A New, Commercially Valuable Chanterelle Species, *Cantharellus californicus* sp. nov., Associated with Live Oak in California, USA[1]

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A New, Commercially Valuable Chanterelle Species, *Cantharellus californicus* sp. nov., Associated with Live Oak in California, USA. The prominent golden chanterelle of California's oak woodlands is characterized as a new species, *Cantharellus californicus* sp. nov., using molecular and morphological data. Our observations indicate that it is the largest *Cantharellus* species in the world, with individual sporocraps commonly weighing 1/2 kilogram (kg) (or 1 pound) or more when mature. Other *Cantharellus* species in California are compared and evaluated, including their known ectomycorrhizal hosts. The California oak chanterelle is an economically valuable species, and some observations on its commercial harvest are presented.

Key Words: Cantharellus, Chanterelle, Internal transcribed spacer (ITS–RFLP), Live oak, Mushroom harvest, Oak chanterelle, Wild edible fungi.

Introduction

Chanterelles (*Cantharellus* spp.) have been harvested for centuries from the forests of Europe, Africa, Asia, and North America, and are among the most widely consumed ectomycorrhizal mushrooms (Danell 1999). The best known species, *Cantharellus cibarius* Fr., was originally described from central France but has been reported from boreal, temperate, and tropical forests around the world (e.g., Corner 1966; Ryvarden et al. 1994). In fact, virtually every medium–sized to large, yellow–orange *Cantharellus* has at one time or another passed under the name *C. cibarius* or been mistaken for that species regardless of its habitat, climate zone, distance from France, and ectomycorrhizal host. In North America, several taxa have passed under the name *C. cibarius,* e.g., four different taxa in Arora (1991), and even within Europe there may be more than one species lumped under that name (Petersen 1979).

As long as chanterelles were consumed locally, their scientific epithets were mostly a matter for academic discussion. But Watling (1997) values worldwide chanterelle production at an estimated USD 1.67 billion annually, and this expanding global trade in chanterelles (Arora 1999) has heightened the need to distinguish and clarify these numerous disparate "forms" or species. Chefs and discerning consumers, on the one hand, want to know what they are buying since the culinary and gastronomic qualities of the different species vary. At the same time, the commercial harvest of chanterelles has spurred interest in better understanding their ecology, physiology, and productivity; some studies, however, have been marred by the use of chanterelles of uncertain identity as noted by Danell (1999).

The tendency to broadly interpret *C. cibarius* as a widespread, highly variable, polymorphic species may in part be a quirk of mycotaxonomic tradition, but also can be attributed to the high degree of inter– and intra–regional variation in yellow–orange chanterelles (hereafter called golden chanterelles), and to a paucity of conserved micro– and macroscopic morphological characters that would make delineation and recognition easier (Smith and Morse 1947; Petersen 1985). Given the limited usefulness of morphological

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characters, the application of molecular markers has proven extremely helpful in defining species boundaries within *Cantharellus*. Genetic studies of North American chanterelles with *C. cibarius*–like morphology have demonstrated significant length variability in the nuclear ribosomal internal transcribed spacer (nrDNA ITS) (Feibelman et al. 1994), and this length variability has been correlated with the presence of previously unrecognized species.

Recent research has made it clear that there are more taxa of golden chanterelles than currently recognized, and that the European *C. cibarius* is not as ubiquitous as once believed. Redhead et al. (1997) identified the principal golden chanterelle of commerce in North America as *C. formosus* Corner, a species associated with conifers, especially hemlock (*Tsuga*) and Douglas–fir (*Pseudotsuga*)), in the Pacific Northwest. They identified and described a second, less prevalent but commercially valuable species with a more vividly colored hymenophore as *C. cibarius* var. *roseocanus* Redhead, Norvell & Danell, associated primarily with spruce (*Picea*) and pine (*Pinus*) in the Pacific Northwest. The authors also made brief reference (Redhead et al. 1997:312) to an "oak–associated species" from California but did not elaborate further.

This oak–associated species is the principal chanterelle of commerce in California and is one of the most prominent fungal features of its extensive live oak woodlands. Despite its large size (specimens weighing 1 kilogram [kg] each are not rare) and frequently poroid, pallid hymenium, it has historically been treated as *C. cibarius* (Smith and Morse 1947; Thiers 1985; Arora 1986, 1991). The reluctance to recognize it as a distinct species seems all the more remarkable given the distinct Mediterranean climate of the California Floristic Province where it occurs, the geographical barriers surrounding the California Floristic Province and its isolation from other regions with a Mediterranean climate, and the exceptionally high level of endemism in the California Floristic Province—nearly 50% for plants (Raven and Axelrod 1978).

Dunham et al. (2003) studied genetic variability within putative *C. formosus* populations using RFLP analysis of the ITS region (ITS 1, ITS 2, and the 5.8s gene) in order to characterize another commercially harvested but previously unrecognized species from Oregon, *C. cascadensis* Dunham, O'Dell & Molina. During that study, a novel ITS genotype from southern California was identified from a single chanterelle collected under oak. The overall length of the ITS region for this collection was slightly shorter than that characterized for *C. formosus* (~1,600 vs. 1,690 base pairs according to Dunham et al. 2003), and it produced a unique RFLP pattern. Meanwhile Arora, while observing and collecting western chanterelles for more than 30 years, had concluded that the California oak chanterelle is a distinct biological entity, morphologically distinguishable from European *C. cibarius* and at least ecologically and geographically distinguishable from the conifer–loving *C. formosus*.

In this study we increased the sampling of chanterelles from California's pure and mixed oak woodlands to verify the presence of this unique chanterelle species, using RFLP analysis of the ITS region to help characterize it. Our primary objectives were to: 1) analyze ITS–RFLP variability from a broad sample of chanterelles to determine the number of chanterelle taxa associated with California's oak woodlands and mixed forests, 2) characterize the geographical distribution of California's oak–associated chanterelles, 3) identify morphological characters useful in differentiating oak–associated chanterelles from other golden chanterelles, and 4) describe any new species of *Cantharellus* based on these genetic and morphological characters.

