KAVAKA 62(2): 11-19 (2026) DOI: 10.36460/Kavaka/62/2/2026/11-19

Broadening the known distribution of *Craterellus aureus* Berk. & M.A. Curtis, a wild edible mushroom from India with morpho-phylogenetic evidence

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(Submitted on 10 September, 2025; Accepted on 22 June, 2026)

ABSTRACT

***Craterellus aureus* is recorded for the first time from East Jaintia Hills and Ri Bhoi district of Meghalaya, India, based on morphological and molecular data. This species is characterised in the field by a trumpet-shaped, bright orange-yellow fruiting body, wavy pileus margin, and dirty white to pale yellow, nearly smooth hymenial surface. Microscopically, diagnostic features are the ellipsoid to broadly ellipsoid smooth basidiospores and absence of clamp connections in all types of hyphae. Comparison of the nearest nrLSU DNA sequences from GenBank confirmed the identity of our record and showed that the species is distributed not only in China, but also in India. This species is also highly valued as an edible mushroom by local tribal communities, highlighting its ethnomycological importance. In this communication, we provide a comprehensive morphological description complemented by illustration, comparisons with similar species, further supported by nrLSU-based phylogenetic analysis.**

Keywords: Basidiomycota, *Craterellus,* Hydnaceae, nrLSU, Meghalaya, Taxonomy

INTRODUCTION

The genus *Craterellus* Pers., together with its sister genus *Cantharellus* Adans., and the genera *Hydnum* L., *Clavulina* J. Schröt., lichen-forming *Multiclavula* R.H. Petersen, and two corticioid genera *Sistotrema* Pers., and *Membranomyces* Jülich, forms a well-supported core cantharelloid clade characterized by the presence of stichic basidia (Pine *et al*., 1999; Hibbett and Binder, 2002). In the current classification of Basidiomycota, these taxa are placed within a single family Hydnaceae of the order Cantharellales, one of the earliest diverging lineages of mushroom-forming Agaricomycetes (Hibbett *et al*., 2014).

Craterellus was established by Persoon in 1825 with *C. cornucopioides* as the type species to separate chanterelles with a hollow stipe from *Cantharellus* (Corner, 1966; Petersen, 1979a). Although the distinction between the genera *Cantharellus* and *Craterellus* has long been debated, traditionally *Craterellus* is characterised by small, funnel-shaped basidiomata with (completely or partly) hollow stipes that may also be much reduced and with or without clamps (Petersen, 1979a). However, Dahlman *et al*., (2000) demonstrated that these genera can be clearly differentiated using nrLSU and nrITS sequence data, and stated that the presence of a hollow stipe appears to be a morphological synapomorphy characteristic of *Craterellus*. However, the subtle morphological differences among species make its classification very complicated. Since the study by Dahlman *et al*., (2000), several phylogenetic analyses along with morphological characteristics have been employed to resolve taxonomic confusion of *Craterellus* (Cao *et al*., 2021; Jiang *et al*., 2025). Moreover, Cao *et al*., (2021) classified *Craterellus* species with several similar morphological characteristics into six subgenera viz. *Cariosi* T. Cao & H. S. Yuan, *Craterellus*, *Imperforati* T. Cao & H. S. Yuan, *Lamelles* T. Cao & H. S. Yuan, *Longibasidiosi* T. Cao and H. S. Yuan, and *Ovoidei* T. Cao and H. S. Yuan, using combined nrITS and nrLSU sequences. *Craterellus* is widely distributed in the temperate regions of the northern hemisphere and is frequently found in the tropics (Jiang *et al*., 2025). Ecologically, it forms ectomycorrhizal associations with a variety of host plants, including members of the Dipterocarpaceae, Fagaceae, Malvaceae, Myrtaceae, Pinaceae, and Salicaceae, and plays a significant role

in forest ecosystems (Jiang *et al*., 2025). *Craterellus* exhibits high species diversity, with approximately 173 taxa recorded, of which up to 68 species are currently accepted (http://www.indexfungorum.org, accessed 5 September 2025). In the Indian subcontinent, 12 species of *Craterellus* have been reported so far, predominantly from northern India (Himachal Pradesh, Uttarakhand, and Jammu & Kashmir), with a few reports from tropical regions (Jharkhand and Kerala) and from northeastern states including Mizoram and Assam (Hembrom *et al*., 2017; Bijeesh *et al*., 2018; Roy *et al*., 2022). Besides its attractive appearance, species of *Craterellus* have gained significant attention for their edibility and medicinal properties and are widely consumed globally (Hembrom *et al*., 2017; Zhang *et al*., 2022; Jiang *et al*., 2025).

