

***Lactifluus parvigerardii* sp. nov., a new link towards
the pleurotoid habit in *Lactifluus* subgen.
Gerardii (Russulaceae, Russulales)**

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Abstract – *Lactifluus parvigerardii*, a new species from subtropical southwestern China, is described. Worldwide, this is the third representative of *Lactifluus* subgen. *Gerardii* with coloured latex, as in the Asian *L. ochrogalactus* and the American *L. petersenii*. Microscopically, this new species differs from *L. ochrogalactus* in having thin-walled hyphae in the pileipellis and robust macrocystidia in the hymenium. Compared with *L. petersenii*, *L. parvigerardii* has distant lamellae and heavily ornamented spores. Despite this morphological similarity to the *L. ochrogalactus*-*L. petersenii* clade phylogenetic analysis placed *L. parvigerardii* close to *L. uyedae*, taking a basal position in a strictly pleurotoid subclade. It is a key species demonstrating additional morphological and molecular diversity within *Lactifluus* subgen. *Gerardii*.

Biogeography / *Lactifluus* / Phylogeny / subtropical China / Taxonomy

INTRODUCTION

Macrofungi with an eastern North American – East Asian disjunct distribution are of special biogeographical interest and are expected to have different evolutionary histories (Wu & Mueller 1997; Mueller *et al.* 2001; Yang 2005; Li *et al.* 2009; Wang & Liu 2010). The dark-colored milkcap, *Lactarius gerardii* Peck, is one of the putative representatives with this suggested distribution (Wu & Mueller 1997). Originally described from New York by Peck (1873), the species was later recorded from Japan and China (Hongo 1971; Ying *et al.* 1991). Later Le *et al.* (2007) reported “*Lactarius* aff. *gerardii*” from Thailand and found that *L. gerardii* is a species complex forming a clade separate from the other members of *Lactarius* subgen. *Plinthogalus*, notwithstanding the striking

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morphological similarities with this well-defined subgenus. Stubbe *et al.* (2010) demonstrated that the white-spored species of *L.* subgen. *Plinthogalus*, as represented by *L. gerardii* and *L. petersenii* Hesler & A.H. Sm., form a separate clade. This new clade was described as *Lactarius* subgen. *Gerardii* (A.H. Sm. & Hesler) Stubbe, which now has been transferred to the genus *Lactifluus* with its species, based on molecular phylogenetic results (Stubbe *et al.* 2012). It contained not only these white-spored *Plinthogali* but, surprisingly, also the pleurotoid *Lactifluus uyedae* (Singer) Verbeke and its allies. The subgenus as a whole is an eastern North American and subtropical-tropical Australasian disjunct group.

Some members of the *Lactifluus gerardii* complex have occasionally been reported from China, geographically situated in between eastern North America and Australasia. Ying (1991) reported *Lactarius gerardii*, its two varieties (var. *subrubescens* (A.H. Sm. & Hesler) Hesler & A.H. Sm. and var. *facicola* (A.H. Sm. & Hesler) Hesler & A.H. Sm.) and *Lactarius subgerardii* Hesler & A.H. Sm. from southwestern China and described a new species *Lactarius atrovelutinus* J.Z. Ying from the same region, all of which were later included in *Lactarius* subgen. *Gerardii* and then recombined into *Lactifluus* (Stubbe *et al.* 2010; Stubbe *et al.* 2012). *Lactarius ochrogalactus* M. Hashiya, a species with yellowish-brown latex but also in the subgenus *Gerardii* was reported from Southwestern China by Wang *et al.* (2006). In the dataset provided by Stubbe *et al.* (2010), vouchers from China are represented in only two of the 30 well-supported clades.

A recent survey of *Lactarius s.l.* in China provided many new collections belonging to the *Lactifluus gerardii* complex and a first tentative analysis showed the diversity of this complex in China to be largely underestimated (unpubl. data). Among these collections, one taxon with dull yellowish latex led our attention to *Lactifluus ochrogalactus* (Hashiya) X.H. Wang and *Lactifluus petersenii* (Hesler & A.H. Sm.) Stubbe, the only representatives in the subgenus known to have coloured latex right from the start. However, phylogenetic analysis gave an unexpected result placing it in the subclade for pleurotoid species. The new species is here described as *Lactifluus parvigerardii* and its phylogenetic importance and morphological features are discussed and illustrated.



