Leptota in California: species with a hymeniform pileus covering

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Abstract: Eight Leptota species with a hymeniform pileus covering that are known in California are presented and discussed. Leptota phaeoderna is described as new; this species is characterized by a dark pileus surface, which splits open into small patches around the umbo, and the absence of an annulus. Leptota neophana, a species with an annulus and a closed brown pileus surface, and L. lilacea, with a conspicuous dark annulus, are both recorded for the first time west of the Rocky Mountains. The identity of L. neophana is reviewed and clarified based on morphological and molecular data. The type collection of L. rufipes was studied, and L. rufipes was placed in synonymy with Cystolepiota seminuda. A key to the species is given.

Key words: Agaricaeae, biodiversity, Callitropsis macrocarpa, nrITS and EF1-α sequences, taxonomy, type studies

INTRODUCTION

Leptota (Pers.) Gray is represented in the highly diverse state of California by at least 25 species, 30% of which are still undescribed. This genus is less species-rich than Leucoagaricus (Locq.) ex Singer (Vellinga 2004a), which also contains many undescribed species in California. Several Leptota species have been described from the state in the past (e.g. Murrill 1912; Sundberg 1971, 1989; Vellinga 2007), but an overview of the genus is still lacking. The group of species with a hymeniform pileus covering was the focus of this article. Basidiocarps of these species are small, with a pileus covering that either covers the pileus homogeneously or splits open into small patches or flat scales, depending on the presence or absence of an intercellular matrix that binds the individual cells. An annulus can be present or absent; the spores are ellipsoid or bullet-shaped, and small (less than 8 μm long), and the spore walls do not react strongly with Melzer’s reagent and Congo red. One species has only one nucleus per spore (Kühner 1945, Vellinga and Huijser 1999), whereas the other species have two, as is usual in Leptota. Cheilocystidia are present or absent. The morphological differences among the species are often subtle (Vellinga and Huijser 1999), but nrITS sequence data support the morphologically recognized species. However species with a hymeniform pileipellis do not form a monophyletic group (Vellinga 2003).

This group has been accommodated in 1–3 sections based on morphological characters, according to various authors. Singer (1986) put all species in section Cristatae (Kühner ex Wasser) Bon, regardless of spore shape, but Bon (1993) placed them in three sections (in two subgenera) by distinguishing species with bullet-shaped spores (in sect. Cristatae) from species with ellipsoid spores in subgenus Paralepiotula Bon. He then divided this subgenus in two: sect. Integrilegii (Kühner ex Bon) Bon for species with a pileus covering that does not split open and only one nucleus per spore and sect. Lilaceae Bon for species whose pileus covering breaks open into scales and have binucleate spores.

Phylogenetic analyses based on molecular data failed to resolve many of these differences (Vellinga 2003). However they clearly showed that species with bullet-shaped spores and a hymeniform pileus covering, such as L. cristata, belong with ellipsoid-spored species and a similar pileus covering and not with species with spurred spores and a trichodermal pileus covering. The bullet-shaped spores arose once in this clade of ellipsoid-spored species; the more pronouncedly spurred spores in the group of species with trichodermal or cutis-like pileus covering (L. boudieri Bres., L. castanea Quél.) evolved independently.

The molecular data (Vellinga 2003) also did not support a separate section for L. rufipes, which differs from the other species in the uninucleate spores. The isolated and unresolved positions of Leptota lilacea Bres., L. ochraceofulva P.D. Orton and L. pyrochroa Malençon, outside the core group of species with a hymeniform pileus covering, came as a surprise (Vellinga 2003) because morphologically they are not distinct in essential characters from the rest of the hymeniform species.

Despite several articles on species in this group from California (Sundberg 1971, 1989; Vellinga 2001a, b) naming problems still persist. The identity of L. neophana Morgan, described from Preston, Ohio, (Morgan 1906) is at the center of the problem:

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because at least three different interpretations of this species have been published (Smith 1954, Sundberg 1989, Bizio et al. 1993). This species again has been studied and is here redescribed from modern Californian collections, according to the original description by Morgan (1906). As a result the species described as L. neophana sensu Sundberg (1989) is in need of a new name and is described as L. phaeoderna.

