

FLORISTIC INVESTIGATIONS OF THE OZARK PLATEAU NATIONAL WILDLIFE
REFUGE AND THE GENUS *QUERCUS* IN OKLAHOMA

By

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PREFACE

This thesis comprises two chapters, each of which encompasses one aspect of my master's research conducted between 2006 and the present. Written in the format of papers appearing in the *Proceedings of the Oklahoma Academy of Science*, Chapter I describes the results of a floristic survey of three tracts of the Ozark Plateau National Wildlife Refuge located in the Boston Mountains ecoregion in Adair County, Oklahoma. Written in more or less traditional thesis format, Chapter II offers a taxonomic treatment of the genus *Quercus* in Oklahoma which is to be incorporated in the forthcoming *Flora of Oklahoma*. The taxonomic keys for the sections and species of the genus have already been inserted in *Keys and Descriptions of the Vascular Plants of Oklahoma*.

Partial financial support for my floristic work on the Ozark Plateau National Wildlife Refuge was provided by the U.S. Fish and Wildlife Service. I offer special thanks to refuge manager Steve Hensley for providing financial support and assisting me in conducting my research. I also offer special thanks to Ronald J. Tyrl for serving as my major professor, contributing to my training as a taxonomist, and offering encouragement throughout my program. Thanks are due several individuals for their contributions: Patricia Folley for confirming and annotating my collections of specimens in the Cyperaceae; Michael Powell for examining my specimens of *Quercus* from Cimarron County, allowing me access to the Herbarium at the Sul Ross State University, and giving me a map with hand written directions for finding the species of *Quercus* in Big Bend National Park and the Guadalupe Mountains; Clayton Russell for treating me like family during my many collecting trips to the Gittin Down Mountain Tract; and Claude Liver for his hospitality and interesting stories. I offer additional

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CHAPTER I

A CHECKLIST OF THE VASCULAR PLANTS ENCOUNTERED IN THE GITTIN DOWN MOUNTAIN, LIVER, AND VARMINT TRACTS OF THE OZARK PLATEAU NATIONAL WILDLIFE REFUGE IN ADAIR COUNTY, OKLAHOMA

ABSTRACT

In a two-year (2007–2009) inventory of the Gittin Down Mountain, Liver and Varmint tracts of the Ozark Plateau National Wildlife Refuge in Adair County, Oklahoma, 392 species in 275 genera and 85 families were encountered. Three hundred sixty (91.8%) of the species were native to North America. Constituting 23.6% of the flora, the Asteraceae and Poaceae were the largest families. *Quercus*, *Carex*, *Desmodium*, and *Dichanthelium* were the largest genera present. Eighty-two species were new records for Adair County. Species designated threatened or endangered by The Endangered Species Program of the United States Fish & Wildlife Service were not discovered. Thirteen species—*Brachyelytrum erectum*, *Carex cephalophora*, *Castanea pumila* var. *ozarkensis*, *Clematis virginiana*, *Corallorhiza odontorhiza*, *Desmodium pauciflorum*, *Dicentra cucullaria*, *Dryopteris felix-mas*, *Elymus hystrix*, *Monotropa uniflora*, *Silene regia*, *Triphora trianthophora*, and *Urtica dioica*—designated rare (S1 or S2) by the Oklahoma Natural Heritage Inventory were documented as present.

INTRODUCTION

Encompassing approximately 1,215 hectares in eight disjunct tracts throughout northeastern Oklahoma, the Ozark Plateau National Wildlife Refuge (OPNWR) was established in 1985 by the U.S. Fish and Wildlife Service (USFWS). These tracts were protected because of the cave hibernacula that they provide for the federally listed endangered *Myotis grisescens* (gray bat), *Myotis sodalis* (Indiana bat), and *Corynorhinus townsendii ingens* (big eared bat). Use of these caves by bats and other mammals such as bear and tapir has been dated by skeletal remains to the last Ice Age (Czaplewski et al., 2002). In addition, these caves also are critical habitat for the federally listed endangered *Cambarus aculabrum* (cave crayfish), and threatened *Amblyopsis rosae* (ozark cave fish) and *Noturus placidus* (Neosho madtom) (USFWS, 2002). Restriction of these species to these areas/caves is believed to be the result of deforestation, pollution, and other anthropogenic disturbances in their natural ranges (USFWS, 2002; O'Shea and Brogan, 2003; Hensley, 2004). Caves on the refuge have been gated to eliminate or minimize further human disturbance.

An additional function of the OPNRW is the protection of large continuous stands of Ozark forest essential for migratory birds nesting in interior forests (USFWS, 2002).

The refuge was known initially as the Oklahoma Bat Caves National Wildlife Refuge until 1995 when the name was changed to reflect a change to the ecosystem approach to cave management and protection (Hammond, 2009). As the refuge has evolved the USFWS has partnered with a number of other agencies and groups including: the Oklahoma Department of Wildlife Conservation, The Nature Conservancy, the Trust for Public Lands, The Oklahoma Natural Heritage Inventory, the Arkansas

Game and Fish Commission, the U.S. Forest Service, the Cherokee Nation, Oklahoma university, conservation and caving organizations, and private land owners (USFWS, 2000; Hensley, 2004).

A crucial aspect of the ecosystem approach to management of the OPNWR is a thorough knowledge of the plants and vegetation present. Surveys of the refuge's vascular flora formally began with the work of Hayes (2003) on the Sally Bull Hollow Tract in Adair County. Gard (2009) continued her inventory of the hollow and also survey adjacent parcels of land known as the Eagle Pass and Workman Mountain Tracts. The inventories reported in this thesis are of the Gittin Down Mountain, Liver, and Varmint Tracts, also in Adair County but approximately four to ten km further west. Objectives of this work were four: (1) to compile a list of the woody and herbaceous species present in each tract; (2) to provide, using GPS coordinates, a summary of the geographical locations of any species listed as "rare" by the Oklahoma Natural Heritage Inventory (2006); and (3) to prepare two sets of voucher specimens documenting the species present. This work will provide baseline information that can be used in making decisions about the management of the refuge's vegetation. The summary of locations of rare taxa will facilitate monitoring of these species. The voucher specimens will provide a permanent record of the refuge's flora and provide a reference resource for refuge personnel.

ECOGEOGRAPHY OF THE OPNWR REGION IN ADAIR COUNTY

Geology & Soils—The OPNWR and Adair County are situated in the Boston Mountains Level III ecoregion (Woods et al., 2005) at the southwest edge of the area

commonly known as the Oklahoma Ozarks. Comprising a series of fault blocks with steep escarpment faces and gentle dip slopes visible as irregular hills and ridges separated by narrow and broad valleys, this area is considered to have the roughest topography of the Ozarks (Soil Conservation Service, 1965; Unklesbay and Vineyard, 1992). The meandering creeks and intermittent streams have cut through the ridges and the major drainages are parallel to the fault lines which, in general, have a northeast orientation (Soil Conservation Service, 1965). Their sources are seepage (trickles) from escarpment faces, heavy flows from the mouths of upland caves, or a few springs that flow year-round (Goodman, 1977).

The parent rock strata of the region are limestone, sandstone, and marine shale of the Pennsylvanian and Mississippian ages (Branson and Johnson, 1972), with Atoka sandstone of the Pennsylvanian typically forming the surface rocks (Soil Conservation Service, 1965). Weathering of the limestone imparts the characteristic variability of the region—sinkholes, ridges, crevices, caves, and troughs (Goodman, 1977). Caves are formed from weathering processes between the Hale layer, in the Lower Morrow series of the Pennsylvanian system, and the Pitkin layer, in the Upper Chesterian series of the Mississippian System (Russell, 1971). The Hale layer often comprises the primary parent material of upland forests while simultaneously acting as a ceiling above all cave entrances and hallways. Roots are visible along the ceiling of certain corridors of the caves.

Soils in this region are generally highly weathered ultisols characteristic of temperate/humid climates under forest vegetation (Hoagland, 2000). The Soil Conservation Service (1965) cites four series—Hector, Linker, Etowah, and

Greendale— and five associations—Linker Fine Sandy Loams, Hector-Linker Fine Sandy Loams, Hector Complex, Bodine Silt Loams, Etowah-Greendale—to be present in various parts of the refuge. Along the ridgelines the Hector complex and Hector-Linker Fine Sandy Loams occur. In the valley floors and creek beds, Bodine Silt Loams and Etowah-Greendale soils dominate. Linker Fine Sandy Loams are frequently associated with seasonally moist embankments of the lowland creek drainages.

Climate—Adair County’s climate is characterized as warm-temperate with cool winters and hot humid summers (Oklahoma Climatological Survey, 2008). Average annual precipitation is 111 cm. March and April are typically the wettest months, whereas August and September are the driest. With irregular showers and storms occurring throughout the year, annual precipitation can vary considerably. The town of Stillwell located approximately 5 km northeast of the three tracts received 130 cm of precipitation in 2001, but only 107 cm in 2002 (Oklahoma Climatological Survey, 2002). The average growing season is 203 days, with the last spring freeze about 8 April and the first fall freeze about 28 October (Johnson and Duchon, 1995).

Vegetation—The natural vegetation of the Boston Mountains ecoregion is primarily oak-hickory deciduous forest (Bruner, 1931; Duck and Fletcher, 1943; Vankat, 1992; Woods et al., 2005). Fifteen of the forest associations of Hoagland (2000) are present. The broader valleys have been cleared for pastures. There is no formal account of the fire history of the area. Recollections of local residents such as Clayton Russell, Claude Liver, Neva Kirk, and Nancy Swaney, and Steve Hensley, refuge manager (all personal

communications), indicate that fires occur sporadically, cover areas of varying sizes, and burn until they die out naturally or are extinguished by local firefighters. Personal observations of previously burned areas revealed little damage to both the canopy and understory trees, the fires burning primarily the accumulated understory litter and the grasses and forbs in the forest openings

Although the area is considered to have high botanical diversity (Hoagland, 2000), only one general survey of the flora of the region has been conducted. Charles Wallis (1959) collected 328 species in Adair County for a doctoral dissertation in the 1950s. Surveys of three tracts in the OPNWR were conducted by Hayes (2003) and Gard (2009). The survey reported here thus represents the fourth floristic study of the area.

CHARACTERISTICS OF THE THREE TRACTS

The three tracts surveyed in this study are located in Adair County approximately 5 km south of the town of Stilwell via county roads. The characteristics of each tract are described in the following paragraphs.

Gittin Down Mountain Tract (GDMT)—This tract (35°45'40.18"N and 94°43'45.17"W) encompasses 182 hectares on the top and east-facing slope of a wide ridge oriented more or less North–South. Relief is approximately 100 m (340–440 m) and below the irregularly undulating ridgeline, the east-face consists of gentle to steep rocky slopes and intermittent vertical rock faces. A small stream arising from seeps and springs on the slope flows out of the tract in the southeast corner. This corner also exhibited the

greatest diversity in habitats due to the irregular topography of the slope. The vegetation is dense upland forest with the exception of the of tract's northwest corner which is savannah presumably due to past clearing. The ridgetop and upper portions of the east-facing slope burned in the early spring of 2007, the first year of the collecting reported here.

Liver Tract (LT)— This 41 hectare tract (35°43'21.56"N and 94°44'31.42"W) surrounds the source of Greasy Creek which originates in the saddle between the two tallest hills of a N–S oriented series collectively known as Welch Mountain. The majority of the tract comprises undulating, shallow, north- and south-facing slopes with occasional low escarpments that descend from the relatively level tops of the hills. Elevation ranges between 320 and 400 m on the tract. Near its source in the eastern part of the tract, the broader creek floodplain is bordered by more open forests on the slopes. Westward, the creek floodplain narrows and is bordered by dense forests as it flows into the broad valley on the west side of the tract. Signs of recent fire were not apparent.

Varmint Tract (VT)— This 27 hectare tract (35°43'21.56"N to 94°44'31.42"W) encompasses a small stretch of land primarily on the south side of Tributary No. 22 of Sallisaw Creek which flows to the southeast. The creek is the north edge of a steep, north-facing, boulder laden slope with a distinct bluff line approximately 10 m high. This slope descends from a relatively level upland ridge. Elevation within the tract ranges from 340 to 364 m. Dense forest cover the slope. Signs of fire were not apparent.

METHOD OF SURVEY

The three tracts were visited on 41 occasions during the growing seasons of 2006, 2007, and 2008. Visits began in late March or early April and continued through October of each year. A total of 78 man-days were spent in the field.

Surveying involved traversing each tract repeatedly on foot using topographic maps, compass, and global positioning unit in order to encounter as many different habitats and species as possible. Using compass bearings and topographic maps, transects were established to grid each tract so that it could be searched completely. Depending upon the topography and uniformity of vegetation, the distances between parallel transects varied from 100 to 400 m. In addition, an attempt was made to find as many different ecological habitats—different environments characterized by physical, chemical, and biotic features—as possible (Palmer et al., 1995, 2002; Palmer, 2007). Eleven species listed as S1, S2, or S3 by the Oklahoma Natural Heritage Inventory (ONHI) (2006) were of particular interest.

As the tracts were explored, species were identified and recorded as present. Information about their abundance, habit, features of their habitat, and associated species was recorded in writing. Relative abundance of a species was based on density of populations and the five category system — abundant, frequent, occasional, infrequent, rare—of Palmer and coworkers (1995) was used.

Two or more voucher specimens of each species encountered were collected; one to be deposited in the OSU Herbarium (OKLA) and one to be laminated and given to personnel of the refuge. An attempt was made to collect specimens in flower and/or fruit. Standard collecting and herbarium techniques were used in the preparation of the

specimens and labels (Radford et al., 1974). When plants of species listed as S1, S2, or S3 by ONHI were encountered, they were not collected; rather their presence recorded and the global positioning system (GPS) coordinates of their position recorded for subsequent transmittal to USFWS. Some of the abundant, easily recognized dominant species, e.g., *Fraxinus pennsylvanica*, present in all three tracts were not vouchered, but rather their presence simply recorded in the tract lists.

Identification of unknown species was accomplished by using state and regional floras (Waterfall, 1969; Correll and Johnston, 1970; Flora of the Great Plains Association, 1983; Tyrl et al., 2007) and the resources of the OSU Herbarium. Intraspecific taxa were not identified unless it was necessary to determine a species' rarity on the Oklahoma Natural Heritage Inventory's 2006 *Working List of Rare Oklahoma Plants*.

As the survey progressed, lists of the species in each tract were compiled. The *PLANTS Database* (USDA NRCS, 2009) served as the nomenclatural reference for the scientific and common names used and the designation of each species nativity. At the conclusion of the study, a single list was compiled.

RESULTS and DISCUSSION

Flora of The Three Tracts—Three hundred and ninety-two species in 275 genera, 85 families, 2 classes, and 3 divisions were encountered in this inventory of the three tracts of the OPNWR (Table 1; Appendix I). Constituting 23.6% of the flora, the Asteraceae with 30 genera and 51 species and the Poaceae with 25 genera and 38 species were

the largest families. The largest genera were *Quercus* and *Carex* each with 7 species and *Desmodium* and *Dichantheium* each with 5 species.

Table 1. Taxa encountered in the Gittin Down Mountain, Liver, and Varmint Tracts of the Ozark Plateau National Wildlife Refuge. Intraspecific taxa are not included in the table, because they were only recognized if necessary to determine a species' rarity on the Oklahoma Natural Heritage Inventory's 2006 *Working List of Rare Oklahoma Plants*.

	Families	Genera	Species		Total
			Native	Introduced	
Pteridophyta	4	9	11	0	11
Coniferophyta	2	2	2	0	2
Magnoliophyta					
Magnoliopsida	71	214	280	26	306
Liliopsida	8	50	67	6	73
Total Taxa	85	275	360	32	392

In the Gittin Down Mountain (GDMT) Tract, 311 species in 236 genera and 82 families were encountered. In the Liver Tract (LT) 287 species in 212 genera and 75 families were recorded, whereas in the Varmint Tract, 336 species in 200 genera and 78 families were recorded.

Three hundred sixty of the 392 species encountered in this study (91.8%) were native to North America. This percentage is similar to those reported by Hayes (91.3%; 2003) and Gard (92%; 2009) for other tracts of the refuge in Adair County. In

comparison, the native proportion of the total flora of Oklahoma (2,540 species) is 86% (ONHI, 2006). The 32 introduced species are listed in Table 2. These species were

Table 2. Thirty-two introduced species encountered in the Gittin Down Mountain, Liver, and Varmint Tracts of the Ozark Plateau National Wildlife Refuge, Adair County, Oklahoma.

<i>Achillea millefolium</i> ^a	<i>Lonicera japonica</i>	<i>Saponaria officinalis</i>
<i>Albizia julibrissin</i>	<i>Melilotus officinalis</i>	<i>Setaria pumila</i>
<i>Arctium minus</i>	<i>Microstegium vimineum</i>	<i>Sorghum halepense</i>
<i>Belamcanda chinensis</i>	<i>Nasturtium officinale</i>	<i>Stellaria media</i>
<i>Bromus arvensis</i>	<i>Perilla frutescens</i>	<i>Taraxacum officinale</i>
<i>Datura stramonium</i>	<i>Plantago lanceolata</i>	<i>Trifolium dubium</i>
<i>Ipomoea coccinea</i>	<i>Poa compressa</i>	<i>Trifolium hybridum</i>
<i>Kummerowia stipulacea</i>	<i>Potentilla recta</i>	<i>Verbascum thapsus</i>
<i>Lamium purpureum</i>	<i>Prunus persica</i>	<i>Veronica arvensis</i>
<i>Lespedeza cuneata</i>	<i>Rosa multiflora</i>	<i>Veronica polita</i>
<i>Leucanthemum vulgare</i>	<i>Rumex crispus</i>	

^aThis species is listed as both introduced and native in the *Plants Database* (2009).

encountered along old dirt roads and tracks, ATV trails, and man-made clearings throughout the tracts. With the exception of the annual grasses in the larger clearings, none of these taxa were particularly abundant. *Lespedeza cuneata*, *Lonicera japonica*,

and *Sorghum halepense*, although typically considered invasive had not established large colonies or stands in the three tracts.

Eighty-two species encountered in the three tracts represented new records for Adair County (Hoagland et al., 2004; Appendix 2). Twenty-one of these species were also encountered by Gard (2009) who was surveying the Sally Bull Hollow, Eagle Pass, and Workman Mountain tracts of the refuge at the same time this study was being conducted. The discovery of these new records is not unexpected because of the lack of extensive collecting heretofore. As noted above, only one general survey of the flora of the region has been conducted. Although Charles Wallis (1959) collected 328 species in Adair County, he did not collect in any of the tracts of the OPNWR.

Two plant species—*Platanthera leucophaea*, eastern prairie fringed orchid, and *P. praeclara*, western prairie fringed orchid—designated threatened by The Endangered Species Program of the USFWS (2001) were not encountered. As their common names suggest, they are tallgrass prairie species and such habitats do not occur in the three tracts. Thirteen species designated rare (S1 or S2) in Adair County by the ONHI (2006, 2009) were documented as present in the three tracts (Table 3). This inventory ranks a species' rarity at both state (S) and global (G) levels on a scale of 1–5. A ranking of 1 designates a plant as being critically imperiled (5 or fewer sites of occurrence or very few remaining individuals or acreage); 2 if it is imperiled (6-20 occurrences or few individuals or acreage remaining); 3 if it is rare and local in its range (or found locally in a restricted range with 21-100 sites); 4 if apparently secure, but may be quite rare in parts of its range, especially at the edges; and 5 if demonstrably secure, however it may

be quite rare at the distributional limits of its range (ONHI, 2006). Additionally, a listing of 'T' means the plant is threatened.

Table 3. Taxa designated rare by the Oklahoma Natural Heritage Inventory (2006, 2009) discovered in the Gittin Down Mountain, Liver, and Varmint Tracts of the Ozark Plateau National Wildlife Refuge. Global, federal, and state natural heritage rankings follow the taxon names.

<i>Brachyelytrum erectum</i>	G5	S1		
<i>Carex cephalophora</i>	G5	S2		
<i>Castanea pumila</i> var. <i>ozarkensis</i>	G5	T3	S2	
<i>Clematis virginiana</i>	G5	S1	S2	
<i>Corallorhiza odontorhiza</i>	G5	S1		
<i>Desmodium pauciflorum</i>	G5	S1		
<i>Dicentra cucullaria</i>	G5	S2		
<i>Dryopteris felix-mas</i>	G5	S1		
<i>Elymus hystrix</i>	G5	S2	S3	
<i>Monotropa uniflora</i>	G5	S1		
<i>Silene regia</i>	G3	S1		
<i>Triphora trianthophora</i>	G4	G3	S2	S3
<i>Urtica dioica</i>	G5	S2		

At the time this study was initiated, ONHI (2006) listed only 11 species as rare in Adair County and 5 species on this list were encountered. On 22 December 2009, ONHI

issued an updated list and an additional 7 species were discovered to have been present. GPS coordinates of the populations of the 5 species on the 2006 list were recorded and transmitted directly to Steve Hensley, Refuge Manager of OPNWR.

Observations of Vegetation and Species—Hoagland (2000) recognized 15 forest associations in the area of Adair County occupied by the OPNRW tracts. In this study, no attempt was made to formally identify these associations as the three tracts were surveyed; emphasis was placed on finding as many species as possible.

In the following paragraphs, observations of the vegetation made while collecting species are summarized.

The canopy and subcanopy of the upland forests of all three tracts were dominated by: *Quercus stellata*, *Q. velutina*, *Q. shumardii*, *Q. marilandica*, *Q. falcata*, *Q. rubra*, *Carya cordiformis*, *C. ovata*, *Ulmus rubra*, *U. americana*, *U. alata*, *Cercis canadensis*, *Cornus florida*, *Celtis laevigata*, *Diospyros virginiana*, *Ostrya virginiana*, and *Prunus mexicana*. On the mesic slopes and the northeast-facing slope of Gittin Down Mountain *Q. alba* and *Q. muehlenbergii* were abundant in addition to the other hardwood species.

In the northern part of the GDMT, the oaks form a woodland with distinct openings in the canopy. The woodland is dominated by both red/black and white oak species with the trees having diameters at breast height (DBH) equal to or greater than 40 cm which constitute old-growth size classes as defined by Kennedy and Nowacki (1997). Herbaceous species in this tract also were more abundant than in the other two tracts. *Triophora trianthophora*, *Spiranthes cernua*, and *Monotropa uniflora* were

frequently discovered. In the summer, species encountered included: *Lobelia spicata*, *Salvia azurea*, *Asclepias* spp., *Eryngium yuccifolium*, *Coreopsis palmata*, *Erigeron strigosus*, *Symphotrichum* spp., *Liatris* spp., *Smallanthus uvedalius*, *Toxicodendron radicans*, *Brachyelytrum erectum*, *Chasmanthium latifolia*, *Helianthus hirsutus*, *Croton lindheimerianus*, *Croton monanthogynous*, *Melothria pendula*, *Desmodium* spp., *Lespedeza* spp., *Hypericum punctatum*, *Hypericum hypericoides*, *Pycnanthemum tenuifolium*, *Gillenia stipulata*, *Urtica chamaedryoides*, *Elephantopus carolinianus*, *Phytolacca americana*, and *Solidago missouriensis*.

On shaded slopes in all tracts, localized populations, sometimes quite extensive, of *Diarrhena americana*, *Rubus* spp., *Chasmanthium latifolium*, *Brachyelytrum erectum*, *Symphoricarpos orbiculatus*, *Desmodium* spp., *Rhus aromatica*, and *Toxicodendron radicans* were encountered. Also on these slopes, *Dryopteris felix-mas*, *Polystichum acrostichoides*, *Adiantum pedatum*, *Polygonum* spp., *Sanicula canadensis*, *Urtica* spp., *Impatiens capensis*, *Botrychium biternatum*, *Osmorhiza longistylus*, *Staphylea trifolia*, and *Lindera benzoin* were abundant.

In both the Liver and Varmint tracts, herbs were especially abundant along the creeks. Species included: *Osmorhiza longistylis*, *Impatiens capensis*, *Mimulus alatus*, *Polygonum* spp., *Scrophularia marilandica*, *Samolus valerandi*, *Physalis* spp., *Hydrangea arborescens*, *Cuphea viscosissima*, *Rudbeckia* spp., *Echinacea purpurea*, *Platanus occidentalis*, *Gleditsia triacanthos*, *Dichanthelium* spp., *Urtica* spp., and *Juncus* spp. As an aside, many of the same species were encountered in the southeastern corner of the GDMT associated with a natural spring and the stream to which it gives rise.

In the Varmint Tract, in addition to the herbaceous diversity along the creek, fern species including: *Dryopteris felix-mas*, *Polystichum acrostichoides*, and *Adiantum pedatum* were especially abundant along the escarpment. An ATV trail in the western part of the tract was characterized by the presence of *Kumerowia stipulacea*, *Lespedeza cuneata*, and *Juniperus virginiana*. The eastern portion of the escarpment was dominated by a canopy of large trees of *Quercus rubra* and *Q. velutina* that formed a dense canopy. *Tilia americana* was the most abundant understory tree in this area.

In the Liver Tract, the understory of the upland forests in the southern half of the tract as dominated primarily by *Desmodium* spp., *Lespedeza* spp. and a few grasses including *Brachyelytrum erectum*. In the moist western portion of the tract most of the spring flowering species such as *Trilium viridescens*, *Corydalis flavula*, *Dicentra cucullaria*, *Viola* spp., *Podophyllum peltatum*, *Impatiens pallida*, and *Arisaema* spp. Ferns that were abundant along Greasy Creek include *Pellaea atropurpurea*, *Dryopteris felix mas*, and *Polystichum acrostichoides*. They are established in cracks of the limestone escarpments or the shallow soils of stony slopes. In the summer, *Osmorhiza longistylis*, *Perilla frutescens*, *Salvia lyrata*, *Diodia teres*, *Sanicula canadensis*, *Plantago rugelii*, *Euphorbia dentate*, *Croton glandulosa*, *Echinacea purpurea*, and *Chasmanthium latifolium* are abundant.

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Appendix 1. Vascular plant taxa of the Gittin Down Mountain, Liver, and Varmint Tracts of the Ozark Plateau National Wildlife Refuge, Adair, County, OK. Nomenclature follows the PLANTS Database (USDA, NRCS, 1999). Taxa are arranged alphabetically by family, and species. Abundance is according to Palmer et al. (1995). U.S. Nativity indicates if a species is native to North America or is introduced PLANTS Symbol is the identification code assigned to each species listed in PLANTS database.

Family	Species	Common Name	Abundance	Tracts	Origin	Symbol
Acanthaceae	<i>Dicliptera brachiata</i> (Pursh) Spreng.	branched foldwing	Occasional	GLV	Native	DIBR2
	<i>Ruellia humilis</i> Nutt.	fringeleaf wild petunia	Occasional	GLV	Native	RUHU
Aceraceae	<i>Acer negundo</i> L.	boxelder	Infrequent	GV	Native	ACNE2
	<i>Acer saccharum</i> Marsh.	sugar maple	Occasional	GLV	Native	ACSA3
Amaranthaceae						
	<i>Amaranthus hybridus</i> L.	slim amaranth	Infrequent	L	Native	AMHY
Anacardiaceae	<i>Rhus aromatica</i> Aiton	fragrant sumac	Occasional	GLV	Native	RHAR4
	<i>Rhus glabra</i> L.	smooth sumac	Occasional	GLV	Native	RHGL
Apiaceae	<i>Toxicodendron radicans</i> (L.) Kuntze	eastern poison ivy	Occasional	GLV	Native	TORA2
	<i>Chenopodium album</i> L.	lambsquarters	Occasional	GLV	Native	CHAL7
	<i>Eryngium yuccifolium</i> Michx.	button eryngo	Occasional	GL	Native	ERYU
	<i>Osmorhiza longistylis</i> (Torr.) DC.	longstyle sweetroot	Infrequent	GLV	Native	OSLO
	<i>Sanicula canadensis</i> L.	sanicle	Frequent	GLV	Native	SANIC
	<i>Taenidia integerrima</i> (L.) Drude	yellow pimpernel	Infrequent	G	Native	TAIN
	<i>Trepocarpus aethusae</i> Nutt. ex DC.	whitenymph	Infrequent	L	Native	TRAE2
	<i>Zizia aurea</i> (L.) W.D.J. Koch	golden zizia	Frequent	L	Native	ZIAU
Apocynaceae	<i>Amsonia tabernaemontana</i> Walter	eastern bluestar	Infrequent	L	Native	AMTA2
	<i>Apocynum cannabinum</i> L.	Indianhemp	Occasional	GV	Native	APCA
Aquifoliaceae	<i>Ilex decidua</i> Walter	possum haw	Occasional	GLV	Native	ILDE
Araceae	<i>Arisaema dracontium</i> (L.) Schott	green dragon	Occasional	GLV	Native	ARDR3
	<i>Arisaema triphyllum</i> (L.) Schott	Jack in the pulpit	Occasional	GLV	Native	ARTR
Aristolochiaceae						
	<i>Asarum canadense</i> L.	Canadian wildginger	Infrequent	GV	Native	ASCA
Asclepiadaceae						
	<i>Asclepias tuberosa</i> L.	butterfly milkweed	Infrequent	GLV	Native	ASTU
	<i>Asclepias variegata</i> L.	redring milkweed	Infrequent	G	Native	ASVA
	<i>Asclepias verticillata</i> L.	whorled milkweed	Occasional	GL	Native	ASVE
	<i>Cynanchum laeve</i> (Michx.) Pers.	honeyvine	Occasional	GLV	Native	CYLA
	<i>Matelea baldwyniana</i> (Sweet) Woodson	Baldwin's milkvine	Occasional	G	Native	MABA3

Family	Species	Common Name	Abundance	Tracts	Origin	Symbol
	<i>Matelea gonocarpus</i> (Walter) Shinnery	angularfruit milkvine	Occasional	G	Native	MAGO
Aspleniaceae	<i>Asplenium platyneuron</i> (L.) Britton, Sterns & Poggenb.	ebony spleenwort	Occasional	GLV	Native	ASPL
	<i>Asplenium rhizophyllum</i> L.	walking fern	Occasional	GLV	Native	ASRH2
Asteraceae	<i>Achillea millefolium</i> L.	common yarrow	Occasional	GL	Introduced	ACMI2
	<i>Ageratina altissima</i> (L.) King & H. Rob.	white snakeroot	Occasional	G	Native	AGAL5
	<i>Ambrosia artemisiifolia</i> L.	annual ragweed	Frequent	GLV	Native	AMAR2
	<i>Ambrosia bidentata</i> Michx.	lanceleaf ragweed	Occasional	GLV	Native	AMBI2
	<i>Ambrosia psilostachya</i> DC.	Cuman ragweed	Occasional	GLV	Native	AMPS
	<i>Ambrosia trifida</i> L. var. <i>trifida</i> f. <i>integrifolia</i> (Muhl. ex Willd.) Fernald	great ragweed	Rare	G	Native	AMTRT2
	<i>Ambrosia trifida</i> L.	great ragweed	Occasional	G	Native	AMTR
	<i>Amphiachyris dracunculoides</i> (DC.) Nutt.	prairie broomweed	Infrequent	LV	Native	AMDR
	<i>Antennaria parlinii</i> Fernald	Parlin's pussytoes	Occasional	GL	Native	ANPA9
	<i>Arctium minus</i> Bernh.	lesser burdock	Infrequent	V	Introduced	ARMI2
	<i>Arnoglossum plantagineum</i> Raf.	Indian pliantain	Occasional	G	Native	ARPL4
	<i>Bidens bipinnata</i> L.	Spanish needles	Occasional	GLV	Native	BIBI7
	<i>Bidens aristosa</i> (Michx.) Britton	bearded beggarticks	Infrequent	L	Native	BIAR
	<i>Centaurea americana</i> Nutt.	American star-thistle	Occasional	GLV	Native	CEAM2
	<i>Chrysopsis pilosa</i> Nutt.	soft goldenaster	Infrequent	GL	Native	CHPI8
	<i>Cirsium altissimum</i> (L.) Hill	tall thistle	Occasional	GLV	Native	CIAL2
	<i>Conoclinium coelestinum</i> (L.) DC.	blue mistflower	Infrequent	LV	Native	COCO13
	<i>Conyza canadensis</i> (L.) Cronq.	Canadian horseweed	Frequent	GLV	Native	COCA5
	<i>Coreopsis palmata</i> Nutt.	stiff tickseed	Occasional	G	Native	COPA10
	<i>Echinacea pallida</i> (Nutt.) Nutt.	pale purple coneflower	Occasional	G	Native	ECPA
	<i>Echinacea purpurea</i> (L.) Moench	eastern purple coneflower	Occasional	LV	Native	ECPU
	<i>Elephantopus carolinianus</i> Raeusch.	Carolina elephantsfoot	Frequent	GLV	Native	ELCA3
	<i>Erechtites hieracifolia</i> (L.) Raf. ex DC.	American burnweed	Occasional	G	Native	ERHI2
	<i>Erigeron strigosus</i> Muhl. ex Willd.	prairie fleabane	Occasional	GLV	Native	ERST3
	<i>Eupatorium altissimum</i> L.	tall thoroughwort	Frequent	G	Native	EUAL3
	<i>Eupatorium serotinum</i> Michx.	late flowering boneset	Occasional	GLV	Native	EUSE2

Family	Species	Common Name	Abundance	Tracts	Origin	Symbol
	<i>Fleischmannia incarnata</i> (Walter) King & H. Rob.					
		pink thoroughwort	Occasional	GLV	Native	FLIN2
	<i>Gamochaeta purpurea</i> (L.) Cabrera	rabbit tobacco	Occasional	G	Native	GAPU3
	<i>Grindelia papposa</i> G.L. Nesom & Suh	Spanish gold	Infrequent	L	Native	GRPA8
	<i>Helenium amarum</i> (Raf.) H. Rock	yellowdicks	Occasional	GLV	Native	HEAM
	<i>Helenium flexuosum</i> Raf.	purplehead sneezeweed	Occasional	V	Native	HEFL
	<i>Helianthus grosseserratus</i> M. Martens	sawtooth sunflower	Occasional	G	Native	HEGR4
	<i>Helianthus hirsutus</i> Raf.	hairy sunflower	Occasional	GLV	Native	HEHI2
	<i>Helianthus mollis</i> Lam.	ashy sunflower	Occasional	G	Native	HEMO2
	<i>Heliopsis helianthoides</i> (L.) Sweet	smooth oxeye	Frequent	GLV	Native	HEHE5
	<i>Heterotheca subaxillaris</i> (Lam.) Britt. & Rusby					
		camphorweed	Occasional	L	Native	HESU3
	<i>Hieracium gronovii</i> L.	queendevil	Occasional	GLV	Native	HIGR3
	<i>Ionactis linariifolius</i> (L.) Greene	flaxleaf whitetop aster	Rare	G	Native	IOLI2
	<i>Lactuca canadensis</i>	Canada lettuce	Occasional	L	Native	LACA
	<i>Lactuca ludoviciana</i> (Nutt.) Riddell	biannual lettuce	Occasional	L	Native	LALU
	<i>Leucanthemum vulgare</i> Lam.	oxeye daisy	Infrequent	G	Introduced	LEVU
	<i>Liatriis aspera</i> Michx.	tall blazing star	Occasional	GL	Native	LIAS
	<i>Liatriis elegans</i> (Walter) Michx.	pinkscale blazing star	Infrequent	GL	Native	LIEL
	<i>Liatriis squarrosa</i> (L.) Michx.	scaly blazing star	Occasional	G	Native	LISQ
	<i>Packera obovata</i> (Muhl. ex Willd.) W.A. Weber & A. Löve					
		roundleaf ragwort	Frequent	GLV	Native	PAOB6
	<i>Parthenium integrifolium</i> L.	wild quinine	Infrequent	GL	Native	PAIN2
	<i>Pyrrhopappus carolinianus</i> (Walter) DC.					
		Carolina desert-chicory	Occasional	GLV	Native	PYCA2
	<i>Ratibida pinnata</i> (Vent.) Barnhar	prairie coneflower	Occasional	GLV	Native	RAPI
	<i>Rudbeckia hirta</i> L.	blackeyed Susan	Occasional	GL	Native	RUHI2
	<i>Rudbeckia triloba</i> L.	brown-eyed Susan	Occasional	GLV	Native	RUTR2
	<i>Smallanthus uvedalius</i> (L.) Mack. ex Small					
		hairy leafcup	Occasional	GLV	Native	SMUV
	<i>Solidago canadensis</i> L.	Canada goldenrod	Occasional	GLV	Native	SOCA6
	<i>Solidago ulmifolia</i> Muhl. ex Willd.	elmleaf goldenrod	Occasional	GLV	Native	SOUL2
	<i>Solidago missouriensis</i> Nutt.	Missouri goldenrod	Occasional	GLV	Native	SOMI2

Family	Species	Common Name	Abundance	Tracts	Origin	Symbol
	<i>Symphyotrichum anomalum</i> (Engelm.) G.L. Nesom	manyray aster	Infrequent	G	Native	SYAN2
	<i>Symphyotrichum drummondii</i> (Lindl.) G.L. Nesom var. <i>drummondii</i>	Drummond's aster	Frequent	G	Native	SYDRD
	<i>Symphyotrichum patens</i> (Aiton) G.L. Nesom var. <i>patentissimum</i> (Lindl. ex DC.) G.L. Nesom	late purple aster	Infrequent	GLV	Native	SYPAP
	<i>Taraxacum officinale</i> F.H. Wigg.	common dandelion	Infrequent	GLV	Introduced	TAOF
	<i>Verbesina alternifolia</i> (L.) Britton ex Kearney	wingstem	Occasional	GLV	Native	VEAL
	<i>Verbesina helianthoides</i> Michx.	gravelweed	Occasional	G	Native	VEHE
	<i>Verbesina virginica</i> L.	white crownbeard	Occasional	GLV	Native	VEVI3
	<i>Vernonia baldwinii</i> Torr.	Baldwin's ironweed	Occasional	GL	Native	VEBA
	<i>Vernonia gigantea</i> (Walter) Trel.	giant ironweed	Occasional	LV	Native	VEGI
	Balsaminaceae					
	<i>Impatiens capensis</i> Meerb.	jewelweed	Occasional	GLV	Native	IMCA
	Berberidaceae <i>Podophyllum peltatum</i> L.	mayapple	Frequent	GLV	Native	POPE
	Betulaceae <i>Ostrya virginiana</i> (P. Mill.) K. Koch	hophornbeam	Frequent	GLV	Native	OSVI
	Bignoniaceae <i>Campsis radicans</i> (L.) Seem. ex Bureau	trumpet creeper	Frequent	GLV	Native	CARA2
	Boraginaceae <i>Cynoglossum virginianum</i> L.	wild comfrey	Occasional	GLV	Native	CYVI
	<i>Hackelia virginiana</i> (L.) I.M. Johnston	beggarslice	Frequent	GLV	Native	HAVI2
	<i>Lithospermum canescens</i> (Michx.) Lehm.	hoary puccoon	Occasional	GL	Native	LICA12
	Brassicaceae <i>Arabis canadensis</i> L.	sicklepod	Occasional	GLV	Native	ARCA
	<i>Arabis laevigata</i> (Muhl. ex Willd.) Poir.	smooth rockcress	Occasional	GLV	Native	ARLA
	<i>Cardamine concatenata</i> (Michx.) Sw.	cutleaf toothwort	Frequent	GLV	Native	CACO26
	<i>Cardamine parviflora</i> L.	sand bittercress	Frequent	GLV	Native	CAPA12
	<i>Lepidium densiflorum</i> Schrad.	common pepperweed	Frequent	G	Native	LEDE
	<i>Nasturtium officinale</i> W.T. Aiton	watercress	Infrequent	G	Introduced	NAOF
	Cactaceae <i>Opuntia macrorhiza</i> Engelm.	twistspine pricklypear	Infrequent	GLV	Native	OPMA2
	Campanulaceae					
	<i>Campanulastrum americanum</i> (L.) Small	American bellflower	Occasional	GLV	Native	CAAM18
	<i>Lobelia cardinalis</i> L.	cardinalflower	Rare	V	Native	LOCA2

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	<i>Lobelia inflata</i> L.	Indian-tobacco	Infrequent	GL	Native	LOIN
	<i>Lobelia spicata</i> Lam.	palespike lobelia	Occasional	GLV	Native	LOSP
Caprifoliaceae	<i>Lonicera japonica</i> Thunb.	Japanese honeysuckle	Infrequent	GLV	Introduced	LOJA
	<i>Sambucus nigra</i> L. ssp. <i>canadensis</i> (L.) R. Bolli	American black elderberry	Occasional	GL	Native	SANIC4
	<i>Symphoricarpos orbiculatus</i> Moench	coralberry	Frequent	GLV	Native	SYOR
	<i>Viburnum rufidulum</i> Raf.	rusty blackhaw	Occasional	GLV	Native	VIRU
Caryophyllaceae	<i>Dianthus armeria</i> L.	Deptford pink	Infrequent	GL	Native	DIAR
	<i>Saponaria officinalis</i> L.	bouncingbet	Infrequent	G	Introduced	SAOF4
	<i>Silene stellata</i> (L.) W.T. Aiton	widowsfrill	Frequent	GLV	Native	SIST
	<i>Silene regia</i> Sims	royal catchfly	Occasional	G	Native	SIRE2
	<i>Stellaria media</i> (L.) Vill.	common chickweed	Frequent	GV	Introduced	STME2
Celastraceae	<i>Euonymus atropurpureus</i> Jacq.	burningbush	Occasional	G	Native	EUAT5
Clusiaceae	<i>Hypericum hypericoides</i> (L.) Crantz	St. Andrew's cross	Occasional	GLV	Native	HYHY
	<i>Hypericum punctatum</i> Lam.	spotted St. Johnswort	Occasional	GV	Native	HYPV
Commelinaceae	<i>Commelina erecta</i> L.	whitemouth dayflower	Occasional	G	Native	COER
	<i>Tradescantia ohiensis</i> Raf.	bluejacket	Occasional	GLV	Native	TROH
	<i>Tradescantia ozarkana</i> E.S. Anderson & Woodson	Ozark spiderwort	Rare	GL	Native	TROZ
Convolvulaceae	<i>Ipomoea coccinea</i> L.	redstar	Occasional	GLV	Introduced	IPCO3
	<i>Ipomoea pandurata</i> (L.) G.F.W. Mey.	man of the earth	Occasional	GLV	Native	IPPA
Cornaceae	<i>Cornus drummondii</i> C.A. Mey.	roughleaf dogwood	Occasional	GLV	Native	CODR
	<i>Cornus florida</i> L.	flowering dogwood	Frequent	GLV	Native	COFL2
Crassulaceae	<i>Sedum pulchellum</i> Michx.	widowscross	Infrequent	G	Native	SEPU
Cucurbitaceae	<i>Melothria pendula</i> L.	Guadeloupe cucumber	Occasional	GLV	Native	MEPE3
Cupressaceae	<i>Juniperus virginiana</i> L.	eastern redcedar	Occasional	GLV	Native	JUVI
Cyperaceae	<i>Carex albicans</i> Willd. ex Spreng.	whitetinge sedge	Occasional	GL	Native	CAAL25
	<i>Carex cephalophora</i> Muhl. ex Willd.	oval-leaf sedge	Infrequent	G	Native	CACE
	<i>Carex grisea</i> Wahlenb.	inflated narrow-leaf sedge	Infrequent	G	Native	CAGR24

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	<i>Carex hirsutella</i> Mack.	fuzzy wuzzy sedge	Infrequent	G	Native	CAHI6
	<i>Carex oligocarpa</i> Schkuhr ex Willd.	richwoods sedge	Occasional	G	Native	CAOL2
	<i>Carex retroflexa</i> Muhl. ex Willd.	reflexed sedge	Infrequent	G	Native	CARE9
	<i>Carex socialis</i> Mohlenbr. & Schwegm.	low woodland sedge	Infrequent	G	Native	CASO
	<i>Cyperus lupulinus</i> (Spreng.) Marcks	Great Plains flatsedge	Infrequent	LV	Native	CYLU2
	<i>Cyperus odorata</i> L.	fragrant flatsedge	Infrequent	L	Native	CYOD
	<i>Cyperus strigosus</i> L.	strawcolored flatsedge	Infrequent	LV	Native	CYST
	<i>Eleocharis lanceolata</i> Fern.	daggerleaf spikerush	Occasional	GLV	Native	ELLA
	<i>Scirpus atrovirens</i> Willd.	green bulrush	Infrequent	L	Native	SCAT2
	<i>Scleria oligantha</i> Michx.	littlehead nutrush	Occasional	GLV	Native	SCOL2
Dryopteridaceae						
	<i>Cystopteris tennesseensis</i> Shaver	Tennessee bladder fern	Occasional	GV	Native	CYTE3
	<i>Dryopteris filix-mas</i> (L.) Schott	male fern	Infrequent	GL	Native	DRFI2
	<i>Polystichum acrostichoides</i> (Michx.) Schott	Christmas fern	Occasional	GLV	Native	POAC4
	<i>Woodsia obtusa</i> (Spreng.) Torr.	bluntlobe cliff fern	Infrequent	GLV	Native	WOOB2
Ebenaceae	<i>Diospyros virginiana</i> L.	common persimmon	Occasional	GLV	Native	DIVI5
Ericaceae	<i>Vaccinium arboreum</i> Marsh.	farkleberry	Infrequent	G	Native	VAAR
Euphorbiaceae						
	<i>Acalypha monococca</i> (Engelm. ex Gray)	threeseed mercury	Frequent	GLV	Native	ACMO4
	<i>Acalypha ostryifolia</i> Riddell	pineland threeseed mercury	Infrequent	GLV	Native	ACOS
	<i>Chamaesyce nutans</i> (Lag.) Small	eyebane	Occasional	LV	Native	CHNU9
	<i>Croton glandulosus</i> L.	vente conmigo	Frequent	GLV	Native	CRGL2
	<i>Croton lindheimerianus</i> Scheele	threeseed croton	Infrequent	GLV	Native	CRLI2
	<i>Croton monanthogynus</i> Michx.	prairie tea	Infrequent	GLV	Native	CRMO6
	<i>Crotonopsis michauxii</i> G. L. Webster	Michaux's croton	Occasional	GLV	Native	CRMI 8
	<i>Euphorbia corollata</i> L.	flowering spurge	Infrequent	GLV	Native	EUCO10
	<i>Euphorbia dentata</i> Michx.	toothed spurge	Frequent	GLV	Native	EUDE4
	<i>Phyllanthus caroliniensis</i> Walter	Carolina leaf-flower	Infrequent	G	Native	PHCA9
Fabaceae	<i>Albizia julibrissin</i> Durazz.	silktree	Infrequent	G	Introduced	ALJU
	<i>Amphicarpaea bracteata</i> (L.) Fernald	American hogpeanut	Occasional	GLV	Native	AMBR2
	<i>Astragalus canadensis</i> L.	Canadian milkvetch	Infrequent	G	Native	ASCA11
	<i>Baptisia</i> Vent.	wild indigo	Infrequent	G	Native	BAPTI

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	<i>Cercis canadensis</i> L.	eastern redbud	Frequent	GLV	Native	CECA4
	<i>Chamaecrista fasciculata</i> (Michx.) Greene	partridge pea	Occasional	GLV	Native	CHFA2
	<i>Chamaecrista nictitans</i> (L.) Moench	sensitive partridge pea	Infrequent	GLV	Native	CHNI2
	<i>Clitoria mariana</i> L.	Atlantic pigeonwings	Occasional	GLV	Native	CLMA4
	<i>Crotalaria sagittalis</i> L.	arrowhead rattlebox	Occasional	G	Native	CRSA4
	<i>Dalea candida</i> Michx. ex Willd.	white prairie clover	Occasional	G	Native	DACA7
	<i>Desmanthus illinoensis</i> (Michx.) MacMill. ex B.L. Rob. & Fernald	Illinois bundleflower	Infrequent	L	Native	DEIL
	<i>Desmodium canescens</i> (L.) DC.	hoary ticktrefoil	Occasional	GLV	Native	DECA8
	<i>Desmodium glutinosum</i> (Muhl. ex Willd.) Wood	pointedleaf ticktrefoil	Frequent	GL	Native	DEGL5
	<i>Desmodium laevigatum</i> (Nutt.) DC.	smooth ticktrefoil	Occasional	GL	Native	DELA2
	<i>Desmodium paniculatum</i> (L.) DC.	panickedleaf ticktrefoil	Occasional	GL	Native	DEPA6
	<i>Desmodium pauciflorum</i> (Nutt.) DC.	fewflower ticktrefoil	Occasional	GLV	Native	DEPA7
	<i>Desmodium sessilifolium</i> (Torr.) Torr. & A. Gray	sessile ticktrefoil	Occasional	G	Native	DESE
	<i>Galactia regularis</i> (L.) Britton, Sterns & Poggenb.	eastern milkpea	Infrequent	L	Native	GARE2
	<i>Gleditsia triacanthos</i> L.	honeylocust	Occasional	GLV	Native	GLTR
	<i>Kummerowia stipulacea</i> (Maxim.) Makino	Korean clover	Infrequent	LV	Introduced	KUST
	<i>Lespedeza cuneata</i> (Dum.-Cours.)G. Don	sericea lespedeza	Infrequent	GLV	Introduced	LECU
	<i>Lespedeza hirta</i> (L.) Hornem.	hairy lespedeza	Occasional	L	Native	LEHI2
	<i>Lespedeza repens</i> (L.) W. Bart.	creeping lespedeza	Frequent	GLV	Native	LERE2
	<i>Lespedeza virginica</i> (L.) Britt.	slender lespedeza	Occasional	GLV	Native	LEVI7
	<i>Melilotus officinalis</i> (L.) Lam.	yellow sweetclover	Occasional	GLV	Introduced	MEOF
	<i>Mimosa quadrivalvis</i> L.	fourvalve mimosa	Occasional	GLV	Native	MIQU2
	<i>Senna marilandica</i> (L.) Link	Maryland senna	Occasional	GV	Native	SEMA11
	<i>Strophostyles helvola</i> (L.) Elliott	amberique-bean	Occasional	GLV	Native	STHE9
	<i>Strophostyles leiosperma</i> (Torr. & Gray) Piper	slickseed fuzzybean	Frequent	GLV	Native	STLE6

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	<i>Stylosanthes biflora</i> (L.) Britton, Sterns & Poggenb.	sidebeak pencilflower	Occasional	GLV	Native	STBI2
	<i>Tephrosia virginiana</i> (L.) Pers.	Virginia tephrosia	Occasional	G	Native	TEVI
	<i>Trifolium dubium</i> Sibth.	suckling clover	Frequent	GV	Introduced	TRDU2
	<i>Trifolium hybridum</i> L.	alsike clover	Infrequent	L	Introduced	TRHY
	<i>Vicia minutiflora</i> F.G. Dietr.	pygmyflower vetch	Occasional	GLV	Native	VIMI
Fagaceae	<i>Castanea pumila</i> (L.) Mill. var. <i>ozarkensis</i> (Ashe) Tucker	Ozark chinkapin	Rare	G	Native	CAPUO
	<i>Quercus alba</i> L.	white oak	Occasional	GL	Native	QUAL
	<i>Quercus falcata</i> Michx.	southern red oak	Frequent	GLV	Native	QUFA
	<i>Quercus macrocarpa</i> Michx.	bur oak	Occasional	GL	Native	QUMA2
	<i>Quercus marilandica</i> Münchh.	blackjack oak	Occasional	GL	Native	QUMA3
	<i>Quercus muehlenbergii</i> Engelm.	chinkapin oak	Occasional	GLV	Native	QUMU
	<i>Quercus prinoides</i> Willd.	dwarf- chinkapin oak	Infrequent	G	Native	QUPR
	<i>Quercus rubra</i> L.	northern red oak	Frequent	GLV	Native	QURU
	<i>Quercus shumardii</i> Buckley	Shumard's oak	Occasional	GL	Native	QUSH
	<i>Quercus stellata</i> Wengen.	post oak	Frequent	GL	Native	QUST
	<i>Quercus velutina</i> Lam.	black oak	Frequent	GLV	Native	QUVE
Fumariaceae	<i>Corydalis flavula</i> (Raf.) DC.	yellow fumewort	Frequent	GLV	Native	COFL3
	<i>Dicentra cucullaria</i> (L.) Bernh.	Dutchman's breeches	Occasional	GLV	Native	DICU
Geraniaceae	<i>Geranium carolinianum</i> L.	Carolina geranium	Occasional	G	Native	GECA5
Hippocastanaceae	<i>Aesculus glabra</i> Willd.	Ohio buckeye	Infrequent	GV	Native	AEGL
Hydrangeaceae	<i>Hydrangea arborescens</i> L.	wild hydrangea	Occasional	GLV	Native	HYAR
Iridaceae	<i>Belamcanda chinensis</i> (L.) DC.	blackberry lily	Infrequent	V	Introduced	BECH
Juglandaceae	<i>Carya cordiformis</i> (Wengen.) K. Koch	bitternut hickory	Occasional	GLV	Native	CACO15
	<i>Carya ovata</i> (P. Mill.) K. Koch	shagbark hickory	Frequent	GLV	Native	CAOV2
	<i>Carya texana</i> Buckley	black hickory	Frequent	GLV	Native	CATE9
	<i>Juglans nigra</i> L.	black walnut	Occasional	GLV	Native	JUNI
Juncaceae	<i>Juncus secundus</i> P. Beauv. ex Poir.	lopsided rush	Occasional	G	Native	JUSE
	<i>Juncus tenuis</i> Willd.	poverty rush	Infrequent	GV	Native	JUTE
	<i>Juncus interior</i> Weigland	inland rush	Occasional	G	Native	JUIN2

