

***Calocybe kinabaluensis* (Lyophyllaceae, Agaricales), a new species from Kinabalu UNESCO Global Geopark, Sabah, Northern Borneo, Malaysia**

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Abstract

Calocybe kinabaluensis sp. nov. was collected and described from Kinabalu UNESCO Global Geopark in Sabah, Malaysia. Morphological and phylogenetic evidence were used to delimit the collections as a new species. The species is characterized by its small to medium-sized basidiomata, deep blue to indigo-blue pileus with an irregularly lobed and undulate margin, and whitish to pale cream adnate to decurrent lamellae. Microscopically, it is distinguished by ovoid to broadly ellipsoid basidiospores, a cutis-type pileipellis, and the presence of cheilocystidia. Phylogenetic analyses of concatenated ITS and LSU sequences and ITS-only sequences distinguish this species from the molecularly closely related taxa, including *C. cyanella* and *C. longisterigma*. A detailed description and illustrations of the new species as well as comparative notes with other blue-capped taxa are provided. This research represents the first description of a new *Calocybe* species from Sabah, Malaysia, expanding current knowledge of the genus and highlighting the region as a significant area for future fungal diversity investigations.

Key words: Agaricales, Basidiomycota, Kinabalu Park, Phylogeny, *Rugosomyces*, Taxonomy

Introduction

The genus *Calocybe* Kühner ex Donk, typified with *C. gambosa* (Fr.) Donk, represents one of the most taxonomically significant lineages within the family Lyophyllaceae Jülich (Agaricales Underw.). Initially, *Calocybe* was proposed as a section within *Lyophyllum* P. Karst (Kühner & Romagnesi, 1953). It was subsequently elevated to generic status based on distinctive morphological characteristics, a classification later corroborated by molecular phylogenetic analyses (Hofstetter *et al.* 2002, Matheny *et al.* 2006, Garnica *et al.* 2007). Characterized by a tricholomatoid to collybioid habit and usually vivid pileus pigmentation, its circumscription was originally based on the siderophilous granulation of the basidia, a feature first emphasized by Kühner (1938) and later validated by Donk (1962). A major historical conflict involved the status of *Rugosomyces* Raithelh. (1979), a genus originally established for species characterized by a rugose pileus and a cellular pileipellis and later emended by Bon (1991) to also include species with a trichoderm pileipellis. While morphological treatments (Bon, 1991, 1999, Kalamees 2004) maintained it as distinct from *Calocybe*, multi-gene phylogenetic analyses have demonstrated that *Rugosomyces* is nested within the *Calocybe* core clade (Hofstetter *et al.* 2014, Bellanger *et al.* 2015, Vizzini *et al.* 2015). Previous studies by Chinese mycologists have further consolidated this synonymy (recognizing *Rugosomyces* as a heterotypic junior synonym) based on extensive multi-locus analyses (Qi *et al.* 2022, Mu & Bau 2023, Hu *et al.* 2024, Liu *et al.* 2025). These studies also confirm that

the diagnostic characters once used to define *Rugosomyces* represent homoplastic traits that have evolved multiple times within *Calocybe*. In the past, *Calocybe* included several large-bodied tropical taxa, such as *C. indica* Purkay. & Chandra (Shashikant *et al.* 2022). Nonetheless, a thorough morphological reevaluation, coupled with multi-gene phylogenetic data, revealed that these species are without siderophilous granules and exhibit remarkably resilient basidiomata, warranting their reclassification into the genus *Macrocybe* Pegler & Lodge (Pegler *et al.* 1998, Nath *et al.* 2023). Therefore, *Macrocybe indica* is the correct name for the tropical species that is cultivated worldwide, and excluding this species has greatly refined the taxonomic limits of *Calocybe* species (Razzaq *et al.* 2026).

Modern molecular evidence has led to a clearer demarcation between *Calocybe* and several related genera: (a) *Tricholomella* Kalamees, (typified with *T. constricta* (Fr.) Zerova ex Kalamees) segregated from *Calocybe* due to its tricholomatoid, thick-fleshy, with a white partial veil, an usually rooting stipe, echinulate to elliptic basidiospores, and because it grows in disturbed, man-made environments, frequently in proximity to sites where nitrogen compounds are accumulated (Kalamees 2004, 1994), (b) *Gerhardtia* Bon, typified with *G. borealis* (Fr.) Contu & A. Ortega (= *G. incarnatobrunnea* (Ew. Gerhardt) Bon), is a distinct genus characterized by verruculose or irregular basidiospores and lack of clamp connections (Vizzini *et al.* 2015, 2017), (c) *Calocybella* Vizzini, Consiglio & Setti, was established to accommodate *Rugosomyces pudicus* Bon & Contu, distinguished by its strictly collybioid habit, a reddening context, and distinct phylogenetic position (Vizzini *et al.* 2015, 2017). Micromorphological characterizations remain pivotal for taxonomic resolution at the species level. Basidiospores in *Calocybe* are typically smooth and vary in size and shape, which represent the key diagnostic features for species delimitation (Xu *et al.* 2019, Li *et al.* 2017). However, morphological overlaps in pileus coloration, basidiomata size, and subtle microscopic characteristics often complicate species identification, highlighting the necessity of integrative methodologies.

Recent taxonomic research increasingly integrates morphology with multi-locus phylogenetic frameworks. The nuclear ribosomal internal transcribed spacer (ITS) region is still the universal fungal barcode for fungal species identification. However, it often lacks sufficient resolution on its own to confidently support the description of novel taxa. Other loci, such as RNA polymerase II gene (RPB2) and Translation Elongation Factor 1- α (*TEF1- α*), have proven instrumental in elucidating species complexes and validating new taxa within Lyophyllaceae (Bellanger *et al.* 2015, Qi *et al.* 2022). *Calocybe* species are mostly saprotrophic, occurring in grasslands, forest litter, and soils that are rich in organic matter. They assist with nutrient cycling and the turnover of organic matter. The humid tropical climates of southeast Asia, characterized by rapid decomposition processes, likely support ecological niches that differ from those in temperate regions, where the genus has been studied more thoroughly (Graziosi *et al.* 2025).

Kinabalu Park, a UNESCO World Heritage and Global Geopark site in Sabah, Malaysian Borneo, is renowned for its exceptional biodiversity, steep elevation changes, and diverse forest ecosystems that range from lowland dipterocarp to subalpine vegetation (Goh *et al.* 2013, Justine *et al.* 2025). E. J. H. Corner led the Royal Society expeditions to Mount Kinabalu, contributing significantly to documenting Sabah's fungal diversity (Watling and Ginns, 1998). His monographic treatments were the first in English to demonstrate the exceptional diversity of Southeast Asian macrofungi (Watling and Ginns, 1998). He published specific taxonomic studies on Bornean mushrooms, including the genera *Phylloporus* Quél. (Corner 1970) and *Ramaria* Fr. ex Bonord. (Corner 1976). Additionally, he provided detailed reports on the 1961 expedition results (Corner 1962) and the unique flora of Mount Kinabalu East (Corner 1965). Despite the strong likelihood of undocumented diversity, relatively few *Calocybe* records have been reported from this region, and there are no thorough taxonomic studies available. The current study conducts the taxonomic evaluation of a *Calocybe* species from Kinabalu Park using an integrative framework that combines comprehensive morphological characterization with phylogenetic analyses based on ITS and the large subunit of ribosomal DNA (LSU) sequence data.

Materials and methods

Sampling site and Sample collections

Three samples of the mushroom were collected via opportunistic sampling from Bundu Tuhan Trail (6°00'04"N 116°31'43"E), Silau-Silau Trail (6°00'42"N 116°32'24"E), and Liwagu Trail (6°0'39"N 116°32'46"E) Kinabalu Park, Sabah, Malaysia, during field trips on 25 February, 1 November, and 19 November 2025, respectively. The study map was created using QGIS 3.44.3 software (<https://qgis.org/download/>).

Macroscopic morphology

Fresh basidiomata were photographed in situ using an Olympus TG-5 digital camera, and macromorphological characteristics, including pileus shape, size, color, surface texture, lamellae attachment and spacing, stipe features, and overall habit, were recorded from fresh specimens. Color descriptions followed Kornerup and Wanscher (1978). The dimensions of basidiomata were measured in the field, and specimens were subsequently dried in an electric dehydrator (Primada Food Dehydrator MPD68, Malaysia) at 40–45°C for 48 hours. Voucher specimens have been deposited in the Borneensis Collection (BORH), Institute for Tropical Biology and Conservation (ITBC), Universiti Malaysia Sabah (UMS), Kota Kinabalu, Sabah, Malaysia.

