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# An Updated Infrageneric Classification of the North American Oaks (*Quercus* Subgenus *Quercus*): Review of the Contribution of Phylogenomic Data to Biogeography and Species Diversity

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**Abstract:** The oak flora of North America north of Mexico is both phylogenetically diverse and species-rich, including 92 species placed in five sections of subgenus *Quercus*, the oak clade centered on the Americas. Despite phylogenetic and taxonomic progress on the genus over the past 45 years, classification of species at the subsectional level remains unchanged since the early treatments by WL Trelease, AA Camus, and CH Muller. In recent work, we used a RAD-seq based phylogeny including 250 species sampled from throughout the Americas and Eurasia to reconstruct the timing and biogeography of the North American oak radiation. This work demonstrates that the North American oak flora comprises mostly regional species radiations with limited phylogenetic affinities to Mexican clades, and two sister group connections to Eurasia. Using this framework, we describe the regional patterns of oak diversity within North America and formally classify 62 species into nine major North American subsections within sections *Lobatae* (the red oaks) and *Quercus* (the white oaks), the two largest sections of subgenus *Quercus*. We also distill emerging evolutionary and biogeographic patterns based on the impact of phylogenomic data on the systematics of multiple species complexes and instances of hybridization.

**Keywords:** biodiversity; distribution; hybridization; oak; phylogeny; systematics



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## 1. Introduction

The oaks (*Quercus*, Fagaceae) comprise more than 435 species distributed across temperate and tropical regions of the northern hemisphere [1–3]. They are among the best-known and most ecologically significant forest trees in North America (including Mexico) and Eurasia, shaping forest and savanna ecosystems [4] and the diversity of urban forests [5,6], and molding the development of human civilization and mythology [7–10]. Oaks are united by a suite of distinctive floral traits—in particular, pendant male catkins and tricarpetate female flowers with linear styles and expanded stigmas—and a signature fruit trait: the circular single fruit or acorn seated within a cup-shaped extra-floral accessory structure, a specialized involucre called a cupule. The cupule is the defining feature of Fagaceae. While other genera of the family feature acorns and valveless rounded cupules, the combination of floral character states shared by oaks is unique within the family [11,12].

The most recent classification system of *Quercus* recognizes eight sections within two subgenera, subgenus *Quercus* (ca. 295 spp.) and subg. *Cerris* (ca. 140 spp. [3]; see Table 1). This old dichotomy between oak subgenera, which dates to the early Eocene, was recognized in early molecular studies of the genus and family [13,14] and is robustly supported by an extensive RAD-seq (next-generation DNA sequencing) phylogenomic study of a comprehensive worldwide sample of species [15]. The two subgenera represent a deep biogeographic split among modern taxa: subg. *Cerris* is restricted to Europe, Asia, and northern Africa; and subg. *Quercus*, the American oak clade, is largely restricted to the Americas except for two dispersals back to Eurasia. Eight sections of the genus are

also supported by a combination of RAD-seq data and macro- and microscopic characters, most notably patterns of pollen ornamentation viewed under SEM [3]. These subtle yet well-established differences in pollen exine, and their correlation with phylogenomic data, give us high confidence in the basic split between subgenera and the pollen subtypes that correspond to each of the recognized sections [3,16].

**Table 1.** Current Infrageneric classification of the genus *Quercus* [3]. The total number of species with in each infrageneric group is provided, including the number of species within the Flora of North America (FNA) region and the number treated within this study.

<i>Quercus</i> L.	Sections	No. of Species Total/FNA	No. of Species Treated Here
subg. <i>Quercus</i>		297/92	
	<i>Lobatae</i> Loud.	120/39	37
	<i>Protobalanus</i> (Trel.) Schwarz	5/5	
	<i>Ponticae</i> Stef.	2/1	
	<i>Virentes</i> Loud.	7/4	
	<i>Quercus</i>	150/53	45
subg. <i>Cerris</i> Oerst.		138	
	<i>Cyclobalanopsis</i> (Oerst.) Benth. & Hook. f.	90	
	<i>Cerris</i> Dumort.	13	
	<i>Ilex</i> Loud.	35	

Fossilized pollen has been used to pin the modern sections in time and space, serving as an invaluable resource to interpret paleobiogeography and to time-calibrate the global oak phylogeny [15,16]. Time-calibrated phylogenomic analyses, combined with fossil and modern oak species distributions, support an initial split in the American oak clade between the red oaks, sect. *Lobatae*, and the remainder of the clade between ca. 54 and 48 Ma (= million years ago). The non-*Lobatae* American oak clade sections exhibit high ecological diversity, with several striking contrasts between three early-diverging clades—sects. *Protobalanus*, *Ponticae* and *Virentes*—and the main radiation of white oaks, sect. *Quercus*. These early-branching lineages are species-poor, two to seven species each, restricted in distribution, and evergreen to wintergreen in habit. By contrast, sect. *Quercus*, with approximately 150 species of white oak, has the broadest distribution of all forest trees in the Northern Hemisphere [3]. This may be owing to the evolution of deciduousness and other traits associated with a range of continental climates, an exceptionally high range of functional diversity that sets the American oaks up as a model clade for understanding tree diversification and ecology [17,18]. The other main branch of the American oaks and the sister group to these lineages, sect. *Lobatae*, comprises the second largest clade next to the white oaks. It forms a remarkably parallel radiation to the white oaks with respect to distribution, habit, and morphology [17,19]. There is, however, an important point of ecological distinction between these two large oak clades: *Lobatae* show lower levels of diversification in western North America, especially in the California Floristic Province (CA-FP) and xeric woodlands of the American southwest [20]. The reasons for this ecological distinction between the clades may be key to understanding coexistence of these sections in the Americas, and the consequent interaction between diversification and tree diversity in oaks [17,21,22].

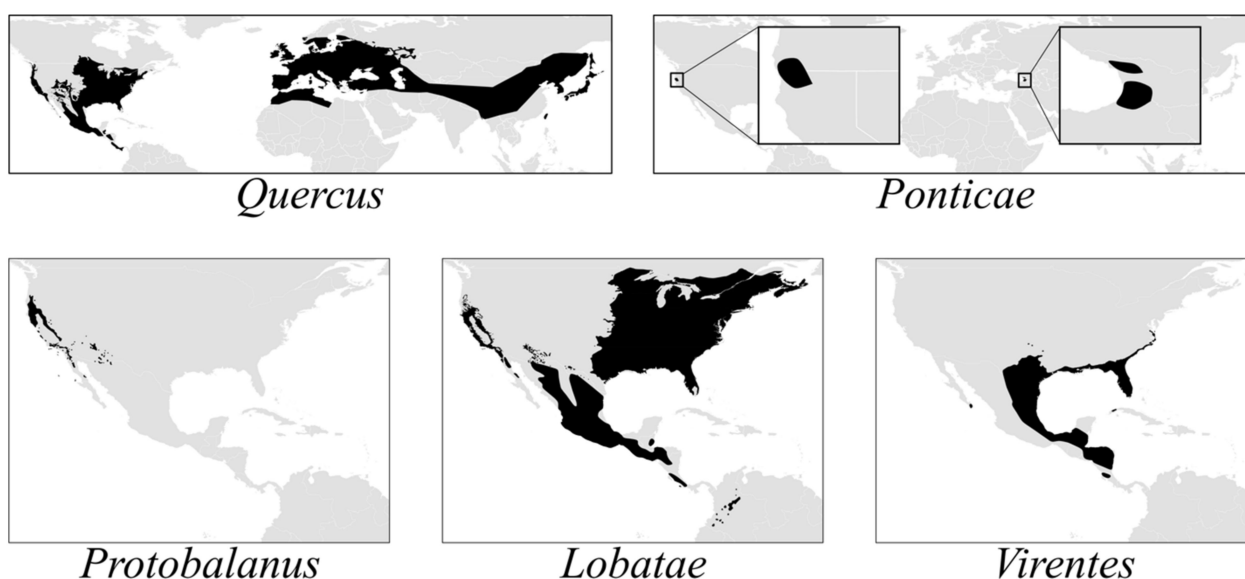
The sectional classification for *Quercus* [3] is solid and unlikely to change. In this paper, we present a subsectional classification for the American oak clade based largely on our phylogenomic work of the past five years [15,19,23–25]. Our current sampling of

species for RAD-seq analysis stands at roughly 250 taxa: A total of 177 from subg. *Quercus*, the American oak clade, and 73 from subg. *Cerris*, the Eurasian oak clade. Within subg. *Quercus*, our coverage is nearly complete for the 92 species treated within the *Flora of North America* (FNA north of Mexico [1]). This phylogenomic work reveals compelling continental patterns of oak diversity at the broadest and narrowest phylogenetic scales. At the scale of entire clades, the early-branching clades as well as many other lineages within the two largest sections of subg. *Quercus*, sects. *Lobatae* (red oaks) and *Quercus* (white oaks), are distributed exclusively within North America north of Mexico (hereafter, “the FNA region”). It is also clear that the number of species within the FNA region with relationships to species outside the region is relatively low, limited to a single species of sect. *Ponticae* and a single clade in sect. *Quercus*, as discussed below. Thus, the oak flora of the FNA region is nearly a self-contained unit for study. At the same time, within regional clades, multiple radiations of taxa have been sampled at the population level for both our global phylogeny and as part of earlier stand-alone studies targeting the fine-scale systematics of challenging species complexes [23,25–28]. These enable the same dataset that informs classification to provide insight into species taxonomy. With this framework in place, we are well positioned to provide a phylogenetically-driven and timely bookend on the systematics of the taxa treated in the FNA region.

Our goals with this review are: (1) To describe the biogeographic patterns of oak diversity within North America; (2) to formally classify 62 species into nine well-sampled monophyletic subsections; and (3) to review the impact of phylogenomic data on the systematics of multiple species complexes and distill the results of hypothesis testing involving hybridization within the flora.

### 1.1. Phylogeny and Biogeography of the Oak Flora in North America

The American oak clade (*Quercus* subg. *Quercus*) comprises three endemic lineages—sects. *Lobatae*, *Protobalanus* and *Virentes*—and two Holarctic or transcontinental lineages—sects. *Ponticae* and *Quercus* (Figure 1). Sections *Lobatae*, *Protobalanus*, and *Quercus* likely arose in what is now the boreal zone. Middle Eocene pollen records from Axel Heiberg Island (79°55'N, 88°58' W) indicate the presence of modern oak lineages at high latitudes in North America by c. 45 Ma [29]. As temperatures at high latitudes decreased by ca. 3–5 °C during the Eocene–Oligocene climate transition 34 Ma [30], *Lobatae* and *Quercus* were pushed southward toward their modern-day distributions (Figure 1). A parallel pattern of vicariance in the red oaks and the white oaks is evident from the phylogeny, with each section diverging into a western clade centered in the California Floristic Province (CA-FP) sister to an eastern North American clade. The red oaks and white oaks then radiated simultaneously in the CA-FP and eastern North America before diverging from an eastern North American ancestor to diversify in Mexico and Central America.



**Figure 1.** Distributions of the five oak sections of the American oak clade (*Quercus* subgenus *Quercus*). Maps were generated using species maps provided by Little [31,32], as refined by recent studies [17] and herbarium records.

The oak flora of the FNA region contains a high level of global phylogenetic diversity—all five sections of subgenus *Quercus*, including the relictual sections *Ponticae* (*Q. sadleriana* only) and *Protobalanus* (five species), which are restricted to the CA-FP or, in the case of *Q. chrysolepis* and *Q. palmeri* of section *Protobalanus*, range from the CA-FP to the adjacent southwest. Our work suggests that older crown group ages [15] and plastome divergences [13,33] are associated with many of these deeply divergent subclades, a pattern consistently in contrast to the more recently derived subclades containing mostly Mexican and Central American species. These nested clades contain three unrelated red oak species and two distinct groups of white oak species in the FNA region, which suggests multiple recent dispersal events or range extensions from Mexico back into the southwestern edge of the FNA region [19].

### 1.2. Patterns of Ecological Diversity

A broad overview of North American species diversity and community assembly published in 2018, based on tree species within U.S. Forest Service Forest Inventory and Analysis (FIA) plots [17,18], shows that FNA oak diversity peaks in the southeastern piedmont and coastal plain regions [18]. While these analyses did not include ca. 30 oak shrubs and small tree species, they demonstrate the broad distribution of oak diversity in the FNA region. What they miss most significantly is the impressive level of shrub and small tree diversity in the CA-FP and adjacent desert biomes of the southwest that accounts for about 18 species across four sections, or roughly two-thirds of the species of smaller stature within the flora. While the addition of these species changes little to the initial observation that the uplands of eastern and central North America are the least diverse areas for oaks, this diversity is important to understanding the role of oak phylogenetic diversity in a range of ecological and evolutionary contexts, including community assembly and ecosystem functions of non-forested oak-dominated ecosystems.

The broad geographic and ecological distribution of oaks across at least eight distinct North American biomes has generated a complex array of foliar adaptations, especially within the two main species-rich sections, *Lobatae* and *Quercus*. While each of the sections covers a broad ecological and geographic range, these ranges begin to subdivide and segregate regionally. Eastern North American subclades *Stellatae* (section *Quercus*) and *Phellos* (section *Lobatae*), here treated as subsections, centered in the piedmont and coastal plain, highlight previously unsuspected close relationships between lobe-leaved and non-lobe-leaved species. In the southeast, the added presence of generally non-lobe-leaved species

of sect. *Virentes* (live oaks) with already diverse communities of sympatric oak species revealed a clear pattern of phylogenetic sorting and convergent evolution among species from the three sections along moisture and fire gradients [26,34].

For species placed within western clades of red and white oaks and centered on the CA-FP—subclades *Dumosae* (sect. *Quercus*) and *Agrifoliae* (sect. *Lobatae*), here treated as subsections—a combination of sclerophylly and deciduousness has presumably evolved in response to drought. In each case, phylogenies resolved the lobe-leaved deciduous species sister to more diverse clades of mostly sclerophyllous shrub species [23,27,35]. This parallel distinction between leaf habit and species diversity in the white and red oaks of the CA-FP suggests an increase in diversification rate in response to decreasing summer precipitation and general support for the hypothesis of convergent patterns of foliar evolution. Additional complexity in the evolution of character states of leaf persistence is observed within the most diverse clades of red and white oaks along abiotic gradients southward into Mexico and Central America, demonstrating sympatric and strongly parallel diversification in climatic niche and leaf habit increasing in rate with the move into Mexico [19].

### 1.3. Classification of the American Oak Clade: Species Level Systematics

The ecological and biogeographic segregation of species within sections suggests a biological rationale for naming subsections, beyond the practical ramifications of any classification system for the writing of keys and identification of species. At the species level, phylogenetic relationships among oak species remain difficult to resolve with confidence, especially for a group well known for hybridization [24,36,37]. But recent studies using a range of DNA markers suggest that hybridization does not pose an insurmountable barrier to achieving that goal [24,26,36,38–41]. Population-level sampling is critical to establishing that oak species show genetic cohesion, and the use of reduced-representation next-generation sequencing data on exemplars across species ranges has provided robust evidence for the existence of species boundaries even among closely related species occurring in sympatry (e.g., [42–46]). A species level analysis of sect. *Virentes* stands out as the first oak study with complete phylogenomic sampling of any oak clade, using RAD-seq data and including multiple accessions throughout the range of each species, to generate a phylogeny and provide the context needed to guide a range of comparative investigations [26]. Since then, two more clades, treated here as subsections *Dumosae* and *Agrifoliae*, have been comprehensively sampled and analyzed [23,27,35,47].

