Persoonia 30, 2013: 77–93
www.ingentaconnect.com/content/nhn/pimj

RESEARCH ARTICLE

http://dx.doi.org/10.3767/003158513X666268

A comprehensive molecular phylogeny of the *Mortierellales* (*Mortierellomycotina*) based on nuclear ribosomal DNA

L. Wagner[1,2], B. Stielow[3], K. Hoffmann[1,2], T. Petkovits[4], T. Papp[4], C. Vágvölgyi[4], G.S. de Hoog[3], G. Verkley[3], K. Voigt[1,2]*

Key words

internal transcribed spacer
large subunit ribosomal DNA
taxonomic revision
Zygomycetes
Zygomycota

Abstract The basal fungal order *Mortierellales* constitutes one of the largest orders in the basal lineages. This group consists of one family and six genera. Most species are saprobic soil inhabiting fungi with the ability of diverse biotransformations or the accumulation of unsaturated fatty acids, making them attractive for biotechnological applications. Only few studies exist aiming at the revelation of the evolutionary relationships of this interesting fungal group. This study includes the largest dataset of LSU and ITS sequences for more than 400 specimens containing 63 type or reference strains. Based on a LSU phylogram, fungal groups were defined and evaluated using ITS sequences and morphological features. Traditional morphology-based classification schemes were rejected, because the morphology of the *Mortierellales* seems to depend on culture conditions, a fact, which makes the identification of synapomorphic characters tedious. This study belongs to the most comprehensive molecular phylogenetic analyses for the *Mortierellales* up to date and reveals unresolved species and species complexes.

Article info Received: 17 June 2012; Accepted: 2 January 2013; Published: 13 March 2013.

INTRODUCTION

The order Mortierellales – from historical aspects on morphology and systematics to modern approaches in fungal identification

The *Mortierellales* are a long known, species rich order of the basal fungi. With nearly 100 described species, the *Mortierellales* is one of the largest basal fungal orders. However, only 13 genera are described in one family, the *Mortierellaceae* (Kirk et al. 2008, and Species Fungorum January 2013). Out of these genera six are currently accepted with one potential additional genus recently described (Kirk et al. 2008, Jiang et al. 2011, Table 1). The first species of the type genus was described by Coemans (1863) as *Mortierella polycephala*, originally isolated from a mushroom. The name *Mortierella* was given in tribute to M. Du Mortier, the president of the Société de Botanique de Belgique (Coemans 1863). Nevertheless, the common lifestyle of those fungi is as soil inhabiting saprobic organisms on decaying organic matter. Only one species is occasionally described from animal fungal infections (de Hoog et al. 2009). Many mortierellean species possess the ability to produce polyunsaturated fatty acids or to convert organic compounds, making them highly interesting organisms for biotransformations and other biotechnological applications (Holland 2001, Higashiyama et al. 2002).

As many basal fungal species, the *Mortierellales* possess a reduced macro- and micromorphology with only few morphological characters available for differentiation. Examples of micromorphological features are shown in Fig. 1 and 2. Overall appearance of the colonies is the typical zonate, rosette-like growth (Fig. 1a) and the often occurring garlic-like odour. Colonies are in general white to light-grey, young mycelium is coenocytic and septate in aged cultures. Asexual spores are produced in sporangia or sporangiola and are passively released (e.g., Fig. 1h, s). The sporangiophores could be widened at the base (e.g., Fig. 1o) and variously branched (e.g. Fig. 1h, l). A columella is never protruding into the sporangium. Sexual reproductive structures (zygospores, Fig. 2r) are often surrounded by a hyphal sheat. Variously shaped chlamydospores and stylospores are also possible (Fig. 1w, 2l) (Zycha et al. 1969, Gams 1977). Morphological identification based solely on asexual features, leading to the aforementioned traditional classification. *Mortierella* was furthermore divided into nine sections based on morphology: *Actinomortierella*, *Alpina*, *Haplosporangium*, *Hygrophila*, *Mortierella*, *Schmuckeri*, *Simplex*, *Spinosa* and *Stylospora* (Gams 1977).

Judging from the proposed total number of fungi with 1.5 million species and the current number of described and registered species with 75 000 (Hawksworth 2001) it seems likely that also for the order *Mortierellales* an unknown percentage of undescribed species may exists, a fact which might influence phylogenetic analyses. Yet, a recent study challenged previous estimations of the potential number of undescribed fungal species and proposed that, at least for *Mortierella*, nearly all species are most likely described already (Nagy et al. 2011). Based on this knowledge, phylogenetic analyses including sequences of an extensive amount of type and reference strains could reveal the natural evolutionary relationships.

Nevertheless, the phylogenetic position of the *Mortierellales* is controversial discussed. They are either placed within the subphylum *Mucoromycotina* (Hibbett et al. 2007) or elevated to an own subphylum, the *Mortierellomycotina* (Hoffmann et al. 2011). Furthermore, relationships within this order are also

[1] University of Jena, School of Biology and Pharmacy, Institute of Microbiology, Department of Microbiology and Molecular Biology, Jena Microbial Resource Collection, Neugasse 25, 07743 Jena, Germany;
corresponding author e-mail: Kerstin.voigt@hki-jena.de.
[2] Leibniz-Institute for Natural Product Research and Infection Biology (HKI), Department of Molecular and Applied Microbiology, Beutenbergstrasse 11a, 07745 Jena, Germany.
[3] Centraalbureau voor Schimmelcultures, CBS-KNAW Fungal Biodiversity Centre, P.O. Box 85167, 3508 AD Utrecht, The Netherlands.
[4] University of Szeged, Faculty of Science and Informatics, Department of Microbiology, 6726 Szeged, Közép fasor 52, Hungary.

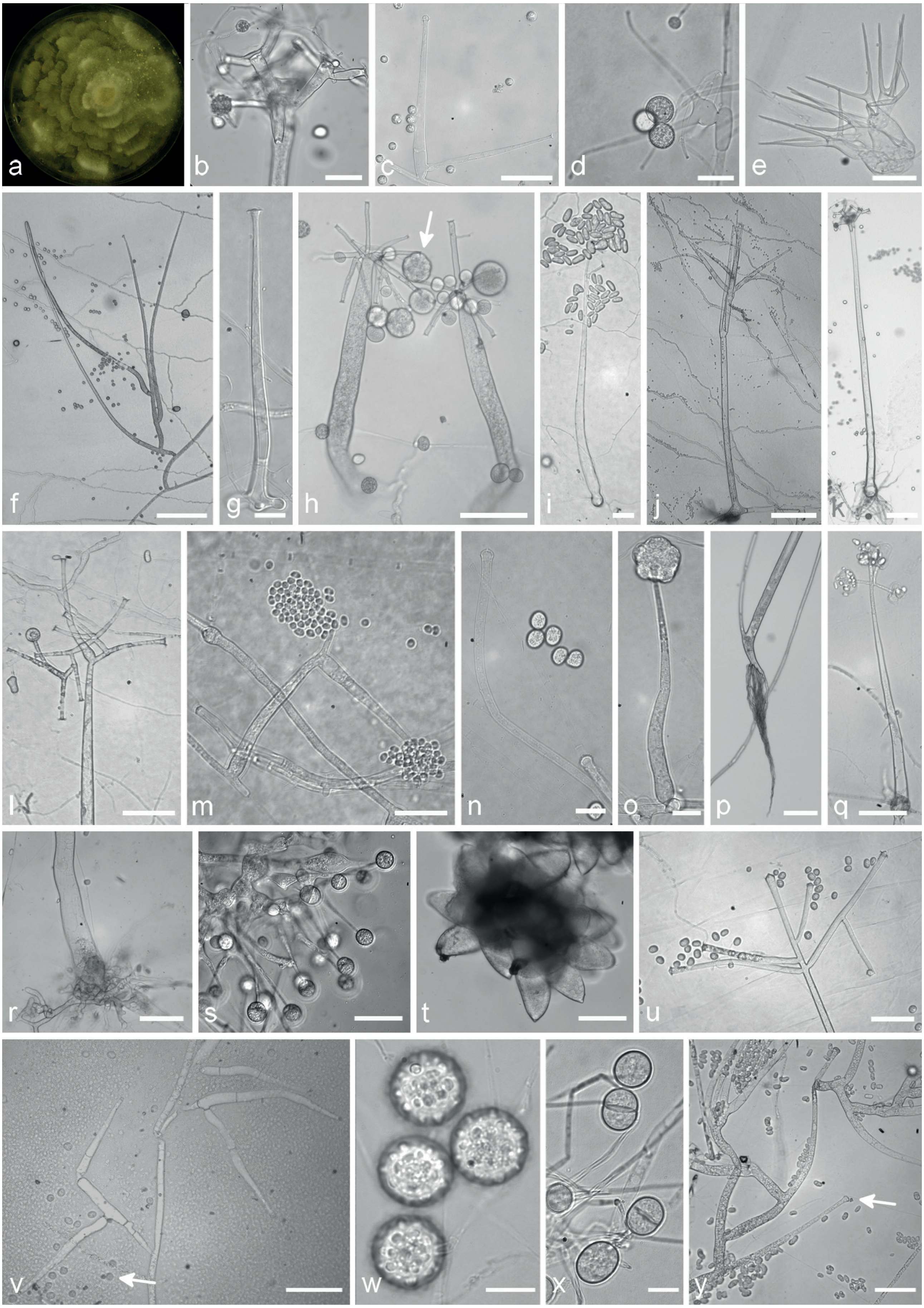

Fig. 1 Typical morphological structures of different isolates of the *Mortierellales*, which are suitable for species delimitation. a. *M. zychae* CBS 316.52, macroscopic shape of a growing culture with the typical zonate growth; b. *M. hypsicladia* CBS 116202, acrotonous branching of a sporangiophore; c. *M. epicladia* CBS 355.76, sporangiophore and sporangiospores; d. *M. zonata* CBS 228.35, basitonous branched sporangiophore with sporangioles; e. *Gamsiella multidivaricata* CBS 227.78, typical branched sporangiophores; f. *M. elongata* FSU 9721, basitonous branched sporangiophore; g. *M. alpina* FSU 2698, sporangiophore; h. *M. polycephala* FSU 867, sporangiospores with sporangia (arrow) and sporangiospores; i. *Mortierella* cf. *wolfii* CBS 614.70, sporangiophore with elongated

Table 1 Chronological overview of descriptions and name changes for accepted genera in the order *Mortierellales* Caval.-Sm. 1998 [MB#90555]. The order consists of several genera and one family, the *Mortierellaceae* A. Fisch. 1892 [MB#81029]. Data based on MycoBank and IndexFungorum (accessed 7 January 2013).

Year	Genus	Synonyms	Type species	Number of described species	MycoBank no.
1863	*Mortierella* Coem.	*Actinomortierella* Chalab. 1968 *Carnoya* Dewèvre 1893 *Haplosporangium* Thaxt. 1914 *Azygozygum* Chesters 1933 *Naumoviella* Novot. 1950	*M. polycephala*	91	MB#20345
1914	*Dissophora* Thaxt.	none	*D. decumbens*	3	MB#20187
1936	*Modicella* Kanouse	none	*M. malleola*	2	MB#20336
1967	*Aquamortierella* Embree & Indoh	none	*A. elegans*	1	MB#20047
2004	*Gamsiella* (R.K. Benj.) Benny & M. Blackw.	none	*G. multidivaricata*	1	MB#28820
2004	*Lobosporangium* M. Blackw. & Benny	*Echinosporangium* Malloch 1967	*L. transversale*	1	MB#28819
2011	*Echinochlamydosporium* X.Z. Jiang, X.Y. Liu & Xing Z. Liu	none	*E. variabile*	1	MB#511829

MB = Mycobank: http://www.mycobank.org; IndexFungorum: http://www.indexfungorum.org.

poorly understood and were extensively analysed only in few studies until now (Nagy et al. 2011, Petkovits et al. 2011). Our study contributes to the effort to elucidate natural phylogenetic relationships based on one of the largest datasets assembled so far. This study concerns the extension of previous datasets and facilitates an approach to molecular identification of the *Mortierellales*. We surveyed the diversity of the *Mortierellales* including a re-evaluation of the morphology based classifications. This study based on the broad sampling of specimens which are maintained at the fungal culture collections CBS (Centraalbureau voor Schimmelcultures, Utrecht, The Netherlands) and JMRC (Jena Microbial Resource Collection, Jena, Germany).

MATERIALS AND METHODS

Taxon sampling, culture conditions and light microscopic investigations

For this study, a total of 421 isolates were obtained from the Centraalbureau voor Schimmelcultures (CBS, Utrecht, The Netherlands) and the Jena Microbial Resource Collection (JMRC, Jena, Germany) (Table 2). Strains were cultivated on malt-extract medium (3 % malt extract, 0.5 % yeast extract) for DNA isolation and on oatmeal agar (OA, 3 %), soil extract agar (Gams 1969) or synthetic nutrient deficient agar (SNA, Nirenberg 1981) for morphological examinations. Cultivation was done at 20–37 °C for 7–20 days depending on the requirements of the fungus to sporulate. The light microscopical examinations shown in Fig. 1 and 2 were performed with an Axiophot (Zeiss, Germany). The best method to observe microscopic features is to grow cultures directly on cover slips.

