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## New species and new record of *Crepidotus* (Crepidotaceae, Agaricales) from Sikhote-Alin, Russia

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### Abstract

During ongoing surveys of the fungi of the Sikhote-Alin mountain range, Russian Far East, two species of *Crepidotus* were discovered. Of these, one species, *C. sokolovii*, is new to science, while *C. indicus* represents new Russian record. *Crepidotus sokolovii* is characterized by dull ochre-brown, greyish-brown or tawny pileus, globose, verrucose ornamented basidiospores and flexuous heteromorphic cheilocystidia. Herein, we fully describe and illustrate *C. sokolovii* and provide description and new distributional data for *C. indicus*. The results of phylogenetic analyses of nrITS+nLSU sequences support the recognition of these two species. Photographs, detailed morphological description, line drawings, and comparisons with related species are provided.

**Key words:** Agaricomycetes, Basidiomycota, nrITS, nrLSU, molecular phylogeny, Primorsky Krai, taxonomy

### Introduction

*Crepidotus* (Fries 1821: 272) Staude (1857: 71) is a rather large genus of Agaricales, including saprophytic fungi mostly with pleurotoid basidiomata, pale brown to yellowish spore print and typically a stipe that is absent or poorly developed. The genus was originally established by Fries (1821: 272) as a tribe *Crepidotus* in *Agaricus* L. (1753: 1171) series *Dermminus* characterized by pleurotoid habit and ferruginous spores. Later, Staude (1857) raised the tribe *Crepidotus* Fr. to generic rank with *Crepidotus mollis* (Schaeff. 1774: 49) Staude (1857: 71) as the type species. Currently, the genus encompasses about 330 known species (<https://www.catalogueoflife.org>, accessed on 2 April 2025). The systematic position of the genus *Crepidotus* remained controversial until recently, as it was placed either in the family Crepidotaceae (Jülich 1981, Moser 1983, Singer 1986, Hawksworth *et al.* 1995), Strophariaceae (Kühner 1980), Cortinariaceae (Bas 1988, Kirk *et al.* 2001) or Inocybaceae (Kirk *et al.* 2008). In recent phylogenetic high-ranking taxonomic systems incorporating the latest molecular phylogeny data (He *et al.* 2019, 2024, Hyde *et al.* 2024) the family Crepidotaceae has been reevaluated within a broader phylogenetic framework of Agaricales, including *Crepidotus* as the type genus of a family and six other genera, representing a distinct lineage of dark-spore euagarics. Among morphological characteristics of the genus *Crepidotus*, microscopic characters such as basidiospores, hymenial cystidia and pileipellis structure are of the greatest taxonomic importance. The majority of species characterized by ornamented basidiospores and hyphae with clamp connections are assigned to the subgenus *Dochmiopus* (Pat.) Pilát (1887: 113), while species with smooth basidiospores and without clamps are mostly classified to subgenus *Crepidotus* (Senn-Irlet 1995, Consiglio & Setti 2008, Han *et al.* 2024).

A literature-based investigation from different regions indicated that thirty-five species of the genus have been recorded from Russia (Bolshakov *et al.* 2021). The aim of the study was to register new data and expand knowledge about the diversity of agaricoid fungi of the Russian Far East. During our studies on the diversity of fungi of the Sikhote-Alin mountain range, we found two species of *Crepidotus*, of which one species, *C. sokolovii*, is new to science and the other, *C. indicus*, represents a new record for Russia. The newly discovered taxa morphologically correspond to the subgen. *Dochmiopus*. We used both morphological and molecular approaches to verify the delimitation of these species. Phylogenetic analyses were applied to assess the relationships between the newly described species and members of the *Crepidotus* subgen. *Dochmiopus*, which have globular and ornamented basidiospores.

## Materials & Methods

### Morphological examination

The research is based on a study of three of the author's own collections. Macroscopic morphological characters were recorded in the fresh specimens and color-coded with codes from the RAL Design System plus D2 (RAL D2 Colour fan, edition 2018, Germany). The collections were examined using standard microscopic techniques (Cléménçon 2009). The microscopical slides for the study were prepared with 5% KOH and Congo Red in 1% ammonia. Colours and measurements of microscopic structures were obtained in KOH, but the measurements of cheilocystidia were made under Congo Red using an Axiolab 5 light microscope equipped with AxioCam MRc5 camera (CarlZeiss, Germany). For scanning electron microscopy (SEM), individual lamellae were mounted on a stub, coated with gold, and examined under a Jeol JSM 6390LA scanning electron microscope (JEOL Ltd., Japan). Basidiospore dimensions are given following the form (a)b–c(d), with b–c representing 10 and 90 percentiles, the extremes (a, d) enclosed in parentheses, (n) means the number of spores measured and  $L_{av}$  and  $W_{av}$  are the mean value of length and width of the total spores measured. Q indicates the basidiospore length/width ratio,  $Q_{av}$  represents the mean length/width quotient of the total basidiospores measured. The studied specimens were deposited in the Mycological Herbarium of the Komarov Botanical Institute, Saint Petersburg (LE F).

### Molecular techniques

DNA was extracted from small fragments of dried basidiomata. The procedure of DNA extraction completely corresponded to the manufacturer's protocol of the Phytosorb Kit (ZAO Syntol, Russia). The following primers were used for amplification and sequencing: ITS1F-ITS4 (White *et al.* 1990, Gardes & Bruns 1993) for the ITS1-5.8S-ITS2 fragment; LROR and LR5 for part of the nrLSU region (White *et al.* 1990, Vilgalys & Hester 1990). PCR products were purified applying the CleanMag DNA PCR (Evrogen, Russia). Sequencing was performed with an ABI model 3500 Genetic Analyzer (Applied Biosystems, CA, USA). Raw data were edited and assembled in MEGA 11 (Tamura *et al.* 2021).

All microscopic and molecular studies of specimens were carried out at the Center for collective use of scientific equipment "Cellular and molecular technology of studying plants and fungi" (Komarov Botanical Institute of the Russian Academy of Sciences, St. Petersburg).

