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INOCYBE SWATENSIS (AGARICALES), A NEW SPECIES OF THE *INOCYBE GRAMMATA* GROUP AND FIRST REPORT OF *INOCYBE* SECT. *ALBODISCAE* FROM ASIA

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Abstract

Inocybe swatensis sp. nov., is described here based on ITS and LSU sequence data and comparison of its micro- and macromorphological characters with other closely related species. The taxon is characterized by distinctive bicolored, light to dull orangish-brown basidiomata, thick-walled cheilo- and pleurocystidia, small basidia, and angular basidiospores within the *Inocybe grammata* group. This species occurs as a highly-supported lineage based on phylogenetic analyses of ITS and LSU data. This is the first report of *Inocybe* section *Albodiscae* from Asia.

Key words: Biodiversity, ITS, Phylogeny, Systematics, New species.

Introduction

During our biodiversity assessment of the macrofungi of the humid temperate coniferous forests of the Swat Valley KP Pakistan, a unique species of *Inocybe* was found which turned out to be a member of the *Inocybe grammata* group in *Inocybaceae* (Agaricales). According to Matheny & Kudzma (2019), this monophyletic cosmopolitan family circumscribes 1050 species and forms mycorrhizal associations with up to 23 families of vascular plants. The most recent classification of *Inocybaceae*, based on a six-gene phylogenetic analysis, divides the family into seven genera elevating some subgenera and clades of *Inocybe* to generic status (Matheny *et al.*, 2020). The largest and most widespread genus, *Inocybe*, now in its restricted sense, contains an estimated 850 species worldwide that can be distinguished by the presence of pleurocystidia and basidiospores that are amygdaliform, elliptic, subcylindrical, angular, nodulose, or spinose, typically with a distinct apiculus. However, if the pleurocystidia are absent then the basidiospores are nodulose or long projectile-shaped. *Inocybe* (sen. str.) is confirmed as ectomycorrhizal based on anatomical studies (Agerer, 1987), stable isotope analysis (Mayor *et al.*, 2009), synthesis experiments (Chu-Chou & Grace, 1981; Cripps & Miller, 1995), and molecular evaluation of plant roots (Ryberg *et al.*, 2009; Tedersoo & Smith, 2013) A few species in the genus also form orchid mycorrhizae (Ryberg *et al.*, 2008; Roy *et al.*, 2009).

Inocybe grammata, characterized microscopically by the presence of thick-walled cystidia and somewhat small, nearly angular basidiospores with relatively few or obscure nodules (Vauras, 1997), has been the subject of numerous taxonomic treatments and phylogenetic studies (Matheny *et al.*, 2022). In a multigene phylogenetic study (Ryberg *et al.*, 2010), *I. grammata* was recovered as sister to the rest of what is now recognized (Matheny *et al.*, 2020) as the genus *Inocybe* but with poor support. Matheny *et al.*, (2022) formally recognized eight species in the *I. grammata* group and accommodated them in the newly described section, *Inocybe* sect. *Albodiscae*. Among the eight species of *Inocybe* sect. *Albodiscae* there is no representative from Asia. We confirm the occurrence of our new species of *Inocybe* from the Swat Valley, Pakistan in *I.* sect. *Albodiscae* through morphological and phylogenetic analyses based on ITS and LSU sequence data. This study extends the geographic range of *I.* sect. *Albodiscae* to Asia and increases the number of species in this section to nine.

Materials and Methods

Collections: A total of four specimens were collected from two nearby areas within the mixed coniferous forests of Nalkot, Matta Swat Valley, Pakistan, where they were observed growing in close proximity. Specimens were photographed in the field and were dried on a warm-air fan at 40-50ºC, preserved in plastic bags, and deposited in the Islamia College Fungarium Peshawar, Pakistan (ICFP) and the Fungarium of the Illinois Natural History Survey (ILLS), Champaign, IL, USA.

Morphological studies: Material was rehydrated in 5% KOH and examined using a Labomed-V2000 and an Olympus CX22RFS1 light microscope. For observations of the pileipellis, a radial-epithelial section was made approximately halfway between the margin and the center of the pileus. Basidiospores were observed under 100X magnification and basidia, cystidia (cheilocystidia and pleurocystidia), pileipellis and stipitipellis were observed under 40X. A minimum of 40 measurements were taken for basidiospores and 20 for the other microscopic features. Dimensions of basidiospores are given as (a-) b-c (-d), where the range b-c represented 90% of the measured values (5th to 95th percentiles) and extreme values (a and d), whenever present, (a < 5th percentile, d > 95th percentile), are given in parentheses. Q refers to the length/width ratio of basidiospores.

