Mycosphere 13(2): 207–280 (2022) www.mycosphere.org ISSN 2077 7019
Article – Special issue
Doi 10.5943/mycosphere/si/1f/7

Evolutionary relationships and allied species of *Pyronemataceae*, with segregation of the novel family *Pyropyxidaceae*

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Zeng M, Gentekaki E, Zeng XY, Tian Q, Zhao Q, Hyde KD 2022 – Evolutionary relationships and allied species of *Pyronemataceae*, with segregation of the novel family *Pyropyxidaceae*. Mycosphere 13(2), 207–280, Doi 10.5943/mycosphere/si/1f/7

Abstract

Pyronemataceae is the largest family within *Pezizomycetes*, members of which are distinguished by the shape and color of apothecia, the shape and ornamentation of ascospores, and the presence of carotenoids. Within *Pyronemataceae*, the *Otidea* lineage was previously elevated to the family level based on multiple gene analyses. However, this was controversial as the family was embedded in *Pyronemataceae sensu stricto* redefined by Hansen et al. Herein, we re-elevate the *Otidea* lineage to *Otideaceae* at the family rank level. Meanwhile, using a combination of morphology, phylogeny and divergence times estimates, we propose the new family *Pyropyxidaceae* to accommodate the *Pyropyxis* lineage containing *Jafnea*, *Micronematobotrys*, *Pyropyxis,* and *Smardaea*. The *Pyropyxis* lineage is phylogenetically distinct and branches off *Otideaceae* and the rest of *Pyronemataceae sensu stricto.* The monophyly of *Otideaceae* and *Pyropyxidaceae* has maximum statistical support. These two families have specific morphological features that set them apart from the rest of *Pyronemataceae sensu stricto*. *Pyropyxidaceae* has short hyphoid or moniliform hairs, while *Otideaceae* has abundant tomentum on the basal of apothecia. Both families lack true ascomatal hairs and carotenoids. Divergence times estimates place the crown of *Pyropyxidaceae* split at 141 Mya in the Early Cretaceous. The ancestral character state of ascomata in *Pyronemataceae*, *Pyropyxidaceae* and *Otideaceae* was the apothecium represented by epigeous taxa. Within *Pyronemataceae*, the hypogeous ascomata independently arose at least twice in distantly related lineages at 99 and 31 Mya. Moreover, cleistothecia and gymnothecia independently arose only once at approximately 38 Mya. Besides, we collected 37 allied collections of *Pyronemataceae sensu stricto*, including six new species, *viz.*, *Melastiza verruculosa*, *Otidea guttulata*, *O. macrospora*, *O. ovalispora*, *O. subleporina* and *Scutellinia verruculosa*. All new species are introduced based on morphological characters and phylogeny.

Submitted 20 December 2022, Accepted 28 December 2022, Published 29 December 2022
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Keywords – 6 new species – 1 new family – *Pezizales* – taxonomy – evolution

Introduction

Pyronemataceae Corda is the largest family in *Pezizales* (*Pezizomycetes*). This family produces epigeous, semi-hypogeous to hypogeous ascomata with a variety of shapes; sessile to stalked, discoid to cupulate, and pulvinate to folded, with most members presenting true ascomatal hairs (Perry et al. 2007, Hansen et al. 2013, Pfister 2015). Members of this family are distinguished by pigmented paraphyses, inamyloid asci, and smooth to ornamented ascospores (Pfister 2015). The family contains approximately 80 genera, but molecular data is available for only two-thirds of them (Perry et al. 2007, Hansen et al. 2013, Ekanayaka et al. 2018, Wijayawardene et al. 2020, 2022). The concept of a broadly circumscribed *Pyronemataceae* was originally widely accepted (Korf 1972, Korf 1973, Perry et al. 2007, Kirk et al. 2008). A stricter concept of *Pyronemataceae*, which is limited to *Pyronema* with or without *Coprotus*, has also been proposed (Rifai 1968, Kimbrough 1970, 1989). Other genera were adopted in three currently not accepted/controversial families, namely *Aleuriaceae*, *Humariaceae*, and *Otideaceae* (Eckblad 1968, Le Gal 1969, Korf & Zhuang 1991a, b). Subsequent phylogenetic inferences at the order and family levels resulted in new families to accommodate genera, which were originally placed in the broad *Pyronemataceae* (Perry et al. 2007, Pfister et al. 2008, Hansen et al. 2013, Ekanayaka et al. 2018). Hansen et al. (2013) redefined *Pyronemataceae sensu stricto* based on its monophyly within *Pezizomycetes*. It includes the broadly circumscribed *Pyronemataceae*, excluding some genera based on their closer phylogenetic relationships with other families (Hansen et al. 2013). Recent extensions and amendments within *Pyronemataceae* followed the strict concept put forth by Hansen et al. (Sun & Guo 2010, Hansen & Olariaga 2015, Lindemann et al. 2015, Olariaga et al. 2015, Van Vooren et al. 2015a, 2017, 2021, Lindemann & Alvarado 2017, Alvarado et al. 2018, Van Vooren & Vega 2018a, Xu et al. 2018, 2022, Grupe et al. 2019, Saitta 2019, Vega et al. 2019, Eckstein et al. 2021a, Lindemann et al. 2022). The current consensus refutes the original concept of *Otideaceae*, whose family rank remains controversial.

Eckblad (1968) established *Otideaceae* to accommodate *Otidea* and the related genera *Ascosparassis*, *Geopyxis*, *Sowerbyella*, and *Tarzetta*, all of which produce larger, sessile or stipitate apothecia without bright orange to red colors. Korf (1972, 1973) reduced *Otideaceae* to subfamily rank (*Otideoideae*) comprising three tribes within *Pyronemataceae sensu lato*. *Ascosparassis*, *Otidea* and *Psilopezia* were placed in the tribe *Otideeae*, *Tarzetta* was placed in the tribe *Jafneeae*, while *Geopyxis* and *Sowerbyella* were apportioned into two separate subfamilies (Korf 1972, 1973). However, several subsequent studies accepted the family rank of *Otideaceae* (e.g. Eriksson & Hawksworth 1993, Yao & Spooner 1996a, Wang & Pfister 2001). Phylogenetic inferences using combined genetic marker matrices lead to further clarify the relationship between *Pyronemataceae* and *Otideaceae*. Multi-locus phylogenetic analyses of *Pyronemataceae* and *Pezizomycetes* did not support the previously proposed close relationships among *Geopyxis*, *Otidea*, *Psilopezia*, *Sowerbyella*, and *Tarzetta* (Hansen et al. 2013, Ekanayaka et al. 2018). Instead, *Otidea* along with *Acervus*, *Arpinia*, *Monascella*, and *Warcupia* grouped together and nested within *Pyronemataceae* (Hansen et al. 2013, Ekanayaka et al. 2018). Recently, many *Otidea*-related new taxa, especially *Otidea* spp., were assigned to *Pyronemataceae* rather than *Otideaceae* (Hansen et al. 2013, Hansen et al. 2015, Olariaga et al. 2015, Ekanayaka et al. 2016, Xu et al. 2018, 2022, Zeng et al. 2020). Ekanayaka et al. (2018) accepted the family rank of *Otideaceae* due to the basal placement of the *Otidea*-lineage within *Pyronemataceae sensu stricto*. However, the statistical support for the *Otideaceae* node, *Pyronemataceae* node, and sister relationship for these two families was not significant (Ekanayaka et al. 2018).

Phylogenetic studies have been used to support or reject hypotheses about the placement of specific fungal groups (Hyde et al. 2017, Hongsanan et al. 2017). Currently, molecular clock analyses are being commonly applied to infer evolutionary events in the fungal tree, hence providing additional evidence to stabilize the ranking of fungal taxa (Beimforde et al. 2014, Phukhamsakda et al. 2016, Samarakoon et al. 2016, Liu et al. 2017, 2018a, Zeng et al. 2019, 2022, Zhang et al. 2019, Hyde et al. 2021). Using fossil data to calibrate the molecular clock, one can estimate divergence times of lineages and further speculate on ancestral character states, biogeographic origin, diversification, and host associations (Sung et al. 2008, O'Donnell et al. 2011, Du et al. 2012, Bonito et al. 2013, Sochorová et al. 2019, Samarakoon et al. 2022). Phylogenetic analyses have pointed towards *Pezizomycetes* and *Orbiliomycetes* being the "basal", early diverging *Pezizomycotina* lineages, hence they are significant to evolutionary studies interrogating this diverse group of fungi (James 2006, Schoch et al. 2009a, b, Ebersberger et al. 2012, Kumar et al. 2012, Beimforde et al. 2014, Liu et al. 2017). Some studies on the estimated divergence time of *Pezizomycetes* have extrapolated the crown age of the group, which ranges from the Carboniferous (310 Mya) to the Devonian (413 Mya) (Table 1). Others have focused on smaller groups involving *Geomoriaceae* (Kraisitudomsook et al. 2020), *Helvellaceae* (Zhao 2016, Kraisitudomsook et al. 2020), *Morchellaceae* (O'Donnell et al. 2011, Du et al. 2012, Liu et al. 2018b, Kraisitudomsook et al. 2020, Lü et al. 2021), *Pyronemataceae* (Alvarado et al. 2016, Sochorová et al. 2019), and *Tuberaceae* (Bonito et al. 2013, Murat et al. 2018).

In this study, dozens of discomycetes were collected from China and Thailand. Morphological descriptions were performed, and phylogenetic trees were inferred using LSU, *tef-1α*, *rpb2*, and SSU genetic markers. Our analyses show that these samples belong to eight genera of *Pezizales*, including six new species from three genera. Based on morphology, phylogeny, and divergence time estimates, we propose a new family separated from *Pyronemataceae*.

Table 1 The estimated divergence times for the *Pezizomycetes* crown in previous studies.

Geological period	Time (Mya)	References
Carboniferous	~310	Gueidan et al. (2011)
Carboniferous	317 (213–407)	Prieto & Wedin (2013)
Devonian	413 (292–554)	Beimforde et al. (2014)
Devonian	368 (275–456)	Ekanayaka et al. (2017)

Materials & Methods

Sample collection, morphological study and deposition

Fresh samples were collected from dead wood or soil from southwestern China and Thailand and dried using a dehydrator or allochroic silica gel for moisture absorption. The fruiting bodies placed in silica gel were then used for DNA extraction. Information for all samples and materials was recorded. Subsequently, morphological and molecular information was obtained. The herbarium specimen labeled "*Peziza*" (HKAS90031) was also acquired from the Herbarium of Cryptogams Kunming Institute of Botany Academia Sinica (KUN-HKAS) for morphological and phylogenetic studies.

Morphological examinations were performed using a Motic SMZ-168 stereoscope and digital images were recorded with a Nikon Eclipse Ni compound microscope equipped with a Nikon DS-Ri2 camera. Dried samples were rehydrated in pure water or 5% KOH solution and stained with Cotton Blue, Congo Red, and Melzer's reagent solutions. Measurements of microscopic characteristics were performed using the Tarosoft® Image Frame Work program v.0.9.7. Q is the ratio of ascospore length/width, while **Q** is the average of at least 20 Q ± standard deviation, and indicates the ascospore shape. Adobe Photoshop CS6 (Adobe Systems, USA) was used to make photoplates.

The specimens were deposited at the Herbarium of Mae Fah Luang University (MFLU) and the Herbarium of Cryptogams, Kunming Institute of Botany Academia Sinica (KUN-HKAS). Facesoffungi and Index Fungorum numbers were obtained as in Jayasiri et al. (2015) and Index Fungorum (2022) respectively for new taxa. The newly generated data were added to the Greater Mekong Subregion webpage (Chaiwan et al. 2021).

DNA extraction, PCR amplification and sequencing

Genomic DNA extraction was carried out directly from the fruiting bodies using *Trelief*™ Plant Genomic DNA extraction kit. Polymerase chain reaction (PCR) was used to amplify partial fragments of the large subunit ribosomal RNA (LSU), translation elongation factor 1-alpha (*tef-1α*), second largest subunit of RNA polymerase II (*rpb2*), and small subunit ribosomal RNA (SSU), using the corresponding primer pairs LR0R/LR5, 983F/2218R, fRPB2-5f/fRPB2-7cR, and NS1/NS4 (Vilgalys & Hester 1990, White et al. 1990, Liu et al. 1999, Rehner & Buckley 2005). Amplifications were performed in a 25 µL reaction volume containing 9.5 µL of sterile deionized water, 12.5 µL of 2×Power Taq PCR MasterMix (ABM Inc. Canada), 1 µL of each primer (10 µM stock) and 1 µL DNA template. An applied Biosystems 2720 thermocycler (Foster City, CA, USA) was used for amplification under the following conditions: initial denaturation at 94 °C for 5 min, followed by 35 cycles (LSU, *tef-1α* & SSU) or 40 cycles (*rpb2*) of denaturation at 94 °C for 50 s, annealing at 56 °C for 50 s (LSU, *tef-1α* & SSU) or 55 °C for 2 min (*rpb2*), extension at 72 °C for 1 min, and a final extension at 72 °C for 10 min. PCR products were verified on 1 % agarose electrophoresis gels stained with ethidium bromide, further purified and sequenced by Beijing Tsingke Biological Engineering Technology and Services Co., Ltd (Beijing, P.R. China). Newly-generated sequences were deposited in GenBank.

Phylogenetic analysis

DNASTAR Lasergene SeqMan Pro v.7.1.0 (44.1) was used for sequence assembly. The dataset spanned the diversity of *Pezizomycetes* and included 272 taxa from nine families and 77 genera. An effort was made to include as many pyronemataceous representatives as possible and to use sequences from the type (if available). Taxa from eight additional families were added to also assess the monophyly of *Pyronemataceae*. Two *Orbilia* strains were used as outgroup. Strains for which a single genetic marker was available were omitted from our analyses as they affected phylogenetic reconstruction and divergence time estimates. Assembled sequences were used as queries against GenBank to check for contamination and assemble the datasets for each genetic marker (Table 2). The datasets were aligned using MAFFT v.7.110 available online (Katoh & Standley 2013), followed by trimming using TrimAl v.1.2. (Capella-Gutiérrez et al. 2009) with a gap threshold of 0.4 for LSU and 0.5 for *tef-1α*, *rpb2* and SSU. Individual trimmed datasets were used to infer phylogenies for each genetic marker to assess the topological congruence of the four datasets (data not shown). The four datasets were combined and assembled into a supermatrix using Sequence Matrix v.1.8 (Vaidya et al. 2011). AliView v.1.19-betalk was used to convert the ".fasta" format to ".phylip" and ".nexus" (Larsson 2014).

Maximum likelihood (ML) phylogenies were inferred using IQ-Tree on the web server (http://iqtree.cibiv.univie.ac.at/; Trifinopoulos et al. 2016), while Bayesian inference (BI) analysis was executed on the CIPRES Science Gateway v.3.3 platform (https://www.phylo.org/portal2/login!input.action; Miller et al. 2010) using MrBayes v.3.2.7a on XSEDE (Huelsenbeck & Ronquist 2001, Ronquist et al. 2012). For the IQ tree, analysis was carried out using default options and statistical support was derived from 1000 ultrafast bootstrap replicates. The jModelTest v.2.1.10 (Darriba et al. 2012) was used to select the best-fit model (see phylogenetic analyses in the results section) for the BI analysis for each gene based on the Akaike information criterion (Posada & Buckley 2004). Markov Chain Monte Carlo Sampling (MCMC) was conducted to calculate posterior probabilities (PP) (Rannala & Yang 1996, Huelsenbeck & Ronquist 2001). Two runs comprising six simultaneous Markov Chains each were run for 10,000,000 generations and trees were sampled every 100th generation (Cai et al. 2005). The first 25% of the trees were discarded as burn-in and analysis was stopped when the standard deviation of split frequencies reached 0.01.

Phylogenetic trees were viewed and edited using FigTree v.1.4.2 (http://tree.bio.ed.ac.uk/software/figtree/) and Adobe Illustrator CS5 (Adobe Systems, USA).

Table 2 GenBank accession numbers used in this study.

Species name	Location	Voucher/Strain number	LSU	*tef-1α*	*rpb2*	SSU	References
Acervus beijingensis	**China: Beijing**	**HMAS 78150**	**HM197754**	**KP993492**	**KP993484**	**DQ787815**	**Zhuang et al. (2011)**
Acervus epispartius	USA: New York	s.n. (FH)	DQ220305	–	–	–	Perry et al. (2007)
Acervus globulosus	**China: Yunnan**	**HKAS 88987**	**KX765253**	**KX765255**	**KX765254**	**–**	**Ekanayaka et al. (2016)**
Acervus globulosus	China: Yunnan	HKAS 124374	OP291059	OP352492	OP352522	OP291009	This study
Acervus stipitatus	**China: Yunnan**	**MFLU 16-0607**	**KX765256**	**KX765258**	**KX765257**	**MG859244**	**Ekanayaka et al. (2016)**
Aleuria aurantia	Sweden	KH.04.81 (FH)	KC012661	KC109217	JX943815	–	Hansen et al. (2013)
Aleuria bicucullata	USA: MA	BAP 526 (FH)	KC012662	KC109218	JX943816	–	Hansen et al. (2013)
Aleurina imaii	–	HMAS 57707	KP993478	KP993494	KP993486	–	https://www.ncbi.nlm.nih.gov/nuccore/KP993478
Aleurina imaii	China: Sichuan	HKAS 124375	OP291076	OP352503	OP352530	OP291026	This study
Aleurina imaii	China: Sichuan	HKAS 124377	OP291077	OP352504	OP352531	OP291027	This study
Aleurina tenuiverrucosa	Austria	GF201802030	MW553849	–	–	–	https://www.ncbi.nlm.nih.gov/nuccore/MW553849
Anthracobia macrocystis	Denmark	KH.01.35 (C)	KC012663	–	JX943777	–	Hansen et al. (2013)
Anthracobia rehmii	France: Charente-maritime	FV2017090601	MW476531	–	–	–	Van Vooren et al. (2021)
Anthracobia sp.	Ecuador	TL-11709	KC012664	KC109219	JX943778	–	Hansen et al. (2013)
Arpinia inops	Norway	C F-54586	DQ220315	–	–	–	Perry et al. (2007)
Arpinia luteola var. *pallidorosea*	Italy: Liguria	GDOR:2950	MW884557	MW892386	MW892391	–	Carbone et al. (2021)
Ascodesmis nigricans	Netherlands	CBS 389.68	DQ168335	KC109221	JX943761	–	Hansen et al. (2013)
Ascodesmis sphaerospora	–	AFTOL-ID 920	FJ176858	FJ238391	FJ238346	FJ176804	Schoch et al. (2009a)
Aurantiolachnea solsequia	**France**	**LY NV 2016.10.11**	**MW546544**	**MW544629**	**MW544614**	**–**	**Van Vooren et al. (2021)**
Aurantiolachnea solsequia	Italy	TUR-A 208919	MW546543	MW544628	MW544613	–	Van Vooren et al. (2021)
Balsamia aestivalis	Sweden	KH.10.133 (S)	MK100250	MK113869	MK113840	–	Hansen et al. (2019)
Balsamia platyspora	Finland: Varsinais-suomi	TUR206101(TUR)	MK100252	MK113871	MK113841	–	Hansen et al. (2019)

Table 2 Continued.

Species name	Location	Voucher/Strain number	LSU	*tef-1α*	*rpb2*	SSU	References
Byssonectria deformis	France	N.V. 2009.04.09	KP309866	–	–	–	Lindemann et al. (2015)
Byssonectria deformis	Norway	HD Alta 00.014 (C)	DQ220356	KC109245	JX943795	–	Perry et al. (2007)
Byssonectria fusispora	Germany	U.L. 174-13	KP309864	–	–	–	Lindemann et al. (2015)
Byssonectria terrestris	Denmark	KS-94-4 (C)	AY500531	–	AY500504	–	Hansen et al. (2005)
Chaetothiersia cupressicola	Spain	LY NV 2020.01.04	MW546546	–	MW544616	–	Van Vooren et al. (2021)
Chaetothiersia laricina	**Italy**	**TUR-A 208918**	**MW546545**	**–**	**MW544615**	**–**	**Van Vooren et al. (2021)**
Cheilymenia crucipila	Norway	KH.03.63 (FH)	DQ220320	KC109283	JX943803	–	Perry et al. (2007)
Cheilymenia fimicola	USA: California	BAP 432 (FH)	DQ220322	–	–	–	Perry et al. (2007)
Cheilymenia granulata	Sweden	KH.08.66 (S)	KC012670	KC109225	JX943809	–	Hansen et al. (2013)
Cheilymenia sclerotiorum	Sweden	KH.08.32 (S)	KC012671	KC109227	JX943807	–	Hansen et al. (2013)
Cheilymenia sclerotiorum	Norway	KH.03.115 (FH)	DQ220324	KC109226	–	–	Perry et al. (2007)
Cheilymenia stercoraria	Belgien	U.L. 240	KX592807	–	–	–	Lindemann & Alvarado (2017)
Cheilymenia theleboloides	China: Sichuan	HKAS 82899	MG871314	MG980685	MG980704	–	Ekanayaka et al. (2018)
Cheilymenia vitellina	Denmark	KH.01.32 (C)	DQ220325	KC109228	JX943808	–	Hansen et al. (2013)
Cheilymenia vitellina	China: Yunnan	HKAS 104645	OP291078	OP352505	OP394213	OP291028	This study
Cheilymenia vitellina	China: Yunnan	HKAS 104646	OP291079	OP352506	OP394214	OP291029	This study
Choiromyces meandriformis	USA: Iowa	RH691	FJ809794	JX022550	JQ954471	–	Bonito et al. (2010)
Cupulina montana	**Switzerland**	**G 00262366**	**KY364073**	**–**	**–**	**–**	**Van Vooren et al. (2017)**
Cupulina ascophanoides	Slovakia	U.L. 131	KY928060	–	–	–	Perry et al. (2007)

Table 2 Continued.

Species name	Location	Voucher/Strain number	LSU	*tef-1α*	*rpb2*	SSU	References
***Desertella* sp.**	**USA**	**CBS 140199**	**MH878153**	**–**	**–**	**–**	**Vu et al. (2019)**
Donadinia echinacea	**China: Yunnan**	**HKAS 107659**	**MW079923**	**MW094269**	**–**	**MW080008**	**Zeng et al. (2021)**
Fallacidiscus helveticus	**Switzerland**	**ETH: ZT Myc 61122**	**MW546576**	**MW544643**	**MW544627**	**–**	**Lindemann et al. (2022)**
Fallacidiscus helveticus	Switzerland	ETH: ZT Myc 61123	MW546577	–	–	–	Lindemann et al. (2022)
Genabea fragilis	Spain: Asturias	MA56986	KJ938720	–	–	–	Alvarado et al. (2016)
Genabea hyalospora	Spain: León	AH:46360	MG019781	–	MG004577	–	Alvarado et al. (2018)
Genea brunneocarpa	**Spain: Valladolid**	**AH 44112**	**KJ938725**	**KJ938948**	**–**	**–**	**Alvarado et al. (2016)**
Genea dentata	**France: Loire-Atlantique**	**AH 44121**	**KJ938730**	**KJ938946**	**–**	**–**	**Alvarado et al. (2016)**
Genea hispidula	**USA: Minnesota**	**FLAS: F-61550**	**MG019784**	**MG004550**	**–**	**–**	**Alvarado et al. (2018)**
Genea sphaerica	Germany: Grockstädt	AH44161	KJ938753	KJ938940	–	–	Alvarado et al. (2016)
Genea lespiaultii	France: Charente-Maritime	AH44137	KJ938739	KJ938938			Alvarado et al. (2016)
Genea verrucosa	Greece: Katsimidi Attica	AH44208	KJ938766	KJ938955			Alvarado et al. (2016)
Geopora arenicola	Denmark	KS-94-173 (C)	DQ220336	–	–	–	Perry et al. (2007)
Geopora cercocarpi	**USA**	**SOC1590**	**HQ283091**	**–**	**–**	**–**	**Southworth & Frank (2011)**
Geopora cervina	Norway	KH.03.61 (FH)	DQ220344	KC109235	JX943785	DQ646527	Perry et al. (2007)
Geopora clausa	Spain: Canary Islands	OSC 58245	MK446230	–	–	–	Grupe et al. (2019)
Geopora clausa	Portugal	MA46927	JX424576	–	–	–	Healy et al. (2013)
Geopora cooperi	USA	BAP 517 (FH)	KC012678	KC109236	JX943787	–	Hansen et al. (2013)
Geopora sp.	Norway	KH.03.109 (FH)	DQ220345	KC109238	JX943786	–	Hansen et al. (2013)
Geopyxis aleurioides	**Canada**	**TUR 078772**	**NG_060674**	**KU932434**	**KU932570**	–	**Wang et al. (2016)**
Gilkeya compacta	USA: California	OSC:148044	MG019790	MG004555	MG004581	–	Alvarado et al. (2018)

Table 2 Continued.

Species name	**Location**	**Voucher/Strain number**	**LSU**	***tef-1α***	***rpb2***	**SSU**	**References**
Gilkeya compacta	Mexico: Tlaxcala	FLAS: F-58964	MG019788	MG004553	MG004579	–	Alvarado et al. (2018)
Helvella pezizoides	**Sweden**	**O-253366 (H061)**	**KY772945**	**KY772854**	**–**	**–**	**Skrede et al. (2017)**
Heydenia arietina	Switzerland	AL-0701	HQ596525	–	–	–	Leuchtmann & Clémençon (2012)
Hoffmannoscypha pellita	USA: Michigan	DHP 297 (FH)	DQ220343	–	–	–	Perry et al. (2007)
Hoffmannoscypha pellita	Germany	GH20100409	HQ993571	–	–	–	Stielow et al. (2013)
Humaria hemisphaerica	Norway	KH.03.100 (FH)	DQ220353	KC109244	JX943824	DQ646529	Perry et al. (2007)
Humaria hemisphaerica	Norway	KH.03.10 (FH)	KC012683	–	JX943825	–	Hansen et al. (2013)
Humaria hemisphaerica	China: Yunnan	HKAS 104654	OP291080	OP352507	OP394215	OP291030	This study
Humaria hemisphaerica	China: Sichuan	HKAS 104695	OP291081	OP352508	OP394216	OP291031	This study
Humaria hemisphaerica	China: Yunnan	HKAS 124378	OP291082	OP352509	OP394217	OP291032	This study
Humaria sp.	France: Savoie	LY 2013.08.52	MG019801	MG004566		–	Alvarado et al. (2018)
Humaria sp.	USA: Florida	FLAS: F-61552	MG019795	MG004560	MG004583	–	Alvarado et al. (2018)
Humaria sp.	USA: Iowa	FH 823752	MG019791	MG004556	MG004582	–	Alvarado et al. (2018)
Jafnea semitosta	USA: IA	ISC-443551	MT350430	–	–	–	https://www.ncbi.nlm.nih.gov/nuccore/MT350430
Jafnea fusicarpa	China: Hubei	420526MF0730	MH668008	–	–	–	Wang et al. (2020)
Jafnea fusicarpa	China: Hebei	HKAS 90031	OP291096	–	–	OP291046	This study
Lamprospora aneurae	**Germany: Postdam**	**B 70 0005997**	**MZ343191**	**–**	**–**	**MZ343180**	**Eckstein et al. (2021a)**
Lamprospora ascoboloides	Norway	KH.03.54 (FH)	DQ220358	KC109246	JX943840	DQ646531	Hansen et al. (2013)
Lamprospora campylopodis	Germany: Niedersachsen	48633	MF066054	MK569289	–	MK569364	Egertová et al. (2018a)
Lamprospora dictydiola	Czech Republic	PRM 945794 (Ldic)	MF754056	MF754054	–	MK569365	Egertová et al. (2018b)

Table 2 Continued.

Species name	**Location**	**Voucher/Strain number**	**LSU**	***tef-1α***	***rpb2***	**SSU**	**References**
Lamprospora hispanica	Spain: Mallorca	B 70 0100986	MN394599	MN366468	–	MW242827	Eckstein et al. (2021b)
Lamprospora sylvatica	**Ukraine: Zakarpattia Oblast**	**PRM 946415 (UA1)**	**MG947604**	**MK569290**	**–**	**MK569367**	**Egertová et al. (2018a)**
Lasiobolidium boudieri	France	L.D. 31.08.04	MW546548	MW544631	MW544617	–	Van Vooren et al. (2021)
Lasiobolidium coprophilum	**Netherlands**	**MAAS RB 01127**	**MW546549**	–	–	–	Van Vooren et al. (2021)
Lasiobolidium orbiculoides	**USA: California**	**CBS 344.73**	**NG_057745**	**KC109313**	**JX943757**	**NG_062375**	Hansen et al. (2013)
Lasiobolidium parvisporum	Spain	E.R.D. 7668	MW546552	MW544632	MW544618	–	Van Vooren et al. (2021)
Lasiobolidium spirale	**USA**	**TRTC 41942**	**MW546555**	–	–	–	Van Vooren et al. (2021)
Lasiobolidium spirale	**USA**	**TRTC 41596**	**MW546554**	–	–	–	Van Vooren et al. (2021)
Lasiobolidium spirale	**USA**	**CBS 782.70**	**NG_057747**	**KC109249**	**JX943804**	**NG_061054**	Hansen et al. (2013)
Lasiobolidium trachysporum	**Spain**	**LY NV 2019.04.14**	**MW546553**	**–**	**–**	**–**	Van Vooren et al. (2021)
Lasiocupulina mediterranea	Albania	LY:N.V. 2018.07.01	MK238282	–	–	–	Van Vooren & Vega (2018a)
Lasiocupulina mediterranea	**Albania**	**HBG:M.V. 180702-01**	**MK238281**	**–**	**–**	**–**	**Van Vooren & Vega (2018a)**
Leucoscypha leucotricha	Denmark	KS-94-174 (C)	DQ220365	–	–	–	Perry et al. (2007)
Lotinia verna	**–**	**SESTAO 2003040401**	**KP195729**	**KP195727**	**–**	**–**	**https://www.ncbi.nlm.nih.gov/nuccore/KP195729**
Lotinia verna	–	SESTAO 2002061101	KP195728	KP195726	–	–	https://www.ncbi.nlm.nih.gov/nuccore/KP195728
Melastiza contorta	Sweden	KH 01.06 (C)	AY500539	KC109250	AY500505	DQ646536	Hansen et al. (2005)
Melastiza cornubiensis	Norway	KH.03.43 (FH)	DQ646524	KC109252	JX943811	DQ646537	Hansen & Pfister (2006)

Table 2 Continued.

