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Amanita indogrisea, a new species of *Amanita* subg. *Amanitina* sect. *Roanokenses* from India

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Abstract

Amanita indogrisea is described here as a new species from coniferous forests in the Union Territory of Jammu and Kashmir, India based on morpho-anatomy and molecular data. This species is characterized by its small to medium-sized basidiomata, ash grey to lilac-grey pileal surface with ash grey to greyish brown pulverulent-floccose to felted veil remnants, ash grey to greyish-white stipes with ovoid to ellipsoid basal bulb, ellipsoid to elongated basidiospores (10.5–15.0 × 7.0–10.0 µm) and the absence of clamps in all tissues. Molecular phylogenetic analysis based on nuclear ribosomal large subunit (nrLSU) sequences confirmed its identity as a new species nested within *A.* subgen. *Amanitina* sect. *Roanokenses.* Description of the new species is provided in this study.

Introduction

The genus *Amanita* Pers. is cosmopolitan in geographical distribution comprising species with ecological and economic importance (Corner & Bas 1962, Bas 1969, Yang 1997, Cui et al. 2018). Most species in this genus form ectomycorrhizal (ECM) associations with a wide range of host trees. The monophyletic genus *Amanita* has been divided into three subgenera namely, *Amanita*, *Amanitina* (E. J. Gilbert) E. J. Gilbert, & *Lepidella* (E.J. Gilbert) Vesely. These three subgenera are further divided into eleven sections (Yang et al. 2018). Within the subg. *Amanitina,* members of the sect. *Roanokenses* Singer ex Singer are characterized by amyloid basidiospores, appendiculate pileus, stipe with bulbous base, volval remnants often as warts, floccose, powder, verrucae, patches on pileus and stipe base, and the presence or absence of clamps (Singer 1962, Cui et al. 2018). To date, the genus includes 612 validly published species all over the world and from India 73 species have been reported so far (Kumar et al. 2021, Tulloss & Yang 2021).

During macrofungal surveys to different parts of the Union Territories of J&K, an interesting species of *Amanita* was found. This species is proposed in the present publication as new and are presented here with detailed macro- and micromorphological descriptions together with illustrations, nrLSU-based phylogenetic analyses and comparisons with related species.

Materials and Methods

Macro- and micromorphology study

Macromorphological characters were recorded from the fresh young to matured basidiomata from the field or at the base camp, and collected samples were dried within a wooden drier and deposited in the Central National Herbarium (CAL) located at Howrah, Kolkata (Holotype) and herbarium of the Department of Botany, University of Jammu (HBJU) (Paratype). Colour codes description was followed from the Methuen Handbook of Colour (Kornerup & Wanscher 1978). Micromorphological features were observed with a compound microscope (Olympus CH20i) from dry materials mounted in 5% KOH, 1% Phloxine, Melzer's reagent and 1% Congo red. Biometric variables are after Yang (1997) and Cui et al. (2018). Drawings of microscopic elements were made with a camera lucida at 1000× magnification. Microphotography was made with the respective dedicated cameras attached to the compound microscopes Olympus CX23.

DNA extraction, PCR amplification and sequencing

A Plant II Kit (Macherey-Nagel) was used to isolate nuclear genomic DNA from 100 mg of dried sample (AKS–0028). For LSU amplification, LR0R (ACCCGCTGAACTTAAGC) and LR5 (TCCTGAGGGAAACTTCG) primers were used (Vilgalys & Hester 1990). PCR amplification reactions were carried out in a 20 µl reaction volume which contained 1× Phire PCR buffer (contains 1.5 mM $MgCl_2$), 2 mM each dNTPs (dATP, dGTP, dCTP and dTTP), 1 µl DNA, 0.2 µl Phire Hotstart II DNA polymerase enzyme, 0.1 mg ml–1 BSA and 3% DMSO, 0.5 M Betaine, 5 pM of forward and reverse primers. PCR amplification was carried out in a PCR thermal cycler (Gene Amp PCR System 9700, Applied Biosystems) programmed for 2 min at 96 °C, followed by 30 cycles of 30 sec at 96 °C, 40 sec at 50 °C, and a final stage of 4 min at 60 °C. The PCR products were purified with QIAquick Gel Extraction Kit (QIAGEN, Germany) and then subjected to Sanger sequencing in an automated DNA sequencer (ABI3730xl DNA Analyzer, Applied Biosystems, USA) were carried out at Rajiv Gandhi Centre for Biotechnology, Thiruvananthapuram. The sequences generated from collections of the new species were deposited in GenBank with the accession numbers OK206078, OK206079 (Table 1).