Molecular sequencing and phylogenetic analyses: Genomic DNA was extracted from portions of lamellae through a modified NaOH extraction (Osmundson *et al.*, 2013); 200 µL 0.5M NaOH was added to ~75 mg of dried tissue, ground with a micropestle, centrifuged at 14000 RPM for 2 minutes, and 5 µL of the resulting supernatant added to 495 µL 100 mM Tris-HCl buffered with NaOH to pH 8.5-8.9 (Tris-HCl-DNA extraction solution). ITS and LSU regions of nuclear rDNA were amplified using the primer pairs ITS1F-ITS4 and LR0R-LR6 (Vilgalys & Hester, 1990; White *et al.*, 1990; Gardes and Bruns, 1993). Polymerase chain reactions (PCR) were performed in a total volume of 25 µL including 12.5 µL of the GoTaq® Green Master mix (Promega, Madison, Wisconsin, USA), 2 µL each of primer pairs, 1 µL of 50% DMSO, 1 µL of BSA, 3.5 µL of PCR grade water, and 3 µL of template DNA. PCR amplification was completed on a Bio-Rad PTC 200 thermal cycler under the following parameters: an initial 2-minute denaturation step at 94°C, followed by 40 cycles of 30 seconds at 94°C, 20 seconds at 55°C (for ITS region) or 58°C (for LSU region), and 1 minute at 72°C, with a final extension step of 10 minutes at 72°C. PCR products were visualized on a 1% TBE agarose gel containing ethidium bromide and purified with the Wizard® SV Gel and PCR Clean-Up System (Promega, Madison, Wisconsin, USA). Template DNA was used in 10 µL sequencing reactions with BigDye® Terminator v3.1 (Applied Biosystems, Foster City, California, USA) using a combination of the following primers: ITS1F, ITS2, ITS3, ITS4, LROR, LR3, LR3R and LR6 (Vilgalys & Hester, 1990; White *et al.*, 1990; Gardes & Bruns, 1993; Rehner & Samuels, 1995). Sequences were generated in both directions on an Applied Biosystems 3730XL high throughput capillary sequencer at the W.M. Keck Center at the University of Illinois Urbana-Champaign. Sequences and chromatograms were assembled, corrected and initially aligned in Sequencher 4.9 (Gene Codes Corp., Ann Arbor, Michigan). Further alignment was performed with MUSCLE 3.6 (Edgar 2005) followed by manual correction. Sequences were deposited in GenBank (http://www.ncbi.nlm.nih.gov).

The online tool BLAST and databases at GenBank (http://www.ncbi.nlm.nih.gov/) were used to check for possible PCR-product contamination and to identify and retrieve available highly similar *Inocybe* ITS and LSU sequences for the phylogenetic analyses (Fig. 5). Sequences in the NCBI database with similarity up to 92% and 100% query cover for ITS and up to 95% identity and 98% query cover for LSU were downloaded and included in the phylogenetic analyses along with all sequences of *I.* sect. *Albodiscae* from recent publications (Table 1). The holotype sequences (NR154687, NG057043) of *Auritella robusta* Matheny & Bougher from Australia were used to root the ITS and LSU trees, respectively. The datasets for the phylogenetic trees were aligned using MUSCLE in SEAVIEW software version 5.0.5 (Gouy *et al.*, 2010). We used jModelTest 2.1.6 (Darriba *et al.*, 2012) to verify the best nucleotide substitution model using the Akaike information criterion. The Maximum Likelihood analyses were performed using RAxML v.8 (Stamatakis, 2014) with the XSEDE tool (8.2.12) on the CIPRES Science Gateway v.3.3 portal (Miller *et al.*, 2010), the GTRGAMMA model and 1000 bootstrap replicates. The results obtained from these analyses were processed using RAxML online tool, and the phylogenetic trees were constructed using FigTree v1.4.3, with bootstrap values labelled on the nodes/branches. Finally, branches in the phylogenetic tree with bootstrap values equal to or exceeding 70% in the Maximum Likelihood analysis were considered to be supported.

Results and Discussion

Phylogenetic analyses: The final datasets consisted of 58 and 28 sequences of ITS and LSU, respectively. Both the ITS and LSU trees represent nearly the same topography with *Inocybe swatensis* sp. nov. occurring in the same strongly-supported clade with *Inocybe grammatoides* Esteve-Rav., Pancorbo & E. Rubio and *Inocybe acriolens* (Figs. 3, 4).

Taxonomy:

Inocybe swatensis I. Ahmad & A.N. Mill., sp. nov. (Figs. 1, 2)

MycoBank: MB851471
Etymology: The specific epithet refers to the type location, Swat, a district of Pakistan.

