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ORIGINAL ARTICLE

Kaziboletus, a new boletoid genus of Boletaceae associated with *Shorea robusta* in Bangladesh

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Abstract

A bolete putatively associated with *Shorea robusta*, morphologically resembling *Leccinum*, *Leccinellum*, and *Spongispora* but distinct genetically, was collected in Bangladesh. DNA analyses of four gene fragments (nrLSU, *TEF1-α*, *RPB1*, and *RPB2*) placed this bolete in the subfamily Leccinoideae of the family Boletaceae, but representing a distinct generic lineage. Phylogenetically, the new bolete is sister to a clade comprising morphologically closely related stipitate-pileate genera: *Leccinum*, *Leccinellum*, and *Spongispora*; and sequestrate genera: *Chamonixia*, *Octaviania*, *Rossbeevera*, and *Turmalinea*. Nevertheless, some morphological differences and host preference together with the molecular inferences distinguish the new bolete from *Leccinum*, *Leccinellum*, and *Spongispora*. This lineage is described as a monotypic genus *Kaziboletus* and is typified by *K. rufescens*. It is circumscribed by a context that turns pale red or reddish orange when exposed, a scurfy stipe with conspicuous longitudinal striations from the apex to just above the base, elongated to cylindrico-fusoid smooth basidiospores 17–19 × 5.5–6.5 µm, the presence of sparse hymenial cystidia, an epithelium pileipellis, and putative ectomycorrhizal with *S. robusta* in Bangladesh. Morphological descriptions, illustrations, line drawings, and comparisons with allied taxa/genera are provided. A key to the genera morphologically similar to *Kaziboletus* is also provided.

Keywords Asian distribution, · Dipterocarpaceae, · Leccinoideae, · Tropical bolete

Introduction

Boletaceae Chevall. is a species-rich fungal family in the order Boletales E.-J. Gilbert. Within the family, many species are important because of their ecological and economical value (Arora 2008; Sitta and Floriani 2008; Sitta and Davoli 2012; Cui et al. 2016). Boletes are attractive to mushroom pickers as they can be easily recognized in the field by their brilliant colors and usually large basidiomata with fleshy context and tubular hymenophore instead of a lamellar configuration (Corner 1972; Wu et al. 2014). Most species of the Boletaceae form ectomycorrhizal symbioses (ECMs) with various plants including Dipterocarpaceae Blume (Hong 1979; Watling and Lee 1995, 1998; Lee et al. 2003; Sirikantaramas et al. 2003; Yuwa-Amornpitak et al. 2006; Peay et al. 2010; Brearley 2012; Hosen and Li 2017; Wu et al. 2018). In Southeast Asia and the Indian subcontinent, Dipterocarpaceae are important ECMs host plants. *Shorea robusta* C.F. Gaertn., a broad-leaved tree in the plant family Dipterocarpaceae, is a native species on the Indian subcontinent. A considerable number of fungi have previously been reported with an association to *S. robusta* (Tulloss and Bhandary 1992; Dutta et al. 2015; Hosen et al. 2013, 2015; Hosen and Li 2015, 2017; Parihar et al. 2018a, b); however, Wu et al. (2018) hypothesized that new boletoid taxa await discovery, if more intensive collecting to be done in that region.

This article is dedicated to Dr. Kazi M. Badruddoza, a national emeritus scientist and founder of modern agriculture of Bangladesh.

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Since the development of an excellent phylogenetic framework of the Boletaceae by Wu et al. (2014), ca. 35 new genera have been erected and established in that family, mostly from East Asia (Zhao et al. 2014; Zeng et al. 2014; Orihara et al. 2016; Wu et al. 2016; Zhang and Li 2018), Southeast Asia (Wu et al. 2018; Khmelnitsky et al. 2019; Vadthanarat et al. 2019), and Europe (Gelardi et al. 2014a, b, c; Vizzini 2014a, b). Wu et al. (2014) showed seven major clades at the subfamily levels, Leccinoideae is one of the subfamilies, and includes 14 genera (Wu et al. 2018). A recent study by Kuo and Ortiz-Santana (2020) merged several well-known sequestrate (*Chamonixia* Rolland, *Octaviania* Vittad., *Rossbeevera* T. Lebel & Orihara, and *Turmalinea* Orihara & N. Maek.) and stipitate-pileate (*Leccinum* Gray and *Leccinellum* Bresinsky & Manfr. Binder) genera into a single large genus *Leccinum* in subfamily Leccinoideae. Orihara et al. (2021) argued against this broad concept of *Leccinum* because of the lack of backbone resolution in the evolutionary tree, and because several other major clades of stipitate-pileate taxa (*Leccinum* and/or *Leccinellum*) within Leccinoideae were poorly resolved. Furthermore, Orihara et al. (2021) pointed that synonymy of these sequestrate and stipitate-pileate genera with *Leccinum* is premature and may result in the loss of information of evolutionary history. In an earlier study, Lebel et al. (2012) also argued against the collapse of five genera (*Chamonixia*, *Leccinum*, *Leccinellum*, *Rossbeevera*, and *Octaviania*) into *Leccinum* because of the lack of support at the genus level, and the presence of remarkable morphological and molecular characters supporting them as distinct genera within Leccinoideae. In this study, we follow the traditional classification and interpretation of Lebel et al. (2012) and Orihara et al. (2016, 2021).

In Bangladesh, only five putatively ECMs fungi have been reported previously in association with *S. robusta* (Hosen et al. 2013, 2015; Hosen and Li 2015, 2017). During studies of boletes in Bangladesh in association with *S. robusta*, the first author found several collections of the same bolete which were superficially similar to a species of *Leccinum*, *Leccinellum*, or *Spongispora* G. Wu et al. Surprisingly, however, the nrLSU sequence derived from the new bolete collection matched only 86.78% with the known species of *Leccinum* available in GenBank. Molecular phylogenetic analyses of 4-gene, i.e., the nuclear ribosomal large subunit (nrLSU), translation elongation factor-1α (*TEF1-α*), the largest subunit of RNA polymerase II (*RPB1*), and the second largest subunit of RNA polymerase II (*RPB2*) along with detailed morphological observation did not place the new bolete with either *Leccinum*/*Leccinellum* or *Spongispora*. Rather, the evidence supports a separate generic lineage distinct from those genera. Therefore, this new generic lineage is formally described as a new genus in the subfamily Leccinoideae of the family Boletaceae.

