
Lactarius* in Northern Thailand: 1. *Lactarius* subgenus *Piperites

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This paper reports on *Lactarius* subgenus *Piperites* from northern Thailand and is the first in a series resulting from a complete revision of the genus for the area. Five taxa are described as new for science: *Lactarius formosus*, *L. austrotorminosus*, *L. austrozonarius*, *L. alboscrobiculatus* and *L. alboscrobiculatus* var. *roseopurpureus*. Three other new species are described and illustrated, but not formally described. *Lactarius akahatsu* and *L. hatsudake*, described from Japan, are recorded for Thailand, and *L. purpureus*, described from Thailand in 1966 is also listed here with new records. Species concepts and comparisons with species of other continents are based on morphological and molecular data (ITS-region).

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

Introduction

In tropical forests of South-East Asia, knowledge of the genus *Lactarius* is poor and fragmentary, although the genus is one of the more important ectomycorrhizal genera in these ecosystems, associated with *Fagaceae* (*Castanopsis*, *Lithocarpus*), *Dipterocarpaceae* (*Dipterocarpus*) and *Pinaceae* (*Pinus*). Recent studies of the genus are available for Papua New Guinea (Verbeken and Horak, 1999, 2000) and for Java (Verbeken *et al.*, 2001). This paper deals with northern Thailand species in *Lactarius* subgenus *Piperites* and is part of a larger study of the entire genus in this area.

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The seasonal climate in northern Thailand is ideal for the presence of *Lactarius* and the ectotrophic forests that occur there are likely to host a diversity of species in the genus. The physical geography of northern Thailand includes all of the highest peaks in Thailand (Doi Inthanon 2565 m). The climate of northern Thailand is strongly seasonal. The annual rainfall varies from 1100 to 1500 mm, with over 80% of the annual rainfall within the 6 months rainy season (from May to October). The months of December, January and February are virtually without rain (Gardner *et al.*, 2000). Three vegetation zones are recognized in the forests: lowland forests (<800 m), mid-elevation forests (800–1200 m), and highland forests (1200–2565 m). The floral composition of the mid-elevation forest is transitional between lowland and highland forests, containing a proportion of both lowland and highland species and resulting in some of the most species-rich forests in northern Thailand (Gardner *et al.*, 2000). Many of the forests of northern Thailand contain members of the *Fagaceae* (*Quercus* spp., *Castanopsis* spp.), *Dipterocarpaceae* (*Dipterocarpus* spp.), and *Pinaceae* (*Pinus* spp.). These three plant families contain the major hosts of ectomycorrhizal fungi such as *Lactarius*.

The studies in similar areas revealed a high diversity of ectomycorrhizal fungi. Watling has studied boletes from south Asia throughout Malaysia and Thailand with equivalent, temperate spring and autumn seasons (Watling, 2001). Verbeken and Horak studied *Lactarius* in Papua New Guinea where the climate is similar to the climate in South-East Asia (Verbeken and Horak, 1999, 2000; Verbeken *et al.*, 2001).

Few species of *Lactarius* have been recorded from Thailand (Heim, 1962): *L. roseophyllus* and *L. purpureus* have been described from northern Thailand and the European *L. volemus* is reported. Of these species, only *L. purpureus* is a representative of *Lactarius* subgenus *Piperites* (Heim, 1962).

The subgenus is very well represented in temperate regions and is treated here in a broad sense, covering the subgenera '*Lactarius*' (*Deliciosi*), *Colorati*, *Piperites* and *Tristes* as defined by Hesler and Smith (1979) and Bon (1983). The representatives are characterized by a slimy to sticky, rarely dry pileus, often hairy and/or with concentric zones; a dry or sticky stipe which is often scrobiculate; the pileipellis is an ixocutis to an ixotrichoderm, more rarely a cutis to a trichoderm. In temperate regions the subgenus is subdivided in different sections, using the colour and colour changes of the latex as a major character.

Molecular data were used here to primarily aid in delimiting species concepts, and for comparisons with species from other continents. Moreover,

the inferred phylogeny can be used to test current sectional concepts and to aid in recognizing different groups within this subgenus.

Materials and methods

Morphological approach

The study is based on collections made by Le and Desjardin during the period 2003–2006, augmented with collections of Verbeken and Walleyne made in June 2004.

The studied material is deposited in the following herbaria: Herbarium Universitatis Gandavensis (GENT), Herbarium of Chiang Mai University (CMU), and San Francisco State University (SFSU).

Macromorphological features are all based on fresh material and document all aspects of size, shape, colour and colour changes, texture, odor and taste, and latex features (Hesler and Smith, 1979). Features of both young and old fruit bodies were recorded. The colours were described in daylight using terms and notations in a colour guide by Kornerup and Wanscher (1978). Latex colour was recorded as it was exuded from the mushroom, from a drop placed on a glass slide held over white paper, and from a drop placed directly on white paper. We also observed changes of the latex on the context or lamellae. Latex colour changes through time were also recorded. The reaction of tissue of the pileus and latex to the chemicals FeSO_4 and KOH (2.5%–10%) was noted. Pictures of the fruit bodies will be published on the *Russulales* News website (<http://www.mtsn.tn.it/russulales-news/>).

Micromorphological characters were documented from the analyses of dried material. Spores were observed in Melzer's reagent for measurements and drawings; all other structures in 2–5% KOH or Congo-red. For each collection at least 20 spores were measured. Spores were measured in side view in Melzer's reagent, excluding the ornamentation and measurements are given as (MINa) $[AVa - 2 \cdot SD] - AVa - AVb - [AVb + 2 \cdot SD]$ (MAXb) in which AVa = lowest mean value for the measured collections, AVb = greatest mean value and SD = standard deviation calculated for the measurements of one collection. Q stands for "quotient length/width" and is given as (MINQa) $Qa - Qb$ (MAXQb) in which Qa, resp. Qb, stand for the lowest, respectively the highest, mean quotient for the measured specimens. All pertinent micromorphological features were illustrated with the aid of a drawing tube attached to an Olympus CX-41 research compound microscope. For the details of description and terminology of micromorphological features see Verbeken (1998).

Molecular approach

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 the ITS1-F primer (Gardes and Bruns, 1993) and the 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 (accession numbers in 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 (S1673, M3027).

Neighbor joining analysis was performed with PAUP* 4b10 (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.

Maximum likelihood analyses were performed using PAUP*. The model of sequence evolution was optimized using likelihood ratio tests as implemented in Modeltest. Gaps were treated as missing data and phylogenies

Table 1. Specimens used for the phylogenetic analyses.

Species	Origin	Collection number (herbarium)	GenBank accession number or UNITE
<i>L. akahatsu</i>	Japan, Tottori	22601 (TMI)	EF141556
<i>L. akahatsu</i>	Thailand	LTH162 (GENT)	EF141544
<i>L. alboscrobiculatus</i>	Thailand	LTH175 (GENT)	EF141538
<i>L. alboscrobiculatus</i>	Thailand	LTH257 (GENT)	EF141539
<i>L. alboscrobiculatus</i> var. <i>roseopurpureus</i>	Thailand	LTH148 (GENT)	EF141540
<i>L. aurantiacus</i>		UE 11.10.2004-4	UDB000887
<i>L. austrotorminosus</i>	Thailand	LTH111 (GENT)	EF141531
<i>L. austrotorminosus</i>	Thailand	LTH130 (GENT)	EF141532
<i>L. austrotorminosus</i>	Thailand	LTH191 (GENT)	EF141533
<i>L. austrozonarius</i>	Thailand	LTH129 (GENT)	EF141535
<i>L. austrozonarius</i>	Thailand	LTH299 (GENT)	EF141536
<i>L. controversus</i>		AV2000-117	UDB000859
<i>L. deliciosus</i>	Italy	JV 96-457 (GENT)	DQ922490
<i>L. deterrimus</i>	Slovakia	JN 2001-053 (GENT)	DQ922515
<i>L. formosus</i>	Thailand	LTH382 (GENT)	EF141549
<i>L. hatsudake</i>	Thailand	LTH167 (GENT)	EF141545
<i>L. hatsudake</i>	Japan, Kagoshima	24414 (TMI)	EF141555
<i>L. lacunarum</i>		UE 04.09.2004-4	UDB000878
<i>L. porninsis</i>	Slovakia	JN 2001-082 (GENT)	DQ922547
<i>L. purpureus</i>	Thailand	LTH99 (GENT)	EF141541
<i>L. purpureus</i>	Thailand	LTH120 (GENT)	EF141542
<i>L. purpureus</i>	Papua New Guinea	E4552	EF141543
<i>L. repraesentaneus</i>			AY331011
<i>L. sanguifluus</i>	Belgium	JN 2000-008 (GENT)	AY332547
<i>L. scrobiculatus</i>			AF140262, AF140263
<i>L. sp.</i>	Thailand	LTH93 (GENT)	EF141550
<i>L. sp.</i>	Thailand	LTH100 (GENT)	EF141551
<i>L. sp.</i>	Thailand	LTH374 (GENT)	EF141552
<i>L. sp.1</i>	Thailand	LTH174 (GENT)	EF141548
<i>L. sp.2</i>	Thailand	LTH351 (GENT)	EF141546
<i>L. sp.3</i>	Thailand	LTH332 (GENT)	EF141534
<i>L. speciosus</i>	USA, North Carolina	AV 04/206	EF141547
<i>L. subsericatus</i>			AF140261
<i>L. torminosus</i>			DQ367908, AY336959
<i>L. uvidus</i>			AY606957, AJ534936
<i>L. zonarius</i>		UE 27.09.2002-4	UDB000865
<i>L. aff. wenquanensis</i>	Thailand	LTH143 (GENT)	EF141537
Outgroup			
<i>L. sp. (Plinthogali)</i>	Thailand	LTH281 (GENT)	EF141554
<i>L. sp. (Plinthogali)</i>	Thailand	LTH325 (GENT)	EF141553
<i>L. lignyotus</i>	Germany		AY606949

were obtained using the heuristic search option and TBR branch swapping. Bootstrap support for branches was calculated with 100 bootstrap replicates with a rearrangement limit of 10000.

Results

Key to the species

1. Latex orange or vinaceous red from the beginning2
1. Latex white or yellow when exuded, unchanging or eventually changing to another colour ..3
2. Latex orange remaining so or eventually slowly becoming vinaceous red; pileus pale orange to orange; spore ornamentation up to 0.7 μm high **1. *L. akahatsu***
2. Latex reddish brown (vinaceous red) from the beginning; pileus pale greyish wine red to pinkish; spores somewhat heavier ornamented (up to 1 μm) **2. *L. hatsudake***
3. Latex changing to violet, purplish or bright yellow4
3. Latex unchanging, white and remaining so6
4. Latex changing to bright yellow **3. *L. sp. 1***
4. Latex changing to violet or purplish5
5. Pileus with distinctly hairy margin and with glutinous hairs on the surface, changing quickly to dark purple when bruised; latex becoming dark purple; spore ornamentation up to 0.6(1.6) μm high, composed of rather broad and rounded ridges with inamyloid plage **4. *L. formosus***
5. Pileus at most ciliate at margin, not changing when bruised; latex becoming reddish lilac; spore ornamentation up to 1.7(2) μm high, composed of spiny, acute ridges with distally amyloid plage **5. *L. sp. 2***
6. Context changing to pink; pileus surface viscid, smooth, zonate with striate margin, light yellow, staining pinkish white to brownish orange when bruised **6. *L. sp. 3***
6. Context unchanging; not with this combination of characters7
7. Margin of pileus distinctly hairy, tomentose and remaining so8
7. Margin of pileus smooth or slightly tomentose when young, glabrescent10
8. Stipe not or hardly scrobiculate; pileus with dominant pinkish tinges, strongly or vaguely zonate **7. *L. austrotorminosus***
8. Stipe distinctly scrobiculate with large and abundant scrobicules, pileus yellowish, strongly zonate9
9. Spore ornamentation 2.5 (3.5) μm high **8. *L. austrozonarius***
9. Spore ornamentation 0.5 (0.8) μm high **9. *L. aff. wenquanensis***

10. Pileus, lamellae and stipe remarkably unicolourous reddish purple; pileus surface scaly; lamellae distant to close **10. *L. purpureus***
10. Pileus with pale whitish colours (sometimes locally purplish); pileus surface smooth; lamellae crowded 11
11. Pileus whitish, without purple spots; taste acrid; context unchanging
..... **11. *L. alboscrobiculatus***
11. Pileus whitish with local purplish spots; taste mild; context staining greyish colour by the latex **12. *L. alboscrobiculatus* var. *roseopurpureus***

1. *Lactarius akahatsu* Tanaka, Bot. Mag. (Tokyo) 4: 394 (1890) (Figs 1a,b)

Synonyms:

≡ *L. hatsudake* var. *akahatsu* (Tanaka) Kawam., Bot. Mag. (Tokyo) 28: 525 (1914)

= *L. deliciosus* f. *virescens* S. Imai, Bot. Mag. (Tokyo) 49: 607 (1935) *Misapplication:*

L. deliciosus sensu Yasuda (1913); *sensu* Kobayshi (1939)

Type: not selected, described from Japan.

Pileus 60–120 mm diam., plano-convex to widely infundibuliform, irregular; margin straight to very irregular-wavy, (translucently) striate (up to 12 mm); surface smooth, sticky, greasy to slightly viscid, weakly zonate in some specimens, with distinct zones near the margin in other specimens, zones consisting of watery spots; colour partly pale orange (4A4/5 near the centre), deeper orange in other places (5A/B6 to 6A7/8), more whitish orange when dry, with emerald green shades when older. *Lamellae* decurrent with a small tooth, distant, abundant; colour orange (5A5) but staining greenish when bruised, dirty brownish orange when older; edge entire, paler. *Stipe* 30–46 × 11–20 mm, irregularly cylindrical, tapering downwards, central to slightly eccentric; surface smooth, slightly viscid; colour orange-buff (5A4–6). *Context* rather firm, ± 6 mm thick in the pileus, hollow in the stipe, pale cream to whitish but soon pinkish buff to pale orange when cut, especially underneath the pileipellis; colour unchanging; smell agreeable, sweetish or flowery; taste agreeable, mild, like nuts. *Latex* scarce, bright orange (6A8) to deep orange.

Spores 7.5–7.9–8.4 × 5.5–6–6.5 (6.8) μm, broadly ellipsoid to ellipsoid (n = 120, Q = 1.22–1.33–1.44); ornamentation up to 0.5 μm high, of rather broad ridges and isolated warts, forming a rather complete reticulum; plage distally slightly amyloid, ± centrally additional amyloid spots often present. *Basidia* 35–50 × 9–10 μm, subclavate, 4-spored, often containing oil-droplets; sterigmata 3.5–5 μm long. *Pleuromacrocystidia* very scarce, 50–55 × 6–8 μm, emergent, fusiform with a moniliform apex, contents needle-shaped, thin-walled. *Pseudocystidia* abundant, 4–5.5 μm broad, not or slightly emergent, often tortuous; contents oleiferic. *Lamellar edge* sterile without cheilomacrocystidia; cheiloleptocystidia 9.5–22 × 4–8 μm, subclavate to irregular, hyaline or with ochre granular contents (in 10% KOH), thin-walled.

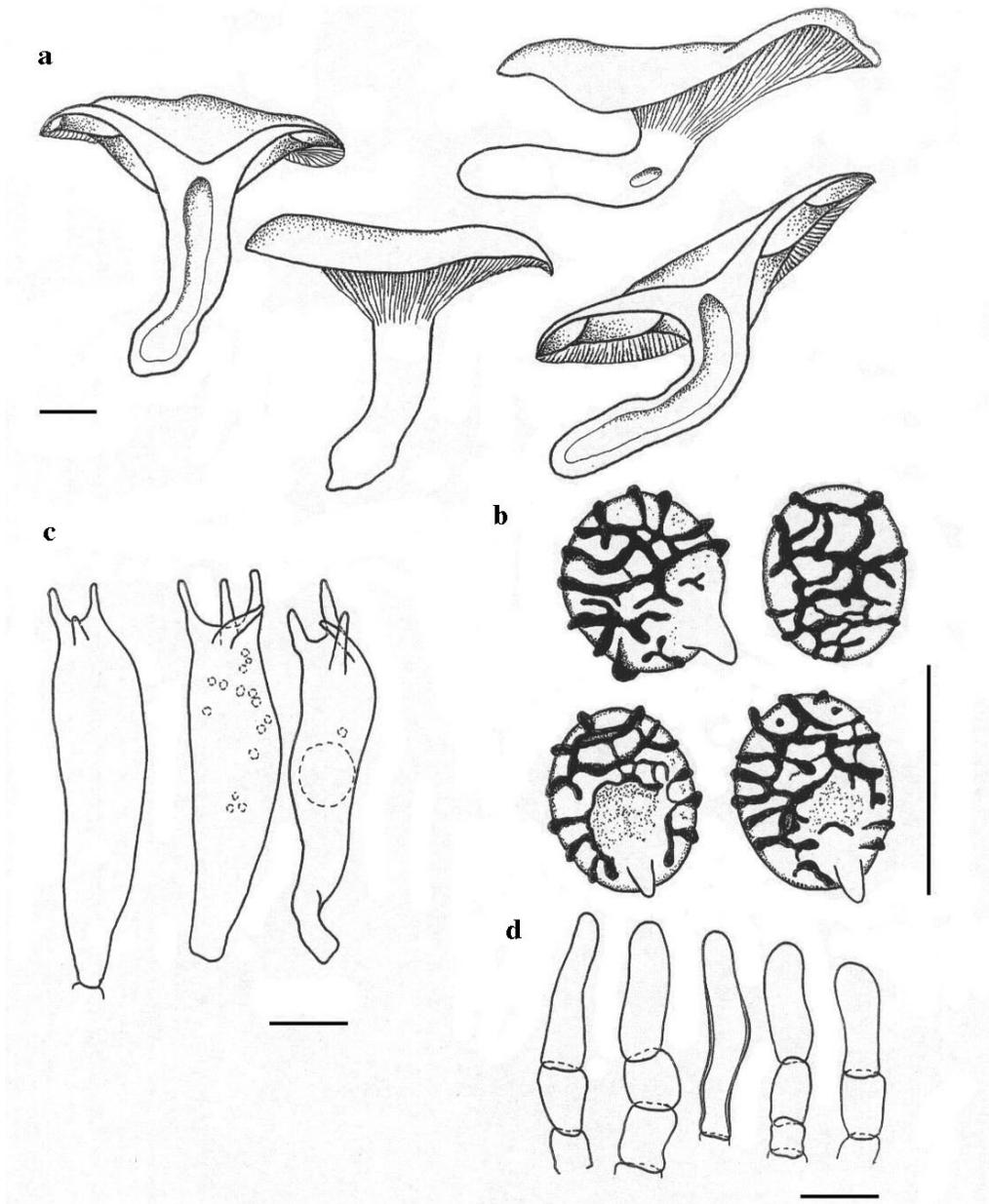


Fig. 1a. *Lactarius akahatsu*. **a.** Basidiocarp. **b.** Spores. **c.** Basidia. **d.** Marginal cells. Scale bars = 10 mm (basidiocarp) and 10 μ m.

