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DNA barcoding in *Mucorales*: an inventory of biodiversity

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Abstract The order *Mucorales* comprises predominantly fast-growing saprotrophic fungi, some of which are used for the fermentation of foodstuffs but it also includes species known to cause infections in patients with severe immune or metabolic impairments. To inventory biodiversity in *Mucorales* ITS barcodes of 668 strains in 203 taxa were generated covering more than two thirds of the recognised species. Using the ITS sequences, Molecular Operational Taxonomic Units were defined by a similarity threshold of 99 %. An LSU sequence was generated for each unit as well. Analysis of the LSU sequences revealed that conventional phenotypic classifications of the *Mucoraceae* are highly artificial. The LSU- and ITS-based trees suggest that characters, such as rhizoids and sporangiola, traditionally used in mucoralean taxonomy are plesiomorphic traits. The ITS region turned out to be an appropriate barcoding marker in *Mucorales*. It could be sequenced directly in 82 % of the strains and its variability was sufficient to resolve most of the morphospecies. Molecular identification turned out to be problematic only for the species complexes of *Mucor circinelloides*, *M. flavus*, *M. piriformis* and *Zygorhynchus moelleri*. As many as 12 possibly undescribed species were detected. Intraspecific variability differed widely among mucorealean species ranging from 0 % in *Backusella circina* to 13.3 % in *Cunninghamella echinulata*. A high proportion of clinical strains was included for molecular identification. Clinical isolates of *Cunninghamella elegans* were identified molecularly for the first time. As a result of the phylogenetic analyses several taxonomic and nomenclatural changes became necessary. The genus *Backusella* was emended to include all species with transitorily recurved sporangiophores. Since this matched molecular data all *Mucor* species possessing this character were transferred to *Backusella*. The genus *Zygorhynchus* was shown to be polyphyletic based on ITS and LSU data. Consequently, *Zygorhynchus* was abandoned and all species were reclassified in *Mucor*. Our phylogenetic analyses showed, furthermore, that all non-thermophilic *Rhizomucor* species belong to *Mucor*. Accordingly, *Rhizomucor endophyticus* was transferred to *Mucor* and *Rhizomucor chlamydosporus* was synonymised with *Mucor indicus*. Lecto-, epi- or neotypes were designated for several taxa.

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INTRODUCTION

The order *Mucorales* represents a phylogenetically ancient group of fungi comprising predominantly saprotrophs inhabiting soil, dung and dead plant material, as well as several parasites on plants and on other fungi. Mucoralean strains have been used for centuries in the fermentation of traditional Asian and African food such as tempeh or furu (fermented tofu) (Nout & Aidoo 2010), and they also play a role in the production of several kinds of cheese (Hermet et al. 2012). On the other hand, some members of the *Mucorales* are responsible for the spoilage of fresh and manufactured food (Pitt & Hocking 2009).

Mucoralean fungi are also known to be involved in human infection. Mucormycoses are still very rare, but their incidence is increasing in hosts with severe immune or metabolic impairment, e.g. due to hemomalignancy, hematopoietic stem cell transplantation or uncontrolled ketoacidotic diabetes mellitus (Skiada et al. 2011). Infections often take a dramatic course and have a high mortality rate. In risk group patients such as those with leukemia or allogenic bone marrow transplant an increase of 8 % and 2 %, respectively, has been noted (Greenberg et al. 2004). In part the clinical strains belong to the same species as the ones used in food fermentation. For example, *Mucor circinelloides* is used for starter cultures in Asian food (Hesseltine 1983, Nout & Aidoo 2010), but is also able to infect patients with an impaired immune system (e.g. Khan et al. 2009).

Mucorales are among the best represented groups in fungal culture collections. They easily grow in axenic culture and they have been used as model organisms since the late 19th century. A large share of all species described in the order are represented today by living cultures publicly available in fungal reference collections. For example, the Centraalbureau voor Schimmelcultures (www.cbs.knaw.nl) possesses 135 ex-type or authentic strains out of 227 currently accepted species. This is a unique situation, compared e.g. with dermatophytes which were described around the same period (Sabouraud 1910).

Problematic for the nomenclatural stability of the *Mucorales* is the practice of many early authors to designate a living strain as 'type' although this was permitted by the International Code of Botanical Nomenclature. Since 2000 Art. 8.4 of ICBN has allowed deposition of metabolically inactive cultures as types (Greuter et al. 2000). In order to link these original strains to the

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respective names we designated the vial with the lyophilised strain that was prepared at time of its accession as lectotypes. If the original strain was not lyophilized in the year of its accession we lectotypified the name by the original illustration and designated the original strain as epitype. In the case of *Zygorhynchus exponens* a neotype was chosen because the original figures were not specific and no other authentic material is known to exist.

Taxonomy of *Mucorales* has traditionally been based upon microscopic morphology and mating experiments. The classical works of Maria A.A. Schipper (Schipper 1973, 1975, 1976, 1978a, b, 1979, 1984, 1986, 1990, Schipper & Samson 1994, Schipper & Stalpers 1984, 2003) provided model studies and have long remained satisfactory for the identification of major species. A large number of names were synonymised. However, molecular phylogeny has revealed that diversity within and between species is much larger than anticipated, and this has led to a proliferation of the number of taxa recognised. Since the older, morphological synonyms were a priori omitted from most studies, the respective names remained obscure and were not included in nomenclatural comparisons. New names are being introduced today for species that do not match any of the known taxa deposited in GenBank. Verification of the ex-type strains of older, still valid names may prove that some of the new names are later synonyms, and that the historical names have to be re-installed.

DNA barcoding was originally aimed to allow faster and more precise species identification. However, the accuracy of this method strongly depends on completeness of taxon sampling and on taxonomic elaboration (Meyer & Pauley 2005). Since polyphyly was revealed with molecular data in many morphology-based families and genera (O'Donnell et al. 2001, Voigt & Wöstemeyer 2001), several groups have been revised using molecular phylogenetic analyses, e.g. *Actinomucor* (Zheng & Liu 2005, Khan et al. 2008), *Apophysomyces* (Álvarez et al. 2010b), *Cunninghamella* (Liu et al. 2001), *Lentamyces* (Hoffmann & Voigt 2009), *Lichtheimia* (Alastruey-Izquierdo et al. 2010), *Pilobolus* (Foos et al. 2011), *Rhizopus* (Abe et al. 2006, 2007, 2010, Liu et al. 2007, Gryganskyi 2010), *Saksenaea* (Álvarez et al. 2010a), *Siepmannia* (Kwaśna & Nirenberg 2008a, b) and *Umbelopsis* (Meyer & Gams 2003). However, some genera, e.g. *Absidia* s.str., *Circinella* and relatives, or *Syncephalastrum* have not been revised using molecular data. The largest mucorelean group, *Mucor* and its relatives, has been investigated only fragmentarily focusing on certain clades (Jacobs & Botha 2008, Budziszewska et al. 2010, Álvarez et al. 2011, Madden et al. 2011, Hermet et al. 2012). Only a few publications (Abe et al. 2007, Alastruey-Izquierdo et al. 2010, Gryganskyi 2010, Hermet et al. 2012) use at least two unlinked molecular markers and apply sufficient strain and taxon sampling to adopt concepts of genealogical concordance phylogenetic species recognition (GCPSR, Taylor et al. 2000) satisfactorily. As a consequence, the criteria of good taxonomy are insufficiently met, and many species in *Mucorales* are poorly delimited. It was, therefore, the primary aim of the present study to inventory the genetic diversity of *Mucorales* deposited in the CBS culture collection and to highlight critical groups that need to be studied by a multi-locus approach. Our paper provides DNA barcodes for all ex-type and authentic strains of *Mucorales* available in the CBS culture collection, and makes these data available by open access as reference for subsequent studies on biodiversity and taxonomy.

Recently, the Fungal Barcoding Consortium (Schoch et al. 2012) proposed the rDNA internal transcribed spacer (ITS) as a universal DNA barcode marker for fungi. In our study ITS was also applied because of its discriminative power in *Mucorales* (Meyer & Gams 2003, Kwaśna et al. 2006, Schwarz et al. 2006, Vitale et al. 2012). The ITS region is highly variable between members and is not alignable over the entire order. ITS sequences of some species differ to such an extent that they could not be aligned confidently with their putative sibling species. To establish the phylogenetic position of species and to acquire an overview of the entire order that includes all groups recognized on the basis of molecular data, the D1/D2 region of the large subunit (LSU) rDNA was sequenced from one strain of each Molecular Operational Taxonomic Unit (MOTU). A MOTU is defined by ITS similarities with mutual threshold values of > 99 %. Using this approach a species can be represented by a single or by several MOTUs depending on intraspecific variability.

Analyses of the ITS region as a single locus can not be used to define species boundaries, but, conversely, hypotheses on species limits can be developed by plotting morphospecies on the ITS trees. Therefore only those taxonomic rearrangements were made that did not require exact knowledge on species limits. These revisions will be discussed, and nomenclatural status of names analysed.

ITS barcodes of 668 strains in 203 taxa (178 species, 19 varieties, 6 forms) were generated for this study covering 78.4 % of the recognized species in *Mucorales*. Seventy-six percent of the species are represented by ex-type strains or other authentic material. LSU sequences were generated for 43.5 % of the strains. Special attention was paid to the inclusion of a high proportion of clinical strains predominantly provided by the Spanish National Center for Microbiology in Madrid (Spain) and the Postgraduate Institute of Medical Education and Research in Chandigarh (India). The paper focuses on the genera *Actinomucor*, *Mucor* and allies, *Rhizomucor* and *Rhizopus* because ITS trees have been published for the remaining medically important genera: *Apophysomyces* (Álvarez et al. 2010b), *Cunninghamella* (Liu et al. 2001), *Lichtheimia* (Alastruey-Izquierdo et al. 2010), *Saksenaea* (Álvarez et al. 2010a) and *Syncephalastrum* (Vitale et al. 2012).

In main traits we follow the nomenclature of the species provided by Species Fungorum (http://www.speciesfungorum.org) based largely on the 10th edition of the Dictionary of the Fungi. We adopted the family structure by Hoffmann et al. (2013).

MATERIALS AND METHODS

Strains

A total number of 668 mucoralean strains belonging to 178 species, 19 varieties and 6 formae and covering 78.4 % of the currently accepted species was studied. For 22.2 % of the taxa it was possible to include five or more strains per lowest taxonomic level (form, variety or species), 60.1 % of the taxa were represented by 2 or more isolates. Ex-type strains or other authentic material was available for 75.8 % of the studied species. In order to cover intraspecific variability, strains from the most distant localities and from a wide range of substrates were selected. Special attention was paid to the inclusion of clinical isolates. Studied strains originated from the reference collection of the CBS-KNAW Fungal Biodiversity Centre (CBS; Utrecht, The Netherlands), the Instituto de Salud Carlos III National Centre of Microbiology (CNM-CM; Madrid, Spain), the Departments of Medical Microbiology (PGIMER; Chandigarh, India) or the Belgian Co-ordinated Collections of Micro-organisms (IHEM; Brussels, Belgium). The studied strains, source information and GenBank accession numbers are listed in Table 1.

DNA extraction, PCR amplification, cloning and sequencing

Genomic DNA was extracted in most cases from 2d-old cultures grown on malt extract agar (MEA 5 %, Oxoid, Badhoevedorp,

(text continues on p. 26)

Table 1 Source information and GenBank accession numbers of the studied strains. Strains marked with an asterisk belong to different genera based on their ITS- or LSU-sequences: * *Absidia idahoensis* CBS 103.91 belongs to *Circinella*; ** *Circinella lacrymispora* CBS 101757 belongs to *Gongronella*, *** *Circinella simplex* CBS 428.80 belongs to *Mucor*. Ex-type strains are designated by: T = ex-type strain, ET = ex-epitype strain, HT = ex-holotype strain, IT = ex-isotype strain, LT = ex-lectotype strain, NT = ex-neotype strain, PT = ex-paratype strain, ST = ex-syntype strain and AUT = authentic material. Type information was checked with original literature only for those taxa that are treated in the taxonomy part; the remaining data were derived from the CBS database.

Strain number	Species	Species name at the beginning of the study	Status	Country	Source	ITS	LSU
CBS 125.68	*Absidia anomala*		T	Cuba	soil	JN205815	JN206593
CBS 126.68	*Absidia californica*		T	USA	dung of rat		JN206583
CBS 314.78	*Absidia californica*			USA	dung of mouse	JN205816	JN206582
CBS 101.28	*Absidia coerulea*			USA	dung of rabbit	JN205818	JN206585
CBS 102.28	*Absidia coerulea*			USA	soil	JN205821	JN206584
CBS 104.08	*Absidia coerulea*			n.a.	soil	JN205811	HM849703
CBS 628.70B	*Absidia coerulea*			Denmark	forest soil	JN205812	
CBS 101.59	*Absidia cuneospora*		T	USA	sandy soil		JN206580
CBS 102.59	*Absidia cuneospora*			USA	clay soil	JN205819	JN206579
CBS 100.08	*Absidia cylindrospora* var. *cylindrospora*			n.a.	n.a.	JN205822	JN206588
CBS 127.68	*Absidia cylindrospora* var. *nigra*		T	USA	soil of pastured hardwood		JN206589
CBS 153.63	*Absidia cylindrospora* var. *rhizomorpha*		T	Honduras	rhizosphere of *Musa sapientum*		JN206594
CBS 102.35	*Absidia fusca*		T	Germany	soil of pine forest	JN205814	HM849707
CBS 346.97	*Absidia fusca*	*A. cylindrospora* var. *nigra*		Netherlands	myxomycete	JN205817	
CBS 100.48	*Absidia glauca*			Germany	manure, in asparagus field	JN205820	JN206581
CBS 101.08	*Absidia glauca*		T	n.a.	n.a.	JN205810	HM849705
CBS 101.29	*Absidia heterospora*		T	France	soil of pine forest		JN206595
CBS 103.91	*Absidia idahoensis**		T	USA	brood chamber of *Nomia melanderi*	JN205847	
CBS 697.68	*Absidia macrospora*		T	former Czechovakia	soil		HM849704
CBS 100.62	*Absidia pseudocylindrospora*		T	Tanzania	virgin soil		JN206591
CBS 128.68	*Absidia psychrophilia*		T	Canada	ambrosia beetle; gland		JN206587
CBS 115583	*Absidia repens*		IT	UK, England	wallpaper	JN205813	HM849706
CBS 187.64	*Absidia spinosa* var. *biappendiculata*		IT	USA	*Comandra pallida*; leaf		JN206592
CBS 106.08	*Absidia spinosa* var. *spinosa*			n.a.	n.a.	JN205809	JN206590
CBS 100.09	*Actinomucor elegans*			n.a.	n.a.	JN205827	JN206491
CBS 100.22	*Actinomucor elegans*			USA	n.a.	JN205828	
CBS 111556	*Actinomucor elegans*					JN205826	
CBS 154.86	*Actinomucor elegans*			Egypt	n.a.	JN205829	HM849686
CBS 338.72	*Actinomucor elegans*			Nepal	soil	JN205824	
CBS 117697	*Actinomucor elegans* var. *kuwaitiensis*	*A. kuwaitiensis*	T	Kuwait	human; wound	JN205823	JN206493
CBS 111558	*Actinomucor elegans* var. *meitauzae*	*A. taiwanensis*		n.a.	n.a.	JN205825	JN206492
CBS 476.78	*Apophysomyces elegans*		T	India	soil of mango orchard	JN206279	
CBS 477.78	*Apophysomyces elegans*			India	soil of grassy site	JN206280	JN206536
CBS 658.93	*Apophysomyces variabilis*	*A. elegans*	T	Netherlands Antilles	human; osteomyelitis	JN206281	HM849695
CBS 128.70	*Backusella circina*		T	USA	soil with lichens	JN206258	JN206529
CBS 129.70	*Backusella circina*		PT	USA	soil	JN206257	
CBS 323.69	*Backusella circina*			Japan	n.a.	JN206259	
CBS 382.95	*Backusella circina*			China	forest soil	JN206256	
CBS 907.73	*Backusella circina*			Japan	n.a.	JN206260	
CBS 786.70	*Backusella indica*	*M. recurvus* var. *indicus*	LT (designated here)	India	n.a.	JN206255	JN206526
CBS 107.09	*Backusella lamprospora*		T of *Mucor dispersus*	Norway	n.a.	JN206269	
CBS 118.08	*Backusella lamprospora*		T	Switzerland	n.a.	JN206268	JN206531
CBS 195.28	*Backusella lamprospora*			USA	fallen leaf	JN206271	JN206530
CBS 244.67	*Backusella lamprospora*			France	moist wall	JN206270	
CBS 568.70	*Backusella oblongielliptica*	*Mucor oblongiellipticus*	LT (designated here)	Japan	agaric	JN206278	JN206533
CBS 569.70	*Backusella oblongispora*	*Mucor oblongisporus*	NT (designated here)	Japan	soil	JN206251	JN206407
CBS 196.71	*Backusella recurva*	*M. recurvus* var. *recurvus*				JN206265	JN206523
CBS 317.52	*Backusella recurva*	*M. recurvus* var. *recurvus*		Macedonia	decaying wood	JN206262 (c1)	
CBS 318.52	*Backusella recurva*	*M. recurvus* var. *recurvus*	ET (designated here)	USA	*Fragaria*; diseased root	JN206261	JN206522
CBS 673.75	*Backusella recurva*	*M. recurvus* var. *recurvus*		Australia	soil	JN206263 (c1) JN206264 (c2)	JN206524

Table 1 (cont.)

Strain number	Species	Species name at the beginning of the study	Status	Country	Source	ITS	LSU
CBS 538.80	*Backusella* sp.	*M. recurvus* var. *recurvus*		Egypt	*Medicago sativa*	HM999964	HM849692
CBS 562.66	*Backusella tuberculispora*	*Mucor tuberculisporus*	LT (designated here)	India	n.a.	JN206267	
CBS 570.70	*Backusella tuberculispora*	*Mucor tuberculisporus*		Japan	cultivated soil	JN206266	
CBS 564.66	*Backusella variabilis*	*Mucor variabilis*	LT (designated here)	India	excrements of human	JN206254 (c1) JN206253 (c3)	JN206528
CBS 421.70	*Benjaminiella multispora*		IT	India	humus-rich soil	JN206243	JN206410
CBS 158.60	*Benjaminiella poitrasii*		T	USA	dung of rat	JN206241	JN206411
CBS 103.89	*Benjaminiella youngii*		T	Spain	dung of lizard	JN206242	JN206409
CBS 130.59	*Blakeslea trispora*			Panama	soil	JN206227	
CBS 137.49	*Blakeslea trispora*			Indonesia	*Hibiscus rosa-sinensis*; flower	JN206229	
CBS 198.80	*Blakeslea trispora*			Sweden	n.a.	JN206228	
CBS 564.91	*Blakeslea trispora*	*B. sinensis*	PT of *B. sinensis*	China	soil	JN206230	JN206515
CBS 116.24	*Chaetocladium brefeldii*			n.a.	n.a.	JN206020	JN206519
CBS 136.28	*Chaetocladium brefeldii*			n.a.	dung of horse	JN206019	
CBS 156.74	*Chaetocladium brefeldii*			Netherlands	litter	JN206022	JN206520
CBS 162.82	*Chaetocladium brefeldii*			Netherlands	dung of rat	JN206021	
CBS 811.69	*Chaetocladium jonesiii*			Norway	meadow soil	JN206023	
CBS 172.67	*Chlamydoabsidia padenii*		T	USA	*Pisum sativum*; root	JN206294	JN206586
CBS 120.25	*Choanephora cucurbitarum*	*C. infundibulifera* f. *cucurbitarum*		n.a.	n.a.	JN206231	
CBS 150.51	*Choanephora cucurbitarum*	*C. infundibulifera* f. *cucurbitarum*		n.a.	n.a.	JN206232	
CBS 178.76	*Choanephora cucurbitarum*	*C. infundibulifera* f. *cucurbitarum*	T. of *C. heterospora*	India	dead insect	JN206235	
CBS 445.72	*Choanephora cucurbitarum*	*C. infundibulifera* f. *cucurbitarum*		n.a.	n.a.	JN206234	
CBS 674.93	*Choanephora cucurbitarum*	*C. infundibulifera* f. *cucurbitarum*		China	n.a.	JN206233	JN206514
CBS 153.51	*Choanephora infundibulifera*	*C. infundibulifera* f. *infundibulifera*		n.a.	n.a.	JN206236	JN206513
CBS 155.51	*Choanephora infundibulifera*	*C. infundibulifera* f. *infundibulifera*		n.a.	n.a.	JN206237	
CBS 155.58	*Choanephora infundibulifera*	*C. infundibulifera* f. *infundibulifera*		Japan	n.a.	JN206238	
CBS 172.62	*Circinella angarensis*			USA	dung of rodent	JN205848	
CBS 173.62	*Circinella angarensis*		NT	USA	dung	JN205849	JN206551
CBS 140.28	*Circinella chinensis*		T	Japan	n.a.	JN205855	JN206549
CBS 101757	*Circinella lacrymispora***		T	Argentina	soil	JN206289	JN206608
CBS 102.16	*Circinella minor*	*C. umbellata*		n.a.	n.a.	JN205860	
CBS 142.81	*Circinella minor*			Netherlands	dung of mouse	JN205861	JN206552
CBS 143.56	*Circinella minor*			n.a.	n.a.	JN205862	
CBS 107.13	*Circinella muscae*		T of *C. sydowii*	n.a.	gold mine, depth of 600 m	JN205854	JN206550
CBS 141.28	*Circinella muscae*			n.a.	n.a.	JN205853	JN206548
CBS 159.49	*Circinella muscae*			Indonesia	soil	JN205851	
CBS 342.79	*Circinella muscae*			Netherlands	preserved meat	JN205852	
CBS 720.76A	*Circinella muscae*			USA	n.a.	JN205850	
CBS 428.80	*Circinella simplex****			Colombia	paramo soil under undisturbed vegetation	JN206213	JN206445
CBS 101.16	*Circinella umbellata*			n.a.	dung of dog	JN205857	JN206553
CBS 160.49	*Circinella umbellata*			Italy	air	JN205858	HM849722
CBS 195.74	*Circinella umbellata*			Kuwait	soil	JN205856	
CBS 837.97	*Circinella umbellata*			Germany	dung of mouse	JN205859	
CBS 158.50	*Cokeromyces recurvatus*		T	USA	dung of rabbit	JN206244	HM849699
CBS 168.59	*Cokeromyces recurvatus*			USA	dung of rat	JN206245	JN206408
CBS 151.80	*Cunninghamella bertholletiae*	*C. elegans*		USA	human; lung (leukemic patient)	JN205875	
CBS 182.84	*Cunninghamella bertholletiae*			USA	human	JN205877	
CBS 186.84	*Cunninghamella bertholletiae*			USA	human; lung (leukemic patient)	JN205876	
CBS 190.84	*Cunninghamella bertholletiae*			USA	human; heart, patient with lymphosarcoma	JN205878	HM849701
CBS 191.84	*Cunninghamella bertholletiae*			USA	human; tibia	JN205879	
CBS 372.95	*Cunninghamella bertholletiae*	*C. polymorpha*		China	forest soil	JN205872	
CBS 373.95	*Cunninghamella bertholletiae*	*C. polymorpha*		China	rotten log	JN205873	
CBS 693.68	*Cunninghamella bertholletiae*	*C. polymorpha*	NT of *C. polymorpha*	former Yugoslavia	soil	JN205871	JN206600
CBS 779.68	*Cunninghamella bertholletiae*	*C. polymorpha*		n.a.	n.a.	JN205874	JN206599
CNM-CM3628	*Cunninghamella bertholletiae*			Spain	human; sputum	JN205881	

CNM-CM3650	*Cunninghamella bertholletiae*			Spain	human; skin	JN205880	
CBS 158.28	*Cunninghamella binariae*	*C. elegans*		n.a.	n.a.	JN205888	JN206602
CBS 481.66	*Cunninghamella binariae*	*C. elegans*		Brazil	soil	JN205889	JN206603
CBS 133.27	*Cunninghamella blakesleeana*		T	Switzerland	n.a.	JN205865	
CBS 177.36	*Cunninghamella blakesleeana*			n.a.	n.a.	JN205868	
CBS 224.64	*Cunninghamella blakesleeana*			Canada	*Linum issitatissimum*	JN205870	
CBS 433.84	*Cunninghamella blakesleeana*			Kuwait	n.a.	JN205867	
CBS 720.85	*Cunninghamella blakesleeana*	*C. elegans*		Croatia	decaying fruit	JN205866	
CBS 782.68	*Cunninghamella blakesleeana*			n.a.	n.a.	JN205869	JN206601
CBS 100178	*Cunninghamella clavata*		T	n.a.	n.a.	JN205890	JN206604
CBS 362.95	*Cunninghamella clavata*			China	soil	JN205891	
CBS 156.28	*Cunninghamella echinulata*		NT	n.a.	n.a.	JN205895	HM849702
CBS 656.85	*Cunninghamella echinulata*			Egypt	soil	JN205896	JN206598
CBS 766.68	*Cunninghamella echinulata*			n.a.	n.a.	JN205894	
CBS 545.75	*Cunninghamella echinulata* var. *antarctica*	*C. antarctica*	T	Chile	soil	JN205893	JN206597
CBS 167.53	*Cunninghamella elegans*			Canada	*Linum usitatissimum*; seed	JN205882	HM849700
CBS 318.78	*Cunninghamella elegans*	*C. phaeospora*		Turkey	soil under shrub vegetation	JN205886	
CBS 773.68	*Cunninghamella elegans*			former Czechoslovakia	n.a.	JN205887	
CBS 781.68	*Cunninghamella elegans*	*C. phaeospora*		n.a.	n.a.	JN205885	
CNM-CM5114	*Cunninghamella elegans*			Spain	human; lung, biopsy sample	JN205884	
CBS 168.53	*Cunninghamella homothallica*		T	Japan	soil	JN205863	JN206605
CBS 347.69	*Cunninghamella intermedia*	*C. phaeospora*	T of *C. brunnea*	India	n.a.	JN205892	JN206606
CBS 692.68	*Cunninghamella phaeospora*		NT	Indonesia	soil	JN205864	HM849697
CBS 989.96	*Cunninghamella vesiculosa*		T	India	soil of *Shorea robusta* forest	JN205897	HM849693
CBS 695.76	*Dichotomocladium elegans*			USA	dung of rodent	JN205840	HM849715
CBS 714.74	*Dichotomocladium elegans*		T	USA	dung of mouse	JN205839	JN206555
CBS 164.61	*Dichotomocladium hesseltinei*		T	India	soil of a cultivated field	JN205841	JN206556
CBS 439.76	*Dichotomocladium robustum*			USA	dung of mouse	JN205842	
CBS 440.76	*Dichotomocladium robustum*		T	USA	dung of mouse	JN205843	JN206557
CBS 243.57	*Ellisomyces anomalus*		T	USA	dung of lizard	JN205992	JN206423
CBS 697.76	*Ellisomyces anomalus*			USA	dung of mouse	JN205993	
CBS 290.86	*Fennellomyces heterothallicus*		AUT	India	dung of house lizard	JN205844	JN206540
CBS 292.86	*Fennellomyces heterothallicus*		AUT	India	dung of shrew		JN206539
CBS 158.54	*Fennellomyces linderi*		T	USA	poplin	JN205846	HM849723
CBS 190.32	*Gilbertella persicaria*	*G. persicaria* var. *persicaria*	T	USA	*Prunus persica*; fruit	HM999958	HM849691
CBS 246.59	*Gilbertella persicaria*	*G. persicaria* var. *persicaria*		USA	trickling filter plant	JN206222	
CBS 325.71A	*Gilbertella persicaria*	*G. persicaria* var. *persicaria*		Indonesia	*Saccharum officinarum*; leaf	JN206220	
CBS 325.71D	*Gilbertella persicaria*	*G. persicaria* var. *persicaria*		Indonesia	wood	JN206225	
CBS 403.51	*Gilbertella persicaria*	*Rhizopus stolonifer*		Japan	n.a.	JN206221	
CBS 421.77	*Gilbertella persicaria*	*G. persicaria* var. *persicaria*		Pakistan	soil	JN206223	
CBS 442.64	*Gilbertella persicaria*	*G. persicaria* var. *indica*	T of *G. persicaria* var. *indica*	India	n.a.	JN206219	
CBS 532.77	*Gilbertella persicaria*	*G. persicaria* var. *persicaria*		India	dung of mouse		JN206517
CBS 565.91	*Gilbertella persicaria*	*G. hainanensis*	T of *G. hainanensis*	China	dung of swine	JN206226	
CBS 785.97	*Gilbertella persicaria*	*Mucor thermophilus*		n.a.	n.a.	JN206218	
CBS 102.44	*Gongronella butleri*			Italy	n.a.	JN206284	
CBS 157.25	*Gongronella butleri*		T of *G. urceolifera*	Indonesia	*Cocos nucifera*; root		JN206607
CBS 179.28	*Gongronella butleri*			n.a.	n.a.	JN206286	
CBS 216.58	*Gongronella butleri*		T of *Mucor vesiculosus*	UK	garden soil	JN206285	HM849698
CBS 415.67	*Gongronella butleri*			Brazil	soil	JN206288	
CBS 969.73	*Gongronella butleri*			Chile	volcanic ash soil	JN206287	
CBS 244.62	*Gongronella lacrispora*		T	USA	dooryard soil		JN206609
CBS 162.75	*Halteromyces radiatus*		T	Australia	mud from mangrove forest, contaminated with effluent	JN206290	JN206596
CBS 223.63	*Helicostylum cordense*		IT	India	forest soil	JN206193	JN206506
CBS 169.57	*Helicostylum elegans*			UK	dead isopod (woodlouse)		JN206471
CBS 107.23	*Helicostylum pulchrum*			n.a.	n.a.	JN206053	
CBS 258.59	*Helicostylum pulchrum*		T of *H. venustellum*	UK, England	isopod, on the underside of a disturbed pine stump	JN206054	
CBS 259.68	*Helicostylum pulchrum*			Germany	air-dried raw sausage	JN206052	
CBS 639.69	*Helicostylum pulchrum*			USA	spoiled beef crackling	JN206055	
CBS 197.68	*Hesseltinella vesiculosa*		IT	Brazil	rice-field soil		JN206610

Table 1 (cont.)

