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A re-evaluation of the genus *Myceliophthora* (Sordariales, Ascomycota): its segregation into four genera and description of *Corynascus fumimontanus* sp. nov.

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Abstract: Based on a number of isolates of *Myceliophthora* (Chaetomiaceae, Sordariales, Ascomycota) recently isolated from soil samples collected in USA, the taxonomy of the genus was re-evaluated through phylogenetic analyses of sequences from the nuc rDNA internal transcribed spacer region and genes for the second largest subunit of RNA polymerase II and translation elongation factor 1α. Members of *Myceliophthora* were split into four monophyletic clades strongly supported by molecular and phenotypic data. Such clades correspond with *Myceliophthora*, now restricted only to the type species of the genus *Corynascus*, which is re-established with five species, the new monotypic genus *Crassicarpon* and also the new genus *Thermothelomyces* (comprising four species). *Myceliophthora lutea* is mesophilic and a permanently asexual morph compared to the members of the other three mentioned genera, which also are able to sexually reproduce morphs with experimentally proven links to their asexual morphs. The asexual morph of *M. lutea* is characterized by broadly ellipsoidal, smooth-walled conidia with a wide, truncate base. *Crassicarpon thermophilum* is thermophilic and heterothallic and produces spherical to cuneiform, smooth-walled conidia and cleistothecial ascomata of smooth-walled, angular cells and ascospores with a germ pore at each end. *Corynascus* spp. are homothallic and mesophilic and produce spherical, mostly ornamented conidia and cleistothecial ascomata with textura epidermoidea composed of ornamented wall cells, and ascospores with one germ pore at each end. *Thermothelomyces* spp. are thermophilic, heterothallic and characterized by similar ascomata and conidia as *Corynascus* spp., but its ascospores exhibit only a single germ pore. A dichotomous key to distinguish *Myceliophthora* from the other mentioned genera are provided, as well as dichotomous keys to identify the species of *Corynascus* and *Thermothelomyces*. A new species, namely *Corynascus fumimontanus*, characterized by verrucose ascomatal wall cells and irregularly shaped ascospores, is described and illustrated.

Key words: Chaetomiaceae, *Crassicarpon*, Pezizomycotina, soilborne fungi, *Thermothelomyces*

Introduction

Myceliophthora spp. (Chaetomiaceae, Sordariales) traditionally were characterized by the production of one-celled, subhyaline to reddish brown, smooth-walled to verrucose, globose to pyriform blastoconidia, sessile or arising on swollen protrusions from the vegetative hyphae, solitary or in short chains, and show a narrow basal scar due to their rhexolytic dehiscence (Oorschot 1980). Mycelia and conidia of *Myceliopthora* spp. are mostly hyaline or nearly so, with the only exception of the conidia of *Myceliophthora hinnulea*, which become dark brown with age, and the mycelium of *Myceliopthora vellerea*, which is pale brown. The conidiogenesis in *Myceliophthora* spp. is similar among them, producing holoblastic conidia, sessile (frequently named as aleuroconidia) or on micronematous to semimicronematous conidiophores, mostly solitary but also grouped in short chains of 2–4 conidia. Sessile holoblastic conidia are also present in other members of the family Chaetomiaceae, that is *Thielavia arenaria*, *Thielavia microspora* and *Thielavia subthermophila* (Mouchacca 1973). *Myceliophthora* spp. are mostly found in soil but they also have been reported on compost used for growing mushrooms (Costantin and Matruchot 1894), some species being parasites of mushrooms (Costantine 1892) and rarely infecting human (Hoog et al. 2000).

The genus *Myceliophthora* was erected by Costantin (1892) to accommodate the mycoparasitic fungus *Myceliophthora lutea*, characterized by pyriform to globose conidia born terminally or laterally on aerial

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hyphae, sometimes with a basal short pedicel, and occasionally producing an additional apical conidium. Later three new species were added to the genus, they are *Myceliophthora sulphurea* Goddard (Goddard 1913), *Myceliophthora fusca* Doyer (Doyer 1927) and *Myceliophthora inflata* Burnside (Burnside 1928). van Oorschot (1977, 1980) revised the genus and transferred three additional species, *Myceliophthora fergusii* (Klopotek) Oorschot and *Myceliophthora thermophila* (Apinis) Oorschot from *Chrysosporium* and *Myceliophthora vellerea* (Sacc. & Speg.) Oorschot from *Sporotrichum*. The same author excluded *M. fusca*, *M. inflata* and *M. sulphurea* from the genus. *Myceliophthora fusca* was thought to be identical to *Ptychogaster rubescens* Boud., the anamorph of the basidiomycete *Punctularia atropurpurascens* (Berk. & Br.) Petch; *M. inflata* was synonymized with *Taifanglania inflata* (Burnside) Z.Q. Liang, Y.F. Han & H.L. Chu; and *M. sulphurea* was found indistinguishable from *Chrysosporium merdarium* (Ehrenb.) J.W. Carmich. More recently *Myceliophthora hinnulea* Awao & Udagawa (Awao and Udagawa 1983) was described.

The sexual morphs of *Myceliophthora* have been included in several genera belonging to different orders and even classes, *Arthroderma* (*Arthroderma tuberculatum* Kuehn; order Onygenales; class Eurotiomycetes), *Corynascus* (*Corynascus* spp.; order Sordariales; class Sordariomycetes) and *Ctenomyces* (*Ctenomyces serratus* Eidam; order Onygenales; class Eurotiomycetes) (Oorschot 1980, Guarro et al. 1985, Stchigel et al. 2000). Some of these sexual morphs from heterothallic species have been obtained in vitro by crossing sexually compatible strains, as is the case for *Arthroderma tuberculatum*, *Myceliopthora thermophila*/*Corynascus heterothallicus* and *Myceliophthora fergusii*/*Corynascus thermophilus* (Klopotek 1974, 1976). On the other hand, crossings of isolates of *Myceliophthora gutulata*, *Myceliophthora hinnulea* and *Myceliophthora lutea* have never been reported to produce their sexual stage. The homothallic species of *Corynascus* produced ascomata in monospore cultures on several culture media (von Arx et al. 1984; Oorschot 1980). *Myceliophthora* spp. linked with their sexual morph have never been treated as a *Myceliophthora*-like asexual stage.

The genus *Corynascus* was proposed by von Arx in 1973 based on two species of *Thielavia* (i.e. *Thielavia novoguineensis* Udagawa & Y. Horie and *Thielavia sepedonium* C.W. Emmons) that possess ascospores with two germ pores, one at each end, as opposed to species of *Thielavia* that have only a single germ pore. Three additional species of *Thielavia* also were transferred under the same criteria to *Corynascus*, (i.e. *Thielavia heterothallica* Klopotek, *Thielavia setosa* Dade and *Thielavia thermophila* Fergus & Sinden Klopotek (Klopotek 1974, von Arx 1975, von Arx et al. 1984). In 1978 *Corynascus setosus* moved to *Chaetomidium* (Lodha 1978). In the current century, three new species have been included in *Corynascus* (i.e. *Corynascus sexualis* Stchigel, Cano & Guarro, *Corynascus similis* Stchigel, Cano & Guarro and *Corynascus verrucosus* Stchigel, Cano & Guarro [Stchigel et al. 2000]).

