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Infundibulicybe trachyspora, a New Species from Northeastern China Based on Morphology and Molecular Phylogeny

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Abstract

Infundibulicybe trachyspora is described as a new species from northeastern China. The species is characterized by clitocyboid to omphalioid habit, carneous, greyish-yellow to brownish pileus, brown to dark reddish-brown, longitudinally fibrillose-striate stipe, non-amyloid, non-smooth spores, the absence of cystidia and the presence of clamp connections. A comprehensive description of the species is provided together with photo-illustrations and comparisons with phenotypically similar and phylogenetically related species. The nuclear ribosomal internal transcribed spacer (ITS) region and the nuclear, large subunit rDNA (nrLSU) region of the new species was sequenced and analyzed. The phylogenetic analysis supported the novelty of the species and its placement within the genus. Furthermore, a discussion on the proposal to establish a new section is made, and a key is provided for the *Infundibulicybe* species reported from China.

Introduction

The genus *Infundibulicybe* Harmaja was initially proposed for *Clitocybe* sect. *Infundibuliformes* (Fr.) in the restricted delimitation used by Harmaja [1, 2]. The species of this genus are mainly characterized as slightly depressed to infundibuliform pileus, decurrent lamellae, smooth, inamyloid spores that are mostly lacrymoid in shape, abundant clamp connections and the lack of hymenial cystidia, and in particular, mycelia that cannot reduce nitrate and cyanophobic spore walls [2, 3]. Matheny et al. [4] recognized the genus in the Agaricales and as a sister group of the Tricholomatoid clade based on multilocus analysis of a six-gene region supermatrix was re-certified by Binder et al. [5]. Subsequently, Dentinger et al. proposed the suborder Tricholomatineae Aime, Dentinger & Gaya for four families, including *Infundibulicybe* species as "*Incertae sedis*" within it [6]. He et al. [7] also treated the genus as "*Incertae sedis*" suggesting it remained with an uncertain familial placement.

Recent molecular analysis has increased the accuracy of fungal identification and the accumulated sequence data also provide an advantage of promptly discovering new or rare species [8–11]. Presently, 26 species have been recognized in *Infundibulicybe* [2, 3, 12, 13]. In China, only 8 of those species have been identified (with some species under *Clitocybe*): *Infundibulicybe alkaliviolascens* (Bellù) Bellù, *I. altaica* (Singer) Harmaja (≡*Clitocybe altaica* Singer), *I. geotropa* (Bull.) Harmaja (=*Clitocybe geotropa* (Bull.) Quél.), *I. gibba* (Pers.) Harmaja [=*Clitocybe gibba* (Pers.) P. Kumm.], *I. hongyinpan* L. Fan & H. Liu, *I. rufa* Q. Zhao, K.D. Hyde, J.K. Liu & Y.J. Hao, *I. subsalmonea* (Lamoure) N. Schwab (≡*Clitocybe subsalmonea* Lamoure), *I. trulliformis* (Fr.) Gminder {=*Clitocybe trulliformis* (Fr.) P. Karst. [as '*trullaeformis*']} [12–18]. The present study describes a new species, *Infundibulicybe trachyspora*, from northeastern China based on morphology and molecular phylogenetic analyses and documents *Infundibulicybe* species reported in China.

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Materials and Methods

Sampling and Morphological Analysis

The basidiocarps were collected in Sep 2020 in the forests dominated by *Larix olgensis* of northeastern China (Jilin Province). Specimens were preserved and deposited in the Herbarium Mycology of Jilin Agricultural Science and Technology University (HMJU). Conventional macro-morphological characters and detailed anatomy of the specimens were recorded from fresh collections and photographic illustrations. Color names are given in parentheses according to the color chart by Kornerup and Wanscher [19]. For microscopic studies, sections of dried basidiocarps were rehydrated in 3% KOH, subsequently stained in Congo red solution, Melzer's reagent and Cotton blue, and then observed under an Olympus BX 53 (Tokyo, Japan) light microscope (Nikon, Tokyo, Japan) at either 40, 100, 400, 600, and 1000 magnifications. To evaluate the range of basidiospore size, 20 basidiospores each from one specimen of every collection were measured. The notation [n/m/p] indicates that measurements were made on "n" randomly selected spores from "m" basidiocarps of "p" collections. Q = the quotient of length and width in any one basidiospore; Qm = average of Q. The procedure for scanning electron microscopy followed that of Xu et al. [20], and an FEI Quanta 200FE-SEM (JEOL Ltd., Japan) was used at an accelerating voltage of 5–10 kV.