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	<i>Luzula bulbosa</i> (Alph. Wood) Smyth & Smyth	bulbous woodrush	Infrequent	GL	Native	LUBU
Lamiaceae	<i>Clinopodium arkansanum</i> (Nutt.) House	limestone calamint	Infrequent	L	Native	CLAR5
	<i>Lamium purpureum</i> L.	purple deadnettle	Occasional	GLV	Introduced	LAPU2
	<i>Lycopus americanus</i> Muhl. ex W. Bartram	American water horehound	Occasional	LV	Native	LYAM
	<i>Monarda punctata</i> L.	spotted beebalm	Infrequent	LV	Native	MOPU
	<i>Monarda fistulosa</i> L.	wild bergamot	Infrequent	G	Native	MOFI
	<i>Monarda russeliana</i> Nutt. ex Sims	redpurple beebalm	Occasional	GLV	Native	MORU
	<i>Perilla frutescens</i> (L.) Britt.	beefsteakplant	Frequent	GLV	Introduced	PEFR4
	<i>Prunella vulgaris</i> L.	common selfheal	Occasional	GLV	Native	PRVU
	<i>Pycnanthemum tenuifolium</i> Schrad.	mountainmint	Occasional	GLV	Native	PYTE
	<i>Salvia azurea</i> Michx. ex Lam.	azure blue sage	Occasional	GLV	Native	SAAZ
	<i>Salvia lyrata</i> L.	lyreleaf sage	Frequent	GLV	Native	SALY2
	<i>Scutellaria ovata</i> Hill	heartleaf skullcap	Occasional	GL	Native	SCOV
	<i>Teucrium canadense</i> L.	Canada germander	Occasional	GLV	Native	TECA3
Lauraceae	<i>Lindera benzoin</i> (L.) Blume	northern spicebush	Infrequent	GLV	Native	LIBE3
	<i>Sassafras albidum</i> (Nutt.) Nees	sassafras	Occasional	GLV	Native	SAAL5
Liliaceae	<i>Allium canadense</i> L.	meadow garlic	Frequent	GLV	Native	ALCA3
	<i>Camassia scilloides</i> (Raf.) Cory	Atlantic camas	Occasional	G	Native	CASC5
	<i>Erythronium americanum</i> Ker Gawl.	dogtooth violet	Occasional	GLV	Native	ERAM5
	<i>Nothoscordum bivalve</i> (L.) Britton	crowpoison	Frequent	GLV	Native	NOBI2
	<i>Polygonatum biflorum</i> (Walter) Elliot	Solomon's seal	Infrequent	GLV	Native	POBI2
	<i>Trillium viridescens</i> Nutt.	tapertip wakerobin	Occasional	GLV	Native	TRVI5
	<i>Uvularia grandiflora</i> Sm.	largeflower bellwort	Infrequent	G	Native	UVGR
Lythraceae	<i>Cuphea viscosissima</i> Jacq.	blue waxweed	Infrequent	LV	Native	CUVI
Malvaceae	<i>Sida spinosa</i> L.	prickly fanpetals	Infrequent	GV	Native	SISP
Monotropaceae	<i>Monotropa uniflora</i> L.	Indianpipe	Rare	GV	Native	MOUN3
Moraceae	<i>Maclura pomifera</i> (Raf.) Schneid.	Osage orange	Occasional	GLV	Native	MAPO
	<i>Morus rubra</i> L.	red mulberry	Occasional	GLV	Native	MORU2

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Nyctaginaceae							
	<i>Mirabilis albida</i> (Walt.) Heimerl	white four o'clock	Infrequent	GLV	Native	MIAL4	
Oleaceae	<i>Fraxinus pennsylvanica</i> Marsh.	green ash	Occasional	GLV	Native	FRPE	
Onagraceae	<i>Gaura longiflora</i> Spach	longflower bee blossom	Infrequent	GLV	Native	GALO3	
	<i>Ludwigia alternifolia</i> L.	seedbox	Infrequent	V	Native	LUAL2	
	<i>Oenothera biennis</i> L.	evening-primrose	Infrequent	GLV	Native	OEBI	
Ophioglossaceae							
	<i>Botrychium biternatum</i> (Sav.) Underwood						
		sparselobe grapefern	Occasional	GLV	Native	BOBI	
Orchidaceae	<i>Corallorhiza odontorhiza</i> (Willd.) Poir.	autumn coralroot	Rare	G	Native	COOD7	
	<i>Spiranthes tuberosa</i> Raf.	little lady's tresses	Occasional	G	Native	SPTU	
	<i>Triphora trianthophora</i> (Sw.) Rydb.	three birds	Occasional	G	Native	TRTR3	
Oxalidaceae	<i>Oxalis dillenii</i> Jacq.	woodsorrel	Frequent	GLV	Native	OXDI2	
	<i>Oxalis violacea</i> L.	violet woodsorrel	Occasional	GLV	Native	OXVI	
Papaveraceae	<i>Sanguinaria canadensis</i> L.	bloodroot	Occasional	GLV	Native	SACA13	
Passifloraceae	<i>Passiflora incarnata</i> L.	passion flower	Occasional	GLV	Native	PAIN6	
	<i>Passiflora lutea</i> L.	yellow passionflower	Frequent	GLV	Native	PALU2	
Phytolaccaceae							
	<i>Phytolacca americana</i> L.	American pokeweed	Frequent	GLV	Native	PHAM4	
Pinaceae	<i>Pinus echinata</i> Mill.	loblolly pine	Rare	G	Native	PITA	
Plantaginaceae							
	<i>Plantago aristata</i> Michx.	largebracted plantain	Occasional	GLV	Native	PLAR3	
	<i>Plantago lanceolata</i> L.	narrowleaf plantain	Frequent	V	Introduced	PLLA	
	<i>Plantago rugelii</i> Decne.	blackseed plantain	Frequent	GLV	Native	PLRU	
Plantanaceae	<i>Platanus occidentalis</i> L.	sycamore	Occasional	GLV	Native	PLOC	
Poaceae	<i>Aristida purpurea</i> Nutt.	purple threeawn	Infrequent	GLV	Introduced	ARPU9	
	<i>Arundinaria gigantea</i> (Walter) Muhl.	giant cane	Infrequent	GL	Native	ARGI	
	<i>Andropogon gerardii</i> Vitman	big bluestem	Occasional	GL	Native	ANGE	
	<i>Andropogon virginicus</i> L.	broomsedge bluestem	Occasional	GL	Native	ANVI2	
	<i>Brachyelytrum erectum</i> (Schreb. ex Spreng.) P. Beauv.						
			bearded shorthusk	Frequent	GLV	Native	BRER2
		<i>Bromus arvensis</i> L.	field brome	Infrequent	GL	Introduced	BRAR5
	<i>Bromus pubescens</i> L.	bald brome	Occasional	GLV	Introduced	BARRA2	

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	<i>Chasmanthium latifolium</i> (Michx.) Yates	Indian woodoats	Frequent	GLV	Native	CHLA5
	<i>Cinna arundinacea</i> L.	Sweet woodreed	Occasional	V	Native	CIAR2
	<i>Danthonia spicata</i> (L.) P. Beauv. ex Roem. & Schult.	poverty oatgrass	Frequent	GLV	Native	DASP2
	<i>Diarrhena americana</i> P. Beauv.	American beakgrass	Frequent	GL	Native	DIAM
	<i>Dichantherium acuminatum</i> (Sw.) Gould & C.A. Clark	tapered rosette grass	Occasional	GLV	Native	DIAC2
	<i>Dichantherium boscii</i> (Poir.) Gould & C.A. Clark	Bosc's panicgrass	Occasional	GLV	Native	DIRA
	<i>Dichantherium laxiflorum</i> (Lam.) Gould	openflower rosette grass	Occasional	GL	Native	DILA9
	<i>Dichantherium linearifolium</i> (Scribn. ex Nash) Gould	slimleaf panicgrass	Infrequent	GL	Native	DILI2
	<i>Dichantherium malacophyllum</i> (Nash) Gould	softleaf rosette grass	Occasional	GL	Native	DIMA5
	<i>Dichantherium oligosanthes</i> (Schult.) Gould	Heller's rosette grass	Occasional	GLV	Native	DIOL
	<i>Digitaria sanguinalis</i> (L.) Scop.	hairy crabgrass	Occasional	L	Native	DISA
	<i>Echinochloa crus-galli</i> (L.) P. Beauv.	barnyardgrass	Occasional	V	Native	ECCR
	<i>Elymus hystrix</i> L.	eastern bottlebrush grass	Rare	GLV	Native	ELHY
	<i>Elymus virginicus</i> L.	Virginia wildrye	Occasional	GLV	Native	ELVI3
	<i>Eragrostis hirsuta</i> (Michx.) Nees	bigtop lovegrass	Occasional	GL	Native	ERHI
	<i>Festuca subverticillata</i> (Pers.) Alexeev	nodding fescue	Occasional	G	Native	FESU3
	<i>Glyceria striata</i> (Lam.) Hitchc.	fowl mannagrass	Occasional	L	Native	GLST
	<i>Leersia virginica</i> Willd.	whitegrass	Occasional	GL	Native	LEVI2
	<i>Melica nitens</i> (Scribn.) Nutt. ex Piper	threeflower melicgrass	Occasional	GL	Native	MENI
	<i>Microstegium vimineum</i> (Trin.) A. Camus	Nepalese browntop	Occasional	LV	Introduced	MIVI
	<i>Muhlenbergia sobolifera</i> (Muhl. ex Willd.) Trin.	rock muhly	Occasional	GLV	Native	MUSO
	<i>Panicum anceps</i> Michx.	beaked panicgrass	Occasional	GLV	Native	PAAN
	<i>Panicum flexile</i> (Gattinger) Scribn.	wiry panicgrass	Occasional	V	Native	PAFL

Family	Species	Common Name	Abundance	Tracts	Origin	Symbol
	<i>Poa compressa</i> L.	Canada bluegrass	Infrequent	GLV	Introduced	POCO
	<i>Poa sylvestris</i> A. Gray	woodland bluegrass	Infrequent	L	Native	POSY
	<i>Schizachyrium scoparium</i> (Michx.) Nash	little bluestem	Occasional	G	Native	SCSC
	<i>Setaria pumila</i> (Poir.) Roem. & Schult.	yellow foxtail	Infrequent	GLV	Introduced	SEPU8
	<i>Sorghum halepense</i> (L.) Pers.	Johnsongrass	Infrequent	GLV	Introduced	SOHA
	<i>Sphenopholis obtusata</i> (Michx.) Scribn.	prairie wedgescale	Infrequent	G	Native	SPOB
	<i>Steinchisma hians</i> (Elliot) Nash	gaping grass	Infrequent	L	Native	STHI3
	<i>Tridens flavus</i> (L.) Hitchc.	purpletop tridens	Infrequent	L	Native	TRFL2
Polemoniaceae						
	<i>Phlox divaricata</i> L.	wild blue phlox	Occasional	GLV	Native	PHDI5
	<i>Phlox pilosa</i> L.	downy phlox	Infrequent	G	Native	PHPI
Polygonaceae	<i>Polygonum convolvulus</i> L.	black bindweed	Occasional	GLV	Native	POCO10
	<i>Polygonum hydropiperoides</i> Michx.	swamp smartweed	Infrequent	GLV	Native	POHY2
	<i>Polygonum punctatum</i> Ell.	dotted smartweed	Infrequent	GLV	Native	POPU5
	<i>Polygonum scandens</i> L.	false buckwheat	Occasional	G	Native	POSC3
	<i>Polygonum virginianum</i> L.	jumpseed	Frequent	GLV	Native	POVI2
	<i>Rumex crispus</i> L.	curly dock	Infrequent	V	Introduced	RUCR
Portulacaceae	<i>Claytonia virginica</i> L.	Virginia springbeauty	Frequent	GLV	Native	CLVI3
	<i>Phemeranthus parviflorus</i> (Nutt.) Kiger	sunbright	Infrequent	V	Native	PHPA29
Primulaceae	<i>Dodecatheon meadia</i> L.	pride of Ohio	Rare	V	Native	DOME
	<i>Samolus valerandi</i> L.	seaside brookweed	Occasional	GLV	Native	SAVA3
Pteridaceae	<i>Adiantum pedatum</i> L.	northern maidenhair	Occasional	GLV	Native	ADPE
	<i>Cheilanthes alabamensis</i> (Buckl.) Kunze	Alabama lipfern	Occasional	G	Native	CHAL5
	<i>Cheilanthes lanosa</i> (Michx.) D.C. Eaton	hairy lipfern	Occasional	G	Native	CHLA2
	<i>Pellaea atropurpurea</i> (L.) Link	purple cliffbrake	Infrequent	GL	Native	PEAT2
Ranunculaceae						
	<i>Anemone virginiana</i> L.	tall thimbleweed	Occasional	GLV	Native	ANVI3
	<i>Aquilegia canadensis</i> L.	red columbine	Occasional	GLV	Native	AQCA
	<i>Thalictrum thalictroides</i> (L.) Eames & Boivin	rue anemone	Frequent	GLV	Native	THTH2
	<i>Clematis virginiana</i> L.	devil's darning needles	Infrequent	GLV	Native	CLVI5

Family	Species	Common Name	Abundance	Tracts	Origin	Symbol
	<i>Ranunculus fascicularis</i> Muhl. ex Bigelow					
		early buttercup	Occasional	V	Native	RAFA
	<i>Ranunculus sceleratus</i> L.	cursed buttercup	Infrequent	V	Native	RASC3
Rhamnaceae	<i>Frangula caroliniana</i> (Walt.) Gray	Carolina buckthorn	Frequent	GLV	Native	FRCA13
Rosaceae	<i>Agrimonia pubescens</i> Wallr.	soft agrimony	Occasional	GLV	Native	AGPU
	<i>Crataegus crus-galli</i> L.	cockspur hawthorn	Occasional	GL	Native	CRCR2
	<i>Datura stramonium</i> L.	Jimsonweed	Occasional	G	Introduced	DAST
	<i>Fragaria virginiana</i> Duchesne	Virginia strawberry	Occasional	GLV	Native	FRVI
	<i>Geum canadense</i> Jacq.	white avens	Occasional	GLV	Native	GECA7
	<i>Gillenia stipulata</i> (Muhl. ex Willd.) Baill.					
		American ipecac	Occasional	GLV	Native	GIST5
	<i>Potentilla recta</i> L.	sulphur cinquefoil	Occasional	GL	Introduced	PORE5
	<i>Prunus americana</i> Marsh.	American plum	Occasional	GL	Native	PRAM
	<i>Prunus persica</i> (L.) Batsch	peach	Infrequent	GL	Introduced	PRPE3
	<i>Rosa multiflora</i> Thunb.	multiflora rose	Infrequent	LV	Introduced	ROMU
	<i>Rubus allegheniensis</i> Porter	Allegheny blackberry	Occasional	GLV	Native	RUAL
	<i>Rubus occidentalis</i> L.	black raspberry	Occasional	GLV	Native	RUOC
Rubiaceae	<i>Cephalanthus occidentalis</i> L.	common buttonbush	Occasional	V	Native	CEOC2
	<i>Diodia teres</i> Walt.	poorjoe	Frequent	GLV	Native	DITE2
	<i>Diodia virginiana</i> L.	Virginia buttonweed	Infrequent	V	Native	DIVI3
	<i>Galium aparine</i> L.	stickywilly	Occasional	GLV	Native	GAAP2
	<i>Galium pilosum</i> Ait.	hairy bedstraw	Frequent	GLV	Native	GAPI2
	<i>Galium triflorum</i> Michx.	fragrant bedstraw	Infrequent	G	Native	GATR3
	<i>Houstonia pusilla</i> Schoepf	tiny bluet	Infrequent	GLV	Native	HOPU3
Salicaceae	<i>Populus deltoides</i> Bartram ex Marsh.	eastern cottonwood	Frequent	V	Native	PODE3
	<i>Salix caroliniana</i> Michx.	coastal plain willow	Infrequent	GLV	Native	SACA5
Saxifragaceae	<i>Heuchera americana</i> L.	American alumroot	Occasional	GL	Native	HEAM6
	<i>Penthorum sedoides</i> L.	ditch stonecrop	Infrequent	V	Native	PESE6
	<i>Saxifraga virginiana</i> Michx.	early saxifrage	Occasional	GLV	Native	SAVI5
Scrophulariaceae						
	<i>Aureolaria grandiflora</i> (Benth.) Pennell	false foxglove	Infrequent	LV	Native	AUGR
	<i>Lindernia dubia</i> (L.) Pennell	yellow seedfalse pimpernell	Infrequent	G	Native	LIDU
	<i>Minuartia patula</i> (Michx.) Mattf.	pitcher's stitchwort	Infrequent	G	Native	MIPA6

Family	Species	Common Name	Abundance	Tracts	Origin	Symbol
	<i>Mimulus alatus</i> Aiton	sharpwing monkeyflower	Occasional	GLV	Native	MIAL2
	<i>Penstemon tubiflorus</i> Nutt.	white wand beardtongue	Occasional	GLV	Native	PETU
	<i>Scrophularia marilandica</i> L.	carpenter's square	Occasional	V	Native	SCMA2
	<i>Veronica polita</i> Fr.	gray field speedwell	Infrequent	G	Introduced	VEPO
	<i>Veronica arvensis</i> L.	corn speedwell	Occasional	G	Introduced	VEAR
	<i>Verbascum thapsus</i> L.	common mullein	Frequent	GLV	Introduced	VETH
Solanaceae	<i>Physalis longifolia</i> Nutt.	longleaf groundcherry	Infrequent	V	Native	PHLO4
	<i>Physalis pubescens</i> L.	husk tomato	Infrequent	GV	Native	PHPU7
	<i>Solanum carolinense</i> L.	Carolina horsenettle	Occasional	GLV	Native	SOCA3
	<i>Solanum elaeagnifolium</i> Cav.	silverleaf nightshade	Occasional	V	Native	SOEL
	<i>Solanum ptycanthum</i> Dunal	West Indian nightshade	Occasional	GL	Native	SOPT7
Smilacaceae	<i>Smilax bona-nox</i> L.	saw greenbrier	Occasional	GLV	Native	SMBO2
	<i>Smilax herbacea</i> L.	smooth carrionflower	Occasional	GLV	Native	SMHE
	<i>Smilax rotundifolia</i> L.	roundleaf greenbrier	Frequent	GLV	Native	SMRO
Staphyleaceae	<i>Staphylea trifolia</i> L.	American bladdernut	Occasional	GLV	Native	STTR
Tiliaceae	<i>Tilia americana</i> L.	American basswood	Occasional	GLV	Native	TIAM
Ulmaceae	<i>Celtis occidentalis</i> L.	common hackberry	Frequent	GLV	Native	CEOC
	<i>Celtis laevigata</i> Willd.	sugar berry	Occasional	G	Native	CELA
	<i>Ulmus americana</i> L.	American elm	Occasional	L	Native	ULAM
	<i>Ulmus alata</i> Michx.	winged elm	Frequent	GLV	Native	ULAL
	<i>Ulmus rubra</i> Muhl.	slippery elm	Infrequent	GLV	Native	ULRU
Urticaceae	<i>Boehmeria cylindrica</i> (L.) Sw.	smallspike false nettle	Occasional	GLV	Native	BOCY
	<i>Parietaria pensylvanica</i> Muhl. ex Willd.	Pennsylvania pellitory	Occasional	GLV	Native	PAPE5
	<i>Pilea pumila</i> (L.) A. Gray	Canadian clearweed	Occasional	GLV	Native	PIPU2
	<i>Urtica chamaedryoides</i> Pursh	heartleaf nettle	Occasional	GLV	Native	URCH3
	<i>Urtica dioica</i> L.	stinging nettle	Frequent	V	Native	URDI
Verbenaceae	<i>Glandularia canadensis</i> (L.) Nutt.	rose mock vervain	Occasional	GLV	Native	GLCA2
	<i>Phryma leptostachya</i> L.	American lopseed	Occasional	GLV	Native	PHLE5
	<i>Verbena urticifolia</i> L.	white vervain	Occasional	GLV	Native	VEUR
	<i>Verbena simplex</i> Lehm.	narrowleaf vervain	Occasional	L	Native	VESI
Violaceae	<i>Viola bicolor</i> Pursh	field pansy	Occasional	GLV	Native	VIBI
	<i>Viola pedata</i> L.	birdfoot violet	Occasional	G	Native	VIPE
	<i>Viola pubescens</i> Aiton	downy yellow violet	Occasional	GLV	Native	VIPU3

Family	Species	Common Name	Abundance	Tracts	Origin	Symbol
Vitaceae	<i>Viola sororia</i> Willd.	common blue violet	Occasional	GL	Native	VISO
	<i>Parthenocissus quinquefolia</i> (L.) Planch.	Virginia creeper	Occasional	GLV	Native	PAQU2
	<i>Vitis cinerea</i> (Engelm.) Engelm. ex Millard	graybark grape	Occasional	GLV	Native	VICI2
	<i>Vitis rotundifolia</i> Michx.	muscadine	Occasional	GLV	Native	VIRO3

Appendix 2. Eighty-two species collected in the Gittin Down Mountain, Liver, and Varmint Tracts of the Ozark Plateau National Wildlife Refuge which represent new county records for Adair County.

<i>Acalypha monococca</i>	<i>Croton lindheimerianus</i>
<i>Amanthus hybridus</i>	<i>Crotonopsis michauxii</i>
<i>Ambrosia artemisiifolia</i>	<i>Cyperus lupulinus</i>
<i>Ambrosia trifida</i> var <i>trifida</i> f. <i>integrifolia</i>	<i>Cyperus odorata</i>
<i>Amphiachyris dracunculoides</i>	<i>Cyperus strigosus</i>
<i>Arisaema dracontium</i>	<i>Datura stramonium</i>
<i>Aristida purpurea</i>	<i>Desmanthus illinoensis</i>
<i>Arundinaria gigantea</i>	<i>Clematis virginiana</i>
<i>Asplenium rhizophyllum</i>	<i>Clinopodium arkansanum</i>
<i>Astragalus canadensis</i>	<i>Desmodium pauciflorum</i>
<i>Botrychium biternatum</i>	<i>Dicentra cucullaria</i>
<i>Brachyelytrum erectum</i>	<i>Dichanthelium linearifolium</i>
<i>Carex albicans</i>	<i>Dichanthelium malacophyllum</i>
<i>Carex grisea</i>	<i>Diodia teres</i>
<i>Centaurea americana</i>	<i>Echinochloa cruss-galli</i>
<i>Cheilanthes alabamensis</i>	<i>Eupatorium altissimum</i>
<i>Cheilanthes lanosa</i>	<i>Galactia regularis</i>
<i>Chenopodium album</i>	<i>Galium aparine</i>
<i>Desmodium canescens</i>	<i>Galium pilosum</i>
<i>Croton glandulosus</i>	<i>Geum canadense</i>

<i>Gillenia stipulata</i>	<i>Ranunculus sceleratus</i>
<i>Grindelia papposa</i>	<i>Rubus occidentalis</i>
<i>Ipomoea coccinea</i>	<i>Rumex crispus</i>
<i>Lespedeza cuneata</i>	<i>Samolus valerandi</i>
<i>Liatris aspera</i>	<i>Sanicula canadensis</i>
<i>Liatris elegans</i>	<i>Saponaria officinalis</i>
<i>Lycopus americanus</i>	<i>Scirpus atrovirens</i>
<i>Matelea gonocarpos</i>	<i>Senna marilandica</i>
<i>Melilotus officinalis</i>	<i>Silene regia</i>
<i>Minuartia patula</i>	<i>Smilax herbacea</i>
<i>Monarda punctata</i>	<i>Solanum elaeagnifolium</i>
<i>Nasturtium officinale</i>	<i>Solidago canadensis</i>
<i>Opuntia macrorhiza</i>	<i>Solidago missouriensis</i>
<i>Oxalis dillenii</i>	<i>Strophostyles leiosperma</i>
<i>Phemeranthus parviflorus</i>	<i>Taenidia integerrima</i>
<i>Physalis longiflora</i>	<i>Trepocarpus aethusae</i>
<i>Poa compressa</i>	<i>Trifolium hybridum</i>
<i>Poa sylvestris</i>	<i>Triphora trianthophora</i>
<i>Prunus americana</i>	<i>Urtica dioica</i>
<i>Prunus persica</i>	<i>Veronica polita</i>
<i>Quercus falcata</i>	<i>Vitis rotundifolia</i>

CHAPTER II

A FLORISTIC TREATMENT OF THE GENUS *QUERCUS* IN OKLAHOMA

INTRODUCTION

Oklahoma exhibits a highly diverse vascular flora that comprises 173 families, 850 genera, and 2,465 species (Tyrl et al., 2007). These numbers of taxa reflect the diversity of environmental and ecological gradients in the state— climate, elevation, topography, geology, soils, and biota. Species representative of the eastern deciduous forest, the Rocky Mountains, the Chihuahuan and Sonoran Deserts, the Gulf and Atlantic Coastal Plains, and the Ozark Mountains meet those of the central grasslands that extend across the state from north to south (Duck and Fletcher, 1943; Tyrl et al., 2007).

Urnaldy Theodore Waterfall was the first taxonomist to compile a comprehensive key for the identification of the vascular plant species in Oklahoma. His *Keys to the Flora of Oklahoma* (1969) provided diagnostic characters for all species, but unfortunately lacked accompanying morphological descriptions essential for confirming the identities of unknown plants. Use of this publication required continual checking of the morphological descriptions in other floristic treatments such as *Gray's Manual of Botany* (Fernald, 1950), *Manual of the Vascular Plants of Texas* (Correll and Johnston, 1970), *Flora of the Great Plains* (Great Plains Flora Association, 1986), and the *Flora of Missouri* (Steyermark, 1963). A modern treatise on the flora of Oklahoma including

morphological descriptions of all taxa, current classifications of families and genera, and species, and current nomenclature is needed.

To meet this need, the non-profit corporation Flora Oklahoma Incorporated was formed in 1983 to provide a modern treatment of the vascular plants of Oklahoma (Tyrl et al., 2007). The goal of this organization is the eventual publication of the *Flora of Oklahoma*; a taxonomic work that will furnish its users keys and descriptions for all families, genera, and species in the state. In order to provide students and others needing to identify plants current keys and descriptions as soon as possible, the Editorial Committee of the corporation has sequentially published portions of its work as they were completed. Publications to date include *Key to the Vascular Plants of Oklahoma* (1994), which consisted of just a key to families; *Key and Descriptions for the Vascular Plant Families of Oklahoma* (1997); *Identification of Oklahoma Plants* (2003), which included keys to genera; and *Keys and Descriptions for the Vascular Plants of Oklahoma* (2007) which comprised keys to the genera and species of all families. The descriptions of species and genera of all families will accompany the keys when the *Flora of Oklahoma* is finally published. The editorial committee has invited many plant taxonomists to write treatments of selected families, genera, and species. A treatment of the genus *Quercus* in the family Fagaceae and additional information is contributed here. Specific objectives of my work were four: (1) to compile a list of Oklahoma taxa of *Quercus*; (2) to describe the range of morphological variation of each taxon present in the state; (3) to write technical descriptions of each taxon; and (4) to construct a key permitting the rapid and accurate identification of all taxa. The descriptions and key will be submitted to the Editorial Committee of the Flora of Oklahoma Project.

In the following sections the results of a literature review of the taxonomy and biology of *Quercus* and other members of the Fagaceae are presented followed by a review of how the treatment of *Quercus* was prepared. The chapter concludes with the key for identification of sections and species, and the description of each species.

TAXONOMY AND BIOLOGY OF THE FAGACEAE

The Fagaceae, or beech family, comprises a diverse group of hardwood angiosperms broadly distributed south of 60° latitude primarily in the Northern Hemisphere and equatorial Polynesia (Nixon, 1997a). In both temperate and tropical regions, its members are prominent in most forests, woodlands, savannas, and scrublands (Cooper, 1902; Wang, 1961; Backer and Bakhuizen Van Den Brink, 1965; Vankat, 1979; Boucher, 1981; Nixon and Crepet, 1987; Ellenberg, 1988; Nixon, 1997a; Peterson and Boyd, 1998; Li et al., 1999; Terradas, 1999; Hoagland, 2000; Ozel, 2000; Tang, 2006; Nixon, 2006; Tang and Ohsawa, 2009). Importance of this family is obvious in terms of biomass (Nixon, 1993b; Nixon, 1997a; Hoagland, 2000; Manos and Stanford, 2001), and ecologically significant considering the numerous fungal, insect, avian, and mammal relationships that have evolved with it (Brodkorb, 1972;; Stone et al., 2008; Xiao et al., 2009). The oldest fossils attributable to modern taxa are from the late Cretaceous (Muller, 1981; Jones, 1986; Cronquist, 1988; Manos and Steele, 1997; Manos et al., 2001); however, numerous fossils from the early Tertiary exhibit possible relationships as well (Crepet and Daghljan, 1980; Daghljan and Crepet, 1983; Manchester, 1983; Axelrod, 1983; Zhou, 1993; Nixon, 1993a; 1993b; Manos and Stanford, 2001).

Genera of the family are traditionally distinguished by the production of cupules subtending one or more nuts, and early taxonomists and cladists recognized that these structures were commonly derived (Jones, 1986; Cronquist, 1988; Nixon and Crepet, 1989; Nixon, 1997a; Manos, 2001; Singh, 2004; Manos, 1997; Manos et al., 2001; Oh and Manos, 2008). Recent molecular evidence has also supported the family as monophyletic (Manos et al., 1993; Manos and Steele, 1997; Manos et al., 2001; Li et al., 2004; Oh and Manos, 2008). As summarized in Table 1, the Fagaceae is presently thought to comprise 9 genera and about 900 species worldwide (Nixon and Crepet, 1989; Nixon, 1997a; Deng et al., 2006).

Germination syndromes have been considered the most informative morphological indicators of phylogeny among the genera and are supported by molecular studies of plastomes (Manos et al., 1993), internally transcribed spacer (ITS) regions (Manos et al., 2001), and single copy nuclear gene (CRC) sequences (Oh and Manos, 2008). Genera exhibiting the hypogeous germination syndrome include *Quercus*, *Castanopsis*, *Chrysolepis*, *Colombobalanus*, *Lithocarpus*, and *Castanea*; whereas *Fagus*, *Trigonobalanus*, *Colombobalanus*, *Formenodendron* produce seedlings via the epigeous germination syndrome.

Hypogeous germination is particularly advantageous because the cotyledons remain below ground, and thus, may be protected from fire and herbivory (Brose et al., 2005). Furthermore, the energy conserved within the tissue is more likely to facilitate primary root development essential for vegetative growth and seedling establishment (Brose et al., 2005). In addition, it appears that established seedlings exhibit vigorous

Table 1. Genera, number of species, and geographical distribution of the Fagaceae (Nixon and Crepet, 1989; Nixon, 1997a; Deng et al., 2006).

<u>Genus</u>	<u>Number of Species</u>	<u>Principal Geographic Distribution</u>
<i>Castanea</i> L.	10–12	North America, Europe, Asia
<i>Castanopsis</i> (D.Don) Spach	120	tropical and subtropical Asia
<i>Chrysolepis</i> Helmq.	2	West Coast of North America
<i>Colombobalanus</i> Nixon & Crepet	1	South America
<i>Fagus</i> L.	10	North America, Europe, Asia
<i>Fomenadendron</i> Nixon & Crepet	1	subtropical Asia
<i>Lithocarpus</i> Blume	340	Asia, Polynesia, West Coast of North America
<i>Quercus</i> L.	400–500	North America, Central America, West Indies, South America, Europe, Asia
<i>Trigonobalanus</i> Forman	1	Polynesia

root development following removal of the aerial stem; a trait that facilitates vegetative regeneration of the plant (Sander and Clark, 1971; Conard, 1987; Sander, 1990a, b; Sullivan, 1994a, b, c; Fryer, 2008).

As its name implies, in epigeous germination, the cotyledons are carried above ground by elongation of the hypocotyl and thus are more susceptible to disturbance.

Four genera of the Fagaceae exhibit this syndrome: *Fagus*, *Trigonobalanus*, *Formanodendron*, and *Colombobalanus*. Of the four, *Fagus* is the only globally widespread taxon. It is competitive ecologically with genera possessing hypogeous germination (Barnes et al., 1998). Establishing in moist soils and shades, it, however, does exhibit less vigorous vegetative regeneration following disturbance (Tubbs and Houston, 1990). The other three genera appear to have declined from comparable widespread geographical distributions 70 million years ago to isolated, nearly extinct populations (Jones, 1986).

Regardless of germination syndrome, evergreen species in the family have higher endemism (Cannon and Manos, 2003; Sun, 2006; Nixon, 2006; Tang and Ohsawa, 2009). Deciduous species, including those of *Fagus*, *Castanea*, and *Quercus* are currently the most widespread.

As is apparent in Table 1, five genera — *Quercus* (oak), *Fagus* (beech), *Castanea* (chestnut), *Castanopsis* (chinquapin), and *Lithocarpus* (tanoak) — are relatively widespread, contain most of the species in the family, and relatively well known. The other four are less well known, restricted in distribution, and either monotypic or with just two species.

Historically, taxonomists have had different opinions about how to classify several of the genera. For example, early taxonomists submerged *Formanodendron* and *Colombobalanus* in *Trigonobalanus*. These monotypic genera, however, are different in pollen and floral morphology, as well as geographic distribution (Nixon and Crepet, 1989; Huang et al., 1998; Tropicos, accessed April 2009). *Colombobalanus*

excelsa is endemic to Columbia, whereas *Formanodendron doichangensis* is endemic to regions of Thailand and China and *Trigobalanus* occurs only in Polynesia.

Also illustrative of this difference in taxonomic opinion is *Chrysolepis*, a genus comprising two species that are endemic to the evergreen forests along the West Coast of the United States (Nixon, 1997a; Little, 1979). At one time, this genus was submerged in the Asian genus *Castanopsis* (McKee, 1990), but subsequent taxonomic work (Hjelmquist, 1948; Forman, 1966) revealed that the two taxa differ in cupule structure.

Lithocarpus, both morphologically and ecologically similar to *Chrysolepis*, comprises one species in North America and 339 in Asia and Polynesia (Nixon, 1997; Little, 1981; Tappeiner et al., 1990; McKee, 1990).

Historically, the family also included the genus *Nothofagus*, commonly known as the southern beech, but it is now placed in its own family on the basis of molecular phylogenetic studies (Angiosperm Phylogeny Group, 2009). It is a genus of about 35 species of trees and shrubs native to temperate and tropical South America and Australasia.

In the deciduous forest of North America, three genera—*Fagus*, *Castanea*, and *Quercus*—dominate (Nixon, 1997a). Typically encountered as massive trees with smooth bark, *Fagus*, or beech, has ovate, serrate leaves and trigonous nuts subtended by a 3- or 4-valved muricate husk. Forests of Asia and North America in which *Fagus* is prominent have high species diversity when compared with forests of Europe, which in some cases, may consist solely of this genus (Peters, 1997). In North America, a single species with two varieties is native (Little, 1979; Nixon, 1997a). *Fagus grandifolia* var.

grandifolia occurs throughout the eastern deciduous forest of the United States and Canada, and reaches its western distributional limits along the eastern edge of Oklahoma in LeFlore and McCurtain counties (Little, 1981; Hoagland et al., 2000). Variety *mexicana* is endemic to the cloud forests of Mexico where it is increasingly in danger of extinction (Williams-Linera, 2002; Rowden et al., 2004). *Fagus* nuts are relished by wildlife (Halls, 1977) as are the exposed cotyledons due to epigeous germination (Manos et al., 2001). The species is highly tolerant of shade which allows it to compete with other less shade tolerant members of the beech family when fire is suppressed (Barnes et al., 1998). The species in the United States is used for high quality structural timber and fuel wood; however, regeneration has been difficult in recent times (Tubbs and Houston, 1990). In addition to the native species, the introduced *Fagus sylvatica*, commonly known as the European beech, is cultivated in North America.

Historically encountered as massive trees dominating the canopy of eastern forests, *Castanea*, known as chestnut or chinquapin or chinkapin, is represented in North America by three native species: *C. dentata*, *C. ozarkensis*, and *C. pumila* (Nixon 1997a). They all have elliptic to lanceolate leaves with serrations that terminate in awns (Jones, 1986). The nuts are globose or flattened on one side and subtended by a 2- to 4-valved spinose husk. Once highly managed for in North America because of its edible nuts and rot resistant wood, the genus is now considered endangered because of its susceptibility to chestnut blight (Vankat, 1979). In Europe and Asia, the genus exhibits higher disease resistance (Huang et al. 1999). *Castanea dentata*, a once dominant forest tree in the eastern deciduous forest of North America (Vankat, 1979; Nixon,

1997a), was decimated by fungal blight, *Cryphonectria parasitica*, in about 50 years following the initial 1904 outbreak (Dirr, 1998). The disappearance of *C. dentata* in the canopy of the eastern deciduous forest resulted in replacement by *Quercus* and *Carya* (Braun, 1950; Woods and Shanks, 1959; Vankat, 1979; Barnes et al., 1998). Although *Castanea dentata* did not occur in Oklahoma (Little, 1979; Nixon, 1997a; Russell, 1987), the fungal pathogen spread into the state decimating populations of *Castanea ozarkensis* and *C. pumila*.

Although the aerial portions of *Castanea* is killed by the fungus, the rootstocks typically survive and produce new shoots from a burl-like tissue called the “root collar” at their apices (Paillet, 1993). These shoots grow to varying heights, usually about 5–7 meters, become infected with the fungus, and die back (Paillet, 2002). I observed similar die back of *C. ozarkensis* in Adair County Oklahoma. In the growing season of 2007, a small tree with a diameter of 7 cm at breast height was observed dying back to ground level. In the growing season of 2008, new sprouts emerged from the crown and grew 1–1.5 meters tall. Nixon (1997) reported that populations of *C. pumila* have been rediscovered in New York. This species ranged as far west as the southeastern corner of Oklahoma at one time. It can be distinguished from the other two species by its densely pubescent twigs (Nixon, 1997a). With a natural tendency for vegetative regeneration, it has exhibited vigor despite some susceptibility to fungal blight and has been observed to produce nuts on the young sprouts of both wild and cultivated individuals (Sullivan, 1994a). Restoration of the genus in North America is of particular interest to foresters and arborists, and may be possible via special breeding programs in conjunction with enhanced cultural measures (Griffin, 2000).

BIOLOGY AND TAXONOMY OF *QUERCUS*

Biology—Without question, the best known and most important genus of the Fagaceae is *Quercus*, or the oak genus (Muller, 1951b; Johnson et al., 2002; Logan, 2005). Estimates of the number of species range between 400 and 500 throughout in its geographical range throughout North and Central America, northwestern South America, Europe, Asia, and north Africa (Nixon, 1997b; Manos et al., 1999). A few naturalized populations occur in South Africa and Australia (Watt and Breyer-Brandwijk, 1963; Hewson, 1989). Nixon (1993b) estimated that 220-225 species are present in the Americas; Mexico being the center of diversity with 135-150 species. Within its natural range, *Quercus* accounts for most of the distribution of the Fagaceae outside the temperate deciduous forests and mixed broad-leaf-evergreen forests in the northern hemisphere where it is one of the dominant species (Manos et al., 1999; Nixon, 2006). Unequivocal fossil evidence from Texas places its origin as far back as 30 million years ago, although fossils from Oregon suggest that modern *Quercus* may have emerged as far back as the Eocene (Crepet and Daghljan, 1980; Crepet and Nixon, 1989; Nixon, 1993b).

Economic Significance—For early humans, the genus was a highly valued food crop and source of medicine (Nixon, 1997b; Moermann, 1998; Schonbeck and Frey, 2005), and in some instances it continues to be used for those purposes (Czygan et al., 1994; Roberts et al., 2001). The contributions that oak barrels impart to the flavor and color of wine was first recognized by the Romans (McNeil, 2001), and these properties are now considered to have medicinal value as well (Towey and Waterhouse, 1996; Gil et al., 2006; Saucier et al., 2006; Canas et al., 2008). Cultivation of oaks also dates to the Romans (Terredas, 1999). Currently, *Quercus* accounts for approximately one-third to one half of the hardwood saw timber volume

in the eastern United States; with the most highly valued stocks of wood used in furniture, flooring, cabinets, trim, veneer, barrels, artwork, planks, railroad ties, pulpwood, and as fuel (Brown, 1949; Irgens-Moller, 1955; Olsen, 1974; Solomon, 1987; Craig et al., 2001; Stein et al., 2003; Howard, 2003; Cafferty, 2005; Samuelson and Hogan, 2006; Cassens, 2007). The fast growing nature of eastern North American species bolstered demand for exports to other continents during the late 20th Century (Luppold, 1984; Luppold and Baumgras, 1995; American Hardwoods Export Council, n.d.). Slower growing, drought tolerant species of the forests, woodlands, and savannahs to the west are locally valued for the wildlife habitat, fuel wood, and the cheap lumber they provide (Vines, 1982; Stahl and McElvaney, 2003; Samuelson and Hogan, 2006; Abella, 2008). In Oklahoma, *Quercus* is the primary hardwood tree grown for timber stock, as well as the leading hardwood used in the output of veneer, saw logs, and pulpwood (Miller et al., 1993; Howell and Johnson, 2003; Johnson et al., 2008). The most productive oak timberland consists of plantings south of the Canadian River where the length of the growing season and the amount of precipitation are the greatest (Rosson, 2001).

Replacement of oak by other species in both harvested and protected forests has become a problem in Oklahoma (Kabrick et al., 2007). While site quality greatly impacts the successfulness of oak regeneration in the eastern quarter of the state, the absence of environmental disturbance, for example fire, has undermined the quality of oak woodlands in the rest of Oklahoma (Phillips et al., 2005). Innovational strategies in commercial harvesting that simultaneously promote the ecological integrity of less economically important biota are an additional concern (Johnson, 2002; Berg et al., 1994; Anglestam, 1996; Bauhus et al., 2009). The economic value of forests, woodlands, and savannahs in the central and western parts of Oklahoma are simultaneously suffering because of successive replacement by *Juniperus*

virginiana (Bidwell et al., 2006). Ultimately, the exclusion of fire has supported the proliferation of tree species of lower value in areas historically dominated by oak (Nowacki and Abrams, 2008). Because the use of fire regimes as a management tool is difficult to reestablish in many instances, costly restoration management, e.g., mechanical removal of understory and planting of seedlings, may need be implemented to prevent further degradation of oak ecosystems (Johnson, 1992; Brudvig and Asbjornsen, 2007; Bauhus et al., 2009). Oaks are naturally adapted to disturbance (Johnson, 1992; Nowacki and Abrams, 2008), and their ecosystems spanning the North American continent were actively managed for by Native Americans using fire (Abrams, 1986; Abrams, 1992; Batek et al., 1999; Johnson et al., 2002; Nowacki and Abrams, 2008). The size, and thus, energy reserves in acorns are increased by their proximity to photosynthetic leaves (Kormanik et al., 1998; Gribko et al., 2002). Leaves exposed to light in the upper canopy have been observed to be the primary positions for fruit set in closed canopy oak forests (Drake, 1991; Beck, 1992; Gribko et al., 2002). Other effects include a previous year's masting (Sork et al., 1993), weather, pollination success, disease, herbivores, and genetics have influences as well (Johnson, 1994; Gribko et al., 2002). Disturbance that creates light infiltration of the canopy and decreases the influence of shade tolerant vegetation simultaneously bolsters growth of advance regeneration and vegetative regeneration of oak (Crow, 1992; Meiners & Minkovic, 2002; Spetich et al., 2002; Brudvig and Asbjornsen, 2007; Kabrick et al., 2007).

Wildlife Significance—*Quercus* is one of the most important genera for wildlife in North America. In addition to providing shelter and nest sites, it is a most valuable food source. The acorns of most species are highly preferred by songbirds, gamebirds, and

both large and small mammals (Hardin and Evans, 1977; Bernardo et al., 1992; Aquilani et al., 2003; Keyser and Ford, 2005; Greenberg et al., 2007). Fossilized nut caches indicate a relationship between ancient vertebrates and species of *Quercus* shortly after the radiation of mammals (Manchester, 1983, 1987; Gee et al., 2003). The effects of acorns on the fecundity of mammals are documented (Johnson et al., 2002). Black bears (*Ursus americanus*) are known to forage acorns (Landers et al., 1979), as was evidenced by their accelerated behaviors to cause losses to crops and livestock in years of low mast production in Minnesota (Rogers, 1976). The health of bears in the southeastern forests of the United States has been related to their diet of eastern oak species (Vaughan, 2002). Whereas most bears (Urdidae), deer (Cervidae), hogs (Suidae), possums (Didelphidae), raccoons (Procyon), skunks (Mephitidae), and rodents (Muridae) are detrimental to the fate of acorns, squirrels (Sciuridae) facilitate their odds for dispersal and proliferation (Johnson, 2002). Similar caching behaviors have been observed among Asian and American squirrel populations (Xiao et al., 2009); these adaptations over broad geographic areas parallel the similar widespread distributions of oaks (Axelrod, 1983; Manos et al., 1999). This relationship has been estimated to have persisted since the Eocene based on the fossil records of oaks, squirrels, and nut caches (Manchester, 1983, 1987; Gee et al., 2003). Jays (*Cyanocitta*) have an equally distant origin (Brodkorb, 1972); their behaviors of dispersal, nut caching, and establishment of oak seedlings from small sized acorns being especially important in America and Europe (Darley-Hill and Johnson, 1981; Scarlet and Smith, 1991; Moore and Swihart, 2006; Pons and Pausas, 2007). While foraging of acorns and

habitation of oak forests by other bird species is apparent, none are known that compare as significantly to the proliferation of oak.

Canopy disturbance from fire has been demonstrated as an adequate tool for the maintenance of native bird species habitat in the eastern deciduous forest (EDF) (Hardin and Evans, 1977; Johnson, 1992; Aquilani et al., 2003; Greenberg et al., 2007). In the shinnery oak grasslands, endemic bird species, such as the endangered Lesser Prairie Chicken (*Typanachus pallidicinctus*), have depended on the constant removal of tall shoots by natural and anthropogenic sources of fire (Axelrod, 1983; Peterson and Boyd, 1998; Boyd and Bidwell, 2001; 2002; Bailey and Thompson, 2005). Throughout various oak vegetation types, diverse species of insects (Taper et al., 1986; Mopper and Simberloff, 1995; Allison and Schultz, 2005; Hayward and Stone, 2005; Ikai and Hijii 2007; Liljeblad, et al. 2008), fungi (Marçais and Delatour, 1996; McDonald et al., 1998; Appleton et al., 2003), and microorganisms (Nienhaus, 1989; Gribko et al., 2002) are suited to them, and in some instances are obligate (Johnson, 2002; Manos and Stanford, 2001).

Oklahoma has a diverse assemblage of oak dominated ecosystems including Crosstimbers, oak woodland, oak savannah, oak-hickory forests, oak-pine forests, shinnery oak grasslands, and oak-pinon-juniper scrubland (Tyrl et al., 2002). The only counties without at least a small, historically significant (Bruner, 1931; Duck and Fletcher, 1943; Rice and Penfound, 1959; Vankat, 1979; Little, 1981; Boyd and Peterson, 1998; Hoagland et al., 1999; Hoagland, 2000; Dyer, 2006) occurrence of oak are Texas and Beaver Counties in the panhandle (Williams, 1973; Little, 1971; Little, 1976; Stein et al., 2003; Oklahoma Vascular Plants Database, 2008).

Taxonomy—The genus *Quercus* is represented in North America by 90 species in three sections (Table 2) (Irgens-Moller, 1955; Nixon, 1993a, 1997). Species from elsewhere in the world have been introduced as ornamentals and may eventually naturalize (Gilman and Watson, 1994; Goelz and Carlson, 1997; Katzur and Haubold-Rosar, 2004; Nixon and Muller, 1997).

Table 2. Sections of the genus *Quercus* in North America (Irgens-Moller, 1955; Nixon, 1993a, 1997).

<u>Section</u>	<u>Common Name</u>
<i>Lobatae</i> Loudon	red or black oaks
<i>Protobalanus</i> (Trelease) A. Camus	golden cup or intermediate oaks
<i>Quercus</i> (including Sections <i>Ilex</i> and <i>Cerris</i>)	white oaks

Representatives of Section *Lobatae* (red or black oaks) and Section *Protobalanus* (golden-cup oaks) are present only in the Americas (Nixon, 1997a). In contrast, Section *Quercus* (white oaks), are found in tropical and temperate forests to desert scrublands of the northern hemisphere in North and Central America, Eurasia, and North Africa (Nixon, 1993a, 1997a). The section is now interpreted to include species belonging to the formerly recognized Section *Ilex* (Hungarian oaks) and Section *Cerris* (Turkish oaks), all of which are endemic to Eurasia (Irgens-Moller, 1955; Nixon, 1993a; Borgardt and Nixon, 2003).

The three sections are distinguished on the basis of differences in morphology

(Camus, 1934–1954; Nixon, 1993b, 1997; Ozel, 2000), anatomy (Hardin, 1979a, b; Jones, 1986), palynology (Bussotti and Grassoni, 1997; Solomon, 1983a, 1983b), physiology (Bonner, 1971, 1974; Ozcan, 2007), ontology (Mogenson, 1965; Cottam et al., 1982; Manos, 1997a; Boavida et al., 2001; Borgadt and Nixon, 2003; Deng et al., 2008) in addition to reproduction, genetics, ecology, and geography .

Most commonly encountered in North America are the white oaks and red or black oaks. In *Species Plantarum* (1753), Linnaeus grouped white oaks from Europe and North America together and thus informally recognized Section *Quercus*. J.C. Loudon in his 1830 *Hortus Britannicus* distinguished red or black oaks from white oaks on the basis of leaf lobe morphology when he established his group *Loba'te* or Section *Lobatae* as it is now known (Nixon, 1993b). Although recognized as distinct evolutionary lineages, the two sections are closely related. Their geographical and ecological association throughout most of their range in North America is suggestive of evolutionary convergence (Cavender-Bares et al., 2004). Species of the two sections have similar karyotypes. There is uniformity in chromosome number with $2n = 24$ (Duffield, 1940; Ohri and Ahuja, 1990; D'Emerico et al., 1993; Nixon, 1997; Jensen, 1997; Chokchaichamnankit et al., 2006; Dzialuk et al., 2007). Variability in chromosome structure and the localization of ribosomal genes between and within sections is also similar to some extent (D'Emerico et al., 1993; Zoldo et al., 1998; Zoldos et al., 1999). The phylogeny of the two sections is supported by the cladistic analyses of molecular data (Manos et al., 1999; Oh and Manos, 2008).

In Oklahoma, the 24 native species of *Quercus* are present in all counties with the exception of Beaver and Texas in the Panhandle (Little, 1981; Oklahoma Vascular

Plants Database, 2008). Section *Quercus* is the more ecologically diverse section, with its members occupying both the driest sands in the western part of the state (Tucker, 1961; Peterson and Boyd, 1998) and the wettest soils in the eastern part (Clark and Benforado, 1981; Wharton et al., 1982; Mitsch and Gosselink, 2000). This ecological versatility is exhibited by species of the section throughout the northern hemisphere (Nixon, 1993b), and may be greatly attributable to the broad range of adaptations in the roots of species in the section (Peterson and Boyd, 1998; Burke et al., 2004). In contrast, Section *Lobatae* does not exhibit the species diversity or ecological breadth that Section *Quercus* does (Nixon 1993b; Cavender-Bares et al., 2004; Haney et al., 2008). This is illustrated in arid western Oklahoma where moisture limits the distribution of species of the section (Bruner, 1931).

Reproductive Characters & Taxonomy—Although the sections of *Quercus* are for the most part well delineated on the basis of a wealth of information as outlined above, problems in distinguishing individual plants of Sections *Quercus* and *Lobatae* do occur (Nixon, 1993b; Borgadt and Nixon, 2003). In Oklahoma, morphology of the pistillate flowers and maturation of the acorns are the best means of distinguishing the two sections and their respective species. Aspects of these features are outlined below.

Morphology of the staminate catkins in the genus exhibits considerable plasticity and are not of significant value in distinguishing sections and species (Muller, 1951b; Nixon, 1997b). In contrast, the pistillate flower is quite useful (Muller, 1951b). In Section *Lobatae*, there is a flange of tissue arising from the peduncle that surrounds the cupule at the base of the pistil (Figure 1). Nixon (1993b) described this flange as an unequivocally effect character for delineation of the section and evidence for the

section's monophyly. In Section *Quercus* there are stipules that at times will subtend the pistillate flowers, but nothing morphologically comparable to the flange in Section *Lobatae* (Figure 2).

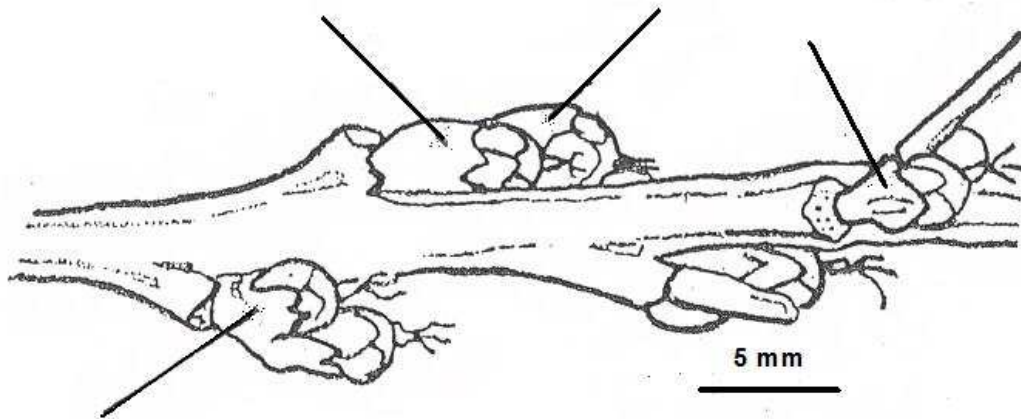


Figure 1. Pistillate flowers of *Quercus velutina*. Lines indicate flanges extending from peduncles and subtending individual flowers. Drawing by Will Lowry.

