doi:10.5598/imafungus.2017.08.02.03

IMA FUNGUS · 8(2): 245–257 (2017)

Multigene phylogeny of *Endogonales*, an early diverging lineage of fungi associated with plants

Alessandro Desirò[1], William R. Rimington[2], Alison Jacob[2], Natalie Vande Pol[1], Matthew E. Smith[3], James M. Trappe[4], Martin I. Bidartondo[2,5], and Gregory Bonito[1]

[1]Department of Plant Soil and Microbial Sciences, Michigan State University, East Lansing, MI 48824, USA; corresponding author e-mail: adesiro@msu.edu
[2]Department of Life Sciences, Imperial College London, London SW7 2AZ, UK
[3]Department of Plant Pathology, University of Florida, Gainesville, FL 32611, USA
[4]Department of Forest Ecosystems and Society, Oregon State University, Corvallis, OR 97331, USA
[5]Jodrell Laboratory, Royal Botanic Gardens, Kew, Richmond, Surrey TW9 3DS, UK

Abstract: *Endogonales* is a lineage of early diverging fungi within *Mucoromycota*. Many species in this order produce small sporophores ("sporocarps") containing a large number of zygospores, and many species form symbioses with plants. However, due to limited collections, subtle morphological differentiation, difficulties in growing these organisms *in vitro*, and idiosyncrasies in their rDNA that make PCR amplification difficult, the systematics and character evolution of these fungi have been challenging to resolve. To overcome these challenges we generated a multigene phylogeny of *Endogonales* using sporophores collected over the past three decades from four continents. Our results show that *Endogonales* harbour significant undescribed diversity and form two deeply divergent and well-supported phylogenetic clades, which we delimit as the families *Endogonaceae* and *Densosporaceae* fam. nov. The family *Densosporaceae* consists of the genus *Densospora, Sphaerocreas pubescens*, and many diverse lineages known only from environmental DNA sequences of plant-endosymbiotic fungi. Within *Endogonaceae* there are two clades. One corresponds to *Endogone* and includes the type species, *E. pisiformis*. Species of *Endogone* are characterized by above- and below-ground sporophores, a hollow and infolded sporophore form, a loose zygosporangial hyphal mantle, homogeneous gametangia, and an enigmatic trophic mode with no evidence of ectomycorrhizal association for most species. For the other clade we introduce a new generic name, *Jimgerdemannia* gen. nov. Members of that genus (*J. flammicorona* and *J. lactiflua* species complexes, and an undescribed species) are characterized by hypogeous sporophores with a solid gleba, a well-developed zygosporangial hyphal mantle, heterogeneous gametangia, and an ectomycorrhizal trophic mode. Future studies on *Densosporaceae* and *Endogonaceae* will be important for understanding fungal innovations including evolution of macroscopic sporophores and symbioses with plants.

Key words:
Densosporaceae
Endogone
endophytes
Jimgerdemannia
multigene phylogeny

Article info: Submitted: 24 June 2017; Accepted: 27 September 2017; Published: 3 October 2017.

INTRODUCTION

Endogonales is an order of early diverging fungi that belong to the subphylum *Mucoromycotina* and is represented by the single family *Endogonaceae*. This family currently includes five genera: *Endogone* (Link 1809; with *E. pisiformis* as the type of the genus), *Peridiospora* (Wu & Lin 1997), *Sclerogone* (Warcup 1990*)*, *Youngiomyces* (Yao *et al.* 1995) and the fossil genus *Jimwhitea* (Krings *et al.* 2012) reported from Middle Triassic formations. These fungi are rarely collected and phylogenetic affiliations of several taxa still need to be tested with molecular data. Some species of *Endogone* participate in ecto- or endomycorrhizal associations with diverse vascular and non-vascular plants (Warcup 1990, Walker 1985, Field *et al.* 2015a, Yamamoto *et al*. 2017a). Similar to the obligately biotrophic arbuscular mycorrhizal fungi in *Glomeromycotina* (Spatafora *et al.* 2016), many lineages of *Endogonales* cannot be maintained *in vitro*. However, a few have been successfully isolated and maintained axenically in the laboratory with extensive efforts (Berch & Fortin 1982, Berch & Castellano 1986, Field *et al.* 2015b; Yamamoto *et al.* 2017b). Recent studies indicate that ectomycorrhizal symbioses and endosymbioses with several lineages of land plants have emerged independently more than once (Tedersoo & Smith 2013, Field *et al.* 2015a, Orchard *et al.* 2017a, Yamamoto *et al.* 2017a). Recently, Tedersoo & Smith (2017) considered four ectomycorrhizal lineages in *Mucoromycotina*: the "/densospora lineage" (*Endogone* group C *sensu* Yamamoto *et al.* 2017a) comprising members of the genus *Densospora* (McGee 1996) and uncultured ectomycorrhizal fungi associated with *Eucalyptus* and *Nothofagus* (Tedersoo *et al.* 2008); the "/endogone1 lineage" (*Endogone* group B *sensu* Yamamoto *et al.* 2015) which includes members of the *Endogone flammicorona* (Trappe & Gerdemann 1972) and *E. lactiflua* (Berkley & Broome 1846) complex; the "/endogone2 lineage" with *Endogone tuberculosa* (Lloyd 1918), *Youngiomyces aggregatus* (Yao *et al.* 1995) and, potentially, *Sclerogone eucalypti* (Warcup 1990). *Endogone tuberculosa* and *S. eucalyptii* were reported to grow axenically (Warcup 1990) but no sequence data are available for these taxa so there is no information about their phylogenetic position. The "/endogone3 lineage" is based on environmental DNA sequences putatively related to the saprotrophic *E. pisiformis* and generated from *Quercus* ectomycorrhizas (Yamamoto *et al.* 2017b). The ectomycorrhizal fungal lineages "/endogone2" and "/endogone3" were both within *Endogone* group A (*sensu* Yamamoto *et al.* 2015).

It has recently been hypothesized that mutualistic *Mucoromycotina* fungi related to *Endogone* played a crucial role during the colonization of terrestrial environments by early land plants (Bidartondo *et al.* 2011, Desirò *et al.* 2013, Field *et al.* 2015a). These studies highlight the ecology of *Endogone*-like *Mucoromycotina* fungi as plant-fungal symbionts, and challenge the paradigm of *Glomeromycotina* as the ancestral fungal mutualists of land plants (Field *et al.* 2015a). Similar to *Glomeromycotina*, *Endogone* can harbour Mollicutes-related endobacteria (MRE) in their mycelia and spores (Desirò *et al.* 2015). Even though the biology of these bacteria is still poorly understood, MRE might have played a role in the evolution of symbiotic interactions between plants and fungi (Bonfante & Desirò 2017). Given that *Endogonales* represent an early origin of a symbiotic nutrition mode by fungi, independent from arbuscular mycorrhizal *Glomeromycotina* and ectomycorrhizal *Dikarya*, there is now renewed interest in the diversity and evolutionary relationships of this early diverging group of fungi (Bidartondo *et al*. 2011, Desirò *et al*. 2013, Field *et al*. 2015b, Orchard *et al*. 2017b).

The genus *Endogone* comprises species that produce sporophores ("sporocarps") containing a large number of zygospores. *Endogone* is among the earliest lineages in the fungal kingdom to produce macroscopic sporophores. The sporophores are the result of sexual reproduction by compatible apposed gametangia that lead to the production of zygospores. Sporophores of *Endogone* are sequestrate or enclosed and often hypogeous, although some epigeous species may produce sporophores within or upon heavily decayed wood or twigs, decaying polypore basidiomes, leaf litter, or amongst mosses and liverworts (Gerdemann & Trappe 1974, Tandy *et al.* 1975, Yamamoto *et al.* 2015). Given their range in diversity, morphology, and growth habits, the taxonomy and systematics of *Endogone* and related lineages have been in a state of flux over the past 200 years (Stürmer 2012).

As currently circumscribed, while *Endogonales* contains four extant genera (see above), there is poor resolution of the phylogenetic relationships of the taxa within the order, and still uncertainty whether *Sphaerocreas pubescens* (Saccardo 1882), members of *Densospora* (McGee 1996), and numerous *Endogone*-related *Mucoromycotina* associated with plants belong to *Endogonales*. Even though they are distributed across temperate and tropical habitats in the Northern and Southern Hemispheres, sporophores of most of these fungi are rarely collected and molecular data are limited or not available. Further, there are idiosyncratic challenges when working with *Endogonales* rDNA, because ITS rDNA does not amplify or sequence well, or is degenerate (Tedersoo *et al.* 2016). Consequently, *Endogonales* are often conspicuously underrepresented in environmental molecular surveys and databases (e.g. GenBank) that rely on rDNA markers (Větrovský *et al.* 2015). Moreover, when detected, these fungi are difficult to place within a phylogenetic and taxonomic framework.

To address these limitations, we generated a multigene phylogeny for *Endogonales* based on rDNA (18S; 28S) and protein coding genes (EF1-α; RPB2) from a global sampling of *Endogone* sporophores, and integrated available *Endogonales* and environmental DNA sequences into this phylogeny. We also employed the RPB2 gene for the first time as a marker to enhance the phylogenetic resolution of *Endogonales*. Our results provide a phylogenetic placement of two *Endogone* species that were previously unresolved and define two families within *Endogonales*: *Endogonaceae* and *Densosporaceae* fam. nov. Within *Endogonaceae,* we delimit two deeply divergent monophyletic lineages that differ in morphology, sporing habit, and potentially also ecology. We introduce *Jimgerdemannia* gen. nov. to accommodate one of these two lineages, and also synonymize *Youngiomyces* with *Endogone s. str*.

METHODS

Collections sampled

Dried fungarium specimens of *Endogone flammicorona*, *E. incrassata* (Thaxter 1922), *Endogone lactiflua*, *E. oregonensis* (Gerdmann & Trappe 1974), *E. pisiformis* (Link 1908), *E. tuberculosa*, and unidentified *Endogone* were obtained from private collections or the following institutions: University of Florida Herbarium (FLAS), Michigan State University Herbarium (MSC), National Herbarium of Victoria (MEL), Oregon State University Herbarium (OSC), and Western Australian Herbarium (PERTH). In total, 45 collections of *Endogone* from Australia, Italy, Mexico, the United Kingdom, and USA were analyzed (Table 1).

Molecular analyses

A small fragment of gleba tissue from each sporophore was sampled and genomic DNA extracted with a CTAB-based method (Doyle 1991). All PCR reactions were carried out with DreamTaq Green PCR Master Mix (Thermo Fisher Scientific, Waltham, MA). A fragment of the 18S rRNA gene was amplified with primers EndAD1f (Desirò *et al.* 2013) and EF3 (Smit *et al.* 1999). For samples that failed to amplify, PCR products were diluted 1:10 in sterile water and used as template for a semi-nested PCR with the reverse primer EndAD2r (Desirò *et al.* 2013). The PCR conditions followed those of Desirò *et al.* (2013). The ITS2 region and a partial fragment of the 28S rRNA gene were amplified with a semi-nested PCR approach. The first PCR was carried out with the new primers EndAD7f (5'-CTGCTAAATAGYTAKGCCAAC-3', designed on the 18S rRNA gene) and EndAD28Sr (5'- CATTAMGY-CAGCGACCYAAG-3', designed on the 28S rRNA gene). The

Table 1. List of the *Endogonaceae* sporophores analyzed in this study and available relative information about voucher as herbarium and/or collector number (when both are available, collector numbers are in parentheses), site and date of collection.

