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Hysterangiales revisited: expanded phylogeny reveals new genera and two new suborders

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Abstract: *Hysterangiales* (*Phallomycetidae*, *Agaricomycetes*, *Basidiomycota*) is a diverse, nearly cosmopolitan order of predominantly hypogeous, sequestrate, ectomycorrhizal fungi. Expanding on previously published phylogenies, we significantly increased sampling of *Hysterangiales* specimens, emphasizing representatives from Australia. Using protein-coding genes *atp6* (adenosine triphosphate synthase subunit 6) and *tef1* (translation elongation factor 1- α), we recovered 26 provisional novel genera, and corroborated existing genera and families. Further, two new suborders (*Phallogastrineae* subord. nov. and *Hysterangineae* subord. nov.) and a new family (*Phallogastraceae* fam. nov.) are described, and three new combinations made to *Phallogaster*. Aspects of classification and biogeography are presented.

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INTRODUCTION

Hysterangiales (*Phallomycetidae*, *Agaricomycetes*, *Basidiomycota*) was established in 2006 to accommodate a phylogenetically refined *Hysterangiaceae* and relatives (Hosaka *et al.* 2006). *Hysterangiales* comprises a wide array of predominantly hypogeous, sequestrate, ectomycorrhizal fungi, but some taxa in the basal lineage (*Phallogastraceae*) are epigeous and non-mycorrhizal. *Hysterangiales* possess a range of unusual morphologies (Fig. 1), such as basidiomes with a powdery spore mass (and often with a sterile core) in the *Mesophelliaceae* (Trappe *et al.* 1996), the gelatinized or cartilaginous gleba with translucent columella in *Gallaceaceae* and *Hysterangiaceae*, or the utricle-encased spores of many *Mesophelliaceae* and *Hysterangiaceae* (Castellano & Beever 1994; Fig. 2). Like many truffle-like fungi, *Hysterangiales* often have distinct odours, which attract small animals for spore dispersal via mycophagy (*e.g.* Fogel & Trappe 1978, Claridge & May 1994). The characteristics of being mostly hypogeous and nearly universally dependent on other organisms for dispersal, combined with their worldwide (excluding Antarctica) distribution and diversity, have led to the consideration of multiple biogeographic scenarios for *Hysterangiales*, ranging from ancient Pangaean vicariance to recent long-distance dispersal (Hosaka *et al.* 2008).

Hysterangiales taxa are remarkably abundant and highly diverse in Australia (a major impetus for the present study), particularly the endemic family *Mesophelliaceae*. Ectomycorrhizal *Myrtaceae* and *Nothofagaceae* species are the primary symbionts

of *Hysterangiales* in Australasia. Another impetus for the present study is that numerous novel Australasian *Hysterangiales* taxa yet to be formally described have been known for over a decade but generic boundaries were not strongly supported (Hosaka 2005, Hosaka *et al.* 2006, 2008). We expanded on previous work initiated by Hosaka *et al.* (2006, 2008) by sampling extensively from Australian specimens, which corroborated known genera (both formally described and provisional) and families, and elucidated additional provisional novel genera.

MATERIALS AND METHODS

Collections referred to in this study are housed at various fungaria including AD, ATH, BRI, OSC, and MEL. Collections were initially sorted into morphotaxa based on macro- and micro-characters, and a broad selection of material encompassing as many genera as possible were then sampled for molecular analyses. This included some material from non-Australasian taxa that had not previously been sampled, to better support previous taxonomic hypotheses. Thin sections of fungal tissue were mounted in KOH, Melzers' reagent and occasionally Congo Red + KOH to examine peridium and glebal structure, and spore size, shape, presence of a utricle, and ornamentation. Imaging was completed using either an Olympus BX-52 microscope with DP-73 camera and measurement tools using Olympus cellSens standard (v. 1.16) or a Zeiss/Moticam 10 camera system.

Adenosine triphosphate synthase subunit 6 (*atp6*; mitochondrial) and translation elongation factor 1- α (*tef1*;



Fig. 1. Examples of a range of basidiome morphologies in *Hysterangiales*. **A–C.** *Phallogastraceae* **A.** "Gen. prov. 1" (AU, photo credit M. Castellano). **B.** *Phallogaster (Trappea) phillipsii* (photo credit N. Siegel). **C.** *Phallogaster saccatus* (photo credit D. Mitchell/B. Roody); **D–F.** *Gallaceaceae*. **D.** *Austrogautieria* sp. (NZ, photo credit K. Hosaka). **E.** *Gallacea eburnea* (photo credit N. Siegel). **F.** *Gallacea scleroderma* (photo credit N. Siegel); **G–I.** *Hysterangiaceae*. **G.** *Aroramyces* sp. (AU, photo credit M. Castellano). **H.** *Hysterangium* sp. (AU, photo credit Castellano). **I.** *Hysterangium* sp. (NZ, photo credit K. Hosaka); **J–L.** *Mesophelliaceae*. **J.** *Chondrogaster* sp. (photo credit M. Castellano). **K.** "Gen. prov. 3" (photo credit M. Castellano). **L.** *Mesophellia* sp. (photo credit D. Catcheside); **M–O.** *Mesophelliaceae*. **M.** *Nothocastoreum cretaceum* (photo credit D. Catcheside). **N.** *Castoreum radicans* (photo credit M. Castellano). **O.** *Gummiglobus pachytrix* (photo credit M. Castellano). Scale bars = 10 mm.

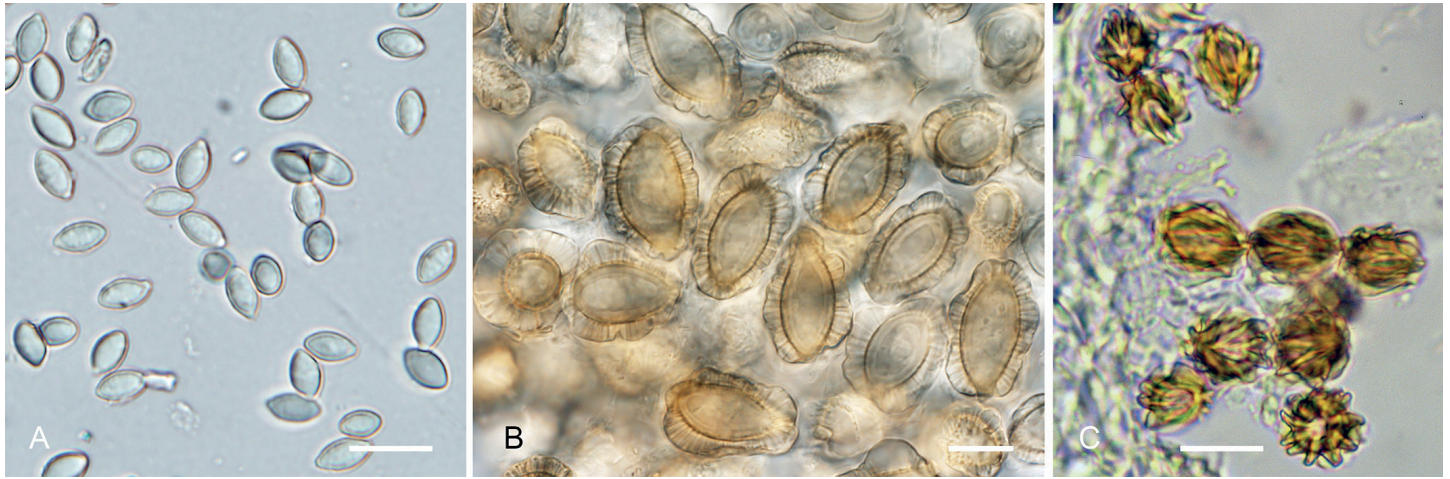


Fig. 2. Three spore types observed in *Hysterangiales*. **A.** *Mesophellia brevispora* (photo credit M. Castellano): smooth, no utricle. **B.** "*Genus prov. 7*" (photo credit N. Davoodian): ornamented, utricle present. **C.** *Austrogautieria* (photo credit T. Lebel): ribbed, no utricle. Scale bars = 10 μ m.

nuclear) nucleotide sequence data for *Hysterangiales* available on GenBank were downloaded. Further, new *atp6* and *tef1* sequences were generated for 99 *Hysterangiales* specimens, as well as one specimen of *Phallales* and one specimen of *Cantharellales* to use as outgroup (Table 1). For these newly sequenced specimens, DNA was extracted from dried herbarium material with the E.Z.N.A. Forensic DNA Kit (Omega Bio-tek). A portion of the mitochondrial protein-coding gene *atp6* was PCR amplified with ATP6-3 and ATP6-2 primers (Kretzer & Bruns 1999) using the following cycling protocol: 95 °C for 5 min; 8 cycles of 94 °C for 35 s, 37 °C for 55 s, 72 °C for 60 s; 35 cycles of 72 °C for 60 s, 94 °C for 35 s, 45 °C for 55 s; 72 °C for 2 min. A portion of the nuclear protein-coding gene *tef1* was PCR amplified with EF1-983F and EF1-1567R, or EF1-1953R, primers (Rehner & Buckley 2005) using the following cycling protocol: 95 °C for 5 min; 10 cycles of 94 °C for 30 s, 65 °C for 60 s, 72 °C for 90 s; 30 cycles of 94 °C for 45 s, 55 °C for 60 s, 72 °C for 70 s; 72 °C for 5 min. Sanger sequencing was conducted in forward and reverse directions at the Australian Genome Research Facility (Melbourne, Victoria, Australia). Sequences are deposited in GenBank (Table 1).

Each gene was aligned using MAFFT online (Katoh *et al.* 2017), visually inspected, and manually adjusted as required. Phylogenetic analyses of each individual gene were conducted using the methods outlined in the next paragraph. Dendrograms from these analyses were then compared using PHYLO.IO (Robinson *et al.* 2016) to assess concordance. The topologies between each gene were found to be almost completely concordant at the generic level and below, corroborating all genera and species (with the exception of specimen H381 which appeared in different positions). Also, many relationships between genera were corroborated between *atp6* and *tef1*. In the individual gene analyses, higher taxonomic levels (e.g. family, suborder) were either not recovered or recovered with low support.

