBS 167.61. **Malaysia**, Selangor, isolated from *Elaeis guineensis*, 19 March 1974, T. L.Huan, culture ex-type CBS 399.97 = IMI 183184 = MUCL 39402.

Notes: The ascomata of *H. malaysiensis* resemble those of *H. quadrangulata* and the ascospores are similar to those of *H. seminuda*. *Humicola malaysiensis* can be distinguished from *H. quadrangulata* by limoniform rather than quadrangular ascospores and from *H. seminuda* by the production of longer ascomata necks.

Humicola mutabilis X. Wei Wang & Houbraken, **sp. nov.** MycoBank MB824438. Fig. 18.

Etymology: The epithet refers to the production of ascomata of different shapes.

Micromorphology: *Ascomata* superficial, solitary, leaden black with buff or amber hairs in reflected light, ovoid, obpyriform, urniform or irregular, with 1–3 ostioles, usually apically non-converging, 125–200 µm high, 50–140 µm diam. *Ascomatal wall* brown, *textura angularis*, often with pale to hyaline, amorphous and deliquescent cells surrounding the ostiolar opening in surface view. *Terminal hairs* arising from the wall cell around the ostioles, seta-like with a swollen basal cell 3–6 µm diam, sometimes absent. *Lateral hairs* mainly surrounding apex, seta-like, tapering and fading towards the tips. *Asci* clavate, with spore-bearing part 25–35 × 10–14 µm and stalks about 12–25 µm long, with 8 irregularly arranged ascospores, evanescent. *Ascospores* olivaceous brown when mature, limoniform, biapiculate, bilaterally flattened, (8.5–)9–10.5(–11.5) × (6.5–)7–8.5(–10) × 5–6(–6.5)

µm, with an apical germ pore. *Conidia* globose to subglobose, sometimes obovoid or pyriform, subhyaline to olivaceous, lateral or terminal on hyaline hyphae or short branches of hyphae, solitary, 6–12.5 µm diam.

Culture characteristics: Colonies on OA 43–49 mm diam after 7 d at 25 °C; edge crenate; aerial hyphae sparse and distributing irregularly; soluble pigment honey to isabelline; reverse olivaceous grey to dark mouse grey caused by soluble pigment and immersed hyphae with a large number of dark conidia in the medium. Colonies on CMA similar to those on OA, 43–49 mm diam after 7 d at 25 °C; obverse showing relatively dense aerial hyphae which distributed radially from the centre; soluble pigment honey to isabelline; reverse olivaceous grey to dark mouse grey. Colonies on MEA 41–47 mm diam after 7 d at 25 °C; edge entire or crenate; obverse primrose to buff, texture floccose; sporulation absent, reverse sienna caused by soluble pigment and immersed conidia in the medium. Colonies on PCA 39–46 mm diam after 7 d at 25 °C; edge entire; aerial hyphae absent; soluble pigment isabelline; reverse isabelline to dark mouse grey.

Material examined: **Israel**, Mt. Carmel, isolated from soil, unknown date, T. Leisinger (**holotype** CBS H-23485, culture ex-type CBS 779.71).

Notes: The ex-type strain of *H. mutabilis* was deposited in CBS as *Chaetomium seminudum*. *Humicola mutabilis* is morphologically similar to *H. seminuda* (= *C. seminudum*) and *H. degenerans*. This species can be distinguished by its ascomata that often possess 2–3 ostiolar pores and appear variable in shape, and by its buff or amber coloured hairs (in reflected light) that mainly arise from wall cells around the beak. The ascomata of *H. seminuda* and *H. degenerans* rarely possess more than one ostiolar pore and are regular in shape. The terminal ascomatal hairs of *H. seminuda* arise from the extension of the adjacent ostiolar cells and are limited in length, while terminal ascomatal hairs of *H. degenerans* are absent or sparsely produced.

Humicola olivacea X. Wei Wang & Samson, Stud. Mycol. 84: 203. 2016. MycoBank MB818848. Fig. 19.

Micromorphology: *Somatic hyphae* hyaline, subhyaline, pale olivaceous to honey or greyish sepia, 1–2.5 µm wide. *Conidia* produced laterally or intercalary on hyphae, or terminally on the short branches of hyphae, single-celled, olivaceous to dark brown, with dark brown thick wall when old, solitary, sometimes 2(–8) in chains or in cluster, globose, subglobose or broad obovate, (7.5–)8–9.5(–11) × (7–) 7.5–9(–10) µm.

Culture characteristics: Colonies on OA 39–45 mm diam after 7 d at 25 °C; edge entire; obverse olivaceous; aerial mycelium thin, smoke grey; reverse mouse grey. Colonies on CMA similar to those on OA, 38–44 mm diam after 7 d at 25 °C. Colonies on MEA 42–48 mm diam after 7 d at 25 °C; edge entire; aerial mycelium white; texture floccose; reverse pale luteous to greyish sepia. Colonies on PCA 34–40 mm diam after 7 d at 25 °C; edge entire; aerial mycelium sparse, white to pale luteous; reverse slightly pale luteous.

Material examined: **USA**, isolated from dust, 2009, E. Whitfield & K. Mwange, culture ex-type CBS 142031 = DTO 319-C7.

Notes: The ex-type of *H. olivacea* was examined using the inclined coverslip culture method to determine how the conidia arise from the hyphae. Pigmented aerial hyphae were observed

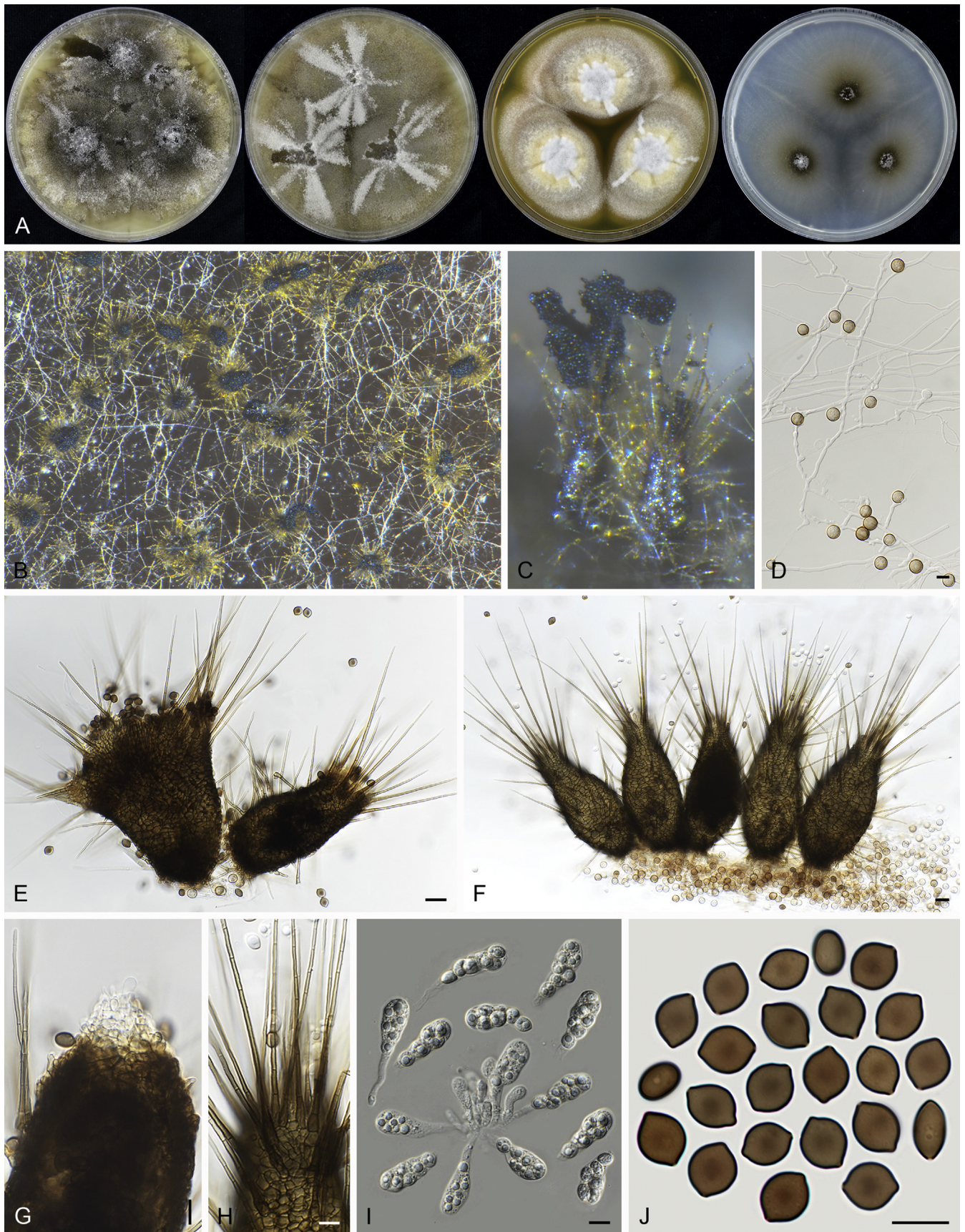


Fig. 18. *Humicola mutabilis* (CBS 779.71, ex-type culture). **A.** Colonies from left to right on OA, CMA, MEA and PCA after 2 wk incubation. **B.** Mature ascomata on OA, top view. **C.** Mature ascomata on OA, side view. **D.** Hyphae and conidia. **E–F.** Ascomata together with conidia mounted in lactic acid. **G–H.** Structures of the apices of ascomata. **I.** Asci. **J.** Ascospores. Scale bars: E–F = 20 μ m; G–I = 10 μ m.

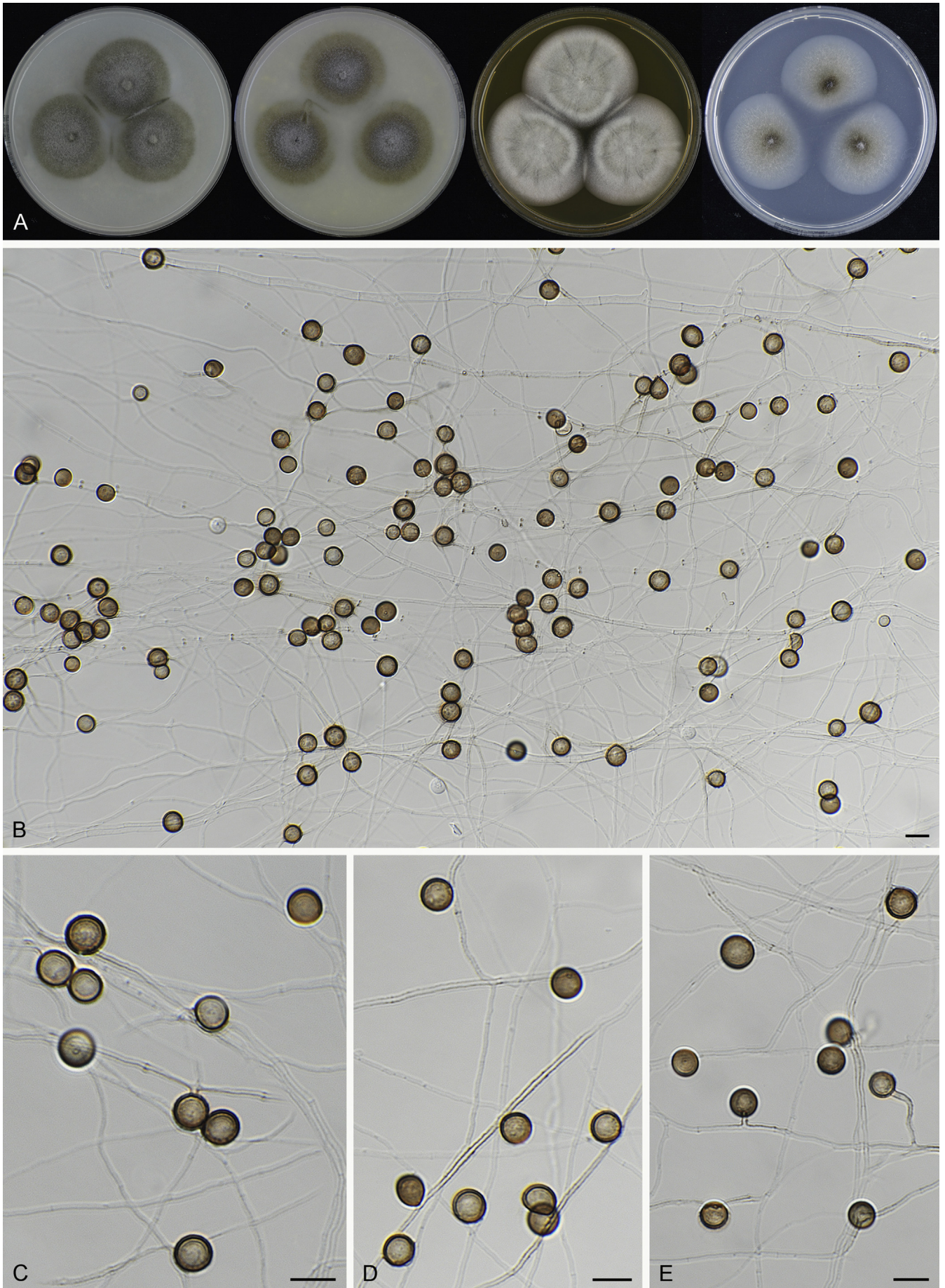


Fig. 19. *Humicola olivacea* (CBS 142031, ex-type culture). **A.** Colonies from left to right on OA, CMA, MEA and PCA after 1 wk incubation. **B–E.** Hyphae and conidia. Scale bars = 10 μ m.

in *H. olivacea*. The majority of *Humicola* species usually only produce hyaline aerial hyphae. The conidia were produced laterally, intercalary on hyphae, or terminally on the short branches on hyphae. These short branches on hyphae become slightly pigmented (Fig. 19-E) and these are similar to the pigmented hyphae present in aerial mycelium (Fig. 19-D, E).

Humicola pinnata (L.M. Ames) X. Wei Wang & Houbraken, **comb. nov.** MycoBank MB824440. Fig. 20.

Basionym: *Chaetomium pinnatum* L.M. Ames, Monograph *Chaetomiaceae*: 33. 1963.

Micromorphology: *Ascomata* superficial, ostiolate, olivaceous buff to citrine green in reflected light because of ascomatal hairs, subglobose, ovoid or obpyriform, 80–195 µm high, 45–130 µm diam, usually with a short conical to short cylindrical ostiolar beak. *Ascomatal wall* brown, *textura angularis* in surface view. *Terminal hairs* flexuous, distinctly septate, 2–3 µm diam near the base, multi-branched in the upper part, forming a net to keep the ascospore masses, with the branches strongly constricted at septa, appearing to be composed of a chain of fusiform or cymbiform hyaline to subhyaline cells. *Lateral hairs* seta-like or flexuous. *Asci* clavate to fusiform, with spore-bearing portion 21.5–27.5 × 8–11.5 µm and stalks 5–12.5 µm long, with 8 biseriate ascospores, evanescent before ascospores mature. *Ascospores* olivaceous brown when mature, limoniform, biapiculate or umbonate at both ends, bilaterally flattened, (6.5–) 7–8 × 5–6(–6.5) × (3.5–)4–5 µm, with an apical germ pore. *Conidia* globose to oblate, sometimes ovoid, hyaline to subhyaline, lateral, intercalary or terminal on the hyphae or short branches of hyphae, without conidiophore differentiation, solitary, 6.5–9.5 µm diam.

Culture characteristics: Colonies on OA 38–44 mm diam after 7 d at 25 °C; edge entire; obverse honey to greenish olivaceous because of ascomatal hairs mixed with ascospore masses, aerial hyphae absent; soluble pigment absent; reverse olivaceous buff. Colonies on CMA similar to those on OA, 36–42 mm diam after 7 d at 25 °C. Colonies on MEA 39–45 mm diam after 7 d at 25 °C; edge entire; aerial mycelium thin; soluble pigment absent; reverse ochreous to fulvous. Colony growth on PCA 31–37 mm diam after 7 d at 25 °C; edge entire; aerial hyphae absent; soluble pigment absent; reverse uncoloured.

Material examined: USA, Arizona, Colorado National Forest, isolated from dead wood, unknown date, G.W. Martin, ex-type culture CBS 467.66.

Notes: von Arx et al. (1986) reduced this species to a synonym of *Chaetomium homopilatum* (classified as *Humicola homopilata* in this paper). *Humicola pinnata* produces asci and ascospores that are similar to those of *Humicola homopilata*. However, the terminal hairs of *H. pinnata* are multi-branched in the upper part with the branches strongly constricted at the septa, while the ascomatal hairs of *H. homopilata* are distinctively different and usually unbranched, seta-like, or slightly undulate or flexuous. The four-gene phylogeny clearly shows that *H. pinnata* is a separate species, distinct from *H. homopilata*.

Humicola pulvericola X. Wei Wang, Houbraken & Seifert, **sp. nov.** MycoBank MB824444. Fig. 21.

Etymology: The epithet refers to dust, the original substrate from which the ex-type strain was isolated.

Micromorphology: *Somatic hyphae* hyaline, 1.5–3 µm wide. *Conidia* produced laterally or intercalary on hyphae, occasionally terminally on the short branches of hyphae, single-celled, olivaceous to dark brown, with dark brown thick wall when old, solitary, sometimes two in chain, smooth, subglobose, or oblate, occasionally piriform to clavate, (7.5–)8.5–11.5(–14) × (5.5–) 7.5–9(–11) µm. *Acremonium-like conidiophores* unbranched, occasionally branched, aseptate or septate, 13–30 × 1–3 µm. *Conidiogenous cells* phialidic. *Conidia* in basipetal chains, sometimes in false heads, hyaline, aseptate, smooth, obovoid, usually with a truncated base and a rounded apex, 2.5–4 × 1–2(–2.5) µm.

Culture characteristics: Colonies on OA 51–57 mm diam after 7 d at 25 °C; edge entire or undulate; aerial mycelium thick, white, buff, pale luteous or ochreous; reverse ochreous to olivaceous black. Colonies on CMA similar to those on OA, 46–52 mm diam after 7 d at 25 °C; aerial mycelium white, salmon to peach. Colonies on MEA 46–52 mm diam after 7 d at 25 °C; edge entire; aerial mycelium thick, white, salmon or pale luteous; reverse dark brick. Colonies on PCA 39–45 mm diam after 7 d at 25 °C; edge entire; aerial mycelium sparse, white to pale luteous; reverse slightly pale luteous.

Material examined: Mexico, isolated from house dust by dilution-to-extinction, 2009, K. Mwangi & E. Whitfield (**holotype** CBS H-23486, culture ex-type CBS 144165 = DTO 318-G9). South Africa, isolated from house dust by dilution-to-extinction, 2009, K. Mwangi & E. Whitfield, culture CBS 144166 = DTO 319-B7.

Notes: Conidia together with an acremonium-like morph were observed on slide cultures prepared using the inclined coverslip method. This species is morphologically similar to *H. piriformis*, but can be distinguished by larger conidia (8.5–11.5 × 7.5–9 µm vs 7–7.5 µm). The species is also characterised by its floccose colonies with thick mycelium on OA and PCA.

Humicola quadrangulata X. Wei Wang & Houbraken, **sp. nov.** MycoBank MB825446. Fig. 22.

Etymology: The epithet refers to the quadrangular ascospores of this fungus.

Micromorphology: *Ascomata* superficial, ostiolate, usually covered by thick aerial hyphae, leaden black in reflected light, elongate obpyriform, obclavate or ampulliform below, apically attenuated to a cylindrical, thread-like neck with a slightly conical apex, 290–610 µm high, 55–110 µm diam at the widest part, with the neck part usually 160–450 µm long, 18–32 µm wide in the mid. *Ascomatal wall* brown, composed of angular and irregular cells or elongated to cylindrical cells at the neck part in surface view. *Terminal hairs* arising from the limited extension of the adjacent ostiolar cells with pointed tips, smooth, the majority less than 50 µm long, 2–3 µm diam near the base, usually with one of them extending to up to 260 µm long and 3–4 µm diam near the base. *Lateral hairs* sparse, seta-like, tapering and fading towards the tips. *Asci* narrowly clavate to clavate, occasionally cylindrical, with spore-bearing part 23–39 × 10.5–15(–17) µm and stalks 5–20 µm long, with 8 biseriate ascospores, evanescent. *Ascospores* olivaceous brown when mature, quadrangular or nearly so in face view, bilaterally flattened, (9.5–)10–10.5 × (8.5–)9–10(–10.5) × 5.5–6.5 µm, with an apical germ pore. *Conidia* globose or subglobose, abundant, usually arising laterally from the aerial hyphae, hyaline to subhyaline, 5.5–14 µm diam.

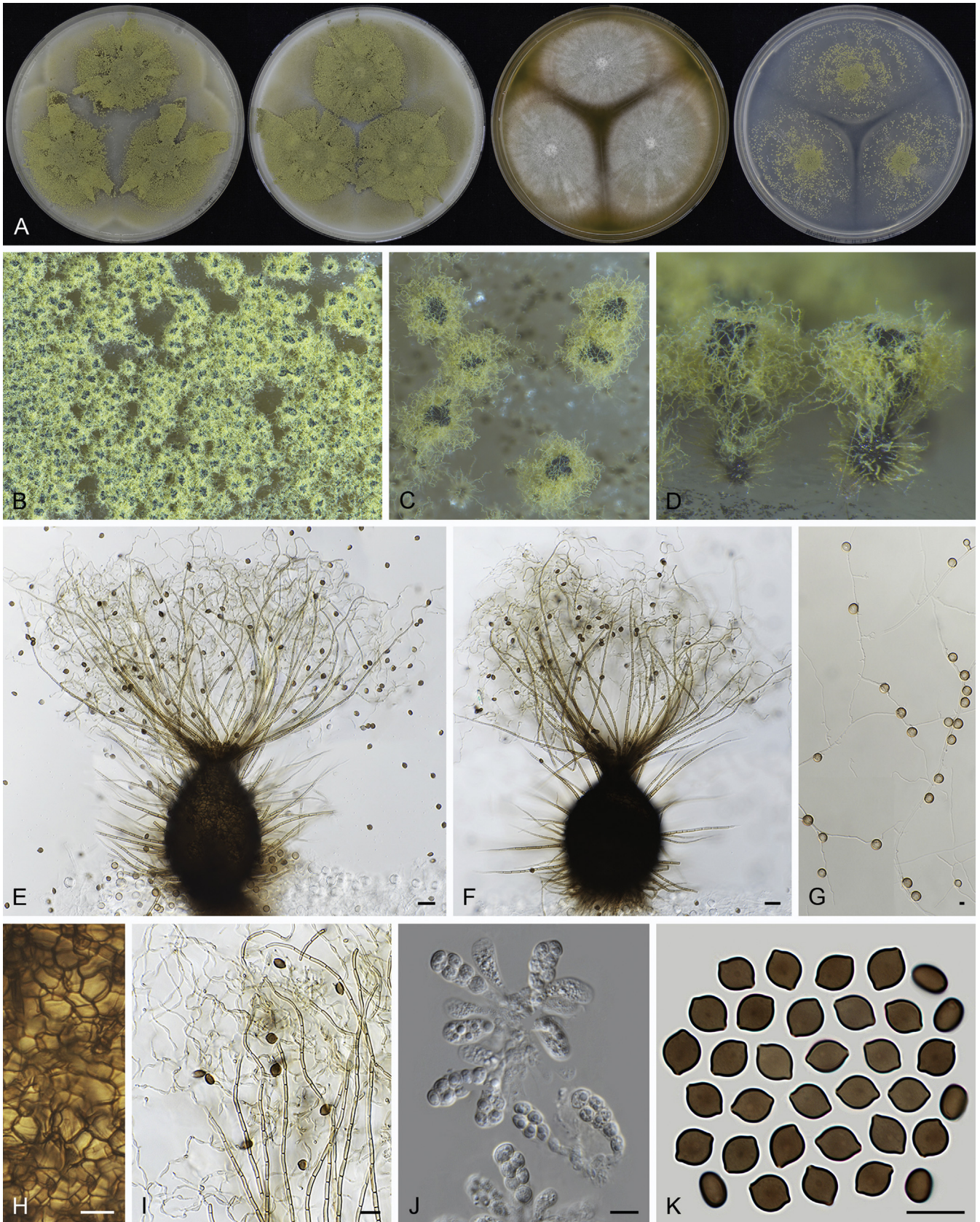


Fig. 20. *Humicola pinnata* (CBS 467.66, ex-type culture). **A.** Colonies from left to right on OA, CMA, MEA and PCA after 3 wk incubation. **B.** Part of the colony on OA. **C.** Mature ascomata on OA, top view. **D.** Mature ascomata on OA, side view. **E–F.** Ascomata mounted in lactic acid. **G.** Hyphae and conidia. **H.** Structure of ascomatal wall in surface view. **I.** Terminal ascomatal hairs. **J.** Asci. **K.** Ascospores. Scale bars: E–F = 20 μ m; G–K = 10 μ m.

Culture characteristics: Colonies on OA 28–34 mm diam after 7 d at 25 °C; edge fimbriate to crenate; aerial hyphae thick, white; soluble pigment mouse grey to dark mouse grey; reverse partly mouse grey to dark mouse grey. Colonies on CMA similar to those on OA, 21–27 mm diam after 7 d at 25 °C. Colonies on

MEA 25–31 mm diam after 7 d at 25 °C; edge entire or slightly crenate; aerial mycelium thick, white; sporulation absent; reverse partly dark brick to sepia. Colony on PCA 24–30 mm diam after 7 d at 25 °C; edge fimbriate to crenate; about, aerial mycelium relatively sparse; soluble pigment absent; reverse uncoloured.

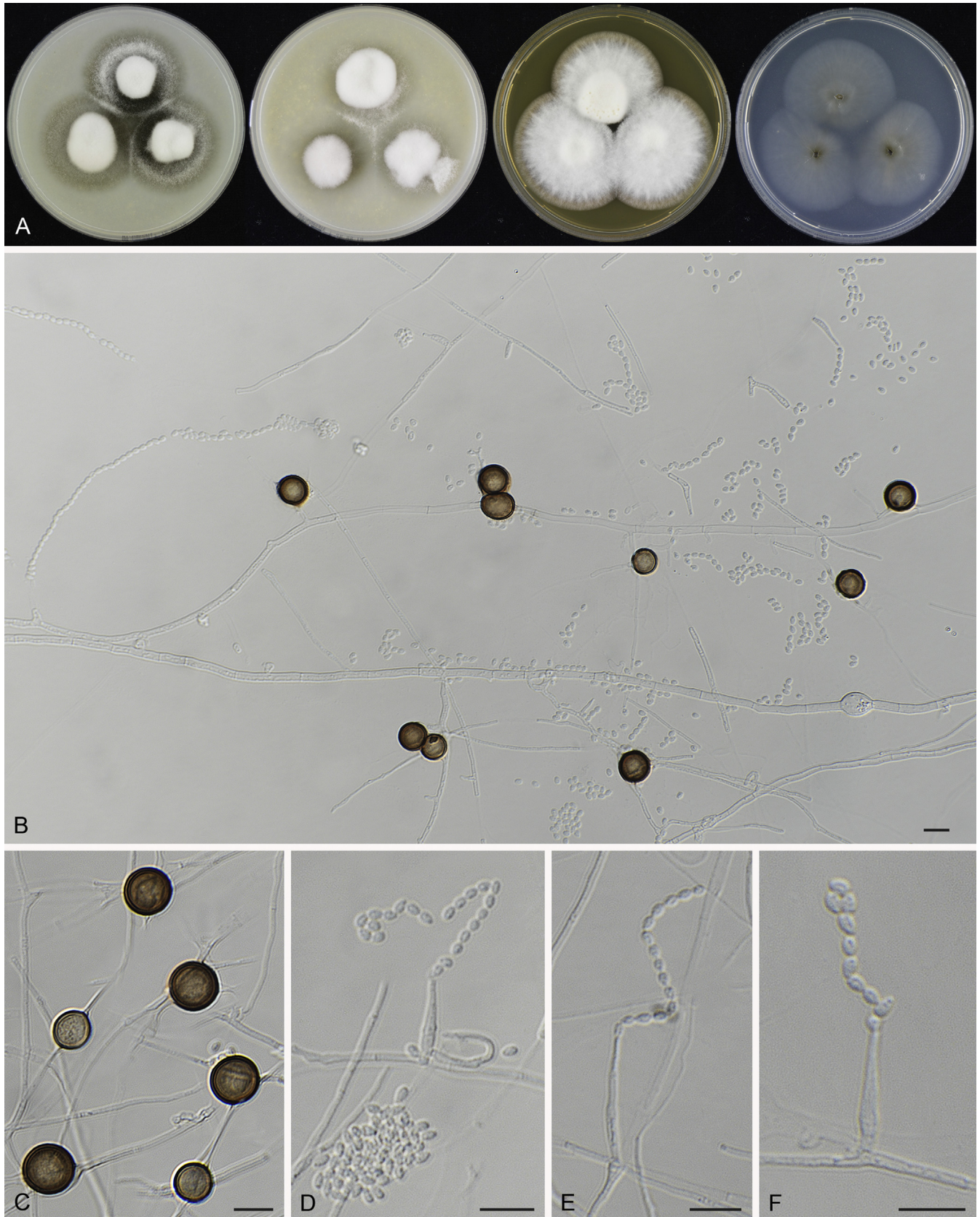


Fig. 21. *Humicola pulvericola* (CBS 144165, ex-type culture). **A.** Colonies from left to right on OA, CMA, MEA and PCA after 1 wk incubation. **B.** Hyphae, thick-walled conidia and acronium-like synanamorph. **C.** Hyphae and thick-walled conidia. **D–F.** Acronium-like synanamorph. Scale bars = 10 μ m.

Material examined: Brazil, Corcovado, isolated from soil, unknown date, R.F. Castaneda-Ruiz (**holotype** CBS H-23487, culture ex-type CBS 111771).

Notes: The ex-type strain was deposited as *Chaetomium cuyabenoensis* in CBS. *Humicola quadrangulata* can be

easily distinguished from *Humicola cuyabenoensis* (Fig. 8) by the production of quadrangular ascospores without umbonate ends and ascomata with a shorter neck without lateral hairs.

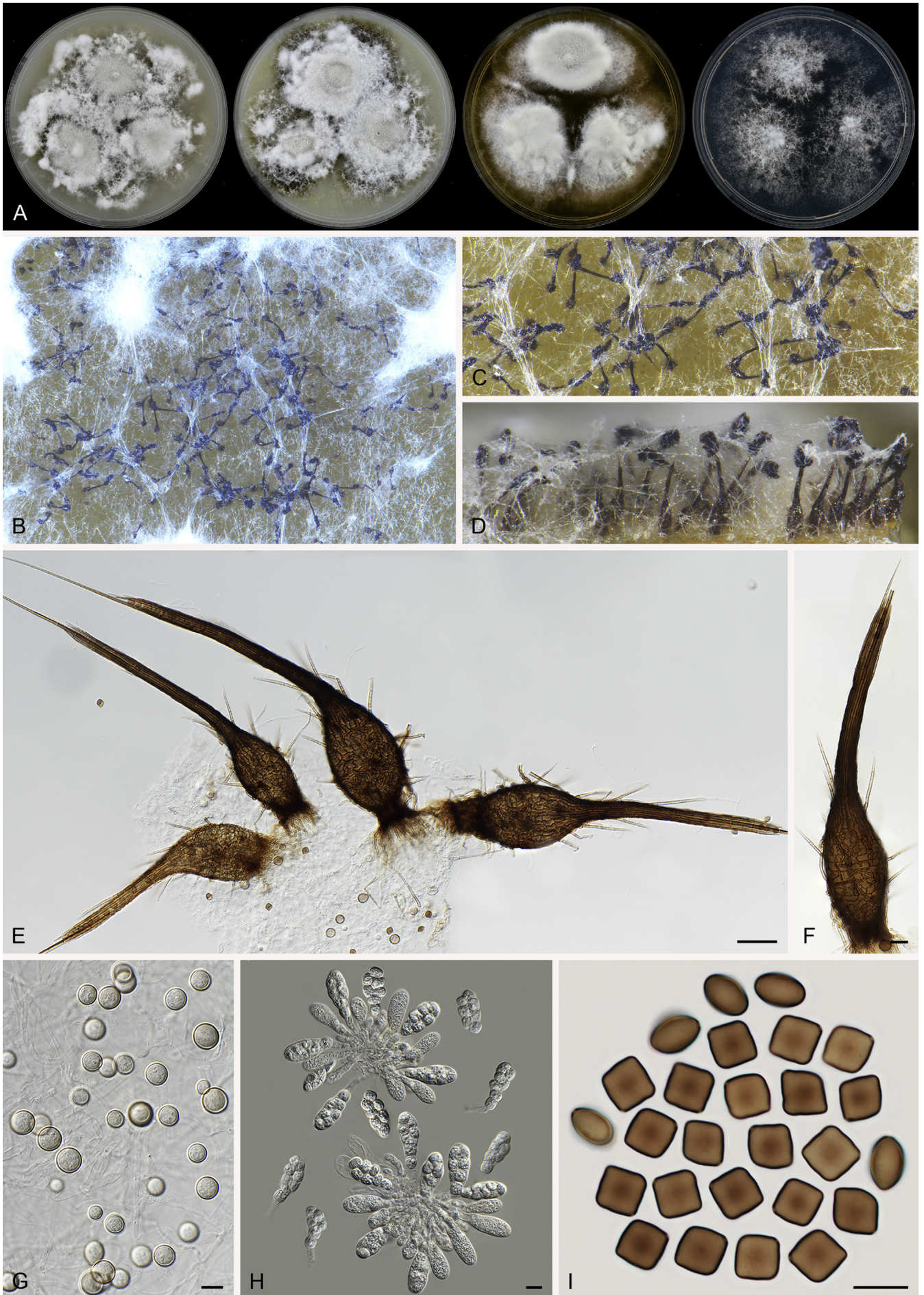


Fig. 22. *Humicola quadrangulata* (CBS 111771, ex-type culture). **A.** Colonies from left to right on OA, CMA, MEA and PCA after 4 wk incubation. **B.** Part of the colony showing immersed ascomata above which aerial mycelium was removed. **C.** Mature ascomata on OA, top view. **D.** Mature ascomata on OA, side view. **E–F.** Ascomata mounted in lactic acid. **G.** Hyphae and conidia. **H.** Asci. **I.** Ascospores. Scale bars: E = 50 μm ; F = 20 μm ; G–I = 10 μm .

Humicola seminuda (L.M. Ames) X. Wei Wang & Houbraken, **comb. nov.** MycoBank MB824447. Fig. 23.

Basionym: *Chaetomium seminudum* Ames, Mycologia 41: 642. 1949.

Synonym: *Farrowia seminuda* (Ames) D. Hawksw., Persoonia 8: 181. 1975.

Micromorphology: Ascomata superficial, obpyriform or ovoid, ostiolate, with a short conical to short cylindrical ostiolar beak, usually apically converging, 130–200 µm high, 50–90 µm diam. Ascomatal wall brown, *textura angularis* with the beak part composed of vertically elongated cells in surface view. *Terminal hairs* arising from the limited extension of the adjacent ostiolar cells with pointed or round tips, 1.5–3 µm diam near the base. *Lateral hairs* sparse, seta-like, and relatively long near the ostioles. *Asci* clavate to fusiform, with spore-bearing part 20–35 × 11–16.5 µm and stalks 3.5–10 µm long, with 8 irregularly arranged ascospores, evanescent before ascospores become mature. *Ascospores* olivaceous brown when mature, limoniform, bilaterally flattened, apiculate to umbonate at both ends, (8–) 8.5–9.5 × 7.5–8.5 × (4.5–)5–6 µm, with an apical germ pore. *Conidia* globose to subglobose, sometimes ellipsoidal or obovoid, subhyaline to pale olivaceous, lateral, or terminal on the hyphae or short branches of hyphae, solitary, sometimes two in chains, 8–10.5(–11) µm diam, up to 12 µm long when obovoid.

Culture characteristics: Colonies on OA 48–54 mm diam after 7 d at 25 °C; edge entire; obverse greenish black because of the formation of ascomata; aerial hyphae sparse or absent; soluble pigment buff to honey; reverse honey to hazel. Colonies on CMA similar to those on OA, 45–51 mm diam after 7 d at 25 °C. Colonies on MEA 32–38 mm diam after 7 d at 25 °C; edge entire; aerial mycelium white; soluble pigment absent; reverse cinnamon to sienna. Colony on PCA 42–48 mm diam after 7 d at 25 °C; edge entire; aerial mycelium white; soluble pigment absent; reverse uncoloured.

Material examined: **Lectotype designated here:** Figs 23–29 illustrated by L.M. Ames based on ex-type culture from Iowa, USA in Mycologia 41: 643. 1949. MBT381349. **Canada,** Ontario, isolated from soil, 13 Apr. 1981, A. Carter & S.A. Redhead, MBT381345 (**epitype designated here,** CBS H-23488, culture ex-epitype CBS 368.84); Ontario, isolated from soil under *Thuja occidentalis*, Sep 1964, G.C. Bhatt, culture CBS 549.69. **China,** isolated from leaf fragment in soil, 25 Apr 1958, G. Sörgel, culture CBS 153.59; Xinjiang, Khanas, isolated from soil under yak dung, June 2002, X.W. Wang, culture CBS 119767.