Material and methods

Specimen collection and deposition

The specimens were collected from tropical Bangladesh in association with *Shorea robusta*, described and deposited in the Cryptogamic Herbarium of Kunming Institute of Botany, Chinese Academy of Sciences, Kunming, China (KUN-HKAS), and in the private herbarium of the first author (PHI).

Morphological studies

Macromorphological descriptions were based on field notes and documented with photographs. Color codes were derived from Kornerup and Wanscher (1981). Micromorphological observations were made from dried specimens mounted in H_2O, 5% aqueous KOH (w/v) and Congo Red. Melzer's solution was used to check any amyloid reaction of basidiospores and tissues. Line drawings were made freehand. In the description of basidiospore measurements, the notation [n/m/p] was used, in which *n* basidiospores were measured from *m* basidiomata of *p* collections. Dimensions for basidiospores are given as (a–)b–c(–d), in which "b–c" contains a minimum of 90% of the measured values and extreme values "a" and "d" are given in parentheses, whenever necessary. *Q* denotes the length/width ratio of a measured basidiospore, Q_m denotes the average of n basidiospores, and SD is their standard deviation. Results are presented as $Q_m \pm SD$. Basidiospores were also observed using a scanning electron microscope (SEM) and following the protocol in Hosen et al. (2013).

DNA extraction, PCR amplification, and sequencing

Protocols for genomic DNA extraction, PCR amplification, and sequencing followed those described in Hosen et al. (2013) and Wu et al. (2014), and references cited therein. In this study, one nuclear ribosomal and three nuclear protein encoding genes were used: 1) the nuclear ribosomal large subunit (nrLSU), 2) the protein encoding gene for translation elongation factor-1α (*TEF1-α*), 3) the protein encoding gene for the largest subunit of RNA polymerase II (*RPB1*), and 4) the protein encoding gene for the second largest subunit of RNA polymerase II (*RPB2*). LR0R/LR5 (Vilgalys and Hester 1990), ef1-983F/ef1-1567R (Rehner and Buckley 2005), rpb1-BF/rpb1-BR (Wu et al. 2014) and rpb2-BF/rpb2-BR (Wu et al. 2014) primer pairs were used for the amplification of nrLSU, *TEF1-α*, *RPB1*, and *RPB2* fragments, respectively. PCR products were purified with a Gel Extraction & PCR Purification Combo Kit (Spincolumn; Bioteke, Beijing, China). Samples were sequenced using the same primers as in the original PCR amplifications.

DNA sequence alignments and dataset assembly

The newly obtained nrLSU sequences from the new bolete were used as a query in a Blast search to compare with those already deposited in GenBank. The closest matches and reference sequences were then retrieved, mainly from recent phylogenetic studies (Desjardin et al. 2011; Orihara et al. 2012a, 2016; Hosen et al. 2013, 2019; Nuhn et al. 2013; Wu et al. 2014, 2018; Vadthanarat et al. 2018; Khmelnitsky et al. 2019; Kuo and Ortiz-Santana 2020). First, a nrLSU dataset was reconstructed which consisted of 360 nrLSU sequences of Boletales (data not shown). In this dataset, almost all representative genera of Boletaceae were included and the new bolete appeared in the subfamily Leccinoideae with moderate Bootstrap (BS) support. Following the nrLSU analysis, representative species/genera of the subfamily Leccinoideae, within which the new bolete nested, were considered for the 4-gene analyses. For the 4-gene analyses, a total of 67 samples of Boletaceae were retained from the nrLSU taxon set, and subsequently available sequences of *TEF1-α*, *RPB1*, and *RPB2* were retrieved from GenBank (Table 1). Additionally, five samples from the three genera *Binderoboletus* T.W. Henkel & M.E. Sm., *Ionosporus* Khmeln., and *Rhodactina* Pegler & T.W.K. Young were included in the 4-gene dataset to determine the phylogenetic affinity among genera within Leccinoideae. Each single-gene dataset was aligned in MAFFT v.6.8 using the E-INS-i strategy (Katoh et al. 2005), and manually edited in BioEdit v.7.0.9 (Hall 1999). The single-gene aligned datasets were then concatenated using Phyutility (Smith and Dunn 2008) for combined phylogenetic analyses. MrModeltest 2.3 (Nylander 2004) was used to select the best-fit substitution model of evolution for each aligned dataset separately with Akaike information criterion (AIC). The selected models were GTR+I+G, GTR +I+G, SYM+G, and K80+I+G for nrLSU, *TEF1-α*, *RPB1,* and *RPB2* datasets, respectively.

Phylogenetic analyses

The maximum likelihood (ML) method was conducted with RAxML v.7.2.6 (Stamatakis 2006). As RAxML only supports the GTR model, GTRGAMMAI was used for analysis of the 4-gene dataset. The phylogenetic tree was inferred by a single analysis with four partitions (one for each gene). All parameters in the ML analysis were set as default, and BS support values were obtained with 1000 replicates. Support values from bootstrapping runs (MLB) were mapped on the best ML tree using the "-f a" option of RAxML and "-x 12345" as a random seed to invoke the novel rapid bootstrapping algorithm.

Bayesian inference (BI) analysis was conducted with MrBayes 3.2 (Ronquist and Huelsenbeck 2003). Individual best-fitting substitution models were assigned to four different partitions. Partitioned Bayesian analysis with four chains was conducted by setting 6 million generations under the selected evolutionary models. Trees were sampled every 100 generations and posterior probabilities (PP) calculated after discarding the first 25% of the samples as the burn-in. At the end of the run, the average deviation of split frequencies was 0.006.

Results

Molecular phylogenetic results

A total of nine sequences from three collections of the bolete species was obtained and submitted to GenBank (Table 1). The final 4-gene dataset consisted of 181 sequences (nrLSU: 67, *TEF1-α*: 61, *RPB1*: 18, *RPB2*: 35; Table 1) from 72 bolete samples, and *Boletus edulis* Bull. as the outgroup taxon. The aligned dataset consisted of 3017 characters with gaps (nrLSU: 927, *TEF1-α*: 642, *RPB1*: 784, *RPB2*: 664) of which 1754 were constant, 270 were parsimony uninformative and 999 are parsimony informative, and was submitted to TreeBASE (S25339). Both ML and BI analyses produced almost the same topologies; thus, only the ML tree is presented (Fig. 1). In the phylogenetic analyses, the new bolete appears on a long branch in the subfamily Leccinoideae, and clusters with the stipitate-pileate genera *Leccinum*, *Leccinellum*, and *Spongispora*, as well as the sequestrate genera *Chamonixia*, *Octaviania*, *Rossbeevera*, and *Turmalinea* with moderate support (70% ML BS, PP = 0.97). Although the new bolete is nested in a well-supported leccinoid clade, its closest sister relationship with other genera remains unclear. However, the new bolete lineage always forms a clade basal/sub-basal to *Chamonixia*, *Octaviania*, *Leccinum*, *Leccinellum*, *Turmalinea*, and *Rossbeevera*. The ML analysis of the 4-gene matrix resulted in the phylogenetic tree shown in Fig. 1.