Fig. 1. *Lactifluus parvigerardii* (holotype): basidiomata.

MATERIALS AND METHODS

The macroscopical descriptions of sporocarps are based on fresh material and micromorphological study on dried material. Basidiospores were observed in Melzer's reagent and measured in side view, excluding ornamentation and apiculus. Statistical citation of measures follows Yang (2000). All other micromorphological structures were revived in 5% KOH, then mounted with Congo-red (aqueous reagent). Presence or absence of hyphal incrustations was checked using distilled water. All drawings, except those of the basidiospores, were made using a drawing tube installed on a Nikon E400 microscope. Colour codes are from Kornerup and Wanscher (1961).

One basidiocarp of *L. parvigerardii* was used for isolating total DNA. Total DNA extraction, protocols for PCR amplification and sequencing followed Wang *et al.* (2009), except that the amplification conditions were adjusted as follows: denaturation at 95°C for 5 min, 35 cycles of 1 min at 94°C, 1.5 min at 53°C, 2 min at 72°C, and a final extension of 10 min at 72°C. The primers ITS1-F/ITS4 (White *et al.* 1990), LR0R/LR5 (R. Vilgalys lab "<http://www.biology.duke.edu/fungi/mycolab/primers.htm>") and bRPB2-6f and fRPB2-7cR (Liu *et al.* 1999) were used to amplify the ITS region of the nuc rDNA, part of the LSU nuc rDNA, and the region between conserved domains 6 and 7 of the second largest subunit of the RNA polymerase II (*rpb2*), respectively.

To verify its taxonomic position within *Lactifluus* subgen. *Gerardii*, a preliminary phylogenetic analysis was run with the dataset and protocol of Stubbe *et al.* (2010) which contains *Auriscalpium vulgare* as outgroup, several species of *Russula*, and species of the different subgenera within *Lactarius* and *Lactifluus*. For the final analysis, a reduced dataset was used. Besides *L. parvigerardii*, 26 taxa were selected from the dataset of Stubbe *et al.* (2010) to cover representative clades of *Lactifluus* subgen. *Gerardii* and those comprising Chinese samples (Fig. 3, Tab. 1). *Lactarius volemus*, which is also a member of *Lactifluus* and has been shown to be the closest taxon of the subgenus, was selected for rooting purpose. Multiple sequence alignments were manually adjusted in BioEdit, after prior automatic alignment with MAFFT v6 (Katoh & Toh 2008) using setting L-INS-I for the ITS region and FFT-NS-I for LSU and *rpb2*. Ambiguously aligned sections of the ITS alignment to be eliminated for further analyses were selected with Gblocks v0.91b (Castresana 2000) using default settings except for maximum number of contiguous nonconserved positions (6), minimum length of a block (8) and allowed gap positions (with half). The *rpb2* intron was also excluded from the analysis. In a previous study of *Lactifluus* subgen. *Gerardii* no conflicts were detected between the analyses of the nuclear ribosomal DNA (ITS and LSU) and *rpb2* (Stubbe *et al.* 2010), allowing for the analysis of the concatenated alignment. A rapid bootstrapping (BS) algorithm of 1000 replicates was executed in RAxML, followed by a heuristic maximum likelihood (ML) search for the best tree using the GTRMIX model. Data partitioning with parameters estimated for each partition was as follows: ITS1 + ITS2, 5.8S, LSU, *rpb2* codon positions 1 + 2 and *rpb2* codon position 3.

Table 1. Specimens and GenBank accession numbers of DNA sequences used in the molecular analyses

