
Lactarius* in Northern Thailand: 2. *Lactarius* subgenus *Plinthogali

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This paper reports on *Lactarius* subgenus *Plinthogali* from Northern Thailand and is the second in a series resulting from a complete revision of the genus for the area. Four taxa are described as new for science: *L. crassiusculus*, *L. lavandulus*, *L. friabilis* and *L. subplinthogalus* var. *chiangmaiensis*. *Lactarius oomsisiensis* and *L. montoyae* are reported for the first time outside Papua New Guinea and India respectively. Phylogenetic analysis of the ITS sequence was used to test conspecificity and support species delimitations. *Lactarius* aff. *gerardii* is reported in Thailand; however, our results demonstrate *L. gerardii* is a species complex forming a separate clade from the other members of *L.* subg. *Plinthogali*.

Key words: macromorphology, micromorphology, molecular phylogeny, *Russulales*, taxonomy.

Introduction

Lactarius is a genus of ectomycorrhizal macrofungi with an estimated 500 species around the globe. Within *Lactarius*, subgenus *Plinthogali* forms a morphologically and molecularly well-defined group. Species in this subgenus produce medium-sized, moderately fleshy basidiomes, further recognized by a more or less velutinous pileus in dry conditions, with mostly dull pileus colours (cream, greyish, brownish, blackish, brown), and a concolourous stipe. The majority of species exhibit a pinkish or reddish discoloration of the context or latex, but also yellow, lilac, blue, violet, brown and from red to black

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discolorations are known. Some species do not exhibit any discolorations at all.

The spores are globose to subglobose, bearing high ornamentations in a reticulate or zebroid pattern, usually with a distally amyloid plage. The pileipellis structure is most typically a palisade containing intracellular, brownish pigmentation, although sometimes it may be a trichoderm or trichopalysade. The presence of macrocystidia is rare in this subgenus. Phylogenetic analyses of *Russulaceae* so far confirm the monophyly of *L.* subgenus *Plinthogali* (Nuytinck *et al.*, 2003; Eberhardt and Verbeken, 2004; Shimono *et al.*, 2004). Currently, over 70 species and about 15 varieties have been described worldwide. A satisfactory sectional division has not yet been accomplished. The latest proposal from Verbeken (2000) divides *Lactarius* subg. *Plinthogali* into three sections: *Lactarius* sect. *Nigrescentes* characterized by watery latex, the context turning pinkish or reddish before finally turning black and by the presence of macrocystidia; *Lactarius* sect. *Pseudofuliginosi* characterized by an ixotrichoderm in the pileipellis and by the latex drying greyish-brownish. Both these sections are strictly African and comprise only seven taxa. All remaining species are lumped together in *Lactarius* sect. *Plinthogali*. North America and Africa contain the largest known diversity, with over 20 species reported from each continent. Europe, which can be considered a well-studied area, harbors only 10 species. From Asia, though a vast and diverse continent, a mere 15 species have been described so far, of which 10 are from South-East Asia, viz., Java (Verbeken *et al.*, 2001), Papua New Guinea (Verbeken and Horak, 1999, 2000; Verbeken *et al.*, 2002), Malaysia (Stubbe *et al.*, 2007) and Singapore (Masse, 1914). This low number is solely the consequence of the lack of mycological surveys. However, a study *L.* subgenus *Piperites* in Thailand (Le *et al.*, 2007) and a revision of *L.* sect. *Deliciosi* in Asia (Nuytinck *et al.*, 2006) have presented five new species within *L.* subgenus *Piperites* and recent research on *Russulaceae* in India and China has revealed numerous new species, suggesting a potentially high species richness in the whole of Asia (Sharma and Das 2003; Das *et al.*, 2003, 2004a,b, 2005a,b, 2006; Das and Sharma 2004; Wang and Verbeken 2006). Between 2003 and 2006 numerous specimens of *Lactarius* were collected in Northern Thailand. This paper is the second in a series revising *Lactarius* for the region and the first report of representatives of *Lactarius* subg. *Plinthogali* from Thailand. The vegetation in this area constitutes of mid- and high-elevation rainforests and is dominated by ectomycorrhizal trees belonging to the *Dipterocarpaceae*, *Fagaceae* and *Pinaceae*.

Materials and methods

Morphological approach

The study is based on collections made by Huyen T. Le and D.E. Desjardin during the period 2003-2006, augmented with collections of A. Verbeke and R. Walley made in June 2004. The studied material is deposited in the following herbaria: Herbarium Universitatis Gandavensis (GENT), Herbarium of Chiang Mai University (CMU), San Francisco State University (SFSU), and the Mushroom Research Centre (MRC). Terminology and protocol has been adopted from Le *et al.* (2007). Colour codes refer to Kornerup and Wanscher (1978). Photographs of the fruit bodies will be published on the *Russulales* News website (<http://www.mtsn.tn.it/russulales-news/>).

Molecular approach

Molecular data were used primarily as an aid in delimiting species, and for comparisons with species from other continents.

DNA preparation. DNA was extracted from dried material. Small parts of the lamellae were crushed in a bead beater and DNA was extracted using the PrepMan Ultra kit (Applied Biosystems, USA). Instructions as given by the manufacturer were followed. These DNA extractions were purified using JetQuik columns (Genomed, Germany).

PCR and direct sequencing of the ITS region. The ITS region was amplified using ITS1-F primer (Gardes and Bruns, 1993) and ITS 4 primer (White *et al.*, 1990). When amplification failed intermediate primers ITS2 and ITS3 (White *et al.*, 1990) were also used. The PCR program was initiated by a 5 min. denaturation step at 94°C, followed by 35 cycles of 30 sec at 94°C, 30 sec at 55°C and 45 sec at 70°C. The polymerization was completed by an incubation of 7 min. at 70°C. The obtained PCR products were purified using ExoSAP (USB, USA). DNA sequencing reactions were performed with the ABI PRISM® BigDye™ Terminators v3.1 Cycle Sequencing Kit using the same primers on an ABI PRISM® 3130xl DNA Sequencer. Sequences were deposited in GenBank (table 1).

Data analysis. Sequence chromatograms were inspected visually and sequences initially aligned using Clustal X (Thompson *et al.*, 1997). The alignment results were edited by hand with the BioEdit Sequence Alignment Editor version 7.0.3 (Hall, 1999) and the matrix was submitted to TreeBase (No. SN3365). Neighbor joining analysis was performed with PAUP* 4b10

Table 1. Specimens used for the phylogenetic analyses.

Species	Origin	Collection number (herbarium)	GenBank accession number
<i>L. angiocarpus</i>	Africa	Arora 00-448	AY606942
<i>L. fuliginosus</i>	Belgium	AV 2000-120	EF560657
<i>L. acris</i>	France	AV 97-520	EF560659
<i>L. aff. gerardii</i>	Thailand	LTH270	EF560685
<i>L. aff. gerardii</i>	Thailand	LTH246	EF560686
<i>L. aff. gerardii</i>	Thailand	LTH295	EF560687
<i>L. azonites</i>	Belgium	JN 2002-010	EF560658
<i>L. crassiusculus</i>	Thailand	LTH439	EF560681
<i>L. crassiusculus</i>	Thailand	LTH12	EF560682
<i>L. crassiusculus</i>	Thailand	LTH398	EF560683
<i>L. crassiusculus</i>	Thailand	LTH369	EF560684
<i>L. crassiusculus</i>	Thailand	LTH281 (GENT)	EF141554
<i>L. friabilis</i>	Thailand	LTH325 (GENT)	EF141553
<i>L. friabilis</i>	Thailand	AV-RW04/115 (=LTH147)	EF560663
<i>L. friabilis</i>	Thailand	LTH355	EF560664
<i>L. friabilis</i>	Thailand	LTH399	EF560665
<i>L. friabilis</i>	Thailand	LTH310	EF560666
<i>L. friabilis</i>	Thailand	LTH390	EF560667
<i>L. gerardii</i>	USA	AV 05-235	EF560688
<i>L. lavandulus</i>	Thailand	LTH314	EF560676
<i>L. lavandulus</i>	Thailand	LTH315	EF560677
<i>L. lignyotus</i>	Germany	Lw098	AY606949
<i>L. montoyae</i>	Thailand	LTH218	EF560671
<i>L. montoyae</i>	Thailand	LTH48	EF560672
<i>L. montoyae</i>	India	K. Das 1065	EF560673
<i>L. oomsisiensis</i>	Thailand	LTH172	EF560678
<i>L. oomsisiensis</i>	Thailand	AV-RW04/055 (=LTH122)	EF560679
<i>L. oomsisiensis</i>	Papua New Guinea	E4545(=RH6181)	EF560680
<i>L. pterosporus</i>	Belgium	LVL 2002-019	AY331013
<i>L. romagnesii</i>	Belgium	RW 4024	EF560662
<i>L. ruginosus</i>	Czech Rep.	RW - AV 3147	EF560660
<i>L. lavandulus</i>	Thailand	DED7469	EF560675
<i>L. lavandulus</i>	Thailand	AV-RW04/102 (=LTH144)	EF560674
<i>L. subplinthogalus</i> var. <i>chiangmaiensis</i>	Thailand	LTH260	EF560668
<i>L. subplinthogalus</i> var. <i>chiangmaiensis</i>	Thailand	LTH13	EF560669
<i>L. subplinthogalus</i> var. <i>chiangmaiensis</i>	Thailand	LTH420	EF560670
<i>L. subruginosus</i>	Italy	MTB 95091501	EF560661
Outgroup			
<i>Lactarius volemus</i>	France	RW 1228	AY606959
<i>Russula nigricans</i>		FO46761	AY606963

(Swofford, 2002), using maximum likelihood (ML) distances. The ML-distance parameters were estimated using Modeltest version 3.7 (Posada and Crandall, 1998). Maximum parsimony (MP) analyses were performed with PAUP* using 1000 heuristic searches, employing TBR branch swapping and random sequence addition. Other settings were: gaps treated as missing, all characters of type unordered and equally weighted, multistate characters interpreted as uncertainty, starting trees obtained via stepwise addition, one tree held at each step during stepwise addition, steepest descent option not in effect, branches collapsed (creating polytomies) if minimum branch length is zero, and MulTrees option in effect. Bootstrap supports were evaluated using 1000 bootstrap replicates with 10 heuristic searches per replicate, random sequence addition and TBR branch swapping.

Results

This paper reports on the Thai representatives of *Lactarius* subgenus *Plinthogali* and describes four new taxa: *L. crassiusculus*, *L. friabilis*, *L. lavandulus* and *L. subplinthogalus* var. *chiangmaiensis*. *Lactarius oomsisiensis* Verbeke and Halling is reported for the first time outside Papua New Guinea and *L. montoyae* K. Das and J.R. Sharma is reported for the first time outside India, raising the total number of Thai species to six. Many collections have been made of *L. aff. gerardii*. Though always considered a well-defined species within *L. subg. Plinthogali*, our molecular analyses indicate *L. gerardii* Peck is in fact a species complex forming a separate clade from the other members of the *L. subg. Plinthogali*. Unpublished data (Stubbe *et al.*) confirm its exclusion from *L. subg. Plinthogali*.

Key to species

1. Pileus and stipe brown; lamellae pale, often with brownish margin; spore ornamentation higher than 1.5 μm , forming a complete reticulum 2
 1. Not with this combination of characters; pileus cream-coloured, orange brown or coffee-and-milk coloured; spore ornamentation 1.5-2.5 μm high, zebroid or forming an incomplete reticulum 3
2. Lamellae distant; context and latex remaining white *L. aff. gerardii*
2. Lamellae close; context and lamellae staining purplish grey or violet *L. lavandulus*
3. Lamellae close; pleuromacrocytidia present *L. crassiusculus*
3. Lamellae distant to subdistant; pleuromacrocytidia absent 4
4. Lamellae orange brown; context changing from white to orange pinkish/dirty pinkish
 - *L. oomsisiensis*
4. Not with this combination of characters; lamellae whitish or cream coloured 5

5. Pileus coffee-and-milk coloured with an olive brown tinge; context turning pink, spores reticulate..... *L. friabilis*
 5. Pileus coloured otherwise; spores zebroid 6
6. Pileus greyish brown; context and latex unchanging, thin-fleshy in cap; spores winged with ridges up to 2.5 µm high *L. montoyae*
 6. Pileus pale greyish brown to greyish orange; context turning pinkish to greyish orange, not thin-fleshy in cap; spore ornamentation never reaching 2.5 µm high
 *L. subplinthogalus* var. *chiangmaiensis*

***Lactarius crassiusculus* H.T. Le & Stubbe, sp. nov.** (Figs 1, 2, 3a, 3b, 10)
 MycoBank: 510722

Etymology: *crassiusculus*: ‘moderately thick’ because of the moderately thick context of the pileus.

Pileus 8-40 mm in diam., primo convexus tum planoconvexus ad infundibuliformem, in centro interdum subumbonatus, crassiusculus, leviter rugulosus, pallide albidus, griseocremeus ad pallide brunneum. *Lamellae* decurrentes, confertae, pallide cremeae vel pallide aurantiae, brunnescentes. *Stipes* 12-40 mm longus, 3-10 mm crassus, griseocremeus, brunnescens. *Contextus* crassiusculus, albidus vel sordide rosescens. *Latex* albus, aurantiacescens vel rosescens, tum brunnescens. *Basidiosporae* 6.5-7.5-8.6 × 6.0-7.1-8.2 µm, globosae ad subglobosas, cristis usque ad 2-2.5 µm altis ornatae, reticulatae; macula suprahilaris distale amyloidea. *Pleuromacrocystidia* abundantia, 40-80(95) × 8-13 µm, emergentia. *Cheilomacrocystidia* abundantia. *Pileipellis* bistrata; elementa suprapellis subcylindrata, 10-50 × 2-7 µm; subpellis pseudoparenchymata. *Stipitipellis* trichoderma.

Holotypus hic designatus: THAILAND: Chiang Mai Province, Mae Taeng Distr., Tung Joaw village, N19°08.07' E.098°38.09', 1423 m alt., rainforest dominated by *Castanopsis armata*, *Lithocarpus* sp. and *Pinus kesiya*, solitary to gregarious on the soil among leaves, 15/06/2005, Huyen T. Le 281 (CMU; *isotypus* SFSU, GENT).