Strain number	Species	Species name at the beginning of the study	Status	Country	Source	ITS	LSU
CBS 254.85	*Hyphomucor assamensis*			Malaysia	*Burmannia*	JN206212	JN206440
CBS 415.77	*Hyphomucor assamensis*		T	India	n.a.	JN206211	JN206439
CBS 174.67	*Lentamyces parricida*		NT	UK	grassland soil, surface layer	JN206293	JN206535
CBS 100.17	*Lichtheimia corymbifera*	*Mycocladus corymbifer*		n.a.	n.a.	GQ342885	GQ342942
CBS 100.51	*Lichtheimia corymbifera*	*Mycocladus corymbifer*		n.a.	n.a.	GQ342886	GQ342939
CBS 102.48	*Lichtheimia corymbifera*	*Mycocladus corymbifer*		India	mouldy shoe	GQ342888	GQ342910
CBS 115811	*Lichtheimia corymbifera*	*Mycocladus corymbifer*		Germany	indoor air	GQ342887	GQ342932
CBS 429.75	*Lichtheimia corymbifera*	*Mycocladus corymbifer*	NT	Afghanistan	soil	GQ342878	GQ342903
CBS 100.31	*Lichtheimia corymbifera*	*Mycocladus corymbifer*		n.a.	aborted cow	GQ342879	GQ342914
CBS 101040	*Lichtheimia corymbifera*	*Mycocladus corymbifer*		France	human; keratomycosis	GQ342882	GQ342918
CBS 109940	*Lichtheimia corymbifera*	*Mycocladus corymbifer*		Norway	human; finger tissue	GQ342881	GQ342917
CBS 120580	*Lichtheimia corymbifera*	*Mycocladus corymbifer*		France	human; lung	GQ342884	GQ342919
CBS 120581	*Lichtheimia corymbifera*	*Mycocladus corymbifer*		France	human; bronchia	GQ342883	GQ342948
CBS 120805	*Lichtheimia corymbifera*	*Mycocladus corymbifer*		France	human; bone	GQ342880	GQ342915
CBS 519.71	*Lichtheimia corymbifera*	*Absidia griseola*	T of *Absidia griseola*	Japan	n.a.	GQ342889	GQ342904
CBS 100.28	*Lichtheimia hyalospora*	*Mycocladus blakesleeanus*; *Absidia blakesleeana*	T of *Absidia blakesleeana*	USA	*Bertholletia excelsa*; nut	GQ342896	GQ342902
CBS 100.36	*Lichtheimia hyalospora*	*Mycocladus blakesleeanus*; *Absidia blakesleeana*		n.a.	n.a.	GQ342898; GQ342897	GQ342943
CBS 102.36	*Lichtheimia hyalospora*	*Mycocladus blakesleeanus*; *Absidia blakesleeana*	T of *Absidia cristata*	Ghana	*Manihot esculenta*; stem	GQ342895	GQ342907
CBS 518.71	*Lichtheimia hyalospora*	*Mycocladus blakesleeanus* var. *atrosporus*; *Absidia blakesleeana* var. *atrospora*	T of *Absidia blakesleeana* var. *atrospora*	Japan	n.a.	GQ342894	GQ342944
CBS 173.67	*Lichtheimia hyalospora*	*Mycocladus hyalosporus*; *Absidia hyalospora*	NT	Philippines	fermented food taosi	GQ342893	GQ342905
CBS 291.66	*Lichtheimia ornata*	*Mycocladus corymbifer*	T of *Absidia ornata*	India	dung of bird	GQ342891	GQ342946
CNM-CM4978	*Lichtheimia ornata*			Spain	human; wound	GQ342892	JN206554
CBS 958.68	*Lichtheimia ornata*	*Mycocladus corymbifer*		n.a.	n.a.	GQ342890	GQ342936
CBS 100.24	*Lichtheimia ramosa*	*Mycocladus corymbifer*		n.a.	n.a.	GQ342876	GQ342941
CBS 100.49	*Lichtheimia ramosa*	*Mycocladus corymbifer*		Indonesia	dung of cow	GQ342858	GQ342940
CBS 100.55	*Lichtheimia ramosa*	*Mycocladus corymbifer*		n.a.	n.a.	GQ342851	GQ342938
CBS 101.51	*Lichtheimia ramosa*	*Mycocladus corymbifer*		Netherlands	Guinea pig; lung	GQ342859	GQ342945
CBS 101.55	*Lichtheimia ramosa*	*Mycocladus corymbifer*		Switzerland	human; cornea	GQ342865	GQ342947
CBS 103.35	*Lichtheimia ramosa*	*Mycocladus corymbifer*	T of *Absidia gracilis*	n.a.	*Musa sapientum*; fruit	GQ342847	GQ342908
CBS 124198	*Lichtheimia ramosa*	*Mycocladus corymbifer*		Netherlands	culture contaminant	GQ342848	GQ342906
CBS 223.78	*Lichtheimia ramosa*	*Mycocladus corymbifer*		n.a.	cocoa soil	GQ342877	GQ342934
CBS 271.65	*Lichtheimia ramosa*	*Mycocladus corymbifer*		n.a.	n.a.	GQ342875	GQ342937
CBS 582.65	*Lichtheimia ramosa*	*Mycocladus corymbifer*	NT	Ghana	*Theobroma cacao*; seed	GQ342874	GQ342909
CBS 649.78	*Lichtheimia ramosa*	*Mycocladus corymbifer*		India	cultivated field soil	GQ342849	GQ342912
CBS 713.74	*Lichtheimia ramosa*	*Mycocladus corymbifer*		n.a.	n.a.	GQ342856	GQ342935
CNM-CM2166	*Lichtheimia ramosa*	*Mycocladus corymbifer*		Spain	human; sputum	GQ342863	GQ342926
CNM-CM3590	*Lichtheimia ramosa*	*Mycocladus corymbifer*		Spain	human	GQ342869	GQ342924
CNM-CM4119	*Lichtheimia ramosa*	*Mycocladus corymbifer*		Spain	human; skin	GQ342862	GQ342923
CNM-CM4228	*Lichtheimia ramosa*	*Mycocladus corymbifer*		Spain	human; skin	GQ342861	GQ342922
CNM-CM4253	*Lichtheimia ramosa*	*Mycocladus corymbifer*		Spain	human; skin	GQ342860	GQ342921
CNM-CM4261	*Lichtheimia ramosa*	*Mycocladus corymbifer*		Spain	human; lung	GQ342854	GQ342953
CNM-CM4337	*Lichtheimia ramosa*	*Mycocladus corymbifer*		Spain	human; skin	GQ342852	GQ342920
CNM-CM4427	*Lichtheimia ramosa*	*Mycocladus corymbifer*		Spain	human; bronchoaspirate	GQ342853	GQ342931
CNM-CM4537	*Lichtheimia ramosa*	*Mycocladus corymbifer*		Spain	human; skin	GQ342873	GQ342930
CNM-CM4849	*Lichtheimia ramosa*	*Mycocladus corymbifer*		Spain	human; skin	GQ342855; GQ342868	GQ342929
CNM-CM5111	*Lichtheimia ramosa*	*Mycocladus corymbifer*		Spain	human; sputum	GQ342871	GQ342928
CNM-CM5171	*Lichtheimia ramosa*	*Mycocladus corymbifer*		Belgium	human	GQ342864	GQ342927

AS 3.4808	*Lichtheimia ramosa*	*Mycocladus corymbifer*	T of *Absidia idahoensis* var. *thermophila*	China	soil	GQ342867	GQ342955
CBS 112528	*Lichtheimia ramosa*	*Mycocladus corymbifer*		Germany	human; wound, double infection with Candida albicans	GQ342850	GQ342913
CBS 124197	*Lichtheimia ramosa*	*Mycocladus corymbifer*		Greece	human; abscess of the flank	GQ342870	GQ342951
CBS 269.65	*Lichtheimia ramosa*	*Mycocladus corymbifer*		n.a.	n.a.	GQ342857	GQ342949
CNM-CM1638	*Lichtheimia ramosa*	*Mycocladus corymbifer*		Spain	human; gastric juice	GQ342866	GQ342954
CNM-CM3148	*Lichtheimia ramosa*	*Mycocladus corymbifer*		Spain	human; corneal exudate	GQ342872	GQ342925
CBS 420.70	*Lichtheimia sphaerocystis*	*Mycocladus* aff. *blakesleeanus*		India	n.a.	GQ342900	GQ342933
CBS 647.78	*Lichtheimia sphaerocystis*	*Mycocladus* aff. *blakesleeanus*		India	dung of mouse	GQ342899	GQ342911
CBS 648.78	*Lichtheimia sphaerocystis*	*Mycocladus* aff. *blakesleeanus*		India	soil	GQ342901	GQ342916
CBS 388.35	*Mucor abundans*	*M. hiemalis* f. *silvaticus*	NT (designated here)	Germany	forest soil	JN206111	
CBS 521.66	*Mucor abundans*			Russia	forest soil	JN206110	JN206457
CBS 244.58	*Mucor aligarensis*			UK	human; ear	JN206057	
CBS 993.70	*Mucor aligarensis*		T	India	soil	JN206056	JN206461
CBS 185.77	*Mucor amphibiorum*			Central America	diseased *Dendrobates* sp.	JN206170	
CBS 763.74	*Mucor amphibiorum*		T	Germany	amphibian	HM999957	HM849688
CNM-CM2934	*Mucor amphibiorum*			Germany	human	JN206171	
CBS 210.80	*Mucor ardhlaengiktus*		ET (designated here)	India	garden soil	JN206172	JN206504
CBS 528.73	*Mucor ardhlaengiktus*			Mozambique	*Gossypium*; seed	JN206173	
CBS 650.78	*Mucor ardhlaengiktus*	*M.* aff. *variisporus*		India	dung of lizard	JN206174	JN206499
CBS 292.63	*Mucor azygosporus*		IT	USA	dung of lizard	JN206187	JN206497
CBS 251.53	*Mucor bacilliformis*		T	USA	soil	JN206083	JN206451
CBS 573.70	*Mucor bacilliformis*			Japan	agaric	JN206084	JN206452
CBS 293.63	*Mucor bainieri*		IT	India	forest soil	JN205995	JN206424
CBS 129.41	*Mucor brunneogriseus*	*M. plumbeus*	T	Netherlands	aphid	JN205910	
CBS 124110	*Mucor circinelloides* (non of the described formae)			Hawaii island, USA	*Morinda citrifolia*; fermented fruit juice	JN205996	JN206430
CBS 202.28	*Mucor circinelloides* (non of the described formae)	*M. circinelloides* f. *janssenii*		n.a.	n.a.	JN205994	JN206418
CBS 338.71	*Mucor circinelloides* (non of the described formae)	*M. hiemalis* f. *hiemalis*		Turkey	n.a.	JN205998	
CBS 526.68	*Mucor circinelloides* (non of the described formae)	*M. circinelloides* f. *janssenii*		Armenia	soil	JN206015	JN206426
CBS 635.65	*Mucor circinelloides* (non of the described formae)	*M. hiemalis* f. *hiemalis*		UK, England	faeces of diseased *Apis mellifera*	JN205997	JN206428
CBS 846.73	*Mucor circinelloides* (non of the described formae)	*M. flavus*		Chile	soil	JN206014	
CNM-CM5225	*Mucor circinelloides* (non of the described formae)			Austria	human	JN205999	
CBS 108.16	*Mucor circinelloides* f. *circinelloides*			Japan	n.a.	JN205954	JN206413
CBS 111555	*Mucor circinelloides* f. *circinelloides*	*M. hiemalis*		China	sufu starter	JN205943	
CBS 111560	*Mucor circinelloides* f. *circinelloides*	*M. racemosus* f. *racemosus*		Vietnam	sufu, chao	JN205957	
CBS 121702	*Mucor circinelloides* f. *circinelloides*	*M. ramosissimus*		Spain	commercial honey	JN205966	
CBS 123973	*Mucor circinelloides* f. *circinelloides*			Germany	human; thigh necrosis after trauma	JN205958	
CBS 172.27	*Mucor circinelloides* f. *circinelloides*			n.a.	*Artocarpus*; fruit	JN205967	
CBS 192.68	*Mucor circinelloides* f. *circinelloides*			Netherlands	dung of pig	JN205959	
CBS 194.68	*Mucor circinelloides* f. *circinelloides*			South Africa	n.a.	JN205972	
CBS 195.68	*Mucor circinelloides* f. *circinelloides*		NT	Netherlands	air	JN205961	HM849680
CBS 196.68	*Mucor circinelloides* f. *circinelloides*			Turkey	*Triticum aestivum*	JN205968	
CBS 239.35	*Mucor circinelloides* f. *circinelloides*		T of *M. griseoroseus*	Germany	soil	JN205942	
CBS 247.35	*Mucor circinelloides* f. *circinelloides*			Germany	air	JN205962	
CBS 295.34	*Mucor circinelloides* f. *circinelloides*			Ukraine	n.a.	JN205955	
CBS 384.95	*Mucor circinelloides* f. *circinelloides*	*Rhizomucor variabilis* var. *regularior*	T of *Rhizomucor variabilis* var. *regularior*	China	human; face	JN205933	HM849679
CBS 394.68	*Mucor circinelloides* f. *circinelloides*			Netherlands	thawing beef meat	JN205969	
CBS 416.77	*Mucor circinelloides* f. *circinelloides*	*M. rouxii*		n.a.	fermenting rice, component of ‘Chinese yeast’	JN205934	JN206412
CBS 479.70	*Mucor circinelloides* f. *circinelloides*			Finland	soil	JN205973	
CBS 480.70F	*Mucor circinelloides* f. *circinelloides*			India	garden soil	JN205956	
CBS 480.70G	*Mucor circinelloides* f. *circinelloides*			n.a.	n.a.	JN205965	

Table 1 (cont.)

Strain number	Species	Species name at the beginning of the study	Status	Country	Source	ITS	LSU
CNM-CM2437	*Mucor circinelloides* f. *circinelloides*			Spain	human; nail	JN205939	
CNM-CM2541	*Mucor circinelloides* f. *circinelloides*			Spain	human; nail	JN205944	JN206414
CNM-CM2922	*Mucor circinelloides* f. *circinelloides*			Spain	human; wound exudate	JN205963	
CNM-CM3112	*Mucor circinelloides* f. *circinelloides*			Spain	human; peritoneal dialysis	JN205945	
CNM-CM3178	*Mucor circinelloides* f. *circinelloides*			Spain	human; urine	JN205946	
CNM-CM3510	*Mucor circinelloides* f. *circinelloides*			Spain	human; reservoir	JN205947	
CNM-CM3785	*Mucor circinelloides* f. *circinelloides*			Spain	human; catheter (low respiratory tract infection)	JN205948	
CNM-CM3926	*Mucor circinelloides* f. *circinelloides*			Spain	human; arm wound (traumatism with arm amputation)	JN205949	
CNM-CM4299	*Mucor circinelloides* f. *circinelloides*			Spain	human; skin (surgical wound)	JN205950	
CNM-CM4366	*Mucor circinelloides* f. *circinelloides*			Spain	human; wound exudate (polytraumatism, esplenomectomy)	JN205974	JN206415
CNM-CM4526	*Mucor circinelloides* f. *circinelloides*			Spain, Canaries	human; otic exudate	JN205953	
CNM-CM4569	*Mucor circinelloides* f. *circinelloides*			Spain	human; bronchioaspirate (acute lymphoblastic leukemia B cells)	JN205951	
CNM-CM4621	*Mucor circinelloides* f. *circinelloides*			Spain	human; skin of arm (burned patient)	JN205970	
CNM-CM4895	*Mucor circinelloides* f. *circinelloides*			Spain	human; exudate (traumatism)	JN205975	
CNM-CM4974	*Mucor circinelloides* f. *circinelloides*			Spain	human; wound skin	JN205952	
CNM-CM5071	*Mucor circinelloides* f. *circinelloides*			Spain	human; bronchioaspirate	JN205938	
CNM-CM5169	*Mucor circinelloides* f. *circinelloides*			Belgium	human	JN205971	
IHEM 16415	*Mucor circinelloides* f. *circinelloides*			Italy	human; skin of hand, trauma	JN205964	
IHEM 20006	*Mucor circinelloides* f. *circinelloides*			Belgium	human; wound	JN205936	
IHEM 21105	*Mucor circinelloides* f. *circinelloides*			France	human	JN205937	
IHEM 21158	*Mucor circinelloides* f. *circinelloides*			Belgium	human; wound (burned patient)	JN205960	
IHEM 21426	*Mucor circinelloides* f. *circinelloides*			Belgium	human (burned patient)	JN205935	
IHEM 22323	*Mucor circinelloides* f. *circinelloides*			Belgium	human	JN205941	
CBS 116.08	*Mucor circinelloides* f. *griseocyanus*		T	Norway	soil	JN206003	JN206421
CBS 198.28	*Mucor circinelloides* f. *griseocyanus*			n.a.	n.a.	HM999951	JN206420
CBS 223.56	*Mucor circinelloides* f. *griseocyanus*			Netherlands	n.a.	JN206000	
CBS 366.70	*Mucor circinelloides* f. *griseocyanus*			Netherlands	canned strawberries	JN206001	
CBS 698.68	*Mucor circinelloides* f. *griseocyanus*			South Africa	*Zea mays*	JN206002	
CBS 144.93	*Mucor circinelloides* f. *janssenii*	*M.* aff. *ramosissimus*		USA?	human; thigh	JN206012	
CBS 185.68	*Mucor circinelloides* f. *janssenii*		T of *M. kurssanovii*	Russia	grassland soil	JN206006	
CBS 204.68	*Mucor circinelloides* f. *janssenii*			n.a.	iguana; lung	JN206010	
CBS 205.68	*Mucor circinelloides* f. *janssenii*		NT (designated here)	South Africa	forest soil	HM999952	JN206425
CBS 206.68	*Mucor circinelloides* f. *janssenii*			India	n.a.	JN206004	
CBS 227.29	*Mucor circinelloides* f. *janssenii*			n.a.	n.a.	JN206008	
CBS 232.29	*Mucor circinelloides* f. *janssenii*		T of *M. tenellus*	France	n.a.	JN206007	
CBS 243.67	*Mucor circinelloides* f. *janssenii*			South Africa	human	JN206005	
CBS 365.70	*Mucor circinelloides* f. *janssenii*			n.a.	dung of *Dixippus morosus*	JN206009	
CBS 762.74	*Mucor circinelloides* f. *janssenii*			Netherlands	milk powder	JN206011	JN206416
CBS 108.17	*Mucor circinelloides* f. *lusitanicus*		T	n.a.	n.a.	JN205980	
CBS 111228	*Mucor circinelloides* f. *lusitanicus*	*M. racemosus* f. *racemosus*		China	sufu starter, from sufu factory	JN205991 (c1) JN205989 (c3)	JN206429
CBS 111229	*Mucor circinelloides* f. *lusitanicus*	*M. indicus*		China	sufu starter, from sufu factory	JN205983 (c2) JN205990 (c4)	
CBS 236.35	*Mucor circinelloides* f. *lusitanicus*	*M. fragilis*		Germany	*Tremella*	JN205979	JN206422
CBS 242.33	*Mucor circinelloides* f. *lusitanicus*			n.a.	n.a.	JN205987	
CBS 253.35	*Mucor circinelloides* f. *lusitanicus*			USA	*Zea mays*; grain	JN205988	
CBS 276.49	*Mucor circinelloides* f. *lusitanicus*			n.a.	n.a.	JN205984	
CBS 633.65	*Mucor circinelloides* f. *lusitanicus*			South Afrika	*Zea mays*	JN205986	
CBS 847.72	*Mucor circinelloides* f. *lusitanicus*			Portugal	n.a.	JN205981	
CBS 851.71	*Mucor circinelloides* f. *lusitanicus*			n.a.	n.a.	JN205982	
CBS 968.68	*Mucor circinelloides* f. *lusitanicus*			Mexico	n.a.	HM999953	JN206419
CBS 969.68	*Mucor circinelloides* f. *lusitanicus*			Russia	forest soil	JN205985	JN206427

CBS 293.66	*Mucor ctenidius*	*Backusella ctenidia*		USA	desert soil	JN205976	JN206417
CBS 433.87	*Mucor ctenidius*	*Backusella ctenidia*		Kenya	dead plant material	JN205978	
CBS 696.76	*Mucor ctenidius*	*Backusella ctenidia*		USA	dung of pack rat	JN205977	
CBS 156.51	*Mucor durus*	*Circinella rigida*	ET (designated here)	UK, England	soil	JN206112	JN206456
CBS 484.66	*Mucor durus*	*Circinella rigida*		Ukraine	soil	JN206113	
CBS 385.95	*Mucor endophyticus*	*Rhizomucor endophyticus*	HT	China	*Triticum aestivum*; leaves	JN206159	JN206448
CBS 141.20	*Mucor exponens*	*Zygorhynchus exponens* var. *exponens*	NT (designated here)	Germany	n.a.	JN206206	JN206441
CBS 404.58	*Mucor exponens*	*Zygorhynchus exponens* var. *smithii*	LT of *Z. exponens* var. *smithii* (designated here)	UK, England	ploughed field soil	JN206208	
CBS 508.48	*Mucor exponens*	*Zygorhynchus exponens* var *exponens*		Germany	n.a.	JN206207	
CBS 251.35	*Mucor falcatus*		HT	Germany	honeycomb	JN206250	JN206509
CBS 252.35	*Mucor falcatus*			Germany	dung of rabbit	JN206249	
CBS 126.70	*Mucor flavus*		T of *M. mephitis*	USA	dung of mouse	JN206049	JN206469
CBS 182.90	*Mucor flavus*			Czech Republic	floor of room in cave, used for speleotherapy	JN206065	JN206472
CBS 197.71	*Mucor flavus*		T of *M. meridionalis*	Ukraine	dung of wood mouse	JN206066	JN206470
CBS 210.71	*Mucor flavus*		T of *M. peacockensis*	India	dung of peacock	JN206050	JN206462
CBS 230.35	*Mucor flavus*		T of *M. attenuatus*	Germany	dung of roe	JN206061	JN206464
CBS 234.35	*Mucor flavus*		NT	Germany	n.a.	JN206051	JN206468
CBS 664.67	*Mucor flavus*			Finland	forest litter	JN206064	
CBS 681.73	*Mucor flavus*			Germany	wheat field soil	JN206069 (c2) JN206070 (c3)	JN206473
CBS 893.73	*Mucor flavus*		NT of *M. sciurinus*	Russia	forest soil	JN206062 (c1) JN206063 (c2)	JN206465
CBS 992.68	*Mucor flavus*			Antarctica	coastal gravel flat covered by *Bryum argenteum*	JN206067 (c1) JN206068 (c3)	JN206467
CBS 230.29	*Mucor fuscus*		T of *M. petrinsularis* var. *echinosporus*	France	n.a.	JN206204	
CBS 254.48	*Mucor fuscus*		T of *M. bedrchanii*	Germany	n.a.	JN206203	
CBS 282.78	*Mucor fuscus*			France	cheese	JN206201	JN206442
CBS 313.78	*Mucor fuscus*			France	cheese	JN206200	
CBS 530.77	*Mucor fuscus*			India	dung of mouse	JN206202	
CBS 336.68	*Mucor fusiformis*	*Zygorhynchus psychrophilus*	HT	Finland	*Picea abies*; brown needle	JN206157	JN206447
CBS 114.08	*Mucor genevensis*		T	Switzerland	soil	JN206041	JN206435
CBS 404.71	*Mucor genevensis*			Ukraine	dung of field-mouse	JN206042 (c1) JN206043 (c2)	
CBS 535.78	*Mucor genevensis*			USA	n.a.	JN206045 (c1) JN206046 (c3) JN206047 (c4)	JN206436
CBS 564.75	*Mucor genevensis*			Netherlands	*Malus sylvestris*; fruit	JN206044 (c3)	
CBS 383.95	*Mucor gigasporus*			China	soil	JN206246	
CBS 566.91	*Mucor gigasporus*		T	China	soil	JN206247	JN206494
CBS 186.87	*Mucor grandis*		T	India	dung of mouse	JN206252	JN206527
CBS 174.27	*Mucor guiliermondii*		T	Russia	dung of *Periplaneta americana*	JN206082	JN206475
CBS 252.85	*Mucor heterogamus*	*Zygorhynchus heterogamus*		Netherlands	cattle feed	JN206161 (c1) JN206162 (c4)	JN206490
CBS 338.74	*Mucor heterogamus*	*Zygorhynchus heterogamus*		Sweden	sediment in drain pipe	JN206169 (c1) JN206168 (c4)	JN206488
CBS 405.58	*Mucor heterogamus*	*Zygorhynchus heterogamus*	ET (designated here)	n.a.	n.a.	JN206167	JN206487
CBS 580.83	*Mucor heterogamus*	*Zygorhynchus heterogamus*		Netherlands	sandy soil in potato field	JN206163	JN206486
CBS 594.83	*Mucor heterogamus*	*Zygorhynchus heterogamus*		Colombia	soil	JN206164 (c3) JN206165 (c4)	JN206485
CBS 115.18	*Mucor hiemalis*	*M. hygrophilus*		n.a.	n.a.	JN206127	
CBS 118522	*Mucor hiemalis*			Denmark	agricultural soil	JN206138	
CNM-CM2540	*Mucor hiemalis*			Spain	human; nail	JN206140	
CNM-CM5229	*Mucor hiemalis*			Spain	human; nail	JN206141	
Fungiscope AS72	*Mucor hiemalis*			Austria	human	JN206142	
CBS 106.09	*Mucor hiemalis* f. *corticola*		T	Norway	n.a.	JN206130	
CBS 362.68	*Mucor hiemalis* f. *corticola*			Russia	forest soil	JN206132	JN206449

Table 1 (cont.)