Species or original identification	Voucher	Location	GenBank Accession n ^o		
			ITS	LSU	rpb2
<i>L. aff. gerardii</i>	<i>E.Nagasawa</i> , TMI15534 (TMI)	Tottori, Japan	GU258229	GU265586	GU258323
<i>L. aff. gerardii</i>	<i>X.H.Wang</i> 1768 (HKAS)	South Korea	GU258225	GU265583	GU258319
<i>L. aff. gerardii</i>	<i>KIINA</i> 126 (GENT)	Hunan , China	GU258227	GU265584	GU258321
<i>L. aff. gerardii</i>	<i>H.D.Zheng</i> 101 (HKAS)	Yunnan, China	GU258226	–	GU258320
<i>L. aff. gerardii</i>	<i>H.T.Le</i> 394 (GENT)	Chiang Mai, Thailand	GU258249	GU265610	GU258347
<i>L. aff. gerardii</i>	<i>H.T.Le</i> 431 (GENT)	Chiang Mai, Thailand	GU258251	GU265612	GU258349
<i>L. aff. gerardii</i>	<i>M.Christensen</i> 04-259 (GENT)	Nepal	GU258234	GU265592	GU258329
<i>L. aff. gerardii</i>	<i>D.Stubbe</i> 07-502 (GENT)	Sri Lanka	GU258238	GU265596	GU258333
<i>L. aff. gerardii</i>	<i>K.Das</i> 4062 (BSD)	Uttaranchal, India	GU258228	GU265585	GU258322
<i>L. aff. uyedae</i>	<i>G.Gates/D.Ratkowsky</i> 17-02-05	Tasmania, Australia	GU258294	GU265657	GU258397
<i>L. atrovelutinus</i>	<i>D.Stubbe</i> 06-003 (GENT)	Selangor, Malaysia	GU258231	GU265588	GU258325
<i>L. bicolor</i>	<i>D.Stubbe</i> 06-229 (GENT)	Negeri Sembilan, Malaysia	GU258221	GU265577	GU258313
<i>L. gerardii s.l.</i>	<i>D.Stubbe/R.Walleyn</i> 07-373 (GENT)	Chiang Mai, Thailand	GU258242	GU265603	GU258340
<i>L. gerardii s.l.</i>	<i>A.Verbeke</i> n 05-235 (GENT)	Tennessee, U.S.A.	EF560688	GU265614	GU258351
<i>L. ochrogalactus</i>	<i>E.Nagasawa</i> 80-102 = <i>typus</i> (TMI)	Tottori, Japan	GU258280	–	GU258381
<i>L. parvirgerardii</i>	<i>X.H.Wang</i> 2415 (HKAS) = <i>typus</i> (KUN)	Guizhou, China	JF975641	JF975642	JF975643
<i>L. petersenii</i>	<i>A.Verbeke</i> n 05-267 (GENT)	North Carolina, U.S.A.	GU258282	GU265643	GU258383
<i>L. petersenii</i>	<i>A.Verbeke</i> n 05-282 (GENT)	Tennessee, U.S.A.	GU258285	GU265646	GU258386
<i>L. reticulatovenosus</i>	<i>E.Horak</i> 6472 = <i>typus</i> (GENT)	Java, Indonesia	GU258286	GU265649	GU258389
<i>L. subgerardii</i>	<i>A.Verbeke</i> n 05-269 (GENT)	North Carolina, U.S.A.	GU258263	GU265625	GU258362
<i>L. subgerardii</i>	<i>A.Verbeke</i> n 05-285 (GENT)	Tennessee, U.S.A.	GU258267	GU265629	GU258366
<i>L. uyedae</i>	<i>MCA</i> 584 (VPI)	Japan	–	AF218562	–
<i>L. wirrabara</i>	<i>J.E.Tonkin</i> 1000 (MEL)	Victoria, Australia	GU258292	GU265655	GU258395
<i>L. wirrabara</i>	<i>P.Leonard</i> 40509	South Island, New Zealand	GU258287	GU265650	GU258390
<i>L. wirrabara</i>	<i>G.Gates/D.Ratkowsky</i> 24-01-2004	Tasmania, Australia	GU258307	GU265667	GU258407
<i>L. wirrabara</i>	<i>G.Gates/D.Ratkowsky</i> 12-07-2003	Tasmania, Australia	GU258306	GU265666	GU258406
<i>Lactarius volemus</i>	<i>A.Verbeke</i> n 05-394 (GENT)	U.S.A	GU258300	GU265660	GU258400
<i>Lactarius volemus</i>	<i>A.Verbeke</i> n 07-079 (GENT)	Belgium	GU258301	GU265661	GU258401
<i>Lactarius volemus</i>	<i>H.T.Le</i> 321 (GENT)	Thailand	GU258302	GU265662	GU258402

RESULTS

Taxonomy

Lactifluus parvigerardii X.H. Wang & D. Stubbe, sp. nov.