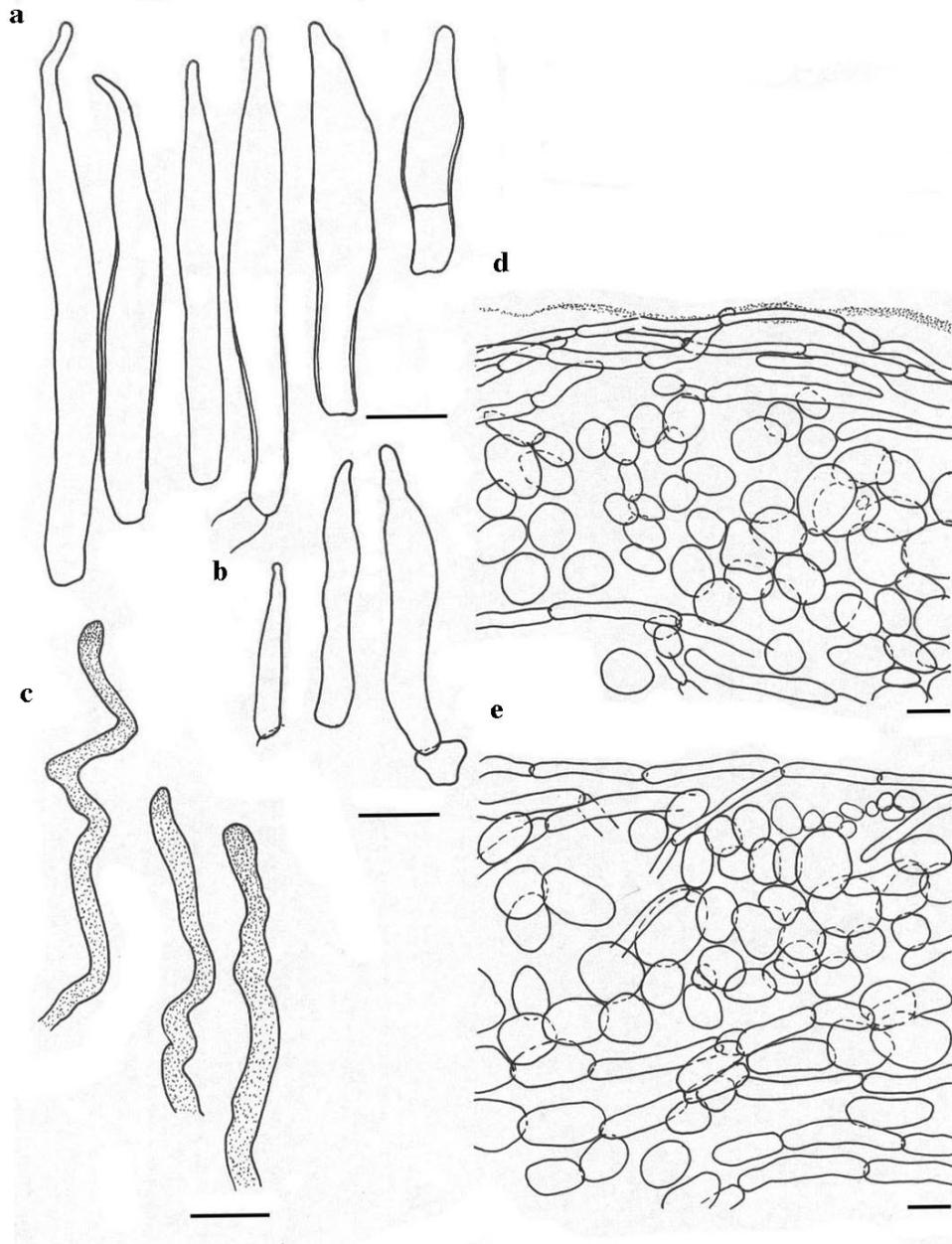


Fig. 1b. *Lactarius akahatsu*. **a.** Pleuromacrocystidia. **b.** Cheiloleptocystidia. **c.** Pleuropseudocystidia. **d.** Pileipellis. **e.** Stipitipellis. Scale bars = 10 μ m.

Pileipellis an ixocutis, 50–250 µm thick; composed of mostly strongly shrivelled and gelatinised hyphae in the upper layer, hyphae 1–3 µm diam. *Stipitipellis* a cutis, 70–100 µm thick, composed of thin-walled, strongly interwoven hyphae 2–4 µm diam.; no shrivelled hyphae present. *Clamp connections* absent.

Habitat: On the ground in lowland *Pinus kesiya* forests.

Distribution: Described from Japan where the species occurs with *Pinus densiflora*, *P. thunbergii*, *P. liuchuensis* etc. and introduced on the Bonin Islands (Hongo, 1960, 1977). Recorded here for the first time from Thailand.

Material examined: JAPAN, Tottori, Tottori-shi, Uemachi (Bairian), under planted *Pinus thunbergii* in garden, 27 September 1997, leg. E. Nagasawa, TMI 22601 (TMI) – THAILAND, Chiang Mai Prov., Mae Teng Distr., Tung Joaw village, forest trail, 1300 m alt., N19°08.07' E98°38.90', secondary forest with *Pinus kesiya*, *Castanopsis* etc., 20 June 2004, leg. R. Walley & A. Verbeken 2004-015 (GENT), leg. Huyen T. Le 115 (CMU, SFSU) – ibid., road side, 1350 m alt., under *Pinus kesiya*, 21 June 2004, leg. R. Walley & A. Verbeken 2004-036 (GENT), leg. Huyen T. Le 121 (CMU, SFSU) – Chiang Mai Prov., Mae Teng Distr., Highway 1095 at 22 km marker, 750 m alt., N19°07.57' E98°45.65', xeric broad-leaf forest (*Dipterocarpus* spp. + teak) with *Pinus kesiya*, under *Pinus*, 23 June 2004, leg. R. Walley & A. Verbeken 2004-076 (GENT), leg. Huyen T. Le 127 (CMU, SFSU) – ibid., solitary to gregarious on the soil, rainforest dominated by *Dipterocarpus* sp. and *Pinus kesiya* trees, 21 June 2005, Huyen T. Le 287 (CMU, GENT, SFSU) – ibid., solitary to gregarious on the soil under *Pinus kesiya* trees, rain forest dominated by *Dipterocarpus* sp. and *Pinus kesiya* trees, 04 June 2006, Huyen T. Le 392 (CMU, GENT, SFSU) – ibid., solitary on the soil under *Pinus kesiya* trees, rain forest dominated by *Dipterocarpus* sp. and *Pinus kesiya* trees, 11 June 2006, Huyen T. Le 424 (CMU, GENT, SFSU) – Chiang Mai Prov., Mae Teng Distr., Huai Nam Dang National Park, nature trail, 1530 m alt., N19°18.29' E98°35.88', forest with *Pinus kesiya*, *Dipterocarpus* sp., Bamboo & scattered *Castanopsis*, 28 June 2004, leg. R. Walley & A. Verbeken 2004-141 (GENT), leg. Huyen T. Le 162 (CMU, SFSU) – ibid., solitary on the soil and pine leaves, forest with *Pinus kesiya*, *Dipterocarpus* sp., Bamboo & scattered *Castanopsis*, 29 June 2005, Huyen T. Le 330 (CMU, GENT, SFSU).

Discussion: Molecular analysis revealed such a close relationship between these Thai collections and the Japanese *L. akahatsu* that they can be considered conspecific. The description above is entirely based on Thai material.

Lactarius akahatsu seems to be a common species in Japan, characterised by its generally orange appearance and orange latex that slowly becomes red on the context. It is unmistakably different from *L. hatsudake*, a species with red latex from the beginning. The Japanese specimens differ from the ones collected in Thailand by the behaviour of the latex, which slowly becomes vinaceous red or stays orange respectively. Microscopically pleuro- and cheilomacrocytidia are more abundant in the Japanese collections.

L. akahatsu is appreciated as an edible mushroom in Thailand.

2. *Lactarius hatsudake* Tanaka, Bot. Mag. (Tokyo) 4: 393 (1890) (Figs 2a,b)*Synonym:*?= *L. lividatus* Berk. & M.A. Curtis, Proc. Amer. Acad. Arts & Sciences 4: 119 (1860)*Type:* not selected, described from Japan.

Pileus 30–100 mm diam., at first convex with an incurved margin, sometimes with a papilla, then expanded and margin bent downwards to slightly incurved, finally widely infundibuliform; margin sometimes slightly translucently striate; surface smooth, greasy to slightly viscid when wet, zonate, especially near the margin; colour pale reddish buff to dirty brownish pink or with ochraceous tinges (7/8B3/4), sometimes with a darker centre (8C5), zones dull red, older or discoloured specimens very light orange or with a greenish ochraceous centre, discolouring bluish green in age (25F6), slightly hygrophanous. *Lamellae* decurrent, rather crowded to subdistant, often branched, rather broad, colour dull, pale reddish when young, vinaceous red when mature, becoming more ochraceous, mixed with greenish or bluish green in age; edge entire, paler. *Stipe* 15–40 × 6–20 mm, short, tapering downwards, becoming hollow, glabrous, colour dull reddish (9C/D5), often covered with a white layer, without scrobicules, with a white zone at the apex. *Context* firm in the centre of the pileus to very thin at the margin, white to buff, staining vinaceous red (10/11C5) underneath the pileipellis or on the entire pileus surface and underneath the stipitipellis, later becoming greenish; smell indistinct to sweet, agreeable; taste mild. *Latex* scarce, vinaceous red (11D6/7), unchanging. *Spore deposit* unknown.

Spores 7.7–8.3–9–9.7 × 5.6–6.2–6.6–7.5 μm, broadly ellipsoid to ellipsoid (n = 180, Q = 1.21–1.30–1.39–1.54); ornamentation up to 0.8 (1) μm high, composed of conspicuous, large, but rather faint amyloid spots connected with mainly thick ridges but also with scarcer thin ridges, forming an irregular, dense and almost complete network, some isolated warts present; plage often with an irregular, faintly amyloid pattern or distally amyloid. *Basidia* 40–52 × 8–14 μm, subclavate, 4-spored; sterigmata 4.5–8 μm long. *Pleuromacrocystidia* very scarce but more abundant close to the lamella edge, 42–48 × 7–9 μm, emergent, subfusiform, with a moniliform or acute apex, thin-walled. *Pseudocystidia* abundant, 2.5–5 μm diam., not to slightly emergent, cylindrical to tortuous, with an ochre-yellow content. *Lamellar edge* sterile with scarce cheilomacrocystidia but macrocystidia mostly abundant close to the edge; cheiloleptocystidia mostly 8–16 × 3.5–6 μm but rarely very conspicuous and emergent, up to 35–40 μm long, subclavate to cylindrical or more irregular, hyaline, thin-walled; cheilomacrocystidia 24–35 × 4.5–6 μm, subfusiform with a moniliform apex, content needle-shaped or granular, thin-walled. *Pileipellis* an ixocutis, 50–300 μm thick, of mainly shriveled and gelatinised hyphae in the top layer, deformed and swollen hyphae also present;

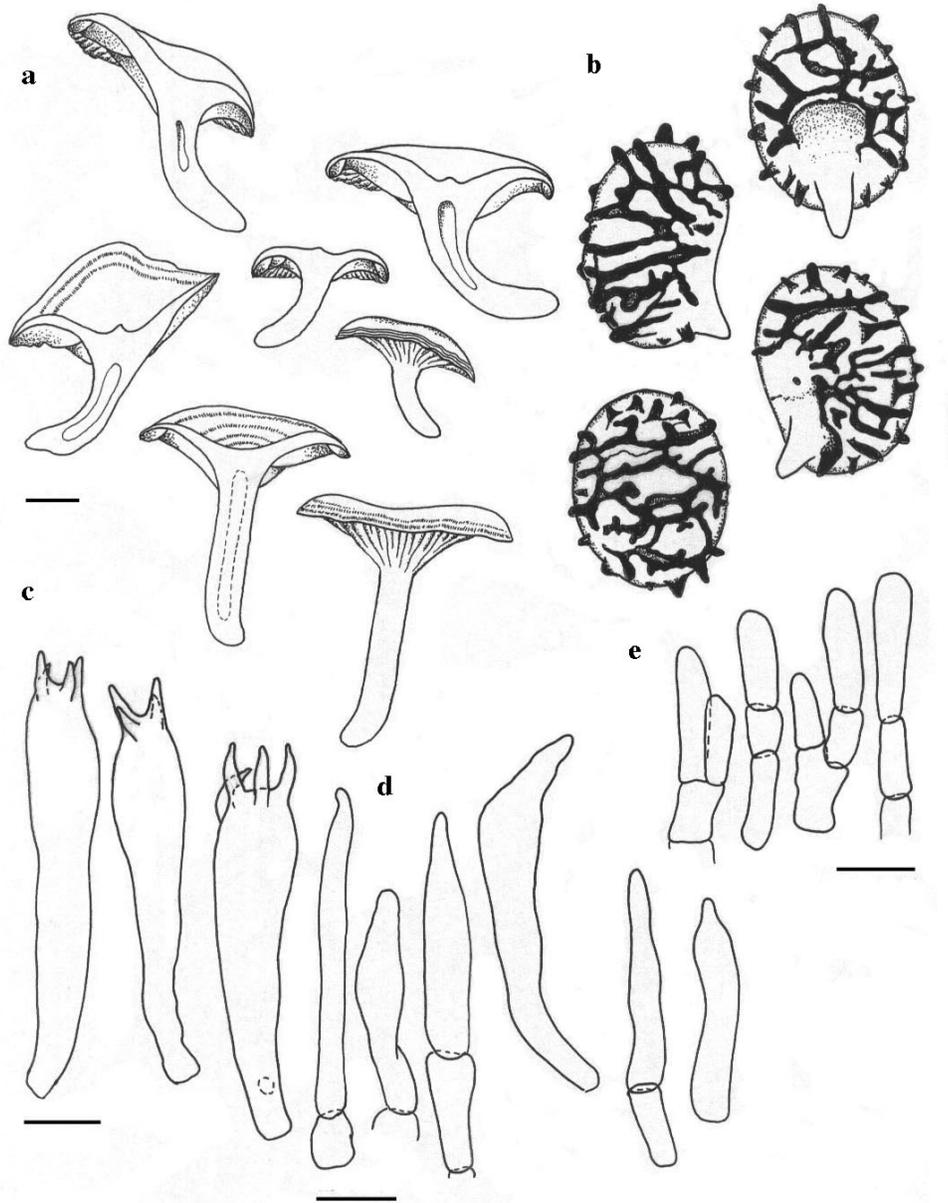


Fig. 2a. *Lactarius hatsudake*. **a.** Basidiocarp. **b.** Spores. **c.** Basidia. **d.** Pleuromacrocytidia. **e.** Marginal cells. Scale bars = 10 mm (basidiocarp) and 10 μ m.

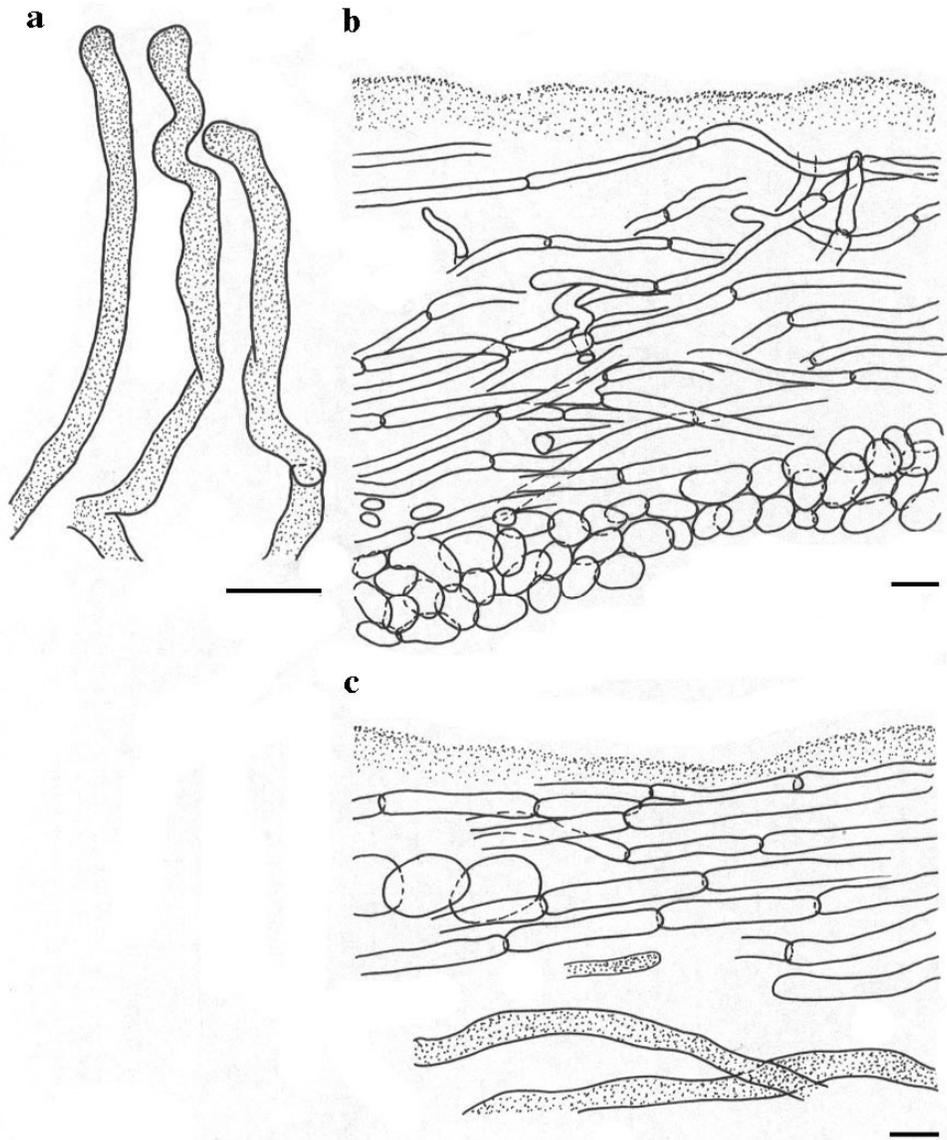


fig. 2b. *Lactarius hatsudake*

Fig. 2b. *Lactarius hatsudake*. **a.** Pleuropsudocystidia. **b.** Pileipellis. **c.** Stipitipellis. Scale bars = 10 μ m.

hyphae 1–6 µm broad, thin-walled. *Stipitipellis* a cutis, 30–70 µm thick, of thin-walled, strongly interwoven hyphae 2–6 µm broad; no shriveled or gelatinised hyphae. *Clamp connections* absent.

Habitat: Under *Pinus kesiya*.

Distribution: Recorded from China, Japan, the Bonin Islands, eastern Russia, Korea, Thailand and Taiwan. Under *Pinus* spp. such as *P. thunbergii*, *P. densiflora*, *P. liuchuensis*, *P. yunnanensis*, *P. kesiya*; in Japan in lowland forests and gardens etc., abundant in (early) autumn; in Yunnan (Southwest China) throughout the mushroom season (May to September) (Tanaka, 1890; Nagasawa, 1998; X.H. Wang, pers. comm.).

Material examined: JAPAN, Kagoshima, Aira-gun, Makizono-cho, Oonami-yama, 1060–1300 m alt., under *Pinus densifolia*, in mixed coniferous and hardwood forest, 27 October 2000, leg. E. Nagasawa & T. Fujita, TMI 24414 (TMI) – THAILAND, Chiang Mai Prov., Mae Teng Distr., Tung Joaw village, forest trail, 1300 m alt., N19°08.07' E98°38.90', secondary forest, under *Pinus kesiya*, on a steep wall of red soil along the trail, 20 June 2004, leg. R. Walley & A. Verbeken 2004-014 (GENT), leg. Huyen T. Le 110 (CMU, SFSU) – *ibid.*, secondary forest with *Pinus kesiya*, *Castanopsis* etc., 30 June 2004, leg. R. Walley & A. Verbeken 2004-159 (GENT), leg. Huyen T. Le 167 (CMU, SFSU) – *ibid.*, secondary forest with *Pinus kesiya*, *Castanopsis* etc., 07 August 2004, Huyen T. Le 215 (CMU, SFSU) – *ibid.*, secondary forest with *Pinus kesiya*, *Castanopsis* etc., 16.07.2005, Huyen T. Le 354 (CMU, GENT, SFSU) – *ibid.*, secondary forest with *Pinus kesiya*, *Castanopsis* etc., 03 August 2005, Huyen T. Le 367 (CMU, GENT, SFSU) – Chiang Mai Prov., Mae Teng Distr., Huai Nam Dang National Park, nature trail, 1530 m alt., N19°18.29' E98°35.88', forest with *Pinus kesiya*, Bamboo, scattered *Castanopsis*, 28 June 2004, leg. R. Walley & A. Verbeken 2004-134 (GENT), leg. Huyen T. Le 158 (CMU, SFSU) – *ibid.*, forest with *Pinus kesiya*, Bamboo, scattered *Castanopsis*, 28 June 2004, leg. R. Walley & A. Verbeken 2004-138 (GENT), leg. Huyen T. Le 159 (CMU, SFSU) – *ibid.*, forest with *Pinus kesiya*, Bamboo, scattered *Castanopsis*, 28 June 2004, leg. R. Walley & A. Verbeken 2004-139 (GENT), leg. Huyen T. Le 160 (CMU, SFSU) – *ibid.*, forest with *Pinus kesiya*, *Dipterocarpus* sp., Bamboo & scattered *Castanopsis*, 29 June 2005, Huyen T. Le 331 (CMU, GENT, SFSU) – Chiang Mai Prov., Mae Teng Distr., Ban Pha Deng village, Pathummikaram Temple, forest trail, 1050 m alt., N19°06.28,8" E98°44.47,3", solitary to gregarious on the soil and leaves, near the trail, rain forest dominated by *Castanopsis armata*, *Dipterocarpus* sp., *Pinus kesiya*, 12 June 2006, leg. Roy Halling and Huyen T. Le, Huyen T. Le 428 (CMU, GENT, SFSU).

Discussion: *Lactarius hatsudake* is one of the highly prized edible mushrooms in Japan and large parts of China and probably also in Korea and eastern Russia (Nagasawa, 1998; Wang *et al.*, 2004, Nuytinck *et al.*, 2006). It is not known as an edible species in Thailand.

Lactarius hatsudake is characterised by its wine red latex and its association with *Pinus* spp. The size of the basidiocarps is quite variable, e.g., very small to rather large basidiocarps are often encountered together (X.H. Wang, pers. comm.). Microscopically the heavy spore ornamentation with the large but faintly amyloid spots is typical and a reliable feature for identification.