Materials and Methods

MATERIAL EXAMINED

To characterize the ITS–RFLP diversity present within California's chanterelles, samples were taken from eight counties throughout the state (Fig. 1) during the years 2003–2005. Dried voucher materials from all analyzed collections were deposited in the mycological herbariums at Oregon State University (OSC) and University of California–Berkeley (UC) as well as at San Francisco State University (Table 1). Most collections were made in pure live oak (*Quercus*) woodlands and in oak woodlands with other potential ectomycorrhizal angiosperms present, such as *Arctostaphylos*, *Arbutus*, and *Lithocarpus*. We also made a special effort to sample *Cantharellus* collections from evergreen forests containing tanoak, *Lithocarpus densiflorus* Rehd., mixed with ectomycorrhizal conifers such as western hem-

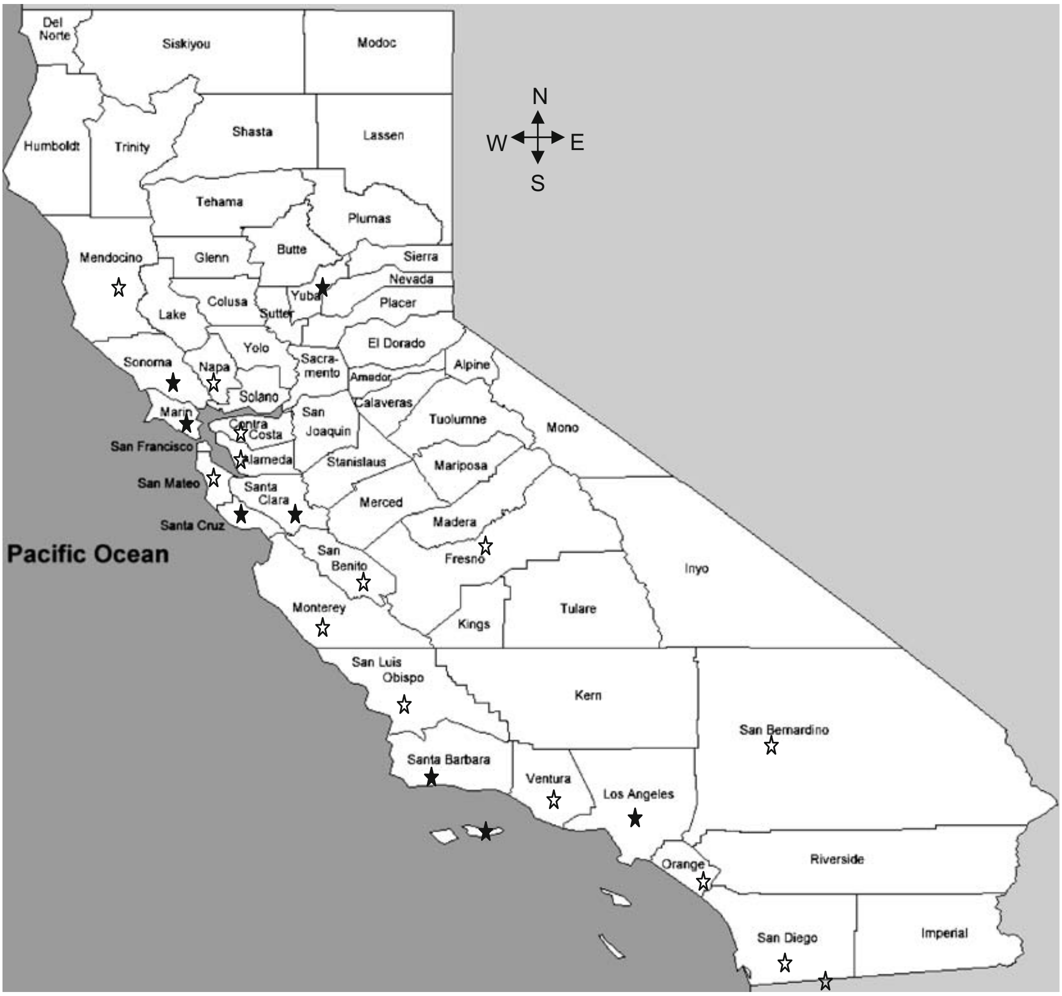

Fig. 1. California counties in which *Cantharellus californicus* was found during this study (filled stars) or in which it has been reliably reported (open stars).

lock, *Tsuga heterophylla* Sargent, Douglas–fir, *Pseudotsuga menziesii* (Mirb.) Franco, and pine, especially *Pinus muricata* D. Don.

RESTRICTION FRAGMENT LENGTH POLYMORPHISM (ITS–RFLP) ANALYSIS

After grinding a small amount of fresh or dried tissue in 1 ml of lysis buffer (100 mM Tris, 10 mM EDTA, 2% sodium dodecyl sulfate, 1 mg/ml proteinase–K, pH 8.0), each sample was incubated for 1.5 hours at 55°C and DNA was extracted using a standard phenol/chloroform emulsification and precipitation (Maniatis et al. 1982). Resulting pellets were vacuum–dried and re–suspended in 50 to 200 µl of sterile TE buffer (10 mM Tris, 1 mM EDTA). Unquantified DNA samples were diluted 10 to 1,000–fold prior to use and the polymerase chain reaction (PCR) was attempted on successive 10–fold dilutions until amplification of the desired nrDNA region was achieved. The entire ITS region spanning the 3′ end of the 18S, ITS–1, 5.8S, ITS–2, and 5′ end of the 28S was amplified with the fungal specific primer ITS1–F (Gardes and Bruns 1993) and ITS4 (White et al. 1990). All amplifications of nrDNA regions were carried out in 40 µl volumes that contained 3 µl of diluted template. Final concentrations of PCR mix components were 20 µl of premix C (Epicenter Technologies), 0.2 µM of each primer,

Table 1. COLLECTION NUMBERS (OSC EXCEPT AS NOTED), LOCATIONS, AND HABITATS ASSOCIATED WITH SAMPLES USED IN MOLECULAR ANALYSES.