Preparation of genomic DNA, PCR amplification and DNA sequencing

Genomic DNA was prepared from mycelia grounded to a fine powder in liquid nitrogen followed by purification (Cenis 1992) or living cultures alternatively, using the Jetquick general DNA clean up kit (Genomed) or a high-throughput 96-well plate extraction (Ivanova et al. 2006) following the given protocols. The PCR for the amplification of the ITS1-5.8S-ITS2 nuclear ribosomal DNA region uses ITS5/ITS1 and ITS4 under standard or semi-nested conditions (White et al. 1990, Stielow et al. 2009). PCR for amplifying the partial 28S rDNA (LSU) was done using the standard primers LR0R and LR5 or the NL-primer (http://www.biology.duke.edu/fungi/mycolab/primers.htm). The primers differ only in their annealing temperature (55 °C or 60 °C). Increasing cycle extension time (90 s/cycle) was done in some cases to improve amplification. PCR products were directly purified using FastAP thermosensitive alkaline phosphatase and shrimp alkaline phosphatase (Fermentas, Thermo Scientific) or using the GeneClean protocol (Vogelstein & Gillespie 1979). The cycle-sequencing reaction was set up using ABI big dye terminator v. 3.1, following the manufactures instructions or by using a quarter of the suggested volumes (modified manufactures protocol), followed by bidirectional sequencing with a laboratory capillary electrophoresis system (Life Technologies 3730XL DNA analyser). Sequences were evaluated with Chromas Lite (Technelysium Pty. Ltd.). Sequencing primers were the same as used for PCR. Manually correction and assembling of forward and reverse sequences was done using the Biolomics database (www.bio-aware.com) (Vu et al. 2012) or Seqman (v. 7.2.1). Sequences were deposited at NCBI GenBank (Table 2).

Alignments and phylogenetic analyses

A total of 364 sequences of ITS and 213 sequences of LSU were generated in this study. For the extension of the dataset additional sequences were retrieved from GenBank (Table 2). A total of 15 sequences were excluded and 562 were subjected to further analyses (298 ITS and 263 LSU sequences). Alignments were performed with MAFFT v. 6.833 (Katoh 2008) as implemented in EPoS (Griebel et al. 2008). Maximum Likelihood analyses were carried out using RAxML (Stamatakis 2006) provided by the CIPRES Science Gateway v. 3.2 (http://www.phylo.org). RAxML was run under the default settings with the

Fig. 1 (cont.)
sporangiospores; j. *M. parvispora* FSU 10759, sporangiophores; k. *M. hypsicladia* CBS 116202, typical sporangiophore with rhizoid; l. *Mortierella* cf. *wolfii* CBS 614.70, acrotonous branching of a sporangiophore; m. *Mortierella* sp. FSU 10557, sporangiophore and sporangiospores; n. *M. paraensis* CBS 547.89, tips of a sporangiophore with a pseudocolumella and sporangiospores; o. *M. alpina* FSU 2698, sporangiophore with unmatured sporangia; p. *M. nanthalensis* CBS 610.70, typical rhizoid of a sporangiophore; q. *M. wolfii* CBS 651.93, sporangiospores with unusual remain of the sporangia cover (arrow); r. *M. strangulata* CBS 455.67, rhizoid of the sporangiophore; s. *Gamsiella multidivaricata* CBS 227.78, sporangiophores with sporangioles; t. *Lobosporangium transversale* CBS 357.67, typical sporangia, arranged in clusters, containing numerous spherical sporangiospores; u. *M. gamsii* FSU 10538, acrotonous branching of a sporangiophore and sporangiospores; v. *Dissophora decumbens* CBS 592.88, septate sporangiophores along a hypha and sporangiospore (arrow); w. *M. polycephala* FSU 867, stylospores; x. *Gamsiella multidivaricata* CBS 227.78, sporangiola containing spores; y. *M. kuhlmanii* CBS 157.71, branching pattern of the basitonous part of the sporangiophore and elongated sporangiospores, pseudocolumella. — Scale bars: b, c, s–u, x = 30 µm; d, e, i = 20 µm; f, j, k, p = 100 µm; g, n, o, w = 10 µm; h, l, m, q, r, v, y = 50 µm.

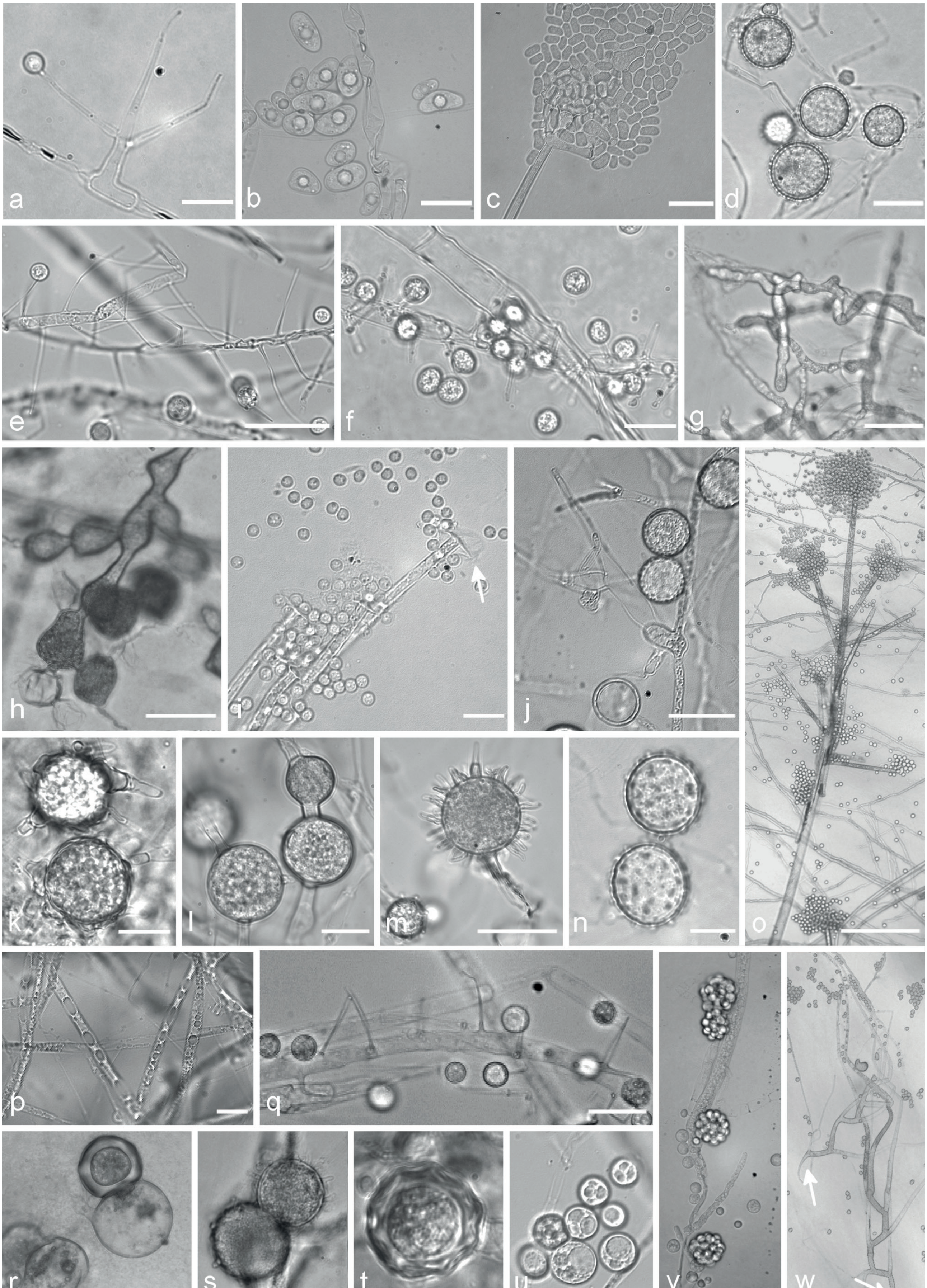

Fig. 2 Typical morphological structures of different isolates of the *Mortierellales*, which are suitable for species delimitation. a. *M. verticillata* CBS 315.52, sporangiophore with a sporangiola; b. *M. elongata* FSU 9721, elongated sporangiospores containing central oil droplets; c. *M. wolfii* CBS 651.93, cracked sporangia releasing sporangiospores, on acrotonous branched tip of the sporangiophore; d. *M. indohii* CBS 720.71, stylospores; e. *M. schmuckeri* CBS 295.59, sporangiophores alongside a hypha with sporangiola; f. *M. claussenii* CBS 294.59, sporangiophores along a hypha with sporangiola; g. *M. clonocystis* CBS 357.76, typical swollen hyphae; h. *M. zychae* FSU 719, typical swollen hyphae arranged in clusters; i. *M. parvispora* FSU 10759, tip of a sporangiophore,

following adjustments: GTRGAMMA for bootstrapping and final tree inference with 1 000 bootstrap iterations. The resulting phylogenetic trees which based on the LSU sequences were used to identify clusters of strains. For these clusters MAFFT alignments of the ITS region were computed and RAxML analyses performed. Subsequent alignments are crucial since ITS is in general highly diverse on higher level classification. If a group of sequences contains a high number of a repetitive species not all sequences were included in the ITS tree. Alignments and trees are deposited in TreeBASE2 under http://purl.org/phylo/treebase/phylows/study/TB2:S13827.

RESULTS AND DISCUSSION

Phylogenetic analyses and relationships within the Mortierellales based on single-locus analyses

According to previous studies (White et al. 2006, Petkovits et al. 2011), the major genus of the *Mortierellales*, *Mortierella*, appears as paraphyletic genus since the genera, *Dissophora*, *Gamsiella* and *Lobosporangium* are nested within. Since there is no sequence data or living material available for *Aquamortierella* and *Modicella* (White et al. 2006) these genera were not included. Due to lacking species material the newly proposed and described genus *Echinochlamydosporium* (Jiang et al. 2011) was also excluded from the current analysis. Although the pre-molecular classification schemes defined morphologically well-supported clades (Linnemann 1941, Zycha et al. 1969, Gams 1977) these clades could not be retained in any molecular based analyses (White et al. 2006, Petkovits et al. 2011, this study). The present study extended a previous study by addition of sequence information for 407 specimens. One isolate, *Mortierella mutabilis*, was excluded due to miss-fitting morphological characteristics. The morphology of *M. mutabilis* is in contradiction with its original description (Linnemann 1941) and resembles *Gamsiella multidivaricata* in all morphological features as well its molecular data. Since only one isolate is available, we postpone its phylogenetically analysis till additional material is available. Nineteen species were additionally included with a total of 115 sequences. Out of these sequences 57 sequences were generated for ITS, 58 for LSU and 1 ITS sequence was retrieved from GenBank.

Out of 421 specimens in total, 213 sequences for LSU and 364 sequences for ITS were generated. The dataset was supplemented with additional sequences form GenBank (69 LSU and 11 ITS sequences) (Table 2).

A first phylogenetic tree based on LSU sequences from 266 taxa was generated to define placement and relationships of all sequences generated in this study (data not shown). A subset of all relevant groups and isolates was taken for the final tree of the LSU dataset (Fig. 3, just for better overview). The final alignment contains 781 characters and 101 taxa. For subsequent deep-level analyses seven artificial subsets out of eight clades of this tree were defined referring to the previously published group delimitations (Petkovits et al. 2011). For each group the ITS1-5.8S rDNA-ITS2 sequences were aligned and analysed with Maximum Likelihood although the backbone of the underlying LSU tree is not resolved (Fig. 3). Groups are mainly located on one branch ('monophyletic') except for the under-represented *chienii/selenospora*-group which was combined and aligned together with the most basal group. Taking these groups as single taxa sets allows alignments providing phylogenetic signals with higher resolution on deep level classification. The alignments of the subsets consists of the following numbers of taxa and characters: subset 1: 58/816 (means 58 taxa and 816 characters, Fig. 4); subset 2: 36/636 (Fig. 5); subset 3: 38/701 (Fig. 6); subset 4: 17/710 (Fig. 7); subset 5: 18/761 (Fig. 8); subset 6: 60/703 (Fig. 9); subset 7: 73/688 (Fig. 10).

Our results do not allow for the revelation of the natural relationships between different species or between groups of species since the clades are poorly supported in the LSU tree. But definition of boundaries between the species/species groups is possible and the presented species groups are in full accordance with the twelve large clades distinguished in a previous study (Petkovits et al. 2011). Because the current dataset is more comprehensive, we will keep, but also extend some of the groups.