Species name	Location	Voucher/Strain number	LSU	*tef-1α*	*rpb2*	SSU	References
Melastiza cornubiensis	Denmark	KH.01.017 (C)	DQ220367	KC109251	JX943810	–	Hansen et al. (2013)
Melastiza cornubiensis	China: Sichuan	HKAS 104702	OP291083	OP352510	OP394218	OP291033	This study
Melastiza cornubiensis	China: Sichuan	HKAS 104703	OP291084	OP352511	OP394219	OP291034	This study
Melastiza cornubiensis	China: Yunnan	HKAS 124379	OP291085	OP352512	OP394220	OP291035	This study
Melastiza flavorubens	Iceland	DHP 04.570 (FH)	DQ220369	KC109253	JX943812	–	Hansen et al. (2013)
Melastiza verruculosa	**China: Yunnan**	**HKAS 124366**	**OP291086**	**OP352513**	**OP394221**	**OP291036**	**This study**
Melastiza verruculosa	China: Yunnan	HKAS 124367	OP291087	–	OP394222	OP291037	This study
Micronematobotrys verrucosus	China: Beijing	E3-2181	FJ025222	–	–	FJ025225	Sun & Guo (2010)
Micronematobotrys verrucosus	China: Beijing	O15-2161	FJ025221	–	–	FJ025224	Sun & Guo (2010)
Miladina lecithina	USA	KH.04.22 (FH)	DQ220372	KC109255	JX943793	–	Hansen et al. (2013)
Miladina lecithina	Sweden	KH.03.156 (FH)	DQ220371	KC109254	JX943792	DQ646538	Hansen et al. (2013)
Monascella botryosa	**Spain**	**CBS 233.85**	**MH873558**	**KC109256**	**JX943831**	**–**	**Vu et al. (2019)**
Moravecia hvaleri	Norway	RK 97.44	DQ220373	–	–	–	Perry et al. (2007)
Myrmecocystis cerebriformis	USA: California	FLAS: F-58962	MG019802	MG004567	MG004588	–	Alvarado et al. (2018)
Myrmecocystis mediterranea	**Spain: Girona**	**BCN: JMV910209-2**	**MG019811**	**MG004574**	**–**	**–**	**Alvarado et al. (2018)**
Myrmecocystis microspora	**Spain: Segovia**	**AH:46367**	**MG019812**	**MG004575**	**–**	**–**	**Alvarado et al. (2018)**
Neottiella aphanodictyon	Norway	HD Finn.86.35 (C)	DQ220376	–	–	–	Perry et al. (2007)
Neottiella gigaspora	**China: Sichuan**	**HKAS 104669**	**MK589293**	**MK577716**	**–**	**–**	**Yuan et al. (2020)**
Neottiella rutilans	Poland: Karkonosze	46853	MK569313	MK569288	–	MK569336	Sochorová et al. (2019)
Neottiella vivida	Czech Republic	PRM 945797 (NVZla)	MF066068	MF754051	–	MK569337	Sochorová et al. (2019)

Table 2 Continued.

Species name	Location	Voucher/Strain number	LSU	*tef-1α*	*rpb2*	SSU	References
Octospora affinis	Czech Republic: Liska	PRM 945798 (OAfZla)	MF754075	MF754045	–	MK569347	Egertová et al. (2018b)
Octospora americana	**USA: Louisiana**	**S F43718 (2055)**	**MN967346**	**MT078729**	**–**	**MN994516**	**Sochorová et al. (2020)**
Octospora axillaris	Czech Republic: Olomouc	PRM 954016	MW242829	MW430761	–	MW242828	Sochorová et al. (2021)
Octospora conidiophora	South Africa	ZE71/18	MK569322	MK569293	–	MK569356	Sochorová et al. (2019)
Octospora humosa	Czech Republic	PRM 945802 (OHZla)	MF754074	MF754043	–	MK569343	Egertová et al. (2018b)
Octospora hygrohypnophila	Norway	KH.03.30 (FH)	DQ220379	KC109258	JX943836	DQ646539	Hansen et al. (2013)
Octospora kelabitiana	Malaysia: Sarawak	ZE61/16	MF754064	MF754049	–	MK569376	Egertová et al. (2018b)
Octospora melina	Iceland	DHP-04.552 (FH)	KC012689	KC109259	JX943837	–	Hansen et al. (2013)
Octospora neerlandica	Germany	PRC 4691	MZ343185	–	–	MZ343176	Eckstein et al. (2021a)
Octospora orthotrichi	Croatia: Vela Draga canyon	HR8	MK569314	MK569311	–	MK569342	Sochorová et al. (2019)
Octospora pseudoampezzana	Czech Republic: Stramberk	OP1	MF754069	MF754050	–	MK569339	Egertová et al. (2018b)
Octospora roxheimii	USA	KH.05.01 (FH)	KC012690	–	JX943838	–	Hansen et al. (2013)
Octospora rubens	Germany: Gross Pampau	MV20131018-05	MW221930	MW219145	–	MW206791	Sochorová et al. (2021)
Octospora oscarii	**Germany: Rote Warte**	**B 70 0100532**	**MZ343190**	**–**	**–**	**MZ343178**	**Eckstein et al. (2021a)**
Octospora doebbeleri	**Czech Republic**	**PRM 954007 (DEVh)**	**MW152148**	**MW159137**	**–**	**MW152156**	**Sochorová et al. (2021)**
Octospora sp.	Norway	KH.03.136 (FH)	DQ220384	KC109260	JX943839	–	Hansen et al. (2013)
Octosporopsis erinacea	Malaysia: Pa Lungan	DUM20/1	MF754057	MF754041	–	MK569338	Egertová et al. (2018b)
Octosporopsis nicolai	Portugal: Lisboa	MV20130205-1	KF771035	KF771043	–	–	Lindemann et al. (2014)

Table 2 Continued.

Species name	**Location**	**Voucher/Strain number**	**LSU**	***tef-1α***	***rpb2***	**SSU**	**References**
Orbicula parietina	Canada: Ontario	CBS 166.71	MH871829	–	–	–	Vu et al. (2019)
Orbilia auricolor	–	AFTOL-ID 906	DQ470953	DQ471072	DQ470903	DQ471001	Spatafora et al. (2006)
Orbilia vinosa	–	AFTOL-ID 905	DQ470952	DQ471071	–	DQ471000	Spatafora et al. (2006)
Otidea alutacea	Sweden	KH.09.178 (S)	KM823191	KM823259	KM823385	–	Hansen & Olariaga (2015)
Otidea alutacea	Norway	KH.09.133 (S)	KM823185	KM823253	KM823381	–	Hansen & Olariaga (2015)
Otidea alutacea	China: Sichuan	HKAS 104674	OP291060	OP352493	–	OP291010	This study
Otidea alutacea	China: Sichuan	HKAS 104699	OP291061	OP352494	–	OP291011	This study
Otidea borealis	**Finland**	**S F-242694**	**KM823197**	**KM823265**	**KM823390**	**–**	**Hansen & Olariaga (2015)**
Otidea bufonia	Sweden	KH.09.172 (S)	JN941097	KM823272	KM823397	JN941217	Hansen & Olariaga (2015)
Otidea bufonia	France	NV 2009.11.01 (S)	JN941085	KM823270	KM823395	JN941221	Hansen & Olariaga (2015)
Otidea bufonia	China: Sichuan	HKAS 124376	OP291062	OP352495	OP352523	OP291012	This study
Otidea formicarum	**Finland**	**H6003549**	**KM823211**	**KM823281**	**KM823409**	**–**	**Hansen & Olariaga (2015)**
Otidea guttulata	**China: Sichuan**	**HKAS 104692**	**OP291063**	**OP352496**	**–**	**OP291013**	**This study**
Otidea guttulata	China: Sichuan	HKAS 104693	OP291064	–	–	OP291014	This study
Otidea guttulata	China: Sichuan	HKAS 104711	OP291065	–	–	OP291015	This study
Otidea hanseniae	**China: Gansu**	**XF007**	**KU987028**	**KU987035**	**–**	**–**	**Xu et al. (2018)**
Otidea korfii	**China: Sichuan**	**Z.W. Ge 1913**	**KU987029**	**KU987036**	**–**	**–**	**Xu et al. (2018)**
Otidea korfii	China: Sichuan	HKAS 104682	OP291066	OP352497	–	OP291016	This study
Otidea korfii	China: Sichuan	HKAS 104685	OP291067	OP352498	OP352524	OP291017	This study
Otidea leporina	**Finland: Etelae-Karjala**	**H6003548**	**KM823222**	**KM823292**	**–**	**–**	**Hansen & Olariaga (2015)**
Otidea leporina	France	NV 2008.09.28 (S)	KM823214	KM823284	KM823411	–	Hansen & Olariaga (2015)
Otidea macrospora	**China: Sichuan**	**HKAS 104688**	**OP291068**	**–**	**OP352525**	**OP291018**	**This study**
Otidea macrospora	China: Sichuan	HKAS 124370	OP291069	OP352499	–	OP291019	This study
Otidea nannfeldtii	**Finland**	**H6002902**	**KM823228**	**KM823297**	**KM823426**	**–**	**Hansen & Olariaga (2015)**
Otidea olivaceobrunnea	China: Sichuan	HKAS 104680	OP291070	OP352500	OP352526	OP291020	This study

Table 2 Continued.

Species name	Location	Voucher/Strain number	LSU	*tef-1α*	*rpb2*	SSU	References
Otidea ovalispora	**China: Yunnan**	**HKAS 104658**	**OP291071**	**–**	**OP352527**	**OP291021**	**This study**
Otidea ovalispora	China: Yunnan	HKAS 124368	OP291072	OP352501	OP352528	OP291022	This study
Otidea platyspora	Sweden	KH.09.163 (S)	KM823238	KM823308	KM823438	–	Hansen & Olariaga (2015)
Otidea propinquata	France	NV 2008.09.15 (S)	KM823240	KM823310	KM823440	–	Hansen & Olariaga (2015)
Otidea propinquata	China: Sichuan	HKAS 104694	OP291073	–	–	OP291023	This study
Otidea pseudoformicarum	**China: Yunnan**	**HKAS 101386**	**KY498606**	**–**	**MG980709**	**–**	**Hyde et al. (2018)**
Otidea pseudoleporina	**USA**	**rh101910 (OSC)**	**KM823243**	**KM823313**	**KM823443**	**–**	**Hansen & Olariaga (2015)**
Otidea purpureogrisea	**China: Sichuan**	**Z.W. Ge 863**	**KU987023**	**KU987032**	**KU987037**	**–**	**Xu et al. (2018)**
Otidea subformicarum	**Spain**	**S F242696**	**KM823495**	**–**	**–**	**–**	**Olariaga et al. (2015)**
Otidea subleporina	**China: Yunnan**	**HKAS 104663**	**OP291074**	**OP352502**	**OP352529**	**OP291024**	**This study**
Otidea subleporina	Chian: Sichuan	HKAS 124369	OP291075	–	–	OP291025	This study
Parascutellinia carneosanguinea	Norway	KH.03.34 (FH)	DQ220388	KC109265	JX943823	DQ646541	Hansen et al. (2013)
Parascutellinia carneosanguinea	Iceland	DHP 04.530 (FH)	KC012694	KC109266	–	–	Hansen et al. (2013)
Paratricharina poiraultii	Portugal	U.L. 178-14	KP052789	KP052790	KP052791	–	Van Vooren et al. (2015a)
Paratricharina poiraultii	Spain	U.L. 179-14	KP052785	KP052786	KP052787	–	Van Vooren et al. (2015a)
Paratricharina multiguttulata	Hungary: Sopron	MSTR P 04356	MW158783	MW161231	MW161233	–	Lindemann et al. (2021)
Paratricharina multiguttulata	**Germany: Thuringia**	**MSTR P 19992**	**MW158782**	**MW161230**	**MW161232**	**–**	**Lindemann et al. (2021)**
Parawilcoxina inexpectata	**Spain**	**LY NV 2019.09.17**	**MW546564**	**MW544639**	**MW544624**	**–**	**Van Vooren et al. (2021)**
Perilachnea flavobrunnea	Hungary	TUR-A 208916	MW546560	MW544636	MW544621	–	Van Vooren et al. (2021)
Perilachnea hemisphaerioides	Switzerland	LY NV 2014.06.12	MW546557	MW544634	MW544619	–	Van Vooren et al. (2021)

Table 2 Continued.

Species name	Location	Voucher/Strain number	LSU	*tef-1α*	*rpb2*	SSU	References
Perilachnea ochraceoflava	**Italy**	**TUR-A 208917**	**MW546561**	**MW544637**	**MW544622**	**–**	**Van Vooren et al. (2021)**
Picoa lefebvrei	Israel	AH19584	JN392188	–	–	–	Zitouni-Haouar et al. (2015)
Picoa juniperi	Iran	AH39287	JN392181	–	–	–	Zitouni-Haouar et al. (2015)
Planamyces parisiensis	France	CBS:143165	MG386093	–	MG386141	–	Crous et al. 2017
Plectania sichuanensis	**China: Sichuan**	**HKAS 107664**	**MW079927**	**MW094271**	**MW085093**	**MW080012**	**Zeng et al. (2021)**
Pseudaleuria fibrillosa	Italy: Sicily	MCVE:30135	MK720106	MK722152	MK722153	–	Saitta (2019)
Pseudaleuria quinaultiana	USA: Oregon	NSW 7107 (OSC)	DQ220389	–	–	–	Perry et al. (2007)
Pseudombrophila bulbifera	Germany	U.L. 155	KX592810	KX592792	–	–	Lindemann & Alvarado (2017)
Pseudombrophila theioleuca	USA	DHP 3498 (FH)	KC012696	KC109269	JX943756		Hansen et al. (2013)
Pseudopithyella minuscula	USA: CA	mh 675 (FH)	AY945849	FJ238387	DQ017600	AF006317	Hansen et al. (2013)
Pseudosarcosoma latahense	–	AFTOL-ID 954	FJ176860	FJ238392	–	FJ176806	Schoch et al. (2009a)
Pseudotricharina intermedia	Greece	GK 6904	KT861361	KT861363	KT861365	–	Van Vooren et al. (2015b)
Pseudotricharina intermedia	**Spain**	**ST 25011493**	**KT861360**	**KT861362**	**KT861364**	**–**	Van Vooren et al. (2015b)
Pyronema domesticum	USA	AFTOL-ID 949	DQ247805	DQ471093	DQ247795	DQ247813	Schoch et al. (2006)
Pyronema omphalodes	United Kingdom	CBS 283.31	MH866665	–	–	–	Vu et al. (2019)
Pyropyxis rubra	Canada: Ontario	K. Egger 323 (DAOM)	DQ220405	KC109310	JX943775	–	Hansen et al. (2013)
Pyropyxis rubra	Canada: Ontario	K. Egger 289 (DAOM)	DQ220404	KC109311	JX943776	–	Hansen et al. (2013)
Ramsbottomia asperior	Norway	HD Finn.00.07 (C)	DQ220406	KC109278	JX943796	–	Perry et al. (2007)
Ramsbottomia crechqueraultii	USA	DHP 06.608 (FH)	KC012698	KC109279	–	–	Hansen et al. (2013)

Table 2 Continued.

Species name	**Location**	**Voucher/Strain number**	**LSU**	***tef-1α***	***rpb2***	**SSU**	**References**
Rhodotarzetta rosea	Norway: Nordland	HD Rana 75.081	DQ220414	–	–	–	Perry et al. (2007)
Rhodotarzetta rosea	Norway	KH.03.107 (FH)	DQ220413	KC109281	JX943833	DQ646550	Hansen et al. (2013)
Rhodoscypha ovilla	Norway: Nordland	HD Rana 79.060 (C)	DQ220411	–	–	–	Perry et al. (2007)
Rhodoscypha ovilla	Sweden	KH.08.007	KC012699	KC109280	JX943834	–	Hansen et al. (2013)
Rhodoscypha ovilla	China: Sichuan	HKAS 104677	OP291088	OP352514	–	OP291038	This study
Sarcoscypha coccinea	–	AFTOL-ID 930	FJ176859	–	FJ713615	FJ176805	Schoch et al. (2009a)
Scutellinia barlae	Denmark	KH.01.023 (C)	DQ220415	–	–	–	Perry et al. (2007)
Scutellinia blumenaviensis	Costa Rica	KH.02.55 (FH)	DQ220416	–	–	–	Perry et al. (2007)
Scutellinia colensoi	China: Hubei	420526MF0304	MH668015	–	–	–	Wang et al. (2020)
Scutellinia colensoi	China: Yunnan	HKAS 104661	OP291089	OP352515	OP394223	OP291039	This study
Scutellinia colensoi	China: Yunnan	HKAS 124372	OP291090	OP352516	OP394224	OP291040	This study
Scutellinia colensoi	China: Yunnan	HKAS 124583	OP291091	OP352517	OP394225	OP291041	This study
Scutellinia geneospora	Japan: Yaku Island	R.P. Korf and S.C. Gruff. Discomycetes exsiccati #70 (FH)	DQ220418	–	–	–	Perry et al. (2007)
Scutellinia hyperborea	Denmark	ALL-94-14 (C)	DQ220419	–	–	–	Perry et al. (2007)
Scutellinia hyperborea	Norway	KH.03.116 (FH)	KC012702	–	JX943801	–	Hansen et al. (2013)
Scutellinia jejuensis	**Korea: Jeju**	**KUS-F52411**	**GU361609**	**–**	**–**	**–**	**Han et al. (2010)**
Scutellinia jungneri	Thailand: Payao	MFLU 22-0113	OP291092	OP352518	OP394226	OP291042	This study
Scutellinia nigrohirtula	China: Hubei	420526MF0257	MH668011	–	–	–	Wang et al. (2020)
Scutellinia pennsylvanica	USA: New York	DHP 105 (FH)	DQ220420	–	–	–	Perry et al. (2007)
Scutellinia scutellata	USA	AFTOL-ID 62	DQ247806	–	DQ247796	DQ247814	Schoch et al. (2006)

Table 2 Continued.

Species name	Location	Voucher/Strain number	LSU	*tef-1α*	*rpb2*	SSU	References
Scutellinia sinosetosa	China: Yunnan	HKAS 124373	OP291093	OP352519	–	OP291043	This Study
Scutellinia sp.	USA: Massachusetts	BAP 427 (FH)	DQ220422	–	–	–	Perry et al. (2007)
Scutellinia sp.	Ecuador: Carchi	TL-11648	KC012705	–	JX943797	–	Perry et al. (2007)
Scutellinia subhirtella	Denmark	C F-55440	DQ220423	–	–	–	Perry et al. (2007)
Scutellinia cf. *subhirtella*	Norway	KH.03.117 (FH)	KC012704	KC109286	–	–	Hansen et al. (2013)
Scutellinia trechispora	Denmark	KH.01.37 (C)	DQ220425	–	JX943798	–	Perry et al. (2007)
Scutellinia trechispora	China: Hubei	420526MF0468	MH668012	–	–	–	Wang et al. (2020)
Scutellinia verruculosa	**China: Sichuan**	**HKAS 104667**	**OP291094**	**OP352520**	**OP394227**	**OP291044**	**This study**
Scutellinia verruculosa	China: Sichuan	HKAS 124371	OP291095	OP352521	OP394228	OP291045	This study
Sepultariella semi-immersa	France	N.V. 2006.09.27	KY364074	–	–	–	Van Vooren et al. (2017)
Sepultariella patavina	Georgia	N.V. 2013.08.71	KY364076	–	–	–	Van Vooren et al. (2017)
Smardaea amethystina	Denmark	KH-97-132 (C)	AF335176	–	–	–	Hansen et al. (2013)
Smardaea reticulosperma	France	MPU: JCD 265-84	MT273649	–	MT274694	–	https://www.ncbi.nlm.nih.gov/nuccore/MT273649
Smardaea verrucispora	Italy: Roma	AMB 17161	MK025554	–	–	–	Agnello et al. (2019)
Sowerbyella angustispora	China: Beijing	HKAS 89982	MG871334	–	MG980722	–	Ekanayaka et al. (2018)
Sowerbyella imperialis	–	CL2004.105 (C)	DQ220427	KC109290	JX943817	DQ646551	Perry et al. (2007)
Sowerbyella radiculata	USA: New Mexico	KH.04.30 (FH)	DQ220428	KC109291	JX943818	–	Hansen et al. (2013)
Sowerbyella meridionalis	**Spain: Catalunya**	**LSS20190103**	**MT741965**	**MT741957**	**MT741958**	**–**	**Rubio et al. (2021)**

Table 2 Continued.

Species name	Location	Voucher/Strain number	LSU	*tef-1α*	*rpb2*	SSU	References
Spaniodiscus fuckelii	Switzerland	U.R. 1000-1016	MW546563	MW544638	MW544623	–	Lindemann et al. (2022)
Spaniodiscus fuckelii	**France**	**MPU: JCD 135-84**	**MT273654**	**MT274710**	**–**	**–**	**Lindemann et al. (2022)**
Sphaerosporella brunnea	USA: Massachussetts	KH.03.04 (FH)	DQ220433	KC109302	JX943779	–	Perry et al. (2007)
Sphaerosporella hinnulea	Norway	HD Rana 81.104 (C)	DQ220431	–	–	–	Perry et al. (2007)
Sphaerosporium lignatile	USA: Wisconsin	MICH:254984	MN749494	–	–	MN756649	Song et al. (2019)
Spooneromyces helveticus	Sweden	JS08.030 (S)	KC012707	KC109292	JX943813	–	Hansen et al. (2013)
Spooneromyces laeticolor	Denmark	HFG 88.013 (C)	DQ220434	KC109293	JX943814	–	Hansen et al. (2013)
Tarzetta alnicola	**France**	**LY:NV 2017.08.36**	**MN712256**	–	–	–	Van Vooren et al. (2019)
Terracavicola echinospora	**Mexico**	**FLAS JT 19275**	**MK278727**				**Grupe et al. (2019)**
Tricharina praecox	Norway	KH.03.101 (FH)	DQ646525	KC109298	JX943788	DQ646552	Hansen et al. (2013)
Tricharina striispora	–	MUCL:41297	JQ836560	–	JQ836564	–	https://www.ncbi.nlm.nih.gov/nuccore/JQ836560
Tricharina sp.	Ecuador	TL-10051 (C, QCA)	DQ220447	KC109299	JX943789	–	Hansen et al. (2013)
Tricharinopsis herinkii	**Czech Republic**	**PRM 772405**	**MN386012**	**–**	**–**	**–**	**Lindemann et al. (2022)**
Trichophaea abundans	Denmark	KH.01.36 (C)	DQ220449	KC109300	JX943780	–	Van Vooren et al. (2021)
Trichophaea contradicta	Switzerland	G RD 27.03.246.02	MW546567	MW544640	MW544625	–	Van Vooren et al. (2021)
Trichophaea dougoudii	France	LY N.V. 2015.08.13	KX982242	–	–		Van Vooren (2016)
Trichophaea hybrida	Iceland	AMNH-49682	DQ220455	–	–	–	Perry et al. (2007)
Trichophaea hybrida	USA: Colorado	KH.04.39 (FH)	DQ220454	KC109304	–	–	Perry et al. (2007)

Table 2 Continued.

Species name	Location	Voucher/Strain number	LSU	*tef-1α*	*rpb2*	SSU	References
Trichophaea hybrida	USA: Vermont	DHP 30.8.2000 (FH)	DQ220453	–	–	–	Perry et al. (2007)
Trichophaea minuta	Canada: Ontario	CBS 236.57	MH869247	KC109305	JX943781	–	Vu et al. (2019)
Trichophaea pseudogregaria	France	LY NV 2013.08.71	MW546566	–	–	–	Van Vooren et al. (2021)
Trichophaea saccata	**England**	**CBS 804.70**	**DQ220451**	**KC109306**	**JX943782**	**–**	**Hansen et al. (2013)**
Trichophaea woolhopeia	Denmark	KH.01.033 (C)	DQ220460	KC109307	–	DQ646553	Perry et al. (2007)
Trichophaeopsis asturiensis	**Spain**	**LY NV 2013.06.19**	**MW546572**	**–**	**–**	**–**	**Van Vooren et al. (2021)**
Trichophaeopsis tetraspora	Denmark	C F-47525 (C)	DQ220463	–	–	–	Perry et al. (2007)
Tuber indicum	China	HKAS44333	MG871340	MG980702	MG980725	–	Ekanayaka et al. (2018)
Warcupia terrestris	Canada: British Columbia	CBS 891.69	DQ220467	KC109308	JX943832	–	Hansen et al. (2013)
Wilcoxina mikolae	USA: Wyoming	WS 36 (SFSU)	DQ220468	–	–	–	Hansen et al. (2013)
Wilcoxina rehmii	USA: California	sn	AF266706	–	–	–	Perry et al. (2007)
Wilcoxina verruculosa	**China: Sichuan**	**HKAS 104676**	**MN449993**	**MN447536**	**–**	**–**	**Hyde et al. (2020)**
Wilcoxina sp.	Belgium	LY NV 2016.09.01	MW546575	–	–	–	Van Vooren et al. (2021)
Wilcoxina sp.	France	G.M. 20160801	MW546574	–	–	–	Van Vooren et al. (2021)
Wolfina aurantiopsis	USA	DHP 04-599 (FH)	AY945859	KC109212	DQ017605	–	Hansen et al. (2013)

Note: Names in red indicate newly-described species in this study. Names in bold indicate type collections. Names in blue indicate newly sequenced collections

Molecular clock analysis

The dataset used for phylogenetic inferences was also used in the divergence time estimations. Two secondary calibrations were set according to divergence times estimates from previous studies as follows: the *Pezizomycetes* crown node was set in the normal distribution (mean = 317 Mya, SD = 37 Mya) (Prieto & Wedin 2013, Alvarado et al. 2016). The *Tuberaceae* crown node was also set in the normal distribution (mean = 156.9 Mya, SD = 9 Mya) (Bonito et al. 2013, Alvarado et al. 2016).

Divergence time analyses were carried out using BEAST v1.10.4 (Suchard et al. 2018). Aligned sequence data were partitioned separately for LSU, *tef-1α*, *rpb2*, and SSU. The XML file of each gene was constructed using BEAUTI v1.10.4. (BEAST package). Substitution models for all genes were the same as in the BI analysis (see phylogenetic analyses in the results section) (Darriba et al. 2012). An uncorrelated relaxed clock model was used with a lognormal distribution of rates for each gene estimated. The Yule speciation process was set as the tree prior. Default was used for all of the other priors. Four independent Monte Carlo Markov Chains were run for 350,000,000 generations with a sampling frequency every 10,000 generations. The log files were combined in LogCombiner v.1.10.4 (BEAST package) with the first 10% of trees discarded as burn-in. The combined log file was evaluated for convergence and stationarity in Tracer v1.6 (Rambaut et al. 2013), ensuring that the effective sample size (ESS) for all parameters was above 200. Trees were summarized as maximum clade credibility (MCC) trees in TreeAnnotator (BEAST package).

Ancestral character states analyses

Bayesian Binary MCMC (Markov chain Monte Carlo) (BBM) was used as implemented in RASP v.4.2. (Reconstruct Ancestral State in Phylogenies) (Yu et al. 2015, 2020). The morphological character of ascomata was mapped over the inferred phylogeny: a. apothecium; b. hypogeous; c. semi-hypogeous; d. gymnothecium; e. cleistothecium; f. unknown or asexual. Parameters were set as follows: number of cycles 1,000,000; number of chains 10; frequent of samples 100; discard samples 100; temperature: 0.1; state frequencies: estimated (F81); among-site rate variation Gamma+(G). Trees were viewed and edited in RASP v.4.2. and Adobe Illustrator CS5 (Adobe Systems, USA).

Results

Phylogenetic analysis

The phylogenetic tree of *Pyronemataceae*, *Otideaceae* and related taxa was inferred using 272 taxa and four genes, including *Orbilia auricolor* (AFTOL-ID 906) and *O. vinosa* (AFTOL-ID 905) as the outgroup taxa (Fig. 1). The alignment comprised 3638 characters (LSU: 1–876 bp; *tef-1α*: 877–1861 bp; *rpb2*: 1862–2584 bp; SSU: 2585–3638 bp). This likelihood of the best-scoring IQ tree was -81209.613. The best-fit models for each gene were GTR+I+G for LSU, TIM1+I+G for *tef-1α*, SYM+I+G for *rpb2*, and TIM2+I+G for SSU. The BI analysis converged at 5,740,000 generations. The topologies of IQ and BI trees were similar.

The backbone phylogeny of *Pyronemataceae* and *Otideaceae*

In the inferred phylogenetic tree, *Pyronemataceae* is divided into six lineages (L1–L6) comprising 198 pyronemataceous strains from 51 genera. These lineages were determined based on results obtained in this and other studies (Perry et al. 2007, Hansen et al. 2013). Based on the dataset we selected in this study, 40 genera are monophyletic, while several others are polyphyletic and dispersed across several clades, with *Trichophaea* and *Octospora* being the most representative. Statistical support for the lineages varied: Lineage 1 with 94BS; Lineage 2 with 81BS/100PP; Lineage 3 with 73BS; Lineage 4 with 90BS/0.98PP; Lineage 5 with 100BS/100PP; and Lineage 6 with 79BS/0.93PP.