Notes: The holotype of *Chaetomium seminudum* seems to be lost. However, the protologue contains the illustrations that are designated here as the lectotype of *C. seminudum*, the basionym of *H. seminuda*. This species is morphologically similar to *H. mutabilis* and *H. degenerans* but can be distinguished by the apical structure of ascomata, which usually possess terminal hairs arising from the extension of the adjacent ostiolar cells, and these terminal hairs are limited in length resembling to those of *H. mutabilis*.

Humicola semispiralis (Udagawa and Cain) X. Wei Wang & Houbraken, **comb. nov.** MycoBank MB824448. Fig. 24.

Basionym: *Chaetomium semispirale* Udagawa & Cain, Canad. J. Bot. 47: 1947. 1969.

Micromorphology: Ascomata superficial, ostiolate, with ascomatal hairs pale buff to olivaceous buff in reflected light, spherical, ellipsoidal to ovoid, 270–380 µm high, 190–320 µm diam.

Ascomatal wall brown, composed of angular to irregular cells in surface view. *Terminal hairs* partly straight to flexuous, partly spirally coiled in the upper part, septate, verrucose, 2.5–4.5 µm diam near the base. *Lateral hairs* straight or flexuous. *Asci* clavate, with spore-bearing portion 20–26 × 9–12 µm and stalks 11–21.5 µm long, with 8 biseriate ascospores, evanescent. *Ascospores* olivaceous brown to brown when mature, limoniform, umbonate at both ends, bilaterally flattened, (8–) 8.5–9.5(–10) × (6–)6.5–8 × 4.5–5.5(–6) µm, with an apical germ pore. *Conidia* globose to oblate, sometimes ovoid, hyaline, subhyaline to olivaceous, usually lateral on the hyphae or short branches of hyphae, without conidiophore differentiation, solitary, (8.5–)9–11 µm diam.

Culture characteristics: Colonies on OA 36–42 mm diam after 7 d at 25 °C; edge entire; aerial mycelium irregularly distributing, thick, white; texture cottony; soluble pigment ochreous to umber; reverse pale luteous, ochreous to umber. Colonies on CMA similar to those on OA, 37–43 mm diam after 7 d at 25 °C. Colonies on MEA 39–45 mm diam after 7 d at 25 °C; edge entire; non-sporulating, aerial mycelium thick, buff to ochreous; texture floccose; reverse apricot to sienna caused by soluble pigment. Colony on PCA 34–40 mm diam after 7 d at 25 °C; edge entire; aerial mycelium sparse; soluble pigment absent; reverse uncoloured.

Material examined: **Canada,** isolated from herbarium specimen of the type of *C. semispirale* by A. Carter, culture ex-isotype CBS 723.97. The type of *C. semispirale* was originally isolated from contaminated filter paper, 1958, S. Udagawa & R.F. Cain.

Notes: von Arx et al. (1986) considered *Chaetomium semispirale* (= *Humicola semispiralis*) to be a synonym of *Chaetomium sphaerale*. Based on the original descriptions and our examination of these two species, *H. semispiralis* can be easily distinguished from *H. sphaerale* by its larger ascospores (8.5–9.5 × 6.5–8 × 4.5–5.5 µm vs 7–7.5 × 5.5–6.5 × 4–4.5 µm), and by the characters of its terminal hairs.

Two groups of species of *Humicola* described by de Bertoldi (1976), i.e. i) *H. aurea*, *H. lutea*, *H. piriforme* and *H. repens*, and ii) *H. glauca*, *H. nivea* and *H. sardiniae*, are closely related to *H. semispiralis* based on their ITS sequences and are discussed in the “Doubted or excluded species” section below. Other strains and other ITS sequences deposited in GenBank and identified as *H. fuscoatra* (e.g. KU945926) also seem to belong to this complex, Multigene and morphological analyses of these strains must be completed to determine whether these are synonyms of *H. semispiralis*, or whether this is a phylogenetic species complex.

Humicola sphaerale (Chivers) X. Wei Wang & Houbraken, **comb. nov.** MycoBank MB824449. Fig. 25.

Basionym: *Chaetomium sphaerale* Chivers, Proc. Amer. Acad. Arts 48: 84. 1912.

Micromorphology: Ascomata superficial, ostiolate, with ascomatal hairs buff to pale luteous in reflected light, ellipsoidal to ovoid, 240–340 µm high, 190–275 µm diam. Ascomatal wall brown, composed of angular to irregular cells in surface view. *Terminal hairs* flexuous to undulate, septate, verrucose, 2–3.5 µm diam near the base. *Lateral hairs* straight or flexuous. *Asci* clavate, with spore-bearing portion 22–30 × 8–13 µm and stalks about 12–26 µm long, with 8 biseriate ascospores,

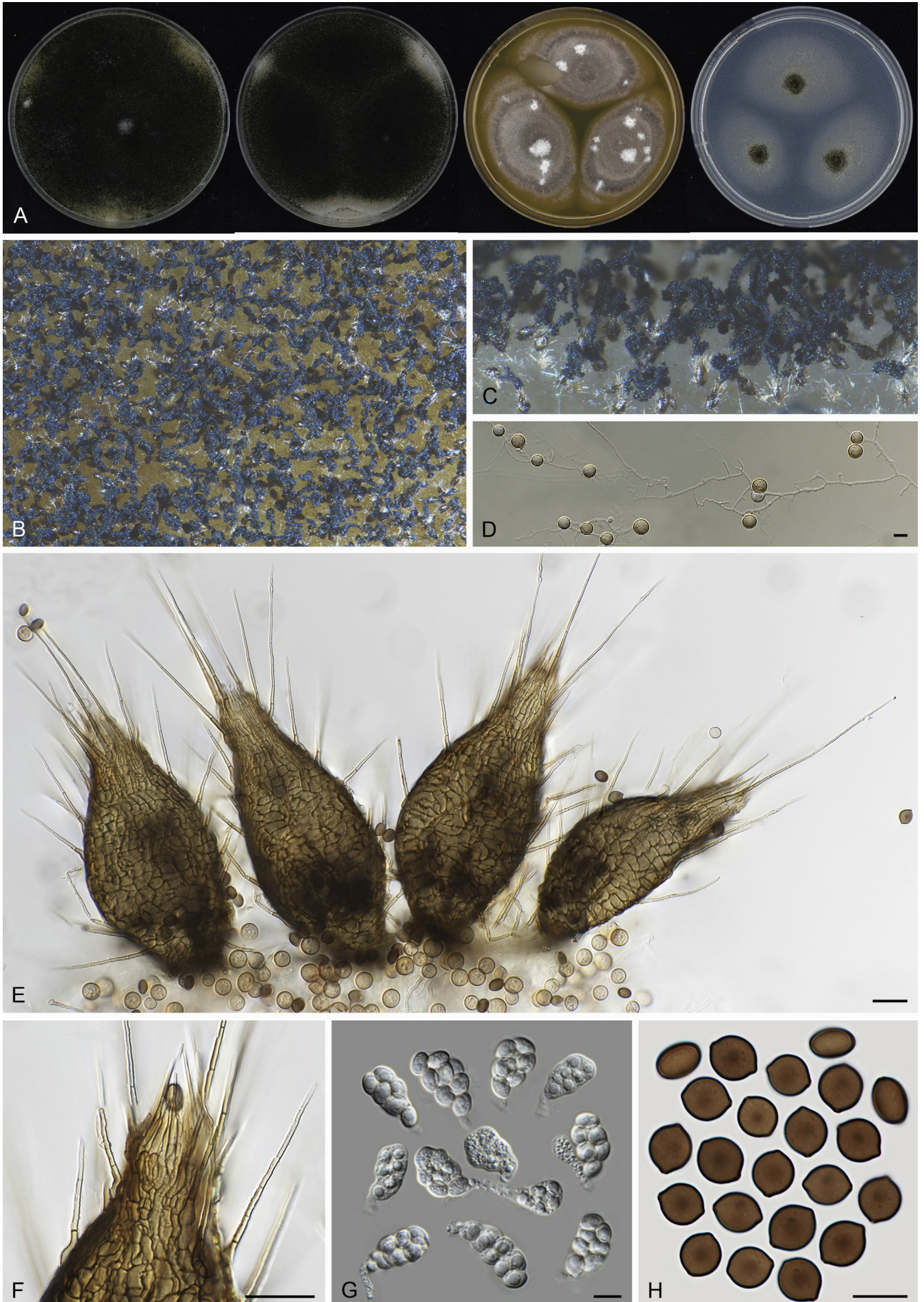


Fig. 23. *Humicola seminuda* (CBS 368.84, ex-epitype culture). **A.** Colonies from left to right on OA, CMA, MEA and PCA after 3 wk incubation. **B.** Mature ascomata on OA, top view. **C.** Mature ascomata on OA, side view. **D.** Hyphae and conidia. **E.** Ascomata together with conidia mounted in lactic acid. **F.** Structures of the apex of an ascoma. **G.** Asci. **H.** Ascospores. Scale bars: D, F = 20 μ m; E, G, H = 10 μ m.

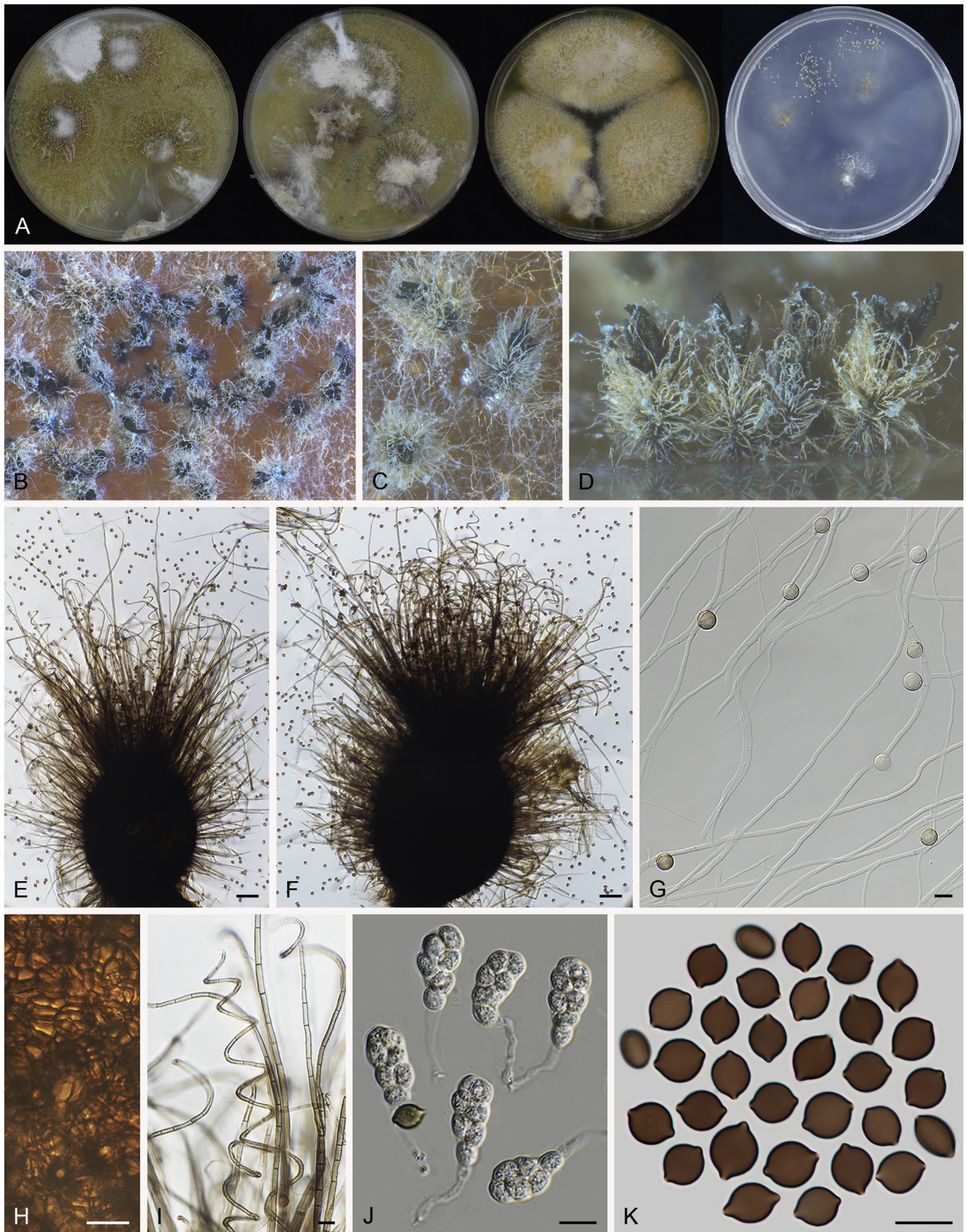


Fig. 24. *Humicola semispiralis* (CBS 723.97, ex-isotype culture). **A.** Colonies from left to right on OA, CMA, MEA and PCA after 4 wk incubation. **B.** Part of the colony. **C.** Mature ascomata on OA, top view. **D.** Mature ascomata on OA, side view. **E–F.** Ascomata mounted in lactic acid. **G.** Hyphae and conidia. **H.** Structure of ascomatal wall in surface view. **I.** Terminal ascomatal hairs. **J.** Asci. **K.** Ascospores. Scale bars: E–F = 50 μ m; G–K = 10 μ m.

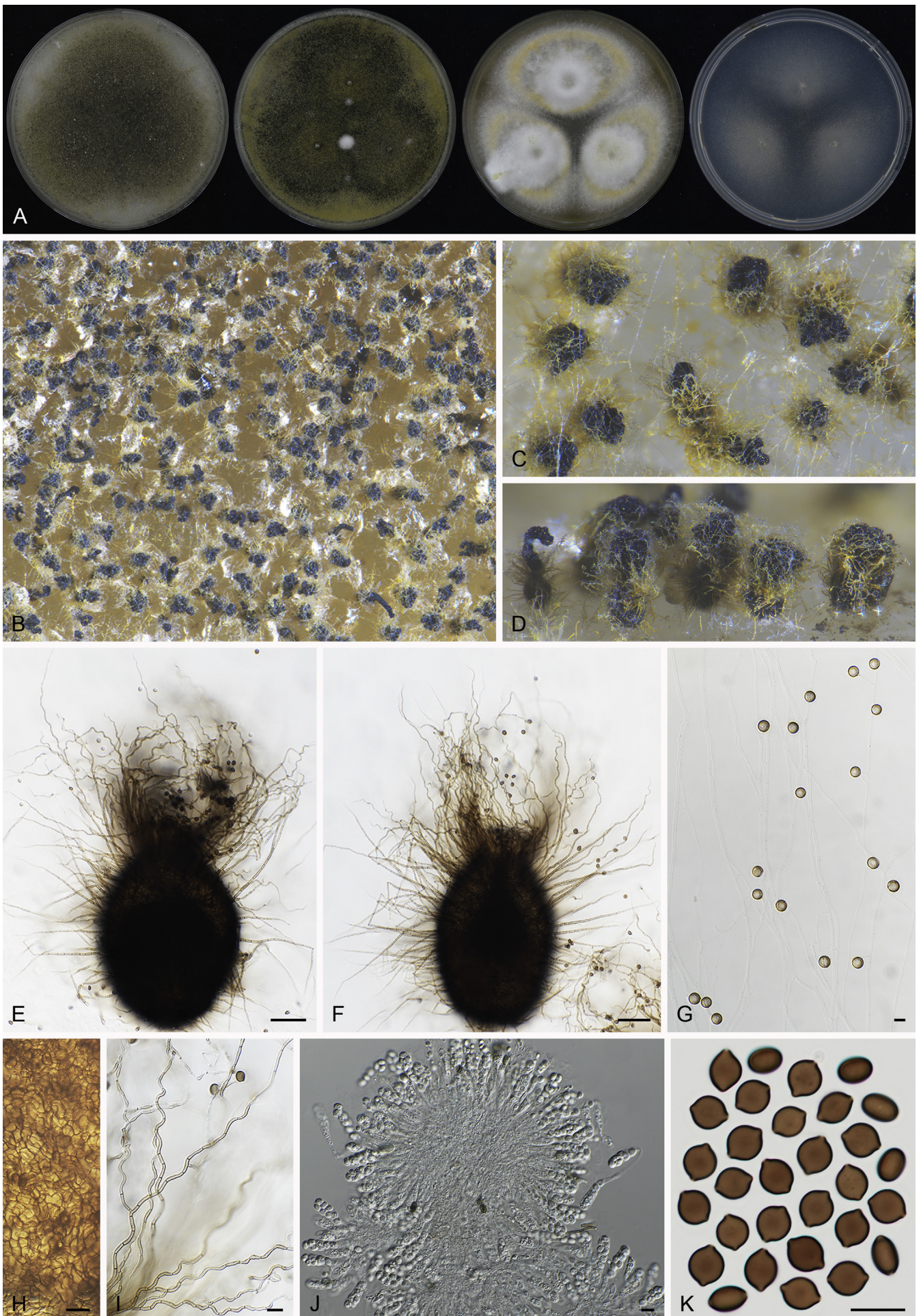


Fig. 25. *Humicola sphaeralis* (CBS 985.87, ex-epitype culture). **A.** Colonies from left to right on OA, CMA, MEA and PCA after 4 wk incubation. **B.** Part of the colony. **C.** Mature ascomata on OA, top view. **D.** Mature ascomata on OA, side view. **E–F.** Ascomata mounted in lactic acid. **G.** Hyphae and conidia. **H.** Structure of ascomatal wall in surface view. **I.** Terminal ascomatal hairs. **J.** Asci. **K.** Ascospores. Scale bars: E–F = 50 μm ; G–K = 10 μm .

evanescent. *Ascospores* olivaceous brown to brown when mature, limoniform, umbonate at both ends, bilaterally flattened, (6.5–) 7–7.5(–8) × 5.5–6.5 × 4–4.5 µm, with an apical germ pore. *Conidia* globose to oblate, sometimes ovoid, hyaline, subhyaline to olivaceous, usually lateral on the hyphae or short branches of hyphae, without conidiophore differentiation, solitary, 9–12 µm diam.

Culture characteristics: Colonies on OA 42–48 mm diam after 7 d at 25 °C; edge entire; aerial mycelium absent; soluble pigment buff to honey or absent; reverse isabelline. Colonies on CMA similar to those on OA, 42–48 mm diam after 7 d at 25 °C. Colonies on MEA 45–51 mm diam after 7 d at 25 °C; edge entire; non-sporulating; aerial mycelium thick, white to pale luteous; texture floccose; reverse fuscous black caused by soluble pigment. Colony on PCA 37–43 mm diam after 7 d at 25 °C; edge entire; about, aerial mycelium sparse or absent; soluble pigment absent; reverse uncoloured.

Material examined: France, isolated from soil, unknown date, F. Seigle-Murandi, culture CBS 985.87. USA, Reading, Mass., isolated from a culture of caterpillars, unknown date, A.H. Chivers (holotype, New York Botanical Garden Specimen ID 01050440).

Notes: CBS 985.87 was deposited as *Chaetomium semispirale*, however, its relatively small ascospores, flexuous to undulate and branched, but never spirally coiled ascomatal hairs correspond well with the characters of the type of *C. sphaerale*. Chivers (1912) described *C. sphaerale* producing ascospores measuring 7.3–8.1 × 6.4 µm. von Arx et al. (1986) re-described *C. sphaerale*, and in his description, the ascospores were 7.5–9 × 6–7 × 4–5 µm, which is larger than in the original description. Our measurement of the type (6–7.5 × 5–6.5 × 4–4.5 µm) confirmed that the size of the ascospores of *C. sphaerale* is less than 8 × 6.5 µm in face view. The holotype was originally collected in the USA, and epitypification of this species awaits recollection from the type locality.

Humicola subspiralis (Chivers) X. Wei Wang & Houbraken, **comb. nov.** MycoBank MB824450. Fig. 26.

Basionym: *Chaetomium subspirale* Chivers, Proc. Amer. Acad. Arts 48: 84. 1912.

Micromorphology: *Ascomata* superficial, ostiolate, grey white in reflected light because of the ascomatal hairs, spherical, ellipsoidal to ovoid, 240–320 µm high, 185–260 µm diam. *Ascomatal wall* brown, composed of angular to irregular cells in surface view. *Terminal hairs* straight or slightly flexuous, undulate to spirally coiled and attenuated in the upper part, septate, 2.5–4.5 µm diam near the base. *Lateral hairs* similar to the terminal ones, but shorter. *Asci* clavate, with spore-bearing portion 18–25 × 6–9 µm and stalks 8–25(–31) µm long, with 8 biseriate ascospores, evanescent. *Ascospores* olivaceous brown when mature, limoniform, biapiculate or umbonate at both ends, bilaterally flattened, 5–6.5(–7) × 4.5–5.5(–6) × 3–4 µm, with an apical germ pore. *Conidia* absent. *Acremonium-like conidiophores* unbranched, occasionally branched, aseptate or septate, 6–24 × 1.2–3 µm, with phialidic conidiogenous cells. *Conidia* in basipetal chains, sometimes in false heads, hyaline, aseptate, smooth, obovoid, usually with a truncated base and a rounded apex, 2–3.5 × 1–1.5 µm.

Culture characteristics: Colonies on OA 34–40 mm diam after 7 d at 25 °C; edge entire; aerial mycelium absent; soluble

pigment violaceous black to olivaceous black or absent; reverse leaden black. Colonies on CMA similar to those on OA, 34–40 mm diam after 7 d at 25 °C. Colonies on MEA 30–36 mm diam after 7 d at 25 °C; edge entire; non-sporulating; aerial mycelium pale smoke grey; texture floccose; soluble pigment umber; reverse fuscous black. Colonies on PCA 32–38 mm diam after 7 d at 25 °C; edge entire; aerial mycelium absent; soluble pigment; reverse uncoloured.

Material examined: China, Chungking, isolated from leaf fragments in soil, 8 Feb 1958, G. Sörgel, culture CBS 148.58; Guangdong Pro., isolated from soil, Aug 2004, X.W. Wang, culture CBS 119768. USA, New England, isolated from cow dung, unknown date A.H. Chiver (holotype, New York Botanical Garden Specimen ID 01050446).

Notes: According to Chivers (1912), the diagnostic characters of *Chaetomium subspirale* (= *Humicola subspiralis*) are the ascomatal hairs, especially its lateral hairs, which are different from those of most other species in being undulate to spirally coiled. No asexual stage of this species was mentioned by Chivers. In two subsequent studies, thick-walled conidia were found (Carter 1982, von Arx et al. 1986). In our study, rather than thick-walled conidia, an acremonium-like synanamorph was observed in both cultures. von Arx et al. (1986) pointed out that thick-walled conidia could occasionally be absent in CBS 148.58. *Humicola subspiralis* can potentially produce both thick-walled conidia and an acremonium-like synanamorph. Further study may find out which factors determine its anamorph type.

Humicola udagawae (Sergejeva ex Udagawa) X. Wei Wang & Houbraken, **comb. nov.** MycoBank MB824451. Fig. 27.

Basionym: *Chaetomium udagawae* (Sergejeva) Sergejeva ex Udagawa, Trans. Mycol. Soc. Japan 20: 476. 1979.

Synonym: *Chaetomium udagawae* Sergejeva, Novosti Syst. Nizsh. Rast. P.110. 1965.

Micromorphology: *Ascomata* superficial, often covered by white aerial hyphae, usually obovoid and without ostiolar beak, with an inconspicuous ostiole, 100–180 µm high, 70–140 µm diam. *Ascomatal wall* brown, *textura angularis* in surface view. *Ascomatal hairs* seta-like, difficult to distinguish terminal or lateral, straight, unbranched or simply branched, septate, slightly granulate, olivaceous brown, tapering and fading towards the tips, with a swollen basal cell, 2–4.5 µm diam near the base. *Asci* clavate, with spore-bearing part 20–28 × 9–15 µm and stalks 7–17 µm long, with 8 biseriate ascospores, evanescent. *Ascospores* olivaceous brown when mature, limoniform, bilaterally flattened, umbonate at both ends, 8–9.5(–10.5) × 6.5–7.5(–8.5) × 4.5–5.5(–6) µm, with an apical germ pore. *Conidia* globose to subglobose, occasionally obovoid or obpyriform, hyaline, pale olivaceous, lateral, or terminal on the hyphae or short branches of hyphae, occasionally intercalary, solitary, 7–10.5 µm high, 6.5–10.5 µm wide.

Culture characteristics: Colonies on OA 38–44 mm diam after 7 d at 25 °C; edge entire; aerial mycelium white; texture cottony; soluble pigment olivaceous grey; reverse grey olivaceous. Colonies on CMA 37–43 mm diam after 7 d at 25 °C; edge entire; aerial mycelium white; texture cottony; soluble pigment olivaceous grey; reverse greyish sepia to fulvous. Colonies on MEA 36–42 mm diam after 7 d at 25 °C; edge entire; aerial mycelium thick, white to buff; texture cottony; reverse ochreous. Colony on PCA 36–42 mm diam after 7 d at 25 °C; edge entire; aerial mycelium absent; soluble pigment absent; reverse uncoloured.

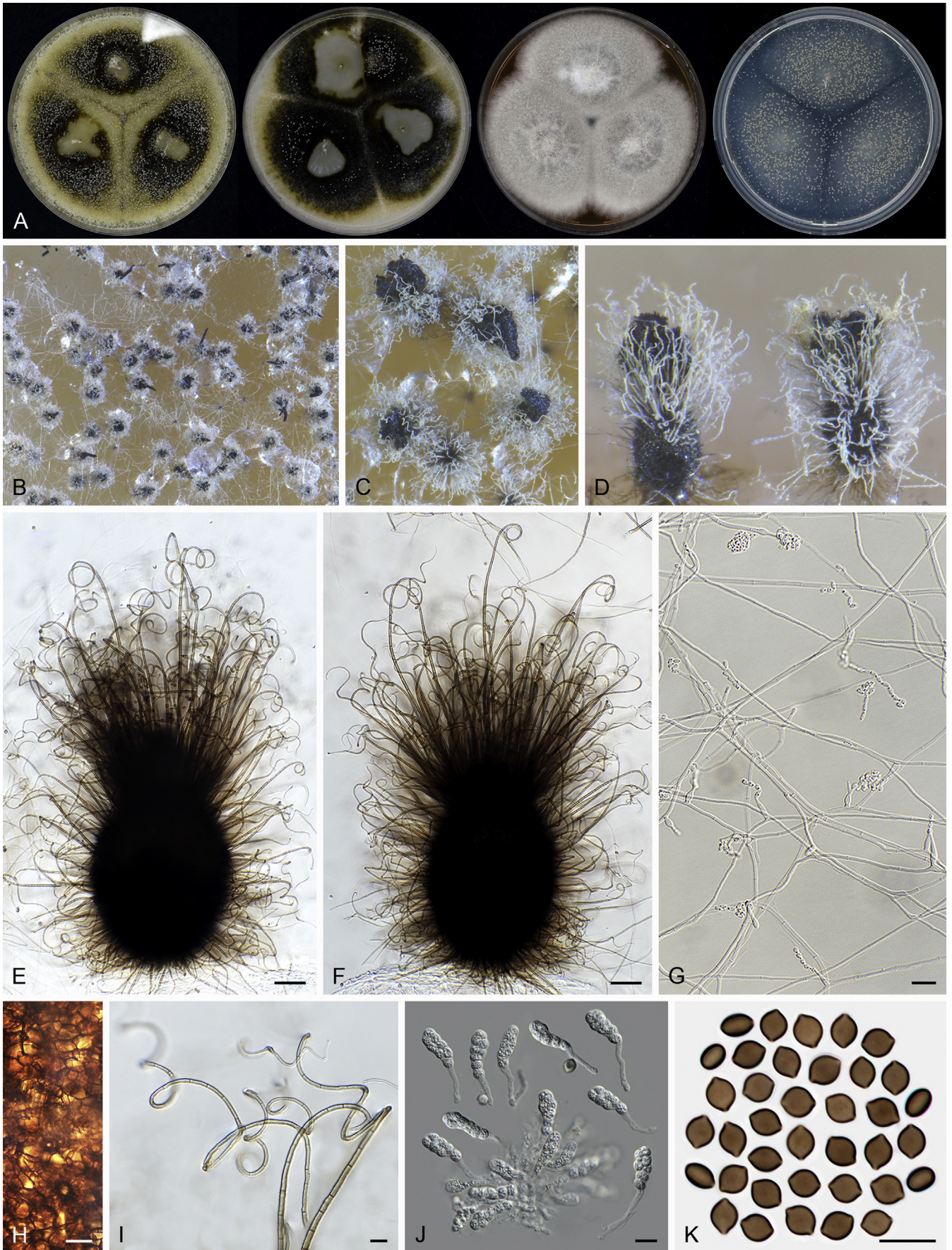


Fig. 26. *Humicola subspiralis* (CBS 148.58). **A.** Colonies from left to right on OA, CMA, MEA and PCA after 3 wk incubation. **B.** Part of the colony. **C.** Mature ascomata on OA, top view. **D.** Mature ascomata on OA, side view. **E–F.** Ascomata mounted in lactic acid. **G.** Hyphae, conidiophores and conidia of acremonium-like synanamorph. **H.** Structure of ascomatal wall in surface view. **I.** Terminal ascomatal hairs. **J.** Asci. **K.** Ascospores. Scale bars: E–F = 50 μm ; G–K = 10 μm .

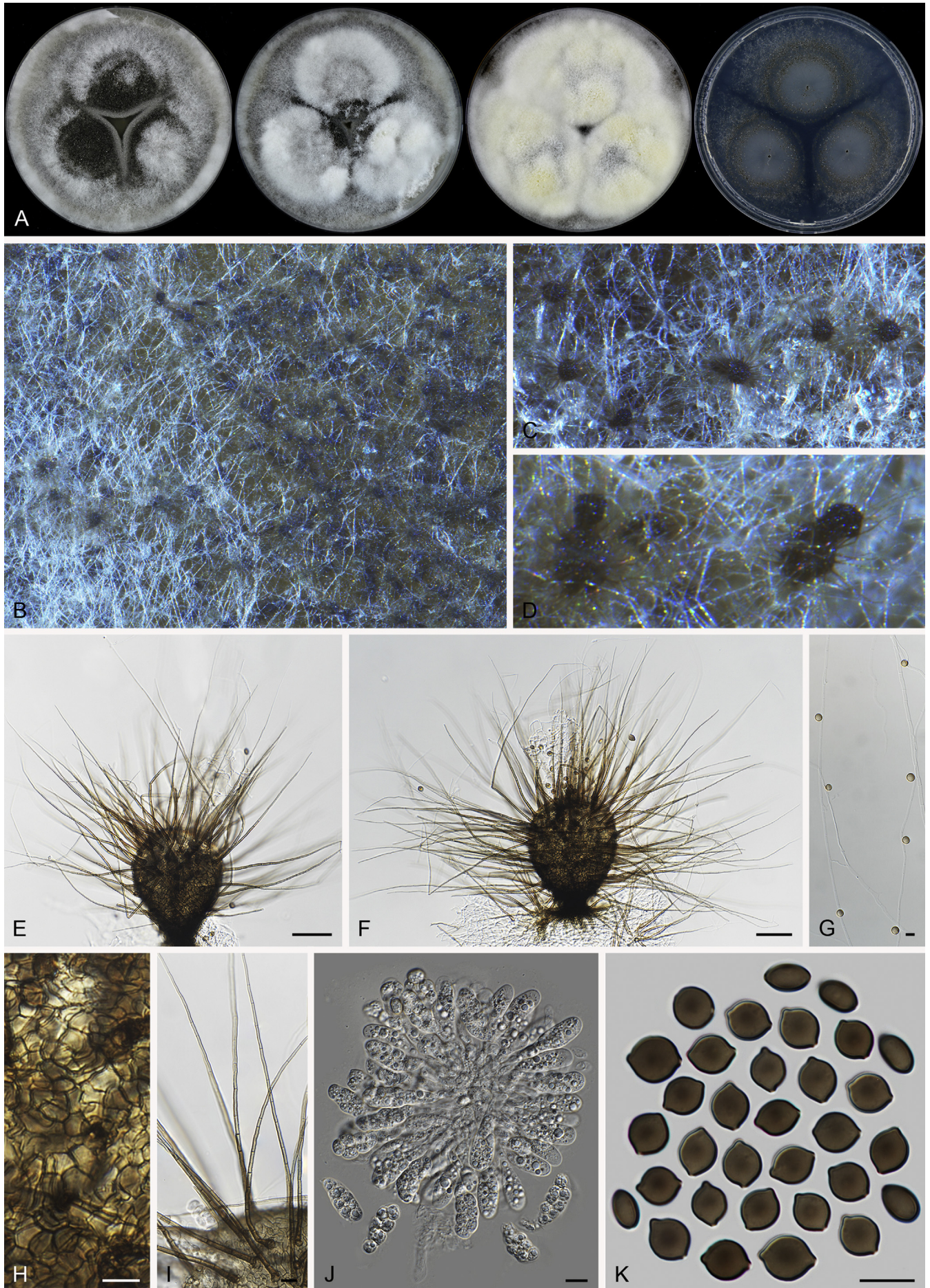


Fig. 27. *Humicola udagawae* (CBS 337.68, ex-type culture). **A.** Colonies from left to right on OA, CMA, MEA and PCA after 2 wk incubation. **B.** Part of the colony. **C.** Mature ascomata on OA, top view. **D.** Mature ascomata on OA, side view. **E–F.** Ascumata mounted in lactic acid. **G.** Hyphae and conidia. **H.** Structure of ascomatal wall in surface view. **I.** Terminal ascomatal hairs. **J.** Asci. **K.** Ascospores. Scale bars: E–F = 50 μm ; G–K = 10 μm .

Material examined: **Unknown country**, unknown substrate, unknown date, K.S. Sergejeva, culture ex-type CBS 337.68.

Notes: This species is characterised by obovoid ascomata without ostiolar beak, and inconspicuous ostiole openings.

Humicola wallefii (J.A. Mey. & Lanneau) X. Wei Wang & Houbraken, **comb. nov.** MycoBank MB824452. Fig. 28.

Basionym: *Chaetomium wallefii* J.A. Mey. & Lanneau, Bull. Soc. Mycol. France. 83: 320. 1967.

Micromorphology: Somatic hyphae hyaline, 1–3 µm wide. Conidia usually originating on the side of vegetative hyphae, single-celled, solitary, sometimes two in chain or a few in cluster, usually slightly tuberculate, olivaceous brown, globose, subglobose or oblate, (7–)7.5–9.5(–13) µm high, (7–)7.5–9.5(–10) µm wide. Sexual morph degenerated in the culture examined in this study. *Fide Meyer & Lanneau (1967):* Ascumata ostiolate, dark brown, subglobose or ovoid, solitary, 150–280 × 100–180 µm, setifera, grey-green or dark grey-brown. Ascumatal hairs flexuous to undulate, septate, 2–2.5 µm diam. Asci clavate, up to 50 × 7–8 µm, with 8 ascospores, evanescent. Ascospores light brown, limoniform, bilaterally flattened, biapiculate, 6.5–8 × 4.5–6.5 µm, with an apical germ pore.

Culture characteristics: Colonies on OA 32–38 mm diam after 7 d at 25 °C; edge entire; aerial mycelium white; texture floccose; reverse isabelline to brown vinaceous. Colonies on CMA similar to that on OA, 32–38 mm diam after 7 d at 25 °C; reverse primrose to straw. Colonies on MEA 35–41 mm diam after 7 d at 25 °C; aerial mycelium white; texture floccose; reverse pale luteous to ochreous. Colonies on PCA 28–34 mm diam after 7 d at 25 °C; edge entire; about, translucent, aerial mycelium white, sparse, reverse uncoloured.

Material examined: **Zaire**, Lumbumbashi, isolated from soil, unknown date, J. Meyer, ex-type culture CBS 147.67 = IMI 126039.

Notes: This species originally produced ascumata and was treated as a synonym of *Chaetomium homopilatum* (von Arx et al. 1986). The ex-type culture of *Humicola wallefii* at CBS only produces conidia. The conidia of *H. wallefii* are slightly tuberculate, while they are smooth in most other *Humicola* species.

Mycothermus D.O. Natvig et al. ex X. Wei Wang, Houbraken & D. O. Natvig, **gen. nov.** MycoBank MB824453.

Type species: *Mycothermus thermophilus* (Cooney & R. Emers.) X. Wei Wang, Houbraken & D. O. Natvig.

Micromorphology: Somatic hyphae hyaline to subhyaline, Chlamydo-spores holothallic, thick-walled, brown, produced intercalary, laterally or terminally, solitary or in chains or clusters, smooth to verrucose, doliiform, globose, subglobose, oblong or obovoid. Thermophilic.

Notes: The genus *Mycothermus* and its type species were invalidly published (Art. 42.1) with a single identifier (MB 807382) (Natvig et al. 2015). Here we validate these two names. Based on *rpb2* sequence data as well as a multi-gene phylogeny, this genus represents a sister lineage to *Remersonia*.

Mycothermus thermophiloides X. Wei Wang & Houbraken, **sp. nov.** MycoBank MB824455. Fig. 29.

Etymology: The epithet to the phenotypic similarity of this species to *My. thermophilus*.