Molecular evidence shows that the genetic variability in *L. hatsudake* is high, which might indicate that our species concept is relatively broad here (Nuytinck, 2005). Moreover, this molecular variability is also confirmed by morphological diversity. The collections from Thailand showed a striking hygrophanous colour change of the cap that is not reported for the Chinese collections. It is possible that at least several varieties can be distinguished within *L. hatsudake* but more observations on fresh material are needed. The description above is based entirely on Thai material.

3. *Lactarius* sp. 1

(Fig. 3)

Pileus 44 mm diam., deeply infundibuliform; surface viscid, zonate, especially in outer half, greyish yellow (4AB4); margin wavy, smooth, neither hairy nor striate. *Lamellae* decurrent with tooth, crowded, with 3 lamellulae between 2 lamellae, sometimes forked, narrow, 2.5 mm broad, greyish yellow (4AB5), becoming greyish orange-brown (5BC6). *Stipe* 41 × 18 mm, cylindrical, central, hollow, viscid, smooth, greyish yellow (4B5) at apex, pale yellow (3A4) at base. *Context* rather thin, 2 mm in pileus, hollow in stipe, light yellow (4AB4), unchanging with KOH 10% and FeSO₄; taste slightly acid; smell sweet. *Latex* immediately bright yellow. *Spore deposit* white cream.

Basidiospores 6.7–8.3–9.9 (10.2) × 5.9–7–8(8.5) μm, (Q = 1.09–1.19–1.37, n = 20), subglobose to broadly ellipsoid, rarely ellipsoid; ornamentation up to 1 μm high, composed of rather irregular ridges, never forming a complete reticulum, often with a slight zebroid aspect; plage distinctly but faintly distally amyloid. *Basidia* 30–41 × 6.5–9 μm, with sterigmata 4–9 × 1.2–2 μm, sometimes thick-walled, 4-spored, sometimes 2-spored, subclavate to cylindrical, with hyaline or granular contents. *Pleuromacrocytidia* 24–65 × 3–6.5(8) μm, locally abundant, slightly emergent, sometimes with granular and guttate contents, fusiform, irregularly cylindrical to slightly tortuous, some branching, thin-walled or very slightly thick-walled. *Pleuropseudocystidia* 3.0 μm diam., not abundant, not emergent, with lactiferous content, thin-walled, tortuous to cylindrical. *Lamellae edge* heteromorphous; marginal cells cylindrical to short-clavate, 17–23 × 5.0–8.3 μm, slightly thick-walled, hyaline, sometimes 1-septate. *Hymenophoral trama* of interwoven, filamentous hyphae. *Pileipellis* an ixocutis, 60–90 μm thick, composed of hyphae 4–5 μm broad; underlying layer composed of filamentous hyphae and sphaerocytes. *Stipitipellis* a trichoderm, 40–80 μm thick; pleuropseudocystidia present; underlying layer composed of filamentous hyphae and sphaerocytes. *Clamp connections* absent.

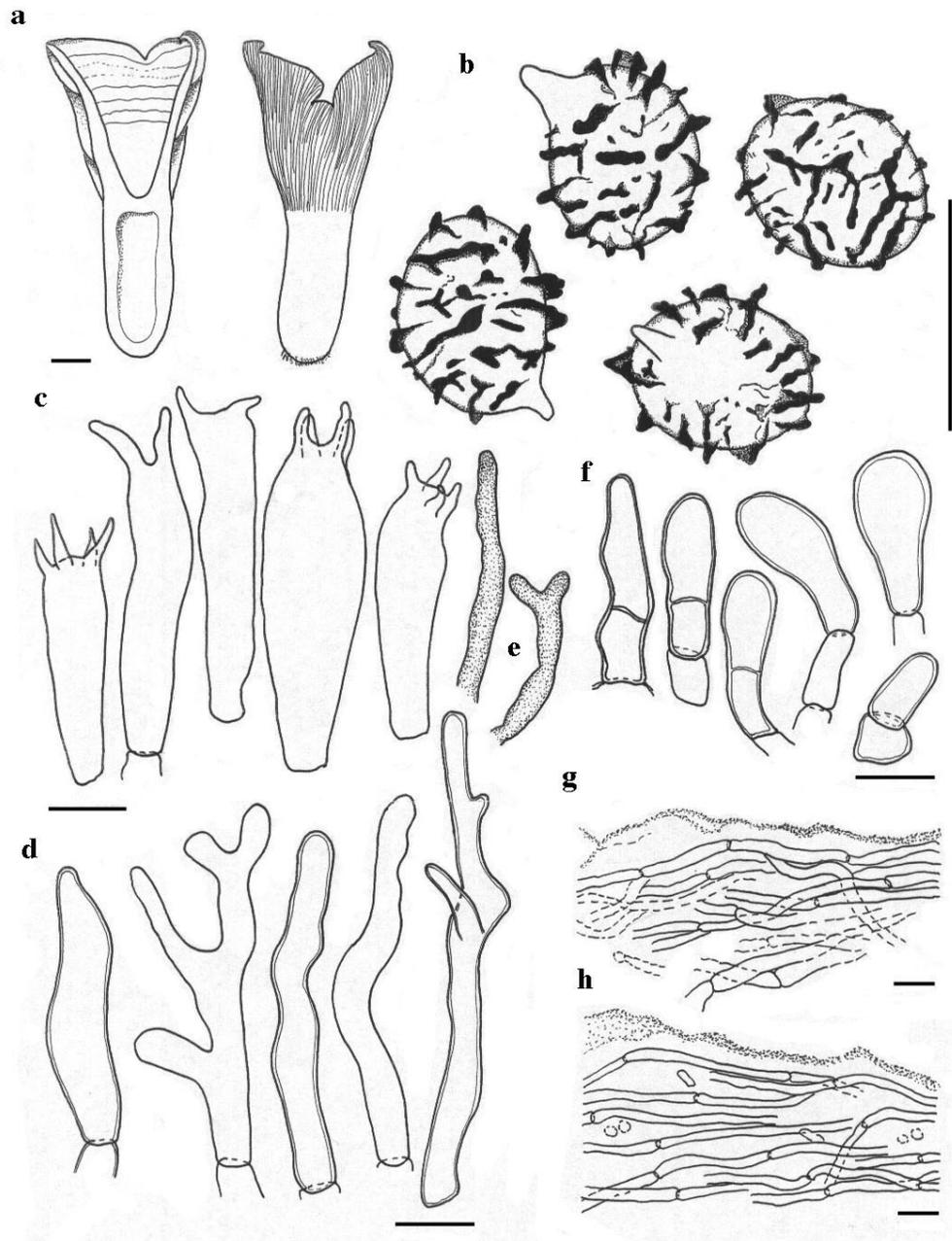


Fig. 3. *Lactarius* sp.1. **a.** Basidiocarp. **b.** Spores. **c.** Basidia. **d.** Pleuromacrocystidia. **e.** Pleuropseudocystidia. **f.** Marginal cells. **g.** Pileipellis. **h.** stipitipellis. Scale bars = 10 mm (basidiocarp) and 10 μ m.

Habitat and distribution: Known from this specimen only, growing in rainforest dominated by *Castanopsis armata* and *Pinus* sp., probably associated with *Castanopsis*.

Material examined: THAILAND, Chiang Mai Prov., Doi Inthanon National Park, Hwy 1009 at 25 km marker, N18°32.54' E098°33.51', 1076 m alt., solitary in the soil among pine leaves, rainforest dominated by *Castanopsis armata* and *Pinus* sp., 03 June 2004, leg. Huyen T. Le 174 (CMU, SFSU, GENT).

Discussion: The only available specimen is in rather poor condition, which makes it hard to observe the pilei- and stipitipellis and the hymenial elements. Therefore we prefer not to propose it as a new species, although its macromorphological features are distinctive. To our knowledge, it appears to be the only representative of the subgenus with bright yellow latex in Thailand.

This species is well characterized by a pale, zonate pileus without tomentose margin and latex that is immediately yellow. A similar species with yellow latex, described from Papua New Guinea is *L. xanthogalus* Verbeken & E. Horak. *Lactarius* sp. 1 differs from *L. xanthogalus* by the less zebroid spore ornamentation. Though there is a slightly zebroid aspect to the spores, it is never as pronounced as in *L. xanthogalus*.

The position of this species in the phylogenetic analyses is unclear. Its position varies from a very long branch within *L.* subgenus *Piperites* (Fig. 13) to the very base of the subgenus (tree not shown); but in some of the MP trees it falls outside this subgenus. In all of our analyses, *L.* sp. 1 was never included in the *Russularia* clade and therefore we prefer to include the species in subgenus *Piperites*. The taxonomic delimitations of the subgenera *Piperites* and *Russularia* is problematic, not only from a morphological but also from a molecular point of view (Eberhardt, 2000).

A European species with yellow latex, *L. chrysorrhoeus* Fr., also has a doubtful position between *L.* subgenera *Piperites* and *Russularia*. It differs significantly from *L.* sp. 1 in forming a pileipellis without slime layer.

4. *Lactarius formosus* H.T. Le & A. Verbeken, sp. nov. (Figs 4a,b)
Mycobank: 510282.

Pileus 27 mm diam., planoconvexus, leviter depressus, cum papilla parva; pileipellis viscida, zonata, squamulosa, griseolutea, purpurascens. Stipes 40 mm longus, 6 mm crassus, pileo concolorus, luteoalbus, purpurascens, scrobiculatus. Lamellae subdecurrentes, densae, ad 1 mm latae, luteoalbae. Contextus griseoalbus, purpureoalbus, gustu mitis. Latex cremeus ad luteoalbus. Sporae globosae ad ellipsoideae, 8–9.7–11.3(11.6) × 7.4–8.8–10.1 μm, reticulatae, cristis usque ad 0.6(1.6) μm altis ornatae; macula suprahilaris non amyloidea. Basidia 48–77 × 13–18 μm, subclavata, tetraspora. Pleuromacrocystidia abundantia, 35–90 × 8–13 μm, emergentia, subfusiformia. Pleuropsseudocystidia non abundantia, emergentia, 8–11 μm diam., cylindrata vel tortuosa. Pileipellis cutis vel trichoderma, 120–140 μm crassa.

Holotypus: THAILAND, Chiang Mai Prov., Mae Taeng Dist., Tung Joaw village, N19°08.07' E098°38.09', 1423 m alt., solitary in soil amongst leaves, in rainforest dominated by

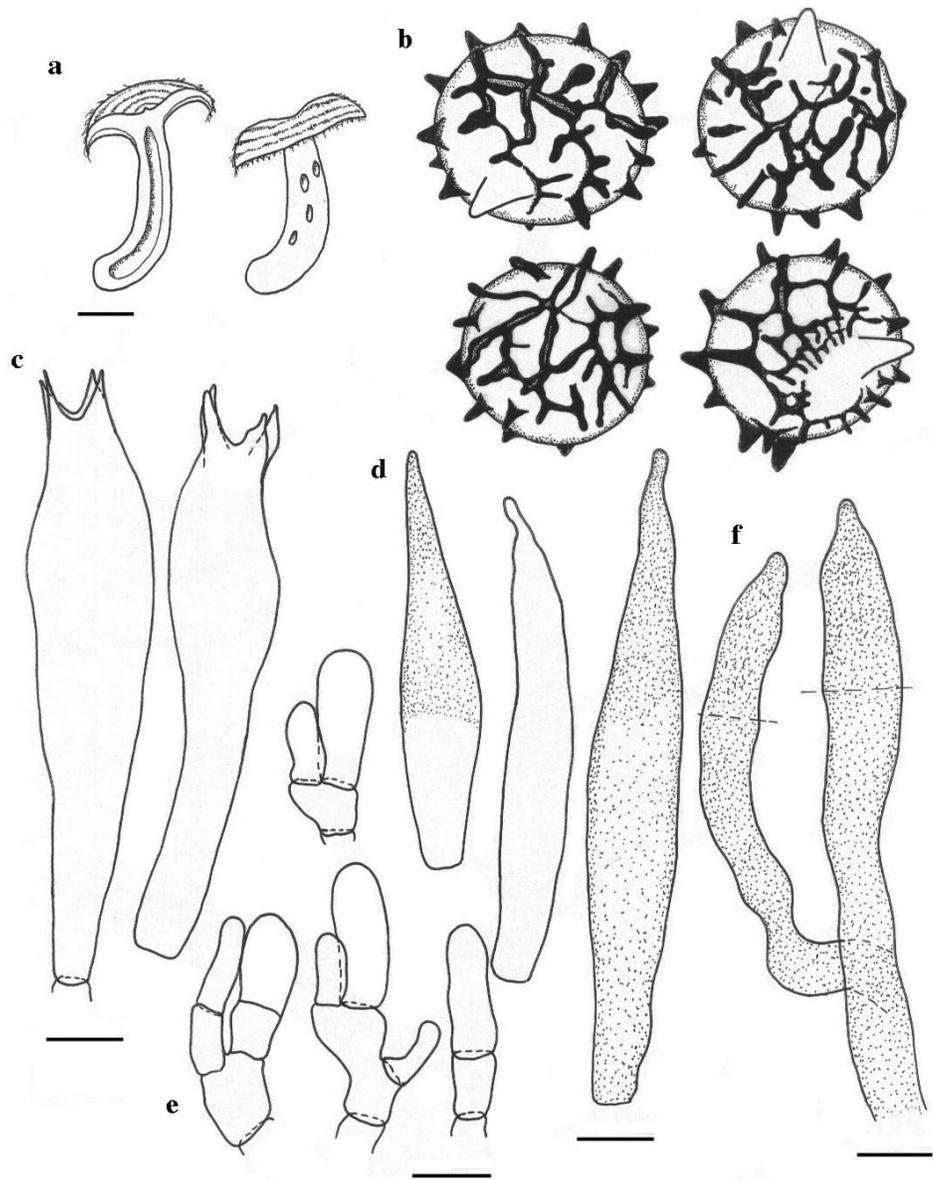


Fig. 4a. *Lactarius formosus*. **a.** Basidiocarp. **b.** Spores. **c.** Basidia. **d.** Pleuromacrocystidia. **e.** Marginal cells. **f.** Pleuropseudocystidia. Scale bars = 10 mm (basidiocarp) and 10 μ m.

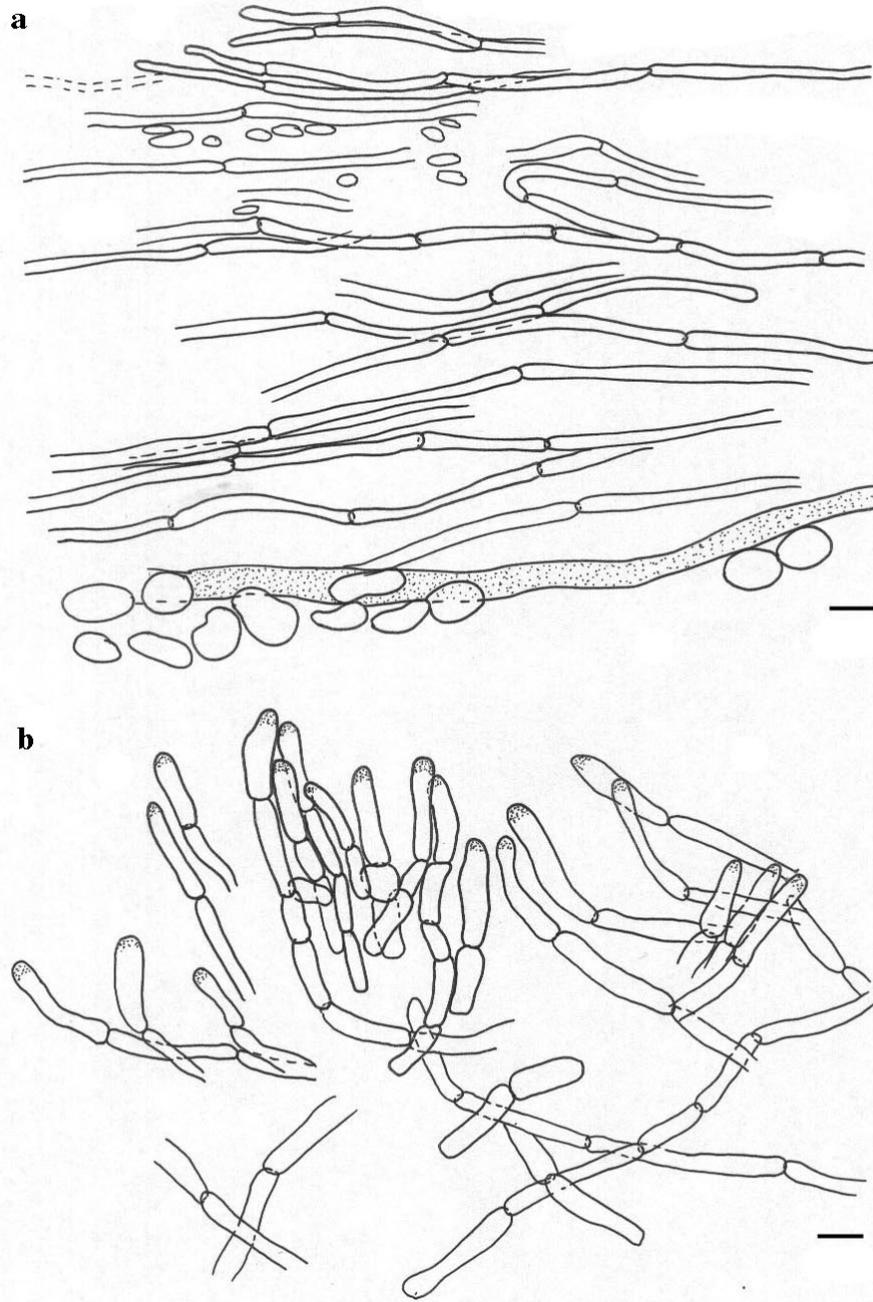


Fig. 4b. *Lactarius formosus*. **a.** Pileipellis. **b.** Stipitipellis. Scale bars = 10 μ m.

Castanopsis armata and *Pinus kesiya*, 16 October 2005, Huyen T. Le 382 (**holotypus** CMU; **isotypes** GENT, SFSU).

Pileus 27 mm diam., plano-convex with slight central depression and a very small papilla; surface viscid, zonate, scaly, covered with bundles of glutinous hairs, greyish yellow to yellowish buff with some olivaceous tones, changing quickly to dark purple (14F4) when bruised or broken; margin hairy. *Lamellae* subdecurrent, close to crowded, up to 1 mm broad, with 3 series of lamellulae, yellowish white (4A2), becoming dark ruby (12F4) when bruised or broken; edge dark purple (14F5). *Stipe* 40 × 6 mm, tapering upwards, central, greasy to dry, scrobiculate, yellowish white (4A2) at apex, concolourous with pileus, quickly changing to dark purple (14EF5) when bruised. *Context* 2.5 mm thick in pileus, greyish white to purplish white (14A2), hollow in stipe, pale yellow (3A3) with KOH 10%, dull yellow (3B3) with FeSO₄; smell distinct; taste mild. *Latex* cream to yellowish white (4A2), staining the lamellae dark purple, pale yellow (3A3) to brownish orange (5C4) with KOH 10%. *Spore deposit* unknown.

Basidiospores 8–9.7–11.3 (11.6) × 7.4–8.8–10.1 μm, (n = 20, Q = 1.01–1.1–1.38), globose to ellipsoid; ornamentation up to 0.6 (–1.6) μm high, composed of rather broad ridges, forming a mostly complete reticulum; plage inamyloid. *Basidia* abundant, 48–77 × 13–18 μm, with sterigmata 2–7 μm long, 4-spored, hyaline, sometimes with granular and guttate contents, thin-walled, subclavate. *Pleuromacrocystidia* abundant, 35–90 × 8–13 μm, emergent, subfusiform, with a mucronate to moliniform apex, hyaline or with granular contents, thin-walled. *Pleuropseudocystidia* not abundant, 8–11 μm wide, emergent up to 30 μm, tortuous to cylindrical, with lactiferous contents, thin-walled. *Hymenophoral trama* composed of filamentous hyphae. *Lamellae edge* sterile; marginal cells 11–21 × 3.5–7 μm, abundant, hyaline, 1-septate, cylindrical, thin-walled; cheilocystidia 29–60 × 8–9 μm, hyaline, subfusiform, similar to pleuromacrocystidia but smaller, with mucronate to moliniform apex. *Pileipellis* a cutis to a trichoderm, 120–140 μm thick; underlying layer composed of thin-walled filamentous hyphae and sphaerocytes. *Stipitipellis* a trichoderm, 90–130 μm thick composed of thin-walled hyphae; underlying layer composed of sphaerocytes and filamentous thin-walled hyphae.

Habitat and distribution: solitary in the soil among leaves near *Pinus kesiya* and *Castanopsis armata*.

Material examined: THAILAND, Chiang Mai Prov., Mae Taeng Dist., Tung Joaw village, N19°08.07' E098°38.09', 1423 m alt., rainforest dominated by *Castanopsis armata* and *Pinus kesiya*, 16 October 2005, leg. Huyen T. Le 382 (**holotype** CMU; **isotype** GENT, SFSU).