Species	Voucher/Collector No	Collection Site	Collection Date
Endogone incrassata	MEXU 26467	Volcano Nevado de Colima National Park, Jalisco, Mexico	25 Sep. 2009
Endogone incrassata	T32417	Cofre de Perote, Veracruz, Mexico	17 Sep. 2007
Endogone incrassata	T32492	San José Teacalco, Tlaxcala, Mexico	21 Sep. 2007
Endogone oregonensis	OSC 130614	Polk, Oregon, USA	23 Feb. 2008
Endogone oregonensis	T36235	Benton County, Oregon, USA	14 March 2013
Endogone oregonensis	AD153	Monmouth, Oregon, USA	29 Dec. 2015
Endogone pisiformis	AD152	Corvallis, Oregon, USA	11 March 2017
Endogone pisiformis	FLAS F-59194 (MES1451)	Bartlett Experimental Forest, Carroll County, New Hampshire, USA	11 Aug. 2015
Endogone pisiformis	OSC 80931 (T28028)	Benton, Oregon, USA	7 Feb. 2002
Endogone pisiformis	OSC 112172 (T31477)	Washington, USA	24 April 2006
Endogone pisiformis	OSC 149839 (T37049)	White Mountain National Forest, Carroll County, New Hampshire, USA	17 Aug. 2015
Endogone pisiformis	T37093	Lane County, Oregon, USA	21 May 2013
Endogone sp.	MEL 2024690	Loftia Recreation Park, Adelaide Hills, Australia	26 Aug. 1984
Endogone sp.	FLAS F-59071 (MES866)	Ordway-Swisher Reserve, Melrose, Florida, USA	23 Feb. 2015
Endogone sp.	PERTH 7567251	Atherton, Queensland, Australia	7 May 1991
Endogone sp.	PERTH 7591853	Cape York, Australia	-
Endogone sp.	PERTH 7603037	Bluewater Park, Queensland, Australia	13 April 1989
Endogone sp.	PERTH 7648049	Dwellingup, Australia	10 May 2002
Endogone sp.	PERTH 7648847	Dwellingup, Australia	25 June 2002
Endogone sp.	PERTH 7672527	Mount Windsor Tableland, Queensland, Australia	2 Feb. 1992
Endogone sp.	PERTH 8092931	Leeuwin-Naturaliste National Park, Australia	17 May 2007
Endogone sp.	PERTH 8127840	Karakamia Sanctuary, Australia	4 Oct. 2006
Endogone sp.	PERTH 8473986	Boorabbin National Park, Australia	20 Aug. 2009
Endogone sp.	T26631	Bournda National Park, Australia	22 Nov. 2000
Endogone tuberculosa	OSC 146000 (T34145)	Australian Capital Territory, Australia	14 May 2010
Jimgerdemannia flammicorona	AD002	Veglio, Piemonte, Italy	7 Sep. 2013
Jimgerdemannia flammicorona	MSC 0242545 (AD239)	Lake Lansing Park North, Haslett, Michigan, USA	7 Oct. 2016
Jimgerdemannia flammicorona	MSC 0242546 (AD244)	Lake Lansing Park North, Haslett, Michigan, USA	7 Oct. 2016
Jimgerdemannia flammicorona	AD245	Lake Lansing Park North, Haslett, Michigan, USA	7 Oct. 2016
Jimgerdemannia flammicorona	GB716	Lake Lansing Park North, Haslett, Michigan, USA	13 Sep. 2015
Jimgerdemannia flammicorona	MSC 0242548 (GB737)	Lake Lansing Park North, Haslett, Michigan, USA	17 Sep. 2015
Jimgerdemannia flammicorona	RH932	Ledges State Park, Iowa, USA	27 June 2009
Jimgerdemannia flammicorona	T33849	Bosque la Primavera, Jalisco, Mexico	2 Oct. 2009
Jimgerdemannia flammicorona	T33851	Bosque la Primavera, Jalisco, Mexico	2 Oct. 2009
Jimgerdemannia lactiflua	AD001	Veglio, Piemonte, Italy	7 Sep. 2013
Jimgerdemannia lactiflua	MSC 0242547 (AD251)	Mason, Michigan, USA	13 Oct. 2016
Jimgerdemannia lactiflua	AD256	Mason, Michigan, USA	13 Oct. 2016
Jimgerdemannia lactiflua	AM2190	Cavola, Emilia Romagna, Italy	22 July 2000
Jimgerdemannia lactiflua	CH9142	Derbyshire, United Kingdom	12 Nov. 2012
Jimgerdemannia lactiflua	T32409	Cofre de Perote, Veracruz, Mexico	17 Sep. 2007
Jimgerdemannia lactiflua	T32490	San José Teacalco, Tlaxcala, Mexico	21 Sep. 2007
Jimgerdemannia lactiflua	T32544	Huamantla, Tlaxcala, Mexico	23 Sep. 2007
Jimgerdemannia lactiflua	T32674	Miquihuana, Tamaulipas, Mexico	2 Aug. 2008
Jimgerdemannia sp.	T34745-A	Main Ranges National Park, Queensland, Australia	3 June 2010
Jimgerdemannia sp.	T34745-B	Main Ranges National Park, Queensland, Australia	3 June 2010

cycling conditions were: an initial step at 95 °C for 5 min, 30 cycles at 95 °C for 30 s, 55 °C for 30 s, 72 °C for 1 min 15 s and a final extension step at 72 °C for 7 min. The PCR amplicons were then diluted and used as template for the second PCR with the forward primers ITS3 (White *et al.* 1990), fITS9 (Ihrmark *et al.* 2012) or LR0R (Vilgalys & Hester 1990) in combination with EndAD28Sr. The cycling conditions for the second step of the semi-nested PCR were: an initial step at 95 °C for 5 min, 27 cycles at 95 °C for 30 s, 55 °C for 30 s, 72 °C for 1 min and a final extension step at 72 °C for 7 min. A partial fragment of the elongation factor 1 alpha (EF1-α) gene was amplified with the primers 983F and 2218R (Rehner & Buckley 2005). The cycling conditions in this case were: an initial step at 95 °C for 5 min, 35 cycles at 95 °C for 30 s, 55 °C for 30 s, 72 °C for 1 min and a final extension step at 72 °C for 7 min. When amplification was not successful, PCR products were diluted and used as template for a semi-nested PCR with the new forward primer EndADef1f (5'-TWCACVCTYGGYGTGCGTC-3') and PCR conditions as detailed above with 27 cycles. A partial fragment of the second largest subunit of RNA polymerase II (RPB2) gene was amplified with the new primers RPB2AD3f (5'-GAAGGTCARGCKTGYGGTC-3') or RPB2AD2f (5'-ATTCATCCSAGTATGATTC-3') and RPB2AD1r (5'- AASGGTGTRGCRTCACCTTC-3'). The cycling conditions were: an initial step at 95 °C for 5 min, 35 cycles at 95 °C for 30 s, 55 °C for 30 s, 72 °C for 1 min and a final extension step at 72 °C for 7 min. When amplification with these two primer combinations was unsuccessful, a semi-nested PCR was attempted with forward primers RPB2AD2f or RPB2AD1f (5'- ATGGARGARTTTGARAAGCC-3'). The semi-nested PCR conditions were as detailed above with 27 cycles. All PCR amplicons were purified and either sequenced directly or cloned with the TOPO-TA cloning kit (Thermo Fisher Scientific). The PCR amplicons or cloned fragments were sequenced with an ABI 3730XL DNA Analyzer (Applied Biosystems, Foster City, CA). The DNA sequences generated in this study are deposited in GenBank (MF478989-MF479111).

Phylogenetic analyses

Sequences were assembled and curated in Geneious v.8.1.7 (Kearse *et al.* 2012), and were used as queries for conducting BLAST searches (Altschul *et al.* 1990). Four single-locus datasets were created (i.e. 18S, 28S, EF1-α, RPB2). The datasets included 123 sequences generated in this study and 187 obtained from the NCBI and UNITE databases. In particular, we used sequences generated from the recently described *Bifiguratus adelaidae* (Torres-Cruz *et al*. 2017), *Calcarisporiella thermophila*, *Densospora nuda* and *D. solicarpa*, several *Endogone* spp., *Sphaerocreas pubescens*, *Youngiomyces aggregatus* (syn. *E. aggregata*, see below) and other undescribed *Mucoromycotina* spp., *Mortierella verticillata* (NRRL 6337) (*Mortierellomycotina*) was included as outgroup in single-locus analyses. The 18S, 28S, EF1-α and RPB2 datasets included 140, 67, 65 and 34 taxa, respectively (Supplementary Table 1). Datasets were aligned with MAFFT (Katoh & Standley 2013) or MUSCLE (Edgar 2004) and then manually edited. The ITS2 region and introns of EF1-α and RPB2 genes were excluded from subsequent analyses. Each alignment was then trimmed with GBlocks v.0.91b (Castresana 2000) using the least stringent conditions. The single-locus alignments had a total of 1 435 (18S), 877 (28S), 839 (EF1-α), and 904 (RPB2) nucleotide positions. We also created a concatenated dataset that included, when available, all four loci for 56 taxa (Supplementary Table 1). *Densospora solicarpa* (DAR 69421; DAR 74956; Tedersoo *et al*. 2016), *Sphaerocreas pubescens* (NBRC 109377) and an unidentified *Mucoromycotina* sp. (MES1534; Truong *et al.* 2017) were used as outgroups in the multi-locus analysis. Missing loci were treated as missing data. Because the four single-locus trees appeared largely congruent, they were combined after aligning and trimming steps described above. The concatenated alignment had a total of 3568 nucleotide positions. Trimmed single-locus and concatenated alignments were deposited in TreeBase (http://purl.org/phylo/treebase/phylows/study/TB2:S21409).

Prior to phylogenetic inferences, best-fit nucleotide substitution models were estimated for each dataset by using jModelTest v.2.1.9 (Darriba *et al.* 2012). Phylogenetic analyses were carried out using MrBayes v.3.2.6 (Ronquist *et al.* 2012) and RAxML v.8.2.4 (Stamatakis 2014). A Markov chain Monte Carlo was run for five million generations under the TIM3+I+G (18S, 28S), TrN+G (EF1-α) and TrNef+I (RPB2) nucleotide substitution models. A partitioned analysis was carried out for the concatenated dataset and run for five million generations using the models as above for the 28S and RPB2 partitions; the TrN+I+G and TIM2ef+G nucleotide substitution models were applied for the 18S and EF1-α partitions. Maximum likelihood analyses were carried out under the GTRCAT nucleotide substitution model with the "autoMR" option for bootstrap replicates (Pattengale *et al.* 2010).

RESULTS

Specimens examined and phylogenetic analyses

In total, 45 *Endogone* specimens were analyzed in this study. Thirty-three specimens were identified morphologically and 12 were unidentified (Table 1). Previously used primer pairs (Bidartondo *et al.* 2011, Desirò *et al.* 2013) together with new primer combinations designed in this study allowed us to amplify all of the four target genes from 19 out of 45 specimens. For the other 26 specimens, three (12 specimens), two (13 specimens) or one (1 specimen) gene sequences were successfully generated (Supplementary Table 1). Most missing gene sequence data were of the ITS-28S rRNA region, which is known to be problematic for *Endogonales* (Tedersoo *et al.* 2016). The RPB2 gene also proved challenging to amplify and sequence. Although primer bias cannot be excluded, multiple factors such as age and preservation mode of the samples may affect DNA integrity and therefore PCR success (Osmundson *et al.* 2013). Indeed, most amplification failures were from specimens collected in the 1980s and 1990s whereas three or four target genes were amplified for most of the specimens collected within the last 10 years.

Single- and multi-locus phylogenetic reconstructions showed two deeply divergent and well-supported mono-phyletic groups within *Endogonaceae*. The first group corresponded to the genus *Endogone* whereas the second represents the new genus *Jimgerdemannia*. The *Endogone* clade included the type species, *E. pisiformis*, together with *Youngiomyces aggregatus* (syn. *E. aggregata*; see below), *E. corticioides*, *E. incrassata*, *E. magnospora*, *E. oregonensis*, *E. tuberculosa*, all the unidentified *Endogone* specimens investigated, and several environmental sequences. The *Endogone* group was divided into two clades. The first clade encompassed *E. pisiformis* and its sister lineage *E. corticioides* (Figs 1–2, Supplementary Figs 1–2). Interestingly, putative ectomycorrhizal *Endogone* sequences (Yamamoto *et al.* 2017a) were nested within the *pisiformis-corticiodes* clade together with a clade constituted by environmental DNA sequences generated from fungal symbionts of liverworts (Bidartondo *et al.* 2011) (Fig. 2, Supplementary Fig. 2). The second clade included *E. aggregata*, *E. incrassata*, *E. magnospora*, *E. oregonensis*, *E. tuberculosa,* and unidentified *Endogone* specimens. The position of the taxa within this clade was not clearly resolved by single-locus analyses, however, our multigene phylogeny supported the placement of *E. oregonensis* as the most basal taxon within this clade and *E. incrassata* as sister group to the *Endogone* species complex that contains *E. aggregata*, *E. magnospora,* and *E. tuberculosa* (Fig. 1).