Pileus 8-40 mm diam., convex when young, becoming plano-convex and depressed to almost infundibuliform, centre sometimes subumbonate, margin regular, somewhat wavy when older; surface dry and smooth to slightly rugulose, pale whitish, greyish cream (4B2/3) to pale brown (5BCD3/4), sometimes with olive brown tinges (4D3/4) in centre. *Lamellae* decurrent, close to crowded (12-16 L+1/1cm), 1-3 mm broad, 3 series of lamellulae, pale cream coloured to pale orange (3/4/5A2-3), when bruised staining at first greyish orange or dirty pinkish (6/7B5/6) but ultimately becoming brown (6DE5). *Stipe* 12-40 × 3-10 mm, more or less cylindrical, central or slightly eccentric; surface dry, smooth, greyish cream to dark cream coloured, staining brown (7C4-7E8) when bruised. *Context* moderately thick, 1.5-3 mm thick at mid-radius in pileus, solid or hollow in stipe, white, unchanging or because of the latex staining dirty pinkish, sometimes also yellowish, but later on becoming greyish brown; smell not remarkable or fragrant; taste mild or slightly acrid. *Latex* abundant, white, within a few minutes turning orange or pinkish (6A7-7B4-8B5), ultimately becoming dark coffee-and-milk coloured, grey brown or dark brown (8EF5).

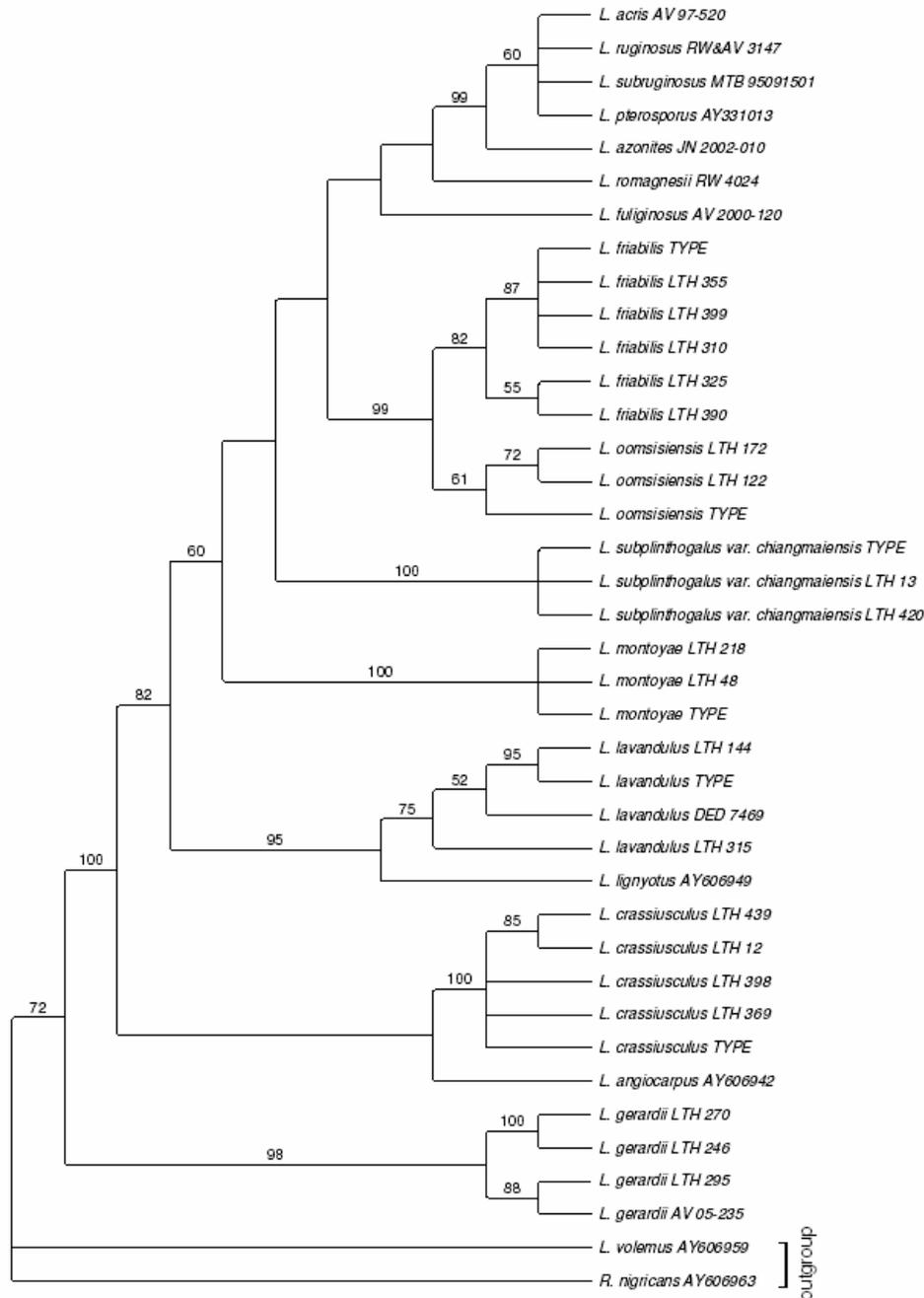


Fig. 1. MP phylogeny of *Lactarius* subgenus *Plinthogali* in Northern Thailand based on ITS sequences. The 50% majority rule consensus tree resulting from the Maximum Parsimony analysis with the bootstrap values higher than 50% added on the internal nodes.

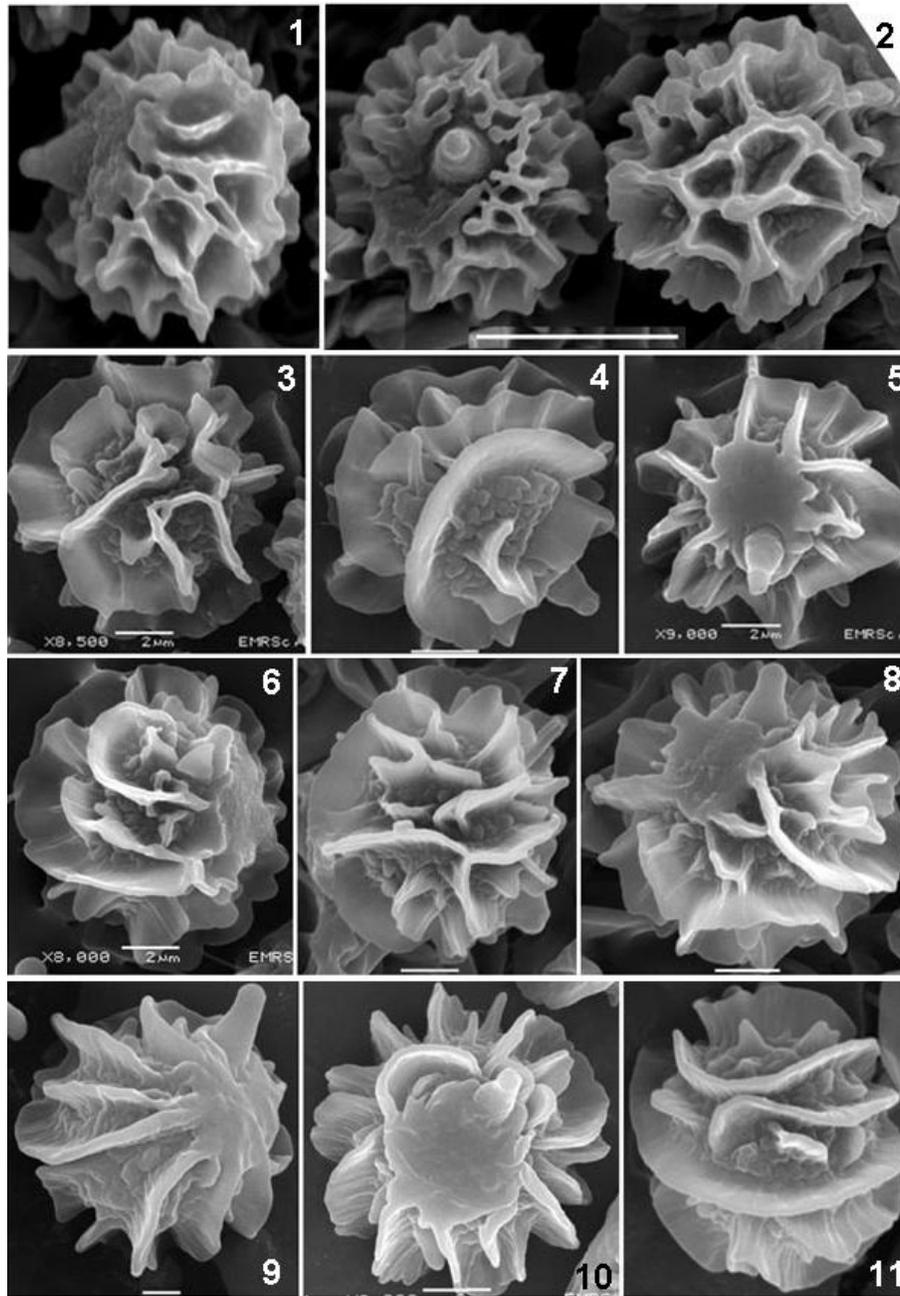


Fig. 2. SEM photogram of *Lactarius* basidiospores. *L. lavandulus* (1, 2) Huyen T. Le 314; *L. crassiusculus* (3, 4, 5) Huyen T. Le369; *L. friabilis* (6, 7, 8) Huyen T. Le 147; *L. montoyae* (9, 10, 11) H. T. Le 218; *L. oomsisiensis* (12, 13, 14) H. T. Le 172; *L. subplinthogalus* var. *chiangmaiensis* (15, 16, 17) Huyen T. Le 260; *L. aff. gerardii* (18, 19, 20) H. T. Le 270. Scale bar = 6 μ m (1, 2); = 2 μ m (3, 4, 5, 6, 7, 8, 10, 14, 17); = 1 μ m (9, 12, 13, 15, 16, 18, 19, 20).