Micromorphology: Somatic hyphae hyaline, 1.5–6(–7) µm wide. Chlamydo-spores holothallic, thick-walled, brown, superficial or immersed, produced laterally, intercalary on hyphae, or terminally on the short side branches of hyphae, single-celled, occasionally 2-celled, solitary, sometimes two in chains, smooth to spinose, globose, subglobose, oblate or obovoid, (9.5–) 11–15(–19) × (9–)10.5–12(–16) µm.

Culture characteristics: Colonies on OA more than 70 mm diam after 7 d at 37 °C; edge entire; aerial hyphae sparse or absent; obverse pale mouse grey to mouse grey because of the formation of chlamydo-spores; reverse uncoloured to pale smoke grey. Colonies on CMA similar to those on OA, more than 70 mm diam after 7 d at 37 °C. Colonies on MEA more than 70 mm diam after 7 d at 37 °C; edge crenate, aerial hyphae white to smoke grey; obverse fluccose; reverse greyish sepia. Colonies on PCA more than 70 mm diam after 7 d at 37 °C; edge crenate or lobate; aerial hyphae absent; obverse pale mouse grey to mouse grey because of the formation of chlamydo-spores; reverse uncoloured to olivaceous grey.

Material examined: **USA**, Indiana, isolated from soil, unknown date, M.R. Tansey (**holotype** CBS H-23489, culture ex-type CBS 183.81).

Mycothermus thermophilus (Cooney & R. Emers.) X. Wei Wang, Houbraken & D. O. Natvig, **comb. nov.** MycoBank MB824454. Fig. 30.

Basionym: *Torula thermophila* Cooney & R. Emers., Thermophilic Fungi: 92. 1964.

Synonyms: *Scyrtalidium thermophilum* (Cooney & R. Emers.) Austwick, New Zealand J. Agric. Res. 19: 29. 1976.

Mycothermus thermophilus (Cooney & R. Emers.) D.O. Natvig et al., *Mycologia* 107: 321. 2015, nom. inval. (Art. 42.1).

Humicola insolens Cooney & R. Emers., Thermophilic Fungi: 72. 1964.

Humicola grisea var. *thermoides* Cooney & R. Emers., Thermophilic Fungi: 72. 1964.

Micromorphology: Somatic hyphae hyaline, 1–6(–7) µm wide. Chlamydo-spores holothallic, thick-walled, brown, superficial or immersed, varying in morphology in different isolates, intercalary or lateral on the hyphae, or terminal on the short side branches of hyphae, solitary or in chains or in clusters, smooth, doliiform, globose, subglobose, oblong or obovoid, (5.5–) 7–14(–22) × (4.5–)6–11 (–16) µm. Occasionally with spinose ornamentation.

Culture characteristics: Colonies on OA more than 70 mm diam in 7 d at 37 °C; edge entire or crenate; obverse smoke grey, buff to hazel because of the formation of chlamydo-spores, aerial mycelium sparse; reverse smoke grey or hazel. Colonies on CMA more than 70 mm diam in 7 d at 37 °C; edge entire or crenate; obverse smoke grey to greenish olivaceous or hazel because of the formation of chlamydo-spores, aerial mycelium sparse; reverse ochreous to cinnamon. Colonies on MEA more than 70 mm diam in 7 d at 37 °C; edge lobate, crenate or slightly fimbriate; aerial mycelium grey white, smoke grey, vinaceous buff or greyish sepia, texture floccose; reverse olivaceous buff to greenish olivaceous or isabelline. Colonies PCA more than 70 mm diam in 7 d at 37 °C; edge lobate or crenate; aerial mycelium sparse or absent; obverse colourless or pale mouse grey to mouse grey because of the formation of chlamydo-spores; reverse uncoloured to olivaceous grey.

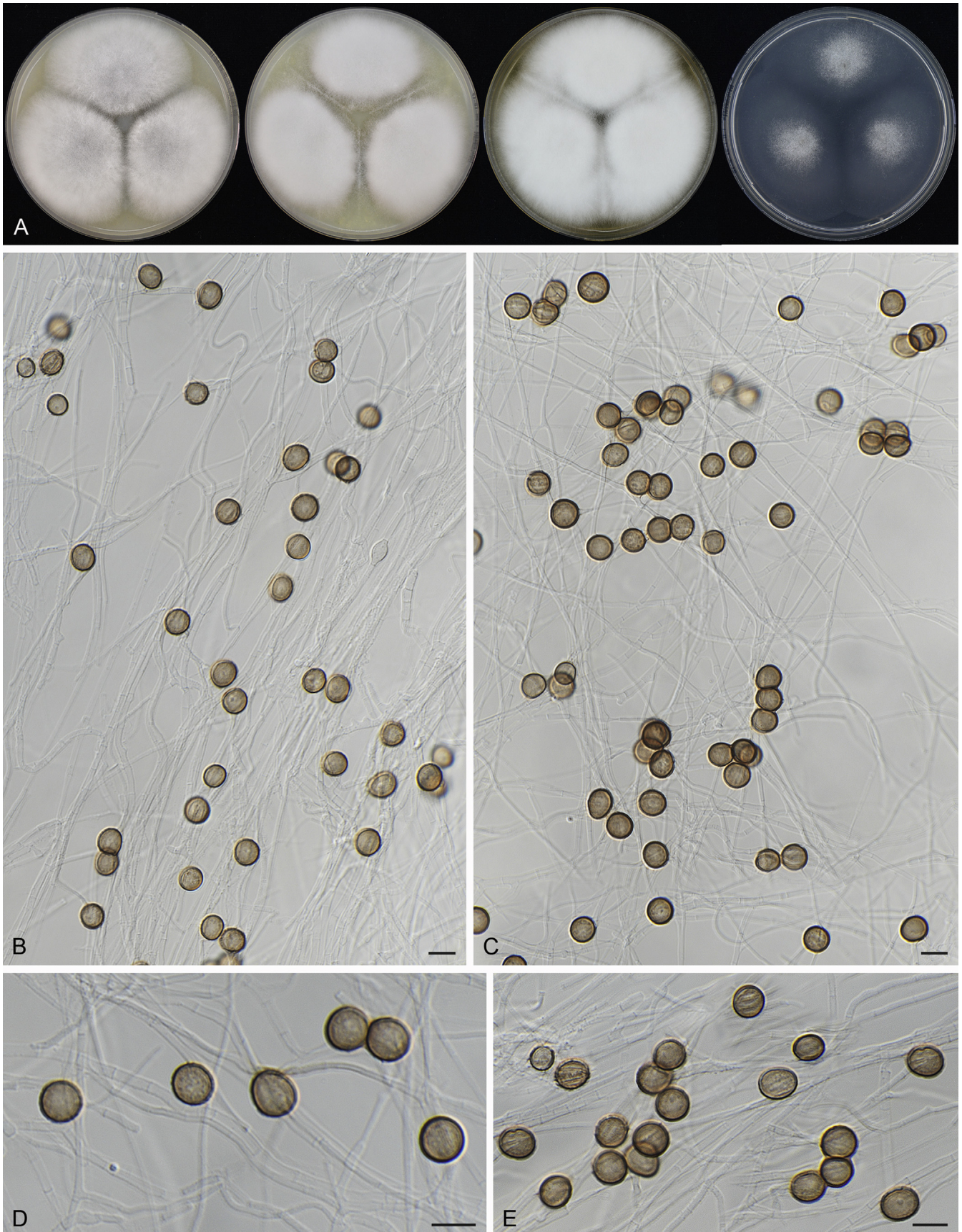


Fig. 28. *Humicola wallefii* (CBS 147.67, ex-type culture). **A.** Colonies from left to right on OA, CMA, MEA and PCA after 2 wk incubation. **B–E.** Hyphae and conidia. Scale bars = 10 μ m.

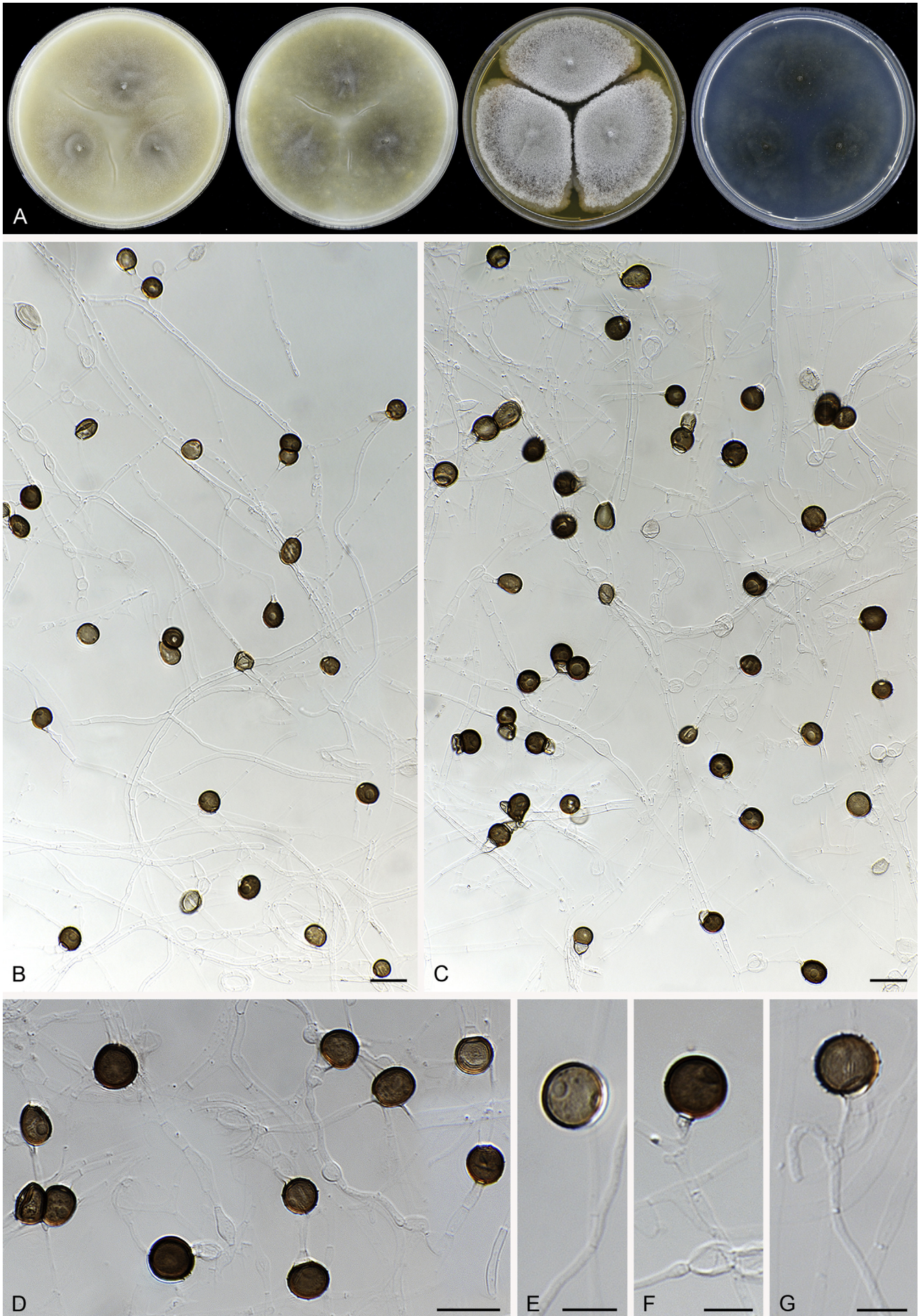


Fig. 29. *Mycothermus thermophiloides* (CBS 83.81 ex-type). **A.** Colonies from left to right on OA, CMA, MEA and PCA after 1 wk incubation. **B–G.** Hyphae and chlamydospores. Scale bars: B–D = 20 μm ; E–G = 10 μm .

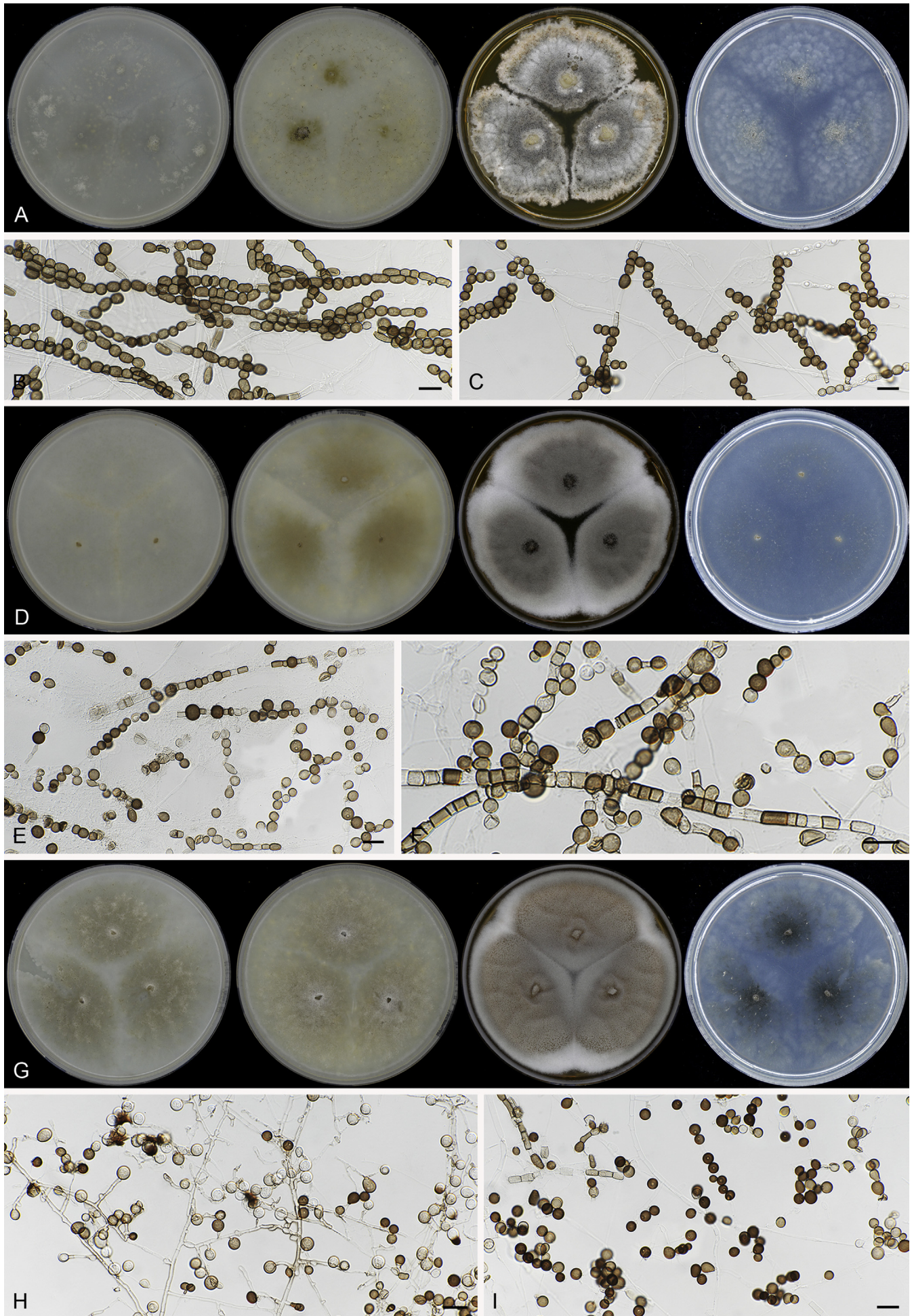


Fig. 30. *Mycothermus thermophilus* (A–C: CBS 625.91, ex-type culture; D–F: CBS 626.91 ex-type of *Humicola insolens*; CBS 627.91 ex-type of *Humicola grisea* var. *thermoides*). A, D, G. Colonies from left to right on OA, CMA, MEA and PCA after 1 wk incubation. B–C, E–F, H–I. Hyphae, and chlamydospores. Scale bars = 20 μm.

Material examined: **Switzerland**, Zürich, Gossau, isolated from mushroom compost, 10 Apr. 1963, C.L. Fergus, culture CBS 226.63. **USA**, Nevada, isolated from chicken nest straw, 1950, D.G. Cooney, holotype of *Torula thermophila*, UC 1206525, culture ex-type CBS 625.91 = ATCC 16463; California, isolated from rotting guayule shrub, 1944, P.J. Allen, J. Naghski & S.R. Hoover, culture ex-type of *Humicola insolens* CBS 626.91 = ATCC 16454 = NBRC 107640; California, isolated from dung of elephant dung, 1948, D.G. Cooney, culture ex-type of *Humicola grisea* var. *thermoidea* CBS 627.91 = ATCC 16453; California, Berkeley, unknown substrate, unknown date, R.E. Smith, culture CBS 392.69.

Notes: The three isolates noted above were designated as types of three different taxa by Cooney & Emerson (1964). The ex-type culture CBS 625.91 of *Torula thermophila* has relatively thick vegetative hyphae, 1–7 µm wide. Its chlamydo-spores usually form from the swelling of the cells of superficial hyphae, appear intercalary in chains, doliiform, oblong or subglobose, (5.5–)7.5–12(–16) × (4.5–)6–9.5(–11) µm. CBS 626.91, the ex-type culture of *Humicola insolens*, produces similar hyphae, 1–6 µm wide. The chlamydo-spores are intercalary or lateral on superficial or immersed hyphae, solitary or in chains, globose, subglobose, doliiform, oblong or obovoid, (6–)7–14(–22) × (5.5–)7–11 (–16) µm. CBS 627.91, the ex-type culture of *Humicola grisea* var. *thermoidea* produces relatively thin hyphae, 1–4 µm wide. Its chlamydo-spores are usually produced laterally or terminally on short side branches of superficial or immersed hyphae, commonly solitary, globose, subglobose, or obovoid, (8–)9–11.5(–13) × (7–)8–10.5(–12) µm. Germ pores were observed on some spores of CBS 626.91 and CBS 627.91. Each isolate produces thick-walled cells intercalary within the hyphae, a common character.

Natvig *et al.* (2015) noticed the close phylogenetic relationship of the ex-type cultures of *Torula thermophila* (basionym of *Mycothermus thermophilus*), *Humicola insolens* and *Humicola grisea* var. *thermoidea*. In their description of *My. thermophilus*, they quoted the original description of *Torula thermophila* and did not incorporate the morphological diversity of the newly recognised *My. thermophilus* (as shown in Fig. 30).

Remersonia Samson & Seifert, Can. J. Bot. 75: 1160. 1997. MycoBank MB27809.

Type species: *Remersonia thermophila* (Fergus) Seifert & Samson.

Synonym: *Synnmukeyjiomyces* K. R. Aneja & R. Kumar, Adv. Microbial Biotech. (in: J.P. Teware *et al.*): 2. 1999, *nom. inval.* Art. 37.1, *fide* Seifert *et al.* (2011), based on the protologue.

Notes: The type species of *Remersonia* was originally described as *Stilbella thermophila* (Fergus 1964). *Stilbella* is a typical synnematus hyphomycete with phialidic conidiogenous cells and slimy conidia, which is considered to be an anamorphic form in *Bionectriaceae*, *Hypoceales* (Seifert *et al.* 2011). Based on a detailed study of the type and supplementary isolates, *Remersonia* was proposed by Seifert *et al.* (1997) for this species. *Remersonia* is different from *Stilbella* in its thermotolerant growth and percurrently-extending conidiogenous cells. Their sequence data of 18S and 28S ribosomal DNA showed that this genus belonged to the *Sordariales*. The synonymous genus *Synnmukeyjiomyces* was described two years after *Remersonia*, apparently based on the same species (as *S. thermophilus* "(Lindau)" K. R. Aneja & R. Kumar, apparently confusing the original author of the genus *Stilbella* Lindau as the author of the species epithet *thermophila*).

The four *Remersonia* isolates studied here belong to two different species (Figs 1, 2). Unfortunately, the ex-type culture of *R. thermophila* in the CBS collection is no longer viable. Natvig *et al.* (2015) showed, based on a phylogenetic analysis of a

combined sequence dataset (ITS, *tub2*, *mcm7*, *rpb1* and *rpb2*), that *R. thermophila*, represented by the ex-type, is a close relative of *Mycothermus* in the *Chaetomiaceae*. To supplement their data, we sequenced the the same fragment of *tub2* for our four *Remersonia* isolates and six isolates of *My. thermophilus*, including the ex-type culture of *My. thermophilus* and two more representatives that were used in the study of Natvig *et al.* (2015). Three of our four isolates (Fig. 3) are conspecific with *R. thermophila*, and CBS 784.85 is a novel species which is described below. The close relationship between *Remersonia* and *Mycothermus* is also confirmed.

Remersonia tenuis X. Wei Wang, Houbraken & Seifert, *sp. nov.* MycoBank MB824456. Fig. 31.

Etymology: The epithet refers to the relatively narrow conidia of this species.

Micromorphology: Synnemata on OA 250–520 µm tall, scattered, sparse, often forming between two colonies, cylindrical and capitate, unbranched, slender, hyaline. Stipe 10–37 µm wide, smooth. Hyphae of stipe 1.5–2.5 µm wide, parallel and interweaving with each other through most of stipe. Conidiophores unbranched or branched once. Conidiogenous cells 13–110 µm long, 3–4.5 µm wide, proliferating percurrently and forming nodose annellations, 1–4.5 µm between annellations. Conidial mass measures (50–)100–400 µm in diam, slimy, hyaline to straw, globose to subglobose when wet, becoming dry and pyriform or fusiform in a few minutes, with columns of laterally adhered conidia tending to poke out of the conidial mass. Conidia (9.5–)11.5–16.5(–18.5) × (2.5–)3.5–4.5 (–5) µm, hyaline, oblong, clavate or ellipsoidal, sometimes slightly curved, with a truncate base and rounded apex.

Culture characteristics: Colonies on OA more than 70 mm diam in 7 d at 37 °C; edge entire; obverse uncoloured, occasionally fawn; aerial mycelium absent; reverse uncoloured. Colonies on CMA more than 70 mm diam in 7 d at 37 °C; edge entire; obverse uncoloured or olivaceous buff; aerial mycelium absent; reverse uncoloured. Colonies on MEA 37–43 mm diam in 7 d at 37 °C; edge entire; obverse olivaceous buff, with radiating furrows, producing numerous synnemata; reverse ochreous. Colonies on PCA more than 70 mm diam in 7 d at 37 °C; edge entire; aerial mycelium absent; reverse uncoloured.

Material examined: **India**, Hyderabad, isolated from dung of horse, unknown date, M.N. Rao (**holotype** CBS H-18610, culture ex-type CBS 784.85 = IMI 295313 = JCM 10546).

Notes: This species can be distinguished from *R. thermophila* by smaller conidia (11.5–16.5 × 3.5–4.5 µm vs 13–22.5 × 5–7 µm), and its faster growth rate at 37 °C (Table 2). Figs. 3–8 in Seifert *et al.* (1997) are the ex-type strain and thus represent *R. tenuis* rather than *R. thermophila* as labelled; the difference in conidial size and conidiophore branching is also evident from that figure.

Remersonia thermophila (Fergus) Seifert & Samson, Canad. J. Bot. 75: 1160. 1997. MycoBank MB437277. Figs 32–34.

Basionym: *Stilbella thermophila* Fergus, Mycologia 56: 277. 1964.

Micromorphology: Synnemata on OA 170–1100 µm tall, scattered to gregarious, cylindrical to clavate, capitate, unbranched, hyaline, sometimes fulvous to sepia when old. Stipe 5–320 µm wide in the mid part, smooth. Hyphae of stipe 1.5–3.5 µm wide, parallel and interweaving with each other through most of stipe.

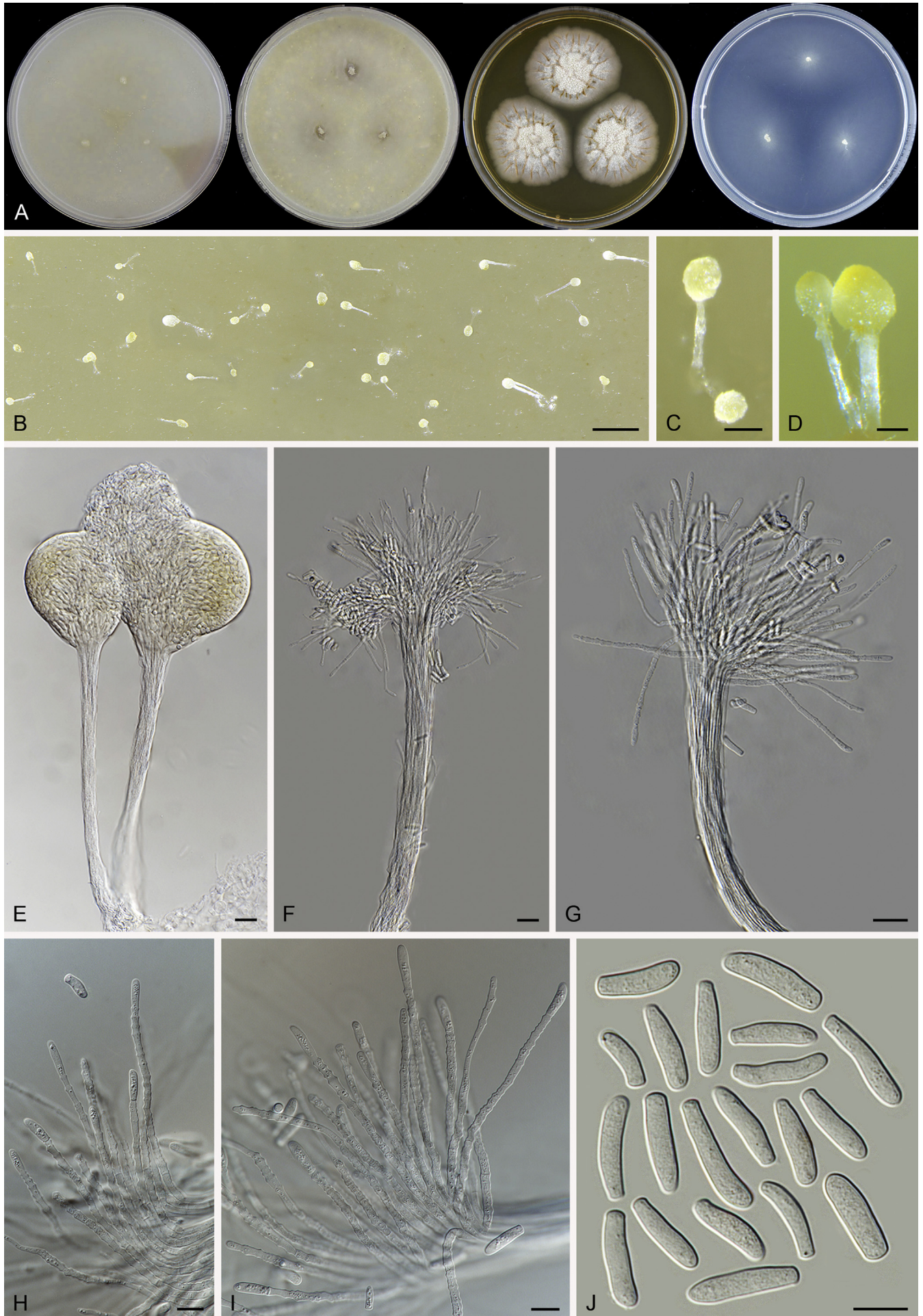


Fig. 31. *Remersonia tenuis* (CBS 784.85). **A.** Colonies from left to right on OA, CMA, MEA and PCA after 1 wk incubation. **B.** Part of the colony on OA. **C–D.** Synnemata on OA. **E–G.** Synnemata mounted in lactic acid. **H–I.** Conidiogenous cells. **J.** Conidia. Scale bars: B = 500 μm ; C–D = 200 μm ; E–F = 50 μm ; G = 20 μm ; H–J = 10 μm .

Conidiophores unbranched or simply branched once to twice. Conidiogenous cells 14–90 µm long, 3.5–6.5 µm wide, proliferating percurrently and forming nodose annellations, 1.5–26.5 µm between annellations. *Conidial mass* 50–1 300 µm in diam, slimy, hyaline, straw or pure yellow, globose or subglobose when wet, becoming dry and pyriform or fusiform in a few minutes. *Conidia* (10.5–)13–22.5(–26.5) × (4.5–)5–7(–9) µm, hyaline, oblong, clavate or ellipsoidal, occasionally pyriform, sometimes slightly curved, with a truncate base and rounded apex.

Culture characteristics: Colonies on OA 36–55 mm diam in 7 d at 37 °C; edge entire to lobate or crenate; obverse smoke grey to vinaceous buff, or fawn to olivaceous, often with radiating furrows starting from the central point, sometimes forming several dark brick to sepia concentric and crenate rings; aerial mycelium absent; reverse uncoloured, straw, olivaceous buff, fawn or olivaceous. Colonies on CMA 26–39 mm diam in 7 d at 37 °C; edge entire, lobate or crenate; obverse fawn, or pale isabelline; aerial mycelium absent; reverse fawn, olivaceous or isabelline. Colonies on MEA 26–46 mm diam in 7 d at 37 °C; edge entire, lobate, crenate or fimbriate; obverse buff, fawn to vinaceous grey, producing numerous synnemata and often mixed with aerial hyphae; reverse uncoloured, or ochreous to cinnamon, or fulvous to umber. Colonies PCA 10–38 mm diam in 7 d at 37 °C; edge lobate, crenate or fimbriate; aerial mycelium absent; reverse buff or uncoloured.

Material examined: **Netherlands**, Horst, isolated from compost, Apr. 1987, G. Straatsma, culture CBS 643.91; Horst, isolated from compost, Jun. 1991, G. Straatsma, culture CBS 645.91. **Switzerland**, Gossau-Zürich, isolated from mushroom compost during peak heating, 1962, C.L. Fergus, culture CBS 540.69 = MUCL 15081.

Notes: This species exhibit a high morphological diversity in colony characters, synnemata, conidiophores and conidiogenous cells, but conidial size and shape are consistent between different isolates (Figs 32–34, Table 2).

Staphylotrichum J.A. Mey. & Nicot, Bull. Soc. Mycol. France 72: 322. 1957. MycoBank MB10065.

Type species: *Staphylotrichum coccosporum* J.A. Mey. & Nicot.

Micromorphology: *Asexual morphs* usually of two types: type one macronematous, possessing conidiophores arising from an intercalary, thick-walled, pigmented foot cell, usually pigmented and thick-walled in the lower part, tapering and fading towards the tips, apically branched, with denticle-like

conidiogenous cells terminally on the tops of the branches; type two micronematous, with cylindrical or denticle-like conidiogenous cells arising directly from hyphae rather than apical branches of macronematous conidiophores. *Conidia* holoblastic, solitary, single-celled, smooth or slightly verrucose, hyaline to pale brown, usually globose, subglobose or obovoid. *Sexual morph* absent or present. *Ascomata* superficial, or covered by aerial hyphae, ostiolate, elongate obpyriform, obclavate or ampulliform below, usually apically attenuated to a cylindrical, thread-like neck which is composed of fused basal part of the terminal hairs. *Terminal hairs* seta-like or whip-like, fused at the lower part to form a channel through which a column of ascospores emerges from the ascomata, smooth. *Asci* clavate to fusiform, with 8 irregularly-arranged ascospores, evanescent. *Ascospores* broad limoniform to nearly globose, often somewhat biapiculate, bilaterally flattened, with an apical germ pore.

Notes: *Staphylotrichum* is well known for its apically branched macronematous conidiophores (Fig. 58G–I). Our observations showed that micronematous formation of conidia on hyphae (Fig. 58F) is also a very common character in the asexual *Staphylotrichum* species. Eight *Staphylotrichum* isolates were selected for this study, including the ex-type strain of the type species, all originally deposited as *S. coccosporum* in CBS. In the *rpb2* and four-locus phylograms, the “*Chaetomium longiculleum*” clade split the “*S. coccosporum*” clade into two separate subclades, indicating a close relationship between these sexual and asexual organisms. Production of micronematous, occasionally even macronematous asexual morphs in sexually reproducing species is additional morphological support that the “*Chaetomium longiculleum*” clade represents the sexual morph of *Staphylotrichum*. Fig. 43 shows the colony morphology of the asexual species in the genus.

Staphylotrichum acaciicola X. Wei Wang & Houbraken, **sp. nov.** MycoBank MB824457. Fig. 35.

Etymology: The epithet refers to *Acacia karroo*, the substrate from which the type strain was isolated.

Micromorphology: *Somatic hyphae* hyaline or subhyaline, producing macronematous conidia mixed with micronematous ones. *Macronematous conidiophores* arising from a thick-walled L-shaped or cylindrical, brown to dark brown foot cell, brown to

Table 2. Morphological differences between *Remersonia* isolates.

	<i>R. thermophila</i> , CBS 540.69 (Fig. 32)	<i>R. thermophila</i> , CBS 643.91 (Fig. 33)	<i>R. thermophila</i> , CBS 645.91 (Fig. 34)	<i>R. tenuis</i> , CBS 784.85 (Fig. 31)
Height of synnemata on OA	300–1 100 µm	170–550 µm	330–900 µm	300–520 µm
Width of synnema stipes	5–20.5 µm	13–85 (–145) µm	26–320 µm	12–37 µm
Conidiogenous cells	30–90 × 4.5–6.5 µm	15–70 × 4–5.5 µm	14–55 × 3.5–6 µm	13–110 × 3–4.5 µm
Distance between annellations	6–26.5 µm	2–8.5 µm	1.5–4.5 µm	1–4.5 µm
Diam of conidial masses	50–230 µm	70–500 µm	170–1 300 µm	100–400 µm
Dimensions conidia	(11–)15–22.5(–26.5) × (4.5–)5–7(–9) µm	(10.5–)13–20(–26) × (4.5–)5–6.5(–7) µm	(10.5–)13–18(–22.5) × 5–6(–7) µm	(10.5–)13–18(–22.5) × 5–6(–7) µm
Colony diam on OA (7 d, 37 °C)	49–55 mm	44–50 mm	36–42 mm	> 70 mm
Colony diam on CMA (7 d, 37 °C)	33–39 mm	26–32 mm	26–32 mm	> 70 mm
Colony diam on MEA (7 d, 37 °C)	40–46 mm	28–34 mm	26–32 mm	37–43 mm
Colony diam on PCA (7 d, 37 °C)	32–38 mm	24–30 mm	10–16 mm	> 70 mm

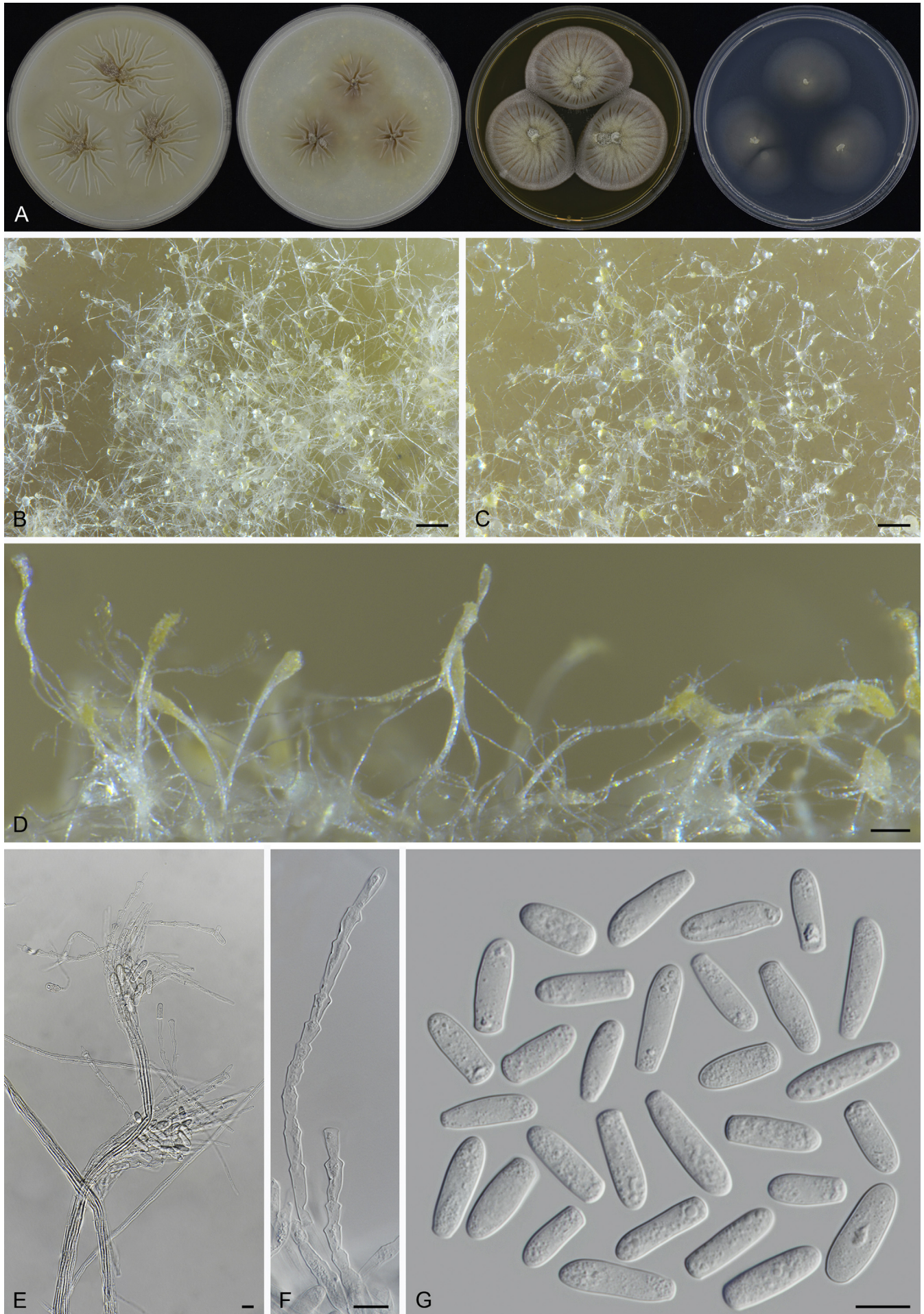


Fig. 32. *Remersonia thermophila* (CBS 540.69). **A.** Colonies from left to right on OA, CMA, MEA and PCA after 1 wk incubation. **B–C.** Synnemata on OA, top view. **D.** Synnemata on OA, side view. **E.** Synnemata mounted in lactic acid. **F.** Conidiogenous cells. **G.** Conidia. Scale bars: B–C = 500 μ m; D = 100 μ m; E–G = 10 μ m.