DNA Extraction, PCR and Sequencing

Genomic DNA was isolated from dried specimens using an M5 Fungal Genomic DNA Kit (Mei5 Biotechnology Co., Ltd, Beijing, China) according to the manufacturer's instructions. Polymerase chain reaction (PCR) and DNA sequencing were performed with the primers ITS1 and ITS4 [21] for the ITS region; LROR and LR7 [22] for the nrLSU region. The cycling parameters were as follows, ITS: 5 min at 94 ℃ for one cycle; 30 s at 94 ℃, 30 s at 53 ℃, 30 s at 72 ℃ for 33 cycles, 5 min at 72 ℃ for one cycle; nrLSU: 4 min at 94 ℃ for one cycle; 45 s at 94 ℃, 40 s at 46 ℃, 40 s at 72 ℃ for 30 cycles, 4 min at 72 ℃ for one cycle. The PCR amplification products were examined on a 1% agarose gel and checked by a JY 600 electrophoresis apparatus (Beijing JUNYI Electrophoresis Co., Ltd, Beijing, China). Sequencing was completed by BGI Co., Ltd, Beijing, China.

Phylogenetic Analyses

The newly generated sequences in this study were compared with the representative sequences in the GenBank database using the BLASTn algorithm. Since the accessible gene markers of *Infundibulicybe* species are limited in GenBank databases, this study mainly focuses on the ITS and nrLSU regions for phylogenetic analyses to obtain a representative topological structure. Based on the BLASTn results and outcomes of recent phylogenetic studies focused on *Infundibulicybe* [3, 12, 13, 18, 23–25], sequences were retrieved from GenBank databases, then were aligned automatically with MAFFT 7.0 [26] using '–auto' strategy and normal alignment mode. Aligned sequences were visually inspected and manually adjusted using MEGA 7.0. ModelFinder [27] determined the best-fitted substitution model using the Akaike information criterion (AIC). GTR + F + I + G4 was chosen as the best model for both ITS and ITS-LSU analyses. Phylogenetic analyses using Bayesian Inference (BI) analyses and Maximum Likelihood (ML) analyses were subsequently conducted on MrBayes 3.2.2 [28] and IQ-TREE [29], respectively. Four incrementally heated simultaneous Monte Carlo Markov Chains (MCMC) were run over 10 M generations for the BI analyses. Trees were sampled every 1000 generations resulting in a broad sampling of 10,001 trees. The first 2500 trees were discarded as burn-in (25%). For the ML analyses, statistical supports were obtained using nonparametric bootstrapping with 1000 replicates. The resulting consensus trees were visualized using FigTree 1.4.3 (http://tree.bio.ed.ac.uk/software/figtree/). The significance threshold was set at ≥ 0.90 for Bayesian posterior probability (PP) and ≥ 70% for ML bootstrap proportions (BP). All the sequences used in this study are listed in Table 1.

Results

Phylogenetic Analyses

The ITS data matrix comprised 49 sequences (including 41 from GenBank). This dataset was 860 bp long and contained 404 (47.0%) variable sites. The combined ITS-LSU dataset matrix comprised 33 sequences (including 26 from GenBank). Both BI and ML approaches resulted in the same tree topology, as such only the ML trees are shown with Bayesian PP values (left) and MLBP values (right) for each node (Figs. 1, 2). Phylogenetic analysis based on ITS and ITS-nrLSU sequences showed similar results, the new species grouped in the genus *Infundibulicybe* and represented a distinct monophyletic lineage.

Taxonomy

Infundibulicybe trachyspora J. Z. Xu, J. C. Qin & Yu Li, sp. nov.

Figures 3, 4, and 5.

Mycobank No. MB 842,075.

