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Phylogenomic systematics of *Lanmaoa* (Boletaceae) reveals cryptic diversity, resolves global evolutionary relationships, and suggests a novel psychoactive lineage

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ABSTRACT

The genus *Lanmaoa* is a globally distributed, economically important group of mushroom-forming fungi in the family Boletaceae containing edible and psychoactive species. Despite the growing interest in its hallucinogenic properties, the fundamental systematics of this genus remains poorly resolved due to limited taxon sampling and limited genetic characterization. This study combines a comprehensive sampling of all *Lanmaoa* species, including 21 type specimens, with whole genome sequencing of 53 specimens. A phylogeny of *Lanmaoa* is generated based upon an alignment of 1515 single-copy orthologs and recovers full statistical support at all major nodes, resolving evolutionary relationships in the genus. Phylogenomic analysis of previously unsequenced type specimens supports several taxonomic changes, including six novel combinations and the discovery of four novel species, two of which are described here—*Lanmaoa fallax*, sp. nov. and *Lanmaoa carbonilivor*, sp. nov.—resulting in a total recognition of 17 species in the genus. Genome mining of *Lanmaoa asiatica* fails to detect canonical biosynthetic genes associated with psilocybin or ibotenic acid production, suggesting the presence of a novel psychoactive compound. This study establishes a comprehensive genomic foundation for *Lanmaoa* systematics, enabling future research to more robustly explore the evolutionary history and secondary chemistry of the genus.

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KEYWORDS

Boletaceae; psychoactive mushroom; systematics; taxonomy; 7 new taxa

INTRODUCTION

Lanmaoa G. Wu, Zhu L. Yang & Halling is a genus of mushroom-forming fungi in the family Boletaceae that contains economically important edible and psychoactive taxa (Wu et al. 2016; Dai et al. 2024). *Lanmaoa* species are characterized by their combination of typically thin hymenophore that bruises blue and an interwoven trichodermium to a subcutis pileipellis (Wu et al. 2016). The type species of the genus, *Lanmaoa asiatica* G. Wu & Zhu L. Yang, was described from a food market in Yunnan, China, where it is regularly consumed by locals and reported to elicit hallucinogenic effects when undercooked (Arora 2008; Wu et al. 2016; Li et al. 2022; Dai et al. 2024). The chemical basis of these reported hallucinogenic effects remains unknown.

The molecular basis for the genus *Lanmaoa* originates from a three-gene phylogenetic analysis of the family Boletaceae in which the undescribed “carminipes clade” was identified, which was composed of four taxa labeled as “*Boletus bicolor* var. *borealis*,” “*Boletus carminipes*,” “*Boletus pseudosensibilis*,” and “*Boletus*

pulverulentus” (Nuhn et al. 2013). A later, four-gene analysis of the Boletaceae, which included additional specimens, also recovered these taxa in a monophyletic undescribed clade (“Clade 49”) composed of seven taxa (Wu et al. 2014).

Based on these phylogenetic findings, the genus *Lanmaoa* was erected, and a set of morphological traits was proposed to distinguish species in this genus (Wu et al. 2016). However, subsequent studies have found these traits to be variable within the genus and shared with species in other Boletaceae genera, effectively undermining their diagnostic utility (Chai et al. 2018). Additionally, most of the vouchers sequenced in the phylogenetic studies by Nuhn et al. (2013) and Wu et al. (2014) were not type specimens. As a result, the species that the phylogeny was presumed to represent and which formed the inferred basis for their taxonomic transfer to *Lanmaoa* may be incorrect.

Among the 12 currently accepted species of *Lanmaoa*, only one has a publicly available internal transcribed spacer (ITS) barcode—the universal fungal DNA barcode used for species-level identification

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(Schoch et al. 2012). Moreover, type specimens from five *Lanmaoa* species have never been sequenced at any genetic locus. Such an absence of molecular data from the original type material prevents unambiguous linkage between modern collections and the correct taxonomic names. Without the reliability of DNA-verified identification, the high degree of morphological variability and convergence observed in Boletaceae mushrooms can make species identification exceedingly difficult (Tremble et al. 2024). This fact not only obscures the true diversity and evolutionary relationships in *Lanmaoa* but also undermines the reliability, accuracy, and utility of specimens deposited in public databases and herbarium collections. Moreover, as *Lanmaoa* species are popular globally traded commercial products, frequent misidentification of wild edible mushrooms with potentially poisonous lookalikes is a both well-documented and serious concern for public food safety and medical practitioners that highlights the need for greater taxonomic understanding (Pérez-Moreno et al. 2020; Zhang et al. 2021).

The phylogenetic studies of *Lanmaoa* performed to date have utilized only one to four genetic loci and have been limited by incomplete taxonomic and geographic sampling (Nuhn et al. 2013; Wu et al. 2014; Chai et al. 2018, 2019). As a result, a comprehensive and well-supported phylogeny for the genus *Lanmaoa* has not yet been achieved. Despite increasing interest in the intriguing psychoactive properties of *L. asiatica*, limited phylogenetic characterization and incomplete sampling hinders a robust understanding of the true diversity, evolutionary relationships, and secondary chemistry of this genus.

This study aimed to (i) reconstruct a robust phylogeny of *Lanmaoa* using whole genome sequences from 53 specimens covering all previously described *Lanmaoa* species, including 21 type specimens, (ii) clarify taxonomic boundaries through molecular analysis of type material, and (iii) investigate the genetic basis of psychoactive compounds in *L. asiatica*.

MATERIALS AND METHODS

Sampling.—To capture potentially novel species and mislabeled collections, voucher specimens deposited in herbaria under the genus name *Lanmaoa* (or respective basionyms), or under the names of the most morphologically similar bolete mushrooms typically misidentified with *Lanmaoa* (e.g., *Boletus bicolor*, *Baorangia bicolor*, *Boletus sensibilis*), were requested for study. Additionally, specimens of *Lanmaoa* and the colloquial “bicolor bolete” lookalikes were donated by citizen scientists across North

America, either as preserved specimens identified as *Lanmaoa* spp. or *Baorangia bicolor* on iNaturalist and Mushroom Observer or as specimens collected fresh during the summer-fall season of 2023 and 2024 (SUPPLEMENTARY TABLE 1).

