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First report of *Caloboletus guanyui* (Boletaceae) in India: Taxonomic and phylogenetic insights from Mizoram

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Abstract

The family Boletaceae primarily consists of ectomycorrhizal fungi, which are essential for maintaining the health of forest ecosystems. These fungi form symbiotic relationships with trees, facilitating nutrient exchange and enhancing plant growth. In the present study, specimens of *Caloboletus guanyui* were collected from the Mizoram University campus during the rainy season of 2023. Identification was based on both morphological characteristics and molecular analysis of the ITS region of rDNA, with phylogenetic analysis further confirming the distinctiveness of *Caloboletus guanyui* from closely related species within the genus *Caloboletus* Vizzini. This medium-sized to large bolete is characterized by its dirty-white to pale-brown pileus and the basidiospores are elliptic-fusiform (spindle-shaped) to subfusiform 9.5–11.5 × 3.5–4.5 µm. This study represents the first recorded occurrence of *Caloboletus guanyui* in the tropical moist deciduous forests of Mizoram, India, thereby expanding the known distribution of this species. These new findings enhance our understanding of bolete diversity in India, particularly within the unique forest ecosystems of Mizoram.

Keywords

Boletales; ectomycorrhizal fungi; macrofungi; phylogeny; taxonomy

Introduction

Boletaceae Chevall., is a monophyletic group of fleshy, sequestrate, or pileate-stipitate macrofungi with a lamellate or tubular hymenophore (1). It has been widely studied worldwide, contributing valuable insights into their morphology, molecular phylogeny, and ecology. Advancements in molecular tools for studying Boletes have greatly increased the number of recognized genera in this family. Around 1,200 species and 100 genera of Boletaceae have been documented globally, with 65 genera proposed based on molecular evidence (2). However, due to their morphological complexity and the limited phylogenetic data on the numerous species and genera, our understanding of their systematics and evolution remains rather rudimentary (3). Macrofungi from the basidiomycete family Boletaceae Chevall., is a large, cosmopolitan family with abundant species and are ecologically and commercially significant. They are rich in nutrients and have potential health-promoting properties, making them valuable not only for their ecological roles but also as functional foods that can contribute to human health (4-6). They are integral components of the Indian ecosystem, contrib-

uting significantly to nutrient cycling and soil health through their roles as decomposers. Their ectomycorrhizal associations with various tree species enhance nutrient availability and plant resilience, thereby facilitating forest dynamics and promoting biodiversity (7). Currently, boletoid mushrooms comprising 96 species from 27 genera have been documented in India (8).

The genus *Caloboletus* Vizzini is characterized by yellow to olive-yellow tubes and occasionally orange to red pores that turn bluish when injured. It has a distinctly bitter taste due to specific chemical compounds, calopin and cyclocalopin (9). They are primarily found in subtropical and temperate zones within the Holarctic region and are commonly associated with plants from the Pinaceae and Fagaceae (10). The genus differs from all other genera of Boletaceae in its yellowish or reddish surface of the stipe, bluish color changed when bruised and pilleipellis composed of interwoven filamentous hyphae (11). Limited information is available on *Caloboletus* species in India. *Caloboletus calopus* (reported as *Boletus calopus*) and *Caloboletus rubriceps* (reported as *Boletus rubripes*) has been reported from Sikkim, India (12-13). This was further noted in a comprehensive checklist of 88 species within the Boletaceae family, which reported no additional *Caloboletus* species (14). Furthermore, based on the descriptions provided, Zhao et al. (10) suggested that the Indian specimen identified by Das (13) as *B. rubripes* likely corresponds to *C. panniformis*. The genus *Caloboletus* Vizzini display distinct geographical patterns as *C. calopus* and *C. radicans* remain confined to Europe, while *C. firmus* and *C. inedulis* are limited to North and Central America. In East Asia, several species, including *C. panniformis*, *C. yunnanensis*, *C. taienus*, and *C. xiangtoushanensis*, have been documented (9-10,15).

