
Descriptions and taxonomy of the Asian representatives of *Lactarius* sect. *Deliciosi*

Jorinde Nuytinck¹, Xiang-Hua Wang² and Annemieke Verbeken^{1*}

¹Ghent University, Department of Biology, Research Group Mycology, K.L. Ledeganckstraat 35, 9000 Gent, Belgium

²Kunming Institute of Botany, Chinese Academy of Sciences, Kunming 650204, P.R. China

Nuytinck, J., Wang, X.H. and Verbeken, A. (2006). Descriptions and taxonomy of the Asian representatives of *Lactarius* sect. *Deliciosi*. *Fungal Diversity* 22: 171-203.

Nine Asian species belonging to *Lactarius* sect. *Deliciosi* are described and illustrated in detail in this paper. Representatives of all of these species were included in a molecular phylogenetic study focusing on the worldwide phylogeny of this section based on ITS and partial glyceraldehyde-3-phosphate dehydrogenase gene sequences. The detailed results of this analysis will be published elsewhere but we concluded that all Asian species, except for *L. thakalorum*, form well separated and well supported branches. *Lactarius thakalorum* is possibly conspecific with the European *L. sanguifluus*, but more research is needed here. *Lactarius deliciosus* seems to be one of the rare species in this section that occurs in both Asia and Europe. *Lactarius horakii* is described as a new species. Two other new species were discovered but insufficiently detailed macroscopical notes prevent us from describing them as new species yet. Several unidentified and poorly known taxa are briefly discussed.

Key words: *Dapetes*, *Lactarius deliciosus*, *Lactarius horakii*, microscopy, morphology

Introduction

In Asia, the knowledge of the genus *Lactarius* Pers. is poor and fragmentary. Several publications focused on *Lactarius* species associated with mainly *Fagales* (*Castanopsis*, *Lithocarpus*, *Nothofagus*) from the tropical, mostly montane rainforests of South-East Asia (Verbeken and Horak, 1999, 2000; Verbeken *et al.*, 2002). In Japan, the study of *Lactarius* is relatively well advanced. Sixty species are recorded for this country, most of which receive European or North American names. A general, critical overview of the reported species and the proportion of endemic species does not yet exist for the Asian continent. One of the major problems to be overcome is the lack of modern and illustrated descriptions and revisions from this continent (Verbeken, 2001).

*Corresponding author: A. Verbeken; e-mail: Mieke.Verbeken@UGent.be

Thirteen names have so far been published from Asia in *Lactarius* sect. *Deliciosi* (Fr.: Fr.) Redeuilh, Verbeken & Walley (syn. sect. *Dapetes* (Fr. ex J. Kickx f.) Burl.): seven species, three varieties, one form and two invalid names. We recognize five of those seven species here; we add *L. deliciosus* (L.: Fr.) Gray to the list and give descriptions of three new species. This brings the total number of species to nine. Only one of the three new species is effectively published as detailed macroscopical descriptions lack for the other two species. More taxa undoubtedly will be discovered, as more fieldwork will be done in this underexplored area. Several unidentified collections and insufficiently known taxa are listed at the end of this paper. Furthermore, the species concept we (provisionally) apply here is wider than our species concept in a well-studied region as Europe. This is for example reflected in the large genetical and morphological variability we observed in *L. hatsudake* Tanaka (this study and Nuytinck *et al.*, in prep.).

All nine Asian species described here were included in a molecular phylogenetic analysis of this section on a worldwide scale, based on ITS and partial glyceraldehyde-3-phosphate dehydrogenase gene sequences (Nuytinck *et al.*, pers. observ.). Although this analysis indicates a possible conspecificity of *L. thakalorum* Bills & Cotter with *L. sanguifluus* (Paulet) Fr., *L. thakalorum* is provisionally maintained as a separate species here. In the discussion under *L. thakalorum* we give an overview of the morphological differences with *L. sanguifluus*. More evidence, in the form of more, well-documented collections, is needed to come to a confident conclusion on the eventual conspecificity. The description of *L. deliciosus* that we provide here is entirely based on specimens collected in China (Guizhou, Yunnan and Sichuan). A description based on European collections can be found in Nuytinck and Verbeken (2005). These descriptions were kept separately in order to maintain information on the regional differences in the morphology of this species.

Materials and methods

This study is based on herbarium material obtained from BPI, H, HKAS, RMS, TMI and ZT or deposited in GENT. Macroscopical characters are based on observations on fresh collections or are compiled from literature and field notes attached to herbarium collections. Colour codes are according to Kernerup and Wanscher (1962). Microscopic measurements and drawings were made under oil immersion at 1000× with a Zeiss Axioscop 2 microscope and drawing tube. All observations and measurements [except for the spores] were made in Congo red in L4 (7.2 g KOH, 160 mL glycerine, 840 mL dH₂O, 7.6 g NaCl and 5 mL Invadin (Ciba-Geigi), Clémenton, 1972]. Where

necessary a short pre-treatment in 10% KOH was used to rehydrate the tissue. Basidia lengths exclude sterigmata lengths. We use the term cheiloleptocystidia for the thin-walled, mostly clavate to irregularly shaped cystidia, without specific content and with a rounded apex on the lamella edge. Observations and measurements of basidiospores were made in Melzer's reagent. Spores were measured in side view, excluding ornamentation and 20 spores were measured for every collection mentioned under the examined collections section. Measurements are given as (MIN) $[Ava-2 \times SDa] - Ava - Avb - [Avb+2 \times SDb]$ (MAX) in which Ava = lowest mean value for the measured collections, Avb = greatest mean value and SDa/b = standard deviation of the lowest and greatest mean value respectively. MIN is the lowest value measured, MAX the highest value; MIN and MAX are only given when they exceed $[Ava-2 \times SDa]$ or $[Avb+2 \times SDb]$ respectively. Q stands for 'quotient length/width' and is given as MINQ – $Qa - Qb$ – MAXQ in which Qa and Qb stand for the lowest and the highest mean quotient of the measured specimens respectively. MINQ/MAXQ stands for the minimum/maximum value over the quotients of all available measured spores. For species that were microscopically described using only one specimen, the measurements are given as (MIN) $[Av-2 \times SD] - Av - [Av+2 \times SD]$ (MAX) in which Av is the mean value of the 20 spores measured from that collection and as MINQ – Q – MAXQ in which Q stands for the mean quotient of the measured spores.

Scanning electron photographs were taken with a JEOL JSM-5600 LV microscope. Small pieces of lamellae were taken from dried specimens and soaked overnight in strongly diluted ammonia. The material was then treated with 70% ethanol (2×15 min.) and dimethoxymethane (2×30 min.), before being submitted to the process of critical point drying. This was done with a BAL-TEC CDP 030 dryer. The samples were then coated with gold in a JEOL JFC-1200 Fine Coater for 60 sec. at 8 Pa and 30 mA, until a 15 nm thick layer covered the spores.

Results

Lactarius akahatsu Tanaka, Bot. Mag. (Tokyo) 4: 394 (1890) (Figs. 1, 2)

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* Kobayashi (1939)

Type: not selected, described from Japan.

Introduction: We did not observe fresh *L. akahatsu* collections from Japan and thus had to adapt the macroscopical description from the original

description and other literature data (Tanaka, 1890; Hongo, 1977). Microscopical features were observed on herbarium material from Japan (one collection only). Obviously, more collections from other localities are needed to arrive at a reliable and detailed description of *L. akahatsu*.

Description: Macroscopical description compiled from Tanaka (1890) & Hongo (1977): *Pileus* 2-10 cm diam., at first convex with an incurved margin, then flattened to depressed; margin smooth, becoming slightly undulated, rather thin and acute; surface smooth, glabrous, viscid when moist, zoned; colour orange to brownish-orange (6A/B6), then pale, margin pale orange, staining green with age. *Lamellae* decurrent, rather thin, crowded; colour orange (5A6-6A6), staining green where bruised. *Stipe* 3-6 × 1.2-2 cm, subequal, sometimes curved, more or less rugulose, becoming hollow, concolorous with the pileus to pruinose. *Latex* scarce, orange, slowly becoming vinaceous red on the context; taste mild or slightly acid.

Microscopical observations on *L. akahatsu* TMI 22601 (TMI), collected in Japan: *Spores* 8-8.5-9.1 (9.3) × 5.9-6.4-7 μm, broadly ellipsoid to ellipsoid (Q = 1.22-1.33-1.44); ornamentation up to 0.7 μm high, of rather broad ridges and some isolated warts and short ridges, forming an almost complete reticulum; plage distally slightly amyloid, often with scattered, light amyloid spots. *Basidia* 45-55 × 9-11 μm, subclavate to almost cylindrical, 4-spored, content sometimes slightly granular or with oil-droplets; sterigmata 4.5-6.5 μm long. *Pleuromacrocystidia* rather abundant but hardly visible, 30-50 × 6-8.5 μm, not to slightly emergent, fusiform with an obtuse to (more rarely) capitate apex, with a needle-shaped content, thin-walled. *Pseudocystidia* rather abundant, (2) 3-5 μm broad, not to slightly emergent, cylindrical but tortuous near the base, content oleiferic. *Lamella edge* sterile with quite abundant cheilomacrocystidia; cheiloleptocystidia 11-25 × 3-5 μm, subclavate to irregular, hyaline or with a pale brownish to ochre, granular content (observation in 10% KOH); cheilomacrocystidia 19-25 × 4-6 μm, subfusiform but often irregular, with a moniliform apex, hyaline or with a granular content, thin-walled. *Pileipellis* an ixocutis, 90-120 μm thick, with only very few shrivelled hyphae.

Habitat: On the ground in lowland *Pinus* forests, widely distributed along with *Pinus* spp., such as *P. densiflora*, *P. thunbergii*, *P. liuchuensis* etc., found in the autumn (to the winter on the Bonin Islands) (Nagasawa, 1998).

Distribution: Reported from Japan and introduced on the Bonin Islands (Hongo, 1960, 1977).

Collections examined: JAPAN, Tottori, Tottori-shi, Uemachi (Bairian), under planted *Pinus thunbergii* in garden, 27.09.1997, leg. E. Nagasawa, TMI 22601 (TMI).

Discussion: *Lactarius akahatsu* seems to be a common species in Japan, characterised by its generally orange appearance and orange latex that slowly

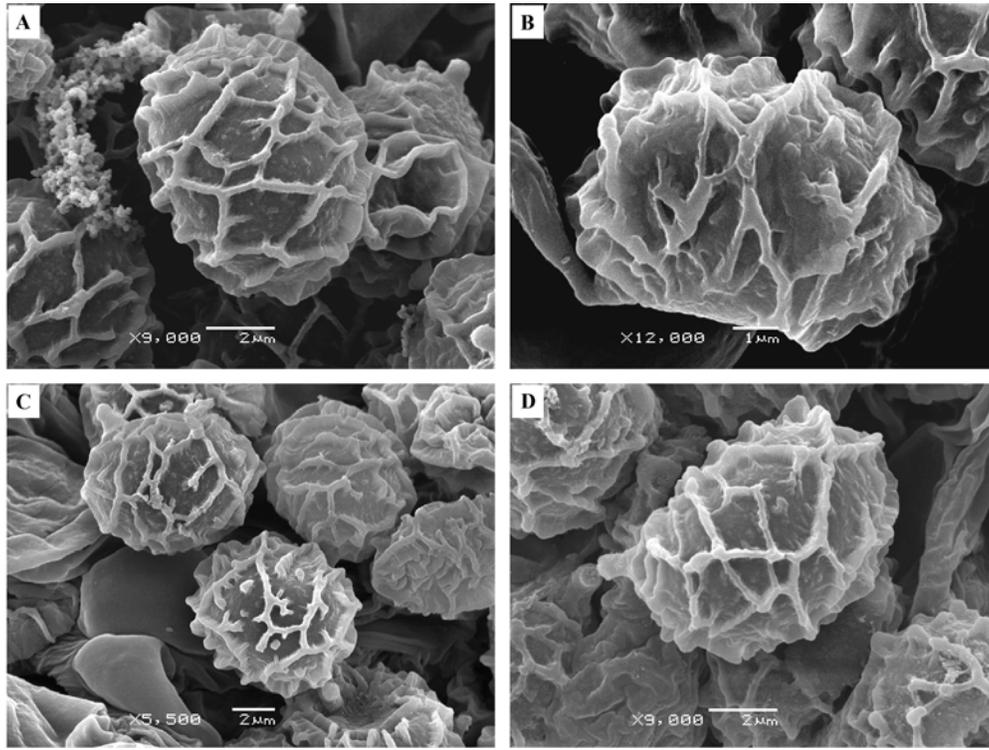


Fig. 1. SEM images of the spores of **A.** *L. akahatsu* A. Verbeken 2004-141; **B.** *L. hatsudake* TMI24414; **C.** *L. laeticolor* TMI23149; **D.** *L. sp. 2* M. Härkönen KIINA 35.

becomes red on the context. It is unmistakably different from *L. hatsudake*, a species with red latex from the beginning. Tanaka (1890) moreover, remarks that the lamellae in *L. akahatsu* are narrower than those of *L. hatsudake*.

The descriptions by Tanaka (1890) and Hongo (1977) include short notes on the microscopy. Tanaka (1890) reports much larger spores ($9-11 \times 6-8 \mu\text{m}$). The microscopical description by Hongo (1977), that mentions abundant cheilomacrocystidia but pleuromacrocystidia difficult to demonstrate, corresponds best with our observations on collection 22601 (TMI). The pleuromacrocystidia we observed on collection TMI 22601 are remarkable in that their shape is slightly different from the pleuromacrocystidia in most other members of *Lactarius* sect. *Deliciosi*. The apex is obtuse to (more rarely) capitate here, while a moniliform apex is observed in most species. Certainly, more observations on more collections are needed to confirm these findings.