The *Otideaceae* taxa formed a strongly supported clade (100BS/1.00PP) sister to *Pyronemataceae* and this relationship has nearly maximum support (98BS/1.00PP). *Otideaceae* was separated into six monophyletic clades, comprising 43 strains from six genera, *viz.*, *Acervus*, *Arpinia*, *Monascella*, *Otidea*, *Planamyces*, and *Warcupia*. *Monascella*, *Planamyces*, and *Warcupia* are represented by single strains. Five *Acervus* strains formed a clade of maximum support (100BS/1.00PP), which was sister to the clade formed by the previous three genera. Two *Arpinia* strains were sister to the genus *Otidea*, which is represented by 33 strains, with nearly maximum statistical support (99BS/1.00PP).

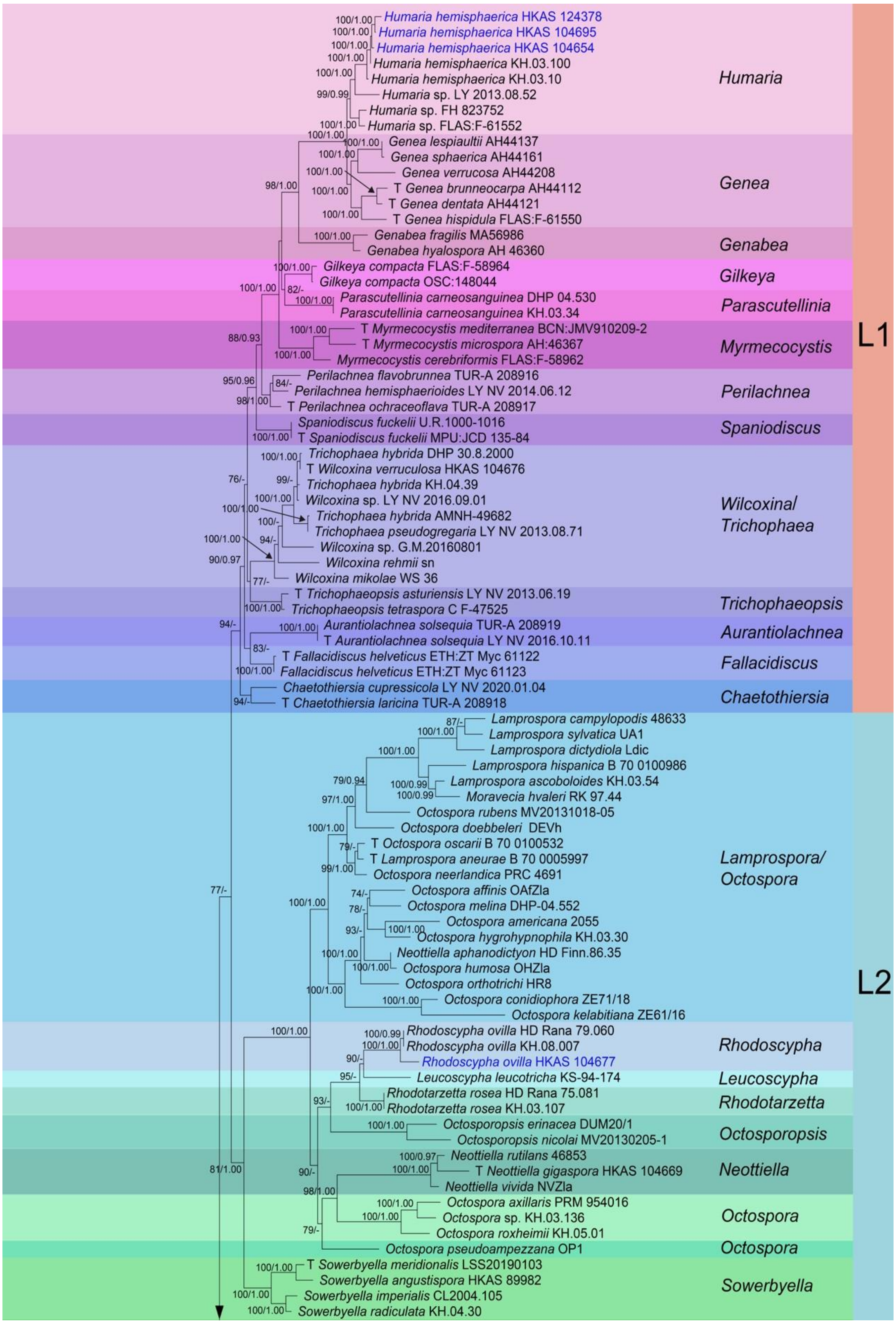

Figure 1 – Phylogenetic tree of combined sequence data (LSU, *tef-1α*, *rpb2* & SSU) inferred from 272 taxa and 3638 sites. Ultrafast bootstrap support values for IQ-tree (BS) and Bayesian posterior probabilities (PP) greater than 70% and 0.90, respectively are indicated at the nodes in this order. Names in red indicate newly described species and names in blue stand for newly sequenced collections. *Orbilia auricolor* (AFTOL-ID 906) and *Orbilia vinosa* (AFTOL-ID 905) represent the outgroup. The letter T preceding taxa names denotes the type.

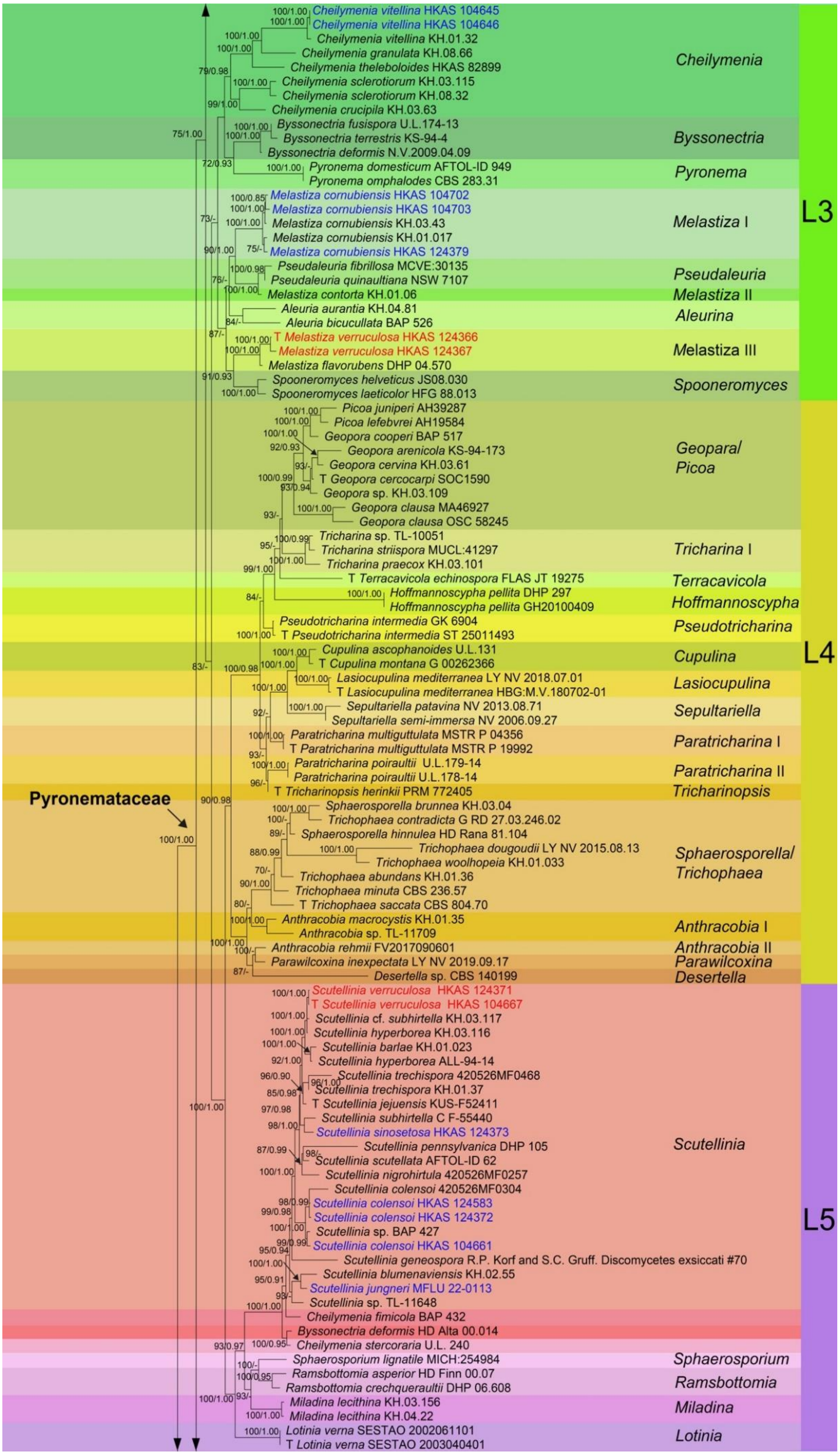

Figure 1 – Continued.

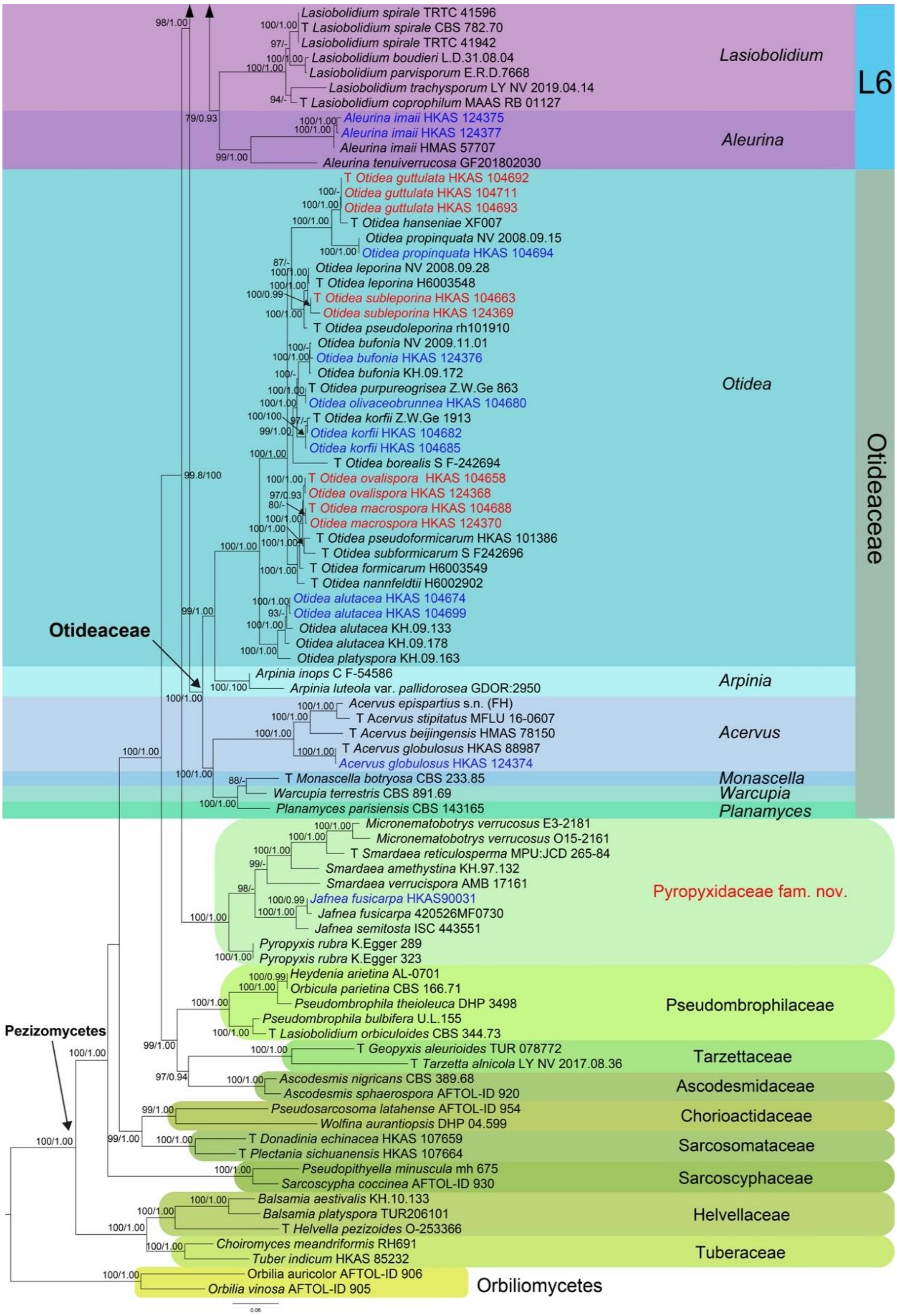

Figure 1 – Continued.

The placement of new collections in this study

Our 37 collections belong to eight genera, namely, *Acervus*, *Aleurina*, *Cheilymenia*, *Humaria*, *Melastiza*, *Otidea*, *Rhodoscypha*, and *Scutellinia* within *Pyronemataceae* and *Otideaceae* based on morphology and phylogeny. Overall, the new collections are distributed in each lineage except for lineage 4. The new species are situated in lineages 3, 5 and *Otideaceae*.

Within lineage 1, three *Humaria* collections are grouped with two *H. hemisphaerica* strains forming a clade of maximum support (100BS/1.00PP). Within lineage 2, a new Chinese collection of *Rhodoscypha ovilla* clustered sister to a clade of two European *R. ovilla* strains with maximum support (100BS/1.00PP). The polyphyletic *Melastiza* is separated into three main groups in lineage 3. One represented by five *Melastiza cornubiensis* strains (three of which are from this study), one formed by *Melastiza flavorubens* and our new species *Melastiza verruculosa* (represented by two strains). Besides, the single strain *Melastiza contorta* (KH 01.06) is sister to the genus *Pseudaleuria*. Two *Cheilymenia vitellina* samples collected from a morel cultivation greenhouse clustered with the *C. vitellina* strain (KH 01.32), further sister to *Cheilymenia granulata*. Within lineage 5, we first determined the phylogenetic positions of *Scutellinia jungneri* and *Scutellinia sinosetosa*. The new species *Scutellinia verruculosa* (represented by two strains) groups with other two *Scutellinia* strains, *Scutellinia* cf. *subhirtella* (KH 03.117) and *Scutellinia hyperborea* (KH 03.116) in a clade of maximum support (100BS/1.00PP). Besides, three *Scutellinia colensoi* collections group with another *S. colensoi* strain and an undetermined *Scutellinia* strain in a maximum supported clade (100BS/1.00PP). Four newly-introduced species and eight collections are placed in *Otideaceae*. The placement of the four new taxa has nearly maximum statistical support.

Pyropyxidaceae* fam. nov. segregates from *Pyronemataceae sensu stricto

Based on a broad taxon sampling and four genes, *Jafnea*, *Micronematobotrys*, *Pyropyxis*, and *Smardaea* are clustered, forming a *Pyropyxis* lineage of maximum statistical support (100BS/1.00PP), which branches off the *Pyronemataceae*+*Otideaceae* clade. These results are similar to Hansen et al. (2013). We establish the new family *Pyropyxidaceae* to accommodate the *Pyropyxis* lineage, which was originally adopted into *Pyronemataceae sensu stricto* (Hansen et al. 2013).

Within *Pyropyxidaceae*, there are mainly three clades, involving four genera. *Pyropyxis* is basal to this family. The hyphomycetous genus *Micronematobotrys* represented by two *Micronematobotrys verrucosus* strains is nested within *Smardaea*. *Jafnea* is sister to the clade formed by these two genera, and one *Jafnea fusicarpa* strain sequenced from herbarium is sister to *J. fusicarpa* (420526MF0730) with maximum support (100BS/0.99PP).

Estimation of divergence times

The BEAST analysis yielded over 200 effective sample sizes for all relevant parameters. Divergence time estimates and the chronogram are illustrated in Fig. 2. The topology of the maximum clade credibility (MCC) tree resembles that obtained from the combined data in IQ-tree and BI analyses. The estimated crown age of *Pezizomycetes* (332 Mya) is similar to previous studies (Gueidan et al. 2011, Prieto & Wedin 2013, Ekanayaka et al. 2017), as is the node age for *Tuberaceae* (154 Mya) (Bonito et al. 2013). The *Pyropyxidaceae* lineage diverged from the *Pyronemataceae* and *Otideaceae* approximately 243 Mya (199−291) in the Late Triassic. The crown age of this family is around 141 Mya (86−200). The split of *Otideaceae* and *Pyronemataceae* occurred around 230 Mya (188−274) in the Late Triassic. The crown age of *Otideaceae* is about 202 Mya (159−250), while that of *Pyronemataceae* is 209 Mya (171−257). Additional divergence times of other selected families are shown in Table 3.

Ancestral character states reconstruction

Ancestral states are depicted on all nodes, mapped on the consensus evolution analysis as pie charts. Reconstruction of ancestral character states of ascomatal types in *Pyronemataceae*, *Pyropyxidaceae* and *Otideaceae* are shown in Fig. 3 using time-calibrated maximum clade credibility trees. The corresponding character states for all terminal taxa were coded based on previous studies. Six ascomatal types were depicted on the trees.

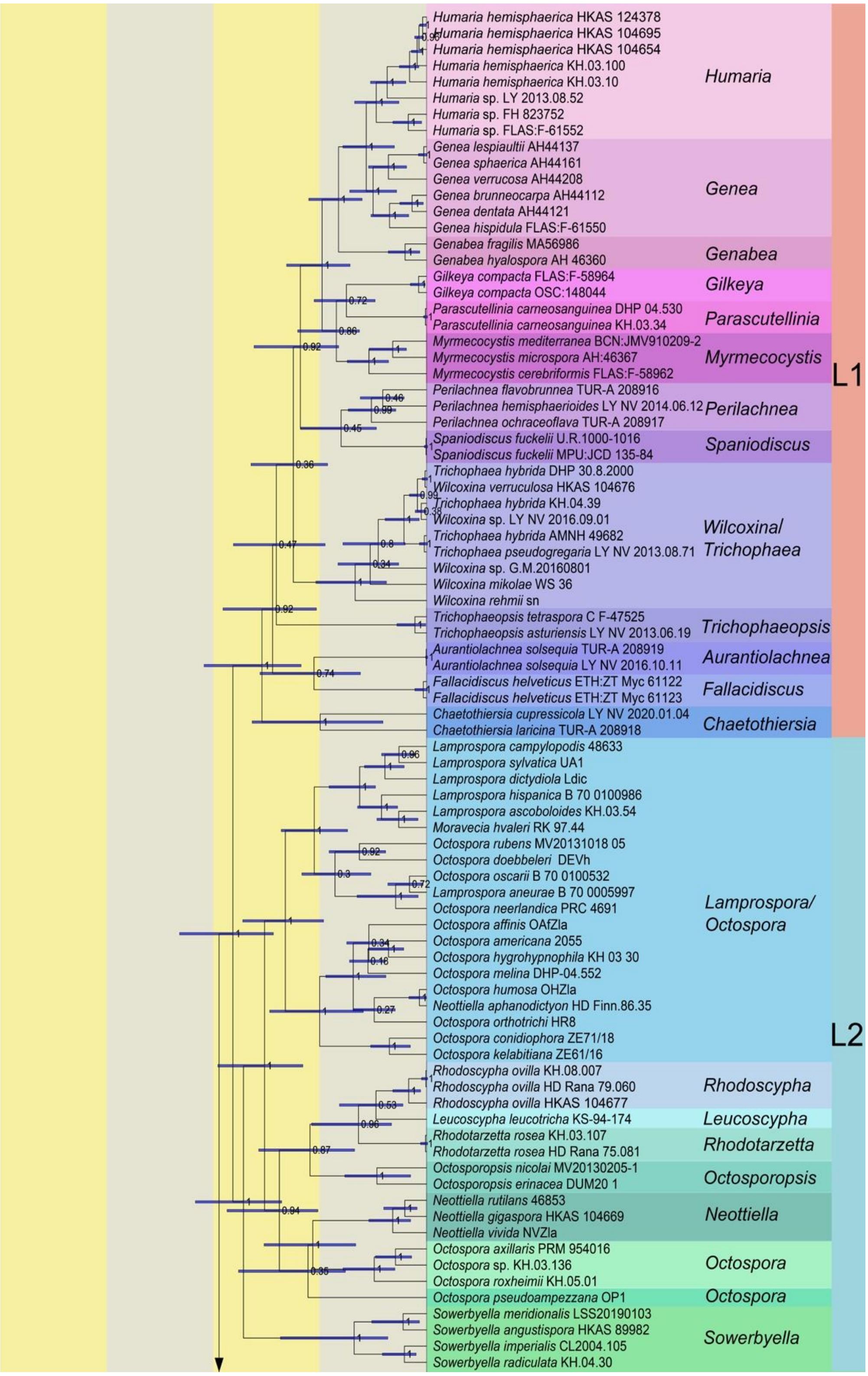

Figure 2 – Time calibrated phylogeny of extant *Pyronemataceae*, *Otideaceae*, *Pyropyxidaceae* and other selected taxa from *Pezizomycetes*. Divergence times were estimated with maximum clade credibility (MCC) tree under a relaxed clock model. Numbers at nodes indicate posterior probabilities for node support, bars correspond to the 95% highest posterior density (HPD) intervals. Numbers in the red circles indicate the secondary calibration (1, 2) points. Numbers in the blue circles indicate the median age and 95% HPD (Table 3).

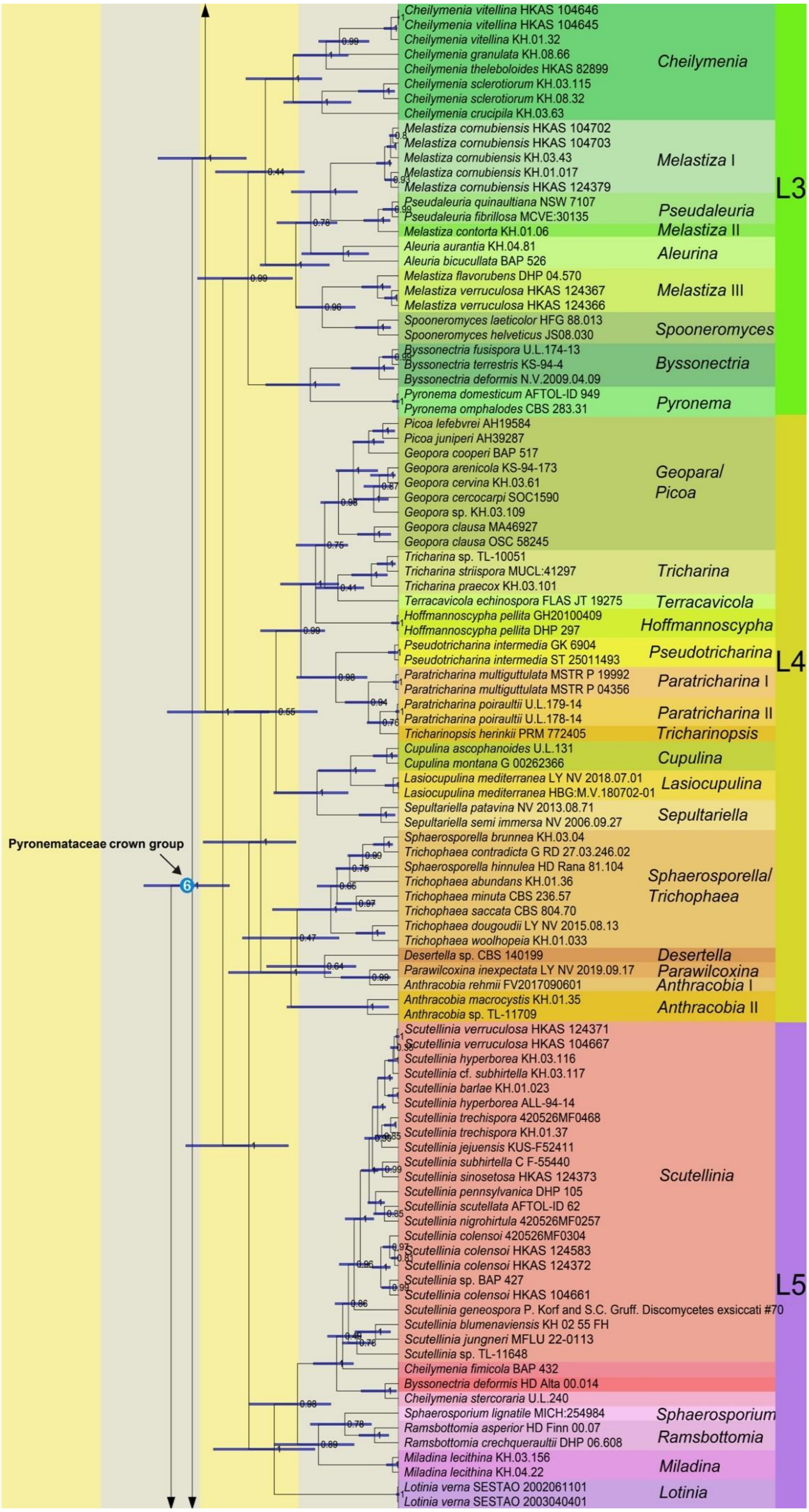

Figure 2 – Continued.

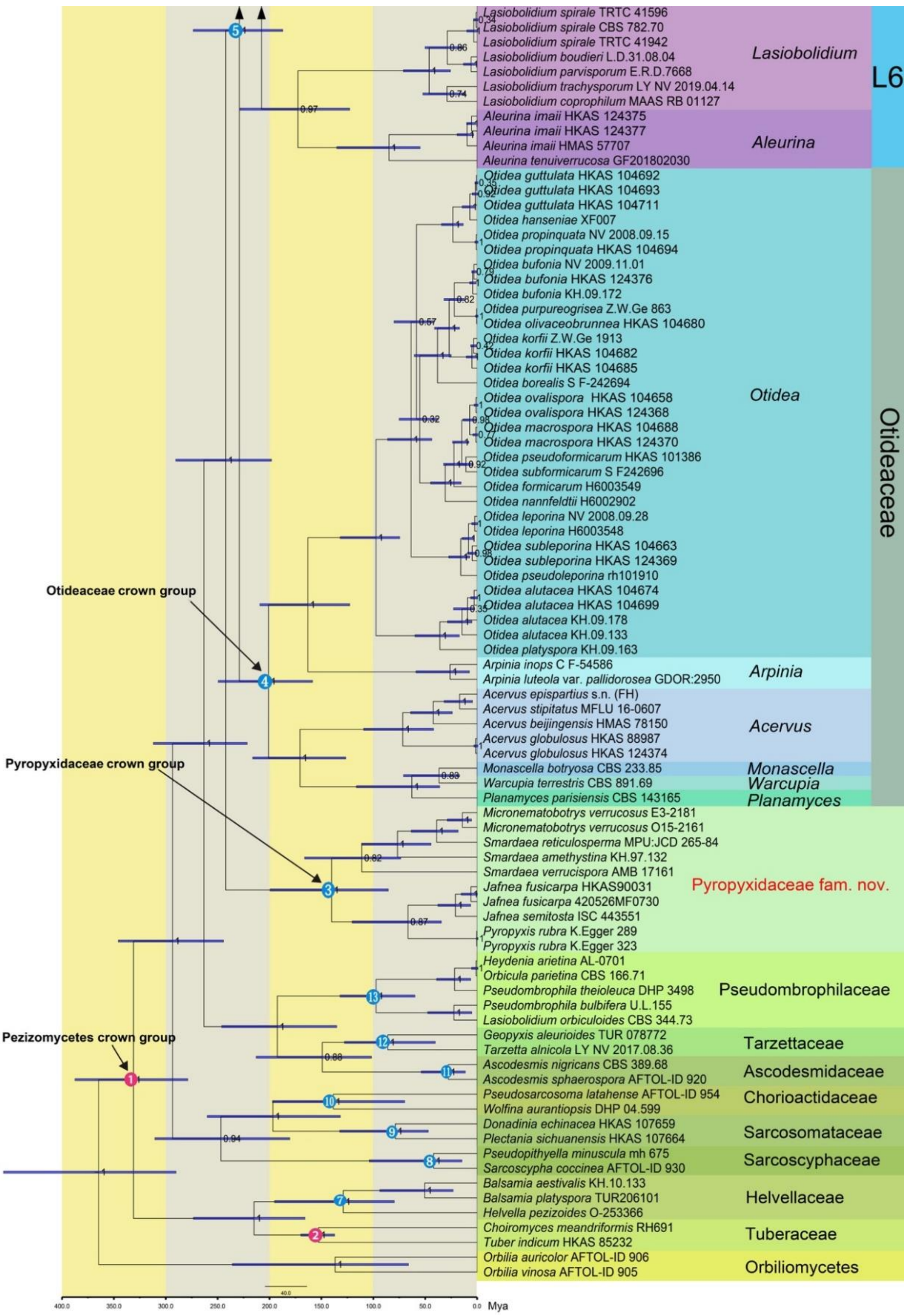

Figure 2 – Continued.

Table 3 Divergence times estimates (Mya) with 95% credibility intervals (CI).

Nodes	Group	Node age (Mya)	Geological time scales
1	*Pezizomycetes* crown group	332 (280−388)	Early Carboniferous
2	*Tuberaceae* crown group	154 (138−171)	Late Jurassic
3	*Pyropyxidaceae* crown group	141 (86−200)	Early Cretaceous
4	*Otideaceae* crown group	202 (159−250)	Late Triassic
5	*Otideaceae*−*Pyronemataceae*	230 (188−274)	Late Triassic

Table 3 Continued.

