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A systematic overview of *Descolea* (*Agaricales*) in the *Nothofagaceae* forests of Patagonia

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Research highlights

The genus *Descolea* is emended in light of new and historical Patagonian collections.

A new sequestrate *Descolea* species is described from Patagonia.

Two sequestrate species of *Cortinarius* (*Thaxterogaster*) are transferred to the genus *Descolea*.

Morphological variation within *Descolea* and key characters for delimiting this genus are discussed.

Abstract

The descolea clade includes species of ectomycorrhizal basidiomycetes in the genera *Descolea*, *Setchelliogaster*, *Descomyces*, and *Timgrovea* that are known primarily from the Southern Hemisphere. Taxa in this group produce basidiomes that range in morphology from typical epigeous mushrooms (*Descolea*) and secotioid taxa (*Setchelliogaster*) to fully gasteroid species (*Descomyces* and *Timgrovea*). High intraspecific morphological variation has been reported in several species within this clade, suggesting that careful morphological and molecular studies are needed to refine species concepts. Molecular analyses of fresh Patagonian collections in conjunction with taxonomic studies have confirmed high variability in key morphological features, including overall sporocarp form, spore shape and dimensions, universal veil remnants and cuticle configuration. Based on our synthesis, we emend the genus *Descolea* to include sequestrate species. We describe the new sequestrate taxon *Descolea inferna* sp. nov. from *Nothofagaceae* forests in Patagonia and we propose *Thaxterogaster squamatus* as a synonym of our new combination *Descolea brunnea*. We also formalize the identity of *Descolea pallida* as a synonym of *D. antarctica* and provide new specimens of *Thaxterogaster archeuretus*, a species that has not been encountered since the original discovery during the expeditions of Roland Thaxter in 1905-1906. Here we re-describe and transfer this species to *Descolea* as *D. archeureta*. We also discuss diagnostic features that can be used to delimitate the four known South American taxa in the descolea clade.

Keywords: *Setchelliogaster*, *Descomyces*, *Timgrovea*, secotioid, hypogeous, South America.

1. Introduction

Close affinities between the genus *Descolea* and the sequestrate taxa *Setchelliogaster*, *Descomyces*, and *Timgrovea* have been previously inferred based on morphology (Lago et al. 2001) and also via molecular data (Peintner et al. 2001, Tedersoo and Smith 2013). This group of fungi has been referred to as the ‘descolea clade’ by Peintner et al (2001) or the /descolea lineage by Tedersoo and Smith (2013). Multilocus phylogenetic studies suggest that this lineage belongs to the family *Bolbitiaceae* and is distantly related to other macroscopically similar, brown-spored lineages of ectomycorrhizal fungi (e.g. *Cortinarius*, *Hebeloma*, *Hymenogaster*) (Matheny et al. 2006). Taxa within the descolea clade produce basidiomes that range in morphology from typical agaricoid mushrooms (*Descolea*) or secotioid taxa (*Setchelliogaster*) to fully gasteroid forms (*Descomyces* and *Timgrovea*). These are ectomycorrhizal fungi that are mostly restricted to forests of Australasia and southern South America. They are usually associated with *Nothofagaceae* and *Myrtaceae* host plants but at least two epigeous species have been reported from Asia with other hosts (e.g. *D. flavoannulata* in Japan and Siberia, *D. pretiosa* in India) (Horak 1971, Bougher and Castellano 1993, Tedersoo et al. 2010). Taxa in the descolea clade have brown limoniform spores that lack a germ pore but always have a more or less hyaline, ornamented utricle that covers the spores. The ornamented utricle is present in epigeous *Descolea* species (Singer 1949) but is much more developed and obvious in many of the sequestrate taxa in this group (Bougher and Castellano 1993, Danks et al. 2010). A fully developed universal veil that may remain until maturity is also frequent in some taxa within this group but it is not obvious in all collections or species (Horak 1971).

Pouzar (1958) erected the genus *Setchelliogaster* to accommodate species of the descolea clade that produce secotioid basidiomes with *Setchelliogaster tenuipes* (Setch.) Pouzar (=*Secotium tenuipes* Setch.) as the type species.The genera *Descomyces* and *Timgrovea* were originally described by Bougher and Castellano (1993) to accommodate hypogeous sequestrate taxa originally placed in the genus *Hymenogaster* (which is phylogenetically aligned with epigeous species of *Alnicola* and *Hebeloma* – Matheny et al. 2006). Bougher and Castellano (1993) recognized that *Descomyces* and *Timgrovea* shared some morphological similarities with the agaricoid species of *Descolea* as well as the secotioid species of *Setchelliogaster* but they reasoned that these fully sequestrate lineages were morphologically and ecologically unique and therefore required separate genus-level recognition. However, molecular analyses of Peintner et al. (2001) and the morphological analysis by Lago et al (2001) have confirmed the close and complex relations between *Descolea*, *Descomyces*, *Timgrovea* and *Setchelliogaster* and suggest that further taxonomic and phylogenetic studies are needed (Lago et al. 2001, Peintner et al. 2001). Although Peintner et al. (2001) confirmed the close evolutionary relationships among these lineages, their phylogenetic analyses suggested that gasteroid and secotioid taxa (e.g. *Descomyces*, *Timgrovea* and *Setchelliogaster*) likely arose multiple times due to convergent evolution.

High morphological variation was reported for some species within the descolea clade by Lago et al. (2001), who found high variability in the spore dimensions and also in the presence and morphology of cystidia. They concluded that broader species concepts are needed within this lineage to accommodate variable intraspecific morphological features. They also determined that generic boundaries are not always clear. For example, the generic boundary between *Descolea* (epigeous, agaricoid basidiomes) and *Setchelliogaster* (secotioid basidiomes) is transgressed by some taxa (e.g. *Descolea maculata*, *D. gunni*) that can produce basidiomes of both types (Lago et al. 2001). This exceptional intraspecific variability was previously described by Cribb (1956), when she studied the spore morphology and development of *Descomyces albus* (Berk.) Bougher and Castellano (as *Hymenogaster albus*).

There are currently 15 accepted species and five varieties of *Descolea* (according to Index Fungorum http: //www.indexfungorum.org/) but only two described species are known from Patagonia. *Descolea antarctica* was described from the forests of Tierra del Fuego by Singer (1951) as the type species, whereas *Descolea pallida* was later described by Horak (1971) from Valdivian forests of coastal Chile. *Descolea pallida* was separated from *D. antarctica* based on the geographic distribution as well as the spore size and color differences of the cap and veil remnants. However, both Singer (1954) and Horak (1971) discussed the difficulty in differentiating these two species by their morphological characteristics.

In addition, the sequestrate taxa within the clade are taxonomically confused for several reasons. First, the original species descriptions for some of the sequestrate taxa are based on specimens preserved in liquid rather than fresh collections and this made it challenging to accurately describe these taxa (Halling 1981). Second, there are longstanding issues regarding the proper generic names to use for gasteroid and secotioid taxa so some species have been described in different genera. Third, some prominent taxonomists have disagreed about nomenclatural synonyms and the proper names to use for these taxa, leaving the final number of species in doubt. Amidst this ongoing debate Index Fungorum currently lists six species in the genus *Descomyces*, five in *Timgrovea* and seven species plus three varieties in *Setchelliogaster*.

In the light of the morphological plasticity of basidiomes and the difficulty in establishing limits between agaricoid and secotioid genera, some authors have responded by transferring species with secotioid basidiomes to *Descolea* (e.g. *Descolea tenuipes* (Setch.) Neville & Poumarat, *Descolea gunnii* (Berk. ex Massee) Horak). However the acceptance of those names is not yet complete and currently some authors still treat hypogeous species under the sequestrate genus names (e.g. Cortez et al. 2008, Nouhra et al. 2008, Pennington et al 2011)

The first discoveries of brown-spored, sequestrate basidiomycetes from Patagonia came from the expedition of Roland Thaxter, who visited *Nothofagaceae* forests in Chile and Argentina during an extended collecting trip in 1905-1906 (Halling 1981). Thaxter took notes in the field but there are no photographs of his collections. Due to the difficulties of traveling in the early 1900's, he was unable to dry all specimens and could only keep small portions of each specimen in liquid preservatives. His preserved collections and notes were returned to the Farlow Herbarium at Harvard University and were later studied and described by Dodge and Zeller (1934) and Halling (1981).

Among Thaxter's collections from Patagonia, Zeller and Dodge (1934) examined a sequestrate specimen (Hymenogaster No. 1, FH accession #4635) that they identified as the previously described Tasmanian species *Hymenogaster albellus* Massee & Rodway (Massee and Rodway 1898). Horak (1963) later described a morphologically similar taxon under the name *Hypogea brunnea* Horak. This species was later transferred by Singer (1971) to *Setchelliogaster* as *S. brunneus* (Horak) Singer. Although Horak (1979) identified Thaxter's collection as *S. brunneus*, this material was discussed by Dodge and Zeller (1934) and morphologically characterized by Halling (1981) under the name *Hymenogaster albellus*.

In a detailed revision of Thaxter's materials, Halling (1981) also described two new *Thaxterogaster* species, *T. squamatus* and *T. archeuretus*. *Thaxterogaster squamatus* was distinguished by its limoniform, utriculate spores, two-spored basidia and notable veil remnants whereas *T. archeuretus* was distinguished by four-sterigmate basidia, and limoniform, utriculate spores that are smaller than any other known utriculate *Thaxterogaster* species.