Genomic data of seven type specimens that were revealed to belong to the *Lanmaoa* and *Baorangia* clades in Tremble et al. (2024) were incorporated in this study (SUPPLEMENTARY TABLE 2). All other type specimens of currently accepted *Lanmaoa* species were requested from their respective holding institutions.

Based on previously published phylogenies of the genus *Lanmaoa* and the family Boletaceae, taxa from the closely related genera of *Cyanoboletus* and *Baorangia* were used as outgroups in the single-gene ITS tree (Chai et al. 2018; Tremble et al. 2024). Genomes for four species in *Cyanoboletus* and *Baorangia* each were selected to serve as outgroups in the phylogenomic tree.

DNA extraction and sequencing.—Approximately 10 mg of dried tissue from each specimen was homogenized in 2.0-mL screw-cap tubes containing a single 3.0 mm and eight 1.5 mm stainless steel beads using a BeadBug microtube homogenizer (Sigma-Aldrich, Saint Louis, Missouri; catalog no. Z763713) for 120 s at a speed setting of 3500 rpm. Next, DNA was extracted using the Monarch Genomic DNA Purification Kit (New England Biolabs, Ipswich, Massachusetts; catalog no. T3010) with the Monarch gDNA Tissue Lysis Buffer (catalog no. T3011) using double the volume of lysis buffer, 1 h of lysis incubation at 56 C, and 600 µL of wash buffer during each of the wash steps.

Aliquots of 2 µL of eluted DNA from each sample underwent polymerase chain reaction (PCR) and barcode sequencing. Samples were amplified using the PCR primers ITS-8 F (5'-AGTCGTAACAAGGTTTCCGTAGGTG-3') and ITS-6 R (5'-TTCCCGCTTCACTCGCAGT-3'), which were designed for higher-specificity amplification of Agaricomycetes (Dentinger et al. 2010), and submitted for Sanger sequencing on the reverse strand at the DNA sequencing core facility at the University of Utah. Sequencing chromatograms were processed by trimming the 5' and 3' ends to conserved motifs 5'-CATTA- and -GACCT-3' following the method in Dentinger et al. (2010) for downstream analysis.

Genomic DNAs were sequenced using 2 × 150 paired-end sequencing on the Illumina NovaSeq sequencing platforms (Illumina, San Diego, California) at the Genomics Core Facility at the University of Utah (Salt Lake City, Utah) and Novogene Corporation (Sacramento, California). All newly generated ITS and

whole genome sequences generated in this study have been uploaded to GenBank (SUPPLEMENTARY TABLES 1 and 2).

Single-gene phylogenetic analysis.—To construct a wide-coverage genetic data set of *Lanmaoa* species diversity, and to inform the selection of representative taxa for whole genome sequencing, phylogenetic analysis was performed on a data set of newly generated ITS sequences and all publicly available ITS sequences for *Lanmaoa* spp. from the National Center for Biotechnology Information (NCBI) (SUPPLEMENTARY TABLE 1). Public sequences were collected using the query “*Lanmaoa*[ORGN] AND ‘internal transcribed spacer,’” yielding 75 results. To capture sequences that may have been misidentified but belong to *Lanmaoa*, additional queries were performed with taxa suspected to belong to *Lanmaoa* but are currently classified in the genus *Boletus* (*B. bicolor*, *B. sensibilis*, *B. “sensibilior,” B. recapitulatus*). Further, the top 50 BLASTn hits of a *Lanmaoa asiatica* ITS sequence (MG030477.1) were also included. Sequences shorter than 400 bp were discarded from the analysis to avoid excessive gaps in the alignment. Finally, ITS sequences were included from Tremble et al. (2024) of seven type specimens (*B. rubissimus*, *L. carminipes*, *L. pseudosensibilis*, *B. miniatopallescens*, *B. sensibilis* var. *subviscidus*, *B. bicolor* var. *subreticulatus*, and *Lanmaoa borealis*) that were revealed to belong to the *Lanmaoa* and *Baorangia* clades.

All ITS sequences were aligned using MAFFT 7.397 (Katoh et al. 2019) with the L-INS-i algorithm. Aligned ITS sequences were manually trimmed to the conserved motifs mentioned previously. A maximum likelihood gene tree was inferred using IQ-TREE 2.0.3 (Minh et al. 2020) with automatic model selection in ModelFinder (Kalyaanamoorthy et al. 2017) and ultra-fast bootstrapping (Hoang et al. 2018) with 1000 replicates. The phylogenetic tree was visualized in FigTree (<http://tree.bio.ed.ac.uk/software/figtree/>).

Genome assembly, ortholog extraction, and phylogenomic analysis.—Raw sequencing reads were quality-filtered and adapter-trimmed using fastp 0.20.1 (Chen et al. 2018) with default settings. Genome assemblies were produced from quality-filtered reads using MEGAHIT (1.2.9) (Li et al. 2016) using eight k-mer values ($k = 21, 29, 39, 59, 79, 99, 119, 141$) and the flags “-no-mercy” and “-min-count 3.” From each genome, 1764 highly conserved single-copy orthologs were identified using BUSCO with the “basidiomycota_odb10” data set. Orthogroups that were present in

less than 95% of taxa were removed using SEGUL (Handika and Esselstyn 2024). Retained orthologs were aligned using MAFFT 7.397 (Katoh et al. 2019) with the L-INS-i algorithm, and maximum likelihood gene trees were inferred using IQ-TREE 2.0.3 (Minh et al. 2020) with automatic model selection in ModelFinder (Kalyaanamoorthy et al. 2017) and ultra-fast bootstrapping (Hoang et al. 2018) with 1000 replicates. A summary-coalescent species tree was constructed from the resulting gene trees using ASTRAL-Hybrid implemented in ASTER* (1.15) (Zhang and Mirarab 2022). A partitioned concatenated data set of all aligned retained orthologs was generated using SEGUL and used to estimate branch lengths in substitutions/site, with the summary-coalescent species tree serving as a topological constraint using the “-te” option in IQ-TREE.