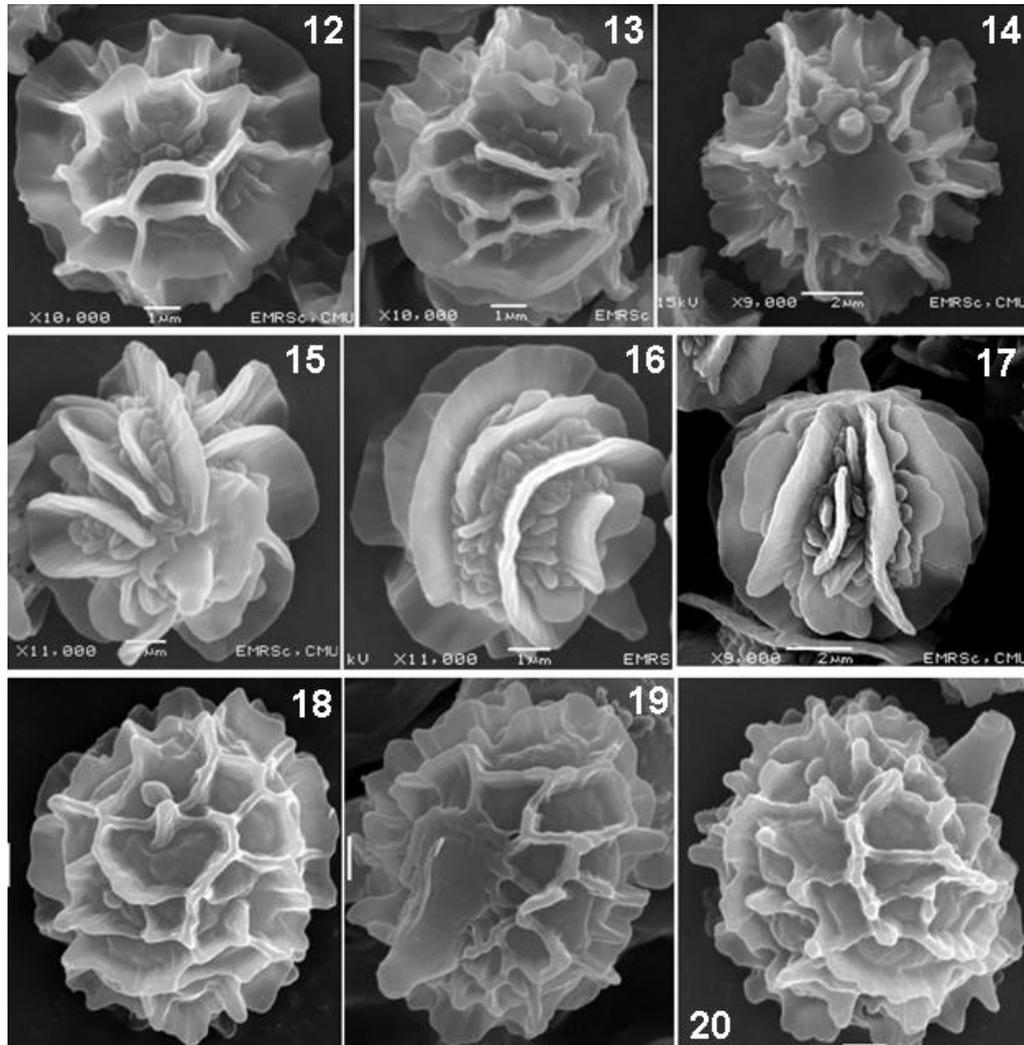


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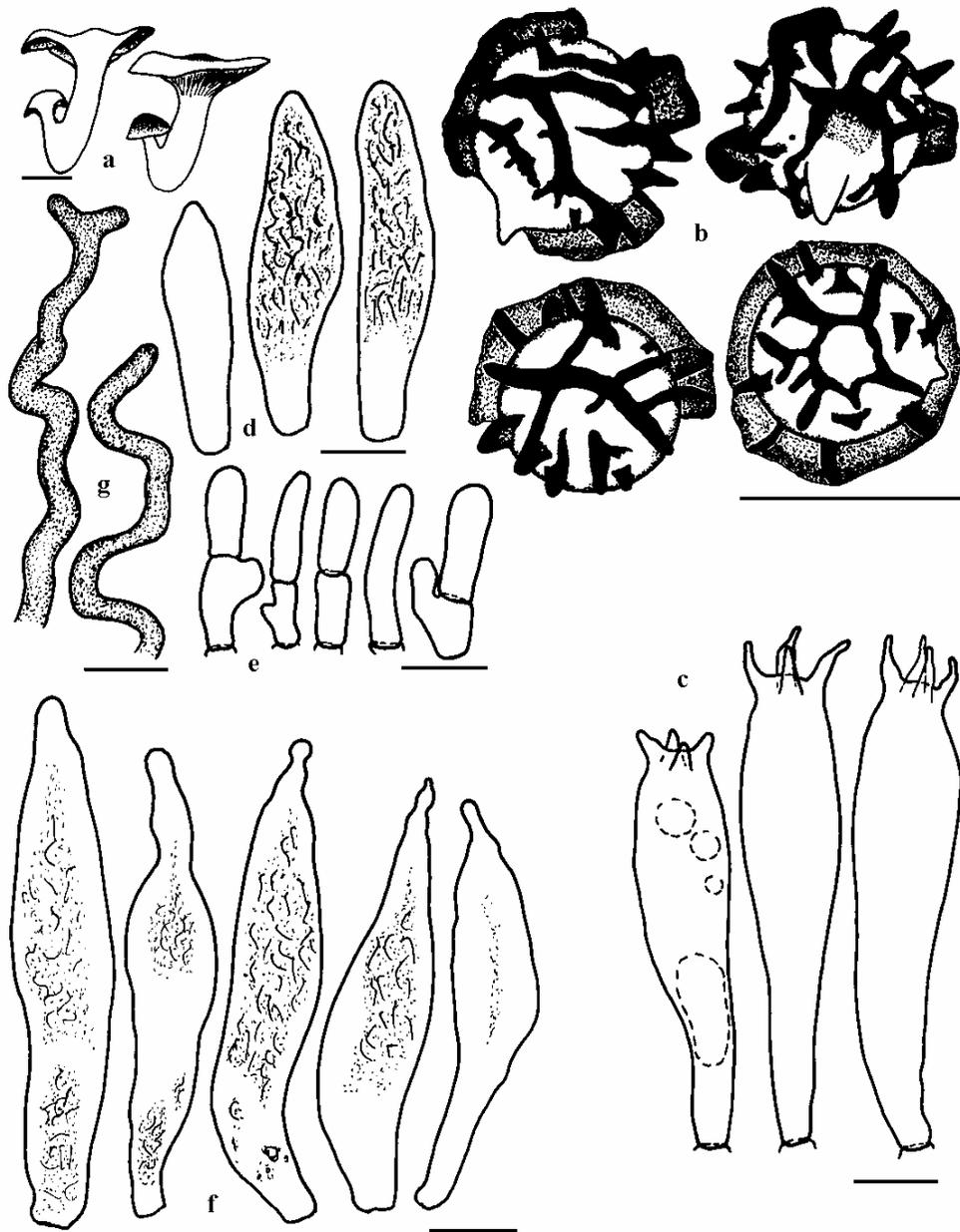


Fig. 3a. *Lactarius crassiusculus*. a. basidiomes. b. basidiospores, c. basidia, d. cheilomacrocystidia, e. cheiloleptocystidia, f. pleuromacrocystidia, g. pleuropseudocystidia. Scale bars = 10 mm (basidiomes) and 10 μ m.

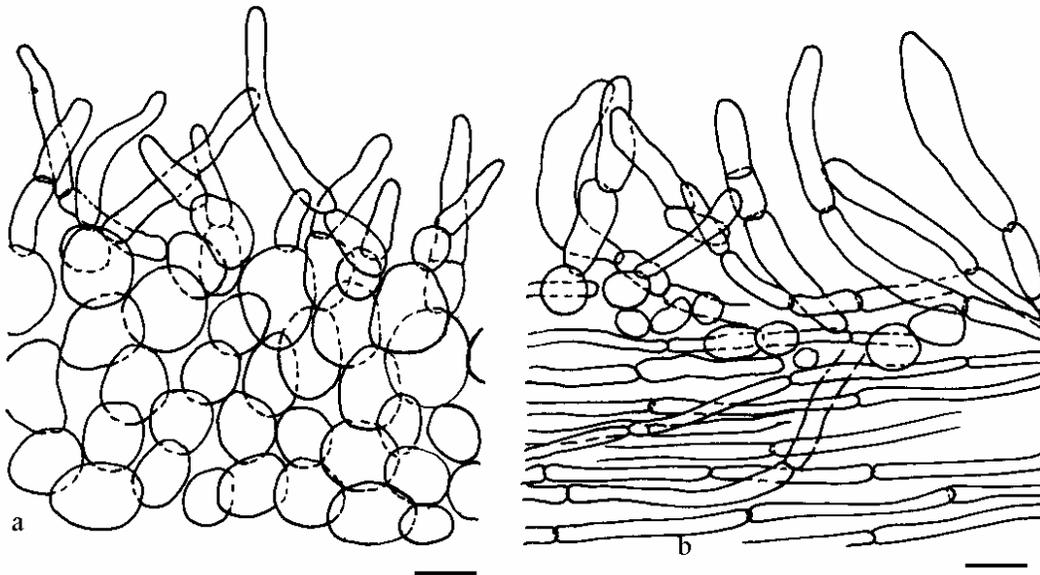


Fig. 3b. *Lactarius crassiusculus*. a. pileipellis, b. stipitipellis. Scale bars = 10 μ m.

Spore print greyish orange (observed in LTH 281). *Basidiospores* (5.5) 6.7–7.6–8.1–8.6 (9.5) \times (5.3) 6.4–7.1–7.6–8.1 (8.8) μ m (Q = 1.01–1.06–1.17; n = 100), globose to subglobose; ornamentation amyloid, forming an incomplete to almost complete reticulum with rather wide meshes, composed of firm ridges; ridges often with a slightly split aspect, < 2–2.5 μ m high, mostly with smooth or somewhat irregular edges, sometimes slightly crenulate; minute isolated warts present between the ridges; plage mostly distally amyloid.

Basidia 40–70 \times 10–15 μ m, subclavate to clavate, 4-spored, hyaline sometimes with guttate contents; sterigmata 3–6 \times 1–2 μ m. *Pleuromacrocystidia* abundant to very abundant, 40–80(95) \times 8–13 μ m, emergent, subcylindrical, subclavate or subfusiform, apex obtuse, acute, capitate or submoniliform, containing needle-like crystals, thin-walled. *Pleuropseudocystidia* abundant to moderately abundant, 2.5–5.5(6) μ m diam., not or slightly emergent, slender, cylindrical, tortuous, thin-walled. *Lamellar edge* mostly sterile, sometimes basidia present but mainly composed of cheiloleptocystidia and cheilomacrocystidia; cheilomacrocystidia abundant, 40–60 \times 9–11 μ m, subclavate to fusiform, similar to pleuromacrocystidia, contents granular or with needle-like crystals, thin-walled; cheiloleptocystidia 10–25 \times 2.5–8 μ m, cylindrical to subfusiform or narrowly clavate, hyaline, thin-walled. *Hymenophoral trama* predominantly filamentous; lactifers abundant. *Pileipellis* a palisade, 60–90 μ m thick, hyaline or containing a faint brownish intracellular pigmentation in the upper layers; suprapellis composed of subcylindrical,

terminal elements that are $10\text{-}50 \times 2\text{-}6.5 \mu\text{m}$, sometimes septate, oblique to almost periclinal, rather thin-walled but cell walls often somewhat refringent; subpellis composed of several layers of inflated, more or less isodiametric cells, $10\text{-}20 \mu\text{m}$ diam. *Stipitipellis* a trichoderm, $50\text{-}80 \mu\text{m}$ thick, sometimes inflated hyphal elements present, hyaline; hyphae $3\text{-}5(10) \mu\text{m}$ diam., thin-walled; terminal cells $18\text{-}35 \times 4\text{-}8 \mu\text{m}$, recumbent or erect, thin-walled.

Habitat and distribution: Growing on soil and leaves in mid- to high-elevation broadleaf or mixed forests with *Castanopsis*, *Lithocarpus* and *Pinus*. So far only known from Northern Thailand.

Material Examined: THAILAND: Chiang Mai Province, Mae Taeng Distr., Tung Joaw village, $N19^{\circ}08.07' E.098^{\circ}38.09'$, 1423 m alt., rainforest dominated by *Castanopsis armata*, *Lithocarpus* sp. and *Pinus kesiya*, solitary to gregarious on the soil among leaves, 15/06/2005, Huyen T. Le 281 (**holotypus:** CMU; **isotype:** SFSU, GENT) – Chiang Mai Province, Doi Inthanon National Park, along Highway 1009 at 25 km marker, $N18^{\circ}32.56' E098^{\circ}33.51'$, 1073 m alt., forest dominated by *Castanopsis* spp. and *Pinus* spp., 04/08/2005, leg. R. Zhao, Huyen T. Le 369 (CMU, SFSU, GENT) – *ibid.*, 05/06/2006, leg. M.A. Neves, Huyen T. Le 398 (CMU, SFSU, GENT) – Chiang Mai Province, Mae Teng Distr., Highway 1095 at 22 km marker, $N19^{\circ}07.57' E98^{\circ}45.65'$, 750 m alt., mixed forest dominated by *Dipterocarpus* spp. and *Pinus kesiya*, under *Pinus* sp., 02/07/2003, Huyen T. Le 12 (CMU, SFSU, GENT) – Chiang Mai Province, Doi Suthep-Pui National Park, Sangasahasri Lane to Huai Kok Ma village, $N18^{\circ}48.62' E098^{\circ}54.60'$, 1150 m alt., in primary montane forest with *Castanopsis* spp. and *Lithocarpus polistachyus*, 13/06/2006, leg. T. Osmundson, Huyen T. Le 439 (CMU, SFSU, GENT).

Notes: *Lactarius crassiusculus* is a pale, cream to pale brown coloured, medium-sized mushroom, with a moderately fleshy cap, dense lamellae, and latex turning pink and later on brownish. It is microscopically easily distinguished by the abundant macrocystidia, which are absent in the other Thai species. Although, macrocystidia are uncommon in *L.* subg. *Plinthogali*, the molecular analyses clearly confirm the position of *L. crassiusculus* within this subgenus (Fig. 1). Morphologically, this classification is supported by the dull pileus colours, the pink discoloration of the latex, the globose spores with high ($2\text{-}2.5 \mu\text{m}$) reticulate ornamentation and the palisade in the pileipellis. Among the collected specimens certain morphological characters were not always consistent. In Huyen T. Le 369 a yellow discoloration of the context occurred after its turning pink, a character not observed in the other specimens. The ultimately brown discoloration of the latex was not as strong in every specimen. And Huyen T. Le 281 differed from the other specimens in having a hollow stipe. To eliminate any doubts concerning their conspecificity, all specimens were included in the molecular analyses. In all trees the specimens form a separate clade. We therefore interpret the observed morphological differences as part of intraspecific variability.

Lactarius oomsisiensis Verbeken & Halling, Austr. Syst. Bot. 15: 768 (2002).

(Figs 1, 2, 4, 10)

Pileus 50-110 mm diam., depressed to slightly infundibuliform with small papilla; margin irregularly wavy, sometimes reflexed; surface dry, strongly radially rugose but smoother towards the margin, mostly pale coffee-and-milk coloured, locally with a more orange tinge (5BC5), with very fine, darker spots, becoming brownish grey when older or bruised. *Lamellae* broadly adnate, distant (3-6 L+l/cm), up to 15 mm broad, brittle, with subtle venations between the lamellae, up to 4 lamellulae between 2 lamellae, orange brown (6D4/7); edge entire, concolourous. *Stipe* 50-70 × 10-16 mm, central, equal or tapering downwards and often slightly curved at the base, more or less cylindrical; surface smooth, dry, whitish, cream coloured, somewhat brownish pink when touched (5B3/4). *Context* thick, 4-9 mm thick at mid-radius in pileus, solid in stipe, cream coloured (4A2), slowly turning pale brownish orange or dirty pinkish (7B5/6, 7C7), especially just beneath the surface of the stipe, unchanging with 10% KOH or FeSO₄; smell mild, unremarkable or faintly rancid; taste mild, sometimes slightly acrid. *Latex* abundant, white, drying somewhat cream-coloured; unchanging with 10% KOH.

Spore print colour unknown. *Basidiospores* (5.6) 6-7-7.6-8.5 × (5.4) 5.7-6.8-7.3-8.3 μm (Q = 1.01-1.02-1.04-1.11; n = 100), globose to subglobose; ornamentation amyloid, forming an incomplete reticulum, composed of irregular ridges; ridges up to 1.5-2.0 μm high, rather acute, often with more or less crenulate edges; abundant, small, isolated warts present; plage distally to almost totally amyloid. *Basidia* 40-60 × 10-16 μm, subclavate to clavate, 4-spored, contents often guttate; sterigmata 3-9 × 1.5-2.5 μm. *Pleuromacrocystidia* absent. *Pleuropseudocystidia* 3-8 μm diam., abundant to very abundant, mostly emergent, cylindrical and smooth or more or less tortuous and irregular, sometimes branching towards the top, with crystalline or guttate contents, thin-walled. *Lamellar edge* mostly sterile; cheiloleptocystidia 15-40 × 3-7 μm, cylindrical, subcylindrical to fusiform, thin-walled, hyaline. *Hymenophoral trama* heteromerous, composed of hyphae intermixed with sphaerocysts; lactifers abundant. *Pileipellis* a trichopalisade to palisade, 40-80 μm thick, containing brown, intracellular pigmentation in the upper layers; suprapellis composed of subcylindrical to subfusiform terminal elements, 15-30 × 2-7 μm, mostly recumbent or oblique, thin-walled; subpellis composed of inflated cells, often somewhat elongated, 5-14 μm diam., a few to several layers thick, thin-walled. *Stipitipellis* a trichoderm, 20-60 μm thick; hyphae 2.5-5 μm diam., hyaline; terminal elements 13-37 × 2.5-5 μm, subcylindrical to subfusiform, upright to recumbent, thin-walled, hyaline.