OSC #	Species	County	Dominant Overstory
122878 (t)	*Cantharellus californicus*	Marin	*Q. agrifolia*
122879	*C. californicus*	Marin	*Q. agrifolia*
122880	*C. californicus*	Marin	*Q. agrifolia*
122881	*C. californicus*	Marin	*Q. agrifolia*
122882	*C. californicus*	Marin	*Q. agrifolia*
122883	*C. californicus*	Marin	*Q. agrifolia*
122884	*C. californicus*	Santa Cruz	*Q. agrifolia & Q. parvula* var. *shrevei*
122885	*C. californicus*	Santa Cruz	*Q. agrifolia*
122886	*C. californicus*	Santa Cruz	*Q. agrifolia*
122890	*C. californicus*	Santa Cruz	*Pseudotsuga menziesii & Quercus* spp.
122891	*C. californicus*	Santa Cruz	*Q. parvula* var. *shrevei*
122892	*C. californicus*	Santa Cruz	*Lithocarpus densiflorus & Sequoia sempervirens*
122897	*C. californicus*	Los Angeles	*Quercus agrifolia*
122898	*C. californicus*	Los Angeles	*Q. agrifolia*
122902	*C. californicus*	Marin	*Q. agrifolia*
122903	*C. californicus*	Marin	*Q. agrifolia*
122904	*C. californicus*	Marin	*Q. agrifolia*
122905	*C. californicus*	Santa Clara	*Q. agrifolia*
122906	*C. californicus*	Santa Clara	*Q. agrifolia*
122907	*C. californicus*	Santa Clara	*Q. agrifolia & Arctostaphylos glauca*
122908	*C. californicus*	Santa Clara	*Q. agrifolia & A. glauca*
122909	*C. californicus*	Santa Clara	*Q. agrifolia & A. glauca*
122910	*C. californicus*	Santa Clara	*Q. agrifolia & A. glauca*
122911	*C. californicus*	Santa Cruz	*Q. agrifolia*
122912	*C. californicus*	Santa Cruz	*Q. agrifolia*
122913	*C. californicus*	Santa Cruz	*Q. agrifolia*
122914	*C. californicus*	Santa Cruz	*Q. agrifolia*
122915	*C. californicus*	Santa Cruz	*Q. agrifolia*
122916	*C. californicus*	Santa Cruz	*Q. agrifolia & Pseudotsuga menziesii*
122917	*C. californicus*	Santa Cruz	mixed hardwoods with *P. menziesii*
122918	*C. californicus*	Santa Cruz	*Quercus parvula* var. *shrevei*
122919	*C. californicus*	Santa Cruz	*Q. parvula* var. *shrevei* & *Pseudotsuga menziesii*
UC1860230	*C. californicus*	Santa Barbara	*Q. agrifolia* & *Q. pacifica* Nixon & C. H. Mull.
UC1860231	*C. californicus*	Santa Barbara	*Quercus* spp. & *Pinus muricata*
122920	*C. californicus*	Sonoma	*Q. agrifolia*
122921	*C. californicus*	Yuba	*Q. wislizenii* & *Q. kelloggii*
122922	*C. californicus*	Yuba	*Q. wislizenii* & *Q. kelloggii*
122887	*C. subalbidus*	Mendocino	mixed hardwoods
122896	*C. subalbidus*	Mendocino	mixed hardwoods with *Pseudotsuga menziesii*
122888	*C. formosus*	Mendocino	mixed hardwoods with *Pinus muricata*
122889	*C. formosus*	Mendocino	mixed hardwoods
122893	*C. formosus*	Mendocino	mixed hardwoods with *Pseudotsuga menziesii*
122894	*C. formosus*	Mendocino	mixed hardwoods with *P. menziesii*
122895	*C. formosus*	Mendocino	mixed hardwoods with *P. menziesii*
122899	*C. formosus*	Sonoma	*Pinus muricata*
122900	*C. formosus*	Sonoma	*P. muricata*
122923	*C. formosus*	Mendocino	*Pseudotsuga menziesii*
122924	*C. formosus*	Mendocino	mixed hardwoods with *P. menziesii*

Table 1. (CONTINUED)

OSC #	Species	County	Dominant Overstory
122925	*C. formosus*	Santa Cruz (?)	mixed hardwoods with *P. menziesii* (?)
122926	*C. formosus*	Sonoma	mixed hardwoods with *P. menziesii*
122901	*C. cibarius* var. *roseocanus*	Sonoma	*Pinus muricata*
122927	*C. cibarius* var. *roseocanus*	Mendocino	mixed hardwoods with *P. muricata*

All species identifications were confirmed with ITS-RFLP analysis. All counties are located in the state of California, U.S.A. Dominant tree species are as noted, with "mixed hardwoods" connoting various mixtures of oak (*Quercus* spp.), madrone (*Arbutus menziesii*), manzanita (*Arctostaphylos* spp.), and/or tanoak (*Lithocarpus densiflorus*). (t) = type collection.

and 0.75 units of DNA polymerase. Following an initial denaturation period at 95°C for 3 min., reactions were subject to 35 PCR cycles with the following profile: Denaturation at 95°C for 1 min., primer annealing at 52°C for 1 min., and primer extension at 72°C for 90 s. Following the 35th cycle, samples were subjected to a final extension of 72°C for 10 min.

Unpurified PCR products amplified with ITS1–F and ITS4 were digested separately with three restriction enzymes known to differentiate all recently described chanterelle species: *Alu*, *Hinf I*, and *HaeIII* (Dunham et al. 2003). Restriction fragments were electrophoretically separated on 3% agarose gels (2% Nu–Sieve agarose, 1% SeaKem LE agarose; FMC Bio-Products), stained with ethidium bromide, and scored against a 100 bp ladder using the Alpha Imager 2000 documentation and analysis system V 3.2 (Alpha Innotech Corp.). Each collection sampled in this study was assigned to an ITS type that summarized information from the three restriction enzyme profiles. Thus, collections with different ITS type designations are considered to represent different species.