Genome mining for psychoactive biosynthetic gene clusters.—Biosynthetic gene mining was performed on the genome assembly from the holotype of *Lanmaoa asiatica* (HKAS 54094). Gene prediction followed by reciprocal-best BLAST (RBB) was used to identify homologs of genes involved in the production of psilocybin and ibotenic acid. The psilocybin biosynthetic genes searched for were PsiD (tryptophan decarboxylase), PsiK (kinase), PsiM (methyltransferase), and PsiH (cytochrome P450) based on the publicly available chromosomal level assembly for *P. cubensis* (GenBank accession PRJNA700437) (McKernan et al. 2021). The ibotenic acid genes searched for were IboA (adenylation), IboC (cytochrome P450), IboD (decarboxylase), IboF flavin-dependent monooxygenase (FMO), IboG1 pyridoxal phosphate (PLP), IboG2 (PLP), and IboH (hydroxylase) based on the publicly available *Amanita muscaria* genome assembly (GenBank accession PRJNA207684) (Kohler et al. 2015).

Gene prediction was performed using AUGUSTUS (3.5.0) (Stanke et al. 2008). Following gene prediction, the top hits for each biosynthetic gene were determined using BLASTp with default parameters to search for homologs in the predicted translated protein sequences in the *Lanmaoa asiatica* genome. Additional biosynthetic genes clusters involved in secondary metabolite production were examined using antiSMASH (8.0.0) (Blin et al. 2025).

Morphological description of novel species.—Macroscopic features, macrochemical reactions, and habitat of novel species were described through examination of field photographs and original collection notes of fresh voucher specimens. Microscopic features

were observed with a Zeiss Axioscope 5 compound microscope equipped with Nomarski differential interference contrast (DIC) optics (Oberkochen, Germany) and measured from dried material rehydrated in 5% KOH. Spore images were captured in bright field using the equipped Axiocam 705 color camera, and measurements were made in the Zeiss ZEN blue (3.7) software program. Spore dimensions were calculated from 20 individual spores in profile view and are reported as (minimum)low range–high range(maximum).

RESULTS

Sampling.—Type specimens for 11 of the 12 currently accepted species of *Lanmaoa* were successfully acquired. The one exception, *Lanmaoa fragrans*, was described in 1835 (Vittadini 1835) and has no physical collection designated as a type specimen. However, this is a commonly collected and reliably identifiable species, and the voucher of *L. fragrans* acquired from the same country as the original typification was used and is designated here as an epitype. A total of 77 voucher specimens from seven countries were acquired from both herbarium specimens and citizen scientist donations (SUPPLEMENTARY TABLE 1).

Single-gene phylogenetic analysis.—The single-locus ITS sequence alignment was composed of 930 nucleotide sites and 202 sequences, consisting of 125 publicly available sequences from GenBank and 77 newly generated sequences from this study (SUPPLEMENTARY DATA). One hundred seventy-six sequences were confirmed as members of *Lanmaoa*, while 26 sequences from the genus *Baorangia* served as outgroup taxa.

Phylogenetic analysis revealed that five of the eight voucher specimens labeled as *Boletus bicolor* were in fact members of the genus *Lanmaoa*, belonging to three different species, while only three specimens belonged in the genus *Baorangia*. This finding suggests that unrecognized *Lanmaoa* diversity is mislabeled and unrecognized in collection archives under incorrect taxonomic names due to their misidentification with morphologically similar taxa. Similarly, of the 125 public ITS sequences incorporated, 21 were labeled on NCBI as *Boletus bicolor*; phylogenetic analysis revealed 19 (90.4%) of these to belong to *Lanmaoa*, with only two being *Baorangia bicolor*.

The single-gene ITS phylogeny (SUPPLEMENTARY FIG. 1) recovered 16 species clades in the genus *Lanmaoa*. Six clades were identified that represent taxa previously unrecognized in *Lanmaoa*: one species from Colombia, one from Indo-Himalaya, and four from USA. These clades were primarily composed of collections

identified as “*Boletus bicolor*,” “*Boletus* sp.,” “Boletaceae sp.,” or “Boletales sp.” To ensure comprehensive sampling and identify potentially novel *Lanmaoa* species, representative specimens from each unique clade in the ITS tree were selected for whole genome sequencing.

Genome sequencing and assembly.—Whole genome sequences were successfully generated for 11 of the 12 acquired type specimens. The holotype of *Lanmaoa sublurida* (FLAS-F-15869) collected in Florida by Murrill in 1937 was acquired, but DNA could not be successfully extracted. A modern voucher specimen from the type locality (UT-M0002418) that shared 100% ITS sequence identity to collections identified as *L. sublurida* by Farid et al. (2021) was used instead.

Newly generated whole genome sequences of 46 specimens resulted in an average of 41 122 958 paired-end reads per specimen (SUPPLEMENTARY TABLE 2). On average, genome assemblies possessed an assembly N50 of 10.0 kbp (thousand base pairs), total assembly length of 60.0 Mbp (million base pairs), 48 772 contigs, and a BUSCO score of 95.5%. A total of 1759 BUSCO genes were extracted.

Phylogenomic analysis.—Seven previously published genome assemblies from Tremble et al. (2024) were combined with 46 newly sequenced genomes, yielding a final data set of 45 *Lanmaoa* specimens and eight outgroup taxa, including 21 type specimens. After filtering to retain only BUSCO genes represented in over 95% of samples, the final phylogenomic matrix comprised 1515 single-copy orthologs. A summary-coalescent species tree based on individual gene trees recovered full statistical support (local posterior probability = 1.0) across all major nodes of the phylogeny (FIG. 1).

Whole genome sequencing and phylogenomic analysis of type specimens supported multiple taxonomic changes. Of the 12 currently described *Lanmaoa* species, 11 formed a monophyletic group, while one species, *Lanmaoa borealis* (A.H. Sm. & Thiers) Bessette, Nuhn & Halling, was resolved within the genus *Baorangia*. Additionally, *Lanmaoa pseudosensibilis* (A.H. Sm. & Thiers) G. Wu, Halling & Zhu L. Yang was found to be conspecific with *Lanmaoa carminipes* (A.H. Sm. & Thiers) G. Wu, Halling & Zhu L. Yang.

