Leucoagaricus decipiens and La. erythrophaeus, a new species pair in sect. Piloselli

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Abstract: Leucoagaricus decipiens and La. erythrophaeus, are described as new from Sardinia, Italy, and California, USA, respectively. These sister species show distinct reddening when touched on all parts of the basidiocarps and darken on drying. Their collariate lamellae, broadly cylindrical to utriform cheilocystidia and trichodermal pileus covering distinguish them morphologically from other species in sect. Piloselli, while nrITS and EF1- α sequences distinguish them from each other. Leucoagaricus erythrophaeus has been known under the name Lepiota roseifolia, but the type collection of this species does not fit the interpretation.

Key words: Agaricaceae, biodiversity, Mediterranean, nrITS and EF1-α sequences

INTRODUCTION

The mycofloras of the Mediterranean area in Europe and the north coastal region in California, North America, are rich in species belonging to Leucoagaricus Locq. ex Singer in the Leucoagaricus/Leucocoprinus clade of the Agaricaceae (e.g. Bon 1993, Candusso and Lanzoni 1990, Vellinga 2004). Several pairs of closely related morphologically almost identical species, one of them occurring in Europe the other in western North America, have been recognized based on analyses of nrITS sequences (Vellinga 2004, Vellinga and Sundberg 2008). Another such pair of species is presented here, consisting of one species recently discovered in Sardinia, Italy, the other one well known and widespread in California but as it turned out, hiding under the name L. roseifolia Murrill. Both species are described as new and presented with descriptions and illustrations.

The new species morphologically belong to Leu-

coagaricus section *Piloselli* (Kühner ex) Singer, a section that harbors those species whose basidiocarps stain red when bruised and discolor green with ammonia; blackening of the basidiocarps can follow the reddening. Cells of the basidiocarps are filled with dark granules or a brown pigment that can be seen especially well in ammonia or KOH. In some species the whole basidiocarp will turn black with age and on drying; in others the reaction is much more subdued and restricted to the lamella edge for example.

The species in this section are recognized based on morphological features such as the colors and color reactions, the size and shape of the basidiocarps, the shape of the cheilocystidia and in particular the presence or absence of an apical excrescence, the structure of the pileus covering and the shape of the spores.

MATERIALS AND METHODS

Macroscopic characters were noted for fresh material. Color annotations in the macroscopical description follow the Flora of British Fungi Colour Identification Chart (Anonymous 1969). Microscopic studies are based on dried material, and observations were made on mounts in these reagents: lamellae and spores in Congo red in 10%ammonia, followed by 5% KOH or 10% ammonia; pileus covering, stipitipellis and annular tissue in 10% ammonia; spores in Cresyl blue in water and Melzer's reagent. Terminology is according to Vellinga and Noordeloos (2001). The notation [55,3,2] indicates that measurements were made on 55 spores in three samples in two collections. These abbreviations are used: avl for average length, avw for average width, Q for quotient of length and width and avQ for average quotient. L. is used for Lepiota, La. for Leucoagaricus and Lc. for Leucocoprinus.

Material was deposited at UC, except where otherwise noted. Herbarium abbreviations are according to Holmgren and Holmgren (1998).

DNA was extracted with a QIAGEN DNeasy® Blood and Tissue kit (QIAGEN, Valencia, California). The nrITS region was amplified with the ITS-1F/ITS-4 primer set with an MJ PTC- 100^{TM} thermocycler (Applied Biosystems, Foster City, California) under conditions described by Gardes and Bruns (1993). Part of the elongation factor 1- α gene (EF1- α) was amplified with primers EF1-983F and EF1-1567R (Rehner and Buckley 2005) according to the protocol developed by Rehner and Buckley (2005). PCR products were cleaned with $0.5~\mu$ L ExoSAP IT (USB Corp., Cleveland, Ohio) per reaction and cycled at 37 C for 45 min, followed by 80 C for 15 min. Sequencing was performed with Big Dye chemistry and an ABI PRISM 3100 Genetic Analyzer (both from Applied Biosystems,