Moser and Horak (1975) suggested that *Thaxterogaster* was nested within *Cortinarius* and the paraphyly of *Cortinarius* and polyphyly of *Thaxterogaster* were later verified using molecular data by Peintner et al. (2001). Based on these studies that focused on a subset of species, all described *Thaxterogaster* species were subsequently transferred to *Cortinarius* (Peintner et al. 2002). However, some taxa such as *Cortinarius squamatus* (Halling) Peintner & Moser have spores and cystidia that suggest an evolutionary relationship with *Descolea* rather than *Cortinarius*. These findings suggest that a critical review of sequestrate taxa currently treated in the genus *Cortinarius* is needed to determine the phylogenetic and taxonomic affinities of these taxa.

Based on Thaxter's materials, a hypogeous sequestrate species was described by Dodge and Zeller (1934) as *Hymenogaster fragilis*. However, this species was later transferred to *Thaxterogaster* (Smith apud Singer 1962) and synonymized with *Setchelliogaster tetrasporum* Singer by Horak (1979) under the new combination *Setchelliogaster fragilis* (Zeller & C.W. Dodge) E. Horak. Halling (1981) provides a detailed discussion of the morphology of this species based on Thaxter's original collections. Peintner et al. (2001) confirmed the affiliation of this taxon within the genus *Cortinarius* under the name *C. fragilis* (Zeller & C.W. Dodge) Peintner & Moser using DNA sequences from Australian specimens. This relationship has been recently confirmed based on South American material; Chilean collections of "*Hymenogaster fragilis*" are related to *Cortinarius* and not *Setchelliogaster* (F. Kuhar, unpublished data).

Recent collecting expeditions during 2008–2016 in Patagonian *Nothofagaceae* forests have yielded numerous collections of both epigeous and hypogeous members of the descolea clade. Microscopic analyses of these specimens indicate the difficulty of using morphological features to assign these specimens to described species and suggest that molecular studies are needed to resolve these problems. Furthermore, a recent study of ectomycorrhizal fungal communities of Patagonian *Nothofagaceae* species (*Nothofagus dombeyi*, *Lophozonia obliqua*, and *L. alpina*) suggests that at least two taxa in the descolea clade can be locally common on ectomycorrhizal roots (referred to as '*Descomyces* sp. 1' and '*Descolea* sp. 1') (Nouhra et al 2013).

The purpose of this study was to critically assess the morphology and molecular phylogeny of members of the descolea clade to determine their diversity in Patagonian *Nothofagaceae* forests. Our main goals were to determine the number of species that are present based on both morphological and molecular data and also to ascertain the best taxonomic names and genus-level placement for each of these phylogenetically distinct taxa. We also reviewed the published taxonomic literature and examined type specimens of hypogeous sequestrate taxa described from Patagonia to determine appropriate names and synonyms.

2. Materials and Methods

Specimens (e.g. *Descolea*, *Descomyces*, and *Setchelliogaster* among other taxa) were collected in spring and autumn 2008–2016, photographed and dried on a forced air drier.

Additional specimens were obtained from the following herbaria: Florida Museum of Natural History (FLAS), the Farlow Herbarium at Harvard University (FH), the New York Botanical Garden (NY), Herbario del Museo Botánico de Córdoba (CORD), Universidad Nacional de La Plata Herbarium (LP) and Museo Nacional de Historia Natural de Chile (SGO). New collections were deposited at FH, FLAS, SGO, and CORD. Dried material was rehydrated and mounted in water, 3% KOH, Melzer's reagent, and cotton blue. Spores were measured in 3% KOH solution. Spore measurements include the hilar appendix but do not include spore ornamentation or the utricle. Length and width measurements were used to calculate length to width ratios (Qr).At least 20 different measurements were averaged to estimate all size values. Variation in the cuticle was also observed and characterized by examining thin cross-sections from multiple specimens of each species.

DNA was extracted from basidiomes following a modified cetyltrimethylammonium bromide (CTAB) method (Gardes and Bruns, 1993) or using the Extract n' Amp DNA extraction kit (Sigma-Aldrich, St. Louis, MO, USA) following manufacturers protocols. PCR for the internal transcribed spacer region (ITS1–5.8s–ITS2, hereafter referred to as ITS) was performed with forward primers ITS1F and reverse primers ITS4 or ITS4B. The PCR conditions were: 94°C for 5 min followed by 35 cycles of 1 min at 94°C, 1 min at 55°C and 2 min at 72°C, followed by 7 min at 72°C. The PCR products were visualized on 1.5% agarose gels with SYBR Green I (Molecular Probes, Eugene, OR, USA) and purified with ExoSAP®-IT (USB) following the manufacturer's instructions. Sanger sequencing was conducted at the Interdisciplinary Center for Biotechnology Research at the University of Florida and in Macrogen (Seoul, South Korea). Sequences were edited with Sequencher v.4.1 (Gene Codes Inc., Ann Arbor, MI, USA).

The obtained sequences were used as "Blastn" search queries against the UNITE database (https: //unite.ut.ee/) and "Megablast" search queries against Genbank (http: //www.ncbi.nlm.gov).Available high quality, vouchered ITS sequences of the genera *Timgrovea*, *Setchelliogaster*, *Descomyces* and *Descolea* were included in the analysis. We also included ectomycorrhizal (ECM) root tip sequences of '*Descomyces* sp. 1' and '*Descolea* sp. 1' obtained by Nouhra et al. (2013) from the roots of Patagonian *Nothofagaceae* species. High quality sequences of the genera *Cortinarius* and *Hebeloma* were used as outgroups, as in Paintner et al. (2001). All sequences analyzed are listed in the Table 1.

Sequences were aligned using L-INS-i strategy as implemented in MAFFT v 7.0 (Katoh and Standley 2013). The aligned matrix is available from TreeBASE (http://purl.org/phylo/treebase/phylows/study/TB2:S21186). Ambiguously aligned regions were eliminated using Gblocks (Castresana 2000) available fom http: //molevol.cmima.csic.es/castresana/Gblocks.html, allowing smaller final blocks, gap positions within the final block and less strict flanking positions for a less stringent selection. Maximum likelihood (ML) analysis was performed in PHYML as implemented on the South of France bioinformatics platform (http: //www.atgc-montpellier.fr/phyml/) (Guindon and Gascuel 2003; Guindon et al. 2010) using the GTR+G+I substitution model as estimated in PHYML. Bootstrap support values were calculated with 1,000 repetitions. Bayesian analyses were conducted with MrBayes (Huelsenbeck and Ronquist 2001). The analyses were run for 10,000,000 generations starting with a random tree and employing four simultaneous chains. The first 80,000 generations (i.e., 8,000 trees) were discarded as the burn-in. TRACER1 (http: //evolve.zoo.ox.ac.uk/software.html/tracer/) was used to ensure that stationarity was achieved after the first 100,000 generations. Maximum Parsimony (MP) analyses were performed using PAUP 4.0 (Swofford 2002). Support values given in the text correspond to Maximum Likelihood Bootstrap (BS) and Bayesian Posterior Probabilities (PP).

3. Results

3.1 Phylogenetic analysis

Analyses based on ITS rDNA confirmed that members of the descolea clade (e.g. species of *Timgrovea*, *Descomyces*, *Setchelliogaster* and *Descolea*) are closely related and form a strongly supported monophyletic group (BS 1.00; PP 0.99) (Fig 1). The placement of secotioid and sequestrate taxa across multiple branches of the phylogeny indicate that sequestrate forms have arisen multiple times within the descolea clade (as previously determined by Peintner et al. 2001).

Regardless of their preliminary morphological determinations, the Patagonian sequences from sequestrate and epigeous descolea clade taxa were resolved into four different well-supported clades. Epigeous specimens from across a wide geographical range and morphologically identified as *Descolea antarctica* and *D. pallida* were resolved in just one clade with minimal ITS variation (0.02%) among specimens (BS 1.00; PP 0.99) (Fig 1). These results indicate that these should be treated as a single morphologically variable taxon *D. antarctica*.

Despite the high morphological variation among the sequestrate specimens, we resolved three distinct clades that can be distinguished based on both macroscopic and microscopic characters. One of the well-supported sequestrate clades BS (1.00, PP 1.00) (*Descolea brunnea*) showing 0.03% ITS variation includes morphologically variable specimens initially identified under different genera and species names. However, all collections are brownish in color, have spores >17 µm, and have two spores per basidium.

A second well-supported monophyletic clade of almost identical ITS sequences (BS 0.93, PP 0.99) (Fig 1) includes a small number of sequestrate specimens from northern Patagonia. Specimens in this group have a distinctly yellow color when fresh, have spores smaller than 17 µm in length, and four spores per basidium. Members of this clade do not fit the descriptions of any known species and are described below as *Descolea inferna* sp. nov. based on unique morphological and molecular characters.

Two other sequestrate collections form a third well supported clade. After detailed study and comparison with the *Cortinarius archeurethus* (=*Descolea archeureta* comb. nov.) holotype collection, one of them (MES1786) was matched to *C. archeurethus*. The second collection (MES1584) was too rotten at the time of collection to be morphologically characterized but is also regarded here as *Cortinarius* aff. *archeuretus* (=*Descolea archeureta* comb. nov. based on molecular data).

3.2 Taxonomy

Our phylogenetic results and evidence from previous studies (e.g. Lago et al. 2001, Peintner et al. 2001) indicate that the descolea clade is a monophyletic ectomycorrhizal lineage with high intraspecific morphological variation and multiple origins of secotioid and gasteroid forms. In order to avoid polyphyletic entities resulting from the process of convergent evolution to sequestrate forms, we emend the genus *Descolea* to include secotioid and sequestrate taxa that belong to the descolea clade.