Figs 1-2

Mycobank: MB 561807

Basidioma minutissima. *Latex translucido-atroflavus immutabilis*. *Sporae albae in cumulo, subcomplete spinosoreticulatae. Pileipellis vallum, cellulis non incrassatis. Macrocyttidia abundantia, robusta. Species affinis Lactario ochrogalacto et L. petersenio propter lactem atroflavum, sed basidiomis minutissimis et lacte cum carne immutabilibus. Species similis L. reticulatovenoso, sed lacte atroflavo et macrocyttidiis robustis.*

Typus: China, Guizhou Province, Daozhen County, Yangxi, along main road from Daozhen to Yangxi, growing under trees of Fagaceae, on soil, alt. 2000 m, N02°58.88' E102°18.24', 28 July 2010, X.H. Wang 2415 (KUN F61367).

Etymology: referring to the similarity of *L. gerardii* but with small basidiomata.

Basidiomata (Fig. 1) small, fragile. **Pileus** 7-15 mm in diam., concave at first, then infundibuliform, occasionally lobate, yellowish brown (5F5) when young, paler (5E5) at maturity, often locally paler; centre bluntly papillate or not; surface velvety, dry, often strongly rugulose; margin often crenate. **Context** 0.3-0.7 mm thick in the pileus, whitish, not discoloring when bruised. **Lamellae** 1-2 mm broad, pale yellow (3A2-3A3), subdistant to distant, decurrent. **Stipe** 10-15 × 1-3 mm, equal or tapering towards base, ochraceous-brown or brownish, sub-hollow; apex paler; base with white tomentum. **Latex** dull-yellowish, watery, unchanging. **Spore print** white.

Basidiospores (6.0) 7-8.5 (9.0) × 5.5-7.0 μm [Q = (1.09) 1.17-1.33 (1.36), Q = 1.24 ± 0.05] (70/3/1), subglobose to ellipsoid; ornamentation 0.5-0.8 (1) μm high, composed of conical warts interconnected by fine lines, not forming a complete reticulum; plage centrally amyloid. **Basidia** 37-48 × 9-11 μm, clavate, 4-spored. **Pseudocystidia** not seen. **Pleuromacrocyttidia** abundant, 70-80 × 9-12 μm, robust, cylindrical, subclavate, with dense intracellular contents, arising deeply from the subhymenium or even the hymenophoral trama, not projecting beyond the layer of basidia. **Lamellar edge** sterile; cheilomacrocyttidia absent. **Hymenophoral trama** with globose cells, lacking typical rosettes. **Lactifers** not abundant, 8-10 μm thick, with dense contents, not forming pseudocystidia towards hymenium. **Pileipellis** a palisade, 80-100 μm thick; suprapellis composed of subcylindrical terminal elements, 15-50 × 4-6 μm, 1- or 2-celled, sometimes tapering towards apex; subpellis composed of 3-4 layers of isodiametric cells, 20-25 × 15-25 μm, thin-walled. **Stipitipellis** a trichoderm, locally a trichopalisade, 30-50 μm thick, with brown, intracellular pigmentation throughout pellis; terminal elements 10-40 × 4-7 (9) μm, subcylindrical, often tapering towards apex, rarely with swollen apex, thin-walled. **Tomentum** at stipe base composed of aggregate hyphae; hyphae 2-3 μm in diam., slightly thick-walled, not inflating, with round and thin-walled apex.

Habitat: on the ground, in fagaceous forest.

Material examined: CHINA, Guizhou Province, Daozhen County, Yangxi, July 28, 2010, X.H. Wang 2415 (KUN F61367, holotype).