Mizoram is unique in many aspects such as rich floristic composition, high annual precipitation undulated topography and varying types of forest ecosystem which is complemented by a variety of macrofungi found throughout its different districts (16-18). More than 264 macrofungal species have been documented in Mizoram. Among these, the order Boletales includes two main families, Boletaceae (7 genera, 11 species) and Sclerodermataceae (2 genera, 3 species), making a total of 14 species within the order Boletales (19). Although macrofungi have been studied in particular areas over the past decades, there is still a lack of documented fungal species from Mizoram compared to other states in India. This highlights a knowledge gap, particularly regarding *Caloboletus* species in India, suggesting the potential for a wider distribution of this genus. In light of this, the present study describes and illustrates *C. guanyui* for the first time from the tropical moist deciduous forests of Mizoram University, Mizoram, India.

Materials and Methods

Three specimens were collected during July–August 2023 from the campus of Mizoram University, Aizawl Mizoram, India, located between the coordinates 23° 45'25" N to 23° 43'37" N latitude and 92° 38'39" E to 92° 40'23" E longitude. The forested regions of the campus are characterized by porous, sandy loam, and humus-rich soils, which provide a fertile environment for vegetation. Mizoram University campus covers an area of approximately 980 acres (Fig. 1).

Fig. 1. Map of the Mizoram University campus [adapted from Lalchhuanawma (28)].

Morphological studies

The collected specimens were maintained in paper bags for transport to the laboratory and identified using standard macroscopic (pileus, context, hymenophore, tubes, stipe, and odor) and microscopic (basidiospores, basidia, cystidia, pileipellis, and stipitipellis) characteristics in consultation with relevant literature (3,9-11,20). Photographs of the fruiting bodies were taken using Nikon-D7500. Location, date, temperature (°C), relative humidity (RH), elevation, coordinates and type of plants prevailing in the collection area of the specimen and their habits were documented. Color description was based on Kornerup and Wanscher (21). The macroscopic description, including shape, size, and color of the basidiocarps were documented from fresh sample in the fields. Microscopic characteristics were examined from both fresh and dried specimens using a light microscope (Carl ZEISS Axio Lab.A1) after sectioning and directly staining with 5% potassium hydroxide (KOH), Lactophenol cotton blue (LPCB) and Melzer's reagent (Hi-ARTM, India). Sections of the pileipellis were cut radially and perpendicularly halfway between the center and the margin of the pileus. For the stipitipellis, sections were taken from the middle part along the longitudinal axis of the stipe. Microscopic structures were drawn freehand to capture fine details observed under the microscope more precisely.

DNA extraction, PCR and sequencing of the specimen

For molecular identification, following Zothanzama et al. (18) and reference therein, a small piece of tissue from the fruiting body of the specimen was added to a sterile 1.7 mL

micro centrifuge tube with glass beads and 500 µL of cetyltrimethylammonium bromide (CTAB) lysis buffer, then vortexed for 1 minute. After a brief centrifugation, the supernatant was transferred to a new tube and incubated at 65°C for 20 minutes. Following this, 500 µL of chloroform (Hi-ARTM, India) was added, mixed, and the mixture was centrifuged at 13,000 rpm for 5 minutes. The upper layer of the supernatant was transferred to another tube, and two-thirds of the volume was mixed with isopropanol and stored at -20°C. After 5 minutes at room temperature, the mixture was centrifuged at 15,000 rpm for 7 minutes. The supernatant was removed, and the pellet was washed with 500 µL of 70% ethanol (Hi-ARTM, India), and then centrifuged at 15,000 rpm for 3 minutes. The ethanol was evaporated, and the DNA pellet was re-suspended in 100 µL of sterile water. PCR reactions were set up in 0.2 mL tubes with 12.5 µL GoTaq Green Mastermix (Promega), 9.5 µL nuclease-free water, 1 µL forward primer (5 µM), 1 µL reverse primer (5 µM), and 1 µL fungal DNA template, making up the volume up to 25.5 µL. PCR was performed with primers ITS1-F and ITS4-R using the following conditions: 94°C for 5 minutes, followed by 35 cycles of 94°C for 1 minute, 52°C for 1 minute, and 72°C for 1 minute, with a final extension at 72°C. PCR products were checked by electrophoresis on a 1% agarose gel with SYBR green and visualized using a Gel Documentation System. Sequencing was done using Sanger sequencing with both primers. Consensus sequences were trimmed and aligned using BioEdit and compared to GenBank entries using BLASTn. The aligned sequences were analyzed with Clustal W.