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Foster City, California). Sequences were edited and contigs assembled with Sequencher 4.2.2 (Gene Codes Corp., Ann Arbor, Michigan). Newly produced sequences were deposited in GenBank. The sequences of new species were compared with those from other species in sect. Piloselli (with the exception of the species group of La. americanus [Peck] Vellinga). nrITS sequences were aligned by partial order alignment (Lee et al. 2002), and the EF1-α sequences were aligned with Clustal X 2.09 (Larkin et al. 2007); alignments are deposited in TreeBase (S2466 for the study, M4696 and M4697 for the matrices). Maximum parsimony option in PAUP* (Swofford 2002) was used for phylogenetic analysis. Cystolepiota seminuda (Lasch) Bon was chosen as outgroup for the nrITS sequence analyses and L. magnispora Murrill for EF1-α data (Fig. 1). Analyses were performed only to determine whether the sequences matched existing sequences of previously sequenced species and were not used to hypothesize about the phylogeny of section Piloselli.

TAXONOMY

Leucoagaricus decipiens Contu, Vizzini & Vellinga, sp. nov. FIG. 2

MycoBank MB 513553

TYPE. ITALY. Sardinia: prov. Sassari, Calangianus, loc. Catala, Stazzo Luciano, under *Alnus glutinosa* in a wet area, 7 Sep 2002, M. Contu. (HOLOTYPE designated here, UC).

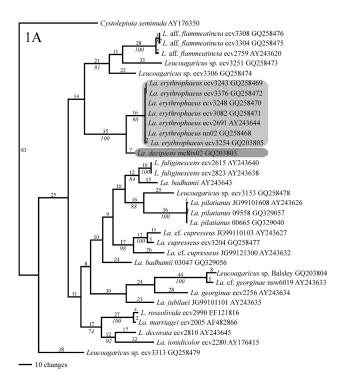
Etymology. The epithet "decipiens" refers to the Latin verb "dēcipere" (to ensnare) and therefore meaning a deceptive, not obvious species.

Pileus 15–40 mm, parce carnosus, fragillimus, convexus dein explanatus, obtuse umbonatus, ad medium brunneus vel lilaceo-brunneus et in squamulis brunneis excoriato, aliunde albido, margine haud striata. Lamellae confertae, collariatae, albae. Stipes 45–85 3–6 mm (usque ad 8 mm ad basim), clavatus, haud bulbosus, albo-floccosus, annulo simplice albido cum margine brunneo obtecto. Caro fragillima, alba, tactu leviter rubescens dein brunnescens. Odor saporque debiles. Sporarum pulvis alba.

Sporae 5.9–7.2(–7.8) \times 3.9–4.6 µm, ellipso-ovoideae, obtusae, dextrinoideae. Pleurocystidia nulla. Cheilocystidia 30–50 \times 8.0–15 µm, plerumque clavata, interdum utriformia vel lanceolata, tenuitunicata, haud incrustata, in siccis succo brunneo impleta. Operimentum pilei trichodermicum, ex hyphis cylindro-fusoideis usque ad 300 \times 17 µm formatum, pariete brunnea ad basim obtectis in siccis pigmento brunneo impletum. Fibulae absentes.

Leucoagarici erythrophaei similis, sed in spatii interne transcripti sequentia ("ITS").

Pileus 15–40 mm, thin, fragile, convex to planoconvex, with rounded to inconspicuous and low umbo, entirely brown (mainly Umber 18 or Date Brown 24), sometimes with faint lilac hues (Date Purplish 22), smooth and glabrous to slightly tuftedtomentose, radially cracking toward margin into dense but not imbricate squamules, paler than at



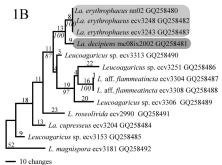


FIG. 1. A. Phylogram based on parsimony analyses of the nrITS region of species in *Leucoagaricus* sect. *Piloselli*. One of 44 MPT is depicted. *Cystolepiota seminuda* was chosen as outgroup. The numbers above branches refer to the number of changes; bootstrap values, based on 1000 replicates, are indicated in italics below branches. B. Phylogram based on parsimony analyses of EF1-α sequences. One of two MPT is given here. *Lepiota magnispora* was chosen as outgroup. The numbers above branches refer to the number of changes; bootstrap values, based on 1000 replicates, based on 1000 replicates, are indicated in italics below the branches.

