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Phylogenetic re-evaluation of *Thielavia* with the introduction of a new family *Podosporaceae*

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Abstract: The genus *Thielavia* is morphologically defined by having non-ostiolate ascomata with a thin peridium composed of *textura epidermoidea*, and smooth, single-celled, pigmented ascospores with one germ pore. *Thielavia* is typified with *Th. basicola* that grows in close association with a hyphomycete which was traditionally identified as *Thielaviopsis basicola*. Besides *Th. basicola* exhibiting the mycoparasitic nature, the majority of the described *Thielavia* species are from soil, and some have economic and ecological importance. Unfortunately, no living type material of *Th. basicola* exists, hindering a proper understanding of the classification of *Thielavia*. Therefore, *Thielavia basicola* was neotypified by material of a mycoparasite presenting the same ecology and morphology as described in the original description. We subsequently performed a multi-gene phylogenetic analyses (*rpb2*, *tub2*, ITS and LSU) to resolve the phylogenetic relationships of the species currently recognised in *Thielavia*. Our results demonstrate that *Thielavia* is highly polyphyletic, being related to three family-level lineages in two orders. The redefined genus *Thielavia* is restricted to its type species, *Th. basicola*, which belongs to the *Ceratostomataceae* (*Melanosporales*) and its host is demonstrated to be *Berkeleyomyces rouxiae*, one of the two species in the "*Thielaviopsis basicola*" species complex. The new family *Podosporaceae* is sister to the *Chaetomiaceae* in the *Sordariales* and accommodates the re-defined genera *Podospora*, *Trangularia* and *Cladorrhinum*, with the last genus including two former *Thielavia* species (*Th. hyalocarpa* and *Th. intermedia*). This family also includes the genetic model species *Podospora anserina*, which was combined in *Triangularia* (as *Triangularia anserina*). The remaining *Thielavia* species fall in ten unrelated clades in the *Chaetomiaceae*, leading to the proposal of nine new genera (*Carteria*, *Chrysanthotrichum*, *Condenascus*, *Hyalosphaerella*, *Microthielavia*, *Parathielavia*, *Pseudothielavia*, *Stolonocarpus* and *Thermothielavioides*). The genus *Canariomyces* is transferred from *Microascaceae* (*Microascales*) to *Chaetomiaceae* based on its type species *Can. notabilis*. *Canariomyces* is closely related to the human-pathogenic genus *Madurella*, and includes three thielavia-like species and one novel species. Three monotypic genera with a chaetomium-like morph (*Brachychaeta, Chrysocorona* and *Floropilus*) are introduced to better resolve the *Chaetomiaceae* and the thielavia-like species in the family. *Chrysocorona lucknowensis* and *Brachychaeta variospora* are closely related to *Acrophialophora* and three newly introduced genera containing thielavia-like species; *Floropilus chiversii* is closely related to the industrially important and thermophilic species *Thermothielavioides terrestris* (syn. *Th. terrestris*). This study shows that the thielavia-like morph is a homoplastic form that originates from several separate evolutionary events. Furthermore, our results provide new insights into the taxonomy of *Sordariales* and the polyphyletic *Lasiosphaeriaceae*.

Key words: *Ceratostomataceae*, *Chaetomiaceae*, Multi-gene phylogeny, Non-ostiolate ascomycetes, Taxonomy, 54 Taxonomic novelties.

Taxonomic novelties: new family: *Podosporaceae* X. Wei Wang & Houbraken; **New genera:** *Brachychaeta* X. Wei Wang & Houbraken, *Carteria* X. Wei Wang & Houbraken, *Chrysanthotrichum* X. Wei Wang & Houbraken, *Chrysocorona* X. Wei Wang & Houbraken, *Condenascus* X. Wei Wang & Houbraken, *Floropilus* X. Wei Wang & Houbraken, *Hyalosphaerella* X. Wei Wang & Houbraken, *Microthielavia* X. Wei Wang & Houbraken, *Parathielavia* X. Wei Wang & Houbraken, *Pseudothielavia* X. Wei Wang & Houbraken, *Stolonocarpus* X. Wei Wang & Houbraken, *Thermothielavioides* X. Wei Wang & Houbraken; **New species:** *Acrophialophora teleoafricana* X. Wei Wang & Houbraken, *Canariomyces vonarxii* X. Wei Wang & Houbraken, *Carteria arctostaphyli* X. Wei Wang & Houbraken, *Chrysanthotrichum allolentum* X. Wei Wang & Houbraken, *Chrysanthotrichum leptolentum* X. Wei Wang & Houbraken, *Pseudothielavia subhyaloderma* X. Wei Wang & Houbraken; **New combination:** *Acrophialophora jodhpurensis* (Lodha) X. Wei Wang & Houbraken, *Brachychaeta variospora* (Udagawa & Y. Horie) X. Wei Wang & Houbraken, *Canariomyces arenarius* (Mouch.) X. Wei Wang & Houbraken, *Canariomyces microsporus* (Mouch.) X. Wei Wang & Houbraken, *Canariomyces subthermophilus* (Mouch.) X. Wei Wang & Houbraken, *Chrysanthotrichum lentum* (van Warmelo) X. Wei Wang & Houbraken, *Chrysanthotrichum peruvianum* (Goch.) X. Wei Wang & Houbraken, *Chrysocorona lucknowensis* (J.N. Rai & J.P. Tewari) X. Wei Wang & Houbraken, *Cladorrhinum hyalocarpum* (Arx) X. Wei Wang & Houbraken, *Cladorrhinum intermedium* (Stchigel & Guarro) X. Wei Wang & Houbraken, *Condenascus tortuosus* (Udagawa & Y. Sugiy.) X. Wei Wang & Houbraken, *Floropilus chiversii* (J.C. Cooke) X. Wei Wang & Houbraken, *Hyalosphaerella fragilis* (Natarajan) X. Wei Wang & Houbraken, *Microthielavia ovispora* (Pidopl. *et al.*) X. Wei Wang & Houbraken, *Parathielavia appendiculata* (M.P. Srivast. *et al.*) X. Wei Wang & Houbraken, *Parathielavia hyrcaniae* (Nicot) X. Wei Wang & Houbraken, *Parathielavia kuwaitensis* (Moustafa) X. Wei Wang & Houbraken, *Podospora bulbillosa* (W. Gams & Mouch.) X. Wei Wang & Houbraken, *Pseudothielavia arxii* (Stchigel & Guarro) X. Wei Wang & Houbraken, *Pseudothielavia hamadae* (Udagawa) X. Wei Wang & Houbraken, *Pseudothielavia terricola* (J.C. Gilman & E.V. Abbott) X. Wei Wang & Houbraken, *Stolonocarpus gigasporus* (Moustafa & Abdel-Azeem) X. Wei Wang & Houbraken, *Thermothielavioides terrestris* (Apinis) X. Wei Wang & Houbraken, *Triangularia anserina* (Rabenh.) X. Wei Wang & Houbraken, *Triangularia allahabadensis* (*M.P. Srivast. et al.*) X. Wei Wang & Houbraken, *Triangularia bellae-mahoneyi* (C. Boucher *et al.*) X. Wei Wang & Houbraken, *Triangularia comata* (Milovtz.) X. Wei Wang & Houbraken, *Triangularia longicaudata* (Cain) X. Wei Wang & Houbraken, *Triangularia pauciseta* (Ces.) X. Wei Wang & Houbraken, *Triangularia phialophoroides* (Mouch. & W. Gams) X. Wei Wang & Houbraken, *Triangularia pseudoanserina* (C. Boucher *et al.*) X. Wei Wang & Houbraken, *Triangularia pseudocomata* (C. Boucher *et al.*) X. Wei Wang & Houbraken, *Triangularia pseudopauciseta* (C. Boucher *et al.*) X. Wei Wang & Houbraken, *Triangularia setosa* (G. Winter) X. Wei Wang & Houbraken, *Triangularia verruculosa* (C.N. Jensen) X. Wei Wang & Houbraken; **Typifications: Neotypifications:** *Thielavia basicola* Zopf, *Chaetomium trilaterale* var. *chiversii* J.C. Cooke; **Lectotypifications & Epitypifications:** *Chaetomium jodhpurense* Lodha, *Chaetomium lucknowense* J.N. Rai & J.P. Tewari, *Coniothyrium terricola* J.C. Gilman & E.V. Abbott, *Schizothecium fimicola* Corda.

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INTRODUCTION

The genus *Thielavia* (*Th.*) was established by Zopf (1876) based on *Th. basicola*, which was found in association with the hyphomycete *Thielaviopsis basicola*, and the former was once considered to be the sexual morph of the latter. McCormick (1925) showed that *Th. basicola* was not genetically connected to *Thielaviopsis basicola*, and that they represented two different organisms. Historically, *Thielavia* was once assigned in *Eurotiales* (Saccardo 1882–1931, Booth 1961). Booth (1961) defined *Thielavia* as having dark spherical ascocarps, with a thin pseudoparenchymatous wall without sutures or an ostiole; broadly clavate to ovate, unitunicate asci with 4–8 ascospores, which usually become deliquescent as spores mature; oval to fusoid, brown to black ascospores with one or more germ pores.

The advances in the studies of ontogenetic characters challenged the position of *Thielavia* in *Eurotiales* (Luttrell 1951). With the increasing number of species described in the genus, the similarity between *Thielavia* and *Chaetomidium* became gradually clear. *Chaetomidium* was considered to be the non-ostiolate counterpart of *Chaetomium* (*Ch.*) and was consistently placed in the *Chaetomiaceae* (Zopf 1881, Saccardo 1882). *Chaetomidium* was characterised by non-ostiolate ascomata with well-developed ascomatal hairs, while species with glabrous ascomata were placed in *Thielavia* (Zopf 1881, Saccardo 1882, Whiteside 1962, von Arx 1975). In 1967, von Arx classified *Thielavia* in his newly proposed family *Thielaviaceae* in *Pyrenomycetes* (*Sordariomycetes*), followed by von Arx & Mahmood (1968) and von Arx *et al.* (1988). *Thielaviaceae* is, however, an invalidly introduced family because no Latin description was provided in the original paper (Art. 39.1, Melbourne). Malloch & Cain (1973) suggested the presence or absence of setae or hairs on the ascomata as a criterion of insufficient taxonomic value at genus level. In their broad concept, *Chaetomidium* was treated as a synonym of *Thielavia* and nearly all *Chaetomidium* species were transferred to the latter genus. They also considered *Thielavia* to be closely related to *Chaetomium*, possessing a similar morphology in colony, ascospores, ascocarp initials, ascocarp vestiture and conidial morphs, but differing in having ascocarps without ostioles. In contrast to Malloch & Cain (1973), von Arx (1975) maintained both genera: *Thielavia* for the species with non-ostiolate, glabrous, setose or tomentose ascomata having a thin wall composed of *textura epidermoidea*, and *Chaetomidium* for species with non-ostiolate ascomata having a pseudoparenchymatous wall covered by straight, undulate or circinate and pigmented hairs.

Thielavia sensu Booth (1961) was considered to be a heterogeneous group even without the addition of *Chaetomidium* species (Mouchacca 1973, von Arx 1973, 1975), and there were several attempts to homogenise this genus. *Coniochaetidium* (= *Coniochaeta*) was proposed in *Coniochaetaceae* to accommodate species producing ascospores with a germ slit (Malloch & Cain 1971). *Corynascus* was established for species characterised by ascospores with two germ pores, one at each end, and by the formation of a chrysosporium-like conidial morph (von Arx 1973). Species producing ascospores with two germ pores, but lacking a chrysosporium-like conidial morph, were classified in the genus *Corynascella* (von Arx 1975). *Thielavia* was then restricted to those species having non-ostiolate ascomata with a wall of *textura epidermoidea* and ascospores with a single distinct germ pore (von Arx 1975).

Thielavia sensu von Arx represented the contemporary concept of the genus in which over 40 species have been described. Based on further studies of morphological and ontogenetic characters, *Thielavia* was transferred to *Sordariales* (Hawksworth *et al.* 1983). Following this assignment, the invalid *Thielaviaceae* was not accepted and the genus was widely accepted in the *Chaetomiaceae* (*Sordariales*) (Barr 1990, Eriksson & Hawksworth 1993, Alexopoulos *et al.* 1996, Kirk *et al.* 2008).

Thielavia species exhibit a diverse ecology. The type species is usually associated with *Thielaviopsis basicola*, appearing fungicolous in culture, while almost all the other taxa are saprobes. Most of the species in the genus are found in soil, including desert or soda soils at pH levels up to 11 (von Arx 1975, von Arx *et al.* 1998, Guarro *et al.* 2012, Grum-Grzhimaylo *et al.* 2016). Some species can be coprophilous, endophytes, lichenicolous and even marine-derived (Stchigel *et al.* 2003, Moustafa & Abdel-Azeem 2008, Qadri *et al.* 2014, Han *et al.* 2017). Different species present different growth temperature in culture. Although the majority of species are mesophilic, the genus also includes psychrotolerant, thermotolerant and thermophilic species (Apinis 1963, von Arx *et al.* 1988, Stchigel *et al.* 2002, 2003, Moustafa & Abdel-Azeem 2008, van den Brink *et al.* 2015). The thermotolerant and thermophilic species represent a potential reservoir of industrial-relevant enzymes (Kallio *et al.* 2011, Lu *et al.* 2013, van den Brink *et al.* 2015). Among them, *Th. terrestris* is the most eminent species. Genome analyses and enzymological studies showed that this thermophilic species is able to produce enzymes with biotechnological applications, including the hydrolysis of all major polysaccharides found in biomass (Berka *et al.* 2011, de Vries *et al.* 2011, Syed *et al.* 2014, Xu *et al.* 2015, Woon *et al.* 2016, Gao *et al.* 2017, García-Huante *et al.* 2017). The capacity of *Th. arenaria* to degrade bisphenol A and reduce its acute toxicity presents its bioremediation potential in pollutant removal processes (Mtibaà *et al.* 2018). Several species were found to produce bioactive metabolites, such as inhibitors of prostaglandin biosynthesis in *Th. terricola* (Kitahara *et al.* 1981), antifungal compounds active against *Candida albicans* in *Th. subthermophila* (Qadri *et al.* 2014), and antifouling activities in a *Thielavia* sp. (Han *et al.* 2017). On the other hand, the thermotolerant species *Th. subthermophila* has been reported as the causal agent of keratitis (Theoulakis *et al.* 2009) and fatal cerebral mycoses (Badali *et al.* 2011).

Molecular data have proved that the morphologically-defined *Chaetomidium* was polyphyletic with no evidence showing a relationship with *Thielavia* species (Greif *et al.* 2009, Wang *et al.* 2016b). The genus *Chaetomidium* now has been synonymised with *Chaetomium* (Wang *et al.* 2016b). The separation of *Coniochaeta*, *Corynascus* and *Corynascella* from *Thielavia* was also phylogenetically supported (van den Brink *et al.* 2012, 2015, Maharachchikumbura *et al.* 2016, Wang *et al.* 2016a). Stchigel *et al.* (2002) performed the first phylogenetic study of *Thielavia* on the basis of ITS-5.8S rDNA sequences, including 17 representative species. They selected isolate CBS 229.82 as the representative of the type species, *Th. basicola*, although the pure culture of this isolate grows well on the medium and has no association with *Thielaviopsis basicola*, and its morphology was not compared with the original description in the protologue of *Thielavia basicola*. In their phylogenetic tree,

16 *Thielavia* species and *Melanocarpus thermophilus* (the only reference that is not a *Thielavia* species in their study) formed a moderately supported clade, which was distant from *Th. intermedia*. Based on a five-locus phylogeny of 45 isolates representing 32 species of seven morphologically defined genera in *Chaetomiaceae*, van den Brink *et al.* (2015) showed that ten representative *Thielavia* species clustered in six distant clades throughout the *Chaetomiaceae*. However, the type species, *Th. basicola* was not included in their study, and no taxonomic conclusions were made. In our recent studies of the *Chaetomiaceae*, *Thielavia antarctica* was located in the genus *Trichocladium* (Wang *et al.* 2019), and one isolate (CBS 541.76) that was mentioned as *Th. minuta* by Stchigel *et al.* (2002) was transferred to the genus *Melanocarpus* (Wang *et al.* 2016a). These studies demonstrated that the morphologically-defined *Thielavia* are not monophyletic.

The phylogenetic location of the type species is the key step in the taxonomic studies of *Thielavia*. Since neither a holotype specimen nor ex-type culture of *Th. basicola* were available, our first priority was to obtain suitable material in order to typify the type species. Isolate CBS 178.82 has been used as a representative strain for *Th. basicola*. It presented a morphology well agreeing with the original description of *Th. basicola* (Zopf 1876) and grew in close association with a hyphomycete fungus (its host) possessing the typical morphology of *Thielaviopsis basicola* in culture (von Arx *et al.* 1988). Thus, we targeted the strain CBS 178.82 as a candidate for a neotype. Our research started in identifying its host.

Traditionally defined *Thielaviopsis basicola* has been reclassified in a newly proposed genus *Berkeleyomyces* separate from *Thielaviopsis sensu stricto* (Nel *et al.* 2018). *Thielaviopsis* has a tumultuous taxonomic history. Several recent studies resolved the taxonomy of *Thielaviopsis basicola* and allied genera/species (Mbenoun *et al.* 2014, de Beer *et al.* 2014, Nel *et al.* 2018). Mbenoun *et al.* (2014) epitypified the type species of *Thielaviopsis*, *Thielaviopsis ethacetica*, and transferred it to *Ceratocystis sensu lato*. De Beer *et al.* (2014) phylogenetically resurrected and redefined the genus *Thielaviopsis*. The genus was considered to produce both sexual and asexual morphs, and characterised by the distinctly digitate or stellate appendages on the globose basal part of the ascomata. *Thielaviopsis basicola*, however, was not included in their study. Nel *et al.* (2018) introduced *Berkeleyomyces* to accommodate the traditionally defined *Thielaviopsis basicola*, in which two species were included: *B. basicola* and a new cryptic species, *B. rouxiae*. In their study, no sexual morph was observed in the two *Berkeleyomyces* species, and these two species were morphologically undistinguishable. There is no information, however, which of the two *Berkeleyomyces* species is associated with the holotype of *Thielavia basicola* described by Zopf (1876).

The success in molecular identification of both the sexual *Thielavia* member and its asexual host in the culture of CBS 178.82 enabled us to resolve the taxonomy of *Thielavia*. The aims of the present study were: (i) to resolve the phylogenetic placement of each of the species available in *Thielavia*; (ii) to re-evaluate the phylogenetic relationships between *Thielavia* species and their related taxa; (iii) to re-describe and illustrate the species available in culture that were formerly described in *Thielavia* and those that are related to the studied *Thielavia* species.

MATERIALS AND METHODS

Isolates

Thirty-three *Thielavia* strains were obtained from the CBS culture collection (CBS) housed at the Westerdijk Fungal Biodiversity Institute (WI), Utrecht, the Netherlands. More isolates potentially related to the obtained *Thielavia* strains were selected based on a preliminary phylogenetic analysis of LSU sequences from the in-house database of WI (Vu *et al.* 2019), as well as several cultures of the *Chaetomiaceae* maintained in the Institute of Fungus Resources housed at Guizhou University in China. All the strains used in this study are listed in Table 1.

DNA isolation and sequencing

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 internal transcribed spacer 1 and 2 including the intervening 5.8S nrDNA (ITS), the D1/D2 domains of the 28S nrDNA (LSU) and a part of the DNA-directed RNA polymerase II second largest subunit gene (*rpb2*) and the β-tubulin gene (*tub2*) were selected for phylogenetic inference. In addition, the partial translation elongation factor 1-α (*tef1*-α) gene region was used to delimit species in the *Th. arenaria* species complex, which was amplified with the primers EF1-728 & EF1-2Rd combined with EF1-983F & EF1-2218R (Carbone & Kohn 1999, S. Rehner, AFTOL, http://aftol.org/). The PCR conditions and primers used for PCR amplification and sequencing were the same as those described by Wang *et al.* (2019). Each amplicon was sequenced in both directions using the same set of 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).

Ascomatal formation of the fungicolous *Th. basicola* was induced by growing the culture CBS 178.82 on cornmeal agar (CMA) covered with a cellophane membrane. The young ascomata formed along the edge of the colony (Fig. 7A) were collected for genomic DNA extraction. DNA extraction and PCR amplification were performed as described above. Each of the ITS, LSU *rpb2* and *tub2* amplicons was purified and cloned into pGEM-T vector (Promega, USA). The recombinant plasmids were transformed into *E. coli* DH5α cells (Sambrook *et al.* 1989). About 20–30 recombinant colonies containing the positive plasmids were randomly picked up for each of the amplicons. The colonies were heated at 100 °C for 10 min to release the recombinant DNA fragments, and then were used for sequencing as described above.

Data sets and phylogeny

Novel sequences generated in this study were deposited in GenBank (http://www. ncbi.nlm.nih.gov, Table 1, *tef1*-α marked directly in the phylogenetic tree, Fig. 5). Additional sequences of representative species belonging to the *Chaetomiaceae* were obtained from previous studies (Wang *et al.* 2016a, b, 2019). *Rpb2* reference sequences of other *Sordariales* members were obtained from GenBank and added to our *rpb2* dataset to delimit

Table 1. Details of strains used in this study.

Current name	Culture accession number[1]	previous identification (if different)	Origin	GenBank accession numbers[2]		
				ITS & LSU	*rpb2*	*tub2*
Ceratostomataceae						
Microthecium fimicola	CBS 967.97	*Sphaerodes fimicola*	*Coriolus flabelliformis*, Papua New Guinea	**MK926777**	**MK876739**	**MK926877**
M. quandrangulatum	CBS 112763 **T**	*Sphaerodes quandrangularis*	Soil, Spain	**MK926778**	**MK876740**	**MK926878**
M. retisporum	CBS 995.72	*Sphaerodes retispora* var.*inferior*	Soil, Japan	**MK926779**	**MK876741**	**MK926879**
M. tenuissimum	CBS 112764 **T**	*Sphaerodes tenuissima*	Soil, Spain	**MK926780**	**MK876742**	**MK926880**
M. zobelii	CBS 268.62	*Melanospora zobelii*	Dung of roe, Netherlands	**MK926781**	**MK876743**	**MK926881**
M. zobelii	CBS 341.73	*Melanospora zobelii*	*Coriolus flabelliformis*, Papua New Guinea	**MK926782**	**MK876744**	**MK926882**
Thielavia basicola	CBS 178.82 **NeoT**	n/a[3]		**MK926783**	**MK876745**	**MK926883**
Ceratocystidaceae						
Berkeleyomyces basicola	CBS 341.33	*Thielaviopsis basicola*	Pathogenic *Primula* sp., Netherlands	**MK926784**	**MK876746**	**MK926884**
B. rouxiae	CBS 178.82	*Thielaviopsis basicola*	Diseased root of *Phaseolus vulgaris*, Host of *Thielavia basicola*	**MK926785**	**MK876747**	**MK926885**
Chaetomiaceae						
Acrophialophora ellipsoidea	CBS 102.61	*Acrophialophora levis*	Soil, Belgium	**MK926786**	**MK876748**	**MK926886**
	CGMCC 3.17487	n/a	Compost, China	**MK926787**	**MK876749**	**MK926887**
Acro. fusispora	CBS 380.55 **T**	n/a	Forest soil, India	**MK926788**	**MK876750**	**MK926888**
Acro. hechuanensis	GZUIFR-H08-1 **T**	n/a	Soil, Chongqing City, China	**MK926789**	**MK876751**	**MK926889**
Acro. jodhpurensis comb. nov.	CBS 602.69 **eT**	*Chaetomium jodhpurense*	Substrate unknown, Pakistan	**MK926790**	**MK876752**	**MK926890**
	CBS 509.84	*Chaetomium jodhpurense*	Soil, Kenya	**MK926791**	**MK876753**	**MK926891**
Acro. major	GZUIFR-H57-2 **T**	n/a	Soil,	**MK926792**	**MK876754**	**MK926892**
Acro. nainiana	CBS 100.60 **T**	n/a	Farm soil,India	**MK926793**	**MK876755**	**MK926893**
	CBS 417.67	n/a	Soil, India	**MK926794**	**MK876756**	**MK926894**
Acro. teleoafricana sp. nov.	CBS 281.79 **T**	*Chaetomium jodhpurense*	Soil, Sudan	**MK926795**	**MK876757**	**MK926895**
	CBS 280.79	*Chaetomium jodhpurense*	Soil, Sudan	**MK926796**	**MK876758**	**MK926896**
Brachychaeta variospora gen. et comb. nov.	CBS 414.73 **T**	*Chaetomium variosporum*	Soil, Thailand	**MK926797**	**MK876759**	**MK926897**
Canariomyces arenarius comb. nov.	CBS 507.74 **T**	*Thielavia arenaria*	Desert soil, Egypt	**MK926798**	KM655438	**MK926898**
Can. microsporus comb. nov.	CBS 276.74 **T**	*Thielavia microspora*	Desert soil, Egypt	**MK926799**	**MK876760**	**MK926899**
	CBS 161.80	*Thielavia microspora*	Leaf of *Thymus*, Japan	**MK926800**	**MK876761**	**MK926900**
	CBS 808.73	*Thielavia microspora*	Saline desert soil, Kuwait	**MK926801**	**MK876762**	**MK926901**
Can. notabilis	CBS 548.83 **T**	n/a	Litter of *Phoenix canariensis*, Spain	**MK926802**	**MK876763**	**MK926902**
	CBS 508.74	*Thielavia arenaria*	Desert soil, Egypt	**MK926803**	KM655439	**MK926903**
Can. subthermophilus comb. nov.	CBS 509.74 **T**	*Thielavia subthermophila*	Desert soil, Egypt	**MK926804**	**MK876764**	**MK926904**
Can. vonarxii sp. nov.	CBS 160.80 **T**	*Thielavia subthermophila*	Dried flower of *Hibiscus*, Sudan	**MK926805**	**MK876765**	**MK926905**
	CBS 251.85	*Canariomyces notabilis*	Substrate unknown, Nigeria	**MK926806**	**MK876766**	**MK926906**

Table 1. (Continued).

Current name	Culture accession number[1]	previous identification (if different)	Origin	GenBank accession numbers[2]		
				ITS & LSU	*rpb2*	*tub2*
Carteria arctostaphyli gen. et sp. nov.	CBS 229.82 **T**	*Thielavia basicola*	*Arctostaphylos uva-ursi*, Switzerland	**MK926807**	**MK876767**	**MK926907**
Chrysanthotrichum allolentum gen. et sp. nov.	CBS 644.83 **T**	*Chaetomium lentum*	Soil, USA	**MK926808**	**MK876768**	**MK926908**
Chrysan. lentum comb. nov.	CBS 339.67 **T**	*Chaetomium lentum*	Soil, South Africa	**MK926809**	**MK876769**	**MK926909**
Chrysan. leptolentum sp. nov.	CBS 126.85 **T**	*Chaetomium lentum*	Dung of elephant, Kenya	**MK926810**	**MK876770**	**MK926910**
	CBS 127.85	*Chaetomium lentum*	Dung of moose or deer, Canada	**MK926811**	**MK876771**	**MK926911**
Chrysan. peruvianum comb. nov.	CBS 732.68 **T**	*Thielavia peruviana*	High mountain tundra soil, Peru	**MK926812**	**MK876772**	**MK926912**
Chrysocorona lucknowensis gen. et comb. nov.	CBS 727.71 **eT**	*Chaetomium lucknowense*	Dung of deer, India	**MK926813**	**MK876773**	**MK926913**
	CBS 124.85	*Chaetomium lucknowense*	Dung of burro, Venezuela	**MK926814**	**MK876774**	**MK926914**
	CBS 562.67	*Chaetomium lucknowense*	Dung of rabbit, Germany	**MK926815**	**MK876775**	**MK926915**
	CBS 385.66	*Chaetomium lucknowense*	Soil and vegetable detritus, Venezuela	**MK926816**	**MK876776**	**MK926916**
Condenascus tortuosus gen. et comb. nov.	CBS 610.97	*Thielavia tortuosa*	Soil, India	**MK926817**	**MK876777**	**MK926917**
Floropilus chiversii gen. et comb. nov.	CBS 558.80 **NeoT**	*Chaetomium chiversii*	Dung of moose, Canada	**MK926818**	**MK876778**	**MK926918**
Hyalosphaerella fragilis gen. et comb. nov.	CBS 456.73 **T**	*Thielavia fragilis*	Rhizosphere of *Pennisetum typhoideum* in garden soil, India	KX976693 + KX976791	**MK876779**	KX977042
Madurella fahalii	CBS 129176 **T**	n/a	Mycetoma of a man's foot, Sudan	**MK926819**	**MK876780**	**MK926919**
Mad. mycetomatis	CBS 109801 **T**	n/a	Foot mycetoma of a woman, Sudan	**MK926820**	**MK876781**	**MK926920**
Mad. pseudomycetomatis	CBS 129177 **T**	n/a	Mycetoma of a man's lower jaw, China	**MK926821**	**MK876782**	**MK926921**
	CBS 217.55	n/a	Man hand, Argentina	**MK926822**	**MK876783**	**MK926922**
	CBS 124574	n/a	Black grains discharged by a case of mycetoma, China	**MK926823**	**MK876784**	**MK926923**
Mad. tropicana	CBS 201.38 **T**	n/a	Man foot, Indonesia	**MK926824**	**MK876785**	**MK926924**
	CBS 206.47	n/a	Man foot, Netherlands	**MK926825**	**MK876786**	**MK926925**
Microthielavia ovispora gen. et comb. nov.	CBS 165.75 **T**	*Thielavia ovispora*	Root of *Avena sativa*, Ukraine	**MK926826**	**MK876787**	**MK926926**
Parathielavia appendiculata gen. et comb. nov.	CBS 723.68 **T**	*Thielavia appendiculata*	Leaf of *Punica granatum*, India	**MK926827**	**MK876788**	**MK926927**
	CBS 731.68	*Thielavia appendiculata*	Dung of rabbit, Wales	KM655330 + KM655369	KM655402	KX977041
	CBS 417.73	*Thielavia appendiculata*	Unknown substrat and country	**MK926828**	**MK876789**	**MK926928**
Par. hyrcaniae comb. nov.	CBS 353.62 **T**	*Thielavia hyrcaniae*	Sand dune soil, Iran	KM655329 + KM655368	KM655401	KX977043
Par. kuwaitensis comb. nov.	CBS 945.72 **T**	*Thielavia kuwaitensis*	Desert soil, Kuwait	KM655332 + KM655371	KM655404	KX977044
	CBS 119771	*Thielavia kuwaitensis*	Soil, China	**MK926829**	**MK876790**	**MK926929**

(*continued on next page*)

Table 1. (Continued).

Current name	Culture accession number[1]	previous identification (if different)	Origin	GenBank accession numbers[2]		
				ITS & LSU	*rpb2*	*tub2*
Pseudothielavia arxii gen. et comb. nov.	CBS 603.97 **T**	*Thielavia arxii*	Soil, Chile	**MK926830**	**MK876791**	**MK926930**
	CBS 102199	*Thielavia arxii*	Soil, Chile	**MK926831**	**MK876792**	**MK926931**
Pse. hamadae comb. nov.	CBS 499.83 **T**	*Chaetomium hamadae*	Soil, Japan	**MK926832**	**MK876793**	**MK926932**
Pse. subhyaloderma sp. nov.	CBS 473.86 **T**	n/a	Forest soil, Papua New Guinea	**MK926833**	**MK876794**	**MK926933**
Pse. terricola comb. nov.	CBS 165.88 **eT**	*Thielavia terricola*	Soil, USA	KX976694 + KX976792	**MK876795**	KX977045
	CBS 487.74	*Thielavia terricola*	Kernel of *Arachis hypogaea*, USA	**MK926834**	**MK876796**	**MK926934**
Stellatospora terricola	CBS 811.95 **T**	n/a	Paddy soil, Japan	**MK926835**	**MK876797**	**MK926935**
Stolonocarpus gigasporus gen. et comb. nov.	CBS 112062 **T**	*Thielavia gigaspora*	Dung of *Camelus dromedarius*, Egypt	**MK926836**	**MK876798**	**MK926936**
Thermothielavioides terrestris gen. et comb. nov.	CBS 117535 **T**	*Thielavia terrestris*	Soil, UK	**MK926837**	**MK876799**	**MK926937**
	CBS 492.74	*Thielavia terrestris*	Soil, Japan	**MK926838**	**MK876800**	**MK926938**
	CBS 546.86	*Thielavia terrestris*	Unknown substrat and country	**MK926839**	**MK876801**	**MK926939**
	CBS 351.90	*Thielavia terrestris*	Cellulose in soil, Malaysia	**MK926840**	**MK876802**	**MK926940**
Lasiosphaeriaceae						
*Apiosordaria microcarpa**	CBS 692.82 **T**	n/a	Rice-field soil, Japan	**MK926841**	**MK876803**	**MK926941**
*Podospora decidua**	CBS 254.71 **T**	n/a	Dung of hare, Birao	**MK926842**	**MK876804**	**MK926942**
*Pod. fabiformis**	CBS 112043 **T**	n/a	Animal dung, Australia	**MK926843**	**MK876805**	**MK926943**
*Pod. fibrinocaudata**	CBS 315.91 **T**	n/a	Dung of dusky footed wood rat, USA	**MK926844**	**MK876806**	**MK926944**
*Pod. glutinoides**	CBS 116865	n/a		**MK926845**	**MK876807**	**MK926945**
*Pod. inaequalis**	CBS 356.49 **T**	n/a	Daucus carot seed, USA	**MK926846**	**MK876808**	**MK926946**
*Pod. longicollis**	CBS 368.52 **T**	n/a	Deteriorating material, Panama	**MK926847**	**MK876809**	**MK926947**
*Pod. prolifica**	CBS 250.71 **T**	n/a	Dung of *Cobus defassa*, Central African Republic	**MK926848**	**MK876810**	**MK926948**
*Pod. selenospora**	CBS 109403 **T**	n/a	Forest soil, Chile	**MK926849**	**MK876811**	**MK926949**
Zopfiella karachiesis	CBS 657.74	n/a	Arid soil, Egypt	**MK926850**	**MK876812**	**MK926950**
Z. marina	CBS 155.77 **T**	n/a	Marine mud, Taiwan, China	**MK926851**	**MK876813**	**MK926951**
Z. pilifera	CBS 413.73 **T**	n/a	Soil, Japan	**MK926852**	**MK876814**	**MK926952**
Z. submersa	CBS 698.96 **T**	n/a	Submerged dead culms, Iraq	**MK926853**	**MK876815**	**MK926953**
Z. tabulata	CBS 230.78	n/a	Dung of porcupine, Quebec, Canada	**MK926854**	**MK876816**	**MK926954**
Z. tardifaciens	CBS 670.82 **T**	n/a	Dung of cow, Argentina	**MK926855**	**MK876817**	**MK926955**
Podosporaceae fam. nov.						
Cladorrhinum foecundissimum	CBS 180.66 **T**	n/a	Soil, Netherlands	**MK926856**	**MK876818**	**MK926956**
Clad. hyalocarpum comb. nov.	CBS 322.70 **T**	*Thielavia hyalocarpa*	Soil, Netherlands	**MK926857**	**MK876819**	**MK926957**
	CBS 102198	*Thielavia hyalocarpa*	Forest soil, Spain	**MK926858**	**MK876820**	**MK926958**
Clad. intermedium comb. nov.	CBS 433.96 **T**	*Thielavia intermedia*	Soil, India	**MK926859**	**MK876821**	**MK926959**

Table 1. (Continued).

Current name	Culture accession number[1]	previous identification (if different)	Origin	GenBank accession numbers[2]		
				ITS & LSU	*rpb2*	*tub2*
	CBS 100257	*Thielavia* sp.	Soil, Tunisia	**MK926860**	**MK876822**	**MK926960**
Podospora bulbillosa comb. nov.	CBS 304.90 **T**	*Cladorrhinum bulbillosum*	Desert soil, Egypt	**MK926861**	**MK876823**	**MK926961**
Pod. fimicola	CBS 482.64 **eT**	n/a	Dung of cow, Switzerland	**MK926862**	**MK876824**	**MK926962**
	CBS 990.96	n/a	Dung of horse, New Zealand	**MK926863**	**MK876825**	**MK926963**
*Triangularia anserina comb. nov.***	S mat+ **T**	*Podospora anserina*				
	CBS 433.50	*Podospora pauciseta*	Dung of cow, Canada	**MK926864**	**MK876826**	**MK926964**
Trian. allahabadensis comb. nov.	CBS 724.68 **T**	*Sordaria allahabadensis*	Flower of *Carica papaya*, India	**MK926865**	**MK876827**	**MK926965**
Trian. backusii	CBS 539.89 **T**	*Apiosordaria backusii*	Soil, USA	**MK926866**	**MK876828**	**MK926966**
	CBS 106.77	n/a	Sandy soil, Japan	**MK926867**	**MK876829**	**MK926967**
Trian. bambusae	CBS 352.33 **T**	*Triangularia bambusae*	Shoot of *Bambusa* sp., unknown country	**MK926868**	**MK876830**	**MK926968**
Trian. longicaudata comb. nov.	CBS 252.57 **T**	*Zopfiella longicaudata*	Dung of horse, Canada	**MK926869**	**MK876831**	**MK926969**
Trian. pauciseta comb. nov.	CBS 451.62	*Podospora pauciseta*	Dung of cow, Argentina	**MK926870**	**MK876832**	**MK926970**
Trian. phialophoroides comb. nov.	CBS 301.90 **T**	*Cladorrhinum phialophoroides*	Desert sandy soil, Egypt	**MK926871**	**MK876833**	**MK926971**
Trian. setosa comb. nov.	CBS 311.58	*Podospora setosa*	Soil, UK	**MK926872**	**MK876834**	**MK926972**
	CBS 369.59	*Podospora setosa*	Dung of horse, UK	**MK926873**	**MK876835**	**MK926973**
Trian. verruculosa comb. nov.	CBS 148.77	*Apiosordaria verruculosa*	Soil, Japan	**MK926874**	**MK876836**	**MK926974**
Sordariaceae						
Boothiella tetraspora	CBS 887.97	n/a	Sand, Spain	**MK926875**	**MK876837**	**MK926975**
	CBS 334.67	n/a	Soil, Pakistan	**MK926876**	**MK876838**	**MK926976**

*: Generic affiliation remains to be re-evaluated.
**: Sequences obtained from genome.
[1] **T**: ex-type strains; **eT**: ex-epitype strain designated in this study; **NeoT**: ex-neotype strain designated in this study.
[2] Sequences generated in this study indicated in **bold**.
[3] n/a: No name changed.

the family *Chaetomiaceae* and to study the relationship between *Chaetomiaceae* and non-chaetomiaceae species. Those reference sequences retrieved from GenBank database or from the released genomic data were marked directly in the phylogenetic trees (Figs 1, 2, 4, 6; in parentheses behind the strain numbers). The phylogenetic relationships of *Thielavia* species with related taxa were further studied in a combined ITS, LSU, *rpb2* and *tub2* data set. Additionally, several small datasets were made to identify the host member in the culture CBS 178.82 (ITS and *rpb2*), determining the taxonomic placement of *Th. basicola* (LSU), and to delimit species in the *Th. arenaria* species complex (*tub2* and *tef1*-α) and the *Podospora anserina/pauciseta/comata* species complex (ITS, *Rchr3*, *Rchr4*, and *Rchr6*). Alignments were made using the web interface MAFFT v. 7 (Katoh & Standley 2013), followed by manual adjustments with MEGA v. 6 (Tamura *et al.* 2013). Phylogenetic analyses were performed using Maximum-Likelihood (ML) and Bayesian Inference (BI) approaches under RAxML-HPC2 on XSEDE 8.2.10 (Stamatakis 2014) using the Cipres Science gateway portal (Miller *et al.* 2010) and MrBayes v. 3.2.6 (Ronquist *et al.* 2012), respectively. For BI, the best evolutionary model for each locus was determined using MrModeltest v. 2.0 (Nylander 2004). The Maximum-Likelihood analysis used the GTRGAMMA model. Obtained trees were viewed in FigTree v. 1.1.2 (Rambaut 2009) and subsequently visually prepared and edited in Adobe® Illustrator® CS6. Confident branch support is defined as Bayesian posterior probabilities (PP) $\geq$ 0.95 and maximum likelihood bootstrap values (ML-BS) $\geq$ 70 %.

Morphology

Colony morphology and microscopic morphology were examined as described by Wang *et al.* (2019). In short, strains were grown on OA, cornmeal agar (CMA), malt extract agar (MEA) and potato carrot agar (PCA) at 25 °C (or 37 °C for *Thermothielavioides terrestris*) in darkness. After 7 d incubation, colony diameters on the various media were measured. Incubation on OA continued and growth was monitored until informative structures such as ascomata, asci, ascospores and/or an asexual morph were observed. Morphological data on those structures were obtained from microscopic slides under a Nikon Eclipse 80i compound microscope equipped with differential interference

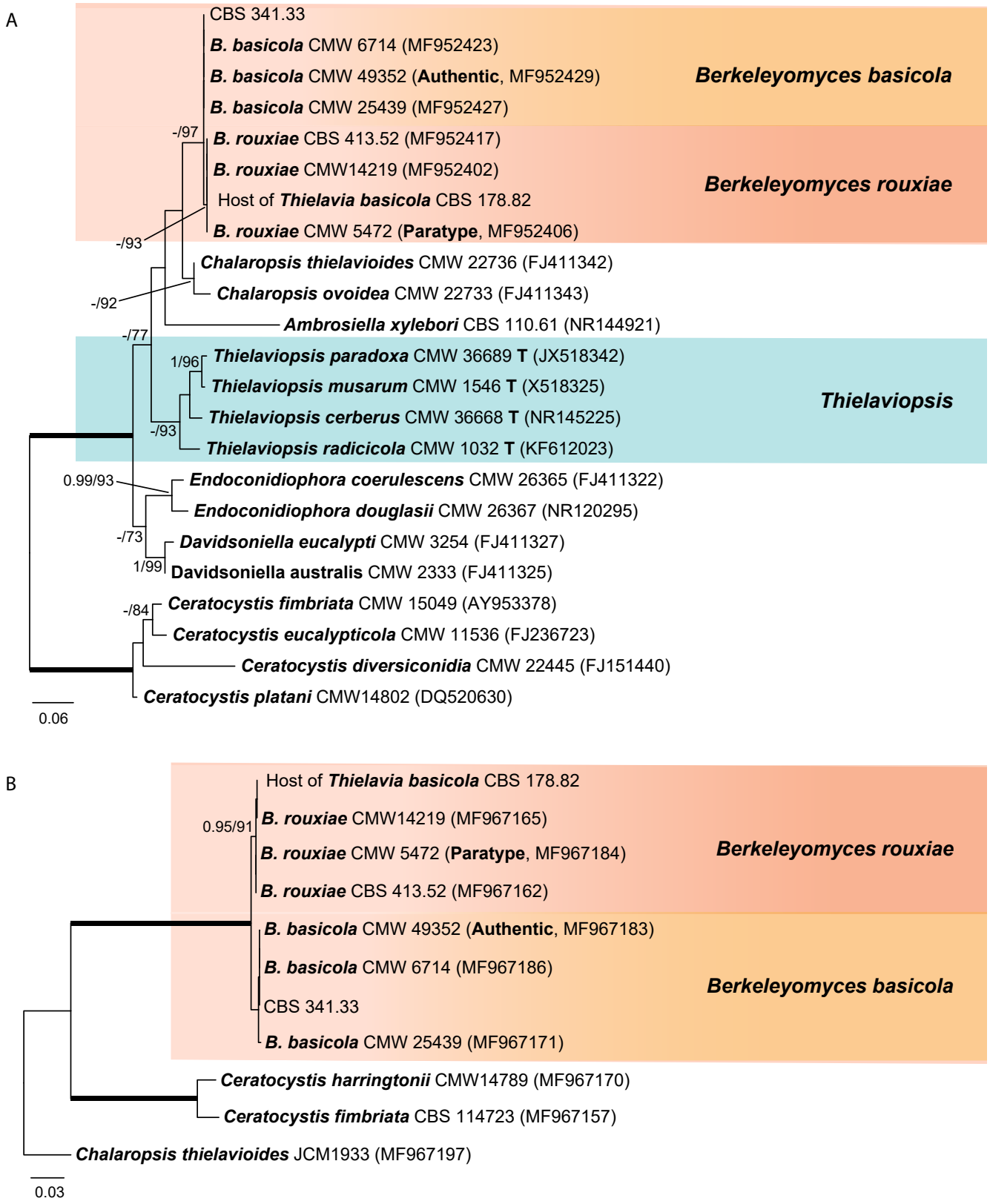


Fig. 1. Phylogenetic identification of the host partner in the culture CBS 178.82 based on the separate analyses of partial gene sequences of ITS (**A**) and *rpb2* (**B**). Maximum-Likelihood (ML) trees are showed with the confidence values indicated at the notes: the posterior probabilities from the Bayesian analysis before the backslash, bootstrap proportions from the ML analysis after the backslash. The "-" means lacking statistical support (<70 % for bootstrap proportions from ML analysis; <0.95 for posterior probabilities from Bayesian analysis). The branches with full statistical support (PP = 1.0; ML-BS = 100 %) are highlighted by thickened branches. Targeted genus/species clades are discriminated with boxes in different colours. The scale bar shows the expected number of changes per site. Type strains are marked with "**T**" after the culture number. The ITS tree is rooted with the *Ceratocystis* clade containing four species. The *rpb2* tree is rooted with *Chalaropsis thielavioides* JCM1933.

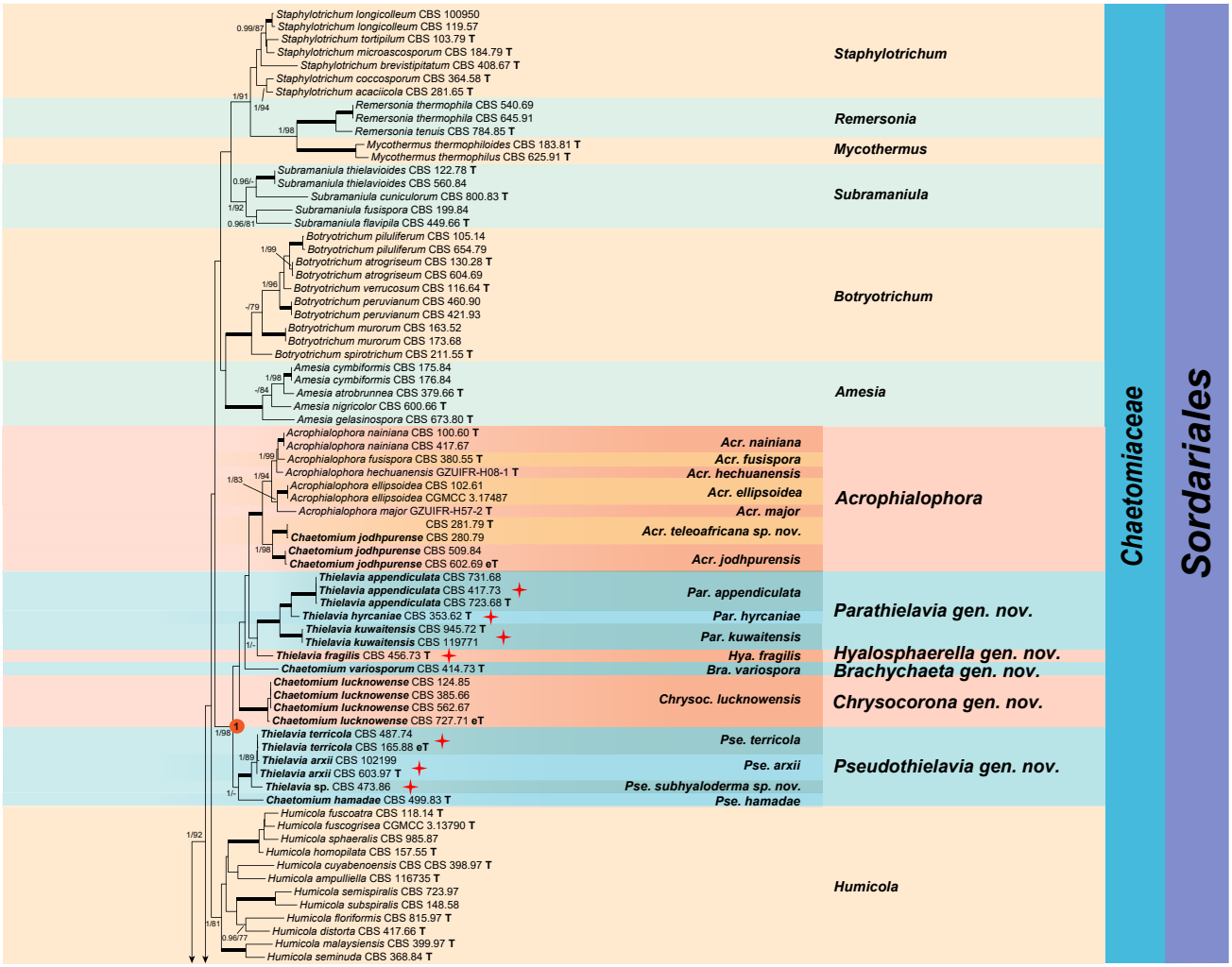


Fig. 2. Phylogenetic tree inferred from ML analysis of the partial *rpb2* gene region alignment. The confidence values are indicated at the notes same to Fig. 1. Genus/species clades in the *Chaetomiaceae* and potential family/genus lineages in the other traditional family are discriminated with boxes in different colours. Type strains are marked with "**T**" after the culture number. "**eT**" or "**NeoT**" represents the ex-epitype or ex-neotype designated in the this study. Thielavia-like strains are indicated with a red star on its right side. The reference sequences retrieved from GenBank database or from the released genomic data were marked behind the strain numbers. The scale bar shows the expected number of changes per site. The tree is rooted with three species in the *Microascales*.

contrast (DIC) illumination, and from observation under Nikon SMZ 1500 dissecting-microscope. At least 30 measurements were made for all morphologically informative features.

RESULTS

Phylogeny

The matrix statistics and related characters resulting from the phylogenetic analyses of all the datasets in the present study are summarised in Table 2.

Phylogenetic identification of the host of *Thielavia basicola* (Fig. 1)

The ITS and *rpb2* sequences generated from the host of *Th. basicola* in culture CBS 178.82 were added and aligned with the sequences used in Nel *et al.* (2018). The asexual host in the culture CBS 178.82 resides in the ITS (Fig. 1A) and *rpb2* (Fig. 1B) phylograms with three strains identified as *Berkeleyomyces rouxiae*. The reference strain CBS 341.33 clusters in the sister clade *Berkeleyomyces basicola*. These two species proved to be separated from the *Thielaviopsis* lineage as shown in the ITS tree (Fig. 1A).

Phylogeny of morphologically identified *Thielavia* species and potentially related taxa

The *rpb2* and the concatenated ITS, LSU, *tub2* and *rpb2* sequences data set were both used to resolve the phylogenetic positions of the studied *Thielavia* species. Thirty-three strains that were previously described or identified in *Thielavia* and 34 additional strains were included in our study. The latter 34 strains were found to be related to the targeted species based on a preliminary phylogenetic analysis of LSU sequences (data not shown) and the majority of them belonged to the *Chaetomiaceae*, *Lasiosphaeriaceae* and *Sordariaceae* in *Sordariales*. In the *Chaetomiaceae*, five representative species of *Acrophialophora* (nine strains), five *Madurella* species (eight strains), *Boothiella* (two strains) and six chaetomium-like species (16 strains) were selected, which were not yet included in our previous studies within this family. Twenty-seven species presumably belonging to the *Lasiosphaeriaceae* were included

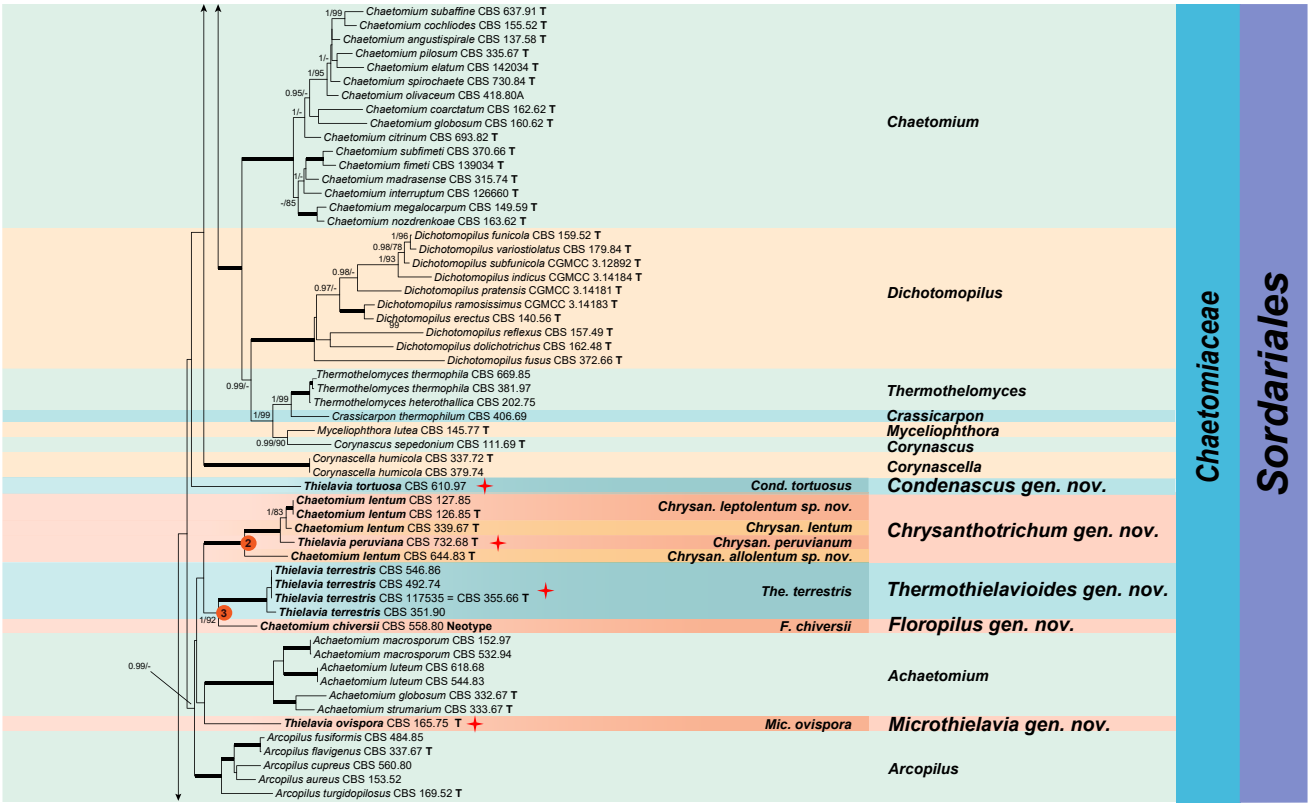


Fig. 2. (Continued).

which were traditionaly identified in the genera *Apiosordaria*, *Cladorrhinum*, *Podospora*, *Triangularia* or *Zopfiella*. The remaining strains were traditionally identified in *Stellatospora* (considered to be in the *Sordariaceae*), *Microthecium* (six isolates) in the *Ceratostomataceae* (*Melanosporales*) or *Canariomyces notabilis* (considered to be in the *Microascaceae*, *Microascales*).

Rpb2 phylogeny (Fig. 2)

The *rpb2* data set contained sequences of 283 strains. Compared with the four-locus concatenated dataset, 26 additional species of *Lasiosphaeriaceae* were included, representing the genera *Bombardia*, *Cercophora*, *Corylomyces*, *Jugulospora*, *Lasiosphaeria*, *Rinaldiella*, *Strattonia* and *Schizothecium*. Seven species belonging to *Gelasinospora*, *Neurospora* and *Sordaria* in *Sordariaceae* were included in the analysis, as well as *Xylaria hypoxylon*, a representative of the order *Xylariales*. *Microascus trigonosporus* and the two species of *Berkeleyomyces* (*Microascales*) were selected as outgroup species, based on the phylogenetic relationships between orders in the *Sordariomycetes* (Maharachchikumbura *et al.* 2016). The ML tree topology confirmed the tree topology obtained from the BI analysis, and therefore, only the ML tree is presented with the PP values indicated at the nodes.

The resulting phylogenetic tree resolved the 33 studied *Thielavia* strains as 18 species-level clades (marked with an orange star) in 11 generic lineages. Fifteen species-level clades belonged to six well-supported main clades (indicated with 1–6 in red circle boxes at the nodes). The remaining three strains formed single lineages in the *Chaetomiaceae*: *Thielavia tortuosa* (CBS 610.97), *Th. ovispora* (CBS 165.75) and the strain CBS 229.82 which was once used as a representative strain of *Th. basicola* (Stchigel *et al.* 2002). Four of the recognised main clades belonged to the *Chaetomiaceae* (Clades 1–4; PP = 1 and ML-BS $\geq$ 92 %). Clade 1 (PP = 1; ML-BS = 98 %) grouped into six lineages: three encompassing *Thielavia* species, two chaetomium-like species (*Ch. lucknowense* and *Ch. variosporum*) and the existent genus *Acrophialophora*. Clade 2 (PP = 1; ML-BS = 100 %) consisted of *Th. peruviana* (ex-type CBS 732.68) and four isolates of *Ch. lentum*, which were split into three species lineages. In Clade 3 (PP = 1; ML-BS = 92 %), *Ch. chiversii* (ex-type CBS 558.80) clustered close but separate from the thermophilic species *Th. terrestris*. Clade 4 (PP = 1; ML-BS = 100 %) consisted of four generic lineages: *Th. gigaspora* (ex-type CBS 112062) clustered close but separate from the existent genus *Madurella* and an unknown lineage (G2B); *Th. arenaria* and *Th. subthermophila* grouped with the type species of *Canariomyces*, *Can. notabilis*, which formed a sister clade to another species, *Th. microspora*.

The fifth main clade (Clade 5, PP = 1 and ML-BS = 80 %) was part of the polyphyletic *Lasiosphaeriaceae* containing three fully-supported generic lineages (PP = 1 and ML-BS = 100 %). Two "*Thielavia*" species, *Th. hyalocarpa* and *Th. intermedia*, grouped with the type species of *Cladorrhinum*, *Clad. foecundissimum*. Two isolates of *Podospora fimicola*, the type species of *Podospora* (*Pod.*), grouped with *Clad. bulbillosum*. The third lineage contained members of five genera: *Apiosordaria*, *Cladorrhinum*, *Podospora*, *Triangularia* and *Zopfiella*. The type species of both *Apiosordaria* (*A. verruculosa*, 1967) and *Triangularia* (*Trian. bambusae*, 1934) were included in this lineage. The type species of *Zopfiella*, *Z. tabulata* (ex-type CBS 230.78, marked with a red triangle on the right), was located in another lineage, distant from Clade 5 in the polyphyletic *Lasiosphaeriaceae*. In Clade 6 (PP = 1 and ML-BS = 100 %), the representative isolate of the type species *Th. basicola*, CBS 178.82, clustered close but separate from the genus *Microthecium* in the *Ceratostomataceae*

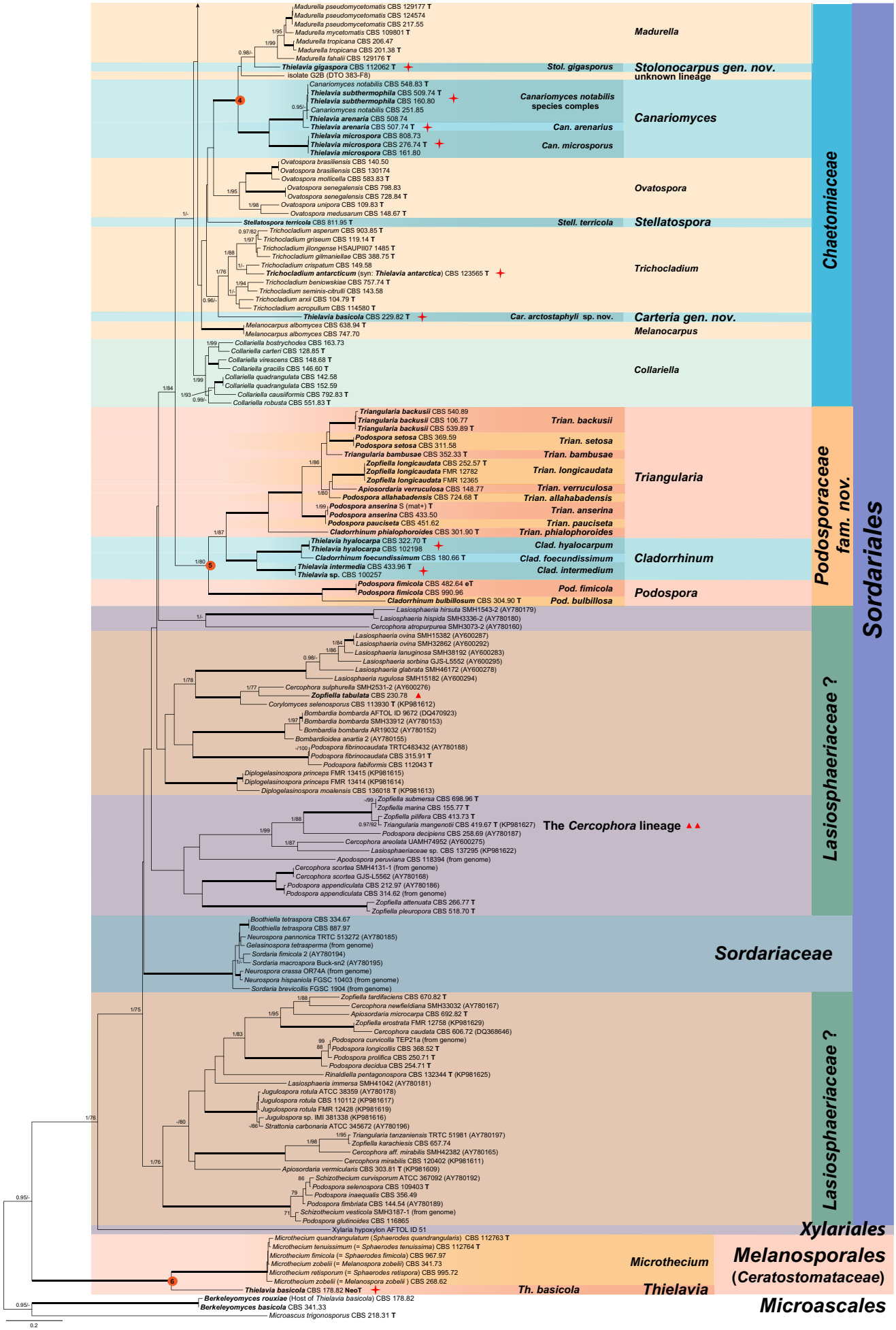


Fig. 2. (Continued).