In a recent phylogenetic study (van den Brink et al. 2012), *Corynascus* spp. grouped together with the type species of *Myceliophthora* (*M. lutea*), and based on the current fungal nomenclature (McNeill et al. 2012), the name *Myceliophthora* was chosen while *Corynascus* was considered a synonym. In the same study *Myceliophthora vellerea* was placed far from *M. lutea*, clustering with *C. serratus* and *A. tuberculatum* in a different and phylogenetically distant clade (family Arthrodermataceae), being therefore excluded from *Myceliophthora*. *Myceliophthora* is restricted currently to those species belonging to the family Chaetomiaceae (Sordariales), characterized by the production of cleistothecial ascomata with an ascomata wall of textura epidermoidea, unitunicate asci and one-celled, ellipsoidal or broadly fusiform, brownish ascospores, usually with a distinct germ pore at each end (Stchigel et al. 2000, Guarro et al. 2012). Zhang et al. (2014) described the new species *Myceliophthora guttulata* Y. Zhang & L. Cai, from a soil sample in China. The following 11 species of *Myceliophthora* currently are accepted (i.e. the already mentioned *M. fergusii*, *M. guttulata*, *M. heterothallica*, *M. hinnulea*, *M. lutea*, *M. thermophila*, in addition to *M. novoguineensis* [Udagawa & Y. Horie] van den Brink & Samson, *M. sepedonium* [C.W. Emmons] van den Brink & Samson, *M. sexualis* [Stchigel, Cano & Guarro] van den Brink & Samson, *M. similis* [Stchigel, Cano & Guarro] van den Brink & Samson, and *M. verrucosa* [Stchigel, Cano & Guarro] van den Brink & Samson [van den Brink et al. 2012, Zhang et al. 2014]).

During a survey on soilborne ascomycetes from Great Smoky Mountains National Park (USA), several fungi belonging to *Myceliophthora* were isolated. Becausee some of these isolates could not be properly identified, a phylogenetic and phenotypic study was conducted to better define the boundaries between *Myceliophthora* and related genera, resulting in the proposal of two new genera and one new species.

MATERIALS AND METHODS

Soil sampling and isolation of fungi.—Soil samples were collected in Aug 2008 in Great Smoky Mountains National Park (35.60, −83.52), USA, located in Tennessee and North Carolina and containing more than 2100 square kilometres.

This area is mainly composed of cove hardwood, hemlock, northern hardwood, pine-oak and spruce-fir forests (Whittaker 1956) and includes more than 1570 species of vascular plants of which 130 are native trees (Sharkey 2001). To carry out the isolation of soilborne ascomycetes we followed a previously described protocol for activation of the dormant ascospores using acetic acid (Stchigel et al. 2001). Fungal structures of those specimens that developed in the primary cultures were examined under the stereomicroscope and transferred with a sterile needle to Petri dishes containing oatmeal agar (OA; oatmeal flakes, 30 g; agar-agar, 20 g; tap water, 1 L), and incubated at 15, 25 and 35 C.

Phenotypic study.—Fungal isolates were grown on OA, potato-carrot agar (PCA; grated potatoes, 20 g; grated carrot, 20 g; agar-agar, 20 g; L-chloramphenicol, 100 mg; 1% w/v dieldrin™ in dimethyl-ketone, 20 drops; tap water, 1 L) and potato dextrose agar (PDA; Pronadisa, Madrid, Spain) at 5, 15, 25, 30, 35, 40, 45 and 50 C. Color notations in parentheses in the species descriptions are from Kornerup and Wanscher (1984). Fertile fungal structures were mounted and measured in lactic acid. Photomicrographs were obtained with a Zeiss Axio Imager M1 light microscope. The scanning electron microscope (SEM) techniques used were described by Figueras and Guarro (1988). SEM micrographs were taken with a Jeol JSM 840 at 15 keV.

Phylogenetic studies.—DNA of the isolates was extracted and purified directly from fungal colonies according to the Fast DNA Kit protocol (MP Biomedicals, Solon, Ohio). The amplification of the internal transcribed spacer region (ITS) of the nuc rDNA (ITS1-5.8S-ITS2) and partial segments of the translation elongation factor 1-α (*EF*1) and RNA polymerase II (*RPB*2) loci was performed for all isolates, according to Cano et al. (2004) (ITS) and Houbraken et al. (2007) (*RPB*2 and *EF*1). The sequences of these amplicons were obtained with the protocol of the Taq Dye-Deoxy Terminator Cycle Sequencing Kit, and PCR products were purified and sequenced by Macrogen Europe (Amsterdam, the Netherlands) with a 3730XL DNA analyzer (Applied Biosystems). Consensus sequences were obtained with SeqMan (7.0.0; DNASTAR, Madison, Wisconsin), and the sequences were aligned with Clustal X 2.0 (Larkin et al. 2007) followed by manual adjustments with a text editor. Sequences retrieved from GenBank and included in these analyses are provided (TABLE I). The phylogenetic analyses was carried out with MEGA 5.21 of the combined dataset (ITS, *RPB*2, *EF*1) of our isolates, the type and reference strains of the accepted species of *Myceliophthora*, the type strain of *Corynascella inaequalis* and one strain of *Thielavia terricola*, *Chaetomidium arxii* and *Chaetomium globosum*, using the type strain of *Hypocrea aurantefussa* and a strain of *Nectria pseudotrichia* as outgroups, (Tamura et al. 2011). The combined dataset was tested for incongruence with the partition homogeneity test (PHT) as implemented in PAUP* (Swofford 2002). Maximum likelihood (ML) analysis was conducted on the dataset using the Tamura-Nei model, with gamma distribution and the pairwise deletion of gaps option. The robustness of branches was assessed by bootstrap analysis with 1000 replicates. Bayesian inference (BI) was carried out with MrBayes 3.1 following the parameters detailed in Alvarez et al. (2010). The sequences generated in this study are deposited in GenBank, and the alignments used in the phylogenetic analyses are deposited in TreeBASE: (www.treebase.org, accessionURL: http://purl.org/phylo/treebase/phylows/study/TB2:S16736).

RESULTS

The individual alignments used in the combined dataset were 473 bp (ITS), 634 bp (*EF1*) and 499 bp (*RPB2*), and the final total alignment was 1606 bp, 361 bp of which were parsimony informative. Because the result of the partition homogeneity test showed that the dataset for the three loci were congruent ($P = 0.508$), they were combined into a single dataset. ML analysis produced a single tree (FIG. 1). Three of our recently collected American isolates (CBS 137294, CBS 135878, CBS 137791) grouped in a main clade (71% bs and less than 0.95 bayesian posterior probability [pp]) with the type strains of *M. lutea*, *M. novoguineensis*, *M. sepedonium*, *M. sexualis* and *M. similis*. This clade was divided into two sister clades. The first one included the type strain and other strains of *M. lutea* (100% bs/1 pp), which were characterized by holoblastic, pyriform to globose, thick- and smooth-walled hyaline conidia, broadly truncate at the base, sometimes with a pedicel, borne terminally or laterally on aerial hyphae (FIG. 2). *Myceliophthora lutea* is mesophilic, with an optimal growth at 30–35 C. The second sister clade (99% bs/1 pp) grouped species that previously were included in *Corynascus*, including the type species of this genus. For this reason we think *Corynascus* should be re-established. Within the *Corynascus* spp. sister clade our isolate CBS 137294 formed a terminal branch, although at significant distance, together with *M. sexualis* (100% bs/1 pp). This isolate had both asexual and sexual morphs, the latter being characterized by cleistothecial ascomata with an ascomatal wall of textura epidermoidea composed of verrucose cells, and irregularly-shaped ascospores with a germ pore at each end. Its conidia were globose, yellowish and verrucose (FIG. 3). The optimal growth of this fungus was at 35–40 C. This combination of features does not match any known species. Its most closely related species, *M. sexualis*, can be differentiated by the absence of an asexual morph and ascomata composed of verrucose cells and limoniform ascospores. The type strains of *M. novoguineensis*, *M. sepedonium*, *M. sexualis*, *M. similis* and *M. verrucosa*, all grouped in the same clade, being characterized by their homothallism, in contrast with the members of the other clades, and by the production of

TABLE I. Isolates and reference strains of the genus *Myceliophthora* and related genera included in this study

