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

Zeng M1,2,3, Gentekaki E2,3*, Zeng XY4, Tian Q5, Zhao Q1,6* and Hyde KD1,2,3,7*

1Yunnan Key Laboratory of Fungal Diversity and Green Development, Key Laboratory for Plant Diversity and Biogeography of East Asia, Kunming Institute of Botany, Chinese Academy of Sciences, Kunming, Yunnan 650201, P.R. China
2School of Science, Mae Fah Luang University, Chiang Rai, 57100, Thailand
3Center of Excellence in Fungal Research, Mae Fah Luang University, Chiang Rai, 57100, Thailand
4Department of Plant Pathology, College of Agriculture, Guizhou University, Guiyang 550025, China
5School of Life Science and Technology, Center for Informational Biology, University of Electronic Science and Technology of China, Chengdu 611731, P.R. China
6Institute of Applied Fungi, Southwest Forestry University, Kunming 650224, P.R. China
7Innovative Institute for Plant Health, Zhongkai University of Agriculture and Engineering, Haizhu District, Guangzhou 510225, P.R. China

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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 *Pyropyx* lineage containing *Jafnea*, *Micronematobotrys*, *Pyropyx*, and *Smardaeae*. The *Pyropyx* 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 hyploid 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 epigean 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.
Keywords – 6 new species – 1 new family – Pezizales – taxonomy – evolution

Introduction

Pyrenomataceae 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, Wijayarwardene et al. 2020, 2022). The concept of a broadly circumscribed Pyrenomataceae was originally widely accepted (Korf 1972, Korf 1973, Perry et al. 2007, Kirk et al. 2008). A stricter concept of Pyrenomataceae, which is limited to Pyronema with or without Coprotus, has also been proposed (Rifai 1968, Kimbrough 1970, 1989).


Eckblad (1668) 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 (Otideeae) comprising three tribes within Pyrenomataceae sensu lato. Ascosparassis, Otidea and Psilopezia were placed in the tribe Otideae, Tarzetta was placed in the tribe Jafneeeae, 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 Pyrenomataceae and Otideaceae. Multi-locus phylogenetic analyses of Pyrenomataceae 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 Pyrenomataceae (Hansen et al. 2013, Ekanayaka et al. 2018). Recently, many Otidea-related new taxa, especially Otidea spp., were assigned to Pyrenomataceae 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 Pyrenomataceae sensu stricto. However, the statistical support for the Otideaceae node, Pyrenomataceae 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,

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.

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<tr>
<th>Geological period</th>
<th>Time (Mya)</th>
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<tr>
<td>Devonian</td>
<td>368 (275–456)</td>
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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-1a, 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://iqt.tree.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.

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<th>tef-1α</th>
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<td>sn</td>
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<td>–</td>
<td>–</td>
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<td>MN449993</td>
<td>MN447536</td>
<td>–</td>
<td>–</td>
<td>Hyde et al. (2020)</td>
</tr>
<tr>
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<td>LY NV 2016.09.01</td>
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<td>–</td>
<td>–</td>
<td>–</td>
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</tr>
<tr>
<td><em>sp.</em></td>
<td>France</td>
<td>G.M. 20160801</td>
<td>MW546574</td>
<td>–</td>
<td>–</td>
<td>–</td>
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</tr>
<tr>
<td><em>aurantiopsis</em></td>
<td>USA</td>
<td>DHP 04-599 (FH)</td>
<td>AY945859</td>
<td>KC109212</td>
<td>DQ017605</td>
<td>–</td>
<td>Hansen et al. (2013)</td>
</tr>
</tbody>
</table>

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

<table>
<thead>
<tr>
<th>Nodes</th>
<th>Group</th>
<th>Node age (Mya)</th>
<th>Geological time scales</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>Pezizomycetes crown group</td>
<td>332 (280–388)</td>
<td>Early Carboniferous</td>
</tr>
<tr>
<td>2</td>
<td>Tuberaeaceae crown group</td>
<td>154 (138–171)</td>
<td>Late Jurassic</td>
</tr>
<tr>
<td>3</td>
<td>Pyropyxidaceae crown group</td>
<td>141 (86–200)</td>
<td>Early Cretaceous</td>
</tr>
<tr>
<td>4</td>
<td>Otideaeeae crown group</td>
<td>202 (159–250)</td>
<td>Late Triassic</td>
</tr>
<tr>
<td>5</td>
<td>Otidea–Pyronemataceae</td>
<td>230 (188–274)</td>
<td>Late Triassic</td>
</tr>
</tbody>
</table>
Table 3 Continued.