Table 1 Species list and DNA sequence information employed for phylogenetic analysis

Species	Collection	GenBank accession numbers		Location
		ITS	LSU	
Ampulloclitocybe clavipes	AFTOL-ID 542 / PBM 2474	AY789080	AY639881	–
Catathelasma ventricosum	AFTOL-ID 1488 / PBM 2403	DQ486686	DQ089012	Oregon, USA
Catathelasma imperiale	KM55154 / DAOM225247	GQ981498	AF261402	–
Cleistocybe vernalis	ADP 050,506 (WTU)	EF416917	EF416916	Washington, USA
Clitocybe dealbata	HC95cp3	AF357061	AF223175	–
C. metachroa	13,056; GLM 45,882	JF907806	AY207155	Italy; Germany
C. nebularis	CBS362.65	AF357063	AF223217	–
C. nebularis	AFTOL-ID 1495 / PBM 2259	DQ486691	DQ457658	Washington, USA
C. nebularis	MKACC 50,146; EL10_98	AY521248	AY586685	–
C. nebularis	Vrh2004	DQ149728	–	–
C. nebularis	BJTCFM405	MH581235	–	Shanxi Province, China
C. vibecina	839; GLM 45,888	JF907821	AY207160	–
Infundibulicybe alkaliviolascens	**HMJU509**	**MW880700**	**MW880706**	**Ningxia Hui Autonomous Region, China**
I. alkaliviolascen	HMAS 253,292	KT951209	–	Beijing, China
I. alkaliviolascen	HMAS 253,280	KT951212	–	Beijing, China
I. alkaliviolascen	HMAS 253,290	KT951210	–	Beijing, China
I. alkaliviolascen	HMAS 253,286	KT951211	–	Beijing, China
I. alkaliviolascen	HMAS 253,294	KT951208	–	Beijing, China
I. catinus	I	HM631720	–	Linthal, France
I. gibba	AFTOL-ID 1508 / JCS 0704B	DQ490635	DQ457682	Massachusetts, USA
I. gibba	BJTCFM099	MH581237	–	Shanxi Province, China
I. gibba	ASIS22667	KF668320	–	–
I. gibba	ASIS22552	KF668316	–	–
I. gibba	TENN61223	FJ596815	–	Tennessee, USA
I. gibba	MLS052	GU188436	–	USA
I. gibba	L	HM631721	–	Dimaro, Italy
I. gibba	C	HM631714	–	Magnola, Italy
I. gibba	B	HM631713	–	Stava, Italy
I. gibba	A	HM631712	–	Monte Venere, Italy
I. gibba	NBRC30524	AB301608	–	Japan
I. gibba	**HMJU356**	**MW880697**	**MW880703**	**Liaoning Province, China**
I. gibba	**HMJU393**	**MW880698**	**MW880704**	**Liaoning Province, China**
I. gibba	**HMJU505**	**MW880699**	**MW880705**	**Liaoning Province, China**
I. geotropa	ALV4344	KT122792	KT122793	–
I. hongyinpan	BJTCFM187	MH581239	–	Shanxi Province, China
I. hongyinpan	BJTCFM216	MH581240	–	Shanxi Province, China
I. hongyinpan	BJTCFM392	MH581238	–	Shanxi Province, China
I. kotanensis	LAH35902	MN017278	–	Khyber Pakhtunkhwa Province, Pakistan
I. kotanensis	LAH35902	MN017274	–	Khyber Pakhtunkhwa Province, Pakistan
I. mediterranea	C	HM631724	–	Magnola, Italy
I. rufa	HKAS83492	KX239810	–	Sichuan Province, China
I. rufa	HKAS82911	KX239809	–	Sichuan Province, China
I. rufa	HKAS87760	KX239808	–	Sichuan Province, China
I. rufa	HKAS87727	KX239807	–	Sichuan Province, China
I. rufa	HKAS87741	KX239806	–	Sichuan Province, China
I. trachyspora	**HMJU744**	**MW736885**	**MW880692**	**Jilin Province, China**
I. trachyspora	**HMJU758**	**MW913424**	**–**	**Jilin Province, China**
I. trachyspora	**HMJU850**	**MW880701**	**MW880707**	**Jilin Province, China**

Table 1 (continued)