After the assessment of the individual gene phylogenies, *atp6* and *tef1* were concatenated, resulting in an alignment of 1 464 sites long with 223 terminals. MrBayesS v. 3.2.7a (Ronquist *et al.* 2012) was used via the CIPRES REST API (Miller *et al.* 2015) for Bayesian inference (BI) analysis. An analysis using default priors and the following parameters was run for 20 000 000 generations; nstopts: 6, nucmodelopts: 4by4, rateopts: gamma, nrunsval: 2, nchainsval: 4, tempval: 0.200, swapfreqval:

1, nswapsval: 1, samplefreqval: 1 000, burninfracval: 0.5, vparam.stopval: 0.003, sump_burninfrac: 0.5, sumpnrns: 2, sumt_burninfrac: 0.5, sumtnruns: 2, sumtntrees: 1. The average potential scale reduction factor reported for all parameters was 1.038. The alignment and resultant consensus phylogram is deposited in TreeBASE under study number 27527. To corroborate our topology and support values, we conducted additional separate analyses using different outgroup taxa (*Gaeastrales*), extended generations (ranging from 22 000 000 to 59 000 000), different models of rate variation among sites, and different partitions *i.e.* one partition, two partition (each gene), or multi-partition (codon positions for each gene, as well as introns for *tef1*) analyses. We also conducted maximum likelihood (ML) analysis using RAxML software (Stamatakis *et al.* 2008) via the CIPRES REST API with the following options; dna_gtrcat: GTRGAMMA, select_analysis: fa, choose_bootstrap: x, bootstrap_value: 1 000. Taxon names at individual terminals in the phylogram are field-based, verbatim identifications, from various mycologists.

RESULTS

The BI analysis recovered *Hysterangiales* (Bayesian posterior probability, *bpp* = 1) with the four constituent families *Gallaceaceae*, *Hysterangiaceae*, *Mesophelliaceae*, and *Phallogastraceae fam. nov.* (all *bpp* = 1), containing numerous described and undescribed genera (Supplementary Fig. S1, Fig. 3 - Parts 1,2,3). In total, 26 provisional undescribed genera were inferred (25 *Hysterangiales* and 1 *Phallales*). The results of the additional BI analyses and ML analysis were not substantively different from our primary BI analysis, corroborating all taxa indicated in Fig. 3 and Table 1. *Phallogastraceae* is accommodated by a newly established suborder, *Phallogastrineae* (described below, Fig. 3 - Part 1), and the families *Mesophelliaceae* (Fig. 3 - Part 1), *Hysterangiaceae* (Fig. 3 - Part 2) and *Gallaceae* (Fig. 3 - Part 3) are accommodated in the new suborder *Hysterangineae*. *Trappeaceae* is not in *Hysterangiales*, since the type species of *Trappea*, *T. darkeri*, is inferred to be in *Phallales* based on this and previous analyses (Hosaka *et al.* 2006, Sulzbacher *et al.* 2016; Fig. 3 - Part 3, Table 1). Neither *Trappea pinyonensis* nor *T. phillipsii* belong in *Trappea* given their position within *Phallogastraceae* (Xu & Luo 2003, Hosaka *et al.* 2006; Fig. 3 - Part 1); the combination to

Phallogaster is made here. It should be noted that true *Protuber* lies outside of *Hysterangiales*, since the type (*P. maracuja*) and related species belong in *Protophallaceae*, *Phallales* (Trierweiler-Pereira *et al.* 2014). Thus, *Protuber* *hautuensis*, *P. nothofagi*, and all other taxa appearing in Fig. 3 - Part 3) labelled as *Protuber* are not true members of the genus (this includes *P. canescens*, which is a synonym of *Ileodictyon gracile* in *Phallaceae*, *Phallales*).

Taxonomy

Order *Hysterangiales* K. Hosaka & Castellano

Phallogastrineae Castellano, T. Lebel, Davoodian & K. Hosaka, **subord. nov.** MycoBank MB 838485.

Basidiomes sequestrate, small (0.2 cm wide) to larger (up to 5 cm long and 3 cm wide), subglobose to irregularly subovoid, with a tapered to irregularly shaped base, single or caespitose, with white rhizomorphs (rhizomorphs sometimes discolouring pinkish). Basidiome surface smooth to velvety to finely tomentose, white to clay white (discolouring pinkish to salmon buff to reddish or faint lilac). *Peridium* 160–2 000 µm thick. *Columella* branched, whitish to semi-translucent, gelatinized. *Gleba* varies from green, olivaceous green, greyish olive to pale olive; gelatinized, loculate, locules small. *Basidia* clavate to narrowly clavate to irregularly cylindrical, thin-walled, hyaline, 6–8-spored. *Sterigmata* small to indistinct. *Spores* smooth, elongate-ellipsoid to oblong, thin-walled, utricle absent, hyaline singly, olive buff to honey yellow or pale green in mass. *Clamp connections* present.

Phylogenetic taxon definition of the suborder: The largest crown clade containing *Phallogaster saccatus* Morgan 1893, but not *Hysterangium clathroides* Vittad. 1831, *Mesophellia arenaria* Berk. 1857, and *Gallacea scleroderma* (Cooke) Lloyd 1905. This is a maximum crown-clade definition (Hibbett *et al.* 2018).

Type family: Phallogastraceae Castellano, T. Lebel, Davoodian & K. Hosaka *non Phallogastraceae* Locq., *De Taxia Fungorum: I. Syllabus 1A*: 56. 1974.

Phallogastraceae Castellano, T. Lebel, Davoodian & K. Hosaka, **fam. nov.** MycoBank MB 838484.

Basidiomes sequestrate, small (0.2 cm wide) to larger (up to 5 cm long and 3 cm wide), subglobose to irregularly subovoid, with a tapered to irregularly shaped base, single or caespitose, with white rhizomorphs (rhizomorphs sometimes discolouring pinkish). Basidiome surface smooth to velvety to finely tomentose, white to clay white (discolouring pinkish to salmon buff to reddish or faint lilac). *Peridium* 160–2 000 µm thick. *Columella* branched, whitish to semi-translucent, gelatinized. *Gleba* varies from green, olivaceous green, greyish olive to pale olive; gelatinized, loculate, locules small. *Basidia* clavate to narrowly clavate to irregularly cylindrical, thin-walled, hyaline, 6–8-spored. *Sterigmata* small to indistinct. *Spores* smooth, elongate-ellipsoid to oblong, thin-walled, utricle absent, hyaline singly, olive buff to honey yellow or pale green in mass. *Clamp connections* present. *Odour* sometimes fetid. Species apparently saprotrophic, occurring on decaying wood or leaves, or partially buried in litter.

Type genus: Phallogaster Morgan, *J. Cincinnati Soc. Nat. Hist.* **15**: 171. 1893.

Notes: Phallogastraceae Locq. (1974) is invalid in accordance with Art. 39:1 of the Shenzhen code. This is the only clade in *Hysterangiales* with an apparently non-mycorrhizal habit. Although the number of taxa is thus far very limited, the phylogenetic relationships within the family/suborder strongly indicate reciprocal monophyly of the Northern Hemisphere (“*Phallogaster* clade”) and Southern Hemisphere clades (“*Gen. prov. 1*”) (Fig. 3 - Part 1).

In addition to a traditional morphology-based description for the corresponding suborder (*Phallogastrineae subord. nov.*), we have also applied a phylogenetic taxon definition for the suborder (see Hibbett *et al.* 2018). More taxon sampling in the future may require further amendment of the morphological definition of the suborder, whereas our phylogenetic taxon definition of *Phallogastrineae* will remain stable.

Phallogaster pinyonensis (States) K. Hosaka, Castellano, Davoodian & T. Lebel, **comb. nov.** MycoBank MB 838487.

Basionym: Trappea pinyonensis States, *Mycotaxon* **41**: 128. 1991. MycoBank MB 129849.

Typus: USA, Arizona, Walnut Canyon National Monument, Coconino County, on sandy soil under *Pinus edulis*, 10 Oct. 1986, *J. States* AHF-530 (**holotype** ASC).

Phallogaster phillipsii (Harkn.) K. Hosaka, Castellano, Davoodian & T. Lebel, **comb. nov.** MycoBank MB 840085.

Basionym: Hysterangium phillipsii Harkn., *Proceedings of the California Academy of Sciences* **1**(8): 255. 1899. MycoBank MB 187085.

Synonym: Trappea phillipsii (Harkn.) Castellano, *Mycotaxon* **38**: 7. 1990. MycoBank MB 127551.

Typus: USA, California, Wire Bridge, Placer County, in soil, associated with *Quercus*, Jan. 1899, *C.L. Phillips* (Harkness 234, **holotype** BPI)

Notes: Although the species was not included in the phylogenetic analysis in this study, it has clearly been demonstrated to be the sister taxon to *Phallogaster (Trappea) pinyonensis* by Hosaka *et al.* (2006). Its basidiome surfaces stain pinkish when bruised, which is also a common characteristic with other species in the genus *Phallogaster*.

Excluded taxa

Trappea cinnamomea A-S. Xu & D.Q. Luo, *Mycosystema* **22**: 192. 2003. MycoBank MB 489004.

Notes: Based on the original description of *T. cinnamomea* (Xu & Luo 2003), its basidiome surfaces have the staining reaction to pink, which is similar to *Trappea phillipsii* and *T. pinyonensis*. However, we so far have no access to the specimens and no DNA data from the species are currently available. Until more definitive evidence becomes available, we keep this taxon in the genus *Trappea*.

Hysterangineae Castellano, T. Lebel, Davoodian & K. Hosaka, **subord. nov.** MycoBank MB 838486.

Basidiomes sequestrate, hypogeous or epigeous, and can be small (0.1 cm wide) to larger (up to 10 cm wide), subglobose to