Discussion: The species is striking in the field because of the quick colour change to violet in all parts combined with a hairy, viscid, zonate pileus and a scrobiculate stipe.

The species is similar to the European *L. repraesentaneus* Britzelm. and the North American *L. speciosus* Burl., two species with violet staining latex that also share the hairy pileus with bearded margin and a scrobiculate stipe. The spore ornamentation of this new Asian species is very different from both temperate species. *L. speciosus* has spinose warts and ridges hardly forming a reticulum, while *L. repraesentaneus* has a denser but lower incomplete to complete reticulum. In the field *L. formosus* differs by the much smaller and more slender basidiomes while the temperate species are both robust and larger. Since only one specimen has been found up to now, we do not know whether this is a consistent differentiating character. The colour of the basidiome is bright yellow in *L. repraesentaneus* and pinkish buff to cinnamon buff in *L. speciosus*.

L. repraesentaneus is recorded from China by Wang and Xie (1984) and from Japan by Nagasawa (1998) and Imazeki *et al.* (1988), but on the basis of the colour picture of the latter, which shows an upside down specimen only, it is hard to judge whether it represents the same taxon as ours.

Molecular data indicates that *L. formosus* differs clearly from *L. repraesentaneus* and from *L. speciosus*. These three morphologically very similar species do not always form one clade. Whether *L. formosus* indeed belongs to subgenus *Piperites* is not always clear in the molecular phylogenies (see under general discussion). Its exact position needs a more thorough molecular approach based on more specimens.

5. *Lactarius* sp. 2 (Figs 5a,b)

Pileus 35–45 mm diam., infundibuliform with papilla, sticky, hairy, scaly when young, light brown (5D4-5 and 6D5) in center, light greyish yellow (4AB4) to light brown (6D6) on margin, olive brown (4F4) in center when old; margin wavy, ciliate, with small triangles of hairs that are pendulous. *Lamellae* decurrent, dense (33L+l/cm), close to crowded, with 3 series of lamellulae, 2–3 mm broad, pale yellow (4A2-3) to brownish orange (5C4-5), greyish violet (15D6) when bruised or broken. *Stipe* 50 × 9–12 mm, cylindrical, curved, eccentric to central, greasy, smooth, orange white (5A2) to pale yellow (4A3) at apex, pale greyish orange (5AB3) to pale greyish yellow (4AB3) at base, brownish grey (8C2) to greyish Magenta (14DE5) when broken or bruised. *Context* rather firm in pileus, 3.0–3.5 mm thick in pileus, hollow in stipe, pale greyish orange (5AB3) and pinkish (12A2) changing to dark purple (14F4–5) when cut, with zonation in pileus, pale yellow (3A4) with 10% KOH no reaction with FeSO₄; taste mild; smell strong. *Latex* white, abundant, changing to reddish lilac (14B3). *Spore deposit* unknown.

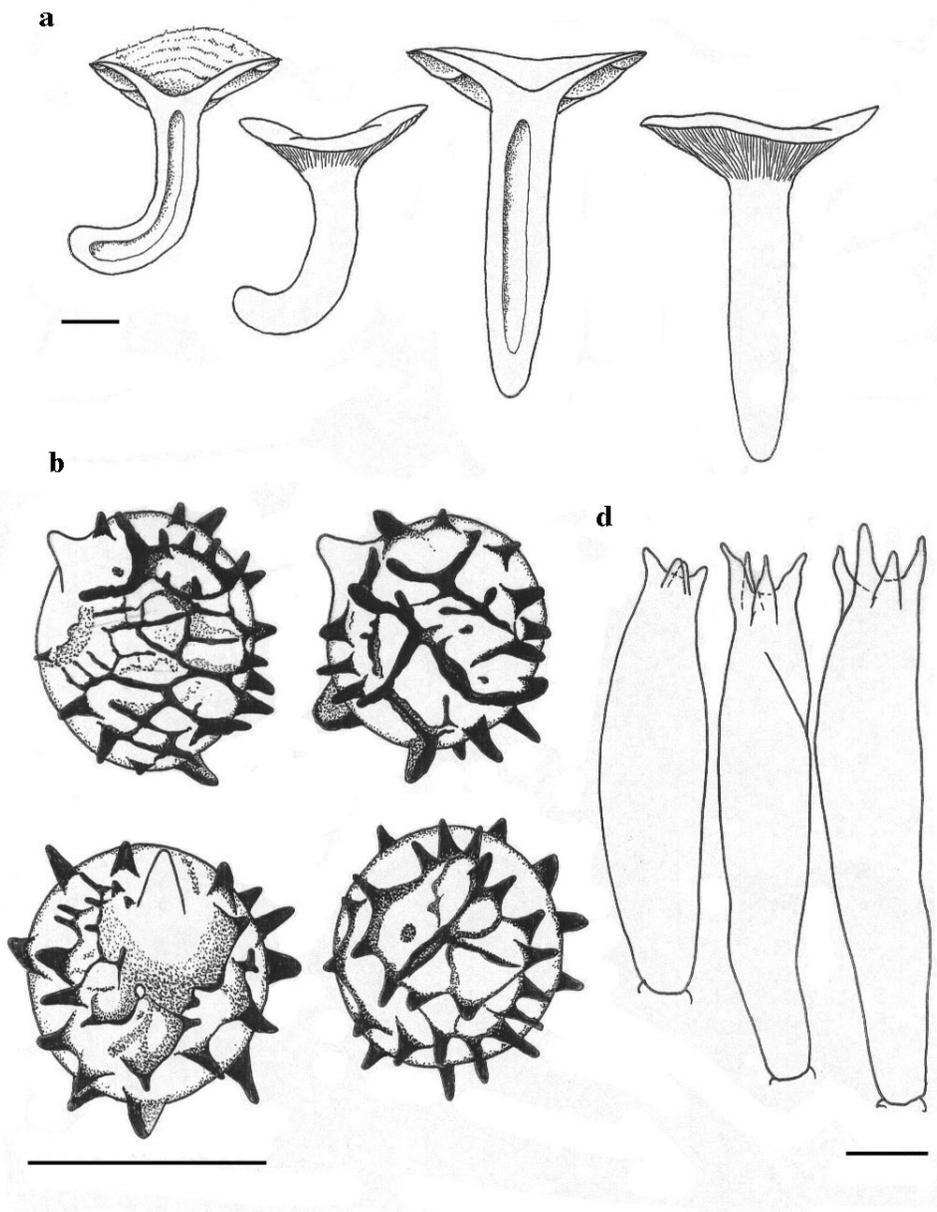


Fig. 5a. *Lactarius* sp. 2. **a.** Basidiocarp. **b.** Spores. **c.** Basidia. Scale bars = 10 mm (basidiocarp) and 10 μ m.

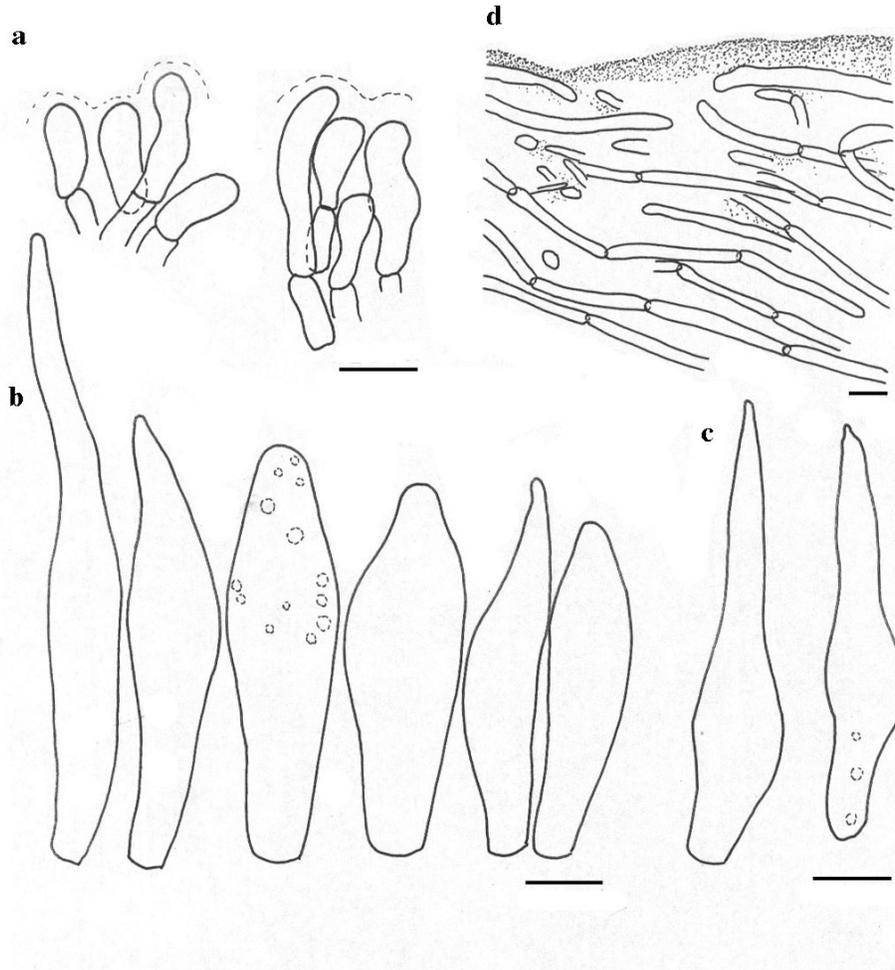


Fig. 5b. *Lactarius* sp. 2. **a.** Marginal cells. **b.** Pleuromacrocystidia. **c.** Cheiloleptocystidia. **d.** Pileipellis. Scale bars = 10 μ m.

Basidiospores 8–8.7–9.8–11.8 \times (7.2) 7.7–8.8–9.9–10.3 μ m, (n = 40, Q = 1.01–1.14–1.3), globose to broadly ellipsoid; ornamentation up to 0.8(–2.0) μ m high, composed of spiny, acute, irregular ridges forming an almost complete reticulum; plage distally amyloid. *Basidia* 55–68 \times 12–15 μ m, with sterigmata 4–7 \times 2–2.8 μ m, 4-spored, thin-walled, subclavate to cylindrical. *Pleuromacrocystidia* 45–90 \times 9–18 μ m, abundant, emergent, with hyaline and guttate contents, subclavate to fusiform or irregular-fusiform, tapering upwards with a mucronate apex, thin-walled. *Pleuropseudocystidia* very scarce, only

observed at the lamella edge, not emergent. *Hymenophoral trama* composed of interwoven hyphae and lactiferous hyphae. *Lamellar edge* sterile, embedded in a thin slime layer; marginal cells 15–30 × 4–7 µm, abundant, hyaline, thin-walled, subclavate, sometimes tapering upwards with a mucronate apex; cheilomacrocytidia 56–63 × 12 µm, abundant, emergent, thin-walled, fusiform, always tapering to a mostly acute apex; contents guttate. *Pileipellis* an ixocutis, 140–240 µm thick; underlying layer composed of filamentous hyphae and sphaerocytes. *Stipitipellis* a cutis, 35–40 µm thick; underlying layer composed of sphaerocytes and filamentous thin-walled hyphae. *Clamp connections* absent.

Habitat and distribution: solitary to gregarious on the soil among leaves.

Material examined: THAILAND, Chiang Mai Prov., Mae Taeng Dist., Tung Joaw village, N19°08.07' E098°38.09', 1423 m alt., rainforest dominated by *Castanopsis armata* and *Pinus kesiya*, 16 July 2005, leg. Zhao Ruilin and Huyen T. Le, Huyen T. Le 351 (CMU, SFSU, MRC).

Discussion: This species is characterized by remarkable colour changes, viz., the latex turns reddish-lilac and stains the lamellae greyish-violet, while the context changes to black-purple.

Violet staining *Piperites* species are well-represented in Europe and North America, where they are accepted in *L.* subsect. *Uvidini* Konr. and *L.* subsect. *Aspideini* Singer of sect. *Uvidi* (Konr.) Bon. The first subsection is characterized by violaceous to brownish or greyish colours in the pileus and the second subsection by cream to bright yellowish colours. According to this criterion, the Thai species described above would belong to *L.* subsect. *Uvidini*, but the colour of milk and context is much more reddish than in all European species, and *Lactarius* sp. 2 is phenetically unlike any of the temperate species.

No violet-staining *Piperites* species have been described from Asia so far. Although some violet-staining species are depicted in Imazeki *et al.* (1988) under European names, they are different from *L.* sp. 2. The ITS sequence of this species is very similar to that of *L. formosus* (Fig. 13). In all analyses they form a clade with a 100% bootstrap support. We prefer not to describe the Thai species formally until more specimens and field data are obtained from which taxonomic and phylogenetic conclusions may be drawn.

6. *Lactarius* sp. 3 (Fig. 6)

Pileus 54 mm diam., convex with depressed center; surface viscid, smooth, zonate, with striate margin, light yellow (4A5) in center, pale yellow (4A3–4) on margin, pinkish white (7A2) to brownish orange (7C5) when bruised. *Lamellae* crowded, decurrent with small tooth, 2–3 mm broad with 3 lamellulae between 2 lamellae, light yellow (4A4–5), grey-brownish red (7BC5) when bruised or broken. *Stipe* 27 × 10 mm, tapering downwards,

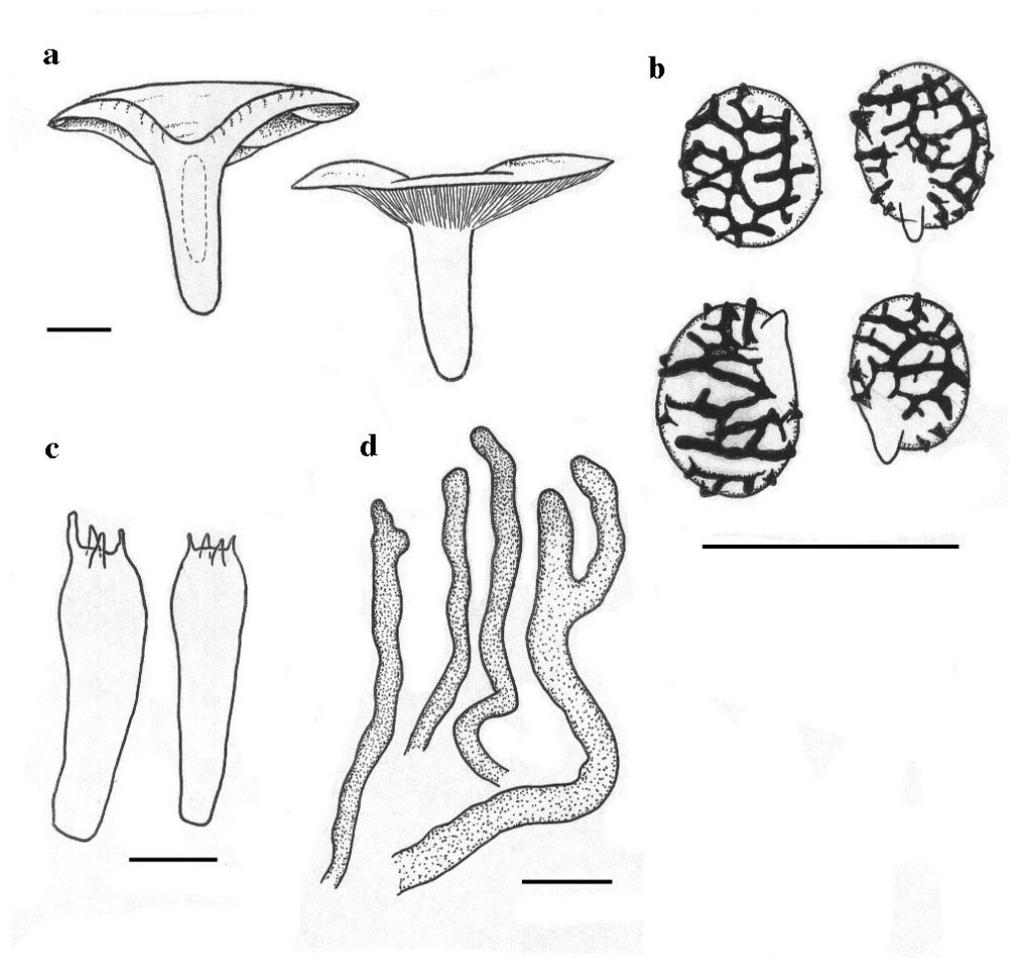


Fig. 6. *Lactarius* sp. 3. **a.** Basidiocarp. **b.** Spores. **c.** Basidia. **d.** Pleuropseudocystidia. Scale bars = 10 mm (basidiocarp) and 10 μ m.

central to eccentric; surface greasy, smooth, orange white (5A2) at apex, pale yellow (4A3) at base. *Context* 4–5 mm thick in pileus, white, soft, solid in stipe, zonation in pileus, staining to pinkish white (7A2), yellowish white (4A2) with 10% KOH, unchanging with FeSO₄; smell sweet; taste mild. *Spore deposit* unknown.

Basidiospores (4.8)5.3– 6.6– 7.7 \times 4.4– 4.9–5.4 μ m, (n = 20, Q = 1.07– 1.3–1.5), subglobose to ellipsoid; ornamentation up to 0.7 μ m high, mostly forming a complete reticulum; plage amyloid. *Basidia* 33–36 \times 9–12 μ m, with sterigmata 3–6 \times 1–1.5 μ m, 4-spored, thin-walled, subclavate, hyaline. True

pleurocystidia absent. *Pleuroseudocystidia* 3–5 μm diam., abundant, emergent up to 45 μm , tortuous to cylindrical, thin-walled. *Hymenophoral trama* composed of filamentous hyphae. *Pileipellis* an ixocutis, 45–53 μm thick, underlying layer composed of filamentous hyphae, thin-walled. *Stipitipellis* a cutis, 30–50 μm thick.

Habitat and distribution: solitary on the soil among leaf litter under *Castanopsis* sp. and *Pinus kesiya*.

Material examined: THAILAND, Chiang Mai Province, Huai Nam Dang National Park, nature trail, 1530 m alt., N19°18.29' E98°35.88', forest with *Pinus kesiya*, *Dipterocarpus* sp., Bamboo & scattered *Castanopsis*, 29.06.2005, leg. Amy Honan, Huyen T. Le 332 (CMU, GENT, SFSU).

Discussion: The species is striking by the pink colour change of the context, which is unknown in *L.* subgenus *Piperites*. Furthermore, it is characterized by a very viscid, pale and zonate pileus surface and by zones in the pileus context.

Because we have only a single specimen in moderate condition, we prefer to wait for more records before formally describing this potential new species. In the molecular phylogeny this species clearly belongs to *L.* subgenus *Piperites* and is often closely allied with *L. controversus* Pers.: Fr.

7. *Lactarius austrotorminosus* H.T. Le & A. Verbeken, sp. nov. (Figs 7a,b)
MycoBank: 510280

Pileus 30–80 mm diam., planoconvexus, leviter depressus, ad infundibuliformis, cum papilla parva; pileipellis squamulosa, strigosa, pallide griseoaurantia, pallide rosea. Stipes 30–70 mm longus, 5–16 mm crassus, cylindratus, leviter scrobiculatus. Lamellae subdecurrentes ad decurrentes, densae, 1–2 mm latae, pallide luteae. Contextus pallide cremeus, gustu acris. Latex albus, immutabilis. Sporae globosae ad late ellipsoideae, (6.5)6.7–7.5–8.4 \times 5.8–6.4–7.0 μm , incomplete reticulatae, leviter zebroideae, cristis usque ad 1(1.5) μm altis ornatae; macula suprahilaris non amyloidea. Basidia 35–60 \times 8–10 μm , subclavata ad cylindrata, tetraspora. Pleuromacrocystidia abundantia, 40–75 \times 5–11 μm , emergentia, subfusiformia ad cylindrata. Pleuroseudocystidia abundantia, non emergentia, 3–6 μm diam., cylindrata vel tortuosa. Pileipellis cutis vel trichoderma, 30–80 μm crassa.

Holotypus: THAILAND, Chiang Mai Prov., Doi Suthep Natl. Park, Sangasabhasri Lane to Huai Kok Ma village, N19°48.62' E98°54.60', primary montane rainforest with *Dipterocarpus*, *Castanopsis*, in exposed soil along trail, 24 June 2004, Huyen T. Le 130 (**holotypus** CMU; **isotypus** SFSU, GENT).