Phylogenetic analyses

To construct the phylogeny of major lineages, representative taxa from the primary species were selected. Model testing and Maximum Likelihood (ML) phylogenetic analyses were performed using RAxMLGUI 2.0 (22), with recommended parameters to determine the best tree topology and bootstrap support values from 1000 search replicates, which were summarized in FigTree. Model testing was conducted using the inbuilt ModelTest-NG program (23). GTR+I+G was selected and found to be the optimal substitution model based on the corrected Akaike Information Criterion (24).

Results and Discussion

The description of the specimen, including macroscopic and microscopic characteristics, habitat, known distribution, an illustration of the fruiting bodies and a phylogenetic tree of the specimen with related species obtained using the Maximum Likelihood method based on the ITS region is presented.

Caloboletus guanyui N.K. Zeng, H. Chai & S. Jiang

Description of the specimen

Macroscopic characters: Pileus 5.5–11 cm diam., convex to nearly flat; surface dry, finely tomentose, white to pale brown. Context 0.6–2 cm thick, white, bruising bluish when injured, then back to white. Hymenophore poroid, depressed around apex of stipe; pores subround, 0.3–0.6 mm diam., reddish brown, then yellowish brown, bruising bluish black when injured; tubes 0.6–1.2 cm, yellowish then changing to bluish when injured. Stipe 5.5–9.5 x 0.8–1.6 cm, central, subcylindrical, solid, surface dry, covered with pale brown to reddish brown, minute squamules; context white; with white basal mycelium, Odor indistinct. *Microscopic characters*: Basidiospores 9.5–11.5 × 3.5–4.5 µm (n=30), elliptic-fusiform (spindle-shaped) to subfusiform, yellowish brown in KOH, smooth. Basidia 20–32 × 6.5–8.5 µm (n=30), clavate, thin-walled, yellowish in KOH; 4-spored, sterigmata 3.2–4 µm. Cheilocystidia 26–43 × 7–10 µm, fusiform, thin-walled, yellowish in KOH. Pleurocystidia 34–45 × 6–11.5 µm, fusiform, thin-walled, colorless to yellowish in KOH. Pileipellis a trichoderm about 100–200 µm thick, composed of slightly interwoven, 5–8.5 µm wide, thin-walled hyphae; terminal cells 26–35 × 5.5–10.5 µm, clavate or subclavate, with obtuse apex. Stipitipellis hymeniform, 80–100 µm, composed of thin-walled emergent hyphae, clavate, subclavate, fusiform, four-spored basidia. Clamp connections absent.

Habitat

Gregarious on the ground in tropical moist deciduous forests dominated by *Aporusa octandra* (Buch.-Ham. ex D.Don) A.R.Vickery, *Castanopsis tribuloides* (Sm.) A.DC., and *Saurauia punduna* Wall.; during summer and fall, in monsoon season.

Distribution and Ecology

Japan (25), southeastern and southern China (20), and India (present report). This species grows on soil, typically in habitats with a mixed canopy of both understory and canopy trees, alongside fallen tree trunks and a layer of leaf litter covering the ground.

Specimen examined

India, Mizoram, Aizawl district, Mizoram University campus, on soil, elevation 848 m (2782.15 ft), 26 July 2023 (24.3°C and 87.1% RH), 23°44'21.8"N 92°39'58.7"E, Thachunglura VL and Zohmangaiha C, MZU/JZT-VL/2022/036 (Fig. 2).

Notes

Phylogenetic tree of *C. guanyui* and related species obtained with Maximum Likelihood method based on the ITS region. Numbers below the branches are bootstrap percentage values based on 1000 replicates, ML/MP bootstrap support values greater than 50% (Fig. 3). *Fomitopsis eucalypticola* was used as outgroup. The sequence of our fungal isolate *C. guanyui* from Mizoram, India was compared to 36 corresponding sequences of reference fungal taxa in the database and the list of species, voucher number, GenBank accession number and locality used for the analysis is given in Table 1.