Strain number	Species	Species name at the beginning of the study	Status	Country	Source	ITS	LSU
CBS 365.68	*Mucor hiemalis* f. *corticola*			Austria	soil	JN206133	
CBS 366.68	*Mucor hiemalis* f. *corticola*			Austria	soil	JN206139	
CBS 532.78	*Mucor hiemalis* f. *corticola*			Netherlands	soil	JN206145	
CBS 533.78	*Mucor hiemalis* f. *corticola*			Netherlands	greenhouse soil under *Lycopersicon esculentum*	JN206146	
CBS 107.19	*Mucor hiemalis* f. *hiemalis*		T of *M. vallesiacus*	Switzerland	n.a.	JN206137	
CBS 110.19	*Mucor hiemalis* f. *hiemalis*		T of *M. hiemalis* var. *toundrae*	Switzerland	n.a.	JN206136	
CBS 117.08	*Mucor hiemalis* f. *hiemalis*		T of *M. adventitius* var. *aurantiacus*	Switzerland	n.a.	JN206143	
CBS 123972	*Mucor hiemalis* f. *hiemalis*			Germany	human; sputum	JN206128	
CBS 201.65	*Mucor hiemalis* f. *hiemalis*		NT	USA	n.a.	JN206125	HM849683
CBS 242.35	*Mucor hiemalis* f. *hiemalis*		IT of *M. hiemalis* var. *griseus*	Germany	forest soil	JN206134	
CBS 328.92	*Mucor hiemalis* f. *hiemalis*			Italy	lake sediment, submerged	JN206135	
CBS 337.71D	*Mucor hiemalis* f. *hiemalis*			Norway	soil	JN206131	
CBS 454.71	*Mucor hiemalis* f. *hiemalis*			n.a.	dung of rabbit	JN206126	
CBS 528.78	*Mucor hiemalis* f. *hiemalis*			Netherlands	agaric	JN206144	
CBS 980.68	*Mucor hiemalis* f. *hiemalis*			Netherlands	*Coccinella*	JN206129	
CBS 255.36	*Mucor inaequisporus*		T	Ghana	*Spondias mombin*; fruit	JN206177	JN206502
CBS 351.50	*Mucor inaequisporus*			Indonesia	*Musa sapientum*; fruit	JN206178	JN206500
CBS 496.66	*Mucor inaequisporus*			Japan	*Diospyros kaki*; immature fruit	JN206179	JN206501
CBS 120.08	*Mucor indicus*			n.a.	n.a.	JN206182	
CBS 120585	*Mucor indicus*			India	human; muscle	JN206180	
CBS 123974	*Mucor indicus*			Germany	human; gastrointestinal infection	JN206181	
CBS 226.29	*Mucor indicus*		ET (designated here)	Switzerland	n.a.	HM999956	HM849690
CBS 414.77	*Mucor indicus*	*Ascidiophora* sp.		India	dung of berber goat	JN206185	
CBS 422.71	*Mucor indicus*			Indonesia	*Dioscorea*; tuber	JN206186	
CBS 535.80	*Mucor indicus*			South Africa	sorghum malt	JN206184	
CBS 671.79	*Mucor indicus*			Indonesia	n.a.	JN206183	
CBS 100164	*Mucor irregularis*	*M. hiemalis* f. *luteus*		China	human; nasolabial infection	JN206153	
CBS 103.93	*Mucor irregularis*	*Rhizomucor variabilis*	T of *Rhizomucor variabilis*	China	human; hand	JN206150	HM849684
CBS 609.78	*Mucor irregularis*	*M. hiemalis* f. *hiemalis*		Nigeria	garden soil	JN206152	
CBS 654.78	*Mucor irregularis*	*M.* aff. *variosporus*		India	owl pellet	JN206151	
CBS 700.71	*Mucor irregularis*	*M. hiemalis* f. *luteus*	T	India	soil	JN206154	JN206450
CBS 977.68	*Mucor irregularis*	*M. hiemalis* f. *hiemalis*		India	n.a.	JN206155 (c1) JN206156 (c2)	
CBS 154.69	*Mucor japonicus*	*Zygorhynchus japonicus*	NT (designated here)	Russia	forest soil	JN206158	JN206446
CBS 638.74	*Mucor lanceolatus*	*M. fuscus*		France	cheese	JN206205	JN206443
CBS 143.85	*Mucor laxorrhizus*		NT	UK	lake mud	JN206209	JN206444
CBS 237.66	*Mucor laxorrhizus*			Ukraine	peat	JN206210	
CBS 243.35	*Mucor luteus*	*M. hiemalis* f. *luteus*	T	Germany	n.a.	HM999954	HM849685
CBS 244.35	*Mucor luteus*	*M. hiemalis* f. *luteus*		Germany	n.a.	JN206148	
CBS 301.74	*Mucor luteus*	*M. hiemalis* f. *luteus*		Germany	n.a.	JN206149	
CBS 567.70A	*Mucor luteus*	*M. hiemalis* f. *luteus*		Japan	agaric	JN206147	
CBS 215.27	*Mucor megalocarpus*	*Zygorhynchus macrocarpus*	ET (designated here)	France	n.a.	JN206160	JN206489
CBS 204.28	*Mucor microsporus*		T of *M. cylindrosporus*	France	n.a.	JN206272	JN206521
CBS 245.35	*Mucor microsporus*			Austria	soil	JN206273	
CBS 586.67	*Mucor minutus*		T of *M. griseoochraceus* var. *minuta*	India	n.a.	JN206048	JN206463
CBS 216.27	*Mucor moelleri*	*Zygorhynchus moelleri*		France	n.a.	JN206116	
CBS 380.29	*Mucor moelleri*	*Zygorhynchus moelleri*		Netherlands	wood mixed with soil	JN206119	
CBS 406.58	*Mucor moelleri*	*Zygorhynchus moelleri*	NT (designated here)	USA	soil	JN206121	
CBS 444.65	*Mucor moelleri*	*Zygorhynchus moelleri*	LT of *M. saximontensis* (designated here)	USA	soil	JN206114	HM849682
CBS 460.51	*Mucor moelleri*	*Zygorhynchus moelleri*		UK, England	culture contaminant	JN206120	
CBS 501.66	*Mucor moelleri*	*Zygorhynchus moelleri*		Austria	soil	JN206118	
IHEM 21156	*Mucor moelleri*	*Zygorhynchus moelleri*		France	human	JN206115	

CBS 402.58	*Mucor moelleri* f. *californiensis*	*Zygorhynchus californiensis*	ET (designated here)	USA	soil	JN206117	
CBS 531.77	*Mucor mousanensis*			India	dung of mouse	JN206016	
CBS 721.76	*Mucor mousanensis*			Taiwan	dung of *Rattus norvegensis*	JN206018	
CBS 999.70	*Mucor mousanensis*		T	India	dung of mouse	JN206017	JN206434
CBS 228.29	*Mucor mucedo*		T of *M. murorum*	Russia	n.a.	JN206088	
CBS 296.35	*Mucor mucedo*			Germany	dung of rabbit	JN206090	
CBS 525.68	*Mucor mucedo*			Armenia	dung of field-mouse	JN206087	
CBS 542.66	*Mucor mucedo*			Ukraine	water	JN206086	
CBS 640.67	*Mucor mucedo*		NT	Netherlands	cow; nose effluent	JN206085	HM849687
CBS 834.73	*Mucor mucedo*			n.a.	dung of dog	JN206093 (c1) JN206091 (c2)	
CBS 836.73	*Mucor mucedo*	*M. piriformis*		Germany	wheat field soil	JN206092 (c1)	
CBS 987.68	*Mucor mucedo*			Netherlands	dung of rabbit	JN206089	JN206480
CBS 110662	*Mucor multiplex*	*Zygorhynchus multiplex*	HT	China	paddy field soil	JN206166	JN206484
CBS 735.70	*Mucor nederlandicus*			n.a.	n.a.	JN206176	JN206503
CBS 120.71	*Mucor odoratus*			USA	n.a.	JN206195	
CBS 130.41	*Mucor odoratus*		T	Denmark	laboratory air	JN206197	JN206495
CBS 179.76A	*Mucor odoratus*			Germany	dung of cow	JN206196	
CBS 201.71	*Mucor odoratus*			Netherlands	dung of horse	JN206198	
CBS 572.70	*Mucor odoratus*			Japan	soil	JN206194	
CBS 417.77	*Mucor parviseptatus*	*M. laxorrhizus* var. *ovalisporus*	T	Australia	sandy heath soil	JN206108	JN206453
CBS 522.79	*Mucor parviseptatus*	*M. laxorrhizus* var. *ovalisporus*		Austria	soil	JN206109	
CBS 111230	*Mucor piriformis*			n.a.	n.a.	JN206030 (c1)	
CBS 169.25	*Mucor piriformis*		NT	n.a.	*Pyrus communis*; decaying fruit	JN206028	HM849681
CBS 175.27	*Mucor piriformis*			France	n.a.	JN206029	
CBS 256.85	*Mucor piriformis*			USA	soil and decaying pear fruit	JN206031	
CBS 527.68	*Mucor piriformis*			Romania	river water	JN206034	JN206476
CBS 528.68	*Mucor piriformis*			Russia	ant hill	JN206032	
CBS 177.46	*Mucor plasmaticus*			UK, England	dung of rabbit	JN206076 (c1) JN206077 (c4)	
CBS 275.49	*Mucor plasmaticus*			Netherlands	dung of mouse	JN206078 (c2) JN206079 (c4)	JN206483
CBS 402.73	*Mucor plasmaticus*			Russia	dung of forest-mouse	JN206081 (c1) JN206080 (c4)	
CBS 226.32	*Mucor plumbeus*			Canada	forest soil	JN205916	
CBS 284.78	*Mucor plumbeus*			Netherlands	lettuce	JN205914	
CBS 295.63	*Mucor plumbeus*			Zaire	leaf litter	JN205912	
CBS 312.78	*Mucor plumbeus*			Netherlands	horse meat	JN205915	
CBS 630.74	*Mucor plumbeus*			France	cheese	JN205918	
CBS 633.74	*Mucor plumbeus*			Switzerland	cat; subcutaneous tissue	JN205913	
CBS 634.74	*Mucor plumbeus*			Germany	human; biopsy material	HM999955	HM849677
CBS 814.96	*Mucor plumbeus*			Sweden	wheat bran	JN205917	
CBS 652.78	*Mucor prayagensis*	*M.* aff. *variisporus*		India	dung of shrew	JN206189 (c1) JN206190 (c3)	JN206498
CBS 816.70	*Mucor prayagensis*		T	India	n.a.	JN206188	JN206496
CBS 111557	*Mucor racemosus* f. *racemosus*	*M. circinelloides* f. *circinelloides*		China	sufu starter	JN205902	
CBS 113.08	*Mucor racemosus* f. *racemosus*	*M. racemosus* f. *sphaerosporus*	IT of *M. dimorphosporus*	Switzerland	n.a.	JN205909	
CBS 204.74	*Mucor racemosus* f. *racemosus*	*M. sinensis*	T of *M. sinensis*	China	soya cheese	JN205899	
CBS 222.81	*Mucor racemosus* f. *racemosus*			Netherlands	*Juglans regia*; nut	JN205906	
CBS 260.68	*Mucor racemosus* f. *racemosus*		NT (designated here)	Switzerland	n.a.	JN205898	HM849676
CBS 271.86	*Mucor racemosus* f. *racemosus*	*M. racemosus* f. *sphaerosporus*		Spain, Tenerife	dung	JN205900	
CBS 369.71	*Mucor racemosus* f. *racemosus*			Finland	human; skin	JN205905	
CBS 616.63	*Mucor racemosus* f. *racemosus*			n.a.	*Agapornis*; lung	JN205903	
CBS 636.67	*Mucor racemosus* f. *racemosus*	*M. racemosus* f. *chibinensis*	NT (designated here) of *M. racemosus* f. *chibinensis*	Russia	grassland soil	JN205904	
CBS 657.68	*Mucor racemosus* f. *racemosus*			Belgium	contaminated cheese	JN205901	
CBS 660.66	*Mucor racemosus* f. *racemosus*	*M. racemosus* f. *chibinensis*		Ukraine	halva	JN205911	
CBS 661.66	*Mucor racemosus* f. *racemosus*			Austria	soil	JN205908	
CNM-CM2569	*Mucor racemosus* f. *racemosus*			Spain	human; nail	JN205929	
CNM-CM3862	*Mucor racemosus* f. *racemosus*			Spain	human	JN205930	

Table 1 (cont.)

Strain number	Species	Species name at the beginning of the study	Status	Country	Source	ITS	LSU
CBS 115.08	*Mucor racemosus* f. *sphaerosporus*		IT	Norway	n.a.	JN205919	JN206433
CBS 143.70	*Mucor racemosus* f. *sphaerosporus*			n.a.	storage rot of *Cucurbita maxima*	JN205925	
CBS 238.35	*Mucor racemosus* f. *sphaerosporus*			Germany	wood	JN205920	
CBS 347.87	*Mucor racemosus* f. *sphaerosporus*			USA	soil and litter	JN205924	
CBS 538.78	*Mucor racemosus* f. *sphaerosporus*			Germany	sausage	JN205922	
CBS 539.78	*Mucor racemosus* f. *sphaerosporus*			France	cheese	JN205923	
CBS 571.70	*Mucor racemosus* f. *sphaerosporus*	*M. plasmaticus*		Japan	dung of horse	JN205926	
CBS 574.70	*Mucor racemosus* f. *sphaerosporus*			Japan	steamed sweet potato	JN205921	
CBS 634.78	*Mucor racemosus* f. *sphaerosporus*	*M. racemosus* f. *racemosus*		France	cheese	JN205927 (c2) JN205928 (c4)	
CBS 135.65	*Mucor ramosissimus*		NT	Uruguay	human; nasal lesion	JN205932	HM849678
CBS 598.78	*Mucor saturninus*			Netherlands	fruit body of *Hygrophoropsis aurantiaca*	JN206074	
CBS 599.78	*Mucor saturninus*			Netherlands	chicken leg	JN206073 (c3) JN206075 (c4)	
CBS 974.68	*Mucor saturninus*		NT	Netherlands	soil	JN206072	JN206458
CBS 249.35	*Mucor silvaticus*	*M. hiemalis* f. *silvaticus*		Germany	soil of *Picea forest*	JN206122	JN206455
CBS 412.71	*Mucor silvaticus*	*M. hiemalis* f. *silvaticus*	NT (designated here)	Denmark	forest soil	JN206124	
CBS 509.66	*Mucor silvaticus*	*M. hiemalis* f. *silvaticus*		Germany	forest soil	JN206123	
CBS 122.23	*Mucor* sp.	*M. plasmaticus*		Germany	n.a.	JN206040	JN206479
CBS 125018	*Mucor* sp.			France	strawberries	JN206038 (c1) JN206039 (c2)	JN206478
CBS 334.71	*Mucor* sp.	*M. hiemalis* f. *hiemalis*		Benin	tropical vegetable	JN206248	JN206518
CBS 541.78	*Mucor* sp.	*M. circinelloides* f. *griseocyanus*		South Africa	*Zea mays*	JN206013	JN206431
CBS 608.78	*Mucor* sp.	*M. circinelloides* f. *griseocyanus*		USA	gymnosperm litter	JN205931	JN206432
CBS 837.73A	*Mucor* sp.	*M. piriformis*		Netherlands	*Ribes rubrum*	JN206033	JN206482
CBS 100.66	*Mucor strictus*		T of *M. kanivcevii*	Ukraine	grassland soil	JN206035	JN206477
CBS 368.71A	*Mucor strictus*			Norway	soil of dried up bog	JN206036	
CBS 576.66	*Mucor strictus*		NT	Austria	soil at lake shore	JN206037	
CBS 221.71	*Mucor ucrainicus*		T	Ukraine	dung of mouse	JN206191	
CBS 674.88	*Mucor ucrainicus*			Germany	soil of litter layer	JN206192	JN206507
CBS 837.70	*Mucor variisporus*		T	India	n.a.	JN206175	JN206508
CBS 148.69	*Mucor zonatus*		T	Germany	soil	JN206104	JN206454
CBS 183.76	*Mucor zonatus*			Sweden	forest soil under *Picea abies*	JN206106 (c3) JN206107 (c4)	
CBS 529.83	*Mucor zonatus*			Sweden	mould-infected *Pinus* wood	JN206105	
CBS 416.67	*Mucor zychae* var. *zychae*		T	India	manured soil	JN206199	
CBS 186.68	*Mycotypha microspora*			Germany	decaying wood	JN206215	
CBS 230.32	*Mycotypha microspora*		T	Netherlands	*Citrus aurantium*; peel, contaminant	JN206217	JN206510
CBS 610.92	*Mycotypha microspora*			Germany	washroom in hospital	JN206216	
CBS 109960	*Mycotypha* sp.	*M. microspora*		Thailand	human; pus of wound	JN206214	JN206511
CBS 412.66	*Parasitella parasitica*		T	USA	*Paeonia*	JN206027	JN206438
CBS 152.69	*Parasitella* sp.	*P. parasitica*		n.a.	n.a.	JN206024 (c1) JN206025 (c3)	JN206437
CBS 207.28	*Parasitella* sp.	*P. parasitica*		USA	n.a.	JN206026	
CBS 113.76	*Phascolomyces articulosus*		T	Panama	dung of bat		JN206547
CBS 112.20	*Phycomyces blakesleeanus*	*P. blakesleeanus* var. *piloboloides*	T	Germany	n.a.	JN206303	
CBS 188.27	*Phycomyces blakesleeanus*			USA	n.a.	JN206304	
CBS 269.32	*Phycomyces blakesleeanus*	*P. blakesleeanus* var. *piloboloides*		Germany	n.a.	JN206309	
CBS 270.32	*Phycomyces blakesleeanus*			Germany	n.a.	JN206305	HM849662
CBS 282.35	*Phycomyces blakesleeanus*			Netherlands	n.a.	JN206306	
CBS 284.35	*Phycomyces blakesleeanus*			Germany	n.a.	JN206308	
CBS 286.35	*Phycomyces blakesleeanus*	*P. blakesleeanus* var. *piloboloides*		Germany	n.a.	JN206307	
CBS 131.23	*Pilaira anomala*			n.a.	n.a.	JN206097	
CBS 396.71C	*Pilaira anomala*			UK, Scotland	dung of rabbit	JN206099	

CBS 424.70	*Pilaira anomala*			UK	dung	JN206101	
CBS 695.68	*Pilaira anomala*			Netherlands	dung	JN206098	JN206460
CBS 699.71	*Pilaira anomala*			Germany	dung of cow	JN206100	
CBS 181.26	*Pilaira moreaui*			France	n.a.	JN206094	JN206459
CBS 411.67	*Pilaira moreaui*	*Backusella lamprospora*		India	n.a.	JN206095	
CBS 496.71	*Pilaira moreaui*			Germany	dung of cow	JN206096	
CBS 523.68	*Pilaira moreaui* var. *caucasica*	*P. caucasica*	T	Armenia	dung of mouse	JN206299	JN206532
CBS 302.83	*Pilobolus umbonatus*			Netherlands	dung of deer	JN206274	HM849665
CBS 425.50	*Pilobolus umbonatus*			Germany	n.a.	JN206275	
CBS 962.68	*Pirella circinans*		T	India	soil	JN206102	JN206512
CBS 524.68	*Pirella naumovi*		T	Armenia	dung of mouse	JN206103	JN206474
CBS 588.88	*Pirella* sp.	*P. circinans*		USA	beneath Joshua trees	JN206071	JN206481
CBS 153.58	*Poitrasia circinans*		T	Trinidad and Tobago	soil	JN206239	JN206516
CBS 647.70	*Poitrasia circinans*			Sri Lanka	soil	JN206240	
CBS 661.86	*Protomycocladus faisalabadensis*			India	dung of rodent		JN206558
CBS 205.77	*Radiomyces embreei*			USA	dung of lizard (?)	JN206291	HM849663
CBS 206.77	*Radiomyces embreei*			USA	dung of pack rat	JN206292	
CBS 254.60	*Radiomyces embreei*		T	USA	dung of mouse		JN206538
CBS 255.60	*Radiomyces spectabilis*		T	USA	dung of lizard		JN206537
CBS 182.67	*Rhizomucor miehei*		T	USA	retting *Parthenium argentatum*	HM999959 (c1) HM999960 (c2) HM999961 (c4)	HM849717
CBS 209.77A	*Rhizomucor miehei*			USA	soil	JN206322 (c1) JN206321 (c2)	
CBS 360.92	*Rhizomucor miehei*			Australia	human; kidney and liver (leukemic patient)	JN206318	
CBS 429.70	*Rhizomucor miehei*			UK, England	*Hordeum*; stored grains	JN206319 (c1) JN206320 (c4)	
CBS 179.69	*Rhizomucor pusillus*	*R. tauricus*	T of *R. tauricus*	Ukraine	forest soil	JN206310	
CBS 219.31	*Rhizomucor pusillus*			n.a.	pig; kidney	JN206311	
CBS 354.68	*Rhizomucor pusillus*		ET (designated here)	Netherlands	corn meal	JN206312	HM849716
CBS 425.78	*Rhizomucor pusillus*			USA	soil	HM999962	
CNM-CM2752	*Rhizomucor pusillus*			Spain	human; sputum	JN206313	
CNM-CM2935	*Rhizomucor pusillus*			n.a.	n.a.	JN206314	
CNM-CM2974	*Rhizomucor pusillus*			Spain	human; peritoneal fluid	JN206315	
CNM-CM4727	*Rhizomucor pusillus*			Spain	human; biopsy sample	JN206316	
CNM-CM5124	*Rhizomucor pusillus*			Spain	human; lung, biopsy sample	JN206317	
CBS 340.62	*Rhizopus americanus*	*R. sexualis* var. *americanus*	T	USA	air	HM999967 (c3)	HM849674
CBS 109939	*Rhizopus arrhizus* var. *arrhizus*	*R. oryzae*		Canada	human; dermal lesions of back	JN206330	
CBS 110.17	*Rhizopus arrhizus* var. *arrhizus*	*R. oryzae*	T of *R. maydis*	Switzerland	n.a.	JN206327	
CBS 112.07	*Rhizopus arrhizus* var. *arrhizus*	*R. oryzae*	T of *R. oryzae*	Netherlands	n.a.	JN206323	HM849659
CBS 118614	*Rhizopus arrhizus* var. *arrhizus*	*R. oryzae*		Turkey	human; palate	JN206326	
CBS 125017	*Rhizopus arrhizus* var. *arrhizus*	*R. oryzae*		Greece	human; sinus (leukemic patient)	JN206332	
CBS 146.90	*Rhizopus arrhizus* var. *arrhizus*	*R. oryzae*		Netherlands	human; palatum molle	JN206324	
CBS 286.55	*Rhizopus arrhizus* var. *arrhizus*	*R. oryzae*		n.a.	rabbit brain	JN206328	
CBS 330.53	*Rhizopus arrhizus* var. *arrhizus*	*R. oryzae*	T of *R. boreas*	Japan	n.a.	JN206331	
CBS 438.76	*Rhizopus arrhizus* var. *arrhizus*	*R. oryzae*	NT of *Amylomyces rouxii*	Thailand	Look Pang (sweet fermented glutenous rice)	JN206329	
CBS 515.94	*Rhizopus arrhizus* var. *arrhizus*	*R. oryzae*		Singapore	tempeh	JN206325	
Chakrabarti710113	*Rhizopus arrhizus* var. *arrhizus*			India	human	JN206333	
CBS 111231	*Rhizopus arrhizus* var. *delemar*	*R. oryzae*		n.a.	n.a.	JN206338	
CBS 111760	*Rhizopus arrhizus* var. *delemar*	*R. oryzae*		Vietnam	starch-based rice wine starters	JN206334	
CBS 120593	*Rhizopus arrhizus* var. *delemar*	*R. oryzae*		France	human; lung	JN206340	
CBS 392.95	*Rhizopus arrhizus* var. *delemar*	*R. oryzae*	T of *R. delemar* var. *multiplicisporus*	n.a.	air	JN206336	
CBS 402.51	*Rhizopus arrhizus* var. *delemar*	*R. oryzae*	T of *R. javanicus* var. *kawasakiensis*	Japan	n.a.	JN206339	
CBS 544.80	*Rhizopus arrhizus* var. *delemar*	*R. oryzae*		South Africa	sorghum malt	JN206337	
CBS 607.68	*Rhizopus arrhizus* var. *delemar*	*R. oryzae*		n.a.	spaghetti	JN206341	
Chakrabarti710104	*Rhizopus arrhizus* var. *delemar*			India	human	JN206335	
CBS 427.87	*Rhizopus caespitosus*		T	India	n.a.	HM999965	HM849671
CBS 111232	*Rhizopus homothallicus*			India	n.a.	JN206365	JN206404

Table 1 (cont.)

Strain number	Species	Species name at the beginning of the study	Status	Country	Source	ITS	LSU
CBS 336.62	*Rhizopus homothallicus*		T	Guatemala	tropical desert soil	HM999968	HM849670
CBS 117.43	*Rhizopus lyococcus*	*R. stolonifer* var. *reflexus*		Netherlands	*Hordeum vulgare*; grain	JN206375	
CBS 320.35	*Rhizopus lyococcus*	*R. stolonifer* var. *reflexus*		n.a.	n.a.	JN206373	JN206534
CBS 398.95	*Rhizopus lyococcus*			n.a.	n.a.	JN206374	
CBS 111563	*Rhizopus microsporus*			Vietnam	sufu starter: rice wine tablet	JN206363	
CBS 357.93	*Rhizopus microsporus* var. *azygosporus*		T	Indonesia	tempeh	JN206343	HM849666
CBS 359.92	*Rhizopus microsporus* var. *azygosporus*			Australia	human; liver of premature infant, necrotising enterocolitis	JN206342	
CBS 294.31	*Rhizopus microsporus* var. *chinensis*		T of *R. bovinus*	France	cow foetus	JN206351	
CBS 344.29	*Rhizopus microsporus* var. *chinensis*		T of *R. pypmaeus*	Russia	n.a.	JN206360	
CBS 388.34	*Rhizopus microsporus* var. *chinensis*		T of *R. chinensis* var. *liquefaciens*	Japan	n.a.	JN206354	
CBS 394.34	*Rhizopus microsporus* var. *chinensis*		T of *R. pseudochinensis* var. *thermosus*	Japan	n.a.	JN206359	
CBS 537.80	*Rhizopus microsporus* var. *chinensis*			South Africa	sorghum malt	JN206355	
CBS 631.82	*Rhizopus microsporus* var. *chinensis*		T	China	bread	JN206344	HM849668
CBS 112285	*Rhizopus microsporus* var. *microsporus*			Mozambique	maize; ground nuts	JN206364	JN206403
CBS 308.87	*Rhizopus microsporus* var. *microsporus*			Australia	human; hand, necrotic tissue	JN206357	
CBS 699.68	*Rhizopus microsporus* var. *microsporus*		NT	Ukraine	soil	HM999970	HM849669
CBS 112587	*Rhizopus microsporus* var. *oligosporus*			Indonesia	tempeh	JN206358	
CBS 228.95	*Rhizopus microsporus* var. *oligosporus*			Indonesia	tempeh	JN206348	
CBS 337.62	*Rhizopus microsporus* var. *oligosporus*		NT	Indonesia	probably from tempeh	JN206362	
CBS 338.62	*Rhizopus microsporus* var. *oligosporus*			Indonesia	tempeh fermentation	JN206352	
CBS 102277	*Rhizopus microsporus* var. *rhizopodiformis*			n.a.	human; rhinocerebral infection	JN206356	
CBS 118987	*Rhizopus microsporus* var. *rhizopodiformis*			France	human; cutaneous lesion	JN206346	
CBS 196.77	*Rhizopus microsporus* var. *rhizopodiformis*			USA	herbal tea from *Borbonia cordata*	JN206361	
CBS 220.92	*Rhizopus microsporus* var. *rhizopodiformis*			Netherlands	human; lung	JN206347	
CBS 258.79	*Rhizopus microsporus* var. *rhizopodiformis*			Sweden	dust in saw mill	JN206349	
CBS 343.29	*Rhizopus microsporus* var. *rhizopodiformis*		T of *R. pusillus*	Russia	n.a.	JN206353	
CBS 536.80	*Rhizopus microsporus* var. *rhizopodiformis*		NT	South Africa	sorghum malt	HM999971	JN206402
CBS 607.73	*Rhizopus microsporus* var. *rhizopodiformis*			former Yugoslavia	stored cereals	JN206345	HM849667
CBS 113206	*Rhizopus microsporus* var. *tuberosus*			China	koji in brewery	JN206350	
CBS 138.95	*Rhizopus schipperae*		T	USA	human; bronchial wash of patient with myeloma	HM999969	HM849672
CBS 336.39	*Rhizopus sexualis*		T	UK	*Fragaria*; decaying fruit	HM999966	HM849673
CBS 126.83	*Rhizopus* sp.	*R. stolonifer*		n.a.	ragi	JN206368	
CBS 442.74	*Rhizopus* sp.	*R. stolonifer*		Netherlands	coffee-ground	JN206367	
CBS 926.87	*Rhizopus* sp.	*R. stolonifer*		Spain, Tenerife	*Spartocytisus supranubius*; stem	JN206366	JN206406
CBS 133.90	*Saksenaea oblongispora*	*S. vasiformis*		Brazil	rain forest soil	JN206282 (c1) JN206283 (c3)	HM849694
CBS 405.63	*Spinellus fusiger*			n.a.	n.a.	JN206298	HM849664
CBS 515.75	*Spinellus fusiger*			Netherlands	fruit bodies of *Mycena galericulata*	JN206297	
CBS 633.80	*Spinellus fusiger*			Germany	fruit body of *Mycena* cf. *leptocephala*	JN206295	
CBS 894.73	*Spinellus fusiger*			Switzerland	fruit body of *Mycena pura*	JN206296	
CBS 195.77	*Sporodiniella umbellata*			Ecuador	*Umbonia*	JN206372	JN206405
CBS 122.12	*Syncephalastrum monosporum*	*S. racemosum*		Switzerland	n.a.	HM999977 (c1) HM999976 (c2)	JN206575
CBS 568.91	*Syncephalastrum monosporum* var. *cristatum*		T	China	soil	HM999975	HM849720
CBS 567.91	*Syncephalastrum monosporum* var. *monosporum*		T	China	soil	HM999974	HM849719
CBS 120811	*Syncephalastrum racemosum*			France	human; skin	HM999979 (c1) HM999980 (c4)	
CBS 199.81	*Syncephalastrum racemosum*			Kuwait	tidal mud-flat soil	HM999972	HM849718
CBS 213.78	*Syncephalastrum racemosum*		T of *S. verruculosum*	India	air	HM999978	JN206578

