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Lepiota condylospora, a new species with nodulose spores in section *Lilaceae* from northern Thailand

PHONGEUN SYSOUPHANTHONG^{1,2,3,8}, NARITSADA THONGKLANG^{1,2,9*}, SAMANTHA C. KARUNARATHNA^{4,6,10}, PETER E. MORTIMER^{4,6,11}, KEVIN D. HYDE^{2,7,12} & ELSE C. VELLINGA^{5,13}

¹Center of Excellence in Fungal Research, Mae Fah Luang University, Chiang Rai 57100, Thailand.

²School of Science, Mae Fah Luang University, Chiang Rai 57100, Thailand.

³Ecology Division, Biotechnology and Ecology Institute, Ministry of Science and Technology, P.O.Box: 2279, Vientiane Capital, Laos.

⁴Key Laboratory for Plant Diversity and Biogeography of East Asia, Kunming Institute of Botany, Chinese Academy of Sciences, Kunming 65201, China.

⁵Department of Plant and Microbial Biology, University of California at Berkeley, Berkeley, CA 94720–3102, USA.

⁶Centre for Mountain Futures, Kunming Institute of Botany, Chinese Academy of Sciences, Kunming 650201, China.

⁷Institute of Plant Health, Zhongkai University of Agriculture and Engineering, Haizhu Campus, Guangzhou 510225, China.

⁸✉ laofungi@gmail.com; <https://orcid.org/0000-0002-1275-2459>

⁹✉ fah_naritsada@hotmail.com; <http://orcid.org/0000-0001-9337-5001>

¹⁰✉ samanthakarunarathna@gmail.com; <https://orcid.org/0000-0001-7080-0781>

¹¹✉ petermortimer@mac.com; <https://orcid.org/0000-0003-3188-9327>

¹²✉ kdhyde3@gmail.com; <https://orcid.org/0000-0002-2191-0762>

¹³✉ ecvellinga@comcast.net; <https://orcid.org/0000-0003-4171-0554>

*Corresponding author: ✉ fah_naritsada@hotmail.com

Abstract

During our studies of the genus *Lepiota* in northern Thailand we collected a putatively new species with a distinct morphology and ITS nrDNA profile from Chiang Mai Province. The new species, *Lepiota condylospora*, is characterized by the presence of reddish brown to brownish orange or brown squamules on the pileus surface, triangular basidiospores with two lateral knobs, and a hymenidermal pileipellis composed of broadly to narrowly clavate elements. Two genetically distinct species of *Lepiota* section *Lilaceae* having triangular spores with two lateral knobs are compared with *L. condylospora*: *Lepiota fraterna*, from Papua New Guinea, differs in having larger basidiospores and cheilocystidia; while *L. cristata* var. *macrospora*, from China, has bigger basidiomata. A full description, color photographs, line drawings and a phylogenetic tree to show the position of the new species are provided.

Keywords: Agaricaceae, hymeniderm, lepiotaceous fungi, phylogeny, taxonomy

Introduction

The macrofungi in northern Thailand are extremely diverse with numerous new taxa being discovered (Zhao *et al.* 2016, Chen *et al.* 2017, Hyde *et al.* 2018). This paper deals with a putatively new species of the genus *Lepiota* (Pers.) Gray (1821: 1) sect. *Lilaceae* M. Bon (1981: 11) from Chiang Mai (Thailand). Species in this section are characterized by a hymenidermal pileipellis made up of tightly packed clavate to narrowly clavate elements and subglobose to ellipsoid or spurred basidiospores (Bon 1981). Section *Lilaceae* is clearly different from the other five sections of *Lepiota* based on morphological and molecular data (Vellinga 2001a, Vellinga 2003). However, some species were placed in other sections of *Lepiota* because of their spurred spores (Bon 1981, Horak 1981, Candusso & Lanzoni 1990). Vellinga and Huijser (1998), and Vellinga (2001a, 2010) discussed the history of section *Lilaceae* and gave an overview of European and western North American species. Liang *et al.* (2009) investigated the species with spurred spores related to *Lepiota cristata* (Bolton) P. Kumm. (1871: 137) in China, using DNA sequences from three gene regions, *viz.*, ITS and IGS nrDNA as well as mtSSU rDNA. These authors showed that *L. fraterna* var. *macrospora* Zhu L. Yang (1984: 124), a species with lateral knobs on the spores, was actually related to the clade of *L. cristata*, while

another morphologically very similar variant with spurred spores lacking lateral knobs, was not. This taxon was later described as *L. cristatanea* J.F. Liang & Zhu L. Yang (2011: 116).