Seven of the eight species presented here co-occur in one small area, containing several Monterey cypress (Callitropsis macrocarpa (Hartw.) D.P. Little; syn. Cupressus macrocarpa Hartw.; Hesperocyparis macrocarpa (Hartw.) Bartel) plantations on an east-facing slope south of San Francisco, and one of these seven is not known from any other location in California. These Monterey cypress groves are notable for being rich in species of Lepiota and Leucoagaricus (Vellinga 2004a).

The species are treated in checklist format in alphabetical order, with a nomenclator and references to descriptions and illustrations in the literature. Species new to science and the newly recorded species are fully described. Additional morphological information is provided for several species, including the number of nuclei per spore, an important diagnostic character. An identification key is provided to aid recognition of the species.

**MATERIALS AND METHODS**

Standard methods for describing basidiocarps were applied with the terminology of Vellinga and Noordeloos (2001). Color annotations in macroscopic descriptions are from Munsell® soil color charts (1975). The notation [115,7,6] means that measurements were made on 115 spores in seven samples in six collections. These abbreviations are used: l for number of lamellae, 1 for number of lamellulae between two lamellae, aval for average length, aw for average width, Q for quotient of length and width and avQ for average quotient. Herbarium material was used to count the number of nuclei per spore. Nuclei were stained with a 4′, 6-diamidino-2-phenylindole, dihydrochloride (DAPI) solution (1 μg/mL) and observed with a fluorescence microscope with E550–575 BPass and E670 LP 397 filters. Herbarium abbreviations follow Holmgren and Cleveland, Ohio) and cycled at 37 °C for 45 min, followed 15 min at 80 °C. Sequencing was performed with Big Dye chemistry and an ABI PRISM 3100 Genetic Analyzer (Applied Biosystems, Foster City, California). Sequences were edited and contigs assembled with Sequencer 4.2.2 (Gene Codes Corp., Ann Arbor, Michigan). The nrITS sequences were aligned by partial order alignment (Lee et al. 2002), and the EF1-α sequences were aligned with Clustal X 2.0.9 (Larkin et al. 2007); PAUP* 4.0b81 (Swofford 2002) performed the phylogenetic analysis. Five species representative of the major clades in Lepiota were chosen for comparison. Chamaemyces fracidus (Fr.) Donk serves as an outgroup because it is basal in the Lepiota (Vellinga 2004b). Dermoloma inconspicuum Dennis was included in the analysis because it recently was shown to belong to the Agaricaceae (Kropp 2008); it shares the hymeniform pileus covering with the species treated here. All 30 newly produced sequences have been deposited in GenBank. (Accession numbers are listed with the collections examined and in Figs. 1, 6.) Alignments are deposited in TreeBase under provisional number SN4563.

Sequence data were used only to establish that the morphological differences were in concordance with sequence differences, not to establish a phylogenetic hypothesis for genus Lepiota or the species with a hymeniform pileus covering.

**TAXONOMY**


   _Lepiota castaneidisca_ was described from California by Murrill (1912), subsequently considered synonymous with _L. cristata_ (under _L. conspurcata_ [Willd.] Morgan) by the same author (Murrill 1914), treated as a species with ellipsoid spores by Sundberg (1967) and later as a synonym of _L. cristata_ (Sundberg 1989). Vellinga (2001) realized that there was indeed a taxon that differs from _L. cristata_ in California with a rounded red-brown pileus instead of a distinctly umbонate pileus with orange-like tinges and used the name _L. castaneidisca_ for it. The nrITS sequences neatly support the recognition of two species (Fig. 1). _L. cristata_ and _L. castaneidisca_ are indistinguishable microscopically. The spores are slightly metachromatic in Cresyl blue and have two nuclei. _Lepiota castaneidisca_ is known from California north into Washington (Birkebak pers comm).


   = _Agaricus cristatus_ Bolton, A history of fungusses
Fig. 1. One of 10,000 most parsimonious trees based on a dataset of 70 nrITS sequences of *Lepiota* species with a hymeniform pileus covering, five species representative of the major clades in *Lepiota* (indicated by *), *Dermoloma inconstipicium* and *Chamaemyces fracidus* as outgroup (76 in total). Two hundred seventy-one characters were parsimony informative. Species occurring in California are highlighted; the other hymeniform species are from Europe, with the exception of *D. inconstipicium* from Central and South America. Numbers above branches indicate branch length, numbers in italics below branches are an indication of the bootstrap support. Bootstrap support was calculated based on 50,000 replicates done in fast-stepwise-addition, with groups with > 70% support retained.
Lepiota cristata is a widespread species complex known from the temperate northern hemisphere (Vellinga 2001b; Liang, Xu and Yang 2009). nrITS sequences show considerable variation in this species even within collections from the same area (e.g. the three collections from Ann Arbor, Michigan, fall into two clearly different groups based on nrITS sequences and a small sample from California shows three distinct nrITS types [Vellinga 2001b]), but a correlation with morphology has not been made, and at this point it is unclear whether these nrITS variants represent different species. Several infraspecific taxa have been described, but because their status has to be confirmed with molecular data they are not listed here. Note that the description by Sundberg (1989) includes L. castaneidisca and hence is not listed under selected descriptions.

