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

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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.

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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 morpho-

logical 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 sporangia 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 sheath. Variously shaped chlamydozoospores and stylozoospores 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 exist, 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

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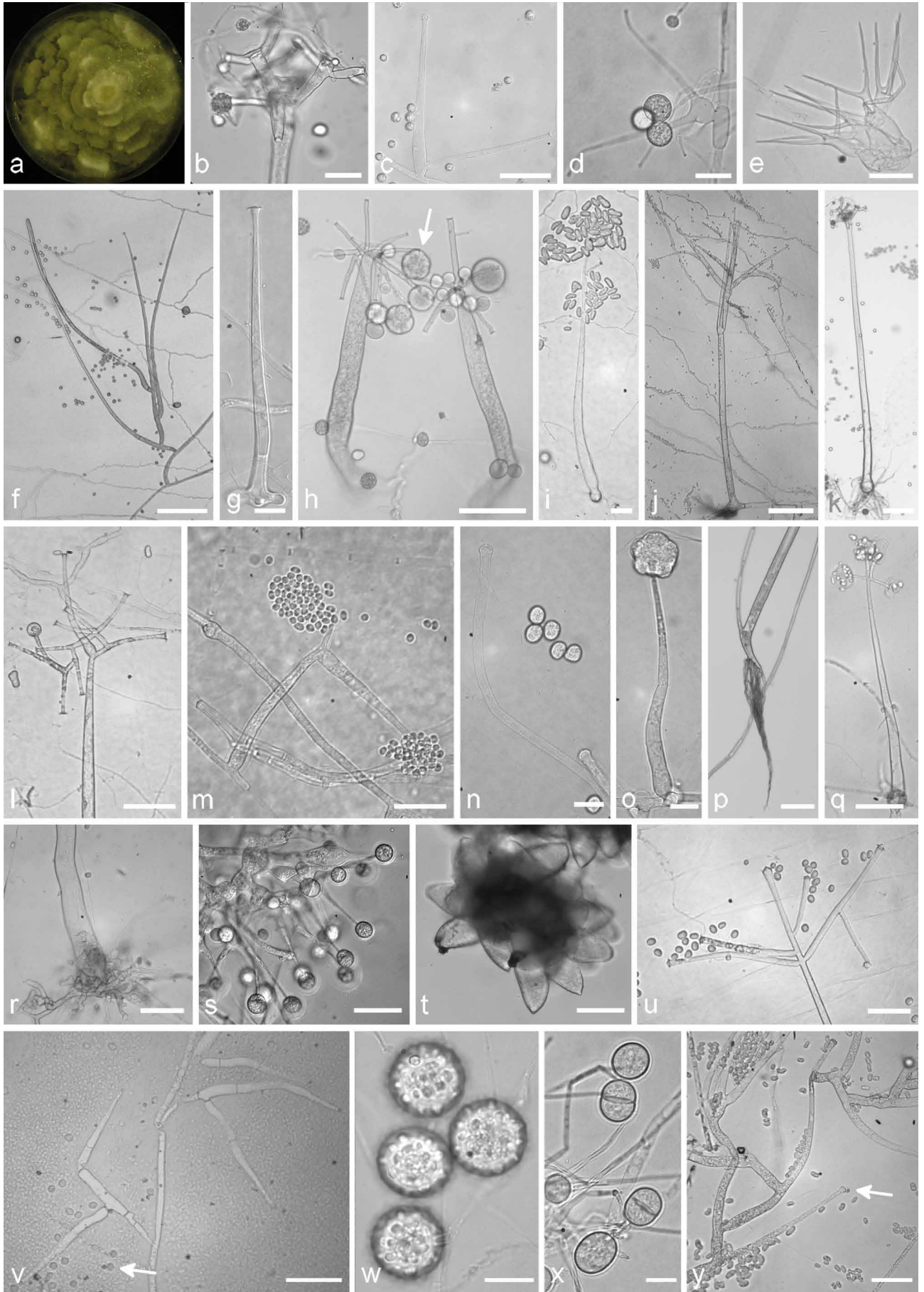


Fig. 1 Typical morphological structures of different isolates of the *Mortierellales*, which are suitable for species delimitation. a. *M. zychnae* CBS 316.52, macroscopic shape of a growing culture with the typical zonate growth; b. *M. hypsicladia* CBS 116202, acrotonous branching of a sporangiophore; c. *M. epicladia* CBS 355.76, sporangiophore and sporangiospores; d. *M. zonata* CBS 228.35, basitonous branched sporangiophore with sporangioles; e. *Gamsiella multidivariata* 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	<i>Mortierella</i> Coem.	<i>Actinomortierella</i> Chalab. 1968 <i>Carnoya</i> Dewèvre 1893 <i>Haplosporangium</i> Thaxt. 1914 <i>Azygozygum</i> Chesters 1933 <i>Naumoviella</i> Novot. 1950	<i>M. polycephala</i>	91	MB#20345
1914	<i>Dissophora</i> Thaxt.	none	<i>D. decumbens</i>	3	MB#20187
1936	<i>Modicella</i> Kanouse	none	<i>M. malleola</i>	2	MB#20336
1967	<i>Aquamortierella</i> Embree & Indoh	none	<i>A. elegans</i>	1	MB#20047
2004	<i>Gamsiella</i> (R.K. Benj.) Benny & M. Blackw.	none	<i>G. multivaricata</i>	1	MB#28820
2004	<i>Lobosporangium</i> M. Blackw. & Benny	<i>Echinosporangium</i> Malloch 1967	<i>L. transversale</i>	1	MB#28819
2011	<i>Echinochlamyosporium</i> X.Z. Jiang, X.Y. Liu & Xing Z. Liu	none	<i>E. variabile</i>	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. hypsycladia* 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 unmaturing 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 multivaricata* 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 multivaricata* 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.