A few species of *Lepiota* have been reported from the tropical forests of Thailand (Soytong 1994, Chandrasrikul 1996, Ruksawong & Flegel 2001, Chandrasrikul *et al.* 2008), although their micromorphological features have not been investigated in detail. Advanced studies of *Lepiota* in Thailand incorporating molecular evidence were later carried out by Sysouphanthong *et al.* (2011, 2012, 2016), Tibpromma *et al.* (2017), and Hyde *et al.* (2020). So far, *L. cristata* is the only species in section *Lilaceae* reported from Thailand (Soytong 1994, Chandrasrikul *et al.* 2011, Sysouphanthong *et al.* 2013). However, although there are species of *Lepiota* resembling *L. cristata* with spurred spores thought to occur in northern Thailand the taxonomy was based on morphology alone (Soytong 1994). In the present work, the taxonomic status of new collections resembling *L. cristata* having spurred spores with lateral knobs is re-evaluated with the aid of morphological and molecular data.

Materials and methods

Collecting and material examination

All samples were collected in deciduous forests of Chiang Mai Province (Northern Thailand). After collection, specimens were brought to the laboratory at the Mushroom Research Center (Chiang Mai, Thailand), and studied macro- and microscopically. The specimens were dried in a hot air dryer (30–40 °C) for 24 hours, and deposited in the herbarium of Mae Fah Luang University (MFLU, Thailand). Colour features were described comparing fresh material with the colour charts of Kornerup and Wanscher (1978). Terminology followed Vellinga (2001b). Microscopical characteristics were measured and illustrated from dry specimens, using a drawing tube attached to an Olympus CX-41 microscope. Water and 2.5–10% KOH were used as mounting media to study colour features; spores were examined in Melzer's reagent, Cotton Blue and Cresyl Blue, and structures were drawn from mounts in ammoniacal Congo Red. 25 spores were measured in side-view from each basidioma of each collection. The notation [75,3,3] indicates that measurements were made on 75 spores from three samples from three collections. The following abbreviations are used: l for length, w for width, avl for average length, avw for average width, Q for quotient of length and width and avQ for average quotient.

Phylogenetic study

DNA was extracted from dried herbarium collections using Biospin Fungus Genomic DNA Extraction Kit (Bioer Technology Co., Hangzhou, China) following the manufacturer's protocols. Primers ITS1F and ITS4 (White *et al.* 1990, Gardes & Bruns 1993) were used to amplify the ITS nrDNA region by PCR. The PCR-amplified products were purified and sequenced by the Shanghai Sangon Biological Engineering Technology & Services Co. (Shanghai, China). The sequences were edited and contigs assembled using Sequencher 4.2.2 (Gene Codes Corporation, Ann Arbor, MI, USA). Finally, the edited ITS nrDNA sequences were deposited in GenBank.