In the phylogenetic analysis, our species *C. guanyui* (PQ288749) is clustered within the *C. guanyui* clade, which is highlighted in blue colour. This clade also includes sequences of *C. guanyui* submitted by Chai et al. (20) such as MH885364, MH885365, and MH885366, indicating a close phylogenetic relationship among them. Additionally, this

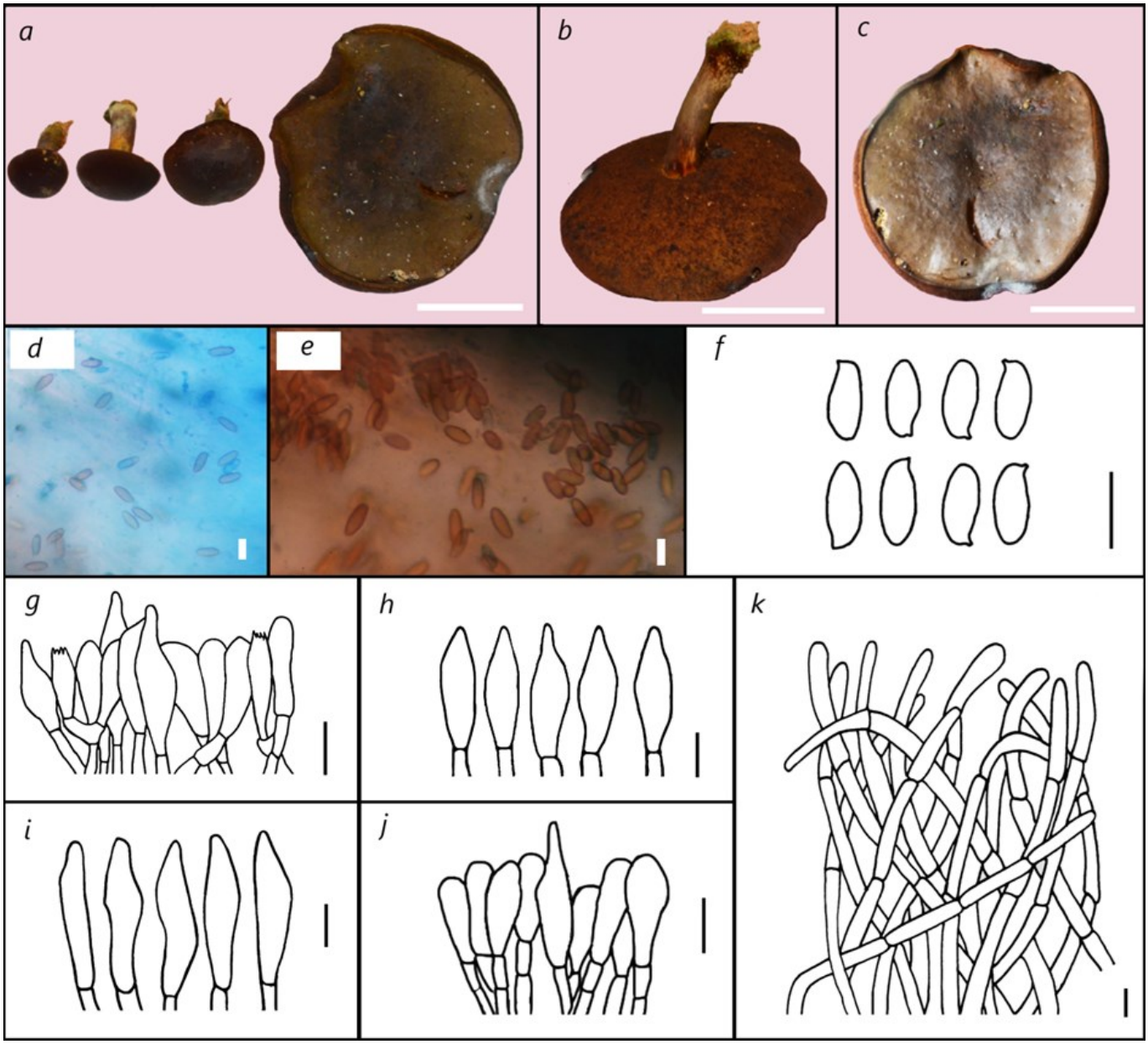

Fig. 2. *Caloboletus guanyui* . **a**-**c**: Basidiomata close-ups , **d**-**f**: Basidiospores, **g**: Basidia and Pleurocystidia, **h**: Cheilocystidia, **i**: Pleurocystidia, **j**: Stipitipellis and **k**: Pileipellis. (Scale bars: **a**-**c**: 5cm, **d**-**k**: 10 µm).