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

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 apothecial 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

   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).

   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)

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 sub-stipitate. *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 H₂O] (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-1a*: OP352493; SSU: OP291010), HKAS 104699 (LSU: OP291061; *tef-1a*: OP352494; SSU: OP291011).

Notes – This species is characterized by ear-shaped, split, sometime cupulate, sub-stipitate apothecia, pale yellowish-brown receptacle surface, ectic excipulum with sparse resinous exudates, brown hymenium, oblong ellipsoid ascospores (Olariaga et al. 2015). Multiple-gene analyses based on *LSU*, *ITS*, *tef-1a*, 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.


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 H₂O] (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.
One hundred and ten taxa are included in the combined analyses which comprise 3283 characters (LSU: 1–840 bp; ITS: 841–1462 bp; tef-1a: 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-1a: 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-1a: 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 mirabilis 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 mirabilis 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.

Saprobie 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 H2O] (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.

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 H₂O] (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.

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, ochre 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, ochre, 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, filamentous, 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 [20/11, in H2O] (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-1a: 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)

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 H₂O] (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).

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).

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

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

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

Holotype – HKAS 104658

**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.

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,
Otididea propinquata (P. Karst.) Harmaja, Karstenia 15: 32 (1976)

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, substipitate, 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. 0.9 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, oculerate, inamyl oid, with a long pedicel and a crozier at the base. Ascospores [20/1/1, in H₂O] (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 a.s.l., 15 August 2018, Ming Zeng, ZM 19 (HKAS 124368, paratype).


Notes – This species is sister to another new species, Otidea macrospora introduced in this study, and further clades with Otidea pseu doformicarum (Fig. 5). Although our species is morphologically similar to Otidea pseu doformicarum 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 subleporina M. Zeng, Q. Zhao & K.D. Hyde, sp. nov.

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 H₂O] (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 distinct 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.

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 Pyromenataceae 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.

   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)  
   Index Fungorum number: IF 103019; Facesoffungi number: FoF 04247
   Saprobie 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 dark 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 H2O] (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)  
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 H₂O] (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).


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, sepaete, with a pointed end. *Medullary excipulum* 55–100 μm thick, composed of *textura intricata*, 3–6 μm broad hyaline hypheae. *Paraphyses* 2–3 μm broad, filiform, hyaline, apex enlarged, 6–10 μm broad. *Asci* 210–250 × 15–20 μm, 8-spored, cylindrical, operculate, inamylid, with a long pedicel and a crozier at the base. *Ascospores* [20/1/1, in H₂O] (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 tetraspera* (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 *Aeuria* 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, *Aeuria* 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.
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 H₂O] (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).


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.

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

Etyymology: 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, inamylloid, with a long pedicel and a crozier at the base. Ascospores [20/1/1, in H2O] (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-leaf forest, elev. 683 m asl., 10 June 2018, Ming Zeng, Zeng 018 (HKAS 124367, paratype); ibid., elev. 568 m asl., 11 June 2018, Ming Zeng, Zeng 025 (HKAS 124367, holotype); ibid., elev. 568 m asl., 11 June 2018, Ming Zeng, Zeng 025 (HKAS 124367, paratype).


Notes – Our new species is similar 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 *Pseudeuleuria*, 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_{2}O] (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-1a: 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_{2}O] (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).

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 red. The newly described species are indicated in blue. Names in bold indicate type collections.

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

Saprobic on soil. Sexual morph: *Apothecia* 0.2–0.5 cm broad, 500–800 μm high, scattered to gregarious, golden 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 H2O] (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-1a: 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).

Fig. 23

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 H2O] (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).

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*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.

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 H2O] (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).