Phylogenetic analysis

In this study, 43 nrLSU sequences of *Amanitaceae*, including two nrLSU sequences of our proposed new species were used for phylogenetic analysis (Table 1). Species in the subg. *Amanitina* core clade with high similarity to our new species and availability

Figure1. ***Amanita indogrisea*** (holotype). (a–e) Young and mature basidiomata in the coniferous forest. (f) Basidia at different stages of development (LM). (g) Light micrograph (LM) of basidiospores. (h) Universal veil remnants. Scale bars: a–e = 20 mm; f–g =10 µm; h =20 µm.

of sequences of *Amanita* in public databases like GenBank (Clark et al. 2016) and relevant published literature (Cui et al. 2018, Hosen et al. 2018) were selected for phylogenetic analysis. The nrLSU dataset was then aligned with Mafft v.6.8 (Katoh & Standley 2013) and manually adjusted with BioEdit v.7.0.9 (Hall 1999) using default settings. Phylogenetic analysis of nrLSU sequences was undertaken based on Maximum Likelihood (ML) criteria computed in RAxML GUI 2.0 (Edler et al. 2019). 1000 bootstrap replicates were analysed to obtain nodal support values. Bayesian inference was computed independently twice in MrBayes v.3.2.2 (Ronquist et al. 2012), under different models. The best-fit substitution model was carried out in MrModeltest 3.7 (Posada & Crandall 1998). Bayesian posterior probabilities were calculated in two simultaneous runs with the MCMC algorithm (Largent & Simon 1999). Markov chains were run for 10 million generations, saving a tree every 100th generation. Default settings in MrBayes were used for the incremental heating scheme for the chains (three heated and one cold chain), unconstrained branch length [unconstrained: exponential (10.0)] and uninformative topology (uniform) priors. The first 25 % of trees were discarded as burn-in material (Hall 2004). *Limacella illinita* was selected as the outgroup for the molecular phylogenetic analysis.

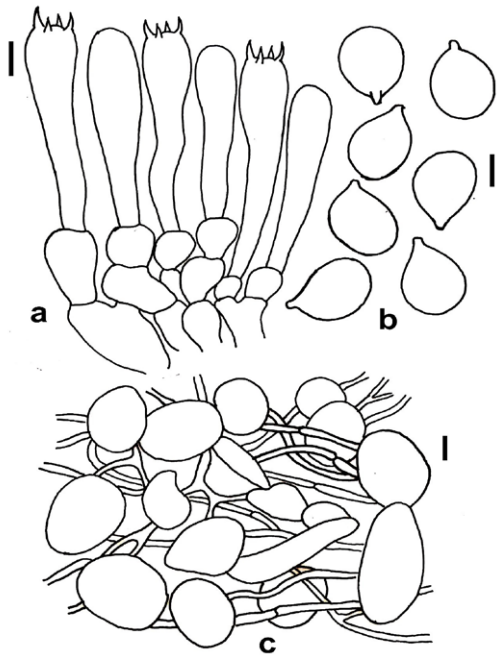

Figure 3. Microscopic features of *Amanita indogrisea* (1850 holotype). (a) Basidia and elements of subhymenium. (b) Basidiospores. (c) Universal veil remnants. Scale bars: a-c =10 µm.