Diagnosis: *Inocybe swatensis* differs from the morphologically similar species *Inocybe grammatoides* and *I. acriolens* by having dull orangish basidiomata, smaller basidia and cheilocystidia. It forms a distinct lineage in the phylogenetic analyses and differs from the other two species by 90–92 % in the ITS and 94-95 % in the LSU.

Holotype: Pakistan, KP, Swat, Matta, Nalkot, Aug 08, 2019. Ishtiaq Ahmad, ICFP # SK1901 (*Isotype*: ILLS00122424); GenBank ITS: OR625717, LSU: OR625719.

Description (macromorphological features): Pileus 2 - 3.5 cm, round, campanulate with papilla, straight, radially fibrillose, deflexed conic, pallid to light orange (7.5YR 8/1), disc and margins dull orangish brown (7.5YR 6/4) to reddish brown (7.5R 4/6) in the rest of the cap upon maturity. KOH-negative, context firm, white and not changing upon exposure. Odor faint, *Lamellae* Free and approximate to sinuate. Crowded with several tiers of lamellulae; light yellowish pink (5YR 9/4) to yellowish pink (5YR 7/4), up to 3 mm deep, margins slightly eroded. *Stipe* 30 - 65 × 5 mm, grey at the top (7.5YR8/2) and lighter at the base (7.5YR8/1), central, cylindrical, hollow, subbulbous, smooth, equal and free, annulus absent. *Bulb* 0.5 cm, light grey (10Y8/8), abrupt to marginate. *Taste* not recorded.

Micromorphological features: Basidiospores (5) 6–8 (9) × (4) 5–6 (7), Q = 1.1–1.7 µm, avQ = 1.4, angular to metuloid, a few ellipsoid, hyaline in 5% KOH. Basidia (21) 22–28 (29) × (6.4) 7–9.3 (9.5) µm, clavate, truncate, rostrate, frequently bisporic and rarely tri- and tetrasporic. Cheilocystidia (25.5) 31.5–44.5 (49) × (5.5) 5.6–7.3 (8.1) µm, narrowly clavate, subcapitiate, oblong, truncate, thin-walled, apices obtuse, crystalliferous and hyaline in 5% KOH. Pleurocystidia (47) 48.5–64.5 (65.5) × (12.5) 13.5–19 µm, narrowly clavate, obtuse, utri-form, mucronate, thick-walled, apices obtuse, crystalliferous and hyaline in 5% KOH. Pileipellis 2.2–7.6 µm, regular, ixotrichoderm, septate, no clamp connections seen, hyaline in 5% KOH. Stipitipellis 2.3–7.6 µm, regular, ixocutis, septate and clamp connections present.

Habitat and distribution: This species was found in mixed coniferous forests dominated by *Pinus wallichiana* and *Abies pindrow* in the Nalkot region of Matta, Swat Valley, Pakistan. Specimens were collected from moss-covered soil at elevations ranging from 1,800 to 2,000 meters.

Additional specimen examined: Pakistan, KP, Swat, Matta, Nalkot, Aug 09, 2019. Shahid Ali, ICFP # SK1990; GenBank ITS: OR625718, LSU: OR625720.

Notes: The genus *Inocybe* is common at varying elevations in the coniferous and oak forests in the Swat region of Pakistan due to a mix of cool and humid environments (Jabeen *et al.*, 2016; Khalid, 2022). *Inocybe swatensis* is characterized by the presence of a bicolored light to orangish brown pileus that is hemispherical, campanulate and radially fibrillose. The presence of angular to metuloid basidiospores and the presence of thick-walled cheilo- and pleurocystidia distinguish it as a new species within the section. *I.* sect. *Albodiscae*. The other eight members of this section occur in Europe and North and/or Central America. With the addition of this Asian species *I. swatensis* Ahmed & Mill. the total number of species in the group increases to nine, and expands the geographic range of the section *Albodiscae*. *Inocybe swatensis* is similar to the closely-related *Inocybe grammatoides* in the size and campanulate shape of the pileus (Crous *et al.*, 2019). However, *I. grammatoides* has a very light pale brown pileus and larger basidia and cheilocystidia compared to the dull orangish pileus and smaller basidia (21–29 × 6.5–9.5 µm) and cheilocystidia (25.5–49 × 5.5–8 µm) of *I. swatensis* (Cho *et al.,* 2021). The other phylogenetically closely related species is *Inocybe acriolens* with which *Inocybe swatensis* shares the same size, similar shape of the pileus and similar habitat and hosts, but differs in the color of the pileus, and by the very rare existence of metuloid basidiospores and complete absence of ellipsoid basidiospores in the latter (Grund & Stuntz, 1975). Moreover, *Inocybe swatensis* differs from *Inocybe acriolens* by having a longer and darker stipe, smaller basidia, pleurocystidia, and cheilocystidia and larger basidiospores (5–9 × 4–7). Other phylogenetically similar species are the recently described new species, *Inocybe albodiscoides* Matheny from Washington, USA and *Inocybe panamica* Matheny & Corrales reported from Panama and Costa Rica (Matheny *et al.*, 2022). *Inocybe albodiscoides* differ from *Inocybe swatensis* by having different hosts such as *Pseudotsuga, Arbutus* and *Thuja*, whereas *I. swatensis* is found under *Pinus* and *Quercus* spp. *Inocybe albodiscoides* also differ from *I. swatensis* due to its occurrence on acidic soil and having larger basidiomata with a whitish to slightly brownish pileus. *Inocybe panamica* differs from *I. swatensis* by having larger basidiomata with a whitish to slightly brownish pileus and larger cystidia. All three taxa share the same climatic and edaphic conditions, although they occur on different continents with *I. grammatoides* occurring in Germany and *I. acriolens* occurring in the USA and Canada (Ahmad, 2017; Matheny *et al.*, 2022).