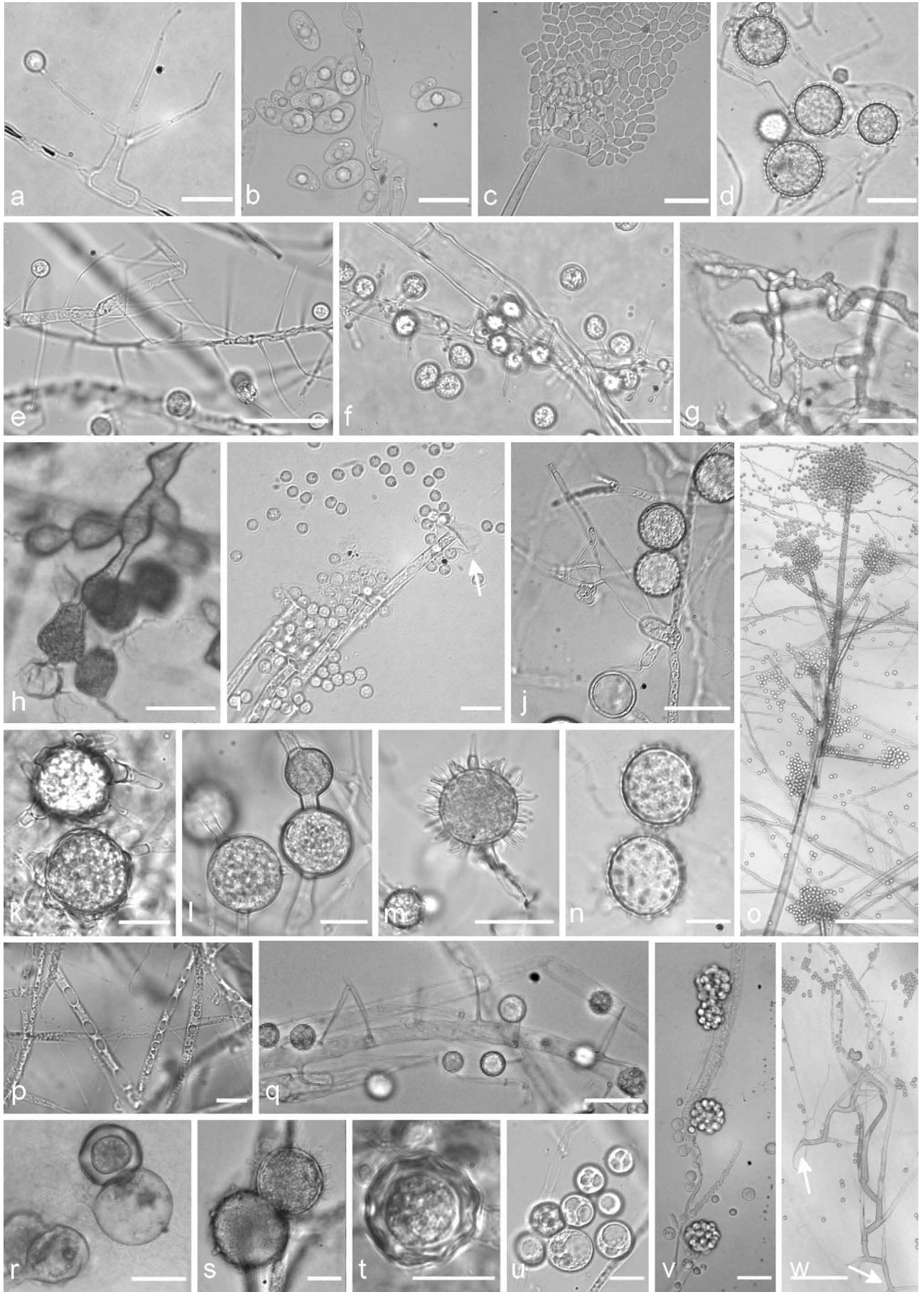


Fig. 2 Typical morphological structures of different isolates of the *Mortierellales*, which are suitable for species delimitation. a. *M. verticillata* CBS 315.52, sporangiophore with a sporangia; b. *M. elongata* FSU 9721, elongated sporangiospores containing central oil droplets; c. *M. wolfii* CBS 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 sporangia; f. *M. clausenii* CBS 294.59, sporangiophores along a hypha with sporangia; g. *M. clonocystis* CBS 357.76, typical swollen hyphae; h. *M. zychnae* FSU 719, typical swollen hyphae arranged in clusters; i. *M. parvispora* FSU 10759, tip of a sporangiophore, white arrow points to a spore; j. *M. parvispora* FSU 10759, spore; k. *M. parvispora* FSU 10759, spore; l. *M. parvispora* FSU 10759, spore; m. *M. parvispora* FSU 10759, spore; n. *M. parvispora* FSU 10759, spore; o. *M. parvispora* FSU 10759, hyphae with clusters of spores; p. *M. parvispora* FSU 10759, hyphae; q. *M. parvispora* FSU 10759, hyphae with spores; r. *M. parvispora* FSU 10759, spore; s. *M. parvispora* FSU 10759, spore; t. *M. parvispora* FSU 10759, spore; u. *M. parvispora* FSU 10759, spores; v. *M. parvispora* FSU 10759, hyphae with spores; w. *M. parvispora* FSU 10759, hyphae, white arrows point to spores.