Species	Collection	GenBank accession numbers		Location
		ITS	LSU	
I. trachyspora	**HMJU851**	**MW880702**	**MW880708**	**Jilin Province, China**
Musumecia bettlachensis	TO-HG2284	JF926520	JF926521	Alsace, France
Mycena galericulata	AFTOL-ID 727 / PBM2407	DQ404392	AY647216	–
Mycena plumbea	AFTOL-ID 1631 / PBM 2718	DQ494677	DQ470813	–
Paralepistopsis amoenolens	TO AV2004	JQ585653	JQ585654	France
Pseudoclitocybe cyathiformis	TO-HG2285	JF926522	JF926523	Tuscany, Italy
Pseudoclitocybe cyathiformis	LE258346	HM191730	–	Russia
Pseudoclitocybe expallens	TO-HG2286	JF926524	JF926525	Tuscany, Italy
Singerocybe adirondackensis	H.E. Bigelow18199	HQ902912	HQ902914	Arizona, USA
Singerocybe adirondackensis	H.E. Bigelow18252	JX514121	HQ902915	Arizona, USA
Singerocybe alboinfundibuliformis	HKAS 73,150	JX514127	JX514109	Yunnan Province, China
Singerocybe alboinfundibuliformis	HKAS 73,262	JX514126	HQ902915	Yunnan Province, China
Singerocybe phaeophthalma	TO-HG1147	FM877684	–	Friuli Venezia Giulia, Italy
Singerocybe umbilicata	HKAS 77,290	KF208450	–	Yunnan Province, China
Trichocybe puberula	TO-HG1148	FM877683	FM877680	Ettingen, Switzerland
Trichocybe puberula	L 0,053,903	FM877682	FM877681	Vauclusotte, France
Tricholoma aestuans	AFTOL-ID 497 / PBM 2494	DQ494699	AY700197	Massachusetts, USA
Tricholoma saponaceum	AFTOL-ID 672 / PBM 2514	DQ494700	AY647209	–

The newly generated sequences are given in bold

Type China, Jilin Province, Jilin City, Zuojia Town, (44°3′55″ N, 126°6′8″ E, elevation 349 m), on the ground under mixed forests dominated by *Larix olgensis* Henry, 1 Sep 2020, J.Z. Xu (holotype, HMJU 744, Genbank accession numbers: ITS, MW736885; LSU, MW880692; RPB1, OL677427; RPB2, OL677428).

Etymology The epithet derives from the non-smooth spores.

Diagnosis Distinguished by the clitocyboid to omphalioid habit, a carneous, greyish-yellow to brownish pileus, a brown to dark reddish-brown, longitudinally fibrillose-striate stipe, non-amyloid, non-smooth spores and the presence of clamp connections.

Description Basidiocarp clitocyboid to subomphalioid. Pileus 4.5–8 cm diam., at first plane to slightly depressed in the center, finally subinfundibuliform to umbilicate, sagging at the margin, carneous (3B3) then greyish-yellow to brownish (4B3), and dark brown (6D5) at the center. Surface dry, smooth, glabrous, some with a ring stripe, slightly appearing hygrophanous when water-soaked. Margin always involute, irregular, eroded. Lamellae decurrent, up to 0.3 cm broad, dark cream to yellowish-white (1A2, 1A3), moderately crowded, with lamellulae of 1 or 3 lengths, edges concolorous, entire. Stipe 3.5–7 × 0.5–0.75 cm, cylindrical, concolorous with the center of pileus or slightly lighter, brown to dark reddish-brown (6D5, 7E8), solid, some slightly twisty, surface with fibrous longitudinal stripes.

Basidiospores [60/6/3] 6.5–8.1(8.5) × (3.6)3.8–4.4(4.7) µm, Q = (1.69)1.71–1.87(1.95), Qm = 1.78, cyanophilous, lacrymoid to shortly ellipsoid, apiculate, non-amyloid, surface non-smooth under a light microscope, hyaline. Basidia (20.7)21.5–29.3(33.2) × (4.4)4.7–5.9 µm, subclavate to clavate, hyaline, infertility numerous, 4-spored, sterigmata up to 3.5 µm long. Hymenial cystidia absent. Hymenophoral trama regular to subregular, consisting of parallel, cylindrical to clavate, thin-walled hyphae, hyphae 3.1–9.6 µm wide. Pileipellis as a cutis composed of repent, cylindrical, subparallel, septate, thin-walled hyphae, hyphae 3.9–11.0 µm wide. Stipitipellis similar to the pileipellis. Clamp connections are present.

Habitat Scattered on the ground under mixed forests dominated by *Larix olgensis*.

Distribution Currently, only known from northeastern China (Jilin Province).

