MYCOTAXON

*Volume 112, pp. 393–444* *April–June 2010*

# Lepiotaceous fungi in California, U.S.A. *Leucoagaricus* sect. *Piloselli*

Else C. Vellinga

*ecvellinga@comcast.net*

*Department of Plant and Microbial Biology, University of California at Berkeley*
*Berkeley, CA 94720-3102, U.S.A.*

**Abstract** — Eighteen red-bruising taxa in the *Leucoagaricus/Leucocoprinus* clade (*Agaricaceae*) are listed for California. Thirteen taxa are described in detail, with 7 proposed as new and 2 single specimen collections remaining unnamed. The species, all of which turn green with ammonia and produce spores without a germ pore, fall into 2 morphological groups (not phylogenetically supported): the pileus of one group comprises a trichodermal covering and the pileus surface of the second bears strands of repent, coloured hyphae. New taxa in the latter group are *La. flammeotinctoides* (more robust than *Lepiota flammeotincta* and with clavate cheilocystidia), *La. pyrrhophaeus* with irregular cheilocystidia and copper colours in the dried basidiocarps, and *La. pyrrhulus* with amygdaliform spores. Taxa in the 'trichodermal' group — *L. fuliginescens*, *La. cupresseus*, and *La. erythrophaeus* as well as new species *La. adelphicus*, *La. pardalotus, La. hesperius,* and *La. dyscritus* — are differentiated based on pileus covering, cheilocystidia, and reactions of the lamellae when damaged. The type collections of *L. fuliginescens* and *L. flammeotincta* were studied. DNA sequence data for all species are given and a key to 19 taxa, including *La. georginae* (from Washington), is provided.

**Key words** — biodiversity, *Leucoagaricus badhamii, La. pilatianus,* nrITS, type studies

## Introduction

### Classification

*Leucoagaricus* section *Piloselli* Singer harbours those species within the *Leucoagaricus/Leucocoprinus* clade of the *Agaricaceae* that stain red when bruised and discolour green with ammonia. The concept of this section has been changing over time, and which species belong to it has been subject to debate. Singer (1973) described the section, based on Kühner's work (1936), for species with lamellae that turn pink, have a white or lilac pileus, and a surface that reacts green with ammonia; *Lepiota georginae* (W.G. Sm.) Sacc. was chosen as the type. Locquin (1945) erected *Leucocoprinus* sect. *Anomali* Locq. (as "*Anomalae*") for species that change colour, with *Lc. meleagris* (Sowerby) Locq. and *Lc. brunnescens* (Peck) Locq. as representatives. Heinemann (1973 – the

same year as Singer (1973) described section *Piloselli*) placed the reddening species in *Leucoagaricus* sect. *Anomali* Locq. One complication is that Locquin (1945) and Kühner (1936) did not give Latin descriptons to their infrageneric units, and so the combination of *Leucoagaricus* sect. *Anomali* has never been published validly. Furthermore, Locquin (1945) applied the name *Anomalae* also to a section in *Lepiota* characterized by the absence of clamp connections, and this section has been used in different ways by various authors (e.g. to accommodate species without clamp-connections within *Lepiota*, (Pegler 1986) though they belong to the *Leucoagaricus/Leucocoprinus* clade). A third section where species with a colour change have been placed is *Leucoagaricus* sect. *Annulosi* (Fr.) Singer (Singer 1973), typified by *La. leucothites* (Vittad.) Wasser, a white species that does not change colour and whose spores have a germ pore. Bon (1993) put *La. americanus* (Peck) Vellinga (as *La. bresadolae* (Schulzer) Bon) in *Leucoagaricus* subsect. *Rubescentes* (Wasser) Bon at the same time as he placed *La. meleagris* (Sowerby) Singer, a close relative of *La. americanus*, in sect. *Piloselli*.

Species that turn red, but not green, with ammonia and KOH, such as *La. croceovelutinus* (Bon & Boiffard) Bon & Boiffard, were also accommodated in sect. *Piloselli* (e.g. Bon 1993, Candusso & Lanzoni 1990).

Various authors placed some of those species in *Leucocoprinus* Pat. and other taxa in *Lepiota* (Pers. : Fr.) Gray. For example, Pegler (1986), who held a narrow concept of *Leucoagaricus* Singer and placed many of its species in *Lepiota,* listed *Lc. zeylanicus* (Berk.) Boedijn and *L. holospilota* (Berk. & Broome) Sacc. Other authors, e.g. Reid (1990), accommodated all reddening species in *Leucocoprinus*. Reid (1990) avoided a formal more detailed classification by referring species that stain with ammonia fumes to the "*Leucocoprinus badhamii* complex".

Another complication in understanding the species and their relationships is that the concepts of *La. badhamii* (Berk. & Broome) Singer and *La. americanus* (as *La. bresadolae* in Europe) were mixed up in the literature until Demoulin (1966) put things straight (see also Reid 1990).

*Leucoagaricus* sect. *Piloselli* has been subdivided into two subsections based on the respective absence [subsect. *Pilatianei* Migl. & L. Perrone (Migliozzi & Perrone 1992)] or presence [subsect. *Pilosellini* (Singer) Bon, *Pilatianei*)] of an apical excrescence on the cheilocystidia.

All the above attempts at classifications have been based on European collections. All European taxa, except *L. roseolivida* Murrill (syn. *La. marriagei* D.A. Reid), have a trichodermal pileus covering, whereas species with a cutis or entangled cutis, such as *L. flammeotincta* Kauffm., described from North America had not been taken into consideration.

Phylogenetic analyses of nrLSU and nrITS regions (Vellinga 2004a, 2004b) have shown that the three groups — those that redden with ammonia, those

that turn green with ammonia with spores without a germ pore, and those that turn green and have spores with a germ pore — do not form a monophyletic group. Rather the first and third groups are monophyletic (Vellinga & Sundberg 2008; Vellinga 2004a), while the second one (green with ammonia, no germ pore) is polyphyletic. The nrITS data do not seem to support a simple division of *Leucoagaricus* sect. *Piloselli* into two subsections either, although there are clades comprising species with an apical excrescence on the cystidia (e.g. the clade to which *La. georginae* (W.G. Sm.) Candusso belongs), but the species with clavate or otherwise non-appendiculate cystidia do not form a monophyletic group. Pileus covering characteristics are, unfortunately, also not a good predictor for phylogenetic relationships.

The "*La. americanus* + *La. meleagris*" group takes an isolated position in the *Leucoagaricus*/*Leucocoprinus* clade (Vellinga 2004a).

The red bruising reaction in *Leucoagaricus meleagris* is caused by lepiotaquinone, an amino-1,4-benzoquinone derivative (Aulinger et al. 2000); N.B. the authors identified their specimens as *L. americana*, but the material turned out to be *La. meleagris* (pers. obs.). It is not known whether this same chemical causes the reddening reaction in all species.

**Species recognition**

It has proven impossible to classify every single collection found so far; species recognition based on morphology alone is often challenging.

Specimens in the field look often quite different from those brought home for description and study, as the basidiocarps of many species turn very dark from handling. Furthermore, old, weather-beaten specimens of different species can look very much alike, again because of the colour changes. Microscopical characters often cast the decisive vote in the identification process.

Although the tentative new species thus far represented by only one collection are not formally described, they are described as well as included in the identification key.

No new combinations are made in *Leucoagaricus* for species still accommodated in *Lepiota*, as the taxonomy of this clade is not yet stable (Vellinga 2004a).

**Scope of the article**

The present paper focuses on the California species of section *Piloselli*. Here, for this study, we take the same pragmatic approach as Reid (1990) by covering those species that turn red when scratched and that turn green with ammonia vapours.

Several conspicuous species, some quite common, have been described from California (*L. fuliginescens, La. cupresseus, La. marginatus*), but the group is not

well covered in popular field guides (e.g. Arora 1986) or on web sites (e.g. Wood & Stevens 1996–2009). Species described from California by Murrill (1912) and Burlingham (1945) are now recognized, and their names used again.

The well-known species *L. flammeotincta* turned out to represent a complex of five different species with different nrITS sequences, but with only subtle microscopical differences and an almost identical macroscopical appearance.

The two reddening species with a germ pore in the spores, *La. americanus* and *La. meleagris*, are not treated here, although both fruit occasionally in California; descriptions based on European collections can be found in Vellinga (2001).

Vellinga (2007a) recently presented the lilac and dark pink species *L. roseolivida* and *L. decorata* Zeller with full descriptions and comparisons with the type collections, which are not repeated here.

A description of *Lepiota castanescens* Murrill, a species that stains red with ammonia, has also recently been published (Vellinga & Sundberg 2008). *Leucoagaricus erythrophaeus* was recently described for the interpretation of *L. roseifolia*, but its description is given here as well, as it can easily be confused with some of the other species.

The key below covers all known Californian species in the *Leucoagaricus/ Leucocoprinus* clade that change red on bruising, although some species concepts are not yet completely settled.

### *Leucoagaricus* sect. *Piloselli* in North America

Only a few reddening species have been described for the central, eastern, and southeastern parts of the U.S.A. *Leucoagaricus brunnescens* (Peck) Bon, described from Missouri (Peck 1904), is a small species that initially resembles *L. cristata* (Bolton : Fr.) P. Kumm. but changes colour on drying. Bon (1993) reported it for Europe, but whether it really is the same species is not clear.

*Lepiota mutata* Peck, a white species described from Kansas (Peck 1896) with a scurfy pileus surface that changes brown on drying might belong to section *Piloselli*.

Murrill described several species in the group of species with a germ pore: the widespread *La. americanus*, *L. muticolor* Murrill [from Alabama (Murrill 1914), for type study see Smith (1966)], and *L. sanguiflua* Murrill and *L. tinctoria* Murrill, both from Florida, and featured in an article on this group by Smith & Weber (1987). The last authors introduced an additional species in this group, *L. besseyi* H.V. Sm. & N.S. Weber, characterized by pleurocystidia. Of these species, only *La. americanus* has been encountered in California.

### Diversity, ecology, and distribution

Further investigations and inventories of the state and its diverse habitats will undoubtedly add to the diversity, as we know it now. New species were being

discovered up to the very end of the research for this article, even in material collected from well-studied areas. Recognition of these new species is critical. As is the case with the small brown species in the *L. oculata* group (Vellinga 2007b), many different species co-inhabit the same habitat and locality.

Collecting trips focused on the coastal area from Monterey north to Humboldt County and on the San Francisco Bay area, with occasional surveys of the lower parts of the Sierra Nevada (Yuba and Nevada counties). Some ecological trends are now apparent. Species of the *L. flammeotincta* group, which have never been found under Monterey cypress (*Callitropsis macrocarpa* (Hartw.) D.P. Little (syn. *Cupressus macrocarpa* Hartw.; *Hesperocyparis macrocarpa* (Hartw.) Bartel), do grow under redwood (*Sequoia sempervirens* (D. Don) Endl.) and in forests of various conifer species with tanbark oak (*Notholithocarpus densiflorus* (Hook. & Arn.) Manos et al.) along the coast and inland. *Leucoagaricus cupresseus* is known from two kinds of habitats: Monterey cypress plantings in coastal settings and kitchen gardens. It does not occur in an old east-facing cypress plantation but can fruit abundantly on west facing slopes under cypresses used as wind breaks close to the coast. Only two species (*La. erythrophaeus* and *L. flammeotincta*) were encountered at lower elevations of the central Sierra Nevada, but this habitat is not well investigated for lepiotaceous fungi. Two species seem so far to be restricted to old Monterey cypress plantations (*La. dyscritus* and *La. hesperius,* both described in this paper); in general, this habitat is very rich in lepiotaceous species (Guinberteau et al. 1998, Vellinga 2004b). Distribution data for other west coast states are scarce, but it appears that California has a unique '*Lepiota*' flora, richer in species than the more northern regions. *Leucoagaricus georginae*, however, has been recorded from Washington, but has not been encountered in California, yet. Only *Lepiota fuliginescens*, *L. flammeotincta,* and *L. castanescens* are widespread in the Pacific Coast states. However, for most species distribution and ecological data are still very incomplete.

## Material and methods

Standard methods for describing basidiocarps were applied, using the terminology of Vellinga & Noordeloos (2001). Colour annotations in the macroscopical descriptions are from Munsell™ soil color charts (1975). Microscopical observations were made on dried material. The notation [60,4,3] indicates that measurements were made on 60 spores in four samples in three collections. At least 15 spores were measured per collection. The lamellar characters and spore shape and size were observed in Congo Red in 10% ammonia followed by ammonia only, and the pileus covering was observed in 10% ammonia. The following abbreviations are used: L for number of lamellae, l for number of lamellulae in between two lamellae, avl for average length, avw for average width, Q for quotient of length and width, and avQ for average quotient. The abbreviation *L.* is used for *Lepiota*, *La.* for *Leucoagaricus* and *Lc.* for *Leucocoprinus*.

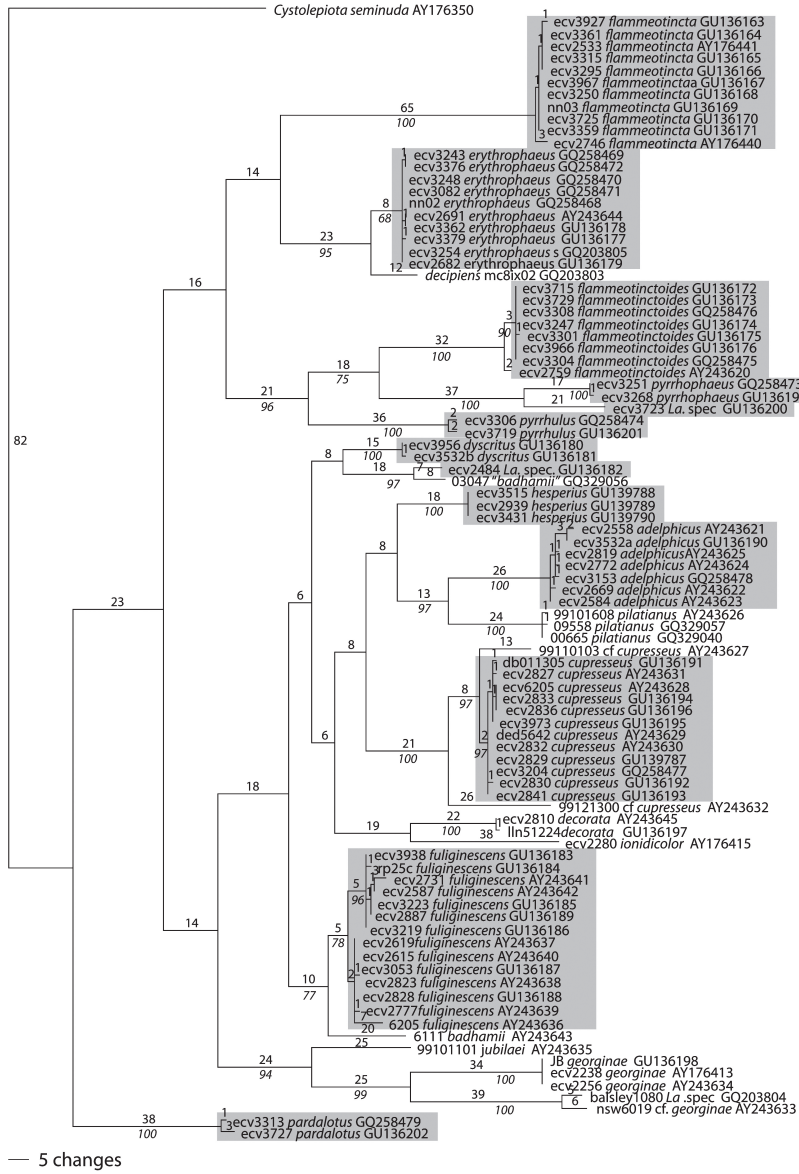


Fig. 1. Phylogram based on parsimony analyses of the nrITS region of species in *Leucoagaricus* sect. *Piloselli*. One of 10,000 MPT's is depicted, based on 305 parsimony informative characters. *Cystolepiota seminuda* was chosen as outgroup. The numbers above branches refer to the number of changes, the ones below the branches are bootstrap values (> 65%). The taxa treated in this paper are highlighted.

All collections are in UC unless otherwise stated. Herbarium abbreviations are according to Holmgren & Holmgren (1998). Latin descriptions of new species have been deposited in MycoBank. For many species, multiple illustrations are given to show the variability among collections belonging to the same species.

DNA was extracted from dried material using a Qiagen DNeasy® Blood and Tissue kit (Qiagen, Valencia, CA, USA). The nrITS region was amplified with the ITS-1F/ITS-4 primer set with an MJ PTC-100™ thermocycler (Applied Biosystems, Foster City, CA, USA) under conditions previously described (Gardes & Bruns 1993). PCR products were cleaned using 0.5 µl of ExoSAP IT (USB Corp, Cleveland, OH, USA) per reaction and cycled at 37°C for 45 min, followed by 80°C for 15 min. Sequencing was performed using Big Dye chemistry and an ABI PRISM 3100 Genetic Analyzer (both from Applied Biosystems, Foster City, CA, USA). Sequences were edited and contigs assembled using Sequencher 4.2.2 (Gene Codes Corporation, Ann Arbor, MI, USA). Newly produced sequences were deposited in GenBank, and their accession numbers listed with the collections.

The nrITS sequences were aligned with the program MAFFT version 6 (Katoh et al. 2002). For the phylogenetic analyses the Maximum Parsimony option in PAUP* v4 (Swofford 2002) was used. The sequence data base was also analyzed by maximum likelihood method (ML) using RAxML version 7.2.3 (Stamatakis et al. 2008); 100 rapid ML bootstraps were performed, and bootstrap values are included in the MP tree of Fig. 1. *Cystolepiota seminuda* (Lasch) Bon was chosen as outgroup. The analyses were only performed to determine whether the sequences matched sequences of previously sequenced species and collections, and were not used to infer a phylogeny of section *Piloselli*.

## Taxonomy

**1. *Lepiota fuliginescens*** Murrill, Mycologia 4: 236. 1912. Figures 2–5

Type study — Smith (1966: 105–106).

Microscopical characters (from Vellinga type study; Figure 2) — Basidiospores [15,1,1] in side-view 6.0–7.6 × 3.9–4.9 µm, avl × avw = 6.7 × 4.4 µm, Q = 1.36–1.64, avQ = 1.52, ellipsoid, some subamygdaliform, in frontal view ellipsoid-ovoid, rather thick-walled, without germ pore, uni-guttulate, congophilous, immediately red-brown in Melzer's reagent (dextrinoid), metachromatic in Cresyl Blue. Basidia not observed. Lamella edge sterile. Cheilocystidia abundant, 27–70 × 8–16 µm, clavate, fusiform-lageniform to clavate with abrupt apical, cylindrical to moniliform appendage (12–28 × 4–6 µm), with brown contents in ammonia. Pleurocystidia absent. Pileus covering a cutis of cylindrical elements, 3–7 µm wide, with green-brown pigment in ammonia, giving rise to tufts of upright elements, 55–220 × 9–19 µm, narrowly fusiform and tapering towards apex or cylindrical with rounded apex, exuding green-brown pigment in ammonia, and with dark granules (as seen in ammonia). Clamp connections not observed.