MORPHOLOGY

Morphological and color data were taken from fresh collections representing the full range in chanterelle color variation (hue and intensity) and sporocarp (fruiting body) shape. Colors were assigned names according to Rayner (1970). Morphological data were recorded before RFLP data were generated so that the more subjective determinations (such as color) were not biased by knowledge of the ITS genotypes. Microscopic observations of spores were made from spore deposits collected from fresh material. Thirty spores were examined from selected collections and mean spore length and width measurements were calculated. Microscopic observations of tissues were made from dried material mounted in 5% KOH at 1000X magnification using the methods of Smith and Smith (1973) and Largent et al. (1977).

Results

RESTRICTION ENZYME ANALYSIS

PCR products amplified using ITS1–F and ITS4 were either ~1490, ~1,600 or ~1690 base pairs in length. In several profiles, particularly those generated with *HaeIII*, the lengths of individual restriction fragments (Table 2) sum to less than the length of the original ITS product. This is due to the high number of recognition sites for this enzyme in the ITS of *Cantharellus* and our inability to detect and accurately size RFLP fragments smaller than 90 bp. *HaeIII* digests typically exhibited several small fragments below this size cut off, which were ignored during RFLP comparisons.

Information pooled from individual restriction fragment profiles was used to characterize four unique RFLP types assigned across the 50 collections analyzed (Tables 1 and 2). Eleven chanterelle collections possessed a ~1690 bp ITS region that produced RFLP profiles identical to those characterized for *C. formosus* (Dunham et al. 2003). Thirty–seven collections possessed an ITS region slightly shorter than that seen in *C. formosus* (~1,600 bp). Although the ITS length is shorter than reported in Dunham et al. (2003), these collections produced RFLP profiles identical to the single collection (OSC 76057) they cited from under *Quercus* in southern California. (It is likely that because Dunham, O'Dell, and Molina examined only a single collection of this type the subtle ITS length difference was misinterpreted as a gel artifact.) Two collections from the current

Table 2. POOLED RESTRICTION FRAGMENT PROFILES USED TO DEFINE *CANTHARELLUS* SPECIES IN THIS STUDY.

	Restriction Fragment Profile			
RFLP type	Alu	Hinf I	HaeIII	ITS size (bp)
C. californicus	1	1	1	~1600
C. formosus	2	2	2	~1690
C. cibarius var. roseocanus	3	3	3	~1490
C. subalbidus	3	3	4	~1490

Values identify restriction fragment profiles for each enzyme. In some cases, the fragment sizes in an RFLP profile do not sum to the size of the original ITS product (1490, 1600, or 1690 bp) because the sizes of fragments below 100 bp were difficult to accurately estimate. Restriction fragment sizes (bp) for each profile are as follows: Alu (1) 740-490-340-120, (2) 540-490-340-200-120, (3) 490-380-250-220-150; Hinf I (1) 750-500-250, (2) 970-500-220, (3) 690-500-300; HaeIII (1) 690-300-180, (2) 780-330-180-170-140-90, (3) 690-310-220-180, (4) 690-170-160-140-100.

study showed ITS–RFLP patterns consistent with *C. subalbidus* Smith & Morse and the remaining two collections exhibited a total ITS length of ~1490 bp and an RFLP profile identical to that reported for *C. cibarius* var. *roseocanus* (Redhead et al. 1997; Dunham et al. 2003).

We found only one species, heretofore undescribed, in California's live oak woodlands.

Cantharellus californicus sp. nov.

Basidiomata terrestres, plerumque quercibus sempervirentibus consociata, monopileata, staturis mediis vel grandibus. Pileus maturitate undulatus vel urceolatus, armeniacus. Hymenium colore pilei suffusum sed pleurumque pallidus, plicarum decurrentium venis transversis aetate profundisque aspectis poroideis compositum. Stipes aequalis vel deorsum contractus, saepe crassusque brevis, similiter pileo coloratus. Contextus crassus, albus, sapore mitis, leviter fragrans, hyphis hyalinis, intertextis, 2–6 µm ad septa crassis, cellulis multis inflatis vesicariis usque ad 7–10 µm. Pileipellis juventute 50 µm crassa, hyphis arcte adpressis, 2–6 µm crassis, contentu luteolis, maturitate implexis. Fibulae dispersae, inconspicuae. Sporae ±9×5 µm, hyalinae, laeves, ellipsoideae vel obtusae. Typus hic designatus: OSC 122878.

Sporocarp monopileate, gymnocarpic, medium–sized to large. Pileus (cap) 8–30 or more cm broad, broadly convex at first, but mature specimens undulating to concave or vase–shaped or irregular with much adhering mud and leaves; surface typically bright to dull yellow–orange (between "Orange" and "Luteous" in Rayner 1970), but at times tinged pale pinkish–apricot (near "Salmon" in Rayner 1970) or mottled because of adhering leaf debris (those areas covered with leaves quite pale); older specimens becoming browner in areas or bleaching out if exposed to bright sunlight, or even with greenish mold or algae; surface typically appearing smooth when wet, but usually with a fine canescence or extremely fine scattered fibrils when young (especially evident in drier conditions); in older specimens traces of the fibrils are most evident at the margin. *Hymenium* composed of blunt, deeply decurrent lamellar folds 1–2 mm thick and 2–4 mm apart; when young these folds forking and anasmatosing; at maturity hymenium markedly intervenose, the cross–veins between the longitudinal folds about 1 mm apart from each other and especially numerous toward the margin of the pileus, becoming shallower and blunter as they approach the stalk or descend it; cross–veins deepening in age (i.e., becoming broader and more highly developed) so that at full maturity the hymenium frequently assumes an almost poroid appearance (Fig. 2); color of the hymenium variable: usually tinged with the pileus color but noticeably paler (between "Saffron" and "Pale Luteous" in Rayner 1970), but in some collections the hymenium is bright yellow–orange like the pileus or shows bright yellow–orange shades toward the margin of the pileus and paler tones toward the stalk, and at other times the hymenium is both paler and slightly pinker than the pileus (near "Salmon" in Rayner 1970); oxidized or bruised areas usually dull, dark ochraceous to orangish–brown. *Stipe* 1.5–4 cm thick and 3–9 cm long, solid, usually equal or tapered toward the base, but sometimes with the base slightly swollen; surface usually colored like the pileus or paler (i.e., like the hymenium), but often darker in places from handling and often

Fig. 2. Mature specimen of *C. californicus* showing the tendency of the hymenium to become poroid (Santa Cruz County, California). (David Arora, all rights reserved).

overlain with slightly darker (ochraceous to brown) fibrils which may or may not break up to form tiny appressed scales; surface often developing dark ochraceous or orangish–brown stains after prolonged handling. *Context* fibrous, very thick at the center of the pileus but only 3 mm near the pileus margin, white except for a tinge of yellow–orange just beneath the surface of the pileus, not staining appreciably within 60 seconds when cut; odor faintly fruity (reminiscent of pumpkin) especially when several are stored together in a paper bag; taste typically mild (but one collection in exceptionally dry conditions was strongly bitter as if impregnated with tannin).