Nodes	Group	Node age (Mya)	Geological time scales
6	*Pyronemataceae* crown group	209 (171−257)	Late Triassic
7	*Helvellaceae* crown group	130 (81−196)	Early Cretaceous
8	*Sarcoscyphaceae* crown group	43 (15−105)	Early Paleogene
9	*Sarcosomataceae* crown group	80 (48−133)	Late Cretaceous
10	*Chorioactidaceae* crown group	139 (71−198)	Early Cretaceous
11	*Ascodesmidaceae* crown group	29 (12−55)	Late Paleogene
12	*Tarzettaceae* crown group	87 (41−129)	Late Cretaceous
13	*Pseudombrophilaceae* crown group	98 (61−133)	Late Cretaceous

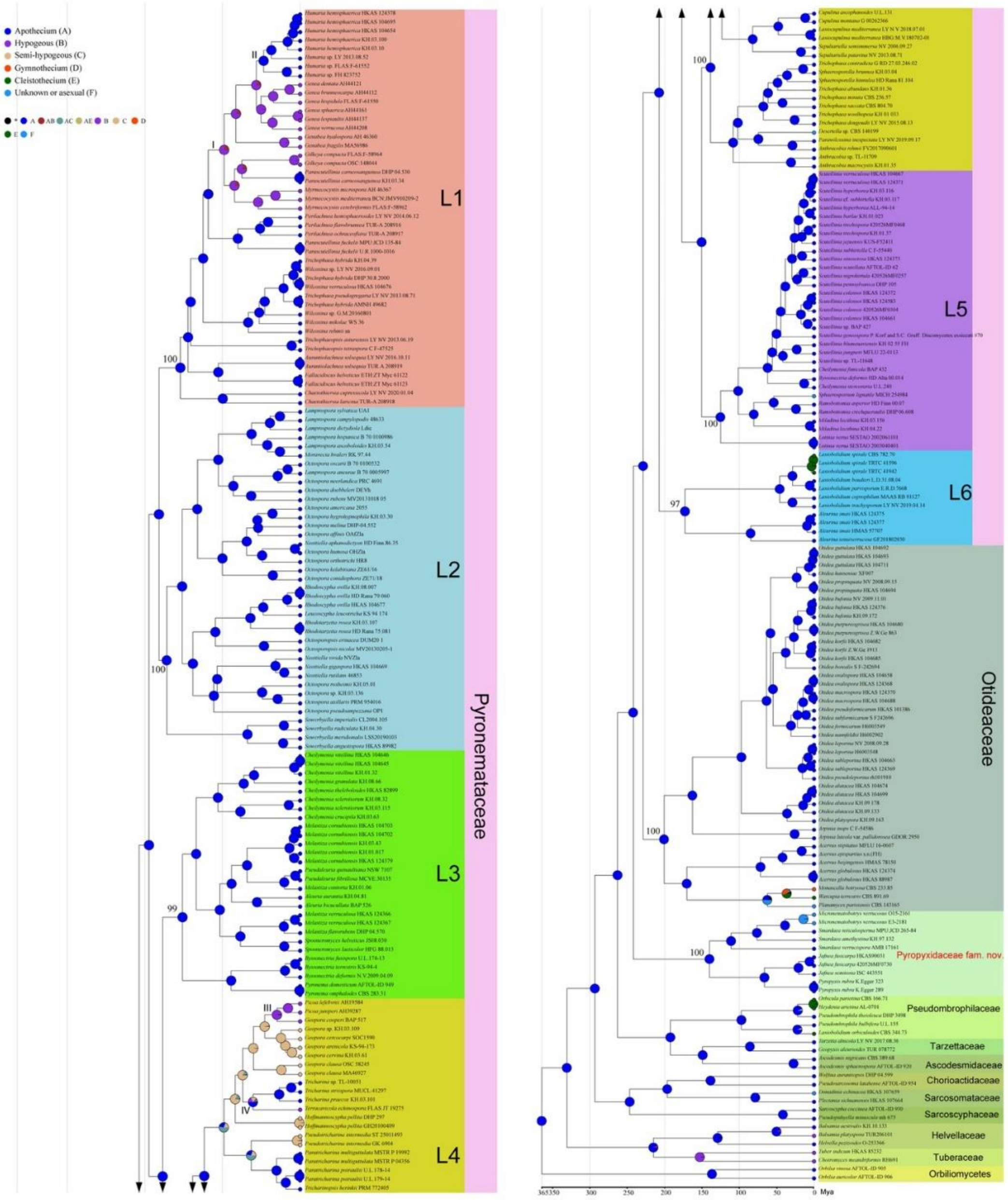

Figure 3 – Reconstruction of ancestral character states focusing on ascomatal characters using Bayesian Binary MCMC (BBM) method.

Based on our analysis, the ancestral ascomata type for the ancestor of *Pyronemataceae*, *Pyropyxidaceae* and *Otideaceae* was the apothecium. *Pyropyxidaceae* members retain this ancestral character, excluding *Micronematobotrys*, for which only the asexual morph is known. Within *Otideaceae*, *Otidea subterranea* independently acquired the hypogeous ascomata (Fig. 5). This species was excluded from our analysis due to only ITS being available (Smith & Healy 2009). Gymnothecia arose only once in *Monascella*, which grouped with the cleistothecial bearing *Warcupia* in this and other analyses (Hansen et al. 2013). The two diverged at approximately 38 Mya. Within *Pyronemataceae*, all ascomatal types are present, except for gymnothecia. Most members of the lineages still retain the apothecia state with specific taxa exceptions in L1, L4 and L6. Cleistothecia independently arose once within *Pyronemataceae* (L6) in *Lasiobolidium spirale*, which diverged approximately 30 Mya from the apothecia-bearing ancestor of *Lasiobolidium*. Hypogeous members have evolved independently at least twice within *Pyronemataceae* in L1 and L4. The estimated dates placed the common ancestor of hypogeous taxa in L1 at 99 Mya (node I), followed by diversification leading to the extant taxa *Genea* (51 Mya), *Genabea* (21 Mya), *Gilkeya* (8 Mya), and *Myrmecocystis* (55 Mya). A reversal from the hypogeous form to the apothecial form occurred in the ancestors of *Humaria* (48 Mya, node II) and *Parascutellinia* (2 Mya), both of which arose independently. Within L4, the hypogeous type arose twice, one is at 31 Mya (node III), one is split from 61 Mya (node IV), while semi-hypogeous arose at least twice.

Taxonomy

Otideaceae Eckblad, Nytt Mag. Bot. 15(1-2): 82 (1968)

Index Fungorum No: IF 81096; Facesoffungi number: FoF 04231

Type genus – ***Otidea*** (Pers.) Bonord.

Notes – This family has various ascomatal forms, including apothecia, hypogeous, gymnothecia, or cleistothecia, with discoid, cupulate, ear-shaped, globose to folded, and even some highly reduced. Paraphyses are filiform to sub-clavate, often straight or curved, sometimes with notches at the apex. Ascospores are mostly ellipsoid and guttulate, with smooth-walled (Olariaga et al. 2015, Ekanayaka et al. 2018). This family contains nine genera *Acervus*, *Arpinia*, *Monascella*, *Otidea*, *Planamyces*, *Warcupia*, *Ascosparassis*, *Diehliomyces* and *Wenyingia*, with the last three lacking sequence data (Ekanayaka et al. 2018). While the attributions of *Diehliomyces* and *Wenyingia* are currently disputed (Van Vooren & Vega 2018b, Pfister & Healy 2021). This family is sister to *Pyronemataceae* with high support (98BS/1.00PP) (Fig. 1). These two also differ morphologically in that the *Pyronemataceae* mostly present carotenoid pigments and has apothecial, cleistothecial, semi-hypogeous to hypogeous ascomata, diverse ascospores with smooth or ornamented walls (Hansen et al. 2013).

Acervus Kanouse, Pap. Mich. Acad. Sci. 23: 149 (1938) [1937]

Index Fungorum No: IF 34

Type species – ***Acervus epispartius*** (Berk. & Broome) Pfister

Notes – This genus has closed ascomata when young, and yellow to orange or red apothecia when mature, with sessile to substipitate, filiform to sub-clavate paraphyses, subcylindrical to cylindrical asci and smooth-walled, guttulate ascospores (Zeng et al. 2020, Pfister & Healy 2021). Ten species are accepted in this genus, all of which are found in soil or rotten wood. In addition, most of this diversity has been reported from China, where nine of the species were reported (Zeng et al. 2020).

Zeng et al. (2020) mistakenly provided the isotype information (TRH:F:11406) of the type species *Acervus epispartius* according to the herbarium information at https://www.gbif.org/occurrence/3460841307, while this herbarium does not match the type in protologue (Berkeley & Broome 1873). Thus, the label "isotype" on the herbarium (TRH:F:11406) is incorrect. Besides, we collected an *Acervus* specimen identified as *A. globulosus* (HKAS 124374) from the original locality of the type specimen (Ekanayaka et al. 2016). This is a common species in tropical regions which was first reported in China and then in Thailand (Ekanayaka et al. 2016, Zeng et al. 2020).

Otidea (Pers.) Bonord., Handb. Allgem. mykol. (Stuttgart): 205 (1851)

Index Fungorum No: IF 3654

Type species – ***Otidea onotica*** (Pers.) Fuckel

Notes – This is an easily recognized genus characterized by cupulate to ear-shaped apothecia, sessile to stipitate, and margin normally split on one side, sometimes entire. Excipulum often with pigmented resinous exudates. Paraphyses are straight or curved to hooked, with or without notches at the apex. Ascospores are ellipsoid to oblong, often with 1−2 guttules, and mostly smooth-walled, rarely with additional small granules (Hansen & Olariaga 2015, Olariaga et al. 2015). Besides, *Otidea subterranea*, a rare hypogeous taxon of this genus, is featured by globose to subglobose ascomata, three layers of peridium, inamyloid asci with eight ascospores and a crozier at base, ellipsoid, uniguttulate ascospore with smooth or roughish walls (Smith & Healy 2009). In a monograph of this genus, Olariaga et al. (2015) accepted 33 species with full descriptions and illustrations or notes. Subsequently, new additions and amendments to species were introduced (Hyde et al. 2018, Xu et al. 2018, 2022, this study). This genus has high species diversity with all species forming a strongly supported monophyletic group (100BS/1.00PP) (Fig. 1).

Otidea alutacea (Pers.) Massee, Brit. Fung.-Fl. (London) 4: 446 (1895) Fig. 4

Index Fungorum number: IF 118687; Facesoffungi number: FoF 04233

Saprobic on soil. Sexual morph: *Apothecia* 1−6 cm broad, 1.5−7 cm high, scattered to gregarious, cupulate to ear-shaped, sessile to substipitate. *Receptacle surface* pale yellowish brown, finely furfuraceous, margin split on one side. *Hymenium* 195−250 µm thick, yellowish brown to brown, slightly darker in color than the receptacle surface, nearly smooth. *Subhymenium* 50−170 µm thick, distinct, and visible as a darker zone of densely arranged cylindrical to swollen cells. *Ectal excipulum* 45−110 µm thick, composed of *textura angularis* to *textura globulosa*, 20−25 × 14−16 µm, yellow, present sparse resinous exudates, with 3−5 µm broad, hyaline to yellowish, short hyphoid hairs from outermost cells. *Medullary excipulum* 250−350 µm thick, composed of *textura intricata*, 3−8 µm broad, hyaline to yellowish or brownish hyphae. *Paraphyses* 2−3 µm broad, filiform, curved at the apex, with yellowish to brownish contents, sometimes embedded in a brown matter at apices, without notches. *Asci* 190−215 × 11−14 µm, 8-spored, cylindrical, operculate, inamyloid, with a long pedicel and a crozier at the base. *Ascospores* [20/1/1, in H_2O] (15.3−) 16.2−18.6 (−19.5) × (7.7−) 7.9−9.2 (−10.2) µm (Q = 1.83−2.27, **Q** = 2.04±0.14), oblong ellipsoid, hyaline, uniseriate, equilateral, rarely slightly inequilateral, rounded at the ends, uniguttulate to biguttulate, sometimes with additional small granules, smooth. Asexual morph: Undetermined.

Material examined – China, Sichuan province, Jiuzhai valley, on mossy soil under a mixed coniferous broad-leaved forest, elev. 3567 m asl., 20 August 2018, Ming Zeng, ZM 46 (HKAS 104674); *ibid.* on soil under a coniferous forest, elev. 3247 m asl., 20 August 2018, Ming Zeng, ZM 73 (HKAS 104699).

GenBank accession numbers – HKAS 104674 (LSU: OP291060; *tef-1α*: OP352493; SSU: OP291010), HKAS 104699 (LSU: OP291061; *tef-1α*: OP352494; SSU: OP291011).

Notes – This species is characterized by ear-shaped, split, sometime cupulate, substipitate apothecia, pale yellowish-brown receptacle surface, ectal excipulum with sparse resinous exudates, brown hymenium, oblong ellipsoid ascospores (Olariaga et al. 2015). Mutiple-gene analyses based on LSU, ITS, *tef-1α*, and *rpb2* show this species as is a complex and is separated into several clades with strong supports (Fig. 5). Further sampling, morphological and molecular studies are required to thoroughly resolve the definition of this species.

Otidea bufonia (Pers.) Boud., Hist. Class. Discom. Eur. (Paris): 52 (1907) Fig. 6

Index Fungorum number: IF 414705; Facesoffungi number: FoF 12752

Saprobic on soil. Sexual morph: *Apothecia* 2−4 cm broad, 2−6 cm high, scattered to gregarious, cupulate to broadly ear-shaped, stipitate. *Stipe* up to 2 cm broad, 2−3 cm high, white, tomentum. *Receptacle surface* dark brown, margin split on one side, sometimes entire. *Hymenium* 150−200 µm thick, dark brown, same in color as receptacle surface or slightly lighter, nearly smooth.

Subhymenium ca. 70 µm thick, distinct, and visible as a darker zone of densely arranged cylindrical to swollen cells. *Stipal ecto-excipulum* 70−90 µm broad, of *textura angularis* to *textura globulosa*, composed of 11−15 × 9−11 µm cells, yellowish, with 5−7 µm broad, short hyphoid hairs, hyaline to yellowish, arising from outmost cells. *Ectal excipulum* 55−110 µm thick, composed of *textura angularis* to *textura globulosa*, 13−15 × 9−12 µm cells, yellow, abundantly present resinous exudates, with 3−5 µm broad, short, hyaline to yellowish, hyphoid hairs. *Medullary excipulum* 320−850 µm thick, composed of *textura intricata*, 3−5 µm broad, yellowish or brownish hyphae, present resinous exudates. *Paraphyses* 2−3 µm broad, filiform, curved and hooked, with yellow to brown contents, without notches. *Asci* 145−172 × 8−10 µm, 8-spored, cylindrical, operculate, inamyloid, with a long pedicel and a crozier at the base. *Ascospores* [20/1/1, in H_2O] (11.8−) 12.5−13.5 (−14.3) × (6−) 6.1−6.7 (−7) µm (Q = 1.78−2.3, **Q** = 2.03±0.12), narrowly ellipsoid to oblong or subfusoid, hyaline, uniseriate, equilateral or inequilateral, rounded at the ends, uniguttulate to biguttulate, sometimes with additional small granules, smooth. Asexual morph: Undetermined.

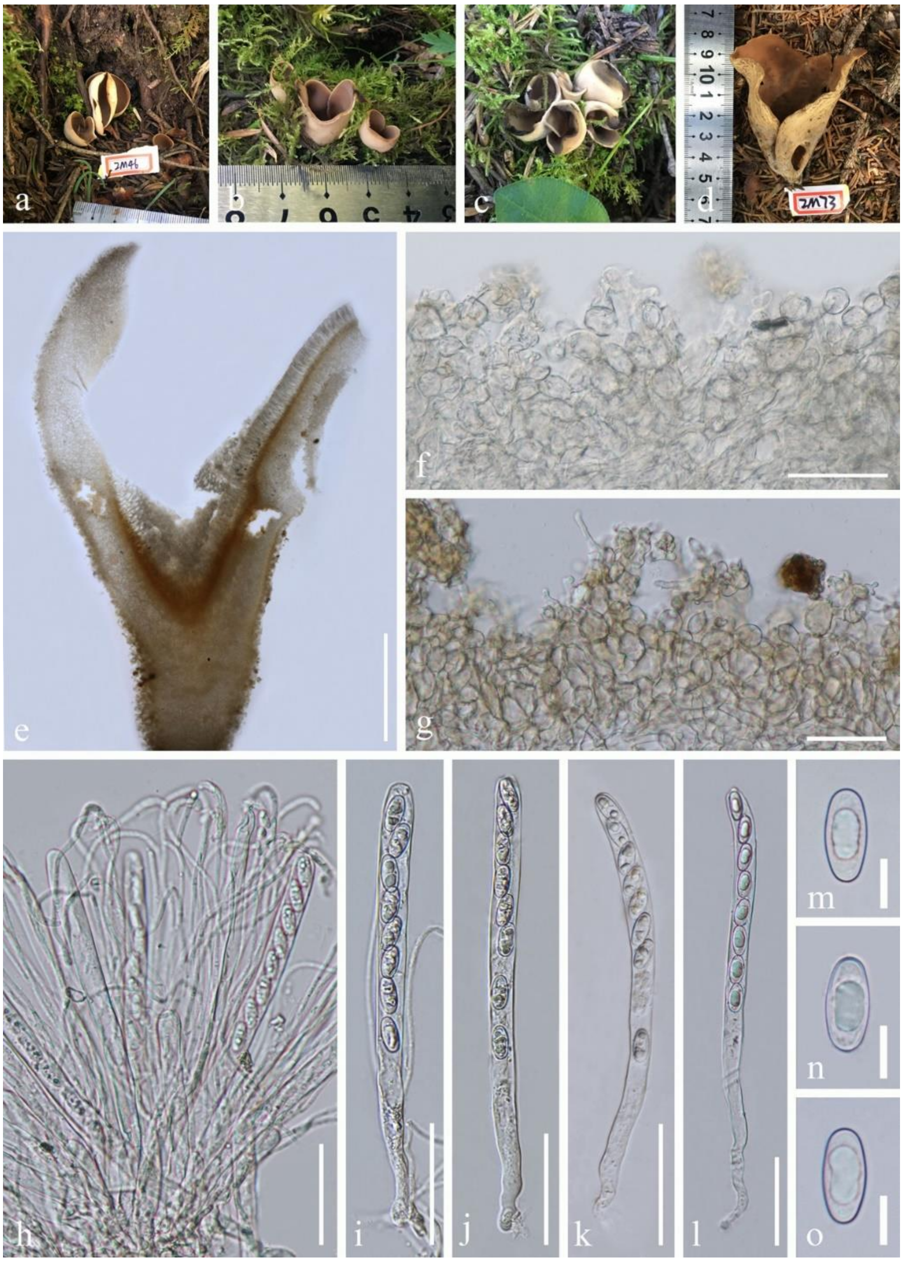

Figure 4 – *Otidea alutacea*. a–d Fresh specimens. a–c HKAS 104674. d HKAS 104699. e Vertical median section of ascomata. f Stipal ecto-excipulum. g Ectal excipulum. h Asci and paraphyses. i–l Asci. m–o Ascospores. Scale bars: e = 1000 µm, f–l = 50 µm, m–o = 10 µm.

Figure 5 – Phylogram generated from combined LSU, ITS, *tef-1α*, and *rpb2* sequence data for *Otidea* species. Related sequences refer to Hansen & Olariaga (2015), Olariaga et al. (2015), and Xu et al

(2018, 2022). One hundred and ten taxa are included in the combined analyses which comprise 3283 characters (LSU: 1−840 bp; ITS: 841−1462 bp; *tef-1α*: 1463−2502 bp; *rpb2*: 2503−3283 bp) in a matrix. *Monascella botryosa* (CBS 233.85) and *Warcupia terrestris* (CBS 891.69) are used as the outgroup taxa. The best-fit models were selected by jModelTest v. 2.1.10 (Darriba et al. 2012) for each gene (LSU & ITS: TIM2+I+G; *tef-1α*: TrNef+I+G; *rpb2*: HKY+I+G). The best-scoring IQ tree with a final likelihood values of -28803.187 is presented. Bootstrap values ≥ 75% (maximum likelihood) and posterior probability values ≥ 0.90 (Bayesian inference) are indicated with thick branches. The tree topology of the IQ-tree analysis is similar to the Bayesian analysis. The newly sequenced collections are indicated in blue. The newly described species are indicated in red. Names in bold indicate type collections.

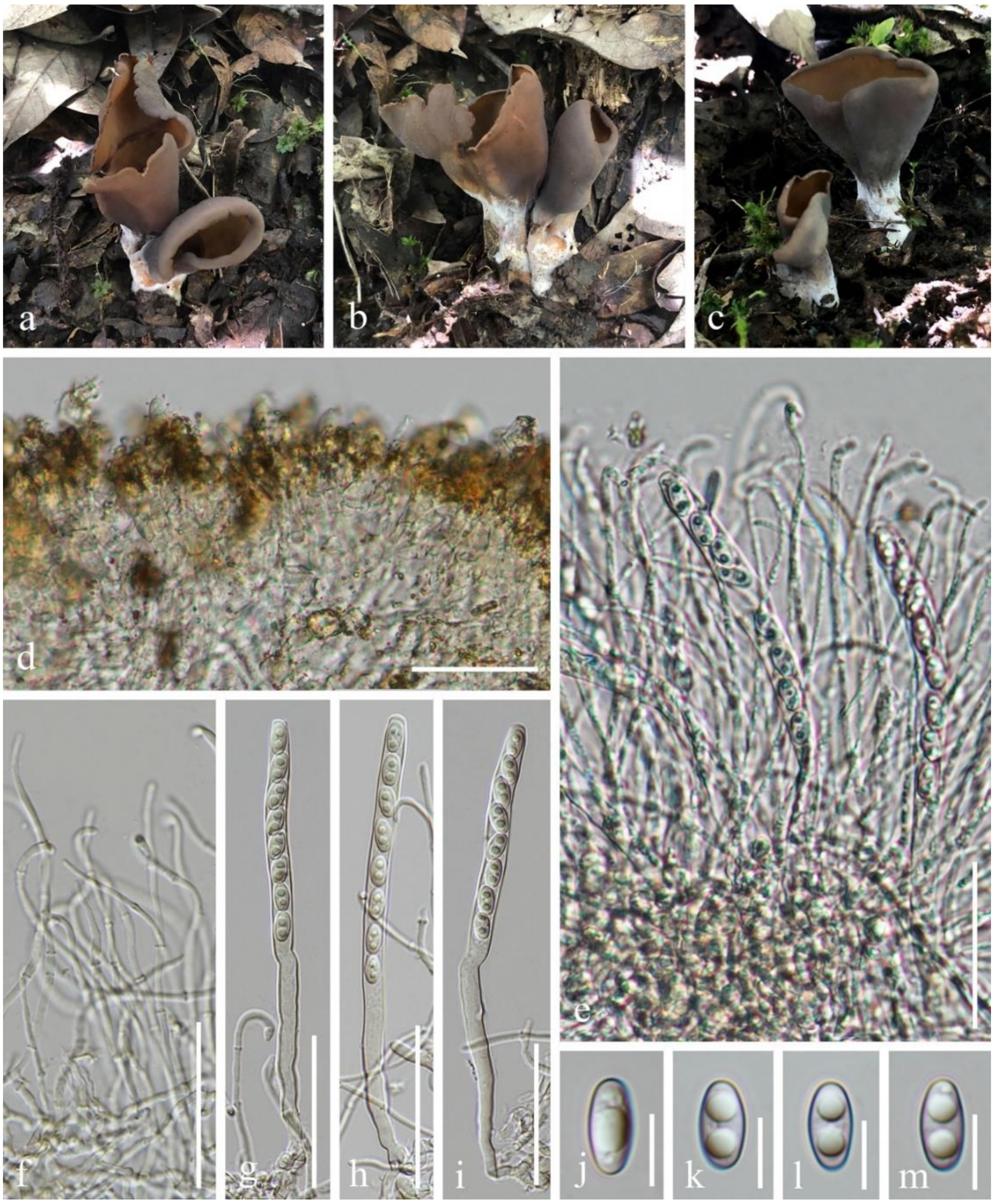

Figure 6 – ***Otidea bufonia*** (HKAS 124376). a–c Fresh specimens. d Ectal excipulum. e Asci and paraphyses. f Paraphyses. g–i Asci. j–m Ascospores. Scale bars: d–i =50 µm, j–m = 10 µm.

Material examined – China, Sichuan province, G318, on soil under a broad-leaved forest, 12 August 2021, Song Wang, ZM 383 (HKAS 124376).

GenBank accession numbers – HKAS 124376 (LSU: OP291062; *tef-1α*: OP352495; *rpb2*: OP352523; SSU: OP291012).

Notes – This species has cup-shaped, ear-shaped, dark brown apothecia with a broad stipe, resinous exudates present in the excipulum, curved and hooked paraphyses, narrowly ellipsoid to sub-fusoid ascospores (Olariaga et al. 2015). The color and ascospores shape of *Otidea filiformis* and *Otidea mirabilisi* resembles those of *Otidea bufonia*. These two differ from *Otidea bufonia* in that resinous exudates in the medullary excipulum are absent or rare. In addition, the receptacle surface of *Otidea mirabilisi* is purple to lilaceous-bluish (Olariaga et al. 2015, Xu et al. 2020). Phylogenetic analyses show that this species is polyphyletic (Fig. 5). Most *Otidea bufonia* strains form a moderately-supported clade (90BS/0.82PP), while the two strains, MCVE 29371 and MCVE 29372, identified by Carbone et al. (2019) group with *Otidea filiformis* introduced by Xu et al. (2022) (Fig. 5). The species limits of *Otidea bufonia* and *Otidea filiformis* should be based on broader taxon sampling, morphological and phylogenetic studies in the future.

Otidea guttulata M. Zeng, Q. Zhao & K.D. Hyde, sp. nov. Fig. 7

Index Fungorum number: IF 900174; Facesoffungi number: FoF 12599

Etymology: The epithet refers to its guttulate ascospores.

Holotype: HKAS 104692

Diagnosis – This species is diagnosed by its ear-shaped to cupulate, substipitate apothecia, yellow and wrinkled receptacle surface, yellow excipulum absent or rarely present resinous exudates, ocher hymenium, yellowish paraphyses with one or two notches and broadly ellipsoid ascospores.

Saprobic on soil. Sexual morph: *Apothecia* 1−3 cm broad, 1.5−4 cm high, scattered to gregarious, broadly ear-shaped, sometimes cupulate, split, substipitate, basal with white to cream tomentum and mycelium. *Receptacle surface* yellow, wrinkled or furfuraceous, margin mostly split. *Hymenium* 200−240 µm thick, ocher, slightly darker in color than receptacle surface, nearly smooth. *Subhymenium* ca. 100 µm thick, distinct, and visible as a darker zone of densely arranged cylindrical to swollen cells. *Ectal excipulum* 75−140 µm thick, composed of *textura angularis* to *textura globulosa*, 23−31 × 17−21 µm cells, yellow, absent or rare with resinous exudates, with short yellow hyphoid hairs, 5−8 µm broad, arising from outmost cells. *Medullary excipulum* 320−580 µm thick, composed of *textura intricata*, 4−10 µm broad, yellow hyphae, absent or rare with resinous exudates at the septa. *Paraphyses* 2−3 µm broad, yellowish, filiform, straight or curved at the apex, with one or two low or distinct notches. *Asci* 180−215 × 11−14 µm, 8-spored, cylindrical, operculate, inamyloid, with a long pedicel and a crozier at the base. *Ascospores* [20/1/1, in H_2O] (14.1−) 14.9−16.3 (−16.9) × (8−) 8.8−10 (−10.2) µm (Q = 1.54−1.81, **Q** = 1.66±0.08), broadly ellipsoid, hyaline, uniseriate, equilateral, rounded at the ends, uniguttulate to biguttulate, rarely with additional small granules, smooth. Asexual morph: Undetermined.

Material examined – China, Sichuan province, Jiuzhai valley, on mossy soil under a mixed coniferous broad-leaved forest, elev. 3247 m asl., 20 August 2018, Ming Zeng, ZM 66 (HKAS 104692, holotype); *ibid*., ZM 67 (HKAS 104693, paratype); *ibid*., elev. 3173 m asl., 22 August 2018, Ming Zeng, ZM 88 (HKAS 104711, paratype).

GenBank accession numbers – HKAS 104692 (LSU: OP291063; *tef-1α*: OP352496; SSU: OP291013), HKAS 104693 (LSU: OP291064; SSU: OP291014), HKAS 104711 (LSU: OP291065; SSU: OP291015).

Notes – We collected three specimens that show consistent morphologies, and are phylogenetically close to *Otidea hanseniae,* which were assigned to a distinct clade. Xu et al. (2018) introduced *Otidea hanseniae* typified by yellowish brown to olivaceous brown hymenium, furfuraceous, even brown pustulate receptacle surface, and pale brown to dark brown excipulum with abundant resinous exudates. Additionally, *Otidea hanseniae* has smaller apothecia (10–18 mm high, 5–12 mm broad) than *Otidea guttulata* (1.5−4 cm high, 1−3 cm broad). These characteristics easily distinguish it from our new species, although *Otidea hanseniae* is not monophyletic in our study as one of *Otidea hanseniae* strain (XF007, holotype) branches out from the clade containing the rest *Otidea hanseniae* and our species. However, our three collections have grouped together with strong support (89BP/0.99PP) (Fig. 5).

Figure 7 – *Otidea guttulata*. a–e Fresh specimens (a, b. HKAS 104693. c, d HKAS 104692, holotype. e HKAS 104711). f Ectal excipulum. g Asci and paraphyses. h Ascus. i Ascus in Congo red. j Ascus in Melzer Reagent. k Apex of an ascus in Congo red. l–o Ascospores. Scale bars: f –j = 50 µm, k, l, n, o = 10 µm, m = 20 µm.