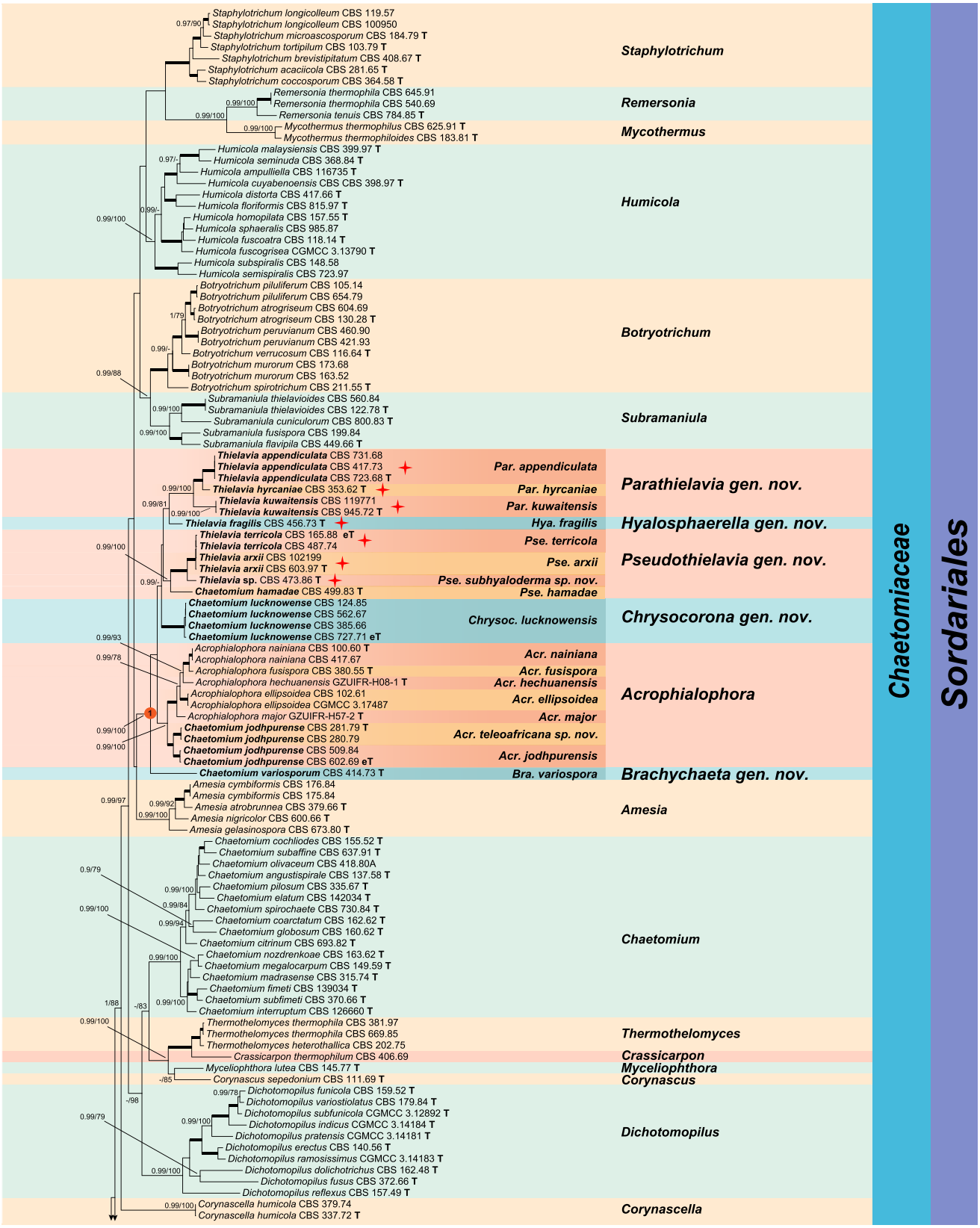


Fig. 3. Phylogenetic tree resulting from ML analysis of the concatenated partial *rpb2*, *tub2*, ITS and LSU gene region alignment, with the confidence values indicated at the notes same to Fig. 1. Genus/species clades in the *Chaetomiaceae* and potential family/genus lineages in the other traditional family are discriminated with boxes in different colours. Type strains are marked with "**T**" after the culture number. "**eT**" represents the ex-epitype designated in this study. Thielavia-like strains are indicated with a red star on its right side. The scale bar shows the expected number of changes per site. The tree is rooted with three species in the *Microascales*.

(*Melanosporales*). Members of the monophyletic family *Sordariaceae* form a distinct lineage, while members of the *Lasiosphaeriaceae* are distributed over at least four unrelated clades (with exception of Clade 5). *Stellatospora terricola* formed a single lineage in the *Chaetomiaceae* rather than in the *Sordariaceae*, while *Boothiella tetraspora* clustered in the *Sordariaceae*.

Four-locus phylogeny (Fig. 3)

The concatenated alignment included 224 isolates, with the same outgroups as in the *rpb2* phylogeny. The sequence dataset consisted of 3 648 characters (including gaps) composed of four

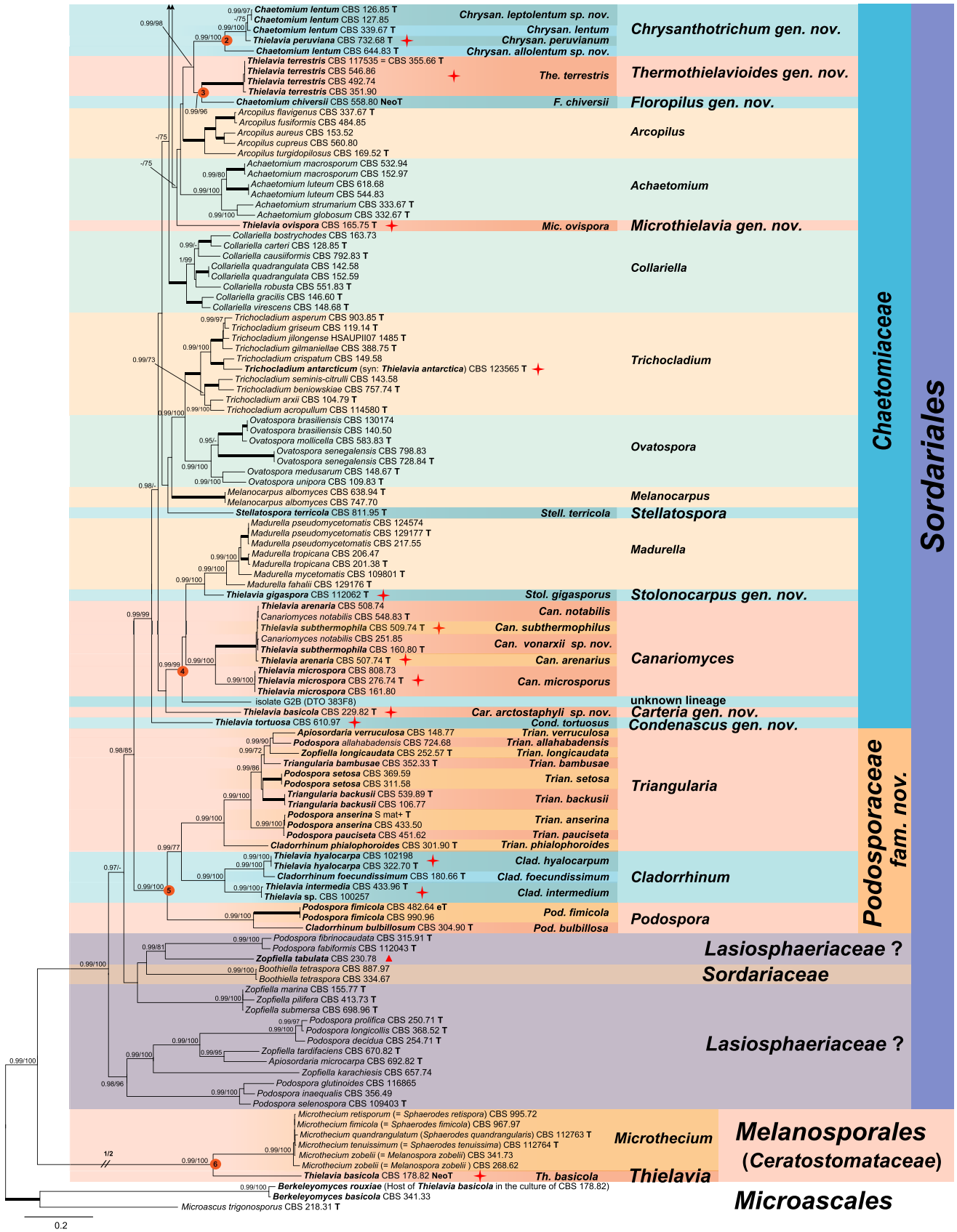


Fig. 3. (Continued).

partitions: 891 characters for *rpb2*, 1 373 characters for *tub2*, 805 characters for ITS and 579 characters for the D1/D2 regions of LSU. All nine thielavia-related clades (Clades 1–6 and three single lineages) recognised in the *rpb2* alignment were supported in the four-locus phylogeny with robust supports (PP = 0.99 and ML-BS $\geq$ 96 %). The phylogenetic relationships of the 11 generic lineages containing "*Thielavia*" species with their related genera were also confirmed with confident support. At the same time, the four-locus phylogeny confirmed the sister relationship between the *Chaetomiaceae* and Clade 5

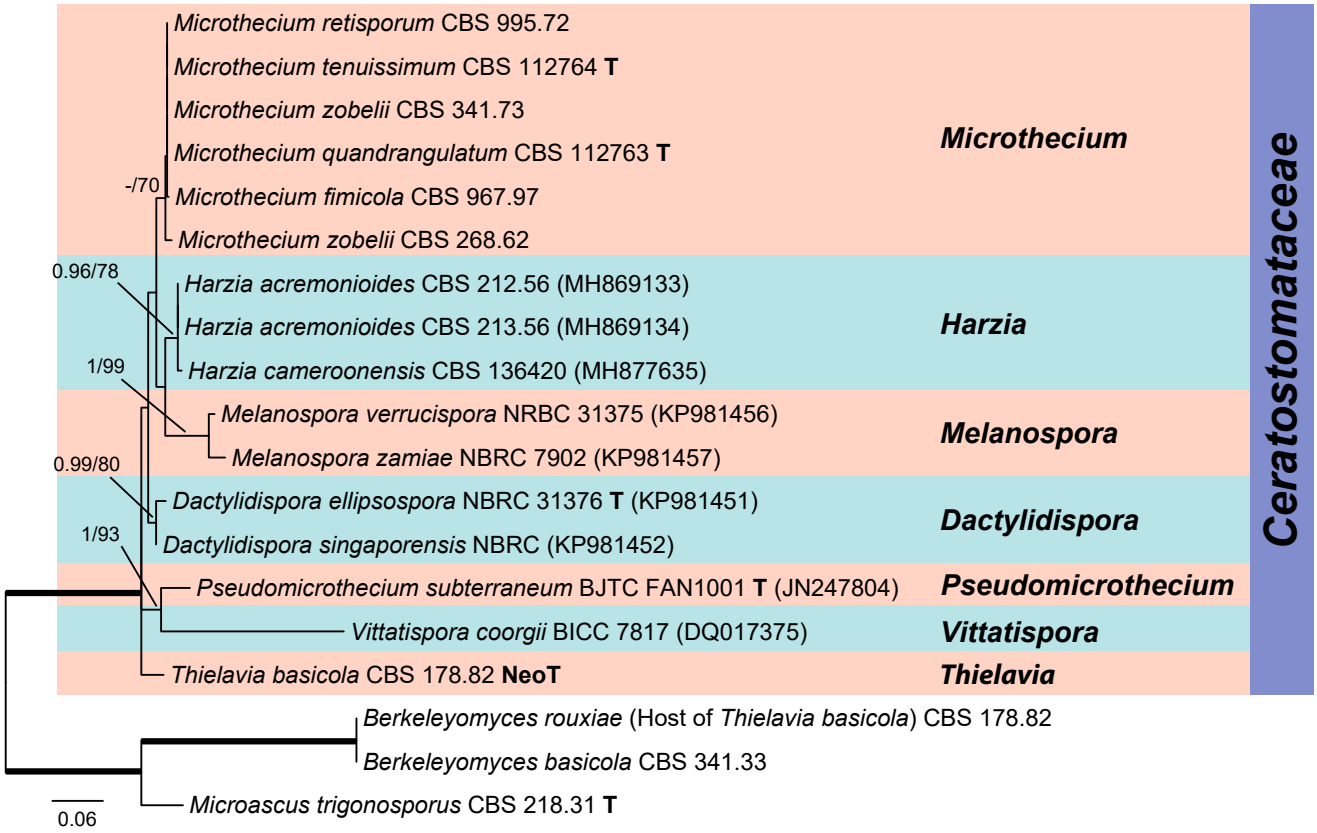


Fig. 4. Phylogenetic confirmation of the placement of *Thielavia basicola* in the *Ceratostomataceae* based on the analysis of the D1/D2 domains of LSU sequences with the confidence values indicated at the notes same to Fig. 1. Targeted genus/species clades are discriminated with boxes in different colours. The scale bar shows the expected number of changes per site. The tree is rooted with two *Berkeleyomyces* species and one *Microascus* species in the *Microascales*.

(PP = 0.98, ML-BS = 85 %), and provided further evidence for the polyphyly of the *Lasiosphaeriaceae*. In addition, the classification of *Stellatospora terricola* in *Chaetomiaceae* and *Boothiella tetraspora* in *Sordariaceae* was confirmed in this phylogenetic analysis.

Confirmation of the placement of *Thielavia basicola* in the *Ceratostomataceae* based on LSU phylogeny (Fig. 4)

The LSU alignment consisted of 19 isolates, including representatives of six genera in the family *Ceratostomataceae*, namely *Dactylidispora*, *Harzia*, *Melanospora*, *Microthecium*, *Pseudomicrothecium* and *Vittatispora*. *Microascus trigonosporus* and the two species of *Berkeleyomyces* residing in the *Microascales* were used as outgroup species. This analysis clearly showed that *Th. basicola* clustered within the *Ceratostomataceae* (PP = 1; ML-BS = 100 %).

Delimitation of species in the *Canariomyces* clade (Fig. 5)

The *rpb2* phylogeny (Fig. 2) failed to differentiate *Th. arenaria*, *Th. subthermophila* and *Can. notabilis*, even though these species are morphologically different (this study, Mouchacca 1973, von Arx 1975, 1984, von Arx *et al.* 1988). Single gene trees based on *tub2* and *tef1*-α data sets were constructed to delimit the species in the *Canariomyces* clade. The *tub2* and *tef1*-α phylogenies were concordant. Four lineages were recognised and these lineages agreed with the observed or reported morphology.

Re-delimitation of *Podospora anserina* and its closely related species (Fig. 6)

To better understand the relationship between *Podospora anserina* and its closely related species, we re-analysed the published sequence data generated by Boucher *et al.* (2017), including ITS sequences and sequences of three other intergenic loci from different chromosomes (*Rchr3*, *Rchr4* and *Rchr6*). Single gene trees were constructed based on each locus. ITS failed to distinguish *Pod. anserina* from *Pod. pauciseta*, *Pod. bellae-mahoneyi* and *Pod. pseudocomata* (Fig. 6A). In contrast, *Rchr3* (Fig. 6B), *Rchr4* (Fig. 6C) and *Rchr6* (Fig. 6D) differentiated all seven species which were accepted by Boucher *et al.* (2017), and *Rchr3* even recognised two subclades within the *P. anserina* clade.

TAXONOMY

Nineteen species are recognised in the 33 studied "*Thielavia*" strains. *Thielavia basicola* is transferred to the *Ceratostomataceae* (*Melanosporales*) based on its phylogenetic affinity with *Microthecium* as well as five other genera in the family (Figs 2–4). Clade 5 is a sister clade to the *Chaetomiaceae* and is proposed as the new family *Podosporaceae*. This family

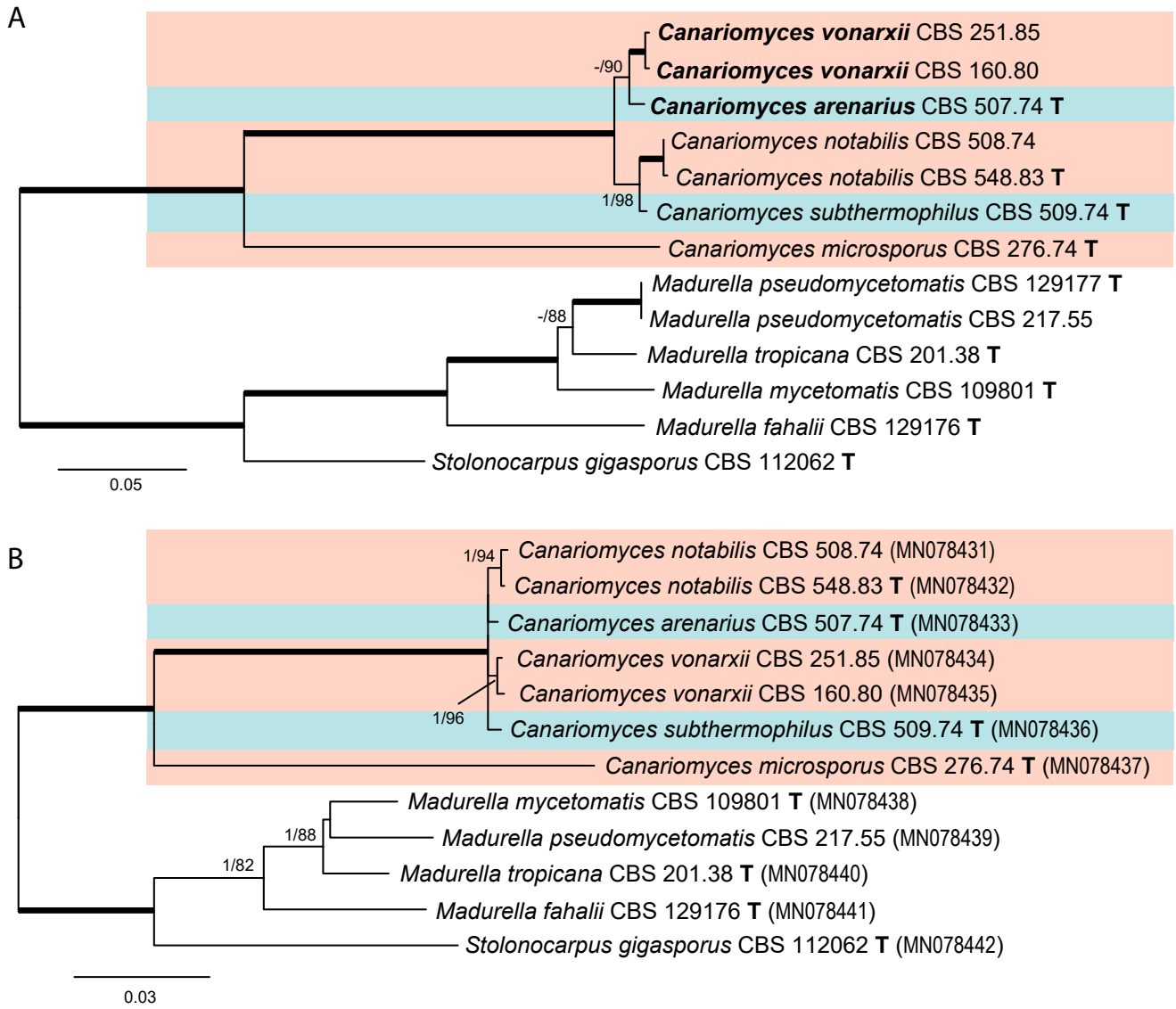


Fig. 5. Delimitation of species in the *Canariomyces* clade based on the separate analyses of partial gene sequences of *tub2* (**A**) and *tef1*-α (**B**). Maximum-Likelihood (ML) trees are showed with the confidence values indicated at the notes same to Fig. 1. Recognised species are discriminated with boxes in different colours. Type strains are marked with "**T**" after the culture number. The scale bar shows the expected number of changes per site. The tree is rooted with the four species of *Madurela* together with the type species of *Stolonocarpus*.

accommodates the three re-defined genera *Cladorrhinum*, *Podospora* and *Triangularia*, which were all previously positioned in the polyphyletic *Lasiosphaeriaceae*. *Thielavia hyalocarpa* and *Th. intermedia* are transferred to *Cladorrhinum* based on their phylogenetic affinities with the type species of this genus. *Canariomyces* was previously classified in the *Microascaceae* and is here transferred to *Chaetomiaceae*. This re-defined genus includes *Th. arenaria*, *Th. microspora* and *Th. subthermophila*. Furthermore, nine new genera in the *Chaetomiaceae* are introduced to accommodate species with a thielavia-morph. These genera are *Carteria*, proposed for CBS 229.82 which was previously identified as *Th. basicola*, but doesn't have an association with *Thielaviopsis basicola*; *Chrysanthotrichum* for *Th. peruviana*, *Ch. lentum* and two new species which are morphologically similar but phylogenetically separate from *Ch. lentum*; *Condenascus* for *Th. tortuosa*; *Hyalosphaerella* for *Th. fragilis*; *Microthielavia* for *Th. ovispora*; *Parathielavia* for *Th. appendiculata*, *Th. hyrcaniae* and *Th. kuwaitensis*; *Pseudothielavia* for *Th. arxii*, *Ch. hamadae*, *Th. terricola* and CBS 473.86 representing a new species which was deposited in the CBS collection as *Ch. hamadae*; *Stolonocarpus* for *Th. gigaspora*; *Thermothielavioides* for the thermophilic species *Th. terrestris*. To clarify the phylogenetic relationships of thielavia-like taxa in the *Chaetomiaceae*, three chaetomium-like single lineages are introduced as new genera. These are *Chrysocorona* to accommodate *Ch. lucknowense*, *Brachychaeta* for *Ch. variosporum* in Clade 1 and *Floropilus* for *Ch. chiversii* in clade 3, which is a sister to *Thermothielavioides*. In addition, the genus *Acrophialophora* is redefined to include two sexually reproducing chaetomium-like species (*Acr. jodhpurensis* and *Acr. teleoafricana*). Our phylogenetic analysis also showed that monotypic *Stellatospora*, typified with *Stell. terricola,* is a genus in the *Chaetomiaceae* and the monotypic genus *Boothiella*, typified with *Booth. tetraspora*, belongs to the *Sordariaceae*. New combinations are provided for those species names where the generic classification changed. Twenty genera and 46 species are (re-)described and illustrated, including the species available that were previously described in *Thielavia* and those that are related to the studied "*Thielavia*" species.

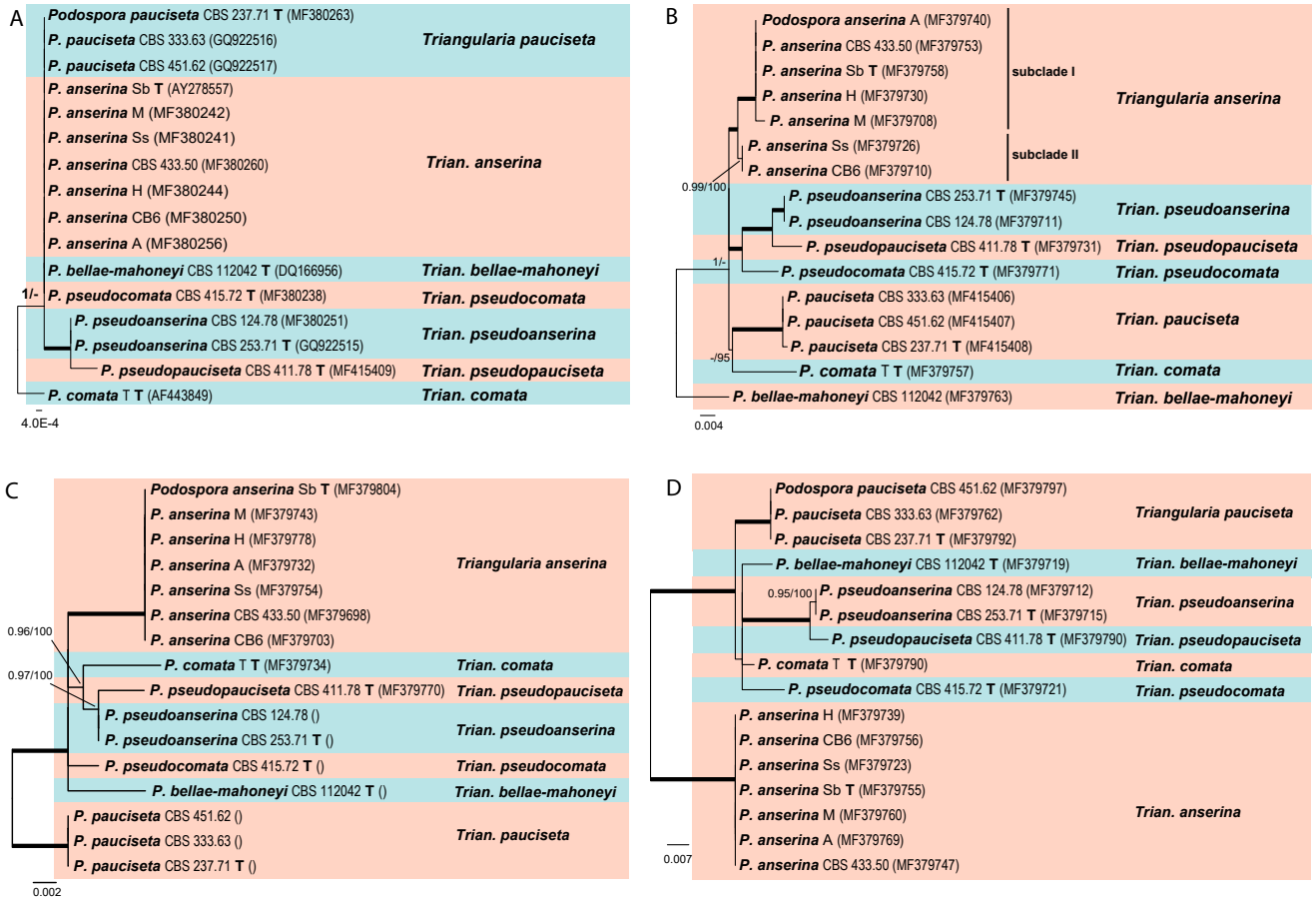


Fig. 6. Delimitation of *Podospora anserina* and its closely related species based on the separate analyses of four loci from Boucher *et al.* (2017): ITS (**A**), Rchr3 on chromosome 3 (**B**), Rchr4 on chromosome 4 (**C**) and Rchr6 on chromosome 6 (**D**). Unrooted ML trees are shown with the confidence values indicated at the notes as in Fig. 1. Recognised species are discriminated with boxes in different colours. Type strains are marked with "**T**" after the culture number. The scale bar shows the expected number of changes per site.

Melanosporales, Ceratostomataceae

Thielavia *Zopf,* Verh. Bot. Vereins. Prov. Brandenburg. 18: 105. 1876.

Micromorphology: Growing in close association with *Berkeleyomyces* species. *Ascomata* superficial, usually solitary, non-ostiolate, globose or subglobose, often surrounded by the conidiophores and conidia of the host. *Ascomatal wall* subhyaline to brown, translucent. *Asci* subglobose to ellipsoidal or ovate, evanescent before ascospores become mature. *Ascospores* 1-celled, brown when mature, smooth, ellipsoidal with attenuated ends, or fusiform, with a germ pore.

Type species: *Thielavia basicola* Zopf.

Notes: *Thielavia basicola* was originally described to develop on the root of the plant species *Senecio elegans* (common names: redpurple ragwort, purple groundsel, wild cineraria and purple ragwort) in Germany and is associated with the morphologicaly defined *Thielaviopsis basicola* (Zopf 1876). The lack of type material of the type species hinders the attempt to properly resolve the taxonomy of *Thielavia*. In the present study, the type species *Th. basicola* is neotypified with CBS H-18808 (see the details below). This material originates from CBS 178.82, a strain isolated from the plant species *Phaseolus vulgaris* (common names: kidney bean, pea bean and French bean) and containing *Th. basicola* and its host which was previously identified as *Thielaviopsis basicola*. The taxonomy of *Thielaviopsis basicola* and allied genera/species was subject of various studies (Mbenoun *et al.* 2014, de Beer *et al.* 2014, Nel *et al.* 2018). Mbenoun *et al.* (2014) epitypified *Thielaviopsis ethacetica* which is the type species of *Thielaviopsis*, and transferred *Thielaviopsis* to the genus *Ceratocystis*. De Beer *et al.* (2014) resurrected and redefined the genus *Thielaviopsis*. *Thielaviopsis* was considered to produce both a sexual and asexual state, and the members of this genus have stellate appendages on the globose basal part of the ascomata. *Thielaviopsis basicola* was not included in their study and this species would not fit in their generic description. More recently, Nel *et al.* (2018) phylogenetically re-evaluated *Thielaviopsis basicola*. They introduced the new genus *Berkeleyomyces* to accommodate *Thielaviopsis basicola* and described a new, cryptic sister species, *B. rouxiae*. These two species are morphologically undistinguishable (Nel *et al.* (2018). In the present study, we obtained ITS, LSU, *rpb2* and *tub2* sequences of both fungi in the culture CBS 178.82. The hyphomycete in CBS 178.82 is identified as *B. rouxiae* (Fig. 1). The host fungus in the culture of Zopf (1876) used for the description of *Th. basicola* could have been *B. rouxiae* or *B. basicola* based on its morphology. The association of *Th. basicola* in CBS 178.82 with *Berkeleyomyces* (= *Thielaviopsis basicola sensu lato*) and the substrate (isolated from plant roots) agrees with the original description of *Th. basicola* (Zopf 1876). Even though CBS 178.82 originates from Canada and the holotype is from Germany, and their plant host species differ, still von Arx *et al.* (1988) used CBS 178.82 as a representative strain for *Th. basicola*. Our morphological examination of CBS 178.82 confirmed that the

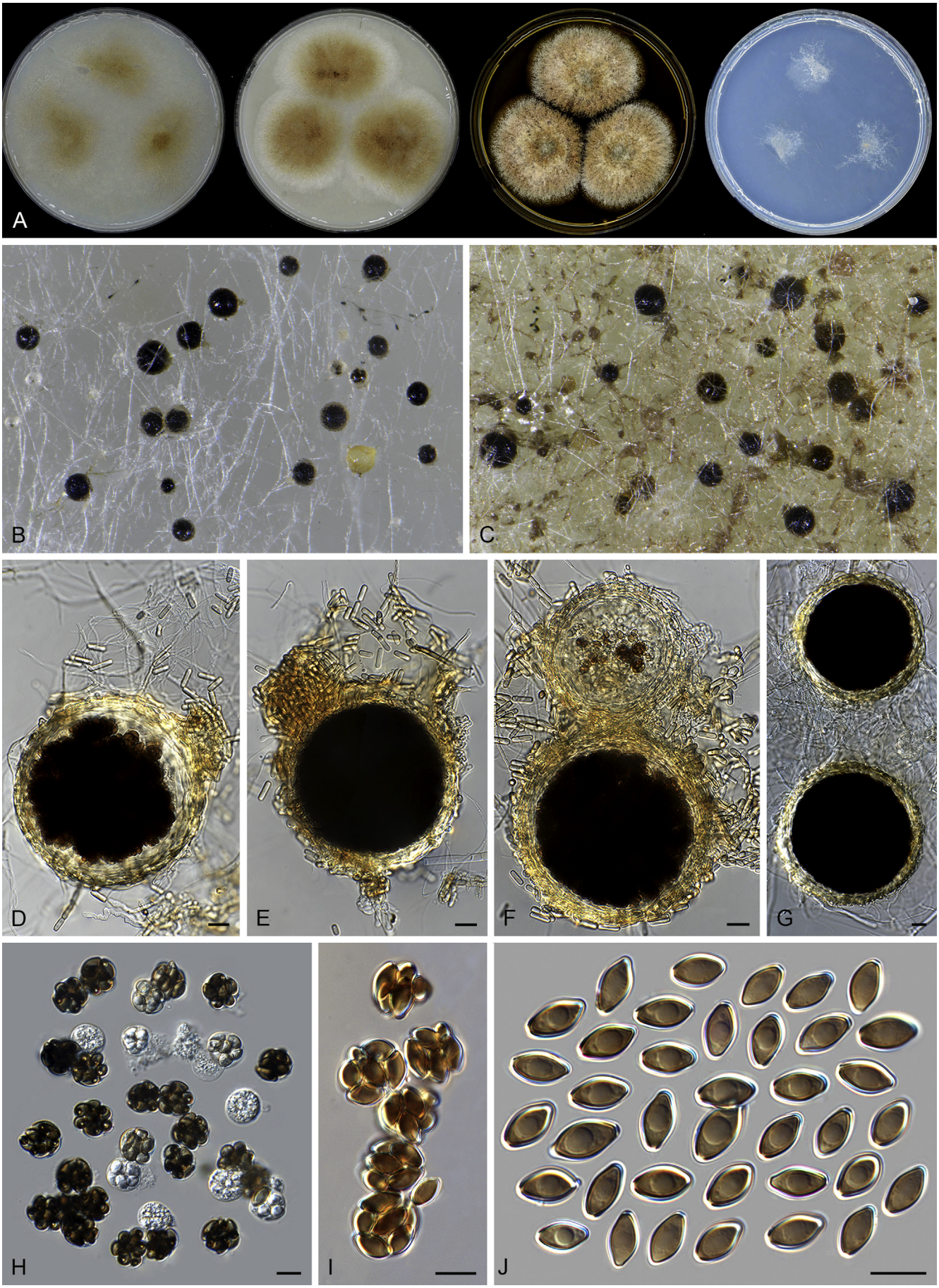


Fig. 7. *Thielavia basicola* growing with its host *Berkeleyomyces rouxiae* (CBS 178.82, ex-neotype culture). **A.** Colonies from left to right on OA, CMA, MEA and PCA after 10 d incubation. **B.** Part of the 2-wk old colony on CMA covered with a cellophane membrane to show ascomata, top view. **C.** Part of the 5-wk old colony on CMA covered with a cellophane membrane to show ascomata surrounded by host fungus, top view. **D–G.** Ascomata surrounded by asexual structures of the host, mounted in lactic acid. **H–I.** Asci. **J.** Ascospores. Scale bars: D–G = 20 µm; H–J = 10 µm.

Table 2. A summary of matrix statistics for each alignment analysed phylogenetically in this study.

Analyses	ITS		*rpb2*		4-locus combined	LSU	*tub2*	*tef1*-α	*Rchr3*	*Rchr4*	*Rchr6*
	Berkeleyomyces [1]	*P. anserina*[5]	*Berkeleyomyces* [1]	*Thielavia*[2]	*Thielavia*[2]	*Ceratostomataceae*[3]	*Canariomyces*[4]	*Canariomyces*[4]	*P. anserina*[5]	*P. anserina*[5]	*P. anserina*[5]
Characters of alignments											
Number of ingroup taxa	19	16	10	280	221	16	7	7	16	16	16
Number of outgroup taxa	4	0*	1	3	3	3	6	5	0*	0*	0*
Number of nucleotide characters including gaps	530	518	1016	900	3648	577	703	1440	838	755	524
Number of constant characters	345	514	830	315	1355	365	424	1088	756	727	467
Number of parsimony-informative characters	111	1	128	551	2009	168	190	201	30	13	42
Number of parsimony-uninformative characters	74	3	58	34	284	44	89	151	52	15	15
Statistics for the Bayesian analyses											
Substitution model	GTR+I+G	HKY	K80	GTR+I+G	GTR+I+G for each	GTR+G	HKY+G	GTR+G	SYM	HKY	K80
Number of generated trees	2385	168	84	31878	13053	1513	5	45	1109	1500	1180
Number of trees discarded as the ''burn-in'' phase	596	42	21	7969	3263	378	1	11	277	375	295
Number of trees used for final tree	1789	126	63	23909	9790	1135	4	34	832	1125	885

*: indicating an unrooted tree.

[1] Dataset for identification of the host (asexual partner) in the culture of CBS 178,82.

[2] Dataset for taxonomic study of morphologically identified *Thielavia* and potentially related taxa.

[3] Dataset for determining the phylogenetic placement of *Thielavia basicola* in the family *Ceratostomataceae*.

[4] Dataset for delimitation of species in the *Canariomyces* clade.

[5] Dataset for delimitation of "*Podospora anserina*" and its closely related species.

sexually reproducing fungus agrees well with the original description of the holotype of *Th. basicola* (Fig. 7), and the hyphomycete fits with the description of *Berkeleyomyces* species as noted above (Fig. 8). Phylogenetic analyses (Figs 2–4) indicated that the *Th. basicola* strain in CBS 178.82 clustered close, but separate from *Microthecium* and five other genera in the family *Ceratostomataceae* (*Melanosporales*).

Microthecium, *Melanospora* and *Sphaerodes* in the *Ceratostomataceae* have a tumultuous taxonomic history with conflicts between morphology and phylogeny (Cannon & Hawksworth 1982, Zhang & Blackwell 2002, Schultes *et al.* 2017). In the

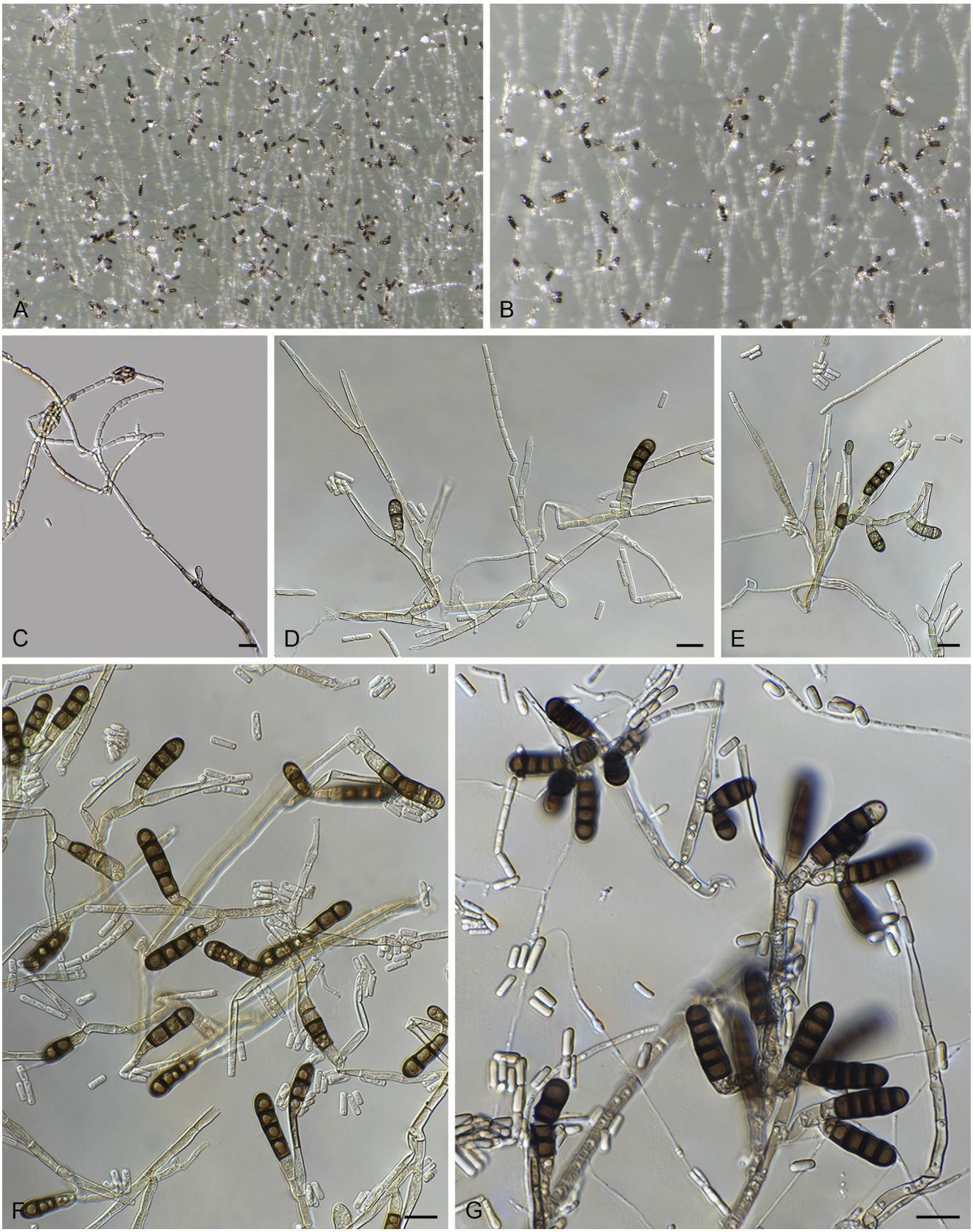


Fig. 8. *Berkeleyomyces rouxiae*, host of *Thielavia basicola* (CBS 178.82). **A–B.** Part of the colony on TSA, showing thick-walled conidia arising from aerial hyphae. **C–G.** Dimorphic synanamorphs: conidiophores, phialides and two types of conidia. Scale bars: C–G = 10 µm.

past, many *Microthecium* species were transferred to *Melanospora* or *Sphaerodes*, including those selected in this study as the representatives of *Ceratostomataceae* (Figs 2, 3). A recent study (Marin-Felix *et al.* 2018) phylogenetically re-evaluated the taxonomy of *Melanospora* and related taxa. *Melanospora* was restricted to species producing ostiolate ascomata whose neck is composed of intermixed hyphae, and having a phialidic asexual morph. *Sphaerodes* was treated as a synonym of *Microthecium*. *Microthecium* was re-established for *Melanospora* and *Sphaerodes* species without the typical characters of *Melanospora* described above. An analysis of a LSU dataset including representative species of six genera in *Ceratostomataceae* confirmed the placement of *Th. basicola* in this family (Fig. 4).

Species in the order *Melanosporales* (comprises the family *Ceratostomataceae*) are characterised by the production of usually translucent ascomata, unitunicate asci, and unicellular, pigmented ascospores with germ pores or germ slits (Marin-Felix *et al.* 2018). *Thielavia basicola* produces translucent ascomata, unitunicate asci, and unicellular, pigmented ascospores with a germ pore, fitting in the family *Ceratostomataceae*. Moreover, most of the species in the *Ceratostomataceae* are known to be parasitic on or closely associated with other fungi, including basidiomycetes and sexual and asexual reproducing ascomycetes (Jeffries & Young 1994, Harveson 1999, Zhang & Blackwell 2002, Marin-Felix *et al.* 2018). These data provide robust support for the phylogenetic placement of *Th. basicola* in the *Ceratostomataceae*, rather than *Chaetomiaceae*. As a consequence, the *Thielavia* species classified in the latter family should be combined in other or new genera.

Thielavia basicola Zopf, Verh. Bot. Vereins Prov. Brandenburg 18: 105. 1876. Fig. 7.

Micromorphology: *Ascomata* superficial, usually solitary, non-ostiolate, globose or subglobose, often surrounded by the conidiophores and conidia of the host (*Berkeleyomyces rouxiae*), (80–)105–260 µm diam. *Ascomatal wall* subhyaline to brown, translucent, composed of 4–6 layers of cells. *Asci* subglobose to ellipsoidal or ovate, 14–19 × 12.5–17 µm, usually without visible stalks, containing eight irregularly-arranged ascospores, evanescent, but often persistent until ascospores mature. *Ascospores* 1-celled, brown when mature, smooth, fusiform, umbonate at both ends, (8.5–)9.5–11.5(–13.5) × (5–)5.5–7 µm, with an apical germ pore. *Asexual morph* not observed.

Culture characteristics (mixed with the host): On OA with an entire edge, 40–46 mm diam in 7 d at 25 °C, obverse fawn due to conidia of the host, reverse uncoloured. On CMA similar to those on OA, 35–41 mm diam in 7 d at 25 °C. On MEA with an entire or slightly crenate edge, 37–43 mm diam in 7 d at 25 °C, texture floccose due to the host, obverse vinaceous buff to fawn, reverse fawn. On PCA transparent, with a crenate edge, 22–28 mm diam in 7 d at 25 °C, with sparse aerial mycelium, obverse vinaceous buff, reverse uncoloured.

Typus: **Canada**, Ontario, Toronto, isolated from diseased root of *Phaseolus vulgaris*, Mar. 1981, A. Carter (CBS H-18808, **neotype designated here**, MBT 385801, culture ex-neotype CBS 178.82 = MUCL 40417).

Notes: Our attempts in finding the holotype of *Th. basicola* in B (Botanischer Garten und Botanisches Museum Berlin-Dahlem, Germany), HAL (Martin-Luther-Universität, Halle-Wittenberg, Halle, Germany) and K (Royal Botanic Gardens, Kew, UK) were unsuccessful. The holotype of this species seems to be lost. There are two strains deposited as *Th. basicola* in the CBS culture collection: CBS 178.82 and CBS 229.82. The two isolates produce similar ascomata and asci in shape. CBS 229.82 grows independently on the agar media, while CBS 178.82 grows in close association with *Berkeleyomyces rouxiae* (Fig. 8). This association hampered the use of CBS 178.82 as it was often poorly sporulating and difficult to obtain sequence data from its culture. Probably that is why CBS 229.82 was once used as a representative strain of *Th. basicola* (Stchigel *et al.* 2002). After successfully inducing ascomata production of CBS 178.82 in the present study (Fig. 7B, C), morphological examination showed that CBS 178.82 produces fusiform and larger ascospores (9.5–11.5 × 5.5–7 µm *vs* 8–9 × 4.5–5.5 µm) than the ellipsoidal ones of CBS 229.82. The former strain also produced larger ascomata than those of CBS 229.82 (105–260 µm *vs* 25–85 µm diam). The holotype of *Th. basicola* was described with ascomata developing on roots of *Senecio elegans* in association with *Thielaviopsis basicola*, measuring 80–170 µm diam, containing fusiform ascospores 9–12 × 5–6.5 µm (*fide* Booth 1961, von Arx 1975). It is clear that the morphology and ecology of CBS 178.82 fits that of the holotype of *Th. basicola* quite well. To stabilize the use of the species name, we propose the specimen CBS H-18808 from the strain CBS 178.82 as the neotype of *Th. basicola*.

The morphology of *Microthecium tenuissimum* (syn.: *Sphaerodes tenuissima*) is also presented in this study as a representative species in the *Ceratostomataceae* (Fig. 9). This species possesses a similar morphology to that of *Th. basicola*: non-ostiolate and translucent ascomata, evanescent asci which are often persistent until ascospores mature, and fusiform and pigmented ascospores with two apical germ pores.

Sordariales, Chaetomiaceae

Acrophialophora Edward, Mycologia 51: 784. 1961.

Micromorphology of ***asexual species***: *Hyphae* hyaline or pigmented, branched, septate. *Conidiophores* arising laterally from hyphae, differentiated to be thick-walled, warty, unbranched, erect, pigmented, fading towards tips, or reduced to conidiogenous cells. *Conidiogenous cells* phialidic, flask-shaped, swollen at the base, taping to a narrow neck, either on differentiated conidiophores, arranged in whorls or verticils near or at the apex, or on undifferentiated aerial hyphae, in latter case solitary, sometimes proliferating. *Conidia* 1-celled. formed in basipetal chains, hyaline to subhyaline, ovoid, ellipsoidal to fusiform, smooth or punctate. *Sexual morph* not observed in the known asexual species. *Micromorphology of* ***sexual species***: *Ascomata* superficial, ostiolate, subglobose to ovate. *Ascomatal wall* brown, of *textura intricata* in surface view. *Terminal hairs* flexuous or undulate, occasionally branched, brown, septate. *Lateral hairs* flexuous. *Asci* fasciculate, clavate or fusiform, stalked, containing eight biseriate or irregularly-arranged ascospores, evanescent. *Ascospores* 1-celled, olivaceous brown when mature, smooth, 1-celled, fusiform or ellipsoidal, with a subapical or lateral germ pore. *Asexual morph* not observed in the known asexual species.

Type species: *Acrophialophora nainiana* Edward.

Notes: Both *rpb2* and four-locus phylogenies indicated that *Acrophialophora* is closely related to three genera (*Parathielavia*, *Hyalosphaerella* and *Pseudothielavia*) containing thielavia-like

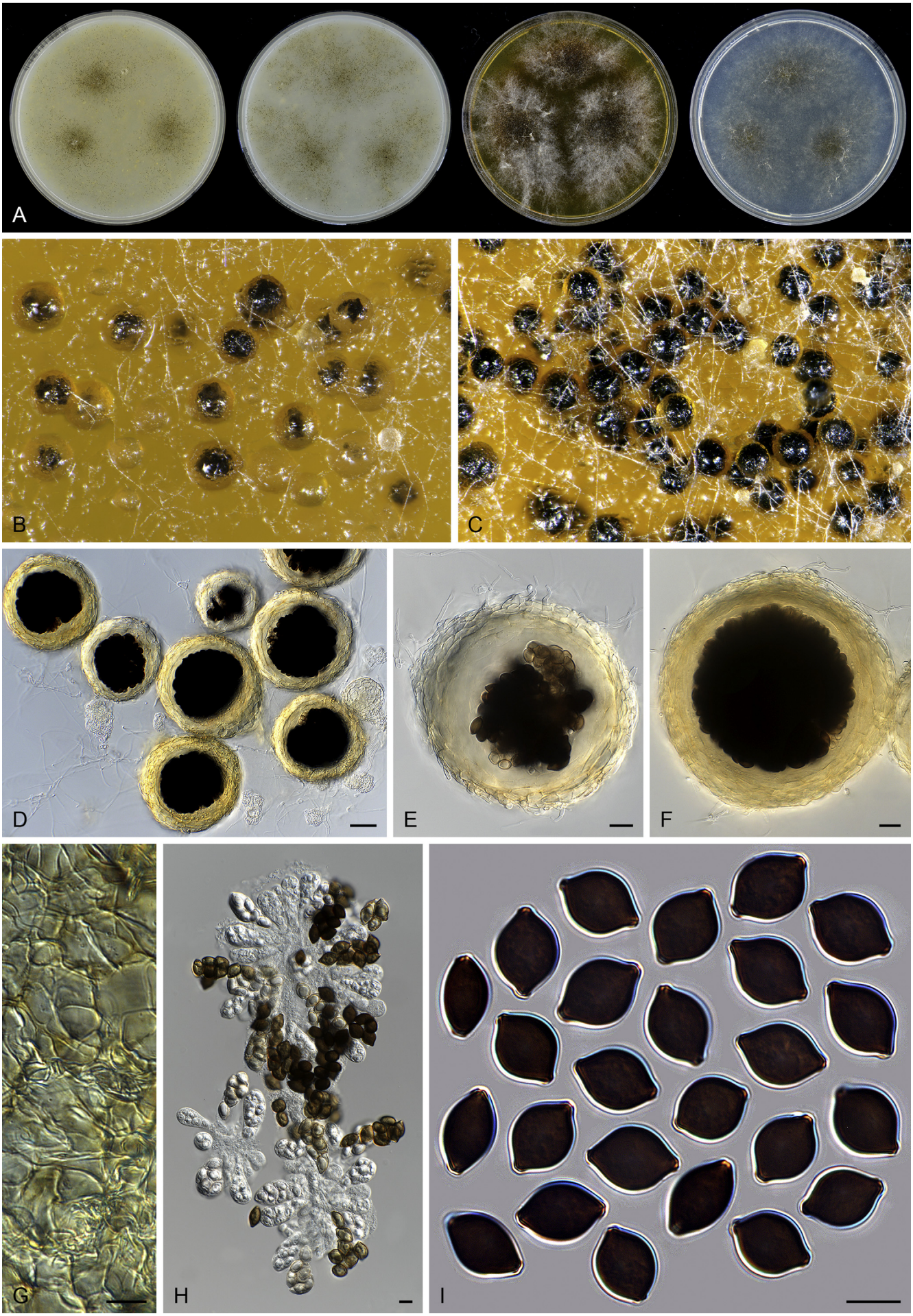


Fig. 9. *Microthecium tenuissimum* (CBS 112764, ex-type culture). **A.** Colonies from left to right on OA, CMA, MEA and PCA after 3 wk incubation. **B–C.** Mature ascomata on MEA, top view. **D–F.** Ascomata mounted in lactic acid. **G.** Structure of ascomatal wall in surface view. **H.** Asci. **I.** Ascospores. Scale bars: D = 50 µm; E–F = 20 µm; G–I = 10 µm.

species and two genera (*Chrysocorona*, *Brachychaeta*) with former *Chaetomium* species in Clade 1 (Figs 2, 3). The taxonomy of this genus was therefore treated in the present study to better show the phylogenetic position of the related "*Thielavia*" species in the *Chaetomiaceae*. Five traditional *Acrophialophora* species were selected as representatives of the genus (*Acr. ellipsoidea*, *Acr. fusispora*, *Acr. hechuanensis*, *Acr. major* and *Acr. nainiana*). Two sexual species (*Acr. jodhpurensis* and *Acr. teleoafricana*) formerly classified in *Chaetomium*, clustered in the monophyletic *Acrophialophora* clade (PP $\geq$ 0.99, ML-BS = 100, Figs 2, 3). The generic description thus was emended to include these sexually reproducing species.

Edward (1961) introduced *Acrophialophora* based on its distinct conidiophores and phialides and suggested it to be closely related to the genus *Paecilomyces*. However, Dal Vesco & Peyronel (1968) treated the type species of the genus, *Acr. nainiana*, as a synonym of *Paecilomyces fusisporus* and also Barron (1968) did not accept *Acrophialophora* as separate genus from *Paecilomyces*. In the subsequent study of Samson & Mahmood (1970), *Acrophialophora* was reintroduced and they emphasized the differences from *Paecilomyces* species in the presence of pigmented hyphae and pigmented conidiophores with thick and verrucose walls, and the presence of proliferating phialides. Three *Acrophialophora* species were accepted in *Acrophialophora sensu* Samson & Mahmood, *Acr. fusispora*, *Acr. levis* and *Acr. nainiana*, each being thermotolerant and producing more or less differentiated conidiophores. The morphological concept of *Paecilomyces* was demonstrated to be polyphyletic by the phylogenetic analysis of SSU sequences (Luangsa-ard *et al.* 2004). The type species *Pae. variotii* and its thermophilic relatives belong in the order *Eurotiales*, *Paecilomyces farinosus* and its related mesophilic species belong to the order *Hypocreales*, while the monophialidic species *Pae. inflatus* was moved to *Phialemonium* as *Ph. inflatum* in the *Cephalothecaceae* (Perdomo *et al.* 2013). On the other hand, many more monophialidic species were described in *Paecilomyces* (Matushima 1971, Liang *et al.* 2006a, b, Liang *et al.* 2007). In 2009, Liang *et al.* proposed the genus *Taifanglania* and transferred eight monophialidic *Paecilomyces* species to *Taifanglania*. Recent phylogenetic evidence using ITS, SSU and *tub2* sequences showed that *Acrophialophora* and *Taifanglania* are congeneric, and *Taifanglania* was therefore treated as a synonym of *Acrophialophora* (Zhang *et al.* 2015). Their emended genus *Acrophialophora* contained 16 thermotolerant species with an optimal growth temperature between 35–40 °C.

Acrophialophora is commonly known as an asexual genus because the majority of species produce only the asexual state and no species is known to form both asexual and sexual states. Species of the five closely related genera are all known to produce sexual states. *Parathielavia* and *Hyalosphaerella* produce non-ostiolate ascomata. The majority of *Pseudothielavia* species also produce non-ostiolate ascomata with the exception of *Pse. hamadae* which possesses ascomata with an inconspicuous ostiole and covered by sparse and hyaline hypha-like hairs (Fig. 37), quite different from the sexual *Acrophialophora* species that produce ascomata with a conspicuous ostiole and covered by well-developed flexuous or undulate ascomatal hairs (Figs 13, 16). The monotypic genus *Chrysocorona* can be distinguished from sexual *Acrophialophora* species by its ascomata covered by amber to luteous and arcuate ascomatal hairs usually with numerous short and easily-exfoliated branches near the tips (Fig. 28). *Brachychaeta* can be distinguished by its ascomata covered by its short, yellow-green, arcuate or flexuous and unbranched ascomatal hairs and by its irregularly-shaped ascospores.

Acrophialophora ellipsoidea Yu Zhang & L. Cai, Mycologia 107: 772. 2015. Fig. 10.

Micromorphology: *Sexual morph* not observed. *Somatic hyphae* hyaline, 1.0–4 µm wide. *Conidiophores* reduced to conidiogenous cells. *Conidiogenous cells* arising laterally from hyphae, phialidic, usually solitary, flask-shaped or obclavate, swollen near base, tapering abruptly to a narrow neck, 8–16 × 2.5–4.5 µm. *Conidia* 1-celled, formed in basipetal chains, hyaline, ellipsoidal or ovoid, smooth, (4–)5.5–7(–9) × (2–)2.5–3 µm.

Culture characteristics: On OA with an entire edge, 34–40 mm diam after 7 d at 25 °C, obverse white and floccose due to aerial mycelium, reverse buff. On CMA similar to those on OA, with a relative thin layer of aerial mycelium. On MEA with an entire edge, 17–23 mm diam after 7 d at 25 °C, texture floccose, obverse white to buff, reverse luteous to orange. On PCA 17–23 mm diam after 7 d at 25 °C; edge entire; with sparse aerial mycelium, reverse uncoloured.

Material examined: **Belgium**, Luik, isolated from soil, date unknown, J.L. Ramaut (CBS 102.61). **China**, Guangxi, isolated from compost, Oct. 2011, W.Q. Ma (CGMCC 3.17487).

Notes: Acrophialophora ellipsoidea can be recognised by its solitary conidiogenous cells (reduced conidiophores) producing smooth, ellipsoidal or ovoid conidia, rather than fusiform conidia as in most of the other studied species. CBS 102.61 was deposited in the CBS culture collection as *Acr. levis*. *Acrophialophora ellipsoidea* produces conidiogenous cells and conidia similar to those of *Acr. levis*, but can be distinguished by the absence of differentiated conidiophores which are pigmented in *Acr. levis* and have a coarsely warty surface in the lower part. Samson & Mahmood (1970) mentioned that differentiated conidiophores were also often absent in *Acr. levis*. Based on Zhang *et al.* (2015), the two species are closely related, but cluster in two distinct clades. Our examined strains CGMCC 3.17487 and CBS 102.61 group with CGMCC 3.15256, the ex-type of *Acr. ellipsoidea*. Further study is needed to determine the taxonomic value of conidiophore complexity in *Acrophialophora*.

Acrophialophora fusispora (S.B. Saksena) Samson, Acta Bot. Neerl. 19: 805. 1970. Fig. 11.
Basionym: *Paecilomyces fusisporus* S.B. Saksena, J. Indian Bot. Soc. 32: 188. 1953.

Micromorphology: *Sexual morph* not observed. *Somatic hyphae* hyaline, 1–4 µm wide. *Conidiophores* simple, hyaline, smooth, cylindrical or slightly clavate, 3.5–13 × 3–4 µm, or reduced to conidiogenous cells. *Conidiogenous cells* phialidic, generating apically on conidiophores in verticils, or arising laterally from hyphae and solitary, often proliferating, obclavate or flask-shaped, swollen near base, tapering gradually or abruptly to a narrow neck, (4–)9–22 × 2.5–4(–4.5) µm. *Conidia* 1-celled, formed in basipetal chains, hyaline to subhyaline, ellipsoidal, fusiform or ovoid, with warts which are usually striated or spirally arranged, (5–)6–8 (–11) × 2.5–4(–5) µm.