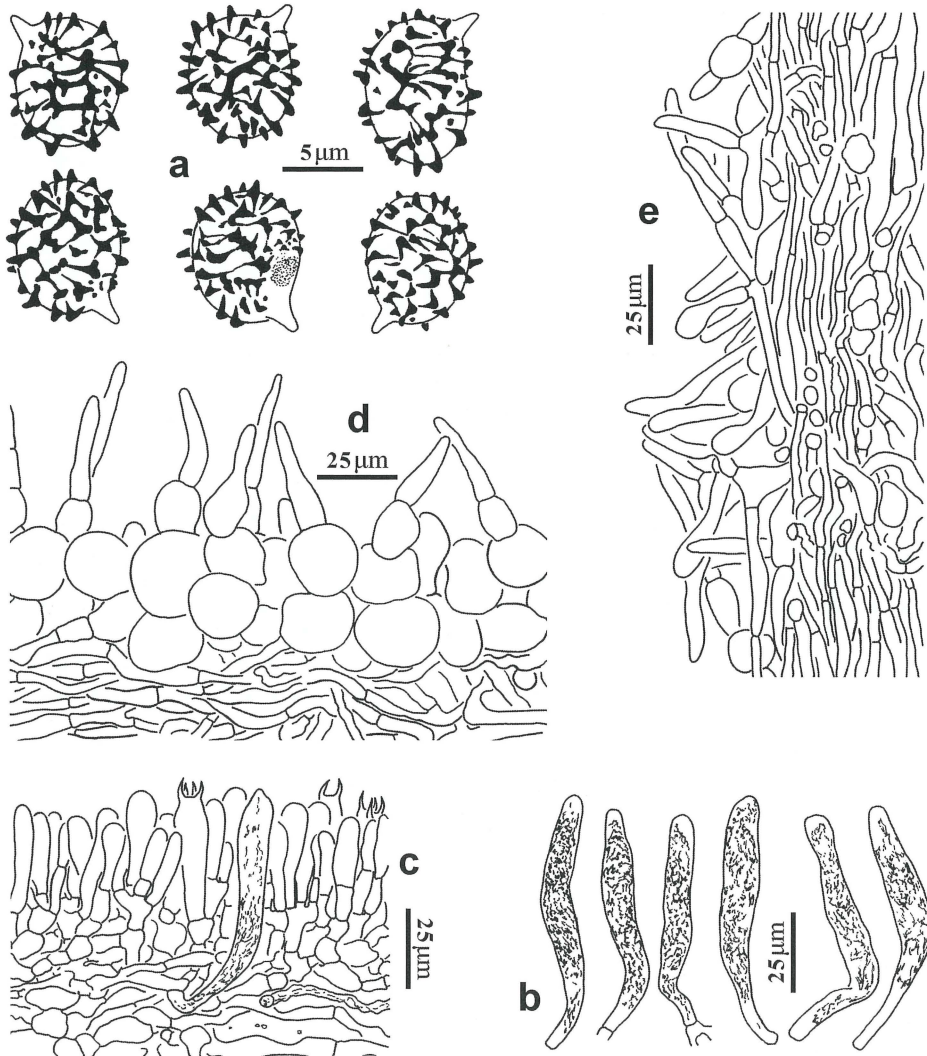


Fig. 2. *Lactifluus parvigerardii* (holotype): **a.** basidiospores, **b.** pleuromacrocystidia, **c.** hymenium, **d.** pileipellis, **e.** stipitipellis.

Phylogenetic Analysis

The preliminary phylogenetic analyses confirmed that *L. parvigerardii* is nested well within *Lactifluus* subgen. *Gerardii* with *Lactarius volemus* as the closest relative for the subgenus. For the final analysis, 32% of the ITS alignment was eliminated after processing with Gblocks. The excluded *rpb2* intron was approximately 70 base pairs long. The concatenated alignment used for the phylogenetic analyses is 2164 base pairs long. The analysis produced a highly resolved phylogram with strong support for nearly all clades. The monophyletic nature of *Lactifluus* subgen. *Gerardii* as a whole is confirmed and the overall

structure of the tree is in line with the results of Stubbe *et al.* (2010). The *L. ochrogalactus-L. petersenii* clade remains a basal clade in the phylogeny, and is separated by high support values from the rest of the subgenus. Also in a basal position is the pleurotoid clade of *L. uyedae* and associated species. *Lactifluus parvigerardii* joins the *L. uyedae* clade at the base, supported by a BS support value of 79. The dataset is made available on Treebase (S12337).

