Agrifoliae: the California Red Oaks

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ABSTRACT

Like water from an incredibly slowly leaking faucet the recognition of the four species (Fig. 1) of the California Floristic Province (CA-FP) native Red Oaks (*Quercus*, section *Lobatae*, series *Agrifoliae*) has dripped out one at a time over nearly two hundred years. The eleven currently accepted taxa – four species including eight varieties plus three named hybrids – were each described by different authors, most prior to 1890. A recent study (Hauser et al. 2017) combining both morphological and molecular analysis has finally examined all eleven taxa simultaneously. Morphometric and DNA sequence (RAD-Seq) results are in general agreement, confirming the four California Red Oak species to be distinct while also identifying two samples as F1 hybrids. Here we describe and interpret the taxonomic history of the *Agrifoliae* and provide a detailed synthesis of the findings which have consequences to biodiversity and conservation concerns. We conclude that: 1) DNA analysis establishes the *Agrifoliae* to be a discrete clade separate from and sister to the combined Eastern North America and Mexican Red Oaks, splitting from them roughly 30 million years ago; 2) *Q. wislizeni* is not composed of two varieties as described by Engelmann; 3) *Q. parvula* var. *tamalpaisensis* is of hybrid origin, not a variety of *Q. parvula*; 4) DNA analysis reveals an unnamed F1 hybrid (*Q. kelloggii* × *Q. parvula* var. *shrevei*); and 5) both morphological and DNA analyses suggest *Q. parvula* var. *parvula* is a hybrid, but sample sizes are too small to confirm this.

Keywords: hybridization, introgression, *Lobatae*, morphometrics, phylogeny, *Quercus* hybrids, RAD-Seq, taxonomy

The convoluted taxonomic history of the Agrifoliae

Luis Née's 1801 description of *Quercus agrifolia* (Fig. 1C) – collected by the Spanish Malaspina Expedition of 1789-1794 ostensibly in both Monterey and, incorrectly, Canada – constitutes the first California Red Oak taxon still recognized today (Née 1801). Like all of the others to follow, *Q. agrifolia* is a morphotaxon, defined by its unique combination of morphological characters: the spiny leaves and sharply pointed fruit which distinguish *Q. agrifolia* from oaks found in Europe and the Eastern United States. Another half century elapsed before botanists began teasing out other California Red Oak taxa.

In 1855 Kellogg described *Q. arcoglandis*, from material collected by Colonel Ransom near Fort Tejon in Kern County (Kellogg 1855). The type specimen and Kellogg's drawings are presumed destroyed by the fire following the 1906 San Francisco earthquake. Even without these, Kellogg's surviving published description defines an evergreen oak different from *Q. agrifolia*. Today, the California Red Oak matching Kellogg's description near Fort Tejon are those now called *Q. wislizeni* (Fig. 1D).

Nine years after Kellogg's publication, Swiss-French botanist Alphonse P. De Candolle described *Q. wislizeni* (A. DC. 1864) relying on material he thought to have been gathered in either 1846 or 1847 by Friedrich Wislizenus in the mountains of Mexico to the west of Chihuahua near Cosiquiriachi, altitude 7,000 ft., where Wislizenus was imprisoned during the Mexican-American War. Collected material was forwarded to De Candolle by German-born botanist Georg Engelmann – fellow German-born expat, Wislizenus's close friend, and St. Louis medical-practice partner.

The naming by De Candolle of a high-elevation Mexican oak might have had little to do with California Red Oak taxonomic history today except that nearly 30 years after Wislizenus's collection 69-year-old Engelmann published a surprising modification to collection location and date. He changed them from the mountains of Mexico in 1846-1847 during Wislizenus's Mexican-American War imprisonment, to the Sierra foothills of California in 1851 during Wislizenus's extended honeymoon. Engelmann wrote that the revised location was along the "American Fork of Sacramento River," neglecting to include "near Auburn" (also noted on the type specimen's label). In the same publication Engelmann devoted half a sentence to his description of a new variety, *Q. wislizeni* var. *frutescens* (Engelmann 1878), complementing his other shrubby variants: *Q. agrifolia* var. *frutescens* (Engelmann 1880) and *Opuntia fragilis* var. *frutescens* (Engelmann 1845), both no longer recognized.

But previously in 1853 – before the published descriptions of either *Q. arcoglandis* or *Q. wislizeni* – a United States military and scientific expedition had made its way down the Zuni and Colorado Rivers. While crossing the mountains towards San Diego expedition members collected material from a holly-leaved oak near Santa Ysabel subsequently examined by John Torrey and described as a new species: *Q. oxyadenia* (Torrey 1853). This would have been the second California evergreen oak to be recognized, but because of its morphological similarity to *Q. agrifolia, Q. oxyadenia* was not widely accepted as a separate species and was relegated to synonymy under *Q. agrifolia*. Ignored for nearly 80 years *Q. oxyadenia* was eventually resurrected by John Thomas Howell as *Q. agrifolia* var. *oxyadenia* (Howell 1931).