The *Jimgerdemannia* clade included *J. flammicorona* and *J. lactiflua*, and an undescribed *Jimgerdemannia* sp. (T34758-A and T34758-B). In contrast to the *Endogone* clade, the relationships within *Jimgerdemannia* were well resolved; *J. flammicorona* and *J. lactiflua* are sister groups, while the undescribed *Jimgerdemannia* sp. (T34758-A and T34758-B) is sister of the *flammicorona-lactiflua* clade (Fig. 1, Supplementary Figs 1–3). Curiously, phylogenetic reconstructions showed two distinct *J. flammicorona* clades. Furthermore, several environmental fungal sequences retrieved from hornworts and liverworts clustered together with *Jimgerdemannia* sp. (T34758-A and T34758-B) or were closely related to it (“group E” *sensu* Desirò *et al.* 2013) (Fig. 2, Supplementary Figs 1–2). A third group (“groups D and H“ *sensu* Desirò *et al.* 2013) comprised *Mucoromycotina* spp. associated with bryophytes and ferns (Bidartondo *et al*. 2011; Desirò *et al*. 2013; Rimington *et al*. 2015; Field *et al.* 2016) and a fine root endophyte (Orchard *et al*. 2017a) nested between the *Endogone* and *Jimgerdemannia* clades (Fig. 2, Supplementary Fig. 2). Finally, *Jimgerdemannia* was sister of a clade of hornwort- and liverwort-associated fungi (“group G” *sensu* Desirò *et al.* 2013), whereas a second clade encompassing DNA sequences retrieved from the liverwort *Neohodgsonia mirabilis* was the first diverging clade of *Endogonaceae* (Fig. 2).

All the sporophore and environmental DNA sequences described above were included within a monophyletic clade referred to here as *Endogonaceae*. A more distantly related monophyletic sister group mostly consisted of environmental *Mucoromycotina* sequences generated from undescribed fungal symbionts of early diverging land plants. Several well-supported phylogroups were present in this clade. Fine root endophytes (Orchard *et al*. 2017a) clustered within two phylogroups whereas a third very diverse phylogroup encompassed numerous environmental *Mucoromycotina* sequences, *Densospora nuda*, *D. solicarpa*, *Sphaerocreas pubescens*, an unidentified *Mucoromycotina* sp. (MES1534) (Truong *et al*. 2017), and uncultured ectomycorrhizal *Mucoromycotina* (Tedersoo *et al.* 2008). Below we circumscribe this monophyletic sister lineage that has been referred to previously as the *Sphaerocreas-Densospora* clade (Yamamoto *et al.* 2015, Truong *et al.* 2017) as the new family *Densosporaceae*.

TAXONOMY

Densosporaceae Desirò, M.E. Sm., Bidartondo, Trappe & Bonito, **fam. nov.**
MycoBank MB821851

Type genus: *Densospora* McGee 1996.

Diagnosis: The family *Densosporaceae* is erected here to apply to all descendants of the node “D” defined in the phylogeny (Fig. 2) as the terminal *Densosporaceae* clade. We define *Densosporaceae* as the least inclusive clade containing the genus *Densospora* and *Sphaerocreas pubescens* (*sensu* Hirose *et al*. 2014), but also environmental DNA sequences generated from fungal symbionts of non-vascular and vascular plants (JF414222, JF414224, KC708392, KC708404, KC708409, KC708417, KC708436, KJ952212, KJ952213, UDB002714).

Discussion: Most of the phylogenetic diversity within *Densosporaceae* is known from environmental DNA sequences generated from fungal symbionts of bryophytes, rather than from sporophore collections. Consequently, we have used these environmental DNA sequences to help define this family. Taxa within *Densosporaceae* have previously been classified as belonging to *Endogonales* and *Glomerales*, and some are currently classified as *incertae sedis* (http://www.indexfungorum.org/). However, single-locus and multigene phylogenetic reconstructions resolve *Densosporaceae* as a distant sister clade of *Endogonaceae* within the order *Endogonales*. *Densosporaceae* encompasses multiple divergent monophyletic clades that mostly comprise undescribed *Mucoromycotina* lineages, but also species such as *Densospora nuda*, *D. solicarpa* and *Sphaerocreas pubescens* that produce sporophores. Like *Endogonaceae*, fungi in *Densosporaceae* are frequently associated with liverworts, hornworts (Bidartondo *et al*. 2011, Desirò *et al.* 2013, Hirose *et al.* 2014), lycopods and ferns (Rimington *et al.* 2015). Some short NGS sequences from fine root endophytes (*Glomus tenue s. lat.*) associated with *Trifolium* roots (Orchard *et al.* 2017a) also cluster within *Densosporaceae*. Furthermore, sequences from ectomycorrhizal fungi associated with *Eucalyptus* and *Nothofagus* (Tedersoo *et al.* 2008) and an unidentified *Mucoromycotina* sp. (MES1534; Truong *et al.* 2017) are placed within this clade.

Jimgerdemannia Trappe, Desirò, M.E. Sm., Bonito & Bidartondo, **gen. nov.**
MycoBank MB821846

Etymology: In honour of James (“Jim”) W. Gerdemann, researcher and professor, who was instrumental in bringing

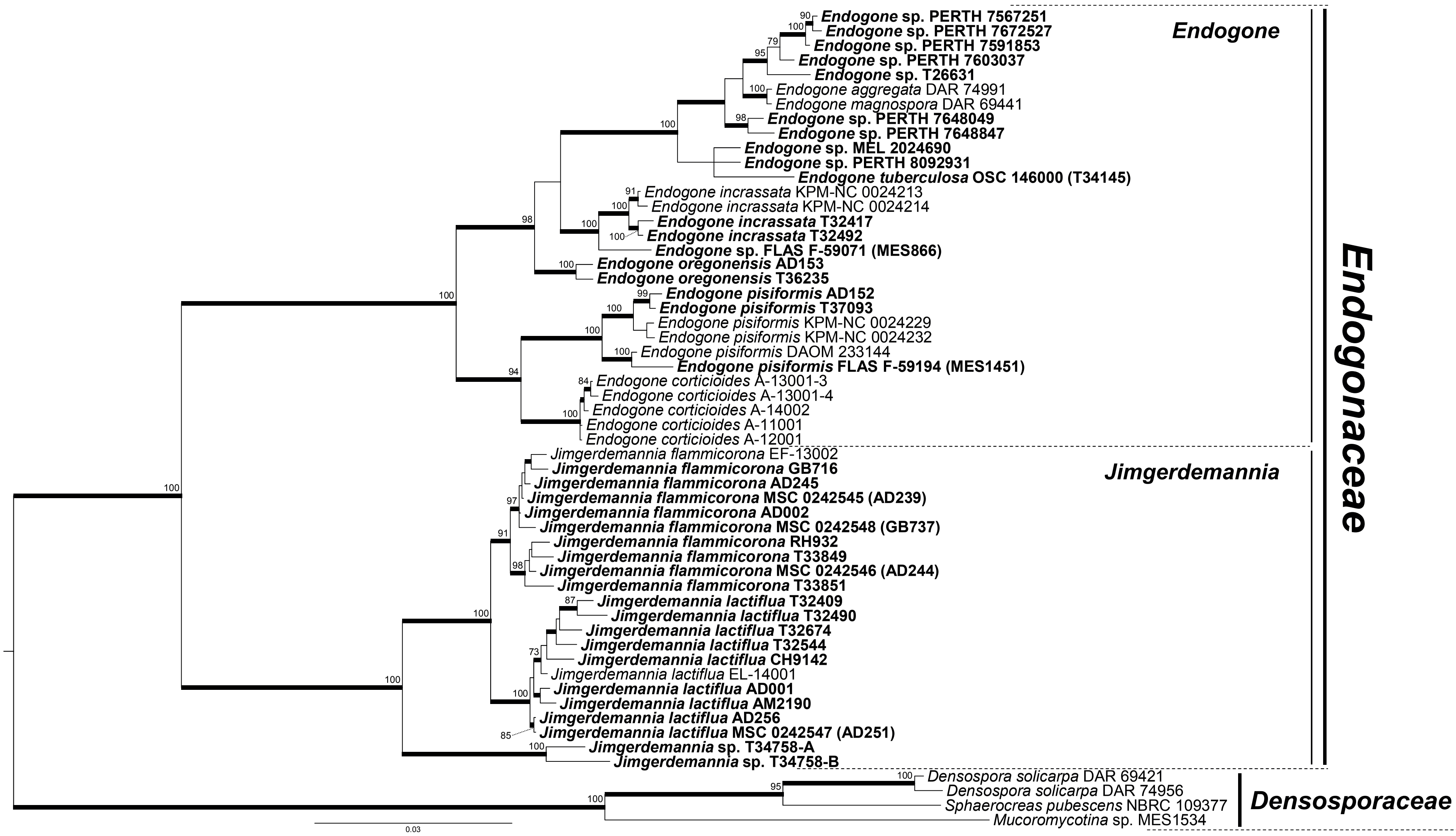


Fig. 1. Phylogenetic reconstruction of *Endogonaceae* based on a concatenated dataset of 18S, 28S, EF1-α and RPB2 sequences. The family *Densosporaceae*, represented by *Densospora solicarpa, Sphaerocreas pubescens* and an unidentified *Mucoromycotina* sp., was used as outgroup. The tree shows the topology obtained with the Bayesian method; branches with Bayesian posterior probabilities ≥0.95 are thickened and ML bootstrap support values ≥70 are shown. Specimens analyzed in this study are in bold.

Endogonales and *Glomerales* into modern taxonomy before the advent of DNA and phylogenetic analyses. *Type species*: *Jimgerdemannia flammicorona* (Trappe & Gerd.) Trappe *et al.* 2017.

Diagnosis: Differs from *Endogone* by pairing a large gametangium with a small one, the tip of the small one fusing to the side of the large one.

Discussion: The zygospore typically buds from the tip of the large gametangium or occasionally from the junction of the two gametangia. Spores typically becoming enveloped in tightly appressed hyphae that fuse at maturity with the spore wall to form a surface ornamentation. Spores are distributed randomly among the glebal hyphae, and not clustered. Phylogenetic analyses confirm that *Jimgerdemannia* and *Endogone s. str.* represent separate lineages within *Endogonaceae*. All known *Jimgerdemannia* species putatively form ectomycorrhizas with various species of *Pinaceae* and the sporophores of taxa of this group are usually hypogeous among host rootlets.

Jimgerdemannia flammicorona (Trappe & Gerd.) Trappe, Desirò, M.E. Sm., Bonito, Bidartondo, **comb. nov.**
MycoBank MB821847
Basionym: *Endogone flammicorona* Trappe & Gerd., *Trans. Brit. Mycol. Soc.* **59**: 405 (1972).

Jimgerdemannia lactiflua (Berk. & Broome) Trappe, Desirò, M.E. Sm., Bonito & Bidartondo, **comb. nov.**
MycoBank MB 821853
Basionym: *Endogone lactiflua* Berk. & Broome, *Ann. Mag. Nat. Hist.*, ser. 1, **18**: 81 (1846).

Discussion: *Jimgerdemannia flammicorona* and *J. lactiflua* have been compared in detail by Trappe & Gerdemann (1972), and demonstrated to form ectomycorrhizas with *Pinus contorta*, *P. lambertiana*, *P. monticola*, *P. peuce*, *P. radiata*, *P. strobus* and *Pseudotsuga menziesii*. These taxa are common and sporulate in beds of *Pinaceae* seedlings in Europe and North America (Fassi & Palenzona 1969, Fassi *et al.* 1969, Chu-Chou & Grace 1979, 1984). *Jimgerdemannia lactiflua* was reported to form mycorrhizas and produce sporophores on three-month old *Pinus contorta* nursery seedlings (Walker 1985). These species are widely distributed in *Pinus radiata* plantations in Australia and New Zealand, where they were likely accidentally introduced with imported seedlings in the early 20th century (Chu-Chou & Grace 1984, Trappe, unpubl.). Both species commonly appear in faeces (scats) of bush rats (*Rattus fuscipes*) in *Pinus radiata* plantations in Australia (Trappe, unpubl) and are also found in small mammal droppings in North America (Maser *et al.* 1978).

Endogone Link, *Ges. Naturf. Freunde Berlin Mag. Neuesten Entdeckt. Gesammten Naturk.* **3**: 33 (1809).

Type species: *Endogone pisiformis* Link 1809.

Synonym: *Youngiomyces* Y.-J. Yao, *Kew Bull.* **50**: 350 (1995).

Diagnosis: Differs from *Jimgerdemannia* by pairing two gametangia of similar size that fuse near their tips and the zygospores mostly then budding from the junction of the two.

Discussion: Spores mostly not enveloped in appressed hyphae, or, if so then the hyphae not fused with the spore wall to form a surface ornamentation at maturity. Spores either distributed randomly among the glebal hyphae or clustered in discrete aggregations separated by hyphal tissue. Phylogenetic analyses reveal that *Endogone s. str.* (as circumscribed here) and *Jimgerdemannia* represent separate lineages within *Endogonaceae*. In contrast to the ectomycorrhizal *Jimgerdemannia*, most *Endogone s. str.* species are either putatively saprotrophic or perhaps fungicolous and may be either hypogeous or epigeous, the latter sporing on various substrates. Ectomycorrhizas putatively identified as related to *E. pisiformis* were detected in oak forest in Japan (Yamamoto *et al*. 2017a). Even though their functional role is unknown, some taxa within the *Endogone* clade have been documented as symbionts of liverworts.