Throughout this paper, our work rests on a concept of oak species as populations of individuals that cohere genomically in a subset of the genome that is likely shared across all members of the species, barring early-generation hybrids [48,49]. While the mechanisms maintaining species boundaries in oaks very likely differ across the range of even a single species, and while those mechanisms maintained across a species' range may vary in strength across the range, it remains the case that we are able to recognize most oak species ecologically and morphologically [50–52]. In addition, as individual cases of species pairs and species clusters are investigated with increasing amounts of molecular data, sampled from across the genome, they converge with very few exceptions on genomic clusters that accord with recognizable species [23,38,53–56]. Exceptions will no doubt result from incomplete divergence, as time since speciation is likely a key factor in resolving oak species, even with the application of multiple criteria [48]. Our work thus far has shown that clades from the FNA region often vary in their depth of relative species divergence, with several examples that suggest we are capturing various stages of diversification, ranging from isolation by distance on the California Channel Islands (e.g., sect. *Protobalanus*, subsect. *Dumosae*) to differentiation in ecological niche space in both coastal and continental regions (e.g., sect. *Virentes*, subsect. *Prinoideae*).

Analogous to the argument that has been made for plant species as a whole [56], the correlation between morphological patterns of similarity and genomic evidence for reproductive barriers suggests that our use of the species category in oaks is both mean-



ingful and based on an integrative approach using multiple criteria [48]. Where studies have found difficulty distinguishing morphological and ecological species using molecular data (e.g., [57,58]), returning with higher numbers of markers generally recovers clusters that cleanly separate the species (e.g., [43,59]). This suggests that there may be genomic heterogeneity in *where* and *how much* of the genome is shared within species vs. among species, even if the regions of the genome that distinguish recently diverged oak species may be few and far between [60] and interspersed with regions that exchange relatively freely between species. At the same time, it gives us good reason to expect that species we are able to recognize ecologically and morphologically will also cohere genomically, so long as we look closely enough.

Moreover, in spite of taxonomic difficulties at the species level, our RAD-seq work already cited and ongoing work based on sequence-capture data [37,61] strongly support the clades we recognize as subsections in the current work (Figure 2). Given our sampling to date and the strong phylogenetic support, the timing is reasonable to recognize subsections for the FNA region. To complete the American oak clade (*Quercus* subg. *Quercus*), better sampling of the Mexican and Central American taxa is needed and ongoing.

## 2. Materials and Methods

### *Taxonomic Treatment*

In the treatments that follow, all references to phylogenetic resolution are based on RAD-seq data cited here [15,19,23–27,36,62] unless otherwise indicated. Three of the American sections are relatively small and are not divided into subsections: These are sect. *Ponticae* (2 species, one of which is in the FNA region), sect. *Protobalanus* (5 species), and sect. *Virentes* (7 species, 4 of which are in the FNA region).

Numbers in parentheses indicate the number of species in the FNA region out of the total number of species estimated for the clade, following previous work [1,3]. Species indicated with an asterisk are subshrubs, shrubs, or small trees; all others are trees. Section descriptions are not here; for these, we refer the reader to the most recent classification of the genus [3]. Our subsectional descriptions are based on previous classifications, species-level treatments, and morphological studies cited below, including new observations made from herbarium specimens.

## 3. Results and Discussion

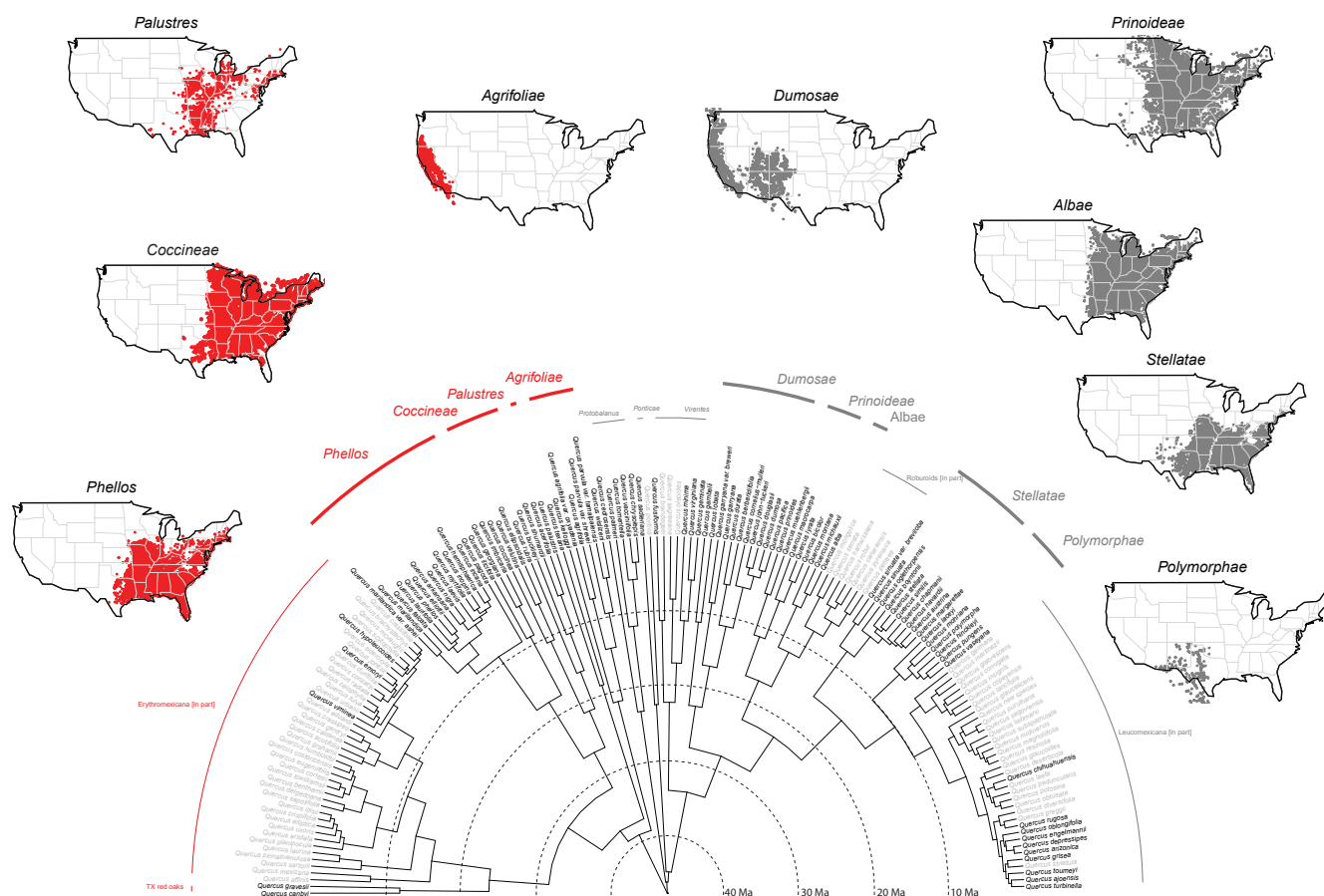
### 3.1. Section *Protobalanus* (5/5)

**Includes:** \* *Q. cedrosensis* C.H. Muller, *Q. chrysolepis* Liebm., \* *Q. palmeri* (Engelm.) Engelm., *Q. tomentella* Engelm., \* *Q. vacciniifolia* Kellogg

The *Protobalanus* oaks are the only truly evergreen American group, with leaves persisting up to three years. Three of the species are shrubs or small trees. All species of the section are in the FNA region, and two of them extend south into Mexico. Defining features of the section include apiculate stamens and a mostly lateral position of abortive ovules [3,63]. Trichome variation is especially informative in this species complex [64]. The most widespread species, *Q. chrysolepis*, is also one of the most variable North American oaks, with juvenile leaf morphology and branching habit, sucker shoots, shade forms, or shoots of individuals in ecologically extreme habitats often resembling other species of the complex [1]. The section includes one of the two island endemic species in the FNA region, *Q. tomentella* (California Channel Islands; Isla Guadalupe, Mexico). Clonal reproduction is common in *Q. tomentella* [65] and reported to be extreme in *Q. palmeri* from the Jarupa Hills of southern California, the site of a 13,000 year-old clone [66].

*Quercus cedrosensis* appears to be the earliest branch in the clade, followed by *Q. palmeri*. The remaining taxa are not cleanly resolved as subclades with our current sample, suggesting a recent divergence history and likely continued gene flow between the two species pairs, *Q. chrysolepis*–*Q. vacciniifolia* and *Q. chrysolepis*–*Q. tomentella* [65,67]. Phylogeographic studies of *Protobalanus* using plastid data showed a north-south discontinuity in California, perhaps related to an ancient disjunction within the complex that limited

seed dispersal [13]. More recently, Ortego et al. [67] detected two lineages within a paraphyletic *Q. chrysolepis* using RAD-seq data and population genetic analyses. Their work demonstrates the existence of a southern lineage sharing a most recent common ancestor with *Q. tomentella*, divergence between the southern and northern lineages at about 5 Ma, consistent with our fossil-calibrated estimate [15].



**Figure 2.** Time tree/chronogram of the five sections of the American oak clade (*Quercus* subgenus *Quercus*) adapted from [19], with distribution maps for the nine subsections recognized within sections *Lobatae* and *Quercus*. Shown in boldface are 88 of the 92 taxa that occur within the FNA region. Ma = million years ago. Maps are based on specimen data used in [19], excluding specimen records from cultivation and from outside the range of the species; additionally, populations of *Q. havardii* from west of eastern Arizona were excluded as their taxonomic status and possible hybrid origin are uncertain [68,69]. Additional specimen data from SEINet were included for the *Coccineae* in North Carolina, which were undersampled. Code for generating maps and phylogenetic tree is archived in GitHub (<https://github.com/andrew-hipp/2021-oak-classification>, Release v0.95-1, 2021-06-06) and Zenodo (DOI: 10.5281/zenodo.4905230).

Both the fossil record and expanded ancestral range predicted by niche modeling for *Q. chrysolepis* suggest *Protobalanus* once were more widely distributed [70,71]. Plastome sharing between the California white oak *Q. engelmannii* and sect. *Protobalanus* and deep plastome splits between sects. *Quercus* and *Protobalanus* further support a long history of co-occurrence of the two sections in the CA-FP [13,33]. A center of diversification in western North America suggests a long-term presence in the region and perhaps farther south given the deep phylogenetic divergence of *Q. cedrosensis* and its extended range south along the Baja coast to Cedros Island, Mexico.

### 3.2. Section *Ponticae* (1/2)

**Includes:** \* *Q. sadleriana* R. Br. Ter

*Quercus sadleriana* is one of the most distinctive oaks from western North America (CA-FP) and the FNA region's solitary member of this ditypic section. The combination of its isolated range and chestnut-like, shallowly lobed leaves reminiscent of the white oak species of both eastern North America and Asia likely led to its placement in monotypic groups by both Trelease ([72]; as series *Sadlerianae*) and Camus ([73–75]; subsect. *Sadleriana*). Our analyses conclusively place it sister to *Q. pontica* K. Koch from the Caucasus Mountains, supporting a placement that had previously been shown correctly based on nuclear ribosomal DNA alone, but not robustly supported [76]. Together they form a distinct Holarctic lineage within subg. *Quercus*. *Ponticae* are quite similar in their shallowly lobed, chestnut-like leaves, large stipules, large leaf buds with loosely attached scales, and shrubby, rhizomatous habit. They also share the derived features of basal abortive ovules, glabrous endocarp, and annual fruit maturation with sects. *Virentes* and *Quercus* [3].

Qualitatively, both species occupy similar latitudes and ecological zones that overlap strongly in the mean values of 19 climatic variables [77], despite being longitudinally separated by 165°. There is morphological evidence that *Q. sadleriana* hybridizes with *Q. garryana* ([78]; A. Keuter, pers. comm.) and strong molecular evidence that ancient introgression occurred between *Q. pontica* and the roburoid white oaks of Eurasia [26,39]. This history of introgression has interfered with the accuracy of phylogenetic estimation within the white oaks and become a model for examining the impact of introgression on the mosaic of phylogenetic signals within the oak genome [15,24,37,79].

Given the nested phylogenetic position of *Ponticae* within the American oak clade, it seems reasonable to hypothesize an origin in the Americas followed by dispersal to Eurasia. Undoubtedly, *Ponticae* are relicts of a once more widespread species group although there is no macrofossil evidence that can be definitively attributed to the group [3].

### 3.3. Section *Virentes* (4/7)

**Includes:** *Q. fusiformis* Small, *Q. geminata* Small, \* *Q. minima* (Sarg.) Small, *Q. virginiana* Mill.

Although sect. *Virentes* has long been considered one of the best-demarcated species groups of the American oaks [34,80], until recently its relationship to the white oaks was unclear. All phylogenomic data place *Virentes* sister to sect. *Quercus* with strong support. Section *Virentes* is uniquely characterized by the combination of fused stellate trichomes on the leaf undersides; seeds with fused cotyledons; and the presence of a cotyledonary tube in seedling development [3,80]. Section *Virentes*' consistent and distinct morphology across vegetative and reproductive features support a long and divergent history within the American oak clade.

The lineage is unusual within the FNA region and globally in being restricted to low-elevation habitats, occurring largely on well-drained sandy soils or volcanic tuff [34]. Ecological separation of the taxa by climate and environmental factors is well studied [24], including clear demonstration of flowering time as an isolating mechanism between *Q. virginiana* and *Q. geminata* [81].

Population-level studies support the placement of the four FNA taxa into two main clades [24]. One comprises three species from the southeastern FNA region: The widespread *Q. virginiana* and more narrowly distributed sister species-pair of *Q. geminata* and *Q. minima*. These species form the sister to a Central American clade of *Q. sagraena* Nutt. and *Q. oleoides* Schltdl. and Cham. In the southwest, *Q. fusiformis* and *Q. brandegeei*, a narrow endemic from the southern tip of Baja California, diverge early from the rest of the complex. A discontinuous distribution across the southwest of the FNA region and extension south suggests allopatric speciation, driven by range contraction and isolation by distance [82]. Long distance dispersal also seems likely in explaining the origin of the Antillean *Q. sagraena* (Cuban oak) from a mainland progenitor similar to *Q. oleoides* [26].

The distribution of *Virentes* suggests physiological adaptations to temperate climates with mild winters or seasonally dry tropical climates. Vulnerability to freezing and tolerance of drought have likely influenced historical patterns of migration and the current



restricted distribution of the group [17]. Although a temperate origin within the FNA region, followed by east-west dispersion and subsequent migration south seems plausible, the timing remains elusive. With no reliable fossil record for modern *Virentes* [3], the age of the crown group is dependent on sampling, phylogenetic estimation, and the use of fossil constraints derived from other oak lineages. The wide range of crown group estimates from 11 to 23 Ma is likely due to these variables [16,26], a reminder of the uncertainty and potential disparities in the timing of the pattern of oak diversification across studies.

