The Oak (*Quercus*) Biodiversity of California and Adjacent Regions[1]

Kevin C. Nixon[2]

Abstract

Twenty species of oak (*Quercus*) are known from California. The white oak group is the most diverse, and includes a complex of scrub oak species that are often encountered in chaparral, mixed forest and desert margin habitats. The Protobalanus group (e.g., *Quercus chrysolepis*) is a unique and distinctive clade of western North American species that appears to be most closely related to the white oak group. Within the white oaks and red oaks (black oaks), the majority of California species do not have obvious, close relationships to species outside of the region. In addition, these species either have lobed leaves (e.g., *Q. kelloggii, Q. lobata, Q. garryana*) or have leaves that appear to be derived from ancestors with lobed leaves by reduction (e.g., *Q. dumosa, Q. berberidifolia, Q. john-tuckeri, Q. cornelius-mulleri, Q. agrifolia*). Lobed leaves, such as those found in numerous oaks of the eastern U.S., are characteristic of species from temperate or cold climates, but not any of the more tropical species, thus suggesting a temperate ancestry for the bulk of California oak species in the white oak and red oak groups. In contrast, the Protobalanus group, which is truly evergreen and has entire or merely dentate leaves, probably has a more tropical origin.

Introduction

The genus *Quercus* is one of the most important groups of woody plants in many regions of the Northern Hemisphere. Oaks dominate various temperate, subtropical, and tropical forest types, and are also a major component of several chaparral and scrub vegetations. Although the popular conception of oaks is of a temperate tree that dominates temperate forests of North America and Europe, the center of diversity for the genus in the New World is in the montane forests of Mexico (Nixon 1993a), where oaks species occur as mostly evergreen and semi-evergreen trees, as the sole dominant, or often in association with pine. However, numerous shrub species also occur in association with these forests, sometimes as dominants in chaparral vegetation. Less known are the truly tropical species of *Quercus*, occurring at elevations from near sea level to 1,500 m on both the Atlantic and Pacific slopes, from Mexico to Panama, with one species in Colombia. According to the most recent estimate there are 202 species of *Quercus* in the New World (Fagaceae, in Flora Mesoamericana). Mexico has the greatest number of species (Nixon 1993a; Nixon and Muller 1992, 1993), with ca. 140 *(table 1)*. California, with 20 species, is moderately diverse relative to other areas in North America, but is far less diverse than an equivalent sized area of Central or Southern Mexico. Aside from Mexico, other "hotspots" for *Quercus* occur in subtropical-

[1] An abbreviated version of this paper was presented at the Fifth Symposium on Oak Woodlands: Oaks in California's Changing Landscape, October 22-25, 2001, San Diego, California.

[2] Associate Professor, L. H. Bailey Hortorium, Department of Plant Biology, Cornell University, Ithaca, New York 14853.

temperate China and southeast Asia. The southeastern U.S. is another moderate center of *Quercus* diversity, especially the coastal gulf and Atlantic states.

Our present understanding of the generic relationships within family Fagaceae indicates that the genus *Quercus* is monophyletic, and that the genus *Lithocarpus* (Tanoak) is not a part of the *Quercus* clade (Nixon 1984, 1989, 1993b; Manos and others 1993, 1999, 2001). The similar "acorn" fruits of *Lithocarpus* represent independent convergent evolution from more complex multi-fruited dichasial cupules such as found in *Fagus*, *Castanea*, *Chrysolepis* and the trigonobalanoid genera (Nixon 1989; Nixon and Crepet, 1989; Crepet and Nixon 1989a, 1989b; Nixon 1997a, 1997b, 1997c). It is interesting to note that both *Lithocarpus* and *Chrysolepis*, members of subfamily Castaneoideae, are insect-pollinated, while all *Quercus* are wind-pollinated. This difference is reflected in profound differences in flowers and inflorescences between the two groups. Little is known about pollination in California *Lithocarpus*, although small beetles have been observed visiting the flowers (Verne Grant, personal communication), which have an unpleasant odor similar to that of chestnut flowers.

Table 1—*Distribution of* Quercus *species in the New World.*

Area	Number of species	Number of endemics
New World	202	202
Latin America	148	89
Mexico	140	81
Central America	25	8
Costa Rica	14	0
Mexico/Canada/U.S.	194	186
United States	89	46
California	20	7

The California Oaks

The California oaks have been the subject of almost constant taxonomic upheaval for the past century. This is in large part due to improved methods of study but, more importantly, because of more attention to careful fieldwork and consideration of the variation in the context of both morphology and ecological parameters and distribution. Much credit must be given to John Tucker (University of California, Davis, Emeritus) for setting the groundwork for more recent taxonomic studies of California oaks with a series of seminal papers that began to disassemble the broad and variable populations of scrub oaks into component taxa and to firmly establish the hybrid nature of several populations, both widespread (e.g., *Q.* X *alvordiana*) and restricted (e.g., *Q.* X *munzii*). The taxonomy presented here would not have been possible without Tucker's earlier work, as well as the work of the late C. H. Muller, whose interests focused more on Mexican and tropical American oaks. It is satisfying that both of these students of California oaks have been largely in agreement with the newer findings and taxonomy presented here (see Tucker 1993; Muller, personal communication).

The 20 species of *Quercus* found within the political boundaries of California fall into three different Sections (Nixon 1993b, Nixon 1997d): Section Quercus (the white oaks), Section Lobatae (the red or black oaks, often referred to Subg. *Erythrobalanus*), and Section Protobalanus (the intermediate or golden oaks). Within

each Section, I have provided only informal groupings that should not be considered to represent monophyletic groups, with the exception of subsection Glaucoideae (see below).