Group 1 – selenospora and parvispora (Fig. 4, some morphological features are displayed in Fig.1j, 2i) contains the two most basal groups of the LSU tree (Fig 3). *Mortierella selenospora* clusters well with *M. chienii* (Bootstrap support BS = 100 %). *Mortierella chienii* was not included in the previous study (Petkovits et al. 2011). In cases where the morphological identification does not match the position of the strain in the ITS tree the strains were designated as *Mortierella* sp. with the epithet in quotation marks. Strains which are very distinct, not part of a clade and consequently might represent undescribed species are highlighted in blue. The selenospora clade also contains the questionable *M. wolfii* CBS 614.70 which shows different characteristics (e.g. no thermotolerance) to the original *M. wolfii* strains although the sporangiospores are ellipsoidal to kidney-shaped like those of *M. wolfii*. A detailed analysis of the morphology and several molecular markers is needed to clarify the status of this particular strain. The other group termed 'parvispora' contains also the species *M. alliacea*, *M. basiparvispora*, *M. fimbricystis*, *M. jenkinii*, *M. macrocystis*, *M. macrocystopsis*, *M. sossauensis* in addition to the previously included species (*M. cystojenkinii*, *M. dichotoma*, *M. elongatula*, *M. parvispora*, *M. pulchella*, *M. turficola*; Petkovits et al. 2011). *Mortierella alliacea*, *M. chienii*, *M. cystojenkinii*, *M. elongatula*, *M. macrocystis*, *M. macrocystopsis*, *M. pulchella* and *M. sossauensis* form well-supported clades and the morphologically defined species boundaries are well reflected in the ITS tree (Fig. 4). The parvispora-jenkinii-complex consists predominantly of strains morphologically identified as *M. jenkinii* or *M. parvispora*. These two species differ mainly by the shape of their sporangiospores: ellipsoidal for *M. jenkinii* and globose for *M. parvispora*. This distinction is not supported by the ITS tree, mixing both types of spores. The strain *M. basiparvispora* CBS 517.72 is also clustering in this complex, but is differing morphologically from the ex-type strain of this species, which was not included in this study (Gams 1976). A detailed revision of this species in relation to *Mortierella* will be needed.

(text continues on p. 88)

Fig. 2 (cont.)
sporangia leaving a collar (arrow), globose sporangiospores; j. *M. lignicola* CBS 207.37, sporangiophores, sporangiola (arrow 1), stylospores (arrow 2); k. *M. exigua* CBS 655.68, chlamydospores with typical outgrowing hyphae; l. *M. gemmifera* CBS 134.45, chlamydospores; m. *M. hypsicladia* CBS 116202, stylospores with projections; n. *M. polygonia* CBS 685.71, stylospores; o. *M. nanthalensis* CBS 610.70, acrotonous branching part of a sporangiophore; p. *M. alpina* FSU 2698, oil droplets containing hypha; q. *M. camargensis* CBS 221.58, sporangiophores along a hypha with sporangiola; r. *M. epigama* CBS 489.70, zygospores; s. *M. echinosphaera* CBS 575.75, chlamydospores; t. *M. microszygospora* CBS 880.97, microzygospore; u. *M. camargensis* CBS 221.58, oil droplets containing spheric sporangiola; v. *Dissophora decumbens* CBS 592.88, sporangiophores with sporangia; w. *M. paraensis* CBS 547.89, two sporangiophores with typical basitonous branchings (arrows mark the basal part). — Scale bars: a, b, i, n, p, r, u = 10 μm; c, j, q = 20 μm; d, e, g, h, m, v = 30 μm; f, k, l, s, t = 15 μm; o = 250 μm; w = 100 μm.

Table 2 Strains used in this study.

Original name	Strain numbers	Microscopic identification	Type status	Locality	Substrate	Accession no. ITS	Accession no. LSU
Dissophora decumbens	CBS301.87, FSU9780	*D. decumbens*		Kingston, Rhode Island	ground-up litter of Quercus-Acer woodland, incubated at 0°C for two months	JX976001	HQ667354.1
	CBS592.88, FSU801	*D. decumbens*		Rhode Island	ground-up Quercus and Acer leaves, incubated at 0°C for 21 months	HQ630276.1	HQ667355.1
Dissophora ornata	CBS347.77, FSU9782	–	Holotype of *Mortierella ornata*	Cordillera Central, Cauca en Huila, Parque Nacional del Puracé, Colombia	soil, in mountain forest under Weinmannia, Clusia etc., alt. 3100 m	HQ630278.1	HQ667357.1
	CBS348.77, FSU9783	–	Holotype of *Mortierella ornata*	Cordillera Central, Cauca en Huila, Parque Nacional del Puracé, Colombia	soil, in mountain forest under Weinmannia, Clusia etc., alt. 3100 m	JX976036	HQ667356.1
Gamsiella multidivaricata	CBS227.78, FSU9784	*G. multidivaricata*	Isotype of *Mortierella multidivaricata*	Moskva, Sokolniki Park, Russia	decaying stump	JX975871	HQ667355.1
Lobosporangium transversale	CBS357.67, FSU9785	–	Type of *Echinosporangium transversale*	Nevada, Virginia City	soil	–	HQ667404.1
Mortierella acrotona	CBS386.71, FSU9788	–	Type of *Mortierella acrotona*	Jaipur, Rambagh Palace Hotel, Rajasthan	soil	JX975921	HQ667405.1
Mortierella alliacea	CBS106.78	–		France	gymnosperm litter	JX976019	KC018349
	CBS894.68	–		Tirol, Obergurgl, Austria	alpine raw humus soil	JX975990	JX976148
Mortierella alpina	CBS110518	–		South Africa	soil, dry sandy highveld grassland	JX975906	–
	CBS210.32, FSU9789	*M. alpina*	Authentic strain of *Mortierella renispora*	Victoria	sandy loam soil	JX975853	HQ667421.1
	CBS219.35	–		–		JX976018	KC018359
	CBS250.53	–		–		JX975955	KC018184
	CBS384.71C	–		Jaipur, Rambagh Palace Hotel, Rajasthan	soil	JX976098	JX976154
	CBS387.71	–		Gran Canaria, Spain	soil, under *Pinus canariensis*	JX976038	KC018378
	CBS396.91	–		Washington	air bladder of juvenile fish	JX975994	KC018375
	CBS529.72	–		North Carolina	pasture soil	JX976124	KC018320
	CBS585.81	*M. kuhlmanii*		Netherlands	agricultural soil	JX976132	JX976152
	CBS608.70	–		Netherlands	agricultural soil	JX976046	KC018438
	CBS696.70	*M. cystojenkinii*		Wageningen, Mansholtlaan, Netherlands	agricultural soil	JX975947	KC018328
	FSU2698	*M. alpina*		Argentinia		JX976004	KC018272
	FSU6524	*M. alpina*		Geisenheim, Germany		JX976045	KC018273
Mortierella ambigua	CBS373.96	–		Fukiagehama, Kagoshima, Japan	soil of salt marsh	JX976062	JX976147
	CBS450.88	–		–		JX976067	KC018411
	CBS457.66	–		Armenia	soil	JX976041	KC018398
	CBS474.96	–		Ootomi, Iriomotejima Island, Okinawa, Japan	calcareous soil in ditch	JX976056	KC018416
	CBS521.80	–		Delhi, India	dung	JX976120	KC018423
Mortierella amoeboidea	CBS889.72, FSU9790	*M. alpina*	Type of *Mortierella amoeboidea*	Teutoburger Wald, Beller Holz, Germany		JX976073	HQ667422.1
Mortierella angusta	CBS293.61, FSU9791	*M. angusta*	Neotype of *Mortierella polycephala* var. *angusta*	Chesh., Delamere Forest, England	podzol soil, pH up to 2.8	JX976061	HQ667358.1
Mortierella antarctica	CBS194.89	–		Northern Foothills, Northern Victoria Land, Antarctica	soil	JX976087	KC018345
	CBS195.89	–		Northern Victoria Land, Edmonson Point, Antarctica	soil	JX975843	–
	CBS196.89	–		Northern Victoria Land, Cape King, Antarctica	soil	JX976059	–
	CBS609.70, FSU9792	–	Type of *Mortierella antarctica*	near Hallett Station, Antarctica	soil, rock crevice near glacier	JX975907	HQ667503.1
Mortierella armillariicola	CBS105.78	–		Putten, Schovenhorst, Netherlands		JX976100	KC018432
	CBS914.73, FSU9793	–	Type of *Mortierella armillariicola*	Baarn, Groeneveld, Netherlands	attacked by *Dipodascus armillariae*	JX975924	HQ667446.1
Mortierella bainieri	CBS220.35	–		former West-Germany		JX975901	KC018324
	CBS272.71	*M. kuhlmanii*		South Carolina	soil under *Pinus taeda*	JX975964	JX976155
	CBS273.71	*M. kuhlmanii*		South Carolina	soil under *Pinus taeda*	JX975920	KC018355
	CBS442.68	–		Georgia	soil from pine forest	JX975864	KC018331
	CBS508.81	–		Getzbach near Eupen, Belgium		JX975844	KC018393
	CBS552.80	–		Eifel, Hundsbachtal near Gerolstein, Germany		JX975850	JX976174
Mortierella basiparvispora	CBS517.72	–		Valdivia, Cordillera Pelada, Chile	soil, under *Fitzroya cupressoides*	JX976048	JX976167

Mortierella beljakovae	CBS102878	–		Toronto High Park, Ontario	infrabuccal pellet of *Camponotus pennsylvanicus* (carpenter ant) on Pinus	JX976090	KC018350
	CBS109594	–		Toronto, High Park, Ontario	infrabuccal pellet of *Camponotus pennsylvanicus*, in mature Pinus tree	JX975848	KC018449
	CBS109595	–		Zweifaller Wald near Aachen, Germany	infrabuccal pellet of *Formica rufa*	JX976129	KC018358
	CBS109596	–		St. Andrews, Annesley House, New Brunswick	infrabuccal pellet of *Camponotus pennsylvanicus*, in Pinus tree	JX975971	JX976170
	CBS109597	–		Scarborough, Ontario	infrabuccal pellet of *Camponotus pennsylvanicus*, in mature Pinus tree	JX975918	KC018433
	CBS109655	–		Bayerischer Wald, Pfahl bei Viechtach, Germany	infrabuccal pellet of *Camponotus herculeanus*, in *Picea abies*	JX975869	JX976171
	CBS109658	–		Zweifaller Wald near Aachen, Germany	infrabuccal pellet of *Formica rufa*	JX976051	KC018376
	CBS109659	–		Utrecht, Lage Vuursche, Netherlands	infrabuccal pellet of *Formica rufa*	JX975998	KC018340
	CBS123.72, FSU9794	*M. beljakovae*	Type of *Mortierella beljakovae*	Rovensk region, Sarna, Ukraine	soil, coniferous forest	JX976126	HQ667428.1
	CBS267.71	–		North Carolina	seedling, *Pinus teada*	JX976072	KC018346
	CBS268.71	–		North Carolina	seedling, *Pinus teada*	JX976043	KC018323
	CBS274.71	–		South Carolina	root, *Pinus taeda*	JX976011	KC018388
	CBS275.71	–		South Carolina	root, *Pinus taeda*	JX975913	KC018401
	CBS276.71	–		South Carolina	root, *Pinus taeda*	JX975937	KC018442
	CBS806.68	–		North Carolina	bark of root, Pinus	JX975987	KC018397
Mortierella biramosa	CBS370.95, FSU9795	*M. biramosa*	Type of *Mortierella wuyishanensis*	Wuyi, Fujian, China	forest soil	JX976094	HQ667389.1
	CBS506.81	–		Odenwald, Oberer Buntsandstein, Germany	decaying fine root, 30 yr old, on acidic loamy soil	JX975963	KC018407
	CBS550.80	–		Odenwald, Germany	rootlet	JX976064	KC018419
Mortierella bisporalis	CBS145.69	–		Italy		JX975857	KC018377
	FSU9675	*M. bisporalis*		–		JX975953	JX976176
Mortierella camargensis	CBS110638	–		Soest, Smickel, Netherlands	thatch of roof	JX976024	–
	CBS221.58, FSU9796	*M. camargensis*	Type of *Mortierella camargensis*	Camargue, Bois des Rièges, France	sandy soil	JX975949	HQ667408.1
Mortierella capitata	CBS110640	–		Berlin, Königin-Luise-Straße, near BBA, Germany	soil with Armadillidium	JX975923	JX976163
	CBS293.96	–		Naganohara, Gunma, Japan	garden soil	JX976123	KC018334
	CBS859.70	–		North Carolina	pillbug gut	JX976008	KC018395
Mortierella chienii	CBS287.96	–		Amakubo, Tsukuba, Ibaraki, Japan	soil under *Quercus mirsinifolia* forest	JX976013	KC018427
	CBS289.96	–		Nanamagari, Yokohama, Kanagawa, Japan	soil under *Castanopsis sieboldii* forest	JX975898	JX976161
	CBS290.96	–			soil under *Miscanthus sinensis*	JX976075	KC018373
	CBS292.96	*M. selenospora*		Shitoko, Yakushima Island, Kagoshima, Japan	soil under *Ficus microcarpa* forest	JX975951	JX976153
	CBS554.73	*M. selenospora*		Kuang-Miau Co., 16 km E of Tainan, Taiwan	soil from bamboo grove	JX975912	KC018381
Mortierella chlamydospora	CBS120.34, FSU9799	–	Syntype of *Azygozygum chlamydosporum*		infected by *Rhizoctonia solani*	JX975942	HQ667430.1
	CBS529.75	–		Netherlands	soil	JX975927	–
Mortierella claussenii	CBS790.85	–		–		JX976012	JX976159
Mortierella clonocystis	CBS357.76, FSU9801	*M. clonocystis*	Type of *Mortierella clonocystis*	Gran Canaria, Spain	soil, under *Apollonias canariensis*	JX975899	HQ667395.1
Mortierella cogitans	CBS879.97, FSU9802	–	Type of *Mortierella cogitans*	Nagano, Sanada, Sugadaira M.R.C., Japan	decaying tree bark	JX976017	HQ667360.1
Mortierella cystojenkinii	CBS456.71, FSU9803	*M. cystojenkinii*	Type of *Mortierella cystojenkinii*	Wageningen, Netherlands	agricultural soil	JX976030	HQ667504.1
	CBS660.82	–		Bakkeveen, Netherlands	Pinus forest	JX975868	KC018325
Mortierella decipiens	CBS873.68	–		Kiel-Kitzeberg, Germany	wheat field soil	–	JX976173
Mortierella dichotoma	CBS221.35, FSU9804	*M. dichotoma*	Syntype of *Mortierella dichotoma*	former West-Germany	dung of mouse	JX975842	HQ667393.1
Mortierella echinosphaera	CBS574.75	–		near Wageningen, Netherlands	soil	JX976060	KC018370
	CBS575.75, FSU9805	*M. echinosphaera*	Holotype of *Mortierella echinosphaera*	Aalsmeer, Netherlands		JX976015	HQ667431.1
Mortierella echinula	CBS282.71	–		Iceland	soil	JX975948	–
Mortierella elongata	CBS110517	–		Alti Mountains, South Africa	soil, grassland, summer rainfall region	JX976042	KC018348
	CBS122.71	–		Georgia, Monroe, USA	soil, under golf turf-grass	JX976000	KC018396
	CBS126.71, FSU823	*M. elongata*		Wageningen, Netherlands	agricultural soil	JX976101	KC018279
	CBS208.71	–		Netherlands	greenhouse soil	JX975995	JX976135