Endogone pisiformis, undoubtedly the most widely distributed species of the genus, has been reported from Asia, Europe, and North America and proliferates on diverse substrates, including forest litter, brown-cubical rotted wood, decaying polypore basidiomes, and among mosses. It sometimes produces sporophores at the edge of melting snowbanks or immersed in meltwater on saturated organic matter. It can grow in pure culture (Jabaji-Hare & Charest 1987) and produce zygospores *in vitro* in the absence of mycorrhiza formation (Berch & Castellano 1986). *Endogone tuberculosa* and *Youngiomyces aggregatus* (i.e. *E. aggregata*) were reported to grow on agar media (Warcup 1990). However, molecular tools should be applied to validate these findings. Yamamoto *et al*. (2017b) showed a limited vegetative growth of *E. corticioides* in pure culture. Warcup (1990) inoculated various *Eucalyptus* spp. with *Y. aggregatus* (i.e. *E. aggregata*) and *E. tuberculosa*. Although ectomycorrhizas formed, the methods used did not preclude contamination by other fungi, so the results were inconclusive.

Endogone carolinensis (Y.-J. Yao) Desirò, M.E. Sm., Bonito, Bidartondo & Trappe, **comb. nov.**
MycoBank MB821852
Basionym: *Youngiomyces carolinensis* Y.-J. Yao, *Kew Bull.* **50**: 351 (1995).

Discussion: The key feature used to distinguish *Youngiomyces* from *Endogone* was that in *Youngiomyces* the zygosporangium has two, three, or four openings (Yao *et al.* 1995). However, *E. pisiformis,* and rarely *E. incrassata,* have been reported to have zygosporangia with two openings (Yamamoto *et al.* 2015). Although the type of the genus *Youngiomyces* (*Y. caroliniensis*) was not included in our phylogeny, the phylogenetic position of *Y. aggregatus* is nested deep within the *Endogone* clade (Fig. 1), close to *E. magnospora* and other *Endogone* species devoid of multiple openings in their zygosporangia. For those reasons, and in line

Fig. 2. Phylogenetic reconstruction of *Endogonales* based on 18S rDNA sequences. The node "D" defines the family *Densosporaceae*. *Mortierella verticillata* was used as outgroup. The tree shows the topology obtained with the Bayesian method; branches with Bayesian posterior probabilities ≥0.95 are thickened and ML bootstrap support values ≥70 are shown. Sequences generated in this study are in bold.

with Yamamoto *et al.* (2015), we synonymize *Youngiomyces* with *Endogone s. str.* This requires recombining the type species *Y. carolinensis* into *Endogone s. str.* and returning the other species assigned to *Youngiomyces* to their original status as *Endogone* species: *E. aggregata, E. multiplex*, and *E. stratosa*.

DISCUSSION

Single-locus and multigene phylogenetic analyses using rDNA and single-copy protein-coding genes resolved the phylogeny of *Endogonales* into two monophyletic clades showing a deep divergence with significant support. Based on these results, we revised the taxonomy of *Endogonales* and introduced the new family *Densosporaceae*. We

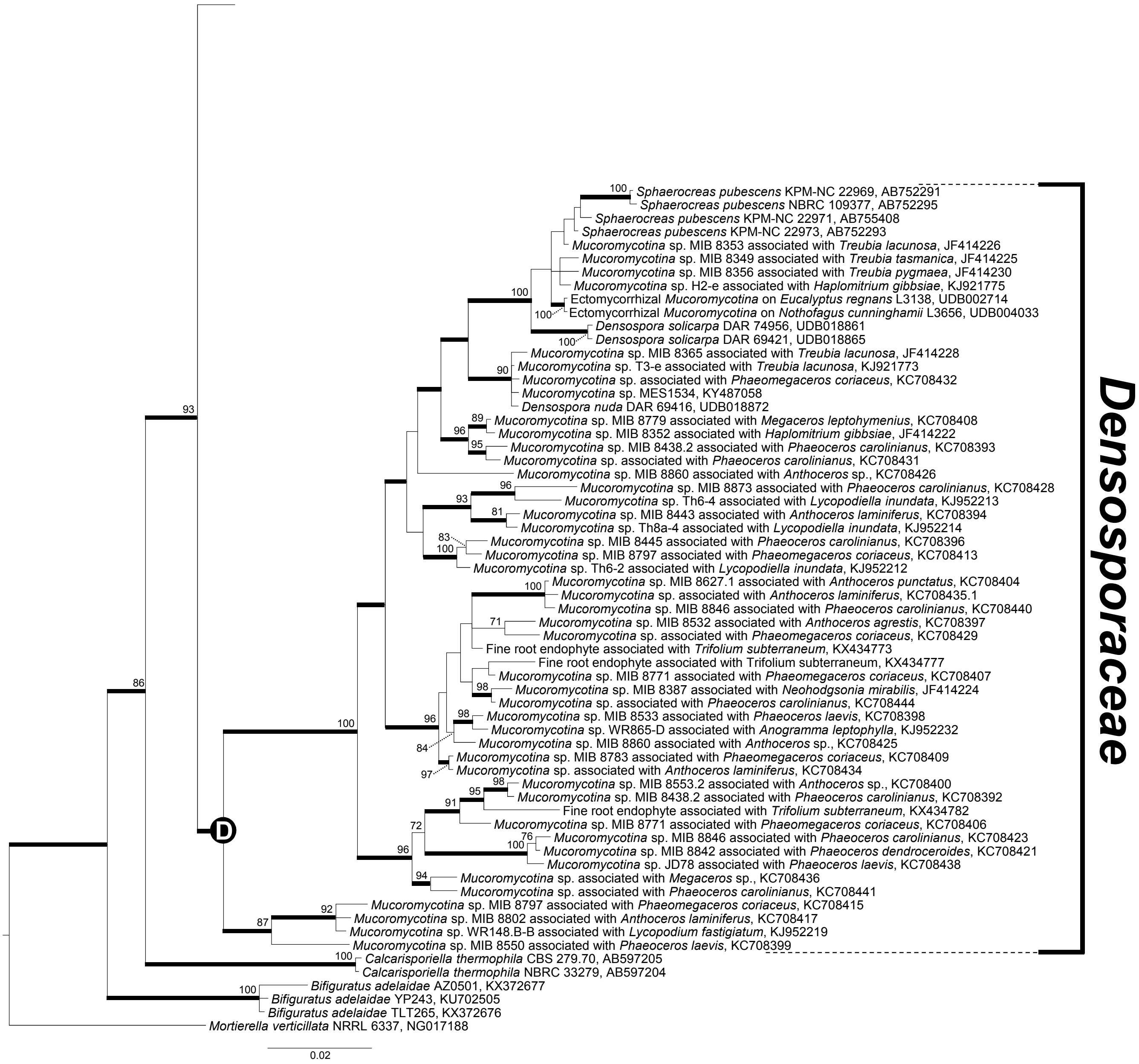


Fig. 2. (Continued).

also introduced the new genus *Jimgerdemannia* within *Endogonaceae* and synonymized the genus *Youngiomyces* with *Endogone s. str*. The new genus *Jimgerdemannia* includes two species, *J. flammicorona* and *J. lactiflua*, and an undescribed *Jimgerdemannia* lineage, which is sister to the *flammicorona-lactiflua* clade. Furthermore, we also provided a more detailed phylogenetic placement for *E. oregonensis* and placed *E. tuberculosa* within the genus *Endogone*: the single-locus and multigene phylogeny placed *E. oregonensis* and *E. turberculosa* together with *E. aggregata*, *E. incrassata*, *E. magnospora* and several unidentified *Endogone* spp. within a clade that is sister to the *corticioides-pisiformis* clade.

Jimgerdemannia appears sister to *Endogone*. However, when environmental *Mucoromycotina* sequences were included in the phylogenetic reconstructions, several additional novel clades were detected within *Endogonaceae*. Furthermore, *Jimgerdemannia* was sister to a clade consisting of DNA sequences belonging to fungi associated with liverworts and hornworts ("group G" *sensu* Desirò *et al.* 2013). Similarly, *Endogone* is nested within a monophyletic group that also included two clades of fungal symbionts of liverworts, hornworts and ferns ("groups D and H" *sensu* Desirò *et al.* 2013). Sequences from a taxon of fine root endophytes (*Glomus tenue*) associated with roots of *Trifolium* (Orchard *et al.* 2017a) clusters within one of these two clades ("group D" *sensu* Desirò *et al.* 2013). However, the fine root endophyte sequences are short NGS reads (*ca*. 200 bp) so their placement will need to be revisited based on longer sequences for better resolution. Lastly, all other *Endogonaceae* sequences are sister to a clade of fungal sequences retrieved from the thallus of the liverwort *Neohodgsonia mirabilis* (Field *et al.* 2016).

A number of points can be made regarding the morphology, sporing habit and ecology of *Jimgerdemannia*. In particular, species in this genus have a developed zygosporangial hyphal mantle and heterogeneous gametangia. They usually produce below ground sporophores and are considered ectomycorrhizal with *Pinaceae* (Fassi *et al.* 1969, Fassi & Palenzona 1969, Chu-Chou & Grace 1979, Walker 1985; Warcup, 1990). Interestingly, our results show that sequences from fungal symbionts of hornworts and liverworts are closely related to an undescribed *Jimgerdemannia* sp. This indicates that this *Jimgerdemannia* species might engage in symbiotic interactions with early diverging land plant lineages. We cannot rule out the possibility that members of this genus can form ectomycorrhizas on some hosts and be endophytic or form other biotrophic interactions with other hosts.

In contrast, taxa in *Endogone* have a loose zygosporangial hyphal mantle and homogeneous gametangia. They may have hypogeous or epigeous sporophores. Most *Endogone* species are saprotrophic or perhaps fungicolous and have generally been considered non-ectomycorrhizal. However, Warcup (1990) reported mycorrhiza formation on *Eucalyptus* spp. inoculated with *E. aggregata* (syn. *Youngiomyces aggregatus*) and *E. tuberculosa*. Although ectomycorrhizas formed, molecular confirmation is needed to verify the fungal identity and exclude potential contamination by other fungi. Curiously, Yamamoto *et al.* (2017a) recently reported ectomycorrhizas on two oak root tips putatively formed by a novel lineage related to *E. corticioides* and *E. pisiformis*. It is interesting to note that phylogenetic reconstructions based on the EF1-α gene placed sequences from fungal symbionts associated with the liverworts *Treubia lacunosa* and *T. pygmaea* (Bidartondo *et al*. 2011) close to the ones retrieved from oak roots, suggesting the possibility that some *Endogone* species might associate with multiple plant partners.

Phylogenetic reconstructions placed *Youngiomyces aggregatus* (i.e. *E. aggregata*), the only representative of the genus *Youngiomyces* in our study, within *Endogone*. It has recently been shown that the key morphological character used to distinguish *Youngiomyces* from *Endogone* (i.e. a zygosporangium with two to four openings) can also be observed in *E. pisiformis* and rarely in *E. incrassata* (Yamamoto *et al.* 2015). Based on this rationale, we synonymize *Youngiomyces* with *Endogone s. str.*

Densospora nuda, *D. solicarpa*, and *Sphaerocreas pubescens*, short DNA sequences from environmental sequencing of fine root endophytes (*Glomus tenue*), and numerous environmental *Mucoromycotina* sequences clustered together within a diverse and well supported monophyletic clade that we name *Densosporaceae* here. This group has previously been referred to as the *Sphaerocreas-Densospora* clade (Yamamoto *et al.* 2015, Truong *et al.* 2017). Due to limited taxon and/or gene sampling in previous (Lin *et al.* 2014; Spatafora *et al.* 2016) and present studies, there is still uncertainty regarding the diversity and relationships among *Densosporaceae* and the phylogenetic position of *Endogonales* within *Mucoromycotina*. However, in our analyses the monophyletic *Densosporaceae* is sister to the monophyletic *Endogonaceae*. Most of the DNA sequences included in *Densosporaceae* were undescribed *Mucoromycotina*. *Densospora*, *Sphaerocreas pubescens*, an unidentified *Mucoromycotina* sp. (MES1534; Truong *et al.* 2017), and uncultured ectomycorrhizal *Mucoromycotina* spp. (Tedersoo *et al.* 2008) clustered within a monophyletic clade together with several liverwort- and hornwort-associated lineages. The remaining clades were formed by fungal DNA sequences retrieved from liverworts, hornworts, lycopods, and ferns, whose identity is unknown. Some of these apparently undescribed taxa are also similar to short DNA reads of fine root endophytes in the *Glomus tenue* species complex (Orchard *et al.* 2017a).