Fig. 1. Basidiomata of *Inocybe swatensis* sp. nov.: A, ICFP # SK190; B, ICFP # SK1990.

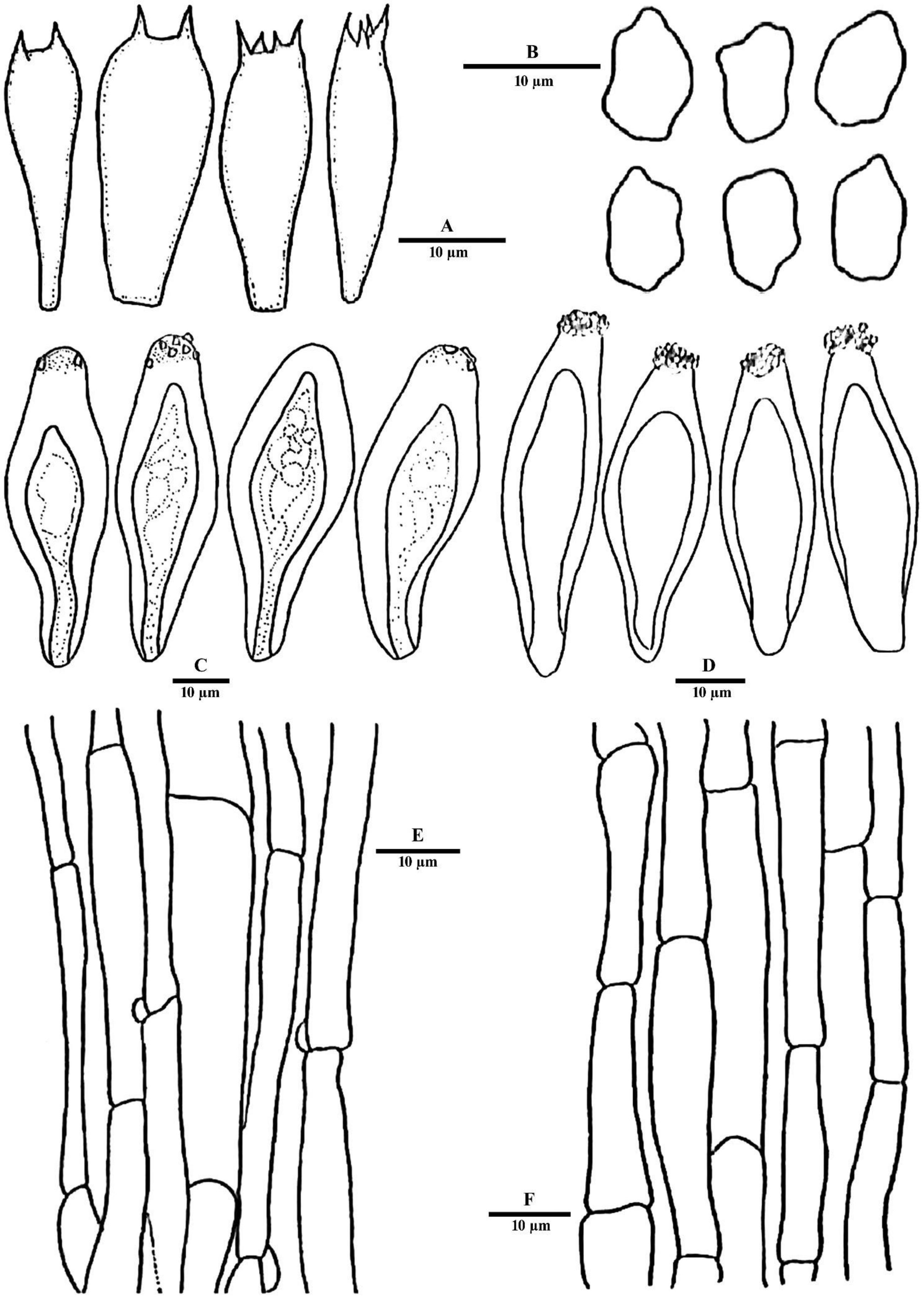

Fig. 2. Microscopic characters of *Inocybe swatensis* sp. nov.: A, Basidia; B, Basidiospores; C, Pleurocystidia; D, Cheilocystidia; E, Stipitipellis; F, Pileipellis.

Table 1. Taxa of *Inocybe* and *Auritella* included in the molecular phylogenetic analyses.

Species	Specimen voucher / isolate	Geographic origin	GenBank		Reference / Authors from GenBank
			ITS	LSU	
Auritella robusta	HO:572018	Australia	NG154687	NG057043	(Matheny & Bougher, 2017)
I. acriolens	ACAD:11669	Canada	MG489945	ON113314	(Matheny *et al*., 2022)
I. acriolens	RAS869	USA	ON116979	JN974981	(Matheny *et al*., 2022)
I. acriolens	LVK15086	USA	ON116978	ON113312	(Matheny *et al*., 2022)
I. adorabilis	STU: SMNS-STU-F-0901641	Austria	OK057161	---	(Bandini *et al*., 2022)
I. adorabilis	STU: SMNS-STU-F-0901582	Austria	OK057159	---	(Bandini *et al*., 2022)
I. adorabilis	STU SMNS-STU-F-0901582	Austria	NR176168	---	(Bandini *et al*., 2022)
I. albodiscoides	JK189 (MO484645)	USA	ON116980	ON113316	(Matheny *et al*., 2022)
I. albodiscoides	PBM554	USA	ON116981	EU307819	(Matheny *et al*., 2022)
I. amelandica	M80	Hungary	MW354976	---	(Csizmár *et al*., 2021)
I. amelandica	M31	Hungary	MW354975	---	(Csizmár *et al*., 2021)
I. beninensis	HLA0390	Benin	NR184903	---	(Aïgnon *et al*., 2022)
I. beninensis	HLA0390	Benin	MN096196	---	(Aïgnon *et al*., 2022)
I. boreogodeyi	TUR A204256	Sweden	NR184491	---	Vauras &Larsson
I. boreogodeyi	JV31472	Sweden	OM859009	---	Vauras & Larsson