center; margin white, nonstriate and without appendiculate velar remains. Lamellae crowded, narrow, free or attached to a collarium, white, with concolorous finely scalloped edge. Stipe $45-85 \times 3-6$ mm (< 8 mm wide toward base), clavate, white, finely floccose-pubescent, at first stuffed, then hollow. Annulus simple, located at the middle of stipe, white with brownish underside. Context thin, fragile, whitish, turning orange to red with handling. Mature and

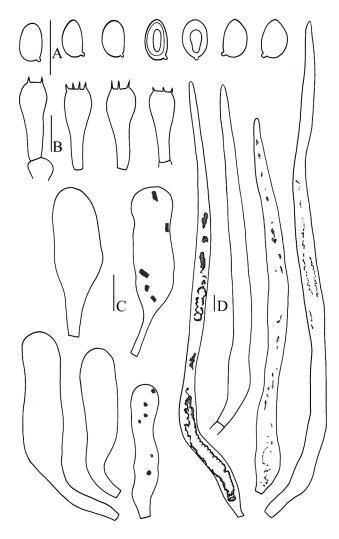


FIG. 2. Leucoagaricus decipiens. A. spores; B. basidia; C. cheilocystidia (all from holotype, MC7xii2002); D. elements of the pileus covering (from MC8xii02); brown contents of cystidia and pileus covering elements are not indicated. Bars = $10~\mu m$.

dried specimens are entirely dark brown. *Odor* weak, indistinct; *taste* mild. *Spore print* white.

Basidiospores [55,3,2] 5.9–7.2(–7.8) \times 3.9–4.6 μm, avl \times avw = 6.5–6.6 \times 4.2 μm, Q = 1.4–1.7 (–1.85), avQ = 1.55–1.6, ellipsoid, with rounded apex to slightly amygdaliform in side view, in frontal view ellipsoid, with evident hilar appendage, without germ pore, thin-walled, usually with a large central guttule, hyaline, smooth, dextrinoid, congophilous, and metachromatic in Cresyl blue. Basidia 17–27 \times 7.0–8.5 μm, 4-spored, narrowly clavate; subhymenium consisting of polygonal elements. Hymenophoral trama made up of large colorless hyphae. Pleurocystidia absent. Lamella edge sterile; cheilocystidia abundant, 30–50 \times 8.0–15 μm, usually cylindrical with rounded apex and with pedicel, sometimes utriform or narrowly clavate,

often with long pedicel, thin-walled not encrusted at apex, with brownish contents and dark granules in dried specimens due to the reaction of intracellular pigments with ammonia. *Pileus covering* a trichoderm made up of long hyphae with terminal cylindrical elements $200-300 \times 11-17~\mu m$, and also some short clavate elements, usually tapering toward apex, and with widest just above base; pigment brown, parietal in lower half of the cells, but also intracellular, dark brown in old and dried specimens; connecting hyphae repent and full of dark granules in ammonia. *Annulus* consisting of cylindrical to allantoid, sometimes branching hyphae, $4-21~\mu m$ wide, mostly with thickened walls. *Stipitipellis* a cutis of cylindrical hyphae. *Clamp connections* absent.

Macrochemical reactions. Lamellae, pileus and stipe surface with NH₄OH: emerald green then dark redvinaceous; pileus surface with KOH 4%: instantaneously emerald green but soon bright red with green halo.

Habitat and distribution. Terrestrial, in small groups, in moist areas, under Alnus glutinosa. September. At present known only from Sardinia, Italy.

Collections examined. ITALY, Sardinia, prov. Sassari, Calangianus, loc. Catala, under *Alnus glutinosa*, 7 Sep 2002 (Holotype, UC) and 8 Sep 2002, *M. Contu* (nrITS GQ203803; EF1-α GQ258481; UC).

Comments.—Leucoagaricus decipiens belongs morphologically to subsect. Pilatiani Migl. & L. Perrone because of the nonappendiculate cheilocystidia.