Craterellus aureus Berk. & M.A. Curtis was originally described from Guangdong Province, southern China, and is characterized by a light yellow to greenish yellow pileus, white to yellowish white hymenophore, broad basidiospores, and lack of aromatic odour (Zhong *et al*., 2018). We found this species in 2023 and 2024 during macrofungal forays in the East Jaintia Hills and Ri-Bhoi districts of Meghalaya, India. In Meghalaya, this species is regarded as a delicacy by the Khasi and Jaintia tribal communities and is commonly sold in local markets during the rainy season. In this article, we provide detailed information on the morphology, anatomy and nrLSU DNA sequence of this collection. The record is further compared with similar reports from around the world. The aim of this study is to improve our insight into the taxonomy, phylogeny and distribution of *Craterellus aureus*.

MATERIALS AND METHODS

Morphological study

Thorough and extensive macrofungal forays to the East Jaintia Hills and Ri-Bhoi districts of Meghalaya, India, were undertaken during the post-monsoon season of 2023 and 2024 (September to October), leading to the collection of several fresh, young, and mature basidiomata belonging to Hydnaceae. Macromorphological characterizations were recorded from fresh specimens in the field or at a basecamp. Photographs of fresh basidiomata were taken both in the field and in the basecamp using a Canon EOS 200D DSLR camera and OnePlus Nord CE. Colour codes and terminology used hereafter follow the Methuen Handbook of Colour (Kornerup and Wanscher, 1978). After that, the specimens were dried with a field drier at 45–50°C. Micromorphological features were examined at the Mycology Laboratory, Botanical Survey of India, Eastern Regional Centre, Shillong. Freehand sections were made from dried specimens and mounted in 3–5% potassium hydroxide (KOH), 1% phloxine, and 1% Congo red, applied separately. Microscopic observations were conducted using an OLYMPUS CX-43 compound microscope equipped with a Magcam DC Plus 10 camera for microphotography. Illustrations of anatomical features were prepared using a drawing tube attached to the same microscope at 1000× magnification. Measurements were carried out using MagVision Standard software dedicated to the OLYMPUS CX-43. Basidium length measurements excluded the sterigmata. Basidiospores were observed in Cotton Blue reagent and Melzer's reagent and measured in side view. Basidiospore measurements and length/width ratios (Q) were represented as: minimum–mean–maximum. Twenty measurements were taken for all the micromorphological structures. The subgeneric classification used in this study followed Cao *et al*., (2021). Part of the studied material was deposited at ASSAM, Shillong, India (herbarium abbreviations follow Index Herbariorum, Thiers, updated continuously).

DNA extraction, polymerase chain reaction (PCR) and sequencing

Genomic DNA was extracted from 100 mg of dried basidiome with the InstaGeneTM Matrix Genomic DNA isolation kit (Biorad, USA) following the manufacturer's instructions. PCR amplification, and cycling conditions were in accordance with those described in Ghosh *et al*., (2024). The partial sequences of nrLSU region were amplified using the primers LR0R and LR5 (Gardes and Bruns, 1993). The amplified PCR products were separated on a 1% agarose gel and the bands visualised under UV light, after which the products were sent to Barcode Bioscience (Bangalore, India) for sequencing. The chromatograms of the raw sequences were checked, assembled and edited using Geneious Prime® 2024.0.7 (https://www.geneious.com/). The newly generated consensus sequences were prepared using Geneious Prime® 2024.0.7 and finally submitted to GenBank to procure the accession numbers.