It must be noted that remnants of the peduncles and aborted flowers can appear somewhat bract-like in species of both sections at acorn maturity. The aborted flowers may reach various sizes before growth ceases and may persist as the fertilized pistils mature and expand. Pistillate flowers in *Quercus* remain microscopic until a few months before maturation (Bonner and Vozzo, 1987). Differences among species typically are only discernable near the time of fruit maturation in late summer and early fall. Maturation of the acorns in Section *Quercus* occurs in one growing season, whereas in Section *Lobatae* maturation takes two growing seasons, albeit a few species of the latter section mature annually in California (Nixon, 1993b; Nixon, 2002). Because

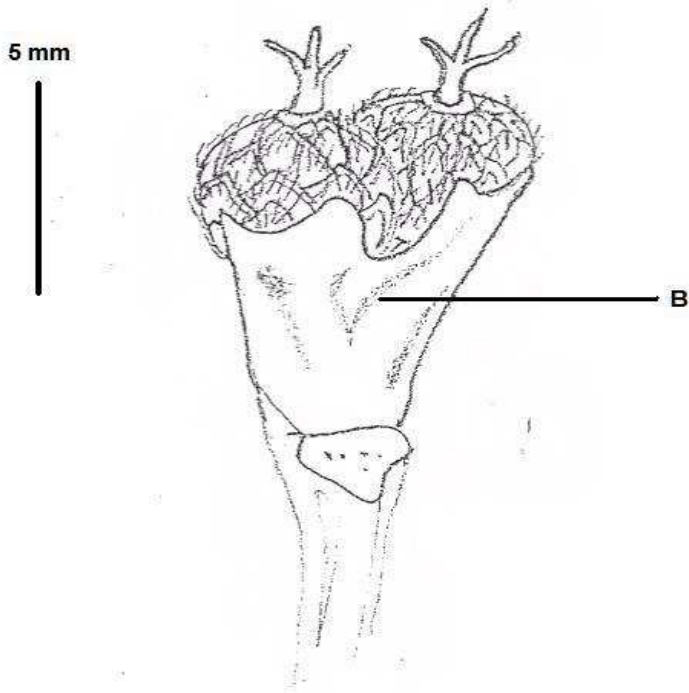
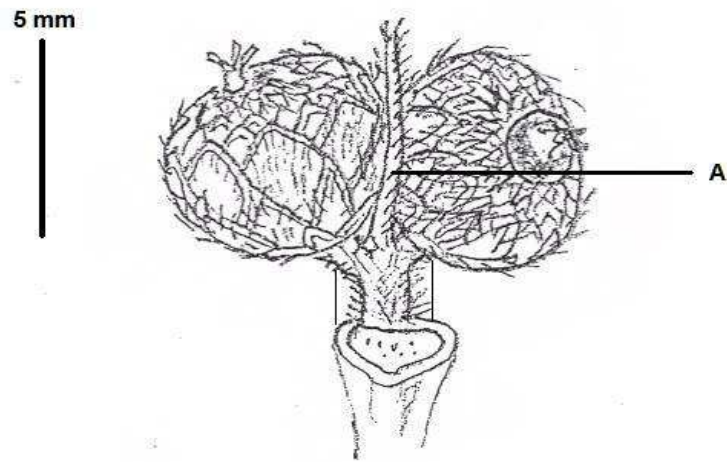


Figure 2. Upper: Pistillate flowers of *Quercus margaretta* (Sect. *Quercus*) subtended by pubescent stipule (A). Lower: Pistillate flowers of *Quercus velutina* (Sect. *Lobatae*) subtended by glabrous flange (B). Drawing by Will Lowry.

Section *Lobatae* has two generations of acorns on first and second year twigs, the flange that subtends the flower is exceptionally apparent late in the first season. By acorn maturity in the second season, the flange may begin to blend into the texture and color of the peduncle from which it extends.

De Candolle was the first to separate sections of the genus using the differences of the orientation of aborted ovules between the sections, and since then it has been used by a multitude of classifications (Borgardt and Nixon, 2003). Those of Section *Quercus* are oriented basally, whereas in Section *Lobatae* they are apical (Borgardt and Nixon, 2003). These aborted ovules are more conspicuous at the apices of the nuts in Section *Lobatae*, but in order to see them the pericarp must first be removed from the nut.

The pistillate flowers also differ in the appearance of their cupule scales. Cupules subtending the nut in Section *Lobatae* bear scales that remain flattened and appressed into maturity, with exception of some of the larger fruited species, whereas the scales of cupules in Section *Quercus* are frequently basally creased or tuberculate at maturity, with exception of some of the smaller fruited species. Persistently silvery pubescent or tomentose cupules are a typical feature of Section *Quercus*. In contrast, in Section *Lobatae*, the pubescence is variously deciduous, but rarely persists after winter weathering removes it. Cupules that appear silver or white are covered by pubescence whereas the tissue of scales is actually colored by various photosynthetic pigments. Hints of the underlying pigmentation sometimes occur when the cupules appear greenish, reddish, or purple tinged. A golden appearance is created by the reflectance of the yellow pigmentation off of the silver or whitish hairs while the darker purple, red

and greenish pigments seem to cause a silvery cupule in Section *Quercus*. In a few species, e.g., *Q. alba*, there is an actual coating of a golden-colored “wax”. This phenomenon is more commonly seen on scales of cupules in Section *Lobatae*. They are typically orange to red, but can appear silvery or golden from dense silver, red, or golden tomentum; in addition to a “wax” coating in the eastern deciduous species.

Cupule shape does not appear to be a reliable means of distinguishing among species or sections. Although cupule width at the rims is influenced by the expansion of the nut; there are few species in which that the cupule rim does not appear to grip the nut. In Section *Lobatae*, the cupule is often more dish-shaped than in Section *Quercus*; though this is not uniformly so and is often variable among acorns of the same tree.

The inner indumentum of cupules has been used traditionally in the past to differentiate sections—Section *Lobatae* characterized as tomentose—but reliance on this feature should be avoided because higher magnification (>100x) reveals that the supposedly glabrous inner cupules of acorns in Section *Quercus* are indeed tomentose. Because this tomentum is silvery and quite minute, the cupules may appear glabrous due to reflection of the colored pigments of the tissue. Furthermore, *Q. alba*, *Q. havardii*, *Q. macrocarpa*, *Q. mohriana*, and *Q. turbinella* seem to produce conspicuous tomentum on the inner surface of the cupules that is discernable to the naked eye. The pubescence covering the nuts among species in each section is much more reliable. Only one species in Section *Quercus*—*Q. macrocarpa*—produces nuts that are covered with tomentum in the area of contact with the cupule. However, the tomentum that covers nuts of both sections may be weathered off before winter, or simply rubbed off. Using the character depends on obtaining fresh material that has been handled gently.

Trichomes & Taxonomy—Hairs (trichomes) also can be used to distinguish sections, and in some cases species. Using electron microscopy, Hardin (1979a, b) classified the eastern oak species of North America by the presence, absence, and persistence of eight types of hairs covering the adaxial and abaxial leaf surfaces. Five of these hair types can be grouped together as “stellate” using the traditional phytographic definition. Because the names he used for these hairs require extensive knowledge of electron microscopy to fully appreciate, they are not used in this treatment. However, combinations of features exhibited by the stellate hairs are distinguishable using an ordinary dissecting scope, and can be used to categorize hair types of individual species.

Stellate hairs generally consist of multiple appendages from a subtending base or stalk, termed “rays”. Stellate hair types can be differentiated based on persistence, location, color, basal or stalked attachment, and ray number, aspect, length, and straightness. The pubescence of oak leaves coincides with early stages of development (Hardin, 1979a, b). Some oak species produce leaves that shed a majority of their initial hairs before becoming fully expanded; this is especially true for hairs borne on the adaxial surfaces (Hardin, 1979a, b). Other species retain them on one or both surfaces, but generally produce fewer hair cells on the adaxial surfaces (Hardin, 1979a, b). The western most species in Oklahoma in some instances retain hairs on both surfaces of the leaves, perhaps to avoid excessive levels of radiation and desiccation (Karabournitis et al., 1992). Loss of pubescence on mature leaves in many eastern oak species is believed to reflect a transition from morphological to chemical defenses via heightened levels of tannins (Johnson, 1975). Persistence of hairs, and in some

instances different pubescence types, has also been related to sun exposure and leaf placement in the canopy. The retention of hairs on shaded leaves of *Q. velutina* has been correlated with protection from herbivory (LeCorff and Marquis, 1999; Lill et al., 2006). Like other leaf characters, hair morphology and density may vary with position of the leaf in the tree's canopy, and thus the collection of leaves from different tiers of the canopy must be performed to gather data for complete species descriptions (Blue and Jensen, 1989). The need to do this is especially important when attempting to identify *Q. velutina*, *Q. macrocarpa*, *Q. muehlenbergii*, and *Q. lyrata*. In Oklahoma, members of Section *Quercus* produce leaves bearing hairs that are generally persistent, with exception of *Q. alba*. Some species of the section may lose many hairs during the growing season, but usually some are retained along the midribs. In contrast, a majority of the species in Section *Lobatae* shed the hairs covering the leaf surfaces except for small tufts in the vein axils of the abaxial surfaces.

With respect to hair color, different species can have hairs that are described as silvery, white, sulphurous yellow, or red. Coloration of stellate trichomes is the result of exudates produced by the base or stalk below the rays. These exudates in some species may form amber-colored, crystalline projections on the leaf surfaces that are conspicuous with magnification. The hardened projection typically envelops the base of the stellate hairs. Rays are colorless unless otherwise lightly "glazed". Silvery and white hairs generally lack exudates that otherwise would give them a sulphurous yellow to red appearance. Silvery hairs tend to be translucent and white hairs opaque. Leaves of *Q. incana*, *Q. macrocarpa*, *Q. muehlenbergii*, *Q. mohriana*, *Q. virginiana*, and *Q. sinuata* often appear to lack exudates completely. However, following a drying cycle of 2 or

more months, sulphurous yellow highlights within the bases of the white hairs sometimes appear. As illustrated in Figure 3, bases of stellate hairs range from sessile (A-E) to inconspicuously stalked or conspicuously stalked (F-H) at 70 x magnification. In this treatment of the genus, stalks are considered conspicuous when longer than 0.1 mm, and inconspicuous when less. The only species in Section *Quercus* that produces conspicuously stalked hairs is *Q. margaretta*. In most species of Section *Lobatae* this hair type is observed in the vein axils of the abaxial sides of leaves. Species with stalked hairs never have appressed rays, with the exception of hybrid individuals. Hybrids between species that only produce sessile hairs with appressed rays and species that produce stalked hairs may exhibit stalked hairs with appressed rays. Appressed rays generally arise from sessile bases. Sometimes the rays may be both appressed and ascending to erect. In general however, species of Section *Quercus* do not have individual hairs with both appressed and ascending to erect rays (Hardin 1979a, b). However, some species produce more than one type of hair; some sessile with appressed rays others sessile or inconspicuously stalked with ascending rays (Hardin 1979a, b). Fortunately, a single type dominates in most cases, and the other type will be sparsely distributed over the leaf surface (Hardin 1979a, b). Hairs with erect or appressed rays have straight to inconspicuously curving rays. In Section *Lobatae*, sessile hairs may have combinations of appressed, ascending, and erect rays (Hardin 1979a, b). In many individuals the appressed and erect rays may be straighter than those ascending. While diagnostic of all species in the section with the exception of *Q. incana*, they are characteristically always shed from the surfaces, with exception of *Q. falcata* and sometimes *Q. velutina*.

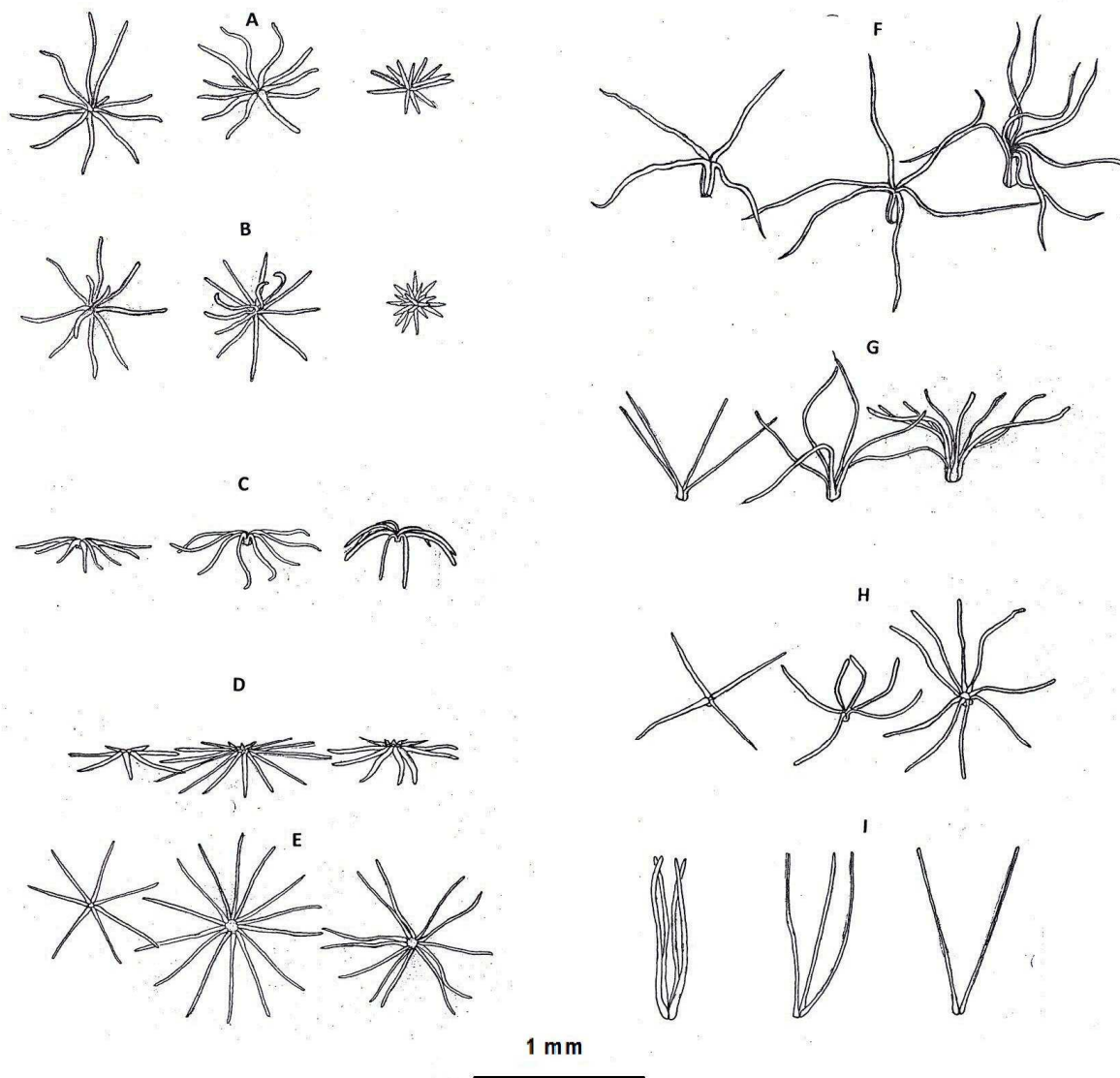


Figure 3. Hair types encountered in species of *Quercus*. A: side view of sessile hairs with appressed to ascending or erect rays. B: paradermal view of hairs in A. C: side view of sessile and inconspicuously stalked hairs with inconspicuously ascending and/or descending rays. D: side view of sessile hairs with appressed rays. E: paradermal view of hairs in C and D. F: side view of conspicuously stalked hairs with ascending to erect rays. G: side view of inconspicuously stalked hairs with ascending to erect rays. H: paradermal view of hairs in F and G. I: side view of erect hairs. Drawings by Will Lowry.

Three other hair types—bulbous, uniseriate, and sericeous— are useful in the classification and identification of oaks; however, they can only be clearly viewed at 70 x or higher magnification (Hardin 1979a, b). Bulbous hairs are barely visible at 40 x magnification (Figure 4). They resemble white or yellow grains of sand distributed along the leaf veins in most instances, but can be distinguished by the uniformity in their shape when present in significant densities. They are most useful species in distinguishing *Q. stellata* and *Q. havardii* from other morphologically similar species. These two species bear so many in some individuals, that it appears at 30–70 x magnification as though the abaxial surfaces of the leaves are covered with sand.

Uniseriate hairs cover the leaf surfaces and are composed of a single oblong cell or multiple cells forming an oblong-shaped structure (Figure 4). These hairs tend to be equal to or less than 1 mm in length. Color of these hairs, whether uni- or multicellular can be variable or uniform.

The third hair type is the sericeous hair. It is a straight, translucent, unicellular trichome typically 0.5–3 mm long. Were it not for the fact that they are antorsely appressed and lying directly on top of the veins, they would be visible to the naked eye.

Recognition of Sections in Oklahoma—As noted above, only two sections of *Quercus* are present in Oklahoma. With a few exceptions, they can be distinguished by a suite of easily visible morphological characters. In descending order of reliability, they include the following: (1) the presence or absence of the flange of tissue subtending each pistillate flower; (2) maturation of the nuts in one or two growing seasons i.e., mature acorns on the previous season's wood or current season's wood; and (3)

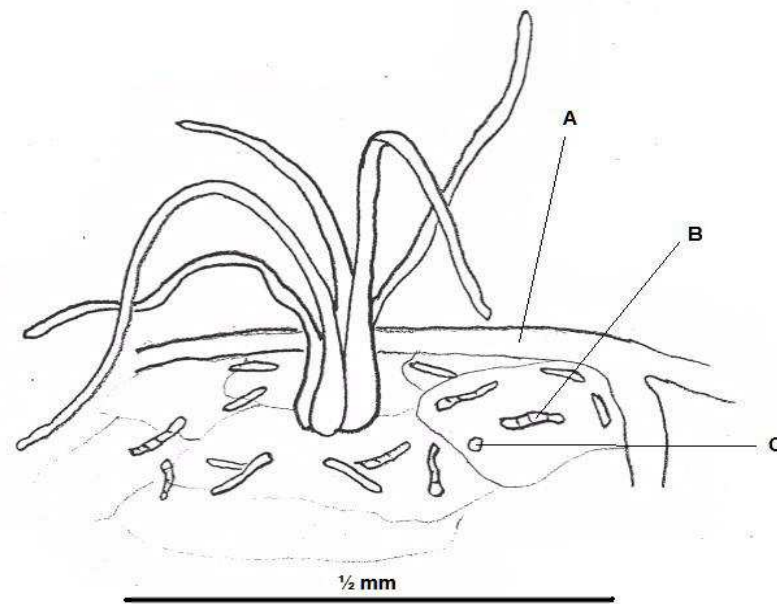


Figure 4. Leaf surface of *Quercus stellata* with uniserrate and bulbous hairs associated with sessile stellate hair. A: vein. B: uniserrate hair. C: bulbous hair. Drawing by Will Lowry.

presence or absence of awns along the leaf margins.

Awns are extensions of the veins extending beyond the body of the leaf blades and are characteristic of the species of Section *Lobatae*. Exceptions are *Q. turbinella*, *Q. x pauciloba*, and *Q. virginiana* in Section *Quercus*. Fortunately, these three species are geographically restricted in the state, and thus the presence or absence of awns is for the most part effective in distinguishing the two sections.

Characters of the cupule that include tuberculate scales and a blackened callus should be used with caution. The tomentose nature of the inner cupule is not an effective character. As noted above, it is difficult to see in some taxa and the ability to

feel the tomentum relies on the sensitivity of the nerve endings in the finger as well. The location of aborted ovules at the apices or bases of the nuts appear as small black spots, but are only useful when the pericarps are removed to reveal intact tissues. However, if nuts are collected when fresh, the distribution of hairs covering them will reveal the section to which it belongs, with the exception of *Q. macrocarpa*. The sessile hairs covering the leaf surfaces of most species in section *Lobatae* are caducous, and therefore do not assist in identification when only mature leaves are present.

Hybridization in *Quercus*—The genus is famous, or perhaps more appropriately infamous, for the hybridization that occurs among its species. Numerous putative hybrids have been described in the taxonomic literature and more than 100 of these have been given species names (Palmer, 1948). Hybridization occurs only among species of the same section (Cottam et al., 1982) and typically produces solitary trees or small populations of intermediate individuals (Hardin, 1975). In some instances, most notably the *Q. undulata* complex, large populations of intergrading, intermediate individuals distributed over a wide geographic area may be present (Tucker, 1961). Hybridization occurs in both Section *Quercus* and Section *Lobatae*, and to a lesser extent in Section *Protobalanus* (Nixon, 1997).

In addition to obscuring taxonomic clarity in many instances (Tucker, 1961; Muller, 1951b; Nixon, 1993b), observations of *Quercus* hybrids have revealed some of the most interesting contradictions to the biological species concept (Grant, 1971; Van Valen, 1976; Petit et al., 1993; Nixon, 1993b; Ishida et al., 2006). Some taxonomists (Grant, 1971; Van Valen, 1976) have argued against using species in the genus

because the frequency at which hybrids are formed challenges the biological species concept . They proposed using the syngameon concept—a group of genetically related, discrete morphological units that are interfertile to varying degrees—for *Quercus*. The more common view (Tucker, 1961; Hardin, 1975; Rosen, 1979; Cracraft, 1982; Whittmore and Schaal, 1991; Nixon, 1993b), however, is that the ability to interbreed is simply a pleisomorphic character state that does not really negate the historical concept of species in *Quercus* based on phenotype, ecology, geography, sexual incompatibility among species, and numerous fossils related to extant taxa. Furthermore, the infraspecific diversity exhibited within many species of *Quercus* is considered to be reflective of the processes that lead to speciation (McDougal and Parks, 1986; Kriebel et al., 1988; Steiner et al., 1995; Hess and Stoyhoff, 1998; Magni et al., 2005; Cavender-Bares, 2007).

The significance of hybridization in *Quercus* is perhaps not that it creates problems for the taxonomist but that it may result in the disappearance of distinct taxa (species). Current knowledge about climate change and successive vegetation migrations following the last glacial thaw has lead to proposals that hybridization in *Quercus* serves as a mechanism of invasion of one species by another via “pollen-swamping (Hardin, 1975; Petit et al., 1993; Julyan, 2006). Those species with the highest level of endemism, such as *Q. buckleyi* (Stein et al., 2003), may be more at risk of disappearance via hybridization (Dorr and Nixon, 1985), because the environmental barriers that encouraged the divergence of the species are no longer in place (Abrams, 1986, 1992; Rieseberg, 1997). As described in the treatment of *Q. x pauciloba*,

observations of oaks in Tesequite Canyon in Cimarron County may reflect this phenomenon.

Historically, hybrids in *Quercus* were treated as a variety or subspecies of one of the parental species depending upon the resemblance of the hybrid plants leaves to those of the putative parent or as a named hybrid if the hybrid plants were obviously intermediate between two parental species (Sargent, 1918; Trelease, 1924; Bartlett, 1951). In most cases, the hybrid individual is a solitary plant or in close proximity to morphologically similar plants that have presumably backcrossed to one of the parental species (Bartlett, 1951; Hardin, 1975; Whittemore and Shaal, 1993). When considering how to formally recognize hybrids (nothotaxa), the taxonomist must weigh the usefulness of using a hybrid name (McNeill et al., 2006). For example, Tucker, Cottam, and Drobnik (1961) proposed that formal recognition of the conspicuously intermediate, numerous, and far ranging hybrids between *Q. gambelii* and *Q. turbinella* was warranted and thus used *Q. x pauciloba* for them.

Encountering a hybrid between species that are morphologically quite similar is possible, but is greatly complicated by the lack of conspicuous intermediacy which characterizes hybrids between quite different species. (Hardin, 1979a, b). Likewise, problems in detection may arise when encountering hybrids produced by crosses among three species (Thomson, 1977). A third complication in understanding hybridization in *Quercus* is that leaves of hybrids within a hybrid-complex may appear similar to those of species not involved in the formation of the complex (Bartlett, 1951). This probably reflects conservation of leaf traits through evolutionary time (Cavender-Bares, 2001). The allelic influences on ecological and morphological plasticity of hybrids

are poorly understood (Ishida et al., 2003). In some instances, hybrid crosses are only detectable through molecular analysis (McDougal and Parks, 1986; Jensen, 1989; Whittemore and Schaal, 1991; Buck and Bidlack, 1998; Burgella et al., 2009).

METHODOLOGY: PREPARATION OF THE TREATMENT

Preparation of this treatment of *Quercus* in Oklahoma began with an extensive review of the floristic and then the taxonomic literature. Floras examined included: *Keys to the Flora of Oklahoma* (Waterfall, 1969), *Flora of North America* (Flora of North America Editorial Committee, 1997), *Flora of New Mexico* (Wooten and Stanley, 1915), *Flora of Indiana* (Deam, 1940), *Flora of Illinois* (Jones, 1945), *Gray's Manual of Botany* (Fernald, 1950), *Manual of the Vascular Plants of Texas* (Correll and Johnston, 1970), *Flora of the Great Plains* (Great Plains Flora Association (1986), *Flora of Missouri* (Steyermark, 1963), and *Colorado flora: Eastern Slope* (Weber, 1990). *Biological Abstracts* was used to locate journal articles addressing specific aspects of the classification and/or nomenclature of species of *Quercus* occurring in Oklahoma. A list of taxa present in Oklahoma was compiled (Table 3). It served as the basis for the subsequent development of the species descriptions.

As the literature was reviewed, herbarium specimens of the genus in the OSU herbarium (OKLA), the Robert Bebb Herbarium (OKL), and the United States Herbarium (US) were identified and examined. In order to determine the range of morphological variation exhibited by each species, 65 characters were scored (Table 4). These character states were entered into Excel spreadsheets to insure recording of the same data for all taxa and to facilitate comparisons during construction of the key. Information

Table 3. Species and infraspecific taxa of *Quercus* occurring in Oklahoma based on a literature survey and an examination of herbarium specimens.

<i>Quercus</i> section <i>Quercus</i>	white oak section
<i>Q. alba</i> L.	white oak
<i>Q. x drummondii</i> Nixon & Muller	Liebmann's sand post oak
<i>Q. x fernowii</i> Trelease	none
<i>Q. gambelii</i> Nuttall	Gambel oak
<i>Q. havardii</i> Rydberg	Havard Oak
<i>Q. lyrata</i> Walter	overcup oak
<i>Q. macrocarpa</i> Michaux	bur oak
<i>Q. margaretta</i> (Ashe) Ashe	sand post oak
<i>Q. mohriana</i> Buckleyi	Mohr oak
<i>Q. muehlenbergii</i> Englemann	chinkapin oak
<i>Q. x pauciloba</i> Rydberg	wavy leaf oak
<i>Q. prinoides</i> Willdenow	dwarf chinkapin
<i>Q. sinuata</i> var. <i>breviloba</i> (Torr.) Muller	bastard oak
<i>Q. stellata</i> Wangenheim	post oak
<i>Q. x stelloides</i> Palmer	none
<i>Q. turbinella</i> Greene	Sonoran scrub oak
<i>Q. virginiana</i> Miller	southern live oak
<i>Quercus</i> section <i>Lobatae</i>	red or black oak section
<i>Q. buckleyi</i> Nixon & Dorr	Buckley oak
<i>Q. falcata</i> Michaux	southern red oak

<i>Q. incana</i> W. Bartram	bluejack oak
<i>Q. marilandica</i> Münchhausen	blackjack oak
<i>var. marilandica</i>	
<i>var. ashei</i> Sudworth	
<i>Q. pagoda</i> Rafinesque	cherrybark oak
<i>Q. palustris</i> Münchhausen	pin oak
<i>Q. phellos</i> Linnaeus	willow oak
<i>Q. nigra</i> Linnaeus	water oak
<i>Q. rubra</i> Linnaeus	red oak
<i>Q. shumardii</i> Buckley	Shumard oak
<i>Q. velutina</i> Lamarck	black oak

extracted from herbarium labels and the Oklahoma Vascular Plants Database (2008) was used to generate distributional maps and information about the ecology of each species. As the description of each taxon was written, I made a line drawing to illustrate its major diagnostic features. Abbreviation of the author name or names following each taxon's scientific name according to Brummitt and Powell (1992).

As the work progressed, field trips were conducted in order: (1) to determine if species known only from one or two historical collections, e.g., *Q. michauxii*, were still present in the state; (2) to determine if species, e.g., *Q. margaretta*, reported by Nixon and Muller (1997), but not by Little (1981), Waterfall (1969), or Taylor and Taylor (1994) were indeed present in the state; and (3) to gain an understanding of the morphology

Table 4. Sixty-five morphological characters examined and scored in order to generate taxon descriptions in *Quercus*.

Plant Form	Hairs of Adaxial Surfaces (continued)
habit	basal attachment
height	ray number
hardiness	ray length
	ray aspect of divergence
Bark	ray straightness
color	Hairs of Abaxial Surfaces
outer form	type
inner appearance	color
Branch Form	basal attachment
aspect	ray number of stellate hairs
	ray length of stellate hairs)
Terminal Buds	divergence of rays of stellate hairs
shape in cross section	straightness of rays of stellate hairs
three dimensional shape	
length	Catkins
color	length
surface texture	
Leaves	Mature Acorns
shape	shape
width	length
length	number per inflorescence
thickness	range in length of peduncle
shape of apices	
shape of margins	Cupules of Acorns
sinuses depth	shape
base shape	diameter
adaxial color	depth
adaxial texture	coverage of nut
abaxial color	color
abaxial texture	scale appression
petiole length	scale shape at rims
petiole texture	scale size at rims
stipule persistence	scale shape
	scale texture
Hairs of Adaxial Surfaces	scale margin color
type	scale margin texture
color	scale base dimension
	color of callus

Nuts	length
shape	color
diameter	texture of distal fraction in white oaks

and range of variation exhibited by species presumed to be involved in hybridization events. These trips are summarized in Table 5.

Table 5. States and numbers of localities visited, and growing seasons of visits in this study of *Quercus*.

<u>State</u>	<u>Number of Localities Visited</u>	<u>Growing Season of Visits</u>
Oklahoma	587	2006–2009
Kansas	7	2009
Missouri	4	2007–2009
Arkansas	4	2007–2009
New Mexico	12	2007–2009
Texas	25	2007–2008
Colorado	7	2008–2009

RESULTS AND DISCUSSION: FLORISTIC TREATMENT OF *QUERCUS*

Based on the work conducted in this study, the oak flora of Oklahoma comprises 24 species and 4 named hybrids. Putative hybrids are not included. In the following paragraphs, keys to the two sections and the species of each section are given. They are followed by the descriptions of each taxon considered to be present in Oklahoma. It is important to note that each taxon's description reflects only the range of its morphological variation in Oklahoma. To provide context, the family description and

key to its three genera that was prepared by the Editorial Committee of the Flora of Oklahoma Project (Tyril et al., 2007) also are included.

As work progressed, the problems—morphological variability, phenotypic plasticity, and extreme hybridization—that have plagued other individuals (Palmer, 1948; Bartlett, 1951; Tucker, 1961; 1970; 1971; Tucker et al., 1961; Hardin, 1975; Morrison-Hill and Buck, 1980; Buck and Bidlack, 1998) working with *Quercus* became apparent. Traditional reliance on leaf features such as overall shape, margin type, appearance of apices and bases, and gross pubescence are inadequate (Muller, 1951b). Fortunately, detailed studies by Hardin (1979a, b), Tucker and Muller (1958) of trichome attributes, in particular Tucker (1961) has proven to be useful in clarifying relationships among species and detecting hybrids. Illustrative of this are the clarifications of the presence of *Q. margaretta*, *Q. gambelii*, *Q. turbinella*, *Q. x pauciloba*, *Q. drummondii*, and *Q. x stelloides* in the state.

FAGACEAE B.C.J. Dumortier

Beech Family

Plants trees or shrubs; deciduous or evergreen; monoecious. **Leaves** simple; alternate; blades entire to variously toothed or lobed; awns present or absent; venation pinnate; stipules present, caducous. **Inflorescences** of 2 types, staminate and pistillate different; axillary. **Staminate Inflorescences** catkins; pendulous; elongate or globose; bracts present or absent, caducous. **Pistillate Inflorescences** solitary flowers or clusters of 2 to 4; bracts present, fused forming involucre cupules (caps) or husks that completely or partially enclose flowers. **Flowers** produced before leaves or simultaneously with or after leaves, imperfect, staminate and pistillate similar; perianths in 1-series. **Calyces**

radially symmetrical. **Sepals** 4 to 8; fused. **Petals** absent. **Stamens** 4 to 20. **Pistils** 1; compound, carpels 3 to 7; stigmas 3; styles 3; ovaries inferior; locules 3 to 7; placentation axile; ovules 2 per locule. Gynoecial rudiments occasionally present. **Fruits** nuts; subtended by involucre cupules (caps) in *Quercus* (=acorn) or enclosed in spiny or prickly husks that are dehiscent at maturity in *Castanea* and *Fagus*. **Seeds** 1.

The family is represented in Oklahoma by 3 genera, 28 species, and 4 nothospecies. *Quercus*, oak, is the largest genus of woody plants in the state and is found in virtually all wooded habitats. *Fagus*, beech, and *Castanea*, chestnut, are uncommon and encountered in the extreme eastern portion of the state. The nuts are an important food for wildlife.

Key to Genera

1. Buds at twig apices multiple. Nuts subtended by cap-like involucre cupules (=acorn). ***Quercus***
1. Buds at twig apices solitary or absent. Nuts enclosed in spiny or muricate husks.
 2. Bark of mature trees smooth. Buds 4 times longer than wide; apices acute, shiny. Staminate catkins globose. Involucres muricate. Nuts trigonous. ***Fagus***
 2. Bark of mature trees furrowed. Buds 1.5–2 times longer than wide; apices obtuse or rounded; dull. Staminate catkins elongate. Involucres spiny. Nuts rounded or slightly flattened on 1 side. ***Castanea***

Quercus C. Linnaeus

Oak

Plants trees or shrubs; deciduous or evergreen. **Terminal Buds** 3-9; clustered. **Bark** whitish gray or brown or black or red tinged; smooth or furrowed or scaly or flaky. **Leaves** pinnately lobed or serrate-crenate or entire or revolute; lobe apices acute or acuminate or rounded, awns present or absent. **Staminate Flowers** borne in elongate, pendulous catkins. **Pistillate Flowers** 1 per involucre cupule (cap). **Mature Acorns** borne on previous or current year's wood; involucre scales of cupules flattened or keeled or with bases thickened; bases of cupules with or without darkened or pubescent callus; inner surfaces of cupules tomentose or glabrous or glabrate.

The genus is represented in Oklahoma by 24 species, 3 varieties, 4 named hybrids, and numerous putative hybrid individuals.

Key to Sections

- 1. Principal veins of leaves excurrent as awns or mucros.
 - 2. Leaf margins conspicuously revolute. **Quercus**
 - 2. Leaf margins of various types, but not revolute. **Lobatae**
- 1. Principal veins of leaves not excurrent as awns or mucros.
 - 3. Mature pistillate flowers and acorns borne on previous year's wood. Pistillate flowers subtended by appressed flange from peduncles. Involucre scales of cupules flattened. Bases of cupules without darkened or pubescent callus. Nuts wholly tomentose. **Lobatae**

3. Mature pistillate flowers and acorns borne on current year's wood. Pistillate flowers not subtended by appressed flange from peduncles. Involucral scales of cupules thickened. Bases of cupules with darkened or pubescent callus. Nuts glabrous to tomentose on surfaces outside cupules (except in *Q. macrocarpa*). **Quercus**

Section *Lobatae* J.C. Loudon

Black Oaks. Red Oaks

Plants trees; deciduous, sometimes tardily so. **Terminal Buds** with apices acute. **Bark** smooth or deeply furrowed, not scaly or flaky. **Leaves** pinnately lobed to entire; lobe apices acute or acuminate, awns typically present, but sometimes absent on mature leaves. **Pistillate Flowers** with calyces free from ovaries, forming flanges; styles linear-spathulate. **Mature Acorns** borne on previous year's wood; involucral scales of cupules flattened; bases of cupules without darkened or pubescent callus; inner surfaces of cupules tomentose.

1. Leaf margins entire or denticulate, and/or apically undulate to sinuate and basally entire. Lobes, if present, rounded or obtuse to broadly acute. Petioles rarely longer than 10 mm long.
2. Leaves linear-lanceolate to lanceolate or elliptic or oblong; lobes absent.
3. Leaf margins denticulate. Awns 2-5; both apical and marginal.
4. Abaxial surfaces of blades silvery green or grey; densely pubescent. Stellate hairs of abaxial surfaces with rays

appressed. Abaxial midribs densely stellate, especially at bases. Petioles densely stellate. Leaf bases rounded to cuneate. ***Q. incana***

(including hybrids involving *Q. incana*)

4. Abaxial surfaces of blades light to coppery green, glabrous to glabrate except for dense tufts of red stellate hairs in vein axils. Stellate hairs of abaxial surfaces with rays ascending. Abaxial midribs glabrous to sparsely stellate near bases.

Petioles glabrous to sparsely stellate. Leaf

bases attenuate to cuneate. ***Q. nigra***

(including hybrids involving *Q. nigra*)

3. Leaf margins entire. Awns 1; only apical.

5. Leaves 4-6 times longer than wide. Bud scales glabrous, except for ciliolate scale margins.

Abaxial surfaces of leaves light to yellow-green; glabrous to glabrate except for dense tufts of stellate hairs along midribs or in vein axils. Stellate hairs of abaxial surfaces with rays raised. ***Q. phellos***

5. Leaves 2-4 times longer than wide. Bud

scales tomentose or pubescent distally. Abaxial surfaces of blades silvery green or grey; uniformly densely pubescent. Stellate hairs of abaxial surfaces with rays appressed. ***Q. incana***

2. Leaves spatulate to oblanceolate or obovate to
obtrullate-rhomboidal, occasionally obdeltoid; lobes,
when present, rounded or obtuse to broadly acute.
6. Blades of mature leaves 6-18 cm wide. Cupules covering
1/3-1/2 of mature nuts.
7. Abaxial surfaces of blades covered with dense stellate
hairs that are persistent. **Q. falcata**
7. Abaxial surfaces of blades covered with stellate
hairs that are deciduous. **Q. marilandica**
6. Blades of leaves 2.5-6 cm wide. Cupules covering
1/4-1/3 of mature nuts.
8. Leaves spatulate to oblanceolate; bases
attenuate to cuneate. Petioles glabrous to glabrate.
Twigs glabrous. Plants large trees. Branches
typically ascending in canopy, typically alive. **Q. nigra**
8. Leaves obovate to obtrullate-rhomboidal; bases cordate
to rounded. Petioles densely to sparsely stellate pubescent.
Twigs densely to sparsely stellate pubescent. Plants colonial shrubs
or small, reproductive at less than or equal to 2 m tall.
Branches typically descending in lower half of canopy;
typically dead..... **Q. marilandica**
1. Leaf margins pinnately lobed to pinnately cleft
or pinnately parted. Lobe apices acute to acuminate.

Petioles always equal to or greater than 20 mm long

9. Abaxial surfaces of blades densely stellate pubescent.

Twigs densely and conspicuously pubescent.

10. Hairs of leaves, petioles and twigs silvery and/or rusty red pubescent. Hairs readily deciduous, easily rubbed off.

Bases of all leaves truncate or cuneate. Apices of involucreal scales of cupules spreading to reflexed. **Q. velutina**

10. Hairs of leaves, petioles and twigs densely sulphurous yellow pubescent. Hairs persistent, not easily rubbed off. Bases of at least some of leaves oblique or U-shaped. Apices of involucreal scales of cupules tightly appressed.

11. Shade leaves without expanded lobes. Terminal buds terete in cross-section..... **Q. falcata**

11. Shade leaves with expanded lobes. Terminal buds 5-angled in cross-section..... **Q. pagoda**

9. Abaxial surfaces of blades glabrous, or only with red tomentum in vein axils. Twigs sparsely and inconspicuously pubescent.

12. Blade sinuses extending less than 2/3 distance to midribs.

13. Terminal buds 7-12 mm long; uniformly pubescent.

Apices of involucreal scales of cupules spreading or reflexed.

Adaxial surfaces dark green; glossy after drying. Cupules

covering 1/2 of mature nuts. Nuts subglobose to ovoid. **Q. velutina**

13. Terminal buds 2- 12 mm long; distally pubescent or only

distal scales pubescent along margins. Apices of involucre scales of cupules tightly appressed. Adaxial surfaces pale green; dull after drying. Cupules covering 1/3-1/4 of mature nuts. Nuts ovoid to oblong. ***Q. rubra***

12. Blade sinuses extending more than 2/3 distance to midribs.

14. Terminal bud scales uniformly pubescent; 8-12 mm long. Involucre scales of cupules spreading to reflexed. ***Q. velutina***

14. Terminal bud scales glabrous or pubescent only in distal 1/2; 4-8 mm long. Involucre scales of cupules tightly appressed.

15. Cupules covering 1/5-1/4 of mature nuts; 3-6 mm deep. Leaves oblong to narrowly elliptic. ***Q. palustris***

15. Cupules covering 1/4-1/3 of mature nuts; 7-16 mm deep. Leaves broadly elliptic to obovate.

16. Terminal buds distally pubescent, margins of bud scales ciliate. Petioles and twigs sparsely stellate or villous. Abaxial blade surfaces coppery green; tufts of stellate hairs in vein axils minute to inconspicuous. Leaves 5-10 cm long. ***Q. buckleyii***

16. Terminal buds glabrous, margins of bud scales erose. Petioles and twigs glabrous. Abaxial blade surfaces dark to light green; tufts of stellate

hairs in vein axils conspicuous.

Leaves 10-20 cm long. *Q. shumardii*

Section *Quercus*

White Oaks

Plants trees or shrubs; deciduous or evergreen. **Terminal Buds** with apices obtuse or rounded. **Bark** smooth or scaly or flaky. **Leaves** pinnately lobed or serrate-crenate or entire or revolute; lobe apices rounded, awns absent. **Pistillate Flowers** with calyces fused to ovaries, not forming flanges; styles usually abruptly spatulate. **Mature Acorns** borne on current year's wood; involucre scales of cupules keeled or with bases thickened; bases of cupules with darkened or pubescent callus; inner surfaces of cupules inconspicuously tomentose.

1. Leaf margins conspicuously revolute. Bark dark brown to black. *Q. virginiana*
(including *Q. fusiformis*)

1. Leaf margins not conspicuously revolute. Bark gray to whitish grey.

2. Blades deeply lobed with at least some of the sinuses extending
half way to midribs.

3. Plants shrubs or sometimes shrubs and small trees intermixed.

4. Plants of Black Mesa area, Cimarron County.

5. Leaf margins with "finger-like" lobes.

Awns not present. Cupules 12- 24 mm

wide. Nuts 11-16 mm in diameter. Twigs glabrous.

Abaxial leaf surfaces bearing only silver stellate

Hairs with 1-5 rays. ***Q. gambelii***

5. Leaf margins with serrate or deltoid lobes. Awns sometimes present. Cupules 8-12 mm wide. Nuts 8-11 mm in diameter. Twigs yellow; densely stellate or rarely glabrous. Abaxial leaf surfaces bearing yellow or red or silver stellate hairs with 5-12 rays.

6. Leaves never longer than 5.2 cm; margins always bearing awns both at apices and lateral lobes. Abaxial leaf surfaces always covered with red uniseriate hairs. ***Q. turbinella***

6. Leaves sometimes longer than 5.2 cm; margins not bearing awns or awns occasionally present. Abaxial leaf surfaces usually covered with red or silvery uniseriate hairs. ***Q. x pauciloba***

4. Plants of the southwestern quarter of the state.

6. Cupules 15-30 mm wide. Involucral scales loosely appressed to reflexed at rims. ***Q. havardii***

(including hybrids involving *Q. havardii*)

6. Cupules 8-15 mm wide. Involucral scales tightly appressed at rims.

7. Leaf blades 6.5 cm long or longer.

Plants trees; to 5 m tall.. ***Q. x pauciloba***

(including hybrids with *Q. mohriana*)

7. Leaf blades 2.5-5 cm long. Plants small

trees or colonial shrubs; to 2 m tall.

8. Adaxial surfaces of leaves dark green;

not glaucous. Abaxial surfaces of leaves

white to cream; conspicuously densely

stellate pubescent, secondary veins not visible.

Young twigs silvery stellate to black. Awns

not present..... ***Q. mohriana***

8. Adaxial surfaces of leaves brownish green

or gray; glaucous. Abaxial surfaces of leaves

silvery green or yellow; glaucous. Young twigs

sulphurous yellow or red. Awns sometimes

present..... ***Q. x pauciloba***

3. Plants trees.

9. Abaxial surfaces of leaves glabrous to glabrate except for

stellate hairs on midribs. Lobes all “finger-like” to “antler-like”.

10. Abaxial surfaces of leaves glabrate to glabrous..... ***Q. alba***

10. Abaxial surfaces glabrous except for dense

stellate hairs along midribs. ***Q. x fernowii***

9. Abaxial surfaces of leaves densely to sparsely

stellate or villous. Lobes not “finger-like” to “antler-like”.

11. Primary lateral lobes of leaves typically 1 or 2 per side;

Cupules covering 1/4-1/2 of mature nuts; 20 mm wide

or less. Involucral scales flat or creased. Catkins 5-8 cm long.

Stellate hairs on abaxial surfaces of leaves all alike;

4- to 8-rayed, rays ascending.

12. Stellate hairs on abaxial surfaces of leaves
sessile to inconspicuously stalked (less than
0.1 mm tall). ***Q. stellata***

12. Stellate hairs on abaxial surfaces of leaves
conspicuously stalked (0.1-0.2 mm tall).

13. Twigs reddish to dark brown; glabrous to
glabrate; bulbous hairs not present. ***Q. margaretta***

13. Twigs silvery to sulphurous yellow;
densely stellate pubescent; bulbous hairs
present (dense along midribs)..... ***Q. x drummondii***

11. Primary lateral lobes of leaves typically 2-4 per side.

Cupules covering 1/2 to all of mature nuts;
22 mm wide or more. Involucral scales
conspicuously awned or tuberculate. Catkins
1-4 cm long. Stellate hairs on abaxial surfaces of
leaves of 2 forms; sun leaves bearing sessile
hairs with 8- to 16-rays that are appressed to
inconspicuously ascending, shade leaves
bearing sessile to inspicuously stalked hairs
with 2- to 6 rays that are erect.

14. Apices of leaf lobes acute. Inner bark visible;
reddish tinged. Cupules covering 3/4 to nearly
all of mature nuts; rim margins often
lacerated due to fruit maturation; not fringed. **Q. lyrata**
14. Apices of leaf lobes rounded. Inner bark not visible.
Cupules covering 1/2-3/4 of mature nuts; rims not
lacerate; fringed with exception of acorns heavily
shaded during development. **Q. macrocarpa**
2. Blades entire or toothed; sinuses not extending half way
to midribs.
15. Leaf margins uniformly serrate; teeth 9-14 per side.
16. Plants trees to 20 m tall. Blade margins with
10-15 teeth per side. Plants not reproductive
when 50 cm tall. **Q. muehlenbergii**
16. Shrubs or small trees to 4 m tall. Blade margins with
9 or 10 teeth per side. Some plants reproductive
when 50 cm tall.
17. Twigs dark red; glabrous..... **Q. prinoides**
(including *Q. prinoides* x *Q. muehlenbergii*)
17. Twigs sulphurous to silvery yellow;
densely stellate pubescent. **Q. x stelloides**
15. Leaf margins entire or toothed. Teeth, if present, 2-8 per side.
18. Plants of Black Mesa area, Cimarron County.

19. Leaf blades 6.5 cm long or longer.

Plants trees; to 5 m tall. **Q. x pauciloba**

(including hybrids with *Q. mohriana*)

19. Leaf blades 2.5-5 cm long. Plants small

trees or colonial shrubs; to 2 m tall.

20. Adaxial surfaces of leaves dark green;

not glaucous. Abaxial surfaces of leaves

white to cream; conspicuously densely

stellate pubescent, secondary veins not visible.

Young twigs silvery stellate to black. Awns

not present..... **Q. mohriana**

20. Adaxial surfaces of leaves brownish green

or gray; glaucous. Abaxial surfaces of leaves

silvery green or yellow; glaucous. Young twigs

sulphurous yellow or red. Awns sometimes

present. **Q. x pauciloba**

18. Plants of the body of the state.

21. Stellate hairs of abaxial surfaces of leaves

with rays appressed.

22. Petioles 3 mm long or less.

Cupules covering 1/8-1/4 of mature

nuts. Involucral scales flat; ovate.

Leaf margins entire or

- 1- to 3- toothed..... **Q. sinuata var. breviloba**
22. Petioles 7 mm long or more. Cupules covering 1/4-1/3 of mature nuts. Involucral scales creased or tuberculate; deltoid to lanceolate. Leaf margins uniformly 3- to 8-toothed.
23. Twigs dark red; glabrous. **Q. prinoides**
23. Twigs sulphurous yellow; stellate. **Q. x stelloides**
21. Stellate hairs of abaxial blades surfaces of leaves with rays ascending.
24. Cupules 20-25 mm in diameter. Involucral scales of 2 shapes; linear at cupule rims, ovate at cupule bases; those at rims 2-2.5 mm longer than those at bases. **Q. havardii**
24. Cupules 10-18 in diameter. Involucral scales all alike; ovate at both cupule rims and bases; those at rims shorter than those at bases..... **Q. mohriana**

***Quercus alba* L. White Oak**

Plants trees; to 30 m in height; deciduous. **Bark of Trunks** whitish gray to black tinged; papery to scaly; inner bark not exposed. **Primary Branches** slightly ascending to horizontal. **Twigs** 1.5-4 mm in diameter; reddish brown; glabrous to glabrate. **Terminal Buds** terete to slightly angular in cross-section; sub-globose to ovoid; 0.5-5 mm long; reddish brown; sparsely silvery tomentose or glabrous. **Leaves** obovate to broadly elliptic; 4-14.5 cm wide; 5-24.5 cm long; thin to thick; chartaceous to coriaceous; apices rounded to obtuse or emarginate to "antler-like"; margins 4- to 7-lobed; lobes "finger-like" to "antler-like", entire or 2(4) "pointed"; sinuses deep, extending equal to or greater than 1/2 distance to midribs; bases cuneate to acute or acuminate; adaxial surface dark green, glossy, glabrous or glabrate; abaxial surfaces white or light green, dull, glabrous or glabrate; petioles 5-38 mm long, glabrous or glabrate; stipules caducous. **Hairs of Adaxial Surfaces** like those of abaxial surfaces. **Hairs of Abaxial Surfaces** caducous; stellate; silvery; sessile to inconspicuously stalked; 4- to 16- rayed; rays 0.1-0.8 mm long, inconspicuously ascending to ascending, straight to curling; antrorsely setaceous along midribs. **Catkins** 5-10 cm long. **Mature Acorns** oblong or ovoid; 22-32 mm long; solitary or in clusters of 2 or 3; sessile or pedunculate, peduncles to 25 mm long. **Cupules** deeply bowl- to saucer-shaped; 18-30 mm in diameter; 4-13 mm deep, enclosing 1/4 of nuts; yellow to silvery or black; scales tightly appressed, those at cupule rims abruptly reduced in size, ovate to circular, silvery tomentose and/or golden waxy, margins red to silver or black in distal 1/2-1/3, glabrate to tomentose, bases conspicuously tuberculate, callus black. **Nuts** ellipsoidal to oblong; 13-22 mm in diameter; 15-30 mm long; light brown to dark brown; glabrous.

A native species, *Q. alba* occurs across the eastern half of the United States with the exception of the southern two-thirds of Florida and Louisiana (Little, 1971). In Oklahoma, the species is encountered in the eastern quarter of the state in three ecoregions: the Ozark Highlands, Boston Mountains, and Ouachita Mountains. . Individuals reaching a DBH equal to or greater than 40 cm are indicative of old growth forest (Kennedy and Nowacki, 1997), and can be found in the mesic valleys of these ecoregions. In the Ouachita Mountains, associations with *Q. velutina* are especially common in the uplands (Erye, 1980). Individuals of *Q. alba* are found in deep to shallow soils that retain moisture throughout a long portion of the growing season (Dirr, 1998). Planted seedlings exhibit greater basal diameters and numbers of leaves in mechanically induced canopy gaps of savannah woodland than in undisrupted levels of canopy cover (Brudvig and Asbjornsen, 2007). White oak has been in cultivation since 1724 (Olsen, 1974; Vines, 1982).

Known to surpass 200 years in age, *Q. alba* produces acorns relished by songbirds, gamebirds, many mammals, and insects (Van Dersal, 1938; Tirmenstein, 1991). Acorn production may commence as early as 20 years of age and continue well pass 200 years; however, prolific nut crops are limited to 4–10 year cycles (Olsen, 1974; Rogers, 1990; Bonner, 2008). Frequent anthropogenic fires in eastern Oklahoma woodlands encourage the prolific sprouting of juvenile trees (Rogers, 1990; Tirmenstein, 1991). Members of the Cherokee and Delaware tribes in Oklahoma used the bark as an antidiarrheal, emetic and febrifuge (Moerman, 1998).

A characteristic feature of the species is that the leaves in the upper canopy exhibit longer lobing in contrast to the shaded leaves (Figures 5 and 6).

Based on his collections in Oklahoma, Hardin (1975) described putative hybrids of *Q. alba* with *Q. stellata* (= *Q. x fernowii* Trelease), *Q. macrocarpa* (= *Q. x bebbiana* C. K. Schneider), and *Q. muehlenbergii* (= *Q. x deamii* Trelease). Hybrids with *Q. muehlenbergii* were treated as *Q. x deamii* until fruits of the type tree were grown and observed to have the morphology of a backcross to either *Q. macrocarpa* or *Q. muehlenbergii* rather than *Q. alba* (Bartlett, 1951; Hardin, 1975). Hardin (1979) also recognized a hybrid between *Q. alba* and *Q. margaretta* in his taxonomic treatment of the foliar trichomes of the eastern oak species. These hybrids between *alba* and *margaretta* may be common in the southeastern quarter of the state where the two species occur together geographically and ecologically.

Individuals of *Q. alba* with conspicuously shallow leaf lobes were recognized as forma *latiloba* by William Trelease (Trelease, 1924; Vines, 1982). However, it is more likely that such individuals are hybrids between *Q. alba* and *Q. stellata* (Hardin, 1979).