Culture characteristics: On OA 30–36 mm diam after 7 d at 25 °C; edge entire; obverse ochraceous, reverse buff to saffron. On CMA 29–35 mm diam after 7 d at 25 °C; edge entire; obverse rosy buff,

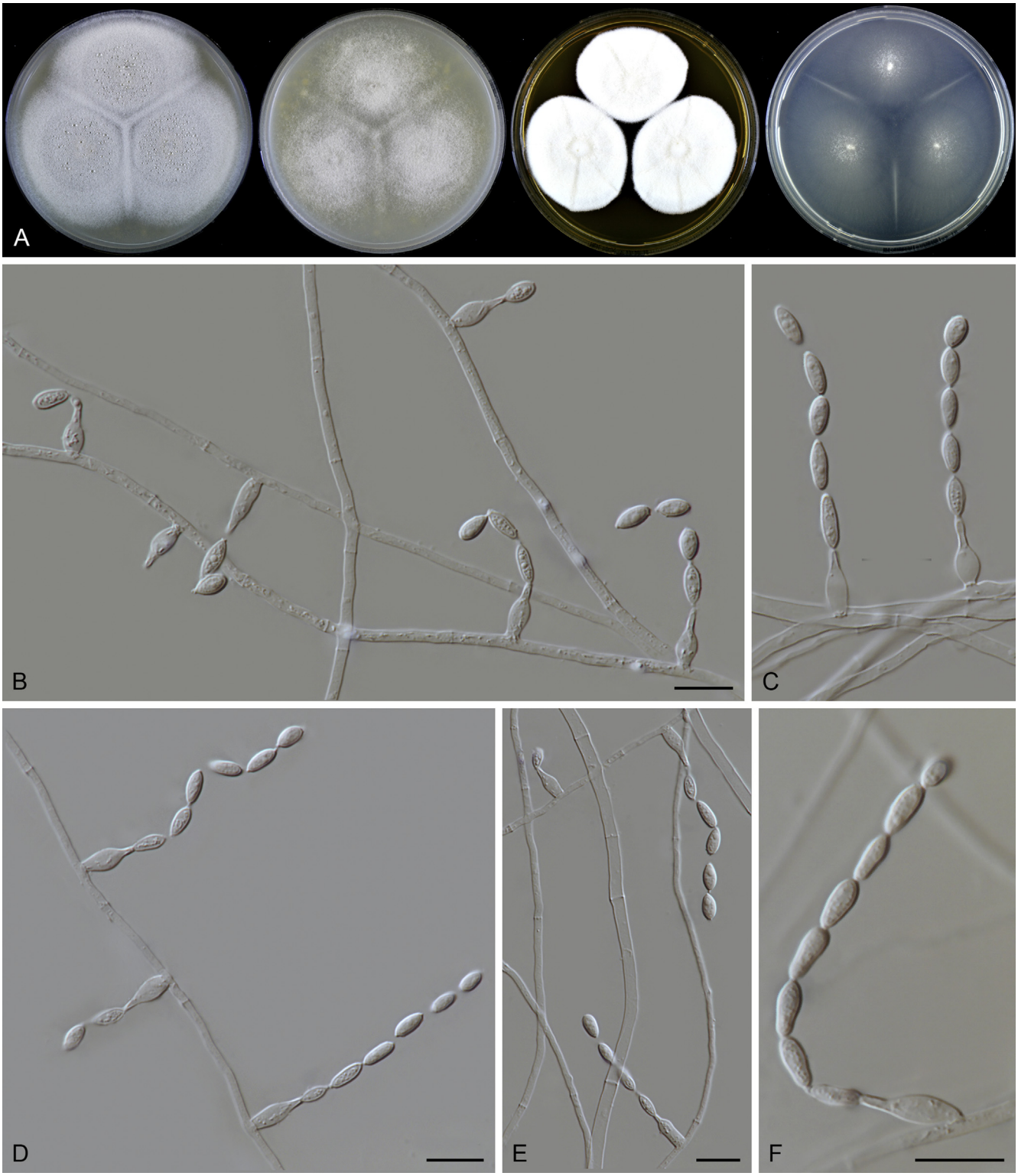


Fig. 10. *Acrophialophora ellipsoidea* (CBS 102.61). **A.** Colonies from left to right on OA, CMA, MEA and PCA after 2 wk incubation. **B–F.** Hyphae, phialidic conidiogenous cells and conidia. Scale bars: B–F = 10 µm.

reverse buff. On MEA 24–30 mm diam after 7 d at 25 °C, edge slightly crenate; obverse buff, reverse saffron to orange. On PCA 16–22 mm diam after 7 d at 25 °C; edge entire or slightly crenate; with sparse aerial mycelium, reverse uncoloured.

Typus: **India**, Sagar, Patharia Forest, isolated from forest soil, date unknown, S.B. Saksena (culture ex-type CBS 380.55 = ATCC 22556 = IMI 057442 = LSHB Pa64 = UAMH 10771).

Notes: According to Samson & Mahmood (1970), *Acr. fusispora* produces darkly pigmented conidiophores measuring up to 1.2 mm long. In our examination of the ex-type, conidiophores were absent, or when present, hyaline and less than 15 µm in length. This is another example to show that the presence of pigmented conidiophores may not be a stable character. Also, the spiral ornamentation reported on the surface of the conidia was not as prominently present as the previous description (Samson & Mahmood 1970). These morphological variations might be caused by the long-term preservation of CBS 380.55. *Acrophialophora fusispora* is closely related to *Acr. hechuanensis* and *Acr. nainiana*. It can be distinguished from *Acr.*

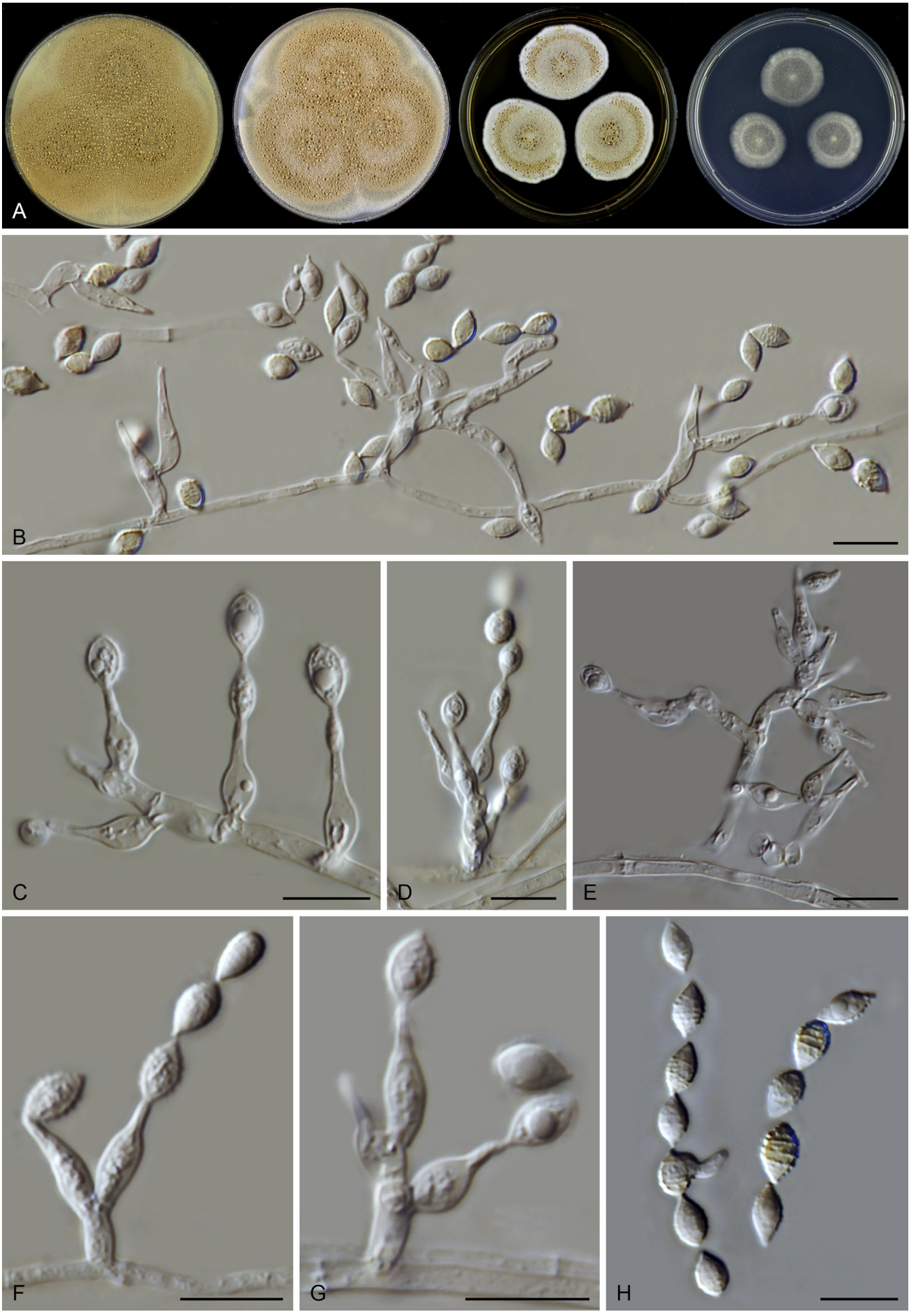


Fig. 11. *Acrophialophora fusispora* (CBS 380.55, ex-type culture). **A.** Colonies from left to right on OA, CMA, MEA and PCA after 18 d incubation. **B–G.** Hyphae, phialidic conidiogenous cells and conidia. **H.** Conidia. Scale bars = 10 µm.

hechuanensis by ornamented and larger conidia (6–8 × 2.5–4 µm *vs* 5–6 × 2–3.5 µm). *Acrophialophora nainiana* differs from both *Acr. fusispora* and *Acr. hechuanensis* by its larger conidia (6–8.5 × 3.5–4.5 µm) and by the persistent presence of well-developed conidiophores which are pigmented, warty and up to 1300(–1500) µm long with conidiogenous cells borne apically in verticils.

Acrophialophora hechuanensis (Z.Q. Liang, Y.F. Han, H.L. Chu & R.T.V. Fox) Yu Zhang & L. Cai, Mycologia 107: 775. 2015. Fig. 12.
Basionym: *Taifanglania hechuanensis* Z.Q. Liang, Y.F. Han, H.L. Chu & R.T.V. Fox, Fungal Diversity 34: 72. 2009.

Micromorphology: *Sexual morph* not observed. *Somatic hyphae* hyaline, 1.5–4 µm wide. *Conidiophores* usually reduced to conidiogenous cells. *Conidiogenous cells* arising laterally from hyphae, phialidic, often proliferating or solitary, obclavate or flask-shaped, swollen near base, tapering abruptly to a narrow neck, (4–)8–19 × 2.5–4 µm. *Conidia* 1-celled, formed in basipetal chains, sometimes formed in heads at apex of the conidiogenous cells, hyaline, smooth, fusiform or ovoid, usually with a spine-like extension at the base, (4–)5–6 (–8) × 2–3.5 (–4) µm.

Culture characteristics: On OA with an entire edge, 32–38 mm diam after 7 d at 25 °C, texture floccose, obverse white or pale white, reverse buff to saffron. On CMA 32–38 mm diam after 7 d at 25 °C, texture floccose, edge entire or slightly crenate; obverse white, reverse pale luteous. On MEA with an entire edge, 32–38 mm diam after 7 d at 25 °C; obverse rosy buff, with a relative thick layer of aerial mycelium, reverse orange. On PCA with an entire edge, 27–33 mm diam after 7 d at 25 °C, with sparse aerial mycelium, reverse uncoloured.

Typus: **China**, Chongqing, Hechuan, isolated from soil, 2003, Y.F. Han & Z.Q. Liang (culture ex-type GZUIFR-H08-1).

Notes: *Acrophialophora hechuanensis* produces smooth conidia, like *Acr. ellipsoidea*, but can be distinguished by usually fusiform conidia with a spine-like extension at base, often proliferating conidiogenous cells, and by the presence of simple conidiophores. Moreover, conidia of *Acr. hechuanensis* are formed not only in chains, but also in heads (Fig. 12F). This species was designated as the type species of *Taifanglania*, a genus characterized by lacking conidiophores (or maximally having simple conidiophores), and having hyaline, solitary phialides, with a swollen base and tapering into a thin neck, and hyaline, smooth walled conidia (Liang *et al.* 2009). This study supports the conclusion of Zhang *et al.* (2015) that *Taifanglania* is congeneric with *Acrophialophora*.

Acrophialophora jodhpurensis (Lodha) X. Wei Wang & Houbraken, ***comb. nov.*** MycoBank MB829844. Fig. 13.
Basionym: *Chaetomium jodhpurense* Lodha, J. Indian Bot. Soc. 43: 132. 1964.

Micromorphology: Ascomata superficial, greyish yellow-green due to ascomatal hairs in reflected light, subglobose to ovate, ostiolate, 130–220 µm high, (100–)120–180 µm diam. *Ascomatal wall* brown, composed of *textura intricata* in surface view. *Terminal hairs* flexuous or undulate, occasionally branched, brown, septate, 1.5–3 µm diam near base. *Lateral hairs* flexuous. *Asci* fasciculate, clavate or fusiform, spore-bearing part 30–43 × 12.5–17 µm, with stalks 6–19 µm long, containing eight biseriate or irregularly arranged ascospores, evanescent. *Ascospores* 1-celled, olivaceous brown when mature, smooth, fusiform or ellipsoidal, (11–)13–14.5(–16) × (5.5–)6–7(–7.5) µm, with a subapical or lateral germ pore. *Asexual morph* not observed.

Culture characteristics: On OA with entire edge, 25–31 mm diam in 7 d at 25 °C, often with mouse grey concentric rings due to the formation of ascomata, without aerial mycelium, fuscous black around the colonies due to coloured exudates diffusing into the medium, reverse olivaceous black. On CMA with a slightly crenate edge, 26–32 mm diam in 7 d at 25 °C, obverse mouse grey due to ascomata, without aerial mycelium, with fuscous black exudates diffusing into the medium and a concentric ascomata ring around the pale center, reverse pale mouse grey. On MEA with a crenate edge, 22–28 mm diam in 7 d at 25 °C, obverse pale olivaceous grey to olivaceous grey due to aerial mycelium, without coloured exudates, reverse olivaceous grey. On PCA with a slightly crenate edge, 30–36 mm diam in 7 d at 25 °C, with sparse ascomata, without aerial mycelium, with olivaceous exudates diffusing into the medium, reverse buff to olivaceous.

Typus: **Lectotype of *Chaetomium jodhpurense* designated here**: fig. 8 in Lodha, J. Indian Bot. Soc. 43: 132, 1964 (based on the original culture from rabbit dung collected at Jodhpur, Rajasthan, India), MBT385817. **Pakistan**, Peshawar, substrate and date unknown, T. Mahmood (CBS H-10019, **epitype designated here**, MBT385818, culture ex-epitype CBS 602.69).

Notes: Four strains maintained as *Ch. jodhpurense* in the CBS collection were studied. These strains cluster with other strictly asexual *Acrophialophora* species with statistical support in both the *rpb2* (PP = 1, ML-BS = 100 %; Fig. 2) and the four-locus phylogeny (PP = 0.99, ML-BS = 100 %; Fig. 3). As a result, they are transferred to the genus *Acrophialophora*. Phylogenetically, the four studied *Ch. jodhpurense* strains split into two species lineages and the other one is described here as a novel species, *Acr. teleoafricana* (Fig. 16, see below). The thermotolerant nature of the sexual species (Zhang *et al.* 2017) also matches with the genus *Acrophialophora*. Since the type specimen seemed to be lost (von Arx *et al.* 1986), an illustration in the protologue is designated here as the lectotype of *Ch. jodhpurense* and CBS 602.69 is selected as the ex-epitype culture in order to fix the application of the species name. This strain was collected in Pakistan, adjacent to the country (India) of the holotype location. Furthermore, the morphology of the species lineage represented by CBS 602.69 matches with the protologue (Lodha 1964).

Acrophialophora major (Z.Q. Liang, H.L. Chu & Y.F. Han) Yu Zhang & L. Cai, Mycologia 107: 775. 2015. Fig. 14.
Basionym: *Paecilomyces inflatus* var. *major* Z.Q. Liang, H.L. Chu & Y.F. Han, J. Fungal Res. 2: 43. 2004.
Synonyms: *Paecilomyces major* (Z.Q. Liang, H.L. Chu & Y.F. Han) Z.Q. Liang, H.L. Chu & Y.F. Han, J. Fungal Res. 4: 47. 2006.
Taifanglania major (Z.Q. Liang, H.L. Chu & Y.F. Han) Z.Q. Liang, Y.F. Han & H.L. Chu, Fungal Diversity 34: 74. 2009.

Micromorphology: Sexual morph not observed. *Somatic hyphae* hyaline, 1–3.5 µm wide. *Conidiophores* reduced to conidiogenous cells. *Conidiogenous cells* arising laterally from hyphae, phialidic, solitary, sometimes proliferating, flask-shaped or obclavate, swollen near base, tapering abruptly to a narrow neck, (4–)7.5–12 × 2–4.5(–5) µm. *Conidia* 1-celled,

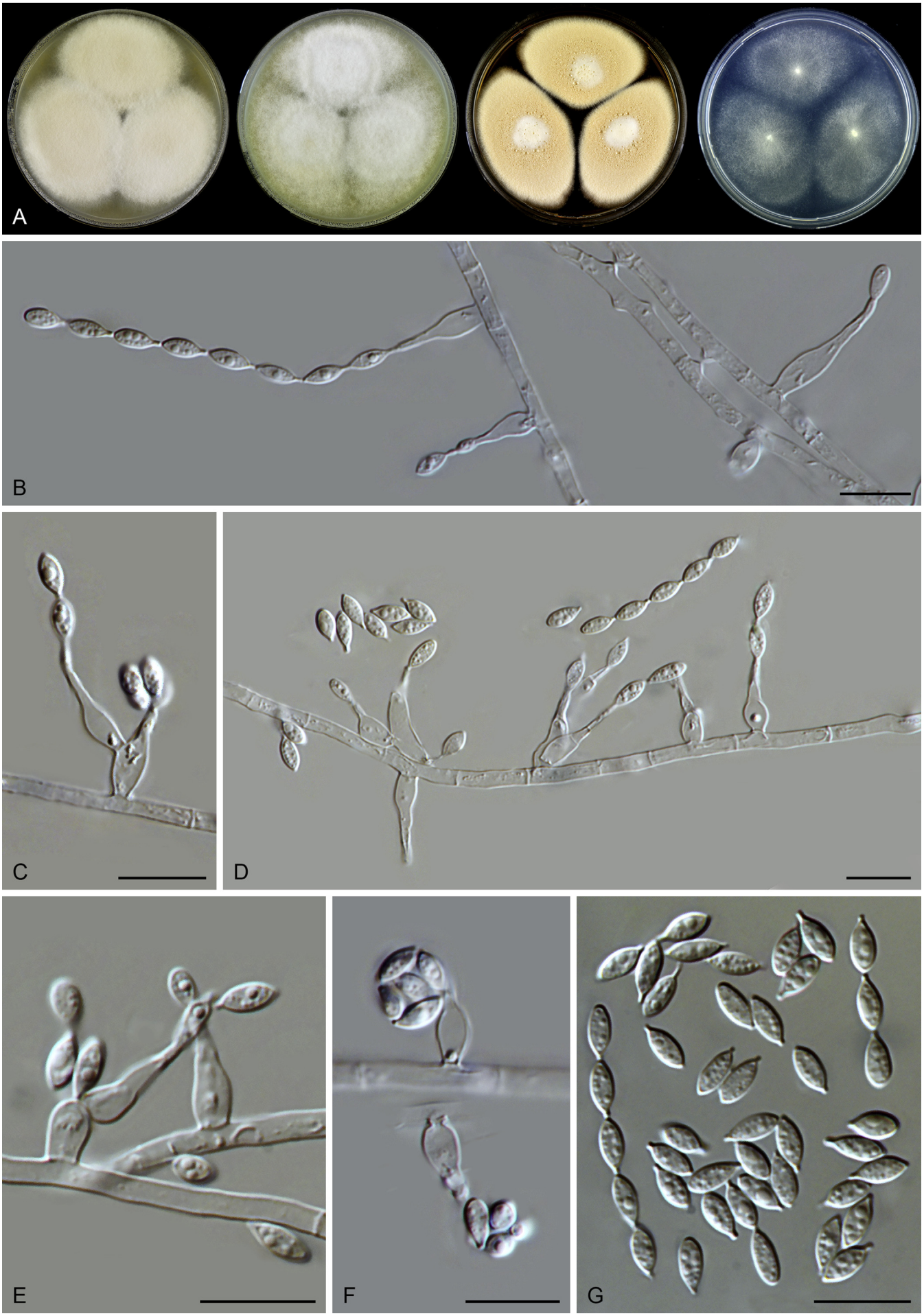


Fig. 12. *Acrophialophora hechuanensis* (GZUIFR-H08-1, ex-type culture). **A.** Colonies from left to right on OA, CMA, MEA and PCA after 18 d incubation. **B–F.** Hyphae, phialidic conidiogenous cells and conidia. **G.** Conidia. Scale bars = 10 μm.

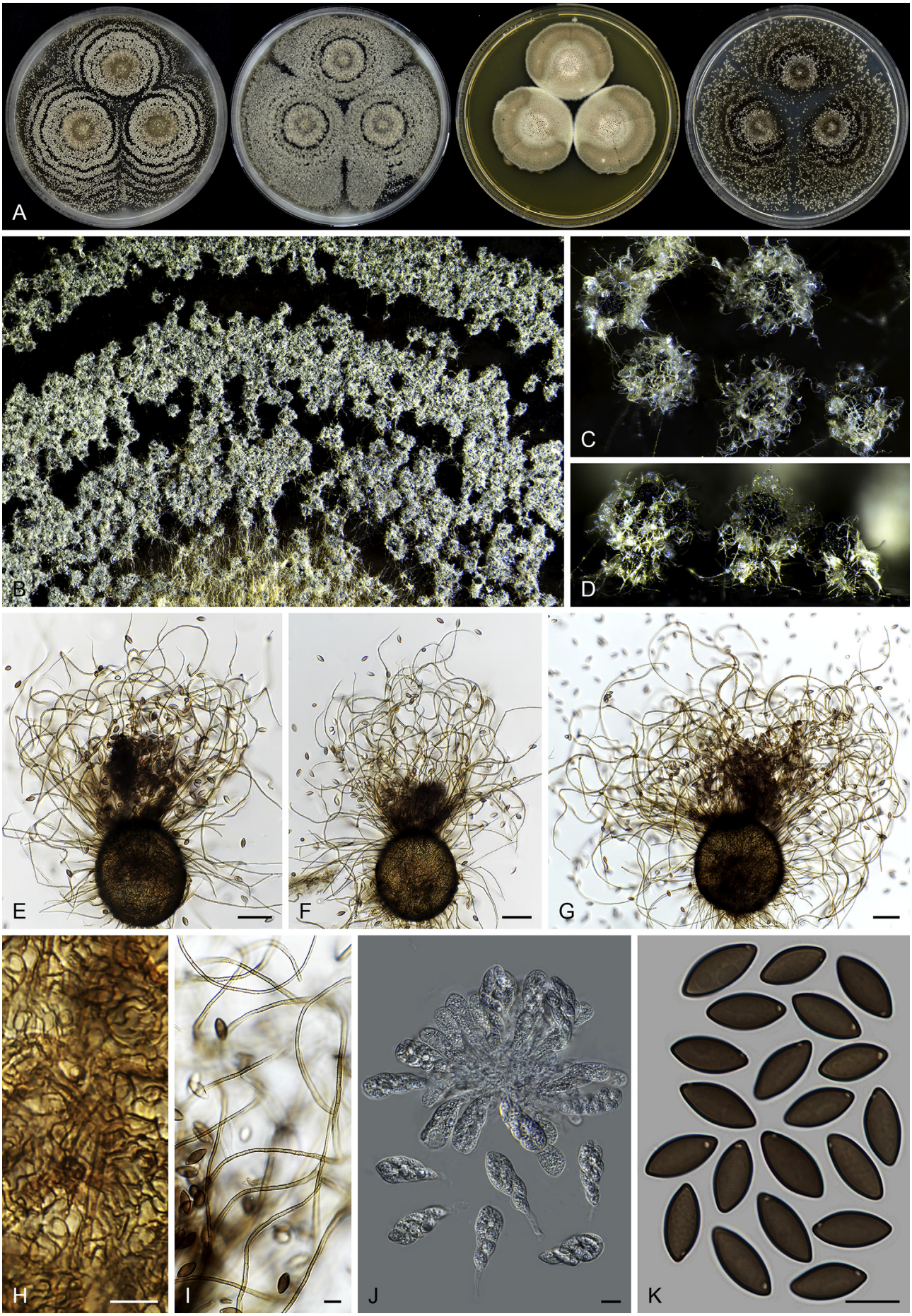


Fig. 13. *Acrophialophora jodhpurensis* (CBS 602.69, ex-epitype culture). **A.** Colonies from left to right on OA, CMA, MEA and PCA after 4 wk incubation. **B.** Part of the colony on OA. **C.** Mature ascomata on OA, top view. **D.** Mature ascomata on OA, side view. **E–G.** Ascomata mounted in lactic acid. **H.** Structure of ascomatal wall in surface view. **I.** Terminal ascomatal hairs. **J.** Asci. **K.** Ascospores. Scale bars: E–G = 50 µm; H–K = 10 µm.

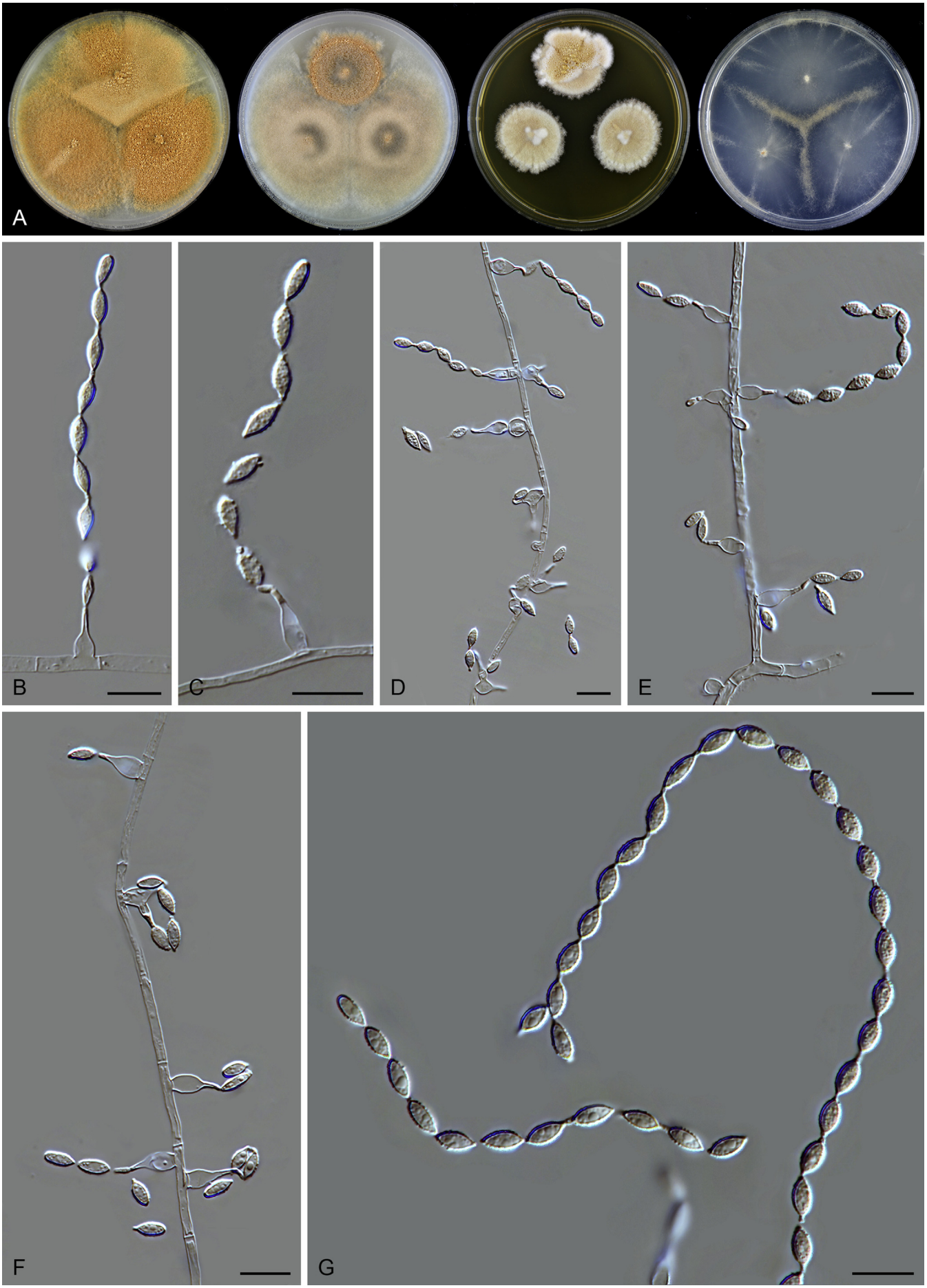
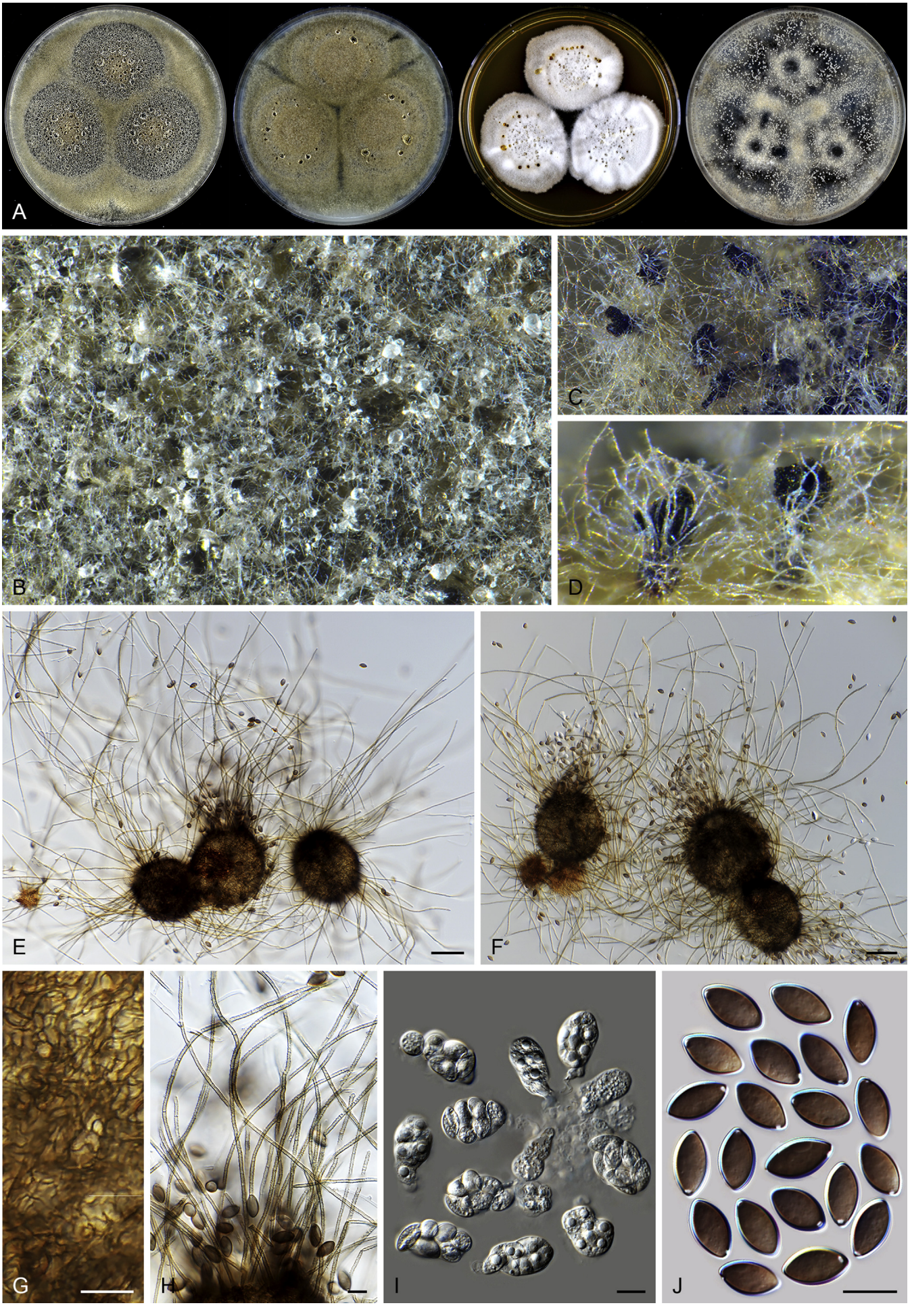


Fig. 14. *Acrophialophora major* (GZUIFR- H57-2, ex-type culture). **A.** Colonies from left to right on OA, CMA, MEA and PCA after 18 d incubation. **B–F.** Hyphae, phialidic conidiogenous cells and conidia. **G.** Conidia. Scale bars = 10 µm.

Fig. 15. *Acrophialophora nainiana* (CBS 100.60, ex-type culture). **A.** Colonies from left to right on OA, CMA, MEA and PCA after 2 wk incubation. **B.** Hyphae, conidiophores and conidia. **C–E.** Conidiophores, conidiogenous cells and macronematous conidia. **F–G.** Phialidic conidiogenous cells and micronematous conidia arising from hyphae. **H.** Conidia. Scale bars: B = 20 µm; C–H = 10 µm.


A
B
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formed in basipetal chains, hyaline, ellipsoidal, fusiform or ovoid, smooth to ornamented with sparse warts which are irregularly or slightly spirally arranged, (6–)6.5–7.5(–8.5) × 2.5–3.5 µm.

Culture characteristics: On OA with an entire edge, 27–33 mm diam after 7 d at 25 °C, obverse saffron, reverse buff to pale luteous. On CMA with an entire or crenate edge 27–33 mm diam after 7 d at 25 °C, obverse rosy buff or saffron, reverse rosy buff. On MEA with a crenate or fimbriate edge, 20–26 mm diam after 7 d at 25 °C, obverse rosy buff to saffron, reverse orange with ochraceous margin. On PCA with an entire edge, 28–34 mm diam after 7 d at 25 °C, without aerial mycelium, reverse uncoloured.

Typus: **China**, Tangshan, Hebei Province, isolated from soil, 2003, H.L. Chu, Y.F. Han & Z.Q. Liang (culture ex-type GZUIFR-H57-2).

Additional material examined: **China**, Tengchong, Yunnan, isolated from soil, 2003, Y.F. Han & Z.Q. Liang (GZUIFR- H52-1).

Notes: Based on our examination of *Acr. major*, the majority of conidia are ornamented with sparse warts which are irregularly or slightly spirally arranged and this slightly differs from the observation reported in Liang *et al.* (2009). *Acrophialophora major* is morphologically similar to *Acr. hechuanensis*, but can be distinguished by ornamented and larger conidia (6.5–7.5 × 2.5–3.5 µm *vs* 5–6 × 2–3.5 µm) and by less proliferating conidiogenous cells.

Acrophialophora nainiana Edward, Mycologia 51: 784. 1961. Fig. 15.

Micromorphology: *Sexual morph* not observed. *Somatic hyphae* hyaline or pale brown often where conidiophores bearing, 1–4 µm wide. *Conidiophores* arising laterally from hyphae, septate, unbranched, erect, warty, pigmented, fading towards tips, 2–5.5 µm wide, (300–)600–1300(–1500) µm long. *Conidiogenous cells* born apically in whorls or in verticils on conidiophores or arising directly from hyphae, phialidic, flask-shaped, swollen at the base, tapering abruptly to a narrow neck, sometimes proliferating, 7.5–15 × 2.5–5 µm. *Conidia* 1-celled, formed in basipetal chains, hyaline to subhyaline, ovoid, ellipsoidal to fusiform, smooth to sparsely punctate, (5–)6–8.5(–10.5) × (2.5–)3.5–4.5(–5) µm.

Culture characteristics: On OA with an entire edge, 32–38 mm diam after 7 d at 25 °C, obverse hazel to olivaceous, reverse olivaceous. On CMA with an entire edge, 24–30 mm diam after 7 d at 25 °C, obverse olivaceous buff to olivaceous, reverse olivaceous. On MEA with an entire edge, 17–23 mm diam after 7 d at 25 °C, obverse white and floccose, reverse pale luteous to luteous at the edge. On PCA with an entire edge, 17–23 mm diam after 7 d at 25 °C, obverse grey white to vinaceous buff due to aerial mycelium, reverse buff.

Typus: **India**, Allahabad, isolated from farm soil, 1957, J.C. Edward (culture ex-type CBS 100.60 = ATCC 22555 = IMI 076567 = LSHB BB399 = UAMH 10774).

Additional material examined: **India**, Allahabad, isolated from soil, collection date and collector unknown, (CBS 417.67 = IARI 1316).

Notes: In our study of the five representatives, asexually reproducing *Acrophialophora* species, *Acr. nainiana*, the type species of the genus, is the only one where typically differentiated pigmented conidiophores were observed. Conidia of this species are produced on phialides on differentiated conidiophores or on solitary phialides on hyphae. The conidia of *Acr. nainiana* are larger than those of the other studied *Acrophialophora* species. Conidiophores of the four other examined species were often absent, or simple and hyaline. The observed conidia of the ex-type culture were less distinctly ornamented as reported by Samson & Mahmood (1970). In their description, the conidia were ornamented with a fine echinulation which is sometimes slightly spirally arranged, while the conidia we observed were smooth to sparsely punctate. It seems evident that differentiated pigmented conidiophores and conidial ornamentation are variable characters in the genus and its species.

Acrophialophora teleoafricana X. Wei Wang & Houbraken, ***sp. nov.*** MycoBank MB829843. Fig. 16.

Etymology: Name refers to a sexual species of *Acrophialophora* isolated from Africa.

Micromorphology: Ascomata superficial, greyish yellow-green due to ascomatal hairs in reflected light, subglobose to ovate, ostiolate, 90–185 µm high, 90–150 µm diam. *Ascomatal wall* brown, of *textura epidermoides* or *intricata* in surface view. *Terminal hairs* flexuous or slightly undulate, brown, septate, 1.5–3 µm diam near base. *Lateral hairs* flexuous. *Asci* fasciculate, clavate or fusiform, spore-bearing part 20–30 × 11.5–17 µm, with stalks 3–7.5 µm long, containing eight biseriate or irregularly-arranged ascospores, evanescent. *Ascospores* 1-celled, olivaceous brown when mature, smooth, ellipsoidal to fusiform, 11–12.5(–13.5) × (5.5–)6–7 µm, with a subapical or lateral germ pore. *Asexual morph* not observed.

Culture characteristics: On OA with an entire edge, 22–28 mm diam in 7 d at 25 °C, obverse buff due to mycelium and mouse grey in the central part due to ascomata, with olivaceous grey exudates diffusing into the medium, reverse smoke grey to olivaceous grey or mouse grey. On CMA with an entire edge, 26–32 mm diam in 7 d at 25 °C, obverse buff due to mycelium mixed with ascomata, with olivaceous grey exudates diffusing into the medium, reverse pale mouse grey to mouse grey. On MEA with a slightly crenate edge, 21–27 mm diam in 7 d at 25 °C, obverse floccose, buff to smoke grey due to aerial mycelium, with coloured exudates diffusing into the medium, reverse dark mouse grey with a pale luteous edge. On PCA with an entire edge, 27–33 mm diam in 7 d at 25 °C, obverse buff due to mycelium, reverse olivaceous to dark mouse grey due to exudates diffusing into the medium.

Typus: **Sudan**, isolated from soil, collection date unknown, B.P.R. Vittal (**holotype** CBS H-23631, culture ex-type CBS 280.79).

Additional material examined: **Sudan**, isolated from soil, collection date unknown, B.P.R. Vittal (CBS 281.79).

Notes: Acrophialophora teleoafricana is a sister to *Acr. jodhpurensis* in both the *rpb2* (PP = 1, ML-BS = 98 %; Fig. 2) and the

Fig. 16. *Acrophialophora teleoafricana* (CBS 280.79, ex-type culture). **A.** Colonies from left to right on OA, CMA, MEA and PCA after 3 weeks 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.** Structure of ascomatal wall in surface view. **H.** Ascomatal hairs. **I.** Asci. **J.** Ascospores. Scale bars: E–F = 50 µm; G–J = 10 µm.

four-locus phylogram (PP = 1, ML-BS = 100 %; Fig. 3). The two species are morphologically similar, but *Acr. teleoafricana* can be distinguished from *Acr. jodhpurensis* by shorter ascospores (11–12.5 × 6–7 µm *vs* 13–14.5 × 6–7 µm) and shorter asci (20–30 × 11.5–17 µm *vs* 30–43 × 12.5–17 µm).

Brachychaeta X. Wei Wang & Houbraken, ***gen. nov.*** MycoBank MB829842.

Etymology: Name refers to the short ascomatal hairs on the ascomata of the type species of this genus.

Micromorphology: *Ascomata* superficial, subglobose, ostiolate. *Ascomatal wall* brown, of *textura epidermoidea* in surface view. *Terminal hairs* arcuate or flexuous, brown, septate, less than 180 µm long. *Lateral hairs* flexuous. *Asci* fasciculate, clavate or fusiform, stalked, containing eight biseriate ascospores, evanescent. *Ascospores* 1-celled, brown when mature, smooth, ellipsoidal, ovate or reniform, often irregular, with two apical germ pores. *Asexual morph* not observed.

Type species: *Brachychaeta variospora* (Udagawa & Y. Horie) X. Wei Wang & Houbraken.

Notes: Brachychaeta is a new chaetomium-like genus proposed for a single lineage in Clade 1 (Figs 2, 3). This lineage was basal in Clade 1, however, statistical support is lacking and the relationship of this monotypic genus with other genera in Clade 1 remains unknown. *Brachychaeta* can be easily distinguished from the other five related genera in Clade 1 (Figs 2, 3) by producing ostiolate ascomata covered by short and arcuate or flexuous ascomatal hairs and by irregularly-shaped ascospores with two apical germ pores.

Brachychaeta variospora (Udagawa & Y. Horie) X. Wei Wang & Houbraken, ***comb. nov.*** MycoBank MB829845. Fig. 17.
Basionym: *Chaetomium variosporum* Udagawa & Y. Horie, Rep. Tottori Mycol. Inst. 10: 430. 1973.

Micromorphology: Ascomata superficial, greyish yellow-green due to ascomatal hairs in reflected light, subglobose, ostiolate, 140–200 µm high, 120–180 µm diam. *Ascomatal wall* brown, of *textura epidermoidea* in surface view. *Terminal hairs* arcuate or flexuous, brown, septate, 2–3.5 µm diam near base, less than 180 µm long. *Lateral hairs* flexuous. *Asci* fasciculate, clavate or fusiform, spore-bearing part 35–47 × 14.5–18 µm, with stalks 8–16 µm long, containing eight biseriate ascospores, evanescent. *Ascospores* 1-celled, brown when mature, smooth, ellipsoidal, ovate or reniform, often irregular, (13–)14.5–17(–18) × (9–)10–12(–14) µm, with two apical germ pores. *Asexual morph* not observed.

Culture characteristics: On OA with an entire edge, 20–26 mm diam in 7 d at 25 °C, without aerial mycelium, obverse honey to greenish olivaceous, citrine or sometimes luteous due to coloured exudates diffusing into the medium, reverse citrine. On CMA with an entire edge, 18–24 mm diam in 7 d at 25 °C, without aerial mycelium, obverse orange due to coloured exudates diffusing into the medium, covered with pale mouse grey to mouse grey ascomata, reverse saffron or citrine. On MEA with a slightly crenate edge, 11–17 mm diam in 7 d at 25 °C, obverse floccose, grey white or pale olivaceous grey, without coloured exudates, reverse olivaceous grey. On PCA with a slightly crenate edge, 17–23 mm diam in 7 d at 25 °C, without aerial mycelium and coloured exudates, reverse greenish olivaceous to iron grey.

Typus: **Thailand**, Lodpure Muang, isolated from soil, date unknown, S. Udagawa (culture ex-type CBS 414.73 = IMI 172986 = NHL 2698).

Notes: *Brachychaeta variospora* forms a single lineage in Clade 1. The ascomata of *Bra. variospora* morphologically resemble those of *Collariella gracilis* (see fig. 25 in Wang *et al.* 2016a). These two species are phylogenetically distant. This species can also be easily distinguished from *Col. gracilis* by its larger and often irregular ascospores (14.5–17 × 10–12 µm *vs* 10–12.5 × 6–7.5 µm) with two germ pores. In contrast, the ascospores of *Col. gracilis* are regularly ellipsoidal or fusiform with one germ pore.

Canariomyces Arx, Persoonia 12: 185. 1984.

Micromorphology: *Ascomata* superficial, solitary to aggregated, non-ostiolate, often covered by subhyaline to brown aerial hyphae, black, globose or subglobose. *Ascomatal wall* brown, non-translucent, *textura angularis* in surface view. *Asci* obvoid, ellipsoidal or subglobose, usually without visible stalks, containing eight irregularly-arranged ascospores, evanescent. *Ascospores* 1-celled, dark brown when mature, smooth, ellipsoidal, with attenuated ends, with a subapical or apical germ pore. *Conidiogenous cells* reduced to a hyphal cell, monoblastic, laterally producing conidia. *Conidia* solitary or in basipetal chains, subhyaline to pigmented, obovoid, pyriform or clavate.

Type species: *Canariomyces notabilis* Arx.

Notes: According to the original description, two types of conidia were observed in the type species of *Canariomyces*: “type I conidia” are formed terminally on hyphae or on short branches of hyphae in a basipetal chain; “type II conidia” are produced laterally from hyphae, solitary and appressonium-like. *Canariomyces* was assigned in the family *Microascaceae* (*Microascales*) mainly based on its sessile asci, ascomatal wall and type I conidia, which are similar to those of *Scedosporium desertorum* and several other species in *Microascaceae* (von Arx 1984). Based on our phylogenetic analyses of the *rpb2* and the combined four-locus datasets, *Canariomyces* belongs in *Chaetomiaceae*, and is closely related to *Madurella* and *Stolonocarpus* (Figs 2, 3). *Canariomyces* is morphologically different from *Madurella* and *Stolonocarpus*. *Madurella* gained attention as the fungal etiologic agent of mycetoma, a chronic subcutaneous inflammatory disease often occurring on extremities. *Madurella* species usually produce only sterile (non-sporulating) hyphae and sparse aerial mycelium, growing restrictedly in culture and often producing buff, cinnamon, sienna or orange exudates diffusing into the agar (Fig. 18). *Stolonocarpus* also produces non-ostiolate ascomata, but can be distinguished from *Canariomyces* by cylindrical (rather than obvoid to subglobose) asci, larger ascospores (25.5–28.5 × 14–15.5 µm *vs* less than 20 × 12 µm) and by the absence of a conidial state.

The ex-type strains of *Th. arenaria* (CBS 507.74), *Th. microspora* (CBS 276.74) and *Th. subthermophila* (CBS 509.74) clustered within the *Canariomyces* lineage represented by the type species *Can. notabilis* (ex-type CBS 548.83). These four species also have similar culture characteristics, ascomata and asci shapes. We therefore transfer *Th. arenaria*, *Th. microspora* and *Th. subthermophila* to *Canariomyces*.

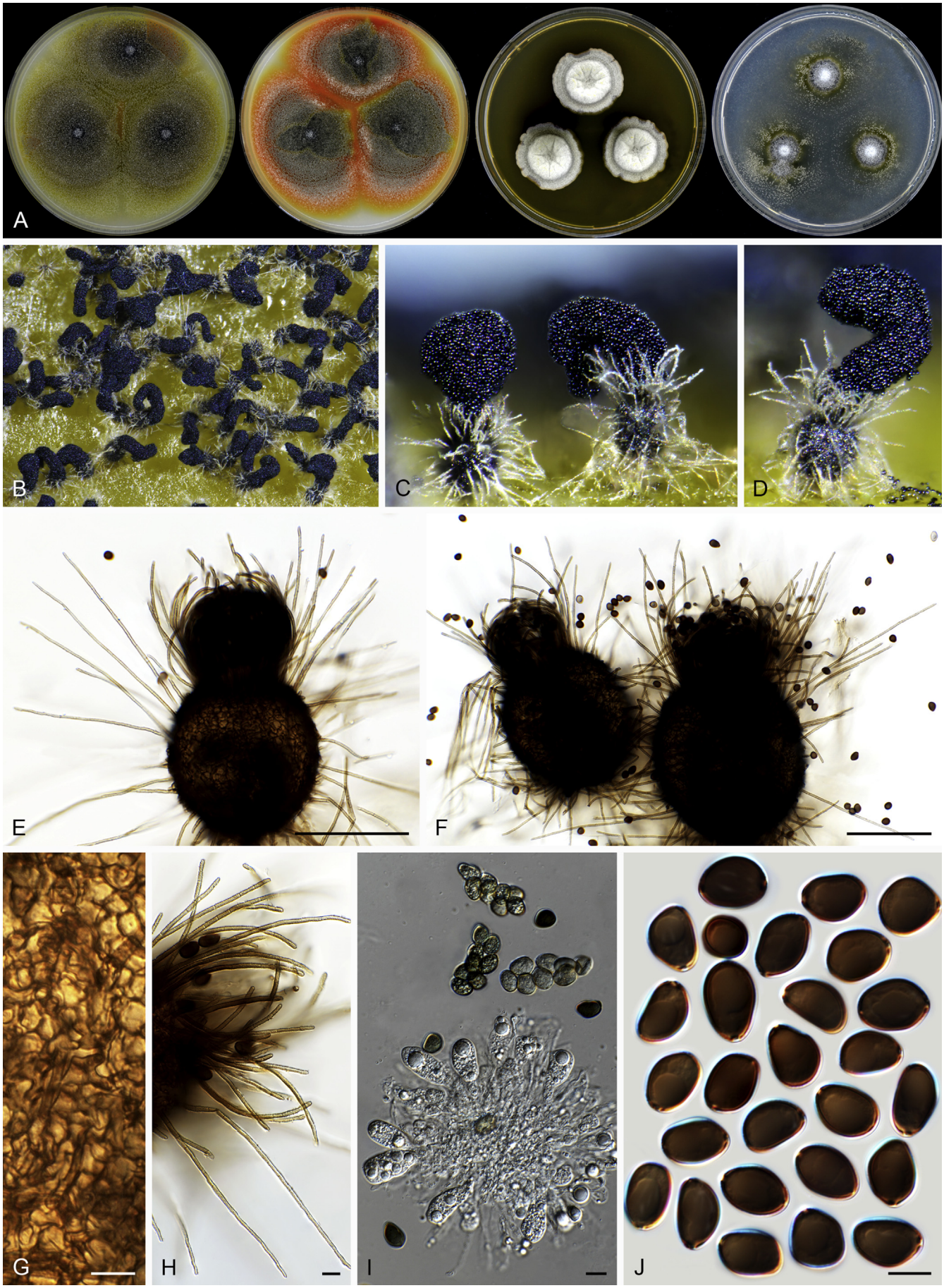


Fig. 17. *Brachychaeta variospora* (CBS 414.73, ex-type culture). **A.** Colonies from left to right on OA, CMA, MEA and PCA after 3 wk incubation. **B.** Mature ascomata on OA, top view. **C–D.** Mature ascomata on OA, side view. **E–F.** Ascomata mounted in lactic acid. **G.** Structure of ascomatal wall in surface view. **H.** Ascomatal hairs. **I.** Asci. **J.** Ascospores. Scale bars: E–F = 100 µm; G–J = 10 µm.

The *Canariomyces* strains seem to degenerate easily. In this study, we only observed type II conidia in CBS 548.83 (ex-type of *Can. notabilis*) using the inclined coverslip method (Wang *et al.* 2019), but its type I conidia and sexual structures were not observed. The ex-type strains of *Th. arenaria* and *Th. subthermophila* also degenerated. Strain CBS 507.74 507.74 produced asexual structures together with empty ascomata with no asci and ascospores inside (Fig. 19). This makes the use of morphological characters for classification of *Can. notabilis* and related species challenging. Several studies (Mouchacca 1973, von Arx 1975, von Arx 1984, von Arx *et al.* 1988) accepted *Can. arenarius*, *Can. notabilis* and *Can. subthermophilus* as separate species mainly based on the difference in their ascospore sizes (Table 3). As both the *rpb2* and the combined four-locus phylogenies were unable to differentiate these three species well (Figs 2, 3), further phylogenetic analyses were made based on partial *tub2* (which has proved to be a good marker to delimit species in the *Chaetomiaceae*, Wang *et al.* 2016b) and *tef1*-α sequences. In the resulting trees (Fig. 5), five lineages were recognised in *Canariomyces*. In the *tub2* phylogeny (Fig. 5A), *Can. notabilis* clustered closely but separate from the *Th. subthermophila* clade, which differ in their ascospore size (11–14 × 7–8.5 µm *vs* 14–19 × 8–10 µm, Tab. 3). Also an unnamed clade clustered close, but separate from the *Th. arenaria* clade, both also differing in their ascospore size (15–18.5 × 9.5–11 µm *vs* 8–12.5 × 5–7.5 µm, Tab. 3). As a result, five species are accepted, including a novel one. Further morphological and phylogenetic work is required to confirm the recognition of these species.

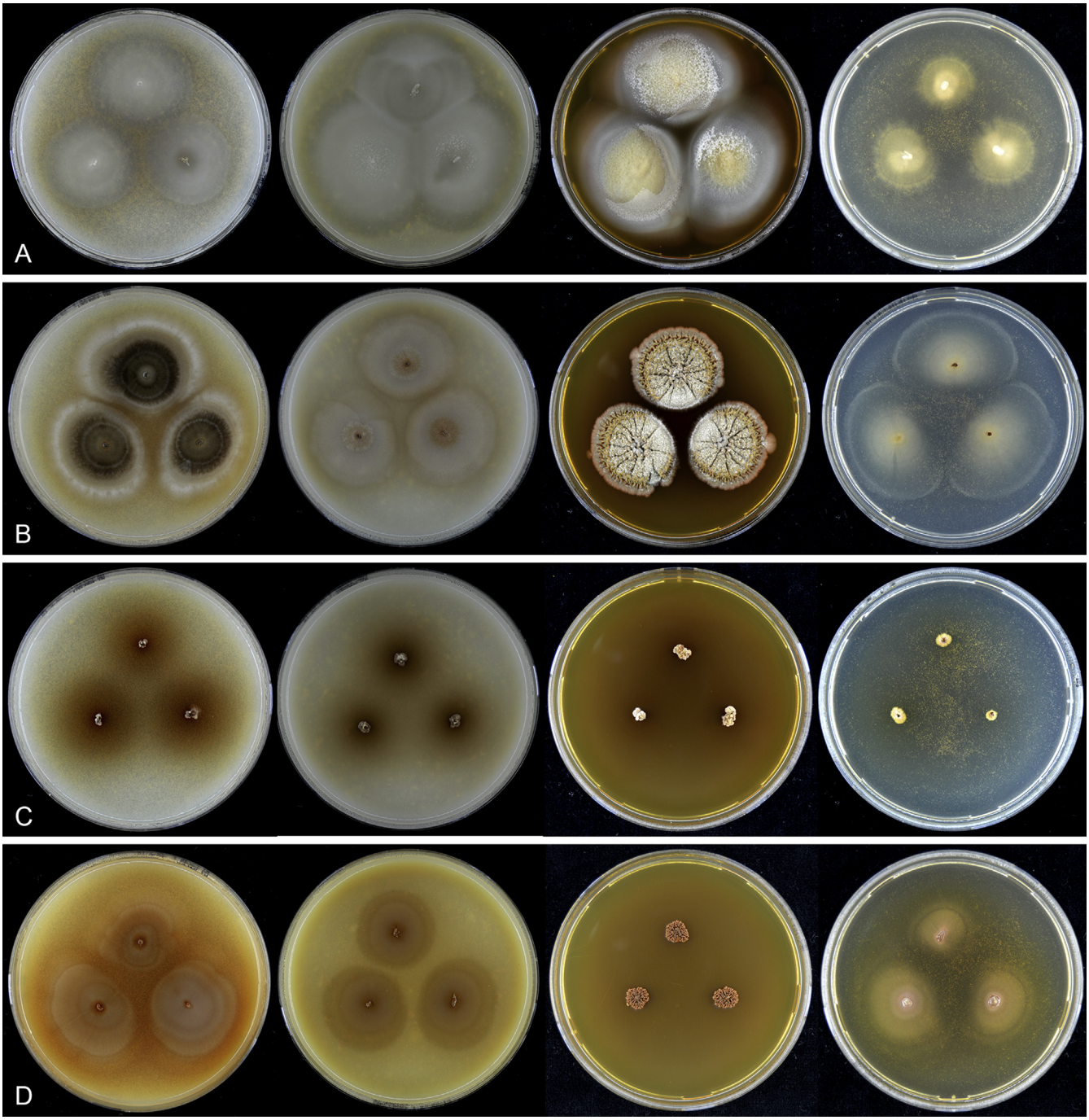


Fig. 18. Colony morphology of *Madurella*. **A.** *Madurella fahalii* (ex-type CBS 129176). Colonies from left to right on OA, CMA, MEA and PCA after 3 wk incubation. **B.** *Madurella mycetomatis* (ex-neotype CBS 109801). Colonies from left to right on OA, CMA, MEA and PCA after 3 wk incubation. **C.** *Madurella pseudomycetomatis* (ex-type CBS 129177). Colonies from left to right on OA, CMA, MEA and PCA after 3 wk incubation. **D.** *Madurella tropicana* (ex-type CBS 201.38). Colonies from left to right on OA, CMA, MEA and PCA after 3 wk incubation.

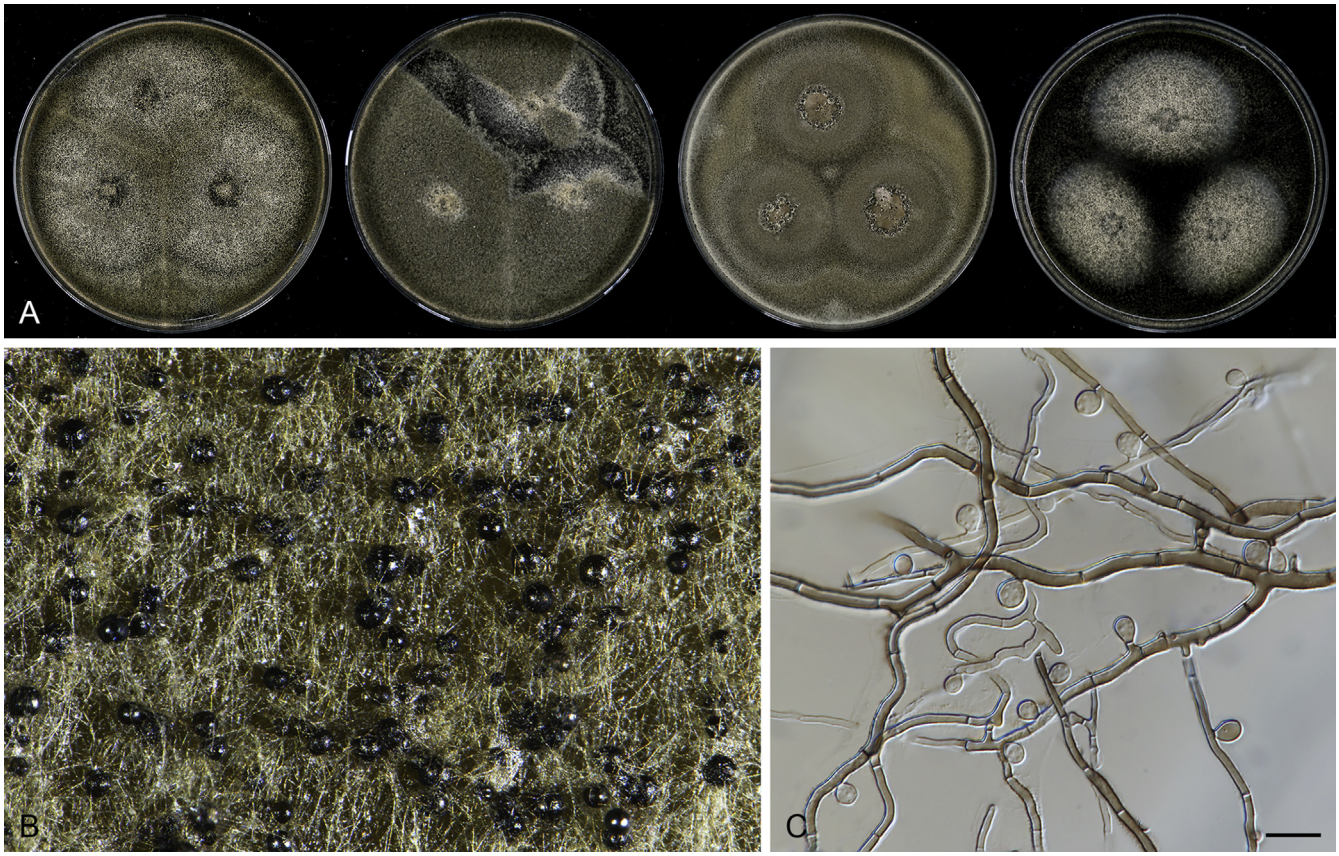


Fig. 19. *Canariomyces arenarius* (CBS 507.74, ex-type culture). **A.** Colonies from left to right on OA, CMA, MEA and PCA after 4 wk incubation. **B.** Part of the colony on OA, showing sterile ascomata, top view. **C.** Hyphae, conidiogenous cells and conidia. Scale bar: C = 10 µm.