Dataset preparation, sequence alignment and phylogenetic analysis

To determine the identity of the recently collected *Craterellus* specimens from Meghalaya, India, the newly generated nrLSU sequences were analysed using BLASTn searches against the GenBank database (https://www.ncbi.nlm.nih.gov/genbank). Additional sequences with high similarity (that exhibited a minimum of 97% identity and 95–100% query coverage) were downloaded from the National Centre for Biotechnology Information (NCBI, www.ncbi.nlm.nih.gov) databases, as well as the sequences of the described species from relevant publications (Hembrom *et al*., 2017; Zhang *et al*., 2022; Jiang *et al*., 2025). The nrLSU dataset was prepared in notepad and aligned using the online version of MAFFT v.7 (https://mafft.cbrc.jp/alignment/software/), employing FFT-NS-2 (Katoh *et al*., 2002), with a 200PAM/k = 2 scoring matrix, a gap opening penalty of 1.53, and an offset value of 0.0. The trailing ends of the nrLSU alignment were trimmed in BioEdit v. 7 (Hall, 1999). Based on Nagy *et al*, (2012), phylogenetically informative insertion and deletion (indel) positions in the nrLSU alignment were coded using FastGap v.1.2 to refine the nucleotide alignment (Borchsenius, 2009), applying the simple indel coding method of Simmons *et al*. (2000). For partitioned analysis with mixed data, thfe alignment of each dataset (nrLSU and INDELS or binary matrix) was prepared as a separate file. Then, in the NEXUS file, each dataset was specified as an independent partition (e.g. DNA_part and Binary_part). The partitioned alignment was analysed based on maximum likelihood (ML) method by IQ-TREE v3.1.2 (Wong *et al*., 2026) using the NEXUS file as input, employing the best models (TN+F+I+R2 for LSU and JC2+FQ+ASC+R2 for INDELS or binary matrix) determined by ModelFinder (Kalyaanamoorthy *et al*., 2017) based on the Bayesian Information Criterion (BIC). Branch support was estimated using 1000 replicates of SH-like approximate likelihood ratio test (SH-aLRT) (Guindon *et al*., 2010) and ultrafast bootstrap (UFBoot) replicates (Hoang *et al*., 2018). Branches were considered reliable when both SH-aLRT ≥ 80% and UFBoot ≥ 95% (Minh *et al*., 2020).

RESULTS

Taxonomic study

Craterellus aureus Berk. & M.A. Curtis, Proc. Amer. Acad. Arts & Sci. 4: 123, 1860 **Figures 2 and 3.**

GenBank: LSU= PV701244 & PV929287

Basidiomata medium to large-sized, 15–60 mm high, solitary to gregarious, soft to more or less leathery to brittle when fresh. Pileus 25–50 mm in diam., infundibuliform to broadly infundibuliform with age; surface dry, glabrous, sometimes faintly tomentose, egg yolk yellow to deep orange (4–5A8); margin plane or applanate when young, becoming irregularly wavy or lobed at maturity, entire. Pileus context 1–1.2 mm thick, chalky white (3A1) to pale white (1A2). Hymenophore dirty white to pale yellow (4A2), nearly smooth, covering entire underside of pileus, with age descending onto the stipe apex. Stipe 22–80 × 5–25 mm, central, hollow, initially cylindrical, sometimes flattening due to lateral confluency with other stipes, usually curved, irregularly expanded upward; surface smooth, concolorous with hymenophore, brown when bruised. Basal mycelium chalky white (1A1). Smell fruity. Taste mild. Spore print not obtained.

Basidiospores 7.5–8.3–9.0 × 5.1–6.7–7.6 µm, [Q = 1.1–1.3–1.5] ellipsoid to broadly ellipsoid, smooth, inamyloid, hyaline or yellowish in KOH. Basidia 66–100 × 6–8 µm, narrowly clavate, without clamp connections, irregularly flexuous, pale yellowish in KOH, devoid of contents; wall thin, 4–6-sterigmate, sterigmata 5–9 µm long. Cystidia absent. Pileipellis intricate, cutis with some upwardly directed hyphal tips, composed of cylindrical pilear hyphae (4–7 µm wide), faintly pale yellow in KOH; terminal cells 20–60 × 5–8 µm, subcylindrical to subclavate with obtuse apex. Clamp connections absent in all tissues.

Habitat: Solitary to gregarious, under mixed tropical broadleaf forests.