Spores yellowish in mass, subglobose to ellipsoid, containing large oil droplets, smooth, measuring 9.30 ± 0.18 µm (7–12 µm) × 6.45 ± 0.12 µm (5–8 µm), Q = 1.50 ± 0.05 (1.13–1.95). Basidia 80–95 × 6–9 µm, with incurved sterigmata and 4–8 spores per basidium. Context composed of hyaline, thin–walled, interwoven hyphae 2–6 µm broad at the septa but often inflated up to 7–10 (12) um. Clamp connections present, scattered, and inconspicuous. Pileipellis ±50 µm thick, in youth with subparallel, tightly appressed hyphae 2–6 µm broad at the septa, the cell contents light yellow, in age the pellis becoming disrupted and the hyphae tangled.

Material Examined. Arora 0501/OSC 122878 (holotype, Marin County, California, Jan. 6, 2005); Arora 0502/OSC 122879 (Marin County, California, Jan. 6, 2005); Arora 0503/OSC 122880 (Marin County, California, January 6, 2005), etc. (see Table 1).

Habitat. Solitary to gregarious in leaf litter in association with coast live oak (*Quercus agrifolia* Née) or sometimes other oaks (*Q. parvula* var. *shrevei* (C.H. Mull.) Nixon, *Q. wislizenii* A. DC., *Q. kelloggii* Newberry, *Q. chrysolepis* Liebm.); also found with tanoak (*Lithocarpus* *densiflorus*) and possibly other hosts in regions where live oaks occur; common to abundant, usually fruiting between November and April but collections have been made during every month of the year. Some of the most productive areas are with spreading live oaks at the edges of pastures, as embodied by the local saying, "where branches touch the ground, chanterelles abound."

Morphological Comparisons. C. californicus is an impressive and beautiful mushroom in its prime. It most closely resembles its nearest relative, the Pacific golden chanterelle (*C. formosus*), showing the same range of color except for the grayish–brown (fuscous) fibrillosity seen in the pileus of *C. formosus* in dry weather (Redhead et al. 1997). In *C. californicus*, as in *C. formosus*, the hymenium is typically paler than the cap (Fig. 3), but exceptions are not uncommon. OSC 122882, for instance, was bright yellow–orange overall, including the hymenium, while OSC 122881 had a pale, faintly pinkish hymenium (a color noted in Corner's original description of *C. formosus*). Both *C. californicus* and *C. formosus* can have a finely fibrillose–squamulose to smooth cap depending on weather conditions, but in *C. formosus* the fibrillose layer is more highly developed, causing young, protected pilei in dry weather to have a dusky or fuscous cast not normally seen in *C. californicus*. *C. californicus*, on the other hand, forms consistently larger fruiting bodies: Fully mature specimens found under mature, spreading live oaks commonly weigh more than half a kilogram (1 lb.) each and individuals in excess of one kilogram are not rare (Fig. 4). No other monopileate species of *Cantharellus* in the world has been reported to regularly produce such massive fruiting bodies. *C. californicus* also differs from *C. formosus* in having a more consistently and markedly poroid hymenium when fully mature (Fig. 2). However, this character is of limited usefulness in the field because individual fruiting bodies often take several weeks to mature fully and many are seen or collected before the hymenium becomes poroid.

C. formosus, in contrast, is large only under exceptional conditions; it rarely exceeds a half kilogram in weight and has a more highly developed gray–brown or dusky fibrillose pileal layer (see Redhead et al. 1997). Also, it typically has a slimmer, longer stipe and is associated with

Fig. 3. *C. californicus*, young and mature specimens (Marin County, California). (David Arora, all rights reserved).

Fig. 4. Occasional mushroom picker Cathy Aubron holding a large monopileate specimen of *C. californicus* weighing 1 kg (Alameda County, California). (Debbie Viess, all rights reserved).

conifers. The larger size of *C. californicus* plus its thicker stalk, stockier stature, and association with live oak separate it from *C. formosus* under most circumstances. However, *C. californicus* tends to be modest in size when growing in mixed evergreen forests, and distinguishing it from *C. formosus* can then be problematic, especially in wet conditions. In such instances, geographical area may be the best indicator of species: In the coastal mixed evergreen forests from Sonoma County northward where tanoak is common but live oak is absent, all collections we examined were *C. formosus* (10 collections), *C. cibarius var. roseocanus* (2 collections), or *C. subalbidus* (2 collections). South of San Francisco, however, *C. californicus* repeatedly turned up in mixed evergreen forests that included coastal live oak or Shreve oak (OSC 122890, OSC 122891, OSC 122911, OSC 122917), as well as on one site where tanoak was the only ectomycorrhizal host present (OSC 122892).

C. cibarius var. *roseocanus* tends to be somewhat larger than *C. formosus* according to Redhead et al. (1997), but is typically smaller than *C. californicus* and can usually be distinguished by its brighter, yellower hymenium and lesser tendency to develop ochraceous to orangish–brown stains after handling. As already noted, in most collections the hymenium of *C. californicus* is paler than the cap, though tinged with the cap color, whereas Redhead et al. (1997) describe the hymenium of *C. cibarius* var. *roseocanus* as bright yellow–orange. However, in our experience it is not uncommon to encounter collections of *C. californicus* in which the hymenium is brightly colored, and we encountered one collection of *C. cibarius* var. *roseocanus* in which the hymenium was rather pale. As far as we know, however, the two species are not sympatric: in California, *C. cibarius* var. *roseocanus* appears to be limited to the northern coast where live oaks are absent while *C. californicus* occurs to the south and/or inland where live oaks are abundant.