By 1887 all California evergreen Red Oaks were considered to be either *Q. agrifolia* or *Q. wislizeni* until fieldwork on Santa Cruz Island by botanist and Episcopal rector Edward Lee Greene. He noted a shrubby oak similar to but distinct from *Q. wislizeni*,

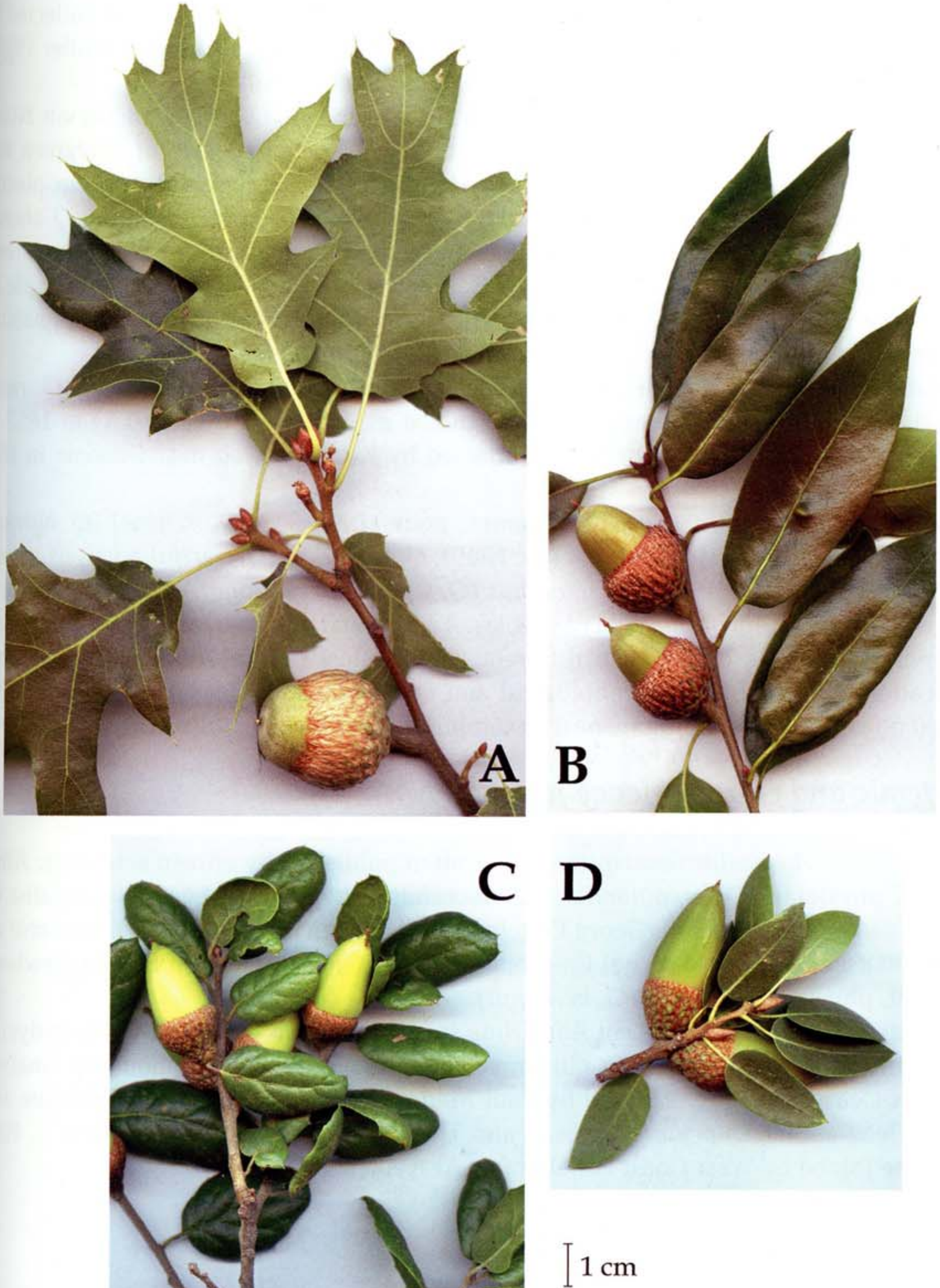

Figure 1/ Examples of the four *Agrifoliae* species of *Quercus*. Deciduous: (A) *Quercus kelloggii*; Evergreen: (B) *Q. parvula* (var. *shrevei* shown); (C) *Q. agrifolia* (var. *agrifolia* shown); (D) *Q. wislizeni*.

calling it *Q. parvula* (Greene 1887). However, shortly thereafter he reluctantly stepped away from his new species deciding it was best lumped together with *Q. wislizeni* because of its similarity to Mt. Tamalpais oaks previously identified as *Q. wislizeni* (Greene 1889-1890).

Expansion of California's evergreen Red Oak count from two to three again seemed likely when in 1938 Cornelius H. Muller described *Q. shrevei* from material collected by botanist Forrest Shreve in Big Sur's Palo Colorado River canyon in 1918 (Muller 1938). But as with Torrey's *Q. oxyadenia*, *Q. shrevei* was also ignored.

More than 110 years after De Candolle's description of *Q. wislizeni*, Kevin Nixon determined that this taxon included not one but two distinct species of evergreen Red Oaks (Nixon 1980; Nixon and Muller 1994). He resurrected Greene's *Q. parvula*, placing the Santa Cruz Island and nearby mainland trees there and recombined Muller's *Q. shrevei* as *Q. parvula* var. *shrevei* (Fig. 1B), where he assigned the majority of the coastal trees.

The final addition to the current list of California evergreen Red Oaks was made by S.K. Langer with his description of *Q. parvula* var. *tamalpaisensis* from a small number of trees on or near Mt. Tamalpais in Northern California (Langer 1993).

California's only native deciduous Red Oak – originally confused with *Q. rubra* from the Eastern United States – was recognized as *Q. kelloggii* (Fig. 1A) in 1857 by Newberry, described from a specimen collected by Karl Hartweg near Sonoma in 1848 (Newberry 1857).