Hongo (1977) thinks *L. akahatsu* is very closely related to or even conspecific with *L. semisanguifluus*. He concludes this mainly because of the colour change of the latex. Singer (1986) suggests the same. Imai (1935)

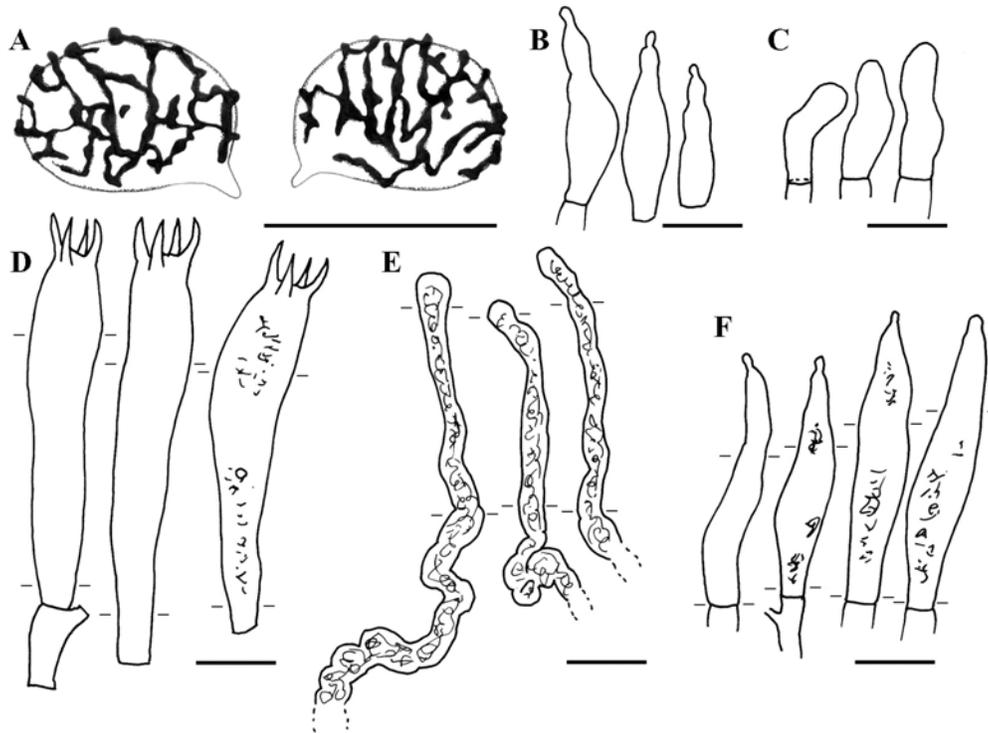


Fig. 2. *Lactarius akahatsu*: **A.** spores; **B.** cheilomacrocystidia; **C.** cheiloleptocystidia; **D.** basidia; **E.** pseudocystidia; **F.** pleuromacrocystidia. From TMI 22601. Bars = 10 μ m, small bars indicate the height of the hymenium.

suggests *L. akahatsu* and *L. deliciosus* are conspecific. He distinguishes a form growing in *Pinus* and *Picea* woods (*L. deliciosus* f. *virescens*), and a form from *Abies* woods that does not discolour greenish (*L. deliciosus* f. *laeticolorus*). Our molecular approach reveals that *L. akahatsu* is a species well separated from all other species in *Lactarius* sect. *Deliciosi*. The exact position in the section remains unclear.

Molecular analysis also indicates a very close relationship between this Japanese collection and several Thai collections made by Verbeken, in collaboration with Huyen Thanh Le and Dennis Desjardin (Le *et al.*, pers. observ.). The Japanese specimens differ from the ones collected in Thailand by the behaviour of the latex, which slowly becomes vinaceous red in Japanese specimens, but remains orange in Thai specimens. Microscopically, pleuro- and cheilomacrocystidia are more abundant in the Japanese collection.

Lactarius deliciosus (L.: Fr.) Gray, Nat. Arr. Br. Pl. 1: 624 (1821) (Fig. 3)*Basionym:*= *Agaricus deliciosus* L., Species Pl.: 1172 (1753)*Synonyms:*= *Lactaria lateritia* Pers., Tent. Disp. Meth. Fung.: 64 (1797)= *L. deliciosus* var. *lamelliporus* (Barla) Sacc., Sylloge Fungorum 5: 438 (1887)= *Agaricus deliciosus* var. *lamelliporus* Barla, Champ. Prov. Nice: 35 (1859)= *L. deliciosus* var. *pini* Vassilkov, [Edible and poisonous fungi of central parts Europ. distr. U.S.S.R.]: 60 (1948), nom. inval., nom. nud.= *L. pinicola* Smotl. ex Z. Schaef., Schweiz. Z. Pilzk. 48: 141 (1970)= *L. deliciosus* var. *pinicola* Smotl., Atlas hub jedlých a nejedlých [Atlas of edible and inedible fungi]: 219 (1947), nom. inval., nom. nud.= *L. deliciosus* f. *rubescens* J.A. Schmitt, Z. Pilzk. 39: 238 (1974)= *L. deliciosus* var. *lateritius* J. Blum ex J. Blum, Lactaires: 216 (1976)*Type:* not selected, described from southern Sweden.

Description: *Pileus* 3-9 cm diam., sometimes larger, convex with an inrolled margin and a slightly depressed centre when young, becoming infundibuliform; surface smooth, viscid; colour pale orange, yellowish to greyish-orange, often with darker spots or concentric zones, especially when young, becoming bluish-green when bruised. *Lamellae* (slightly) decurrent, rather crowded, often forked near the stipe; colour pale orange to yellowish but often more intense than the pileus colour, when bruised discolouring greenish to bluish. *Stipe* 2-4 × 0.6-2 cm, cylindrical or tapering near the base; surface smooth, scrobicules present in most basidiocarps; colour pale orange to yellowish, whitish near the lamellae, discolouring greenish when bruised. *Context* hollow in the stipe, white in the central parts, very pale orange near the pilei- and stipitipellis, orange above the lamellae, unchanging to rarely slowly becoming red (uncertain observation), discolouring bluish-green. *Latex* scarce, orange to reddish; taste sometimes slightly acrid.

Spores 7.2-8.8-8.8-9.3 × 5.7-6.4-6.6-7.3 μm, subglobose to ellipsoid, mainly broadly ellipsoid (Q = 1.13-1.24-1.33-1.43); ornamentation up to 0.7 μm high, of rather thick ridges and quite some isolated warts and short ridges, forming an incomplete or seldom almost complete reticulum; plage inconspicuous and with scattered amyloid spots to slightly amyloid distally. *Basidia* 40-60 × 8-11 μm, subclavate, 4-spored, often containing oil-droplets or with a granular content. *Pleuromacrocystidia* rather abundant, 40-62 × 5.5-10.5 μm, emergent, subfusiform, with a moniliform or capitate apex, with a granular to needle-shaped content, thin-walled. *Pseudocystidia* not very abundant, 2-4 μm broad, rarely emergent, rather slender, tortuous in the lower part, content oleiferic and ochre-brown coloured. *Lamella edge* sterile with abundant cheilomacrocystidia; cheiloleptocystidia 6-20 × 2.5-6 μm, subclavate to almost cylindrical but often bent or irregular, hyaline, thin-walled; cheilomacrocystidia 24-35 × 4-6 μm, subfusiform, with a moniliform

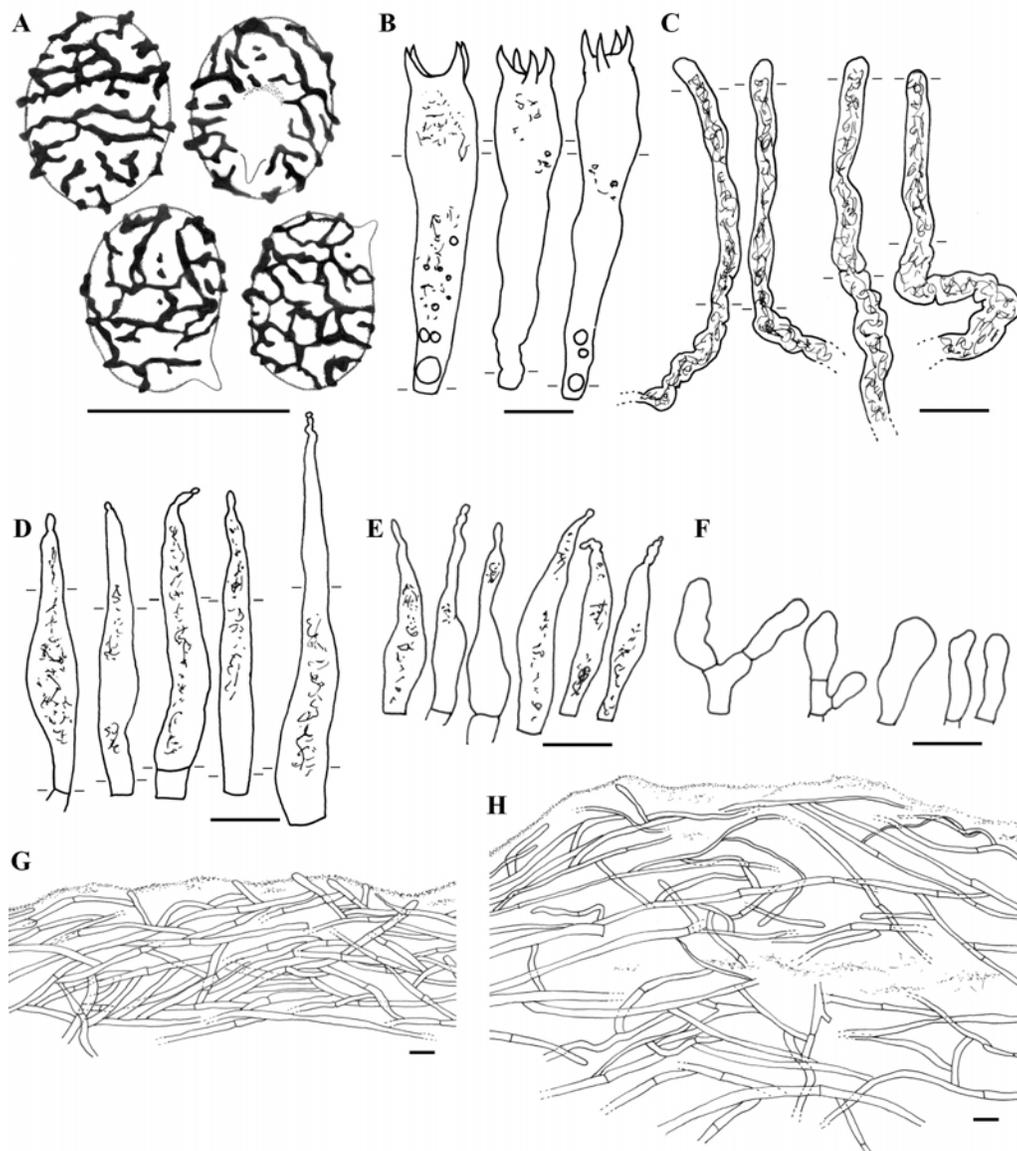


Fig. 3. *Lactarius deliciosus*: **A.** spores; **B.** basidia; **C.** pseudocystidia; **D.** pleuromacrocytidia; **E.** cheilomacrocytidia; **F.** cheileptocystidia; **G.** section through the stiptipellis; **H.** section through the pileipellis. From HKAS 29133, HKAS 31054, HKAS 31722, HKAS 32125, HKAS 33954, HKAS 38286 and HKAS 39045. Bars = 10 μ m, small bars indicate the height of the hymenium.

apex, often with a granular content, thin-walled. *Subhymenium* composed of globose to more irregularly-shaped, small cells. *Hymenophoral trama* irregularly filamentous; with remarkably abundant and broad lactifers. *Pileipellis* an ixocutis, 100-350 μm thick, of strongly interwoven hyphae, 1-6 μm diam., shrivelled and gelatinised hyphae abundant near the surface. *Stipitipellis* an ixocutis, up to 100 μm thick, of regularly shaped and strongly interwoven hyphae, 2-4 μm diam., only very few shrivelled hyphae.

Habitat: Growing under *Pinus yunnanensis* and other *Pinus* species.

Distribution: The examined material was collected in three Chinese provinces: Guizhou, Yunnan and Sichuan.

Collections examined: CHINA, Guizhou Prov.: Weining county, Heishitou, 15.09.1993, M. Zang 3610, HKAS 29133 (HKAS) – Yunnan Prov.: Lijiang county, Yunshanping, 3400 m a.s.l., *Picea* and *Pinus densata*, 08.10.1994, Tanaka & P.G. Liu 94-37, HKAS 28382 (HKAS) – Yunnan Prov.: Lijiang county, Yulong Mountain, under *Pinus densata*, 29.07.1995, M. Zang 12, HKAS 30003 (HKAS) – Yunnan Prov.: Lijiang county, Yulong Mountain, Ganhaizi, 04.08.1995, M. Zang 12555, HKAS 30127 (HKAS) – Sichuan Prov.: Xiaojin county, Rilong, Shuangqiaogou, 3400 m a.s.l., 23.08.1996, M.S. Yuan 2503, HKAS 30958 (HKAS) – Sichuan Prov.: Luding county, Hailuogou, 2600 m a.s.l., 28.08.1996, M.S. Yuan 2513, HKAS 30970 (HKAS) – Sichuan Prov.: Luding county, Hailuogou, 3000 m a.s.l., 02.09.1996, M. Zang 2584, HKAS 31054 (HKAS) – Yunnan Prov.: Qujing City, 04.10.1997, X.H. Wang 171, HKAS 31722 (HKAS) – Sichuan Prov.: Xiaojin county, Rilong, 3200 m a.s.l., *Picea*, *Betula*, *Populus*, 19.07.1998, M.S. Yuan 3020, HKAS 33954 (HKAS) – Yunnan Prov.: near the city of Baoshan, 1800 m a.s.l., *Pinus yunnanensis*, 30.09.1998, Z.L. Yang 2574, HKAS 32125 (HKAS) – Sichuan Prov.: Hongyuan county, Shuajingsi, 3500 m a.s.l., *Picea*, *Betula*, 22.08.1998, M.S. Yuan 3471, HKAS 33824 (HKAS) – Yunnan Prov.: Lijiang county town, 2000 m a.s.l., 11.09.1999, P.Q. Sun 4537, HKAS 34741 (HKAS) – Yunnan Prov.: Chuxiong, Zixishan, *Pinus yunnanensis*, 11.07.2001, F.Q. Yu 437, HKAS 39044 (HKAS) – Yunnan Prov.: Lijiang county, Laojunshan, 2800 m a.s.l., *Pinus yunnanensis*, 29.07.2001, Z.L. Yang 3109, HKAS 38286 (HKAS) – Yunnan Prov.: Kunming, Heilongtan Park, 1890 m a.s.l., *Pinus yunnanensis*, 11.10.2001, F.Q. Yu 769, HKAS 39045 (HKAS).

