Lactarius in California and Beyond: 
Introduction to Subgenera and Species of Lactarius in California

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Nomenclature and History

The genus *Lactarius* was established under the orthographic variant *Lactaria* by Persoon (1797) who later reduced the genus *Lactaria* to a section of *Lactifluus* within the genus *Agaricus* (Persoon, 1801). De Candolle (1805) perpetuated Persoon's original name *Lactaria* but substituted *Lactaria* for *Lactifluus* as a section of *Agaricus* (Donk, 1962). Although S.F. Gray (1821) restored *Lactarius* to generic rank as an orthographic variant of *Lactaria* in *A Natural Arrangement of British Plants*, Fries (1821) recognized this group as "tribus" *Galorrhoeus* within the genus *Agaricus*. Fries (1825) subsequently raised *Galorrhoeus* to generic rank but later abandoned the name *Galorrhoeus* and began using *Lactarius* without citing an author (Fries, 1836-1838). Thus, the valid name *Lactarius* clearly dates to S.F. Gray (1821) in the Friesian period and to *Lactaria* in the pre-Friesian era.

The development of subgeneric and sectional concepts for *Lactarius* in North America has proceeded from the work of Burlingham (1907, 1908, 1910), Kauffman (1918), Singer (1986), and Hesler and Smith (1979) to the framework employed here. The synopsis of *Lactarius* presented is patterned after Hesler and Smith (1979) with two notable exceptions. First, the generic name *Lactarius* has been conserved by the *International Code of Botanical Nomenclature* with *Lactarius piperatus* designated as the type of the genus. Since *L. piperatus* is the type of the genus, the subgenus and section within which it resides must be designated as subgenus and section *Lactarius*, respectively. As such, Hesler and Smith's (1979) subgenus and section *Lactifluus* become subgenus and section *Lactarius*. Second, the taxa previously included in Hesler and Smith's (1979) subgenus *Lactarius* must now be placed in section with a different name. Since the earliest available name is *Dapetes*, Hesler and Smith's (1979) subgenus *Lactarius* must now be placed in section with a different name. Since the earliest available name is *Dapetes*, Hesler and Smith's (1979) subgenus *Lactarius* is recognized as subgenus *Dapetes*. The classification outlined in the synopsis should be compared with that of Singer (1986), not because the classification presented here is better, rather that Singer’s system is worldwide in scope and includes a number of sections and subsections not known from the northern hemisphere.

Knowledge of *Lactarius* in North America has resulted from the work of relatively few mycologists. While Peck (1907) described several new species of *Lactarius*, including *L. rufulus* and *L. xanthogalactus* from California, Earle (1902a, 1902b) and Burlingham (1907, 1908, 1910) were the first mycologists to produce monographic treatments of *Lactarius* in North America. Burlingham’s contribution to the *North American Flora* project brought together most of the previous knowledge of *Lactarius* in North America and provided the foundation for future work on the genus. Burlingham spent several winters in California, Oregon, and Washington collecting fungi and later published a treatment of the species of *Lactarius* she encountered along the Pacific coast (1913). Coker's (1918) monograph of the *Lactariaceae* of North Carolina was an important regional study as were Kauffman's (1918) for Michigan and Murrill's for Florida (1938, 1942, 1943, 1948). Hesler and Smith's early studies of *Lactarius* (1960a, 1960b, Smith and Hesler 1962) were the most comprehensive for North America until the publication of the *Lactarius* monograph in 1979. Subsequent papers which discuss species of *Lactarius* include those by Bills (1986) and Methven (1985, 1992, 1993, 1997, 1998). Methven’s (1997) monograph of *Lactarius* in California represents the culmination of more than fifteen years of study. Methven (1997) was careful to point out, however, that additional taxa will undoubtedly be collected and described from California.
Introduction

Morphology of the Basidiomata

Within the family Russulaceae, the appearance of latex when the basidiomata are cut or mechanically damaged can be used to separate Lactarius from Russula. In general, individual taxa within Lactarius are rarely identifiable by a single character but are distinguished by "suites" of characters which, although consistent within a taxon, accommodate variation encountered in the field. The importance of field and laboratory characters are treated briefly in the following discussion. Additional information can be found in the publications of Burlingham (1908), Hesler and Smith (1979), and Methven (1992, 1993, 1997). Color terms and alphanumeric designations are from Kornerup and Wanscher (1978).

Macroscopic Characters

Pileus

The coloration of the pileus is more useful in identification of taxa than other features (size; shape - convex to plane or uplifted; disc - depressed, umbilicate or umbonate; margin - glabrous, pubescent or bearded; surface - glabrous, velutinous, pubescent or fibrillose as well as dry, moist, subviscid or viscid; zonation - present or absent). It is important to note both the color of immature and mature pilei and any discolorations which develop. Immature pilei are generally more darkly colored than mature pilei. The odor of the pileus context or flesh is useful in the identification of certain taxa but reported as "not distinctive" (i.e., fungoid) for the majority of taxa. Following drying, the basidiomata of L. cocoseolens and L. rubidus have an odor of coconut and maple sugar respectively. The taste of the pileus context can be a valuable taxonomic character although it is virtually impossible to separate the taste of the context from the taste of the latex. The taste is described as bitter, acrid or not distinctive (i.e., fungoid). Pieces of the flesh should be chewed up to 60 seconds to determine whether or not the taste is distinctive and definable.

Lamellae

The spacing, coloration and staining reactions of the lamellae are more useful in identification than other characters (attachment - adnate to subdecurrent; forking - present near the stipe in most taxa; lamellulae - present in one or more tiers). Although most taxa feature lamellae which are close to subdistantly spaced, it is important to note when the lamellae are crowded, as in L. piperatus (Fr.) S. F. Gray, or distant, as in L. lignyotus Fr. Immature lamellae are white to pale yellow or pale orange. As the lamellae mature, more pronounced yellow or orange tints often develop. As the lamellae mature, more pronounced yellow or orange tints often develop. It is important to record any discoloration of the lamellae as the basidiomata mature and staining reactions which result from mechanical injury.