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/phyloids/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 multivaricata* 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 from 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. wolffii* CBS 614.70 which shows different characteristics (e.g. no thermotolerance) to the original *M. wolffii* strains although the sporangiospores are ellipsoidal to kidney-shaped like those of *M. wolffii*. 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. fimbriocystis*, *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, chlamydo-spores with typical outgrowing hyphae; l. *M. gemmifera* CBS 134.45, chlamydo-spores; m. *M. hypsicladia* CBS 116202, stylospores with projections; n. *M. polygonia* CBS 685.71, stylospores; o. *M. nanthaleensis* 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, zygosporangia; s. *M. echinosphaera* CBS 575.75, chlamydo-spores; t. *M. microzygospora* 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
<i>Dissophora decumbens</i>	CBS301.87, FSU9780	<i>D. decumbens</i>		Kingston, Rhode Island	ground-up litter of Quercus-Acer woodland, incubated at 0°C for two months	JX976001	HQ667354.1
	CBS592.88, FSU801	<i>D. decumbens</i>		Rhode Island	ground-up Quercus and Acer leaves, incubated at 0°C for 21 months	HQ630276.1	HQ667355.1
<i>Dissophora ornata</i>	CBS347.77, FSU9782	–	Holotype of <i>Mortierella ornata</i>	Cordillera Central, Cauca en Huila, Parque Nacional del Puracé, Colombia	soil, in mountain forest under Weimannia, Clusia etc., alt. 3100 m	HQ630278.1	HQ667357.1
	CBS348.77, FSU9783	–	Holotype of <i>Mortierella ornata</i>	Cordillera Central, Cauca en Huila, Parque Nacional del Puracé, Colombia	soil, in mountain forest under Weimannia, Clusia etc., alt. 3100 m	JX976036	HQ667356.1
<i>Gamsiella multidivariata</i>	CBS227.78, FSU9784	<i>G. multidivariata</i>	Isotype of <i>Mortierella multidivariata</i>	Moskva, Sokolniki Park, Russia	decaying stump	JX975871	HQ667355.1
<i>Lobosporangium transversale</i>	CBS357.67, FSU9785	–	Type of <i>Echinosporangium transversale</i>	Nevada, Virginia City	soil	–	HQ667404.1
<i>Mortierella acrotoma</i>	CBS386.71, FSU9788	–	Type of <i>Mortierella acrotoma</i>	Jaipur, Rambagh Palace Hotel, Rajasthan	gymnosperm litter	JX975921	HQ667405.1
<i>Mortierella alliacea</i>	CBS106.78	–		France	alpine raw humus soil	JX976019	KC018349
	CBS894.68	–		Tirol, Oberburg, Austria	soil, dry sandy highveld grassland	JX975990	JX976148
<i>Mortierella alpina</i>	CBS110518	–		South Africa	sandy loam soil	JX975906	–
	CBS210.32, FSU9789	<i>M. alpina</i>	Authentic strain of <i>Mortierella renispora</i>	Victoria		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 <i>Pinus canariensis</i>	JX976038	KC018378
	CBS396.91	–		Washington	air bladder of juvenile fish	JX975994	KC018375
	CBS529.72	–		North Carolina	pasture soil	JX976124	KC018320
	CBS585.81	<i>M. kuhlimanii</i>		Netherlands	agricultural soil	JX976132	JX976152
	CBS608.70	–		Netherlands	agricultural soil	JX976046	KC018438
	CBS696.70	<i>M. cystojenkini</i>		Wageningen, Mansholtlaan, Netherlands	agricultural soil	JX975947	KC018328
	FSU2698	<i>M. alpina</i>		Argentina	agricultural soil	JX976004	KC018272
	FSU6524	<i>M. alpina</i>		Geisenheim, Germany	soil of salt marsh	JX976045	KC018273
<i>Mortierella ambigua</i>	CBS373.96	–		Fukuiyama, Kagoshima, Japan		JX976062	JX976147
	CBS450.88	–		–		JX976041	KC018411
	CBS457.66	–		Armenia	soil	JX976067	KC018398
	CBS474.96	–		Ootomi, Iriomotejima Island, Okinawa, Japan	calcareous soil in ditch	JX976056	KC018416
	CBS521.80	–		Delhi, India	dung	JX976120	KC018423
<i>Mortierella amoeboides</i>	CBS889.72, FSU9790	<i>M. alpina</i>	Type of <i>Mortierella amoeboides</i>	Teutoburger Wald, Beller Holz, Germany		JX976073	HQ667422.1
<i>Mortierella angusta</i>	CBS293.61, FSU9791	<i>M. angusta</i>	Neotype of <i>Mortierella polycephala</i> var. <i>angusta</i>	Chesh., Delamere Forest, England	podzol soil, pH up to 2.8	JX976061	HQ667358.1
<i>Mortierella antarctica</i>	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	–
<i>Mortierella armillariicola</i>	CBS609.70, FSU9792	–	Type of <i>Mortierella antarctica</i>	near Hallett Station, Antarctica	soil, rock crevice near glacier	JX975907	HQ667503.1
	CBS105.78	–		Puuten, Schovenhorst, Netherlands		JX976100	KC018432
	CBS914.73, FSU9793	–	Type of <i>Mortierella armillariicola</i>	Baarn, Groeneveld, Netherlands	attacked by <i>Dipodascus armillariae</i>	JX975924	HQ667446.1
<i>Mortierella bainieri</i>	CBS220.35	–		former West-Germany		JX975901	KC018324
	CBS272.71	<i>M. kuhlimanii</i>		South Carolina	soil under <i>Pinus taeda</i>	JX975964	JX976155
	CBS273.71	<i>M. kuhlimanii</i>		South Carolina	soil under <i>Pinus taeda</i>	JX975920	KC018355
	CBS442.68	–		Georgia	soil from pine forest	JX975864	KC018331
	CBS508.81	–		Getzback near Eupen, Belgium		JX975844	KC018393
	CBS552.80	–		Eifel, Hundsbachtal near Gerolstein, Germany		JX975850	JX976174
<i>Mortierella basipanvispora</i>	CBS517.72	–		Valdivia, Cordillera Pelada, Chile	soil, under <i>Fitzroya cupressoides</i>	JX976048	JX976167