Section Lobatae Red or Black Oaks

1. *Quercus agrifolia* Nee
2. *Quercus kelloggii* Newb.
3. *Quercus parvula* Greene var. *parvula*

   Quercus parvula var. *shrevei* (Muller) Nixon & Muller
4. *Quercus wislizeni* A. DC. var. *wislizeni*

   Quercus wislizeni var. *frutescens* Engelm.

Section Protobalanus Intermediate or Golden Oaks

5. *Quercus chrysolepis* Liebm.
6. *Quercus vaccinifolia* Kellogg
7. *Quercus tomentella* Engelm.
8. *Quercus palmeri* (*Quercus dunnii* is a synonym).

Section Quercus White Oaks

Prinoideae group

9. *Quercus sadleriana* R. Brown, Campst.

Glaucoideae group

10. *Quercus engelmannii* Greene

California lobed-leaf white oaks

11. *Quercus lobata* Nee
12. *Quercus douglasii* H. & A.
13. *Quercus garryana* Dougl. var. *garryana*

    Quercus garryana var. *breweri* Jeps.

    Quercus garryana var. *semota*

California scrub white oaks

14. *Quercus dumosa* Nutt. *sensus stricto*
15. *Quercus berberidifolia* Liebm. (formerly often called *Q. dumosa*)
16. *Quercus john-tuckeri* Nixon & Muller

17. *Quercus pacifica* Nixon & Muller

18. *Quercus cornelius-mulleri* Nixon & Steele

19. *Quercus durata* Jeps. var. *durata*

Quercus durata var. *gabrielensis* Nixon & Muller

Sonoran scrub oak group

20. *Quercus turbinella* Greene

Additionally, there are two white oak complexes that are sometimes recognized as species but are considered to be derived from hybrid swarms, and possibly are stabilized nothospecies:

Quercus X *alvordiana* (*Quercus john-tuckeri* X *Quercus douglasii*)

Quercus X *acutidens* (*Q. engelmannii* X *Q. cornelius-mulleri*)

Within each section, essentially every possible hybrid combination has been reported for species that occur sympatrically. There are absolutely no verified cases of hybridization between species from different sections within the California oaks. Outside of California, very few intersectional hybrids have been claimed to have been produced experimentally, but these reports have not been verified with modern genetic or molecular methods. Therefore, until proven otherwise, it must be assumed that intersectional hybrids do not occur in the wild.

California oaks inhabit and dominate a large number of habitats, and have become symbolic of the Californian region. The majority of species are evergreen or subevergreen. This is especially true of the species of the Protobalanus group (e.g., *Q. chrysolepis*), which have leathery leaves that may persist as green, functional leaves for several years. This can be easily seen even in herbarium specimens, and the persistence of leaves for more than 2 years is unusual in the California region and is probably restricted to Protobalanus and the white oak *Q. sadleriana*. When evaluating leaf persistence from either a phylogenetic or ecologic perspective, it should be noted that juvenile oaks, as well as stump sprouts that exhibit "juvenile" growth, often have leaves that have a more leathery, spiny form, and much longer persistence than typical adult foliage. In some cases, species which exhibit leaf persistence of only 12-18 months in adult trees may produce leaves that persist for 24-36 months on stump sprouts and saplings (e.g., *Q. virginiana*; Nixon 1984, 1997).

Relationships of California Oaks

Currently, there are no explicit phylogenies, either morphological or molecular, that treat the California oaks in any detail. This problem is compounded by the large number of species within the genus outside of California that must be considered as potential relatives and therefore included in any thorough analysis. A recent broader molecular analysis of *Quercus* using the ITS and matK genes (Manos and others 2001) included some species of California oak, but resulted in almost no relevant resolution, and is highly suspect due to problems with paralogy in the ITS gene (Vazquez 2001; see also Sanderson and Doyle 1992). It is possible to say at this point only that each of the three sections that occur in North America is likely to be monophyletic based on both morphological and molecular data. Molecular and

morphological analyses that include California species are ongoing, but for the present, we can only make inferences about relationships based on the occurrence of specific character complexes that might be considered synapomorphies (shared, derived diagnostic features) for particular groups. Such speculations should be taken as a basis for developing sampling strategies for further work on the phylogeny of California oaks and as a general framework for evaluating the ecological parameters within the group.

Another issue that is relevant to the production of a phylogeny for California *Quercus* is the propensity of oaks to form hybrid swarms, with the result that it is unlikely that the evolutionary patterns among interfertile species are fully hierarchic. Such deviations from regularly divergent patterns may result in lack of resolution in cladograms, in large variances in positions of taxa, and/or results that seem improbable based on other data. In any case, the presumed mode of speciation (or lack thereof) in *Quercus* argues for cautious interpretations of any presumed phylogenetic patterns, whether derived from formal analyses, or merely based on the occurrence of a few characters as is the case in most of the discussions presented here. It is possible that for any given species of *Quercus*, past hybridization has produced a pattern of relationship to other species that is not hierarchic, and cannot be fully expressed in any hierarchic branching diagram. The resolution of such questions awaits more intensive study of the genus at the molecular level, and perhaps the development of novel approaches to data analysis.