clade is distinct from other *Caloboletus* species (*C*. *calopus* and *C*. *panniformis*) which occupy separate branches in the phylogeny. The bootstrap support and clear clustering further confirm the genetic affinity of PQ288749 within the *C*. *guanyui* clade. Although some species, such as *C*. *griseoflavus*, *C*. *taienus*, *C*. *xiangtoushanensis* and *Neoboletus infuscatus* share several common morphological characteristics with our specimen (*C*. *guanyui*) such as the size of the pileus, pores, stipe, basidiospores, and basidia. Therefore, their distinct morphological features are compared in Table 2.

C. *guanyui*, characterized by medium to large basidiomata, was initially described by Hongo (25) under the name *Boletus quercinus*. However, this name was invalid because Schrader (26) had already used it for a different species. To resolve this, Chai et al. (20) proposed *C*. *guanyui* as the correct name for this species. Morphologically, *C*. *taienus* and *C*. *xiangtoushanensis* were also characterized by a reddish pore. However, *C*. *guanyui* can be easily distinguished from these two species by the colour of its pileus, which is characterized by dirty-white to pale-brown (20). Moreover, the pileus of *C*. *guanyui* is larger than that of both *C*. *taienus* and *C*. *xiangtoushanensis*. It is known that *C*. *guanyui* can be distinguished from *N*. *infuscatus* by its smaller basidiomata, the absence of a pruina layer on the pileus and stipe surfaces, a white context, a stipe densely covered with pale brown to reddish-brown squamules, and a stipe context that remains unchanged in color when injured (27). Moreover, it can be differentiated from *C*. *griseoflavus* by its stipe densely covered with pale brown to reddish-brown squamules and its smaller basidiospores.

Sequencing of the ITS region of rRNA and phylogenetic analysis further showed that the Mizoram sample matched GenBank accession *C*. *guanyui* from China (MH885366, MH885365 and MH885364) in a well-supported clade. Morphological evidence, molecular phylogenetic analyses, and ecological data collectively confirm that the specimen of *Caloboletus* from Mizoram is *C*. *guanyui*, a distinct species and separate from *C*. *griseoflavus*, *C*. *taienus*, *C*. *xiangtoushanensis* and *N*. *infuscatus*. Our collec-