Stipe

The characters of the stipe (size; shape - cylindrical, clavate, terete; surface - glabrous, pruinose or fibrillose-streaked and dry, subviscid or viscid; presence or absence of scrobiculations; basal tomentum) are of limited taxonomic value. The coloration of the stipe is paler than or concolorous with the pileus and, if present, the scrobiculations are darker in color. The context or flesh of the stipe is described as solid, stuffed or hollow, and is concolorous with the pileus context.
Latex

Although the latex is usually white or whey-like (similar to watery skim milk) when exuded, the latex may be colored when exuded or become colored on exposure to the air. The color, color changes, staining reactions, and taste of the latex are indispensable in identification. Without detailed notes on color, color changes, staining reactions, and taste of the latex, most specimens cannot be identified with any degree of certainty. This situation is particularly problematic with herbarium specimens that lack notes. One of the basidiomata should be cut lengthwise and the lamellae cut in the field, the color of the latex noted, and latex applied to the surface of a white field label. Any changes in the color of the latex and/or staining reactions on the lamellae, context, and field label should be apparent upon return to the laboratory. Discolorations or staining reactions which develop overnight are of questionable value but should be recorded. The taste of the latex is described as bitter, acrid or not distinctive (i.e., fungoid). A mechanical cut across the lamellae, apex of the stipe surface or tangential section of the pileus will provide enough latex to be applied to the tip of the tongue. Sixty seconds should be allowed for the development of taste.

Basidiospore Deposit

The color of the basidiospores in mass ranges from white to pale yellow. The color of the basidiospores in mass should only be recorded from moderate or heavy deposits which have been allowed to air dry overnight. Changes in coloration have been noted depending on the "thickness" of the deposit, environmental conditions, manner in which the deposit was dried (air dried versus mechanically dried), and light under which the deposit was observed. As such, little taxonomic emphasis is placed on the color of the basidiospores in mass.

Microscopic Characters

Pileipellis

The pileipellis includes all differentiated layers covering over the pileus context. The types of pileipellis observed in Lactarius are taxonomically important in the delimitation of subgenera, sections, and species. The following pileipellis types, descriptions, and illustrations are used to define individual taxa:

Cutis (Fig. 1) - A layer of repent, loosely interwoven hyphae appressed to the pileus surface which radiate from the disc to the margin.

Modified cutis (Fig. 2) - Similar to a cutis but with scattered, inflated cells.

Ixocutis (Fig. 3) - A simple cutis in which the hyphae secrete gelatinized material or become gelatinized and produce a conspicuous gelatinous layer.

Ixolattice (Fig. 4) - Intermediate between an ixocutis and an ixotrichodermium. The hyphal elements become branched and entangled to form an intricate lattice. An ixolattice may arise from a thick ixocutis which gradually expands as the hyphae gelatinize or as an ixotrichodermium which collapses.

Cellular (Fig. 5) - A layer 1-3 (4) cells deep of isodiametric or vesiculose cells originating from an interwoven layer of hyphae. Limited to taxa in subgenus Russularia.

Palisade (Fig. 6) - A cellular layer in which the terminal cells become oriented vertically to the pileus surface and form a turf. Limited to taxa in subgenus Russularia.
Pileipellis

**Trichodermium (Figs. 7,8)** - An upright layer of hyphal elements arising from an interwoven layer of filamentous hyphae or scattered, inflated cells.

**Fascicles of projecting hyphae (Fig. 9)** - Clusters of hyphae which project from the surface of the pileipellis.

**Modified trichodermium (Fig. 10)** - A trichodermium modified when the cells of the hyphal elements become inflated and packed tightly together by enlarging hyphal cells. The ultimate and penultimate cells of the elements elongate to produce a turf and the inflated cells often form a cellular layer. Limited to taxa in subgenus Plinthogalus.

**Ixotrichodermium (Figs. 11-12)** - A highly developed gelatinous layer into which hyphal elements of unequal length project and resemble a turf of grass.

Basidiospores

Basidiospores are measured in profile and reported without the height of the ornamentation. Most taxa produce basidiospores in the 7-9.5 x 6-7.5 um range with ornamentation which ranges from 0.5-1.5 um in height. Basidiospore size is reported as a range of sizes into which most of the basidiospores measured fit rather than as absolute values. Basidiospore sizes included in parentheses are extremes for a given size range. Basidiospores measured from squash mounts are often 0.5-1 um smaller than those measured from deposits. The shape of the basidiospores (globose, subglobose, broadly ellipsoid, ellipsoid) is reported as a range to include the variation frequently observed. The ornamentation of the basidiospores is a composite structure of the fundamental exosporium and disintegrating perisporium. In *Lactarius* the basidiospore ornamentation stains dark blue to bluish black in Melzer's reagent and is described as being amyloid. Portions of the basidiospore wall which are not covered with amyloid ornamentation appear yellow in Melzer's reagent. The patterns of ornamentation ranges from isolated, spinose elements to a heavily deposited complete reticulum. The following basidiospore ornamentation types, descriptions, and illustrations are used to define individual taxa:

**Isolated elements (Fig. 13)** - Warts and isolated elements lacking amyloid connecting lines between the elements.

**Broken reticulum (Fig. 14)** - Warts and ridges organized so that if connected the ornamentation would form a reticulum.

**Partial reticulum (Fig. 15)** - Ridges and warts fused in places to form enclosed areas which are often hexagonal in outline. Isolated warts and ridges scattered on the basidiospore surface.

**Complete reticulum (Fig. 16)** - Warts and ridges almost completely fused into meshes. Isolated warts and ridges rare to absent.