Table 2 (cont.)

Original name	Strain numbers	Microscopic identification	Type status	Locality	Substrate	Accession no. ITS	Accession no. LSU
	CBS276.89	–		Quebec	(black fly)	JX976111	KC018452
	CBS279.62	–		Kiel-Kitzeberg, Germany	wheat field soil	JX976089	KC018417
	CBS344.66	–		Alaska	tundra soil	JX976081	KC018322
	FSU532	*M. elongata*		–		JX975976	KC018281
	FSU822, CBS125.71	*M. elongata*		Wageningen, Netherlands	agricultural soil	JX975978	KC018282
	FSU9721	*M. elongata*		Münchenroda, Germany		JX975894	KC018284
Mortierella elongatula	CBS488.70, FSU9808	–	Type of *Mortierella elongatula*	former West-Germany	municipal waste	JX975967	HQ667425.1
	CBS661.70	–		Braunschweig, Germany	municipal waste	JX976069	KC018431
Mortierella epicladia	CBS246.75	–		Suriname	soil, under *Elaeis guineensis*	JX975890	KC018361
	CBS355.76, FSU9809	*M. epiclada*	Type of *Mortierella epicladia*	Gran Canaria, Spain	soil, under *Apollonias canariensis*	JX976130	HQ667396.1
	CBS356.76	–		Gran Canaria, Spain	soil, under *Apollonias canariensis*	JX975972	–
	CBS555.89	–		Pará, 200 km SE from Belém, Capitâo Poço, Brasil	rain forest soil	JX975991	JX976150
Mortierella epigama	CBS161.76	*M. epigama*		Exeter, Hatherly Laboratories, England	compost heap	JX976109	JX976158
	CBS489.70, FSU9810	*M. epigama*	Type of *Mortierella epigama*	former West-Germany	municipal waste	JX976057	HQ667367.1
	CBS881.97	–		Kagoshima, Kamei, Tokunoshima-Island, Japan	old dung of cow	JX976053	KC018445
Mortierella exigua	CBS358.76	–		Gran Canaria, Spain	soil, under *Apollonias canariensis*	JX976113	KC018439
	CBS510.63	–		Kiel-Kitzeberg	agricultural soil	JX975863	JX976134
	CBS655.68, FSU9811	*M. exigua*	Type of *Mortierella sterilis*	Allahabad, India	farm soil	JX976047	HQ667406.1
	CBS865.68	–		Kiel-Kitzeberg, Germany	wheat field soil	JX976070	–
Mortierella fatshederae	CBS388.71	–		Gran Canaria	soil, under *Pinus canariensis*	JX976003	JX976136
Mortierella fimbricystis	CBS943.70	–	Type of *Mortierella fimbricystis*	South Patagonia, Puerto Edwards near Beagle Canal, Argentinia	centre of moss cushion, in very wet bog	GU559986.1	JX976172
Mortierella formicicola	CBS109589	–		Brampton, Ontario	infrabuccal pellet of *Camponotus pennsylvanicus*, in house (windowsill)	JX975933	JX976140
Mortierella gamsii	CBS110630	–		Boekrijk, Belgium	soil with Porcellio	JX976106	KC018410
	CBS253.36, FSU9813	*M. gamsii*	Syntype of *Mortierella spinosa*	former West-Germany	forest soil	JX975968	HQ667415.1
	CBS314.52, FSU9814	*M.* cf. *gamsii*	Syntype of *Mortierella spinosa*	former West-Germany	forest soil	JX975892	HQ667384.1
	CBS551.73, FSU824	*M. gamsii*		North Carolina	pasture soil	JX976079	JX976177
	CBS552.73, FSU825	*M. gamsii*		Alleghany County, North Carolina	pasture soil	JX975984	KC018285
	CBS749.68, FSU9812	*M. gamsii*	Type of *Mortierella gamsii*	Baarn, Maarschalksbos, Netherlands	soil		HQ667416.1
	FSU2057	*M. gamsii*		–		JX976118	KC018287
Mortierella gemmifera	CBS124.72	–		Meerdinkbos near Winterswijk, Netherlands	soil, humus layer	JX975909	KC018390
	CBS134.45, FSU9815	*M. gemmifera*	Type of *Mortierella gemmifera*	near Nottingham, England	soil from pine forest	JX975931	HQ667371.1
	CBS383.85	–		Spanderswoud near Bussum, Netherlands	soil, in pine forest	JX976121	JX976157
	CBS661.82	–		Bakkeveen, Netherlands	*Endogone lactiflua*, Pinus forest	JX975989	KC018360
Mortierella globalpina	CBS226.78	–		Katwijk, Netherlands	sand dune soil	JX976006	JX976160
	CBS718.88	–		Japan		JX975925	–
Mortierella globulifera	CBS108.68	–		Schweden		JX975847	KC018332
	CBS746.68	–		Netherlands	agricultural soil	JX976026	KC018371
	CBS857.70, FSU826	–		England	decaying needle	JX975910	HQ667369
	CBS858.70, FSU9817	*M. globulifera*	Neotype of *Mortierella globulifera*	England	decaying root	JX975915	HQ667368.1
	CBS867.68	–		Tirol, Obergurgl, Austria	alpine raw humus soil	JX976107	JX976165
Mortierella histoplasmatoides	CBS321.78, FSU9819	–	Type of *Mortierella histoplasmatoides*	Louisiana	dung	HQ630309.1	HQ667386.1
Mortierella horticola	CBS305.52, FSU9820	*M. horticola*	Syntype of *Mortierella horticola*	former West-Germany		JX975874	HQ667399.1
	CBS869.68	–		Kiel-Kitzeberg	wheat field soil	JX976058	JX976138
	CBS254.76	–		Wageningen, Netherlands	agricultural soil	JX976021	JX976166
Mortierella humilis	CBS180.72	–		Piedmont, North Carolina	forest soil	JX976125	KC018436
	CBS181.72	–		Piedmont, North Carolina	soil	JX975887	KC018405
	CBS222.35, FSU9821	–	Syntype of *Mortierella humilis*	Mexico	soil from Pinus forest	HQ630325.1	HQ667401.1
	CBS363.95	–		Shennongjia, Hubei, China	forest soil	JX976097	KC018443

	CBS443.68, FSU828	*M. humilis*		South Carolina	bark of stump	JX976002	HQ667402
	CBS745.68, FSU829	*M. humilis*		Baarn, Eemnesserweg 90, Netherlands	soil	JX975867	HQ667403
Mortierella hyalina	CBS100563	–		Schoharie Co., New York		JX976023	KC018356
	CBS115655, FSU9822	*M. hyalina*	Isotype of *Hydrophora hyalina*	North of London, Rothamsted, England	roots	HQ630355.1	HQ667432.1
	CBS117.74	–		Boekesteyn near 's-Graveland, Netherlands		JX976083	KC018392
	CBS117152	–		Graz, Austria	soil and chees mixture used as food for mites by E. Ebermann	JX975977	KC018394
	CBS166.25	–		Netherlands	seed	JX975928	–
	CBS167.25	–		–		JX975895	KC018406
	FSU10532	*M. hyalina*		Austria		JX975992	KC018289
	FSU509	*M. hyalina*		–		JX975981	KC018291
Mortierella hypsicladia	CBS116202, FSU9825	*M. hypsicladia*	Type of *Mortierella hypsicladia*	Kyushu Isl., Kariu Cave, Japan	bat dung in cave	JX975866	HQ667379.1
	CBS116203		Authentic strain of *Mortierella hypsicladia*	Kyushu Isl., Kariu Cave, Japan	bat dung in cave	JX975872	KC018369
Mortierella indohii	CBS220.72			Naaldwijk, Netherlands	greenhouse soil	JX975993	KC018408
	CBS331.74, FSU830	*M. indohii*		Lienden, Netherlands	root	JX975860	KC018292
	CBS460.75, FSU831	*M. indohii*		Athens, Georgia	dung of animal	JX975878	HQ667438
	CBS478.95			Chengdu, Sichuan, China	soil	JX975903	KC018347
	CBS528.75			South Africa	bagasse in chicken farm	JX976044	KC018451
	CBS665.70			Wageningen, Netherlands	agricultural soil	JX975956	KC018357
	CBS720.71, FSU9826	*M. indohii*	Isotype of *Mortierella indohii*	Athens, Georgia	dung of animal	JX975856	HQ667377.1
Mortierella jenkinii	CBS188.73			Nottingham, England	turf layer of golf green, received fungicidal treatment for long period	JX975999	KC018389
	CBS666.75C			Sweden	soil under *Picea abies*	–	JX975873
	CBS667.70			Wageningen, Netherlands	agricultural soil	JX976088	KC018422
	CBS850.70			Wageningen, Netherlands	agricultural soil	JX975849	KC018352
	CBS965.73C			Sweden	forest soil	JX976117	JX976139
Mortierella kuhlmanii	CBS157.71, FSU9827	*M. kuhlmanii*	Type of *Mortierella kuhlmanii*	South Carolina, Miley	stump	JX975846	HQ667372.1
	CBS269.71				stump, *Pinus taeda*	JX975935	KC018384
	CBS270.71			Patrick, South Carolina	stump	JX975851	JX976142
	CBS271.71			South Carolina	seedling	JX975883	KC018338
Mortierella lignicola	CBS100594			–		JX975889	–
	CBS116.65			Wageningen, Netherlands	black soil	JX975965	KC018402
	CBS207.37, FSU9828	*M. lignicola*	Type of *Haplosporangium lignicola*	Sierra Nevada de Santa Marta, Colombia	rotten wood	JX976095	HQ667435.1
	CBS313.52, FSU9829	*M. lignicola*	Type of *Mortierella sepedonioides*	former West-Germany	soil under *Pinus sylvestris*	JX976127	HQ667434.1
Mortierella longigemmata	CBS653.93			Höglwald, Germany	soil	JX976055	JX976162
Mortierella macrocystis	CBS110716			De Veluwe	oak forest soil	JX976084	–
	CBS314.85			former West-Germany	rootlet of gymnosperm	JX975974	JX976169
	CBS431.81			Cundinamarca, páramo Cruz Verde, Colombia	soil	JX975897	KC018437
	CBS482.73			former West-Germany	soil	JX975862	–
	CBS937.69			Baarn, Pekingtuin, Netherlands	soil	JX975881	KC018341
Mortierella macrocystopsis	CBS302.87			South Kingstown, Rhode Island	soil under *Pinus resinosa* and *Pinus strobus*	JX975908	KC018362
	CBS387.91	*M. cystojenkinii*		Norway	soil	JX976105	JX976144
	CBS520.88			Rhode Island	soil	JX976078	–
	CBS528.87			South Kingstown, Rhode Island	forest soil, under *Pinus resinosa* and *Pinus strobus*	JX975946	JX976164
Mortierella microzygospora	CBS880.97, FSU9831	*M. microzygospora*	Type of *Mortierella microzygospora*	Shiga, Maibara, Japan	soil in hedge	JX976027	HQ667394.1
Mortierella minutissima	CBS226.35			former West-Germany		JX976092	JX976168
	CBS277.71, FSU832	*M. minutissima*		Georgia	forest soil	JX975938	KC018293
	FSU2735	*M. zonata*		–		JX976103	KC018318
Mortierella minutissima var. *dubia*	CBS307.52, FSU9832		Syntype of *Mortierella minutissima* var. *dubia*	former West-Germany	soil	JX976122	HQ667400.1
Mortierella nantahalensis	CBS610.70, FSU9834	*M. nantahalensis*	Type of *Mortierella nantahalensis*	Joyce Kilmer Memorial Forest in the Nantahala National Forest, North Carolina	soil	JX976022	HQ667388.1
Mortierella oligospora	CBS101758			Pennsylvania	supplement to mushroom culture	JX976032	KC018327
	CBS191.79			Elephant White Nile Island, Sudan	soil	JX975966	JX976151

Table 2 (cont.)