Microscopic examination of spores and tissues from three *C. californicus* collections revealed little information useful in differentiating it from either *C. formosus* or *C. cibarius* var. *roseocanus*. The spore size for *C. californicus* overlaps with those reported for other western chanterelle species (Dunham et al. 2003). Other microscopic characteristics were typical of those reported for species with *C. cibarius*–like morphologies (Smith and

Morse 1947; Corner 1966; Smith 1968; Petersen 1979; Redhead et al. 1997; Dunham et al. 2003). These similarities suggest that molecular evolution within the genus is proceeding at a more rapid pace than changes in microscopic morphology.

Distribution and Abundance. Figure 1 shows the localities for *C. californicus* verified during the course of our study plus some additional counties where its presence has been reported by reliable sources. Many years of field experience by the senior author (Arora) indicate that the California oak chanterelle is abundant in the coastal hills from Santa Barbara and the Lompoc–San Luis Obispo region north to Marin and Napa counties. To the north of Marin County its range swings inland, following the live oak belt through Sonoma and Mendocino counties, but it is absent—or largely absent—in coastal Sonoma and Mendocino counties where live oak woodlands are likewise absent. At the other end of its range, as one moves south from Santa Barbara, *C. californicus* becomes harder to find, i.e., it is more infrequent and/or more erratic in appearance as the climate becomes more arid and its preferred live oak habitat is increasingly restricted to canyons and ravines. It has also been found in extreme northern Baja California (Nahara Ayala, pers. comm.) and on the Channel Islands (UC 1860230, UC 1860231).

C. californicus also occurs in the extensive oak woodlands of the Sierra Nevada foothills, but is far less abundant there than near the coast, perhaps because of the hotter, drier summers. We examined collections from Placer County in the Sierra Nevada foothills associated with *Q. wislizenii* and possibly *Q. kelloggii* (OSC 122921, OSC 122922).

Host Associations

Our sampling design was not specifically intended to define ectomycorrhizal host associations for California's chanterelle species but we did detect some apparent linkages. In the oak woodlands and oak savannas that cover much of California from coastal Marin County and inland Mendocino County south to northern Baja California, and in the Sierra Nevada foothills, we found one predominant species of golden chanterelle, *C. californicus*, associated abundantly with coast live oak (*Q. agrifolia*), frequently with Shreve oak (*Q. parvula* var. *shrevei*), occasionally with interior live oak (*Q. wislizenii*), and rarely with California black oak (*Q. kelloggii*). As the latter two oak species show a preference for drier sites or those with longer, hotter, drier summers, the possibility exists that *C. californicus* is more frequently associated with those trees than our field experience suggests, but that it simply doesn't fruit as often as it does along the coast.

Collections from the mixed evergreen forests of coastal northern California, however, presented a very different picture. Three species, *C. formosus*, *C. cibarius* var. *roseocanus*, and the white chanterelle *(C. subalbidus)*, were identified during the course of our study, and according to knowledgeable commercial sources, a fourth species, *C. cascadensis*, occurs in northern California as far south as Mendocino County (Connie Green and Trent Valvo, pers. comm.). It is important to note that tanoak (*Lithocarpus densiflorus*) is a conspicuous component of these northern evergreen coastal forests but live oaks are not.

The collections of *C. cibarius* var. *roseocanus* made during this study had pine in the vicinity, but pure stands of pine in Sonoma County yielded both *C. cibarius* var. *roseocanus* and *C. formosus*. Habitats with hemlock or Douglas–fir but no pine, on the other hand, had only *C. formosus* and *C. subalbidus*. Collection 0515 of *C. subalbidus* from a mixed hardwood forest (no conifers present) in coastal Mendocino County is noteworthy because *C. subalbidus* is widely reported as a conifer associate (Dunham et al. 2003). That it is able to mycorrhize with tanoak or other angiosperms (*Arbutus, Arctostaphylos*) raises the possibility that the *C. formosus* found in California's northern coastal mixed forests may be mycorrhizally linked with tanoak, manzanita and madrone as well as with conifers.

In the mixed evergreen forests of coastal central California, our results were dramatically different: All collections we examined were *C. californicus* with one possible exception (OSC 122925—positively identified as *C. formosus* but unfortunately accompanied by cryptic habitat and site data). These mixed evergreen forests differ from their northern counterparts, however, in that live oaks (either *Q. agrifolia* or *Q. parvula* var. *shrevei*) are usually present.

While *C. californicus* is apparently restricted to the climate zone favored by live oaks (hot, dry summers and cool, moist winters), it would certainly be selectively advantageous for any chanterelle species to be able to mycorrhize alternate hosts. Some very small sporocarps of *C.*

californicus (OSC122892) from Santa Cruz County were apparently associated with tanoak, as the only other tree species at the collection site was redwood, *Sequoia sempervirens* Endl., which is not known to be ectomycorrhizal. What appeared to be *C. californicus* also has been observed growing on rocky ground under canyon live oak (*Q. chrysolepis*) in the Sierra Nevada foothills at 1,200 meters (m) (or 4,000 feet) in Fresno County, and under the same species of oak in the San Bernardino Mountains at elevations of 1,500 to 2,000 m (or 5,000 to 6,000 feet; Steven Pencall, pers. comm.). Possible association with other oak species, with madrone (*Arbutus menziesii* Pursh), and with manzanita (*Arctostaphylos* spp., especially tree–sized species such as *A. glauca* Lindl.), has been postulated by some mushroom collectors but not verified. What seems clear, however, is that as one gains distance from the live oak woodlands that form the heart of its range, the California oak chanterelle decreases dramatically in frequency or disappears entirely. As already stated, we were not able to find it in northern coastal California where live oak does not occur but other potential hosts such as *Lithocarpus* are abundant.