Results

Phylogenetic inferences

A nrLSU dataset was made for investigating the phylogenetic relationships of the proposed new species. *Amanita indogrisea* (GenBank OK206078, OK206079) is phylogenetically close to *A. longipes* (GenBank HQ539704). All species clustered together in a clade with the sequences of *Amanita eriophora* (HQ539672*), A. cinereovelata* (KP259291) and *A. griseofarinosa* (MH486563). Within this clade *Amanita indogrisea* is closest to *A. longipes* and supported by a 70/0.94 % bootstrap value (**Fig.1**) The resulting phylogenetic tree is presented in **Fig. 1.**

Amanita indogrisea A. Kumar, Mehmood & Sharma Y.P sp. nov. **Figures 2 & 3**

MycoBank: - MB841264
GenBank: nrLSU: OK206078 (Holotype)
OK206079 (Paratype)

DIAGNOSIS: *Amanita indogrisea* differs from all the known species of *Amanita* strips *cinereoconia* by the combination of following characters: ash grey to lilac-grey pileal surface with ash grey to greyish brown pulverulent-floccose to felted volval remnants, ovoid to ellipsoid basal bulb, ellipsoid to elongated basidiospores (10.5–15.0 × 7.0–10.0 µm), and the absence of clamps in all tissues.

TYPIFICATION: India, Jammu & Kashmir, Doda, Dhossa, 33°0'42.41"N, 75°58'9.86"E. Scattered on the ground in coniferous forest dominated by *Abies pindrow* and *Picea smithiana*; 04 August 2021, Anil Kumar (AKS–0028); (The Central National Herbarium (CAL 1850 holotype), Howrah, Kolkata and Herbarium of the Department of Botany, University of Jammu (HBJU 845 Paratype).