I. boreogodeyi	JV31473	Sweden	OM859010	---	Vauras & Larsson
I. calocephala	TENN:066460	Australia	---	KJ756455	(Matheny & Bougher, 2017)
I. calocephala	TENN 066460	Australia	---	NG057234	(Matheny & Bougher, 2017)
I. calocephala	REH9133	Australia	---	KJ756456	(Matheny & Bougher, 2017)
I. comis	STU SMNS-STU-F-0901599	Austria	NR176170	---	(Bandini *et al*., 2022)
I. comis	STU: SMNS-STU-F-0901598	Austria	OK057189	---	(Bandini *et al*., 2022)
I. comis	STU: SMNS-STU-F-0901599	Austria	OK057190	---	(Bandini *et al*., 2022)
I. farinosipes	TENN:066494	Australia	---	KC305404	(Braaten *et al*., 2014)
I. farinosipes	TENN:066628	Australia	---	KC305406	(Braaten *et al*., 2014)
I. fibrillosibrunn	---	Australia	---	KC305398	(Braaten *et al*., 2014)
I. fibrillosibrunn	PERTH:8318816	Australia	---	KC305397	(Braaten *et al*., 2014)
I. fibrillosibrunn	E5971 (WTU)	Australia	---	EU307848	(Braaten *et al*., 2014)
I. flavipes	HLA0363	Benin	MT994601	---	(Aïgnon *et al*., 2022)
I. flavipes	UNIPAR:MR00383	Togo	NR184904	---	(Aïgnon *et al*., 2022)
I. glabripes	STU: SMNS-STU-F-0900979	Germany	NR185422	---	(Bandini *et al*., 2021)
I. glabripes	STU: SMNS-STU-F-0900979	Germany	MW845881	---	(Bandini *et al*., 2021)
I. glabripes	MTB52	Germany	MN947389	---	Khokon & Polle
I. gracilior	PDD:72707	New Zealand	KY827277	---	(Horak, 2018)
I. gracilior	PDD:98239	New Zealand	KY827278	---	(Horak, 2018)
I. gracilior	PDD:98239	New Zealand	NR160467	---	(Horak, 2018)
I. grammata	TENN:074834	USA	---	ON113319	(Matheny *et al*., 2022)
I. grammata	EL102B06	Sweden	---	FN550885	(Ryberg *et al*., 2010)

Table 1. (Cont'd.).