Three hybrid *Agrifoliae* have been named, none after 1949: *Q.* ×*chasei* (*Q. agrifolia* var. *agrifolia* × *kelloggii*) (McMinn et al. 1949); *Q.* ×*ganderi* (*Q. agrifolia* var. *oxyadenia* × *kelloggii*) (Wolf 1944); and *Q.* ×*morehus* (*Q. wislizeni* × *kelloggii*) (Kellogg 1863).

Each of these 11 *Agrifoliae* taxa (4 species, 4 additional varieties, and 3 named hybrids) is a morphotaxon described by a different author, most before 1890. Until the recent publication of a combined morphological and DNA analysis (Hauser et al. 2017) there existed no single study simultaneously examining all of the *Agrifoliae* taxa.

Academic and citizen science join hands

Historically, *Agrifoliae* descriptions were often published by citizen scientists: Albert Kellogg, physician (*Q. arcoglandis*, *Q.* ×*morehus*); Stephen K. Langer, naturalist (*Q. parvula* var. *tamalpaisensis*); Georg Engelmann, physician (*Q. wislizeni*, *Q. wislizeni* var. *frutescens*); Edward Lee Greene, Episcopal rector (*Q. parvula*); John Strong Newberry, geologist, physician, explorer (*Q. kelloggii*).

Echoing this history, the recent *Agrifoliae* study paired lab work and DNA analysis at Duke University with concurrent citizen science fieldwork and morphometric analysis. The East Coast academic team led by Paul Manos included postdoctoral associate John McVay, lead author Duncan A. Hauser, and The Morton Arboretum's Andrew L. Hipp; they were joined by West Coast collaborator Al Keuter.

Morphological studies

Trees sampled for the study were generally morphologically typical representatives of *Agrifoliae* taxa; less typical specimens were only collected when necessary to preserve close proximity of sympatric sample populations. The exception was *Q. agrifolia* which was so variable at or near every sample locality that "typical" representatives could not be easily determined (though all shared annual fruit maturation unique to *Q. agrifolia* among the *Agrifoliae*). Type localities were sampled for eight of the eleven named taxa – all except *Q. agrifolia* var. *agrifolia*, *Q.* ×*morehus*, and *Q.* ×*chasei*. Sympatric taxa were also sampled at the type localities. Too late to include in the study, the *Q.* ×*chasei* holotype tree was not collected and morphologically examined until May 2017.