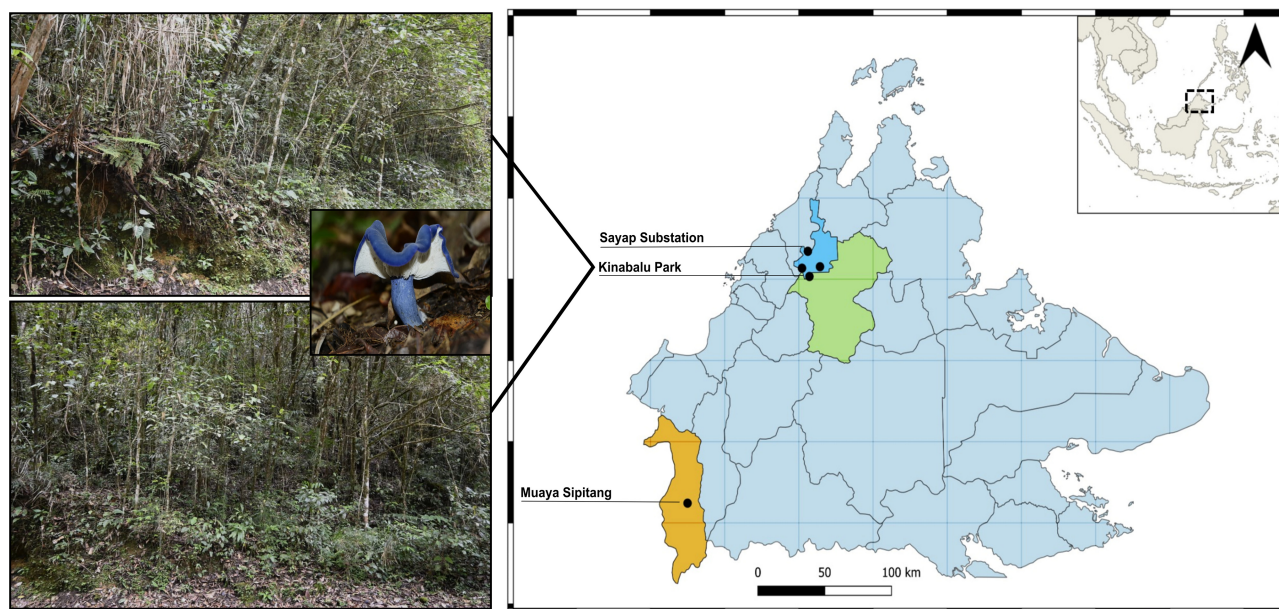


FIGURE 1. Map showing the habitat and geographical locations of the sampling sites in Sabah, Malaysia. The study map was created using QGIS 3.44.3 software (<https://qgis.org/download/>).

Microscopic morphology

For microscopic examination, dried samples were mounted in 3% potassium hydroxide (KOH) and 1% Congo red or Melzer's reagent, and then a compound microscope (Leica DM2500 LED, Germany) was used at magnifications up to $\times 1000$. All measurements were taken from the sections mounted in 1% Congo red and Melzer's reagent. For each specimen, a minimum of 30 basidiospores, 30 basidia, 20 cheilocystidia, and 30 widths of pileipellis were measured from three different basidiomata (Ma *et al.* 2024; Li *et al.* 2025).

A scanning electron microscope was used to examine basidiospores. Small tissues from a dried sample were fixed in 2.5% glutaraldehyde prepared in 0.1 M phosphate buffer (pH 7.2) overnight at 4 °C, rinsed three times, and post-fixed in 1% osmium tetroxide for 1 h at 4 °C. The sample was dehydrated using 70% ethanol and dried by critical-point drying with CO₂. Dried materials were mounted on aluminium stubs with carbon adhesive, sputter-coated with a thin gold-palladium layer (≈ 10 nm) and examined under a scanning electron microscope at 5–10 kV and 6000 $\times$ magnifications (Razzaq *et al.* 2026).

DNA extraction, PCR amplification and sequencing

Genomic DNA extraction was performed using E.Z.N.A Fungal DNA Mini Kit (Omega Bio-Tek, USA) according to the manufacturer's instructions. Primer pairs were used for the amplification of the nuclear rDNA regions, including ITS regions using primers ITS1/ITS4, and LSU region using primers LROR/LR5 (White *et al.* 1990). All PCR amplifications were performed using a Bio-Rad T100 Thermal Cycler. Amplification of the ITS and LSU regions followed the protocol by Vizzini *et al.* (2015) with minor modifications. For ITS, an initial denaturation step at 95°C for 5 min, followed by 35 cycles of denaturation at 94°C for 1 min, annealing at 55°C for 1 min, extension at 72°C for 1 min, and a final extension at 72°C for 10 min. For LSU, an initial denaturation at 94°C for 5 min, followed by 35 cycles of denaturation at 94°C for 30 s, annealing at 53°C for 30 s, extension at 72°C for 40 s, and a final extension at

72°C for 10 min. Agarose gel electrophoresis was performed to visualize PCR products using 1% agarose gels. After electrophoresis, the bands of PCR products were visualized via UV light at 312 nm. For sequencing, the successfully amplified PCR products were sent to Apical Scientific Sdn. Bhd., Selangor, Malaysia for Sanger sequencing. The quality of the newly produced sequences were checked and edited. Then, the contiguous sequences were deposited in GenBank (<http://www.ncbi.nlm.nih.gov/genbank>; Table 1).

TABLE 1. GenBank accession details of ITS and LSU sequences used for phylogenetic analyses in this study.

Species	Collection No	ITS	LSU	Location	References
<i>Calocybe aurantiaca</i>	SYAU FUNGI 006 ^T	NR_156304	NG_058937	China	Li <i>et al.</i> (2017)
<i>Calocybe aurantiaca</i>	YU0095	PV962310	-	China	Li <i>et al.</i> (2017)
<i>Calocybe betulicola</i>	HMJAU48269(2)	OR771920	OR771925	China	Ma <i>et al.</i> (2024)
<i>Calocybe badiofloccosa</i>	HMJU00097	OK649911	OK649881	China	Unpublished
<i>Calocybe badiofloccosa</i>	HMJU00098	MN172332	MN172334	China	Unpublished
<i>Calocybe carnea</i>	CBS552.50	AF357028		Switzerland	Hofstetter <i>et al.</i> (2002)
<i>Calocybe coacta</i>	HMJU269 ^T	OK649907	OK649875	China	Unpublished
<i>Calocybe convexa</i>	SYAU FUNGI 008 ^T	NR_156303	NG_058936	China	Li <i>et al.</i> (2017)
<i>Calocybe carnea</i>	MV-1007	PQ653449	-	Sweden	Unpublished
<i>Calocybe carnea</i>	FR2014052	KP192592	-	France	Bellanger <i>et al.</i> (2015)
<i>Calocybe carnea</i>	K(M):250529	MZ159709	-	United Kingdom	Unpublished
<i>Calocybe carnea</i>	MQ22-KEG090-HRL3511	OQ321901	-	Canada	Unpublished
<i>Calocybe cyanea</i>	RVPR10June97 ^T	AF261400	-	USA	Moncalvo <i>et al.</i> (2002)
<i>Calocybe cyanella</i>	ERP2	MG663232	-	USA	Unpublished
<i>Calocybe cyanella</i>	Mushroom Observer.org/335843	OM655210	-	Mexico	Unpublished
<i>Calocybe cystidiosa</i>	HMJAU48265	OR771915	-	China	Ma <i>et al.</i> (2024)
<i>Calocybe cystidiosa</i>	HMJAU48266	OR771916	-	China	Ma <i>et al.</i> (2024)
<i>Calocybe cystidiosa</i>	HMJAU48267	OR771917	-	China	Ma <i>et al.</i> (2024)
<i>Calocybe chrysenteron</i>	HFRG CG231024	PV031083	-	United Kingdom	Unpublished
<i>Calocybe constricta</i>	HC84/75	AF357036	-	Switzerland	Unpublished
<i>Calocybe decolorata</i>	SYAU FUNGI 004 ^T	NR_156302	NG_058938	China	Li <i>et al.</i> (2017)
<i>Calocybe decolorata</i>	HMJAU48262	OR771922	OR771927	China	Ma <i>et al.</i> (2024)
<i>Calocybe decurrens</i>	HMJU382 ^T	-	MW444857	China	Unpublished
<i>Calocybe decurrens</i>	HMJU383	OK649913	OK649883	China	Unpublished
<i>Calocybe erminea</i>	HMJU00097	OK649911	OK649881	China	Unpublished
<i>Calocybe erminea</i>	HMJU00100 ^T	MN172331	MN172333	China	Unpublished
<i>Calocybe erminea</i>	B212-2	PX683783	PX683785	Pakistan	Unpublished
<i>Calocybe erminea</i>	B212-1	PX683782	PX683784	Pakistan	Unpublished
<i>Calocybe fulvipes</i>	HMJU00317 ^T	MT071590	-	China	Unpublished
<i>Calocybe fulvipes</i>	HMJU3027	OK649910	OK649880	China	Unpublished
<i>Calocybe fulvipes</i>	HMJU 319	MW406907	-	China	Unpublished
<i>Calocybe gambosa</i>	HC78/64	AF357027	-	Switzerland	Unpublished
<i>Calocybe gambosa</i>	TUB 011576	-	DQ071716	Germany	Garnica <i>et al.</i> (2007)
<i>Calocybe gambosa</i>	HMJAU65330	OQ028837	-	China	Unpublished
<i>Calocybe gambosa</i>	HKAS 134249	PV706722	-	China	Lu <i>et al.</i> (2025)
<i>Calocybe gambosa</i>	HBAU15712	MZ144137	-	China	Unpublished
<i>Calocybe hebelomoides</i>	HMJAU59766	PX411667	-	China	Unpublished
<i>Calocybe hebelomoides</i>	HUP 10254	MW672342	-	Pakistan	Unpublished