Species	Specimen voucher / isolate	Geographic origin	GenBank		Reference / Authors from GenBank
			ITS	LSU	
I. grammata	PBM2602	USA	---	JN974977	(Ryberg & Matheny, 2012)
I. grammatoides	KR-M-0044740	Germany	MT006018	ON113320	(Matheny *et al*., 2022)
I. grammatoides	KR-M-0044823	Germany	MT005896	ON113321	(Matheny *et al*., 2022)
I. grammatoides	KR-M-0044811	Germany	MT005891	MH024881	Scholler
I. grammatoides	KR-M-0044790	Germany	MT005870	---	Scholler
I. hystrix	iNAT:16529443	USA	ON366738	---	Plischke *et al*.,
I. hystrix	TENN:071097	Canada	KX897428	---	Matheny *et al*.,
I. hystrix	iNAT:16475137	USA	MZ197993	---	Taylor
I. leptocystis	HMAS 269548	China	KJ810596	---	Wei
I. leptocystis	HMAS 269629	China	KJ810597	---	Wei
I. leptospermi	TENN:066567	Australia	KP308757	---	Matheny& Bougher (2017)
I. leptospermi	TENN:066610	Australia	KP308759	---	Matheny& Bougher (2017)
I. leptospermi	CANB:574560	Australia	KP308753	---	Matheny& Bougher (2017)
I. meirensongia	FHMU: U3157	China	MZ322672	---	(Bhunjun *et al*., 2022)
I. meirensongia	FHMU:3156	China	MZ322671	---	(Bhunjun *et al*., 2022)
I. mellita	TENN:066622	Australia	---	KP170949	Matheny& Bougher
I. mellita	PERTH:08320373	Australia	---	KP170950	Matheny& Bougher
I. nitidiuscula	UBC: F15950	---	HQ604259	---	Berbee *et al*.,
I. nitidiuscula	UBC:F17940	---	HQ604260	---	Berbee *et al*.,
I. panamica	AC265 (ARIZ)	Panama	ON116989	KJ756456	(Matheny *et al*., 2022)
I. panamica	AC98 (ARIZ)	Panama	ON116988	JN974980	(Matheny *et al*., 2022)
I. panamica	AC59 (UCH)	Panama	ON116987	---	(Matheny *et al*., 2022)
I. panamica	NY:01034372	Costa Rica	ON116990	---	(Matheny *et al*., 2022)
I. pseudoscabellif	XC2011-59	France	ON129692	---	Bellanger
I. pseudoscabellif	STU: SMNS-STU-F-0901635	Germany	OK057173	---	(Bandini *et al*., 2022)
I. pseudoscabellif	STU: SMNS-STU-F-0901636	Germany	OK057174	---	(Bandini *et al*., 2022)
I. swatensis sp. nov	ICFP # SK1901	Pakistan	OR625717	OR625719	Current work
I. swatensis sp. nov	ICFP # SK1990	Pakistan	OR625718	OR625720	Current work
I. subfibrosoides	MES-2512	Chile	MT367480	---	Caiafa *et al*.,
I. subfibrosoides	MES543 (FLAS)	Chile	KP636879	---	Matheny *et al*.,
I. urceolicystis	JV1109F (KUO) holotype BAN276	Finland	MF804315	---	(Oertel & Bandini, 2014)
I. urceolicystis	STU: SMNS-STU-F-0901615	Finland	OK057175	---	(Bandini *et al*., 2022)
I. urceolicystis	STU: SMNS-STU-F-0901633	Germany	OK057171	---	(Bandini *et al*., 2022)
I. velicopia	S.D. Russell ONT iNaturalist 130298298	USA	OP749515	---	(Russell, 2022)
I. velicopia	LVK18412X	USA	ON116998	---	(Matheny *et al*., 2022)
I. velicopia	TENN: 065364	USA	ON116999	---	(Matheny *et al*., 2022)
I. velicopia	NY: 01034370	Costa Rica	ON117001	---	(Matheny *et al*., 2022)