Pileus 30–80 mm diam., convex with slightly depressed center to broadly infundibuliform, slightly depressed and involute at margin, with very small papilla; surface scaly, especially scaly when young, hairy and strigose, with zones of hairs, especially zonate in the centre, pale greyish orange (6AB3–4) to pale orange or pink (5A3) when young, light orange (5A4) in center and pale yellow (4A2–3) on margin when old; greyish orange (5B3–4) where bruised; margin incurved when young, very hairy, wavy, with small triangles of

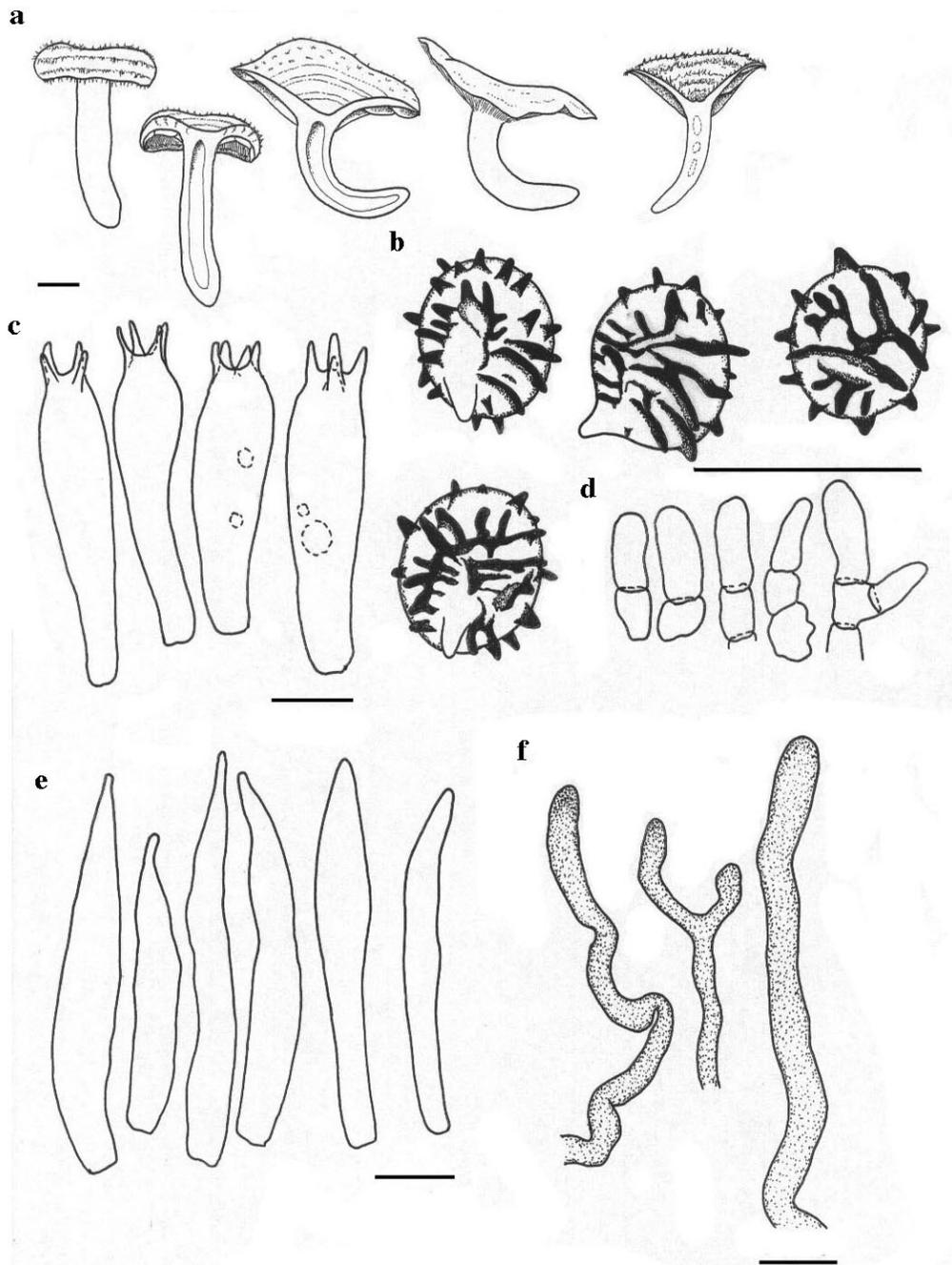


Fig. 7a. *Lactarius austrotorminosus*. **a.** Basidiocarp. **b.** Spores. **c.** Basidia. **d.** Marginal cells. **e.** Pleuromacrocystidia. **f.** Pleuropseudocystidia. Scale bars = 10 mm (basidiocarp) and 10 μm.

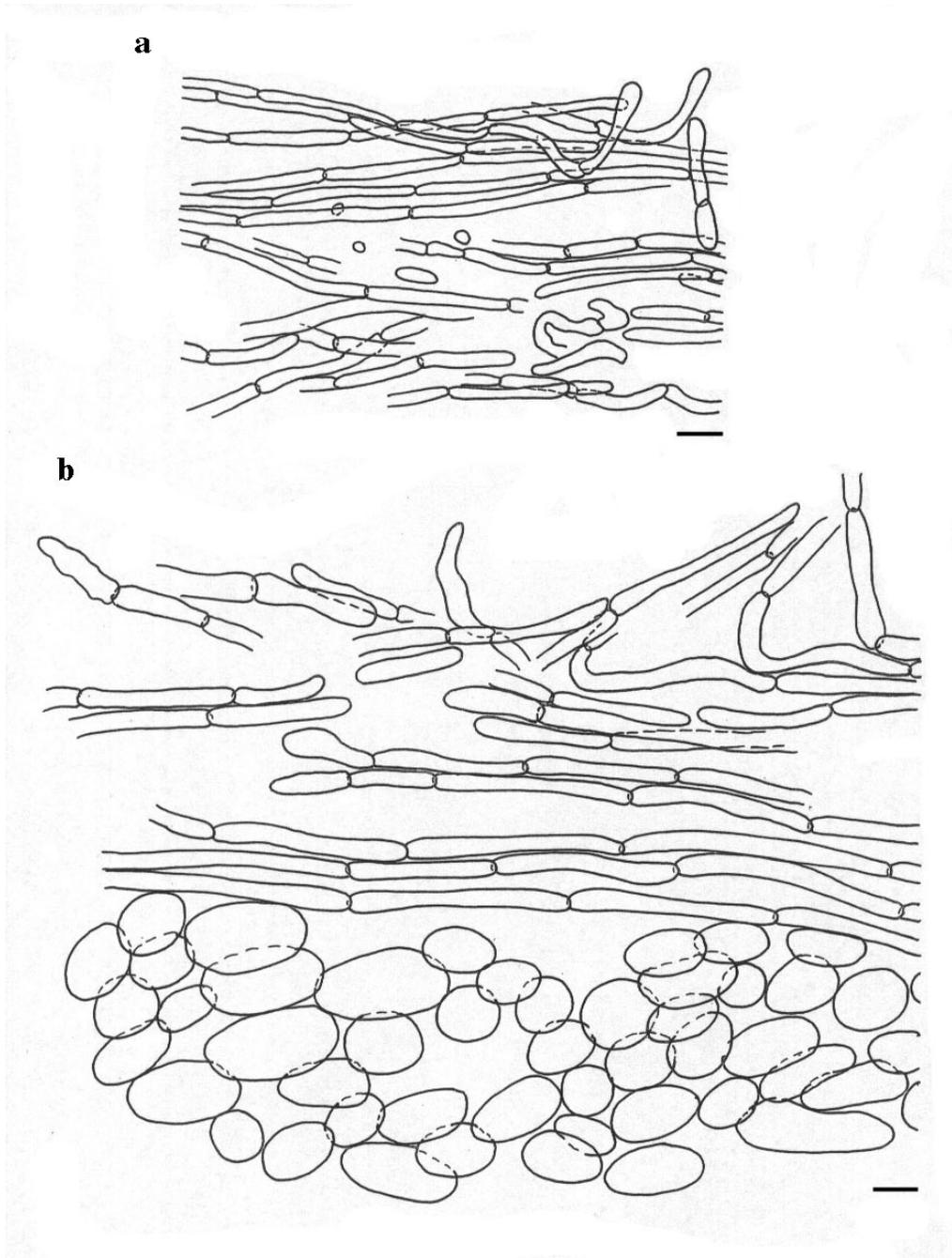


Fig. 7b. *Lactarius austrotorminosus*. **a.** Pileipellis. **b.** Stipitipellis. Scale bars = 10 μ m.

pendulous hairs. *Lamellae* subdecurrent to decurrent, crowded, dense (33L+l/cm), with abundant lamellulae of different lengths, with 3 lamellulae between 2 lamellae, 1–2 mm broad, pale yellow (4A3–4), brownish orange (5CD5) when broken or bruised. *Stipe* 30–70 × 5–16 mm, cylindrical, curved, tapering downwards, smooth, greasy, with small scrobicules, yellowish white (4A2) near gills, light greyish orange (5AB3) or orange white (5A1–2), locally more dirty or brownish pink, with paler to whitish zone on top (4A1–2, 5A2) and base; some specimens scrobiculate with light yellow (4B4–5) scrobicules, brownish orange (6C4) when broken or bruised. *Context* rather firm in pileus, 2.5–5 mm thick in pileus, hollow in stipe, brownish cream near pileus, pinkish cream near gills, with zonation present inside the pileus, pale yellow (3A3) with 10% KOH, unchanging with FeSO₄; taste slightly acrid to very acrid; smell sweetish, agreeable. *Latex* white, unchanging, unchanging with 10% KOH. *Spore deposit* white.

Basidiospores 6–7–7.5–8.3 × 4.5–6–6.5–7.3, (n = 80, Q = 1.05–1.17–1.3), subglobose to broadly ellipsoid; ornamentation up to 1 (–1.5) μm high, composed of ridges forming an incomplete reticulum, with slight zebroid aspect; plage inamyloid. *Basidia* 35–60 × 8–10 μm, with sterigmata 2–7 × 1–2 μm, (1–) 4-spored, sometimes with pigmentation, with guttate and granular contents, thin-walled, subclavate to cylindrical. *Pleuromacrocyttidia* 40–75 × 5–11 μm, very abundant, emergent, subfusiform to cylindrical, with acute or moniliform apex, hyaline, sometimes with granular and needle-like contents, thin-walled. *Pleuropseudocyttidia* abundant, not emergent, 3–6 μm diam., thin-walled, tortuous to cylindrical, tapering upwards at apex. *Hymenophoral trama* composed of interwoven, filamentose hyphae and lactiferous hyphae. *Lamellar edge* heteromorphous; marginal cells 10–25 × 4–7 μm, cylindrical, hyaline, sometimes with pigmentation, thin-walled, 1-septate. *Pileipellis* a cutis to a trichoderm, 30–80 μm thick, composed of hyphae 3–4 μm diam., thin- to slightly thick-walled; underlying layer composed of filamentous hyphae and sphaerocytes; lactifers present. *Stipitipellis* a trichoderm, 20–50 μm thick; underlying layer composed of filamentous hyphae and sphaerocytes. *Clamp connections* absent.

Habitat and distribution: solitary on the soil under *Castanopsis diversifolia* in primary montane forest.

Material examined: THAILAND, Chiang Mai Prov., Doi Suthep-Pui National Park, Sangasahasri Lane to Huai Kok Ma village, N18°48.62' E098°54.60', 1145 m alt., solitary on the soil under *Castanopsis diversifolia* in primary montane forest, dominated by *Castanopsis* spp., *Lithocarpus polistachyus* and other trees, 30 June 2003, leg. D. E. Desjardin, DED 7596 (GENT, CMU, SFSU) – *ibid.*, primary montane rainforest with *Dipterocarpus*, *Castanopsis* etc., in naked soil along trail, 24 June 2004, leg. A. Verbeken & R. Walley 04/84 (GENT), leg. Huyen T. Le 130 (**holotypus** CMU; **isotypes** SFSU, GENT) – *ibid.*, on soil and leaves, in

rain forest dominated by *Castanopsis* and *Lithocarpus* trees, 24 July 2004, leg. Huyen T. Le 191 (CMU, GENT SFSU, MRC) – *ibid.*, solitary on the soil amongst leaves of *Castanopsis armata*, rainforest dominated by *Castanopsis armata* and *Lithocarpus polistachyus* and other trees, 22 June 2005, leg. Huyen T. Le 290 (CMU, GENT, SFSU) – *ibid.*, solitary on the soil amongst leaves of *Castanopsis armata*, rainforest dominated by *Castanopsis armata*, *Lithocarpus polistachyus* and other trees, 24 June 2005, leg. Huyen T. Le 301 (CMU, GENT, SFSU) – Chiang Mai Prov., Mae Taeng Distr., Tung Joaw village, forest trail, 1300 m alt., N19°08.07' E98°38.90', secondary forest with *Pinus kesiya*, *Castanopsis*, 13 June 2004, leg. Huyen T. Le 111 (CMU, GENT, SFSU).

Discussion: *Lactarius austrotorminosus* is easily recognized in the field by the pinkish orange colours and the strongly hairy strigose, zonate pileus. It resembles the European species *L. torminosus* (Schaeff.: Fr.) Pers. and *L. torminosulus* Knudsen & T. Borgen. Both European taxa differ by the more reticulate and lower spore ornamentation and the distinct ixocutis as a pileipellis structure. In addition, the ITS data (Fig. 13) clearly indicate that the Thai *L. austrotorminosus* is distinct from European *L. torminosus*.

The most similar Asian species appears to be *L. strigosus* Verbeke & E. Horak, described from Papua New Guinea. *L. strigosus* has smaller basidiocarps (up to 35 mm diam.) and the spores are less zebroid and have a more spiny and acute aspect. *Lactarius atrosquamulosus* X. He, described from China, is possibly related and shares the zebroid aspect of the spore ornamentation, but has very small basidiocarps (up to 10 mm diam.) and more purplish tinges. Macroscopically specimen Huyen T. Le 111 is distinctive because of the orange, strongly zonate cap with ciliate margin and the pale and slender stipe, but the ITS data show that the specimen belongs to *L. austrotorminosus*.

8. *Lactarius austrozonarius* H.T. Le & A. Verbeke, sp. nov. (Figs 8a,b)
Mycobank: 510281

Pileus 50–135 mm diam., *convexus ad planoconvexus et depressus, infundibuliformis; pileipellis zonata, viscida, pallide lutea, squamulosa, margine barbato. Stipes* 25–115 mm longus, 15–35 mm crassus, *cylindratus ad subcylindratus vel ventricosus, irregularis, pallide luteus, valde scrobiculatus. Lamellae subdistantes, decurrentes, usque ad 11 mm latae, cremeae, a latice griseobrunnescens. Contextus cremeus, albidus, leviter grisescens, gustu acris. Latex albus, immutabilis. Sporae subglobosae ad late ellipsoideae, 8.5–10.2–11.8(12) × 8.1–9.2–10.2 μm, incomplete reticulatae, leviter zebroideae, cristis locale usque ad 2.5(3.5) μm altis ornatae; macula suprahilaris non amyloidea. Basidia* 50–65 × 13–18 μm, *subclavata, tetraspora. Pleuromacrocystidia abundantia, 55–100 × 9–20 μm, emergentia, subclavata ad subfusiformia. Pseudopleurocystidia abundantia, 6–9 μm diam., cylindrata vel tortuosa. Pileipellis ixocutis vel ixo trichoderma, 90–240 μm crassa.*

Holotypus: THAILAND, Chiang Mai Prov., Doi Suthep-Pui Nat. Park, Sangasabhasri Lane to Huai Kok Ma village, N19°48.62' E98°54.60', primary montane rainforest with *Dipterocarpus*, *Castanopsis*, 24 June 2004, leg. Huyen T. Le 129 (**holotypus** CMU; **isotypes** SFSU, GENT).

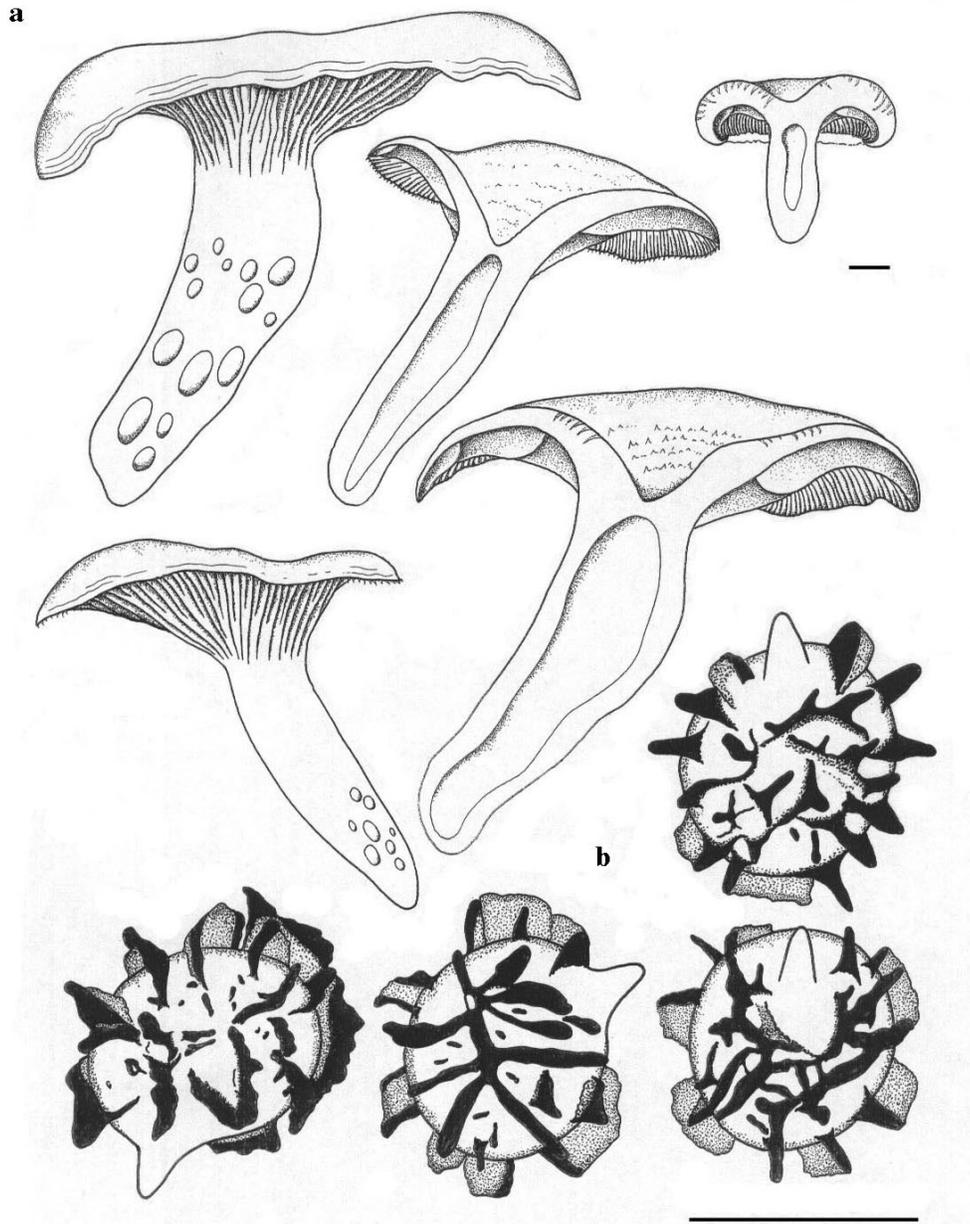


Fig. 8a. *Lactarius austrozonarius*. **a.** Basidiocarp. **b.** Spores. Scale bars = 10 mm (basidiocarp) and 10 μ m.