Taxonomy

Kaziboletus Iqbal Hosen & Zhu L. Yang, **gen. nov.**

MycoBank No.: MB 833238.

Etymology: The genus name "*Kaziboletus* (Lat.)" honors Dr. Kazi M. Badruddoza, a national emeritus scientist and founder of modern agriculture of Bangladesh.

Diagnosis: Pileus 30–60 mm broad, epigeous, stipitate-pileate with a tubular hymenophore. Pileus glabrous to rimose, red to dark reddish brown when young, becoming off white to cream-white or gray to grayish white with age. Hymenophore tubular, free, depressed around the stipe, white to cream white. Stipe central, cylindrical, covered with reddish brown scabrous squamules when young, becoming grayish brown at maturity, longitudinal striations with fine cross lines present from the apex almost to the base, the ridges somewhat

Table 1 List of collections included in the molecular phylogeny

Name of the species	Voucher number	Origin	GenBank accession number				Associated publication
			nrLSU	*TEF1-α*	*RPB1*	*RPB2*	
Binderoboletus segoi	Henkel 8035	Guyana	–	–	LC043079	–	Henkel et al. 2016
Boletaceae sp.	LAM 0421	Malaysia	KY091033	–	–	–	None
Boletus edulis	HMJAU4637	Russia	KF112455	KF112202	KF112586	KF112704	Wu et al. 2014
Borofutus dhakanus	HKAS 73789*	Bangladesh	JQ928616	JQ928576	Q928586	JQ928597	Hosen et al. 2013
Chamonixia brevicolumna	DBG-F-23359	USA	MK601728	MK721082	–	MK766290	Kuo and Ortiz-Santana 2020
Chamonixia caespitosa	OSC 117571	–	EU669260	–	–	–	None
Ionosporus australis	REH9784-non	Australia	–	–	–	MH712036	Khmelnitsky et al. 2019
Ionosporus longipes	Lee 1180	Malaysia	–	–	–	MH712031	Khmelnitsky et al. 2019
Kaziboletus rufescens	**HKAS 74705**	**Bangladesh**	**JQ928620**	**JQ928579**	**JQ928589**	**JQ928599**	This study
Kaziboletus rufescens	**HKAS 74706***	**Bangladesh**	**JQ928618**	**JQ928578**	**JQ928588**	**JQ928600**	This study
Kaziboletus rufescens	**PHI-14**	**Bangladesh**	**MN615938**	–	–	–	This study
Leccinellum aff. *crocipodium*	HKAS 76658	China	KF112447	KF112252	KF112595	KF112728	Wu et al. 2014
Leccinellum albellum	KUO-07241101	USA	MK601746	MK721100		MK766308	Kuo and Ortiz-Santana 2020
Leccinellum corsicum	Buf4507	USA	KF030347	KF030435	KF030389	–	Nuhn et al. 2013
Leccinellum crocipodium	KUO-07050707	USA	MK601749	MK721103	–	MK766311	Kuo and Ortiz-Santana 2020
Leccinellum lepidum	K(M)-142974	Italy	MK601751	MK721105	–	MK766312	Kuo and Ortiz-Santana 2020
Leccinellum pseudoscabrum	DPL-11432	USA	MK601752	MK721106	–	MK766313	Kuo and Ortiz-Santana 2020
Leccinellum sp.	HKAS 53427	China	KF112488	KF112253	KF112596	KF112727	Wu et al. 2014
Leccinellum sp.	HKAS 57592	China	KF112446	–	KF112594	KF112726	Wu et al. 2014
Leccinellum viscosum	BOS-478	Belize	MK601755	MK721109	–	–	Kuo and Ortiz-Santana 2020
Leccinum aff. *duriusculum*	KPM-NC-0017830	Japan	JN378510	JN378448	–	–	Orihara et al. 2012a
Leccinum aff. *schistophilum*	KPM-NC-0017841	Japan	KC552055	KC552096	–	–	Orihara et al. 2016
Leccinum aurantiacum	L-0342207	France	MK601759	MK721113	–	MK766318	Kuo and Ortiz-Santana 2020
Leccinum cf. *duriusculum*	KUO-09120708	USA	MK601761	MK721115	–	MK766320	Kuo and Ortiz-Santana 2020
Leccinum holopus	BOS-569	USA	MK601762	MK721116	–	–	Kuo and Ortiz-Santana 2020
Leccinum rugosiceps	DPL-11186	USA	MK601771	MK721125	–		Kuo and Ortiz-Santana 2020
Leccinum aff. *scabrum*	HKAS 57266	China	KF112248	KF112442	KF112590	KF112722	Wu et al. 2014
Leccinum snellii	BOS-579	USA	MK601773	MK721127	–	MK766331	Kuo and Ortiz-Santana 2020
Leccinum sp.	HKAS 52538	China	KF112441	KF112247	KF112589	KF112721	Wu et al. 2014
Leccinum sp.	DPL-11382	USA	MK601786	MK721140		MK766344	Kuo and Ortiz-Santana 2020
Leccinum variicolor	HKAS 57758	China	KF112445	KF112251	KF112591	KF112725	Wu et al. 2014
Leccinum versipelle	KPM-NC-0017833	Japan	JN378514	JN378454	–	–	Orihara et al. 2012a
Leccinum versipelle	DLC2002-122	USA	MK601778	MK721132	–	MK766336	Kuo and Ortiz-Santana 2020
Leccinum violaceotinctum	BOS-327	Belize	MK601779	MK721133	–	MK766337	Kuo and Ortiz-Santana 2020
Leccinum vulpinum	KPM-NC-0017834	Japan	JN378516	JN378456	–	–	Orihara et al. 2012a
Octaviania asterosperma	FH-284311	USA	MK601796	MK721150	–	MK766353	Kuo and Ortiz-Santana 2020
Octaviania cyanescens	PNW FUNGI 5603	USA	JN378502	JN378438	–	–	Orihara et al. 2012a
Octaviania decimae	KPM-NC-0017763	Japan	JN378465	JN378409	–	–	Orihara et al. 2012a
Octaviania etchuensis	KPM-NC-0017822	Japan	JN378492	JN378433	–	–	Orihara et al. 2012a
Octaviania hesperi	KPM-NC-0017793	Japan	JN378480	JN378422	–	–	Orihara et al. 2012a
Octaviania japonimontana	KPM-NC-0017812	Japan	JN378486	JN378428	–	–	Orihara et al. 2012a
Octaviania kobayasii	KPM-NC-0017785	Japan	JN378477	JN378419	–	–	Orihara et al. 2012a