Description of modern material (Figs 3–5)—Pileus 35–90 mm, convex when young, expanding to plano-convex without, or more rarely with, umbo,

pale brown or pale grey (e.g. 10 R 4/3–2.5 YR 4/2; 5 YR–7.5 YR 5/3–4) when young, velvety all over, later with closed covering at centre or umbo (e.g. 7.5 YR 5/3) only and around centre splitting up into grayish patches (7.5 YR 6/3–6/4) forming a concentrical pattern close to centre and radial pattern in outer ¼ of radius, on whitish background, paler around centre than at umbo, and discolouring red at first, to dark purple brown to dark brown with age; margin exceeding lamellae. Lamellae, L = 70–90, l = 0 or 1(–3), very crowded, free and remote from stipe, subventricose to distinctly ventricose, up to 5–7

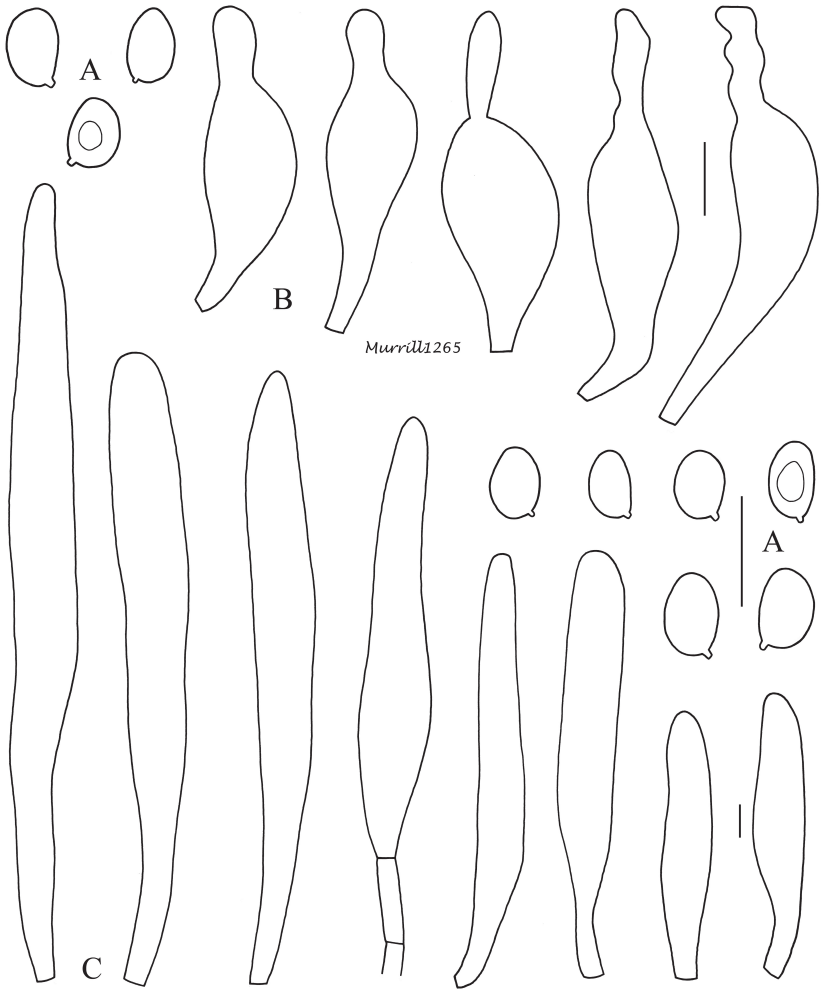


Fig. 2. *Lepiota fuliginescens* — A. spores; B. cheilocystidia;
C. elements of pileus covering.(all from holotype collection). Scale bars 10 µm.

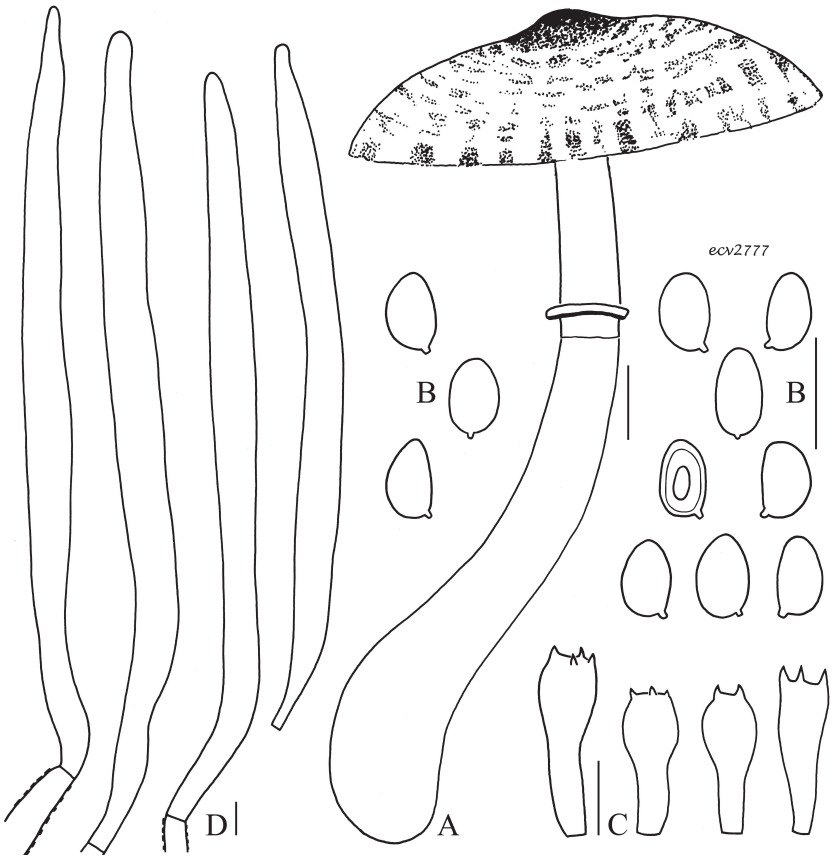


Fig. 3. *Lepiota fuliginescens* — A. Basidiocarp; B. spores, basidia, elements of pileus covering (all from ecv2777). Scale bar 10 mm (A); microscopic features 10 µm.

mm wide, white when young, to whitish with pinkish sheen, discolouring immediately under pressure to orange-red, changing to almost black, with age often vinaceous-purplish pink coloured, with cystidiose edge starting white, but rapidly changing to dark especially near pileus margin and contrasting with rest of lamellae. Stipe 60–125 × 5–16 mm, cylindrical but with up to 20 mm wide base, whitish all over when young, but rapidly changing when damaged to red, changing to dark brown with age, short fibrillose all over, but especially so above annulus, hollow, and white-tomentose at base. Annulus an ascending or descending cuff and a short, 2 mm wide, flaring part, sturdy, at first white and with rim concolourous with pileus centre, soon changing to dark brown, especially at edge. Context in pileus white at first, changing when cut via

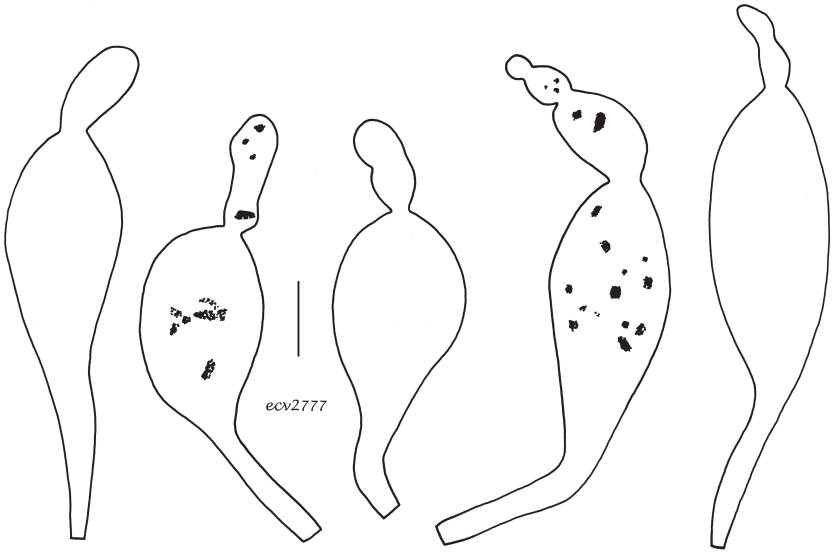


Fig. 4. *Lepiota fuliginescens* – Cheilocystidia (from collection ecv2777). Scale bar 10 µm.

yellow to orange-red, or directly orange, in places; discoloration soon fading; in stipe white and shiny, or whitish and non-changing. Smell like the rubber component of the smell of *Lepiota cristata*, indistinct, slightly rancid.

Chemical tests — KOH 3% on lamella surface first red, changing to green.

Dried specimens dark with dark lamellae.

Basidiospores [296,19,19] in side view 5.8–8.8 × 3.5–5.2 µm, avl × avw = 6.1–7.3 × 3.8–4.5 µm, Q = 1.3–2.1, avQ = 1.6–1.85, ellipsoid to oblong, often amygdaliform, in frontal view ovoid or ellipsoid to oblong, uniguttulate, congophilous, dextrinoid, metachromatic in Cresyl blue, without germ pore. Basidia 15–30 × 6.0–9.0(–12) µm, 4-spored, rarely intermixed with some 2-spored ones. Lamella edge sterile. Cheilocystidia 19–60 × 6.0–25 µm, in most cases with apical, moniliform to cylindrical excrescence, 2.0–33 × 2.0–9.0 µm, with clavate to lageniform body, with dark granules and green-brown diffuse pigment in ammonia; in fresh material with green contents in ammonia. Pleurocystida absent. Pileus covering trichodermal, made up of upright long and relatively slender to more squat and relatively short elements, 58–330 × 10–27 µm, rarely with predominantly short elements not exceeding 100 µm; elements with rounded apex, slightly thick-walled, with brown intracellular (often in blobs) and dark brown (at base of elements) to pale brown (at apex) parietal pigment; in fresh material with some elements with

blue-green contents in ammonia; repent hyphae on pileus surface cylindrical, with incrusting pigment especially in the cells just below the upright elements, and also with brown granular pigment (all pigment observations in ammonia). Clamp connections absent.

Habitat and distribution – Solitary to gregarious in small groups, terrestrial on litter-rich soil, in various forest types, e.g. *Callitropsis macrocarpa* stands, under *Sequoia sempervirens* and other conifers in mixed woods, throughout coastal northern California, also in the Pacific Northwest, not uncommon. November to March in California, fruiting earlier in more northern regions.

Collections examined – U.S.A., **Washington**, Skagit Co., Whidbey Island, Deception Pass State Park, 28-X-1995, S.A. Trudell 95-301-01. **California,** Alameda Co., Berkeley, UC-Berkeley campus, on the bank of Strawberry Creek, 6 December 2001, E.C. Vellinga 2777 (nrITS AY243639); ibidem, 7 January 2002, E.C. Vellinga 2823 (nrITS AY243638). Marin Co., Mount Tamalpais, Alpine-Kent Pump Road, 21 November 2001, E.C. Vellinga 2731 (nrITS AY243641); Point Reyes NP, southern part, 25 November 2003, R. Pastorino 11-25-c (nrITS GU136184); Point Reyes NP, along Olema Trail, 31 October 2009, S.P. Schechter (coll. E.C. Vellinga 4092); Mendocino Co., Jackson State Demonstration Forest, 22 November 2003, E.C. Vellinga 3128. Hendy Woods SP, 25 November 2002, E.C. Vellinga 2887 (nrITS GU136189). Navarro River Redwood SP, 25 November 2002, E.C. Vellinga 2903 and 2904. San Mateo Co., San Francisco Watershed, 8 December 2000, E.C. Vellinga 2587 (nrITS AY243642); ibidem, 23 December 2002, E.C. Vellinga 2974; ibidem, 25 February 2003, E.C. Vellinga 3053 (nrITS GU136187); ibidem, 5 December 2003, E.C. Vellinga 3159; ibidem, 25 November 2008, E.C. Vellinga 3938 (nrITS GU136183). San Mateo County Memorial Park, 4 November 2004, E.C. Vellinga 3219 (nrITS GU136186) and 3223 (nrITS GU136185). Moss Beach, 27 February 2001, F. Stevens (coll. E.C. Vellinga 2615) (nrITS AY243640); ibidem, 10 March 2001, E.C. Vellinga 2619 (nrITS AY243637); ibidem, 11 January 2002, E.C. Vellinga 2828 (nrITS GU136188); 28 January 2003, E.C. Vellinga 3029 and 3030.

Comments — *Lepiota fuliginescens* is very closely related to the European species *La. badhamii* (Fig. 1). Morphologically the two are very similar, with only the spores of *L. fuliginescens* slightly smaller than those of *La. badhamii*. The differences in sequence data and in distribution warrant the recognition of two species. The sequence (GQ329056) from a collection in the Museo di Storia Naturale in Venice (MCVE), labled *La. badhamii,* represents a different, unknown, species.

*Lepiota fuliginescens* is quite variable, both in macroscopic characters and in shape and size of the elements of the pileus covering. The two groups within *L. fuliginescens* that can be distinguished based on nrITS sequences (Fig. 1) are not characterized by any corresponding morphological characters, though one of the two groups based on nrITS sequences seems to be characterized by short elements in the pileus covering, wheras the sizes of the pileus covering elements in the second group are very variable.

*Lepiota fuliginescens* and *La. badhamii* differ from the other species in section *Piloselli* by the combination of relatively big basidiocarps, a trichodermal pileus

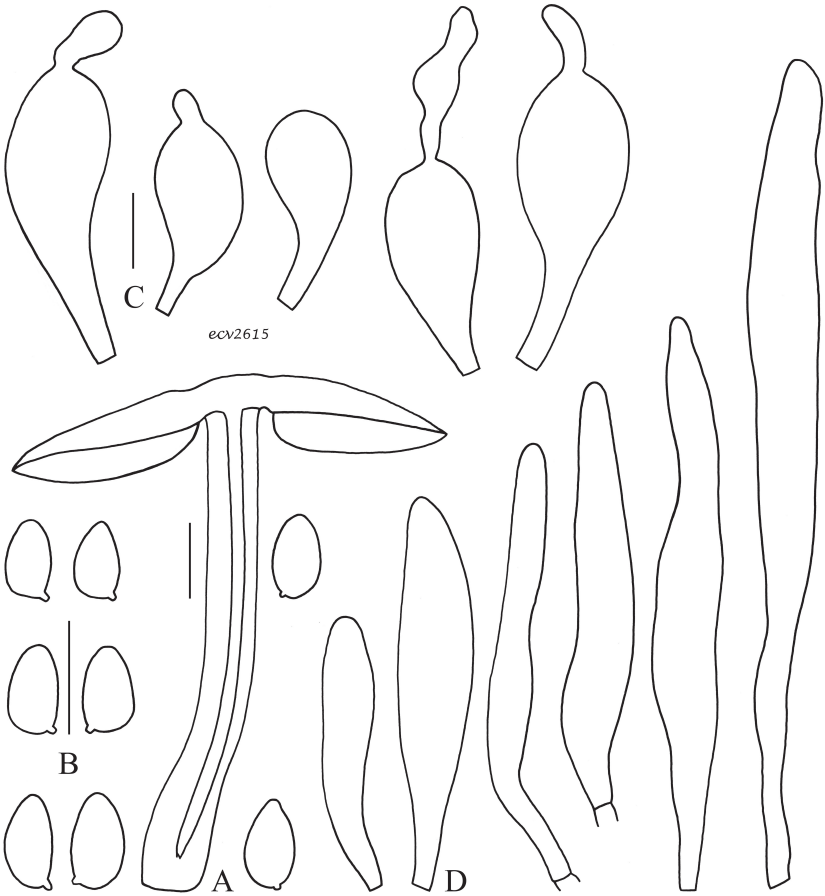


Fig. 5. *Lepiota fuliginescens* — A. Basidiocarp; B. spores; C. cheilocystidia; D. elements of pileus covering (all from ecv2615). Scale bar 10 mm (A); microscopic features 10 µm.

covering, clavate cheilocystidia with an apical excrescence, and amygdaliform to ellipsoid spores. The young specimens are very pale, but darken rapidly. *Leucoagaricus georginae*, reported from Washington, is much smaller with cystidioid elements on the pileus, but shares the cystidial characters with *L. fuliginescens*.

The type collection of *L. roseifolia* Murrill turned out to have clavate cheilocystidia with an apical excrescence (Vellinga et al. 2010), just like those of *L. fuliginescens*, but the lamellae of the dried specimen were not as dark coloured as those of *L. fuliginescens*. Modern day interpretations of *L. roseifolia* depict it as a different species, with clavate, non-appendiculate, cheilocystidia;

that species has recently been described as *La. erythrophaeus* (Vellinga et al. 2010). Sundberg (1967) recorded the cheilocystidia of *L. roseifolia* as clavate and elongate clavate, sometimes rostrate. He might have included *L. fuliginescens* in this description of *L. roseifolia*, a species otherwise lacking in his overview of lepiotaceous fungi in California.

*Lepiota fuliginescens* is known from a range of habitats, and is not, like *La. cupresseus*, restricted to habitats dominated by *Callitropsis macrocarpa*.

**2. *Leucoagaricus cupresseus*** (Burl.) Boisselet & Guinb., Bull. Féd. Ass. mycol. médit., n.s. 19: 34. 2001. FIGURES 6 & 7

≡ *Lepiota cupressea* Burl., Mycologia 37: 53. 1945.

TYPE STUDY — Sundberg (1976: 381–383).

SELECTED DESCRIPTIONS — Boisselet & Guinberteau (2001: 35–36); Burlingham (1945: 53–54).

PILEUS 30–120 mm, convex, irregularly convex, truncate convex when young, expanding to plano-convex with central depression with or without low broad umbo, often a bit irregular, at centre with pink-brown (5–7.5 YR 6/3–4 when young, later 7.5 YR 5/4) tufty-tomentose covering, around centre breaking open and more scaly-tufty, and with age in outer ¼ of radius radially arranged and streaked, darker to dark brown with age and with rain, on white background, when scratched turning red (both covering and background); margin exceeding lamellae for more than 2 mm in young specimens. LAMELLAE, L = 100–150, l = 0–3, crowded to very crowded, free and up to 6 mm from stipe, not ventricose, up to 10 mm wide, white at first, cream-white with age, with white cystidiose edge which turns dark brown with age, and immediately orange when damaged. STIPE 50–140 × 7–25 mm, cylindrical, in most specimens with big bulbous base, 25–50 mm wide, white at first, longitudinally innately fibrillose, often white-tomentose at base, shiny, orange when scratched or handled, turning ugly dark brown, hollow, protruding into pileus in some specimens. ANNULUS with ascending or descending white cuff, often relatively long, with small flaring white dull-tomentose part with thickened rim, changing orange when touched and turning dark brown with age. CONTEXT in pileus thick, white and dull, not changing colour when cut, except where knife stuck on pileus covering and there orange-red, in stipe white and orange in places, in younger specimens especially strongly orange-red in bulb, brownish in bulb in older specimens. SMELL indistinct, fungoid to slightly astringent. SPORE PRINT white.

CHEMICAL TESTS — KOH 3% on lamellae green to greenish.

DRIED SPECIMENS with dark lamellae.

BASIDIOSPORES [210,14,14] in side view 6.1–9.3 × 3.9–5.4 µm, avl × avw = 6.7–7.5 × 4.1–4.7 µm, Q = 1.4–2.0, avQ = 1.53–1.69, ellipsoid to oblong, amygdaliform,

some with faint papilla, in frontal view ellipsoid to obovoid, uni-guttulate, congophilous, dextrinoid, metachromatic in Cresyl blue. Basidia 16–28 × 6.0–8.5 µm, 4-spored. Lamella edge sterile. Cheilocystidia 23–89 × 6.0–16 µm, variable in shape, clavate, fusiform-clavate, lageniform-utriform, cylindrical, some lageniform with rather abrupt excrescence, or with subcapitate apex, with dark granules and contents in ammonia. Pleurocystidia absent. Pileus covering trichodermal with upright elements arising from a cutis of repent brown incrusted hyphae; upright terminal elements (50–)80–350 × 8.0–20 µm, in some collections in the smaller ranges, in others long and slender, cylindrical to narrowly fusiform, with parietal brown pigment, especially in lower half of the cells. Clamp connections absent.

Habitat and distribution — Growing solitarily or in small groups under *Callitropsis macrocarpa* and always close to the coast, in west facing groves and under trees planted as wind breaks etc., known from Pacific Grove and Point Lobos in Monterey Co., northward to San Francisco and the Berkeley Marina on the San Francisco Bay; occasionally in kitchen gardens and on compost heaps. December-March.