Section Lobatae (The Red or Black Oaks)

The "Evergreen" Red Oaks of California—The California red (or black) oaks comprise one deciduous, lobed-leaf species, and three evergreen (or subevergreen) species. Because of the mild climate of California, close proximity to Mexico, and the sclerophyllous evergreen habit of *Q. agrifolia*, *Q. wislizeni*, and *Q. parvula*, one might expect that the closest living relatives of these species would be among the evergreen species of Mexico. However, based on morphological data, there appear to be no obvious connections between the California red oaks and the Mexican red oaks. The California red oaks have a series of features that are not known in Mexican oak species. In general, the sclerophyllous evergreen oaks of Mexico are either truly entire, completely lacking teeth, or have simple teeth, with one tooth per secondary vein. There are a few exceptions to this pattern of venation, both in the white oaks and red oak groups (e.g., the *Q. crassifolia* complex), but none of these species show any particular other features that would suggest a relationship to the California red oaks. While the relationships of *Q. wislizeni* and *Q. parvula* remain ambiguous, the relationships of both *Q. agrifolia* and *Q. kelloggii* seem to be with temperate lobed-leaf red oaks. *Quercus agrifolia* has a leaf venation pattern that appears to be derived from a lobed-leaf form, while *Q. parvula* and *Q. wislizeni* do not. This suggests a possible relationship between *Q. agrifolia* and *Q. kelloggii* or another extinct lobed leaf red oak. *Quercus agrifolia* and *Q. kelloggii* often form hybrids where they are in contact, which tends to be at the lower elevational limits of *Q. kelloggii*.

Quercus wislizeni—Quercus wislizeni (often incorrectly spelled *wislizenii*) is a rather straightforward species that inhabits dry slopes of interior valleys, often in association with the white oak *Q. douglasii*. The leaves are entire or toothed *(fig. 1)*. The most problematic aspects of this species are the extensive swarms of putative hybrids with *Q. agrifolia* and *Q. parvula* var. *shrevei* that occur in the Bay Area (discussed below under *Q. parvula*), where interior valley habitats and more coastal

habitats interdigitate more freely due to lower elevations in the Coast Ranges than occur to the south. In southern California, from the Transverse ranges south, *Q. wislizeni* does not typically attain tree stature, and usually has numerous trunks. These populations appear to be genetically distinct and separable as *Q. wislizeni* var. *frutescens*. It should be noted, however, that various individuals and small populations of *Q. wislizeni* var. *wislizeni,* particularly in the foothills of the Sierra Nevada, may have a scrubby form, which seems more environmentally induced.

Figure 1 *Quercus wislizeni* , typical leaf from lower side. Palomar, San Diego County.

Quercus parvula—Confusion persists about the species status *Q. parvula*. This species is highly distinctive and separable from *Q. wislizeni* on the basis of several characters including twig and bud pubescence, leaf form, and acorn shape and size (Nixon 1980, Tucker 1993). The shrubby populations (*Q. parvula* var. *parvula*) are restricted to Santa Cruz Island and a few populations in mainland Santa Barbara County (Nixon 1980, Nixon and Muller 1994). The tree form (*Q. parvula* var. *shrevei*) is a straight tall tree of relatively mesic habitats, often found on the margins of coast redwood forests (*Sequoia sempervirens*) extending within the fog belt from the Santa Lucia Mountains to a few localities north of San Francisco. In contrast, *Q. wislizeni* is a species typical of drier interior slopes and foothills. However, several populations of evergreen red oaks from the Bay Area and northward exhibit a morass of conflicting characters, indicating a hybrid swarm between *Q. parvula* var. *shrevei* (the mainland coastal tree form of *Q. parvula*) and both *Q. agrifolia* and *Q. wislizeni* (Nixon 1980). Apparently these problematic populations were the basis of the synonymy of *Q. parvula* under *Q. wislizeni* by the eastern North American oak taxonomist Jensen (1997) in his treatment of the red oak group for Flora North America. It should be noted that *Q. parvula* var. *parvula* in common garden cultivation with *Q. wislizeni* at Davis, California, and in the hot Central Valley,

maintain the distinct features, including habit, leaf, twig and acorn characters, typical of *Q. parvula* in coastal habitats (J. Tucker, personal communication). The features that separate *Q. parvula* from *Q. wislizeni* in remote populations are as great or greater than almost any pair of species of North American *Quercus*, and the occurrence of intermediates, even in large swarms, is not unusual, even between species considered to be only distantly related. The evidence overwhelmingly supports the conclusion that the contact and subsequent hybridization between *Q. parvula* and *Q. wislizeni* are secondary events, and that the two species have a separate history and should be recognized as distinct.

Quercus kelloggii—Quercus kelloggii, the California black oak, is a winter-deciduous species with deeply lobed leaves reminiscent of the lobed-leaf red oaks of Eastern North America *(fig. 2)*. It is mostly restricted to higher elevations, except in the north Coast Ranges. No particular eastern species of lobed-leaf oak is particularly close to *Q. kelloggii* in morphological features, and its overall relationships must await further study.

Figure 2 *Quercus kelloggii*, typical leaf from above. Palomar, San Diego County.

Section Protobalanus (The Golden Oaks)

The Protobalanus group of oaks is mainly restricted in range to the southwestern U.S. and adjacent Mexico. Trelease (1924) considered this group to be intermediate in most features between the red oaks and the white oaks. It is perhaps the most distinctive group of North American oaks, and appears to be more closely related to the white oak group than to the red oak group, based on both morphological analyses (Nixon 1993) and molecular analyses (Manos and others 1999, 2001). All species in this group are truly evergreen, with leaves persisting more than 1 year, and often as many as 3 years. Fruition is biennial as in the red oak group, but because the

branches bearing fruit often do not grow in the second year, specimens may appear to have annual fruit and thus may be called "pseudoannual." This condition may be a result of resource allocation, and is seen in various Mexican red oaks as well as California *Lithocarpus*.

Quercus tomentella—Quercus tomentella, the "Island Oak" is restricted to the larger Channel Islands, and also is found on Guadalupe Island off the coast of Baja California, Mexico, the type locality for the species. It is a tree species that resembles *Q. chrysolepis* in general form, but has larger, thicker leaves with more prominent regular teeth and a somewhat corrugated leaf blade *(fig. 3)*.

Figure 3 *Quercus tomentella*, specimen from type locality, Guadalupe Island, Mexico (*Cerda 2*, MEXU).