Taxa	Strain	Source	GenBank accession Nos.		
			ITS	EF1	RPB2
Chaetomidium arxii	FMR 12364	Soil, Gran Canaria, Spain	KP204014[a]	KP204012[a]	KP204013[a]
Chaetomium globosum	CBS 148.51	Man, Greifswald, Germany	GU563374	KC485028	NT_165981
Corynascella inaequalis	CBS 331.75[T]	Soil, Kirovograd, Ukraine	KP204017[a]	KP204015[a]	KP204016[a]
Corynascus fumimontanus	CBS 137294[T] (=FMR 12372[T])	Soil, Great Smoky Mountains National Park, Tennessee	LK932694[a]	LK932719[a]	LK932733[a]
Corynascus novoguineensis	CBS 359.72[T]	Soil, Papua New Guinea	HQ871762	HQ871733	HQ871838
	NBRC 9556	Soil, unknown location	LK932698[a]	LK932716[a]	LK932731[a]
Corynascus sepedonium	CBS 111.69[T]	Soil, Uttar Pradesh, India	HQ871751	HQ871734	HQ871827
	CBS 632.67	Unknown source, Russia	HQ871759	HQ871744	HQ871830
	IMI 378521	Soil, Ajmer, India (ex-type strain of *Corynascus similis*)	AJ224201	LK932715[a]	LK932730[a]
Corynascus verrucosus	IMI 378522[T]	Soil, Quilmes, Argentina	AJ224203	LK932723[a]	LK932726[a]
	CBS 137791 (=FMR 12369)	Soil, Great Smoky Mountains National Park, Tennessee	LK932699[a]	LK932717[a]	LK932732[a]
	CBS 135878 (=FMR 12783)	Soil, Great Smoky Mountains National Park, Tennessee	LK932695[a]	LK932718[a]	LK932734[a]
Corynascus sexualis	IMI 378520[T]	Soil, Jaipur, India	AJ224202	LK932714[a]	LK932729[a]
Crassicarpon thermophilum	CBS 406.69[T]	Mushroom compost, Pennsylvania, USA; MT −	HQ871794	HQ871732	HQ871715
	CBS 405.69	Mushroom compost, Pennsylvania, USA; MT +	HQ871793	HQ871731	HQ871714
Hypocrea aurantefussa	CBS 119284[T]	Partly decorticated branches on ground, Weins, Austria	FJ860728	FJ860613	FJ860520
Myceliophthora lutea	CBS 145.77[T]	Hay, UK	HQ871775	HQ871722	HQ871816
	MUCL 10070	Unknown source, Natick, USA	LK932701[a]	LK932710[a]	LK932724[a]
	MUCL 10071	Unknown	LK932702[a]	LK932711[a]	LK932725[a]
Nectria pseudotrichia	CBS 641.83	Wood, Edo Tachira, Venezuela	HM534899	HM534878	HM534889
Thermothelomyces guttulata	CGMCC 3.15185[T]	Soil, China	KC352943	KC352946	KC352949
	CGMCC 3.15186	Soil, China	KC352944	KC352947	KC352950
Thermothelomyces heterothallica	CBS 202.75[T]	Garden soil, Germany	HQ871771	HQ871710	HQ871798
	CBS 203.75	Soil, Indiana, USA	HQ871772	HQ871711	HQ871800
	CBS 137789 (=FMR 13215)	Soil, Great Smoky Mountains National Park, Tennessee	LK932697[a]	LK932721[a]	LK932736[a]
	FMR 5174	Soil, Spain	LK932692[a]	LK932712[a]	LK932727[a]
	FMR 5175	Soil, Spain	LK932693[a]	LK932713[a]	LK932728[a]
Thermothelomyces hinnulea	CBS 597.83[T]	Cultivated soil, Japan	HQ871791	HQ871719	HQ871813
	CBS 544.82	Soil, New Zealand	HQ871790	HQ871718	HQ871812

TABLE I. Continued

Taxa	Strain	Source	GenBank accession Nos. ITS	EF1	RPB2
Thermothelomyces thermophila	CBS 117.65[T]	Dry pasture soil, UK	HQ871764	HQ871705	HQ871803
	CBS 381.97	Man, HIV positive patient, unknown location	HQ871766	HQ871707	HQ871805
Thielavia terricola	FMR 12786	Soil, Gran Canaria, Spain	LK932696[a]	LK932720[a]	LK932735[a]

[T] Type strains. [a] Sequences derived from this work. CBS = Centraalbureau voor Schimmelcultures, Utrecht, the Netherlands; CGMCC = China General Microbial Culture Collection, China; FMR = Facultat de Medicina, Reus, Spain; IMI = International Mycological Institute, England; MUCL = Belgian Co-ordinated Collections of Micro-organisms, Belgium; NBRC = Biological Resource Center, Chiba, Japan.

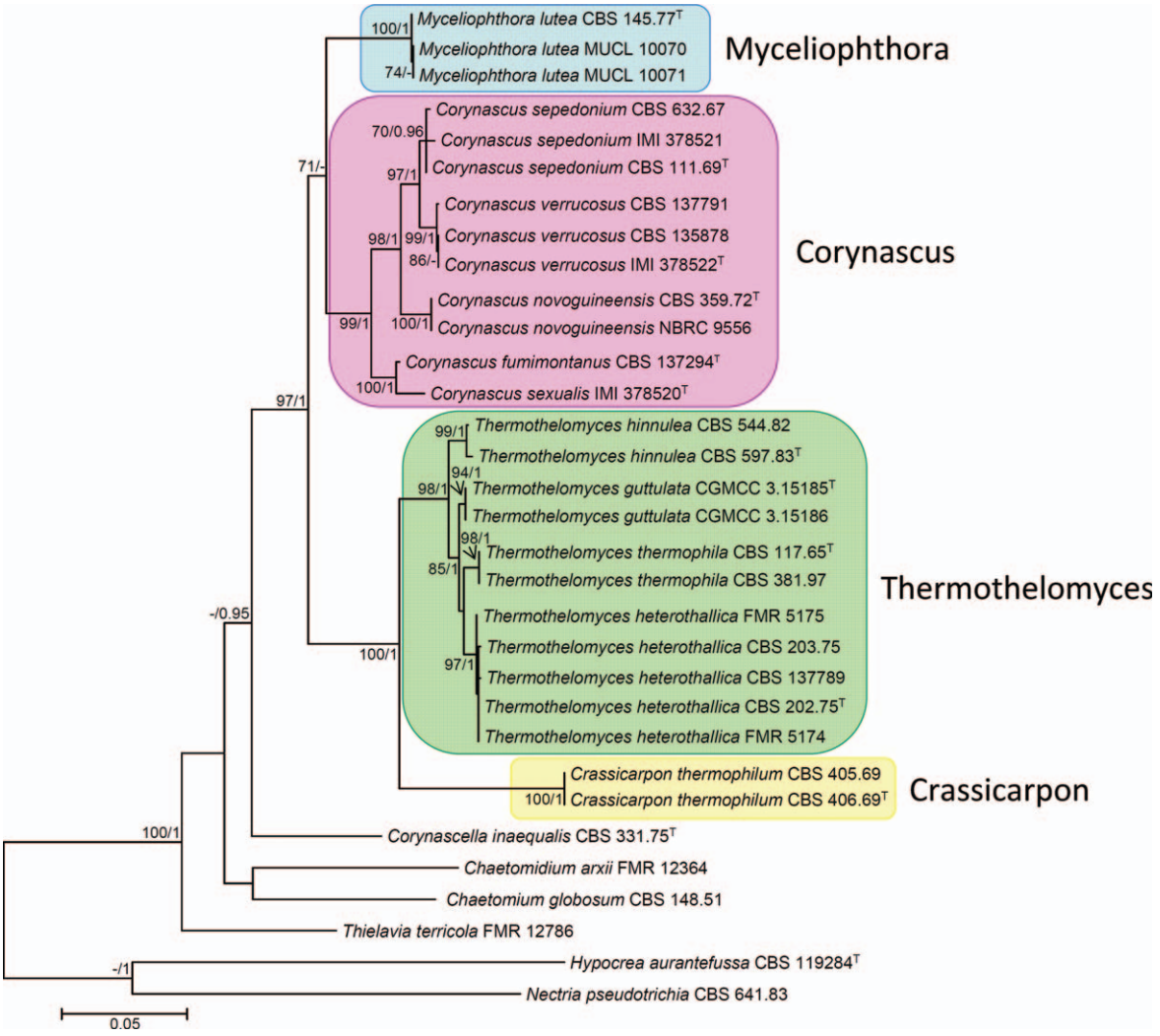

FIG. 1. Maximum-likelihood (ML) tree obtained from the combined DNA sequence data from three loci (ITS, *EF1* and *RPB2*) of our isolates, selected strains previously included in the genus *Myceliophthora*, the type strain of *Corynascella inaequalis* and one strain of *Thielavia terricola*, *Chaetomidium arxii* and *Chaetomium globosum*. The type strain of *Hypocrea aurantefussa* and a reference strain of *Nectria pseudotrichia* were used as outgroup. Bootstrap support values ≥ 70/Bayesian posterior probability scores ≥ 0.95 are indicated along branches. Branch lengths are proportional to distance. Type strains of the different species are indicated with [T].