Original name	Strain numbers	Microscopic identification	Type status	Locality	Substrate	Accession no. ITS	Accession no. LSU
	CBS381.71			Jaipur, Rambagh Palace Hotel, Rajasthan	soil	JX976033	KC018368
Mortierella paraensis	CBS343.89			Pará, Capitão Poço, Brazil	forest soil, virgin forest	JX975944	KC018329
	CBS547.89, FSU9835	*M. paraensis*	Type of *Mortierella paraensis*	Pará, 200 km SE from Belém, Capitão Poço, Brasil	rain forest soil	HQ630353	HQ667429.1
Mortierella parazychae	CBS868.71, FSU9836	*M. parazychae*	Type of *Mortierella parazychae*	Treek near Amersfoort, Netherlands	decaying wood, with *Botryobasidium subcoronatum*	JX975985	HQ667362.1
Mortierella parvispora	CBS304.52, FSU9837	*M. parvispora*	Syntype of *Mortierella gracilis*	former West-Germany	soil	JX975859	–
	CBS311.52, FSU9838		Syntype of *Mortierella parvispora*	former West-Germany	soil	JX976076	HQ667373.1
	CBS315.61, FSU834	*M. parvispora*		Cheshire, Delamere Forest, England	soil, iron-humus podzol	JX976104	HQ667374.1
	CBS316.61, FSU835	*M. parvispora*		Cheshire, Delamere Forest, England	soil, iron-humus podzol	JX976029	HQ667375.1
	CBS445.68			Wageningen, Netherlands	beet-field soil	JX976049	KC018414
	FSU2736	*M. jenkinii*		–		JX976093	KC018295
Mortierella polycephala	CBS227.35			–		JX976096	KC018321
	CBS293.34	*M. hyalina*		Netherlands		JX976050	JX976137
	CBS327.72, FSU866	*M. polycephala*		Lincs., Gibraltar Point, England	salt-marsh soil under *Spartina townsendii*	JX976085	JX976175
	CBS328.72, FSU867	*M. polycephala*		UK	soil	JX976102	KC018296
	CBS456.66, FSU759	*M. polycephala*		near Kiev, Ukraine	dung of wood mouse	JX976034	KC018297
	FSU696	*M. polycephala*		–		JX976035	KC018298
Mortierella polygonia	CBS248.81			Sexbierum, Netherlands	clay soil under *Solanum tuberosum*	JX975891	JX976145
	CBS685.71, FSU9839		Type of *Mortierella polygonia*	Wageningen, Netherlands	agricultural soil	JX975900	HQ667378.1
Mortierella pseudozygospora	CBS779.86			Kingston, North Woods, Univ. of Rhode Island Campus, Rhode Island	soil under Quercus-Acer woodland, about sea level, upper 5 cm depth	JX975960	KC018353
	CBS780.86			Peace Dale, Hazard Tract, Rhode Island	soil, under *Pinus strobus* and *Pinus resinosa* woodland, from upper 5 cm depth, soil temp. 2.5°C	JX975880	JX976143
Mortierella pulchella	CBS205.86			Netherlands	root	JX976031	KC018366
	CBS312.52, FSU9840		Authentic strain of *Mortierella pulchella*	former West-Germany	root	JX976054	HQ667427.1
	CBS675.88			Berlin, Grunewald, Jagen 91, Germany	soil, litter layer	JX976082	KC018440
Mortierella reticulata	CBS110044			Lanark near Branxholme, Victoria	dung of *Perameles gunnii*	JX975980	–
	CBS223.29			–		JX975973	–
	CBS241.33			–		JX976116	JX976133
	CBS415.81			Toronto, Ontario	dung of mouse, collected in a house	JX975877	–
Mortierella rishikesha	CBS652.68, FSU9842		Type of *Mortierella rishikesha*	Rishikesh, India	forest soil	JX976110	HQ667385.1
Mortierella rostafinskii	CBS522.70, FSU9844		Neotype of *Mortierella rostafinskii*	near Bainbridge, Georgia	soil under *Pinus elliottii* var. *elliottii*	JX975885	HQ667436.1
Mortierella sarnyensis	CBS122.72, FSU9845	*M. sarnyensis*	Type of *Mortierella sarnyensis*	Rovensk region, near Sarny, Ukraine	coniferous forest	JX975957	HQ667390.1
Mortierella schmuckeri	CBS156.78			Madhya Pradesh and Uttar Pradesh regions, India	soil, from ravines	JX975854	KC018372
	CBS295.59, FSU9846	*M. schmuckeri*	Syntype of *Mortierella schmuckeri*	Queretaro, Mexico	soil, under *Opuntia* sp., pH 6.7	JX976112	HQ667414.1
	CBS777.86			Shoshone National Forest, Horse Creek Campground, Wyoming	soil, upper 10 cm, under *Pseudotsuga menziesii*, alt. 2500 m	JX976099	KC018413
Mortierella sclerotiella	CBS529.68, FSU9847	*M. sclerotiella*	Type of *Mortierella sclerotiella*	Ukraine	dung of mouse	JX975988	HQ667387.1
Mortierella selenospora	CBS452.88			Cibodas, Indonesia	soil	JX976037	KC018429
	CBS811.68, FSU9848	*M. selenospora*	Type of *Mortierella selenospora*	Horst, Netherlands	mushroom compost, together with *Entomophthora coronata* and *Aphanocladium album*	JX975875	HQ667419.1
Mortierella simplex	CBS110.68			Wageningen, Netherlands	oat-field soil	JX975982	–
	CBS243.82			Baarn, C. Dopperlaan 18, Netherlands	compost heap	JX975870	JX976156
Mortierella sossauensis	CBS153.76C			Schweden	forest soil under *Picea abies*	JX976063	JX976146
	CBS176.74	*M. clonocystis*		Athens, Georgia	Greenhouse soile	JX975926	KC018428
	CBS281.71			South Carolina	root	JX975911	KC018447
	CBS890.72			Ireland	peat soil	JX975865	KC018385
	CBS898.68			Lincs., Gibraltar Point, England	salt-marsh soil	JX975970	KC018374
Mortierella sp.	FSU10519	*M. alpina*		Austria		JX975959	KC018258

	FSU10520	*M. alpina*		Austria		JX975969	KC018259
	FSU10522	*M. alpina*		Austria		JX975930	KC018261
	FSU10523	*M. alpina*		Austria		JX976114	KC018262
	FSU10551	*M. alpina*		Austria		JX975852	KC018269
	FSU10555	*M. alpina*		Austria		JX975996	KC018315
	FSU10558	*M. alpina*		Austria		JX975884	KC018271
	FSU10683	*M. alpina*		Austria		JX976039	–
	FSU10696	*M. alpina*		Austria		JX976108	–
	FSU10706	*M. alpina*		Austria		JX976068	–
	FSU10715	*M. alpina*		Austria		JX976080	–
	FSU10716	*M. alpina*		Austria		JX975879	–
	FSU8712	*M. alpina*		Wehlen, Mosel, Germany		JX975845	KC018274
	FSU8722	*M. alpina*		Wehlen, Mosel, Germany		JX975961	KC018275
	FSU8736	*M. alpina*		Wehlen, Mosel, Germany		JX976119	KC018276
	FSU8737	*M. alpina*		Wehlen, Mosel, Germany		JX975902	KC018277
	FSU8738	*M. alpina*		Wehlen, Mosel, Germany		JX976010	KC018278
	CBS118520			Græse, Zealand, Denmark	agricultural soil	JX975936	JX976149
	FSU10767			Austria		JX975929	–
	FSU10792			Austria		JX976014	–
	FSU10797			Austria		JX975950	–
	FSU10541	*M. elongata*		Austria		JX975876	KC018310
	FSU10771	*M. elongata*		Austria		JX976131	–
	FSU8711	*M. elongata*		Wehlen, Mosel, Germany		JX976071	KC018283
	FSU10538	*M. gamsii*		Austria		JX975858	KC018286
	FSU10535	*M. humilis*		Austria		JX976052	–
	FSU1954	*M. hyalina*		–		JX975861	KC018290
	FSU10804	*M. minutissima*		Austria		JX976020	–
	FSU10552	*M. parvispora*		Austria		JX976009	KC018294
	FSU10712			Austria		JX975941	–
	FSU10730			Austria		JX975916	–
	FSU10753			Austria		JX976016	–
	FSU10758			Austria		JX976005	–
	FSU10759	*M. parvispora*		Austria		JX975934	–
	FSU10789			Austria		JX976065	–
	FSU10530			Austria		JX975893	KC018306
	FSU10540			Austria		JX975986	KC018309
	FSU10557			Austria		JX975932	–
	FSU2188			–		JX975945	KC018316
	FSU10534	*M. verticillata*		Austria		JX975914	KC018317
Mortierella strangulata	CBS455.67, FSU9849	*M. strangulata*	Neotype of *Mortierella strangulata*	Baarn, Groeneveld, Nmetherlands	dung, of fox ?	JX975997	HQ667437.1
Mortierella stylospora	CBS211.32, FSU9850	*M. stylospora*	Type of *Mortierella stylospora*	Victoria	sandy loam	JX976086	HQ667359.1
Mortierella turficola	CBS430.76			Heseper Veen near Coevorden, Netherlands	decaying *Sphagnum recurvum*	JX975919	KC018444
	CBS431.76			Heseper Veen near Coevorden, Netherlands	decaying *Sphagnum recurvum*	JX976025	KC018333
	CBS432.76, FSU9851	*M. turficola*	Neotype of *Mortierella turficola*	Heseper Veen near Coevorden, Netherlands	decaying *Sphagnum recurvum*	JX975952	HQ667426.1
	CBS433.76			Heseper Veen near Coevorden, Netherlands	decaying *Sphagnum recurvum*	JX975939	KC018424
	CBS547.76			Cauca en Huila, Cordillera Central, Parque Nacional del Puracé, 3100 m alt., Colombia	soil from mountain forest under *Weinmannia* etc.	JX975896	KC018339
	CBS581.80			Netherlands	Trio compost	JX976040	KC018409
Mortierella verticillata	CBS130.66			Lancashire, Freshfield, England	sandy forest soil	JX976007	KC018326
	CBS131.66			Lancashire, Freshfield, England	sandy forest soil	JX975886	KC018446
	CBS220.58, FSU9853	*M. verticillata*	Type of *Haplosporangium fasciculatum*	Fontainebleau, France	soil under *Betula* sp.	JX975905	JN940873.1
	CBS225.35, FSU9854	*M. verticillata*	Syntype of *Mortierella marburgensis*	former West-Germany		JX975940	JQ040251.1
	CBS279.71			South Carolina		root	JX975917	KC018426

Table 2 (cont.)