Additional specimen examined China, Jilin Province, Jilin City, Zuojia Town, on the ground under mixed forests dominated by *Larix olgensis*, 1 Sep 2020, J.Z. Xu, HMJU 850, GenBank accession numbers: ITS, MW880701; LSU, MW880707; same location, 1 Sep 2020, J.Z. Xu, HMJU 851, Genbank accession numbers: ITS, MW880702; LSU,

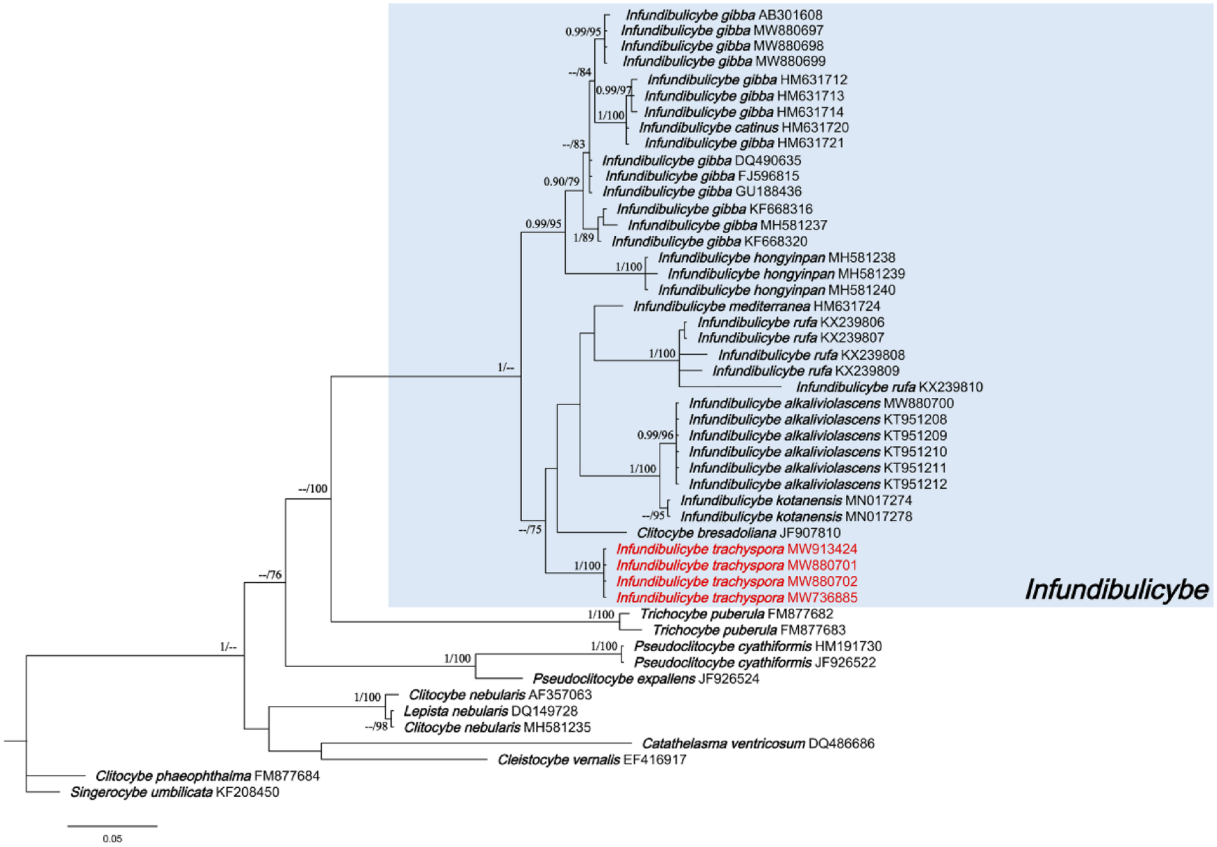

Fig. 1 50% majority rule Bayesian phylogenetic analysis of *Infundibulicybe* based on ITS sequences, with *Singerocybe* species as outgroup taxa. Nodes were annotated if supported by ≥ 0.90 Bayesian PP (left) or ≥ 70% ML BP (right) values. For each sequenced taxon, the Genbank number is given. The new species are in red (Color figure online)

MW880708; same location, 1 Sep 2020, J.Z. Xu, HMJU 758, Genbank accession numbers: ITS, MW913424.