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TABLE 1. (Continued)

Species	Collection No	ITS	LSU	Location	References
<i>Calocybe ionides</i>	HC77/133	AF357029.2	-	Switzerland	Hofstetter <i>et al.</i> (2002)
<i>Calocybe ionides</i>	MZ063039	MZ063039	-	China	Ma <i>et al.</i> (2024)
<i>Calocybe ionides</i>	HMJAU65349	OQ945186	-	China	Ma <i>et al.</i> (2024)
<i>Calocybe kinabaluensis</i>	BORH/F03591^T	PX915575	PX915578	Sabah Malaysia	This study
<i>Calocybe kinabaluensis</i>	BORH/F03592	PX915576	PX915579	Sabah Malaysia	This study
<i>Calocybe kinabaluensis</i>	BORH/F03593	PX963765	PX963766	Sabah Malaysia	This study
<i>Calocybe lilacea</i>	SYAU-FUNGI-067	OM203539	OM341409	China	Qi <i>et al.</i> (2022)
<i>Calocybe lilacea</i>	SYAU-FUNGI-066 ^T	OM203538	OM341407	China	Qi <i>et al.</i> (2022)
<i>Calocybe longisterigma</i>	SYAU-FUNGI-0	OM203542	OM341408	China	Qi <i>et al.</i> (2022)
<i>Calocybe naucoria</i>	HC80/103	AF357030	-	Switzerland	Hofstetter <i>et al.</i> (2002)
<i>Calocybe naucoria</i>	FR2013213	KP192543	-	France	Bellanger <i>et al.</i> (2015)
<i>Calocybe obscurissima</i>	HBAU15474	MW862295	-	China	Unpublished
<i>Calocybe obscurissima</i>	HFRG_LG211104_1	OQ133619	-	United Kingdom	Unpublished
<i>Calocybe obscurissima</i>	MJ23-234	PV121730	PV122031	France	Unpublished
<i>Calocybe obscurissima</i>	NFSG_20241107_01JB	PX396681	-	United Kingdom	Unpublished
<i>Calocybe obscurissima</i>	FR2014101	KP192650	-	France	Bellanger <i>et al.</i> (2015)
<i>Calocybe obscurissima</i>	HC79/181	AF357031	-	Switzerland	Hofstetter <i>et al.</i> (2002)
<i>Calocybe onychina</i>	FR2014064	KP192622	-	France	Bellanger <i>et al.</i> (2015)
<i>Calocybe pseudoflammula</i>	-	PQ613507	-	China	Unpublished
<i>Calocybe pseudoflammula</i>	HBAU15678	MW862362	-	China	Unpublished
<i>Calocybella pudica</i>	AMB 15997	KP858003	KP858008	Italy	Vizzini <i>et al.</i> (2015)
<i>Calocybella pudica</i>	AMB 15996	KP858002	KP858007	Italy	Vizzini <i>et al.</i> (2015)
<i>Calocybella pudica</i>	AMB 15995	KP858001	KP858006	Italy	Vizzini <i>et al.</i> (2015)
<i>Calocybella pudica</i>	AMB 15994	KP858000	KP858005	Italy	Vizzini <i>et al.</i> (2015)
<i>Calocybe persicolor</i>	HC80/99	AF357026	-	Switzerland	Hofstetter <i>et al.</i> (2002)
<i>Calocybe pilosella</i>	TR gmb 00931 ^T	NR_184873	-		
<i>Calocybe subochracea</i>	SYAU-FUNGI-1071	OM203541	OM341411	China	Qi <i>et al.</i> (2022)
<i>Calocybe</i> sp.	GG255-86	GU234094	-	Netherlands	Unpublished
<i>Calocybe</i> sp.	CAON-RH19-515	MW084663	MW084703	USA	Unpublished
<i>Calocybe</i> sp.	120119MFBPC280	MW554178	-	China	Unpublished
<i>Calocybe</i> sp.	BBF: GC13100202	ON543944	-	China	Bellanger <i>et al.</i> (2015)
<i>Calocybe</i> sp.	ANT78QFB2868	MN992505	-	Canada	Unpublished
<i>Calocybe vinacea</i>	HMJU:5135	NR-186979	NG_243053	China	Unpublished
<i>Calocybe vinacea</i>	HMJU5160	OK649909	OK649877	China	Unpublished
<i>Calocybe violacea</i>	HMJAU65325	OQ024178	OQ024180	China	Unpublished
<i>Calocybe violacea</i>	HMJAU65324 ^T	OQ024177	OQ024179	China	Unpublished
<i>Gerhardtia borealis</i>	AMB 15993	KP858004	KP858009	Italy	Vizzini <i>et al.</i> (2015)
<i>Gerhardtia borealis</i>	MO558376	PV009796	-	USA	Unpublished
<i>Gerhardtia foliicola</i>	HMJAU 57050	MW590671	MW600428	China	Rao <i>et al.</i> (2021)
<i>Gerhardtia foliicola</i>	HKAS 118364	PV018319	PV018316	China	Wang <i>et al.</i> (2025)
<i>Gerhardtia foliicola</i>	OMDL iNat # 222144252	PX094335	-	USA	Unpublished
<i>Gerhardtia sinensis</i>	GDGM 29981	KU563151	KU563152	China	Li <i>et al.</i> (2017)
<i>Myochromella</i> sp.	‘PNW04’	MG890331	-	USA	Unpublished
<i>Myochromella</i> sp.	JK199	ON478198	-	USA	Unpublished

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TABLE 1. (Continued)

Species	Collection No	ITS	LSU	Location	References
<i>Myochromella</i> sp.	SC10521	PP556185	-	China	Unpublished
<i>Myochromella</i> sp.	SC10521-0507	PV611072	-	China	Unpublished
<i>Ossicaulis lachnopus</i>	LEBIN 3575	OP605496	OP605516	China	Wei <i>et al.</i> (2023)
<i>Ossicaulis lachnopus</i>	LEBIN 3559	OP605497	OP605517	China	Wei <i>et al.</i> (2023)