The presence of several clades constituted only by environmental DNA sequences indicates that there are several undescribed genera and species in *Endogonales*, so additional phylogenetic studies are needed based on additional fresh specimens. In particular, sequence data are needed for several described but rare species of *Endogone, Peridiospora,* and *Sclerogone* to determine whether or not these fungi really belong to *Endogonaceae*. Species of *Peridiospora* and *Sclerogone* were not sampled in this study and sequences for these two fungal lineages were not available in public databases. However, preliminary data indicate that *Peridiospora* might be phylogenetically related to *Glomeromycotina*, not *Mucoromycotina* (C Walker & MI Bidartondo, unpubl.). Additional molecular data from putatively related taxa could help in identifying and providing a taxonomic placement for some of these diverse and enigmatic fungi, and further clarify the taxonomy of *Endogonales* and *Mucoromycotina*.

Similar to *Endogone* and *Jimgerdemannia*, *Densospora* and *Sphaerocreas pubescens* produce sporophores. *Densospora tubiformis* can form ectomycorrhizas (Warcup 1985; McGee 1996) and *Densospora* sporophores are often found on the soil surface. However, *S. pubescens* sporulates on decaying wood or twigs, and also leaf litter or rotten basidiomes of *Polyporaceae*. This suggests a possible fungicolous behaviour but little information is available on this fungus (Hirose *et al.* 2014). *Endogone* species also sporulate on gametophores of mosses as well as rotten wood or twigs, and rarely on old polypore basidiomes (Yamamoto *et al.* 2015). *Sphaerocreas pubescens* was also considered to be a saprotroph on the basis of failed mycorrhizal synthesis experiments (McGee & Trappe 2002). However, sequences retrieved from fungal symbionts associated with liverworts and hornworts suggest that these fungi are biotrophic (Hirose *et al*. 2014).

Notwithstanding that their ecology remains poorly understood, our results support the hypothesis that lineages of *Mucoromycotina* co-evolved independently with different lineages of vascular and non-vascular plants, among them the early diverging bryophytes whose ancestors were involved in the colonization of terrestrial environments. As such, *Endogonales* provides essential context for studying the origin, evolution and biology of plant-fungal symbioses. However, many challenges remain regarding *Endogonales*, including difficulties in collecting sporophores and detecting these fungi in environmental surveys, and the integration of environmental data with collection-based datasets.

Further sampling and research is needed to provide a more comprehensive investigation of *Endogonales*. This group of fungi requires urgent attention to: (1) provide a formal name to the clades of environmental DNA sequences related to *Endogone*, *Jimgerdemannia*, and *Densosporaceae*; (2) provide taxonomic descriptions of the potentially novel species of *Endogone* and *Jimgerdemannia* used in this study; (3) generate molecular data in order to place species of *Peridiospora* and *Sclerogone* within a phylogenetic framework; (4) investigate the fine root endophytes of vascular plants and the undescribed *Mucoromycotina* spp. of early diverging land plants for taxonomic treatment; (5) shed light on the ecophysiology and trophic status of the various different lineages within *Endogonales*; and (6) clarify taxonomic inconsistencies between *Sphaerocreas pubescens* (*sensu* Hirose *et al*. 2014) and *Sclerocystis* in *Glomeromycotina*.

As we enter the "-omics" age it will be possible to use both fungal genomes and plant microbiomes to facilitate future studies of *Endogonales,* which are rapidly emerging as a key group of fungi to study. It will be critical to understand more about the evolution and trophic modes of this group of fungi in order to elucidate the origin and evolutionary history of plant-fungal symbioses. The ecology of many species of *Densosporaceae* and *Endogonaceae* is likely to be mycorrhizal (or mycorrhiza-like in rootless plants) involving carbon and nutrient transfer between fungus and plant host. This has only been tested thus far for a few liverwort species (Field *et al.* 2015b, 2016). Genomic data have the potential to determine the physiological abilities and differences among symbiotic and free-living species, and to clarify the position of *Endogonales* within the kingdom *Fungi* (i.e. their relationships to other *Mucoromycota* and particularly to the arbuscular mycorrhizal *Glomeromycotina*). Genome data will also enable functional metabolomic and transcriptomic studies of these fungi in symbiosis with their hosts in order to decipher their intriguing plant-fungal interactions.

ACKNOWLEDGEMENTS

We wish to thank Amer Montecchi, Begoña Aguirre-Hudson, Carolina Piña-Páez, Caroline Hobart, Christopher Walker, Efren Cazares, Kris Jacobson, Michael Castellano, Peter McGee, Roberto Garibay-Orijel, Rosanne Healy, R. Stephens, S. Loring, Michigan State University Herbarium, National Herbarium of Victoria, New Zealand Fungal and Plant Disease Collection, Oregon State University Herbarium, Royal Botanic Gardens Kew, Royal Botanical Garden of Madrid, University of Florida Herbarium, and Western Australian Herbarium that generously provided fungal specimens. Christopher Walker is also thanked for valuable comments on the manuscript, and Joey Spatafora, Mario Palenzona and Gian Maria Niccolò Benucci for their help in hunting *Endogone* and *Jimgerdemannia* sporophores in the field. AD and GB were supported through the US National Science Foundation (NSF) DEB 1737898 and Michigan State University AgBioResearch NIFA project MICL02416. MIB and AJ received support from a NERC standard grant (NE/N00941X/1) and WRR received support from a NERC studentship (DTP SSCP). MES received support from NSF grants DEB 1354802 (Symbiotic ectomycorrhizal fungi in southern South America) and DEB 1441677 (The Zygomycetes Genealogy of Life (ZyGoLife)- the conundrum of Kingdom Fungi) as well as the University of Florida's Institute for Food and Agricultural Sciences (IFAS).

REFERENCES

Altschul SF, Madden TL, Schäffer AA, Zhang J, Zhang Z, *et al.* (1997) Gapped BLAST and PSI-BLAST: a new generation of protein database search programs. *Nucleic Acids Research* **25**: 3389–3402.

Berch SM, Castellano MA (1986) Sporulation of *Endogone pisiformis* in axenic and monoxenic culture. *Mycologia* **78**: 292–295.

Berch SM, Fortin JA (1983) *Endogone pisiformis*: axenic culture and associations with *Sphagnum*, *Pinus sylvestris*, *Allium cepa*, and *Allium porrum*. *Canadian Journal of Botany* **61**: 899–905.

Berch SM, Fortin JA (1982) Germination of zygospores of *Endogone incrassata*. *Mycologia* **74**: 861–864.

Berkeley MJ, Broome CE (1874) Enumeration of the fungi of Ceylon. Part II. *Botanical Journal of the Linnean Society* **14**: 29-141.

Berkeley MJ, Broome CE (1846) Notices of British hypogaeous fungi. *Annals and Magazine of Natural History* **18**: 73–82.

Bidartondo MI, Read DJ, Trappe JM, Merckx V, Ligrone R, *et al.* (2011) The dawn of symbiosis between plants and fungi. *Biology Letters* **7**: 574–577.

Bonfante P, Desirò A (2017) Who lives in a fungus? The diversity, origins and functions of fungal endobacteria living in *Mucoromycota*. *The ISME Journal* **11**: 1727–1735.

Chu-Chou M, Grace LJ (1984) *Endogone flammicorona* and *Tuber* sp. as mycorrhizal fungi of *Pinus radiata* in New Zealand. *New Zealand Journal of Botany* **22**: 525–531.

Chu-Chou M, Grace LJ (1979) *Endogone flammicorona* as a mycorrhizal symbiont of Douglas fir in New Zealand. *New Zealand Journal of Forest Science* **9**: 344–347.

Castresana J (2000) Selection of conserved blocks from multiple alignments for their use in phylogenetic analysis. *Molecular Biology and Evolution* **17**: 540–552.

Darriba D, Taboada GL, Doallo R, Posada D (2012) jModelTest 2: more models, new heuristics and parallel computing. *Nature Methods* **9**: 772.

Desirò A, Faccio A, Kaech A, Bidartondo MI, Bonfante P (2015) *Endogone*, one of the oldest plant-associated fungi, host unique Mollicutes-related endobacteria. *New Phytologist* **205**: 1464–1472.

Desirò A, Duckett JG, Pressel S, Villarreal JC, Bidartondo MI (2013) Fungal symbioses in hornworts: a chequered history. *Proceedings of the Royal Society of London, B*: *Biological Sciences* **280**: 20130207.

Doyle J (1991) DNA protocols for plants. In: *Molecular techniques in taxonomy* (GM Hewitt, AWB Johnston & JPW Young, eds): 283–293. Berlin: Springer.

Edgar RC (2004) MUSCLE: multiple sequence alignment with high accuracy and high throughput. *Nucleic Acids Research* **32**: 1792–1797.

Fassi B, Fontana A, Trappe JM (1969) Ectomycorrhizae formed by *Endogone lactiflua* with species of *Pinus* and *Pseudotsuga*. *Mycologia* **5**: 412–414.

Fassi B, Palenzona M (1969) Mycorrhizal synthesis between *Pinus strobus*, *Pseudotsuga menziesii* and *Endogone lactiflua*. *Allionia* **15**: 105–114.

Fassi B (1965) Ectotrophic mycorrhizae produced by *Endogone lactiflua* Berk, on *Pinus strobus* L. *Allionia* **11**: 7–15.

Field KJ, Rimington WR, Bidartondo MI, Allinson KE, Beerling DJ, *et al.* (2016) Functional analysis of liverworts in dual symbiosis with *Glomeromycota* and *Mucoromycotina* fungi under a simulated Palaeozoic CO2 decline. *The ISME Journal* **10**: 1514–1526.

Field KJ, Pressel S, Duckett JG, Rimington WR, Bidartondo MI (2015a) Symbiotic options for the conquest of land. *Trends in Ecology and Evolution* **30**: 477–486.

Field KJ, Rimington WR, Bidartondo MI, Allinson KE, Beerling DJ, *et al.* (2015b) First evidence of mutualism between ancient plant lineages (*Haplomitriopsida* liverworts) and *Mucoromycotina* fungi and its response to simulated Palaeozoic changes in atmospheric CO2. *New Phytologist* **205**: 743–756.

Gerdemann JW, Trappe JM (1974) *Endogonaceae* in the Pacific Northwest. *Mycological Memoirs* **5**: 1–76.

Hirose D, Degawa Y, Yamamoto K, Yamada A (2014) *Sphaerocreas pubescens* is a member of the *Mucoromycotina* closely related to fungi associated with liverworts and hornworts. *Mycoscience* **55**: 221–226.

Ihrmark K, Bödeker IT, Cruz-Martinez K, Friberg H, Kubartova A, *et al.* (2012) New primers to amplify the fungal ITS2 region–evaluation by 454-sequencing of artificial and natural communities. *FEMS Microbiology Ecology* **82**: 666–677.

Jabaji-Hare SH, Charest PM (1987) Ultrastructural and cytochemical observations on the somatic phase of *Endogone pisiformis* (*Endogonaceae*). *Mycologia* **79**: 433–444.

James TY, Kauff F, Schoch CL, Matheny PB, Hofstetter V, *et al.* (2006) Reconstructing the early evolution of *Fungi* using a six-gene phylogeny. *Nature* **443**: 818–822.

Katoh K, Standley DM (2013) MAFFT multiple sequence alignment software version 7: improvements in performance and usability. *Molecular Biology and Evolution* **30**: 772–780.

Kearse M, Moir R, Wilson A, Stones-Havas S, Cheung M, *et al.* (2012) Geneious Basic: an integrated and extendable desktop software platform for the organization and analysis of sequence data. *Bioinformatics* **28**: 1647–1649.

Krings, M, Taylor TN, Dotzler N, Persichini G (2012) Fossil fungi with suggested affinities to the *Endogonaceae* from the Middle Triassic of Antarctica. *Mycologia* **104**: 835–844.

Lin K, Limpens E, Zhang Z, Ivanov S, Saunders DG, *et al.* (2014) Single nucleus genome sequencing reveals high similarity among nuclei of an endomycorrhizal fungus. *PLoS Genetics* **10**: p.e1004078.

Link HF (1809) Observationes in ordines plantarum naturales. *Dissertatio I. Magazin der Gesellschaft Naturforschenden Freunde Berlin* **3**: 3–42.

Lloyd CG (1918) Mycological Notes 56. *Mycological Writings* **5**: 797–812.

Maser C, Trappe JM, Nussbaum RA (1978) Fungal-small mammal interrelationships with emphasis on Oregon coniferous forests. *Ecology* **59**: 799–809.

McGee PA, Trappe JM (2002) The Australian zygomycetous mycorrhizal fungi. II. Further Australian sporocarpic *Glomaceae*. *Australian Systematic Botany* **15**: 115–124.