We have extensively studied the Patagonian species and provide molecular evidence for the placement of these taxa as well as an overview of the synonyms that have been historically used. We also recombine other sequestrate taxa that putatively belong to the descolea clade based on available evidence, including a combination of morphological, host association, and biogeographical data. For example, several sequestrate taxa treated below were first described from South America and collected under exotic ectomycorrhizal *Myrtaceae* of Australasian origin. We have identified a few additional species that have been treated in various genera of the descolea clade (e.g. *Descomyces*) but seem likely to belong to other fungal lineages. We conservatively refrain from transferring these outlier taxa and provide a rationale for excluding these from *Descolea* until more data are available.

Descolea (Sing.) emend. Kuhar, Nouhra & M.E. Smith.

Basidiomes agaricoid to secotioid or fully gasteroid. Stipe sometimes reduced to a turbinate base that easily breaks apart in some secotioid basidiomes and remains only as a percurrent columella in fully gasteroid basidiomes. Spore wall ornamentation, if present, of exosporial - perisporial origin, frequently constituting an embedding utricle. Type: *Descolea antarctica* Sing., Lilloa, 23: 527. (1950).

Descolea inferna Kuhar, Nouhra & M.E. Smith sp. nov. (figs 2E and 3E-F)

MycoBank No.: MB817784

UNITE SH: SH444912.07FU

Type: **Argentina**: Neuquén, Huiliches, Lanín National Park, path to Mirador Curruhé Grande, *Araucaria araucana* and *Nothofagus dombeyi* mixed forest, 17 May 2015, Rosanne Healy (holotype CORD MES1315), Isotype FLAS-F-60295, GenBank accession: ITS = KY523090.

Diagnosis: Basidiomes secotioid, not exposing the hymenophore, yellow, hypogeous. Stipe turbinate and fragile. Basidia bearing 2-3-4 sterigmata. Spores 14 - 17 × 8.5 - 9.5 beaked to sublimoniform.

Etym.: from the latin *infernus*, “of the lower world”, in reference to the hypogeous habit of this species.

Basidiomes 2 × 2.5 cm, hypogeous, globose to depressed, incurvate, not exposing the hymenophore at maturity, dry, smooth, devoid of scales or other visible velum remnants, yellowish, turning brown in age. Pileal (peridial) trama 0.5 - 2 mm thick. Hymenophore galericulate (fully enclosed, refered to in literature on gasteroid fungi as a gleba), hyaline to white when immature, reddish brown in age, consisting of irregular locules up to 0.2 mm diam. Stipe 0.4 - 1 × 0.5 1.1 cm, reduced, constituted by a fragile sterile turbinate base that easily breaks apart, percurrent through as a narrow columella, dry, whitish to yellow.

Spores 14 - 17 × 8.5 - 9.5 µm (Qr=1.72), slightly beaked to sublimoniform, covered by a pigmented irregular utricle of variable thickness that frequently leaves the smooth rostrum uncovered. Cuticle consisting of inflated terminal elements interwoven with cylindrical hyphae (7 - 15 µm) incrusted with yellowish pigments. Pileal (peridial) trama of thick hyphae organized in a hyaline inner layer of thin walled hyphae and an outer layer of thick-walled elements with golden yellow content. Cystidia 20 - 35 × 4 - 9 µm, claviform to capitate, rare in some collections. Basidia 28 - 33 × 10 - 15 µm, clavifom, bearing four (occasionally two - three) sterigmata.

Habitat habit and distribution: hypogeous, in wet habitats, under *Nothofagus pumilio*, *N. dombeyi* and *N. antarctica* in North Patagonia in Argentina and Chile.

Other specimens examined: **Argentina**: Neuquén, Nahuel Huapi National Park, 17 km north of Villa La Angostura, near Lago Espejo, under *N.dombeyi*, 28 March 1988, R. Halling (Halling 5915). Río Negro, Nahuel Huapi National Park, halfway to Tronador, open *N. antarctica* forest, 9 May 2015, M. E.Smith, (CORD, FLAS-F-60291, MES1132), GenBank accessions: ITS KY523086; Los Rápidos, *N.antarctica* forest, 11 May 2015, M.E. Smith, (CORD, FLAS-F-60293, MES1228); near Lago Hess, open *N.antarctica* forest, 16 May 2016, L. Fernandez, (CORD, FLAS-F-60304, MES2067), GenBank accessions: ITSKY523099. **Chile**: Osorno, Puyehue National Park, below Antillanca Ski Area, on the edge of the road near dry riverbed area, with *N.pumilio*. 6 May 2016, R. H. Healy, (FLAS-F-60299, MES 1730, SGO 167980), GenBank accessions: ITSKY523095.

Additional notes: Descolea inferna is one of the four *Descolea* species known from the *Nothofagaceae* forests of Patagonia. This species is readily distinguished from the epigeous *D. antarctica* by its gasteroid, hypogeous fruiting habit. Although *Descolea inferna* is superficially similar to *Descolea brunnea*, the new taxon *D. inferna* is differentiated by a yellow pileus (peridium), four-sterigmate basidia and spores that are 14–17 × 8.5–9.5 µm (compared to those of *D. brunnea* which are 17.5 - 22 (24) × 8.5 - 13 µm). S imilar species described in the literature are *Cortinarius archeuretus* (Halling) Peintner & M.M. Moser (transferred below to *Descolea* as *D. archeureta*), with smaller spores (12-14 × 6.5-7.5) and dull purplish brown basidiomes, and the highly variable *Setchelliogaster australiensis* G.W. Beaton, Pegler & T.W.K. Young (transferred below to *Descolea* as *D. australiensis*), with larger asymmetrical spores (11 - 18.3 (20.8) × 6.3 - 9.9 (11.5) µm) and lacking hymenial cystidia. One specimen collected by Halling and deposited in NY as "*Hymenogaster*" (Halling 5915) is a specimen of *D. inferna*. This collection was annotated by Dr. Michael Castellano in 1993 as "*Descomyces* sp. nov."

Descolea alba (Berk) Kuhar, Nouhra, & M.E. Smith comb. nov.
MycoBank No.: MB817791
UNITE SH: SH300040.07FU
Basionym: *Rhizopogon albus* sensu Berkeley, English Flora 5(2): 229. 1836.
Synonyms: *Hymenogaster albus* Berk., Ann. Mag. nat. Hist., Ser. 1 13: 349. 1844.
Hymenangium album Klotzsch, in Dietrich, Fl. Regn. Boruss. 7: 466. 1839.
*Splanchnomyces albus (*Klotzsch) Corda, in Zobel, Icon.fung. (Prague) 6: 40, tab. 8: 82. 1854.
Descomyces albus (Berk.) Bougher & Castellano, Mycologia 85(2): 280 (1993)
Hymenogaster klotzschii Tul. & C. Tul., Fungi hypog. 64. 1851.
Hymenogaster cerebellum Cavara, Atti Ist. Bot. R. Univ. Pavia, 2 Sér. 3: 211-229 (1893)

Descolea albella (Massee et Rodway) Kuhar, Nouhra, & M.E. Smith comb. nov.
MycoBank No.: MB817793
UNITE SH: SH300097.07FU
Basionym: *Hymenogaster albellus* Massee & Rodway in Massee, Kew Bull. Misc. Inform. 1898.
Synonyms: *Descomyces albellus* (Massee et Rodway) Bougher et Castellano, Mycologia 85(2): 290. 1993.
Hymenogaster zeylanicus Petch, Ann. Roy. Bot. Gard. (Peradeniya) 6: 207. 1917.
Hymenogaster maideni Rodway, Pap. & Proc. Roy.Soc. Tasmania 1920: 157. 1921.

Descolea angustispora (A.A. Francis & Bougher) Kuhar, Nouhra, & M.E. Smith comb. nov.

MycoBank No.: MB817795

UNITE SH: SH281415.07FU

Synonym: *Descomyces angustisporus* A.A. Francis & Bougher, Australas. Mycol. 23(1): 15. 2004.

Descolea antarctica Singer (figs 2A and 3B)

MycoBank No.: MB296578

UNITE SH: SH300036.07FU

Singer, Lilloa, 23: 527. (1950).

Synonyms: *Descolea pallida* E. Horak, Persoonia 6: 237 (1971).

Descolea lepiotiformis Raith., Hongos Argentinos 2: 128 (1977).

Pseudodescolea lepiotiformis (Raith.) Raith., Metrodiana 9: 48 (1980).

Descolea recedens sensu Singer, Sydowia 9: 407 (1955)

Specimens examined: **Argentina**: Chubut, Parque Nacional los Alerces, Sendero a Puerto Chucao,*N. dombeyi* and *Austrocedrus chilensis* mixed forest, 8 May 2013, F. Kuhar (EN382), GenBank accessions: ITS KY523077. Neuquén, Nahuel Huapi National Park, Ultima Esperanza/Lago Espejo Trail, *N. antarctica* and *N. dombeyi* mixed forest, 13 May 2015, P. B. Matheny (CORD, FLAS-F-60294, MES1242), GenBank accessions: ITS KY523089.Río Negro, Nahuel Huapi National Park, Los Rapidos, under *N. antarctica*. 11 May 2015, B. Matheny (CORD, FLAS-F-60292, MES 1195), GenBank accessions: ITS KY523088; road to Tronador below Pampa Linda, 14 May 2016, M. E. Smith & F. Kuhar (CORD, FLAS-F-60303, MES2016), GenBank accessions: ITS = KY523098. Tierra del Fuego, Ushuaia, Paso de las ovejas, solitary under *N. pumilio* 20 Feb 2015, C. Truong (CT-4237), GenBank accessions: ITS = MF085057; Valle Andorra, solitary, *N. antarctica* spot near transition to *N. pumilio* 16 Feb2015, C. Truong (CT-4235). GenBank accessions: ITS = MF085056. **Chile**: Los Ríos, Ranco, Along road T-80 between La Union and Hueicolla before Alerce Costero natural monument, mixed forest with *N. dombeyi*, *Lophozonia alpina*, and mixed *Myrtaceae,* 1 May 2015, M. E. Smith (FLAS-F-60286, MES917, SGO 167983), GenBank accessions: ITS KY523081.