Quercus chrysolepis—Quercus chrysolepis is the most commonly encountered member of the Protobalanus group in California. It tends to grow in moist canyons and on steep north slopes, hence the common name "Canyon Live Oak." The leaves of *Q. chrysolepis* are distinctive, with numerous golden glandular hairs when young, but becoming glaucous with age *(fig. 4)*. Extensive hybridization has been reported between *Q. chrysolepis* and *Quercus vaccinifolia* in the Sierra Nevada, with *Quercus palmeri* in Arizona, and in isolated pockets on the Channel Islands with *Quercus tomentella*.

Figure 4 *Quercus chrysolepis*, lower leaf surface of young leaf, with glandular hairs. Palomar, San Diego County.

Quercus palmeri—Much confusion surrounds the correct name for this species, which in some of the older literature was called *Quercus dunnii*. The latter name was proposed by Kellogg only as a provisional name, and is not valid under the rules of nomenclature. Although *Q. dunnii* was later accepted by the author, in the meantime *Q. palmeri* had been published as a species and therefore it is the oldest valid name for this species. *Q. palmeri* is a rarely encountered species in southern California, and is more common in parts of Central and Western Arizona, and in Baja California, Mexico. This bimodal Arizona-Baja California distribution may indicate a preference for summer rains, and explain the spotty California distribution as mostly due to attrition with an increasing Mediterranean climate. The leaves of *Q. palmeri* are among the spiniest of any oak species, and the species produces thickets that are virtually impenetrable by large mammals such as humans.

Quercus vaccinifolia—Quercus vaccinifolia, or the huckleberry oak, is a low shrub of high montane areas, mostly on the west slope of the Sierra Nevada. It bears a strong resemblance to the shrubby Mexican endemic *Quercus cedrosensis,* found from near the California-Mexican border south, to the closed-cone pine forests of coastal Baja California, and also on higher elevations on Cedros Island.

Section Quercus (The White Oaks)

The ”Prinoideae” group—*Quercus sadleriana* is a rather unique shrub species of the Siskiyou region of northern California that is truly evergreen and has toothed leaves with regularly-spaced secondary veins reminiscent of some eastern North

American species such as *Q. montana* (often called *Q. prinus*; see Nixon and Muller 1997).

"Lobed-leaf White Oaks"—*Quercus lobata*, *Q. garryana*, and *Q. douglasii* are deciduous trees with deeply to moderately lobed leaves (although some individuals of *Q. douglasii* may have unlobed or essentially unlobed leaves, either entire or more commonly irregularly toothed). Within this lobate group, *Q. garryana* shows strong similarities to *Q. gambelii*, a Rocky Mountain species that tends to form multiple trunks. The shrub varieties *Q. garryana* var. *breweri* and *Q. garryana* var. *semota* both are very suggestive of the habit (and montane habitat) of *Q. gambelii*. It is likely that the *Q. garryana-gambelii* complex represents a vicariant distribution of a more widespread ancestral species that has been fractionated with drying trends in the climate of the western U.S. since the Tertiary.

"Scrub White Oaks"—The scrub white oaks (*Q. dumosa sensu lato*, *Q. "turbinella*" and *Q. durata*) have been a source of taxonomic controversy and confusion. A simple interpretation of this problem is that leaf form is highly convergent in scrub oaks, and traditional taxonomies relied too heavily on leaf form without attention to other features, in particular acorn morphology and leaf vestiture. This resulted in a very broad concept of *Q. dumosa* throughout the state. More recent studies, beginning with Nixon and Steele (1981), began to detect a pattern of variation in features of the trichomes, acorns, and habitat that suggest at least 5 species should be recognized from the traditional *Q. dumosa* complex: *Q. dumosa sensu stricto*, *Q. berberidifolia*, *Q. john-tuckeri*, *Q. cornelius-mulleri*, and *Q. pacifica* (Nixcn and Steele 1981; Nixon and Muller 1994, 1997). Each of these species has a very distinctive set of characteristics, and a specific geographic range, as discussed below.

All of the California scrub white oak species (with the exception of the eastern *Q. turbinella*) have a leaf form that appears to be derived from a lobed leaf, as evidenced by the typically branched secondary veins, multiple marginal teeth associated with each secondary vein, irregular tooth spacing, and often deeper sinuses separating groups of teeth derived from each secondary *(fig. 5)*. In other words, these species often have leaves that appear to be small lobed leaves in which the sinuses have been reduced to minor indentations. In contrast, the numerous scrub oaks of the interior southwestern U.S. and mainland Mexico generally have secondary veins that are not highly branched, more typically one tooth per secondary vein, and regularly spaced teeth without obvious variation in depth of sinuses separating the secondaries. Without any complete and robust phylogenies for American *Quercus*, the interpretation of these patterns remains speculative, but strongly suggest that the California scrub oaks were derived directly from lobed-leaf ancestors in common with such species as *Q. garryana*, *Q. lobata*, and *Q. douglasii* (and this species may present a good model for a transition to a smaller, less lobed leaf).

Quercus dumosa Nutt. *sensu stricto*—The type specimen of *Q. dumosa* was collected by the well-known naturalist Thomas Nuttall during the voyage that was the subject of the book *Two Years Before the Mast* (Dana 1840). The type locality is listed as "hills near Santa Barbara" and indeed material similar to the type specimen occurs locally in the foothills that are now part of Santa Barbara, such as on the upper grounds of the Santa Barbara Botanic Garden. This material differs markedly from the common forms of more interior localities that have traditionally been called *Q. dumosa*. Several characters separate the type material of *Q. dumosa* from the widespread species now called *Q. berberidifolia* (Nixon and Muller 1997). These

characters are significant in the context of oak systematics, and populations bearing these characters are found only in very restricted habitats in low hills near the coast, often on very loose sandstones or granitics, in association with species often referred to as "soft chaparral," as opposed to the "hard chaparral" habitat of *Q. berberidifolia* in higher and more interior localities. One of the most distinctive features of the species is an erect, usually twisted, multi-rayed trichome on the lower leaf surface *(fig. 6),* unlike any other scrub oak. *Q. dumosa sensu stricto* is perhaps one of our rarest and most threatened species, known only in these coastal habitats from Santa Barbara County south to northern Baja California. It is unknown from the Channel Islands. Many of the habitats where *Q. dumosa* would be expected have been destroyed by development, and represent some of the most expensive and desirable real estate in southern California. Because of the former wider application of the name *Q. dumosa*, there probably has been some confusion and resistance regarding the rare status of this species. Anyone doubting the distinctness of the species is encouraged to visit Torrey Pines State Park, in San Diego County, one of the last remaining populations that is relatively intact and accessible.