McGee PA (1996) The Australian zygomycetous mycorrhizal fungi: the genus *Densospora* gen. nov. *Australian Systematic Botany* **9**: 329–336.

Orchard S, Hilton S, Bending GD, Dickie IA, Standish RJ, *et al.* (2017a) Fine endophytes (*Glomus tenue*) are related to *Mucoromycotina*, not *Glomeromycota*. *New Phytologist* **213**: 481–486.

Orchard S, Standish RJ, Dickie IA, Renton M, Walker C, *et al.* (2017b) Fine root endophytes under scrutiny: a review of the literature on arbuscule-producing fungi recently suggested to belong to the *Mucoromycotina*. *Mycorrhiza* **27**: 619–638.

Osmundson TW, Robert VA, Schoch CL, Baker LJ, Smith A, *et al.* (2013) Filling gaps in biodiversity knowledge for macrofungi: contributions and assessment of an herbarium collection DNA barcode sequencing project. *PLoS One* **8**: E62419.

Pattengale ND, Alipour M, Bininda-Emonds OR, Moret BM, Stamatakis A (2010) How many bootstrap replicates are necessary? *Journal of Computational Biology* **17**: 337–354.

Rehner SA, Buckley E (2005) A *Beauveria* phylogeny inferred from nuclear ITS and EF1-α sequences: evidence for cryptic diversification and links to *Cordyceps* teleomorphs. *Mycologia* **97**: 84–98.

Rimington WR, Pressel S, Duckett JG, Bidartondo MI (2015) Fungal associations of basal vascular plants: reopening a closed book? *New Phytologist* **205**: 1394–1398.

Ronquist F, Teslenko M, van der Mark P, Ayres DL, Darling A, *et al.* (2012) MrBayes 3.2: efficient Bayesian phylogenetic inference and model choice across a large model space. *Systematic Biology* **61**: 539–542.

Saccardo PA (1882) Fungi boreali-Americani. *Michelia* **2**: 564–582.

Smit E, Leeflang P, Glandorf B, Van Elsas JD, Wernars K (1999) Analysis of fungal diversity in the wheat rhizosphere by sequencing of cloned PCR-amplified genes encoding 18S rRNA and temperature gradient gel electrophoresis. *Applied and Environmental Microbiology* **65**: 2614–2621.

Spatafora JW, Chang Y, Benny GL, Lazarus K, Smith ME, *et al.* (2016) Zygomycete genealogy of life (ZyGoLife): a phylum-level phylogenetic classification of zygomycete fungi based on genome-scale data. *Mycologia* **108**: 1028–1046.

Stamatakis A (2014) RAxML version 8: A tool for phylogenetic analysis and post-analysis of large phylogenies. *Bioinformatics* **30**: 1312–1313.

Stürmer SL (2012) A history of the taxonomy and systematics of arbuscular mycorrhizal fungi belonging to the phylum *Glomeromycota*. *Mycorrhiza* **22**: 247–258.

Tandy PA (1975) Sporocarpic species of *Endogonaceae* in Australia. *Australian Journal of Botany* **23**: 849–866.

Tedersoo L, Smith ME (2017) Ectomycorrhizal fungal lineages: detection of four new groups and notes on consistent recognition of ectomycorrhizal taxa in high-throughput sequencing studies. In: *Biogeography of Mycorrhizal Symbiosis* (Tedersoo L, ed.): 125–142. Springer International Publishing.

Tedersoo L, Liiv I, Kivistik PA, Anslan S, Kõljalg U, *et al.* (2016) Genomics and metagenomics technologies to recover ribosomal DNA and single-copy genes from old fruit-body and ectomycorrhiza specimens. *MycoKeys* **13**: 1.

Tedersoo L, Smith ME (2013) Lineages of ectomycorrhizal fungi revisited: foraging strategies and novel lineages revealed by sequences from belowground. *Fungal Biology Reviews* **27**: 83–99.

Tedersoo L, Jairus T, Horton BM, Abarenkov K, Suvi T, *et al.* (2008) Strong host preference of ectomycorrhizal fungi in a Tasmanian wet sclerophyll forest as revealed by DNA barcoding and taxon-specific primers. *New Phytologist* **180**: 479–490.

Thaxter R (1922) A revision of the *Endogoneae*. *Proceedings of the American Academy of Arts and Sciences* **57**: 289–350.

Torres-Cruz TJ, Tobias TL, Almatruk M, Hesse CN, Kuske CR *et al.* (2017) *Bifiguratus adelaidae* gen. et sp. nov., a new member of *Mucoromycotina* in endophytic and soil-dwelling habitats. *Mycologia* **109**: 363–378.

Trappe JM, Gerdemann JW (1972) *Endogone flammicorona* sp. nov., a distinctive segregate from *Endogone lactiflua*. *Transactions of* *the British Mycological Society* **59**: 403–407.

Truong C, Mujic AB, Healy R, Kuhar F, Furci G, *et al.* (2017) How to know the fungi: combining field inventories and DNA-barcoding to document fungal diversity. *New Phytologist* **214**: 913–919.

Větrovský T, Kolařík M, Žifčáková L, Zelenka T, Baldrian P (2015) The rpb2 gene represents a viable alternative molecular marker for the analysis of environmental fungal communities. *Molecular Ecology Resources* **16**: 388–401.

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

Walker C (1985) *Endogone lactiflua* forming ectomycorrhizas with *Pinus contorta*. *Transactions of the British Mycological Society* **84**: 353–355.

Warcup JH (1990) Taxonomy, culture and mycorrhizal associations of zygosporic *Endogonaceae. Mycological Research* **94**: 173–178.

Warcup JH (1985) Ectomycorrhizal formation by *Glomus tubiforme*. *New Phytologist* **99**: 267–272.

Warcup JH (1975) A culturable *Endogone* associated with eucalyptus. In: *Endomycorrhizas* (Sanders FE, Mosse B, Tinker PB, eds): 53–63. London: Academic Press.

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

Wu CG, Lin SJ (1997) *Endogonales* in Taiwan: a new genus with unizygosporic sporocarps and a hyphal mantle. *Mycotaxon* **64**: 179–188.

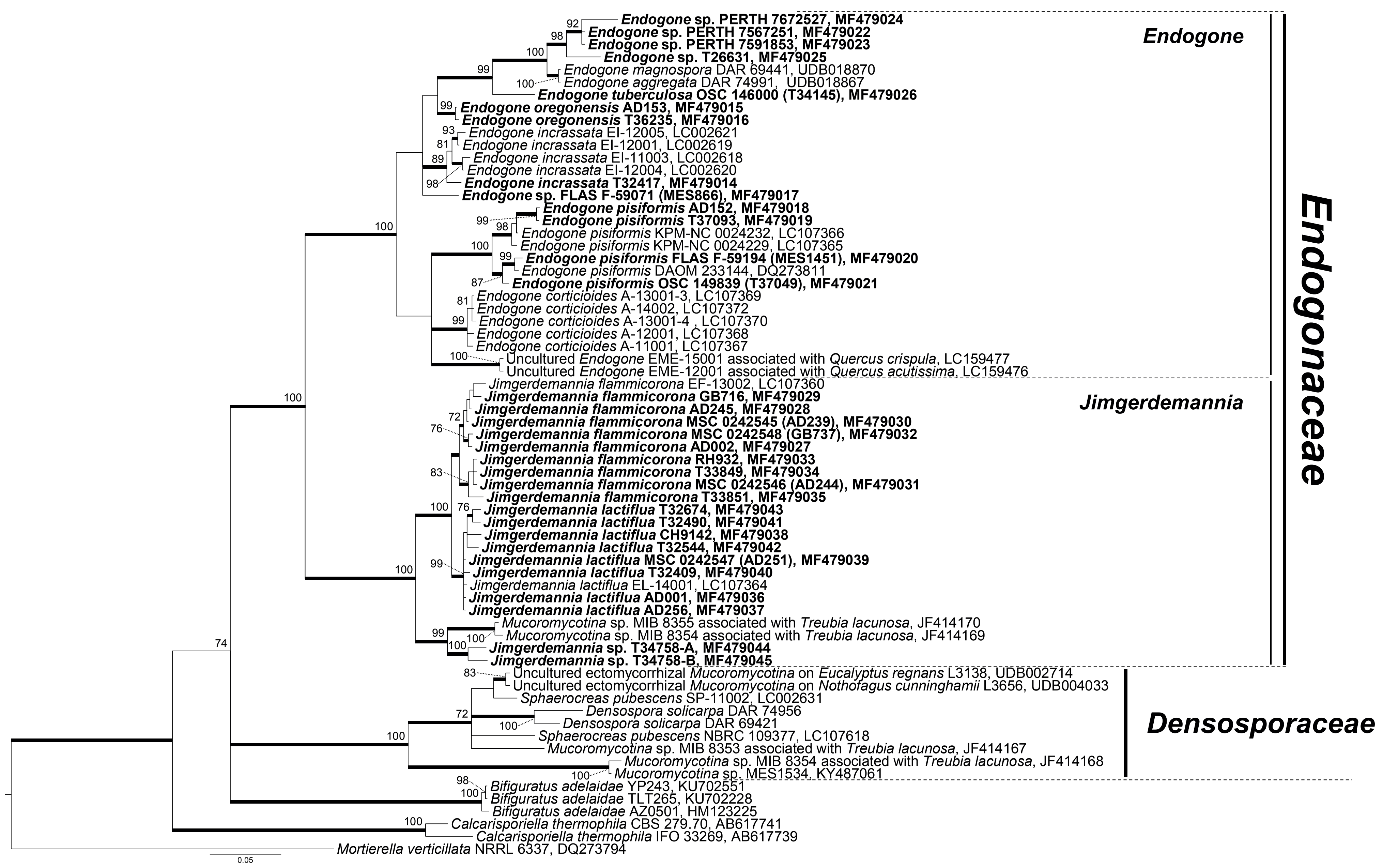
Yamamoto K, Endo N, Degawa Y, Fukuda M, Yamada A (2017a) First detection of *Endogone* ectomycorrhizas in natural oak forests. *Mycorrhiza* **27**: 295–301.

Yamamoto K, Degawa Y, Takashima Y, Fukuda M, Yamada A (2017b) *Endogone corticioides* sp. nov. from subalpine conifer forests in Japan and China, and its multi-locus phylogeny. *Mycoscience* **58**: 23–29.

Yamamoto K, Degawa Y, Hirose D, Fukuda M, Yamada A (2015) Morphology and phylogeny of four *Endogone* species and *Sphaerocreas pubescens* collected in Japan. *Mycological Progress* **14**: 86.

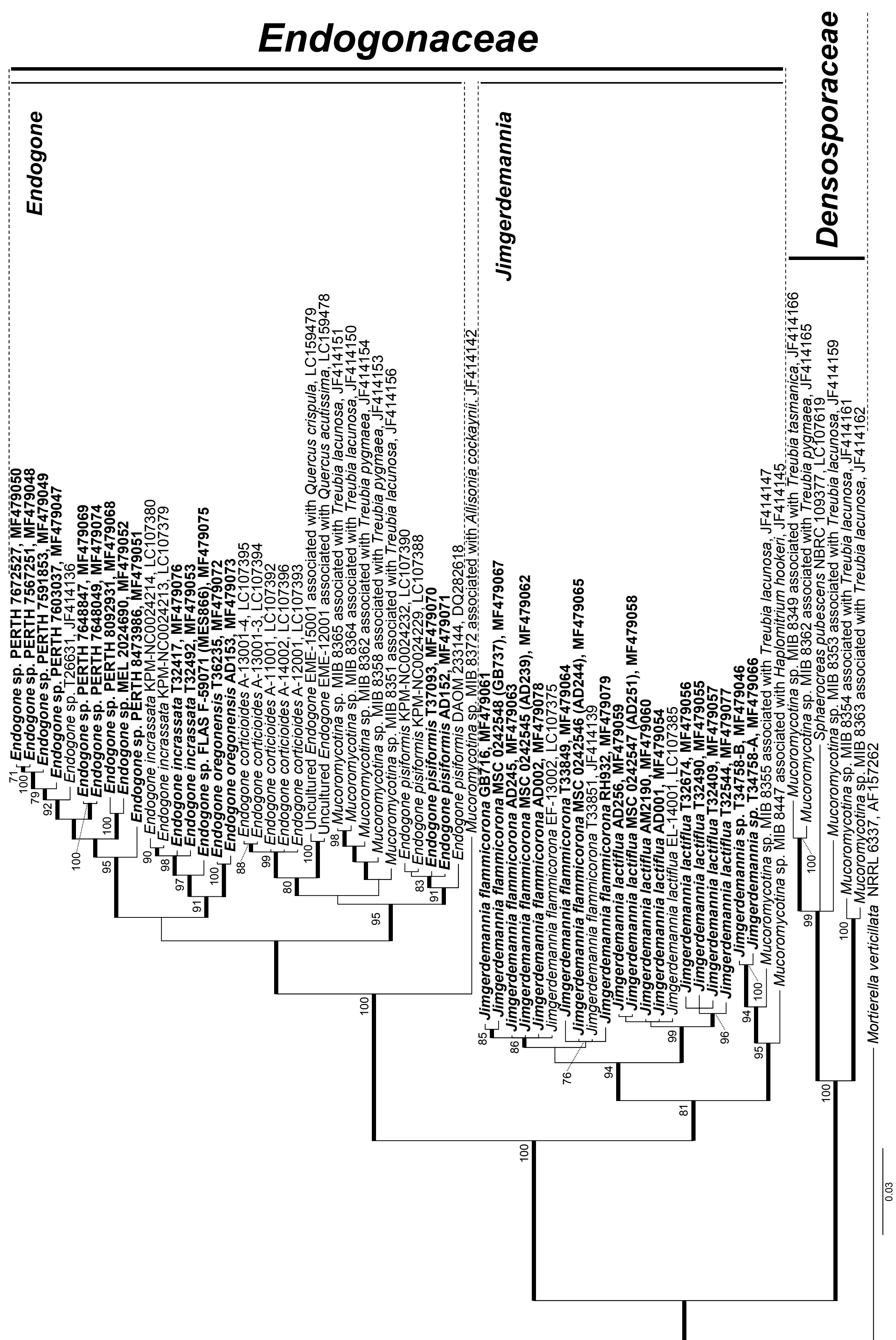
Yao YJ, Pegler DN, Young TWK (1995) *Youngiomyces*, a new genus in *Endogonales* (*Zygomycotina*). *Kew Bulletin* **50**: 349–357.