Additional notes: Both Horak and Singer identified morphological differences between *Descolea* specimens collected in the far south of Patagonia (‘the Fuegian region’) and those from forests of northern Patagonia (Horak 1971, Singer 1954, Singer 1969). *Descolea pallida* was described by Horak (1971) to accommodate collections from northern Patagonia that had smaller spores, yellow veil remnants, and lighter colored caps. However, both Horak and Singer recognized that the two ‘species’ (*D. antarctica* and *D. pallida*) were challenging to differentiate from one another. Singer (1954, in German) expressed “I’m not entirely sure if the Patagonian species (*D. pallida*, [not yet officially described in 1954]) is different from the Fuegian one (*D. antarctica*)... The form and ornamentation of the spores is the same.” Later, Singer (1969) considered *D. antarctica* as a synonym of the Australian species *Descolea recedens* (Cooke & Mass.) Sing. (= *Agaricus recedens* Cooke & Massee). Our phylogenetic analysis, which includes light yellow colored specimens from coastal Chile (e.g. *D. pallida*) and darker colored specimens from Tierra del Fuego (*D. antarctica*), confirms that these two species are synonyms that represent intraspecific color and size variants (Fig 2a). During field collections we also observed color variation in both the caps and partial veil remnants within individual collections, consistent with the idea that species within the descolea clade exhibit high morphological plasticity (Cribb 1956, Lago et al. 2001, Neville et al. 2004). Our phylogenetic analysis also rejects the hypothesis that *D. antarctica* from South America is a synonym of *D. recedens* from Australia (Fig1).

Descolea archeureta (Halling) Kuhar, Nouhra, & M.E. Smith comb. nov. (figs 2D and 3A)
MycoBank No.: MB819433
Basionym: *Thaxterogaster archeuretus* Halling, Mycologia 73: 861. 1981.
Synonym: *Cortinarius archeuretus* (Halling) Peintner & M.M. Moser, Mycotaxon 81: 178. 2002

Additional notes: Halling (1981) studied historical specimens collected by Thaxter in Chile and described the new species *Thaxterogaster archeuretus* Halling (= *Cortinarius archeuretus* (Halling) Peintner & M.M. Moser). Morphological analysis of the holotype specimen at the Farlow Herbarium (FH accession #7775A, Thaxter’s “Fungus Hypogeous No. 6”) indicated that the spores have a hyaline utricle and 4-spored basidia. The spores are also distinctly smaller than those of other sequestrate Patagonian *Descolea* species. Although spore size has proven not to be a conclusive feature to consistently delimit species, it can be useful when used in combination with other diagnostic characters. One feature that can be used to separate *D. archeureta* from other South American *Descolea* species is a thick hyaline utricle that is more translucent than the other Patagonian species. No additional collections of *D. archeureta* were found at the herbaria (FH, LPS, BAFC, CORD, or NY). However, two fresh collections recently found in northern Patagonia (2016) morphologically match the type at FH.

Specimens examined: **Chile**: Los Lagos, Puyehue National Park, foothills of Volcan Puyehue,up the road past El Caulle north of Rio Golgol, under *N. dombeyi*, 1 May 2016, Rosanne Healy (FLAS-F-60300, MES1786, SGO 167981) GenBank accessions: ITS KY523096; foothills of Volcan Puyehue, up the road past El Caulle, north of Rio Golgol, under *N. dombeyi* 4 May 2016, Rosanne Healy (FLAS-F-60296, MES1584, SGO 167982), GenBank accessions: ITS KY523092. Magallanes, Punta Arenas, Fungus Hypogeous No. 6, Feb 1906 (precise date unknown), Holotype preserved in liquid, Roland Thaxter (FH accession #7775A).

Descolea australiensis (G.W. Beaton, Pegler & T.W.K. Young) Kuhar, Nouhra, & M.E. Smith comb. nov.

MycoBank No.: MB 817800

Basionym: *Setchelliogaster australiensis* G.W. Beaton, Pegler & T.W.K. Young, Kew Bull. 40(1): 169. 1985.

Descolea brunnea (Horak) Kuhar, Nouhra, & M.E. Smith comb. nov. (figs 2B-C and 3C-D)

MycoBank No.: MB817785

UNITE SH: SH300035.07FU

Basionym: *Hypogaea brunnea* Horak, Sydowia 17: 279. 1964.

Synonyms: *Setchelliogaster brunneus* (Horak) Sing. apud Petersen. Petersen, Evol. High. Basidiomyc. 468. 1971

Thaxterogaster squamatus Halling, Mycologia 71: 853. 1981.

Cortinarius squamatus (Halling) Peintner & M.M. Moser, Mycotaxon 81: 182. 2002.

Hymenogaster albellus sensu Dodge & Zeller, Ann. Mo. Bot. Gard. 21: 669. 1934.

Additional notes: Several names have been used to refer to this common South American sequestrate *Descolea* species, including *Cortinarius squamatus*, *Hypogaea brunnea*, *Setchelliogaster brunneus*, and *Thaxterogaster squamatus*. This is a highly variable taxon that is present across a wide range of *Nothofagaceae* forests at varying altitudes and latitudes. However, a combination of molecular and morphological evidence suggests that these are the same taxon (thus we treat the names listed above as synonyms). Patagonian collections of sequestrate basidiomes with two sterigmata and large spores formed a well supported clade (Fig 1a) and include specimens with highly variable pileal (peridial) structures, including variable cuticle construction and presence of universal veil scales. Scales are present in some basidiomes but others are totally devoid of scales. For example, specimen EN214 was originally identified as *Thaxterogaster squamatus* based on the obvious and persistent scales. Rostrate (limoniform) and non-rostrate spores also occur within this highly variable species and in some cases both spore types can be observed within the same basidiome. We have also found that in some cases the apical area of the spore darkens in 3%KOH even if it does not protrude from beneath the utricle. Scales are also present in the type collection of *Hypogaea brunnea* Horak and *T. squamatus* Halling.

Descolea brunnea was first collected by Thaxter and later considered by Zeller and Dodge to be *Hymenogaster albellus* (= *Descolea albella*) from Australia. However, the specimens examined by Zeller and Dodge are fragmentary and had no stipe remnants. This morphological feature is important because it can be used to distinguish between *D. brunnea* from South America (typically with a short stipe that is easily separable from the pileus) and *D. albella* (=*H. albellus*) from Australia (typically lacking a stipe).

Horak (1964) described this species as *Hypogaea brunnea.* In Horak's original description, the species was depicted with broadly ellipsoid to sublimoniform spores and our examination of the *H. brunnea* isotype (LPS 38225) confirms these observations. Since spores in the type of *Hypogaea brunnea* are utriculate, Singer (1971) correctly identified this taxon as a member of the descolea clade and transferred the species to *Setchelliogaster* as *S. brunneus* (Horak) Sing.

The same species was later described by Halling (1981) as *Thaxterogaster squamatus* based on Thaxter's Fungus Hypogeous No. 7 from Punta Arenas, Chile. *Thaxterogaster squamatus* was described as having limoniform spores (and therefore seemed different from the broadly ellipsoid spores depicted in the original publication that described *H. brunnea*). However, the *T. squamatus* holotype at FH has urticulate spores that range in shape from limoniform to broadly ellipsoid to limoniform. Although variable, these spores match the morphology of *D. brunnea*. We have also confirmed that *D. brunnea* is a common ECM symbiont of *Nothofagaceae* species near Punta Arenas and at other coastal sites in Chile (see collections MES160 and MES538 listed below).