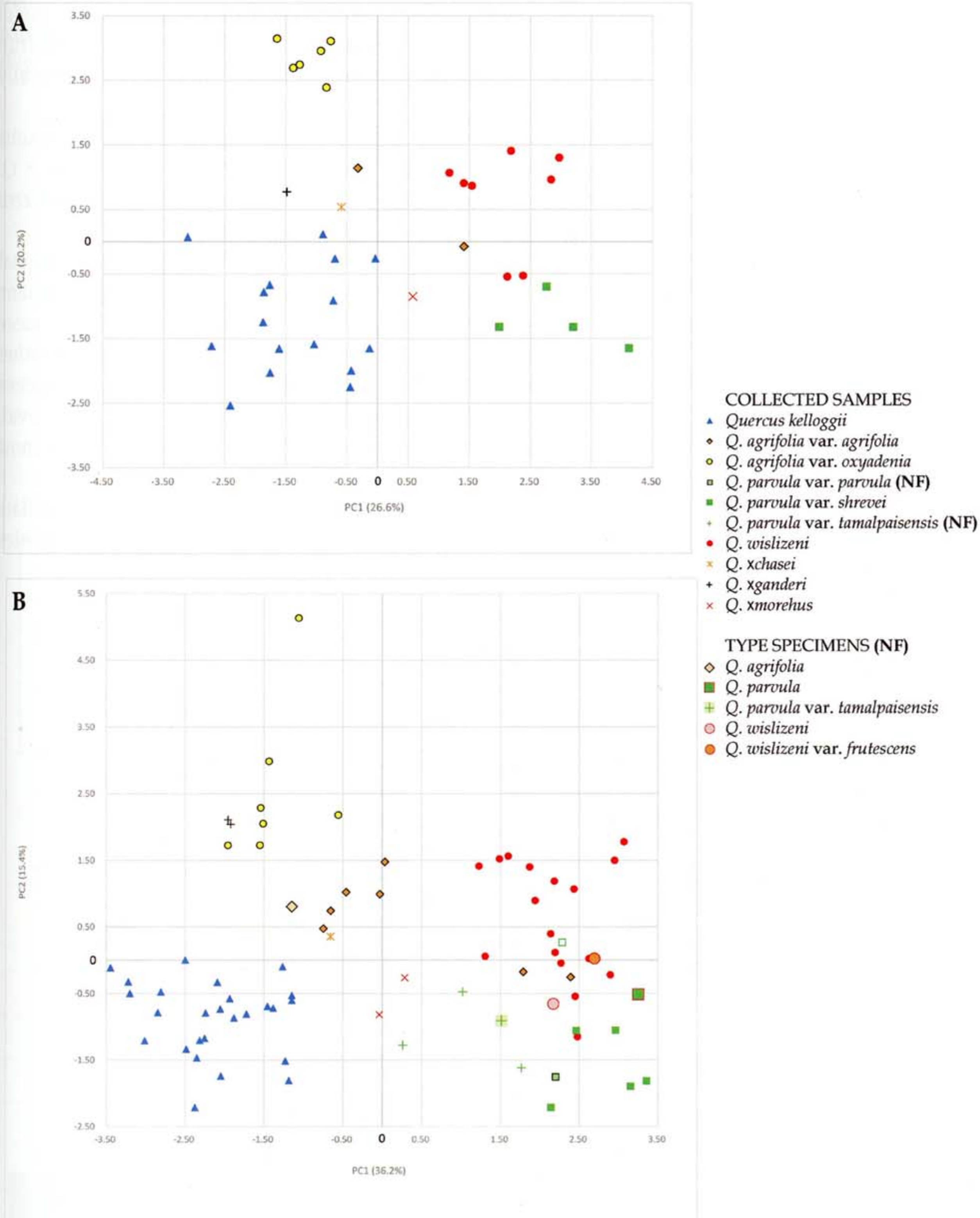

Figure 2/ PCA analyses of morphometric data. (A) PCA of leaf and assembled fruit characters (39 trees, 13 leaf + fruit characters). (B) Leaf-only PCA (77 trees, 12 leaf-only variables) including measurements from digitized herbarium sheets of type specimens. NOTE: Legend entries marked (NF) specify taxa lacking measurable assembled fruit; together with the type specimens they appear only in B.

Roughly 18,000 morphological measurements and assessments produced useful multivariate and univariate results. The multivariate analysis of leaf + assembled fruit measurements demonstrated segregation of the major *Agrifoliae* taxa to be generally consistent with current taxonomy (Fig. 2A).

Type specimens were included in leaf-only measurements (Fig. 2B). The results suggest the *Q. parvula* var. *parvula* lectotype is a hybrid (*Q. parvula* var. *shrevei* × *Q. wislizeni*). Of further note, the holotypes of *Q. wislizeni* and, particularly, *Q. wislizeni* var. *frutescens* did not fall separately from the *Q. wislizeni* samples.

This study's multivariate analysis of *Q. wislizeni* is consistent with the taxon's original description (De Candolle 1864). Engelmann's later portrayal of *Q. wislizeni* (Engelmann 1878) is entirely different (leaves "2-4 inches long … petioles 5-9 lines long"), more accurately describing *Q. kelloggii* or *Q.* ×*morehus* than *Q. wislizeni* or any of the other evergreen *Agrifoliae*. In contrast, Engelmann's description of *Q. wislizeni* var. *frutescens* in the same publication ("in var. *frutescens* the leaves are only 1-1½ inches long, oval, entire, or often very sharply and deeply lobed-dentate; petioles 1-2 lines long") most closely matches De Candolle's description of *Q. wislizeni*.

Leaf-only measurements of *Q. parvula* var. *tamalpaisensis* suggest both an intermediate morphology between *Q. parvula* var. *shrevei* and *Q. wislizeni* as well as possible affinities with *Q. kelloggii* (Fig. 2B).