A BLAST search (Altschul *et al.* 1990) revealed that the specimens analyzed are related to the monophyletic clade where *Lepiota cristata* nests, which includes all species with spurred spores and a hymenidermal pileus covering. Sequences of 76 specimens from 4 distinct species in this group were therefore retrieved from GenBank (JN224822–JN224823). A sequence of *Lepiota aspera* (Pers.) Qué. (1886: 5) was used as the outgroup (Table 1) because the species is in another section (*Echinatae*). The final dataset including 79 sequences was first aligned using MAFFT (Kato *et al.* 2002, Kato and Toh 2008) and minimally adjusted after that. A maximum parsimony (MP) heuristic search was performed in PAUP* 4.0 b10 (Swofford 2002), setting 1000 heuristic searches, TBR branch swapping and random sequence addition. Other settings were as follows: gaps were treated as missing; all characters are of type unordered and all equally weighted; multistate taxa are interpreted as uncertain; starting trees were obtained via stepwise addition; one tree was held at each step during stepwise addition; the steepest descent option was not in effect; branches were collapsed (creating polytomies) if minimum branch length was zero, and MulTrees option was in effect. Bootstrap support (BS) values were calculated using 1000 bootstrap replicates with 10 heuristic searches per replicate, random sequence addition and TBR branch swapping. A maximum likelihood (ML) analysis was performed with RAxML (Stamatakis *et al.* 2008). All free model parameters were estimated by RAxML using a general time-

reversible (GTR) substitution matrix and a proportion of invariable sites estimate. One hundred rapid ML bootstrap analyses were performed.

TABLE 1. ITS nrDNA sequences and their GenBank accession numbers used for the phylogenetic analyses.

Species	Locality	Herbarium and collection number	ITS GenBank accession number	References
<i>Lepiota aspera</i>	Netherlands	L-ecv 2233	AY176354	Vellinga (2004)
<i>L. castaneidisca</i>	USA	UC-ecv 2591	AF391054	Vellinga (2001a)
<i>L. castaneidisca</i>	USA	UC-ecv 2594	AF391055	Vellinga (2001a)
<i>L. castaneidisca</i>	USA	UC-ecv 2599	AF391056	Vellinga (2001a)
<i>L. castaneidisca</i>	USA	UC-ecv 2300	AF391057	Vellinga (2001a)
<i>L. castaneidisca</i>	USA	UC-ecv 2308	AF391058	Vellinga (2001a)
<i>L. castaneidisca</i>	USA	UC-ecv 2309	AF391059	Vellinga (2001a)
<i>L. castaneidisca</i>	USA	UC-ecv 2311	AF391060	Vellinga (2001a)
<i>L. castaneidisca</i>	USA	UC-ecv 2312	AF391061	Vellinga (2001a)
<i>L. castaneidisca</i>	USA	UC-ecv 2395	AF391062	Vellinga (2001a)
<i>L. castaneidisca</i>	USA	UC-ecv 2411	AF391063	Vellinga (2001a)
<i>L. castaneidisca</i>	USA	UC-ecv 2410	AF391064	Vellinga (2001a)
<i>L. castaneidisca</i>	USA	UC-ecv 2516	AF391065	Vellinga (2001a)
<i>L. condylospora</i>	Thailand	MFLU 09-0048	JN224822	This study
<i>L. condylospora</i>	Thailand	MFLU 09-0173	JN224823	This study
<i>L. cristata</i>	USA	UC-ecv 2780	GQ203806	Vellinga (2010)
<i>L. cristata</i>	USA	UC-ecv 2747	GQ203814	Vellinga (2010)
<i>L. cristata</i>	USA	UC-ecv 2750	GQ203815	Vellinga (2010)
<i>L. cristata</i>	USA	DUKE 1582	LCU85327	Johnson (1999)
<i>L. cristata</i>	China	HKAS 45492	EU081935	Liang & Yang (2009)
<i>L. cristata</i>	China	HKAS 5800	EU081936	Liang & Yang (2009)
<i>L. cristata</i>	China	HKAS 49258	EU081937	Liang & Yang (2009)
<i>L. cristata</i>	China	HKAS 49160	EU081938	Liang & Yang (2009)
<i>L. cristata</i>	China	HKAS 46370	EU081939	Liang & Yang (2009)
<i>L. cristata</i>	China	HKAS 46153	EU081940	Liang & Yang (2009)
<i>L. cristata</i>	China	HKAS 45651	EU081941	Liang & Yang (2009)
<i>L. cristata</i>	China	HKAS 49292	EU081942	Liang & Yang (2009)
<i>L. cristata</i>	China	HKAS 46345	EU081943	Liang & Yang (2009)
<i>L. cristata</i>	China	HKAS 46333	EU081944	Liang & Yang (2009)
<i>L. cristata</i>	China	HKAS 45830	EU081946	Liang & Yang (2009)
<i>L. cristata</i>	China	HKAS 46344	EU081947	Liang & Yang (2009)
<i>L. cristata</i>	China	HKAS 45928	EU081950	Liang & Yang (2009)
<i>L. cristata</i>	China	HKAS 50915	EU081953	Liang & Yang (2009)
<i>L. cristata</i>	China	KKAS 49286	EU081955	Liang & Yang (2009)
<i>L. cristata</i>	China	HKAS 45975	EU081956	Liang & Yang (2009)
<i>L. cristata</i>	China	HKAS 46348	EU081957	Liang & Yang (2009)
<i>L. cristata</i>	China	HKAS 7547	EU081958	Liang & Yang (2009)
<i>L. cristata</i>	China	HKAS 49367	EU081960	Liang & Yang (2009)
<i>L. cristata</i>	China	HKAS 11366	EU081961	Liang & Yang (2009)
<i>L. cristata</i>	China	HMJAU 1029	EU081962	Liang & Yang (2009)