Specimens examined: **Argentina**: Neuquén, halfway between San Martín de los Andes and Hua Hum, Mixed *Lophozonia obliqua* and *L. nervosa* forest 18 May 2015, R. Healy (CORD, MES1351). Río Negro, Nahuel Huapi National Park, Los Rapidos, *N. antarctica* forest, 8 May 2015, F. Kuhar (FLAS-F-60289, MES1102). GenBank accessions: ITSKY523084; Laguna Frías, 5 Apr 1962, Horak, (LPS 38225, isotype of *Hypogaea brunnea*); Nahuel Huapi National Park, Mascardi Lake, *Nothofagus dombeyi* forest, 9 May 2010, E. Nouhra (CORD EN214), GenBank accessions: ITS KY523078; Puerto Blest, pure *N. dombeyi* stand, 10 May 2015, M. E. Smith (CORD, MES1155), GenBank accessions: ITS KY523087; Mascardi Lake with *N. dombeyi*, 8 May 2015, G. Furci (CORD, FLAS-F-60290, MES1113), GenBank accessions: ITS KY523085; Los Rapidos, *N. antarctica* forest, 13 May 2016, F. Kuhar & R. Healy (CORD, FLAS-F-60301, MES1894). GenBank accessions: ITS KY523097; Los Rapidos, near Lago Los Moscos, *N. antarctica*, 16 May 2016, A. Mujic (CORD, FLAS-F-60305, MES2095); Lago Hess, *N. antarctica* and *N. dombeyi*, 18 May 2016, F. Kuhar (CORD, FLAS-F-60306, MES2149); 1 km before Lago Hess, *N. antarctica* and *N. dombeyi*, 18 May 2016, A. Mujic (CORD, FLAS-F-60307, MES2167); Road to Tronador, before Pampa Linda by the river, *N. antarctica*, 14 May 2016, E. Nouhra (CORD, FLAS-F-60302, MES1976). **Chile**: Aysén, Reserva Natural Melimoyu, mixed *Nothofagaceae* forest, 12 Mar 2012, M. E. Smith and D. H. Pfister (FH, FLAS-F-60284, MES538), GenBank accessions: ITS KY523079; Reserva Patagonia Sur, Valle California, *Nothofagaceae* forest, 15 Mar 2012, M. E. Smith and D. H. Pfister (FH, FLAS-F-60285, MES565). GenBank accessions: ITS KY523080. Los Lagos, Puyehue National Park, below Antillanca, *N. dombeyi* forest in dense patches of *Chusquea coleou*, 5 May 2015, P. Sandoval (MES1059, SGO 167989); near the Antillanca lodge, *Nothofagaceae* forest, 15 Mar 2015, R. Healy (FLAS-F-60287, MES996 SGO 167985). GenBank accessions: ITS KY523082; above the Antillanca lodge right near the ski slope, *N. antarctica* and *N. pumilio* mixed forest, 5

May 2015, M.E. Smith (FLAS-F-60288, MES1048 SGO 167986), GenBank accessions: ITS = KY523083; on the road to Antillanca lodge with *N. pumilio*, 3 May 2016, P. Sandoval (MES1515, SGO 167984). GenBank accessions: ITS KY523091; foothills of Volcan Puyehue, with *N. dombeyi*, 4 May 2016, A. B. Mujic (FLAS-F-60297, MES1586, SGO 167988), GenBank accessions: ITS KY523093; Anticura, Sendero La Princesa with *N. dombeyi*, 5 May 2016, A. B. Mujic (FLAS-F-60298, MES1687, SGO 167987), GenBank accessions: ITS KY523094; below Antillanca, 5 Jun 2015, M. E. Smith (MES1079). Magallanes, Punta Arenas, Feb 1906, R. Thaxter, Hymenogaster No. 1(FH 4635); Feb 1906, R. Thaxter, Fungus Hypogeous No. 7 (FH accession #7775B, holotype of *Cortinarius squamatus*); Reserva Nacional Magallanes, Summit, Las Minas, Mixed *Nothofagaceae* forest, 21 Mar 2008, M. E. Smith and D. H. Pfister (FH, FLAS-F-60283, MES160).

Descolea ferruginea (Cribb) Kuhar, Nouhra, & M.E. Smith comb. nov.
MycoBank No.: MB817790
UNITE SH: SH300052.07FU
Basionym: *Gymnoglossum ferrugineum* Cribb, Paps. Dept. Bot. Univ. Queensland 3: 157. 1958.
Synonyms: *Timgrovea ferruginea* (Cribb) Bougher et Castellano, Mycologia 85(2): 290. 1993.
Hymenogaster areolatus (Cribb) A. H. Smith, Mycologia 58: 109. 1966.
Gymnoglossum areolatum Cribb, Paps. Dept. Bot. Univ. Queensland 3: 158. 1958.

Descolea fusispora (Trappe & Claridge) Kuhar, Nouhra, & M.E. Smith comb. nov.
MycoBank No.: MB 817796
Basionym: *Descomyces fusisporus* Trappe & Claridge, in Nouhra, Domínguez, Daniele, Longo, Trappe & Claridge, Mycologia 100(5): 753. 2008

Descolea giachinii (Trappe, V.L. Oliveira, Castellano & Claridge) Kuhar, Nouhra, & M.E. Smith comb. nov.
MycoBank No.: MB817797
Basionym: *Descomyces giachinii* Trappe, V.L. Oliveira, Castellano & Claridge, in Giachini, Oliveira, Castellano and Trappe, Mycologia 92(6): 1172. 2000.

Descolea javanica (Höhnel) Kuhar, Nouhra, & M.E. Smith comb. nov.

MycoBank No.: MB817794

Basionym: *Hymenogaster javanicus* Höhnel, Sitzungsber. Kaiserl. Akad. Wiss., Math.-Naturwiss. C1. Abt. 1, 117: 1017. 1908.

Synonym: *Descomyces javanicus* (Höhnel) Bougher et Castellano, Mycologia 85(2): 290. 1993

Additional notes: Hymenogaster javanicus was collected by F. Von Höhnel on the island of Java and described in 1909 (von Höhnel, 1909). Although the habitat of mixed tropical forest does little to illuminate the host associations, it is likely that ectomycorrhizal *Myrtaceae* were originally present in these forests prior to human disturbance. Smith and Schmull (2010) translated von Höhnel's description of *H. javanicus* from German to English, examined von Höhnel's collections, and provided microscopic photos as well as reproductions of von Höhnel's original line drawings. All that remains of the *H. javanicus* type specimen is a single preserved slide. Smith and Schmull (2010) nonetheless confirmed the observations of von Höhnel (1909) and Bougher and Castellano (1993). Smith and Schmull (2010) and Bougher and Castellano (1993) accepted this species as a member of the descolea clade.

Descolea macrospora (Cunningham) Kuhar, Nouhra, & M.E. Smith comb. nov.

MycoBank No.: MB817788

Basionym: *Hymenogaster macrosporus* Cunningham non Knapp & Soehner, Proc. Linn. Soc. New South Wales 59: 171. 1934.

Synonym: *Timgrovea macrospora* (Cunningham) Bougher et Castellano, Mycologia 85(2): 290. 1993.

Descolea reticulata (Cunningham) Kuhar, Nouhra, & M.E. Smith comb. nov.

MycoBank No.: MB817792

Basionym: *Hymenogaster reticulatus* G. H. Cunningham, Proc. Linn. Soc. New South Wales 59: 171. 1934.

Synonyms: *Timgrovea reticulata* (Cunningham) Bougher et Castellano Mycologia 85(2): 290. 1993.

Hymenogaster reticulatus Zeller & Dodge in Dodge and Zeller, Ann. Missouri Bot. Gard.21: 656. 1934.

Gymnoglossum reticulatum Cribb, Paps. Dept. Bot. Univ. Queensland 3: 159. 1958.

Descolea subtropica (Cribb) Kuhar, Nouhra, & M.E. Smith comb. nov.

MycoBank No.: MB817789

Basionym: *Hymenogaster subtropicus* Cribb, Paps. Dept. Bot. Univ. Queensland 3: 127. 1956.

Sinonym: *Timgrovea subtropica* (Cribb) Bougher et Castellano, Mycologia 85(2): 290. 1993.

Descolea tenuipes (Setch.) Neville & Poumarat, in Neville, Poumarat & Ivaldi, Bull. Soc. mycol. Fr. 120(1-4): 68. 2005.

MycoBank No.: MB312266

UNITE SH: SH281414.07FU

Basionym: *Secotium tenuipes* Setch., J. Mycol. 13(6): 239. 1907.

Synonyms: *Setchelliogaster tenuipes* var. *tenuipes* (Setch.) Pouzar, Česká Mykol. 12(1): 34. 1958.

Setchelliogaster tenuipes var. *rheophyllus* (Bertault & Malençon) G. Moreno & M.P. Martín [as '*rheophylla*'], Mycotaxon 78: 262. 2001.

Descolea tenuipes (Setch.) Neville & Poumarat, in Neville, Poumarat & Ivaldi, Bull. Soc. mycol. Fr. 120(1-4): 68. 2005 (2004) var. *tenuipes Naucoria rheophylla* Bertault & Malençon, in Malençon and Bertault, Champignon Supérieurs du Maroc 1: 427. 1970.

Setchelliogaster rheophyllus (Bertault & Malençon) G. Moreno & Kreisel, in Moreno, Kreisel, Galán, Feddes Repert. 108(7-8): 567. 1997

Descolea rheophylla (Bertault & Malençon) Malençon, Beih.Sydowia 8: 258. 1979 (2004)

Additional notes: We consider the combination proposed by Neville et al. (2004) as a valid nomenclatural proposal.

Descolea varians (Trappe & Claridge) Kuhar, Nouhra, & M.E. Smith comb. nov.

MycoBank No.: MB817798

Basionym: *Descomyces varians* Trappe & Claridge, in Nouhra, Domínguez, Daniele, Longo, Trappe and Claridge, Mycologia 100(5): 754. 2008.

4. Discussion

4.1 Morphological Traits

The high degree of morphological convergence associated with the sequestration process has often caused confusion for taxonomists in the past. The delimitation of many genera was based on features that we now know correspond to degrees of sequestration, aligned under the concept of phylogenetic “series” as in Malençon (1931) or Bougher and Castellano (1993). This resulted in polyphyletic sequestrate taxa such as *Thaxterogaster*, *Setchelliogaster*, or *Descomyces* being nested within paraphyletic agaricoid genera such as *Cortinarius* and *Descolea*. Convergent features in the sequestrate representatives (thick walled, mostly globose and heavily ornamented spores) were also used to group these species together in large genera like *Hymenogaster sensu lato*. However, with the use of molecular data and careful microscopic study, it is often possible to see morphological features that help to clarify evolutionary relationships.