Collections Examined — U.S.A., **California,** Alameda Co., Berkeley, Berkeley Marina, 17 December 2002, leg. T.D. Bruns & P. Boynton (coll. E.C. Vellinga 2950); ibidem, 22 December 2002, E.C. Vellinga 2958; ibidem, 30 January 2003, E.C. Vellinga 3041 & 3042; ibidem, 28 February 2004, E.C. Vellinga 3204 (nrITS GQ258477); ibidem, 9 January 2005, E.C. Vellinga 3339; ibidem, 15 December 2006, E. C. Vellinga 3538 & 3539; Berkeley, Keeler Ave, 5 January 2009, E.C. Vellinga 3973 (nrITS GU136195). Monterey Co., Moss Landing, Castroville Moss Landing cemetery, 13 January 2002, E.C. Vellinga 2831 (nrITS AY243628), 2832 (nrITS AY243630) & 2833 (nrITS GU136194); Pacific Grove, Esplanade Park, 13 January 2002, E.C. Vellinga 2836 (nrITS GU136196) & 2841 (nrITS GU136193); unknown locality (at Fungus Fair of the Fungus Federation of Santa Cruz), 12 January 2002, E.C. Vellinga 2829 (nrITS GU139787) and 2830 (nrITS GU136192). San Francisco Co., San Francisco, Sunset Blv, D.E. Desjardin 5642 (USFS); San Francisco, Land's end, 12 January 2006, D. Bojantchev (nrITS GU136191). San Mateo Co., Moss Beach, Fitzgerald Marine Reserve, 11 January 2002, E.C. Vellinga 2827 (nrITS AY243631); ibidem, 28 January 2003, E.C. Vellinga 3038.

Comments — *Leucoagaricus cupresseus* has mainly been found in *Callitropsis macrocarpa* litter in coastal groves and under rows of trees planted as wind breaks. It has also been found in France, again under *C. macrocarpa,* on the Atlantic coast and in the Mediterranean area (Boisselet & Guinberteau 2001), but the one French specimen analyzed differed in nrITS sequence (Genbank accession number AY243627)from the Californian collections (Vellinga 2004b) (Fig. 1).

*Leucoagaricus cupresseus* is highly variable; a whole range of sizes was found in the basidiocarps growing in one row of planted cypresses (compare coll. ecv2832, and 2833; Fig. 7). The spores can vary from having a rounded apex

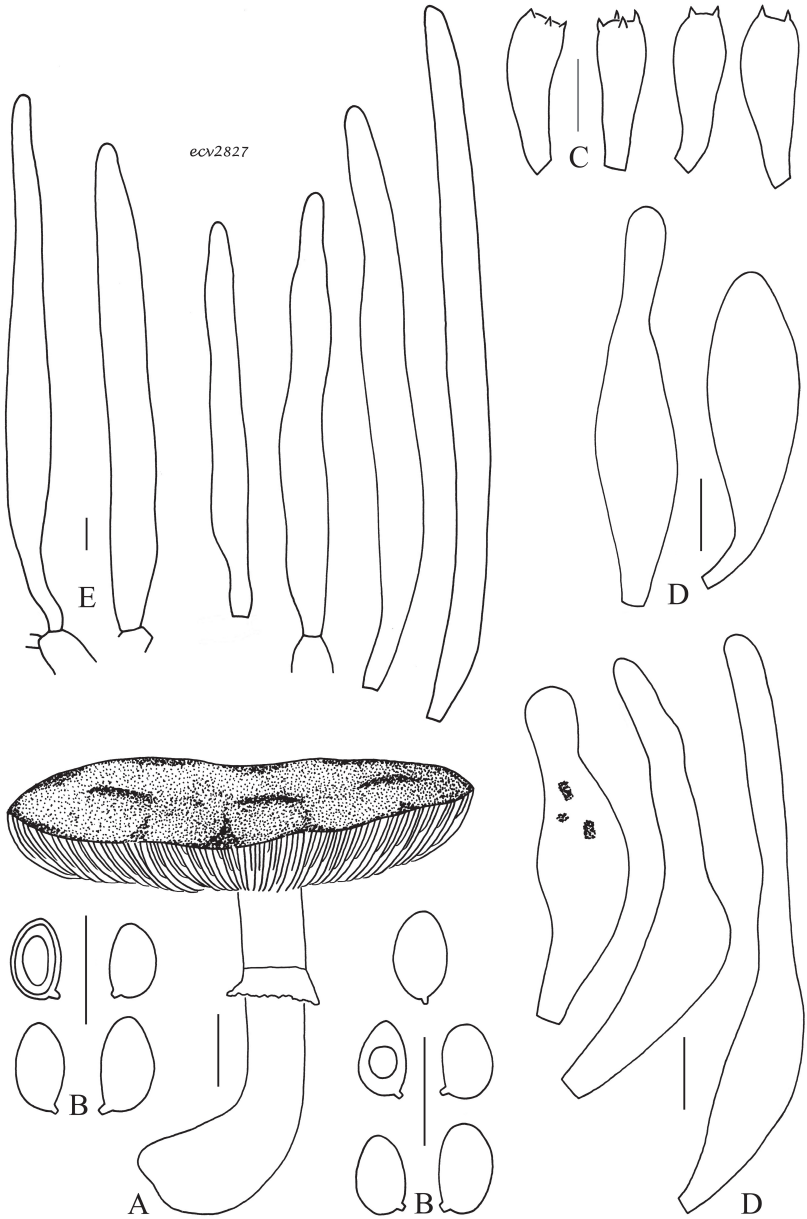


Fig. 6. *Leucoagaricus cupresseus* — A. Basidiocarp; B. spores; C. basidia; D. cheilocystidia; E. elements of pileus covering (all from ecv2827). Scale bar 10 mm (A); microscopic features 10 µm.

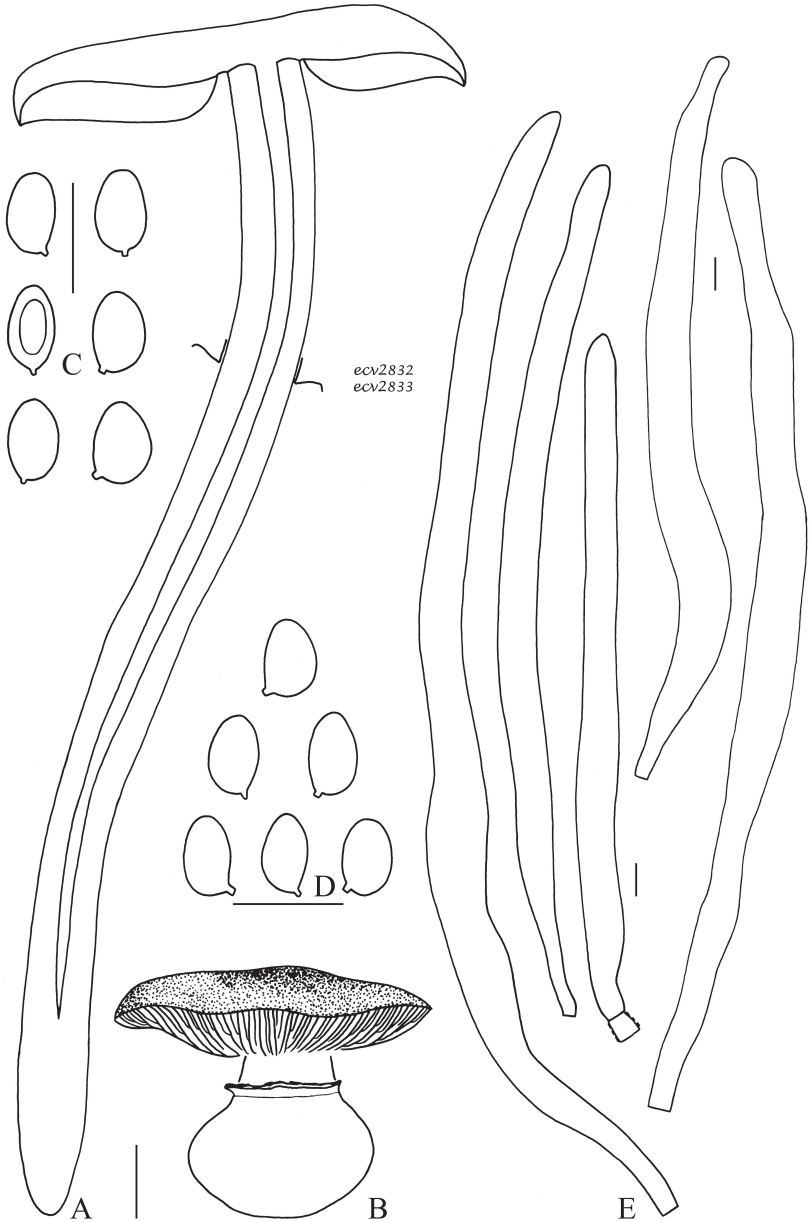


Fig. 7. *Leucoagaricus cupresseus* — Basidiocarps (A from collection ecv2833, B from ecv2832); spores (C from ecv2833, D from ecv2833); E, elements of pileus covering (from ecv2832) Scale bar 10 mm (A); microscopic features 10 µm.

to being amygdaliform and acuminate. Shape and size of the cheilocystidia are also very variable.

In the collections studied the cheilocystidia are predominantly utriform to lageniform, and clavate cystidia occur but are in the minority. Other authors (Sundberg 1976, Boisselet 2002) reported clavate cheilocystidia as the most common type.

*Leucoagaricus marginatus* (Burl.) Boisselet is very close to *La. cupresseus* and might actually represent a different variant. Burlingham (1945), who described both species in the same paper, did not compare the two directly; she only compared *L. marginata* with *L. rubrotinctoides* Murrill and *L. decorata*. *Leucoagaricus marginatus* differs from *La. cupresseus* in the pale reddish lilac pileus center (Burlingham 1945), and both are similar in stature and microscopical characters. Sundberg (1976), who studied the type collections of the two species, did not comment on their differences or taxonomic placement. Boisselet (2002) listed differences between two French species identified by him as *La. cupresseus* and *La. marginatus* respectively. The differences are gradual and some might be weather or age dependent, such as the differences in the ammonia reaction. The spores in the type collection of *La. cupresseus* are more amygdaliform than in *La. marginatus* and the elements of the pileus covering in *La. cupresseus* are more attenuated towards apex than in *La. marginatus* (Sundberg 1976).

*Leucoagaricus pseudopilatianus* Migl. et al. and its varieties *roseodiffractus* Migl. & Resta and *rugosoreticulatus* Migl. & Resta from southern Europe come very close and might well be identical to the French collections of *La. cupresseus* (Migliozzi et al. 2001, Migliozzi & Resta 2001). *Leucoagaricus pseudopilatianus* is a rather robust pale pink brownish species, with rounded (not attenuated), upright elements in the pileus covering, clavate cheilocystidia and amygdaliform spores with an indistinct apical papilla; the basidiocarps turn black on drying. This species was described at the same time that Boisselet & Guinberteau (2001) and Boisselet (2002) reported the French occurrences of *La. cupresseus* and *La. marginatus*.

The type collection of *Leucoagaricus cupresseus* was collected in the cypress groves of Point Lobos, south of Monterey, on the Pacific coast (Burlingham 1945). This is one of the two places in the world where *Callitropsis macrocarpa* occurs in native, not planted, groves (the other being just north of Point Lobos along the '17 Mile drive', also along the coast). *Callitropsis macrocarpa* has been planted in many parts of the world, but the occurrence of a species identical to or very closely related to *La. cupresseus* has only been confirmed for France (Boisselet & Guinberteau 2001, Boisselet 2002). Data on the mycoflora of cypress-dominated landscapes are lacking for other regions.

**3. *Leucoagaricus adelphicus*** Vellinga, **sp. nov.** FIGURES 8 & 9

MycoBank MB 515363

Leucoagarico pilatiano *similis, sed sine odore ligni cedri, etiam in nucleari spatii interne transcipti ("nrITS") ordine differt.*

**Holotypus** — "U.S.A., California, San Mateo County, San Francisco watershed, 8 Dec 2002, E.C. Vellinga 2584 (UC)." (nrITS AY243623).

Etymology: *adelphicus* is the Latinized form of the Greek word αδελφικος, brotherly or sisterly, because of the closeness to *La. pilatianus*.

Pileus 32–55 mm, plano-convex with or without broad low umbo to plano-concave with age, pale brown to brown, pinkish brown or orange-brown, (5 YR 5/3–4, 5 YR 4/3, 7.5 YR 7–6/4–6) to slightly darker at umbo than at rest of pileus, rather evenly coloured over pileus or with radiating streaks of colour on pale cream background, or much paler at margin (up to 5 YR 8/2–3), velvety tufty all over, and those tufts more crowded at centre than at margin; pileus surface when scratched slighty orange discolouring; margin conspicuously lighter than rest of pileus and fringed, exceeding lamellae. Lamellae moderately crowded to very crowded, 1(–3) lamellulae in between 2 lamellae, free and remote from

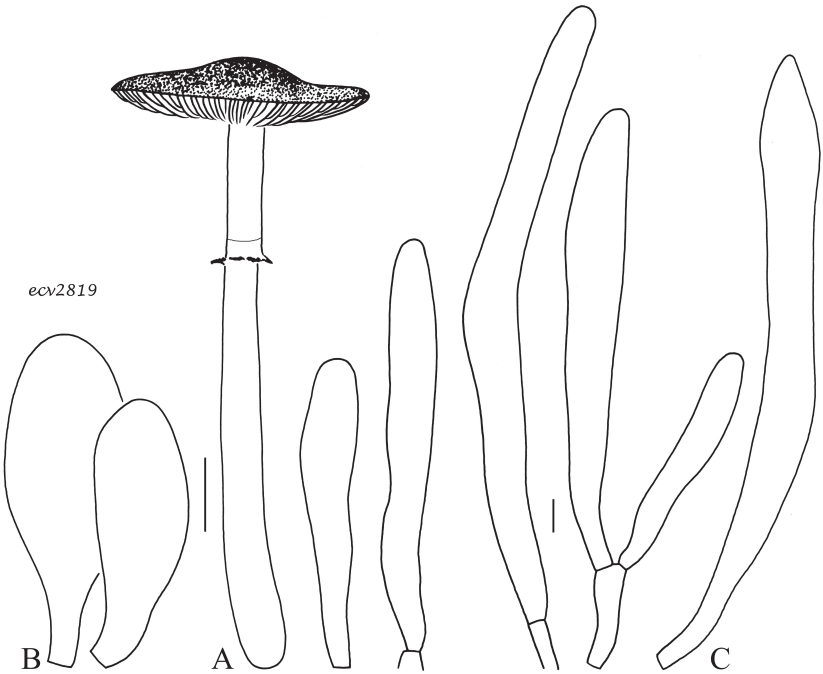


Fig. 8. *Leucoagaricus adelphicus* — A. Basidiocarp; B. cheilocystidia; C. pileus covering elements (all from ecv2819). Scale bar 10 mm (A); microscopic features 10 µm.

stipe, subventricose to ventricose up to 4 mm wide, white but slightly yellowish-pinkish, not changing colour on damaging, with white eroded cystidiose edge. Stipe 50–80 × 5–9 mm, cylindrical but in most specimens slightly widened at base, in upper part whitish with pinkish sheen, in lower half orange-brown from touching, white tomentose at base, hollow. Annulus an ascending or descending cuff with a small flaring part, white with dark rim. Context in pileus white and dull, rather thick, at centre orange-red from cutting, in stipe cortex white to pale brown and shiny. Smell none, fungoid to astringent.

Lamellae of dried specimens not discoloured, pale.

Basidiospores [75,5,5] in side view 5.9–7.6 × 3.4–4.4 µm, avl × avw = 6.2–6.6 × 3.9–4.0 µm, Q = 1.43–1.89, avQ = 1.58–1.66, ellipsoid to oblong with round apex and flattened abaxial side, in frontal view ellipsoid to oblong and symmetrical, thick-walled, smooth, without germ pore, with guttule, congophilous, dextrinoid, metachromatic in Chresyl blue. Basidia 17–28 × 6.5–13 µm, most 4-spored, a few 2-spored. Lamella edge sterile. Cheilocystidia 20–52 × 6.5–16 µm, clavate, broadly clavate, narrowly clavate, some narrowly utriform to cylindrical, with brown pigment and inclusions in ammonia. Pleurocystida absent. Pileus covering resembling a felted mat, trichodermal with upright elements, either solitary or in tufts, 77–317 × 9–20 µm, rarely not exceeding 200 µm in length, widest at 1/4 or 1/3 of length, and tapering towards apex, rarely blunt and relatively wide, with middle brown parietal pigment, but pale at tips. Clamp connections absent.

Habitat and distribution — Solitary or in small groups, terrestrial and saprotrophic, in plantations of *Callitropsis macrocarpa*, in woods of *Quercus agrifolia* Nee, in *Eucalyptus* plantings, or in mixed conifer-broadleaf forests of central coastal California, November to January.

Additional collections Examined — U.S.A., **California,** Alameda Co., Oakland, 15 November 2001, D. Viess & D. Rust (coll. E.C. Vellinga 2669) (nrITS AY243622); Contra Costa Co., Tilden Regional Park, 26 November 2000, E.C. Vellinga 2558 (nrITS AY243621); ibidem, 4 Dececmber 2001, E.C. Vellinga 2772 (nrITS AY243624); ibidem, 6 January 2002, E.C. Vellinga 2819 (nrITS AY243625). San Mateo Co., San Francisco Watershed, 5 December 2003, E.C. Vellinga 3153 (nrITS GQ258478); ibidem, 1 December 2006, E.C. Vellinga 3532A (nrITS GU136190).

Comments — *Leucoagaricus adelphicus* is morphologically and molecularly close to the European species *La. pilatianus* (Demoulin) Bon & Boiffard with which the following characters are shared: a warm brown, plushy-velvety-tomentose pileus surface, pale lamellae in dried specimens, basidiocarps not changing much colour on aging or when scratched; cheilocystidia clavate, and pileus covering made up of erect long, tapering elements. *Leucoagaricus adelphicus* lacks the typical cedar wood smell of *La. pilatianus,* and differs considerably in nrITS sequences from *La. pilatianus*.

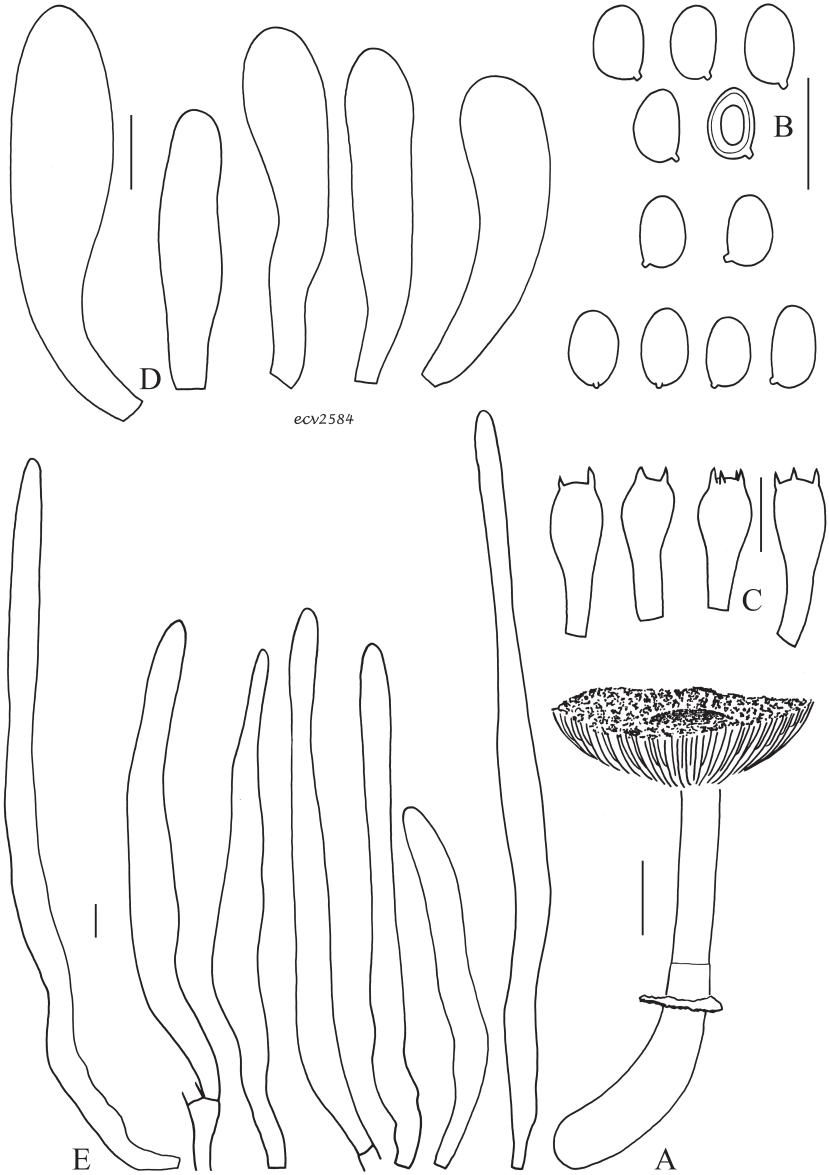


Fig. 9. *Leucoagaricus adelphicus* — A. Basidiocarp; B. spores; C. basidia; D. cheilocystidia; E. elements of pileus covering (all from holotype, collection ecv2584). Scale bar 10 mm (A); microscopic features 10 µm.