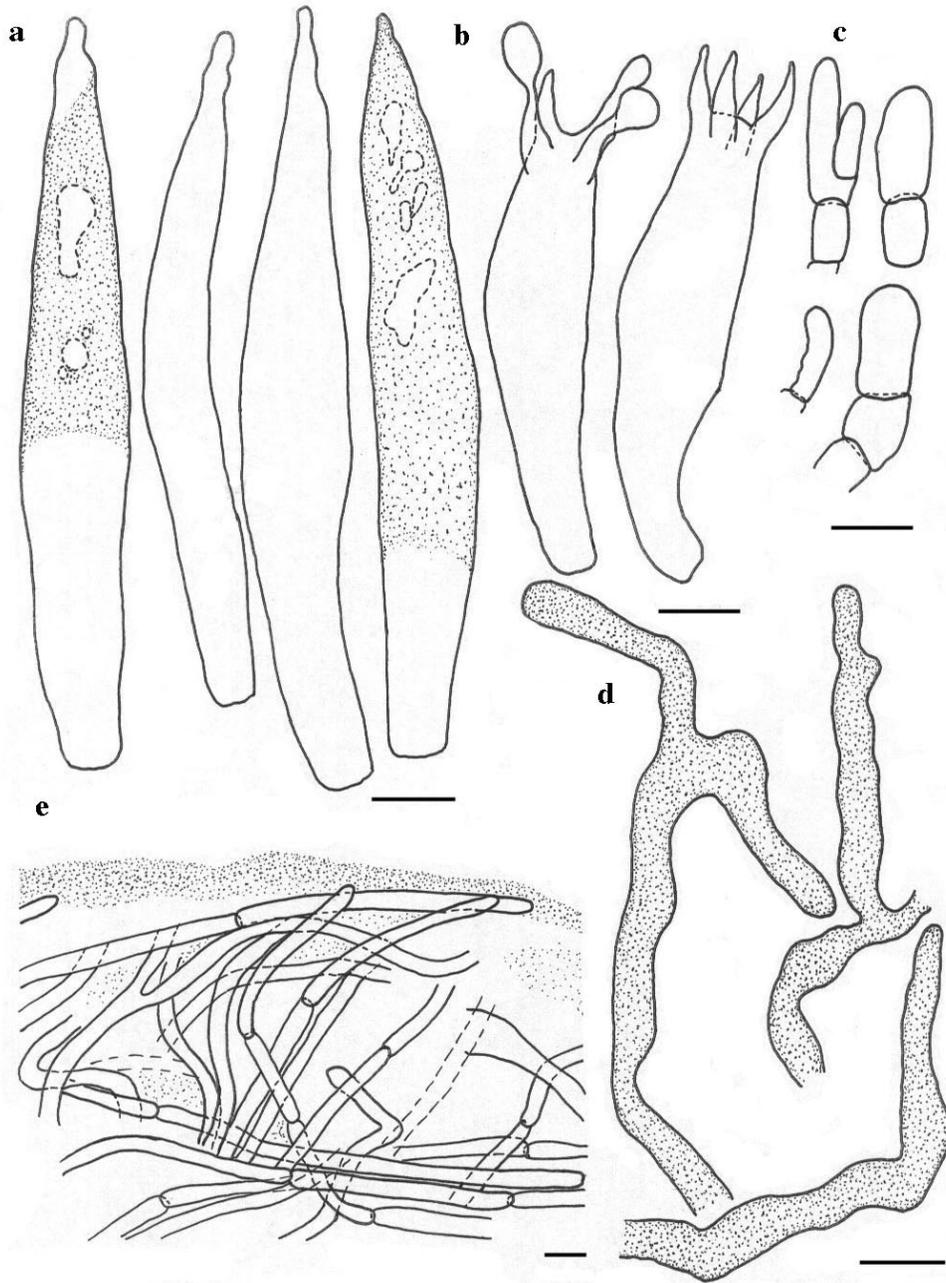


Fig. 8b. *Lactarius austrozonarius*. **a.** Pleuromacrocystidia. **b.** Basidia. **c.** Marginal cells. **d.** Pleuropseudocystidia. **e.** pileipellis. Scale bars = 10 μ m.

Pileus 50–135 mm diam., convex with distinct depression and inrolled margin to plano-convex with deep funnel-shaped depression, infundibuliform; surface pale yellow (3A2–3 in young specimens) or slightly darker and more brownish (sometimes 4B5 in older specimens) with darker to reddish brown scales, with darker zonations, more orange brown on disc, viscid, not hygrophanous, in some specimens woolly; zonations sometimes formed out of the woolly covering, sometimes formed out of watery spots; distinct scales present in some specimens, composed of ascending hairs especially in the center, sometimes dirty brown mottled; margin involute and strongly tomentose in young specimens, bearded, then decurved and with hairs forming pendulous agglutinations, brownish to dirty reddish brown; margin not striate but some slightly grooved aspect visible in between the zonations. *Lamellae* subdistant (6 L+l/cm), decurrent with very long tooth (more than 10 mm in some specimens), with abundant lamellulae (especially short ones), brittle, rather thick, up to 11 mm broad, cream-coloured, staining dirty greyish brown by the latex with some pinkish brown shade; some intervention present close to the stipe in young specimens; edge concolourous, entire. *Stipe* 25–115 × 15–35 mm, cylindrical in younger basidiomes to subcylindrical and ventricose or very irregular in older basidiomes, tapering downwards; surface pale yellow (3A2–3) or darker, locally dirty brownish, smooth, often with very large, ellipsoid scrobicules that are sometimes concolourous, sometimes slightly darker. *Context* very firm and thick in the pileus, hollow in the stipe, cream-coloured to whitish, with watery zonation present inside the pileus, changing slowly greyish when cut; taste very acrid after a while in young specimens, less distinct in older specimens; smell sweetish, like *Lactarius zonarius*. *Latex* very abundant, white to watery cream-coloured, unchanging, but staining paper slowly yellowish, staining lamellae dirty greyish brown, but unchanging when drying; taste burning acrid.

Basidiospores 7.2–8.9–10.5–12.2 × 7–8.4–9.2–10.2 μm (n = 160, Q = 1–1.05–1.14–1.28(–1.33) subglobose to broadly ellipsoid; ornamentation up to 2.5 (–3.5) μm high, forming an incomplete reticulum, often in a partly spiral pattern, composed of acute and locally high ridges that are connected by lower and fines lines; plage inamyloid. *Basidia* 50–65 × 13–18 μm, sterigmata 5–11 × 2–3.5 μm, hyaline, 4-spored, thin-walled, subclavate. *Pleuroseudocystidia* abundant, rarely emergent, 6–9 μm diam., thin-walled, tortuous to cylindrical, with lactiferous contents. *Pleuromacrocystidia* abundant, sometimes with refringent contents, emergent and arising from deep in the subhymenium, 55–100 × 9–20 μm, subclavate to subfusiform with tapering, sometimes moniliform, sometimes rather rounded apex, thin-walled; contents granular and guttate. *Hymenophoral trama* composed of interwoven, filamentous hyphae.

Lamellar edge heteromorphous; marginal cells hyaline, thin-walled, 13–26 × 3–8 µm, 1-septate, shortly clavate, irregularly cylindrical to fusiform. *Pileipellis* an ixocutis to an ixotrichoderm, 90–240 µm thick, underlying layer composed of filamentous hyphae and sphaerocytes. *Stipitipellis* an ixocutis, 70–160 µm thick, underlying layer composed of filamentous hyphae and sphaerocytes. *Clamp connections* absent.

Habitat and distribution: solitary on the soil, in rainforest dominated by *Castanopsis* sp., *Dipterocarpus* sp., and *Lithocarpus* sp.; so far only known from Thailand.

Material examined: THAILAND, Chiang Mai Prov., Doi Suthep-Pui Nat. Park, Sangasabhasri Lane to Huai Kok Ma village, N19°48.62' E98°54.60', 1145 m alt., primary montane rainforest with *Dipterocarpus*, *Castanopsis* etc., 24.06.2004, leg. A. Verbeken & R. Walley 04/81 (GENT), leg. Huyen T. Le 129 (Holotypus CMU, Isotypes SFSU, GENT) – *ibid.*, solitary on the soil amongst leaves of *Castanopsis armata*, rainforest dominated by *Castanopsis armata*, *Lithocarpus polistachyus* and other trees, 24 June 2005, leg. Huyen T. Le 299 (CMU, GENT, SFSU) – *ibid.*, solitary on the soil amongst leaves of *Castanopsis armata*, rainforest dominated by *Castanopsis armata*, *Lithocarpus polistachyus* and other trees, 02 July 2005, leg. Huyen T. Le and Dennis E. Desjardin, Huyen T. Le 338 (CMU, GENT, SFSU) – *ibid.*, solitary on the soil amongst leaves of *Castanopsis armata*, rainforest dominated by *Castanopsis armata*, *Lithocarpus polistachyus* and other trees, 07 June 2006, leg. Huyen T. Le and Dennis E. Desjardin, Huyen T. Le 413 (CMU, GENT, SFSU) – *ibid.*, solitary on the soil amongst leaves of *Castanopsis armata*, rainforest dominated by *Castanopsis armata*, *Lithocarpus* sp. and other trees, 13 June 2006, leg. Huyen T. Le and Dennis E. Desjardin, Huyen T. Le 438 (CMU, GENT, SFSU) – Chiang Mai Prov., Doi Suthep-Pui National Park, Huai Kok Ma village, N18°48.402' E98°54.617', 1146 m alt., primary montane rainforest with *Castanopsis*, *Lithocarpus* etc., 14 August 2003, leg. Huyen T. Le 43 (CMU, GENT, SFSU) – *ibid.*, on soil, primary montane forest with *Castanopsis* spp., *Lithocarpus polistachyus* and other trees, 14 August 2003, leg. Huyen T. Le 44 (CMU, GENT, SFSU) – *ibid.*, on soil, primary montane forest with *Castanopsis* spp., *Lithocarpus polistachyus* and other trees, 14 August 2003, leg. Huyen T. Le 47 (CMU, GENT, SFSU) – *ibid.*, on soil, primary montane forest with *Castanopsis* spp., *Lithocarpus polistachyus* and other trees, 29 August 2003, leg. Huyen T. Le 54 (CMU, GENT, SFSU) – *ibid.*, solitary on soil, relatively wet forest, primary montane forest with *Castanopsis* spp., *Lithocarpus polistachyus* and other trees, 07 October 2003, leg. Huyen T. Le 82 (CMU, GENT, SFSU) – *ibid.*, solitary on soil, relatively wet forest, primary montane forest with *Castanopsis* spp., *Lithocarpus polistachyus* and other trees, 07 October 2003, leg. Huyen T. Le 83 (CMU, GENT, SFSU).

Discussion: *Lactarius austrozonarius* is very similar to *L. austroscrobiculatus* Verbeken & E. Horak, described from Java (Verbeken *et al.*, 2001). It differs by the dominantly yellow colours while *L. austroscrobiculatus* is characterized by pale flesh-coloured, pale hazel and pale lilac tinges. Furthermore, the spores of *L. austrozonarius* are more ellipsoid and with higher ornamentation than those of *L. austroscrobiculatus*.

L. austrozonarius is recognizable in the field by its large basidiomes with zonate, viscid cap and hairy margin, distinct scrobicules on the stipe and white, unchanging latex. Based on overall morphological features, the species belongs

to *Lactarius* subgenus *Piperites* sect. *Zonarii*. Both, *L. austroscrobiculatus* and *L. austrozonarius* differ from all other known representatives of *L.* section *Zonarii* by the very dense reticulum and very high spore ornamentation. Most other species have rather low ornamented spores and a less dense reticulum. The two specimens of *L. austrozonarius* included in the molecular analyses cluster with a bootstrap support of 100% and are well-separated from all other species in *L.* subgenus *Piperites*. It should be noted that in our ITS phylogenies, sect. *Zonarii* is polyphyletic (see also Eberhardt, 2000), and hence the exact relationships of *L. austrozonarius* remain unclear.

Macroscopically, *L. austrozonarius* is also reminiscent of *L. wenquanensis* Y. Wang & Z.X. Xie, described from China (Wang and Xie, 1984), which shares the large basidiomes with yellowish colours, very scrobiculate stipe and zonate pileus with hairy margin. The latex in *L. wenquanensis* is also white and unchanging. Microscopically however, the spores of *L. wenquanensis* are ornamented with isolated ridges and warts of up to 1 μm high and connected by fine lines.

9. *Lactarius* aff. *wenquanensis* Y. Wang & Z.X. Xie, Acta Mycologica Sinica 3(2): 81-86 (1984) (Fig. 9)

Pileus 35–76 mm diam., convex to plano-convex, infundibuliform in age; surface viscid, zonate (with about 7 distinct zones especially in outer half), pale yellow (3A3–4), but slightly darker in the center and in the glutinous hairs; margin decurved, very hairy and tomentose when young (with hairs up to 5 mm long), later with hairs forming glutinous triangles on top of the zonate outer part. *Lamellae* decurrent, rather dense (12–14 L+1/cm), with abundant lamellulae (at least 3 between 2 lamellae), 5 mm broad, yellowish white (3A2); edge entire, concolourous. *Stipe* 35–55 \times 8–13 mm, cylindrical, curved, scrobiculate, concolourous with lamellae, yellowish white (3A2–3), darker in the scrobicules, with whitish zone at the top. *Context* rather firm in the pileus, hollow in the stipe, cream-coloured, unchanging; smell sweet, apple-like; taste very acrid. *Latex* rather abundant, white, drying cream, changing to bright yellow with KOH. *Spore deposit* unknown.

Basidiospores 5.8–7.3–8.6 \times 5.3–5.9–6.5 μm , (n = 20, Q = 1.1–1.23–1.4), broadly ellipsoid, sometimes subglobose or ellipsoid; ornamentation up to 0.5(–0.8) μm high, composed of ridges forming an incomplete reticulum with some isolated irregular warts present; plage inamyloid. *Basidia* 35–45 \times 9–10 μm , with sterigmata 5–7 \times 1.2–1.5 μm , thin-walled, 4-spored, subclavate to cylindrical, with guttate contents. *Pleuromacrocystidia* 54–76 \times 9.5–12 μm , emergent, abundant, subclavate to subfusiform with tapering, sometime moliniform, sometimes rather round apex, thin-walled; needle-like to granular

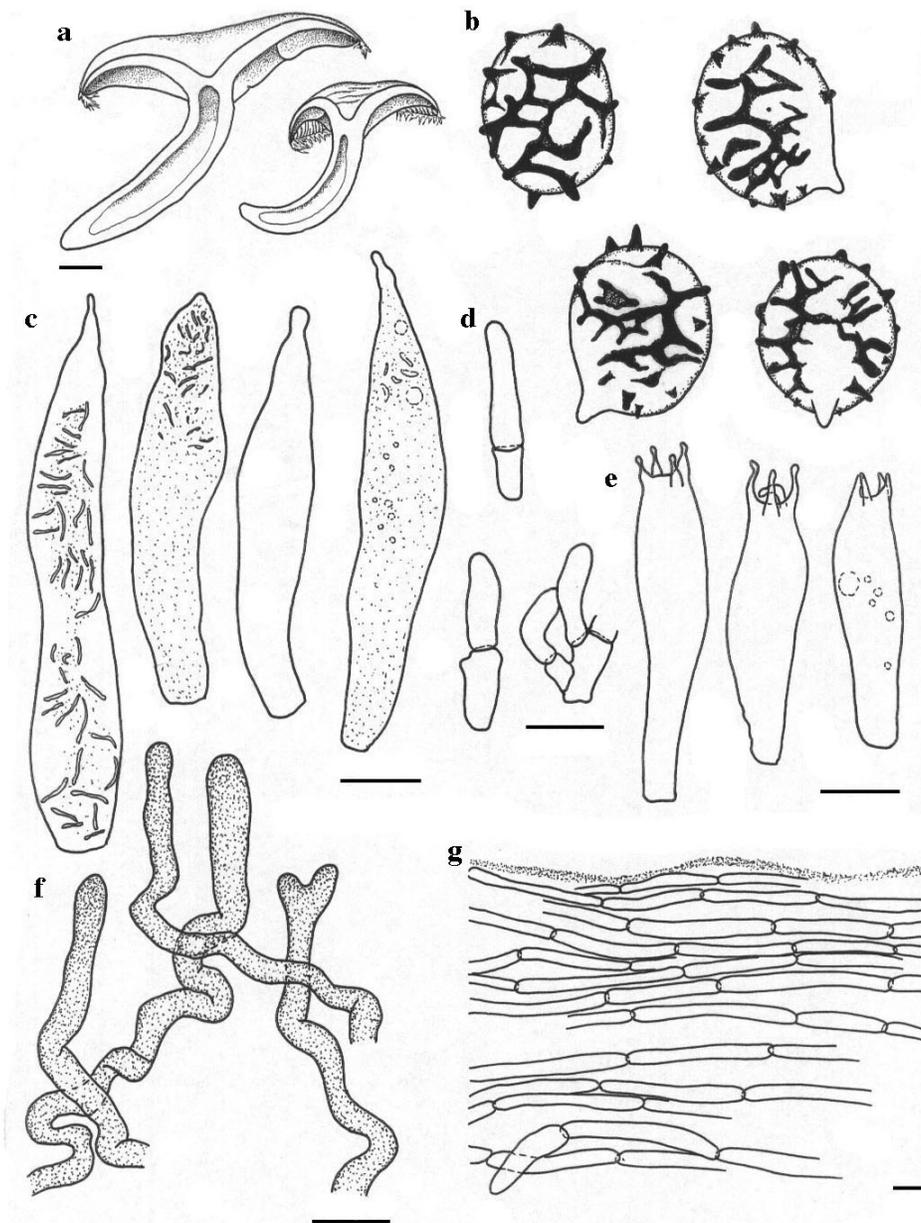


Fig. 9. *Lactarius* aff. *Wenquanensis*. **a.** Basidiocarp. **b.** Spores. **c.** Pleuromacrocystidia. **d.** Marginal cells. **e.** Basidia. **f.** Pleuropseudocystidia. **g.** pileipellis. Scale bars = 10 mm (basidiocarp) and 10 μ m.

contents. *Pleuropseudocystidia* 4–5.5 µm diam., abundant, emergent up to 20–35 µm, with lactiferous contents, thin-walled, tortuous to cylindrical. *Lamellar edge* sterile, composed of marginal cells that are cylindrical, 15–33 × 3–4.5 µm, thin-walled, hyaline. *Hymenophoral trama* composed of interwoven, filamentous hyphae; lactifers abundant. *Pileipellis* an ixocutis, 60–130 µm thick, composed of hyaline, thin-walled hyphae 2–5 µm diam.; underlying layer composed of filamentous hyphae and sphaerocytes mixed, abundant pleuropseudocystidia and lactifers. *Stipitipellis* an ixocutis, 40–60 µm thick. *Clamp connections* absent.

Habitat and distribution: gregarious on the soil, among leaf litter; probably only known from Thailand, possibly conspecific with *L. wenquanensis* known from China.

Material examined: THAILAND, Chiang Mai Prov., Doi Inthanon Natl. Park, junction of Highway 1009 and road to Mae Chem, N19°31.58' E 98°29.64', 1700 m alt., humid montane rainforest with *Quercus*, *Castanopsis*, *Lithocarpus echinops* etc., 25 June 2004, leg. A. Verbeken & R. Walley 04/100 (GENT), leg. Huyen T. Le 143 (CMU, SFSU).

Discussion: The species is characterized by the firm basidiomes with pale yellow, viscid and zonate pileus with very long hairs at the margin that form glutinous triangles and with a distinctly scrobiculate stipe. The latex is white and unchanging and the taste is very acrid. *L. wenquanensis* is the phenetically most similar species to the Thai taxon, but we do not have access to type material of *L. wenquanensis* so our determination is only provisional.

Most Asian look-a-likes have bright yellow latex (e.g. *L. abbotanus* K. Das & J.R. Sharma). A similar species with unchanging, white latex is *L. changbainensis* Y. Wang & Z.X. Xie, but the latter species differs in the subcinnamon colour of the pileus and the smooth margin.

The molecular data (Fig. 13) suggest a close relationship with *L. torminosus*, suggesting that *L. aff. wenquanensis* belongs to *L. sect. Piperites*, a section that is characterized by a sticky pileus with tomentose, hairy margin and white, unchanging latex. The Thai species also shows some features that are typical for *L. sect. Zonarii* (e.g. the sweet apple-like smell, strongly zonate cap, scrobiculate stipe), but as mentioned before the sections within *L. subgenus Piperites* are not yet clearly delimited and traditional European and American classification systems of this subgenus are not confirmed by the molecular data.

10. *Lactarius purpureus* R. Heim ex R. Heim, Rev. Mycol. (Paris) 30: 236. 1962 (1965) (Figs 10a,b)

Type: Heim Th63 (PC), Thailand, Chiang Mai Prov., West of Chiang Mai, ancient forest of Doi Suthep, on a wet gully slope with *Dipterocarpus* sp., 05.12.1957.