The utricle, a more or less translucent discontinuous membrane that covers the basidiospores of some fungi (often treated as an “exosporium” – Lago et al. 2001), was used as a key feature to recognize sequestrate genera (*Descomyces* and *Timgrovea*) within the *Bolbitiaceae* by Bougher and Castellano (1993). Specifically, they recognized the sequestrate genera *Timgrovea*, *Setchelliogaster* and *Descomyces*. This utricle is structured in its exosporial layer as columns or ridges under a smooth surface. However, coarsely distributed verrucae leaving a smooth apex in limoniform spores of some *Cortinarius* (Supplementary Fig 1) were alternatively interpreted as an utricle or as individual ornamentations with the subsequent placement of species having “utricle like structure”or “densely verrucose” spores in different genera by different authors (Singer in Petersen 1971, Horak 1979). For example, the heavily verrucose limoniform spores of *Cortinarius fragilis* were the main reason that this species was treated in the genus *Setchelliogaster*, despite the cortinarioid cuticle of the cap and the absence of a true urticle (Horak 1979, Lago et al. 2001). Our results suggest that truly utriculate spores are found in all species in the descolea clade but do not occur within the genus *Cortinarius*. Increasing visual contrast with Cotton Blue or Toluidine Blue (Clemençon et al. 2012), and the use of differential interference contrast (DIC) microscopy in spore observations (Halling 1981), can help to differentiate the presence of dense spore ornamentation versus a continuous utricle partially covering the spore surface.

Although highly variable, sterile hymenial elements ranging from slightly capitate cystidia to protruding basidioles are common within the Patagonian species. This variation is congruent with the observations of Lago et al. (2001) that found this feature to be correlated with the hymenium maturity. The cylindrical pigmented hyphae that Horak (1971) proposed as an additional difference between the two agaricoid morphotypes (e.g. *Descolea antarctica* and *D. pallida*) are present in all collections studied but in highly variable proportions. This could be the cause of different colorations observed in the veil remnants and again, in possible correlation with maturity stages. Finally, Singer's (1969) observation that occasional basidia bearing less than four sterigmata produce larger spores may be an explanation for the high variability of this feature.

Together this suite of morphological characters (utriculate spores, capitate cystidia, and celluloderm) can be used to consistently differentiate taxa in the descolea clade from those in the cortinarius clade. The importance of these characters was previously recognized by Singer (1969). He also suggested that the apical gap in the utricle is actually a germ pore, a feature that he interpreted as phylogenetically linking *Descolea* to the *Bolbitiaceae* (which have germ pores on their spores) and excluding the genus from *Cortinariaceae* (which lack germ pores on their spores) (Peintner et al. 2004; Mishra 2005).

4.2 Excluded Species

Several brown-spored sequestrate taxa have previously been considered members of the descolea clade (e.g. placed in *Timgrovea*, *Descomyces* or *Setchelliogaster*) but exhibit morphological, ecological, or biogeographical features that are not consistent with this phylogenetic placement. We know that taxa in the descolea clade: 1) have brown, utriculate spores, 2) are mostly native to Australasia and southern South America, and 3) are found primarily with host trees in the *Nothofagaceae* or *Myrtaceae*. Only a few exceptional species of *Descolea* are found in Asia with Northern Hemisphere host plants (Tedersoo et al. 2010). Taxa that are inconsistent with these three key features are likely to belong to other fungal lineages and are therefore considered here outside of the descolea clade.

Bougher and Castellano (1993) transferred the Chinese species *Hymenogaster kwangsiensis* B. Liu to the genus *Timgrovea* probably based on the reticulate spore ornamentation forming polygonal alveoli. However, this species is known only from Asia and has a spore morphology that is quite different from most other sequestrate species in the descolea clade. Specifically, it lacks the characteristic limoniform, utriculate spores. The type is unavailable for study but the combination of spore morphology and biogeography suggest that this taxon probably belongs to a different group.

Another species that does not fit well within the descolea clade is *Setchelliogaster aurantius* (Zeller) Singer & A.H. Sm. This species was originally described as *Secotium aurantium* Zeller from the Trinidad Mountains of Cuba (Zeller 1947). Although this species was transferred by Singer to *Setchelliogaster*, it was originally described by Zeller as being bright orange with a “phalloid” appearance, white rhizomorphs, and smooth brown spores (Zeller 1947). The combination of morphology and biogeography clearly excludes this taxon from the descolea clade and suggests that it is likely a member of the *Phallomycetideae*.

Setchelliogaster tetrasporus was described by Singer (1971) from Valdivian forests of *Nothofagus dombeyi* and *Araucaria araucana* in Chile and discussed by Horak (1979). This species has recently been considered by Horak (1979) to be a synonym of *Cortinarius fragilis* (Zeller & C.W. Dodge) Peintner & M.M. Moser. However, the published descriptions along with our analysis of the holotype (SGO) and fresh specimens (MES129, MES143, MES144) indicate that *Setchelliogaster tetrasporus* shows morphological affinity with *Cortinarius sclerospermus* Peintner & M.M. Moser. This taxon is retained for now in the genus *Setchelliogaster* but will be treated in a future taxonomic work to revise the sequestrate Cortinarius species of South America.

4.3 Ecological Aspects

The mycorrhizal status of *Descolea* species in Patagonia is well established. Palfner (2008) demonstrated that *D. antarctica* was the most abundant fungal symbiont on post-fire seedlings of *Lophozonia alpina,* suggesting that *D. antarctica* behaves as an early stage symbiont in the *Nothofagaceae* forests. Both *D. antarctica* and *D. brunnea* were also common on ECM root tips of three *Nothofagaceae* species sampled by Nouhra et al. (2013) (see also Fig 1). These two species are also among the most common ECM species on seedlings of *Nothofagus* (F.

Kuhar, unpublished data). *Descolea brunnea* also produces abundant basidiomes from high elevation sites down to sea level, as well as over a wide latitudinal range (Nouhra et al. 2012 as *Thaxterogaster squamatus*). This suggests that these two *Descolea* species are strong competitors and can be dominant in many different types of *Nothofagaceae* ECM communities. Alberdi et al. (2007) found that *N. dombeyi* seedlings were more photosynthetically active when inoculated with *D. antarctica* or *Pisolithus tinctorius* than non-ECM seedlings, and that plants colonized by *D. antarctica* were less physiologically stressed than seedlings inoculated with *P. tinctorius*. Since the sequestrate basidiomes of *D. brunnea* may constitute an important source of spore inoculum, a deeper knowledge of the ecology of *D. brunnea* could facilitate its use as a greenhouse inoculant to produce ectomycorrhizal *Nothofagaceae* seedlings for reforestation.

In addition to being common in the environment, many *Descolea* species can also be grown in pure culture on diverse media types. Cultures of *Descolea* species typically produce whitish colonies with a yellow center and have capitate cystidia (Bougher and Castellano, 1993).Valenzuela et al. (2008) successfully cultured *D. antarctica* on malt extract agar and report capitate cystidia on the mycelium, a feature that we have also confirmed (F. Kuhar, unpublished data). Álvarez et al. (2004) reported that *D. antarctica* also has highly adaptable enzymes (i.e. phosphatases, amylases, cellulases) that are active over a wide pH and temperature range. In a later experiment Valenzuela et al. (2008) characterized several enzyme activities and suggested that *D. antarctica* can utilize a wide range of nutrient sources for growth in axenic culture. The importance of the enzyme machinery of ectomycorrhizal fungi has been extensively discussed (e.g. Baldrian 2009) and conclusive evidence of their role as important degraders of organic matter has been summarized and emphasized by Lindahl and Tunlid (2015). Available data suggest that species of *Descolea* may be among the most saprotrophically active ectomycorrhizal fungi.

5. Conclusion

The genus *Descolea* is represented in Patagonia by four species. Here we have placed the hypogeous, secotioid taxa (D. *archeureta*, *D. brunnea* and *D. inferna*) in the genus *Descolea* along with the epigeous agaricoid type species *Descolea antarctica*. We found that several features constitute excellent criteria to recognize members of the genus *Descolea*: capitate cystidia, inflated cuticular elements, perisporial utricle with an apical gap, limoniform to sublimoniform spores and the tendency towards fewer sterigmata in the sequestrate species. The high intra-species or even intra-individual morphological variation is a common feature that makes some species challenging to differentiate without molecular data. Despite the taxonomic difficulties that are caused by this variation, it is also possible that this morphological plasticity might contribute to the ecological adaptability of species in this group to different environmental conditions.

6. Acknowledgments

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Captions to the figures

Figure 1: **Phylogenetic Analyses**

One of three most parsimonious trees (722 steps) showing the phylogenetic placement of the Patagonian species within the monophyletic genus *Descolea*. Significant parsimony bootstrap, maximum likelihood bootstrap values and Bayesian posterior probabilities are indicated as well as basidiome morphologies. Species of *Cortinarius* and *Hebeloma* were used as the outgroup.

Figure 2: **Basidiomes**

Fresh specimens of the Patagonian *Descolea* species. A, *Descolea antarctica*; B and C, *Descolea brunnea*; D, *Descolea archeureta*; E, mature specimen of *Descolea inferna* with missing stipe. Scale bar = 10 mm.