Evidence for historical introgression between parapatric species pairs suggests hybridization during periods of range overlap or long-distance transmission of pollen [36]. For the FNA taxa, introgression among sympatric *Virentes* is clear from morphology and genomic data, but the degree of gene flow is modulated by the strength of ecological isolating mechanisms [26]. Differences in flowering time (*Q. virginiana* vs *Q. geminata*) and drought tolerance (*Q. fusiformis* vs *Q. virginiana*) work to maintain reasonably distinct genetic patterns of species cohesion. However, niche differentiation in fire response and habit between *Q. minima* and *Q. geminata*, two species with broadly overlapping flowering times, are less effective ecological barriers to gene flow. Mixed populations of *Q. virginiana*, *Q. minima*, and *Q. geminata* at the northern extent of sympatry in North Carolina appear to show elevated levels of morphological intergradation, possibly a result of habitat destruction and breakdown of ecological isolating mechanisms (P.S. Manos, pers. obs.).

#### 4. Section Lobatae—(37/ca. 120)

*Lobatae* occupy a range of habitats throughout the Americas, with just one species, *Q. humboldtii* Bonpl., extending into northern Colombia [83,84]; this is the only oak species of any section to range into South America, where it is ecologically important in a diverse array of forest types [85,86]. *Lobatae* are defined by long styles encircled at their base by a perigon, a skirt-like perianth structure [3,87]. Most *Lobatae* species have biennial fruit, but three unrelated species within the FNA region bear annual fruit (*Q. agrifolia*, *Q. emoryi*, and *Q. elliotii*), and a fourth unrelated species, *Q. hypoleucoides*, is polymorphic [88].

The earliest branch within *Lobatae* is a clade we treat here as subsect. *Agrifoliae*, distributed largely within the CA-FP. It is sister to a succession of subclades distributed from eastern North America to well south of the FNA region. Four of these clades are densely sampled in our phylogenetic work and treated below as subsects., but a fifth group within the FNA region, informally known as the Texas red oaks (e.g., *Q. canbyi* Cory and Parks = *Q. graciliformis* C.H. Muller; = *Q. gravesii* Sudw.), may or may not contain other rare, unsampled species that occur in Texas (e.g., *Q. rubusta* C.H. Muller and *Q. tardifolia* C.H. Muller). The placement of this group between the grade formed by temperate subsects. and the large clade formed by all other *Lobatae* south of the FNA region seems to geographically parallel the white oak biogeographic patterns (Figure 2). However, additional studies are needed to evaluate the possibility that the taxonomic complexities in the Trans-Pecos Region represent relictual hybrid populations or rare taxa with relationships to species within subsect. *Coccineae* or to Mexican taxa [1,72,89,90]. With our limited sample, the Texas Red oak group is the provisional sister to the clade formed by all other *Lobatae* south of the FNA region, informally called *Erythromexicana*, whose distributions suggest at least two major hotspots of species richness: The Northern Sierra Madre Orientale and Serranías Meridionales of Jalisco [91]. Three additional species within the FNA region, *Q. emoryi* Torr., *Q. hypoleucoides* A. Camus, and *Q. viminea* Trel., are clearly related to three different subclades within *Erythromexicana*.

Reconstruction of the timing and biogeography of the *Lobatae* phylogeny suggests an initial diversification of red oaks within the FNA region, followed by movement south into Mexico about 15 million years ago, associated with an increased net diversification rate most likely attributable to increased speciation rate [19]. This increase in species diversification rate was likely a response to the combination of tectonic movement, volcanism, and climatic oscillations that generated a mosaic of seasonal montane habitats in Mexico [92,93]. One major barrier to the *Lobatae* diversification was the Nicaraguan De-

pression [93]. As with the parallel and equally rapid diversification of white oaks, species diversity is considerably lower southward to Costa Rica.

In this subsectional treatment, we re-classify a total of 29 species of sect. *Lobatae* recovered in our global analysis, and resolved with high confidence into four clades.

#### 4.1. *Quercus* subsect. *Agrifoliae* (Trel.) A. Camus, Monogr. Genre *Quercus* 3: 46. 1952

*Q.* subsect. *Californicae* A. Camus, Monogr. Genre *Quercus* 3: 426. 1952.

**Shrubs and trees** to 30 m; **Bark** gray, dark brown to black, smooth or with wrinkled rings perpendicular to trunk axis or shallowly sinuous-furrowed to deeply furrowed, occasionally cross-checked into islands; **Twigs** slender, pubescent to glabrous; **Buds** light brown to reddish brown, ovoid to conic 3–9 mm; **Leaves** deciduous to evergreen, petiole 2–40 mm; **Leaf blade** circular to elliptic, ovate, obovate to oblong or narrowly lanceolate; base obtuse, rounded to cordate; margin entire or spinose with up to 30 awns or with 7–11 acute lobes and 13–30 awns; apex acute, attenuate, blunt to rounded; surfaces abaxially glabrous to densely pubescent with multiradiate trichomes or with small axillary tufts of 4–8 rayed fasciculate trichomes; **Acorns** biennial or annual, cup thin to thick, sometimes proximally tuberculate, deeply and narrowly cup-shaped, turbinate or U-shaped to deeply bowl-shaped, scales sometimes obtuse proximally to more acute distally, tips ragged or loose especially along distal cup edge, nut ovoid, oblong, conic to broadly ellipsoid; cotyledons distinct.

**Distribution:** California, north to OR, south to Mexico (B.C.) (see Figure 2)

**Includes:** *Q. agrifolia* Née (the type), *Q. kelloggii* Newb., \* *Q. parvula* Greene, \* *Q. wislizeni* A.DC.

The distinct nature of the red oaks of the CA-FP was recognized by Trelease, who viewed them as an isolated lineage and treated them as series *Agrifoliae* (pages 205, 206 in [70]). His treatment was mostly followed by Camus, although she classified the deciduous species *Q. kelloggii* into a monotypic subsection. Despite the contrast in leaf habit, species of *Agrifoliae* share a suite of diagnostic features including a deep cup and oblong nut and with cup scale tips generally appearing ragged or loose and occasionally inrolled.

*Agrifoliae* have been the subject of recent morphometric and genetic studies, resulting in intense scrutiny of the eleven named taxa, which include four species, four varieties, and three named hybrids [22,47,94]. These studies all demonstrate that the lobe-leaved deciduous species *Q. kelloggii* is sister to the remaining subevergreen species, in support of Camus' recognition that it is taxonomically distinct. Tests for introgression based on the molecular genetic data also demonstrate that *Q. kelloggii* hybridizes with every species in the complex, but there is yet no evidence that F<sub>1</sub> hybrids backcross to parental species in nature [23,95]. This potential barrier to introgression, with F<sub>1</sub> hybrids an apparent dead-end between *Q. kelloggii* and the remainder of the section, is of broad interest: Hybridization between oak species with distinctly different leaf habits is striking on its own [96,97], and biologically, the limits on introgression within any oak section is poorly understood. We also note that the divergence time estimate between *Q. kelloggii* and the remainder of the subsection is roughly 20 Ma, among the oldest splitting times inferred within crown groups among the major oak groups within subg. *Quercus*. The deep divergence separating *Q. kelloggii* from the other California red oaks may contribute to the maintenance of reproductive isolation in the subsection. Nonetheless, at finer phylogenetic scales, lingering taxonomic problems at the varietal level in *Agrifoliae* appear to be mainly due to hybridization (see references above).

Within the subevergreen complex, *Q. agrifolia* is sister to *Q. parvula* + *Q. wislizeni*. Within each of these species, recognized varieties correspond to north-south extremes in species distribution and values in sets of continuous morphological traits [94]. For the coastally distributed *Q. parvula*, there is strong support for var. *shrevei* (C.H. Muller) Nixon as the only valid variety whereas both var. *tamalpaisensis* and var. *parvula* have complex genetic backgrounds that likely involve gene flow from different combinations of subevergreen species [47]. While more study is needed, our findings indicate that the

narrowly endemic *Q. parvula* var. *tamalpaisensis* S.K. Langer represents a hybrid population that is roughly 60% *Q. wislizeni* and 40% *Q. parvula* var. *shrevei*. In this case, leaf size is notably larger in the introgressed populations, well outside the range of the parental species [23].

Disentangling *Q. parvula* var. *shrevei* from *Q. wislizeni* demonstrates that two main taxa span coastal and interior areas of the CA-FP. Molecular dating analysis [23] is consistent with the hypothesis proposed by Axelrod in 1983 [98] that *Q. parvula* and *Q. wislizeni* split from a common ancestor approximately 10–12 Ma. The fossil record shows that the *Q. wislizeni* + *Q. parvula* clade likely originated within what is now the Great Basin, east of the Sierra Nevada [99,100], with the lineage that would become modern *Q. parvula* moving westward in response to the drying climate following uplift of the Sierra Nevada. *Quercus wislizeni* is the more drought-tolerant taxon that also later moved west, following the westward movement of *Q. parvula*. As the climate continued to dry in the region, *Q. wislizeni* continued to expand westward with *Q. parvula* contracting even farther west, eventually resulting in its current coastal distribution.

One other coastal red oak, *Q. agrifolia*, is well supported except that the southernly distributed var. *oxyadenia* (Torr.) J.T. Howell, while morphologically and elevationally distinct (>750 m), is weakly supported by molecular data [23,95]. In this case, it's possible that the var. *oxyadenia* morphology has arisen multiple times in response to climatological differences in the drier, higher elevation and more southerly environments in which it is found. Future studies should include disjunct Baja populations of *Q. agrifolia* to test the hypothesis that a distinct genetic entity with the morphology of var. *oxyadenia* inhabits the more isolated areas farther south, and that widespread interbreeding between the var. *agrifolia* and var. *oxyadenia* forms has confounded that distinction just north within the FNA region.

#### 4.2. *Quercus subsect. Palustres* (Trel.) A. Camus, *Monogr. Genre Quercus* 3: 360. 1952

**Large trees** to 25 m; **Bark** gray, brown, with flat ridges and shallow to broad fissures; **Twigs** slender, glabrous; **Buds** gray to reddish brown, ovoid 3–7 mm; **Leaves** deciduous, petiole 20–60 mm; **Leaf blade** ovate, elliptic, obovate; base cuneate to truncate; margin with 5–11 lobes, and 9–30 awns, lobes acute to distally expanded, apex acute to acuminate; surfaces abaxially glabrous except for conspicuous axillary tufts of fasciculate trichomes; **Acorns** biennial, cup thin, scale bases visible on inner surface, saucer to deeply goblet shaped with minor to pronounced constriction at the base, scale tips appressed, nut globose to broadly ovoid; cotyledons distinct.

**Distribution:** Northern and Atlantic States, north to Canada (ONT), west to OK, KS, south to eastern TX, LA (see Figure 2)

**Includes:** *Q. palustris* Muenchh. (the type), *Q. texana* Buckley

*Palustres* include two largely allopatric bottomland species with highly similar vegetative features that were recognized by Camus to be distinct among lobe-leaved red oaks within North America. However, both Camus and Trelease thought that *Q. palustris* and *Q. georgiana* were closely related, while our analyses place *Q. georgiana* within subsect. *Phellos*. Although apomorphies are not obvious, phenetic studies using morphological data from leaves and fruit closely clustered *Q. palustris* and *Q. texana* (= *Q. nuttallii* E.J. Palmer) to the exclusion of other lobe-leaved species of *Lobatae* [101].

The first genetic result to suggest that at least *Q. palustris* was divergent from other eastern North American lobe-leaved species was obtained by allozyme analyses [102,103]. Phylogenomic studies confirm the early genetic work and resolve *Palustres* as the first branch among the eastern North American *Lobatae*, sister to the remainder of the section. For the two taxa of *Palustres*, dating analysis also shows a deep split, ca. 20 Ma, a pattern consistent with the branching structure within four of the five early-diverging red oak lineages within the FNA region.

#### 4.3. *Quercus* subsect. *Coccineae* (Trel.) A. Camus, *Monogr. Genre Quercus* 3: 386. 1952

*Q.* subsect. *Velutinae* (Trel.) A. Camus, *Monogr. Genre Quercus* 3: 376. 1952.

**Shrubs and medium to large trees** to 30 m; **Bark** dark brown to black, gray-brown, furrowed, ridges wide, shiny or with scaly fissures; **Twigs** somewhat thick, glabrous or sparsely pubescent; **Buds** reddish brown, tawny, gray, or silver, conic to ovoid-ellipsoid 3–12 mm; **Leaves** deciduous, petiole 20–60 mm; **Leaf blade** circular, ovate, elliptic, ovate to obovate; base cuneate, obtuse to truncate; margin with 5–11 lobes, and 12–55 awns, lobes acute, ovate-oblong, to distally expanded, apex obtuse, acute, to acuminate; surfaces abaxially glabrous or pubescent, trichomes multiradiate or stipitate fasciculate in conspicuous axillary tufts; **Acorns** biennial, cup thin to thick, cup to saucer-shaped, hemispheric to turbinate, scales smooth to tuberculate, scale tips appressed to loose at the margin, nut ovoid, subglobose to oblong; cotyledons distinct.

**Distribution:** Northern and Atlantic States, north to Canada (N.B., N.S., ONT, QUE, P.E.I.), west to KS, OK, TX, south to FL (see Figure 2)

**Includes:** *Q. acerifolia* (Palmer) Stoyanoff and Hess, *Q. buckleyi* Nixon and Dorr, *Q. coccinea* Muenchh. (the type), *Q. ellipsoidalis* E.J. Hill, *Q. rubra* L., *Q. shumardii* Buckland, *Q. velutina* Lam.

The circumscription of this group of eastern North American lobe-leaved tree species by Trelease is nearly fully supported by our analyses. The few exceptions include *Q. velutina* which had been either aligned with *Q. marilandica* or treated as a monotypic [72,75,90], and the inclusion of *Q. gravesii* (= *Q. texana* var. *chesosensis* Sarg.) by Trelease, which we resolved as sister lineage to *Erythromexicana* insofar as we have sampled it to date (see above).

*Coccineae* are defined by a certain phenetic similarity and regional proximity. One distinction shared by many of these species (e.g., *Q. rubra*, *Q. shumardii*) is wide geographic range, which promotes differentiation in morphological, physiological and ecological traits, and patterns of variation that have been variously treated as species and varieties [104,105]. We resolved two subclades that correspond to the main morphological groups that have been generally recognized: 1) (*Q. acerifolia*—*Q. buckleyi*—*Q. shumardii*) + *Q. rubra*; and 2) (*Q. velutina* + *Q. coccinea*) + *Q. ellipsoidalis*.

The first group includes the *Q. shumardii* complex, a cluster of continuously varying morphological forms that have been recognized as varieties and species (e.g., *Q. acerifolia*) [103]. Edaphic specialization appears to be an important driver of differentiation within this complex as *Q. buckleyi* (on limestone in TX and OK), *Q. shumardii* var. *schnneckii* (Britton) Sarg. (uplands west of the Blue Ridge), and *Q. acerifolia* (on sandstone, shales) are all endemic to the south-central Midwest. Additional range extensions of *Q. acerifolia*-like populations on limestone into east central Alabama are likely (W. Finch, pers. comm.), and fine-scale molecular and morphological studies of the complex are underway (Y. Wu, pers. comm.). The taxonomic history of *Q. rubra* involves an intraspecific taxon often associated with the higher elevations in the Appalachians, ca. above 1000 m (e.g., var. *ambigua* (A. Gray) Fernald = var. *borealis* (Michx. f.) Farw.). These populations have been quantitatively distinguished by phenetic analysis of morphometric data [101] and by flavonoid profiles [106], but intergradation between the two morphotypes precludes taxonomic recognition [107]. Additional work is needed to better understand the nature of this clinal pattern of variation.