Lepiota kauffmanii was described as having a “Mars brown” (dark brown) pileus that starts out campanulate, expanding to nearly plane umbonate (Zeller 1933), and was considered synonymous with L. cristata (Smith 1966). The data on the shape of the pileus are not sufficient to determine this unambiguously because they could refer to L. castaneidisca. The microscopical data fall within the variability of both L. castaneidisca and L. cristata, and a decision on its synonymy cannot be made. The following notes were made on the type collection (Fig. 2) (and compare with Smith 1966). Basidiospores [25,2,1] 5.4–6.9 × 3.2–4.2 μm, avl × awv = 6.0–6.3 × 3.6–3.7 μm, Q = 1.45–1.85, avQ = 1.64–1.69, not dextrinoid, not metachromatic in Cresyl blue. Lamella edge sterile, with cheilocystidia forming a sterile band; cheilocystidia colorless, 20–42 × 9–13 μm, sphaeropedunculate to clavate with short to long pedicel, rarely narrowly clavate.

Lepiota cristata grows in relatively nutrient-rich places ranging from natural habitats (especially river beds and other riparian habitats with regular flooding) to ruderal places with strong human influences. Human influence may account for the co-occurrence of several nrITS types within a certain area.


Pileus 31–36 mm, 8–11 mm high, plano-convex to applanate with glabrous dark violet disk, around disk breaking open into radially arranged scales, concolorous with disk; surface white and radially fibrillos上述的内容。在下，Lepiota luteophylla

The type collection of Lepiota lilacea has been examined in detail. The pileus covering of this species is characterized by a dark brown, slightly to moderately viscous, smooth, without germ pore, clustering in groups, slightly and slowly staining in Congo red, nondextrinoid. Unfortunately the number of nuclei could not be assessed.

Knudsen (1978) placed L. luteophylla in genus Cystolepiota Singer, although globose cells are absent from the pileus covering. The separate cells of the pileus covering are difficult to see, so he might have been misled by a section taken parallel to the pileus covering.

Despite many forays at the type locality, a grove of Callitropsis macrocarpa, south of San Francisco, I have never found this species myself. It also is known from Michigan (Smith et al. 1979).


Fig. 5 = Lepiota neophana var. europaea Bizio & Migl., Boll Ass micol ecol Romana 9(27):45. 1993.
**Lepiota neophana**

- **Habit** (from *ecv3955*), *Lepiota neophana*.
- **Spores**. *Lepiota neophana*.
- **Basidia**. *L. cristata*.
- **Lamellae**. *L. neophana*.

Selected description. *Bizio et al.*, Riv Micol 36:228–234. 1993 (as *var. europaea* and *f. papillata*).

**Pileus** 10–38 mm, convex, plano-convex with low or prominent umbo, wavy campanulate to wavy convex with prominent umbo, orange-brown (Mu. 7.5 YR 4/6, 5/6, 6/6, 7/6; 5 YR 4/5, 5 YR 4–5/6, 5 YR 5/8), orange-reddish brown (5 YR 3/4) at center, a bit duller when dry, around center paler orange brown, orange-brown (halfway around radius 5 YR 7/6, 7.5 YR 7–8/5, 5/6, or 7.5 YR 8/4, 10 YR 8/5) to very pale at utmost margin and there cream-colored (10 YR 8/4), smooth and glabrous or radially wrinkled or venose around center, with some radial grooves when old, with slightly uneven margin, and in some specimens with white annular remnants clinging to margin. *Lamellae*. L = 30–40, 1 = 1–5, crowded, moderately crowded, free and close to stipe, ventricose, rarely not ventricose but segmentiform, 2.5–6 mm wide, whitish at first and soon cream-colored (10 YR 8/3–4) to distinctly yellowish (2.5 Y 8/2), with white or concolorous even edge. *Stipe* 27–75 × 2–5 mm, cylindrical or slightly wider at utmost base, pale yellowish brown or cream to cream yellow at apex, and there shiny, slightly darker downward, paler than 5 YR 5/8, with some pinkish brown or even vinaceous tinges in old specimens, hollow, with white rhizomorphs at base. *Anulus* whitish and flaring, without cuff, flimsy, evanescent, rarely as some whitish cream fibrils on both sides of brown rim, often clinging to pileus margin and not at stipe. *Context* thin, cream to yellowish white and dull in pileus, concolorous to stipe surface in stipe. *Odor* sweet lepiotoid and astringent, such as the sweet component of *L. cristata*, with a parsley-soapy component, or like *L. cristata* without the sweet component.