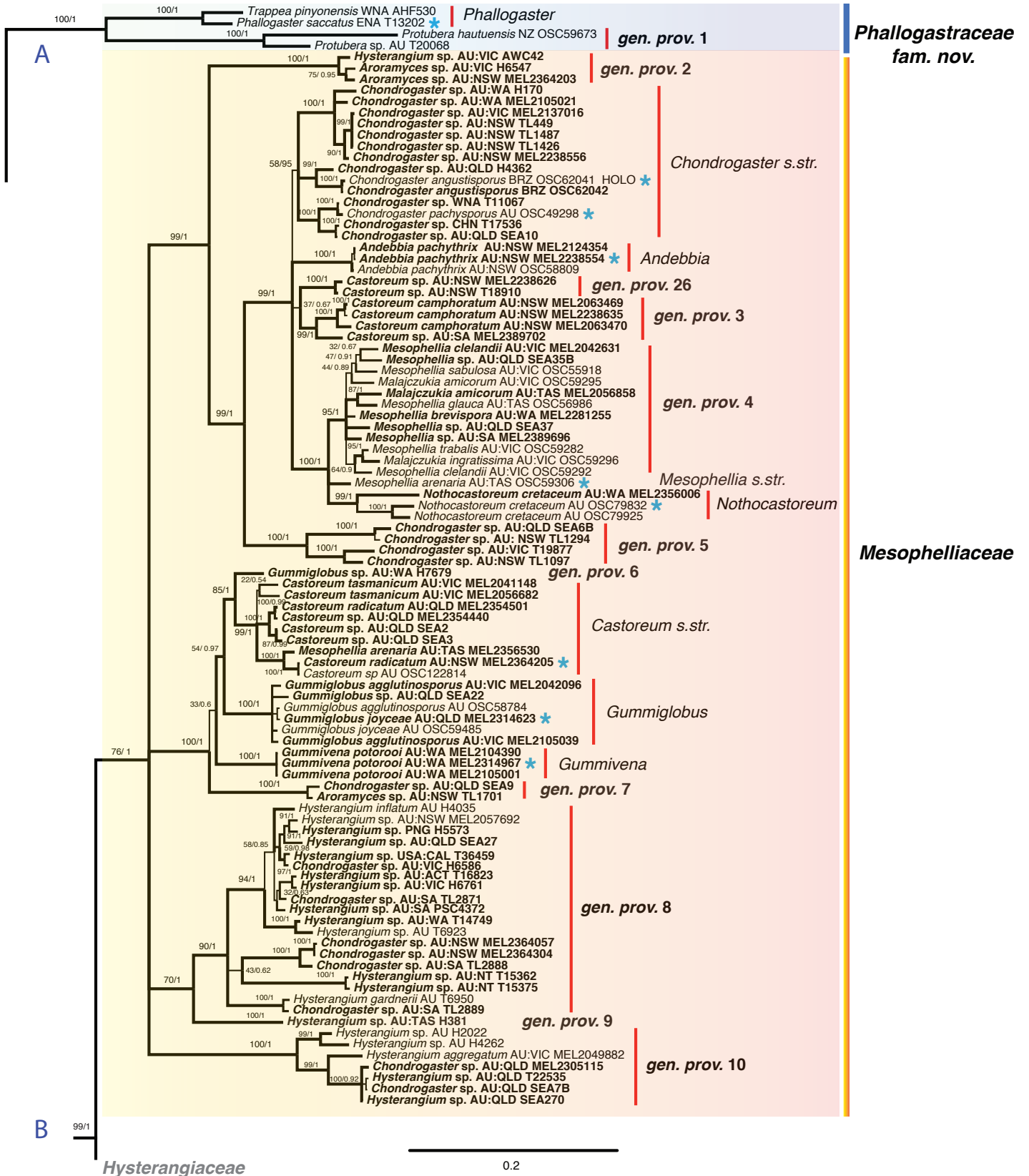


Fig. 3. Part 1. Phylogram from Bayesian analysis showing families and genera within *Hysterangiales*. Node A indicates *Phallogastrineae* subord. nov.; node B indicates *Hysterangineae* subord. nov. Maximum likelihood (ML) bootstrap values / Bayesian posterior probabilities (bpp) are shown at the nodes. The scale bar shows substitutions per site. Where bpp ≥ 0.95 and ML bootstrap $\geq 70\%$, branches are thickened. Type species indicated by a blue asterisk *. The asterisk in parentheses (*) denotes *Ileodictyon*, the currently accepted genus for *Protubera canescens*. Australian (AU) States and Territories indicated by: WA (Western Australia), NT (Northern Territory), QLD (Queensland), NSW (New South Wales), VIC (Victoria), TAS (Tasmania), SA (South Australia). United States (USA) states indicated by: ARIZ (Arizona), CAL (California), COL (Colorado), ID (Idaho), OR (Oregon). Other geographic areas indicated as follows: NZ (New Zealand), NewCal (New Caledonia), PNG (Papua New Guinea), BRZ (Brazil), MEX (Mexico), WNA (western North America), ENA (eastern North America), CHN (China), Guyana (Guyana), SSA (southern South America), NSA (northern South America), ASIA (Asia), SEASIA (southeast Asia), SING (Singapore), THAI (Thailand), IND (India), EUR (Europe), COSTA (Costa Rica), ZIMB (Zimbabwe).

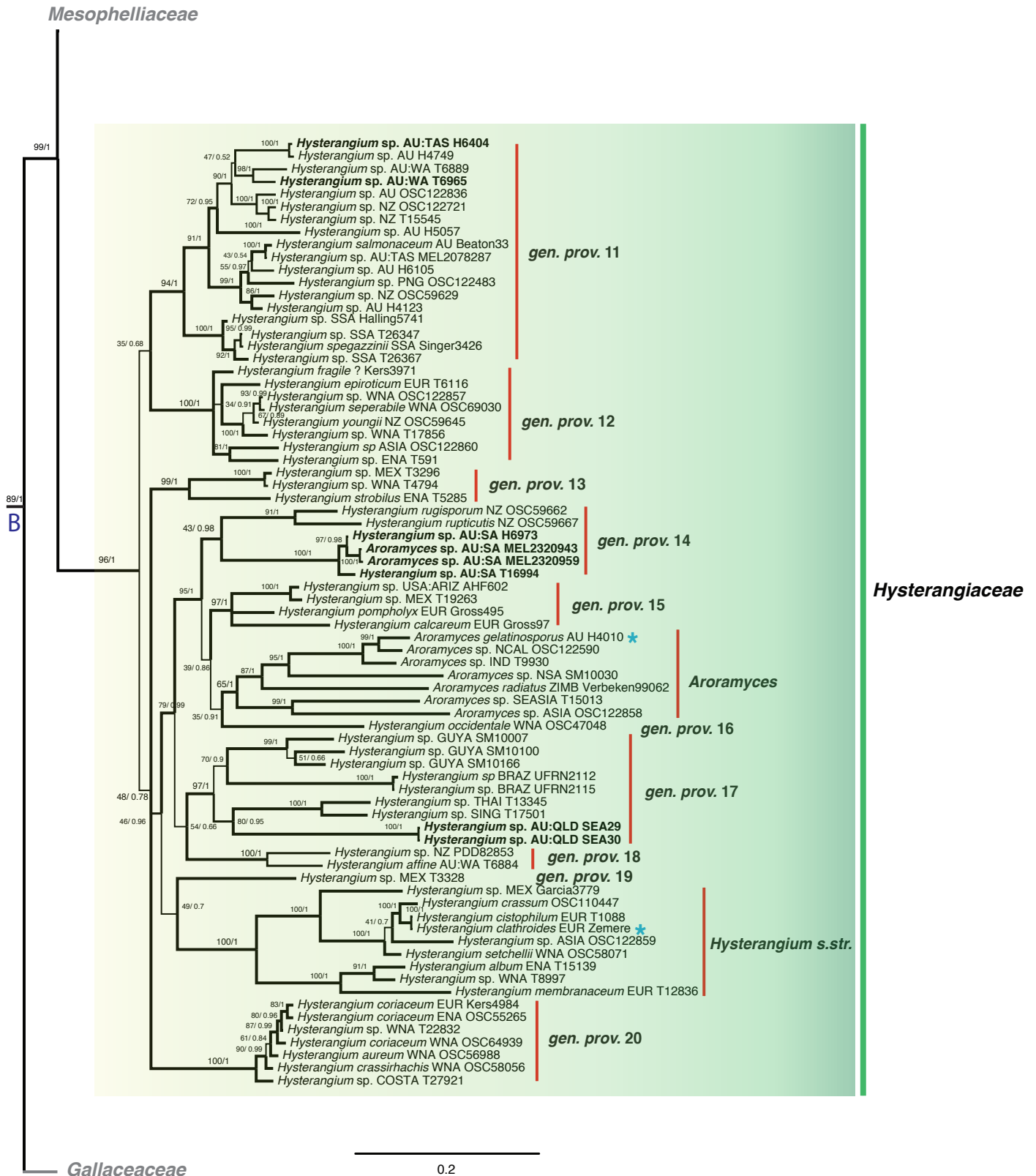


Fig. 3. (Continued) - Part 2.

irregularly subovoid without tapered base, single or gregarious, often covered with adhering sand and soil or encased in debris and rootlets, usually with conspicuous white to off-white rhizomorphs at base or along sides of basidiomata. Basidiome surface smooth to velvety to finely tomentose, often white to off-white in colour and often discolouring pinkish, reddish, yellowish or brownish, but purple to violet in some species. Peridium adherent to often readily separable from gleba,

elastic, glutinous or hard and brittle, 1–4-layered, sometimes incorporating mycorrhizae. *Columella* branched, whitish to semi-translucent and gelatinized or a soft to corky or rubbery central core or lacking such structures. *Gleba* varies from green, olivaceous green, greyish olive, brown to ochraceous or pinkish; gelatinous to cartilaginous or with a powdery spore mass at maturity, often with labyrinthine to elongated to circular locules. *Basidia* clavate to narrowly clavate to irregularly cylindrical,

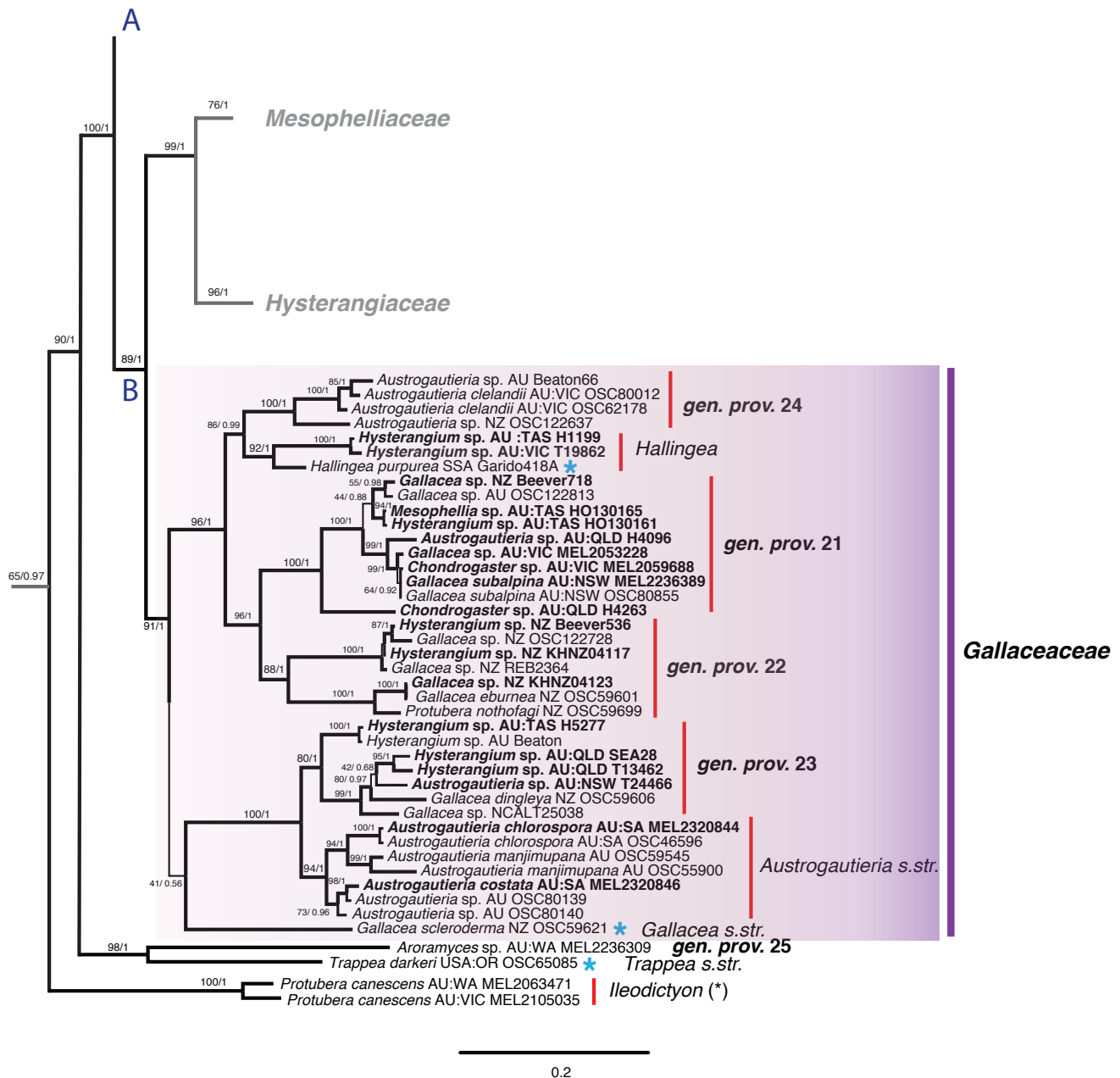


Fig. 3. (Continued) - Part 3.

thin-walled, hyaline, mostly 4-spored. Spores ellipsoid to oblong to fusoid, smooth to minutely verrucose or with long spines beneath a utricle, or sometimes with longitudinal ridges, thin- to thick-walled, often covered with a wrinkled to inflated or ephemeral utricle, hyaline, pale green, or brown in KOH, inamyloid, sometimes weakly dextrinoid. Odour faint, fetid, or sometimes sweet. Clamp connections present or absent. All species are presumably ectomycorrhizal with various vascular plants including *Dipterocarpaceae*, *Fagaceae*, *Myrtaceae*, *Nothofagaceae*, and *Pinaceae*.