Discussion: Molecular evidence shows that the included Asian collection of *L. deliciosus* is conspecific with the European ones (Nuytinck *et al.*, pers. observ.). Small microscopical differences we observed are the slightly smaller spores, the more abundant pleuromacrocytidia and the ixocutis of the stipe in the Asian specimens. The abundance of pleuromacrocytidia is however a variable feature within many species in *Lactarius* sect. *Deliciosi*. Hesler and Smith (1979) mention that the occurrence of a cutis or ixocutis as stipe cuticle can also be variable within a species.

Quite some variability is observed in the macromorphology of *L. deliciosus* in Asia. Some collections consist of smaller basidiocarps with dirty, ochraceous to pale orange colours, often with green hues; they are rather slender and never have very incurved margins; they grow with *Pinus*. Other collections are more robust and have brighter orange tinges, especially in the lamellae; the margins are often inrolled; they also grow under *Pinus*. Both

types are very commonly sold on the markets in Yunnan, often mixed. A third, less common type from higher elevations has pure but rather pale orange colours and grows in *Abies-Picea* forests; the former two forms are clearly duller in colour. All these collections do not differ microscopically; they were not yet included in any molecular analysis.

Concerning the variability of the microscopical characters, collection HKAS 28382 is the only one that shows significantly larger spores (8.7-9.5-10.3 (10.5) × (6.6) 6.7-7.3-8 μm, Q = 1.21-1.29-1.43). Macroscopically this collection fits into the range of *L. deliciosus*.

Lactarius hatsudake Tanaka, Bot. Mag. (Tokyo) 4: 393 (1890) (Figs. 1, 4, 5)

Synonyms:

?= *L. lividatus* Berk. & M.A. Curtis, Proc. Amer. Acad. Arts & Sciences 4: 119 (1860)

?= *L. sanguifluus* var. *asiaticus* Dörfelt, Kiet & A. Berg, Feddes Repert. 115: 169 (2004)

Type: not selected, described from Japan.

Description: *Pileus* 3-10 cm diam., at first convex with an incurved margin, then expanded and margin bent downwards to slightly incurved, finally widely infundibuliform; surface smooth, greasy to slightly viscid when wet, zoned, 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). *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* 1.5-4 × 0.6-2 cm, short, tapering downwards, becoming hollow; surface glabrous; colour dull reddish (9C/D5), often covered with a white layer, scrobicules absent, 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 in 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 (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. *Pleuromacro*

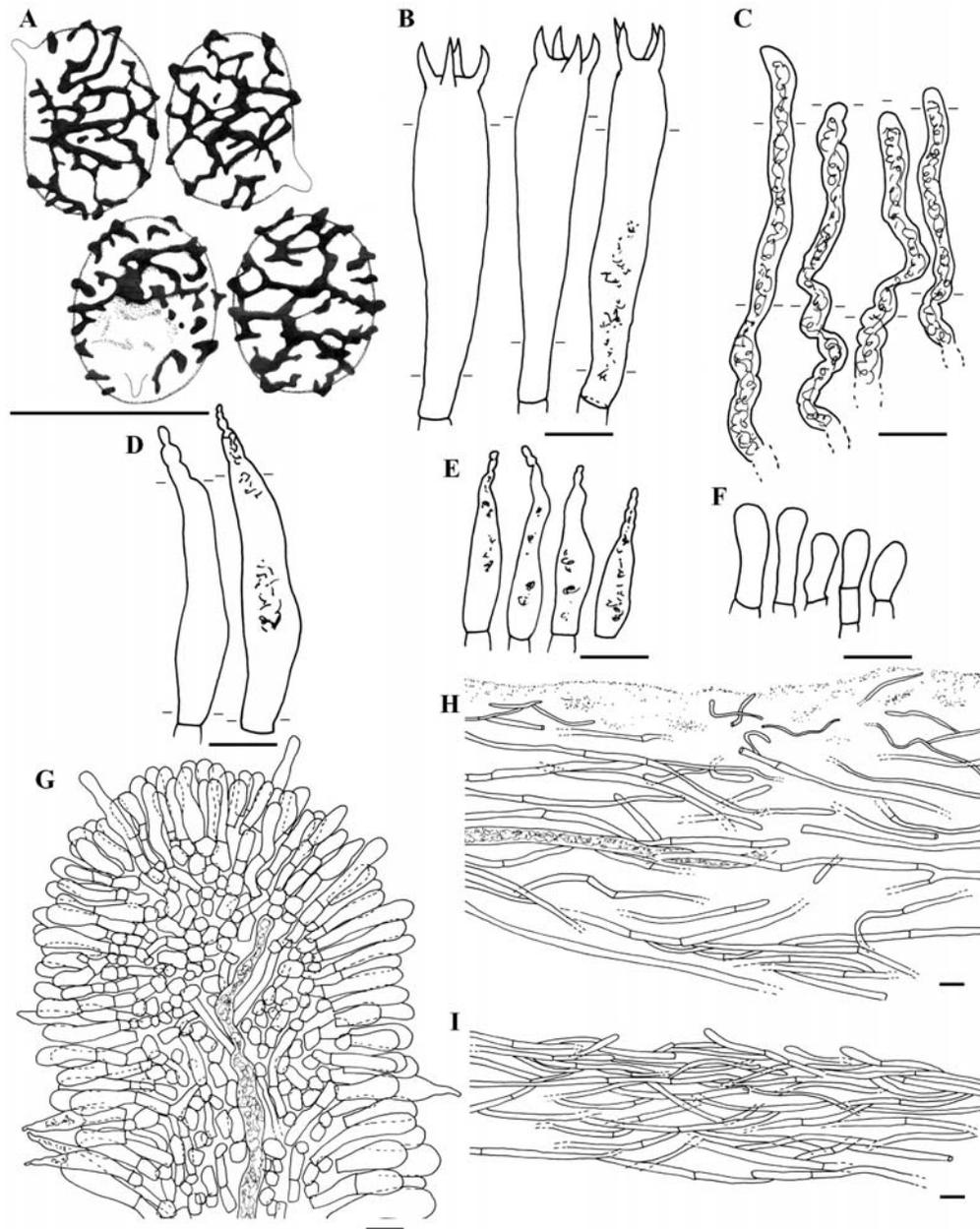


Fig. 4. *Lactarius hatsudake*: **A.** spores; **B.** basidia; **C.** pseudocystidia; **D.** pleuromacrocystidia; **E.** cheilomacrocystidia; **F.** cheileptocystidia; **G.** lamella edge; **H.** section through the pileipellis; **I.** section through the stipitipellis. From HKAS 31714, HKAS 38746, HKAS 39032, HKAS 39047, HKAS 39354, TMI 22646 and TMI 24414. Bars = 10 μ m, small bars indicate the height of the hymenium.

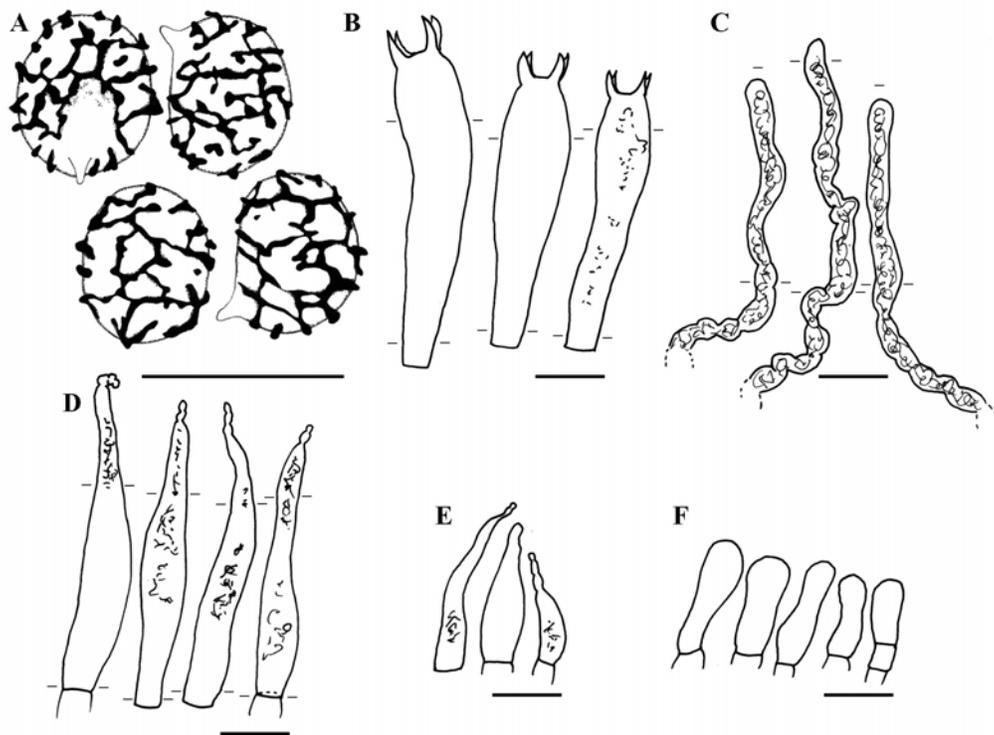


Fig. 5. *Lactarius hatsudake*: **A.** spores; **B.** basidia; **C.** pseudocystidia; **D.** pleuromacrocystidia; **E.** cheilomacrocystidia; **F.** cheileptocystidia. From M. Härkönen KIINA 62 and HKAS 39378. Bars = 10 μ m, small bars indicate the height of the hymenium.

cystidia very scarce but more abundant close to the lamella edge, 42-48 \times 7-9 μ m, emergent, subfusiform, with a moniliform or acute apex, thin-walled. *Pseudocystidia* abundant, 2.5-5 μ m diam., not to slightly emergent, cylindrical to tortuous, with an ochre-yellow content. *Lamella edge* sterile with scarce cheilomacrocystidia but macrocystidia mostly abundant close to the edge; cheileptocystidia mostly 8-16 \times 3.5-6 μ m but rarely very conspicuous and emergent, up to 35-40 μ m long, subclavate to cylindrical or more irregular, hyaline, thin-walled; cheilomacrocystidia 24-35 \times 4.5-6 μ m, subfusiform with a moniliform apex, content needle-shaped or granular, thin-walled. *Subhymenium* composed of mainly small, \pm isodiametric, irregularly arranged cells. *Hymenophoral trama* irregularly filamentous, with abundant lactifers. *Pileipellis* an ixocutis, 50-300 μ m thick, of mainly shrivelled and gelatinised hyphae in the top layer, deformed and swollen hyphae also present; hyphae thin-walled and 1-6 μ m broad. *Stipitipellis* a cutis, 30-70 μ m thick, of thin-

walled, strongly interwoven hyphae, 2-6 μm broad; no shrivelled or gelatinised hyphae.

Habitat: 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 (southwestern China) throughout the mushroom season (May to October) (Tanaka, 1890; Nagasawa, 1998; own observations).

Distribution: Recorded from China, Japan, the Bonin Islands, eastern Russia and Korea.

Collections examined: CHINA, Yunnan Prov.: Lunan county, Stone Forest, 11.10.1995, P.G. Liu & Y. Doi, HKAS 29734 (HKAS) – Yunnan Prov.: Kunming, Ciba, 1900 m a.s.l., 30.08.1997, X.H. Wang 50, HKAS 31714 (HKAS) – Yunnan Prov.: Kunming, Longtougjie, 1900 m a.s.l., 03.09.1997, X.H. Wang 60, HKAS 31715 (HKAS) – Yunnan Prov.: Songming county, Baiyi, 2000 m a.s.l., *Pinus yunnanensis*, 22.07.1998, X.H. Wang 407, HKAS 32067 (HKAS) – Yunnan Prov.: near the city of Baoshan, 1800 m a.s.l., under *Pinus yunnanensis*, 30.09.1998, Z.L. Yang 2577, HKAS 32124 (HKAS) – Yunnan Prov.: Songming county town, 28.08.1999, X.H. Wang 911, HKAS 39349 (HKAS) – Yunnan Prov.: Wuding county, Shizishan, *Pinus yunnanensis*, 05.07.2000, X.H. Wang 992, HKAS 39354 (HKAS) – Yunnan Prov.: Kunming Botanical Garden, 1900 m a.s.l., under *Pinus yunnanensis* & *Quercus*, 17.07.2000, X.H. Wang 1014, HKAS 39355 (HKAS) – Yunnan Prov.: Kunming, Laobailong, 2000 m a.s.l., *Pinus yunnanensis*, 24.07.2000, F.Q. Yu 12, HKAS 39034 (HKAS) – Yunnan Prov.: Kunming, Heilongtan Park, 1890 m a.s.l., *Pinus yunnanensis*, 06.09.2000, F.Q. Yu 395, HKAS 39031 (HKAS) – Yunnan Prov.: Kunming, Qiongzhusi, 2000 m a.s.l., *Pinus yunnanensis*, 14.09.2000, F.Q. Yu 413, HKAS 38689 (HKAS) – Yunnan Prov.: Nanjian county, Zhonghuashan, 1940 m a.s.l., *Pinus yunnanensis*, 13.08.2001, M. Zang 13859, HKAS 38541 (HKAS) – Yunnan Prov.: Kunming, Laobailong, 2000 m a.s.l., under *Pinus yunnanensis*, 14.08.2001, F.Q. Yu 512, HKAS 39047 (HKAS) – Yunnan Prov.: Chuxiong, Zixishan, 2200 m a.s.l., *Pinus yunnanensis*, 23.08.2001, F.Q. Yu 541, HKAS 39032 (HKAS) – Yunnan Prov.: near Gongshan county town, 2000 m a.s.l., *Pinus yunnanensis*, 06.09.2001, F.Q. Yu 703, HKAS 39035 (HKAS) – Yunnan Prov.: Kunming Botanical Garden, 1900 m a.s.l., 06.09.2001, L.F. Zhang 88, HKAS 38454 (HKAS) – Yunnan Prov.: Gongshan county town, 07.09.2001, X.H. Wang 1391, HKAS 38746 (HKAS) – JAPAN, Tottori, Tottori-shi, Iwakura (Exp. For.), under *Pinus densiflora*, 17.10.1997, leg. E. Nagasawa, TMI 22646 (TMI) – Kagoshima, Aira-gun, Makizono-cho, Oonami-yama, 1060-1300 m a.s.l., under *Pinus densifolia*, in mixed coniferous and hardwood forest, 27.10.2000, leg. E. Nagasawa & T. Fujita, TMI 24414 (TMI) – Tottori, Tottori-shi, Hamasaka, Tottori Sand Dune, in *Pinus thunbergii* woods, 07.11.2000, leg. T. Hongo & E. Nagasawa, TMI 24398 (TMI).