Otidea korfii Pfister, F. Xu & Z.W. Ge, Mycol. Progr. 17(1-2): 83 (2017) [2018] Fig. 8

Index Fungorum number: IF 816085; Facesoffungi number: FoF 12753

Saprobic on soil. Sexual morph: *Apothecia* 0.5−2 cm broad, 2−4 cm high, scattered to gregarious, broadly ear-shaped, substipitate, basal with white to cream tomentum. *Receptacle surface* yellow-brown, mustard, margin involute, split on one side. *Hymenium* 180−220 µm thick, cream yellow or pastel yellow, slightly lighter in color than receptacle surface, nearly smooth. *Subhymenium* 90−110 µm thick, distinct, and visible as a darker zone of densely arranged cylindrical to swollen cells. *Ectal excipulum* 85−120 µm, composed of *textura angularis* to *textura globulosa*, 25−35 × 20−25 µm cells, yellow to yellow-brown, present resinous exudates, with 4.5−8 µm, short, hyaline to yellowish hyphoid hairs. *Medullary excipulum* 250−380 µm, composed of *textura intricata*, 5−8 µm broad, hyaline to yellowish hyphae, seldom present resinous exudates. *Paraphyses* 2−3.5 µm broad, filiform, curved and hooked, yellowish, containing small, refractive, light brownish to yellowish guttules, without notches. *Asci* 160−200 × 10−12 µm, 8-spored, cylindrical, operculate, inamyloid, with a long pedicel and a crozier at the base. *Ascospores* [20/1/1, in H_2O] (13.8−) 14−15.2 (−16) × (7.4−) 7.6−8.1 (−8.5) µm (Q = 1.76−2.05, **Q** = 1.86±0.08), oblong ellipsoid to sub-fusoid, hyaline, uniseriate, equilateral or sometimes slightly inequilateral, rounded at the ends, uniguttulate to biguttulate, sometimes with additional small granules, smooth. Asexual morph: Undetermined.

Material examined – China, Sichuan province, Jiuzhai valley, on mossy soil under a mixed coniferous broad-leaved forest, elev. 3567 m asl., 20 August 2018, Ming Zeng, ZM 54 (HKAS 104682); *ibid.*, ZM 57 (HKAS 104685).

GenBank accession numbers – HKAS 104682 (LSU: OP291066; *tef-1α*: OP352497; SSU: OP291016), HKAS 104685 (LSU: OP291067; *tef-1α*: OP352498; *rpb2*: OP352524; SSU: OP291017).

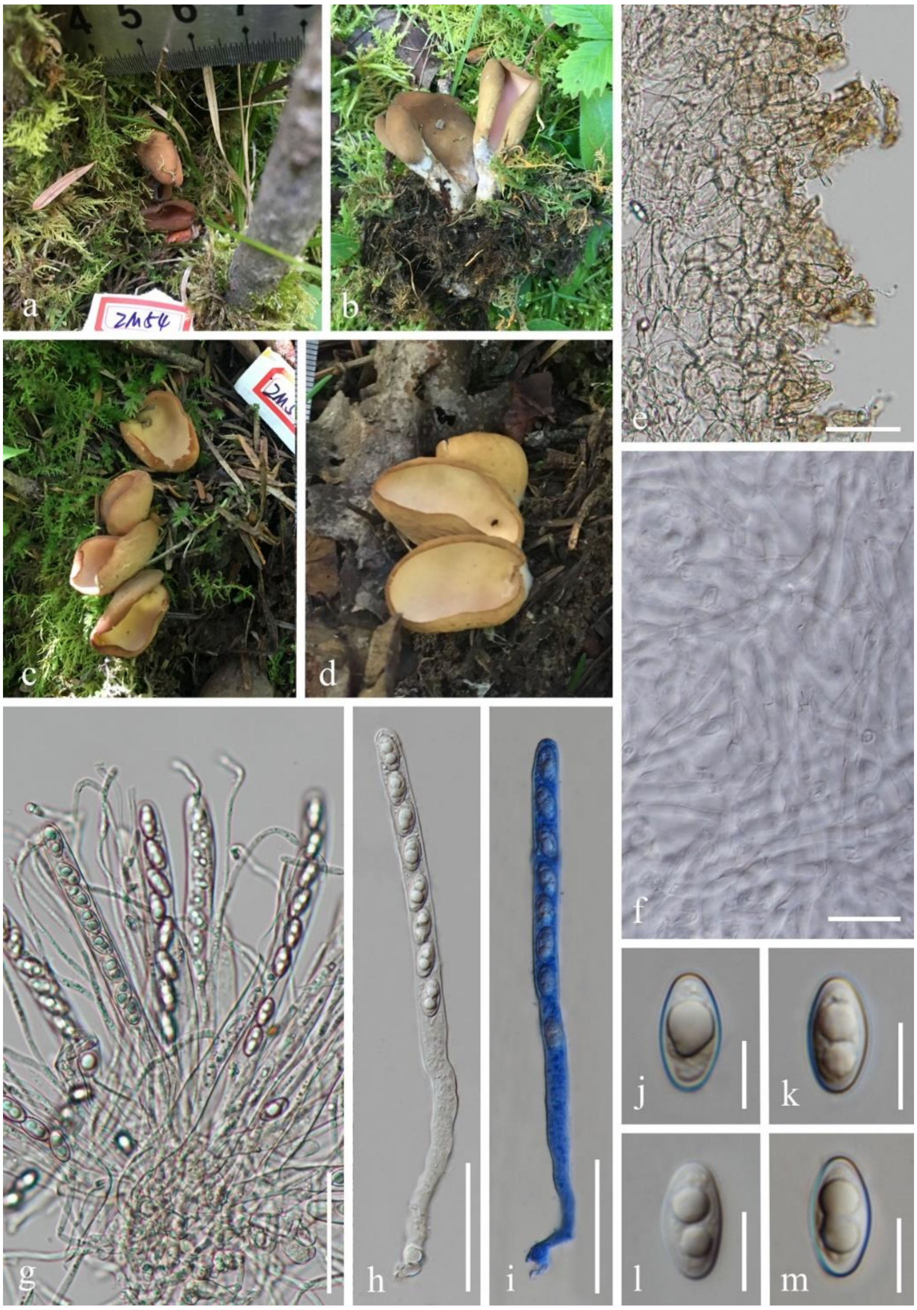

Figure 8 – *Otidea korfii*. a–d Fresh specimens (a, b HKAS 104682. c, d HKAS 104685). e Ectal excipulum. f Medullary excipulum. g Asci and paraphyses. h Ascus. i Ascus in Cotton blue. j–m Ascospores. Scale bars: e–i = 50 µm, j–m = 10 µm.

Notes – This species is featured by broadly ear-shaped, substipitate apothecia, yellowish brown to mustard receptacle surface, pale yellow or pastel yellow hymenium, lighter than receptacle surface in color, curved paraphyses, ellipsoid to subfusoid ascospores (Xu et al. 2018). Our two collections cluster with the holotype of *Otidea korfii* as a well-supported (100BS/1.00PP) lineage within *Otidea* (Fig. 6).

Otidea macrospora M. Zeng, Q. Zhao & K.D. Hyde, sp. nov. Fig. 9

Index Fungorum number: IF 900175; Facesoffungi number: FoF 12600

Etymology: The epithet refers to the larger size of ascospores.

Holotype: HKAS 104688

Diagnosis – This species is recognized by broad ear-shaped or cupulate, substipitate apothecia, ocher hymenium and darker than receptacle surface, yellowish and curved paraphyses with 1−4 district notches, and large ascospores.

Saprobic on soil. Sexual morph: *Apothecia* 0.8−3.5 cm broad, 2−4 cm high, scattered to gregarious, broadly ear-shaped, split, or cupulate, substipitate, basal with white to cream tomentum and mycelium. *Receptacle surface* yellow, margin mostly split on one side, rarely entire. *Hymenium* ca. 260 µm thick, ocher, darker in color than receptacle surface, nearly smooth. *Subhymenium* ca. 65 µm thick, distinct, and visible as a darker zone of densely arranged cylindrical to swollen cells. *Ectal excipulum* 120−200 µm thick, composed of *textura angularis* to *textura globulosa*, 23−32 × 18−24 µm cells, yellow to brownish, present resinous exudates, with 5−9 µm, short, hyaline to yellow hyphoid hairs, arising from outmost cells. *Medullary excipulum* 150−300 µm thick, composed of *textura intricata*, 6−9 µm broad, hyaline to yellowish hyphae. *Paraphyses* 3−4 µm broad, with yellow contents, filiform, mostly curved at the apex, with 1−4 district notches close to the apex. *Asci* 235−270 × 13−15 µm, 8-spored, cylindrical, operculate, inamyloid, with a long pedicel and a crozier at the base. *Ascospores* [20/1/1, in H_2O] (16.2−) 17.5−20.2 (−21) × (8.1−) 9.6−12.2 (−13.3) µm (Q = 1.60−2.01, **Q** = 1.74±0.11), ellipsoid to broadly ellipsoid, hyaline, uniseriate, equilateral, rounded at the ends, uniguttulate to biguttulate, smooth. Asexual morph: Undetermined.

Material examined – China, Sichuan province, Jiuzhai valley, on soil under a mixed coniferous broad-leaved forest, elev. 3247 m asl., 20 August 2018, Ming Zeng, ZM 62 (HKAS 104688, holotype); *ibid.*, elev. 2845 m asl., 21 August 2018, Ming Zeng, ZM 74 (HKAS 124370, paratype).

GenBank accession numbers – HKAS 104688 (LSU: OP291068; *rpb2*: OP352525; SSU: OP291018), HKAS 124370 (LSU: OP291069; *tef-1α*: OP352499; SSU: OP291019).

Notes – This species is sister to another new species, *Otidea ovalispora* in this study. These two have different morphological features. Compared to the other species in the same clade (Fig. 5), this species mainly differs in that it has larger ascospores than *Otidea ovalispora* (9.6−11.2 × 5.6−6.3 µm), *Otidea pseudoformicarum* (8–10 × 5–7 µm), *Otidea formicarum* (9.5–11× 6–7 µm), and *Otidea subformicarum* (10.5–12 × 6–6.5 µm) (Olariaga et al. 2015, Hyde et al. 2018). Based on the morphology and phylogeny, we introduce the new species *O. macrospora* in this study.

Otidea olivaceobrunnea Harmaja, Phytotaxa 2: 49 (2009) Fig. 10

Index Fungorum number: IF 543326; Facesoffungi number: FoF 12601

Saprobic on soil. Sexual morph: *Apothecia* 1.5−2 cm broad, 2.5−4 cm high, gregarious, ear-shaped, split, stipitate. *Stipe* 3−6 mm broad, 0.7−1.7 cm long, terete, solid, brownish, basal with white to cream tomentum and mycelium. *Receptacle surface* dark brown to yellowish brown, darker than hymenium in color, margin mostly deeply split on one side. *Hymenium* 190−220 µm thick, pale brown to olive-brown, nearly smooth. *Subhymenium* 80−100 µm thick, distinct, and visible as a darker zone of densely arranged cylindrical to swollen cells. *Stipal ecto-excipulum* 60−110 µm broad, of *textura angularis* to *textura globulosa*, yellowish to brownish, composed of 13−17 × 9−12 µm cells, with hyphoid hairs, abundant close to the base, 3−5 µm wide, hyaline to brownish. *Ectal excipulum* 70−160 µm thick, composed of *textura angularis* to *textura globulosa*, 13−19 × 8−12 µm cells, yellowish to brownish, abundantly present resinous exudates, with hyphoid hairs, 3−5 µm wide, hyaline to brownish. *Medullary excipulum* 170−270 µm thick, composed of *textura intricata*, 4−6 µm broad hyaline to brownish hyphae, present scarce resinous exudates. *Paraphyses* 2−4 µm broad, with yellow to brownish pigments, filiform, curved at the apex. *Asci* 160−188 × 10−12 µm, 8-spored, cylindrical, operculate, inamyloid, with a long pedicellate and a crozier at the base. *Ascospores* [20/1/1, in H_2O] (14.5−) 15.3−16.9 (−17.5) × (7−) 7.4−8 (−8.2) µm (Q = 1.93−2.50, **Q** = 2.10±0.13), ellipsoid to oblong, hyaline, uniseriate, equilateral or slightly inequilateral, rounded at the ends, uniguttulate to biguttulate, or with additional smaller granules, smooth. Asexual morph: Undetermined.

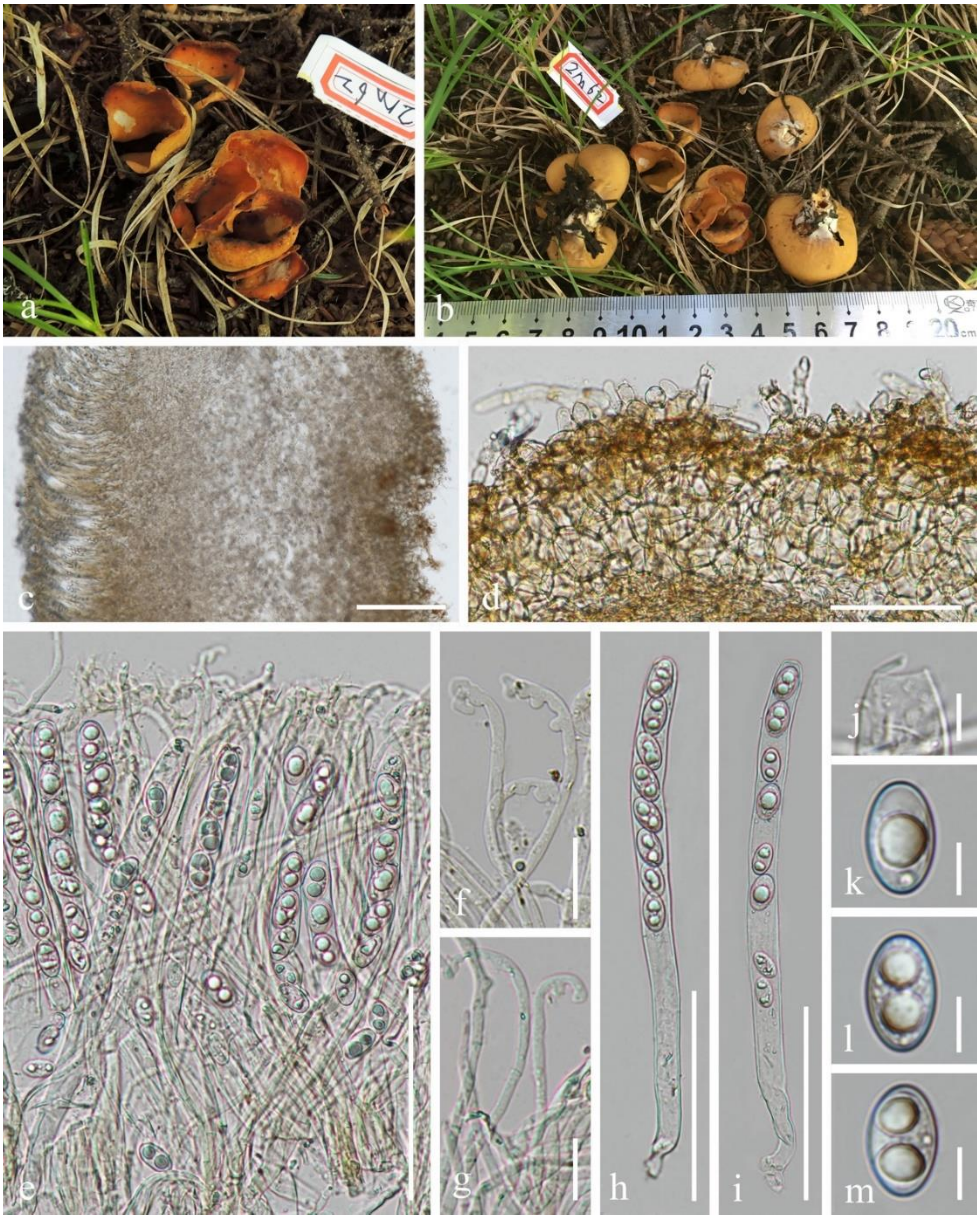

Figure 9 – *Otidea macrospora* (HKAS 104688, holotype). a, b Fresh specimens. c Vertical section of ascomata. d Ectal excipulum. e Asci and paraphyses. f, g Apices of paraphyses. h, i Asci. j Apex of an ascus. k–m Ascospores. Scale bars: c = 200 µm, d, e, h, i = 100 µm, f, g = 20 µm, j–m = 10 µm.

Material examined – China, Sichuan province, Jiuzhai valley, on mossy soil under a mixed coniferous broad-leaved forest, elev. 3559 m asl., 20 August 2018, Ming Zeng, ZM 52 (HKAS 104680).

GenBank accession numbers – HKAS 104680 (LSU: OP291070; *tef-1α*: OP352500; *rpb2*: OP352526; SSU: OP291020).

Notes – This species was established by Harmaja (2009) for the illegitimate *O. olivacea* J.Z.Cao & L.Fan (Cao et al. 1990). The latter was earlier introduced by Bucholtz (1897). This species is mainly distinguished by its olive-brown hymenium, ellipsoid to oblong ascospores (Zhuang 2014). Our collection grouped with *Otidea olivaceobrunnea* (HMAS 23948), further highly supported as a sister taxon to *Otidea purpureogrisea* (Fig. 5).

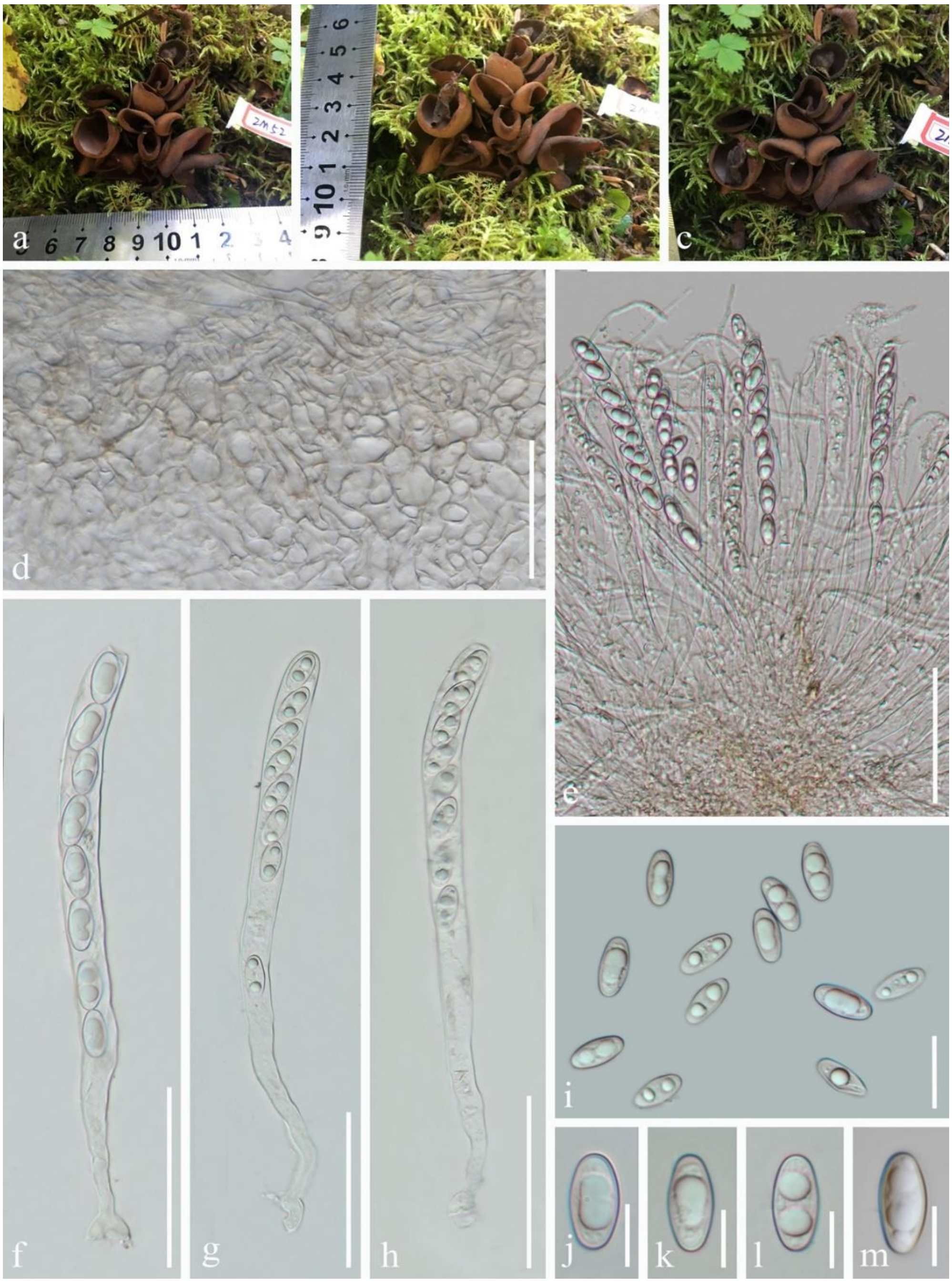

Figure 10 – ***Otidea olivaceobrunnea*** **(**HKAS 104680). a–c Fresh specimens. d Ectal excipulum close to the base. e Asci and paraphyses. f–h Asci. i–m Ascospores. Scale bars: d–h = 50 µm, i = 20 µm, j–m = 10 µm.

Otidea ovalispora M. Zeng, Q. Zhao & K.D. Hyde, sp. nov. Fig. 11

Index Fungorum number: IF 900176; Facesoffungi number: FoF 12602

Etymology – The epithet refers to the ellipsoid shape of ascospores.

Holotype – HKAS 104658

Figure 11 – *Otidea ovalispora* (HKAS 104658, holotype). a–c Fresh specimens. d Stipal ecto-excipulum. e Ectal excipulum. f Asci and paraphyses. g–i Asci. j Apex of an ascus. k–m Ascospores. Scale bars: d–i = 50 µm, j–m = 5 µm.

Diagnosis – This species is characterized by ear-shaped apothecia with a stalk, yellow ocher receptacle surface and hymenium, curved paraphyses without or with 1−3 low notches, and ellipsoid ascospores.

Saprobic on soil. Sexual morph: *Apothecia* 0.5−2.5 cm broad, 1.5−3.5 cm high, scattered to gregarious, ear-shaped, split, stipitate. *Stipe* 2−8 mm broad, 0.6−2 cm long, terete, solid, yellow ocher, nearly smooth, basal with white to cream tomentum and mycelium. *Receptacle surface* yellow ocher, mostly concolorous with hymenium, margin mostly deeply split on one side, sometimes split in excess. *Hymenium* 160−190 µm thick, yellow ocher, nearly smooth. *Subhymenium* ca. 80 µm thick, distinct, and visible as a darker zone of densely arranged cylindrical to swollen cells. *Stipal ecto-excipulum* 30−70 µm thick, of *textura angularis* to *textura globulosa*, brownish to brown, composed of 10−16 × 7−10 µm cells, with hyphoid hairs, abundant close to the base, 2−3 µm broad, brownish, septate, present yellow-brown resinous exudates. *Ectal excipulum* 50−100 µm thick, composed of *textura angularis* to *textura globulosa*, 16−24 × 13−20 µm cells, yellow to brownish, present yellow-brown resinous exudates, with 5−7 µm, short hyphoid hairs. *Medullary excipulum* 130−170 µm thick, composed of *textura intricata*, 3−6 µm broad, hyaline to yellowish hyphae, present yellow-brown resinous exudates. *Paraphyses* 2−3 µm broad, yellowish, filiform, mostly curved at the apex, without or with 1−3 low notches close to the apex. *Asci* 155−178 × 10−11.5 µm, 8-spored, cylindrical, operculate, inamyloid, with a long pedicel and a crozier at the base. *Ascospores* [20/1/1, in H_2O] (9.7−) 9.6−11.2 (−13.1) × (5.4−) 5.6−6.3 (−7) µm (Q = 1.64−2.06, **Q** = 1.76±0.11), ellipsoid, hyaline, uniseriate, equilateral, rarely slightly inequilateral, rounded at the ends, uniguttulate to biguttulate, smooth. Asexual morph: Undetermined.

Material examined – China, Yunnan province, Shangri-La, on soil under a mixed coniferous broad-leaved forest, elev. 3550 m asl., 15 August 2018, Ming Zeng, ZM 19 (HKAS 104658, holotype); *ibid.*, elev. 3652 m asl., 15 August 2018, Ming Zeng, ZM 31 (HKAS 124368, paratype).

GenBank accession numbers – HKAS 104658 (LSU: OP291071; *rpb2*: OP352527; SSU: OP291021), HKAS 124368 (LSU: OP291072; *tef-1α*: OP352501; *rpb2*: OP352528; SSU: OP291022).

Notes – This species is sister to another new species, *Otidea macrospora* introduced in this study, and further clades with *Otidea pseudoformicarum* (Fig. 5). Although our species is morphologically similar to *Otidea pseudoformicarum* in having an excipulum with resinous exudates and similar ascospores, it differs in that it has substipitate apothecia, smaller asci (115–150 × 7–10 µm), and straight paraphyses (Hyde et al. 2018). Based on these, we introduce the new species *O. ovalispora* here.

Otidea propinquata (P. Karst.) Harmaja, Karstenia 15: 32 (1976) Fig. 12

Index Fungorum number: IF 319059; Facesoffungi number: FoF 12754

Saprobic on soil. Sexual morph: *Apothecia* 1.5−3 cm broad, 2−3 cm high, scattered to gregarious, broadly cup-shaped, substipitata, basal with white to brownish tomentum and mycelium. *Receptacle surface* dark brown, furfuraceous, margin entire, rarely split. *Hymenium* 230−275 µm thick, dark brown, same in color as receptacle surface, nearly smooth. *Subhymenium* ca. 90 µm thick, distinct, and visible as a darker zone of densely arranged cylindrical to swollen cells. *Ectal excipulum* 60−150 µm, composed of *textura angularis* to *textura globulosa*, 23−30 × 19−23 µm cells, yellow to brown, present resinous exudates, with 5−6 µm, short, yellow to brown hyphoid hairs. *Medullary excipulum* 250−400 µm thick, composed of *textura intricata*, 4−8.5 µm broad, yellow to brownish hyphae. *Paraphyses* 2−3.5 µm broad, yellow, filiform, mostly curved at the apex, with 1−4 district notches close to the apex. *Asci* 210−260 × 14−17 µm, 8-spored, cylindrical, operculate, inamyloid, with a long pedicel and a crozier at the base. *Ascospores* [20/1/1, in H_2O] (18−) 18.5−20.2 (−20.8) × (10.5−) 11−11.8 (−12) µm (Q = 1.62−1.84, **Q** = 1.70±0.06), ellipsoid to broadly ellipsoid, hyaline, uniseriate, equilateral, rounded at the ends, uniguttulate to biguttulate, sometimes with additional smaller granules, smooth, sometimes with one de Bary bubble. Asexual morph: Undetermined.

Material examined – China, Sichuan province, Jiuzhai valley, on mossy soil under a mixed coniferous broad-leaved forest, elev. 3247 m asl., 20 August 2018, Ming Zeng, ZM 68 (HKAS 104694).

GenBank accession numbers – HKAS 104694 (LSU: OP291073; SSU: OP291023).

Notes – This species is morphologically easily identified by its broadly cup-shaped, dark brown apothecia with substipitate to stipitate, notched paraphyses with yellow pigments and large ellipsoid ascospores (Olariaga et al. 2015). Our collection clusters with the other two *Otidea propinquata* strains forming a high-supported (100BS/1.00PP) and independent clade within *Otidea* (Fig. 5).

Otidea subleporina M. Zeng, Q. Zhao & K.D. Hyde, sp. nov. Fig. 13

Index Fungorum number: IF 900177; Facesoffungi number: FoF 12603

Etymology – The epithet refers to morphological traits similar to *Otidea leporina*.

Holotype – HKAS 104663

Diagnosis – This species has relatively narrow ear-shaped apothecia with a stalk, concolorous receptacle and hymenium, curved paraphyses with notches, and ellipsoid, guttulate ascospores.

Saprobic on soil. Sexual morph: *Apothecia* 5−8 mm broad, 2.5−3 cm high, scattered to gregarious, ear-shape, split, stipitate. *Stipe* 3−5 mm broad, ca. 2 cm long, terete, solid, brown, nearly smooth, basal with white to cream tomentum and mycelium. *Receptacle surface* brown, mostly concolorous with hymenium, margin involute, mostly deeply split on one side. *Hymenium* ca. 180

µm thick, brown, nearly smooth. *Subhymenium* ca. 70 µm thick, distinct, and visible as a darker zone of densely arranged cylindrical to swollen cells. *Stipal ecto-excipulum* 75−130 µm thick, of *textura angularis* to *textura globulosa*, brownish to brown, composed of 20−30 × 15−19 µm cells, with hyphoid hairs, abundant close to the base, composed of 3−7 µm wide, hyaline to brownish, septate. *Ectal excipulum* 60−120 µm thick, composed of *textura angularis* to *textura globulosa*, 14−19 × 11−14 µm cells, yellow to brownish, with yellow-brown resinous exudates, some outer globose cells irregularly loosely aggregate to a pruinose-like surface, rarely with 4−9 µm, short, swollen hyphoid hairs. *Medullary excipulum* 150−300 µm thick, composed of *textura intricata*, 4−8 µm broad hyaline to brownish hyphae, present yellow-brown resinous exudates. *Paraphyses* 2−3 µm broad, with yellowish contents, filiform, mostly deeply curved at the apex, sometimes with up to 3 low notches close to the apex. *Asci* 155−175 × 10−12 µm, 8-spored, cylindrical, operculate, inamyloid, with a long pedicel and a crozier at the base. *Ascospores* [20/1/1, in H_2O] (9.1−) 10.3−12.8 (−13.8) × (5.8−) 6.1−7.9 (−9.8) µm (Q = 1.38−1.89, **Q** = 1.66±0.15), ellipsoid, hyaline, uniseriate, equilateral, rounded at the ends, uniguttulate to biguttulate, smooth. Asexual morph: Undetermined.

Figure 12 – *Otidea propinquata* (HKAS 104694). a Fresh specimen. b Ectal excipulum. c Asci and paraphyses. d, e Apices of paraphyses. f, g Asci. h Apex of an ascus. i–k Ascospores. Scale bars: b, c, f, g = 50 µm, d, h–k = 10 µm, e = 20 µm.

Material examined – China, Yunnan province, Shangri-La, on mossy soil under a mixed coniferous broad-leaved forest, elev. 3634 m asl., 15 August 2018, Ming Zeng, ZM 29 (HKAS 104663, holotype); China, Sichuan province, S301, on soil under a mixed coniferous broad-leaved forest, elev. 3519 m asl., 20 August 2018, Ming Zeng, ZM 60 (HKAS 124369, paratype).