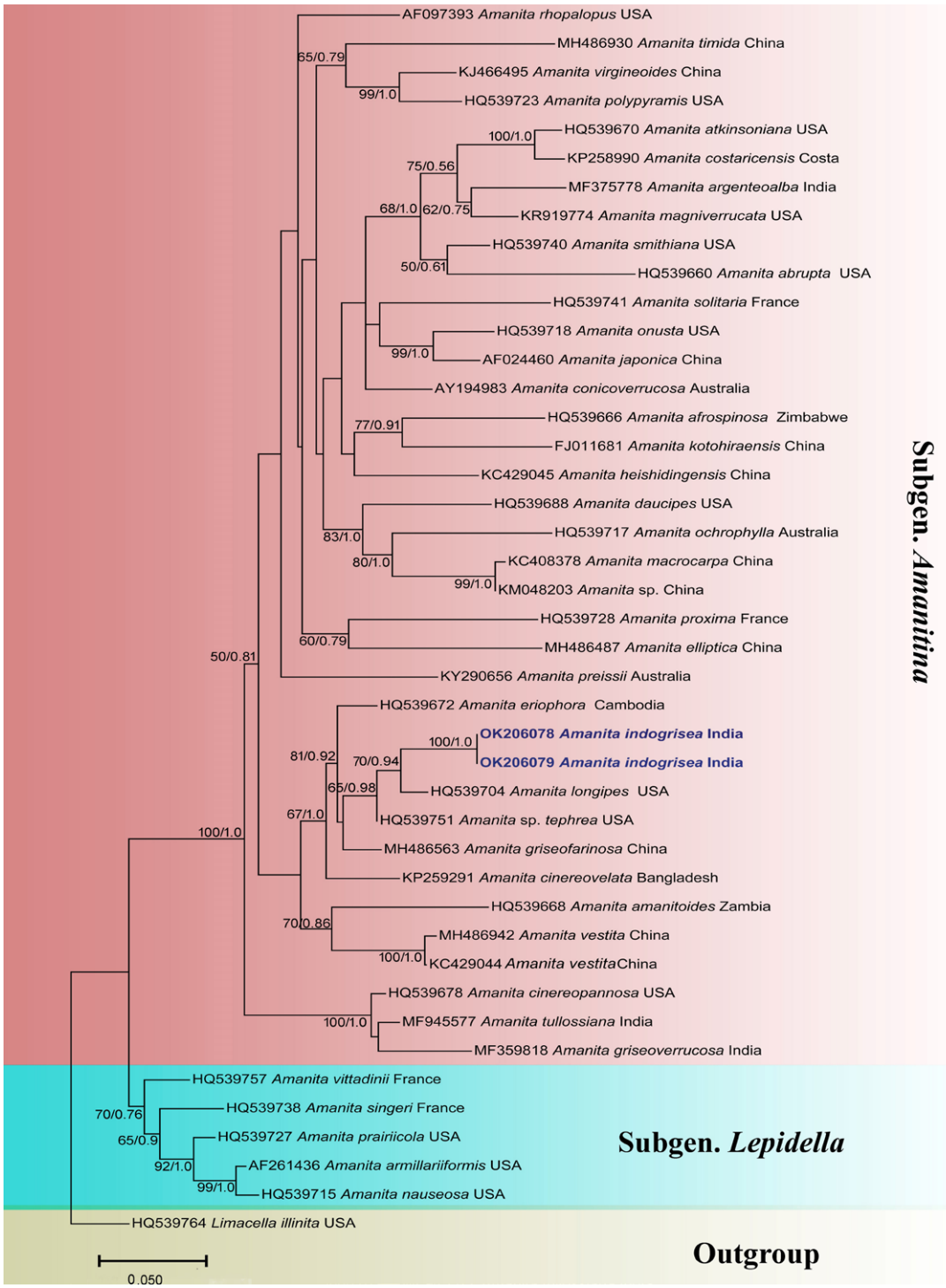

Figure 3. Phylogram resulting from *Amanita indogrisea* nrLSU sequences. Branches are labelled with bootstrap support values (>50 %) obtained from the ML analysis.

ETYMOLOGY: The species epithet '*indo*' refers to the locality of the type specimen from India and '*grisea*' (Latin) "having a grey colour".

DESCRIPTION: *Basidioma* is small to medium-sized. Pileus 20–60 mm in wide, initially globose then convex to plano-convex finally plane, dry, slightly viscid when moist, light greyish to ash grey (1C1–1B2), to lilac-grey (15C2) covered with pulverulent-floccose, volval remnants initially light grey (15B2) to ash grey (1C1–1B2) finally felted to floccose patches greyish brown (6D3–E3) with age, slightly dark brown (6F4) in centre, sometimes depressed at centre, umbo absent, margin non-striate, appendiculate, split with maturity. *Lamellae* 5–8 mm broad, nearly free, close to rather crowded, pure white (1B1), lamellae edge often covered with veil remnants; lamellulae 3–4 tiers, attenuated. *Stipe* 100–130 × 8.0–10.5 mm (excluding bulb), cylindrical, ash grey (1B2) to greyish-white (1B1), densely covered with tomentose, to floccose friable volval remnants, turn blackish when handled; basal bulb ovoid to ellipsoid shaped 20–50 ×20–30 mm. *Annulus* superior, soft, grey (4C1) to lilac-grey (15C2), friable. Context up to 5 mm thick at pileus centre white, stipe context white and stuffed, unchanging when cut or injured. *Taste* not recorded. *Lamellar trama* bilateral, divergent. *Mediostratum* 60–180 µm wide, composed of abundant broadly ellipsoid to elongated inflated cells (15–30 × 10–20 µm), filamentous, undifferentiated hyphae 5–6 µm wide. *Lateral stratum* composed of subglobose, broadly ellipsoid to ellipsoid cells (40–78 × 12–33 µm), filamentous undifferentiated hyphae 4–8 µm wide. *Subhymenium* 30–60 µm thick, hyaline, basidia arising from ellipsoid to irregularly inflated cells (9–20 × 4–6 µm). *Basidia* 65–80 × 10–14 µm, hyaline clavate, 4-spored; sterigmata 3–6 µm long; basal clamp connections absent.

Basidiospores [120/5/3] (9.0–) 10.5–15.0 (–17.0) × (6.0–) 7.0–10.0 (–11.0) µm, [Q=1.33–1.67, Qm = 1.49] ellipsoid to elongated, amyloid, hilar appendix up to 0.6 µm long; Lamellae edge tissue sterile, mainly composed of irregular ellipsoid inflated cells (10–20 × 4–6) µm. *Pileipellis* 80–170 µm thick, in two-layered; non-gelatinized, upper layer 30–70 µm thick, radially arranged filamentous, undifferentiated hyphae 8–13 µm wide; lower layer 50–100 µm thick, filamentous, undifferentiated hyphae 10–15 µm wide, compactly arranged, thin-walled, hyaline. *Universal veil* on pileus composed of irregularly arranged elements: filamentous hyphae 2–6 µm wide, scarce to scattered. *Universal veil* on stipe composed of irregularly arranged elements, filamentous hyphae 2–5 µm wide, abundant to somewhat dominant, subglobose to fusiform to ellipsoid to clavate 55–150 × 35–120 µm, thin-walled, colourless cells. *Stipe context* longitudinally acrophysalidic; acrophysalides 85–130 × 7–20 µm; filamentous undifferentiated hyphae 4.0–10 µm wide. Clamps are absent in all parts of basidioma.