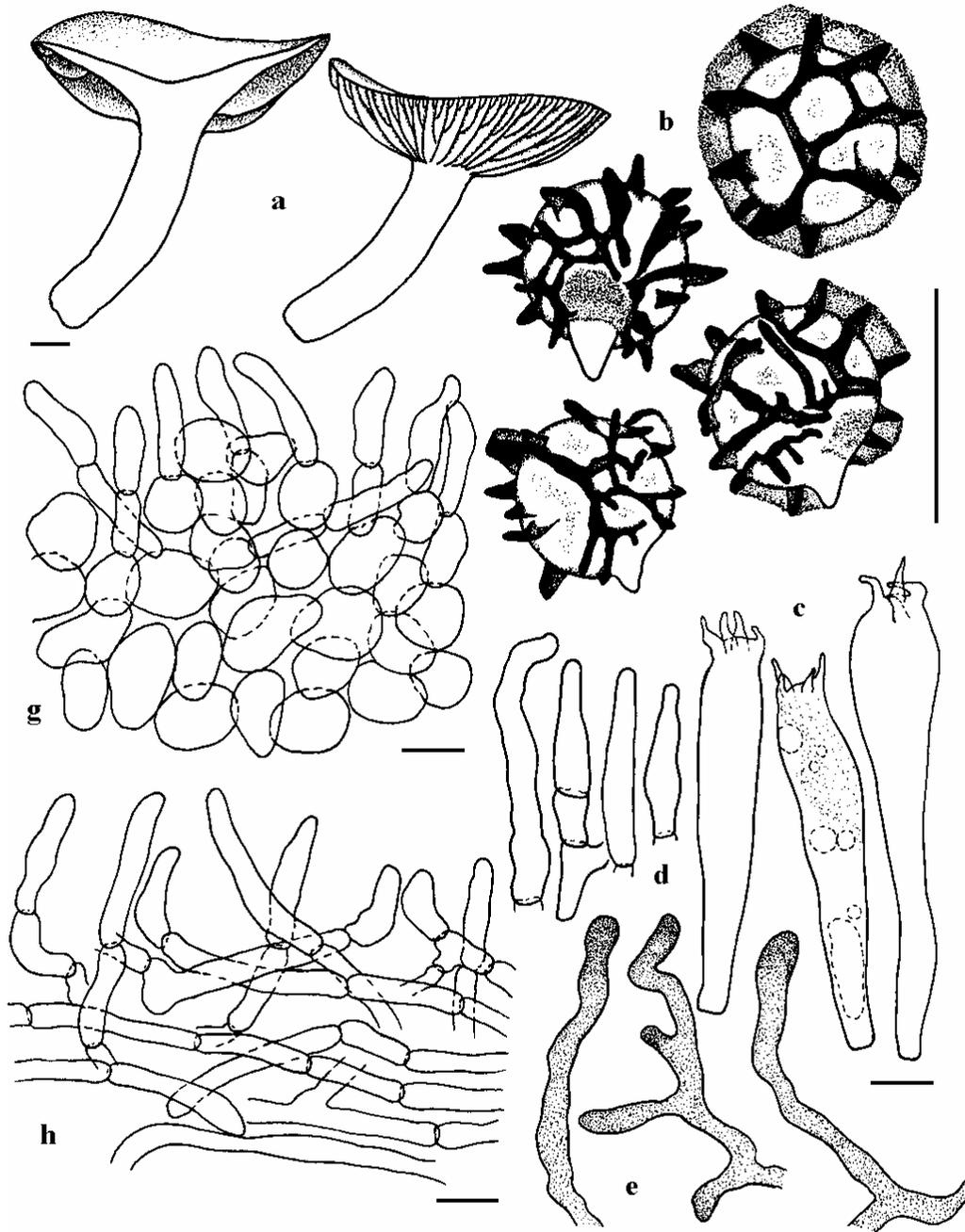


Fig. 4. *Lactarius oomsisiensis*. **a.** basidiomes, **b.** basidiospores, **c.** basidia, **d.** cheiloleptocystidia, **e.** pleuropseudocystidia, **g.** pileipellis, **h.** stipitipellis. Scale bars = 10 mm (basidiomes) and 10 μ m.

Habitat and distribution: Solitary on the soil in mixed forests dominated by *Castanopsis* and *Pinus*, often near *Pinus*. Reported from Papua New Guinea and Thailand.

Material Examined: THAILAND: Chiang Mai Province, Doi Inthanon National Park, along Highway 1009 at 25 km marker, N18°32.54' E098°33.51', 1076 m alt., rainforest dominated by *Castanopsis armata* and *Pinus* sp., 11/06/2004, *Huyen T. Le* 108 (CMU, SFSU, GENT) – *ibid.*, 02/07/2004, *Huyen T. Le* 172 (CMU, SFSU, GENT) – *ibid.*, 27/06/2005, *leg. W. Noparat, Huyen T. Le* 316 (CMU, SFSU, GENT) – *ibid.*, 04/08/2005, *leg. R. Zhao, Huyen T. Le* 368 (CMU, SFSU, GENT) – Chiang Mai Province, Mae Teang Distr., Ban Pha Deng village, near Pathumikaram Temple, 1076m alt., forest dominated by *Dipterocarpus* spp. and *Castanopsis armata*, on the soil near *Shorea* sp., 22/06/2004, *Huyen T. Le* 122 (CMU, SFSU) (= *Verbeken* and *Walley* 04/055, GENT).

Notes: Both morphological and molecular data confirm the conspecificity of these Thai specimens with *Lactarius oomsisiensis* *Verbeken & Halling*, although with low bootstrap support (61%). This species was described originally from Papua New Guinea where it is associated with *Lithocarpus*. The distant and rather dark, orange brown lamellae contrasting with the whitish stipe and the pale brownish cap make this species easily recognizable in the field. Its lamellae are among the darkest in the genus *Lactarius*. Other characteristic features are the rugulose cap surface and the thick context that slowly turns pinkish upon exposure. Microscopic features are the spore ornamentation that forms an incomplete reticulum with ridges up to 2 µm high, the striking abundance of pseudocystidia, and the trichopalisade in the pileipellis.

The Thai specimens differ from the specimens from Papua New Guinea because of their larger dimensions and a mostly mild taste of the latex and, microscopically, in having a trichoderm in the stipitipellis instead of a trichopalisade. We consider these differences as part of the infraspecific variability. In both countries *L. oomsisiensis* is found in lowland to mid-elevation rainforests, dominated by *Dipterocarpaceae* or *Fagaceae*. It is the first time *L. oomsisiensis* has been recorded outside Papua New Guinea, but since its current distribution spans the far ends of Southeast Asia, it would be expected that this species can be found in similar habitats all over the Malesian region.

Lactarius montoyae Das K. & Sharma J.R., Mycotaxon 89: 291 (2004)

(Figs 1, 2, 5, 10)

Pileus 12-66 mm diam., hemispherical when young, becoming plano-convex to infundibuliform when mature, often with subtle, radial pleats towards the margin, becoming more pronounced in older basidiomes; centre slightly depressed, sometimes with small papilla; surface dry, rugulose, greyish brown (5D4/5), browner when young. *Lamellae* adnate, sometimes with small

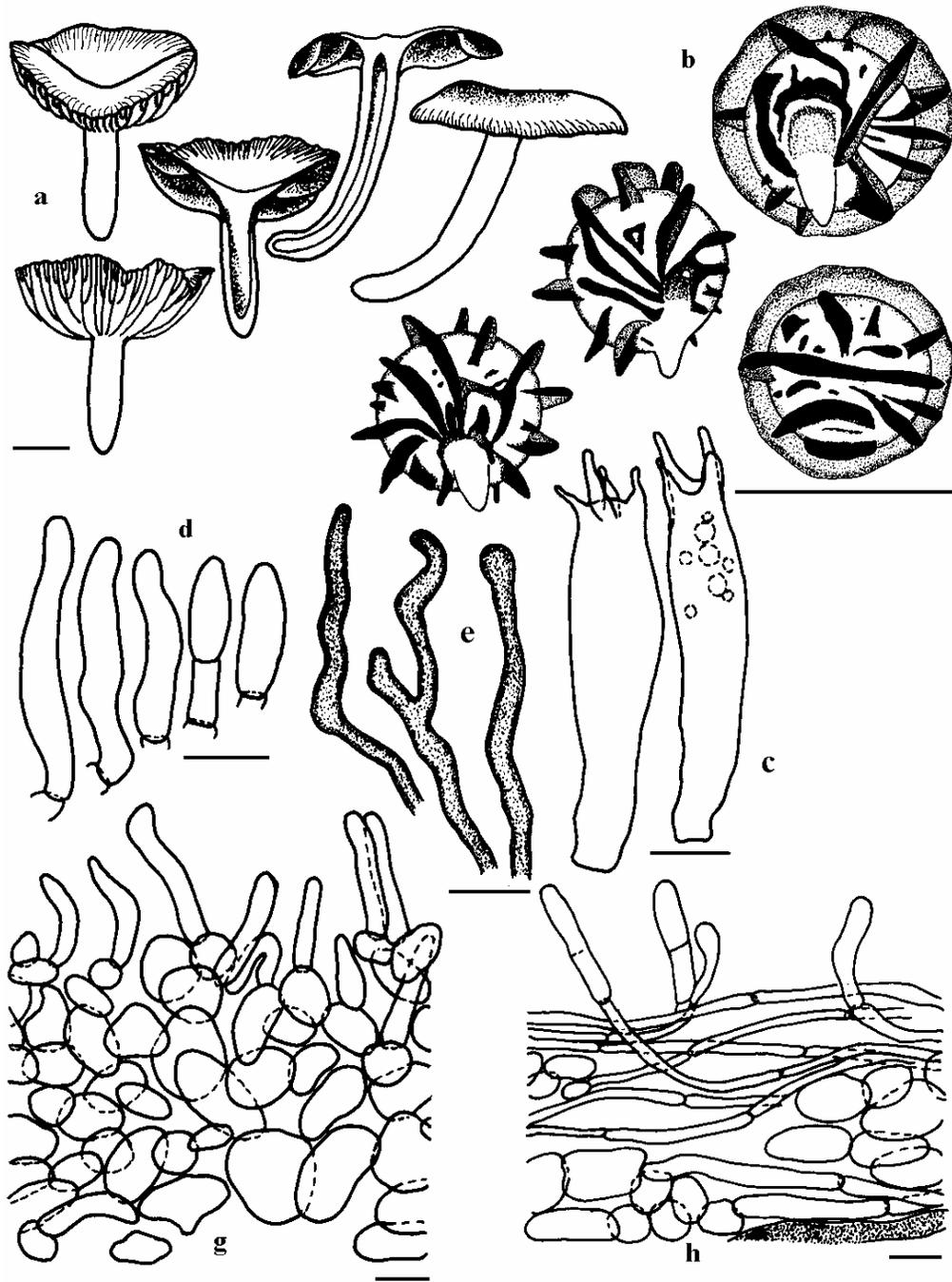


Fig. 5. *Lactarius montoyae*. a. basidiomes, b. basidiospores, c. basidia, d. cheiloleptocystidia, e. pleuropseudocystidia, g. pileipellis, h. stipitipellis. Scale bars = 10 mm (basidiomes) and 10 μm.

decurrent tooth, subdistant to distant, rather broad (3-14 mm), with 3-4 series of lamellulae, dark cream-coloured; edge entire, concolourous. *Stipe* 23-80 × 3-8 mm, equal or slightly tapering downwards or upwards, often curved at the base, cylindrical, central to slightly eccentric; surface dry, smooth, concolourous with pileus or paler and greyer, especially at the apex and base. *Context* brittle, very thin-fleshy in pileus, 0.5-3.5 mm thick at mid-radius, spongy in stipe, white sometimes slowly becoming slightly yellowish white, pale yellowish with 10% KOH, turning pale grey (4C-D1) with FeSO₄; smell fragrant; taste none to slightly sweet. *Latex* white, abundant; unchanging with 10% KOH.

Spore print colour unknown. *Basidiospores* (6.4) 7.5–7.7–8.2–8.6 (9.7) × (6.2) 7.1–7.3–7.8–8.3 (8.8) μm (Q = 1.01–1.04–1.08–1.16; n = 120), globose to subglobose; ornamentation amyloid, winged, ridges firm and often somewhat irregular, < 2.5 μm high, slightly acute, mostly isolated and rather wide-spaced, sometimes branching but never reticulate; ridges often exhibiting a split appearance with often slightly crenulate edges; small warts present between the main ridges; plage distally to totally amyloid. *Basidia* 53-65 × 9-18 μm, subclavate to clavate, 4-spored, hyaline, thin-walled; sterigmata 3-10 × 1.5-2.5 μm. *Pleuromacrocystidia* absent. *Pleuropseudocystidia* 4-11 μm diam., scattered to moderately abundant, emergent or not, tortuous, sometimes branched, thin-walled. *Lamellar edge* sterile; cheiloleptocystidia 17-32 × 4-9 μm, subcylindrical or subfusiform, hyaline, thin-walled. *Hymenophoral trama* mixed, composed of hyphae interwoven with sphaerocysts; lactifers abundant. *Pileipellis* a palisade, 40-90 μm thick, containing intracellular, brown pigmentation in the upper layers; suprapellis composed of erect or recumbent terminal elements, 20-52 × 4-5 μm, long and slender, cylindrical or subfusiform, often septate, thin-walled; subpellis composed of few to several layers of inflated cells, 10-25 μm diam. *Stipitipellis* a trichoderm, 20-90 μm thick, containing brown, intracellular pigmentation in the upper layers.

Habitat and distribution: Solitary on the soil among leaves in mid-elevation rain forests dominated by *Lithocarpus* and *Castanopsis*. Reported from Northern India and Thailand.

Material Examined: THAILAND: Chiang Mai Province, Mae Teng Distr., Pang Sa Det, Mae Sae village, N19°14,59' E98°38.45', 962m alt., wet forest dominated by *Pinus kesiya*, *Castanopsis armata* and *Lithocarpus* sp., 25/08/2004, Huyen T. Le 218 (**holotypus**: CMU; *isotypus*: SFSU, GENT). – Chiang Mai Province, Mae Teng Distr., Ban Pha Deng village, near Pathummikaram Temple, along forest trail, N19°06.28,8' E98°44.47,3', 1050 m alt., rain forest dominated by *Castanopsis armata*, 07/06/2003, Huyen T. Le 42 (CMU, SFSU, GENT). – Chiang Mai Province, Doi Suthep-Pui National Park, Sangasahasri Lane to Huai Kok Ma village, N18° 48,62' E098°54.60', 1146 m alt., primary montane forest with *Castanopsis armata*, *Castanopsis* spp. and *Lithocarpus polystachyus*, 14/08/2003, Huyen T. Le 48 (CMU, SFSU, GENT) – *ibid.*, 24/06/2005, *leg.* D.E. Desjardin, Huyen T. Le 296 (CMU, SFSU, GENT). – Chiang Mai Province, Mae Teng Distr., Ban Mae Sae village, dominated by

Castanopsis armata and *Pinus kesiya*, 05/09/2004, Huyen T. Le 226 (CMU, SFSU, GENT) – Chiang Mai Province, Khun Chae National Park, 963 m alt., N19°04' E99°23', wet forest dominated by *Castanopsis armata*, *Lithocarpus* sp. and *Pinus kesiya*, 10/06/2005, Huyen T. Le 271 (CMU, SFSU, GENT).