The second group within subsect. *Coccineae* includes two widespread species, *Q. coccinea* and *Q. velutina*, and the north-central endemic *Q. ellipsoidalis* [108,109], which has the distinction of being our northernmost member of sect. *Lobatae* [110,111] and, historically, a locus of substantial taxonomic confusion in the upper Midwest (e.g., [111–117]). The question of whether *Q. ellipsoidalis* is distinct from *Q. coccinea* has been studied with AFLP markers [43,118], microsatellites [59], and RAD-seq data [15] using population-level sampling, including many of the morphologically similar red oaks (including *Q. palustris*) that co-occur in the northern part of the FNA region. There is strong evidence for recognizing *Q. ellipsoidalis* as a distinct species based on this fairly broad sampling. Further, there is little evidence for gene flow between *Q. ellipsoidalis* and *Q. coccinea*, which



resolve as largely allopatric sister species, but a low level of ongoing gene flow between *Q. ellipsoidalis* and both *Q. velutina* and *Q. rubra* [43,119–121]. The more distantly related *Q. rubra* and *Q. ellipsoidalis* also show evidence of genomically heterogeneous introgression driven by selection: alleles that distinguish the two species at a gene associated with flowering phenology segregate along moisture gradients and are preferentially shared between species in intermediate environments [122,123]. Genomic study of this species is underway (O. Gailing, pers. comm.). This western Great Lakes species may turn out to be a gateway to broader understanding of speciation in red oaks.

#### 4.4. *Quercus* subsect. *Phellos* (G. Don) A. Camus, Monogr. Genre *Quercus* 3: 293. 1952

*Q.* subsect. *Myrtifoliae* (Trel.) A. Camus, Monogr. Genre *Quercus* 3: 280. 1952; *Q.* subsect. *Nigrae* (G. Don) A. Camus, Monogr. Genre *Quercus* 3: 322. 1952; *Q.* subsect. *Marilandicae* (Trel.) A. Camus, Monogr. Genre *Quercus* 3: 329. 1952; *Q.* subsect. *Laevis* A. Camus, Monogr. Genre *Quercus* 3: 338. 1952; *Q.* subsect. *Pagodifoliae* (Trel.) A. Camus (as *Pagodaefoliae*), Monogr. Genre *Quercus* 3: 343. 1952; *Q.* subsect. *Ilicifoliae* (Oersted) Trel. A. Camus, Monogr. Genre *Quercus* 3: 353. 1952.

**Shrubs or large trees** to 40 m; **Bark** hard, black, roughly furrowed separated by smooth furrows or with rectangular blocks; **Twigs** slender to thick, glabrous or glabrescent or pubescent; **Buds** light brown, reddish-brown to purplish, conic to ovoid 2–10 mm; **Leaves** deciduous or subevergreen, petiole 1.5–60 mm; **Leaf blade** elliptic, ovate, obovate, circular to rhombic; base cuneate, rounded or cordate; margin entire, revolute or with 3–11 lobes, and 1–25 awns, lobes acute, attenuate to falcate; surfaces abaxially glabrous to tomentulous to uniformly pubescent, trichomes multiradiate, rosulate or stipitate fasciculate in axillary tufts; **Acorns** biennial and annual, cup thin to involute, shallow goblet-shaped, saucer to cup-shaped, scale tips appressed to loose at the margin, nut ovoid to subglobose; cotyledons distinct.

**Distribution:** Atlantic and Gulf region States, north to IA, MN, west to OK, TX (see Figure 2)

**Includes:** *Q. arkansana* Sarg., \* *Q. elliotii* Wilbur, *Q. falcata* Michx., *Q. georgiana* M. A. Curtis, *Q. hemisphaerica* Bartram ex Willd., \* *Q. ilicifolia* Wangen., *Q. imbricaria* Michx., *Q. incana* Bartram, \* *Q. inopina* Ashe, *Q. laevis* Walter, *Q. laurifolia* Michx., *Q. marilandica* Muenchh., \* *Q. myrtifolia* Willd., *Q. nigra* L., *Q. pagoda* Raf., *Q. phellos* L. (the type)

The center of species diversity for *Phellos* falls within the North Atlantic Coastal Plain (NACP), a recently recognized global biodiversity hotspot [124]. The combined distributions of eleven of the 16 species conform to the broad outline of the NACP, while the ranges of three of the 11 species, *Q. hemisphaerica*, *Q. phellos* and *Q. nigra*, have expanded from the southeastern coastal plain into adjacent piedmont, likely due to a combination of ecological disturbance and escape from cultivation [107].

Resolution of these 16 species aligns a heterogeneous and variously treated set of species into subsect. *Phellos*, making it the largest subsection within the FNA region. It is clear from previous treatments that a subset of this diversity was recognized as a natural group based on sharing the non-lobed laurel-like leaf type, small acorns, cups covering less than half of the nut, with scales closely appressed (subsect. *Phellos* sensu Camus: *Q. imbricaria*, *Q. incana*, *Q. laurifolia*, *Q. phellos*, *Q. pumila* Walter (= *Q. elliotii*). Other potentially related but phenetically dissimilar taxa with lobed leaves (e.g., *Q. falcata*, *Q. ilicifolia*, *Q. marilandica*) instead were segregated into series and subsections, often consisting of one or two species ([72,75]; see [125] for review).

Our results are generally consistent with more recent studies of flavonoid profiles and leaf architecture across these taxa: the systematics of the eight species treated by Trelease and later by Camus within their concepts *Laurifoliae*, *Marilandicae*, and *Nigrae* cannot be divorced from other taxa within the southeastern FNA region, e.g., *Q. laevis*, *Q. myrtifolia*, and *Q. inopina* [125]. The suggestion of a hybrid origin for many of these taxa [125] does not appear to be supported by phylogenomic study [15,19], which clearly resolves these species, with the caveat that this radiation arose relatively recently, within the last 10 Ma.



More intensive and targeted sampling is generally needed to test specific cases of reticulate evolution, and this clade has yet to be investigated so closely.

Based on population level sampling, we found that several of the lobe-leaved species show a close relationship to species with unlobed leaves. Additionally, although the five subclades resolved in our analyses are not strongly supported, the following preliminary patterns of species relationship suggest that diversification may be traced along several underlying ecological trajectories. For example, the group formed by (*Q. hemisphaerica*—*Q. incana*—*Q. myrtifolia*—*Q. inopina*) share unlobed leaves and occupy core NACP habitats of mostly sandhills; by contrast, the group formed by (*Q. ilicifolia*—*Q. georgiana*—*Q. imbricaria*) tend to occur in upland areas outside of the NACP in various habitats and substrates, including ravines and granitic outcrops, except that *Q. ilicifolia* ranges onto the northern edge of the NACP from New Jersey to Maine. Two other sets of species span sandhills to bottomlands. The larger of the two comprises (*Q. elliotii*—*Q. pagoda*—*Q. phellos*—*Q. laurifolia*—*Q. nigra*—*Q. arkansana*), which includes only three taxa that Camus placed with her concept of *Phellos*. A close relationship between *Q. arkansana* and *Q. nigra* is supported here [125]. The final group ((*Q. laevis* + *Q. marilandica*)—*Q. falcata*) tends to occupy sandy well-drained poor soils spanning coastal areas to adjacent uplands. Two of the tree species often resolved as sister taxa, *Q. laevis* and *Q. marilandica*, share a combination of bark, twig, and foliar characteristics. We also sampled *Q. marilandica* var. *ashei* Sudw. from the type location (Scott Mt.) in the Cross Timbers Region of Oklahoma. The placement of two accessions as sister to var. *marilandica* supports previous evidence to recognize this taxon as distinct [88].

## 5. Section *Quercus*—(45/ca. 150)

The white oaks stand out as the most species rich and most broadly distributed of all oak clades (Figure 1). The center of species diversity, ca. 100 spp., occurs in Mexico [84], but expansion of white oaks into the driest shrublands of the southwest (e.g., *Q. turbinella*, *Q. cornelius-mulleri*) and Intermountain west (*Q. gambelii*), and their extension into the coldest woodlands of the northern Midwest (*Q. macrocarpa*) demonstrate a physiological breadth not seen in the *Lobatae* [17]. Although white oaks share diagnostic features such as basal abortive ovules, glabrous endocarp, and annual fruit maturation with sects. *Virentes* and *Ponticae*, they are easily distinguished from *Virentes* and to a lesser extent *Ponticae* [3].

As with the *Lobatae*, our analyses reveal that the earliest branch of white oaks, which we treat here as subsect. *Dumosae*, is distributed largely within the CA-FP. It is sister to two major clades: One comprises three clades of mostly north temperate species that range from eastern North America to Eurasia, the other, a succession of three clades: the predominantly eastern subsect. *Stellatae*; a predominantly Texan group we treat here as subsect. *Polymorphae*; and the more recently derived Mexican and Central American clade, informally called *Leucomexicana* pending more detailed study. For the FNA region, we sampled every species except for *Q. intricata* Trel. (Trans-Pecos Region; Chihuahuan Desert Region) and *Q. carmenensis* C.H. Muller (Chisos Mts, Sierra del Carmen Region, Coahuila, Mexico); both of these unsampled species are likely to be placed into the groups we have recognized in this treatment. We also place ten additional FNA species distributed along the southwestern edge of the FNA region into at least three subclades within *Leucomexicana*. These species, a mix of shrubs and trees ranging from open chaparral, woodlands, and slopes of the Chihuahuan Desert Region west to the southern CA-FP, had been placed into many different series and subsections by Trelease and Camus. While additional sampling is needed for formal recognition, eight of these species, including *Q. engelmannii* from the CA-FP [35,126,127] and *Q. turbinella* from the Sonoran Desert, fall into one clade, suggesting a distinct east-west regional radiation that straddles the southwestern border of the FNA region that extends into Mexico.

Where the ranges of distantly related white oaks narrowly intersect, species have formed hybrid zones in areas of sympatry. One case study includes the tree species *Q. engelmannii* and two shrub species, *Q. cornelius-mulleri* and *Q. berberidifolia*, both placed

here in subsect. *Dumosae*. Morphological observations of hybridization remain anecdotal, but recent molecular analyses using phylogenetic methods to estimate whether allele sharing is due to gene flow conclude that ancient introgression had shuttled alleles from *Q. cornelius-mulleri* into *Q. engelmannii* [127]. In another case study, *Q. gambelii*, the only white oak of the Intermountain west, and here placed in subsect. *Dumosae* (see below), has long been recognized for hybridizing with white oak species of at least four distinct subclades that we recognize, including *Q. turbinella* and *Q. grisea* of *Leucomexicana* (e.g., [128,129]) and *Q. macrocarpa* of subsect. *Prinoideae* [130]. While recent genetic analyses show that morphologically typical *Q. gambelii* is genetically homogeneous (samples from AZ, CO, NM, UT), there is strong evidence that ancient introgression with *Q. macrocarpa* causes it to be unstable in phylogenomic analyses [25]. The fact that secondary contact zones exist between well separated white oak lineages makes them ideal case studies for ancient introgression and the development of more complete understanding of the nature of the mosaic structure of the oak genome [15,127,131].

Reconstruction of the timing and biogeography of the *Quercus* phylogeny also suggests an initial diversification of white oaks within the FNA region, followed by simultaneous movement south in a pattern closely parallel to *Lobatae*, then across the entire geographic range of Eurasia. The direction of movement, i.e., west through the Beringian Land Bridge or east through the North Atlantic Land Bridges, into Eurasia remains ambiguous, however, recent analyses based on whole plastome genome data also suggest a clear origin of the roburoids within the Americas (B. Wang, P.S. Manos et al. in prep.). The two relatively young and nearly contemporaneous radiations, *Leucomexicana* and roburoids, starting about 15 Ma [15], together account for roughly 75% of the diversity of the section (see Figure 2).

In this subsectional treatment, we re-classify a total of 33 species of sect. *Quercus* recovered in our global analysis, and resolved with high confidence into five clades.

#### 5.1. *Quercus* subsect. *Dumosae* (Trel.) A. Camus, Monogr. Genre *Quercus* 2: 462. 1936

*Q.* subsect. *Douglasiae* (Trel.) Camus, Monogr. Genre *Quercus* 3: 666. 1936; *Q.* subsect. *Lobatae* (Trel.) Camus, Monogr. Genre *Quercus* 3: 681. 1936; *Q.* subsect. *Gambelieae* (Trel.) Camus, Monogr. Genre *Quercus* 3: 694. 1936.

**Shrubs, small to large trees** to 30 m; **Bark** light to dark gray, dark brown, scaly or deeply checkered in age; **Twigs** slender, yellowish, gray, brown or reddish brown, densely puberulent to tomentulose with spreading hairs to glabrate; **Buds** yellowish, brown to reddish brown, ovate, globose, ovoid to fusiform, 1–12 mm; **Leaves** deciduous or subevergreen, petiole 1–20 mm; **Leaf blade** broadly obovate, elliptic, subrotund to ovate or oblong to oblanceolate, deeply to shallowly 4–8 lobed; base truncate, rounded-attenuate, cuneate or cordate; margins entire, irregularly shallowly toothed, coarsely toothed to spinose-toothed or lobed, lobes oblong to spatulate, obtuse, rounded, subacute or blunt; surfaces abaxially grayish to whitish, dull green, yellowish to light green, blue-green to glaucous, waxy or glossy, densely velvety with erect 4–8 rayed fasciculate trichomes or dense to sparsely appressed to semi-erect 8–12 rayed stellate trichomes, sometimes with interlocking or fused rays, becoming glabrous; **Acorns** annual, 1–3 subsessile or pedunculate, cup saucer-shaped, hemispheric, deeply cup-shaped or turbinate, base flat or rounded, scales closely appressed, ovate, weakly to strongly tuberculate, scale tips acute, mostly free often reflexed, nut conic, ovoid to globose, ellipsoid, oblong to fusiform, cylindric or barrel-shaped; cotyledons distinct.

**Distribution:** Pacific States, north to Canada (B.C.), south to Mexico (B.C.) (see Figure 2)

**Includes:** \* *Q. berberidifolia* Liebm., \* *Q. cornelius-mulleri* Nixon and K. P. Steele, *Q. douglasii* Hook. and Arn., \* *Q. dumosa* Nutt. (the type), \* *Q. durata* Jepson, \* *Q. gambelii* Nutt., *Q. garryana* Douglas ex Hook., \* *Q. john-tuckeri* Nixon and C. H. Muller, *Q. lobata* Née, \* *Q. pacifica* Nixon and C. H. Muller

*Dumosae* form the sister group to all white oaks, diverging by at least 40 Ma likely from within the FNA region. Two clades of basically sclerophyllous shrubby species are

nested within an early-branching grade of the two deciduous lobe-leaved species, *Q. lobata* and *Q. garryana* [27]. Fossil leaf compressions attributed to precursors of *Q. lobata* (e.g., *Q. prelobata*) occur well north of the current distribution, indicating a broader ancestral distribution of the stem group going back to the early Miocene, 16–23.5 Ma [99,100].