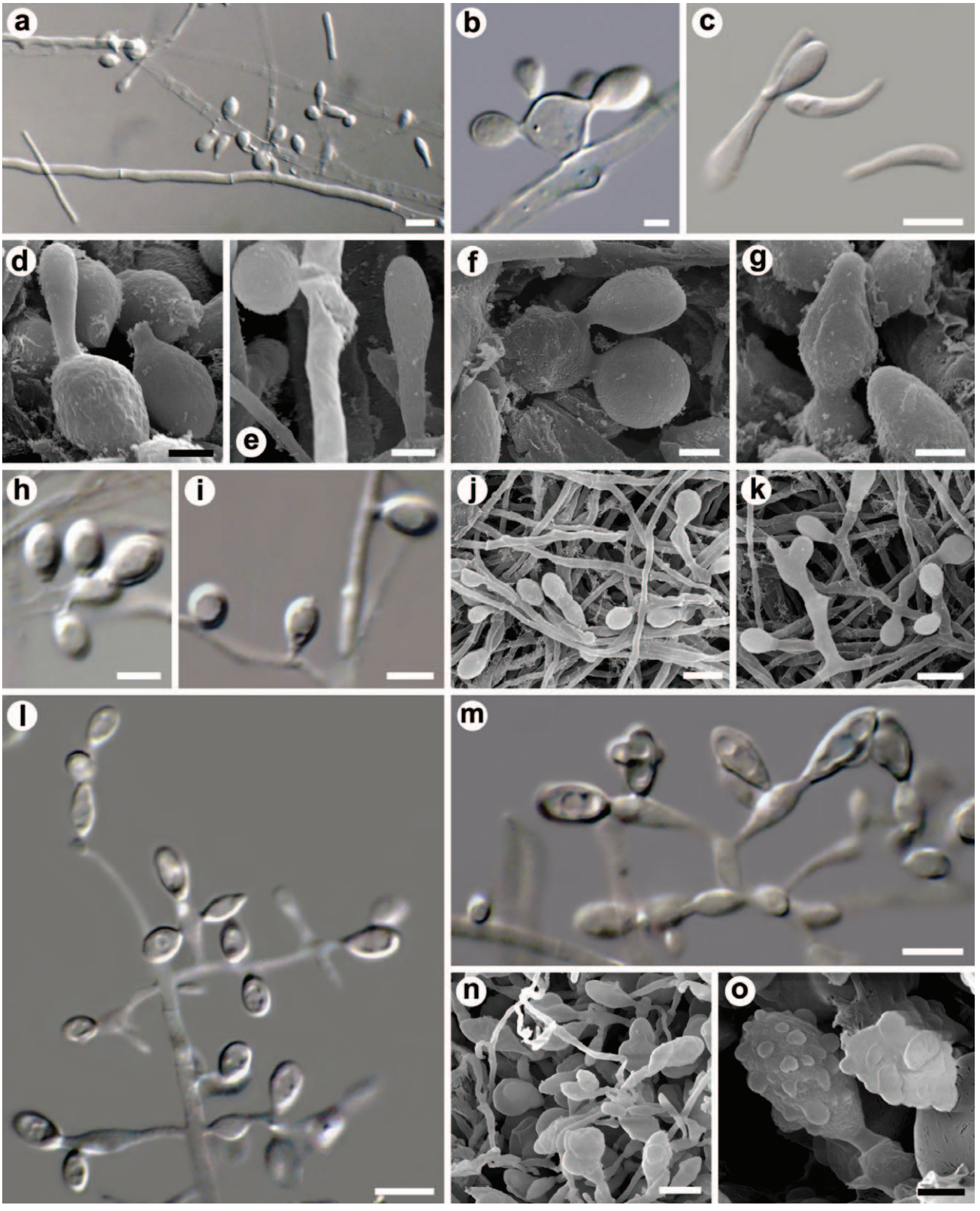

FIG. 2. Asexual morph of the genera *Crassicarpon*, *Myceliophthora* and *Thermothelomyces*. a–g. *Crassicarpon thermophilum* CBS 406.69. a, b. Conidiophores; c–g. conidia. h–k. *Myceliophthora lutea* MUCL 10070. h–k. Conidiophores bearing conidia. l–o. *Thermothelomyces heterothallica* CBS 137789; l–n. Conidiophores bearing terminal and lateral conidia; o. conidium (SEM). Bars: a, l = 10 µm; b, c, h–k, m, n = 5 µm; d–g, o = 2.5 µm.