Notes: *Lactarius montoyae* is a species described originally from Northern India (Kumaon Himalaya). It is recognized by its slender appearance, the rather distant and broad lamellae, a dry, greyish brown cap that in mature basidiomes often develops radial pleats towards the margin and is strikingly thin-fleshy, the mild taste, and the absence of a distinct colour change in the latex or context. Microscopically the main characters are the high, zebroid spore ornamentation (2.5 µm), the palisade structure in the pileipellis and a trichoderm in the stipitipellis. The type description differs slightly in mentioning a trichopalisade in both pilei- and stipitipellis. Since this could be explained by an either more or less pronounced layer of inflated cells, we still consider these descriptions consistent with each other. The ITS-inferred phylogeny places this species definitively in *Lactarius* subgenus *Plinthogali*, and completely supports the conspecificity of the Thai and Indian specimens (Fig. 1). Other species with high, zebroid spore ornamentation that *L. montoyae* could be mistaken for are three species from Europe and North America: *L. ruginosus* Romagn., *L. pterosporus* Romagn. and *L. subplinthogalus* Coker. In contrast to *L. montoyae*, these three species exhibit a pink discoloration in the context and all three have an acrid taste. Furthermore, *L. ruginosus* can be distinguished by the moderately thick context, *L. pterosporus* by its crowded lamellae and wrinkled cap, and *L. subplinthogalus* by its paler and more yellowish colour and the hyaline and short, subcylindrical to broadly clavate terminal elements in the pileipellis.

***Lactarius subplinthogalus* Coker var. *chiangmaiensis* H.T. Le & Stubbe var. nov.** (Figs 1, 2, 6, 10)

Mycobank: 510725

Etymology: *chiangmaiensis*: 'from Chiang Mai' the type locality.

A var. typ. differt pileipellide bistrata et subpellide distincte composata cellulis globosis et a var. typ. differt sporis parvioribus.

Holotypus hic designatus: THAILAND: Chiang Mai Province, Mae Taeng Distr., Ban Mae Sae village, near 50 km marker along Highway 1095, N. 19°14.59', E. 98°38.45', 990 m alt., dominated by *Castanopsis armata*, *Lithocarpus* sp. and *Pinus* sp., 03/06/2005, Huyen T. Le 260 (CMU; *isotypus* SFSU, GENT)

Pileus 15–40 mm diam., convex when young, becoming somewhat infundibuliform with depressed centre when older; margin slightly crenate, sometimes wavy; surface dry, smooth, somewhat rugose, pale greyish brown to greyish orange (5BCD3/4). *Lamellae* adnate or subdecurrent, rather distant, 3–8 mm broad, with 2–3 series of lamellulae, pale yellow (4A3/4), when bruised

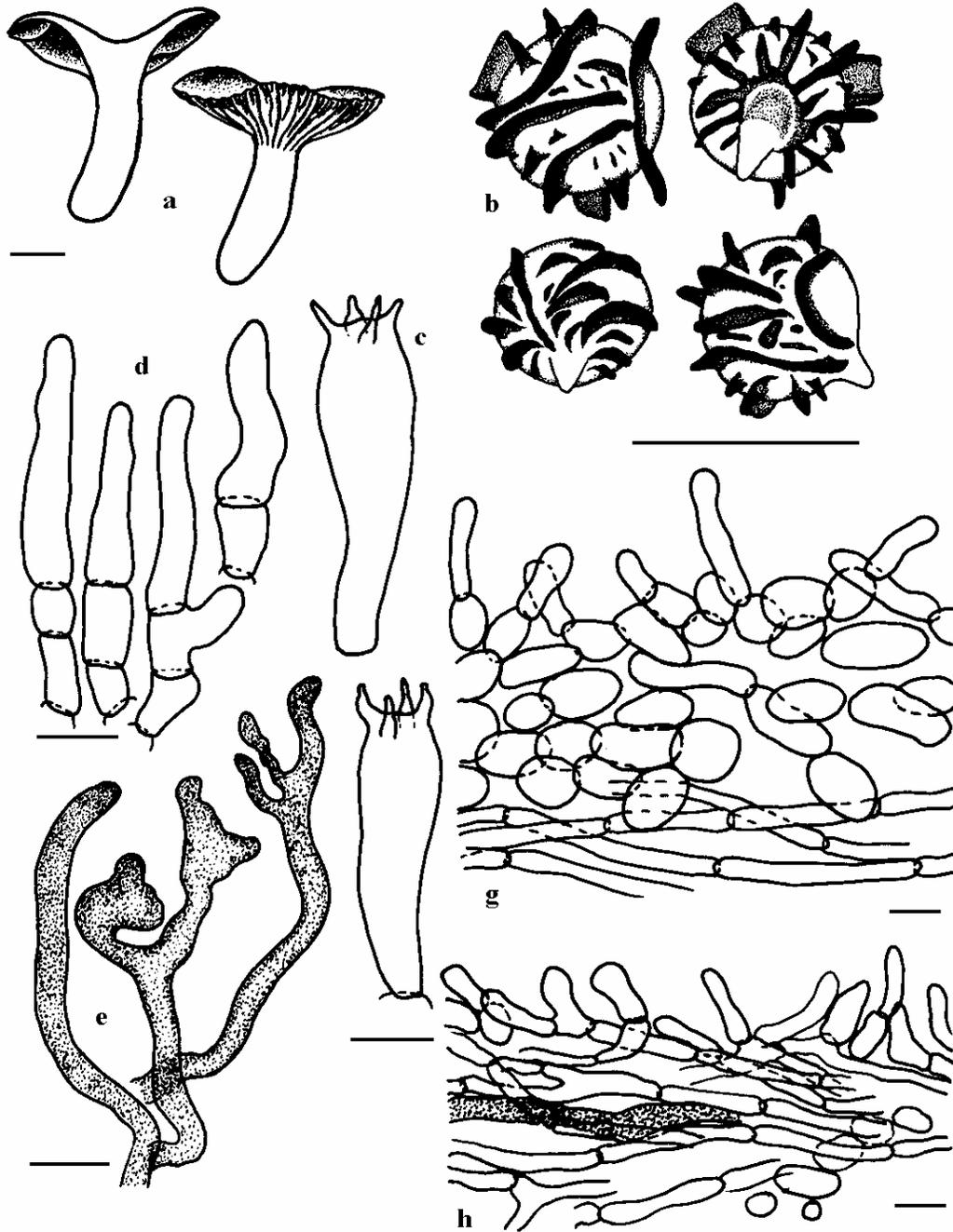


Fig. 6. *Lactarius subplinthogalus* var. *chiangmaiensis*. **a.** basidiomes, **b.** basidiospores, **c.** basidia, **d.** cheileleptocystidia, **e.** pleurospseudocystidia, **g.** pileipellis, **h.** stipitipellis. Scale bars = 10 mm (basidiomes) and 10 μ m.

becoming yellowish grey (4AB3) or pale yellowish brown to pinkish brown (5/6C7); edge entire, concolourous. *Stipe* 13-30 × 3-8 mm, more or less cylindrical, central or slightly eccentric; surface dry, smooth, concolourous with pileus, whitish to cream coloured at apex (5A2/3), somewhat greyer at base (5C3/4). *Context* moderately thick (> 5 mm) in pileus, solid in stipe, yellowish to greyish white (4AB2), turning pink (7A3/4, 7BC4/5) to greyish orange (6B3/4), pale greyish yellow (4AB3) with 10% KOH; smell none or weakly fragrant, sometimes pungent (somewhat reminiscent of sweet peppers); taste not remarkable or mild and fresh, slightly sweet. *Latex* watery white, unchanging or turning pale pinkish in contact with the context.

Spore print colour unknown. *Basidiospores* (6.2) 7.1–7.3–7.9–8.3 (8.8) × (5.6) 6.8–7.2–7.5–8.1 (8.5) μm (Q = 1.01–1.05–1.07–1.16; n = 60), globose to subglobose; ornamentation amyloid, zebroid, 2 (2.2) μm high, with long and shorter ridges, isolated and often with several ridges arranged parallel to one another, almost never branching, never reticulate; edges often finely crenulate; spore surface between the ridges often covered by numerous minute, isolated warts; plage distally amyloid. *Basidia* 35-55 × 11-15 μm, subclavate, 4-spored, often with guttate contents; sterigmata 5-7 × 1-2 μm. *Pleuromacrocystidia* absent. *Pleuropseudocystidia* 3-6 μm diam., scattered to moderately abundant, slightly emergent, subcylindrical and somewhat tortuous, sometimes irregularly branched towards the apex. *Lamellar edge* sterile, composed of cheiloleptocystidia, but basidia present in the immediate vicinity; cheiloleptocystidia 8-32 × 3-7 μm, subfusiform to rather irregular, often narrower towards the apex, hyaline, thin-walled. *Hymenophoral trama* heteromerous, composed of both cellular and filamentous elements; lactifers moderately abundant, containing fine, needle-like crystals. *Pileipellis* a palisade, 45-100 μm thick, containing pale brown, intracellular pigmentation, sometimes a thin mucus layer present, barely covering the terminal elements; suprapellis composed of subcylindrical to subfusiform terminal elements, 15-45 × 3-6 μm, upright, recumbent or almost repent, often septate with a slightly inflated base cell, thin-walled; subpellis composed of a few to several layers of thin-walled, inflated cells, 8-18 × 15-25 μm. *Stipitipellis* a trichoderm to trichopalisade with rather few inflated elements, 30-40 μm thick, hyaline or with light brown, intracellular pigmentation; terminal cells subfusiform or subclavate, 10-35 × 3-5 μm, thin-walled.

Habitat and distribution: Solitary on the soil in mixed, mid-elevation rainforests of *Pinus* and *Castanopsis*, *Lithocarpus* or *Dipterocarpus*. So far only known from Northern Thailand.

Material Examined: THAILAND: Chiang Mai Province, Mae Taeng Distr., Ban Mae Sae village, near 50 km marker along Highway 1095, N. 19°14.59', E. 98°38.45', 990 m alt., dominated by *Castanopsis armata*, *Lithocarpus* sp. and *Pinus* sp., 03/06/2005, *Huyen T. Le* 260

(**holotypus** CMU; **isotypus** SFSU, GENT) – *ibid.*, 09/06/2006, *Huyen T. Le* 420 (CMU, SFSU, GENT) – Chiang Mai Province, Mae Teng Distr., near 22 km marker along Highway 1095, 750 m alt., N19°07.57' E98°45.65', forest dominated by *Dipterocarpus* spp. and *Pinus kesiya.*, *Huyen T. Le* 13 (CMU, SFSU, GENT).

Notes: *Lactarius subplinthogalus* var. *chiangmaiensis* is characterized by its pale greyish brown to greyish orange cap colour, a moderately fleshy cap, distant lamellae, a pinkish orange discoloration of the context, and zebroid spore ornamentation with ridges easily up to 2 µm high. It closely resembles *L. subplinthogalus* Coker, a species that was described from Southeastern United States and has been reported in several countries in Asia (China, Japan, and Nepal). However, *L. subplinthogalus* var. *chiangmaiensis* contains a palisade in the pileipellis, whereas *L. subplinthogalus* var. *subplinthogalus* has a hymeniderm-like to trichopalisadic pileipellis and possesses slightly larger spores (7.5-9 (9.5) × 7-8 µm). Descriptions of the spore ornamentation of *L. subplinthogalus* var. *subplinthogalus*, and of *L. marylandicus* A.H. Sm. & Hesler and *L. pseudofuliginosus* A.H. Sm. & Hesler (both have been synonymized with *L. subplinthogalus* by Hesler and Smith (1979), state that the ridges can be branched, sometimes forming an incomplete reticulum, which is not the case for the Thai specimens. *Lactarius subplinthogalus* var. *chiangmaiensis* is comparable with the European species *L. ruginosus* Romagn., but the former can be distinguished by its clearly more distant lamellae and a denser spore ornamentation with more regular and longer ridges. Phylogenetic analysis of the ITS-sequences confirm their independent status (Fig. 1). *Lactarius montoyae*, which is found in similar habitats as *L. subplinthogalus* var. *chiangmaiensis*, is also a species with distant gills and zebroid spore ornamentation. However, *L. montoyae* differs by lacking any discoloration in context or latex, having a thin fleshed cap and spore ornamentation consisting of slightly thicker and more irregular ridges.

Lactarius friabilis H.T. Le & Stubbe **sp. nov.**

(Figs 1, 2, 7, 10)

MycoBank: 510723

Etymology: *friabilis*: 'brittle'.

Pileus 25-55 mm in diam., planoconvexus, subpapillatus, velutinus, atrocremea ad pallide luteobrunneam. *Lamellae* adnatae vel subdecurrentes, (sub)distantes, rosescentes. *Stipes* 20-45 mm longus, 4-10 mm crassus, albidus, leviter aurantiacescens. *Contextus* albidus, rosescens vel aurantiorosescens. *Latex* albus, imutabilis. *Basidiosporae* (7.0) 7.1-8.0-9.0 × 6.6-7.6-8.5 µm, globosae ad subglobosas, cristis isolatis usque ad 1.5-2(2.5) µm ornatae, macula suprahilaris distale amyloidea. *Pleuromacrocytidia* absentia. *Pileipellis* bistrata; suprapellis ex elementis cylindratis, subfusiformes vel subclavatis, 6-60 × 2-6 µm; subpellis ex hyphis et cellulis inflatis.

Holotypus hic designatus: THAILAND: Chiang Mai Province, Doi Inthanon National Park, near junction of Highway 1009 and road to Mae Chem, N18°31.58' E098°29.64', 1703 m

alt., rain forest dominated by *Quercus* sp., *Lithocarpus echinops*, and *Castanopsis armata*, 25/06/2004, Huyen T. Le 147 (CMU, isotypus GENT (*Verbeken-Walleyn* 04/115), SFSU).