### Phylogenetic analyses

For this study, 3 nrITS sequences and 2 nrLSU sequences were newly generated. In addition, 62 ITS sequences and 46 nrLSU sequences of taxa from *Crepidotus* subgen. *Dochmiopus* and *Neopaxillus dominicanus* and *N. echinospermus* (as an outgroup), were downloaded from the GenBank database ([www.ncbi.nlm.nih.gov/genbank/](http://www.ncbi.nlm.nih.gov/genbank/)) for molecular analyses, using the BLAST application and taxonomic considerations. All the sequences used in this study are listed in Table 1. The sequences of both genetic markers were aligned using MAFFT version 7 (<https://mafft.cbrc.jp/alignment/server/index.html>; Katoh *et al.* 2019) with the FFT-NS-i option and improved where necessary using MEGA11.

**TABLE 1.** List of species used in the phylogenetic analyses.

Species	Voucher/strain	Geographic origin	GenBank accession number		References
			nrITS	nrLSU	
<i>Crepidotus applanatus</i>	SLO 2539	Slovakia	OM832523	OM832558	Jančovičová <i>et al.</i> 2022
<i>C. applanatus</i>	SLO 2551	Slovakia	OM832526	OM832560	Jančovičová <i>et al.</i> 2022
<i>C. applanatus</i>	SLO 2534	Slovakia	OM832521	OM832556	Jančovičová <i>et al.</i> 2022
<i>C. asiaticus</i>	TJB10018	Thailand	MF077339	MF077338	Guzmán-Dávalos <i>et al.</i> 2017
<i>C. asiaticus</i>	TJB9995	Thailand	MF077337	MF077336	Guzmán-Dávalos <i>et al.</i> 2017
<i>C. brunnescens</i>	OMDL K. Canan iNat181616855	-	OR945023	-	Unpublished
<i>C. brunnescens</i>	MO414862	USA	OK346340	-	Unpublished

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**TABLE 1.** (Continued)

Species	Voucher/strain	Geographic origin	GenBank accession number		References
			nrITS	nrLSU	
<i>C. capitatocystidiatus</i>	FFAAS1310 (Type)	China	PQ061270	PQ061255	Han <i>et al.</i> 2024
<i>C. capitatocystidiatus</i>	FFAAS1311	China	PQ061271	PQ061256	Han <i>et al.</i> 2024
<i>C. caspari</i>	FFAAS0343	China	MZ401360	MW581520	Unpublished
<i>C. caspari</i>	FFAAS0342	China	MZ401361	MW581521	Unpublished
<i>C. cesatii</i>	SLO 2613	Germany	PP874212	PP874221	Jančovičová <i>et al.</i> 2024
<i>C. cesatii</i>	SLO 2607	Slovakia	PP874214	PP874223	Jančovičová <i>et al.</i> 2024
<i>C. clavocystidiatus</i>	FFAAS1317	China	PQ061277	PQ061262	Han <i>et al.</i> 2024
<i>C. clavocystidiatus</i>	FFAAS1316	China	PQ061276	PQ061261	Han <i>et al.</i> 2024
<i>C. croceotinctus</i>	iNat126570732	USA	OP470431	-	Unpublished
<i>C. croceotinctus</i>	iNat31834012	USA	MN498116	-	Unpublished
<i>C. crocophyllus</i>	SLO 2588	Slovakia	OM832530	OM832563	Jančovičová <i>et al.</i> 2022
<i>C. crocophyllus</i>	SLO 2433	Slovakia	OM832529	OM832562	Jančovičová <i>et al.</i> 2022
<i>C. ehrendorferi</i>	SLO 2587	Slovakia	OM832534	OM832566	Jančovičová <i>et al.</i> 2022
<i>C. ehrendorferi</i>	SLO 707	Slovakia	OM832532	OM832565	Jančovičová <i>et al.</i> 2022
<i>C. exilis</i>	TBGT17157 (Type)	India	-	MK878548	Kumar <i>et al.</i> 2020
<i>C. flavobrunneus</i>	TBGT15841	India	-	MK567981	Kumar <i>et al.</i> 2022
<i>Crepidotus globisporus</i>	TBGT17341 (Type)	India	-	MK878540	Kumar <i>et al.</i> 2022
<i>C. indicus</i>	<b>LE F-354605</b>	<b>Russia</b>	<b>PV468333</b>	<b>PV468335</b>	<b>Present study</b>
<i>C. indicus</i>	JP81	India	OR827603	-	Unpublished
<i>C. indicus</i>	TBGT15950	India	MK370662	-	Kumar <i>et al.</i> 2018
<i>C. iqbalii</i>	MU248	Pakistan	OQ672617	-	Unpublished
<i>C. iqbalii</i>	LAH36654	Pakistan	MT973498	MW888515	Izhar <i>et al.</i> 2021
<i>C. lamellomaculatus</i>	FFAAS1305 (Type)	China	PQ061265	PQ061250	Han <i>et al.</i> 2024
<i>C. lamellomaculatus</i>	FFAAS1307	China	PQ061267	PQ061252	Han <i>et al.</i> 2024
<i>C. lateralis</i>	PDD 72571	New Zealand	KY827294	-	Horak 2018
<i>C. lateralis</i>	PDD 72508 (Type)	New Zealand	KY827293	-	Horak 2018
<i>C. lundellii</i>	NL-5279	Hungary	-	MK277888	Varga <i>et al.</i> 2019
<i>C. luteolus</i>	16834	Italy	JF907963	-	Osmundson <i>et al.</i> 2013
<i>C. lutescens</i>	HMJAU 37002 (Type)	China	KU762017	-	Ge <i>et al.</i> 2017
<i>C. lutescens</i>	HMJAU 21976	China	KU762016	-	Ge <i>et al.</i> 2017
<i>C. macedonicus</i>	PV773	Hungary	MH780921	-	Unpublished
<i>C. macedonicus</i>	MB19102501	Italy	PP131267	PP125747	Unpublished
<i>C. malachioides</i>	SLO 2391	Slovakia	OM832536	OM832567	Jančovičová <i>et al.</i> 2022
<i>C. malachioides</i>	SLO 2578	Slovakia	OM832538	OM832568	Jančovičová <i>et al.</i> 2022
<i>C. malachius</i>	SLO 2091	Slovakia	OM832541	OM832571	Jančovičová <i>et al.</i> 2022
<i>C. malachius</i>	SLO 2541	Slovakia	OM832546	OM832575	Jančovičová <i>et al.</i> 2022
<i>C. malachius</i>	SLO 2530	Slovakia	OM832543	OM832573	Jančovičová <i>et al.</i> 2022
<i>C. pini</i>	SLO 2579 (Type)	Slovakia	OM832550	OM832580	Jančovičová <i>et al.</i> 2022
<i>C. pini</i>	SLO 2550	Slovakia	OM832549	OM832579	Jančovičová <i>et al.</i> 2022
<i>C. rufidulus</i>	PDD 98272 (Type)	New Zealand	KY827319	-	Horak 2018