Table 1 (continued)

Name of the species	Voucher number	Origin	GenBank accession number				Associated publication
			nrLSU	*TEF1-α*	*RPB1*	*RPB2*	
Octaviania nigrescens	MES270	USA	JN378498	JN378440	–	–	Orihara et al. 2012a
Octaviania nonae	KPM-NC-0017751	Japan	JN378462	JN378406	–	–	Orihara et al. 2012a
Octaviania tasmanica	OSC132097	Australia	JN378494	JN378435	–	–	Orihara et al. 2012a
Pseudoaustroboletus valens	HKAS 82643	China	KM274870	KM274878	–	–	Li et al. 2014
Retiboletus brunneolus	HKAS 52680*	China	KF112424	KF112179	–	KF112690	Wu et al. 2014
Retiboletus fuscus	HKAS 63590	China	KF112417	KF112178	KF112537	KF112691	
Retiboletus griseus	BD210	USA	HQ161858	–	HQ161827	–	Dentinger et al. 2010
Retiboletus kauffmanii	HKAS 63548	China	KF112416	KF112177	KF112536	KF112689	Wu et al. 2014
Retiboletus nigerrimus	HKAS 59699	China	JQ928627	JQ928582	JQ928592	JQ928603	Hosen et al. 2013
Retiboletus sinensis	HKAS 83957	China	KP739291	KP739303	–	–	Zeng et al. 2016
Rhodactina himalayensis	CMU25117*	Thailand	–	MG212603	–	–	Vadthanarat et al. 2018
Rhodactina rostratispora	SV170	Thailand	–	MG212605	–	MG212645	Vadthanarat et al. 2018
Rossbeevera bispora	GDGM 45612	China	MK036346	–	–	MK350308	Hosen et al. 2019
Rossbeevera cryptocyanea	KPM-NC-0017845	Japan	KC552030	KC552072	–	–	Orihara et al. 2016
Rossbeevera eucyanea	TNSF36986*	Japan	HQ693880	KC552068	–	–	Orihara et al. 2016
Rossbeevera griseobrunnea	GDGM45913*	China	MH537793	MK350307	–	MK350311	Hosen et al. 2019
Rossbeevera griseovelutina	TNSF36989*	Japan	KC552031	KC552076	–	–	Orihara et al. 2016
Rossbeevera pachydermis	KPM-NC-0023334	New Zealand	KJ001094	KJ001077	–	–	Orihara et al. 2016
Rossbeevera paracyanea	KPM-NC-0017847	Japan	KC552034	KC552078	–	–	Orihara et al. 2016
Rossbeevera vittatispora	OSC61484	Australia	JN378506	JN378446	–	–	Orihara et al. 2012a
Rossbeevera yunnanensis	HKAS 70689*	China	JN979437	–	–	–	Orihara et al. 2012b
Spongiforma squarepantsii	UC 1860255*	Malaysia	HQ724509	–	–	–	Desjardin et al. 2011
Spongiforma thailandica	DED7873 (holotype)	Thailand	EU685108	KF030436	KF030387	MG212648	Desjardin et al. 2011; Nuhn et al. 2013; Vadthanarat et al. 2018
Spongispora temakensis	SING 0206334*	Singapore	MG672512	MG674377	MG979393	MG674378	Wu et al. 2018
Turmalinea chrysocarpa	HKAS 70601*	China	NG_059488	–	–	KF112729	Wu et al. 2014
Turmalinea mesomorpha subsp. *sordida*	KPM-NC-0018016*	Japan	KC552049	KC552092	–	–	Orihara et al. 2016
Turmalinea persicina	KPM-NC-0018001*	Japan	KC552038	KC552082	–	–	Orihara et al. 2016
Turmalinea yuwanensis	KPM-NC-0018011*	Japan	KC552046	KC552089	–	–	Orihara et al. 2016
Tylocinum griseolum	HAKS 50281*	China	KF112451	KF112284	–	KF112730	Wu et al. 2014
Uncultured Boletaceae	LH37	Malaysia	GQ268714	–	–	–	Peay et al. 2010

An asterisk (*) next to the voucher specimen number indicates holotype material. Newly generated sequences for *Kaziboletus rufescens* are highlighted in bold

anastomosing but not reticulate; basal mycelium whitish. Context white, turning pale red to pale reddish orange in some patches when exposed. Basidiospores light yellow to deep yellow in H_2O and 5% KOH, smooth, elongated to cylindrical, somewhat fusoid. Cystidia mostly fusoid. Pileipellis an epithelium. Clamp connections absent.

Type species: *Kaziboletus rufescens* Iqbal Hosen & Zhu L. Yang

Kaziboletus rufescens Iqbal Hosen & Zhu L. Yang, **sp. nov.** Figs. 2, 3, and 4

MycoBank No.: MB 833239.