<i>Mortierella beljakovae</i>	CBS102878	–	Toronto High Park, Ontario	infrabuccal pellet of <i>Camponotus pennsylvanicus</i> (carpenter ant) on <i>Pinus</i>	JX976090	KC018350
	CBS109594	–	Toronto, High Park, Ontario	infrabuccal pellet of <i>Camponotus pennsylvanicus</i> , in mature <i>Pinus</i> tree	JX975848	KC018449
	CBS109595	–	Zweifaller Wald near Aachen, Germany	infrabuccal pellet of <i>Formica rufa</i>	JX976129	KC018358
	CBS109596	–	St. Andrews, Annesley House, New Brunswick	infrabuccal pellet of <i>Camponotus pennsylvanicus</i> , in <i>Pinus</i> tree	JX975971	JX976170
	CBS109597	–	Scarborough, Ontario	infrabuccal pellet of <i>Camponotus pennsylvanicus</i> , in mature <i>Pinus</i> tree	JX975918	KC018433
	CBS109655	–	Bayrischer Wald, Pfahl bei Viechtach, Germany	infrabuccal pellet of <i>Camponotus herculeanus</i> , in <i>Picea abies</i>	JX975869	JX976171
	CBS109658	–	Zweifaller Wald near Aachen, Germany	infrabuccal pellet of <i>Formica rufa</i>	JX976051	KC018376
	CBS109659	–	Utrecht, Lage Vuursche, Netherlands	infrabuccal pellet of <i>Formica rufa</i>	JX975998	KC018340
	CBS123.72, FSU9794	<i>M. beljakovae</i>	Rovenski region, Sarna, Ukraine	soil, coniferous forest	JX976126	HQ667428.1
	CBS267.71	–	North Carolina	seedling, <i>Pinus taeda</i>	JX976072	KC018346
	CBS268.71	–	North Carolina	seedling, <i>Pinus taeda</i>	JX976043	KC018323
	CBS274.71	–	South Carolina	root, <i>Pinus taeda</i>	JX976011	KC018388
	CBS275.71	–	South Carolina	root, <i>Pinus taeda</i>	JX975913	KC018401
	CBS276.71	–	South Carolina	root, <i>Pinus taeda</i>	JX975937	KC018442
	CBS806.68	–	North Carolina	bark of root, <i>Pinus</i>	JX975987	KC018397
	CBS370.95, FSU9795	<i>M. biramosa</i>	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	acidic loamy soil	JX976064	KC018419
	CBS145.69	–	Italy	rootlet	JX975857	KC018377
	FSU9675	<i>M. bisporalis</i>	–	–	JX975953	JX976176
	CBS110638	<i>M. camargensis</i>	Soest, Smickel, Netherlands	thatch of roof	JX976024	–
	CBS221.58, FSU9796	<i>M. camargensis</i>	Camargue, Bois des Rêges, France	sandy soil	JX975949	HQ667408.1
	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
	CBS287.96	–	Amakubo, Tsukuba, Ibaraki, Japan	soil under <i>Quercus mirsinifolia</i> forest	JX976013	KC018427
	CBS289.96	–	Nanamagari, Yokohama, Kanagawa, Japan	soil under <i>Castanopsis sieboldii</i> forest	JX975898	JX976161
	CBS290.96	<i>M. selenospora</i>	Shitoko, Yakushima Island, Kagoshima, Japan	soil under <i>Miscanthus sinensis</i>	JX976075	KC018373
	CBS292.96	–	Kuang-Miau Co., 16 km E of Tainan, Taiwan	soil under <i>Ficus microcarpa</i> forest	JX975951	JX976153
	CBS554.73	<i>M. selenospora</i>	–	soil from bamboo grove	JX975912	KC018381
	CBS120.34, FSU9799	–	Syntype of <i>Azygogygum chlamydosporum</i>	infected by <i>Rhizoctonia solani</i>	JX975942	HQ667430.1
	CBS529.75	–	Netherlands	soil	JX975927	–
	CBS790.85	–	Gran Canaria, Spain	soil, under <i>Apollonias canariensis</i>	JX976012	JX976159
	CBS357.76, FSU9801	<i>M. clonocystis</i>	Nagano, Sanada, Sugadaira M.R.C., Japan	decaying tree bark	JX975899	HQ667395.1
	CBS879.97, FSU9802	–	–	–	JX976017	HQ667360.1
	CBS456.71, FSU9803	<i>M. cystojenkini</i>	Wageningen, Netherlands	agricultural soil	JX976030	HQ667504.1
	CBS660.82	–	Bakkeveen, Netherlands	<i>Pinus</i> forest	JX975868	KC018325
	CBS873.68	–	Kiel-Kitzeberg, Germany	wheat field soil	–	JX976173
	CBS221.35, FSU9804	<i>M. dichotoma</i>	former West-Germany	dung of mouse	JX975842	HQ667393.1
	CBS574.75	–	near Wageningen, Netherlands	soil	JX976060	KC018370
	CBS575.75, FSU9805	<i>M. echinosphaera</i>	Aalsmeer, Netherlands	soil	JX976015	HQ667431.1
	CBS282.71	–	Iceland	soil	JX975948	–
	CBS110517	–	Atli 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	<i>M. elongata</i>	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	<i>M. elongata</i>		–	agricultural soil	JX975976	KC018281
	FSU822, CBS125.71	<i>M. elongata</i>		Wageningen, Netherlands		JX975978	KC018282
	FSU9721	<i>M. elongata</i>	Type of <i>Mortierella elongatula</i>	Münchenroda, Germany		JX975894	KC018284
<i>Mortierella elongatula</i>	CBS488.70, FSU9808	–		former West-Germany	municipal waste	JX975967	HQ667425.1
	CBS661.70	–		Braunschweig, Germany	municipal waste	JX976069	KC018431
<i>Mortierella epicladia</i>	CBS246.75	–	Type of <i>Mortierella epicladia</i>	Suriname	soil, under <i>Elaeis guineensis</i>	JX975890	KC018361
	CBS355.76, FSU9809	<i>M. epicladia</i>		Gran Canaria, Spain	soil, under <i>Apollonias canariensis</i>	JX976130	HQ667396.1
	CBS356.76	–		Gran Canaria, Spain	soil, under <i>Apollonias canariensis</i>	JX975972	–
	CBS555.89	–		Pará, 200 km SE from Belém, Capitão Poço, Brasil	rain forest soil	JX975991	JX976150
<i>Mortierella epigama</i>	CBS161.76	<i>M. epigama</i>		Exeter, Hatherly Laboratories, England	compost heap	JX976109	JX976158
	CBS489.70, FSU9810	<i>M. epigama</i>	Type of <i>Mortierella epigama</i>	former West-Germany	municipal waste	JX976057	HQ667367.1
	CBS881.97	–		Kagoshima, Kamei, Tokunoshima-Island, Japan	old dung of cow	JX976053	KC018445
<i>Mortierella exigua</i>	CBS358.76	–		Gran Canaria, Spain	soil, under <i>Apollonias canariensis</i>	JX976113	KC018439
	CBS510.63	–		Kiel-Kitzeberg	agricultural soil	JX975863	JX976134
	CBS655.68, FSU9811	<i>M. exigua</i>	Type of <i>Mortierella sterilis</i>	Allahabad, India	farm soil	JX976047	HQ667406.1
	CBS865.68	–		Kiel-Kitzeberg, Germany	wheat field soil	JX976070	–
<i>Mortierella fatischederae</i>	CBS388.71	–		Gran Canaria	soil, under <i>Pinus canariensis</i>	JX976003	JX976136
<i>Mortierella fimbriocystis</i>	CBS943.70	–	Type of <i>Mortierella fimbriocystis</i>	South Patagonia, Puerto Edwards near Beagle Canal, Argentina	centre of moss cushion, in very wet bog	GU559986.1	JX976172
<i>Mortierella formicicola</i>	CBS109589	–		Brampton, Ontario	infrabuccal pellet of <i>Camponotus pennsylvanicus</i> , in house (window sill)	JX975933	JX976140
<i>Mortierella gamsii</i>	CBS110630	–		Boekrijk, Belgium	soil with Porcellio	JX976106	KC018410
	CBS253.36, FSU9813	<i>M. gamsii</i>	Syntype of <i>Mortierella spinosa</i>	former West-Germany	forest soil	JX975968	HQ667415.1
	CBS314.52, FSU9814	<i>M. cf. gamsii</i>	Syntype of <i>Mortierella spinosa</i>	former West-Germany	forest soil	JX975892	HQ667384.1
	CBS551.73, FSU824	<i>M. gamsii</i>		North Carolina	pasture soil	JX976079	JX976177
	CBS552.73, FSU825	<i>M. gamsii</i>		Alleghany County, North Carolina	pasture soil	JX975984	KC018285
	CBS749.68, FSU9812	<i>M. gamsii</i>	Type of <i>Mortierella gamsii</i>	Baarn, Maarschalkerbos, Netherlands	soil	JX976118	HQ667416.1
	FSU2057	<i>M. gamsii</i>		–		JX976118	KC018287
<i>Mortierella gemmifera</i>	CBS124.72	–		Meerdinkbos near Winterswijk, Netherlands	soil, humus layer	JX975909	KC018390
	CBS134.45, FSU9815	<i>M. gemmifera</i>	Type of <i>Mortierella gemmifera</i>	near Nottingham, England	soil from pine forest	JX975931	HQ667371.1
	CBS383.85	–		Spanderswoud near Buessum, Netherlands	soil, in pine forest	JX976121	JX976157
<i>Mortierella globalpina</i>	CBS661.82	–		Bakkeveen, Netherlands	<i>Endogone lactiflua</i> , <i>Pinus</i> forest	JX975989	KC018360
	CBS226.78	–		Katwijk, Netherlands	sand dune soil	JX976006	JX976160
<i>Mortierella globulifera</i>	CBS718.88	–		Japan		JX975925	–
	CBS108.68	–		Schweden	agricultural soil	JX975847	KC018332
	CBS746.68	–		Netherlands	decaying needle	JX976026	KC018371
	CBS857.70, FSU826	–		England	decaying root	JX975910	HQ667369
	CBS5858.70, FSU9817	–		England	decaying root	JX975915	HQ667368.1
	CBS867.68	<i>M. globulifera</i>	Neotype of <i>Mortierella globulifera</i>	Tirol, Oberurg, Austria	alpine raw humus soil	JX976107	JX976165
<i>Mortierella histoplasmatoides</i>	CBS321.78, FSU9819	–	Type of <i>Mortierella histoplasmatoides</i>	Louisiana	dung	HQ630309.1	HQ667386.1
<i>Mortierella horticola</i>	CBS305.52, FSU9820	<i>M. horticola</i>	Syntype of <i>Mortierella horticola</i>	former West-Germany		JX975874	HQ667399.1
	CBS869.68	–		Kiel-Kitzeberg	wheat field soil	JX976058	JX976138
	CBS254.76	–		Wageningen, Netherlands	agricultural soil	JX976021	JX976166
	CBS180.72	–		Piedmont, North Carolina	forest soil	JX976125	KC018436
<i>Mortierella humilis</i>	CBS181.72	–		Piedmont, North Carolina	soil	JX975887	KC018405
	CBS222.35, FSU9821	–	Syntype of <i>Mortierella humilis</i>	Mexico	soil from <i>Pinus</i> forest	HQ630325.1	HQ667401.1
	CBS363.95	–		Shennongjia, Hubei, China	forest soil	JX976097	KC018443