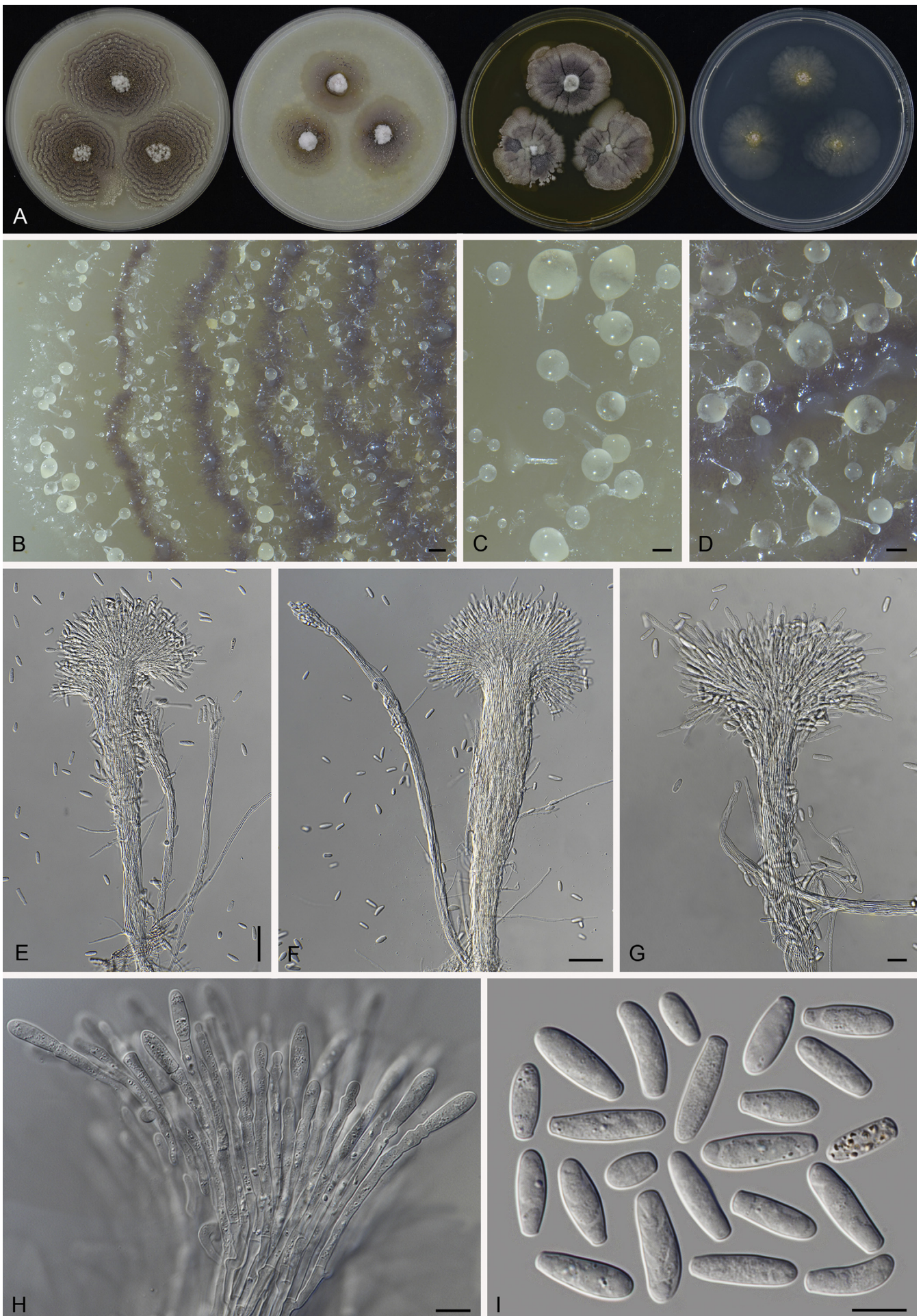


Fig. 33. *Remersonia thermophila* (CBS 643.91). **A.** Colonies from left to right on OA, CMA, MEA and PCA after 1 wk incubation. **B.** Part of the colony on OA. **C–D.** Synnemata on OA. **E–G.** Synnemata mounted in lactic acid. **H.** Parts of conidiophores and conidiogenous cells with conidia. **I.** Conidia. Scale bars: B = 500 μ m; C, D = 200 μ m; E–G = 50 μ m; H–I = 10 μ m.

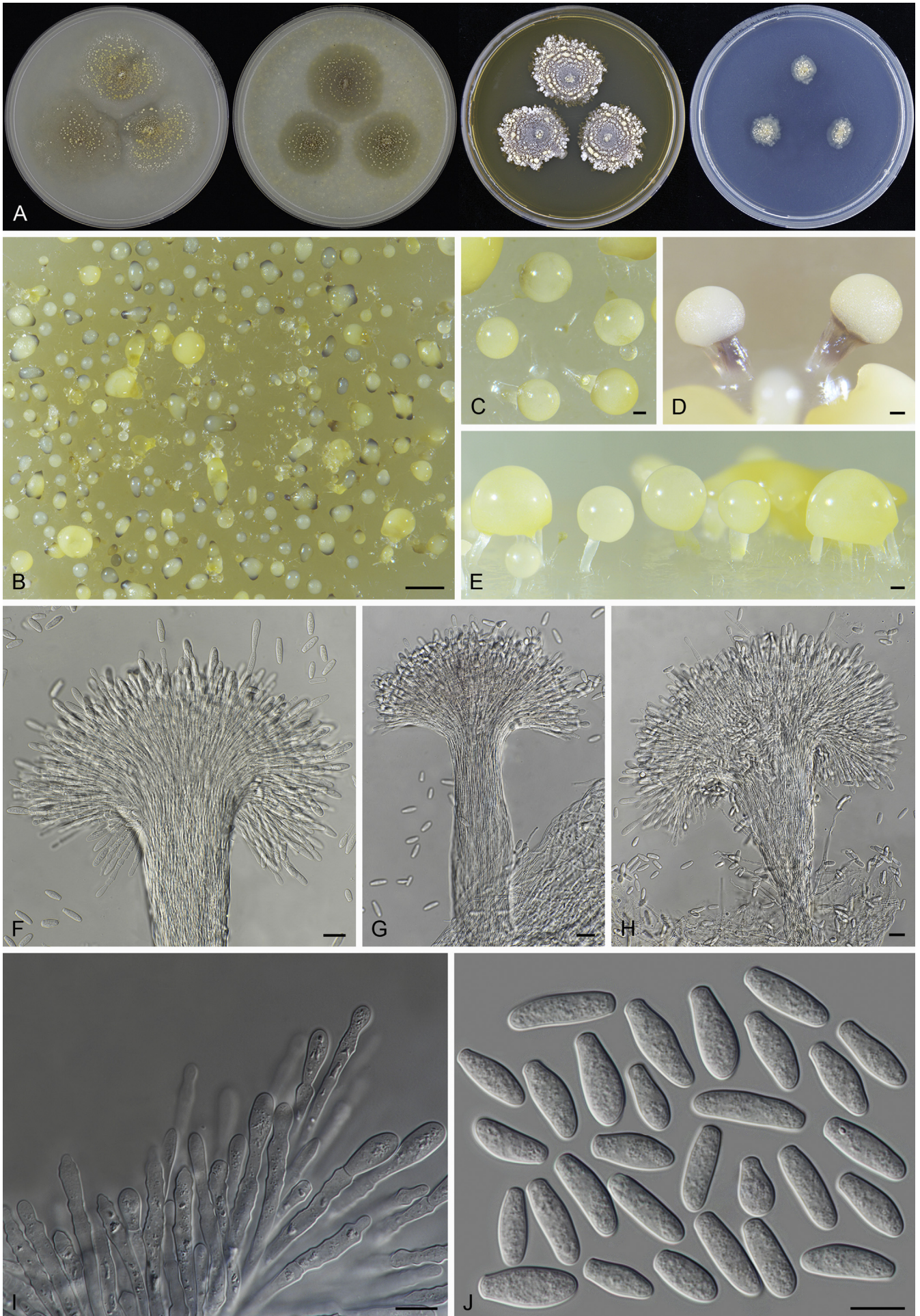


Fig. 34. *Remersonia thermophila* (CBS 645.91). **A.** Colonies from left to right on OA, CMA, MEA and PCA after 1 wk incubation. **B.** Part of the colony on OA. **C.** Synnemata on OA, top view. **D–E.** Synnemata on OA, side view. **F–H.** Synnemata mounted in lactic acid. **I.** Conidiogenous cells. **J.** Conidia. Scale bars: B = 1000 μm ; C, E = 200 μm ; D = 100 μm ; F–H = 20 μm ; I–J = 10 μm .

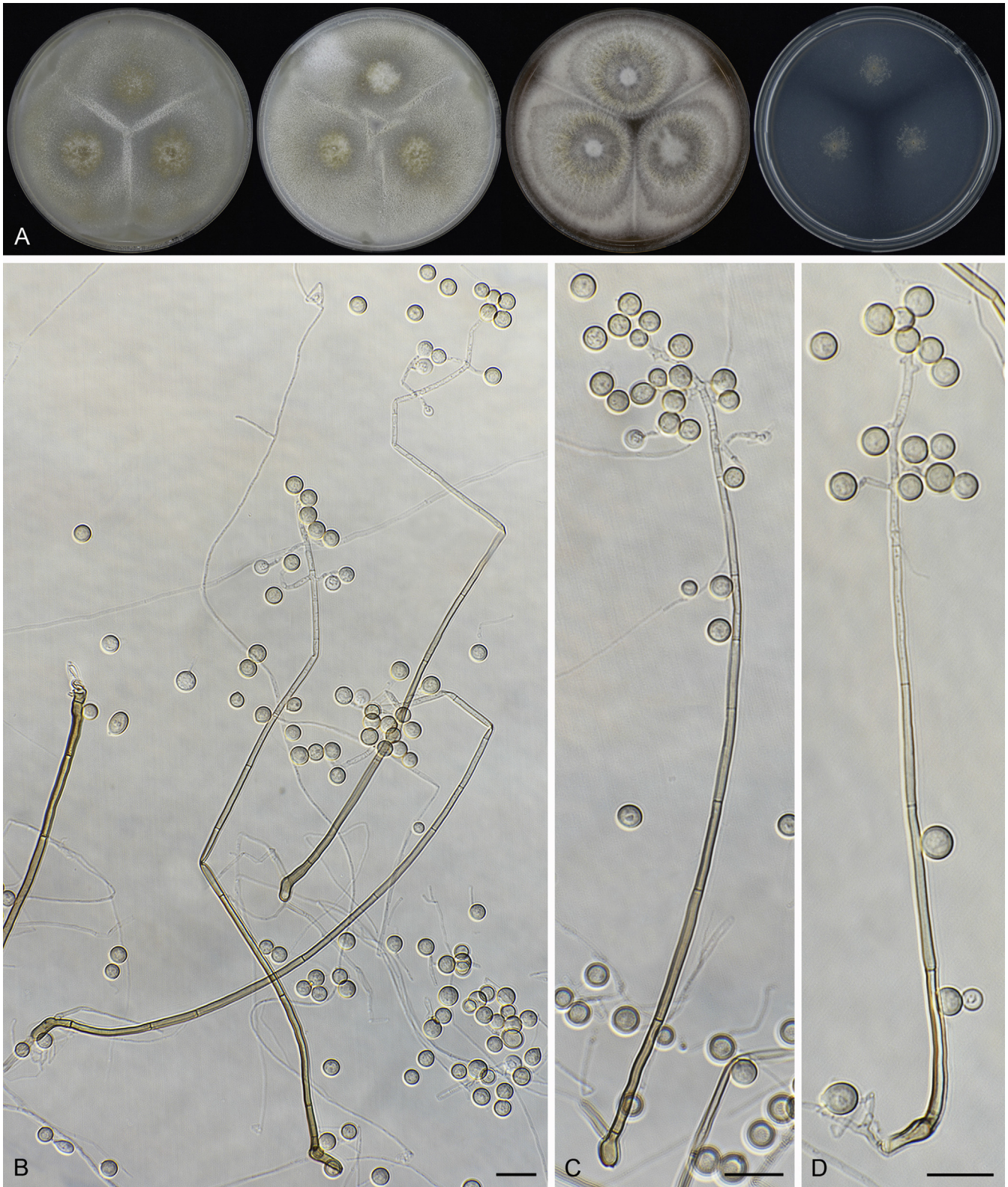


Fig. 35. *Staphylotrichum acaciicola* (CBS 281.65, ex-type culture). **A.** Colonies from left to right on OA, CMA, MEA and PCA after 3 wk incubation. **B–D.** Conidiophores with macronematous conidia and hyphae with micronematous conidia. Scale bars = 20 μm .

dark brown and thick-walled in the lower part, tapering and fading towards the tips, 210–500(–800) μm long, 3–5(–6.5) μm wide near the base, apically branched. *Conidiogenous cells* hyaline, denticle-like to cylindrical, 2–13.5(–15) \times 1–3 μm . *Conidia* pale olivaceous, smooth, single-celled, globose, subglobose or obovoid, (6.5–)7.5–11.5(–14.5) \times (7–)7.5–10(–12.5) μm . *Sexual morph* not observed.

Culture characteristics: Variation in culture characteristics were observed among isolates (Fig. 43). Colonies on OA 50–56 mm diam after 7 d at 25 $^{\circ}\text{C}$; edge entire; obverse pale olivaceous grey (CBS 281.65) or amber with sparse to dense aerial hyphae (CBS 554.89); reverse uncoloured to buff (CBS 281.65), or ochreous (CBS 554.89). Colonies on CMA 46–52 mm diam after 7 d at 25 $^{\circ}\text{C}$; edge entire; obverse white to pale olivaceous grey (CBS

281.65) or amber with white to salmon aerial hyphae (CBS 554.89); reverse buff (CBS 281.65) or pale luteous (CBS 554.89). Colonies on MEA 49–55 mm diam after 7 d at 25 °C; edge entire; obverse floccose and white to buff white (CBS 281.65) or pale luteous because of aerial hyphae (CBS 554.89); reverse fulvous to sepia (CBS 281.65) or sienna (CBS 554.89). Colonies on PCA 48–54 mm diam after 7 d at 25 °C; edge entire; obverse transparent, buff and loosely floccose because of the formation of conidiophores; aerial hyphae absent; reverse uncoloured.

Material examined: **Brazil**, isolated from rainforest soil, unknown date, L. Pfening, culture CBS 554.89. **South Africa**, Potchefstroom, isolated from leaf litter of *Acacia karroo*, unknown date, M.C. Papendorf, (**holotype** CBS H-23490, culture ex-type CBS 281.65). **USA**, Kansas, isolated from soil, unknown date, M. Christensen, culture CBS 127289.

Notes: *Staphylotrichum acaciicola* is phylogenetically closely related to *S. coccosporum*. This species can be distinguished by the production of numerous conidia from micronematous conidiogenous cells on hyphae. In contrast, *S. coccosporum* predominantly produces macronematous conidiogenous cells on conidiophores. In addition, *S. coccosporum* produces relatively broad conidiophores in comparison to those of *S. acaciicola* (4.5–9 µm vs 3–6.5 µm near the base). The colony morphology of *S. acaciicola* varies among different isolates.

Staphylotrichum boninense Nonaka, Miyazaki & Masuma, *Mycoscience* 53: 315. 2012. MycoBank MB561191. **Fig. 36.**

Micromorphology: *Somatic hyphae* hyaline or nearly so, producing macronematous conidia mixed with micronematous ones. *Macronematous conidiophores* arising from a thick-walled L-shaped or cylindrical, brown to dark brown foot cell, brown to dark brown and thick-walled in the lower part, tapering and fading towards the tips, 410–600(–800) µm long, 3.5–5(–7) µm wide near the base, apically branched. *Conidiogenous cells* hyaline, denticle-like to cylindrical, 2–13.5(–16) × 1.5–3 µm, sometimes intercalary in the hyphae. *Conidia* pale olivaceous, single-celled, smooth, globose, subglobose or obovoid, (5–)7–12(–14) µm diam. *Sexual morph* not observed.

Culture characteristics: Colonies on OA 36–42 mm diam after 7 d at 25 °C; edge entire; obverse vinaceous buff to fawn with sparse aerial hyphae; reverse buff. Colonies on CMA 36–42 mm diam after 7 d at 25 °C; edge entire; obverse fawn with greyish white to buff floccose aerial hyphae; reverse uncoloured to buff. Colonies on MEA 41–47 mm diam after 7 d at 25 °C; edge entire; obverse ochreous and floccose because of the aerial hyphae, with an irregular mouse grey ring; reverse rust to bay caused by soluble pigments diffusing into the medium. Colonies on PCA 36–42 mm diam after 7 d at 25 °C; edge entire; obverse pale mouse grey, without aerial hyphae; reverse pale olivaceous grey to smoke grey.

Material examined: **Brazil**, Pista Cláudio Coutinho near Pão de Açúcar, isolated from twig, 12 Oct. 2002, R.F. Castaneda-Ruiz, culture CBS 112059; Pista Cláudio Coutinho near Pão de Açúcar, isolated from leaf litter, 12 Oct. 2005, A. Stchigel & J. Guarro, CBS 112543.

Notes: The two examined *S. boninense* strains share identical ITS and LSU sequences with the type of *S. boninense*. Their morphology also fits the original description of *S. boninense*, and they are therefore identified here as that species. *Staphylotrichum boninense* is morphologically similar to *S. acaciicola*. On OA and CMA, micronematously-produced conidia from hyphae are often predominant. Phylogenetically, *S. boninense* and *S. brevistipitatum* are more closely related to the sexual species

(*S. longicollum*, *S. microascosporum*, *S. tortipilum*) than to *S. acaciicola* and *S. coccosporum* (**Fig. 1**).

Staphylotrichum brevistipitatum X. Wei Wang & Houbraken, **sp. nov.** MycoBank MB824458. **Fig. 37.**

Etymology: The epithet refers to the short conidiophores of this fungus.

Micromorphology: *Somatic hyphae* hyaline or nearly so, producing macronematous conidia mixed with micronematous ones. *Macronematous conidiophores* arising from a thick-walled T-shaped to oblong and brown to dark brown foot cell, brown to dark brown and thick-walled in the lower part, tapering and fading towards the tips, 70–230 µm long, 2.5–5 µm wide near the base, apically branched. *Conidiogenous cells* hyaline, denticle-like to cylindrical, 3–11.5(–19) × 1.5–3 µm. *Conidia* olivaceous, single-celled, smooth to slightly verrucose, globose, subglobose, obovoid or pyriform, (8.5–)9.5–12(–14.5) × (7.5–)9–11.5(–13.5) µm. *Sexual morph* not observed.

Culture characteristics: Variations of culture characteristics were observed among isolates. Colonies on OA 42–48 mm diam after 7 d at 25 °C; edge entire; obverse grey olivaceous and floccose because of aerial hyphae mixed with conidiophores (CBS 408.67) or greenish black without aerial hyphae (CBS 294.55); reverse greenish black. Colonies on CMA 42–48 mm diam after 7 d at 25 °C; edge entire; obverse floccose, greyish white to greyish yellow-green, grey olivaceous at the edge (CBS 408.67), or dark grey olivaceous without aerial hyphae (CBS 294.55); reverse olivaceous black. Colonies on MEA 49–55 mm diam after 7 d at 25 °C; edge entire; obverse floccose and smoke grey to greyish sepia (CBS 408.67), or dark mouse grey with grey mouse aerial hyphae (CBS 294.55); reverse fuscous (CBS 408.67) or chestnut to sepia (CBS 294.55). Colonies on PCA 40–46 mm diam after 7 d at 25 °C; edge entire; obverse transparent, greyish sepia without aerial hyphae; reverse smoke grey or greyish sepia.

Material examined: **South Africa**, Zoeloeland, Empangeni, isolated from leaf litter of *Eucalyptus*, unknown date, A. Eicker (**holotype** CBS H-18521, culture ex-type CBS 408.67). **Zaire**, isolated from soil, unknown date, J.A. Meyer, culture CBS 294.55.

Notes: *Staphylotrichum brevistipitatum* is phylogenetically closely related to *S. boninense*, but can be distinguished by the production of shorter seta-like conidiophores (70–230 µm vs 410–780 µm).

Staphylotrichum coccosporum J.A. Mey. & Nicot. *Bull. Soc. Mycol. France* 72: 323. 1957. MycoBank MB306413. **Fig. 38.**

Micromorphology: *Asexual morph* predominantly producing conidia macronematously from seta-like conidiophores on OA and CMA. *Somatic hyphae* hyaline or nearly so. *Macronematous conidiophores* arising from a thick-walled L-shaped or T-shaped brown to dark brown foot cell, brown to dark brown and thick-walled in the lower part, tapering and fading towards the tips, 250–780 µm long, (3.5–)4.5–9 µm wide near the base, apically branched. *Conidiogenous cells* hyaline, denticle-like to cylindrical, 2–13 × 1.5–3 µm. *Conidia* pale olivaceous, single-celled, globose, subglobose, occasionally obovoid or pyriform, (7.5–)8.5–11.5(–13.5) × (7.5–)8–10(–11) µm. *Sexual morph* not observed.

Culture characteristics: Colonies on OA 39–45 mm diam after 7 d at 25 °C; edge entire; obverse smoke grey to greyish sepia,

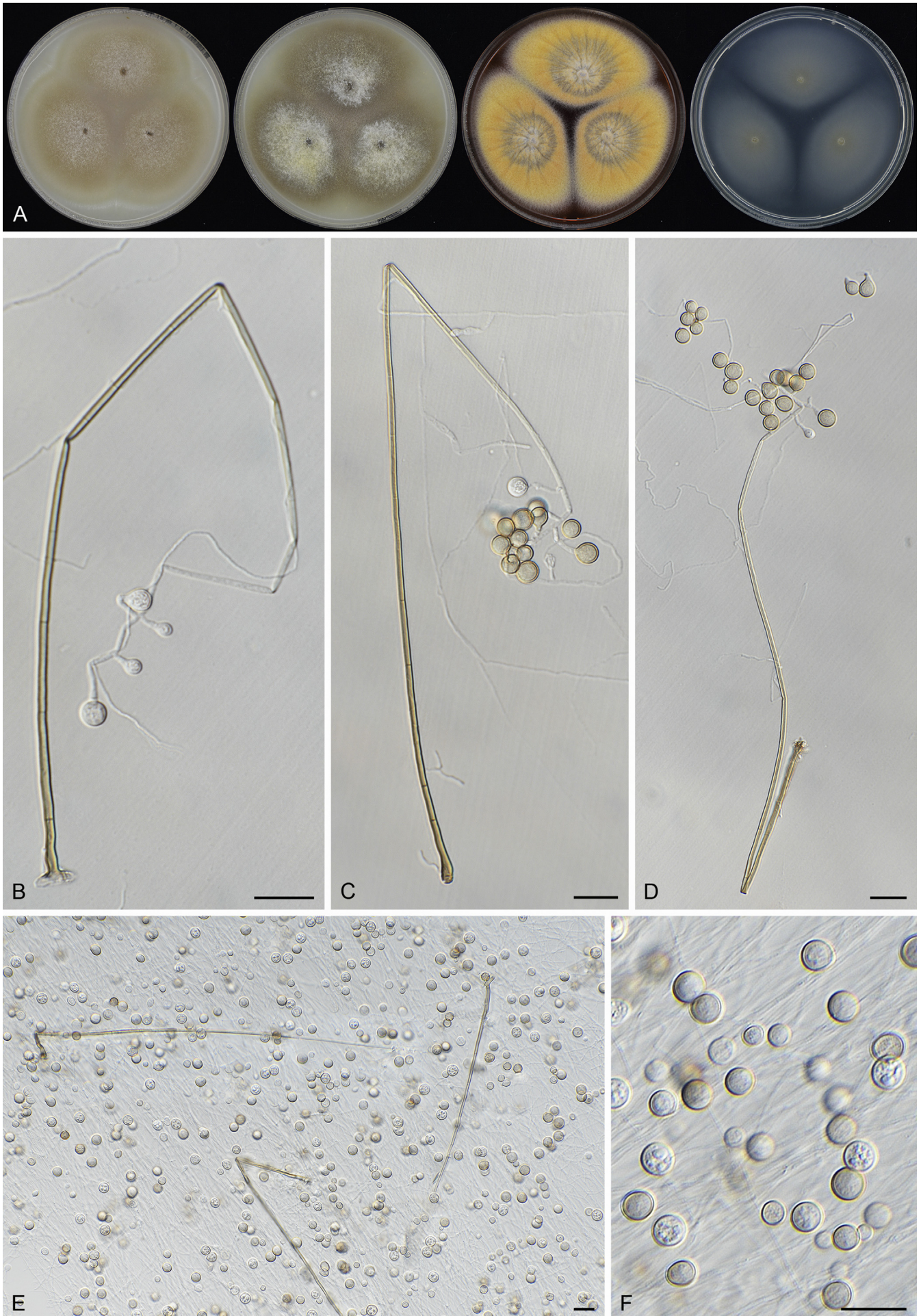


Fig. 36. *Staphylotrichum boninense* (CBS 112059). **A.** Colonies from left to right on OA, CMA, MEA and PCA after 1 wk incubation. **B–E.** Micronematous conidia arising from hyphae and a few conidiophores with macronematous conidia. **F.** Micronematous conidia arising from hyphae. Scale bars = 20 μm.

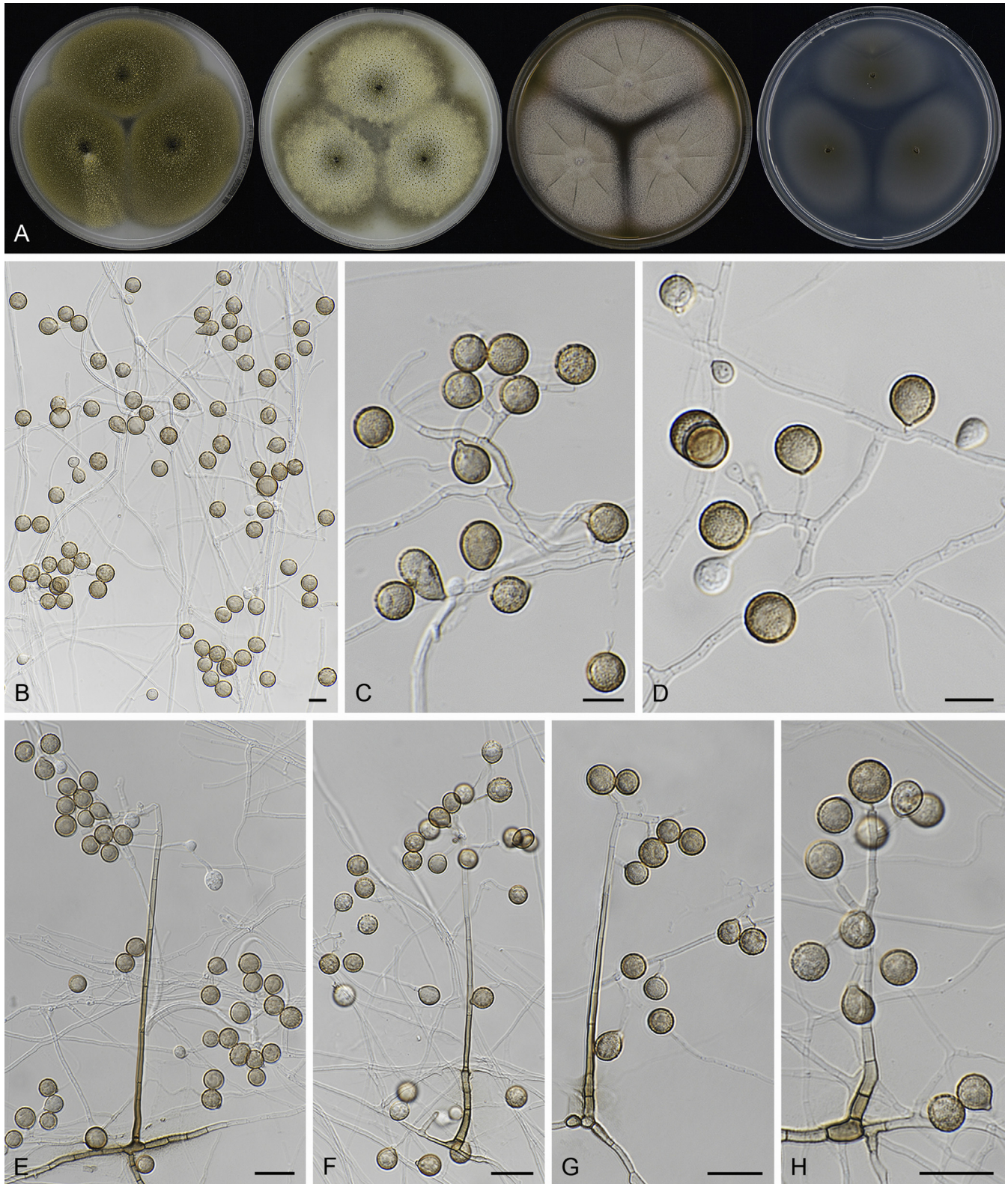


Fig. 37. *Staphylotrichum brevistipitatum* (CBS 408.67, ex-type culture). **A.** Colonies from left to right on OA, CMA, MEA and PCA after 1 wk incubation. **B–D.** hyphae and micronematous conidia. **E–H.** Conidiophores with macronematous conidia and hyphae with micronematous conidia. Scale bars: B–D = 10 μm ; E–H = 20 μm .

floccose because of the formation of numerous conidiophores; reverse uncoloured, buff or umber when old. Colonies on CMA similar to those on OA, 35–41 mm diam after 7 d at 25 °C. Colonies on MEA 43–49 mm diam after 7 d at 25 °C; edge entire; obverse buff and floccose; reverse ochreous to apricot. Colonies on PCA 42–48 mm diam after 7 d at 25 °C; edge entire; obverse transparent, without aerial hyphae; reverse uncoloured.

Material examined: Zaire, Yangambi, isolated from soil, unknown date, J.A. Meyer, culture ex-type CBS 364.58.

Notes: Although *S. coccosporum* predominantly produces conidia macronematously from conidiophores, especially on OA and CMA, the micronematously-produced conidia on hyphae are easy to observe in slides cultures prepared using the inclined coverslip method. Micronematously-produced conidia are common in both sexual and asexual species in *Staphylotrichum*.

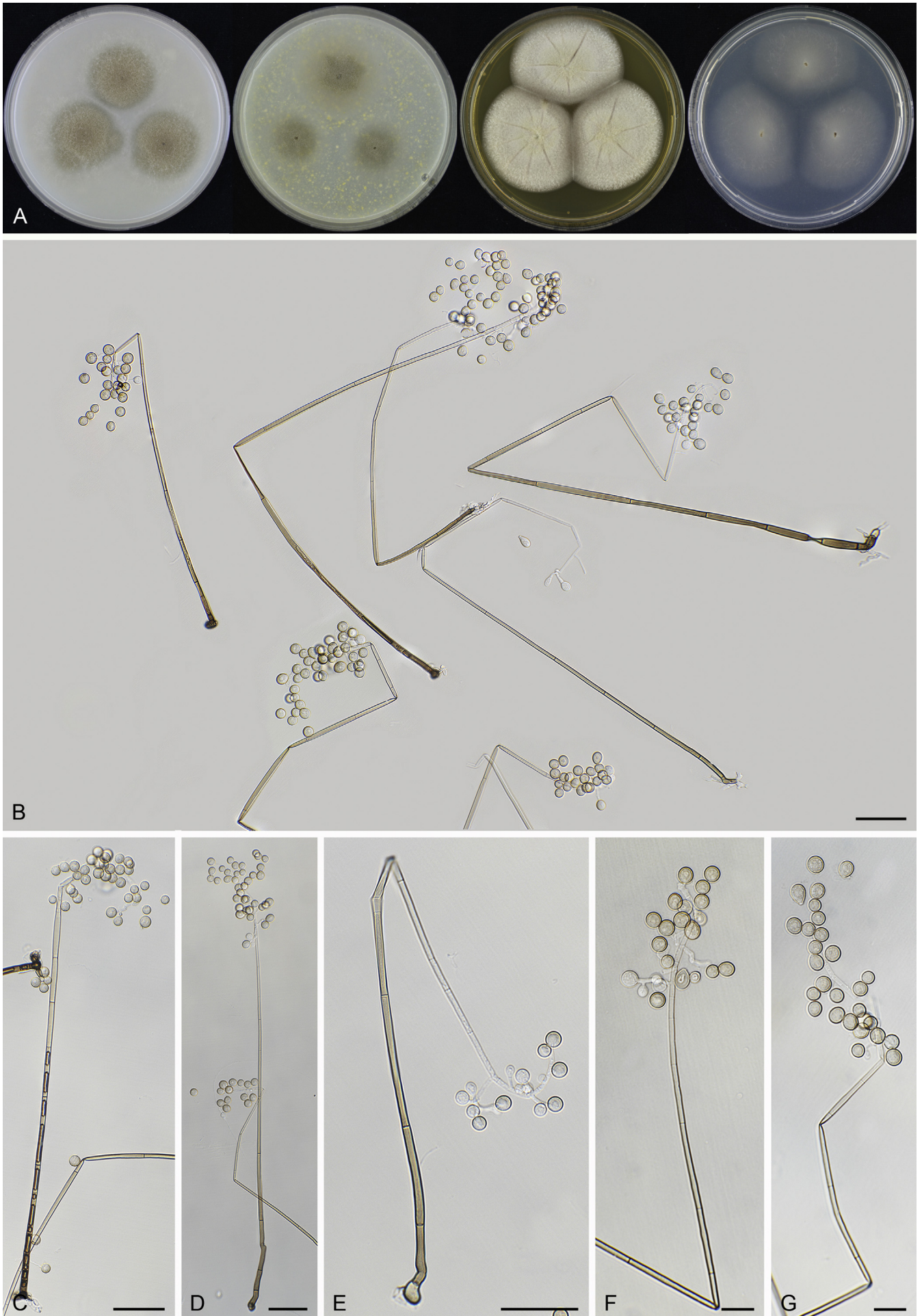


Fig. 38. *Staphylotrichum coccosporum* (CBS 364.58, ex-type culture). **A.** Colonies from left to right on OA, CMA, MEA and PCA after 1 wk incubation. **B–G.** Macronematous conidia. Scale bars: B–G = 20 μ m.

Staphylotrichum longicolleum (Krzemien. & Badura) X. Wei Wang & Houbraken, **comb. nov.** MycoBank MB824459. Figs 39, 40.

Basionym: *Chaetomium longicolleum* Krzemien. & Badura, Acta Soc. Bot. Pol. 23: 748. 1954.

Synonyms: *Chaetocerotostoma longirostre* Farrow, Mycologia 47: 418. 1955.

Chaetomium longirostre (Farrow) L.M. Ames, Monograph Chaetomiaceae: 29. 1963.

Chaetocerotostoma longicolleum (Krzem. & Badura) Badura, Allionia 9: 181. 1964.

Farrowia longicolleum (Krzemien. & Badura) D. Hawksw., Persoonia 8: 174. 1975.

Micromorphology: *Ascomata* superficial, often covered by aerial hyphae, ostiolate, leaden black in reflected light, elongate obpyriform, obclavate or ampulliform below, apically attenuated to a cylindrical, thread-like neck which is composed of fused basal part of the terminal hairs, 55–125 µm diam at the widest part, (300–)550–1300 µm high till the neck excluding the top parts of terminal hairs where the hairs separate with each other, of which, the neck part usually (110–)200–1100 µm high, 25–45 µm wide. *Ascomatal wall* brown, composed of angular cells or elongated to cylindrical cells at the neck part in surface view. *Terminal hairs* seta-like or whip-like, fused at the lower part to form a channel through which a column of ascospores emerge from the ascomata, smooth, brown, septate, 2.5–6 µm diam near the separating base, tapering and fading towards the tips. *Lateral hairs* very sparse, seta-like, tapering and fading towards the tips. *Asci* clavate to fusiform, with spore-bearing part 22.5–34 × 13–20 µm and stalks 6–16 µm long, with 8 irregularly-arranged ascospores, evanescent. *Ascospores* olivaceous brown when mature, broad limoniform to nearly globose, biapiculate, bilaterally flattened, 9–11 (–11.5) × (8–)8.5–10.5 (–11) × (6–)6.5–7.5 µm, with an apical germ pore. *Conidiogenous cell* arising from the hyphae, denticle-like to cylindrical, hyaline, sometimes intercalary. *Conidia* globose or subglobose, sometimes broad obovoid or pyriform, smooth, hyaline, subhyaline to pale olivaceous, lateral or terminal on the hyphae or short branches of hyphae, occasionally on macronematous conidiophores, solitary, sometimes two in chain or a few in cluster, (7–)9–13.5 (–14.5) µm diam.