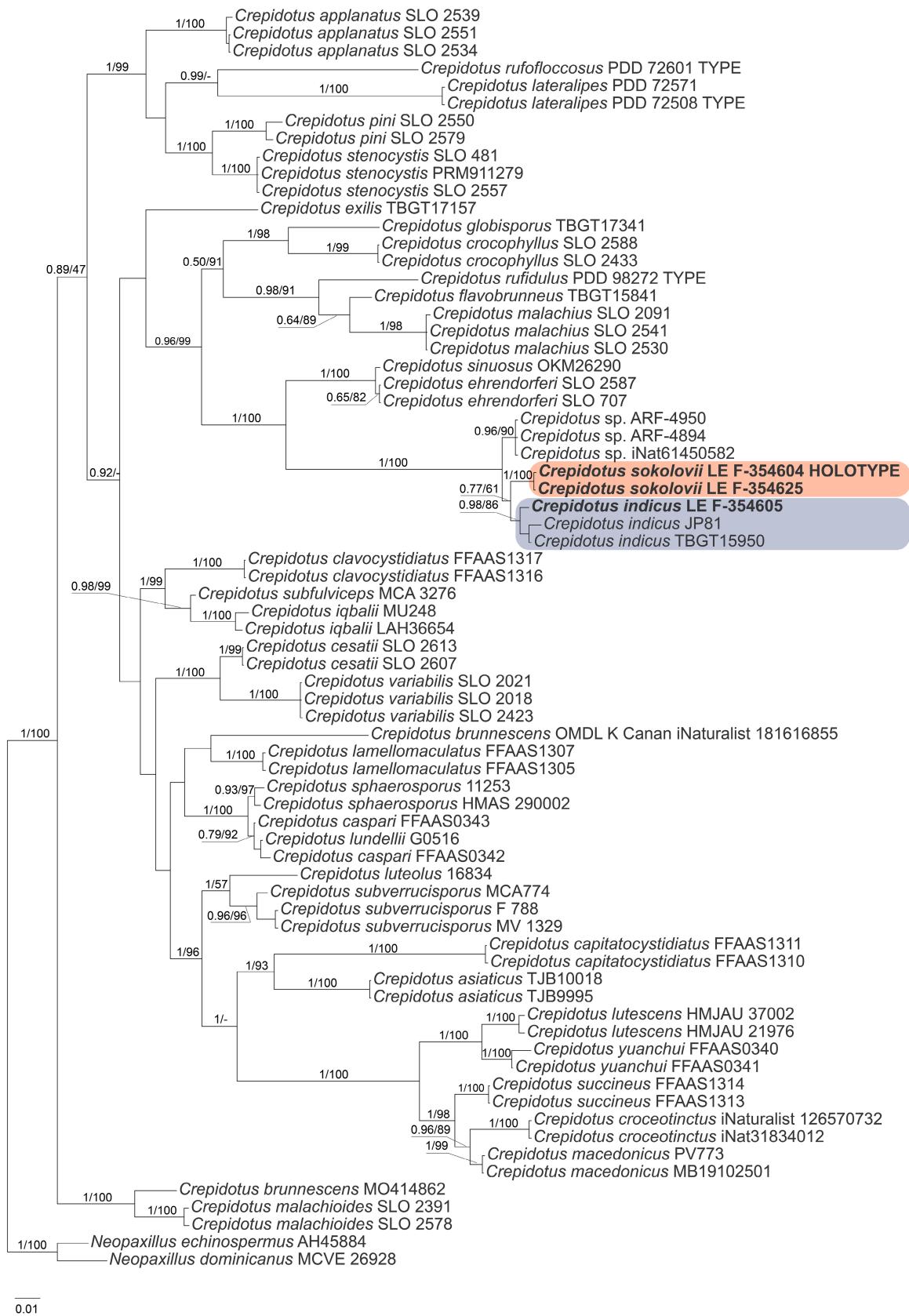
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**TABLE 1.** (Continued)