Table 2 (cont.)

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

Table 2 (cont.)

Original name	Strain numbers	Microscopic identification	Type status	Locality	Substrate	Accession no. ITS	Accession no. LSU
<i>Mortierella wolffii</i>	CBS280.71	<i>M. verticillata</i>	Syntype of <i>Mortierella marburgensis</i>	South Carolina	root	JX976066	KC018404
	CBS315.52, FSU9856	<i>M. verticillata</i>		former West-Germany	forest soil	JX975943	–
	CBS346.66, FSU9852	<i>M. verticillata</i>	Type of <i>Haplosporangium attenuatis-simum</i>	Alaska	tundra soil	JX975855	HQ667397.1
	CBS374.95, FSU9855	<i>M. cf. wolffii</i>		Wuyi, Fujian, China	forest soil	JX976077	HQ667398.1
	CBS614.70, FSU9860	<i>M. wolffii</i>		Matamata, New Zealand	decayed hay	JX975975	HQ667420.1
<i>Mortierella zonata</i>	CBS209.69, FSU9858	<i>M. zonata</i>	Type of <i>Mortierella zonata</i>	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			Limburg, Horst, Netherlands	compost for mushrooms	JX975904	HQ667382.1
	CBS228.35, FSU9863			former West-Germany		JX975983	HQ667433.1
	CBS615.70			Braunschweig-Völknerode, Germany	soil	JX975958	KC018434
	CBS617.76			Cordillera, Central Parque Nacional del Puracé, 3900 m alt.	páramo soil, open vegetation with extensive pasture	JX976028	JX976141
<i>Mortierella zychae</i>	CBS863.68			Ringwood, New Forest, UK	forest soil	JX975888	KC018335
	CBS102879			Toronto High Park, Ontario	pellet of <i>Camponotus pennsylvanicus</i> (carpenter ant)	JX976074	
<i>Umbelopsis isabellina</i>	CBS109599	<i>M. zychae</i>	Type of <i>Mortierella zychae</i>	El Yunque, Rio Blanco Trail, Puerto Rico	infrabuccal pellet of ant	JX975882	
	CBS143.91	<i>M. zychae</i>		former West-Germany		JX976091	
	CBS316.52, FSU9864	<i>M. zychae</i>		Allgäu, Germany	decaying wood	JX975979	HQ667407.1
	CBS531.81	<i>M. zychae</i>		former West-Germany	mushroom casing soil	JX975962	KC018421
	FSU719			–		JX976128	KC018319
	NRRL 1757, 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. epiclada*, *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 sporangia. While *M. minutissima* develops few-spored sporangia, *M. horticola* produces single-spored sporangia. 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. epiclada* 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. epiclada* 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).