The name *Lepiota pulverapella* Zeller was at first considered for the taxon here described as *La. adelphicus*, but that species differs in the robust fruitbodies (also with warm brown colours), its habitat (in a field; Zeller 1933), and in the pileus covering structure and cheilocystidial shape (Sundberg 1995). Habitat, basidiocarp size, and structure of the pileus covering make this an enigmatic species. The context staining yellow when bruised (Zeller 1933) almost suggests a relationship with *La. americanus*, but that species has bigger spores with a germ pore. Zeller (1933) described the lamellae as 'drying a flesh color with darker rosy and vinaceous tinges,' characters absent from *La. adelphicus*. Unfortunately, Sundberg (1995) in his type study did not place the species in a phylogenetic or taxonomic framework or compare it to other described species.

Somewhat similar species are *La. hesperius* and *La. dyscritus*. The former differs in the lamellae that discolour on drying, while the latter shares the pale lamellae but differs in the structure of the pileus covering, which is made up of upright chains of relatively short elements. All three species can fruit at the same time in the Monterey cypress grove of the San Francisco watershed south of San Francisco.

*Leucoagaricus adelphicus* differs from *L. fuliginescens* in the absence of an apical excrescence on the cheilocystidia and the pale colours of the lamellae in dried basidiocarps.

The similar *Leucoagaricus aurantiovergens* A. Gennari & Migl. has longer spores (avQ = 2) and relatively wide elements of the pileus covering (Gennari & Migliozzi 1999). It stains immediately orange on the stipe when bruised. The cheilocystidia are clavate.

A third species from southern Europe, *Leucoagaricus pseudopilatianus*, resembles *La. cupresseus* much more than *La. adelphicus*. Migliozzi & Resta (2001), who published a key to the European species with clavate cheilocystidia, unfortunately did not include *La. cupresseus* and *La. marginatus* in their treatment and discussions.

**4. *Leucoagaricus hesperius*** Vellinga, **sp. nov.** FIGURE 10

MycoBank MB 515366

*Prope* Leucoagaricum adelphicum *et* La. pilatianum, *lamellis rubescentibus differt.*

**Holotypus** — "U.S.A., California, San Mateo County, San Francisco Watershed, 1 December 2006, E.C. Vellinga 3515 (UC)", (nrITS GU139788).

Etymology: *hesperius* is the Latinized form of the Greek word 'εσπεριος meaning 'evening-' and 'western'.

Pileus 30–53 mm, convex to plano-convex with slightly depressed centre, and sometimes with low umbo in centre, plano-concave or wavy with age, evenly pinkish-reddish brown (5–7.5 YR 6–5/4–6), or at centre more dark orange-brown (5 YR 4/6–5/6) and orange-brown around centre, plushy tufty-velutinous all

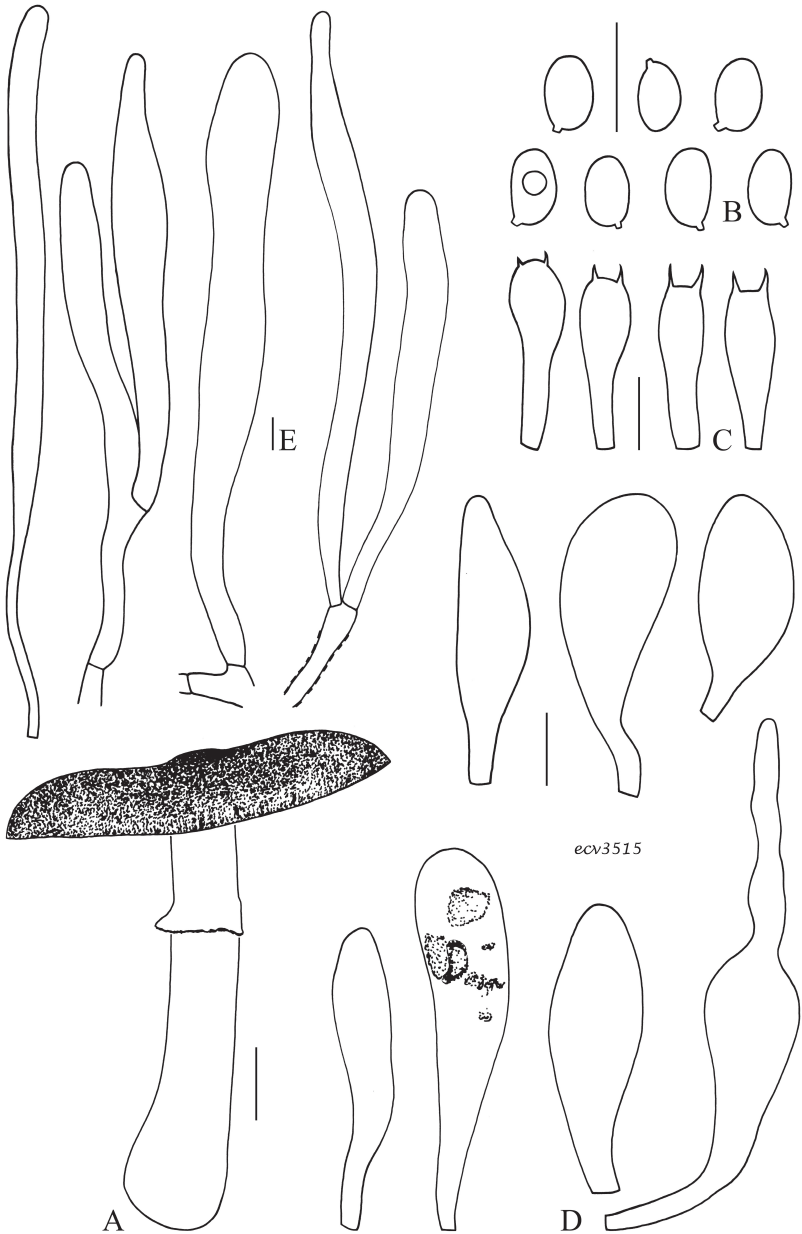


Fig. 10. *Leucoagaricus hesperius* — A. Basidiocarp; B. spores; C. basidia; D. cheilocystidia; E. elements of pileus covering (all from holotype, collection ecv3515). Scale bar 10 mm (A); microscopic features 10 µm.

over, though closed at centre, and on background of radially arranged covering, on a white background; margin cream and exceeding lamellae. Lamellae crowded to rather crowded, free and 1 mm remote from stipe, ventricose to segmentiform, 3–4.5 mm wide, whitish creamy, with age more orange coloured cream, with white cystidiose edge, turning red to almost black with pressure. Stipe 35–77 × 6–10 mm, slightly narrower at apex, widened at base to 14 mm, whitish at utmost apex, pale pinkish-brownish to brownish from handling and with age lower down, innately lengthwise fibrillose, and with fibrils blackening on stipe, hollow. Annulus a descending cuff with ragged upper tear and small flaring part, white with dark brown rim. Context dull, white and thick in pileus, white shiny in stipe. Smell rather indistinct, vaguely like the rubber smell of *L. cristata*.

Chemical tests – Ammonia 10% on pileus, annulus, and lamella edge green; no reaction on surface of lamellae.

Dried specimens with medium to dark pink lamellae.

Basidiospores [70,3,3] in side-view 5.9–8.0 × 3.5–4.7 µm, avl × avw = 6.2–7.1 × 3.8–4.2 µm, Q = 1.3–1.85, avQ = 1.48–1.69, ellipsoid to oblong, with rounded apex, with adaxial side almost straight, and abaxial side convex, in frontal view ellipsoid to oblong, uniguttulate, with smooth thick wall, without a germ pore, congophilous, dextrinoid, metachromatic in Cresyl blue. Basidia 21–28 × 6.5–9.0 µm, 4-spored. Lamella edge sterile. Cheilocystidia 31–73 × 8.5–16 µm, clavate, narrowly clavate, a few fusiform, some with long neck or excrescence (sizes included in measurements), with brown, evenly distributed intracellular pigment in ammonia and sometimes with dark irregular granular contents. Pleurocystidia absent. Pileus covering trichodermal with upright brown-walled elements, some articulated, but most upright elements single-celled; terminal elements 95–325 × 7.5–25 µm, with narrowed rounded apex; pigment brown to pale brown, parietal but also exuding in ammonia, and encrusting in connecting hyphae. Clamp connections absent.

Habitat and distribution — In small groups, terrestrial in cypress duff in east facing *Callitropsis macrocarpa* plantation, only known from one locality south of San Francisco. December.

Additional collections examined — U.S.A., **California,** San Mateo County, San Francisco Watershed, 13 December 2002, E.C. Vellinga 2939 (nrITS GU139789); ibidem, 2 December 2005, E.C. Vellinga 3429, 3430, 3431 (nrITS GU139790).

Comments — *Leucoagaricus hesperius* resembles *La. pilatianus* and *La. adelphicus* but reacts more strongly when damaged, especially on the lamellae.

*Leucoagaricus hesperius* shares the reactions of the lamellae on drying with *L. pulverapella*, which is differentiated by a pileus covering made up of short elements (Sundberg 1995).

5. ***Leucoagaricus dyscritus*** Vellinga, **sp. nov.** FIGURES 11 & 12

MycoBank MB 515365

Leucoagarico adelphico *similis lamellis dilutis non-tinctis, pilei tegumento partibus brevibus aggregatis differt.*

**Holotypus** — "U.S.A., California, San Mateo County, San Francisco Watershed, 5 December 2008, E.C. Vellinga 3956 (UC)", (nrITS GU136180).

Etymology: *dyscritus* is the Latinized form for the Greek δυσκριτος, which means 'difficult to distinguish'; it sounds confusingly similar to the word discrete.

Pileus 20–35 mm, convex with small umbo, velvety to tufty-velvety at centre, dark reddish brown (5 YR 3/4, 4–3/3), around centre with very small radially arranged pinkish brown to reddish brown, (5 YR 4–5/4-6) pyramidal tufts on white to whitish background, very pale at margin and slightly exceeding lamellae, with pressure at margin blackish discoloured. Lamellae crowded to very crowded, free and remote (up to 1 mm) from stipe, subventricose to segmentiform up to 3 mm wide, whitish with white cystidiose edge. Stipe 50–90 × 4–6(–8) mm, slender and cylindrical or laterally compressed, slightly wider at utmost base, white or whitish shiny, discolouring reddish orange

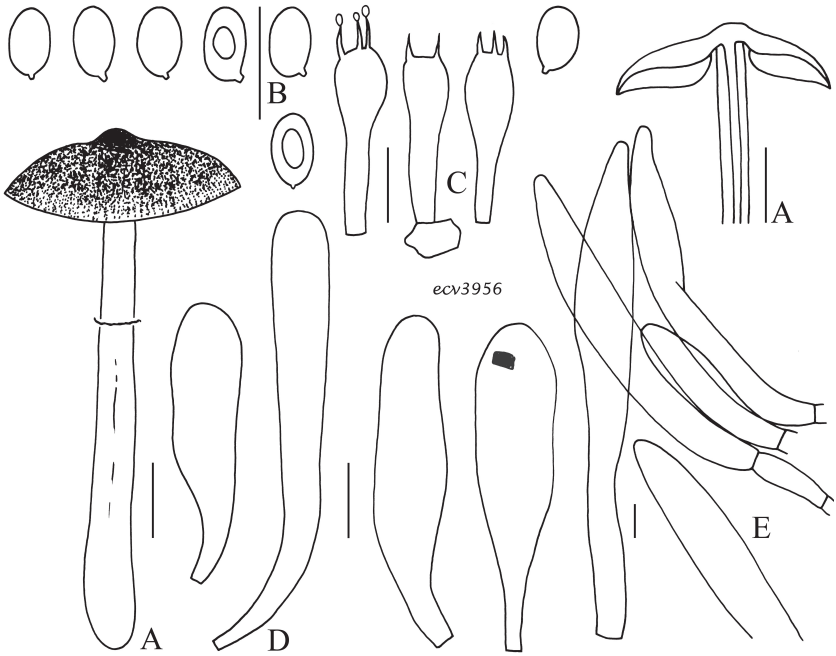


Fig. 11. *Leucoagaricus dyscritus* — A. Basidiocarp; B. spores; C. basidia; D. cheilocystidia; E. elements of pileus covering (all from holotype, collection ecv3956). Scale bar 10 mm (A); microscopic features 10 µm.

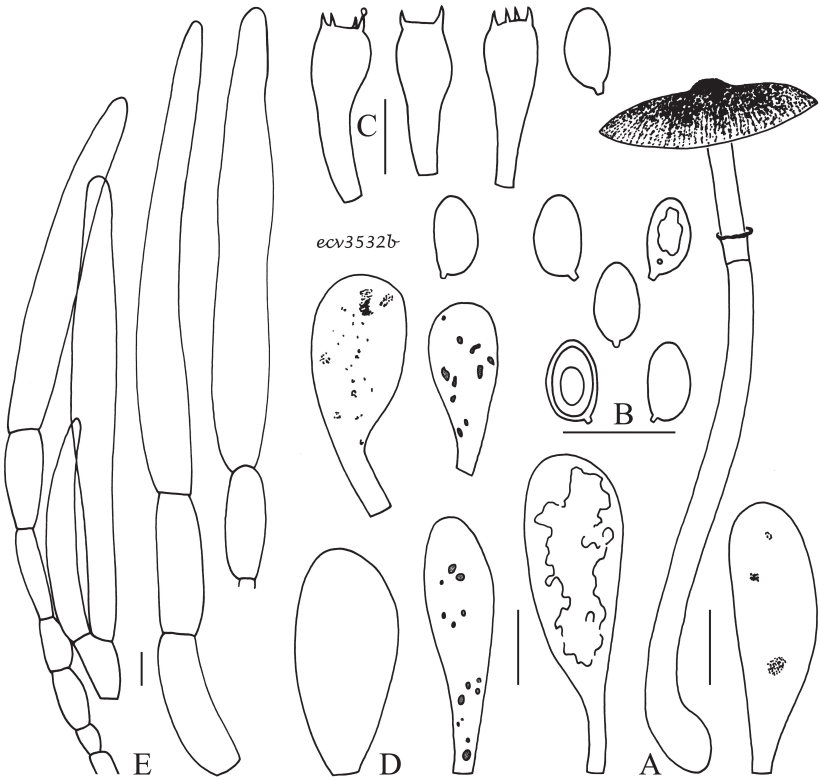


Fig. 12. *Leucoagaricus dyscritus* — A. Basidiocarp; B. spores; C. basidia; D. cheilocystidia; E. elements of pileus covering (all from ecv3532B). Scale bar 10 mm (A); microscopic features 10 µm.

where handled, with dark hairs in lower part, protruding into pileus, hollow. Annulus an ascending cuff and a small flaring part, or just only a funnel-shaped flaring part, white with contrasting very dark to black rim. Context dull and white, quite thick, in pileus, white shiny in stipe. Smell cacao-like fungoid and slightly astringent.

Dried specimens with light lamellae, without any trace of pink.

Basidiospores [80,5,5] in side view 5.1–8.0 × 3.4–4.7 µm, avl × avw = 5.8–7.2 × 3.7–4.1 µm, Q = 1.45–2.05, avQ = 1.56–1.82, ellipsoid to oblong, with rounded apex, in some specimens amygdaliform, in frontal view ellipsoid to oblong, thick-walled, smooth, without germ pore, uniguttulate, congophilous, dextrinoid, metachromatic in Cresyl blue. Basidia 20–25 × 6.5–10.0 µm, 4-spored. Lamella edge sterile. Cheilocystidia 18-55 × 5.5–15 µm, clavate, narrowly clavate to almost cylindrical, fusiform, irregularly lageniform with

rather short neck (up to 14 × 6.0 µm), with dark (not brown, but grey-greenish) granules in ammonia. Pleurocystidia absent. Pileus covering trichodermal with tufts or bundles of upright hyphae, made up of up to 5 elements in a row, with the terminal elements by far the biggest, and most differentiated; terminal elements 40–170 × 10–22 µm, tapering towards apex, with brown intracellular and parietal pigment; pigment exuding in ammonia; pigment parietal and sometimes incrusting in the penultimate elements. Clamp connections absent.

Habitat and distribution – Solitary or in small groups, terrestrial, in duff of *Callitropsis macrocarpa* planting on east-facing slope, November and December. So far, known from the San Francisco Watershed, south of San Francisco.

Additional collections examined — U.S.A., **California,** San Mateo Co., San Francisco Watershed, 10 December 1999, E.C. Vellinga 2389; 5 December 2003, E.C. Vellinga 3152 and 3155; ibidem, 6 December 2005, E.C. Vellinga 3428; ibidem, 1 December 2006, E.C. Vellinga 3532B (nrITS GU136181).

Comments — *Leucoagaricus dyscritus* is characterized by non-staining lamellae and a pileus covering comprising squamules and tufts made up of short elements. In his type study, Sundberg (1995) noted that *L. pulverapella* has a similar pileus covering but differs in the much more robust basidiocarp (7-12 cm across), the pink discolouring lamellae, and its original habitat (Zeller 1933).

Similar species with an equally tomentose-velvety pileus covering that co-inhabit the same Monterey cypress grove south of San Francisco are *La. adelphicus*, with long elements in the pileus covering and non-staining lamellae, and *La. hesperius,* with discolouring lamellae and again a trichoderm made up of long elements. *Leucoagaricus* sp. (collection ecv2484) is much paler in general and has a more squamose pileus covering.

**6. *Leucoagaricus erythrophaeus*** Vellinga in Vellinga et al., Mycologia 102: 450. 2010 (in press; doi:10.3852/09-164).

Misapplied name — *Lepiota roseifolia* sensu Arora (1986: 305); sensu Sundberg (1967: 115–119).

Selected description — Vellinga et al., Mycologia 102: 450–451. 2010.

Pileus 18–60 mm, when young hemispherical with inflexed margin, expanding via convex or widely conical to finally wavy plano-convex to slightly plano-concave, at centre with closed covering, velvety-plushy grey, dark purplish-reddish, to dark brown-black, around centre breaking open into concentrically arranged small fibrillose grayish brownish to dark brown-black squamules, often in bands, on white background, when touched immediately red-orange, changing to dark brown; margin irregular in young specimens, later evening out, exceeding lamellae. Lamellae free, and remote from stipe often attached

to a kind of collarium, moderately crowded to crowded, ventricose, yellowish white, with white cystidiose edge, orange when touched, at least on edge, and edge darkening after being touched. Stipe 55–70 × 4–5 mm, cylindrical in upper 2/3 and widening toward up to 15 mm wide base, pale at apex and in untouched specimens pale over complete length, when touched first orange-red, changing to blackish and dark, cystidiose or hairy-cobwebby over whole length, protruding into pileus, hollow. Annulus an ascending or descending small, white cuff, with a flaring part with fringed edge, turning dark on edge with age and touching. Context white to whitish in pileus, orange where cut but soon vanishing, pale cream-coloured to yellowish in stipe, and orange where cut. Smell indistinct, astringent or lepiotoid. Taste not known.