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TABLE 1. (Continued)

Species	Locality	Herbarium and collection number	ITS GenBank accession number	References
<i>L. cristata</i>	China	HMJAU 0822	EU081963	Liang & Yang (2009)
<i>L. cristata</i>	China	HKAS 46103	EU081965	Liang & Yang (2009)
<i>L. cristata</i>	China	HKAS 45791	EU081966	Liang & Yang (2009)
<i>L. cristata</i>	China	HKAS 46360	EU081967	Liang & Yang (2009)
<i>L. cristata</i>	China	HMJAU 1135	EU081968	Liang & Yang (2009)
<i>L. cristata</i>	China	HKAS 45662	EU081969	Liang & Yang (2009)
<i>L. cristata</i>	China	HKAS 46349	EU081971	Liang & Yang (2009)
<i>L. cristata</i>	China	HMJAU 3430	EU081972	Liang & Yang (2009)
<i>L. cristata</i>	China	HKAS 48786	EU081973	Liang & Yang (2009)
<i>L. cristata</i>	China	HKAS 11210	EU081974	Liang & Yang (2009)
<i>L. cristata</i>	China	RITF 312	EU826492	Liang & Yang (2009)
<i>L. cristata</i>	China	RITF 314	EU826493	Liang & Yang (2009)
<i>L. cristata</i>	Luxembourg	L-ecv 1445	AF391027	Vellinga (2001c)
<i>L. cristata</i>	USA	UC-ecv 2452	AF391040	Vellinga (2001a)
<i>L. cristata</i>	USA	UC-ecv 2449	AF391041	Vellinga (2001a)
<i>L. cristata</i>	Netherlands	L-hah 22IX1993	AF391042	Vellinga (2001a)
<i>L. cristata</i>	Netherlands	L-hah 20IX1989	AF391043	Vellinga (2001a)
<i>L. cristata</i>	China	HKAS 32250	AF391044	Vellinga (2001a)
<i>L. cristata</i>	USA	UC-ecv 2611	AF391045	Vellinga (2001a)
<i>L. cristata</i>	USA	UC-ecv 2401	AF391046	Vellinga (2001a)
<i>L. cristata</i>	USA	UC-ecv 2460	AF391047	Vellinga (2001a)
<i>L. cristata</i>	USA	L-ecv 2285	AF391048	Vellinga (2001a)
<i>L. cristata</i>	USA	UC-ecv 2384	AF391049	Vellinga (2001a)
<i>L. cristata</i>	USA	SFSU-ded 5658	AF391050	Vellinga (2001a)
<i>L. cristata</i>	USA	WTU-pbm 1958	AF391051	Vellinga (2001a)
<i>L. cristata</i>	China	RITF 301	EU826489	Liang & Yang (2009)
<i>L. cristata</i>	China	RITF 308	EU826490	Liang & Yang (2009)
<i>L. cristata</i>	China	RITF 311	EU826491	Liang & Yang (2009)
<i>L. cristata</i>	China	HKAS 45049	EU081954	Liang & Yang (2009)
<i>L. cristata</i>	China	HKAS 49449	EU081945	Liang & Yang (2009)
<i>L. cristata</i>	China	HKAS 48457	EU081949	Liang & Yang (2009)
<i>L. cristata</i>	China	HKAS 45053	EU081948	Liang & Yang (2009)
<i>L. cristata</i>	China	HKAS 51356	EU081959	Liang & Yang (2009)
<i>L. cristatanea</i>	China	HKAS 50183	EU081951	Liang & Yang (2009)
<i>L. cristatanea</i>	China	HKAS 50021	EU081952	Liang & Yang (2009)
<i>L. cristatanea</i>	China	HKAS 43063	EU081970	Liang & Yang (2009)
<i>L. cristatanea</i>	China	RITF 300	EU826488	Liang & Yang (2009)
<i>L. cf. cristata</i>	USA	UC-ecv 2515	AF391052	Vellinga (2001a)
<i>L. cf. cristata</i>	USA	UC-ecv 2542	AF391053	Vellinga (2001a)
<i>L. cf. cristata</i>	USA	UC-ecv 2677	AY176466	Vellinga (2003)
<i>L. cf. cristata</i>	USA	UC-ecv 2714	GQ203807	Vellinga (2010)