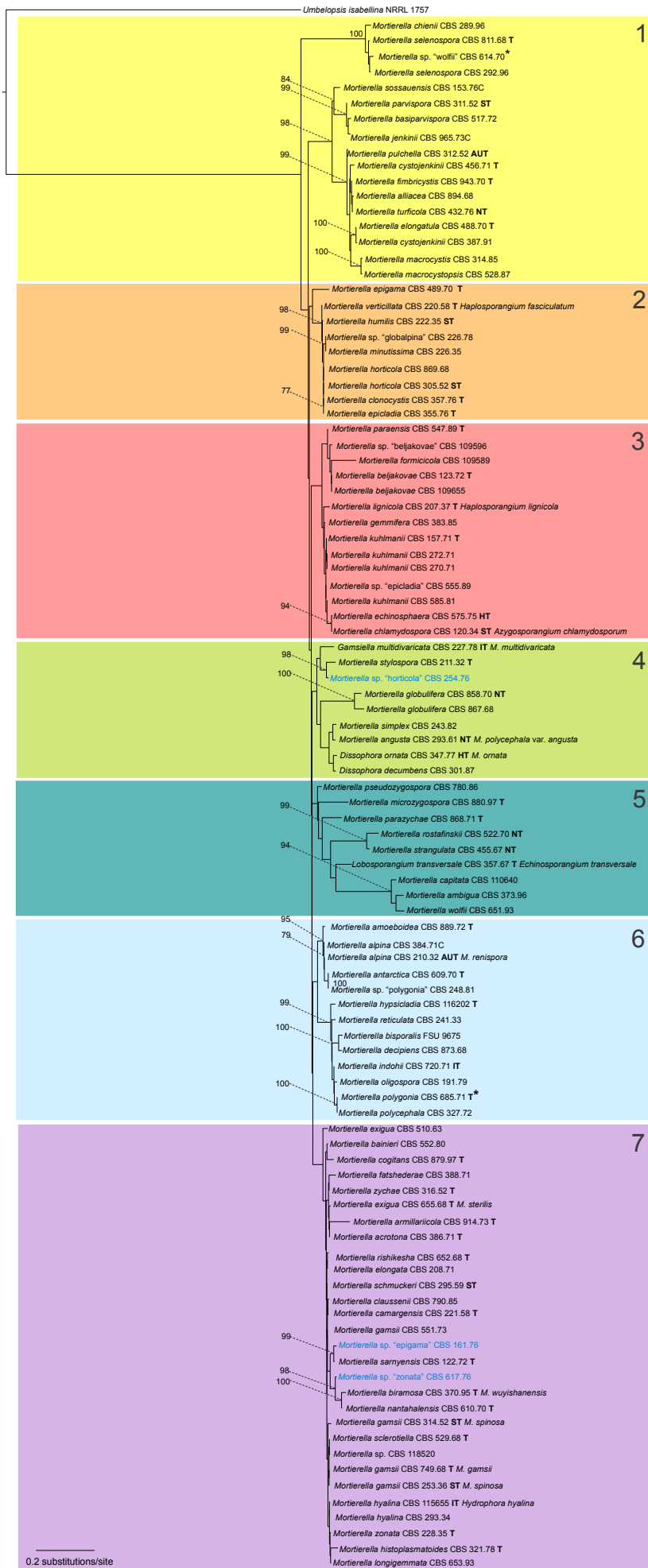


Fig. 3 Maximum Likelihood analysis based on 781 aligned nucleotides of the D1/D2 domain of the large subunit (LSU, 28S) rDNA from 101 taxa (100 ingroup taxa of the *Mortierellales* and 1 outgroup taxon *Umbelopsis* as member of the *Mucorales*, Meyer & Gams 2003). The phylogram based on a MAFFT-Alignment (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.

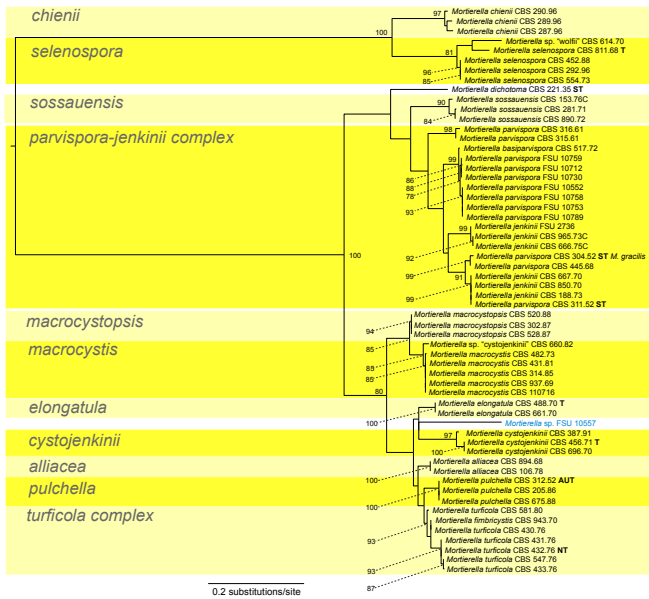


Fig. 4 Maximum Likelihood analysis based on the ITS1-5.8S-ITS2 dataset for clade 1. The phylogram was constructed from a MAFFT-Alignment of 816 aligned nucleotides of 58 taxa. Node support above 75 % is given. The phylogram is midpoint rooted.