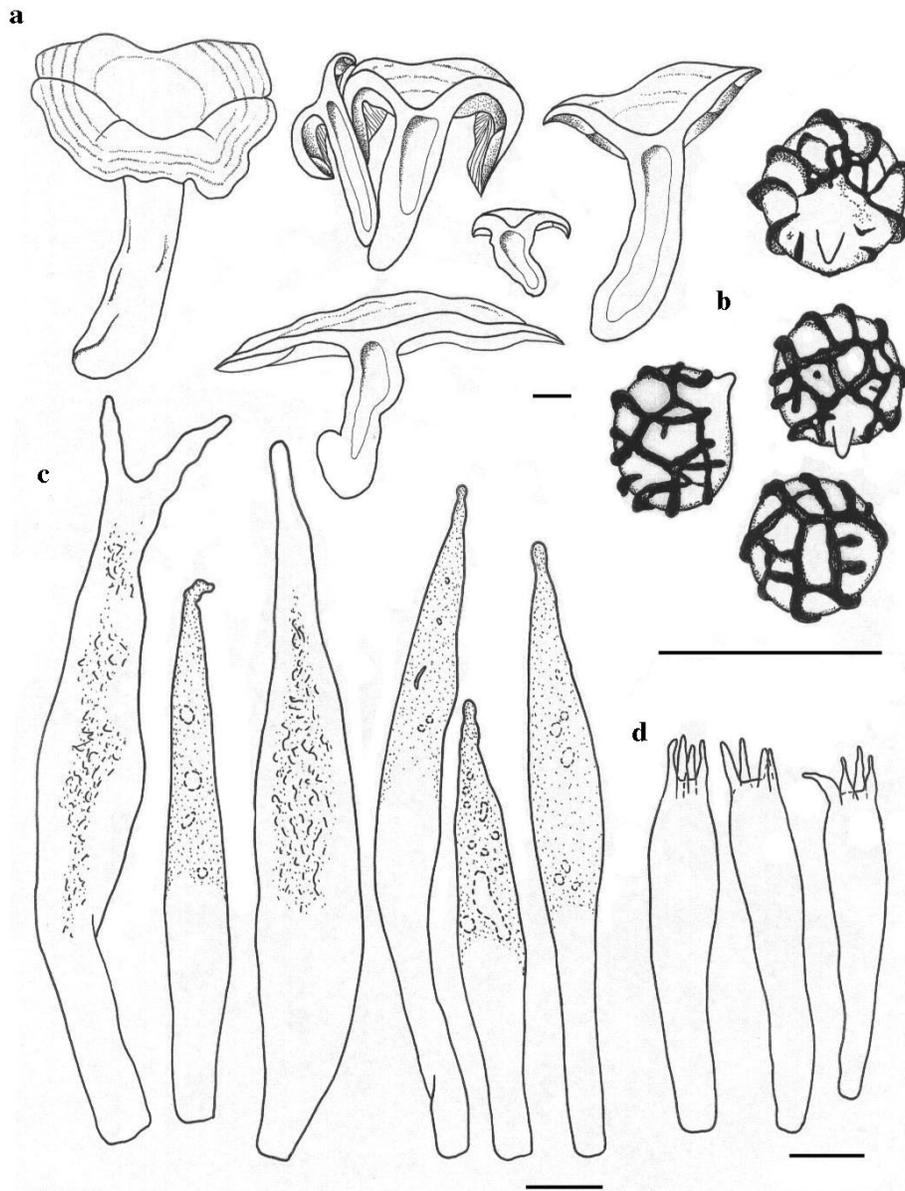


Fig. 10a. *Lactarius purpureus*. **a.** Basidiocarp. **b.** Spores. **c.** Pleuromacrocytidia. **d.** Basidia. Scale bars = 10 mm (basidiocarp) and 10 μ m.

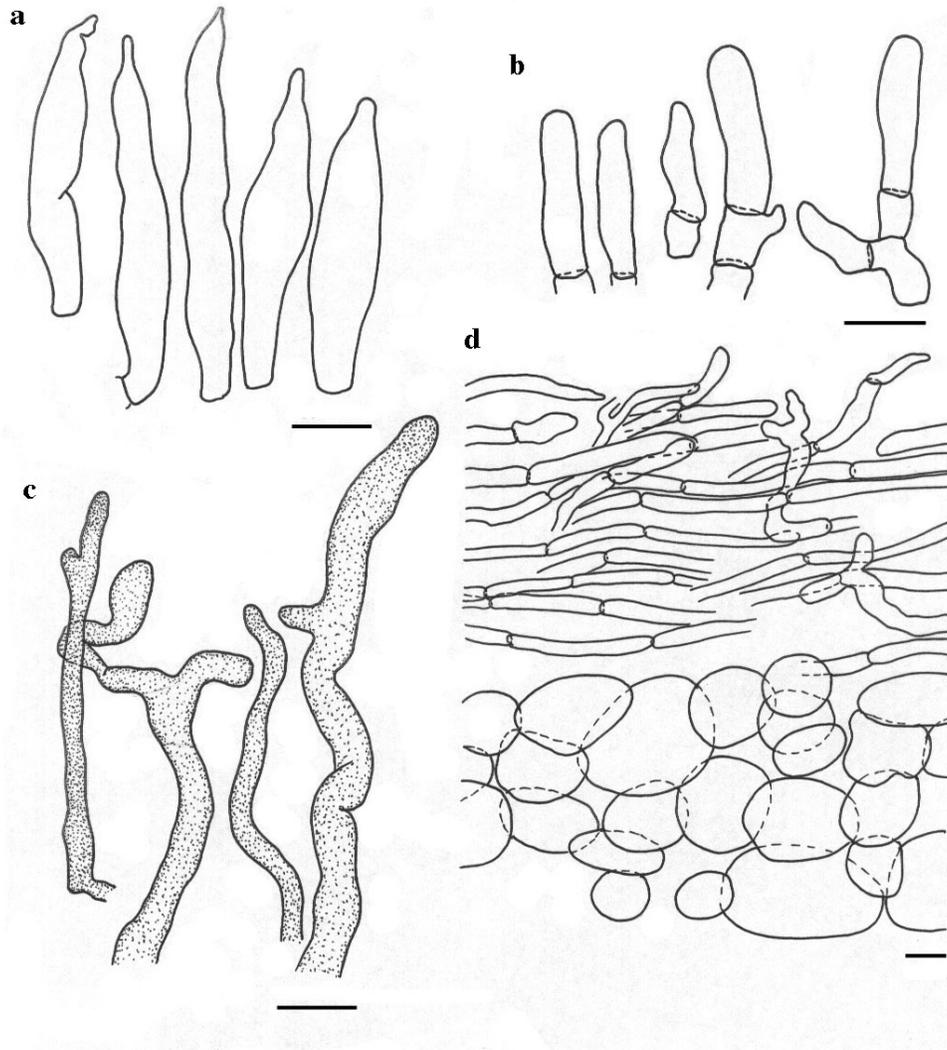


Fig. 10b. *Lactarius purpureus*. **a.** Cheiloleptocystidia. **b.** Marginal cells. **c.** Pleuroseuocystidia. **d.** Pileipellis. Scale bars = 10 μ m (basidiocarp) and 10 μ m.

Pileus 20–115 mm diam., plano-convex with depressed center to almost appanate, becoming widely infundibuliform in age, always somewhat wavy-knotty, irregular; surface with abundant small adpressed scales, slightly to

strongly zonate with multiple zones in some specimens, glabrous, moist to dry but greasy, reddish brown (9C–E5–7), with darker scales on a paler background, darker in the center, paler at the margin; margin incurved to decurved, uplifted in age, very irregular, wavy to flabellate, smooth to slightly tomentose when young, glabrescent. *Lamellae* decurrent with tooth, rather dense (9–12 L+l/cm) with 2–3 series of lamellulae (not always with a regular pattern), reddish brown (9D4–5) when mature, sometimes anastomosing, 2–6 mm broad; edge entire, concolourous. *Stipe* 20–95 × 5.5–20 mm, irregularly cylindrical, sometimes bumpy; surface smooth, concolourous with pileus. *Context* moderately thick and rather firm, 2.5–8 mm thick, thin near the margin, pale pinkish to pale reddish brown in places where eaten by insects, brittle and hollow in stipe, greyish green (29D4–5) with 10%, KOH, unchanging with FeSO₄; taste very acrid; smell fruity acidic, slightly apple-like. *Latex* white, abundant, acrid, unchanging. *Spore deposit* unknown.

Basidiospores 5.2–6–6.8–8.2 × 4.5–5.5–6.4–7.2 μm, (n = 160, Q = 1–1.09–1.2–1.33), globose to broadly ellipsoid; ornamentation up to 1.2 μm high, composed of ridges that are forming a subcomplete reticulum; some isolated warts or short ridges present; plage inamyloid. *Basidia* 40–60 × 7–10 μm, with sterigmata 4–9 × 1.2–2 μm, hyaline, sometimes with refringent contents, thin-walled, 2–4 spored, subclavate to cylindrical. *Pleuromacrocystidia* 44–115 × 8–16 μm, abundant, emergent, subfusiform, with acute or moniliform apex, hyaline, thin-walled. *Pleuropseudocystidia* 3–9 μm diam., abundant, emergent up to 25–40 μm, tortuous to cylindrical, sometimes branching, with lactiferous contents, thin-walled. *Hymenophoral trama* composed of interwoven, filamentous hyphae and lactifers. *Lamellar edge* heteromorphous; marginal cells 12–30 × 4–8 μm, subclavate to subcylindrical, hyaline, thin-walled, 1-septate, forming the top of a multiseptate chain of short elements; cheilomacrocystidia 35–55 × 6–9 μm, rather abundant, fusiform, with tapering to acute, seldom moniliform apex, thin-walled, with needle-like contents. *Pileipellis* a cutis to a trichoderm, 70–160 μm thick, composed of hyphae 2–4 μm diam.; underlying layer composed of sphaerocytes and filamentous hyphae, abundant pleuropseudocystidia and lactifers. *Stipitipellis* a cutis to a trichoderm, 50–80 μm, underlying layer composed of filamentous hyphae and sphaerocytes. *Clamp connections* absent.

Habitat and distribution: Gregarious in soil under *Castanopsis diversifolia* in montane primary forest. *L. purpureus* was described from Thailand and is known also from Papua New Guinea (Verbeken and Horak 2000).

Material examined: THAILAND, Chiang Mai Prov., West of Chiang Mai, ancient forest of Doi Suthep, on a wet gully slope with *Dipterocarpus* sp., 05 December 1957, Heim Th. 63 (PC, Holotypus) – Doi Suthep-Pui National Park, Sangrasabhasri Lane to Huai Kok Ma

village, N18°48.62' E098°54.60', 1145 m alt., primary montane forest with *Castanopsis* spp. and *Lithocarpus polistachyus* and other trees, 22 June 2003, leg. D.E. Desjardin 7556 (CMU, GENT, SFSU) – *ibid.*, primary montane forest with *Castanopsis* spp. and *Lithocarpus polistachyus* and other trees, 30 June 2003, leg. D.E. Desjardin 7600 (CMU, GENT, SFSU) – *ibid.*, primary montane forest with *Castanopsis* spp. and *Lithocarpus polistachyus* and other trees,, solitary to gregarious on soil, 30.05.2004, leg. Huyen T. Le 99 (CMU, GENT, SFSU). – *ibid.*, primary montane forest with *Castanopsis* spp. and *Lithocarpus polistachyus* and other trees, 30 July 2004, leg. Huyen T. Le 207 (CMU, GENT, SFSU) – *ibid.*, primary montane forest with *Castanopsis* spp. and *Lithocarpus polistachyus* and other trees, 02 June 2005, leg. Huyen T. Le 258 (CMU, GENT, SFSU) – *ibid.*, primary montane forest with *Castanopsis* spp. and *Lithocarpus polistachyus* and other trees, 24 June 2005, leg. Huyen T. Le 298 (CMU, GENT, SFSU) – *ibid.*, primary montane forest with *Castanopsis* spp. and *Lithocarpus polistachyus* and other trees,, solitary to gregarious on soil, 24 June 06, leg. Huyen T. Le 446 (CMU, GENT, SFSU) – Doi Suthep-Pui National Park, Huai Kok Ma village, N18°48.402' E98°54.617', 1145 m alt., solitary to gregarious on the soil, primary montane forest with *Castanopsis* spp. and *Lithocarpus polistachyus* and other trees,, 29 August 2003, leg. Huyen T. Le 52 (CMU, GENT, SFSU) – Mae Taeng Distr., Tung Joaw village, N19°08.07' E098°38.09', 1423 m alt., solitary to gregarious on soil and leaves, in evergreen forest dominated by *Castanopsis* sp. and *Pinus* sp., 27 May 2004, leg. Huyen T. Le 94 (CMU, GENT, SFSU) – Mae Teng Distr., Tung Joaw village, hill ridge, N19°08.07' E 98°38.90', 1350 m alt., hypogeous in well decayed leaf litter in drier *Castanopsis*-dominated broadleaved forest, disturbed by fire, 21 June 2004, leg. A. Verbeken & R. Walley 04/35 (GENT), leg. Huyen T. Le 120 (CMU, SFSU).

Discussion: Lactarius purpureus is recognized easily in the field because of the uniformly reddish purple colours, reminiscent of *Hygrophorus russula*, as already indicated in the original diagnosis by Heim (1962). Heim erected a different taxonomic group for this outstanding species, viz., “Squamosi” (invalid). Conspecificity of the Thai and Papua New Guinean specimens is confirmed by the molecular data (Fig. 13).

11. *Lactarius alboscrobiculatus* H.T. Le & A. Verbeken, sp. nov. (Figs 11a,b)
Mycobank: 510283

Pileus 20–120 mm diam., convexus et depressus ad infundibuliformis; pileipellis sicca, laevis ad rugulosa, zonata, alba ad albidocrema. Stipes 25–55 mm longus, 10–30 mm crassus, cylindratus, siccus, laevis, basin versus scrobiculatus, albus ad luteoalbidus. Lamellae subdecurrentes, 2–5 mm latae, cremeae ad albae. Contextus albidus, gustu acris. Latex albus, immutabilis. Sporae globosae ad late ellipsoideae, (5.8)5.8–6.5–7.1 × (5.2)5.3–6.1–6.8 μm, subcomplete reticulatae, cristis usque ad 0.5(1) μm altis ornatae; macula suprahilaris non amyloidea. Basidia 30–65 × 8–11 μm, subclavata ad cylindrata, tetraspora. Pleuromacrocystidia aliquantum abundantia, 33–55 × 4–6 μm, non emergentia, subfusiformia, interdum mucronata. Pseudopleurocystidia non abundantia, 3–8 μm diam., cylindrata vel tortuosa. Pileipellis ixocutis, 60–230 μm crassa.

Holotypus: THAILAND, Chiang Mai Prov., Doi Suthep-Pui National Park, Sangasabhasri Lane to Huai Kok Ma village, N18°48.62' E098°54.60', rainforest dominated by *Castanopsis armata*, *Lithocarpus polistachyus* and other trees, 02 June 2005, leg. Huyen T. Le 257 (**holotypus** CMU; **isotypes** SFSU, GENT).

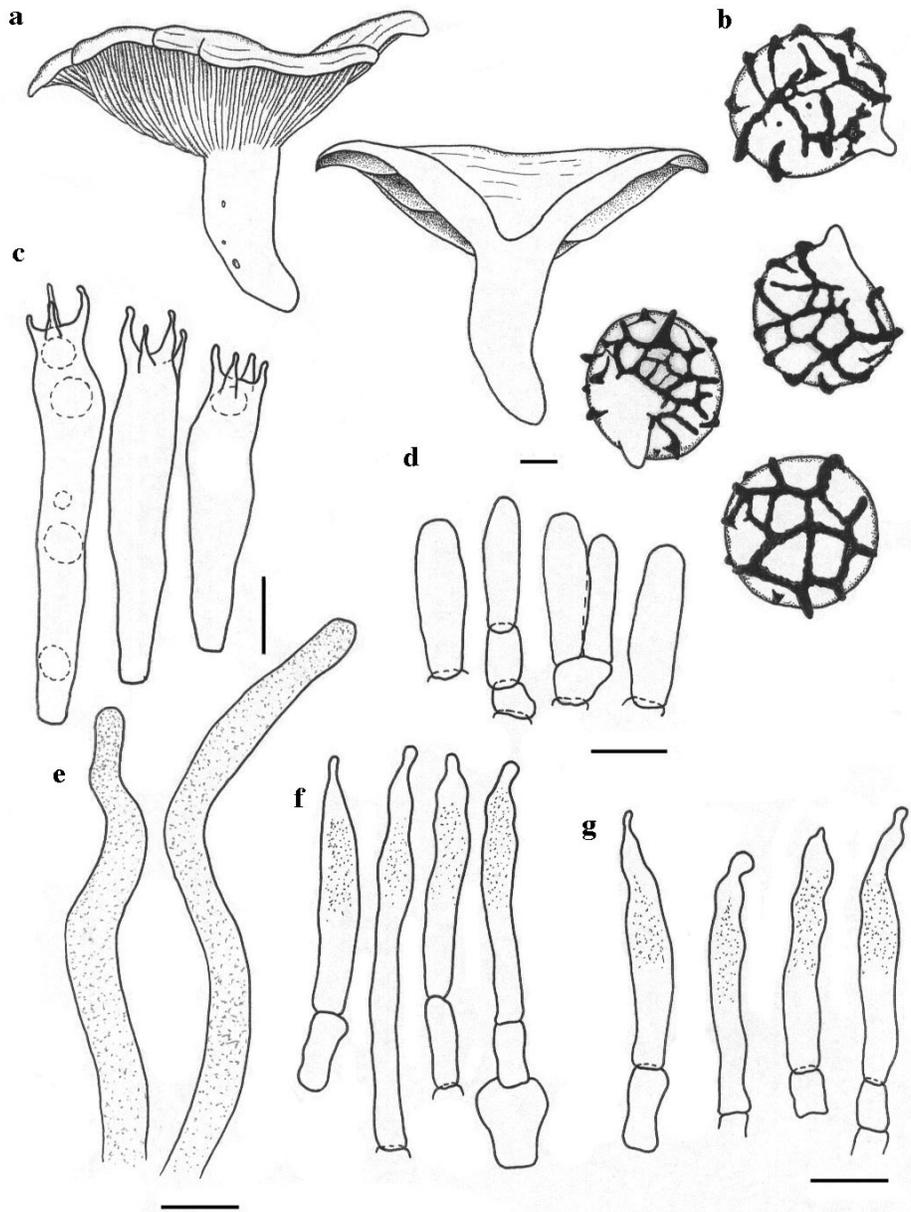


Fig. 11a. *Lactarius alboscrobiculatus*. **a.** Basidiocarp. **b.** Spores. **c.** Basidia. **d.** Marginal cells. **e.** Pleuropseudocystidia. **f.** Pleuromacrocystidia. **g.** Cheiloleptocystidia. Scale bars = 10 mm (basidiocarp) and 10 μ m.

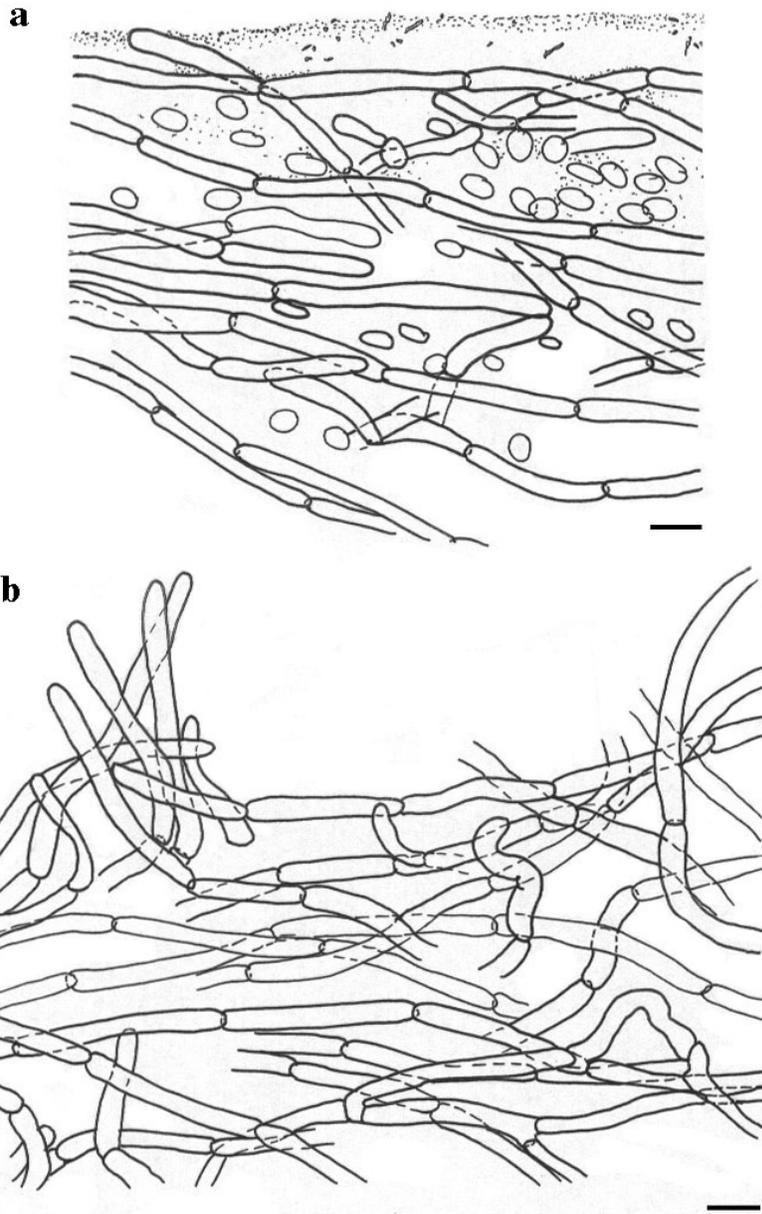


Fig. 11b. *Lactarius alboscrobiculatus*. **a.** Pileipellis. **b.** Stipitipellis. Scale bars = 10 μ m.