Noted: sequences generated in this study are in black bold.

Results and discussion

Phylogeny

Two newly generated ITS nrDNA sequences from the specimens collected at Chiang Mai were compared with those of 76 samples from 4 distinct species with spurred basidiospores and a hymenidermal pileipellis, including European, North American and Asian specimens (Table 1). The phylogenetic analysis (Fig. 1) shows 5 significantly supported clades: the clade of *L. cristata*, including a distinct clade for *L. fraterna* var. *macrospora* with high MP and ML BS values; the clade of *L. castaneidisca* Murrill (1912 : 232) from the USA (Murril 1912); the clade of *L. cf. cristata* from USA; the clade of *L. cristatanea*, and an independent clade including the sequences generated from the samples found at Chiang Mai. These samples are therefore considered different from the other species of the *L. cristata* clade, and a new name is proposed for them below. The new species is maybe related to *Lepiota* cf. *cristata*, although support values are barely significant (70% ML, 68% MP). A subsignificant support for a monophyletic origin of *L. cristata*, *L. castaneidisca*, *L. cf. cristata* and the new species was also observed, although further evidence from additional genetic markers is needed to support this hypothesis.

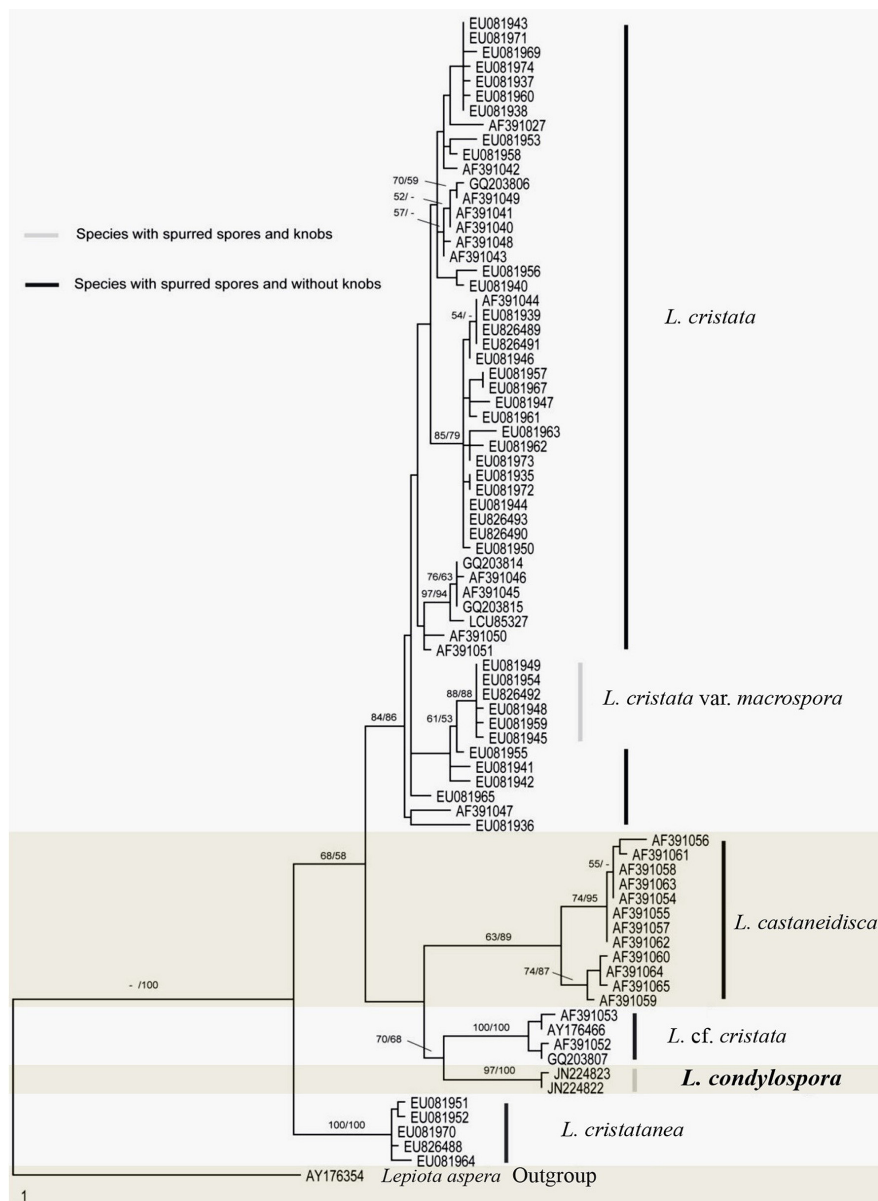