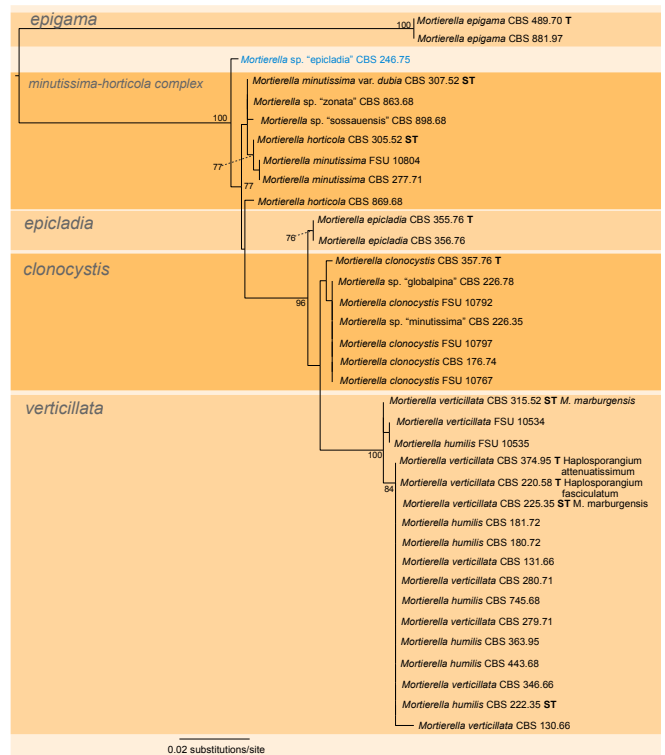


Fig. 5 Maximum Likelihood analysis based on the ITS1-5.8S-ITS2 dataset for clade 2. The phylogram was constructed from a MAFFT-Alignment of 636 aligned nucleotides of 36 taxa. Node support above 75 % is given. The phylogram is midpoint rooted.

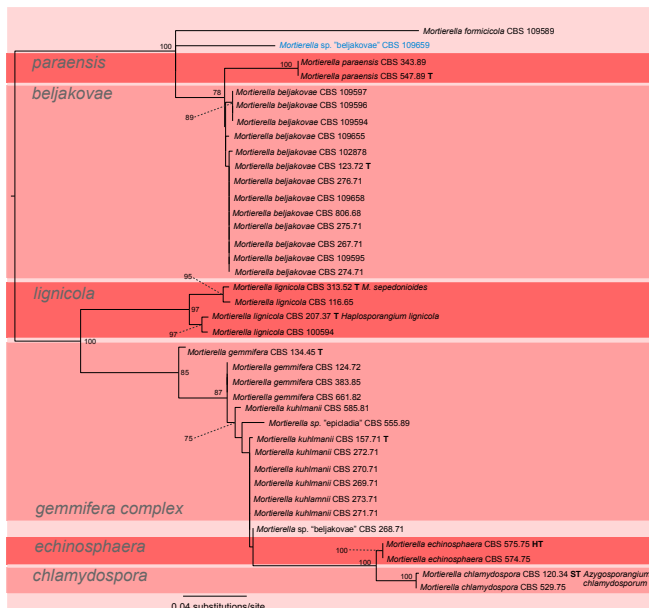


Fig. 6 Maximum Likelihood analysis based on the ITS1-5.8S-ITS2 dataset for clade 3. The phylogram was constructed from a MAFFT-Alignment of 701 aligned nucleotides of 38 taxa. Node support above 75 % is given. The phylogram is midpoint rooted.

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.

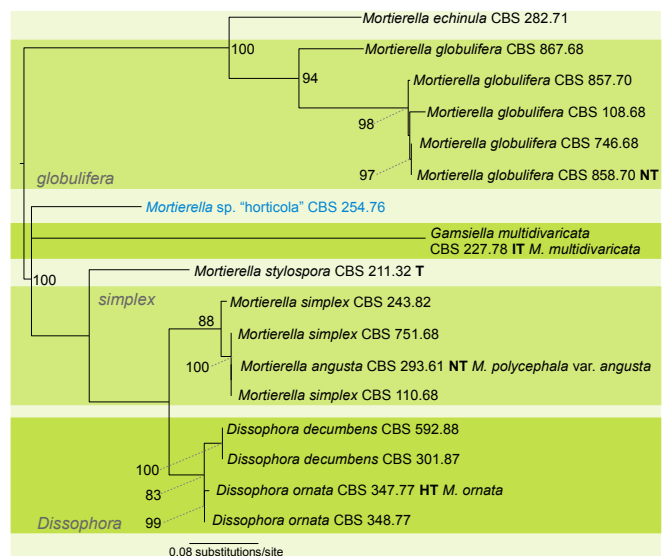


Fig. 7 Maximum Likelihood analysis based on the ITS1-5.8S-ITS2 dataset for clade 4. The phylogram was constructed from a MAFFT-Alignment of 710 aligned nucleotides of 17 taxa. Node support above 75 % is given. The phylogram is midpoint rooted.

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 be 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.

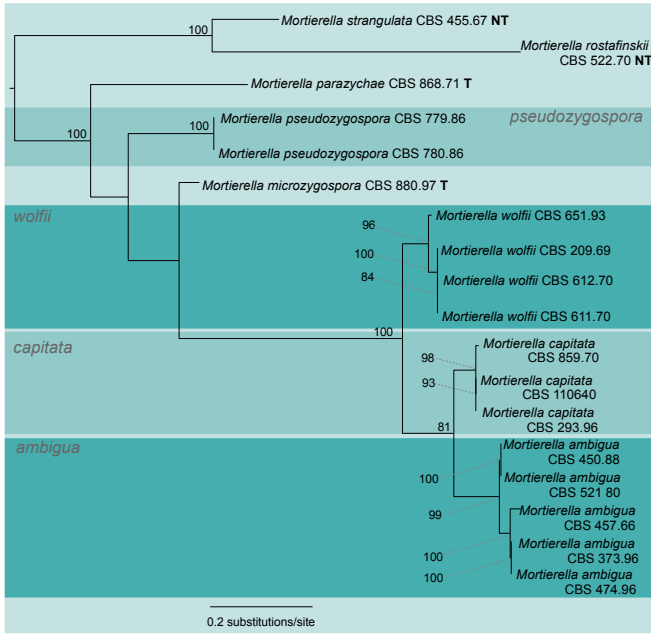


Fig. 8 Maximum Likelihood analysis based on the ITS1-5.8S-ITS2 dataset for clade 5. The phylogram was constructed from a MAFFT-Alignment of 761 aligned nucleotides of 18 taxa. Node support above 75 % is given. The phylogram is midpoint rooted.