**Basidiospores** [115,6,6] 4.1–5.7 × 2.6–3.4 μm, avl × awv = 4.7–4.9 × 2.9–3.2 μm, Q = 1.35–1.9, avQ = 1.55–1.65, in side view ellipsoid to oblong, with flattened or convex adaxial side, ellipsoid to oblong in frontal view, slightly thick-walled, smooth, without germ pore, clustering in groups, not colored to pale pink in Congo red, with pink inner wall in Cresyl blue, nondextrinoid (also after 1 h in Melzer’s reagent), with two nuclei. *Basidia* 18–30 × 5.0–8.0 μm, 4-spored, with clamp connection. *Lamella edge* fertile. *Cheilocystidia* absent. *Pleurocystidia* absent. *Pileus* covering a tightly bound hymeniderm, made up of cells, 23–65 × 10–25 μm, clavate, broadly clavate, to sphaeropedunculate, with short to long pedicel, not obviously pigmented. *Clamp connections* present, especially in hymenium.

**Habitat and distribution.** Solitary to gregarious in small groups, terrestrial in duff, known from Callitropsis macrocarpa stands, Sequoia sempervirens and mixed forests in coastal zone of California, November–December. Distribution outside California unknown.

YMCA woods, eastern part, 27 Aug 2007, R. Healy rh24
nrITS GQ375546, EF1-α GQ375555 (ISC); Webster County, Woodman Hollow State Preserve, 11 Aug 2007, R. Healy rh18 EF1-α GQ375554 and rh39 nrITS GQ375547, EF1-α
GQ375553 (ISC).

*Lepiota neophana* is easy to recognize in the field because of its brown to pale brown strongly umbo-
nate, often slightly radially wrinkled pileus with a light margin, which does not break open into smaller scales and patches, the broadly ventricose yellowish white lamellae and a whitish annulus on the smooth stipe. Microscopically it is characterized by the small binucleate spores, the absence of cheilocystidia and the tightly knit hymenidermal pileus covering. *Lepiota neophana* in the present concept is widely distributed, although rarely recorded.

The species and its name have a long and convoluted history. Morgan (1906) described *L. neophana* from Preston (now New Haven), Hamilton County, Ohio, as, “Pileus fleshy, ovoid then campan-
ulate and expanded, subumbonate, the flesh thin, firm, white; the dermis thin, tough, the surface smooth and glabrous, buff to pale umber, dark brown in the center, the cuticle continuous or at maturity sometimes cracking into irregular areolae. Stipe slender, subequal, tough, fistulous, white above the
annulus, pale umber below, with a white-fibrilloselike cuticle. Lamellae broad, close, white, obtuse behind, free, approximate; spore oblong, obliquely apiculate, 4–5 × 3 mic.

Growing on the ground in woods. Preston, O. Pileus 2–3 cm in diameter; the stipe 3–4 cm long and 2–3 mm thick. The peculiarity of the plant is its toughness in all parts, its subcoreaceous texture.”

The California specimens examined by the present author fit this description very well, although “tough-
ness in all parts” and “subcoreaceous textures” are not characters specifically observed. Murrill (1914) and Kauffman (1924) included the species in their keys but added nothing to Morgan’s description; Murrill (1914) said that it was known only from the type locality.