**Winged elements (Fig. 17)** - A broken to partial reticulum in which the prominences are 1.5-3 um high. Limited to taxa in subgenus Plinthogalus.

**Zebroid (Fig. 18)** - A broken reticulum of unconnected ridges arranged in bands to resemble the stripes of a zebra.
Basidia

The basidia are typically 30-60 x 6-12 μm, clavate, four-sterigmate, hyaline, and thin-walled. Due to the uniformity of the size and shape of the basidia, no taxonomic importance is accorded them.

Pseudocystidia

Pseudocystidia are cystidia which terminate the laticifers or laticiferous hyphae and extend into the hymenium. Pseudocystidia are typically 3-4.5 μm diam, filamentous, undulating, thin-walled, and hyaline. No taxonomic importance is attached to pseudocystidia since their presence is the hymenium is all inclusive.

Macrocystidia

Macrocystidia also terminate the laticifers or laticiferous hyphae and are considered to be specialized forms of pseudocystidia. Macrocystidia are the most prominent structures produced in the hymenium and range in size from 45-90 (120) x 6-15 μm. The shape ranges from cylindric to clavate, fusoid, lanceolate or fusoid-ventricose with apices that range from obtuse to acute or mucronate. Macrocystidia often feature one or more subapical constriction. Due to the variation observed in the size and shape of macrocystidia, often within a single taxon, macrocystidia morphology is generally considered to be of limited taxonomic value. The most useful feature is the presence or absence of macrocystidia in the hymenium.

Cheilocystidia

Cheilocystidia are limited to the lamellar edge. They either resemble immature basidia which do not produce sterigmata or smaller-sized macrocystidia. Due to the variation in the size and shape of cheilocystidia, often within a single taxon, cheilocystidia morphology is generally considered to be of limited taxonomic value. The most useful character is the presence or absence of cheilocystidia on the lamellar edge.

Stipitipellis

The stipitipellis includes all differentiated layers covering the stipe context. Although the same terms used to describe the pileipellis are also applied to the stipitipellis, the structure of the stipitipellis is of limited taxonomic value.
Synopsis of the Genus Lactarius in California

Subgenus Dapetes
L. deliciosus var. areolatus
L. deliciosus var. deliciosus
L. deliciosus var. olivaceosordidus
L. deliciosus var. piceus
L. rubrilacteus

Subgenus Plinthogalus
Section Fumosi
L. pallidolivaceus
Section Plinthogalus
L. fallax var. concolor
L. fallax var. fallax

Subgenus Lactarius
Section Albati
Section Allardii
Section Lactarius
Section Lactifluus

Subgenus Piperites
Section Aspideini
L. aspideoides
L. representaneous
Section Atroviridi
L. necator
L. olivaceo-umbrinus
Section Piperites
Subsection Croceini
L. xanthogalactus
Subsection Piperites
L. controversus
L. pubescens var. betulae
L. subvillosus
L. torminosus var. nordmanensis
Subsection Scrobiculati
L. alnicola var. alnicola
L. resimus var. resimus
L. scrobiculatus var. canadensis
L. scrobiculatus var. montanus
L. scrobiculatus var. pubescens

Subgenus Tristes
Section Colorati
Section Pseudomyxacium
L. argillaceifolius var. megacarpus
L. caespitosus
L. glutigriseus
L. kauffmanii var. kauffmanii
L. pseudomucidus
Section Tristes
L. circellatus var. borealis
Section Violaceo-Maculati
L. californiensis
L. pallescens var. pallescens
L. uvidus var. montanus

Subgenus Russularia
Section Pseudo-Aurantiaci
L. substriatius
L. subviscidus
Section Russularia
L. atrobadius
L. desjardini
L. luculentus var. laetus
L. riparius
L. rufus
L. subflammeus
Section Subsquamulosi
L. alpinus var. mitis
Section Thejogali
L. occidentalis
L. rubidus
L. rufulus
L. thiersii
Section Triviales
L. cocoseolens
L. hygsoni var. americanus
L. manzanitae

1Following the classification system outlined by Hesler and Smith (1979)
2Taxa included in Subgenus Lactarius have not been reported west of the Rocky Mountains including California
3Taxa included in Section Colorati have not been reported from California
Key to California Species of Lactarius

Key to Subgenera of Lactarius

1a. Latex white to whey-like when exuded; basidiomata not staining green .................................. 2
1b. Latex orange or reddish brown when exuded; basidiomata staining dull green ........... Subg. Dapetes

2a. Pileus and stipe velutinous .......................................................... 3
2b. Pileus and stipe not velutinous ....................................................... 4

3a. Pileus white, yellow, orange or red; latex white, copious, unstaining or staining lamellae and flesh brown; macrocystidia frequently present ................................................................. Subg. Lactarius
3b. Pileus brownish grey, light brown, brown or dark brown; latex white, often scant, staining flesh and lamellae pink, lilac or violet; macrocystidia absent .................................... Subg. Plinthogalus

4a. Pileus dry to viscid, yellow, orange, red-orange, red or reddish brown; latex unstaining or staining flesh and lamellae yellow; dextrinoid debris lacking in the pileipellis .............................................................. 5
4b. Pileus viscid, greyish brown, brownish orange or brown; latex staining flesh and lamellae violet to brown; dextrinoid debris present in the pileipellis .............................................................. Subg. Tristes

5a. Basidiomata yellow, yellow-orange or red-orange; pileus surface and margin pubescent to tomentose, often viscid and zonate; stipe > 10 mm thick, scrobiculate .................................................................................................................. Subg. Piperites
5b. Basidiomata bright orange, bright red or reddish brown; pileus glabrous, dry, moist or viscid, azonate; stipe 2-10 mm thick, rarely scrobiculate .............................................................. Subg. Russularia

Key to Species of Subgenus Dapetes

1a. Latex orange when exuded .............................................................. 2
1b. Latex reddish brown when exuded .................................................. L. rubrilacteae