CBS 302.65	*Syncephalastrum racemosum*			Brazil	soil	HM999981 (c2) HM999984 (c4)	HM849721
CBS 370.49	*Syncephalastrum racemosum*			Indonesia	air	HM999983	
CBS 421.63	*Syncephalastrum racemosum*			Zaire	humose soil under *Linum usitatissimum*	HM999973	JN206576
CBS 440.59	*Syncephalastrum racemosum*			USA	soil	HM999982	
CBS 441.59	*Syncephalastrum racemosum*			USA	dung of coyote	HM999985	
CNM-CM2909	*Syncephalastrum racemosum*			Spain	environmental		JN206577
CBS 108947	*Syzygites megalocarpus*			Netherlands	*Amanita rubescens*; decaying fruit body	JN206371 (c1) JN206370 (c3)	
CBS 372.39	*Syzygites megalocarpus*			n.a.	n.a.	JN206369 (c3)	JN206401
CBS 341.55	*Thamnidium elegans*			USA	n.a.	JN206060	JN206466
CBS 411.52	*Thamnidium elegans*			Poland	dung of bat	JN206058	
CBS 641.69	*Thamnidium elegans*			USA	n.a.	JN206059	
CBS 874.69	*Thamnostylum lucknowense*			USA	dung of pack rat	JN205837	JN206546
CBS 690.76	*Thamnostylum nigricans*		NT	Mexico	dung of lizard	JN205838	JN206541
CBS 170.57	*Thamnostylum piriforme*			USA	dung of rat	JN205835	
CBS 182.28	*Thamnostylum piriforme*			USA	*Bertholletia excelsa*	JN205830	HM849724
CBS 233.28	*Thamnostylum piriforme*			USA	dung of rat	JN205832	
CBS 316.66	*Thamnostylum piriforme*		T	France	n.a.	JN205836	JN206544
CBS 412.94	*Thamnostylum piriforme*			Cuba	dung of *Capromys* sp.	JN205834	JN206543
CBS 480.69	*Thamnostylum piriforme*			Canada	soil under *Thuja occidentalis*	JN205831	
CBS 638.69	*Thamnostylum piriforme*			Brazil	dung of pig	JN205833	
CBS 692.76	*Thamnostylum repens*		NT	USA	dung of mouse		JN206542
CBS 104.75	*Thermomucor indicae seudaticae*		T	India	municipal compost	JN206300	HM849661
CBS 446.78	*Thermomucor indicae seudaticae*			Nigeria	*Zea mays*	JN206302	
CBS 447.78	*Thermomucor indicae seudaticae*			Germany	compost	JN206301	
CBS 603.68	*Umbelopsis angularis*		HT	Netherlands	soil	JN206380	HM849710
CBS 212.72	*Umbelopsis autotrophica*			Sweden	forest soil		JN206561
CBS 110039	*Umbelopsis dimorpha*		HT	New Zealand	soil of basaltic parent material	JN206387	HM849709
CBS 117350	*Umbelopsis dimorpha*			USA	soil of native decidious forest	JN206388	
CBS 385.85	*Umbelopsis fusiformis*		T	Australia	soil of forest of *Eucalyptus regnans*	JN206386	JN206560
CBS 919.85	*Umbelopsis fusiformis*			Australia	soil		JN206559
CBS 101745	*Umbelopsis gibberispora*			Japan	*Pinus luchuensis*; decaying needle		JN206565
CBS 109328	*Umbelopsis gibberispora*		T	Japan	*Fagus crenata*; leaf litter	JN206384	JN206564
CBS 100559	*Umbelopsis isabellina*			USA	soil	JN206396	JN206571
CBS 167.80	*Umbelopsis isabellina*			Colombia	fruit body of *Panellus pusillus*	JN206398	
CBS 250.95	*Umbelopsis isabellina*			Netherlands	*Varanus comodoensis*; granulomatous ulcer	JN206399	JN206574
CBS 309.93	*Umbelopsis isabellina*			UK	soil	JN206397	
CBS 560.63	*Umbelopsis isabellina*			Germany	soil of *Larix* forest	JN206400	JN206573
CBS 150.81	*Umbelopsis nana*		T of *U. versiformis*	USA	root	JN206389	
CBS 309.52	*Umbelopsis nana*			Belgium	forest soil	JN206390	
CBS 373.67	*Umbelopsis nana*			Georgia	forest soil	JN206394	
CBS 444.68	*Umbelopsis nana*			USA	pine stump wood	JN206392	
CBS 669.83	*Umbelopsis nana*			Canada	washed mycorrhizal root	JN206393	
CBS 858.68	*Umbelopsis nana*		T of *Mortierella alba*	Poland	forest soil	JN206391	
CBS 499.82	*Umbelopsis ovata*		IT	Australia	*Isopogon ceratophyllus*; rhizoplane	JN206395	JN206572
CBS 101226	*Umbelopsis ramanniana*			USA	soil, wood scraps and other debris	JN206383	JN206566
CBS 112976	*Umbelopsis ramanniana*			New Zealand	litter of ? *Carex* sp.	JN206382	JN206568
CBS 366.95	*Umbelopsis ramanniana*			China	forest soil	JN206385	
CBS 913.85	*Umbelopsis* sp.	*U. vinacea*		Germany	*Picea abies*; root	JN206376	JN206562
CBS 914.85	*Umbelopsis* sp.	*U. angularis*		Germany	root	JN206377	
CBS 559.86	*Umbelopsis* sp.	*U. westeae*		Australia	soil	JN206381	JN206563
CBS 868.85	*Umbelopsis swartii*		T	Australia	soil under *Eucalyptus regnans*	JN206378	JN206567
CBS 212.32	*Umbelopsis vinacea*		AUT	Australia	sandy loam		JN206570
CBS 236.82	*Umbelopsis vinacea*		T of *U. multispora*	Japan	*Fragaria*; root		JN206569
CBS 870.85	*Umbelopsis westeae*		T	Australia	soil of acid heathland	JN206379	
CBS 329.73	*Utharomyces epallocaulus*			India	soil	JN206276	HM849660
CBS 342.73	*Utharomyces epallocaulus*			Mexico	dung of rat	JN206277	
CBS 441.76	*Zychaea mexicana*		T	Mexico	dung of mouse	JN205845	JN206545

The Netherlands) following the protocol given by Möller et al. (1992) with diverse modifications described in detail by Alastruey-Izquierdo et al. (2010). The primer pair V9G (de Hoog & Gerrits van den Ende 1998) and LR3 (Vilgalys & Hester 1990) was used to amplify a DNA segment consisting of the complete ITS region and the D1/D2 region of the LSU. The PCR reaction mixture (25 µl) contained 0.4 µM of each primer, 0.185 mM of each deoxynucleoside triphosphate (GC Biotech, Alphen aan den Rijn, The Netherlands), 10× NH_4 BioTaq Reaction buffer (GC Biotech), 1.5 mM $MgCl_2$, 0.8 U BioTaq DNA polymerase (GC Biotech), and about 20 ng DNA. PCR reactions were conducted on a Thermal cycler 2720 (Applied Biosystems, Nieuwerkerk a/d IJssel, The Netherlands) as follows: one initial cycle at 94 °C for 5 min, followed by 35 cycles of 1 min at 94 °C, 1 min at 53 °C and 2 min at 72 °C, and one final cycle of 7 min at 72 °C. PCR products were analysed in 1 % agarose gels. Direct cycle-sequencing was performed for both strands of the PCR products using the Big dye sequencing kit (Applied Biosystems) and the primer set ITS1 and ITS4 (White et al. 1990) for the complete ITS region, and NL1 and LR3 for the D1/D2 region of the LSU (O'Donnell 1993). Cycle-sequencing products were analysed on an ABI 3730XL automatic sequencer (Applied Biosystems).

In cases where direct sequencing failed or double bands were detected in the agarose gels PCR products were ligated into pGEM-T Easy Vector (Promega, Leiden, The Netherlands) and cloned in *E. coli* JM109 competent cells (Promega) following the manufacturer's instructions. Colony-PCRs were performed using the primer pair M13f (5'-GTAAAACGACGGCCAGT-3') and M13r (5'-GGAAACAGCTATGACCATG-3').

Sequence analyses

Consensus sequences were constructed by means of the SeqMan program v. 7.2.2 (DNASTAR, Lasergene) and deposited in GenBank. A total of 592 ITS sequences (GenBank accession numbers JN205809 to JN206400) and 210 LSU sequences (GenBank accession numbers JN206401 to JN206610) were newly generated for this study. Ninety-two ITS sequences and 113 LSU sequences of strains included in this study were published in previous papers (Alastruey-Izquierdo et al. 2010, Vitale et al. 2012).

The highly diverse ITS sequences were divided in subsets of alignable sequences for phylogenetic analyses. Additionally, a set of LSU sequences was generated representing every MOTU detected in the ITS alignments. The MOTUs were defined by a ≥ 99 % similarity threshold. Similarity values based on the uncorrected distances were calculated with BioNumerics (v. 0.4.61) software (Applied Maths, Sint-Martens-Latem, Belgium).

ITS and LSU sequences were aligned using the server version of the MAFFT program (www.ebi.ac.uk/Tools/mafft) and manually corrected using the program Se-Al v. 2.0a11 (Rambaut 2002; http://tree.bio.ed.ac.uk/software/seal/). All alignments are lodged in TreeBASE (www.treebase.org/). *Mortierella parvispora*, a member of the *Mortierellales*, was selected as outgroup of the LSU tree because the *Mortierellales* is the sibling order of the *Mucorales* (e.g. O'Donnell et al. 2001, Voigt & Wöstemeyer 2001). The ITS trees were rooted by the nearest neighbours of the respective group in the LSU tree. The maximum likelihood algorithm with the server version of RAxML-VI-HPC v. 7.0.0 (Stamatakis et al. 2008) as implemented on the Cipres portal was used to estimate phylogenetic relationships. The robustness of all phylogenetic trees was assessed by bootstrap analyses with 1 000 replicates. ITS trees were only calculated for *Actinomucor*, *Mucor* (4 trees), *Rhizomucor* and *Rhizopus*, but all of the taxa are included in the LSU tree.

Morphology

Strains with a position in the phylogenetic tree that was in conflict with their original classification were verified microscopically. These strains were cultivated on MEA at 24 °C. After 2 and 7 d colonies were observed using a stereomicroscope (SMZ 1500; Nikon) and slides for microscopic examination were made. Fungal material was mounted in lactic acid with cotton blue (2 mg cotton blue/mL lactic acid) and in lactic acid only and examined using a Nikon eclipse 80i microscope (Nikon, Amstelveen, The Netherlands). Measurements were performed using the software NIS-Elements D 3.0 (Nikon). For a few strains mounts from slide cultures were photographed using a Nikon 05SM digital camera.

RESULTS AND DISCUSSION

Performance of ITS and LSU sequencing

Direct sequencing was possible in 82 % of the strains for the ITS and in all strains for the LSU region. ITS sequences of strains that failed direct sequencing could be obtained by cloning in most taxa, while cloning did not solve the problem in the group of *Rhizopus stolonifer*; this was probably due to extended poly-A- and poly-T-regions. In the majority of cloned strains ITS copies differed only by a single basepair. However, in *Syncephalastrum* we found ITS sequences of two types forming two clades in the ITS tree (illustrated in Vitale et al. 2012). Divergent copies of ITS have been found in *Fusarium* (O'Donnell & Cigelnik 1997) and *Laetiporus* (Lindner & Banik 2011). The proportion of strains that had to be cloned was especially high in *Absidia*, *Umbelopsis* and *Syncephalastrum*.

Phylogenetic relationships inferred from LSU data

The family structure of the *Mucorales* revealed by the LSU cladogram in main traits corresponds with that given by Hoffmann et al. (2013), although the *Lichtheimiaceae* and the *Mucoraceae* do not form clades (Fig. 1), probably because our analysis is based on a single locus. Some remaining taxonomic inconsistencies between phenotypic and sequence-based classifications were found, particularly in the upper part of the LSU cladogram (Fig. 1). The *Mycotyphaceae* and the *Choanephoraceae* are nested within the *Mucoraceae* and these families together with the *Backusellaceae*, the *Pilobolaceae* and the *Rhizopodaceae* compose a well-supported clade (*Mucorineae* clade; bootstrap 75 %). The *Mucorineae* clade is dominated by the polyphyletic genus *Mucor* (Fig. 2a), which comprises many groups that are intermingled by other sporangia-forming genera such as *Circinella* p.p. (Fig. 2h), *Parasitella*, *Pilaira*, *Pirella* (Fig. 2f), *Rhizomucor* p.p. (Fig. 2b), and *Zygorhynchus* (Fig. 2d), sporangia- and sporangiola-forming genera such as *Backusella* (Fig. 8) and *Thamnidium* (Fig. 2i), as well as exclusively sporangiola-forming genera such as *Chaetocladium*, *Ellisomyces* (Fig. 2g), *Helicostylum* and *Kirkomyces*. Based on the LSU (Fig. 1) and ITS trees (Fig. 3 to 6), the genera *Backusella*, *Circinella*, *Mucor*, *Rhizomucor* and *Zygorhynchus* appear to be polyphyletic. The lower part of the LSU tree shows a more resolved taxonomy. The majority of genera here are clearly defined and appear to be monophyletic based on our sampling. Exceptions were the paraphyletic genus *Absidia* that includes *Halteromyces* and *Chlamydoabsidia*, and the polyphyletic genera *Circinella* and *Rhizomucor* that are addressed in more detail below.

Although the polyphyly of *Mucor* is indisputable, only few clear lineages within *Mucor* are recognisable. Some of these lineages show a characteristic combination of sporangium size and the branching of the tall sporangiophores: in the *Mucor mucedo* group (Fig. 1), consisting, in addition to the name-giving species

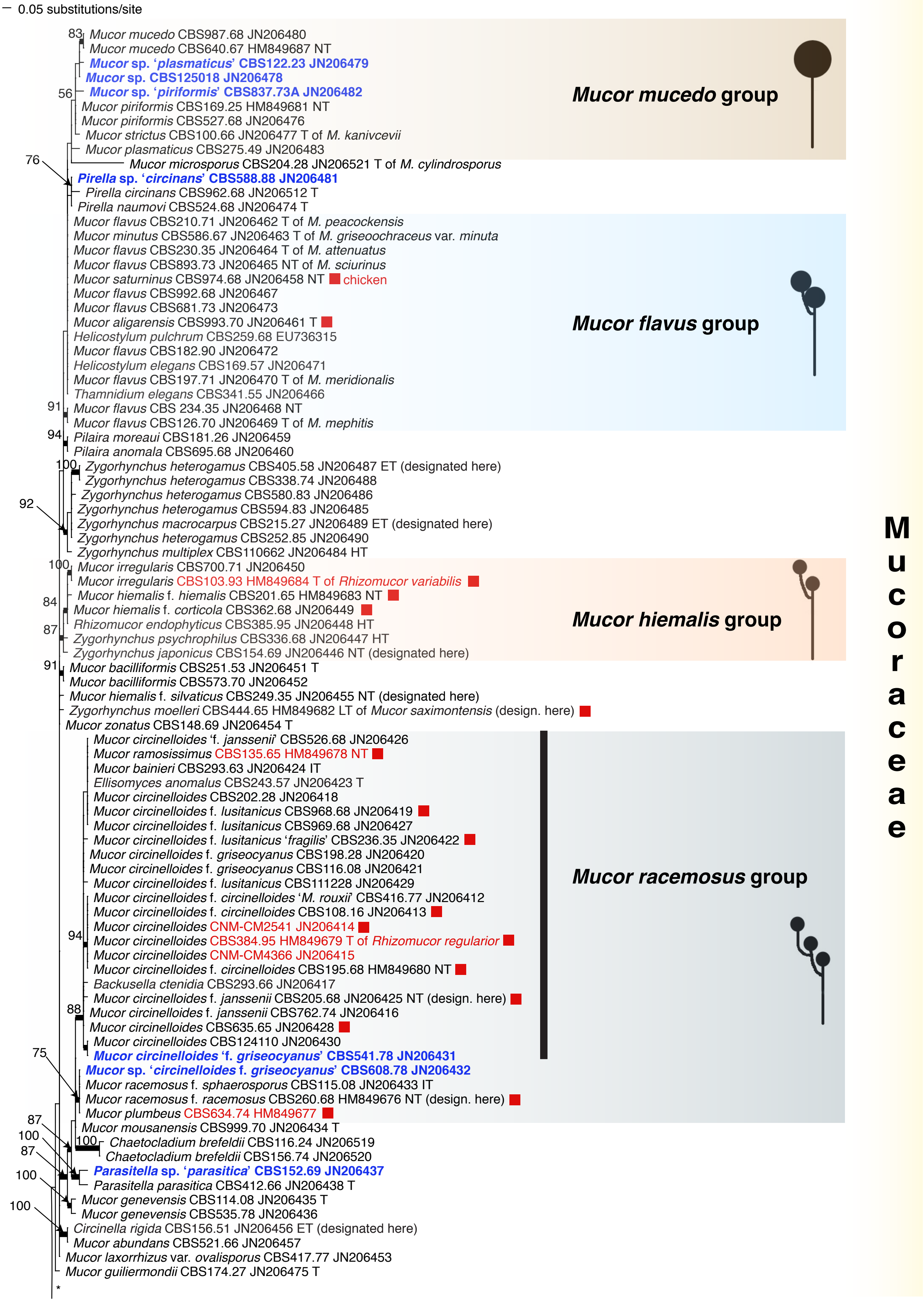


Fig. 1 RAxML phylogram of the *Mucorales* based on the D1/D2 region of the LSU. Each LSU sequence covers for a MOTU in ITS defined by a similarity threshold of 99 %. Branches with bootstrap values of 75 % or higher are printed in **bold**. Morphological groups according to sporangiophore branching and diameter of the sporangium: *Mucor mucedo* group, *M. flavus* group, *M. hiemalis* group, *M. racemosus* group, *M. amphibiorum* group, *M. recurvus* group. Black bar highlights the *Mucor circinelloides* complex. Ex-type strains are designated by: T = ex-type strain, ET = ex-epitype strain, HT = ex-holotype strain, IT = ex-isotype strain, LT = ex-lectotype strain, NT = ex-neotype strain, PT = ex-paratype strain, ST = ex-syntype strain, AUT = authentic material, c = clone, clinical strains are highlighted by red strain and GenBank accession numbers, strains representing MOTUs that comprise clinical strains are marked by red squares. Clinically relevant species are indicated by a red circle if no ITS sequence of a clinical isolate was available for the assignment to a MOTU. Potentially undescribed taxa are indicated by bold blue font.

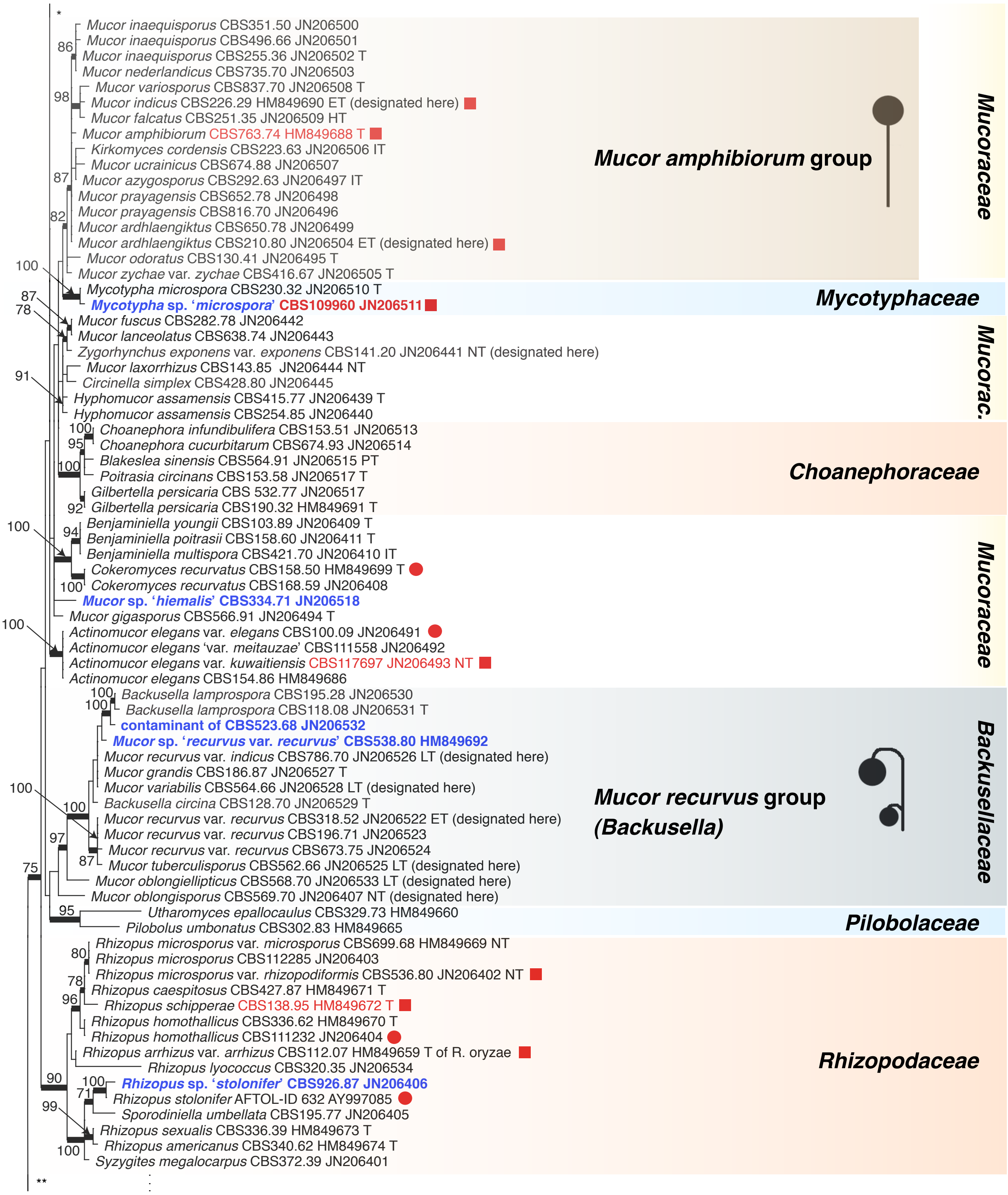
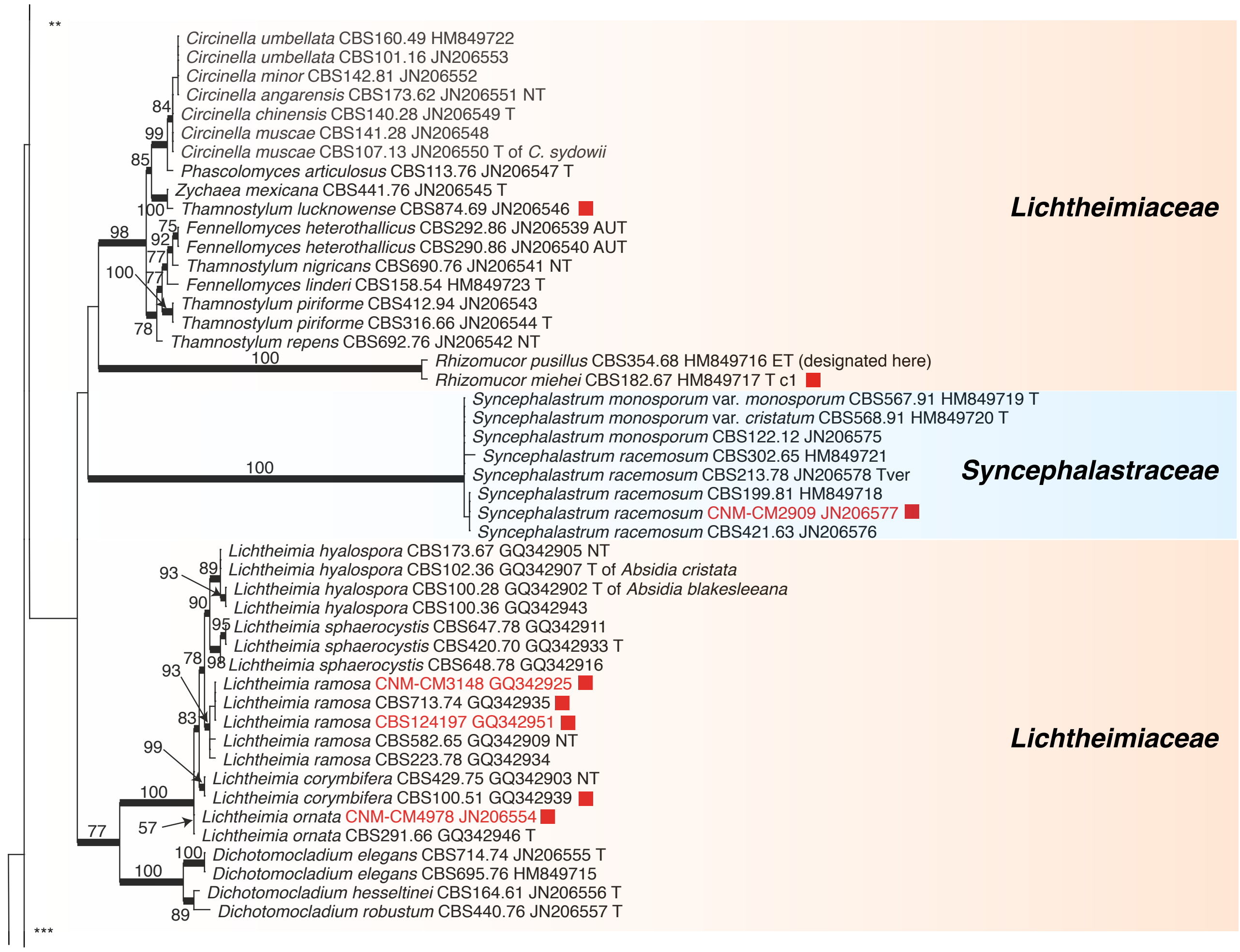


Fig. 1 (cont.)

M. mucedo, of *M. piriformis*, *M. plasmaticus* and *M. strictus*, all form unbranched tall sporangiophores and large sporangia often exceeding 200 µm diam. The morphology of *Mucor strictus* is strongly temperature-dependent. The species develops the typical group morphology only at low temperatures (Schipper 1975: 24). The *Mucor flavus* group, comprising *M. aligarensis*, *M. minutus* and *M. saturninus* in addition to *M. flavus* consists of species developing sympodially branched tall sporangiophores and medium-sized sporangia that are over 80 µm but not exceeding 200 µm diam. A clade including *M. hiemalis*, *M. irregularis*, *M. luteus*, *Rhizomucor endophyticus* and *Zygorhynchus psychrophilus*, the *Mucor hiemalis* group, is characterised by poorly sympodially branched tall sporangiophores and small sporangia not exceeding 80 µm diam. The *Mucor racemosus* group contains *M. circinelloides* with the formae *circinelloides*, *griseocyanus*, *lusitanicus* and *janssenii*, *Mucor bainieri*, *M. plumbeus*, *M. racemosus*, *M. ramosissimus* and *Backusella ctenidia*. The characteristics of this group are repeatedly sympodially branched sporangiophores and small sporangia not exceeding 80 µm diam. Species of the *Mucor amphibiorum* group, namely *M. amphibiorum*, *M. ardhlaengiktus*, *M. azygosporus*, *M. falcatus*, *M. inaequisporus*, *M. indicus*, *M. nederlandicus*, *M. odoratus*, *M. prayagensis*, *M. ucrainicus*, *M. variosporus* and *M. zychae* form − with the exception of *M. indicus* and *M. falcatus* − usually unbranched tall sporangiophores that bear, unlike species of the *M. mucedo* group, small- to medium-sized sporangia (maximum diameter between 70 and 175 µm). The *Mucor recurvus* group comprises *Mucor*



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and *Backusella* species with transitorily recurved sporangiophores and is discussed below in more detail. All of these groups were recognised, to a large extent, by Schipper (1973, 1975, 1976, 1978a).

Phenotypic characters with restricted taxonomic relevance

Genera preferably are defined as monophyletic. This may be in conflict with phenotypic definitions when single characters are concerned. For example, sporangiola-forming taxa such as *Backusella*, *Chaetocladium*, *Ellisomyces*, *Helicostylum*, *Kirkomyces* and *Thamnidium*, appear sporadically among *Mucor* species (Fig. 1, 3, 5, 6) and only the clade consisting of the sporangiola-forming genera *Benjaminiella* and *Cokeromyces* (Fig. 1) possess phylogenetic support. Hence we consider the potential to develop sporangiola in addition to or instead of sporangia as a plesiomorphic character in the *Mucoraceae* that is genetically fixed but not revealed in all species. Consequently, the presence of sporangiola should not be used to define new genera, as was done recently in the newly described genus *Isomucor* (de Souza et al. 2012) with sporangiola as the only distinctive trait. A classical generic criterion is the presence or absence of rhizoids. Our finding of rhizoids in *Mucor* species (Fig. 2c), the genus originally separated from *Rhizomucor* by the absence of rhizoids, and the reclassification of *Rhizomucor* species such as *R. regularior*, *R. variabilis* (Álvarez et al. 2010a), *R. chlamydosporus* and *R. endophyticus* (this paper) into *Mucor* suggests that the potential to form rhizoids might be plesiomorphic in *Mucorales* as well. Homo- and heterothallic species cluster randomly in our trees demonstrating the reduced taxonomic value of this trait. Circinate sporangiophores branches (Fig. 2h), considered to be a characteristic of the genus *Circinella*, evolved at least three times.