Discussion: The macro-description given here is compiled from the original description (Tanaka, 1890) and from field notes attached to collections X.H. Wang 992 (HKAS 39354), X.H. Wang 1014 (HKAS 39355), L.F. Zhang 88 (HKAS 38454). *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).

Lactarius hatsudake is characterised by its wine red latex and its association with *Pinus* spp. The size of the basidiocarps seems very variable;

very small to rather large basidiocarps are often encountered together. Microscopically the heavy spore ornamentation with the large but faintly amyloid spots is typical and a reliable feature for identification.

Although Imai (1935, 1938, 1941) expected *L. hatsudake* to be conspecific to *L. sanguifluus*, both species do not seem to be very closely related. A difference with the indeed macroscopically rather similar *L. sanguifluus* is the absence of scrobicules on the stipe. A recently described variety of *L. sanguifluus* from Vietnam (*L. sanguifluus* var. *asiaticus* Dörfelt, Kiet & A. Berg; Dörfelt *et al.*, 2004) might be conspecific to *L. hatsudake* (see under insufficiently known and doubtful taxa).

Lactarius lividatus was originally described from the Amami-Oshima Islands, south of Japan. According to Neda (1992), who examined the type collection of *L. lividatus*, it is identical with *L. hatsudake*. Lalli and Pacioni (1992) also studied the type and conclude that the type specimen is in very poor condition and that there is not enough evidence to arrive at a precise identification. According to them, the spores and cystidia are of the same type as those of *L. hygrophoroides* Berk. & M.A. Curtis, which belongs to a completely different group.

Molecular evidence shows that the genetic variability in *L. hatsudake* is high, which might indicate that our species concept is relatively wide here. Moreover, this molecular variability is also confirmed by morphological diversity. Collections from Thailand e.g. showed a striking hygrophanous colour change of the cap that is not reported for the Chinese collections (Le *et al.*, pers. observ.). It is possible that at least several varieties can be distinguished within *L. hatsudake* but more observations on fresh material are needed.

Several Chinese collections differ from the other *L. hatsudake* specimens by the broadly ellipsoid spores that have a slightly thinner ornamentation, the very scarce to absent cheilomacrocystidia and the more abundant pleuromacrocystidia, also further away from the edge. One of these collections (M. Härkönen, KIINA 62) was included in our molecular analyses (as *L. hatsudake* China 3) and seemed to be conspecific with or very closely related to *L. hatsudake*. The following is a description of the hymenial characters (Fig. 5):

Spores 7.5-8.3-9 × (5.7) 5.8-6.5-7.2 μm, mostly broadly ellipsoid (Q = 1.21-1.27-1.33); ornamentation up to 0.5 μm high, of medium thick ridges and some scarce isolated warts, forming a rather complete reticulum; plage distally slightly amyloid. *Basidia* 32-46 × 9.5-11 μm, rather short and broad, subclavate, 4-spored; sterigmata 4.5-6 μm long. *Pleuromacrocystidia* abundant to very abundant, 40-50 × 4.5-7 μm broad, emergent, subfusiform with a moniliform to obtuse apex, content granular and refractive, thin-walled.

Pseudocystidia rather abundant, 2-4 μm broad, tortuous, with an ochre, refractive content. *Lamella edge* sterile with very scarce cheilomacrocystidia; cheiloleptocystidia 10-20 \times 4.5-9.5 μm , subclavate, irregularly-shaped to swollen, often with a granular content, thin-walled; cheilomacrocystidia 20-28 \times 4-7 μm , subfusiform with a narrowing to moniliform apex, thin-walled.

Collections examined: CHINA, Hunan Prov.: Wulingyuan World Heritage Area, Zhangjiajie, Matianya, 1000 m a.s.l., N29°19' E110°27', forest with planted *Cunninghamia lanceolata*, *Pinus massoniana* and *Cryptomeria fortunei*, under young, cultivated *Pinus massoniana*., 16.09.1999, M. Härkönen KIINA 62 (H, GENT) – Yunnan Prov.: Tengchong county, Jietou, Datang, under *Pinus yunnanensis*, 04.08.2000, X.H. Wang 1098, HKAS 39378 (HKAS) – Yunnan Prov.: Wuding county, Shizishan, 2300 m a.s.l., *Pinus yunnanensis*, 17.08.2000, F.Q. Yu 141, HKAS 39033 (HKAS).

***Lactarius horakii* Nuytinck & Verbeken, sp. nov.** (Fig. 6)

MycoBank number: MB500971.

Etymology: Named after the collector, Prof. Dr. E. Horak, for his important contribution to the study of a.o. *Lactarius* in the Southeast Asian region.

Latin description: Pileus 45-65 mm diam., primo planoconvexus margine incurvo, tum depressus ad infundibiliformis, interdum papillatus in centro; pileipellis laevis, viscida, ex purpureo rubrobrunnea, juventute pallide rosea ad griseorosea, cum zonis concentricis fuscis, aetate provecta pallidior, azonata, flavovirens. Lamellae breve decurrentes, confertae, saepe anastomosae, pallide roseae, virescentes. Stipes 40-45 mm longus, 9-10 mm crassus, cylindricus, siccus, purpureogriseus ad pallide roseus, virescens, tomento albo virescenti. Contextus albidus, virescens, gustu mitis ad amarum. Latex vinosus.

Sporae late ellipsoideae ad ellipsoideae, 7.2-7.7-8.2 \times (5.3) 5.4-5.8-6.2 μm , ornatae cristis usque ad 0.5 μm altis, dense subreticulatae, macula suprahilaris leviter distale amyloidea. Basidia 35-45 \times 7-9 μm , subclavata ad subcylindrata, tetraspora. Pleuromacrocystidia abundantia prope marginem lamellaris, 35-55 \times 6-8 μm , emergentia, fusiformia. Pseudocystidia abundantia. Cellulae marginales 7.5-15 \times 2.5-5 μm , subclavatae ad irregularis. Pileipellis ixocutis, 50-100 μm crassa. Ad terram in silva coniferarum (*Pinus merkusii*). Indonesia, Java, Bogor, Mt. Salak, Curug Nangka, 910 m, 02.01.2000, Horak 8336 (holotypus ZT, isotypus GENT).

***Holotype:* Horak 8336 (ZT!, isotype GENT!)** 02.01.2000, Indonesia, Java, Bogor, North slope of Mt. Salak, Curug Nangka, 910 m a.s.l., under *Pinus merkusii* (native to Sumatra), planted in secondary broad-leaf montane rainforest, on soil.

Description: Pileus up to 4.5-6.5 cm diam., plano-convex when young with an incurved margin, when expanding becoming depressed with straight margins to deeply infundibuliform, occasionally papillate in the centre; margin translucently-striate, entire to eroded; surface glabrous, sticky when moist, reddish-brown with a pale purplish tinge and with conspicuously darker ring-like zones when young, mature specimens light pink (6-8A2) to greyish-pink (8C4), aged specimens changing to dirty pale beige and losing zoned aspect, staining lemon-green (30A6/7) to lime-green (27/28B8). *Lamellae* shortly decurrent, crowded, often anastomosing at the base; colour pale pink (8/9A/B2), greening upon bruising; edge slightly paler. *Stipe* 4-4.5 \times 0.9-1 cm,

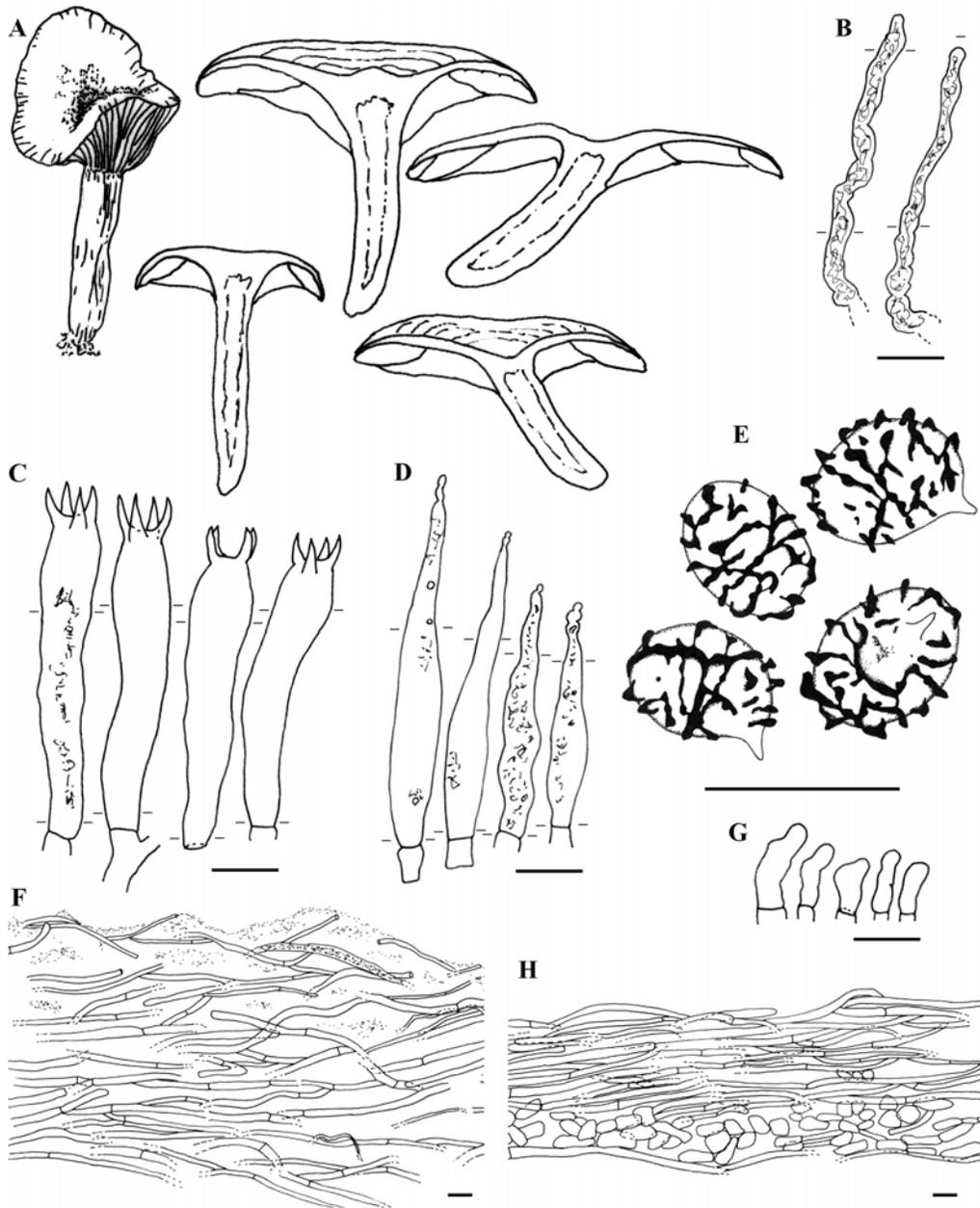


Fig. 6. *Lactarius horakii*: **A.** basidiocarps (life size); **B.** pseudocystidia; **C.** basidia; **D.** pleuromacrocystidia; **E.** spores; **F.** section through the pileipellis; **G.** cheiloleptocystidia; **H.** section through the stipitipellis. From E. Horak 8336 and E. Horak 9983. Bars = 10 μ m, small bars indicate the height of the hymenium.

cylindric, equal or slowly tapering towards the base, apex often costate otherwise smooth; surface dry, purple-grey (8C4) to pale pink (6-8A2), base and especially upon handling turning to pale or deep green; whitish mycelial tomentum or rhizomorphic strands present at base, this basal tomentum turning blue-green. *Context* hollow in the stipe; whitish to pale beige, lower half of the stipe blue-green, rind of stipe and above the lamellae blood red-brown, becoming pale to deep green after exposure; smell not distinctive to pleasant; taste mild to bitter. *Latex* vinaceous red (10/11D/E8).