Smith (1966) studied the type collection and noted, “Spores 4–5.5 × 2.2–2.8 μm, cylindric to broadly ellipsoid in face view and inequilateral in profile view, wall smooth, not thickened, spores adhering together in mounts in Melzer’s sol.; very pale rusty brown to unstained; basidia 13–16 × 4.4–5 μm, 4-spored, hyaline in KOH; pleurocystidia lacking; cheilocystidia lacking, the gill edges fertile; gill trama very compact, interwoven to subparallel, hyaline in KOH, very pale in Melzer’s sol.; pileus trama floccose, hyaline in KOH, very pale yellow in Melzer’s sol.; cuticle a hymeniform layer of pyriform cells 15–26 × 5–10 μm, hyaline in KOH, scarcely

staining in Melzer’s sol., the surface of the pileus not smooth but with frequent elevations and depressions, ruptured in some places and the cuticle missing over part of the surface; clamp connections lacking.”

Franco-Molano also studied the type collection and noted that spores are “inamyloid, ellipsoid to cylindric, (3.6)4.5–6.3 × 2.7–3.6 μm, Q = 1.52,” clamp connections are present (New York Botanical Garden’s Virtual Herbarium http://sweetgum.nybg.org/vh/specimen.php?irn=816627). The sizes of the microscopic characters provided by Smith (1966) are smaller than those found in the California specimens, but the spore sizes provided by Franco-Molano agree much better.

However *Lepiota neophana* has been interpreted in several other ways. Smith (1954) reported a species from Michigan under this name. The pileus is described as, “Pileus 1–3 cm. broad, obtuse to almost globose when young, becoming broadly conic to almost plane, with or without a slight umbo, cuticle continuous at first, remaining smooth on disc, sometimes splitting radially on the margin and showing the white flesh, not truly scaly but the cuticle soon rupturing into small irregular areolae or furfuraceous patches at least toward the margin, disc near army brown, remainder wood brown or having a faint vinaceous tint or ‘avellaneous’. ” The Michigan collection is described microscopically with basidium-like cheilocystidia and faintly dextrinoid spores; clamp connections are said to be absent. Neither the pileus covering rupturing into small areolae nor the basidium-like cheilocystidia fit the original de-
scription of *L. neophana*.

A different interpretation of *Lepiota neophana* is presented by Sundberg (1989) from California. He described a dark almost black species with a pileus covering that cracks open; cheilocystidia and clamp connections are present and numerous. Here again characters of the pileus covering, both color and structure, do not fit the original description. The presence of cheilocystidia is another deviating char-
acter. This taxon is described in this paper as the new species *L. phaeoderma*.

Italian authors described a new variety and a new forma of *Lepiota neophana*, both of which are in good agreement with the description by Morgan, although in general their specimens are paler (Bizio, Migliozzi and Zecchin 1993; type study by Vellinga and Huijser 1999). The California specimens presented here fit their descriptions of the species very well, and this was a decisive factor in considering the name *L. neophana* for these collections. The umbonate pileus with the narrow light margin, the absence of cheilocystidia, and spore characters, all fit very well. Unfortunately no molecular data back this up.
Lepiota thiersii sequences of Lepiota rufipes. L. neophana has a or might appear to justify proper (Lasch) Bon after the globose and L. phaeoderma from California 2.4–2.8 L. neophana 2.5 Lepiota species in which the second nucleus of is also similar to L. rufipes 4.6 Leucoagaricus sequences (F support retained.

Fig. 6. The one most parsimonious tree, based on a dataset of EF-1α sequences of L. neophana from California and Iowa, L. phaeoderma, and with L. magnispora and L. cf pseudoheleveola as outgroups. One hundred three characters were parsimony informative. Numbers above branches indicate branch length, numbers in italics below branches indicate percentage bootstrap support, based on a full heuristic search with 10,000 replicates and groups with > 70% support retained.

Recent collections from northern Iowa (see collections examined) have the same morphological characters as the ones from California but differ slightly in nrITS and more significantly and consistently in EF1-α sequences (Figs. 1, 6). For the time being I refrain from describing the California specimens as a separate taxon; there is no reason to do so on morphological grounds, and to describe a new taxon on molecular data alone seems premature. Sampling is limited and geographically restricted to only two regions (California and Iowa). The existence of L. neophana var. europaea might appear to justify describing the California specimens as another variety. However there is no accepted basis for erecting varietal rank on sequence data.

It might be confusing that the name Lepiota neophana is now used for a different species than the one Sundberg (1989) applied it to, especially because both species co-occur in the same area. Unfortunately the age of the type collection (more than 100 y) rules out any easy use of molecular data. Furthermore there are conflicting interpretations of the species as shown and the likelihood that a species found in Ohio also grows in California might not seem great. Nonetheless the original description, the type studies, the European interpretation of this species and last but not least modern collections from the same general area as where the type was collected support my identification.