Species identification by DNA barcoding

In our study the ITS region turned out to be an appropriate DNA barcoding marker in *Mucorales* because of its power to discriminate the currently accepted species, including predominantly morphologically defined species (morphospecies), and also all species in *Mucor* (Hermet et al. 2012), *Lichtheimia* (Alastruey-Izquierdo et al. 2010) and *Rhizopus* (Abe et al. 2007) recognized by GCPSR studies. The statement of Schwarz et al. (2006) that ITS is able to discriminate most but not all clinically relevant members of *Mucorales* was due to the fact that the authors treated *R. azygosporus* as a separate species, while now it is classified as a variety of *R. microsporus* (Zheng et al. 2007). Indeed the taxonomy of the *Mucoraceae* is unsatisfactory according to current molecular characteristics and consequently identification by DNA barcoding is reliable only for species that form clearly delimited clades in the ITS trees. In *Rhizomucor* (Fig. 11) and *Rhizopus* (Fig. 10), all species can be identified by their ITS sequence, and even two varieties of *Rp. arrhizus* proved to be distinguishable (see sections on *Rhizomucor* or *Rhizopus*, respectively). ITS data also separate a surprisingly high number of species of *Mucor* and its allies as monophyletic groups (Fig. 2–5), allowing reliable species identification despite unclear generic boundaries. Problematic for molecular identification are the species complexes of *Mucor circinelloides*, *M. flavus*, *M. piriformis* and *Zygorhynchus moelleri*. The complex of *Mucor circinelloides* constitutes a supported

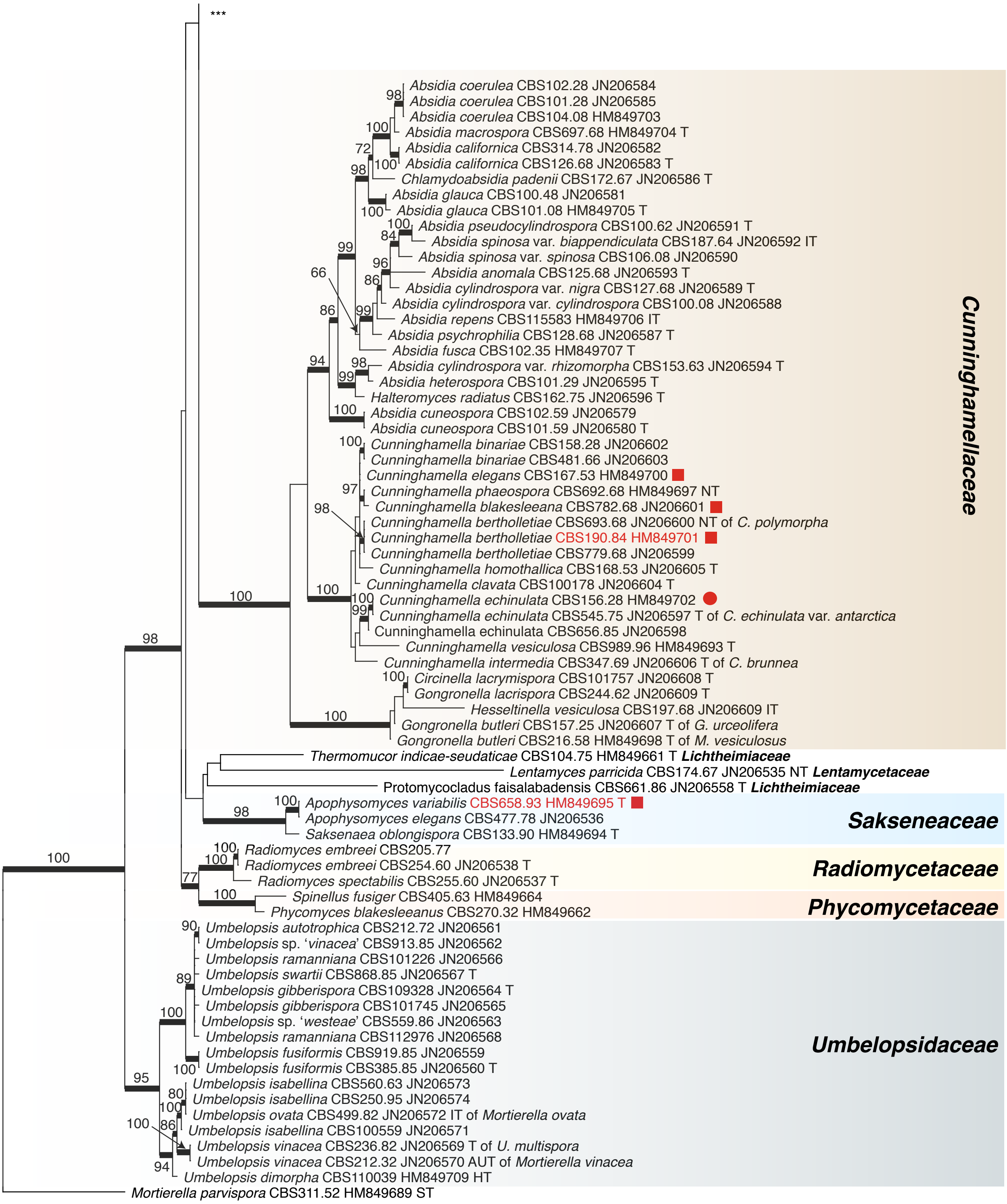

Fig. 1 (cont.)

clade (bootstrap support 88 %) in the LSU phylogram (Fig. 1) and comprises all formae of *M. circinelloides* but also other species such as *M. bainieri* and *M. ramosissimus*, *Ellisomyces anomalus* and *Backusella ctenidia* that cannot be separated by ITS and LSU data from *M. circinelloides* (Fig. 5). All formae of *M. circinelloides* described by Schipper (1976) can be discriminated by their ITS sequences, but there are several strains in the complex with a *M. circinelloides* morphology that do not group in any of these formae (see sections *Mucor* and *Backusella*).

Criteria for taxonomic changes based on ITS and LSU data

In general, multilocus studies are needed to establish boundaries between taxa forming sister clades in single-locus trees. However, in this stage of research we consider ITS and LSU data sufficient to justify taxonomic changes in the following cases: 1) synonymy if the ex-type strains have identical ITS sequences (in case the ITS sequences are identical but large morphological differences have been reported we maintain varieties or formae); 2) attribution of the species rank to varieties or formae if they appear distant to the type variety or forma in ITS and LSU trees; 3) reclassifications based on polyphyly shown by ITS and LSU data (e.g. *Zygorhynchus*); and 4) extension of a genus based on ITS and LSU analyses and morphological synapomorphies (e.g. *Backusella*).

Fig. 2 Morphological diversity of *Mucoraceae*. a. CBS 243.35 *Mucor luteus*, sporangiophore and sporangium with collar, columella and sporangiospores; b. CBS 385.95 *Rhizomucor endophyticus* (recombined into *Mucor endophyticus* in this paper), sporangiophore with columella and collar; c. CBS 243.35 *Mucor luteus*, rhizoids formed on glass slides; d. CBS 110662 *Zygorhynchus multiplex* (recombined into *Mucor multiplex* in this paper), zygospore; e. CBS 385.95 *Rhizomucor endophyticus* (recombined into *Mucor endophyticus* in this paper), zygospore; f. CBS 588.88 *Pirella circinans*, lateral sporangium; g. CBS 243.57 *Ellisomyces anomalus*, multispored sporangiola; h. *Circinella rigida* (recombined into *Mucor durus* in this paper), circinate sporangiophore branch with apophysate sporangium; i. CBS 341.55 *Thamnidium elegans*, multispored sporangiola. — Scale bars = 10 µm, except c = 100 µm.

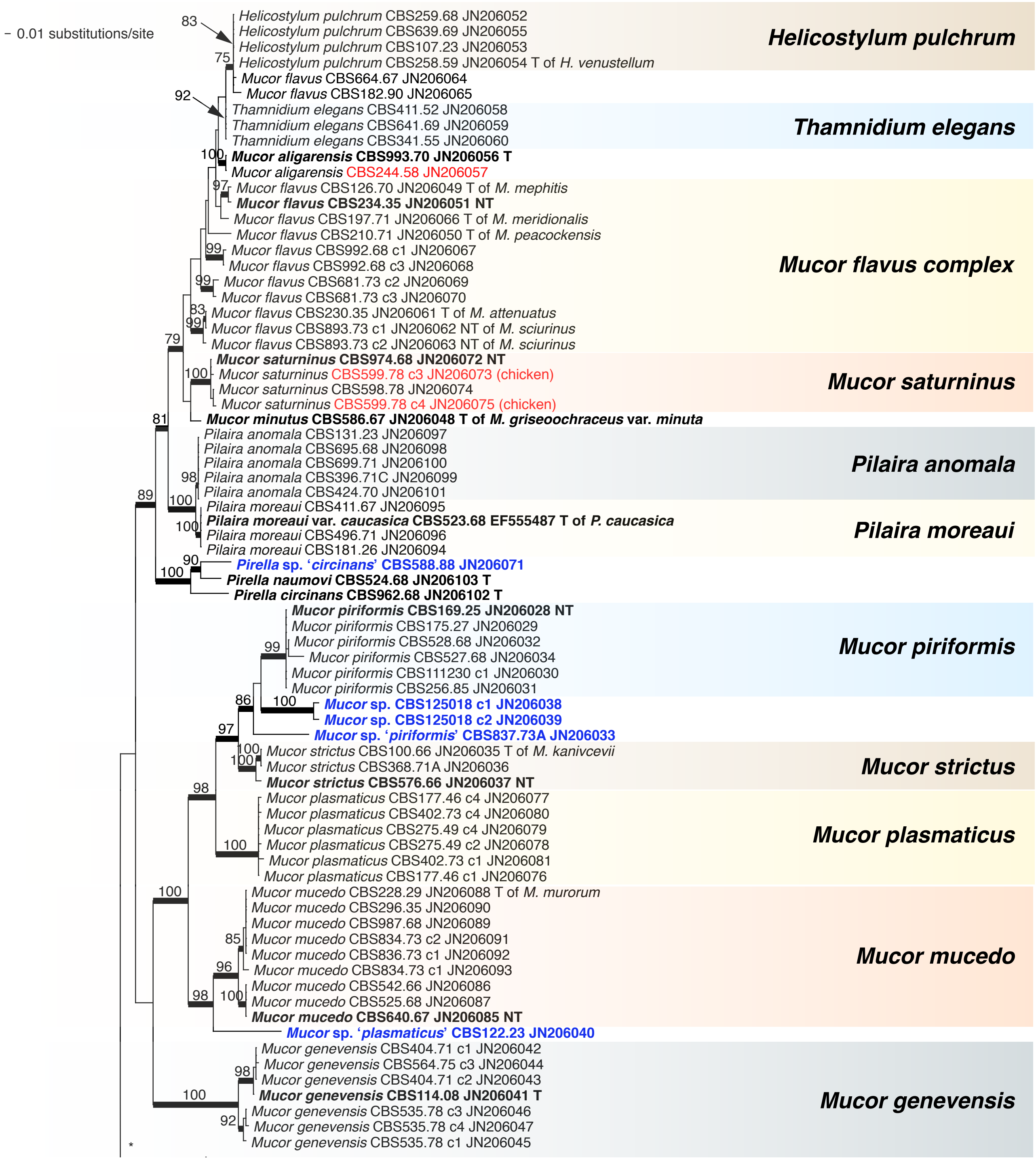

Fig. 3 RAxML phylogram of the *Mucor mucedo* group, *M. flavus* group, *M. hiemalis* group and related taxa based on the ITS region. Branches with bootstrap values of 75 % or higher are printed in **bold**. Ex-type strains are designated by: T = ex-type strain, ET = ex-epitype strain, HT = ex-holotype strain, IT = ex-isotype strain, LT = ex-lectotype strain, NT = ex-neotype strain. Ex-type strains of currently accepted taxa are printed in **bold**. Clones are specified by a 'c' followed by the clone number. Clinical strains are highlighted by red strain and GenBank accession numbers, non-human hosts are given in brackets. Potentially undescribed taxa are indicated by bold blue font. Morphological identifications are given in quotation marks.

Species concepts: conflicts between grouping in the ITS trees and mating results

The broad species concepts in *Mucor* maintained by Schipper (1973, 1975, 1976, 1978a), based on positive matings, are partly in conflict with the grouping in our ITS trees. Species in the sense of Schipper, e.g. *Mucor circinelloides*, *M. hiemalis* (including *M. luteus*) and *M. flavus* are not monophyletic. Their clades include other species or even other genera showing that the simple presence of zygospores is not a sufficient marker for conspecifity. However, a detailed study of their size, shape, colour and number may allow to differentiate between inter- and intraspecific zygospores, as shown for *Mucor irregularis* (Schell et al. 2011) and *Lichtheimia* (Alastruey-Izquierdo et al. 2010). Consequently, the study of zygospores should not be devaluated by our results but is ideally combined with multi-locus studies to recognize species.

Detection of undescribed species by DNA barcoding

Twelve MOTUs are revealed by ITS sequencing that deviate considerably from species included in this study and might represent undescribed taxa (indicated by bold blue font in all trees). The species to which they had previously been assigned, on the basis of morphological features, are given in quotation marks. In order to establish whether these MOTUs deserve species rank we have initiated multilocus-analyses

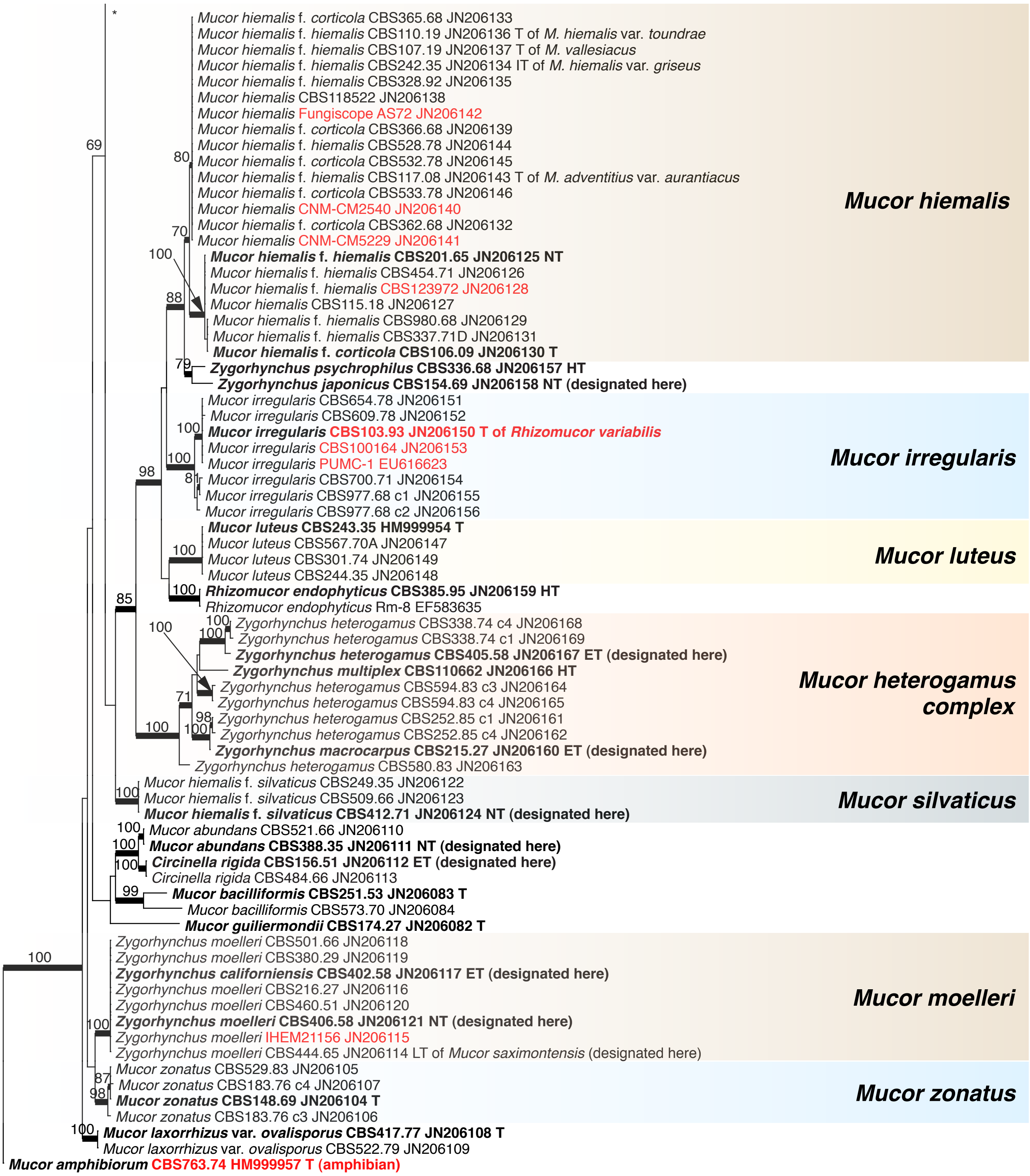

Fig. 3 (cont.)

and detailed morphological studies, which will be published in subsequent papers. Regardless of the question if these MOTUs represent undescribed species, our results suggest that the used phenotypic criteria for species recognition in the *Mucorales* underestimated existing diversity.

The ITS sequences of numerous strains of *Absidia* and *Umbelopsis* could not be obtained by direct sequencing and not all of them could be cloned. Our ITS dataset is therefore incomplete for these genera.

ITS barcoding detected cryptic species, but conversely revealed growth-reduced mutants of existing taxa that had been maintained incorrectly as separate species. Examples include *Mucor sinensis*, which is synonymised with *M. racemosus* f. *racemosus* below, alleged *Mucor ramosissimus* strains that proved to belong to *M. circinelloides* f. *circinelloides* or f. *janssenii*, and *Rhizomucor tauricus* which is a synonym of *Rm. pusillus.*

Intraspecific variability

Intraspecific variability differs widely among mucorealean species and genera. The following dissimilarity values were obtained for the ITS region of species represented by at least 5 strains: *Backusella circina* (0 %), *Choanephora cucurbitarum* (0.5 %), *Circinella muscae* (1.6 %), *Cunninghamella bertholletiae* (1.0 %), *C. blakesleeana* (0.9 %), *C. echinulata* (13.3 %), *Gilbertella persicaria* (1.2 %), *Gongronella butleri* (1.1 %), *Lichtheimia corymbifera* (2.0 %), *L. hyalospora* (6.3 %), *L. ramosa* (7.6 %), *Mucor circinelloides* (5.3 %), *M. fuscus* (0.2 %), *M. hiemalis* (4.1 %), *M. indicus* (0.9 %), *M. irregularis* (2.6 %), *M. mucedo* (3.5 %), *M. odoratus* (0.3 %), *M. piriformis* (0.6 %), *M. plumbeus* (0.2 %), *M. racemosus* (2.1 %), *Phycomyces blakesleeanus* (0 %), *Pilaira anomala* (0 %), *Rhizomucor pusillus* (0.2 %), *Rhizopus arrhizus* incl. var. *delemar* (1.2 %), *R. lyococcus* (0.7 %), *R. microsporus* (2.8 %), *Thamnostylum piriforme* (1.6 %), *Umbelopsis nana* (0 %) and *Zygorhynchus moelleri* (0 %). Complete identity might be the result of undersampling. High dissimilarity values of morphologically defined species such as *Cunninghamella echinulata* could be caused by the inclusion of more than one species. However, the taxonomically well-elaborated genus *Lichtheimia* also contains species with more than 5 % dissimilarity suggesting that intraspecific variability can be comparatively high in *Mucorales*.

In agreement with Nilsson et al. (2006) we did not find a unifying threshold for intraspecific variability, a result that should caution against formal ITS-based species delimitation. On the other hand, the ≥ 99 % identity threshold given by Balajee et al. (2009) for comparative ITS sequence identification using GenBank in *Mucorales* is not covering the intraspecific variability of several clinically important species. Our data suggest that a distinct identity threshold has to be defined for every species for a reliable ITS-based identification. GCPSR studies will be required beforehand to define species boundaries in species with conflicting morphological and ITS data especially in those that are part of a species complex.

Clinically relevant taxa

Clinical strains are highlighted by red strain numbers and GenBank accession numbers in all figures. Strains representing a clinically relevant MOTU are marked either by a red square (assignment to the respective MOTU by ITS comparison) or by a red circle (assignment to the respective MOTU by morphology) in the LSU tree (Fig. 1). The following genera contain species that are involved in human opportunistic infections: *Actinomucor*, *Apophysomyces*, *Cokeromyces*, *Cunninghamella*, *Lichtheimia*, *Mucor*, *Rhizomucor*, *Rhizopus*, *Saksenaea*, *Syncephalastrum*, and possibly *Mycotypha*, *Thamnostylum* (Xess et al. 2012) and *Zygorhynchus*, the latter genus being synonymised with *Mucor* below. The recently described clinically relevant species of *Apophysomyces*, viz. *A. ossiformis* and *A. trapeziformis* (Álvarez et al. 2010b) and of *Saksenaea*, viz. *S. erythrospora* as well as the pathogenic *S. vasiformis* (Álvarez et al. 2010a) were not included in our study.

No clinical strains of the following species were included in the present study, but clinical relevance of the species, resp. strains originating from clinical samples were reported by other authors: *Cokeromyces recurvatus* (e.g. Ryan et al. 2011), *Cunninghamella blakesleeana* (García Rodríguez et al. 2012), *C. echinulata* (Lemmert et al. 2002), *Mucor ardhlaengiktus* (as *M. ellipsoideus*), *M. circinelloides* f. *lusitanicus* (as *M. lusitanicus*) (Álvarez et al. 2011), *Rhizopus homothallicus* (Chakrabarti et al. 2010), *Rhizopus stolonifer* (de Hoog et al. 2000) and *Thamnostylum lucknowense* (Xess et al. 2012). A clinical strain treated as *Mucor fragilis* by Álvarez et al. (2011) is assigned to *M. circinelloides* below.

The involvement of *Zygorhynchus moelleri* and a possibly undescribed *Mycotypha* species in human mucormycoses has not been proven: strain IHEM 21156 of *Zygorhynchus moelleri* was isolated by J.P. Bouchara at the University Hospital Angers (France) in 2004 but the exact source is unknown, and *Mycotypha* strain CBS 109960 was isolated by N. Poonwan from pus of a wound in the RMSC Pitsunalok (Thailand) in 2002. There is also no case report on *Mucor plumbeus* but the source of isolation of strain CBS 634.74 (human biopsy material) and CBS 633.74 (subcutaneous tissue of a cat) suggest a pathogenic potential of this species. *Mucor aligariensis* was isolated in 1958 from human and *M. saturninus* in 1978 from chicken, but no proven case reports have been published. Based on their maximum growth temperatures (< 30 °C, Schipper 1978a) the involvement of these species in infections is questionable.

The clinical strain CNM-CM 5114 (JN205884*)* isolated in 2008 from a lung biopsy specimen in Barcelona (Spain) was diagnosed as *Cunninghamella elegans* by a 99.2 % similarity of the ITS region with the ex-neotype strain of this species CBS 160.28 (AF254928). This is the first time that the involvement of *C. elegans* in human infection has been documented molecularly.

The recent detection of species with clinical relevance, such as *Cunninghamella echinulata* (Lemmert et al. 2002), *Lichtheimia ornata* (Alastruey-Izquierdo et al. 2010), *Mucor ardhlaengiktus* (as *M. ellipsoideus*, Álvarez et al. 2011) or *Rhizopus homothallicus* (Chakrabarti et al. 2010) shows that basically all mucorealean taxa, including species regarded as strictly environmental, should be included in the database for molecular identification of clinical strains. Molecular identification by BLAST searches of GenBank may lead to wrong conclusions because of incomplete sampling, inconsistent nomenclature and a high percentage of misidentified taxa (Bridge et al. 2003, Nilsson et al. 2006, Bidartondo et al. 2008, Lian et al. 2011).

The following taxa have been reported from proven case studies (de Hoog et al. 2000, Gomes et al. 2011): *Actinomucor elegans*, *Apophysomyces variabilis*, *A. trapeziformis* (Weddle et al. 2012), *Cokeromyces recurvatus*, *Cunninghamella bertholletiae*, *C. elegans*, *Lichtheimia corymbifera*, *L. ramosa*, *Mucor amphibiorum*, *M. ardhlaengiktus* (Sugui et al. 2011), *M. circinelloides* (f. *circinelloides*, f. *janssenii*, f. *lusitanicus*), *M. hiemalis*, *M. irregularis* (syn. *Rhizomucor variabilis*), *M. luteus* (syn. *M. hiemalis* f. *luteus*), *M. indicus*, *M. racemosus* f. *racemosus*, *M. ramosissimus*, *Rhizopus microsporus*, *Rp. arrhizus*, *Rp. homothallicus*, *Rp. schipperae*, *Rp. stolonifer*, *Rhizomucor miehei*, *Rm. pusillus*, *Saksenaea vasiformis*, *S. erythrospora* (Hospenthal et al. 2011) and *Syncephalastrum racemosum.*

The forma *circinelloides* of *Mucor circinelloides* contains the highest number of clinical isolates in *Mucor* and forms a well-supported clade (bootstrap 95 %). Two groups within forma

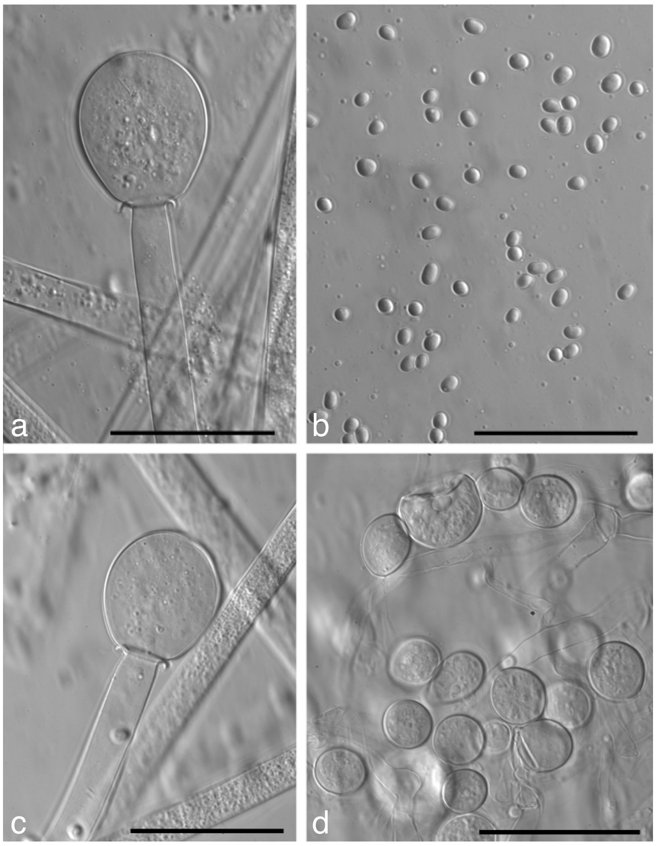

Fig. 4 CBS 388.35 *Mucor abundans*. a, c. Sporangiophore with columella and collar; b. sporangiospores; d. chlamydospores. — Scale bars = 50 µm.

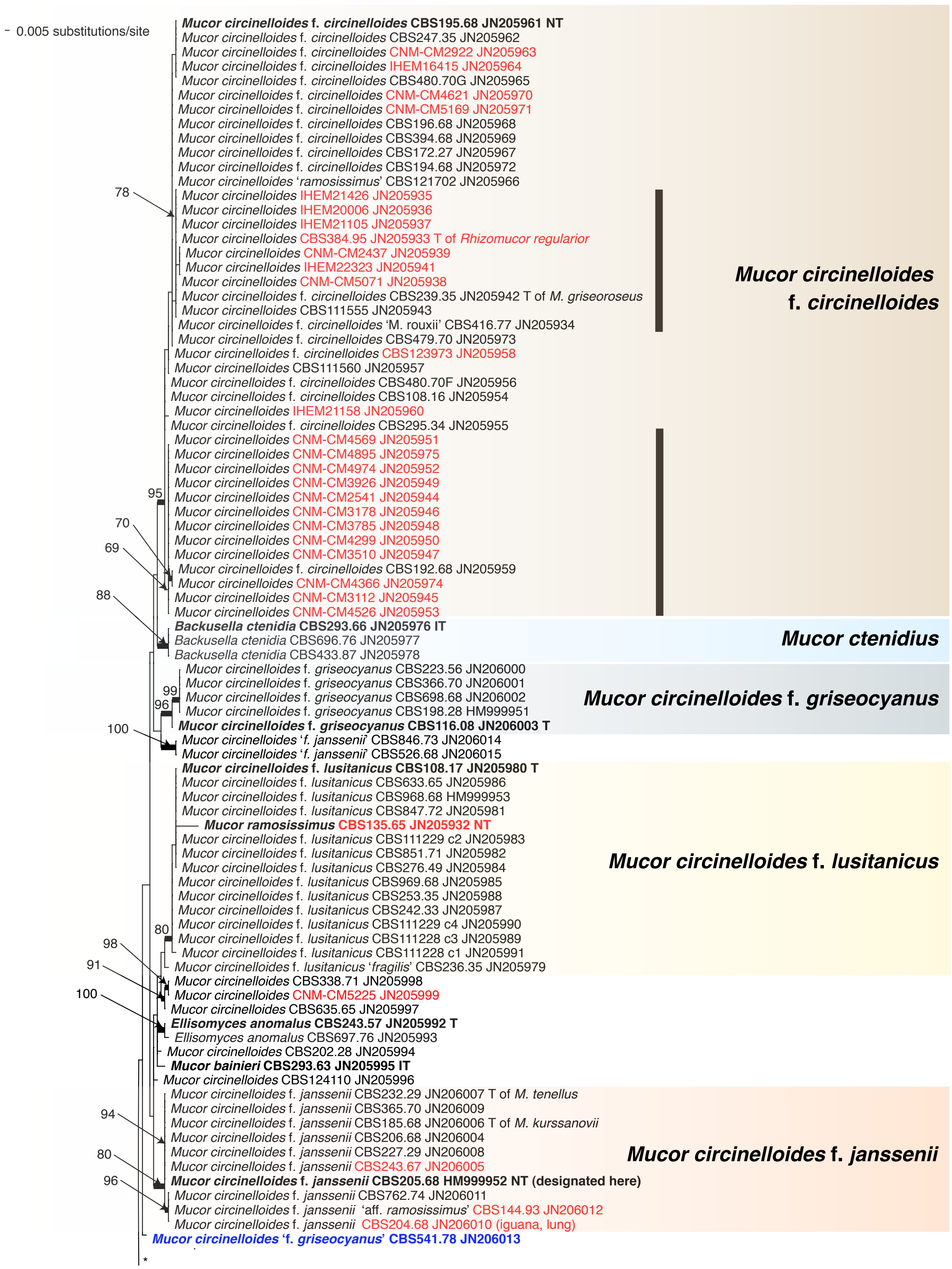

Fig. 5 RAxML phylogram of the *Mucor racemosus* group and related taxa based on the ITS region. Branches with bootstrap values of 75 % or higher are printed in **bold**. Ex-type strains are designated by: T = ex-type strain, ET = ex-epitype strain, IT = ex-isotype strain, NT = ex-neotype strain. Ex-type strains of currently accepted taxa are printed in **bold**. Clones are specified by a 'c' followed by the clone number. Clinical strains are highlighted by red strain and GenBank accession numbers, non-human hosts are given in brackets. Potentially undescribed taxa are indicated by bold blue font. Morphological identifications are given in quotation marks. Black bars indicate groups within *Mucor circinelloides* f. *circinelloides* including a large number of clinical strains.