Known distributions: Eastern China (Jiangxi Province) and southern China (Guangdong and Hainan Provinces, Hong Kong).



Figure 1: Phylogram generated from a maximum likelihood (ML) analysis in IQ-TREE v3.1.2 based on nrLSU sequences of *Craterellus* species, with *Hydnum minus* and *H. cremeoalbum* used as outgroup taxa. Support values from the SH-like approximate likelihood ratio test (SH-aLRT ≥ 80%) are shown to the left of the "/", and ultrafast bootstrap values (UFBoot ≥ 95%) are shown to the right, positioned above or below the branches at the nodes. Two Indian collections of *Craterellus aureus* are highlighted in blue and bold font in the phylogram.

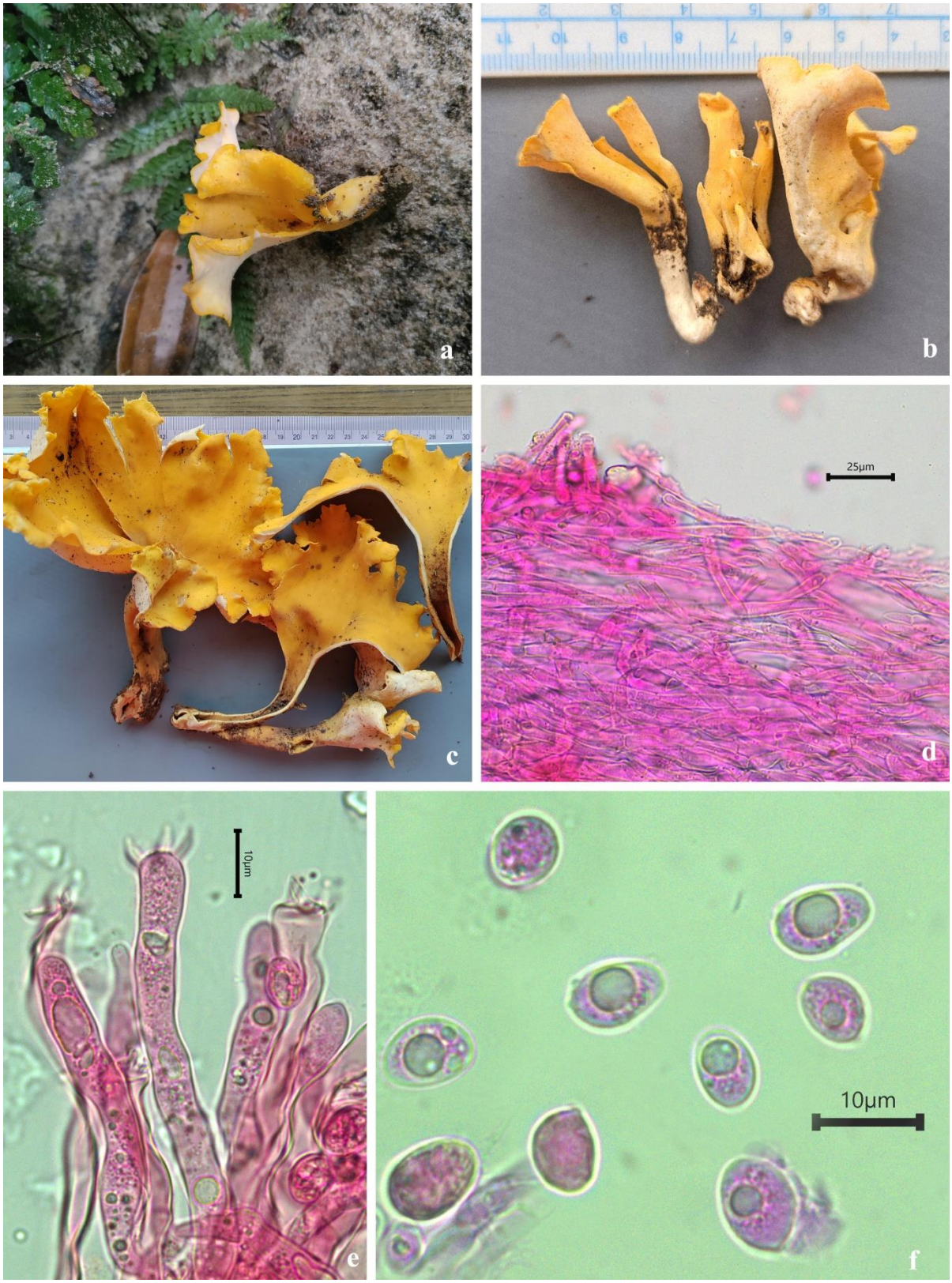


Figure 2: *Craterellus aureus*. a–c. Basidiomata in the field and at the basecamp; **d**. Elements of pileipellis; **e**. Basidia; **f**. Basidiospores. Scale bars: **d** = 25 µm; **e-f** = 10 µm