FIGURE 1. MP phylogenetic tree of *Lepiota* species related with *L. cristata* based on ITS nrDNA sequences. *Lepiota aspera* is used as the outgroup. Parsimony tree scores for the consistency index (CI) = 0.672, retention index (RI) = 0.874, rescaled consistency index (RC) = 0.587, and homoplasy index (HI) = 0.328, length = 424. ML/MP bootstrap support values equal to or higher than 50% are indicated above the branches. All herbarium abbreviations in the phylogeny follow Index Herbariorum (Thiers 2019). The new species is indicated in black bold.

Taxonomy

Lepiota condylospora Sysouphanthong, K.D. Hyde & Vellinga, *sp. nov.* Figs. 2, 3.

Mycobank no.:—MB 833709

Faces of fungi no.:—FoF 07071

Diagnosis:—*Lepiota condylospora* has spurred spores and a hymenidermal pileus covering. It differs from *L. cristata* var. *cristata*, *L. cristatanea*, and *L. castaneidisca* in the nodulose spores with two lateral knobs, and from *L. cristata* var. *macrospora* and *L. fraterna* E. Horak (1980: 124) in the size of its basidiomata and spores.

Holotype:—THAILAND. Chiang Mai Province: Mae Taeng District, near deciduous forest of Pong Dueat Village, dominant by *Castanopsis spp.* and *Lithocarpus spp.*, N 16° 06' 16.1", E 99° 43' 07.9", 780–805 m, 4 July 2007, *P. Sysouphanthong* (MFLU 09–0048, **holotype**); ITS rDNA sequence GenBank JN224822.

Etymology:—‘*condylospora*’ derived κονδυλος (G) wart, and spora (L) (derived from σπορά (G), seed), spore, because of the lateral knobs on the spores.