Unfortunately no professional picture or macroscopical drawing of this new species is available.

Leucoagaricus decipiens is morphologically very close to the western American species formerly known as L. roseifolia Murrill, here described as the new species La. erythrophaeus, which has longer ($< 9.0 \, \mu m$) spores, and longer ($< 93 \, \mu m$) cheilocystidia. The nrITS and EF1- α sequences clearly distinguish the two species. The variability of La. decipiens is poorly known because it is only known at present from one locality where it was collected on two consecutive days in Sep 2002 and has never been seen again; Sardinia experienced exceptionally wet and warm weather during the summer of 2002. A few European species are morphologically close to L. decipiens.

Leucoagaricus brunneolilacinus Babos differs in having a pileus covered by brown-lilaceous erect pyramidal squamules, smaller spores up to 5 μ m long, shorter cheilocystidia (15–25 μ m), and a pileipellis consisting of shorter elements mixed in young basidiocarps with scattered globose cells (Babos 1980, 1985). Leucoagaricus jubilaei (Joss.) Bon has a pileus with distinct amethyst or purplish tinges at the disk, longer spores (< 8 μ m long) and cylindrical pileus surface hyphae with short terminal elements

($< 100 \mu m long$), which do not taper toward the base (e.g. Migliozzi and Coccia 1989).

Leucoagaricus brunnescens (Peck) Bon in the interpretations of Bon (1993) and Migliozzi and Perrone (1992) comes very close to La. decipiens. The collection studied by Migliozzi and Perrone (1992) differs because of the longer spores (< 8 μm) and pileus surface hyphae with obtuse and short (< 150[-200] μm) terminal elements. Bon (1993) described the lamellae as "subcollariées", a character also observed in La. decipiens and La. erythrophaeus. Bon (1993) also stated that the cheilocystidia could be incrusted. Bon (1981) studied the type collection of L. brunnescens Peck, but except for commenting that it is close to La. jubilaei but differs in the simple cylindrical cells on the pileus he did not list its characters. Leucocoprinus brunnescens (Peck) Pegler sensu Pegler (1983) is a different species altogether, characterized by the narrowly lageniform to broadly appendiculate cheilocystidia, spores with a faint germ pore and a pileus covering composed of repent hyphae with short terminal elements, 35-80 µm long.

Leucoagaricus pseudopilatianus Migl., Rocabruna & Tabarés is a much more robust species, with clavate cheilocystidia, spores with a distinct apical papilla and pileus covering elements with rounded blunt apices; the dried material, including the lamellae, is dark to almost black (Migliozzi et al. 2001).

Finally, *Lepiota roseolivida* Murrill (in Europe better known as *La. marriagei* [D.A. Reid] Bon) is a slender fragile species with a pink-lilac pileus covering, composed of repent hyphae (Vellinga 2006, Migliozzi and Perrone 1991). It does not turn black on drying, although it can turn green when exposed to ammonia.

Leucoagaricus erythrophaeus Vellinga, sp. nov.

FIGS 3, 4

MycoBank MB 513552

Misapplied name. *Lepiota roseifolia sensu* Arora, Mushr. Demystif., Ed. 2:305. 1986; sensu Sundberg, Fam. *Lepiotaceae* California: 115–119. 1967.

TYPE. UNITED STATES OF AMERICA. California, Humboldt County, Arcata, Community Forest, 9 Nov 2004, *E.C. Vellinga 3243* (UC).

Etymology. Erythrophaeus is derived from two Greek words: ερυθρος, red, bloody, and φαιος, dark, because of the bright red reaction and the subsequent change into dark colors.