Notes Infundibulicybe trachyspora, characterized by the clitocyboid to subomphalioid habit, a carneous, greyish-yellow to brownish pileus, moderately crowded, narrow lamellae, a brown to dark reddish-brown, longitudinally fibrillose-striated stipe, cyanophilous, non- amyloid and smooth spores and the presence of clamp connections. Morphologically, *I. trachyspora* shares similarities with *Infundibulicybe gigas* (Harmaja) Harmaja in crowed and narrow lamellae and lacrymoid to short ellipsoid spores. But *I. gigas* showed bigger size in pileus and stipe as compared in *I. trachyspora* (*I. gigas*, pileus diameter 9–28 cm, stipe 4–11 × 1.2–3.8 cm; *I. trachyspora*, pileus diameter 9–28 cm, stipe 3.5–7 × 0.5–0.75 cm) [2, 30]. *Infundibulicybe lapponica* resembles *I. trachyspora* having a medium-sized pileus, but it differs in the minutely scaly to the areolate surface of the pileus, which is smooth in *I. trachyspora* [1]. The new species recently described from China, *I. rufa*, resembles *I. trachyspora* in the smooth pileus and the longitudinally striated stipe. However, *I. rufa* produces a reddish pileus and stipe, *I. trachyspora* has a carneous, greyish-yellow to brownish pileus and a brown to dark reddish-brown stipe, *I. rufa* shows ixocutis hyphae in pileipellis, but *I. trachyspora* shows cutis hyphae. In addition, *I. rufa* differs from *I. trachyspora* by the incurved, wavy to undulate pileus margin (appeared to the species *I. kotanensis* M. Ishaq, M. Fiaz & A.N. Khalid, also described from Pakistan) [12, 25]. *Infundibulicybe hongyinpan* is also a new species from China growing on the ground under mixed forests dominated by *Larix olgensis* in autumn, just like *I. trachyspora*. But the pileus color of *I. hongyinpan* is reddish-brown, of *I. trachyspora* is calcareous, greyish-yellow to brownish. There is a more remarkable feature that *I. trachyspora* produces non-smooth spores absent in all *Infundibulicybe* species.

Discussion

The Status of *Infundibulicybe trachyspora*

Based on morphology and phylogenetic analyses, *I. trachyspora* was maintained as a new taxon in the genus *Infundibulicybe*. In ITS and combined ITS-nrLSU phylogenetic