Figure 5 *Quercus dumosa* , lower leaf surface, and sublobate form. Specimen from 32 km north of Ensenada, Baja California Norte, Mexico (*Wiggins & Gillespie 3999*, MEXU).

Quercus durata—Quercus durata is the only American species of *Quercus* that has a restricted distribution on serpentine. Prior to the naming *of Q. durata* var. *gabrielensis* (Nixon and Muller 1994), the species could be considered a true serpentine endemic, and this can still be said of the population referred to var. *durata*, from Santa Barbara County northward. *Q. durata* var. *gabrielensis,* differing in having larger leaves, a more open growth form, larger abaxial leaf trichomes, and more glabrate upper leaf surface, occurs on open gneiss-derived barren soils in the

San Gabriel Mountains of Los Angeles County. Further ecological work is needed to determine if var. *gabrielensis* is edaphically restricted, and the chemical nature of the soils on which it occurs. The nature of the leaf and twig pubescence, acorn shape, size, and cup morphology, as well as the sublobate leaves of *Q. durata,* suggest a possible relationship with *Q. garryana* and *Q. gambelii*, two deciduous tree species with lobed leaves and probably temperate affinities.

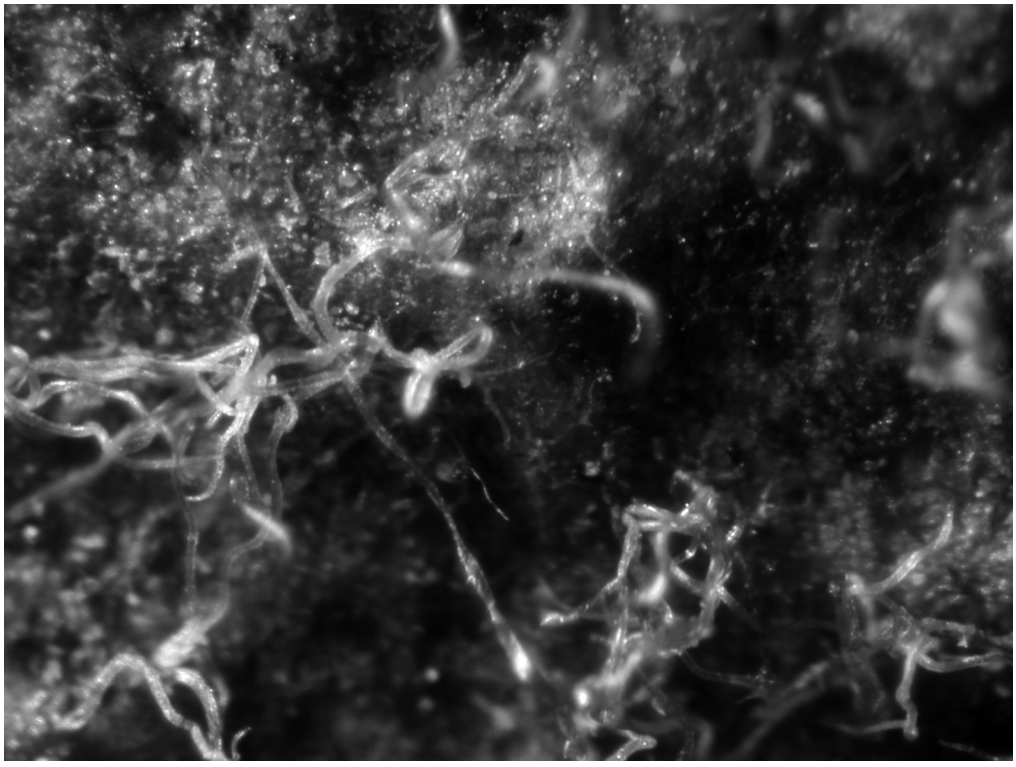

Figure 6 *Quercus dumosa*, sparse, erect, curly trichomes of lower leaf surface, as viewed through dissecting microscope. Field of view is ca. 2 mm across. (*Wiggins & Gillespie 3999*, MEXU).

Quercus berberidifolia—*Quercus berberidifolia* might be considered the "default" scrub oak of the Coast Ranges of Central California. While probably closely related to *Q. john-tuckeri* (formerly called *Q. turbinella* var. *californica*), it occupies more mesic habitats than that species and than *Q. cornelius-mulleri*. It occurs on a variety of soils, while *Q. durata* is restricted to serpentine soils from Santa Barbara County to the north (*Q. durata* var. *gabrielensis* occurs on non-serpentine, but barren gneiss soils, in the San Gabriel Mountains of Los Angeles County). Diagnostic features of *Q. berberidifolia* include the typical usually 7-8 rayed flat stellate trichomes of the lower leaf surface (in contrast to twisted, erect trichomes of *Q. dumosa sensu stricto* and the much larger erect, straight trichomes with fewer rays, found in both varieties of *Q. durata*), a relatively flat waxy leaf with a squarrose or rounded-attenuate base (in contrast to the tapered or acute base and spatulate leaf of *Q. pacifica*), and a usually barrel-shaped, rounded or blunt acorn (in contrast to the sharply acute acorns of both *Q. dumosa sensu stricto* and *Q. pacifica*). Hybrids and/or suspected hybrids occur wherever the scrub oaks come into contact, and given the wide distribution of *Q. berberidifolia*, it is not surprising that putative

hybrids occur with *Q. dumosa sensu stricto* (e.g., Santa Barbara County, at mid-elevation and ridges above populations *of Q. dumosa*) and with both *Q. john-tuckeri* and *Q. durata*.