GenBank accession numbers – HKAS 104663 (LSU: OP291074; *tef-1α*: OP352502; *rpb2*: OP352529; SSU: OP291024), HKAS 124369 (LSU: OP291075; SSU: OP291025).

Notes – Phylogenetic analyses of *Otidea* (Fig. 5) show a sister relationship to *Otidea leporina*. Besides, these two species cluster with another morphologically similar species *Otidea pseudoleporina*, forming a district clade in *Otidea* (Fig. 5). While *Otidea leporina* and *Otidea pseudoleporina* differ in their larger apothecia, and darker hymenium than the receptacle. In addition, our new species has slightly broader asci (10−12 µm) compared to *Otidea leporina* (9−10.5 µm) and *Otidea pseudoleporina* (9−10 µm) (Olariaga et al. 2015). These differences support the establishment of the new species herein.

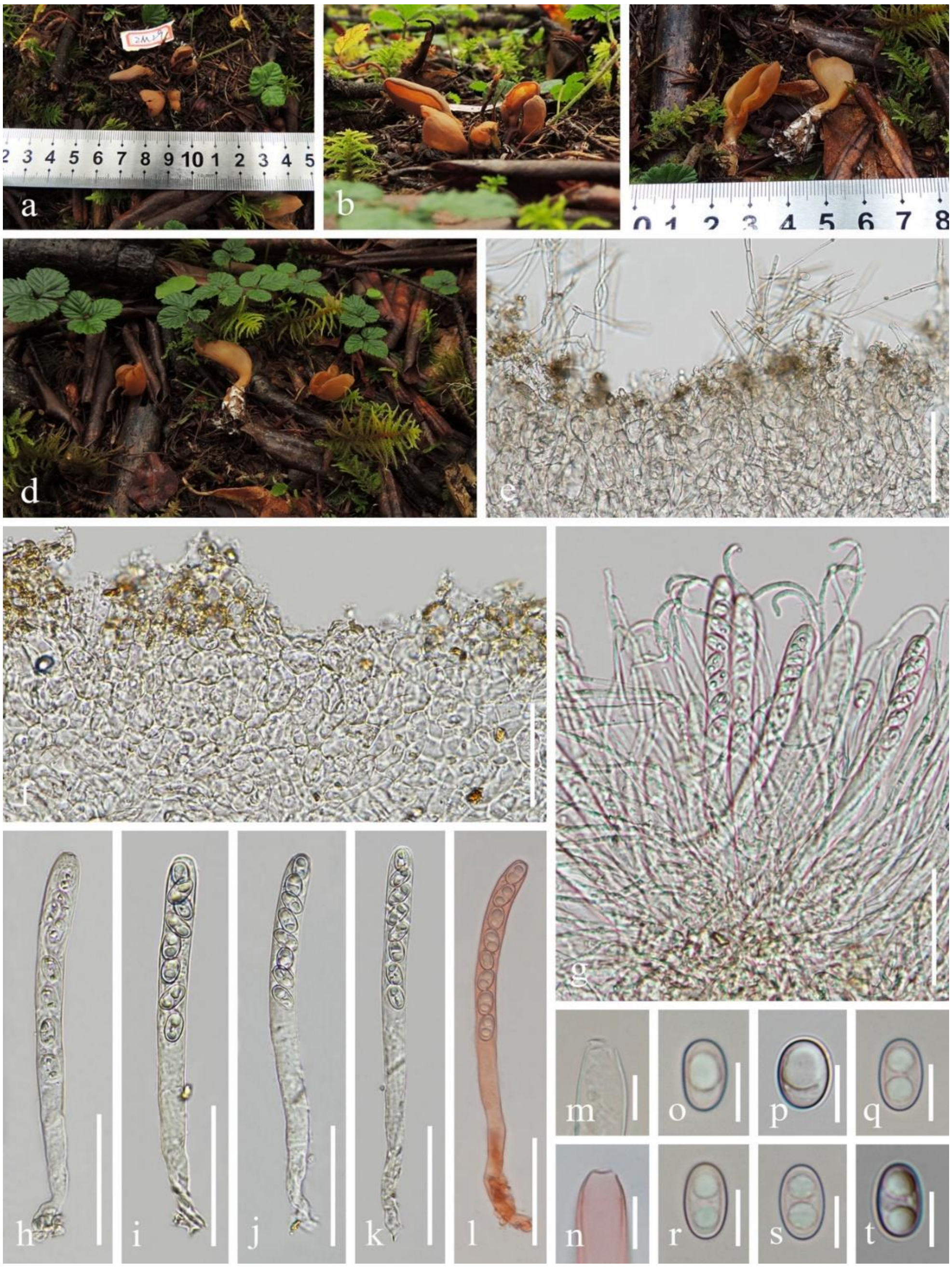

Figure 13 – *Otidea subleporina* (HKAS 104663, holotype). a–d Fresh specimens. e Stipal ecto-excipulum. f Ectal excipulum. g Asci and paraphyses. h–k Asci. l Ascus in Congo red. m Apex of ascus. n Apex of ascus in Congo red. o–t Ascospores. Scale bars: e, f = 100 µm, g–l = 50 µm, m–t = 10 µm.

Pyronemataceae Corda [as ‘Pyronemaceae’], Anleit. Stud. Mykol., Prag: 149 (1842)

Index Fungorum number: IF 81322; Facesoffunginumber: FoF 04243

Type genus – ***Pyronema*** Carus

Notes – This family is highly diverse morphologically and ecologically, containing larger taxa from epigeous to hypogeous, even cleistothecial. The most recently accepted circumscription of *Pyronemataceae* accepted 70 genera (Wijayawardene et al. 2020, 2022), including some new genera, which were established recently (Hansen et al. 2013, Lindemann et al. 2022). In this study, the members of this family are reduced to approximately 60 genera based on the acceptance of *Otideaceae* as defined by Ekanayaka et al. (2018) and the segregation of the new family *Pyropyxidaceae*.

Aleurina Massee, Bull. Misc. Inf., Kew (no. 138): 131 (1898)

Index Fungorum number: IF 25886

Type species – ***Aleurina tasmanica*** Massee

Notes – This genus is recognized by cupulate to discoid apothecia, olivaceous, green-brown to brown hymenium, brown to red-brown receptacle surface, ellipsoid and guttulate ascospores with ornamentation (Zhuang & Korf 1986, Zhuang 2014). This genus is mostly found in soil but was also reported from rotten wood (Zhuang & Korf 1986). Eleven species are accepted in this genus. Zhuang & Korf (1986) contributed the most valuable monograph to date, which includes ten species. The eleventh species was introduced by Dougoud & Roffler (2006).

Aleurina imaii (Korf) W.Y. Zhuang & Korf, Mycotaxon 26: 374 (1986) Fig. 14

Index Fungorum number: IF 103019; Facesoffungi number: FoF 04247

Saprobic on soil. Sexual morph: *Apothecia* up to 15 mm broad, 8 mm high, scattered to gregarious, sessile. *Receptacle* concave to shallow cupulate, receptacle surface olivaceous to pale brown or green-brown, with pustule, margin conspicuous, entire, slightly involute. *Hymenium* 250−270 µm thick, green-brown to brown, darker than receptacle surface, nearly smooth. *Subhymenium* ca. 55 µm thick, distinct, and visible as a darker zone. *Ectal excipulum* 90−200 µm thick, composed of *textura angularis* to *textura globulosa*, 20−27 × 16−21 µm cells, outmost cells darker brown, middle cells olivaceous to green, innermost cells pale brown to deep yellow, with 3−5 µm broad, hyphoid hairs, abundant close to the base, pale brown, septate, with a rounded end. *Medullary excipulum* 150−280 µm thick, composed of *textura intricata*, 3−5 µm broad yellow hyphae. *Paraphyses* 3−5 µm broad, filiform, straight, with yellow to brown contents, apex enlarged slightly, 5−7 µm broad. *Asci* 225−260 × 14−18 µm, 8-spored, cylindrical, operculate, inamyloid, with a long pedicel and a crozier at the base. *Ascospores* [20/1/1, in H_2O] (19.5−) 19.9 −21.3 (−22) × (10.6−) 11.1−12.3 (−13.5) µm (Q = 1.53−2.01, **Q** = 1.76±0.1) (excluding ornamentation), ellipsoid, uniseriate, equilateral, biguttulate, rounded at the ends, ornamented with round warts, 1−2 µm broad, up to 2 µm high. Asexual morph: Undetermined.

Material examined – China, Sichuan province, G318, on soil under a broad-leaved forest, 12 August 2021, Song Wang, ZM 382 (HKAS 124375); *ibid.*, ZM 384 (HKAS 124377).

GenBank accession numbers – HKAS 124375 (LSU: OP291076; *tef-1α*: OP352503; *rpb2*: OP352530; SSU: OP291026), HKAS 124377 (LSU: OP291077; *tef-1α*: OP352504; *rpb2*: OP352531; SSU: OP291027).

Notes – This species is recognized by olivaceous to brown apothecia, deep-colored excipulum and paraphyses, ellipsoid, guttulate ascospores with distinct warts (Zhuang 2014). Our two collections strongly group (100BS/1.00PP) with *Aleurina imaii* (HMAS 57707) forming a distinct subclade within *Aleurina* (Fig. 1).

Cheilymenia Boud., Bull. Soc. mycol. Fr. 1: 105 (1885)

Index Fungorum number: IF 990

Type species – ***Cheilymenia stercorea*** (Pers.) Boud.

Notes – This genus features yellow to orange or red-orange apothecia with setaceous hairs. Setae are typically straight, brown, septate, with simple or furcate basal, forming from the inner excipulum. Ascospores are ellipsoid to oblong, normally unguttulate, with refractive contents (Zhuang 2014). This genus contains more than 60 genera, with approximately ten having molecular data. In our phylogenetic analysis and others (Perry et al. 2007, Hansen et al. 2013), *Cheilymenia* is not monophyletic. Most strains are grouped into one clade, while *C. fimicola* (BAP 432) and *C. stercoraria* (U.L.240) are phylogenetically close to *Scutellinia* (Fig. 5).

Figure 14 – ***Aleurina imaii***. a–e Fresh specimens (a–c HKAS 124375. d, e HKAS 124377). f Ectal excipulum and part medullary excipulum. g Asci and paraphyses. h–j Asci. k–m Ascospores. n Ascospore in Cotton blue. Scale bars: f–j = 100 µm, k–n = 10 µm.

Cheilymenia vitellina (Pers.) Dennis, British Cup Fungi & their Allies: 27 (1960) Fig. 15

Index Fungorum number: IF 328161; Facesoffungi number: FoF 12596

Saprobic on soil. Sexual morph: *Apothecia* up to 8 mm broad, 2−3 mm high, solitary, sessile, setose. *Receptacle* shallowly discoid to cupulate, receptacle surface concolorous with the hymenium, sparsely covered setaceous hairs, margin conspicuous, entire, sometimes involute, with abundant setae. *Hymenium* ca. 230 µm thick, bright orange, nearly smooth. *Ectal excipulum* 95−215 µm thick, composed of *textura angularis* to *textura globulosa*, 22−36 × 18−29 µm cells, pale brown or yellow to yellowish, with setae from the inner layer, up to 550 µm long, up to 35 µm broad at the base, pale brown, septate, with obtuse ends, simple or sometimes branched once at the base. *Medullary excipulum* 100−190 µm thick, composed of *textura intricata*, 4−7 µm broad hyaline hyphae.

Paraphyses 3−5 µm broad, with pale brown to yellow pigments, filiform, apex enlarged slightly, 4−5.5 µm broad. *Asci* 175−200 × 10−13 µm, 8-spored, cylindrical, operculate, inamyloid, with a long pedicel and a crozier at the base. *Ascospores* [20/1/1, in H_2O] (16−) 16.1−17.5 (−18.8) × (7−) 8−9.2 (−9.4) µm (Q = 1.76−2.32, **Q** = 1.96±0.12), ellipsoid, uniseriate, equilateral, rounded at the ends, refractive, smooth, containing 1−2 de Bary bubbles. Asexual morph: Undetermined.

Material examined – China, Yunnan province, Shangri-La, on the soil where morels are cultivated, elev. 3321 m asl., 14 August 2018, Ming Zeng, ZM 04 (HKAS 104645); *ibid.*, ZM 05 (HKAS 104646).

GenBank accession numbers – HKAS 104645 (LSU: OP291078; *tef-1α*: OP352505; *rpb2*: OP394213; SSU: OP291028), HKAS 104646 (LSU: OP291079; *tef-1α*: OP352506; *rpb2*: OP394214; SSU: OP291029).

Notes – This species is recognized by yolk-yellow apothecia with setaceous hairs, pigmented paraphyses, and ellipsoid ascospores with smooth-walled. Our species group with another Danish *Cheilymenia vitellina* (Perry et al. 2007) with strong support (100BS/1.00PP), and there are no significant morphological differences between our species with *C. vitellinia* (Kaya et al. 2016). Hence, we accept these two strains as *C. vitellina*.

Figure 15 – *Cheilymenia vitellina*. a–d Fresh specimens (a, b HKAS 104645. c, d HKAS 104646). e Ectal excipulum. f Seta. g Asci and paraphyses. h, i Asci. j Ascus in Cotton blue. k Apex of ascus in Cotton blue. l–o Ascospores. Scale bars: e, g–j = 50 µm, f = 100 µm, k–o = 10 µm.

Humaria Fuckel, Jb. nassau. Ver. Naturk. 23-24: 320 (1870) [1869-70]

Index Fungorum number: IF 2375

Type species – ***Humaria hemisphaerica*** (F.H. Wigg.) Fuckel

Notes – This genus has deep cupulate, sessile apothecia with setae, grey-white or pale brown hymenium, ellipsoid, and guttulate ascospores with ornamentations (Zhuang 2014). *Humaria* was used to define two genera with different concepts by Fuckel (1870) and Boudier (1885), until McNeill et al. (2006) substantiated the legitimacy of *Humaria* Fuckel. Nonetheless, several issues remain unresolved in *Humaria*. Currently, 17 estimated species are recognized within this genus (Kirk et al. 2008, Niazi et al. 2021).

Humaria hemisphaerica (F.H. Wigg.) Fuckel, Jb. nassau. Ver. Naturk. 23-24: 322 (1870) [1869-70] Fig. 16

Index Fungorum number: IF 120602; Facesoffungi number: FoF 04249

Saprobic on soil. Sexual morph: *Apothecia* 0.5−2 cm broad, 0.5−1.5 cm high, scattered to gregarious, cupulate, with brown, rigid, straight, tapering hairs, sessile. *Receptacle* deeply concave, receptacle surface yellow-brown to brown, covered brown setae, margin conspicuous, entire, with abundant setae. *Hymenium* ca. 300 µm thick, grey-white, nearly smooth. *Subhymenium* 40−65 µm thick, distinct, and visible as a darker zone. *Ectal excipulum* 110−200 µm, of *textura angularis* to *textura globulosa*, 27−36 × 21−29 µm, hyaline to yellowish, with setae from outer layer, up to 1000 µm long, 20 µm broad at the base, brown, septate, with a pointed end. *Medullary excipulum* 55−100 µm thick, composed of *textura intricata*, 3−6 µm broad hyaline hyphae. *Paraphyses* 2−3 µm broad, filiform, hyaline, apex enlarged, 6−10 µm broad. *Asci* 210−250× 15−20 µm, 8-spored, cylindrical, operculate, inamyloid, with a long pedicel and a crozier at the base. *Ascospores* [20/1/1, in H_2O] (20.3–) 21−23.4 (−25.2) × (11.4–) 12.1−13.4 (−13.9) µm (Q = 1.59−1.98, **Q** = 1.61±0.11), ellipsoid, hyaline, uniseriate, equilateral, rounded at the ends, uniguttulate, ornamented with irregular small warts. Asexual morph: Undetermined.

Material examined – China, Yunnan province, Shangri-La, on mossy soil under a mixed coniferous broad-leaved forest, elev. 3652 m asl., 15 August 2018, Ming Zeng, ZM 14 (HKAS 104654); China, Sichuan province, Jiuzhai valley, on mossy soil under a mixed coniferous broad-leaved forest, elev. 3247 m asl., 20 August 2018, Ming Zeng, ZM 69 (HKAS 104695); China, Yunnan province, Kunming, Kunming Institute of Botany, on soil, elev. 1892 m asl., 23 September 2021, Hongli Su, ZM392 (HKAS 124378).

GenBank accession numbers – HKAS 104654 (LSU: OP291080; *tef-1α*: OP352507; *rpb2*: OP394215; SSU: OP291030), HKAS 104695 (LSU: OP291081; *tef-1α*: OP352508; *rpb2*: OP394216; SSU: OP291031), HKAS 124378 (LSU: OP291082; *tef-1α*: OP352509; *rpb2*: OP394217; SSU: OP291032).

Notes – This is a common species with worldwide distribution. It is distinguished by deeply concave apothecia with brown setose hairs, grey-white hymenium, ellipsoid, guttulate ascospores with small warts. In our phylogenetic analysis, the three new collections clade within the other two *Humaria hemisphaerica* strains in a clade of maximum support (100BS/1.00PP) (Fig. 1). So, we identified these three collections as *H. hemisphaerica* here.

Melastiza Boud., Bull. Soc. mycol. Fr. 1: 106 (1885)

Index Fungorum number: IF 3097

Type species – ***Melastiza cornubiensis*** (Berk. & Broome) J. Moravec

Notes – This genus is distinguished by yellow, orange to red apothecia with short, brown to yellow-brown hairs, guttulate, reticulate or warty ascospores (Zhuang 2014). Previously, except for the vague and insufficient descriptions of *Melastiza laxmannii* and *Melastiza phaeoloma* (Boudier 1907), nine additional *Melastiza* species were accepted and divided into two groups based on the ornamentations of ascospores: 1). Ascospores with coarsely raised reticulum, containing *Melastiza carbonicola* (Moravec 1972), *Melastiza cornubiensis* (Moravec 1992, 1994), *Melastiza latispora* (Moravec 1994, Van Vooren 2017), *Melastiza rozei* (Yao & Spooner 1995a), *Melastiza rubra* (Mass Geesteranus 1967), *Melastiza tetraspora* (Dissing 1993); 2). Ascospores with warts and pustules, containing *Melastiza boudieri* (Le Gal 1958), *Melastiza contorta* (Yao & Spooner 1995b), *Melastiza flavorubens* (Korf 1971, Moravec 1994). Moravec (1994) hypothesized the close relationships between *Melastiza* and *Aleuria*, and their receptacle characteristics were insufficient for generic delimitation. Thus, *Melastiza* was merged into the genus *Aleuria* as one of its subgenera (Moravec 1994). Nonetheless, most authors insisted that *Melastiza* be an independent genus in *Pyronemataceae* based on the differences in micromorphology (Mass Geesteranus 1967, Yao & Spooner 1995b, Zhuang 2014, Van Vooren 2017, Šandová 2019). In the phylogenetic analyses, *Aleuria* is monophyletic nesting within *Melastiza* (Perry et al. 2007, Hansen et al. 2013, Van Vooren et al. 2015a), and this is also confirmed in our study (Fig. 1). *Melastiza* is not monophyletic with strains dispersing across the tree (Fig. 1) confirming previous studies (Hansen et al. 2013).

Figure 16 – *Humaria hemisphaerica*. a–f Fresh specimens (a–c HKAS 104654. d, e HKAS 104695. f HKAS 124378). g Setae. h Ectal excipulum and hairs in Cotton blue. i Asci and paraphyses.

j–l Asci. m–p Ascospores. q Ascospore in Cotton blue. Scale bars: c = 1000 µm, g = 200 µm, h–l = 100 µm, m–q = 15 µm.

Melastiza cornubiensis (Berk. & Broome) J. Moravec, Mycotaxon 44(1): 68 (1992) Fig. 17

Index Fungorum number: IF 358476; Facesoffungi number: FoF 12597

Saprobic on sandy soil. Sexual morph: *Apothecia* 2−15 mm broad, 1−2 mm high, scattered to gregarious, sessile, pubescent. *Receptacle* discoid to shallowly saucer-shaped, receptacle surface red-brown, darker in color than hymenium, covered setaceous hairs, margin conspicuous, entire. *Hymenium* 230−260 µm thick, orange to red, nearly smooth. *Ectal excipulum* 70−270 µm thick, composed of *textura angularis* to *textura globulosa*, 29−37 × 24−30 µm cells, hyaline to brownish, with 55−140 µm long, 5−11 µm broad setaceous hairs, arising from outer layer, brown, septate, rounded end. *Medullary excipulum* 60−170 µm thick, composed of *textura intricata*, 5−10 µm broad, hyaline to brownish hyphae. *Paraphyses* 2−4 µm broad, subhyaline to brownish, filiform, apex enlarged, 5−7 µm broad. *Asci* 216−245 × 11−14 µm, 8-spored, cylindrical, operculate, inamyloid, with a long pedicel and a crozier at the base. *Ascospores* [20/1/1, in H_2O] (16.1−) 16.6−18.5 (−20) × (9.1−) 9.7−10.6 (−10.9) µm (Q = 1.52−1.96, **Q** = 1.73±0.1) (excluding ornamentation), ellipsoid, uniseriate, equilateral, rounded at the ends, biguttulate, ornamented with cyanophilous raised reticulum, ca. 0.5 µm broad. Asexual morph: Undetermined.

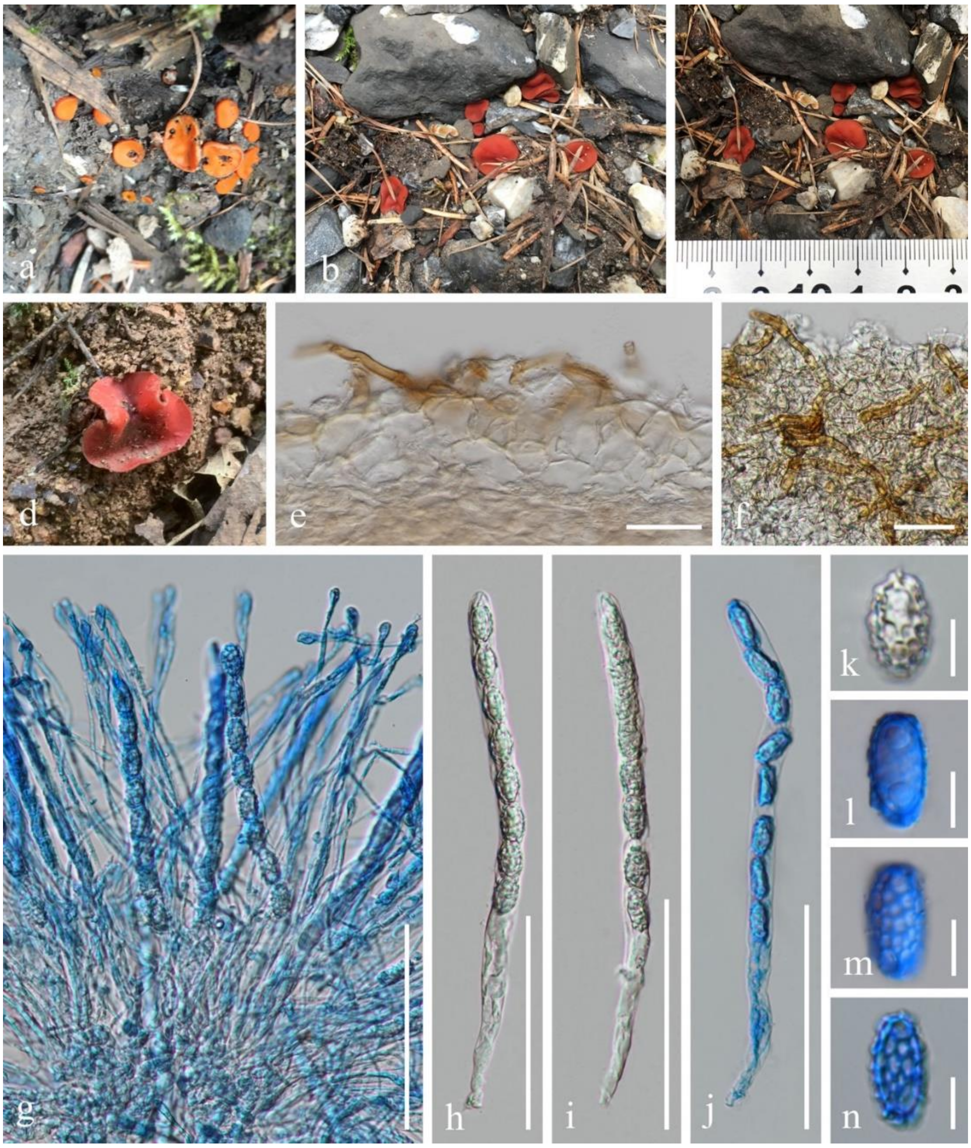

Figure 17 – *Melastiza cornubiensis*. a–d Fresh specimens (a HKAS 104702. b, c HKAS 104703. d HKAS 124379). e, f Ectal excipulum and hairs. g Asci and paraphyses in Cotton blue. h, i Asci. j Ascus in Cotton blue. k Ascospore. l–n Ascospores in Cotton blue. Scale bars: e, f = 50 µm, g–j = 100 µm, k–n = 10 µm.

Material examined – China, Sichuan province, Jiuzhai valley, on sandy soil, elev. 2751 m asl., 21 August 2018, Ming Zeng, ZM 77 (HKAS 104702); *ibid*., ZM 78 (HKAS 104703); China, Yunnan province, Kunming, on sandy soil, elev. 1950 m asl., 21 November 2021, Shucheng He, ZM 396 (HKAS 124379).

GenBank accession numbers – HKAS 104702 (LSU: OP291083; *tef-1α*: OP352510; *rpb2*: OP394218; SSU: OP291033), HKAS 104703 (LSU: OP291084; *tef-1α*: OP352511; *rpb2*: OP394219; SSU: OP291034), HKAS 124379 (LSU: OP291085; *tef-1α*: OP352512; *rpb2*: OP394220; SSU: OP291035).

Notes – This species is recognized by yellow to orange or red, discoid apothecia, brown setae with rounded ends, filiform paraphyses with enlarged apex, and reticulate, biguttulate ascospores. We collected three samples that are anatomically consistent with *Melastiza cornubiensis*, while there are some differences in the color of apothecia. In the phylogenetic tree, the three strains cluster with two *Melastiza cornubiensis* strains forming a clade with maximum statistical support.

Melastiza verruculosa M. Zeng, Q. Zhao & K.D. Hyde, sp. nov. Fig. 18

Index Fungorum number: IF 900178; Facesoffungi number: FoF 12598

Etymology: The epithet refers to its ascospores with pustules.

Holotype: HKAS 124366

Diagnosis – This species is distinguished by orange sessile apothecia with setaceous hairs, pigmented paraphyses, uniguttulate ascospores ornamented by distinctly rounded pustules connecting with ridges.

Saprobic on sandy soil. Sexual morph: *Apothecia* 3−7 mm broad, 0.5−1.5 mm high, scattered to gregarious, sessile, pubescent, basal with brownish mycelia. *Receptacle* discoid to shallowly saucer-shaped, receptacle surface darker in color than hymenium, brown when dry, covered setaceous hairs, margin conspicuous, entire. *Hymenium* ca. 320 µm thick, orange when fresh, yellow to orange when dry, nearly smooth. *Ectal excipulum* 40−200 µm thick, composed of *textura angularis* to *textura globulosa*, 19−25 × 12−17 µm cells, inner cells hyaline, outermost cells brown, with 40−200 µm long, 7−11 µm broad setaceous hairs, dark brown, septate, obtuse end; basal with 9−11 µm broad, brown hyphoid hairs. *Medullary excipulum* 30−200 µm thick, composed of *textura intricata*, 2−4 µm broad hyaline hyphae. *Paraphyses* 2−4 µm broad, subhyaline to yellowish, filiform, apex enlarged, 5−8 µm broad. *Asci* 250−270 × 11−15 µm, 8-spored, cylindrical, operculate, inamyloid, with a long pedicel and a crozier at the base. *Ascospores* [20/1/1, in H_2O] (13.7−) 14.4−16.3 (−17.3) × (9.5−) 10−10.8 (−11) µm (Q = 1.31−1.69, **Q** = 1.47±0.09) (excluding ornamentation), ellipsoid, uniseriate, equilateral, rounded at the ends, uniguttulate, rarely biguttulate, cyanophilous ornamented with mostly rounded pustules, up to 2.5 µm high, 3.0 µm broad, connecting by narrow ridges, pustules at poles of ascospores are enlarged and form spherical apiculi, up to 3.5 µm high, 4.5 µm broad. Asexual morph: Undetermined.

Material examined – China, Yunnan province, Xishuangbanna, Jinghong, on sandy soil under a broad-leave forest, elev. 683 m asl., 10 June 2018, Ming Zeng, Zeng 018 (HKAS 124366, holotype); *ibid*., elev. 568 m asl., 11 June 2018, Ming Zeng, Zeng 025 (HKAS 124367, paratype).

GenBank accession numbers – HKAS 124366 (LSU: OP291086; *tef-1α*: OP352513; *rpb2*: OP394221; SSU: OP291036), HKAS 124367 (LSU: OP291087; *rpb2*: OP394222; SSU: OP291037).

Notes – Our new species is similar to *M. boudieri*, *M. contorta*, and *M. flavorubens* in having pustulate ascospores. Compared to *M. boudieri* which lacks molecular data, *M. boudieri* has reddish apothecia and larger ascospores (18.5 × 10.5 µm) (Moravec 1994). Besides, *M. contorta* which is phylogenetically sister to *Pseudaleuria*, has irregularly warty ascospores, only rarely rounded (Yao & Spooner 1995b). *Melastiza flavorubens* differs in that it has fine pustules, and ascospores with a cluster of small oil drop at each end (Maas Geesteranus 1975). Our new species (represented by two strains) grouped with *M. flavorubens* forming a clade, which is sister to *Spooneromyces* (91BS/0.93PP). Based on both morphological and phylogenetic evidence, the new species *M. verruculosa* was introduced in this study. This is the third *Melastiza* species found in China, after *M. cornubiensis* and *M. rubra* (Zhuang 2014).