2a. Flesh and lamellae staining reddish brown ....................................... 3
2b. Flesh and lamellae not staining reddish brown .................................. 4

3a. Macrocystidia present; coastal and montane coniferous-deciduous forests in association with Picea sitchensis .......................................................... L. deliciosus var. piceus
3b. Macrocystidia absent; coastal and montane coniferous-deciduous forests .......................................................... L. delicosus var. areolatus

4a. Macrocystidia present; pileus with greyish green colors masking golden yellow to brownish yellow ground color on scarcely mature basidiomata; coastal coniferous-deciduous forests in association with Picea sitchensis .......................................................... L. deliciosus var. olivaceosordidus
4b. Macrocystidia absent; pileus greyish orange to brownish orange, staining dull green at maturity; coastal and montane coniferous-deciduous forests .......................................................... L. deliciosus var. deliciosus
Key to Species of Subgenus Plinthogalus

1a. Pileus and stipe brown to dark brown; coastal coniferous-deciduous forests in association with *Picea sitchensis* ........................................ 2
1b. Pileus brownish grey to light brown; stipe white to pale orange; coastal and montane coniferous-deciduous forests .................................. *L. pallidiolivaceus*

2a. Lamellae marginate; margins grey brown to dark brown ............... *L. fallax* var. *fallax*
2b. Lamellae not marginate, white to light yellow overall ............... *L. fallax* var. *concolor*

Key to Species of Subgenus Tristes

1a. Lamellae and flesh staining lilac to violet ........................................ 2
1b. Lamellae and flesh not staining lilac to violet .................................. 4

2a. KOH not producing a green reaction on pileus surface; basidiospore ornamentation > 0.5 um high ................................................................. 3
2b. KOH producing a green reaction on pileus surface; basidiospore ornamentation < 0.5 um high ............................................................. *L. uvidus* var. *montanus*

3a. Pileus greyish yellow, brownish orange or light brown; pileipellis an ixtrotichodermium, collapsing to an ixolattice; stipitipellis an ixocutis ... *L. pallescens* var. *pallescens*
3b. Pileus greyish red on disc, orange grey to brownish orange toward margin; pileipellis an ixocutis; stipitipellis a simple cutis ........................................ *L. californiensis*

4a. Stipe dry; stipitipellis a simple cutis .................................................. 5
4b. Stipe distinctly viscid; stipitipellis an ixocutis to ixolattice .................. 6

5a. Pileus obscurely zonate, greyish ruby; lamellae not staining; basidiospore ornamentation zebroid in profile ........................................ *L. circellatus* var. *borealis*
5b. Pileus greyish yellow to brownish orange or light brown; lamellae staining brown; basidiospore ornamentation not zebroid in profile .... *L. argillaceifolius* var. *megacarpus*

6a. Basidiospores 7-9.5 x 6-8 um, ornamentation > 0.5 um high ............... 7
6b. Basidiospores 9-11.5 x 7.5-8.5 um, ornamentation < 0.5 um high; montane coniferous forests in association with *Abies* spp. ...................... *L. caespitosus*

7a. Pileus (1) 2-7 cm diam, brownish orange to greyish orange or greyish brown to light brown; stipe 3-10 (15) mm diam; latex white, unchanging or drying pale yellow ............... 8
7b. Pileus 5-15 (30) cm diam, brown to dark brown; stipe 10-30 mm diam; latex white, slowly drying grey-green ............................................... *L. kauffmanii* var. *kauffmanii*
8a. Pileus and stipe greyish brown to light brown, slimy viscid; latex white, slowly drying yellow; coastal coniferous-deciduous forests ....................... *L. pseudomucidus*
8b. Pileus and stipe brownish orange to greyish orange, subviscid; latex white, unchanging; montane coniferous forests in association with *Tsuga* spp. .......... *L. glutigriseus*
Key to Species of Subgenus Piperites

1a. Pileus and stipe olive brown to dark green; lamellae staining olive brown; KOH staining pileus surface magenta to purple ............................................. 2
1b. Pileus and stipe differently colored; lamellae not staining olive brown; KOH not staining pileus surface magenta to purple ............................................. 3

2a. Basidiospores 6-8 um wide, ornamentation ≥ 0.5 um high; coastal coniferous forests in association with Picea sitchensis .................. L. olivaceo-umbrinus
2b. Basidiospores 4.5-6 um wide, ornamentation ≤ 0.5 um high; in association with Betula spp., introduced .................. L. nectar

3a. Basidiospores 7.5-9 (10) x 6-7.5 um or larger ............................................. 4
3b. Basidiospores 6-7.5 x 4.5-6 um ............................................. 10

4a. Lamellae and flesh staining violet to lilac ............................................. 5
4b. Lamellae and flesh not staining violet to lilac ............................................. 6

5a. Pileus surface coarsely fibrillose; pileus margin bearded; stipe scrobiculate .................. L. representans
5b. Pileus surface glabrous; pileus margin glabrous; stipe not scrobiculate .................. L. aspideoides

6a. Latex white, quickly changing to yellow on exposure ............................................. 7
6b. Latex white, unchanging or slowly changing to pale yellow on exposure ............................................. 9

7a. Pileus margin initially tomentose; pileus pale yellow ............................................. 8
7b. Pileus margin initially pruinose to glabrous; pileus initially greyish orange to brownish orange then reddish brown .................. L. xanthogalactus

8a. Pileus pale yellow; pileus margin initially tomentose then glabrous; montane coniferous forests, often semihypogeous .................. L. scrobiculatus var. montanus
8b. Pileus yellowish orange; pileus margin densely bearded; coastal coniferous-deciduous forests .................. L. scrobiculatus var. canadensis