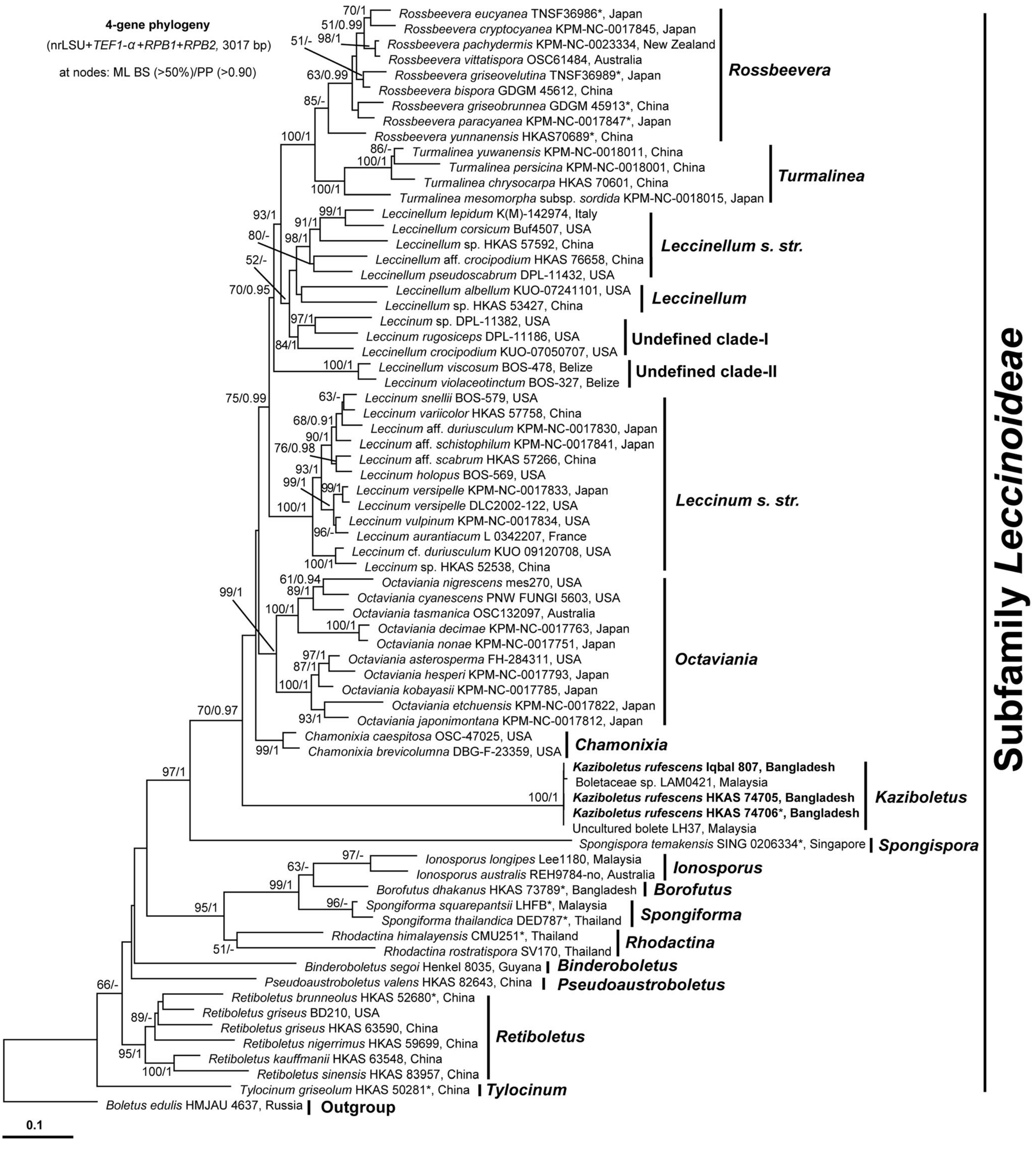


Fig. 1 Phylogenetic relationships of the genera of subfamily Leccinoideae inferred from 4-gene (nrLSU, *TEF1-α*, *RPB1*, and *RPB2*) dataset of 72 samples of Boletaceae using maximum likelihood (ML). Bootstrap (BS) values derived from ML (BS > 50%) and posterior probabilities (PP) from Bayesian Inference (BI) (PP = 0.90) analyses are shown above or beneath the branches at nodes. *Kaziboletus rufescens* gen. et sp. nov. is highlighted in bold. Voucher specimen number for each species is provided after the species name followed by country name. An asterisk next to the voucher specimen number indicates holotype material

Etymology: The epithet "*rufescens*" (Lat.) refers to the context which changes from white to pale red or reddish orange in some patches when exposed.

Typification: **Bangladesh:** Dhaka division, Gazipur, Bhawal National Park, latitude 24°45'N 90°50'E, elevation 20 m, 29 July 2011, Iqbal 304 (HKAS 74706, holotype; PHI-13, isotype).

Description: Basidiomata small to medium-sized. *Pileus* 30–60 mm, convex to hemispherical, sometimes with an irregular to wavy margin; surface dry, covered with pale reddish brown (9D7–8, 9C8) to pale brown (10C7–8) squamules when young, gray to grayish white (10B1, 10C1) at maturity, brownish gray when wet, becoming rimose to rugulose with age or during some stage of development; context up to 8 mm thick, solid, white to cream white, turning slightly pale red (8A4–5) to pale reddish orange (7A6–7) in some patches on exposure. *Hymenophore* tubulose, free, depressed around the stipe, white to creamy white, turning slightly brown when injured; tubes 7–10 mm long, pores angular or round up to 1 mm broad. *Stipe* 40–75 × 8–12 mm, central, cylindrical, attenuated upwards, scabrous, covered with reddish brown (when young) to gray brown (at maturity)