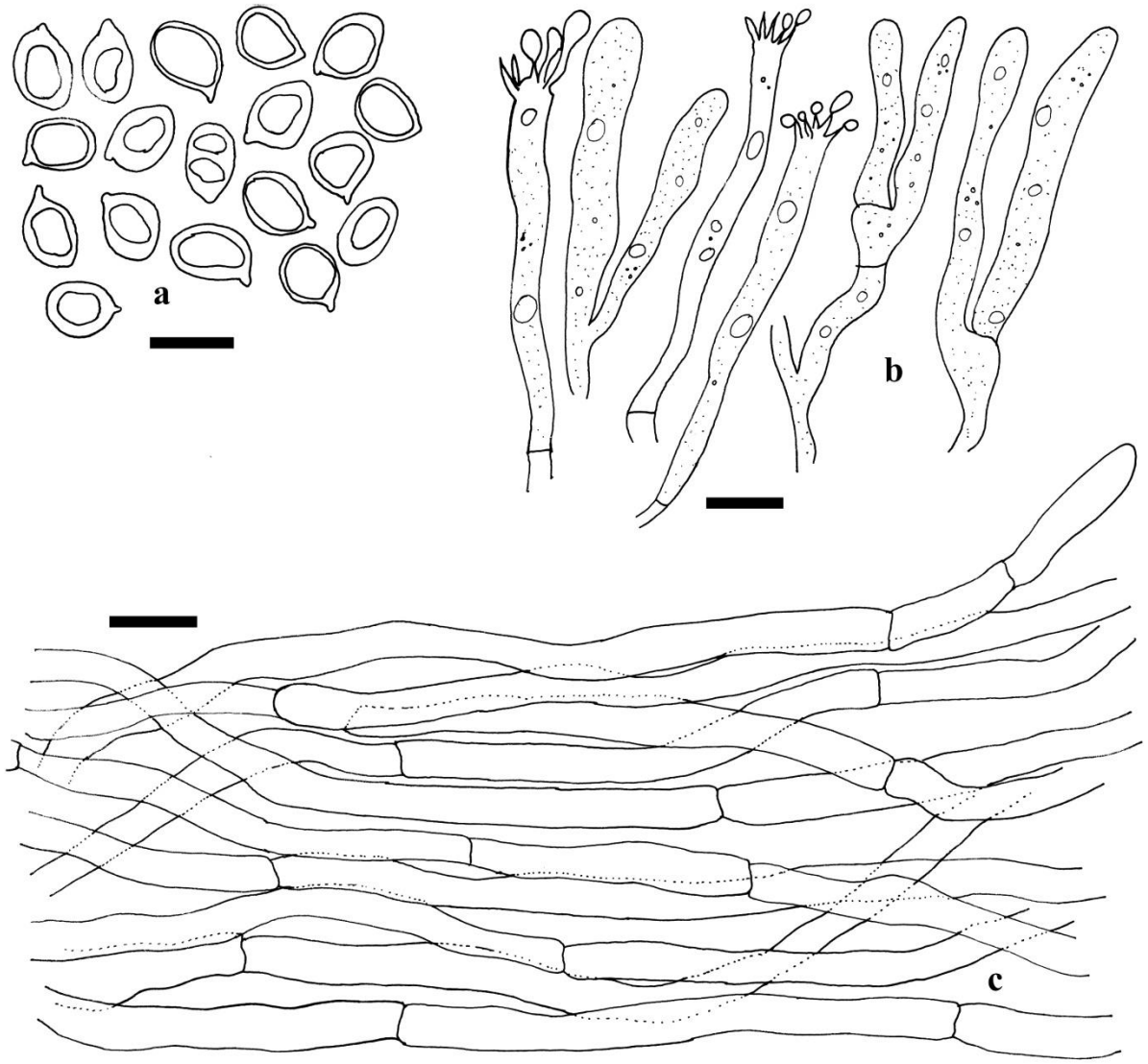


Figure 3: Line drawings of *Craterellus aureus*. **a**. Basidiospores; **b**. Basidia and basidioles; **c**. Elements of pileipellis. Scale bars: **a–c** = 10 µm

Specimens examined: India, Meghalaya, Ri-Bhoi district, Nongkhyllem, 260 m a.s.l, 25°56'3.54"N, 91°46'26.83"E, 16th September 2023, Y. Mahesh and D. Tudu, DC ML-179 (ASSAM F-023); ibid., East Jaintia hills, Moopun, 25°22'01.56"N, 092°14'33.82" E, 1274 m a.s.l, 17th October 2024, D. Chakraborty and D. Tudu, ML 24-138 (ASSAM F-024).

Phylogenetic inferences

The final nrLSU data matrix of *Craterellu*s comprises 75 sequences and 954 nucleotide sites plus 111 binary characters. The dataset contained 469 distinct patterns, 316 parsimony-informative, 41 singleton sites and 597 constant sites. The ML tree was constructed with log-likelihood of –6257.334. The model for LSU is: TN+F+I+R2 with parameters: 2.61123, 4.82994; Frequencies are: 0.294323, 0.175205, 0.279278, 0.251194; Proportion of invariable sites is: 0.468303; and Gamma shape parameters are: 0.424754, 0.787984, 0.106943, 6.22108. The model for the INDEL is: JC2+FQ+ASC+R2 with Gamma shape parameters are: 0.922328, 0.20731, 0.0776719, 10.4129.

In our phylogenetic analysis (**Figure 1**) based on nrLSU sequences, two collections of Indian *Craterellus aureus* (accession nos. PV701244 & PV929287) are nested within the *C. aureus* / *C. luteus* clade, alongside samples collected from China, indicating their strong similarity or conspecificity with the Chinese collections with a strong support (SH-aLRT = 91.6%, UFBoot = 97%). In the phylogram (**Figure 1**), the *C. aureus* / *C. luteus* clade appears as a single, closely clustered group due to the lack of branch resolution. Based on our phylogenetic