Phylogenomic analysis supported the transfer of five species from *Boletus* to *Lanmaoa*: *Boletus rubissimus* A. H. Sm., *Boletus carminiporus* Bessette, Both & Dunaway, *Boletus pyrrhosceles* Halling, *Boletus recapitulatus* D. Chakr., K. Das, Baghela, S.K. Singh & Dentinger, and *Boletus miniatopallescens* A.H. Sm. & Thiers. Among these, *B. rubissimus* and *B. pyrrhosceles*

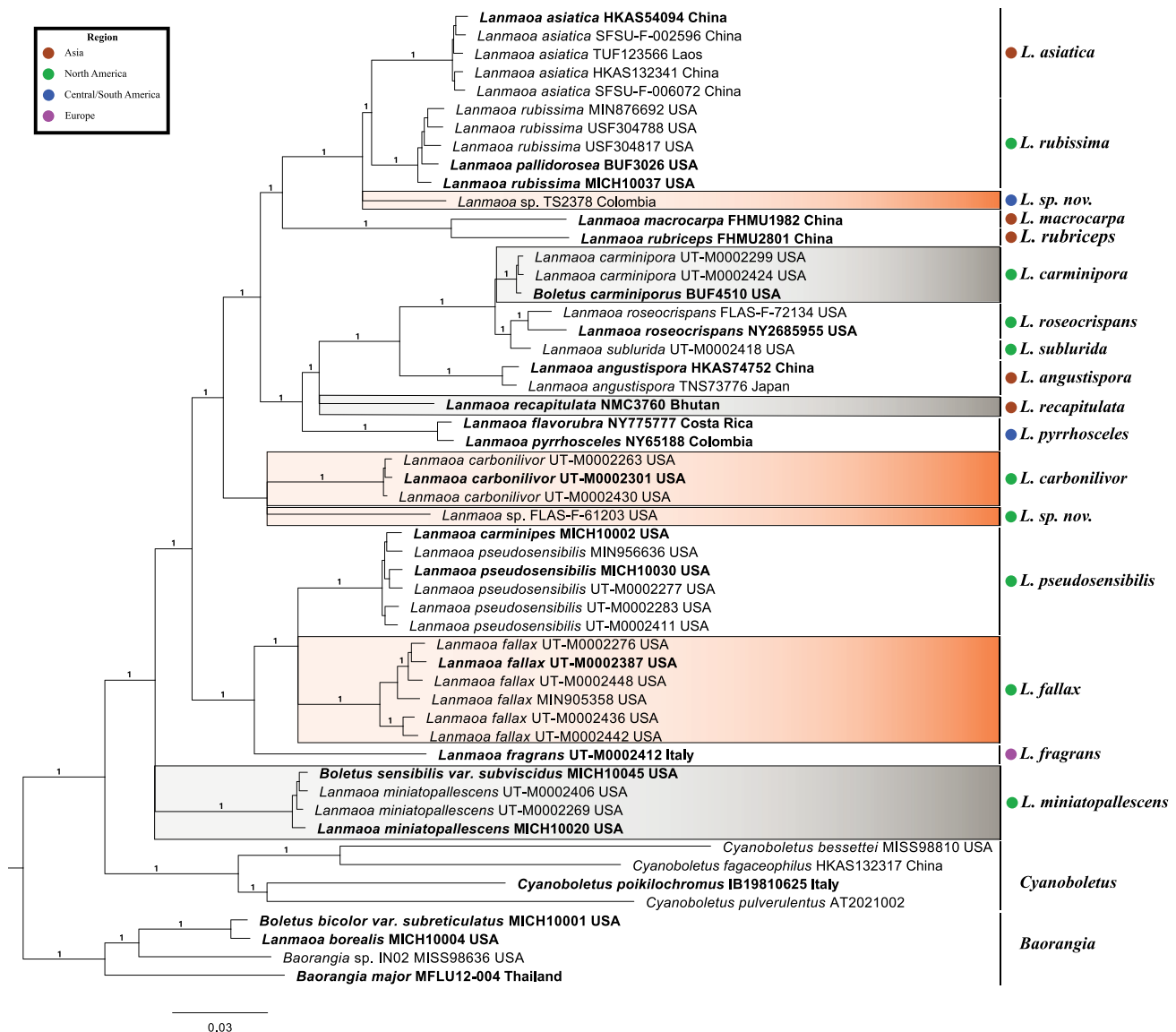


Figure 1. Summary-coalescent phylogeny of 1515 individual gene trees. Branch lengths in substitutions/site were estimated using maximum likelihood in IQ-TREE. Clades highlighted in orange and gray signify newly identified species and combinations in the genus *Lanmaoa*, respectively. Tip labels highlighted in bold denote type specimens. Branch labels represent ultrafast bootstrap support values with 1000 replicates. Scale bar shows substitutions per site.

were found to be conspecific with the previously named *Lanmaoa pallidrosea* and *L. flavorubra*, respectively. Due to nomenclatural priority, these earlier names are adopted in this study. Likewise, the holotype of *B. sensibilis* var. *subviscidus* A.H. Sm. & Thiers was found to be conspecific with *B. miniatopallescens*. However, the holotype of *Boletus sensibilis* Peck remains unsequenced and therefore cannot be confirmed as a member of *Lanmaoa*. Altogether, five new combinations are proposed, three of which represent previously unrecognized members of *Lanmaoa*.

Additionally, four novel species were discovered, two of which are described in this study—*Lanmaoa fallax*

(FIG. 2) and *Lanmaoa carbonilivora* (FIG. 3). Two other novel species remain undescribed due to insufficient material. One of the undescribed novel species was collected in Colombia and is closely related to *L. asiatica* and *L. rubissima*. The other novel undescribed species is sister to *Lanmaoa carbonilivora* and comes from a single collection from Florida.