Culture characteristics: Colonies on OA 44–53 mm diam after 7 d at 25 °C; edge entire; aerial mycelium white, yellow, luteous or amber; soluble pigment saffron, salmon to vinaceous or brick; reverse colourless, or saffron, salmon, cinnamon. Colonies on CMA similar to those on OA, 40–50 mm diam after 7 d at 25 °C; but aerial mycelium relatively thick, producing more ascomata. Colonies on MEA 46–52 mm diam after 7 d at 25 °C; edge entire; non-sporulated, aerial mycelium white to saffron; texture floccose; soluble pigment absent, or vinaceous to brick along the edge; reverse saffron, apricot to violaceous black. Colonies on PCA 43–55 mm diam after 7 d at 25 °C; edge entire; aerial mycelium sparse, white to honey or absent; soluble pigment rosy buff to rosy vinaceous or absent; reverse uncoloured or pale vinaceous.

Material examined: **Madagascar**, isolated from soil under *Theobroma cacao* and *Piper nigrum*, unknown date, G. Doguet, culture CBS 119.57. **Jamaica**, Ocho Rios, isolated from woodland soil, unknown date, A. Carter, culture CBS 562.80 = TRTC 45836. **Panama**, Barro Colorado Island, isolated from soil, 1952,

W.M. Farrow, isotype of *Chaetocerotostoma longirostre*, New York Botanical Garden Specimen ID01050425. **Venezuela**, isolated from leaf litter, Nov. 1997, R. F. Castañeda, culture CBS 100950 = INIFAT C98/35.

Notes: *Chaetomium longirostre* was separated from *C. longicolleum* by its much longer ascomatal neck (<800 µm vs >1000 µm) and a narrower spore exit channel (Ames 1963). The holotype of *Ch. longicolleum* seems to be lost. Hawksworth (1975) designated a slide from Krzemieniewska & Badura (BPI–A 121) as lectotype. This slide is unavailable for study. Hawksworth (1975) observed that the ascomatal neck varied considerably, even within a single isolate. Our examination confirmed Hawksworth's observation that the ascomatal necks can be (110–)200–1100 µm high and 20–45 µm wide. The size of ascospores and the width of terminal hairs near the base are diagnostic characters in this species. The holotype was originally collected in Poland. Epitypification of the species is deferred until a culture is reisolated from the type locality.

Staphylotrichum microascosporum X. Wei Wang & Houbraken, **sp. nov.** MycoBank MB824460. Fig. 41.

Etymology: The epithet refers to the small ascospores of this species.

Micromorphology: *Ascomata* superficial, ostiolate, often covered by aerial hyphae, leaden black in reflected light, elongate obpyriform, obclavate or ampulliform below, apically attenuated to a cylindrical, thread-like neck which is composed of fused basal part of the terminal hairs, 65–110 µm diam at the widest part, (340–)430–760 µm high till the neck excluding the top parts of terminal hairs where the hairs separate with each other, of which, the neck part usually (170–)230–600 µm high, 18–28 µm wide. *Ascomatal wall* brown, composed of angular cells or elongated to cylindrical cells at the neck part in surface view. *Terminal hairs* seta-like or whip-like, fused at the lower part to form a channel through which a column of ascospores emerge from the ascomata, smooth, brown, septate, (3–)4.5–6.5 µm diam near the separated base, tapering and fading towards the tips. *Lateral hairs* very sparse, seta-like, tapering and fading towards the tips. *Asci* clavate to fusiform, with spore-bearing part 22–29 × 13–18.5 µm and stalks 6–18 µm long, with 8 irregularly-arranged ascospores, evanescent. *Ascospores* olivaceous brown when mature, broad limoniform to nearly globose, biapiculate, bilaterally flattened, 8–9.5 (–10) × 7.5–9 × 6–7 µm, with an apical germ pore. *Conidiogenous cell* arising from the hyphae, denticle-like to cylindrical, hyaline, sometimes intercalary. *Conidia* globose, subglobose, sometimes broad obovoid or pyriform, hyaline, subhyaline to pale olivaceous, lateral or terminal on the hyphae or short branches of hyphae, solitary, 8–13.5 µm diam.

Culture characteristics: Colonies on OA 31–37 mm diam after 7 d at 25 °C; edge entire; aerial mycelium sparse, pale luteous or white; soluble pigment ochreous; reverse ochreous to fulvous. Colonies on CMA similar to those on OA, 29–35 mm diam after 7 d at 25 °C. Colonies on MEA 28–34 mm diam after 7 d at 25 °C; edge crenate; non-sporulated; aerial mycelium ochreous, sometimes white or salmon; texture floccose; reverse apricot caused by soluble pigment. Colonies on PCA 26–32 mm diam after 7 d at 25 °C; edge entire; aerial mycelium sparse, ochreous; soluble pigment absent; reverse uncoloured.

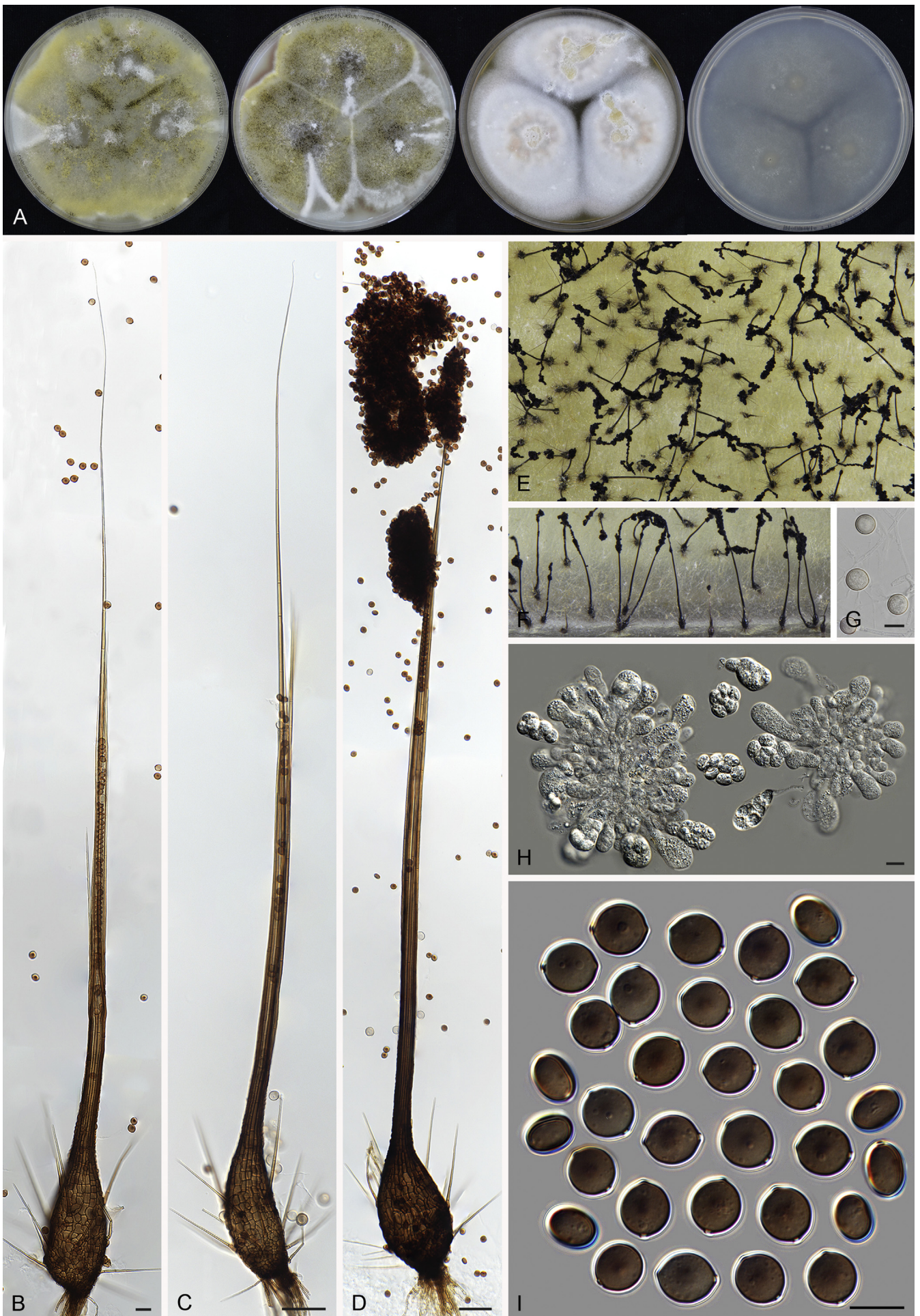


Fig. 39. *Staphylotrichum longicollum* (CBS 119.57). **A.** Colonies from left to right on OA, CMA, MEA and PCA after 5 wk incubation. **B–D.** Ascomata mounted in lactic acid. **E.** Part of the colony on OA showing mature ascomata from top view. **F.** Mature ascomata on OA, side view. **G.** Micronematous conidia arising from short sides of hyphae (denticales). **H.** Asci. **I.** Ascospores. Scale bars: B = 20 μ m; C–D = 50 μ m; G–I = 10 μ m.

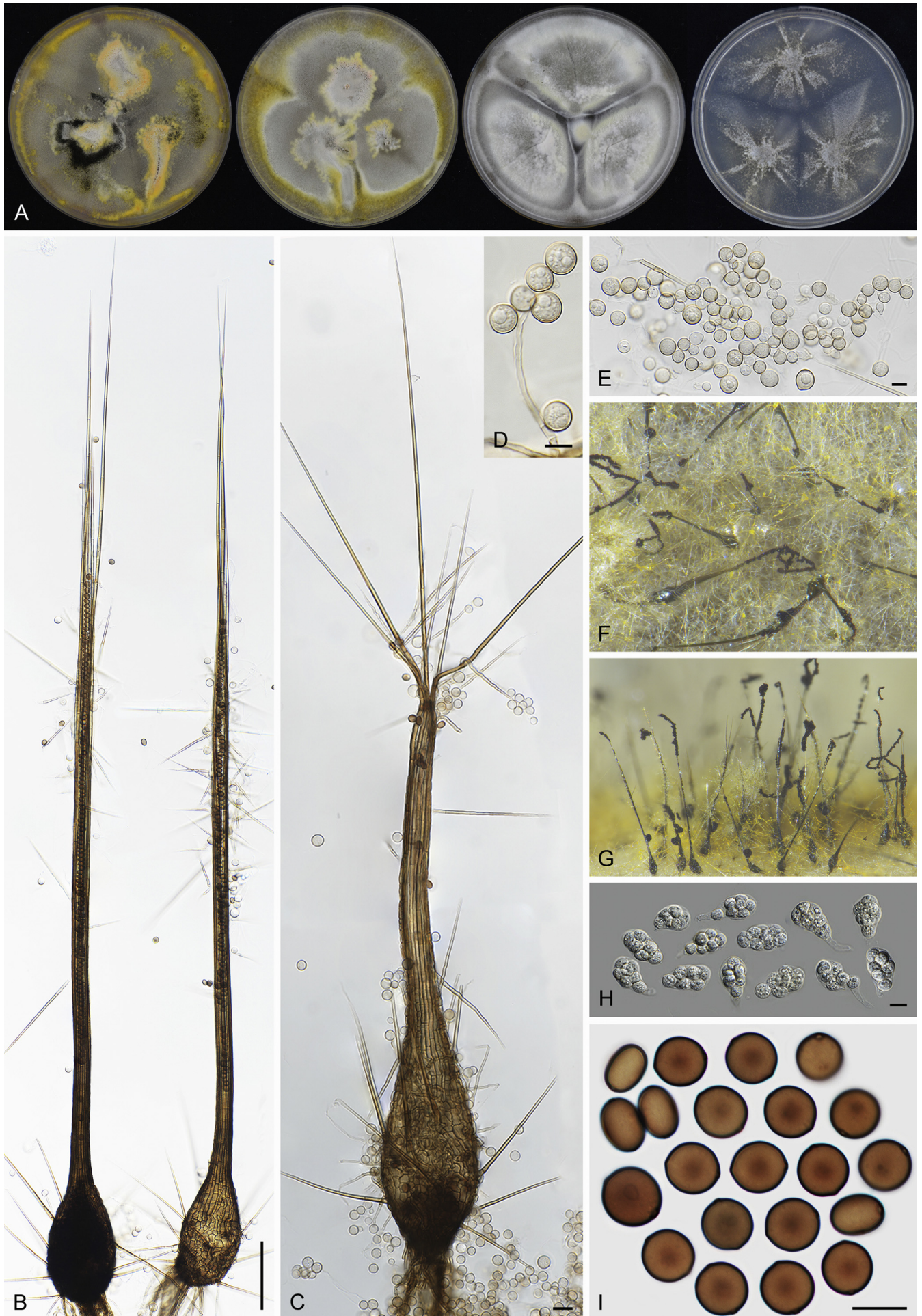


Fig. 40. *Staphylotrichum longicoleum* (CBS 100950). **A.** Colonies from left to right on OA, CMA, MEA and PCA after 5 wk incubation. **B–C.** Ascomata and macronematous conidiophores attached to neck and terminal hairs of ascomata mounted in lactic acid. **D.** A macronematous conidiophore and conidia. **E.** Micronematous conidia. **F.** Part of the colony on OA showing mature ascomata from top view. **G.** Mature ascomata on OA, side view. **H.** Asci. **I.** Ascospores. Scale bars: B = 100 μ m; C = 20 μ m; D, E, H, I = 10 μ m.

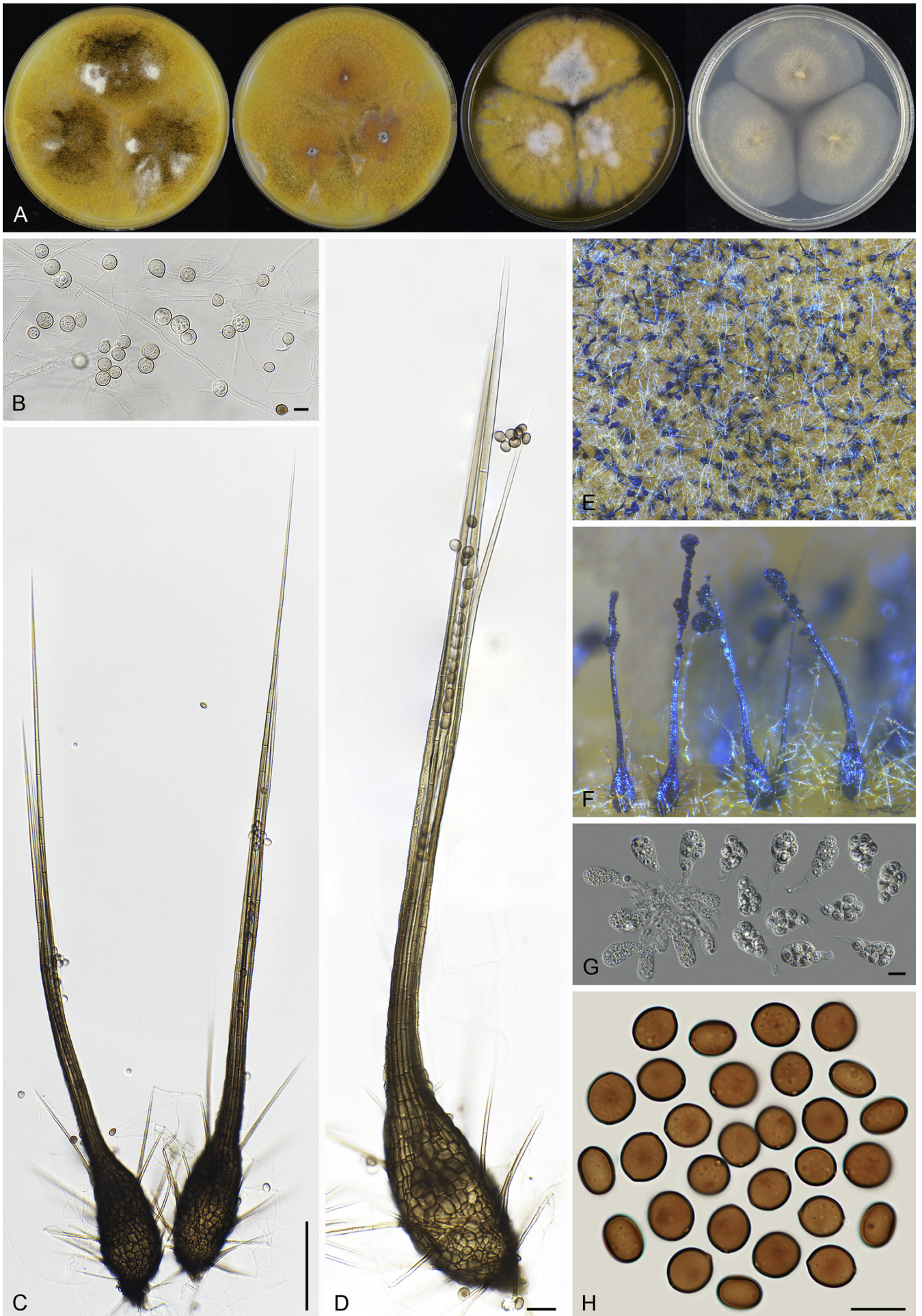


Fig. 41. *Staphylotrichum microascosporum* (CBS 184.79, ex-type culture). **A.** Colonies from left to right on OA, CMA, MEA and PCA after 4 wk incubation. **B.** Micronematous conidia. **C–D.** Ascomata mounted in lactic acid. **E.** Part of the colony. **F.** Mature ascomata on OA, side view. **G.** Asci. **H.** Ascospores. Scale bars: C = 100 μ m; D = 20 μ m; B, G–H = 10 μ m.

Material examined: Sudan, White Nile Island, isolated from soil from *Mangifera* orchard, unknown date, B.P.R. Vittal (**holotype** CBS H-12643, culture ex-type CBS 184.79).

Notes: *Staphylotrichum microascosporum* produces smaller ascospores than the other known *Staphylotrichum* species (8–9.5 × 7.5–9 × 6–7 µm vs 9–11 × 8.5–10.5 × 6.5–7.5 µm).

Staphylotrichum tortipilum X. Wei Wang & Houbraken, **sp. nov.** MycoBank MB824461. Fig. 42.

Etymology: The epithet refers to the slightly twisted terminal hairs of this species.

Micromorphology: *Ascomata* superficial, ostiolate, leaden black in reflected light, elongate obpyriform, obclavate or ampulliform below, apically attenuated to a cylindrical, thread-like neck which is composed of fused basal part of the terminal hairs, (60–) 85–140 µm diam at the widest part, 530–1330 µm high till the neck excluding the top parts of terminal hairs where the hairs separate with each other, of which, the neck part usually 340–1050 µm high, 22–36 µm wide. *Ascomatal wall* brown, composed of angular cells or elongated to cylindrical cells at the neck part in surface view. *Terminal hairs* seta-like or whip-like, fused at the lower part to form a channel through which a column of ascospores emerge from the *ascomata*, smooth, brown, septate, 4.5–8 µm diam near the separating base, often twisted in the lower part, tapering and fading towards the tips. *Lateral hairs* sparse, seta-like, tapering and fading towards the tips. *Asci* clavate to fusiform, with spore-bearing part 28–35 × 14.5–18.5 µm and stalks 6.5–14.5 µm long, with 8 irregularly-arranged ascospores, evanescent. *Ascospores* olivaceous brown when mature, broad limoniform to nearly globose, biapiculate, bilaterally flattened, 10–10.5 (–11) × (8.5–)9–10(–10.5) × 6.5–7.5(–8) µm, with an apical germ pore. Conidiogenous cell arising from the hyphae, denticle-like to cylindrical, hyaline, occasionally intercalary. *Conidia* globose, subglobose, sometimes broad obovoid or pyriform, hyaline, subhyaline to pale olivaceous, lateral or terminal on the hyphae or short branches of hyphae, solitary, (8.5–)10.5–14 µm diam, up to 16.5 µm long when pyriform.

Culture characteristics: Colonies on OA 37–43 mm diam after 7 d at 25 °C; edge entire; aerial mycelium sparse, white to pale luteous or salmon; soluble pigment pale luteous to ochreous; reverse fulvous. Colonies on CMA similar to those on OA, 35–41 mm diam after 7 d at 25 °C; reverse fulvous, orange or apricot. Colonies on MEA 36–43 mm diam after 7 d at 25 °C; edge crenate; non-sporulated; aerial mycelium thick, white to salmon; texture floccose; reverse rust to chestnut caused by soluble pigment. Colonies on PCA 31–37 mm diam after 7 d at 25 °C; edge entire; aerial mycelium rare; soluble pigment absent; reverse uncoloured.

Material examined: USA, North Carolina, isolated from dung of *Pine vole*, 20 Jul. 1976, G.L. Benny (**holotype** CBS H-12642, culture ex-type CBS 103.79).

Notes: *Staphylotrichum tortipilum* can be distinguished from *S. longicolleum* and *S. microascosporum* by larger *ascomata* (85–140 µm vs 55–125 µm diam at the widest part) and broader terminal hairs (4.5–8 µm vs 2.5–6.5 µm diam near the separated base), which are often twisted in the lower part.

Trichocladium Harz. Bull. Soc. Imp. Naturalistes. Moscou 44: 125. 1871. MycoBank MB10278.

Lectotype species: *Trichocladium asperum* Harz, fide Clements & Shear (1931)

Micromorphology: *Asexual morphs* diverse, with conidia from hyaline to pigmented on differentiated conidiophores or from conidiogenous cells, sometimes with acromonium-like conidia, or with hyaline micro-sclerotia, or absent. *Ascomata* superficial or immersed in the thick mycelium, ostiolate to nonostiolate. *Asci* typically cylindrical with 8 (4) uniseriate ascospores, sometimes clavate to fusiform with 8 biseriate ascospores, evanescent. *Ascospores* typically broadly ovate, bilaterally flattened, sometimes ellipsoidal and non-flattened, with an apical germ pore.

Notes: In a synopsis of the hyphomycete concept of *Trichocladium* (Goh & Hyde 1999), 18 species were accepted on the basis of morphological characters. Although the type specimens of only three species were available for our study, two (*T. ismailiense*, *T. pyriforme*) proved to be outside the *Chaetomiaceae* (data not shown).

Trichocladium is morphologically diverse as phylogenetically delimited here (Figs 1, 2), including four closely related subclades, each encompassing a high diversity in morphology. Subclade 1 includes the lectotype species *T. asperum*, which produces pigmented, solitary, monoblastic (1–) 2 (– multicelled) conidia on somewhat differentiated conidiophores, and conidial secession is easily observed in old cultures. Subclades 2 and 3 only contain sexual species that produce ostiolate *ascomata*, such as *Trichocladium crispatum* (= *Chaetomium crispatum*), *T. acropullum* (= *Chaetomium acropullum*) or non-ostiolate *ascomata*, such as *T. antarcticum* (= *Thielavia antarctica*) and *T. arxii* (= *Chaetomidium arxii*). Species in subclade 4 produce hyaline asexual structures (conidia), like those produced by *T. beniowskiae* (= *Beniowskia macrospora*), or only poorly differentiated structures, such as those of *T. amorphum*. Sexual stages are present (e.g. *T. seminis-citrullii*) or absent in subclade 4.

In the dual nomenclature era, *Trichocladium* was used for strictly asexually reproducing hyphomycetes. Here, six new combinations are proposed based on sexually reproducing species (previously classified in *Chaetomidium*, *Chaetomium*, *Thielavia*). Five asexually reproducing species were originally described in other genera (*Beniowskia*, *Gilmaniella*, *Humicola*, *Monodictys*) and those species lack typical *trichocladium*-like conidiophores and conidia. It is unlikely that these sexually reproducing species and the species described in the genera mentioned above would have earlier described names in *Trichocladium* itself. The new *Trichocladium* species described here produce thick-walled intercalary cells and microsclerotia-like structures. These structures are also atypical for *Trichocladium*.

Trichocladium acropullum (X. Wei Wang) X. Wei Wang & Houbraken, **comb. nov.** MycoBank MB824462. Fig. 44.

Basionym: *Chaetomium acropullum* X. Wei Wang, Nova Hedwigia 80: 414. 2005.

Micromorphology: *Ascomata* superficial, sometimes covered by sparse aerial hyphae, nearly spherical to oblate, ostiolate, 170–260 µm high, 150–280 µm diam. *Ascomatal wall* around the apical ostiolar pore composed of angular and thick-walled dark brown cells, in the lower part dextrinoid, translucent and pale yellowish brown, cellular structure indistinct at first, then becoming yellowish brown to brown, with angular or irregular cells (*textura angularis*) when mature. *Terminal hairs* arising around the ostiole, regularly spirally coiled with flexuous lower part, punctulate or verrucose, 3–4.5 µm diam near the base. *Lateral hairs* seta-like or flexuous, tapering and fading towards the tips. *Asci* cylindrical, with



Fig. 42. *Staphylotrichum tortipilum* (CBS 103.79, ex-type culture). **A.** Colonies from left to right on OA, CMA, MEA and PCA after 4 wk incubation. **B.** Ascomata mounted in lactic acid. **C.** Terminal ascomatal hairs. **D.** Part of the colony on OA showing mature ascomata in top view. **E.** Mature ascomata on OA, side view. **F.** Micronematous conidia. **G.** Asci. **H.** Ascospores. Scale bars: B = 100 μ m; C = 20 μ m; F–H = 10 μ m.

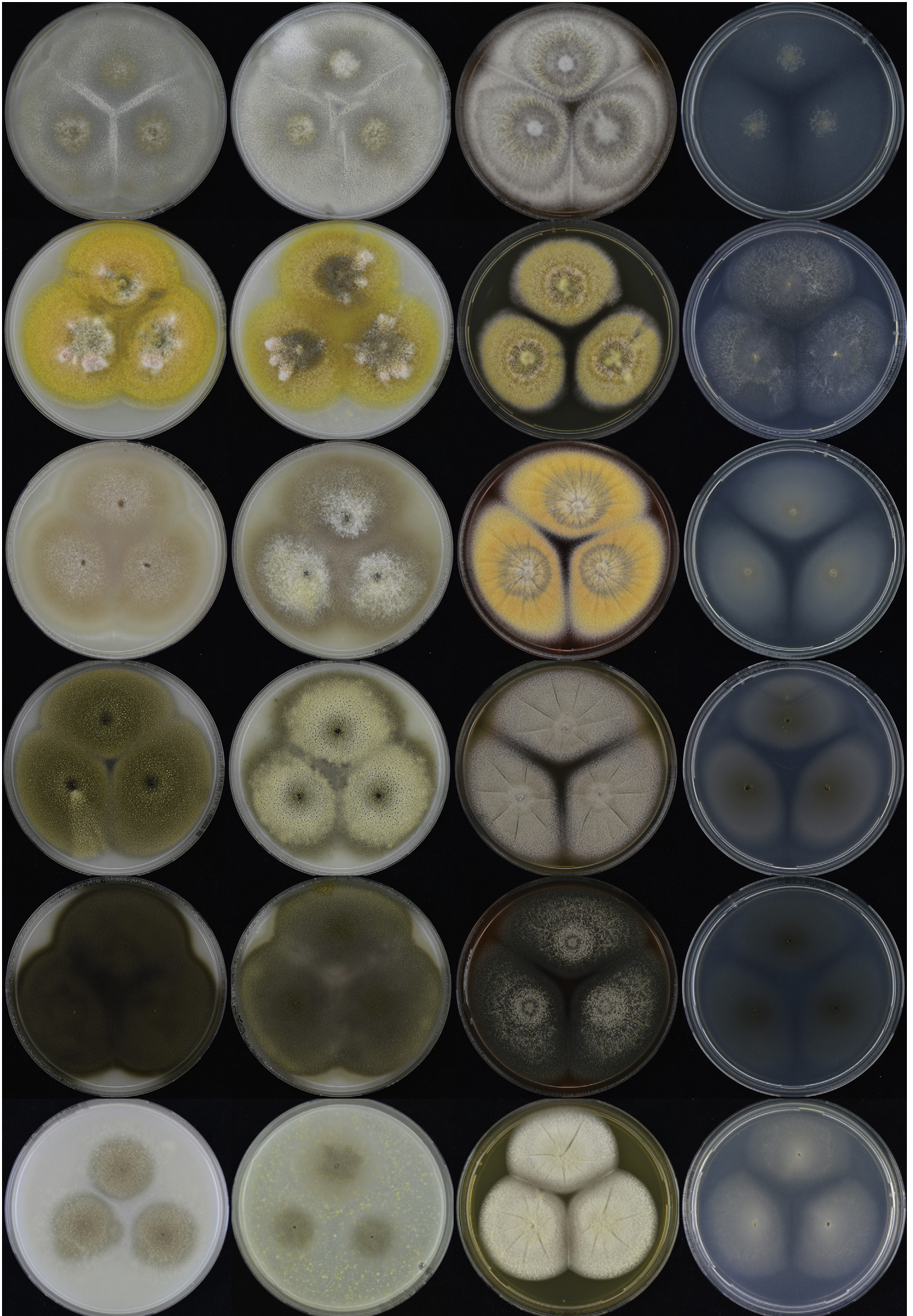


Fig. 43. Diversity of colony morphology in *Staphylotrichum*. From left to right on OA, CMA, MEA and PCA. From top to bottom CBS 281.65 (*S. acaciicola*), CBS 554.89 (*S. acaciicola*); CBS 112543 (*S. boninense*); CBS 408.67 (*S. brevistipitatum*), CBS 294.55 (*S. brevistipitatum*); CBS 364.58 (*S. coccosporum*).

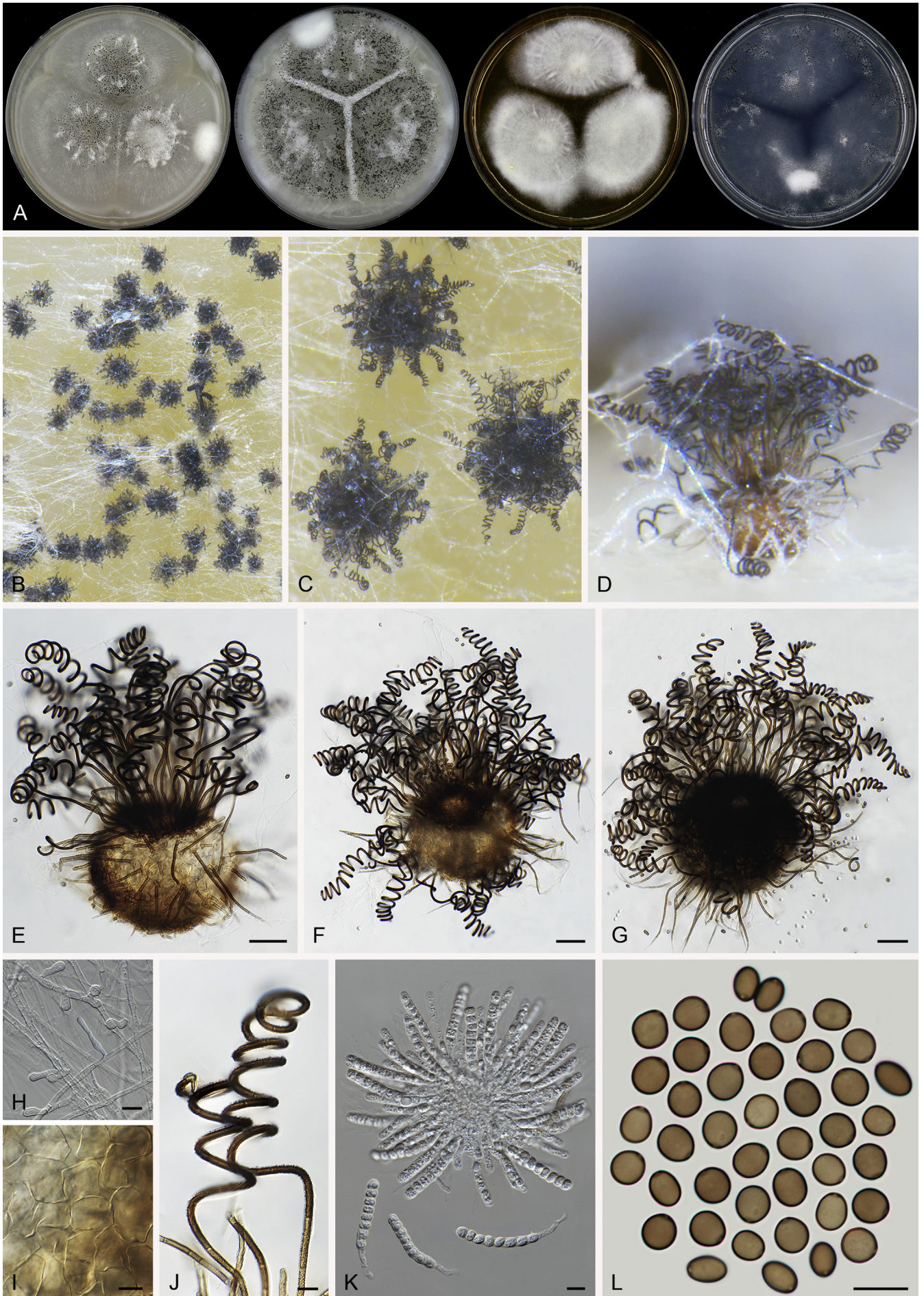


Fig. 44. *Trichocladium acropullum* (CBS 114580, ex-type culture). **A.** Colonies from left to right on OA, CMA, MEA and PCA after 6 wk incubation. **B.** Part of the colony. **C.** Mature ascomata on OA, top view. **D.** Mature ascomata on OA, side view. **E–G.** Ascomata mounted in lactic acid. **H.** Hyphae and chlamyospore-like structures on hyphae. **I.** Structure of ascumatal wall in surface view. **J.** Terminal ascumatal hairs. **K.** Asci. **L.** Ascospores. Scale bars: E–G = 50 μ m; H–L = 10 μ m.

spore-bearing part 36–49 × 6–7 µm and stalks 8.5–19 µm long, with 8 uniseriate ascospores, evanescent. *Ascospores* olivaceous to olivaceous brown when mature, subglobose to ellipsoidal, or ovate in face view, bilaterally flattened, (5.5–)6–7.5(–10) × (5–)5.5–6.5(–7) × 4–5(–5.5) µm, with an apical and often slightly protuberant germ pore. *Conidia* formed laterally or apically on substrate hyphae, hyaline to subhyaline, clavate, ovate, subglobose or irregularly shaped, often two or more in chains, 5–17 × 3–6(–7.5) µm.

Culture characteristics: Colonies on OA 26–32 mm diam after 7 d at 25 °C; edge entire; aerial mycelium thin or thick, white, irregularly distributed; texture cottony; soluble pigment absent; reverse uncoloured. Colonies on CMA similar to those on OA, 26–32 mm diam after 7 d at 25 °C. Colonies on MEA 24–30 mm diam after 7 d at 25 °C; edge lobate; non-sporulating; aerial mycelium thick, white to sulphur yellow; texture floccose; soluble pigment absent; reverse uncoloured. PCA 24–30 mm diam after 7 d at 25 °C; edge entire or slightly crenate, aerial mycelium sparse; soluble pigment absent; reverse uncoloured.

Material examined: China, Hubei, Shennongjia, isolated from garden soil, June 2003, X.W. Wang, ex-type culture CBS 114580. Iran, East Azerbaijan Prov., Bostanabad, isolated from leaf of *Hordeum vulgare*, 4 Jun. 2005, B. Asgari, culture CBS 126783.

Notes: The asexual structures of this species are similar to those observed in the cultures of *T. seminis-citrulli* (= *Chaetomium seminis-citrulli*) and *T. amorphum* (see below), supporting their close relationships.

Trichocladium amorphum X. Wei Wang & Houbraken, **sp. nov.** MycoBank MB824463. Fig. 45.

Etymology: The epithet reflects the poorly differentiated asexual structure of this species.

Micromorphology: *Somatic hyphae* hyaline, 1.5–6 µm wide. *Asexual structures* appearing cylindrical arthroconidia or swollen chlamydospores at the earlier stage, intercalary in hyphae, composed of hyaline, thick-walled cells, which can be solitary or in pairs or chains, later appearing several subglobose cells in clusters, or a mass of subglobose to angular cells like a hyaline microsclerotium, with the cells 6–25 × 2–6 µm when cylindrical, 4.5–11 µm diam when subglobose to angular. *Sexual morph* not observed.

Culture characteristics: Colonies on OA 47–53 mm diam after 7 d at 25 °C; edge entire; with aerial mycelium thin and white; texture loosely floccose; soluble pigment absent; reverse uncoloured. Colonies on CMA similar to those on OA, 45–51 mm diam after 7 d at 25 °C. Colonies on MEA 44–50 mm diam after 7 d at 25 °C; edge entire; aerial mycelium relatively thick, white; texture floccose; soluble pigment absent; reverse uncoloured. Colonies on PCA 41–47 mm diam after 7 d at 25 °C; edge entire; aerial mycelium thin or absent; soluble pigment absent; reverse uncoloured.