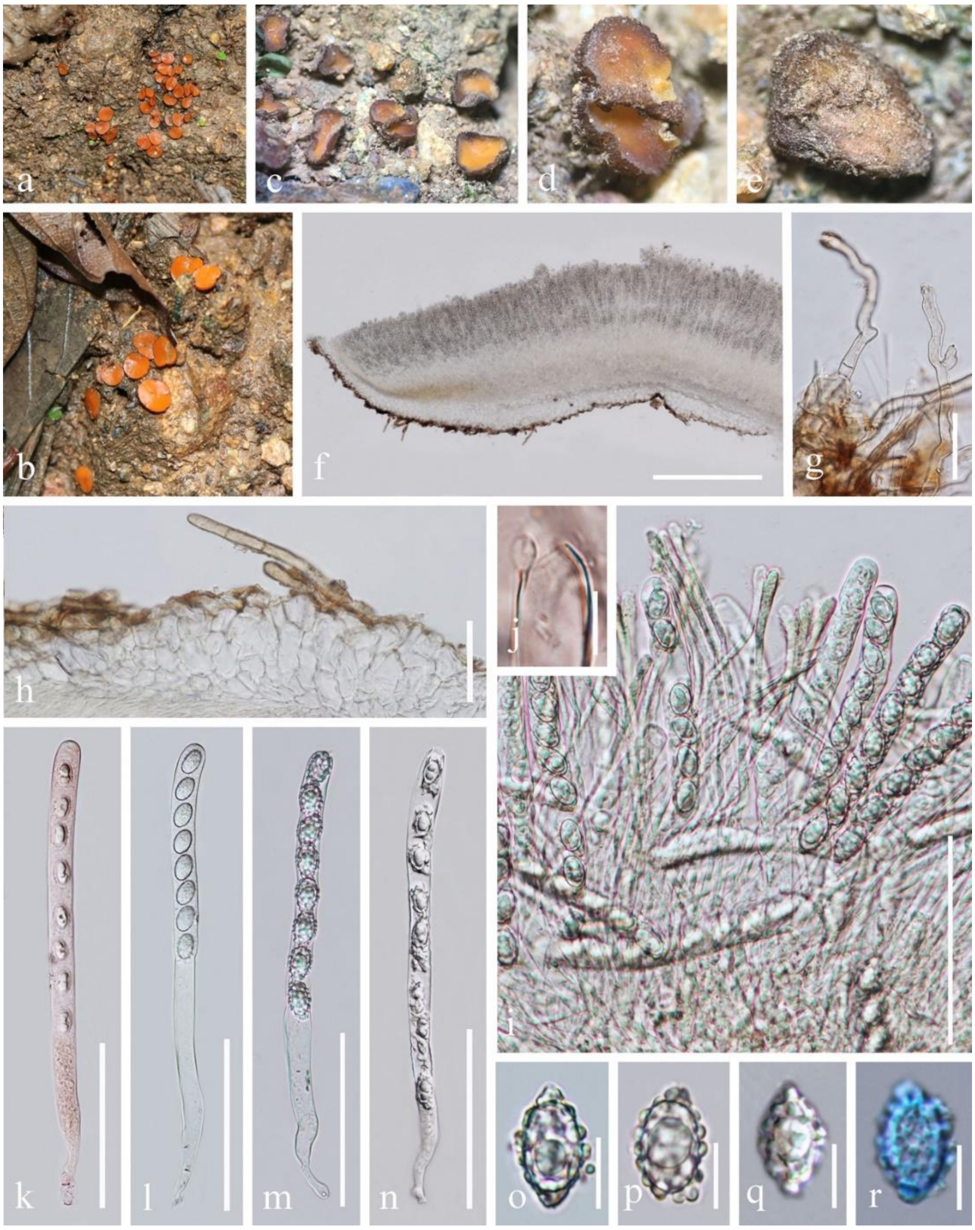

Figure 18 – *Melastiza verruculosa* (HKAS 124366, holotype). a, b Fresh specimens. c–e Dry specimens. f Vertical section of ascomata. g Basal hyphoid hairs. h Ectal excipulum. i Asci and paraphyses. j Apex of ascus in Congo red. k Ascus in Congo red. l–n Asci. o–q Ascospores. r Ascospore in Cotton Blue. Scale bars: f = 500 μm, g, h = 50 μm, i, k–n = 100 μm, j, o–r = 10 μm.

Rhodoscypha Dissing & Sivertsen, Mycotaxon 16(2): 442 (1983)

Index Fungorum number: IF 4717

Type species: ***Rhodoscypha ovilla*** (Peck) Dissing & Sivertsen

Notes – This genus is featured by pink, cupulate apothecia with thick-walled, refractive hairs, and fusiform, guttulate ascospores with smooth or fine ornamentations (Dissing & Sivertsen 1983). This is a mono-specific genus with *Rhodoscypha ovilla* as type. The genus is sister to the *Leucoscypha*, but this relationship is not strongly supported (Fig. 1).

Rhodoscypha ovilla (Peck) Dissing & Sivertsen, Mycotaxon 16(2): 447 (1983) Fig. 19

Index Fungorum number: IF 109230; Facesoffungi number: FoF 12604

Saprobic on soil. Sexual morph: *Apothecia* 3 mm broad, 3 mm high, solitary, cupulate, deeply concave, pubescent, sessile. *Receptacle* cupulate, receptacle surface pink, covered tomentum, margin conspicuous, undulate. *Hymenium* ca. 450 µm thick, coral pink, slightly darker in color than receptacle surface. *Subhymenium* ca. 60 µm thick, distinct, and visible as a darker zone. *Ectal excipulum* 55−115 µm thick, composed of *textura angularis* to *textura globulosa*, 19−24 × 13−17 µm cells, pinkish, with up to 250 µm long, up to 15 µm broad hairs, hyaline, thick-walled, strongly refractive tapering to an obtuse end. *Medullary excipulum* 30−90 µm thick, composed of *textura intricata*, 5−8 µm broad hyphae, hyaline to pinkish. *Paraphyses* 4−8 µm broad, with pinkish pigments, filiform, apex enlarged, 7−10 µm broad. *Asci* 440−465 × 17−25 µm, 8-spored, cylindrical, operculate, inamyloid, with a long pedicel and a crozier at the base. *Ascospores* [20/1/1, in H_2O] (34.1−) 36.1−42.4 (−45.8) × (14−) 15.2−17.1 (−17.2) µm (Q = 2.11−2.7, **Q** = 2.43±0.16), hyaline, fusiform, uniseriate or overlapping, equilateral, rarely slightly inequilateral, mostly biguttulate, occasionally uniguttulate, ornamented with visible warts in the light microscope. Asexual morph: Undetermined.

Material examined – China, Sichuan, Jiuzhai valley, on soil under a mixed coniferous broad-leaved forest, elev. 3559 m asl., 20 August 2018, Ming Zeng, ZM 49 (HKAS 104677).

GenBank accession numbers – HKAS 104677 (LSU: OP291088; *tef-1α*: OP352514; SSU: OP291038).

Notes – This species is distinguished by pink, pubescent apothecia with undulate margin, and fusiform ascospores with distinct fine warts (Zhuang et al. 2014). Our collection is sister to the clade formed by two European *R. ovilla* strains (HD Rana 79.060 & KH.08.007) with maximum support (100BP/1.00PP). While there are no significant differences in morphology with other materials, particularly the Chinese materials examined by Zhuang (2014).

Scutellinia (Cooke) Lambotte, Mém. Soc. roy. Sci. Liège, Série 2 14: 299 [prepr.] (1887) [1888]

Index Fungorum number: IF 4973

Type species – ***Scutellinia scutellata*** (L.) Lambotte

Notes – *Scutellinia* is a large and complicated genus in *Pyronemataceae*. Index fungorum (2022) has 280 estimated records. Of these, many species were excluded from the genus or transferred to other genera, while some remain *nomen dubium* (Schumacher 1988, 1990, Yao & Spooner 1996b, Moravec 1997, Calonge et al. 2006, Zhuang 2013). At present, more than 100 species are accepted in this genus (Kirk et al. 2008, Angelini et al. 2022, Wijayawardene et al. 2020, 2022), with most sharing reddish, orange-red to brownish red apothecia with yellow to brown setae, subglobose to ellipsoid ascospores with divers ornamentations (Schumacher 1990). Based on the most recent phylogeny by Angelini et al. (2022), 50 phylogenetic species were recognized.

Scutellinia colensoi Massee ex Le Gal, Bull. trimest. Soc. mycol. Fr. 83(2): 356 (1967) Fig. 20

Index Fungorum number: IF 521660; Facesoffungi number: FoF 12605

Saprobic on dead wood. Sexual morph: *Apothecia* up to 8 mm broad, 3 mm high, scattered to gregarious, with brown, rigid, straight, tapering hairs, sessile. *Receptacle* discoid to concave, receptacle surface orange-brown, slightly darker than hymenium, covered brown setae, margin conspicuous, entire with hairs. *Hymenium* ca. 250 µm thick, orange. *Ectal excipulum* 60−100 µm thick, of *textura angularis* to *textura globulosa*, 22−28 × 14−17 µm cells, hyaline to yellowish, outermost cells elongate to forming brownish hyphoid hairs, especially close to the base, 7−13 broad µm; with 140−300 µm long, 10−16 µm broad, dark brown, septate, setose hairs from inner layer, with a simple base and pointed end. *Medullary excipulum* 80−130 µm thick, composed of *textura intricata*, 3−7 µm broad hyaline hyphae. *Paraphyses* 2−3 µm broad, filiform, hyaline, apex enlarged, 6−9 µm broad. *Asci* 229−254× 13−16 µm, 8-spored, cylindrical, operculate, inamyloid, with a long pedicel and a crozier at the base. *Ascospores* [20/1/1, in H_2O] (17.8−) 18−20.1 (−21.8) × (10.6−) 10.9−12.5

(−13.6) µm (Q = 1.51−1.79, **Q** = 1.63±0.09) (excluding ornamentation), ellipsoid, hyaline, uniseriate, equilateral, rounded at the ends, uniguttulate to biguttulate, ornamented with rounded or irregular warts, up to 1.5 µm broad, 1.0 µm high, partly interconnected to form a network. Asexual morph: Undetermined.

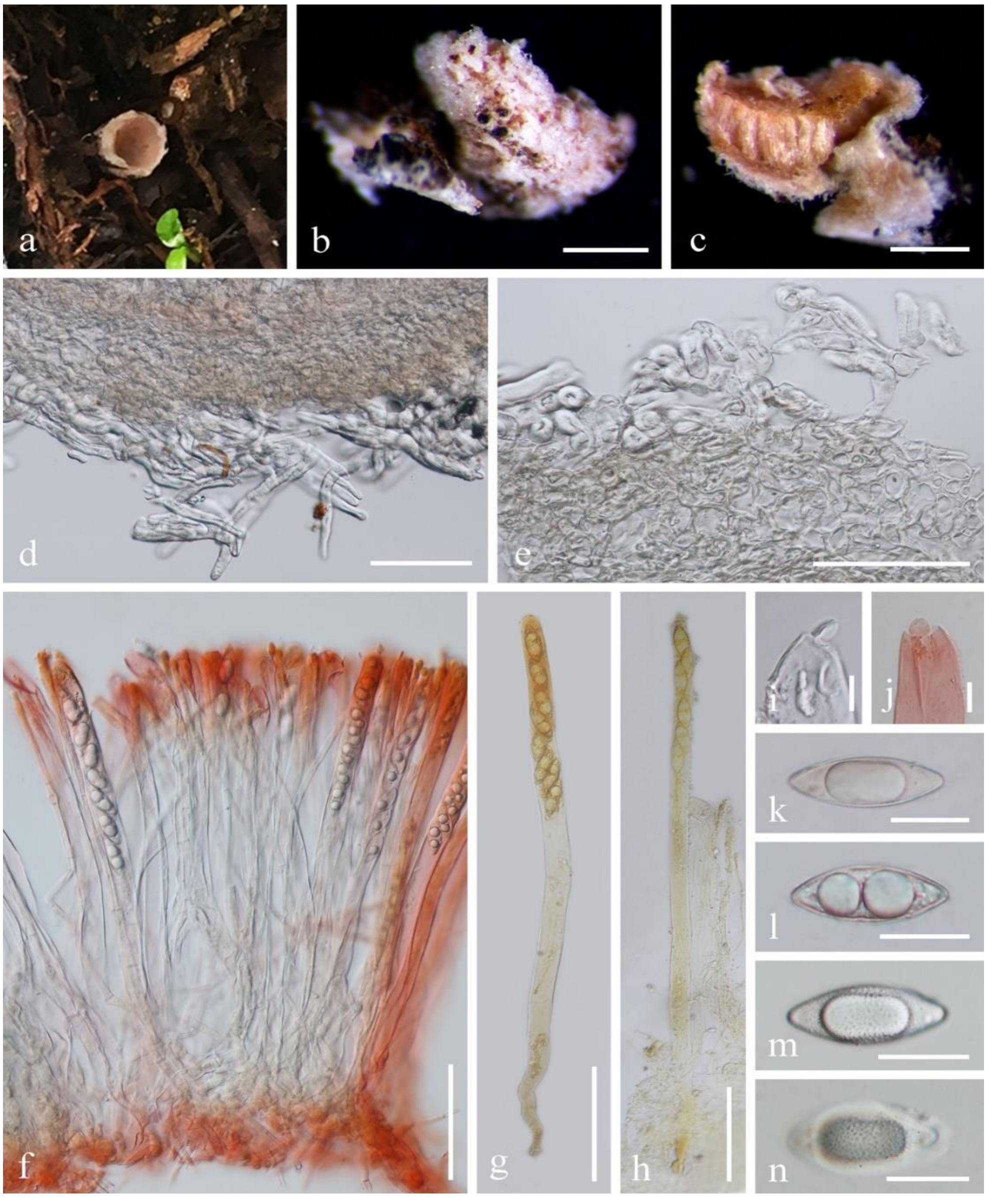

Figure 19 – *Rhodoscypha ovilla* (HKAS 104677). a Fresh specimen. b, c Dry specimens. d Hairs. e Ectal excipulum and hairs. f Asci and paraphyses in Congo red. g, h Asci in Melzer reagent. i Apex of ascus. j Apex of ascus in Congo red. k–n Ascospores. Scale bars: b, c = 500 µm, d–h = 100 µm, i, j = 10 µm, k–n = 20 µm.

Material examined – China, Yunnan province, Shangri-La, on unidentified dead wood under a mixed coniferous broad-leaved forest, 15 August 2018, Ming Zeng, ZM 26 (HKAS 104661); China, Yunnan, Jingdong, on soil, 3 August 2019, Ming Zeng, ZM 125 (HKAS 124372); *ibid.*, 4 August 2019, Ming Zeng, ZM 131 (HKAS 124583).

GenBank accession numbers – HKAS 104661 (LSU: OP291089; *tef-1α*: OP352515; *rpb2*: OP394223; SSU: OP291039), HKAS 124372 (LSU: OP291090; *tef-1α*: OP352516; *rpb2*: OP394224; SSU: OP291040), HKAS 124583 (LSU: OP291091; *tef-1α*: OP352517; *rpb2*: OP394225; SSU: OP291041).

Notes – This species is characterized by orange apothecia, brown setae with a simple base and up to 300 µm long, and ellipsoid ascospores with irregularly raised warts, partly interconnected (Zhuang 2014). Our three *Scutellinia* collections grouped with *Scutellinia colensoi* (420526MF0304) and *Scutellinia* sp. (BAP 427) forming a clade of maximum support (100BS/1.00PP) in the combined tree (Fig. 1). In the ITS phylogeny of *Scutellinia* (Fig. 21), these three collections also clustered with two *S. colensoi* (MT386360 and AY220831) strains to form a high-supported clade (99BS/1.00PP).

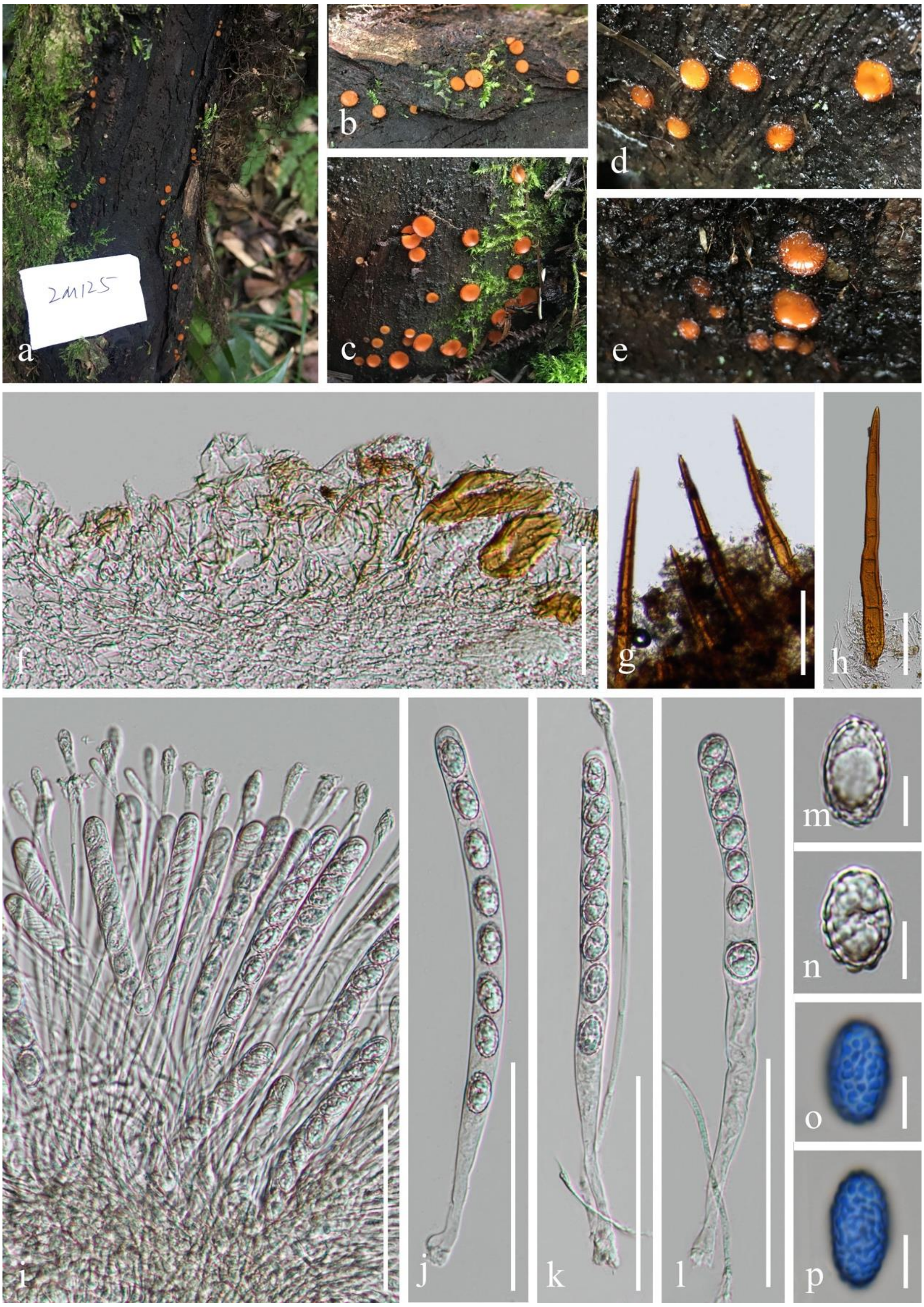

Figure 20 – *Scutellinia colensoi*. a–e Fresh specimens (a, b HKAS 124372. c HKAS 104661. d, e HKAS 124583). f Ectal excipulum. g, h Hairs. i Asci and paraphyses. j–l Asci. m, n Ascospores. o, p Ascospores in Cotton blue. Scale bars: f–l = 100 µm, m–p = 10 µm.

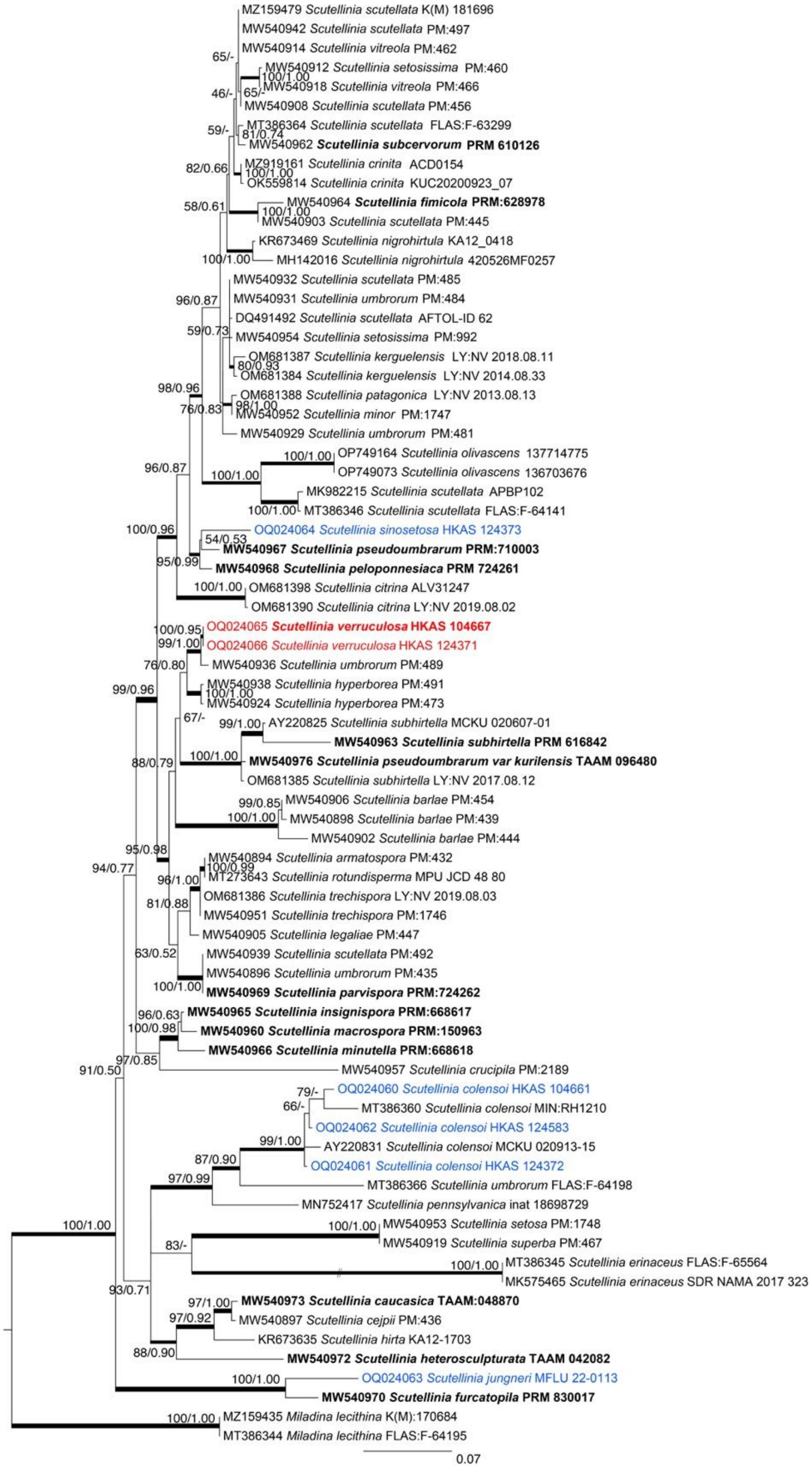

Figure 21 – Phylogenetic tree of ITS sequence data for *Scutellinia* species. Related sequences refer to Angelini et al. (2022). Seventy-five taxa are included in the analyses which comprise a matrix of 584 characters. Two *Miladina lecithina* strains (K(M):170684 and FLAS:F-64195) are used as the outgroup taxa. The best-fit model (TIM2+I+G) was selected by jModelTest v. 2.1.10 (Darriba et al. 2012). The best-scoring IQ tree with a final likelihood values of -5947.836 is presented. Bootstrap values ≥ 75% (maximum likelihood) and posterior probability values ≥ 0.90 (Bayesian inference) are

indicated with thick branches. The tree topology of the IQ-tree analysis is similar to the Bayesian analysis. The newly sequenced collections are indicated in blue. The newly described species are indicated in red. Names in bold indicate type collections.

Scutellinia jungneri (Henn.) Clem., Bull. Torrey bot. Club 30: 90 (1903) Fig. 22

Index Fungorum number: IF 521660; Facesoffungi number: FoF 12606

Saprobic on soil. Sexual morph: *Apothecia* 0.2−0.5 cm broad, 500−800 µm high, scattered to gregarious, golden yellow or yellow-orange when fresh, brown when dry, with brown, rigid, straight, tapering hairs, sessile. *Receptacle* concave, receptacle surface golden yellow or yellow-orange, concolorous with the hymenium, covered brown setae, margin conspicuous, entire with setae. *Hymenium* 190−240 µm thick, yellow. *Ectal excipulum* 120−220 µm thick, of *textura angularis* to *textura globulosa*, hyaline, inner cells 33−45 × 20−34 µm; outermost cells 46−66 × 23−35 µm, elongate to forming hyaline hyphoid hairs, especially close to the base, 7−12 µm; with 150−600 µm long, dark brown, septate setae, arising from inner layer, with simple or furcate base, and pointed end. *Medullary excipulum* 150−600 µm thick, composed of *textura intricata*, 5−7 µm broad, hyaline hyphae. *Paraphyses* 2−4 µm broad, filiform, with yellow pigments, apex enlarged, 5−8 µm broad. *Asci* 189−223× 11−13 µm, 8-spored, cylindrical, operculate, inamyloid, with a long pedicel and a crozier at the base. *Ascospores* [20/1/1, in H_2O] (14.5−) 15.2−16.8 (−17.6) × (8.7−) 9.3−10.7 (−11.1) µm (Q = 1.41−1.87, **Q** = 1.6±0.12) (excluding ornamentation), ellipsoid, hyaline, uniseriate, equilateral, rounded at the ends, biguttulate, ornamented with rounded or irregularly warty, up to 2 µm broad, 1.5 µm high, partly interconnected to form a network. Asexual morph: Undetermined.

Material examined – Thailand, Phayao province, Phu Lang Ka, on soil under a broad-leaved forest, 17 December 2017, Yuanpin Xiao, ZM 01 (MFLU 22-0113).

GenBank accession numbers – MFLU 22-0113 (LSU: OP291092; *tef-1α*: OP352518; *rpb2*: OP394226; SSU: OP291042).

Notes – This species is recognized by yellow apothecia with abundant setae, biguttulate ascospores with irregular warts. In morphology, this species is similar to *Scutellinia margaritacea*, *Scutellinia nigrohirtula* and *Scutellinia setosa* in having yellow to yellowish orange apothecia (Schumacher 1990, Choi et al. 2012, Zhuang 2014). While the ascospores of *S. margaritacea* (27.0−32.8 × 14.2−18.8 µm) and *S. nigrohirtula* (19.4−26.5 × 13.8−16.6 µm) are larger than this species. Besides, *S. setosa* has almost smooth ascospores with many small guttules (Schumacher 1990, Choi et al. 2012). Until now, this species lacks molecular data to clarify its phylogenetic position. We provide the first molecular data for this species in this study. Based on the ITS analysis, this species is sister to *Scutellinia furcatopila* (PM 830017) forming a basal clade within *Scutellinia* (Fig. 21).

Scutellinia sinosetosa W.Y. Zhuang & Zheng Wang, Mycotaxon 69: 352 (1998) Fig. 23

Index Fungorum number: IF 447085; Facesoffungi number: FoF 12607

Saprobic on soil. Sexual morph: *Apothecia* 5−8 mm broad, up to 3 mm high, scattered to gregarious, sessile. *Receptacle* concave, receptacle surface orange-red, covered brown, rigid, straight, tapering setae, margin conspicuous, entire with setae. *Hymenium* 230−285 µm thick, orange-red. *Ectal excipulum* 175−235 µm thick, of *textura angularis* to *textura globulosa*, yellowish to brownish, 55−80 × 40−70 µm cells; outermost cells elongate to forming brownish hyphoid hairs, especially close to base, 13−20 µm broad; with up to 350 µm long, 35 µm broad, dark brown, septate setae, arising from inner layer, with simple or bifurcate base and pointed end. *Medullary excipulum* 70−150 µm thick, composed of *textura intricata*, 7−11 µm broad hyaline hyphae. *Paraphyses* 2−4 µm broad, filiform, with yellowish pigments, apex enlarged, 6−9 µm broad. *Asci* 240−270× 14−18 µm, 8-spored, cylindrical, operculate, inamyloid, with a long pedicel and a crozier at the base. *Ascospores* [20/1/1, in H_2O] (16.2−) 18.1−21 (−21.6) × (12.2−) 12.6−14 (−14.4) µm (Q = 1.28−1.58, **Q** = 1.48±0.09) (excluding ornamentation), ellipsoid, hyaline, uniseriate, equilateral, rounded at the ends, uniguttulate to biguttulate, ornamented with low indistinct irregular raised, partly interconnected to form a reticulation, sometimes containing one de Bary bubble. Asexual morph: Undetermined.

Material examined – China, Yunnan Province, Jingdong, on soil under a mixed coniferous broad-leaved forest, 4 August 2019, Ming Zeng, ZM 137 (HKAS 124373).

GenBank accession numbers – HKAS 124373 (LSU: OP291093; *tef-1α*: OP352519; SSU: OP291043).

Figure 22 – *Scutellinia jungneri* (MFLU 22-0113). a Fresh specimen. b, c Dry specimens. d Vertical section of ascomata. e Excipulum in Congo red. f Hairs. g Asci and paraphyses. h Apices of paraphyses. i Paraphyses in the middle. j Ascus in Melzer's reagent. k, l Asci in Congo red. m–q Ascospores. Scale bars: e–g, j–l = 50 μm, h–i = 10 μm, m–q = 10 μm.