Phylogenetic taxon definition of the suborder: The largest crown clade containing *Hysterangium clathroides* Vittad. 1831, but not *Phallogaster saccatus* Morgan 1893. This is a maximum crown-clade definition (Hibbett *et al.* 2018).

Type family: *Hysterangiaceae* E. Fisch., in Engler & Prantl, *Nat. Pflanzenfam.*, Teil. I (Leipzig): 304. 1899. [1900]

Notes: The *Hysterangineae* is exclusively composed of sequestrate taxa which are ectomycorrhizal with various vascular plants insofar as inferred from available studies. Most species in *Hysterangineae* have rather specific ectomycorrhizal hosts, usually restricted to a single plant family. For example, species distributed in the Southern Hemisphere are associated with *Myrtaceae* (mostly with *Eucalyptus* spp. and/or *Kunzea/Leptospermum* spp.) or *Nothofagaceae* (Castellano & Beaver 1994, Hosaka *et al.* 2008).

This suborder is much more speciose than *Phallogastrineae* and many more new species, especially from Australia, remain to be described for all three families, *i.e.*, *Hysterangiaceae*, *Mesophelliaceae* and *Gallaceaceae*. We believe that the family-level phylogeny is robust (Fig. 3, Supplementary Fig. S1), but more taxon sampling in the future may require further amendment of the morphological definition of the suborder. Therefore, as is the case for *Phallogastrineae*, we have also applied a phylogenetic taxon definition approach as summarized by Hibbett *et al.* (2018).

Table 1. Tabulation of specimens and sequences used in this study. Clade names are from Fig. 3. Generic names (genus verbatim determination) without a species name (species verbatim determination) are based on field identification; collections with species names (species verbatim determination) were examined micromorphologically. Australian (AUS) States and Territories indicated by: WA (Western Australia), NT (Northern Territory), QLD (Queensland), NSW (New South Wales), VIC (Victoria), TAS (Tasmania), SA (South Australia), SA (South Australia). Extra-Australian areas are indicated in bold. United States (USA) states indicated by: AZ (Arizona), CA (California), CO (Colorado), ID (Idaho), OR (Oregon). Other geographic areas indicated as follows: NZ (New Zealand), NEWCAL (New Caledonia), PNG (Papua New Guinea), BRZ (Brazil), MEX (Mexico), WNA (western North America), ENA (eastern North America), CHN (China), GUYANA (Guyana), SSA (southern South America), NSA (northern South America), ASIA (Asia), SEASIA (southeast Asia), SING (Singapore), THAI (Thailand), IND (India), EUR (Europe), COSTA (Costa Rica), ZIMB (Zimbabwe). Novel DNA sequences generated for this study are indicated by GenBank accessions in **bold**.

Clade	Genus verbatim determination	Species verbatim determination	Collector or Herbarium ID	Geography	ATP6	TEF1	Family	Suborder (Order)
Cantharellaceae	<i>Cantharellus</i>	sp.	TL2893	SA	MT828543	MW302303	Cantharellaceae	(Cantharellales)
<i>Geastrum</i>	<i>Geastrum</i>	<i>fimbriatum</i>	OSC60730	USA - OR	DQ218887	DQ219226	Geastraceae	(Geastrales)
	<i>Geastrum</i>	<i>floriforme</i>	OSC29328	USA - CO	DQ218769	DQ219227	Geastraceae	(Geastrales)
	<i>Geastrum</i>	<i>fornicatum</i>	MEL2087743	NSW	DQ218888	DQ219228	Geastraceae	(Geastrales)
	<i>Geastrum</i>	<i>pectinatum</i>	MEL2096557	VIC	DQ218889	DQ219229	Geastraceae	(Geastrales)
	<i>Geastrum</i>	<i>recolligens</i>	OSC41996	USA - ID	DQ218770	DQ219230	Geastraceae	(Geastrales)
<i>Geastrum</i> (<i>Radiigera</i>)	<i>Radiigera</i>	<i>fuscogleba</i>	OSC58979	—	DQ218896	DQ219234	Geastraceae	(Geastrales)
Gen. prov. 25 Lebel & Davoodian	<i>Aroramyces</i>	sp.	MEL2236309	WA	MW438321	MW302302	Trappeaceae	(Phallales)
<i>Trappea</i>	<i>Trappea</i>	<i>darkeri</i>	OSC65085	USA - OR	DQ218938	DQ219292	Trappeaceae	(Phallales)
<i>Ileodictyon</i>	<i>Protuberia</i> [<i>Ileodictyon</i>]	<i>canescens</i> [<i>gracile</i>]	MEL2063471	WA	DQ218931	DQ219283	Clathraceae	(Phallales)
	<i>Protuberia</i> [<i>Ileodictyon</i>]	<i>canescens</i> [<i>gracile</i>]	MEL2105035	VIC	DQ218932	DQ219284	Clathraceae	(Phallales)
<i>Phallogaster</i>	<i>Trappea</i>	<i>pinyonensis</i>	AHF530	WNA	DQ218884	DQ219221	Phallogastraceae	Phallogastrineae (Hysterangiales)
	<i>Phallogaster</i>	<i>saccatus</i>	T13202	ENA	DQ218882	DQ219217	Phallogastraceae	Phallogastrineae (Hysterangiales)
Gen. prov. 1 Hosaka	<i>Protuberia</i>	sp.	T20068	AUS	DQ218883	DQ219220	Phallogastraceae	Phallogastrineae (Hysterangiales)
	<i>Protuberia</i>	<i>hautuensis</i>	OSC59673	NZ	DQ218801	DQ219218	Phallogastraceae	Phallogastrineae (Hysterangiales)
Gen. prov. 24 Castellano & Hosaka	<i>Austrogautieria</i>	sp.	Beaton66	AUS	DQ218820	DQ219133	Gallaceae	Hysterangineae (Hysterangiales)
	<i>Austrogautieria</i>	sp.	OSC122637	NZ	DQ218819	DQ219132	Gallaceae	Hysterangineae (Hysterangiales)
<i>Hallingea</i>	<i>Austrogautieria</i>	<i>clelandii</i>	OSC62178	VIC	DQ218816	DQ219126	Gallaceae	Hysterangineae (Hysterangiales)
	<i>Austrogautieria</i>	<i>clelandii</i>	OSC80012	VIC	DQ218817	DQ219127	Gallaceae	Hysterangineae (Hysterangiales)
	<i>Hallingea</i>	<i>purpurea</i>	Garido418A	SSA	n/a	DQ219145	Gallaceae	Hysterangineae (Hysterangiales)
	<i>Hysterangium</i>	sp.	H1199	TAS	MW449866	MW302288	Gallaceae	Hysterangineae (Hysterangiales)
	indet.		T19862	VIC	MW048610	MW302289	Gallaceae	Hysterangineae (Hysterangiales)
Gen. prov. 21 Hosaka	<i>Austrogautieria</i>	sp.	H4096	QLD	MW417403	MW302309	Gallaceae	Hysterangineae (Hysterangiales)
	<i>Chondrogaster</i>	sp.	MEL2059688	VIC	MW048613	MW302306	Gallaceae	Hysterangineae (Hysterangiales)
<i>Chondrogaster</i>	<i>Chondrogaster</i>	sp.	H4263	QLD	MW048615	MW302290	Gallaceae	Hysterangineae (Hysterangiales)
<i>Gallacea</i>	<i>Gallacea</i>	sp.	Beever718	NZ	MW449882	MW302308	Gallaceae	Hysterangineae (Hysterangiales)
<i>Gallacea</i>	<i>Gallacea</i>	sp.	OSC122813	AUS	DQ218829	DQ219144	Gallaceae	Hysterangineae (Hysterangiales)
<i>Gallacea</i>	<i>Gallacea</i>	sp.	MEL2053228	VIC	MW048612	MW264846	Gallaceae	Hysterangineae (Hysterangiales)

Table 1. (Continued).