9a. Pileus pale yellow; pileus margin pubescent; flesh slowly staining pale yellow; coastal coniferous-deciduous forests .................. L. alnicola var. alnicola
9b. Pileus light orange to greyish orange; pileus margin tomentose; flesh not staining; montane coniferous-deciduous forests in association with Abies spp., Salix spp., and Populus spp. .................. L. torminosus var. nordmanensis

10a. Latex white, quickly changing to yellow on exposure ............................................. 11
10b. Latex white, unchanging or slowly changing to pale yellow on exposure ............................................. 12

11a. Pileus milk white, developing greyish orange stains, viscid; pileus margin bearded; coastal and montane coniferous-deciduous forests .................. L. resimus var. resimus
11b. Pileus light yellow, moist to dry; pileus margin pubescent; montane coniferous forests in association with Abies spp. and Pinus spp. .................. L. scrobiculatus var. pubescens

12a. Pileus and stipe pale yellow, light orange or brownish orange; lamellae not pink ............................................. 13
12b. Pileus and stipe white; lamellae pink ............................................. L. controversus
13a. Pileus zonate, light orange zones alternating with brownish yellow to brownish orange zones; pileus margin tomentose; coastal and montane coniferous-deciduous forests

13b. Pileus azonate, pale yellow to pale orange; margin densely bearded; in association with Betula spp, introduced

Key to Species of Subgenus Russularia

1a. Pileipellis a palisade of vesiculose to clavate cells which form a layer 3-5 cells thick

2a. Odor of basidiomata not distinctive when fresh or dried

2b. Basidiomata with odor of maple sugar when dried; pileus and stipe light brown to reddish brown; coastal and montane coniferous-deciduous forests in association with Quercus spp

3a. Pileus and stipe trama lacking conspicuous rosettes of sphaerocysts; not associated with Alnus spp

3b. Pileus and stipe trama with conspicuous rosettes of sphaerocysts; pileus brown to dark brown; lamellae staining reddish brown; coastal and montane coniferous-deciduous forests in association with Alnus spp

4a. Pileus 1-3 cm diam, cinnamon to ochraceous-tawny; basidiospores 8.5-10.5 x 7.5-9 um, subglobose to broadly ellipsoid; amyloid ornamentation a broken to nearly complete reticulum; coastal coniferous-deciduous forests in association with Pinus spp

4b. Pileus 3-7 cm diam, reddish brown; basidiospores 7-9 um diam, subglobose; amyloid ornamentation a broken reticulum; coastal coniferous forests in association with Quercus spp

5a. Pileus not becoming squamulose to fibrillose-scaly at maturity; pileipellis a cutis, ixocutis, ixolattice or ixotrichodermium

5b. Pileus becoming squamulose to fibrillose-scaly at maturity; pileipellis a modified cutis of loosely arranged hyphae aggregated into tufts or short fascicles; coastal coniferous-deciduous forests in association with Alnus spp

6a. Latex white to whey-like, changing to yellow or staining tissues yellow

6b. Latex white to whey-like, not changing to yellow or staining tissues yellow

7a. Pileus orange to reddish orange, viscid; pileus margin translucent-striate; hypodermium filamentous; coastal and montane coniferous-deciduous forests

7b. Pileus brownish orange to reddish brown, subviscid; pileus margin not translucent-striate; hypodermium cellular; coastal coniferous-deciduous forests in association with Picea spp

8a. Stipe moist to dry, not viscid; stipitipellis a cutis

8b. Stipe viscid to subviscid; stipitipellis an ixocutis to ixolattice

9a. Pileus viscid to subviscid; pileipellis an ixocutis, ixolattice or ixotrichodermium

9b. Pileus moist to dry but not viscid; pileus reddish brown; latex burning acrid; coastal coniferous-deciduous forests in association with Pinus

L. subvillosus
L. pubescens var. betulae
L. rubidus
L. occidentalis
L. thiersii
L. rufulus
L. alpinus var. mitis
L. substriatus
L. subviscidus
L. rufus
10a. Pileipellis an ixocutis .......................... 11
10b. Pileipellis an ixotrichodermium or modified ixotrichodermium .......................... 12

11a. Pileus 2-4 cm diam, brownish orange to reddish brown; taste not distinctive; basidiospores 7-9.5 x 5.5-7 μm, broadly ellipsoid; amyloid ornamentation a broken to partial reticulum; montane coniferous-deciduous forests in seepage areas in association with Abies spp, Alnus spp, and Salix spp .......................... L. riparius

11b. Pileus 5-7 cm diam, light orange to greyish orange; taste acrid; basidiospores 5.5-7 x 5.5-6.5 μm, subglobose; amyloid ornamentation a partial to complete reticulum; coastal coniferous-deciduous forests .......................... L. desjardinii

12a. Pileus brownish orange to orange brown or reddish brown; basidiospores 7.5-10 x 6.5-9.5 μm; amyloid ornamentation a broken reticulum; hypodermium filamentous with scattered inflated cells .......................... 13

12b. Pileus dark vinaceous-brown; basidiospores 6.5-8 x 6-7 μm; amyloid ornamentation a complete reticulum; hypodermium filamentous, lacking inflated cells; coastal coniferous-deciduous forests in association with Sequoia sempervirens .......................... L. hysginus var. americanus

13a. Pileus reddish brown; lamellae close to subdistant, not staining; taste acrid; basidiospores 7.5-9 x 6.5-7.5 μm .......................... L. subflammeus

13b. Pileus brownish orange to light brown; lamellae crowded, staining brown; taste not distinctive; basidiospores 8-10 x 7-8.5 μm .......................... L. luculentus var. laetus

14a. Pileipellis an ixotrichodermium collapsing to an ixolattice; hypodermium filamentous .......................... 15

14b. Pileipellis a modified ixotrichodermium; hypodermium cellular, each cell giving rise to one or more hyphal-like extensions; pileus and stipe blackish red; lamellae staining dark red; coastal coniferous-deciduous forests in association with Pinus spp, Picea spp, and Alnus spp .......................... L. atrobaadius