In total, seven novel *Lanmaoa* taxa were recognized—composed of three new combinations and four new species—bringing the total number of accepted species in the genus to 17. These species cover a widespread geographic distribution: nine are known from North America, five from Asia, two from Central/South

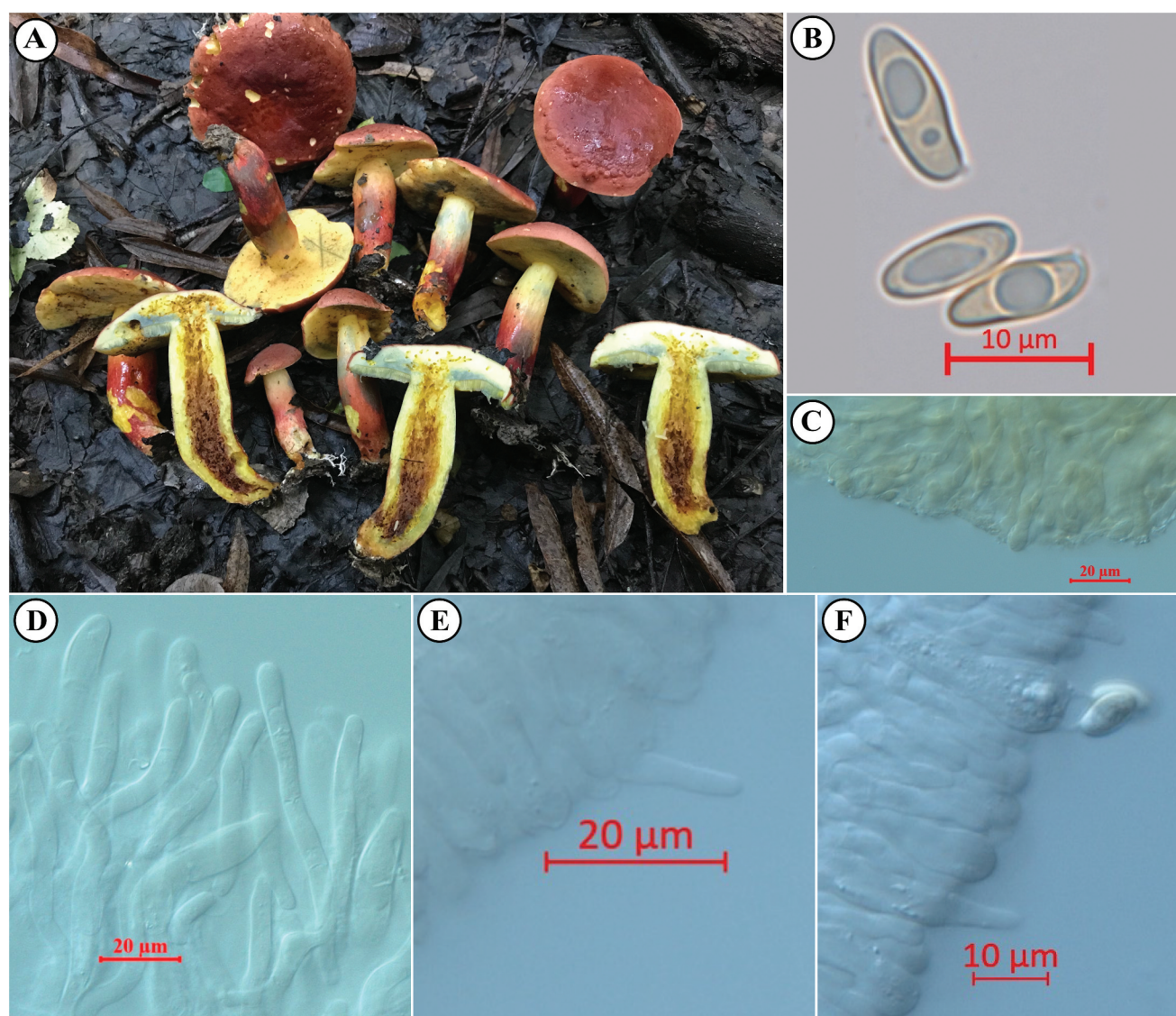


Figure 2. Basidiomata and micromorphological characteristics of *Lanmaoa fallax*. A. Fresh basidiomata (UT-M0002387; image permission Logan Wiedenfeld). B. Spores in KOH (UT-M0002387). C. Stipitipellis (UT-M0002387). D. Pileipellis (UT-M0002387). E. Pleurocystidium (UT-M0002387). F. Basidium (UT-M0002387).

America, and one from Europe. All *Lanmaoa* spp. appear to form ectomycorrhizal associations exclusively with *Quercus* host trees, except two: *L. asiatica* and *L. recapitulata*, which have been reported to grow with *Pinus* and *Betula*, respectively (Chakraborty et al. 2015; Wu et al. 2016). Finally, all the red-pored species of *Lanmaoa* (*L. pyrrhosceles*, *L. recapitulata*, *L. subulrida*, *L. angustispora*, and *L. carminipora*) have been recovered as a monophyletic clade.

Genome mining for psychoactive biosynthetic gene clusters.—The RBB results from the holotype of *Lanmaoa asiatica* (HKAS 54094) found no close hits with any of the psilocybin or ibotenic acid biosynthetic genes (see SUPPLEMENTARY DATA). The predicted

biosynthetic gene cluster (BGC) types from running antiSMASH on *Lanmaoa asiatica* (HKAS 54094) included NRPS, NRPS-like, Terpene, Hybrid (T1PKS + Terpene), and Fungal RiPP-like (see SUPPLEMENTARY DATA). The only matches to known BGCs were atromentin and (+)- δ -cadinol.

TAXONOMY

Baorangia bicolor (Kuntze) G. Wu, Halling & Zhu
L. Yang

Index Fungorum IF551143

Typus: Peck s.n.