Clade	Genus verbatim determination	Species verbatim determination	Collector or Herbarium ID	Geography	ATP6	TEF1	Family	Suborder (Order)
Gen. prov. 22 Castellano	<i>Gallacea</i>	<i>subalpina</i>	MEL2236389	NSW	MW048614	MW302307	Gallaceaceae	Hysterangineae (Hysterangiales)
	<i>Gallacea</i>	<i>subalpina</i>	OSC80855	NSW	DQ218827	DQ219142	Gallaceaceae	Hysterangineae (Hysterangiales)
	<i>Hysterangium</i>	sp.	HO130161	TAS	MW438331	MW302304	Gallaceaceae	Hysterangineae (Hysterangiales)
	<i>Mesophellia</i>	sp.	HO130165	TAS	MW048611	MW302305	Gallaceaceae	Hysterangineae (Hysterangiales)
	<i>Gallacea</i>	sp.	OSC122728	NZ	DQ218828	DQ219143	Gallaceaceae	Hysterangineae (Hysterangiales)
	<i>Gallacea</i>	sp.	REB2364	NZ	DQ218825	DQ219140	Gallaceaceae	Hysterangineae (Hysterangiales)
	<i>Gallacea</i>	sp.	KHNZ04123	NZ	MW449865	MW302293	Gallaceaceae	Hysterangineae (Hysterangiales)
	<i>Gallacea</i>	<i>eburnea</i>	OSC59601	NZ	DQ218766	DQ219138	Gallaceaceae	Hysterangineae (Hysterangiales)
	<i>Hysterangium</i>	sp.	Beever536	NZ	MW417402	MW302291	Gallaceaceae	Hysterangineae (Hysterangiales)
	<i>Hysterangium</i>	sp.	KHNZ04117	NZ	MW438330	MW302292	Gallaceaceae	Hysterangineae (Hysterangiales)
	<i>Protuberia</i>	<i>nothofagi</i>	OSC59699	NZ	AY574786	DQ219219	Gallaceaceae	Hysterangineae (Hysterangiales)
	<i>Austrogautieria</i>	sp.	T24466	NSW	MW438326	MW302299	Gallaceaceae	Hysterangineae (Hysterangiales)
	<i>Gallacea</i>	sp.	T25038	NEWCAL	DQ218826	DQ219141	Gallaceaceae	Hysterangineae (Hysterangiales)
	<i>Gallacea</i>	<i>dingleyae</i>	OSC59606	NZ	DQ218824	DQ219137	Gallaceaceae	Hysterangineae (Hysterangiales)
Gen. prov. 23 Hosaka	<i>Hysterangium</i>	sp.	H5277	TAS	MW048616	MW302294	Gallaceaceae	Hysterangineae (Hysterangiales)
	<i>Hysterangium</i>	sp.	SEA28	QLD	MW438329	MW302297	Gallaceaceae	Hysterangineae (Hysterangiales)
	<i>Hysterangium</i>	sp.	T13462	QLD	MW048617	MW302298	Gallaceaceae	Hysterangineae (Hysterangiales)
	<i>Hysterangium</i>	sp.	KandGBeaton	AUS	DQ218790	DQ219174	Gallaceaceae	Hysterangineae (Hysterangiales)
	<i>Austrogautieria</i>	sp.	OSC80139	AUS	DQ218763	DQ219130	Gallaceaceae	Hysterangineae (Hysterangiales)
	<i>Austrogautieria</i>	sp.	OSC80140	AUS	DQ218764	DQ219131	Gallaceaceae	Hysterangineae (Hysterangiales)
	<i>Austrogautieria</i>	<i>chlorospora</i>	MEL2320844	SA	MW048618	MW302295	Gallaceaceae	Hysterangineae (Hysterangiales)
	<i>Austrogautieria</i>	<i>chlorospora</i>	OSC46596	AUS	DQ218761	DQ219125	Gallaceaceae	Hysterangineae (Hysterangiales)
	<i>Austrogautieria</i>	<i>costata</i>	MEL2320846	SA	MW438327	MW302296	Gallaceaceae	Hysterangineae (Hysterangiales)
	<i>Austrogautieria</i>	<i>manjimupana</i>	OSC55900	AUS	DQ218818	DQ219128	Gallaceaceae	Hysterangineae (Hysterangiales)
	<i>Austrogautieria</i>	<i>manjimupana</i>	OSC59545	AUS	DQ218762	DQ219129	Gallaceaceae	Hysterangineae (Hysterangiales)
	<i>Gallacea</i>	<i>scleroderma</i>	OSC59621	NZ	AY574787	DQ219139	Gallaceaceae	Hysterangineae (Hysterangiales)
	<i>Hysterangium</i>	sp.	H6404	TAS	MW417406	MW302282	Hysterangiaceae	Hysterangineae (Hysterangiales)
	<i>Hysterangium</i>	sp.	Halling5741	SSA	DQ218781	DQ219158	Hysterangiaceae	Hysterangineae (Hysterangiales)
<i>Hysterangium</i>	sp.	T26347	SSA	DQ218873	DQ219204	Hysterangiaceae	Hysterangineae (Hysterangiales)	
Gen. prov. 11 Hosaka	<i>Hysterangium</i>	sp.	T26367	SSA	DQ218874	DQ219205	Hysterangiaceae	Hysterangineae (Hysterangiales)
	<i>Hysterangium</i>	sp.	OSC122836	AUS	DQ218865	DQ219196	Hysterangiaceae	Hysterangineae (Hysterangiales)

Table 1. (Continued).

Clade	Genus verbatim determination	Species verbatim determination	Collector or Herbarium ID	Geography	ATP6	TEF1	Family	Suborder (Order)
Gen. prov. 12 Castellano	<i>Hysterangium</i>	sp.	T15545	NZ	DQ218837	DQ219161	Hysterangiaceae	Hysterangineae (Hysterangiales)
	<i>Hysterangium</i>	sp.	H4123	AUS	DQ218845	DQ219176	Hysterangiaceae	Hysterangineae (Hysterangiales)
	<i>Hysterangium</i>	sp.	H4749	AUS	DQ218861	DQ219192	Hysterangiaceae	Hysterangineae (Hysterangiales)
	<i>Hysterangium</i>	sp.	H5057	AUS	DQ218862	DQ219193	Hysterangiaceae	Hysterangineae (Hysterangiales)
	<i>Hysterangium</i>	sp.	H6105	AUS	DQ218864	DQ219195	Hysterangiaceae	Hysterangineae (Hysterangiales)
	<i>Hysterangium</i>	sp.	MEL2078287	TAS	DQ218843	DQ219173	Hysterangiaceae	Hysterangineae (Hysterangiales)
	<i>Hysterangium</i>	sp.	OSC122483	PNG	DQ218867	DQ219198	Hysterangiaceae	Hysterangineae (Hysterangiales)
	<i>Hysterangium</i>	sp.	OSC122721	NZ	DQ218866	DQ219197	Hysterangiaceae	Hysterangineae (Hysterangiales)
	<i>Hysterangium</i>	sp.	OSC59629	NZ	DQ218853	DQ219184	Hysterangiaceae	Hysterangineae (Hysterangiales)
	<i>Hysterangium</i>	"irregular"	T6965	WA	MW438322	MW302283	Hysterangiaceae	Hysterangineae (Hysterangiales)
	<i>Hysterangium</i>	"rhodocarpaceum"	T6889	WA	DQ218858	DQ219189	Hysterangiaceae	Hysterangineae (Hysterangiales)
	<i>Hysterangium</i>	<i>salmonaceum</i>	Beaton33	AUS	DQ218785	DQ219165	Hysterangiaceae	Hysterangineae (Hysterangiales)
	<i>Hysterangium</i>	<i>spagazzinii</i>	Singer3426	SSA	DQ218787	n/a	Hysterangiaceae	Hysterangineae (Hysterangiales)
	<i>Hysterangium</i>	sp.	OSC122857	WNA	DQ218851	DQ219182	Hysterangiaceae	Hysterangineae (Hysterangiales)
	<i>Hysterangium</i>	sp.	OSC122860	ASIA	DQ218860	DQ219191	Hysterangiaceae	Hysterangineae (Hysterangiales)
Gen. prov. 13 Castellano	<i>Hysterangium</i>	sp.	T17856	WNA	DQ218857	DQ219188	Hysterangiaceae	Hysterangineae (Hysterangiales)
	<i>Hysterangium</i>	sp.	T591	ENA	DQ218840	DQ219170	Hysterangiaceae	Hysterangineae (Hysterangiales)
	<i>Hysterangium</i>	<i>epiroticum</i>	T6116	EUR	DQ218779	DQ219155	Hysterangiaceae	Hysterangineae (Hysterangiales)
	<i>Hysterangium</i>	<i>fragile</i>	Kers3971	—	DQ218780	DQ219156	Hysterangiaceae	Hysterangineae (Hysterangiales)
	<i>Hysterangium</i>	<i>separabile</i>	OSC69030	WNA	DQ218786	DQ219166	Hysterangiaceae	Hysterangineae (Hysterangiales)
	<i>Hysterangium</i>	<i>youngii</i>	OSC59645	NZ	DQ218789	DQ219169	Hysterangiaceae	Hysterangineae (Hysterangiales)
	<i>Hysterangium</i>	sp.	T3296	MEX	DQ218842	DQ219172	Hysterangiaceae	Hysterangineae (Hysterangiales)
	<i>Hysterangium</i>	sp.	T4794	WNA	DQ218846	DQ219177	Hysterangiaceae	Hysterangineae (Hysterangiales)
	<i>Hysterangium</i>	<i>strobilus</i>	T5285	ENA	DQ218788	DQ219168	Hysterangiaceae	Hysterangineae (Hysterangiales)
	<i>Aroramycetes</i>	sp.	MEL2320943	SA	MW218374	MW302286	Hysterangiaceae	Hysterangineae (Hysterangiales)
	<i>Aroramycetes</i>	sp.	MEL2320959	SA	MW218375	MW302287	Hysterangiaceae	Hysterangineae (Hysterangiales)
	<i>Hysterangium</i>	<i>rugisporum</i>	OSC59662	NZ	DQ218784	DQ219164	Hysterangiaceae	Hysterangineae (Hysterangiales)
	<i>Hysterangium</i>	<i>rupticutis</i>	OSC59667	NZ	DQ218838	n/a	Hysterangiaceae	Hysterangineae (Hysterangiales)
	<i>Hysterogaster</i>	sp.	H6973	SA	MW218372	MW302284	Hysterangiaceae	Hysterangineae (Hysterangiales)
	<i>Hysterogaster</i>	sp.	T16994	VIC	MW218373	MW302285	Hysterangiaceae	Hysterangineae (Hysterangiales)
<i>Hysterangium</i>	sp.	AHF602	USA - AZ	DQ218854	DQ219185	Hysterangiaceae	Hysterangineae (Hysterangiales)	

Table 1. (Continued).