Pileus 18–60 mm, in juventute hemisphaericus cum margine inflexo deinde convexus, postremo plano-convexus vel leviter plano-concavus, ad medium integrus et griseo-velutinus, obscure rubro-purpureus vel obscure nigro-brunneus, aliunde in squamulis fibrillosis obscure

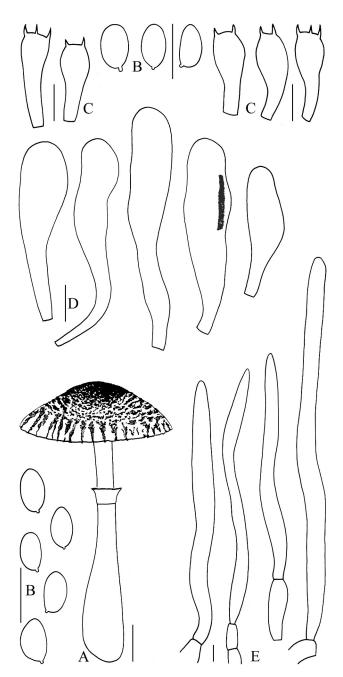


FIG. 3. Leucoagaricus erythrophaeus. A. basidiocarp; B. spores; C. basidia; D. cheilocystidia; E. elements of the pileus covering (all from holotype, ecv3243); brown contents of cystidia and pileus covering elements are not indicated. Bars = 1 cm (basidiocarp) and 10 μm (microscopical characters).

rubro-purpureis vel obscure nigro-brunneis in contexto albo excoriatus, tactu statim rubro-aurantius sed ad brunneum vergens. Lamellae sat confertae vel confertae, liberae, distantes, saepe collariatae, albo-flavidae, tactu rubescentes, acie cystidiosa, alba, tactu brunnescente obtectae. Stipes $55-70\,\times\,4-5$ mm, cylindricus sed versus basim, in tertio inferiore, clavatus, albus, tactu primo rubro-aurantius dein nigrescens atque obscurus; annulo adscendente, simplice,

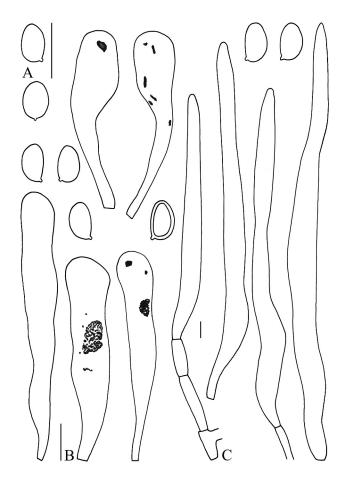


FIG. 4. Leucoagaricus erythrophaeus. A. spores; B. cheilocystidia; C. elements of the pileus covering (all from ecv3254); brown contents of cystidia and pileus covering elements are not indicated. Bars = $10 \mu m$.

fimbriato, albo margine tactu brunnescente obtecto. Caro in pileo alba vel albida sed fracta leviter et fugaciter aurantians, in stipite pallide cremeo-albida vel flavida, fracta aurantians. Odor haud peculiaris, adstringens vel lepiotoideus

Basidiosporae 5.9– 8.8×3.5 – $4.9 \, \mu m$, ellipsoideae vel ellipsoideo-amygdaliformes, aliquae oblongae et leviter amygdaliformes, dextrinoideae. Pleurocystidia nulla. Cheilocystidia 30– 75×8.0 – $14.0 \, \mu m$, strictiter clavata, strictiter utriformia usque ad irregulariter cylindracea et pedicellata, succo brunneo atque granulis in ammonia brunnescentibus impleta. Operimentum pilei ad medium trichodermicum, versus marginem in cute sed cum aliquis hyphis ascendentibus formatum, ex hyphis elongatis usque ad $350 \times 20 \, \mu m$ formatum; apices hyphae fusoideis vel saepe etiam rotundatis vel capitatis; hyphae pariete brunnea ad basim obtectae, saepe etiam granulis brunneis vel succo brunneo impletis. Fibulae absentes.

Leucoagarici decipienti similis, sed in spatii interne transcripti sequentia ("ITS").