Quercus cornelius-mulleri—Quercus cornelius-mulleri was the first of the four segregate species of *Q. dumosa sensu lato* to be recognized. The nature of the vestiture of the lower leaf surface, with dense whitish stellate trichomes that are microscopically fused into plates, is one of the most prominent features of this species *(fig. 7)*. However, it is easily recognized by the dense neat habit, large-tapered cylindric fruit, and bicolored leaves, whitish on the lower surface *(fig. 8)*. It is restricted to dry washes and slopes, mostly on granitics and sands, in the interior desert margins and Juniper and Piñon woodlands of San Bernardino, Riverside and San Diego Counties, south into northern Baja California. Among the best places to observe this species are in Joshua Tree National Monument and along most of the east-west roads in San Diego County on the western margins of the Colorado Desert in Juniper and Piñon woodlands.

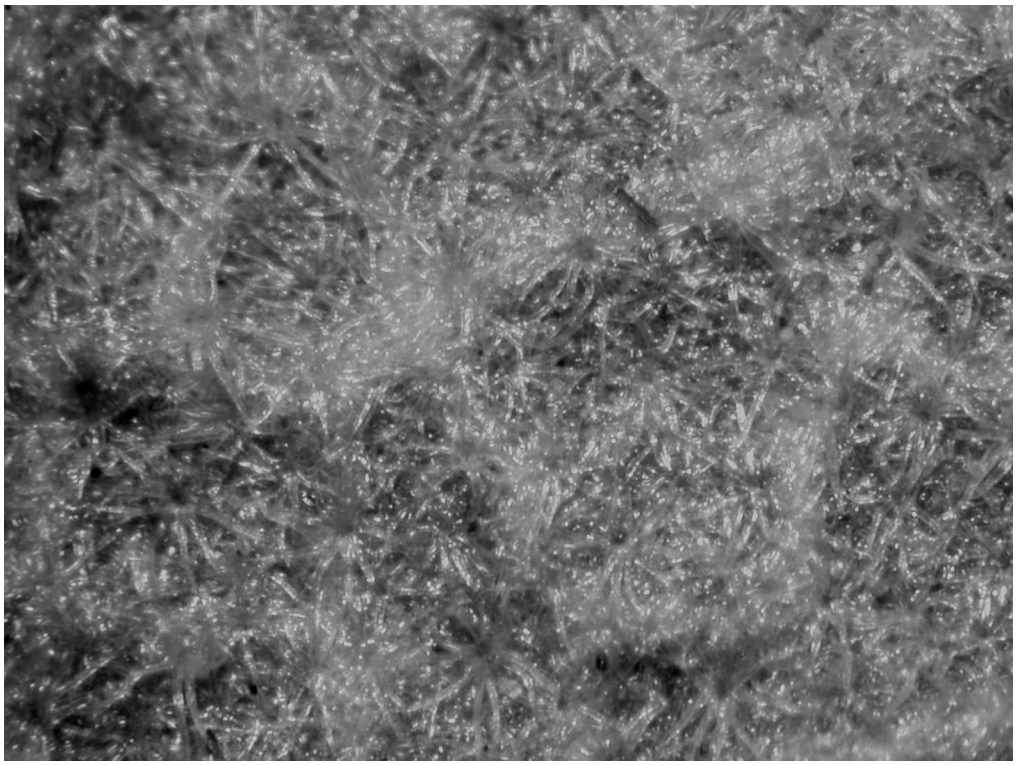

Figure 7 *Quercus cornelius-mulleri*, dense overlapping covering of flat fused-stellate trichomes of the lower leaf surface, as viewed through dissecting microscope. Field of view is ca. 2 mm across. (*Bourell, Patterson & Timbrook 2960*, MEXU).

Figure 8 *Quercus cornelius-mulleri*, typical leaf, with dense whitish trichomes on lower surface. Photographed near Banner, San Diego County.

Like other California scrub oaks, *Q. cornelius-mulleri* probably is related to a group of lobed-leaf species of white oak. A likely candidate, based on vestiture of the leaves, fruit and cup form, and papery bark characteristics, is the species group that includes the species *Q. sinuata*, *Q. pungens* and *Q. vaseyana,* with a distribution from the southeastern U.S. to Arizona and northern Mexico. However, *Q. cornelius-mulleri* also shares certain features with *Q. lobata*, in particular the large tapered acorns*,* and a relationship with that species cannot be excluded.

Quercus pacifica—Quercus pacifica is restricted in distribution to the three channel islands Santa Cruz, Santa Catalina, and Santa Rosa (Nixon and Muller 1994, 1997). It closely resembles *Q. berberidifolia*, but differs in having consistently spatulate leaves with a narrowed leaf base, and acute-tapered fruit, with thinner cups. Leaf vestiture otherwise is similar to *berberidifolia*, but that species has typically square or rounded-attenuate leaf bases and blunter, heavier fruit. It is likely that *Q. pacifica* is phylogenetically close to *Q. berberidifolia* or possibly represents a nothospecies derived from intergradation between *Q. berberidifolia* and *Q. douglasii*. This would be consistent with the widespread occurrence on the channel islands of a lobed-leaf small tree referred to *Q*. X *macdonaldii*, and interpreted to be a stabilized hybrid between *Q. lobata* and *Q. pacifica*, suggesting that widespread hybridization has occurred on the islands between the scrub oaks and either *Q. lobata* or *Q. douglasii*, neither of which occur in abundance, but are found in isolated pockets.