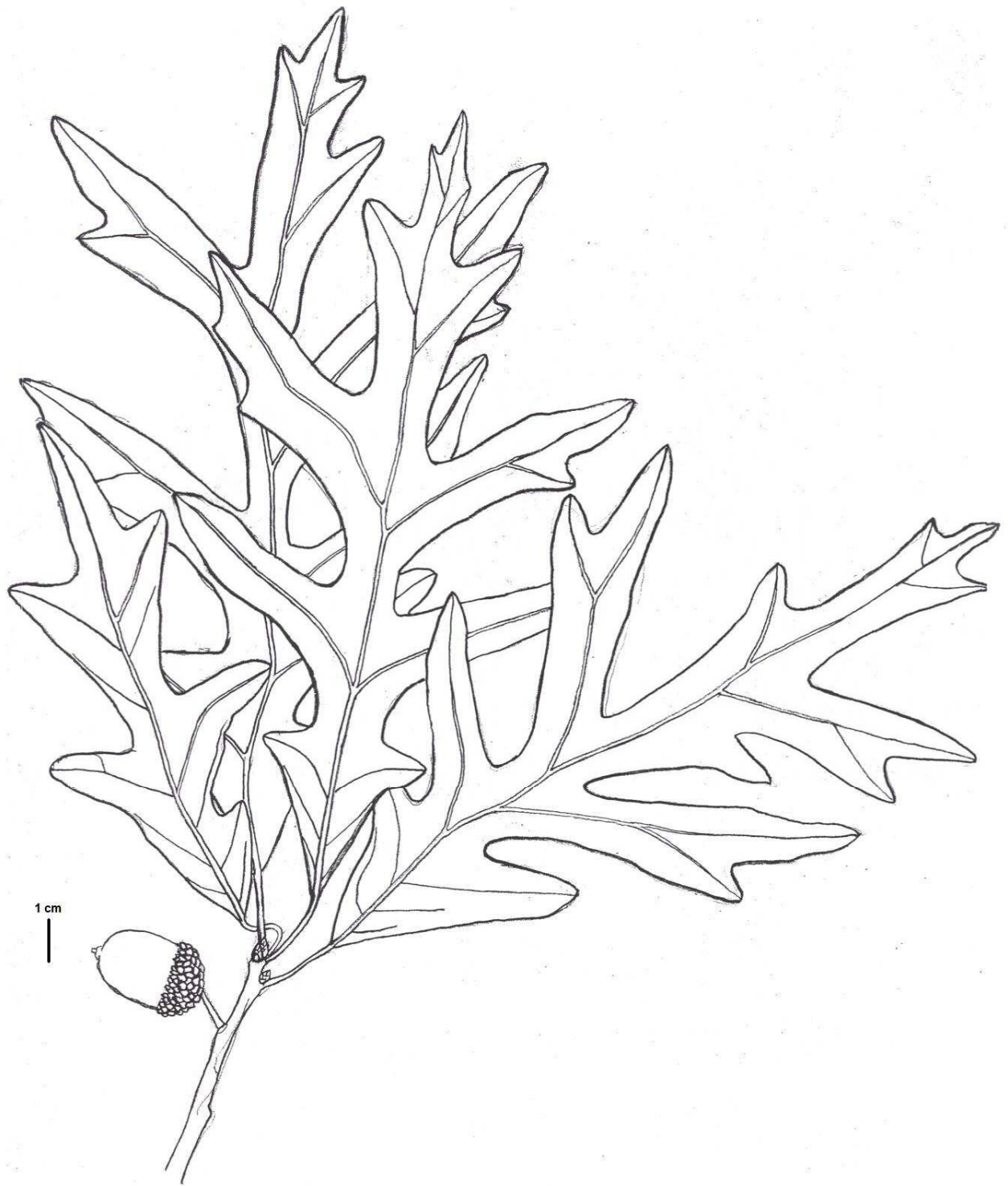


Figure 5. Foliage (sun leaves) and acorn of *Quercus alba* specimen collected in Lake Eucha State Park, Delaware County, Oklahoma.

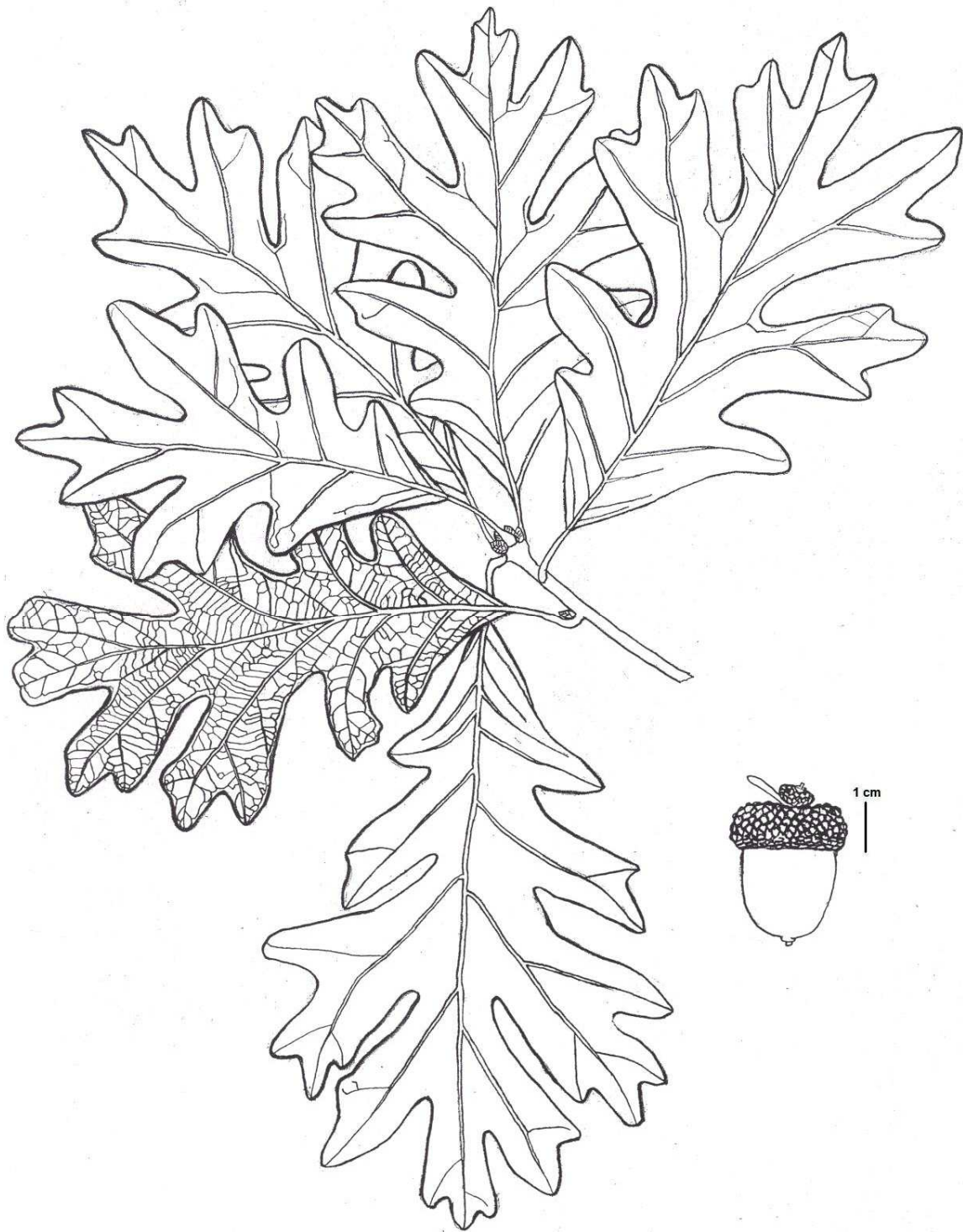


Figure 6. Foliage (shade leaves) and acorn of *Quercus alba* specimen collected on Rich Mountain, LeFlore County, Oklahoma.

***Quercus buckleyi* Nixon & Dorr. Buckley Oak**

Plants trees or shrubs forming clones; 2-18 m in height; deciduous. **Bark of Trunks** grey to black; smooth; inner bark not exposed. **Primary Branches** ascending to horizontal. **Twigs** 2-3.5 mm in diameter; reddish brown to gray; sparsely stellate to glabrate; hairs silvery. **Terminal Buds** terete to slightly angled in cross-section; ovoid to broadly fusiform; 4-7 mm long; reddish brown to dark brown or gray; distally silvery pubescent, sometimes ciliate only along scales margins. **Leaves** ovate to elliptic or orbicular; 5-9.3 cm wide; 5.5-10 cm long; thick; chartaceous; apices acute to attenuate; margins 5- to 9-lobed; lobes oblong to spatulate or broadly obovate, apically 2- to 8-toothed and expanded; sinuses deep, extending equal to or greater than 3/4 distance to midribs; awns 25-61, along expanded margin of lobe apices and/or terminating teeth; bases cuneate to truncate; adaxial surfaces dark to light green, glossy, glabrate; abaxial surfaces coppery green, glossy, glabrate except for inconspicuous or conspicuous tufts of rust colored pubescence in vein axils; petioles 20-45 mm long, sparsely pubescent to glabrate, hairs like those in vein axils of abaxial midribs; stipules caducous. **Hairs of Adaxial Surfaces** like those of abaxial surface; but caducous. **Hairs of Abaxial Surfaces** persistent in axils of midribs to wholly deciduous; stellate; silvery to reddish tinged in vein axils; sessile to inconspicuously or conspicuously stalked; 4- to 12-rayed; rays 0.3-0.7 mm long, appressed to erect or ascending, curling to straight. **Catkins** 4-10 cm long. **Mature Acorns** narrowly ovoid to ellipsoidal; 15-20 mm long; solitary or in clusters of 2 or 3; sessile or pedunculate, peduncles to 9 mm long. **Cupules** bowl-shaped; 5-12 mm in diameter; 5-10 mm deep; enclosing 1/3-1/4 of nuts; silvery and reddish brown to silvery and orange-brown; scales tightly appressed, deltoid to oblong

to ovate or oval, densely silvery to sulphurous yellow tomentose, margins red colored to obscured by tomentum, bases thickened to conspicuously tuberculate, callus absent.

Nuts ovoid to ellipsoidal; 7-14 mm in diameter; 14-18 mm long; light brown to brown; tomentose.

Quercus buckleyi is endemic to central Oklahoma and Texas (Dorr and Nixon, 1985; Jensen, 1997). Its specific epithet honors the frontier botanist and geologist Samuel Botsford Buckley (1809-1884) who described over 200 species of vascular plants from Texas. A climax woodland or forest species, it thrives in the shallow to moderately deep, silty or clayey soils of uplands, ridgelines, and hillsides that are underlain by limestone, sandstone, or granite. Its leaf features and a high root to shoot ratio are believed to be adaptations for surviving in these habitats (Balok and Hilaire, 2002). Associations with *Q. shumardii*, *Q. stellata*, *Q. marilandica* var. *asheii*, *Q. sinuata* var. *breviloba*, *Q. muehlenbergii*, *Celtis occidentalis*, *C. laevigata*, *Juniperus virginiana* and *Juniperus asheii* are typical in the woodlands of the Arbuckle and Wichita Mountains (Hoagland, 2000). The preference of deer to browse this species greatly reduces survival of its seedlings, and thus, the primary mode of reproduction is asexual via root sprouts with the formation of clones (Russel and Fowler, 2004).

On the Edwards Plateau of Texas, its shrub habit provides a primary nesting habitat for the Black Capped Vireo (*Vireo atricapilla*), an endemic and endangered species of Texas and Oklahoma (Bailey and Thompson, 2005).

Individuals of *Q. buckleyi* have been confused with the morphologically similar *Q. shumardii* and *Q. texana* (Dorr and Nixon, 1985; Jensen, 1997). For example, leaves of *Q. buckleyi* have expanded lobe characters like those of *Q. shumardii*; however, the

abaxial leaf surfaces have inconspicuous tufts of pubescence in the vein axils. Equally diagnostic are the smaller sizes of the leaves and nuts in comparison to those of *Q. shumardii*. The nut size and shape are similar to those of *Q. texana*, causing problems in identification with this species when narrow leaf forms have been collected (Dorr and Nixon, 1985).

The smooth bark characteristic of *Q. buckleyi* is likely due to the vigorous vegetative regeneration exhibited by the crown. However, large diameter trunks with smooth bark can often be found amidst numerous dead and/or vegetative sprouts of the same individual. This feature sets the species apart from similar looking species as well as any other character.

Hybridization and resulting backcrosses with *Q. shumardii* can be found as far north as Payne County. These hybrid plants resemble *Q. rubra* or *Q. x riparia*, but produce smaller fruits. The most conspicuous hybrids have leaves with finger-like lobes. Introgression with *Q. marilandica* var. *asheii* occurs throughout the Wichita Mountains. Because of the phenotypic plasticity of *Q. marilandica*, a morphological analysis of this complex is not likely to be as informative as a molecular based one.

Sometimes superficially resembling species in the white oak section (Eskew, 1938), *Q. buckleyi* can be identified by the silver stellate hairs in the axils of the midribs and secondary veins of its leaves, and by the complete covering of tomentum on the nuts.

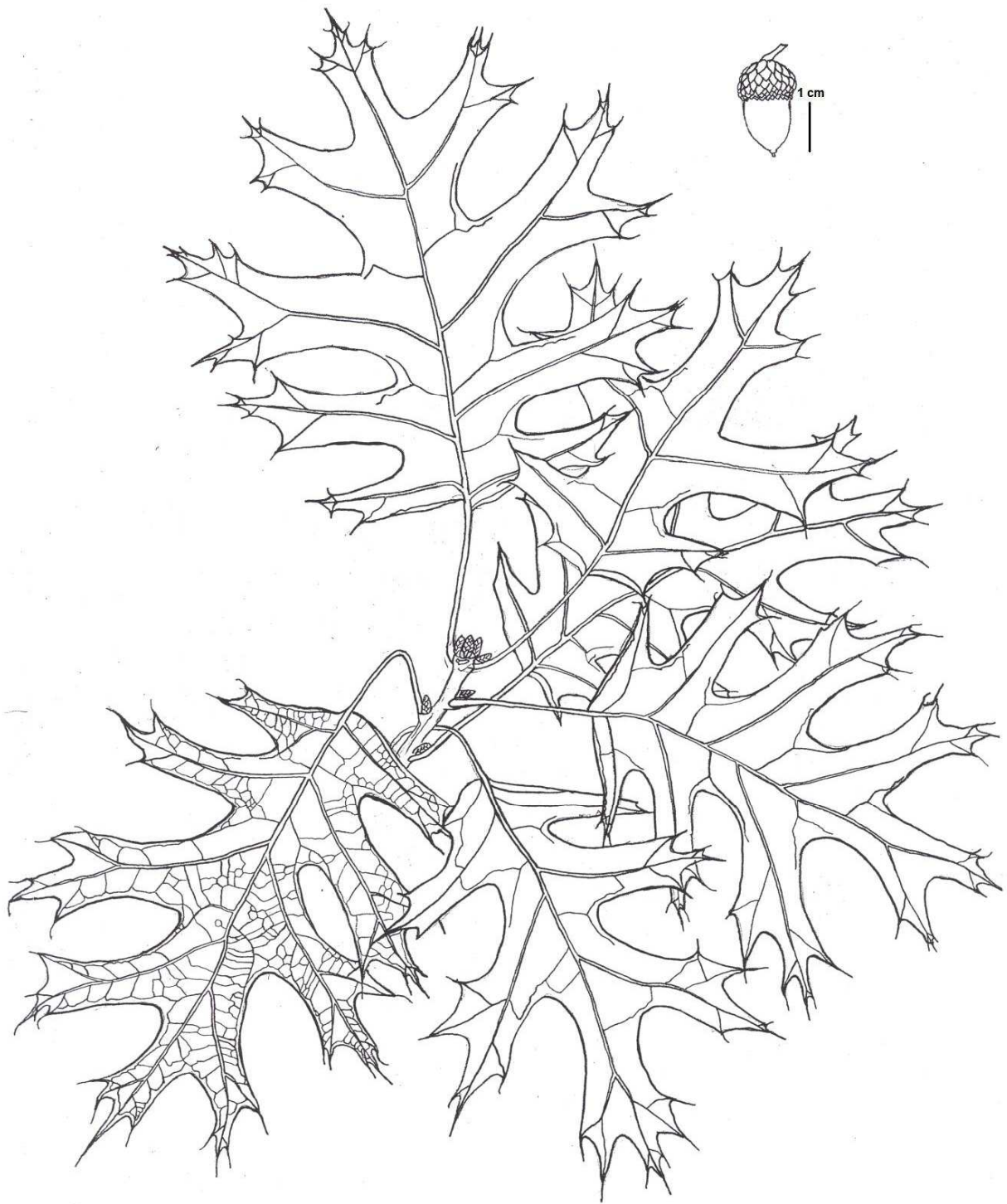


Figure 7. Foliage and acorn of *Quercus buckleyi* specimen collected at Bromide Hill near Sulphur, Murray County, Oklahoma.

***Quercus x drummondii* (Liebmann) Nixon and Muller Liebmann's Sand Post Oak**

Plants trees or shrubs; to 8 m in height; deciduous. **Bark of Trunks** whitish gray; scaly to blocky; inner bark not exposed. **Primary Branches** ascending to horizontal. **Twigs** 3.5-6 mm in diameter; reddish brown to silvery or sulphurous yellow; glabrate to densely stellate; hairs sulphurous yellow. **Terminal buds** terete in cross-section; ovoid; 2-6 mm long; reddish brown; sparsely silvery and/or golden pubescent, sometimes pubescent only along scale margins. **Leaves** obovate to elliptic or orbicular; 5-15 cm wide; 5-15 cm long; thick; coriaceous; apices rounded to obtuse or truncate to emarginate; margins 1- to 3-lobed; lobes oblong to broadly oblanceolate to spatulate, apically entire to 2-toothed and expanded; sinuses deep, extending 1/2-3/4 distance to midribs; bases cordate to rounded or truncate; adaxial surfaces dark to blue green, dull to glossy, sparsely pubescent to glabrate; abaxial surfaces sulphurous yellow or silver tinged green, dull; petioles 3-10 mm long, densely stellate to glabrate; hairs conspicuous, conspicuously stalked, raised and spreading to erect; stipules caducous. **Hairs of Adaxial Surfaces** like those of abaxial surfaces; but consistently deciduous. **Hairs of Abaxial Surfaces** persistent to deciduous; stellate; silvery; scattered to crowded; conspicuously stalked; 4- to 12-rayed; rays firmly attached to base, 0.6-1.2 mm long, raised and divergently spreading to stiffly erect, straight to curling; bulbous or uniseriate, silvery or golden, appressed, less than or equal to 0.1 mm long. **Hairs of Abaxial Midribs** like those of abaxial surfaces. **Catkins** 5-8 cm long. **Mature Acorns** ovoid to oblong; 8-21 mm long; solitary or paired; sessile or pedunculate, peduncles to 25 mm long. **Cupules** bowl- to saucer-shaped; 15-20 mm in diameter; 5-10 mm deep; enclosing 1/4-1/3 of nuts; silvery to golden tinged rusty brown; scales tightly or loosely

appressed, those at cupule rims reduced in size or lanceolate, those at cupule bases ovate, silvery or golden tomentose, margins reddish, tomentulose, bases flattened or thickened and/or creased, callus black to rust colored at maturity. **Nuts** ovoid to oblong; 10-20 mm in diameter; 11-20 mm long; dark brown with blackened stripes; glabrous or distal 3/4-1/2 tomentose.

This taxon was first collected and named as a new species by Liebmann in 1854. In 1924, Trelease published the binomial *Q. pseudomargaretta* for the taxon; this name, of course being a nomenclatural synonym. When Muller (1951b) studied Liebmann's type specimen and trees from the type locality, he concluded that they represented individuals of an exceptionally "stabilized" population of a hybrid between *Q. stellata* and *Q. margaretta* and that *Q. drummondii* was a nothospecies., hence the insertion of the "x" in the name. Features of this hybrid are illustrated in Figure 8.

Quercus x drummondii occurs throughout the southeastern quarter of the United States (Muller, 1951b; Nixon and Muller, 1997). Like *Q. margaretta*, it is usually encountered on well drained sandy to sandy loam soils of Quaternary age (Tucker and Muller, 1958). Large populations in the absence of either parental species are mostly encountered in the Cross Timbers of Oklahoma and Texas, whereas to the east it is more likely encountered as solitary trees or small populations. Contrary to the previously published range maps for the taxon (Nixon and Muller, 1997; Stein et al., 2003), well developed stands are found along the major rivers in both the north and south halves of the state.

Individuals intermediate with *Q. prinoides* and likely forming a few trihybrid mottes occur in Payne County (Figure 9). Individuals near the Deep Fork River in

Okmulgee County and in Boiling Springs State Park in Woodward County appear to share affinities with *Q. macrocarpa*.

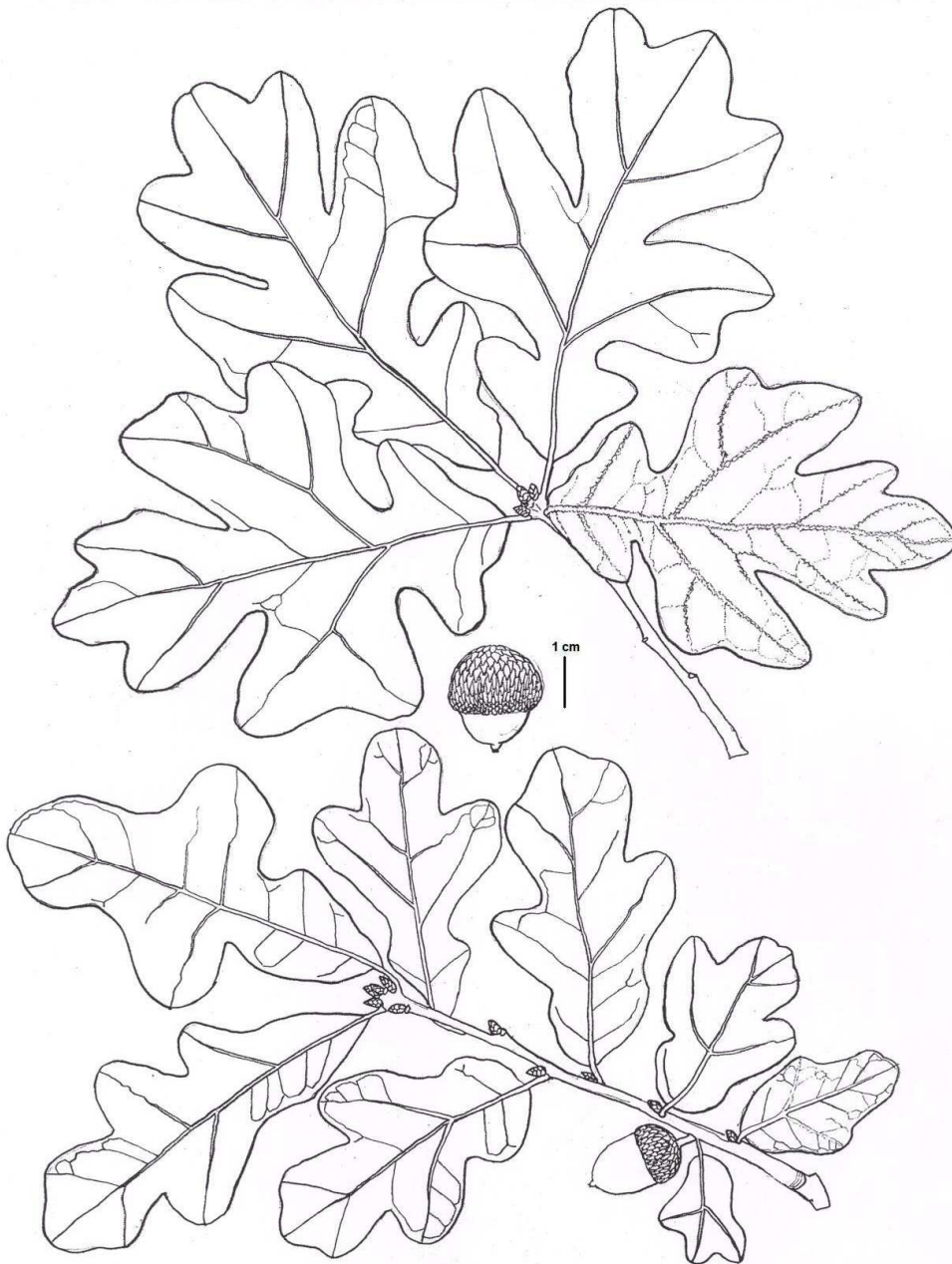


Figure 8. Foliage and acorn of *Q. x drummondii* specimen collected near the Cimarron River, Payne County, Oklahoma.

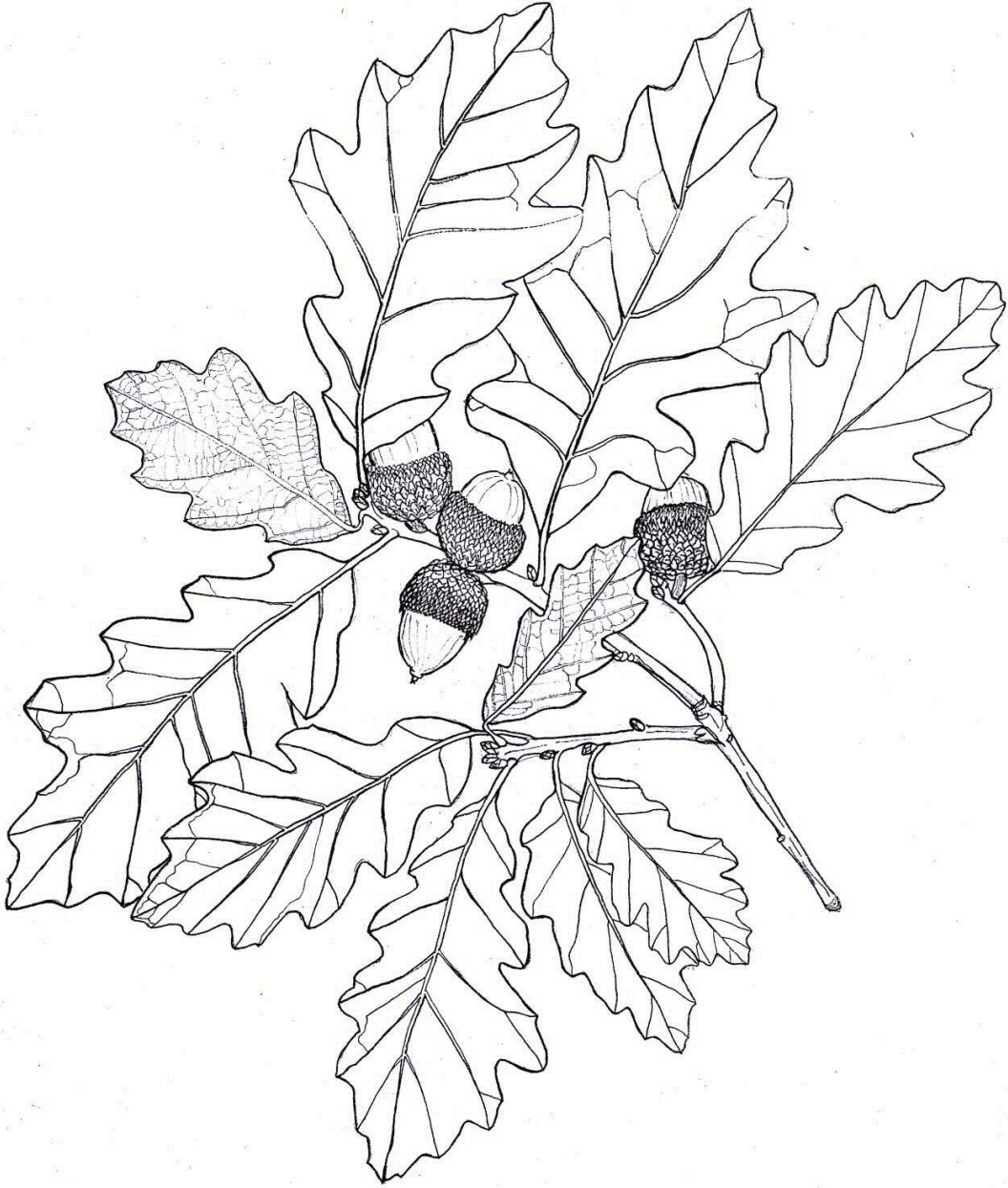


Figure 9. Foliage and acorn of putative trihybrid among *Quercus x drummondii* and *Quercus prinoides* collected near the Cimarron River, Payne County, Oklahoma.

***Quercus falcata* Michx. Southern Red Oak**

Plants trees; to 37 m tall; deciduous. **Bark of Trunks** gray to brown to black; smooth to coarsely ridged; orange inner bark often exposed by fissures or furrows. **Primary Branches** ascending to horizontal. **Twigs** 2-4 mm in diameter; reddish brown to sulphurous yellow; glabrate to densely stellate; hairs sulphurous yellow. **Terminal buds** 5-angled in cross-section; ovoid to ellipsoidal; 4-8 mm long; dark to light reddish brown; densely silvery and/or sulphurous yellow pubescent to glabrous, sometimes with a glabrous band parallel to margin. **Leaves** ovate to obovate; 7-17 cm wide; 10-31 cm long; thin to thick; chartaceous; apices acute to attenuate; margins 3- to 11-lobed; terminal lobes 2x longer than lateral lobes, lobes falcate to lanceolate or oblong to deltoid, entire to apically 1- to 3- toothed and constricted; sinuses deep, extending greater than or equal to 3/4 distance to midribs; awns 5-20, present along margins and/or at lobe apices; bases cuneate to rounded or broadly u-shaped; adaxial surfaces dark green, glossy, sparsely stellate; abaxial surfaces sulphurous yellow to golden yellow or yellow tinged green, dull, densely pubescent; petioles 20-60 mm long, sparsely to densely pubescent; hairs like those of leaf surfaces. **Hairs of Adaxial Surfaces** like those of abaxial surfaces; but persistent only along midribs. **Hairs of Abaxial Surfaces** persistent; stellate; sulphurous yellow covering surfaces to reddish tinged in vein axils, sessile covering surface to inconspicuously stalked in vein axils, 8- to 16-rayed; rays 0.1-0.5 mm long covering surfaces and 0.5-1.5 mm long in vein axils of midrib, appressed to erect, straight to curling; bulbous, sulphurous to golden, appressed, less than 0.1 mm long; setaceous, silvery to sulphurous yellow, 0.5-3.0 mm long. **Catkins** 5-8 cm long. **Mature Acorns** turbinate to ovoid; 12-22 mm long; solitary

or in clusters of 2 or 3; sessile or pedunculate, peduncles to 7 mm long. **Cupules** bowl-shaped; 10-20 mm in diameter; 5-10 mm deep; enclosing 1/3-1/2 of nuts; orange-brown; scales tightly appressed; flattened; oval to oblong; sparsely sulpherous yellow to silvery tomentose, margins red to dark orange colored or obscured by tomentum, bases flattened, callus absent. **Nuts** ovoid to globose; 10-18 mm in diameter; 10-20 mm long; light brown to orange brown; tomentose.

The specific epithet of this species reflects the sickle-shaped lobes of the leaves. It is found throughout the southeastern United States, with exception of extreme southern Florida (Little, 1971). In Oklahoma, individuals are encountered primarily in the southeastern quarter of the state on a variety of soils ranging from deep sandy loams in lowlands to stony loams of upland bluffs (Hoagland, 2000). This species is considered a dominant in the southern half of the eastern Deciduous Forest (Waggoner, 1975; Carey, 1992a).

Juvenile twigs and abaxial leaf surfaces are a bright sulpherous yellow due to dense pubescence, whereas the adaxial leaf surfaces are dark red to blackish green. The surface hairs of the juvenile leaves are stellate and setaceous on the veins. Those of the adaxial surface frequently become loose and are shed during expansion and maturation of the leaves. The twigs shed their hairs throughout the growing season to varying degrees. In the early summer, individuals may have red glabrous twigs to densely stellate twigs. Depending on their position in the canopy, mature leaves can exhibit extremely variable margins and sinuses on the same tree (Muller, 1951b; Vines, 1982; Jensen, 1989). The leaves of individual trees within stands or between stands can also exhibit such variation (Muller, 1951b; Vines, 1982). The tendency of the leaves

to smolder for a long period after a fire, especially when compared to leaves of other oak species, suggests an ecological role as fire facilitators (Kane et al., 2008).

Individuals with thin bark have been described as susceptible to fire damage and subsequent heart rot (Farmer et al., 1969; Belanger, 1990). Hollow trees may serve as habitat for cavity nesting birds (Hardin and Evans, 1977). Profuse acorn production occurs at 1- or 2-year intervals (Olsen, 1974; Bonner, 2008).

Hybrids are reported with other members of Section *Lobatae* in the state with exception of *Q. rubra*, *Q. palustris*, and *Q. buckleyi* (Little, 1979; Jensen, 1997). Hybrids are reported (Palmer, 1948) with *Q. incana* (= *Q. x subintegra* (Englemann) Trelease), *Q. marilandica*, *Q. nigra* (= *Q. x garlandensis* E. J. Palmer), *Q. phellos* (= *Q. x ludoviciana* Sarg.), *Q. shumardii* (= *Q. x jorii* Trelease), and *Q. velutina* (= *Q. x willdenowiana* (Dippel) Zamble). Near the entrance to the Spiro Mounds State Park in LeFlore County is a stand of individuals that appear to be hybrids between *Q. falcata* and either *Q. shumardii* or *Q. rubra*.

Some taxonomists (Waterfall, 1969; Little, 1985; Taylor and Taylor, 1994) treat *Q. falcata* and *Q. pagoda* as conspecific and recognize two varieties. The treatments of Jensen (1989; 1997) and Nixon (1997) maintaining them as distinct species are followed here.



Figure 10. Foliage and immature acorns of *Q. falcata* specimen collected in the Liver Tract of the Ozark Plateau National Wildlife Refuge, Adair County, Oklahoma.

***Quercus x fernowii* Trel.**

Plants trees; to 20 m in height; deciduous. **Bark of Trunks** whitish gray; scaly; inner bark not exposed. **Primary Branches** slightly ascending to horizontal. **Twigs** 1.5-4 mm in diameter; reddish brown to sulphurous yellow; glabrate to stellate; hairs silvery to sulphurous yellow. **Terminal buds** terete in cross-section; sub-globose to ovoid; 0.5-5 mm long; reddish brown to dark brown; sparsely tomentose or glabrous, hairs silvery. **Leaves** obovate to elliptic-obovate; 5.0-10.5 cm wide; 10.5-14.5 cm long; thick; coriaceous; apices rounded to obtuse or emarginate; margins uniformly 2- to 4-lobed; lobes "finger-like" to spatulate, entire or apically toothed; sinuses shallow or deep, extending 1/3-2/3 distance to midribs; bases rounded to acute; adaxial surface dark green, glossy, glabrous or glabrate; abaxial surfaces light green, dull, scabrous, glabrate except for stellate hairs adjacent midribs or wholly stellate; petioles 5-10 mm long, glabrate; hairs like those adjacent midribs; stipules caducous. **Hairs of Adaxial Surfaces** like those of abaxial surfaces; but deciduous. **Hairs of Abaxial Surfaces** persisting along midribs or wholly persistent; stellate; silvery; sessile to inconspicuously stalked, (less than 0.1 mm tall); 6- to 8-rayed; rays 0.2-0.5 mm long, inconspicuously ascending to ascending, straight to curling; uniserrate, silvery, equal to or less than 0.3 mm long, appressed, straight. **Hairs of Abaxial Midribs** sericeous, persistent or caducous, scattered, silvery, 0.5-1.5 mm long, closely antorsely appressed, straight. **Catkins** 5-10 cm long. **Mature Acorns** oblong or ovoid; 12-24 mm long; solitary or in clusters of 2 or 3; sessile or pedunculate, peduncles to 25 mm long. **Cupules** deeply bowl- to saucer-shaped; 15-20 mm in diameter; 6-9 mm deep, enclosing 1/3-1/2 of nuts; silvery; scales tightly appressed, those at cupule rims abruptly reduced in size, ovate to

oval, silvery tomentose, margins reddish in distal 1/2-1/3 or obscured by dense tomentum, bases keeled to tuberculate, callus black. **Nuts** globose to oblong; 9-20 mm in diameter; 10-23 mm long; light brown to dark brown; glabrous.

Originally described as a distinct species by Trelease in 1917, this taxon is now recognized to be a hybrid between *Q. alba* and *Q. stellata* (Hardin, 1975). This nothospecies is named in honor of Bernhard Eduard Fernow, the first Chief of the Division of Forestry in the U.S. Department of Agriculture (Little, 1979). Individuals of *Quercus x fernowii* are common throughout the eastern fifth of the state in the forested mountains where *Q. alba* occupying the lower slopes meets *Q. stellata* occupying the upper slopes. Backcrosses with *Q. stellata* are frequent in Oklahoma because of the abundance of the species, continued distribution to the west, and the prevailing winds from the west and southwest (Hardin, 1975).

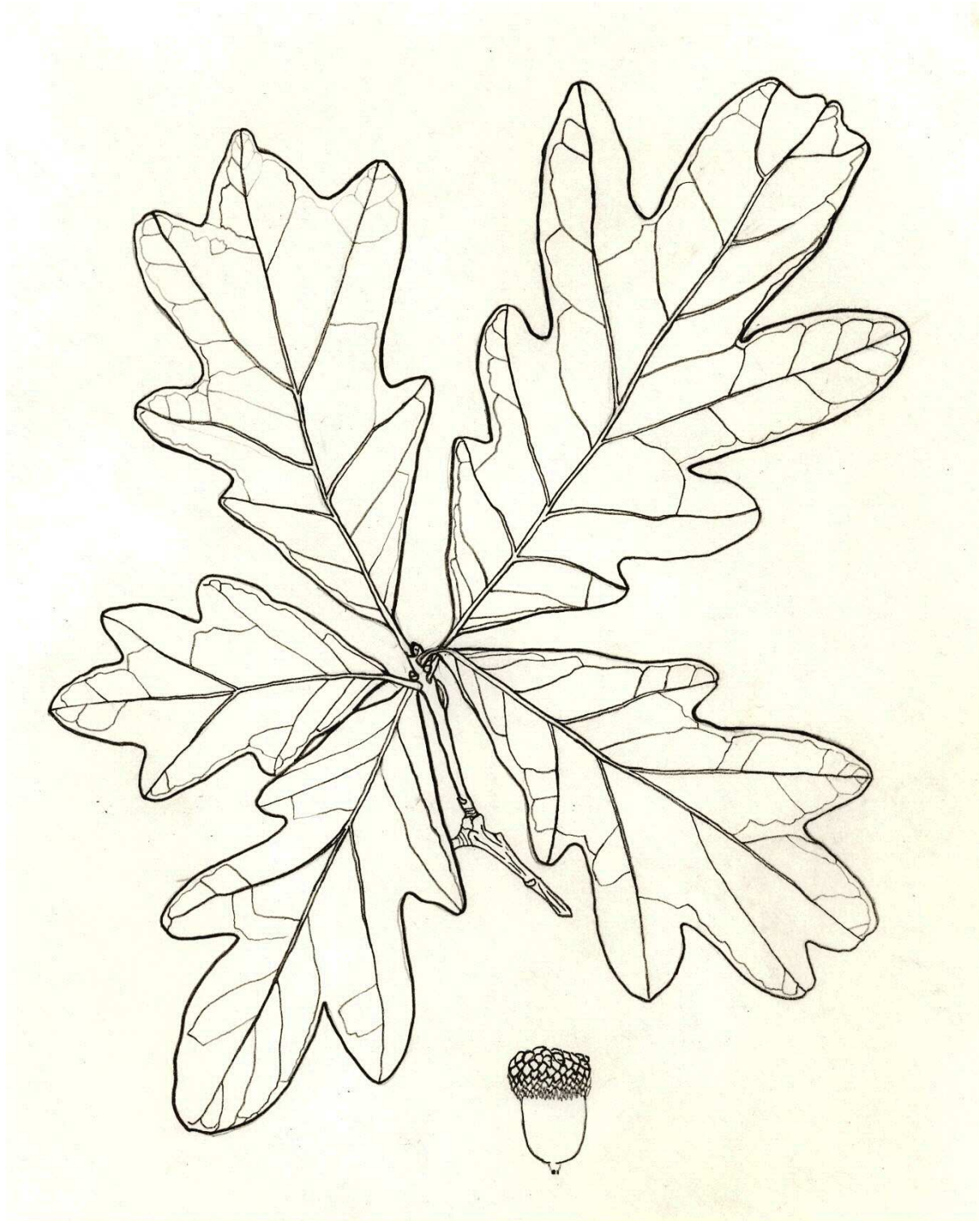


Figure 11. Foliage and acorn of *Quercus x fernowii* specimen collected on Sparrow Hawk Mountain in Cherokee County, Oklahoma.

***Quercus gambelii* Nutt. Gambel Oak**

Plants trees or colony forming shrubs; to 5 m in height; deciduous. **Bark of Trunks** whitish gray to orange and/or black tinged; scaly to roughly ridged to plated; inner bark not exposed. **Primary Branches** ascending to horizontal. **Twigs** 1.5-4 mm in diameter; reddish brown; glabrate. **Terminal buds** terete in cross-section; ovoid; 0.5-3 mm long; dark brown; red and/or silvery pubescent, frequently only ciliate along scale margins. **Leaves** obovate to elliptic; 2.5-9.9 cm wide; 4.8-14.5 cm long; thin; subcoriaceous or coriaceous; apices acute to rounded or emarginate; margins uniformly 4- to 6-lobed; lobes oblong, apically entire or emarginate; sinuses deep, extending equal to or greater than 3/4 distance to midribs; bases truncate or cuneate; adaxial surfaces dark to blue green, glossy or dull, scaberulous to scabrous, sparsely to densely pubescent; abaxial surfaces silvery tinged blue or green, dull, scaberulous and reticulately ribbed to scabrous, sparsely to densely pubescent; petioles 4-15 mm long, glabrate to sparsely setaceous, hairs antrorsely appressed; stipules caducous. **Hairs of Adaxial Surfaces** like those of abaxial surfaces; but sparse and frequently reduced in size. **Hairs of Abaxial Surfaces** persistent; stellate, silvery, sessile to inconspicuously stalked (less than 0.1 mm long), 1- to 5(8)- rayed; rays 0.2-0.5 mm long, ascending to erect, straight to slightly curving; uniserrate, silvery, appressed, equal to or less than 0.3 mm long. **Catkins** 2-4 cm long. **Mature Acorns** oblong; 17-23 mm long; solitary or in clusters of 2 or 3; sessile or pedunculate, peduncles to 10-30 mm long. **Cupules** deeply bowl- to saucer-shaped; 12-24 mm in diameter; 6.5-11 mm deep, enclosing 1/4-1/3 of nuts; silvery; scales tightly appressed, those at cupule rims abruptly reduced in size, deltoid to oval, silvery tomentose, margins reddish in distal 1/2-1/3, tomentulose to tomentose,

bases slightly to conspicuously tuberculate, callus black. **Nuts** oblong; 11-16 mm in diameter; 16-21 mm long; light brown; glabrous.

Quercus gambelii was named by Thomas Nuttall in honor of William Gambel; a naturalist from Philadelphia that discovered it in 1844 (Little, 1981). It is a dominant tree or shrub (Figure 11) throughout the southwestern United States at elevations between 1000-3030 m (Nixon and Muller, 1997). Elevation is important in the distribution of the species, and has led taxonomists to hypothesize (Julyan and Smith, 2006) about ancient climate changes as disjunction populations of the species may be separated by hundreds of miles of desert. In Oklahoma, it only occurs in the northwestern corner of the Panhandle.

Plants are typically found on soils that are highly weathered, well drained, loamy to calcareous, and deep to shallow. Associations with *Juniperus monosperma*, *Pinus edulis*, and *Opuntia polyacantha* occur from Black Mesa to the foothills of the Rocky Mountains (Hoagland, 2000). Some plants in Oklahoma exhibit a stem diameter at breast height (DBH) of 15–20 cm; a value correlated with individuals over 100 years of age according to Abella (2008). About 66% of individuals with these diameters were alive five years after a prescribed fire, whereas less than 20% of individuals with a DBH of 5 cm or less survived (Abella and Fulé, 2008). Sprout regeneration after felling can lead to mottes formed from multiple clones. Dense stands serve as prime refuges and food sources for mule deer, elk and other mammals (Lauver et al., 1989; Simonin, 2000). Native Americans used the nuts for food and medicine while the bark and twigs were used for shelter and tools (Moerman 1998).

This species has hybridized frequently and extensively with drought tolerant, *Q. mohriana* and *Q. turbinella* (Tucker et al. 1961). Hybridization with *Q. turbinella* is most common and wide ranging. Examination of herbarium specimens deposited in Oklahoma herbaria and plants growing in Cimarron County suggest that typical, pure *Q. gambelii* may no longer occur in Oklahoma. Only specimens collected by Elbert L. Little (#36,016) and U.T. Waterfall (#8700) in 1980 and 1948 near a natural spring in Tesequite Canyon in Cimarron County appear to be the most recent collections of typical *Q. gambelii* when compared to a photograph of the type specimen (A. Fendleri no. 810). However, even these collections should be considered atypical according to the herbarium specimen annotations made by J.M. Tucker. This is because he discovered that the stellate hairs on the abaxial leaf surfaces are more frequently 6- to 8-rayed in contrast to the 1- to 4-rayed hairs characteristic of "typical" *Q. gambelii* found 120 miles to the west in the Rocky Mountains.

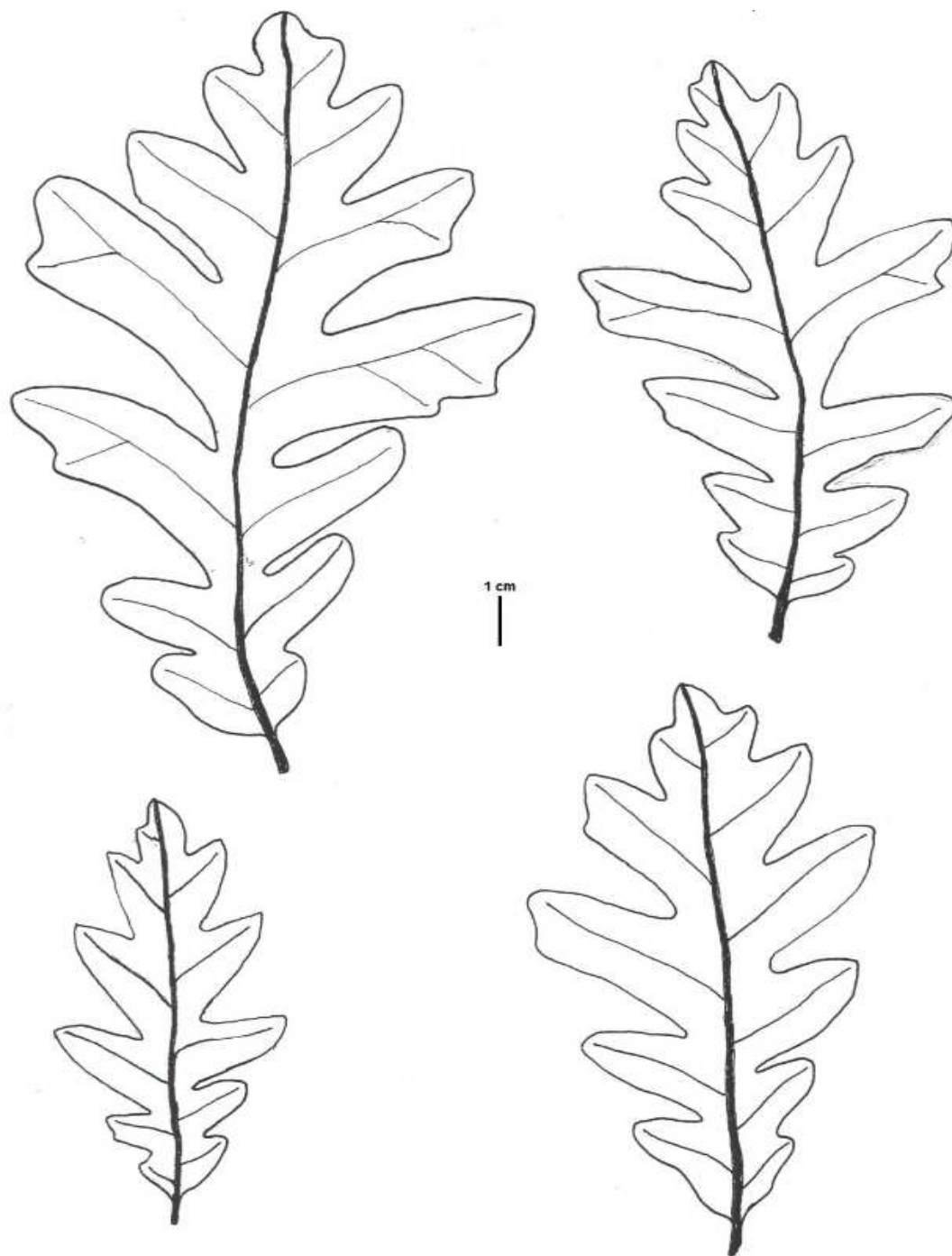


Figure 12. Leaves *Quercus gambelii* collected in Tesequite Canyon, Cimarron County, Oklahoma prior to 1980. Drawn from herbarium specimens of Little and Waterfall.

***Quercus harvardii* Rydb. Shinnery Oak**

Plants colony forming shrubs; to 2.5 m in height; deciduous. **Bark of Trunks** whitish gray to blackish tinged; smooth or scaly; inner bark not exposed. **Primary Branches** ascending to horizontal. **Twigs** 1-2 mm wide; reddish orange to reddish brown; glabrate to sparsely stellate, hairs silvery or sulphurous yellow. **Terminal buds** terete in cross-section; globose to subglobose; equal or less than 2 mm long; reddish brown to orange red; glabrous, sometimes merely reddish ciliate along scale margins. **Leaves** obovate to ovate, or lanceolate to oblanceolate, or oblong to elliptic; 1.8-5 cm wide; 5.5-10.2 cm long; thick; coriaceous; apices rounded or acute; margins entire or undulate or 2- or 5-toothed, teeth serrate to undulate-crenate; sinuses shallow, extending equal to or less than 1/2 distance to midribs; bases rounded to cuneate; adaxial surfaces grey green to light green, glossy, sparsely pubescent to glabrate; abaxial surfaces silvery or yellowish tinged green or white, scabrous and/or reticulately ribbed, yellow glandular, densely to sparsely pubescent; petioles 0.5-7 mm, sparsely glabrate to sparsely stellate, hairs like those of adaxial surfaces but sparse; stipules deciduous. **Hairs of Adaxial Surfaces** like those of abaxial surfaces but sparse. **Hairs of Abaxial Surfaces** persistent; stellate; silvery to sulphurous yellow; sessile to minutely stalked; 8- to 18-rayed; rays 0.1-0.5 mm long, appressed to inconspicuously ascending to ascending, mostly curling to crimped or sparingly straight; bulbous or uniseriate, silvery or golden, appressed, less than or equal to 0.1 mm long. **Catkins** 2-3 cm long. **Mature Acorns** campanulate to ovoid; 17-30 mm long; solitary or in clusters of 2 or 3; sessile or pedunculate, peduncles

to 10 mm long. **Cupules** deeply bowl- to campanulate-shaped; 20-25 mm in diameter; 10-17 mm deep; enclosing 1/2-1/3 of nuts; silvery to golden tinged rusty red; scales loosely appressed, sometimes only reflexed at cupule rims, those at rims acicular, those at cupule bases deltoid to ovate, silvery or golden tomentose, margins red, glabrous to obscured by dense tomentum, bases keeled or conspicuously tuberculate, callus rust colored at maturity. **Nuts** ellipsoidal to oblong; 10-16 mm in diameter; 16-25 mm long; yellowish tinged red to reddish brown; glabrate.

The specific epithet of *Q. havardii* honors the botanist and U.S. Army surgeon Valéry Havard who collected plants in Texas while stationed there (Vines, 1982; Little, 1981). Typically forming dense stands, the species is the dominant of the shinnery oak grasslands of western Oklahoma (Little, 1979; Tyrl, et al., 2002). Historically, it blanketed the southern Great Plains in southeastern New Mexico, southwestern Oklahoma and north-central Texas (Muller, 1952; Little, 1976; Peterson and Boyd, 1998). In Oklahoma, the largest populations are encountered in sandy soils of ancient, stabilized sand dunes, plains, and riverbeds along the western edge of the state (Little, 1981; Peterson and Boyd, 1998; Hoagland and Buthod, 2007). Populations are typically encountered in deep sand, but may also be established in loams with higher clay, silt, and organic matter content (Tyrl et al. 2002; Peterson and Boyd, 1998). Frequently, the species is associated with *Q. stellata* in fence rows. Reported sightings in Cimarron County have not been accompanied by convincing plant material, and the plants observed may have been confused with *Q. x pauciloba*, which all exhibits clonal reproduction from a similar appearing underground system (Saunier and Wagle, 1965).

Some individuals have been estimated to be a thousand years or more old (Mayes, 1994). Reproduction is mostly asexual with the formation of colonies. Rhizomes have been reported to have the width of a human thigh, extend to depths of six meters, and cover an expanse of 43,000 square meters (Muller, 1951a; McIlvain, 1954, 1956; Dhillion et al., 1994; Mayes 1994; Gucker, 2006). When aerial stems are removed from the rhizomes of 18-20 year old individuals, buds will regenerate new stems within 1-2 months (Peterson and Boyd, 1998; Boyd et al., 2001). These physiological responses suggest that the species evolved under conditions of intensive grazing and repeated fires (Peterson and Boyd, 1998; Boyd & Bidwell 2001).