Description:—*Pileus* 5–16 mm diam, first hemispherical or conical, expanding to campanulate, umbonate or plano-convex, with a wide umbo and inflexed margin; with a orangish brown to brown (7C6, 6E8) central calotte (sometimes reduced to the umbo), and irregularly shaped brown (6E8) squamules scattered toward the margin on a white fibrillose background; margin with only a few squamules, fringed, exceeding lamellae when mature. *Lamellae* free, crowded, ventricose, 3 mm deep, white to yellowish white (4A2), with floccose eroded white edge. *Stipe* 30–50 × 1–1.5 mm, cylindrical to slightly tapering to apex, with white to orange-white (6A2) background, covered by white fibrils, staining light brown (7D5) when touched, sometimes with brown (6E8) squamules at base zone. *Annulus* cuff-like, white, cottony or fibrillose, with or without brown (6E8) squamules at the edge, attached at the upper part of the stipe. *Context* white to orange-white (6A2) in the pileus, 1–1.5 mm wide; orange-white (6A2) at the top of the stipe, light brown (7D5) towards its base. *Smell* strong and acrid. *Taste* mild and sweet. *Spore* print white.

Basidiospores [75,3,3] 5.0–7.5 (–8.5) × 3.5–5.5 μm, avl × avw = 6.2 × 4.3 μm, Q = 1.3–2.0, Qav = 1.6, in side-view ellipsoidal to triangular, with an acute apex, in front-view star-like, with two lateral knobs, dextrinoid, more or less congophilous, cyanophilous, not metachromatic. *Basidia* 15–18 × 6.0–8.0 μm, 4-spored, rarely 2-spored, clavate, wider in the middle and narrower towards base and apex, with internal drops and granules visible in Congo Red, with basal clamp-connection. Lamella edge sterile. *Cheilocystidia* 17–29 × 10–15 μm, irregularly clavate, narrowly clavate or narrowly pyriform, sphaeropedunculate. *Pleurocystidia* none seen. *Pileipellis* a hymeniderm composed of more or less clavate elements, 16–66 × 9–23 μm, pale yellow, with hyaline or granular hyphae in the innermost layer, 3–13 μm wide, with clamp-connections. *Stipitipellis* (squamules) a hymeniderm similar to pileipellis. *Clamp-connections* present in all tissues.

Habitat and distribution:—growing in small to large groups, rarely solitary, on humus rich soil with dead leaves and deciduous wood in mixed forests dominated by *Castanopsis spp.* and *Lithocarpus spp.*; only known from Chiang Mai province, northern Thailand.

Additional materials examined:—THAILAND. Chiang Mai: Mae Taeng Dist., near Forest of Pong Dueat Village, N 16° 06' 16.1", E 99° 43' 07.9", alt, 780–805 m, 30 July 2008, *P. Sysouphanthong*, MFLU 09–0173; Chiang Mai, Mae Rim Dist., Mae Sa Valley, 12 July 2008, *P. Sysouphanthong*, MFLU 09–0136.

Discussion

Lepiota condylospora is a slender species with a campanulate, hemispherical to convex-umbonate pileus. It is recognized by the brownish orange to brown squamules on the pileus surface, the triangular basidiospores with two lateral knobs, and a hymenidermal pileipellis composed of clavate elements. So far, two species of *Lepiota* with laterally knobbed basidiospores and a hymenidermal pileipellis have been described: *L. fraterna* E. Horak, originally described from Papua New Guinea (Horak 1981), and *L. cristata* var. *macrospora* (Zhu L. Yang) Liang & Yang from southwest China (Liang & Yang 2011). *Lepiota condylospora* differs from *L. fraterna* in the bigger spores and cheilocystidia as well as the non-striate pileus margin (Horak 1981). Unfortunately, no ITS sequences of *L. fraterna* are available yet. *Lepiota condylospora* closely resembles *L. cristata* var. *macrospora* in most morphological characteristics, but the basidiomata are smaller, and the ITS sequences are notably different, suggesting that *L. cristata* var. *macrospora* nests within the

clade of *L. cristata*. It is fascinating that this spore shape which is quite bizarre to the human eye, has evolved several times in this clade, and one wonders what the ecological advantages of this are. It seems that this new species is rare; three specimens were only found in Chiang Mai, two specimens in Mae Taeng District, and a specimen in Mae Rim District; and it is not found in other parts of Thailand.