Supplementary Figure 1



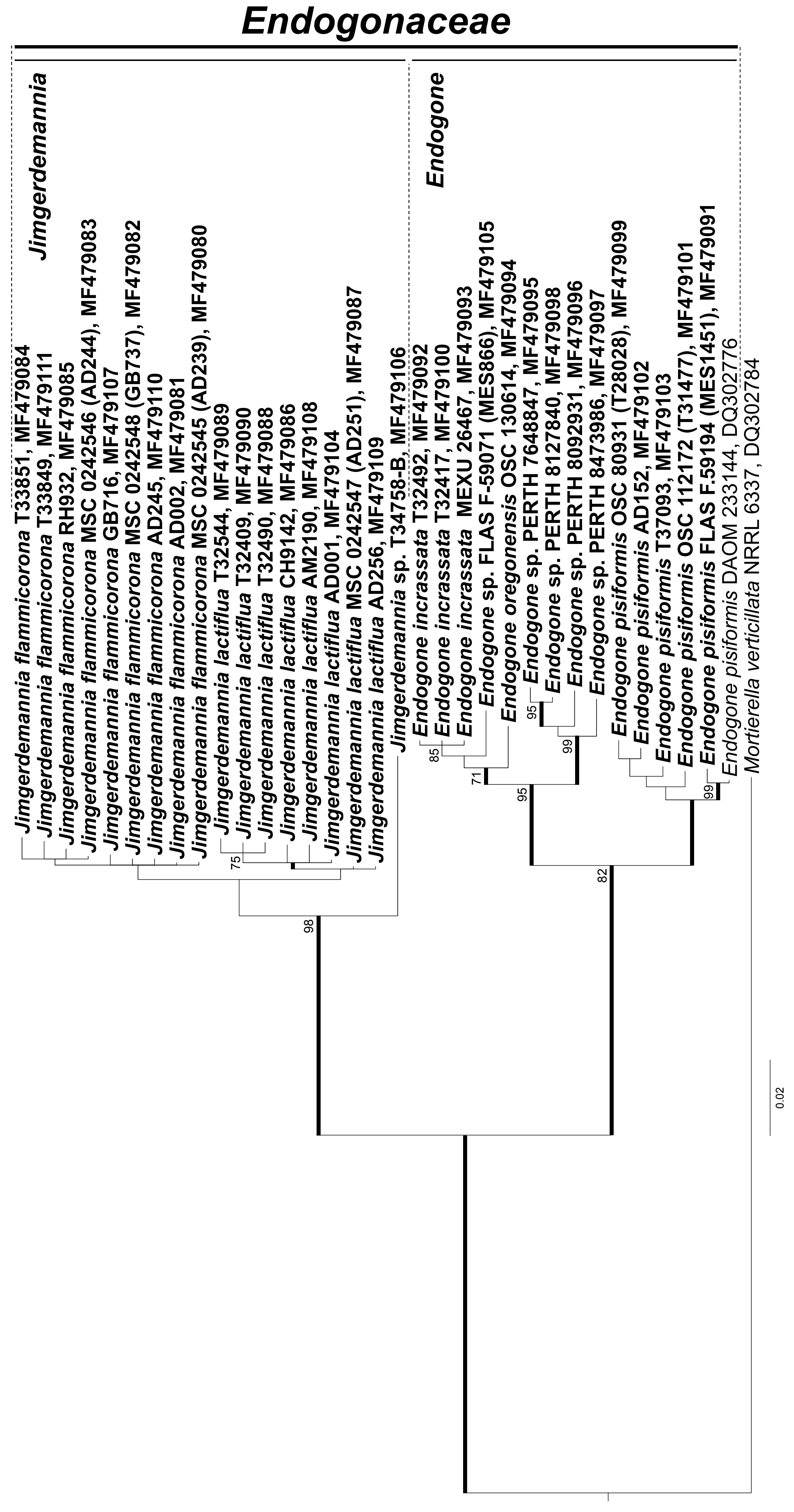
Supplementary Fig. 1. Phylogenetic reconstruction of *Endogonales* based on 28S rDNA sequences. *Mortierella verticillata* was used as outgroup. The tree shows the topology obtained with the Bayesian method; branches with Bayesian posterior probabilities ≥0.95 are thickened and ML bootstrap support values ≥70 are shown. Sequences generated in this study are in bold.

Supplementary Figure 2



Supplementary Fig. 2. Phylogenetic reconstruction of *Endogonales* based on EF1-α sequences. *Mortierella verticillata* was used as outgroup. The tree shows the topology obtained with the Bayesian method; branches with Bayesian posterior probabilities ≥0.95 are thickened and ML bootstrap support values ≥70 are shown. Sequences generated in this study are in bold.

Supplementary Figure 3



Supplementary Fig. 3. Phylogenetic reconstruction of *Endogonaceae* based on RPB2 sequences. *Mortierella verticillata* was used as outgroup. The tree shows the topology obtained with the Bayesian method; branches with Bayesian posterior probabilities ≥0.95 are thickened and ML bootstrap support values ≥70 are shown. Sequences generated in this study are in bold.

Supplementary Table 1

Supplementary Table 1. List of the specimens and related DNA sequences used in the phylogenetic reconstructions carried out in this study. The table shows the GenBank or UNITE accession number of each specimen divided by gene (18S, 28S, EF1-α, RPB2). The specimens analyzed in this study are in bold. The numbers at the apex of each specimen indicate whether that specimen was used in the 18S (1), 28S (2), EF1-α (3), RPB2 (4) and/or multigene (*) phylogenetic reconstruction.

Specimen	GenBank/UNITE Accession No.			
	18s	28s	Ef1-α	RPB2
Bifiguratus adelaidae AZ0501[1,2]	KX372677	HM123225	-	-
Bifiguratus adelaidae TLT265[1,2]	KX372676	KU702228	-	-
Bifiguratus adelaidae YP243[1,2]	KU702505	KU702551	-	-
Calcarisporiella thermophila CBS 279.70[1,2]	AB597205	AB617741	-	-
Calcarisporiella thermophila IFO 33269[2]	-	AB617739	-	-
*Calcarisporiella thermophila*NBRC 33279[1]	AB597204	-	-	-
Densospora nuda DAR 69416[1]	UDB018872	-	-	-
Densospora solicarpa DAR 69421[1,2,*]	UDB018865	UDB018864	-	-
Densospora solicarpa DAR 74956[1,2,*]	UDB018861	UDB018860	-	-
Endogone aggregata DAR 74991[1,2,*]	UDB018868	UDB018867	-	-
Endogone corticioides A-11001[1,2,3,*]	LC107350	LC107367	LC107392	
Endogone corticioides A-12001[1,2,3,*]	LC107351	LC107368	LC107393	-
Endogone corticioides A-13001-3[1,2,3,*]	LC107352	LC107369	LC107394	-
Endogone corticioides A-13001-4[1,2,3,*]	LC107353	LC107370	LC107395	-
Endogone corticioides A-14002[1,2,3,*]	LC107355	LC107372	LC107396	-
Endogone incrassata EI-11003[2]	-	LC002618	-	-
Endogone incrassata EI-12001[2]	-	LC002619	-	-
Endogone incrassata EI-12004[2]	-	LC002620	-	-
Endogone incrassata EI-12005[2]	-	LC002621	-	-
Endogone incrassata KPM-NC 0024213[1,3,*]	LC107337	-	LC107379	-
Endogone incrassata KPM-NC 0024214[1,3,*]	LC107338	-	LC107380	-
***Endogone incrassata* MEXU 26467**[1,4]	KJ952220	-	-	**MF479093**
***Endogone incrassata* T32417**[1,3,4,*]	JF414200	**MF479014**	**MF479076**	**MF479100**
***Endogone incrassata* T32492**[1,3,4,*]	JF414199	-	**MF479053**	**MF479092**
Endogone magnospora DAR 69441[1,2,*]	UDB018869	UDB018870	-	-
***Endogone oregonensis* AD153**[1,2,3,*]	**MF478989**	**MF479015**	**MF479073**	-
***Endogone oregonensis* OSC 130614**[1,4]	JF414196	-	-	**MF479094**
***Endogone oregonensis* T36235**[1,2,3,*]	**MF478990**	**MF479016**	**MF479072**	**-**
***Endogone pisiformis* AD152**[1,2,3,4,*]	**MF478991**	**MF479018**	**MF479071**	**MF479102**
Endogone pisiformis DAOM 233144[1,2,3,4,*]	DQ322628	DQ273811	DQ282618	DQ302776
***Endogone pisiformis* FLAS F-59194 (MES1451)**[1,2,4,*]	**MF478992**	**MF479020**	-	**MF479091**
Endogone pisiformis KPM-NC 0024229[1,2,3,*]	LC107346	LC107365	LC107388	-
Endogone pisiformis KPM-NC 0024232[1,2,3,*]	LC107348	LC107366	LC107390	-
***Endogone pisiformis* OSC 80931 (T28028)**[1,4]	JF414194	-	-	**MF479099**
***Endogone pisiformis* OSC 112172 (T31477)**[1,4]	KC708389	-	-	**MF479101**
***Endogone pisiformis* OSC 149839 (T37049)**[1,2]	**MF478993**	**MF479021**	-	-
***Endogone pisiformis* T37093**[1,2,3,4,*]	**MF478994**	**MF479019**	**MF479070**	**MF479103**
***Endogone* sp. FLAS F-59071 (MES866)**[1,2,3,4,*]	**MF478995**	**MF479017**	**MF479075**	**MF479105**
***Endogone* sp. MEL 2024690**[1,3,*]	**MF478996**	-	**MF479052**	-
***Endogone* sp. PERTH 7567251**[2,3,*]	-	**MF479022**	**MF479048**	-
***Endogone* sp. PERTH 7591853**[2,3,*]	-	**MF479023**	**MF479049**	-
***Endogone* sp. PERTH 7603037**[1,3,*]	**MF478997**	-	**MF479047**	-
***Endogone* sp. PERTH 7648049**[1,3,*]	KM594019	-	**MF479074**	-
***Endogone* sp. PERTH 7648847**[1,3,4,*]	KM594020	-	**MF479069**	**MF479095**
***Endogone* sp. PERTH 7672527**[1,2,3,*]	**MF478998**	**MF479024**	**MF479050**	-
***Endogone* sp. PERTH 8092931**[1,3,4,*]	**MF478999**	-	**MF479068**	**MF479096**
***Endogone* sp. PERTH 8127840**[1,4]	**MF479000**	-	-	**MF479098**
***Endogone* sp. PERTH 8473986**[3,4]	-	-	**MF479051**	**MF479097**

Supplementary Table 1. (Continued).