Sequence alignment and phylogenetic analysis

The newly generated sequences of the studied specimens were compared with public sequences using BLASTn analysis (<https://www.ncbi.nlm.nih.gov/geo/query/blast.html>). Based on BLASTn results and morphological similarities, the relevant sequences were obtained. The ITS and concatenated ITS-LSU datasets were used to infer phylogenetic relationships of the studied taxa. For the ITS dataset, a total of 95 sequences were included, comprising three sequences of the newly described species. The ITS sequences were aligned using Bioedit (<https://bioedit.software.informer.com/7.1>) resulting in an alignment of 888 nucleotide positions, with 711 distinct patterns, 494 parsimony-informative sites, 85 singleton sites, and 309 constant sites. For the concatenated (ITS-LSU) dataset, 69 sequences were analyzed, including the ITS and LSU sequences of the new species. The concatenated alignment comprised 2307 nucleotide positions, containing 1050 distinct patterns, 612 parsimony-informative sites, 306 singleton sites, and 1389 constant sites. Two isolates of *Ossicaulis sichuanensis* S.W. Wei, Q. Wang & Y. Li (SC10172, SC10171) were selected as outgroups for ITS and concatenated (ITS-LSU) analyses because they are phylogenetically close to *Calocybe*, but clearly distinct (Vizzini *et al.* 2015). The sequences were manually edited and aligned using AliView (Larsson, 2014). Using RAXML-HP2 on ACCESS v. 8.2.12, 1000 nonparametric bootstrap iterations were used to conduct bootstrap (BS) analysis (Kalyaanamoorthy *et al.* 2017). To ascertain the suitable model of base substitution, JModelTest2 on XSEDE v. 2.1.6 was used to analyze the model for the dataset (Darriba *et al.* 2012). The model TrNef+G was identified as the best-fit model of nucleotide substitution and the other parameters include lsetnst = 6; rates—gamma; prset revmatpr fixed 1.0000, 1.7639, 1.0000, 1.0000, 3.1308, 1.000; and shapepr = fixed 0.725 (Song *et al.* 2023). Finally, MrBayes v. 3.2.7a was used to execute Bayesian Inference (BI) analysis, to infer the posterior probabilities (PP) of the most likelihood phylogeny (<https://nbisweden.github.io/MrBayes>) (Ronquist and Huelsenbeck 2003). Five million generations of four Markov chains were executed, for two runs with a tree sampled every 1000 generations. Clades with bootstrap support (BS) $\geq 70\%$ and posterior probabilities of (PP) $\geq 90\%$ were considered as significant support. Phylogenetic trees were visualized using FigTree v1.4.4 (<https://evomics.org/resources/software/molecular-evolution-software/figtree/>) and edited with Adobe Illustrator v27.6.1. The sequence alignments used for phylogenetic analyses have been submitted to TreeBASE (<https://www.treebase.org>) (submission ID: 32503).

Results

Phylogenetic analyses

Both BS and BI estimations recovered the same phylogenetic topology for the ITS-LSU concatenated dataset. Therefore, the BS tree with both bootstrap support (BS) and Bayesian posterior probability (PP) values are presented (Fig. 2, SUPPL. Fig.1). The phylogenetic tree includes representatives of *Calocybe*, *Myochromella* V. Hofst., Cléménçon, Moncalvo & Redhead, *Gerhardtia*, *Calocybella*, and *Ossicaulis* Redhead & Ginns. Sequences assigned to *Calocybe* were intermingled within a strongly supported clade, showing that these taxa are closely related. The three isolates from this study (BORH/F03591, BORH/F03592, and BORH/F03593) cluster in a well-supported clade (BS = 100%, PP = 1), sister to a clade comprising *Calocybe cyanella* sequences (BS = 100%, PP = 1). This phylogenetic placement supports the recognition of a new phylogenetic lineage namely *Calocybe kinabaluensis* sp. nov. The genus *Calocybella*, represented by *Calocybella pudica* (Bon & Contu) Vizzini, Consiglio & Setti is supported as a distinct lineage sister to *Gerhardtia* with strong bootstrap support (BS = 97%, PP = 1.00).

In the ITS phylogenetic tree, species representing the genera *Calocybe*, *Myochromella*, *Gerhardtia*, and *Calocybella* were included (SUPPL. Fig.1). *Calocybella pudica* established a distinct basal lineage with robust bootstrap support and Bayesian posterior probability values (BS = 97%; PP = 1.00) and distinctly segregated from genus *Calocybe*. Similarly, *Gerhardtia*, represented by *G. borealis*, *G. sinensis* T.H. Li, Ting Li, C.Q. Wang & W.Q. Deng, and *G.*

TABLE 2. Comparison of macro and micro features of *Calocybe kinabaluensis* with other described blue-capped *Calocybe* species.

Specimen	Fungarium Code	Pileus color	Pileus size (cm)	Stipe (cm)	Pileipellis Type	Basidiospores (µm)	Basidia (µm)	Hymenial cystidia	Distribution	References
<i>Calocybe betulicola</i>	HMJAU48265	violet	2.0–3.5	1.5–3.0 × 0.5–0.8	cutis	(2.0)3.0–6.0 × (2.0)3.0–4.0	4.0–6.0 × 10.0–19.0; 2- or 4-spored	Absent	China	Ma <i>et al.</i> 2024
<i>Calocybe cyanella</i>	F-734 (FH)	dusky violet-blue	3.0	3.0 × 0.3	cutis	4.5 × 2.5–3.3	4.8–5.5 × 18.5–22.5	Absent	USA	Singer <i>et al.</i> 1978
<i>Calocybe cyanea</i>	K(N);56506	dark violet or deep purple	15–60	3.0–6 × 15–60	-	(3–)3.6–5	4–6.4 × 14.6–23.5	Absent	USA	Baroni <i>et al.</i> 1999
<i>Calocybe ionides</i>	HMJAU48264	violet to purple-black	1.3–2.8	1.5–3.0 × 0.1–1.2	Trichoderm pileipellis	(3.0)4.0–6.0 × s (2.0)2.2–3.0	3.0–6.0 × 12.0–19.0	Absent	Europe and China	Bon 1999; Kalamees 2004, Ma <i>et al.</i> 2024
<i>Calocybe kinabaluensis</i>	BORH/F03591–3593	bluish to blue-grey	3.4–12	5.5–12.9 × 0.5–2.6	cutis	2.2–3.5 × 2.6–3.8	3.5–7.1 × 15.4–23.6 2–4 spored	Present	Malaysia	This study
<i>Calocybe violacea</i>	HMJAU65324	Purple to bluish-purple	2.5–3.5	4.5–7.5 × 0.5–1	cutis	(5.7) 6.4–6.7 (7.6) × (2.6) 3.0–3.2 (3.4)	5–7 × 15–24	Absent	China	Mu & Bau, 2023

foliicola (Har. Takah.) N. Endo, S. Ushijima, Nagas., Sotome, Nakagiri & N. Maek., formed a separate, well-supported clade (BS = 95%, PP = 1.00). The taxa within the genus *Myochromella* also formed a distinct clade (BS = 92%, PP = 1.00). Within *Calocybe* sensu lato, different species-level clades, including *C. gambosa*, *C. decolorata* X.D. Yu & Jia J. Li, *C. convexa* X.D. Yu & Jia J. Li, *C. ionides* (Bull.) Donk, *C. badiofloccosa* J.Z. Xu & Yu Li, and *C. cystidiosa* A. Ma, J.J. Hu, B. Zhang, & Y. Li, were resolved with strong statistical results. Within the *Calocybe* clade, different species such as *C. carnea* (Bull.) Donk, *C. obscurissima* (A. Pearson) M.M. Moser, *C. pseudoflammula* (J.E. Lange) M. Lange ex Singer, and *C. cyanella* Singer ex Redhead & Singer formed a distinct well-supported clade. The three collections from this study (BORH/F03591, BORH/F03592, BORH/F03593) grouped together in a separate, well supported monophyletic group (BS = 100%, PP = 1.00). Therefore, they are described as a new species, *Calocybe kinabaluensis*. This lineage is distinctively separate from its closely related taxa, established as an independent branch.