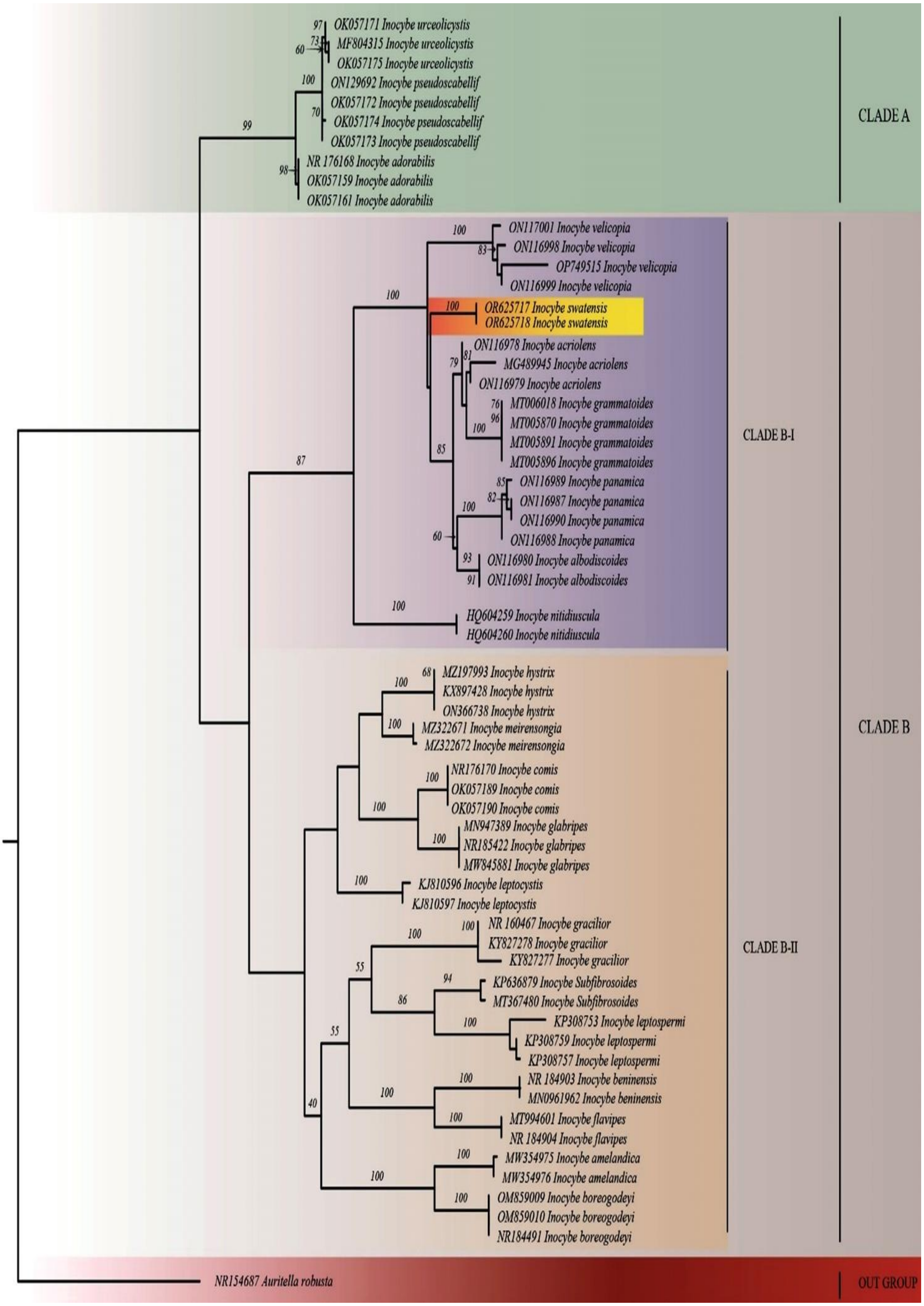

Fig. 3. Phylogenetic tree of *Inocybe spp.* based on ITS sequences. *Inocybe swatensis* is highlighted in yellow. Numbers above or below branches represent bootstrap values. A sequence of the holotype of *Auritella robusta* is used to root the tree.