Spores 6.8-7.3-7.7-8.2 × (5.1) 5.2-5.6-5.8-6.2 μm, mainly broadly ellipsoid to sometimes ellipsoid (Q = 1.25-1.32-1.34-1.43); ornamentation up to 0.5 μm high, composed of medium broad ridges and some isolated warts forming a rather dense, incomplete to almost complete reticulum; plage very slightly amyloid distally. *Basidia* 35-45 × 7-9 μm, subclavate to subcylindric, hyaline or with a needle-like content, 4-spored; sterigmata up to 5.2 μm high. *Pleuromacrocystidia* abundant near the lamella edge, scarce elsewhere, 35-55 × 6-8 μm, emergent, fusiform, with an acute to moniliform apex, with needle- to cube-shaped crystals, thin-walled. *Pseudocystidia* abundant, 3-4 μm broad, cylindrical to tortuous, not to slightly emergent, with a refringent content. *Lamella edge* sterile without cheilomacrocystidia; cheiloleptocystidia 7.5-15 × 2.5-5 μm, subclavate to irregularly shaped, hyaline, thin-walled. *Subhymenium* irregular, appearing like angular cells, more or less arranged in rows. *Hymenophoral trama* irregularly filamentous, with abundant, ochre coloured lactifers. *Pileipellis* an ixocutis, 50-100 μm thick, composed of thin-walled hyphae ± parallel to the surface; with abundant shrivelled and gelatinous hyphae in the surface layer, hyphae 1-4 μm diam. *Stipitipellis* a cutis, 30-50 μm thick, composed of hyaline hyphae with somewhat refractive walls, arranged parallel to the surface; no shrivelled or gelatinised hyphae.

Habitat and distribution: Only known from montane rainforest in Java, probably associated with *Pinus*.

Collections examined: INDONESIA, Java, Bogor, north slope of Mt. Salak, Curug Nangka, 910 m a.s.l., under *Pinus merkusii* (native to Sumatra), planted in secondary broad-leaf montane rainforest, on soil, 02.01.2000, E. Horak 8336 (ZT), holotype – Java, Bogor, north slope of Mt. Salak, Curug Nangka, 910 m a.s.l., under *Pinus merkusii* (native to Sumatra), planted in secondary broad-leaf montane rainforest, on soil, 01.11.2000, leg. A. Retnovati, AWW 30, E. Horak 9983 (ZT).

Discussion: *Lactarius horakii* is a small species with reddish-brown colours in the pileus, a purple-grey stipe and red latex. It was collected in montane rainforest under *Pinus merkusii*. It has rather densely ornamented, small spores (7.3-7.7 × 5.6-5.8 μm on average), which are mostly broadly ellipsoid.

Our molecular analyses reveal a close relationship to *L. hatsudake*. The most striking morphological differences with *L. hatsudake* are the general colour of the basidiocarps (*L. hatsudake* often has orange tinges) and the size of the basidiocarps. Microscopically the spores of *L. horakii* are clearly smaller than those of *L. hatsudake* ($8.3\text{-}9 \times 6.2\text{-}6.6 \mu\text{m}$ on average in *L. hatsudake*) and *L. horakii* lacks cheilomacrocytidia.

Lactarius laeticolor (S. Imai) Imazeki ex Hongo, Acta Phytotax. Geobot 18: 139 (1959) (Figs. 1, 7)

Basionym:

≡ *L. deliciosus* f. *laeticolor* S. Imai, Bot. Mag. (Tokyo) 49: 607 (1935), as '*laeticolorus*'

Synonyms:

≡ *L. laeticolor* (S. Imai) Imazeki, Genshoku-Kinoko: 153 (1959), as '*laeticolorus*', nom. inval., no basionym indicated

= *L. deliciosus* var. *japonicus* Kawam., The Japanese fungi: 55 (1929)

≡ *L. japonicus* (Kawam.) Lar.N. Vassiljeva, Agarics and Boletes (*Agaricales*) of the Primorsk Region: 302 (1973)

Type: not selected, described from Japan.

Description: Spores $8\text{-}9\text{-}10 \times 6.4\text{-}7.1\text{-}7.8 \mu\text{m}$, broadly ellipsoid to ellipsoid ($Q = 1.16\text{-}1.27\text{-}1.39$); ornamentation composed of medium thick ridges and some isolated warts, forming a rather complete network, ornamentation up to $0.5 \mu\text{m}$ high; plage distally amyloid. *Basidia* $42\text{-}50 \times 8\text{-}12 \mu\text{m}$, subclavate, 4-spored, often containing oil-droplets and fine granules; sterigmata $4\text{-}6 \mu\text{m}$ long. *Pleuromacrocytidia* not very abundant, $65\text{-}92 \times 7.5\text{-}9 \mu\text{m}$, subfusiform with a capitate or moniliform apex, very tall and conspicuous, strongly emergent, typically with crystal-shaped content in the base, thin-walled. *Pseudocytidia* rather abundant, $2.5\text{-}4 \mu\text{m}$ broad, cylindrical to tortuous, sometimes slightly emergent, mostly not, with an ochre-yellow content. *Lamella edge* sterile with quite abundant cheilomacrocytidia; cheiloleptocytidia $9\text{-}16 \times 3.5\text{-}6 \mu\text{m}$, subclavate or more irregular, hyaline or with a fine granular content, thin-walled; cheilomacrocytidia $32\text{-}45 \times 5\text{-}7 \mu\text{m}$, subfusiform with a moniliform apex, emergent, content needle-shaped, thin-walled. *Subhymenium* composed of small and rounded, irregularly arranged cells. *Hymenophoral trama* containing abundant lactifers. *Pileipellis* an ixocutis, $250\text{-}300 \mu\text{m}$ thick, of very widely spaced, shrivelled hyphae; hyphae $1\text{-}5 \mu\text{m}$ diam. *Stipitipellis* an ixocutis.

Habitat: Associated with *Abies* (*A. firma*, *A. sachalinensis*, ...), summer to autumn.

Distribution: Japan (Hokkaido, Honshu, Kyushu & Bonin Islands), Korea.

Collections examined: JAPAN, Tottori, Tottori-shi, Ochidani, in *Abies firma-Castanopsis cusoidata* woods, 06.11.1998, leg. E. Nagasawa *et al.*, TMI 23149 (TMI) – KOREA, O.K. Miller 21714 (RMS), originally identified as *L. salmonicolor*.

Discussion: No detailed macroscopical description is available for this species. *Lactarius laeticolor* is described as very distinctive in its bright orange

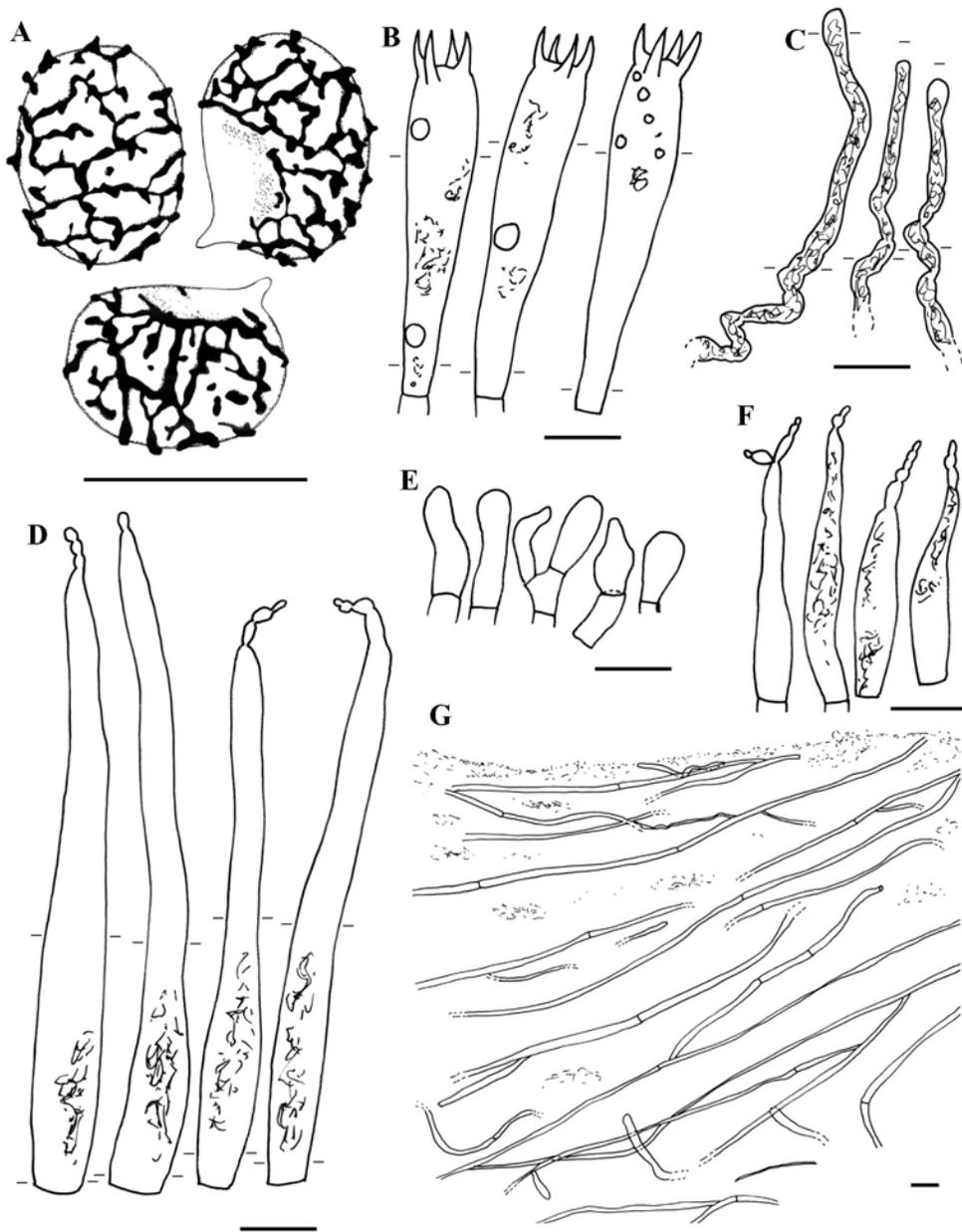


Fig. 7. *Lactarius laeticolor*: **A.** spores; **B.** basidia; **C.** pseudocystidia; **D.** pleuromacrocytidia; **E.** cheiloleptocystidia; **F.** cheilomacrocytidia; **G.** section through the pileipellis. From TMI 23149. Bars = 10 μ m, small bars indicate the height of the hymenium.

colouration of the entire basidiocarp, its viscid pileus and stipe surface in wet conditions and the presence of concentric zones on the cap. The latex is described as reddish-orange, not discolouring with time (Nagasawa, 1998). The pictures in Imazeki *et al.* (1988) show distinct, large scrobicules on the stipe. The greenish discolouration is absent or very limited in *L. laeticolor*. All these features (except maybe the colour reaction of the latex) remind very strongly of *L. salmonicolor*, a European species also associated with *Abies*, and to a lesser extent of *L. thynos*. Microscopically these three species are very similar by the presence of an ixocutis on the stipe and the presence of strongly emergent pleuromacrocyttidia. In our molecular phylogeny these three species are clearly distinct but together form a rather well supported group, confirming their close relationship (Nuytinck *et al.*, pers. observ.). Synonymising *L. laeticolor* with *L. salmonicolor* however (as done in Heilmann-Clausen *et al.*, 1998 and Eberhardt *et al.*, 2000) is incorrect.

Lactarius subindigo Verbeke & E. Horak, Australian Syst. Bot. 13: 651 (2000) (Fig. 8)

Misapplication:

= *L. indigo* *sensu* Imazeki *et al.* (1988), Nagasawa (1998) and probably several other authors (see under discussion).

Holotype: Horak 71-189 (CANB), Isotypes (GENT!, ZH), Papua New Guinea: Morobe District, Bulolo, Watut

Description (macroscopy adapted from Verbeke and Horak, 2000): *Pileus* up to 7 cm diam., at first convex with a strongly incurved margin, centre sometimes with a conical papilla, becoming depressed to umbilicate in mature specimens, papilla absent; margin non-striate; surface viscid if moist, glabrous in dry condition, conspicuously and persistently zonate; colour conspicuously blue-green, centre turning pale ochre in age. *Lamellae* arcuate to decurrent, very dense, up to 4 mm wide, with numerous lamellulae; colour brilliant blue-green, turning dark green when bruised; edge entire, concolorous. *Stipe* 1-3 × 0.4-1 cm, cylindrical, equal or gradually attenuated towards the base; surface dry, glabrous, scrobiculate, concolorous with the pileus or paler, hollow, solitary (or rarely in pairs). *Context* brittle, immediately staining blue-green, in base turning to orange on exposure; smell fruity; taste mild. *Latex* milky, immediate blue on exposure. *Spore deposit* unknown.

KOH no reaction, *HCl* no reaction, *NH₃* no reaction.