Original name	Strain numbers	Microscopic identification	Type status	Locality	Substrate	Accession no. ITS	Accession no. LSU
	CBS280.71			South Carolina	root	JX976066	KC018404
	CBS315.52, FSU9856	*M. verticillata*	Syntype of *Mortierella marburgensis*	former West-Germany	forest soil	JX975943	–
	CBS346.66, FSU9852			Alaska	tundra soil	JX975855	HQ667397.1
	CBS374.95, FSU9855	*M. verticillata*	Type of *Haplosporangium attenuatissimum*	Wuyi, Fujian, China	forest soil	JX976077	HQ667398.1
Mortierella wolfii	CBS614.70, FSU9860	*M.* cf. *wolfi*		Matamata, New Zealand	decayed hay	JX975975	HQ667420.1
	CBS209.69, FSU9858	*M. wolfii*		Keele, England	coal spoil tip soil	HQ630303.1	HQ667380.1
	CBS611.70, FSU9857			Morrinsville, New Zealand	lung, dying from mycotic pneumonia	HQ630306.1	HQ667383.1
	CBS612.70, FSU9859			New Zealand	decayed hay	HQ630304.1	HQ667381.1
	CBS651.93, FSU9862	*M. wolfii*		Limburg, Horst, Netherlands	compost for mushrooms	JX975904	HQ667382.1
Mortierella zonata	CBS228.35, FSU9863	*M. zonata*	Type of *Mortierella zonata*	former West-Germany		JX975983	HQ667433.1
	CBS615.70			Braunschweig-Völkenrode, Germany	soil	JX975958	KC018434
	CBS617.76			Cordillera, Central Parque Nacional del Puracé, 3900 m alt.	páramo soil, open vegetation with extensive pasture	JX976028	JX976141
	CBS863.68			Ringwood, New Forest, UK	forest soil	JX975888	KC018335
Mortierella zychae	CBS102879			Toronto High Park, Ontario	pellet of *Camponotus pennsylvanicus* (carpenter ant)	JX976074	
	CBS109599			El Yunque, Rio Blanco Trail, Puerto Rico	infrabuccal pellet of ant	JX975882	
	CBS143.91			former West-Germany		JX976091	
	CBS316.52, FSU9864	*M. zychae*	Type of *Mortierella zychae*	Allgäu, Germany	decaying wood	JX975979	HQ667407.1
	CBS531.81			former West-Germany	mushroom casing soil	JX975962	KC018421
	FSU719	*M. zychae*		–		JX976128	KC018319
Umbelopsis isabellina	NRRL1757, CBS100559			Wisconsin	soil	JN943789.1	JN940879.1

Group 2 – verticillata-humilis (Fig. 5, some morphological features are displayed in Fig. 1c, 2a, g, r) is a group that also contains the genera *M. clonocystis*, *M. epicladia*, *M. epigama*, *M. horticola* and *M. minutissima*. The topology is similar to the one previously published (Petkovits et al. 2011) but includes some morphologically misidentified specimens. *Mortierella zonata* CBS 863.68 and *M. sossauensis* CBS 898.68 are well separated from any other members of their species. The main cluster of *M. sossauensis* is closely related to the parvispora-jenkinii complex (Fig. 4) while the type strain of *M. zonata* is related to *M. hyalina* and *M. bainieri* (Fig. 10). After a profound morphological revision *M. zonata* CBS 863.68 and *M. sossauensis* CBS 898.68 should be renamed and included in the M. minutissima-M. horticola complex, which makes this phylogenetic group of *M. minutissima-M. horticola* indistinguishable by ITS sequences although both species could be distinguished by the number of their spores in the sporangiola. While *M. minutissima* develops few-spored sporangiola, *M. horticola* produces single-spored sporangiola. This suggests that the number of spores per sporangium is not strictly fixed in this group and is therefore not of taxonomic relevance. The single specimen CBS 246.75 resembles *M. epicladia* but it clusters distantly from the ex-type material CBS 355.76 which is close to *M. clonocystis* (Fig. 5). Since no other known species group together with CBS 246.75, this might be a so far undescribed species. CBS 226.78 was originally deposited as *M. globalpina* and CBS 226.35 as *M. minutissima* but molecular data of both species currently resembles *M. clonocystis*, indicating an original misapplication or a contamination. Morphology of both species was checked twice and both species were finally assigned to *M. clonocystis.* The morphospecies *M. clonocystis*, *M. epicladia* and *M. epigama* are well recognized by the ITS tree while *M. verticillata* and *M. humilis* form another species complex. Another apparent cluster, the *M. verticillata-M. humilis* cluster, contains strains including type strains of both species. Based on ITS sequences, a differentiation is not possible. Sequences are similar between 98–100 %. Both species are morphologically similar without any significant differences. Consequently both species should be synonymized.

Group 3 – lignicola (Fig. 6, some morphological features are displayed in Fig. 1n, y, 2j, l, s, w). This group contains the species *Mortierella beljakovae*, *M. chlamydospora*, *M. echinosphaera*, *M. formicicola*, *M. gemmifera*, *M. kuhlmanii*, *M. lignicola* and *M. paraensis.* Several of the morphologically defined species, namely *M. beljakovae*, *M. chlamydospora*, *M. echinosphaera*, *M. formicicola*, *M. lignicola* and *M. paraensis*, are nicely detected by the molecular data. *Mortierella chlamydospora* and *M. echinosphaera* appear to be closely related as they are sister groups (BS = 100 %). The species *M. gemmifera* and *M. kuhlmanii* are morphologically very similar (complex is supported by BS = 85 %) and differ just gradually by spore shape and chlamydospores. The ex-type strains of both species differ just by 12 different base pairs in the ITS sequences (= 98 %). The original morphological identification of strain CBS 268.71 could not be verified because it did not sporulate under different conditions, but its molecular data places it between the gemmifera-complex, *M. chlamydospora* and *M. echinosphaera*. The strains CBS 109659 and CBS 555.89 were not examined morphologically and assigned as *Mortierella* sp. since their original descriptions does not correspond with the molecular data.

Group 4 – mutabilis, globulifera and angusta (Fig. 7, some morphological features are displayed in Fig. 1e, s, v, x, 2v). This group contains two of the three included non-*Mortierella* genera: *Gamsiella* and *Dissophora*. The genus *Gamsiella* does not cluster with any other mortierellean species, although it was reported to be sister with *M. mutabilis* (Petkovits et al. 2011).

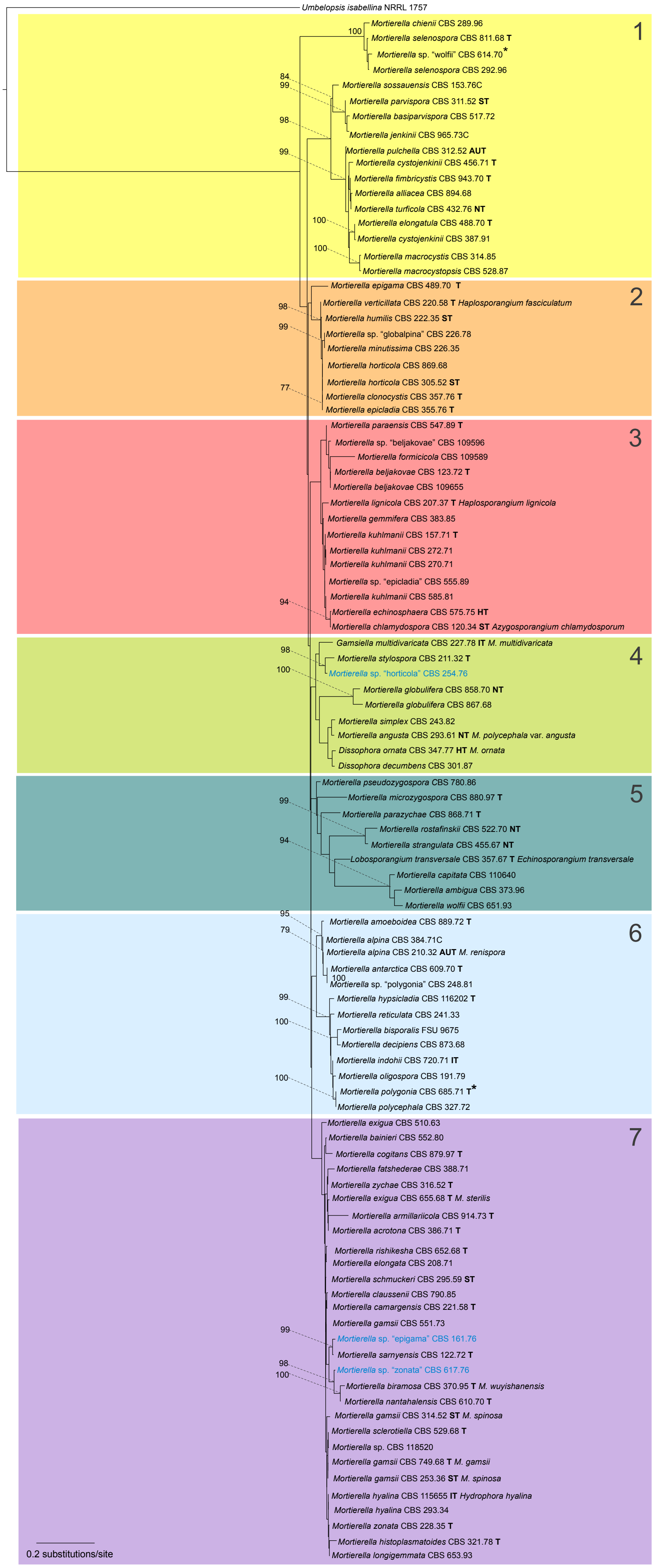

Fig. 3 Maximum Likelihood analysis based on 781 aligned nucleotides of the D1/D2 domain of the large subunit (LSU, 28S) rDNA from 101 taxa (100 ingroup taxa of the *Mortierellales* and 1 outgroup taxon *Umbelopsis* as member of the *Mucorales*, Meyer & Gams 2003). The phylogram based on a MAFFT-Alignment (L-ins-I). Node supports above 75 % is given. The tree defines 7 groups: groups 1–7, which are more profoundly analysed in individual analyses based on the ITS1-5.8S-ITS2 shown in Fig. 4–10. The strains named *Mortierella* sp. 'epithet' are strains with an originally different assignment based on morphology. Blue marked strains are potential new species.

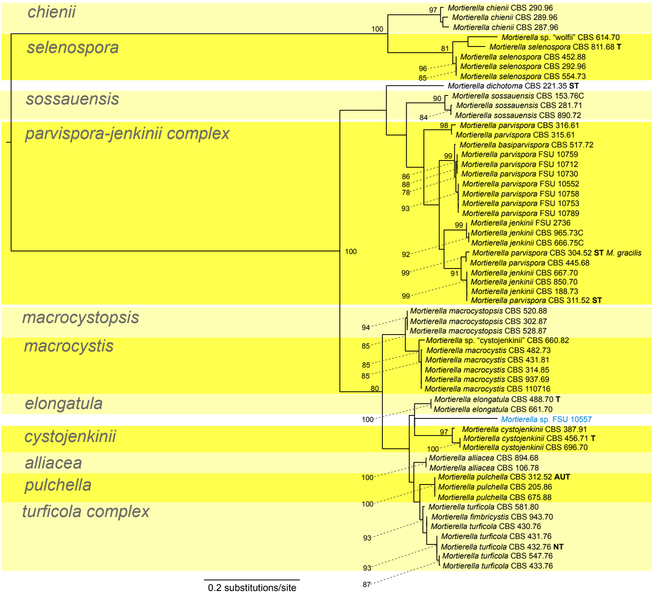

Fig. 4 Maximum Likelihood analysis based on the ITS1-5.8S-ITS2 dataset for clade 1. The phylogram was constructed from a MAFFT-Alignment of 816 aligned nucleotides of 58 taxa. Node support above 75 % is given. The phylogram is midpoint rooted.

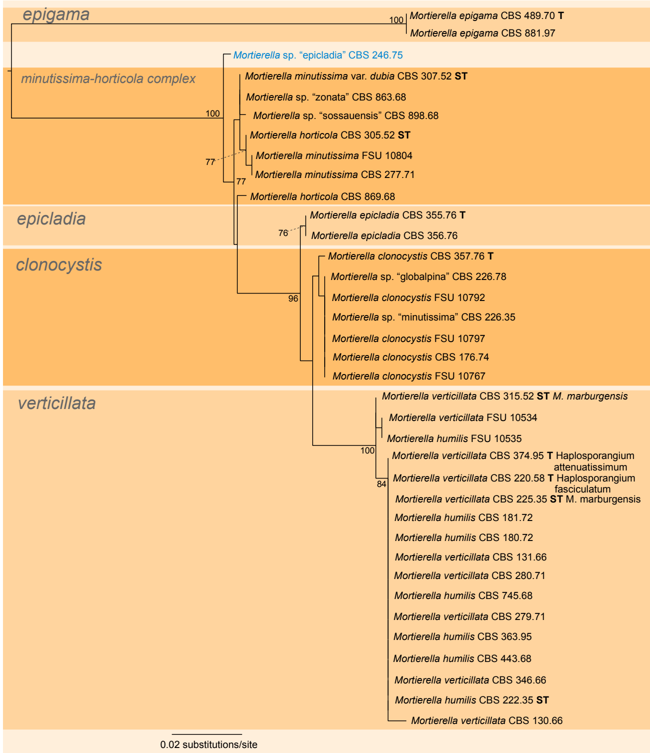

Fig. 5 Maximum Likelihood analysis based on the ITS1-5.8S-ITS2 dataset for clade 2. The phylogram was constructed from a MAFFT-Alignment of 636 aligned nucleotides of 36 taxa. Node support above 75 % is given. The phylogram is midpoint rooted.