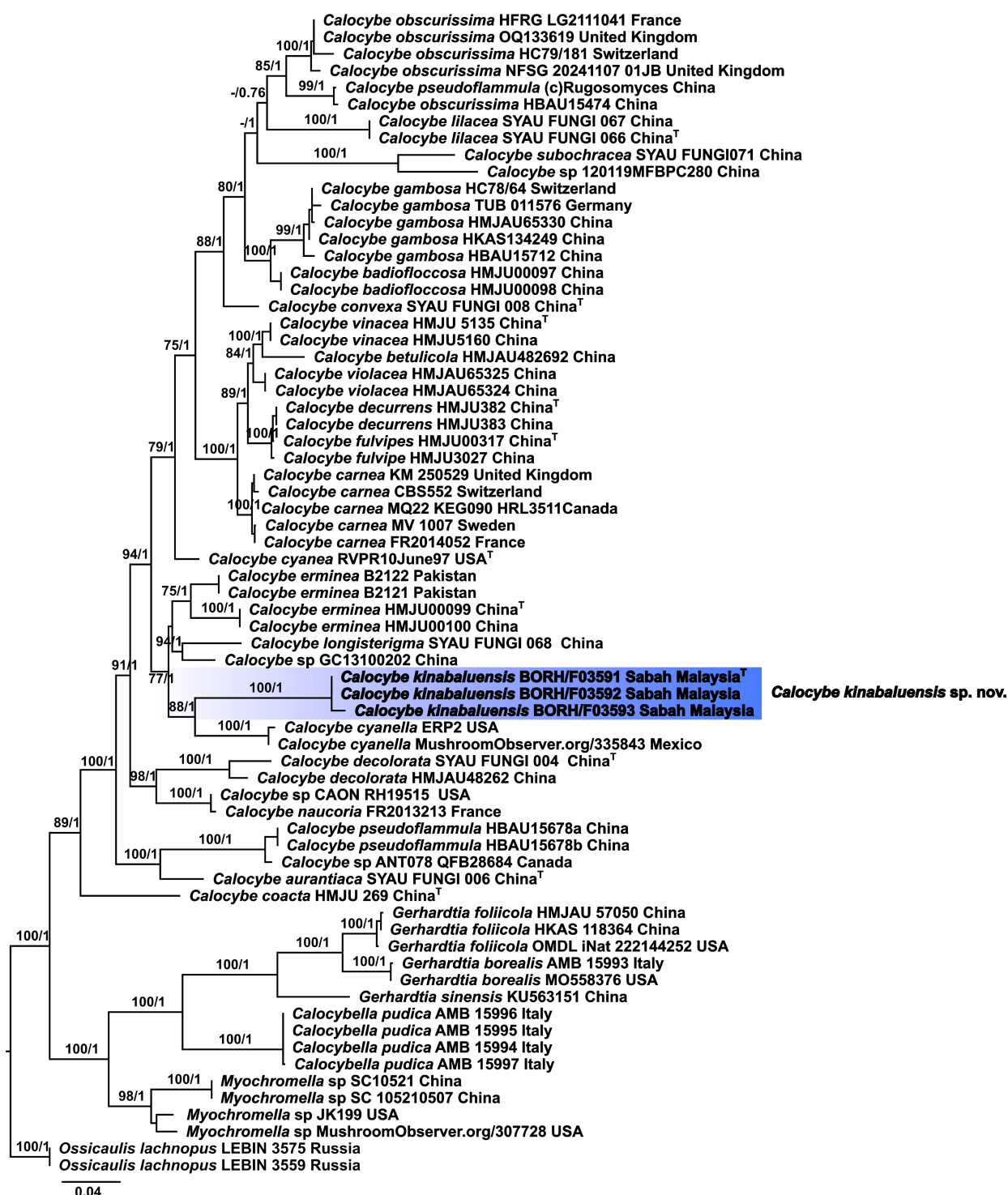


FIGURE 2. Maximum likelihood phylogram of *Calocybe* based on the combined ITS and LSU sequences. Bootstrap support (BS $\geq$ 75% and PP $\geq$ 0.95) is annotated on the branches. The new species is bold.

Taxonomy

Calocybe kinabaluensis Sathiya Seelan, J.S, Kasmin, J Usimin, N.A & Vizzini *sp. nov.* Figures. 3–7
MycoBank number: MB86214

Diagnosis:—differs from closely related species by its convex to plano-convex, deep blue indigo colored pileus, white lamellae, deep blue to indigo-blue stipe, relatively smaller basidiospores, cutis pileipellis, and presence of cheilocystidia.

Etymology:—Refers to Mount Kinabalu, Sabah, Malaysia, where the type specimen was collected.

Holotype:—MALAYSIA. Sabah: Bundu Tuhan Trail, Kinabalu Park, (6°00'04"N 116°31'43"E), elevation 900–1700 m, on forest soil, 25 February 2025, Jamil Kasmin and Jaya Seelan Sathiya Seelan (BORH/F03591, holotype!).

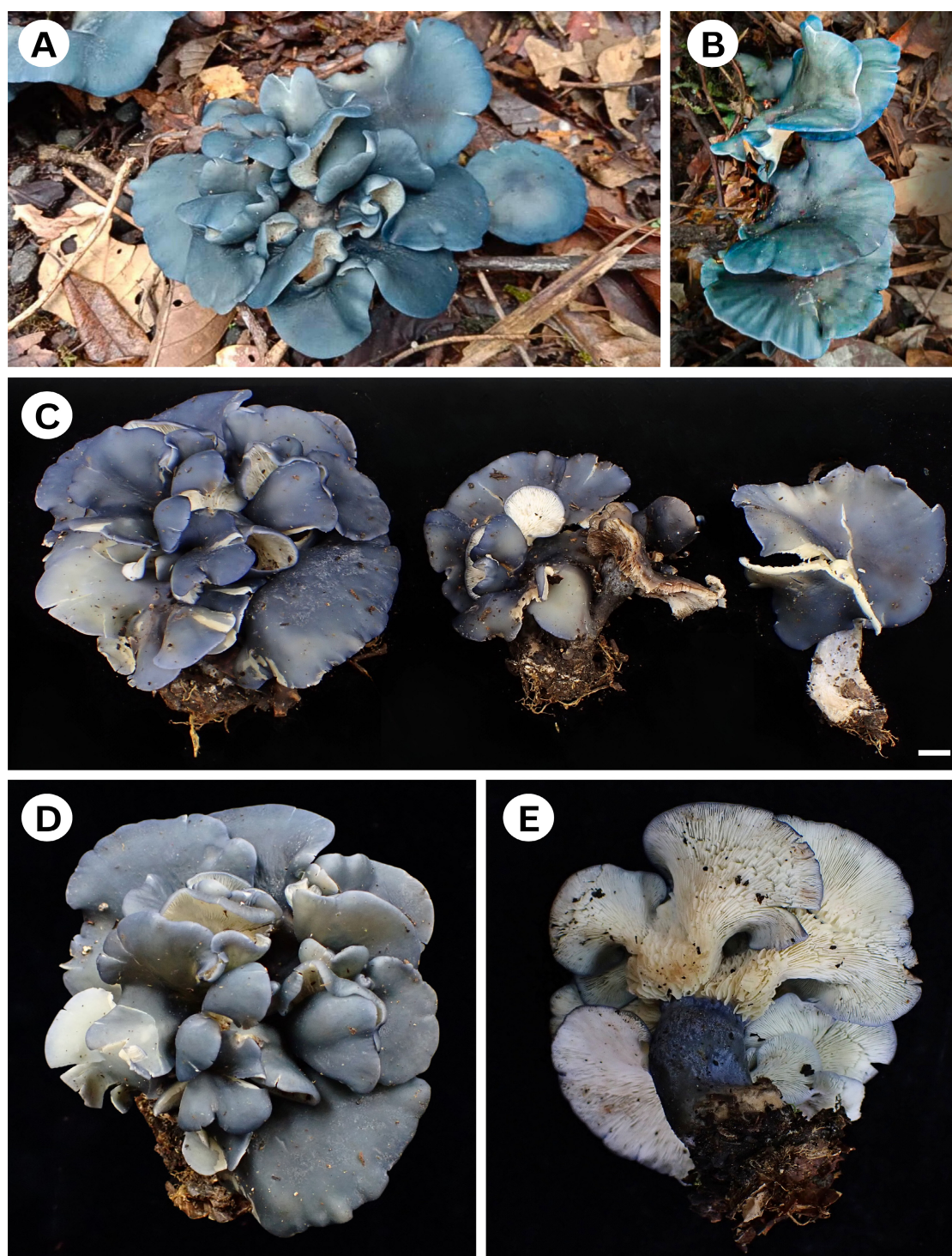


FIGURE 3. Macroscopic features of *Calocybe kinabaluensis* (BORH/F03591) (Holotype). **A** and **B**. Basidiomata in habitat. **C**. Basidiomata (Scale bars: 1 cm). **D**. Wavy pileus margin. **E**. Decurrent lamellae.