Pileus 20–120 mm diam., convex and depressed to infundibuliform; surface dry, smooth to rugose, zonate from center to margin, white to white cream-colour; margin wavy, smooth. *Lamellae* subdecurrent, 2–5 mm broad, with 3–4 lamellulae between two lamellae, sometimes furcate to intervenose, close to crowded, concolourous with pileus, cream to yellowish white (2A2). *Stipe* 25–55 × 10–30 mm, cylindrical to tapering downwards, central, dry, smooth, scrobiculate at base, white to yellowish white (1A1–2) at apex, pale yellow (2A2–3). *Context* 4.5–11 mm in pileus, solid in stipe, yellowish white, greenish grey white (1A–B2) at apex, pale yellow with 10%; KOH, unchanging with FeSO₄; smell fresh, agreeable; taste acrid. *Latex* white to cream. *Chemical reactions* unknown. *Spore deposit* unknown.

Basidiospores (5–)6.5–7.3–8.3 × 4.8–5.8–7 μm, (n = 80, Q = 1–1.07–1.14–1.3), globose to broadly ellipsoid; ornamentation up to 0.5 (–1) μm high, forming an almost complete reticulum; plage inamyloid. *Basidia* 30–62 × 8–11 μm, sterigmata 3–8 × 1–1.8 μm, thin-walled, 4-spored, subclavate to cylindrical, hyaline, sometimes with guttate contents. *Pleuromacrocystidia* rather abundant especially near the edge, but not easy to observe, 33–55 × 4–6 μm, not emergent, sometimes with granular contents, subfusiform, with mucronate apex, thin-walled. *Pleuropseudocystidia* 3–8 μm diam., not abundant, emergent up to 30–36 μm, narrowly cylindrical, tortuous or cylindrical, with lactiferous contents, thin-walled. *Hymenophoral trama* interwoven, composed of filamentous hyphae and sphaerocytes. *Lamellar edge* sterile, composed of marginal cells that are narrowly cylindrical, 14–45 × 3–6.5 μm, thin-walled, hyaline. *Pileipellis* an ixocutis, 60–230 μm thick, composed of hyaline, thin-walled hyphae, with abundant pseudocystidia and lactiferous hyphae (4–6.5 μm diam.); underlying layer composed of filamentous hyphae and sphaerocytes. *Stipitipellis* a cutis to a trichoderm, 50–170 μm thick; underlying layer composed of filamentous hyphae and sphaerocytes. *Clamp connections* absent.

Habitat and substrate: solitary on the soil under *Castanopsis armata* and *Pinus*; so far known only from Thailand.

Material examined: THAILAND, Chiang Mai Prov., Doi Inthanon National Park, Hwy 1009 at 25 km marker, N18°32.54' E098°33.51', 1076 m alt., rainforest dominated by *Castanopsis armata* and *Pinus* sp., 11 June 2004, leg. Huyen T. Le 107 (CMU, GENT, SFSU) – *ibid.*, rainforest dominated by *Castanopsis armata* and *Pinus* sp., 03 July 2004, leg. Huyen T. Le 175 (CMU, GENT, SFSU) – *ibid.*, rainforest dominated by *Castanopsis armata* and *Pinus kesiya*, 27 June 2005, leg. Huyen T. Le 318 (CMU, GENT, SFSU) – Chiang Mai Prov., Doi Suthep-Pui National Park, Sangasabhasri Lane to Huai Kok Ma village, N18°48.62' E098°54.60', 1145 m alt., rainforest dominated by *Castanopsis* spp. and *Lithocarpus polistachyus* and other trees, 02 June 2005, leg. Huyen T. Le 257 (**holotype** CMU; **isotypes** GENT, SFSU).

Discussion: The species is recognized in the field by the overall white to whitish colours, a zonate pileus, and white, unchanging latex and by the relatively short stipe (compared to the rather large pileus diameter). A striking character, visible when cutting the basidiomes, is the presence of a strong zonation inside the pileus context (which seems to be a continuation of the zones on the cap surface). These zones are watery and white and are present especially in the outer half of the pileus but sometimes fill the pileus almost completely. For further discussions see under *L. alboscrobiculatus* var. *roseopurpureus* below.

12. *Lactarius alboscrobiculatus* var. *roseopurpureus* H.T. Le & A. Verbeken,
var. nov. (Fig. 12)

Mycobank: 510284

A var. typ. differt coloribus purpureis vel roseis in pileo, gustu mitis et lamellis grisescentibus.

Holotypus: THAILAND, Chiang Mai Prov., Doi Inthanon National Park, Hwy 1009 at 25 km marker, 1050 m alt., N18°32.54' E98°33.51', xeric forest with *Pinus kesya*, *Castanopsis*, *Lithocarpus*, 25.06.2004, Huyen T. Le 148 (**holotypus** CMU; **isotypes** SFSU, GENT).

Pileus 35–68 mm diam., convex to deeply infundibuliform; surface viscid, zonate with most narrow and distinct zones near the extreme margin and some vaguer zones towards center, margin smooth to slightly tomentose when young, glabrescent, colours reminiscent of *Lactarius controversus*, white, cream-coloured, yellowish white (2A2), locally with purplish pink spots or shades. *Lamellae* decurrent with long tooth, moderately distant (9–10 L+1/cm), with abundant lamellulae, yellowish white (3A2), staining greyish by the latex (where cut). *Stipe* 25–40 × 9–15 mm, irregularly cylindrical, dry, whitish cream-coloured with reddish brown spots, scrobiculate, with smaller or larger scrobicules especially in lower half; scrobicules dark flesh-coloured to dirty pink. *Context* very firm, hollow in stipe, white and with zones present inside the pileus, in some places very distinct watery greyish and a bit pinkish in the zones, slightly pinkish underneath the pileipellis, turning greyish when cut (slowly), unchanging with FeSO₄ and 10% KOH; taste agreeable, remarkable, not acrid; smell sweet, fruity. *Latex* white, slightly cream-coloured, unchanging, unchanging with 10% KOH. *Spore deposit* unknown.

Basidiospores 6–7.4–8.5 × 5.8–6.5–7.5 μm, (n = 20, Q = 1–1.14–1.3), globose to broadly ellipsoid; ornamentation up to 0.5 (–0.8) μm high, forming an almost complete reticulum; plage inamyloid. *Basidia* 45–50 × 10–11 μm, with sterigmata 6–8 × 1.2–1.6 μm, thin-walled, 4-spored, subclavate to cylindrical, with guttate contents. *Pleuromacrocystidia* abundant near the lamella edge, difficult to observe, not emergent, 35–45 × 7–10 μm, subclavate, thin-walled. *Pleuropseudocystidia* 4–8 μm diam., not abundant, emergent up to

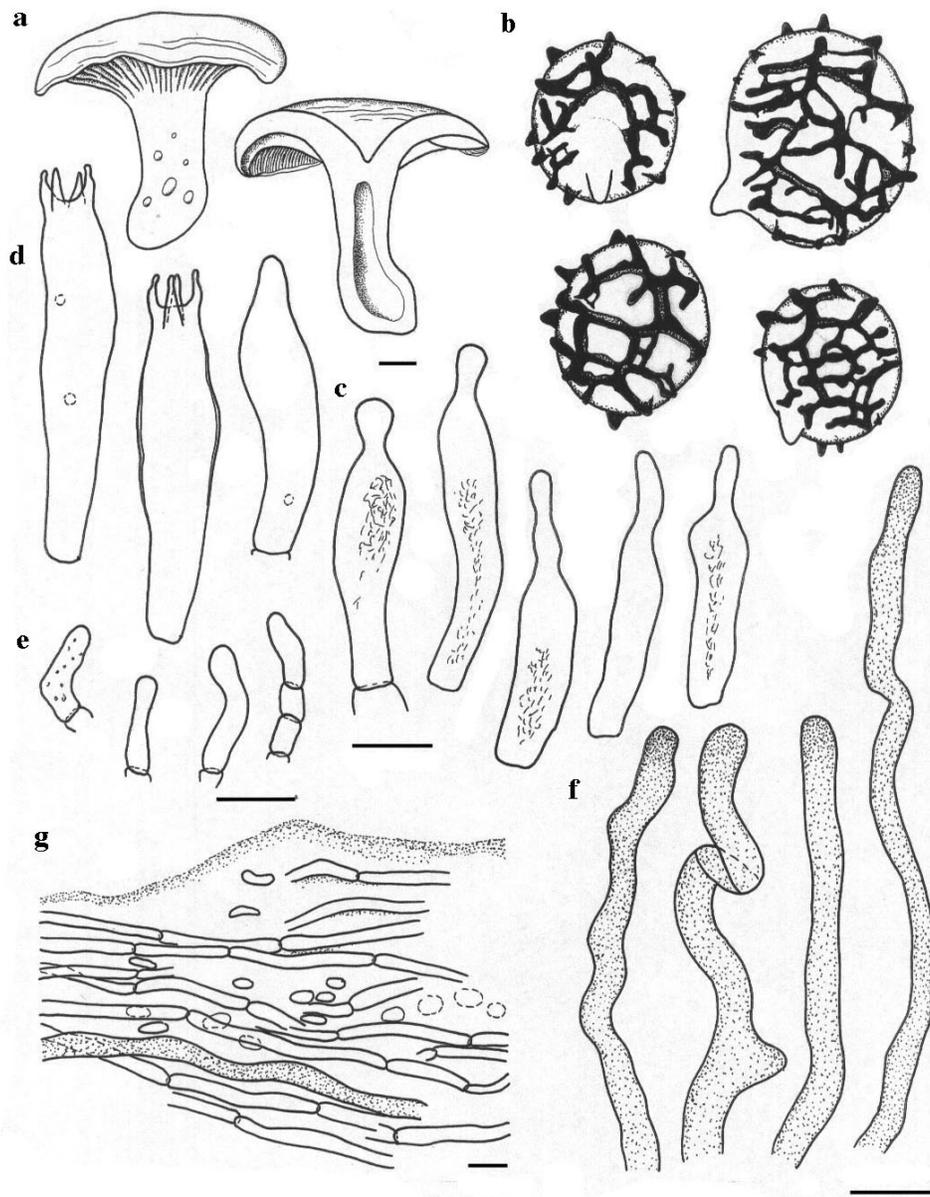


Fig. 12. *Lactarius alboscrobiculatus* var. *Roseopurpureus*. **a.** Basidiocarp. **b.** Spores. **c.** Pleuromacrocystidia. **d.** Basidia. **e.** marginal cells. **f.** Pleuropseudocystidia. **g.** Pileipellis. Scale bars = 10 mm (basidiocarp) and 10 μ m.

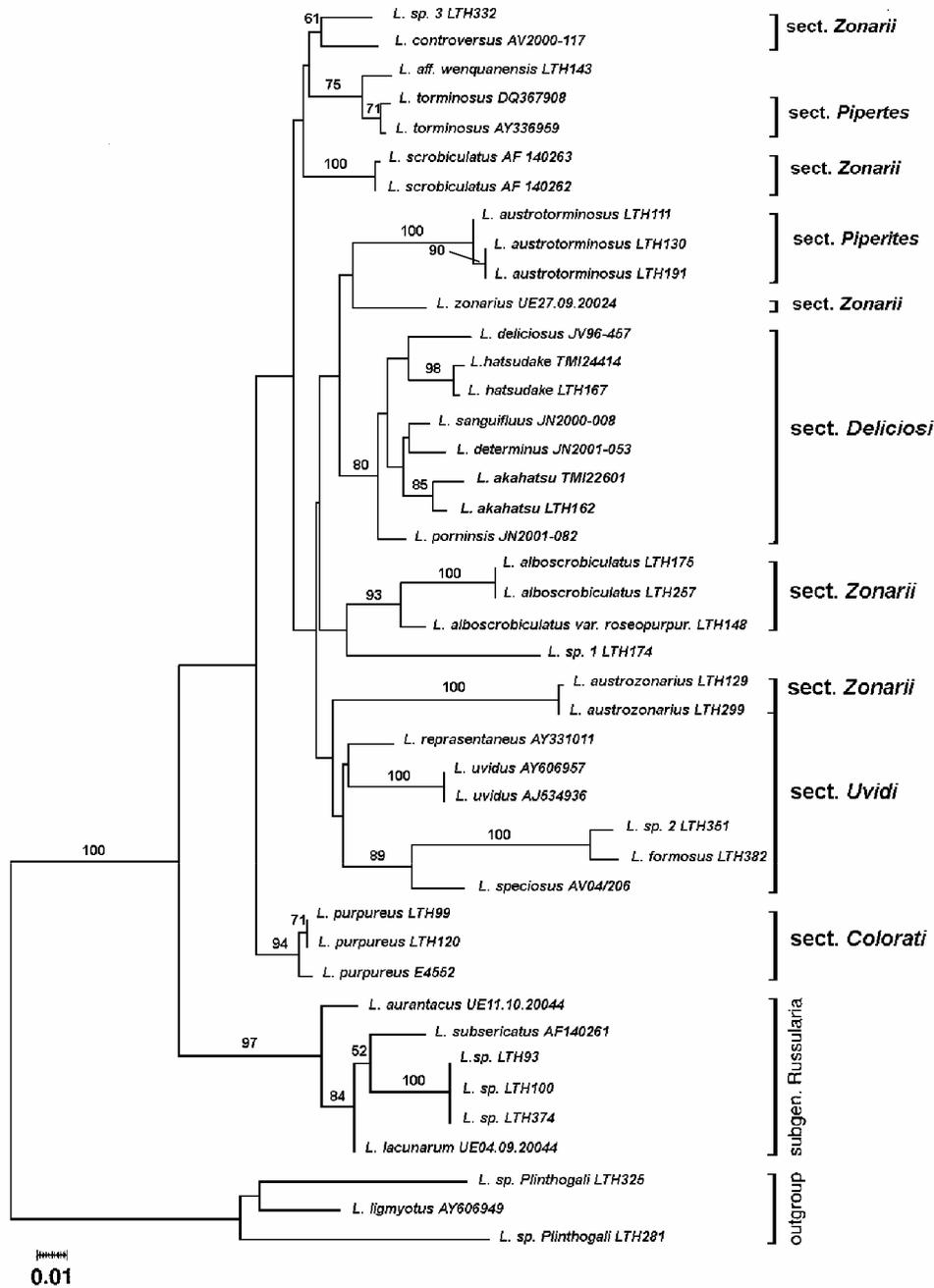


Fig. 13. ML phylogeny of *Lactarius* subgenus *Piperites* in Northern Thailand based on ITS sequences. The TrN+I+G model was used as model of sequence evolution. Bootstrap percentages > 50% are indicated above the branches. The scale bar represents the number of substitutions/site.

50 µm, with lactiferous or oleiferous contents, thin-walled, tortuous to cylindrical. *Lamellar edge* sterile, composed of marginal cells; marginal cells narrowly cylindrical to irregular, 12–21 × 3.0–3.5 µm, thin-walled. *Hymenophoral trama* composed of interwoven, hyaline hyphae. *Pileipellis* an ixocutis, 50–80 µm thick, composed of hyaline hyphae; abundant pleuropseudocystidia and lactifers present; underlying layer composed of filamentous hyphae and sphaerocytes. *Clamp connections* absent.

Habitat and Distribution: solitary under *Castanopsis* sp., *Lithocarpus* sp. and *Pinus* sp.; so far known only from Thailand.

Material examined: THAILAND, Chiang Mai Prov., Doi Inthanon National Park, Hwy 1009 at 25 km marker, 1050 m alt., N18°32.54' E98°33.51', xeric forest with *Pinus kesiya*, *Castanopsis*, *Lithocarpus*, 25 June 2004, leg. A. Verbeken & R. Walley 04/118 (GENT), leg. Huyen T. Le 148 (**holotypus** CMU; **isotypes** SFSU, GENT).

Discussion: This taxon differs from the type variety of *L. alboscrobiculatus* by the presence of purplish pink colours in the pileus, the absence of an acrid taste and the greyish colour change of the lamellae by the latex. Because we could not observe any microscopical difference between this specimen and the other specimens belonging to *L. alboscrobiculatus*, we prefer to describe it as a variety of the same species. Furthermore it should be noted that in the morphologically very similar European species *L. controversus*, entirely white collections are known besides collections with distinct purplish pink tinges. *Lactarius controversus*, however, always has a burning acrid taste, and narrow, very small basidiospores with a less complete reticulum. No Asian look-a-likes are known thus far.

The ITS phylogeny (Fig. 13) shows that the two specimens of *Lactarius alboscrobiculatus* form a clade with 100% bootstrap support, and that *L. alboscrobiculatus* var. *roseopurpureus* is a sister taxon with 93% bootstrap support. Surprisingly the molecular data indicate that *L. alboscrobiculatus* is not closely related to *L. controversus*.

Discussion

Is the subgenus well-represented in Northern Thailand?

Prior to this paper, the only known species of *L.* subgenus *Piperites* in Thailand was *L. purpureus*. This study raised the number to 11 species and one variety, this out of a total number of about 50 *Lactarius* species for the area (unpublished results). In Europe, more than one third of all *Lactarius* species belongs to *L.* subgenus *Piperites*, in North America also one third of all *Lactarius* species belong to this subgenus. In Africa the subgenus is very poorly represented with two species out of a total of 89. In another well-studied

Asian area, Papua New Guinea, the *Lactarius* mycoflora now counts 9 *Piperites* representatives out of a total of 31 species.

The subgenus is thus rather well-represented, but what is striking here is the absence of certain sections in the subgenus. Species with yellow staining latex are common in Europe and North America (*L.* sect. *Scrobiculati*), but seem to be lacking here. In the Thai material only one specimen (considered here as *L.* sp. 1) has yellow latex and its position in the molecular phylogeny is uncertain. The diversity of the purple staining species (*L.* sect. *Uvidi*) is also relatively low. In the temperate the regions well-represented section *Glutinosi* is up to now not known in northern Thailand.

Taking into account the current exploration rate of the area, we expect more species to be found. Whether the described diversity here is representative for a larger area (Thailand, South-East Asia) is hard to conclude. A superficial comparison with Southern China (comparable climate and vegetation) revealed almost no species in common (Wang, pers. comm.), which suggests that the northern Thailand *Lactarius* flora is unique, but which can partly also be explained by incomplete knowledge of the diversity.

A new macromorphological character in Lactarius

Although the general look of the *Piperites* representatives in northern Thailand is very similar to the temperate species and generally the species are easily recognized in the field as belonging to this subgenus, there is one striking new macromorphological character: the zonation of the pileus context. It seems that the zonation of the pileipellis, which is often observed in *Lactarius* and especially in *L.* subgenus *Piperites*, continues inside the context. This is often very obvious and it covers the entire diameter of the pileus. The character was first observed in *Russula zonaria* (*R.* subsect. *Ochricomptae*), described from Doi Suthep-Pui, Thailand (Buyck and Desjardin, 2003) where it occurs in soil under *Dipterocarpus* in primary montane forest. The zonation of the pileus context occurs in five of the here mentioned taxa. This character has also been observed in *L.* aff. *subzonarius* (Huyen T. Le *et al.*, unpubl. res.), a Thai species belonging to *L.* subgenus *Russularia*. Attention should be paid to this feature in *Lactarius* from other areas.

Infrasubgeneric classification

Based on morphology, the described species belong to sections *Deliciosi*, *Uvidi*, *Piperites*, *Zonarii* and *Colorati*. For the moment the molecular phylogeny does not confirm this division of subgenus *Piperites* into sections

(see also Eberhardt, 2000). Only the species belonging to *L.* sect. *Deliciosi* form a well-supported clade based on LSU, ITS and *gpd* sequences (Nuytinck, 2005). The ML tree in Fig. 13 shows that the sections *Zonarii* and *Piperites* are polyphyletic. Besides that, the ITS analyses here once more draw attention to the problematic delimitation of the subgenera *Piperites* and *Russularia*. The ML tree in Fig. 13 shows *L.* sect. *Uvidi* as a monophyletic group within *L.* subgenus *Piperites*, but the NJ and MP analyses show a different picture (trees not shown). In the NJ tree, *L. formosus*, *L. sp. 2* and *L. speciosus* are basal to both *L.* subgenus *Piperites* and *Russularia*, while *L. uvidus* and *L. repraesentaneus* belong to *L.* subgenus *Piperites*, but they don't cluster together. The MP 50% majority rule consensus tree of 1453 shortest trees shows *L. formosus*, *L. sp.2*, *L. speciosus*, *L. repraesentaneus* and *L. uvidus* as a paraphyletic group at the base of *L.* subgenus *Piperites*. Interestingly, *L. purpureus*, a species with all characteristics of *L.* sect. *Colorati*, is embedded in subgenus *Piperites*, which supports the abandonment of *L.* subgenus *Colorati*. It is clear that the sampling in this phylogenetic study is too limited to conclude on the monophyly of *L.* subgenus *Piperites* and *Russularia* and the sections within. Also, ITS sequences alone are not sufficient to answer these questions.

For species delimitation the ITS region is very well-suited in this subgenus (Eberhardt, 2000; Nuytinck, 2005). When trying different analysis methods (NJ, MP, ML) the position of the subgroups (sections, subsections) in the trees is very variable but terminal species clades are stable. Although there sometimes is a strong morphological resemblance of the Thai species to the European or American species, there is no conspecificity.

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