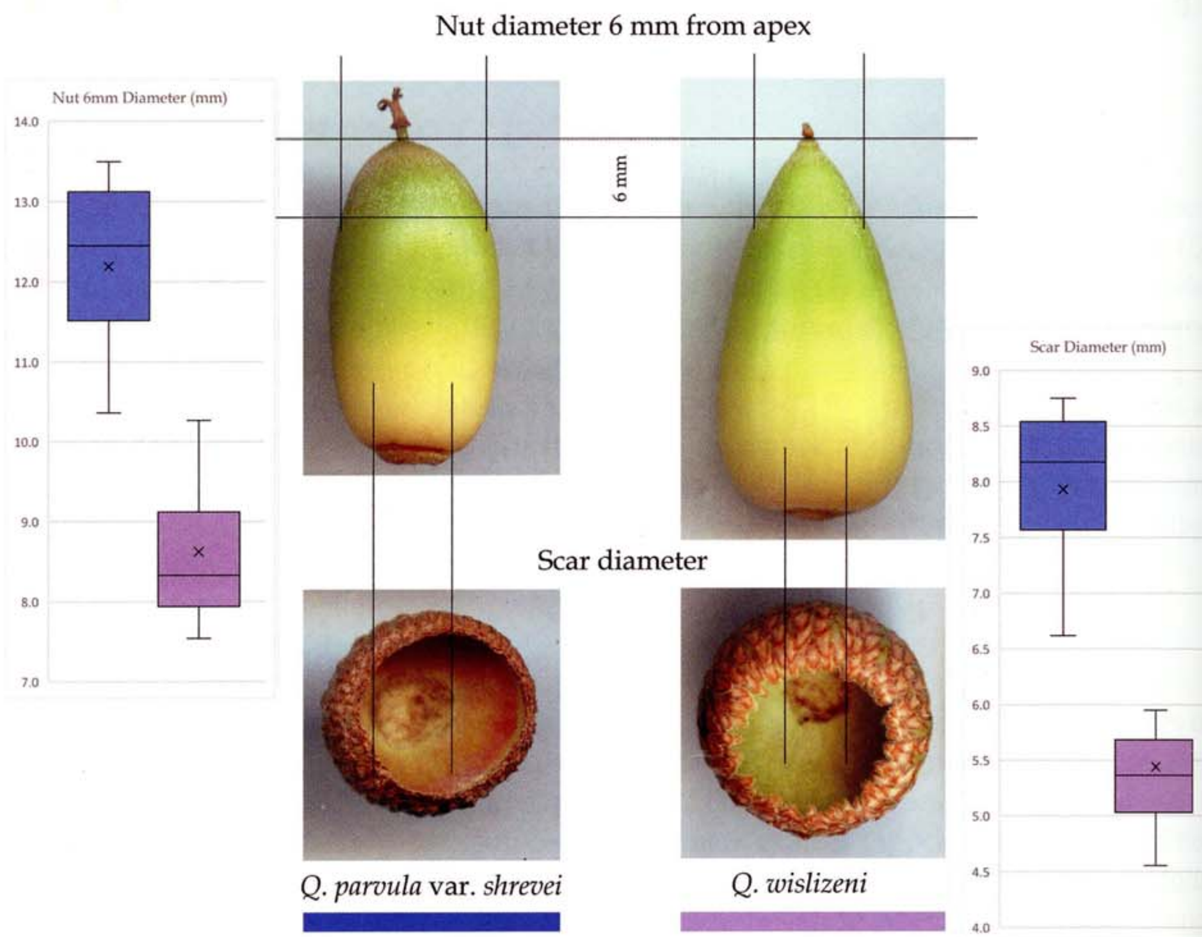

Figure 3/ *Quercus parvula* var. *shrevei* and *Q. wislizeni* fruit comparison. Box-and-whisker charts show inclusive medians; 1st and 4th quartiles limit the boxes, median line and mean marker are displayed inside the boxes.

Univariate analysis identified useful measurements for distinguishing *Q. wislizeni* from *Q. parvula*: differing fruit scar diameter (smaller in *Q. wislizeni*) and, especially, pointed nuts (*Q. wislizeni*) versus blunt, measured as the diameter 6 mm from the apex (Fig. 3).

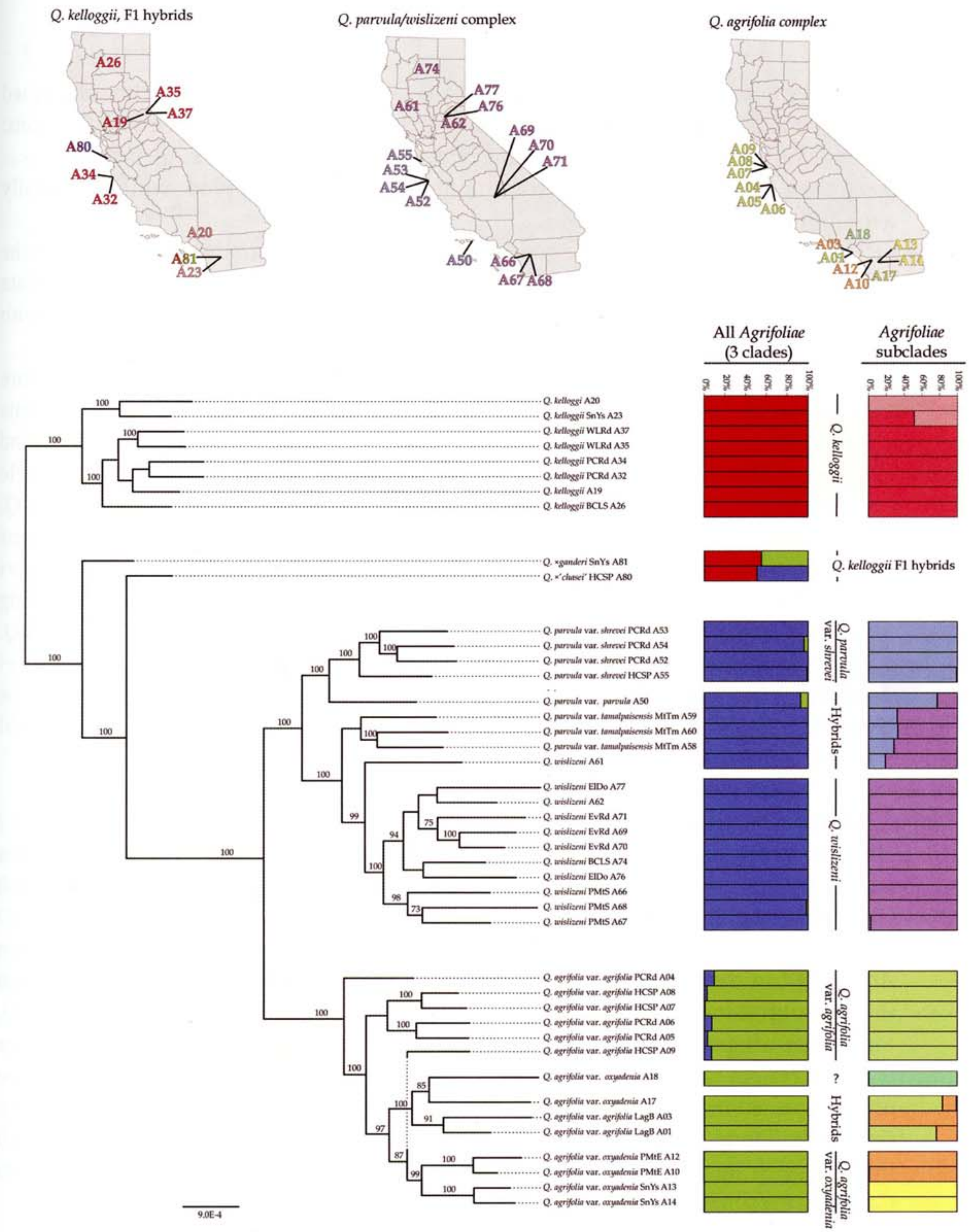

Figure 4/ Phylogenetic tree (left) and STRUCTURE analyses (colored bars) of *Agrifoliae* samples. Left column colored bars = all *Agrifoliae* as a single group (three clades). Right column colored bars = each of the three clades isolated to identify their subclades: (1) *Quercus kelloggii*, two subclades; (2) *Q. parvula*/*Q. wislizeni* complex, two subclades; (3) *Q. agrifolia* complex, four subclades.