Species	Voucher/strain	Geographic origin	GenBank accession number		References
			nrITS	nrLSU	
<i>C. rufofloccosus</i>	PDD 72601 (Type)	New Zealand	KY827296	-	Horak 2018
<i>C. sokolovii</i>	<b>LE F-354604 (Type)</b>	<b>Russia</b>	<b>PV468332</b>	<b>PV468334</b>	<b>Present study</b>
<i>C. sokolovii</i>	<b>LE F-354625</b>	<b>Russia</b>	<b>PV468331</b>	-	<b>Present study</b>
<i>C. sphaerosporus</i>	11253	-	JF907960	-	Osmundson <i>et al.</i> 2013
<i>C. sphaerosporus</i>	HMAS 290002	-	MK966514	-	Unpublished
<i>C. sinuosus</i>	OKM26290	-	-	AF367945	Unpublished
<i>C. stenocystis</i>	SLO 481	Slovakia	OM832552	-	Jančovičová <i>et al.</i> 2022
<i>C. stenocystis</i>	SLO 2557	Slovakia	OM832553	OM832581	Jančovičová <i>et al.</i> 2022
<i>C. stenocystis</i>	PRM911279	Czech Republic	MF621030	MF621024	Jančovičová <i>et al.</i> 2017
<i>C. subfulviceps</i>	MCA 3276	Spain	-	FJ947117	Aime <i>et al.</i> 2009
<i>C. subverrucisporus</i>	MCA774	-	-	AF367948	Unpublished
<i>C. subverrucisporus</i>	F 788	Sweden	PQ652383	PQ652383	Unpublished
<i>C. subverrucisporus</i>	MV 1329	Sweden	PQ653210	PQ653210	Unpublished
<i>C. succineus</i>	FFAAS1313 (Type)	China	PQ061273	PQ061258	Han <i>et al.</i> 2024
<i>C. succineus</i>	FFAAS1314	China	PQ061274	PQ061259	Han <i>et al.</i> 2024
<i>C. variabilis</i>	SLO 2423	Slovakia	MT055887	OM832584	Jančovičová <i>et al.</i> 2020, 2022
<i>C. variabilis</i>	SLO 2021	Slovakia	MT055889	OM832585	Jančovičová <i>et al.</i> 2020, 2022
<i>C. variabilis</i>	SLO 2018	Slovakia	MT055880	OM832583	Jančovičová <i>et al.</i> 2020, 2022
<i>C. yuanchui</i>	FFAAS0340	China	MZ401362	-	Na <i>et al.</i> 2022
<i>C. yuanchui</i>	FFAAS0341	China	MZ401363	MW581519	Na <i>et al.</i> 2022
<i>Crepidotus</i> sp.	ARF 4950	USA	OP580197	-	Unpublished
<i>Crepidotus</i> sp.	ARF 4894	USA	OP580196	-	Unpublished
<i>Crepidotus</i> sp.	iNat61450582	USA	OP028507	-	Unpublished
<i>Neopaxillus dominicanus</i>	MCVE 26928	Dominican Republic	JN033216	JN033217	Vizzini <i>et al.</i> 2012
<i>N. echinospermus</i>	AH45884	Brazil	KY468512	KY468511	Unpublished

Newly generated sequences for this study are in bold.

Phylogenetic analyses were performed with Maximum Likelihood (ML) and Bayesian Inference (BI) methods for combined nrITS+nLSU dataset. The most likely model of evolution was GTR+G determined through Akaike information criterion (AIC) function in FindModel web server (<http://www.hiv.lanl.gov/content/sequence/findmodel/findmodel.html>) for combined dataset. Maximum likelihood analysis was run on IQ-Tree web server (<http://iqtree.cibiv.univie.ac.at/>; Trifinopoulos *et al.* 2016) with 1000 rapid bootstrap replicates. BI analysis was performed with MrBayes 3.2.7 software (Ronquist *et al.* 2012), for two independent runs, each with 5 million generations under described model and four chains with sampling every 100 generations. To check for convergence of MCMC analyses and to get estimates of the posterior distribution of parameter values, Tracer v1.7.1 was used (Rambaut *et al.* 2018). We accepted the result where the ESS (Effective Sample Size) was above 200 and the PSRF (Potential Scale Reduction Factor) was close to 1. Branches with bootstrap support (BS) and posterior probabilities (PP) values greater than or equal to 70% and 0.90, respectively, were considered significantly supported (Hillis & Bull 1993, Alfaro *et al.* 2003). Tree topologies were then edited and visualized in iTOL (Letunic & Bork 2019). In order to best understand the relationships between the different species, an interspecific genetic distances for nrITS region were calculated in MEGA 11 with GTR+G model. Newly generated sequences were deposited in GenBank with corresponding accession numbers.



**FIGURE 1.** Combined phylogenetic nrITS+nLSU topology from Bayesian analysis for taxa from *Crepidotus* subgen. *Dochmiopus*, with *Neopaxillus dominicanus* and *N. echinospermus* as an outgroup. Posterior probability and Bootstrap support values (PP/BS) are shown on the branches. All sequences are labeled with taxon name and voucher or isolate number. The sequences generated for this study are indicated in bold.

## Results

### Molecular phylogeny

The combined dataset of nrITS+nLSU sequences for members of *Crepidotus* subgen. *Dochmiopus* contained 1757 characters, including gaps (nrITS: 1–859 and nrLSU: 860–1757). Both Bayesian and Maximum likelihood analyses produced the same topology. Therefore, we present only the BI tree with both PP and BS values (Fig. 1). Phylogenetic analyses showed that all species involved formed distinct clades or independent lineages, which is consistent with earlier studies (Han *et al.* 2024).

The present molecular data indicate that our two collections from Russian Far East were grouped together and from highly supported (PP = 1.00, BS = 100 %) monophyletic clade, which is described here as a new species *C. sokolovii*. Our other collection is closely related to *C. indicus*. Both species are nested in the same clade together with sequences of unidentified collections *Crepidotus* sp., probably a new undescribed taxon, from the USA (OP028507, OP580196 and OP580197). However, our collection of *C. indicus* from Russia is clustered together with the Indian collections, including a paratype (TBGT15950), into one strongly supported clade (PP = 0.98, BS = 86 %) and their nrITS sequences are 2 % distant from the American sequences (corresponding to twenty-two different nucleotides including gaps in the whole region). The nrITS interspecific distances ranged from 2.2 % to 2.8 % for *C. sokolovii* and *Crepidotus* sp. and *C. indicus*, respectively, which is sufficient to consider these taxa as separate species.