analysis, as well as previous phylogenetic studies (Zhang *et al*., 2022; Jiang *et al*., 2025), *C. luteus* is revealed to be a later synonym of *C. aureus*, with both taxa previously reported from China.

DISCUSSION

Our recent collections phylogenetically clustered within the *Craterellus aureus* / *C. luteus* lineage described from China, with strong statistical support (**Figure 1**). The holotype of *C. luteus* T.H. Li and X.R. Zhong, originally described from Guangdong Province, southern China, is characterized by robust and large basidiomata, a bright yellow cap, a white hymenophore, and longer basidiospores [(8.5–) 9–11(–12.5) µm] (Zhong *et al*., 2018). However, Zhang *et al*., (2022) demonstrated that their collections of *C. aureus* Berk. & M.A. Curtis [(originally from Hong Kong, southern China (Berkeley and Curtis, 1860)] share highly similar sequences with the holotype of *C. luteus* and also exhibit nearly identical basidiospore sizes to the originally described *C. aureus*. Based on these findings, Zhang *et al*., (2022) treated *C. luteus* as a later synonym of *C. aureus*, as both taxa were described from southern China and occur in similar climatic and vegetational conditions. Indian collections also have basidiospores of remarkably similar size to those of *C. aureus*, although Indian specimens have larger basidiomata (up to 60 mm high) than the holotype (20 mm high) (Petersen, 1979b).