Tree median nut diameters 6 mm from the apex and fruit scar diameters are generally consistent beginning late July until the fruit reach maturity in October or November; during the same time period nut length may nearly triple, making it a poor key character (Keuter 2013-2017, unpublished data).

DNA analyses

Sampled populations were selected to include as many different species or named hybrids of *Agrifoliae* at each sample location as possible. Other selection considerations:

- type localities were sampled if known and sympatric with other *Agrifoliae*;
- proximate populations in mixed communities were sampled while generally avoiding atypical specimens.

Restriction site associated DNA sequencing (RAD-Seq) was conducted on most of the same samples examined morphologically. Phylogenetic analysis of the RAD-Seq data disclosed the samples to be segregated into clades which are consistent to species with the morphological results and current taxonomy.

We also analyzed the RAD-Seq data to investigate population-level genetic structure and the assignment of individuals to broader genotypic groups. Not only did this analysis output cluster into the same clades as those identified by the phylogenetic and morphological analyses, but it provided additional insight into the levels of genetic admixture between species across the entire sample and in subclades (Fig. 4): (1) *Q. parvula* var. *shrevei* and *Q. wislizeni* are shown to be distinct taxa; (2) two specimens identified morphologically as hybrids are F1 hybrids, one of them the *Q. ×ganderi* holotype tree. However, the other F1 hybrid is most likely the currently unnamed pairing of *Q. kelloggii* and *Q. parvula* var. *shrevei* – provisionally named "*Q. ×wootteni.*" (3) *Q. parvula* var. *tamalpaisensis* is revealed to be a hybrid between *Q. parvula* var. *shrevei* and *Q. wislizeni*. (4) The single *Q. parvula* var. *parvula* specimen analyzed is shown to be a hybrid between *Q. parvula* var. *shrevei* and *Q. wislizeni*, consistent with morphological analysis of the lectotype.

DNA analysis results:

A. *Quercus kelloggii* is separated into Northern and Southern California subclades which are not readily distinguishable morphologically; more study of Southern California populations is needed.

B. There is no evidence of introgression between *Q. kelloggii* and the evergreen *Agrifoliae* in the test samples except in the two F1 hybrids. This could suggest that introgression beyond F1 is rare – although Wolf's garden plantings of *Q. ×morehus* offspring and field observations suggest otherwise (Wolf 1938) – or it could reflect the relative ease with which *Q. kelloggii* × evergreen *Agrifoliae* phenotypic admixture was observed and avoided during population selection for this study. Dodd and Papper have also reported avoiding unexpected *Q. kelloggii* introgression in their sampling, except in a single collection from Palo Colorado Canyon (personal communication, 2018).

C. *Quercus parvula* var. *shrevei* is distinct from and sister to *Q. wislizeni*.

D. The lone *Q. parvula* var. *parvula* sample is an introgressed hybrid (*Q. parvula* var. *shrevei* × *Q. wislizeni* × *Q. agrifolia*). Another recent study has similarly found *Q. parvula* var. *parvula* to have a complex genetic background (Dodd and Papper 2019).

E. *Quercus parvula* var. *tamalpaisensis* samples from the type locality are all introgressed hybrids (*Q. parvula* var. *shrevei* × *Q. wislizeni*).

F. C. and D. imply that *Q. parvula* var. *shrevei* (originally *Q. shrevei* C.H. Mull.) is the only valid variety of *Q. parvula*; more study needed.

G. *Quercus agrifolia*-complex samples were segregated into four subclades: 1. Central California coast. Southern California; 2. Santa Ysabel (*Q. oxyadenia* type locality); 3. Palomar Mountain; 4. San Gabriel Mountains. Central California samples showed introgression with *Q. parvula-wislizeni*-complex. Laguna Beach and U.S./ Mexican border samples showed introgression between subclades 1 and 3; more study is needed.

Figure 5/ Hermaphroditic flowers, *Quercus agrifolia* var. *agrifolia*, August 8, 2018.

DNA analysis further suggests the divergence of the California Red Oaks from the Eastern North America (ENA) Red Oaks occurred ~10 million years before the later separation of the bulk of the Mexican Red Oaks from the ENA Red Oaks ~20 Ma. Surprisingly, despite the physical proximity of Mexico to California, the Mexican Red Oaks are more closely related to the ENA Red Oaks than to the California Red Oaks.

Our estimate of the divergence between *Q. parvula* and *Q. wislizeni* is consistent with the hypothesis that the split occurred approximately 10-12 Ma (Axelrod 1983).

Differences between DNA and morphological results:

- While morphological analysis identified clear separation between *Q. agrifolia* var. *oxyadenia* and *Q. agrifolia* var. *agrifolia*, DNA analysis suggested Southern California *Q. agrifolia* to be more complex and deserving of additional study.
- Morphological measurements suggested *Q. kelloggii* influence in Tamalpais oak although DNA analysis did not find California black oak introgression.
- The morphological characters analyzed suggested *Q. agrifolia* var. *agrifolia* influence in the "*Q.* ×*chasei*" sample but DNA analysis did not find evidence of *Q. agrifolia* admixture.