HABIT AND HABITAT: Scattered on the ground in coniferous forest dominated by *Abies pindrow* and *Picea smithiana*; basidioma found in August to October.

ADDITIONAL SPECIMENS EXAMINED: India, Jammu and Kashmir, district Doda, Bhalessa, Dhossa, 33°0'42.41"N, 75°58'9.86"E, alt. 2410 m a.s.l., 04 August 2021, Anil Kumar (AKS–0032, AKS-0039); Kishtwar, Chatroo, 2068 m a.s.l, 25 August, 2020, Roshi Sharma (RA–0108).

Discussion

Morphological characters and molecular data derived from nrLSU sequences placed the present species (*Amanita indogrisea*) into subgen. *Amanitina* sect. *Roanokenses*. Based on the Bas key, the present species keyed out in (subsect. *Solitariae*) stirps *Cinereoconia*. In stirps *Cinereoconia*, *Amanita indogrisea* is closely related to *A. cinereoconica* G.F. Atk., *A. griseofarinosa* Hongo, *A. odorata* Beeli, *A. pelioma* Bas, *A. lutescens* Hongo, *A. vestita* Corner & Bas, *A. tullossiana* Hosen et al., *A. griseovelata* D.A. Reid, A. *pallidoflavescens* Dav. T. Jenkins, and *A. viridissima* Wartchow.

Amanita cinereoconica, can be differentiated from *A. indogrisea* by its pale yellowish grey to pale umber pileus, elongated to rooting bulb, cylindrical to elongate basidiospores 8.5–11.5 × 5–6.5 µm (Bas 1969). *Amanita griseofarinosa*, can be segregated from *A. indogrisea* by its brownish grey pileus, subglobose to broadly ellipsoid basidiospores 8.5–10 × 7–9 µm (Bas 1969).

Likewise, *A. odorata*, differs from our species by its brownish olive to olivaceous brown pileus, pinkish-white lamellae and elongate to cylindric basidiospores 9.5–13 × 4.5–5.5 µm (Bas 1969). While

Table 1. Information of nrLSU sequences retrieved for phylogenetic purpose, their sequence accession number, country of origin and reference to published work where those sequences were obtained.