## Taxonomy

### *Crepidotus sokolovii* E.F. Malysheva, *sp. nov.* (Figs. 2, 3)

MycoBank: MB858726

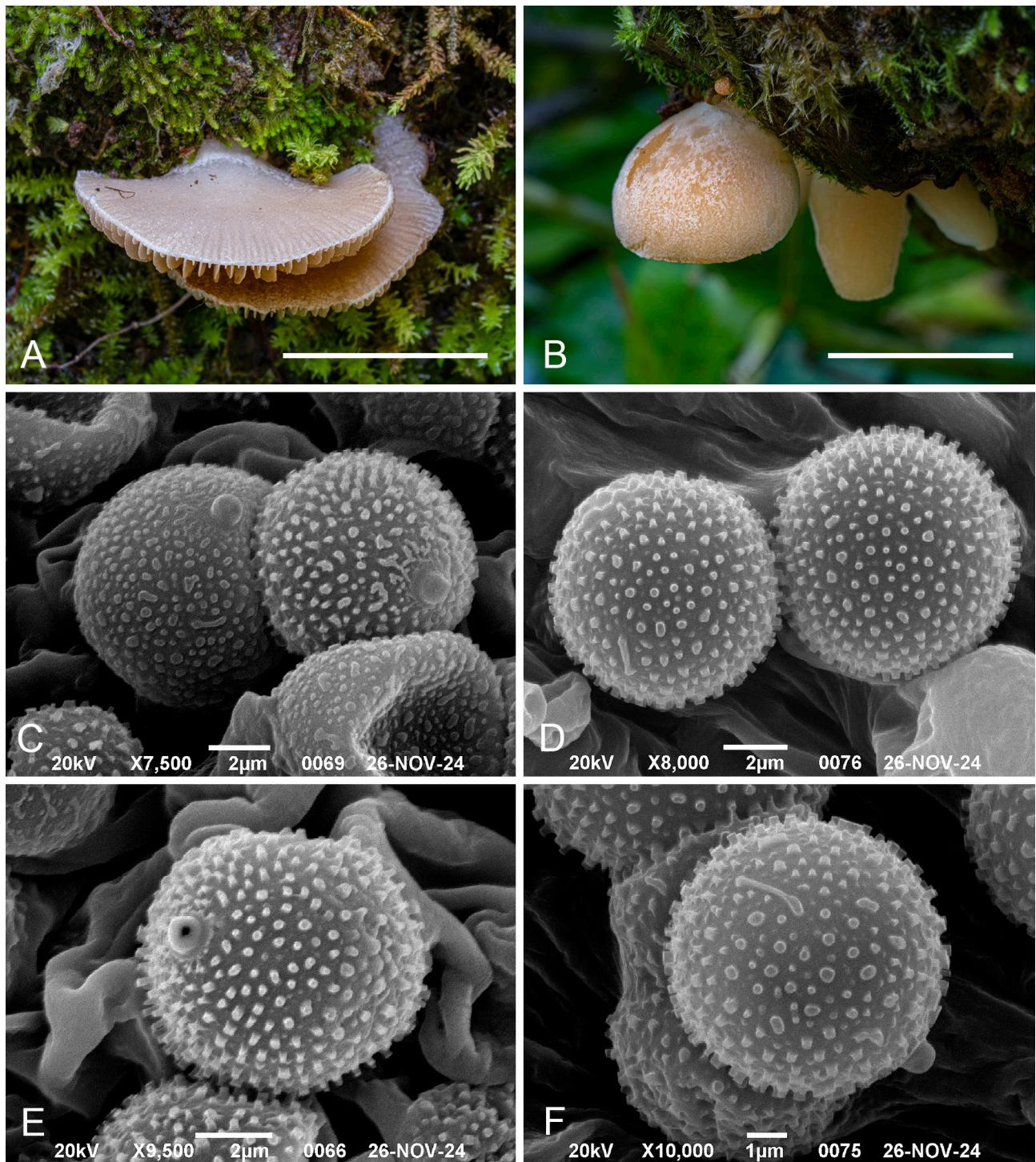
*Diagnosis*:—Basidiomata small, semicircular to flabelliform, laterally attached to the substrate with pseudostipe, with even and sulcate margin; surface of pileus dry, slightly pruinose, dull ochre-brown, greyish-brown or tawny; basidiospores (5.8)–6.7–8.8(–9.8) × (5.8)–6.5–8.2(–9.6) µm, globose to subglobose, verrucose ornamented; cheilocystidia flexuous heteromorphic, often with apical papilla.

*Holotype*:—Russia. Primorsky Krai, Sikhote-Alin State Nature Biosphere Reserve, vicinity of Zimoveiny field reserve station, 45°08'20.90" N, 136°18'54.30" E, floodplain coniferous-broadleaved forest (with *Pinus koraiensis* and *Populus maximowiczii*), on a mossy, large fallen trunk of *Populus maximowiczii*, 20 Aug. 2024, V. Malysheva (LE F-354604). GenBank nrITS: PV468332; nrLSU: PV468334.

*Etymology*:—In honor of Vladimir Sokolov, Sikhote-Alin State Nature Biosphere Reserve staff member, for his invaluable help in organising mycological research in the Reserve and many years of work on preserving the unique nature of this region.

*Description*:—*Pileus* 10–15 mm, semicircular to flabelliform, plano-convex to applanate, laterally attached to the substrate with pseudostipe, with even and distinctly striate-sulcate margin; surface of pileus dry, not hygrophanous, slightly pruinose and tomentose along the margin and at the point of attachment to the substrate, dull ochre-brown, greyish-brown or tawny (Bamboo beige RAL 050 70 10, Amber grey RAL 050 70 20 or Medium brown RAL 050 60 30). *Lamellae* moderately crowded, ventricose, uniformly beige to cinnamon (Soft greige RAL 060 80 10, Peanut butter RAL 060 70 20), then spotted; lamellar edge minutely fimbriate, whitish. *Stipe* absent or rudimentary. *Spore print* yellowish brown (Camel brown RAL 060 50 40).