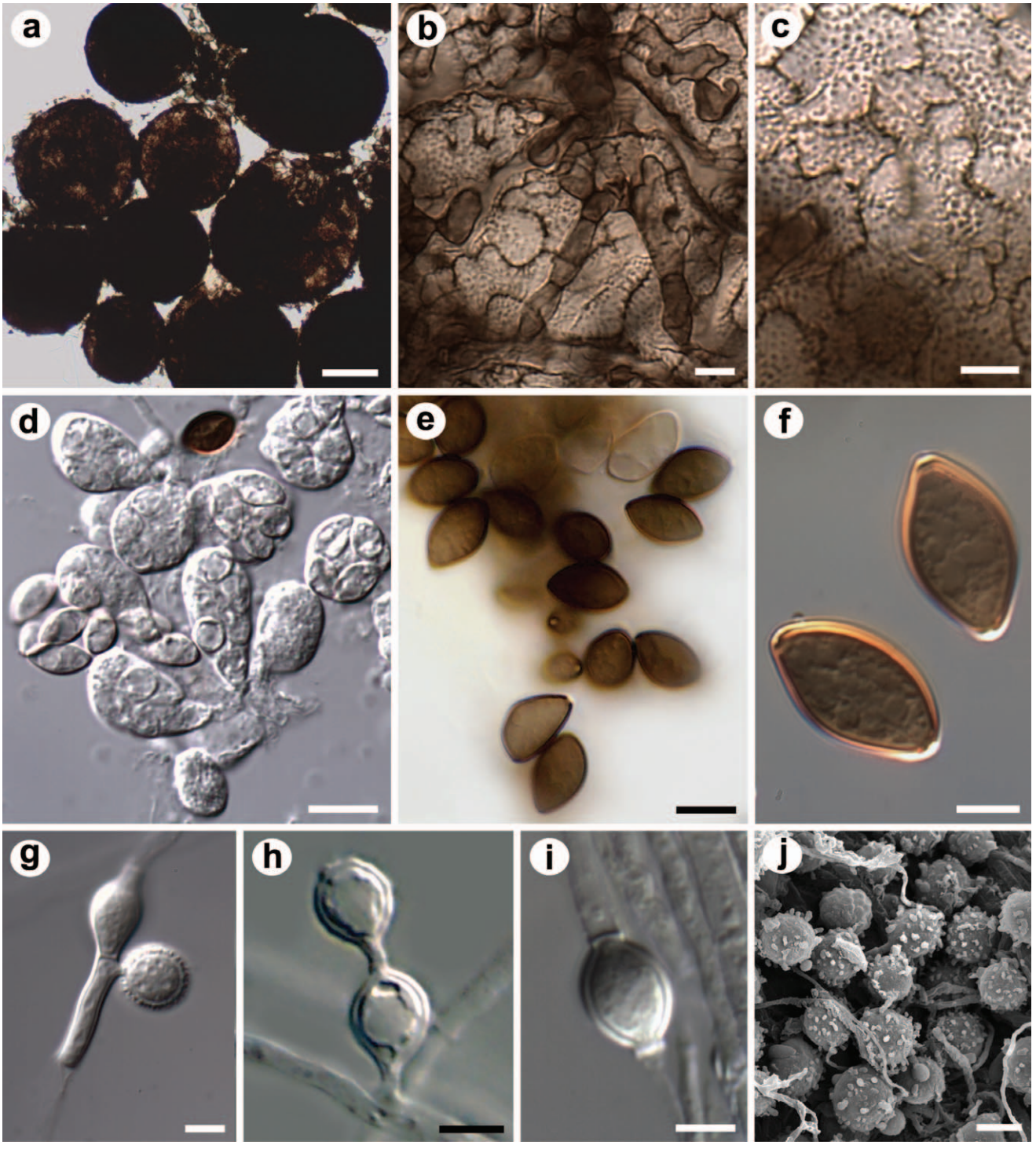

FIG. 3. *Corynascus fumimontanus* CBS 137294. a. Ascomata. b. Irregular network of distorted hyphae on the ascomatal wall. c. Detail of the ascomatal wall. d. Asci. e, f. Ascospores. g. Sessile conidia. h. Conidia on short inflated protusion. i. Intercalary conidia. j. Conidia (SEM). Bars: a = 50 µm; b, c, f–j = 5 µm; d = 15 µm; e = 10 µm.

cleistothecial ascomata of textura epidermoidea and ornamented (mostly reticulate) ascomata wall cells, and brown ascospores with a distinct germ pore at each end (FIG. 4). The asexual morph was observed in all these species with the exception of *M. sexualis*, as was reported by Stchigel et al. (2000), and was characterized by holoblastic, spherical or nearly so, hyaline to pale yellow conidia with an ornamented cell wall, except for *M. novoguineensis*, which produced smooth-walled conidia, sessile or on short protrusions,

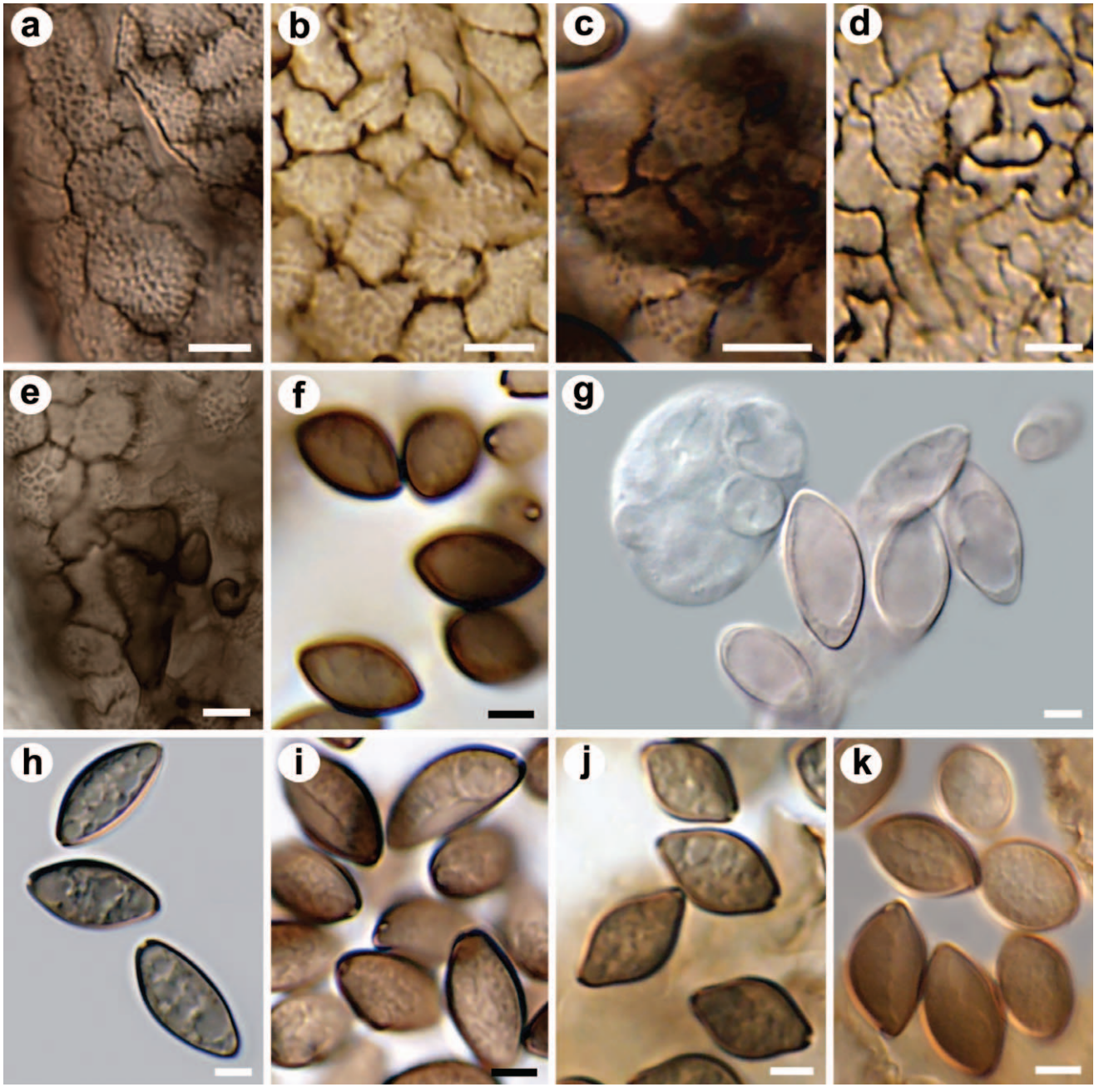

FIG. 4. Sexual morphs of the species of *Corynascus*. *Corynascus fumimontanus* CBS 137294. a. Detail of ascomata wall. f. Ascospores. *Corynascus novoguineensis* NBRC 9556. b. Detail of ascomata wall; g. Ascus and immature pinkish ascospores; h. Ascospores. *Corynascus sepedonium* IMI 378521. c. Detail of ascomata wall; i. Ascospores. *Corynascus sexualis* IMI 378520. d. Detail of ascomata wall. j. Ascospores. *Corynascus verrucosus* CBS 137791. e. Detail of ascomata wall. k. Ascospores. Bars: a–k = 5 µm.

sometimes also on swollen, sometimes catenate, conidiogenous cells (FIG. 5). These species were mesophilic with an optimal growth at 25–40 C. The type strains of *M. sepedonium* and *M. similis* grouped together in the same clade with a nucleotide identity over 99%. Morphologically both species were distinguished only by the shape of the ascospores and the position of the germ pores (i.e. irregularly shaped ascospores with two subapical germ pores in *M. similis*) and broadly fusiform ascospores with two apical germ pores in *M. sepedonium*.

The other species of *Myceliophthora* (i.e. *M. fergusii*, *M. guttulata*, *M. heterothallica*, *M. hinnulea*, *M. thermophile*) were located in two distinct, well-supported sister clades, each of them representing a new genus. The first contains the type strains of *M.*