In addition to the nine *Dumosae* taxa that occur in the Pacific States, we expand the subsection to include *Q. gambelii*, consistent with the high degree of leaf and trichome similarity between *Q. gambelii* and *Q. garryana sensu lato* [132]. *Quercus gambelii* is a curiously widespread species that consists of many isolated but weakly differentiated populations [77]. It was the eponymous center of the 11-species Treleasian series *Gambelieae*, but all those taxa have subsequently been subsumed into *Q. gambelii* or are otherwise not recognized. It was never classified with other lobed-leaved species [72,74,90]. Its uncertain systematic affinities may have been partly a consequence of its isolated geography. In the northern part of its range, it is often the only oak species within the Intermountain west. But in the southwest, *Q. gambelii* is surrounded by and often sympatric with multiple species representing at least four subjects. of white oaks, resulting in a rich taxonomic and ecological literature describing patterns of natural hybridization [128,129,133,134].

However, its uncertain position may be due to its cryptic morphology, a lobedness that may derive in part from an ancient history of introgression with eastern lobed white oaks. Our phylogenomic studies detected a primary signal of phylogenetic history between *Q. gambelii* and *Q. lobata* as the branches leading to accessions of both species formed a clade [25]. The position of this clade was determined to be unstable in the phylogenetic space between *Dumosae* and *Prinoideae*. Our work, based on tests designed to detect secondary phylogenetic signals due to introgression, suggests that ancient hybridization between *Q. gambelii* and *Q. macrocarpa* is the likely cause of phylogenetic uncertainty in the placement of this species. Our inference of historical rather than contemporary gene flow is further supported by the fact that *Q. gambelii*, *Q. macrocarpa*, and *Q. lobata* are strongly monophyletic across analyses. If ongoing gene flow were the cause of phylogenetic instability, we would expect some individuals of these species to switch positions between species or become dragged to phylogenetically intermediate positions themselves. Instead, all individuals of these species form separate clades by species.

Thus *Q. gambelii* seems to have arisen from allopatric speciation within the formerly widespread range of *Q. lobata* or the ancestral complex formed by *Q. lobata* and the named varieties of *Q. garryana* [20,25]. In this scenario, uplift of the Sierra Nevada, increasing aridity, and other developing north-south barriers isolated populations of ancestral *Q. gambelii* during the Miocene. The aridity of the Great Basin would have forced the nascent species eastward, into mesic woodlands, and to the southeast, along the foothills of the Rocky Mountains into its current elevational range of 1000 to 3000 m. While *Q. gambelii* does not currently overlap in range with *Q. lobata*, *Q. garryana*, or *Q. macrocarpa*, periods of range expansion during warm and wet periods over the last 5 million years likely generated extensive secondary contact zones between *Q. gambelii* and *Q. macrocarpa* [99]. In addition to our genetic results, support for historical range extension and hybridization comes from morphological evidence observed in outlier populations of *Q. gambelii* in the Black Hills of South Dakota and *Q. macrocarpa* in northeastern New Mexico [130].

The main diversification within *Dumosae* involves an array of mostly shrub species, including *Q. pacifica*, the second taxon endemic to the California Channel Islands, that have vexed systematists for well over a century [20,132,135]. It was suggested that all of the California shrub species, except for *Q. turbinella* are derived from a lobe-leaved ancestor similar to *Q. lobata*. Nixon [122] outlined anatomical evidence for this relationship, noting the venation pattern shared between sclerophyllous shrub species and lobe-leaved species, specifically branched secondary veins, multiple and irregularly spaced teeth, and an often coarse pattern of lobation. This pattern contrasts with the condition of secondary veins that rarely branch, generally resulting in one tooth per secondary vein and regularly spaced teeth, like those of *Q. turbinella* and other shrub species in the southwestern FNA region

and Mexico. Our analyses confirm this hypothesis, while in-depth studies have generated additional patterns of species relationships within the shrub diversity of *Dumosae*.

By ca. 15 Ma, the nested crown lineage of *Dumosae* diverged into two clades, one clade comprising *Q. pacifica*—*Q. dumosa* and a distinct well supported subclade of (*Q. cornelius-mulleri*–(*Q. john-tuckeri* + *Q. douglasii*)), and the other clade formed by a grade of population samples representing the widespread *Q. berberidifolia*, within which are nested two separate subclades of *Q. durata* var. *durata* and var. *gabrielensis* Nixon and C.H. Muller [27,35,127]. This overall pattern and taxonomy are consistent with previous morphological work that segregated the narrow endemic *Q. dumosa* from *Q. berberidifolia* and recognized the parapatrically distributed *Q. cornelius-mulleri* and *Q. john-tuckeri* to be distinct from previous taxonomic treatments (see [132] for review). The nested position of the tree species *Q. douglasii* within the shrub clade formed by *Q. cornelius-mulleri* and *Q. john-tuckeri* is an interesting example of an evolutionary reversal back to the tree habit. The timing of divergence of the nested crown clade of shrubby species, from *Q. pacifica* through the *Q. berberidifolia* clade, is consistent with the hypothesis of Kim et al. (2018) [127]: Diversification of the shrub species coincides with mid-Miocene development of the Mediterranean climate in the CA-FP [136]. The onset of this climate regime would have increased the frequency of fire, potentially favoring shrubs over trees. The evolution of *Q. douglasii*, a tree with shrub-like traits, may have been enabled by ecological opportunity in the relatively mesic foothills of the Sierra Nevada.

Recent demographic studies of gene flow among different combinations of shrub species suggest that hybridization continues to promote taxonomic uncertainty while ecology and climate reinforce genomic cohesiveness and identity [35,127,137]. The full complement of genetic analyses confirms that most of the morphologically-defined species of *Dumosae* are cohesive and often ecologically isolated to some degree. One notable exception stands out from studies of the *Q. berberidifolia*—*Q. durata* complex, which have revealed the most challenging case to date. *Quercus durata* appears to have arisen twice from within *Q. berberidifolia*, despite the generally clear taxonomic distinctions between *Q. berberidifolia* and *Q. durata*. While *Q. durata* var. *durata* is well separated, albeit nested, within *Q. berberidifolia*, var. *gabrielensis* is only weakly distinguished [27,127]. This distinction likely involves ecological isolation, as *Q. durata* var. *durata* mostly occurs on serpentine soils. Such cases may be more widespread in oaks than we suspect and bear closer investigation.

## 5.2. *Quercus* subsect. *Prinoideae* (Trel.) A. Camus, Monogr. Genre *Quercus* 2: 434. 1936

*Q.* subsect. *Lyratae* (Oersted) A. Camus, Monogr. Genre *Quercus* 2: 723. 1936; *Q.* subsect. *Macrocarpae* (Trel.) A. Camus, Monogr. Genre *Quercus* 2: 738. 1936.

**Shrubs or large trees** to 30–50 m; **Bark** dark gray to light gray, thin flaky to papery, scaly, flat-ridged or with thick plates underlying scales; **Twigs** coarse, slender to moderate, gray, tan, reddish brown, fine-pubescent to villous becoming glabrate or with round to radiating flat corky wings; **Buds** gray, brown, red-brown, subrotund to broadly ovoid 1–4 mm; **Leaves** deciduous, deciduous or persistent stipules, petiole 4–30 mm; **Leaf blade** moderate to large, lanceolate, obovate to narrowly elliptic or broadly obovate; base rounded, truncate, cuneate to acute; margins regularly undulate, toothed or shallow-lobed to deeply lobed; surfaces abaxially glaucous to light green, tomentose, trichomes erect long-rayed fasciculate and small stellate; **Acorns** annual, 1–3 on thin to stout peduncle, cup hemispheric, cup-shaped, turbinate to goblet-shaped or spheroid, base rounded, scales closely appressed to laterally connate, moderately to prominently keeled, tuberculate or coarsely thickened and fringed at the margin with short awns, nut ovoid-ellipsoid or oblong; cotyledons distinct.

**Distribution:** Atlantic States and Mississippi Valley, north to Canada (MAN, N.B., ONT, QUE, SASK), south to the mountains of western TX, NM, and northeastern Mexico (COAH, N.L., HGO, TAMPS) (see Figure 2)

**Includes:** *Q. bicolor* Willd., *Q. lyrata* Walter, *Q. macrocarpa* Michx., *Q. muehlenbergii* Engelm., \* *Q. prinomides* Willd. (the type)



*Prinoideae* form the sister to a moderately sized temperate clade that spans eastern North America and Eurasia. The five species we recognize here share a common set of trichomes and similar cup scale morphology. Camus classified *Q. montana* and *Q. michauxii* in her concept of subsect. *Prinoideae*, while recognizing *Q. lyrata* and *Q. macrocarpa* in separate monotypic groups. Our analyses placed the former species pair with *Q. alba*, consistent with their lack of the trichome types observed across all *Prinoideae* [138,139].

Extensive population sampling and analysis resolved a deep split within the crown group, ca. 20 Ma, pairing tree species *Q. muehlenbergii* and shrub *Q. prinoides* sister to a well-supported group of (*Q. macrocarpa*- (*Q. lyrata* + *Q. bicolor*)). As with morphology, our data are unable to detect a clean separation between the widespread and ecologically distinct “species-pair,” *Q. muehlenbergii* (limestone) and *Q. prinoides* (sands, shales). Further studies are needed to understand the ecological processes behind the weak genetic separation of taxa, despite the heritable differences observed in *Q. prinoides*, such as the shrub habit and early maturation to flower and fruit [132]. It may be that the situation in *Q. muehlenbergii* mirrors that of *Q. berberidifolia* and *Q. durata*, in which the same phenotype has arisen more than once due to parallel selective processes across the range of the more widespread species.

### 5.3. *Quercus* subsect. *Albae* (G. Don) A. Camus, *Monogr. Genre Quercus* 2: 728. 1936

**Large trees** to 30 m; **Bark** dark gray or brown with V-shaped furrows or light brown to gray, scaly; **Twigs** moderate, green, brown to reddish brown, glabrous or fine-pubescent to sparse spreading hairs, becoming glabrous; **Buds** gray, light brown, reddish-brown, ovoid 3–6 mm; **Leaves** deciduous, petiole 5–30 mm; **Leaf blade** moderate, broadly obovate to narrowly elliptic or narrowly obovate; base cuneate to acute or rounded acuminate to broadly cuneate; margins regularly toothed or moderately to deeply lobed; surfaces abaxially light green or yellowish; trichomes solitary, appressed, and erect or appressed, 1–2 rayed fasciculate, persistent to quickly shed; **Acorns** annual, 1–3 sessile or pedunculate, cup shallowly cup-shaped to hemispheric or deeply goblet shaped, base rounded, rim thin to moderate, scales concentric to laterally connate or loosely to closely appressed, slightly keeled to prominently tuberculate, nut ovoid-ellipsoid, cylindric or oblong; cotyledons distinct.

**Distribution:** Atlantic States and Mississippi Valley, north to Canada (ONT, QUE), south to eastern TX, northern FL (see Figure 2)

**Includes:** *Q. alba* L. (the type), *Q. michauxii* Nutt., *Q. montana* Willd.

The three *Albae* species are quite divergent with respect to morphology, especially features of the bark and cup scales. Although the leaves of *Q. alba* are generally described as glabrous and frequently are at maturity [130], fasciculate trichomes are present in the early stages of leaf development, and simple trichomes may persist as the leaf expands. *Quercus michauxii* and *Q. montana* also share fasciculate trichomes, but these are persistent, and erect with long rays in the former and appressed with short rays in the latter. *Albae*, as delimited here, lack the stellate trichomes observed in *Prinoideae* [138,139]. Our analyses break-up the so-called chestnut group of the FNA region (*Q. michauxii*, *Q. montana*, *Q. muehlenbergii*, *Q. prinoides*, *Q. sadleriana*), leading to the distribution species with the ‘prinoid’ or ‘castaneoid’ leaf shape into three distinct temperate clades of white oaks: *Albae*, *Ponticae*, and *Prinoideae*.

*Albae* combine morphological elements of the prinoids and roburoids to form one of the most genetically cohesive oak subclades of the FNA region. The relationships among the three species (*Q. montana*—(*Q. michauxii* + *Q. alba*)) are well supported and based on strong sampling. The sister group relationship of *Albae* to the roburoids extends the signature pattern of early-diverging deciduous shallowly and deeply lobe-leaved species from the FNA region to Eurasia. This biogeographic connection has been difficult to estimate phylogenetically as a result of ancient hybridization between the *Q. pontica* sublineage of *Ponticae* and ancestral roburoids in Eurasia [24].



#### 5.4. *Quercus* subsect. *Stellatae* (Trel.) A. Camus, Monogr. Genre *Quercus* 2: 710. 1936

*Q.* subsect *Confusae* (Trel.) A. Camus, Monogr. Genre *Quercus* 2: 671. 1936; *Q.* subsect *Durandiae* (Trel.) A. Camus, Monogr. Genre *Quercus* 2: 676. 1936.

**Shrubs, often rhizomatous, moderate to large trees** to 30 m; **Bark** light gray or whitish, light brown, scaly or flaky to papery and exfoliating; **Twigs** slender to moderately thick,, densely tomentose, sparsely pubescent, glabrate; **Buds** gray to reddish-brown, ovoid to globose to acute at the apex, 1–6 mm; **Leaves** deciduous to wintergreen, petiole 1–15 mm; **Leaf blade** small to moderately large, obovate to narrowly elliptic, oblong to oblanceolate or rounded 3-dentate to obtriangular; base rounded-attenuate, acute to cordate, cuneate or obtuse; margins undulated, revolute, entire or shallow, moderate to deeply lobed, 3–5 lobes rounded, spatulate or sinuate; surfaces abaxially silvery, grayish, dull to yellowish green or dark green, trichomes dense to scattered, 3–10-rayed stipitate fasciculate, stellate, often becoming glabrate; **Acorns** annual, 1–3 subsessile or pedunculate, cup thin, deeply cup-shaped, goblet-shaped, turbinate, hemispheric, base rounded or constricted, cup scales gray to brown, thin, tightly appressed, flattened to only slightly tuberculate, scale tips acute, nut ovoid, globose, barrel-shaped to elliptic; cotyledons distinct.

**Distribution:** Atlantic States west to eastern NM, north to southern IA, southeastern NY (see Figure 2).

**Includes:** *Q. austrina* Small, \* *Q. boyntonii* Beadle, \* *Q. chapmanii* Sarg., \* *Q. havardii* Rydberg, *Q. margarettae* Ashe, *Q. oglethorpensis* W.H. Duncan, *Q. similis* Ashe, \* *Q. sinuata* Walter, *Q. stellata* Wangenh. (the type)

*Stellatae* comprise a balanced mix of trees of various size and low-growing shrubs that occupy mainly lowlands including deep sands, alluvial flatwoods, and bottomlands. Species of this subsection are more or less distributed in the southeast of the FNA region, strongly overlapping in range and habitat type with species of the red oak clade *Phellos*. The placement of *Q. havardii* within this subsection expands the range farther west to eastern New Mexico.