Pileus 25-55 mm diam., plano-convex, centre slightly depressed, often with an inconspicuous papilla; margin somewhat irregularly wavy and striate to slightly grooved, becoming irregularly crenate when older; surface velutinous, dry, dark cream-coloured (4B3/4, 5A2) to pale yellowish brown (5DE4-5) or warm coffee-and-milk coloured and with an olive brown tinge (4DE4) (slightly reminiscent of the colours of *L. fluens* Boud.), but paler towards the margin; extreme margin dark cream-coloured. *Lamellae* adnate or subdecurrent, rather distant to subdistant, 4-10 mm broad, often interconnected by anastomosing veins, abundant, short lamellulae present, whitish (5A2) or pale yellow to greyish yellow (4(5)AB3/4), staining pinkish, orange-pinkish or brownish pinkish by the latex; edge entire, concolourous. *Stipe* 20-45 × 4-10 mm, central or slightly eccentric, rather slender, equal or slightly tapering downwards, sometimes curved at base; surface dry, smooth, paler than lamellae, yellowish white (4/5A2/3), staining slightly dirty orangish pink (6C3/4) to orange (6A8) when bruised. *Context* rather thin in pileus, stuffed in stipe, white, staining pinkish or orange-pinkish after cutting (5A3, 6B4, 7A5, 7B6, 7C8, 8B5), remaining white in the centre of the stipe; smell faintly fragrant or mealy-spermatoc, reminiscent of *L. azonites* (Bull.) Fr. *Latex* abundant, white or watery white, drying pinkish, unchanging when isolated.

Spore print colour unknown. *Basidiospores* (6.3) 7.8–7.9–8.4–9.1 × (5.8) 7.1–7.5–7.8–8.7 (8.9) μm (Q = 1.01–1.04–1.08–1.15; n = 120), globose to subglobose; ornamentation amyloid, a somewhat dense but incomplete reticulum with various free terminal ends, composed of rather irregular ridges that are 1.5-2 (2.5) μm high, more or less acute, sometimes with a split appearance and mostly irregularly crenulate edges; numerous isolated warts and short ridges present; plage distally amyloid. *Basidia* 35-75 × 10-15 μm, subclavate to clavate, mostly 4-spored but 1- and 2-spored basidia also present, sometimes with granular or guttate contents; sterigmata 2.5-10 × 1-3 μm. *Pleuromacrocystidia* absent. *Pleuropseudocystidia* 4-9 μm diam., scattered to moderately abundant, emergent, irregularly cylindrical, somewhat tortuous, sometimes branched. *Lamellar edge* mostly sterile; cheiloleptocystidia 6-36 × 3-7 μm, subcylindrical, subfusiform or subclavate, hyaline or with granular contents, thin-walled. *Hymenophoral trama* heteromerous; sphaerocytes intermixed with often somewhat inflated hyphae; lactifers moderately abundant to abundant. *Pileipellis* a trichopalysade to palysade, rather thin, 40-90 μm thick, containing pale brown, intracellular pigmentation, cell walls thin or slightly thickened and refringent, often a thin mucus layer present; suprapellis composed of long and slender terminal elements, 6-60 × 2-6 μm, cylindrical, subfusiform, sometimes subclavate, sometimes septate, mostly recumbent to

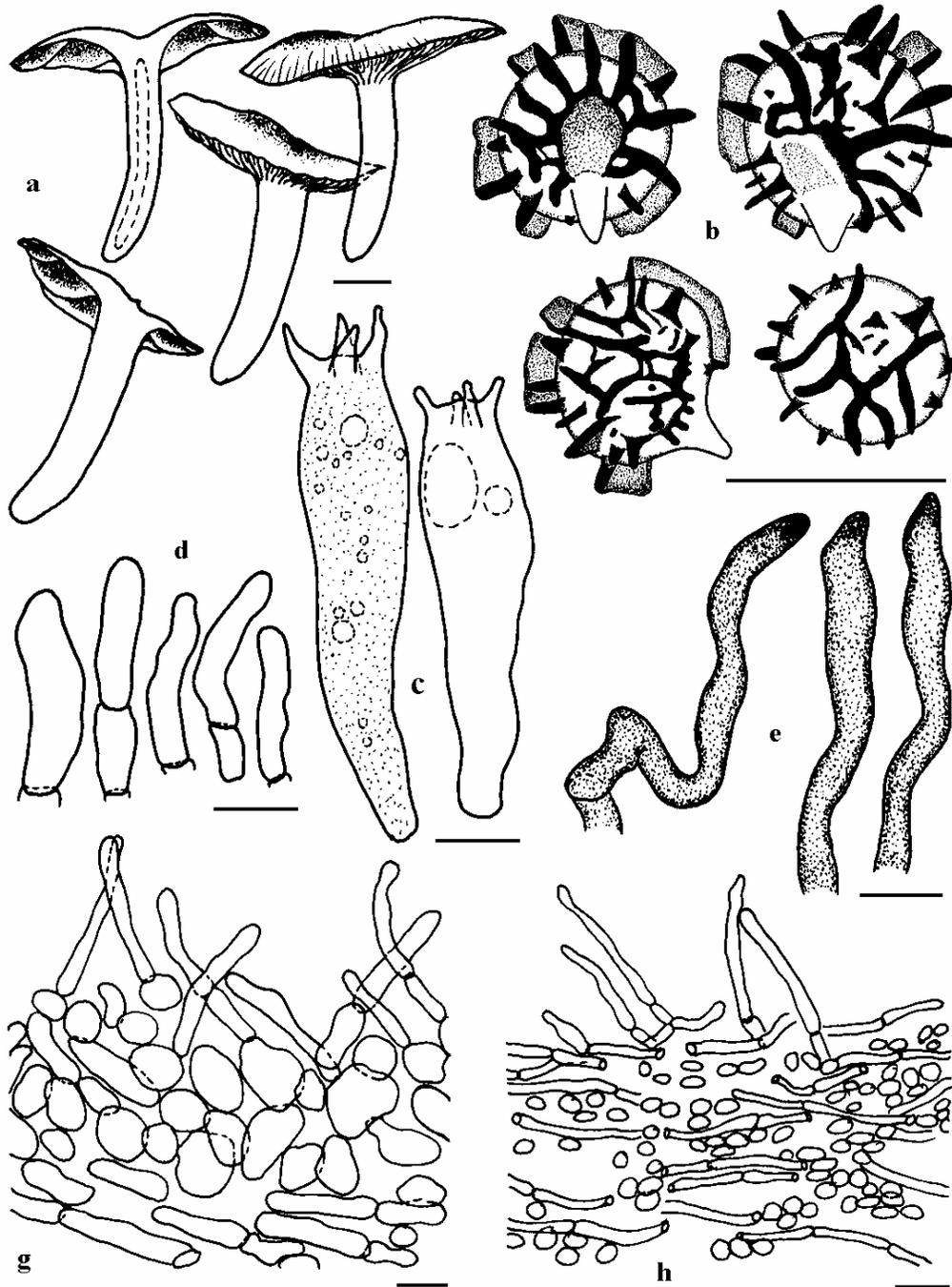


Fig. 7. *Lactarius friabilis*. **a.** basidiomes, **b.** basidiospores, **c.** basidia, **d.** cheiloleptocystidia, **e.** pleuropseudocystidia, **g.** pileipellis, **h.** stipitipellis. Scale bars = 10 mm (basidiomes) and 10 μ m.

repent, also upright; subpellis composed of few layers of inflated cells and hyphal elements, 10-25 × 10-15 μm, isodiametrically or irregularly shaped. *Stipitipellis* a cutis or trichoderm, 30-80 μm thick, hyaline.

Habitat and distribution: Solitary on the soil in montane mid-elevation rainforest with *Quercus*, *Lithocarpus*, *Castanopsis*, *Dipterocarpus* or *Pinus*.

Material Examined: THAILAND: Chiang Mai Province, Doi Inthanon National Park, near junction of Highway 1009 and road to Mae Chem, N18°31.58' E098°29.64', 1703 m alt., rain forest dominated by *Quercus* sp., *Lithocarpus echinops*, and *Castanopsis armata*, 25/06/2004, *Huyen T. Le* 147, (= *Verbeken-Walleyn* 04/115) (**holotypus** CMU, **isotype** GENT, SFSU) – Chiang Mai Province, Doi Suthep-Pui National Park, Sangasahasri Lane to Huai Kok Ma village, on soil and leaves, N18°48.62' E98°54.60', 1145 m alt., primary montane forest with predominantly *Castanopsis armata*, *Castanopsis* sp., *Schima wallichii* and *Lithocarpus polystachyus*, 24/06/2005, *leg.* D. E. Desjardin, *Huyen T. Le* 310 (CMU, SFSU, GENT) – *ibid.*, 21/07/2005, *Huyen T. Le* 355 (CMU, SFSU, GENT) – Chiang Mai Province, Doi Inthanon National Park, near 25 km marker along Highway 1009, N18°32' E098°33', 1076 m alt., rainforest dominated by *Castanopsis armata* and *Pinus* sp., 05/06/2005, *Huyen T. Le* 399 (CMU, GENT, SFSU) – Chiang Mai Province, Doi Inthanon National Park, near 22 km marker along Highway 1009, N18°32.54' E98°33.51', 1076 m alt., rainforest dominated by *Castanopsis armata* and *Pinus kesiya*, solitary on the soil, 27/06/2005, *Huyen T. Le* 325 (CMU, SFSU, GENT) – Chiang Mai Province, Mae Taeng Distr., near 22 km marker along Highway 1095, 750 m alt., N19°07.57' E98°45.65', forest dominated by *Dipterocarpus* spp. and *Pinus kesiya*, under *Pinus* sp., 04/06/2006, *leg.* R. Halling, *Huyen T. Le* 390 (CMU, SFSU, GENT).

Notes: In the field, *L. friabilis* might be confused with *L. subplinthogalus* var. *chiangmaiensis* due to the pale colours, the distant and broad lamellae, and the pink staining of the context. However, microscopically *L. friabilis* is easily distinguished by its reticulate spore ornamentation, whereas *L. subplinthogalus* var. *chiangmaiensis* has a distinctly zebroid ornamentation. In *Huyen T. Le* 325, cells with conspicuously thickened cell walls were observed in the pileipellis. However, these cells were equal in shape and size with the other pileipellis elements, and cells with intermediate cell wall thickness were present. We therefore do not consider them as true lamprocystidia. Similar thick-walled cells have been observed in *Huyen T. Le* 390, but in far lesser abundance. Pileipellis elements with refringent and slightly thickened cell walls were present in all specimens. Molecular analyses confirm all specimens belong to the same clade (Fig. 1). Within this clade, *Huyen T. Le* 325 and *Huyen T. Le* 390 were persistently grouped together, apart from the other specimens. No other differing characters were found except the thick-walled pileipellis elements. Because this appears to be a variable character, we find it precarious to describe them as a separate taxon and consider the abundance of thick-walled pileipellis elements as part of the variability within the species.

***Lactarius lavandulus* H.T. Le & Stubbe sp. nov.** (Figs 1, 2, 8a, 8b, 10)

Mycobank: 510724

Etymology: lavandulus: 'lavender-violet'

Pileus 24-46 mm in diam., planoconvexus ad infundibuliformis, papillata, rugosa, leviter striata, atrobrunnea ad luteobrunneam. *Lamellae* adnatae ad decurrentes, confertae, albidae, purpurascens vel violascens. *Stipes* 35-70 mm longus, 4-6 mm crassus, luteobrunneus ad pallide brunneum. *Context* albidus, violascens, gustu mitis. Latex abundans, albus, immutabilis. *Basidiosporae* (7.3) 7.4-8.0-8.6 × (6.7) 6.9-7.4-8.0 μm, globosae ad subglobosae, reticulatae, macula suprahilaris distale amyloidea. *Pleuromacrocystidia* absentia. *Pileipellis* bistrata; suprapellis ex elementis subcylindratis, subfusiformes vel clavatis, 10-33 × 3-13 μm, pigmento atrobrunneo; subpellis ex cellulis inflatis, pigmento atrobrunneo.

Holotypus hic designatus: THAILAND: Chiang Mai Province, Doi Inthanon National Park, on Highway 1009 at 22 km marker, N18°32.54' E98°33.51', alt. 1076 m; dominated by *Castanopsis* spp. and *Pinus kesiya*, 27/06/2005, leg. D.E. Desjardin, Huyen T. Le 314 (CMU, isotypus SFSU, GENT).

Pileus 24-46 mm diam., plano-convex to infundibuliform with central papilla; surface dry, rugose, weakly striate on the margin, dark brown (6/8F8) to yellowish brown (5E8), paler towards the margin. *Lamellae* adnate to subdecurrent, close, 2-6 mm broad, 3-4 series of lamellulae, yellowish white (3A1/2) to pale yellow (4A3), staining purplish grey (12E4) or deep violet (16D8) when bruised; edge entire, concolourous, sometimes brown. *Stipe* 35-70 × 4-6 mm, central, equal to somewhat tapering upwards, cylindrical, often curved at the base, surface dry, smooth, yellowish brown (5E5) to pale brown (5D4/5), paler towards the base, to brownish white at the base. *Context* 1.5-3 mm thick in pileus, stuffed to hollow in stipe, white, staining deep violet (16D8), becoming pale yellow (4A4) with 10% KOH, brownish grey (5D3) with FeSO₄; smell distinct, strong; taste mild. *Latex* abundant, watery white, unchanging when isolated.