FIGURE 2. Basidiomata of *L. condylospora* (a, MFLU090136; b, MFLU0900032). Photographs: P. Sysouphanthong.

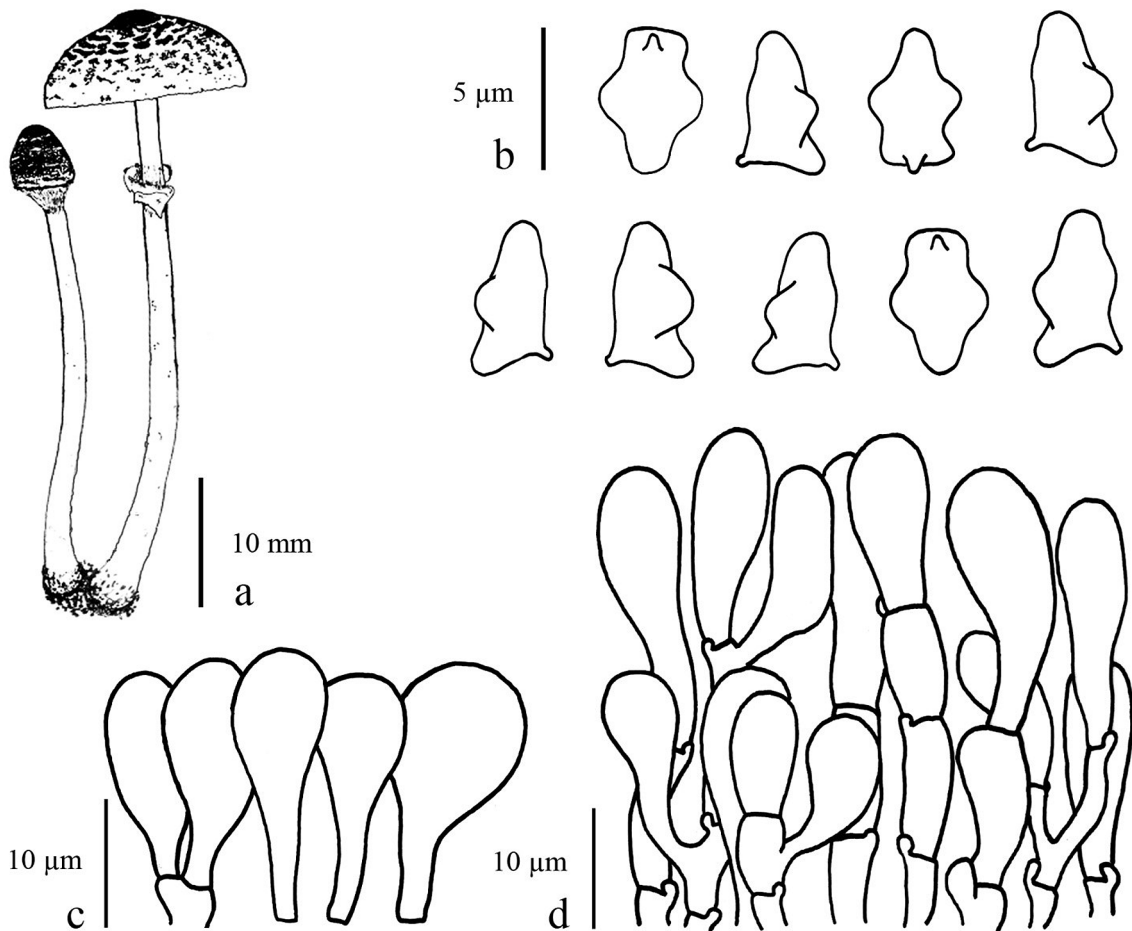


FIGURE 3. *Lepiota condylospora* (MFLU 0900032, holotype). a: Basidiomata, b: basidiospores, c: cheilocystidia, d: pileipellis. Drawings: P. Sysouphanthong.

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