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, inamylloid. 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, ellipsoid, 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 Smardea. 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

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)

Index Fungorum number: IF 332669; Facesoffungi number: 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 H₂O] (24.2−25.8)−(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 Ascii 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).


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 ovoid 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.


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).


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 Svrček (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


Notes – This species was established based on *Ascobolus amethystinus* (Svrček 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 *Diehlomyces*, 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, Planamycetes, 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 ornamentations, but Otideaceae has almost ellipsoid and guttulate ascospores with smooth walls.

Our analyses show that the ancestors of Pyronemataceae, Otideaceae and Pyropyxidaceae had epigeous ascomata. Hypogeous ascomata are present in two distinctly 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, Grule 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.

<table>
<thead>
<tr>
<th>Hypogeous Taxa</th>
<th>Crown age (Mya)</th>
<th>Associated plants (Genus)</th>
<th>Crown age (Mya)</th>
<th>References</th>
</tr>
</thead>
<tbody>
<tr>
<td>Genea/Genabea</td>
<td>51 (29–72.9)/21</td>
<td><em>Abies</em></td>
<td>48.6</td>
<td>Xiang et al. (2015)</td>
</tr>
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<td></td>
<td>(7.3–36.7)</td>
<td><em>Betula</em></td>
<td>6.6</td>
<td>Yang et al. (2019)</td>
</tr>
<tr>
<td></td>
<td></td>
<td><em>Carpinus</em></td>
<td>9.9</td>
<td>Yang et al. (2019)</td>
</tr>
<tr>
<td></td>
<td></td>
<td><em>Castanea</em></td>
<td>19.8</td>
<td>Zhou et al. (2021)</td>
</tr>
<tr>
<td></td>
<td></td>
<td><em>Corylus</em></td>
<td>36.3</td>
<td>Yang et al. (2018)</td>
</tr>
<tr>
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<td></td>
<td><em>Fagus</em></td>
<td>53</td>
<td>Renner et al. (2016)</td>
</tr>
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<td></td>
<td><em>Lithocarpus</em></td>
<td>51</td>
<td>Kua &amp; Cannon (2017)</td>
</tr>
<tr>
<td></td>
<td></td>
<td><em>Nothofagus</em></td>
<td>72.1</td>
<td>Sauquet et al. (2012)</td>
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<td><em>Pinus</em></td>
<td>93.7</td>
<td>Ran et al. (2018)</td>
</tr>
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<td></td>
<td></td>
<td><em>Quercus</em></td>
<td>Ca. 52</td>
<td>Zhou et al. (2022)</td>
</tr>
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<td></td>
<td><em>Salix</em></td>
<td>43.8</td>
<td>Wu et al. (2015)</td>
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<td><em>Tsuga</em></td>
<td>42.2</td>
<td>Havill et al. (2008)</td>
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<td>Gilkeya</td>
<td>8.4 (2.3–16.1)</td>
<td><em>Abies</em></td>
<td>48.6</td>
<td>Xiang et al. (2015)</td>
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<td></td>
<td><em>Quercus</em></td>
<td>Ca. 52</td>
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<tr>
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<td></td>
<td><em>Pinus</em></td>
<td>98.77</td>
<td>Jin et al. (2021)</td>
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<td>Myrmecocystis</td>
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<td><em>Abies</em></td>
<td>48.6</td>
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<td>Picoa</td>
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<td>Ca. 52</td>
<td>Zhou et al. (2022)</td>
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<td>Hypogeous Taxa</td>
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<td>Associated plants (Genus)</td>
<td>Crown age (Mya)</td>
<td>References</td>
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<td>98.77</td>
<td>Jin et al. (2021)</td>
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<td><em>Quercus</em></td>
<td>Ca. 52</td>
<td>Zhou et al. (2022)</td>
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<tr>
<td>Terracavicola</td>
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<td><em>Juniperus</em></td>
<td>43.66</td>
<td>Mao et al. (2010)</td>
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<td><em>Pinus</em></td>
<td>98.77</td>
<td>Jin et al. (2021)</td>
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<td></td>
<td><em>Quercus</em></td>
<td>Ca. 52</td>
<td>Zhou et al. (2022)</td>
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</table>

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