Spore print yellowish white (4A2). *Basidiospores* (7.3) 7.4-8.0-8.1-8.8(9.0) × (6.7) 6.8-7.4-7.5-8.3 μm (Q = 1.02-1.07-1.08-1.14; n = 40), globose to subglobose; ornamentation amyloid, a complete and dense reticulum of fine, somewhat irregular ridges and interconnected spines ≤ 1-1.5 μm high, only few isolated warts present; plage distally amyloid. *Basidia* 40-50 × 9-13 μm, subclavate to subcylindrical, often with guttate contents, 4-spored; sterigmata 5-7 × 1.5-2 μm. *Pleuromacrocystidia* absent. *Pleuropseudocystidia* 3-5 μm diam., moderately abundant, often emergent, cylindrical, tortuous, sometimes branching, thin-walled. *Lamellar edge* sterile; cheiloleptocystidia 17-50 × 4-8 μm, long and slender, subcylindrical to subfusiform, sometimes clavate, hyaline or with brown, intracellular pigmentation, thin-walled. *Hymenophoral trama* predominantly filamentous with somewhat inflated hyphae, and scattered sphaerocysts. *Pileipellis* a palisade tending towards trichopalisade, or when subpellis reduced, tending towards hymeniderm, 40-90 μm thick; terminal elements 10-33 × 3-13 μm, subfusiform, subcylindrical or

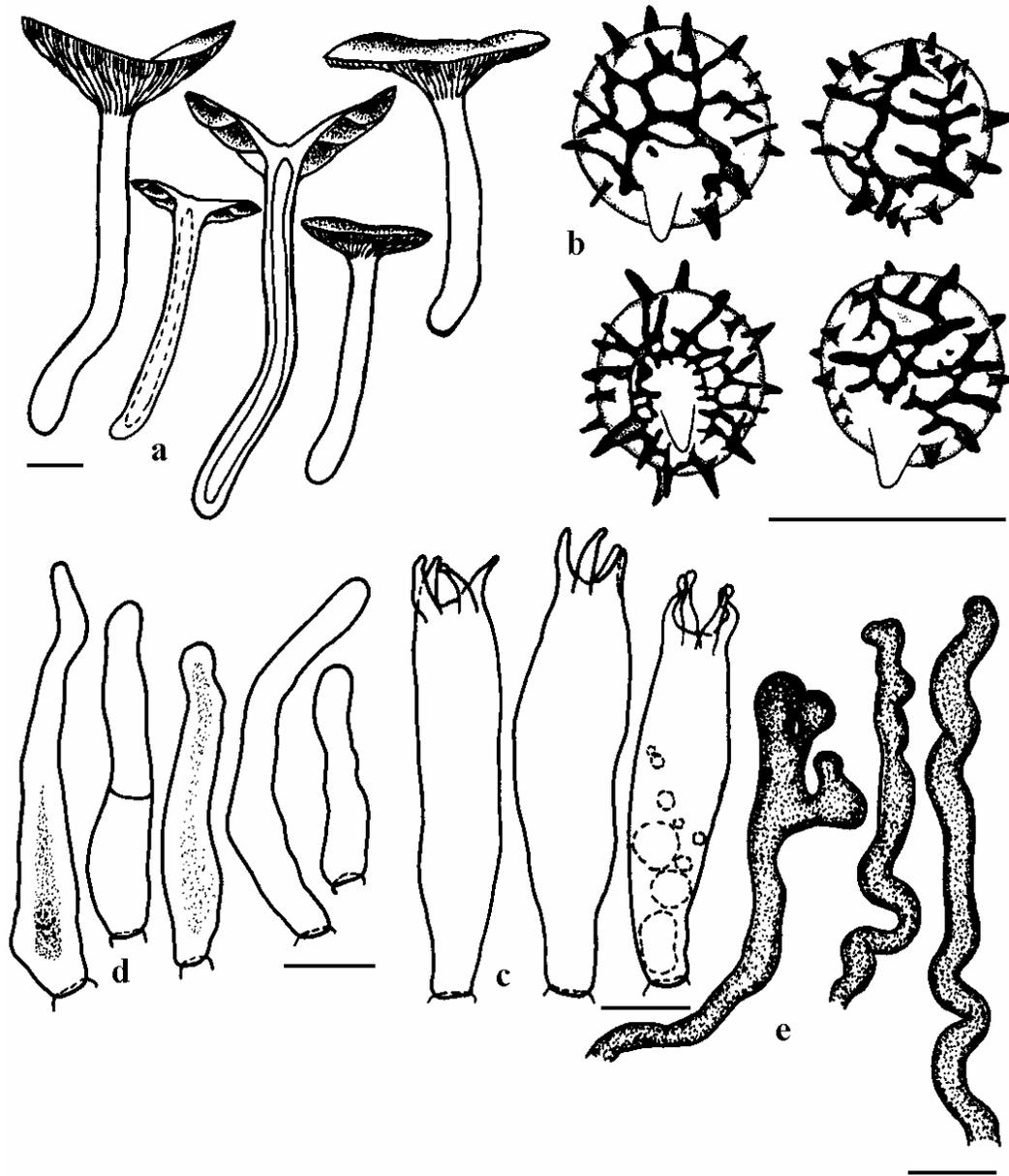


Fig. 8a. *Lactarius lavandulus*. a. basidiomes, b. basidiospores, c. basidia, d. cheiloleptocystidia, e. pleuropseudocystidia. Scale bars = 10 mm (basidiomes) and 10 μ m.

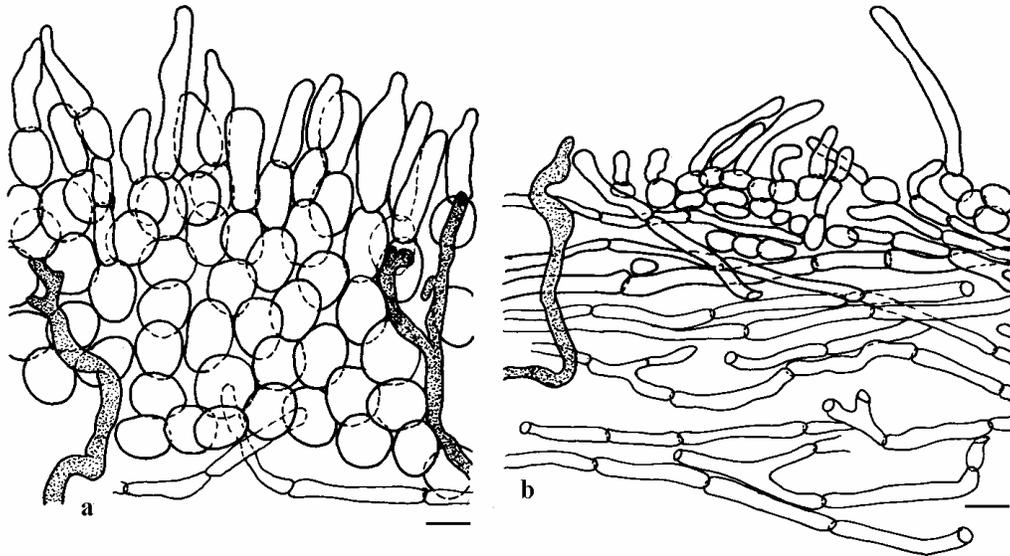


Fig. 8b. *Lactarius lavandulus*: a. pileipellis, b. stipitipellis. Scale bars = 10 μ m.

clavate, upright, containing dark brown, intracellular pigmentation; subpellis composed of a few to several layers of inflated cells, with dark brown, intracellular pigmentation in the upper cell layers. *Stipitipellis* a trichoderm, 40-60 μ m thick, containing dark brown, intracellular pigmentation in upper layers; hyphae 2-6 μ m diam.; terminal elements repent or recumbent.

Habitat and distribution: Growing solitary or gregarious in mixed, montane rainforests with *Castanopsis* and *Pinus*. So far only known from Northern Thailand.

Material Examined: THAILAND: Chiang Mai Province, Doi Inthanon National Park, on Highway 1009 at 22 km marker, N18°32.54' E98°33.51', alt. 1076 m; dominated by *Castanopsis* spp. and *Pinus kesiya*, 27/06/2005, leg. D.E. Desjardin, Huyen T. Le 314 (**holotypus** CMU, **isotype** SFSU, GENT) – *ibid.*, 27/06/2005, leg. A. Honnan, Huyen T. Le 315 (CMU, SFSU, GENT) – Chiang Mai Province, Doi Inthanon National Park, on Highway 1009 at 22 km marker, N18°32.54' E98°33.51', alt. 1076 m; dominated by *Castanopsis* spp. and *Pinus kesiya*, 25/06/2004, Huyen T. Le 144 (CMU, SFSU) = *Verbeken-Walleyn* 04/102 (GENT) – *ibid.*, scattered under *Quercus* sp. and *Pinus kesiya*, 26/06/2003, DED 7576 (CMU, SFSU, GENT) – Chiang Mai Province, Doi Suthep-Pui National Park, Sangasabhasri Lane to Huai Kok Ma village, N18°48.62' E098°54.60', alt. 1200 m, solitary on the soil under *Quercus* sp. in montane primary rain forest dominated by *Castanopsis* spp. and *Lithocarpus polystachyus*, 06/07/2002, DED 7469 (CMU, SFSU, GENT).

Notes: The brown cap with the small papilla, the concolourous stipe that is somewhat long and slender compared to the cap diameter and the pale, dense lamellae give *L. lavandulus* a stature comparable with the blackish brown *L. lignyotus* Fr. In addition to the different colour, *L. lavandulus* is distinguished

by staining purplish grey in the lamellae when bruised and by a strikingly violet discoloration of the context. The description is based on the collections *Huyen T. Le* 314 and *Huyen T. Le* 315 which both clearly displayed a violet colour reaction. However, the colour reaction appears to be subject to variability. The other collections did not exhibit any obvious violet discoloration in the context, but a similar purplish brown to blackish staining was observed in the lamellae. The results of the phylogenetic analysis of the ITS-sequence did not show segregation between the violet staining and non violet staining specimens (Fig. 1). This violet colour reaction is reminiscent of the North American species *L. lignyotus* var. *nigroviolascens* (Atk. in Burl.) Hesler & A.H. Sm. and *L. lignyotus* var. *marginatus* (A.H. Sm. & Hesler) Hesler & A.H. Sm. Comparison with the type material of both varieties revealed distinct differences in spore ornamentation and pileipellis structure. *Lactarius lignyotus* var. *nigroviolascens* (Atkinson 24257, CUP) possesses spores bearing an incomplete and fairly wide-spaced reticulum of irregular and rather acute warts partially interconnected by fine lines. Spore ornamentation of *L. lignyotus* var. *marginatus* (Smith 63004, MICH) consists of higher and coarser warts interconnected by fine lines, the warts often being blunt and slightly broader towards the apex. Its pileipellis is an unambiguous trichopalisade with elongated, chain-like arranged, inflated elements and slender terminal cells. These observations rule out conspecificity between the Thai and North American species.

Lactarius* aff. *gerardii Peck, Bull. Buffalo Soc. Nat. Sci. 1: 57 (1873)

(Figs 1, 2, 9, 10)

Pileus 20-90 mm diam., plano-convex with papilla to slightly depressed or subumbilicate with irregular papilla, sometimes applanate; surface dry, glabrous to slightly velvety, sometimes smooth but in centre mostly radially rugulose and towards the margin veined or grooved, dark yellowish brown (5D4, 5EF6, 5F7) and dark brown (6F7/8) near the margin; margin irregularly crenulate or wavy, in older specimens sometimes faintly, translucently striate. *Lamellae* decurrent to deeply decurrent with tooth, subdistant to distant, 1.5-11 mm broad, yellowish white (2/3A2) to pale yellow (4A3), 2-3 lamellulae between 2 lamellae; edge smooth, often brown (5E3/4) on the entire length. *Stipe* 30-82 × 6-17 mm, central to eccentric, equal or tapering downwards, cylindrical; surface dry, smooth or with shallow longitudinal wrinkles, concolourous with pileus, dark brown (5/6F7/8) or yellowish brown (5E7), the base often paler (5D5) or even whitish. *Context* 1.5-6 mm thick in pileus, hollow in stipe, white, unchanging; yellowish white with 10% KOH, pale

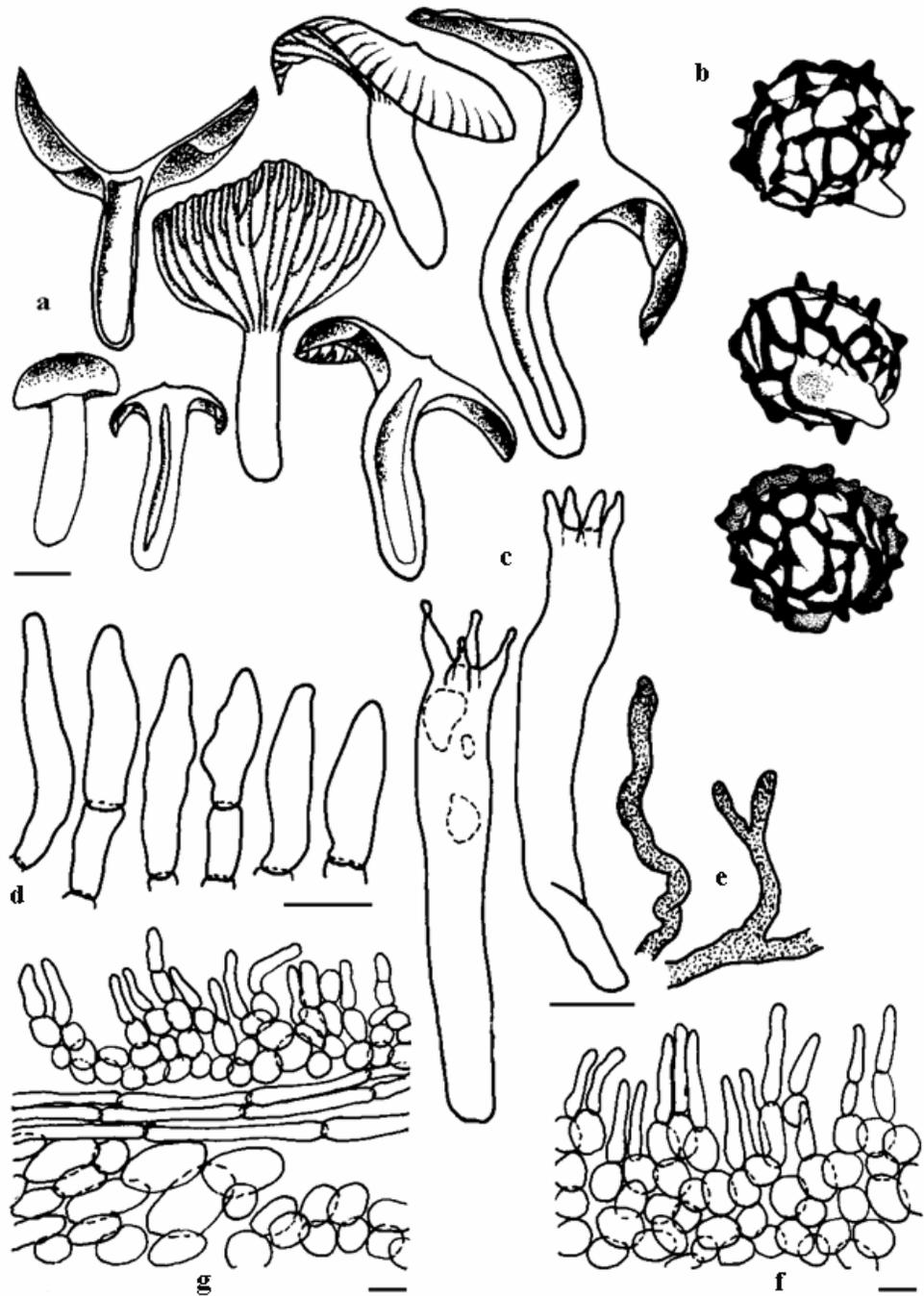


Fig. 9. *Lactarius* aff. *gerardii*. **a.** basidiomes, **b.** basidiospores, **c.** basidia, **d.** cheiloleptocystidia, **e.** pleuropseudocystidia, **f.** pileipellis, **h.** stipitipellis. Scale bars = 10 mm (basidiomes) and 10 μ m.