Canariomyces arenarius (Mouch.) X. Wei Wang & Houbraken, ***comb. nov.*** MycoBank MB829846. Fig. 19.
Basionym: *Thielavia arenaria* Mouch., Bull. Trimestriel Soc. Mycol. France 89: 308. 1973.

Micromorphology: Description *fide* von Arx (1975) and von Arx *et al.* (1988): *Ascomata* non-ostiolate, globose, black, 60–120 µm diam. *Ascomatal wall* composed of *textura epidermoidea* and covered by dark hyphae. *Ascospores* 1-celled, brown when mature, smooth, fusiform or ellipsoidal, 8–12 × 5–6.5 µm. *Conidiogenous cells* reduced to a hyphal cell, monoblastic, laterally producing conidia. *Conidia* borne laterally, terminally or intercalary on the aerial hyphae, spherical or broadly clavate, hyaline or light brown, 4–8 × 3–5 µm.

Culture characteristics: On OA with an entire edge, 32–38 mm diam in 7 d at 25 °C, texture floccose, obverse mouse grey to dark mouse grey due to ascomata and aerial mycelium, reverse leaden black. On CMA similar to those on OA. On MEA with an entire edge, 29–35 mm diam in 7 d at 25 °C, texture floccose, obverse smoke grey to olivaceous grey, reverse black. On PCA with an entire edge, 28–34 mm diam in 7 d at 25 °C, obverse black, with smoke grey, reverse pale olivaceous grey with black margin.

Typus: **Egypt**, Kharga, isolated from desert soil, date unknown, J. Mouchacca (culture ex-type CBS 507.74).

Notes: Only sterile ascomata and the asexual morph were observed during the morphological examination of the ex-type

Table 3. Comparison of asci, ascospores and conidia between the five *Canariomyces* species.

Species names	Asci	Ascospores	Conidia
Can. arenarius	17–26 × 15–20 µm (M)	9–12.5 × 6–7.5 µm (M) 8–12 × 5–6.5 µm (A1)	3.5–8 × 2–6 µm (M) 4–8 × 3–5 µm (A1)
Can. microsporus	15–22 × 11–15 µm (M) 15–25 × 10–15 µm (A) 15–24 × 11–17 µm (W)	7.5–11 × 5–6 µm (M) 8–10 × 5.5–6.5 µm (A1) 7.5–9 × 4.5–6 µm (W)	4–10 × 2.5–4 µm (M) 4–10 × 3–5 µm (A1) 4–10.5 × 2–3.5 µm (W)
Can. notabilis	20–26 µm (A2)	11–14 × 7–8.5 µm (A2)	Type I: 9–16 × 5–7 µm (A2) Type II: 3–5 µm (A2)
Can. subthermophilus	23–32 × 20–25 ìm (M)	13–17 × 7.5–9.5 µm (M) 14–19 × 8–10 µm (A1)	4–18 × 3–5 µm (M) 4–7 × 3–4 µm (A1)
Can. vonarxii	26–45 × 22–38 µm (W)	15–18.5 ×9.5–11 µm (W)	3–7.5 × 2.5–5.5 µm (W)

(M): from Mouchacca (1973); **(A1)**: from von Arx (1975); **(A2)**: from von Arx (1984); **(W)**: from the present study.

strain (Fig. 19). According to literature (Mouchacca 1973, von Arx 1984, Tab. 3), this species has ascospores (8–12 × 5–6.5 µm) smaller than those of *Can. notabilis* (11–14 × 7–8.5 µm), *Can. subthermophilus* (13–17 × 7.5–9.5 µm) and *Can. vonarxii* (15–18.5 × 9.5–11), but larger than those of *Can. microsporus* (7.5–9 × 4.5–6 µm).

Canariomyces microsporus (Mouch.) X. Wei Wang & Houbraken, ***comb. nov.*** MycoBank MB829847. Fig. 20.
Basionym: *Thielavia microspora* Mouch., Bull. Trimestriel Soc. Mycol. France 89: 300. 1973.

Micromorphology: Ascomata superficial, solitary to aggregated, non-ostiolate, often covered by subhyaline to brown aerial hyphae in 1.5–3.5 µm diam, black, globose or subglobose, 85–120 µm diam. *Ascomatal wall* brown, non-translucent, composed of irregular or angular cells. *Asci* ellipsoidal to ovoid, spore-bearing part 13–19 × 11–17 µm, with short stalks 2–5 µm long, containing eight irregularly arranged ascospores, evanescent. *Ascospores* 1-celled, dark brown when mature, smooth, ellipsoidal, with attenuated ends, (7.5–)8–8.5(–9) × 4.5–5.5(–6) µm, with an apical or slightly subapical germ pore. *Conidiogenous cells* reduced to a hyphal cell, monoblastic, laterally producing conidia. *Conidia* laterally produced on aerial hyphae subhyaline, obovoid to clavate, 4–10.5 × 2–3.5 µm.

Culture characteristics: On OA with an entire edge, 31–37 mm diam in 7 d at 25 °C, texture floccose, obverse pale mouse grey to black due to ascomata and aerial mycelium, reverse pale olivaceous. On CMA similar to those on OA, 30–36 mm diam in 7 d at 25 °C, obverse pale mouse grey to olivaceous grey. On MEA with an entire edge, 35–41 mm diam in 7 d at 25 °C, texture floccose, obverse grey white to smoke grey, reverse black. On PCA with an entire edge, 35–41 mm diam in 7 d at 25 °C, with sparse aerial mycelium, obverse pale olivaceous grey to dark mouse grey, reverse dark mouse grey.

Typus: **Egypt**, Kharga, isolated from desert soil, date unknown, J. Mouchacca (culture ex-type CBS 276.74).

Additional material examined: **Japan**, isolated from leaf of imported *Thymus* sp., date and collector unknown (CBS 161.80).

Notes: The ex-type culture of *Can. microsporus*, CBS 276.74, is degenerated and does not produce a sexual state. The above description is based on CBS 161.80. *Canariomyces microsporus* exhibits the culture characteristics and asexual morph that match *Canariomyces*. Phylogenetic analyses unambiguously place this species in *Canariomyces,* distant from the other species in the genus (Figs 2, 3, 5). This species can be distinguished from the other known species in the genus by having the smallest ascospores (8–8.5 × 4.5–5.5 µm) and elongated conidia (4–10.5 × 2–3.5 µm).

Canariomyces notabilis Arx, Persoonia 12: 185. 1984.

Micromorphology: Description *fide* von Arx (1984): Hyphae at first hyaline, partly becoming brown especially in advancing regions, often closely septate, 2–5 µm. *Ascomata* superficial, non-ostiolate, globose, glabrous, dark brown or black, 120–180 µm diam. *Ascomatal wall* dark brown, non-translucent, composed of angular or irregular cells. *Asci* spherical or broadly obovate, sessile, 8-spored, evanescent, 20–26 µm diam. *Ascospores* 1-celled, brown and often with 2 or 3 darker, longitudinal bands when mature, smooth, ellipsoidal or broadly fusiform, with attenuated ends, 11–14 × 7–8.5 µm. *Conidiogenous cells* reduced to a hyphal cell, monoblastic, laterally producing conidia. *Conidia* spherical, ellipsoidal or clavate, formed terminally from hyphae or short branches of hyphae in basipetal chains, 1-celled or 2-celled, 9–16 × 5–7 µm (type I); or formed laterally from hyphae, solitary, 1-celled, appressonium-like, 3–5 µm long (type II).

Culture characteristics (*fide* von Arx 1984): On corn meal agar with a daily growth rate of 2.5–3.5 mm at 28 °C, texture floccose or fasciculate, exudate present, orange or ochraceous.

Typus: **Spain**, Canary Islands, Gran Canaria, Maspalomas, isolated from litter of *Phoenix canariensis*, Oct. 1982, J.A. von Arx (culture ex-type CBS 548.83).

Notes: We failed to observe the sexual state and type I conidia of this species because of the degeneration of the ex-type culture. The genome of CBS 508.74 is sequenced by the US Department of Energy Joint Genome Institute (JGI, http://genome.jgi.doe.gov/) and this strain is identified as *Can. notabilis*. Within the genus, *Can. notabilis* produces ascospores in intermediate size (Tab. 3). It is closely related to *Can. subthermophilus* (Fig. 5A), but can be distinguished by smaller ascospores (11–14 × 7–8.5 µm *vs* 14–19 × 8–10 µm, Tab. 3).

Canariomyces subthermophilus (Mouch.) X. Wei Wang & Houbraken, ***comb. nov.*** MycoBank MB829848.
Basionym: *Thielavia subthermophila* Mouch., Bull. Trimestriel Soc. Mycol. France 89: 297. 1973.

Micromorphology: Description *fide* Mouchacca (1973)*: Ascomata* non-ostiolate, globose, black, 60–120 µm diam. *Ascomatal wall* composed of *textura epidermoidea* and covered by dark hyphae. *Ascospores* 1-celled, brown when mature, smooth, fusiform or ellipsoidal, 13–17 × 7.5–9.5 µm. *Conidiogenous cells* reduced to a hyphal cell, monoblastic, laterally producing conidia. *Conidia* borne laterally, terminally or intercalarary on the aerial hyphae, spherical or broadly clavate, hyaline or light brown, 4–8 × 3–5 µm.

Typus: **Egypt**, Kharga, isolated from desert soil, date unknown, J. Mouchacca (culture ex-type CBS 509.74).

Notes: We generated molecular data from the ex-type stain, but failed to obtain morphological data. More work is needed to confirm the morphology and phylogeny of this species.

Canariomyces vonarxii X. Wei Wang & Houbraken, ***sp. nov.*** MycoBank MB829849. Figs 21, 22.

Etymology: Named after J.A. von Arx, who introduced the genus *Canariomyces*.

Micromorphology: Ascomata superficial, solitary to aggregated, non-ostiolate, often covered by subhyaline to brown aerial hyphae in 1–4.5 µm diam, black, globose or subglobose, 80–200 µm diam. *Ascomatal wall* brown, non-translucent, *textura angularis* in surface view. *Asci* subglobose to ellipsoidal, 26–45(–47) × 22–38 µm, usually without visible stalks, containing eight irregularly-arranged ascospores, evanescent. *Ascospores* 1-celled, dark brown when mature, smooth, ellipsoidal, with attenuated ends, (13.5–)15–18.5(–19.5) × (8.5–)9.5–11(–12) µm, with a subapical, or occasionally apical germ pore. *Conidiogenous cells* reduced to a hyphal cell, monoblastic,

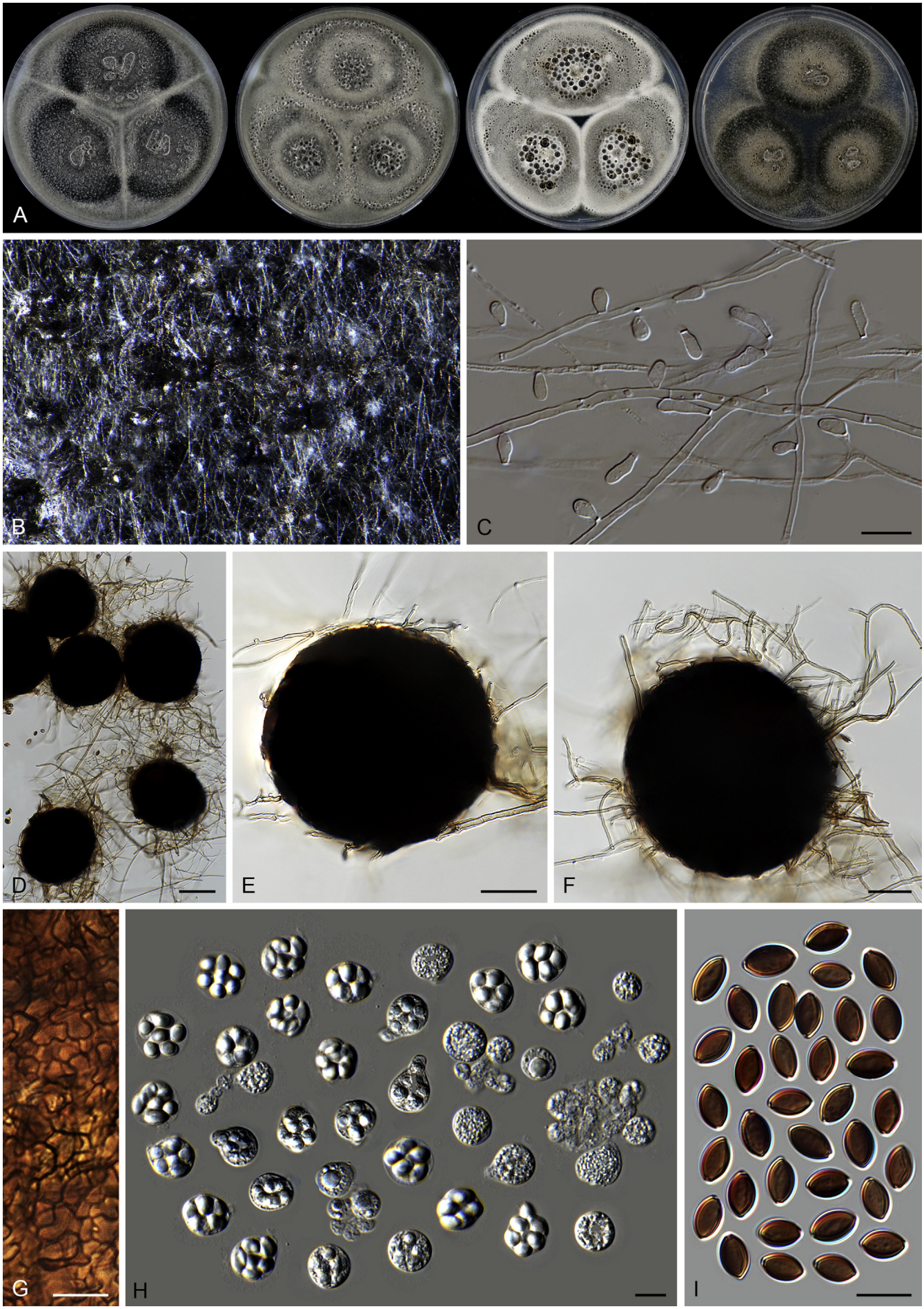


Fig. 20. *Canariomyces microsporus* (CBS 161.80). **A.** Colonies from left to right on OA, CMA, MEA and PCA after 4 wk incubation. **B.** Part of the colony on OA, showing mature ascomata, top view. **C.** Hyphae, conidiogenous cells and conidia. **D–F.** Ascomata mounted in lactic acid. **G.** Structure of ascomatal wall in surface view. **H.** Asci. **I.** Ascospores. Scale bars: C, G–I = 10 µm; D = 50 µm; E–F = 20 µm.

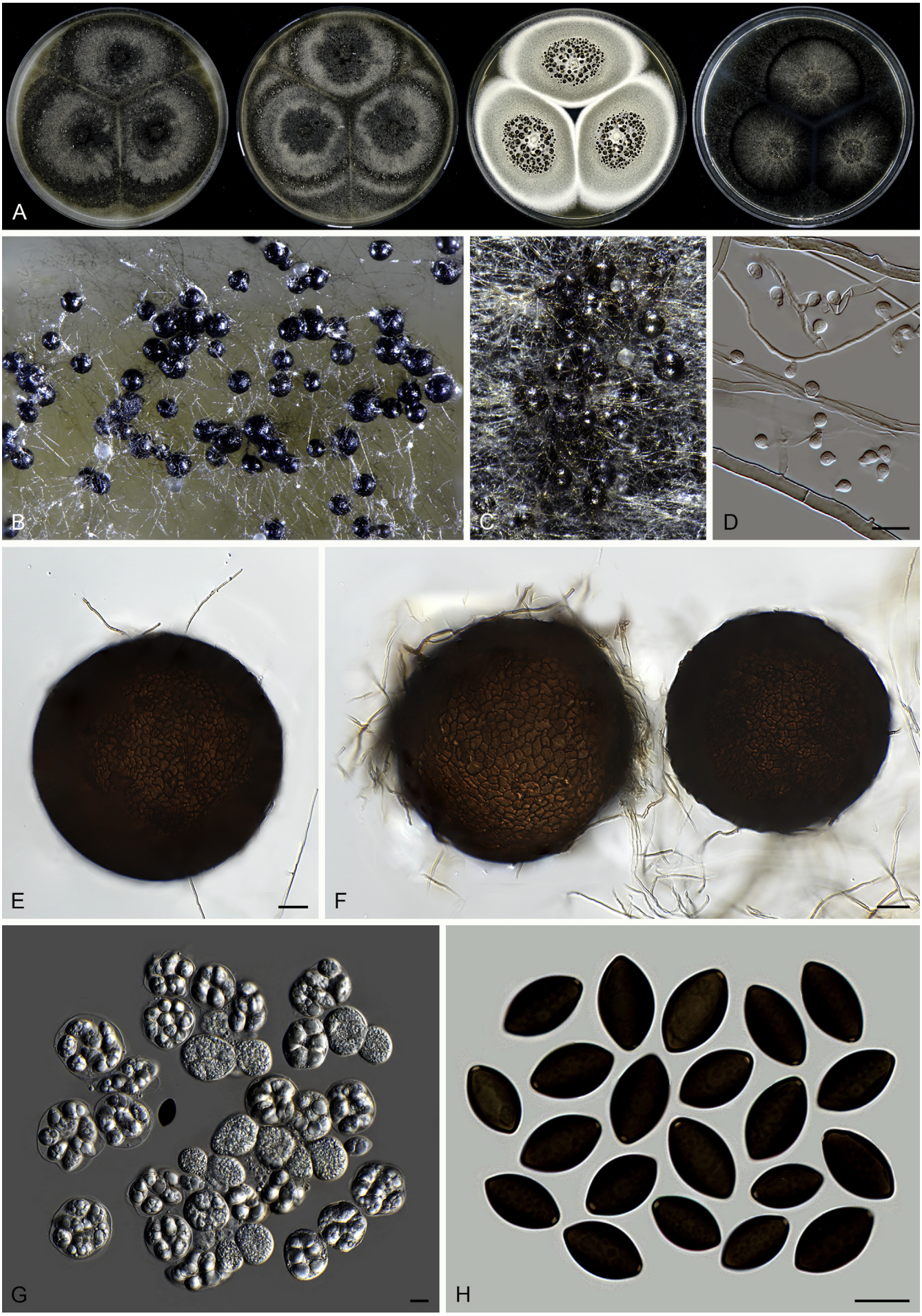


Fig. 21. *Canariomyces vonarxii* (CBS 160.80, ex-type culture). **A.** Colonies from left to right on OA, CMA, MEA and PCA after 4 wk incubation. **B.** Mature ascomata on PCA, top view. **C.** Mature ascomata on OA, top view. **D.** Hyphae, conidiogenous cells and conidia. **E–F.** Ascomata mounted in lactic acid. **G.** Asci. **H.** Ascospores. Scale bars: D, G–H = 10 µm; E–F = 20 µm.

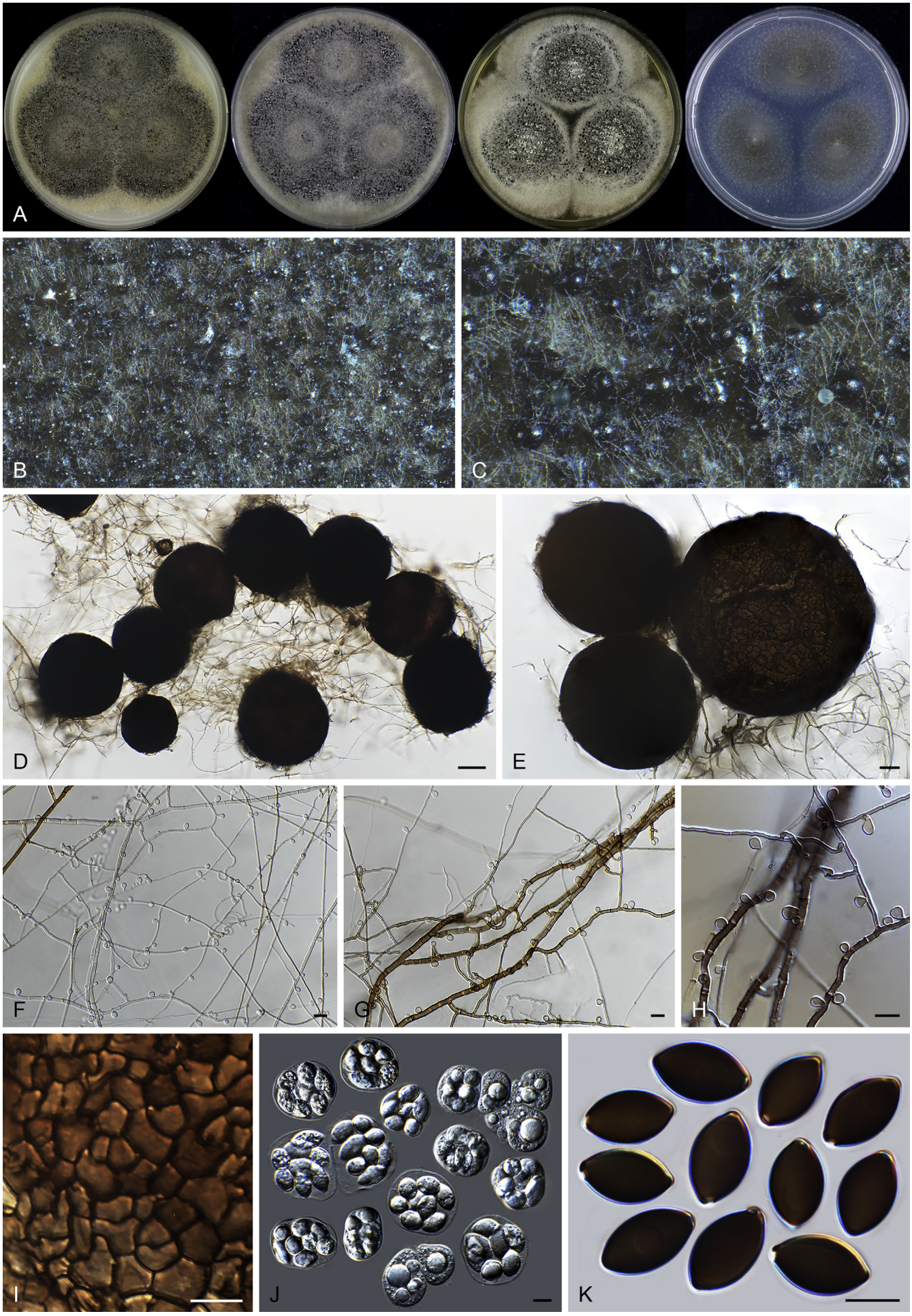


Fig. 22. *Canariomyces vonarxii* (CBS 251.85). **A.** Colonies from left to right on OA, CMA, MEA and PCA after 4 wk incubation. **B–C.** Part of the colony on OA, showing mature ascomata, top view. **D–E.** Ascomata mounted in lactic acid. **F–H.** Hyphae and conidia. **I.** Structure of ascomatal wall in surface view. **J.** Asci. **K.** Ascospores. Scale bars: D = 50 µm; E = 20 µm; F–K = 10 µm.

laterally producing conidia. *Conidia* laterally produced on aerial hyphae, subhyaline to pigmented, obovoid or pyriform, (2.5–)3–7.5 × 2.5–5.5 µm.

Culture characteristics: On OA with an entire edge, 27–33 mm diam in 7 d at 25 °C, texture floccose, obverse buff to olivaceous grey due to ascomata and aerial mycelium, reverse pale mouse grey to mouse grey. On CMA similar to those on OA. On MEA with an entire or slightly crenate edge, 26–32 mm diam in 7 d at 25 °C, texture floccose, obverse olivaceous buff to mouse grey or dark mouse grey due to ascomata and aerial mycelium, reverse hazel. On PCA with an entire edge, 27–33 mm diam in 7 d at 25 °C, with sparse aerial mycelium, obverse olivaceous grey, reverse pale olivaceous grey to olivaceous grey.

Typus: **Sudan**, isolated from a dried flower of *Hibiscus* sp., date unknown, S. Udagawa (**holotype** CBS H-18817, culture ex-type CBS 160.80 = NHL 2831).

Additional material examined: **Nigeria**, substrate unknown, date and collector unknown (CBS 251.85).

Notes: Strain CBS 160.80 was deposited in the CBS collection as *Th. subthermophila* and CBS 251.85 was deposited as *Can. notabilis*. Phylogenetic analyses of *tub2* and *tef1*-α showed that these two strains belong to the same species, separate from the other species in the genus (Fig. 5). In the *tub2* phylogeny, *Can. vonarxii* is closely related to *Can. arenarius* (Fig. 5A), but can be distinguished by its larger ascospores (15–18.5 × 9.5–11 µm *vs* 8–12.5 × 5–7.5 µm, Tab. 3). This species also differs from *Can. notabilis* by having larger ascospores (15–18.5 × 9.5–11 µm *vs* 11–14 × 7–8.5 µm) and from *Can. subthermophilus* by wider ascospores (9.5–11 µm *vs* 7.5–9.5 µm).

Carteria X. Wei Wang & Houbraken, ***gen. nov.*** MycoBank MB829850.

Etymology: Named after Dr Adrian Carter, who collected the ex-neotype culture of *Th. basicola* that made the re-evaluation of *Thielavia* possible.

Micromorphology: *Ascomata* superficial or immersed in medium, solitary to aggregated, non-ostiolate, globose or subglobose. *Ascomatal wall* brown, semi-translucent, composed of *textura epidermoidea* or *angularis* in surface view. *Asci* subglobose, ellipsoidal or obovate, without visible stalks, containing eight irregularly-arranged ascospores, evanescent. *Ascospores* 1-celled, olivaceous brown when mature, smooth, ellipsoidal, attenuated at both ends, with an apical or slightly subapical germ pore. *Asexual morph* not observed.

Type species: *Carteria arctostaphyli* X. Wei Wang & Houbraken.

Notes: *Carteria* is a monotypic genus represented by *Car. arctostaphyli*. This genus forms a unique lineage in the *Chaetomiaceae* and no close relatives were found. *Carteria* produces asci and ascospores similar to those of *Thielavia sensu stricto* in shape; however, its ascomatal wall is not translucent, which is different from *Thielavia* and other genera in the *Ceratostomataceae*. Moreover, *Thielavia sensu stricto* is not able to grow on agar media without a fungal host, while *Carteria* can. A new genus is proposed to accommodate this distinct fungus.

Carteria arctostaphyli X. Wei Wang & Houbraken, ***sp. nov.*** MycoBank MB829851. Fig. 23.

Etymology: Name refers to *Arctostaphylos*, the original substrate of the type strain.

Micromorphology: Ascomata superficial, occasionally immersed in medium, solitary to aggregated, often covered by aerial mycelium, non-ostiolate, olivaceous black in reflected light, spherical or subspherical, 25–85 µm diam. *Ascomatal wall* brown, semi-translucent, composed of *textura epidermoidea* or *angularis* in surface view. *Asci* subglobose, ellipsoidal or obovate, 14–18.5 × 11.5–16 µm, without visiable stalks, containing eight irregularly-arranged ascospores, evanescent. *Ascospores* 1-celled, olivaceous brown when mature, smooth, ellipsoidal, attenuated at both ends, (7–)8–9(–9.5) × 4.5–5.5 µm, with an apical or slightly subapical germ pore. *Asexual morph* not observed.

Culture characteristics: On OA with an entire or slightly crenate edge, 7–13 mm diam in 7 d at 25 °C, obverse white to pale smoke grey due to masses of ascomata mixed with aerial mycelium, with smoke grey margin, usually without coloured exudates, reverse fawn. On CMA similar to those on OA, obverse white to pale mouse grey, with hazel margin due to dark immersed hyphae, reverse fawn to hazel. On MEA with a crenate edge, 9–15 mm diam in 7 d at 25 °C, texture floccose, obverse white due to aerial mycelium, with radiating furrows on the margins, reverse fuscous black cinnamon with a thin margin in sienna. On PCA transparent, with an entire edge, 9–15 mm diam in 7 d at 25 °C, with sparse aerial mycelium, obverse smoke grey, without coloured exudates, reverse dark mouse grey.

Typus: **Switzerland**, Graubünden, Davos, Parsenn, isolated from *Arctostaphylos uva-ursi*, date unknown, B. Widler (**holotype** CBS H-23640, culture ex-type CBS 229.82).

Notes: Strain CBS 229.82 was deposited as one of the two isolates of *Th. basicola* in the CBS culture collection. Phylogenetic data shows that CBS 229.82 and the ex-neotype strain of *Th. basicola* CBS 178.82 belong to two different orders. *Carteria arctostaphyli* produces smaller asci (25–85 µm *vs* 105–260 µm diam) and smaller ascospores (8–9 × 4.5–5.5 µm *vs* 9.5–11.5 × 5.5–7 µm) than those of *Th. basicola*. Furthermore, the pure culture of *Car. arctostaphyli* grows well on the agar media.

Chrysanthotrichum X. Wei Wang & Houbraken, ***gen. nov.*** MycoBank MB829852.

Etymology: Name refers to the ascomatal hairs looking like the flower of the plant genus *Chrysanthemum*.

Micromorphology: Ascomata superficial, globose, subglobose or ovoid, ostiolate or non-ostiolate. *Ascomatal wall* brown, composed of irregular cells. *Ascomatal hairs* smooth to verrucose, brown, septate, arcuate around the ostiole of ostiolate ascomata, apically circinate or coiled, with flexuous lateral hairs; or short and flexuous around non-ostiolate ascomata, sometimes slightly undulate or apically circinate. *Asci* fasciculate, clavate or fusiform, stalked, containing eight biseriate or irregularly-arranged ascospores, evanescent, occasionally persistent until ascospores mature. *Ascospores* 1-celled, olivaceous brown when mature, smooth, elongated ellipsoidal with attenuated ends to fusiform or elongated fusiform, with an apical germ pore. *Asexual morph* not observed.

Type species: *Chrysanthotrichum lentum* (Van Warmelo) X. Wei Wang & Houbraken.

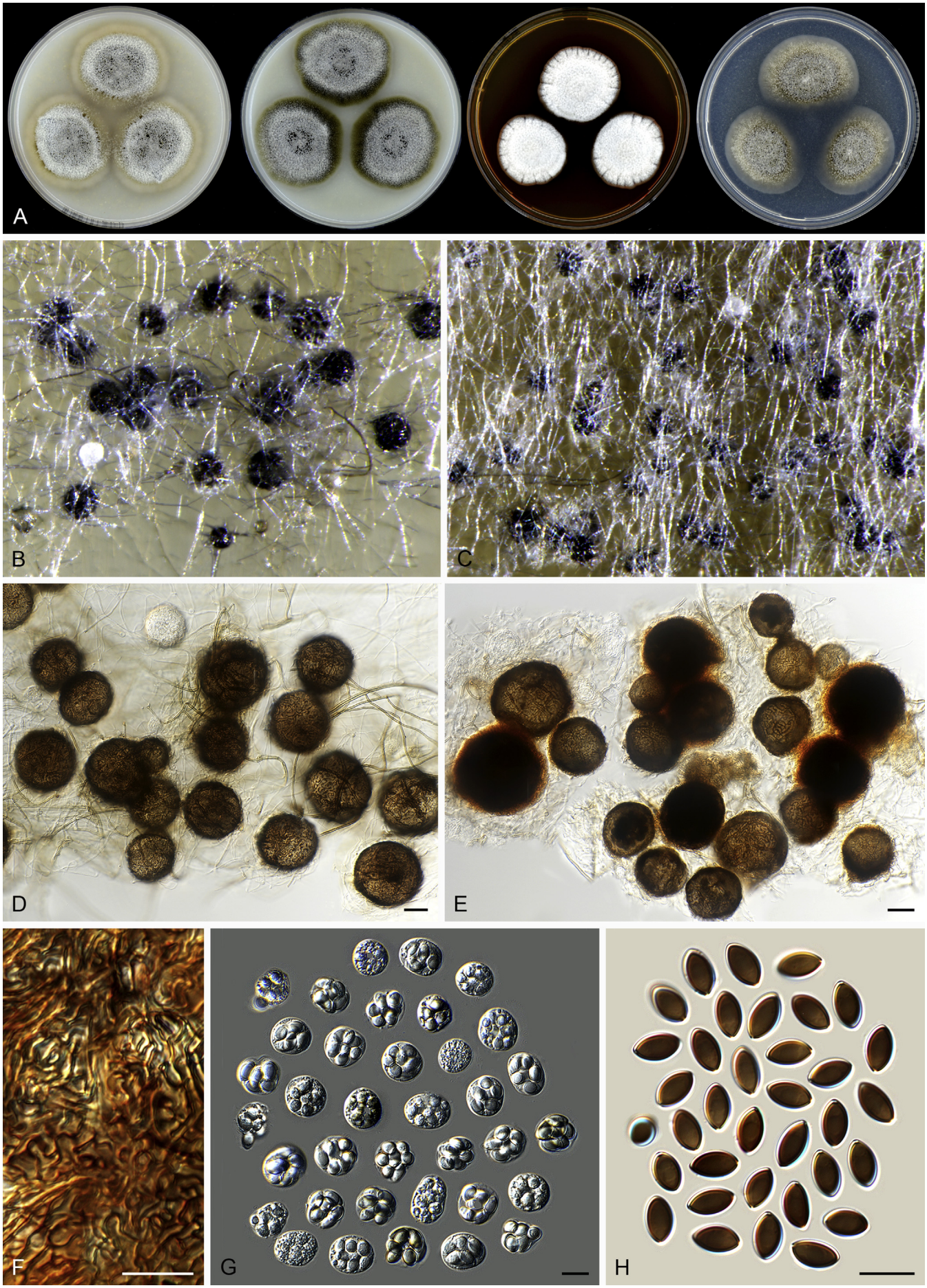


Fig. 23. *Carteria arctostaphyli* (CBS 229.82, ex-type culture). **A.** Colonies from left to right on OA, CMA, MEA and PCA after 4 wk incubation. **B–C.** Part of the colony on OA, showing mature ascomata, top view. **D–E.** Ascomata mounted in lactic acid. **F.** Structure of ascomatal wall in surface view. **G.** Asci. **H.** Ascospores. Scale bars: D–E = 20 µm; F–H = 10 µm.

Notes: This genus is closely related to the monotypic genera *Thermothielavioides* and *Floropilus* (in Clade 3), two new genera introduced in this study (Fig. 3; PP = 0.99; BS = 98 %). *Chrysanthotrichum* includes mesophilic species, while *Thermothielavioides* is introduced for the thermophilic species *The. terrestris* (syn.: *Th. terrestris*). *Floropilus* differs from *Chrysanthotrichum* by its arcuate ascomatal hairs with undulate to loosely coiled upper parts. Furthermore, colonies of *Floropilus* often have amber or luteous exudates on OA and CMA (Fig. 30). The ex-type strain of *Th. peruviana* clustered with three strains in Clade 2, which were deposited as *Ch. lentum* in the CBS culture collection. Phylogenetic analysis showed that these strains fell into four different lineages (Figs 2, 3). Therefore, they are treated as different species in the genus *Chrysanthotrichum*.

Chrysanthotrichum allolentum X. Wei Wang & Houbraken, ***sp. nov.*** MycoBank MB829853. Fig. 24.

Etymology: Name refers to a fungus morphologically similar but separate from *Chrysanthotrichum lentum*.

Micromorphology: Ascomata superficial, olivaceous buff to greenish olivaceous in reflected light due to ascomatal hairs, subglobose, ostiolate, 65–110 µm high, 70–115 µm diam. *Ascomatal wall* brown, composed of *textura epidermoidea* in surface view. *Terminal hairs* arcuate, apically coiled or circinate and tapering towards tips, finely verrucose, brown, septate, (3.5–)4–5.5 µm diam near base. *Lateral hairs* flexuous. *Asci* clavate or fusiform, spore-bearing part 18.5–26.5 × 9–12.5 µm, with stalks 7.5–14 µm long, containing eight biseriate or irregularly-arranged ascospores, evanescent. *Ascospores* 1-celled, olivaceous when mature, smooth, elongated ellipsoidal with attenuated ends to fusiform, (8.5–)9–10(–10.5) × 5–6.5(–7) µm, with an apical germ pore. *Asexual morph* not observed.

Culture characteristics: On OA with an entire edge, 28–34 mm diam in 7 d at 25 °C, with a thin layer of aerial mycelium, obverse greenish olivaceous due to ascomatal hairs, reverse mouse grey due to coloured exudates diffusing into the medium. On CMA similar to those on OA, reverse olivaceous buff. On MEA with an entire edge, 22–28 mm diam in 7 d at 25 °C, texture floccose, obverse pale olivaceous grey, reverse leaden black due to coloured exudates diffusing into the medium. On PCA with a slightly crenate edge, 29–35 mm diam in 7 d at 25 °C, obverse uncoloured, without aerial mycelium, reverse uncoloured.

Typus: **USA**, California, Cachuma Lake, isolated from soil, date unknown, M. Dreyfuss (**holotype** CBS H-23634, culture ex-type CBS 644.83).

Notes: *Chrysanthotrichum allolentum* is phylogenetically distant from the three other species in the genus (Figs 2, 3). Morphologically, this species can be distinguished by its terminal hairs which usually have longer coiled apices than *Chrysan. lentum* (Fig. 25) and *Chrysan. leptolentum* (Fig. 26), while *Chrysan. peruvianum* can be easily distinguished by its non-ostiolate ascomata and elongated fusiform ascospores (Fig. 27)

Chrysanthotrichum lentum (Van Warmelo) X. Wei Wang & Houbraken, ***comb. nov.*** MycoBank MB829855. Fig. 25.
Basionym: *Chaetomium lentum* Van Warmelo, Mycologia 58: 850. 1967.

Micromorphology: Ascomata superficial, olivaceous black in reflected light due to ascomatal hairs, subglobose or ovoid, ostiolate, 55–85 µm high, 55–100 µm diam. *Ascomatal wall* brown, composed of irregular cells. *Terminal hairs* arcuate, apically circinate or slightly coiled, verrucose, brown, septate, (3.5–)4–7 µm diam near base. *Lateral hairs* flexuous. *Asci* fasciculate, clavate or fusiform, spore-bearing part 20–28 × 9.5–12.5 µm, with stalks 5.5–9.5 µm long, containing eight biseriate or irregularly-arranged ascospores, evanescent, occasionally persistent until mature. *Ascospores* 1-celled, olivaceous brown when mature, smooth, elongated ellipsoidal with attenuated ends to fusiform, (7.5–)9–10.5 × (5–)5.5–6(–6.5) µm, with an apical germ pore. *Asexual morph* not observed.

Culture characteristics: On OA with an entire edge, 27–33 mm diam in 7 d at 25 °C, without aerial mycelium, obverse leaden black due to ascomatal hairs, reverse olivaceous grey to iron grey due to coloured exudates diffusing into the medium. On CMA similar to those on OA, reverse dark mouse grey. On MEA with an entire edge, 27–33 mm diam in 7 d at 25 °C, obverse floccose, smoke grey with leaden black ascomata scattering on the surface, reverse fuscous black due to coloured exudates diffusing into the medium. On PCA with an entire edge, 28–34 mm diam in 7 d at 25 °C, obverse olivaceous grey to dark mouse grey due to coloured exudates diffusing into the medium, with sparse white aerial mycelium, reverse olivaceous grey to dark mouse grey.

Typus: **South Africa**, Johannesburg, isolated from soil, K.T. van Warmelo, date unknown (culture ex-type CBS 339.67).

Note: This species can be distinguished from *Chrysan. allolentum* by producing terminal hairs that are circinate or with short coiled apices. *Chrysanthotrichum lentum* is closely related to *Chrysan. leptolentum* and *Chrysan. peruvianum* in a well-supported lineage (PP $\geq$ 0.99, BS = 100 %; Figs 2, 3). The latter deviates from *Chrysan. lentum* by its non-ostiolate ascomata and elongated fusiform ascospores (Fig. 27), and *Chrysan. leptolentum* differs from *Chrysan. lentum* by thinner ascomatal hairs (2.5–5 µm *vs* 4–7 µm diam near base) and thinner ascospores (9–10 × 4.5–5.5 µm *vs* 9–10.5 × 5–6.5 µm).

Chrysanthotrichum leptolentum X. Wei Wang & Houbraken, ***sp. nov.*** MycoBank MB829856. Fig. 26.

Etymology: Name refers to *Chrysan. lentum* with relatively slender ascomatal hairs.

Micromorphology: Ascomata superficial, grey olivaceous in reflected light due to ascomatal hairs, subglobose or ovate, ostiolate, 75–125 µm high, 70–125 µm diam. *Ascomatal wall* brown, composed of irregular cells. *Terminal hairs* arcuate, apically circinate or coiled, smooth or finely punctulate, brown, septate, 2.5–5 µm diam near base. Lateral hairs flexuous. *Asci* fasciculate, clavate or fusiform, spore-bearing part 18–29 × 8–10.5 µm, with stalks 6–12 µm long, containing eight biseriate ascospores, evanescent. *Ascospores* 1-celled, brown when mature, smooth, elongated ellipsoidal with attenuated ends to fusiform, (8.5–)9–10 × 4.5–5.5 µm, with an apical germ pore. *Asexual morph* not observed.

Culture characteristics: On OA with an entire edge, 27–33 mm diam in 7 d at 25 °C, without aerial mycelium, or occasionally with sparse white aerial mycelium, obverse olivaceous grey due to ascomatal hairs, reverse fuscous black due to

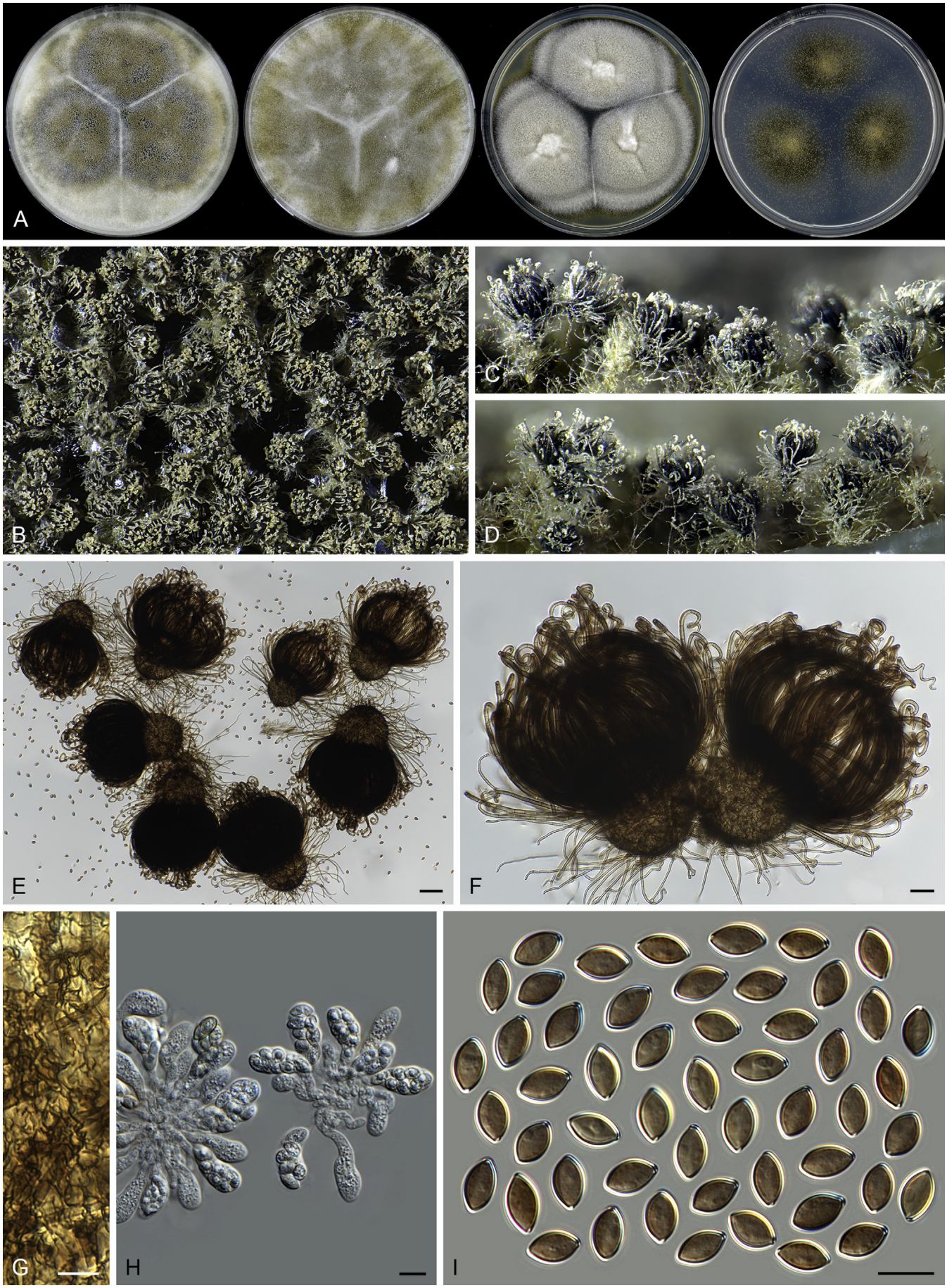


Fig. 24. *Chrysanthotrichum allolentum* (CBS 644.83, ex-type culture). **A.** Colonies from left to right on OA, CMA, MEA and PCA after 3 wk incubation. **B.** Part of the colony on OA. **C.** Mature ascomata on OA, top view. **D.** Mature ascomata on OA, side view. **E–F.** Ascomata mounted in lactic acid. **G.** Structure of ascomatal wall in surface view. **H.** Asci. **I.** Ascospores. Scale bars: E = 50 µm; F = 20 µm; G–I = 10 µm.

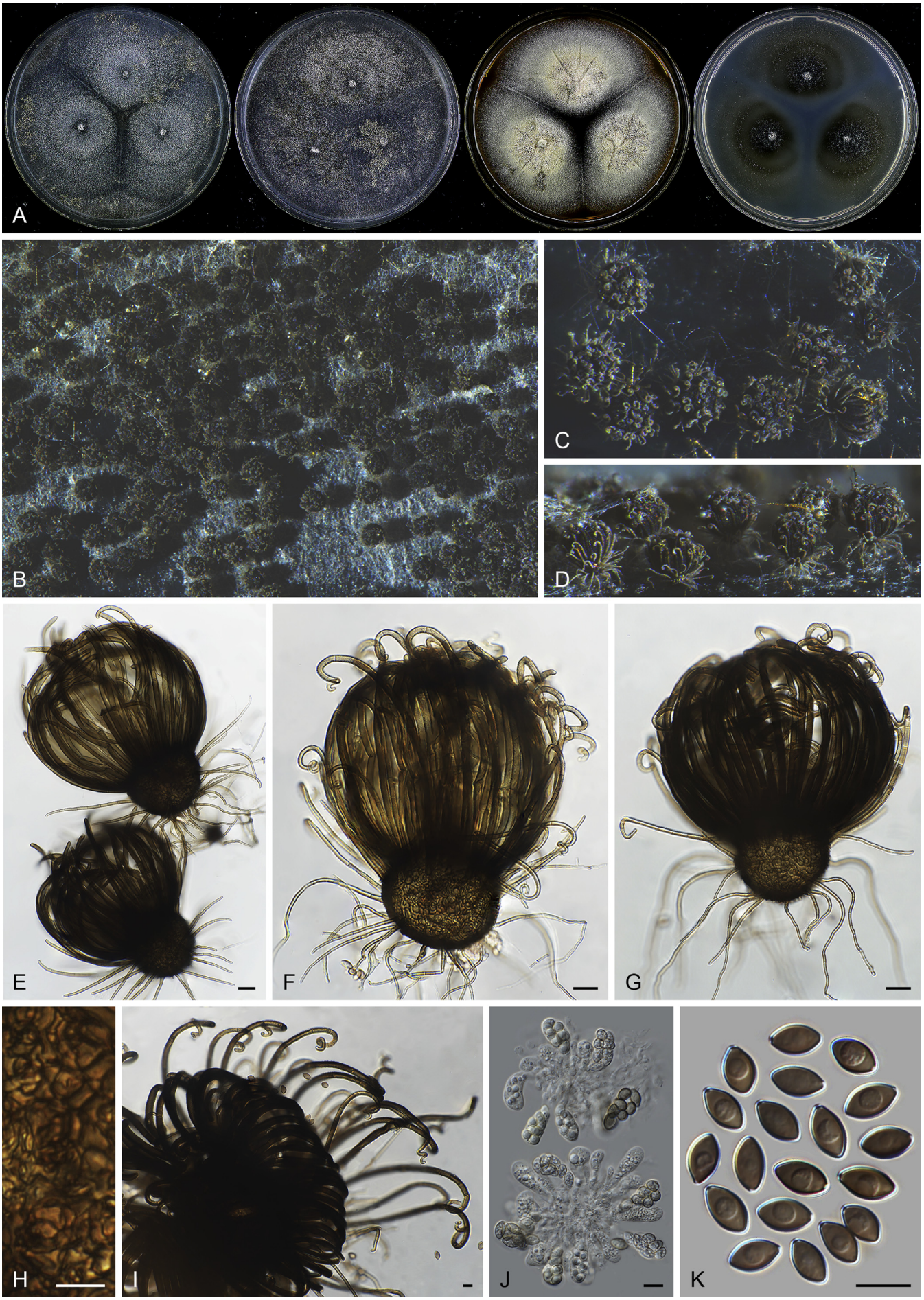


Fig. 25. *Chrysanthotrichum lentum* (CBS 339.67, ex-type culture). **A.** Colonies from left to right on OA, CMA, MEA and PCA after 5 wk incubation. **B.** Part of the colony on OA. **C.** Mature ascomata on OA, top view. **D.** Mature ascomata on OA, side view. **E–G.** Ascomata mounted in lactic acid. **H.** Structure of ascomatal wall in surface view. **I.** Terminal ascomatal hairs. **J.** Asci. **K.** Ascospores. Scale bars: E–G = 20 µm; H–K = 10 µm.

Fig. 26. *Chrysanthotrichum leptolentum* (CBS 126.85, 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–G.** Ascomata mounted in lactic acid. **H.** Structure of ascomatal wall in surface view. **I.** Terminal ascomatal hairs. **J.** Asci. **K.** Ascospores. Scale bars: E–G = 20 µm; H–K = 10 µm.

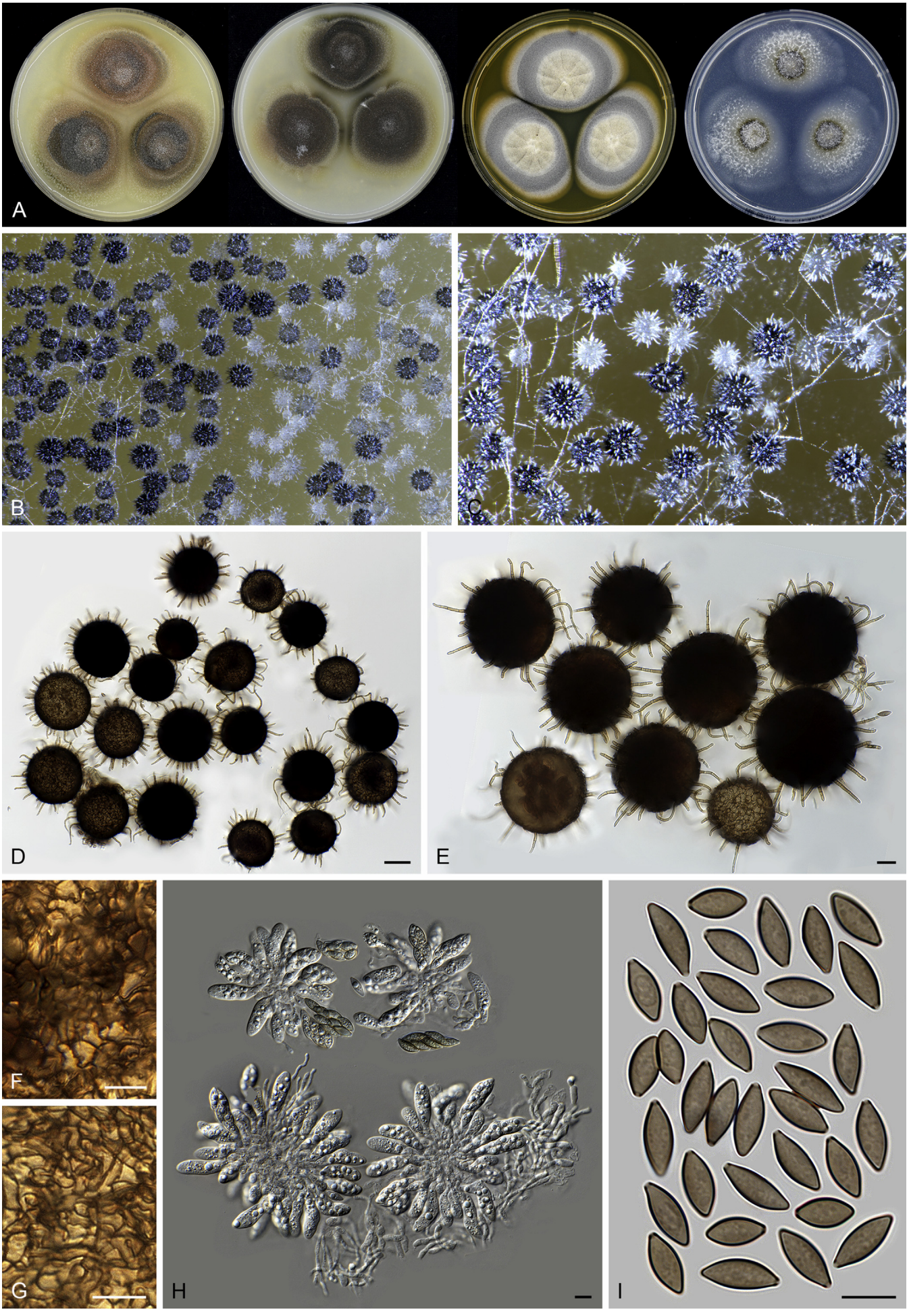


Fig. 27. *Chrysanthotrichum peruvianum* (CBS 732.68, ex-type culture). **A.** Colonies from left to right on OA, CMA, MEA and PCA after 3 wk incubation. **B–C.** Mature ascomata on OA, top view. **D–E.** Ascomata mounted in lactic acid. **F–G.** Structure of ascomatal wall in surface view. **H.** Asci. **I.** Ascospores. Scale bars: D = 50 µm; E = 20 µm; F–I = 10 µm.

coloured exudates diffusing into the medium. On CMA similar to those on OA. On MEA with an entire edge, 28–34 mm diam in 7 d at 25 °C, obverse floccose, smoke grey, reverse greenish black due to coloured exudates diffusing into the medium. On PCA with a slightly crenate edge, 24–30 mm diam in 7 d at 25 °C, obverse greenish black due to coloured exudates diffusing into the medium, with sparse white aerial mycelium, reverse olivaceous grey to iron grey.

Typus: **Kenya**, Mt. Kenya, Naro Moro Track, isolated from dung of elephant, 13 Jul. 1966, R.F. Cain, H.D. Griffin & J.C. Krug (**holotype** CBS H-23633, culture ex-type CBS 126.85).

Additional material examined: **Canada**, Ontario, Haliburton Co., Dorset, isolated from dung of moose or deer, 21 Sep. 1980, D.G. Lahaie (CBS 127.85).

Notes: *Chrysanthotrichum leptolentum* and *Chrysan. lentum* are closely related. For the morphological comparison, see notes of *Chrysan. lentum*.

Chrysanthotrichum peruvianum (Goch.) X. Wei Wang & Houbraken, ***comb. nov.*** MycoBank MB829857. Fig. 27.
Basionym: *Chaetomidium peruvianum* Goch., Mycologia 60: 1118. 1968.
Synonym: *Thielavia peruviana* (Goch.) Malloch & Cain, Mycologia 65: 1067. 1973.

Micromorphology: Ascomata superficial, solitary to aggregated, non-ostiolate, leaden black when mature in reflected light due to the dark ascomatal wall, spherical, pilose, 70–120 µm diam. *Ascomatal wall* brown, semi-translucent, composed of *textura epidermoidea* in surface view. *Ascomatal hairs* brown, short, flexuous, sometimes slightly undulate or apically circinate, smooth, septate, 2.5–4.5 µm diam near base, less than 100 µm long. *Asci* fusiform or clavate, spore-bearing part 25–38 × 8.5–13 µm, with stalks 6–12 µm long, containing eight biseriate or irregularly-arranged ascospores, evanescent, occasionally persistent until mature. *Ascospores* 1-celled, olivaceous when mature, smooth, elongated fusiform, often inequilateral, (9–)11–13.5(–14.5) ×5–6 µm, with an apical germ. *Asexual morph* not observed.

Culture characteristics: On OA with an entire edge, 12–18 mm diam in 7 d at 25 °C, without or with sparse aerial mycelium, obverse mouse grey or olivaceous grey due to the masses of ascomata, or ochraceous to cinnamon or fulvous due to coloured exudates diffusing into the medium, reverse olivaceous grey, with margin fulvous. On CMA similar to those on OA. On MEA with an entire edge, 15–21 mm diam in 7 d at 25 °C, texture slightly floccose, obverse pale smoke grey, with a mouse grey ring near margin, reverse greenish black. On PCA with an entire edge, 13–19 mm diam in 7 d at 25 °C, without white aerial mycelium mainly in the central part, obverse pale olivaceous grey, without coloured exudates, reverse dark mouse grey in the central part.

Typus: **Peru**, near Manazo, isolated from high mountain tundra soil, 1 Jan. 1963, S.E. Gochenaur (culture ex-type CBS 732.68).

Notes: *Chrysanthotrichum peruvianum* is morphologically distinctly different from the three other species in the genus in producing non-ostiolate ascomata. Interestingly, this species is phylogenetically closer to *Chrysan. lentum* and *Chrysan. leptolentum* than to *Chrysan. allolentum*, while the latter three species are morphologically similar. The presence of ostiolate and non-ostiolate ascomata in this genus makes these species good examples to study divergent and convergent evolution of this character.

Chrysocorona X. Wei Wang & Houbraken, ***gen. nov.*** MycoBank MB829858.

Etymology: Name refers to ascomata covered by orange crowns composed of ascomatal hairs.

Micromorphology: *Ascomata* superficial, amber to luteous due to ascomatal hairs in reflected light, subglobose or ellipsoidal, ostiolate. *Ascomatal wall* brown, composed of *textura angularis* in surface view. *Terminal hairs* arcuate, verrucose, with numerous short, flexuous and easily-exfoliated branches near the apical part, brown, septate, usually constricted at the septa, verrucose. *Lateral hairs* flexuous. *Asci* fasciculate, clavate, fusiform or pyriform, stalked, containing eight irregularly-arranged ascospores, evanescent. *Ascospores* 1-celled, olivaceous brown when mature, smooth, 1-celled, ellipsoidal, with a slightly subapical germ pore. *Asexual morph* not observed.

Type species: *Chrysocorona lucknowensis* (J.N. Rai & J.P. Tewari) X. Wei Wang & Houbraken.

Notes: *Chrysocorona* is a newly proposed monotypic chaetomium-like genus closely related to three thielavia-like genera (*Hyalosphaerella*, *Parathielavia*, *Pseudothielavia*), *Acrophialophora* and another chaetomium-like genus (*Brachychaeta*) in Clade 1. In the combined tree (Fig. 3), Bayesian analysis indicates that *Chrysocorona* is basal to the three thielavia-like genera (PP = 0.99); however, this is not supported in the ML analysis (BS <70 %). The genus can be distinguished from *Brachychaeta* and the two sexual species of *Acrophialophora* by its arcuate and brightly coloured terminal ascomatal hairs having numerous short branches near the apical part.

Chrysocorona lucknowensis (J.N. Rai & J.P. Tewari) X. Wei Wang & Houbraken, ***comb. nov.*** MycoBank MB829859. Fig. 28.
Basionym: *Chaetomium lucknowense* J.N. Rai & J.P. Tewari, Canad. J. Bot. 40: 1380. 1962.
Synonym: *Chaetomium venezuelense* L.M. Ames, Monograph of the *Chaetomiaceae*: 42. 1963.

Micromorphology: Ascomata superficial, amber to luteous due to ascomatal hairs in reflected light, subglobose or ellipsoidal, ostiolate, 115–175 µm high, 90–120 µm diam. *Ascomatal wall* brown, composed of textura angularis in surface view. *Terminal hairs* arcuate, 3–4.5 µm diam near base, with numerous short, flexuous and easily-exfoliated branches near the apical part, brown, septate, usually constricted at the septa, verrucose. *Lateral hairs* flexuous. *Asci* fasciculate, clavate, fusiform or pyriform, spore-bearing part 23–31.5 × 11.5–15.5 µm, with stalks 9–19.5 µm long, containing eight irregularly arranged ascospores, evanescent. *Ascospores* 1-celled, olivaceous brown when mature, smooth, ellipsoidal, (9.5–)10–11.5(–12) × 6–7 µm, with a slightly subapical germ pore. *Asexual morph* not observed.