Several species look similar to L. neophana or might otherwise be confused with it. Lepiota thiersii has a pileus covering that splits open into small patches and scales but is microscopically similar to L. neophana. Lepiota lupephylla is also similar to L. neophana but has a dark brown pileus and deep yellow lamellae. Lepiota subneophana Murrill, described from Florida (Murrill 1943), despite its name is a Leucoagaricus species with a silky pileus surface with metachromatic spores and without clamp connections (Akers 1997).

Another species also described by Morgan is close to L. neophana and has its own problems. Morgan (1906) described Lepiota rufipes Morgan as, “Pileus a little fleshy, convex, smooth and glabrous, white. Stipe slender, smooth and glabrous, rufescent, paler at the summit; the annulus evanescent. Lamellae broad, close, white, free, approximate; spores oblong, 4–5 × 3 μm. Growing on the ground in woods among old leaves; Preston, O. Pileus about a centimeter in diameter, the stipe 2–3 cm long.”

This description could apply to a specimen of Cystolepiota seminuda (Lasch) Bon after the globose cells have been washed off by rain, but the European interpretation of Lepiota rufipes is a species with a hymeniform pileus covering within Lepiota proper (Kühner and Maire 1937). In this interpretation the species has a pale, cream to pinkish pileus that does not break open into scales, no annulus, small uninucleate spores, and narrowly clavate cheilocystidia (Vellinga and Huijser 1999). This taxon is one of the few Lepiota species in which the second nucleus of the developing spores migrates back to the base of the basidia instead of staying put (Kühner 1945). It shares with L. neophana the tightly knit pileus covering but differs in the presence of cheilocystidia and uninucleate spores. Lepiota rufipes features in the account of the Michigan species by Smith (1954) as a rare species with a white, almost chalky pileus becoming sordid with age. The rest of the characters are in concordance with those reported by the European authors. Smith (1966) did not include L. rufipes in her studies on North American type collections. Fortunately the original Morgan collection of L. rufipes was located in the ISC herbarium with “type” written in pencil on the envelope. Little remained of the original basidiocarp, but these characters could be noted (Fig. 7): basidiospores [20,1,1] in side view and frontal view 4.1–4.9 × 2.4–2.8 μm, avl × avw = 4.6 × 2.5 μm, Q = 1.65–2.05, avQ = 1.85, oblong to subcylindrical, smooth, without germ pore, not congophilous, not dextrinoid, slightly metachromatic in Cresyl blue; basidia 4-spored; cystidia not observed,
partly due to the state of the dried collection; lamella trama regular; pileus covering an epithelium made up of noncolored globose to subglobose, rarely sphaeropedunculate elements, 17–40 μm diam; clamp connections present.

The relatively narrow spores and the epithelioid pileus covering support synonymy with *Cystolepiota semenuda* (Lasch) Bon, as the description already suggested. Accordingly the Eurasian species, commonly referred to as *L. rufipes*, must be described as new.

6. **Lepiota phaeoderma** Vellinga, sp. nov. MycoBank MB 514125


**Selected description.** Sundberg, Mycotaxon 34:245–247. 1989 (as *L. neophana*).

*Lepiotae hymenodermati* similis pileo coloribus atris stipitis basi sine squamulis differt.

Holotypus “USA. California: San Mateo County, San Francisco watershed, 10 Feb 1970, H.D. Thiers HDT 24773.” (HOLOTYPE designated here, SFSU)

**Etymology.** The epithet *phaeoderma* is a transliteration and latinization of Greek words ἡξιός, meaning dark, and δέρμα, skin, because of the dark pileus covering.

**Pileus** 22–26 mm, broadly campanulate with broad umbo when young, later wavy plano-convex with broad umbo, almost black at center (10 YR 3–2/1), and smooth, around center breaking open into very small dark brown (10 YR 3/3), smooth patches on white to whitish background, very pale at margin; margin just exceeding lamellae. **Lamellae**, L. = 45–50, 1 = 1–3, rather crowded to moderately crowded, free and very close to stipe, slightly ventricose up to 3.5 mm wide, rounded near stipe, whitish, cream-colored with slightly pinkish sheen; edge white and cystidiose. **Stipe** 32–45 × 3.5–5.5 mm, cylindrical, cream at apex, lower down with whitish fibrillose, when young with slightly fluffy covering over pink-brown or pink-red background, later without any ornamentation or annulus, hollow, with white mycelial cords at base. **Annulus** absent. **Context** white and rather thick in pileus, cream-colored in stipe apex, pinkish brown toward base. **Odor** strong, astringent, like the rubber odor of *Lepiota cristata*, or in addition fruity.