Material examined: USA, Laramie, Wyoming, isolated from greenhouse soil, unknown date, M. Christensen (**holotype** CBS H-23491, culture ex-type CBS 127763).

Notes: The ex-type culture was deposited as *Sporendonema* sp. in CBS, and the investigated culture could represent a contaminant of the original specimen. *Trichocladium seminis-citrulli* and *T. amorphum* produce similar asexual structures. The close relationship of these two species is also supported by the

four-gene phylogeny. The poor development of the structures in the cultures of these two species could reflect unmet nutritional requirements in the media employed.

Trichocladium antarcticum (Stchigel & Guarro) X. Wei Wang & Houbraken, **comb. nov.** MycoBank MB824464. Fig. 46.

Basionym: *Thielavia antarctica* Stchigel & Guarro, Mycologia 95: 1225. 2003.

Micromorphology: *Ascomata* superficial, often immersed in thick aerial mycelium, solitary to aggregated, non-ostiolate, glabrous, dark brown, globose, 150–360 µm diam. *Ascomatal wall texture* epidermoidea to intricata. *Asci* numerous, cylindrical to elongate clavate, with spore-bearing part 25–51 × 8.5–16.5 µm, without conspicuous stalks, with 8 uniseriate or biseriate ascospores. *Ascospores* brown, broadly ovoid, bilaterally flattened, (7.5)8–9.5(10.5) × 7–9(10) × 4.5–6.5 µm, with an apical germ pore at the attenuated end. *Acremonium-like conidiophores* arising laterally or terminally from aerial hyphae, unbranched or simply branched, hyaline, aseptate or septate, 4–31 × 2–4.5 µm, with phialidic conidiogenous cells. *Conidia* in false heads or in basipetal chains, one-celled, smooth, obovoid, usually with a truncated base and a rounded apex, 2.5–4.5 × 2–3.5 µm.

Culture characteristics: Colonies on OA 30–36 mm diam after 7 d at 25 °C; edge lobate; with thick and white aerial mycelium; texture floccose; soluble pigment absent; reverse uncoloured. Colonies on CMA similar to those on OA, 30–36 mm diam after 7 d at 25 °C. Colonies on MEA 31–37 mm diam after 7 d at 25 °C; edge lobate; with thick aerial mycelium; white or yellowish white; texture floccose; reverse luteous to saffron. Colonies on PCA 27–33 mm diam after 7 d at 25 °C; edge undulate or lobate; aerial mycelium thin or absent; soluble pigment absent; reverse uncoloured.

Material examined: Antarctica, isolated from *Usnea* cf. *aurantio-atra*, Nov. 1996, A.M. Stchigel, culture ex-type CBS 123565 = FMR 7920; CBS 135876 = FMR 7290.

Notes: The cultures of *T. antarcticum* remained sterile at 25 °C in dark. Incubation of the culture near the window at a temperature around 20 °C and a day-night rhythm induced sporulation. When compared to the original description (Stchigel *et al.* 2003), the size of ascomata (150–360 µm vs 250–450 µm diam) and ascospores (8–9.5 × 7–9 × 4.5–6.5 µm vs 9–11 × 8–10 × 6.5–7 µm) of the ex-type were slightly smaller in this study. In the original publication, cylindrical asci with uniseriate ascospores were described; however, we observed elongate clavate or broad cylindrical asci with biseriate ascospores as well (Fig. 46I). All the other morphological characters fit with the original description. This species was described in *Thielavia*, but phylogenetic analysis clearly showed that it belongs to *Trichocladium*.

Trichocladium arxii (Benny) X. Wei Wang & Houbraken, **comb. nov.** MycoBank MB824465. Fig. 47.

Basionym: *Chaetomidium arxii* Benny, Mycologia 80: 832, 1980.

Micromorphology: *Ascomata* superficial, non-ostiolate, greenish black, with numerous grey olivaceous to olivaceous grey ascomatal hairs in reflected light, spherical or nearly so, 130–230 µm diam. *Ascomata walls* consisting of cephalothecoid plates which are composed of radially elongated cells and surrounded by lines of dehiscence in surface view. *Ascomatal hairs* dark brown, seta-like and covering the whole ascomata, smooth, 2.5–4 µm near

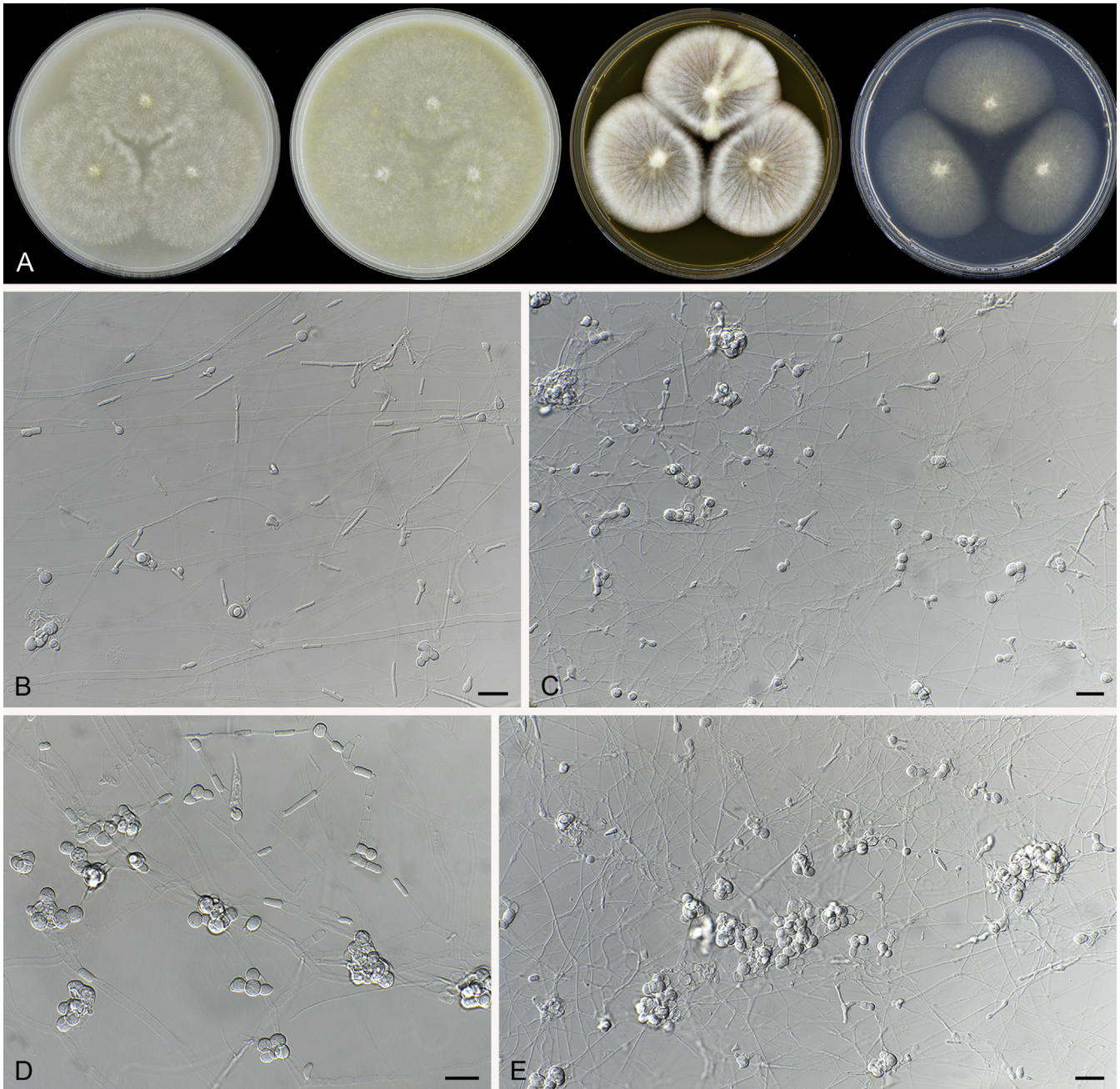


Fig. 45. *Trichocladium amorphum* (CBS 127763, ex-neotype culture). **A.** Colonies from left to right on OA, CMA, MEA and PCA after 1 wk incubation. **B–E.** Hyphae, and the developmental changes of conidiophores and asexual structures on hyphae from young (B) to relatively old (E). Scale bars = 20 µm.

the base. *Asci* clavate or fusiform, with spore-bearing part 34–50 × 18–20.5 µm and stalks 10.5–25 µm long, with 8 biseriolate ascospores, evanescent. *Ascospores* olivaceous brown when mature, ellipsoidal, (10.5–)12.5–14(–17) × (8–)9–11(–12) µm, with an apical germ pore. *Asexual morph* not observed.

Culture characteristics: Colonies on OA 36–42 mm diam after 7 d at 25 °C; edge entire; aerial mycelium absent; soluble pigment buff to pale luteous; reverse buff to pale luteous. Colonies on CMA 36–42 mm diam after 7 d at 25 °C; edge entire; aerial mycelium sparse; soluble pigment pale luteous; reverse pale luteous. Colonies on MEA 29–35 mm diam after 7 d at 25 °C; edge entire; aerial mycelium white; texture floccose; reverse apricot to sienna. Colony growth on PCA 34–40 mm

diam after 7 d at 25 °C; edge entire, aerial mycelium absent; soluble pigment absent; reverse uncoloured.

Material examined: USA, California, isolated from dung of kangaroo rat, 29 Jul. 1974, G.L. Benny, ex-type CBS 104.79.

Notes: The genus *Chaetomidium* was synonymised with *Chaetomium*, and three *Chaetomidium* species were transferred to *Chaetomium*, including the type species *C. fimeti* (Wang *et al.* 2016a). In the study of Hernández-Restrepo (2017), *Chaetomidium arxii* clustered with *Trichocladium asperum* in their LSU tree. This is confirmed in our study using a larger data set. The phylogenetic placement of *T. arxii* in *Trichocladium* confirmed the polyphyly of the traditional “*Chaetomidium*” first shown by Greif *et al.* (2009). More study is needed to determine the phylogenetic relationships of the other “*Chaetomidium*” species.

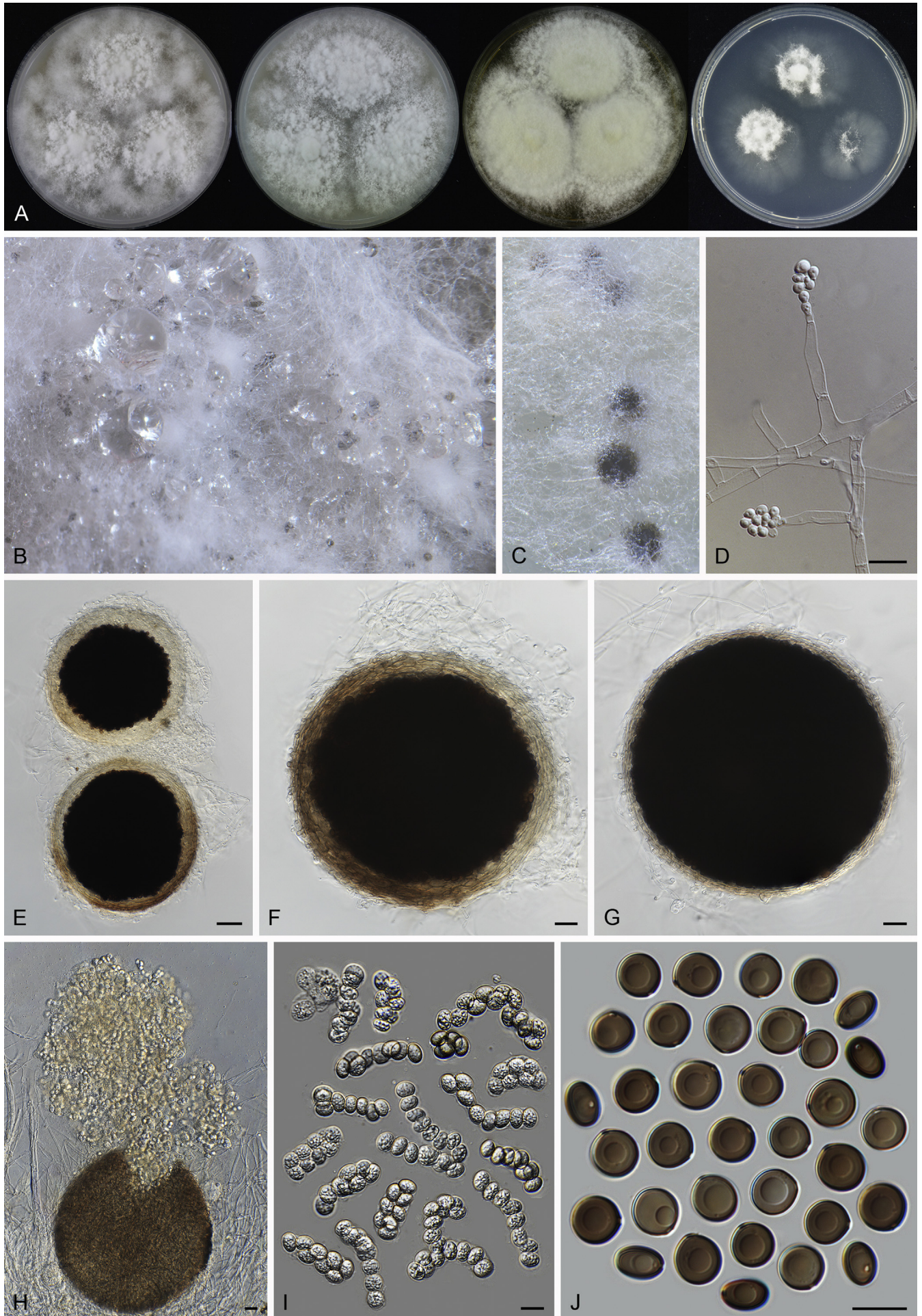


Fig. 46. *Trichocladium antarcticum* (FMR 7920 = CBS 123565, ex-type culture). **A.** Colonies from left to right on OA, CMA, MEA and PCA after 2 wk incubation. **B.** Part of the colony. **C.** Mature ascomata immersed in mycelium on OA, top view. **D.** Conidiophores and conidia. **E–G.** Ascomata mounted in lactic acid. **H.** A ruptured young ascoma, showing ascomatal wall structure in surface view and masses of asci flooding from the rupture. **I.** Asci. **J.** Ascospores. Scale bars: D, I, J = 10 μm ; E = 50 μm ; F–H = 20 μm .

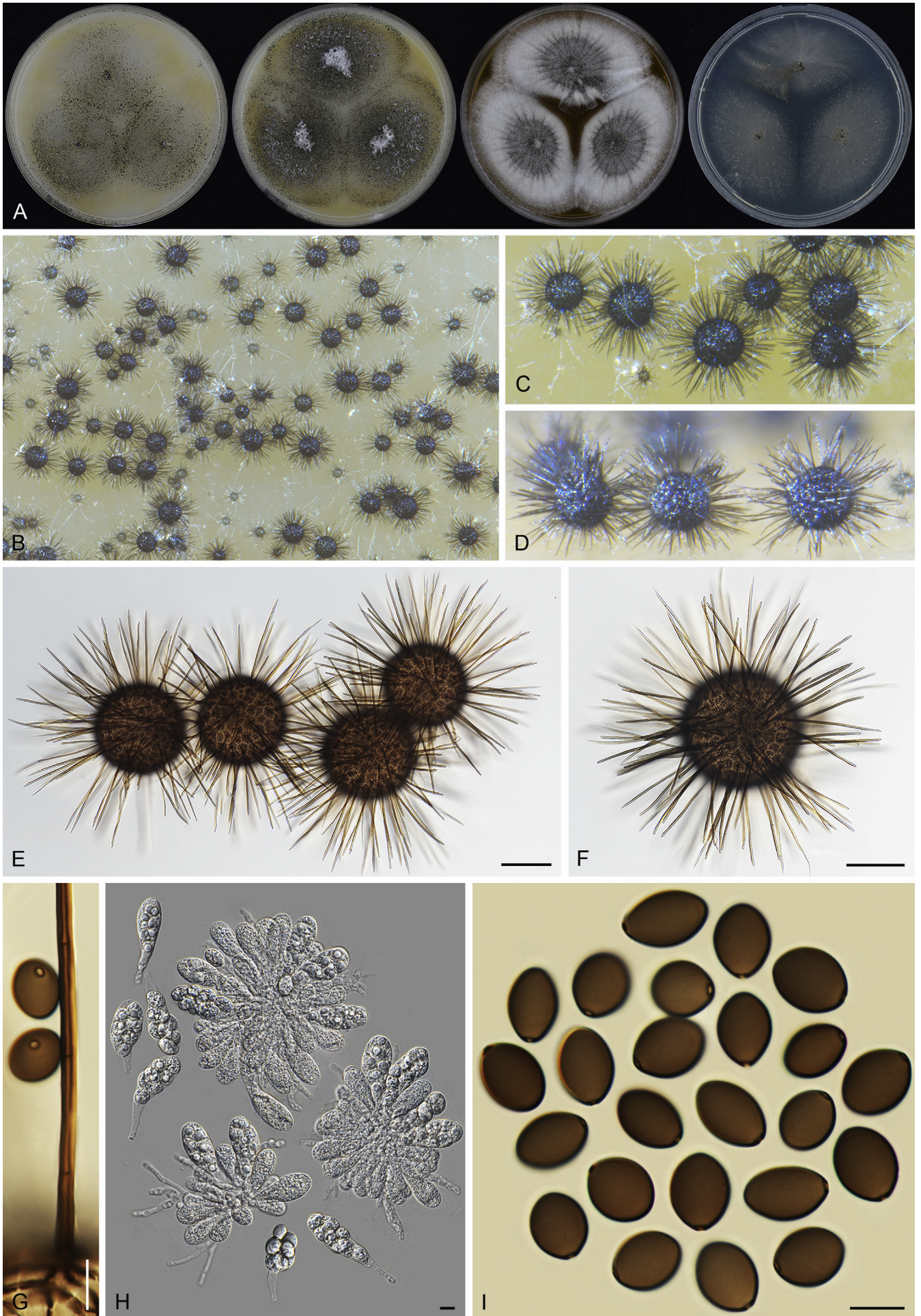


Fig. 47. *Trichocladium arxii* (CBS 104.79, ex-type culture). **A.** Colonies from left to right on OA, CMA, MEA and PCA after 4 wk incubation. **B–C.** Mature ascomata on OA, top view. **D.** Mature ascomata on OA, side view. **E–F.** Ascomata mounted in lactic acid. **G.** Part of a terminal ascomal hair together with two ascospores. **H.** Asci. **I.** Ascospores. Scale bars: E–F = 100 μ m; G–I = 10 μ m.

Trichocladium asperum Harz, Bull. Soc. Imp. Naturalistes. Moscou 44: 125. 1871. MycoBank MB171452. Figs 48, 49.

Synonyms: *Sporidesmium asperum* Corda, Icon. fung. 2: 6. 1838.

Dicoccum asperum (Corda) Sacc., Syll. fung. 4: 342. 1886.

Monodictys aspera (Corda) S. Hughes, Canad. J. Bot. 36: 785. 1958.

Piricauda aspera (Corda) R.T. Moore, Rhodora 61: 96. 1959.

Micromorphology: Somatic hyphae hyaline, 1.5–3.5 µm wide. Conidiophores hyaline, originating laterally or terminally from the hyphae, cylindrical, unbranched or branched 1–2 times, sometimes verticillate, 2–4.5 µm wide, up to 21.5 µm long, sometimes reduced to intercalary conidiogenous loci in the hyphae. Conidia solitary, 1- to 2-celled, occasionally 3-celled, usually with germ pore in each cell, obovate, pyriform, ellipsoid, constricted at the septa, conspicuously warted, (10.5–)14–21.5(–26) × (9–)10–19.5(–20) µm, olivaceous brown to dark brown, sometimes with a basal cell paler than the others, seceding from the mycelium when mature usually together with a part of conidiogenous cell.

Culture characteristics: Colonies on OA 43–49 mm diam after 7 d at 25 °C; edge entire; obverse olivaceous black, with grey white to smoke grey, sparse floccose aerial hyphae; reverse olivaceous grey to greenish black. Colonies on CMA similar to those on OA similar, 41–53 mm diam after 7 d at 25 °C; reverse buff to pale luteous. Colonies on MEA 47–42 mm diam after 7 d at 25 °C; edge entire; obverse iron grey; aerial mycelium sparse, pale mouse grey; texture floccose; reverse cinnamon. Colonies on PCA 44–50 mm diam after 7 d at 25 °C; edge entire; obverse olivaceous grey to iron grey; aerial mycelium sparse, pale mouse grey; reverse olivaceous grey to dark mouse grey.

Material examined: **Lectotype re-designated here:** tab II Fig. 1 illustrated by Harz in Bull. Soc. Imp. Moscou 44, 1871, reproduced here as Fig. 48. MBT 380604. **Belgium,** Kontich, isolated from agricultural soil, 28 Jan. 1964, G.L. Hennebert, culture CBS 112.67 = MUCL 6092. **Germany,** Edersee, Nieder-Werbe, isolated from acidic soil, unknown date, E. Falk, ex-epitype culture CBS 903.85. **The Netherlands,** unknown substrate, unknown date, C.M. Berkhout, culture CBS 140.21. **Unknown country,** unknown substrate, unknown date, O. da Fonseca, culture CBS 157.22.

Notes: In 1871, Harz published the generic name *Trichocladium* for three species, but did not designate the type species for the genus. In 1931, Clements & Shear lectotypified *Trichocladium asperum* as the type species of *Trichocladium* (followed by Hughes 1952). The descriptions of *T. asperum* Harz and *Sporidesmium asperum* Corda are based on different specimens, and the latter should therefore not be regarded as the basionym of *T. asperum*. For this reason, an illustration in the protologue of *Trichocladium asperum* Harz is reproduced and re-designated here as the lectotype of *T. asperum* (Fig. 47). This lectotype replaces the lectotype designated in error by Hernández-Restrepo et al. (2017), which is based on the illustration of *Sporidesmium asperum* Corda (MBT375510).

Hambleton et al. (2005) found that ITS sequences of *Humicola grisea* and *Trichocladium asperum* were identical. In a phylogram based on LSU sequences, *Humicola grisea* clustered together with *Trichocladium asperum* (Hernández-Restrepo et al. 2017). This study confirms the close relationship between *T. griseum* (= *H. grisea*) and *T. asperum*; however, they are regarded as separate species based on their distinct morphology and differences in other genes.

Trichocladium beniowskiae (M.D. Mehrotra) X. Wei Wang & Houbraken, **nom. nov.** MycoBank MB824466. Fig. 50.

Basionym: *Beniowskia macrospora* M.D. Mehrotra, Sydowia 17: 149. 1964.

Etymology: The epithet refers to the genus *Beniowskia*, from which the species is transferred.

Micromorphology: Somatic hyphae hyaline, 2–6 µm wide. Conidiophores hyaline, originating laterally or terminally from the hyphae, hypha-like in the lower part, often consisting of swollen cells in chains or branched chains in the upper part, 2–5 µm wide near the base, up to 220 µm long, with the top swollen conidiogenous cells 5–10 µm wide. Conidia solitary to in short chains, single-celled, smooth, hyaline, globose or subglobose, (10–)14–20.5(–29.5) µm diam.

Culture characteristics: Colonies on OA 56–62 mm diam after 7 d at 25 °C; edge entire; obverse luteous to orange caused by soluble pigment; aerial mycelium white, irregularly distributing;

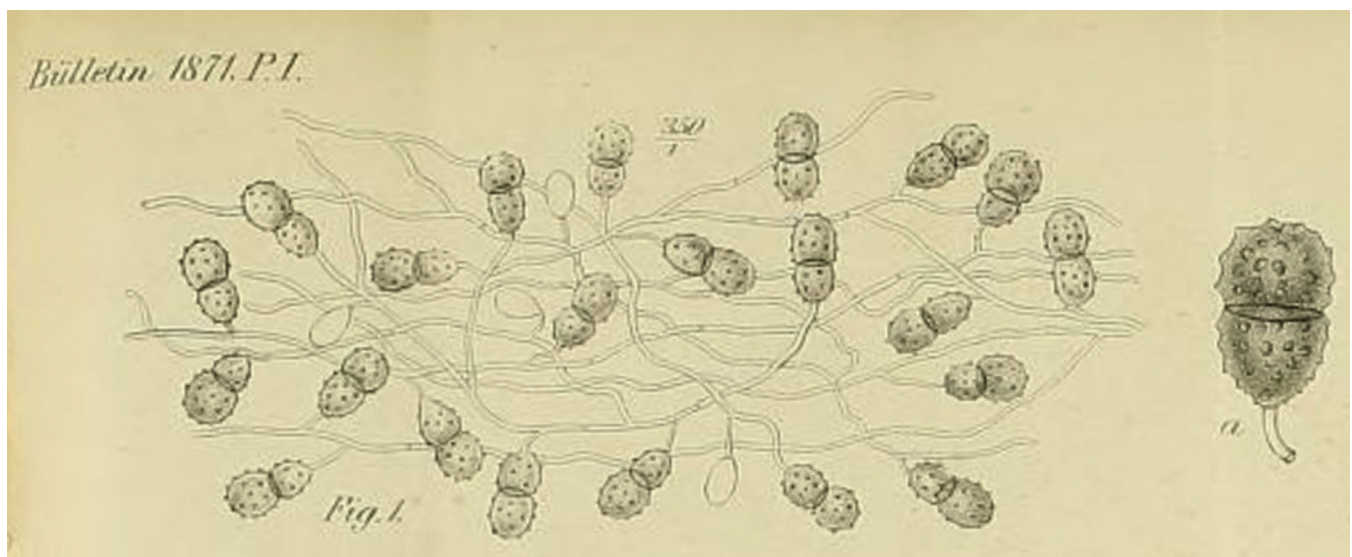


Fig. 48. *Trichocladium asperum*. Illustrated by Harz (1871, Bull. Soc. Imp. Moscou 44: Tab II Fig. 1), selected as a lectotype in this study.

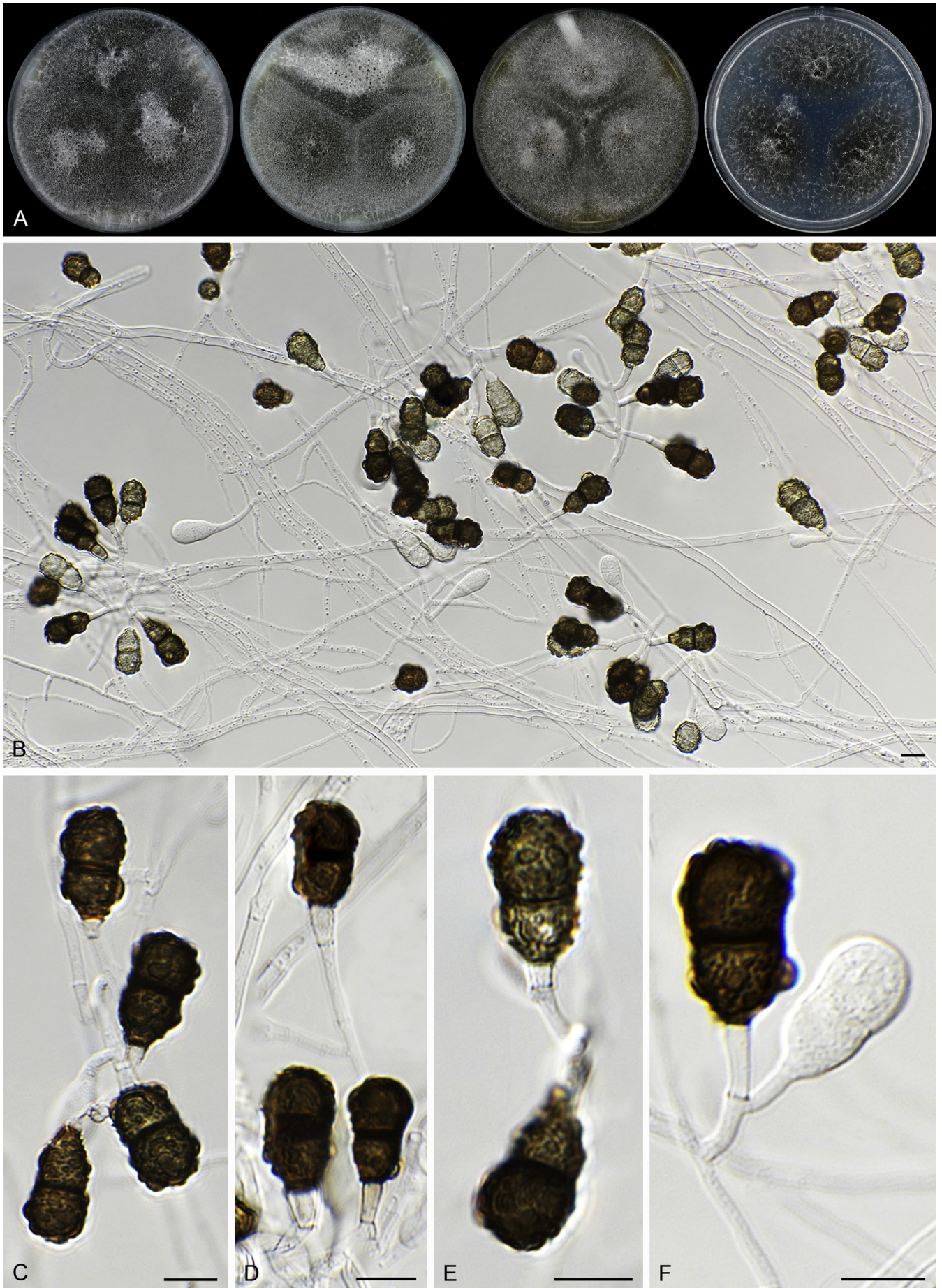


Fig. 49. *Trichocladium asperum* (CBS 903.85, ex-epitype culture). **A.** Colonies from left to right on OA, CMA, MEA and PCA after 2 wk incubation. **B–F.** Hyphae, conidiophores and conidia. Scale bars = 10 μ m.

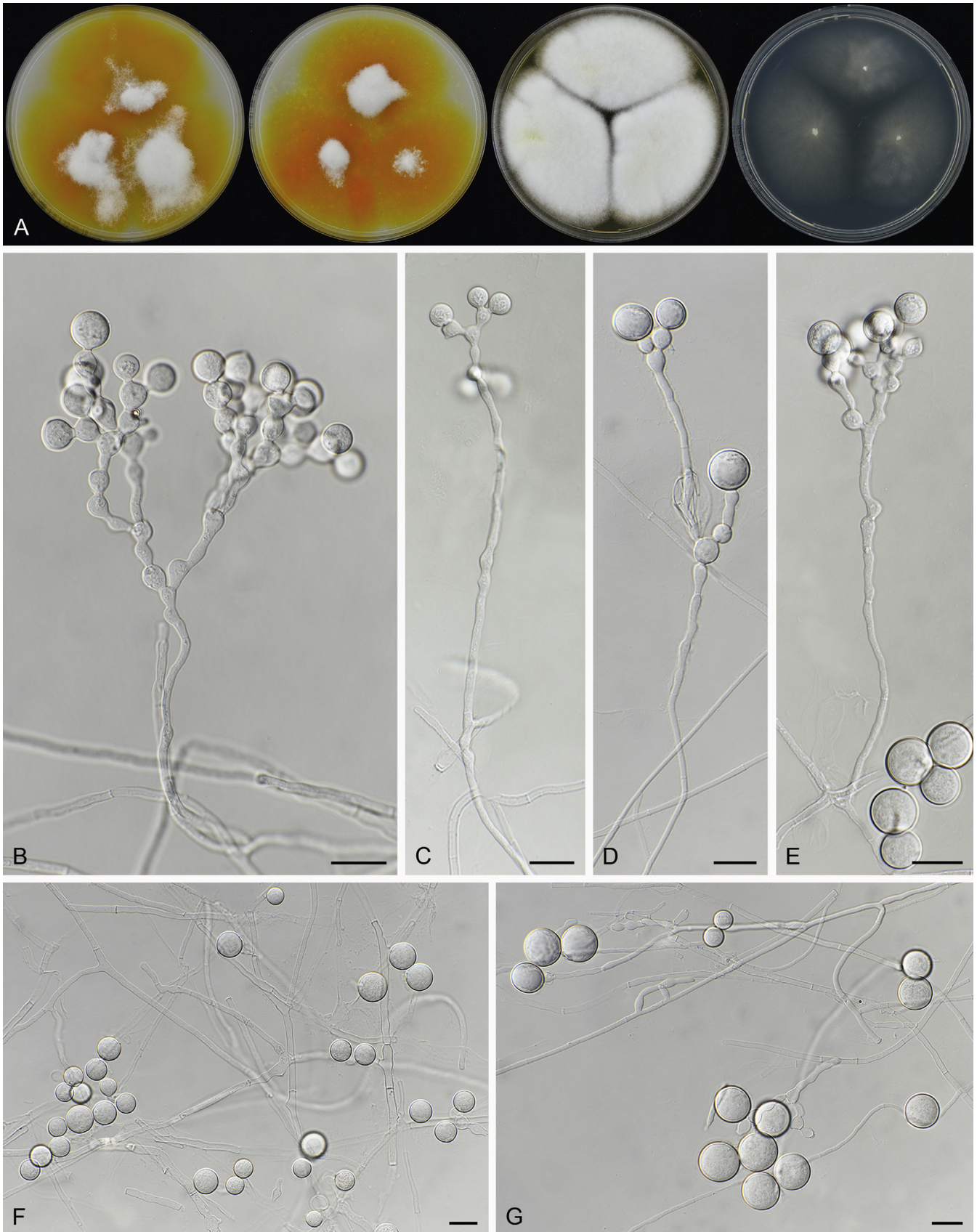


Fig. 50. *Trichocladium beniowskiae* (CBS 757.74, ex-type culture). **A.** Colonies from left to right on OA, CMA, MEA and PCA after 1 wk incubation. **B–E.** Hyphae, conidiophores, conidiogenous cells and developing conidia. **F–G.** Hyphae, conidiophores and mature conidia. Scale bars = 20 µm.

texture floccose; reverse pale luteous to saffron. Colonies on CMA similar to those on OA, 56–62 mm diam after 7 d at 25 °C. Colonies on MEA 61–67 mm diam after 7 d at 25 °C; edge entire; aerial mycelium white, texture floccose; reverse luteous to

orange. Colonies on PCA 47–53 mm diam after 7 d at 25 °C; edge entire; aerial mycelium absent; reverse uncoloured.

Material examined: **India**, isolated from dried leaves of an unidentified grass, unknown date, M.D. Mehrotra, ex-type culture, CBS 757.74 = IMI 099625.

Notes: The type species of *Beniowskia*, *B. sphaeroidea*, is a grass pathogen that produces monoblastic conidia on sporodochia (Hanlin 1987) ornamented with coiled hyphae. *Beniowskia macrospora* (= *Trichocladium beniowskiae*) differs from *B. sphaeroidea* by the absence of coiled ornamenting hyphae on its sporodochia, the pattern of conidiophore branching, and its larger conidia (Mehrotra 1964). Although considered a synonym of *B. sphaeroidea* (Index Fungorum; <http://www.indexfungorum.org>, Aug. 2015), the differences in morphological characters make this unlikely. Hanlin (1987) noted that his attempts to culture *B. sphaeroidea* failed, in contrast to the ability of *B. macrospora* to grow *in vitro*. In our examination of CBS 757.74, no sporodochia were observed on any of the four media. Phylogenetic analyses clearly indicated that *B. macrospora* is a member of the *Trichocladium* lineage, but it remains uncertain whether this species is actually congeneric with the type of *Beniowskia*. Unfortunately, no type material of *B. sphaeroidea* was available for study and the phylogenetic position of the genus *Beniowskia* remains unknown. The name *Trichocladium macrospora* already exists, and therefore a new species epithet is required.

Trichocladium crispatum (Fuckel) X. Wei Wang & Houbraken, **comb. nov.** MycoBank MB824467. Figs 51, 52.

Basionym: *Sphaeria crispata* Fuckel, Fungi Rhenani no. 2022. 1867.

Synonym: *Chaetomium crispatum* Fuckel, Symb. Mycol. P. 90. 1870.

Micromorphology: Ascumata superficial on the aerial mycelium, mouse grey in reflected light because of the ascumata hairs, nearly spherical to ovoid, ostiolate, 150–320 µm high, 140–280 µm diam. Ascumatal wall brown, composed of angular to irregular cells in surface view. **Terminal hairs** arising around the ostiole, regularly spirally coiled with circinate to coiled apex and straight to flexuous lower part, occasionally with coiled branches, strongly verrucose or warty, 3–4.5 µm diam near the base, 5–8 µm diam in the coiled part. **Lateral hairs** seta-like or flexuous, tapering and fading towards the tips. **Asci** cylindrical, with spore-bearing part 52–66 × 6.5–9.5 µm and stalks 18–31 µm long, with 8 uniseriate ascospores, evanescent. **Ascospores** olivaceous to olivaceous brown when mature, broad ovate to limoniform in face view, often slightly biapiculate, bilaterally flattened, (8.5–)9–10(–11) × (7–)7.5–8.5 × 5–6.5 µm, with an apical germ pore at the attenuated end. Asexual morph not observed.