Figure 3: **Microscopy**

Light micrographs at 1000X magnification showing microscopic features of Patagonian *Descolea* collections: A, *Descolea archeureta*; B, *Descolea antarctica*; C, mature spores of *Descolea brunnea*; D, bispored basidium of *D. brunnea;* E, tetrasporic basidium of *Descolea inferna;* F, mature spore of *D. inferna*. Scale bar = 10 µm.**Supplementary Figure 1**: **Sequestrate *Cortinarius* spores**

Light micrographs at 1000X of sublimoniform to limoniform spores of two sequestrate *Cortinarius* species showing the lack of utricle: A-B, *Cotrinarius sclerospermus* LPS38212; C and D, *Cortinarius sphaerocephalus* FK14036 (CORD) Scale bar = 5 µm.

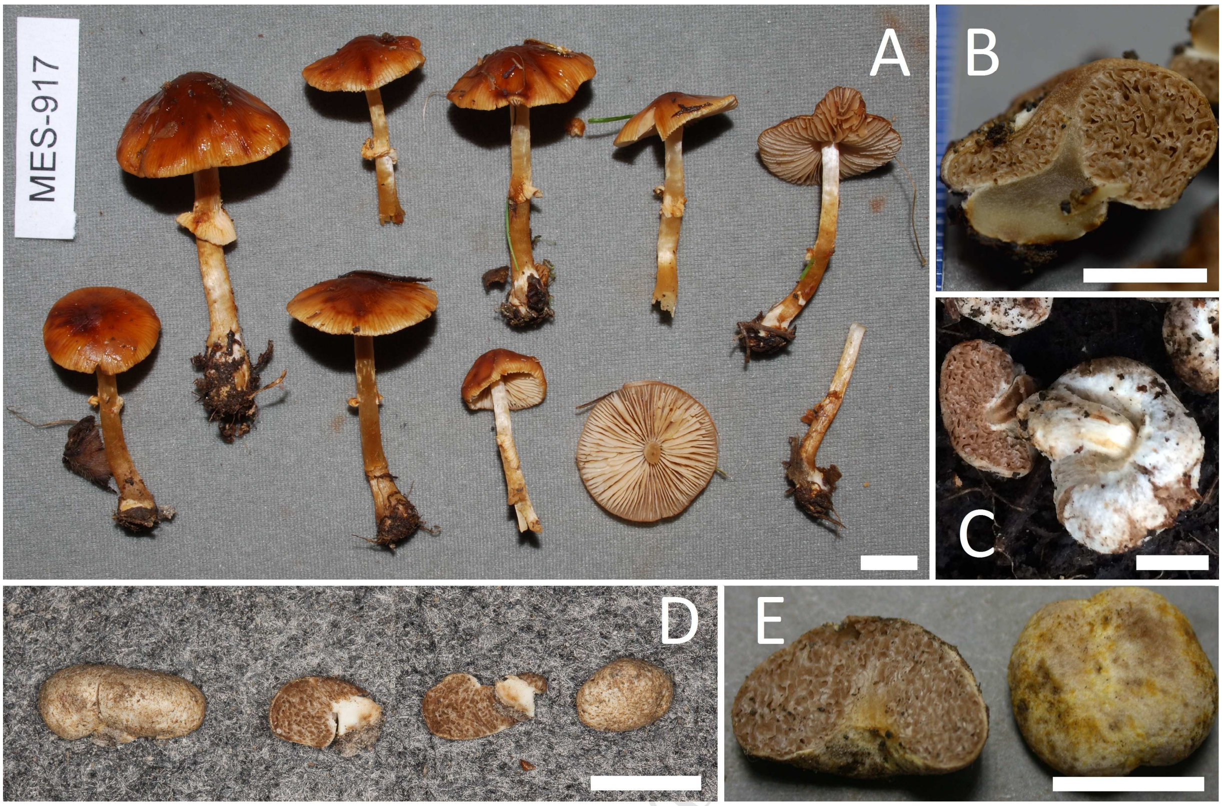
Table 1: List of sequences analyzed

Specimen and location data is provided for each sequence used in the phylogenetic analyses. Personal collections are indicated with surnames and herbarium acronyms are from Thiers, B. Index Herbariorum: A global directory of public herbaria and associated staff. New York Botanical Garden's Virtual Herbarium. http: //sweetgum.nybg.org/ih/.

GenBank Accession Number	Species	Origin	Voucher	Source
KY523092	*Cortinarius archeuretus*	Continental Patagonia	MES1584	FLAS
KY523096	*Cortinarius archeuretus*	Continental Patagonia	MES1786	FLAS
NR131815	*Cortinarius badiovinaceus*	Austria	IB19500061	IB
NR130311	*Cortinarius caesiocolor*	Europe	Kytö00-029	H
NR130313	*Cortinarius obsoletus*	Europe	G00262069	CJB
KY523078	*Cortinarius squamatus*	Continental Patagonia	EN214	FLAS
AF325646	*Descolea antarctica*	Tierra del Fuego	IB19630883	IB
MF085056	*Descolea antarctica*	Tierra del Fuego	CT4235	FLAS
MF085057	*Descolea antarctica*	Tierra del Fuego	CT4237	FLAS
KY523077	*Descolea antarctica*	Continental Patagonia	EN382	FLAS
KY523088	*Descolea antarctica*	Continental Patagonia	MES1195	FLAS
KY523089	*Descolea antarctica*	Continental Patagonia	MES1242	FLAS
KY523098	*Descolea antarctica*	Continental Patagonia	MES2016	FLAS
KY523081	*Descolea antarctica*	Continental Patagonia	MES917	FLAS
AF325647	*Descolea antarctica*	New Zealand	NZ5182	Horak
KY523083	*Descolea brunnea*	Continental Patagonia	MES1048	FLAS
KY523084	*Descolea brunnea*	Continental Patagonia	MES1102	FLAS
KY523085	*Descolea brunnea*	Continental Patagonia	MES1113	FLAS
KY523087	*Descolea brunnea*	Continental Patagonia	MES1155	FLAS
KY523091	*Descolea brunnea*	Continental Patagonia	MES1515	FLAS
KY523093	*Descolea brunnea*	Continental Patagonia	MES1586	FLAS
KY523094	*Descolea brunnea*	Continental Patagonia	MES1687	FLAS

KY523097	*Descolea brunnea*	Continental Patagonia	MES1894	FLAS
KY523079	*Descolea brunnea*	Continental Patagonia	MES538	FLAS
KY523080	*Descolea brunnea*	Continental Patagonia	MES565	FLAS
KY523082	*Descolea brunnea*	Continental Patagonia	MES996	FLAS
KY523086	*Descolea inferna*	Continental Patagonia	MES1132	FLAS
KY523090	*Descolea inferna*	Continental Patagonia	MES1315	FLAS
KY523095	*Descolea Inferna*	Continental Patagonia	MES1730	FLAS
KY523099	*Descolea inferna*	Continental Patagonia	MES2067	FLAS
JX968155	*Descolea maculata*	Europe	WU21819	WU
AF325657	*Descolea phlebophora*	Australia	E4912	Bougher
JX178627	*Descolea phlebophora*	New Zealand	OTA60177	OTA
AF325649	*Descolea recedens*	Australia	E4459	Bougher
JX178628	*Descolea recedens*	New Zealand	OTA60312	OTA
AF325645	*Descomyces albellus*	Australia	Tr17168	OSC
GU479276	*Descomyces albus*	Europe	it53	DSMZ
DQ328125	*Descomyces angustisporus*	Australia	H7216	H
DQ328058	*Descomyces angustisporus*	Australia	H7216	H
AF325644	*Descomyces sp.*	New Zealand	Tr12624	OSC
DQ328211	*Descomyces sp.*	Australia	TRAPPE14397	OSC
NR119686	*Hebeloma plesiocistum*	Europe	LIPJVG1021214	LIP
NR120177	*Hebeloma theobrominum*	Europe	HJB1000080	HJB
KC110674	*Hebeloma velutipes*	New Zealand	PDDPL3404	PDD
JX316330	*Patagonia root tip*	Continental Patagonia	-	CORD
JX316348	*Patagonia root tip*	Continental Patagonia	-	CORD
AF325627	*Setchelliogaster australiensis*	Australia	Cla.2679	Trappe&Claridge
AF325628	*Setchelliogaster australiensis*	Australia	Cla.2621	Trappe&Claridge
DQ328184	*Setchelliogaster sp.*	Australia	TRAPPE14175	OSC
DQ328214	*Setchelliogaster sp.*	Australia	TRAPPE14281	OSC
AF325624	*Setchelliogaster tenuipes*	Australia	Tr24776	OSC
AF099363	*Setchelliogaster tenuipes*	Europe	BCC-MPM2703	M&R.GenBank
DQ328083	*Timgrovea ferruginea*	Australia	H5803	H
DQ328116	*Timgrovea ferruginea*	Australia	H5803	H
DQ328128	*Timgrovea ferruginea*	Australia	H5803	H
KP191836	*Timgrovea sp.*	Australia	MELKV636	MEL
DQ328180	*Timgrovea sp.*	Australia	H4162	H
DQ328182	*Timgrovea sp.*	Australia	H4574	H
DQ328207	*Timgrovea sp.*	Australia	H4146	H

KP191843	*Timgrovea sp.*	Australia	MEL2364426	MEL
DQ328219	*Timgrovea sp.*	Australia	H5655	H