Spores 5.8-6.6-7.5-8.3 × (4.3) 4.5-5.3-5.9-6.5 μm, broadly ellipsoid, rarely subglobose or ellipsoid (Q = 1.10-1.23-1.27-1.39); ornamentation up to 0.5 μm high, of low but medium thick, strongly fragmented ridges, forming a very incomplete reticulum; plage not to distally slightly amyloid; apiculus often strikingly broad and large. *Basidia* 30-70 × (3) 6-9 μm, subclavate to

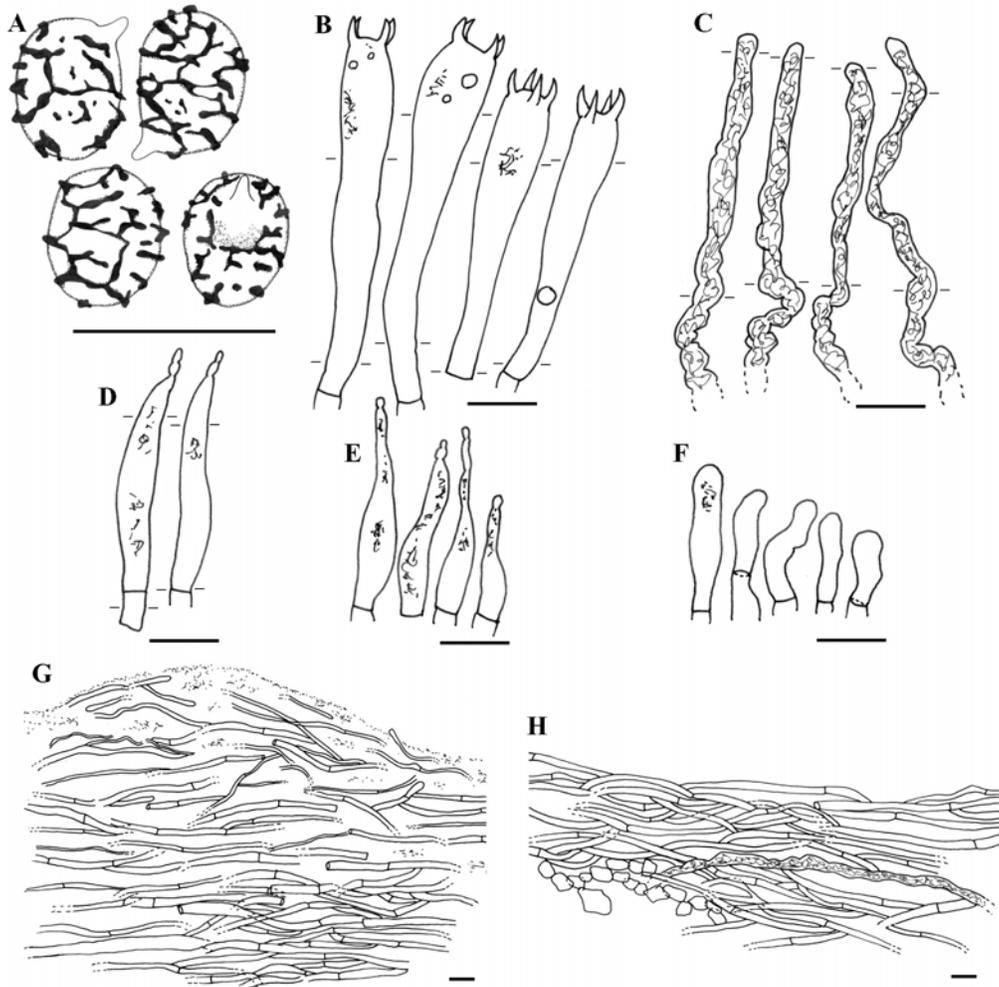


Fig. 8. *Lactarius subindigo*: **A.** spores; **B.** basidia; **C.** pseudocystidia; **D.** pleuromacrocystidia; **E.** cheilomacrocystidia; **F.** cheileptocystidia; **G.** section through the pileipellis; **H.** section through the stipitipellis. From M. Härkönen KIINA 114, RPB 547, K. Das 3030, KCS 475 and E. Horak 71-189 (isotype). Bars = 10 μm , small bars indicate the height of the hymenium.

mostly \pm cylindric, 4-spored, containing oil-droplets or with a fine granular content; sterigmata 3-7 μm long. *Pleuromacrocystidia* very scarce, only present relatively close to lamella edge, 35-40 \times 6-7 μm , subfusiform with a moniliform apex, containing needle-shaped crystals or with a granular content, slightly emergent, thin-walled. *Pseudocystidia* abundant, 3-7 μm broad, \pm cylindric or tortuous, not to slightly emergent, with a deep ochre content. *Lamella edge* sterile, composed of mainly cheileptocystidia with very scarce cheilomacrocystidia; cheileptocystidia 8-25 \times 3.5-8 μm , subclavate to more

irregular, hyaline, thin-walled; cheilomacrocytidia 17-35 × 4-7 µm, subfusiform with a moniliform apex, slightly emergent, with a needle-shaped or granular content, thin-walled. *Subhymenium* composed of small, ± isodiametric cells, irregular. *Hymenophoral trama* irregular, composed of short hyphae and very abundant lactifers with a deep ochre-brown content. *Pileipellis* an ixocutis, 50-150 µm thick, with a thin slime-layer, composed of interwoven, hyaline hyphae, 1-6 µm diam., only few shrivelled hyphae present. *Stipitipellis* a cutis, 30-80 µm thick, composed of strongly interwoven, ± parallel hyphae, 2.5-5 µm diam.; lactifers with deep ochre content present close to surface.

Habitat: Described from broad-leaf rainforest dominated by *Castanopsis acuminatissima* and *Lithocarpus* spp.; recorded under *Quercus leucotrichophora* and *Q. semecarpifolia* in India and in both *Pinus* and broad-leaf forests with *Castanopsis* and *Quercus* in Japan (as *L. indigo*, Nagasawa, 1998).

Distribution: Described from Papua New Guinea, also found in India (Uttaranchal, north India) and see Sharma and Das (2003), China (Hunan, China) and Japan (infrequent in the south of Tohoku district; as *L. indigo* in Imazeki *et al.*, 1988; Nagasawa, 1998), summer to autumn.

Collections examined: CHINA, Hunan Prov.: Wulingyuan World Heritage Area, Zhangjiajie, Matianya, N29° E110°, 19.09.1999, M. Härkönen KIINA 114 (H, GENT), specimen bought from two local (commercial) mushroom pickers – INDIA, Uttaranchal, Pauri Garhwal, Adwani, ~1900 m a.s.l., *Quercus leucotrichophora* & *Rhododendron arboreum*, 15.08.1999, RPB 547 (RMS) – Uttaranchal, Tehri Pauri, Majharatal forest, In deciduous forest, associated with *Quercus semecarpifolia*, 23.09.2000, K. Das 3030 (GENT) – Garhwal, Pauri, Near Hanuman Mandir (forest behind college campus), *Quercus leucotrichophora* & *Rhododendron arboreum*, 5.08.2002, KCS 475 (RMS) – PAPUA NEW GUINEA, Morobe, Bulolo, road to Watut, 1000 m a.s.l., montane broad-leaf forest dominated by *Castanopsis acuminatissima*-*Lithocarpus* spp. on soil, 21.10.1971, E. Horak 71-189 (GENT), isotype.

Discussion: *Lactarius subindigo* has small basidiocarps, blue latex (except in the very base of the stipe) and blue tinges in the pileus and stipe. Microscopically it is characterised by its very small spores and very scarce pleuro- and cheilomacrocytidia. From the ecology notes attached to the examined collections, *L. subindigo* seems to be associated with both *Castanopsis* and *Quercus*.

We observed some variability in the spacing of the lamellae on the herbarium specimens we examined. The Chinese specimen (KIINA 114) for example clearly has more widely spaced lamellae. The size and shape of the spores is also variable. Two Indian collections (KCS 475 and RPB 547) have very small spores (5.7-5.8 × 4.8 µm on average) that are subglobose to mostly broadly ellipsoid (Q = 1.16-1.22 on average).

The original description of *L. subindigo* states that pleuro- and cheilomacrocytidia are absent. The pleuromacrocytidia, erroneously illustrated in Fig. 2, p. 653 (Verbeken and Horak, 2000) show basidia-like cells, very unusual for pleuromacrocytidia in *Lactarius* sect. *Deliciosi*. Pleuro- and cheilomacrocytidia are present however in *L. subindigo* (also observed in the type collection), but are very scarce.

L. subindigo differs microscopically from *L. indigo* by the smaller spores that are ornamented with slightly wider and more rounded ridges. Both species are macroscopically very similar and many of the *L. subindigo* collections examined for this study were originally identified as *L. indigo*. Moreover, *L. indigo* has often been reported from Asia (Hongo and Yokoyama, 1978; Imazeki *et al.*, 1988; Bills and Cotter, 1989; Wu and Mueller, 1997); these records should be critically re-checked. Surprisingly, the very close relationship of *L. indigo* and *L. subindigo*, as supposed by Verbeken and Horak (2000), is not confirmed by molecular phylogenetic analyses. Both ITS and *gpd* data place *L. indigo* and *L. subindigo* in different clades in *Lactarius* sect. *Deliciosi*. This means blue coloured latex originated at least twice independently in this section (Nuytinck *et al.*, pers. observ.).

Lactarius thakalorum Bills & Cotter, Mem. New York Bot. Garden 49: 193 (1989) (Fig. 9)

Description (adapted from Bills and Cotter, 1989): *Pileus* 1.8-7.2 cm diam., convex-depressed with an involute to incurved margin when young, soon shallowly to deeply depressed with an incurved margin, finally deeply depressed with an uplifted, lobed or undulating margin; margin glabrous, sometimes eroded in age; surface dry to moist, waxy, greasy or viscid, slightly rugulose, glabrous, concentrically zonate in young to medium-aged specimens, azonate in age; colour mottled pink to greyish-red (4A/B3/4, 7/8B4, 8A2, 10C5), sometimes with pale reddish-purple hues, fading to pale yellow (4A2/3) with scattered reddish-purple hues, developing deep green to greyish-green stains in age (25D-F6-8). *Lamellae* decurrent, close to subdistant, slightly intervenose, with many lamellulae, sometimes forked; colour greyish-pink (10B2) to orange (6A6), becoming greyish-orange (8B3) to pale orange (5/6B4) and finally pale yellow (4B4) to pale orange (6A2), with dull green stains (25D/E6, 24E7) where injured or in age. *Stipe* (1) 2-6 × 0.5-1 cm, equal or enlarged towards base; surface dry, with a white canescent bloom, concolorous with the pileus, developing green stains in age, with a white mycelium and deep orange mycelial strands attached to the base. *Context* brittle, becoming partially hollow in the stipe, 5-7 mm thick at junction of stipe and lamellae, white, becoming reddish-orange to reddish-brown (7B6/7 to

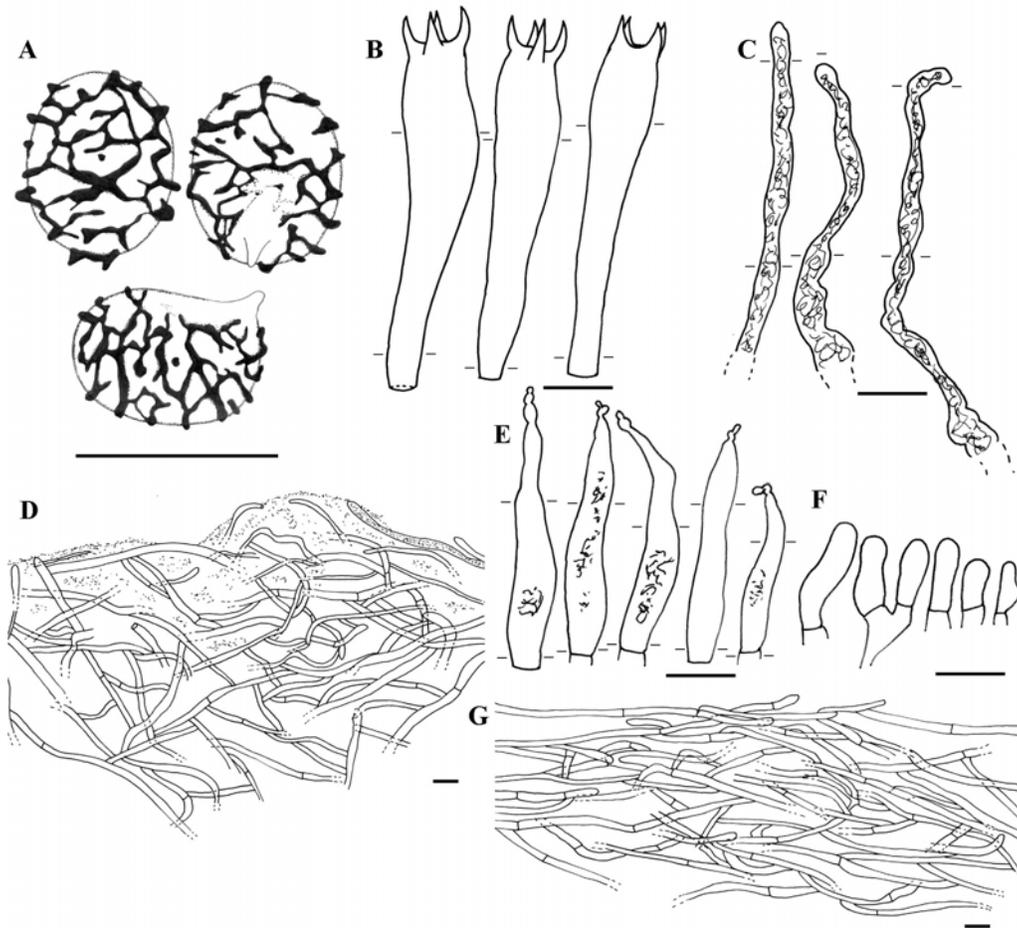


Fig. 9. *Lactarius thakalorum*: **A.** spores; **B.** basidia; **C.** pseudocystidia; **D.** section through the pileipellis; **E.** macrocystidia close to the edge; **F.** cheiloleptocystidia; **G.** section through the stipitipellis. From VC 1313 (type). Bars = 10 μ m, small bars indicate the height of the hymenium.

9/10D7) from the latex, with a distinct reddish-brown line above the lamellae, sometimes with light orange hues at the base of the stipe; smell fragrant, fungoid; taste mild to slightly bitter or unpleasant. *Latex* reddish-brown (8-10E/F8), scant. *Spore deposit* pale yellow-orange (4A3/4).

FeSO₄ no reaction, *KOH* no reaction, *NH₄OH* no reaction.

Spores (8.2) 8.3-9.1-10 \times 6.3-6.9-7.5 μ m, broadly ellipsoid to ellipsoid (Q = 1.22-1.32-1.43); ornamentation composed of rather large and high warts (up to 1 μ m high) interconnected with thick and thin ridges, some isolated smaller warts present, forming a nearly complete reticulum with small meshes; plage ornamented with fine and faintly amyloid lines and small warts or not

amyloid. *Basidia* 40-55 × 10-12 µm, subclavate, 4-spored; sterigmata 5-6 µm high. *Pleuromacrocystidia* rather abundant near the lamella edge but becoming scarce elsewhere, 35-60 × 6-8 µm, subfusiform, with a moniliform apex, often containing needle-shaped crystals, thin-walled. *Pseudocystidia* 2-5 µm broad, narrowly cylindrical and often tortuous, with refractive ochre content, mostly not emergent. *Lamella edge* sterile; cheiloleptocystidia 10-20 × 3-5 µm, abundant, subclavate to irregular cylindrical, hyaline, thin-walled; cheilomacrocystidia 25-40 × 4-7 µm, rather scarce on the edge but very abundant just beneath, emergent, subfusiform, with an acute to moniliform apex, often containing needle-shaped crystals. *Subhymenium* irregular, composed of angular to rounded, small cells. *Hymenophoral trama* irregular, containing abundant lactifers and interwoven hyphae. *Pileipellis* an ixocutis, 90-150 µm thick, with a thin slime-layer, composed of tightly interwoven, narrow, septate and rarely branching hyphae, 1-2 µm diam.; gelatinised and shrivelled hyphae abundant. *Stipitipellis* a cutis, 40-70 µm thick, consisting of interwoven, hyaline hyphae with somewhat refractive walls, 2-4 µm diam.; no shrivelled or gelatinised hyphae present.