15a. Taste acrid, odor not distinctive; hypodermium filamentous; stipitellis an ixocutis expanding into an ixolattice .......................... L. manzanitae

15b. Taste not distinctive, odor of coconut; hypodermium filamentous with scattered inflated cells; stipitellis an ixocutis .......................... L. cocoseolens
A synoptic key is included to facilitate identification of species of *Lactarius*. It may be of value, for example, when characters utilized in the dichotomous key are not readily apparent. Unlike the dichotomous key, where entry into the key must be entered at the first couplet, the synoptic key may be entered at any point. The following features of the synoptic key should be noted:

1. A number in *italics* indicates that a species is listed under more than one alternative; that is, the species shows variation with respect to the character in question.
2. Color terms in the key should be interpreted as indicating a range; i.e., from dilute to dense, bright to dull, and pure to impure.
3. Species 4, 5, 19, 30, and 44 are characterized in part on the basis of their type descriptions and published reports. All other species are characterized from firsthand observations on fresh and dried material.
4. If there are but two choices (see character 3.3), then species numbers are listed only for the choice with fewer taxa; the alternate choice is given, but placed in parentheses.

**Taxa Included in Synoptic Key**

1. *Lactarius alnicola* var. *alnicola*
2. *Lactarius alpinus* var. *mitis*
3. *Lactarius argillaceifolius* var. *megacarpus*
4. *Lactarius aspideoides*
5. *Lactarius atrobadius*
6. *Lactarius caespitosus*
7. *Lactarius californiensis*
8. *Lactarius circellatus* var. *borealis*
9. *Lactarius controversus*
10. *Lactarius cocoseolens*
11. *Lactarius deliciosus* var. *areolatus*
12. *Lactarius deliciosus* var. *deliciosus*
13. *Lactarius deliciosus* var. *olivaceosordidus*
14. *Lactarius deliciosus* var. *piceus*
15. *Lactarius desjardinii*
16. *Lactarius fallax* var. *concolor*
17. *Lactarius fallax* var. *fallax*
18. *Lactarius glutigriseus*
19. *Lactarius hysginus* var. *americanus*
20. *Lactarius kauffmanii* var. *kauffmanii*
21. *Lactarius luculentus* var. *laetus*
22. *Lactarius manzanitae*
23. *Lactarius necator*
24. *Lactarius occidentalis*
25. *Lactarius olivaceo-umbrinus*
26. *Lactarius pallescens* var. *pallescens*
27. *Lactarius pallidiolivaceus*
28. *Lactarius pseudomucidus*
29. *Lactarius pubescens* var. *betulae*
30. *Lactarius representaneous*
31. *Lactarius resimus* var. *resimus*
32. *Lactarius riparius*
33. *Lactarius rubidus*
34. *Lactarius rubrilacteus*
35. *Lactarius rufulus*
36. *Lactarius rufus*
37. *Lactarius scrobiculatus* var. *canadensis*
38. *Lactarius scrobiculatus* var. *montanus*
39. *Lactarius scrobiculatus* var. *pubescens*
40. *Lactarius subflammeus*
41. *Lactarius substriatus*
42. *Lactarius subvillosus*
43. *Lactarius subviscidus*
44. *Lactarius tiersii*
45. *Lactarius torminosus* var. *nordmanensis*
46. *Lactarius uvidus* var. *montanus*
47. *Lactarius xanthogalactus*
Synoptic Key to California Species of *Lactarius*

Pileus

1.1 Color

a. white - 9, 31
b. pale yellow, light yellow - 1, 4, 29, 30, 31, 38, 39
c. greyish yellow - 26
d. light orange, pale orange, yellowish orange, orange - 1, 3, 13, 14, 15, 22, 29, 30, 34, 37, 41, 42, 45
e. brownish yellow, brownish orange, greyish orange - 2, 3, 6, 7, 10, 11, 12, 13, 14, 15, 18, 21, 22, 26, 27, 29, 32, 34, 37, 41, 42, 43, 44, 45, 47
f. light brown, brown, dark brown - 2, 3, 6, 16, 17, 20, 21, 22, 23, 24, 25, 26, 27, 28, 32, 33, 43
g. greyish brown - 28
h. reddish brown - 21, 32, 33, 35, 36, 40, 43, 44, 46, 47
i. dark vinaceous brown - 19
j. olive brown - 23, 25
k. greyish red, dull red, greyish ruby - 8, 46, 47
l. dark green - 23
m. blackish red - 5

1.2 Color Changes

a. orange - 26
b. greyish orange, brownish orange - 26, 31, 38, 46
c. pink, vinaceous, lavender brown - 9
d. greyish green, dull green - 11, 12, 13, 14, 34
e. none - 1, 2, 3, 4, 5, 6, 7, 8, 10, 15, 16, 17, 18, 19, 20, 21, 22, 23, 24, 25, 27, 28, 29, 30, 32, 33, 35, 36, 37, 40, 41, 42, 43, 44, 45, 47

1.3 Surface Moisture

a. dry - 16, 44
b. dry to moist - 2, 12, 14, 17, 24, 27, 33, 35, 36, 43
c. moist to subviscid - 1, 8, 13, 23, 39, 40, 45
d. subviscid to viscid - 3, 7, 9, 11, 15, 21, 25, 29, 30, 34, 38, 41, 42, 46, 47
e. viscid - 4, 5, 6, 10, 18, 19, 20, 22, 26, 28, 31, 37

1.4 Surface Texture

a. glabrous - 3, 4, 5, 6, 7, 8, 10, 11, 12, 13, 14, 15, 18, 19, 20, 21, 22, 24, 26, 28, 31, 32, 33, 34, 35, 36, 38, 40, 41, 43, 44, 46, 47
b. velutinous - 16, 17, 27
c. appressed fibrillose, fibrillose-scaly - 1, 2, 9, 23, 25, 29, 30, 31, 37, 38, 39, 42, 45
d. squamulose - 2