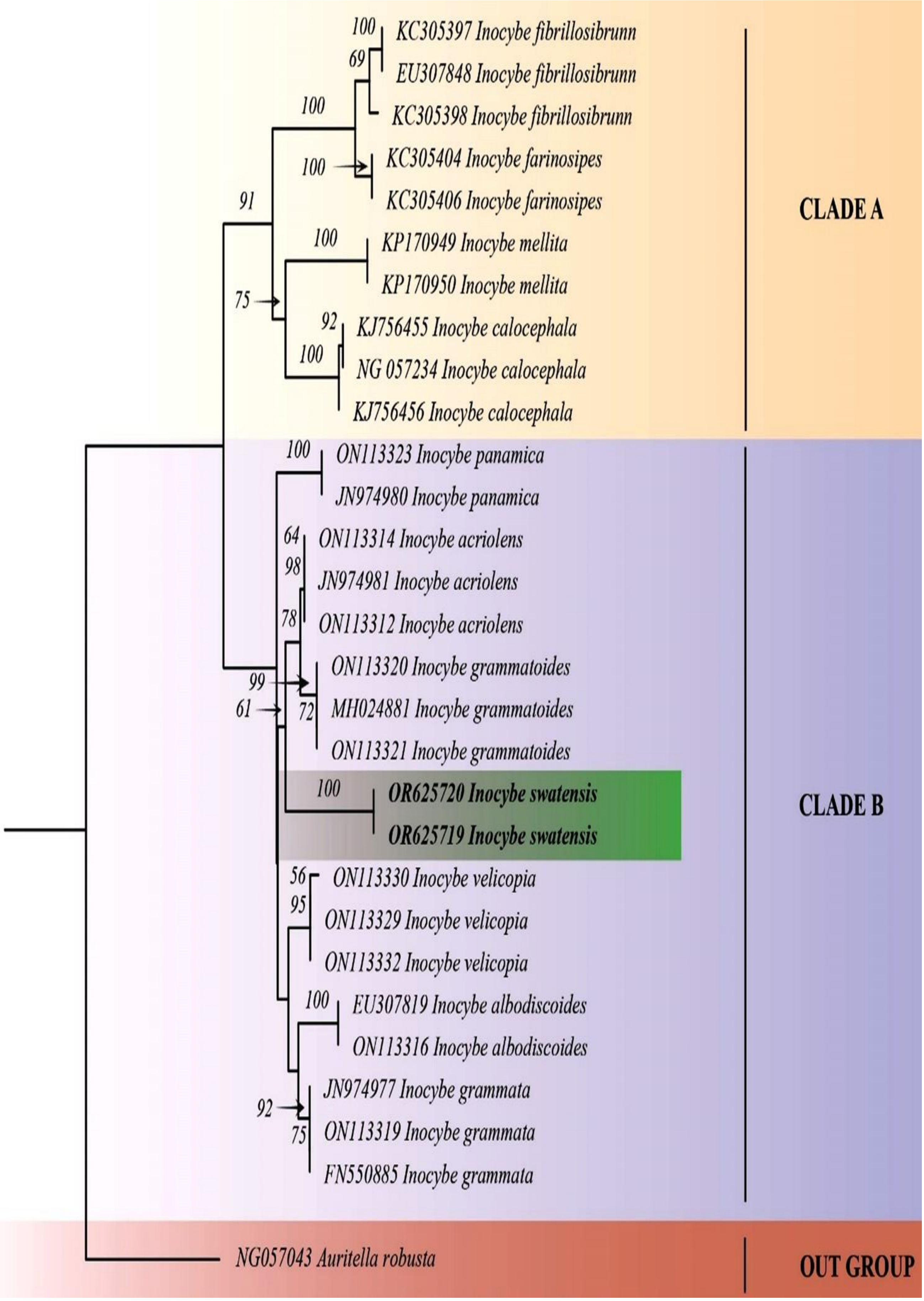

Fig. 4. Phylogenetic tree of *Inocybe* spp. based on LSU sequences. *Inocybe swatensis* is highlighted in green. Numbers above or below branches represent bootstrap values. A sequence of the holotype of *Auritella robusta* is used to root the tree.
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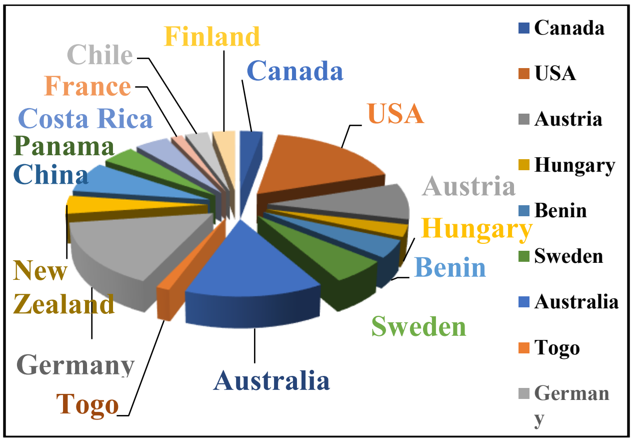

Fig. 5. Global distribution of the members of the *Inocybe grammata* group based on sequence data deposited in NCBI GenBank.

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