Culture characteristics: On OA with an entire edge, 27–33 mm diam in 7 d at 25 °C, without aerial mycelium, olivaceous grey to violaceous black because of pigmented exudates diffusing into the medium, with luteous or orange ascomata mainly distributing near the edges, reverse mouse grey. On CMA similar to those on OA, obverse presenting orange due to the dense formation of ascomata. On MEA with an fimbriate

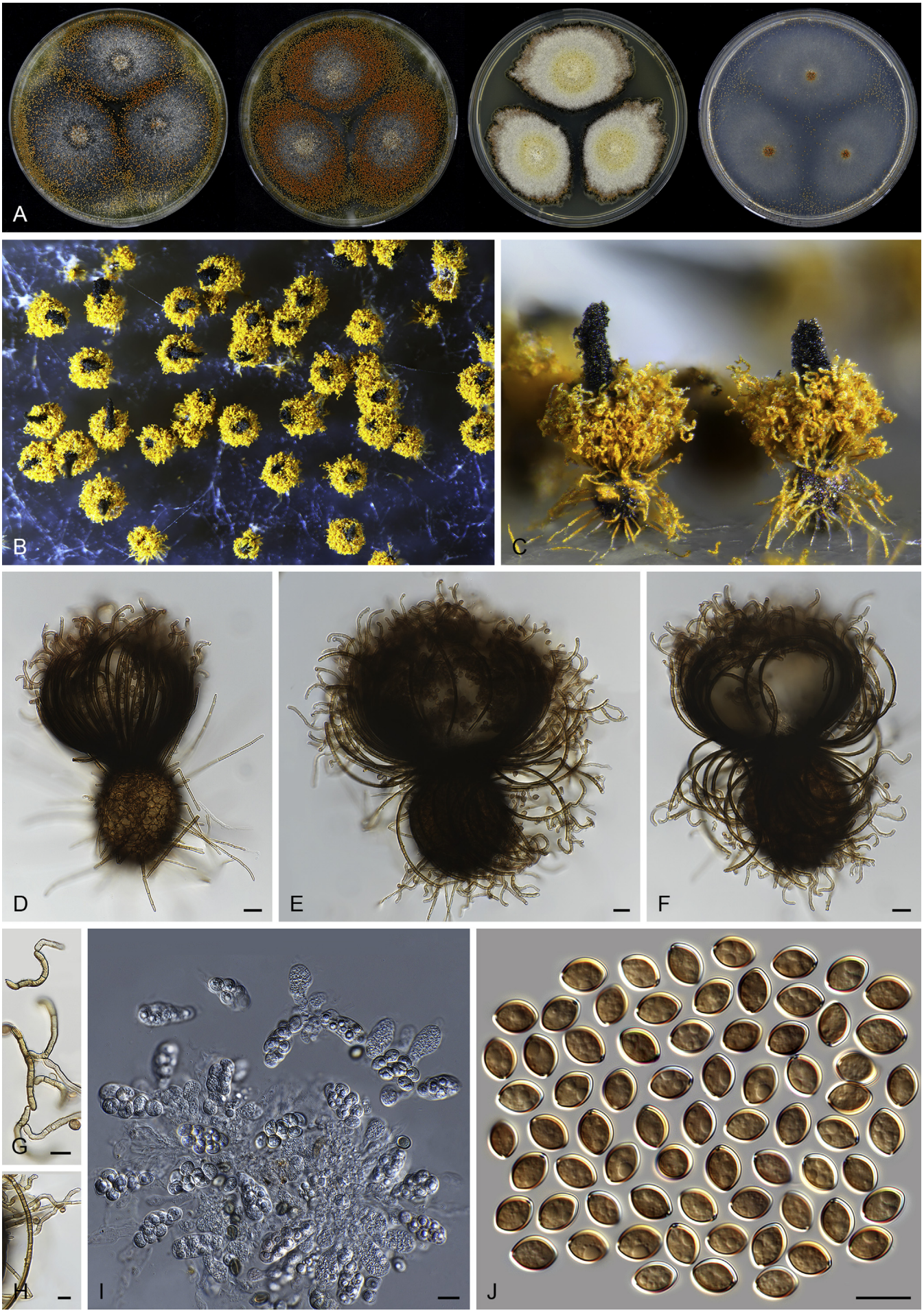


Fig. 28. *Chrysocorona lucknowensis* (CBS 727.71, ex-epitype culture). **A.** Colonies from left to right on OA, CMA, MEA and PCA after 4 wk incubation. **B.** Mature ascomata on OA, top view. **C.** Mature ascomata on OA, side view. **D–F.** Ascomata mounted in lactic acid. **G–H.** Terminal ascomatal hairs. **I.** Asci. **J.** Ascospores. Scale bars: D–F = 20 µm; G–J = 10 µm.

edge, 24–30 mm diam in 7 d at 25 °C, texture floccose, obverse buff to pale luteous, or rosy buff at the edge due to the formation of young ascomata, reverse mouse grey due to exudates diffusing into the medium. On PCA with an entire edge, 27–33 mm diam in 7 d at 25 °C, without aerial mycelium, sparsely forming ascomata mainly in the central point, without coloured exudates, reverse uncoloured or olivaceous grey under ascomata in the central point.

Typus: **Lectotype of *Chaetomium lucknowense* designated here**: figs 16–28 illustrated by J.N. Rai and J.P. Tewari based on original culture from soil in Uttar Pradesh, India, in Canadian Journal of Botany 40: 1380, 1962, MBT385833. **India**, Bharatpur, isolated from dung of deer, Jan. 1971, B.C. Lodha (CBS H-10081, **epitype designated here**, MBT385834, culture ex-epitype CBS 727.71).

Additional material examined: **Germany**, isolated from dung of rabbit, date unknown, H.K. Seth (CBS 562.67). **Venezuela**, State Sucre, isolated from dung of donkey, 14 Jul. 1972, J.C. Krug (CBS 124.85); isolated from soil and vegetable detritus, date unknown, L.M. Ames (CBS 385.66, ex-type of *Ch. venezuelense* L.M. Ames).

Note: In Clade 1, both *Chrysocorona* and *Brachychaeta* are monotypic genera and produce arcuate terminal ascomatal hairs. The type species *Chrysoc. lucknowensis* can be distinguished from *Bra. variospora* by amber to luteous ascomatal hairs with short branches near the apical part which easily fall off, and by ellipsoidal (rather than irregular) and smaller ascospores (10–11.5 × 6–7 µm *vs* 14.5–17 × 10–12 µm) with one (rather than two) germ pore.

Condenascus X. Wei Wang & Houbraken, ***gen. nov.*** MycoBank MB829860.

Etymology: Name refers to the aggregated ascomata and densely congregated asci.

Micromorphology: *Ascomata* superficial, usually aggregated and mixed with aerial mycelium, globose or subglobose, non-ostiolate, glabrous. *Ascomatal wall* brown, semi-translucent, composed of angular or irregular cells. *Asci* cylindrical, twisted, stalked, containing eight uniseriate ascospores, evanescent. *Ascospores* 1-celled, olivaceous brown when mature, smooth, fusiform, with a subapical or oblique germ pore. *Asexual morph* not observed.

Type species: Condenascus tortuosus (Udagawa & Y. Sugiy.) X. Wei Wang & Houbraken.

Note: The four-locus concatenated tree showed that this is a monotypic genus forming a single, basal lineage in the *Chaetomiaceae* and no closely related genera were found in the present study. *Condenascus* produces dense conglomerations of asci in the ascomata, similar to *Trichocladium antarcticum* (syn.: *Th. antarctica*, figs 16–22 in Stchigel *et al.* 2003; fig. 46H in Wang *et al.* 2019). However, *Condenascus* can be easily distinguished from *Tri. antarcticum* by its twisted asci and large, fusiform ascospores, sparse mycelium and by the lack of an asexual state.

Condenascus tortuosus (Udagawa & Y. Sugiy.) X. Wei Wang & Houbraken, ***comb. nov.*** MycoBank MB829861. Fig. 29.
Basionym: *Thielavia tortuosa* Udagawa & Y. Sugiy., Trans. Mycol. Soc. Japan 22: 197. 1981.

Micromorphology: Ascomata superficial, usually aggregated, often covered by or mixed with aerial mycelium, dark slate blue in reflected light, globose or subglobose, non-ostiolate, glabrous,130–400 µm diam. *Ascomatal wall* brown, semi-translucent, composed of angular or irregular cells. *Asci* fasciculate, densely congregated in the ascomata, cylindrical, twisted, spore-bearing part 108–146 × 13–21.5 µm, with stalks 6–12 µm long, containing eight uniseriate ascospores, evanescent. *Ascospores* 1-celled, olivaceous brown when mature, smooth, fusiform, (25–)26–29(–30.5) × (13.5–)14–16(–16.5) µm, with a subapical or oblique germ pore. *Asexual morph* not observed.

Culture characteristics: On OA with a crenate edge, 18–24 mm diam in 7 d at 25 °C, obverse pale mouse grey due to masses of ascomata mixed with aerial mycelium, with white margin because of aerial mycelium, without coloured exudates, reverse uncoloured or buff. On CMA similar to those on OA. On MEA with a crenate edge, 37–43 mm diam in 7 d at 25 °C, obverse pale olivaceous grey due to aggregated ascomata mixed with white aerial mycelium, or white to buff due to aerial mycelium that covers the ascomata, reverse ochraceous or cinnamon. On PCA transparent, with an entire edge, 18–24 mm diam in 7 d at 25 °C, without aerial mycelium, obverse smoke grey in the centre with a ring around the centre due to ascomata, without coloured exudates, reverse uncoloured.

Material examined: **India**, Jaipur, isolated from soil, 30 Oct. 1995, J. Guarro (representative culture CBS 610.97).

Notes: The holotype was isolated from imported spices (thyme plant) in Japan (Udagawa & Sugiyama 1981) and the original location of the holotype is unknown. The ex-type culture CBS 691.82 deposited in the CBS culture collection has died. The examined isolate CBS 610.97 morphologically matches with the protologue (Udagawa & Sugiyama 1981) and was used as the representative of this species in this study.

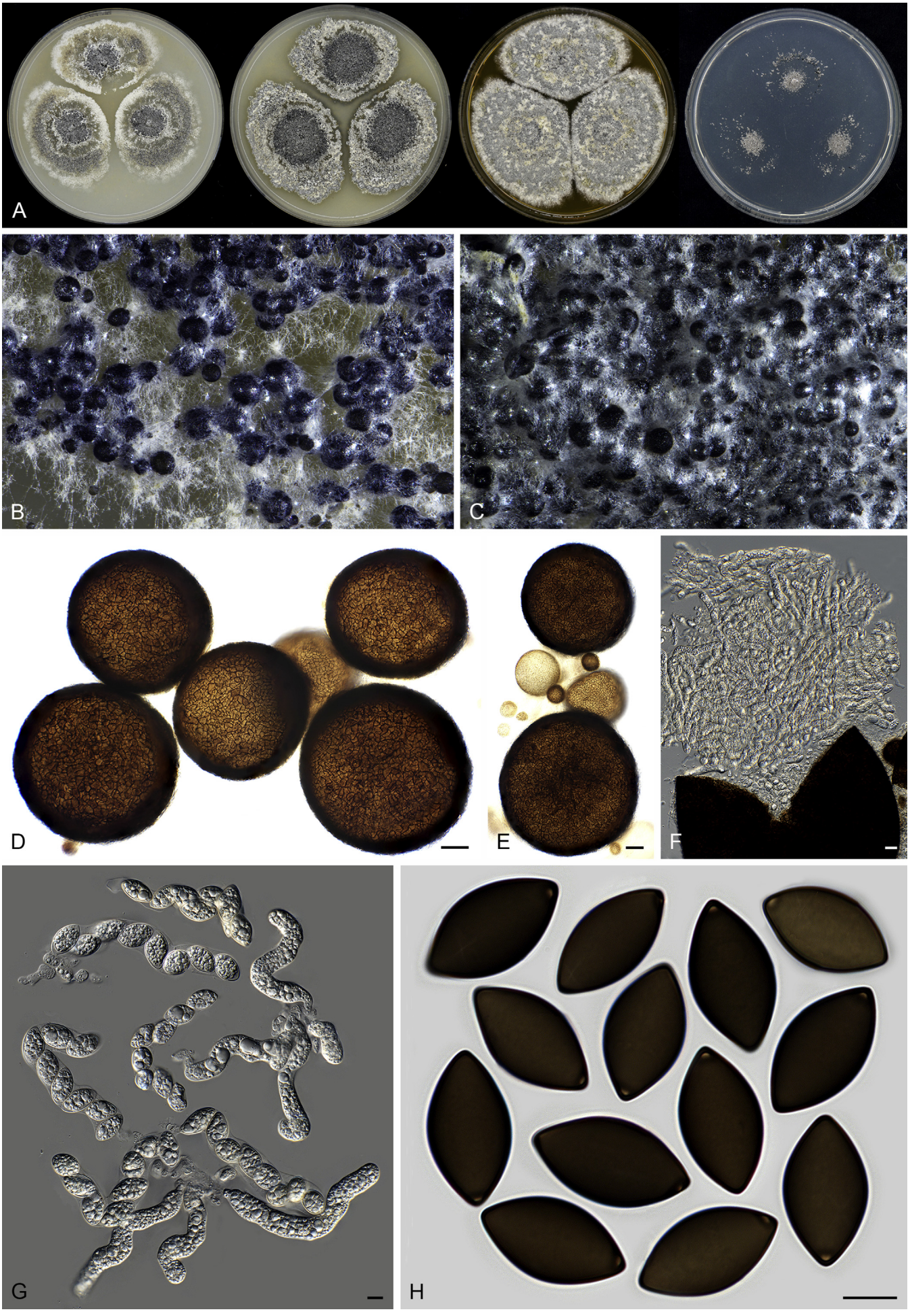
Floropilus X. Wei Wang & Houbraken, ***gen. nov.*** MycoBank MB829862.

Etymology: Name refers to the arcuate terminal hairs with undulate or loosely coiled upper parts hairs which look like a flower covering the ascomata of the fungus.

Micromorphology: *Ascomata* superficial, subglobose, ostiolate. *Ascomatal wall* brown, composed of irregular or angular cells. *Terminal hairs* arcuate, with undulate to circinate or loosely coiled upper parts, brown, septate, verrucose. *Lateral hairs* flexuous, undulate or circinate near the apical part. *Asci* fasciculate, pyriform, obovate or clavate, stalked, containing eight irregularly-arranged ascospores, evanescent. *Ascospores* 1-celled, olivaceous brown when mature, smooth, fusiform or ovate, with an apical or slightly subapical germ pore. *Asexual morph* not observed.

Type species: *Floropilus chiversii* (J.C. Cooke) X. Wei Wang & Houbraken.

Notes: *Floropilus* is a chaetomium-like monotypic genus which forms a sister lineage of the newly introduced genus *Thermothielavioides* in Clade 2 (Figs 2, 3). It can be distinguished from *Thermothielavioides* by ostiolate ascomata and by the absence of a conidial state. Moreover, *Thermothielavioides* is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thermophilic, while *Floropilus* is mesophilic. The type species *F. chiversii* produces arcuate terminal ascomatal hairs and coloured exudates, similar to members of *Arcopilus*, but can be distinguished by its terminal ascomatal hairs with undulate apices. *Arcopilus* species produce terminal hairs with incurved, circinate to coiled apices (Wang *et al.* 2016a). Phylogenetic analyses indicated that this species is not closely related to the genus *Arcopilus* (Figs 2, 3). *Floropilus chiversii* will be a good reference species to study how thermophilic and mesophilic species diverged from each other in the evolutionary history of the *Chaetomiaceae*.

Floropilus chiversii (J.C. Cooke) X. Wei Wang & Houbraken, ***comb. nov.*** MycoBank MB829863. Fig. 30.
Basionym: *Chaetomium trilaterale* var. *chiversii* J.C. Cooke, Mycologia 65: 1218. 1973.
Synonym: *Chaetomium chiversii* (J.C. Cooke) A. Carter, Beih. Nova Hedwigia 84: 19. 1986.

Micromorphology: Ascomata superficial, pale mouse grey due to ascomatal hairs in reflected light, subglobose, ostiolate, 60–125 µm high, 50–110 µm diam. *Ascomatal wall* brown, composed of irregular or angular cells. *Terminal hairs* arcuate, apically undulate, brown, septate, verrucose, 2–3.5 µm diam near base. *Lateral hairs* flexuous, undulate or circinate near the apical part. *Asci* fasciculate, pyriform, obovate or clavate, spore-bearing part 16–24.5 × 10–15.5 µm, with stalks 5–6 µm long, containing eight irregularly arranged ascospores, evanescent. *Ascospores* 1-celled, olivaceous brown when mature, smooth, fusiform or ovate, (9.5–)10–11.5(–12) × 6–7 µm, with an apical or slightly subapical germ pore. *Asexual morph* not observed.

Culture characteristics: On OA with an entire or slightly crenate edge, 21–27 mm diam in 7 d at 25 °C, texture floccose, obverse honey, often with amber or luteous drops of exudates on the surface, reverse honey to ochraceous due to coloured exudates diffusing into the medium. On CMA similar to those on OA, 16–22 mm diam in 7 d at 25 °C, obverse pale olivaceous grey, reverse saffron or citrine. On MEA with a crenate edge, 21–27 mm diam in 7 d at 25 °C, irregularly wrinkled, obverse floccose, honey or hazel, reverse orange. On PCA with an entire edge, 25–31 mm diam in 7 d at 25 °C, without aerial mycelium, without coloured exudates, reverse uncoloured or pale luteous.

Typus: **Canada**, Ontario, Timiskaming District, Burt Lake, isolated from dung of moose, date unknown, A. Carter (CBS H-10077, **neotype of *Chaetomium trilaterale* var. *chiversii* designated here** MBT386363, culture ex-neotype CBS 558.80 = IMI 250966 = MUCL 40052 = TRTC 48533).

Notes: This species was originally described as a variety of *Ch. trilaterale* based on a strain from the USA (Cooke 1973). Carter (1986) raised this variety to species level based on CBS 558.80, because the ex-type culture of *Ch. trilaterale* var. *chiversii* was unavailable (von Arx *et al.* 1986). Therefore, the herbarium specimen CBS H-10077, a dried culture of CBS 558.80, is designated here as the neotype of this species.

Hyalosphaerella X. Wei Wang & Houbraken, ***gen. nov.*** MycoBank MB829864.

Etymology: Name refers to the small spherical non-ostiolate ascomata with translucent walls.

Micromorphology: *Ascomata* immersed in the medium, solitary to aggregated, non-ostiolate, spherical, glabrous, usually less than 120 µm diam. *Ascomatal wall* subhyaline, translucent, thin, composed of *textura epidermoidea* in surface view. *Asci* clavate to pyriform, stalked, containing eight irregularly-arranged ascospores, evanescent. *Ascospores* 1-celled, olivaceous brown when mature, smooth, 1-celled, ovoid, ellipsoidal or reniform, often inequilateral, with an apical germ pore at the most attenuated end. *Asexual morph* not observed.

Type species: *Hyalosphaerella fragilis* (Natarajan) X. Wei Wang & Houbraken.

Notes: The monotypic genus *Hyalosphaerella* forms a single lineage which is a sister to another thielavia-like lineage *Parathielavia* in Clade 1 (Figs 2, 3). *Hyalosphaerella* can be distinguished from *Parathielavia* by the production of immersed ascomata with a subhyaline and translucent ascomatal wall. The subhyaline and translucent ascomatal wall of the type species of *Hyalosphaerella* is reminiscent of that of *Boothiella* in the *Sordariaceae*. However, *Boothiella* differs from *Hyalosphaerella* by the production of cylindrical and 4-spored asci, larger ascomata and larger ascospores. For detailed comparison see notes of *Hya. fragilis*.

Hyalosphaerella fragilis (Natarajan) X. Wei Wang & Houbraken, ***comb. nov.*** MycoBank MB829865. Fig. 31.
Basionym: *Chaetomidium fragile* Natarajan, Proc. Indian Natl. Sci. Acad., B. 37: 124. 1972.
Synonym: *Thielavia fragilis* (Natarajan) Arx, Stud. Mycol. 8: 8. 1975.

Micromorphology: Ascomata immersed in the medium, solitary to aggregated, non-ostiolate, leaden black when mature in reflected light due to the dark ascospores inside, spherical, glabrous, 50–115 µm diam. *Ascomatal wall* subhyaline, translucent, thin, composed of *textura epidermoidea* in surface view. *Asci* clavate to pyriform, spore-bearing part 23.5–36.5 × 13.5–20 µm, with stalks 5–13 µm long, containing eight irregularly arranged ascospores, evanescent. *Ascospores* 1-celled, olivaceous brown when mature, smooth, ovoid, ellipsoidal or reniform, often inequilateral, (10–)11–13 (–14.5) × (6–)6.5–7.5(–8.5) µm, with an apical germ pore at the most attenuated end. *Asexual morph* not observed.

Culture characteristics: On OA with an entire edge, 49–55 mm diam in 7 d at 25 °C, without aerial mycelium, obverse olivaceous grey due to masses of ascomata, with margin olivaceous buff to honey due to coloured exudates diffusing into the medium, reverse isabelline. On CMA with an entire edge, 37–43 mm diam in 7 d at 25 °C, without aerial mycelium, obverse olivaceous grey due to masses of ascomata, without coloured exudates, reverse uncoloured. On MEA with an entire or slightly crenate edge, 41–47 mm diam in 7 d at 25 °C, with white aerial mycelium, texture floccose, obverse white, reverse ochraceous to fulvous. On PCA with an entire edge, 43–49 mm diam in 7 d at 25 °C, without aerial mycelium,

Fig. 29. *Condenascus tortuosus* (CBS 610.97). **A.** Colonies from left to right on OA, CMA, MEA and PCA after 3 wk incubation. **B–C.** Mature ascomata on OA, top view. **D–E.** Ascomata mounted in lactic acid. **F–G.** Asci. **H.** Ascospores. Scale bars: D–E = 50 µm; F = 20 µm; G–H = 10 µm.

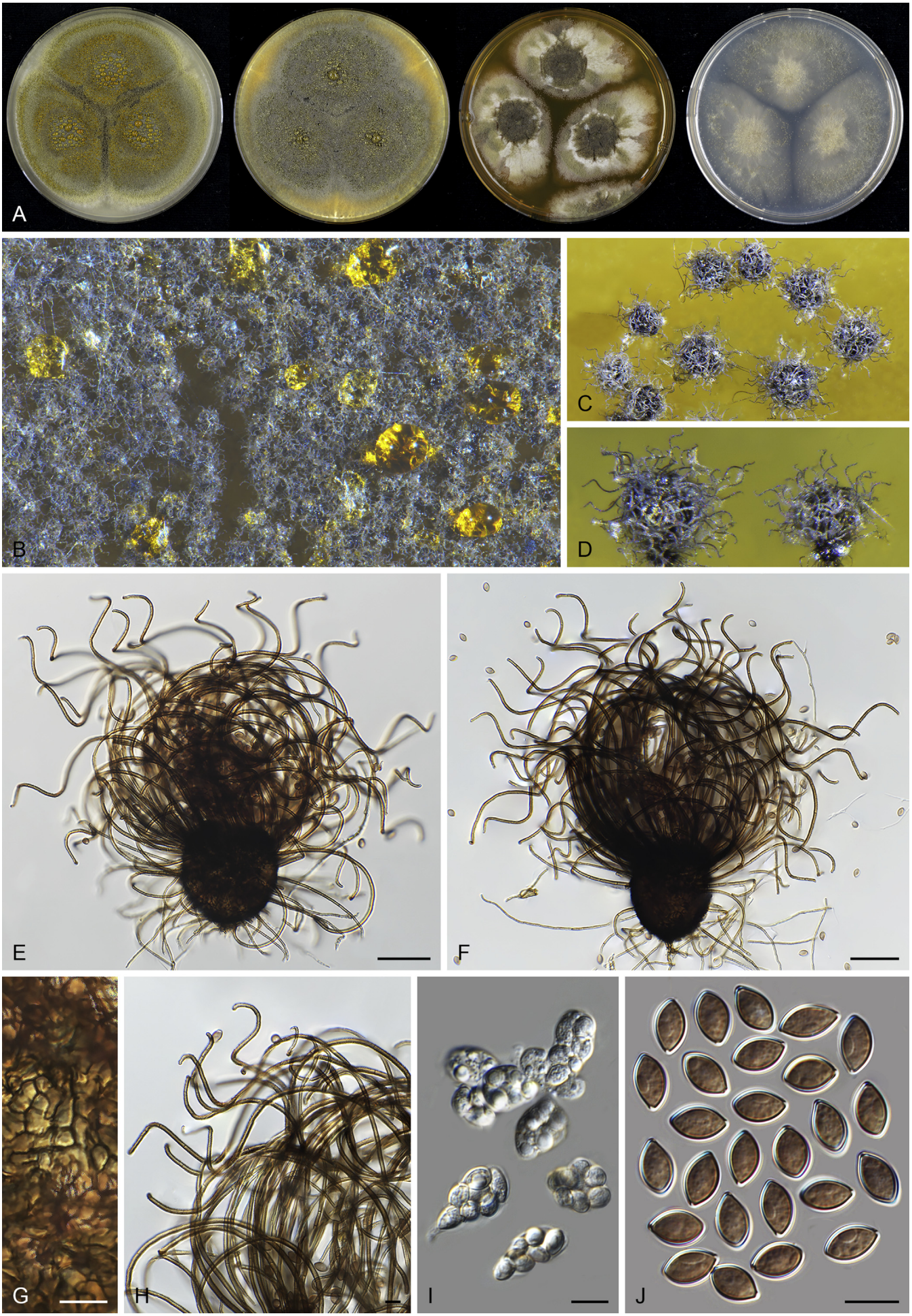


Fig. 30. *Floropilus chiversii* (CBS 558.80, ex-type culture). **A.** Colonies from left to right on OA, CMA, MEA and PCA after 3 wk incubation. **B.** Part of the colony on OA. **C.** Mature ascomata on OA, top view. **D.** Mature ascomata on OA, side view. **E–F.** Ascomata mounted in lactic acid. **G.** Structure of ascomatal wall in surface view. **H.** Terminal ascomatal hairs. **I.** Asci. **J.** Ascospores. Scale bars: E–F = 50 µm; G–J = 10 µm.

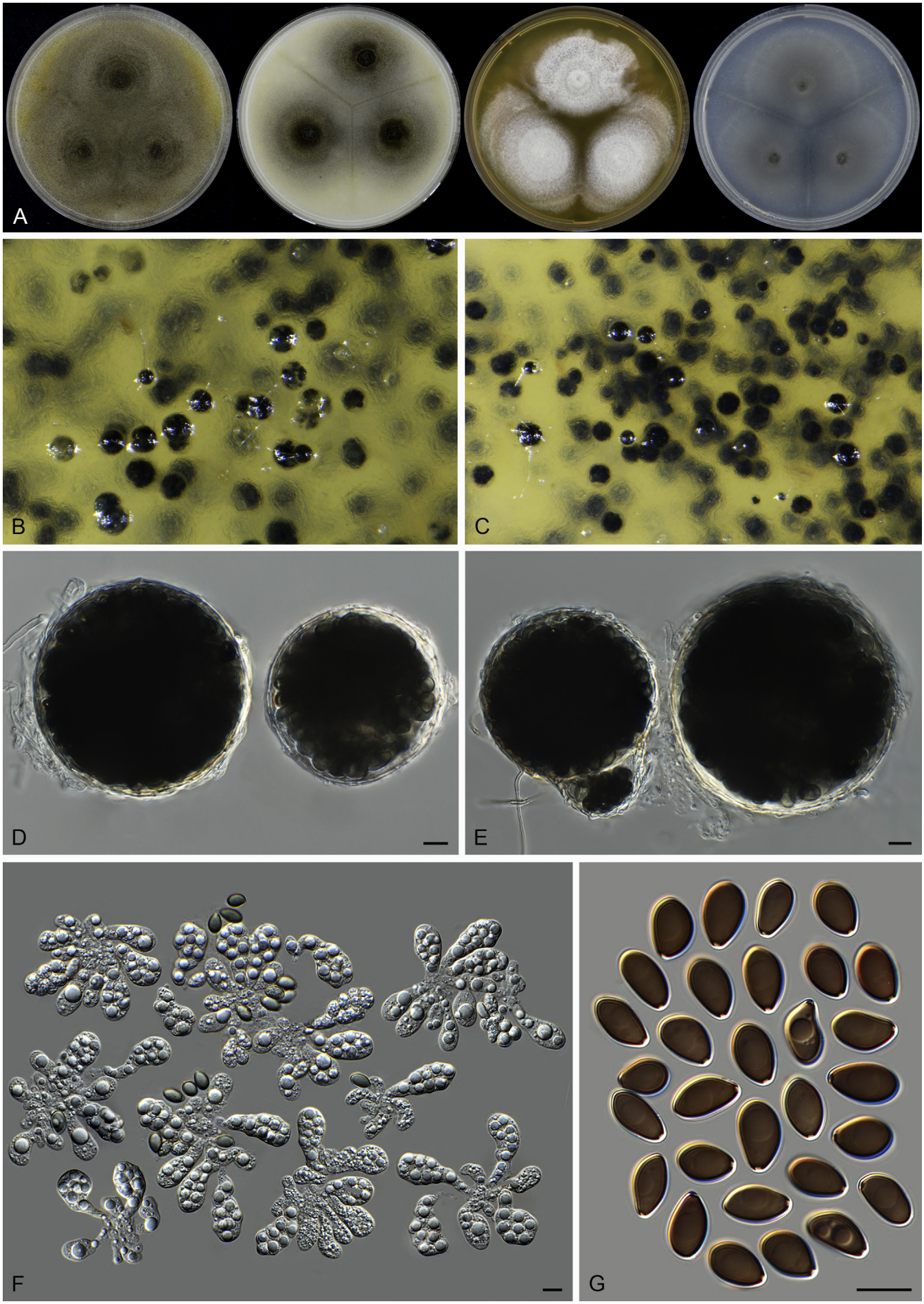


Fig. 31. *Hyalosphaerella fragilis* (CBS 456.73, ex-type culture). **A.** Colonies from left to right on OA, CMA, MEA and PCA after 3 wk incubation. **B–C.** Mature ascomata on OA, top view. **D–E.** Ascomata mounted in lactic acid. **F.** Asci. **G.** Ascospores. Scale bars: D–E = 20 µm; F–G = 10 µm.

obverse pale olivaceous grey, without coloured exudates, reverse pale olivaceous grey.

Typus: **India**, Tamil Nadu, isolated from rhizosphere of *Pennisetum typhoideum* in garden soil, 27 Oct. 1966, K. Natarajan (culture ex-type CBS 456.73).

Notes: *Hyalosphaera fragilis* is morphologically similar to *Pse. subhyaloderma* in ascomata, asci and ascospores, but can be distinguished by immersed ascomata and by lacking aerial mycelium on OA and CMA. Its ascomata with subhyaline and translucent ascomatal wall are also similar to those of *Boothiella tetraspora* in the *Sordariaceae* (Fig. 58). However, *Hya. fragilis* differs from *B. tetraspora* by smaller ascomata (50–115 µm *vs* 115–390 µm diam), 8-spored, clavate to pyriform asci and distinct ascospores (often inequilateral, 11–13 × 6.5–7.5 µm *vs* ellipsoidal to broad ovoid, 17.5–22 ×13–15 µm).

Microthielavia X. Wei Wang & Houbraken, ***gen. nov.*** MycoBank MB829866.

Etymology: Name refers to small and thielavia-like ascomata.

Micromorphology: *Ascomata* immersed or sub-immersed in the medium, solitary to loosely aggregated, small, non-ostiolate, spherical or subspherical, glabrous, usually less than 60 µm diam. *Ascomatal wall* brown, semi-translucent or non- translucent, composed of *textura angularis* in surface view. *Asci* fasciculate, clavate to pyriform, stalked, containing eight irregularly-arranged ascospores, evanescent. *Ascospores* 1-celled, olivaceous when mature, smooth, 1-celled, fusiform or ovoid, attenuated at both ends, with an apical germ pore. *Asexual morph* not observed.

Type species: *Microthielavia ovispora* (Pidopl., Kiril. & Zakharch.) X. Wei Wang & Houbraken.

Notes: *Microthielavia* is one of the three thielavia-like single lineages (*Carteria*, *Condenascus* and *Microthielavia*) in the *Chaetomiaceae*. All three are monotypic and known only from their type species. No close relatives of these three genera have been found. *Microthielavia* can be distinguished from the other genera by its quite small and semi-translucent or non-translucent ascomata which are immersed or sub-immersed in the medium. *Hyalosphaerella* also produces small and immersed ascomata, but can be distinguished by its subhyaline and translucent ascomatal wall. Moreover, the type species of *Hyalosphaerella* has larger ascomata than those of *Mic. ovispora* (50–115 µm *vs* 25–56 µm diam). *Carteria* is also similar to *Microthielavia* in having small and non-ostiolate ascomata, but the type species *Car. arctostaphyli* differs from *Mic. ovispora* by having superficial and slightly larger ascomata (25–85 µm *vs* 25–56 µm diam), subglobose, ellipsoidal or obovate asci without visiable stalks and ellipsoidal ascospores (Fig. 23).

Microthielavia ovispora (Pidopl., Kiril. & Zakharch.) X. Wei Wang & Houbraken, ***comb. nov.*** MycoBank MB829867. Fig. 32.
Basionym: *Thielavia ovispora* Pidopl., Kiril. & Zakharch., Mikrobiol. Zhurn. 35: 724. 1973.
Synonym: *Thielavia kirilenkoae* Beliakova, Mikol. Fitopatol. 8: 73. 1974.

Micromorphology: Ascomata immersed or sub-immersed in the medium, solitary to loosely aggregated, non-ostiolate, leaden black when mature in reflected light, spherical or subspherical, glabrous, 25–56 µm diam. *Ascomatal wall* brown, semi-translucent, composed of *textura angularis* in surface view. *Asci* clavate to pyriform, spore-bearing part 13.5–20.5 ×9–13.5 µm, with stalks 3–7 µm long, containing eight irregularly arranged ascospores, evanescent. *Ascospores* 1-celled, olivaceous when mature, smooth, ovoid to fusiform, attenuated at both ends, (7–)8–9(–9.5) × 5–6 µm, with an apical germ pore. *Asexual morph* not observed.

Culture characteristics: On OA with an entire edge, 18–24 mm diam in 7 d at 25 °C, with sparse aerial mycelium, obverse buff to mouse grey, with margin buff, reverse ochraceous or mouse grey. On CMA with an entire edge, 18–24 mm diam in 7 d at 25 °C, with aerial mycelium, obverse smoke grey, slightly pale luteous due to ascomata mixed with aerial mycelium, reverse isabelline. On MEA with an entire or slightly crenate edge, 13–19 mm diam in 7 d at 25 °C, without aerial mycelium, wrinkled to form radiating furrows, obverse vinaceous buff with fawn margin, reverse ochraceous to orange. On PCA transparent, with an entire edge, 13–19 mm diam in 7 d at 25 °C, obverse near the centre olivaceous grey due to ascomata, with sparse and pale luteous aerial mycelium, without coloured exudates, reverse pale mouse grey, or olivaceous grey near the centre.

Typus: **Ukraine**, Zhitomir region, isolated from the root of *Avena sativa*, 26 Jun. 1962, T.S. Kirilenko (culture ex-type CBS 165.75 = IMI 196525 = VKM F-1596).

Notes: Strain CBS 165.75 was deposited as the ex-type of *Th. kirilenkoae*. The type strains of both *Th. ovispora* and *Th. kirilenkoae* were isolated by T.S. Kirilenko in 1962 originating from the same location and source (Index of Fungi 4: 291. 1971–1980). There is a note written by L.A. Beliakova (the author of *Th. kirilenkoae*) linked to CBS 165.75 and saved in the CBS collection, which indicated that *Th. kirilenkoae* and *Th. ovispora* are based on the same specimen. *Microthielavia ovispora* has priority and *Th. kirilenkoae* is thus reduced to a synonym of *Th. ovispora*. For the morphological comparison, see notes of the genus.

Parathielavia X. Wei Wang & Houbraken, ***gen. nov.*** MycoBank MB829868.

Etymology: Name refers to the morphologically similarity but phylogenetically distance from *Thielavia sensu stricto*.

Micromorphology: *Ascomata* superficial to immersed in the medium, solitary to aggregated, non-ostiolate, spherical to oblate, pilose or glabrous. *Ascomatal wall* brown, semi-translucent, composed of *textura epidermoidea* in surface view. *Asci* clavate, obovoid or pyriform, with stalks, containing eight irregularly arranged ascospores, evanescent, sometimes persistent until ascospores mature. Ascospores 1-celled, olivaceous when mature, smooth, fusiform or ellipsoidal and attenuated at both ends, with a subapical germ pore. *Asexual morph* absent or producing conidia directly on hyphae.

Type species: *Parathielavia hyrcaniae* (Nicot) X. Wei Wang & Houbraken.

Notes: Several thielavia-like species were previously used as the representatives of the genus *Thielavia* (Wang *et al.* 2016a, Wang *et al.* 2019). Phylogenetic analyses in this study included a large sampling of *Chaetomiaceae* members. In the resulting trees (Figs 2, 3), those representative species were split into three

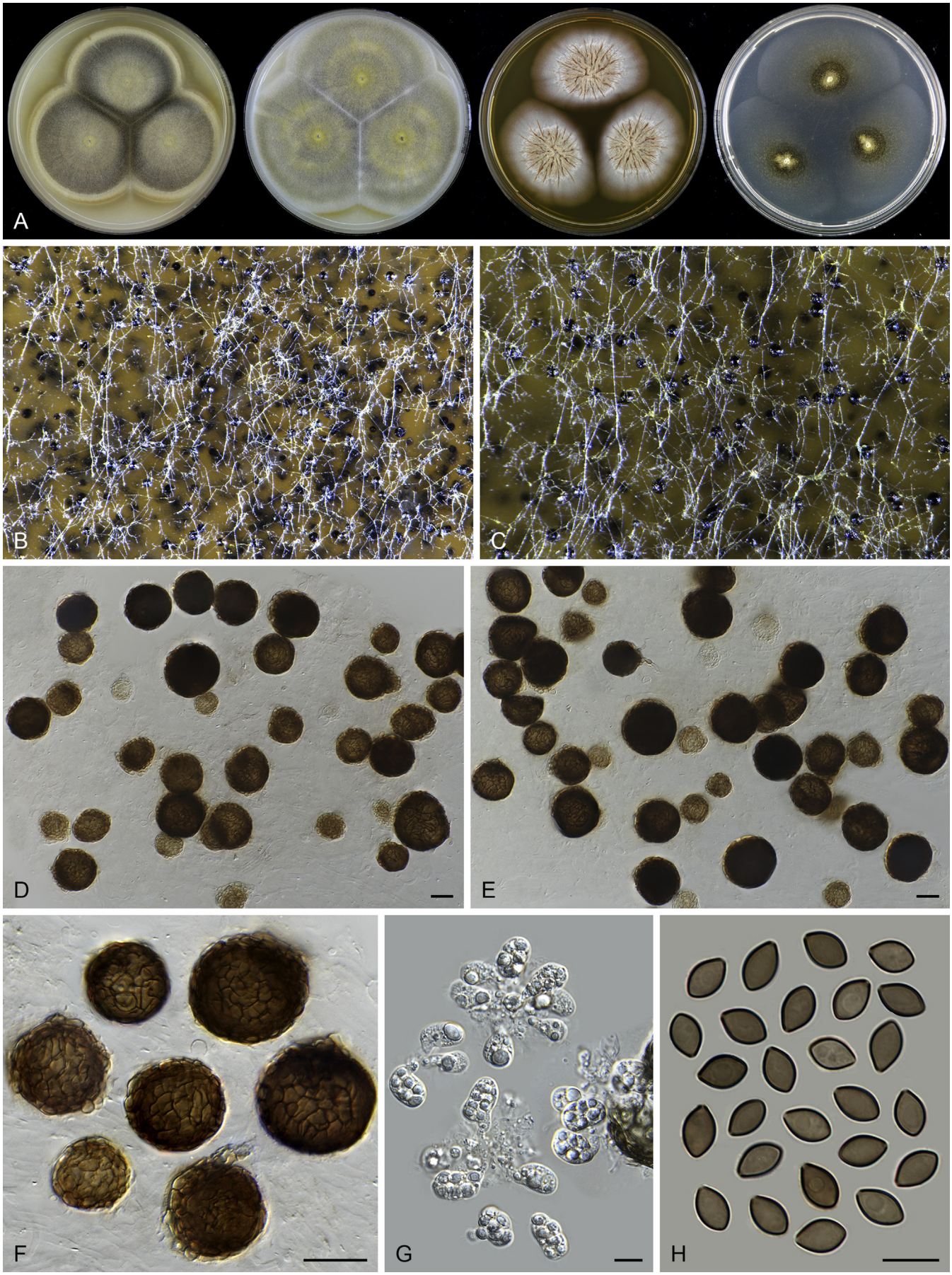


Fig. 32. *Microthielavia ovispora* (CBS 165.75, ex-type culture). **A.** Colonies from left to right on OA, CMA, MEA and PCA after 2 wk incubation. **B–C.** Part of the colony on OA, showing mature ascomata, top view. **D–E.** Ascomata mounted in lactic acid. **F.** Ascomata mounted in lactic acid, showing structure of ascomatal wall in surface view. **G.** Asci. **H.** Ascospores. Scale bars: D–F = 20 µm; G–H = 10 µm.

different lineages and mixed with several non-thielavia-like lineages in Clade 1 in the *Chaetomiaceae*. *Hyalosphaerella*, *Parathielavia* and *Pseudothielavia* were proposed to accommodate those three thielavia-like lineages. These three genera are different from *Thielavia sensu stricto* in having no association with *Berkeleyomyces* species. *Parathielavia* and *Pseudothielavia* also differ in possessing a semi-translucent (rather than translucent) ascomatal wall. *Parathielavia* is most closely related to *Hyalosphaerella*, but differs by its ascomata that are superficial and larger (60–300 µm *vs* 50–115 µm diam) with pigmented and semi-translucent ascomatal walls. It can also be distinguished from *Pseudothielavia* by the ascospores which have a subapical germ pore. *Pseudothielavia* species usually have ascospores with an apical germ pore with the exception of *Pse. arxii* which has ascospores with an oblique to lateral germ pore.

Parathielavia appendiculata (M.P. Srivast., Tandon, Bhargava & A.K. Ghosh) X. Wei Wang & Houbraken, ***comb. nov.*** MycoBank MB829869. Fig. 33.
Basionym: *Thielavia appendiculata* M.P. Srivast., Tandon, Bhargava & A.K. Ghosh, Mycopath. Mycol. Appl. 30: 205. 1966.

Micromorphology: Ascomata superficial, solitary to loosely aggregated, non-ostiolate, leaden black when mature in reflected light due to the dark ascomatal wall, spherical, pilose, (90–)110–235(–280) µm diam. *Ascomatal wall* brown, semi-translucent, composed of *textura epidermoidea* in surface view. *Ascomatal hairs* brown, short, finger-like or tapering towards tips, erect or flexuous, smooth, septate, 2–3.5 µm diam near base, usually less than 20 µm long. *Asci* clavate, spore-bearing part 24–36 × 12.5–17 µm, with stalks 5–14 µm long, containing eight irregularly arranged ascospores, evanescent, sometimes persistent until ascospores mature. *Ascospores* 1-celled, olivaceous when mature, smooth, ellipsoidal to fusiform, attenuated at both ends, (11–)12–14.5(–17) × (6–)6.5–8.5(–9.5) µm, with a subapical germ pore. *Asexual morph* not observed.

Culture characteristics: On OA with an entire edge, 20–26 mm diam in 7 d at 25 °C, with sparse aerial mycelium, obverse usually pale luteous to luteous due to coloured exudates diffusing into the medium, reverse pale luteous to luteous. On CMA similar to those on OA. On MEA with an entire edge, 20–26 mm diam in 7 d at 25 °C, texture floccose, obverse white or pale luteous, reverse orange or sienna. On PCA with an entire edge, 18–24 mm diam in 7 d at 25 °C, without aerial mycelium, obverse uncoloured, without coloured exudates, reverse uncoloured.

Typus: **India**, Jodhpur, isolated from leaf of *Punica granatum*, Nov. 1963, collector unknown (culture ex-type CBS 723.68 = IMI 104944).

Additional material examined: **UK**, Wales, near Aberystwyth, isolated from dung of rabbit, date unknown, H.K. Seth (CBS 731.68). **Unknown**, substrate unknown, date and collector unknown, J.N. Kapoor (CBS 417.73).

Note: This species can be distinguished from the other known thielavia-like species by short, usually finger-like ascomatal hairs and ellipsoidal to fusiform ascospores with a subapical germ pore. Among the three known species in the genus, *Par. hyrcaniae* can be distinguished from *Par. appendiculata* by longer (up to almost 60 µm *vs* less than 20 µm long) and geniculate, flexuous or undulate ascomatal hairs and slightly smaller fusiform ascospores (11–13 × 6–7 µm *vs* 12–14.5 × 6.5–8.5 µm), and *Par. kuwaitensis* differs from *Par. appendiculata* by glabrous ascomata, smaller ascospores (9.5–10.5 × 6–7 µm) and the presence of conidia.

Parathielavia hyrcaniae (Nicot) X. Wei Wang & Houbraken, ***comb. nov.*** MycoBank MB829870. Fig. 34.
Basionym: *Thielavia hyrcaniae* Nicot, Compt. Rend. Hebd. Séances Acad. Sci., Paris 253: 304. 1961.

Micromorphology: Ascomata superficial to immersed in the medium, solitary to aggregated, non-ostiolate, fuscous black when mature in reflected light due to dark ascospores inside, spherical to oblate, pilose, 60–130 µm diam. *Ascomatal wall* brown, semi-translucent, composed of *textura epidermoidea* in surface view. *Ascomatal hairs* olivaceous at the base, tapering and fading towards tips, geniculate, flexuous or undulate, with a swollen basal cell, smooth, septate, 3–6 µm diam near base, usually less than 60 µm long. *Asci* clavate, spore-bearing part 23–28 × 10.5–14.5 µm, with stalks 4–9.5 µm long, containing eight irregularly arranged ascospores, evanescent. *Ascospores* 1-celled, olivaceous or olivaceous brown when mature, smooth, fusiform, sometimes inequilateral, (10–)11–13(–15) × (5.5–)6–7 µm, with a subapical or oblique germ pore. *Asexual morph* not observed.

Culture characteristics: On OA with an entire edge, 22–28 mm diam in 7 d at 25 °C, with sparse aerial mycelium, obverse mouse grey due to ascomata, reverse hazel. On CMA similar to those on OA, 27–33 mm diam in 7 d at 25 °C. On MEA with an entire or slightly crenate edge, 21–27 mm diam in 7 d at 25 °C, texture floccose, obverse mouse grey or buff, reverse apricot to scarlet due to coloured exudates diffusing into the medium. On PCA with an entire edge, 24–30 mm diam in 7 d at 25 °C, without aerial mycelium, obverse pale olivaceous grey, without coloured exudates, reverse fawn.

Typus: **Iran**, southern shore of Caspian Lake, near Nochahr, isolated from sand dune soil, date unknown, J. Nicot (culture ex-type CBS 353.62).

Notes: *Parathielavia hyrcaniae* produces pilose ascomata similar to *Par. appendiculata*. They differ in ascomatal hairs and ascospores. For their morphological comparison, see notes of *Par. appendiculata*.

Parathielavia kuwaitensis (Moustafa) X. Wei Wang & Houbraken, ***comb. nov.*** MycoBank MB829871. Fig. 35.
Basionym: *Thielavia kuwaitensis* Moustafa, Trans. Brit. Mycol. Soc. 66: 336. 1976.

Micromorphology: Ascomata superficial to immersed, or covered by mycelium, solitary to loosely aggregated, non-ostiolate, olivaceous grey to leaden black when mature in reflected light due to the dark ascomatal wall, spherical, glabrous, often covered by more or less mycelium, 130–300 µm diam. *Ascomatal wall* brown, semi-translucent, composed of *textura epidermoidea* in surface view. *Asci* obovoid, pyriform or clavate, spore-bearing part 21–28.5 × 12–17.5 µm, with stalks 3–6.5 µm long, containing eight irregularly arranged ascospores, evanescent, occasionally persistent until ascospores mature. *Ascospores* 1-celled, fulvous to olivaceous brown when mature, smooth, ellipsoidal, attenuated at both ends, (9–)9.5–10.5(–12) × 6–7(–8) µm, with a subapical germ pore. *Conidiogenous cells* reduced to a hyphal cell. *Conidia* 1-celled, hyaline, ellipsoidal, ovoid or subglobose, intercalary, or terminal on hyphae, solitary or two in chains, (7–)8–12(–14) × (6–)7–8.5(–9) µm.

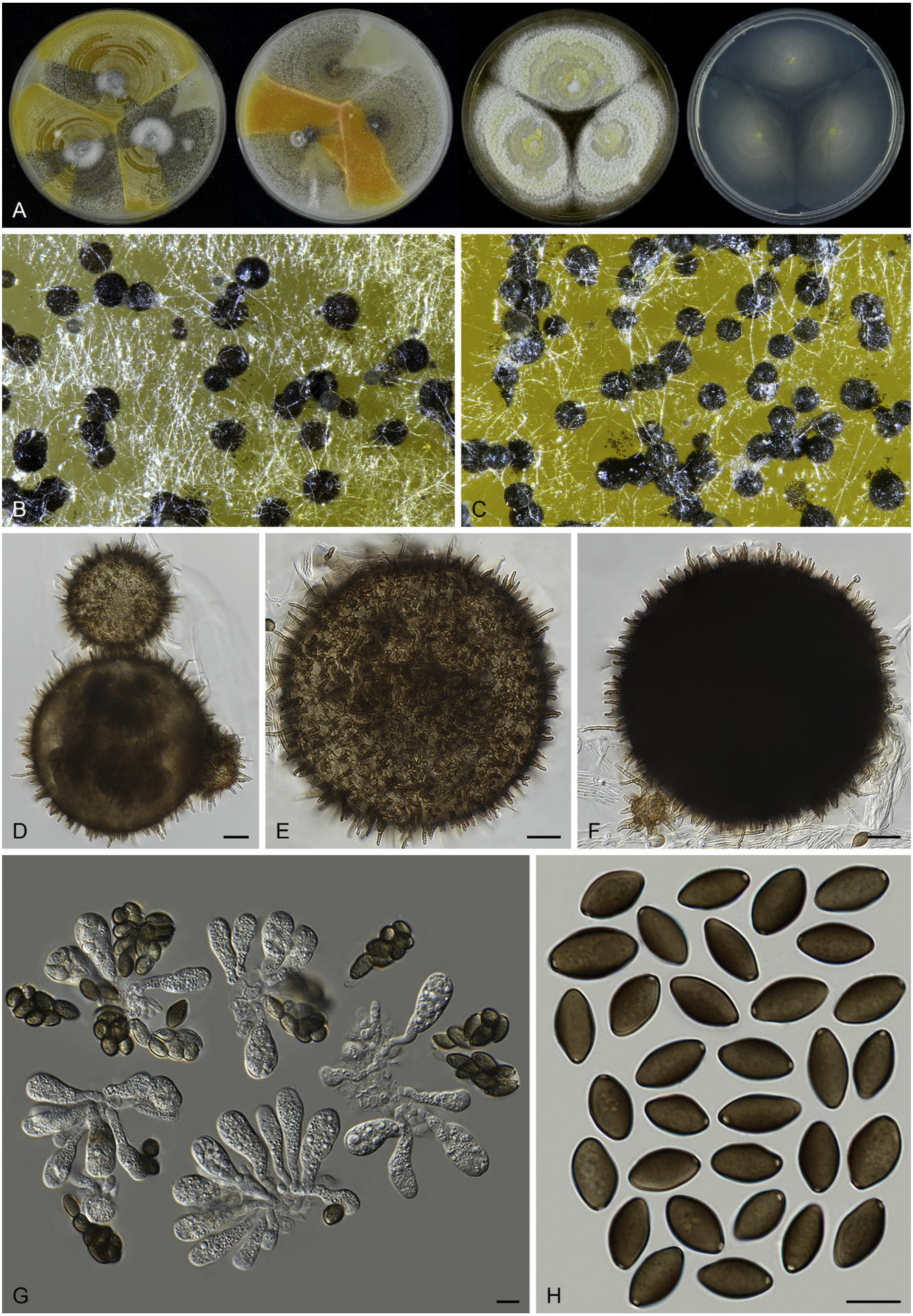
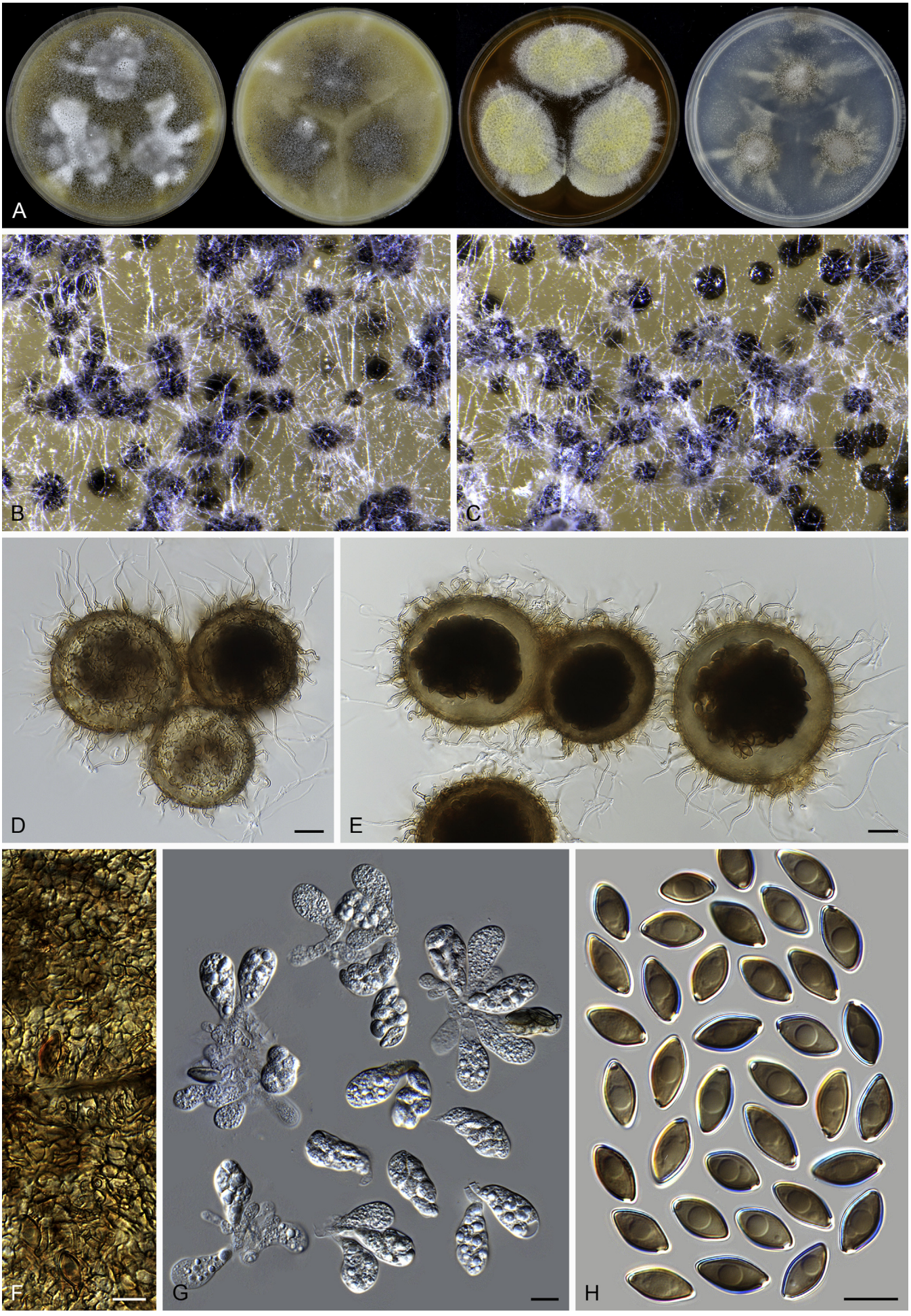


Fig. 33. *Parathielavia appendiculata* (CBS 723.68, ex-type culture). **A.** Colonies from left to right on OA, CMA, MEA and PCA after 3 wk incubation. **B–C.** Mature ascomata on OA, top view. **D–F.** Ascomata mounted in lactic acid. **G.** Asci. **H.** Ascospores. Scale bars: D–F = 20 µm; G–H = 10 µm.


A
B
C
D
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G
H

Culture characteristics: On OA with an entire edge, 21–27 mm diam in 7 d at 25 °C, without or with sparse aerial mycelium, obverse irregularly fawn to olivaceous due to coloured exudates diffusing into the medium, reverse partly olivaceous. On CMA with an entire edge, 20–26 mm diam in 7 d at 25 °C, without or with sparse aerial mycelium, obverse occasionally partly honey to cinnamon due to coloured exudates diffusing into the medium, reverse uncoloured or honey. On MEA with an entire edge, 18–24 mm diam in 7 d at 25 °C, texture floccose, obverse white due to mycelium, reverse ochraceous to fulvous. On PCA with an entire edge, 22–28 mm diam in 7 d at 25 °C, without aerial mycelium, obverse uncoloured, without coloured exudates, reverse uncoloured.

Typus: **Kuwait**, isolated from desert soil, unknown date, A.F. Moustafa (culture ex-type CBS 945.72).

Additional material examined: **China**, Xinjiang, Hetian, Mingfeng county, isolated from desert soil, Aug. 2003, X.W. Wang (CBS 119771 = AS 3.9412).

Notes: *Parathielavia kuwaitensis* differs from the other two species of *Parathielavia* in forming conidia and glabrous ascomata. The ascospores of this species are similar to those of *Canariomyces arenarius* (syn.: *Th. arenaria*). However, *Can. arenarius* can be distinguished from *Par. kuwaitensis* by the production of dark coloured mycelium and by its thermotolerant nature (von Arx 1975, von Arx *et al.* 1988, van den Brink *et al.* 2015). *Parathielavia kuwaitensis* was classified as a mesophilic species (van den Brink *et al.* 2015).

Pseudothielavia X. Wei Wang & Houbraken, ***gen. nov.*** MycoBank MB829872.

Etymology: Name refers to a genus similar to, but different from *Thielavia sensu stricto*.

Micromorphology: *Aerial mycelium* white, usually covering ascomata on OA and CMA. *Ascomata* superficial, occasionally immersed in medium, non-ostiolate, or ostiolate when mature in some species, solitary to aggregated, globose or subglobose, glabrous, or with sparse hypha-like hairs on the ostiolate ascomata. *Ascomatal wall* brown, semi-translucent or translucent, composed of *textura epidermoidea* in surface view. *Asci* clavate to pyriform, with stalks containing eight irregularly arranged ascospores, evanescent. *Ascospores* 1-celled, olivaceous brown when mature, smooth, fusiform, with an apical, oblique or lateral germ pore. *Asexual morph* not observed.

Type species: *Pseudothielavia terricola* (J.C. Gilman & E.V. Abbott) X. Wei Wang & Houbraken.

Notes: Species in this genus present similar culture characteristics. Most of the species produce non-ostiolate ascomata only with the exception of *Pse. hamadae*. The ascomata of *Pse. hamadae* are non-ostiolate at the beginning, but develop an inconspicuous ostiole in time. This genus could be an interesting candidate for studying the genetic relationships between the species with ostiolate and non-ostiolate ascomata. For morphological comparison with the closely related genera, see notes of *Parathielavia*.

Pseudothielavia arxii (Stchigel & Guarro) X. Wei Wang & Houbraken, ***comb. nov.*** MycoBank MB829873. Fig. 36.
Basionym: *Thielavia arxii* Stchigel & Guarro, Mycol. Res. 106: 979. 2002.

Micromorphology: Ascomata superficial, solitary to aggregated, non-ostiolate, leaden black when mature in reflected light due to the dark ascomatal wall and asospores inside, spherical, glabrous, 60–250 µm diam. *Ascomatal wall* brown, semi-translucent, composed of *textura epidermoidea* in surface view. *Asci* clavate to pyriform, spore-bearing part 24–31 × 15–19.5 µm, with stalks 8–18.5 µm long, containing eight irregularly arranged ascospores, evanescent. *Ascospores* 1-celled, olivaceous brown when mature, smooth, fusiform, (11–)12–14.5(–17) ×(6–)6.5–8.5(–9.5) µm, with an oblique to lateral germ pore. *Asexual morph* not observed.