It is interesting to note an analogous situation for *C. cibarius* var. *roseocanus*. Its coastal distribution seems to correspond roughly to that of its favored hosts, Sitka spruce *(Picea sitchensis* [Bong.] Trautv. & C.A. Mey) and shore pine (*Pinus contorta* Dougl.). Our study has confirmed that *C. cibarius* var. *roseocanus* occurs with Bishop pine (*P. muricata*) in Sonoma County, about 100 kilometers (km) (or 60 miles) south of the southernmost point that shore pine and Sitka spruce presently occur, but in more than two decades of collecting we have not found any chanterelle species in pure stands of Bishop pine or Monterey pine (*P. radiata* D. Don) on the Monterey peninsula, a further 360 km (200 miles) to the south. In summary, the distributions of *C. californicus* and *C. cibarius* var. *roseocanus* demonstrate plasticity in the ability of *Cantharellus* species to mycorrhize different hosts, but within certain constraints imposed by climate and/or the distributions of their principal ectomycorrhizal hosts.

Other Species

Thiers' (1985) report of *C. cibarius* var. *pallidifolius* Smith from Mendocino County is likely *C. formosus*, a species that he narrowly interpreted as per Corner's original specifications (Corner 1966). There is nothing in Thiers' description of *C. cibarius* var. *pallidifolius* to eliminate *C. formosus* as redefined by Redhead et al. (1997), and even Thiers (1985) admitted to the similarity. *C. cibarius* var. *pallidifolius*, on the other hand, was originally described from Michigan as a white–stiped species associated with hardwoods. The type collection of *C. cibarius* var. *pallidifolius* was too degraded to analyze, but molecular studies by Feibelman et al. (1994, 1997) give little cause to believe that there are disjunct chanterelle populations of the same species in eastern and western North America, or that there is an eastern member of the *C. formosus*–*C. californicus* clade.

Golden chanterelles have been observed on rare occasions in the high elevation coniferous forests of the Sierra Nevada and in the San Bernardino Mountains in southern California. Their morphology is inconsistent with *C. californicus* (Steven Pencall, pers. comm.), but further investigation is warranted. They may be *C. cibarius* var. *roseocanus*, or *C. formosus*, or another species entirely.

Additional Observations

Sporocarps of *C. californicus* mature slowly, over a period of three to eight weeks or more; this agrees with observations by Redhead et al. (1997) that individual sporocarps of *C. formosus* remain in the ground for up to 100 days. In the heart of its range (e.g., San Luis Obispo County) *C. californicus* comprises, during favorable years, much of the available mushroom biomass in live oak woodlands, at times forming almost a monocrop, yet we have observed few signs of predation by mammals, slugs, or dipteran larvae. Hackman and Meinander (1979) and Danell (1994) likewise demonstrated an extremely low infestation rate for *C. cibarius* as compared to agarics.

Commercial Harvest of *Cantharellus californicus*

C. californicus has been commercially harvested since at least the 1970s. Harvesters have long recognized it as a distinct species which they call the "mud chanterelle"—a tribute to the propensity of the large, mature, gnarled or vase–shaped fruiting bodies for uplifting prodigious amounts of soil and forest debris (Fig. 5). Cleaner, smaller sporocarps with a convex cap are preferred by restaurants and markets, and wholesalers often refer to them by the more appetizing name "California oak chanterelles," or in California, simply "oak chanterelles."

Many chefs, especially those outside California, consider *C. californicus* less desirable than other golden chanterelles (e.g., *C. cibarius, C. formosus*) because the mushrooms are larger than those species (making presentation in a dish more difficult), more fibrous, and not as fragrant as either *C. cibarius* var. *roseocanus* or European *C. cibarius*. Yet *C. californicus* frequently commands higher prices than the other species because it fruits during the winter and spring when other golden chanterelles are unavailable. Arora's observations of the commercial harvest in California and the Pacific Northwest reveal that in a typical year pickers receive USD 1 to USD 5 per pound (or roughly USD 2 to USD 11 per kg) for *C. formosus* versus USD 4 to USD 10 a pound (USD 9 to USD 22 per kg) for *C. californicus* (or higher if selling directly to markets and restaurants). Despite its availability during the winter, the California oak chanterelle has historically been unpopular in Europe because consumers there are accustomed to chanterelles that are smaller, fruitier, more vividly colored, and not as prone to being strongly discolored by oxidation. As a result, California oak chanterelles are sold almost exclusively to the North American market, from California to New York and Toronto.

California restaurant chefs who buy directly from pickers seem the most deeply appreciative of the oak chanterelles. One chef is quoted by Holcomb (2006) as saying:

> There's something exciting about dealing with real people that go out and forage ... and are experts about mushrooms ... there is more connection with the Earth in getting fresh products.

This appreciation is not lost upon those chanterelle pickers who sell directly to chefs. One such picker observes:

> The chefs have got a very hard life slaving away in the hot kitchens and I come waltzing in from the woods in my big Irish sweater with a truck full of these *gorgeous* chanterelles. They never tire of them. Even though they see them every week, they come running out of the kitchen when they see me coming just so they can look in on them. But my value to them is a little bit more than just the product I bring them: I come from *out there*, from the woods, I represent something of a fantasy for them, a kind of longing for a different life that comes through in the food they prepare ...

No statewide records are kept in California, but one well–placed source in the industry (Connie Green, pers. comm.) estimates that in an average year, 50,000 pounds (about 23,000 kg) of *C. californicus* are harvested and sold over a three–month period for a total retail value of nearly USD 1 million. This estimate, which the source stresses is conservative, does *not* include the substantial numbers of chanterelles harvested for personal use, those sold directly by pickers to markets or restaurants (as described above), or the sale of other chanterelle species such as *C. formosus*.

Most of the existing literature on the commercial harvest of wild mushrooms in North America is focused on the Pacific Northwest (e.g., Schlosser and Blatner 1995)—with good reason, as that is where most of the harvest occurs. While it was not the purpose of our study to characterize the commercial harvest of *C. californicus*, Arora has interviewed numerous oak chanterelle pickers over a period of 15 years and has observed both similarities and differences between the commercial harvest of the California oak chanterelle as practiced in central and southern California and the commercial harvest of other mushroom species in northern California and the Pacific Northwest.