The largest acorns of *Q. havardii* are found on stems to a meter in height. These are readily consumed by mammals, game birds, and song birds in the early fall (Tyrl et al., 2002). The species also provides habitat for the endangered prairie chicken (*Typanachus pallidicinctus*) which is endemic to Oklahoma and Texas (Boyd and Bidwell, 2001; 2002). Cattle whose diet consists of 50% or more of this oak may show signs of digestive and urinary tract disorders from toxic accumulations of tannic acids (Marsh et al., 1919; Burrows and Tyrl, 2006). For this reason it has historically been considered undesirable and subject to eradication efforts throughout much of its range. Fortunately, its conservation has become a high priority in Oklahoma, Texas, and New Mexico (Peterson and Boyd, 1998; CCA, 2008).

Mayes and coworkers (1998) performed molecular work showing that the genetic diversity of a population of *Q. havardii* in Texas to be similar to that of species that are reproducing sexually. Muller (1952) and Mayes and coworkers (1998) proposed that interbreeding with *Q. stellata* during past interglacial periods was possibly

responsible for the genetic diversity that they encountered in *Q. havardii*. Many of the seemingly pure clones of *Q. havardii* exhibit leaf shapes comparable to *Q. stellata* (Muller, 1951b). To date there are no accounts of this species or its putative hybrids reproducing from seed in nature, but it is obvious that hybrids are produced (Muller, 1951b; Wiedman and Penfound, 1960; Mayes et al., 1998; Peterson and Boyd, 1998). Muller (1952), as well as Wiedman and Penfound (1960), believed that the hybrids were relicts of past climatic conditions, and that they had survived fire by growing in sheltered habitats where fire did not occur. When considering the natural history of the area occupied by *Q. havardii*, it seems likely that Muller's (1952) assumption about the past introgressions of other species into *Q. havardii* during different environmental conditions is correct. Pollen from F1 and backcrossed generations has likely been a source of genetic diversity in "pure" *Q. havardii*. One-way pollen flow between two species of oak in Portugal that exhibit comparable dynamics of growth strategy to *Q. havardii* and *Q. stellata* has been demonstrated (Boavida et al., 2002). Analysis of the organelle genotypes of the mixed population of these two Portuguese oaks showed evidence that one species remained maternally active and was responsible for the production of F1 generation acorns (Burgarella et al., 2009).

In Oklahoma, *Quercus havardii* hybridizes with *Q. macrocarpa* (= *Q. x andrewsii*), *Q. stellata*, *Q. margaretta* (Figure 14), *Q. mohriana*, and *Q. muehlenbergii* (Sargent, 1918; Waterfall, 1969; Little, 1980). Trihybrid crosses are believed to occur with *Q. gambelii* and *Q. turbinella* in Arizona and Utah (Tucker; 1970). This hybrid has been name variety *tuckeri* by Nixon and Muller (1997). In addition, *Q. x eastwoodii* has been recognized from the region as a hybrid between just *Q. havardii* and *Q. gambelii*

(Welsh et al., 1993, Peterson and Boyd, 1998). Nixon and Muller (1997) believed the variety name is misappropriated by its application to hybrids. Furthermore, type material of the variety, deposited at the Missouri Botanical Gardens, closely resembles currently made collections of *Q. x pauciloba* from northeastern New Mexico and Cimarron County, Oklahoma. Sargent (1918) gave formal variety status to hybrids with *Q. stellata* that he believed were varieties of the latter taxon (Muller, 1951). Intermediate individuals with *Quercus stellata* are the most frequently encountered among others in Oklahoma (Muller, 1951b; 1952; Little, 1979; Nixon and Muller, 1997). Also, fruits resembling the type specimen of *Q. havardii* can be paired with leaves resembling *Q. stellata* (see Plate 27, Muller, 1951b). Often they can be far ranging from underground rhizome; giving the appearance of multiple individuals of the same phenotype when in deed they are clonal. Pettit and Kauffman (1978) discovered that these clonal rhizomes can separate from each other late into maturity (Peterson and Boyd, 1998). Muller (1951) regarded Sargent's (1918) *Q. x andrewsii* as a synonym for *Q. havardii*. Sargent reported the hybrid as being from Dewey County, Oklahoma, and having the parentage of *Q. macrocarpa* and *Q. undulata*. However, *Q. havardii* was recognized as a variety of *Q. undulata* until being recognized as a species by Rydberg (1901) (Tucker, 1961). The likely parentage was between that of *Q. havardii* and *Q. macrocarpa*. Elbert Little Jr. made the first known collection (# 36,505) of *Q. muehlenbergii* x *Q. havardii* from Boiling Springs State Park in 1980. His collections of this individual are deposited in the herbarium at Oklahoma State University and the Bebb herbarium at the University of Oklahoma. Another individual of this cross has since been located at the park. Waterfall (1969) considered small fruited specimens as possibly introgressed with *Q. mohriana*.

These hybrids still occur along the border with Texas; though the influence of *Q. stellata* is mostly developed there.

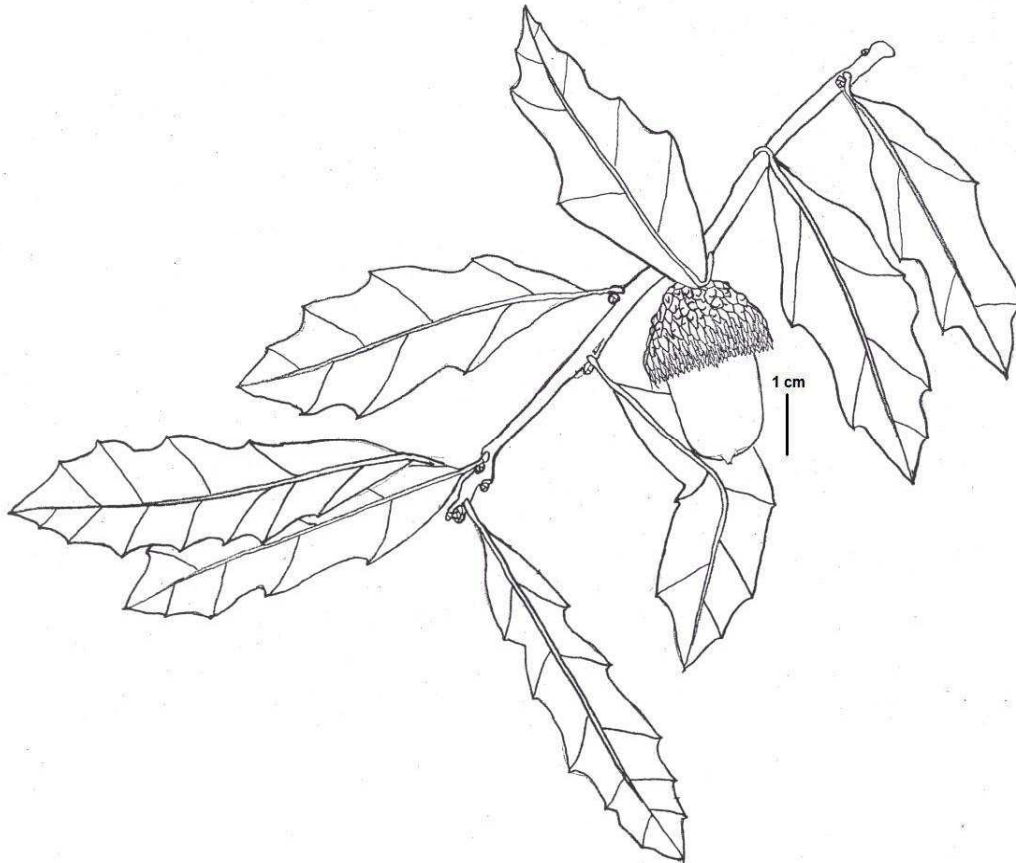


Figure 13. Foliage and acorn of *Q. havardii* specimen collected near Erick in Beckham County, Oklahoma.

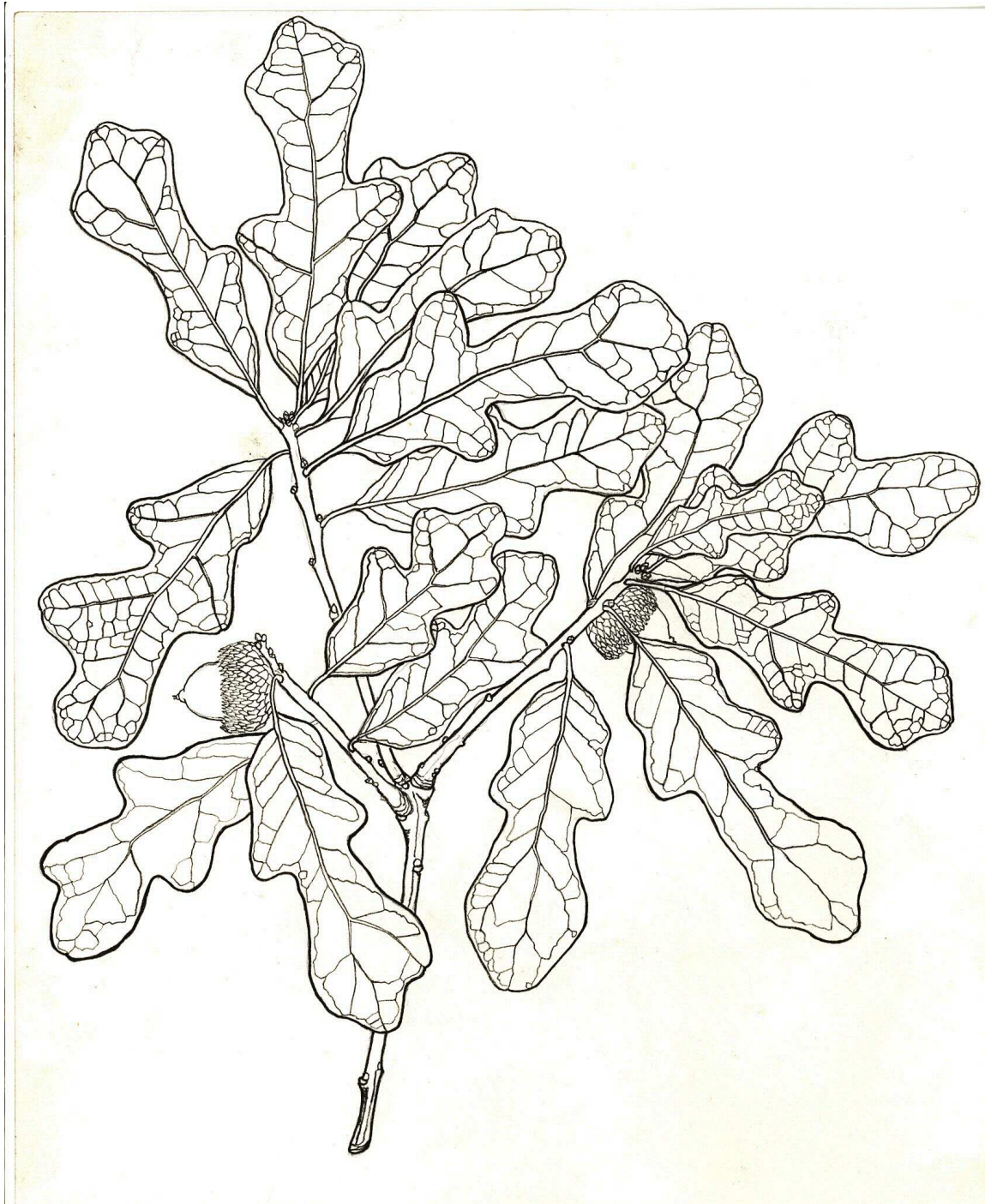


Figure 14. Foliage and acorns of putative hybrid between *Quercus havardii* and *Quercus margaretta* collected in Boiling Springs State Park, Woodward County, Oklahoma.

***Quercus incana* Bartr. Bluejack Oak**

Plants trees; to 17 m tall; deciduous. **Bark of Trunks** grey to black; blocky to roughly ridged; orange inner bark rarely exposed. **Primary Branches** ascending to horizontal to descending; typically twisted. **Twigs** 1-2.5 mm in diameter; silvery to yellowish gray or rarely reddish brown; densely to sparsely silvery stellate, hairs silvery to inconspicuously sulphurous yellow. **Terminal buds** terete in cross-section; 3-5 mm long; ovoid approaching conic; light brown to reddish brown; densely to sparsely silvery pubescent. **Leaves** elliptic-oblong to oblong-oblongate; 1-6.4 cm wide; 3.1-11.2 mm long; thin; coriaceous; apices mucronate to acute or rounded; margins entire to denticulate, teeth dentate; sinuses shallow, extending 1/10-1/3 distance to midribs; awns 0-5, present at teeth apices and/or apex; bases rounded to acute; adaxial surfaces gray green to dark green, dull to glossy, conspicuously stellate to glabrate, except for persistent stellate hairs along midribs; hairs silvery; abaxial surfaces whitish gray to silvery tinged green, dull; petioles 2-10 mm long, densely to sparsely pubescent, hairs like those of leaf surfaces; stipules caducous. **Hairs of Adaxial Surfaces** like those of abaxial surfaces but sparse except near midribs. **Hairs of Abaxial Surfaces** stellate; hairs silvery, except for reddish tinged hairs in vein axils, crowded, sessile, 8- to 12-rayed; rays approx. 0.1-0.4 mm long, those in vein axils approaching longest range, appressed to inconspicuously ascending, straight. **Catkins** 4-5 cm long. **Mature Acorns** ovoid to globose; 17 mm long; solitary or in clusters of 2(3); sessile or pedunculate, peduncles to 4 mm in length. **Cupules** shallowly bowl- or saucer-shaped; 10-15 mm in diameter; 3-6 mm deep; enclosing 1/4-3/8 of nuts; silvery and reddish brown to silvery orange-brown; scales tightly appressed; flattened; ovate to oval;

densely silver tomentose, margins red to dark orange colored or obscured by tomentum, bases flattened, callus absent. **Nuts** globose to ovoid; 10-15 mm in diameter; 10-15 mm long; light brown; pubescent. The foliage and acorn of *Q. incana* are illustrated in Figure 15.

Quercus incana is found in the Gulf and Atlantic Coastal Plains of the southeastern United States; with exception of the southern half of Florida and Louisiana (Little, 1971; Jensen, 1997). Individuals associate frequently with *Q. margaretta* and form intermittent scrublands within the pine-oak association of the eastern Deciduous Forest from Georgia to eastern Oklahoma and Texas (Faust, 1970; Clark, 1971; Correll and Johnston, 1970). In Oklahoma, this scrubland association dominates sandy uplands adjacent to forested bottomlands and tributaries of the Red River in the southeastern quarter of the state (Hoagland, 2000).

Juvenile twigs and abaxial leaf surfaces are yellowish gray pubescent and remain so at maturity, whereas adaxial leaf surfaces are adaxially pinkish, but quickly become bluish green as they mature. Hairs of the adaxial leaf surfaces sometimes shed profusely on heavily shaded individuals, with the exception of hairs on the adaxial midribs which remain densely pubescent near the petiole. Foliage and an acorn of *Q. incana* are illustrated in Figure 13.

The acorns of *Q. incana* are consumed by squirrels, raccoons, deer, quail and turkey (Stein et al., 2003; Sullivan, 1994). Planting and preservation as an understory species in forests of *Pinus palustris* in Texas has been encouraged for its wildlife value (Sullivan, 1994).

The synonym *Q. cinerea* Michx. (1803) is encountered in the older literature (Sargent 1926; Van Dersal, 1938; Howard and Staples, 1983). Bartram (1791) authored the name *Q. incana* and accompanied it with a single verse description in the book he had written about his travels. Some taxonomists began using the binomial *Q. cinerea* published by Michaux, contending that Michaux's description and accompanying artwork satisfied the requirements of valid publication, whereas Barton's name did not (Trelease, 1924; Howard and Staples, 1983). Trelease (1924) believed Bartram's name to be a synonym of *Q. virginiana*, in the Section *Quercus*, even though *Q. incana* is in Section *Lobatae*. Fernald (1944) made an interesting argument for the legitimacy of Bartram's binomial despite the fact that his name is accompanied by only by a single sentence description. He contended that Bartram's writings indicate that he was very familiar with the other oak trees in the region that were similar in morphology, e.g., *Q. virginiana*; a species that he wrote extensively about before mentioning *Q. incana* in his book. Also, it is worth noting that *Q. virginiana* was in cultivation 60 years before Bartram's travels (Olsen, 1974).

Quercus incana also has been used for an oak species native to the Indian subcontinent in Asia (Roxbergh, 1814). Unfortunately, use of *Q. incana* for this Indian taxon is still popular (Gambel, 1984; Azorin-Ortuno et al., 2008; Sharma et al., 2008).

Hybrids are reported between *Q. incana* and other members of Section *Lobatae*, except for *Q. rubra*, *Q. shumardii* and *Q. buckleyi* (Little, 1979; Jensen, 1997). They include: *Q. falcata* (= *Q. x subintegra* (Englemann) Trelease), *Q. marilandica* (= *Q. x cravensis* Little), *Q. nigra* (= *Q. x caduca* Trelease), *Q. phellos*, and *Q. velutina* (= *Q. x podophylla* Trelease) (Palmer, 1948).

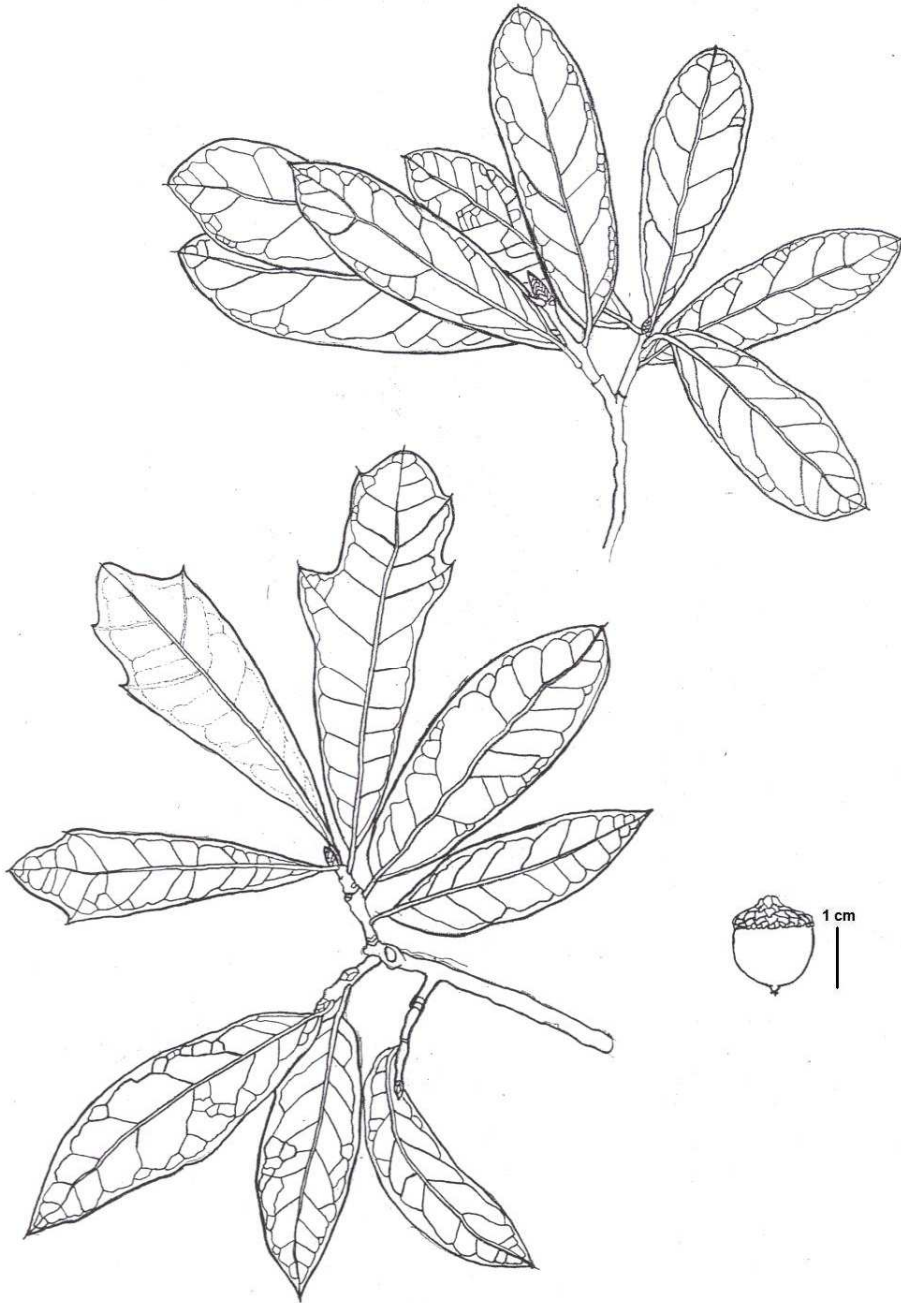


Figure 15. Foliage and acorn *Q. incana* specimen collected in The Nature Conservancy's Boehler Seeps Nature Preserve, Atoka County, Oklahoma.

***Quercus lyrata* Walt. Overcup Oak**

Plants trees; to 24.4 m in height; deciduous. **Bark of Trunks** whitish to dark greenish gray and/or red tinged; scaly to coarsely ridged; reddish inner bark often exposed by fissures or furrows. **Primary Branches** ascending to horizontal. **Twigs** 1-4 mm diameter; reddish brown to gray; glabrate to glabrous. **Terminal buds** terete to slightly angular in cross-section; sub-globose or ovoid to conic; 1-3 mm long; light brown; sparsely silvery pubescent. **Leaves** obovate to elliptic; 5.7-14.1 cm wide; 9.7-18.6 cm long; thin; chartaceous to subcoriaceous; apices acute to obtuse-acute; margins 2- to 7-lobed; lobes deltoid or oblong, apically entire or 1- to 3- toothed and expanded; sinuses deep, extending 1/2-3/4 distance to midribs; bases cuneate to acute; adaxial surfaces dark green, glossy, sparsely pubescent to glabrate; abaxial surfaces coppery green, dull, sparsely pubescent; petioles 8-33 mm long; glabrate to glabrous; stipules persistent below terminal buds. **Hairs of Adaxial Surfaces** like those of abaxial surface of shade leaves; but frequently reduced in size. **Hairs of Abaxial Surfaces** stellate; silvery; scattered and stalked on shade leaves, crowded and sessile on sun leaves; 4-rayed on shade leaves; 8- to 16-rayed on sun leaves; rays 0.5-1 mm long on shade leaves, 0.1-0.5 mm long on sun leaves, ascending to erect on shade leaves, appressed to ascending on sun leaves, straight to slightly curving. **Hairs of Abaxial Midribs** sericeous; silvery; persistent; scattered; sessile; antrorsely appressed; straight to slightly curved. **Catkins** 4-6 cm long. **Mature Acorns** globose; 17-30 mm long; solitary or paired; sessile or pedunculate, peduncles to 40 mm long. **Cupules** globose-shaped; 15-32 mm in diameter; 15-30 mm deep; enclosing more than 3/4 of nuts;

silvery; scales tightly appressed, those at cupule rims abruptly reduced in size, ovate to oblong, silvery tomentose, margins orange in distal 1/3-1/4, tomentulose to obscured by tomentum, bases conspicuously tuberculate to conspicuously keeled, callus black. **Nuts** globose to ovoid; 15-30 mm in diameter; 15-31 mm long; light to dark brown; apices pubescent.

The specific epithet of *Q. lyrata* reflects the shape of the leaves and their resemblance to the musical instrument known as the lyre (Vines, 1982; Figure 16). Individuals are large trees of the Atlantic and Gulf coastal plains (Little, 1971). Disjunct populations occur in Iowa (Shimek, 1922). In Oklahoma, it is found primarily in extreme southeastern McCurtain County and occasionally LeFlore County. Trees occur on clay or silty-clay flats, terraces, or bottoms that are intermediate between low-lying river channels, swamps, or bogs (Clark and Benforado, 1981; Wharton et al., 1982; Mitsch and Gosselink, 2000). They are dominant, only when in association with *Carya aquatica* (Eyre, 1980; Dale, 1984; Sullivan, 1993). Stands of the two species occur in the sloughs and swamps of McCurtain County, Oklahoma (Hoagland 2000). However, little remains of this association in Oklahoma because these habitats were drained and subsequently logged during early statehood (David Weaver, personal communication).

The involucre caps of *Q. lyrata* exhibit an unusual contour that enhances buoyancy of the acorns in water, the primary means of dispersal (Sullivan, 1993; Larsen, 1963). The nuts are preferred by duck, turkey, feral hogs and deer because they are low in tannic acids (Gilman and Watson, 1994). Changes in hydrologic regimes have a detrimental influence on recruitment in old growth stands (McCarthy and Evans, 2000). The roots of *Q. lyrata* have been shown to exhibit both delayed and brief growth

during the growing season as an adaptation to flooding stress when compared to other associated stream terrace oak species (Burke et al., 2004).

Quercus lyrata produces high quality lumber that may serve as cooperage; although the wood may be damaged due to insect borers, prolonged heat stress, or irregular flooding regimes (Stein et al. 2003; Soloman 1990; Phillips et al. 1953).

Hybridization with *Q. alba* was first reported by Palmer (1948), but later interpreted by Hardin (1979) as rare due to the few collections of hybrid individuals in herbaria and quite conspicuous ecological differences between the two species. Muller (1951) was critical of a reported cross with *Q. virginiana* (= *Q. x comptonae* Sargent) based upon his observations of artificially produced hybrids by Ness at College Station, Texas. Some herbarium material from McCurtain County suggests to me introgression with *Q. stellata* (= *Q. x sterettii* Trelease) or *Q. margaretta*.

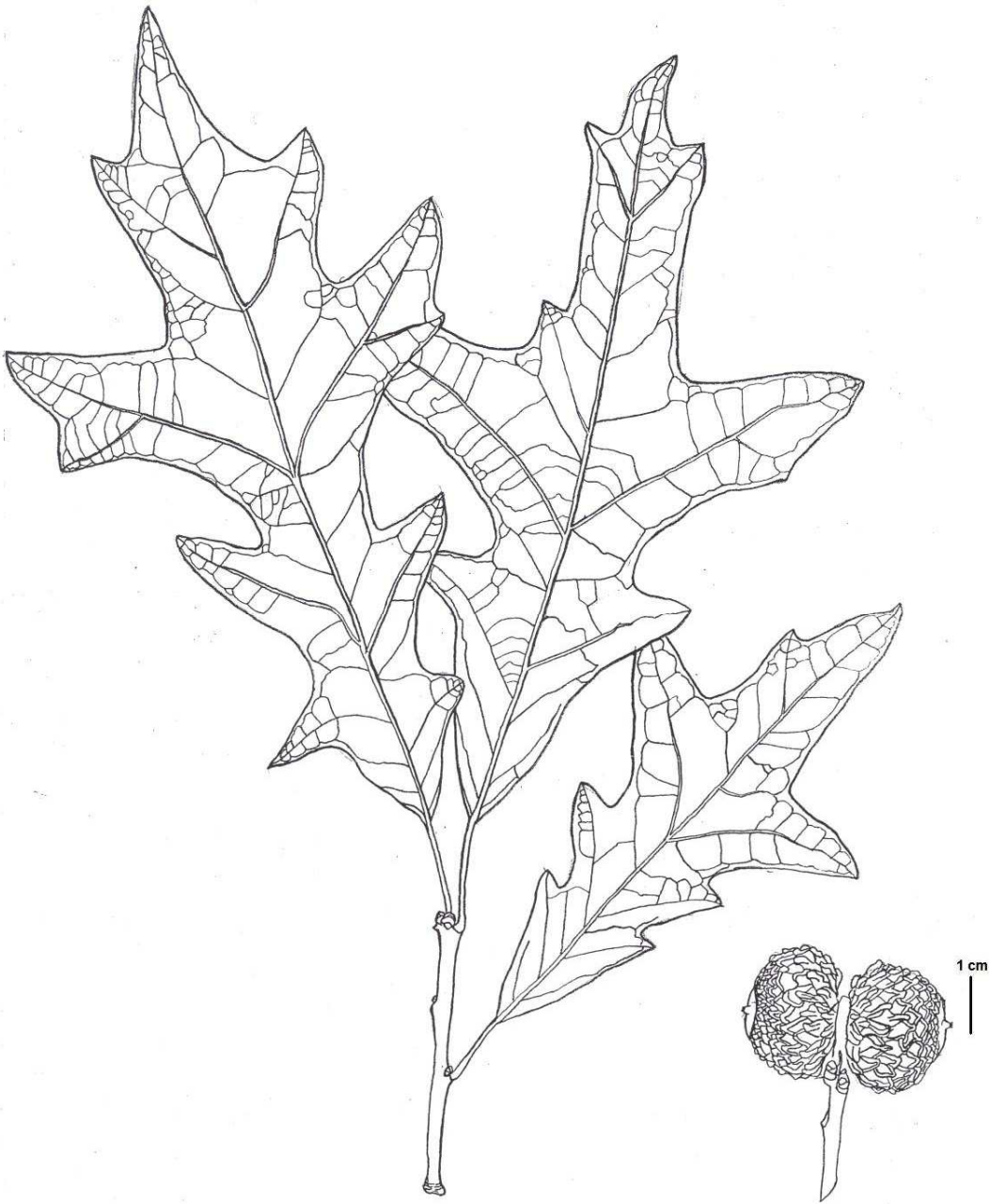


Figure 16. Foliage and acorns of *Q. lyrata* specimen collected in Wister Wildlife Management Area, Latimer County, Oklahoma.

***Quercus macrocarpa* Michx. Bur Oak**

Plants trees; to 30.5 m in height; deciduous. **Bark of Trunks** brownish gray or blackish gray to black; scaly to coarsely ridged; inner bark not exposed. **Primary Branches** ascending to horizontal. **Twigs** 3-6 mm in diameter; reddish brown to grayish brown or sulphurous yellow; glabrate to sparsely stellate, hairs silvery to inconspicuously sulphurous yellow. **Terminal buds** terete in cross-section; ovoid; 2-6 mm long; brown or grayish brown; sparsely silvery pubescent or glabrous. **Leaves** obovate to elliptic; 6-16.9 cm wide; 6.3-35 cm long; thick or thin; coriaceous or chartaceous; apices rounded to obtuse or emarginate; margins 3- to 4-lobed; terminal lobes occasionally flabellate, lateral lobes oblong to obovate, apically entire or 2- to 6- toothed and expanded; sinuses deep, extending 5/10-9/10 distance to midribs; bases rounded to cuneate; adaxial surfaces dark green, glossy, sparsely stellate to glabrate; abaxial surfaces white or light green, dull, densely to sparsely stellate; petioles 10-25 mm long, sparsely pubescent to glabrate; hairs like those of abaxial surfaces; stipules persistent below terminal buds. **Hairs of Adaxial Surfaces** like those of abaxial surfaces; but reduced in density and usually deciduous. **Hairs of Abaxial Surfaces** stellate; silvery; scattered on shade leaves, crowded on sun leaves; inconspicuously stalked on shade leaves, sessile on sun leaves; 4- rayed on shade leaves, 8- to 10-rayed on sun leaves; rays firmly or loosely attached to base, 0.5-1.0 mm long on shade leaves, 0.1-0.5 mm long on sun leaves, ascending to erect on shade leaves, appressed to ascending on sun leaves, straight to slightly curving. **Hairs of Abaxial Midribs** setaceous; silvery; scattered; sessile; antorsely appressed; straight to slightly curved. **Catkins** 3-4 cm long. **Mature Acorns** campanulate to globose; 30-40 mm long; solitary or in clusters of 2 or 3; sessile

or pedunculate, peduncles to 25 mm long. **Cupules** turbinate- to urceolate-shaped; 28-60 mm in diameter; 20-50 mm deep; enclosing more than 1/2 of nuts; golden to silvery; scales tightly appressed, deltoid to ovate, awned, awns to 15 mm long at cupule rims, golden or silvery tomentose, margins reddish or obscured by tomentum, bases tuberculate or greatly thickened, callus black. **Nuts** narrowly ovoid or ellipsoid to oblong; 24-40 mm in diameter; 30-50 mm long; light brown to gray; distal 1/2 tomentose.

Michaux used the specific epithet "*macrocarpa*" to reflect the large size of the nuts (Vines, 1982); they are the largest of any oak species in North America (Nixon and Muller, 1997). The species occurs across central North America, with its distributional boundaries forming a rough triangle from Lake Winnipeg, Canada to the gulf shores of Texas and the southeastern coast of Maine (Little, 1971; Nixon and Muller, 1997). In Oklahoma, it is a climax species of stream terraces, bottomlands, and dry upland habitats (Tyrl et al., 2002), although it rarely occurs at intermediate moisture gradients (Curtis, 1959; Johnson, 1990; Johnson et al., 2002). Occurrence in a diversity of vegetation associations that are found on stream terraces has been reported (Hoagland, 2000).

Shade leaves of *Q. macrocarpa* often exhibit abaxial surfaces with sparse stellate hairs that are inconspicuously stalked, 6- to 8-rayed, 0.5-1.5 mm long, erect to ascending, and straight to curling. This same phenomenon is also exhibited by *Q. muehlenbergii* and can lead to confusion when identifying some individuals in the absence of acorns (Nixon and Muller, 1997). Foliage and acorn of *Q. macrocarpa* are illustrated in Figure 17. Appearance of putative hybrids are illustrated in Figures 18 and 19.

Numerous species of wildlife including songbirds, gamebirds, deer, and numerous other mammals eat the large nuts of *Q. macrocarpa* (Vines, 1982; Welch, 1986; Reichmann, 1987; Tirmenstein, 1988). It is a highly valued timber species that provides structural lumber, flooring, pulpwood, cabinetry, and carpentry articles (Vines, 1982; Tyrl et al, 2002; Stein et al. 2003; Cassens, 2007).

Hybrids between *Q. macrocarpa* and other species of the genus are recognized by the reduced size of their sun leaves, appearance of their stellate hairs (angle of ray divergence and straightness), reduced length or absence of the cupule scale awns at or near the rims, and reduction in nut size. Hybrids including *Q. alba* (= *Q. x bebbiana* Schneider), *Q. margaretta*, *Q. stellata* (= *Q. x guadalupensis* Sargent), *Q. muehlenbergii* (= *Q. x deamii* Trelease), and *Q. havardii* (= *Q. x andrewsii* Sargent) are infrequent throughout the state (Hardin (1975). Some collections from Kiowa and Comanche Counties could possibly be hybrids between *Q. macrocarpa* and *Q. virginiana* (Figure 20) or simply be unusual hybrids between *Q. macrocarpa* and *Q. stellata* (i.e., aberrant *Q. x guadalupensis*). These individuals bear leaves that are conspicuously coriaceous, abaxially reticulate, and sun leaves reduced in size. A herbarium specimen at the University of Oklahoma collected near Kiamichi Mountain is labeled as a hybrid with *Q. lyrata*. Unfortunately, the tree could not be relocated in the wild for further study. A putative hybrid with *Q. margaretta* in Boiling Springs State Park in Woodward County produces large numbers of nuts each year in comparison to the much taller individuals of *Q. margaretta* that surround it. Steffey (1950) determined that introgression of this species with other oaks was taking place in the Cross Timbers by examining the plasticity of *Q. macrocarpa* acorns. Two varieties with conspicuously smaller fruits and reduced awns occur in the Northern Great Plains region, but do not reach Oklahoma (Great Plains Flora Association,

1986). These have recently been shown to be latitudinally divergent from other members of the species due to environmental constraints (Koenig, 2009). Acorns that that develop on shaded branches may not produce awns on scales near the cupule rims, or the acorns may be reduced in size but still producing awns. The following key distinguishes *Q. macrocarpa* and its hybrids with *Q. margaretta*, *Q. stellata*, *Q. havardii*, and *Q. muehlenbergii*.

- 1. Cupules 28-60 mm in diameter; 17–50 mm deep; scales of rims excurrent as awns 5–20 mm long. Nuts 24–40 mm in diameter. *Q. macrocarpa*
- 1. Cupules less than or equal to 24 mm in diameter; 8–15 mm deep; scales of rims acicular or slightly forming fringe less than or equal to 5 mm long. Nuts less than or equal to 20 mm in diameter.
 - 2. Mature acorns globose. Cupules covering half or more of nuts. Nuts 18–22 mm long; globose to ovoid.
 - 3. Twigs dark brown to light brown; glabrous to glabrate.
 - Leaf lobes “finger-like” or rounded. unnamed hybrids at Boiling Springs State Park
 - 3. Twigs densely stellate pubescent; yellowish. Leaf lobes broadly expanded at apices; constricted at bases and middles. *Q. x guadalupensis*
- 2. Mature acorns broadly to narrowly ellipsoid. Cupules covering half or less than half of nuts. Nuts 24–36 mm long; ellipsoidal.
 - 4. Nuts 24–28 mm long; broadly ellipsoidal. Cupules shallowly bowl- to bell-shaped. Trees of western quarter of state. unnamed hybrids in west

4. Nuts 30–37 mm long; narrowly ellipsoidal. Cupules
bowl-shaped. Trees of the body of the state. *Q. x hillii*



Figure 17. Foliage and acorn of *Quercus macrocarpa* specimen collected in Horsethief Canyon, Payne County, Oklahoma.



Figure 18. Foliage and acorn of putative hybrid between *Quercus macrocarpa* and *Quercus stellata* (= *Q. x guadalupensis*) collected near the Cimarron River in southeastern Payne County, Oklahoma.

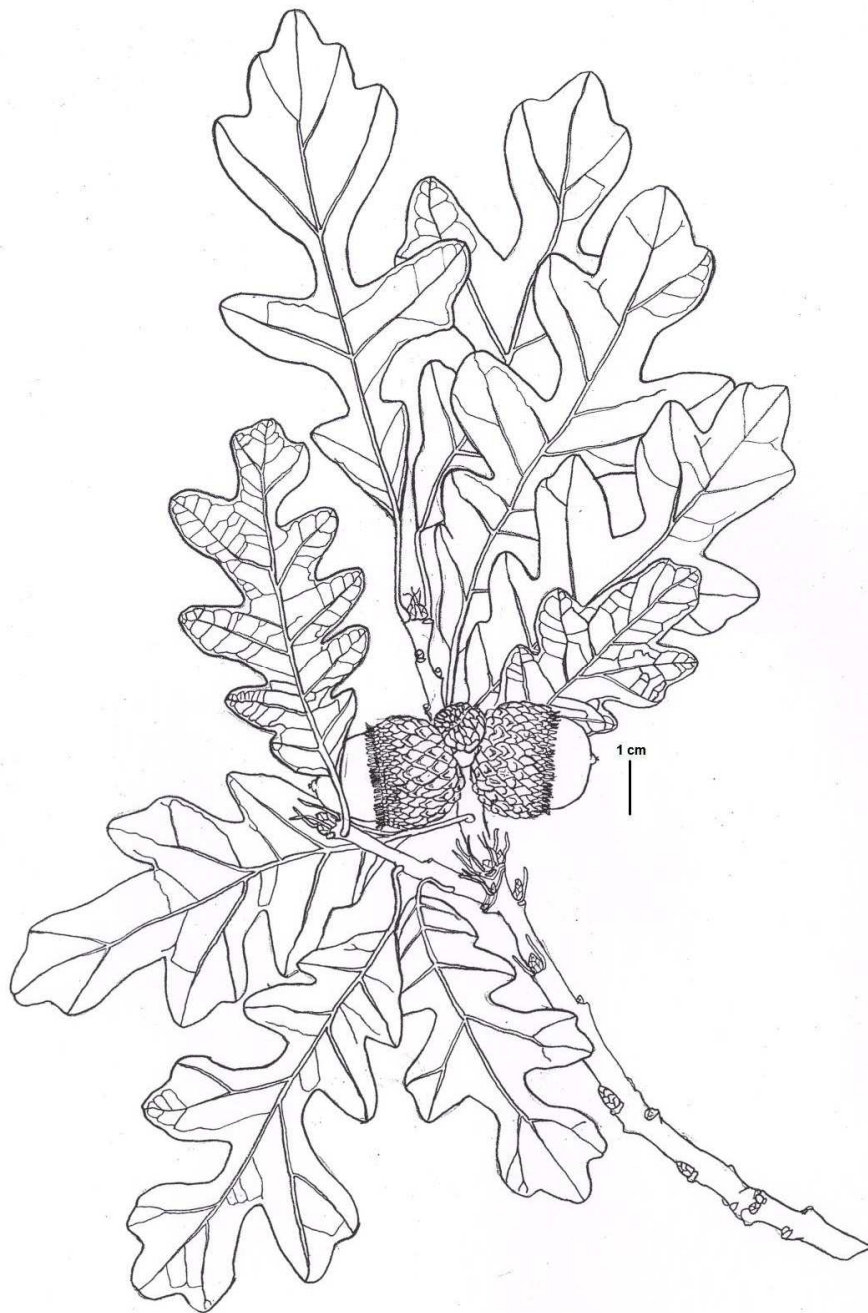


Figure 19. Foliage and acorns of putative hybrid between *Quercus macrocarpa* and *Quercus margaretta* collected in Boiling Springs State Park, Woodward County, Oklahoma.

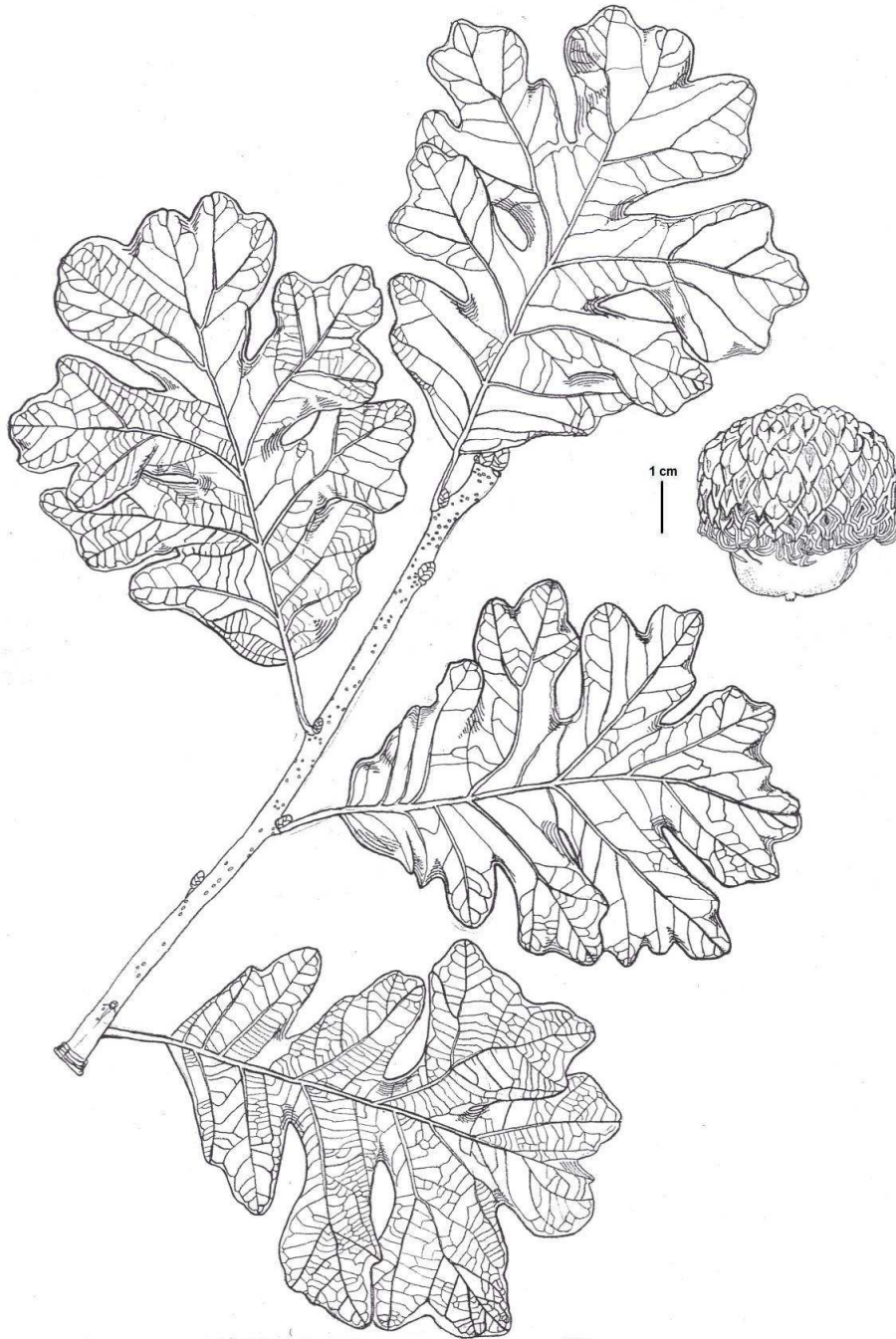


Figure 20. Foliage and acorn of putative hybrid between *Quercus macrocarpa* and *Quercus virginiana* collected on Elk Mountain in the Wichita Wildlife Refuge, Comanche County, Oklahoma.

***Quercus margaretta* Ashe.**

Sand Post Oak

Plants trees or shrubs; to 9.8 m in height; deciduous. **Bark of Trunks** whitish gray; scaly to blocky; inner bark not exposed. **Primary Branches** ascending to horizontal.

Twigs 3.5-4 mm in diameter; reddish brown to dark brown; glabrate to glabrous.

Terminal buds terete in cross-section; ovoid; 2-6 mm long; reddish brown; sparsely silvery and/or golden pubescent, sometimes pubescent only along scale margins.

Leaves obovate to elliptic or orbicular; 3.5-8 cm wide; 7-15 cm long; thick; coriaceous; apices rounded to obtuse or truncate to emarginate; margins 1- or 2-lobed; lobes oblong to broadly oblanceolate to spatulate, apically entire to 2-toothed and expanded; sinuses deep, extending 1/2-3/4 distance to midribs; bases cordate to rounded or truncate; adaxial surfaces dark to blue green, dull to glossy, sparsely pubescent to glabrate; abaxial surfaces sulphurous yellow or silver tinged green, dull; petioles 3-10 mm long, densely stellate to glabrate; hairs like those of abaxial surfaces; stipules caducous. **Hairs of Adaxial Surfaces** like those of abaxial surfaces; but consistently deciduous. **Hairs of Abaxial Surfaces** persistent to deciduous; stellate; silvery; scattered to crowded; conspicuously stalked, leaving pock marks or pustulate protuberances upon removal; 4- to 12-rayed; rays firmly attached to base, 0.6-1.2 mm long, ascending to erect, straight to curling; **Hairs of Abaxial Midribs** like those of abaxial surfaces. **Catkins** 5-8 cm long. **Mature Acorns** ovoid to oblong; 11-21 mm long; solitary or paired; sessile or pedunculate, peduncles to 25 mm long. **Cupules** bowl- to saucer-shaped; 15-20 mm in diameter; 5-10 mm deep; enclosing 1/4-1/3 of nuts; silvery to golden tinged rusty brown; scales loosely appressed at rims, those at cupule rims reduced in size or lanceolate, those at cupule bases ovate, silvery or golden

tomentose, margins reddish, tomentulose, bases flattened or thickened and/or creased, callus black to rust colored at maturity. **Nuts** ovoid to oblong; 10-20 mm in diameter; 11-30 mm long; dark brown with blackened stripes; glabrous or distal 3/4-1/2 tomentose. Foliage and acorns of *Q. margaretta* are illustrated in Figures 21 and 22.

The specific epithet of *Q. margaretta* honors Margaret Henry Wilcox whom married the famous forester and botanist William Willard Ashe (Vines, 1982). It is distributed in the southeastern quarter of the United States (Nixon and Muller, 1997). In Oklahoma, the species dominates woodlands and savannahs on Quaternary sands associated with the major river systems. Soils are mostly well drained, sandy to sandy loams (Tucker and Muller, 1958). In the Gulf Coastal Plain, the most commonly encountered association comprises *Q. margaretta*, *Q. falcata*, and *Q. incana* (Faust, 1970; Clark, 1971; Correll and Johnston, 1970; Cavender-Bares et al., 2004). The northwestern edge of the distribution of this association is in Choctaw and McCurtain Counties (Hoagland, 2000).

Contrary to the previously published range maps for *Q. margaretta* (Nixon and Muller, 1997; Stein et al., 2003), well developed stands are found along major rivers in both the northern and southern halves of the state, with the exception reservoirs along these waterways. Inundation of its habitat by impoundments appears to be the most dramatic impact on distribution of the species. For example, it exhibits vigorous vegetative establishment and regeneration in agricultural fields that line the Arkansas River, but is not seen along the shores of Lake Keystone. Likewise, stands along the Red River are interrupted by the stony shorelines created by the creation of Lake Texoma. Frequently along the banks of the major rivers, stands of *Q. shumardii* will

intermingle with those of *Q. margaretta*. In the sandy loams of the floodplains of the Cimarron and Arkansas Rivers, savannahs of *Q. margaretta* are present.

At places where exposed sandstones or shallow soils of sandstone hills meet sandy floodplains, hybridization between *Q. stellata* and *Q. margaretta* is very common. Cavender-Bares and coworkers (2004) demonstrated that the two species did not overlap along a soil moisture gradient in Florida. This likely explains why hybrid individuals are always only found at these transitions between deep sands and shallower soils over sandstone bedrock. Large creeks that are tributaries of the major rivers in Oklahoma flow for miles before merging with the rivers and thus provide such transition zones for hybrids between the two species.

Although it is difficult to distinguish *Q. margaretta* and *Q. stellata*, differences in habitat, vegetative pubescence, and acorn morphology can differentiate the two taxa. However, this combination of characters is sometimes compromised by hybridization and by seasonal and ecological plasticity of the two species. The easiest time of year to identify *Q. margaretta* is in the spring when its glabrous, reddish brown twigs are easily distinguished from the densely stellate, sulphurous yellow twigs of *Q. stellata*. Also, *Q. margaretta* lacks the bulbous hairs that appear like grains of sand on the blade surfaces and midribs of *Q. stellata* (Hardin, 1979a, b). The coppery red cupule scales subtending the nut are not obscured by dense white pubescence which is exhibited by *Q. stellata*. Also, the scales subtending the rims of the cupules tend to be inconspicuously reflexed or loosely appressed in *Q. margaretta* (Nixon and Muller, 1997). Cupule features are difficult to use in regions where the two species apparently are extensively introgressed. By mid to late spring, all hairs on the foliage of *Q. margaretta* can be distinguished as

stellate with conspicuous stalks (0.1-0.3 mm tall). Using electron microscopy, Hardin (1979a, b) demonstrated that the morphology of hairs in *Q. margaretta* are identical to those conspicuously stalked hair types of Section *Lobatae*. Other species of Section *Quercus* have either sessile or inconspicuously stalked hairs, i.e, stalks less than 0.1 mm tall.

The hybrid between *Q. margaretta* and *Q. stellata* was first collected and named as a new species—*Q. drummondii*—by Liebmann in 1854. In 1924, Trelease published the binomial *Q. psuedomargaretta* for this taxon; this name, of course being a nomenclatural synonym because it lacks priority. When Muller (1951b) studied Liebmann's type specimen and trees from the type locality, he concluded that they represented individuals of an exceptionally "stabilized" population of a hybrid between *Q. stellata* and *Q. margaretta* and that *Q. drummondii* was a nothospecies, hence the insertion of the "x" in the name. Features of this hybrid are illustrated in Figure 8 in the discussion of *Q. x drummondii*. Hybrid individuals are widely distributed in Oklahoma. They can be differentiated from individuals of *Q. margaretta* by their uniserrate and bulbous hairs in addition to their differences in the appearance of the stellate hairs. Some individuals also have the sulphurous yellow twigs of *Q. stellata*. Most individuals tend to have the smaller leaves of *Q. margaretta*.

Quercus margaretta also apparently hybridizes with several other species. Hardin (1975; 1979a) described a hybrid with *Q. alba*, and in my collections of the taxon in Oklahoma, I encountered apparent hybridization with *Q. havardii* (Figure 13), *Q. macrocarpa* (Figure 19), *Q. muehlenbergii*, *Q. prinoides* (Figure 23), and *Q. x stelloides*.

(Figures 47–49). Herbarium specimens deposited in the Bebb Herbarium at the University of Oklahoma suggests that hybridization with *Q. lyrata* may occur also.



Figure 21. Foliage and acorns of *Q. margaretta* specimen collected along the Cimarron River, Payne County, Oklahoma.