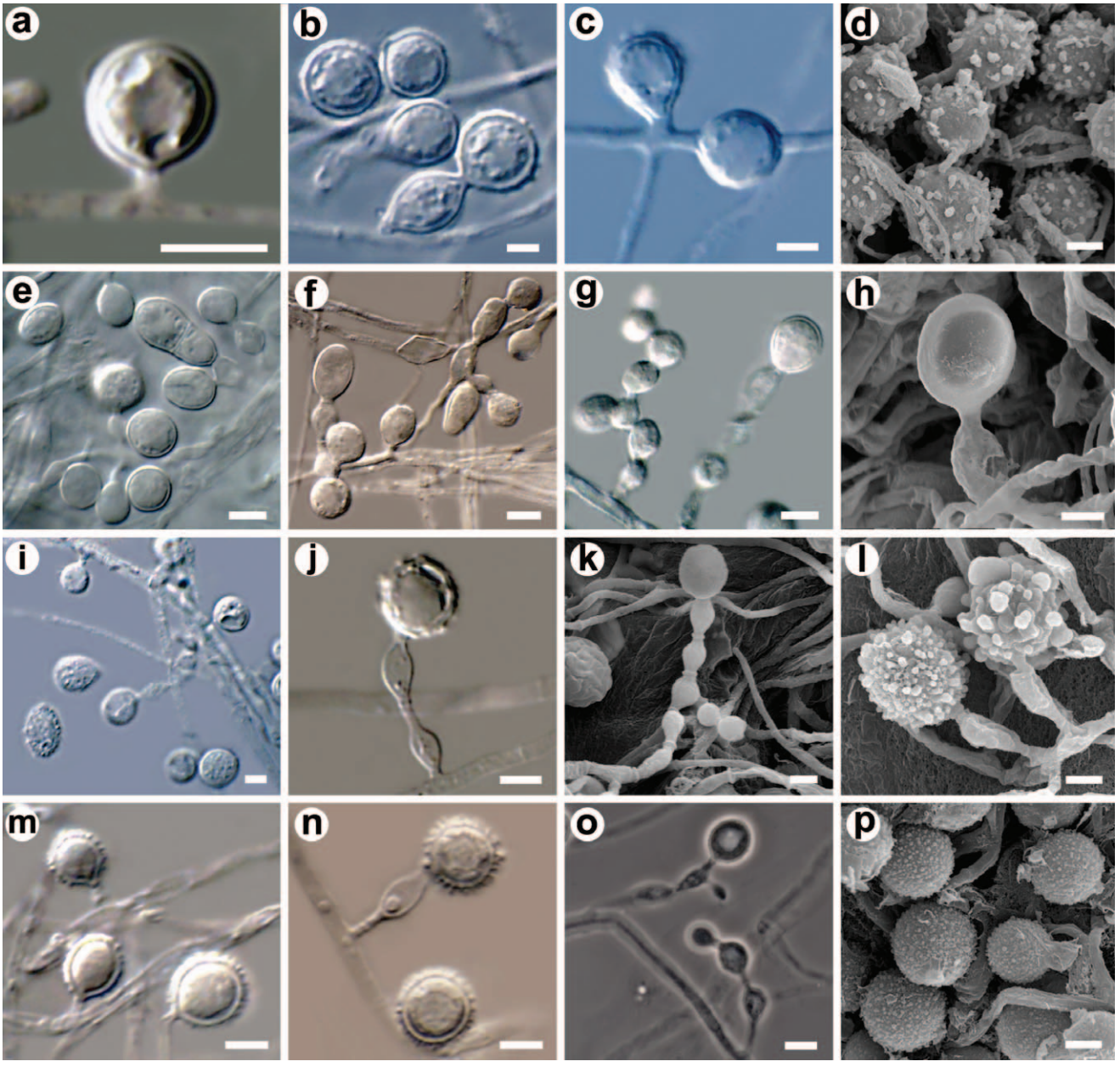

FIG. 5. Asexual morphs of the species of *Corynascus*. a–d. *Corynascus fumimontanus* CBS 137294. a. Sessile conidium; b. Conidia on short inflated protrusion; c. sessile and intercalary conidia; d. conida (SEM). e–h. *Corynascus novoguineensis* NBRC 9556. e. Sessile conidia; f. conidia on short inflated protrusion; g. conidiophores; h. conidium (SEM). i–l. *Corynascus sepedonium* IMI 378521. i. Sessile conidia; j. conidia on short inflated protrusion; k. conidiophore bearing terminal conidium (SEM); l. conidia (SEM). m–p. *Corynascus verrucosus* FMR 12369 (= CBS 137791). m. Sessile conidia; n. conidia on short inflated protrusion; o. conidiophores bearing terminal conidia; p. conida (SEM). Bars: a–c, e–g, i–k, m–o = 5 µm; d, h, l, p = 2.5 µm.

guttulata, *M. heterothallica*, *M. hinnulea* and *M. thermophila* (98% bs/1 pp), and the other includes *M. fergusii* (100% bs/1 pp). The members of both clades were thermophilic, with an optimal growth at 40–45 C. The species in the first clade produced holoblastic, subglobose or obovoid to ellipsoidal conidia truncate at the base, brown, thick-walled and ornamented, with the exception of *M. guttulata* that produces hyaline, smooth-walled and guttulate conidia on terminally and laterally on hyphae (sessile), or on ampulliform to clavate polyblastic conidiogenous cells, sometimes with a short or long basal pedicel (FIG. 2). Only *M. heterothallica* was capable of producing sexual morphs in culture after mating sexually compatible strains. They were dark cleistothecial ascomata with an ascomatal wall of textura epidermoidea, producing ellipsoid to ovoid ascospores with a terminal germ pore. The strains of *M. fergusii* produced holoblastic, hyaline to yellow in mass,

thick- and smooth-walled conidia, sessile or in swollen conidiogenous cells, arising singly or in chains of up to five conidia (FIG. 2). This fungus was also heterothallic, producing cleistothecial ascomata with a thick-walled ascomatal wall of textura angularis and ellipsoidal ascospores, pinkish when young but becoming dark brown, with a germ pore at each end.

The nucleotide identities in the combined dataset among the type strains of *M. fergusii*, *M. lutea*, *M. sepedonium* and *M. thermophila* were ≤ 93%.

TAXONOMY

Based on the molecular and phenotypic results mentioned above, we propose the revalidation of *Corynascus* as a genus distinct from *Myceliophthora*, and the new genera *Thermothelomyces* and *Crassicarpon*. To accommodate the isolate CBS 137294, we propose the new species *C. fumimontanus*.

KEY TO THE GENERA *CORYNASCUS*, *CRASSICARPON*, *MYCELIOPHTHORA* AND *THERMOTHELOMYCES*

1. No growth at 50 C 2
1. Growth at 50 C 3
2. Sexual morph present in culture . . . . . *Corynascus*
2. Sexual morph absent in culture. . . . . *Myceliophthora*
3. Conidia hyaline, spherical to cuneiform, smooth-walled . . . . . *Crassicarpon*
3. Conidia brown, subglobose or obovoid to ellipsoidal; ornamentated or, rarely, smooth . . . . . *Thermothelomyces*

Corynascus Arx, Proc. K. Ned. Akad. Wet., Ser. C, Biol. Med. Sci. 76: 295. 1973. FIGS. 3, 4, 5

Type species: *Corynascus sepedonium* (C.W. Emmons) Arx, Proc. K. Ned. Akad. Wet., Ser. C, Biol. Med. Sci. 76: 292. 1973.

Notes. *Corynascus* is characterized by its mesophilic habit, having an ascomata wall of textura epidermoidea composed of reticulate or verrucose cells, ascospores with a germ pore at each end and yellowish conidia usually verrucose or echinulate to tuberculate, rarely smooth.

MycoBank MB809486

Typification. USA. TENNESSEE: Great Smoky Mountains National Park, Cosby Creek trail, 35.78, −83.22, from forest soil, 01-VIII-2008, *A.N. Miller*, *M. Calduch*, *A.M. Stchigel*. (**holotype** CBS H-21594). **Isotypes** FMR 12372, ILLS 71950. Ex-type cultures FMR 12372, CBS 137294.

Etymology: From the Latin *fumi-*, smoky, and *-montanus*, mountains, referring to the name of the national park where the fungus was isolated.

Diagnosis: This species is characterized by verrucose ascomata wall cells, mostly irregularly shaped ascospores, greenish brown when young, and conidia sessile, intercalary or on swollen conidiogenous cells.