Culture characteristics: On OA with an entire edge, 41–47 mm diam in 7 d at 25 °C, with sparse aerial mycelium, obverse pale olivaceous grey due to masses of ascomata mixed with mycelium, without coloured exudates, reverse buff. On CMA similar to those on OA, 38–44 mm diam in 7 d at 25 °C. On MEA with an entire or slightly crenate edge, 33–39 mm diam in 7 d at 25 °C, texture floccose, obverse white or pale mouse grey, reverse ochraceous. On PCA with an entire edge, 34–40 mm diam in 7 d at 25 °C, without aerial mycelium, obverse smoke grey, without coloured exudates, reverse uncoloured.

Typus: **Chile**, Pascua Island, Hanga-Roa, isolated from soil, date unknown, L. Zaror (culture ex-type CBS 603.97 = FMR 5875).

Additional material examined: **India**, Ajmer, isolated from soil, 2 Nov. 1995, A.M. Stchigel (CBS 102199 = FMR 5765).

Notes: Phylogenetic analyses (Figs 2, 3) failed to differentiate *Pse. arxii* from *Pse. terricola*. *Pseudothielavia arxii* is similar to *Pse. terricola* in culture characteristics, ascomata and asci, but differs in producing ascospores with an oblique to lateral germ pore (Fig. 36H), while those of *Pse. terricola* have an apical germ pore (Fig. 39H). Because of their distinctly different ascospores, we practically accept them as two separate species. Further study is required to deeply re-evaluate the relationship of the two morphological species.

Pseudothielavia hamadae (Udagawa) X. Wei Wang & Houbraken, ***comb. nov.*** MycoBank MB829874. Fig. 37.
Basionym: *Achaetomium hamadae* Udagawa, Trans. Mycol. Soc. Japan 23: 287. 1982.
Synonym: *Chaetomium hamadae* (Udagawa) Arx, Proc. Indian Acad. Sci., Pl. Sci. 94: 343. 1985.

Micromorphology: Ascomata superficial, non-ostiolate when young, forming an inconspicuous ostiole when mature, leaden black in reflected light due to the dark ascomatal wall and masses of ascospores, spherical, or broad ovoid, with a short papillate beak, 160–245 µm high, 140–205 µm diam. *Ascomatal wall* brown, semi-translucent, composed of *textura intricata* in surface view. *Ascomatal hairs* sparse, hypha-like, hyaline or subhyaline, erect or flexuous, smooth, septate, 1.5–3.5 µm diam near base. *Asci* clavate, spore-bearing part 28–41.5 ×

Fig. 34. *Parathielavia hyrcaniae* (CBS 945.72, ex-type culture). **A.** Colonies from left to right on OA, CMA, MEA and PCA after 3 wk incubation. **B–C.** Part of the colony on OA, showing mature ascomata, top view. **D–E.** Ascomata mounted in lactic acid. **F.** Structure of ascomatal wall in surface view. **G.** Asci. **H.** Ascospores. Scale bars: D–E = 20 µm; F–H = 10 µm.

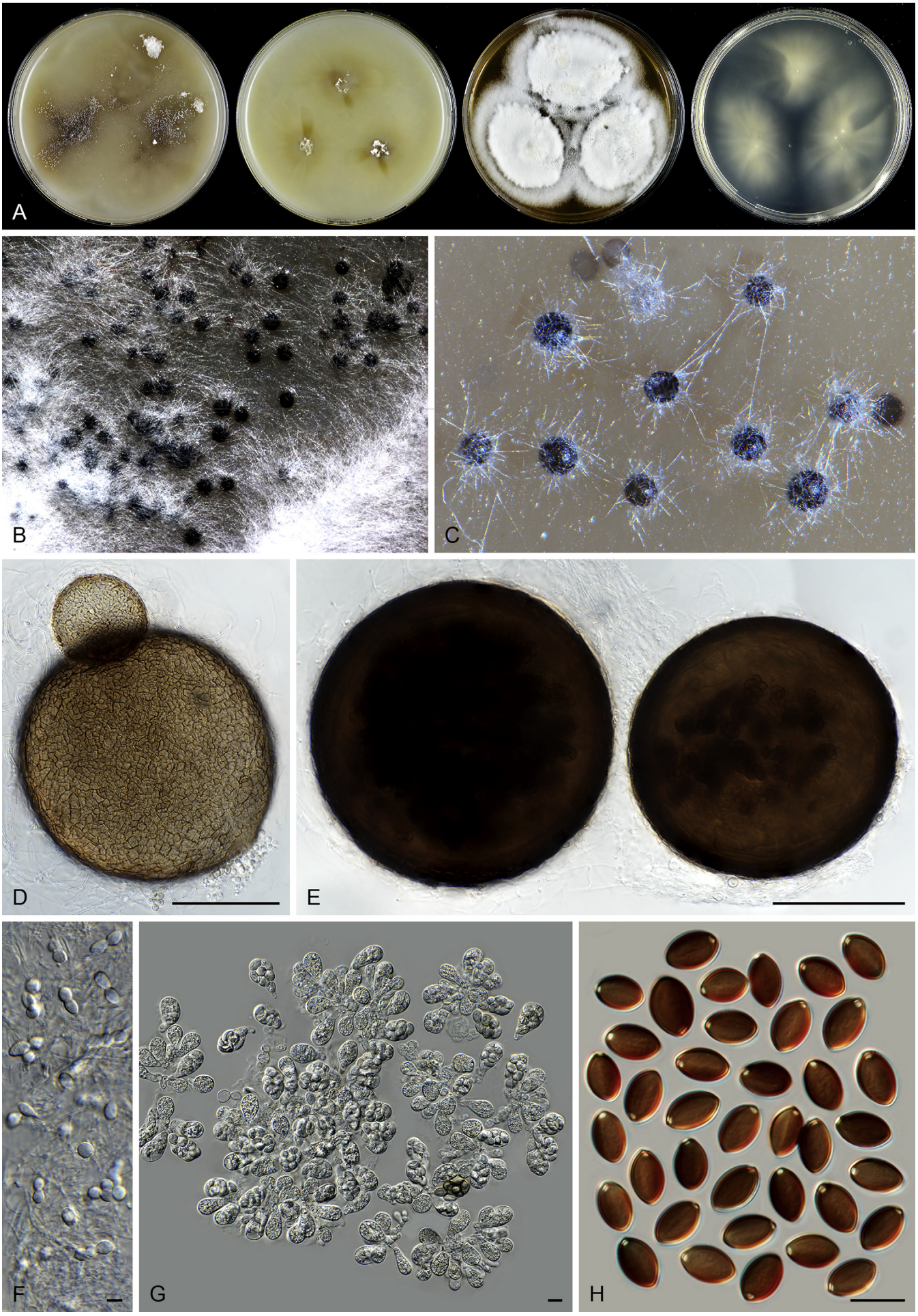


Fig. 35. *Parathielavia kuwaitensis* (CBS 353.62, ex-type culture). **A.** Colonies from left to right on OA, CMA, MEA and PCA after 3 wk incubation. **B–C.** Part of the colony on OA, showing mature ascomata, top view. **D–E.** Ascomata mounted in lactic acid, showing structure of ascomatal wall in surface view in D. **F.** Conidia arising from hyphae. **G.** Asci. **H.** Ascospores. Scale bars: D–E = 100 µm; F–H = 10 µm.

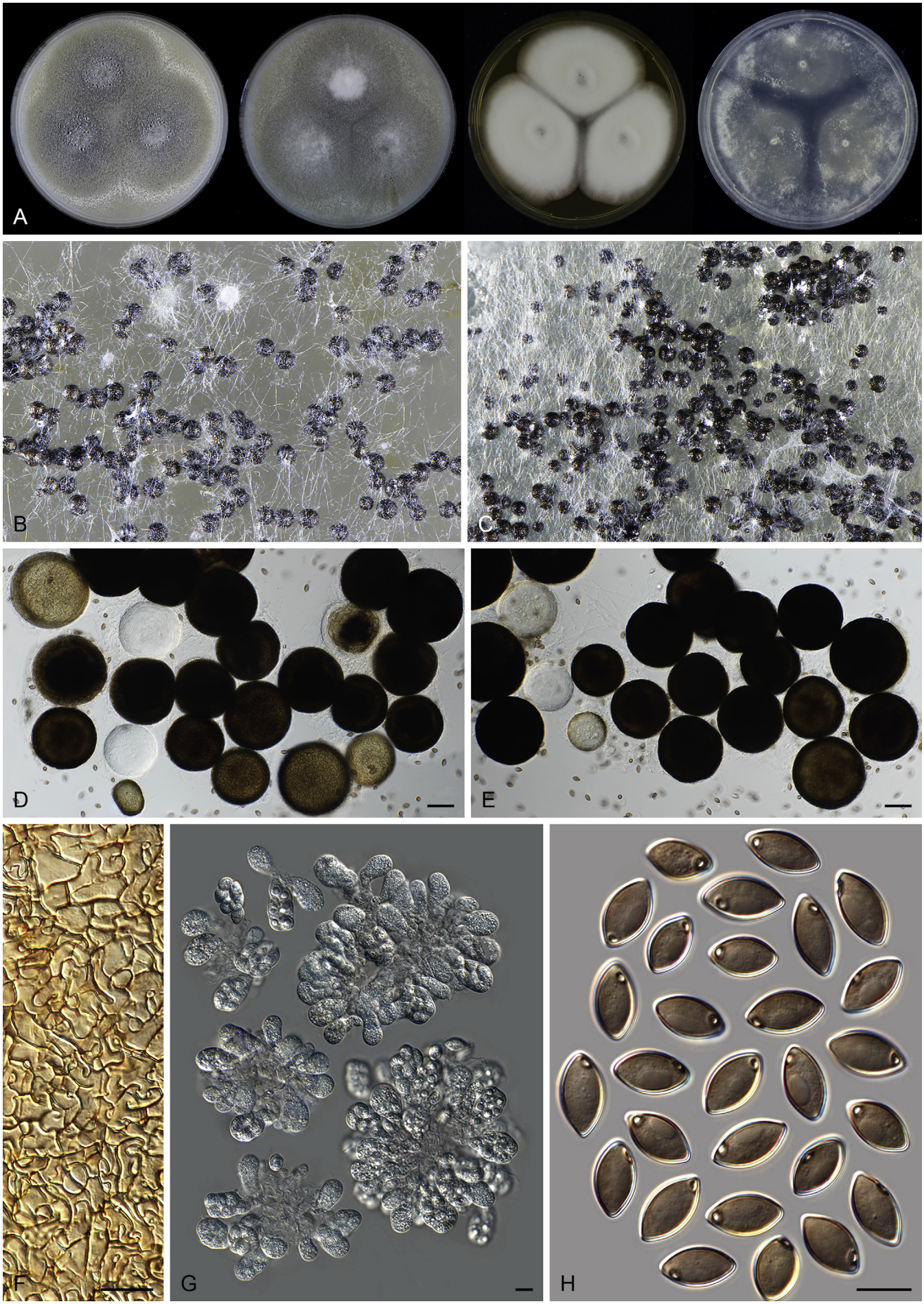


Fig. 36. *Pseudothielavia arxii* (CBS 603.97, ex-type culture). **A.** Colonies from left to right on OA, CMA, MEA and PCA after 2 wk incubation. **B–C.** Mature ascomata on OA, top view. **D–E.** Ascomata mounted in lactic acid. **F.** Structure of ascomatal wall in surface view. **G.** Asci. **H.** Ascospores. Scale bars: D–E = 50 µm; F–H = 10 µm.

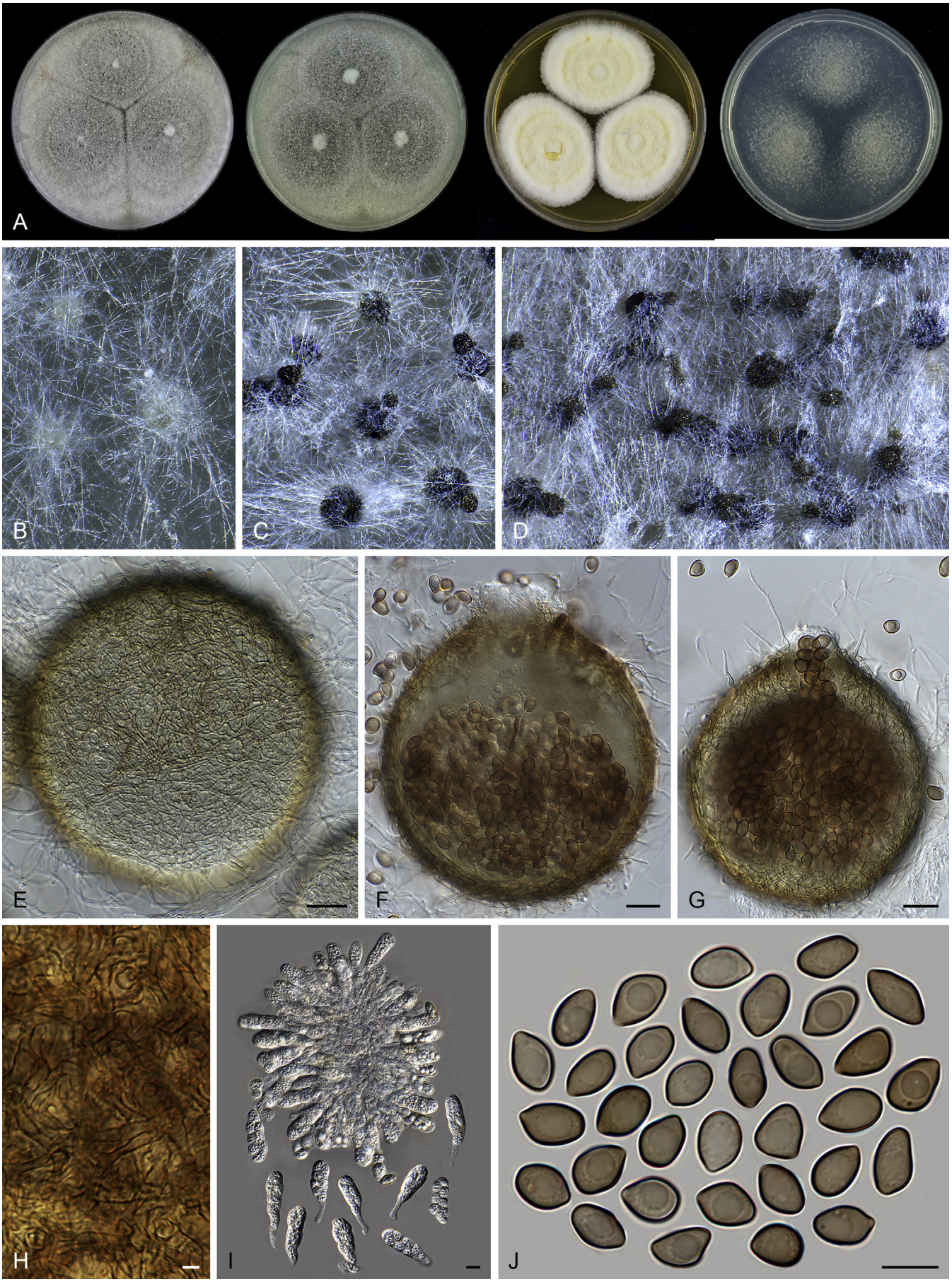


Fig. 37. *Pseudothielavia hamadae* (CBS 499.83, ex-type culture). **A.** Colonies from left to right on OA, CMA, MEA and PCA after 18 d incubation. **B.** Young ascomata on OA. **C–D.** Mature ascomata on OA. **E–G.** Ascomata mounted in lactic acid. **H.** Structure of ascomatal wall in surface view. **I.** Asci. **J.** Ascospores. Scale bars: E–G = 20 µm; H–J = 10 µm.

10–14.5 µm, with stalks 8–19 µm long, containing eight irregularly arranged or biseriate ascospores, evanescent. *Ascospores* 1-celled, olivaceous when mature, smooth, ovoid to irregularly, often inaequilateral, (8–)9.5–11.5(–12) × (6–)6.5–8(–8.5) µm, with an indistinct apical germ at the most attenuated end. *Asexual morph* not observed.

Culture characteristics: On OA with an entire edge, 30–36 mm diam in 7 d at 25 °C, with white aerial mycelium, texture floccose, obverse white or pale olivaceous grey due to mycelium mixed with ascomata, without coloured exudates, reverse buff to honey. On CMA similar to those on OA. On MEA with an entire edge, 26–31 mm diam in 7 d at 25 °C, texture thick floccose, obverse buff, often with two pale luteous concentric rings, reverse saffron. On PCA with an entire edge, 28–34 mm diam in 7 d at 25 °C, without aerial mycelium, obverse smoke grey due to ascomata, without coloured exudates, reverse uncoloured.

Typus: **Japan**, Tosayamada-cho, Kami-gun, isolated from soil, date unknown, S. Udagawa (culture ex-type CBS 499.83 = IMI 288714ii = NHL 2910).

Notes: *Pseudothielavia hamadae* presents an intermediate form between species with ostiolate and non-ostiolate ascomata. This species is mainly characterized by subglobose to broad ovoid ascomata covered by sparse, hyaline hypha-like hairs, with an inconspicuous ostiole and by ovoid to irregularly ascospores with an indistinct apical germ pore.

Pseudothielavia subhyaloderma X. Wei Wang & Houbraken, ***sp. nov.*** MycoBank MB829875. Fig. 38.

Etymology: Name refers to ascomata with translucent walls.

Micromorphology: Ascomata superficial, often covered by white aerial mycelium, occasionally immersed in the medium, solitary to aggregated, non-ostiolate, leaden black when mature in reflected light due to the dark ascomatal wall, spherical, glabrous, 60–185 µm diam. *Ascomatal wall* hyaline, subhyaline to pale mouse grey, translucent, composed of *textura epidermoidea* in surface view. *Asci* clavate to pyriform, spore-bearing part 21–31 × 13–18 µm, with stalks 6–16.5 µm long, containing eight irregularly arranged or biseriate ascospores, evanescent. *Ascospores* 1-celled, olivaceous brown when mature, smooth, ovoid or irregular, often inequilateral, (8.4–)10.5–13(–14) × (6.5–)7–8 µm, with an apical or slightly subapical germ pore at the most attenuated end. *Asexual morph* not observed.

Culture characteristics: On OA with an entire edge, 42–48 mm diam in 7 d at 25 °C, with white aerial mycelium, texture floccose, obverse white or pale olivaceous grey due to masses of ascomata mixed with mycelium, without coloured exudates, reverse uncoloured. On CMA similar to those on OA, 51–57 mm diam in 7 d at 25 °C, with thin aerial mycelium. On MEA with an entire edge, 36–42 mm diam in 7 d at 25 °C, with thick white aerial mycelium, texture floccose, obverse white, reverse cinnamon. On PCA with an entire edge, 34–40 mm diam in 7 d at 25 °C, with white aerial mycelium, obverse white, without coloured exudates, reverse uncoloured.

Typus: **Papua New Guinea**, near Madang, isolated from forest soil, date unknown, R.S. Khan (**holotype** CBS H-6866, culture ex-type CBS 473.86 = TRTC 36863).

Notes: The ex-type culture of *Pse. subhyaloderma* was deposited as *Pse. hamadae* in the CBS culture collection, probably because both species produce irregular ascospores; however, it can be easily distinguished from the latter by the formation of non-ostiolate ascomata. *Pseudothielavia subhyaloderma* and *Hya. fragilis* are not closely related to each other, but morphologically similar in having ascomata with subhyaline and translucent ascomatal wall and ovoid or irregular ascospores. Cultures of *Pse. subhyaloderma* produce aerial mycelium on OA and CMA, and the ascomata of this species are superficial and larger (60–185 µm diam). In contrast, cultures of *Hya. fragilis* lack aerial mycelium on OA and CMA, and their ascomata are immersed in the medium and smaller (50–115 µm diam).

Pseudothielavia terricola (J.C. Gilman & E.V. Abbott) X. Wei Wang & Houbraken, ***comb. nov.*** MycoBank MB829876. Fig. 39.
Basionym: *Coniothyrium terricola* J.C. Gilman & E.V. Abbott, Iowa State Coll. J. Sci. 1: 267. 1927.
Synonym: *Thielavia terricola* (J.C. Gilman & E.V. Abbott) C.W. Emmons, Bull. Torrey Bot. Club 57: 124. 1930.

Micromorphology: Ascomata superficial, solitary to aggregated, non-ostiolate, leaden black when mature in reflected light due to the dark ascomatal wall, spherical, glabrous, 70–200 µm diam. *Ascomatal wall* brown, semi-translucent, composed of *textura epidermoidea* in surface view. *Asci* clavate to pyriform, spore-bearing part 18.5–28.5 × 15.5–22 µm, with stalks 4–9 µm long, containing eight irregularly arranged ascospores, evanescent. *Ascospores* 1-celled, olivaceous brown when mature, smooth, fusiform, (11–)12–14(–14.5) × (6–)7–8.5 µm, with an apical germ pore. *Asexual morph* not observed.

Culture characteristics: On OA with an entire edge, 42–48 mm diam in 7 d at 25 °C, with white aerial mycelium, texture floccose, obverse white or pale olivaceous grey due to masses of ascomata mixed with mycelium, without coloured exudates, reverse buff. On CMA similar to those on OA, 40–46 mm diam in 7 d at 25 °C. On MEA with an entire edge, 45–51 mm diam in 7 d at 25 °C, with thick white aerial mycelium, texture floccose, obverse white, reverse ochraceous to fulvous. On PCA with an entire edge, 38–44 mm diam in 7 d at 25 °C, without aerial mycelium, obverse uncoloured, without coloured exudates, reverse uncoloured.

Typus: **Lectotype of *Coniothyrium terricola* designated here**: Fig. 17 based on the original culture of *Coniothyrium terricola*, isolated from soil in Iowa, USA, in Gilman & Abbott, Iowa State Coll. J. Sci. 1(3): 267, 1927, MBT385836. **USA**, North Carolina, isolated from barren soil, 5 Feb. 1986, J. Shaw (CBS H-24049, **epitype designated here**, MBT387689, culture ex-epitype CBS 165.88 = TRTC 50997).

Additional material examined: **USA**, Gaudsia, isolated from kernel of *Arachis hypogaea*, date unknown, G.A. Gilman (CBS 487.74 = IMI 124876).

Notes: *Pseudothielavia terricola* is widely distributed in the world. The holotype of *Coniothyrium terricola*, the basionym of *Pse. terricola*, was isolated from soil in Iowa, USA. This holotype is neither preserved in FH (Harvard University Herbaria) nor in the ATCC culture collection and seems to be lost. In order to fix the application of the species name, an illustration in the protologue is designated here as the lectotype of this species. CBS 165.88 is selected as the ex-type culture. It is from the same substrate and country, and its morphology agrees well with the protologue (Gilman & Abbott 1927, von Arx 1975). This species is related to *Pse. arxii*. For morphological comparison, see notes of *Pse. arxii*.

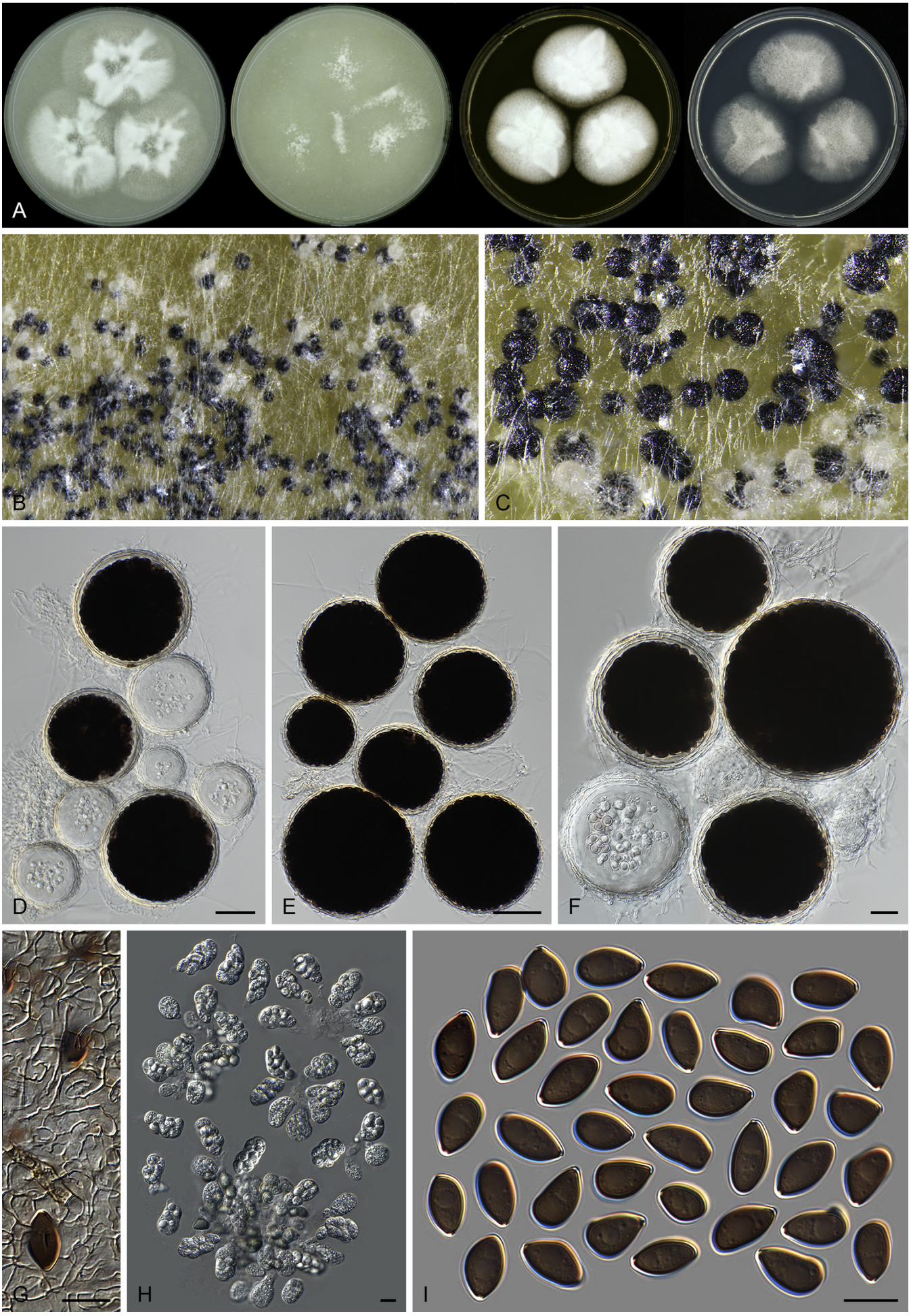


Fig. 38. *Pseudothielavia subhyaloderma* (CBS 473.86, ex-type culture). **A.** Colonies from left to right on OA, CMA, MEA and PCA after 7 d incubation. **B–C.** Mature ascomata on OA, top view. **D–F.** Ascomata mounted in lactic acid. **G.** Structure of ascomatal wall in surface view. **H.** Asci. **I.** Ascospores. Scale bars: D–E = 50 µm; F = 20 µm; G–I = 10 µm.

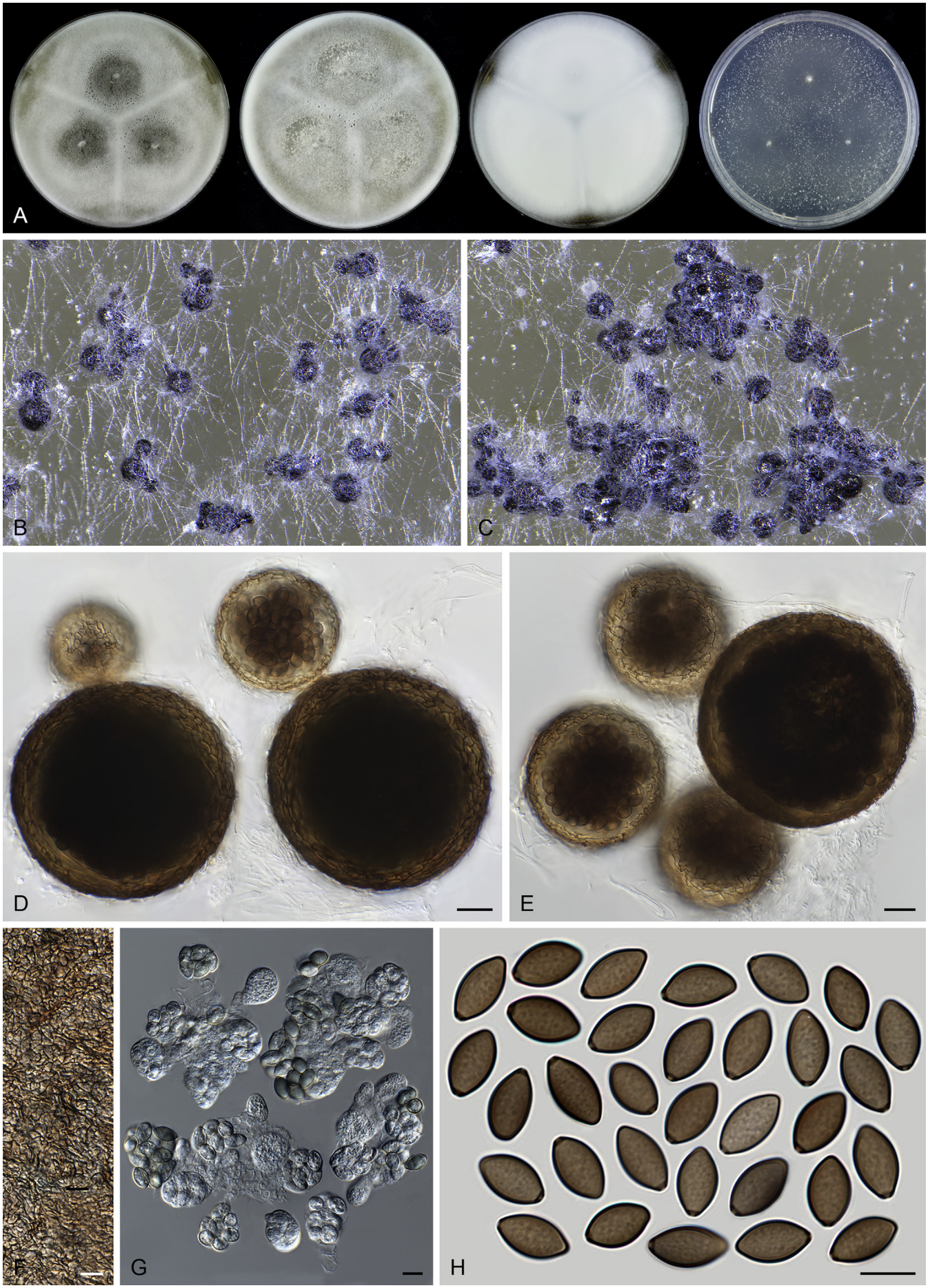
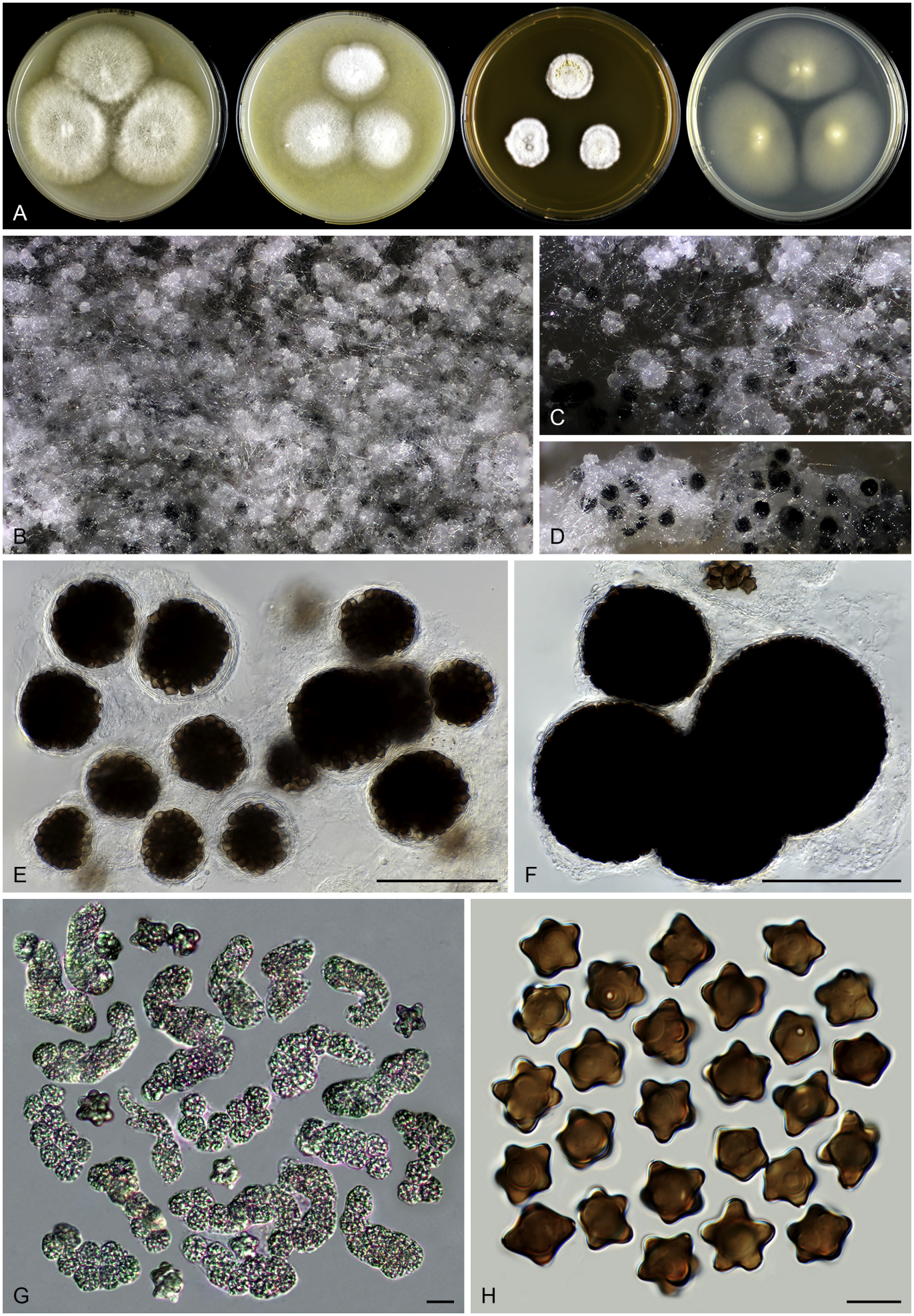


Fig. 39. *Pseudothielavia terricola* (CBS 165.88, ex-epitype culture). **A.** Colonies from left to right on OA, CMA, MEA and PCA after 3 wk incubation. **B–C.** Mature ascomata on OA, top view. **D–E.** Ascomata mounted in lactic acid. **F.** Structure of ascomatal wall in surface view. **G.** Asci. **H.** Ascospores. Scale bars: D–E = 20 µm; F–H = 10 µm.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Stellatospora Tad. Ito & Nakagiri, Mycoscience 35: 413. 1994.

Micromorphology: *Ascomata* usually immersed in the mycelium, solitary to aggregated, non-ostiolate, globose to subglobose. *Ascomatal wall* subhyaline, translucent, composed of depressed cells. *Asci* without visible stalks, 3–8 spored based on the original description, often irregularly-shaped, evanescent. *Ascospores* 1-celled, olivaceous brown when mature, smooth, 1-celled, stellate, with apical germ pores. *Asexual morph* not observed.

Type species: *Stellatospora terricola* Tad. Ito & Nakagiri.

Note: This is a monotypic genus, which was originally regarded to reside in the *Sordariaceae* (Ito & Nakagiri 1994). This classification was followed by Maharachchikumbura *et al.* (2015, 2016), even though Kirk *et al.* (2008) suggested the genus to belong to the *Chaetomiaceae*. The sequences of ITS and the D1/D2 domain of LSU from Vu *et al.* (2019) indicated that the type species, *Stell. terricola* belongs to the *Chaetomiaceae*. Our phylogenetic analyses based on the *rpb2* and the four-locus datasets confirmed that this genus is a single lineage in the *Chaetomiaceae* (Figs 2, 3). No genera or species have been found to be closely related to this genus.

Stellatospora terricola Tad. Ito & Nakagiri, Mycoscience 35: 413. 1994. Fig. 40.

Micromorphology: Ascomata usually immersed in the mycelium, solitary to aggregated, non-ostiolate, globose to subglobose, leaden black when mature in reflected light due to the dark ascospores inside, glabrous, 50–150 µm diam. *Ascomatal wall* subhyaline, translucent, composed of *textura epidermoidea* in surface view. *Asci* elongated clavate, elongated pyriform, dumbbell-shaped or irregularly-shaped, often geniculate or twisted, spore-bearing part 34.5–48.5 × 12–19.5 µm, without visible stalks, containing eight biseriate, irregularly-arranged ascospores, soon evanescent. *Ascospores* 1-celled, olivaceous brown when mature, smooth, stellate, with up to 7–8 papillate protuberances, (8.5–)10.5–13(–16) µm diam, with at least two visible apical germ pores at the ends of protuberances. *Asexual morph* not observed.

Culture characteristics: On OA with an entire edge, 3–9 mm diam in 7 d at 25 °C, with, obverse white due to white aerial mycelium, without coloured exudates, reverse uncoloured or buff. On CMA similar to those on OA. On MEA with an entire or slightly crenate edge, 2–8 mm diam in 7 d at 25 °C, texture floccose, obverse white due to white aerial mycelium, without coloured exudates, reverse ochraceous. On PCA with an entire edge, 1–6 mm diam in 7 d at 25 °C, without aerial mycelium, without coloured exudates, reverse uncoloured.

Typus: **Japan**, Ikeda, Osaka Pref., isolated from paddy soil, May 1966, T. Ito & A. Nakagiri (culture ex-type CBS 811.95 = IFO 32597).

Notes: The unique stellate shape of the ascospores is a diagnostic character to identify *Stell. terricola*. In the original description, the asci were described as "3–8-spored, pyriform to ovate" (Ito & Nakagiri 1994). In our examination, however, no ovate asci containing less than eight spores were observed, but most asci observed were irregularly-shaped (Fig. 40G).

Stolonocarpus X. Wei Wang & Houbraken, ***gen. nov.*** MycoBank MB829877.

Etymology: Name refers to ascomata arising from stolon-like mycelium creeping on or immersed in medium.

Micromorphology: *Mycelium* sparse, composed of olivaceous to brown hyphae, branched, septate, creeping along medium like stolon or immersed in the medium. *Ascomata* superficial, usually arising from aerial mycelium along the edge, subglobose, non-ostiolate. *Ascomatal wall* brown, non-translucent, composed of irregular, angular or elongated cells. *Ascomatal hairs* hypha-like, flexuous, brown, septate, some thicker than the others. *Asci* fasciculate, cylindrical, geniculate or twisted, stalked, containing eight uniseriate or occasionally biseriate ascospores, evanescent. *Ascospores* 1-celled, brown when mature, smooth, ellipsoidal, with attenuated ends, usually over 20 µm long, with an apical germ pore. *Asexual morph* not observed.

Type species: *Stolonocarpus gigasporus* (Moustafa & Abdel-Azeem) X. Wei Wang & Houbraken.

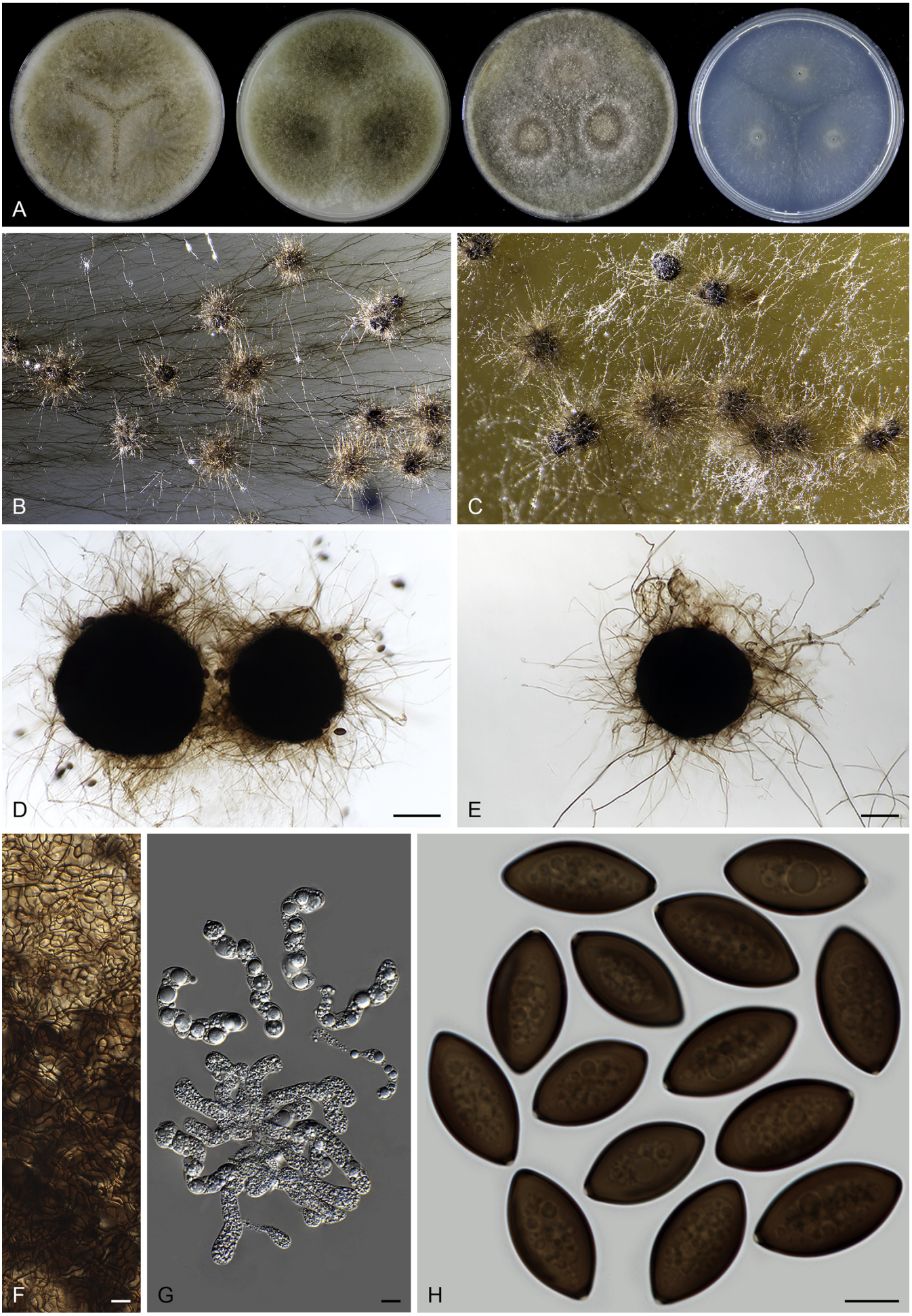
Notes: *Stolonocarpus* is a monotypic genus which is most closely related (PP = 0.99, BS = 100 %; Fig. 3) to *Madurella*, a group of etiologic fungi that can cause human mycetoma. *Madurella* strains often do not sporulate and do not produce a sexual state.

Stolonocarpus gigasporus (Moustafa & Abdel-Azeem) X. Wei Wang & Houbraken, ***comb. nov.*** MycoBank MB829878. Fig. 41. *Basionym*: *Thielavia gigaspora* Moustafa & Abdel-Azeem, Microbiol. Res. 163: 442. 2008.

Micromorphology: Mycelium sparse, composed of pigmented hyphae, branched, septate, often creeping radially along medium like stolon, vinaceous buff to olivaceous in reflected light. *Ascomata* superficial, usually arising from stolon-like mycelium and easily forming along the edge of colonies, fawn to olivaceous due to ascomatal hairs in reflected light, subglobose, non-ostiolate, 160–410 µm diam. *Ascomatal wall* brown, non-translucent, composed of irregular, angular or elongated cells. *Ascomatal hairs* hypha-like, flexuous, partly brown, septate, 1.5–3 µm diam near base, partly dark brown, 3.5–5.5 µm diam near base. *Asci* fasciculate, cylindrical, often geniculate or twisted, spore-bearing part 50–75 × 7.5–13 µm, with stalks 5.5–10 µm long, containing eight uniseriate or occasionally biseriate ascospores, evanescent. *Ascospores* 1-celled, brown when mature, smooth, ellipsoidal with attenuated ends or fusiform, (22.5–)25.5–28.5(–29.5) × (13–)14–15.5 µm, with an apical germ pore. *Asexual morph* not observed.

Culture characteristics: On OA with an entire edge, 38–44 mm diam in 7 d at 25 °C, obverse vinaceous buff to olivaceous due to aerial mycelium with ascomata forming along edge, reverse hazel. On CMA with an entire edge, 29–35 mm diam in 7 d at 25 °C, texture floccose, obverse hazel to isabelline due to aerial mycelium mixed with ascomata, reverse isabelline. On MEA with an entire edge, 44–50 mm diam in 7 d at 25 °C, obverse floccose, vinaceous buff, reverse fawn to

Fig. 40. *Stellatospora terricola* (CBS 811.95, 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.** Asci. **H.** Ascospores. Scale bars: E–F = 100 µm; G–H = 10 µm.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olivaceous due to immered hyphae. On PCA transparent, with an entire edge, 37–43 mm diam in 7 d at 25 °C, with extremely sparse aerial mycelium, without coloured exudates, reverse uncoloured.

Typus: **Egypt**, El-Sheikh Zweid, North Sinai, isolated from dung of *Camelus dromedarius*, 2002, A.F. Moustafa (culture ex-type CBS 112062).

Notes: The type species, *Stol. gigasporus* is distinct from the other known related species in the *Chaetomiaceae* in its sparse, pigmented and stolon-like mycelium which creep radially along medium, ascomata mostly forming along the edge of the colony and large ascospores (25.5–28.5 × 14–15.5 µm). This genus is related to *Madurella* and further study is needed to determine its potential in animal or human infection.

Thermothielavioides X. Wei Wang & Houbraken, ***gen. nov.*** MycoBank MB829879.

Etymology: Name refers to its thermophilic nature and its morphological similarity to *Thielavia sensu stricto*.

Micromorphology: *Ascomata* superficial or covered by aerial mycelium, solitary to aggregated, non-ostiolate, globose or subglobose. *Ascomatal wall* brown, semi-translucent, composed of irregular, angular or elongated cells. *Ascomatal hairs* brown, septate, flexuous, verrucose, tapering and fading to hyaline towards tips. *Asci* fasciculate, ellipsoidal to ovoid, stalked, containing eight biseriate or irregularly-arranged ascospores, evanescent. *Ascospores* 1-celled, olivaceous brown when mature, smooth, ellipsoidal or ovoid, with an apical germ pore at the most attenuated end. *Conidiogenous cells* arising laterally from aerial hyphae, hyaline, phialidic. *Conidia* in basipetal chains, hyaline, aseptate, smooth, obovoid to clavate, usually with a truncated base and a rounded apex. Thermophilic.

Type species: *Thermothielavioides terrestris* (Apinis) X. Wei Wang & Houbraken.

Notes: The monotypic genus *Thermothielavioides* is closely related to *Floropilus* in Clade 3. *Floropilus* is mesophilic and produces chaetomium-like ascomata, while *Thermothielavioides* is thermorphilic with an optimal growth temperature ≥45 °C (van den Brink *et al.* 2015) and has a thielavia-morph.

Thermothielavioides terrestris (Apinis) X. Wei Wang & Houbraken, ***comb. nov.*** MycoBank MB829880. Fig. 42.
Basionym: *Allescheria terrestris* Apinis, *Nova Hedwigia* 5: 68. 1963.
Synonym: *Thielavia terrestris* (Apinis) Malloch & Cain, Canad. J. Bot. 50: 66. 1972.

Micromorphology: *Ascomata* superficial or covered by aerial mycelium, solitary to aggregated, non-ostiolate, lead black in reflected light, globose or subglobose, 80–270 µm diam. *Ascomatal wall* brown, non- translucent or semi-translucent, composed of irregular, angular or elongated cells. *Ascomatal hairs* brown, septate, flexuous, verrucose, tapering and fading to hyaline towards tips, 2–3.5 µm diam near base. *Asci* ellipsoidal to ovoid, spore-bearing part 13.5–20.5 × 6–8 µm, with stalks 4.5–11.5 µm long, containing eight biseriate or irregularly arranged ascospores, evanescent. *Ascospores* 1-celled, olivaceous brown when mature, smooth, ellipsoidal or ovoid, 4–6.5(–7) × (3–)3.5–4.5(–5) µm, with an apical germ pore at the most attenuated end. *Conidiogenous cells* arising laterally from aerial hyphae, hyaline, phialidic, occasionally branched, (6.5–)9–24(–33) × (1–)1.5–3.5 µm. *Conidia* in basipetal chains, hyaline, aseptate, smooth, obovoid to clavate, usually with a truncated base and a rounded apex, (3–)3.5–5(–5.5) × 1.5–2.5(–3) µm.

Culture characteristics: On OA with an entire edge, 53–59 mm diam in 7 d at 37 °C, texture thick floccose, obverse white to pale smoke grey, or rosy buff to hazel, reverse cinnamon to hazel. On CMA similar to those on OA. On MEA with an entire edge, 39–45 mm diam in 7 d at 37 °C, texture thick floccose, obverse white, reverse fawn. On PCA with an entire edge, 41–47 mm diam in 7 d at 37 °C, with sparse aerial mycelium, producing ascomata when growing on cellophane membrane covering the surface of the medium, obverse white to smoke grey, reverse smoke grey.

Typus: **UK**, isolated from dry pasture soil, date unknown, T. Funahashi (culture ex-type CBS 117535 = CBS 355.66).

Additional material examined: **Japan**, Hiroshima, isolated from soil, 11 Jul. 1972, K. Minoura (CBS 492.74 = ATCC 26917 = HUT 4081). **Malaysia**, Pahang, isolated from cellulose in soil from palm oil estate, date unknown, S.C. Cheah (CBS 351.90). **Unknown**, substrate and date unknown, K.F. Gregory (CBS 546.86). **USA**, Indiana, Monroe Co., Kent Farm, isolated from sun-heated soil, 1971, M.R. Tansey (CBS 455.75); Florida, Everglades Nat. Park, 5 km N of Flamingo, isolated from sun-heated dung of rabbit, 1973, M.R. Tansey (CBS 454.75 = IAM 14666).

Notes: This species easily degenerates and produces only conidial morph. Cross cultivation induced the formation of ascomata (Samson *et al.* 1977). Although the culture CBS 117535 = CBS 355.66 was not marked as the ex-type of the species in the CBS database, von Arx (1975) described this culture as the type with the following text: "culture CBS 355.66, type strain, isolated from pasture soil, sent by A.E. Apinis".

Podosporaceae X. Wei Wang & Houbraken, ***fam. nov.*** MycoBank MB829841.

Etymology: Named after *Podospora*, the oldest genus in this family, but differentiating from the existing but invalid name "*Podosporaceae* Hochb. 1930" (Art. 32.1(c), Melbourne).

Micromorphology: *Sexual morph*: *Ascomata* superficial to immersed in medium, solitary or loosely aggregated, ostiolate and ovoid to obpyriform, or non-ostiolate and globose to subglobose, glabrous or possessing hypha-like to seta-like hairs. *Ascomatal wall* membranaceous to coriaceous, usually opaque, in some species semi-translucent. *Asci* cylindrical to elongated clavate or fusiform, stipitate, with or without a thickened ring at apex, (2–)4- or 8- or multi-spored, evanescent or persistent until ascospores mature. *Ascospores* 1-celled and pigmented, or 2-celled and composed of a larger, pigmented upper cell and a smaller, pale or hyaline cell, with or without appendage, usually smooth, in a few species ornamented. *Asexual morph* not observed or cladorrhinum-like: *Conidiophores* micronematous,

Fig. 41. *Stolonocarpus gigasporus* (CBS 112062, ex-type culture). **A.** Colonies from left to right on OA, CMA, MEA and PCA after 2 wk incubation. **B.** Mature ascomata on PCA, top view. **C.** Mature ascomata on OA, top view. **D–E.** Ascomata mounted in lactic acid. **F.** Structure of ascomatal wall in surface view. **G.** Asci. **H.** Ascospores. Scale bars: D–E = 100 µm; F–H = 10 µm.

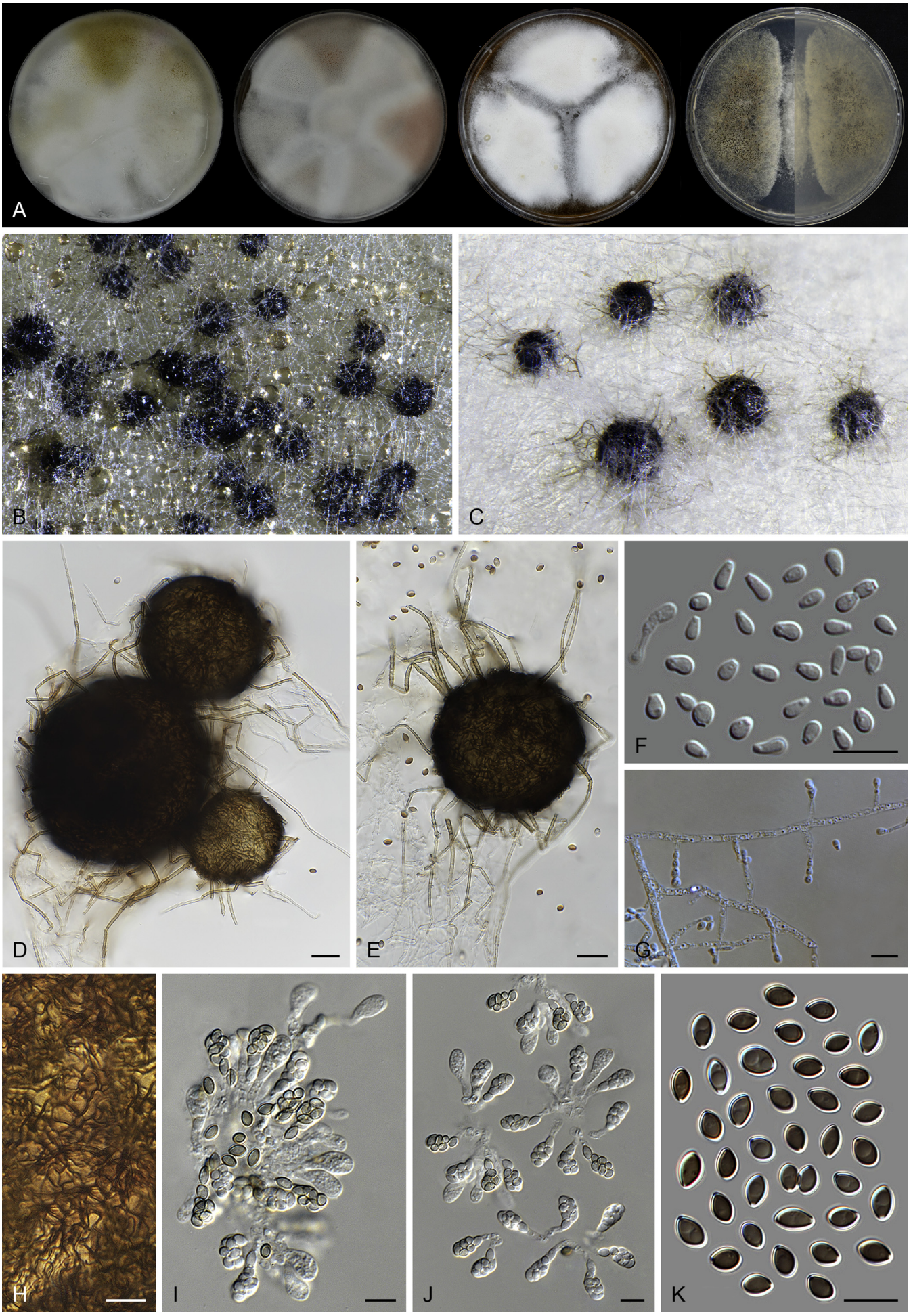


Fig. 42. *Thermothielavioides terrestris* (CBS 492.74). **A.** Colonies from left to right on OA, CMA, MEA and PCA after 4 wk incubation at 37 °C (left half showing obverse colony and right half showing the reverse on PCA). **B–C.** Mature ascomata on PCA, top view. **D–E.** Ascomata mounted in lactic acid. **F.** Conidia. **G.** Hyphae, conidiophores and conidia. **H.** Structure of ascomatal wall in surface view. **I–J.** Asci. **K.** Ascospores. Scale bars: D–E = 20 µm; F–K = 10 µm.

reduced to conidiogenous cells. *Conidiogenous cells* intercalary or occasionally terminal, originating lateral or terminal peg-like structure with a flaring collarette, producing blastic conidia. *Conidia* single-celled, hyaline, smooth, usually with a truncated base and a rounded apex.

Type genus: *Podospora* (Corda) Ces.; other included genera: *Cladorrhinum* Sacc. & Marchal; *Triangularia* Boedijn.

Notes: Previous studies have showed phylogenetic evidence for the polyphyly of the family *Lasiosphaeriaceae*, and noted that the relationships at family and genus level in the *Sordariales* are complicated (Huhndorf *et al.* 2004, Cai *et al.* 2005, Miller & Huhndorf 2005, Cai *et al.* 2006, Zhang *et al.* 2006, Kruys *et al.* 2015). Based on our phylogenetic analyses, a monophyletic lineage, containing species of several different genera, is sister to the *Chaetomiaceae*. The new family name *Podosporaceae* is proposed here to accommodate this sister lineage of the *Chaetomiaceae* (Figs 2, 3). Aside from the molecular data in the present study, a previous study also showed that several *Cercophora* species belonged to this lineage, however, the type species of *Cercophora*, *Cer. mirabilis* grouped with *Triangularia mangenotii* and *Podospora decipiens*, distant from this lineage (Clade A in Cai *et al.* 2006). Although there were not many sequences of *Cercophora* species available for this study, our data enable us to mark the *Cercophora sensu stricto* lineage in the *rpb2* phylogram (marked with double red triangles in Fig. 2).

Podosporaceae Hochb. was invalidly introduced (Art. 32.1(c), Melbourne). Our newly proposed *Podosporaceae* is based on the same type (*Podospora*), but they are differently delimited (phenotype-based *vs* sequence-based). Future studies are required to show the diversity within this family.

Cladorrhinum Sacc. & Marchal, Bull. Soc. Roy. Bot. Belgique 24: 64. 1885.

Micromorphology: *Sexual morph*: *Ascomata* superficial to immersed in medium, solitary or loosely aggregated, non-ostiolate, globose to subglobose, with hypha-like ascomatal hairs or covered by aerial mycelium. *Ascomatal wall* membranaceous, semi-translucent or opaque, composed of *textura intricata* or *epidermoidea* in surface view. *Asci* cylindrical, pyriform, obovoid or fusiform, stalked, without a thickened ring at apex, 8-spored, evanescent. *Ascospores* 1-celled, pigmented, smooth, with an apical germ pore, without appendage. *Asexual morph*: *Conidiophores* micronematous, reduced to conidiogenous cells. *Conidiogenous cells* intercalary or occasionally terminal, originating lateral or terminal peg-like structure with a flaring collarette, producing blastic conidia. *Conidia* single-celled, hyaline, smooth, broad obovoid, ellipsoidal or subglobose, usually with a truncated base and a rounded apex.

Type species: *Cladorrhinum foecundissimum* Sacc. & Marchal.

Notes: *Cladorrhinum* was originally introduced for asexually reproducing species. Our phylogenetic analyses show that two former *Thielavia* species (*Th. hyalocarpa* and *Th. intermedia*) group with the type species of *Cladorrhinum* in the *Podosporaceae* lineage. This genus is therefore redefined to also accommodate sexually reproducing species. Phylogenetic evidence indicated that morphologically-defined traditional *Cladorrhinum* is polyphyletic (Carmarán *et al.* 2015). On the other hand, several sexual genera also produce a cladorrhinum-like state (Mouchacca & Gams 1993, Cai *et al.* 2006). Based on our phylogenetic analyses, only the type species of the traditional *Cladorrhinum* is maintained in the modified genus. The two other studied *Cladorrhinum* species, *Clad. bulbillosum* and *Clad. phialophoroides*, belong to the redefined genera *Podospora* and *Triangularia*, respectively, in the family *Podosporaceae*. More work is required to determine the phylogenetic position of the remaining "*Cladorrhinum*" species.

Cladorrhinum foecundissimum Sacc. & Marchal, Bull. Soc. Roy. Bot. Belgique 24: 64. 1885. Fig. 43.

Micromorphology: *Sexual morph* not observed. *Somatic hyphae* hyaline, 1.0–2.5 µm wide. *Conidiophores* micronematous, reduced to conidiogenous cells. *Conidiogenous cells* intercalary, originating lateral peg-like structure with a flaring collarette, producing lateral blastic conidia. *Conidia* single-celled, hyaline, smooth, broad obovoid, ellipsoidal or subglobose, usually with a truncated base and a rounded apex, (2.5–)3–4(–4.5) × 2.5–3(–3.5) µm.