Notes – The most distinctive feature of this species is its ornamented ascospores under the light microscope. In addition, this species was previously only reported from China (Zhuang & Wang 1998, Zhang 2014). In this study, a *Scutellinia* collection was identified as *S. sinosetosa* based on morphology. We contribute the first molecular data and clarify its phylogenetic position herein. In the ITS inferences (Fig. 21), the species is sister to the type of *Scutellinia pseudoumbrarum* (PRM:710003) with low supports (54BS/0.53PP), then grouped with the type of *Scutellinia peloponnesiaca* (PR 724261) forming a high-supported clade (95BS/0.99PP). While the ascospores of *S. pseudoumbrarum* ornamented with warts up to 2.5 µm wide and 1–2 µm high (Jeannerot 2019). *Scutellinia peloponnesiaca* has globose to subglobose ascospores (Moravec 1974).

Figure 23 – *Scutellinia sinosetosa* (HKAS 124373). a–c Fresh specimens. d Ectal excipulum. e Setae. f Asci and paraphyses. g–j Asci. k–o Ascospores. p Ascospore in Congo red. q, r Ascospores in Cotton blue. Scale bars: d, f–j = 100 µm, e = 200 µm, k–r = 10 µm.

Scutellinia verruculosa M. Zeng, Q. Zhao & K.D. Hyde, sp. nov. Fig. 24

Index Fungorum number: IF 900179; Facesoffungi number: FoF 12608

Etymology: The epithet refers to its ascospores with warts.

Holotype: HKAS 104667

Diagnosis – This species is recognized by orange-red to red apothecia, dark brown, septate seta, broadly ellipsoid to ovoid ascospores with cyanophilic tuberculate warts.

Saprobic on soil. Sexual morph: *Apothecia* 0.3−0.5 cm broad, 0.2−0.3 cm high, scattered, orange-red to red when fresh, with visible hairs at margin, sessile. *Receptacle* concave to discoid, receptacle surface orange-red, almost concolorous with the hymenium, covered brown setae, margin conspicuous, entire, red, with setae. *Hymenium* 270−325 µm thick, orange-red. *Ectal excipulum* 250−320 µm thick, composed of *textura angularis* to *textura globulosa*, 74−93 × 54−70 µm cells, yellowish, with up to 950 µm long, 40 µm broad setae, dark brown, septate, arising from inner layer, with a simple base and pointed end. *Medullary excipulum* 290−450 µm thick, composed of *textura intricata*, 5−12 µm broad hyaline hyphae. *Paraphyses* 3−5 µm broad, filiform, with yellowish pigments and multiple oil droplets, apex enlarged, 6.5−10 µm broad. *Asci* 250−300 × 16−21 µm, 8-spored, cylindrical, operculate, inamyloid, with a long pedicel and a crozier at the base. *Ascospores* [20/1/1, in H_2O] (19.1−) 19.6−21.6 (−21.9) × (13.8−) 14.1−16.4 (−17.9) µm (Q = 1.22−1.44, **Q** =1.35 ±0.06) (excluding ornamentation), broadly ellipsoid to ovoid, hyaline, uniseriate, equilateral, rounded at the ends, uniguttulate, ornamented with cyanophilic tuberculate warts, up to 2.0 µm broad, 1.5 µm high, some containing one de Bary bubbles. Asexual morph: Undetermined.

Figure 24 – *Scutellinia verruculosa*. a–c Fresh specimens (a, b HKAS 104667, holotype. c HKAS 124371). d Ectal excipulum. e Seta. f Asci and paraphyses. g–j Asci. k Apex of asci. l Apex of asci in Melzer's reagent. m–q Ascospores. r Ascospore in Cotton blue. Scale bars: d, e = 150 µm, f–j = 100 µm, k–r =10 µm.

Material examined – China, Sichuan province, Erlang Mountains, on mossy soil under a mixed coniferous broad-leaved forest, elev. 4215 m asl., 17 August 2018, Ming Zeng, ZM 35 (HKAS 104667, holotype); *ibid.*, Danba, on soil, elev. 3713 m asl., 17 July 2019, Ming Zeng, ZM 116 (HKAS 124371, paratype).

GenBank accession numbers – HKAS 104667 (LSU: OP291094; *tef-1α*: OP352520; *rpb2*: OP394227; SSU: OP291044), HKAS 124371 (LSU: OP291095; *tef-1α*: OP352521l; *rpb2*: OP394228; SSU: OP291045).

Notes – According to the descriptions for ornamentations of ascospores in Schumacher (1990), our species is similar to *S. ahmadii*, *S. heterosculpturata*, *S. hyperborea*, *S. paludicola*, *S. patagonica*, *S. subhirtella* and *S. umbrorum* in having tuberculate ornamentation of ascospores. *Scutellinia heterosculpturata* and *S. patagonica*, each represented by a single strain, are phylogenetically distant from our species based on ITS analysis. The *S. hyperborean* and *S. subhirtella* are closely related to our species, however, *S. hyperborean* morphologically differs by having globose to subglobose ascospores, and *S. subhirtella* by having ellipsoid ascospores with slightly pointed ends (Schumacher 1990). Additionally, our new species is sister to one of *S. umbrorum* (MW540936), which has a multifurcate base of hairs (Schumacher 1990). For the other two species which lack molecular data support, *S. ahmadii* differs in that it has short hairs (< 150 μm) and uniguttulate or biguttulate ascospores. *Scutellinia paludicola* however has multiguttulate ascospores (Schumacher 1990, Zhuang 2014). Herein, a new species *S. verruculosa* is proposed.

Pyropyxidaceae M. Zeng, Q. Zhao & K.D. Hyde, fam. nov.

Index Fungorum number: IF 900180; Facesoffunginumber: FoF 12609

Type genus – ***Pyropyxis*** Egger

Saprobic on dead wood or soil, *endophytic* on *Quercus liaotungensis*, *Ulmus macrocarpa* and *Ceratodon purpureus*. Sexual morph: *Ascomata* apothecial, scattered to gregarious, sessile to stipitate, pink, purple, olivaceous to brown, often with short hairs. *Hairs* hyphoid, or moniliform, from ectal excipulum, hyaline to purple or brown, simple or branched, septate. *Hymenium* pale, pink, purple to olivaceous, brown. *Ectal excipulum* composed of *textura angularis* to *textura globulosa*. *Medullary excipulum* composed of *textura intricata*. *Paraphyses* filiform, pigmented, septate, straight or branched, often with slightly enlarged apex. *Asci* 8–spored, operculate, subcylindrical to cylindrical, inamyloid. *Ascospores* globose to subglobose, fusiform to ellipsoid, uniseriate, eguttulate or guttulate, smooth or with ornamentations. Asexual morph: *Conidiophores* mononematous, micronematous, smooth or with ornamentation, unbranched or terminal fertile cells dichotomously branched, hyaline to pale brown. *Conidiogenous cells* polyblastic, integrated, terminal or intercalary, inflated, denticulate, hyaline to pale brown. *Conidia* solitary, aseptate, verrucose to capitate, straight or slight curved, subglobose, ellipsoidal, obovoid, clavate to subcylindrical, sometimes with short denticles, hyaline to pale brown.

Notes – This family was separated from *Pyronemataceae* and introduced to accommodate four genera, *viz.*, *Jafnea*, *Micronematobotrys*, *Pyropyxis* and *Smardaea*. *Micronematobotrys* and *Pyropyxis* are monotypic genera. In the phylogenetic analyses, *Jafnea* is represented by two species, which are grouped together in a clade of maximum support (Fig 1; 100BS/1.00PP). *Smardea* is represented by three species however the three do not group together (Fig. 1). Molecular clock analyses indicate that the newly-proposed family is separated from *Pyronemataceae* and *Otideaceae* around 243 Mya in the Late Triassic (Fig. 2). The family has maximum statistical support (100BS/1.00PP) based on four genes (Fig. 1).

Jafnea Korf, Nagaoa 7: 5 (1960)

Index Fungorum number: IF 2524; Facesoffunginumber: FoF 12610

Saprobic on soil. Sexual morph: *Apothecia* scattered to gregarious, cupulate, villose, stipitate. *Receptacle* deep concave, receptacle surface gray brown to brown, covered brown hairs, margin conspicuous, entire. *Hymenium* whitish, brown to brownish. *Stipal ecto-excipulum* composed of *textura angularis*, brown. *Ectal excipulum* composed of *textura angularis*, brown. *Medullary excipulum* composed of *textura intricata*, hyaline. *Paraphyses* filiform, exceeding the asci, brown, septate, apex enlarged slightly. *Asci* 8–spored, operculate, subcylindrical to cylindrical, inamyloid. *Ascospores* fusiform, uniseriate, hyaline, guttulate, with irregular ornaments. Asexual morph: Undetermined.

Type species – ***Jafnea fusicarpa*** (W.R. Gerard) Korf

Notes – This genus is characterized by pale brown to brown, deep cupulate apothecia with brown hairs, fusiform and ornamented ascospores. Currently, there are three species contained in this genus, *viz.*, *Jafnea fusicarpa*, *Jafnea semitosta*, and *Jafnea pallida*. These three species are easily distinguished by their ornamented ascospores (Korf 1960, Zhuang 2014, Gates & Van Vooren 2016). The former two species have molecular data, while these are lacking in *Jafnea pallida*.

Jafnea fusicarpa (W.R. Gerard) Korf, Nagaoa 7: 5 (1960) Fig. 25

Index Fungorum number: IF 332669; Facesoffunginumber: FoF 12611

Saprobic on soil. Sexual morph: *Apothecia* 1.5−2 cm broad, 1−1.2 cm high, scattered, deep cupulate, villose, stipitate. *Receptacle* deep concave, receptacle surface yellowish brown, covered brown hairs, margin conspicuous, entire. *Stipe* up to 1 cm broad, 1 cm long, terete, solid, brown. *Hymenium* brown. *Stipal ecto-excipulum* 137−179 µm thick, of *textura angularis*, brown, comprised of 30−50 × 13−20 µm cells, with brown, septate, taping to obtuse end hairs. *Ectal excipulum* 70−163 µm thick, of *textura angularis*, brown, 20−30 × 11−16 µm, with up to 250 µm long, 25 µm broad, brownish to brown, septate, taping to obtuse end hairs. *Medullary excipulum* 180−300 µm broad, of *textura intricata*, composed of 2−5 µm broad hyaline hyphae. *Paraphyses* 2−4 µm broad, filiform, exceeding the asci, yellow-brown, septate, apex enlarged, 3−5 µm broad. *Asci* 230−315 × 10−15 µm, 8−spored, operculate, cylindrical, inamyloid. *Ascospores* [20/1/1, in H_2O] (24.2−)25.8−30.9(−33.8) × (9.1−)9.5−10.7(−11.1) µm (Q = 2.38−3.36, **Q** = 2.82±0.3), fusiform, uniseriate, hyaline, biguttulate, ornamented with irregularly raised warts and cushion-shaped apiculi. Asexual morph: Undetermined

Material examined – China, Hebei province, Xinglong, on soil, elev. 1005 m asl., 22 August 2015, Xianghua Wang, 3768 (HKAS 90031).

GenBank accession numbers – HKAS 90031 (LSU: OP291096; SSU: OP291046).

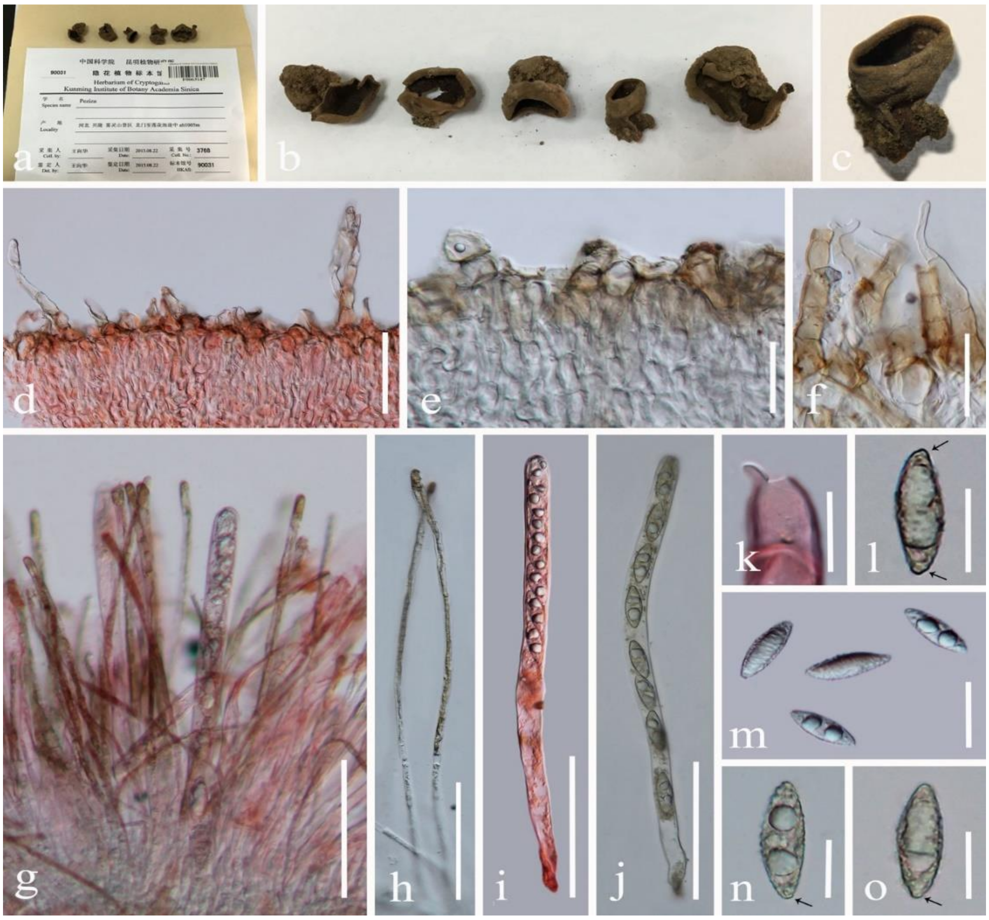

Figure 25 – *Jafnea fusicarpa* (HKAS 90031). a−c Herbarium materials. d Stipal ecto-excipulum in Congo red. e Ectal excipulum. f Hairs. g Asci and paraphyses in Congo red. h Paraphyses. i Ascus in Congo red. J Ascus. k Apex of asci in Congo red. l−o Ascospores. Scale bars: d, g−j = 100 µm, e, f = 50µm, k, l, n, o = 20 µm, m =30 µm.

Notes – This species is similar to *Jafnea semitosta*, which has brown apothecia and irregularly raised warty ascospores. While *J. fusicarpa* has apiculate ascospores, *J. semitosta* lacks the apiculate structure. The presence or absence of apiculi is a very important characteristic to distinguish these two species (Korf 1960, Zhuang 2014).

Micronematobotrys Xiang Sun & L.D. Guo, Mycol. Progr. 9(4): 569 (2010)

Index Fungorum number: IF 543256

For description, see Sun & Guo (2010)

Type species – ***Micronematobotrys verrucosus*** Xiang Sun & L.D. Guo

Notes – This is a hyphomycetous genus, which contains a single species. It is distinguished by smooth or ornamented, micronematous conidiophores, holoblastic, polyblastic conidiogenous cells with minute denticulate, conidia solitary, eguttulate, verrucose to capitate, ellipsoidal or obovoid to clavate, sometime inequilateral (Sun & Guo 2010). In a previous study based on LSU phylogeny, *Micronematobotrys* was represented by three *Micronematobotrys verrucosus* strains, which grouped as and sister to the strain *Greletia reticulosperma* (AY500532) (Sun & Guo 2010). The latter was synonymized under *Smardaea reticulosperma* (Benkert 2005). Thus, *Micronematobotrys* is phylogenetically nested in *Smardaea*, and this is also shown in our study based on extended sampling of *Smardaea* (Fig. 1). Notably, *Micronematobotrys* is an asexual morph, while *Smardaea* is sexual, which raises the possibility of the two being linked in the future.

Micronematobotrys verrucosus Xiang Sun & L.D. Guo, Mycol. Progr. 9(4): 569 (2010)

Index Fungorum number: IF 543334

For description and illustration, see Sun & Guo (2010).

Notes – This is an endophyte species reported from *Quercus liaotungensis* and *Ulmus macrocarpa*. Since there is no available ex-type information in the original publication, we requested a duplicate of the holotype (HMAS 186049) (Fig. 26). At the moment, the morphological examination is not possible. So, we hope to have more samples and molecular data to link and clarify *Micronematobotrys* and *Smardaea* in the future.

Figure 26 – The status of the herbarium of ***Micronematobotrys verrucosus*** (HMAS 186049, duplicate of holotype).

Pyropyxis Egger, Can. J. Bot. 62(4): 705 (1984)

Index Fungorum number: IF 25844

For description, see Egger (1984).

Type species – ***Pyropyxis rubra*** (Peck) Egger

Notes – This is a monotypic genus characterized by deeply cupulate, pink apothecia, ectal excipulum with moniliform hairs, hyaline to orange paraphyses, ellipsoid ascospores with guttules when immature, and eguttulate at maturity. The asexual morph is hyphomycetous. Conidiophores are smooth-walled, hyaline, septate, and dichotomously branched at the apex with swollen ampullae. Conidia solitary, subglobose to elliptical or subcylindrical, brown at maturity, non-septate, and smooth to echinulate (Egger 1984, Filippova et al. 2016).

Pyropyxis rubra (Peck) Egger, Can. J. Bot. 62(4): 705 (1984)

Index Fungorum number: IF 106576

For description and illustration, see Egger (1984) and Filippova et al. (2016).

Notes – This species is introduced based on *Peziza rubra*, and often occurs in post-fire habitats (Egger 1984). This species is similar to *Geopyxis carbonaria* and *Rhodotarzetta rosea* in morphology and all species are pyrophilous. Nonetheless, there are significant differences among these species (Egger 1984, Filippova et al. 2016). *Geopyxis carbonaria* does not contain guttules at any stage, opposite to *R. rosea*, which contains biguttulate ascospores. *Pyropyxis rubra* has biguttulate ascospores, or with several small guttules when immature, but eguttulate when mature (Egger 1984, Filippova et al. 2016). This species is easily cultured in a common medium (PDA) to obtain the anamorphic stage (Filippova et al. 2016).

Smardaea Svrček, Česká Mykol. 23(2): 90 (1969)

Index Fungorum number: IF 5044

For description, see Svrcek (1969).

Type species – ***Smardaea amethystina*** (W. Phillips) Svrček

Notes – This genus is typified by *Smardaea amethystina*, along with other ten species that are currently accepted, viz., *Smardaea australis*, *Smardaea isoldae*, *Smardaea marchica*, *Smardaea microspora*, *Smardaea ovalispora*, *Smardaea planchonis*, *Smardaea protea*, *Smardaea purpurea*, *Smardaea reticulosperma*, and *Smardaea verrucispora* (Svrček 1969, Raymundo & Valenzuela 2021). This genus is distinguished by discoid to cupulate apothecia of purple to dark purple color, pigmented paraphyses, operculate, inamyloid asci, and globose, ellipsoid to fusoid ascospores with smooth, or ornamented walls (Raymundo & Valenzuela 2021). Currently, there are no reports of the asexual morph of *Smardaea*. This genus is polyphyletic with the asexual *Micronematobotrys* nesting within. Wang et al. (2011) reported production of diterpenoid metabolites from a *Smardaea* sp. endophyte, which inhabits *Ceratodon purpureus*.

Smardaea amethystina (W. Phillips) Svrček, Česká Mykol. 23(2): 91 (1969)

Index Fungorum number: IF 339322

For description and illustration, see Svrček (1969), Van Brummelen (1969), Iglesias (2011).

Notes – This species was established based on *Ascobolus amethystinus* (Svrcek 1969). It is similar to *Smardaea isoldae* in their ornamentation and semiglobular apiculi of ascospores. While *S. amethystina* has purple apothecia and smaller ascospores (19.5–22 × 11–12.5 μm), *Smardaea isoldae* differs in its green to olivaceous apothecia and larger ascospores (22–28 × 10–14 μm) (Raymundo & Valenzuela 2021).

Discussion

In this study, we aimed to reveal the phylogenetic relationships within *Pyronemataceae* using broad taxon sampling and inferring phylogenies from a combined four-gene (LSU, *tef-1α*, *rpb2*, and SSU) dataset. Based on the results of the analyses, we resurrected *Otideaceae* and introduced *Pyropyxidaceae*. Both families are successive branching off lineages to the rest of *Pyronemataceae sensu stricto*. The obtained phylogenetic relationships match those of Hansen et al. (2013), but not of Ekanayaka et al. (2018). In Hansen et al. (2013) and this study, *Pyropyxidaceae* comprised the basal lineage in *Pyronemataceae sensu stricto*, instead of *Otideaceae* as described by Ekanayaka et al. (2018). Both *Otideaceae* and *Pyronemataceae* are phylogenetically distinct and their monophyly has maximum statistical support (100BS/1.00PP).

Ekanayaka et al. (2018) redefined the members of *Otideaceae* to contain *Otidea*-lineage taxa and *Ascosparassis*, *Wenyingia* and *Diehliomyces*, all three of which lack molecular data. *Wenyingia* was excluded from *Otideaceae* and placed into *Tarzettaceae* based on the absence of crozier of asci (Van Vooren & Vega 2018b), while Pfister & Healy (2021) accepted the genus in *Otideaceae*. The redefined *Otideaceae* was not accepted in subsequent studies as the circumscribed genera were still described under *Pyronemataceae sensu stricto* (Xu et al. 2018, 2022, Zeng et al. 2020, Wijayawardene et al. 2020, 2022). Herein, *Acervus*, *Arpinia*, *Monascella*, *Otidea*, *Planamyces*, and *Warcupia* clustered together, forming *Otideaceae*, separating from *Pyronemataceae sensu stricto*. *Pyropyxidaceae* comprises *Jafnea* (comprises three species), *Micronematobotrys* (comprises one species), *Pyropyxis* (comprises one species), and *Smardaea* (comprises 11 species). According to the estimates of divergence time in this study, the split of most families occurred during the Triassic−Jurassic, and the node age of most families falls within the Jurassic−Cretaceous (Table 3). Our estimated dates placed the common ancestor of *Otideaceae* at 202 Mya and of *Pyropyxidaceae* at 141 Mya in the Cretaceous.

Morphologically, *Otideaceae* and *Pyropyxidaceae* have features that distinguish them from the rest of *Pyronemataceae sensu stricto*. Both families mostly lack carotenoids, while the rest of *Pyronemataceae sensu stricto* mostly produce ascomata with carotenoids. Carotenoids were subsequently lost in some clades of *Pyronemataceae* containing ectomycorrhizal members hence, the loss may be correlated with a transition to an ectomycorrhizal lifestyle (Hansen et al. 2013). Additionally, true ascomatal hairs are absent in *Otideaceae* and *Pyropyxidaceae* (Hansen et al. 2013). Almost all members of the *Pyropyxidaceae* share short hyphoid or moniliform hairs, while *Otideaceae* has abundant tomentum on the basal of apothecia. Besides, *Pyronemataceae* members have ascospores with smooth or various ornaments, but *Otideaceae* has almost ellipsoid and guttulate ascospores with smooth walls.

Our analyses show that the ancestors of *Pyronemataceae*, *Otideaceae* and *Pyropixidaceae* had epigeous ascomata. Hypogeous ascomata are present in two distantly related lineages (L1 & L4) and arose independently. Semi-hypogeous are present only in L4 and arose at least twice. These types of ascomata are common in *Dikarya* and have evolved independently multiple times. Our divergence time estimates placed the common ancestor of L1 and L4 hypogeous taxa at 99 and 31 Mya, respectively. Similar to other hypogeous taxa, those from L1 and L4 form ectomycorrhizal mutualistic associations with plants. Specifically, *Genea*, *Genabea*, *Geopora*, *Gilkeya*, *Myrmecocystis*, *Picoa*, and *Terracavicola* establish symbioses with roots (Table 4) of *Betulaceae*, *Cistaceae*, *Cupressaceae*, *Fagaceae*, *Nothofagaceae*, *Pinaceae*, *Salicaceae*, and *Sapindaceae* (Smith et al. 2006, Sbissi et al. 2010, Kaounas et al. 2011, Guevara-Guerrero et al. 2012, Alvarado et al. 2016, 2018, Grupe et al. 2019). These genera are associated with multiple plant hosts. The crown age of at least one plant host precedes that of its associated fungi. Hence, the ancestors of these fungi formed plant-based symbioses, which have been postulated to hold a primary role in the evolution of hypogeous taxa diversity.

Based on our phylogenetic analysis, we note some unresolved issues in *Pyronemataceae*. *Lasiobolidium* was accommodated into *Pseudombrophilaceae* based on analyses using a single *Lasiobolidium* strain, the cleistothecial *L. orbiculoides* (CBS 344.73) (Ekanayaka et al. 2018). Wijayawardene et al. (2020, 2022) also accepted this assignment of *Lasiobolidium* with multiple species in the outline of *Pezizomycetes*. A recent study of *Lasiobolidium* based on morphology and phylogeny confirmed its position in the *Pyronemataceae* (Van Vooren et al. 2021). We used all available *Lasiobolidium* sequences to assign the position of this genus in *Pezizomycetes*. Our results are the same as those of Van Vooren et al. (2021). All *Lasiobolidium* strains closely cluster with the three type strains of the type species *L. spirale*, forming a distinct clade of maximum support that is sister to *Aleurina*. The type of *L. orbiculoides* was consistently placed in *Pseudombrophilaceae* (this study, Ekanayaka et al. 2018). Hence, the position of *Lasiobolidium* in *Pyronemataceae* is not in doubt. To resolve the position *L. orbiculoides*, the morphology of the type should be re-examined. In the outline of Wijayawardene et al. (2020, 2022), *Rhodoscypha* and *Rhodotarzetta* were omitted, while *Leucoscypha* was excluded from *Pyronemataceae*. Nonetheless, phylogeny supports the placement of *Leucoscypha*, *Rhodoscypha* and *Rhodotarzetta* in *Pyronemataceae* in this and other studies (Perry et al. 2007, Hansen et al. 2013, Lindemann & Alvarado 2017).

Pyronemataceae comprises a family of high diversity, including species richness, and ecological preferences. Additional collections providing molecular data and morphological characteristics, along with analyses combining various disciplines are necessary to fully understand this complex family.

Table 4 The comparison of median crown or stem ages between hypogeous groups with associated plants.

Hypogeous Taxa	**Crown age (Mya)**	**Associated plants (Genus)**	**Crown age (Mya)**	**References**
Genea/*Genabea*	51 (29−72.9)/ 21 (7.3−36.7)	*Abies*	48.6	Xiang et al. (2015)
		Betula	6.6	Yang et al. (2019)
		Carpinus	9.9	Yang et al. (2019)
		Castanea	19.8	Zhou et al. (2021)
		Corylus	36.3	Yang et al. (2018)
		Fagus	53	Renner et al. (2016)
		Lithocarpus	51	Kua & Cannon (2017)
		Nothofagus	72.1	Sauquet et al. (2012)
		Pinus	93.7	Ran et al. (2018)
		Quercus	Ca. 52	Zhou et al. (2022)
		Salix	43.8	Wu et al. (2015)
		Tsuga	42.2	Havill et al. (2008)
Gilkeya	8.4 (2.3−16.1)	*Abies*	48.6	Xiang et al. (2015)
		Quercus	Ca. 52	Zhou et al. (2022)
		Pinus	98.77	Jin et al. (2021)
Myrmecocystis	54.9 (36.5−75.2)	*Abies*	48.6	Xiang et al. (2015)
		Acer	53.06	Gao et al. (2020)
		Quercus	Ca. 52	Zhou et al. (2022)
Picoa	16.5 (4.6−26.6)	*Helianthemum*	7.8	Aparicio et al. (2017)
		Quercus	Ca. 52	Zhou et al. (2022)
Hypogeous Taxa	**Stem age (Mya)**	**Associated plants (Genus)**	**Crown age (Mya)**	**References**
Geopora cooperi	30.8 (15.5−46.8)	*Abies*	48.6	Xiang et al. (2015)
		Juniperus	43.66	Mao et al. (2010)
		Pinus	98.77	Jin et al. (2021)
		Quercus	Ca. 52	Zhou et al. (2022)
Terracavicola	61.7 (35.7−84.2)	*Juniperus*	43.66	Mao et al. (2010)
		Pinus	98.77	Jin et al. (2021)
		Quercus	Ca. 52	Zhou et al. (2022)

Acknowledgements

We deeply appreciate the suggestions on our manuscript from Prof. Zhuliang Yang. We are grateful to Hongli Su, Shucheng He, Song Wang, and Yuanpin Xiao for collecting samples. The authors would like to thank the Herbarium of Cryptogams, Kunming Institute of Botany Academia Sinica (KUN-HKAS) for allowing us to examine and sequence the herbarium specimens. Dr. Shaun Pennycook (Manaaki Whenua-Landcare Research, New Zealand) is thanked to help to check the Latin name of the new taxa. Chuangen Lin is greatly appreciated for helping to check the description of hyphomycetes. Danfeng Bao is thanked to guide for evolution. Ming Zeng is grateful for MFLU grant number 5971105508 and the dissertation writing grant to support *Pezizomycetes* studies. This study is financed by the Second Tibetan Plateau Scientific Expedition and Research (STEP) Program (Grant No. 2019QZKK0503), the open research project of “Cross-Cooperative Team” of the Germplasm Bank of Wild Species, Kunming Institute of Botany, Chinese Academy of Sciences (Grant No. 292019312511043), Science and Technology Service Network Initiative, Chinese Academy of Sciences (KFJ-STS-QYZD-171). We are thankful for grant entitled Impact of climate change on fungal diversity and biogeography in the Greater Mekong Subregion (Grant No. RDG6130001), the National Research Council of Thailand (NRCT) grant “Total fungal diversity in a given forest area with implications towards species numbers, chemical diversity and biotechnology" (Grant No. N42A650547).

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