Culture characteristics: Colonies on OA 42–48 mm diam after 7 d at 25 °C; edge entire; obverse cottony, smoke grey to grey olivaceous; reverse greenish olivaceous because of the soluble citrine pigments diffusing into the medium. Colonies on CMA similar to those on OA, 42–48 mm diam after 7 d at 25 °C. Colonies on MEA 32–38 mm diam after 7 d at 25 °C; edge entire; obverse olivaceous buff or smoke grey, cottony; reverse fuscous black. Colonies on PCA 35–41 mm diam after 7 d at 25 °C; edge entire; obverse smoke grey or olivaceous buff, loosely cottony; reverse grey olivaceous.

Material examined: The illustration no. 2022 was reproduced here as Fig. 51, which was made by Fuckel on the basis of the holotype of *Chaetomium crispatum* G00127921 (in Conservatoire et Jardin botaniques de la Ville de Genève, Switzerland) and kept together with the type specimen. **Germany**, isolated from estuarine sediment, unknown date, R. Siepmann, MBT381346 (**epitype** designated here, CBS H-23492, culture ex-epitype CBS 149.58). **Netherlands**,

Wageningen, isolated from agricultural soil, unknown date and collector, culture CBS 693.71.

Notes: To stabilise the use of this species name, we propose strain CBS 149.58 as the epitype of *T. crispatum*, which was collected in the same country as the holotype specimen. Morphological features of the epitype fit well with the type as reproduced in Fig. 51.

Trichocladium gilmaniellae (Moustafa) X. Wei Wang & Houbraken, **nom. nov.** MycoBank MB824468. Fig. 53.

Basionym: *Gilmaniella macrospora* Moustafa, Persoonia 8: 332. 1975.

Etymology: The epithet refers to the genus *Gilmaniella*, from which the species is transferred.

Micromorphology: **Somatic hyphae** usually hyaline, thin-walled, 2–4 µm wide, some becoming olivaceous brown and thick-walled when old, 3.5–5 µm wide, with conidia produced on the minimally differentiated conidiophores, on the top of hyphae or on the side of vegetative hyphae. **Conidiophores** hyaline to subhyaline, unbranched, cylindrical, or slightly swollen on the top, 2.5–120 µm long, 2–4 µm wide near top, sometimes lacking where the spores arising from an undifferentiated intercalary conidiogenous cell (a hyphal cell). **Conidia** single-celled, usually solitary, occasionally 2–3 in chains, olivaceous brown to dark olivaceous brown, smooth or slightly verrucose, globose or subglobose, sometimes ellipsoidal, occasionally pyriform, (8.5–) 11–15.5(–22.5) µm diam, with a conspicuous apical, subapical or lateral germ pore which is usually 2–3.5 µm wide.

Culture characteristics: Colonies on OA 39–45 mm diam after 7 d at 25 °C; edge entire; obverse mouse grey to iron grey; aerial mycelium grey white to pale olivaceous grey; texture floccose; reverse pale olivaceous grey. Colonies on CMA 37–43 mm diam after 7 d at 25 °C; edge entire; obverse olivaceous grey to iron grey; aerial mycelium grey white to pale olivaceous grey; texture floccose; reverse pale olivaceous grey. Colonies on MEA 40–46 mm diam after 7 d at 25 °C; edge entire or slightly undulate; aerial mycelium pale olivaceous grey to olivaceous grey; texture floccose; reverse dark mouse grey. Colonies on PCA 33–39 mm diam after 7 d at 25 °C; edge entire; obverse iron grey to greenish black, greyish sepia to olivaceous in the centre; aerial mycelium sparse, smoke grey; reverse iron grey.

Material examined: **Kuwait**, isolated from salt-marsh soil, 1973, A.F. Moustafa, culture ex-type CBS 388.75.

Notes: The genus *Gilmaniella* was considered *incertae sedis* in *Pezizomycotina* and characterized by somewhat differentiated conidiophores and aseptate, pigmented conidia with a conspicuous germ pore (Barron 1964, Kirk et al. 2008). The type species *G. humicola* was described with simple to branched, often inflated conidiophores and having sympodial conidiogenous cells with denticles on which conidia arise (Barron 1964). *Trichocladium gilmaniellae* (= *Gilmaniella macrospora*) produces conidia on monoblastic conidiogenous cells or even on undifferentiated hyphal cells. Furthermore, the conidiogenous cells lack denticles. The species appears very similar to the classic morphological concept of *Humicola grisea*, although the ‘germ pores’ are more obvious. Phylogenetically, *Trichocladium gilmaniellae* resides in a clade with *T. asperum*. The type species of *Gilmaniella*, *G. humicola*, is not a member of the *Chaetomiaceae* (Fig. 1). The epithet *macrospora* is already occupied in *Trichocladium*, namely *T. macrospora* P.M. Kirk, and a new name is therefore proposed.



Fig. 51. *Trichocladium crispatum*. Holotype and illustration no. 2022 made by Fuckel, kept in Conservatoire et Jardin botaniques de la Ville de Genève, Switzerland.

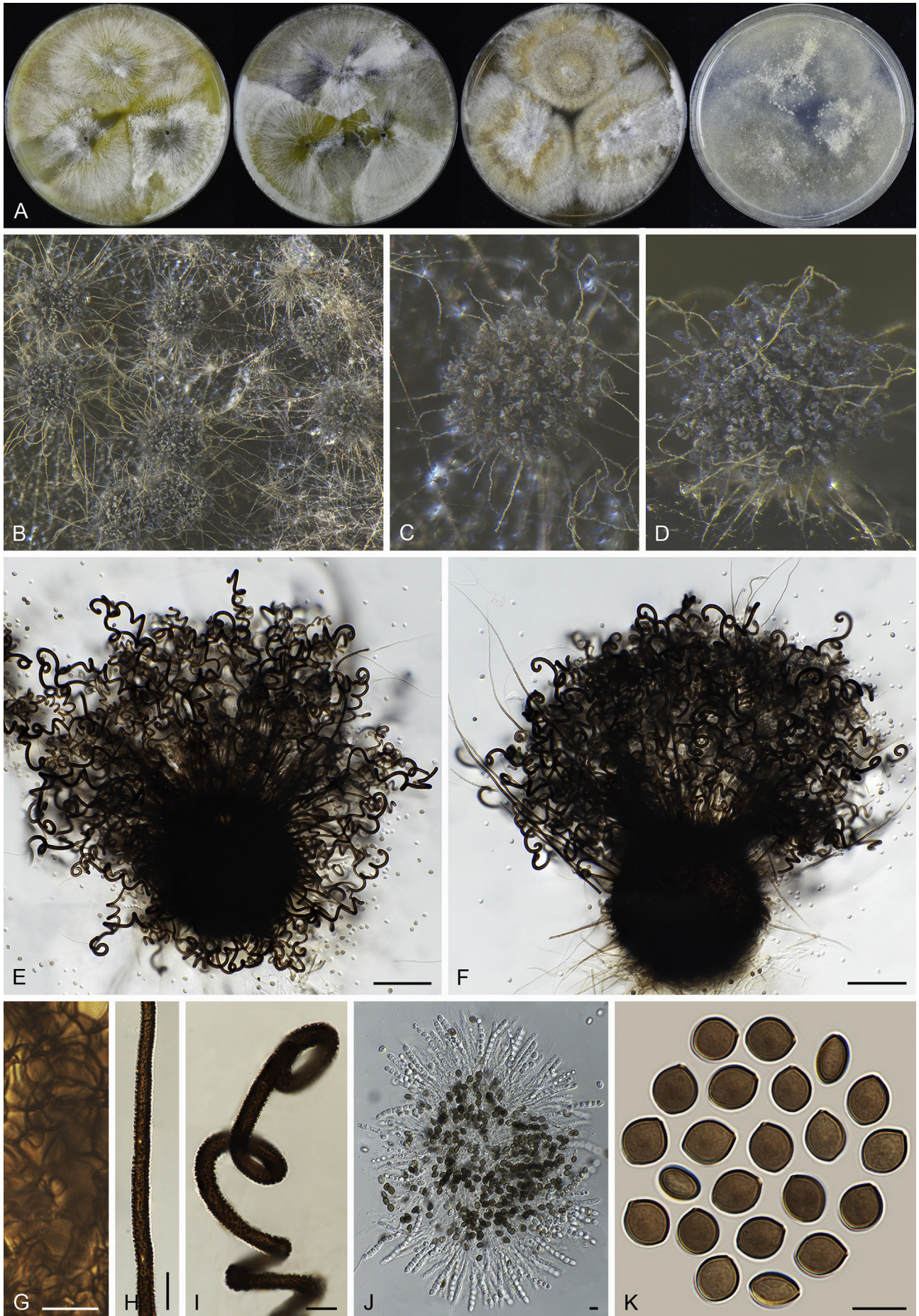


Fig. 52. *Trichocladium crispatum* (CBS 149.58, ex-epitype culture). **A.** Colonies from left to right on OA, CMA, MEA and PCA after 5 wk incubation. **B.** Part of the colony. **C.** A mature ascoma on OA, top view. **D.** A mature ascoma on OA, side view. **E–F.** Ascomata mounted in lactic acid. **G.** Structure of ascocal wall in surface view. **H.** Lower part of a terminal ascocal hair. **I.** Upper part of a terminal ascocal hair. **J.** Asci. **K.** Ascospores. Scale bars: E–F = 100 μ m; G–K = 10 μ m.

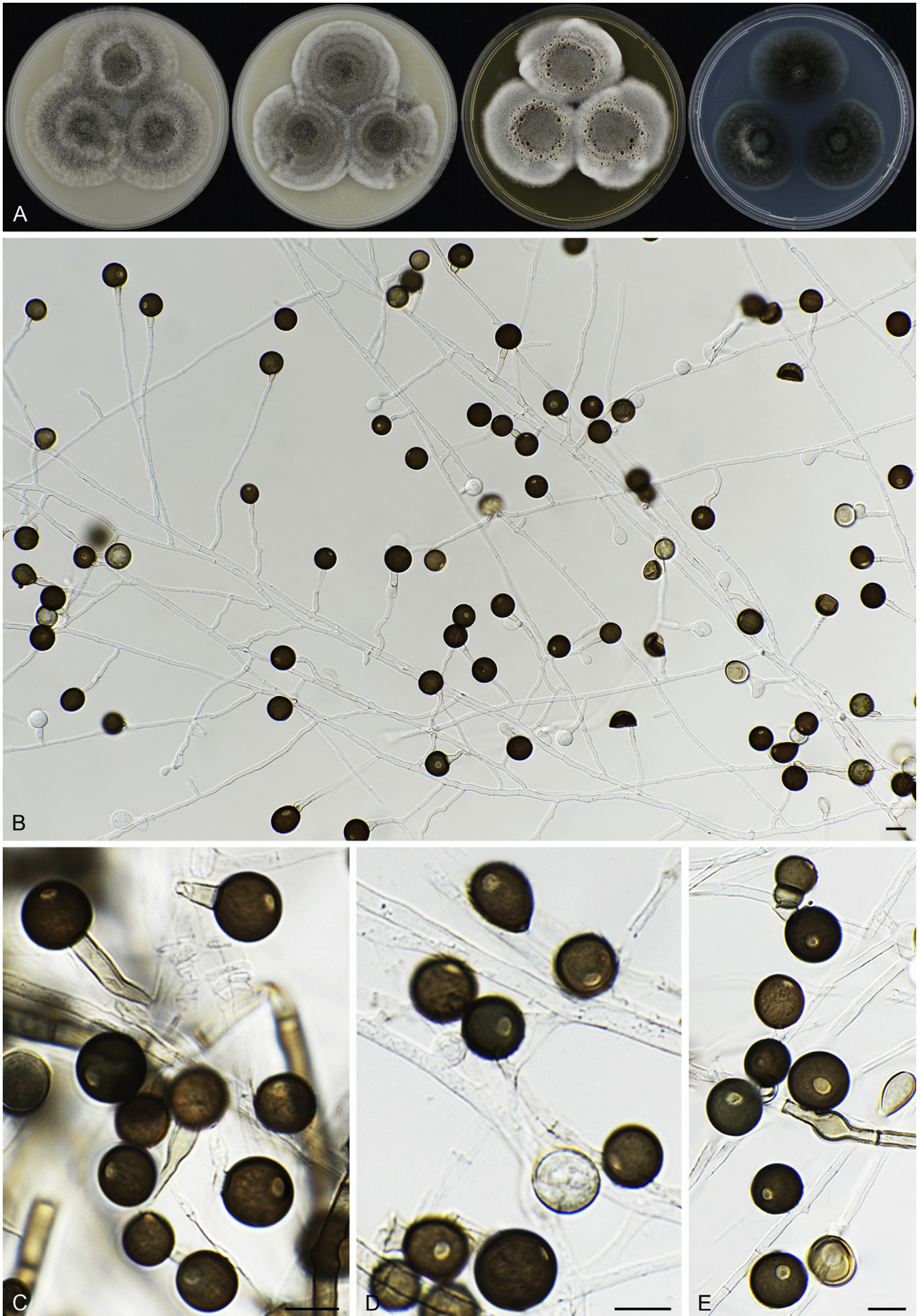


Fig. 53. *Trichocladium gilmaniellae* (CBS 388.75, ex-type culture). A. Colonies from left to right on OA, CMA, MEA and PCA after 1 wk incubation. B. Hyphae, conidiophores and conidia. C–E. Conidia. Scale bars = 10 μ m.

Trichocladium griseum (Traaen) X. Wei Wang & Houbraken, **comb. nov.** MycoBank MB824469. Fig. 54.

Basionym: *Humicola grisea* Traaen, Nytt Mag. Naturvidensk 52: 34. 1914.

Micromorphology: Two types of asexual spores are observed in the culture on OA. *Somatic hyphae* hyaline, 1.2–3 µm wide. *Conidiophores* hyaline or subhyaline, usually pale brown below spores, unbranched, cylindrical, or swelling on the top, 2.5–50 µm long, 2–5 µm wide near top, sometimes lacking where the spores arising from an undifferentiated intercalary conidiogenous cell (a hyphal cell). *Conidia* single-celled, solitary, sometimes 2(–4) in chains or a few in clusters, olivaceous brown to dark olivaceous brown, smooth or slightly verruculose, globose or subglobose, (8–)12–16.5(–18) µm high, (7.5–)12–16(–17.5) µm wide. *Acremonium-like conidiophores* phialidic, formed laterally from hyphae, hyaline, unbranched, 9–21 µm long, 2–2.5 µm wide near the base. *Acremonium-like conidia* formed basipetally in chains, aseptate, obovoid, ellipsoidal, with a truncated base and a rounded apex, 2.5–3.5 × 2–2.5 µm.

Culture characteristics: Colonies on OA 42–48 mm diam after 7 d at 25 °C; edge entire; aerial mycelium pale olivaceous grey to mouse grey; texture floccose; reverse greenish black because of the immersed conidia and soluble pigment. Colonies on CMA similar to those on OA, 39–45 mm diam after 7 d at 25 °C. Colonies on MEA 41–47 mm diam after 7 d at 25 °C; edge entire; aerial mycelium olivaceous grey; texture floccose; reverse greenish black because of the immersed conidia and soluble pigment. Colonies on PCA 37–43 mm diam after 7 d at 25 °C; edge entire; obverse greyish sepia, olivaceous to greenish black; aerial mycelium sparse, grey white; reverse olivaceous black.

Material examined: **China**, Jilin, isolated from soil, Oct. 2009, T.Y. Zhang, CGMCC 3.13888. **Germany**, unknown substrate, unknown date, H.W. Wollenweber, CBS 217.34. **Norway**, isolated from soil, 1914, A.E. Traaen, MBT381347 (designated here as **neotype**, CBS H-23493, ex-neotype culture CBS 119.14 = ATCC 22724 = IMI 075664 = MUCL 8008).

Notes: Strain CBS 119.14 is designated here as the neotype of *H. grisea*. This culture was deposited by A.E. Traaen, who also described *H. grisea*. Two cultures were deposited, CBS 119.14 and ex-type of *H. fuscoatra*, CBS 118.14. A.E. Traaen (1914) didn't designate a type in his paper, and CBS 119.14 is the only extant culture of this species from the original author. *Acremonium-like* synanamorphs were observed in the culture of CBS 119.14, although this structure was not mentioned in the original description of *H. grisea*. The formation of an *acremonium-like* synanamorph is not a stable character and could explain the difference between the original description and our observations (Domsch et al. 2007).

Trichocladium heterothallicum (Yu Zhang & L. Cai) X. Wei Wang & Houbraken, **comb. nov.** MycoBank MB824470.

Basionym: *Chaetomium heterothallicum* Yu Zhang & L. Cai, Fungal Biol. 121: 29. 2017.

Micromorphology: Fide Zhang et al. (2017a) *Ascomata* ostiolate, dark brown, immersed, covered by the aerial mycelium, spherical or nearly so, 160–260 µm diam. *Ascomatal wall* brown, composed of *textura angularis* or *irregularis*. *Ascomatal hairs* numerous, 4–5.5 µm wide near the base, slightly straight below, spirally coiled in the upper part, dark brown, unbranched, nearly smooth. *Asci* cylindrical, with 8 uniseriate ascospores, short-stalked, 60–75 × 7.5–9.5 µm. *Ascospores* light brown,

globose or subglobose, 8.5–11 × 7–9 µm, without distinct germ pore. Heterothallic. *Chlamydospores* present, subhyaline, generally globose, 6–9 µm in diameter, produced in intercalary chains.

Culture characteristics: Fide Zhang et al. (2017a). Colonies up to 52 mm diam. on PDA after 6 d at 25 °C; aerial mycelium abundant, lanose, yellow; soluble pigment orange or absent; reverse yellowish or orange brown.

Notes: Comparison of the sequences from Zhang et al. (2017a) with our dataset revealed a close relationship with *T. amorphum* and the most closely related sexual species is *T. seminis-citrulli* (= *Ch. seminis-citrulli*). *Trichocladium heterothallicum* produces intercalary chlamydospores in chains or in clusters (Zhang et al. 2017a), as do *T. amorphum* and *T. seminis-citrulli*. *Trichocladium heterothallicum* produces cylindrical asci and subglobose ascospores; the asci of *T. seminis-citrulli* are clavate and the ascospores broad ovoid or broad pyriform (Fig. 55).

Trichocladium jilongense (Y.M. Wu & T.Y. Zhang) X. Wei Wang & Houbraken, **comb. nov.** MycoBank MB824471. Fig. 55.

Basionym: *Humicola jilongensis* Y.M. Wu & T.Y. Zhang, Mycotaxon 121: 148. 2012.

Micromorphology: *Somatic hyphae* hyaline to brown, 1.5–3.5 µm wide. *Conidiophores* unbranched, septate with a hyaline and cylindrical basal cell, or aseptate pale brown, ellipsoidal to doliform, sometimes reduced to intercalary conidiogenous loci in the hyphae, cylindrical, originating laterally or terminally from the hyphae, 0–9(–32) µm long. *Conidiogenous cell* pale brown, terminal on conidiophores or intercalary in hyphae, 3–6.5 µm diam. *Conidia* solitary, smooth, olivaceous brown, 1–2(–3) celled, globose, subglobose, obovate, ellipsoid, constricted at the septa, 10–28 × 9.5–15 µm.

Culture characteristics: Colonies on OA 31–37 mm diam after 7 d at 25 °C; edge entire; aerial mycelium thick, greyish white, forming 3–6 concentric and crenate rings; texture floccose; reverse cinnamon to dark brick. Colonies on CMA similar to those on OA, 31–37 mm diam after 7 d at 25 °C. Colonies on MEA 32–38 mm diam after 7 d at 25 °C; edge created; aerial mycelium pale vinaceous buff to smoke grey; texture cottony; reverse sepia to purple slate. Colonies on PCA 28–34 mm diam after 7 d at 25 °C; edge entire; aerial mycelium smoke grey to grey olivaceous; texture floccose; reverse grey olivaceous.

Material examined: **China**, Tibet, isolated from mountain soil, Sept 2007, Y.M. Wu, culture ex-type HSAUP II 071485. **Germany**, isolated from straw-meal-amended field soil, 1984, G.J. Wirth & G. Wolf, culture CBS 195.87.

Notes: This species sometimes produces conidia laterally from conidiogenous loci that are intercalary in the hyphae, similar to what is observed in *Humicola* species. However, the somewhat differentiated conidiophores are easily observed in the culture.

Trichocladium nigrospermum (Schweinitz) X. Wei Wang & Houbraken, **comb. nov.** MycoBank MB824472. Fig. 56.

Basionym: *Acremonium nigrospermum* Schweinitz, Trans. Amer. philos. Soc. 4: 283. 1832.

Synonyms: *Monodictys nigrosperma* (Schwein.) W. Gams Cephalosporium-artige Schimmelpilze: 214. 1971.

Micromorphology: *Somatic hyphae* hyaline, 1.5–4 µm wide. *Conidiophores* hyaline, cylindrical, unbranched, originating laterally or terminally from the hyphae, 2–3.5 µm wide, up to

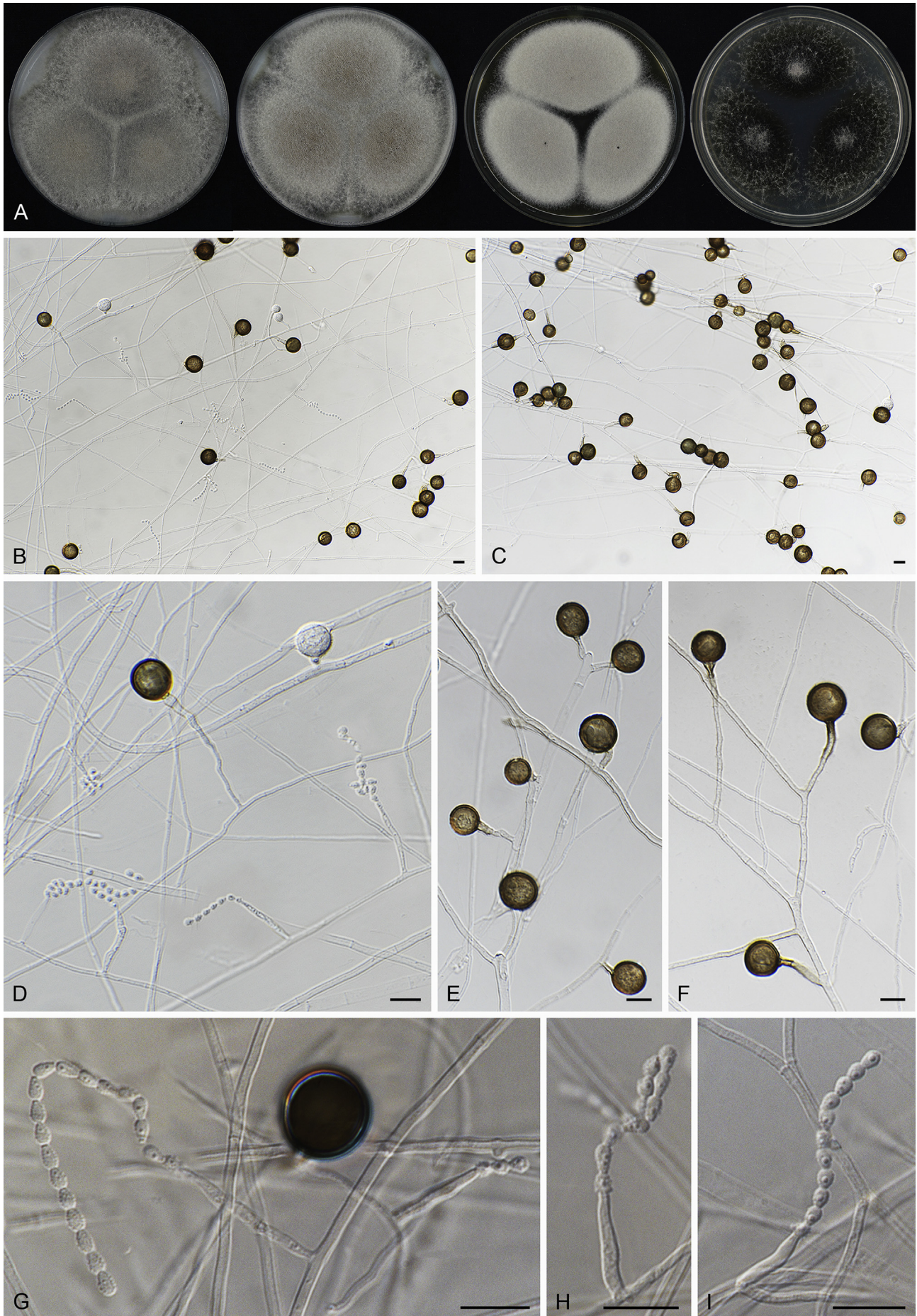


Fig. 54. *Trichocladium griseum* (CBS 119.14, ex-neotype culture). **A.** Colonies from left to right on OA, CMA, MEA and PCA after 2 wk incubation. **B, D, G.** Hyphae, conidiophores, thick-walled conidia and acronium-like synanamorph. **C, E, F.** Hyphae, conidiophores and aleurioconidia. **H–I.** Hyphae, conidiophores and conidia of acronium-like synanamorph. Scale bars = 10 μm.

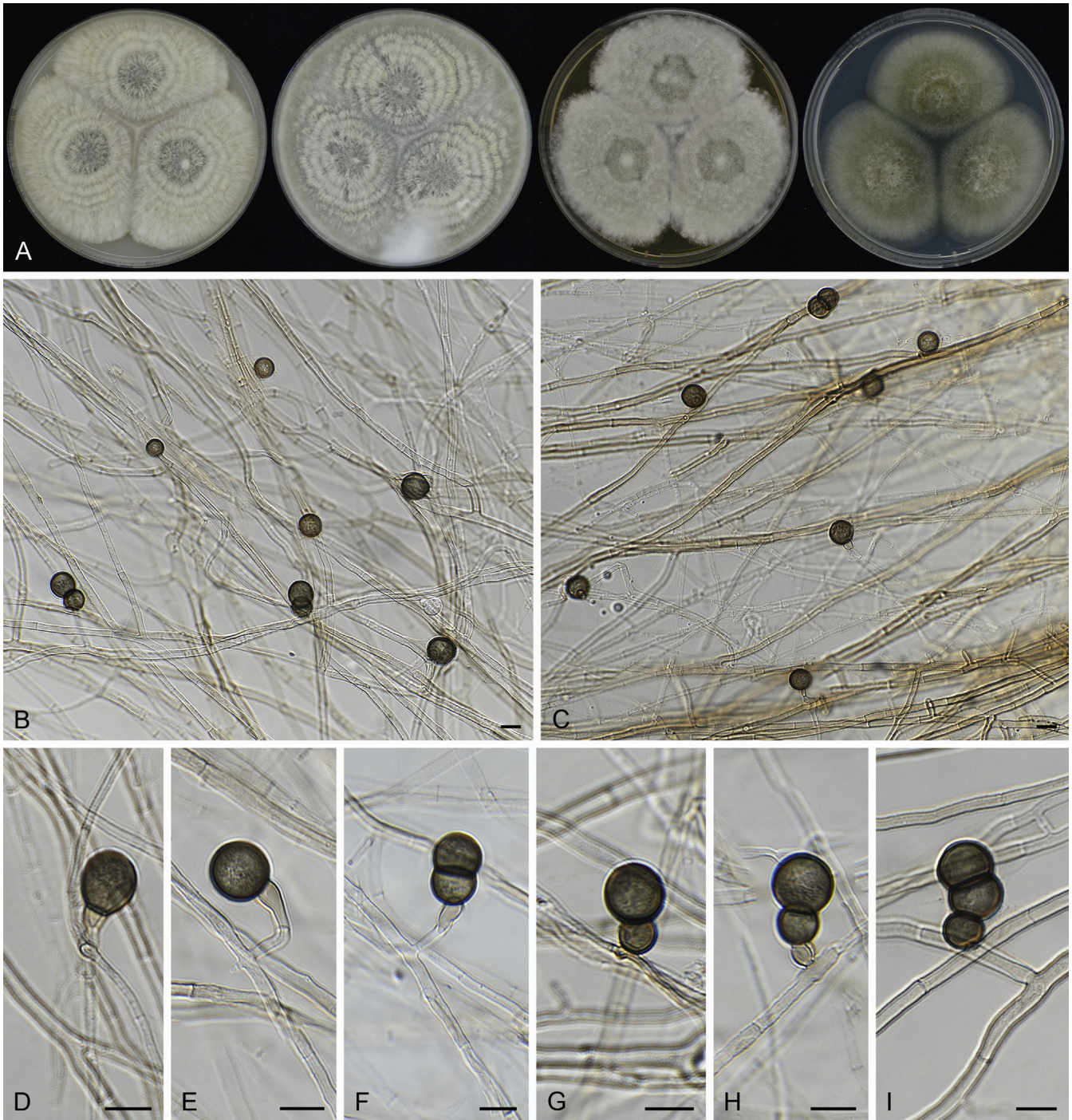


Fig. 55. *Trichocladium jilongensis* (HSAUP II 071485, ex-type culture). **A.** Colonies from left to right on OA, CMA, MEA and PCA after 1 wk incubation. **B–I.** Hyphae, conidiophores and conidia. Scale bars = 10 μ m.

18.5 μ m long, sometimes reduced to intercalary conidiogenous loci in the hyphae. *Conidia* solitary, muriform, obovate, pyriform, ellipsoid, quadrangular or subglobose, constricted at the septa, (9–)13.5–19.5(–22.5) \times (9–)12.5–17(–19) μ m, olivaceous brown to dark brown, sometimes with a basal cell paler than the others.

Culture characteristics: Colonies on OA 36–42 mm diam after 7 d at 25 $^{\circ}$ C; edge entire; obverse greenish black; aerial mycelium pale mouse grey, sparse; reverse greenish black. Colonies on CMA similar to those on OA, 33–39 mm diam after 7 d at 25 $^{\circ}$ C. Colonies on MEA 36–42 mm diam after 7 d at 25 $^{\circ}$ C; edge entire; obverse iron grey; aerial mycelium pale mouse grey, sparse; reverse dark mouse grey to violaceous

black. Colonies on PCA 32–38 mm diam after 7 d at 25 $^{\circ}$ C; edge entire; obverse olivaceous grey to iron grey; with aerial mycelium pale mouse grey, sparse, or absent; reverse olivaceous grey.

Material examined: **The Netherlands**, Utrecht, isolated from meal, unknown date, De Graaff, culture CBS 103.36. **Spain**, Galicia, isolated from forest soil, unknown date, M. Hernández-Restrepo, CBS 132489 = FMR 11941.

Notes: Traditionally, *Monodictys* was characterised by brown muriform conidia produced from monoblastic cylindrical conidiogenous cells (Ellis 1971). From a certain perspective, these can be considered a dictyoconidial analogue to the traditional concepts of the ameroconidial *Humicola* and phragmoconidial *Trichocladium*. Species with such dictyoconidia and ontogeny, originally classified in *Monodictys*, are now scattered over

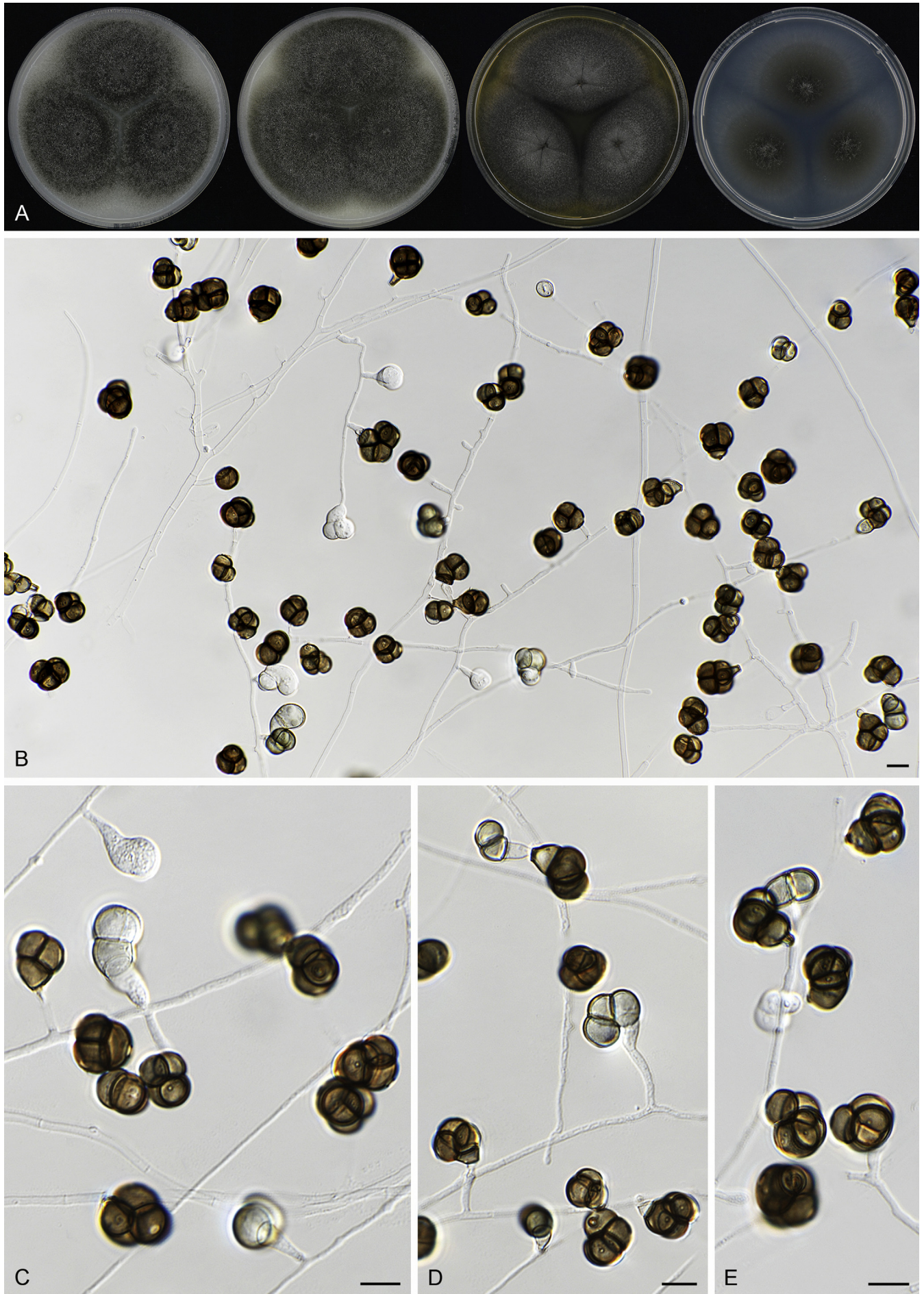


Fig. 56. *Trichocladium nigrosperrum* (CBS 103.36). A. Colonies from left to right on OA, CMA, MEA and PCA after 2 wk incubation. B–E. Hyphae, conidiophores and conidia. Scale bars = 10 μ m.

different classes, i.e. *Dothideomycetes*, *Sordariomycetes* and *Leotiomycetes* (Tanaka *et al.* 2015, Hernández-Restrepo *et al.* 2017). Phylogenetic evidence based on partial LSU sequences (Hernández-Restrepo *et al.* 2017) assigned *Monodictys nigrosperma* to the *Chaetomiaceae* with a close relationship to *Trichocladium*. The four-locus phylogenetic analysis in this study shows that this species belongs to *Trichocladium*. Typification of this species is deferred until representative material from the type locality (USA) is collected.

Trichocladium seminis-citrulli (Sergeeva) X. Wei Wang & Houbraken, **comb. nov.** MycoBank MB824473. Fig. 57.

Basionym: *Chaetomium seminis-citrulli* Sergeeva, Not. Syst. Sect. Crypt. Inst. Bot. Acad. Sci. USSR 11: 113. 1956.

Micromorphology: *Ascomata* usually immersed in thick aerial hyphae, ostiolate, subglobose to broad ovate, mouse grey to dark mouse grey because of the ascomatal hairs, 120–230 µm high, 120–200 µm diam. *Ascomatal wall* translucent, ochreous to brown, composed of angular or irregular cells. *Ascomatal hairs* mainly arising around the ostiole, numerous, spirally coiled with flexuous lower part, 2.5–3.5 µm diam near the base. *Asci* clavate or fusiform, with spore-bearing part 35–48 × 16.5–19 µm and stalks 11–25 µm long, with 8 biseriolate ascospores, evanescent. *Ascospores* rust brown, broad ovoid or broad pyriform, bilaterally flattened, (11.5–)12–13.5(–15) × (9–)10–11(–12) × (7.5–)8–9.5(–10) µm, with an apical and often protuberant germ pore. *Chlamydospore-like structures* intercalary formed in chains or clusters, subglobose or ellipsoidal, hyaline, cylindrical, doliform, 5–12.5 µm diam.