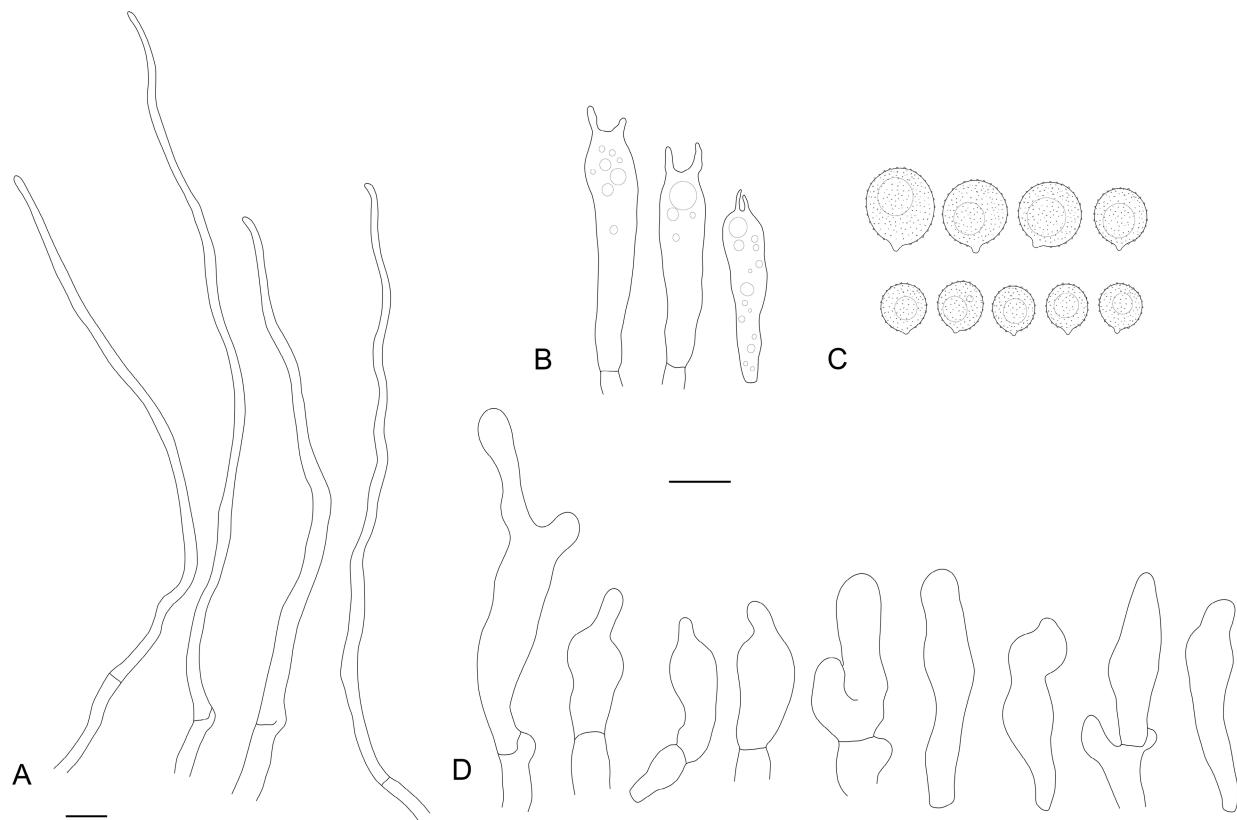
*Basidiospores* (5.8)–6.7–8.8(–9.8) × (5.8)–6.5–8.2(–9.6) µm (n = 100) ( $L_{av}$  = 7.6,  $W_{av}$  = 7.2, Q = 1.0–1.1(1.2);  $Q_{av}$  = 1.1), varying significantly in size even within a single basidioma, globose to subglobose, with a single, large, central oil drop, thick-walled, yellow-brown in KOH, verrucose ornamented (in light microscopy the spores appear punctate; under SEM warts irregular in shape and size, isolated or finely confluent). *Basidia* 27–38 × 8–9 µm, 2-spored, narrowly clavate. *Cheilocystidia* (21.6)–24.0–36.0(–50.5) × (5.5)–5.8–9.0(–10.0) µm, rather abundant, cylindrical, clavate, narrowly utriform, sometimes irregularly branched, with digitate projections, often apically constricted, flexuous, thin-walled. *Pleurocystidia* absent. *Pileal trama* composed of thin-walled, hyaline hyphae, 5.5–8 µm wide. *Pileipellis* a cutis, not-gelatinized, with tufts of erect to semi-erect undifferentiated, narrowly attenuated or filiform apical elements, up to 160 µm in length and 2.5–4 µm wide, thin-walled, hyaline. Clamps present in all tissues.



**FIGURE 2.** Fresh basidiomata and SEM-micrographs of basidiospores of the studied *Crepidotus* species. **A.** Basidiomata of *C. sokolovii* (LE F-354604, holotype). **B.** Basidiomata of *C. indicus* (LE F-354605). **C, E.** Basidiospores of *C. sokolovii* (from holotype). **D, F.** Basidiospores of *C. indicus*. Scale bars for **A–B** = 1 cm.

*Habitat and distribution*:—Solitary, on the bark of fallen, mossy trunks of *Populus*. Currently, only known in the Primorsky Krai, Russia.

*Additional collection examined*:—RUSSIA. Primorsky Krai, Sikhote-Alin State Nature Biosphere Reserve, vicinity of Zimoveiny field reserve station, 45°08'19.30" N, 136°18'33.70" E, floodplain coniferous-broadleaved forest (with *Pinus koraiensis*, *Salix cardiophylla* and *Populus maximowiczii*), on fallen trunk of *Populus maximowiczii*, 21 Aug. 2024, E. Malysheva (LE F-354625). GenBank nrITS: PV468331.



**FIGURE 3.** Microscopic features of *Crepidotus sokolovii* (LE F-354604, holotype). **A.** Terminal elements of pileipellis. **B.** Basidia. **C.** Basidiospores. **D.** Cheilocystidia. Scale bars: **A** = 10  $\mu\text{m}$ ; **B–D** = 10  $\mu\text{m}$ .