Habitat: Scattered to gregarious on the ground in forests and plantations of *Pinus wallichiana* or *P. roxburghii* or in second-growth angiosperm forests mixed with *P. wallichiana* or *P. roxburghii*, 1300-2600 m a.s.l., found from July to October.

Distribution: Only reported from central Nepal.

Collections examined: NEPAL, Dhau-Lagiri Zone, Mustang Distr., upstream of Khobang, 03.09.1985, VC 1313 (BPI), holotype.

Discussion: As explained in the introduction, molecular evidence points towards a possible conspecificity with *L. sanguifluus*. Both taxa seem to differ slightly in several macromorphological features however. *Lactarius thakalorum* is reported to have rather small basidiocarps with a dirty pink to greyish red pileus, fading to pale yellow, while *L. sanguifluus* also has orange tinges in the pileus and has medium-sized to large basidiocarps. Microscopically there are no striking differences.

Lactarius thakalorum has recently been collected in Nepal (M. Christensen) and the study of this documented material might give clues on the eventual close relationship with *L. sanguifluus* and the morphological variability within *L. thakalorum*.

***Lactarius* sp. 1**

(Fig. 10)

Description: Spores 8.1-8.7-9.3 (9.4) × 6-6.5-7.1 µm, broadly ellipsoid to mostly ellipsoid (Q = 1.29-1.34-1.43); ornamentation up to 0.8 µm high, of medium thick to rather fine ridges and many, sometimes elongated warts, forming an irregular, incomplete network; plage very slightly to not amyloid.

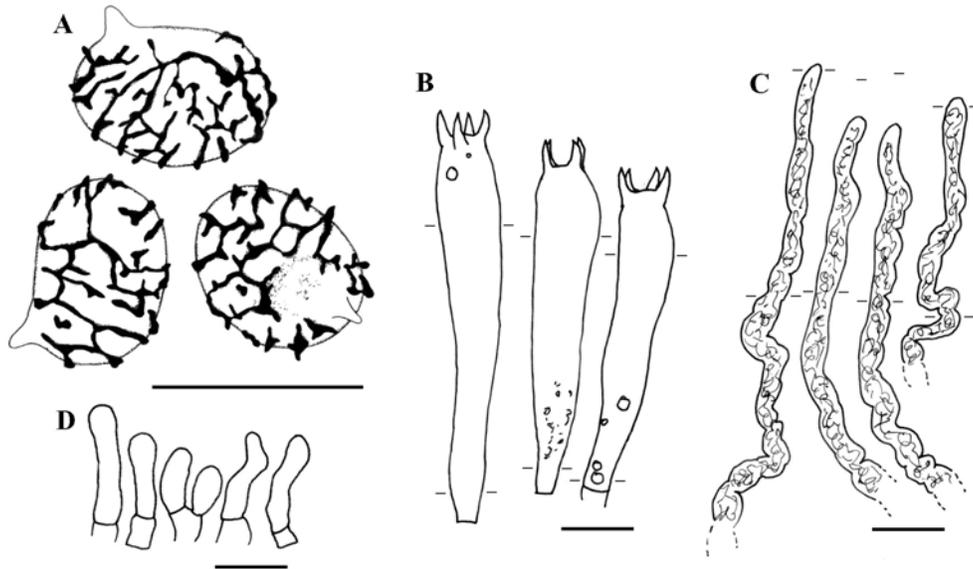


Fig. 10. *Lactarius* sp. 1: **A.** spores; **B.** basidia; **C.** pseudocystidia; **D.** cheiloleptocystidia. From M. Härkönen KIINA 112. Bars = 10 μ m, small bars indicate the height of the hymenium.

Basidia 40-55 \times 7-10 μ m, subclavate to almost cylindrical, mostly 4-spored, often with small oil-droplets; sterigmata 4-5 μ m long. *Pleuromacrocystidia* absent. *Pseudocystidia* abundant, conspicuous, 2.5-4 μ m broad, rarely slightly emergent, tortuous, with a yellowish ochre content. *Lamella edge* sterile, without cheilomacrocystidia; cheiloleptocystidia 7.5-25 \times 2.5-5 μ m, mostly cylindrical, sometimes irregular, often rather long and slender, hyaline, thin-walled. *Subhymenium* of small, irregularly arranged cells. *Hymenophoral trama* with very abundant, ochre-yellow coloured lactifers. *Pileipellis* an ixocutis, up to 200 μ m thick, composed of strongly interwoven, irregularly arranged hyphae, 2-6 μ m diam; few shrivelled or gelatinised hyphae.

Habitat: No information available.

Distribution: Hunan, China.

Collections examined: CHINA, Hunan Prov.: Wulingyuan World Heritage Area, Zhangjiajie, Yuanjiajie village, N29° E110°, 19.09.1999, M. Härkönen KIINA 112 (H, GENT), specimen bought from two local (commercial) mushroom pickers.

Discussion: No detailed information is available on the macroscopy and ecology of this collection. The specimen was bought from local commercial mushroom pickers. From an available picture it can be derived that this species looks similar to *L. hatsudake* but not to *L. quieticolor* while in our molecular phylogenetic analyses this taxon (labelled *L. sp. 1* in Nuytinck *et al.*, pers. observ.) is consistently placed close to *L. quieticolor* and is clearly distinct

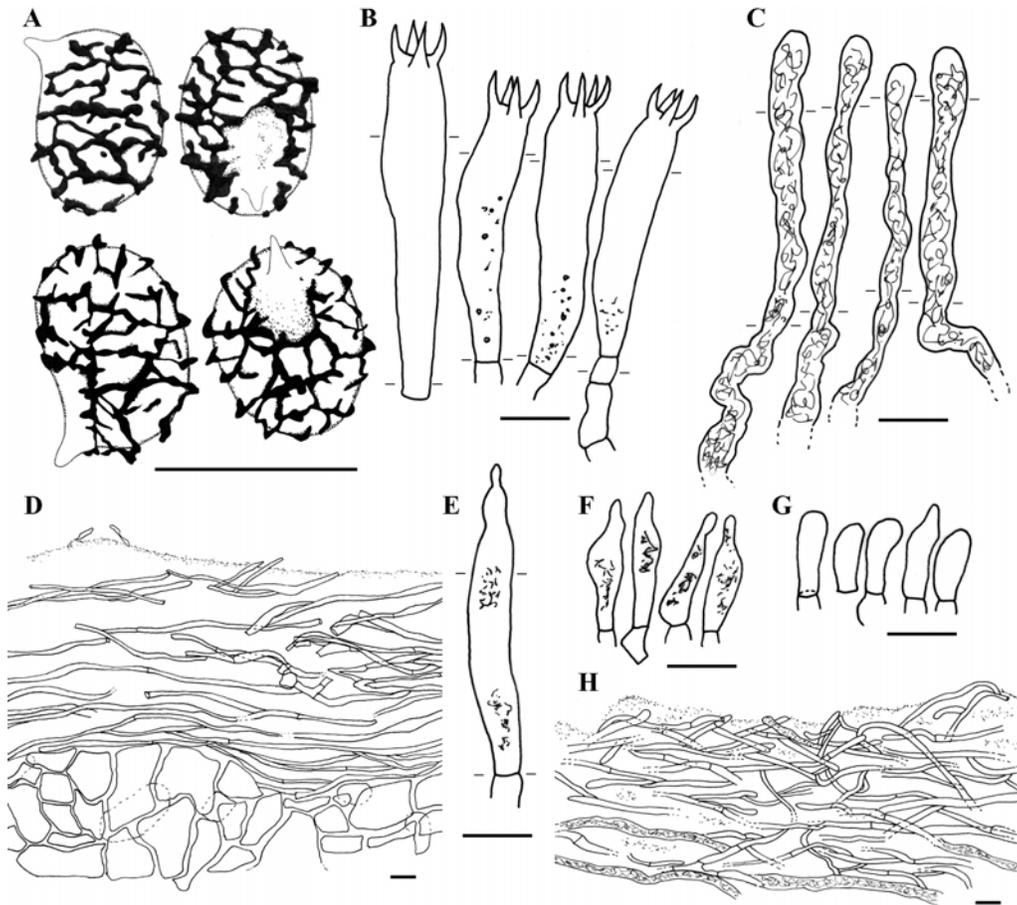


Fig. 11. *Lactarius* sp. 2: **A.** spores; **B.** basidia; **C.** pseudocystidia; **D.** section trough the pileipellis; **E.** macrocystidium; **F.** cheilomacrocystidia; **G.** cheiloleptocystidia; **H.** section through the stipitipellis. From M. Härkönen KIINA 35, 36 and 113. Bars = 10 μ m, small bars indicate the height of the hymenium.

from *L. hatsudake*. It differs microscopically from the both *L. hatsudake* and *L. quieticolor* in the more finely ornamented spores and the absence of pleuro- and cheilomacrocystidia. Many deformed and also 3-spored basidia were observed in this specimen.

***Lactarius* sp. 2**

(Figs. 1, 11)

Description: Spores 7.8-8.4-9.1-10.1 \times 5.6-6.1-6.6-7.2 μ m, broadly ellipsoid to mostly ellipsoid (Q = 1.26-1.36-1.39-1.52); ornamentation up to 0.7 μ m high, composed of rather broad ridges, forming an almost complete, dense reticulum; plage not to distally slightly amyloid. Basidia 50-60 \times 10-12 μ m, subclavate to subcylindric, 4-spored, sometimes with a granular content;

sterigmata 6-8 μm long. *Pleuromacrocystidia* very rare, 60-70 \times 9-11 μm , subfusiform, with a moniliform apex, content somewhat granular, thin-walled. *Pseudocystidia* abundant, 6-10 μm diam., often emergent and broadened at the apex, irregularly cylindric, with ochre-brown intracellular pigmentation. *Lamella edge* sterile with scarce cheilomacrocystidia; cheiloleptocystidia 10-20 \times 4-6 μm , subcylindric to subclavate, thin-walled; cheilomacrocystidia 26-30 \times 6-9 μm , subfusiform, with an obtuse to moniliform apex, often with a granular content, thin-walled. *Subhymenium* composed of small, irregularly shaped and arranged cells. *Hymenophoral trama* with abundant lactifers. *Pileipellis* an ixocutis, 40-70 μm thick, of thin-walled, interwoven hyphae, 2-4 μm diam., and some lactifers. *Stipitipellis* an ixocutis, 30-50 μm thick, of thin-walled, interwoven and mostly gelatinised hyphae, 2-4 μm diam.; some shrivelled hyphae present near the surface; slime-layer very thin.

Habitat: Collected in a forest with planted *Cunninghamia lanceolata*, *Pinus massoniana* and *Cryptomeria fortunei*. Growing under *Pinus massoniana*.

Distribution: Specimens collected in Hunan, China.

Collections examined: CHINA, Hunan Prov.: Wulingyuan World Heritage Area, Zhangjiajie, Matianya, 1000 m a.s.l., N29°19' E110°27', forest with planted *Cunninghamia lanceolata*, *Pinus massoniana* and *Cryptomeria fortunei*, under *Pinus massoniana*., 16.09.1999, M. Härkönen KIINA 35 (H) – Hunan Prov.: Wulingyuan World Heritage Area, Zhangjiajie, Matianya, 1000 m a.s.l., N29°19' E110°27', forest with planted *Cunninghamia lanceolata*, *Pinus massoniana* and *Cryptomeria fortunei*., 16.09.1999, M. Härkönen KIINA 36 (H) – Hunan Prov.: Wulingyuan World Heritage Area, Zhangjiajie, Matianya, N29° E110°, 19.09.1999, M. Härkönen KIINA 113 (H), specimen bought from two local (commercial) mushroom pickers.

Discussion: These specimens (labelled as *L. sp. 2* in Nuytinck *et al.*, pers. observ.) form a distinct, rather basal clade in our phylogenetic analysis and almost certainly represent an undescribed species. Since a detailed macroscopical description is lacking, we do not describe this species as new. It differs microscopically from *L. salmonicolor* and *L. laeticolor* (two species that show a superficial macroscopical resemblance) in the absence of striking pleuromacrocystidia and the heavier spore ornamentation. Specimen KIINA 113 was bought from local mushroom pickers who gave it the local name 'Tsong-jun'.

Unidentified collections from Asia

Apart from the variability described above under *L. deliciosus*, several clearly distinct taxa were collected that are however macroscopically closest to *L. deliciosus*. The microscopical features are described here. None of the

examined specimens were included in our molecular analyses and more collections are needed to come to conclusions.

***Lactarius* sp., collections HKAS 39043 and HKAS 39196** (Fig. 12)

Description: *Pileus* 6-9 cm diam., convex with inrolled margins and a slightly depressed centre when young, becoming infundibuliform; surface smooth, greasy when moist, obscurely zoned; colour dull orange with green tinges, becoming more carrot-orange when mature, centre green to violaceous-blue when young, greenish in mature specimens, whole surface extensively discolouring greenish when bruised. *Lamellae* decurrent, very dense and crowded, often forking; colour carrot-orange, greenish when bruised. *Stipe* 5.5-9 × 1.2-1.6 cm, cylindrical or broader at the base; colour orange but white at the apex, no scrobicules present. *Context* quite firm, hollow in the stipe, whitish, staining orange near the pellis and above the lamellae, unchanging. *Latex* carrot orange, unchanging on the context.