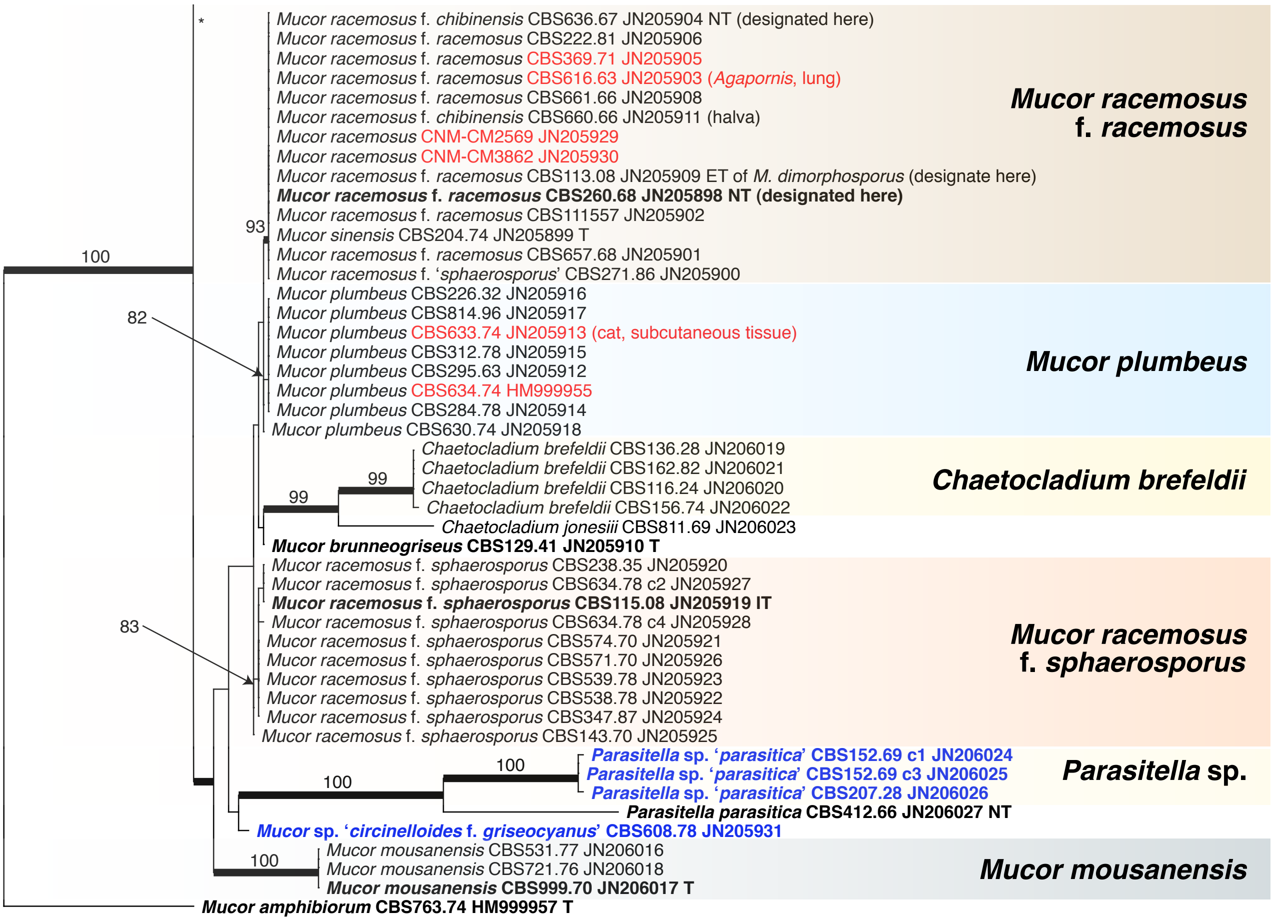

Fig. 5 (cont.)

circinelloides (highlighted by black bars in Fig. 5) contain a large number of clinical strains, which might be explained to high frequency in the human environment, or to an increased virulence. Interestingly, the forma *griseocyanus*, being the only forma of *Mucor circinelloides* that is not able to grow at 37 °C, does not comprise any clinical isolate. In *Mucor racemosus* we found a similar picture: only the forma *racemosus* appears to be involved in human infections, while the forma *sphaerosporus* contains strains only isolated from food and environmental samples. The maximum growth temperature of forma *sphaerosporus* is distinctly lower (28 °C > T_{max} < 25 °C) than that of the clinically relevant forma *racemosus* (37 °C > T_{max} < 30 °C) (Schipper 1976).

Many thermotolerant or thermophilic species (Schipper 1973, 1975, 1976, 1978a, b, 1979, 1984, 1986, 1990, Schipper & Stalpers 1984, Schipper & Samson 1994, de Hoog et al. 2000, Zheng & Chen 2001, Hoffmann et al. 2007, Alastruey-Izquierdo et al. 2010, Álvarez et al. 2010a, b) in the *Mucorales* are opportunistic pathogens of vertebrates, but there is no direct correlation between thermotolerance and pathogenicity. Several taxa including species of *Backusella*, *Cunninghamella* and *Mucor*, as well as *Protomycocladus faisalabadensis* and *Thermomucor indicae-seudaticae* are thermotolerant or even thermophilic, but have never been reported to cause infections.

TAXONOMY

Mucor

Mucor mucedo group, M. flavus group, M. hiemalis group and related taxa

In our ITS tree (Fig. 3) *Mucor flavus* is divided in several small clades that are intermingled with *M. aligarensis*, *Helicostylum pulchrum* and *Thamnidium elegans*. Several ex-type strains of species that were synonymised by Schipper (1975) with *M. flavus* based on positive matings and morphological similarity are placed in other clades than the neotype strain CBS 234.35. Their correct taxonomic status needs to be assessed by more detailed studies.

Only two of the four formae established by Schipper (1973) for *Mucor hiemalis*, viz. f. *hiemalis* and f. *corticola*, constitute a clade in the ITS tree (Fig. 3). This clade is divided into two subclades both composed of strains morphologically assigned to f. *hiemalis* and f. *corticola*. However, the ex-type strains of both formae are located in the same subclade (Fig. 3). For that reason we consider the small differences in the shape of the spores between the formae as taxonomically insignificant. Strains of *Mucor hiemalis* f. *silvaticus* are not part of the well-supported *Mucor hiemalis* clade, not in the ITS (Fig. 3) nor in the LSU tree (Fig. 1). Therefore we treat this taxon as a discrete species. The same applies to *Mucor hiemalis* f. *luteus* that recently was reclassified as *Mucor luteus* (Budziszewska et al. 2010).

No authentic material is known to exist of *Mucor abundans*. The protologue (Povah 1917) describes *M. abundans* as a species with slightly branched sporangiophores, sporangia with a diameter below 100 µm, subglobose to pyriform columellae and small globose to short ellipsoidal sporangiospores. The strains CBS 388.35 (Fig. 4) and CBS 521.66, the latter deposited as *M. abundans* in the CBS collection, match these microscopic characters including the typical size and shape of the sporangiospores. They only differ by features that may have changed during prolonged cultivation such as the colour of the colony or the colour of the young sporangia that are hyaline with a slight yellow tinge in the studied strains instead of yellowish. Schipper (1973) noted the similarity of both strains with *M. abundans* but she considered them too similar to *M. hiemalis* f. *corticola* to recognise a separate species. Our ITS tree (Fig. 3) however, supports the separate position of these strains and therefore we here designate CBS 388.35 (preserved in a metabolically inactive state by lyophilization, batch nr. 472) as the neotype of *Mucor abundans*.

On MEA at room temperature strain CBS 388.35 shows the following features: colonies expanding, cottony, at first white later depending on the intensity of sporulation grey beige or pale grey; reverse uncoloured; sporangiophores slightly sympodially branched, up to 15 µm diam; sporangiophore branches straight; sporangia dark greyish, young hyaline or with a slight yellow tinge, small, up to 70 µm diam; columellae subglobose, ellipsoidal or slightly pyriform (as illustrated by Povah 1917) (Fig. 4a, c), up to 39 by 46 µm in size, often purplish grey; collars distinct; sporangiospores hyaline, smooth, subglobose (3.5–6 µm diam), short ellipsoidal to short cylindrical (4.5–7 by 3.5–5.5 µm) (Fig. 4b); chlamydospores globose, ellipsoidal or pyriform, intercalary, terminally and laterally formed mainly in the submerged mycelium (Fig. 4d); zygospores absent.

Mucor racemosus group and related taxa

Based on our analyses (Fig. 1, 5) *Mucor circinelloides* represents a species complex, which also includes other *Mucor* species and sporangiola-forming taxa. The backbone of the *M. circinelloides* part of the ITS tree is poorly resolved, hampering a decision on the rank of the taxa included. Based on positive matings, Schipper (1976) reduced four species related to *Mucor circinelloides* to formae, namely f. *circinelloides*, f. *griseocyanus*, f. *janssenii* and f. *lusitanicus*. Recently Álvarez et al. (2011) proposed species status for f. *lusitanicus* without considering the positive mating results obtained by Schipper (1976). Strains morphologically assigned to the various formae of *M. circinelloides* form well-supported clades in the ITS tree (Fig. 5), but several additional strains that morphologically belong to *M. circinelloides* are located outside these clades. The strains CBS 338.71 and CBS 635.65, for example, are placed basally to the forma *lusitanicus* clade in the ITS tree (Fig. 5) and develop predominantly globose columellae characteristic of forma *lusitanicus*, but occasionally they develop obovoid columellae typical of forma *circinelloides*. Schipper's (1976) mating results, the presence of intermediate strains and the absence of compensatory base changes (CBC) between f. *circinelloides*, f. *lusitanicus*, and f. *janssenii* (Pawłowska et al. In press) lead us to regard *M. circinelloides* as a single species that consists of several still interbreeding lineages which result in a high intraspecific ITS variability of 5.3 %.

Some confusion exists because of misapplied names for important model strains. Strain CBS 416.77, deposited in the CBS collection by S. Bartnicki-García as *Mucor rouxii*, belongs to *Mucor circinelloides* according to its ITS sequence, a fact that has been noted by several authors (Abe et al. 2006, Schwarz et al. 2006, Liu et al. 2007). Ellis et al. (1976) proposed NRRL 5866 = CBS 438.76 as the neotype for *Amylomyces rouxii* (Calmette 1892) and found it to be conspecific with that of *Rhizopus arrhizus*. Wehmer (1900) incorrectly believed that the strains he isolated represented Calmette's *Amylomyces rouxii* and proposed the name *Mucor rouxii* (Calmette) Wehmer for them. However, he probably studied strains of *Mucor indicus* (Schipper 1978a: 10). Consequently *Mucor rouxii sensu* Wehmer is a synonym of *Mucor indicus*, whereas *Mucor rouxii* (Calmette) Wehmer is *Rhizopus arrhizus*. Strains of *M. indicus* are very similar morphologically to *Mucor circinelloides* at some stages in the life cycle (Schipper 1978a: 10), but the molecular differences between the two species are unambiguous.

Mucor ramosissimus is another member of the *Mucor circinelloides* complex. Its ITS sequence clusters in the well-supported clade of *Mucor circinelloides* f. *lusitanicus*. However, the sequence differs considerably (19 out of 585 basepairs, 3.2 % dissimilarity) from the remaining sequences of *M. circinelloides* f. *lusitanicus*. This is expressed by a long branch in Fig. 5. We therefore retain the species rank for this taxon and await studies on other loci. Other strains that had been identified morphologically as *M. ramosissimus* are positioned distantly in different groups: CBS 144.93 clusters in the *Mucor circinelloides* f. *janssenii* clade and CBS 121702 in the *M. circinelloides* f. *circinelloides* clade. These strains differ by slow growth and possibly represent growth-reduced mutants of these formae.

CBS 236.35, the only strain listed as *Mucor fragilis* in the CBS database, is positioned basally in the *Mucor circinelloides* f. *lusitanicus* clade. As far as we are aware no type material exists for *M. fragilis*. Bainier's (1884) original description assigns the fungus to the *Mucor hiemalis* group because the zygospores are black and bear characteristically roughened stellate spines. Schipper (1976) treated *Mucor fragilis* as a doubtful species because strain CBS 236.35, received as *Mucor fragilis* from Zycha in 1935, deviated from Bainier's description. In agreement with Schipper (1976) we are not using this name and re-identify strain CBS 236.35 as *Mucor circinelloides* f. *lusitanicus*.

Mucor circinelloides f. *janssenii* splits in two groups in the ITS tree (Fig. 5): a first group containing the ex-type strain, and a second group consisting of CBS 144.93, CBS 204.68 and CBS 762.74 at 0.7 % distance. Considering the high degree of sequence diversity in *Mucorales*, expressed for example in an ITS sequence dissimilarity of 2.6 % between *Mucor circinelloides* f. *janssenii* and f. *lusitanicus*, these groups within *jansenii* are being treated as taxonomically insignificant. The ITS sequence of the ex-type strain of the recently described *Mucor velutinosus* (FN650646; Álvarez et al. 2011) is identical to that of CBS 762.74 of f. *janssenii* (data not shown). According to their ITS sequences (data not shown) isolates ATCC1209b (HM754254) and UIC-1 (HQ154609) of *M. circinelloides* forming an unknown group in the phylogenetic analyses of Li et al. (2011) also belong to f. *janssenii* but type material of this form was not included in the study of Li et al. (2011).

The ITS sequence deposited in GenBank (EF203698) for the newly described species *Mucor renisporus* (Jacobs & Botha 2008) is identical to that of CBS 480.70F (data not shown) of *Mucor circinelloides* f. *circinelloides*. However, according to the description given by Jacobs & Botha (2008) the taxa differ significantly in the sizes of sporangia, columellae and sporangiospores. A microscopical study of the ex-type strain of *Mucor renisporus*, and repeated ITS sequencing are necessary to verify conspecifity.

The morphological distinction of f. *racemosus* and f. *sphaerosporus* of *M. racemosus* is ambiguous while they can be clearly differentiated based on ITS data. Some strains of f. *racemosus* such as CBS 271.86 and CBS 113.08 produce a high proportion of spherical sporangiospores.

Mucor racemosus f. *chibinensis* is grouped with *M. racemosus* f. *racemosus* and represents a synonym of the latter. To our knowledge no type material is available for f. *chibinensis*. Schipper (1976) concluded that CBS 636.67 and CBS 660.66 strains matched the protologue of *Mucor chibinensis* (Neophytova 1955) and proposed the name *Mucor racemosus* f. *chibinensis*. Here we designate CBS 636.67 (preserved in a metabolically inactive state by lyophilization, batch nr. 768) as neotype of *Mucor racemosus* f. *chibinensis* because it matches the description of the basionym *M. chibinensis* and it is well described and illustrated (Schipper 1976); in addition the strain was isolated in Russia, corresponding which the geographic origin of the type.

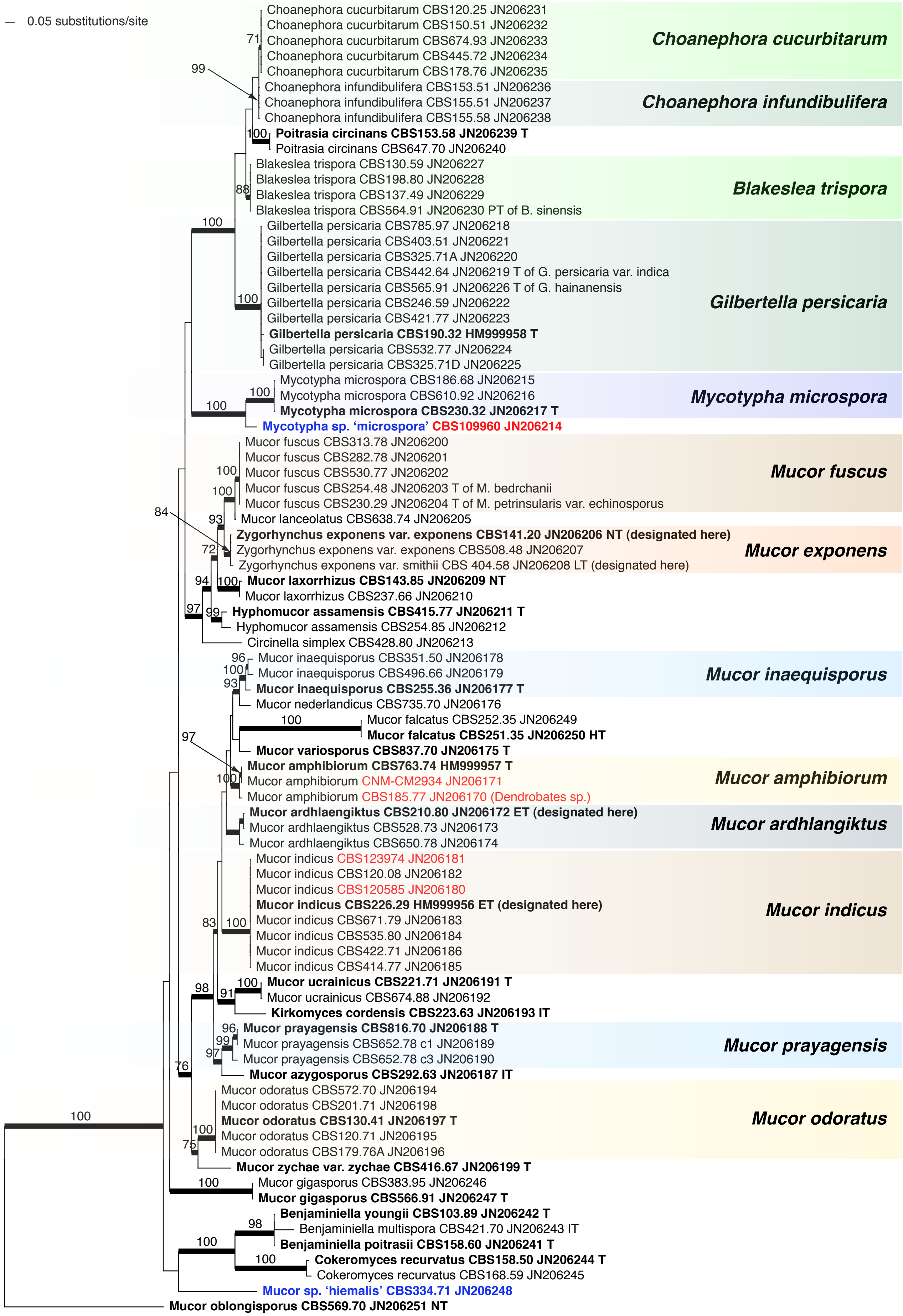

Fig. 6 RAxML phylogram of the *Mucor amphibiorum* group and related taxa based on the ITS region. Branches with bootstrap values of 75 % or higher are printed in **bold**. Ex-type strains are designated by: T = ex-type strain, ET = ex-epitype strain, HT = ex-holotype strain, IT = ex-isotype strain, LT = ex-lectotype strain, NT = ex-neotype strain, PT = ex-paratype strain. Ex-type strains of currently accepted taxa are printed in **bold**. Clones are specified by a 'c' followed by the clone number. Clinical strains are highlighted by red strain and GenBank accession numbers, non-human hosts are given in brackets. Potentially undescribed taxa are indicated by bold blue font. Morphological identifications are given in quotation marks.

Mucor sinensis is considered to be conspecific with *M. racemosus* f. *racemosus* because it groups with the ex-neotype CBS 260.68 of the latter in the ITS tree. It appears to represent a morphological variant or a growth-reduced mutant rather than a separate species.

Mucor amphibiorum group and related taxa

The ITS sequence of the ex-type strain of the recently described *Mucor ellipsoideus* (FN650647, Álvarez et al. 2011) is identical to that of CBS 210.80, the ex-type strain of *Mucor ardhlaengiktus*, except of an A missing at the 3' terminus probably due to low sequence quality (data not shown). The characteristic azygospores described in *M. ardhlaengiktus* (Mehrotra & Mehrotra 1978) appear to be a variable feature that was absent from the strain studied by Álvarez et al. (2011) and from strain CBS 650.78. *Mucor ardhlaengiktus* is the older name (Mehrotra & Mehrotra 1978) and we therefore consider *M. ellipsoideus* as a synonym. The varieties of *Mucor laxorrhizus*, var. *laxorrhizus* and var. *ovalisporus*, appear distantly positioned in the ITS (Fig. 6) and LSU (Fig. 1) trees and as a result we recognize them as separate species.

Mucor ardhlaengiktus B.S. Mehrotra & B.M. Mehrotra, Sydowia 31: 94. 1979 [1978]. — MycoBank MB317921

= *Mucor ellipsoideus* E. Álvarez, Stchigel, Cano, D.A. Sutton & Guarro, in Álvarez et al., Med. Mycol. 49: 67. 2011.

Lectotype. Fig. 1 (Mehrotra & Mehrotra, Sydowia 31: 95. 1979 [1978]), designated here.

Epitype. CBS 210.80 (preserved in a metabolically inactive state by lyophilization, batch nr. 968), designated here.

Specimens examined. CBS 210.80, CBS 528.73, CBS 650.78.

Mucor circinelloides* f. *janssenii (Lendn.) Schipper, Stud. Mycol. 12: 13. 1976. — MycoBank MB348491

Basionym. *Mucor janssenii* Lendn. (as '*janseni*'), Bull. Herb. Boissier 2, Sér. 7: 251. 1908.

≡ *Mucor griseocyanus* Hagem f. *janssenii* (Lendn.) Schipper, Antonie van Leeuwenhoek 36: 486. 1970.

≡ *Circinomucor janssenii* (Lendn.) Arx, Sydowia 35: 18.1982.

= *Mucor tenellus* Y. Ling, Rev. Gén. Bot. 42: 736. 1930.

≡ *Circinella tenella* (Y. Ling) Zycha, Krypt.-Fl. Brandenburg (Leipzig) 6a: 99. 1935.

= *Mucor stagnalis* Novot., Notul. Syst. Inst. Cryptog. Horti Bot. Petropol. 6: 158. 1950.

= *Mucor kurssanovii* Milko & Beliakova, Mikrobiologija 36: 118. 1967.

= *Mucor velutinosus* E. Álvarez, Stchigel, Cano, D.A. Sutton & Guarro, in Álvarez et al., Med. Mycol. 49: 64. 2011.

Neotype. CBS 205.68 (preserved in a metabolically inactive state by lyophilization, batch nr. 605), designated here.

Specimens examined. CBS 144.93, CBS 185.68, CBS 204.68, CBS 205.68, CBS 206.68, CBS 227.29, CBS 232.29, CBS 243.67, CBS 365.70, CBS 762.74.

Notes — Schipper (1970) described *Mucor griseocyanus* f. *janssenii* based on strain CBS 205.68 because no authentic material of *M. janssenii* existed. However, she did not designate CBS 205.68 as the neotype though it was considered as such in the following years. Here we designate strain CBS 205.68 (in a lyophilized state) as neotype of *M. janssenii* because it fits the description of this species morphologically and it is well described (Schipper 1970).

Mucor parviseptatus G. Walther & de Hoog, *nom. nov.* — MycoBank MB800447

≡ *Mucor laxorrhizus* Y. Ling var. *ovalisporus* Schipper, Stud. Mycol. 31: 154. 1989, non *Mucor ovalisporus* (G. Sm.) Pidopl. & Milko, Atlas Mukor. Grib. (Kiev): 61. 1971.

Etymology. The epithet *parviseptatus* refers to the few septa that are formed unconnected with branching of the sporangiophores.

Specimens examined. CBS 417.77 ex-type strain of *Mucor laxorrhizus* var. *ovalisporus*, CBS 522.79.

Mucor racemosus Fresen. f. ***racemosus*** Beitr. Mykol. 1: 12. 1850. — MycoBank MB427116

≡ *Circinomucor racemosus* (Fresen.) Arx, Sydowia 35: 18. 1982.

= *Mucor racemosus* f. *brunneus* Morini, Malpighia 10: 88. 1896.

= *Mucor dimorphosporus* Lendn., Mat. Fl. Crypt. Suisse 3, 1: 93. 1908.

= *Mucor christianensis* Hagem, Ann. Mycol. 8: 268. 1910.

= *Mucor racemosus* var. *christianensis* (Hagem) Naumov, Opred. Mukor. (Mucorales): 46. 1935.

= *Mucor varians* Povah, Bull. Torrey Bot. Club 44: 297. 1917.

= *Mucor pispekii* Naumov, Encycl. Mycol. 9: 47. 1939.

= *Mucor chibinensis* Neophyt., Notul. Syst. Inst. Cryptog. Horti Bot. Petropol. 10: 160. 1955.

= *Mucor racemosus* f. *chibinensis* (Neophyt.) Schipper, Stud. Mycol. 12: 24. 1976.

= *Mucor oudemansii* Váňová, Česka Mykol. 45: 25. 1991.

= *Mucor sinensis* Milko & Beliakova, in Pidopl. & Milko, Atlas Mukor. Grib. (Kiev): 53. 1971.

Neotype. CBS 260.68 (preserved in a metabolically inactive state by lyophilization, batch nr. 87.1018), designated here.

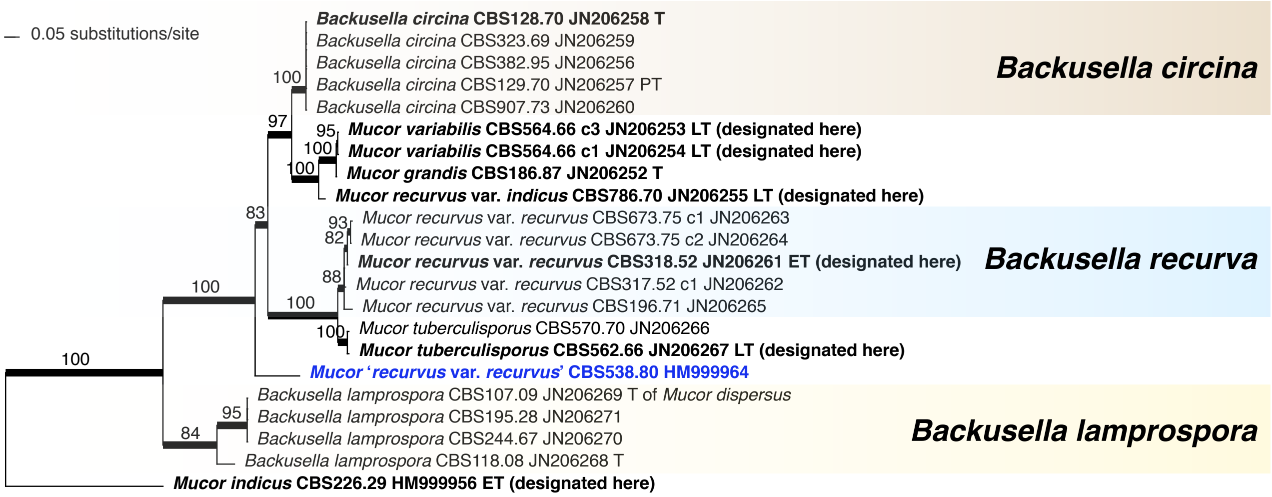

Fig. 7 RAxML phylogram of the *Mucor recurvus* group and *Backusella* based on the ITS region. Branches with bootstrap values of 75 % or higher are printed in **bold**. Ex-type strains are designated by: T = ex-type strain, ET = ex-epitype strain, LT = ex-lectotype strain, PT = ex-paratype strain. Ex-type strains of currently accepted taxa are printed in **bold**. Clones are specified by a 'c' followed by the clone number. Potentially undescribed taxa are indicated by bold blue font. Morphological identifications are given in quotation marks.

Specimens examined. CBS 113.08 ex-lectotype strain of *Mucor dimorphosporus* (lectotype: Fig. 34 (Lendner, Mat. Fl. Crypt. Suisse 3, 1: 93. 1908), designated here; epitype: CBS 113.08, preserved in a metabolically inactive state by lyophilization, batch nr. 479, designated here), CBS 204.74 ex-type strain of *Mucor sinensis*, CBS 222.81, CBS 260.68, CBS 271.86, CBS 369.71, CBS 616.63, CBS 636.67 ex-neotype strain of *Mucor racemosus* f. *chibinensis*, CBS 657.68, CBS 660.66, CBS 661.66, CBS 111557, CNM-CM 2569, CNM-CM 3862.

Notes — Strain CBS 260.68 was used by Schipper (1970) for the description of *Mucor racemosus* f. *racemosus* but not designated as neotype. Here we designate strain CBS 260.68 (in a lyophilized state) as neotype of this species because it is well characterized (Schipper 1970) and because its morphology fully complies with the original description.

Mucor silvaticus Hagem, Skr. Vidensk.-Selsk. Christiana, Math.-Naturvidensk. Kl. 7: 31. 1908. — MycoBank MB182519

≡ *Mucor hiemalis* f. *silvaticus* (Hagem) Schipper, Stud. Mycol. 4: 31. 1973.

Neotype. CBS 412.71 (preserved in a metabolically inactive state by lyophilization, batch nr. 853), designated here.

Specimens examined. CBS 249.35, CBS 412.71, CBS 509.66.

Notes — To our knowledge, authentic material of this species has been lost. Schipper (1973) studied five strains that matched the description of Hagem (CBS 249.35, CBS 250.35, CBS 508.66, CBS 509.66 and CBS 412.71). Schipper's description and drawings are based on CBS 412.71. It was isolated in Denmark, while the remaining strains originated in Germany. Here we designate CBS 412.71 as the neotype of *Mucor silvaticus*, because it was well described and illustrated as *M. hiemalis* f. *silvaticus* in Schipper (1973). Compared to the strains available in international fungal culture collections, it was isolated closest to the locality of the type, Norway.