Dried specimens with pink lamellae.

Basidiospores [228,13,10] in side view 5.9–8.8 × 3.5–4.9 µm, avl × avw = 6.2–7.4 × 3.8–4.2 µm, Q = 1.4–2.05, avQ = 1.61–1.78, ellipsoid to amygdaliform-ellipsoid, some oblong and subamygdaliform, in frontal view ellipsoid, relatively thick-walled, often uniguttulate, without germ pore, congophilous, dextrinoid, metachromatic in Cresyl Blue. Basidia 15–29 × 6.5–9.0 µm, narrowly clavate, with 4 sterigmata. Lamella edge sterile, with a continuous broad band or tufts of cheilocystidia with brown contents. Cheilocystidia 30–75 × 8.0–14.0 µm, narrowly clavate, narrowly utriform, to irregularly cylindrical and narrowed into an often long pedicel, some bifid, with brownish contents and some dark granules in ammonia; in fresh material with green-grey contents in ammonia. Pleurocystidia absent. Pileus covering a trichoderm, towards margin more cutis-like with differentiated terminal elements; terminal elements 96–350 × 9.0–20 µm, most often tapering towards apex, sometimes with blunt and rounded apex, in some specimens with many shorter elements, in others, only with those long elements; elements brown-walled at least in lower part, sometimes also with granulose or diffuse brown contents; repent connecting hyphae with dark granulose contents, sometimes also with parietal and incrusting pigments. Clamp connections absent from all tissues.

Habitat and distribution — In small groups, terrestrial, in different forests, e.g. in northern California mixed *Picea sitchensis* (Bong.) Carrière and *Tsuga heterophylla* Sarg. forests, or *Alnus rubra* Bong. and *Sequoia sempervirens* and in central coastal California *Pseudotsuga menziesii* (Mirb.) Franco with *Sequoia sempervirens* and various other tree species, throughout coastal California from Mendocino Co. northwards. Also reported from lower elevations of the western slope of the central Sierra Nevada, but actual distribution poorly known. End of October through beginning of December.

Collections examined – U.S.A., **California,** Humboldt Co., Arcata, Community Forest, 9 November 2004, E.C. Vellinga 3243 (nrITS GQ258469; Holotype, UC); Patrick's Point SP, 23 October 2003, E.C. Vellinga 3081, 3082 (nrITS GQ258471) and

3083; ibidem, 9 November 2004, E.C. Vellinga 3248 (nrITS GQ258470) and 3254 (nrITS GQ203805); Orrick, along Davison Road, 27 October 2007, N. Nguyen NN02 (nrITS GQ258468); ibidem, 7 November 2009, E.C. Vellinga 4108; Marin Co., near Alpine Lake, 15 November 2005, E.C. Vellinga 3376 (nrITS GQ258472) and 3379 (nrITS GU136177); Point Reyes NP, 31 October 2009, S.P. Schechter (coll. E.C. Vellinga 4094); Mendocino Co., Jackson State Demonstration Forest, 17 November 2001, E.C. Vellinga 2691 (nrITS AY243644); Van Damme SP, 18 November 2001, E.C. Vellinga 2682 (nrITS GU136179); San Mateo Co., San Mateo County Memorial Park, 4 November 2004, E.C. Vellinga 3217; Yuba Co., Tahoe NF, Hornswoggle Campground near Bullards Bar, 9 November 2005, E.C. Vellinga 3358; south of Challenge, along Oregon Hill Road, 10 November 2005, E.C. Vellinga 3362 (nrITS GU136178).

Comments — *Leucoagaricus erythrophaeus* is better known as *Lepiota roseifolia*, but the type study (Vellinga et al. 2010) revealed that *L. roseifolia* is characterized by cheilocystidia with an apical excrescence and relatively broad and short elements on the pileus covering; the dried collection also lacked dark lamellae — all characters that do not fit the modern interpretation of that name.

*Leucoagaricus erythrophaeus* differs from *L. flammeotincta* and allies in the staining lamellae, the pseudocollarium to which the lamellae are attached, and in particular in the structure of the pileus covering that is composed of long often erect (trichodermal) elements. In *L. flammeotincta* s.l., the pileus covering is a cutis composed of strands of repent coloured hyphae. *Leucoagaricus pardalotus* shares the trichodermal pileus covering, is smaller, and has a distinct dark and white pattern on the pileus.

*Lepiota roseifolia* was reported from the Great Smoky Mountains National Park (Smith & Hesler 1938), but microscopical data were lacking, and it might well represent a different species in section *Piloselli*.

*Leucoagaricus decipiens* Contu, Vizzini & Vellinga is the Europan counterpart of *La. erythrophaeus* (Vellinga et al. 2010).

**7. *Leucoagaricus pardalotus*** Vellinga, **sp. nov.** Figure 13

MycoBank MB 515364

Lepiotae flammeotinctae *similis, pilei trichodermalis tegumento, cheilocystidiis cylindricoclavatis, colore minus intense rubescenti differt.*

**Holotypus** — "U.S.A., California, Mendocino Co., Van Damme SP, Fern Creek Canyon, 21 November 2004, E.C. Vellinga 3313," (nrITS GQ258479).

Etymology: *pardalotus* is the latinized form of 'παρδαλωτος', spotted as a leopard, because of the black plushy patches and squamules on the pileus.

Pileus 30–60 mm, convex with faint umbo, plano-convex to plano-concave with umbo, with plushy-velvety deep dark red-brown (5 YR 2.5/2, 7.5 YR 3/2) calotte, around umbo with small, dark brown v-shaped fibrillose squamules, radially arranged, often in streaks, on whitish background; outer 3 mm marginal zone sulcate and white; surface changing to faintly orange when scratched.

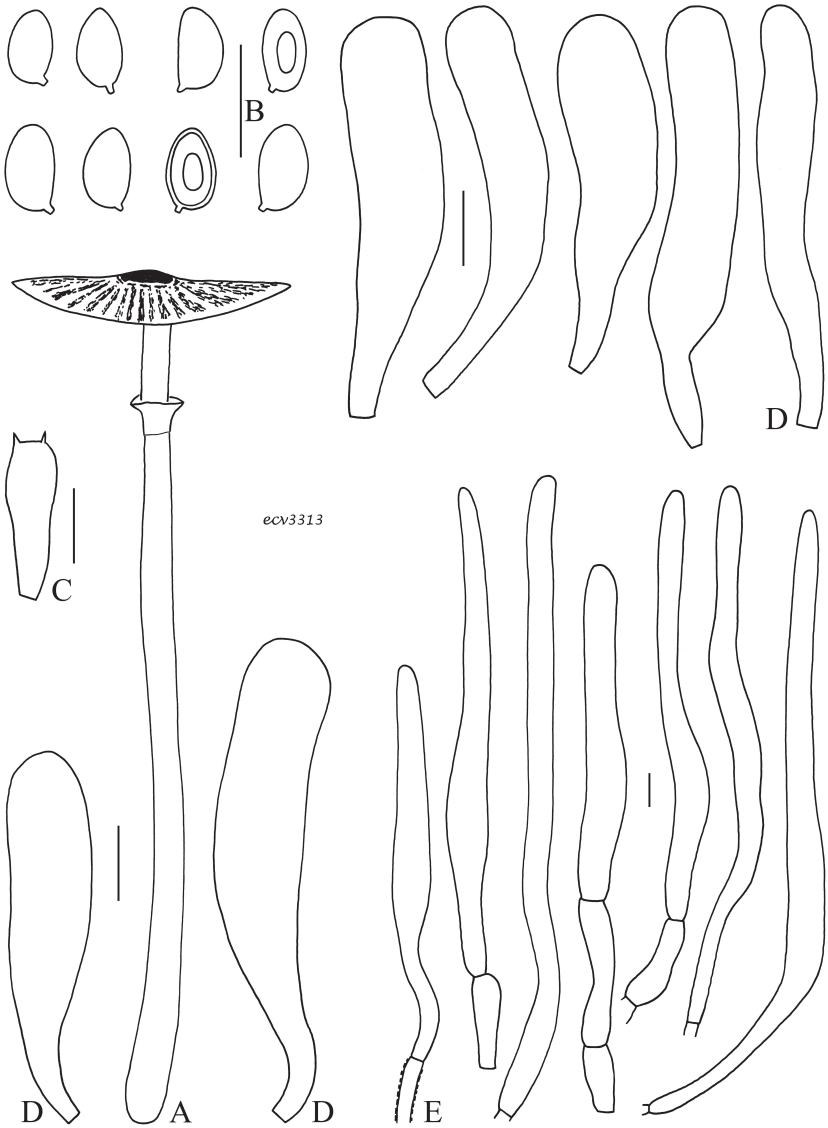


Fig. 13. *Leuocagaricus pardalotus* — A. Basidiocarp; B. spores; C. basidium; D. cheilocystidia; E. pileus covering elements (all from holotype, collection ecv3313). Scale bar 10 mm (A); microscopic features 10 µm.

Lamellae moderately crowded to rather distant, free and remote from stipe, attached to a rudimentary collarium, ventricose or subventricose, cream-greyish, when cut yellow to yellow-orange, with white, distinctly cystidiose-eroded edge, where touched dark brown. Stipe 80–110 × 3–7 mm, gradually widening towards 6-9 mm wide base, pale at apex, shiny but also with cystidia, below annulus brownish, orange to orange-red when touched and turning and staying dark brown, but pale fibrils mitigating the effect, hollow. Annulus made up of an ascending pale cuff and a flaring part, dark brown on under side, white on upper side. Context white to pale creamy in pileus, slightly orange where cut, especially below calotte, pale brown glass-like in stipe. Smell like the rubber component of the smell of *L. cristata*.

Dried specimens with coloured (pinkish) lamellae, and a dark stipe.

Basidiospores [34,2,2] in side view 6.6–8.8 × 3.9–4.7 µm, avl × avw = 7.4–7.5 × 4.3 µm, Q = 1.44–1.92(–2.14), avQ = 1.71–1.74, ellipsoid to oblong, most with straight adaxial side, some amygdaliform, in frontal view ellipsoid to oblong, uni-guttulate, without germ pore, thick-walled, congophilous, dextrinoid, metachromatic in Cresyl Blue. Basidia 18–23 × 7.0–8.5 µm, 4-spored. Lamella edge with tufts of cheilocystidia. Cheilocystidia 26–65 × 8.0–12 µm, narrowly clavate, subutriform, cylindrical and attenuated towards pedicel, often a bit irregular, with brown granular contents in ammonia, but many without contents. Pleurocystida absent. Pileus covering with tufty squamules made up of erect elements, 110–325 × 7.5–12.5 µm, with rounded tips, not attenuated towards apex, with dark brown granular contents and with thickened brown walls; basal connecting hyphae with dark incrusting pigment; hyphae of pileitrama with some dark granules in ammonia. Clamp connections absent.

Habitat and distribution — In small groups, terrestrial and saprotrophic, in damp places in mixed conifer forests on the north Californian coast, November. So far only found in Mendocino County.

Additional collection examined — U.S.A., **California**, Mendocino Co., Jug Handle SR, 19 November 2007, E.C. Vellinga 3727 (nrITS GU136202).

Comments — *Leucoagaricus pardalotus* may be taken for *L. flammeotincta* in the field, but the dense velvety plush calotte and scales and absence of the intense red discolouration on touching, distinguish it. It is one of the most beautiful species in the group. Microscopically the narrowly clavate cheilocystidia and the pileus covering made up of dense patches of upright dark brown elements set it apart from the other species.

The new species looks a bit similar to *Lepiota felina* (Pers.) P. Karst., but the absence of clamp connections, the reddening reactions, the shape of the ring, spores and cystidia all diagnose *La. pardalotus*.

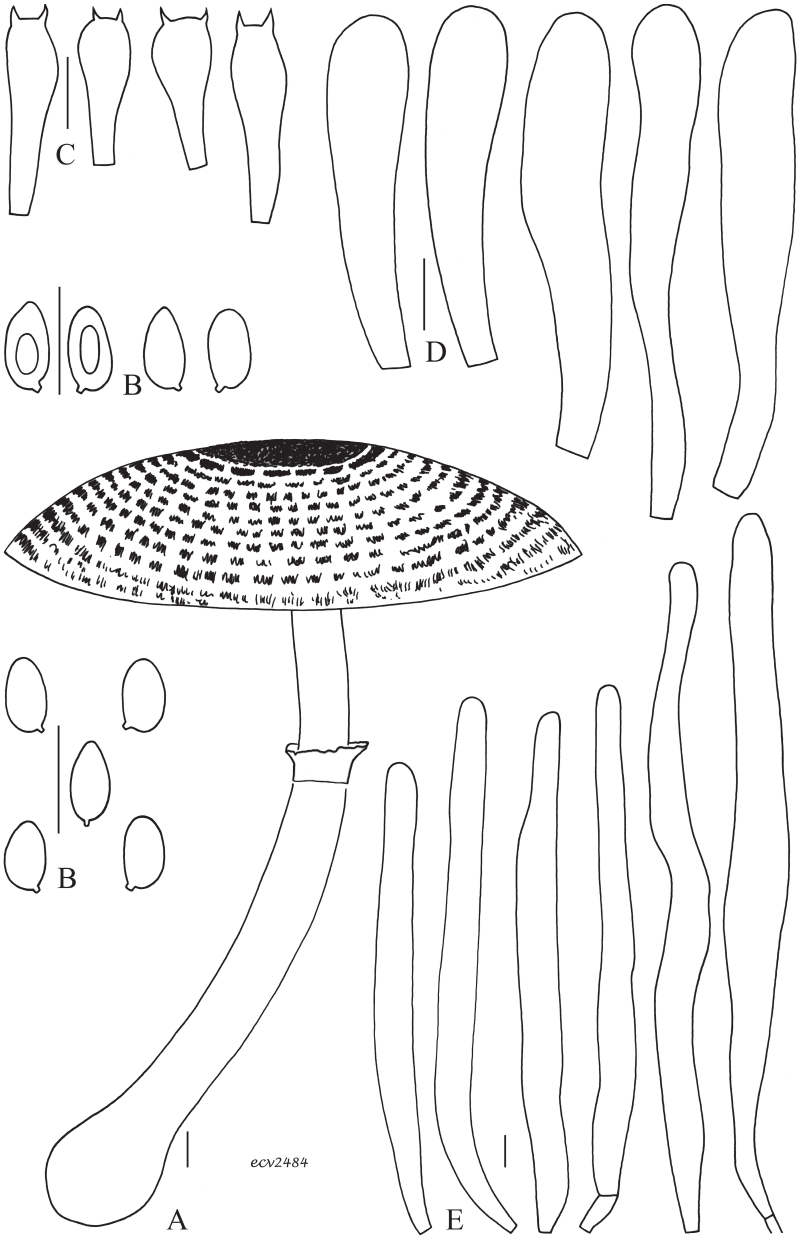


Fig. 14. *Leuocagaricus* sp. (collection ecv2484) — A. Basidiocarp; B. spores; C. basidia; D. cheilocystidia; E. elements of pileus covering.
Scale bar 10 mm (A); microscopic features 10 µm.

**8. *Leucoagaricus*** sp. (collection ecv2484) FIGURE 14

PILEUS 70 mm, plano-convex, dark red-brown (5 YR 3/3) at centre and there closed and plush-like, around centre gradually outwards breaking up into red-brown (5 YR 4/3–5/3) short-fibrillose patches on white background; margin exceeding lamellae. LAMELLAE, L = around 80, l = 1, crowded, free and close to stipe, not ventricose, white, with white-fimbriate edge discolouring dark when touched. STIPE 90 × 8 mm, cylindrical but widened at bulbous, 15 mm wide base, whitish when untouched and staying so above annulus, in lower part with dark brown short fibrils on yellow-brownish background. ANNULUS an ascending cuff with short flaring part with dark purple-brown rim. CONTEXT white, unchanging, thick in pileus, whitish in stipe. SMELL unpleasant, fungoid.

CHEMICAL TESTS — Ammonia 10% or KOH 3% on lamella edge green, remaining basidocarp non-reactive.

DRIED SPECIMEN not discoloured, pale.

BASIDIOSPORES [15,1,1] in side-view 6.0–7.9 × 3.5–4.0 µm, avl × avw = 6.8 × 3.9 µm, Q = 1.61–2.0, avQ = 1.77, oblong to subcylindrical-amygdaliform, with rounded or more pointed apex, in frontal view ovoid with pointed or rounded apex, uniguttulate, congophilous, dextrinoid, metachromatic in Cresyl blue. BASIDIA 21–27 × 6.5–8.5 µm, 4- spored, some, close to lamella edge, thick-walled. LAMELLA EDGE sterile. CHEILOCYSTIDIA 49–75 × 8–11 µm, narrowly clavate, rarely subutriform, without apical excrescence, green in ammonia. PLEUROCYSTIDIA absent. PILEUS COVERING trichodermal, with erect dark brown, cylindrical elements, 125–240 × 11–20 µm, with rounded apex, with parietal pigment; lower, connecting hyphae with incrusting brown pigment. CLAMP CONNECTIONS absent.

HABITAT AND DISTRIBUTION — Solitary, terrestrial in duff, under *Quercus agrifolia,* in central coastal California, November. Found once in the San Francisco Bay area.

COLLECTION EXAMINED — U.S.A., **California**, Contra Costa Co., Tilden Regional Park, 16 November 2000, E.C. Vellinga 2484 (nrITS GU136182).

COMMENTS — This large conspicuous taxon was only found once. It differs from the other species in the pale colours and absence of strong reddening reactions.

**9. *Lepiota flammeotincta*** Kauffman, Papers Mich. Acad. Sci., Arts Letters 4: 331. 1924 (as '*Lepiota flammeatincta*'). FIGURES 15–18

SELECTED DESCRIPTION — Kauffman (1924: 331–332).

TYPE STUDY — Smith (1966: 103–105).

MICROSCOPICAL CHARACTERS (FROM VELLINGA TYPE STUDY; FIGURE 15) — BASIDIOSPORES [21,1,1] in side-view 7.4–9.3 × 4.4–5.0 µm, avl × avw = 7.9 × 4.7 µm, Q = 1.58–1.91, avQ = 1.7, oblong, some subamygdaliform, in frontal

view oblong and not amygdaliform, thick-walled, with central guttule, without germ pore, congophilous, swelling in ammonia and Congo Red, dextrinoid, metachromatic in Cresyl Blue. Basidia 21–30 × 8.0–10 µm, 4-spored. Lamella edge sterile. Cheilocystidia 30–45 × 5.0–9.0 µm, cylindrical, very narrowly clavate, a few wavy, not coloured. Pleurocystidia absent. Pileus covering made up of adnate hyphae, with parietal brown-grey pigment in ammonia, with extracellular red granules, and some elements filled with very dark pigments in clumps; hyphae unified in squamose fibrils; terminal elements cylindrical with rounded apex, 36–119 × 6.5–9.5 µm. Clamp connections not observed.