Pileus and Stipe Context

2.1 Odor

a. maple syrup - 33
b. coconut - 10
c. not distinctive - 1, 2, 3, 4, 5, 6, 7, 8, 9, 11, 12, 13, 14, 15, 16, 17, 18, 19, 20, 21, 22, 23, 24, 25, 26, 27, 28, 29, 30, 31, 32, 34, 35, 36, 37, 38, 39, 40, 41, 42, 43, 44, 45, 46, 47
Pileus and Stipe Context

2.2 Taste

a. acrid - 1, 2, 4, 6, 7, 8, 9, 10, 15, 18, 19, 20, 22, 23, 25, 28, 29, 30, 31, 35, 36, 37, 38, 41, 42, 43, 45
b. not distinctive - 2, 5, 11, 12, 13, 14, 16, 17, 21, 24, 26, 27, 30, 31, 32, 33, 34, 37, 39, 40, 44, 46, 47

2.3 Staining Reactions

a. pale yellow, light yellow, yellow - 1, 6, 10, 29, 31, 37, 38, 39, 41, 47
b. light orange - 16, 17, 27
c. lilac, violet - 4, 7, 26, 30, 46
d. light brown - 37
e. reddish brown - 11, 14, 34
f. unstaining - 2, 3, 5, 8, 9, 10, 12, 13, 15, 18, 19, 20, 21, 22, 23, 24, 25, 28, 32, 33, 35, 36, 40, 42, 43, 44, 45

Latex

3.1 Color

a. white - 1, 2, 4, 5, 6, 7, 8, 9, 10, 15, 16, 17, 18, 19, 20, 21, 22, 23, 24, 25, 26, 27, 28, 29, 30, 31, 32, 35, 36, 37, 38, 39, 40, 41, 42, 43, 44, 45, 46, 47
b. whey-like - 7, 10, 24, 28, 32, 33, 43, 44
c. pale yellow, cream color - 3, 6, 8, 23, 30
d. orange - 11, 12, 13, 14
e. reddish brown - 34

3.2 Color Changes (on drying)

a. pale yellow, yellow - 1, 28, 29, 31, 37, 38, 39, 41, 42, 43, 45, 47
b. grey green - 20
c. unchanging - 2, 3, 4, 5, 6, 7, 8, 9, 10, 11, 12, 13, 14, 15, 16, 17, 18, 19, 21, 22, 23, 24, 25, 26, 27, 30, 32, 33, 34, 35, 36, 40, 44, 46

Lamellae

4.1 Spacing

a. close to subdistant - 2, 3, 5, 6, 7, 10, 11, 13, 14, 18, 20, 21, 22, 24, 26, 27, 28, 29, 32, 33, 35, 36, 40, 41, 42, 43, 44, 45, 47
b. close to crowded - 1, 4, 8, 9, 12, 15, 16, 17, 19, 23, 25, 29, 30, 31, 34, 37, 38, 39, 46

4.2 Color of Faces

a. white, pale yellow, light yellow - 1, 3, 4, 6, 7, 8, 10, 16, 17, 18, 19, 26, 27, 28, 29, 30, 31, 37, 38, 39, 45, 46, 47
b. pale orange, light orange - 1, 2, 3, 7, 10, 11, 12, 13, 14, 15, 18, 20, 21, 22, 23, 24, 25, 26, 27, 29, 30, 31, 32, 33, 34, 35, 36, 37, 40, 41, 42, 43, 44, 45, 46, 47
c. pale pink, pink, pinkish cream - 9
d. pinkish cinnamon, orange cinnamon - 5, 19
e. greyish orange - 32
Lamellae

4.3 Color of Edges
a. brown - 17
b. (concolorous with faces)

4.4 Staining Reactions
a. yellow - 31, 37, 38
b. light orange - 16, 17, 27
c. orange, greyish orange - 26, 41
d. greyish brown, light brown, brown - 3, 6, 18, 20, 23, 25, 28, 37, 38, 39
e. reddish brown - 5, 11, 14, 24, 34
f. olive brown - 23, 25
g. lilac, violet - 4, 7, 26, 30, 46
h. dull green, greyish green - 11, 12, 13, 14, 34
i. unstaining - 1, 2, 8, 9, 10, 15, 19, 21, 22, 29, 32, 33, 35, 36, 40, 42, 43, 44, 45, 47

Stipe

5.1 Color
a. white, pale yellow, light yellow - 1, 3, 4, 7, 8, 9, 19, 26, 27, 29, 30, 31, 37, 38, 39
b. pale orange, light orange, orange - 2, 11, 12, 13, 14, 15, 20, 21, 22, 34, 42, 45, 47
c. yellowish grey, yellowish brown, greyish brown - 6, 8, 23, 24, 29
d. light brown, brown - 16, 17, 23, 25, 28, 33, 40, 43
e. brownish orange, greyish orange - 2, 6, 10, 18, 20, 21, 24, 32, 33, 34, 36, 37, 40, 41, 43, 44, 46, 47
f. olive brown - 23, 25
g. greyish red - 32, 47
h. blackish red - 5
i. reddish brown - 35, 36, 44

5.2 Scrobiculations
a. present - 1, 19, 20, 25, 29, 30, 34, 37, 38, 39, 42
b. absent - 2, 3, 4, 5, 6, 7, 8, 9, 10, 11, 12, 13, 14, 15, 16, 17, 18, 21, 22, 23, 24, 26, 27, 28, 31, 32, 33, 35, 36, 40, 41, 43, 44, 46, 47

5.3 Surface Moisture
a. dry - 8, 11, 12, 14, 16, 17, 19, 21, 24, 27, 31, 33, 34, 35, 36, 37, 38, 39, 44, 45
b. dry to moist - 1, 2, 3, 7, 9, 10, 13, 15, 22, 29, 32, 40, 41, 42, 43, 47
c. moist to viscid - 5