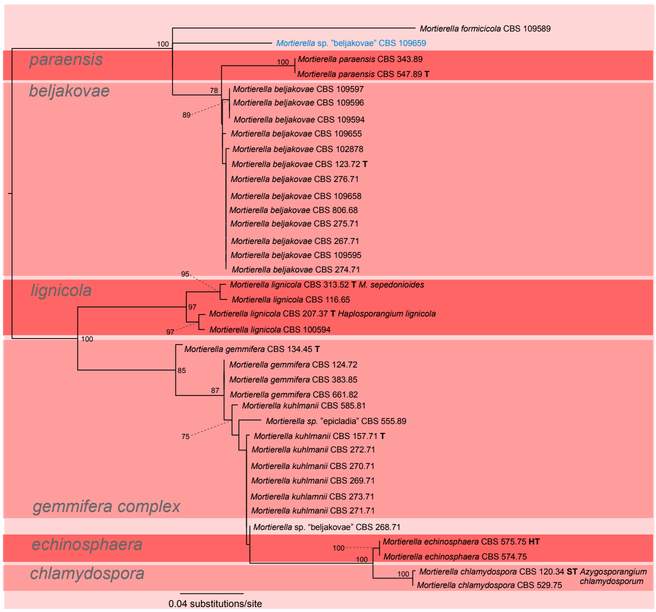

Fig. 6 Maximum Likelihood analysis based on the ITS1-5.8S-ITS2 dataset for clade 3. The phylogram was constructed from a MAFFT-Alignment of 701 aligned nucleotides of 38 taxa. Node support above 75 % is given. The phylogram is midpoint rooted.

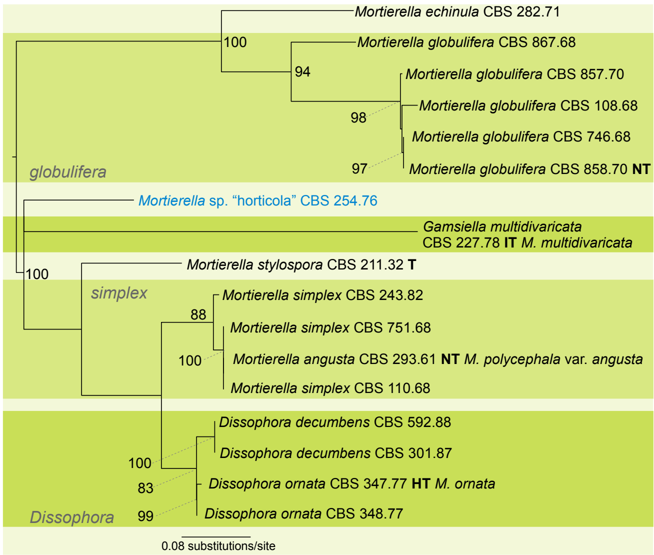

Fig. 7 Maximum Likelihood analysis based on the ITS1-5.8S-ITS2 dataset for clade 4. The phylogram was constructed from a MAFFT-Alignment of 710 aligned nucleotides of 17 taxa. Node support above 75 % is given. The phylogram is midpoint rooted.

A revision of the morphology revealed different features for *M. mutabilis* as originally described. *Mortierella mutabilis* should develop explicitly branched sporangiophores with globose sporangia containing globose to subglobose sporangiospores, for example. But the observed morphology resembles that of *Gamsiella*. Furthermore, LSU and ITS sequences are similar with 100 and 99.8 %, respectively. Based on these data, we are rejecting the previous group named mutabilis (Petkovits et al. 2011). For the final placement of *M. mutabilis*, additional strain material is necessary.

The angusta group is extended by *M. simplex* and consists of the subclades *M. angusta*-*M. simplex* (BS = 88 %) and the subclade *Dissophora* with *D. decumbens* and *D. ornata* (BS = 100 %). *Mortierella simplex* could not by differentiated from *M. angusta* by significant features, suggesting an upcoming synonymization of both species. The globulifera group contains exclusively *M. globulifera* (BS = 94 %). The strain CBS 254.76 formerly identified as *M. horticola* might represent a new species because of its distinct ITS sequence. The ITS sequences of true *M. horticola* strains belong to group 2 (Fig. 5) where the ex-syntype of this species is located.

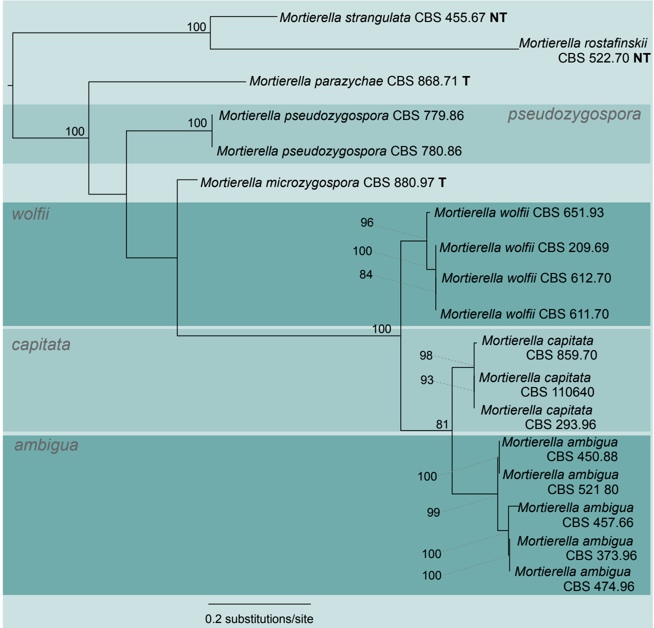

Fig. 8 Maximum Likelihood analysis based on the ITS1-5.8S-ITS2 dataset for clade 5. The phylogram was constructed from a MAFFT-Alignment of 761 aligned nucleotides of 18 taxa. Node support above 75 % is given. The phylogram is midpoint rooted.

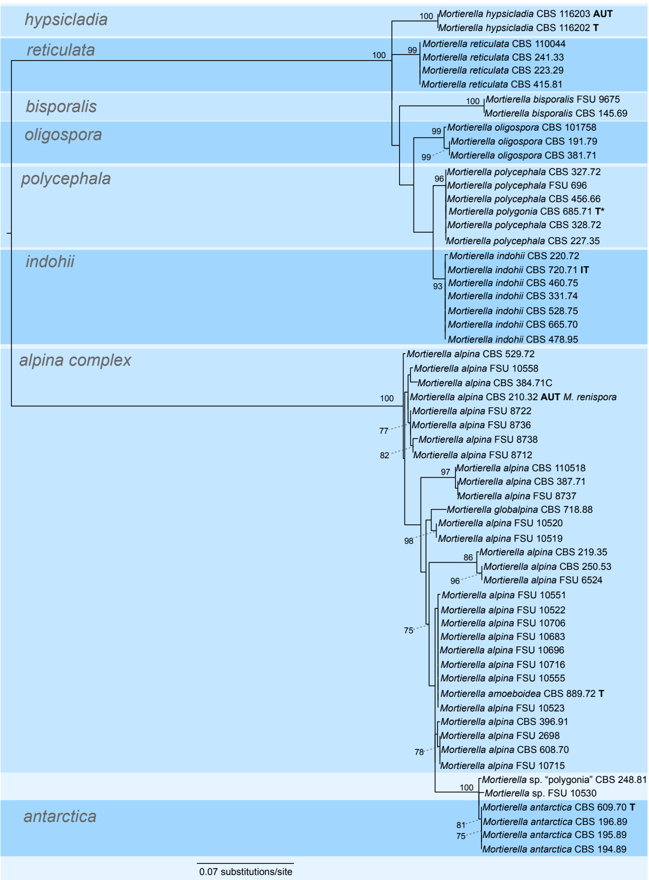

Fig. 9 Maximum Likelihood analysis based on the ITS1-5.8S-ITS2 dataset for clade 6. The phylogram was constructed from a MAFFT-Alignment of 703 aligned nucleotides of 60 taxa. Node support above 75 % is given. The phylogram is midpoint rooted.

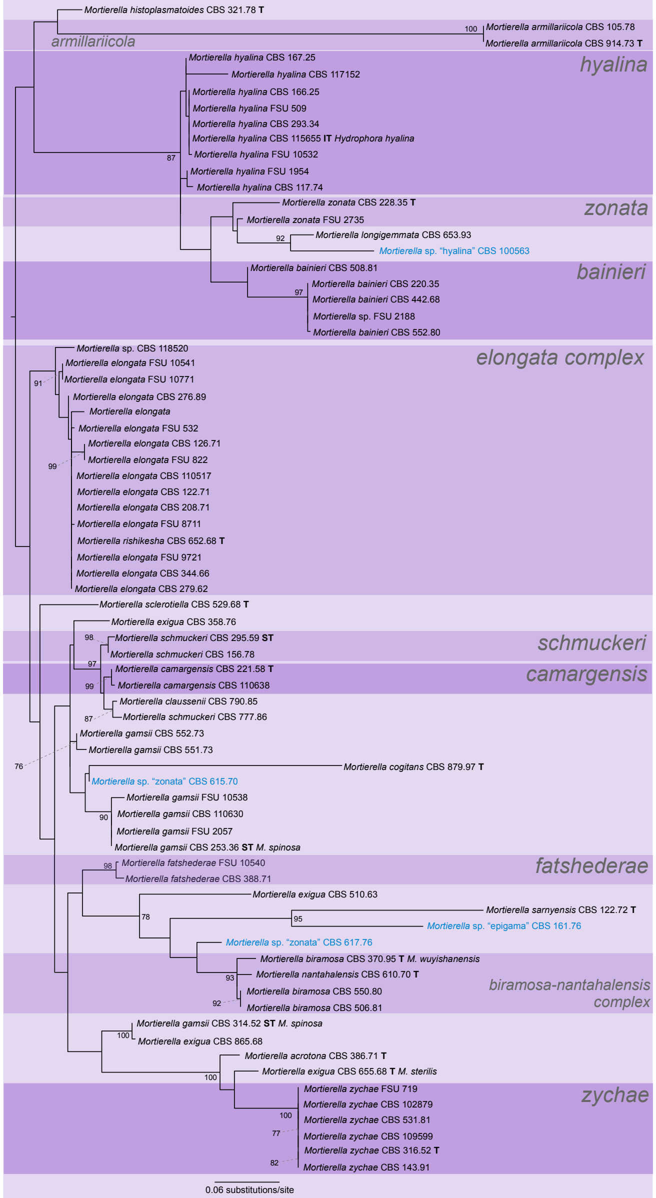

Fig. 10 Maximum Likelihood analysis based on the ITS1-5.8S-ITS2 dataset for clade 7. The phylogram was constructed from a MAFFT-Alignment of 688 aligned nucleotides of 73 taxa. Node support above 75 % is given. The phylogram is midpoint rooted.

Table 3 Summary of isolates which were revised and assigned to different species within this study.

Strain number	Original name	Revised name
CBS585.81	*M. alpina*	*M. kuhlmanii*
CBS696.70	*M. alpina*	*M. cystojenkinii*
CBS272.71	*M. bainieri*	*M. kuhlmanii*
CBS273.71	*M. bainieri*	*M. kuhlmanii*
CBS292.96	*M. chienii*	*M. selenospora*
CBS554.73	*M. chienii*	*M. selenospora*
CBS387.91	*M. macrocystopsis*	*M. cystojenkinii*
FSU2736	*M. parvispora*	*M. jenkinii*
CBS293.34	*M. polycephala*	*M. hyalina*
CBS176.74	*M. sossauensis*	*M. clonocystis*

Group 5 – strangulata and wolfii (Fig. 8, some morphological features are displayed in Fig. 1q, r, 2c, t) contains only few species, which could all be identified by molecular data. The wolfii group (BS = 100 %) is extended in this study by *M. ambigua* (clade support BS = 99 %). *Mortierella ambigua* is sister clade (BS = 81 %) to *M. capitata* (BS = 98 %) and both clades are sister group to *M. wolfii* (BS = 96 %). The strangulata group is retained, containing *M. strangulata* and *M. rostafinskii* (BS = 100 %). *Mortierella microzygospora*, *M. parazychae* and *M. pseudozygospora* were not assigned to any defined group.