Spores 7.9-8.7-8.8-9.5 (9.6) × 6-6.7-6.8-7.3 (7.5) μm, broadly ellipsoid to ellipsoid (Q = 1.22-1.31-1.39); ornamentation up to 0.5 μm high, of moderately thick to rather thick ridges and isolated warts, forming a broken reticulum; plage distally slightly amyloid. *Basidia* 42-50 × 9-10.5 μm, subclavate, 4-spored, often hyaline; sterigmata 4.5-6 μm long. *Pleuromacrocystidia* abundant, especially near the lamella edge, 40-60 × 5-6 μm, subfusiform with a moniliform or capitate apex, emergent, with a granular or needle-like content, thin-walled. *Pseudocystidia* rather abundant, 2-5 μm broad, mostly not emergent, cylindrical to tortuous, with a refractive content. *Lamella edge* sometimes fertile and with very abundant, emergent and striking cheilomacrocystidia; cheiloleptocystidia 11-22 × 3-10 μm, subclavate to more irregular, mostly hyaline, thin-walled; cheilomacrocystidia 32-50 × 4-7 μm, strongly emergent, subfusiform with mostly a moniliform apex, with a needle-shaped content, thin-walled. *Subhymenium* composed of sub-isodiametric cells, irregular. *Hymenophoral trama* composed of short hyphae and abundant, ochre-coloured lactifers. *Pileipellis* an ixocutis, 100-150 μm thick, of strongly interwoven hyphae; shrivelled and gelatinised hyphae present near the surface.

Collections examined: CHINA, Yunnan Prov.: Binchuan county, Jizushan, 2250 m a.s.l., *Pinus yunnanensis*, 16.07.2001, X.H. Wang 1264, HKAS 39196 (HKAS), originally identified as *L. deliciosus* – Yunnan Prov.: Binchuan county, Jizushan, 2300 m a.s.l., *Pinus yunnanensis*, 16.07.2001, F.Q. Yu 467, HKAS 39043 (HKAS), originally identified as *L. akahatsu*.

Discussion: These specimens are strikingly larger and taller than the “typical *L. deliciosus*” sold on the markets in Yunnan. The colours are less bright and the greenish discolouration is much stronger. Microscopically the abundant, large, strongly emergent cheilomacrocystidia are striking. Very large

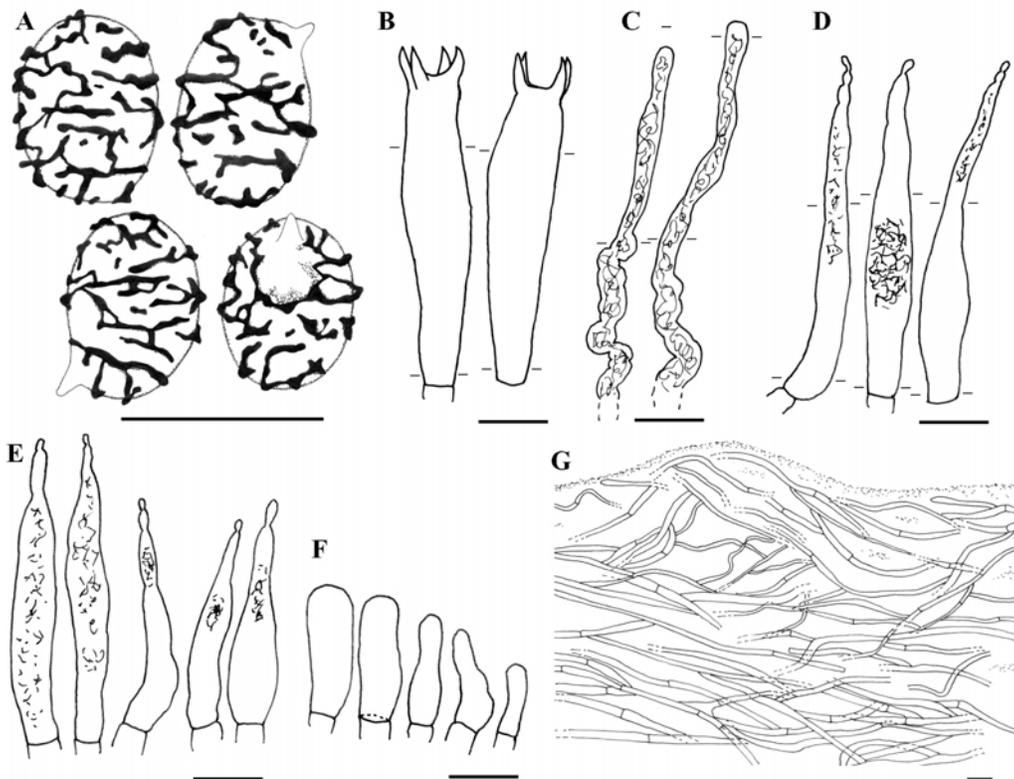


Fig. 12. *Lactarius* sp.: **A.** spores; **B.** basidia; **C.** pseudocystidia; **D.** pleuromacrocystidia; **E.** cheilomacrocystidia; **F.** cheileptocystidia; **G.** section through the pileipellis. From HKAS 39043 and HKAS 39196. Bars = 10 μ m, small bars indicate the height of the hymenium.

(> 10 μ m long) and strongly ellipsoid spores were occasionally observed but no 2-spored basidia were noticed. The examined collections all come from Yunnan.

Insufficiently known and doubtful taxa from Asia

Lactarius ogasawarashimensis S. Ito & S. Imai, Trans. Sapporo Nat. Hist. Soc. 16: 55 (1940)

This species is described as having a pinkish to buff coloured pileus with dark zones, a light blue coloured stipe and olive-buff lamellae. The latex is described as scarce and blue coloured. The spores are 7.5-8.5 \times 7-7.5 μ m. *Lactarius ogasawarashimensis* is described as endemic to the Bonin Islands (from which the name was derived) and is found under *Pinus liuchuensis*. Nothing is known from this taxon except for its original description

(Nagasawa, 1998). It was not typified and there is no similar species described from Asia or elsewhere.

Lactarius sanguineus Teng, unpubl., cited in Fungi of China: 414 (1996), nom. inval., nom. nud.

This name was traced by Korf (1996) in Teng's notes. Comments by Korf (1996): 'This species was not treated in the Chinese version, *Chung-kuo Ti Chen-chun*, 1963. Teng added it in the revised key (above), but the portion of this manuscript containing the description of the fungus and any references as to where it was collected or reported from China has (have) been lost.'

Lactarius deliciosus var. *indicus* Atri, Saini & D.K. Mann, Geobios, New Reports 10: 110 (1991), as 'indica'

Atri *et al.* (1991) reported four varieties of *L. deliciosus* from northwest India: *L. deliciosus* var. *deliciosus*, var. *olivaceosordidus*, var. *areolatus* and var. *indicus*. The latter variety is described as new (as *L. deliciosus* var. *indica*) and is reported to be very similar to *L. deliciosus* var. *deliciosus*. It is different in possessing an azonate pileus, larger spores ($9-10.5 \times 7.5-9 \mu\text{m}$ in var. *indicus* versus $7-9 \times 6-7 \mu\text{m}$ in var. *deliciosus*) and a white spore deposit. We neither examined Indian material of *L. deliciosus* var. *indicus* nor from the other varieties reported to occur in this country. It seems necessary to compare Indian material to both European and Asian type or reference collections as the boundary between the European and Asian mycota is unclear or overlapping. The occurrence of American varieties of *L. deliciosus*, for which it has been shown that they are not conspecific with the Eurasian *L. deliciosus* (Nuytinck *et al.*, pers. observ.), seems highly improbable however.

Lactarius sanguifluus var. *asiaticus* Dörfelt, Kiet & A. Berg, Feddes Repert. 115: 169 (2004)

The original description of this taxon, described from Vietnam, is too incomplete to come to a sure conclusion but it seems to be similar to *L. hatsudake*. An obvious difference is the very small size reported for the basidiocarps (2 to 3 cm diam.). We compared the spores the type specimen of *L. sanguifluus* var. *asiaticus* with both the spores of *L. hatsudake* and *L. horakii* and found a striking resemblance with the spores of *L. hatsudake*. Following spore measurements were recorded for the holotype (*L. sanguifluus* var. *asiaticus* specimen V 107, HAL fungi 1766): $(7.1) 7.2-8-8.9 (9.1) \times 5.4-6-6.6 (6.8) \mu\text{m}$ ($Q = 1.21-1.33-1.49$).

Acknowledgements

The curators of the herbaria BPI, H, HAL, HKAS, RMS, TMI and ZT are thanked for providing us with herbarium specimens. This research was funded by the Institute for the

Promotion of Innovation by Science and Technology in Flanders (IWT), Belgium and the National Natural Science Foundation of China (NSFC, Grant No. 30300002).

References

- Atri, N.S., Saini, S.S. and Mann, D.K. (1991). Further studies on north west Indian agarics – systematics of *Lactarius deliciosus* (Fr.) S.F. Gray. *Geobios, New Reports* 10: 106-110.
- Bills, G.F. and Cotter, H. Van T. (1989). Taxonomy and Ethnomycology of *Lactarius* Sect. *Dapetes* (Russulaceae) in Nepal. *Memoirs of the New York Botanical Garden* 49: 192-197.
- Cléménçon, H. (1972). Zwei verbesserte Präparierlösungen für die mikroskopische Untersuchung von Pilze. *Zietschrift für Pilzkunde* 38: 49-53.
- Dörfelt, H., Kiet, T.T and Berg, A. (2004). Neue Makromyceten-Kollektionen von Vietnam und deren systematische und ökogeographische Bedeutung. *Feddes Repertorium* 115: 164-177.
- Eberhardt, U., Oberwinkler, F., Verbeken, A., Rinaldi, A.C., Pacioni, G. and Comandini, O. (2000). *Lactarius ectomycorrhizae* on *Abies alba*: morphological description, molecular characterisation, and taxonomic remarks. *Mycologia* 92: 860-873.
- Heilmann-Clausen, J., Verbeken, A. and Vesterholt, J. (1998). *The Genus Lactarius. Fungi of Northern Europe 2*. Svampetryk, Denmark.
- Hesler, L.R. and Smith, A.H. (1979). *North American Species of Lactarius*. Ann Arbor, University of Michigan Press.
- Hongo, T. (1960). The Agaricales of Japan 1-3 Russulaceae. *Acta Phytotaxonomica et Geobotanica* 18: 129-146.
- Hongo, T. (1977). Higher fungi of the Bonin Islands I. *Memoirs of the National Science Museum (Tokyo)* 10: 31-41.
- Hongo, T. and Yokoyama, K. (1978). Mycofloristic ties of Japan to the continents. *Memoirs of the Shiga University, Faculty Arts & Science* 26: 76-80.
- Imai, S. (1935). Studies on the Agaricaceae of Japan. II. *Lactarius* in Hokkaido. *Botanical Magazine (Tokyo)* 49: 603-610.
- Imai, S. (1938). Studies on the Agaricaceae of Hokkaido. II. *Journal of the Faculty of Agriculture, Hokkaido University* 43: 179-378.
- Imai, S. (1941). *Studia agaricacearum japonicarum*. III. *Botanical Magazine (Tokyo)* 55: 514-520.
- Imazeki, R., Otani, Y. and Hongo, T. (1988). *Fungi of Japan*. Yama-Kei Publishers Co., Ltd. Tokyo, Japan.
- Korf, R.P. [Ed.] (1996). *Fungi of China*, by S.C. Teng. Mycotaxon, Ltd., Ithaca.
- Kornerup, A. and Wanscher, J.H. (1962). *Farver i Farver*. Politikens Forlag, Copenhagen.
- Lalli, G. and Pacioni, G. (1992). *Lactarius* sect. *Lactifluus* and allied species. *Mycotaxon* 44: 155-195.
- Nagasawa, E. (1998). A preliminary checklist of the Japanese Agaricales II, The suborder Russulineae. *Reports of the Tottori Mycological Institute* 36: 36-71.
- Neda, H. (1992). Proceedings of the 36th annual meeting of the Mycological Society of Japan (in Japanese).
- Nuytinck, J. and Verbeken, A. (2005). Morphology and taxonomy of the European species in *Lactarius* sect. *Deliciosi* (Russulales). *Mycotaxon* 92: 125-168.
- Sharma, J.R. and Das, K. (2003). New and interesting species of *Lactarius* from India. *Mycotaxon* 88: 377-385.

- Singer, R. (1986). *The Agaricales in Modern Taxonomy*. 4th ed. Koeltz Scientific Books, Koenigstein.
- Tanaka, N. (1890). On Hatsudake and Akahatsu, two species of Japanese edible fungi. *Botanical Magazine (Tokyo)* 4: 2-7.
- Verbeken, A. (2001). Worldwide systematics of *Lactarius*: a state of the art. *Micologia e Vegetazione Mediterranea* 16: 71-88.
- Verbeken, A., Bougher, N.L. and Halling, R. (2002). *Lactarius* (Basidiomycota, Russulaceae) in Papua New Guinea. 3. Two new *Lactarius* species in subgenus *Plinthogali*. *Australian Systematic Botany* 15: 765-771.
- Verbeken, A. and Horak, E. (1999). *Lactarius* (Basidiomycota) in Papua New Guinea. 1. Species of tropical lowland habitats. *Australian Systematic Botany* 12: 767-779.
- Verbeken, A. and Horak, E. (2000). *Lactarius* (Basidiomycota) in Papua New Guinea. 2. Species of tropical montane rainforests. *Australian Systematic Botany* 13: 649-707.
- Wang, X.H., Liu, P.G. and Yu, F.Q. (2004). *Color Atlas of Wild Commercial Mushrooms in Yunnan*. Yunnan Science and Technology Press, Kunming.
- Wu, Q.X. and Mueller, G.M. (1997). Biogeographic relationships between the macrofungi of temperate eastern Asia and eastern North America. *Canadian Journal of Botany* 75: 2108-2116.
- Yasuda, A. (1913). Kinrui Zakki (23) (Notes on fungi (23)). *Botanical Magazine (Tokyo)* 27: 560-562.

(Received 18 October 2005; accepted 27 April 2006)