Description of modern material (Figs 16–18) — Pileus (7–)14–45 mm, convex, plano-convex to applanate with small and low umbo, at centre pale grey brown at first, turning to dark brown (7.5 YR 3/2), almost black felted-tomentose, around centre with radially arranged fibrillose v-shaped squamules, starting out very pale, but changing to dark brown with age, on white to pale background which immediately and vividly discolours orange-red on touching, after some time completely dark brown. Lamellae, L = 35–50, l = (0–)1–3, moderately distant to moderately crowded, free and close to stipe, rounded off near stipe, (sub)ventricose, up to 6 mm wide, white to cream with pinkish

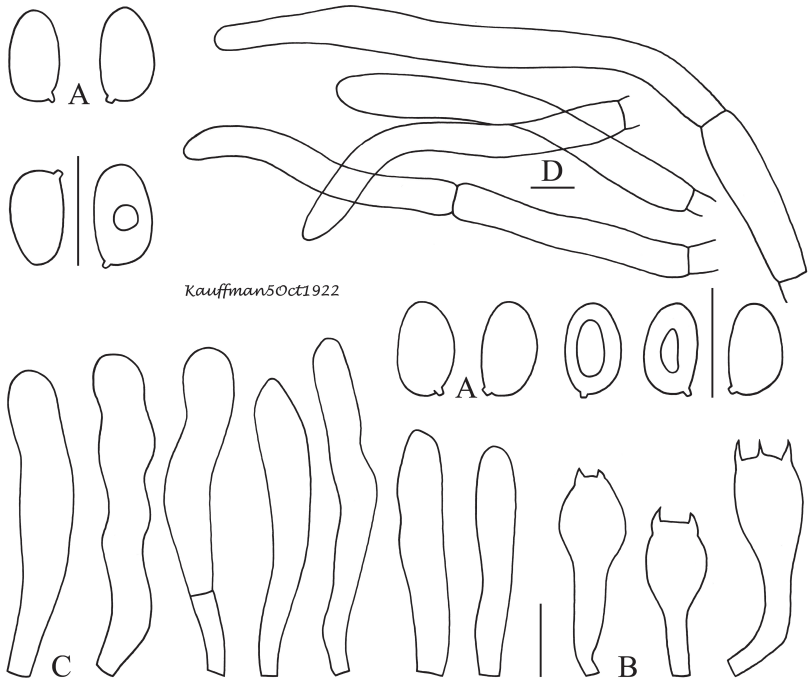


Fig. 15. *Lepiota flammeotincta* — A. spores; B. basidia; C. cheilocystidia; D. pileus covering elements (all from holotype collection). Scale bars 10 µm.

sheen, not changing colours when cut or touched; lamella edge white cystidiose, with some very fine colourless drops when young, dark where touched. Stipe 40–80 × 2.5–4 mm, cylindrical, gradually widening towards 4–7 mm wide base, white at first, but instantly intensely red staining when touched, changing to dark brown fibrillose where touched, lengthwise short-fibrillose hollow, with some white rhizomorphs. Annulus often absent in mature specimens, flimsy, not with a distinct cuff and flaring part, dark on outside, and with a dark rim, white on the inside. Context whitish in pileus, dull rather thick, immediately orange-red when cut; in stipe white at first, shiny, with age pale brownish to glassy yellowish. Smell rubber-like to astringent lepiotoid and unpleasant, sometimes with fruity component.

Chemical tests — KOH 3% on lamellae reddish, on pileus red, on stipe hard to see reaction.

Dried specimens with dark pileus and stipe, but lamellae pale and strongly contrasting with the rest of the basidiocarps.

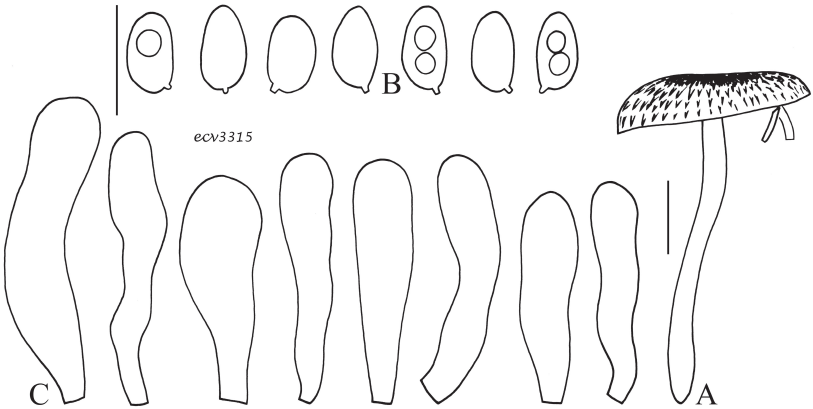


Fig. 16. *Lepiota flammeotincta* — A. basidiocarp; B. spores; C. cheilocystidia (from collection ecv3315). Scale bar 10 mm (A); microscopic features 10 µm.

Basidiospores [146,8,8] in side view 5.9–9.0 × 3.4–5.6 µm, avl × avw = 6.5–7.5 × 3.9–4.5 µm, Q = 1.5–2.1, avQ = 1.65–1.85, (the longer values for collections with a relatively high number of 2-spored basidia), oblong to almost cylindrical, with straight abaxial side, and convex adaxial side, some subamygdaliform, in frontal view oblong to almost cylindrical, thick-walled, smooth, without germ pore, and often uniguttulate, congophilous, dextrinoid, metachromatic in Cresyl blue, with walls swelling in ammonia. Basidia 16.5–32 × 6.5–9.0 µm, 4-spored, but in some collections with a relatively high number with 2 sterigmata. Lamella edge sterile. Cheilocystidia 25–70 × 4.5–12.0(–13.0) µm, cylindrical, cylindrical-wavy (at least a few), more rarely narrowly clavate to narrowly utriform, with some dark brown granules or very pale brown in

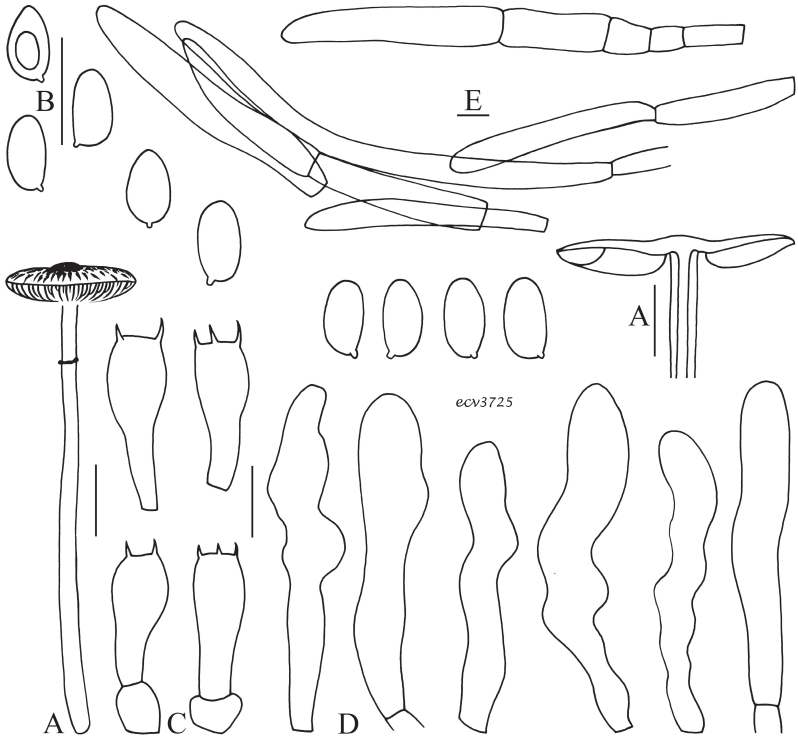


Fig. 17. *Lepiota flammeotincta* — A. Basidiocarp; B. spores; C. basidia; D. cheilocystidia; E. elements of pileus covering (all from collection ecv3725). Scale bar 10 mm (A); microscopic features 10 µm.

ammonia. Pleurocystidia absent. Pileus covering cutis-like with bundles of repent to ascending hyphae, made up of brown-walled, sometimes incrusted cells, also with dark granules and blobs and intracellular brown pigment (in ammonia); extracellular pigment blobs present; terminal elements, 55–180 × 5–16 µm, cylindrical to slightly inflated, not or differentiated with rounded or acuminate tips. Clamp connections not observed.

Habitat and distribution – Solitary or gregarious in small groups, terrestrial and saprotrophic in litter, in different types of coniferous forests, e.g. in coastal pine forests, in coastal mixed forests and in the Sierra foothills, widespread and common, October through December. Also known from Oregon and Washington.

Collections examined – U.S.A., **California,** Humboldt Co., Patrick's Point State Park, 9 November 2004, E.C. Vellinga 3250 (nrITS GU136168); near Orrick, along Davison Road, 10 November 2004, E.C. Vellinga 3266; ibidem, 27 October 2007, N.H. Nguyen 003 (nrITS GU136169); ibidem, 7 November 2009, E.C. Vellinga 4101; Marin Co., Tomales Bay State Park, 28 November 2001, E.C. Vellinga 2746 (nrITS AY176440)

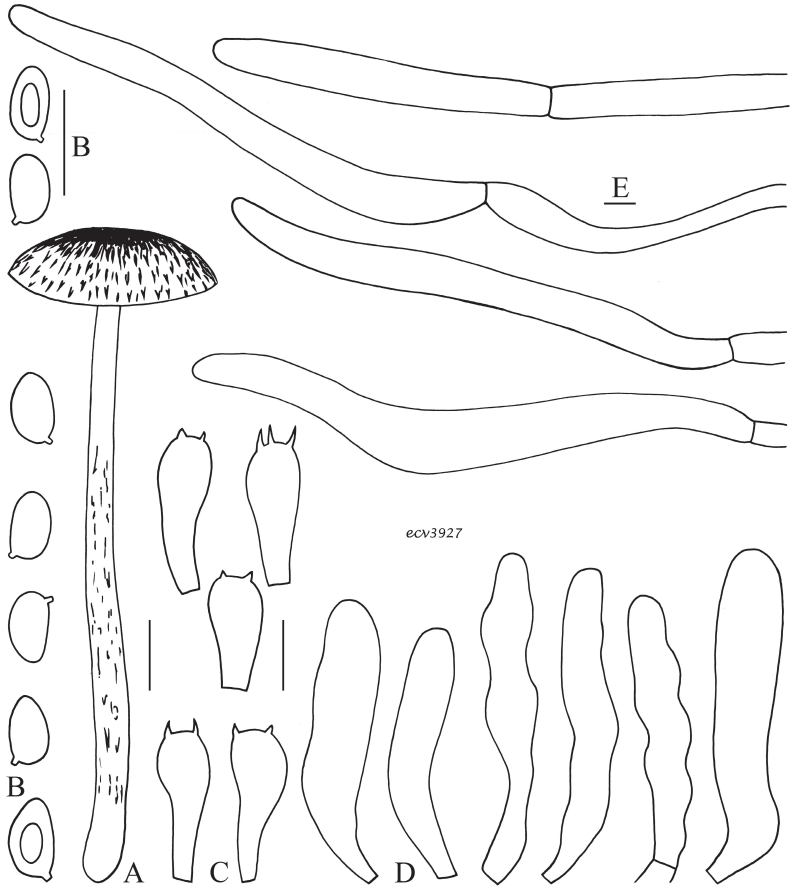


Fig. 18. *Lepiota flammeotincta* — A. Basidiocarp; B. spores; C. basidia; D. cheilocystidia; E. elements of pileus covering (all from ecv3927). Scale bar 10 mm (A); microscopic features 10 µm.

and 2757; ibidem, near Hearts Desire Beach, 22 November 2008, E.C. Vellinga 3927 (nrITS GU136163); Point Reyes NP, 6 October 2001, E.C. Vellinga 2644; Point Reyes NP along Sky Trail, 31 October 2009, S.P. Schechter (coll. E.C. Vellinga 4093); Mendocino Co., Jackson State Demonstration Forest, 18 November 2000, E.C. Vellinga 2533 (nrITS AY176441); ibidem, 17 November 2001, E.C. Vellinga 2704 and 2717; ibidem, 23 November 2002, E.C. Vellinga 2911, 2912 and 2913; ibidem, 20 November 2004, E.C. Vellinga 3295 (nrITS GU136166); Jughandle State Reserve, 19 November 2007, E.C. Vellinga 3725 (nrITS GU136170); Van Damme SP, 19 November 2000, E.C. Vellinga 2529. Nevada Co., San Juan Ridge, near North Columbia Schoolhouse on Tyler Foote Rd, 13 December 2003, E.C. Vellinga 3174; San Mateo Co., San Mateo County Memorial Park, 5 December 2008, F. Stevens et al. (coll. E.C. Vellinga 3967) (nrITS GU136167). Sonoma Co., Salt Point State Park, 22 November 2004, E.C. Vellinga 3315 (nrITS GU136165). Yuba Co., Challenge, along Oregon Rd, 10 November 2005, E.C. Vellinga

3359 (nrITS GU136171) and 3361 (nrITS GU136164). **Oregon,** Clackamas County, Mt Hood near Welches, 5 October 1922, C.H. Kauffman (Holotype, MICH).

Comments — What was thought to represent just one species, *L. flammeotincta,* turned out to be a complex, with two common taxa, *L. flammeotincta*, and *La. flammeotinctoides* (described below), two rarely observed species, and one putative taxon based on a single collection.

The distinction between the two common and most intensely reddening species is microscopical, based on the shape of the cheilocystidia: cylindrical and often wavy-constricted to narrowly clavate in *L. flammeotincta*, and only narrowly clavate, with an occasional cylindrical one, in *La. flammeotinctoides*. The lamellae of the more robust *La. flammeotinctoides* stain reddish, and nrITS sequences distinguish the two species very convincingly.

The other satellite taxa have irregularly shaped, non-cylindrical cheilocystidia, and differ in subtle pileus covering characters or spore shape. *Lepiota flammeotincta* and *La. flammeotinctoides* 'bleed' heavily, the others less so. It is amazing, and frustrating, that species that differ so clearly in sequence data are hard to distinguish morphologically.

The strong reddening reaction of *L. flammeotincta* might be the reason that KOH on the surfaces did not have the chance to turn the tissues green.

Kauffman's (1924) macroscopical description of *L. flammeotincta* is very accurate and complete, an excellent example of good and thorough observation without drowning in unnecessary details.

Smith (1966), who also studied the type collection, noted narrowly clavate cheilocystidia and slightly smaller spores than observed here. Only cylindrical and very narrowly clavate cheilocystidia, some wavy, were observed for this study.

Johnson (1999) included a collection from Costa Rica for which she used the name *L. flammeotincta,* but the nrITS, nrLSU, and mtSSU sequences (GenBank accession numbers U85331, U85296 and U85363 resp.) represent a different, unidentified species.

Unlike *La. erythrophaeus*, *L. fuliginescens*, and *La. adelphicus*, *L. flammeotincta* does not have a sister species in Europe. In fact, all European species of section *Piloselli*, except *L. roseolivida,* have a trichodermal pileus covering.

**10. *Leucoagaricus flammeotinctoides*** Vellinga, **sp. nov.** Figures 19 & 20

MycoBank MB 515367

Lepiotae flammeotinctae *similis, lamellis post tactum discolorentibus, cheilocystidiis (tenuiter) clavatis, nucleari spatii interne transcipti ("nrITS") ordine differt.*

**Holotypus** — "U.S.A., California, Mendocino County, Jughandle SR, 19 November 2007, E.C. Vellinga 3729 (UC)," (nrITS GU136173).

Etymology: The epithet *flammeotinctoides* refers to the resemblance to *L. flammeotincta*; the word combines the Latin '*flammeotincta*' with the suffix '*-oides*' derived

from the Greek, resulting in a more euphonious word than the completely Latin and grammatically correct 'flammeotinctaster' with the same meaning.

Pileus 31–60 mm, plano-convex, to applanate with central depression and (low, broad) umbo to wavy, at first dark grey at umbo, soon dark brown to dark red-brown (5 YR 3/3), plushy velvety-tomentose on umbo, around umbo with concentrical rings of dark brown material as on pileus centre, and further towards margin with small fibrillose radially arranged dark brown scales to small cobwebby fibrils on white background, gradually lighter towards margin to pale brown (7.5 YR 8/2), on pale background and margin; fibrils red when touched, but background not changing colour; marginal zone sulcate in some specimens. Lamellae, L = 50–60, l = 0 1, crowded or moderately crowded, free and 1 mm remote from stipe, some furcate, segmentiform to ventricose, 4–6 mm wide, white-cream to yellowish white coloured, orange near margin, orange-red when touched, with white cystidiose-dentate edge, changing via orange to dark with pressure and age, but this reaction can be slow and weak. Stipe 70–135 × 4–7 mm, slightly narrower at apex, 8–13 mm wide at base, protruding slightly into pileus, white, lengthwise innately fibrillose and hirsute all over, changing instantly to bright orange-red when bruised, turning dark brown with time, hollow. Annulus an ascending white cuff and a small flaring part with dark rim, with dark fibrils as on pileus, and turning completely dark. Context white to whitish and dull in pileus, but where cut (especially under umbo) red or orange but soon fading, shiny to glassy white to pale brownish with age in stipe, orange when cut (fresh specimens). Smell none, indistinct or astringent lepiotoid to rubber-fungoid.

Dried specimens dark with dark lamellae.

Basidiospores [140,8,8] in side view 5.9–8.8 × 3.1–4.6 µm, avl × avw = 6.4–7.8 × 3.5–4.1 µm, Q = 1.5–2.2, avQ = 1.74–1.88, ellipsoid to subcylindrical, with rounded apex, a few subamygdaliform, in frontal view similar as in side-view, thick-walled and smooth, uniguttulate, congophilous, dextrinoid, metachromatic in Cresyl blue. Basidia 18–29 × 6.5–9.5 µm, 4-spored. Lamella edge completely sterile, or with tufts and groups of cystidia. Cheilocystidia 22–53(–75) × 5.0–15.0 µm, clavate, narrowly clavate, narrowly utriform or sublageniform, occasionally cylindrical, a few with really long pedicel, with dark brown contents and big inclusions or granules in ammonia. Pleurocystidia absent. Pileus covering cutis-like made up of strands of mostly repent, more rarely ascending brown-walled hyphae; terminal elements 63–200(–260) × 9.0–15.5 µm, cylindrical to slightly inflated, with rounded apex, or attenuated towards apex; penultimate elements often much shorter; pigment brown parietal and intracellular, exuding out of material in ammonia, with dark brown granules, and can be incrusting in all elements except terminal ones. Clamp connections absent.

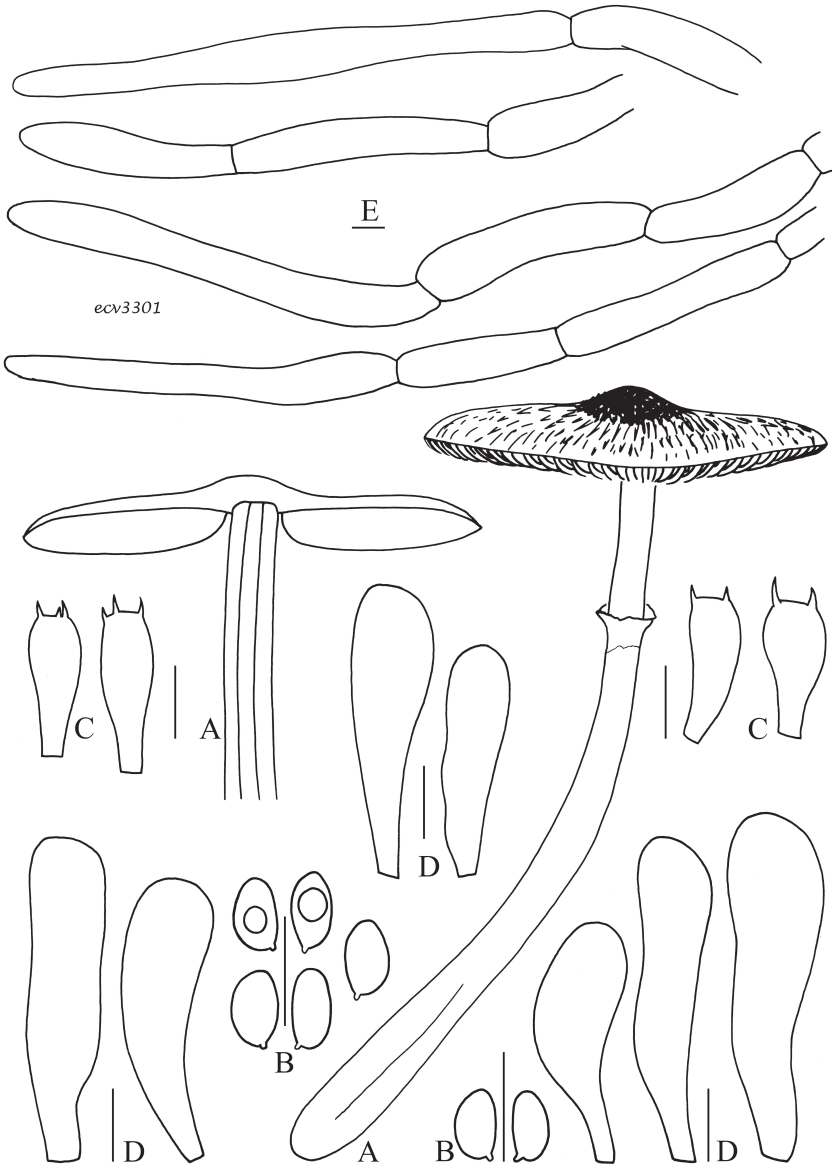


Fig. 19. *Leucoagaricus flammeotinctoides* — A. Basidiocarp; B. spores; C. basidia; D. cheilocystidia; E. elements of pileus covering (all from ecv3301) . Scale bar 10 mm (A); microscopic features 10 μm.