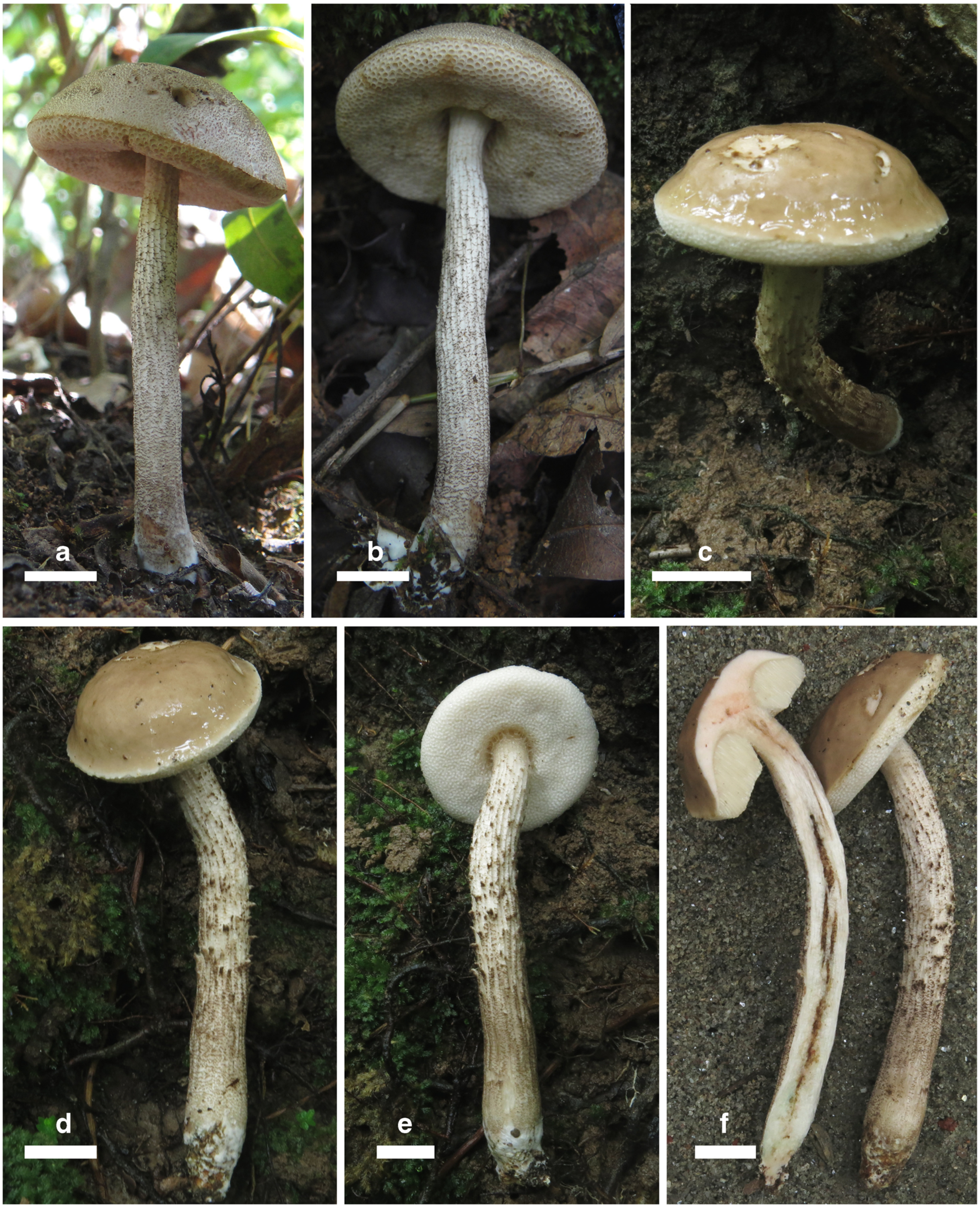


Fig. 2 Basidiomata of *Kaziboletus rufescens*. **a**, **b** HKAS 74706, holotype; PHI-13, isotype; **c**, **d**, **f** PHI-14. *Bars* = 1 cm

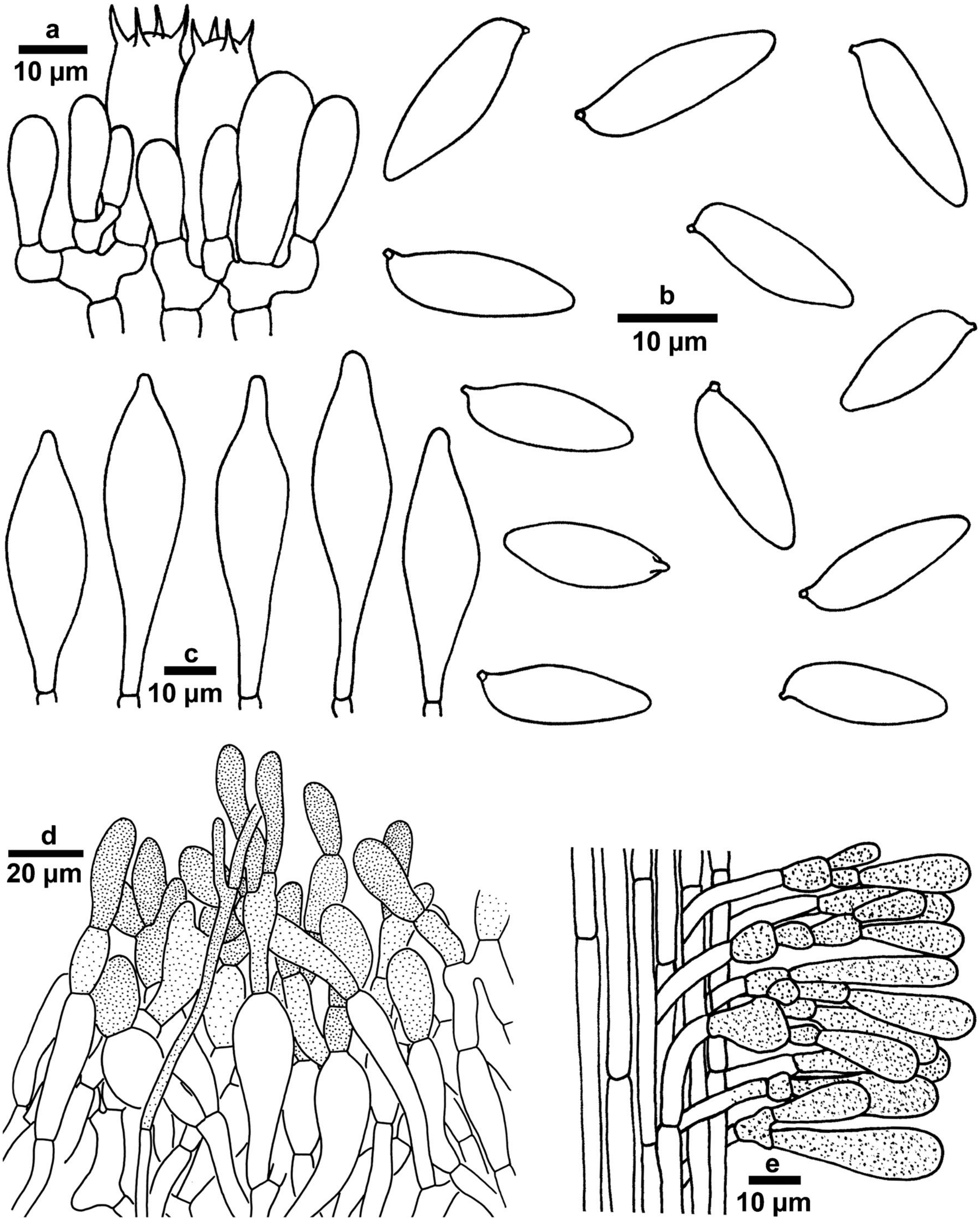
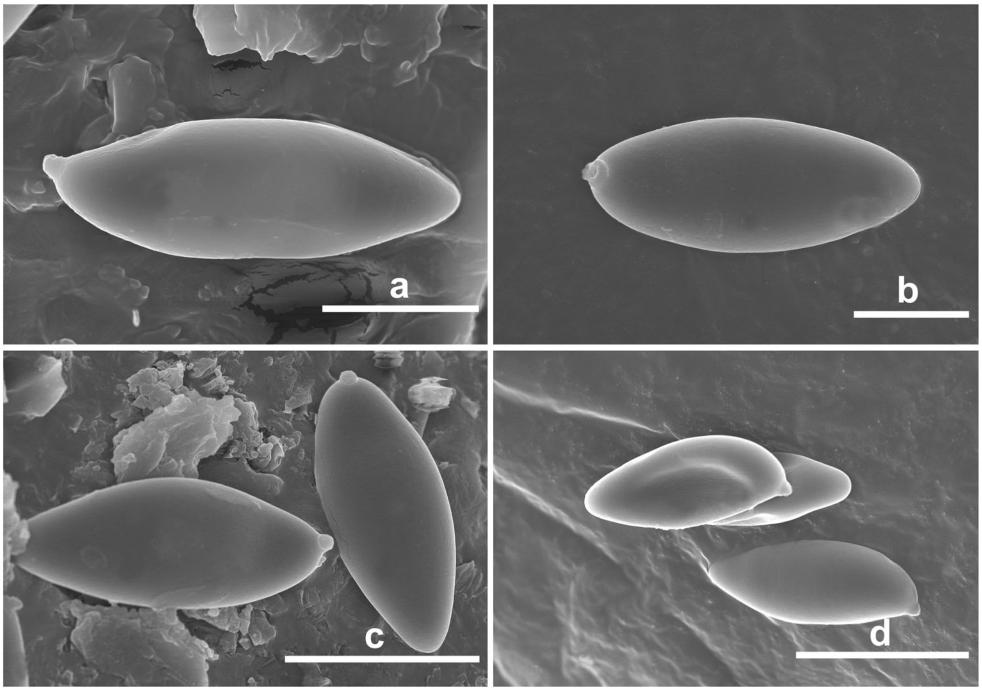