Clade	Genus verbatim determination	Species verbatim determination	Collector or Herbarium ID	Geography	ATP6	TEF1	Family	Suborder (Order)	
Aroramyces	<i>Hysterangium</i>	sp.	T19263	MEX	DQ218849	DQ219180	Hysterangiaceae	Hysterangineae (Hysterangiales)	
	<i>Hysterangium</i>	<i>calcareum</i>	Gross97	EUR	DQ218776	DQ219149	Hysterangiaceae	Hysterangineae (Hysterangiales)	
	<i>Hysterangium</i>	<i>pompholyx</i>	Gross495	EUR	DQ218783	DQ219163	Hysterangiaceae	Hysterangineae (Hysterangiales)	
	<i>Aroramyces</i>	<i>gelatinosporus</i>	H4010	AUS	DQ218809	DQ219118	Hysterangiaceae	Hysterangineae (Hysterangiales)	
	<i>Aroramyces</i>	<i>radiatus</i>	Verbeken99062	ZIMB	DQ218810	DQ219119	Hysterangiaceae	Hysterangineae (Hysterangiales)	
	<i>Aroramyces</i>	sp.	OSC122590	NEWCAL	DQ218814	DQ219123	Hysterangiaceae	Hysterangineae (Hysterangiales)	
	<i>Aroramyces</i>	sp.	OSC122858	ASIA	DQ218813	DQ219122	Hysterangiaceae	Hysterangineae (Hysterangiales)	
	<i>Aroramyces</i>	sp.	SM10030	NSA	DQ218815	DQ219124	Hysterangiaceae	Hysterangineae (Hysterangiales)	
	<i>Aroramyces</i>	sp.	T15013	SEASIA	DQ218811	DQ219120	Hysterangiaceae	Hysterangineae (Hysterangiales)	
	<i>Aroramyces</i>	sp.	T9930	IND	DQ218812	DQ219121	Hysterangiaceae	Hysterangineae (Hysterangiales)	
	Gen. prov. 16 Lebel & Castellano	<i>Hysterangium</i>	<i>occidentale</i>	OSC47048	WNA	AY574825	DQ219162	Hysterangiaceae	Hysterangineae (Hysterangiales)
	Gen. prov. 17 Lebel & Castellano	<i>Hysterangium</i>	sp.	SEA29	QLD	MW438328	MW302300	Hysterangiaceae	Hysterangineae (Hysterangiales)
		<i>Hysterangium</i>	sp.	SEA30	QLD	MW438323	MW302301	Hysterangiaceae	Hysterangineae (Hysterangiales)
		<i>Hysterangium</i>	sp.	SM10007	GUYANA	DQ218869	DQ219200	Hysterangiaceae	Hysterangineae (Hysterangiales)
	<i>Hysterangium</i>	sp.	SM10100	GUYANA	DQ218870	DQ219201	Hysterangiaceae	Hysterangineae (Hysterangiales)	
	<i>Hysterangium</i>	sp.	SM10166	GUYANA	DQ218871	DQ219202	Hysterangiaceae	Hysterangineae (Hysterangiales)	
	<i>Hysterangium</i>	sp.	T13345	THAI	DQ218872	DQ219203	Hysterangiaceae	Hysterangineae (Hysterangiales)	
	<i>Hysterangium</i>	sp.	T17501	SING	DQ218841	DQ219171	Hysterangiaceae	Hysterangineae (Hysterangiales)	
	<i>Hysterangium</i>	sp.	UFRN2112	BRZ	LT635647	LT635645	Hysterangiaceae	Hysterangineae (Hysterangiales)	
	<i>Hysterangium</i>	sp.	UFRN2115	BRZ	LT635648	LT635646	Hysterangiaceae	Hysterangineae (Hysterangiales)	
Gen. prov. 18 Castellano & Lebel	<i>Hysterangium</i>	sp.	PDD82853	NZ	DQ218868	DQ219199	Hysterangiaceae	Hysterangineae (Hysterangiales)	
	<i>Hysterangium</i>	<i>affine</i>	T6884	AUS	DQ218831	n/a	Hysterangiaceae	Hysterangineae (Hysterangiales)	
Gen. prov. 19 Castellano	<i>Hysterangium</i>	sp.	T3328	MEX	DQ218852	DQ219183	Hysterangiaceae	Hysterangineae (Hysterangiales)	
<i>Hysterangium</i>	<i>Hysterangium</i>	sp.	Garcia3779	MEX	DQ218847	DQ219178	Hysterangiaceae	Hysterangineae (Hysterangiales)	
	<i>Hysterangium</i>	sp.	OSC122859	ASIA	DQ218859	DQ219190	Hysterangiaceae	Hysterangineae (Hysterangiales)	
	<i>Hysterangium</i>	sp.	T8997	WNA	DQ218876	DQ219207	Hysterangiaceae	Hysterangineae (Hysterangiales)	
	<i>Hysterangium</i>	<i>album</i>	T15139	ENA	DQ218774	DQ219147	Hysterangiaceae	Hysterangineae (Hysterangiales)	
	<i>Hysterangium</i>	<i>cistophilum</i>	T1088	EUR	DQ218777	DQ219150	Hysterangiaceae	Hysterangineae (Hysterangiales)	
	<i>Hysterangium</i>	<i>clathroides</i>	Zemere	EUR	DQ218832	DQ219151	Hysterangiaceae	Hysterangineae (Hysterangiales)	
	<i>Hysterangium</i>	<i>crassum</i>	OSC110447	—	AY574827	DQ219154	Hysterangiaceae	Hysterangineae (Hysterangiales)	
	<i>Hysterangium</i>	<i>membranaceum</i>	T12836	EUR	DQ218782	DQ219160	Hysterangiaceae	Hysterangineae (Hysterangiales)	

Table 1. (Continued).

Clade	Genus verbatim determination	Species verbatim determination	Collector or Herbarium ID	Geography	ATP6	TEF1	Family	Suborder (Order)
Gen. prov. 20 Castellano	<i>Hysterangium</i>	<i>setchellii</i>	OSC58071	WNA	DQ218839	DQ219167	<i>Hysterangiaceae</i>	<i>Hysterangineae</i> (<i>Hysterangiales</i>)
	<i>Hysterangium</i>	sp.	T22832	WNA	DQ218850	DQ219181	<i>Hysterangiaceae</i>	<i>Hysterangineae</i> (<i>Hysterangiales</i>)
	<i>Hysterangium</i>	sp.	T27921	COSTA	DQ218875	DQ219206	<i>Hysterangiaceae</i>	<i>Hysterangineae</i> (<i>Hysterangiales</i>)
	<i>Hysterangium</i>	<i>aureum</i>	OSC56988	WNA	DQ218775	DQ219148	<i>Hysterangiaceae</i>	<i>Hysterangineae</i> (<i>Hysterangiales</i>)
	<i>Hysterangium</i>	<i>coriaceum</i>	Kers4984	EUR	DQ218833	n/a	<i>Hysterangiaceae</i>	<i>Hysterangineae</i> (<i>Hysterangiales</i>)
	<i>Hysterangium</i>	<i>coriaceum</i>	OSC55265	ENA	DQ218834	n/a	<i>Hysterangiaceae</i>	<i>Hysterangineae</i> (<i>Hysterangiales</i>)
	<i>Hysterangium</i>	<i>coriaceum</i>	OSC64939	WNA	AY574826	DQ219152	<i>Hysterangiaceae</i>	<i>Hysterangineae</i> (<i>Hysterangiales</i>)
	<i>Hysterangium</i>	<i>crassirhachis</i>	OSC58056	WNA	DQ218778	DQ219153	<i>Hysterangiaceae</i>	<i>Hysterangineae</i> (<i>Hysterangiales</i>)
	<i>Aroramyces</i>	sp.	H6547	VIC	MW417410	MW302213	<i>Mesophelliaceae</i>	<i>Hysterangineae</i> (<i>Hysterangiales</i>)
	<i>Aroramyces</i>	sp.	MEL2364203	NSW	MW417417	MW302214	<i>Mesophelliaceae</i>	<i>Hysterangineae</i> (<i>Hysterangiales</i>)
<i>Chondrogaster</i>	<i>Hysterangium</i>	sp.	AWC42	VIC	MW417411	MW302212	<i>Mesophelliaceae</i>	<i>Hysterangineae</i> (<i>Hysterangiales</i>)
	<i>Chondrogaster</i>	sp.	H170	WA	MW438325	MW302215	<i>Mesophelliaceae</i>	<i>Hysterangineae</i> (<i>Hysterangiales</i>)
	<i>Chondrogaster</i>	sp.	H4362	QLD	MW449881	MW302217	<i>Mesophelliaceae</i>	<i>Hysterangineae</i> (<i>Hysterangiales</i>)
	<i>Chondrogaster</i>	sp.	MEL2137016	VIC	MW417412	MW302218	<i>Mesophelliaceae</i>	<i>Hysterangineae</i> (<i>Hysterangiales</i>)
	<i>Chondrogaster</i>	sp.	TL449	NSW	MW417415	MW302219	<i>Mesophelliaceae</i>	<i>Hysterangineae</i> (<i>Hysterangiales</i>)
	<i>Chondrogaster</i>	sp.	TL1487	NSW	MW417414	MW302220	<i>Mesophelliaceae</i>	<i>Hysterangineae</i> (<i>Hysterangiales</i>)
	<i>Chondrogaster</i>	sp.	TL1426	NSW	MW417413	MW302221	<i>Mesophelliaceae</i>	<i>Hysterangineae</i> (<i>Hysterangiales</i>)
	<i>Chondrogaster</i>	sp.	T17536	CHN	MW449874	MW302224	<i>Mesophelliaceae</i>	<i>Hysterangineae</i> (<i>Hysterangiales</i>)
	<i>Chondrogaster</i>	sp.	SEA10	QLD	MW449868	MW302225	<i>Mesophelliaceae</i>	<i>Hysterangineae</i> (<i>Hysterangiales</i>)
	<i>Chondrogaster</i>	sp.	T11067	WNA	MW438324	MW302223	<i>Mesophelliaceae</i>	<i>Hysterangineae</i> (<i>Hysterangiales</i>)
<i>Andebbia</i>	<i>Chondrogaster</i>	sp.	MEL2238556	NSW	MW417405	MW302226	<i>Mesophelliaceae</i>	<i>Hysterangineae</i> (<i>Hysterangiales</i>)
	<i>Chondrogaster</i>	<i>angustisporus</i>	MEL2105021	WA	MW417407	MW302216	<i>Mesophelliaceae</i>	<i>Hysterangineae</i> (<i>Hysterangiales</i>)
	<i>Chondrogaster</i>	<i>angustisporus</i>	OSC62041	BRZ	DQ218822	DQ219135	<i>Mesophelliaceae</i>	<i>Hysterangineae</i> (<i>Hysterangiales</i>)
	<i>Chondrogaster</i>	<i>angustisporus</i>	OSC62042	BRZ	MW449876	MW302222	<i>Mesophelliaceae</i>	<i>Hysterangineae</i> (<i>Hysterangiales</i>)
	<i>Chondrogaster</i>	<i>pachysporus</i>	OSC49298	AUS	DQ218823	DQ219136	<i>Mesophelliaceae</i>	<i>Hysterangineae</i> (<i>Hysterangiales</i>)
	<i>Andebbia</i>	<i>pachythrinx</i>	MEL2124354	NSW	MW449879	MW302227	<i>Mesophelliaceae</i>	<i>Hysterangineae</i> (<i>Hysterangiales</i>)
	<i>Andebbia</i>	<i>pachythrinx</i>	MEL2238554	NSW	MW449880	MW302228	<i>Mesophelliaceae</i>	<i>Hysterangineae</i> (<i>Hysterangiales</i>)
	<i>Andebbia</i>	<i>pachythrinx</i>	OSC58809	NSW	DQ218808	DQ219117	<i>Mesophelliaceae</i>	<i>Hysterangineae</i> (<i>Hysterangiales</i>)
	<i>Castoreum</i>	sp.	MEL2238626	NSW	MW449869	MW302229	<i>Mesophelliaceae</i>	<i>Hysterangineae</i> (<i>Hysterangiales</i>)
	<i>Castoreum</i>	sp.	T18910	NSW	MW417409	MW302230	<i>Mesophelliaceae</i>	<i>Hysterangineae</i> (<i>Hysterangiales</i>)
Gen. prov. 3 Castellano	<i>Castoreum</i>	sp.	MEL2389702	SA	MW417408	MW302241	<i>Mesophelliaceae</i>	<i>Hysterangineae</i> (<i>Hysterangiales</i>)

Table 1. (Continued).