Mucor recurvus group and *Backusella*

The LSU phylogram (Fig. 1) resolved a clade (*Mucor recurvus* group) consisting of *Mucor grandis*, *M. oblongiellipticus*, *M. oblongisporus*, *M. recurvus*, *M. tuberculisporus*, *M. variabilis*, two potentially undescribed species as well as *Backusella circina* and *B. lamprospora* that exclusively unifies taxa with transitorily recurved sporangiophores (Fig. 8). In this clade the sporangiophores are curved during maturation of the sporangium and become upright afterwards. Schipper (1978a) recognised the *Mucor* portion of this group on morphological grounds. The type species of *Backusella*, *B. circina* (Ellis & Hesseltine 1969: 865) (Fig. 8a, b), as well as *B. lamprospora* (Benny & Benjamin 1975: 320) also have been described to form transitorily recurved sporangiophores.

The genus *Backusella* differs from *Mucor* only by the formation of sporangiola in addition to sporangia. However, sporangiola, though in low frequency, have also been described in *Mucor recurvus* var. *indicus* and in *M. tuberculisporus* (Schipper 1978a). In our opinion the clade in the LSU phylogram including *Mucor* and *Backusella* species represents a natural group characterised by transitorily recurved sporangiophores. Consequently, we transfer all *Mucor* species belonging to that clade to the genus *Backusella*. The two varieties of *Mucor recurvus* (var. *recurvus* and var. *indicus*) are located in different supported subclades of our ITS tree (Fig. 7) and likely represent separate species.

Sequence diversity is high in the emended genus *Backusella*. ITS sequences of *M. oblongisporus* CBS 569.70, *M. oblongiellipticus* CBS 568.70, and a contaminant strain of CBS 523.68 deviate significantly from the remaining members of the group and cannot be aligned with confidence. However, their LSU sequences and the formation of transitorily recurved sporangiophores clearly assign these taxa to the emended genus *Backusella*.

Backusella ctenidia is positioned inside the *Mucor circinelloides* complex (Fig. 1, 5) and does not belong in *Backusella*. For that reason we propose transferring it to *Mucor*.

We propose the following emendation for *Backusella*:

Backusella *Ellis & Hesseltine emend. Walther et al.*

Type species. Backusella circina J.J. Ellis & Hesselt.

Sporophores arising directly from the substrate mycelium, simple or sympodially branched, recurved when young, erect at maturity (transitorily recurved), smooth or roughened, producing terminal sporangia and in some species few to many lateral, pedicellate sporangiola. Terminal sporangia columellate, multispored, globose to subglobose, size ranging from 90 to 375 µm diam, nonapophysate, wall encrusted, deliquescent; columellae subglobose, ellipsoidal, slightly pyriform or conical, smooth. Collars small or consisting of needle-shaped spines. Sporangiolar pedicels straight, curved, or recurved, simple or branched, smooth or encrusted. Sporangiola columellate, multi- or unispored; wall verrucose or spinulose or both, persistent. Sporangiospores of sporangia and multispored sporangia identical, large, subglobose, ellipsoidal or irregularly polyhedral, smooth. Columellae, hyphae and sporangiospores in some species with yellowish or brownish content. Zygospores globose to subglobose; wall dark, opaque or translucent, ornamented with conical or rounded projections; suspensors opposed, smooth or roughened, equal or unequal.

Notes — The emended genus *Backusella* includes the following species: *Backusella circina*, *B. grandis*, *B. indica*, *B. lamprospora*, *B. oblongielliptica*, *B. oblongispora*, *B. recurva*, *B. tuberculispora* and *B. variabilis*.

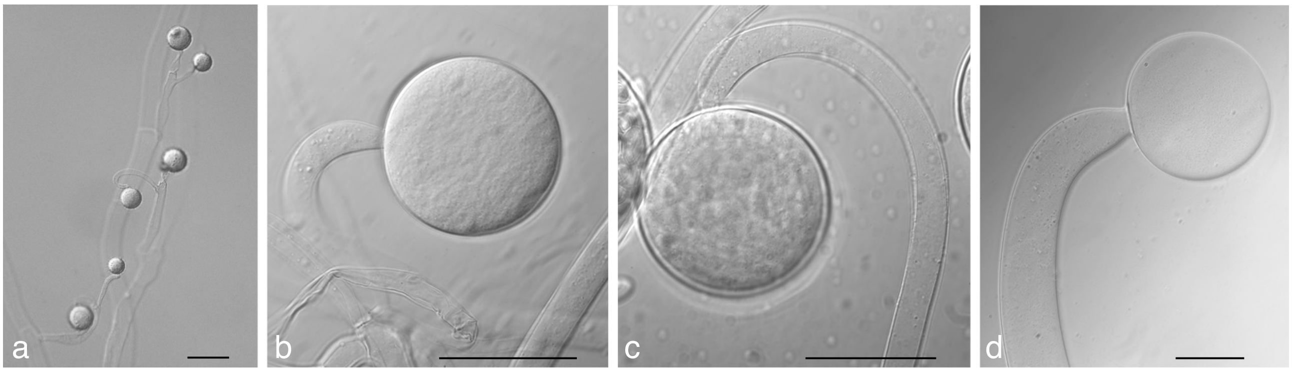

Fig. 8 Morphology of the genus *Backusella*. a, b. CBS 128.70 *Backusella circina*, a. unispored sporangiola; b. transitorily recurved sporangiophore; c. CBS 318.52 *Mucor recurvus* var. *recurvus* (*Backusella recurva* here), transitorily recurved sporangiophore; d. CBS 564.66 *Mucor variabilis* (*Backusella variabilis* here), transitorily recurved sporangiophore. — Scale bar: a = 10 µm, b–d = 50 µm.

Backusella grandis (Schipper & Samson) G. Walther & de Hoog, *comb. nov.* — MycoBank MB800453

Basionym. *Mucor grandis* Schipper & Samson, Mycotaxon 50: 479. 1994.

Specimen examined. CBS 186.87 ex-type strain of *Mucor grandis*.

Notes — The ITS sequence of *Mucor grandis* differs by only 6 basepairs from that of *M. variabilis*, while different clones of *M. variabilis* vary at four positions. The small sequence differences suggest conspecifity but the diameter of the sporangia varies significantly between the species. More detailed taxonomic studies are needed to clarify species limits.

Backusella indica (Baijal & B.S. Mehrotra) G. Walther & de Hoog, *comb. nov.* — MycoBank MB800449

Basionym. *Mucor recurvus* var. *indicus* Baijal & B.S. Mehrotra, Sydowia 19: 207. 1965.

Lectotype. CBS 786.70 (preserved in a metabolically inactive state by lyophilization, batch nr. 344), designated here.

Specimen examined. CBS 786.70.

Backusella oblongielliptica (H. Nagan., Hirahara & Seshita ex Pidopl. & Milko) G. Walther & de Hoog, *comb. nov.* — MycoBank MB800451

Basionym. *Mucor oblongiellipticus* H. Nagan., Hirahara & Seshita, Essays Stud. Fac. Hiroshima Jogakuin College 18: 167. 1969, nom. inval., Art. 36.1
≡ *Mucor oblongiellipticus* H. Nagan., Hirahara & Seshita ex Pidopl. & Milko, Atlas Mukor. Grib. (Kiev): 81. 1971.

Lectotype. CBS 568.70 (preserved in a metabolically inactive state by lyophilization, batch nr. 113), designated here.

Specimen examined. CBS 568.70.

Backusella oblongispora (Naumov) G. Walther & de Hoog, *comb. nov.* — MycoBank MB800452

Basionym. *Mucor oblongisporus* Naumov, Mater. Mykol. Fitopatol. Rossii 1(4): 12. 1915.

Neotype. CBS 569.70 (preserved in a metabolically inactive state by lyophilization, batch nr. 55), designated here.

Specimen examined. CBS 569.70.

Backusella recurva (E.E. Butler) G. Walther & de Hoog, *comb. nov.* — MycoBank MB800448; Fig. 8c

Basionym. *Mucor recurvus* E.E. Butler, Mycologia 44: 561. 1952.

Lectotype. Fig. 1 (Butler, Mycologia 44: 562. 1952).
Epitype. CBS 318.52 (preserved in a metabolically inactive state by lyophilization, batch nr. 717), designated here.

Specimens examined. CBS 196.71, CBS 317.52, CBS 318.52, CBS 673.75.

Backusella tuberculispora (Schipper) G. Walther & de Hoog, *comb. nov.* — MycoBank MB800450

Basionym. *Mucor tuberculisporus* Schipper, Stud. Mycol. 17: 23. 1978.

Lectotype. CBS 562.66 (preserved in a metabolically inactive state by lyophilization, batch nr. 88.1007), designated here.

Specimens examined. CBS 562.66, CBS 570.70.

Backusella variabilis (A.K. Sarbhoy) G. Walther & de Hoog, *comb. nov.* — MycoBank MB800454; Fig. 8d

Basionym. *Mucor variabilis* A.K. Sarbhoy, Trans. Brit. Mycol. Soc. 48: 559. 1965.

Lectotype. CBS 564.66 (preserved in a metabolically inactive state by lyophilization, batch nr. 22), designated here.

Specimen examined. CBS 564.66.

Mucor ctenidius (Durrell & M. Fleming) G. Walther & de Hoog, *comb. nov.* — MycoBank MB800455

Basionym. *Thamnidium ctenidium* Durrell & M. Fleming, Mycologia 58: 797. 1966.
≡ *Backusella ctenidia* (Durrell & M. Fleming) Pidopl. & Milko, Atlas Mukor. Grib. (Kiev): 85. 1971, ex Benny & R.K. Benj., Aliso 8: 325. 1975.

Specimens examined. CBS 293.66 ex-isotype strain of *Thamnidium ctenidium*, CBS 433.87, CBS 696.76.

Pilaira

Recently, Zheng & Liu (2009a) studied the genus *Pilaira* morphologically and reclassified *P. caucasica* as a variety of *P. moreaui*. The variety differed from var. *moreaui* in the size of sporangiophores and sporangiospores (Zheng & Liu 2009a). We found identical ITS sequences for both varieties supporting conspecifity (Fig. 3). We retain both varieties despite of identical ITS sequences because of the clear morphological distinction.

Zygorhynchus

Phenotypically *Zygorhynchus* and *Mucor* differ in the following features. First, species of *Zygorhynchus* are exclusively homothallic, while the majority of *Mucor* species is heterothallic (Watanabe 1994). Second, the suspensors of the zygospores are unequal in *Zygorhynchus* and equal in *Mucor.* Third, the two suspensors originate from the same hypha in *Zygorhynchus*, the '*Zygorhynchus* pattern', while they arise from different hyphae in *Mucor*, the '*Mucor* pattern' (Hesseltine et al. 1959, Schipper 1986). However, these differences are gradual (Schipper 1986). *Zygorhynchus exponens* may develop equal but *Mucor plumbeus* more or less unequal suspensors (Schipper 1986). In *Zygorhynchus exponens* (Hesseltine et al. 1959), *Z. japonicus* (Schipper 1986) and *Z. moelleri* (Green 1927) zygospores are also produced between different hyphae.

Based on our LSU (Fig. 1) and ITS (Fig. 3, 6) data, *Zygorhynchus* is polyphyletic. Our analyses indicate that unequal suspensors and the *Zygorhynchus* pattern of zygospore production do not represent synapomorphies in the genus *Zygorhynchus*, but appear to be convergent characters within *Mucor*. Therefore we recombine all *Zygorhynchus* species in *Mucor*.

The ex-type strains of *Zygorhynchus moelleri* and *Z. californiensis* have identical ITS sequences suggesting conspecifity. However, *Z. californiensis* has regularly globose spores, while the spores of *Z. moelleri* are oblong to ovoidal in shape, 2.0–3.3 × 3.0–6.5 µm (Hesseltine et al. 1959). For that reason we propose reclassifying *Z. californiensis* as a forma of *Z. moelleri*.

The two varieties described in *Zygorhynchus exponens*, var. *exponens* and var. *smithii* differ by only a single basepair in their ITS sequences. Also small morphological differences such as the lighter and browner sporangia and columellae in var. *smithii*, do not justify the maintenance of a separate variety and consequently we consider both varieties as synonymous.

Mucor exponens (Burgeff) G. Walther & de Hoog, *comb. nov.* — MycoBank MB800461

Basionym. *Zygorhynchus exponens* Burgeff, Bot. Abh. 4: 34. 1924.
= *Zygorhynchus exponens* Burgeff var. *smithii* Hesselt., C.R. Benj. & B.S. Mehrotra, Mycologia 51: 179. 1959.

Neotype. CBS 141.20 (preserved in a metabolically inactive state by lyophilization, batch nr. 563), designated here.

Specimens examined. CBS 141.20, CBS 404.58 ex-lectotype strain of *Zygorhynchus exponens* var. *smithii* (lectotype: CBS 404.58, preserved in a metabolically inactive state by lyophilization, batch nr. 40, designated here), CBS 508.48.

Mucor fusiformis G. Walther & de Hoog, *nom. nov.* — MycoBank MB800459

≡ *Zygorhynchus psychrophilus* Schipper & Hintikka, Antonie van Leeuwenhoek 35: 29. 1969, non *Mucor psychrophilus* Milko, in Pidopl. & Milko, Atlas Mukor. Grib. (Kiev): 73. 1971.

Etymology. The epithet refers to the shape of the sporangiospores.

Specimens examined. CBS 336.68 ex-type strain of *Zygorhynchus psychrophilus.*

Mucor heterogamus Vuill., Bull. Séanc. Soc. Sci. Nancy 8: 50. 1887. — MycoBank MB249261

≡ *Zygorhynchus heterogamus* (Vuill.) Vuill., Bull. Trimestriel. Soc. Mycol. France 19: 117. 1903.

Lectotype. Pl. II, f. 27-48 (Vuill., Bull. Séanc. Soc. Sci. Nancy 8. 1887), designated here.
Epitype. CBS 405.58 (preserved in a metabolically inactive state by lyophilization, batch nr. 658), designated here.

Specimens examined. CBS 252.85, CBS 338.74, CBS 405.58, CBS 580.83, CBS 594.83.

Notes — The original material of this species consists of slides labelled as "*Mucor heterogamus* P.V. Zygospores Mis de pain 17-3-86" (Hesseltine et al. 1959). Hesseltine et al. (1959) studied five strains: NRRL 1489, NRRL 1490, NRRL 1491, NRRL 1616 (= CBS 405.58) and a fresh isolate without an NRRL number designated as 'No. 1957' and compared these strains with the original material. The authors found remarkable intraspecific variation in colony appearance, but micromorphologically Vuillemin's material was almost identical with their living cultures except for some differences in lengths of the zygospore projections. Therefore they considered the type material and their strains as conspecific. Here we designate CBS 405.58 (NRRL 1616, preserved in a lyophilized state) verified by Hesseltine et al. (1959) as epitype of *Mucor heterogamus*.

Isolates of *M. heterogamus* vary considerably in their ITS sequences (maximum dissimilarity of 10 %) and might represent a complex of several species. Isolates that were morphologically assigned to *M. heterogamus* form a well-supported group with *Z. multiplex* and *Z. macrocarpus*, but at distances to the designated ex-epitype strain of 10.8 % and 7.7 %, respectively. The precise definition of species boundaries awaits detailed multilocus DNA sequence-based analyses.

Mucor japonicus (Komin.) G. Walther & de Hoog, *comb. nov.* — MycoBank MB800458

Basionym. *Zygorhynchus japonicus* Komin., Mykol. Zentbl. 5: 3. 1915 (1914).

Neotype. CBS 154.69 (preserved in a metabolically inactive state by lyophilization, batch nr. 409), designated here.

Specimen examined. CBS 154.69.

Notes — The authentic strain of *Zygorhynchus japonicus* studied by Kominami (1915) has been lost (Schipper 1986). Strain CBS 154.69 (preserved in a lyophilized state) is selected as neotype of *Z. japonicus* because it resembles the original strain and it is well described and illustrated (Schipper 1986).

Mucor megalocarpus G. Walther & de Hoog, *nom. nov.* — MycoBank MB800456

≡ *Zygorhynchus macrocarpus* Y. Ling, Rev. Gén. Bot. 42: 150. 1930, non *Mucor macrocarpus* Corda, Icon. Fungorum 2: 21. 1838.

Lectotype. Fig. 1 (Ling, Rev. Gén. Bot. 42: 152. 1930), designated here.
Epitype. CBS 215.27 (preserved in a metabolically inactive state by lyophilization, batch nr. 748), designated here.

Specimen examined. CBS 215.27.

Mucor moelleri (Vuill.) Lendn. f. ***moelleri***, Mat. Fl. Crypt. Suisse 3, 1: 72. 1908.

Basionym. *Zygorhynchus moelleri* Vuill., Bull. Trimestriel Soc. Mycol. France 19: 117. 1903.
= *Zygorhynchus vuilleminii* Namysl., Ann. Mycol. 8: 154. 1910.
= *Zygorhynchus vuilleminii* race *agamus* Namysl., Bull. Int. Acad. Sci. Cracovie, Cl. Sci. Math., Ser. B, Sci. Nat. 6: 479. 1911.
= *Zygorhynchus dangeardii* Moreau, Bull. Soc. Bot. France 59: 717. 1912.
= *Mucor saximontensis* Rall, Mycologia 57: 874. 1965.

Neotype. CBS 406.58 (preserved in a metabolically inactive state by lyophilization, batch nr. 656), designated here.

Specimens examined. CBS 216.27, CBS 380.29, CBS 406.58, CBS 444.65 ex-lectotype strain of *Mucor saximontensis* (lectotype: CBS 444.65, preserved in a metabolically inactive state by lyophilization, batch nr. 803, designated here), CBS 460.51, CBS 501.66, IHEM 21156.

Notes — No authentic material of this species is known to be preserved. Hesseltine et al. (1959) reported NRRL 2660 (= CBS 406.58) as the type of *Z. moelleri* but the strain studied by Vuillemin was isolated in Eberswalde (Germany) while NRRL 2660 originated from soil in Wisconsin (USA).

Mucor moelleri f. ***californiensis*** (Hesselt., C.R. Benj. & B.S. Mehrotra) G. Walther & de Hoog, *comb. nov.* — MycoBank MB800460

Basionym. *Zygorhynchus californiensis* Hesselt., C.R. Benj. & B.S. Mehrotra, Mycologia 51: 185. 1959.

Lectotype. Fig. 8–10 (Hesseltine, Benjamin & Mehrotra, Mycologia 51: 176. 1959), designated here.
Epitype. CBS 402.58 (preserved in a metabolically inactive state by lyophilization, batch nr. 90.0055), designated here.

Specimen examined. CBS 402.58.

Mucor multiplex (R.Y. Zheng) G. Walther & de Hoog, *comb. nov.* — MycoBank MB800457

Basionym. *Zygorhynchus multiplex* R.Y. Zheng, Mycotaxon 84: 370. 2002.

Specimen examined. CBS 110662 ex-type strain of *Zygorhynchus multiplex.*

Actinomucor

Currently there are three varieties in *Actinomucor*: *A. elegans* var. *elegans*, var. *meitauzae* (syn. *A. taiwanensis*, Zheng & Liu 2005) and var. *kuwaitiensis* (Khan et al. 2008). Characters distinguishing the varieties are shape, size and ornamentation of the sporangiospores (Zheng & Liu 2005, Khan et al. 2008). The var. *meitauzae* and var. *kuwaitiensis* show reduced growth on Czapek's agar. In contrast to earlier reports (Jong & Yuan 1985), the maximum growth temperature does not discriminate the varieties (Zheng & Liu 2005, Khan et al. 2008). However, the relationships deduced from our ITS data (Fig. 9) contradict current taxonomic concepts. Strains with the characteristics of var. *meitauzae* are scattered over nearly all parts of the tree, and only a part of the strains belonging to var. *elegans* is included in a well-supported clade around the ex-type strain of var. *elegans*. A detailed taxonomic revision is required.

Rhizopus

Based on our phylogenetic trees the genus *Rhizopus* is paraphyletic because *Sporodiniella umbellata* and *Syzygites megalocarpus* cluster among *Rhizopus* species. All currently accepted *Rhizopus* species are well recognizable in the ITS tree. However, three strains of *Rhizopus stolonifer*, CBS 126.83, CBS 442.74 and CBS 926.87, exhibit widely deviating ITS sequences, forming a separate group that may represent a new species. In agreement with our results, Vágvölgyi et al.

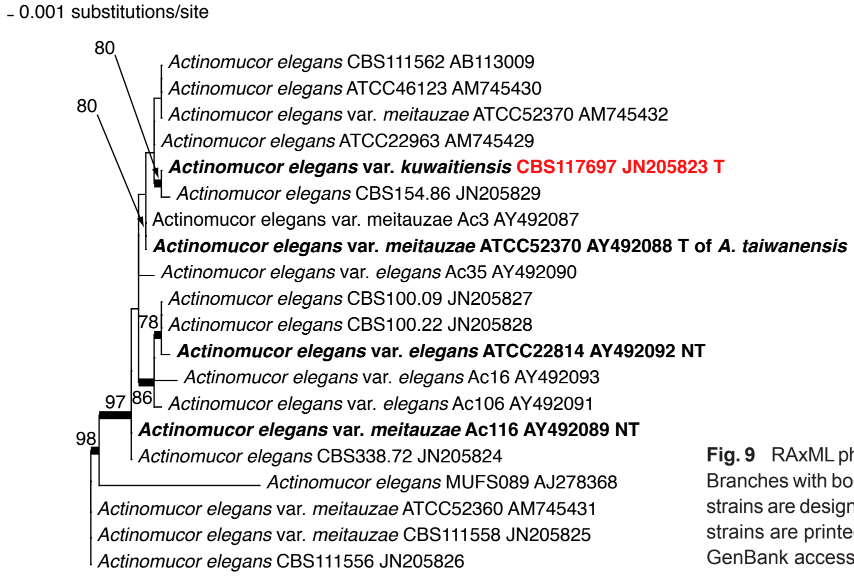

Fig. 9 RAxML phylogram of the genus *Actinomucor* based on the ITS region. Branches with bootstrap values of 75 % or higher are printed in **bold**. Ex-type strains are designated by: T = ex-type strain, NT = ex-neotype strain. Ex-type strains are printed in **bold**. Clinical strains are highlighted by red strain and GenBank accession numbers.

(2004) found strains morphologically assigned to *R. stolonifer* with strongly deviating randomly amplified polymorphic DNA (RAPD) patterns and consequently the authors suspected an undescribed variety or even species. The varieties *arrhizus* and *delemar* of *Rhizopus arrhizus* are also recognized in the ITS tree, in accordance with Abe et al. (2007) and Gryganskyi (2010) who treated them as separate species. Strains identified morphologically as *R. arrhizus* var. *tonkinensis* by Zheng et al. (2007) do not form a separate cluster but are distributed in var. *arrhizus* and var. *delemar* clades. However, by using short tandem repeat motives of IGS rDNA sequences Liu et al. (2008) were able to characterize all three varieties of *R. arrhizus*.

The morphological varieties described in *Rhizopus microsporus* are not supported genetically; a single, supported clade includes strains representing the varieties *microsporus*, *chinensis* and *oligosporus*. ITS sequences of the remaining *R. microsporus* strains that had been assigned morphologically to the varieties *azygosporus*, *chinensis*, *oligosporus*, *rhizopodiformis* and *tuberosus* are all identical. The ITS identities imply in agreement with Liu et al. (2008), Abe et al. (2010) and Dolatabadi et al. (In press) that enlarged size and indistinct ornamentation of sporangiospores have no genetic basis in *R. microsporus*.

Circinella

The genus *Circinella* was erected by van Tieghem & le Monnier (1873) in order to accommodate strains differing from *Mucor* by circinate sporangiophore branches that terminate in globose sporangia with persistent walls (Hesseltine & Fennell 1955). Based on our LSU tree (Fig. 1) *Circinella* is polyphyletic, resolved in a well-supported group around the type species *C. umbellata* within the *Lichtheimiaceae*, and two separate species, *C. simplex* and *C. rigida*, positioned distantly within different clades of *Mucor*. As a consequence, we propose assigning *C. rigida* to *Mucor*. No type material is known to have been preserved of *C. simplex*. We studied five strains of this species but we only obtained good sequence data for CBS 428.80. More detailed taxonomic studies on the numerous strains of this species that are available in public collections are necessary to test its monophyly and to select a neotype. Excluding the unrelated species *C. rigida* and *C. simplex*, the genus *Circinella* is restricted to species that develop sporangiophores either with sterile spines or umbels with circinate branches.

The ex-type strain of *Circinella lacrymispora* clusters with the ex-type strain of *Gongronella lacrispora* in the *Gongronella* clade of the LSU phylogram (Fig. 1). Based on this finding *Circinella lacrymispora* should be reclassified in *Gongronella*. The LSU sequences of *C. lacrymispora* and *G. lacrispora* differ only in 3 basepairs and conspecifity cannot be excluded. We defer recombination until we obtain the ITS sequences of both taxa and until we perform a detailed morphological study.

Mucor durus G. Walther & de Hoog, *nom. nov.* — MycoBank MB800462

≡ *Circinella rigida* G. Sm., Trans. Brit. Mycol. Soc. 34: 19. 1951, non *Mucor rigidus* Léger, Rech. Struct. Mucor (Thèse, Paris): 71. 1895.

Lectotype. Pl. 2, Fig. 7–8 (Smith, Trans. Brit. Mycol. Soc. 34: 17–22. 1951), designated here.

Epitype. CBS 156.51 (preserved in a metabolically inactive state by lyophilization, batch nr. 389), designated here.

Etymology. Named after the rigid wall of the sporangium.

Specimens examined. CBS 156.51, CBS 484.66.

Notes — The species differs markedly from other *Mucor* species by the extremely rigid sporangial walls, the often curved branches of the sporangiophores, the common formation of subsporangial septa and the frequent presence of distinct apophyses (Fig. 2h).

Rhizomucor

All non-thermophilic *Rhizomucor* species, namely *Rm. chlamydosporus*, *Rm. endophyticus*, *Rm. regularior* and *Rm. variabilis* belong to *Mucor* based on our LSU tree (Fig. 1). *Rhizomucor regularior* and *Rm. variabilis* have recently been reclassified: *Rm. variabilis* has been renamed as *Mucor irregularis*, whereas *Rm. regularior* has been synonymised with *M. circinelloides* (Álvarez et al. 2011). Our ITS data (Fig. 3) indicate that *Rhizomucor endophyticus* represents a discrete species closely related to *Mucor luteus*. The ITS sequence of the ex-type strain of *Rm. chlamydosporus* (GenBank EF583634) is identical to that of *Mucor indicus* (data not shown); the morphological description of the species (Zheng & Liu 2009b) fully matches with that of *M. indicus*.

Mucor hiemalis and *M. luteus* develop distinct rhizoids when they grow over glass slides (Fig. 2c). These findings demonstrate that not only *Rhizomucor*, but also *Mucor* species have the ability to produce rhizoids, at least under certain conditions. Consequently, this feature should not be used as sole criterion for the distinction of *Mucor* and *Rhizomucor.*

After removal of the above species, *Rhizomucor* with its type species *Rhizomucor parasiticus* (which is a synonym of *Rm.*

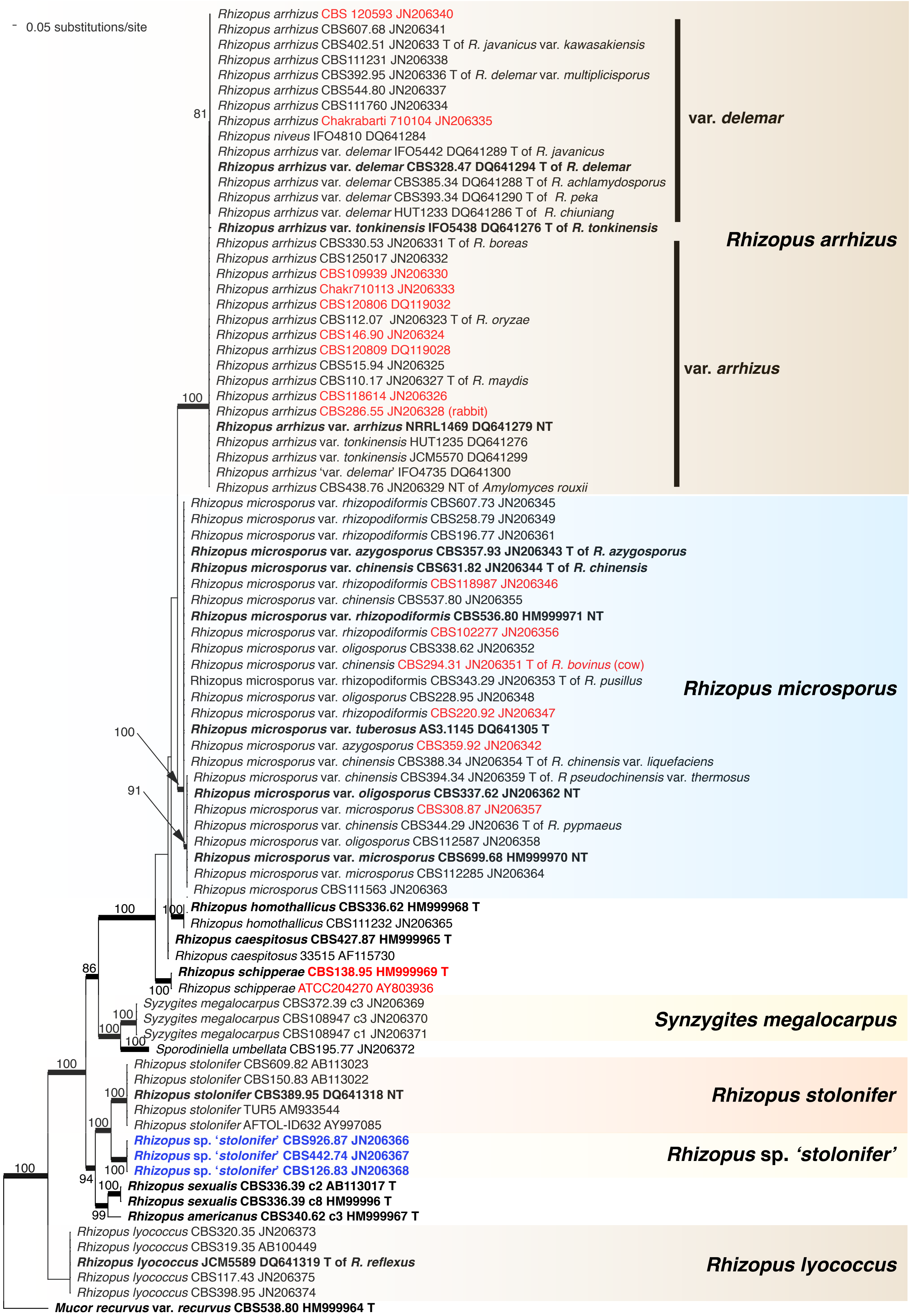

Fig. 10 RAxML phylogram of the genus *Rhizopus* based on the ITS region. Branches with bootstrap values of 75 % or higher are printed in **bold**. Ex-type strains are designated by: T = ex-type strain, NT = ex-neotype strain. Ex-type strains of currently accepted taxa are printed in **bold**. Clones are specified by a 'c' followed by the clone number. Clinical strains are highlighted by red strain and GenBank accession numbers, non-human hosts are given in brackets. Potentially undescribed taxa are indicated by bold blue font. Morphological identifications are given in quotation marks.