DISCUSSION

The combination of the general habit of the basidioma, the palisade structure of the pileipellis, and the white spore print assigned the new species into *Lactifluus* subgen. *Gerardii*. This is further supported by the phylogenetic analysis. Inside the subgenus, the yellowish brown latex is now only found in the Asian *L. ochrogalactus* and North American *L. petersenii* (Hesler & Smith 1979; Hashiya 1994; Wang *et al.* 2006). The new species is the smallest among these three species with coloured latex, but also strikingly small within the whole subgenus. Further, the thin-walled hyphae in the pileipellis and the unchanging latex and context can be used to distinguish *L. parvigerardii* from *L. ochrogalactus*. *Lactifluus petersenii* lacks macrocystidia and has spores with much lower ornamentation (Hesler & Smith 1979; Stubbe *et al.* 2010). The small and thin-fleshed basidiomata of *L. parvigerardii* are also reminiscent of *L. reticulatovenosus* (Verbeken & E. Horak) Verbeken, another member of the same subgenus, but the Indonesian species has more strongly reticulate spores, colourless latex, and lacks macrocystidia (Verbeken & Horak 2001).

Based on morphological-phylogenetic analysis by Stubbe *et al.* (2010), the subgenus *Gerardii* can be divided into three major clades: *L. gerardii* clade, *L. uyedae* clade, and *L. ochrogalactus-L. petersenii* clade. The morphological delimitation between the three clades is clear: dark-coloured basidiomata coupled with reticulate spores for *L. gerardii* clade, white pleurotoid basidiocarps for *L. uyedae* clade, and yellowish-brown(ing) latex & spores ornamented with warts interconnected by fine lines for *L. ochrogalactus-petersenii* clade. Based on this classification, *L. parvigerardii* can easily find its position in the *L. ochrogalactus-L. petersenii* clade. Surprisingly, the molecular analysis demonstrates that *L. parvigerardii* belongs to the *L. uyedae* clade (Fig. 3). Nevertheless, we can find some morphological support for this placement: the stout and abundant macrocystidia, which are usually not present in this subgenus, are shared by *L. parvigerardii* and *L. uyedae* complex; the miniaturization of basidiomata of *L. parvigerardii*, which are less representative in the *L. ochrogalactus-L. petersenii* and *L. gerardii* clade, is typical for the *L. uyedae* Clade (Verbeken 1998; Henkel *et al.* 2000). *Lactifluus parvigerardii* blurred the morphological delimitation between the *L. ochrogalactus* and *L. uyedae* clades.

It is also interesting to note that *L. parvigerardii* lacks pseudocystidia in the hymenium and has only few lactifers in the context. This is a very exceptional feature for milk caps. The continuous series going from presence to complete absence of pseudocystidia (and the associated lactifer network) has so far only been proven to exist within genus *Multifurca* (Buyck *et al.* 2008; Buyck *et al.* 1999; Wang & Liu 2010). The presence of a similar gradient in *Lactifluus*, even if represented solely by *L. parvigerardii* for the moment, blurs the delimitation between milk caps and *Russula* even further.