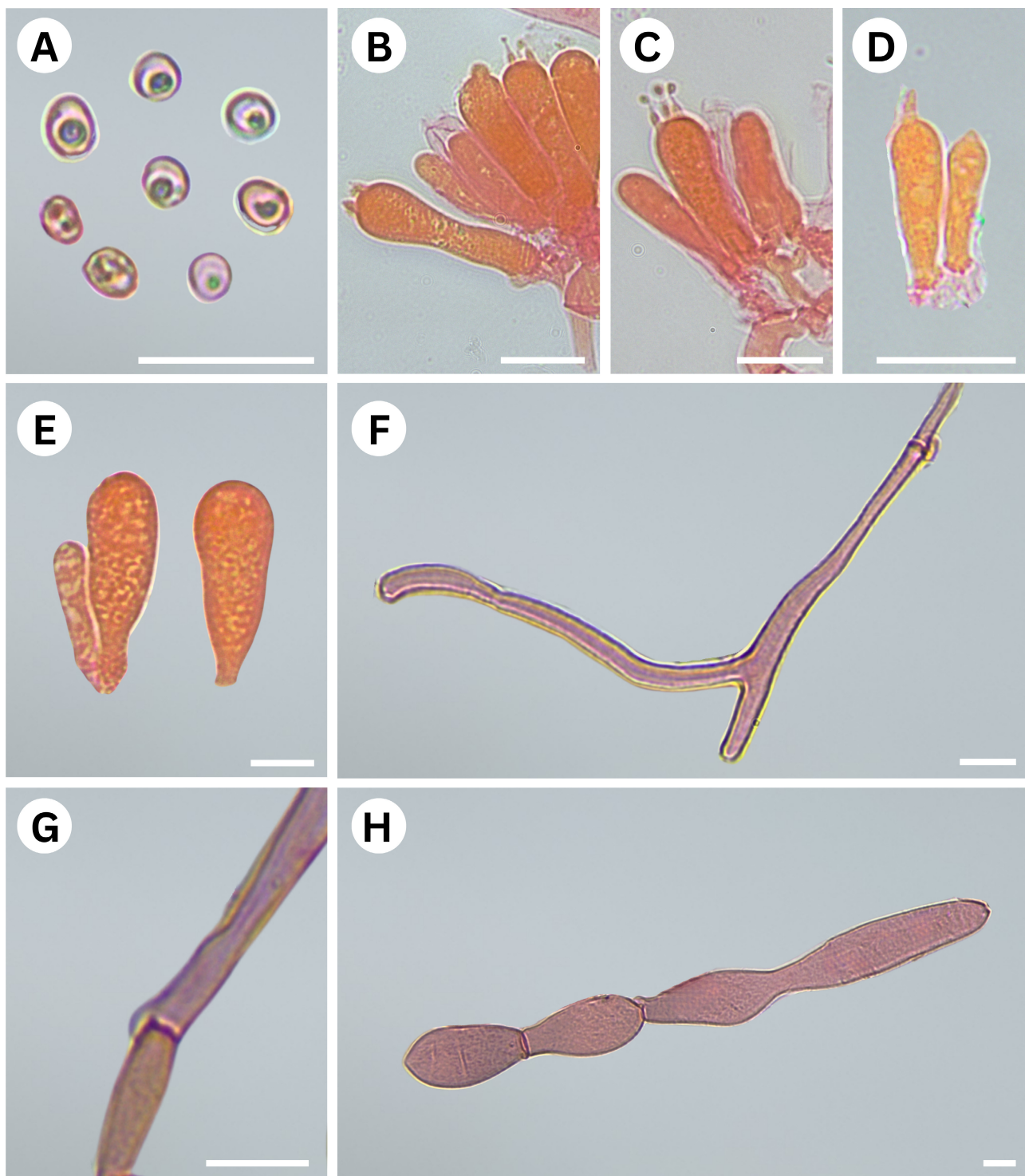


FIGURE 4. Microscopic features of *Calocybe kinabaluensis* (BORH/F03591). **A.** Basidiospores. **B** and **C.** Basidia. **D.** Cheilocystidia. **E.** Basidioles. **F.** Pileipellis structured as a cutis. **G.** Clamp connection. **H.** Stipitipellis hypha. Scale bars **A–H:** 10 μ m.

Description:—*Basidiomata* small to medium-sized (Figure. 3). *Pileus* 34–120 mm wide, convex to plano-convex, form rosette-like clusters, surface dry, smooth to slightly silky, deep blue to indigo-blue (24C5–24C7), margin rounded to irregularly lobed and undulate, eccentric attachment to stipe (Figure. 3D). *Context* 3–7 mm thick, whitish, fleshy to firm. *Lamellae* adnate to slightly decurrent, thin, ventricose near the stipe, narrower towards the pileus margin, crowded; whitish to pale cream (2A1–2B1), edge entire or fimbriate (Figure. 3E). *Stipe* 55–129 $\times$ 5–26 mm, cylindrical to slightly clavate, deep blue to indigo blue (24C5–24C7), white to pale cream towards the base (2A1–2B1), smooth to slightly silky, dry, insertion apparently eccentric (Figure. 3E). Odor indistinct. Taste slightly bitter. Spore print white.

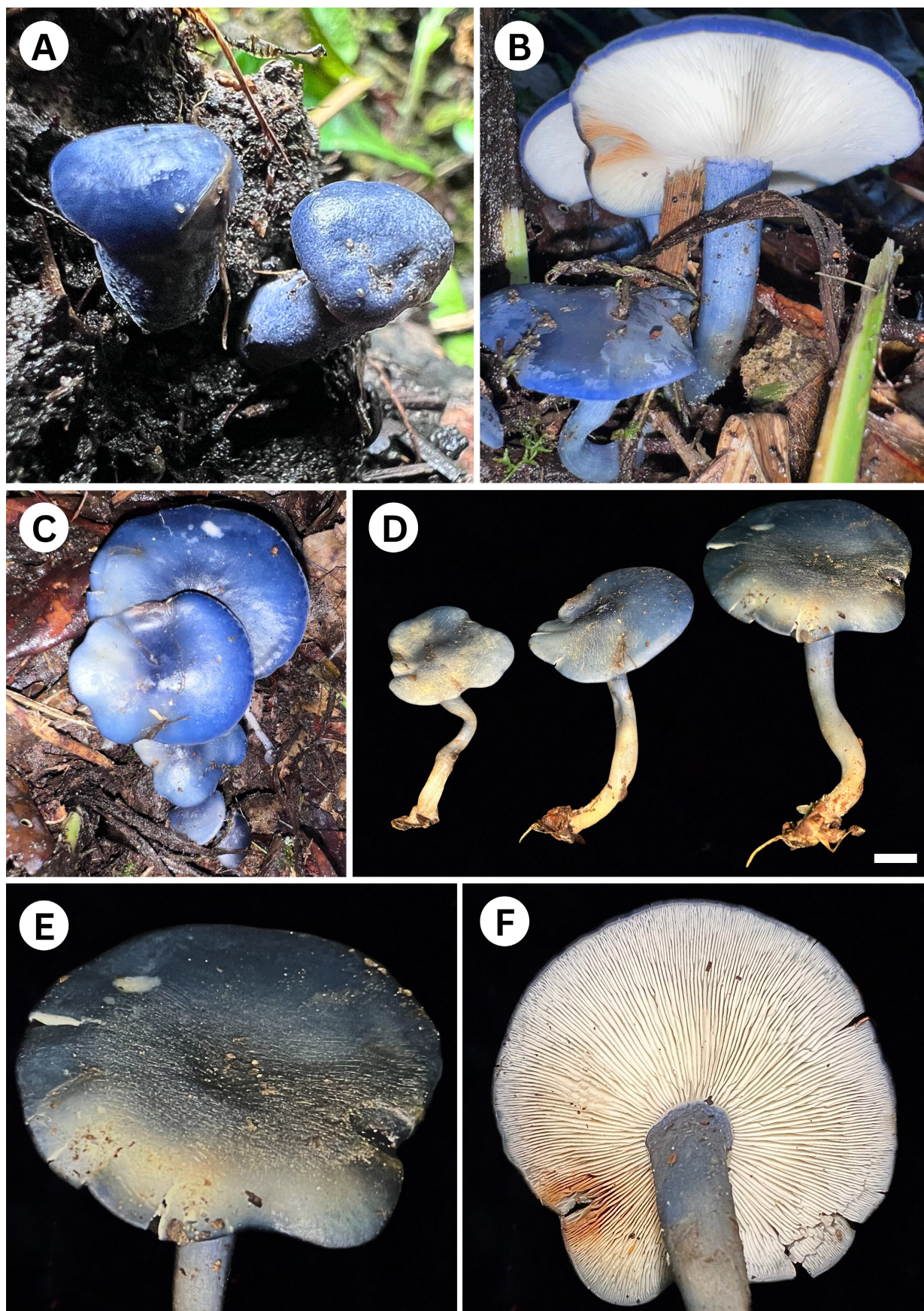


FIGURE 5. Macroscopic features of *Calocybe kinabaluensis* (BORH/F03593) (Paratype). **A.** Immature stage of basidiomata (Young Bud). **B.** Lateral view of basidiomata. **C.** Dorsal view of basidiomata at different development stages (Scale bars: 1 cm). **D–E.** Pileus. **F.** Adnate lamellae.