Group 6 – alpina and polycephala (Fig. 9, some morphological features are displayed in Fig. 1b, g, h, k, o, w, 2d, m, n, p). The polycephala group harbours the type species of the whole genus *Mortierella*: *M. polycephala*. Therefore, this clade resembles the core group of the genus *Mortierella*. Related to *M. polycephala* and well supported in LSU (BS = 99 %) and ITS (BS = 100 %) are the species *M. bisporalis*, *M. hypsicladia*, *M. indohii*, *M. oligospora*, *M. polygonia* and *M. reticulata*. Except for the ex-type strain of *M. polygonia* CBS 685.71 which clusters within the *M. polycephala*, all species form well supported clades (Fig. 9). But judging from the different observed morphology of *M. polygonia*, which is that of *M. polycephala* instead of that originally described (Gams 1976), this strain should be treated as such. Although the strain is sterile, it shows the typical stylospores of *M. polycephala*. A second isolate of *M. polygonia* (CBS 248.81) could not be confirmed as 'true' *M. polygonia* since it does not sporulate, displaying only untypical stylospores and clusters within the alpina-complex (Fig. 9). Therefore the status of this species seems doubtful. *Mortierella alpina* is one of the major species isolated and identified from our environmental samples collected in Austria. *Mortierella alpina* forms a heterogeneous cluster with the two species *M. antarctica* and *M. amoeboidea*. For *M. amoeboidea* again is the observed morphology not identical with the described one and resembles the species indicated by molecular data. This justifies *M. amoeboidea* W. Gams 1976 to be treated as synonym of *M. alpina* Peyronel 1913. One isolate of *M. globalpina* (CBS 718.88) is placed within the alpina complex and one isolate (CBS 226.78) is located in the *M. clonocystis* clade (Fig. 5). Verification by inclusion of the type strain is not possible since this particular strain seems to be dead now.

Group 7 – gamsii (Fig. 10, some morphological features are displayed in Fig. 1a, d, f, p, u, 2b, e, f, h, k, o, q, u) is the largest group in this and our previous study containing 73 taxa. The previous dataset (Petkovits et al. 2011) with the species *Mortierella acrotona*, *M. armillariicola*, *M. biramosa*, *M. camargensis*, *M. cogitans*, *M. elongata*, *M. exigua*, *M. gamsii*, *M. histoplasmatoides*, *M. hyalina*, *M. nantahalensis*, *M. rishikesha*, *M. sarnyensis*, *M. schmuckeri*, *M. sclerotiella*, *M. zonata* and *M. zychae* was extended by *M. bainieri*, *M. claussenii*, *M. fatshederae* and *M. longigemmata*. *Mortierella armillariicola*, *M. bainieri*, *M. fatshederae*, *M. hyalina* and *M. zychae* form monophyletic clades supported by the coherence of several strains (Fig. 10). *Mortierella exigua*, *M. gamsii* and *M. zonata* are polyphyletic. Strains identified as these species appear in different places of the tree. None of the strains of *M. exigua* clusters together with the ex-type strain. For *M. gamsii* at least three divided clusters are present. One sequence of an ex-type strain is placed in the elongata-complex. *Mortierella schmuckeri* forms one monophyletic clade together with *M. claussenii* and *M. camargensis* (BS = 97 %). Due to a lack of sufficient amounts of strains neither the phylogenetic position nor the species coherence of *M. acrotona*, *M. cogitans*, *M. histoplasmatoides*, *M. longigemmata*, *M. nantahalensis*, *M. sclerotiella* and *M. zonata* could be confirmed.

CONCLUSIONS

In order to study and evaluate the monophyly of *Mortierella*, and to address the phylogenetic relationships of other genera in the *Mortierellales*, we analysed one of the largest datasets of LSU and ITS sequences for this order. The genera *Dissophora*, *Gamsiella* and *Lobosporangium* are placed within the genus *Mortierella*. This suggests either a polyphyly of *Mortierella* with the necessity to establish additional genera or the necessity to reduce the existing genera to one. Although our study contains a comprehensive dataset it is still not possible to elucidate all species and species groups of the *Mortierellales*. It was already proposed that additional molecular markers are necessary for a profound phylogenetic study (Petkovits et al. 2011). But our study supports existing and reveals new contradictions to the traditional morphology based classifications (Linnemann 1941, Zycha et al. 1969, Gams 1977). Several species, originally identified as one, appear on different places in the phylogenetic analyses. This might originate either from simple misapplications or from the observed phenomenon of dependency of the phenotype on culture conditions (Petkovits et al. 2011). Furthermore, names of new genera and species published just recently may be superfluous at a nomenclatural level because their respective phylogenetic markers were not compared with the full molecular dataset of the *Mortierellales*, e.g. *Echinochlamydosporium variabile* (Jiang et al. 2011), which may turn out to be a micromorphologically degenerate *Mortierella stylospora*. Here we present the most comprehensive molecular dataset of the *Mortierellales* which is available up to date and facilitates revision of existing and validation of upcoming names. Finally, all these actions will lead to several species name changes and synonymizations. Nevertheless, several species or even groups of species seem to be distinguishable by morphology and phylogeny. The monophyletic clade of *Mortierella* s.str. contains the type species of the genus, *M. polycephala* Coem. 1863. Whether additional species are related to this group and therefore belonging to the genus *Mortierella* needs to be evaluated in further studies. Current data (Petkovits et al. 2011) are contradictory with regard to relationships of species and species groups. Due to the lack of suitable morphological criteria the following species and species groups were misapplied and require taxonomic revision, where indicated nomenclatural synonymization. These are: *M. angusta*, *M. basiparvispora*, *M. carmagensis*, *M. fimbricystis*, *M. gamsii*, *M. gemmifera*, *M. globalpina*, *M. horticola*, *M. humilis*, *M. jenkinii*, *M. kuhlmanii*, *M. minutissima*, *M. parvispora*, *M. rishikesha*, *M. schmuckeri*, *M. simplex*, *M. sossauensis*, *M. turficola*, *M. verticillata* and *M. zonata.*

Underrepresented in this study, but due to the lack of comprehensive additional material, are the species: *M. acrotona*, *M. angusta*, *M. dichotoma*, *M. epicladia*, *M. exigua*, *M. fimbricystis*, *M. formicicola*, *M. longigemmata*, *M. microzygospora*, *M. nantahalensis*, *M. parazychae*, *M. rishikesha*, *M. rostafinskii*, *M. sclerotiella* and *M. strangulata*.

Acknowledgements This research was supported by an international cooperation grant of the German and Hungarian Research Foundations (DFG Vo 772/9-1 and OTKA NN106394) and the Hungarian grant TÉT_10-1-2011-0747. Tamas Petkovits was supported by the European Union and by the European Social Fund (project number: TÁMOP-4.2.2/B-10/1-2010-0012). We like to express our gratitude to Martin Kirchmair (University of Innsbruck, Austria) for collecting and providing environmental strains of *Mortierella* from the alpine region. Also we would like to thank Domenica Schnabelrauch (Max Planck Institute for Chemical Ecology Jena, Germany) and the members of the molecular barcoding team at the CBS Utrecht for technical support in DNA sequencing.

REFERENCES

Cavalier-Smith T. 1998. A revised six-kingdom system of life. Biological Reviews of the Cambridge Philosophical Society 73, 3: 203–266.

Cenis JL. 1992. Rapid extraction of fungal DNA for PCR amplification. Nucleic Acids Research 20, 9: 2380.

Chalabuda TV. 1968. Systemica familiae Mortierella. Novosti Sistematiki Nizshikh Rastenii 5: 120–131.

Chesters CGC. 1933. Azygozygum chlamydosporum nov. gen. et sp. A phycomycete associated with a diseased condition of Antirrhinum majus. Transactions of the British Mycological Society 18, 3: 199–214.

Coemans E. 1863. Quelques hyphomycetes nouveaux. 1. Mortierella polycephala et Martensella pectinata. Bulletin de l'Académie Royale des Sciences de Belgique Classe des Sciences 2, ser. 15: 536–544.

Dewèvre A. 1893. Contribution a l'étude des Mucorinées, avec essai d'une monographie de ces champignons. Grevillea 22, 101: 1–8.

Fischer A. 1892. Mortierellaceae. In: Rabenhorst L, Kryptogamen-Flora von Deutschland, Oesterreich und der Schweiz. Band 1, Abth. IV. Kummer E, Leipzig, Germany: 268–283.

Gams W. 1969. Gliederungsprinzipien in der Gattung Mortierella. Nova Hedwigia 18, 1: 30–44.

Gams W. 1976. Some new or noteworthy species of Mortierella. Persoonia 9, 1: 111–140.

Gams W. 1977. A key to the species of Mortierella. Persoonia 9, 3: 381–391.

Griebel T, Brinkmeyer M, Böcker S. 2008. EPoS: a modular software framework for phylogenetic analysis. Bioinformatics 24: 2399–2400.

Hawksworth DL. 2001. The magnitude of fungal diversity: the 1.5 million species estimate revisited. Mycological Research 105, 12: 1422–1432.

Hibbett DS, Binder M, Bischoff JF, Blackwell M, Cannon PF, et al. 2007. A higher-level phylogenetic classification of the Fungi. Mycological Research 111: 509–547.

Higashiyama K, Fujikawa S, Park EY, Shimizu S. 2002. Production of arachidonic acid by Mortierella fungi. Biotechnology and Bioprocess Engineering 7: 252–262.

Hoffmann K, Voigt K, Kirk PM. 2011. Mortierellomycotina subphyl. nov., based on multi-gene genealogies. Mycotaxon 115, 1: 353–363.

Holland HL. 2001. Biotransformation of organic sulfides. Natural Product Reports 18: 171–181.

Hoog GS de, Guarro J, Gené J, Figueras MJ. 2009. Atlas of clinical fungi, 3rd ed. Centraalbureau voor Schimmelcultures, Utrecht, The Netherlands / Universitat Rovira i Virgili, Reus, Spain.

Ivanova NV, Dewaard JR, Hebert PDN. 2006. An inexpensive, automation-friendly protocol for recovering high quality DNA. Molecular Ecology Notes 6: 998–1002.

Jiang XZ, Yu HY, Xiang MC, Liu XY, Liu XZ. 2011. Echinochlamydosporium variabile, a new genus and species of Zygomycota from soil nematodes. Fungal Diversity 46, 1: 43–51.

Katoh T. 2008. Recent developments in the MAFFT multiple sequence alignment program. Briefings in Bioinformatics 2008, 9: 286–298.

Kirk PM, Cannon PF, Minter DW, Stalpers JA. 2008. Ainsworth & Bisby's dictionary of the fungi. 10th ed. CAB International, Wallingford, UK.

Linnemann G. 1941. Die Mucorineen-Gattung Mortierella Coemans. Pflanzenforschung 23: 1–64.

Malloch D. 1967. A new genus of Mucorales. Mycologia 59: 326–329.

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

Nagy LG, Petkovits T, Kovács GM, Voigt K, Vágvölgyi C, Papp T. 2011. Where is the unseen fungal diversity hidden? A study of Mortierella reveals a large contribution of reference collections to the identification of fungal environmental sequences. New Phytologist 191, 3: 789–794.

Nirenberg HI.1981. A simplified method for identifying Fusarium spp. occurring on wheat. Canadian Journal of Botany 59: 1599–1609.

Novotelnova. 1950. Notulae systematicae e sectione cryptogamica. Instituti Botanici Nominee V.L. Komarovii l'Académie des Sciences de l'URSS 6: 160.

Petkovits T, Nagy LG, Hoffmann K, Wagner L, Nyilasi I, et al. 2011. Data partitions, Bayesian analysis and phylogeny of the zygomycetous fungal family Mortierellaceae, inferred from nuclear ribosomal DNA sequences. PLoS ONE 6, 11: e27507.

Peyronel B. 1913. I germi astmosferici dei fungi con micelio: 17. Dissertation. Padua, Italy.

Stamatakis A. 2006. RAxML-VI-HPC: maximum likelihood-based phylogenetic analyses with thousands of taxa and mixed models. Bioinformatics 22: 2688–2690.

Stielow B, Bubner B, Hensel G, Munzenberger B, Hoffmann P, et al. 2009. The neglected hypogeous fungus Hydnotrya bailii Soehner (1959) is a widespread sister taxon of Hydnotrya tulasnei (Berk.) Berk. & Broome (1846). Mycological Progress 9: 195–203.

Thaxter R. 1914. New or peculiar Zygomycetes. 3: Blakeslea, Dissophora and Haplosporangium, nova genera. Botanical Gazette Crawfordsville 58: 353–366.

Vogelstein B, Gillespie D. 1979. Preparative and analytical purification of DNA from agarose. Proceedings of the National Academy of Sciences of the United States 76, 2: 615–619.

Vu TD, Eberhardt U, Szöke S, Groenewald M, Robert V. 2012. A laboratory information management system for DNA barcoding workflows. Integrative Biology 4, 7: 744–755.

White MM, James TY, O'Donnell K, Cafaro MJ, Tanabe Y, Sugiyama J. 2006. Phylogeny of the Zygomycota based on nuclear ribosomal sequence data. Mycologia 98: 872–884.

White TJ, Bruns T, Lee S, Taylor J. 1990. Amplication 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, San Diego, California.

Zycha H, Siepmann R, Linnemann G. 1969. Mucorales. Eine Beschreibung aller Gattungen und Arten dieser Pilzgruppe. Cramer, Lehre.