The present taxon is morphologically and phylogenetically very similar to *Craterellus odoratus* (Schwein.) Fr. (originally described from North America), sharing features such as funnel-shaped basidiomata, a hollow stipe, narrowly clavate basidia, and clampless hyphae. However, it can be distinguished by its more fragile basidiomata, bright orange pileus, and comparatively larger and narrower basidiospores (8.9–11.8 × 4.4–6.3 µm) (Petersen, 1979b; Lincoff, 1989; Zhong *et al*., 2018; Zhang *et al*., 2022). The previously described Indian taxon *Craterellus odoratus* var. *solidostipite*, reported from northern India, is distantly related, as it possesses abundant clamp connections (Thind and Adlakha, 1956). The only other clampless *Craterellus* described from India, *C. indicus*, is distinct in having a light brownish to sand-coloured pileus and yellowish grey stipe (Kumari *et al*., 2012) and also represents a different lineage within the genus (see **Figure 1**).

CONCLUSIONS

This study reports an expanded distribution of *Craterellus aureus* in India, a species originally described from southern China, supported by morphotaxonomic characterization and nrLSU-based phylogenetic analysis. Although the diversity of *Craterellus* in India has been documented primarily from northern regions, with a few reports from tropical regions such as Jharkhand and Kerala and from northeastern states including Mizoram and Assam, many of these taxa were historically identified largely based on morphological resemblance to European and North American counterparts, often with limited molecular evidence. Our findings demonstrate that the integration of morphological and molecular approaches is essential for accurate species delimitation and can reveal previously unrecognized diversity within Indian *Craterellus*. Furthermore, this study represents the first report of a *Craterellus* species from Meghalaya, using a polyphasic approach.

Key to reported species of *Craterellus* in India

1. Clamp connections absent..... 2
1a. Clamp connections present 3
2. Basidiomata up to 20 mm high; pileus light brownish to sand-coloured..... *C. indicus*
2a. Basidiomata up to 60 mm high; pileus egg yolk yellow to bright orange yellow ..... ***C. aureus***
3. Basidiomata pileate-stipitate; stipe present 4
3a. Basidiomata pleurotoid or cyphelloid; stipe reduced or absent ..... *C. inusitatus*
4. Basidiomata pale yellow to vivid yellow 5
4a. Basidiomata differently coloured 6
5. Pileus imperforate; basidiospores 10.4–13 × 7.2–9 µm ..... *C. shoreae*
5a. Pileus or stipe base perforate 7
6. Pileus perforated at the center, hymenophore with pinkish shades at maturity..... *C. ignicolor*
6a. Stipe base perforated, hymenophore without pinkish shades ..... *C. tubaeformis*
7. Stipe solid 8
7a. Stipe hollow 10
8. Stipe excentric to lateral..... *C. mussooriensis*
8a. Stipe central 9
9. Pileus dark violet, hymenophore vinaceous, crested; basidiospores 7–8 × 5–5.5 µm ..... *C. cymatodermoides*
9a. Pileus greyish brown, hymenophore grey, smooth; basidiospores 9–11.5 × 6–8 µm..... *C. albostrigosus*

10. Pileus typically ≥ 50 mm in diam., blackish brown with appressed black fibrils, basidiospores small, 6–7.5 × 4.5–5 µm ..... *C. dubius*

10a. Pileus typically < 50 mm in diam., differently coloured; basidiospores larger 11

11. Pileus fuliginous black, hymenophore blackish brown, ribbed ..... *C. cornucopioides*

11a. Pileus greyish, hymenophore some shade of greyish, folded 12

12. Basidia 4–6 sterigmate, basidiospores 8–8.8 × 4–5.6 µm ..... *C. cinereus*

12a. Basidia 2–6 sterigmate, basidiospores 9.6–12 × 7.6–9 µm ..... *C. parvogriseus*

ACKNOWLEDGEMENTS

The authors are grateful to the Director, Botanical Survey of India (Kolkata), Head of Office, Eastern Regional Centre, Shillong for providing all facilities. Authors are also thankful to Mr. BBT Tham, Dr. Y. Mahesh and Mr. Sherlang Khonglam for assisting us and providing information to undertake the macrofungal surveys to the forested areas. One of us (AG) is thankful to the Principal, St. Xavier's college (Autonomous), Maharo (Dumka) for providing required facilities for the study.

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