Synonyms: *Boletus bicolor* var. *borealis* A.H. Sm. & Thiers, *Boletes* of Michigan (Ann Arbor):277 (1971),

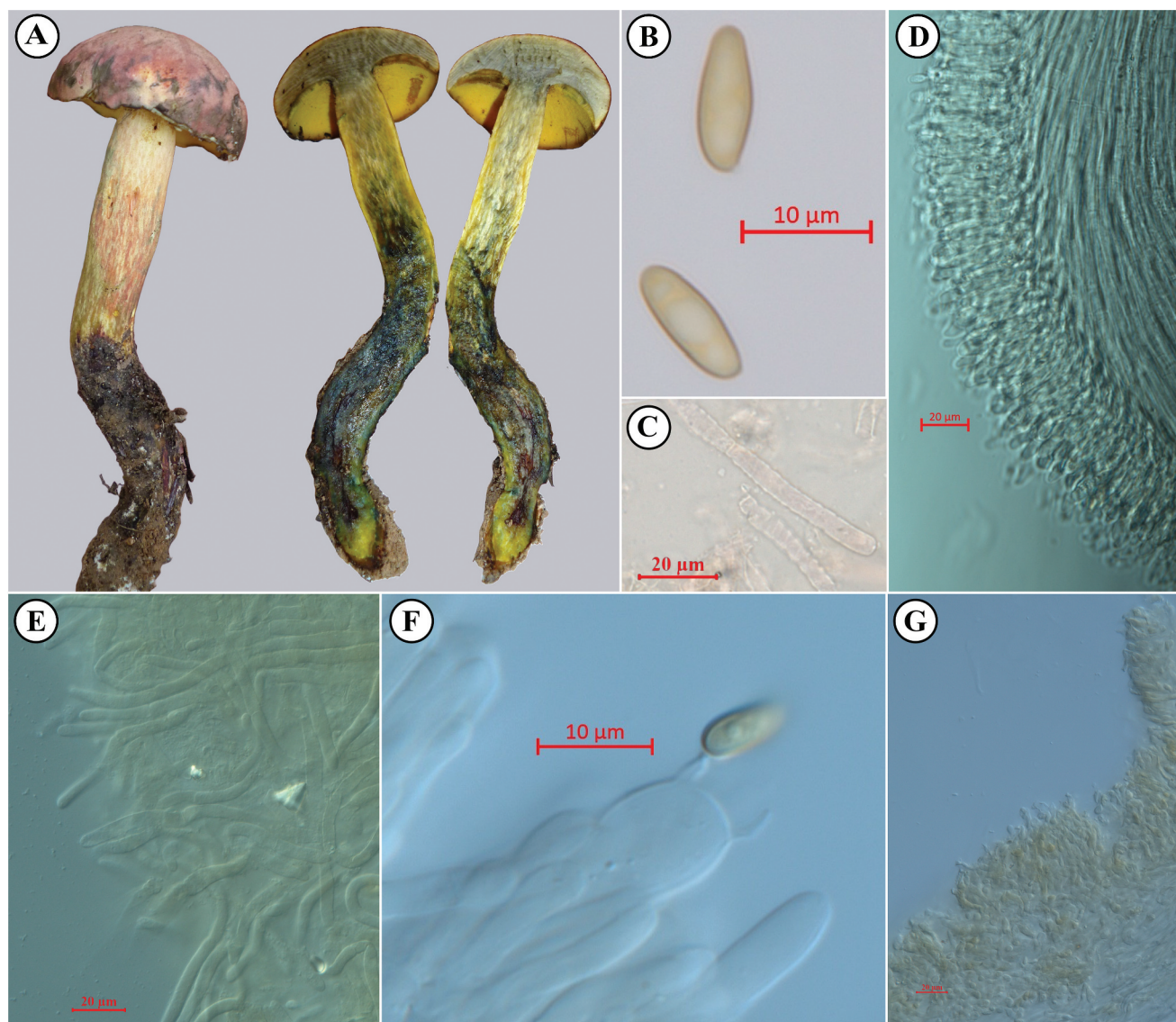


Figure 3. Basidiomata and micromorphological characteristics of *Lanmaoa carbonilivor*. A. Fresh basidiomata (UT-M0002301; image permission Igor Safonov). B. Spores in KOH (UT-M0002301). C. Encrusted hyphae in pileipellis stained with phloxine (UT-M0002301). D. Hymenophore trama and pleurocystidia (UT-M0002301). E. Pileipellis (UT-M0002301). F. Basidium and pleurocystidium (UT-M0002301). G. Stipitipellis (UT-M0002301).

syn. nov.; *Boletus bicolor* var. *subreticulatus* A.H. Sm. & Thiers, *Boletes of Michigan* (Ann Arbor):278 (1971), syn. nov.

Evidence: Phylogenetic; holotypes sequenced (this study).

Notes: *Boletus bicolor* Peck was described from the northeast USA and later combined to *Baorangia bicolor* (Kuntze) G. Wu, Halling & Zhu L. Yang by Wu et al. (2016). Phylogenomic analysis of the two varieties described by Smith and Thiers, *Boletus bicolor* var. *borealis* and *Boletus bicolor* var. *subreticulatus*, also from the northeastern USA, revealed their placement in *Baorangia*.

Lanmaoa fragrans (Vittad.) Vizzini, Gelardi & Simonini

MycoBank MB508332

Typus: Italy, Latium, Oriolo Romano (Viterbo), 450 m, on acidic soil under *Quercus cerris* and *Corylus avellana* with the presence of *Castanea sativa* and *Fagus sylvatica*, 7 Oct 2019, legit. and det. M. Gelardi & F. Costanzo, MG780 (epitype UT-M0002412; isoeotype Matteo Gelardi personal herbarium MG780).

Notes: The original description by Vittadini (1835) lacks designation of a physical type specimen.

Lanmaoa rubissima (A.H. Sm) Domnauer & Dentinger, comb. nov.

Index Fungorum IF903800

Typus: USA, Michigan, Oakland, Haven Hill, Highland State Recreation Area, 42.6413, –83.5637, 25 Jul 1972, A.H. Smith 81187 (holotype MICH 10037).

Basionym: *Boletus rubissimus* A.H. Sm., Persoonia 7(2):325 (1973).

Synonym: *Lanmaoa pallidorozea* (Both) Raspé & Vadthanarat, in Phookamsak et al. Fungal Diversity 95:207 (2019).

Evidence: Phylogenetic; holotype sequenced (Tremble et al. 2024).

Lanmaoa carminipora (Bessette, Both & Dunaway) Domnauer & Dentinger, comb. nov.