Culture characteristics: Colonies on OA 40–46 mm diam after 7 d at 25 °C; edge entire or lobate; aerial mycelium thick, white to primrose or sulphur yellow, irregularly distributing; soluble pigment ochreous to fulvous; reverse ochreous to apricot. Colonies on CMA similar to those on OA, 35–41 mm diam after 7 d at 25 °C; aerial mycelium thicker than those on OA and covering the whole colonies. Colonies on MEA 35–41 mm diam after 7 d at 25 °C; edge lobate to radially striated; aerial mycelium thick, white; reverse orange caused by soluble pigment. Colonies on PCA 34–40 mm diam after 7 d at 25 °C; edge entire; aerial mycelium absent; soluble pigment; reverse uncoloured.

Material examined: Israel, isolated from dung of goat, unknown date, M. Dreyfuss, culture CBS 637.83. Turkmenistan, isolated from dung of fox, unknown date, K.S. Sergejeva, ex-isotype culture CBS 143.58 = IMI 074953 = VKM F-1952.

Notes: The asexual structures of this species were overlooked in the study by von Arx *et al.* (1986). They are very similar to those found in *T. amorphum*, confirming their close relationship; however, *T. amorphum* does not produce sexual spores (Fig. 45).

Trichocladium uniseriatum (Yu Zhang & L. Cai) X. Wei Wang & Houbraken, **comb. nov.** MycoBank MB824475.

Basionym: *Chaetomium uniseriatum* Yu Zhang & L. Cai, Fungal Biol. 121: 33. 2017.

Micromorphology: Fide Zhang *et al.* (2017a). *Ascomata* ostiolate, dark grey to black, immersed and covered by the aerial mycelium, spherical or nearly so, 170–270 µm diam. *Ascomatal wall* brown, composed of *textura angularis* or *irregularis*. *Ascomatal hairs* slightly straight below, spirally coiled in the upper part, dark brown, unbranched, nearly smooth 2.5–3.5 µm wide near the base. *Asci* cylindrical, with 8 uniseriate ascospores, short-

stalked, 52–63 × 8–11 µm. *Ascospores* arranged uniseriately in the ascus, pale brown, ovate or nearly spherical, 8.5–13 × 8–11.5 × 7–9 µm, without distinct germ pore. *Chlamydospores* present, subhyaline, globose or subglobose, 9–11 µm diam, usually in intercalary chains.

Culture characteristics: Fide Zhang *et al.* (2017a). Colonies up to 50 mm diam on PDA after 6 d at 25 °C; aerial mycelium abundant, lanose, yellow; soluble pigment orange or absent; reverse yellow or orange brown.

Notes: Comparison of sequences from Zhang *et al.* (2017a) with our dataset revealed a close relationship between *T. uniseriatum* and *T. heterothallicum*. These species cluster closely with *T. amorphum*. *Trichocladium heterothallicum* and *T. uniseriatum* produce cylindrical asci and intercalary chlamydospores in chains or clusters (Zhang *et al.* 2017a), providing the morphological evidence that both species are related and belong both to the redefined *Trichocladium*.

Doubted or excluded species

Although we have not completed a thorough revision of types of described species of *Humicola* and *Trichocladium*, we are able to provide some data and insight on the following species. The paper by De Bertoldi (1976) was one of the larger studies of *Humicola*, with thirteen new species described, with several species being distinguished by the then-exotic character of DNA base composition (GC %). The ex-types of several of these species are discussed below. Many Chinese *Humicola* species are not included here; most need to be re-collected from their type localities and cultured to reevaluate their phylogenetic relationships. Many older species remain to be reconsidered in modern terms.

Chaetomium tetrasporum S. Hughes, Trans. Brit. Mycol. Soc. 29: 70. 1946. MycoBank 285138.

Notes: CBS 351.77 (ex wheat field soil, Germany) was originally identified as *Chaetomium tetrasporum* and forms a unique lineage in *Trichocladium* (Figs 1, 2), sister to *T. antarcticum* and *T. crispatum*. This culture is sterile, as mentioned by von Arx *et al.* (1986), and the identity could not be confirmed using phenotypic characters. The ex-type strain of *C. tetrasporum* (IMI 005639) was not included in our study, and the taxonomic position of this taxon therefore remains uncertain.

Humicola asteroides Udagawa & Y. Horie, Bulletin of the National Science Museum Tokyo 14: 528. 1971. MycoBank MB504753.

Notes: Based on ITS (GenBank MH444281) and *rpb2* (GenBank MH444284) sequences from the ex-type culture CBS 561.71 (= ATCC 24018 = NHL 2453, isolated from *Coriolus* sp. in Papua New Guinea), this species is remote from the *Chaetomiaceae*, but closely related to some species of *Melanospora* and *Sphaerodes*. The status of this name should be reconsidered in future revisions of *Ceratostomataceae*, *Melanosporales*.

Humicola aurea De Bert., Canad. J. Bot. 54: 2757. 1976. MycoBank MB315239.

Notes: This species belongs to the *Chaetomiaceae* and shares the same ITS sequence (GenBank MH444277, from the ex-type culture CBS 461.76, isolated from nematode-infested soil in Italy)

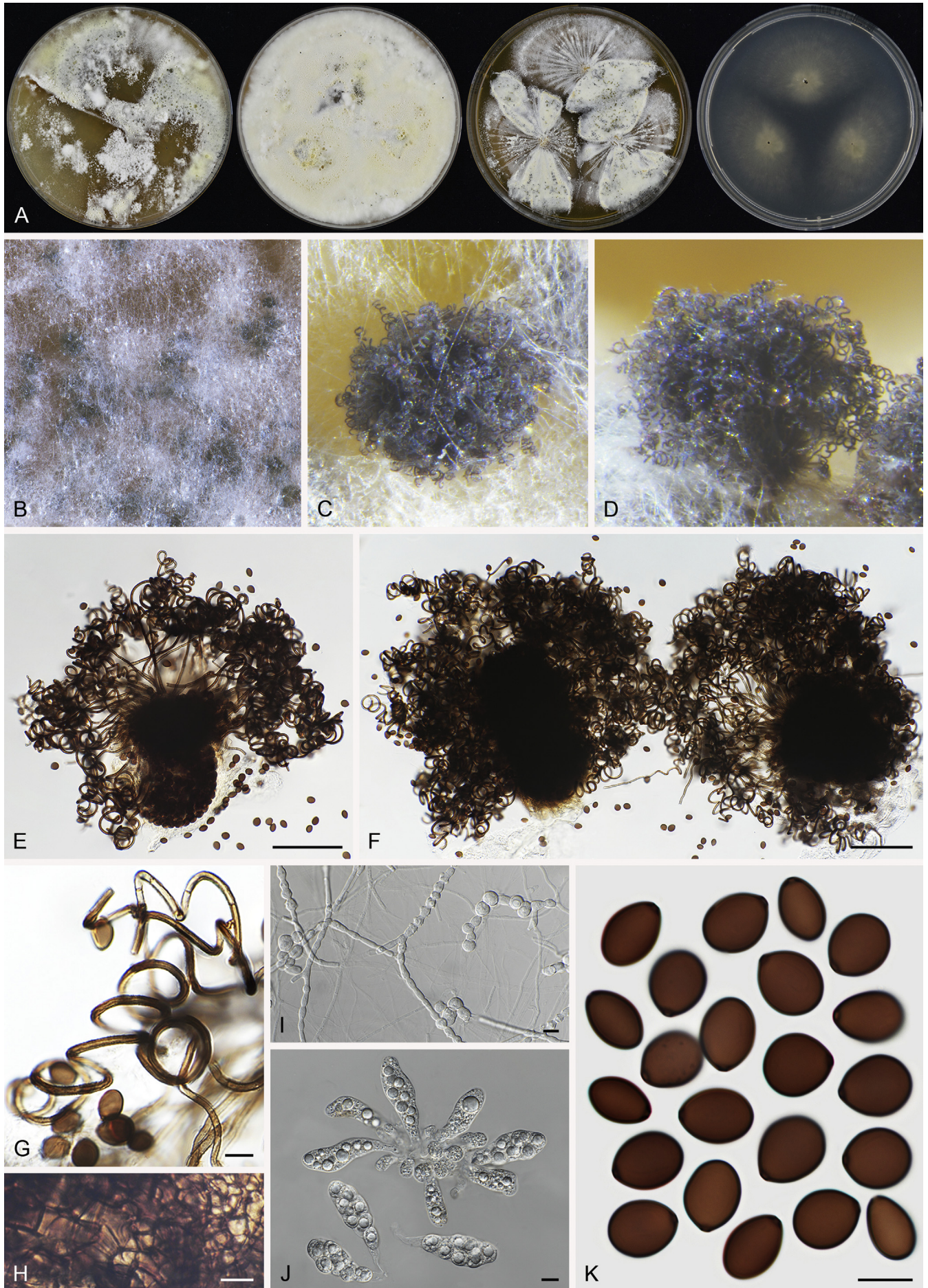


Fig. 57. *Trichocladium seminis-citrulli* (CBS 143.58, ex-type culture). **A.** Colonies from left to right on OA, CMA, MEA and PCA after 5 wk incubation. **B.** Part of the colony. **C.** Mature ascomata on OA, top view. **D.** Mature ascomata on OA, side view. **E–F.** Ascomata mounted in lactic acid. **G.** Terminal ascumal hairs. **H.** Structure of ascumal wall in surface view. **I.** Hyphae and chlamydospore-like structures on hyphae. **J.** Asci. **K.** Ascospores. Scale bars: E–F = 100 μm ; G–K = 10 μm .

with the ex-type cultures of *H. lutea*, *H. repens* and *H. piriforme* (see below). See notes under *H. semispiralis*.

Humicola brunnea* var. *africana Fassat., Česká Mykol. 21: 84. 1967. MycoBank MB332023.

Notes: Our ITS sequence of the ex-type strain (CBS 402.67, CBS 402.67 = ATCC 22630 = CCF 986 GenBank MH494028) is 93 % similar to *Atrocalyx bambusae* (MFLU 11-0150, GenBank KX672149). This is an insufficient match to suggest a genus for this taxon, but its classification should be reconsidered in future studies of the family *Lophiotremataceae*, *Pleosporales*.

Humicola glauca De Bert., Canad. J. Bot. 54: 2757. 1976. MycoBank MB315242.

Notes: This species belongs to the *Chaetomiaceae* and the revised concept of *Humicola* adopted here, and is probably a synonym of *H. semispiralis*, based on ITS (GenBank MH444273) and *tub2* (GenBank MH444286) sequences from the ex-type culture CBS 462.76 (= MUCL 19429, isolated from nematode-infested soil in Italy). A *rpb2* sequence is necessary to confirm this tentative synonymy. Identical ITS sequences were obtained from the ex-type cultures of *H. nivea* and *H. sardiniae*. See also notes under *H. semispiralis* under Taxonomy.

Humicola koreana Hyang B. Lee & T.T.T. Nguyen, Fungal Diversity 78: 94. 2016. MycoBank MB814402.

Notes: *Humicola koreana* produces typical micronematous conidia on denticle-like to cylindrical conidiogenous cells, similar to other *Staphylotrichum* species (Li *et al.* 2016). Only LSU and ITS sequences are available in GenBank. Comparison of these sequences confirmed its morphological affinity *Staphylotrichum*. Typical seta-like conidiophores were not observed in this species, and this might be because of the used growth medium, PDA. More morphological and phylogenetic research is needed to determine the position of *H. koreana*.

Humicola limonisporum Z.F. Zhang & L. Cai, Persoonia 39: 15. 2017. MycoBank MB818248.

Notes: Comparison of the deposited sequences of *H. limonisporum* with our sequence data set indicates that *H. limonisporum* isn't related to *Humicola sensu stricto* as defined in this study (data not shown). The *tub2* and ITS sequence data resolve *H. limonisporum* at the root to the *Staphylotrichum* clade. Based on the *rpb2* sequence dataset, *H. limonisporum* is located at the root of the superclade in which *Staphylotrichum*, *Mycothermus* and *Remersonia* are located. The ascomata of *H. limonisporum* were described to have an "inconspicuous neck" and were covered by undulate to spirally coiled terminal hairs. This ascomata type is not observed in *Staphylotrichum*. The original description of *H. limonisporum* did not give any information about the conidia ontology. More research is needed to determine the phylogenetic placement of *H. limonisporum*.

Humicola lutea De Bert., Canad. J. Bot. 54: 2759. 1976. MycoBank MB315246.

Notes: This species belongs to the *Chaetomiaceae* and the revised concept of *Humicola* adopted here, and is a close relative of *H. semispiralis* based on the ITS (GenBank MH444276) and *tub2* (GenBank MH444288) sequences from the ex-type culture CBS 460.76 (isolated from soil in a *Quercus*

forest in Italy). ITS sequences are identical to those of *H. aurea*, *H. repens* and *H. piriforme*. See notes for *H. semispiralis* under Taxonomy.

Humicola nigrescens Omvik, Mycologia 47: 748. 1955. MycoBank MB298523.

Notes: Based on the ITS (GenBank MH444280) and *rpb2* (GenBank MH444283) sequences from the ex-type culture CBS 208.55 (= ATCC 22714 = IMI 045938 = MUCL 21867, isolated from soil in potato field in Norway), this species belongs to the *Chaetomiaceae* and is probably a synonym of *Trichocladium griseum*. A *tub2* sequence is necessary to confirm this synonymy.

Humicola nivea De Bert., Canad. J. Bot. 54: 2766. 1976. MycoBank MB315248.

Notes: The ex-type culture CBS 469.76 (= MUCL 19436, isolated from the gastroenteric cavity of *Talitrus saltator* in Italy) shares the same ITS sequence (GenBank MH444274) as *H. semispiralis* and the ex-type cultures of *H. glauca* and *H. sardiniae*, suggesting that this species belongs to the *Chaetomiaceae* and the revised concept of *Humicola* adopted here. Sequences of *tub2* and *rpb2* are needed for a conclusive determination of synonymy with *H. semispiralis* (see notes under Taxonomy)

Humicola parvispora Gambogi, G. bot. ital., n.s. 103: 38. 1969. MycoBank MB332028.

Notes: Our ITS sequence of the ex-type strain of *H. parvispora* (CBS 953.68 = ATCC 22715 = MUCL 11820, isolated from forest soil in Italy, GenBank MH444282) does not match other sequenced fungi well, being only 87 % identical with various sequences identified as species of *Preussia*, placed outside and sister to this genus. Although this fungus is obviously not a member of *Chaetomiaceae*, the status of this name should be reconsidered in future revisions of *Sporormiaceae*, *Pleosporales*.

Humicola piriformis De Bert., Canad. J. Bot. 54: 2759. 1976. MycoBank MB315249.

Notes: Only the ITS sequence (GenBank MH444278) is available from the ex-type culture CBS 470.76 (isolated from uncultivated soil in Italy), but shows that this fungus belongs to the *Chaetomiaceae* and the revised concept of *Humicola* adopted here. The ITS sequence is identical to those of *H. aurea*, *H. lutea* and *H. repens*. More work is needed to determine the status of this name. See also notes under *H. semispiralis* in the Taxonomy section.

Humicola repens De Bert., Canad. J. Bot. 54: 2761. 1976. MycoBank MB315250.

Notes: This species belongs to the *Chaetomiaceae* and the revised concept of *Humicola* adopted here, and is sister to *H. lutea*, mentioned above, based on the ITS (GenBank MH444275) and *tub2* (GenBank MH444287) sequences from the ex-type culture CBS 458.76 (isolated from wheat field soil in Italy). The ITS sequence is identical to those of *H. aurea*, *H. lutea* and *H. piriforme*. *Tub2* sequences showed that *H. repens* is probably a separate species from *H. lutea*. See notes under *H. semispiralis* under Taxonomy.

Humicola sardiniae De Bert., Canad. J. Bot. 54: 2761. 1976. MycoBank MB315252.

Notes: This species belongs to the *Chaetomiaceae* and the revised concept of *Humicola* adopted here, and is suggested to be

a synonym of *H. semispiralis*, the same as *H. glauca* mentioned above, based on the ITS (GenBank MH444272) and *tub2* (GenBank MH444285) sequences from the ex-type culture CBS 456.76 (= MUCL 19430, isolated from vineyard soil in Italy). A *rpb2* sequence is awaited for the final determination of synonymy. The ex-type strains of *H. glauca* and *H. nivea* have identical ITS sequences to *H. sardiniae*. See also notes under *H. semispiralis*.

Humicola veronae De Bert., *Canad. J. Bot.* 54: 2766. 1976. MycoBank MB315255.

Notes: Only an ITS sequence (GenBank MH444279) is available now from the ex-type culture CBS 459.76 (= MUCL 19434, isolated from soil from *Quercus* forest in Italy), suggesting that this species belongs to the *Chaetomiaceae* and the revised concept of *Trichocladium* adopted here, where it is in the same subclade with *T. griseum*. Additional sequences and morphological analysis are needed to confirm a robust concept for this species.

Microdochium tainanense (Ts. Watan.) de Hoog & Herm.-Nijh. *Stud. Mycol.* 15: 215. 1977. MycoBank MB317670.

Basionym: *Humicola tainanensis* Ts. Watan., *Trans. Mycol. Soc. Japan* 16: 168. 1975.

Notes: The phylogenetic study of Hernández-Restrepo *et al.* (2016) confirmed the classification of this species in *Microdochium* (*Microdochiaceae*, *Xylariales*).

Staphylotrichum indicum Neeta N Nair, Swapna S & Lini K Mathew, *J. Chem. Pharm. Res.* 7: 1. 2015. MycoBank MB815841.

Notes: The production of thin-walled conidiophores with ornamented conidia was reported on PDA in the original description of *S. indicum* (Nair *et al.* 2015). Sequence data are needed to compare this species with the other species in the genus, and the morphology on PCA remained to be studied.

Staphylotrichum subramanianii Udagawa, *Tropical Mycology*: 150. 1997. MycoBank MB442384.

Notes: This species differs significantly from the other *Staphylotrichum* species by the production of ornamented conidia with several spiral bands (Udagawa 1997). Sequence data are needed to determine whether this species truly belongs to *Staphylotrichum*.

Sporothrix dimorphospora (Roxon & S.C. Jong) Madrid, Gené, Cano & Guarro, *Mycologia* 102: 1200. 2010. MycoBank MB515560.

Basionym: *Humicola dimorphospora* Roxon & S.C. Jong, *Can. J. Bot.* 52: 517. 1974.

Synonym: *Humicolopsis dimorphospora* (Roxon & S.C. Jong) Verona, *G. bot. ital.*, n.s. 111: 88. 1977.

Notes: As summarized by de Beer *et al.* (2013), this species is part of the *Sporothrix inflata* species complex (*Ophiostomatales*); the epithet refers to its synanamorphs, the mycelial *Sporothrix* morph now indicated by its classification, and the humicola-like chlamydospores.

DISCUSSION

The majority of taxonomic studies of *Chaetomiaceae* focus on sexually reproducing species (von Arx *et al.* 1986, 1988, Wang *et al.* 2016b, Zhang *et al.* 2017a,b). In this study, we focused

on integrating hyphomycete genera into the taxonomic outline of this important fungal family. The most important contribution is the linkage of these asexual species to their sexual relatives, more detailed study of the asexual states accompanying perithecial states, and the delimitation of *Humicola*, *Staphylotrichum* and *Trichocladium* as genera including both sexual and asexual species. This is a first step to establish monophyletic concepts for *Humicola* and *Trichocladium* as defined by their type species. The taxonomic positions of other species traditionally classified in *Humicola* and *Trichocladium* but phylogenetically placed outside *Chaetomiaceae* are in a preliminary state and should be a subject for future research; a few names known not to belong to *Chaetomiaceae* are noted above. In addition to these hyphomycetes that lack conidiophores or have micronematous conidiophores, we also studied species of *Botryotrichum*, *Staphylococcum* and *Gilmaniella*, which have similar conidia but more differentiated, branched conidiophores.

Asexual spores in *Humicola* and related genera are produced on vegetative hyphae or on minimally differentiated conidiophores and are usually thick-walled. In the past, several names were used for the description of these thick-walled spores, such as chlamydospores and aleurioconidia (Hambleton *et al.* 2005), botryotrichum-like conidia (Hawksworth 1975, Decock & Hennebert 1997) and conidia (Wu & Zhang 2012, Hernández-Restrepo *et al.* 2017). Typical “botryotrichum-like” conidia are thick-walled and have an irregularly encrusted surface (Domsch *et al.* 2007). In *B. piluliferum*, these conidia are produced on branched conidiophores terminating or intermixed with sterile setae (Wang *et al.* 2016b: Figs 10, 11). The combination of these structures is not observed in any species of *Humicola* and related genera. The term “botryotrichum-like” is therefore not useful to describe the thick-walled spores of *Humicola* and morphologically similar genera in *Chaetomiaceae*.

Based on the discussion in the “Introduction”, the thick-walled spores produced by all species of the redefined genera *Humicola*, *Trichocladium* and *Staphylotrichum* in this study could be considered conidia. In *Humicola*, lateral conidia that arise from a hyphal cell (intercalary conidiogenous cell) are common in each of the investigated species (Fig. 58A–E), which are distinguishable from those in the other genera (Fig. 58 F–N). Such lateral conidia can be used as the diagnostic structures for *Humicola*. Occasionally, *Humicola* conidia can also be produced terminally on the short branches of hyphae which could be interpreted as minimally-differentiated (i.e. micronematous) conidiophores. These short branches show no difference from vegetative hyphae. We can also find spores that are morphologically almost identical to the lateral ones but are intercalary in hyaline vegetative hyphae (such as those in *H. atrobrunnea*, Fig. 6B–C), fitting the usual concept of chlamydospores. Similar conidia are found in several genera and species, including *Trichocladium*, *Staphylotrichum* and *Botryotrichum verrucosum* (= *Thermomyces verrucosum*), where the distinction from the usual concept of chlamydospores is usually clearer. In *Trichocladium*, conidium production is mainly present in “subclade 1” (Figs 1, 2) and this subclade includes the type species *T. asperum*. *Trichocladium* conidiophores are usually pigmented, at least at the upper part, and their conidia are more pigmented and have thicker cell walls than the conidia of *Humicola*. All the *Staphylotrichum* species investigated in this study can also produce conidia on denticle-like conidiogenous cells that arise directly from hyphae (micronematous) in addition to their more

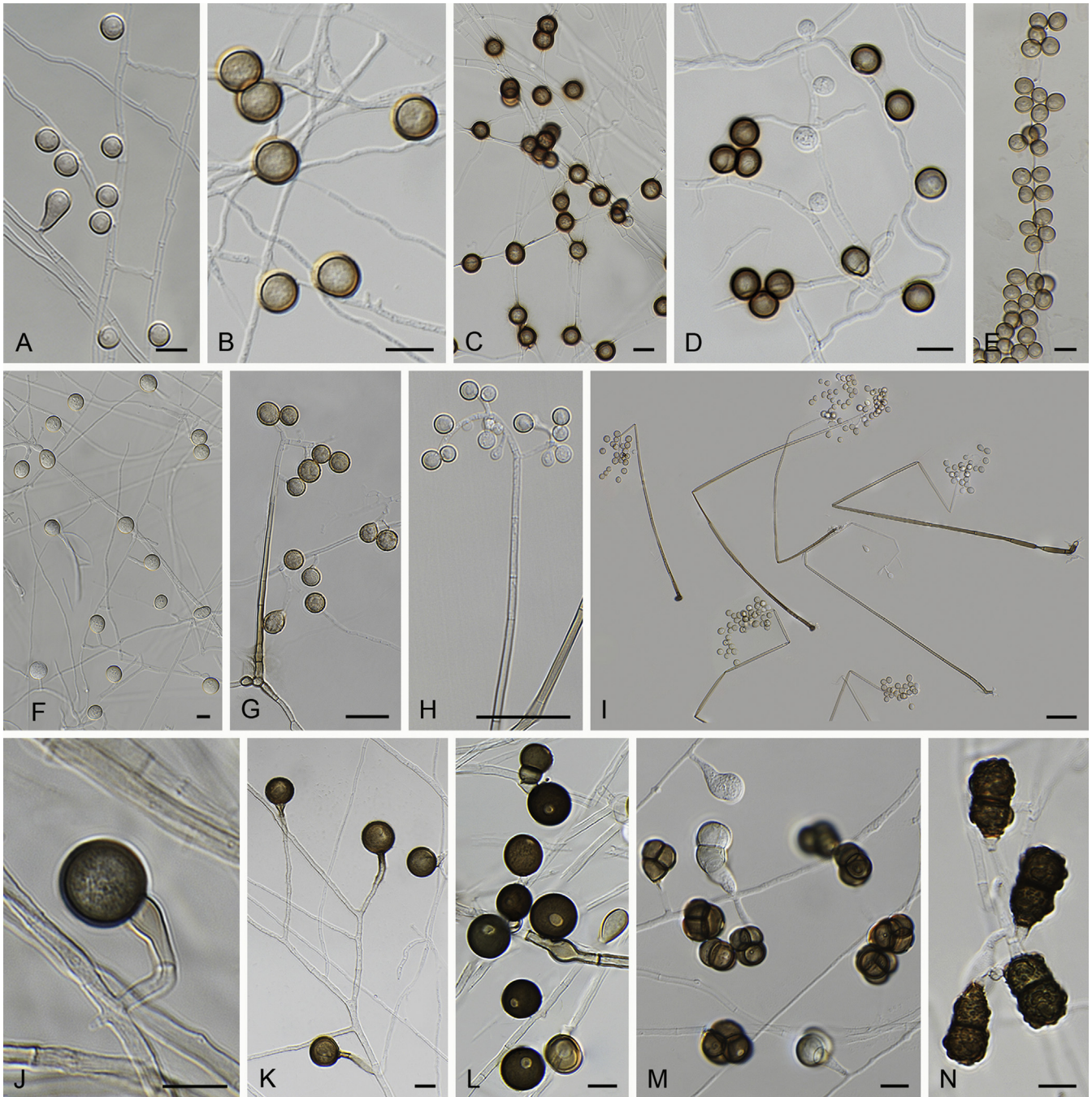


Fig. 58. Morphological differences in the asexual morph of *Humicola*, *Staphylotrichum* and *Trichocladium*. **A–E. *Humicola*:** Hyphae and conidia (A. *Humicola distorta*, ex-type CBS 417.66; B. *H. fuscoatra*, ex-type CBS 118.14; C. *H. longistipe*, ex-type CGMCC 3.13791; D. *H. floriformis*, ex-type CBS 815.97; E. *Humicola fuscobrunnea* ex-type CGMCC 3.13790). **F–I. *Staphylotrichum*:** Hyphae, conidiophores, conidiogenous cells and conidia (F. *S. tortipilum*, ex-type CBS 103.79; G. *S. brevistipitatum*, ex-type CBS 408.67; H–I. *S. coccosporum*, CBS 364.58). **J–N. *Trichocladium*:** Hyphae, conidiophores, conidiogenous cells and conidia (J. *T. jilongense* ex-type HSAUPI07 1485; K. *T. griseum*, ex-neotype CBS 119.14; L. *T. gilmaniellae*, ex-type CBS 388.75; M. *T. nigrospermum*, CBS 103.36; N. *T. asperum*, ex-epitype CBS 903.85). Scale bars: A–F, J–N = 10 μ m; G–I = 20 μ m.

conspicuous conidia on macronematous conidiophores. Both kinds of conidia are almost identical in shape and size (Figs 35–42, 58F–I). These conidia are usually hyaline or nearly so with relatively thin cell walls, morphologically resembling the conidia of *Humicola*. *Staphylotrichum* conidia easily secede from the conidiogenous cells that produce them, while conidia of *Humicola* often do not.

Ascospore morphology is a diagnostic character of sexual *Humicola* species. Ascospores of *Humicola* are limoniform to quadrangular, bilaterally flattened, and have one apical germ pore. They resemble those of *Chaetomium sensu stricto* and of one subclade in *Collariella* (Wang et al. 2016b). No species in the latter genus produces conidia as do the species in *Humicola*.

Furthermore, the limoniform ascospores of *Collariella* species are produced in ascomata with a darkened collar around the ostiolar pore. Perhaps all *Humicola* species are genetically capable of producing both conidia and ascospores. However, some may easily lose their sexual structures after long preservation, may require specific culture conditions, or may be heterothallic, as observed in other genera of *Chaetomiaceae* (e.g. *Myceliophthora*, *Thielavia* and *Trichocladium*).

Acremonium-like synanamorphs were reported in a few *Chaetomium* species, such as *C. elatum* and *C. rectangulare* (Wang et al. 2016a). This study confirmed the occurrence of an acremonium-like morph in several *Humicola* and *Trichocladium* species (e.g. *H. floriformis*, *H. pulvericola*, *H. subspiralis*,

T. griseum). These acromonium-like structures are usually produced together with thick-walled conidia. There is evidence that some *Humicola* species are able to produce ascospores together with thick-walled conidia and acromonium-like conidia, for example, *H. floriformis* (= *Chaetomium floriforme*) (Gené & Guarro 1996). However, we failed to find ascomata in the degenerated cultures of this species. The acromonium-like morphs are phylogenetically scattered in *Chaetomiaceae* and are not an informative character for delimiting clades. Often sparsely produced in culture and hidden by ascomata or more conspicuous pigmented conidia, they are difficult to observe and are often missed. We found the inclined coverglass culturing method helpful for observing those structures. But the lack of diagnostic characters associated with this simple morph, combined with their sparseness, makes them of limited value as a taxonomic character.

The connection of asexual *Staphylotrichum* species to the sexual species *S. longicolleum* (= *Chaetomium longicolleum*) is clearly supported by our morphological and molecular data. The micronematously produced conidia (Fig. 58F) are formed in all investigated sexual *Staphylotrichum* species together with ascomata and ascospores (Figs 35–42). On the other hand, the typical macronematous conidiophores were observed together with sexual structures in one strain of *S. longicolleum* (CBS 100950, Fig. 40C–D). Another noteworthy observation is that the agar medium influences the mode of conidia formation. For example, cultures on PCA produce conidia on typical conidiophores (macronematous), while cultures on OA or CMA often produce numerous micronematous conidia mixed with macronematous ones. The morphological similarity of thick-walled conidia of *Humicola* and micronematous conidia of *Staphylotrichum* can easily result in confusion. Recently, *Humicola koreana* was described without reference to *Staphylotrichum* (Li et al. 2016). Comparison of LSU and ITS sequences deposited in GenBank indicated that this species belongs to *Staphylotrichum* instead of *Humicola*.

Our concept of *Trichocladium* includes a high degree of morphological diversity. Four well-supported subclades occur in *Trichocladium* (Figs 1, 2). There is no morphological rationale for splitting the subclades into separate genera in the *Trichocladium* lineage. Subclade 1 includes species (including the type of the genus, *T. asperum*) that produce thick-walled conidia and these can have a large morphological diversity (Fig. 58J–K). The other three subclades contain species that reproduce sexually. The hyaline asexual structures observed in *T. amorphum* (Fig. 45) and *T. seminis-citrulli* (Fig. 55) might be the undeveloped ascomata. Species with cylindrical asci and ovoid ascospores are found in the subclades 2 and 4, and this character links these two subclades. The phylogenetic distance between the different subclades is low, and this also supports our decision to treat these subclades as one genus.

The redefined concept of *Botryotrichum* (Wang et al. 2016b) results in another example of a group that exhibits highly diverse morphology. *Botryotrichum* included asexual species such as *B. piluliferum*, *B. atrogriseum*; sexual species producing ostiolate ascomata such as *B. murorum* (= *Chaetomium murorum*) and sexual species producing non-ostiolate ascomata such as *B. spirotrichum* (= *Emiliumella spirotricha*). In this study, the asexual species *B. verrucosum* (= *Thermomyces verrucosus*) was added to *Botryotrichum*. This species produces conidiophores and conidia that are distinct from other

Botryotrichum species. Six species were originally described in *Thermomyces*: *Th. dupontii*, *Th. ibadanensis*, *Th. lanuginosus*, *Th. piriformis*, *Th. stellatus* and *Th. verrucosus* (many of these epithets also classified by some authors in *Humicola*, see Index Fungorum; <http://www.indexfungorum.org>, Aug. 2015). Later phylogenetic analyses revealed that *Thermomyces* is polyphyletic. Houbraken & Samson (2011) showed a close relationship between *Talaromyces thermophilus* (= *Th. dupontii*) and *Th. lanuginosus* (*Trichocomaceae*, *Eurotiomycetes*), the type species of the genus. *Thermomyces ibadanensis* shared ITS sequences with *Th. lanuginosus* and might be a synonym of the latter species. *Thermomyces stellatus* belongs to the *Microascaceae* (*Microascales*) and the taxonomic position of *Th. piriformis* is unclear (Houbraken et al. 2014).

Correct identification of a strain is an important step in biological research. The name *Mycothermus thermophilus* was introduced in 2015 (Natvig et al.), and *Humicola insolens* and *Scytalidium thermophilum* are commonly used synonyms of that species. This species attracts attention in biotechnology because of its capability to produce thermostable enzymes and its positive effect in *Agaricus bisporus* cultivation. The older names *H. insolens* and *S. thermophilum* are still frequently used in publications (e.g. Carniel et al. 2017, Meleiro et al. 2017, 2018), leading to confusion among researchers unaware that they are actually working with the organism (e.g. Meleiro et al. 2017, 2018). Furthermore, identification of *My. thermophilus* isolates as *H. insolens* or *S. thermophilum* incorrectly suggest a close relationship with other *Humicola* or *Scytalidium* (*Leotiomyces*) species, which could lead to incorrect assumptions in comparative studies. Besides using the correct name, identification can also be hampered because of the use of an insufficiently precise identification marker. Although ITS is the main fungal barcode, different *Chaetomiaceae* species can share the same ITS sequence (e.g. *Trichocladium asperum* and *T. griseum*, Hambleton et al. 2005) and this locus is therefore not always suitable for species identification (Schoch et al. 2012, Wang et al. 2016a). Wang et al. (2016a) evaluated six loci (LSU, ITS, *tub2*, *rpb1*, *rpb2*, *tef1*) for species of the *Chaetomium globosum* complex, and the *tub2* regions provided the best species resolution (Wang et al. 2016b). Identification using partial *tub2* sequences (600–700 bp; primer pairs T1 & TUB4Rd) is recommended here as the alternative identification marker for all *Chaetomiaceae*. Besides having a good species resolution, this gene also has a high PCR success rate, and public sequence databases (GenBank) are well stocked with beta-tubulin reference sequences. For phylogenetic studies, we recommend sequencing and analysing at least a part of the *rpb2* and *tub2* region. In our experience, the phylogenetic signal in ITS and LSU is low, and these genes are less appropriate for delimiting genera (and species) in *Chaetomiaceae*. Selecting reliable reference sequences is also very important. For example, *Humicola koreana* was described using ITS and LSU sequencing and compared only with *Humicola* species (Li et al. 2016). However, this species belongs to *Staphylotrichum* based on our phylogenetic analyses (data not shown).

Species of *Chaetomiaceae* reported to produce the carcinogenic mycotoxin sterigmatocystin include *Botryotrichum piluliferum*, *Chaetomium cellulolyticum*, *C. longicolleum*, *C. malaysiense*, *C. udagawae*, *C. virescens* and *Humicola fuscoatra* (Rank et al. 2011). The taxonomy of the *Chaetomiaceae* changed significantly in recent years (Wang et al. 2016a,b).

Using the latest taxonomic concepts, none of the reported sterigmatocystin producers belongs to *Chaetomium sensu stricto*. Sterigmatocystin producing species in *Chaetomiaceae* are distributed over four genera and seven species: *Botryotrichum piluliferum* (= *Ch. piluliferum*), *Collariella virescens* (= *Ch. cellulolyticum*, *Ch. virescens*), *Humicola fuscoatra*, *H. malaysiensis* (= *Ch. malaysiense*), *H. udagawae* (= *Ch. udagawae*), *Staphylotrichum longicolleum* (= *Ch. longicolleum*) and *S. tortipilum* (CBS 103.79, listed by Rank *et al.* 2011 under *Ch. longicolleum*). Based on a poorly understood *Chaetomiaceae* taxonomy, Rank *et al.* (2011) speculated that the sterigmatocystin biosynthetic pathway in the *Chaetomiaceae* evolved independently two times. Based on our updated taxonomy and the phylogenetic relationship among the sterigmatocystin producing species (Figs 1, 2), it is tempting to suggest that the pathway evolved at least four times independently. Alternatively, all *Chaetomiaceae* may have part of or the whole sterigmatocystin gene cluster, i.e. the gene cluster is vertically inherited (Rank *et al.* 2011). The immediate precursor for aflatoxin, O-methylsterigmatocystin, is produced by species of *Humicola*, *Collariella* and *Staphylotrichum*, which indicates the potential of *Chaetomiaceae* to produce aflatoxin. Future genome sequencing combined with extrolite analysis of a large set of *Chaetomiaceae* species will give insight into the distribution and origin of the sterigmatocystin pathway and the potential of each of the *Chaetomiaceae* species to produce aflatoxin.

The delimitation of the five genera in this study contributes to an integrated phylogeny of the family *Chaetomiaceae*. The eighteen monophyletic genera currently accepted in the *Chaetomiaceae* are statistically supported in the *rpb2* and the four-locus phylogeny (Figs 1, 2). *Trichocladium* is a sister genus of *Ovatospora* and *Chaetomium*, while *Myceliophthora* and *Dichotomopilus* are closely related to each other. The thermophilic genera *Mycothermus* and *Remersonia* are phylogenetically related. Further studies are needed to establish a comprehensive modern classification of the *Chaetomaceae* and to give better insight into the evolutionary relationships among the species and genera in the family.

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