MES-917
A
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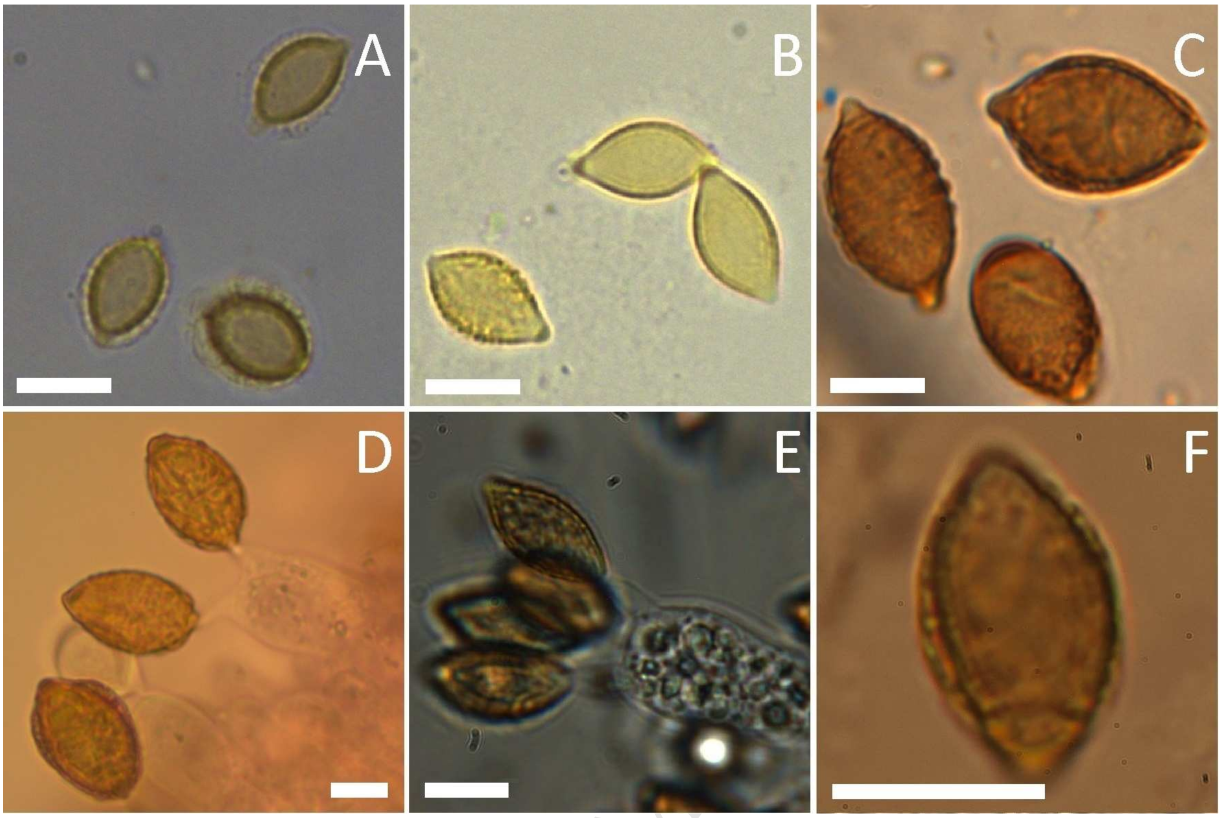
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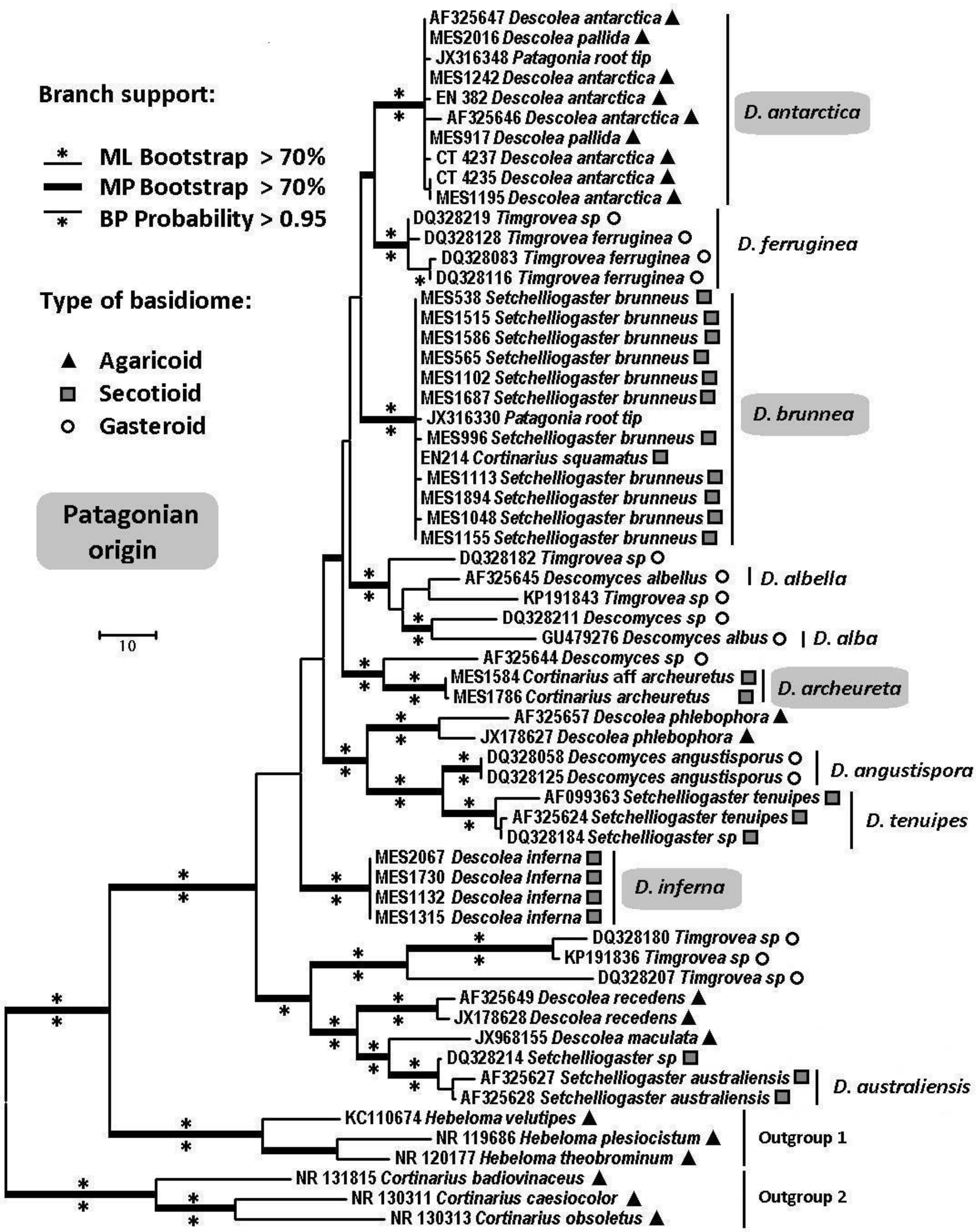

Branch support:
ML Bootstrap > 70%
MP Bootstrap > 70%
BP Probability > 0.95
Type of basidiome:
Agaricoid
Secotioid
Gasteroid
Patagonian origin
10
AF325647 Descolea antarctica
MES2016 Descolea pallida
JX316348 Patagonia root tip
MES1242 Descolea antarctica
EN 382 Descolea antarctica
AF325646 Descolea antarctica
MES917 Descolea pallida
CT 4237 Descolea antarctica
CT 4235 Descolea antarctica
MES1195 Descolea antarctica
D. antarctica
DQ328219 Timgrovea sp
DQ328128 Timgrovea ferruginea
DQ328083 Timgrovea ferruginea
DQ328116 Timgrovea ferruginea
D. ferruginea
MES538 Setchelliogaster brunneus
MES1515 Setchelliogaster brunneus
MES1586 Setchelliogaster brunneus
MES565 Setchelliogaster brunneus
MES1102 Setchelliogaster brunneus
MES1687 Setchelliogaster brunneus
JX316330 Patagonia root tip
MES996 Setchelliogaster brunneus
EN214 Cortinarius squamatus
MES1113 Setchelliogaster brunneus
MES1894 Setchelliogaster brunneus
MES1048 Setchelliogaster brunneus
MES1155 Setchelliogaster brunneus
D. brunnea
DQ328182 Timgrovea sp
AF325645 Descomyces albellus
D. albella
KP191843 Timgrovea sp
DQ328211 Descomyces sp
GU479276 Descomyces albus
D. alba
AF325644 Descomyces sp
MES1584 Cortinarius aff archeuretus
MES1786 Cortinarius archeuretus
D. archeureta
AF325657 Descolea phlebophora
JX178627 Descolea phlebophora
DQ328058 Descomyces angustisporus
DQ328125 Descomyces angustisporus
D. angustispora
AF099363 Setchelliogaster tenuipes
AF325624 Setchelliogaster tenuipes
DQ328184 Setchelliogaster sp
D. tenuipes
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MES1132 Descolea inferna
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D. inferna
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KP191836 Timgrovea sp
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JX178628 Descolea recedens
JX968155 Descolea maculata
DQ328214 Setchelliogaster sp
AF325627 Setchelliogaster australiensis
AF325628 Setchelliogaster australiensis
D. australiensis
KC110674 Hebeloma velutipes
NR 119686 Hebeloma plesiocistum
NR 120177 Hebeloma theobrominum
Outgroup 1
NR 131815 Cortinarius badiovinaceus
NR 130311 Cortinarius caesiocolor
NR 130313 Cortinarius obsoletus
Outgroup 2