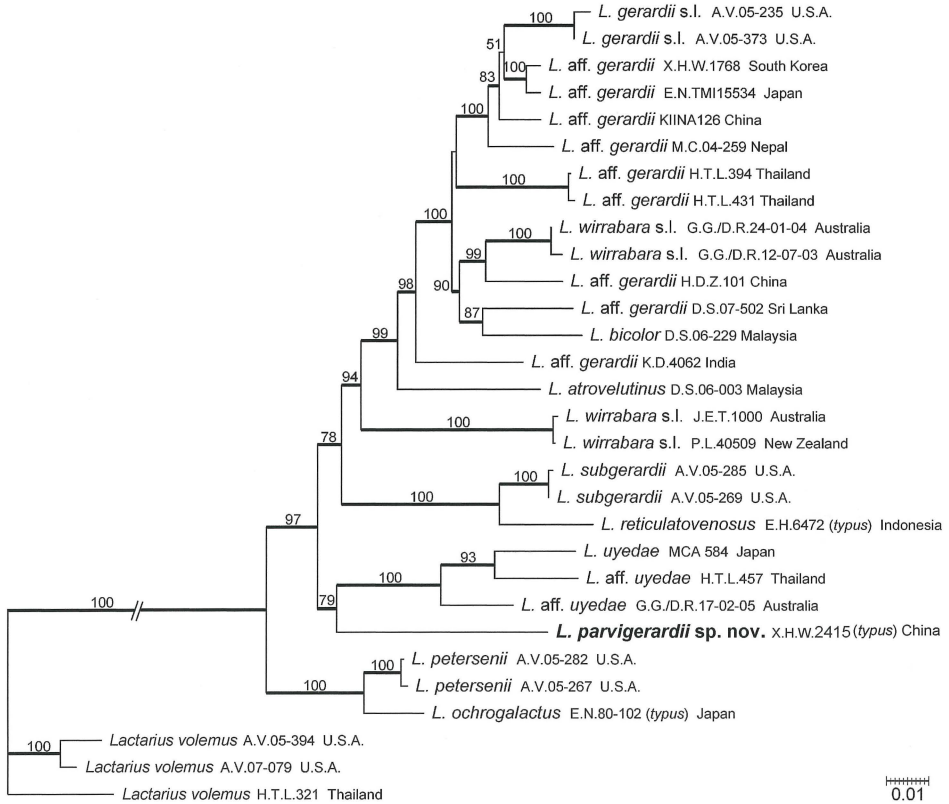


Fig. 3. ML phylogeny of *Lactifluus parvigerardii* and its allies based on the combined analysis of ITS, LSU and *rpb2* sequences, resulting from a 1000 replicates Rapid Bootstrapping algorithm and a ML tree search in RAXML. Bootstrap values are indicated above branches.

The results presented here, along with those by Stubbe *et al.* (2010, 2011) and Verbeken *et al.* (2010), indicate that Australasian collections are represented in all of the major clades within *Lactifluus* subgen. *Gerardii*, whereas North American specimens are less diverse. Following the acceptance of the nomenclatural proposal by Buyck *et al.* (2010), all other species in subgenus *Gerardii* have been transferred to *Lactifluus*. Given that *Lactifluus* is much better represented in tropical regions (Verbeken 1996; Buyck *et al.* 2008), the tropical origin of *Lactifluus* subgen. *Gerardii* seems possible. More sampling, particularly in undersampled and intermediate geographical regions, such as in the vast territory of China or India (Das *et al.* 2011), is needed to understand the evolutionary history and dispersal patterns of *L.* subgen. *Gerardii*.

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REFERENCES

- BUYCK B., HOFSTETTER V., EBERHARDT U., VERBEKEN A. & KAUFF F., 2008 — Walking the thin line between *Russula* and *Lactarius*: the dilemma of *Russula* subsect. *Ochriconpactae*. *Fungal Diversity* 28: 15-40.
- BUYCK B., HOFSTETTER V., VERBEKEN A. & WALLEYN W., 2010 — Proposal to conserve *Lactarius* nom. cons. (Basidiomycota) with a conserved type. *Taxon* 59(1): 295-296.
- BUYCK B., 1999 — Il contributo della microflora tropicale Africana per una classificazione piu naturale delle *Russulaceae*. *Pagine di Micologia* 12: 53-58.
- CASTRESANA J., 2000 — Selection of conserved blocks from multiple alignments for their use in phylogenetic analysis. *Molecular Biology and Evolution* 17: 540-552.
- DAS K. & VERBEKEN A., 2011 — Three new species of *Lactarius* (Russulaceae) from Sikkim, India. *Cryptogamie, Mycologie* 32(4): 365-381.
- HASHIYA M., 1994 — On the undescribed *Lactarius* species collected from Japan. *Proc. of the 38th Annual Meeting of the Mycological Society of Japan*, Tottori, Japan, May 26-27, p. 70 (in Japanese).
- HENKEL T.W., AIME M.C. & MILLER S.L., 2000 — Systematics of pleurotoid Russulaceae from Guyana and Japan, with notes on their ectomycorrhizal status. *Mycologia* 92(6): 1119-1132.
- HESLER L.R. & SMITH A.H., 1979 — North American species of *Lactarius*. Ann Arbor, University of Michigan Press, 841 pp.
- HONGO T., 1971 — Notulae Mycologicae (10). *Faculty of Education Memoirs Shiga University Natural Science* 21: 62-68.
- KATO H. & TOH H., 2008 — Recent developments in the MAFFT multiple sequence alignment program. *Briefings in Bioinformatics* 9: 286-298.
- KORNERUP A. & WANSCHER J.H., 1961 — Farver i Farver. Copenhagen, Politikens Forlag.
- LE H.T., STUBBE D., VERBEKEN A., NUYTINCK J., LUMYONG S. & DESJARDIN D.E., 2007 — *Lactarius* in Northern Thailand: 2. *Lactarius* subgenus *Plinthogali*. *Fungal Diversity* 27(1): 61-94.
- LI Y.C., YANG Z.L., TOLGOR B., 2009 — Phylogenetic and biogeographic relationships of *Chroogomphus* species as inferred from molecular and morphological data. *Fungal Diversity* 38: 85-104.
- LIU Y.J., WEHLEN S. & HALL B.D., 1999 — Phylogenetic relationships among ascomycetes: evidence from an RNA polymerase II subunit. *Molecular Biology and Evolution* 16: 1799-1808.
- MUELLER G.M., WU Q.X., HUANG Y.Q., GUO S.Y., ALDANA-GOMEZ R. & VILGALYS R., 2001 — Assessing biogeographic relationships between North American and Chinese macrofungi. *Journal of Biogeography* 28: 271-281.
- PECK C.H., 1873 — Descriptions of new species of fungi. *Bulletin of Buffalo Society Natural Science* 1: 41-72.
- STUBBE D., LE H.T., WANG X.H., NUYTINCK J., VAN DE PUTTE K. & VERBEKEN A., 2012 — The Australasian species of *Lactarius* subgenus *Gerardii* (Russulales). *Fungal Diversity* 52: 141-167.
- STUBBE D., NUYTINCK J. & VERBEKEN A., 2010 — Critical assessment of the *Lactarius gerardii* species complex (Russulales). *Fungal Biology* 114(2-3): 271-283.
- STUBBE D., WANG X.H. & VERBEKEN A., 2012 — New combinations in *Lactifluus*. 2. *L.* subgenus *Gerardii*. *Mycotaxon* 119: 483-485.
- VERBEKEN A., 1996 — Biodiversity of the genus *Lactarius* Pers. in tropical Africa [PhD dissertation]. Gent: Ghent University.
- VERBEKEN A., 1998 — Studies in tropical African *Lactarius* species. 6. A synopsis of the subgenus *Lactariopsis* (Henn.) R. Heim emend. *Mycotaxon* 86: 387-418.
- VERBEKEN A. & HORAK E., 2001 — Agaricales of Indonesia. 3. New records of the genus *Lactarius* (Basidiomycota, Russulales) from Java. *Sydowia* 53: 261-289.
- VERBEKEN A., NUYTINCK J. & STUBBE D., 2010 — Type studies of six Australian and one New Zealand *Lactarius* species (Basidiomycota, Russulaceae). *Cryptogamie, Mycologie* 31(3): 235-249.