**Basidiospores** [68,4,4] 4.4–6.3 × 2.5–3.4 μm, avl × avw = 4.9–5.2 × 2.9–3.0 μm, Q = 1.5–2.1, avQ = 1.65–1.8, in side view ellipsoid, oblong, a few subcylindrical, with flattened or convex adaxial side, in frontal view ellipsoid to subcylindrical, slightly thick-walled, smooth, without germ pore, clustering in groups, vaguely reacting in Congo red, not dextrinoid (also after 1 h in Melzer’s reagent), with pink inner wall in Cresyl blue, with two nuclei.

**Basidia** 18–29 × 5.5–7.5 μm, 4-spored, with basal clamp connection. **Lamella edge sterile.** Cheilocystidia 18–42 × 5.5–13 μm, clavate to narrowly clavate, some with long pedicel, hyaline and without contents. **Pleurocystidia** absent. **Pileus covering** a hymeniderm made up of 23–60 × 10–16 μm, clavate to narrowly clavate, sphaeropedunculate, with pedicel of varying length, with brown intracellular pigment. **Clamp connections** present in all tissues.

**Habitat and distribution.** Solitary or in small groups, terrestrial and saprotrophic in duff of *Callitropsis macrocarpa* in *C. macrocarpa* stands and in mixed...
woodlands. Nov–Apr. Known from San Mateo, Santa Clara and Butte counties, California, USA

Collections examined. USA. California: Santa Clara County, Palo Alto, Los Tranco Preserve, 21 Nov 2006, D. Smith; California, San Mateo County, San Francisco watershed, 3 Jan 1967, H.D. Thiers (Sundberg 1095) (SFSU); ibidem, 16 Apr 1967, H.D. Thiers HDT 18829 (SFSU); ibidem, 10 Feb 1970, H.D. Thiers HDT 24773 (Holotype, SFSU); ibidem, 7 Jan 2003, E.C. Vellinga 3000, nrITS GQ293810, EF1-a GQ375549; ibidem, 28 Jan 2003, E.C. Vellinga 5016.

Lepiota phaeoderma is easily recognized because of the dark pileus with small patches around the center, the hymeniform pileus covering and the narrowly clavate to clavate cheilocystidia. The stipe has no scales and does not have an annulus.

This is Lepiota neophana Morgan sensu Sundberg (1989), which deviates from the original description by Morgan (1906) in the colors of the pileus and the surface that is cracking open, forming small patches around the umbo. A comprehensive discussion of L. neophana is given above.

Sundberg (1989) gave a thorough description of L. phaeoderma (as L. neophana). The above macroscopic description is based on my own observations of a limited number of collections of this species; the description of the microscopic characters also is based on some of the collections studied by Sundberg (1989).


Macroscopically L. scaberula and its European counterparts L. cystophoroides Joss. & Rioussel and C. cystophora (Malecon) Bon are quite different from the other species treated here, with a much more fibrillose-squamose pileus covering and a distinctly fibrillose-woolly stipe. Microscopically the pileus covering is more cutis-like with clavate to globose upright terminal elements. The more characteristic members of this group have a pileus covering that is either not split up or split up into small patches composed of tightly packed narrowly clavate to clavate cells and a stipe without scales or with a few scales at the base.

Lepiota scaberula is known from a few places in coastal central California.


Lepiota thiersii has a pileus covering that splits open into small patches around a closed disk, a small annulus, and ellipsoid spores; it lacks cheilocystidia. In the field it can be confused with L. castaneidisca but differs in the ellipsoid spores and the presence of cheilocystidia. It differs from L. neophana in the covering that splits open but shares the small ellipsoid spores and the absence of cheilocystidia with that species. The spores show a pink inner wall in Cresyl blue, as do many other species in the group. It differs from L. phaeoderma in the much paler, brown pileus covering, and the absence of cheilocystidia. The interpretation of L. neophana by Smith (1954) actually might refer to this species. Lepiota thiersii occurs in coastal central California but is rarely encountered or more likely rarely recognized.

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**LITERATURE CITED**


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