5.4 Surface Texture
a. glabrous - 1, 2, 3, 4, 5, 6, 7, 8, 9, 10, 11, 12, 13, 14, 15, 18, 19, 20, 21, 22, 23, 24, 25, 26, 28, 29, 30, 31, 32, 33, 34, 35, 36, 37, 38, 39, 40, 41, 42, 43, 44, 45, 46, 47
b. pruinose - 9, 29, 34, 37, 38

c. velutinous - 16, 17, 27
**Basidiospores**

6.1 Shape

a. globose to subglobose - 15, 16, 17, 27, 33, 35
b. subglobose to broadly ellipsoid - 2, 8, 19, 21, 22, 31, 36, 41, 43, 44
c. broadly ellipsoid to ellipsoid - 1, 3, 4, 5, 6, 7, 9, 10, 11, 12, 13, 14, 18, 20, 23, 24, 25, 26, 28, 29, 30, 32, 34, 37, 38, 39, 40, 42, 45, 46, 47

6.2 Length Range

a. 6.5-8 um - 8, 9, 10, 15, 19, 22, 29, 31, 33, 39, 42
b. 7.5-9.5 um - 1, 2, 3, 4, 5, 7, 11, 12, 13, 14, 16, 17, 18, 20, 21, 23, 24, 25, 27, 28, 32, 34, 35, 36, 37, 38, 40, 41, 43, 44, 45, 47
c. 9.5-12 um - 6, 26, 30, 46

6.3 Width Range

a. 4.5-5.5 um - 9, 21, 23, 29, 31, 39, 42
b. 6-7.5 um - 1, 2, 3, 4, 5, 7, 8, 10, 11, 12, 13, 14, 15, 18, 19, 20, 22, 24, 25, 26, 28, 32, 33, 34, 36, 37, 38, 40, 41, 45, 47
c. 7-9 um - 6, 16, 17, 27, 30, 35, 43, 44, 46

6.4 Ornamentation

a. broken reticulum - 8, 30, 37, 40
b. broken to partial reticulum - 2, 3, 4, 5, 6, 7, 9, 11, 12, 13, 14, 16, 17, 19, 20, 21, 22, 23, 24, 25, 26, 29, 31, 32, 33, 34, 35, 36, 39, 41, 42, 43, 44, 45, 46, 47
c. partial to complete reticulum - 1, 6, 10, 15, 18, 19, 27, 28, 38, 44
d. zebroid - 8

6.5 Ornamentation Height

a. ≤ 0.5 um - 2, 3, 6, 7, 8, 9, 10, 11, 12, 13, 14, 15, 19, 22, 31, 32, 34, 35, 36, 37, 38, 39, 42, 44, 45, 46, 47
b. 0.5-1.0 um - 1, 4, 5, 18, 20, 21, 23, 24, 25, 26, 27, 28, 29, 30, 33, 40, 41, 43
c. > 1.0 um - 16, 17

**Cystidia**

7.1 Macrocystidia

a. absent - 11, 12, 16, 17, 27, 33, 35, 44
b. (present)

7.2 Cheilocystidia

a. absent - 9, 27, 32, 35, 38, 39, 44
b. (present)
Pellis

8.1 Pileipellis

a. cutis - 29, 36
b. fascicles of hyphae - 2
c. cellular - 24, 33, 35, 44
d. ixocutis - 1, 3, 4, 7, 8, 9, 11, 12, 14, 15, 19, 23, 25, 30, 31, 32, 34, 37, 38, 39, 42, 45, 46, 47
e. trichodermium - 16, 17, 27, 40
f. ixotrichodermium - 5, 6, 10, 18, 19, 20, 21, 22, 26, 28, 41, 43
g. ixolattice - 5, 7, 19, 22, 26, 46

8.2 Stipitipellis

a. cutis - 1, 2, 7, 8, 9, 11, 12, 14, 15, 16, 17, 19, 21, 24, 25, 27, 29, 30, 31, 32, 33, 34, 36, 37, 38, 39, 40, 41, 42, 43, 44, 45, 47
b. ixocutis - 3, 4, 5, 10, 13, 18, 20, 22, 23, 25, 26, 28
c. ixolattice - 6, 20, 22, 26, 28, 46
d. ixotrichodermium - 30

Habitat and Distribution

9.1 Distribution

a. coastal - 1, 2, 5, 7, 10, 13, 15, 16, 17, 19, 20, 21, 22, 24, 25, 28, 33, 35, 36, 37, 38, 39, 40, 41, 42, 43, 44, 45, 46
b. montane - 4, 6, 8, 9, 18, 32, 38, 39, 45, 46
c. coastal and montane - 3, 11, 12, 14, 26, 27, 30, 31, 34, 41, 42, 47

9.2 Forest Type

a. coniferous - 5, 8, 19, 30, 32, 38, 39, 44, 46
b. deciduous - 18, 35
c. coniferous-deciduous - 1, 2, 3, 4, 6, 7, 9, 10, 11, 12, 13, 14, 15, 16, 17, 20, 21, 22, 24, 25, 26, 27, 28, 31, 33, 34, 36, 37, 40, 41, 42, 43, 45, 47
d. horticultural plantings - 23, 29

9.3 Host Specificity

a. Abies - 6, 30, 32, 38
b. Alnus - 2, 5, 6, 24, 34
c. Arctostaphylos - 22
d. Betula - 23, 29
e. Picea - 5, 13, 14, 16, 17, 21, 25, 30, 43
f. Pinus - 5, 6, 34, 36, 38, 44
g. Populus - 9, 45
h. Quercus - 3, 33, 35, 47
i. Salix - 9, 34, 45
j. Sequoia - 19
k. Tsuga - 18
Literature Cited