Exciting new Agrifoliae *observations*

Subsequent to the Hauser study (Hauser et al. 2017), continuing observations of California Red Oaks have provided unexpected results:

- A single *Quercus agrifolia* var. *agrifolia* tree in Santa Cruz, CA, has developed bisexual flowers (Fig. 5) four consecutive years (the first three years reported in Keuter 2018), described only once before in *Agrifoliae* (Greene 1889).
- Recent observations have revealed that a hybrid of two species distinguished by the time required for fruit maturation – *Q. agrifolia* (annual fruit maturation) × *Q. parvula* var. *shrevei* (biennial fruit maturation) – has simultaneously produced mature crops of both annual and biennial fruit in 2017 (second year study is in progress). While polymorphism in fruit maturation has been observed in section *Cerris* (e.g., *Q. suber*: Díaz Fernández 2000) this is the first report based on hybridizing populations of annual- and biennial-maturing species in the Red Oaks (Fig. 6)

Conclusion

This work represents an exciting and informative example of the power of citizen science and receptive academics. It also generally demonstrates taxonomic congruence between morphological and genetic analysis; however, it does not find support for three of the named varieties of *Agrifoliae*, showing two to be introgressed hybrids and failing to find evidence of the third (see Table 1). It further reveals that the early-branching pattern of *Agrifoliae* relative to all other American Red Oaks mirrors the recently discovered divergence of the *Dumosae* (most California White Oaks) from all other American White Oaks (McVay et al. 2017).

Current taxonomy	**Taxonomy supported by Hauser et al. 2017**
Q. agrifolia Née var. *agrifolia*	*Q. agrifolia* Née var. *agrifolia*
Q. agrifolia Née var. *oxyadenia* (Torr.) J.T. Howell	*Q. agrifolia* Née var. *oxyadenia* (Torr.) J.T. Howell
Q. kelloggii Newb.	*Q. kelloggii* Newb.
Q. parvula Greene var. *parvula*	? likely introgressed hybrid, more study needed
Q. parvula Greene var. *shrevei* (C.H. Mull.) Nixon	*Q. parvula* Greene var. *shrevei* (C.H. Mull.) Nixon
Q. parvula Greene var. *tamalpaisensis* S.K. Langer	NO: introgressed hybrid
Q. wislizeni A. DC. var. *wislizeni*	*Q. wislizeni* A. DC.
Q. wislizeni Engelm. var. *frutescens* Engelm.	NO: indistinguishable from *Q. wislizeni* A. DC.

Table 1/ Comparison of taxa recognized within *Agrifoliae*.

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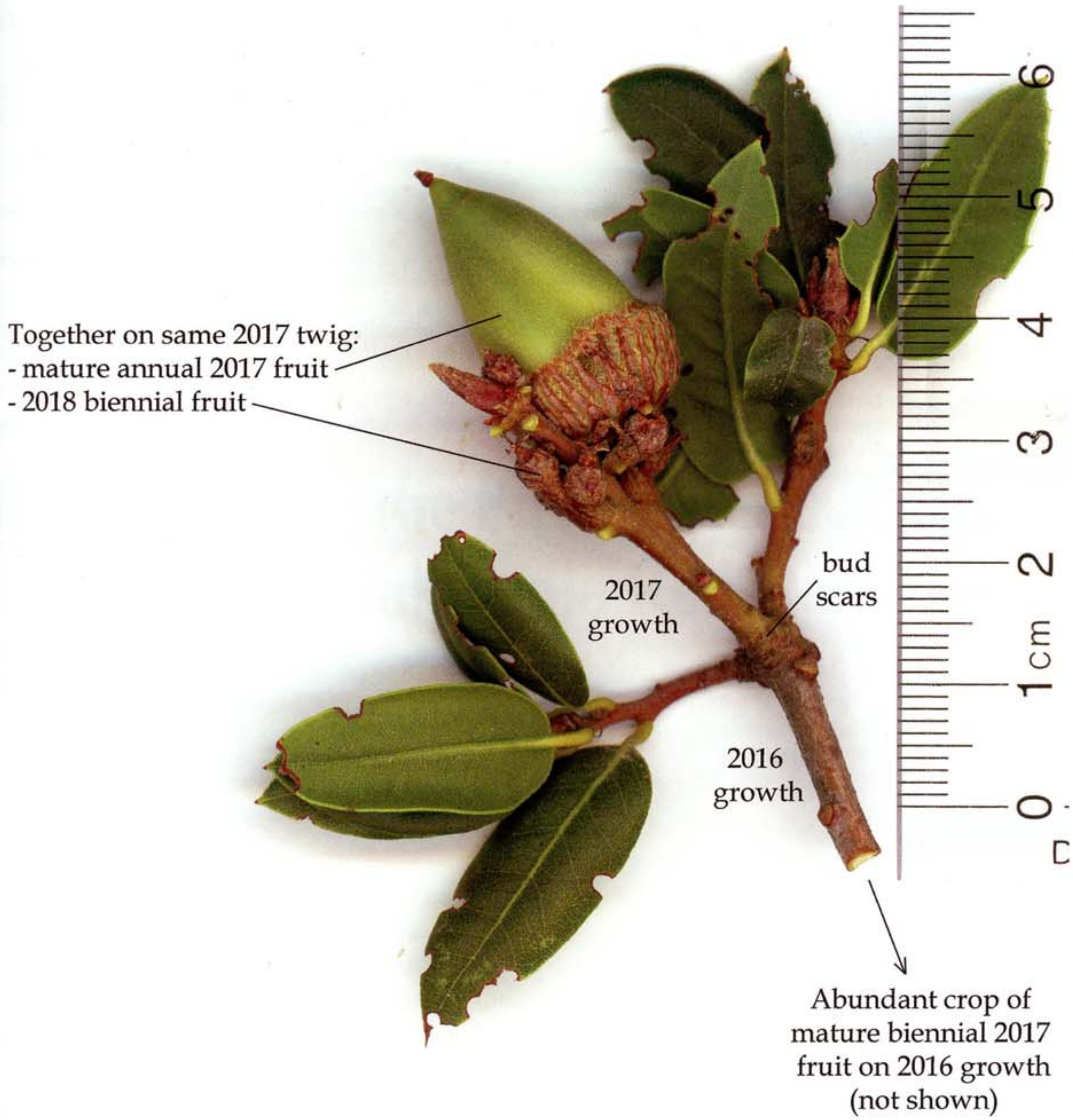