Fig. 3 Microscopic features of *Kaziboletus rufescens* (HKAS 74706). **a** Basidia with basidioles; **b** Basidiospores; **c** Hymenial cystidia (Cheilo- and pleurocystidia); **d** Epithelium pileipellis; **e** Caulocystidia

squamules; conspicuous longitudinal striations present with fine cross lines from the apex to just above the base, the ridges somewhat anastomosing, sometimes sub-reticulate at the apex, the basal half more scabrous than the upper half; context 8 mm thick, solid, white to dull white, staining pale red to reddish orange in some patches, pale blue at stipe base in one specimen (Iqbal 807). *Basal mycelium* white. *Odor and taste* not distinctive.

Basidiospores [60/3/3] (15–)17–19(–21) × 5.5–6.5(–7) µm, elongated to cylindro-fusoid, thin-walled, inamyloid, smooth under light microscope and SEM, pale yellow (1A2–3) to vivid yellow (2A6–8) in H_2O and 5% KOH.

Fig. 4 SEM of smooth basidiospores of *Kaziboletus rufescens* (**a–d** HKAS 74706, holotype). *Bars* = **a**, **b** 5 μm. **c**, **d** 10 μm



Basidia 30–36 (–45) × (9–)10–12 μm, narrowly clavate, clavate or broadly clavate, colorless in H_2O and 5% KOH, thin-walled, 4-spored, occasionally 2- or 3-spored; sterigmata up to 3.5 μm long. *Hymenophoral trama* 100–130 μm wide, boletoid, hyphae cylindrical, 4–10 μm wide, hyaline. *Cheilo- and pleurocystidia* 50–70 × 10–15 μm, scattered, not abundant, fusoid to subfusoid, mucronate, somewhat lanceolate, hyaline, thin-walled, smooth, without encrustation. *Pileipellis* an epithelium, 100–130 μm thick, consisting of 2–3(–5) broadly clavate to pyriform to broadly ellipsoid inflated cells in chains; terminal cells 15–30 (–50) × 10–16 (–20) μm, with yellowish brown to brown vacuolar pigments; sometimes mixed with filamentous hyphae 3–5 μm wide, with brown vacuolar pigments. *Stipe trama* composed of parallel, cylindrical, hyaline hyphae up to 13 μm wide. *Stipitipellis* covered by a hymenium-like structure, composed of clavate to broadly clavate caulocystidia 16–35 × 6–11 μm, with yellowish brown to pale brown vacuolar pigmentation. *Clamp connections* absent in all tissues.

Habit and habitat: Mostly solitary in pure stands of *S. robusta*, and putatively forming ectomycorrhizae with *S. robusta*.

Known distribution: Currently known only from tropical Bangladesh, and possibly Malaysia (based on sequence data).

Additional specimens examined: **Bangladesh**. Dhaka division: Gazipur, Bhawal National Park, elevation 20 m, 5 Jul 2011, Iqbal 154 (HKAS 74705). Rangpur division: Dinajpur, Birol, Kaliganj Sal Baghan, elevation 60–70 m, 7 Aug 2013, Iqbal 807 (PHI-14).

Discussion

The presence of a coarsely scaly or scurfy stipe surface, smooth basidiospores, and fusoid cheilocystidia in the new genus *Kaziboletus* are similar to those of *Leccinum*, *Leccinellum* and *Spongispora*. However, the phylogenetic analyses presented here confirm that *Kaziboletus* cannot be placed in any of these genera. Furthermore, *Leccinum* and *Leccinellum* are most diverse in North America and Europe with most species host specific to the members of Betulaceae Gray, Ericaceae Durande, Fagaceae Dumort., Pinaceae Spreng. ex F. Rudolphi, and Salicaceae Mirb. (Corner 1972; Engel 1978; Singer 1986; Bresinsky and Besl 2003; den Bakker and Noordeloos 2005), while *Kaziboletus* is distributed in tropical South Asia with putative host specificity to *S. robusta*. Although some species of *Leccinum* have been reported from the tropics, for example, in Costa Rica by Halling (1999), Halling and Mueller (2003), Ortiz-Santana and Halling (2009); and in Southeast Asia by Corner (1972) and Horak (2011), their phylogenetic placements largely need to be explored. Furthermore, *Kaziboletus* differs from *Leccinum* and *Leccinellum* by the context that becomes reddish to pale reddish orange in patches when injured (except *L. rugosiceps* (Pk.) Singer and *L. intusrubens* (Corner) Høil), and the presence of longitudinal striations from the apex to just above the base. *Spongispora*, a monotypic genus originally described from Singapore, is easy to separate from the new genus by a coarsely reticulate stipe, a pileus context that turns pale brown on exposure, an interwoven trichodermial pileipellis, broadly ellipsoid to ovoid ornamented basidiospores, and putative association with *Hopea odorata* Roxb. A key is provided for convenience in comparison among the four morphologically closely related genera *Kaziboletus*, *Leccinum*, *Leccinellum*, and *Spongispora*.