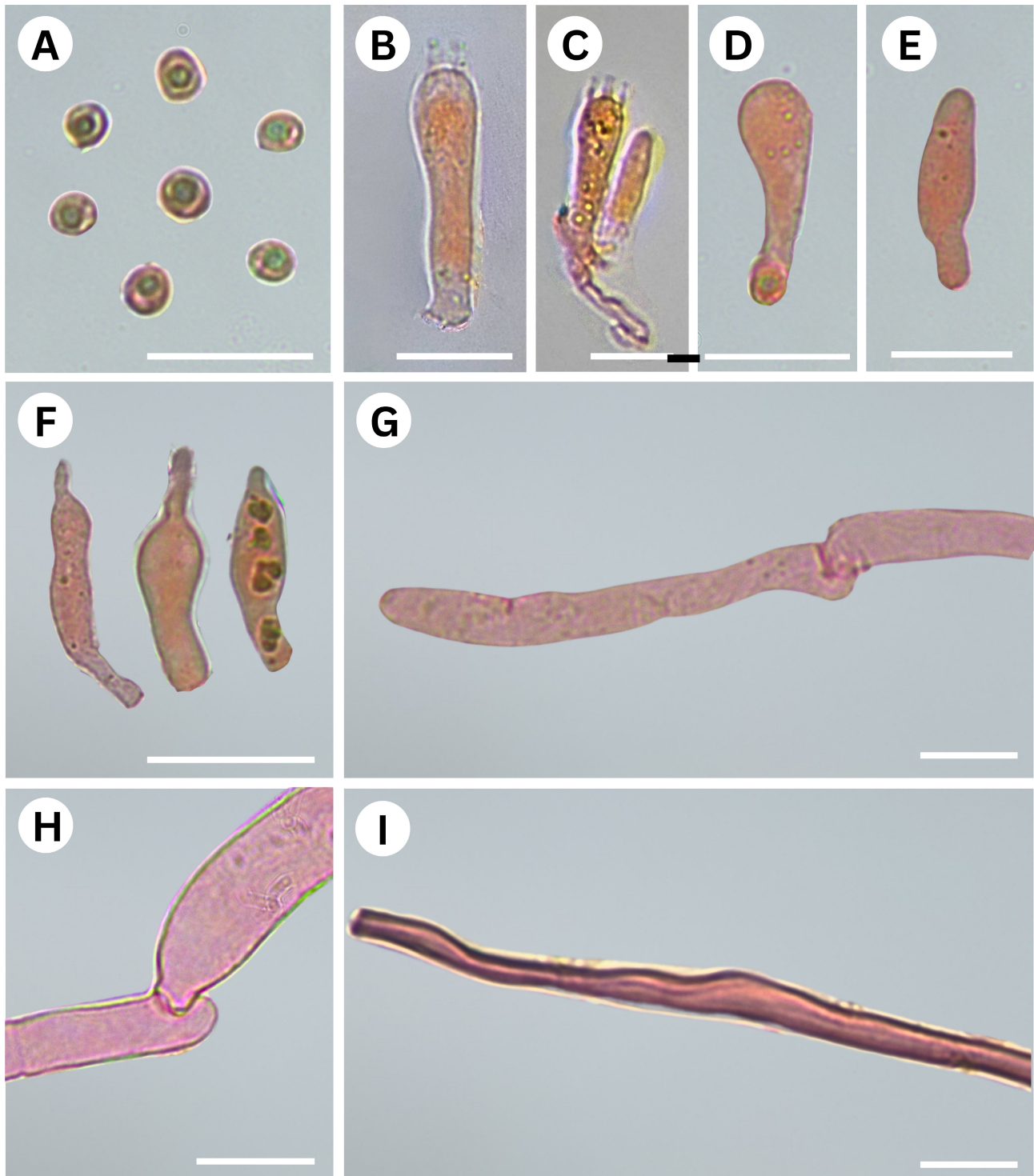


FIGURE 6. Microscopic features of *Calocybe kinabaluensis* (BORH/F03593). **A.** Basidiospores. **B** and **C.** Basidia. **D.** Basidioles. **E** and **F.** Cheilocystidia. **G.** Pileipellis hypha. **H.** Clamp connection. **I.** Stipitipellis hypha. Scale bars **A–H:** 10 μm .

Basidiospores (2.2–) 2.5–3.3 (–3.5) $\times$ (2.6–) 2.8–3.5 (–3.8) μm , av. 3.0 $\times$ 3.1 μm , $Q = 0.82\text{--}1.44$, $Q_m = 1.15 \pm 0.09$, ovoid to ellipsoid, smooth, thin-walled, hyaline, inamyloid (Figure. 4A). Cyanophily was assessed (SUPPL. Fig. 2). *Basidia* 16.5–23.6 $\times$ 4.5–6.9 μm ($\bar{x} = 20.1 \times 5.7 \mu\text{m}$, $n = 30$), 2–4 spored, sterigmata clavate (Figure. 4B–C). *Cheilocystidia* 3.1–5.5 $\times$ 12.7–28.0 μm , thin-walled, hyaline, cylindrical to slightly lageniform, with an apex rounded to slightly swollen, occasionally with short mucronate apex (Figure. 4D). *Pleurocystidia* absent. *Pileipellis* a cutis, hyphae 2.1–10.3 μm wide, hyaline, septate, smooth (Fig. 4F). *Stipitipellis* a cutis, hyphae 2.1–16.9 μm wide, hyaline, septate, smooth (Fig. 4H). *Clamp connections* present in all tissues (Figure. 4G).

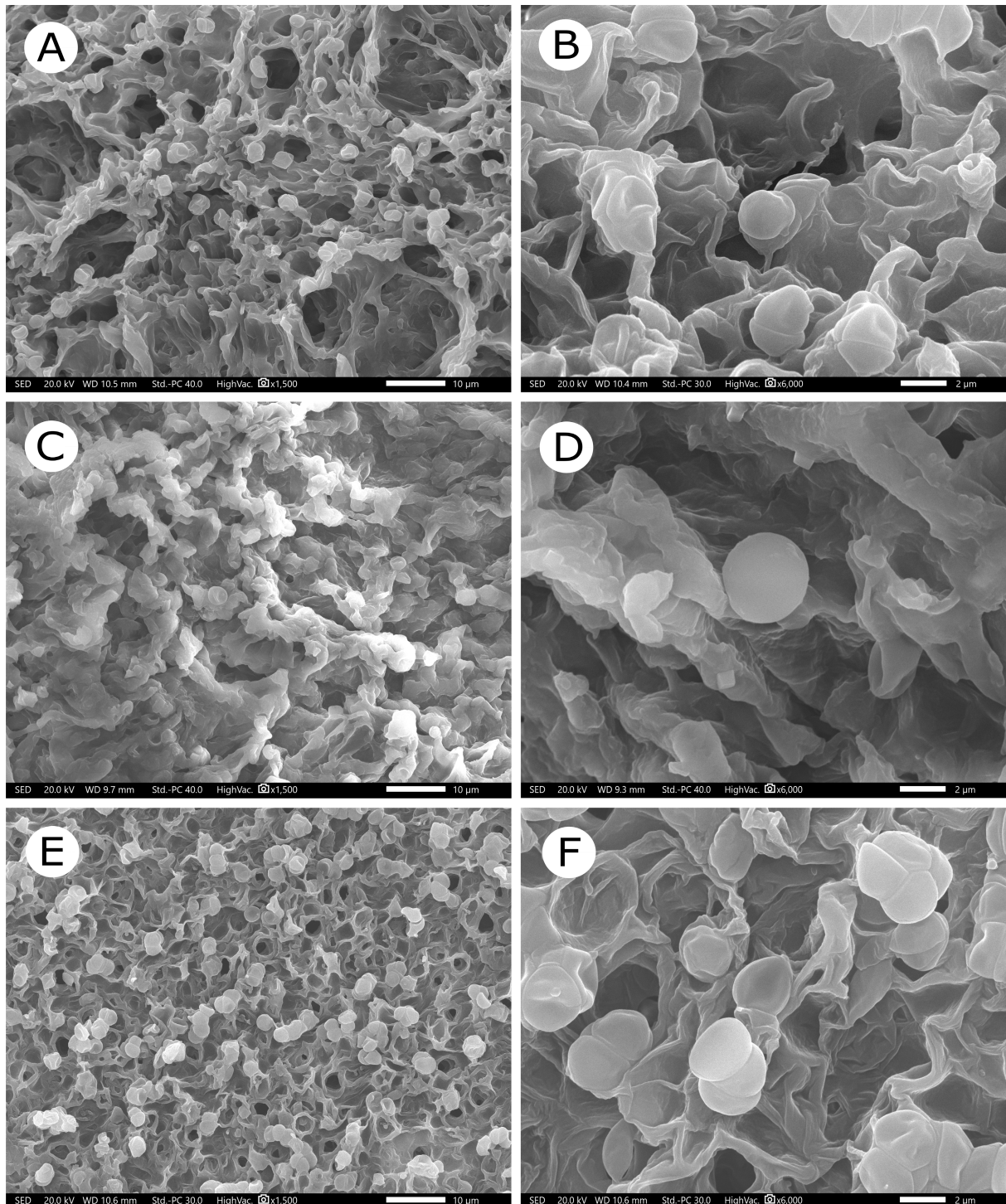


FIGURE 7. Scanning electron micrographs of basidiospores of *Calocybe kinabaluensis*. **A–B.** Specimen BORH/F03591 showing smooth, globose to subglobose basidiospores. **C–D.** Specimen BORH/F03592 with smooth basidiospores. **E–F.** Specimen BORH/F03593 showing smooth basidiospores.