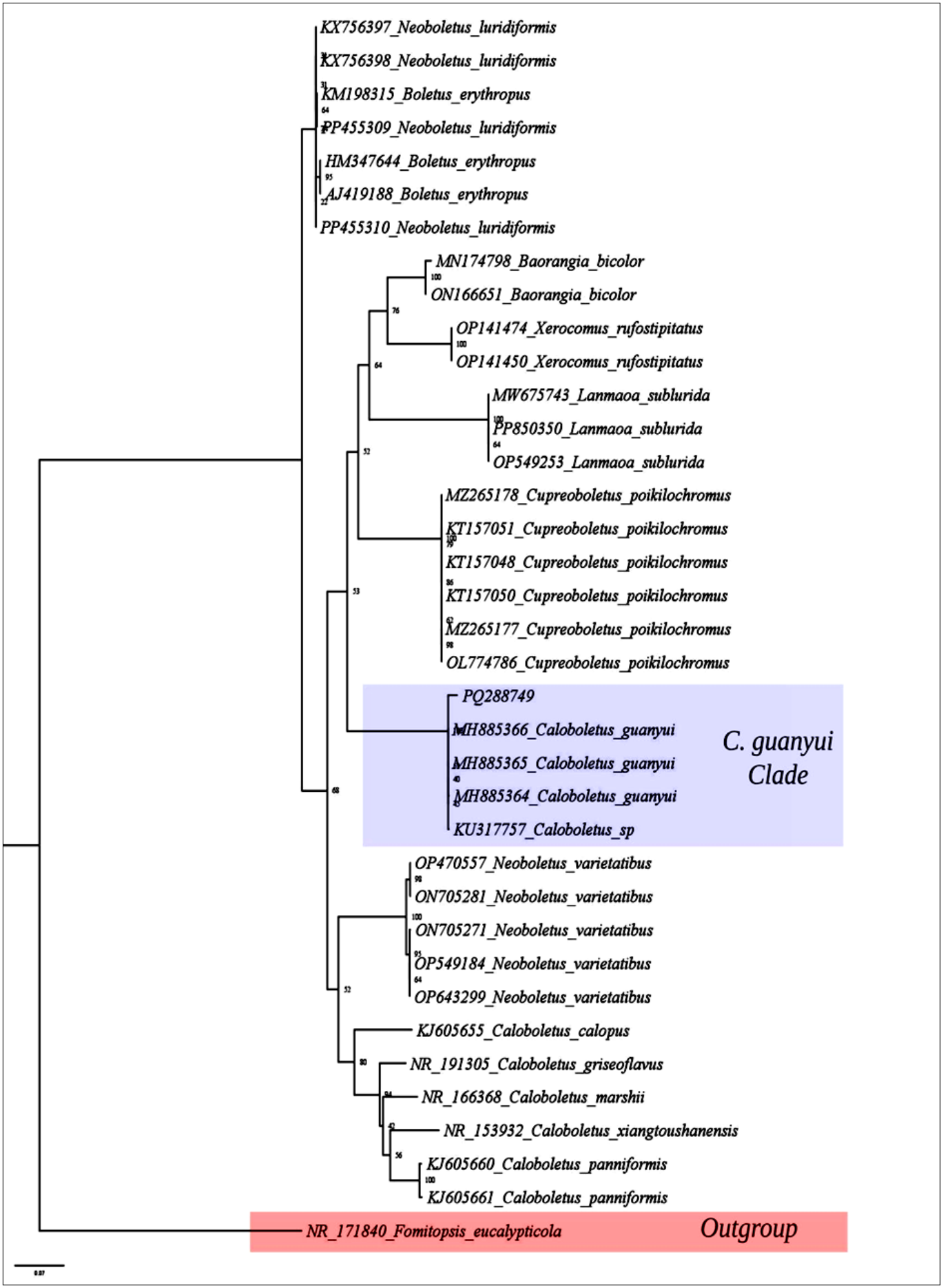

Fig. 3. Phylogenetic tree of *Caloboletus guanyui* and other related taxa.

tion broadens the known distribution of *C. guanyui* to India, aligning it with its presence in East Asian countries such as Japan and China. This suggests that similar environmental factors may be promoting its spread across various regions. Documenting this occurrence in India not only enhances our understanding of *C. guanyui* ecological

Table 1. List of species, voucher, GenBank accession nos. and locality.

No.	Voucher	Accession No.	Species Name	Locality
1	WA0000052272	KX756397	*Neoboletus luridiformis*	Poland
2	WA0000052289	KX756398	*Neoboletus luridiformis*	Poland
3	WU 36064	KM198315	*Boletus erythropus*	Austria
4	U3758	PP455309	*Neoboletus luridiformis*	Sweden
5	UF278	HM347644	*Boletus erythropus*	Portugal
6	-	AJ419188	*Boletus erythropus*	Spain
7	U3759	PP455310	*Neoboletus luridiformis*	Sweden
8	JLF6843	MN174798	*Baorangia bicolor*	USA
9	iNAT:15437268	ON166651	*Baorangia bicolor*	USA
10	PDD 101779	OP141474	*Xerocomus rufostipitatus*	New Zealand
11	JAC16762	OP141450	*Xerocomus rufostipitatus*	New Zealand
12	Farid_631	MW675743	*Lanmaoa sublurida*	USA
13	OMDL K. Canan iNaturalist # 131374134	PP850350	*Lanmaoa sublurida*	USA
14	S.D. Russell ONT iNaturalist 127411460	OP549253	*Lanmaoa sublurida*	USA
15	TUR-A 208927	MZ265178	*Cupreoboletus poikilochromus*	Italy
16	GS 10070	KT157051	*Cupreoboletus poikilochromus*	Italy
17	MG 271a	KT157048	*Cupreoboletus poikilochromus*	Italy
18	GS 11008	KT157050	*Cupreoboletus poikilochromus*	Italy
19	TUR-A 208926	MZ265177	*Cupreoboletus poikilochromus*	Italy
20	SOMF30350	OL774786	*Cupreoboletus poikilochromus*	Bulgaria
21	N.K.Zeng3079	MH885366	*Caloboletus guanyui*	China
22	N.K.Zeng3058	MH885365	*Caloboletus guanyui*	China
23	N.K.Zeng3263	MH885364	*Caloboletus guanyui*	China
24	HKAS74864	KU317757	*Caloboletus sp.*	China
25	S.D. Russell ONT iNaturalist # 129764007	OP470557	*Neoboletus varietatibus*	USA
26	#374573	ON705281	*Neoboletus varietatibus*	USA
27	#249632	ON705271	*Neoboletus varietatibus*	USA
28	S.D. Russell ONT iNaturalist 129866347	OP549184	*Neoboletus varietatibus*	USA
29	S.D. Russell ONT iNaturalist # 129907651	OP643299	*Neoboletus varietatibus*	USA
30	BR5020159063805	KJ605655	*Caloboletus calopus*	Belgium
31	BJTC FM2438	NR_191305	*Caloboletus griseoflavus*	China
32	SFSU Arora11118	NR_166368	*Caloboletus marshii*	USA
33	GDGM 44725	NR_153932	*Caloboletus xiangtoushanensis*	China
34	HKAS77506	KJ605660	*Caloboletus panniformis*	China
35	HKAS77530	KJ605661	*Caloboletus panniformis*	China
36	BJFC:029897	NR_171840	*Fomitopsis eucalypticola*	Australia