Kaziboletus rufescens resembles *Leccinum rugosiceps* because of its rugose pileus, pink or pale red context when injured, and a hymeniform or epithelium pileipellis (Halling and Mueller 2003). However, the latter taxon, originally described from eastern USA, has a large pileus up to 150 mm broad, bright yellow to wax yellow tubes, non-staining stipe context, and association with *Quercus* sp. (Smith and Thiers 1971; Halling and Mueller 2003). Furthermore, phylogenetically, *L. rugosiceps* forms a distinct lineage apart from the *Kaziboletus* clade. Morphologically, *Leccinellum albellum* (Peck) Bresinsky & Manfr. Binder also resembles *K. rufescens*, but the species is distinguished from the latter taxon by its context that never turns pale reddish to reddish orange when exposed, abundant hymenial cystidia, and distribution predominantly within the USA (Smith and Thiers 1971).

The tropical Asian *Leccinum* spp., *L. borneense* (Corner) E. Horak and *L. intusrubens*, originally described from Malaysia (Corner 1972), can also be distinguished from *K. rufescens*. *Leccinum borneense* has an ixocutis as a pileipellis, a pale yellow context and tubes that quickly become blue on bruising, and basidiospores 13–15 × 4–4.5 μm in size. *Leccinum intusrubens* has a context that quickly turns blood red or saffron on exposure and then slowly turns blackish, a pileipellis composed of 2–3 septate moniliform hyphal end cells, and proportionally shorter and narrower basidiospores 11–14 × 5–5.5 μm. No molecular data are available for these Malaysian species of *Leccinum*, and their phylogenetic position can therefore not be assessed in the current study.

It is interesting to note that two nrLSU sequences generated either from mycorrhizal root tips (GQ268714, labelled as uncultured bolete) or basidioma (KY091033, labelled as Boletaceae sp.) from Sarawak, Malaysia are identical to those of *K. rufescens* (Fig. 1), suggesting that *Kaziboletus* may also occur in Southeast Asia. Surprisingly, however, apart from these two nrLSU sequences from Malaysian samples, the nrLSU sequences of *K. rufescens* vary significantly (i.e., matched only 85–86.78%) with the known species of *Leccinum* and other boletoid genera available in GenBank. Prior to proposing the new genus *Kaziboletus*, we carefully consulted the literature of Malaysian boletes (Corner 1972, 1974; Horak 2011), and determined that neither of those Corner boletes appear similar to the new bolete described here. Finally, it may be concluded that though several species of *Leccinum* are described from tropical regions such as Southeast Asia, Africa and South America or Costa Rica, none of these are morphologically identical to the South Asian *K. rufescens*. In accordance with the guidelines set out by Vellinga et al. (2015), *Kaziboletus* has enough morphological differences, host preference, and phylogenetic support to be considered as a distinct genus in Boletaceae.

The molecular phylogenetic results of Wu et al. (2018) distinguished 14 genera in the subfamily Leccinoideae. Shortly after, Khmelnitsky et al. (2019) erected another new Leccinoideae genus, *Ionosporus*, which is phylogenetically closely related to the monotypic genus *Borofutus* Hosen & Zhu L. Yang (Fig. 1). The erection of *Kaziboletus* gen. nov. in this study raises the number of genera in the subfamily Leccinoideae to 16, with all genera appearing to be monophyletic except *Leccinum* and *Leccinellum* (Fig. 1).

Key to the genera morphologically similar to *Kaziboletus*

1\. With tropical and temperate distribution ……..…………2
1* With tropical distribution only.....................................…… 3
2\. Hymenophoral surface yellow when young, pileus context yellowish to white then quickly blackeing when injured; pileipellis a palisade trichoderm; ectomycorrhizal symbioses mainly with Fagaceae and Betulaceae.....……...*Leccinellum*
2* Hymenophoral surface diverse colors but not yellow when young; pileus context whitish to light gray to grayish; pileipellis diverse- trichoderm, hymeniform/ epithelium; ectomycorrhizal symbioses with Pinaceae, Fagaceae, Betulaceae, Caesalpinoid legumes and Dipterocarpaceae……....………………………...*Leccinum*
3\. Pileus context whitish but faintly staining pale brown when injured; stipe almost reticulate and covered by coarse scurfy squamules, basidiospores not smooth, with irregular clefts and warts under SEM; pileipellis a trichoderm composed of cylindrical cells; ectomycorrhizal symbioses with *Hopea odorata* Roxb., known from Singapore…..............…......………..... *Spongispora*
3* Pileus context white to creamy white but turning slightly pale red to pale reddish orange when exposed; stipe surface with sparse coarse, scurfy squamules; basidiospores smooth; pileipellis an epithelium composed of 2–3(5) inflated cells; putatively ectomycorrhizal symbiosis with *Shorea robusta*; known from Bangladesh and possibly Malaysia..………..........….......….... *Kaziboletus*

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Author contribution This is a part of the first author's DSc work was affiliated with the Kunming Institute of Botany, Chinese Academy of Sciences, Kunming 650201, China. MIH and ZLY made conceptualized and designed the study. MIH collected samples from Bangladesh, examined morphological features, analyzed molecular data, and wrote the paper. ZLY has supervised MIH's DSc study, drew the pileipellis structure of *Kaziboletus*, and improved the entire text.

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Data availability The sequences generated in this study are available in the NCBI GenBank (Table 1). Voucher specimens studied in this study are deposited in the Herbarium of Cryptogams, Kunming Institute of Botany, Chinese Academy of Sciences (KUN-HKAS), and in the private herbarium of Iqbal (PHI).

Declarations

Conflict of interest The authors declare no competing interests.

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