Clade	Genus verbatim determination	Species verbatim determination	Collector or Herbarium ID	Geography	ATP6	TEF1	Family	Suborder (Order)
Gen. prov. 4 Castellano & Lebel	<i>Castoreum</i>	<i>camphoratum</i>	MEL2063469	NSW	MW417404	MW302231	Mesophelliaceae	Hysterangiales (Hysterangiales)
	<i>Castoreum</i>	<i>camphoratum</i>	MEL2238635	NSW	MW417416	MW302232	Mesophelliaceae	Hysterangiales (Hysterangiales)
	<i>Castoreum</i>	<i>camphoratum</i>	MEL2063470	NSW	MW449877	MW302233	Mesophelliaceae	Hysterangiales (Hysterangiales)
	<i>Malajczukia</i>	<i>amicorum</i>	MEL2056858	TAS	MW449867	MW302235	Mesophelliaceae	Hysterangiales (Hysterangiales)
	<i>Malajczukia</i>	<i>amicorum</i>	OSC59295	VIC	DQ218792	DQ219208	Mesophelliaceae	Hysterangiales (Hysterangiales)
	<i>Malajczukia</i>	<i>ingratiissima</i>	OSC59296	VIC	DQ218793	DQ219209	Mesophelliaceae	Hysterangiales (Hysterangiales)
	<i>Mesophellia</i>	sp.	SEA37	QLD	MW449875	MW302237	Mesophelliaceae	Hysterangiales (Hysterangiales)
	<i>Mesophellia</i>	sp.	MEL2389696	SA	MW449870	MW302238	Mesophelliaceae	Hysterangiales (Hysterangiales)
	<i>Mesophellia</i>	sp.	SEA35B	QLD	MW438333	MW302239	Mesophelliaceae	Hysterangiales (Hysterangiales)
	<i>Mesophellia</i>	<i>brevispora</i>	MEL2281255	WA	MW449872	MW302236	Mesophelliaceae	Hysterangiales (Hysterangiales)
<i>Mesophellia</i>	<i>Mesophellia</i>	<i>clelandii</i>	MEL2042631	VIC	MW449878	MW302234	Mesophelliaceae	Hysterangiales (Hysterangiales)
	<i>Mesophellia</i>	<i>clelandii</i>	OSC59292	VIC	DQ218795	DQ219211	Mesophelliaceae	Hysterangiales (Hysterangiales)
	<i>Mesophellia</i>	<i>glauca</i>	OSC56986	TAS	DQ218878	DQ219212	Mesophelliaceae	Hysterangiales (Hysterangiales)
	<i>Mesophellia</i>	<i>sabulosa</i>	OSC55918	VIC	DQ218879	DQ219213	Mesophelliaceae	Hysterangiales (Hysterangiales)
	<i>Mesophellia</i>	<i>trabalis</i>	OSC59282	VIC	DQ218880	DQ219214	Mesophelliaceae	Hysterangiales (Hysterangiales)
	<i>Mesophellia</i>	<i>arenaria</i>	OSC59306	TAS	DQ218877	DQ219210	Mesophelliaceae	Hysterangiales (Hysterangiales)
	<i>Nothocastoreum</i>	<i>cretaceum</i>	MEL2356006	WA	MW246680	MW302240	Mesophelliaceae	Hysterangiales (Hysterangiales)
	<i>Nothocastoreum</i>	<i>cretaceum</i>	OSC79832	AUS	DQ218881	DQ219215	Mesophelliaceae	Hysterangiales (Hysterangiales)
	<i>Nothocastoreum</i>	<i>cretaceum</i>	OSC79925	AUS	n/a	DQ219216	Mesophelliaceae	Hysterangiales (Hysterangiales)
	Gen. prov. 5 Lebel	<i>Chondrogaster</i>	sp.	SEA6B	QLD	MW246665	MW302273	Mesophelliaceae
<i>Chondrogaster</i>		sp.	TL1294	NSW	MW246677	MW302274	Mesophelliaceae	Hysterangiales (Hysterangiales)
<i>Chondrogaster</i>		sp.	T19877	VIC	MW246684	MW302275	Mesophelliaceae	Hysterangiales (Hysterangiales)
<i>Chondrogaster</i>		sp.	TL1097	NSW	MW246685	MW302276	Mesophelliaceae	Hysterangiales (Hysterangiales)
<i>Gummiglobus</i>		sp.	H7679	WA	MW449873	MW302242	Mesophelliaceae	Hysterangiales (Hysterangiales)
<i>Castoreum</i>	<i>Castoreum</i>	sp.	SEA2	QLD	MW246674	MW302246	Mesophelliaceae	Hysterangiales (Hysterangiales)
	<i>Castoreum</i>	sp.	SEA3	QLD	MW246668	MW302247	Mesophelliaceae	Hysterangiales (Hysterangiales)
	<i>Castoreum</i>	sp.	OSC122814	AUS	DQ218821	DQ219134	Mesophelliaceae	Hysterangiales (Hysterangiales)
	<i>Castoreum</i>	<i>radicatum</i>	MEL2354501	QLD	MW246672	MW302244	Mesophelliaceae	Hysterangiales (Hysterangiales)
	<i>Castoreum</i>	<i>radicatum</i>	MEL2364205	NSW	MW246690	MW302250	Mesophelliaceae	Hysterangiales (Hysterangiales)
	<i>Castoreum</i>	<i>tasmanicum</i>	MEL2041148	VIC	MW246695	MW302243	Mesophelliaceae	Hysterangiales (Hysterangiales)
	<i>Castoreum</i>	<i>tasmanicum</i>	MEL2056682	VIC	MW246683	MW302248	Mesophelliaceae	Hysterangiales (Hysterangiales)

Table 1. (Continued).

Clade	Genus verbatim determination	Species verbatim determination	Collector or Herbarium ID	Geography	ATP6	TEF1	Family	Suborder (Order)
Gummiglobus	<i>Fusicastoreum</i>	sp.	MEL2354440	QLD	MW246667	MW302245	Mesophelliaceae	Hysterangineae (Hysterangiales)
	<i>Mesophellia</i>	<i>arenaria</i>	MEL2356530	TAS	MW246688	MW302249	Mesophelliaceae	Hysterangineae (Hysterangiales)
	<i>Gummiglobus</i>	sp.	SEA22	QLD	MW246691	MW302252	Mesophelliaceae	Hysterangineae (Hysterangiales)
	<i>Gummiglobus</i>	<i>agglutinosporus</i>	OSC58784	AUS	DQ218830	n/a	Mesophelliaceae	Hysterangineae (Hysterangiales)
	<i>Gummiglobus</i>	<i>agglutinosporus</i>	MEL2042096	VIC	MW246693	MW302251	Mesophelliaceae	Hysterangineae (Hysterangiales)
	<i>Gummiglobus</i>	<i>agglutinosporus</i>	MEL2105039	VIC	MW246670	MW302254	Mesophelliaceae	Hysterangineae (Hysterangiales)
	<i>Gummiglobus</i>	<i>joyceae</i>	MEL2314623	QLD	MW438332	MW302253	Mesophelliaceae	Hysterangineae (Hysterangiales)
	<i>Gummiglobus</i>	<i>joyceae</i>	OSC59485	AUS	DQ218772	n/a	Mesophelliaceae	Hysterangineae (Hysterangiales)
	<i>Gummivena</i>	<i>potorooi</i>	MEL2104390	WA	MW246678	MW302255	Mesophelliaceae	Hysterangineae (Hysterangiales)
	<i>Gummivena</i>	<i>potorooi</i>	MEL2314967	WA	MW246696	MW302256	Mesophelliaceae	Hysterangineae (Hysterangiales)
Gen. prov. 7 Davoodian, Lebel & Castellano	<i>Gummivena</i>	<i>potorooi</i>	MEL2105001	WA	MW246673	MW302257	Mesophelliaceae	Hysterangineae (Hysterangiales)
	<i>Aroramycetes</i>	sp.	TL1701	NSW	MT947437	MT947438	Mesophelliaceae	Hysterangineae (Hysterangiales)
	<i>Chondrogaster</i>	sp.	SEA9	QLD	MT947436	MW264847	Mesophelliaceae	Hysterangineae (Hysterangiales)
	<i>Chondrogaster</i>	sp.	H6586	VIC	MW246682	MW302260	Mesophelliaceae	Hysterangineae (Hysterangiales)
	<i>Chondrogaster</i>	sp.	TL2871	SA	MW246692	MW302262	Mesophelliaceae	Hysterangineae (Hysterangiales)
	<i>Chondrogaster</i>	sp.	MEL2364057	NSW	MW246671	MW302267	Mesophelliaceae	Hysterangineae (Hysterangiales)
	<i>Chondrogaster</i>	sp.	MEL2364304	NSW	MW246697	MW302268	Mesophelliaceae	Hysterangineae (Hysterangiales)
	<i>Chondrogaster</i>	sp.	TL2888	SA	MW246689	MW302269	Mesophelliaceae	Hysterangineae (Hysterangiales)
	<i>Chondrogaster</i>	sp.	TL2889	SA	MW246687	MW302270	Mesophelliaceae	Hysterangineae (Hysterangiales)
	<i>Hysterangium</i>	sp.	T16823	ACT	MW246686	MW302258	Mesophelliaceae	Hysterangineae (Hysterangiales)
Gen. prov. 8 Hosaka	<i>Hysterangium</i>	sp.	T36459	USA - CA	MW246694	MW302259	Mesophelliaceae	Hysterangineae (Hysterangiales)
	<i>Hysterangium</i>	sp.	PSC4372	SA	MW246679	MW302261	Mesophelliaceae	Hysterangineae (Hysterangiales)
	<i>Hysterangium</i>	sp.	H6761	VIC	MW246666	MW302263	Mesophelliaceae	Hysterangineae (Hysterangiales)
	<i>Hysterangium</i>	sp.	SEA27	QLD	MW246681	MW302265	Mesophelliaceae	Hysterangineae (Hysterangiales)
	<i>Hysterangium</i>	sp.	H5573	PNG	MW246669	MW302264	Mesophelliaceae	Hysterangineae (Hysterangiales)
	<i>Hysterangium</i>	sp.	T14749	WA	MW246698	MW302266	Mesophelliaceae	Hysterangineae (Hysterangiales)
	<i>Hysterangium</i>	sp.	T6923	AUS	DQ218855	DQ219186	Mesophelliaceae	Hysterangineae (Hysterangiales)
	<i>Hysterangium</i>	sp.	T15362	NT	MW246675	MW302271	Mesophelliaceae	Hysterangineae (Hysterangiales)
	<i>Hysterangium</i>	sp.	T15375	NT	MW246676	MW302272	Mesophelliaceae	Hysterangineae (Hysterangiales)
	<i>Hysterangium</i>	sp.	MEL2057692	NSW	DQ218848	DQ219179	Mesophelliaceae	Hysterangineae (Hysterangiales)

Table 1. (Continued).