Culture characteristics: On OA with an entire edge, 26–32 mm diam after 7 d at 25 °C; obverse pale luteous due to coloured exudates diffusing into the medium, with aerial mycelium, reverse honey. On CMA similar to those on OA. On MEA with an entire edge, 18–24 mm diam after 7 d at 25 °C, obverse honey due to aerial mycelium and conidia, reverse olivaceous grey due to coloured exudates diffusing into the medium. On PCA translucent, with an entire edge, 23–29 mm diam after 7 d at 25 °C, without aerial mycelium, obverse and reverse honey.

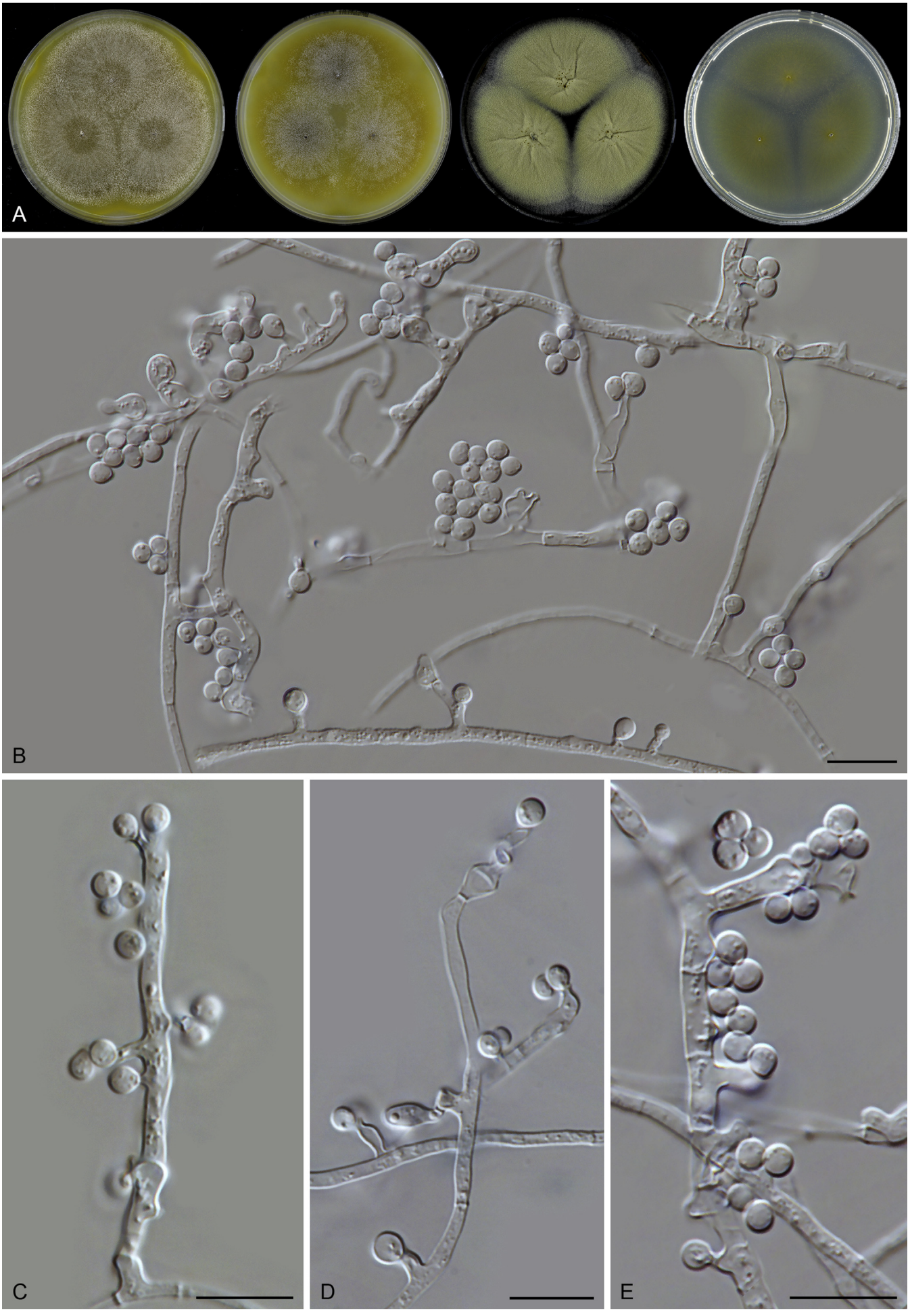
Typus: **Netherlands**, Wageningen, isolated from soil, 22 Jul. 1965, J.H. van Emden (culture ex-neotype CBS 180.66).

Notes: The type species *Clad. foecundissimum* is currently the only asexual species in this genus. This species was originally isolated from dung in Belgium (Marchal 1885). The holotype seems to be lost, and von Arx & Gams (1967) designated a herbarium specimen from CBS 180.66 as the neotype of this species. The ex-neotype strain keeps a strictly asexual reproduction. In contrast, no asexual morph was observed in the closely related species *Clad. hyalocarpum* and *Clad. intermedium*. The latter two species only produced sexual morphs.

Cladorrhinum hyalocarpum (Arx) X. Wei Wang & Houbraken, ***comb. nov.*** MycoBank MB829881. Fig. 44.
Basionym: *Thielavia hyalocarpa* Arx, Stud. Mycol. 8: 6. 1975.

Micromorphology: Ascomata superficial or slightly submersed, occationally immersed in the medium, solitary, often covered by aerial mycelium, non-ostiolate, black, globose, (160–)265–500(–605) µm diam. *Ascomatal wall* brown, semi-translucent, translucent, composed of *textura epidermoidea* or *intricata* in surface view. *Ascomatal hairs* hypha-like, hyaline or subhyaline, 2–4 µm diam near base. *Asci* cylindrical, spore-bearing part 81.5–148 × 11.5–19.5 µm, with stalks 7–20.5 µm long, containing eight uniseriate ascospores, evanescent. *Ascospores* 1-celled, dark brown when mature, smooth, fusiform, (22.5–)24.5–31(–36) × (11.5–)13–15.5(–16) µm, with an apical germ. *Asexual morph* not observed.

Culture characteristics: On OA with an entire edge, over 70 mm diam in 7 d at 25 °C, with floccose aerial mycelium near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the edge, obverse buff or honey due to coloured exudates diffusing into the medium, or white due to aerial mycelium, reverse buff. On CMA similar to those on OA. On MEA with an entire edge, over 70 mm diam in 7 d at 25 °C, texture floccose, obverse grey white, reverse fulvous. On PCA with an entire edge, over 70 mm diam in 7 d at 25 °C, without aerial mycelium, without coloured exudates, reverse uncoloured.

Typus: **Netherlands**, Zuidelijk Flevoland, isolated from soil, 1969, C.V. Subramanian (culture ex-type CBS 322.70).

Additional material examined: **Spain**, Beseit, isolated from forest soil, 14 Mar. 1999, A.M. Stchige (CBS 102198).

Notes: *Cladorrhinum hyalocarpum* is most closely related to *Clad. foecundissimum*, but differ in its ability to produce a sexual state and lacking a conidial state. This species can also be easily distinguished from *Clad. intermedium* by usually superficial or slightly sub-immersed ascomata, cylindrical asci, and larger fusiform ascospores (24.5–31 × 13–15.5 µm *vs* 12.5–14.5 × 9–10 µm).

Cladorrhinum intermedium (Stchigel & Guarro) X. Wei Wang & Houbraken, ***comb. nov.*** MycoBank MB829882. Figs 45, 46.
Basionym: *Thielavia intermedia* Stchigel & Guarro, Mycol. Res. 106: 976. 2002.

Micromorphology: Ascomata immersed or sub-immersed in the medium, solitary, non-ostiolate, fuscous black, globose, 245–460 µm diam. *Ascomatal wall* brown, opaque or semi-translucent, composed of *textura intricata* in surface view. *Ascomatal hairs* hypha-like, hyaline or subhyaline, 0.6–1.5 µm diam near base. *Asci* pyriform, obovoid or fusiform, spore-bearing part 20–35 × 13–21.5 µm, with stalks 14–25 µm long, containing eight irregularly arranged ascospores, evanescent. *Ascospores* 1-celled, olivaceous brown when mature, smooth, ovoid, (10–)12.5–14.5(–15) × (8–)9–10 µm, with an apical germ at the attenuated end. *Asexual morph* not observed.

Culture characteristics: On OA with an entire edge, 55–61 mm diam in 7 d at 25 °C, obverse pale grey to pale mouse grey due to aerial mycelium mixed with ascomata, reverse olivaceous grey due to coloured exudates diffusing into the medium. On CMA similar to those on OA, 52–58 mm diam in 7 d at 25 °C . On MEA with a slightly crenate edge, 55–61 mm diam in 7 d at 25 °C, texture floccose, obverse white, reverse fulvous. On PCA with a crenate edge, 56–62 mm diam in 7 d at 25 °C, without aerial mycelium, obverse mouse grey due to ascomata, without coloured exudates, reverse mouse grey.

Typus: **India**, isolated from soil, 29 Oct. 1995, A.M Stchigel (culture ex-type CBS 433.96 = FMR 5594).

Additional material examined: **Tunisia**, 5 km NW of Ksar Haddada, NW from Tatahouine, 470 m asl, isolated from soil attached to rhizoids of *Grimmia orbicularis*, 11 Apr. 1981, J.P. Frahm (CBS 100257 = ATCC 201454 = TRTC 52049).

Notes: The above description is based on the ex-type culture CBS 433.96 (Fig. 45). The isolate CBS 100257 was deposited as *Th. dacrydioides* J.C. Krug in the CBS culture collection, but no publication was found and the name was probably never validly published. Although this strain differs slightly from CBS 433.96 in colony morphology due to the formation of denser ascomata covered by less aerial mycelium (Fig. 46), our phylogenetic analyses and microscopic examination identified it as *Clad. intermedium*. *Cladorrhinum intermedium* can be easily distinguished from *Clad. hyalocarpum* by immersed or occasionaly sub-immersed ascomata, pyriform, obovoid or fusiform but never cylindrical asci and smaller ovoid ascospores (12.5–14.5 × 9–10 µm *vs* 24.5–31 × 13–15.5 µm).

Podospora Ces., Hedwigia 1: 103. 1856.

Micromorphology: *Sexual morph*: *Ascomata* usually superficial, solitary, ostiolate, ampulliform or papillate. *Ascomatal wall* membranaceous to coriaceous. *Asci* with an apical ring, usually persistent until ascospore mature. *Ascospores* composed of a pigmented, swollen upper cell and a lower hyaline pedicel (or referred to as primary appendage), often with apical and/or basal gelatinous appendages (also referred to as secondary appendages). *Asexual morph*: cladorrhinum-like or not observed. *Conidiophores* micronematous, reduced to conidiogenous cells. *Conidiogenous cells* usually intercalary, originating lateral peg-like structure with a flaring collarette, producing blastic conidia. *Conidia* single-celled, hyaline, smooth, usually with a truncated base and a rounded apex.

Type species: Podospora fimicola (Corda) Ces.

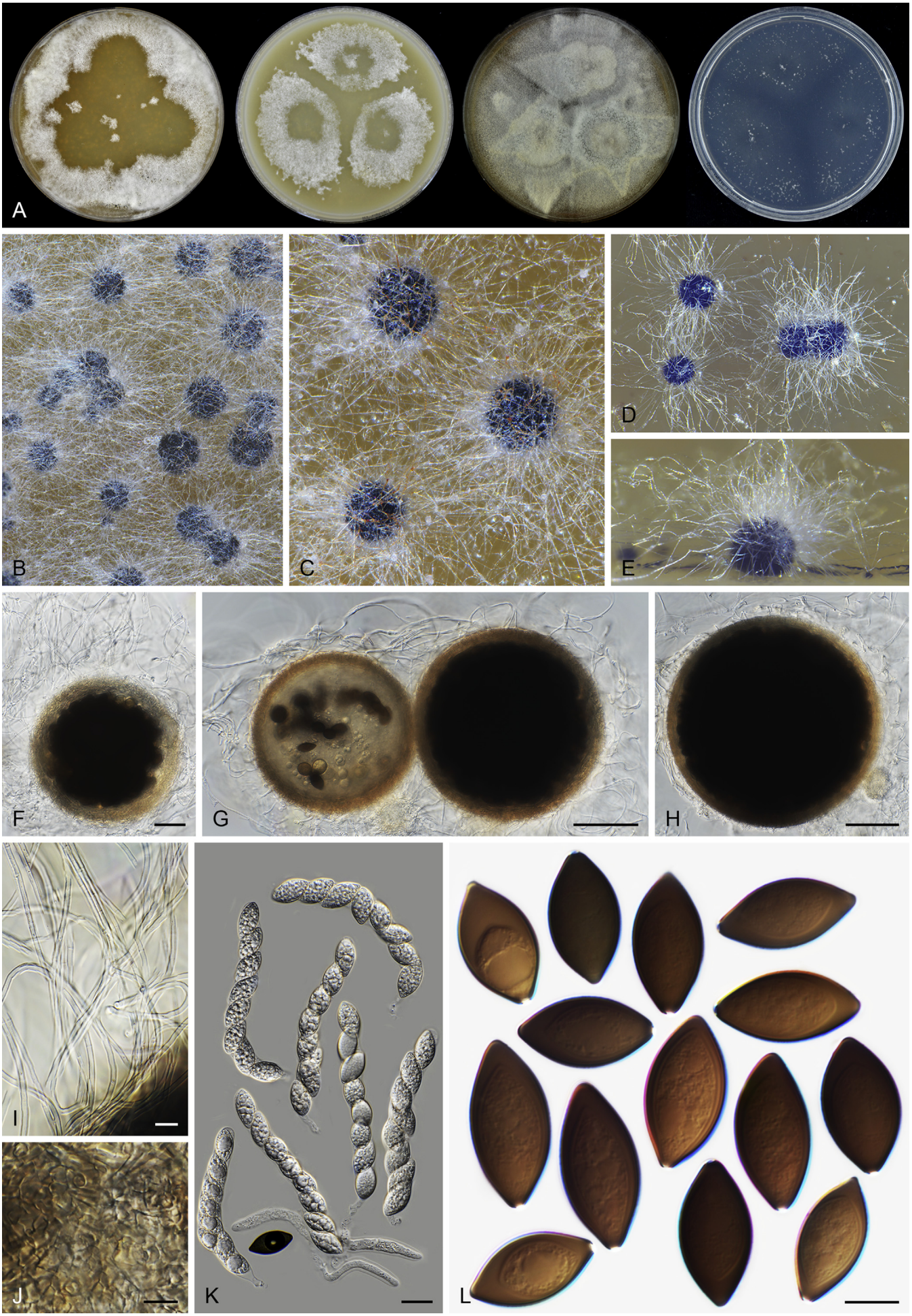
Notes: The genus *Podospora* was validly published in Hedwigia 1(15): 103, Tab. XIV, A, 1–11 (Cesati 1856) with a description later added in Rabenhorst's Klotzschii Herb. Viv. Mycol., Ed. Nova, no. 259 (see Braun 2018, fig. 22). It is a large genus containing over 100 species. Among the species included in this study, only the type species is maintained in *Podospora sensu stricto* based on our phylogenetic analyses. More work is required to determine the additional taxa in the genus.

Podospora bulbillosa (W. Gams & Mouch.) X. Wei Wang & Houbraken, ***comb. nov.*** MycoBank MB829883. Fig. 47.
Basionym: *Cladorrhinum bulbillosum* W. Gams & Mouch., Mycotaxon 48: 425. 1993.

Micromorphology: *Sexual morph* not observed. *Fertile hyphae* hyaline, 1.5–4(–6) µm wide. *Conidiophores* micronematous, reduced to intercalary hyphal conidiogenous cells. *Conidiogenous hyphal cells* 5.5–14 × 2–4 µm, usually producing a single (rarely two) conidiogenous protrusion laterally. *Conidiogenous protrusion* papillate to cylindrical, up to 2.5 µm long, 1–2 µm wide, apically with a flaring collarette opening that produces blastic conidia continuously. *Conidia* single-celled, hyaline, smooth, subglose or broad obovoid, usually with a truncated base and a rounded apex, 2.5–3.5 × 2–3 µm.

Culture characteristics: On OA with an entire edge, over 70 mm diam after 7 d at 25 °C, texture floccose, obverse buff to honey due to aerial mycelium mixed with masses of young ascomata, later becoming dark due to the mature ascomata, reverse buff to cinnamon. On CMA similar to those on OA. On MEA with an entire edge, over 70 mm diam after 7 d at 25 °C, with buff to vinaceous buff aerial mycelium, obverse greyish sepia, reverse fawn. On PCA translucent, with an entire edge, over 70 mm diam after 7 d at 25 °C, without or with sparse aerial mycelium, reverse uncoloured.

Fig. 43. *Cladorrhinum foecundissimum* (CBS 180.66, ex-type culture). **A.** Colonies from left to right on OA, CMA, MEA and PCA after 3 wk incubation. **B–E.** Hyphae, conidiogenous cells and conidia. Scale bars: B–E = 10 µm.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Typus: **Egypt**, New Valley region, Western Desert, isolated from desert soil, 15 Jan. 1993, J. Mouchacca (culture ex-type CBS 304.90 = CBS 979.72K).

Note: Phylogenetic analyses place this species in *Podospora sensu stricto*, sister to *Pod. fimicola*. No sexual state is observed in *Podospora bulbillosa*, while in *Pod. fimicola*, only the sexual morph is present.

Podospora fimicola (Corda) Ces., Hedwigia 1: 103. 1856. Fig. 48.
Basionym: *Schizothecium fimicola* Corda, Icon. Fung. 2: 29. 1838.
Synonyms: *Pleurage fimicola* (Corda) Kuntze, Revis. Gen. Pl. 3: 504. 1898.
Sordaria fimiseda Ces. & De Not., Comment. Soc. Crittog. Ital. 1: 226. 1863.

Micromorphology: Ascomata superficial, purplish grey or iron grey in reflected light, solitary, ampulliform with a short and black beak, ostiolate, 630–1250 µm high, 330–710 µm diam. *Ascomatal wall* brown, opaque, of *textura intricata* or *epidermoidea* in surface view. *Ascomatal hairs* covering the whole ascoma, erect or flexuous, brown, 2.5–5 µm diam near base, less than 75 µm long. *Asci* fasciculate, elongated fusiform, occasionally cylindrical, spore-bearing part 245–320 × 35–60 µm, with stalks (90–) 120–150 µm long, containing eight biseriate (occasionally uniseriate) ascospores, persistent until ascospore mature. *Ascospores* composed of a olivaceous brown cell and a hyaline and clavate or cylindrical pedicel (primary appendage) when mature, of which the pigmented cell ellipsoidal, 44.5–55 × 27.5–46 µm, with an apical germ pore and often with a hyaline and gelatinous apical secondary appendage; the primary appendage at the opposite end, 25–37 × 4.5–6.5(–8) µm, often with hyaline and gelatinous basal secondary appendage. *Asexual morph* not observed.

Culture characteristics: On OA with an entire edge, 31–37 mm diam in 7 d at 25 °C, with sparse aerial mycelium, obverse olivaceous to iron grey due to pigmented hyphae and coloured exudates diffusing into the medium, reverse purplish grey. On CMA similar to those on OA, obverse dark mouse grey. On MEA with a fimbriate edge, 17–23 mm diam in 7 d at 25 °C, obverse hazel due to aerial mycelium, reverse dark slate blue. On PCA with a slightly crenate edge, 25–31 mm diam in 7 d at 25 °C, without aerial mycelium; obverse dark mouse grey, reverse mouse grey to dark mouse grey.

Typus: **Lectotype of *Schizothecium fimicola* designated here**: Tab. XIII, fig. 105, illustrated by Corda based on the holotype collected from dried cow dung in Czech Republic, near Prague, in Corda, Icon. Fung. 2, 1831, MBT 385838. **Switzerland**, Kt. Aargau, Ober-Erlinsbach, Barmelweid, isolated from dung of cow, 21 Aug. 1958, W. Schaffner (CBS H-24048, **epitype designated here**, MBT387690, culture ex-epitype CBS 482.64 = ETH 2812).

Additional material examined: **New Zealand**, Cape Foulwind, South Island, isolated from dung of horse, Aug. 1990, D.P. Mahoney (CBS 990.96).

Notes: The genus *Podospora* is typified by *Pod. fimicola*, which is based on Corda's name *Schizothecium fimicola*. Type material of *S. fimicola* could neither by traced in PRC (Charles University in Prague) nor PRM (National Museum, Prague) and seems to be lost. In order to fix the application of the name, an illustration in the protologue is designated here as the lectotype of *Schizothecium fimicola*, and we selected CBS 482.64 as ex-epitype culture. CBS 482.64 matches with the protologue of the fungus described by Corda (1838) and it was collected on the same substrate and continent as the original material.

Triangularia Boedijn, Ann. Mycol. 32: 302. 1934.
Synonym: *Apiosordaria* Arx & W. Gams, Nova Hedwigia 13: 201. 1967.

Micromorphology: *Sexual morph*: *Ascomata* often superficial, sometimes semi-immersed to immersed in medium, solitary or loosely aggregated, ostiolate and ovoid, obpyriform to ampulliform and with a papilla-like beak, or non-ostiolate and globose to subglobose, glabrous or possessing hypha-like or seta-like hairs. *Ascomatal wall* membranaceous to coriaceous, opaque or semi-translucent, in some species translucent. *Asci* cylindrical to elongated clavate or fusiform, stipitate, without or with a usually inconspicuous apical ring, (2–)4– or 8– or multi-spored, evanescent or persistent until ascospores mature. *Ascospores* often 2-celled, composed of a larger, pigmented upper cell with an apical germ pore, and a smaller, pale or hyaline cell (also referred to as the primary appendage or pedicel when elongated and narrow), in some species without gelatinous appendages (secondary appendages), usually smooth, in a few species ornamented. *Asexual morph* usually cladorrhinum-like or not observed. *Conidiophores* micronematous, reduced to conidiogenous cells. *Conidiogenous cells* intercalary or occasionally terminal, originating lateral or terminal peg-like structure with a flaring collarette, producing blastic conidia. *Conidia* single-celled, hyaline, smooth, usually with a truncated base and a rounded apex.

Type species: *Triangularia bambusae* (J.F.H. Beyma) Boedijn.

Notes: *Triangularia* was morphologically defined by producing cylindrical or clavate asci with a thickened apical ring, 2-celled smooth ascospores, with a larger, pigmented and conical to triangular upper cell and a smaller, paler or hyaline and triangular to hemispherical lower cell, without gelatinous appendages (Guarro & Cano 1988). Our phylogenetic analyses did not support the morphologically defined genus *Triangularia* (Figs 2, 3). Therefore, this genus is redefined which includes morphologically diverse species.

Triangularia pauciseta and related species ("*Podospora anserina/pauciseta/comata* species complex", Boucher *et al.* 2017) needs further attention. *Podospora pauciseta* and *Pod. anserina* are morphologically indistinguishable and the former species was once treated as a synonym of *Pod. pauciseta* (Traversog 1907). At the molecular level, *Pod. anserina* strains differ by one base pair in their ITS sequence in comparison with *Pod. pauciseta*, six base pairs in *rpb2* (total 852 bp) and two base pairs in *tub2* (total 689 bp). Following a polyphasic approach and the taxonomic criteria used in our previous work in the *Chaetomiaceae* (Wang *et al.* 2016a, 2016b, 2019), we would have treated *Pod. anserina* as a synonym of *Pod. pauciseta*, due to the lack of morphological differences and minor sequence differences. A recent study (Boucher *et al.*

Fig. 44. *Cladorrhinum hyalocarpum* (CBS 322.70, ex-type culture). **A.** Colonies from left to right on OA, CMA, MEA and PCA after 4 wk incubation. **B.** Part of the colony on OA. **C–D.** Mature ascomata on OA, top view. **E.** Mature ascomata on OA, side view. **F–H.** Ascomata mounted in lactic acid. **I.** Ascomatal hairs. **J.** Structure of ascomatal wall in surface view. **K.** Asci. **L.** Ascospores. Scale bars: F = 50 µm; G–H = 100 µm; I, J, L = 10 µm; K = 20 µm.

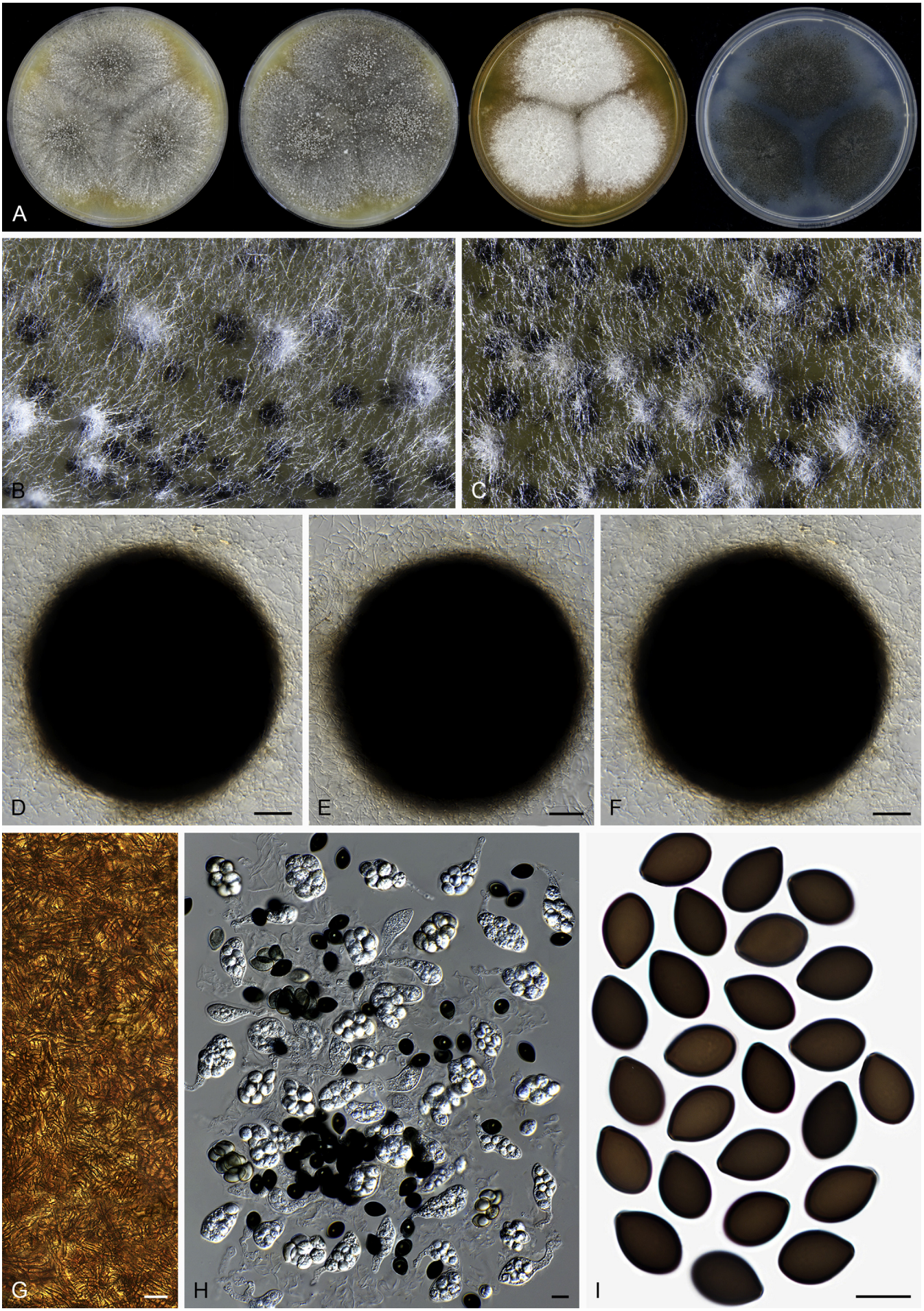

Fig. 45. *Cladorrhinum intermedium* (CBS 433.96, ex-type culture). **A.** Colonies from left to right on OA, CMA, MEA and PCA after 3 wk incubation. **B–C.** Part of the colony showing mature ascomata on OA, top view. **D–F.** Ascomata mounted in lactic acid. **G.** Structure of ascomatal wall in surface view. **H.** Asci. **I.** Ascospores. Scale bars: D–F = 50 µm; G–I = 10 µm.

2017) employed ITS sequences and three new intergenic loci to delimit cryptic species in the *Podospora anserina/pauciseta/comata* species complex (*Rchr3*, on chromosome 3; *Rchr4* on chromosome 4, and *Rchr6* on chromosome 6). Unfortunately, the phylogenetic markers *rpb2* and *tub2*, generally used in the *Chaetomiaceae*, were not included in their study. Based on their phylogenetic analysis, they recognised not only *Pod. anserina*, *Pod. pauciseta* and *Pod. comata*, but also four new species. In addition to the phylogenetic analyses, Boucher *et al.* (2017) performed crosses and pointed out that interspecific crosses were nearly sterile and most F1 progeny is female sterile, demonstrating congruence between their phylogenetic and biologic defined species. Based on the results (Fig. 6) of the re-analysed datasets of Boucher *et al.* (2017), we decided to follow them, and accept all seven species in the *"Podospora anserina/pauciseta/comata* species complex*"*: *Trian. anserina*, *Trian. bellae-mahoneyi*, *Trian. comata*, *Trian. pauciseta*, *Trian. pseudoanserina*, *Trian. pseudocomata* and *Trian. pseudopauciseta*. These species are morphologically identical (Boucher *et al.* (2017) and only the species description of *Trian. pauciseta* is given here.

Triangularia allahabadensis (M.P. Srivast., Tandon, Bhargava & A.K. Ghosh.) X. Wei Wang & Houbraken, ***comb. nov.*** MycoBank MB829884. Fig. 49.
Basionym: *Sordaria allahabadensis* M.P. Srivast., Tandon, Bhargava & A.K. Ghosh, Mycopathol. Mycol. Appl. 30: 203. 1966.

Micromorphology: *Ascomata* superficial, greenish black due to the mass of released ascospores in reflected light, solitary to aggregated, ampulliform with a short beak, ostiolate, 188–350 µm high, 144–325 µm diam. *Ascomatal wall* dark brown, opaque. *Ascomatal hairs* covering the whole ascoma, hypha-like, hyaline to subhyaline, 0.5–1 µm diam near base. *Asci* fasciculate, cylindrical to elongated fusiform, without conspicuous apical ring, spore-bearing part 70–125 × 12–20 µm, with stalks 13–35 µm long, containing eight biseriate or irregularly arranged (occasionally uniseriate) ascospores, evanescent after ascospores become mature. *Ascospores* 1-celled, hyaline when young and continuous with a hyaline and elongated fusiform appendage (9–13.5 × 2.5–3 µm in size and then falling off from mature ascospores), dark brown when mature, smooth, fusiform or navicular (19.5–)21.5–26(–28.5) × (8.5–)10–12 µm, with an apical germ pore. *Asexual morph* not observed.

Culture characteristics: On OA with an entire edge, 31–37 mm diam in 7 d at 25 °C, without aerial mycelium, obverse violaceous black due to ascomata and coloured exudates diffusing into the medium, reverse mouse grey. On CMA similar to those on OA, reverse olivaceous grey. On MEA with an entire edge, 34–40 mm diam in 7 d at 25 °C, with a thin layer of grey white aerial mycelium, sporulating well, obverse olivaceous grey due to coloured exudates diffusing into the medium, reverse dark slate blue. On PCA with an entire edge, 27–33 mm diam in 7 d at 25 °C, without aerial mycelium; obverse pale olivaceous grey or olivaceous grey, reverse mouse grey.

Typus: **India**, Allahabad, isolated from flower of *Carica papaya*, 1964, collector unknown (culture ex-type CBS 724.68 = IMI 104947).

Notes: The ex-type culture CBS 724.68 was deposited as *Podospora austroamericana* in the CBS culture collection. Previous studies showed that these two species are morphologically similar (Srivastava *et al.* 1966, Mirza & Cain 1969). Guarro *et al.* (1991) treated *Sordaria allahabadensis* as a synonym of *Pod. austroamericana* (basionym: *Hypocopra austroamericana* Speg. 1880); however, they did not study the holotype of the latter species. Based on literature (Srivastava *et al.* 1966, Mirza & Cain 1969), *Podospora austroamericana* can be distinguished from *Tri. allahabadensis* by the production of a phialophora-like morph and ascospores with clavate, persistent and broader primary appendages (3.5–4 µm *vs* 2.5–3 µm wide). More work is required to determine the relationship between these two species.

Triangularia anserina (Rabenh.) X. Wei Wang & Houbraken, ***comb. nov.*** MycoBank MB829885.
Basionym: *Malinvernia anserina* Rabenh., Hedwigia 1: 116. 1857.
Synonym: *Sordaria anserina* (Rabenh.) G. Winter, Abh. Naturf. Ges. Halle 13: 99. 1873.
Pleurage anserina (Rabenh.) Kuntze, Revis. Gen. Pl. 3: 504. 1898.
Podospora anserina (Rabenh.) Niessl, Hedwigia 22: 156. 1883.

Description and illustrations: See Boucher *et al.* (2017) and *Triangularia pauciseta* (present study).

Material examined: **Canada**, Ontario, Glenn Morris, isolated from dung of cow, 11 May 1944, R.F. Cain (CBS 433.50 = TRTC 12114). **France**, Normandy, isolated from dung, around 1940, collector unknown, culture ex-epitype of *Malinvernia anserina*, strain S deposited at Museum National d'Histoire Naturelle, Paris n° 6597. **Unknown**, substrate unknown, date and collector unknown, deposited by K. McCluskey (CBS 141519 = ATCC MYA-4624 = DSM 980 = FGSC 10383; CBS 141520 = ATCC MYA-4625 = FGSC 10384).

Notes: The *rpb2* and *tub2* sequences of the ex-epitype strain S (deposited at the Museum National d'Histoire Naturelle, Paris n° 6597) were retrieved from the released genomic data, but we didn't examine the morphology of this strain. *Triangularia anserina* is an important model ascomycete, being used for over a century to study various biological processes such as cell fusion, aging, sexual reproduction, differentiation and development and plant biomass degradation (Silar 2013). *Triangularia anserina*, *Trian. pauciseta* and the other species in this complex are morphologically indistinguishable. For further details, see notes of *Triangularia*.

Triangularia backusii L.H. Huang, Canad. J. Bot. 53: 560. 1975. Fig. 50.
Synonyms: *Zopfiella backusii* (L.H. Huang) Guarro, Int. J. Mycol. Lichenol. 2: 253. 1986.
Apiosordaria backusii (L.H. Huang) Guarro, Trans. Brit. Mycol. Soc. 91: 589. 1988.

Micromorphology: Ascomata superficial, ostiolate, obpyriform to ampulliform with a conical or papilla-like dark-brown to black beak, 350–480 µm high, 290–360 µm wide, covered with hypha-like grey olivaceous to isabelline hairs. *Ascomatal wall* coriaceous, opaque, brown. *Asci* elongated clavate or fusiform, without an apical ring, spore-bearing part 120–210 × 29–39 µm, with stalks 21–40.5 µm long, containing eight biseriate or irregularly-arranged ascospores, evanescent, often persistent till ascospores mature. *Ascospores* 2-celled, smooth under light microscope, obovoid to pyriform, (39–)40–50(–56.5) × (21.5–)23.5–26(–27) µm, of which the upper cell is violaceous black when mature and usually possessing a pale apical stab-like appendage, (28–)30–35.5(–37.5) µm long, with an

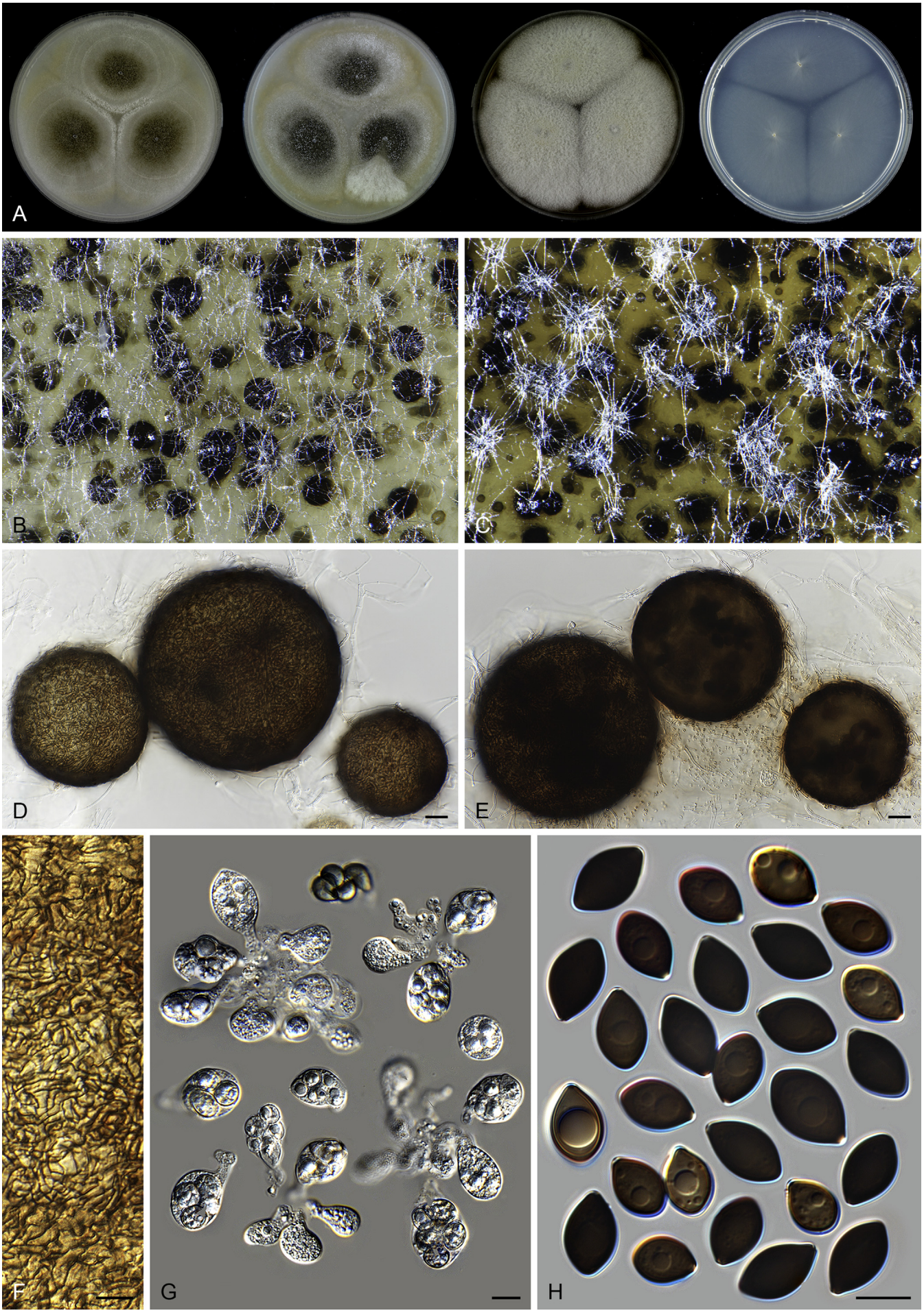

Fig. 46. *Cladorrhinum intermedium* (CBS 100257). **A.** Colonies from left to right on OA, CMA, MEA and PCA after 10 d incubation. **B–C.** Mature ascomata on OA, top view. **D–E.** Ascomata mounted in lactic acid. **F.** Structure of ascomatal wall in surface view. **G.** Asci. **H.** Ascospores. Scale bars: D = 50 µm; E = 20 µm; F–H = 10 µm.

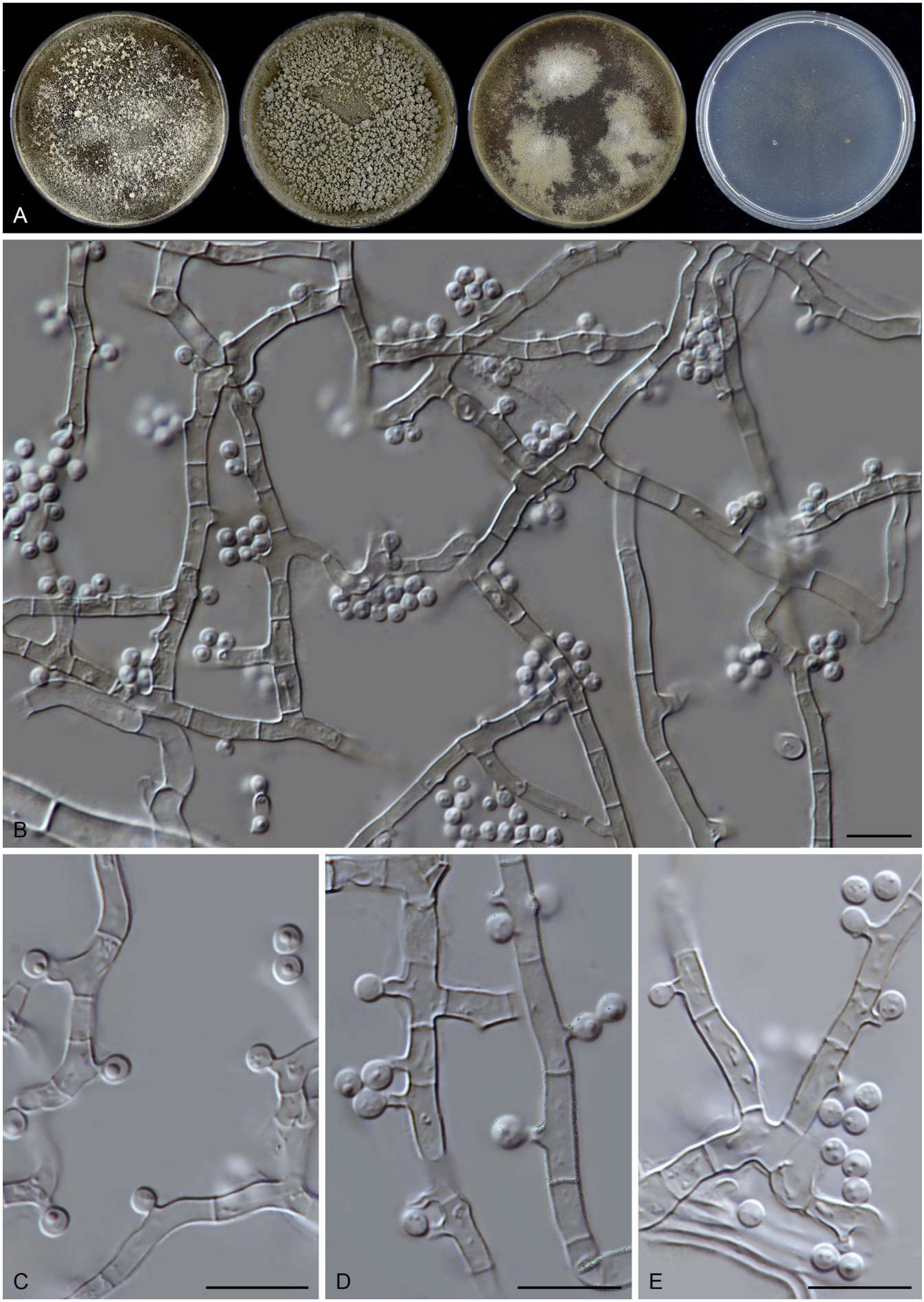

Fig. 47. *Podospora bulbillosa* (CBS 304.90). **A.** Colonies from left to right on OA, CMA, MEA and PCA after 3 wk incubation. **B–E.** Hyphae, conidiogenous cells and conidia. Scale bars: B–E = 10 µm.

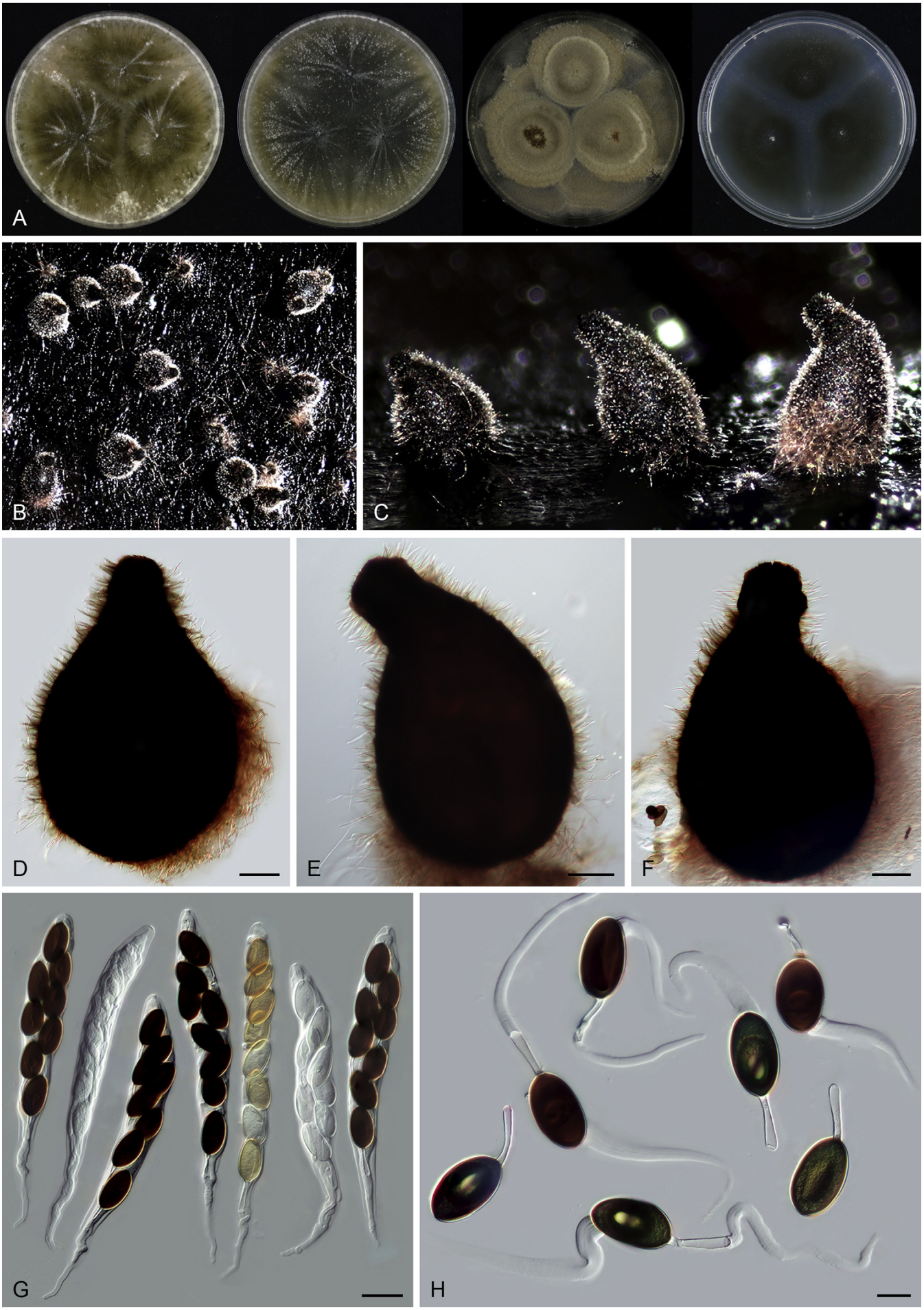

Fig. 48. *Podospora fimicola* (CBS 482.64, ex-epitype culture). **A.** Colonies from left to right on OA, CMA, MEA and PCA after 2 wk incubation. **B.** Mature ascomata on OA, top view. **C.** Mature ascomata on OA, side view. **D–F.** Ascomata mounted in lactic acid. **G.** Asci. **H.** Ascospores. Scale bars: D–F = 100 µm; G = 50 µm; H = 20 µm.

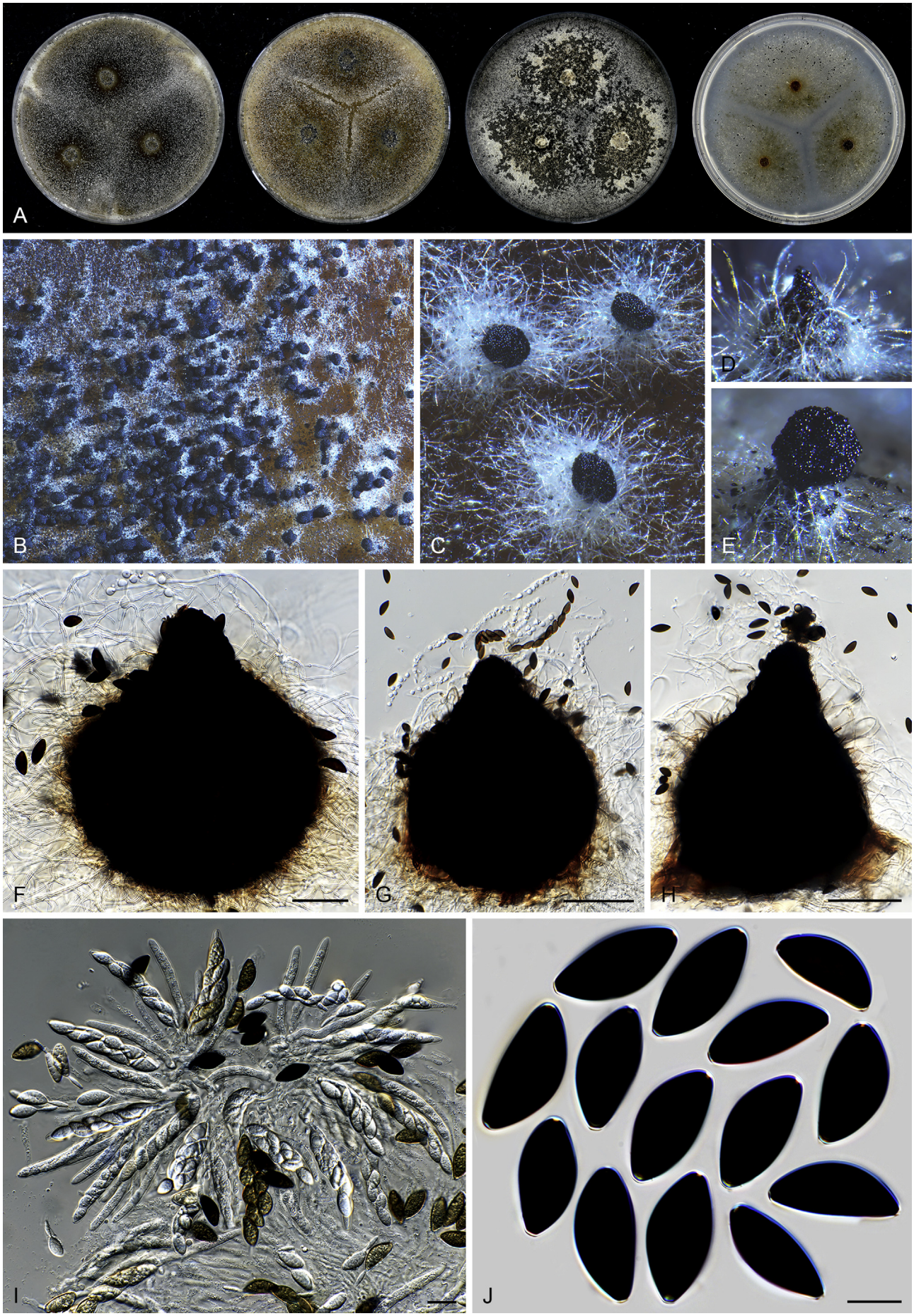

Fig. 49. *Triangularia allahabadensis* (CBS 724.68, ex-type culture). **A.** Colonies from left to right on OA, CMA, MEA and PCA after 4 wk incubation. **B.** Part of the colony on OA. **C.** Mature ascomata on OA, top view. **D–E.** Mature ascomata on OA, side view. **F–H.** Ascomata mounted in lactic acid. **I.** Asci and young ascospores with a primary appendage. **J.** Ascospores. Scale bars: F = 50 µm; G–H = 100 µm; I = 20 µm; J = 10 µm.

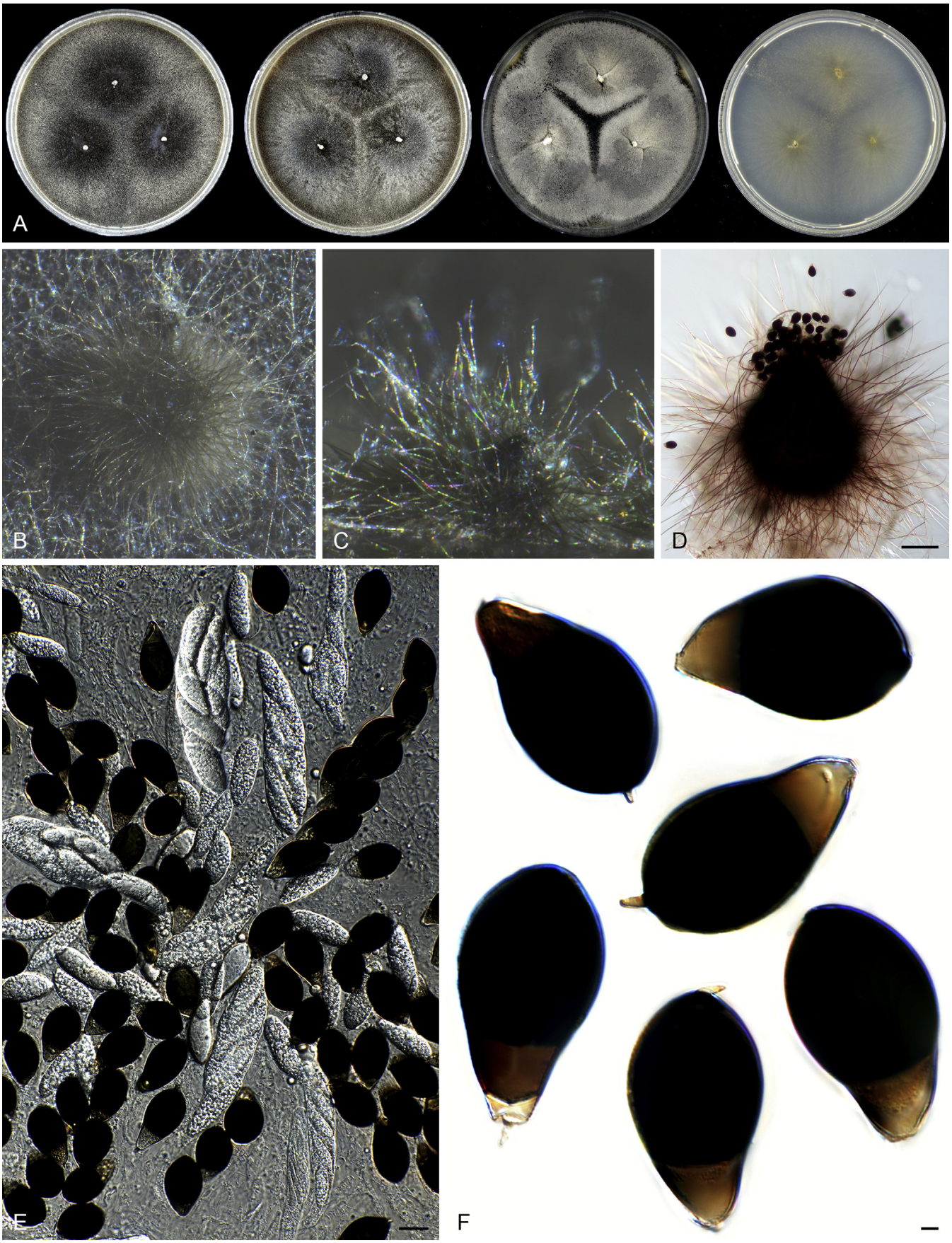

Fig. 50. *Triangularia backusii* (CBS 539.89, ex-type culture). **A.** Colonies from left to right on OA, CMA, MEA and PCA after 4 wk incubation. **B.** Mature ascomata on OA, top view. **C.** Mature ascomata on OA, side view. **D.** Ascomata mounted in lactic acid. **E.** Asci. **F.** Ascospores. Scale bars: D = 100 µm; E = 20 µm; F = 10 µm.

inconspicuous apical germ pore; and the lower cell straw to cinnamon, (10.5–)12–16(–18.5) × (13–)14.5–17(–18) µm, often collapsed at the base. *Asexual morph* not observed.

Culture characteristics: On OA with an entire edge, over 70 mm diam after 7 d at 25 °C, obverse greyish sepia, with a thin layer of smoke grey aerial mycelium, reverse mouse grey. On CMA similar to those on OA, obverse olivaceous, reverse mouse grey. On MEA with an entire edge, over 70 mm diam after 7 d at 25 °C, texture floccose, obverse smoke grey, reverse isabelline. On PCA translucent, with an entire edge, over 70 mm diam after 7 d at 25 °C, without or with sparse aerial mycelium, obverse pale olivaceous grey to pale luteous, reverse pale olivaceous grey or partly pale luteous.

Typus: **USA**, Montgomery Co. in Ohio, isolated from soil, L.H. Huang, date unknown (culture ex-type CBS 539.89 = ATCC 28796 = CBS 273.75).

Additional material examined: **Japan**, Okinawa Pref., isolated from sandy soil by J. Horie, 28 Sep. 1973 (CBS 106.77 = ATCC 34568 = IFM 4533 = IMI 210877 = NHL 2739). **Spain**, Castillejos, Tarragona, isolated from dung of rabbit, J. Guarro, date unknown (CBS 540.89 = ATCC 62830 = FMR 842).

Notes: The name changes of this species illustrate the complication of delimiting of *Apiosordaria*, *Triangularia* and *Zopfiella* morphologically. These three genera share the production of unequally 2-celled ascospores, with one larger, pigmented upper cell (which is occasionally septated) and a smaller, paler or hyaline lower cell, but lacking gelatinous appendages (Guarro & Cano 1988, Guarro *et al.* 1991). *Apiosordaria* species were regarded to produce ornamented ascospores, while the ascospores of *Triangularia* and *Zopfiella* were considered to be smooth walled (Guarro & Cano 1988, Wu *et al.* 2016). *Zopfiella* could be differentiated by the production of non-ostiolate ascomata (Guarro & Cano 1988, Guarro *et al.* 1991). SEM micrographs showed that there were shallow pits on the ascospores of *Trian. backusii*, which were hardly visible under light microscopy (Guarro & Cano 1988). For this reason, the species was transferred to *Apiosordaria* (Guarro & Cano 1988). Our phylogenetic data (Figs 2, 3) do not support the classification of *Trian. backusii* in *Apiosordaria*. Our data show that the morphological characters used for the delimitation of *Apiosordaria* needs to be re-evaluated.

Triangularia bambusae (J.F.H. Beyma) Boedijn, Ann. Mycol. 32: 302. 1934. Figs 51, 52.
Basionym: *Trigonia bambusae* J.F.H. Beyma, Zentralbl. Bakteriol., 2. Abt. 89: 236. 1933.

Micromorphology: Ascomata superficial, sometimes semi-immersed, ostiolate, obpyriform with a conical or papilla-like dark-brown to black beak, 200–370 µm high, 150–275 µm wide, usually covered by hyaline hypha-like hair, sometimes with brown setae near the ostiole. *Ascomatal wall* coriaceous, opaque or slightly semi-translucent, brown. *Asci* cylindrical, with a thickened ring at apex, spore-bearing part 90–125 × 9.5–17 µm, with stalks 16.5–55 µm long, containing eight uniseriate (occasionally biseriate) ascospores, evanescent, sometimes persistent till ascospores mature. *Ascospores* 2-celled, (15.5–)16–18.5(–20) µm long, composed of an upper triangular cell and a lower vinaceous buff cell, of which, the upper triangular cell olivaceous brown when mature, (13–)13.5–15.5(–17) × (9–)9.5–11(–13) µm, with a subapical germ pore; and the lower paler cell,(2–)3–4(–4.5) µm high, (10–)11.5–13.5(–14) µm wide. *Asexual morph* cladorrhinum-like, abundantly present, covering the ascomata. *Conidiogenous cells* terminally or laterally arising from aerial hyphae, hyaline, short cylindrical, slightly tapering, up to 2.5 µm long, 1–1.5 µm wide, apically with a flaring collarette opening in 1.5–2.5 µm wide, which produces blastic conidia continuously. *Conidia* single-celled, hyaline, smooth, subglobose, ellipsoidal or broad obovoid, often with a truncated base and a rounded apex, (2.5–)3–3.5(–4) × (2–)2.5–3(–4) µm.

Culture characteristics: On OA with an entire edge, over 70 mm diam after 7 d at 25 °C, with a layer of white aerial mycelium, obverse salmon to peach due to coloured exudates diffusing into the medium, distributing black dot-like ascomata, reverse peach. On CMA similar to those on OA. On MEA with an entire edge, over 70 mm diam after 7 d at 25 °C, with a thick layer of white aerial mycelium, obverse fulvous due to coloured exudates diffusing into the medium, distributing black dot-like ascomata, reverse apricot. On PCA with an entire edge, over 70 mm diam after 7 d at 25 °C, with a thin layer of white aerial mycelium, obverse and reverse uncoloured, without coloured exudates.

Typus: **Unknown**, isolated from shoot of *Bambusa* sp., Kol. Instituut, date unknown (ex-type culture CBS 352.33).