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 center covered, velvety-plushy gray, dark purplish-reddish, to dark brown-black, around center 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 two-thirds and widening downward to up to 15 mm wide base, pale at apex and in untouched specimens pale over complete length, when touched first orange-red, changing to very dark to black, 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 to yellowish in stipe, and orange where cut. Odor indistinct, astringent or lepiotoid. Taste un-

Basidiospores [273,14,12] in side view $5.9-8.8 \times 3.5 4.9 \mu m$, avl × avw = $6.2-7.4 \times 3.8-4.2 \mu m$, Q = 1.4-2.15, avQ = 1.61-1.78, ellipsoid to amygdaloidellipsoid, some oblong and slightly amygdaloid, in frontal view ellipsoid, relatively thick-walled, often with one guttule, without germ pore, congophilous, metachromatic in Cresyl blue, dextrinoid. Basidia 15- 29×6.5 – $9.0 \, \mu m$, narrowly clavate, with 4 sterigmata. Pleurocystidia absent. Lamella edge sterile, with a continuous broad band or tufts of cheilocystidia with brown contents (in ammonia). Cheilocystidia 30–93 × 8.0-14.0 µm, narrowly clavate, narrowly utriform, to irregularly cylindrical and narrowed into an often long pedicel, some with bifid apex, with brownish contents and some dark granules in ammonia. Pileus covering a trichoderm, toward margin more cutis-like with differentiated terminal elements; terminal elements $96-350 \times 9.0-20 \,\mu\text{m}$, most often tapering toward 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 (in ammonia); repent connecting hyphae with dark granulose contents (in ammonia), 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 and Tsuga heterophylla forests or Alnus rubra and Sequoia sempervirens and in central coastal California Pseudotsuga menziesii with Sequoia sempervirens and various other tree species) end of October through beginning of December, throughout coastal California from Mendocino County northward and in the foothills of the central Sierra Nevada. Actual distribution poorly known.

Collections examined. UNITED STATES OF AMER-ICA. California, Humboldt County, Arcata, Community Forest, 9 Nov 2004, E.C. Vellinga 3243 (nrITS GQ258469; EF1-α GQ258483; Holotype, UC); Patrick's Point SP, 23 Oct 2003, E.C. Vellinga 3081, 3082 (nrITS GQ258471) and 3083; ibidem, 9 Nov 2004, E.C. $Vellinga~3248~(nrITS~GQ258470;~EF1-\alpha~GQ258482)$ and 3254 (nrITS GQ203805); Orrick, along Davidson Road, 27 Oct 2007, N. Nguyen NN02 (nrITS GQ258468; EF1-\alpha GQ258480); Marin County, near Alpine Lake, 15 Nov 2005, E.C. Vellinga 3376 (nrITS GQ258472) and 3379, Mendocino County, Jackson State Demonstration Forest, 17 Nov 2001, E.C. Vellinga 2691 (nrITS AY243644); San Mateo County, San Mateo County Memorial Park, 4 Nov 2004, E.C. Vellinga 3217; Yuba County, Tahoe NF, Hornswoggle Campground near Bullards Bar, 9 Nov 2005, E.C. Vellinga 3358; south of Challenge, along Oregon Hill Road, 10 Nov 2005, E.C. Vellinga 3362.

Comments.—The species herein described as La. erythrophaeus has been known as L. roseifolia Murrill (e.g. Arora 1986, Sundberg 1967, Wood and Stevens 1996–2009). This taxon was interpreted as a species resembling L. flammeatincta Kauffman but with lamellae that turn red when damaged and with age. However L. flammeatincta has lamellae that do not turn red when damaged, despite a vivid and immediate reddening reaction of the stipe and pileus when touched. The type collection of L. roseifolia (collection Murrill 1287 [NY]) was studied (FIG. 5) and was found to differ from La. erythrophaeus.

Murrill (1912) described *L. roseifolia* as, "Pileus regular, convex to subexpanded, solitary, 4 cm. broad; surface dry, shining, innate-fibrillose, radiaterimose, smooth and glabrous at the center, castaneous, blackish-tinted when fresh, assuming a more reddish tint after picking; lamellae free, crowded, slightly ventricose, regular, white when fresh, changing to rose-colored on drying or when bruised; spores ellipsoid, smooth, hyaline, $7{\text -}8 \times 3{\text -}3.5~\mu$; stipe equal, compressed, very long because buried in leaves, hollow, smooth, glabrous, avellaneous-isabelline, white at the apex, 17 cm. long, 5 mm. thick; annulus superior, slight, fixed, fuliginous."