Fig. 10. Basidiocarps of *Lactarius* subgenus *Plinthogali*. 1. *Lactarius lavandulus*. 2. *Lactarius oomsisiensis*. 3. *Lactarius montoyae*. 4. *Lactarius subplinthogalus* var. *chiangmaiensis*. 5. *Lactarius crassiusculus*. 6. *Lactarius friabilis*. 7. *Lactarius* aff. *gerardii*. (Photos 1, 2, 3, 4, 5, 7: Huyen T. Le; 6: Ruben Walley).

orange with FeSO₄; smell not remarkable; taste mild, slightly sweet. *Latex* abundant, white, unchanging; pale yellow with 10% KOH.

Spore print colour unknown. *Basidiospores* 6.6–7.9–9.3 × (5.4)5.8–7.1–8.4 μm (Q = 1–1.12–1.3; n = 20), globose to broadly ellipsoid; ornamentation up to 0.5 (1.8) μm high, forming a ± complete reticulum, ridges broad and stout, rounded, never acute; plage centrally diffusely amyloid. *Basidia* 42–72 × 9.5–11.5 μm, subcylindrical to clavate, hyaline or with guttate content, 4-spored; sterigmata 5–14 × 1.5–3 μm. *Pleuromacrocystidia* absent. *Pleuropseudocystidia* 8–10 μm diam., abundant, emergent, cylindrical and often somewhat tortuous, thin-walled, with lactiferous contents. *Hymenophoral trama* mostly cellular or with frequently septate hyphae; lactifers moderately abundant. *Lamellar edge* sterile; cheiloleptocystidia 22–50 × 3–7 μm, subcylindrical to subfusiform, thin-walled, hyaline or with brown intracellular pigmentation. *Pileipellis* a palisade, 33–100 μm thick, with brown intracellular pigmentation; suprapellis composed of terminal elements (18–37 × 5 μm), subcylindrical, thin-walled; subpellis composed of few to several layers of inflated cells, 9–25 μm diam. *Stipitipellis* a palisade, 25–70 μm thick, containing intracellular, brown pigmentation, sometimes resembling a trichoderm because of a very degenerated subpellis; terminal cells 15–25 × 5–6 μm, subcylindric to subfusiform, thin-walled, erect or oblique; subpellis composed of few layers of inflated cells, sometimes barely forming a layer.

Habitat and distribution: Rather common in June during the beginning of the rainy season, in the mid-elevation rainforests of northern Thailand and southern China. Associated with *Lithocarpus* or *Castanopsis*.

Material Examined: THAILAND: Chiang Mai Province, Mae Taeng Distr., Ban Pa Deng village, at MRC, in montane rain forest, 01/06/2004, *Huyen T. Le* 101 (CMU, GENT, SFSU) – Chiang Mai Province, Doi Suthep-Pui National Park, Sangasahasri Lane to Huai Kok Ma village, N18°48.62' E98°54.60', alt. 1145 m, primary montane rain forest with *Castanopsis* spp. and *Lithocarpus polystachyus*, 30/06/2003, *DED* 7599 (CMU, SFSU, GENT) – *ibid.*, 24/06/2004, *Huyen T. Le* 134 (CMU, SFSU, GENT) – *ibid.*, 24/06/2004, *Huyen T. Le* 135 (CMU, SFSU, GENT) – *ibid.*, 24/06/2005, *Huyen T. Le* 295 (CMU, SFSU, GENT) – *ibid.*, 24/06/2005, *Huyen T. Le* 302 (CMU, SFSU, GENT) – *ibid.*, 02/07/2005, *Huyen T. Le* 343 (CMU, SFSU, GENT) – *ibid.*, *Huyen T. Le* 411 (CMU, SFSU, GENT) – Chiang Mai Province, Mae Taeng dist., Ban Pha Deng village, at the MRC in plot 11, area dominated by *Lithocarpus* spp., 13/09/2004, *Huyen T. Le* 246 (CMU, GENT, SFSU) – Chiang Rai Province, Khun Chae National Park, alt. 963 m, N19°04' E99°23', montane rain forest dominated by *Castanopsis armata*, *Castanopsis* spp. and *Pinus* spp., 10/06/2005, *Huyen T. Le* 270 (CMU, SFSU, GENT) – Chiang Mai Province, Doi Inthanon National Park, junction of highway 1009 and road to Mae Chem, alt. 1703 m, N18°31.58' E98°29.64', montane rain forest dominated by *Castanopsis armata*, *Castanopsis* spp. and *Pinus* spp., 27/06/2005, *leg.* D.E. Desjardin, *Huyen T. Le* 317 (CMU, SFSU, GENT) – *ibid.*, 05/06/2006, *leg.* Osmundoni T., *Huyen T. Le* 400 (CMU, SFSU, GENT) – Chiang Mai Province, Mae Taeng Distr., Mae Sae village, highway 1095, near 55 km marker, N19°14' E98°38', alt. 990 m, *Huyen T. Le* 388 (CMU, SFSU, GENT) – Chiang Mai Province, Mae Teng Distr., Highway 1095 at 22 km marker, alt. 750 m, N19°07.57' E98°45.65',

mixed forest with *Dipterocarpus* spp. and *Pinus kesiya*, under *P. kesiya*, 04/06/2006, *Huyen T. Le* 394 (CMU, SFSU, GENT) – Chiang Mai Province, Doi Inthanon National Park, Highway 1009 at 25 km marker, N18°32.54' E098°33.51', 1076 m alt., montane rain forest dominated by *Castanopsis armata* and *Pinus* sp., 05/06/2006, *Huyen T. Le* 404 (CMU, SFSU, GENT).

Notes: The above description is based on *Huyen T. Le* 270, and is presented here as an example of several similar collections that have been made in the same or other localities in Northern Thailand. All of them are characterized by a dark brown, rugose cap, whitish and distant lamellae often with a dark brown edge, contrasting with the dark brown stipe, and exhibiting no discoloration in context nor latex. The phylogenetic analyses of the Thai specimens show that they indeed form one clade together with the American *L. gerardii* (*Verbeken* 05-235) (Fig. 1). What is more, the analyses reveal within the *gerardii*-group, two highly supported clades that could not be correlated with any distinct morphological findings. A study by *Verbeken, Wang and Stubbe* (in preparation) compares North American collections of *L. gerardii* with East Asian look-a-likes (from China, Korea and Japan) and with the closely resembling Malayan species *L. bicolor* *Massee*. The basidiospores of these East Asian collections appear to be globose to subglobose instead of ellipsoid like those of their American counterparts. Due to this difference, and acknowledging the geographical disjunction, a new subspecies will be described for these East Asian collections. *Lactarius bicolor* differs from *L. gerardii* by the bigger and thin-fleshy basidiocarps, globose to subglobose basidiospores and stouter terminal elements in the pileipellis and lamellar marginal cells.

The phylogenetic analyses presented here also indicate the *gerardii*-complex as a separate clade from the other members of *L. subg. Plinthogali*. Unpublished data (by *Stubbe et al.*) even confirm its complete removal from the subgenus, despite the very fitting morphological characters. In light of these findings and the new collections made in Thailand, a more broad-scaled and molecular approach will be required to untangle the exact nature of the species complex surrounding *L. gerardii*.

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References

- Das, K., Sharma J.R. and Verbeken A. (2003). New species of *Lactarius* from Kumaon Himalaya, India. *Mycotaxon* 88: 333-342.
- Das, K. and Sharma J.R. (2004). *Lactarius* in Kumaon Himalaya – 2: New and interesting species of subgenus *Plinthogali*. *Mycotaxon* 89: 289-296.
- Das, K., Sharma J.R. and Montoya L. (2004a). *Lactarius* (*Russulaceae*) in Kumaon Himalaya. 1. New species of subgenus *Russularia*. *Fungal Diversity* 16: 23-33.
- Das, K., Sharma J.R. Montoya L. (2004b). *Lactarius* in Kumaon Himalaya 3: A new species of subgenus *Lactifluus*. *Mycotaxon* 90: 285-290.
- Das, K., Sharma J.R., Basso, M.T. and Bhatt, R.P. (2005a). *Lactarius* in Kumaon Himalaya 4: A new species of subgenus *Piperites*. *Mycotaxon* 91: 1-7.
- Das, K., Miller, S.L., Sharma, J.R., Sharma, P. and Bhatt, R.P. (2005b). *Russula* in Himalaya 1: A new species of subgenus *Amoenula*. *Mycotaxon* 94: 85-88.
- Das, K., Miller, S.L. and Sharma, J.R. (2006). *Russula* in Himalaya 2: Four new taxa. *Mycotaxon* 95: 205-215.
- Eberhardt, U. and Verbeken, A. (2004). Sequestrate *Lactarius* species from tropical Africa: *L. angiocarpus* sp nov. and *L. dolichocaulis* comb. nov. *Mycological Research* 108: 1042-1052.
- Gardes, M. and Bruns, T.D. (1993). ITS primers with enhanced specificity for basidiomycetes - application to the identification of mycorrhizae and rusts. *Molecular Ecology* 2: 113-118.
- Hall, T.A. (1999). BioEdit: a user-friendly biological sequence alignment editor and analysis program for Windows 95/98/NT. *Nucleic Acids Symposium Series* 41: 95-98.
- Hesler, L.R. and Smith, A.H. (1979). *North American species of Lactarius*. University of Michigan Press, Ann Arbor, USA.
- Kornerup, A. and Wanscher, J.H. (1978). *Methuen Handbook of Colour*. London, Eyre Methuen.
- Le, H.T., Nuytinck, J., Verbeken, A., Desjardin, D.E. and Lumyong, S. (2007). *Lactarius* in Northern Thailand: 1. *Lactarius* subgenus *Piperites*. *Fungal Diversity* 24: 173-224
- Massee, G. (1914). *Fungi Exotici*: XVII. *Kew Bulletin*: 72-76.
- Nuytinck, J., Verbeken, A., Delarue, S. and Walley, R. (2003). Systematics of European sequestrate lactarioid russulaceae with spiny spore ornamentation. *Belgian Journal of Botany* 136: 145-153.
- Nuytinck, J., Wang, X.-H. and Verbeken, A. (2006). Descriptions and taxonomy of the Asian representatives of *Lactarius* sect. *Deliciosi*. *Fungal Diversity* 22: 171-203.
- Posada, D. and Crandal, K.A. (1998). MODELTEST: testing the model of DNA substitution. *Bioinformatics* 14: 817-818.
- Sharma, J.R. and Das, K. (2003). New and interesting species of *Lactarius* from India. *Mycotaxon* 88: 377-385.
- Shimono, Y., Kato, M. and Takamatsu, S. (2004). Molecular phylogeny of *Russulaceae* (Basidiomycetes; *Russulales*) Inferred from the nucleotide sequences of nuclear large subunit rDNA. *Mycoscience* 45: 303-316.
- Stubbe, D., Verbeken, A. and Watling, R. (2007). Blue staining species of *Lactarius* subgenus *Plinthogali* in Malaysia. *Belgian Journal of Botany* 140: 180-195.

- Swofford, D.L. (2002). PAUP*: *Phylogenetic analysis using parsimony and other methods*. Version 4.0b10 edition. Sinauer associates, Sunderland, Massachusetts.
- Thompson, J.D., Gibson, T.J., Plewniak, F., Jeanmougin, F. and Higgins, D.G. (1997). The CLUSTAL X windows interface: flexible strategies for multiple sequence alignment aided by quality analysis tools. *Nucleic Acids Research* 22: 4876-4882.
- Verbeken, A. (1998). Studies in tropical African *Lactarius* species. 5. A synopsis of the subgenus *Lactifluus* (Burl.) Hesler and A.H. Sm. Emend. *Mycotaxon* 66: 363-386.
- Verbeken, A., Bougher, N.L. and Halling, R. (2002). *Lactarius* (Basidiomycota, *Russulaceae*) in Papua New Guinea. 3. Two new *Lactarius* species in subgenus *Plinthogali*. *Australian Systematic Botany* 15: 796-771.
- Verbeken, A. and Horak, E. (1999). *Lactarius* (Basidiomycota) in Papua New Guinea 1. Species of Tropical Lowland Habitats. *Australian Systematic Botany* 12: 767-77
- Verbeken, A. and Horak, E. (2000). *Lactarius* (Basidiomycota) in Papua New Guinea 2. Species in Tropical-montane Rainforests. *Australian Systematic Botany* 13: 649-707.
- Verbeken, A., Horak, E. and Desjardin, D.E. (2001). *Agaricales* of Indonesia. 3. New records of the genus *Lactarius* (Basidiomycetes, *Russulales*) from Java. *Sydowia* 53: 261-289.
- Wang, X.-H. and Verbeken, A. (2006). Three new species of *Lactarius* subgenus *Lactifluui* (*Russulaceae*, *Russulales*). *Nova Hedwigia* 83: 167-176.
- White, T.J., Bruns T., Lee, S.S. and Taylor, J. (1990). Amplification and direct sequencing of fungal ribosomal RNA genes for phylogenetics. In: Innis M.A., Gelfand D.H., Sninsky J.J. and White T.J. (eds.) *PCR protocols: a guide to methods and applications*. Academic Press, New York, U.S.A., 315-322.

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