Specimen	**GenBank/UNITE Accession No.**			
	18s	**28s**	**Ef1-α**	**RPB2**
***Endogone* sp. T26631**[1,2,3,*]	JF414198	**MF479025**	JF414136	-
***Endogone tuberculosa* OSC 146000 (T34145)**[2,*]	-	**MF479026**	-	-
Fine root endophyte OTU0 associated with *Trifolium subterraneum*[1]	KX434773	-	-	-
Fine root endophyte OTU4 associated with *Trifolium subterraneum*[1]	KX434777	-	-	-
Fine root endophyte OTU8 associated with *Trifolium subterraneum*[1]	KX434780	-	-	-
Fine root endophyte OTU10 associated with *Trifolium subterraneum*[1]	KX434782	-	-	-
***Jimgerdemannia flammicorona* AD002**[1,2,3,4,*]	**MF479001**	**MF479027**	**MF479078**	**MF479081**
***Jimgerdemannia flammicorona* AD245**[1,2,3,4,*]	**MF479002**	**MF479028**	**MF479063**	**MF479110**
Jimgerdemannia flammicorona EF-13002[1,2,3,*]	LC107332	LC107360	LC107375	-
***Jimgerdemannia flammicorona* GB716**[1,2,3,4,*]	**MF479003**	**MF479029**	**MF479061**	**MF479107**
***Jimgerdemannia flammicorona* MSC 0242545 (AD239)**[1,2,3,4,*]	**MF479004**	**MF479030**	**MF479062**	**MF479080**
***Jimgerdemannia flammicorona* MSC 0242546 (AD244)**[1,2,3,4,*]	**MF479005**	**MF479031**	**MF479065**	**MF479083**
***Jimgerdemannia flammicorona* MSC 0242548 (GB737)**[1,2,3,4,*]	**MF479006**	**MF479032**	**MF479067**	**MF479082**
***Jimgerdemannia flammicorona* RH932**[1,2,3,4,*]	**MF479007**	**MF479033**	**MF479079**	**MF479085**
***Jimgerdemannia flammicorona* T33849**[1,2,3,4,*]	JF414204	**MF479034**	**MF479064**	**MF479111**
***Jimgerdemannia flammicorona* T33851**[1,2,3,4,*]	**MF479008**	**MF479035**	JF414139	**MF479084**
***Jimgerdemannia lactiflua* AD001**[1,2,3,4,*]	KM594016	**MF479036**	**MF479054**	**MF479104**
***Jimgerdemannia lactiflua* AD256**[1,2,3,4,*]	**MF479009**	**MF479037**	**MF479059**	**MF479109**
***Jimgerdemannia lactiflua* AM2190**[1,3,4,*]	KM594017	-	**MF479060**	**MF479108**
***Jimgerdemannia lactiflua* CH9142**[1,2,4,*]	KM594018	**MF479038**	-	**MF479086**
Jimgerdemannia lactiflua EL-14001[1,2,3,*]	LC107343	LC107364	LC107385	-
***Jimgerdemannia lactiflua* MSC 0242547 (AD251)**[2,3,4,*]	-	**MF479039**	**MF479058**	**MF479087**
***Jimgerdemannia lactiflua* T32409**[1,2,3,4,*]	**MF479010**	**MF479040**	**MF479057**	**MF479090**
***Jimgerdemannia lactiflua* T32490**[1,2,3,4,*]	**MF479011**	**MF479041**	**MF479055**	**MF479088**
***Jimgerdemannia lactiflua* T32544**[1,2,3,4,*]	JF414202	**MF479042**	**MF479077**	**MF479089**
***Jimgerdemannia lactiflua* T32674**[1,2,3,*]	JF414203	**MF479043**	**MF479056**	-
***Jimgerdemannia* sp. T34758-A**[1,2,3,*]	**MF479012**	**MF479044**	**MF479066**	-
***Jimgerdemannia* sp. T34758-B**[1,2,3,4,*]	**MF479013**	**MF479045**	**MF479046**	**MF479106**
Mortierella verticillata NRRL 6337[1,2,3,4]	NG 017188	DQ273794	AF157262	DQ302784
Mucoromycotina sp. 9152.1-D associated with *Neohodgsonia mirabilis*[1]	KR779279	-	-	-
Mucoromycotina sp. associated with *Anthoceros laminiferus*[1]	KC708434, KC708435	-	-	-
Mucoromycotina sp. associated with *Megaceros* sp.[1]	KC708436	-	-	-
Mucoromycotina sp. associated with *Phaeoceros carolinianus*[1]	KC708431, KC708441, KC708444	-	-	-
Mucoromycotina sp. associated with *Phaeomegaceros coriaceus*[1]	KC708429, KC708432, KC708433	-	-	-
Mucoromycotina sp. FT2 associated with *Treubia lacunosa*[1]	KM211581	-	-	-
Mucoromycotina sp. H2-e associated with *Haplomitrium gibbsiae*[1]	KJ921775	-	-	-
Mucoromycotina sp. JD78 associated with *Phaeoceros laevis*[1]	KC708438	-	-	-
Mucoromycotina sp. JD92 associated with *Anogramma leptophylla*[1]	KJ952217	-	-	-
Mucoromycotina sp. MES1534[1,2,*]	KY487058	KY487061	-	-
Mucoromycotina sp. MIB 8349 associated with *Paraphymatoceros coriaceus*[1,3]	JF414225	-	JF414166	-
Mucoromycotina sp. MIB 8349 associated with *Treubia tasmanica*[1]	JF414225	-	-	-
Mucoromycotina sp. MIB 8351 associated with *Treubia lacunosa*[1,3]	-	-	JF414156	-
Mucoromycotina sp. MIB 8352 associated with *Haplomitrium gibbsiae*[1]	JF414222	-	-	-
Mucoromycotina sp. MIB 8353 associated with *Treubia lacunosa*[1]	JF414214, JF414226	-	-	-
Mucoromycotina sp. MIB 8353 associated with *Treubia lacunosa*[2,3]	-	JF414167	JF414159	-

Supplementary Table 1. (Continued).

Specimen	**GenBank/UNITE Accession No.**			
	18s	**28s**	**Ef1-α**	**RPB2**
Mucoromycotina sp. MIB 8354 associated with *Treubia lacunosa*[1,2,3]	JF414215	JF414168, JF414169	JF414161	-
Mucoromycotina sp. MIB 8355 associated with *Treubia lacunosa*[2,3]	-	JF414170	JF414147	-
Mucoromycotina sp. MIB 8356 associated with *Treubia pygmaea*[1]	JF414230	-	-	-
Mucoromycotina sp. MIB 8358 associated with *Treubia pygmaea*[1,3]	JF414220	-	JF414153	-
Mucoromycotina sp. MIB 8362 associated with *Treubia pygmaea*[3]	-	-	JF414154, JF414165	-
Mucoromycotina sp. MIB 8363 associated with *Treubia lacunosa*[1,3]	JF414219	-	JF414162	-
Mucoromycotina sp. MIB 8364 associated with *Treubia lacunosa*[1,3]	JF414227	-	JF414150	-
Mucoromycotina sp. MIB 8365 associated with *Treubia lacunosa*[1,3]	JF414228	-	-	-
Mucoromycotina sp. MIB 8365 associated with *Treubia lacunosa*[1,3]	JF414228	-	JF414151	-
Mucoromycotina sp. MIB 8372 associated with *Allisonia cockaynii*[3]	-	-	JF414142	-
Mucoromycotina sp. MIB 8387 associated with *Neohodgsonia mirabilis*[1]	JF414224	-	-	-
Mucoromycotina sp. MIB 8438.2 associated with *Phaeoceros carolinianus*[1]	KC708392, KC708393	-	-	-
Mucoromycotina sp. MIB 8439 associated with *Paraphymatoceros coriaceus*[1]	JF414225	-	-	-
Mucoromycotina sp. MIB 8443 associated with *Anthoceros laminiferus*[1]	KC708394	-	-	-
Mucoromycotina sp. MIB 8445 associated with *Phaeoceros carolinianus*[1]	KC708396	-	-	-
Mucoromycotina sp. MIB 8447 associated with *Haplomitrium hookeri*[1,3]	JF414213	-	JF414145	-
Mucoromycotina sp. MIB 8448 associated with *Haplomitrium blumei*[1]	JF414211	-	-	-
Mucoromycotina sp. MIB 8478 associated with *Paraphymatoceros* sp.[1]	JF414207	-	-	-
Mucoromycotina sp. MIB 8532 associated with *Anthoceros agrestis*[1]	KC708397	-	-	-
Mucoromycotina sp. MIB 8533 associated with *Phaeoceros laevis*[1]	KC708398	-	-	-
Mucoromycotina sp. MIB 8550 associated with *Phaeoceros laevis*[1]	KC708399	-	-	-
Mucoromycotina sp. MIB 8553.2 associated with *Anthoceros* sp.[1]	KC708400	-	-	-
Mucoromycotina sp. MIB 8627.1 associated with *Anthoceros punctatus*[1]	KC708404	-	-	-
Mucoromycotina sp. MIB 8771 associated with *Phaeomegaceros coriaceus*[1]	KC708406, KC708407	-	-	-
Mucoromycotina sp. MIB 8779 associated with *Megaceros leptohymenius*[1]	KC708408	-	-	-
Mucoromycotina sp. MIB 8783 associated with *Phaeoceros carolinianus*[1]	KC708411	-	-	-
Mucoromycotina sp. MIB 8783 associated with *Phaeomegaceros coriaceus*[1]	KC708409	-	-	-
Mucoromycotina sp. MIB 8792 associated with *Phaeoceros carolinianus*[1]	KC708412	-	-	-
Mucoromycotina sp. MIB 8797 associated with *Phaeomegaceros coriaceus*[1]	KC708413, KC708415, KC708416	-	-	-
Mucoromycotina sp. MIB 8802 associated with *Anthoceros laminiferus*[1]	KC708417	-	-	-
Mucoromycotina sp. MIB 8827 associated with *Phaeoceros carolinianus*[1]	KC708419	-	-	-
Mucoromycotina sp. MIB 8841 associated with *Phaeoceros dendroceroides*[1]	KC708420	-	-	-
Mucoromycotina sp. MIB 8842 associated with *Phaeoceros dendroceroides*[1]	KC708421	-	-	-
Mucoromycotina sp. MIB 8846 associated with *Phaeoceros carolinianus*[1]	KC708423, KC708440	-	-	-
Mucoromycotina sp. MIB 8860 associated with *Anthoceros* sp.[1]	KC708425, KC708426	-	-	-
Mucoromycotina sp. MIB 8861 associated with *Folioceros* sp.[1]	KC708427	-	-	-
Mucoromycotina sp. MIB 8873 associated with *Phaeoceros carolinianus*[1]	KC708428	-	-	-
Mucoromycotina sp. T1-a associated with *Treubia lacunosa*[1]	KJ921770	-	-	-
Mucoromycotina sp. T3-e associated with *Treubia lacunosa*[1]	KJ921773	-	-	-
Mucoromycotina sp. Th6-2 associated with *Lycopodiella inundata*[1]	KJ952212	-	-	-
Mucoromycotina sp. Th6-4 associated with *Lycopodiella inundata*[1]	KJ952213	-	-	-
Mucoromycotina sp. Th8a-4 associated with *Lycopodiella inundata*[1]	KJ952214	-	-	-
Mucoromycotina sp. WR148.B-B associated with *Lycopodium fastigiatum*[1]	KJ952219	-	-	-

Supplementary Table 1. (Continued).

Specimen	**GenBank/UNITE Accession No.**			
	18s	**28s**	**Ef1-α**	**RPB2**
Mucoromycotina sp. WR330-B associated with *Neohodgsonia mirabilis*[1]	KR779282	-	-	-
Mucoromycotina sp. WR343.b-B associated with *Allisonia cockaynei*[1]	KR779277	-	-	-
Mucoromycotina sp. WR865-D associated with *Anogramma leptophylla*[1]	KJ952232	-	-	-
Sphaerocreas pubescens KPM-NC 22969[1]	AB752291	-	-	-
Sphaerocreas pubescens KPM-NC 22971[1]	AB755408	-	-	-
Sphaerocreas pubescens KPM-NC 22973[1]	AB752293	-	-	-
Sphaerocreas pubescens NBRC 109377[1,2,3,*]	AB752295	LC107618	LC107619	-
Sphaerocreas pubescens SP-11002[2]	-	LC002631	-	-
Uncultured ectomychorrizal *Endogone* EME-12001[1,2,3,*]	LC159474	LC159476	LC159478	-
Uncultured ectomychorrizal *Endogone* EME-15001[1,2,3,*]	LC159475	LC159477	LC159479	-
Uncultured ectomycorrhizal *Mucoromycotina* on *Eucalyptus regnans* L3138[1,2]	UDB002714	UDB002714	-	-
Uncultured ectomycorrhizal *Mucoromycotina* on *Nothofagus cunninghamii* L3656[1,2]	UDB004033	UDB004033	-	-