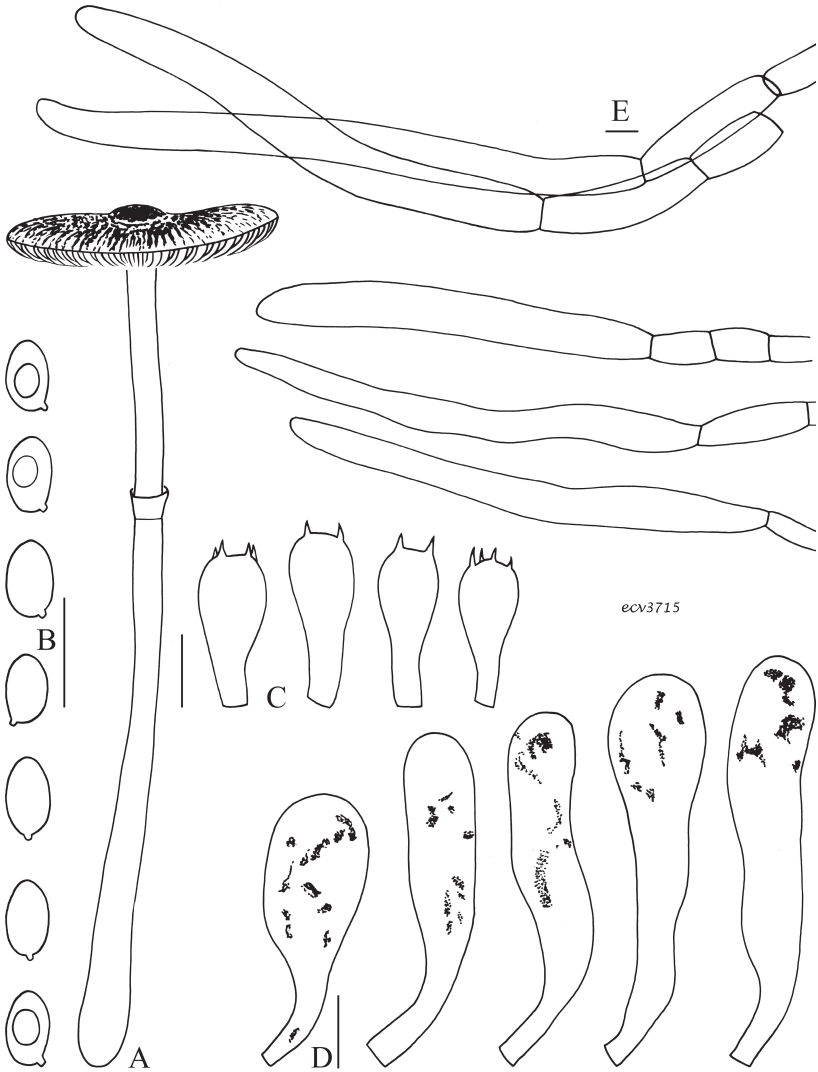


Fig. 20. *Leucoagaricus flammeotinctoides* — A. Basidiocarp; B. spores; C. basidia; D. cheilocystidia; E. elements of pileus covering (all from 3715) . Scale bar 10 mm (A); microscopic features 10 µm.

Habitat and distribution – Solitary to gregarious in small groups, terrestrial and saprotrophic, in coastal mixed coniferous forests, with or without *Sequoia sempervirens*, in northern California, November and early December.

Additional collections examined – U.S.A., **California,** Humboldt Co., Patrick's Point SP, 9 November 2004, E.C. Vellinga 3247 (nrITS GU136174); Marin Co., Samuel P. Taylor State Park, 28 November 2001, E.C. Vellinga 2759 (nrITS AY243620); Mendocino County, Jackson State Demonstration Forest, 20 November 2004, E.C. Vellinga 3301 (nrITS GU136175), 3304 (nrITS GQ258475) and 3308 (nrITS GQ258476); Van Damme SP, along Fern Canyon Trail, 18 November 2007, E.C. Vellinga 3715 (nrITS GU136172); San Mateo Co., San Mateo County Memorial Park, 5 December 2008, F.A. Stevens et al. (collection ecv3966) (nrITS GU136176).

Comments — *Leucoagaricus flammeotinctoides* resembles *L. flammeotincta* in the rapid staining reaction of pileus and stipe, but it differs in the bigger and more robust basidiocarps, the staining lamellae, and the narrowly clavate cheilocystidia. The lamellae are more remote from the stipe than in *L. flammeotincta*. Wavy cylindrical cheilocystidia, so characteristic for *L. flammeotincta*, have never been observed in this species.

It seems to be less common than *L. flammeotincta* s. str., not yet found outside the coastal forests, but its real distribution and occurrence are unknown.

The new species could be confused with *La. erythrophaeus* because of the staining lamellae, but that species has a pseudocollarium to which the lamellae are attached and a trichodermal pileus covering structure.

**11. *Leucoagaricus pyrrhophaeus*** Vellinga, **sp. nov.** Figure 21

MycoBank MB 515369

*A* Lepiota flammeotincta *cheilocystidiis clavatis ad lageniformibus vel irregularibus differt.*

Holotypus — "U.S.A., California, Humboldt County, near Orick, along Davidson's Road, 10 November 2004, E.C. Vellinga 3268 (UC)," (nrITS GU136199).

Etymology: derived from the Greek words πυρρος, 'red, flame-coloured, yellowish-red', and φαιος, 'dark'; chosen because of the reaction of the tissues when exposed to air.

Pileus 25-30 mm plano-convex with low umbo, dark red-brown (2.5 YR 2.5/3) at umbo, around umbo with concentrical and towards margin more radially oriented tufts of fibrils, v-shaped, concolorous with umbo, on white background which easily discolours orange; margin irregularly fringed, exceeding lamellae. Lamellae, L = around 50, l = 0, 1 or 3, moderately crowded, free and remote from stipe, ventricose, whitish with cystidiose edge glistening with some colourless drops; edge discolouring when touched to orange changing to dark brown-black. Stipe 50–70 × 2.5–3 mm, gradually widening downwards to 6 mm wide base, pale pinkish at apex, below annulus with dark fibrils where touched, turning orange, then dark, when scratched, cystidiose-fibrillose above annulus, hollow. Annulus not very elaborate, not a distinct cuff but funnel-shaped, with a broadened rim, pale on the inside, with dark upper rim, and some dark fibrils on outside.

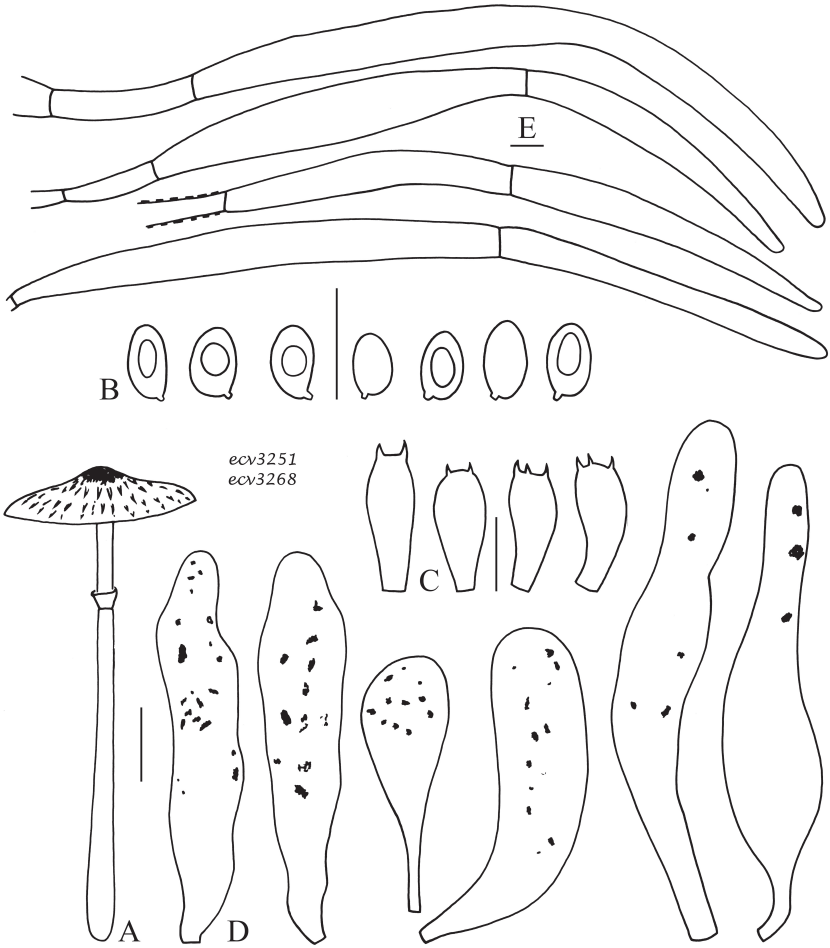


Fig. 21. *Leucoagaricus pyrrhophaeus* — A. Basidiocarp (holotype, collection ecv3268); B. spores; C. basidia; D. cheilocystidia; E. pileus covering elements (all microscopic features from collection ecv3251). Scale bar 10 mm (A); microscopic features 10 µm.

Dried specimens copper coloured, with coloured lamellae.

Basidiospores [35,2,2] in side view 5.5–7.2 × 3.4–4.2 µm, avl × avw = 6.4–6.6 × 3.8 µm, Q = 1.4–2.0, avQ = 1.68–1.75, oblong, with flattened abaxial side, with rounded, non-amygdaliform apex, smooth and thick-walled, with guttule, without germ pore, congophilous, dextrinoid, metachromatic in Cresyl blue. Basidia 13–18 × 6.0–8.0 µm, 4-spored. Lamella edge sterile. Cheilocystidia 30–68 × 9.0–13 µm, irregularly lageniform to utriform, some clavate, some

narrowly lageniform, with brown contents and dark granules in ammonia. Pleurocystidia absent. Pileus covering with repent to upright brown-walled hyphae with brown contents and some dark granules in ammonia, some with incrusting pigments; most typically 3 coloured elements in a row, with the terminal element the biggest, and slightly differentiated, narrowing into acute apex, in most cases elements not widened at the septa; with lowest elements the narrowest or narrowing at base; terminal elements 115–285 × 12–20 µm; penultimate elements up to 25 µm wide. Clamp connections absent.

Habitat and distribution – Solitary or in small groups, terrestrial in coastal coniferous forests of northern California, under *Picea sitchensis*, or in a mixed conifer forest with *Sequoia sempervirens*, *Picea sitchensis* and *Tsuga heterophylla*. So far only found in Humboldt County. November.

Additional collection examined – U.S.A.: California, Humboldt Co., Patrick's Point State Park, 9 November 2004, E.C. Vellinga 3251 (nrITS GQ258473).

Comments — *Leucoagaricus pyrrhophaeus* belongs to the group of species that look very much like *L. flammeotincta*. In particular, it resembles *Leucoagaricus* sp. (collection ecv3723), but differs in the hyphae of the pileus covering with non-inflated elements, resulting in smooth hyphae; *La. pyrrhulus* also comes close but has amygdaliform spores. All three have cheilocystidia that show a certain resemblance to Dr. Seuss creatures. *Leucoagaricus pyrrhophaeus* stains less easily red when touched than *L. flammeotincta* and *La. flammeotinctoides*; furthermore, the cheilocystidial shape also easily separates it from both these species. Thus far, nrITS sequences differentiate these taxa more easily than morphological characters.

**12. *Leucoagaricus pyrrhulus*** Vellinga, **sp. nov.** Figure 22

MycoBank MB 515368

*A* Lepiota flammeotincta *in pileo fibrillis tenuibus, sporis amygdaliformibus, cheilocystidiis clavatis ad lageniformibus differt.*

**Holotypus** — "U.S.A., California, Mendocino County, Jackson Demonstration State Forest, 20 November 2004, E.C. Vellinga 3306 (UC)", (nrITS GQ258474);

Etymology: *pyrrhulus* is derived from the Greek word πυρρος, 'red, flame-coloured, yellowish-red'. Some linguistic freedom has been applied to coin the diminutive, referring to the small fibrils on the pileus surface in comparison to the other species in the complex.

Pileus 15–30 mm, plano-convex to applanate without distinct umbo, dark brown at centre, white around centre with very small dark brown cobwebby fibrils and a dark margin from pressure (after bringing home), with some dark radial streaks from touching, with glistening surface, immediately orange when scratched. Lamellae, L = around 30, l = 0 or 1, moderately crowded, free but not remote from stipe, ventricose, cream with distinctly white cystidiose edge.

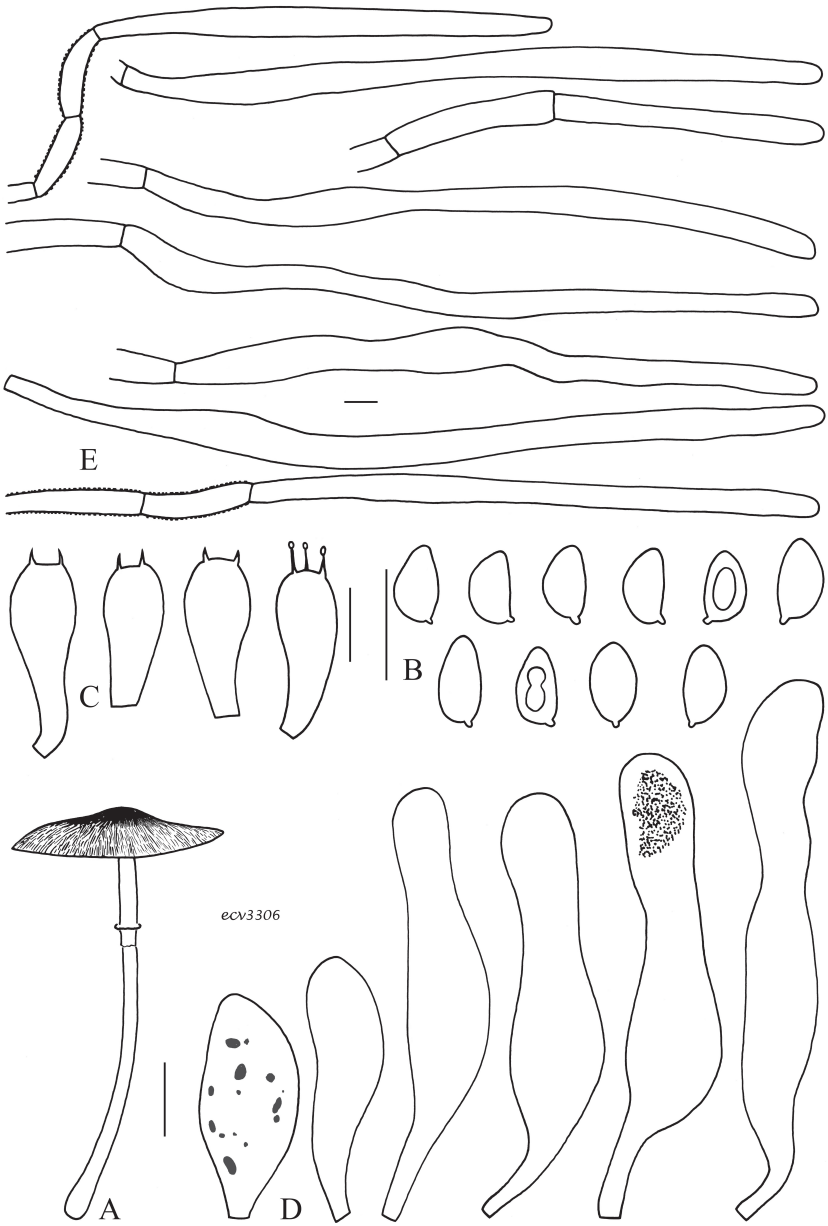


Fig. 22. *Leucoagaricus pyrrhulus* — A. Basidiocarp; B. spores; C. basidia; D. cheilocystidia; E. elements of pileus covering (all from holotype, collection ecv3306). Scale bar 10 mm (A); microscopic features 10 µm.

Stipe 30–50 × 1.5–2.5 mm, cylindrical or slightly widened at base, whitish all over, but dark where touched, hairy cystidiose all over, hollow. Annulus small, with a small ascending cuff, and a small dark flaring part. Smell indistinct.

Dried specimens with pink to dark lamellae.

Basidiospores [20,2,2] in side-view 6.1–7.8 × 3.2–4.4 µm, avl × avw = 6.8–6.9 × 3.7–4.0 µm, Q = 1.6–2.1, avQ = 1.7–1.83, amygdaliform-oblong or oblong with rounded apex, in frontal view oblong-obovoid, smooth, thick-walled, with one or more guttules, congophilous, dextrinoid, metachromatic in Cresyl blue. Basidia 21–26 × 7.0–8.5 µm, 4-spored. Lamella edge sterile. Cheilocystidia 43–67 × 7.0–14 µm, lageniform with long neck, some with subcapitate apex or with moniliform neck, a few clavate, with green-brown contents and dark granules or concretions in ammonia. Pleurocystidia absent. Pileus covering a cutis made up of dark reddish brown hyphae in bundles on top of a yellow-brown lower layer with thin hyphae, some of which have finely incrusting pigment. Hyphae of upper layer with long cylindrical to slightly differentiated terminal elements, 80–250 × 9–13 µm, with rounded, non attenuated tips, with parietal pigment. Clamp connections absent.

Habitat and distribution — Solitary, terrestrial in mixed coniferous forests with *Sequoia sempervirens*, in coastal northern California, found twice near Mendocino, November.

Additional collection examined — U.S.A., **California,** Mendocino Co., Van Damme SP, Fern Canyon, 18 November 2007, E.C. Vellinga 3719 (nrITS GU136201).

Comments — *Leucoagaricus pyrrhulus* is close in general appearance to the other species in the *L. flammeotincta* group, but it has finer fibrils on pileus, does not strongly discolour when touched, and is the only species with amygdaliform spores. It also differs in the shape and size of the cystidia from both *L. flammeotincta* and *La. flammeotinctoides* but the shape of the cheilocystidia is similar to those found in *La. pyrrhophaeus*.

Differences with the undescribed taxon, *Leucoagaricus* sp. (collection ecv3723), are subtle, but again, the amygdaliform spores distinguish *La. pyrrhulus*, and nrITS sequence data clearly separate them. More material is needed to assess the morphological diversity of and the distinctions among these taxa.

**13. *Leucoagaricus*** sp. (collection ecv3723) Figure 23

Pileus 31 mm, wide-conical with umbo, deep dark brown and tomentose at umbo, around umbo with short, small dark radial fibrils on whitish background, not arranged into v-shaped squamules or cobwebby, but individually arranged; background whitish to dirty pale orange where touched. Lamellae, L = around 45, l = 0 or 1, free, but not remote from stipe, moderately spaced, not distant,

nor crowded, subventricose, whitish with pinkish sheen, with white cystidiose edge, changing to yellow when pestered. Stipe 75 × 3 mm, gradually widening downwards to 6 mm, cream coloured when fresh, when picked immediately orange-red, changing to dirty and dark brown, hairy-tomentose, but in lower half with dark fibrils, hollow. Annulus an ascending cuff and a small flaring part which is dark brown and distinctly hairy-tomentose at underside. Context very thin in pileus, white, red at centre from cutting through the umbo, in stipe concolorous with surface. Smell like the sweet and rubber components of the smell of *L. cristata*.