Habit, Habitat, and distribution: Caespitose to gregarious, growing on forest soil and grassland in lower montane forest. Currently known only from the type locality in Mount Kinabalu, Sabah, Malaysia.

Additional Specimens Examined (Paratypes): MALAYSIA. Sabah: Liwagu Trail, Kinabalu Park, 6°0'39"N 116°32'46"E, elevation 1500–1600 m, on soil, 1 November 2025, BORH/F03592; Silau-Silau Trail, Kinabalu Park, 6°00'42"N 116°32'24"E, elevation 1560–1600 m, on forest soil and grassland (Nearby roadside along the Timpohon gate, entrance to Mount Kinabalu), 19 November 2025, Jamil Kasmin, Nur Amanina, Jaya Seelan Sathiya Seelan, (BORH/F03593, paratype!)

Discussion

Based on the molecular and morphological results, we propose the introduction of the new species, *C. kinabaluensis*. The species is clearly nested within the family Lyophyllaceae, confirmed by the presence of siderophilous granulation in the basidia and our phylogenetic analysis (Fig. 2), which places it within the *Calocybe* clade. Morphologically, the new species belongs to the group of five blue-pigmented *Calocybe* species historically placed in the genus *Rugosomyces*. The group is characterized by violaceous to indigo-blue basidiomata and cutis pileipellis. Among these taxa, *C. cyanella* is the most morphologically similar species. *Calocybe cyanella* is described as having blue tones to the pileus and stipe (Singer 1948). Basidiomata of *C. kinabaluensis* can be distinguished from *C. cyanella* by several key characteristics. Firstly, the basidiospores of *C. kinabaluensis* are smaller than those of *C. cyanella*. Basidia in *C. kinabaluensis* are predominantly 2–4-spored basidia, whereas the closely related species possess typical 4-spored basidia, providing an additional micromorphological character that supports its distinction. Furthermore, the pileus of *C. cyanella* is described as dusky violet-blue whereas *C. kinabaluensis* exhibits a deep blue to indigo-blue color with a smooth to slightly silky surface and a margin that is irregularly lobed and undulate (Table 2). From an ecological perspective, *C. cyanella* is traditionally associated with tropical and subtropical habitats in the southern regions of the United States (Bessette *et al.* 2019), whereas *C. kinabaluensis* was collected from forest soil and grassland areas in the lower montane forest of Mount Kinabalu, Sabah, Malaysia, suggesting ecological differentiation under tropical conditions. Phylogenetically, our concatenated ITS and LSU phylogenetic tree shows that *C. kinabaluensis* forms a distinct lineage from *C. cyanella* with high bootstrap support (BS = 100%, PP = 1.00). While both share a cutis-type pileipellis, characteristic of the *Calocybe* group, both genetic and morphological distinctions justify the recognition of the Malaysian sample as a new species.

Calocybe longisterigma X.D. Yu, Ye Zhou & H.B. Guo is another species typically reported from Asia, originally described as a saprotrophic fungus found on grasses in Inner Mongolia (Qi *et al.* 2022). Phylogenetic analyses indicate that *C. longisterigma* is among the taxa most closely related to the novel species. Its principal characteristics include a brownish to orange pileus and stipe, which contrast markedly with the indigo-blue coloration of *C. kinabaluensis*. Additionally, the basidiospores of *C. longisterigma* are of similar size but slightly more ellipsoid than those of the new species. *C. longisterigma* is characterized by elongated sterigmata, whereas in *C. kinabaluensis*, the basidia are clavate with 2–4 spored basidia, and the sterigmata differ in structure.

Calocybe cyanea Singer ex Redhead & Singer has been reported from neotropical regions, typically on well-rotted logs (Baroni *et al.* 1999). The pileus of *C. cyanea* is described as a dark violet or deep purple (Singer 1948, Baroni *et al.* 1999), and its cylindrical stipe is violet at the apex and tomentose at the base (Baroni *et al.* 1999). The lamellae are thick with broad edges and coloration of pale yellow, a stark difference from *C. kinabaluensis* with its thin gills of a pale cream color. Another distinct contrast between *C. cyanea* and our novel species is the stipe coloration, in which the former's stipe is dark to brownish yellow in color. The basidiospores *C. cyanea* are longer, (3–)3.6–5 μm and thick-walled (Baroni *et al.* 1999). Basidia in *C. cyanea* are typically 4-sterigmate, however sometimes 2-sterigmate basidia may occur. *Calocybe kinabaluensis* also exhibited 4-sterigmate basidia in this study. Furthermore, *C. kinabaluensis*, which shows clavate basidia with 2–4 spored, *C. cyanea* exhibits a more typical basidial structure with limited sterigmata, lacking the unusual sterigmatal variability observed in the new species. Additionally, *C. cyanea* lacks hymenial cystidia and its pileipellis is formed by a hymeniform layer of clavate, spheroid, pyriform, often mucronate elements.

Calocybe ionides is a species that grows on leaf litter in temperate and subtropical forests worldwide (Bon 1999, Kalamees 2004, Li *et al.* 2017, Xu *et al.* 2021a, Ma *et al.* 2024). Its pilei are much smaller and stipes significantly shorter than *C. kinabaluensis* (Bon 1999, Kalamees 2004, Ma *et al.* 2024). The color of its pileipellis is closer to violet and purple-black, often darker in the center (Ma *et al.* 2024). This contrasts with the deep blue and indigo coloration of the *C. kinabaluensis* pileipellis. The lamellae are white and crowded, similar to those of our novel species (Ma *et al.* 2024). However, the basidiospores of *C. ionides* are noticeably oblong in shape (5–7 $\times$ 2.5–3.0 μm), unlike the ovoid basidiospores of *C. kinabaluensis* (Bon 1999, Kalamees 2004, Ma *et al.* 2024). Its basidia are clavate with up to four sterigmata, and the species lacks hymenial cystidia. Similarly, *C. kinabaluensis* displays clavate basidia with 2–4 spores basidia, which clearly differentiates it from *C. ionides* and represents a remarkable and diagnostic micromorphological feature of the new species.

Conclusion

The recognition of *C. kinabaluensis* is based on a combination of morphological, ecological, and phylogenetic evidence to define species boundaries, as commonly used in recent studies of descriptions of new fungal species. It is the first *Calocybe* species described from Malaysia. These results broaden current knowledge of *Calocybe* diversity and highlight Malaysia as an underexplored region with significant potential for future fungal taxonomic research.

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CRedit authorship contribution statement

Jaya Seelan Sathiya Seelan, Nur Amanina Binti Usimin, Jamil Kasmin, and Muhammad Shahbaz: Field work, conceptualization, and formal analysis. **Jaya Seelan Sathiya Seelan, Alfredo Vizzini, Ibrahim Ghani Wasti, Nur Amanina Binti Usimin and Muhammad Shahbaz:** Original manuscript writing, figures, initial review, and editing. **Jaya Seelan Sathiya Seelan and Alfredo Vizzini:** Critical review. **Jaya Seelan Sathiya Seelan:** Supervision and final validation.

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Data availability: the nucleotide sequences have been deposited in the NCBI GenBank database (<https://submit.ncbi.nlm.nih.gov/subs>). The accession numbers will be made publicly available upon publication of this article. All other data supporting the findings of this study are available from the corresponding author upon reasonable request.

Declarations

Competing interests: The authors state that they have no conflicts of interest.

Ethical approval: The current research work does not require ethical approval.

Supplementary material

Supplementary Figure S1 provides an additional ITS phylogenetic tree and Figure S2 describes the presence of cyanophily.

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