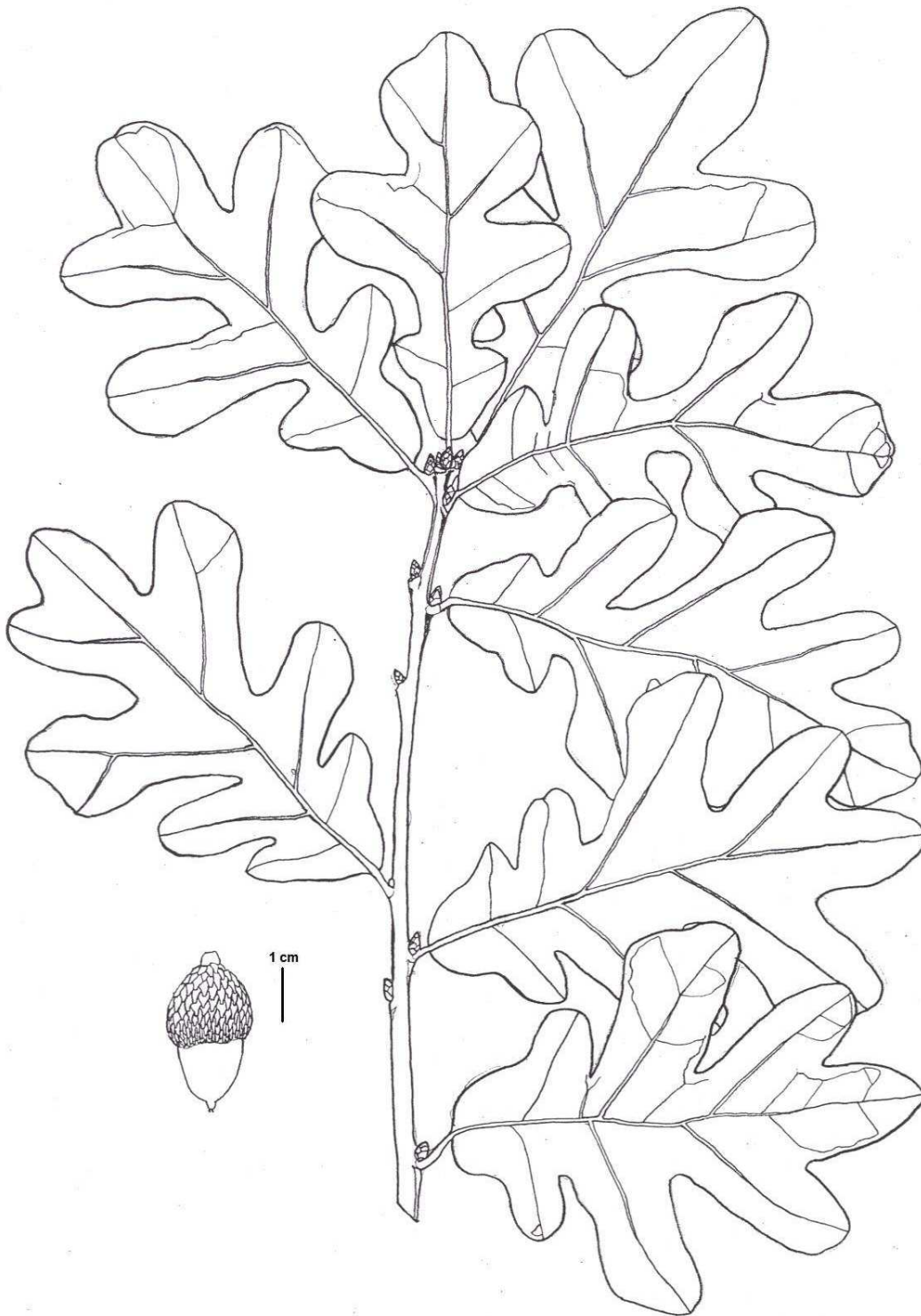


Figure 22. Foliage and acorn of *Q. margaretta* specimen collected along the Cimarron River, Payne County, Oklahoma.

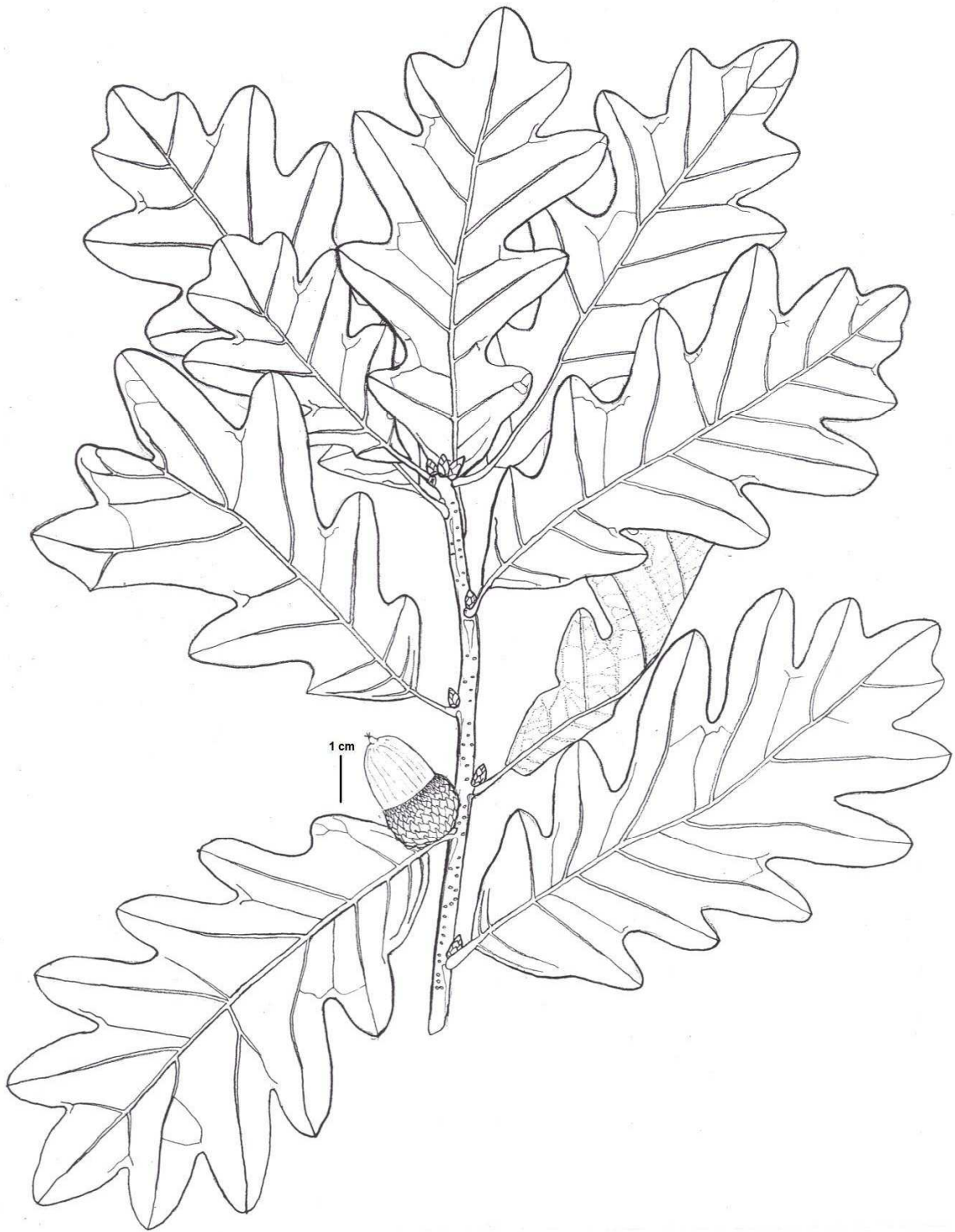


Figure 23. Foliage and acorn of putative hybrid between *Q. margaretta* and *Q. prinoides* collected along the Cimarron River, Payne County, Oklahoma.

***Quercus marilandica* Muenchh.**

Blackjack Oak

Plants trees or colonial shrubs; 2-15 m tall; deciduous. **Bark of Trunks** brownish black to black, rarely grayish; coarsely ridged to blocky; orange inner bark rarely exposed by furrows. **Primary Branches** horizontal to descending, rarely ascending; typically twisted. **Twigs** 2-5 mm in diameter; sulphurous yellow to reddish brown or gray; densely to sparsely stellate or glabrate; hairs silvery to sulphurous yellow. **Terminal buds** 5-angled in cross-section; ovoid to ellipsoidal; 3-10 mm long; silvery to golden or orange or rust colored; densely sulphurous yellow or silvery pubescent to rusty red pubescent, sometimes with a glabrous band parallel to margin. **Leaves** obovate to obtrullate, rarely rhomboidal or obdeltoid or campanulate; 2.2-19 cm wide; 2.5-19 cm long; thick; coriaceous; apices broadly acute to rounded or truncate; margins in distal 1/2-1/3 greatly expanded, entire to denticulate, or undulate to sinuate, or 3- to 5- toothed, teeth broadly dentate or crenate, or 3- to 5- lobed; lobes broadly deltoid to oblong; margins in basal 1/2-2/3 greatly constricted, entire to 1- or 2- toothed; teeth crenate to serrate; sinuses shallow to deep, extending 1/10-1/2 distance to midribs; awns 0-15, at lobe margins and/or at apices; bases rounded to cuneate or cordate; adaxial surfaces dark green to yellowish green, glossy, scaberulous, sparsely pubescent; abaxial surfaces golden to light green, reticulately ribbed, scaberulous, dull or glossy, scaberulous, densely pubescent to glabrate except for inconspicuous or conspicuous rust colored tufts of pubescence in vein axils; petioles 0-10 mm long, densely to sparsely pubescent, hairs like those of leaf surfaces and/or midribs; stipules caducous. **Hairs of Adaxial Surfaces** stellate; silvery to golden tinged; scattered; inconspicuously stalked; 4- to 12-rayed; rays firmly attached to base or stalk; 0.1-0.2 mm long; raised and spreading;

curling to straight. **Hairs of Abaxial Surfaces** stellate; silvery to golden tinged covering surfaces, silvery to reddish tinged in vein axils; scattered covering surfaces, crowded in vein axils; sessile to minutely stalked covering surfaces, conspicuously stalked in vein axils; 4- to 8-rayed covering surfaces, 4- to 12-rayed in vein axils; rays loosely attached to base, firmly attached to stalk, 0.2-1.5 mm long, approaching longer 1/3 of range in vein axils, raised and spreading, approaching erect in vein axils, curling to sparingly straight; filiform-scurfy; golden or intermittently golden and silvery; crowded along vasculature or absent; 0.1-0.5 mm long; appearing adnate to leaf surface. **Hairs of Abaxial Midribs** glabrate or hairs like those of abaxial surfaces; golden to silvery setaceous, crowded to scattered or absent, 0.1-1.5 mm long, antrorsely appressed; straight. **Catkins** 5-7 cm long. **Mature Acorns** turbinate to globose; 12-22 mm long; solitary or in pairs; sessile or pedunculate, peduncles to 10 mm. **Cupules** saucer- to bowl-shaped; 10-20 mm in diameter; 5-10 mm deep; enclosing 1/3-1/2 of nuts; silvery orange-brown to sulphurous yellow brown; scales tightly appressed, tips slightly loose along rims, flattened, ovate to oblong to oval, sparsely sulphurous yellow to silvery tomentose, margins red to dark orange, tomentose to glabrate, bases flattened, callus absent. **Nuts** globose to ovoid to ellipsoidal; 10-15 mm in diameter; 10-20 mm long; brown to orange brown; tomentose.

The specific epithet of *Q. marilandica* refers to Maryland (Vines, 1982), reflecting the location of the species first collection. It is distributed throughout the eastern United States with exception of Florida and the Great Lakes region (Little, 1971). In Oklahoma, it covers the body of the state in association with *Q. stellata* forming the distinctive forests, woods and savannahs of the Cross Timbers. Climatic and terrestrial

features of the state complement this association so well, that it accounts for 70 percent of the total basal area of forests, woodlands and savannahs in the state (Rice and Penfound, 1959; Hoagland et al., 1999). Juvenile twigs are yellow colored while leaf surfaces are reddish adaxially. Pubescence of expanding leaves and twigs is persistent until late summer. Moving from east to west, there is a gradual and continuous change in the growth form of *Q. marilandica* from stout trees of medium stature to rhizomatous shrubs that reproduce both clonally and sexually.

Two relatively distinct varieties of *Q. marilandica* occur in Oklahoma.

Widespread throughout the eastern 3/4 of the state is variety *marilandica* (Figure 24). In the Wichita and Quartz Mountains are populations of variety *asheii* Sudworth (Figure 25) (Bush, 1928; Jensen, 1997). Individuals of this variety are distinguished from variety *marilandica* by their growth form, acorn shape, blade size, texture, and appearance of stellate hairs. These consistent differences may indicate that *asheii* should be recognized as a distinct species (Sudworth, 1922; Bush 1928; Hunt, 1989; Nixon and Muller, 1997). The following couplet offers characters to distinguish the two varieties.

- 1. Individual trees always small or colonial shrubs to 3 m tall. Leaves 2.2-7 cm wide; 2.5-7 cm long. Abaxial leaf surfaces of silvery pubescence in vein axils; not densely uniserrate pubescent. Cupules frequently covering 1/3 of nuts. Nuts glabrate to glabrous. variety *asheii*
- 1. Individual trees 3-10 m tall. Leaves 7-19 cm wide; 7-19 cm long. Abaxial leaf surfaces often reticulately ribbed; densely pubescent to tardily glabrate except for persistent tufts of silvery and/ or rust colored pubescence in vein axils. Densely glandular-scurfy pubescent. Cupules frequently covering 1/3–2/3 of nuts. Nuts densely pubescent. variety *marilandica*

Variety *asheii* is typically encountered on the dry soils of mountain sides, bluffs, and prairie uplands throughout central Oklahoma and Texas (Jensen, 1997). The most extensive populations in the state are found in the Wichita and Quartz Mountains where variety *marilandica* does not occur. Solitary individuals are rare; more common are dense stands or colonies of individuals that exhibit uniform heights 1.5–3 meters tall. Variety *asheii* is known to hybridize with *Q. buckleyi* (Jensen, 1997; Figure 26).

In addition to hybridization with *Q. buckleyi*, *Q. marilandica* hybridizes with other members of Section *Lobatae* (Palmer, 1942, 1948; Little 1979; Hunt, 1989). These include: *Q. falcata*, *Q. incana* (= *Q. x cravensis* Little), *Q. rubra*, *Q. velutina* (= *Q. x bushii* Sargent). The hybrids with *Q. velutina* are quite common on upland sandstones (Figures 27 and 28).

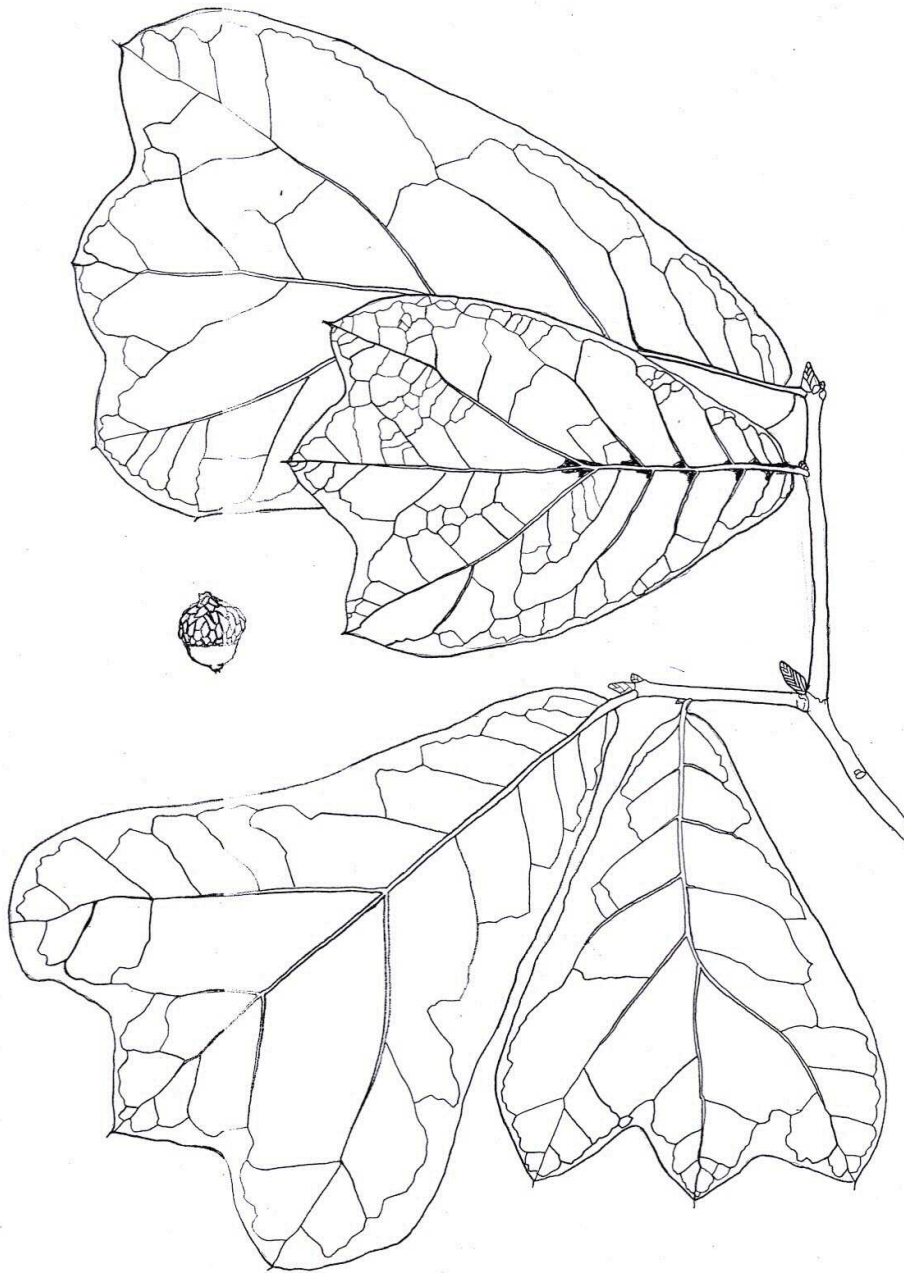


Figure 24. Foliage and acorn of *Quercus marilandica* var. *marilandica* specimen collected along the Cimarron River, Payne County, Oklahoma.

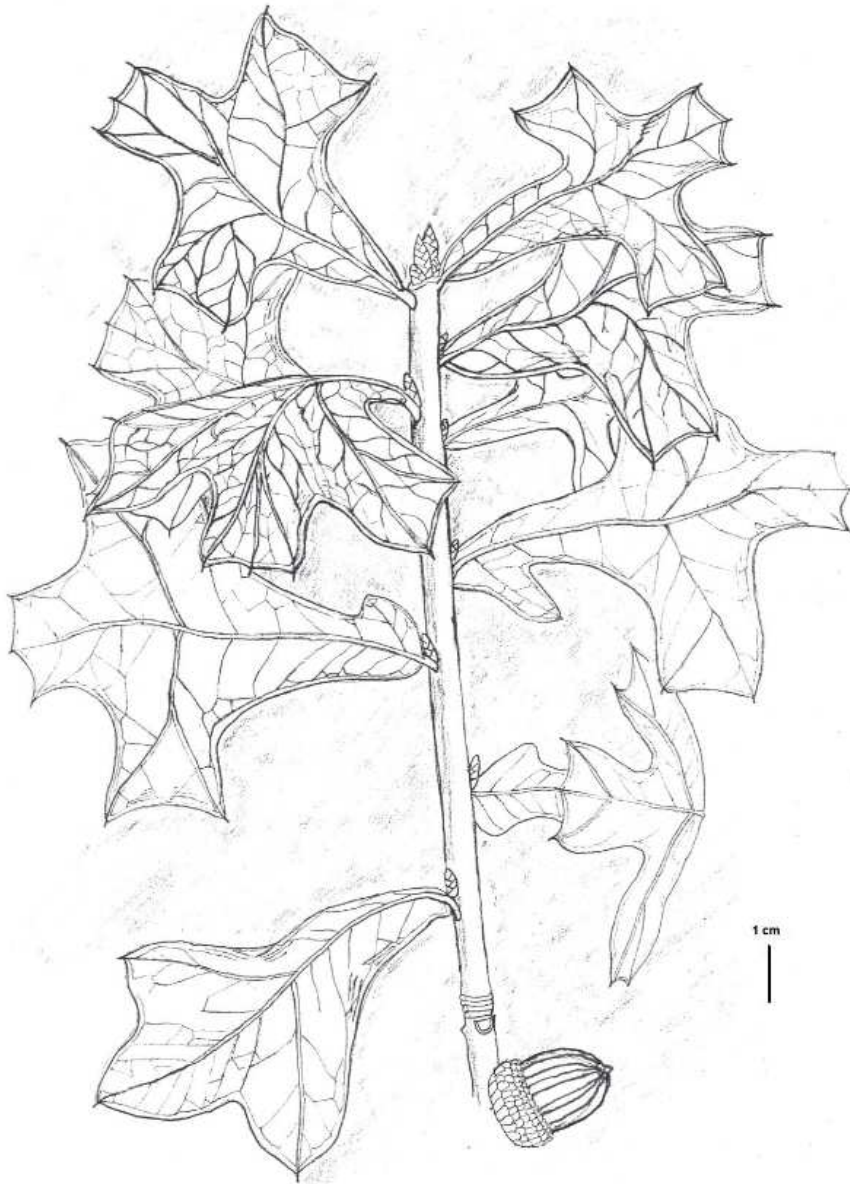


Figure 25. Foliage and acorn of *Quercus marilandica* var. *asheii* specimen collected on Elk Mountain in the Wichita Mountains National Wildlife Refuge, Comanche county, Oklahoma.

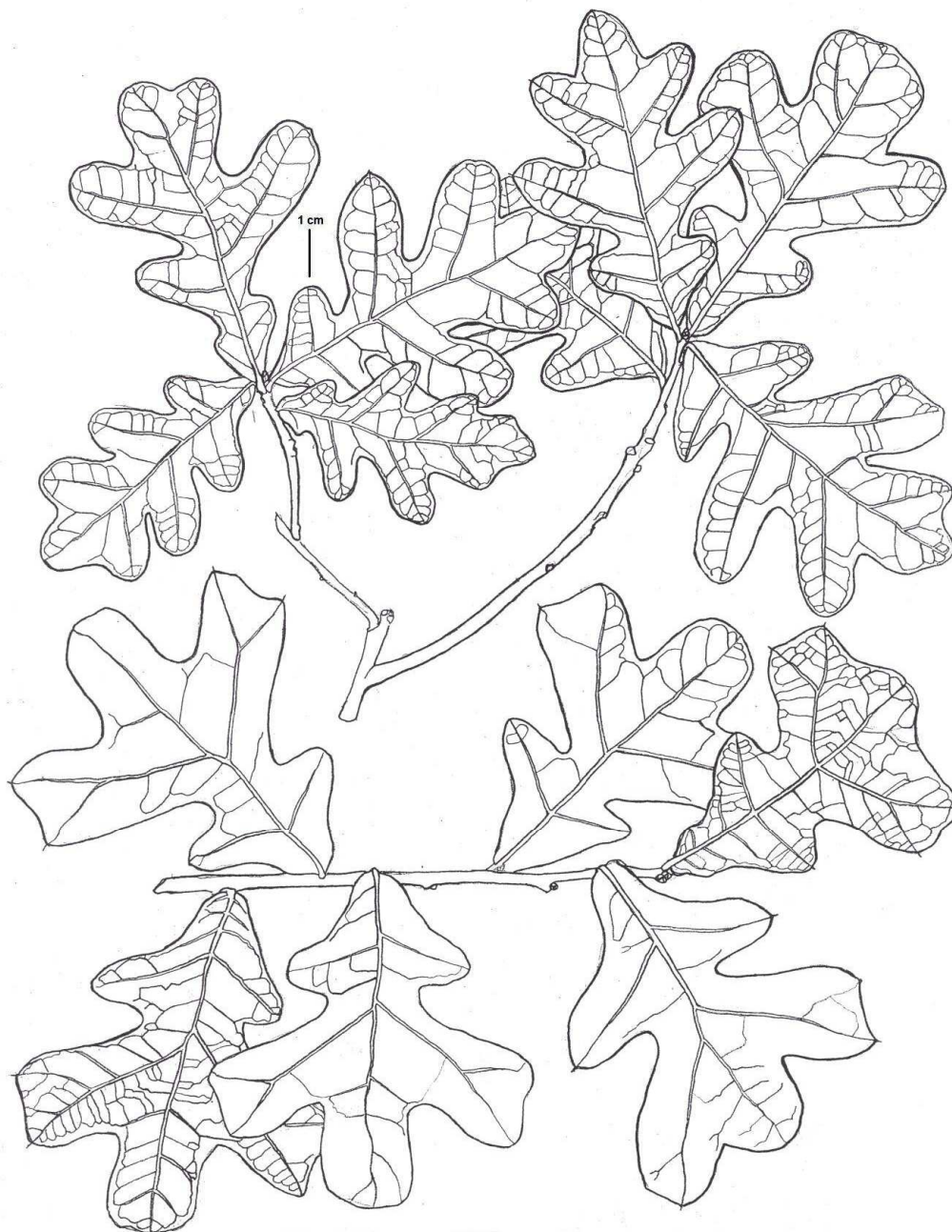


Figure 26. Foliage of hybrids of *Q. marilandica* var. *asheii* and *Q. buckleyi* (above) and *Q. marilandica* var. *asheii* (below) collected on Elk Mountain in the Wichita Mountains National Wildlife Refuge, Comanche County, Oklahoma.

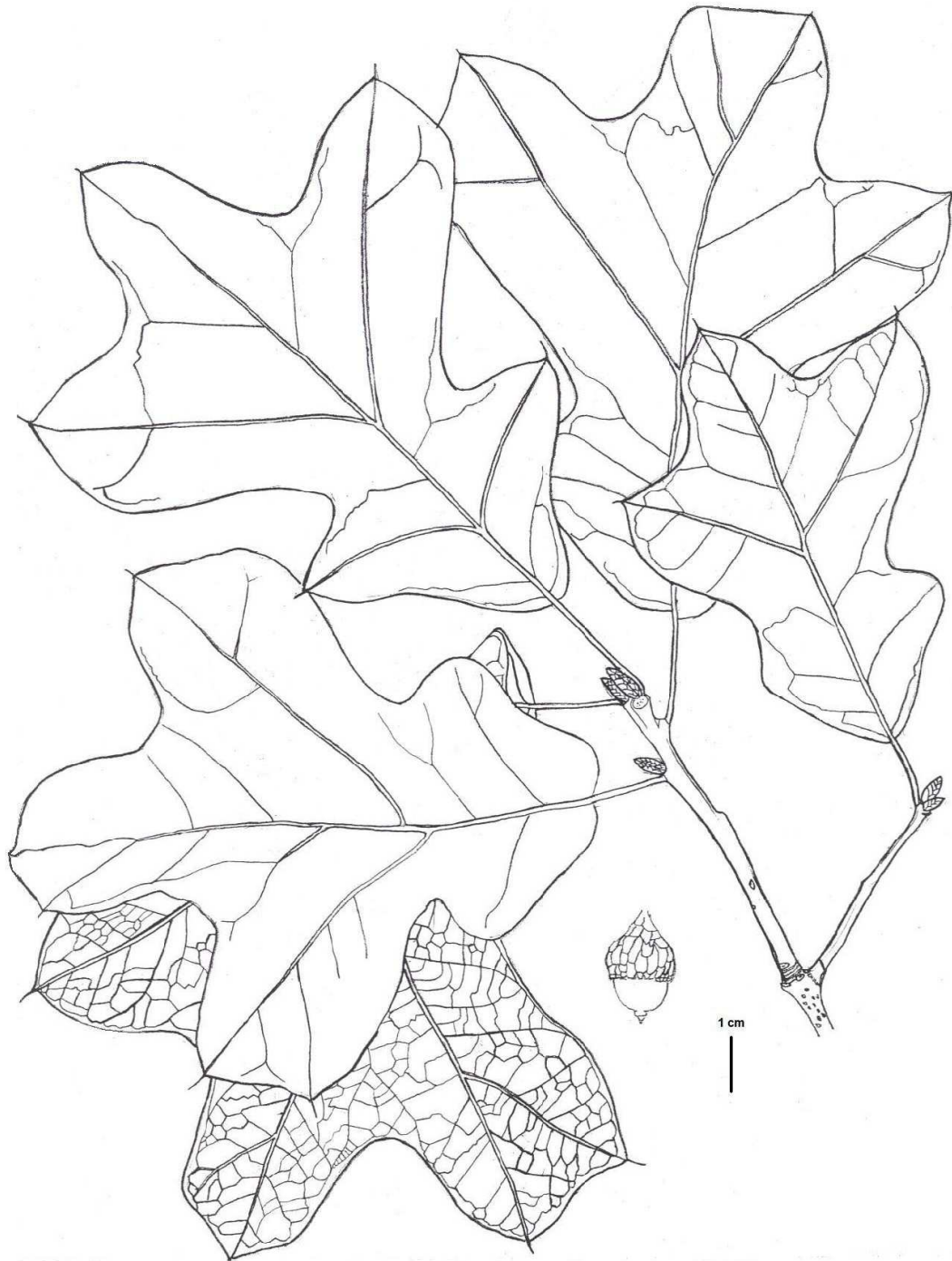


Figure 27. Foliage and acorn of putative hybrid between *Q. marilandica* var. *marilandica* and *Q. velutina* (= *Q. x bushii*) collected in Lake Spavinaw State Park, Mayes County, Oklahoma.



Figure 28. Foliage and acorn of putative hybrid between *Q. marilandica* var. *marilandica* and *Q. velutina* (= *Q. x bushii*) collected near Stillwater, Payne County, Oklahoma.

***Quercus mohriana* Buckley ex Rydb. Mohr oak**

Plants trees or colony forming shrubs; to 4 m in height; subevergreen or deciduous.

Bark of Trunks whitish gray or grayish brown; scaly; inner bark not exposed. **Primary**

Branches horizontal to descending. **Twigs** 2-4 mm in diameter; silvery to black;

densely to sparsely stellate; hairs silvery. **Terminal buds** terete in cross-section; ovoid

to sub-rotund; 2-4 mm long; reddish brown or red; sparsely silvery pubescent,

sometimes merely ciliate along scale margins. **Leaves** elliptic to oblong, or obovate to

ovate, or lanceolate to oblanceolate; 1.3-2.5 cm wide; 2.5-7.5 cm long; moderately thick;

subcoriaceous; apices rounded to acute to mucronate; margins entire to denticulate or

toothed, teeth serrate; sinuses shallow, extending less than or equal to 1/4 distance to

midribs; bases rounded to cuneate or cordate; adaxial blades surfaces dark green,

scaberulous, sparsely stellate to appearing glabrate; abaxial blades surfaces cream to

white, woolly, densely stellate. petioles 2-5 mm long, hairs like those of abaxial

surfaces; stipules caducous. **Hairs of Adaxial Surfaces** like those of abaxial surfaces,

but usually sparse. **Hairs of Abaxial Surfaces** stellate; silvery; densely crowded and

obscuring veins; sessile to inconspicuously stalked; 4- to 6-rayed; rays 0.1-1.2 mm long,

appressed to erect, straight to curling. **Catkins** 2-3 cm long. **Mature Acorns** ovoid to

ellipsoidal; 7-15 mm long; solitary or paired; sessile or pedunculate, peduncles to 15

mm long. **Cupules** urceolate to hemispheric; 10-15 mm in diameter; 5-10 mm deep;

enclosing 1/3-1/2 of nuts; silvery white; scales tightly appressed, those at cupule rims

abruptly reduced, triangular to ovate, silvery white canescent to tomentose, margins red

to reddish brown in distal 1/2-1/4, glabrous, bases conspicuously tuberculate, callus

black. **Nuts** ovoid to ellipsoidal; 8-12 mm in diameter; 10-14 mm long; light brown; glabrous. The foliage and an acorn of *Q. mohriana* are illustrated in Figure 29.

The specific epithet of *Q. mohriana* honors the German botanist and pharmacist Charles Mohr who authored a work on the flora of Alabama (Vines, 1982; Little, 1981). It is distributed from central and southwestern Texas to northeastern New Mexico and southwestern Oklahoma (Little, 1976; Nixon, 1997) although Tucker (1961) questioned whether the species occurred northwest of Palo Duro Canyon in the Texas Panhandle. In Oklahoma, it is reported (Waterfall, 1969; Little, 1985; Nixon, 1997) to occur only in the Limestone Hills geomorphic province in the southwestern corner of the state. Unexpectedly, I collected this species in Cimarron County and careful comparison of its morphology with herbarium specimens collected near the center of its distributional range indicate that my identification is correct.

Its wood is used primarily for fuel or fence posts, and it is important as habitat and food for wildlife (Vines, 1982; Stahl and McElvaney, 2003).

Hybrids of *Q. mohriana* with *Q. grisea*, *Q. gambelii*, *Q. havardii*, *Q. stellata* and *Q. macrocarpa* have been described (Muller, 1951b; Tucker, 1961; Fralish and Franklin, 2002). Muller (1952) stated that intermediate individuals between *Q. mohriana* and *Q. havardii* are restricted to where limestone hills abut sandy plains. Considerable introgression is believed to have occurred in the Big Bend area of Texas, as well as the northeastern region of New Mexico that borders the panhandle of Oklahoma and Texas (Muller, 1951b, 1952; Tucker, 1961).



Figure 29. Foliage and acorn of *Quercus mohriana* specimen collected in Tesequite Canyon, Cimarron County, Oklahoma.

***Quercus muehlenbergii* Engelm. Chinquapin Oak**

Plants trees or shrubs; to 20-34 m tall; deciduous. **Bark of Trunks** whitish gray; scaly to papery; inner bark not exposed. **Primary Branches** ascending to horizontal. **Twigs** 2-4 mm in diameter; dark brown to reddish brown or light brown; glabrous to glabrate. **Terminal buds** terete to slightly angular in cross-section; sub-globose to ovoid; 3-5 mm long; brown or reddish brown or grayish brown; sparsely to densely silvery pubescent, sometimes merely ciliate along scale margins. **Leaves** obovate to ovate, or oblanceolate to lanceolate, or oblong to elliptic; 3-14 cm wide; 4.5-21.5 cm long; thick or thin; coriaceous or chartaceous; apices acute to apiculate; margins 10- to 15-toothed, teeth dentate to serrate or serrate-crenate; sinuses shallow, extending 1/4 or less distance to midribs; bases truncate to cuneate; adaxial surfaces dark green, dull or glossy, sparsely pubescent to glabrate; abaxial surfaces white to light green, densely stellate; petioles 7-28 mm long, sparsely pubescent to glabrate, hairs like those of leaf surfaces; stipules caducous. **Hairs of Adaxial Surfaces** like those of abaxial surface; but sometimes with few rays and consistently deciduous. **Hairs of Abaxial Surfaces** persistent; stellate; silvery; crowded; sessile; 4- to 12-rayed; rays firmly attached to base, 0.3-1.0 mm long, appressed to erect, straight to slightly curving. **Hairs of Abaxial Midribs** sericeous; silvery; scattered; sessile; antrorsely appressed; straight to slightly curved. **Catkins** 4-6 cm long. **Mature Acorns** globose to oblong; 17-29 mm long; solitary or paired; sessile or pedunculate, peduncles to 11 mm long. **Cupules** deeply to shallowly bowl-shaped; 11.5-23.5 mm in diameter; 6-12 mm deep; enclosing 1/4-1/3 of nuts; silvery; scales tightly appressed, those at cupule rims abruptly reduced in size or lanceolate, those at cupule bases deltoid to ovate, silvery tomentose, margins reddish,

tomentulose to obscured by dense tomentum, bases creased to slightly tuberculate, callus black. **Cupules** hemispheric to deeply bowl-shaped; 11.5-23.5 mm in diameter; 6-12 mm deep; enclosing 1/4-1/3 of nuts; silvery to silvery yellow or red; scales tightly appressed, slightly tuberculate to creased and thickened or flattened, narrowly ovate to oblong, abruptly reduced in size at rims, silvery tomentose, margins dark orange, tomentulose or obscured by tomentum. **Nuts** ovoid to oblong; 15-22 mm in diameter; 15-28 mm long; dark brown; glabrous to distal 3/4 tomentose.

The foliage and acorn of *Q. muehlenbergii* are illustrated in Figure 30.

The specific epithet "*muehlenbergii*" honors the botanist and minister G. H. E. Muhlenberg (Vines, 1982; Little, 1981). The binomial *Q. acuminata* was used for this taxon by Sargent (1895). However, Kendig (1979) contended that Michaux's 1801 description of *Q. acuminata* is essentially the same as Muhlenberg's 1799 description of *Q. castanea*, a Mexican oak, and that the two taxa should be considered conspecific. Englemann (1887) published the name *Q. muehlenbergii* as a replacement for *acuminata* (Kendig 1979).

Distributed primarily in the eastern half of the United States, *Q. muehlenbergii* also occurs in central New Mexico and northeastern Mexico (Little 1971; Nixon, 1997). In Oklahoma, it is commonly found in the eastern three-quarters of the body of the state, and to lesser extent westward. Trees occupy a diverse range of habitats including moist uplands, buttes, eroding slopes, and stream terraces that vary in elevation, precipitation, aspect, soils, parent material, light intensity, and vegetation. It is often dominant on the sandstone hills of the prairies and Cross Timbers and the limestone bluffs and ridges of the Ozark Plateau (Tirmenstein, 1991). In the western half of the state it is frequently

associated with other hardwoods on buttes, ridgelines, stream terraces, or sand dunes.

Quercus muehlenbergii is especially important as food for black bears (Rogers, 1976). It provides mast for woodpeckers, songbirds, and large gamebirds (Martin, 1951; Stapanian and Smith, 1984; Reichman, 1987; Van Dersal, 1938; Tirmenstein, 1991). Rabbits, beavers, porcupines, and deer frequently browse young saplings and bark (Van Dersal, 1938; Hannah, 1987). Also, consumption by squirrels, chipmunks, voles, deer, and songbirds has been reported.

Within stands of the species, the leaves of the individual trees may vary in size, shape, and number and appearance of the marginal teeth. It is not uncommon for trees taller than 4 meters to exhibit considerable variation in the appearance of the leaves in the upper and lower canopy (Yokoyama and McGregor, 1951). Shade leaves of both small or large individuals can exhibit stellate hairs with erect rays similar to those of *Q. macrocarpa* (Nixon and Muller, 1997). Vegetative regeneration is vigorous in this species and the resulting coppice growth forms may be mistaken for the morphologically similar *Q. prinoides* (Sanders, 1990a). Leaves with obovate leaves were treated a forma *alexanderi* by U.T. Waterfall (1969), a taxon recognized by William Trelease (1924).

Hybridization of *Q. muehlenbergii* with other species of the genus have been documented or suspected (Little, 1979, 1980; Tucker, 1961; Hardin, 1975; Nixon and Muller, 1997; Buck and Bidlack, 1998). Hybrid plants are recognized by the blade lobing, appearance of stellate hairs (angle of ray divergence and straightness), petiole pubescence, cupule scales, and acorn size. Known hybridizations include *Q. alba*, *Q. havardii*, and *Q. macrocarpa* (= *Q. x deamii* Trelease), the latter being the most

frequently deposited hybrid in state herbaria. Little (1980) identified a single hybrid plant with *Q. havardii* in Boiling Springs State Park in Woodward County. I subsequently, encountered another hybrid of this cross in 2007. Suspected hybrids include: *Q. margaretta*, *Q. prinoides*, *Q. stellata*, and *Q. x drummondii*. Molecular analyses has indicated a relationship between *Q. stellata* and *Q. muehlenbergii* (Buck and Bidlack, 1998), and two hybrid individuals were encountered in this study (Figure 31). Hybrids with *Q. lyrata* are likely though, albeit none have been documented in the state's herbarium collections and I did not encounter any. Hybrids with *Q. gambelii* do not occur in Cimarron County, Oklahoma; however, they are reported from Texas and New Mexico (Tucker, 1961).

In addition, some individuals on Bromide Hill in Murray County, exhibit intermediacy between *Q. muehlenbergii* and *Q. sinuata* var. *breviloba*, as do others with *Q. virginiana* in the Quartz Mountains of Kiowa County. Possible hybridization among *Q. muehlenbergii* and these two species has not yet been reported.

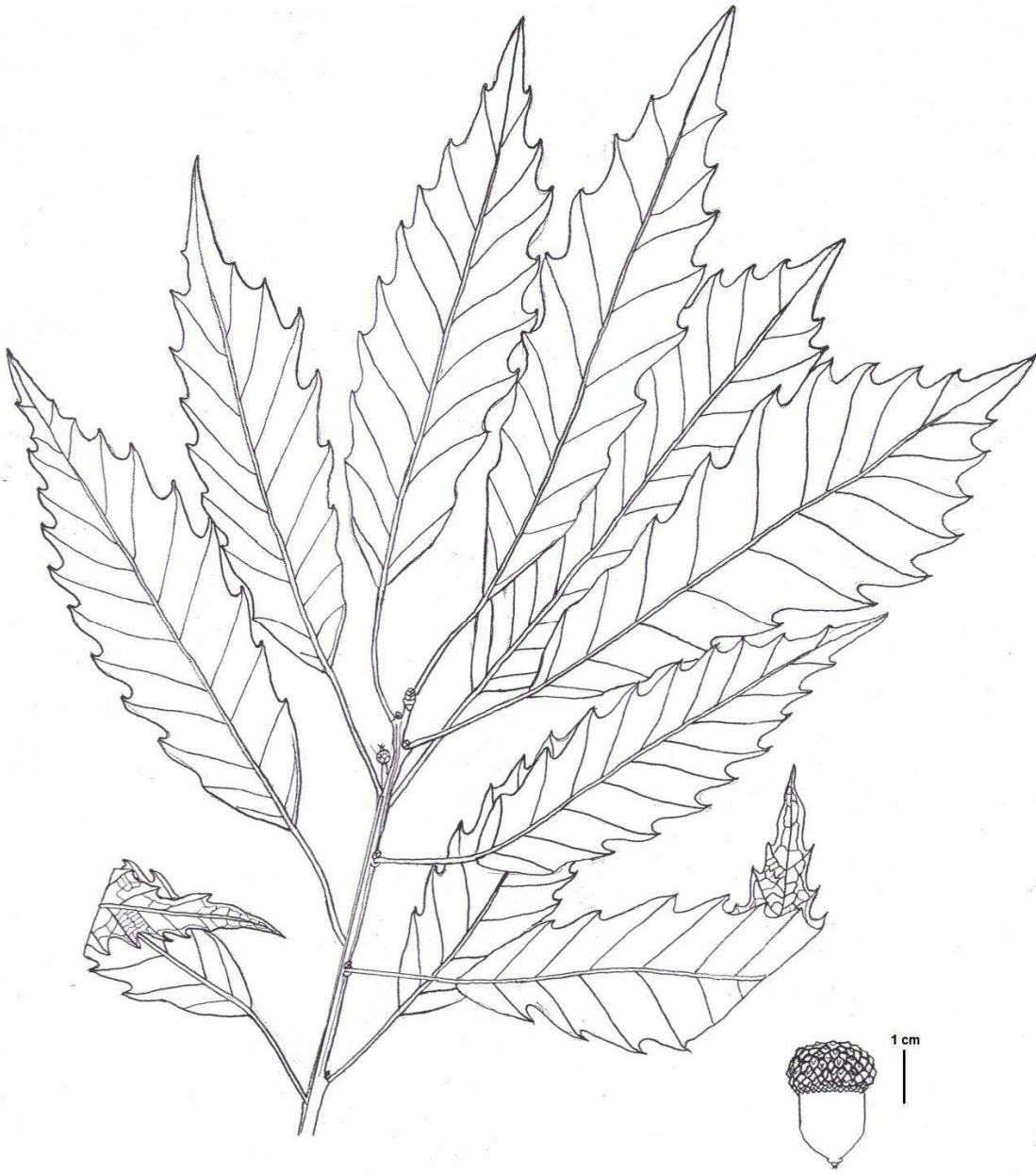


Figure 30. Foliage and acorn of *Quercus muehlenbergii* specimen collected near Mulhall, Payne County, Oklahoma.

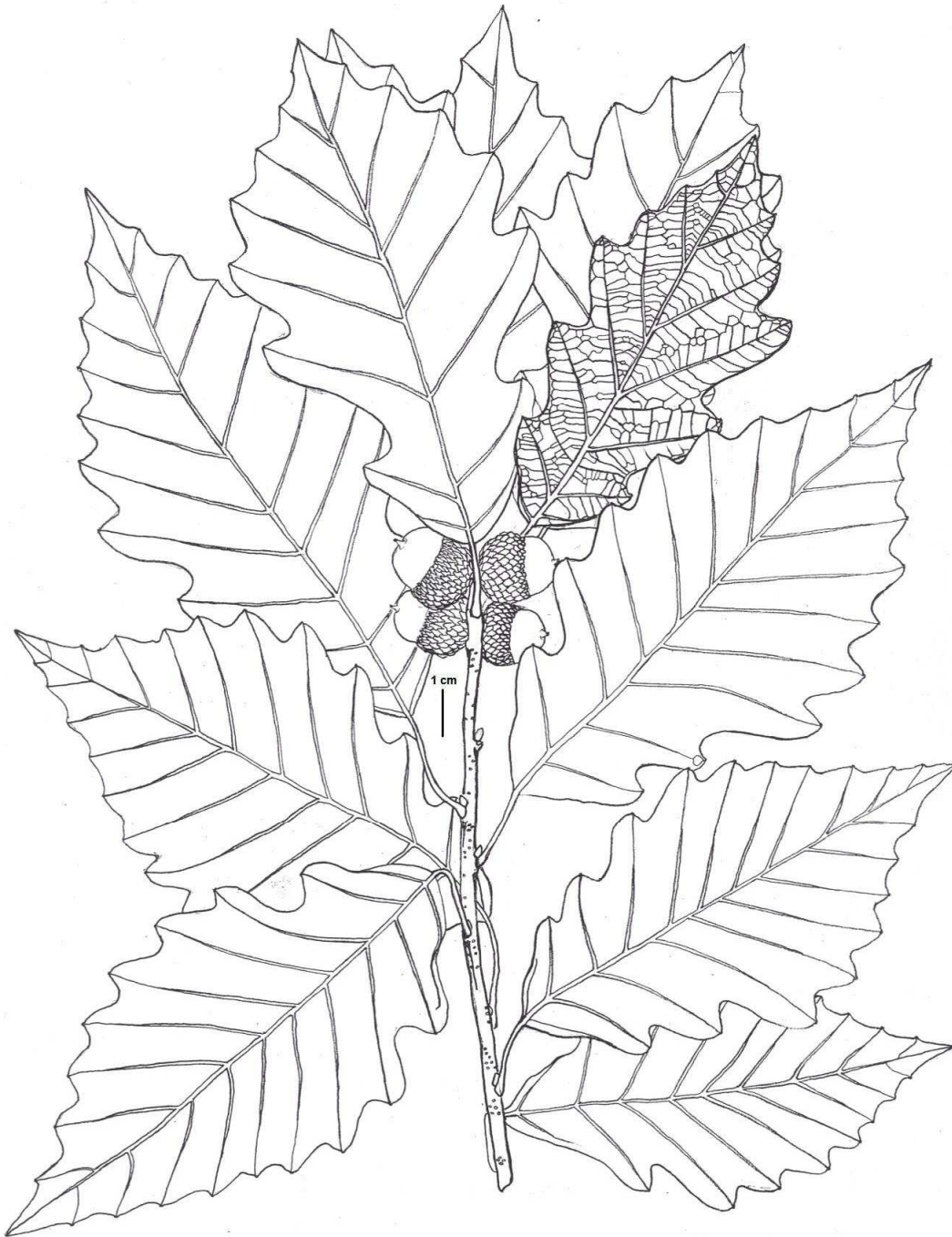


Figure 31. Foliage and acorns of putative hybrid between *Q. muehlenbergii* and *Q. stellata* collected at the southwest city limits of Stillwater, Payne County, Oklahoma.

***Quercus nigra* L. Water Oak**

Plants trees; to 47 m tall; deciduous. **Bark of Trunks** grey to black; smooth to coarsely ridged or scaly ridged; pink inner bark rarely exposed. **Primary Branches** ascending to horizontal. **Twigs** 1-2 mm in diameter; reddish brown to light brown or gray; glabrate. **Terminal buds** terete in cross-section; ovoid approaching conic; 3-5 mm long; silvery brown to reddish brown; distally silvery pubescent. **Leaves** obovate to obtrullate to oblong; 1-6.4 cm wide; 3.1-11.2 cm long; thick; chartaceous to coriaceous; apices rounded to acute; margins in distal 1/3-1/4 slightly to greatly expanded, entire to denticulate or 2- to 3-toothed, teeth broadly crenate to dentate; margins in basal 2/3 greatly constricted, entire; sinuses shallow, extending 1/10-1/2 distance to midribs; awns 0-5, present at margins and/or at lobe apices; bases attenuate to cuneate; adaxial surfaces dark to blue green, glossy, glabrous to glabrate; abaxial surfaces light or coppery green, glossy, glabrate except for inconspicuous to conspicuous tufts of rust colored pubescence in vein axils; **Hairs of Adaxial Surfacea** stellate; silvery; scattered along surfaces; sessile; 6- to 12- rayed; rays 0.1- 0.4 mm long, appressed to ascending, curling to straight. **Hairs of Abaxial Surfaces** stellate; silvery to golden tinged in vein axils; crowded in vein axils; stalked in vein axils; 4- to 12-rayed in vein axils; rays firmly attached to stalk, 0.1-1.0 mm long in vein axils, appressed to erect, curling to straight. **Hairs of Abaxial Midribs** glabrate or sparsely setaceous, golden and/or silvery, scattered or absent, 0.1-1.0 mm long, antorsely appressed; straight. **Catkins** 4-8 cm long. **Mature Acorns** ovoid to globose; 17 mm long; solitary or in clusters of 2 or 3; sessile or pedunculate, peduncles to 5 mm in length. **Cupules** shallowly bowl- to sauce-shaped; 10-15 mm in diameter; 3-6 mm deep; enclosing 1/4-1/3 of nuts; silvery brown to

orange-brown; scales appressed, flattened, ovate to oval, densely silvery tomentose, margins red to dark orange colored to obscured by tomentum, bases flattened, callus absent. **Nuts** globose to ovoid; 10-15 mm in diameter; 10-15 mm long; light brown; tomentose.

The specific epithet of *Q. nigra* reflects the dark color of the bark (Vines, 1982). This species is found throughout the southeastern quarter of United States (Little, 1971; Nixon, 1997; Jensen, 1997). In Oklahoma, it likewise is distributed primarily in the three ecoregions of the southeastern quarter of the state: the Ouachita Mountains, the Arkansas Valley, and the Red River bottomlands of the South Central Plains. *Quercus nigra* is a sub-climax species of lowland forests and periodically flooded soils adjacent wetlands (Carey, 1992a). Trees occupy soils that range from sandy to cherty loams where is commonly associated with other mesic hardwoods (Hoagland, 2000).

The juvenile twigs and leaf surfaces of *Q. nigra* are typically green. The hairs of the juvenile leaves are sparse or absent with exception of the midribs and axils of the abaxial veins. They become loose and are shed during expansion and maturation of the leaves. Hairs of the adaxial leaf surfaces sometimes shed profusely with the exception of the midribs which are densely pubescent near the petioles; a phenomenon also exhibited by hybrids between it and *Q. incana* or *Q. falcata*.

Trees that establish on shallow rocky soils inevitably remain smaller due to restricted root growth, and water and nutrient uptake. Individuals may resprout from the crown after top removal quite effectively at any age with regenerative capacities similar to those exhibited by *Q. phellos* (Putnam, 1951; Streng et al. 1989; Vozzo, 1990; Schlaegal, 1990; Carey, 1992a).

Sargent classified individuals bearing leaves with three lobes and attenuate bases as variety *tridentata* (Jensen, 1997); however, my observations indicate that these two character states may simply be intrapopulational variation rather than a genetic feature typically characteristics of a varietal taxon.

Hybridizations of *Q. nigra* with *Q. incana* (= *Q. x caduca* Trelease), *Q. falcata* (= *Q. x garlandensis* E. J. Palmer), *Q. marilandica* (= *Q. x sterilis* Trelease), *Q. palustris*, *Q. phellos* (= *Q. x capesii* W. Wolf), *Q. rubra*, *Q. shumardii* (= *Q. x neopalmeri* Sudworth), and *Q. velutina* (= *Q. x demareii* Ashe) have been reported (Little, 1979; Hunt, 1989; Jensen, 1997). Hybrids with *Q. falcata* and *Q. phellos* seem to be the most frequently encountered. Hybridization with *Q. buckleyi* has not been reported; undoubtedly due to geographic isolation. In the southeastern corner of the state, these hybrids are easily detected in populations where the trees exhibit a diversity of leaf margins; each distinctly different from other nearby individuals.

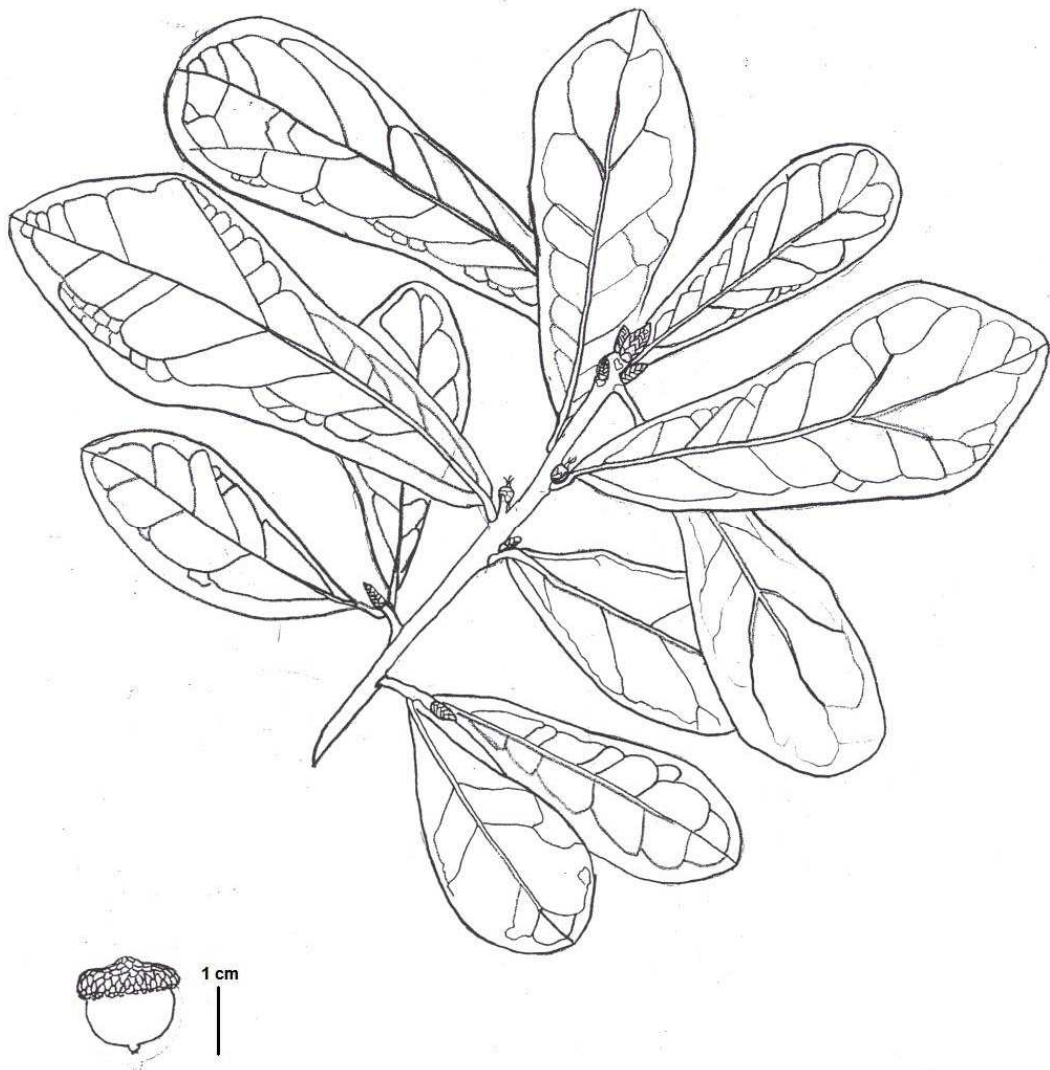


Figure. 32. Foliage and acorn of *Q. nigra* specimen collected along Fouché Maline Creek, Le Flore County, Oklahoma.