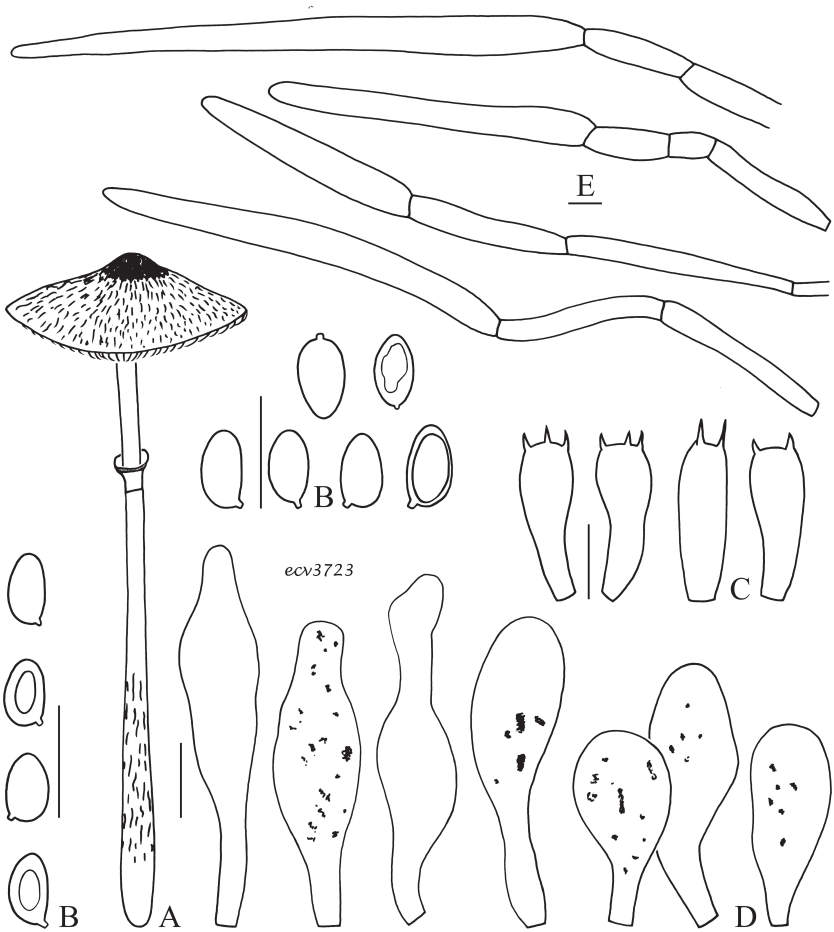


Fig. 23. *Leucoagaricus* sp. (collection ecv3723) — A. Basidiocarp; B. spores; C. basidia; D. cheilocystidia; E. elements of pileus covering. Scale bar 10 mm (A); microscopic features 10 µm.

Dried specimens with red-copper tinges and pinkish lamellae.

Basidiospores [20,1,1] in side view 5.7–7.1 × 3.4–4.0 µm, avl × avw = 6.1 × 3.7 µm, Q = 1.55–1.85, avQ = 1.66, ellipsoid to oblong with slightly straighter adaxial then abaxial side, with rounded apex, a few subamygdaliform, in frontal view ellipsoid to oblong, with guttule, thick-walled, smooth, without germ pore, congophilous, dextrinoid, metachromatic in cresyl blue. Basidia 19–21 × 6.0–7.5 µm, 4-spored. Lamella edge sterile. Cheilocystidia 20–48 × 9.0–13 µm, variable, clavate, more or less lageniform to utriform and relatively long, with brown contents and dark granules in ammonia. Pleurocystidia absent. Pileus covering around centre with repent red-brown-walled hyphae made up of 3–5 coloured elements; terminal elements slightly differentiated and inflated, longer than the penultimate cells, 100–250 × 15–18 µm. Clamp connections absent.

Habitat and distribution – Solitary, terrestrial, in mixed forest, with *Picea sitchensis, Pinus muricata* D. Don, and *Sequoia sempervirens,* only found once, in Mendocino County, November.

Collection examined – U.S.A., **California,** Mendocino Co., Jughandle State Natural Reserve, 19 November 2007, E.C. Vellinga 3723 (nrITS GU136200).

Comments — More material is needed to assess whether this is a species in its own right. This collection is closely related to *La. pyrrhophaeus,* with which it shares the copper colours of the dried specimens. The shape of the pileus covering elements differs slightly in *La. pyrrhophaeus* as the cells in that species do not show inflations at the septa. The differences with the other taxa in the *L. flammeotincta* group are subtle, and pertain to the shape of the spores and cheilocystidia, and colour changes of the basidiocarps.

### Key to the California species in the *Leucoagaricus* /*Leucocoprinus* clade that turn red on bruising

1. Pileus covering lilac or raspberry pink to lilac, fibrillose or plushy tomentose all over
   2. Pileus lilac to pink, fibrillose; basidiocarp slender; pileus covering with repent hyphae; spores amygdaliform . . . . . ***L. roseolivida***
      [not uncommon in California, description in Vellinga (2007a)]
   2. Pileus raspberry pink; basidiocarp sturdy, with pileus width equal to stipe length; pileus covering with upright elements; spores with rounded apex . . . . . ***L. decorata***
      [rare, only known from a few collections in California and Oregon, fruiting relatively late in the season; description in Vellinga (2007a)]
1. Pileus covering starting out very pale, changing to dark brown to black, or predominantly with dark brown to black, brown, grey or brick red colours; background can turn deep raspberry pink with age

3. Basidiocarps staining brick red with age and with ammonia, but not turning green with ammonia; spores with distinct apical papilla. . . . . ***L. castanescens***
[not uncommon in California, common further north, e.g. in Washington; description in Vellinga & Sundberg (2008)]

3. Basidiocarps staining green with ammonia (in strongly reddening species this reaction might be obscured); spores without apical papilla

4. Spores with a germ pore

5. Pileus (70–)100–230 mm with brown squamules; spores with distinct germ pore; elements of pileus covering tapering towards narrow apex; basidiocarps solitary or in small clusters . . . . . ***La. americanus***
[occasionally fruiting in the western states of North America, on wood chips or probably on hidden roots etc., widespread in North American and Europe; type description in Vellinga (2000); description of European material in Reid (1990), and Vellinga (2001)]

5. Pileus 13–50(–80) mm with small, dot-like dark brown squamules (starting out pale grey-brown); spores with indistinct germ pore; elements of pileus covering with blunt apex; basidiocarps in big clusters . . . . . ***La. meleagris***
[occasionally fruiting in the western states of North America, on wood chips etc., widespread and known from eastern North America, Hawaii, Europe and Asia; description of European material in Reid (1990), and Vellinga (2001)]

4. Spores without a germ pore

6. Pileus covering made up of repent hyphae, with or without differentiated terminal elements . . . . . ***L. flammeotincta*** group (5 taxa)

7. Cheilocystidia (at least some) cylindrical and wavy (best seen when lamella edge is severely squashed), most cylindrical to narrowly clavate; lamellae not staining red when damaged . . . . . 9. ***L. flammeotincta*** s. str.

7. Cheilocystidia not wavy at all; lamellae often staining red when damaged

8. Cheilocystidia clavate, narrowly clavate . . . . . 10. ***La. flammeotinctoides***

8. Cheilocystidia variable, from clavate to irregularly utriform, or lageniform

9. Spores amygdaliform; pileus with fine fibrils . . . . . 12. ***La. pyrrhulus***

9. Spores with rounded, non-amygdaliform apex; pileus with v-shaped squamules

10. Pileus covering elements not constricted at septa . . . . . 11. ***La. pyrrhophaeus***

10. Pileus covering elements slightly inflated and constricted at septa . . . . . 13. ***Leucoagaricus*** sp. (collection ecv3723)

6. Pileus covering trichodermal made up of upright elongated, rarely cystidioid, elements

12. Cheilocystidia clavate with terminal, often moniliform, excrescence; basidiocarps starting out rather pale and often developing pink-purple tinges
    13. Basidiocarps medium to large (pileus > 35 mm; stipe 60–125 × 5–16 mm, up to 20 mm at base); pileus covering made up of elongated elements only . . . . . 1. ***L. fuliginescens***
    13. Basidiocarps small to medium (pileus < 35 mm; stipe 13–40 × 1.5–3 mm); pileus covering made up of cystidioid and clavate elements . . . . . ***La. georginae***
    [known from the state of Washington and from Europe; included in the analysis of nrITS sequences of FIG. 1; description of European collections in Vellinga (2001)]
12. Cheilocystidia lacking long terminal excrescence, clavate, narrowly clavate or broadly clavate, fusiform to lageniform, cylindrical, or narrowly utriform
    14. Lamellae staining when damaged
        15. Lamellae attached to a collarium-like structure; cheilocystidia clavate, up to 90 µm long . . . . . 6. ***La. erythrophaeus***
        15. Lamellae not attached to a collarium-like structure; cheilocystidia if clavate, shorter
            16. Basidiocarps sturdy, fleshy (pileus 30–120 mm); pileus with pink-brown tomentose covering, changing to evenly dark brown with age . . . . . 2. ***La. cupresseus***
            16. Basidiocarps medium to small (pileus 30–60 mm); pileus warm red-brown or with dark centre and patches on light background
                17. Pileus warm red-brown all over; cheilocystidia varied, narrowly clavate, clavate, fusiform-utriform to clavate with terminal excrescence . . . . . 4. ***La. hesperius***
                17. Pileus white with very dark centre and a radiating pattern of dark patches on an off-white background; cheilocystidia cylindrical . . . . . 7. ***La. pardalotus***
    14. Lamellae not staining red when damaged (although lamella edge might discolour)
        18. Pileus dark red-brown, fibrillose around centre; cheilocystidia long (50–75 µm long), narrowly clavate . . . . . 8. ***Leuocagaricus*** sp. (collection ecv2484)
        18. Pileus red-brown, warm red-brown, plush-like velvety-tomentose; cheilocystidia clavate, narrowly clavate (up to 55 µm long)
            19. Pileus covering with long elements; cheilocystidia clavate . . . . . 3. ***La. adelphicus***
            19. Pileus covering with bundles of short elements; cheilocystidia narrowly clavate . . . . . 5. ***La. dyscritus***

## Acknowledgments

Thanks are due to all people who contributed to this paper by providing me with collections: Steve Trudell, Buck McAdoo, and Joshua Birkebak from Washington and British Columbia (Canada), Dimitar Bojantchev, Darvin DeShazer, Boleslaw Kuznik, Daniel Nicholson, Fred Stevens, Debbie Viess and David Rust, Mark Lockaby, and Ron Pastorino, Tom Bruns, Primrose Boynton, Nhu Nguyen and Shannon Schechter for Californian collections. The curators at MICH, NY, and SFSU are acknowledged for sending material on loan. The San Francisco Public Utilities Commission made it possible for me to visit the San Francisco watershed where the cypress groves are a treasure trove for *Lepiota* hunters. Jan Frits Veldkamp (Nationaal Herbarium, Leiden, the Netherlands) helped me with the Latin descriptions. John Lennie accompanied me on collecting trips and as always edited my English. Comments by the two reviewers, Dr. Zhu-Liang Yang and Dr. Brian Perry, and by the nomenclature editor, Dr. Shaun Pennycook, were very helpful. Funding by NSF grant DEB 0618293 is gratefully acknowledged.

## Literature cited

Arora D. 1986. Mushrooms demystified. A comprehensive guide to the fleshy fungi. Ed. 2. Ten Speed Press, Berkeley. 959 pp.

Aulinger K. Arnold N, Steglich W. 2000. Metabolites of 2-aminophenol from fruit bodies of *Lepiota americana* (*Agaricales*). Zeitschrift für Naturforschung Section C Journal of Biosciences 55 (5–6): 481–484.

Boisselet P. 2002 ('2001'). *Leucoagaricus marginatus* comb. nov., espèce d'origine californienne retrouvée en France. Bulletin trimestriel de la Societé mycologique de France 117: 183–192.

Boisselet P, Guinberteau J. 2001. *Leucoagaricus cupresseus* (Burlingham) Boisselet & Guinberteau comb. nov., une lépiote cupressicole d'origine américaine récoltée en France. Bulletin de la Féderation des Assocations mycologiques méditerranéennes, n.s. 19: 33–42.

Bon M. 1993. Flore mycologique d'Europe 3. Les Lépiotes. *Lepiotaceae* Roze. Documents mycologiques. Mémoire hors série 3: 1–153.

Burlingham GS. 1945. Noteworthy species of *Lepiota* and *Lactaria*. Mycologia 37: 53–64.

Candusso M, Lanzoni G. 1990. *Lepiota* s.l. Fungi europaei 4. Giovanna Biella, Saronno. 743 pp, 80 pl.

Demoulin V. 1966. Le problème de *Lepiota badhamii* et de *Lepiota rufovelutina*. Lejeunia 39: 1–15.

Gardes M, Bruns TD. 1993. ITS primers with enhanced specificity for basidiomycetes – application to the identification of mycorrhizae and rusts. Molecular Ecology 2: 113–118.

Gennari A, Migliozzi V. 1999 ('1998'). Una nuova entità della sezione *Piloselli, Leucoagaricus aurantiovergens* sp. nov. Rivista di Micologia 41: 291–300.

Guinberteau J, Callac P, Boisselet P. 1998. Inventaire des communautés fongiques liées au *Cupressus macrocarpa* en zone littorale atlantique et données récentes sur les populations sauvages d'*Agaricus bisporus*. Bulletin trimestriel de la Societé mycologique de France 114(2): 19–38. 1998.

Heinemann P. 1973. Leucocoprinées nouvelles d'Afrique centrale. Bulletin du Jardin botanique national de Belgique 43: 7–13.

Holmgren PK, Holmgren NH. 1998 [continuously updated]. Index Herbariorum: A global directory of public herbaria and associated staff. New York Botanical Garden's Virtual Herbarium. http://sweetgum.nybg.org/ih/ [accessed June 2009].

Johnson J. 1999. Phylogenetic relationships within *Lepiota* sensu lato based on morphological and molecular data. Mycologia 91: 443–458.

Katoh K, Misawa K, Kuma K, Miyata T. 2002. MAFFT: a novel method for rapid multiple sequence alignment based on fast Fourier transform. Nucleic Acids Research 30: 3059–3066.

Kauffman CH. 1924. The genus *Lepiota* in the United States. Papers from the Michigan Academy of Science, Arts and Letters 4: 319–344.

Kühner R. 1936. Recherches sur le genre *Lepiota*. Bulletin trimestriel de la Societé mycologique de France 52: 177–238.

Locquin M. 1945. Notes sur les Lépiotes II. Bulletin mensuel de la Societé linnéenne de Lyon 14: 44–52, 53–63, 82–88, 89–100.

Migliozzi V, Perrone L. 1992. Sulle Lepiotee - 8° contributo. Descrizione di *Leucoagaricus brunnescens* (Peck) Bon e creazione della sottosezione *Pilatianei* Migliozzi et Perrone. Bollettino dell'associazione micologica ed ecologica romana 26: 3–9.

Migliozzi V, Resta G. 2001. Note sulla sottosezione *Pilatiani* del genere *Leucoagaricus*, due nuove varietà: *Leucoagaricus pseudopilatianus* var. *rugosoreticulatus* e *Leucoagaricus pseudopilatianus* var. *roseodiffractus*. Micologia e vegetazione mediterranea 15: 129–156.

Migliozzi V, Rocabruna A, Tabarés M. 2001. *Leucoagaricus pseudopilatianus*: una nueva especie de la sección *Piloselli*. Revista Catalana de Micologia 23: 67–74.

Munsell™ soil color charts. 1975. Baltimore.

Murrill WA. 1912. The *Agaricaceae* of the Pacific Coast II. Mycologia 4: 231–262.

Murrill WA. 1914. *Agaricaceae* (pars). North American Flora 10(1): 1–79.

Peck CH. 1896. New species of fungi. Bulletin of the Torrey botanical Club 23: 411–420.

Peck CH. 1904. New species of fungi. Bulletin of the Torrey botanical Club 31: 177–182.

Pegler DN. 1986. Agaric flora of Sri Lanka. Kew Bulletin additional Series 12: 1–519.

Reid DA. 1990. The *Leucocoprinus badhamii* complex in Europe: species which redden on bruising or become green in ammonia fumes. Mycological Research 94: 641–670.

Singer R. 1973. Diagnoses fungorum novorum *Agaricalium* III. Beihefte Sydowia 7: 1–106.

Smith AH, Hesler LR. 1938. Notes on Agarics from Tennessee and North Carolina. Journal of the Elisha Mitchell Scientific Society 54: 261–268 + 2 plates.

Smith HV. 1966. Contributions toward a monograph on the genus *Lepiota*, I. Type studies in the genus *Lepiota*. Mycopathologia et mycologia applicata 29: 97–117.

Smith HV, Weber NS. 1987. Observations on *Lepiota americana* and some related species. Contributions from the University of Michigan Herbarium 16: 211–221.

Stamatakis A, Hoover P, Rougemont J. 2008. A rapid bootstrap algorithm for the RAxML web-Servers. Systematic Biology 75: 758–771.

Sundberg WJ. 1967. The family *Lepiotaceae* in California. Master's thesis, San Francisco State University. 219 pp.

Sundberg WJ. 1976. *Lepiota* sensu lato in California. II. Type studies of *Lepiota cupressea* and *Lepiota marginata*. Mycotaxon 3: 381–386.

Sundberg WJ. 1995. A type study of *Lepiota pulverapella*. Documents mycologiques 25(98–100): 449–451.

Swofford DL. 2002. PAUP*. Phylogenetic Analysis Using Parsimony (*and other methods). Version 4. Sinauer Associates, Sunderland, Massachusetts.

Vellinga EC. 2000. Notes on *Lepiota* and *Leucoagaricus*. Type studies on *Lepiota magnispora*, *Lepiota barssii*, and *Agaricus americanus*. Mycotaxon 76: 429–438.

Vellinga EC. 2001. *Leucoagaricus*. Pp. 85–108, in ME Noordeloos, ThW Kuyper, EC Vellinga (eds). Flora agaricina neerlandica 5. A.A. Balkema Publishers, Lisse/Abingdon/ Exton(PA)/Tokyo.

Vellinga EC. 2004a. Genera in the family *Agaricaceae* — Evidence from nrITS and nrLSU sequences. Mycological Research 108: 354–377.

Vellinga EC. 2004b. Ecology and distribution of lepiotaceous fungi (*Agaricaceae*). Nova Hedwigia 78: 273–299.

Vellinga EC. 2007a. Lepiotaceous fungi in California, U.S.A. — 3. Pink and lilac species in *Leucoagaricus* sect. *Piloselli.* Mycotaxon 98: 213–224.

Vellinga EC. 2007b. Lepiotaceous fungi in California, U.S.A. — 5. *Lepiota oculata* and its look-alikes. Mycotaxon 102: 267–280.

Vellinga EC, Noordeloos ME. 2001. Glossary. Pp. 6–11, in ME Noordeloos, ThW Kuyper, EC Vellinga (eds). Flora agaricina neerlandica 5. A.A. Balkema Publishers, Lisse/Abingdon/Exton (PA)/Tokyo.

Vellinga EC, Sundberg WJ. 2008. Lepiotaceous fungi in California, U.S.A. 6. — *Lepiota castanescens.* Mycotaxon 103: 97–108.

Vellinga EC, Contu M, Vizzini A. 2010. *Leucoagaricus decipiens* and *La. erythrophaeus*, a new species pair in sect. *Piloselli.* Mycologia 110: 447–454, doi:10.3852/09-164.

Wood M, Stevens F. 1996-2008. The fungi of California. www.mykoweb.com/CAF/ [accessed Aug. 2009]

Zeller SM. 1933. New or noteworthy agarics from Oregon. Mycologia 25: 376–391.