Mycelium composed of hyaline to pale yellow, branched, anastomosing, septate, smooth-walled hyphae of 1–2 µm diam. Colonies on PCA attaining 72–75 mm diam in 14 d at 35 C, light yellow with olive patches, olive gray at center, flattened, powdery to granular due to the production of conidia and ascomata, margins fimbriate; reverse pale yellow to light yellow, with olive patches. Ascomata superficial, globose, cleistothecial, brown to dark brown, 50–110 µm diam, ascomata wall of textura epidermoidea, composed of 1–3 layers of irregularly shaped, verrucose, golden brown to brown cells, covered by hyphae anastomosing with the ascomata wall cells. Paraphyses absent. Asci eight-spored, subglobose to broadly ellipsoidal, 24–31 × 15×22 µm, thin-walled, short-stipitate, evanescent. Ascospores one-celled, broadly fusiform to irregularly shaped, 13–17 × 7–9 µm, hyaline to greenish brown when young becoming brown, thick- and smooth-walled, with a conspicuous subterminal to terminal germ pore at each end. Conidiophores micronematous, 1–2.5 µm wide and up to 26 µm long, or semimacronematous, flask-shaped, 5–10 × 3–8 µm. Conidia holoblastic, globose to subglobose, 6–10 µm diam, subhyaline to pale yellow, thick-walled, verrucose, sessile or on swollen conidiogenous cells, and holothallic when intercalary, morphologically similar to the holoblastic ones.

Colonies on PDA attaining 73–75 mm diam in 14 d at 35 C, yellowish white to pale yellow, velvety to powdery, radially folded, umbilicate, lobulate, margins regular; reverse pale yellow to light yellow. Ascomata absent. The minimum and maximum temperature of growth are 15 and 45 C, respectively. Optimal temperature 35–40 C.

Corynascus novoguineensis (Udagawa & Y. Horie) Arx, Proc. K. Ned. Akad. Wet., Ser. C, Biol. Med. Sci. 76: 295. 1973. FIGS. 4b, g, h; 5e–h

Basionym: Thielavia novoguineensis Udagawa & Y. Horie, Bull. natn. Sci. Mus., Tokyo 15: 191. 1972.

≡ *Myceliophthora novoguineensis* (Udagawa & Y. Horie) van de Brink & Samson, in Brink, Samson, Hagen, Boekhout & Vries, Fungal Divers. 52: 206. 2012.

Notes. *Corynascus novoguineensis* is characterized by slightly verrucose ascomata wall cells, pinkish ascospores when young, and smooth-walled conidia. In the original description the immature ascospores were described as greenish brown (Udagawa and Horie 1972).

Corynascus sepedonium (C.W. Emmons) Arx, Proc. K. Ned. Akad. Wet., Ser. C, Biol. Med. Sci. 76: 292. 1973. FIGS. 4c, i; 5i-l

Basionym: Thielavia sepedonium C.W. Emmons, Bull. Torrey bot. Club 59: 417. 1932

≡ *Chaetomidium sepedonium* (C.W. Emmons) Lodha, in Subramanian (Ed.), Taxonomy of Fungi (Proc. int. Symp. Madras, 1973), Pt 1: 248. 1978.

≡ *Myceliophthora sepedonium* (C.W. Emmons) van den Brink & Samson, in Brink, Samson, Hagen, Boekhout & Vries, Fungal Divers. 52: 206. 2012.

= *Thielavia sepedonium* var. *minor* B.S. Mehrotra & Bhattacharjee, Antonie van Leeuwenhoek 32: 391. 1966.

= *Myceliophthora similis* (Stchigel, Cano & Guarro) van de Brink & Samson, in Brink, Samson, Hagen, Boekhout & Vries, Fungal Divers. 52: 206. 2012.

Ascomata superficial, globose, cleistothecial, brown to dark brown, 50–110 µm diam, glabrous, ascomata wall of textura epidermoidea, composed of 1–3 layers of irregularly shaped, reticulate, golden-brown to brown cells. Paraphyses absent. Asci eight-spored, subglobose to broadly ellipsoidal, 26–40 × 20–31 µm, thin-walled, short-stipitate, evanescent. Ascospores one-celled, ellipsoidal to broadly fusiform or navicular in lateral view, 11–23 × 6.5–13 µm, hyaline becoming brown when mature, thick- and smooth-walled, with a conspicuous subterminal to terminal germ pore at each end. Conidiophores micronematous or semimacronematous. Conidia holoblastic, globose to subglobose, 6–12 µm diam, subhyaline to pale yellow, thick-walled, finely echinulate to tuberculate, sessile or on swollen conidiogenous cells.

Notes. Corynascus sepedonium is characterized by reticulate ascomata wall cells and echinulate to tuberculate conidia. The description is from the protolog with slight modifications based on the study of the type strain of *C. similis* (IMI 378521).

Corynascus sexualis Stchigel, Cano & Guarro, in Stchigel, Sagués, Cano & Guarro, Mycol. Res. 104: 880. 2000. FIG. 4d, j

≡ *Myceliophthora sexualis* (Stchigel, Cano & Guarro) van de Brink & Samson, in Brink, Samson, Hagen, Boekhout & Vries, Fungal Divers. 52: 206. 2012.

Notes. Corynascus sexualis differs from the other species of the genus by the lack of asexual morph and its lemon-shaped ascospores.

Corynascus verrucosus Stchigel, Cano & Guarro, in Stchigel, Sagués, Cano & Guarro, Mycol. Res. 104: 884. 2000. FIGS.; 4e, k; 5m–p

≡ *Myceliophthora verrucosa* (Stchigel, Cano & Guarro) van de Brink & Samson, in Brink, Samson, Hagen, Boekhout & Vries, Fungal Divers. 52: 206. 2012.

Notes. Corynascus verrucosus is characterized by verruciform dark brown projections from the ascomata wall, and broadly fusiform ascospores with a subterminal germ pore at each end.

KEY TO THE SPECIES OF *CORYNASCUS*

1. Asexual morph absent; ascospores limoniform *C. sexualis*
1. Asexual morph present; ascospores irregularly shaped, ellipsoidal or fusiform 2
2. Conidia smooth-walled, or nearly so; ascospores pinkish when young . . . . . *C. novoguineensis*
2. Conidia verrucose or tuberculate; ascospores greenish or brownish when young. 3
3. Ascomata wall cells with verrucose projections; ascospores irregularly shaped *C. fumimontanus*
3. Ascomata wall cells reticulated 4
4. Ascomata glabrous; ascospores ellipsoidal to broadly fusiform... . . . . *C. sepedonium*
4. Ascomata with short, brown verruciform projections on entire ascomata wall; ascospores broadly fusiform . . . . . *C. verrucosus*

Crassicarpon Y. Marín, Stchigel, Guarro & Cano, gen. nov. FIG. 2a–g

Type species: Crassicarpon thermophilum (Fergus & Sinden) Y. Marín, Stchigel, Guarro & Cano.

Etymology: From the Greek *Crassum-* and *-karpos*, referring to the thick ascomatal wall.

Diagnosis: Characterized by its thermophilic habit, blackish ascomata with a thick wall of textura angularis, broadly ellipsoidal ascospores with a germ pore at each end, and hyaline, smooth-walled conidia, yellow in mass.

Ascomata superficial or immersed, globose, cleistothecial, dark brown to black, glabrous, ascomatal wall thick, of textura angularis, composed of an outer layer of thick-walled swollen cells, and an inner layer of flattened cells. Asci 4–6-spored, broadly clavate, thin-walled, stalked, evanescent. Paraphyses absent. Ascospores one-celled, broadly ellipsoidal, first hyaline, becoming pink and finally dark brown, smooth- and thick-walled, with a germ pore at each end. Conidiophores micronematous or semimacronematous. Conidia holoblastic, hyaline to yellow in mass with the age, spherical to cuneiform, variable in size, thick- and smooth-walled, sessile or produced in swollen conidiogenous cells, sometimes with short pedicels; secondary apical conidia may be produced. Heterothallic. Thermophilic.

Crassicarpon thermophilum (Fergus & Sinden) Y. Marín, Stchigel, Guarro & Cano, comb. nov. FIG. 2a–g

MycoBank MB809488

Basionym: Thielavia thermophila Fergus & Sinden, Can. J. Bot. 47: 1635. 1969.

≡ *Corynascus thermophilus* (Fergus & Sinden) Klopotek, Arch. Mikrobiol. 98: 366. 1974.

≡ *Chaetomidium thermophilum* (Fergus & Sinden) Lodha, in Subramanian (Ed.), Taxonomy of Fungi (Proc. int. Symp. Madras, 1973), Pt 1: 248. 1978.