***Quercus pagoda* Raf. Cherrybark Oak**

Plants trees; to 20 m tall; deciduous. **Bark of Trunks** gray to brown to black; smooth to coarsely ridged; orange inner bark often exposed by fissures or furrows. **Primary Branches** ascending to horizontal. **Twigs** sulphurous yellow to light brown; densely or sparsely stellate; hairs sulphurous yellow. **Terminal buds** 5-angled in cross-section; ovoid to ellipsoidal; 6-8 mm long; golden to yellow tinged red; densely sulphurous yellow pubescent, sometimes with a glabrous band parallel to margin. **Leaves** broadly elliptic to obovate; 10-17 cm wide; 10-31 cm long; thin to thick; chartaceous; apices acute, from terminal lobe equal in length to the lateral lobes; margins 5- to 11-lobed; deltoid to falcate or oblong, apically entire or 1- to 4- toothed and constricted,; sinuses deep, extending 2/4-3/4 distance to midribs; awns 10-20, present along margins and/or at lobe apices; bases subrounded to cuneate or acute. petioles 20-60 mm long, sparsely to densely pubescent; hairs like those of leaf surfaces. **Hairs of Adaxial Surfaces** like those of abaxial surfaces; but persistent only along midribs. **Hairs of Abaxial Surfaces** persistent; stellate; silvery to sulphurous yellow covering surfaces or reddish tinged in vein axils, sessile covering surface to inconspicuously stalked in vein axils, 8- to 12-(16)-rayed; rays 0.1-0.5 mm long covering surfaces and 0.5-1.5 mm long in vein axils of midribs, appressed to erect, straight to curling; bulbous; sulphurous to golden; appressed; less than 0.1 mm long; setaceous; silvery to sulphurous yellow; 0.5-3.0 mm long. **Hairs of Abaxial Surfaces** like those of abaxial surfaces; setaceous; silvery or sulphurous yellow; 0.5-3 mm long. **Catkins** 5-8 cm long. **Mature Acorns** turbinate to ovoid; 12-22 mm long; solitary or in clusters of 2 or 3; sessile or pedunculate, peduncles to 7 mm long. **Cupules** bowl-shaped; 10-20 mm in diameter; 5-10 mm deep; enclosing

1/3-1/2 of nuts; orange-brown; scales tightly appressed; flattened; oval to oblong; sparsely sulpherous yellow to silvery tomentose, margins red to dark orange colored or obscured by tomentum, bases flattened, callus absent. **Nuts** ovoid to globose; 10-18 mm in diameter; 10-20 mm long; light brown to orange brown; tomentose.

The specific epithet of *Quercus pagoda* reflects the similarity between the shape of its leaves and the tiered organization of an Asian pagoda (Figures 33 and 34). It is distributed in the Atlantic and Gulf coastal plains of the southeastern quarter of the United States, and is characteristically restricted to lowlands and seasonally inundated bottoms (Little, 1971; Jensen, 1989; 1997; Moore and Wilson, 2003). These moisture requirements likely play role in isolating the species from the morphologically similar *Q. falcata* despite frequent hybridization between the two taxa (Jensen, 1989).

In Oklahoma, the species likewise occurs in wet bottomlands in the extreme southeastern corner of the state. The high annual precipitation and long growing seasons of McCurtain County likely permits its establishment on mesic slopes in the Ouachita Mountains, a phenomenon seen in the Appalachian Mountains (Krinard, 1990; Jensen, 1997; Moore and Wilson, 2003). Soils occupied are acidic, silty or clayey loams that tend to be well drained (Moore and Wilson, 2003). Trees become reproductive at 25 years of age with maximum production of nuts between 50 and 75 years of age (Krinard, 1990; Moore and Wilson, 2003). Large crops of nuts are produced every 1 or 2 years (Bonner, 2008).

Some taxonomists (Waterfall, 1969; Little, 1985; Taylor and Taylor, 1994) treat *Q. falcata* and *Q. pagoda* as conspecific, use the binomial *Q. falcata*, and recognize

variety *falcata* and variety *pagodifolia* Elliot. The treatments of Jensen (1989; 1997) and Nixon (1997) maintaining them as distinct species are followed here.



Figure 33. Foliage (sun leaves) and acorn of *Quercus pagoda* specimen collected in the Little River National Wildlife Refuge, McCurtain County, Oklahoma.

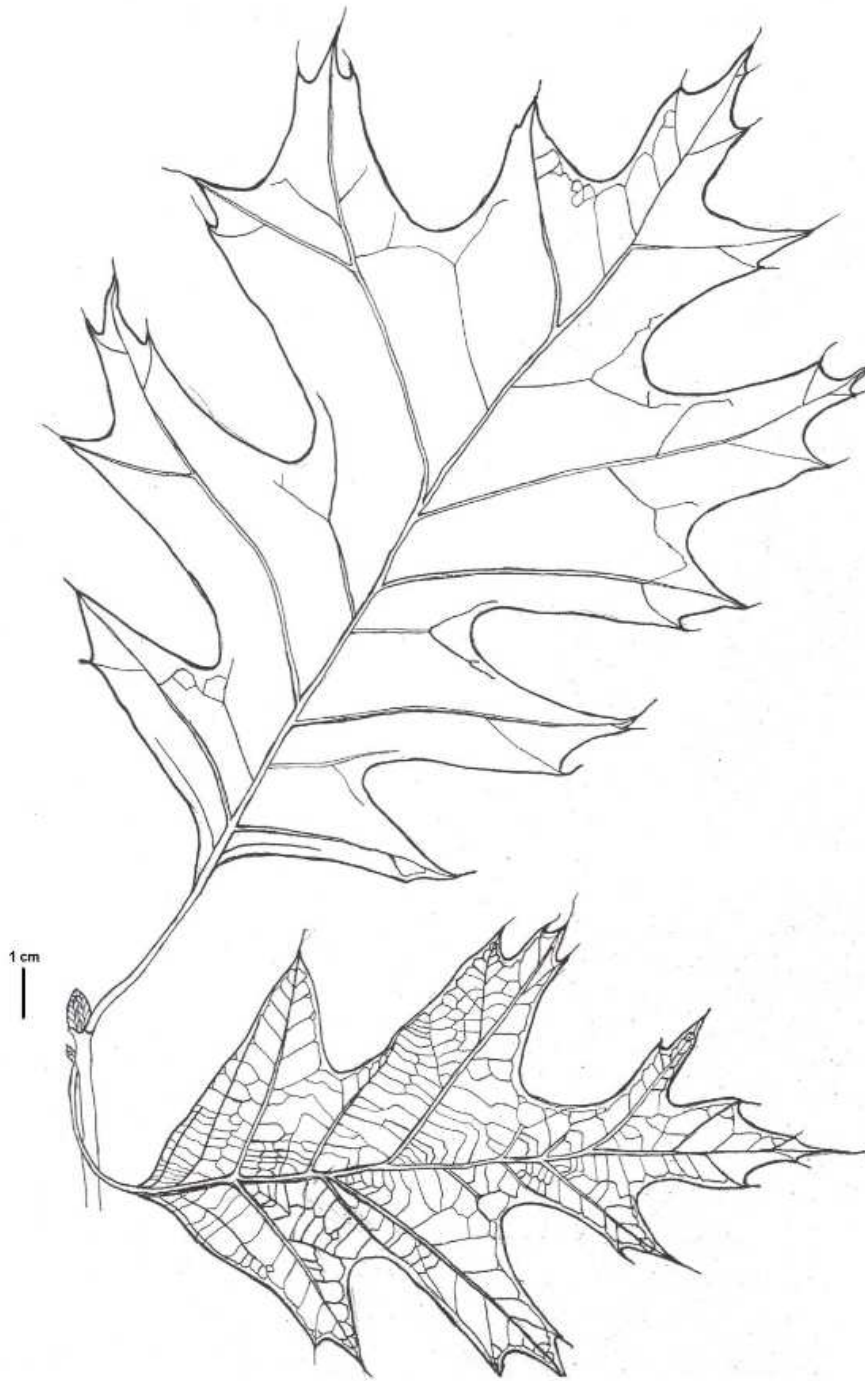


Figure 30. Foliage (shade leaves) of *Quercus pagoda* specimen collected in the Little River National Wildlife Refuge, McCurtain County, Oklahoma.

***Quercus palustris* Muenchh. Pin Oak**

Plants trees; to 34 m tall; deciduous. **Bark of Trunks** brownish gray to gray; smooth to slightly ridged; pink inner bark often exposed by fissures. **Primary Branches** ascending above, horizontal to descending below. **Twigs** 2-3.5 mm in diameter; reddish brown to dark brown or gray; glabrate. **Terminal Buds** terete to slightly angled in cross-section; ovoid to ellipsoidal; 4-7 mm long; reddish brown to grayish brown; apically tomentose to glabrate, sometimes ciliate only along scales margins. **Leaves** orbicular to obovate or ovate; 5-12 cm wide; 5-18 cm long; thin or thick; chartaceous; apices acute to attenuate; margins 5- to 9-lobed; lobes deltoid to lanceolate or oblong, apically 3- to 5- toothed; sinuses deep, extending equal to or greater than 3/4 distance to midribs; awns 10-30, present along margins of lobe apices; bases cuneate to obtuse or truncate; adaxial surfaces dark green, dull or glossy, glabrate; abaxial surfaces light green, glossy, glabrate except for conspicuous or inconspicuous tufts of rust colored pubescence in vein axils; petioles 20-60 mm long, glabrate to glabrous, hairs like those of abaxial midribs; stipules caducous. **Hairs of Adaxial Surfaces** like those of abaxial surface. **Hairs of Abaxial Surfaces** persistent in axils of secondary veins with midribs; stellate; silvery to reddish tinged; sessile to conspicuously stalked; 6-to 16-rayed; rays 0.4-1.4 mm long; appressed to erect; curling to straight. **Catkins** 4-8 cm long. **Mature Acorns** globose to ovoid; 12-16 mm long; solitary or paired; sessile or pedunculate, peduncles to 8 mm long. **Cupules** shallowly saucer-shaped; 10-16 mm in diameter; 2-3.5 mm deep; enclosing 1/4-1/5 of nuts; reddish brown to silvery brown; scales tightly appressed, flattened, deltoid to oval, densely silvery to sulphurous yellow tomentose, margins dark red and glabrous, bases flattened, callus absent. **Nuts** globose; 10-16 mm

in diameter; 10-15 mm long; brown to dark brown; tomentose. Foliage and an acorn of *Q. palustris* are illustrated in Figure 35.

The specific epithet "*palustris*" means "of the marsh" and reflects to an extent the habitat of *Q. palustris*. This species is characteristic of intermittently flooded bottomlands and poorly drained clay soils of uplands of the northeastern United States (Little, 1971; Carey, 1992; Nixon, 1997). In Oklahoma, naturally occurring populations are restricted to lowlands and stream or river terraces primarily in the northeastern quarter of the state, with disjunct populations in Latimer and LeFlore counties (Little, 1971, 1985). The species is common along portions of the Deep Fork, Neosho, and Verdigris Rivers. In addition, it is encountered in prairie hay meadows adjacent to the Neosho River. Soils along these rivers are characterized by high proportions of clay and silt, poor drainage, low to high organic matter, and high to moderate acidity. Natural associations with mesic upland hardwoods are infrequent. Trees that establish themselves near seasonally flooded areas are less likely to suffer fire damage (Haney et al., 2008). The growth habit of *Q. palustris* makes it useful in buffer strip plantings used in watershed protection of agricultural fields because the roots are concentrated close to the trunk, and thus do not inhibit growth of nearby crops (Udawatta et al., 2004). Throughout eastern Oklahoma, cultivars of *Q. palustris* are used ornamentally as shade and specimen trees because of the horizontal orientation of the branches in the lower canopy (Dirr, 1998). The Delaware tribe of Oklahoma used the bark as an analgesic and gastrointestinal aid (Moerman, 1998).

Little (1979), Hunt (1989), and Jensen (1997) cited hybrids of *Q. palustris* with *Q. marilandica*, *Q. nigra*, *Q. phellos* (= *Q. x schochiana* Dieck), *Q. rubra* (= *Q. x*

columnaris Laughlin), *Q. shumardii* (= *Q. x mutabilis* E. J. Palmer & Steyermark), and *Q. velutina* (= *Q. x vaga* E. J. Palmer & Steyermark). There are no confirmed reports of hybridization with *Q. incana*, *Q. falcata*, or *Q. buckleyi*.

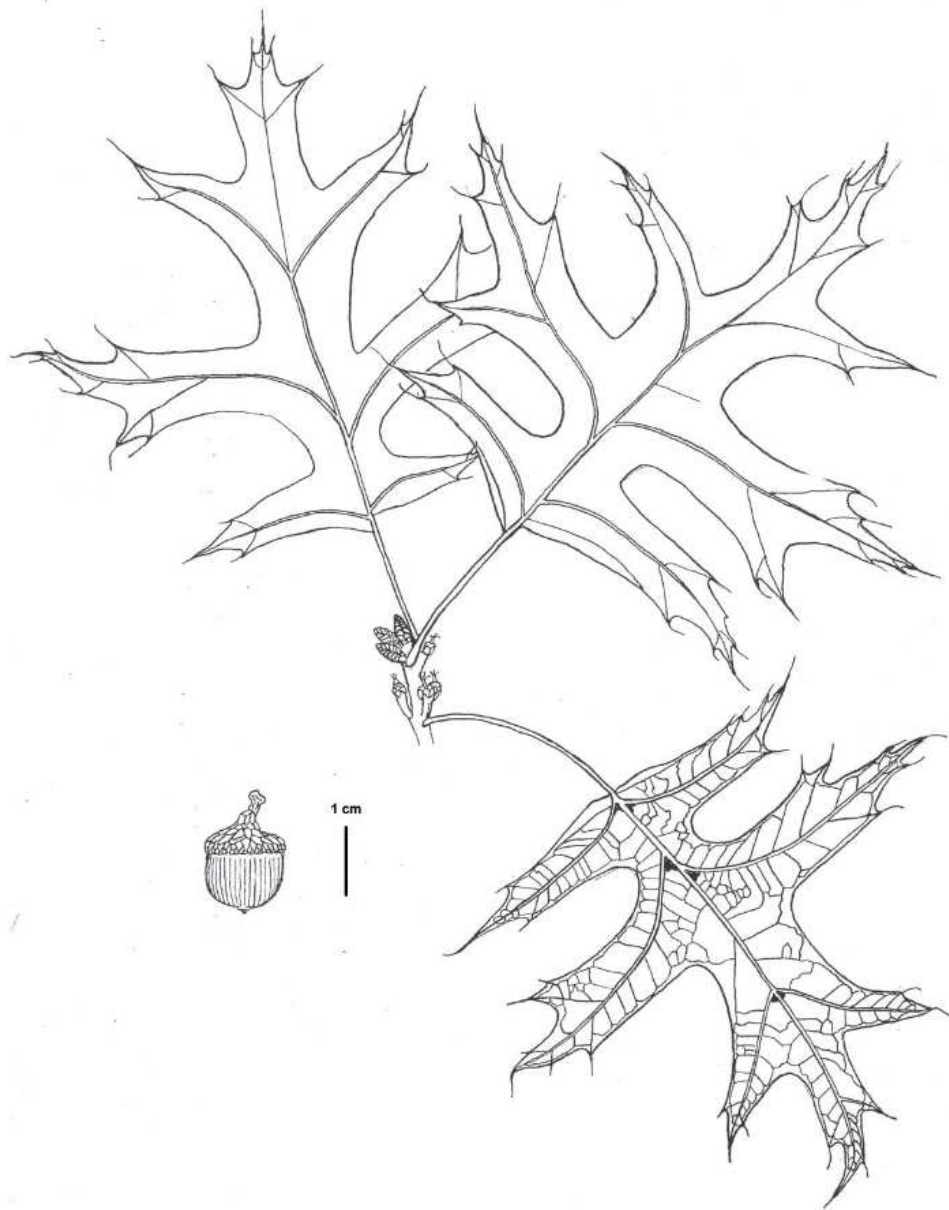


Figure 31. Foliage and acorn of *Q. palustris* specimen collected along the Fouche Maline Creek in Wister Wildlife Management Area, LeFlore County, Oklahoma.

***Quercus x pauciloba* Rydb. Rocky Mountain Scrub Oak**

Plants colony forming shrubs; to 3.5 m in height; deciduous or subevergreen. **Bark of Trunks** whitish gray or brownish gray; scaly to blocky to coarsely ridged; inner bark not exposed. **Primary Branches** horizontal. **Twigs** 2-3 mm in diameter; reddish brown to sulphurous yellow; glabrate to densely stellate, hairs sulphurous yellow. **Terminal buds** terete in cross-section; globose to ovoid; 1.5-3 mm long; yellowish brown to brown; sparsely silvery pubescent, sometimes only pubescent along scale margins. **Leaves** elliptic to ovate or obovate or oblong; 1-5 cm wide; 1.5-8 cm long; coriaceous to subcartilaginous, sometimes thin and indurate; apices mucronate to acute or obtuse to rounded; margins entire to undulate or uniformly 2- to 7-toothed, teeth undulate-serrate to undulate-spinose or dentate to crenate, or 4- to 7- lobed, lobes finger like to deltoid; sinuses shallow or deep, extending equal to or less than 3/4 distance to midribs; awns 0-11, present at apices of teeth and/or lobes; bases rounded to cordate or truncate to cuneate; adaxial blades surfaces silvery green to blue or light gray, scabrous, sparsely stellate; abaxial blades surfaces whitish yellow to silvery blue or green, scabrous to coarsely scabrous; petioles 2-10 mm long, densely stellate; hairs those of abaxial surfaces. **Hairs of Adaxial Surfaces** like those of abaxial surfaces; but sparse and frequently reduced in size. **Hairs of Abaxial Surfaces** persistent; stellate, silvery, sessile to inconspicuously stalked (less than 0.1 mm long), 6- to 12-rayed; rays 0.2-1.0 mm long, ascending to erect, straight to curling; uniserrate; silvery or golden colored; appressed; equal to or less than 0.2 mm long. **Catkins** 2-3 cm long. **Mature Acorns** ovoid to ellipsoidal; 11-20 mm long; solitary or paired; sessile or pedunculate, peduncles to 30 mm long. **Cupules** urceolate to hemispheric; 8-12 mm in diameter; 6-8 mm deep;

enclosing 1/5-1/2 of nuts; silvery white; scales tightly appressed, sometimes slightly reflexed at cupule rims, those at cupule rims reduced in size or lanceolate, those at cupule bases deltoid to ovate, silvery to golden silvery tomentose, margins orange to reddish brown in distal 1/2-1/3, glabrous to tomentulose, bases slightly tuberculate to keeled or thickened to flattened, callus black or rust colored at maturity. **Nuts** ovoid to ellipsoidal; 8-11 mm in diameter; 10-18mm long; light brown; glabrous or pubescent in distal half. Foliage and acorns of this taxon are illustrated in Figures 36 and 37.

Quercus x pauciloba ranges throughout the foothills and canyons of the Rocky Mountains and Chihuahuan and Sonoran deserts of the United States, in some cases hundreds of miles from either parental species (Little, 1979; Tucker, 1961). In Oklahoma it is only found in the northwestern corner of the Panhandle near Black Mesa. Soils consist of well drained and highly weathered sediments. Habitats include foothills, alluvial fans, cuernas, and the escarpments of Tesequite Canyon and Carrizo Creek.

Exactly which species of oaks are present in the Black Mesa area of Cimarron County has confounded taxonomists for decades. *Quercus gambelii*, *Q. pauciloba*, *Q. undulata*, and *Q. mohriana* have all been reported to occur there (Rydberg, 1901; Sargent, 1926; Tucker, 1961; Waterfall, 1969; Little, 1981; Great Plains Flora Association, 1986; Nixon, 1997). Based on the phenotypic and ecological studies of Tucker (1961, 1963, 1970, 1971; Tucker et al., 1961) plants previously identified as *Q. undulata* are classified as the nothospecies *Q. x pauciloba*, a hybrid between *Q. gambelii* and *Q. turbinella*, in this treatment.

John Torrey based his 1828 description of *Q. undulata*, the wavy leaf oak, on plant material of three oak specimens collected by botanists accompanying the 1820

Major Stephen Long Expedition to the Rocky Mountains (Rydberg, 1901; Tucker; 1971). Because he had been misinformed about the collection protocols and the plants he received were morphologically similar, he named them as one species. His classification was accepted for many years (Rydberg, 1901; Sargent, 1905; Trelease; 1924; Muller; 1951b; Waterfall, 1969). Subsequent work by Tucker (1961, 1963, 1970, 1971; Tucker et al., 1961) revealed that the type specimen of Torrey's *Q. undulata* includes plant material of *Q. grisea*, *Q. havardii* and a hybrid plant (see Figure 12, Tucker, 1971). In addition, there is a hand-drawn illustration that conspicuously resembles *Q. havardii* accompanying the species description (see Figure 8, Tucker, 1971). Because the holotype comprises this mixture of taxa, the binomial *Q. undulata* cannot be used.

The hybrid with its distinctive undulate margins on Torrey's herbarium sheet is morphologically similar to plants found throughout the southwestern United States (Tucker, 1961, 1971). Tucker (1961) determined that these undulate margins occurred between hybrids of *Q. gambelii* and other oak species within its range including *Quercus turbinella* (sonoran scrub oak), *Quercus grisea* (gray oak), *Quercus mohriana* (Mohr oak), *Quercus havardii* (shinnery oak), and *Quercus arizonica* (Arizona oak) and described this complex of hybridization as the *Q. x undulata* complex (Tucker, 1961; 1963; 1970; 1971; Tucker et al., 1961).

The binomial *Q. x pauciloba* is based on Rydberg's 1901 publication of *Q. pauciloba*. His morphological description of the taxon describes these intermediate characters of populations extending throughout the Southern Rockies into Oklahoma. It

is understandable that he treated these plants as a species because of their widely distributed, but yet similar phenotypes.

Specimens of *Q. x pauciloba* have been misidentified as *Q. havardii* in the past (Nixon and Muller, 1997). The two taxa can be distinguished, however, by the hybrid's true awns and smaller acorns.



Figure 36. Foliage and acorn of *Q. x pauciloba* specimen collected in Tesequite Canyon, Cimarron County, Oklahoma.

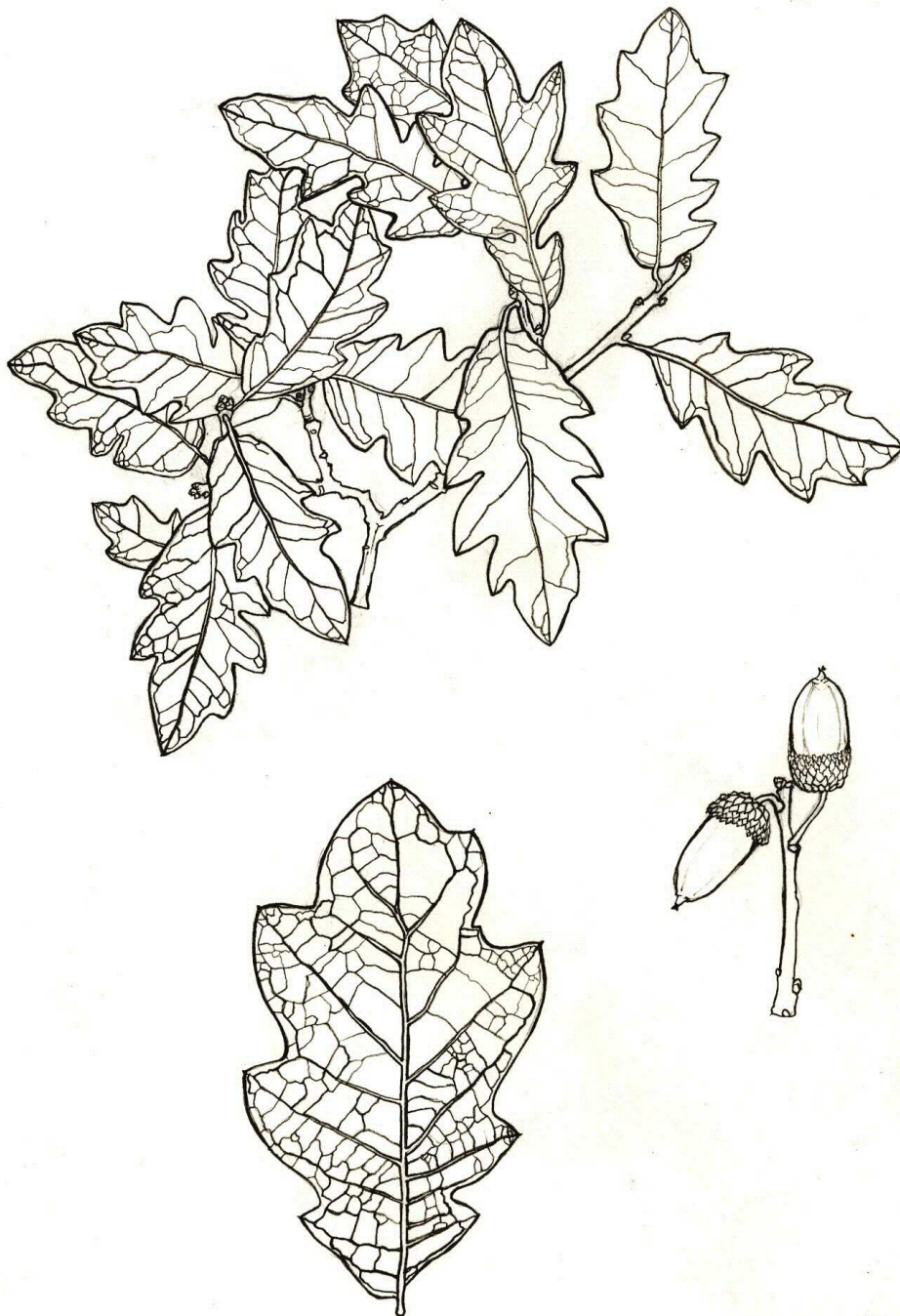


Figure 37. Foliage and acorns of *Q. x pauciloba* specimen collected in Tesequite Canyon, Cimarron County, Oklahoma.

***Quercus phellos* L. Willow Oak**

Plants trees; to 25 m tall; deciduous. **Bark of Trunks** grey to black; smooth to coarsely ridged; orange inner bark rarely exposed. **Primary Branches** ascending to horizontal. **Twigs** 1-2 mm in diameter; reddish brown to light brown or gray; glabrate to sparsely stellate; hairs silvery. **Terminal buds** terete in cross-section; ovoid; 2-4 mm long; light brown to reddish brown; sparsely pubescent to glabrate except for ciliate scale margins. **Leaves** lanceolate to oblong; 1-1.5 cm wide; 5-13 cm long; thin; chartaceous; apices acute to obtuse; margins entire to slightly revolute; awns 0-1, present at apices; bases obtuse to acute; adaxial surfaces light green, dull to glossy, glabrous or glabrate except for inconspicuous pubescence along midribs; abaxial surfaces light green to whitish green, dull, glabrate except for inconspicuous rust colored tufts of pubescence in vein axils; petioles 2-4 mm long, glabrate or sparsely pubescent, hairs like those along adaxial midribs; stipules caducous. **Hairs of Adaxial Surfaces** like those in vein axils of abaxial midribs; but restricted to basal portion of adaxial midribs. **Hairs of Abaxial Surfaces** persistent in axils of secondary veins with midribs; stellate; silvery to reddish tinged; sessile to inconspicuously stalked (less than or equal to 0.1 mm tall); 2- to 10-rayed; rays 0.2-0.7 mm long, ascending to erect, curling to sparingly straight. **Hairs of Abaxial Midribs** like those along midribs; but frequently deciduous. **Catkins** 2-4 cm long; flower clusters crowded. **Mature Acorns** sub-turbinate to globose or ovoid; about 13.5 mm long; solitary or in clusters of 2 or 3; sessile or pedunculate, peduncles to 5 mm long. **Cupules** shallowly bowl- to saucer-shaped; 10-13.5 mm in diameter; 4-8 mm deep; enclosing 1/4-1/3 of nuts; red to light brown; scales appressed, ovate to oval, abruptly reduced in size near rims, densely silvery tomentose, margins red to orange,

tomentulose to glabrous, bases thickened, callus absent. **Nuts** globose; 10-12 mm in diameter; 10-11 mm long; light brown; tomentose. Foliage and acorns of *Q. phellos* are illustrated in Figure 34.

The specific epithet "*phellos*" is the ancient Greek name for the European cork oak *Q. suber*. Found throughout the south and central United States, *Q. phellos* is a late succession forest species of bottomland forests ((Little, 1971; Schlaegel, 1990). In Oklahoma, it is found on sandy to cherty loams of the Gulf Coastal Plain and Ouachita Mountains in the southeastern quarter of the state associated with a variety of other tree species. Associations with *Nyssa sylvatica* and *Carpinus caroliniana* are most common (Hoagland, 2000).

Juvenile twigs and leaf surfaces are yellow-green in color. The hairs of juvenile leaves are sparse or absent with exception of the midribs and abaxial vein axils. Those covering the leaf surface quickly become loose and are shed during expansion and maturation of the leaf. Mature leaves have a tendency to be exceptionally yellow green which is an indicator of borderline chlorosis (Schnelle, 1991). Trees that establish on shallow rocky soils inevitably remain smaller due to restricted root growth, and water and nutrient uptake. Individuals that establish themselves under a dense canopy may exhibit die back, but regenerate by sprouting from their crowns (Schlagael, 1990).

A popular tree in urban horticulture, *Q. phellos* is ideal for both reclamation and ornamental use because of the ease at which it establishes itself in well drained to mucky soils (Dirr, 1998).

Hybrids have been reported with other members of Section *Lobatae* in Oklahoma, with exception of *Q. buckleyi*. These include *Q. falcata* (= *Q. x ludoviciana*

Sargent), *Q. pagoda*, *Q. incana*, *Q. marilandica* (= *Q. x rudkinii* Britton), *Q. nigra* (= *Q. x capesii* W. Wolf), *Q. palustris* (= *Q. x schochiana* Dieck), *Q. rubra* (= *Q. x heterophylla* F. Michaux), *Q. shumardii* (= *Q. x moultonensis* Ashe), *Q. velutina* (= *Q. x filialis* Little) (Palmer, 1948; Little, 1979; Hunt, 1989; Jensen, 1997). In the southeastern corner of the state, hybrids of *Q. phellos* with *Q. nigra* and *Q. pagoda* are the most common. They can be easily recognized by their leaf size, leaf pubescence, and tendency to exhibit leaf margins of both parents on the same tree (Muller, 1951b).

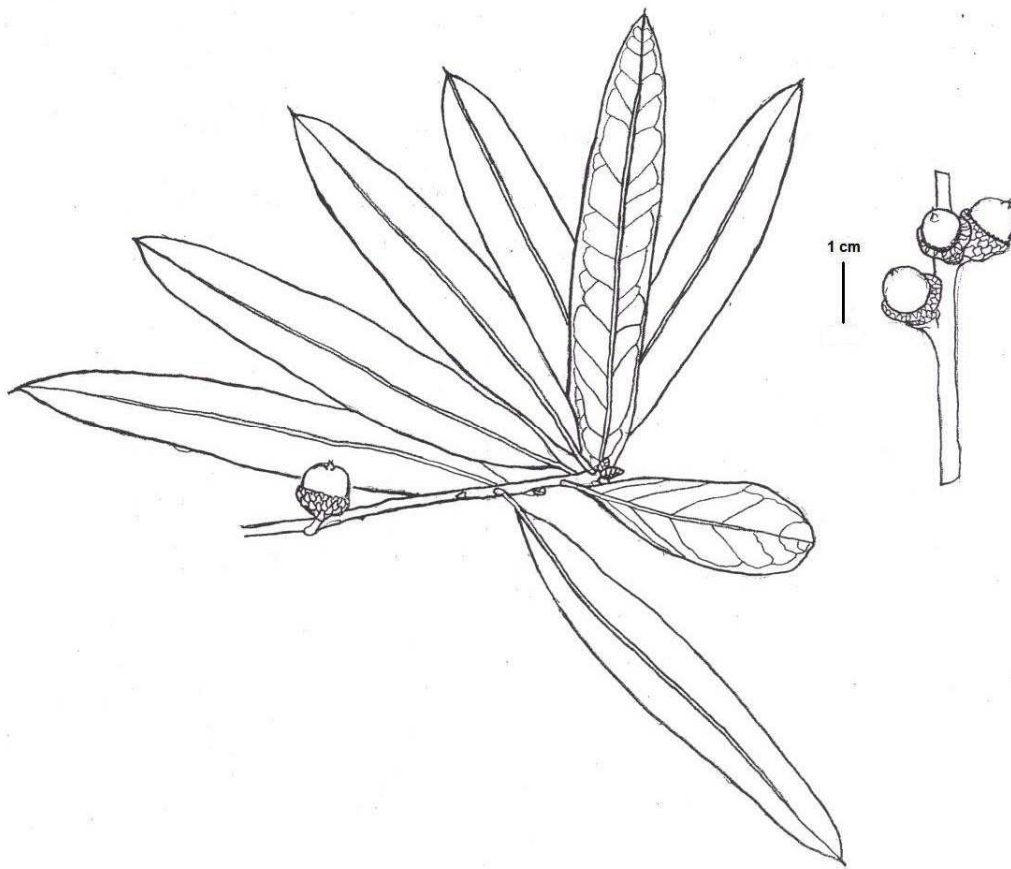


Figure 38. Foliage and acorn of *Quercus phellos* specimen collected along the Red River, McCurtain County, Oklahoma.

***Quercus prinoides* Willd. Dwarf Chinkapin Oak**

Plants trees or shrubs; to 7.6m in height; deciduous. **Bark of Trunks** whitish gray; papery to scaly; inner bark not exposed. **Primary Branches** ascending to horizontal. **Twigs** 2-3 mm diameter; reddish brown or gray; glabrate. **Terminal buds** terete in cross-section; sub-rotund to broadly ovoid; 1-1.5 mm long; light brown or brown or grayish brown; sparsely silvery pubescent, sometimes merely ciliate along scale margins. **Leaves** obovate to ovate, or oblanceolate to lanceolate, or oblong to elliptic; 1.4-11.5 cm wide; 3.4-19.5 cm long; thick; coriaceous; apices acute to apiculate; margins uniformly 5- to 9-toothed, teeth dentate to serrate to serrate-crenate; sinuses shallow, extending 1/10-1/4 distance to midribs; bases truncate to cuneate; adaxial surface dark green, dull or glossy, scaberulous or wax-like, sparsely stellate to glabrate; abaxial surface white to light green, scaberulous to ribbed, densely to sparsely stellate; hairs inconspicuous, sessile, 8- to 10-rayed; rays straight, closely appressed and spreading; petioles 7-28 mm long, sparsely stellate to glabrate; hairs like those of abaxial surfaces; stipules caducous. **Hairs of Adaxial Surfaces** like those of abaxial surface; but usually deciduous. **Hairs of Abaxial Surfaces** persistent; stellate; silvery; sessile; 6- to 12-rayed; rays 0.3-1.0 mm long; appressed; straight to slightly curving. **Catkins** 4-6 cm long. **Mature Acorns** globose to oblong; 11-18 mm long; solitary or paired; sessile or pedunculate, peduncles to 8 mm long. **Cupules** hemispheric; 12-23.5 mm in diameter; 5-12 mm deep; enclosing 1/4-1/2 of nuts; silvery; scales tightly appressed, those at cupule rims abruptly reduced in size or lanceolate, those at cupule bases deltoid to ovate, silvery tomentose, margins reddish, tomentulose to obscured by dense tomentum, bases slightly tuberculate to creased and thickened, callus black.

Nuts ovoid to oblong; 8-22 mm in diameter; 13-28 mm long; dark brown; glabrous to lower 3/4-1/2 tomentose. Foliage and acorns of *Q. prinoides* are illustrated in Figure 39.

The specific epithet of *Q. prinoides* reflects the resemblance of its leaves to those of *Q. prinus* (Vines, 1982). It is distributed throughout the northeastern United States with the exception of Wisconsin and Minnesota (Nixon and Muller, 1997). In the Southeast, the species is present in the northern half of states that border the Gulf Coast and the western half of states that border the southern Atlantic coast (Stein et al., 2003). The western most distribution of the species is in central and northeastern Oklahoma (Nixon and Muller, 1997). Considered to rarely occur on calcareous soils (Nixon and Muller, 1997), these shrubs in Oklahoma are typically encountered on the Permian sands in the west and the upland Permian sandstone and shale in the center of the state. However, throughout its range in North America, this species occurs in soils to those derived from serpentine (Pennell, 1910; Hellmers, 1940; Brown, 1960; Stewart and Rossi, 1981; Copenheaver and Abrams, 2002).

The identity of *Q. prinoides* has been debated for the last century due to differences in opinion as to what characters distinguish it from *Q. muehlenbergii* (Nixon and Muller, 1997). The plasticity exhibited by its leaf shapes and margins certainly exceeds the variability exhibited by its acorn morphology (Meehan, 1885). This variability is seen in many stands of both *Q. prinoides* and the morphologically similar *Q. muehlenbergii* in Oklahoma. *Q. prinoides* becomes reproductive at 3 or 5 years of age with a diameter at breast height of 5–30 mm (Nixon and Muller, 1997).

Two hybrids between *Q. prinoides* were recognized by Little (1979) and include *Q. alba* (= *Q. x faxonii* Trelease) and *Q. stellata* (= *Q. x stelloides* Palmer). Interestingly,

despite the problems of distinguishing *Q. prinoides* and *Q. muehlenbergii*, no reports of hybridization between the two species has been published.

The hybrid *Q. x stelloides* is so common that herbarium collections of it have been overlooked or misidentified. However, the presence of its sulphurous to silvery yellow twigs versus the dark red twigs of *Q. prinoides* can consistently be used to differentiate the hybrid. Usually encountered along the edge of Cross Timbers forests, rhizomatous clones of *Q. prinoides* are often intermingled with those bearing this twig character. Morrison-Hill and Buck (1980) analyzed populations of *Q. prinoides* and *Q. stellata*. They concluded introgression following hybridization was advantageous for the occupation of otherwise unsuitable habitats by *Q. x stelloides* in Oklahoma. Populations that were studied by Morrison-Hill and Buck were revisited in 2007. The individuals present in these populations exhibited some of the greatest variation in this hybrid complex.

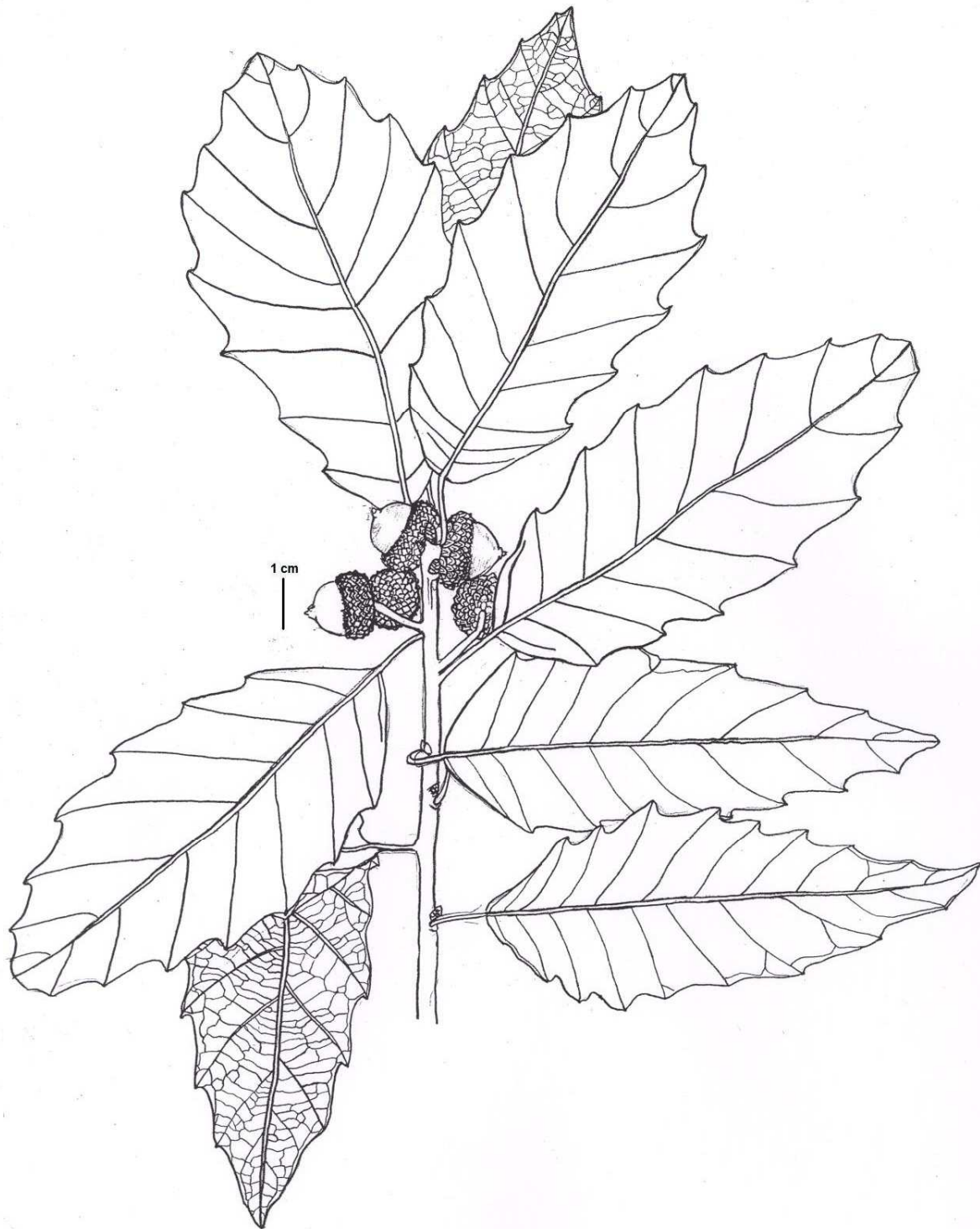


Figure 39. Foliage and acorns of *Quercus prinoides* specimen collected near Mulhall, Kingfisher County, Oklahoma.

***Quercus rubra* L. Northern Red Oak**

Plants trees; to 37 m tall; deciduous. **Bark of Trunks** grey to black; smooth to coarsely ridged; pink inner bark often exposed by fissures or furrows. **Primary Branches** ascending to horizontal. **Twigs** 2.5-4 mm in diameter; reddish brown to dark brown or gray; glabrate. **Terminal buds** terete to slightly angled in cross-section; ovoid to ellipsoidal; 4-7 mm long; dark reddish to silvery brown; distally silvery red pubescent, sometimes ciliate only along scales margins. **Leaves** ovate to obovate; 7.5-16 cm wide; 15-23 cm long; thin or thick; chartaceous; apices broadly acute to attenuate; margins 7- to 11-lobed; lobes deltoid to lanceolate or oblong, apically entire or 1- to 4- toothed and constricted; sinuses deep, extending 1/4-1/2 distance to midribs; awns 13-49, present along margins and/or at lobe apices; bases cuneate to rounded or acute; adaxial surfaces dark green, dull, sparsely pubescent to glabrate; abaxial surfaces light or coppery green, reticulately ribbed, dull or glossy, sparsely pubescent to glabrate except for inconspicuous silvery and/or rust colored tufts of pubescence in vein axils; petioles 25-55 mm long, sparingly pubescent to glabrate, hairs like those covering abaxial midribs; stipules caducous. **Hairs of Adaxial Surfaces** like those covering abaxial surfaces. **Hairs of Abaxial Surfaces** stellate; silvery covering surfaces, silvery and/or reddish tinged in vein axils; sessile to inconspicuously stalked covering surfaces, conspicuously stalked in vein axils; scattered covering surfaces, crowded in vein axils; 6- to 8-rayed covering surfaces, 2- to 12-rayed in vein axils; rays firmly attached, 0.3-1.2 mm long, approaching longer two thirds of length in vein axils, appressed to ascending covering surfaces, ascending to erect in vein axils, curling to straight. **Hairs of Abaxial Midribs** deciduous; stellate like those of abaxial surfaces; silvery setaceous, scattered,

loosely attached, 0.5-1.5 mm long, antrorsely appressed. **Catkins** 8-10 cm long. **Mature Acorns** oblong-ovoid to oblong; 24-32 mm long; solitary or in clusters of 2 or 3; sessile or pedunculate, peduncles to 5 mm long. **Cupules** bowl- or saucer-shaped; 17-28 mm in diameter; 8-15 mm deep; enclosing 1/3-1/4 of nuts; reddish brown to silvery reddish brown; scales tightly appressed, ovate to oval, gradually broadened from rims to bases, sparsely silvery or red tomentose, margins dark red, glabrous or tomentulose, bases flattened to thickened or slightly tuberculate, callus absent or forming black speckles. **Nuts** ellipsoidal to oblong; 15-25 mm in diameter; 20-30 mm long; orange brown to striped or wholly dark brown; tomentose.

Found throughout the eastern half of the United States, with exception of Florida, Louisiana and Texas, *Q. rubra* is a late succession forest species throughout most of its range (Little, 1971). Though mostly restricted the eastern fifth of Oklahoma, disjunct stands occur along the Caney River in Rogers County, the Arkansas River in Tulsa County, and perhaps the Cimarron River in Payne County. The last report is questionable because of the possible occurrence of the southern *Q. buckleyi* with which it might be confused. In the uplands of the Ozark Plateau, this species is a dominant hardwood (Hoagland, 2000). In the Ouachita Mountains, it is frequent along upland creeks or on mesic slopes, but may also be in the dry uplands. Soils that it occupies are moist and well drained to moderately dry. Their texture ranges from the coarse colluvium of uplands to the finer alluvium of stream terraces.

Juvenile twigs are green to yellow in color whereas leaf surfaces are adaxially pink to yellowish and abaxially whitish from dense pubescence. The hairs of juvenile leaves are stellate covering the surfaces and setaceous above the veins (Hardin, 1979).

They become loose and are shed during expansion and maturation of the leaf. This shedding may be delayed until summer for the typical obovate shaped leaves in the lower canopy (Figure 40). Leaves in the upper canopy are usually elliptic to narrowly ovate with margins bearing more lobes and deeper sinuses (Figure 41). Heightened production of nuts occurs at 3–5 year intervals (Bonner, 2008).

Regeneration of the species is important ecologically and economically. Seedling survival has been shown to steadily increase along edge gradients from forest canopies to exposed fields in New Jersey (Meiners & Martinkovic, 2002), Wisconsin (Crow, 1992) and Arkansas (Spetich et al., 2002). Growth rates of seedlings from different populations have shown an inherited effect that is specific to the locality from which they were obtained (Steiner et al., 1995). A field study conducted by Garcia and coworkers (2002) near Quebec, Canada showed that increased seed germination is associated with moist soils devoid of litter, and a laboratory study revealed that seed germination was greater with higher levels of seed moisture content. Greater efficiency of nutrient uptake by planted seedlings of *Q. rubra* in proximity to sprouting oak stumps has been observed in Pennsylvania and is believed due to the effect of pre-established mycorrhizal associations (Dickie et al., 2008). Kabrick and coworkers (2007) concluded that management for regeneration of *Q. rubra* may be enhanced by partitioning landscapes into an ecological classification framework, thus, allowing for the partitioning of suitable regeneration management methods.

Quercus rubra hybridizes and intergrades with other members of Section *Lobatae* including: *Q. marilandica*, *Q. nigra*, *Q. palustris* (= *Q. x columnaris* Laughlin), *Q. phellos* (= *Q. x heterophylla* F. Michaux), and *Q. shumardii* (= *Q. x riparia* Laughlin), *Q. velutina*

(= *Q. x hawkinsii* Sudworth) (Palmer, 1942; Little, 1979; Hunt, 1989, Jensen, 1997).

Hybrids are not reported for *Q. buckleyi*, *Q. falcata*, and *Q. incana*.

The binomial *Q. borealis* Michxaux has been used for this taxon in some taxonomic treatments (Sargent, 1926; Gates, 1938; Jones, 1945; Deam, 1940) and individuals of northern red oak in Canada and the northeastern United States have been called this name for many years. The confusion can be traced to Sargent's interpretation of Linnaeus's original description of the species. Sargent (1915) believed that Linnaeus's binomial *Q. rubra* was best applied to what is now called southern red oak (*Q. falcata*). He stated that Michaux's *Q. borealis* was the correct name for the northern red oak.

However, Linnaeus' *Q. rubra* was a composite name; applied to three or four species of the red oak section but later typified as the present *Q. rubra* by Du Roi (Svenson, 1939; 1945; Little, 1979). More importantly, Michaux in his treatment of the genus in his 1817 *North American Sylva* clearly described the morphological and geographical distinctions among *Q. rubra*, *Q. borealis*, and *Q. falcata*. Subsequently systematic work has revealed that *Q. rubra* and *Q. borealis* are conspecific. McDougal and Parks (1986) demonstrated hybridization between *Q. borealis* and *Q. rubra* using flavanoid profiles from populations of each species in southern Appalachia.

In Oklahoma, Waterfall (1969) treated *Q. borealis* as a variety of *Q. rubra* and used the varietal epithet of Farwell—*borealis* (F. Michaux) Farwell. The difference between the two varieties is the shape and depth of the cupules covering the nuts. Trees with large nuts with 1/4 covered by a flat, saucer-shape cupule are var. *rubra*,

whereas smaller nuts with about 1/3 covered by a cup- or bowl-shaped cupule are var. *borealis* (Jensen, 1997).



Figure 40. Foliage (shade leaves) and acorn of *Quercus rubra* specimen collected on Gittin Down Mountain, Ozark Plateau National Wildlife Refuge, Adair County, Oklahoma.

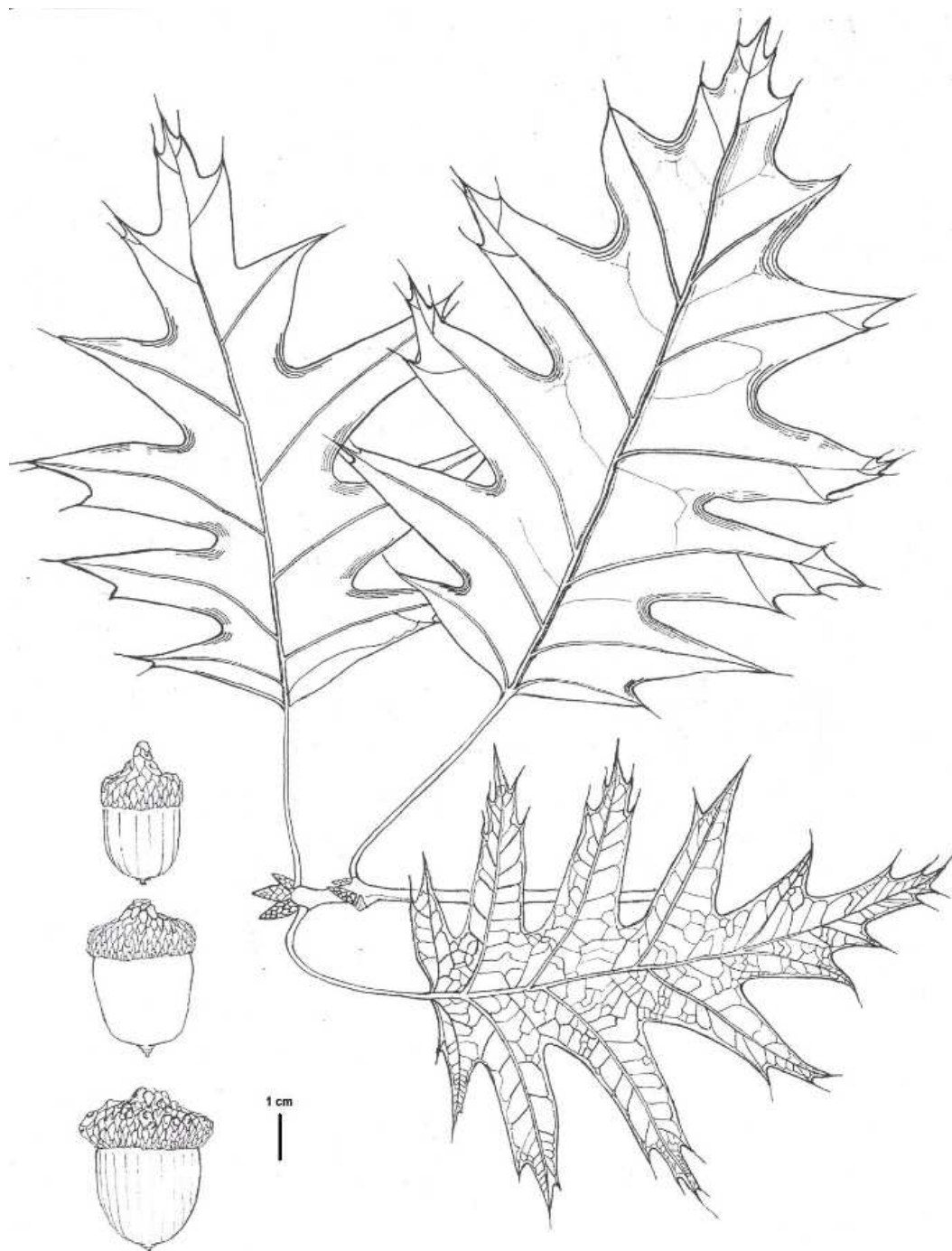


Figure 41. Foliage and acorn of *Quercus rubra* specimen collected in Spavinaw Wildlife Management Area, Delaware County, Oklahoma.