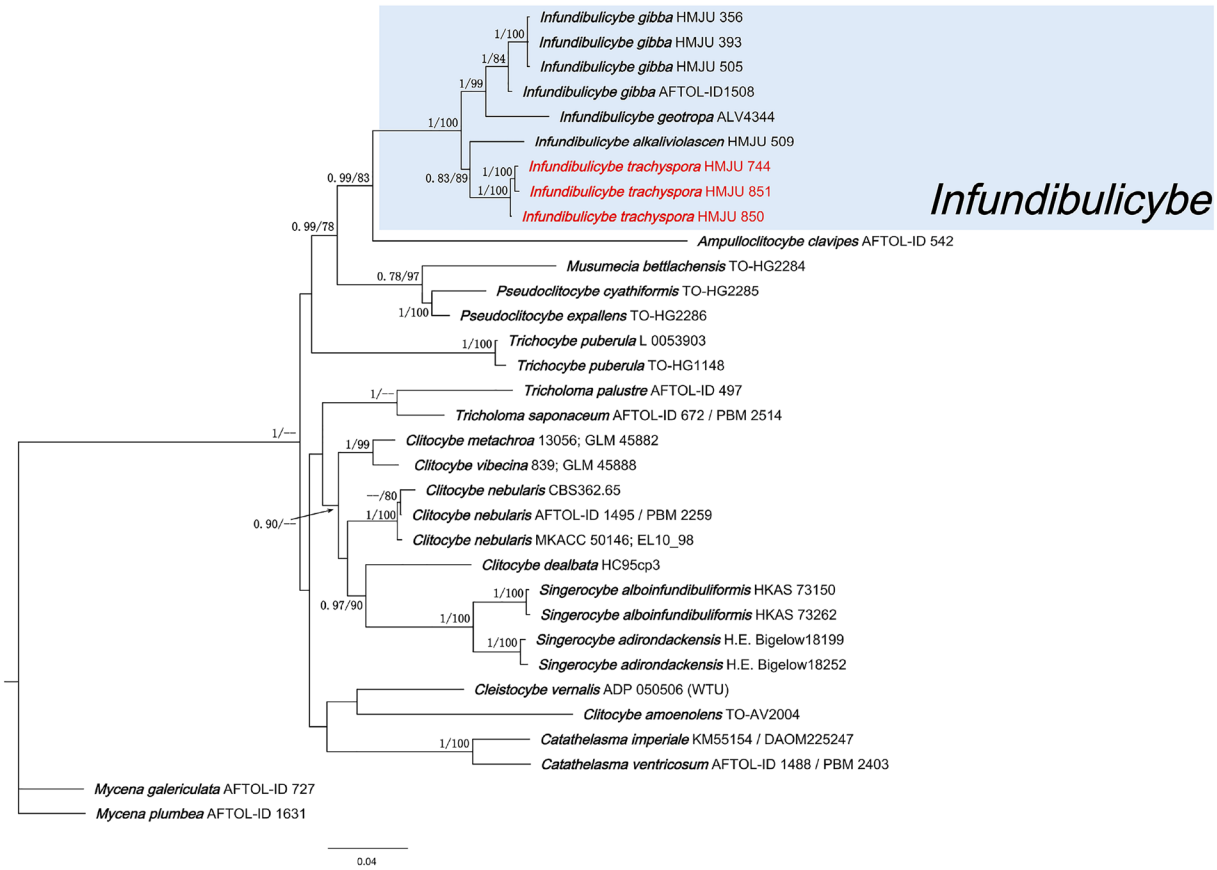

Fig. 2 50% majority rule Bayesian phylogenetic analysis of *Infundibulicybe* based on ITS-nrLSU sequences, with *Mycena* species as outgroup taxa. Nodes were annotated if supported by ≥ 0.90 Bayesian PP (left) or ≥ 70% ML BP (right) values. For each sequenced taxon, the collection number/Specimen voucher number is given. The new species are in red (Color figure online)

Fig. 3 Habitat and basidiocarps of *Infundibulicybe trachyspora* (HMJU 744, holotype)

analyses, *Infundibulicybe* group showed close relationships with *Ampulloclitocybe clavipes* (Pers.) Redhead, Lutzoni, Moncalvo & Vilgalys and *Trichocybe puberula* (Kuyper) Vizzini, which is consistent with previous studies [12, 23–25]. *Ampulloclitocybe clavipes* and *I. trachyspora* both have non-smooth spores and lack cystidia. However, *A. clavipes* produces bulbose-base stipe, *I. trachyspora* produces cylindrical stipe [31]. *Trichocybe puberula* and *I. trachyspora* share the same characteristics in the presence of clamp connections, but *T. puberula* differs from *I. trachyspora* by having cystidia and smooth spores [32].

So far, this genus has no subdivisions and there is no established opinion on the infrageneric classification of *Infundibulicybe*. Meanwhile, the non-smooth spores and the distance of *I. trachyspora* from the other *Infundibulicybe* species suggested that the non-smooth spored species may deserve its section. Additional specimens from different areas are needed to evaluate the status of *I. trachyspora* and reveal the infrageneric classification of *Infundibulicybe*.