Analysis of holotype specimen (Fig. 5).—Basidiospores [22,1,1] in side view $6.9-8.3 \times 3.9-4.9 \mu m$, avl × avw

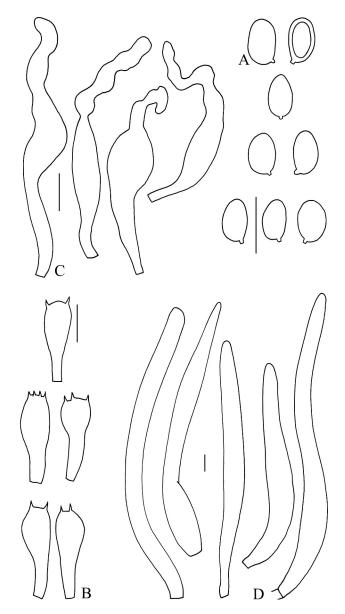


FIG. 5. *Lepiota roseifolia*. A. spores; B. basidia; C. cheilocystidia; D. elements of the pileus covering (all from holotype, Murrill 1287). Bars = $10 \mu m$.

= 7.5 \times 4.4 μ m, Q = 1.52–1.88, avQ = 1.7, ellipsoid to oblong with rounded apex, rarely with pointed apex and amygdaliform, with flattened adaxial side, in frontal view obovoid-ellipsoid, thick-walled, congophilous, dextrinoid, metachromatic in Cresyl blue. Basidia 20–24 \times 7.0–8.5 μ m, 4-spored. Pleurocystidia not observed. Lamella edge sterile; cheilocystidia 38–66 \times 6.0–12 μ m, narrowly clavate to fusiform with in most cases a long moniliform excrescence (included in length of cheilocystidia), rarely only capitulate. Pileus covering with clusters of upright slightly differentiated terminal elements, 80–170 \times 12–19 μ m, brown-walled and with rounded to tapering apex, arising from a cutis made up of cylindrical

brown-walled hyphae. *Clamp connections* not observed. Smith (1966) also studied the type collections of *L. roseifolia*, and our observations are very similar, although she reported longer spores ("8–11 \times 3.6–4.5 μ m, usually 8–9.5 μ m long").

However there are striking differences from the modern interpretation of L. roseifolia in the shape of the cheilocystidia and the fact that the lamellae of the type collection are not dark. The appendiculate cheilocystidia in the type collection of L. roseifolia are similar to those in L. fuliginescens Murrill, a species close to the European species La. badhamii (Berk. & Broome) Singer. The pale lamellae in the type collection of L. roseifolia precludes L. roseifolia and L. fuliginescens from being synonymized. The type collections of L. roseifolia and L. fuliginescens were collected on the same day in a Sequoia sempervirens forest near La Honda in the Santa Cruz Mountains, south of San Francisco (Murrill 1912). It often is not possible to identify the species in section Piloselli in the field because old specimens in particular look very much alike. In California the species often grow in the same habitat and fruit at the same time.

Lepiota roseifolia in the original sense has not yet been rediscovered in the Californian Sequoia sempervirens forests, hence we can only speculate about its position.

Leucoagaricus erythrophaeus is quite variable, in macroscopical and microscopical characters, especially spore size, shape and pigmentation of the pileuscovering elements vary considerably from one collection to the other. It is hard to tell *La. decipiens* and *La. erythrophaeus* apart, although the nrITS and EF1-α sequences clearly distinguish them.

Lepiota flammeatincta differs in the absence of a reddening reaction of the lamellae that are not attached to a collarium, a slender habit, relatively pale (pink or pink-gray) lamellae when dried, and a cutis-like pileus covering made up of repent hyphae.

Several still undescribed species are included (Fig. 1); these differ from the species described here either in the shape of the cheilocystidia or in the structure of the pileus covering. All California species in this group will be treated in a separate paper.

ACKNOWLEDGMENTS

The curator of NY is thanked for sending the type collection of *L. roseifolia* on loan. Remarks by two anonymous reviewers improved the present study. John Lennie made very helpful suggestions regarding presentation, and financial support by NSF grant DEB 0618293 for ECV is gratefully acknowledged.

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