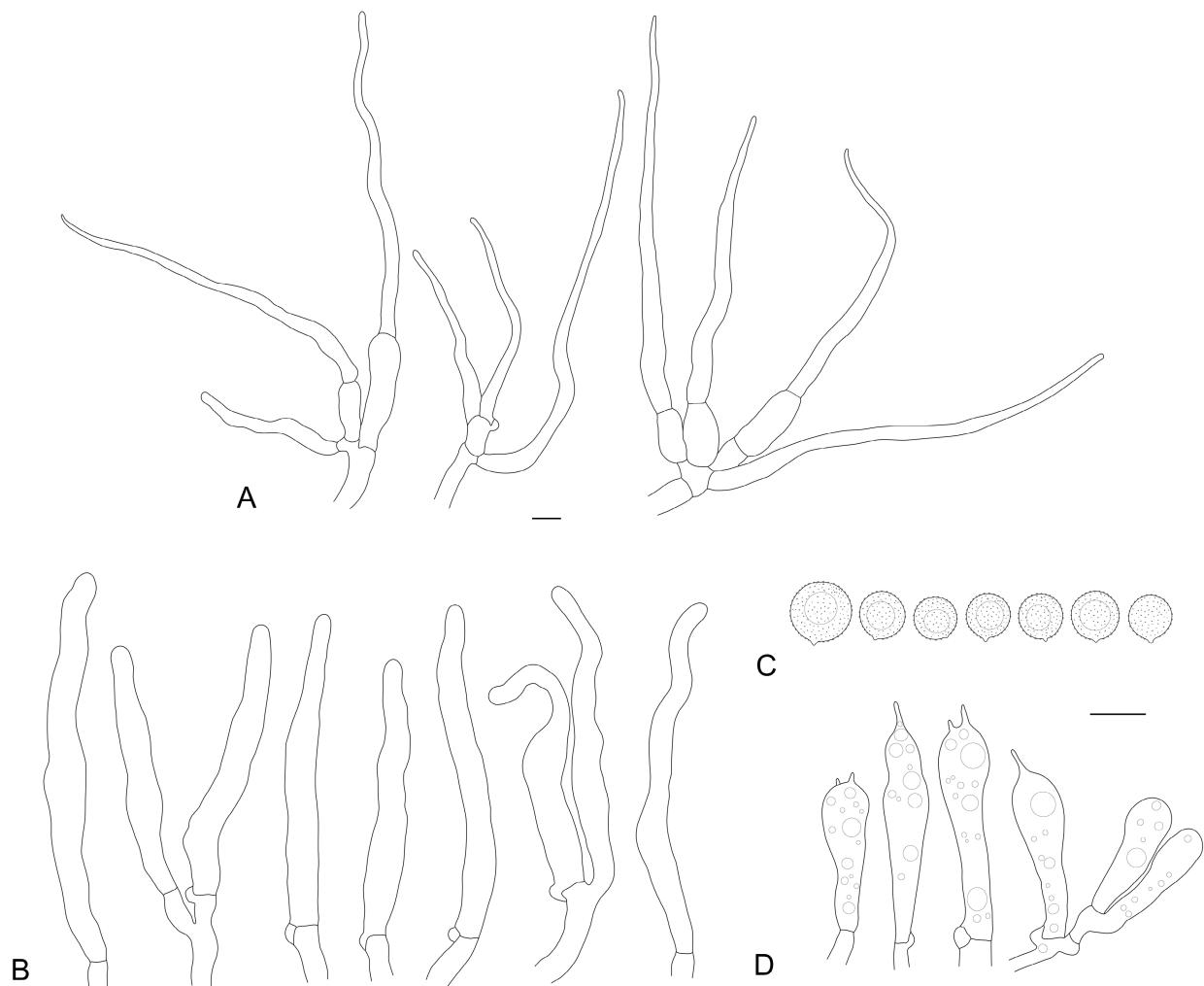
***Crepidotus indicus*** Manojk. & C.K. Pradeep, in Kumar, Vrinda & Pradeep, Cryptog. Mycol. 39(3): 290 (2018) (Figs. 2, 4)

*Pileus* 10–18 mm, semicircular to more or less flabelliform, convex when young, becoming plano-convex, some young basidiomata rather reniform, laterally attached to the substrate, with even, slightly involute margin, hygrophanous; surface of pileus dry, tomentose to pubescent, apricot to orange-pink (Mild orange RAL 060 80 30, Candle yellow RAL 060 70 40), darker on drying (Apricot brown RAL 050 60 40, Orange yellow RAL 050 60 50). *Lamellae* moderately crowded to distant, ventricose, uniformly beige to yellowish-brown (Ash yellow RAL 075 80 40, Apricot yellow RAL 070 80 40); lamellar edge concolorous, entire. *Stipe* absent or rudimentary, with white tomentum. *Spore print* yellowish brown (Peach yellow RAL 060 70 30).

*Basidiospores* (6.1–)6.7–7.8(–8.6)  $\times$  (5.7–)6.5–7.5(–8.3)  $\mu\text{m}$  ( $n = 90$ ) ( $L_{av} = 7.2$ ,  $W_{av} = 6.9$ ,  $Q = 1.0–1.1$ ;  $Q_{av} = 1.0$ ), globose, with a single, large, central oil drop, yellow-brown in KOH, verrucose ornamented (in light microscopy the spores appear punctate; under SEM warts conical, rounded or somewhat short-cylindrical, isolated, rarely confluent), thick-walled. *Basidia* 29–44  $\times$  6.5–8.5  $\mu\text{m}$ , 1- and 2-spored, narrowly clavate. *Cheilocystidia* (42.5–)44.5–66.5(–75.5)  $\times$  (4.5–)5.0–7.5(–8.4)  $\mu\text{m}$ , numerous, projecting above the hymenium, forming a somewhat dense, sterile layer on lamellae margin, flexuous, cylindrical or narrowly fusiform, hyaline, thin-walled, clamped. *Pleurocystidia* absent. *Pileal trama* composed of thin-walled, hyaline hyphae, 6–8  $\mu\text{m}$  wide. *Pileipellis* a trichoderm, composed of hyaline or yellowish, thin-walled hyphae; terminal elements (65–)71–126(–135)  $\times$  4–8  $\mu\text{m}$ , cylindrical or subulate and attenuated, straight or slightly flexuous, subterminal cells often short, ventricose, 10–15  $\mu\text{m}$  wide, thick-walled and somewhat incrusted. Clamps present in all tissues.