Quercus turbinella and Q. john-tuckeri—The name *Q. turbinella* was previously applied to populations to the east of California (Arizona to Texas, into northern Mexico), as well as to populations in California now referred to *Q. john-tuckeri* (mostly interior Central California) and *Q. cornelius-mulleri* (interior desert margins

of southern California). *Quercus turbinella* from Arizona and eastwards has a distinctive fruit, relatively small and borne on a peduncle up to four cm in length. Peduncle length throughout the genus *Quercus* is one of the most useful and consistent characters, and species with elongate peduncles are in the minority (e.g., *Q. robur*, *Q. bicolor*, *Q. virginiana*). While long peduncles are typical of all *Q. turbinella* outside of California, the material previously referred to *Q. turbinella* var. *californica* from Central California has subsessile acorns, as in all other California scrub oaks including *Q. cornelius-mulleri*. Additionally, *Q. turbinella* var. *californica* lacks the distinctive cordate leaf base of typical *Q. turbinella* from the east, and has a host of other more subtle differences, such as thicker, more warty cups, larger, blunter fruit, and trichomes with fewer rays. The Californian material is thus better referred to another species, *Q. john-tuckeri*, which in fact seems to be more similar to the other California scrub oaks such as *Q. berberidifolia* than to typical *Q. turbinella* from Arizona. Examination of leaf form in *Q. turbinella* from Arizona and Mexico also reveals that it has more regular, evenly spaced veins that are not suggestive of a lobate form, in contrast to *Q. john-tuckeri,* which has the typical sublobate form found in other California scrub oaks. Interestingly, there are a few populations of typical *Q. turbinella* in the eastern desert ranges of southern California near the Arizona border, and in Baja California on the eastern slope of the Sierra Juarez and Sierra San Pedro Martir. All of these areas receive significant summer rainfall, and it is likely that the range *of Q. turbinella sensu stricto* is determined by the occurrence of summer rain – further negating the idea that it is conspecific with *Q. john-tuckeri*. The relationships of *Q. trubinella* clearly are with a complex of species to the east, including *Q. ajoensis*, *Q. hinckleyi*, and possibly *Q. toumeyi*, none of which occur in California.

Quercus engelmannii—Quercus engelmannii is a relatively common component of open oak woodlands in mostly interior foothill localities from Los Angeles County (along the foothills of the San Gabriel Mountains) south to similar habitats in Baja California Norte. Although leaf color is variable in this species, most individuals have a bluish cast to the leaf on both surfaces, and some individuals are strikingly blue in color *(fig. 9)*. Because of the superficial similarities between *Q. engelmannii* and the more northern *Q. douglasii* in leaf color and habitat preference, many California botanists have assumed that the two species are closely related. This is not the case. Numerous morphological features indicate a close relationship between *Q. engelmanni* and *Q. oblongifolia*, a very similar species of oak woodland habitats in Arizona, New Mexico, and northern Mexico. *Q. engelmannii* and *Q. oblongifolia* share a more or less identical leaf vestiture, coloration, shape and size of leaves, and an important complex of embryological features. Both species exhibit marked fusion of the cotyledons in the seed (Nixon 1984, 1993a, 1997d), a feature not found in any other species of California oak, and definitely lacking in *Q. douglasii*. In turn, based on several features including the apparent synapomorphy of fused cotyledons, *Q. engelmannii* and *Q. oblongifolia* belong to well-marked clade of about 35 species of *Quercus* from the southwestern U.S. and Mexico, placed in subsection Glaucoideae. A significant number of these species (e.g., *Q. arizonica*, *Q. perpallida*, *Q. depressipes*, *Q. glaucoides*) exhibit glaucous, often bluish leaves in common with *Q. engelmannii*. *Quercus douglasii* is not a member of the Glaucoideae and evidence suggests a closer relationship between it and the California scrub oaks and lobed-leaf white oaks, such as *Q. garryana*. Thus, the bluish color and habitat preference shared by *Q. engelmannii* and *Q. douglasii* should be considered to be convergent.

Figure 9 *Quercus engelmannii*, branch with acorn. Photographed near Palomar, San Diego County.

The complex of species to which *Q. engelmannii* belongs (subsection Glaucoideae) generally occurs in relatively arid areas that receive most rainfall in the summer months. These localities, from the southwestern U.S. to southern Mexico, are some of the driest places that oaks are found in North America. Additionally, the embryological features separating this group are associated with a germination syndrome in which the embryo axis is placed more deeply into the soil, and may be an adaptation to drought, fire, or both (Nixon 1984). Further study of the ecology of the unusual germination syndrome of this group, including *Q. engelmannii*, is needed.

Summary

The 20 recognized species of California oaks include representatives of 3 major lineages, generally treated as sections within *Quercus*. One of these sections (the white oaks) is widespread in the Northern Hemisphere of both the Old and New Worlds and is the most diverse group within California oaks. The higher diversity of the white oak group in California is consistent with its higher diversity in general in arid areas, in contrast to the red oaks. The red oak group includes only four species, one of which (*Q. parvula*) appears to be a relict of wetter coastal habitats both on Santa Cruz Island and the mainland. The third section, Protobalanus, is endemic to the southwestern U.S. and northwestern Mexico, and is perhaps the most distinctive group of North American oaks. Within the white oaks, the scrub oak group is most problematic taxonomically, and the component species (with the exception of *Q. turbinella sensu stricto*) exhibit leaf morphologies that suggest derivation from one or

more lobed-leaf deciduous ancestors. This favors the interpretation that the scrub white oaks were derived from temperate oak ancestors, and are not closely related to scrub oak species of chaparral and woodland habitats to the east and south in summer rain areas of the southwestern U.S. and Mexico. These origins may have ecological significance and should be taken into consideration whenever California oak species are compared with each other, or with species from other areas. One of the best established phylogenetic relationships among California oaks is that of *Q. engelmannii*, often considered to be related to *Q. douglasii*, but which actually belongs to a distinctive group of mostly Mexican species (subsection Glaucoideae), many of which share a bluish leaf color. Members of the Glaucoideae have a unique seed morphology and germination syndrome that may be related to fire or drought adaptation, and which may be important in understanding the ecological parameters controlling the distribution of *Q. engelmannii* in California.