Table 2. Comparative morphological analysis of related *Caloboletus* species.

Species	Pileus	Pores (mm)	Stipe (cm)	Basidiospores (µm)	Basidia (µm)
Caloboletus griseoflavus	3–7.5 cm	Angular or subround; up to 0.5 mm	2.6–6 × 0.8–2 cm	12–15 × 4.5–5.5 µm	32–36 × 9–11 µm
Caloboletus guanyui	5.5–11 cm	Subround; 0.3–0.6 mm	5.5–9.5 × 0.8–1.6 cm	9.5–11.5 × 3.5–4.5 µm	20–32 × 6.5–8.5 µm
Caloboletus taienus	5–7 cm	Angular; 1–3 mm	6–8 × 1.5–2 cm	8–9 × 3–4 µm	25–31× 7–10 µm
Caloboletus xiangtoushanensis	4–9 cm	Angular; 2–3 mm	3–8 × 1–1.5 cm	9–13 × 4–5 µm	25–33× 7–10 µm
Neoboletus infuscatus	6–16 cm	Angular; 2 mm	9–11 × 1.8–2.5 cm	8.5–10.5× 3.5–4.5 µm	31.5–39.5 × 9.5–2.5 µm

preferences but also highlights the significance of India diverse forest ecosystems in supporting distinct and varied macrofungi.

Conclusion

Our study indicates that the geographic distribution of *C. guanyui* now extends into India, showcasing its resilience

to a wide range of environmental circumstances. Characterized by medium-sized to large basidiomata, *C. guanyui* has been identified through morpho-molecular analysis, enriching the fungal diversity of the family Boletaceae in India and representing an especially significant addition to Mizoram. While Mizoram is known for its rich floral diversity, there remains limited information about its wild mushrooms, emphasizing the need for further studies to assess and document the broad range of mushrooms in this region. This situation emphasizes the critical need for comprehensive research initiatives to explore the full potential of these fungi. Such efforts could yield valuable insights into their ecological significance and possible contributions to health, industrial applications, and biotechnological innovations. By investigating the various characteristics and functions of wild mushrooms, we can deepen our understanding of their roles in ecosystems and the potential benefits they offer across different sectors.

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Authors' contributions

VLT, LB, and ZC collected the samples, performed the morpho-molecular studies, contributed to the sequence alignment, constructing phylogenetic tree and prepared the manuscript draft. PKR and JZT assisted in the study design and manuscript review. All authors reviewed and approved the final manuscript.

Compliance with ethical standards

Conflict of interest: Authors do not have any conflict of interests to declare.

Ethical issues: None.

AI Declaration

During the preparation of this work, the author(s) used Artificial Intelligence [Curie] for language editing. After using this tool, the author(s) reviewed and edited the content as needed and take(s) full responsibility for the content of the publication.

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