- WANG X.H., HASHIYA M., VERBEKEN A., 2006 — *Lactarius ochrogalactus*, a new species of the genus *Lactarius* (Russulaceae, Russulales) with yellowish-brown latex. *Mycoscience* 47: 232-234.
- WANG X.H. & LIU P.G., 2010 — *Multifurca* (Russulales), a genus new to China. *Cryptogamie, Mycologie* 31(1): 9-16.
- WANG X.H., YANG Z.L., LI Y.C., KNUDSEN H. & LIU P.G., 2009 — *Russula griseocarnosa* sp. nov. (Russulaceae, Russulales), a commercially important edible mushroom in tropical China: mycorrhiza, phylogenetic position, and taxonomy. *Nova Hedwigia* 88(1-2): 269-282.
- WHITE T.J., BRUNS T., LEE S.S. & TAYLOR J., 1990 — Amplification and direct sequencing of fungal ribosomal RNA genes for phylogenetics. In: INNIS M.A., GELFAND D.H., SNINSKY J.J. & WHITE T.J. (eds), *PCR Protocols, A guide to methods and applications*. Academic Press, Inc., New York, pp. 315-322.
- WU Q.X. & MUELLER G.M., 1997 — Biogeographic relationships between the macrofungi of temperate eastern Asia and eastern North America. *Canadian Journal of Botany* 75: 2108-2116.
- YANG Z.L., 2000 — Type studies on agarics described by N. Patouillard (and his co-authors) from Vietnam. *Mycotaxon* 75: 431-476.
- YANG Z.L., 2005 — Diversity and biogeography of higher fungi in China. In: XU J. (ed), *Evolutionary Genetics of Fungi*. Horizon Bioscience, Norfolk, pp 35-62.
- YING J.Z., 1991 — Studies on the genus *Lactarius* S.F. Gray from China I. New taxa of *Lactarius*. *Acta Mycologica Sinica* 10: 190-199.