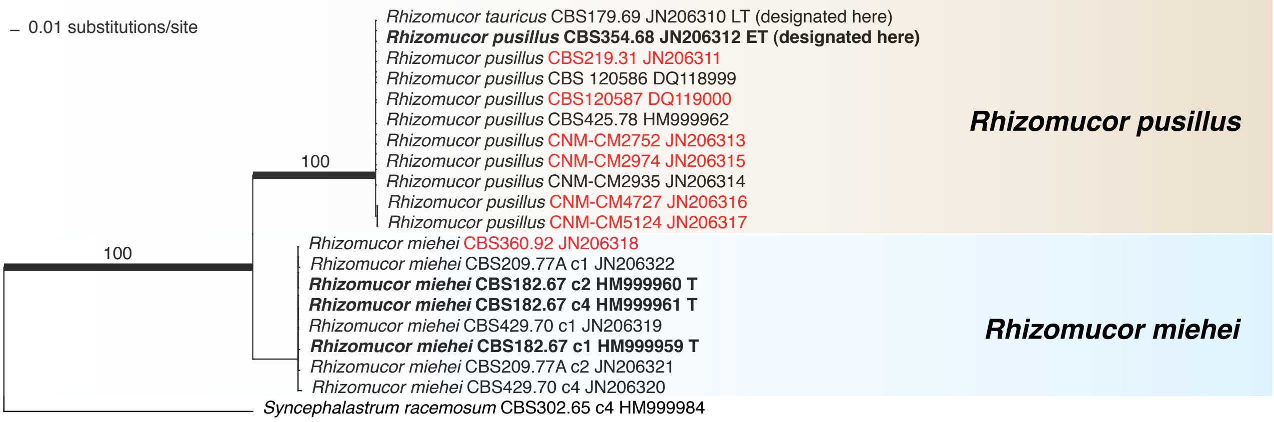

Fig. 11 RAxML phylogram of the genus *Rhizomucor* based on the ITS region. Branches with bootstrap values of 75 % or higher are printed in **bold**. Ex-type strains are designated by: T = ex-type strain, LT = ex-lectotype strain, ET = ex-epitype strain. The identifying ex-type strain of a clade is printed in **bold**. Clones are specified by a 'c' followed by the clone number. Clinical strains are highlighted by red strain and GenBank accession numbers.

pusillus) is monophyletic. The genus is restricted to thermophilic species with predominantly subglobose spores, as was recognized previously by Schipper (1978b) applying only phenotypic characters. Currently four thermophilic *Rhizomucor* species are accepted: *Rm. miehei*, *Rm. nainitalensis*, *Rm. pakistanicus* and *Rm. pusillus*. *Rhizomucor tauricus* is considered to be conspecific with *Rm. pusillus* because their ITS sequences are identical (Fig. 11). Analysis of its carbon source utilization, isoenzyme patterns and PCR-coupled RFLP of the ITS suggested that *Rm. tauricus* represented a heterothallic mutant strain of *Rm. pusillus* (Vágvölgyi et al. 1999).

Rhizomucor nainitalensis forms sporangiospores of different shapes, varying from subglobose to irregularly shaped (Joshi 1982). The sporangiospores of *Rhizomucor pakistanicus* are globose or ovoidal (Mirza et al. 1979). The following description of *Rhizomucor* is slightly modified from Schipper (1978b: 53):

Rhizomucor Lucet & Costantin (1900)

Thermophilic; sporangiophores originating from aerial mycelium, either from short aerial hyphae or from distinct stolons, both with simple or weakly branched rhizoids; sporangiophores branched, each branch bearing a multispored terminal sporangium; sporangia borne in an upright position, globose, dark (coloured), distinctly columellate, non-apophysate; sporangiospores consistently or partly subglobose; zygospores globose, covered with blunt projections, and formed in the aerial mycelium between non-ornamented, isogamous opposed suspensors.

Mucor endophyticus (R.Y. Zheng & H. Jiang) J. Pawłowska & G. Walther, *comb. nov.* — MycoBank MB800463

Basionym. *Rhizomucor endophyticus* R.Y. Zheng & H. Jiang, Mycotaxon 56: 456. 1995.

Specimens examined. CBS 385.95 ex-type strain of *Rhizomucor endophyticus*.

Mucor indicus Lendn., Bull. Soc. Bot. Genève, Ser. 2, 21: 258. 1930. — MycoBank MB267842

≡ *Zygorhynchus indicus* (Lendn.) Arx, Sydowia 35: 16. 1982.
= *Rhizomucor chlamydosporus* R.Y. Zheng, X.Y. Liu & R.Y. Li, Sydowia 61: 142. 2009.

Lectotype. Fig. 1–3 (Lendner, Bull. Soc. Bot. Genève, Ser. 2, 21: 258–260. 1930), designated here.

Epitype. CBS 226.29 (preserved in a metabolically inactive state by lyophilization, batch nr. 679), designated here.

Specimens examined. CBS 120.08, CBS 226.29, CBS 414.77, CBS 422.71, CBS 535.80, CBS 671.79, CBS 120585, CBS 123974.

Rhizomucor pusillus (Lindt) Schipper, Stud. Mycol. 17: 54. 1978. — MycoBank MB322484

Basionym. *Mucor pusillus* Lindt, Arch. Exp. Path. Pharmacol. 21: 272. 1886.

= *Mucor septatus* Bezold, Schimmelmyc. Menschl. Ohres: 97. 1889.
≡ *Rhizomucor septatus* (Bezold) Lucet & Costantin, Archs Parasitol. 4: 362. 1901.
= *Mucor parasiticus* Lucet & Costatin, Compt. Rend. Hebd. Séances Acad. Sci. 129: 1033. 1899.
≡ *Rhizomucor parasiticus* (Lucet & Costantin) Lucet & Costantin, Rev. Gén. Bot. 12: 81. 1900.
≡ *Rhizopus parasiticus* (Lucet & Costantin) Lendn., Mat. Fl. Crypt. Suisse 3: 115. 1908.
= *Mucor buntingii* Lendn., Bull. Soc. Bot. Genève, Ser. 2, 21: 260. 1930.
= *Mucor tauricus* Milko & Schkur., Novosti Sist. Nizsh. Rast. 7: 139. 1970.
≡ *Rhizomucor tauricus* (Milko & Schkur.) Schipper, Stud. Mycol. 17: 62. 1978.
≡ *Rhizomucor pusillus* var. *tauricus* (Milko & Schkur.) R.Y. Zheng, X.Y. Liu & R.Y. Li, Sydowia 61: 144. 2009.

Lectotype. Pl. II.III, Fig. 1–6 (Lindt, Arch. Exp. Path. Pharmacol. 21: 269–298. 1886), designated here.

Epitype. CBS 354.68 (preserved in a metabolically inactive state by lyophilization, batch nr. 85.0901), designated here.

Specimens examined. CBS 179.69 ex-lectotype strain of *Rhizomucor tauricus* (lectotype: CBS 179.69, preserved in a metabolically inactive state by lyophilization, batch nr. 87.3168, designated here), CBS 219.31, CBS 354.68, CBS 425.78, CBS 120586, CBS 120587, CNM-CM 2752, CNM-CM 2935, CNM-CM 2974, CNM-CM 4727, CNM-CM 5124.

Umbelopsis

Our ITS dataset is incomplete for *Umbelopsis* because of the high proportion of strains that needed to be cloned. For that reason, we refrain from taxonomic changes. The ex-type strains of *Umbelopsis dimorpha* and *Umbelopsis nana* possess identical ITS sequences and it is likely that these species are conspecific. The ITS sequences of the ex-type strains of *U. swartii* and *U. westeae*, as well as those of *U. gibberosa* and *U. ramanniana* are very similar necessitating a critical revision of *Umbelopsis* taxonomy.

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REFERENCES

Abe A, Asano K, Sone T. 2010. A molecular phylogeny-based taxonomy of the genus Rhizopus. Bioscience, Biotechnology and Biochemistry 74: 1325–1331.

Abe A, Oda Y, Asano K, Sone T. 2006. The molecular phylogeny of the genus Rhizopus based on rDNA sequences. Bioscience, Biotechnology and Biochemistry 70: 2387–2393.

Abe A, Oda Y, Asano K, Sone T. 2007. Rhizopus delemar is the proper name for Rhizopus oryzae fumaric-malic acid producers. Mycologia 99: 714–722.

Alastruey-Izquierdo A, Hoffmann K, Hoog GS de, Rodriguez-Tudela JL, Voigt K, et al. 2010. Species recognition and clinical relevance of the zygomycetous genus Lichtheimia (syn. Mycocladus, Absidia pp.). Journal of Clinical Microbiology 48: 2154–2170.

Álvarez E, Cano J, Stchigel AM, Sutton DA, Fothergill AW, et al. 2011. Two new species of Mucor from clinical samples. Medical Mycology 49: 62–72.

Álvarez E, Garcia-Hermoso D, Sutton DA, Cano JF, Stchigel AM, et al. 2010a. Molecular phylogeny and proposal of two new species of the emerging pathogenic fungus Saksenaea. Journal of Clinical Microbiology 48: 4410–4416.

Álvarez E, Stchigel AM, Cano J, Sutton DA, Fothergill AW, et al. 2010b. Molecular phylogenetic diversity of the emerging mucoralean fungus Apophysomyces: Proposal of three new species. Revista Iberoamericana de Micología 27: 80–89.

Bainier M. 1884. Nouvelles observations sur les zygospores des Mucorinées. Annales des Sciences Naturelles, Botanique 19: 200–214.

Balajee SA, Borman AM, Brandt ME, Cano J, Cuenca-Estrella M, et al. 2009. Sequence-based identification of Aspergillus, Fusarium, and Mucorales species in the clinical mycology laboratory: Where are we and where should we go from here? Journal of Clinical Microbiology 47: 877–884.

Benny GL, Benjamin RK. 1975. Observations on Thamnidiaceae (Mucorales). New taxa, new combination, and notes on selected species. Aliso 8: 301–351.

Bidartondo MI, Bruns T, Blackwell M, Edwards I, Taylor AFS, et al. 2008. Preserving accuracy in GenBank. Science 21: 1616.

Bridge PD, Roberts PJ, Spooner BM, Pancha G. 2003. On the unreliability of published DNA sequences. New Phytologist 160: 43–48.

Budziszewska J, Piątkowska J, Wrzosek M. 2010. Taxonomic position of Mucor hiemalis f. luteus. Mycotaxon 111: 75–85.

Calmette LCA. 1892. Contribution à l’étude des ferments de l’amidon; la levûre chinoise. Annales de l’Institut Pasteur 6: 604–620.

Chakrabarti A, Marak RSK, Shivaprakash MR, Gupta S, Garg R, et al. 2010. Cavitary pulmonary zygomycosis caused by Rhizopus homothallicus. Journal of Clinical Microbiology 48: 1965–1969.

Dolatabadi S, Walther G, Hoog GS de. In press. Diversity and delimitation of Rhizopus microsporus. Fungal diversity.

Ellis JJ, Hesseltine CW. 1969. Two new members of the Mucorales. Mycologia 61: 863–872.

Ellis JJ, Rhodes LJ, Hesseltine CW. 1976. The genus Amylomyces. Mycologia 68: 131–143.

Foos KM, May NL, Beach DL, Pomper M, Sheehan KB, Ruch DG. 2011. Phylogeny of Pilobolaceae. Mycologia 103: 36–44.

García Rodríguez J, Quiles I, Humala K, Monzon A, Cuenca-Estrella M. 2012. Isolation of Cunninghamella blakesleeana in an immunodepressed patient. Mycoses 55: 463–465.

Gomes MZR, Lewis RE, Kontoyiannis DP. 2011. Mucormycosis caused by unusual Mucormycetes, non-Rhizopus, -Mucor, and -Lichtheimia species. Clinical Microbiology Reviews 24: 411–445.

Green E. 1927. The life-history of Zygorhynchus moelleri Vuill. Annals of Botany 41: 419–435.

Greenberg RN, Scott LJ, Vaughn HH, Ribes JA. 2004. Zygomycosis (mucormycosis): emerging clinical importance and new treatments. Current Opinion in Infectious Diseases 17: 517–525.

Greuter W, McNeill J, Barrie FR, Burdet H-M, Demoulin V, et al. (eds) 2000. International Code of Botanical Nomenclature (St Louis Code). Regnum Vegetabile 138. Koeltz Scientific Books, Königstein.

Gryganskyi AP, Lee SC, Litvintseva AP, Smith ME, Bonito G, et al. 2010. Structure, function, and phylogeny of the mating locus in the Rhizopus oryzae complex. PLoS ONE 5: e15273.

Hermet A, Méheust D, Mounier J, Barbier G, Jany JL. 2012. Molecular systematics within the genus Mucor with special regard to species encountered in cheese. Fungal Biology 116: 692–705.

Hesseltine CW. 1983. Microbiology of oriental fermented foods. Annual Review of Microbiology 37: 575–606.

Hesseltine CW, Benjamin CR, Mehrotra BS. 1959. The genus Zygorhynchus. Mycologia 51: 173–194.

Hesseltine CW, Fennel DI. 1955. The genus Circinella. Mycologia 47: 193–212.

Hoffmann K, Discher S, Voigt K. 2007. Revision of the genus Absidia (Mucorales, Zygomycetes) based on physiological, phylogenetic, and morphological characters; thermotolerant Absidia spp. form a coherent group, Mycocladiaceae fam. nov. Mycological Research 111: 1169–1183.

Hoffmann K, Pawłowska J, Walther G, Wrzosek M, Hoog GS de, et al. 2013. The family structure of the Mucorales: a synoptic revision based on comprehensive multigene-genealogies. Persoonia 30: 57–76.

Hoffmann K, Voigt K. 2009. Absidia parricida plays a dominant role in biotrophic fusion parasitism among mucoralean fungi (Zygomycetes): Lentamyces, a new genus for A. parricida and A. zychae. Plant Biology 11: 537–554.

Hoog GS de, Gerrits van den Ende AHG. 1998. Molecular diagnostics of clinical strains of filamentous basidiomycetes. Mycoses 41: 183–189.

Hoog GS de, Guarro J, Gené F, Figueras MJ. 2000. Atlas of clinical fungi, 2nd ed. Reus, Utrecht.

Hospenthal DR, Chung KK, Lairet K, Thompson EH, Guarro J, et al. 2011. Saksenaea erythrospora infection following combat trauma. Journal of Clinical Microbiology 49: 3707–3709.

Jacobs K, Botha A. 2008. Mucor renisporus sp. nov., a new coprophilous species from Southern Africa. Fungal Diversity 29: 27–35.

Jong SC, Yuan GF. 1985. Actinomucor taiwanensis sp. nov., for manufacture of fermented soybean food. Mycotaxon 23: 261–264.

Joshi MC. 1982. A new species of Rhizomucor from India. Sydowia 35: 100–103.

Khan ZU, Ahmad S, Brazda A, Chandy R. 2009. Mucor circinelloides as a cause of invasive maxillofacial zygomycosis: an emerging dimorphic pathogen with reduced susceptibility to posaconazole. Journal of Clinical Microbiology 47: 1244–1248.

Khan ZU, Ahmad S, Mokaddas E, Chandy R, Cano J, Guarro J. 2008. Actinomucor elegans var. kuwaitiensis isolated from the wound of a diabetic patient. Antonie van Leeuwenhoek 94: 343–352.

Kominami K. 1915. Zygorhynchus japonicus, une nouvelle Mucorinée hétérogame, isolée du sol du Japon. Mycologisches Centralblatt 5: 1–4.

Kwaśna H, Nirenberg HI. 2008a. Siepmannia, a new genus in the Mucoraceae. Mycologia 100: 259–274.

Kwaśna H, Nirenberg HI. 2008b. Validation of the genus Siepmannia (Mucoraceae) and its four species. Polish Botanical Journal 53: 187–188.

Kwaśna H, Ward E, Bateman GL. 2006. Phylogenetic relationships among Zygomycetes from soil based on ITS1/2 rDNA sequences. Mycological Research 110: 501–510.

Lemmert K, Losert H, Rickerts V, Just-Nübling G, Sander A, et al. 2002. Identification of Cunninghamella spec. by molecular methods. Mycoses 45, Suppl. 1: 31–36.

Li CH, Cervantes M, Springer DJ, Boekhout T, Ruiz-Vazquez RM, et al. 2011. Sporangiospore size dimorphism is linked to virulence of Mucor circinelloides. PLoS Pathogens 7: e1002086.

Lian X, Lackner M, Hoog GS de, Gerrits van de Ende AHG, Priha O, et al. 2011. Assessment of identity of filamentous fungi colonizing from water-damaged building materials. Sydowia 63: 49–66.

Lindner DL, Banik MT. 2011. Intragenomic variation in the ITS rDNA region obscures phylogenetic relationships and inflates estimates of operational taxonomic units in genus Laetiporus. Mycologia 103: 731–740.

Liu XY, Huang H, Zheng RY. 2001. Relationships within Cunninghamella based on sequence analysis of ITS rDNA. Mycotaxon 80: 77–95.

Liu XY, Huang H, Zheng RY. 2007. Molecular phylogenetic relationships within Rhizopus based on combined analyses of ITS rDNA and pyrG gene sequences. Sydowia 59: 235–253.

Liu XY, Huang H, Zheng RY. 2008. Delimitation of Rhizopus varieties based on IGS rDNA. Sydowia 60: 93–112.

Lucet A, Costantin J. 1900. Rhizomucor parasiticus, espèce pathogéne de l’homme. Revue Générale Botanique 12: 81–98.

Madden AA, Stchigel AM, Guarro J, Sutton DA, Starks PT. 2011. Mucor nidicola sp. nov., a novel fungal species isolated from an invasive paper wasp nest. International Journal of Systematic and Evolutionary Microbiology doi: 10.1099/ijs.0.033050–0. [Epub ahead of print].

Mehrotra BS, Mehrotra BM. 1978. Another azygosporic species of Mucor from India. Sydowia 31: 94–96.

Meyer CP, Paulay G. 2005. DNA barcoding: Error rates based on comprehensive sampling. PLoS Biology 3: e422.

Meyer W, Gams W. 2003. Delimitation of Umbelopsis (Mucorales, Umbelopsidaceae fam. nov.) based on ITS sequence and RFLP data. Mycological Research 107: 339–350.

Mirza JH, Khan SM, Begum S, Shagufta S. 1979. Mucorales of Pakistan. University of Agriculture, Faisalabad, Pakistan.

Möller EM, Bahnweg G, Sandermann H, Geiger HH. 1992. A simple and efficient protocol for isolation of high molecular weight DNA from filamentous fungi, fruit bodies, and infected plant tissues. Nucleic Acids Research 22: 6115–6116.

Neophytova VK. 1955. Novye vidy gribov iz sfagnovogo torfãnika. (Fungorum species novae e palude sphagnosa.) Notulae Systematicae E Sectione Cryptogamica Instituti Botanici 10: 159–162.

Nilsson RH, Ryberg M, Kristiansson E, Abarenkov K, Larsson K-H, Kõljalg U. 2006. Taxonomic reliability of DNA sequences in public sequence databases: a fungal perspective. PLoS ONE 1: e59.

Nout MJR, Aidoo KE. 2010. Asian fungal fermented food. In: Hofrichter M (ed), Industrial applications. The Mycota, Vol. 10, ed 2: 30–58. Springer, Berlin, Heidelberg.

O'Donnell K. 1993. Fusarium and its near relatives. In: Reynolds DR, Taylor JW (eds), The fungal holomorph: mitotic, meiotic and pleomorphic speciation in fungal systematics: 225–233. CAB International, Wallingford, UK.

O'Donnell K, Cigelnik E. 1997. Two divergent intragenomic rDNA ITS2 types within a monophyletic lineage of the fungus Fusarium are nonorthologous. Molecular Phylogenetics and Evolution 7: 103–116.

O'Donnell K, Lutzoni FM, Ward TJ, Benny GL. 2001. Evolutionary relationships among mucoralean fungi (Zygomycota): evidence for family polyphyly on a large scale. Mycologia 93: 286–296.

Pawłowska J, Walther G, Wilk M, Hoog GS de, Wrzosek M. In press. The use of compensatory base changes analysis of ITS2 as a tool in phylogeny of Mucorales illustrated by 'Mucor circinelloides' group. Organisms Diversity & Evolution.

Pitt JI, Hocking AD. 2009. Fungi and food spoilage. 3rd ed, Springer, New York.

Povah AHW. 1917. A critical study of certain species of Mucor. Bulletin of the Torrey Botanical Club 44: 287–310.

Rambaut, A. 2002. Se–Al. http://tree.bio.ed.ac.uk/software/seal/.

Ryan LJ, Ferrieri P, Powell RD, Paddock CD, Zaki SR, Pambuccian SE. 2011. Fatal Cokeromyces recurvatus pneumonia: report of a case highlighting the potential for histopathologic misdiagnosis as Coccidioides. International Journal of Surgical Pathology 19: 373–376.

Sabouraud R. 1910. Maladies du cuir chevelu. III. – Les maladies cryptogamiques. Les teignes. Masson & Cie, Paris.

Schell WA, O'Donnell K, Alspaugh JA. 2011. Heterothallic mating in Mucor irregularis and first isolate of the species outside of Asia. Medical Mycology 49: 714–723.

Schipper MAA. 1970. Two species of Mucor with oval- and spherical-spored strains. Antonie van Leeuwenhoek 36: 475–488.

Schipper MAA. 1973. A study on variability in Mucor hiemalis and related species. Studies in Mycology 4: 1–40.

Schipper MAA. 1975. On Mucor mucedo, Mucor flavus and related species. Studies in Mycology 10: 1–33.

Schipper MAA. 1976. On Mucor circinelloides, Mucor racemosus and related species. Studies in Mycology 12: 1–40.

Schipper MAA. 1978a. On certain species of Mucor with a key to all accepted species. Studies in Mycology 17: 1–52.

Schipper MAA. 1978b. On the genera Rhizomucor and Parasitella. Studies in Mycology 17: 53–71.

Schipper MAA. 1979. Thermomucor (Mucorales). Antonie van Leeuwenhoek 45: 275–280.

Schipper MAA. 1984. A revision of the genus Rhizopus. 1. The Rhizopus stolonifer-group and Rhizopus oryzae. Studies in Mycology 25: 1–19.

Schipper MAA. 1986. Notes on Zygorhynchus species. Persoonia 13: 97–105.

Schipper MAA. 1990. Notes on Mucorales – 1. Observations on Absidia. Persoonia 14: 133–148.

Schipper MAA, Samson RA. 1994. Miscellaneous notes on Mucoraceae. Mycotaxon 50: 475–491.

Schipper MAA, Stalpers JA. 1984. A revision of the genus Rhizopus. II. The Rhizopus microsporus-group. Studies in Mycology 25: 20–34.

Schipper MAA, Stalpers JA. 2003. Zygomycetes: the order Mucorales. In: Howard DH (ed), Pathogenic fungi in human and animals: 67–125. Marcel Dekker, Inc., USA.

Schoch CL, Seifert KA, Huhndorf S, Robert V, Spouge JL, et al. 2012. The nuclear ribosomal internal transcribed spacer (ITS) region as a universal DNA barcode marker for fungi. Proceedings of the National Academy of Sciences USA 109: 6241–6246.

Schwarz P, Bretagne S, Gantier JC, Garcia-Hermoso D, Lortholary O, et al. 2006. Molecular identification of zygomycetes from culture and experimentally infected tissue. Journal of Clinical Microbiology 44: 340–349.

Skiada A, Pagano L, Groll A, Zimmerli S, Dupont B, et al. 2011. Zygomycosis in Europe: analysis of 230 cases accrued by the registry of the European Confederation of Medical Mycology (ECMM) Working Group on Zygomycosis between 2005 and 2007. Clinical Microbiology and Infection 17: 1859–1867.

Souza JI de, Pires-Zottarelli CLA, Santos JF dos, Costa JP, Harakava R. 2012. Isomucor (Mucoromycotina): a new genus from a Cerrado reserve in state of São Paulo, Brazil. Mycologia 104: 232–241.

Stamatakis A, Hoover P, Rougemont J. 2008. A rapid bootstrap algorithm for the RAxML web-servers. Systematic Biology 75: 758–771.

Sugui JA, Christensen JA, Bennett JE, Zelazny AM, Kwon-Chung KJ. 2011. Hematogenously disseminated skin disease cured by Mucor velutinosus in a patient with acute myeloid leukemia. Journal of Clinical Microbiology 49: 2728–2732.

Taylor JW, Jacobson DJ, Kroken S, Kasuga T, Geiser DM, et al. 2000. Phylogenetic species recognition and species concepts in fungi. Fungal Genetics and Biology 31: 21–32.

Tieghem P van, Monnier G le. 1873. Recherches sur les Mucorinées. Annales des Sciences Naturelles, Botanique 17: 261–399.

Vágvölgyi C, Heinrich H, Ács K, Papp T. 2004. Genetic variability in the species Rhizopus stolonifer, assessed by random amplified polymorphic DNA analysis. Antonie van Leeuwenhoek 86: 181–188.

Vágvölgyi C, Vastag M, Ács K, Papp T. 1999. Rhizomucor tauricus: a questionable species of the genus. Mycological Research 103: 1318–1322.

Vilgalys R, Hester M. 1990. Rapid genetic identification and mapping of enzymatically amplified ribosomal DNA from several Cryptococcus species. Journal of Bacteriology 172: 4238–4246.

Vitale RG, Hoog GS de, Schwarz P, Dannaoui E, Deng S, et al. 2012. Antifungal susceptibility and phylogeny of opportunistic members of Mucorales. Journal of Clinical Microbiology 50: 66–75.

Voigt K, Wöstemeyer J. 2001. Phylogeny and origin of 82 zygomycetes from all 54 genera of the Mucorales and Mortierellales based on combined analysis of actin and translation elongation factor EF-1α genes. Gene 270: 113–120.

Watanabe T. 1994. Two new species of homothallic Mucor in Japan. Mycologia 86: 691–695.

Weddle G, Gandy K, Bratcher D, Pahud B, Jackson MA. 2012. Apophysomyces trapeziformis infection associated with a tornado related injury. The Pediatric Infectious Disease Journal 31: 640–642.

Wehmer, C. 1900. Studien über technische Pilze. VII. Die 'Chinesische Hefe' und der sogenannte Amylomyces (= Mucor Rouxii). Centralblatt für Bakteriologie, Parasitenkunde und Infektionskrankheiten, Abt. II, 6: 353–365.

White TJ, Bruns T, Lee S, Taylor JW. 1990. Amplification and direct sequencing of fungal ribosomal RNA genes for phylogenetics. In: Innis MA, Gelfand DH, Sninsky JJ, White TJ (eds), PCR protocols: a guide to methods and applications: 315–322. Academic Press, Inc., New York, USA.

Xess I, Mohapatra S, Shivaprakash MR, Chakrabarti A, Benny GL, et al. 2012. Evidence implicating Thamnostylum lucknowense as an etiological agent of rhino-orbital mucormycosis. Journal of Clinical Microbiology 50: 1491–1494.

Zheng RY, Chen GQ. 2001. A monograph of Cunninghamella. Mycotaxon 80: 1–75.

Zheng RY, Chen GQ, Huang H, Liu XY. 2007. A monograph of Rhizopus. Sydowia 59: 273–372.

Zheng RY, Liu XY. 2005. Actinomucor elegans var. meitauzae, the correct name for A. taiwanensis and Mucor meitauzae (Mucorales, Zygomycota). Nova Hedwigia 80: 419–432.

Zheng RY, Liu XY. 2009a. Taxa of Pilaira (Mucorales, Zygomycota) from China. Nova Hedwigia 88: 255–267.

Zheng RY, Liu XY. 2009b. More Rhizomucor causing human mucormycosis from China: R. chlamydosporus sp. nov. Sydowia 61: 135–147.