Index Fungorum IF903799

Typus: USA. MISSISSIPPI: Pike County, McComb, 6 Aug 1996, A.E. Bessette 10648 (holotype BUF 4510)

Basionym: *Boletus carminiporus* Bessette, Both & Dunaway, in Bessette, Both, Bessette, Dunaway & Roody, Bull Buffalo Soc Nat Sci 36:234 (1998).

Evidence: Phylogenetic; holotype sequenced (this study).

Lanmaoa recapitulata (D. Chakr., K. Das, Baghela, S.K. Singh & Dentinger) Domnauer & Dentinger, comb. nov.

Index Fungorum IF903797

Typus: INDIA. SIKKIM: East District, Churten, 1454 m, 27.56969, 88.43108, 25 May 2014, K. Das DC 14-001 (holotype CAL, Das DC14-001).

Basionym: *Boletus recapitulatus* D. Chakr., K. Das, Baghela, S.K. Singh & Dentinger, Phytotaxa 236(2):151 (2015).

Evidence: Phylogenetic; voucher sequenced (this study).

Lanmaoa miniatopallescens (A.H. Sm. & Thiers) Domnauer & Dentinger, comb. nov.

Index Fungorum IF903798

Typus: USA. MICHIGAN: Washtenaw County, Chelsea, 42.3181, –84.0206, 1 Aug 1935, A.H. Smith 1692 (holotype MICH 10020)

Basionym: *Boletus miniatopallescens* A.H. Sm. & Thiers, Boletes of Michigan (Ann Arbor):272 (1971).

Synonym: *Boletus sensibilis* var. *subviscidus* A.H. Sm. & Thiers, Boletes of Michigan (Ann Arbor):286 (1971).

Evidence: Phylogenetic; holotype sequenced (Tremble et al. 2024).

Lanmaoa pyrrhosceles (Halling) Domnauer & Dentinger, comb. nov.

Index Fungorum IF903928

Typus: COLOMBIA. NARIÑO: Pasto. km 17 on the road from Pasto to Chachagui, ‘La Josefina’ rural district, 20 Nov 1988, Franco-M. 172 (holotype NY65188).

Basionym: *Boletus pyrrhosceles* Halling, Brittonia 44(3):322 (1992)

Synonym: *Lanmaoa flavorubra* (Halling & M. Mata) G. Wu, Halling & Zhu L. Yang, in Wu, Zhao, Li, Zeng, Feng, Halling & Yang, Fungal Diversity 81:10 (2015).

Evidence: Phylogenetic; holotype sequenced (this study).

Lanmaoa fallax Domnauer, I. Safonov, Kudzma & Dentinger, sp. nov.

Index Fungorum IF903801

Typification: USA. LOUISIANA: Baton Rouge, 18 Jun 2018, L. Wiedenfeld 213 (holotype UT-M0002387). GenBank: ITS = PV694397.

Diagnosis: *Lanmaoa fallax* is phylogenetically closest to *Lanmaoa pseudosensibilis* but differs from the latter by its overall less intense blue-staining in the context that does not fade to brown. *L. fallax* may appear superficially similar to *L. rubissima* but differs from the latter by its lack of odor.

Etymology: The species epithet “fallax” means deceptive and refers to its morphological variability.

Description: Pileus 5–14 cm wide, convex when young, flattening to planar in age, margin distinctly incurved, thin and glabrous marginal band, color variable, rose pink to maroon to deep mahogany, fading to a reddish brown in age, sometimes cracking in age. Cap color unchanged when dehydrated. Hymenophore yellow, becoming olive-yellow in age, blueing when bruised, centrally depressed around the stipe. Stipe: 5–8 cm, not reticulated, cylindrical to ventricose, strongly tapered toward base, smooth, sometimes longitudinally striate with red streaks, color light red to burgundy, darkest at the base, often fading to pale yellow toward apex, cracking in age, lightly blueing where handled and damaged, basal mycelium white. Context lemon yellow in stipe, brightest toward the base fading to pale yellow to white in pileus, erratically and weakly blueing slowly in hymenial and pileal contexts, rarely blueing in stipe, flesh firm and dense, stipe interior frequently consumed by insect larvae, golden yellow when dehydrated, odor not distinctive, taste slightly sweet to indistinct. Spore deposit olive-brown.

Micromorphology: Basidiospores in 5% KOH (8.7–)9.2–10.6(–11.5) × (4.0–)4.1–4.7(–4.9) μm (n = 20), smooth, subfusiform, hyaline to light brown. Basidia clavate, hyaline, 4-sterigmate. Pleurocystidia present, subventricose with a narrow, rounded apex. Pileipellis a loosely interwoven trichodermium with hyphae rounded to obtuse apices, thin-walled, finely

roughened to smooth, hyaline in KOH. Stipitipellis loosely fasciculate, parallel to loosely interwoven hyphae, yellow to ochraceous in KOH. Clamp connections absent.

Habitat and distribution: Growing with *Quercus*. Common across the eastern USA, with a few collections from the western USA.

Additional specimens examined: USA. LOUISIANA: Baton Rouge, 18 Jun 2018, UT-M0002387; *ibid.*, 16 Oct 2017, UT-M0002276; MISSOURI: St. Louis County, 9 Aug 2016, UT-M0002448; PENNSYLVANIA: Bellevue, 40.4964, -80.0546, 4 Jul 2023, UT-M0002446.

Lanmaoa carbonilivor Domnauer, I. Safonov, Kudzma & Dentinger, sp. nov.

Index Fungorum IF903810.

Typification: USA. NEW JERSEY: Stokes State Forest, 200 m, 27 Aug 2017 (**holotype** UT-M0002301). GenBank: ITS = PX991780.

Diagnosis: *Lanmaoa carbonilivor* is morphologically similar to *L. miniatopallescens* but differs from the latter by its overall smaller fruiting body size and distinct curry-like odor.

Etymology: The species epithet refers to the charcoal-black-colored staining on the pileus.