In addition to the five species Camus recognized in her subsect. *Stellatae* (*Q. boyntonii*, *Q. chapmanii*, *Q. margarettae*, *Q. similis*, *Q. stellata*), our expanded delimitation of the group to nine species includes three species—*Q. austrina*, *Q. havardii* [66], and *Q. sinuata*—that had been treated in small subsections of one or two species each, and the unclassified and most recently described oak species east of the Mississippi, *Q. oglethorpensis*. Duncan (1950) [140] had suggested a close affinity of *Q. oglethorpensis* to many of the species placed here based on similarities in cup scales, bark, and leaf epidermal features. Strong similarities in cup shape and well-defined cup scales that are thin, generally narrow, and flat and only slightly tuberculate also support the expansion of the historically recognized post oak subgroup sensu Camus to include four additional species.

*Stellatae* diversified within the last 15 Ma, around the same time as subsect. *Phellos* and clades within *Leucomexicana*. We resolved *Q. sinuata* and *Q. oglethorpensis* as early-branching species, consistent with Duncan's (1950) view that both are somewhat isolated evolutionarily. The remaining seven species are resolved into three moderately supported subclades: *Q. margarettae*—*Q. austrina*; *Q. chapmanii*—*Q. havardii*; and *Q. stellata*, *Q. similis*, and *Q. boyntonii*. Additional population sampling, especially in the southern Gulf states and west into Texas, is needed to better understand the relationship of geography and potential hybridization to this initial estimate of phylogeny.

#### 5.5. *Quercus* subsect. *Polymorphae* (Trel.) A. Camus, Monogr. Genre *Quercus* 2: 561. 1936

**Shrubs, often rhizomatous, small to moderate trees** to 20 m; **Bark** light gray to brown, papery, scaly or deeply furrowed, sometimes exfoliating in long strips; **Twigs** slender, gray, yellowish to light brown, reddish brown, pubescent to tomentose or soon glabrate; **Buds** gray, brown, reddish-brown, round to ovoid or with apex acute, 0.5–10 mm; **Leaves** subevergreen, deciduous, petiole 2–25 mm; **Leaf blade** small to moderate, elliptic, narrowly lanceolate to oblong, ovate, obovate, subrotund or rotund; base rounded, cordate, cordulate or cuneate; margins thick or thin, flat, revolute to regularly undulate-

crisped, entire to toothed, shallowly lobed sometimes with 2–3 spinescent teeth on each side; surfaces abaxially light green, blue-green, dark green, glaucous or whitish, glabrous, floccose or tomentose, trichomes dense to scattered, flat, curly or stiffened stellate, with erect or appressed simple hairs, sometimes becoming glabrous; **Acorns** annual, 1–2 subsessile or pedunculate, cup thin, shallowly to deeply cup-shaped, turbinate, hemispheric or funnel-shaped, cup scales appressed, thickened basally, moderately to strongly tuberculate, scale tips appressed; nut ovoid-ellipsoid, oblong or barrel-shaped, sometimes flattened at both ends; cotyledons distinct or connate.

**Distribution:** Southwestern States AZ, NM, OK, TX, northeastern Mexico south to Guatemala (see Figure 2)

**Includes:** \* *Q. hinckleyi* C.H. Muller, *Q. laceyi* Small, *Q. mohriana* Buckley, *Q. polymorpha* Schltdl. and Cham. (the type), *Q. pungens* Liebm., *Q. vaseyana* Buckley

*Polymorphae* form a small and variable clade that diverged from *Leucomexicana* more than 15 Ma. Of the six recognized taxa, only *Q. hinckleyi* and *Q. polymorpha* share the same Bioregion climate cluster with *Leucomexicana* taxa based on climatic ranges estimated from Worldclim data [77], while the other four species cluster with Eastern North American taxa [19]. The clade is remarkably heterogeneous in morphology and habit, with a patchy distribution in the Chihuahuan Desert Region and adjacent Edwards Plateau except for *Q. polymorpha*, which ranges from southwest Texas, south along the east slope of the Sierra Madre Oriental to Guatemala [83,132].

One well supported subgroup of taxa comprises *Q. hinckleyi*—*Q. pungens*—*Q. vaseyana*. *Quercus pungens* and *Q. vaseyana* have been linked taxonomically, the latter initially treated as a variety of the former, and both classified by Muller (1951) [90] in his series *Vaseyanae*. Muller described and placed *Q. hinckleyi* within series *Glaucoidae*, a group he delimited to include the FNA taxa *Q. laceyi* and *Q. depressipes* Trel. and the widespread Mexican species *Q. glaucoides* M. Martins and Galeotti. Our analyses instead support a regional radiation of taxa, including *Q. laceyi*, while placing the FNA taxa associated with the historical concept of series *Glaucoidae* (e.g., *Q. depressipes*, *Q. engelmannii* Greene, *Q. arizonica* Sarg.) within *Leucomexicana* (Figure 2).

Except for *Q. pungens* and *Q. vaseyana*, none of the taxa treated here within *Polymorphae* have been considered closely related in previous classifications. For example, *Q. laceyi*, *Q. polymorpha*, and *Q. mohriana* were placed in different sets of mostly Mexican taxa: (1) *Q. mohriana* with *Q. arizonica* in subsect. *Arizonicae* sensu Camus [74]; (2) *Q. polymorpha* with *Q. porphyrogenita* Trel. and a few other Mexican taxa of doubtful validity within subsect. *Polymorphae* sensu Camus [83]; and (3) *Q. laceyi* within series *Glaucoidae* sensu Muller, and as noted later [141], with putative affinities to either *Q. porphyrogenita* or eastern North American white oaks.

Our current sampling and high level of resolution and support within section *Quercus* are sufficient to conclude that most of the previous speculation on the disparate affinities of these taxa is not supported. We sampled two accessions of the widespread *Q. polymorpha*, one from the northernmost population in Texas (Dolan Falls, Val Verde Co.) the other from south of Monterrey (Nuevo Leon; Mexico), about 600 km apart, and they fell sister to one another with strong support [15]. Similarly, each taxon with the exception of *Q. hinckleyi* has been sampled from two separate populations, with all individuals of these species forming tight, cohesive clades.

While our sampling in Mexico is preliminary, analyses suggest at least one compelling scenario for the biogeographic history of this clade. Aside from *Q. polymorpha*, these taxa currently form the most narrowly distributed radiation of the North American oak clades, and the timing of the clade's crown diversification coincides closely with the mid-Miocene expansion of arid zones [142]. Species of this clade generally occur on limestone and desert slopes of the southwestern states (AZ, NM, TX, OK) and three north-central states of Mexico (CHIH, COAH, N.L.). The more mesophytic and broadly distributed *Q. polymorpha* sublineage occurs to the south along the east slope of the Sierra Madre Oriental. Current patterns of distribution suggest a concentrated distribution of relictual species of various

habit and climatic niche breadth, with a notable biogeographic disjunction between the *Q. polymorpha* and *Q. mohriana* sublineages by the end of the Pliocene, ca. 3–5 Ma, well after the diversification of main radiation of *Leucomexicanae* [19]. It is likely that the historical range of *Polymorphae* was more widespread farther north and west into the FNA region and south into Mexico during wetter and more mild climates during the late Wisconsin glaciation episode (22–11 thousand years ago). The most distinctive of these taxa, *Q. hinckleyi*, is a narrow endemic of the Trans-Pecos Region, with spinescent, subrotund leaves. It has been called a “climate relict” based on leaf fossil evidence from packrat middens throughout the Pleistocene ([143], for discussion see [144]).

## 6. Conclusions

We have provided a review and synthesis of the systematics of the oaks within the Flora of the North American region, as informed by recent analyses using phylogenomic analyses of nuclear sequence data. A new classification for part of the American oak clade is presented and discussed with reference to biogeographic history, species-level relationships, and previous hypotheses of hybridization. This update on the evolutionary diversification of an ecologically and economically important tree group provides both a capstone and roadmap to guide future studies.

The recognition of oak clades below the sectional level provides an opportunity to revisit some of the most interesting topics in ecology, biogeography, and species biology. From the ecological processes involved in community assembly to the adaptive role of hybridization, species-level phylogenies derived from next-generation DNA sequence data will enhance scientific inquiry and promote targeted hypothesis testing. In practical terms, translating phylogenies into informative classification systems improves our ability to communicate with precision about the independent evolutionary radiations of species across the tree of life.

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## References

1. Nixon, K.C. *Quercus*. In *Flora of North America North of Mexico*; Committee Flora of North America Editorial, Ed.; Oxford University Press: New York, NY, USA, 1997; Volume 3, pp. 445–447.
2. Manos, P.S.; Stanford, A.M. The Historical Biogeography of Fagaceae: Tracking the Tertiary History of Temperate and Subtropical Forests of the Northern Hemisphere. *Int. J. Plant Sci.* **2001**, *162*, S77–S93. [CrossRef]
3. Denk, T.; Grimm, G.W.; Manos, P.S.; Deng, M.; Hipp, A.L. An updated infrageneric classification of the oaks: Review of previous taxonomic schemes and synthesis of evolutionary patterns. In *Oaks Physiological Ecology. Exploring the Functional Diversity of Genus Quercus L.*; Gil-Pelegrín, E., Peguero-Pina, J.J., Sancho-Knapik, D., Eds.; Tree Physiology; Springer: Cham, Switzerland, 2017; pp. 13–38. ISBN 9783319690988.

4. Cavender-Bares, J. Diversity, Distribution, and Ecosystem Services of the North American Oaks. *Int. Oaks* **2016**, *27*, 37–48.
5. Fahey, R.T.; Darling, L.; Anderson, J. Oak Ecosystem Recovery Plan: Sustaining Oaks in the Chicago Wilderness Region; Chicago Wilderness Oak Ecosystem Recovery Working Group; USDA Forest Service and US Fish & Wildlife Service, Chicago, Illinois. 2015. Available online: <http://chicagorti.org/sites/chicagorti/files/OERP-Full-Report-lowres.pdf> (accessed on 12 June 2021).
6. Nowak, D.J.; Hoeft, R.E.I.; Bodine, A.R.; Crane, D.E.; Dwyer, J.F.; Bonnewell, V.; Watson, G. *Urban Trees and Forests of the Chicago Region*; U.S. Department of Agriculture, Forest Service, Northern Research Station: Newtown Square, PA, USA, 2013.
7. Chassé, B. Eating Acorns: What Story Do the Distant, Far, and near Past Tell Us, and Why? *Int. Oaks: J. Int. Oak Soc.* **2016**, *27*, 107–135.
8. Logan, W.B. *Oak: Frame of Civilization*; W.W. Norton & Company Inc.: New York, NY, USA, 2005.
9. Leroy, T.; Plomion, C.; Kremer, A. Oak Symbolism in the Light of Genomics. *New Phytol.* **2020**, *226*, 1012–1017. [\[CrossRef\]](#)
10. Mabey, R. *The Cabaret of Plants: Forty Thousand Years of Plant Life and the Human Imagination*, 1st ed.; W.W. Norton & Company Inc.: New York, NY, USA, 2017; ISBN 9780393353860.
11. Forman, L.L. On the Evolution of Cupules in the Fagaceae. *Kew Bull.* **1966**, *18*, 385. [\[CrossRef\]](#)
12. Nixon, K.C.; Crepet, W.L. TRIGONOBALANUS (FAGACEAE): TAXONOMIC STATUS AND PHYLOGENETIC RELATIONSHIPS. *Am. J. Bot.* **1989**, *76*, 828–841. [\[CrossRef\]](#)
13. Manos, P.S.; Doyle, J.J.; Nixon, K.C. Phylogeny, Biogeography, and Processes of Molecular Differentiation in *Quercus* Subgenus *Quercus* (Fagaceae). *Mol. Phylogenet. Evol.* **1999**, *12*, 333–349. [\[CrossRef\]](#)
14. Oh, S.-H.; Manos, P.S. Molecular Phylogenetics and Cupule Evolution in Fagaceae as Inferred from Nuclear CRABS CLAW Sequences. *Taxon* **2008**, *57*, 434–451.
15. Hipp, A.L.; Manos, P.S.; Hahn, M.; Avishai, M.; Bodénès, C.; Cavender-Bares, J.; Crawl, A.A.; Deng, M.; Denk, T.; Fitz-Gibbon, S.; et al. Genomic Landscape of the Global Oak Phylogeny. *New Phytol.* **2020**, *226*, 1198–1212. [\[CrossRef\]](#) [\[PubMed\]](#)
16. Denk, T.; Grimm, G.W. Significance of Pollen Characteristics for Infrageneric Classification and Phylogeny in *Quercus* (Fagaceae). *Int. J. Plant Sci.* **2009**, *170*, 926–940. [\[CrossRef\]](#)
17. Cavender-Bares, J. Diversification, Adaptation, and Community Assembly of the American Oaks (*Quercus*), a Model Clade for Integrating Ecology and Evolution. *New Phytol.* **2019**, *221*, 669–692. [\[CrossRef\]](#) [\[PubMed\]](#)
18. Cavender-Bares, J.; Kothari, S.; Meireles, J.E.; Kaproth, M.A.; Manos, P.S.; Hipp, A.L. The Role of Diversification in Community Assembly of the Oaks (*Quercus* L.) across the Continental U.S. *Am. J. Bot.* **2018**, *105*, 565–586. [\[CrossRef\]](#) [\[PubMed\]](#)
19. Hipp, A.L.; Manos, P.S.; González-Rodríguez, A.; Hahn, M.; Kaproth, M.; McVay, J.D.; Avalos, S.V.; Cavender-Bares, J. Sympatric Parallel Diversification of Major Oak Clades in the Americas and the Origins of Mexican Species Diversity. *New Phytol.* **2018**, *217*, 439–452. [\[CrossRef\]](#) [\[PubMed\]](#)
20. Nixon, K.C. The Oak (*Quercus*) Biodiversity of California and Adjacent Regions. *Gen. Tech. Rep. USDA For. Serv.* **2002**, PSW-GTR-184, 3–20.
21. González-Rodríguez, A.; García-Oliva, F.; Tapie-Torres, Y.; Morón-Cruz, A.; Chávez-Vergara, B.; Baca-Patiño, B.; Cuevas-Reyes, P. Oak Community Diversity Affects Nitrogen in Litter and Soil. *Int. Oaks J. Int. Oak Soc.* **2019**, *30*, 125–130.
22. Cavender-Bares, J.; Ackerly, D.D.; Baum, D.A.; Bazzaz, F.A. Phylogenetic Overdispersion in Floridian Oak Communities. *Am. Nat.* **2004**, *163*, 823–843. [\[CrossRef\]](#)
23. Hauser, D.A.; Keuter, A.; McVay, J.D.; Hipp, A.L.; Manos, P.S. The Evolution and Diversification of the Red Oaks of the California Floristic Province (*Quercus* Section *Lobatae*, Series *Agrifoliae*). *Am. J. Bot.* **2017**, *104*, 1581–1595. [\[CrossRef\]](#) [\[PubMed\]](#)
24. McVay, J.D.; Hipp, A.L.; Manos, P.S. A Genetic Legacy of Introgression Confounds Phylogeny and Biogeography in Oaks. *Proc. Roy. Soc. B.* **2017**, *284*, 20170300. [\[CrossRef\]](#)
25. McVay, J.D.; Hauser, D.; Hipp, A.L.; Manos, P.S. Phylogenomics Reveals a Complex Evolutionary History of Lobed-Leaf White Oaks in Western North America. *Genome* **2017**, *60*, 733–742. [\[CrossRef\]](#)
26. Cavender-Bares, J.; Gonzalez-Rodriguez, A.; Eaton, D.A.R.; Hipp, A.L.; Beulke, A.; Manos, P.S. Phylogeny and Biogeography of the American Live Oaks (*Quercus* Subsection *Virentes*): A Genomic and Population Genetics Approach. *Mol. Ecol.* **2015**, *24*, 3668–3687. [\[CrossRef\]](#) [\[PubMed\]](#)
27. Fitz-Gibbon, S.; Hipp, A.L.; Pham, K.K.; Manos, P.S.; Sork, V. Phylogenomic Inferences from Reference-Mapped and de Novo Assembled Short-Read Sequence Data Using RADseq Sequencing of California White Oaks (*Quercus* Subgenus *Quercus*). *Genome* **2017**, *60*, 743–755. [\[CrossRef\]](#) [\[PubMed\]](#)
28. Crawl, A.A.; Bruno, E.; Hipp, A.L.; Manos, P.S. Revisiting the Mystery of the Bartram Oak. *Arnoldia* **2020**, *77*, 6–11.
29. McIntyre, D.J. Pollen and Spore Flora of an Eocene Forest, Eastern Axel Heiberg Island. *N.W.T. Geol. Surv. Can. Bull.* **1991**, *403*, 83–97.
30. Liu, Z.; Pagani, M.; Zinniker, D.; DeConto, R.; Huber, M.; Brinkhuis, H.; Shah, S.R.; Leckie, R.M.; Pearson, A. Global Cooling During the Eocene-Oligocene Climate Transition. *Science* **2009**, *323*, 1187–1190. [\[CrossRef\]](#) [\[PubMed\]](#)
31. Little, E.L. *Atlas of United States Trees, Volume 1, Conifers and Important Hardwoods*; Miscellaneous publication; U.S. Dept. of Agriculture, Forest Service: Washington, DC, USA, 1971.
32. Little, E.L. *Atlas of United States Trees, Volume 4, Minor Eastern Hardwoods*; Miscellaneous publication; U.S. Dept. of Agriculture, Forest Service: Washington, DC, USA, 1977.
33. Pham, K.K.; Hipp, A.L.; Manos, P.S.; Cronn, R.C. A Time and a Place for Everything: Phylogenetic History and Geography as Joint Predictors of Oak Plastome Phylogeny. *Genome* **2017**, *60*, 720–732. [\[CrossRef\]](#)