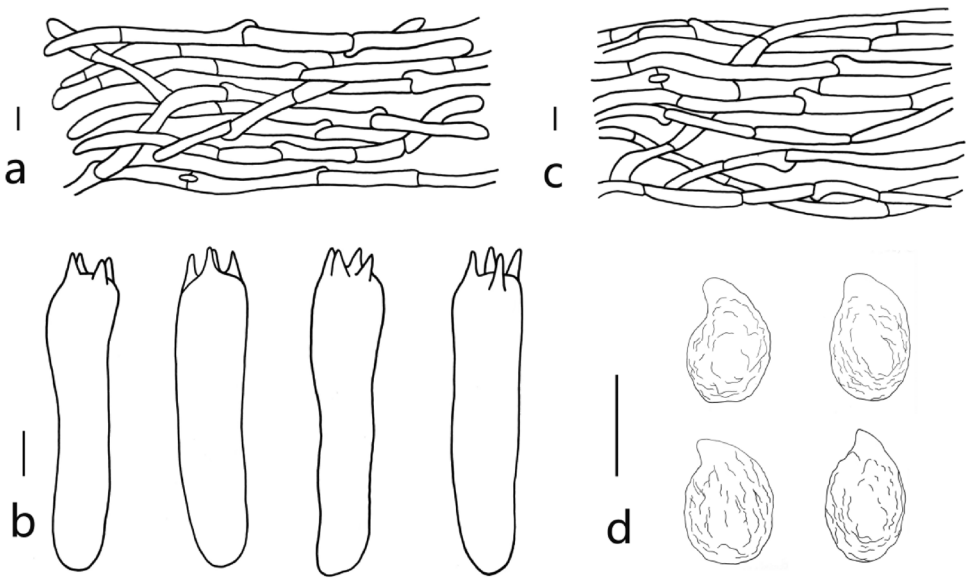

Fig. 4 Microscopic characteristics of *Infundibulicybe trachyspora* (HMJU 744, holotype). **a** Pileipellis. **b** Stipitipellis. **c** Basidia. **d** Basidiospores. Bars: **a**, **b** 10 µm; **c**, **d** 5 µm

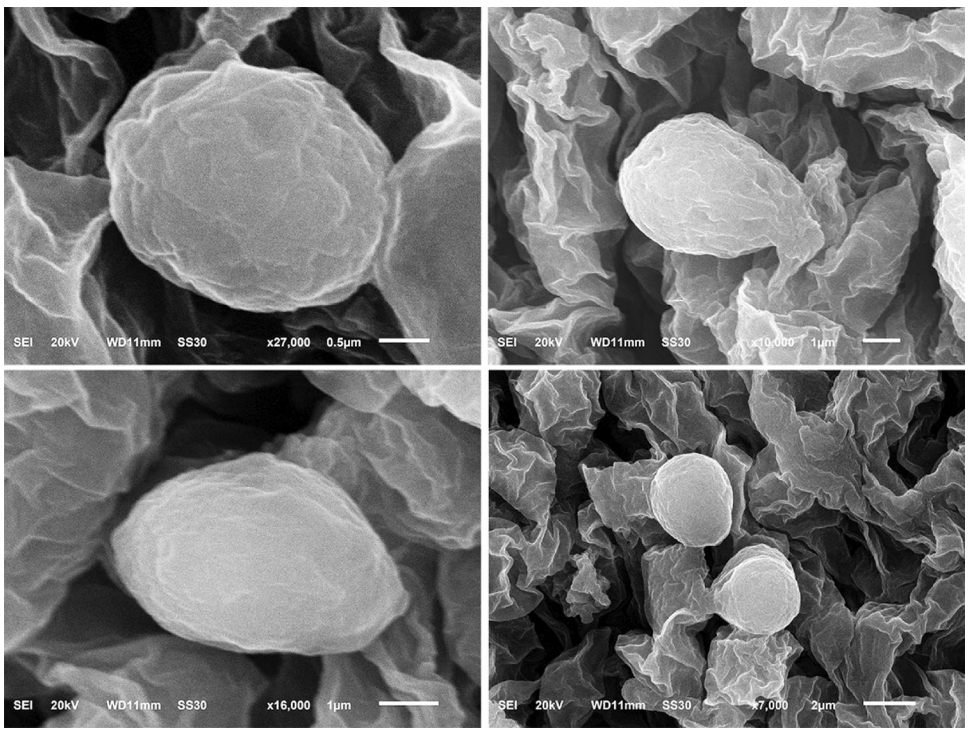

Fig. 5 Scanning electron microscope images of basidiospores of *Infundibulicybe trachyspora* (HMJU 744, holotype)

Key to Chinese Species of *Infundibulicybe*

1a. The color of pileus is red-brown……0.2
1b. The color of pileus is not red-brown……3.
2a. Pileus hygrophanous…….. *I. hongyinpan.*
2b. Pileus not hygrophanous…….. *I. rufa.*
3a. Pileus surface smooth…….. *I. trachyspora.*
3b. Pileus surface not smooth……0.4
4a. The base of stipe with a few rhizoids…….. *I. trullaeformis.*
4b. The base of stipe without rhizoids……5.
5a. Cystidia present…….. *I. altaica.*
5b. Cystidia absent……6.
6a. Stipe diameter > 2 cm ……*I. geotropa.*
6b. Stipe diameter < 2 cm……0.7
7a. Stipe fibrillose…….. *I. alkaliviolascens.*
7b. Stipe not fibrillose…….. *I. subsalmonea.*

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