= *Myceliophthora fergusii* (Klopotek) Oorschot, Persoonia 9: 406. 1977.

≡ *Chrysosporium fergusii* Klopotek, Arch. Mikrobiol. 98: 366. 1974.

Notes. We decided to use the epithet *thermophilum* instead *fergusii*, which had been chosen by van den Brink et al. (2012) for this taxon because *Thielavia thermophila* was the first morph described.

Myceliophthora Costantin, C. r. hebd. Séanc. Acad. Sci., Paris 114: 849. 1892. FIG. 2h–k

Type species. *Myceliophthora lutea* Costantin, C. r. hebd. Séanc. Acad. Sci., Paris 114: 2. 1892. FIG. 2h–k

Notes. *Myceliophthora* is characterized by its mesophilic habit, hyaline and smooth-walled conidia and the lack of sexual morph.

Thermothelomyces Y. Marín, Stchigel, Guarro & Cano, gen. nov. FIGS. 2l–o

MycoBank MB809489

Type species: Thermothelomyces thermophila (Apinis) Y. Marín, Stchigel, Guarro & Cano.

Etymology. From the Greek *thermos-*, hot, *thelo-*, love, and *-myces*, fungi, referring to the thermophilic habit of the fungus.

Diagnosis: Characterized by its thermophilic habit, ascomata with a wall of textura epidermoidea, ellipsoidal ascospores with a single apical germ pore, and hyaline or pale brown conidia, mostly ornamented.

Ascomata immersed to sub-immersed, globose, cleistothecial, black, glabrous, ascomata wall thin, of textura epidermoidea. Asci eight-spored, ellipsoidal, thin-walled, stalked, evanescent. Paraphyses absent. Ascospores ellipsoidal, occasionally irregularly shaped, first hyaline, dark brown to black, thick- and smooth-walled, with one germ pore. Conidiophores micronematous or semimacronematous. Conidia holoblastic, hyaline or pale brown, subglobose, ellipsoidal or obovoid to pyriform, thick-walled, conspicuously verrucose-spinulose or tuberculate, rarely smooth-walled and guttulate, producing terminally or laterally on hyphae, sometimes with short or long pedicels, or on swollen conidiogenous cells in a number of 1–4; occasionally a secondary apical conidium is produced. Heterothallic. Thermophilic.

Thermothelomyces guttulata (Y. Zhang & L. Cai) Y. Marín, Stchigel, Guarro & Cano, comb. nov.

MycoBank MB 809490

Basionym: Myceliophthora guttulata Y. Zhan & L. Cai, Mycol Progress 13: 165. 2014.

Notes. *Thermothelomyces guttulata* is distinguished from the other species by its hyaline, smooth-walled and guttulate conidia.

Thermothelomyces heterothallica (von Klopotek) Y. Marín, Stchigel, Guarro & Cano, comb. nov. FIGS. 2l–o

MycoBank MB809491

Basionym: Thielavia heterothallica von Klopotek, Arch. Mikrobiol. 107: 223. 1976.

≡ *Corynascus heterothallicus* (von Klopotek) von Arx, Dreyfuss & Müller, Persoonia 12: 174. 1984.

≡ *Myceliophthora heterothallica* (von Klopotek) van den Brink & Samson, in Brink, Samson, Hagen, Boekhout & Vries, Fungal Divers. 52: 206. 2012.

Notes. This species is characterized by pale orange-brown, long ellipsoidal, tuberculate conidia and the production of ascomata after mating. The conidia previously were described as hyaline (Klopotek 1974, 1976; van Oorschot 1977).

Thermothelomyces hinnulea (Awao & Udagawa) Y. Marín, Stchigel, Guarro & Cano, comb. nov.

MycoBank MB809492

Basionym: Myceliophthora hinnulea Awao & Udagawa, Mycotaxon 16: 436. 1983.

Notes. This species is characterized by yellowish brown to brown, subglobose to ovate, conspicuously verrucose-spinulose conidia.

Thermothelomyces thermophila (Apinis) Y. Marín, Stchigel, Guarro & Cano, comb. nov.

MycoBank MB809493

Basionym: Sporotrichum thermophilum Apinis, Nova Hedwigia 5: 74. 1963.

≡ *Chrysosporium thermophilum* (Apinis) Klopotek, Arch. Mikrobiol. 98: 366. 1974.

≡ *Myceliophthora thermophila* (Apinis) Oorschot, Persoonia 9: 403. 1977.

Notes. The asexual morph of this species is similar to those of *T. heterothallica* but *T. thermophila* does not produce a sexual morph after mating.

KEY TO THE SPECIES OF *THERMOTHELOMYCES*

1. Conidia smooth-walled and guttulate, (3.8–)4.8–7.2 × 3–5 µm . . . . . *T. guttulata*
1. Conidia with an ornamented surface. 2
2. Conidia 7–12 × 5–10 µm . . . . . *T. hinnulea*
2. Conidia 4.5–11 × 3–4.5 µm . . . . . *T. heterothallica/T. thermophila*[*]

[*] *Thermothelomyces heterothallica* produces ascomata after mating.

DISCUSSION

Based on recent molecular studies that demonstrated that *M. lutea*, the type species of *Myceliophthora*, clustered with some members of the family Chaetomiaceae, that genus was restricted to the species of such family (van den Brink et al. 2012, Zhang et al. 2014); consequently *M. vellerea* (now renamed *Ctenomyces vellereus* [Sacc. & Speg.] P.M. Kirk) and *Myceliopthora* anamorph of *Arthroderma tuberculatum* were transferred to the family Arthrodermataceae, where they were phylogenetically located (van den Brink et al. 2012, Kirk 2014).

In previous phylogenies (van den Brink et al. 2012, 2013) the species of *Myceliophthora* spp. grouped with a confidence value of below 50%, being divided into two main clades (each one composed of one or two terminal clades depending on the nuclear loci employed in the phylogenetic inference) according to their mesophilic and thermophilic habit. However, in our study, in agreement with Zhang et al. (2014), *Myceliophthora* spp. formed a well-supported clade, but the genetic distances among the terminal clades (below of 93% similarity) are such that they should be treated as separate genera. Consequently we proposed to split *Myceliophthora* into four genera, revalidating *Corynascus* and erecting two new genera: *Crassicarpon* and *Thermothelomyces*. Our proposal is also supported by phenotypic data (e.g. *Crassicarpon thermophilum* presents dark, thick-walled ascomata with a wall of textura angularis composed of non-ornamented ascomata wall cells, while the *Corynascus* spp. and *Thermothelomyces* spp. are characterized by the production of many pale, thin-walled ascomata with a wall of textura epidermoidea composed of ornamented ascomata wall cells. The type of ascomata wall previously had been used successfully in the delimitation of genera in Lasiosphaeriaceae (Miller and Huhndorf 2004, 2005; Cai et al. 2005). The number of germ pores in the ascospores is also a distinctive feature because *Corynascus* spp. and *Crassicarpon thermophilum* have one at each end, whereas *Thermothelomyces heterothallica* presents only one. The conidia are produced by similar ontogenetic processes in all four genera but also show morphological differences: both *Myceliophthora lutea* and *Crassicarpon thermophilum* produce hyaline, smooth-walled conidia, but while in the first taxon they are pyriform to globose and produced singly (or rarely in chains up to two conidia), in the second one they are spherical to cuneiform and in chains of up to five conidia. *Corynascus* spp. and *Thermothelomyces* spp. produce mostly ornamented, yellowish conidia, even though *Thermothelomyces* spp. present more complex conidiophores, with ovoid to clavate conidia with a truncate base, whereas in *Corynascus* spp. they are spherical.

Corynascus fumimontanus sp. nov. is easy to distinguish morphologically from the rest of the species of the genus *Corynascus* by its verrucose ascomata wall cells (reticulate in the other species) and its irregularly shaped ascospores. Finally the synonymy of *C. similis* with *C. sepedonium* was proposed due to the high nucleotide identity and the minor morphological differences among them.

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