Taxon	GenBank accession number (nrLSU)	Geographic location	Reference
Amanita costaricensis	KP258990	Costa Rica	Tulloss et al. 2015
Amanita atkinsoniana	HQ539670	USA	Tulloss & Yang 2021
Amanita magniverrucata	KR919774	USA	Tulloss et al. 2015
Amanita argenteoalba	MF375478	India	Mehmood et al. 2018
Amanita smithiana	HQ539740	USA	Tulloss & Yang 2021
Amanita abrupta	HQ539660	USA	Tulloss & Yang 2021
Amanita heishihidingensis	KC429045	China	Li & Cai 2014
Amanita solitaria	HQ539741	France	Tulloss & Yang 2021
Amanita conicoverrucosa	AY194983	Australia	Sawyer et al. 2003
Amanita kotohiraensis	FJ011681	China	Zhang et al. 2015
Amanita japonica	AF024460	China	Weiss et al. 1999
Amanita onusta	HQ539718	USA	Tulloss & Yang 2021
Amanita daucipes	HQ539688	USA	Tulloss & Yang 2021
Amanita ochrophylla	HQ539717	Australia	Tulloss & Yang 2021
Amanita macrocarpa	KC408378	China	Deng et al. 2014
Amanita elliptica	MH486487	China	Cui et al. 2018
Amanita timida	MH486930	China	Cui et al. 2018
Amanita rhopalopus	AF097393	USA	Drehmel et al. 1999
Amanita virgineoides	KJ466495	China	Cai et al. 2014
Amanita polypyramis	HQ539723	USA	Tulloss et al. 2021
Amanita preissii	KY290656	Australia	Unpublished
Amanita cinereopannosa	HQ539723	USA	Tulloss et al. 2021
Amanita griseoverrucosa	MF359818	India	Mehmood et al. 2018
Amanita tullossiana	MF945577	India	Mehmood et al. 2018a
Amanita afrospinosa	HQ539666	Zimbabwe	Tulloss et al. 2021
Amanita proxima	HQ539728	France	Tulloss et al. 2021
Amanita amanitoides	HQ539668	Zambia	Tulloss et al. 2021
Amanita vestita	KC429044	China	Cai et al. 2014
Amanita cinereovelata	KP259291	Bangladesh	Hosen et al. 2015
Amanita indogrisea	OK206078	India	This paper
Amanita indogrisea	OK206079	India	This paper
Amanita eriophora	HQ539672	Cambodia	Tulloss & Yang 2021
Amanita griseofarinosa	Mh486563	China	Cui et al. 2018
Amanita sp.	HQ539751	USA	Tulloss & Yang 2021
Amanita longipes	HQ539704	USA	Tulloss & Yang 2021
Amanita vittadinii	HQ539757	France	Tulloss & Yang 2021
Amanita singeri	HQ539738	France	Tulloss & Yang 2021
Amanita prairiicola	HQ539727	USA	Tulloss & Yang 2021
Amanita nauseosa	HQ539715	USA	Tulloss & Yang 2021
Amanita armillariiformis	AF261436	USA	Moncalvo et al. 2002
Amanita illinita	HQ539764	USA	Tulloss & Yang 2021

as *A. pelioma*, is easily segregated from *A. indogrisea* by its greyish-olive to pale brownish pileus, pale brownish lamellae, and ellipsoid to elongate basidiospores 10–12.5 × 6.5–8 µm (Bas 1969), *A. lutescens* is distinct from *A. indogrisea* by its context turning yellowish when bruised and relatively smaller basidiospores (8–10 × 5.5–6.5 µm) (Bas 1969).

Another species, *A. vestita*, delineates from our taxon by its pale greyish-white pileus, white to brownish stipe, and rooting stipe bulb (Corner & Bas 1962). *Amanita tullossiana,* originally reported from India, could be discerned from *A. indogrisea* by its white annulus, napiform to rooting bulb and stipe covered by recurved scales (Hosen et al. 2018), whereas *A. griseovelata*, separated out from the novel taxon by its slate-grey pileus blackish at central disc, covered pale grey, felty–pruinose universal veil remnants, and subglobose to broadly ellipsoid basidiospores 7–10 × 6.8–8.5 µm (Reid 1980). As described by Jenkins (1986), another closely related member, *A. pallidoflavescens,* has white to silvery white pileus and bears elongate to cylindric basidiospores 8.6–10.2 × 4.7–5.5 µm thus different from *A. indogrisea,* and finally *A. viridissima*, segregates itself from the present species by its green pileus and stipe, pale lamellae and elongate to cylindric basidiospores 9.8–13 × 5.7–8.3 µm (Wartchow 2016).

Phylogenetically, *Amanita indogrisea* is closely related to: *Amanita eriophora* (Berk.) E.-J. Gilbert, *A. cinereovelata* Hosen, and *A. longipes* Bas ex Tulloss & Dav. T. Jenkins (**Fig.1**). *A. eriophora*, segregates from our species by its pale brownish rufescent context on bruising or cutting (Bas 1969). *Amanita longipes* can be easily separated from present species by its pallid greyish pileus, context turning slightly brown when damaged, elongated bulb, elongate to cylindric basidiospores 10.5–13.5 × 5.5–7.5 µm with a higher Q value =1.80 (Tulloss 2005). *Amanita cinereovelata* originally described from Bangladesh differs from *A. indogrisea* due to globose to subglobose basidiospores (8–) 9–10 (– 11)×(7–) 8–9 (–10) µm, presence of clamps at the base of basidia, and its associations with Sal (*Shorea robusta*) forest (Hosen et al. 2015).

Conflict of Interest

This work is original and authors declare that there is no conflict of interest.

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