Clade	Genus verbatim determination	Species verbatim determination	Collector or Herbarium ID	Geography	ATP6	TEF1	Family	Suborder (Order)
	<i>Hysterangium</i>	<i>gardnerii</i>	T6950	AUS	DQ218835	DQ219157	Mesophelliaceae	Hysterangiineae (Hysterangiales)
	<i>Hysterangium</i>	<i>inflatum</i>	H4035	AUS	DQ218836	DQ219159	Mesophelliaceae	Hysterangiineae (Hysterangiales)
Gen. prov. 9 Davoodian	<i>Hysterangium</i>	sp.	H381	TAS	MW449871	MW302281	Mesophelliaceae	Hysterangiineae (Hysterangiales)
Gen. prov. 10 Hosaka	<i>Chondrogaster</i>	sp.	MEL2305115	QLD	MW449861	MW302277	Mesophelliaceae	Hysterangiineae (Hysterangiales)
	<i>Chondrogaster</i>	sp.	SEA7B	QLD	MW449864	MW302280	Mesophelliaceae	Hysterangiineae (Hysterangiales)
	<i>Hysterangium</i>	sp.	H2022	AUS	DQ218856	DQ219187	Mesophelliaceae	Hysterangiineae (Hysterangiales)
	<i>Hysterangium</i>	sp.	H4262	AUS	DQ218773	DQ219146	Mesophelliaceae	Hysterangiineae (Hysterangiales)
	<i>Hysterangium</i>	sp.	T22535	QLD	MW449862	MW302278	Mesophelliaceae	Hysterangiineae (Hysterangiales)
	<i>Hysterangium</i>	sp.	SEA270	QLD	MW449863	MW302279	Mesophelliaceae	Hysterangiineae (Hysterangiales)
	<i>Hysterangium</i>	<i>aggregatum</i>	MEL2049882	VIC	DQ218844	DQ219175	Mesophelliaceae	Hysterangiineae (Hysterangiales)

DISCUSSION

In addition to revealing new taxa, our analysis highlights prominent biogeographic patterns in *Hysterangiales*. Trans-Tasman distributions are numerous throughout *Hysterangiales*; almost every New Zealand lineage inferred in our phylogram is sister to an Australian lineage, at various taxonomic scales. Gondwanan disjunctions are also represented, for example "Gen. prov. 17" (Fig. 3 - Part 2) contains an Australian and paleotropical clade sister to a northeastern South American clade. Some human-mediated introduction events are apparent as well *e.g.* *Chondrogaster angustisporus* (OSC62041 - holotype) is from planted *Eucalyptus* in Brazil (Giachini *et al.* 2000). Hosaka *et al.* (2008) postulated that the *Hysterangiales* originated in Australia or Eastern Gondwana and expanded in range over time, possibly through long-distance dispersal. Sheedy *et al.* (2016) inferred that *Hysterangiales* was the first group of *Agaricomycetes* to become sequestrate in Australia (*ca.* 83 million years ago). The rate of sequestration of *Agaricomycetes* was inferred to have increased in Australia after separation from Antarctica, the timing of which overlaps with the radiation of potential mycorrhizal plant associates as well as the emergence of specialized mycophagous marsupials. Although periods of aridification were evidently not the sole driver of sequestration, they likely had a major influence on the diversity of sequestrate fungi in Australia, including *Hysterangiales* (Sheedy *et al.* 2016).

Our analysis indicates phylogenetic signals for some prominent macroscopic features. In the *Mesophelliaceae*, the clade unifying *Gummivena*, *Gummiglobus*, and *Castoreum* is comprised of species that have gummy-like mycelium and/or outer glebal tissue (Fig. 1N, O). Species in the clade containing *Chondrogaster*, *Andebbia*, *Mesophellia*, *Nothocastoreum*, and related provisional genera have a powdery spore mass at maturity and also incorporate roots and soil in a multi-layered mycelial crust surrounding the basidiome (in *Nothocastoreum* this falls off easily and remains in the soil) (Fig. 1J–M). In provisional genera 8 through 10, the basidiomes are typically encased in a mycelial soil crust, and the glebal tissue is gelatinized. Macroscopic characters of *Hysterangiaceae* overlap somewhat with various clades in the *Mesophelliaceae* and *Gallaceaceae*, including having a gelatinized gleba and varying degrees of rhizomorph development across the surface of basidiomes (Fig. 1G–I). In *Gallaceaceae*, most lineages have a firm, cartilaginous peridium surrounding a gelatinized gleba (Fig. 1D–F), and spores lacking an utricle (Fig. 2A). The condition of having ridged spores (Fig. 2C) is not monophyletic in *Hysterangiales*; this character was previously thought to be diagnostic for the genus *Austrogautieria* (Stewart & Trappe 1985) but now appears in two well-supported, distinct clades in *Gallaceaceae* (*Austrogautieria* and "Gen. prov. 24"; Fig. 3 - Part 3).

Numerous provisional genera and species have been revealed in this study, which will be described by the respective authors of this paper and other collaborators in upcoming publications. We believe our current approach of recognising numerous provisional genera is a more accurate and conservative estimate of diversity than to lump them into fewer, larger genera. In addition to strong phylogenetic signals, each provisional genus is readily distinguishable by macroscopic and microscopic characters, but species level differentiation within genera requires more sampling in many of these taxa. Moreover, our phylogenetic analyses show that some existing genera, such as *Castoreum* and *Gummiglobus* in *Mesophelliaceae*, are closely related to each other within their respective families, but our provisional genera are more distantly related to these existing genera (Fig. 3, Supplementary Fig. S1). More sampling throughout Australasia and South America will likely uncover additional clades and aid in further refining generic and specific boundaries.

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Conflict of interest: The authors declare that there is no conflict of interest.

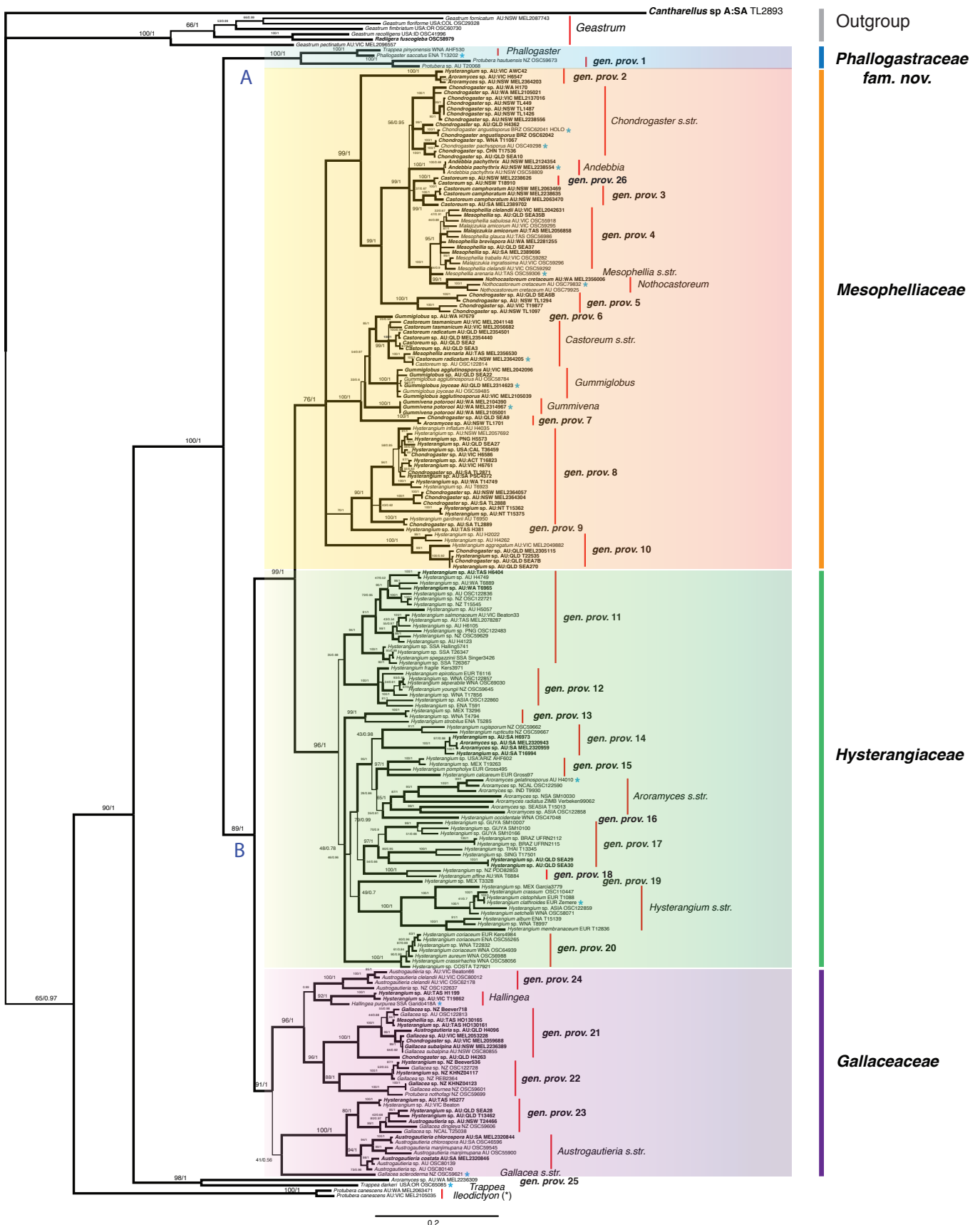
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Fig. S1. Overview Phylogram from Bayesian analysis showing relationship between *Hysterangiales*, some *Phallales* and outgroups (OG). Node A indicates *Phallogastrineae subord. nov.*; node B indicates *Hysterangineae subord. nov.* Maximum likelihood (ML) bootstrap values / Bayesian posterior probabilities (bpp) are shown at the nodes. Where bpp \geq 0.95 and ML bootstrap \geq 70 %, branches are thickened. Type species indicated by a blue asterisk *. The asterisk in parentheses (*) denotes the currently accepted genus for *Protuberia canescens*, *lleodictyon*. Countries and States indicated with same acronyms as Fig. 3.

Figure S1



Supplementary Fig. S1. Overview Phylogram from Bayesian analysis showing relationship between *Hysterangiales*, some *Phallales* and outgroups (OG). Node A indicates *Phallogastrineae subord. nov.*; node B indicates *Hysterangineae subord. nov.* Maximum likelihood (ML) bootstrap values / Bayesian posterior probabilities (bpp) are shown at the nodes. Where $bpp \geq 0.95$ and ML bootstrap $\geq 70\%$, branches are thickened. Type species indicated by a blue asterisk *. The asterisk in parentheses (*) denotes the currently accepted genus for *Protuberana canescens*, *Ileodictyon*. Countries and States indicated with same acronyms as Fig. 3.