34. Muller, C.H. The Live Oaks of the Series Virentes. *Am. Midl. Nat.* **1961**, *65*, 17–39. [\[CrossRef\]](#)
35. Sork, V.L.; Riordan, E.; Gugger, P.F.; Fitz-Gibbon, S.; Wei, X.; Ortego, J. Phylogeny and Introgression of California Scrub White Oaks (*Quercus* Section *Quercus*). *Int. Oaks* **2016**, *27*, 61–74.
36. Eaton, D.A.R.; Hipp, A.L.; González-Rodríguez, A.; Cavender-Bares, J. Historical Introgression among the American Live Oaks and the Comparative Nature of Tests for Introgression. *Evolution* **2015**, *69*, 2587–2601. [\[CrossRef\]](#) [\[PubMed\]](#)
37. Crawl, A.A.; Manos, P.S.; McVay, J.D.; Lemmon, A.R.; Lemmon, E.M.; Hipp, A.L. Uncovering the Genomic Signature of Ancient Introgression between White Oak Lineages (*Quercus*). *New Phytol.* **2020**, *226*, 1158–1170. [\[CrossRef\]](#)
38. Muir, G.; Fleming, C.C.; Schlötterer, C. Species Status of Hybridizing Oaks. *Nature* **2000**, *405*, 1016. [\[CrossRef\]](#)
39. Pearse, I.S.; Hipp, A.L. Phylogenetic and Trait Similarity to a Native Species Predict Herbivory on Non-Native Oaks. *Proc. Natl. Acad. Sci. USA* **2009**, *106*, 18097–18102. [\[CrossRef\]](#)
40. Hipp, A.L. Should Hybridization Make Us Skeptical of the Oak Phylogeny? *Int. Oak J.* **2015**, *26*, 9–18.
41. Hipp, A.L. Oak Research in 2015: A Snapshot from the IOS Conference. *Int. Oak J.* **2016**, *27*, 15–22.
42. Craft, K.J.; Ashley, M.V.; Koenig, W.D. Limited Hybridization between *Quercus lobata* and *Quercus douglasii* (Fagaceae) in a Mixed Stand in Central Coastal California. *Am. J. Bot.* **2002**, *89*, 1792–1798. [\[CrossRef\]](#) [\[PubMed\]](#)
43. Hipp, A.L.; Weber, J.A. Taxonomy of Hill’s Oak (*Quercus ellipsoidalis*: Fagaceae): Evidence from AFLP Data. *Syst. Bot.* **2008**, *33*, 148–158. [\[CrossRef\]](#)
44. Lepais, O.; Petit, R.J.; Guichoux, E.; Lavabre, J.E.; Alberto, F.; Kremer, A.; Gerber, S. Species Relative Abundance and Direction of Introgression in Oaks. *Mol. Ecol.* **2009**, *18*, 2228–2242. [\[CrossRef\]](#) [\[PubMed\]](#)
45. Curtu, A.L.; Gailing, O.; Leinemann, L.; Finkeldey, R. Genetic Variation and Differentiation within a Natural Community of Five Oak Species (*Quercus* spp.). *Plant Biol.* **2007**, *9*, 116–126. [\[CrossRef\]](#) [\[PubMed\]](#)
46. Gailing, O.; Curtu, A.L. Interspecific Gene Flow and Maintenance of Species Integrity in Oaks. *Ann. For. Res.* **2014**, *57*, 5–18. [\[CrossRef\]](#)
47. Dodd, R.; Papper, P. Disentangling the Phylogenetic Network of the California Red Oaks. *Int. Oaks* **2019**, *30*, 203–208.
48. Valencia-A, S. Species Delimitation in the Genus *Quercus* (Fagaceae). *Bot. Sci.* **2021**, *99*, 1–12. [\[CrossRef\]](#)
49. Hipp, A.L.; Whittemore, A.T.; Garner, M.; Hahn, M.; Fitzek, E.; Guichoux, E.; Cavender-Bares, J.; Gugger, P.F.; Manos, P.S.; Pearse, I.S.; et al. Genomic Identity of White Oak Species in an Eastern North American Syngameon. *Ann. Mo. Bot. Garden* **2019**, *104*, 455–477. [\[CrossRef\]](#)
50. Van Valen, L. Ecological Species, Multispecies, and Oaks. *Taxon* **1976**, *25*, 233–239. [\[CrossRef\]](#)
51. Burger, W.C. The Species Concept in *Quercus*. *Taxon* **1975**, *24*, 45–50. [\[CrossRef\]](#)
52. Hardin, J.W. Hybridization and Introgression in *Quercus alba*. *J. Arnold Arbor.* **1975**, *56*, 336–363.
53. Kremer, A.; Hipp, A.L. Oaks: An Evolutionary Success Story. *New Phytol.* **2020**, *226*, 987–1011. [\[CrossRef\]](#) [\[PubMed\]](#)
54. Fitzek, E.; Delcamp, A.; Guichoux, E.; Hahn, M.; Lobdell, M.; Hipp, A.L. A Nuclear DNA Barcode for Eastern North American Oaks and Application to a Study of Hybridization in an Arboretum Setting. *Ecol. Evol.* **2018**, *8*, 5837–5851. [\[CrossRef\]](#) [\[PubMed\]](#)
55. Guichoux, E.; Lagache, L.; Wagner, S.; Léger, P.; Petit, R.J. Two Highly Validated Multiplexes (12-Plex and 8-Plex) for Species Delimitation and Parentage Analysis in Oaks (*Quercus* spp.). *Mol. Ecol. Resour.* **2011**, *11*, 578–585. [\[CrossRef\]](#)
56. Rieseberg, L.H.; Wood, T.E.; Baack, E.J. The Nature of Plant Species. *Nature* **2006**, *440*, 524–527. [\[CrossRef\]](#)
57. Moran, E.V.; Willis, J.; Clark, J.S. Genetic Evidence for Hybridization in Red Oaks (*Quercus* Sect. *Lobatae*, Fagaceae). *Am. J. Bot.* **2012**, *99*, 92–100. [\[CrossRef\]](#)
58. Aldrich, P.R.; Parker, G.R.; Michler, C.H.; Romero-Severson, J. Whole-Tree Silvic Identifications and the Microsatellite Genetic Structure of a Red Oak Species Complex in an Indiana Old-Growth Forest. *Can. J. For. Res.* **2003**, *33*, 2228–2237. [\[CrossRef\]](#)
59. Owusu, S.A.; Sullivan, A.R.; Weber, J.A.; Hipp, A.L.; Gailing, O. Taxonomic Relationships and Gene Flow in Four North American *Quercus* Species (*Quercus* Section *Lobatae*). *Syst. Bot.* **2015**, *40*, 510–521. [\[CrossRef\]](#)
60. Scotti-Saintagne, C.; Mariette, S.; Porth, I.; Goicoechea, P.G.; Barreneche, T.; Bodenes, C.; Burg, K.; Kremer, A. Genome Scanning for Interspecific Differentiation between Two Closely Related Oak Species [*Quercus robur* L. and *Q. petraea* (Matt.) Liebl.]. *Genetics* **2004**, *168*, 1615–1626. [\[CrossRef\]](#) [\[PubMed\]](#)
61. Garner, M.; Pham, K.K.; Whittemore, A.T.; Cavender-Bares, J.; Gugger, P.F.; Manos, P.S.; Pearse, I.S.; Hipp, A.L. From Manitoba to Texas: A Study of the Population Genetic Structure of Bur Oak (*Quercus macrocarpa*). *Int. Oaks J. Int. Oak Soc.* **2019**, *30*, 131–138.
62. Hipp, A.L.; Eaton, D.A.R.; Cavender-Bares, J.; Fitzek, E.; Nipper, R.; Manos, P.S. A Framework Phylogeny of the American Oak Clade Based on Sequenced RAD Data. *PLoS ONE* **2014**, *9*, e93975. [\[CrossRef\]](#) [\[PubMed\]](#)
63. Manos, P.S. *Cladistic Analyses of Molecular Variation of “Higher” Hamamelididae and Fagaceae, and Systematics of Quercus Section Protobalanus*; Cornell University: Ithaca, NY, USA, 1993.
64. Manos, P.S. Foliar Trichome Variation in *Quercus* section *Protobalanus* (Fagaceae). *Sida Contrib. Bot.* **1993**, *15*, 391–403.
65. Ashley, M.V.; Backs, J.R.; Kindsvater, L.; Abraham, S.T. Genetic Variation and Structure in an Endemic Island Oak, *Quercus tomentella*, and Mainland Canyon Oak, *Quercus chrysolepis*. *Int. J. Plant Sci.* **2018**, *179*, 151–161. [\[CrossRef\]](#)
66. May, M.R.; Provance, M.C.; Sanders, A.C.; Ellstrand, N.C.; Ross-Ibarra, J. A Pleistocene Clone of Palmer’s Oak Persisting in Southern California. *PLoS ONE* **2009**, *4*, e8346. [\[CrossRef\]](#)
67. Ortego, J.; Gugger, P.F.; Sork, V.L. Genomic Data Reveal Cryptic Lineage Diversification and Introgression in Californian Golden Cup Oaks (section *Protobalanus*). *New Phytol.* **2018**, *218*, 804–818. [\[CrossRef\]](#)