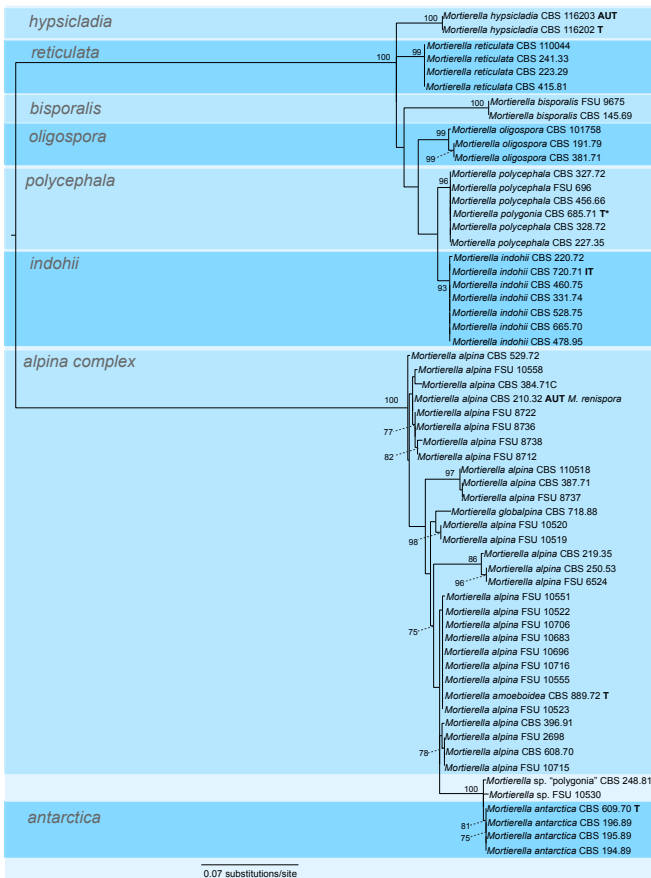


Fig. 9 Maximum Likelihood analysis based on the ITS1-5.8S-ITS2 dataset for clade 6. The phylogram was constructed from a MAFFT-Alignment of 703 aligned nucleotides of 60 taxa. Node support above 75 % is given. The phylogram is midpoint rooted.

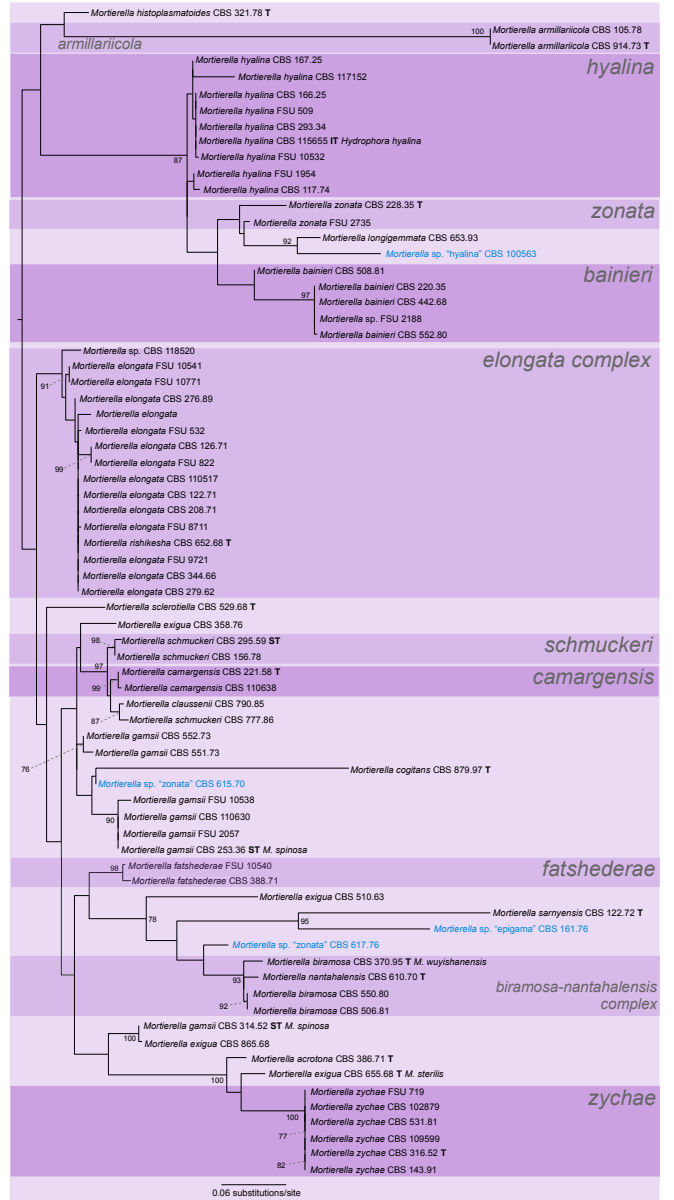


Fig. 10 Maximum Likelihood analysis based on the ITS1-5.8S-ITS2 dataset for clade 7. The phylogram was constructed from a MAFFT-Alignment of 688 aligned nucleotides of 73 taxa. Node support above 75 % is given. The phylogram is midpoint rooted.

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

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

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. rishiksha*, *M. sarnyensis*, *M. schmuckeri*, *M. sclerotiella*, *M. zonata* and *M. zychnae* was extended by *M. bainieri*, *M. clausenii*, *M. fatshederiae* and *M. longigemmata*. *Mortierella armillariicola*, *M. bainieri*, *M. fatshederiae*, *M. hyalina* and *M. zychnae* 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. clausenii* 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. basi-parvispora*, *M. camargensis*, *M. fimbricystis*, *M. gamsii*, *M. gemmifera*, *M. globalpina*, *M. horticola*, *M. humilis*, *M. jenkinsii*, *M. kuhlmanni*, *M. minutissima*, *M. parvispora*, *M. rishiksha*, *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. parazychnae*, *M. rishiksha*, *M. rostafinskii*, *M. sclerotiella* and *M. strangulata*.

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