*Habitat and distribution:*—In small group, on fallen, mossy trunk of *Populus*. Currently, known from India, North America and Asian part of Russia.

*Collection examined:*—RUSSIA. Primorsky Krai, Sikhote-Alin State Nature Biosphere Reserve, vicinity of Zimoveiny field reserve station, 45°08'20.90" N, 136°18'54.30" E, floodplain coniferous-broadleaved forest (with *Pinus koraiensis* and *Populus maximowiczii*), on a mossy, large fallen trunk of *Populus maximowiczii*, 20 Aug. 2024, V. Malysheva (LE F-354605). GenBank nrITS: PV468333; nrLSU: PV468335.



**FIGURE 4.** Microscopic features of *Crepidotus indicus* (LE F-354605). **A.** Terminal elements of pileipellis. **B.** Cheilocystidia. **C.** Basidiospores. **D.** Basidia. Scale bars: **A** = 10 µm; **B–D** = 10 µm.

## Discussion

*Crepidotus sokolovii* is introduced here based on two collections, both found in the Central Sikhote-Alin of the Russian Far East in coniferous-broadleaved forest. The new species is characterized by small basidiomata with dull ochre-brown, greyish-brown or tawny pileus; globose basidiospores, ornamented by warts of significantly variable in size; flexuous cheilocystidia of variable shape, often with apical constriction, and numerous clamps in all tissues.

Morphological characteristics, such as brownish pileus, heteromorphic cheilocystidia and globose ornamented basidiospores reminds European *C. stenocystis* Pouzar (2005: 300) and North American *C. brunnescens* Hesler & A.H. Sm. (1965: 52). However, both species can be separated from *C. sokolovii* by smaller basidiospores ( $L_{av}$  = 6.1–6.2 µm,  $W_{av}$  = 5.8–6.1 µm) and the presence of numerous lageniform or narrowly clavate pileocystidia in pileipellis (Consiglio & Setti 2008, Jančovičová *et al.* 2017). In the phylogenetic tree, these species occupy a very distant position in relation to *C. sokolovii* (Fig. 1).

*Crepidotus ochraceus* Hesler & A.H. Sm. (1965: 26), North American species with ochraceous or dull yellow-brown pileus, differs from *C. sokolovii* mainly by its smooth ellipsoid basidiospores and lack of clamp connections (Hesler & Smith 1965).

*Crepidotus confertus* Hesler & A.H. Sm. (1965: 61) and *C. pallidobrunneus* Hesler & A.H. Sm. (1965: 64), originally described from Michigan and so far known only from the USA, both have relatively larger (1–6 mm) pileus, but significantly smaller basidiospores (4–6 µm) and ventricose or clavate, sometimes capitate, cheilocystidia (Hesler & Smith 1965).

The other morphologically comparable species with similar basidioma colouration, warty globose basidiospores and presence of clamp connections are *C. malachiodoides* Consiglio, Prydiuk & Setti (2008: 303) known from Europe and North America (<https://www.gbif.org/species/7612769>), *C. flavobrunneus* A.M. Kumar & C.K. Pradeep (2022: 318) recently described from India (Kumar *et al.* 2022), and *C. succineus* M.H. Han, L. Zou, Q. Na & Y.P. Ge (2024: 18), originally described from China (Han *et al.* 2024). *Crepidotus malachiodoides* can be distinguished from *C. sokolovii* by its unique hymenidermic pileipellis with capitate pileocystidia, and capitate cheilocystidia (Consiglio & Setti 2008, Jančovičová *et al.* 2014). *Crepidotus flavobrunneus* differs in velvety pileus, smaller basidiospores (5.6–6.4 × 5.6–6.4 µm) and broadly clavate cheilocystidia. *Crepidotus succineus* has smaller basidiospores (5.7–7.0 × 4.7–5.8 µm) and clavate pileocystidia.

Based on phylogenetic analyses, *C. sokolovii* is closely related to *C. sinuosus* Hesler & A.H. Sm. (1965: 66), originally described from the USA (Hesler & Smith 1965), and *C. ehrendorferi* Hauskn. & Krisai (1988: 183), originally described from Austria but currently known from Europe and North America (<https://www.gbif.org/species/5453264>). These species are also characterized by small to medium-sized basidiomata, pale orange, orange buff or ochraceous buff pileus, globose ornamented basidiospores, and flexuous, variable in shape cheilocystidia. *Crepidotus sinuosus* is distinguishable from *C. sokolovii* by its finally pubescent pileus, smaller basidiospores (5–7.5 µm), 4-spored basidia and larger cheilocystidia (Hesler & Smith 1965). *Crepidotus ehrendorferi* can be differentiated by 4-spored basidia and trichoderm pileipellis with rather short, cylindrical or narrowly fusiform terminal elements (Consiglio & Setti 2008, Ripková & Glejdura 2010).

Phylogenetically related species *C. indicus* differs from *C. sokolovii* in brightly coloured, apricot or orange pileus, longer cylindrical or narrowly fusiform cheilocystidia and pileipellis a trichoderm with shorted terminal elements (Kumar *et al.* 2018). The Far Eastern specimen of *C. indicus* studied by us corresponds well to the original description of the species, although it differs from it by the smaller size of the pileus and its brighter colouration, as well as slightly smaller basidiospores. The nrITS sequences of our specimen (LE F-354605) and the paratype specimen of *C. indicus* (TBGT15950) are almost identical (genetic distance less than 1%). The species was originally described from India (Kumar *et al.* 2018), but now several finds are known from the southern regions of the USA and Mexico (GBIF database data confirmed by voucher specimens, [https://www.gbif.org/occurrence/search?taxon\\_key=10820086](https://www.gbif.org/occurrence/search?taxon_key=10820086), accessed on 2 April 2025). Thus, the geographic range of the species, given our collection, appears to be quite extensive. It is likely that *C. indicus* is a warm-climate species and is confined mainly to tropical and subtropical climatic zones. The specimen we studied does not contradict this conclusion, as the Sikhote-Alin region exhibits subtropical influences, particularly in the eastern areas where it is part of the temperate monsoon zone.

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