References

Crepet, William L;. Nixon, Kevin C. 1989a. **Earliest megafossil evidence of Fagaceae: phylogenetic and biogeographic implications.** American Journal of Botany 76: 842-855.

Crepet, William L.; Nixon, Kevin C. 1989b. **Extinct transitional Fagaceae from the Oligocene and their phylogenetic implications.** American Journal of Botany 76: 1493-1505.

Dana, Richard H., Jr. 1840. **Two years before the mast, a personal narrative of life at sea.** New York: Harper and Brothers; 483 p.

Jensen, Richard J. 1997. ***Quercus* section Lobatae.** In: Flora of North America Editorial Committee, eds, Flora of North America North of Mexico. Vol. 3. New York: Oxford University Press; 447-468.

Manos Paul S.; Nixon, Kevin C.; Doyle, Jeffery J. 1993. **Cladistic analysis of restriction site variation within the chloroplast DNA inverted repeat region of selected Hamamelididae.** Syst Bot 18: 551–562.

Manos, Paul S.; Doyle, Jeffery J.; Nixon, Kevin C. 1999. **Phylogeny, biogeography, and processes of molecular differentiation in *Quercus* subg. *Quercus* (Fagaceae).** Molecular Phylogenetics and Evolution. 12: 333-349.

Manos Paul S.; Zhou, Z-K.; Cannon, Charles H. 2001. **Systematics of Fagaceae: phylogenetic tests of reproductive trait evolution.** Int J Plant Sci 162: 1361–1379.

Nixon, Kevin C. 1980. **A systematic study of *Quercus parvula* Greene on Santa Cruz Island and mainland California**. University of California, Santa Barbara. M.A. thesis.

Nixon, Kevin C. 1984. **A biosystematic study of *Quercus* Series Virentes with phylogenetic analyses of Fagales, Fagaceae and *Quercus*.** University of Texas, Austin. Ph.D. dissertation,

Nixon, Kevin C. 1989. **Origins of Fagaceae.** In: Crane, P. R.; Blackmore, S., eds. Syst. Assoc. Spec. Vol. 40B. Evolution, systematics, and fossil history of the Hamamelidae. Vol. 2: 23-43. Oxford: Clarendon Press.

Nixon, Kevin C. 1993a. **The genus *Quercus* in Mexico.** In: Ramamoorthy, T. P.; Bye, Robert; Lot, Antonio; Fa, J., eds. Biological diversity of Mexico: origins and distribution. Oxford: Oxford University Press; 447-458.

Nixon, Kevin C. 1993b. **Infrageneric classification of *Quercus* (Fagaceae) and typification of sectional names.** Annales des Sciences Forestieres 50(suppl. 1): 25s-34s.

Nixon, Kevin C. 1997a. **Fagaceae**. In: Flora of North America Editorial Committee, eds, Flora of North America North of Mexico. Vol. 3. New York: Oxford University Press; 436-437.

Nixon, Kevin C. 1997b. **Chrysolepis**. In: Flora of North America Editorial Committee, eds, Flora of North America North of Mexico. Vol. 3. New York: Oxford University Press; 438-439.

Nixon, Kevin C. 1997c. **Lithocarpus**. In: Flora of North America Editorial Committee, eds, Flora of North America North of Mexico. Vol. 3. New York: Oxford University Press; 442-443.

Nixon, Kevin C. 1997d. **Quercus**. In: Flora of North America Editorial Committee, eds, Flora of North America North of Mexico. Vol. 3. New York: Oxford University Press; 445-447.

Nixon, Kevin C.; Crepet, William L. 1989. ***Trigonobalanus* (Fagaceae): Taxonomic status and phylogenetic relationships.** Amer. J. Bot. 76: 826-841.

Nixon, Kevin C.; Muller, Cornelius H. 1992. **The resurrection of *Quercus laceyi.*** Sida 15: 57-69.

Nixon, Kevin C.; Muller, Cornelius H. 1993. **The *Quercus hypoxantha* complex in Mexico.** Brittonia 45: 146-153.

Nixon, Kevin C.; Muller, Cornelius H. 1994. **New names in California oaks.** Novon 4: 391-393.

Nixon, Kevin C.; Muller, Cornelius H. 1997. ***Quercus* section *Quercus.*** In: Flora of North America Editorial Committee, eds, Flora of North America North of Mexico. Vol. 3. New York: Oxford University Press; 471-506.

Nixon, Kevin C.; Steele, Kelly P. 1981. **A new species of *Quercus* from southern California.** Madroño 28(4):210-219.

Sanderson, Michael J.; Doyle, Jeffery J. 1992. **Reconstruction of organismal and gene phylogenies from data on multigene families: concerted evolution, homoplasy, and confidence.** Systematic Biology 41: 4-17.

Tucker, John M. 1993. **Fagaceae.** In: The Jepson manual. Higher plants of California. Hickman, James C., ed. Berkeley: University of California Press; 657-663.

Vazquez, Lucia. 2001. **Molecular and Morphological Study of *Quercus* series Crassifoliae.** Cornell University. Ph.D. thesis.