Figure 6/ Putative hybrid between *Quercus agrifolia* and *Q. parvula* var. *shrevei* simultaneously producing annual and biennial fruit.

Photographs. Title Page: Al Keuter (*Q. agrifolia* var. *oxyadenia*). Photos in Figures 1, 3, 5, 6: Al Keuter.

Works cited

Axelrod, D.I. 1983. Biogeography of oaks in the Arcto-Tertiary province. *Annals of the Missouri Botanical Garden* 70: 629-657.

De Candolle, A.P. 1864. *Prodromus Systematis Naturalis Regni Vegetabilis*. 16(2.1): 67.

Díaz Fernández, P.M. 2000. Variabilidad de la fenología y del ciclo reproductor de *Quercus suber* L. en la Península Ibérica. Doctoral Thesis, Universidad Politecnica de Madrid.

Dodd, R. and P. Papper. 2019. Disentangling the phylogenetic network of the California red oak clade (*Quercus*, section *Lobatae*, series *Agrifoliae*). *International Oaks* 30: 203-208.

Engelmann, G., and A. Gray. 1845. Plantae Lindheimerianae; an enumeration of the plants collected in Texas, and distributed to subscribers, by F. Lindheimer, with remarks, and descriptions of new species, etc. *Boston J. Nat. Hist*. 5: 245.

Engelmann, G. 1878. About the oaks of the United States. *Trans. Acad. Sci. St. Louis* 3: 396.

Engelmann, G. 1880. *Quercus*. In: *Geological Survey of California (Volume 2: Botany)*, Edited by W.H. Brewer. Cambridge, MA: University Press.

Greene, E.L. 1887. New species, mainly Californian. *Pittonia* 1: 40.

Greene, E.L. 1889-1890. *Illustrations of West American Oaks From Drawings By The Late Albert Kellogg, M.D., text by Edward L.*

Greene. Vols. 1 & 2. San Francisco, CA: Bosqui Engraving and Printing Co.

Hauser, D.A., A. Keuter, J.D. McVay, A.L. Hipp, and P.S. Manos. 2017. The evolution and diversification of the red oaks of the California Floristic Province (*Quercus* Section *Lobatae*, series *Agrifoliae*). *American Journal of Botany* 104(10): 1-15.

Howell, J.T. 1931. A variant of the coast live oak. *Madroño.* 2:38.

Langer, S.K. 1993. A new oak on Mount Tamalpais. *The Four Seasons: Journal of the Regional Parks Botanic Garden* 9(3): 21-30.

Kellogg, A. (1855) 1873. *Proceedings of the California Academy of Natural Sciences.* 1(1): 25. Reprint, *Proceedings of the California Academy of Natural Sciences.* 1(2): 23.

Kellogg, A. 1863. Description of Two New Species of Plants. *Proceedings of the California Academy of Natural Sciences.* 2(1): 36.

Keuter, A. 2018. Observations of hermaphroditic late-season flowering in the red oak *Quercus agrifolia*. *Phytoneuron* 19: 1-5.

McMinn, H.E., E.B. Babcock, and F.I. Righter. 1949. The Chase oak, a new giant hybrid oak from Santa Clara County, California. *Madroño* 10: 51.

McVay, J.D., D. Hauser, A.L. Hipp, and P.S. Manos. 2017. Phylogenomics reveals a complex evolutionary history of lobed-leaf white oaks in western North America. *Genome* 60: 733-742.

Muller, C.H. 1938. Further studies in southwestern oaks. *Amer. Midl. Nat.* 19: 587.

Newberry, J.S. 1857. Botanical Report: No. 1—Report upon the Botany of the Route. *Reports of Explorations and Surveys to Ascertain the Most Practicable and Economical Route for a Railroad from the Mississippi River to the Pacific Ocean* VI(3): 28, f. 6, 89.

Née, L. 1801. *Anales De Ciencias Naturales.* 3: 271.

Nixon, K.C. 1980. A Systematic Study of *Quercus parvula* Greene on Santa Cruz Island and Mainland California. Master's Thesis (unpublished), UCSB.

Nixon, K.C., and C.H. Muller. 1994. New names in California oaks. *Novon* 4(4): 391-393.

Torrey, J. 1853. Botany. In: *Report of an expedition down the Zuni and Colorado Rivers.* Editor: L. Sitgreaves. Washington: Robert Armstrong, Public Printer.

Wolf, C.B. 1944. The Gander oak, a new hybrid oak from San Diego County, California. *Proceedings of the California Academy of Natural Sciences* 25: 177-188.

Wolf, C.B. 1938. California Plant Notes I. *Rancho Santa Ana Botanic Garden Occas. Papers* 1: 47-52.