Description: Pileus 3–6 cm wide, pulvinate to convex, margin incurved slightly undulating, surface dry and smooth, color solid “Morocco red,” fading to brick red to brown in age, occasionally mottled with yellow patches, quickly bruising intense blue fading to charcoal-gray, KOH dark mahogany brown to cherry red, NH₄OH muddy yellow to greenish amber yellow. Context mustard yellow to pale yellow-white, brightest yellow along stipe margin, rapidly staining blue throughout, often most intense bruising in bottom of stipe, slowly fading to brownish gray, KOH orangish brown on the flesh after blueing fades, distinct bouillon/curry odor, taste unknown. Hymenophore adnate, tubes 2–6 mm deep, bright yellow, color not dulling in age, rapidly staining blue to grayish blue when bruised. Stipe 4–7 cm long, equal to ventricose, often tapering downward with a pinched base, solid surface smooth at the apex, pale yellow from base to apex, with faint streaks or patches of red, turning blue when bruised or handled, basal mycelium white. Spore deposit unknown.

Micromorphology: Basidiospores in 5% KOH (9.8–)9.9–11.7(–12.4) × (3.6–)3.7–4.3(–4.5) μm (n = 20), smooth, subfusiform, hyaline to light brown. Basidia clavate, hyaline, 4-sterigmate. Pleurocystidia present, subventricose with a narrow, rounded apex. Pileipellis a poorly differentiated ixotrichoderm to interwoven trichoderm; hyphae narrow, tightly interwoven in a subgelatinous matrix, surface appearing finely

roughened and undulating margin due to ring-like annular incrustations, hyaline to pale yellowish in KOH. Stipitipellis a dense tomentum of erect to suberect, loosely fasciculate hyphae; terminal cells clavate to irregularly inflated, thin-walled, pale yellowish to ochraceous in KOH, often constricted at septa giving a moniliform appearance. Clamp connections absent.

Habitat and distribution: Growing in mixed hardwood forests, presumably with *Quercus* or possibly *Tsuga*. Known only from northeast North America.

Additional specimens examined: USA. NEW JERSEY: Stokes State Forest, 27 Aug 2017, UT-M0002301; *ibid.*, 25 Jun 2017, UT-M0002263; Tourne County Park, 26 Jul 2017, UT-M0002430.

DISCUSSION

Despite its economic importance in China and intriguing chemistry, the genus *Lanmaoa* has been subject to few systematic studies, none of which have incorporated a globally representative sampling of species diversity or utilized sufficient molecular data to completely resolve the evolutionary relationships in the genus. The present study addressed this knowledge gap by combining comprehensive taxon sampling with whole genome sequencing of 53 specimens, including the type specimens of 11 of the 12 previously described species of *Lanmaoa*. Phylogenomic analysis led to the recognition of seven new members in the genus and clarification of species relationships and nomenclature. This study resolved the backbone relationships in the *Lanmaoa* phylogeny with full statistical support, enabling more robust insights and analyses of the evolutionary history of this genus.

The novel species described in this study, *Lanmaoa fallax* and *Lanmaoa carbonilivor*, had been collected for decades in North America but were misidentified and subsequently mislabeled in herbaria under the names of morphologically similar species. This erroneous conflation was not recognized until these specimens underwent genetic sequencing and were revealed to be genetically distinct. In fact, these new species are necessarily closely related to the taxa they were often conflated with. Sequencing of voucher specimens in this study revealed that much cryptic diversity remains hidden under misapplied taxonomic names.

Importantly, the diagnostic macroscopic features originally proposed to differentiate the genus *Lanmaoa*, such as “thickness of hymenophore ½–times that of pileal context” and “context that bruises blue,” are not reliably observed in all species in our expanded and revised classification of *Lanmaoa* and have also been found to occur in distantly related clades of Boletaceae (Wu et al.

2016, 83; Chai et al. 2018). For example, the genus *Hongoboletus*, which was not discovered until after the description of *Lanmaoa*, similarly exhibits an extremely shallow hymenophore relative to the pileal context (Wu et al. 2023).

Such morphological convergence across the wider Boletaceae family has led to erroneous taxonomic identifications, including in *Lanmaoa*. For example, on the basis of fitting the presumed diagnostic morphological characters, combined with phylogenetic evidence of a voucher specimen “2858 *Boletus bicolor* var. *borealis*,” *Boletus bicolor* var. *borealis* was transferred to *Lanmaoa borealis* (Nuhn et al. 2013; Wu et al. 2014). However, the name applied to this voucher specimen turned out to be incorrect, as subsequent sequencing by Tremble et al. (2024) proved that the type specimen of *Boletus bicolor* var. *borealis* actually belongs in *Baorangia*. This finding highlights the potential pitfalls of morphologically based classification and underscores the importance of using molecular methods for accurate identification. Although individual species of *Lanmaoa* can be morphologically distinguished, we are unable to ascertain any individual morphological feature, or set of features, that uniquely differentiates and characterizes the genus *Lanmaoa* from other genera of Boletaceae. The phylogenetic data and analyses generated in this study therefore provide a valuable authenticated basis for future identification and reliable study of *Lanmaoa* species.

Biosynthetic gene mining of the *Lanmaoa asiatica* genome found no close hits with any genes known in the production of mushroom psychoactive compounds. This supports our hypothesis of the presence of a novel unidentified metabolite responsible for the unique hallucinogenic properties of *Lanmaoa asiatica*. This finding corroborates observational and clinical data, which report drastically different psychological and physiological symptoms following *Lanmaoa asiatica* intoxication compared with psilocybin or ibotenic acid (Linchu and Kuang 1991; Dai et al. 2024). The phylogeny and genomic data provided in this study may support future drug discovery efforts, as well as research into the evolution and phylogenetic distribution of the potentially important bioactive secondary chemistry within the genus *Lanmaoa*.

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DISCLOSURE STATEMENT

No potential conflict of interest was reported by the author(s).

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DATA AVAILABILITY STATEMENT

All newly generated ITS and whole genome sequences are deposited on the National Center for Biotechnology Information (NCBI). The accession numbers for each specimen can be found in SUPPLEMENTARY TABLES 1 and 2. All genome assemblies, multiple sequence alignments, and raw tree files are publicly available through Figshare (<https://doi.org/10.6084/m9.figshare.29150444>).

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