Notes: The position of *Tri. bambusae*, the type species of *Triangularia*, determined the phylogenetic placement of this genus in the *Podosporaceae fam. nov. Triangularia bambusae* is most closely related to *Trian. allahabadensis*, *Trian. backusii*, *Trian. longicaudata*, *Trian. setosa* and *Trian. verruculosa* (Figs 2, 3), but can be easily distinguished by its ascospores consisting of a dark and triangular shaped upper cell and a pale, broad and very short lower cell. *Triangularia backusii* and *Trian. verruculosa* also produce 2-celled ascospores, but ascospores of *Trian. backusii* are obovoid to pyriform, and those of *Trian. verruculosa* are unequally fusiform, never having a triangular upper cell. *Triangularia allahabadensis* produces 1-celled fusiform or navicular ascospores with a hyaline, elongated fusiform and easily falling-off appendage. *Triangularia longicaudata* and *Trian. setosa* produce 2-celled ascospores with a persistent hyaline primary appendage.

Triangularia bellae-mahoneyi (C. Boucher, T.S. Nguyen & Silar) X. Wei Wang & Houbraken, ***comb. nov.*** MycoBank MB829886.
Basionym: *Podospora bellae-mahoneyi* C. Boucher, T.S. Nguyen & Silar, Cryptog. Mycol. 38: 497. 2017.

Description and illustrations: See Boucher *et al.* (2017) and *Triangularia pauciseta* (present study).

Notes: This species is accepted based on the phylogenetic analysis using sequence data of the loci *Rchr3*, *Rchr4* and *Rchr6* (Fig. 6) from Boucher *et al.* (2017). This species cannot be recognised by ITS sequences. *Chr3*, *Chr4* and *Chr5* sequences should be generated for identification (Boucher *et al.* 2017). *Tub2* sequencing is recommended for identification of *Chaetomiaceae* (Wang *et al.* 2016b); however, no *tub2* references sequences of this species are available. Future studies including *tub2* sequences should provide information whether this species (and other closely related *Podosporaceae* species) could be identified using this secondary barcode.

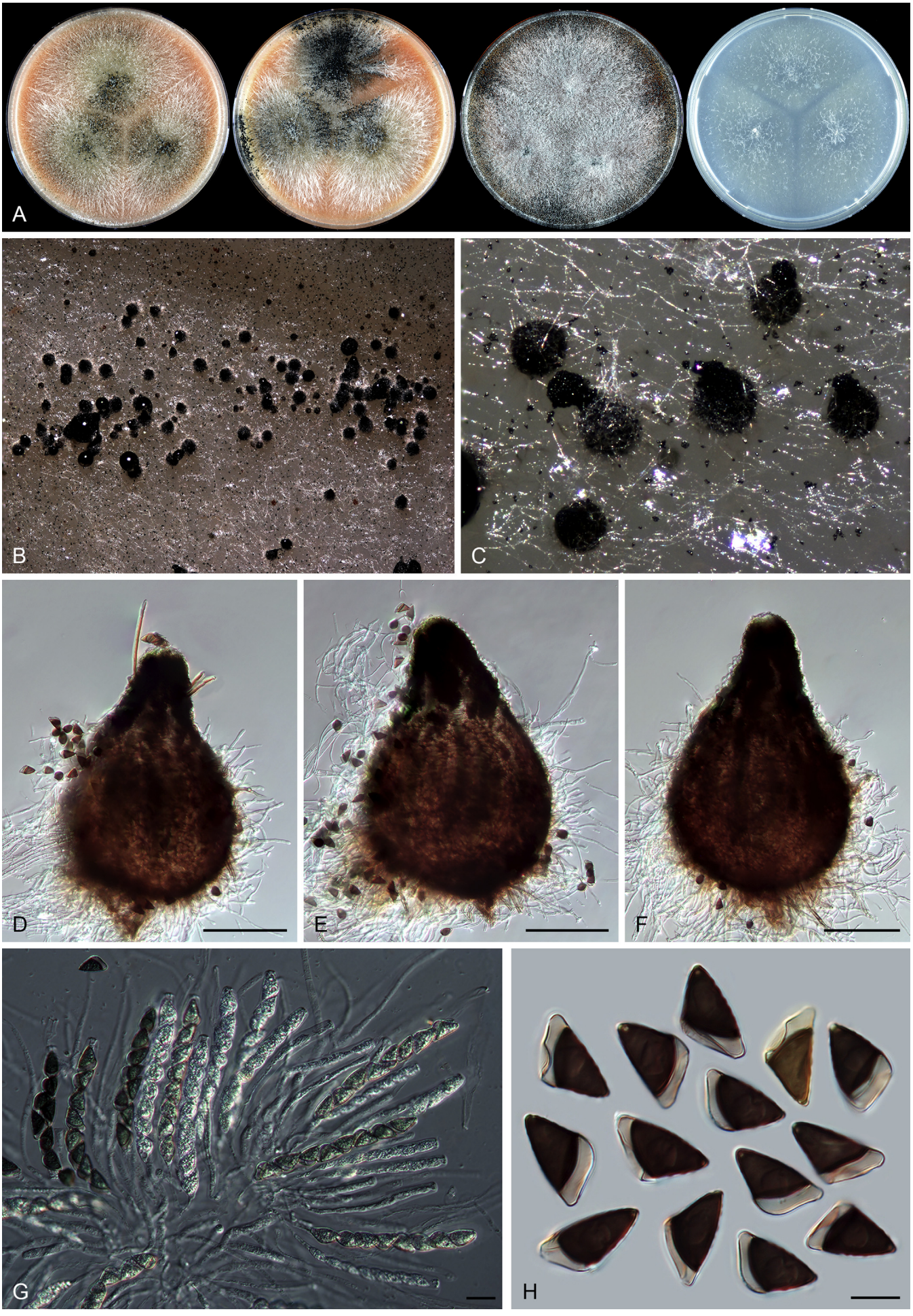

Fig. 51. *Triangularia bambusae* (CBS 352.33, ex-type culture). **A.** Colonies from left to right on OA, CMA, MEA and PCA after 4 wk incubation. **B.** Part of the colony on OA. **C.** Mature ascomata on OA, top view. **D–F.** Ascomata mounted in lactic acid. **G.** Asci. **H.** Ascospores. Scale bars: D–F = 100 µm; G = 20 µm; H = 10 µm.

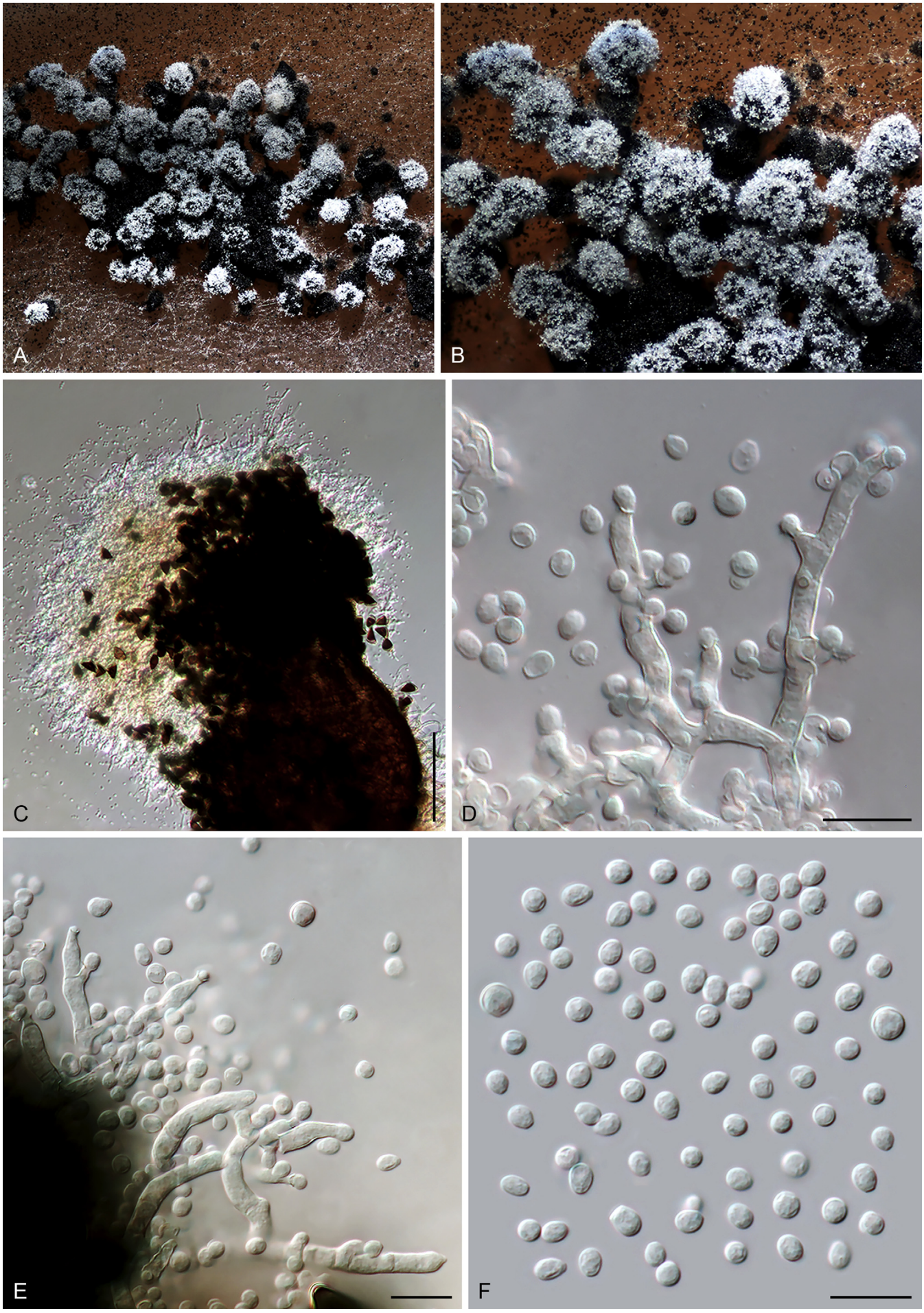

Fig. 52. *Triangularia bambusae* (CBS 352.33, ex-type culture). **A–B.** Asexual structures covering ascomata on OA, top view. **C.** Asexual structures covering an ascoma mounted in lactic acid. **D–E.** Hyphae, conidiogenous cells and conidia. **F.** Conidia. Scale bars: C = 100 µm; D–F = 10 µm.

Triangularia comata (Milovtz.) X. Wei Wang & Houbraken, ***comb. nov.*** MycoBank MB829887.
Basionym: *Podospora comata* Milovtz., Trav. Inst. Bot. Charkov 2: 20. 1937.

Description and illustrations: See Boucher *et al.* (2017) and *Triangularia pauciseta* (present study).

Notes: This species is accepted and transferred to the genus *Triangularia*. For additional information, see notes of *Trian. bellae-mahoneyi*.

Triangularia longicaudata (Cain) X. Wei Wang & Houbraken, ***comb. nov.*** MycoBank MB829888. Fig. 53.
Basionym: *Tripterospora longicaudata* Cain, Canad. J. Bot. 34: 702. 1956.
Synonym: *Zopfiella longicaudata* (Cain) Arx, Proc. Kon. Ned. Akad. Wetensch. C 76: 291. 1973.

Micromorphology: Ascomata superficial to immersed in the medium, fuscous black in reflected light, solitary to aggregated, subglobose, non-ostiolate, 110–245 µm diam. *Ascomatal wall* brown, semi-translucent, composed of irregular or angular cells. *Ascomatal hairs* sparse, hyaline, hypha-like, 2–3.5 µm diam near base. *Asci* fasciculate, cylindrical or elongated fusiform, without an apical ring, spore-bearing part 46–63 × 11–13 µm, with stalks 14–26 µm long, containing eight biseriate or irregularly arranged ascospores, evanescent. *Ascospores* composed of a olivaceous brown cell and a hyaline, cylindrical primary appendage when mature, of which the pigmented cell is ellipsoidal, attenuated at both ends, (11–)12–14.5(–15) × (7.5–)8–9(–9.5) µm, with an apical germ pore; the primary appendage at the opposite end, 9.5–13.5 × 2–3.5(–4) µm. *Asexual morph* not observed.

Culture characteristics: On OA with a lobate edge, 22–28 mm diam in 7 d at 25 °C, with white or buff sparse aerial mycelium or without aerial mycelium, obverse vinaceous buff or ochraceous due to pigmented exudates diffusing into the medium, or mouse grey due to the formation of ascomata, reverse mouse grey. On CMA similar to those on OA, obverse mouse grey to dark mouse grey. On MEA with a crenate or slightly fimbriate edge, 24–30 mm diam in 7 d at 25 °C, irregularly wrinkled, obverse white to mouse grey, with white to grey white aerial mycelium, reverse olivaceous grey. On PCA with a lobate edge, 19–25 mm diam in 7 d at 25 °C, without aerial mycelium; obverse pale olivaceous grey due to the formation of ascomata, reverse uncoloured.

Typus: **Canada**, Ontario, Peel Co., N of Palgrave, isolated from dung of horse, 10 Oct. 1955, R.F. Cain (culture ex-type CBS 252.57 = TRTC 31528).

Notes: *Triangularia longicaudata* was once placed in the genus *Zopfiella* (von Arx 1973). Our phylogenetic analyses indicated that this species is distant from *Zopfiella tabulata*, the type species of the genus *Zopfiella* (authentic strain CBS 230.78, marked with a red triangle in Figs 2, 3). Traditionally, *Zopfiella* is differentiated from *Triangularia* by the production of non-ostiolate ascomata, clavate to cylindrical asci lacking an apical ring, and small ascospores with short hyaline cells (primary appendages), but without gelatinous appendages (Guarro *et al.* 1991). Cai *et al.* (2006) suggested restricting *Zopfiella* to species having ascospores with a septum in the dark upper cell. The taxonomic value of this character and the possible presence of other species than *Zopfiella tabulata*, *Pod. didyma* and *Cercophora sulphurella* in *Zopfiella sensu stricto* needs to be evaluated. *Triangularia longicaudata* produces similar ascospores to those of *Trian. setosa* in shape, but can be distinguished from the latter species by 8-spored asci and smaller ascospores (12–14.5 × 8–9 µm *vs* 17–20.5 × 10.5–12 µm). It can be distinghuised from the other closely related species by the production of non-ostiolate ascomata. For more morphological comparisons, see notes of *Trian. bambusae*.

Triangularia pauciseta (Ces.) X. Wei Wang & Houbraken, ***comb. nov.*** MycoBank MB829889. Fig. 54.
Basionym: *Sphaeria pauciseta* Ces., Rabenhorst, Klotzschii Herb. Viv. Mycol., Cent. 17: no. 1642, 1852.
Synonym: *Podospora pauciseta* (Ces.) Traverso, Fl. ital. crypt., Fungi 2: 431. 1907.

Micromorphology: Ascomata superficial, iron grey to fuscous black in reflected light, solitary to aggregated, ampulliform with a short and black beak, ostiolate, 310–685 µm high, 220–440 µm diam. *Ascomatal wall* brown, semi-translucent, composed of irregular or angular cells. *Ascomatal hairs* arising from the lower half of ascomata, erect or flexuous, subhyaline to pale brown, 1.5–3 µm diam near base, up to 200 µm long. *Asci* fasciculate, cylindrical, apically attenuated, without conspicuous apical ring, spore-bearing part 124–164 × 18.5–24.5 µm, stalks 30–55 µm long, containing four uniseriate ascospores, persistent. *Ascospores* composed of a olivaceous brown cell and a hyaline and cylindrical primary appendage when mature, of which the pigmented cell is ellipsoidal, (30–)31–36(–38) × (14.5–)16–19 µm, with an apical or slightly subapical germ pore and often geminating at or near apex to form a hyaline secondary appendage; the primary appendage at the opposite end, 25–37 × 4.5–6.5(–8) µm. *Asexual morph* cladorrhinum-like (*fide* Mirza & Cain 1969 and Boucher *et al.* 2017): *Conidiophores* micronematous, reduced to conidiogenous cells. *Conidiogenous cells* intercalary, originating lateral peg-like structure with a flaring collarette, producing blastic conidia. *Conidia* single-celled, hyaline, smooth, globose to ovoid, usually with a truncated base and a rounded apex, 1.5–2.5 µm diam.

Culture characteristics: On OA with a crenate edge, 29–35 mm diam in 7 d at 25 °C, without aerial mycelium, obverse vinaceous buff to olivaceous grey due to pigmented hyphae and coloured exudates diffusing into the medium, reverse pale mouse grey to mouse grey. On CMA similar to those on OA, but less sporulating, obverse olivaceous to fuscous black. On MEA with a lobate edge, 23–29 mm diam in 7 d at 25 °C, obverse presenting smoke grey aerial mycelium and olivaceous black ascomata, reverse greenish grey. On PCA with a slightly crenate edge, 25–31 mm diam in 7 d at 25 °C, without aerial mycelium; obverse pale olivaceous grey, reverse uncoloured.

Material examined: **Argentina**, Buenos Aires, Km 38, isolated from dung of cow, date unknown, J.E. Wright (CBS 451.62).

Note: This species has been typified by Boucher *et al.* (2017). We did not study the ex-epitype CBS 237.71, but the phylogenetic analyses indicated that our examined strain (CBS 451.62) clusters with the ex-type of *Trian. pauciseta* in the same species lineage (Fig. 6). *Triangularia pauciseta* and the other species in the "*Podospora anserina/pauciseta/comata* species complex" (Boucher *et al.* 2017) are mainly characterised by 4-spored cylindrical asci, 1-celled ascospores with a hyaline primary appendage at base and a secondary appendage at or near apex.

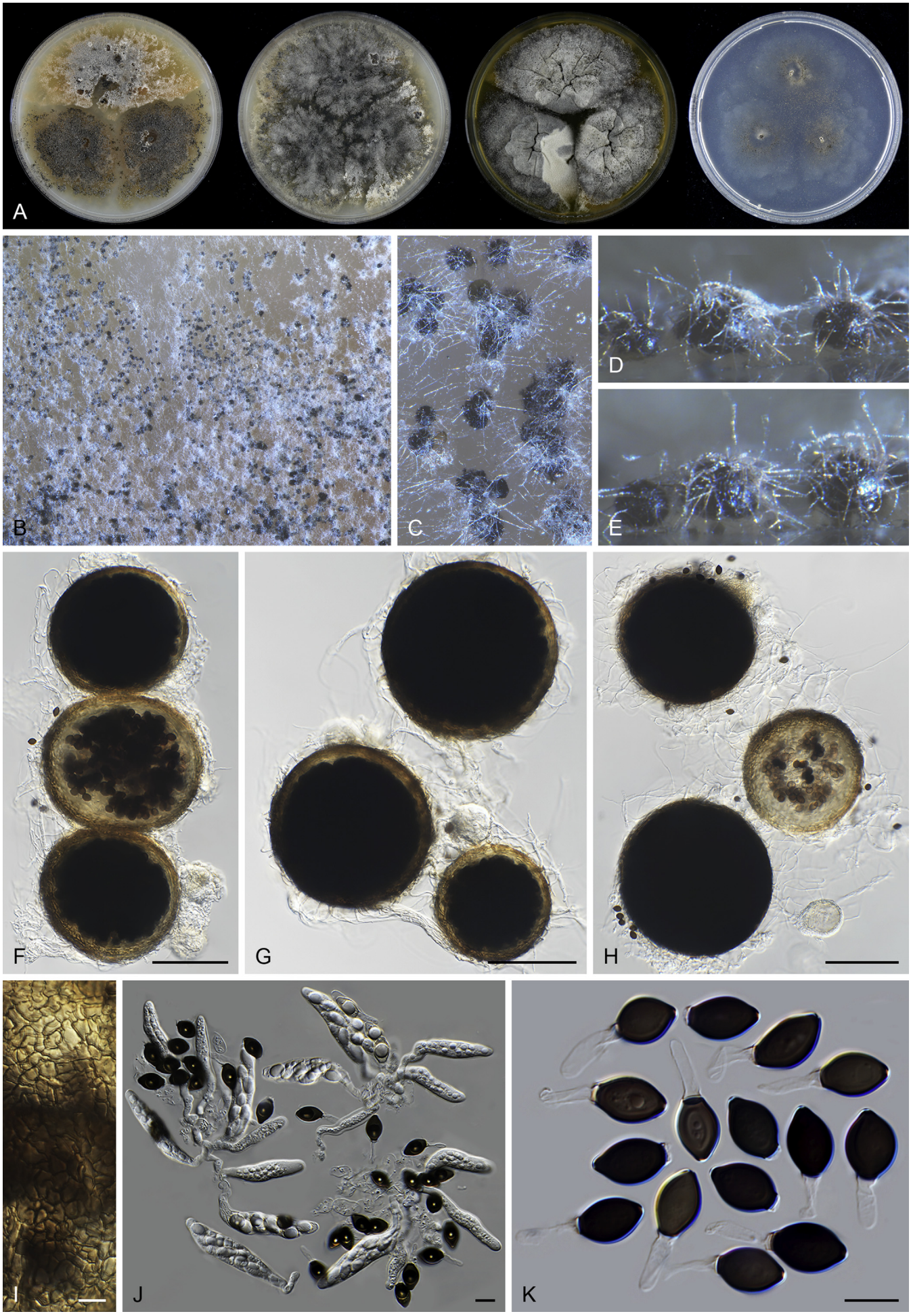

Fig. 53. *Triangularia longicaudata* (CBS 252.57, ex-type culture). **A.** Colonies from left to right on OA, CMA, MEA and PCA after 3 wk incubation. **B.** Part of the colony on OA. **C.** Mature ascomata on OA, top view. **D–E.** Mature ascomata on OA, side view. **F–H.** Ascomata mounted in lactic acid. **I.** Structure of ascomatal wall in surface view. **J.** Asci. **K.** Ascospores. Scale bars: F–H = 100 µm; I–K = 10 µm.

Fig. 54. *Triangularia pauciseta* (CBS 451.62). **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–E.** Ascomata mounted in lactic acid. **F–G.** Asci. **H.** Ascospores. Scale bars: D–E = 100 µm; F = 50 µm; G = 20 µm; H = 10 µm.

These characters can be used to differentiate the species in this species complex from the other known species in the genus.

Triangularia phialophoroides (Mouch. & W. Gams) X. Wei Wang & Houbraken, ***comb. nov.*** MycoBank MB829891. Fig. 55.
Basionym: *Cladorrhinum phialophoroides* Mouch. & W. Gams, Mycotaxon 48: 428. 1993.

Micromorphology: *Sexual morph* not observed. *Somatic hyphae* hyaline, 1.5–5 µm wide. *Conidiophores* phialidic, terminally or laterally arising from aerial hyphae, 7–20 × 2–3 µm, or reduced to intercalary conidiogenous cells that produce lateral blastic conidia. *Conidia* single-celled, hyaline, smooth, broad obovoid, ellipsoidal, elongated ellipsoidal or cylindrical, usually with a truncated base and a rounded apex, 2.5–3.5(–4) × 1.5–2.5 µm.

Culture characteristics: On OA with a slightly crenate edge, 25–31 mm diam after 7 d at 25 °C, obverse dark mouse grey due to pigmented sclerotial masses immerged in the medium, with sparse aerial mycelium, reverse mouse. On CMA similar to those on OA. On MEA with a crenate edge, 18–24 mm diam after 7 d at 25 °C, obverse pale mouse grey due to aerial mycelium and conidia, reverse greenish black. On PCA translucent, with a crenate edge, 22–28 mm diam after 7 d at 25 °C, without sparse aerial mycelium, obverse pale mouse grey, reverse uncoloured.

Typus: **Egypt**, New Valley region, Western Desert, isolated from desert sand soil, 24 Aug. 1990, J. Mouchacca (culture ex-type CBS 301.90).

Notes: This species clustered in the *Triangularia* lineage in both *rpb2* and combined four-locus phylogenetic analyses (*rpb2*: PP = 1, ML-BS = 100 %; Fig. 2 and the four-locus tree: PP = 0.99, ML-BS = 100 %; Fig. 3). No sexual morph was observed in our analysis. On the other hand, we have observed that several sexual species in the re-defined genus *Triangularia* produce cladorrhinum-like asexual structures.

Triangularia pseudoanserina (C. Boucher, T.S. Nguyen & Silar) X. Wei Wang & Houbraken, ***comb. nov.*** MycoBank MB829890.
Basionym: *Podospora pseudoanserina* C. Boucher, T.S. Nguyen & Silar, Cryptog. Mycol. 38: 497. 2017.

Description and illustrations: See Boucher *et al.* (2017) and *Triangularia pauciseta* (present study).

Notes: This species is accepted and transferred to the genus *Triangularia*. For additional information, see notes *Trian. bellae-mahoneyi*.

Triangularia pseudocomata (C. Boucher, T.S. Nguyen & Silar) X. Wei Wang & Houbraken, ***comb. nov.*** MycoBank MB829892.
Basionym: *Podospora pseudocomata* C. Boucher, T.S. Nguyen & Silar, Cryptog. Mycol. 38: 498. 2017.

Description and illustrations: See Boucher *et al.* (2017) and *Triangularia pauciseta* (present study).

Notes: This species is accepted and transferred to the genus *Triangularia*. For additional information, see notes *Trian. bellae-mahoneyi*.

Triangularia pseudopauciseta (C. Boucher, T.S. Nguyen & Silar) X. Wei Wang & Houbraken, ***comb. nov.*** MycoBank MB829893.
Basionym: *Podospora pseudopauciseta* C. Boucher, T.S. Nguyen & Silar, Cryptog. Mycol. 38: 498. 2017.

Description and illustrations: See Boucher *et al.* (2017) and *Triangularia pauciseta* (present study).

Notes: *Triangularia pseudopauciseta* is accepted and transferred to the genus *Triangularia*. For additional information, see notes *Trian. bellae-mahoneyi*.

Triangularia setosa (G. Winter) X. Wei Wang & Houbraken, ***comb. nov.*** MycoBank MB829894. Fig. 56.
Basionym: *Sordaria setosa* G. Winter, Abh. Naturf. Ges. Halle 13: 97. 1873.
Synonym: *Philocopra setosa* (G. Winter) Sacc., Syll. Fung. 1: 249. 1882.
Podospora setosa (G. Winter) Niessl, Hedwigia 22: 156. 1883.
Pleurage setosa (G. Winter) Kuntze, Revis. Gen. Pl. 3: 505. 1898.
Cladochaete setosa (G. Winter) Sacc., Ann. Mycol. 10: 318. 1912.

Micromorphology: Ascomata superficial, mouse grey in reflected light, solitary, ovoid to ampulliform with a short and black beak, ostiolate, 230–590 µm high, 185–410 µm diam. *Ascomatal wall* brown, opaque, of *textura intricata* or *epidermoidea* in surface view. *Ascomatal hairs* arising mainly around the lower half part, hypha-like, erect or flexuous, brown, 1.5–3 µm diam near base. *Asci* fasciculate, fusiform or elongated fusiform, spore-bearing part 145–238 × 25–49(–57) µm, without a conspicuous apical ring, with stalks 21.5–62 µm long, containing numerous irregularly- and densely-arranged ascospores, evanescent or persistent until ascospores mature. *Ascospores* composed of a olivaceous brown cell and a hyaline, cylindrical primary appendage when mature, of which the pigmented cell ellipsoidal, usually with attenuated ends, (15–)17–20.5(–22) × (9–) 10.5–12(–12.5) µm, with an apical germ pore, the primary appendage at the opposite end, 8–12 × 2–3 µm. *Asexual morph* not observed.

Culture characteristics: On OA with an entire edge, 24–30 mm diam in 7 d at 25 °C, without aerial mycelium, obverse vinaceous buff with sparse ascomata mainly along the edge, reverse hazel. On CMA similar to those on OA. On MEA with a fimbriate edge, 18–24 mm diam in 7 d at 25 °C, obverse grey white to vinaceous buff due to aerial mycelium, with numerous ascomata on the surface, reverse saffron to orange. On PCA with a slightly crenate edge, 21–27 mm diam in 7 d at 25 °C, without aerial mycelium, reverse uncoloured.

Material examined: **UK**, Lakenheath Warren, isolated from soil, 1949, J.H. Warcup (CBS 311.58 = LSHTM BB244); isolated from dung of horse, Dec. 1957, C.T. Ingold (CBS 369.59).

Notes: *Triangularia setosa* produces ascospores similar to those of *Trian. longicaudata* in shape, but can be distinguished from the latter species by multi-spored asci (containing more than 64 ascospores) and larger ascospores (17–20.5 × 10.5–12 µm *vs* 12–14.5 × 8–9 µm). For more characters that can be used for morphological comparisons, see notes of *Trian. bambusae*. In the morphologically-defined *Podospora*, species seem to be highly diverse in the number of ascospores in an ascus, including those with 4-spored, 8-spored, 16-spored, 32-spored, 64-spored, 128-spored, 156-spored, 256-spored, 512-spored and 1024-spored asci (Cain 1962, Mirza & Cain 1969). More work is needed to assess the relationships of those species with asci containing different numbers of ascospores. The holotype of the basionym *Sordaria setosa* was collected from goose dung in Leipzig, Germany, and needs to be examined.

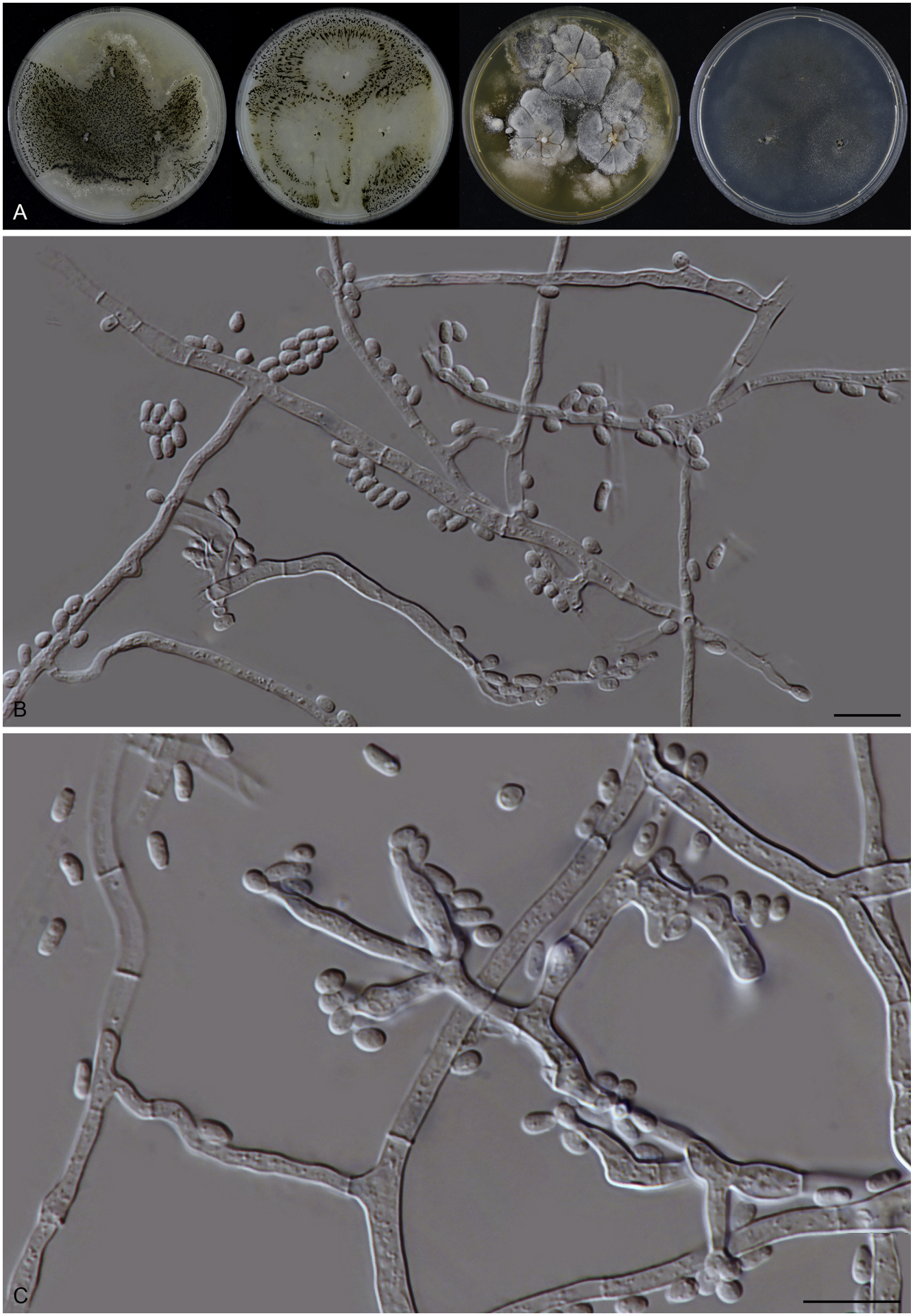

Fig. 55. *Triangularia phialophoroides* (CBS 301.91, ex-type culture). **A.** Colonies from left to right on OA, CMA, MEA and PCA after 3 wk incubation. **B–C.** Hyphae, conidiogenous cells and conidia. Scale bars: B–C = 10 µm.

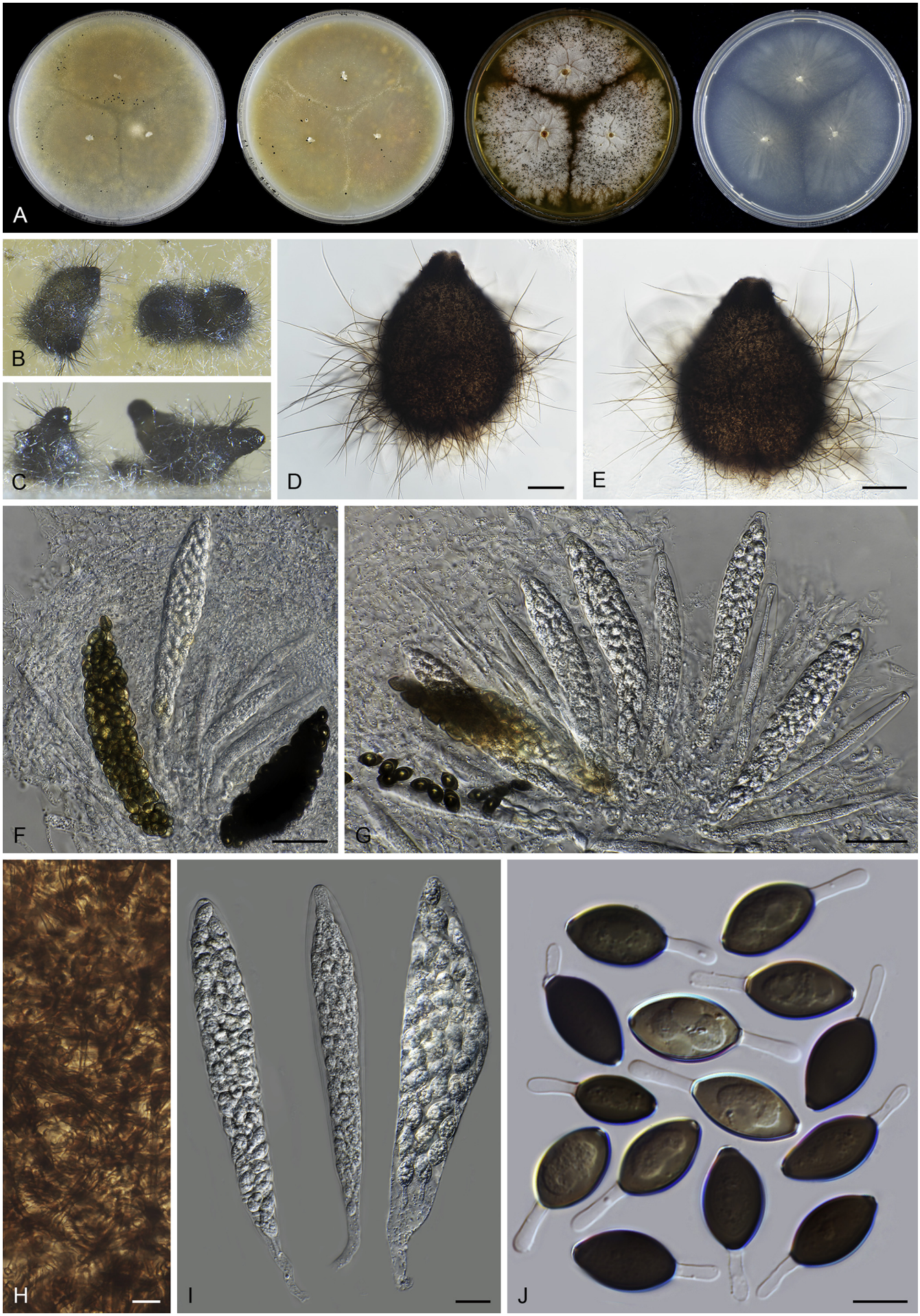

Fig. 56. *Triangularia setosa* (CBS 311.58). **A.** Colonies from left to right on OA, CMA, MEA and PCA after 3 wk incubation. **B.** Mature ascomata on OA, top view. **C.** Mature ascomata on OA, side view. **D–E.** Ascomata mounted in lactic acid. **F, G, I.** Asci. **H.** Structure of ascomatal wall in surface view. **J.** Ascospores. Scale bars: D–E = 100 µm; F–G = 50 µm; H, J = 10 µm; I = 20 µm.

Triangularia verruculosa (C.N. Jensen) X. Wei Wang & Houbraken, ***comb. nov.*** MycoBank MB829895. Fig. 57.
Basionym: *Pleurage verruculosa* C.N. Jensen, Bull. Cornell Univ. Agric. Exp. Sta 315: 472. 1912.
Synonym: *Apiosordaria verruculosa* (C.N. Jensen) Arx & W. Gams, Nova Hedwigia 13: 201. 1967.

Micromorphology: Ascomata superficial to semi-immersed, ostiolate, obpyriform to ampulliform with a papilla-like dark-brown to black beak, 230–340 µm high, 160–260 µm wide, usually with brown setae near the ostiole. *Ascomatal wall* coriaceous, opaque, brown. *Asci* cylindrical, with an apical ring, spore-bearing part 75–115 × 12–18.5 µm, with stalks 19–53 µm long, containing (two to) four uniseriate ascospores, evanescent, often persistent until ascospores mature. *Ascospores* 2-celled, unequally fusiform, umbonate at both ends, (23–) 25.5–28.5(–29.5) µm long, composed of an upper olivaceous brown cell and a lower vinaceous buff cell when mature, of which the upper cell is ornamented with spines up to 2 µm long, (15.5–)18–20 × (12.5–)13–14 µm, with an apical germ pore; and the lower cell smooth, (7–) 8–9.5(–10) × (7–)7.5–8.5(–9) µm. *Asexual morph* cladorrhinum-like (*fide* Mouchacca & Gams 1993): *Conidiophores* micronematous, reduced to conidiogenous cells. *Conidiogenous cells* intercalary or occasionally terminal, originating lateral or terminal peg-like structure with a flaring collarette, producing blastic conidia. *Conidia* single-celled, hyaline, smooth, ovoid to ellipsoid, usually with a truncated base and a rounded apex, 3–3.5 × 2–2.5 µm.

Culture characteristics: On OA with an entire edge, over 70 mm diam after 7 d at 25 °C, with white aerial mycelium, obverse buff to olivaceous grey, reverse pale greenish grey to pale mouse grey. On CMA similar to those on OA. On MEA with an entire edge, over 70 mm diam after 7 d at 25 °C, obverse buff to straw due to aerial mycelium and conidia, with olivaceous grey margin due to ascomata, reverse greenish grey. On PCA an entire edge, over 70 mm diam after 7 d at 25 °C, with sparse aerial mycelium, obverse grey olivaceous to olivaceous grey, reverse olivaceous grey.

Material examined: **Japan**, Niyako-shi, isolated from soil, 2 Aug. 1974, K. Furuya (CBS 148.77 = NHL 2736 = SANK 10374).

Notes: *Apiosordaria verruculosa* is the type species of the genus *Apiosordaria*. This genus was also defined to possess 2-celled ascospores, and was considered to be different from *Triangularia* in the production of ellipsoidal to subglobose ascospores with an upper dark cell which is often ornamented with striate, pitted or verrucose walls, or covered by spines (Arx & Gams 1967, Guarro & Cano 1988). Our *rpb2* and four-locus phylogenetic analyses clearly indicated that *Apio. verruculosa* belongs to the *Triangularia* lineage. *Triangularia* (1934) has priority over *Apiosordaria* (1967), and this species is therefore transferred to the re-defined genus *Triangularia* here, and *Apiosordaria* is synonymized with *Triangularia*. The species remains to be typified.

Triangularia verruculosa is most closedly related to *Trian. allahabadensis*, *Trian. backusii*, *Trian.bambusae*, *Trian. longicaudata*, *Trian. setosa* and *Trian. verruculosa* (Figs 2, 3), but can be easily distinguished by its 2-celled ascospores with the upper cell ornamented with conspicuous spines. For more characters that can be used for morphological comparison, see notes of *Trian. bambusae*.

Sordariaceae

Boothiella Lodhi & J.H. Mirza, Mycologia 54: 217. 1962.

Micromorphology: *Ascomata* superficial to immersed in the medium, solitary to aggregated, non-ostiolate, globose to subglobose. *Ascomatal wall* hyaline, translucent. *Asci* cylindrical, containing four uniseriate ascospores, evanescent. *Ascospores* olivaceous brown when mature, smooth, 1-celled, with apical germ pores. *Asexual morph* not observed.

Type species: *Boothiella tetraspora* Lodhi & J.H. Mirza.

Note: Boothiella is a monotypic genus which was thought to be related to *Thielavia*, but separated from this genus based on its colourless ascomatal wall (Lodhi & Mirza 1962). Later, Eriksson *et al.* (2004) and Kirk *et al.* (2008) classified this genus in the *Sordariaceae*; however, more recently Maharachchikumbura *et al.* (2015, 2016) placed this genus in the *Chaetomiaceae*. Comparison of ITS and LSU (D1/D2 domain) sequences obtained from CBS 334.67 (Vu *et al.* 2019) showed that *Boothiella tetraspora* belongs to the *Sordariaceae*. Our phylogenetic analyses based on *rpb2* and four-locus datasets robustly confirmed the result of Vu *et al.* (2019).

Boothiella tetraspora Lodhi & J.H. Mirza, Mycologia 54: 217. 1962. Fig. 58.
Synonyms: *Thielaviella humicola* Arx & T. Mahmood, Trans. Brit. Mycol. Soc. 51: 611. 1968.
Thielavia tetraspora (Lodhi & Mirza) Arx, The genera of fungi sporulating in pure culture. 115. 1974.

Micromorphology: Ascomata superficial to immersed in the medium, solitary to aggregated, non-ostiolate, globose to subglobose, leaden black when mature in reflected light due to the dark ascospores inside, glabrous, 115–390 µm diam. *Ascomatal wall* subhyaline, translucent, composed of *textura epidermoidea* in surface view. *Asci* cylindrical, spore-bearing part 44–70 × 11.5–17 µm, with stalks 8–26 µm long, without apical structure, containing four uniseriate ascospores, evanescent. *Ascospores* 1-celled, olivaceous brown when mature, smooth, ellipsoidal to broad ovoid, (16.5–)17.5–22(–26.5) × 13–15(–17.5) µm, with an apical germ pore. *Asexual morph* not observed.

Culture characteristics: On OA with an entire edge, over 70 mm diam after 7 d at 25 °C, texture floccose, obverse buff to honey due to aerial mycelium mixed with masses of young ascomata, later becoming umber due to the mature ascomata, reverse buff to ochraceous. On CMA similar to those on OA. On MEA with an entire edge, over 70 mm diam after 7 d at 25 °C, texture floccose, obverse buff to ochraceous due to aerial mycelium mixed with masses of ascomata, reverse umber. On PCA translucent, with an entire edge, over 70 mm diam after 7 d at 25 °C, without or with sparse aerial mycelium, reverse uncoloured.

Material examined: **India**, Kanpur, isolated from soil, 5 Nov. 1995, J. Guarro (CBS 887.97 = FMR 6192). **Pakistan**, Lahore area, isolated from barley field soil, date unknown, S.H. Iqbal (CBS 334.67 = IMI 291723 = MUCL 11462, culture ex-isotype of *Thielaviella humicola*).

Notes: *Boothiella tetraspora* possesses glabrous and subglobose ascomata with subhyaline and translucent ascomatal wall, resembling *Hya. fragilis* and *Pse. subhyaloderma* in the

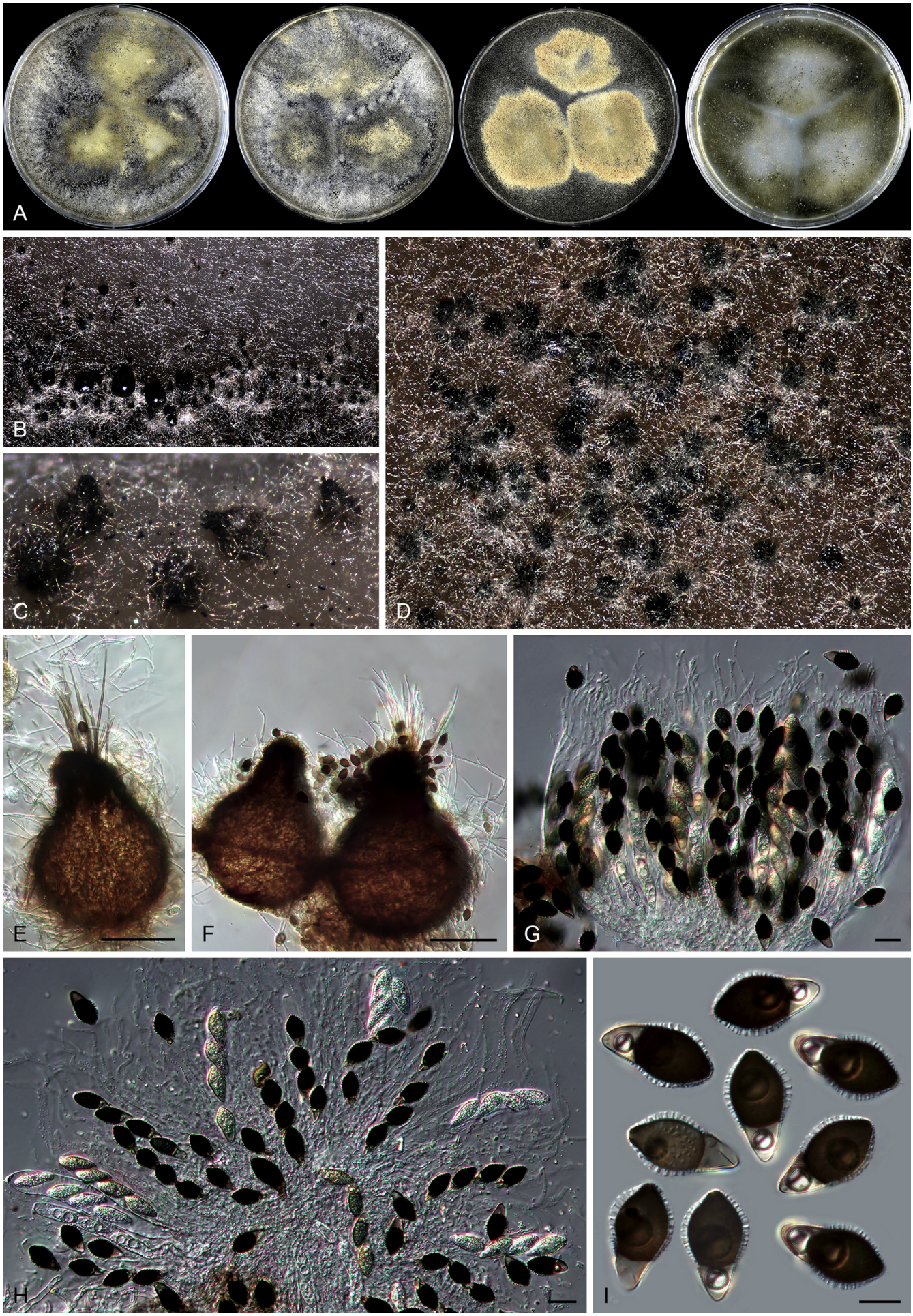

Fig. 57. *Triangularia verruculosa* (CBS 148.77). **A.** Colonies from left to right on OA, CMA, MEA and PCA after 4 wk incubation. **B.** Part of the colony on OA. **C.** Mature ascomata on OA, side view. **D.** Mature ascomata on OA, top view. **E–F.** Ascomata mounted in lactic acid. **G–H.** Asci. **I.** Ascospores. Scale bars: E–F = 100 µm; G–H = 20 µm; I = 10 µm.

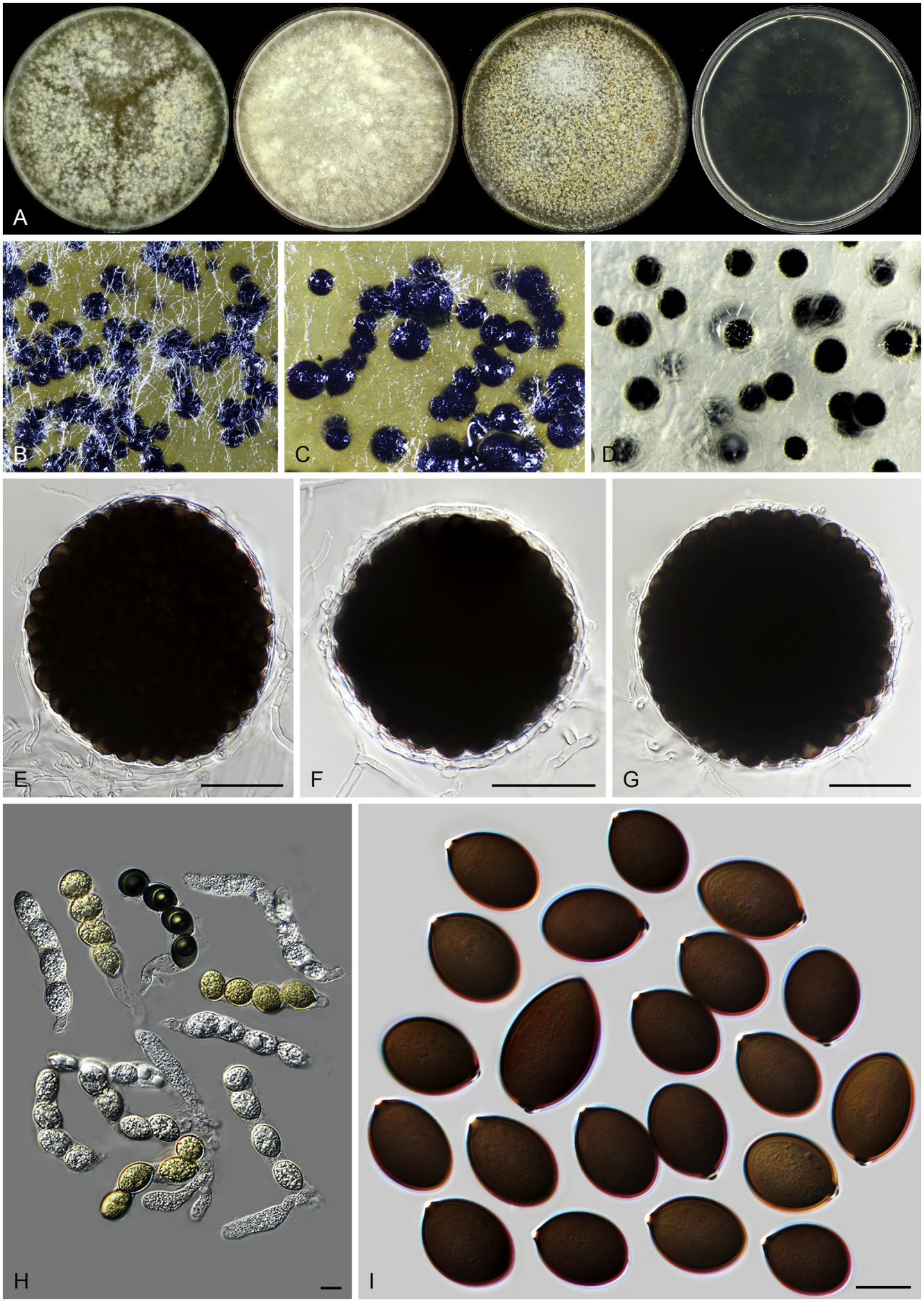

Fig. 58. *Boothiella tetraspora* (CBS 887.97). **A.** Colonies from left to right on OA, CMA, MEA and PCA after 4 wk incubation. **B.** Part of the colony on OA. **C.** Mature ascomata on OA, top view. **D.** Mature ascomata on PCA, top view. **E–G.** Ascomata mounted in lactic acid. **H.** Asci. **I.** Ascospores. Scale bars: E–G = 50 µm; H–I = 10 µm.

Chaetomiaceae, but differs mainly in cylindrical and 4-spored asci. *Hyalosphaerella fragilis* can also be distinguished by smaller ascomata (50–115 µm *vs* 115–390 µm diam), clavate to pyriform asci, smaller and inequilaterally ovoid to reniform ascospores (11–13 × 6.5–7.5 µm *vs* 17.5–22 × 13–15 µm). *Pseudothielavia subhyaloderma* differs by smaller ascomata (60–185 µm *vs* 115–390 µm diam), clavate to pyriform asci and smaller and often irregular ascospores (10.5–13 × 7–8 µm *vs* 17.5–22 × 13–15 µm).

DISCUSSION

Thielavia basicola is neotypified and this species (and genus) is classified in the *Ceratostomataceae* (*Melanosporales*). The remaining 18 studied "*Thielavia*" species fall into two related family-level lineages in the *Sordariales*: the *Chaetomiaceae* and *Podosporaceae fam. nov.* (Figs 2, 3). Seventeen species that were previously classified in *Thielavia* are recognised in the *Chaetomiaceae*, including our previously combined *Trichocladium antarcticum* (Wang *et al.* 2019). These species belong to eleven genera, of which nine are newly described in the present study. The genera containing thielavia-like species are not all closely related to each other and they are mostly intermingled with other genera in the *Chaetomiaceae*. Six of the newly described genera are monotypic: three of them (*Carteria*, *Condenascus*, *Microthielavia*) are lone lineages without known close relatives; *Hyalosphaerella* clusters closely but separate from *Parathielavia* and *Pseudothielavia* within Clade 1; *Thermothielavioides* is closely related to the chaetomium-like ostiolate genus *Floropilus*; and *Stolonocarpus* is basal to *Madurella*. Furthermore, several species cluster within *Canariomyces*; *Chrysan. peruvianum* (syn. *Th. peruviana*) groups with three chaetomium-like ostiolate species in *Chrysanthotrichum*, and *Trich. antarcticum* (syn: *Th. antarctica*) falls in the morphologically diverse genus *Trichocladium*. These results show that the thielavia-like (non-ostiolate, glabrous, setose or tomentose ascomata with a thin wall composed of *textura epidermoidea*) is a homoplastic structure that originated from several separate evolutionary events, similar to what happened in the chaetomidium-like ascomata (Greif *et al.* 2009, Wang *et al.* 2016b). According to Index Fungorum and MycoBank, there are 26 more species which were described in *Thielavia*, but no strains of those species are available in the present study. They are likely to be distant from *Thielavia sensu stricto* because none of them are known to grow in association with any other fungus. Their exact position in the current classification of *Chaetomiaceae* (or other families) remains to be studied in future. As mentioned in the introduction, the morphologically defined *Thielavia* exhibits a diverse ecology. It is required to further study the influence of ecological factors on the divergence of thielavia-like species.

Three re-defined genera are currently classified in the newly proposed family *Podosporaceae*. Based on some previous studies and our phylogenetic analyses, several morphological defined genera in the *Lasiosphaeriaceae* appear to be polyphyletic. For example, the genus *Cladorrhinum* is phylogenetically restricted to the type species (*Clad. foecundissimum*), and also includes two thielavia-like species in which no asexual state was observed. On the other hand, the cladorrhinum-form asexual state has also been reported in several sexually reproducing species, such as *Apiosordaria verruculosa* (von Arx & Gams 1967), *Cercophora samala* (Udagawa & Muroi 1979), *Cercophora striata* (Miller & Huhndorf 2001) and *Podospora fimicola* (Bell & Mahoney 1997). The family *Podosporaceae* corresponds to clade A of Cai *et al.* where species with a cladorrhinum-like asexual state grouped in their Clade A (Cai *et al.* 2006). Our observation supported the study of Cai *et al.* (2006), although we did not include *Cercophora* species in this study, and did not carefully examine the cladorrhinum-like state in all the studied species. The morphologically defined genus *Podospora* is one of the largest genera in the *Lasiosphaeriaceae* and is mainly characterised by producing ascospores with an apical germ pore, a basal hyaline cell, and gelatinous appendages (Mirza & Cain 1969). Nearly 200 species have been described in this genus according to Index Fungorum and MycoBank. Numerous previous studies have provided phylogenetic evidence that the morphologically defined *Podospora* is polyphyletic and taxonomic confusion between this genus and several other genera in the *Lasiosphaeriaceae* exists (Huhndorf *et al.* 2004, Cai *et al.* 2005, Miller & Huhndorf 2005, Cai *et al.* 2006, Zhang *et al.* 2006, Kruys *et al.* 2015). Based on our *rpb2* phylogeny (Fig. 2), the morphologically defined *Podospora* species are distributed over at least seven generic- or even higher-level clades and this confirms that a revision of *Podospora* is necessary. We restrict *Podospora* to a small clade containing the type species *Pod. fimicola* and *Pod. bulbillosa*, an asexually reproducing species which was originally described as *Cladorrhinum bulbillosum*.

The genera *Triangularia* and *Apiosordaria* were defined mainly based on their differences in ascospores morphology. *Triangularia* was characterised by having ascospores composed of two cells: the upper cell is dark and conical or triangular shaped and has a germ pore, and the lower cell is hyaline and triangular or hemisphaerical shaped (Guarro & Cano 1988). The upper cells of the 2-celled ascospores of *Apiosordaria* are also dark pigmented, but ellipsoidal to subglobose, and often ornamented with striate, pitted or verrucose walls (Arx & Gams 1967, Guarro & Cano 1988). In this study, the genus *Triangularia* is redefined, and includes nine species which were previously classified in *Apiosordaria*, *Cladorrhinum*, *Podospora*, *Triangularia* or *Zopfiella*. Our results indicate not only a highly diverse morphology in *Triangularia* (especially in the morphology of their ascospores), but also the polyphyly of the four other traditional genera. Aside from *Cladorrhinum* and *Podospora* (discussed above), the two *Apiosordaria* species included in our *rpb2* phylogram fall in two distant clades: the type species (*Apio. verruculosa*) is combined in *Triangularia* and belongs to the *Podosporaceae*, while *Apio. microcarpa* is related to *Zopfiella tardifaciens* and is classified in a different, maybe new family lineage. Similarly, *Zopfiella* species are scattered throughout the polyphyletic *Lasiosphaeriaceae*, and probably belong to four different family lineages. More work is required to re-evaluate the species of *Apiosordaria*, *Cercophora*, *Podospora*, and *Zopfiella*, as well as additional *Triangularia* species that were not involved in the present study.

Species delimitation is the basic work of taxonomy. *Triangularia anserina* (syn.: *Pod. anserina*) is a model species that has been widely used for over a century to study many biological and genetic phenomena (Silar 2013). Following the taxonomic criteria in our previous work in the *Chaetomiaceae* (Wang *et al.* 2016a, 2016b, 2019), we would have accepted *Trian. anserina* as a synonym of *Trian. pauciseta*, because there are no morphological differences or phylogenetic evidence based on ITS, LSU, *rpb2* or *tub2* sequences to distinguish both species. Boucher *et al.* (2017) recognised seven species in the *Podospora anserina/pauciseta/comata* species complex on the basis

of their phylogenetic analysis of ITS and three new intergenic loci. At the same time they stated that their recognised seven species appeared to poorly mate in culture, pointing towards biological species. ITS has poor resolution in differentiating species (Fig. 6A) and three uncommonly used intergenic loci (*Rchr3*, *Rchr4* and *Rchr6*) were able to differentiate the seven species in the species complex (Fig. 6B–D). Their data challenged to some extent our current phylogenetic delimitation of *Chaetomiaceae* species. It remains to study whether the markers commonly used in *Chaetomiaceae* for phylogeny (LSU, ITS, *tub2* and *rpb2*) and identification (*tub2*) have sufficient resolution in this species complex. There is an opposite situation in the *Chaetomiaceae* where species are phylogenetically indistinguishable but morphologically distinct. One example is the two species in *Pseudothielavia*: *Pse. terricola* and *Pse. arxii*, which are phylogenetically indistinguishable but produce morphologically distinct ascospores. A similar case occurs in *Ch. globosum* and *Ch. cruentum*. Wang *et al.* (2016b) treated *Ch. cruentum* as *Ch. globosum* with the morphological form '*cruentum*'; however, we now prefer to accepted them as separate species as well. Phylogenetic species recognition (PSR) is based on the consensus that "once progeny evolutionary species have formed from an ancestor, changes in gene sequences occur and can be recognized before changes have occurred in mating behavior or morphology" (Taylor *et al.* 2000). We prefer to use a polyphasic approach, combining phenotypic and molecular data, for the delimitation of species in *Chaetomiaceae*. More studies (*e.g.* other loci, genome data) are needed for sufficient recognition of species in the *Chaetomiaceae*.

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