It has been estimated that from half to as much as 85% of North American households participated in the informal economy in some way, and it has been suggested that mushroom buying may represent the largest legal cash–based commerce in North America (Alexander et al. 2002). As elsewhere, most of California's chanterelle transactions are conducted in cash, at least at the point of first sale. However, more than 80% of California's oak woodlands are privately held (Huntsinger and Fortmann 1990; Giusti et al. 2004), and there are few public lands between Napa and Los Angeles counties where chanterelles can be collected legally, even for personal consumption (see Arora 2008, this issue). As a result, most of the commercial picking of California oak chanterelles takes place on private property, hidden from public view, and is much less visible than the commercial harvest of other mushroom species as documented by Arora

Fig. 5. Mature specimens of *C. californicus* growing under live oak, Los Angeles County, California. The tendency of the concave caps to lift up large quantities of soil and forest humus has given them the popular commercial name "mud chanterelles." (David Arora, all rights reserved).

Fig. 6. Chanterelle picker Randex "rounding up" chanterelles. He says: "I always wanted to be a cowboy, and this is as close as it gets, except that I'm roundin' up chanterelles instead of cattle ..."

(1999). The prominent roadside buy stands that typify mushroom commerce in the Pacific Northwest (Love et al. 1998; Arora 1999) are largely absent for California oak chanterelles, and someone not specifically searching for oak chanterelle pickers would be unlikely to encounter them. As many of the best "chanterelle beds" are within easy driving distance of urban centers, a significant but undetermined amount of California oak chanterelles is sold directly by pickers to restaurants and markets (proportionately more so, probably, than for *C. formosus* in the Pacific Northwest). Since the buy stands are crucial focal points for gathering, socializing, and exchanging information (Arora 1999; McLain 2000), the pickers of California oak chanterelles appear to be more atomized than their chanterelle–picking counterparts in Oregon and Washington (Love et al. 1998), and less nomadic. Very few describe themselves as "circuit pickers," i.e., people who travel year–round in search of mushrooms (Arora 1999; McLain 2000). Observations also suggest that compared to pickers in the Northwest (see Schlosser and Blatner 1995), pickers of California oak chanterelles are more likely to be male and Caucasian, and more apt to own a business and/or property or to be gainfully employed or to have (or have had) professional careers. More than a few commercial pickers of oak chanterelles belong to amateur mushroom societies, which McLain et al. (1998) interpret as a sign of being well educated.

Stereotypes of commercial pickers as motivated only by money are unwarranted. As has been noted, nobody gets rich picking and selling chanterelles (Love et al. 1998; Alexander et al. 2002; Pilz et al. 2003) owing in part to the erratic and elusive nature of the crop. Most long–time commercial pickers describe the oak chanterelle harvest as a not–very–reliable but extremely welcome source of seasonal income or pocket money, and as a challenging and rewarding reason to roam and revisit California's oak woodlands. While land–management agencies (and many recreational pickers) tend to divide resource users into mutually exclusive categories—commercial, recreational, and subsistence (Pilz et al. 2003; McLain 2008, this issue)—and often assign purely monetary motivations to the former, in reality these categories are not mutually exclusive: "recreational" pickers often trade their bounty for credit at stores and restaurants, or use them as gifts, and "commercial" pickers often pick for pleasure. In fact, the mushroom gathering narratives of commercial oak chanterelle pickers as told to Arora (including reasons why they engage in the activity) bear a striking resemblance to those of "recreational" pickers as related by Fine (1998:27–56). For example, while picking a prolific patch of chanterelles with Arora in a live oak woodland, David Eichorn, a retired Alameda County school teacher who has picked and sold chanterelles to Chez Panisse and other well–known restaurants for 30 years, suddenly exulted, "It's God's gift to me, to all of us. When I'm out here picking I feel like the luckiest person in the world!" Another teacher, Steve Bowen of San Jose, who sells chanterelles directly to restaurants for USD 8 to USD 12 a pound, says:

> I get well paid which is great because I'm a biology teacher and teachers don't make a lot of money, but mushroom hunting also satisfies a primeval urge. It's one of the few things in life that I find truly satisfying, and the chanterelles are like my little friends.

And then there is Randex (Fig. 6), a chanterelle picker in San Luis Obispo County, who says:

> I lived on a nude beach [in California] for eight years and threw luaos for German tourists. I used to *hate* the rain. Now I love it! Never in my whole life have I ever wanted it to rain so much! Because these guys [mud chanterelles] grow in solid rain ..."

Such spontaneous expressions of excitement, gratitude, and longing tend to support the contention of McLain (2000) that commercial wild mushroom pickers share many of the same motivations as maple syrup producers in Quebec and Vermont (Hinrich 1998), namely, that they pick mushrooms because it is a spiritually and emotionally rewarding, income–producing way of exploring and experiencing the natural world.

Prospects for the Future

It has been demonstrated for several mushrooms, including species of *Cantharellus*, that the removal of sporocarps does not adversely impact future harvests (Jansen and van Dobben 1987; Arnolds 1991; Norvell 1995; Pilz et al. 2003; Egli et al. 2006). There is no particular reason to believe that *C. californicus* is any different in this regard or that it is at risk from the commercial harvest as presently practiced. Of more concern is the destruction and fragmentation of its habitat. Encroaching suburbanization and parcelization of the countryside (Giusti et al. 2004), the razing of live oak woodlands in order to plant vineyards (Merenlender 2000), and the spread of Sudden Oak Death (*Phytophthora ramorum* Werres, deCock & Man), termed "the most aggressive forest disease in the world" (see Rizzo et al. 2005; Fernandez 2008) are rapidly shrinking the extensive live oak woodlands that once defined the quintessential "California landscape," and many of the oak species are not regenerating fast enough to replace themselves (Griffin 1971). These factors have already had adverse impacts on some chanterelle pickers. One claims to have lost one half of his productive oak chanterelle patches in the San Francisco Bay Area to Sudden Oak Death in the space of just five years, while another sadly took Arora to his "100 pound patch" on the outskirts of San Luis Obispo—a grove of oaks that produced 100 or more pounds of chanterelles annually until replaced by condominiums.

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