68. Zumwalde, B.A.; McCauley, R.A.; Fullinwider, I.J.; Duckett, D.; Spence, E.; Hoban, S. Genetic, Morphological, and Environmental Differentiation of an Arid-Adapted Oak with a Disjunct Distribution. *For. Trees Livelihoods* **2021**, *12*, 465. [\[CrossRef\]](#)
69. Tucker, J.M. Studies in the *Quercus undulata* Complex. IV. The Contribution of *Quercus havardii*. *Am. J. Bot.* **1970**, *57*, 71–84. [\[CrossRef\]](#)
70. Bouchal, J.; Zetter, R.; Grímsson, F.; Denk, T. Evolutionary Trends and Ecological Differentiation in Early Cenozoic Fagaceae of Western North America. *Am. J. Bot.* **2014**, *101*, 1332–1349. [\[CrossRef\]](#) [\[PubMed\]](#)
71. Ortego, J.; Gugger, P.F.; Sork, V.L. Climatically Stable Landscapes Predict Patterns of Genetic Structure and Admixture in the Californian Canyon Live Oak. *J. Biogeogr.* **2015**, *42*, 328–338. [\[CrossRef\]](#)
72. Trelease, W. The American Oaks. *Mem. Natl. Acad. Sci.* **1924**, *20*, 1–255.
73. Camus, A.A. *Monographie Du Genre Quercus. Tome I. Genre Quercus. Sous-Genre Cyclobalanopsis et Sous-Genre Euquercus (Section Cerris et Mesobalanu)*; Encyclopédie économique de sylviculture VI.; Editions Paul Lechevalier: Paris, France, 1936.
74. Camus, A.A. *Monographie Du Genre Quercus. Tome II. Genre Quercus. Sous-Genre Euquercus (sections Lepidobalanus et Macrobalanus)*; Encyclopédie économique de sylviculture VII.; Editions Paul Lechevalier: Paris, France, 1938.
75. Camus, A.A. *Monographie Du Genre Quercus. Tome III. Genre Quercus. Sous-Genre Euquercus (sections Protobalanus et Erythrobalanus)*; Encyclopédie économique de sylviculture VIII.; Editions Paul Lechevalier: Paris, France, 1952.
76. Denk, T.; Grimm, G.W. The Oaks of Western Eurasia: Traditional Classifications and Evidence from Two Nuclear Markers. *Taxon* **2010**, *59*, 351–366. [\[CrossRef\]](#)
77. Fick, S.E.; Hijmans, R.J. WorldClim 2: New 1-Km Spatial Resolution Climate Surfaces for Global Land Areas. *Int. J. Climatol.* **2017**, *37*, 4302–4315. [\[CrossRef\]](#)
78. Brown, R. XXX.—Descriptions of Some New or Little-Known Species of Oaks from North-West America. *Ann. Mag. Nat. Hist.* **1871**, *7*, 249–256. [\[CrossRef\]](#)
79. Hipp, A.L. Pharaoh's Dance: The Oak Genomic Mosaic. *Int. Oaks J. Int. Oak Soc.* **2019**, *30*, 53–62.
80. Nixon, K.C. A Biosystematic Study of *Quercus* Series Virentes (the Live Oaks) with Phylogenetic Analyses of Fagales, Fagaceae and *Quercus*. Ph.D. Dissertation, University of Texas, Austin, TX, USA, 1985.
81. Cavender-Bares, J.; Pahlich, A. Molecular, Morphological, and Ecological Niche Differentiation of Sympatric Sister Oak Species, *Quercus virginiana* and *Q. geminata* (Fagaceae). *Am. J. Bot.* **2009**, *96*, 1690–1702. [\[CrossRef\]](#) [\[PubMed\]](#)
82. Muller, C.H. Relictual Origins of Insular Endemics in *Quercus*. In *Proceedings of the Symposium on the Biology of the Channel Islands*; Philbrick, R.N., Ed.; Santa Barbara Botanic Garden: Santa Barbara, CA, USA, 1967; pp. 73–77.
83. Valencia-Avalos, S. Diversidad Del Género *Quercus* (Fagaceae) En México. *Boletín Soc. Botánica México* **2004**, *75*, 33–53.
84. Nixon, K.C. Global and neotropical distribution and diversity of oak (genus *Quercus*) and oak forests. In *Ecology And Conservation of Neotropical Montane Oak Forests*; Springer: Berlin/Heidelberg, Germany, 2006; pp. 3–13.
85. Avella Muñoz, A.; Rangel Churio, J.O. Oak forests types of *Quercus humboldtii* in the Guantiva-La Rusia-Iguaque Corridor (Santandr-Boyacá, Colombia). *Colomb. For.* **2014**, *17*, 100–116. [\[CrossRef\]](#)
86. Fernández-M., J.F.; Sork, V.L. Genetic Variation in Fragmented Forest Stands of the Andean Oak *Quercus humboldtii* Bonpl. (Fagaceae). *Biotropica* **2007**, *39*, 72–78. [\[CrossRef\]](#)
87. Nixon, K.C. Infrageneric Classification of *Quercus* (Fagaceae) and Typification of Sectional Names. *Ann. Sci. For.* **1993**, *50*, 25–34. [\[CrossRef\]](#)
88. Jensen, R.J. *Quercus* Linnaeus sect. *Lobatae* Loudon. In *Flora of North America, North of Mexico*; Flora of North America Editorial Committee, Ed.; Oxford University Press: New York, NY, USA, 1997; Volume 3, pp. 447–468.
89. Griswold, E.; Still, S.; McNeil-Marshall, A. Scouting and Collecting Rare Oaks in the Trans-Pecos for Ex-Situ Conservation, 2016. *Int. Oaks J. Int. Oak Soc.* **2018**, *29*, 125–142.
90. Muller, C.H. The oaks of Texas. In *Contributions from Texas Research Foundations*; Lundell, C.L., Ed.; Texas Research Foundation: Renner, TX, USA, 1951; pp. 40–41.
91. Torres-Miranda, A.; Luna-Vega, I.; Oyama, K. Conservation Biogeography of Red Oaks (*Quercus*, Section *Lobatae*) in Mexico and Central America. *Am. J. Bot.* **2011**, *98*, 290–305. [\[CrossRef\]](#) [\[PubMed\]](#)
92. Torres-Miranda, A.; Luna-Vega, I.; Oyama, K. New Approaches to the Biogeography and Areas of Endemism of Red Oaks (*Quercus* L., Section *Lobatae*). *Syst. Biol.* **2013**, *62*, 555–573. [\[CrossRef\]](#)
93. Rodríguez-Correa, H.; Oyama, K. How Are Oaks Distributed in the Neotropics? A Perspective from Species Turnover, Areas of Endemism, and Climatic Niches. *Int. J. Plant Sci.* **2015**, *176*, 222–231. [\[CrossRef\]](#)
94. Keuter, A.; Manos, P.S. Agrifoliae: The California Red Oaks. *Int. Oaks J. Int. Oak Soc.* **2019**, *30*, 191–202.
95. Dodd, R.S.; Afzal-Rafii, Z. Selection and Dispersal in a Multispecies Oak Hybrid Zone. *Evolution* **2004**, *58*, 261–269. [\[CrossRef\]](#) [\[PubMed\]](#)
96. Jensen, R.J. Identifying Oaks: The Hybrid Problem. *J. Int. Oak Soc.* **1995**, *6*, 47–54.
97. Cottam, W.P.; Tucker, J.M.; Santamour, F.S. *Oak Hybridization at the University of Utah*; State Arboretum of Utah: Salt Lake City, UT, USA, 1982.
98. Axelrod, D.I. Biogeography of Oaks in the Arcto-Tertiary Province. *Ann. Mo. Bot. Gard.* **1983**, *70*, 629–657. [\[CrossRef\]](#)
99. Mensing, S. The Paleohistory of California Oaks. In *Proceedings of the Seventh California Oak Symposium: Managing Oak Woodlands in a Dynamic World*; USDA Forest Service General Technical Reports PSW-GTR-251; Pacific Southwest Research Station: Berkeley, CA, USA, 2014; pp. 35–48.

100. Mensing, S. The History of Oak Woodlands in California, Part I: The Paleoeologic Record. *Calif. Geogr.* **2005**, *45*, 1–38.
101. Jensen, R.J. A Preliminary Numerical Analysis of the Red Oak Complex in Michigan and Wisconsin USA. *Taxon* **1977**, *26*, 399–407. [[CrossRef](#)]
102. Manos, P.S.; Fairbrothers, D.E. Allozyme Variation in Populations of Six Northeastern American Red Oaks (Fagaceae: *Quercus* Subg. *Erythrobalanus*). *Syst. Bot.* **1987**, *12*, 265–373. [[CrossRef](#)]
103. Guttman, S.I.; Weigt, L.A. Electrophoretic Evidence of Relationships among *Quercus* (oaks) of Eastern North America. *Can. J. Bot.* **1989**, *67*, 339–351. [[CrossRef](#)]
104. Hess, W.J.; Stoyanoff, N.A. Taxonomic Status of *Quercus acerifolia* (Fagaceae) and a Morphological Comparison of Four Members of the *Quercus shumardii* Complex. *Syst. Bot.* **1998**, *23*, 89–100. [[CrossRef](#)]
105. Stoyanoff, N.; Hess, W.J. A New Status for *Quercus shumardii* var. *acerifolia* (Fagaceae). *SIDA Contrib. Bot.* **1990**, *14*, 267–271.
106. McDougal, K.M.; Parks, C.R. Elevational Variation in Foliar Flavonoids of *Quercus rubra* L. (Fagaceae). *Am. J. Bot.* **1984**, *71*, 301–308. [[CrossRef](#)]
107. Weakley, A.S. Flora of the Southeastern United States. University of North Carolina Herbarium (NCU), North Carolina Botanical Garden: Chapel Hill, NC, USA, 2020.
108. Trelease, W. The Jack Oak (*Quercus ellipsoidalis*). *Trans. Ill. State Acad. Sci.* **1919**, *12*, 108–118.
109. Jensen, R.J. Lectotypification of *Quercus ellipsoidalis* E.J. Hill. *Taxon* **1979**, *29*, 154–155. [[CrossRef](#)]
110. Maycock, P.F.; Daniel, D.R.; Gregory, R.; Reznicek, A.A. Hill's Oak (*Quercus ellipsoidalis*) in Canada. *Can. Field Nat.* **1980**, *94*, 277–285.
111. Ball, P.W. Hills Oak (*Quercus ellipsoidalis*) in Southern Ontario, Canada. *Can. Field Nat.* **1981**, *95*, 281–286.
112. Overlease, W.R. Genetic Relationships between Three Species of Oaks as Determined by Common Garden Studies with Populations from Michigan, Indiana and Wisconsin. *J. Pa. Acad. Sci.* **1991**, *65*, 71–74.
113. Jensen, R.J.; Depiero, R.; Smith, B.K. Vegetative Characters, Population Variation, and the Hybrid Origin of *Quercus ellipsoidalis*. *Am. Midl. Nat.* **1984**, *111*, 364–370. [[CrossRef](#)]
114. Wadmond, S.C. The *Quercus ellipsoidalis*–*Quercus coccinea* Complex. *Trans. Wisc. Acad. Sci. Arts Lett.* **1933**, *28*, 197–203.
115. Overlease, W.R. A Study of the Relationship between Scarlet Oak (*Quercus coccinea* Muenchh.) and Hill Oak (*Quercus ellipsoidalis* E.J. Hill) in Michigan and Nearby States. *J. Pa. Acad. Sci.* **1977**, *51*, 47–50.
116. Shepard, D.A. The Legitimacy of *Quercus ellipsoidalis* Based on a Populational Study of *Quercus coccinea* in Illinois. Western Illinois University: Macomb, IL, USA, 1993.
117. Shepard, D.A. A Review of the Taxonomic Status of *Quercus ellipsoidalis* and *Quercus coccinea* in the Eastern United States. *Int. Oak J.* **2009**, *20*, 65–84.
118. Hipp, A.L.; Weber, J.A.; Srivastava, A. Who Am I This Time? The Affinities and Misbehaviors of Hill's Oak (*Quercus ellipsoidalis*). *Int. Oak J.* **2010**, *21*, 27–36.
119. Zhang, R.; Hipp, A.L.; Gailing, O. Sharing of Chloroplast Haplotypes among Red Oak Species Suggests Interspecific Gene Flow between Neighboring Populations. *Botany* **2015**, *93*, 691–700. [[CrossRef](#)]
120. Hokanson, S.C.; Isebrands, J.G.; Jensen, R.J.; Hancock, J.F. Isozyme Variation in Oaks of the Apostle Islands in Wisconsin: Genetic Structure and Levels of Inbreeding in *Quercus rubra* and *Q. ellipsoidalis* (Fagaceae). *Am. J. Bot.* **1993**, *80*, 1349–1357. [[CrossRef](#)]
121. Sullivan, A.R.; Owusu, S.A.; Weber, J.A.; Hipp, A.L.; Gailing, O. Hybridization and Divergence in Multi-Species Oak (*Quercus*) Communities. *Bot. J. Linn. Soc.* **2016**, *181*, 99–114. [[CrossRef](#)]
122. Khodwekar, S.; Gailing, O. Evidence for Environment-Dependent Introgression of Adaptive Genes between Two Red Oak Species with Different Drought Adaptations. *Am. J. Bot.* **2017**, *104*, 1088–1098. [[CrossRef](#)] [[PubMed](#)]
123. Lind-Riehl, J.F.; Sullivan, A.R.; Gailing, O. Evidence for Selection on a CONSTANS-like Gene between Two Red Oak Species. *Ann. Bot.* **2014**, *113*, 967–975. [[CrossRef](#)]
124. Noss, R.F.; Platt, W.J.; Sorrie, B.A.; Weakley, A.S.; Means, D.B.; Costanza, J.; Peet, R.K. How Global Biodiversity Hotspots May Go Unrecognized: Lessons from the North American Coastal Plain. *Divers. Distrib.* **2015**, *21*, 236–244. [[CrossRef](#)]
125. Hunt, D.M. *A Systematic Review of Quercus Series Laurifoliae, Marilandicae and Nigrae*; University of Georgia: Athens, GA, USA, 1990.
126. Ortego, J.; Gugger, P.F.; Riordan, E.C.; Sork, V.L. Influence of Climatic Niche Suitability and Geographical Overlap on Hybridization Patterns among Southern Californian Oaks. *J. Biogeogr.* **2014**, *41*, 1895–1908. [[CrossRef](#)]
127. Kim, B.Y.; Wei, X.; Fitz-Gibbon, S.; Lohmueller, K.E.; Ortego, J.; Gugger, P.F.; Sork, V.L. RADseq Data Reveal Ancient, but Not Pervasive, Introgression between Californian Tree and Scrub Oak Species (*Quercus* Sect. *Quercus*: Fagaceae). *Mol. Ecol.* **2018**, *27*, 4556–4571. [[CrossRef](#)] [[PubMed](#)]
128. Tucker, J.M. Studies in the *Quercus undulata* Complex. I. A Preliminary Statement. *Am. J. Bot.* **1961**, *48*, 202. [[CrossRef](#)]
129. Howard, D.J.; Preszler, R.W.; Williams, J.; Fenchel, S.; Boecklen, W.J. How Discrete Are Oak Species? Insights from a Hybrid Zone between *Quercus grisea* and *Quercus gambelii*. *Evolution* **1997**, *51*, 747–755. [[CrossRef](#)]
130. Maze, J. Past Hybridization between *Quercus macrocarpa* and *Quercus gambelii*. *Brittonia* **1968**, *20*, 321–333. [[CrossRef](#)]
131. Leroy, T.; Roux, C.; Villate, L.; Bodénès, C.; Romiguier, J.; Paiva, J.A.P.; Dossat, C.; Aury, J.-M.; Plomion, C.; Kremer, A. Extensive Recent Secondary Contacts between Four European White Oak Species. *New Phytol.* **2017**, *214*, 865–878. [[CrossRef](#)]
132. Nixon, K.C.; Muller, C.H. *Quercus* Linnaeus sect. *Quercus*. In *Flora of North America*; Flora of North America Editorial Committee, Ed.; Oxford University Press: New York, NY, USA, 1997; Volume 3, pp. 471–506.

- 
133. Tucker, J.M. Studies in the *Quercus undulata* Complex. III. The Contribution of *Q. arizonica*. *Am. J. Bot.* **1963**, *50*, 699–708. [[CrossRef](#)]
  134. Swenson, N.G.; Fair, J.M.; Heikoop, J. Water Stress and Hybridization between *Quercus gambelii* and *Quercus grisea*. *West. N. Am. Nat.* **2008**, *68*, 498–507. [[CrossRef](#)]
  135. Nixon, K.C.; Steele, K.P. A New Species of *Quercus* (Fagaceae) from Southern California. *Madroño* **1981**, *28*, 210–219.
  136. Rundel, P.W.; Arroyo, M.T.K.; Cowling, R.M.; Keeley, J.E.; Lamont, B.B.; Vargas, P. Mediterranean Biomes: Evolution of Their Vegetation, Floras, and Climate. *Annu. Rev. Ecol. Evol. Syst.* **2016**, *47*, 383–407. [[CrossRef](#)]
  137. Burge, D.O.; Parker, V.T.; Mulligan, M.; Sork, V.L. Influence of a Climatic Gradient on Genetic Exchange between Two Oak Species. *Am. J. Bot.* **2019**, *106*, 864–878. [[CrossRef](#)]
  138. Hardin, J.W. Patterns of Variation in Foliar Trichomes of Eastern North American *Quercus*. *Am. J. Bot.* **1979**, *66*, 576–585. [[CrossRef](#)]
  139. Thomson, P.M.; Mohlenbrock, R.H. Foliar Trichomes of *Quercus* Subgenus *Quercus* in the Eastern United States. *J. Arnold Arbor.* **1979**, *60*, 350–366.
  140. Duncan, W.H. *Quercus oglethorpensis*—Range Extensions and Phylogenetic Relationships. *Lloydia* **1950**, *13*, 243–248.
  141. Nixon, K.C.; Muller, C.H. The Taxonomic Resurrection of *Quercus laceyi* Small (Fagaceae). *SIDA Contrib. Bot.* **1992**, *15*, 57–69.
  142. Axelrod, D.I. Evolution of the Madro-Tertiary Geoflora. *Bot. Rev.* **1958**, *24*, 433–509. [[CrossRef](#)]
  143. Van Devender, T.R.; Spaulding, W.G. Development of Vegetation and Climate in the Southwestern United States. *Science* **1979**, *204*, 701–710. [[CrossRef](#)] [[PubMed](#)]
  144. Backs, J.R. Genetic Analysis of a Rare Isolated Species: A Tough Little West Texas Oak, *Quercus hinckleyi* C.H. Mull. *J. Torrey Bot.* **2015**, *142*, 302–313. [[CrossRef](#)]