***Quercus shumardii* Buckl. Shumard Oak**

Plants trees; to 29 m tall; deciduous. **Bark of Trunks** grey to black; smooth to coarsely ridged; pink inner bark often exposed by fissures or furrows. **Primary Branches** ascending to horizontal. **Twigs** 2-3.5 mm in diameter; brown to reddish brown or gray; glabrate. **Terminal Buds** terete to 5-angled in cross-section; ovoid to ellipsoidal; 4-7 mm long; reddish brown to grayish dark brown; glabrate to tomentose on upper 1/3, scale margins frequently erose to silver tomentose. **Leaves** orbicular to obovate or ovate; 7.5-16 cm wide; 15-20 cm long; thin to thick; chartaceous; apices acute to attenuate; margins 5- to 9-lobed; lobes spatulate to obovate, apically 3- to 7- toothed and expanded; sinuses deep, extending equal to or greater than 3/4 distance to midribs; awns 15-70, present only along margin of lobe apices; bases cuneate to truncate or broadly acute; adaxial surfaces dark to light green, glossy, glabrate; abaxial surfaces light or yellow green, reticulately ribbed, glossy or dull, glabrate except for conspicuous rust colored tufts of pubescence in vein axils; petioles 20-60 mm long, glabrate, hairs like those of abaxial midribs; stipules caducous. **Hairs of Adaxial Surfaces** caducous. **Hairs of Abaxial Surfaces** stellate; reddish tinged; conspicuously stalked; crowded in vein axils; 6- to 12-rayed; rays firmly to loosely attached, 0.5-1.5 mm long, ascending to erect, tangled to curling or sparingly straight. **Hairs of Abaxial Midribs** caducous. **Catkins** 8-10 cm long. **Mature Acorns** oblong to ovoid or rarely subglobose; 15-32 mm long; solitary or paired; sessile or pedunculate, peduncles to 7 mm long. **Cupules** shallowly bowl- to saucer-shaped; 15-32 mm in diameter; 7-15 mm deep; enclosing 1/3-1/4 of nuts; reddish brown to light brown; scales tightly appressed, ovate to oval, gradually broadened from rims to bases, silvery to yellow tomentose, margins orange to

dark red, glabrous to obscured by dense tomentum, bases thickened to slightly tuberculate, callus absent to forming few black speckles. **Nuts** oblong to ellipsoidal; 20-25 mm in diameter; 25-31 mm long; light brown to brown; tomentose.

Quercus shumardii honors the Texas state geologist Benjamin Franklin Shumard (Little, 1981). Found throughout the south and central United States, it is a dominant tree of the bottomland forests in the region (Little, 1971). In Oklahoma, it typically occurs as solitary trees or small to large stands in bottomlands across the southern half of the state (Hoagland, 2000). It is especially abundant in the southeastern corner. Disjunct populations are encountered in the Wichita Mountains and Caddo Canyons (Little, 1981).

The juvenile twigs of *Q. shumardii* are green to yellow while its leaf surfaces are abaxially pink to yellowish or whitish due to dense pubescence. The surfaces of the juvenile leaves are covered with stellate hairs whereas the hairs above the veins are setaceous. These hairs become loose and shed during expansion and maturation of the leaves in early spring. The leaves are orbicular in the upper canopy (Figure 42) and obovate when growing in shade (Figure 43). The trees grow tall and stand densities are highest when the species is established on deep soils of mesic slopes, stream terraces, and bottomlands. Stand development in sheltered mesic habitats has been correlated with poor vegetative regeneration, and higher hydrolic conductance and gas exchange rates (Cavender-Bares et al., 2001). Those individuals established on shallow and dry rocky soils often exhibit a dwarfed habit and deeply furrowed and blocky scaled bark. This last feature distinguishes them from the morphologically similar upland species *Q. buckleyi* in southwestern Oklahoma (Dorr & Nixon, 1985). Those individuals that are

exceptionally tall in upland habitats often exhibit morphological intermediacy with *Q. rubra*.

Multiple varieties of *Q. shumardii* have been reported to occur in the state. Trees producing shallowly saucer-shaped cupules are considered to be variety *shumardii* (Jensen, 1997), whereas those consistently producing bowl-shaped cupules are recognized as variety *schneckii* (Britton) Sargent (Sargent, 1918). This variety is described by Sargent (1926) as occurring across the northern Gulf Coastal Plain. Variety *acerifolia* Palmer, also treated as a distinct species by Stoyhoff & W. J. Hess (1990) has been applied to a “shumard-like” oak endemic to the Ouachita Mountains of western Arkansas. There are no herbarium collections of it in Oklahoma, but might be expected to occur. It is similar to *Q. buckleyi* in habitat, leaf shape, and stature, but differs in having larger leaves, conspicuous hairs on the abaxial leaf surfaces, and dish-shaped cupules covering the nut (Jensen, 1997). The specific epithet “*acerifolia*” reflects the palmate venation that individuals of this taxon possess; a feature that is definitely not characteristic of the family or genus (Nixon, 1997; Huang et al., 1999). If this venation trait is indeed genetically determined and stabilized (Smith, 1994; White, 2005), then recognition of this taxon via comparative morphological analysis with other oak species (Hess and Stoyhoff, 1998) seems unnecessary. Palmer (1927; 1948) suspected that these individuals resulted from hybridization, but decided to name them as a variety because of their abundance.

Reported hybrids of *Q. shumardii* with other members of Section *Lobatae* include: *Q. buckleyi*, *Q. falcata* (= *Q. x joorii* Trelease), *Q. marilandica* (= *Q. x hastingsii* Sargent), *Q. nigra* (= *Q. x neopalmeri* Sudworth), *Q. palustris* (= *Q. x mutabilis* E. J.

Palmer & Steyermark), *Q. phellos* (= *Q. x moultonensis* Ashe), *Q. rubra* (= *Q. x riparia* Laughlin), and *Q. velutina* (= *Q. x discreta* Laughlin) (Little, 1979; Dorr and Nixon, 1985; Jensen, 1997).

The hybrids between *Q. shumardii* and *Q. buckleyi* occur in the Arbuckle Mountains where stream terraces and calcareous hills abut. These hybrids are a source of confusion regarding the possible absence of *Q. texana* in the state. It is a wetland species that morphologically resembles *Q. shumardii* (Dorr and Nixon, 1985), but does not occur in Oklahoma. Its principal distribution is the lower Mississippi River drainage and extreme eastern Texas. The two species differ in acorn production. Mast years for shumard acorn crops follow a 2- or 3-year cycle in contrast to the 3- or 4-year cycle of *Q. texana* (Olsen, 1974; Bonner, 2008).

Further complicating the issue of whether *Q. texana* is present in the state is the mistaken use of *Q. texana* for *Q. buckleyi* as well as the use of *Q. nuttallii* for *Q. texana* (Dorr and Nixon, 1985). E. J. Palmer's (1927) binomial *Quercus nuttallii* is considered a synonym of *Q. texana* (Dorr and Nixon, 1985; Jensen, 1997). Although Phillips (1953) and Little (1981) reported *Q. nuttallii* to occur in McCurtain County, close examination of herbarium specimens and my field work indicate that all individuals more closely resemble *Q. shumardii*, *Q. velutina*, or *Q. pagoda* rather than *Q. texana*.

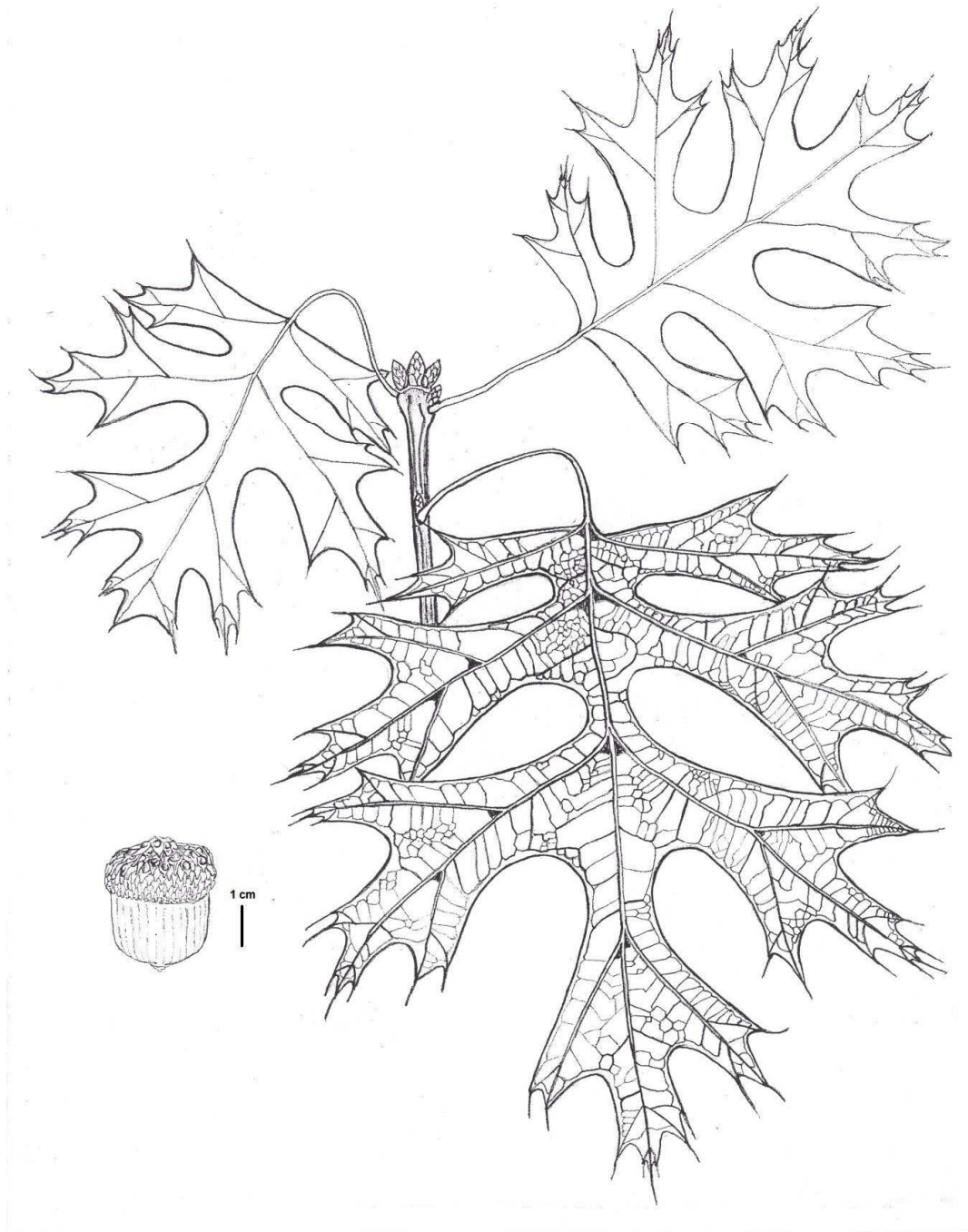


Figure 42. Foliage and acorn of *Quercus shumardii* specimen collected in Robbers Cave State Park, Latimer County, Oklahoma.

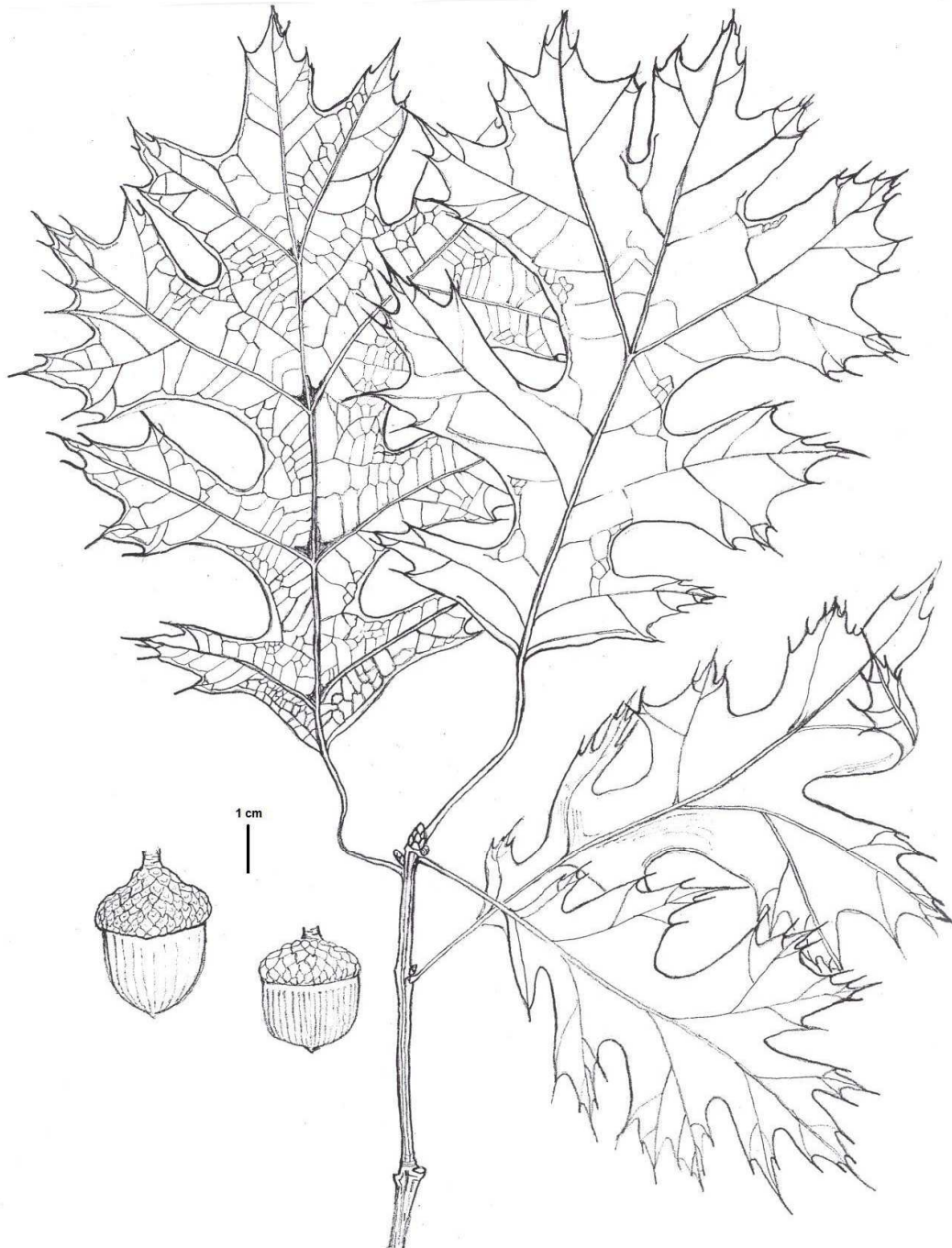


Figure 43. Foliage and acorns of *Quercus shumardii* specimen collected on Gittin Down Mountain, Ozark Plateau National Wildlife Refuge, Adair County, Oklahoma.

***Q. sinuata* Walter var. *breviloba* (Torr.) C. H. Müll. Bastard Oak**

Plants small trees or colony forming shrubs; to 5 m tall; deciduous. **Bark of Trunks** whitish gray to orange tinged, papery to scaly, inner bark not exposed. **Primary Branches** horizontal. **Twigs** 1-2 mm diameter; reddish brown to gray; glabrate to sparsely stellate; hairs silvery. **Terminal buds** terete in cross-section; globose; 1-3 mm long; reddish brown to dark brown; glabrous, sometimes merely ciliate along scale margins. **Leaves** obovate to oblanceolate or elliptic to rhomboidal; 0.8-4.4 cm wide; 4.8-18 mm long; thin to thick; coriaceous; apices rounded to obtuse to obtuse-acute; margins entire to 1- to 3-toothed, teeth undulate to crenate; sinuses shallow, extending 1/3 or less distance to midribs; bases acute to attenuate or rounded to obtuse; adaxial surfaces dark green, glossy, glabrate to sparsely pubescent; abaxial surfaces white to light green, dull, densely pubescent, however, inconspicuously so; petioles 2-8 mm long, glabrate to sparsely pubescent, hairs like those of adaxial/abaxial surfaces; stipules caducous. **Hairs of Adaxial Surfaces** absent or like those of abaxial surfaces but sparse. **Hairs of Abaxial Surfaces** persistent; stellate; silvery; crowded; sessile; 8- to 14-rayed, rays firmly attached to base, equal to or less than 0.2 mm long, closely appressed and spreading, straight to slightly curving. **Hairs of Abaxial Midribs** like those of abaxial blade surfaces but sparse. **Catkins** 1-2 cm long. **Mature Acorns** ovoid to oblong; 7-12 mm long; solitary or paired; sessile or pedunculate, peduncles to 10 mm long. **Cupules** shallowly saucer-shaped; 9-11 mm in diameter; 2.5-7 mm deep; enclosing 1/8-1/4 of nuts; golden and or silvery dark red to black; silvery; scales tightly appressed, those at cupule rims abruptly reduced in size, broadly oval to ovate, silvery

and/or golden tomentose, margins red and/or black, glabrous, bases flattened or slightly keeled near cupule bases, callus black. **Nuts** ovoid to oblong; 7-10 mm in diameter; 7-12 mm long; light brown; glabrous or distal 3/4 tomentose. Foliage and acorns of variety *breviloba* are illustrated in Figure 44.

The specific epithet "*sinuata*" refers to the leaf margins of the species and the variety "*breviloba*" to the short length of the leaves (Vines, 1982). *Quercus sinuata* var. *breviloba* is typically a colony-forming shrub that occurs on limestone and gypsum soils of south-central Oklahoma, central Texas, and eastern Mexico. In western Oklahoma, there are rare occurrences on granite as well as typical stands on limestone (Nixon and Muller, 1997). Variety *sinuata* is a large tree distributed sporadically throughout the southeastern United States and according to (Little, 1977, 1979) no longer occurs in Oklahoma. A single tree is reported (okplanttrees.okstate.edu/index.html) near Broken Bow in McCurtain County, but was not located in this study.

On the Edwards Plateau of Texas, the shrubs of this species provide a primary nesting habitat for the Black Capped Vireo (*Vireo atricapilla*), an endangered species in Texas and Oklahoma (Bailey and Thompson, 2005). The wood was used during the late 19th Century to make splints for baskets, used in the collecting of cotton, as well as the fabrication of screws for the cotton gin (Palmer, 1945).

Although Thomas Walter in his *Flora Caroliniana* (1788) did not designate a type specimen when describing *Q. sinuata* as a new species his description is substantial and clearly differentiates the taxon from the other morphologically similar species (Nixon and Muller, 1997). Historically, some taxonomists believed that the shrubs of variety *breviloba* should be recognized as a distinct species and the binomials *Q. annulata*, *Q.*

durandii, and *Q. breviloba* appear in the literature. Muller, in 1944, formally published the trinomial used in this treatment. He (1951) differentiated variety *breviloba* from Walter's description of the species by describing the leaves as "subtus subglaucus" and the acorns as "mediocribus globosis calyce subplano."

The juvenile leaves of variety *breviloba* are blackish to dark green adaxially and silvery abaxially. Most of the bulbous, and inconspicuously stalked and sessile stellate hairs of the adaxial surface are shed by late spring. The twigs transition from silvery stellate during rapid growth in the spring, to silvery and glabrous by mid summer.

E. J. Palmer (1948) reported hybrids between *Q. stellata* and both variety *breviloba* (= *Q. x mahonia* Palmer) and variety *sinuata* (= *Q. x macnabiana* Palmer). Muller (1952) reported that hybridization could not be verified between *Q. sinuata* var. *breviloba* and *Q. mohriana*, *Q. pungens*, or *Q. virginiana* despite their frequent association together. However, introgression with *Q. virginiana* in the Quartz Mountains seems likely to me, because populations of both species occur in close proximity, and the lack of definition due to visible light transmittance by the rays at 400 x magnification is evident.

Intermediate hair characters have been shown to be indicators of hybridization (Tucker, 1963; Hardin, 1979). Additional information might be gained via electron microscopy of leaf hairs. The fused rays that are otherwise only present in *Q. virginiana* might be detected (Hardin, 1979b).

This phenomenon of change in hair appearance is observed in the hybrids between variety *breviloba* and *Q. stellata* (= *Q. x mahonia*). Differences in the number, size, and aspect of ray divergence can be observed in the hybrids with the aid of a compound microscope and at least 400X magnification. The leaf blades of these

hybrids, however, typically resemble those of *Q. stellata* in outline, and thus most hybrids are misidentified as *Q. stellata*. In the Arbuckle Mountains, some hybrids grow as individuals of *Q. x mahonia* in the Arbuckle Mountains have an arborescent habit and resemble individuals of variety *sinuata*.

A few rare individuals of variety *breviloba* resemble *Q. nigra*. Intermediates with *Q. muehlenbergii* have also been seen also, but none so conspicuous as to be considered an F1 generation. Hybrids with *Q. havardii* are present in the Antelope Hills.

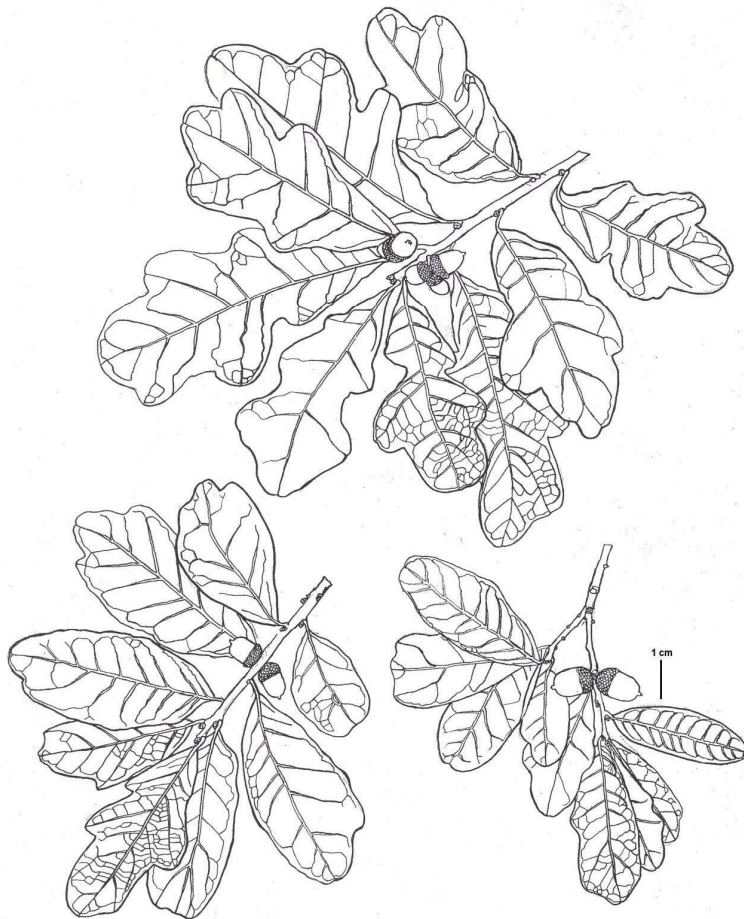


Figure 44. Foliage and acorns of *Q. sinuata* var. *breviloba* specimens collected on Bromide Hill near Sulphur, Murray County, Oklahoma.

***Quercus stellata* Wangerh. Post Oak**

Plants trees; to 25.9 m in height; deciduous. **Bark of Trunks** whitish gray; scaly; inner bark not exposed. **Primary Branches** ascending to horizontal. **Twigs** 2-6 mm diameter; sulphurous yellow; densely stellate; hairs sulphurous yellow. **Terminal buds** terete in cross-section; ovoid; 2-6 mm long; reddish brown or grayish brown; sparsely or densely silvery and/or golden to sulphurous yellow pubescent. **Leaves** obovate to elliptic or circular; 2.3-15.9 cm wide; 4.1-20.5 cm long; thick; coriaceous; apices rounded to obtuse to truncate to emarginate; margins 1- to 2-lobed; lobes semicircular to obovate or oblong to broadly spatulate, apically entire or 1- to 5- toothed and expanded; sinuses deep, extending equal to or greater than 3/4 distance to midribs; bases acute to rounded or cordate; adaxial surface dark to yellow green, scabrous to scaberulous, sparsely stellate; abaxial surface whitish green to silvery green, scabrous to scaberulous, sparsely to densely stellate; petioles 5-15 (30) mm long, densely stellate to glabrate; hairs like those of twigs or leaf surfaces. **Hairs of Adaxial Surfaces** like those of abaxial surfaces; but sparse in comparison. **Hairs of Abaxial Surfaces** persistent to deciduous; stellate; silvery; scattered to crowded; sessile to inconspicuously stalked; 4- to 12-rayed; rays firmly attached to base, 0.3-0.6 mm long, inconspicuously ascending to spreading, straight to curling; bulbous or uniseriate, silvery or golden, appressed, less than or equal to 0.1 mm long. **Hairs of Abaxial Midribs** like those of abaxial surfaces. **Catkins** 5-8 cm long. **Mature Acorns** globose to oblong; 11-21 mm long; solitary or paired; sessile or pedunculate, peduncles to 6-40 mm long. **Cupules** shallowly to deeply bowl-shaped; 9.5-18 mm in diameter; 5-12 mm deep; enclosing 1/3-2/3 of nuts; silvery to golden; scales tightly appressed, those at

cupule rims lanceolate, those at cupule bases ovate, silvery or golden tomentose, margins reddish or silvery to golden, tomentulose to obscured by dense tomentum, bases thickened and/or creased, callus black or absent. **Nuts** ovoid to oblong; 7.5-14 mm in diameter; 9.5-19 mm long; light to dark brown with blackened stripes; glabrous or distal 3/4-1/2 pubescent.

The specific epithet of *Q. stellata* reflects the dense covering of stellate hairs on the leaves and petioles. This species is distributed throughout the eastern half of the United States, with the exception of the Northeast and the southern half of Florida (Little, 1971). In Oklahoma, it occurs across the body of the state except for the extreme northwest corner and the Panhandle (Little, 1981). Trees occupy a variety of soils ranging from deep sands and sandy loams to clays. *Q. stellata* is indicative of dry, sterile, upland soils and commonly associated with *Q. marilandica* in Cross Timbers (Tyril et al., 2002), and the species accounts for nearly 64% percent of the volume of saw timber of the medium and large size classes (Stransky, 1990). This association is especially common in the uplands of the eastern deciduous forest that occur in the state. In the western part of the state, *Q. stellata* is commonly associated with *Q. havardii* (Duck and Fletcher, 1943). Small stands of taller individuals of *Q. stellata* are often encircled by clones of *Q. havardii* that fill the gap between their lower branches and the grass layer (Bruner, 1931). This phenomenon leads to frequent hybridization between the two species along Oklahoma's western border with Texas.

As illustrated in Figures 45 and 46, the leaves of *Q. stellata* are quite variable in shape even in small stands. Figure 46 illustrates how the leaves can even resemble

somewhat those of *Q. marilandica* and has been construed as possible hybridization between the two species.

Quercus stellata hybridizes with other species of Section *Quercus* in the state, with the exception of *Q. gambelli* in Cimarron County (Sargent, 1918; Muller, 1951b; Hardin, 1975; Morrison-Hill and Buck, 1980; Buck and Bidlack, 1998). These hybrids include: *Q. alba* (= *Q. x fernowii* Trelease), *Q. havardii* *Q. lyrata* (= *Q. x sterrettii* Trelease), *Q. macrocarpa* (= *Q. x guadalupensis* Sargent), *Q. margaretta* (= *Q. x drummondii* (Liebm) Nixon & Muller), *Q. mohriana*, *Q. muehlenbergii*, *Q. prinoides* (= *Q. x stelloides* Palmer), *Q. sinuata* var. *breviloba* (= *Q. x mahonii* E. J. Palmer), and *Q. virginiana* (= *Q. x harbisonii* Sargent).

Quercus x fernowii, the hybrid between *Q. stellata* and *Q. alba* is frequently encountered along the eastern edge of the state (Hardin, 1975), so much so that it is formally recognized in this treatment. It is somewhat difficult to distinguish from *Q. margaretta* because both have the oblong lobes and red twigs. *Quercus x stelloides*, the hybrid between *Q. stellata* and *Q. prinoides* is so common that herbarium collections of it are commonly misidentified. The reason for this is that most individuals resemble *Q. prinoides* except for one character— its sulphurous to silvery yellow twigs. The back crosses to *Q. stellata* are rare in occurrence but usually exhibit this color characteristic. It is likely that most individuals looking at these hybrid specimens thought they were looking at aberrant forms of *Q. prinoides*. Backcrosses to *Q. stellata* are distinguished by 3–5 crenate teeth or “finger like” lobes along the margins of the leaves instead of the typical 1 or 2.

Sargent (1918) named several varieties of *Q. stellata* that were later determined to be hybrids with *Q. havardii* (Muller, 1951). These are by far the easiest hybrids to locate in the state. Most occur along fence lines and bar ditches 2–4 miles inland from the major rivers that dissect the extreme western edge of the state. In addition, some hybrid mottes attributed to *Q. stellata* and *Q. havardii* also involve *Q. margaretta* where the three taxa occur together on Quaternary sands.

Examination of herbarium specimens deposited in the Oklahoma State University Herbarium suggest that hybridization occurs with *Q. lyrata*. Unfortunately, the suspected hybrid trees were not relocated. The barely recognizable hybrids of *Q. x guadalupensis* so closely resemble *Q. macrocarpa* that they are best treated as simply a variant of it. Identification of these individuals is really possible only in the field when individuals of *Q. macrocarpa* are nearby allowing immediate comparison of morphologies. Likewise, most individuals of *Q. x drummondii* are identified only by comparing the putative hybrids with nearby individuals of *Q. stellata* and *Q. margaretta*. Hybrids of *Q. virginiana* and *Q. stellata* are only known from the Quartz Mountains. Muller (1951b) and Palmer (1948) used the name *Q. x harbisonii* for this hybrid. Whittmore and Schaal (1991) detected the hybrid plants using chloroplast DNA.

Hybrids of *Q. stellata* and *Q. muehlenbergii* are scattered throughout the state. Buck and Bidlack (1998) used morphological characters and isozyme data to infer this relationship.

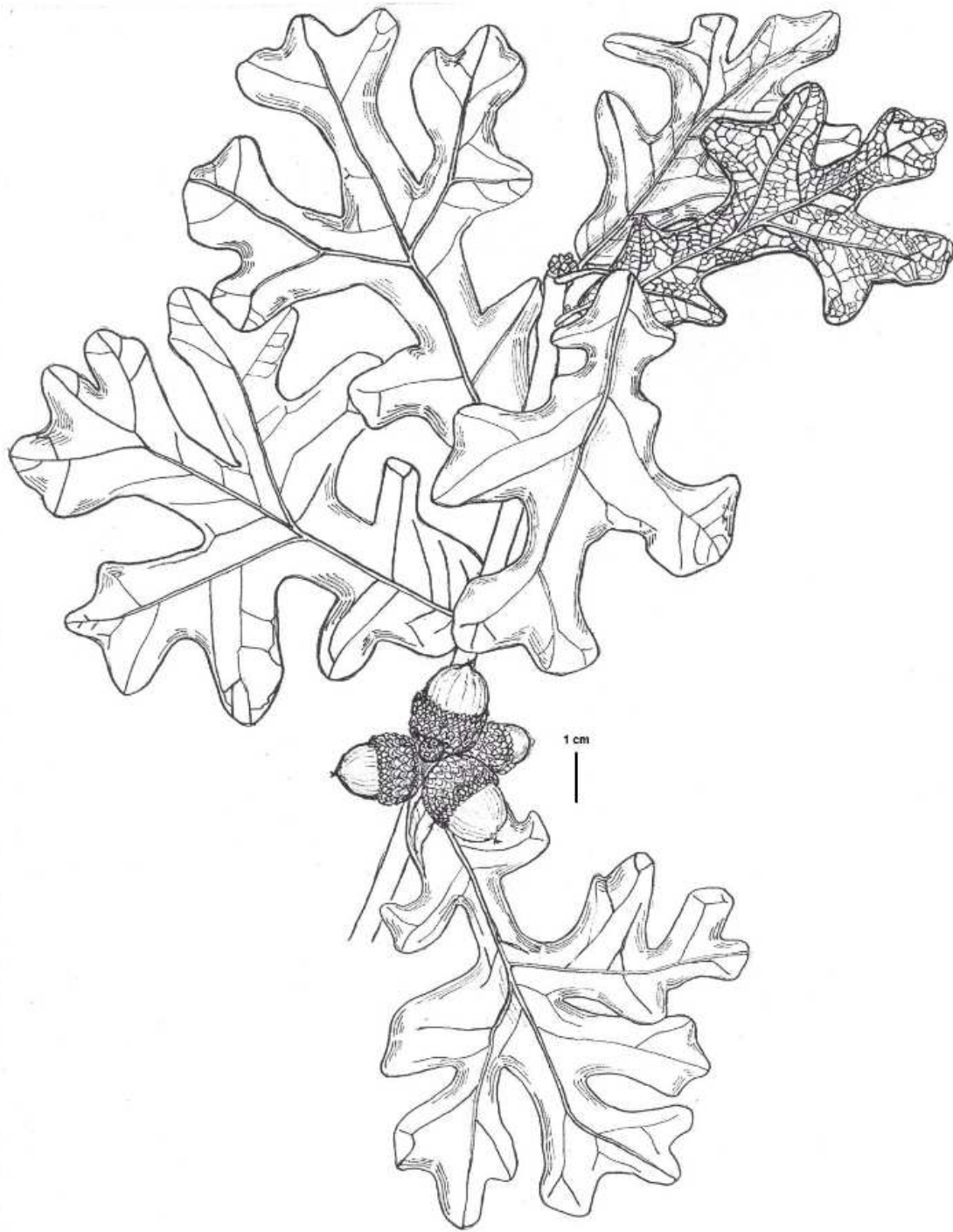


Plate 45. Foliage and acorns of *Quercus stellata* specimen collected from a sandstone butte overlooking Polecat Creek, Tulsa County, Oklahoma.

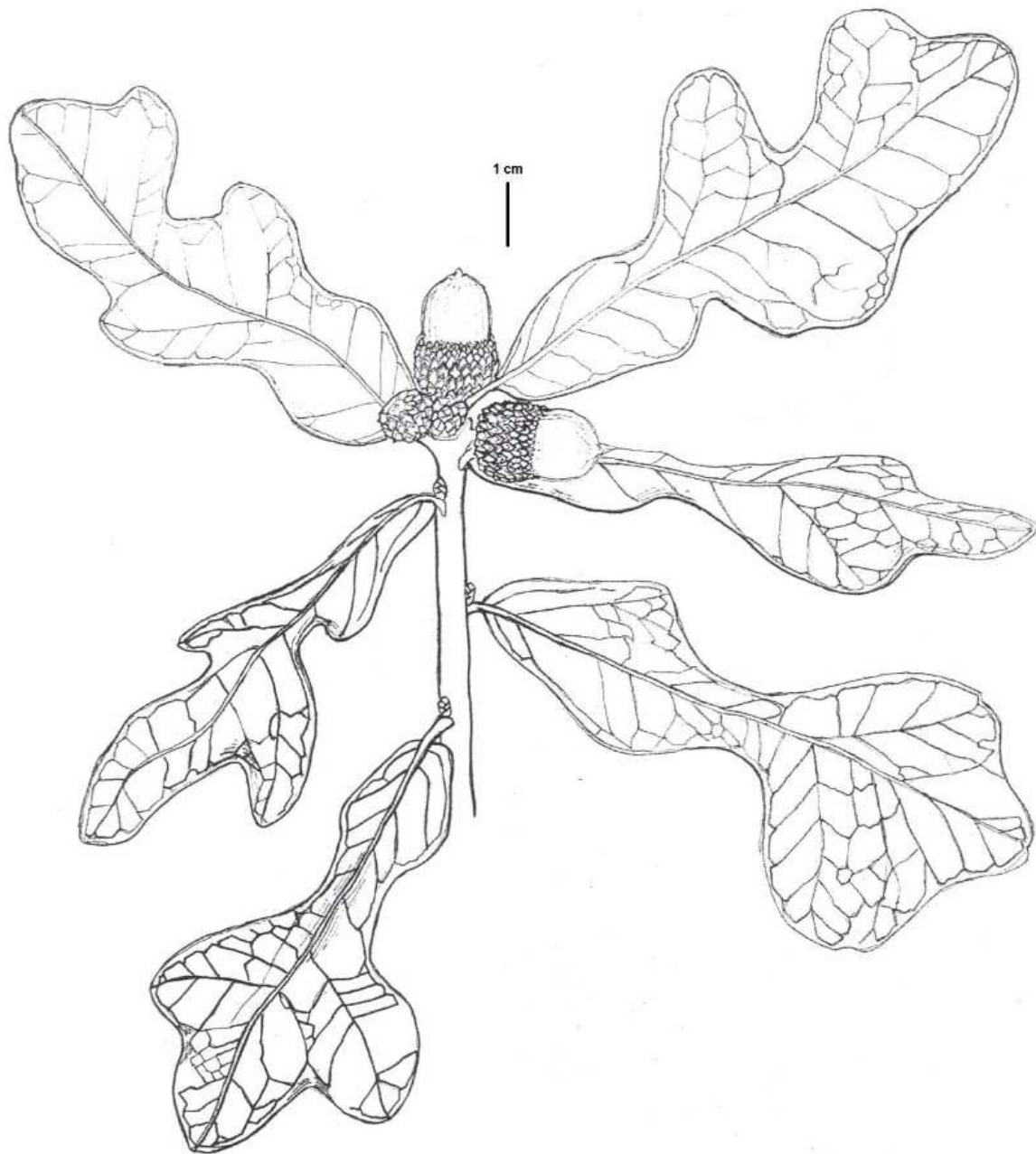


Figure 46. Foliage and acorns of *Quercus stellata* specimen photographed at the Wichita Mountains National Wildlife Refuge, Comanche County, Oklahoma.

***Quercus x stelloides* Palmer**

Plants trees or shrubs; to 7.6m in height; deciduous. **Bark of Trunks** whitish gray; papery to scaly; inner bark not exposed. **Primary Branches** ascending to horizontal. **Twigs** 2-3 mm diameter; reddish brown or sulpherous yellow; glabrate or densely stellate; hairs sulpherous yellow. **Terminal buds** terete in cross-section; sub-rotund to broadly ovoid; 1-1.5 mm long; light brown or brown or grayish brown; sparsely silvery pubescent, sometimes merely ciliate along scale margins. **Leaves** obovate to ovate, or oblanceolate to lanceolate, or oblong to elliptic; 1.4-11.5 cm wide; 3.4-19.5 cm long; thick; coriaceous; apices acute to apiculate; margins uniformly 5- to 9-toothed, teeth dentate to serrate to serrate-crenate, or 3- to 5- lobed, lobes oblong to semicircular; sinuses shallow or deep, extending less than or equal to 3/4 distance to midribs; bases truncate to cuneate; adaxial surface dark green, dull or glossy, scaberulous or wax-like, sparsely stellate to glabrate; abaxial surfaces white to light green, scaberulous to ribbed, densely to sparsely stellate; hairs inconspicuous, petioles 7-28 mm long, sparsely stellate to glabrate; hairs like those of abaxial surfaces; stipules caducous. **Hairs of Adaxial Surfaces** like those of abaxial surfaces; but usually deciduous. **Hairs of Abaxial Surfaces** persistent; stellate; silvery; sessile to inconspicuously stalked; 6- to 12-rayed; rays 0.3-1.0 mm long, appressed to ascending, straight to curling. **Catkins** 4-6 cm long. **Mature Acorns** globose to oblong; 11-28 mm long; solitary or paired; sessile or pedunculate, peduncles to 8 mm long. **Cupules** hemispheric; 12-23.5 mm in diameter; 5-12 mm deep; enclosing 1/4-1/2 of nuts; silvery; scales tightly appressed, those at cupule rims abruptly reduced in size or lanceolate, those at cupule bases deltoid to ovate, silvery tomentose, margins reddish, tomentulose to obscured by dense

tomentum, bases slightly tuberculate to creased and thickened, callus black. **Nuts** ovoid to oblong; 8-22 mm in diameter; 13-28 mm long; dark brown; glabrous to lower 3/4-1/2 tomentose. The foliage and acorns of *Q. x stelloides* are illustrated in Figures 47, 48, and 49.

Quercus x stelloides is a hybrid between *Q. stellata* and *Q. prinoides* (Little, 1979). It occurs where the two species are associated—along the edges of woodlands and forests—an association first described by Palmer (1948). Both species are characterized by their ecological occurrence in dry uplands.

This hybrid is quite common, so much so that many herbarium collections of it are commonly misidentified. The reason for this is that most individuals resemble parental *Q. prinoides* except for one character— its sulphurous to silvery yellow twigs. *Quercus prinoides* has dark red, glabrous twigs. The back crosses to *Q. stellata* are rare in occurrence but usually exhibit this color characteristic as well. It is likely that most individuals looking at these hybrid specimens thought they were looking at aberrant forms of *Q. prinoides*. Backcrosses to *Q. stellata* are distinguished by 3–5 crenate teeth or “finger like” lobes along the margins of the leaves instead of the typical 1 or 2.

Examination of herbarium specimens deposited in the Oklahoma State University Herbarium revealed four collections of *Q. x stelloides* which resembled *Q. prinoides* except for the sulphurous yellow twigs and sparse occurrence of inconspicuously ascending rays of the stellate hairs of the abaxial surfaces of the leaves. Morrison and Buck (1980) studied a population along Bird Creek in Tulsa County which was revisited several times in the 2008 and 2009 growing seasons.

In addition, three populations of hybrid plants in Payne and Noble counties were encountered. In all three populations, individuals with the sulphurous yellow, pubescent twigs were found. Likewise, in all three populations there was at least one individual located nearby that had margins with finger-like lobes or crenate teeth coupled with a single deep sinus entering the median portion of the blade. The plants collected by Palmer (# 14285) and studied by Morrison-Hill and Buck (1980) exhibited these same features. The majority of hybrids seem to backcross to *Q. prinoides* as had been reported previously (Morrison-Hill and Buck, 1980).

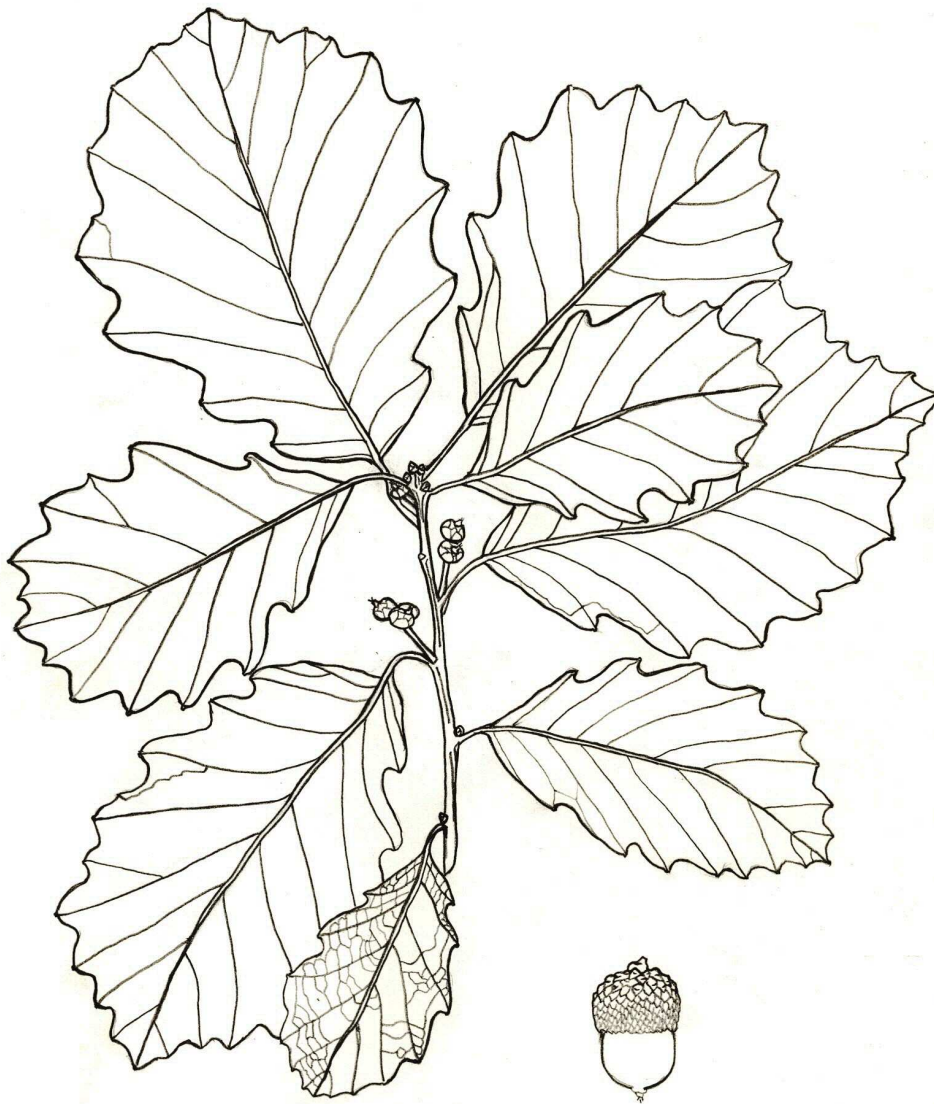


Figure 47. Foliage and acorn of *Quercus x stelloides* specimen collected in Mohawk Park, Tulsa County, Oklahoma.



Figure 48. Foliage and acorn of *Quercus x stelloides* specimen collected in Mohawk Park, Tulsa County, Oklahoma.

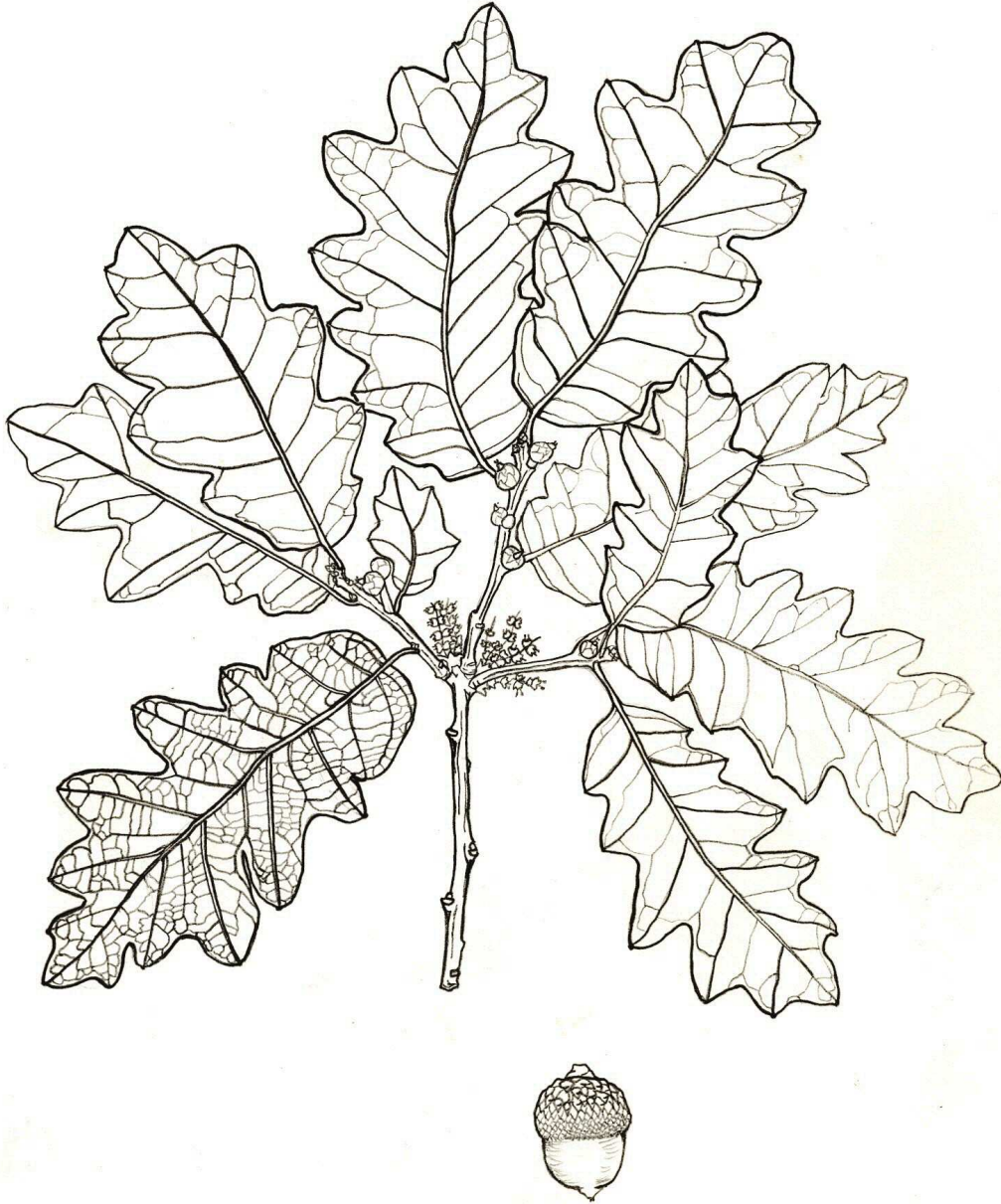


Figure 49. Foliage and acorn of *Quercus x stelloides* specimen collected in Mohawk Park, Tulsa County, Oklahoma.

***Quercus turbinella* Greene Sonoran Scrub Oak**

Plants colony forming shrubs; to 3.5 m in height; deciduous or subevergreen. **Bark of Trunks** whitish gray or brownish gray; scaly to blocky to coarsely ridged; inner bark not exposed. **Primary Branches** horizontal. **Twigs** 2-3 mm in diameter; reddish brown to sulphurous yellow; glabrate to densely stellate, hairs sulphurous yellow. **Terminal buds** terete in cross-section; globose to ovoid; 1.5-3 mm long; yellowish brown to brown; sparsely silvery pubescent, sometimes only pubescent along scale margins. **Leaves** elliptic to ovate or obovate or oblong; 1-2.3 cm wide; 10-5.2 cm long; coriaceous to subcartilaginous, sometimes thin and indurate; apices mucronate to acute or obtuse to rounded; margins entire to undulate or uniformly 2- to 7-toothed, teeth undulate-serrate to undulate-spinose or dentate to crenate; sinuses shallow or deep, extending equal to or less than 1/2 distance to midribs; awns 0-11, present at apices of teeth and/or lobes; bases rounded to cordate or truncate; adaxial blades surfaces silvery green to blue or light gray, scabrous, sparsely stellate; abaxial blades surfaces whitish yellow to silvery blue, scabrous to coarsely scabrous; petioles 2-10 mm long, densely stellate; hairs those of abaxial surfaces. **Hairs of Adaxial Surfaces** like those of abaxial surfaces; but sparse and frequently reduced in size. **Hairs of Abaxial Surfaces** persistent; stellate, silvery; sessile to inconspicuously stalked; 6- to 18-rayed; rays equal to or less than 1.0 mm long, appressed to ascending, mostly curling to crimped or sparingly straight; bulbous; golden to red; appressed; less than or equal to 0.1 mm long. **Catkins** 2-3 cm long. **Mature Acorns** ovoid to ellipsoidal; 11-20 mm long; solitary or paired; sessile or pedunculate, peduncles to 30 mm long. **Cupules** urceolate to hemispheric; 8-12 mm in diameter; 6-8 mm deep; enclosing 1/5-1/2 of nuts; silvery white; scales tightly

appressed, sometimes slightly reflexed at cupule rims, those at cupule rims reduced in size or lanceolate, those at cupule bases deltoid to ovate, silvery to golden silvery tomentose, margins orange to reddish brown in distal 1/2-1/3, glabrous to tomentulose, bases slightly tuberculate to keeled or thickened to flattened, callus black or rust colored at maturity. **Nuts** ovoid to ellipsoidal; 8-11 mm in diameter; 10-18mm long; light brown; glabrous or distal 1/2 pubescent.

Quercus turbinella is distributed in the foothills and canyons of the Rocky Mountains and Chihuahuan and Sonoran deserts of the United States (Little, 1979; Nixon and Muller, 1997). Individuals of this species may be hundreds of miles from other species with which it forms hybrids (Tucker, 1961). In Oklahoma, only two individuals have been encountered and collected in the Black Mesa area of extreme northwestern Cimarron County. They occurred in well drained and highly weathered soil of the Cimarron River. The foliage and acorns of *Q. turbinella* are illustrated in Figure 50.

Like *Q. virginiana*, the spinose margin of the leaves is the feature that distinguishes it from most other species in Section *Quercus* in North America. The Navajo believed that the leaves of the species could ward off evil from dwellings that were covered with its branches. The Kiowa are believed to have concocted a drink from the roots of the species (Moerman, 1998).

Hybrids with other members of Section *Quercus* are reported (Tucker, 1961; Nixon and Muller, 1997). The most notable example is its hybridization with *Q. gambelii* to form the nothospecies *Q. x pauciloba* previously called *Q. undulata* by many taxonomists (Tucker, 1961, 1963, 1970, 1971; Tucker et al., 1961).

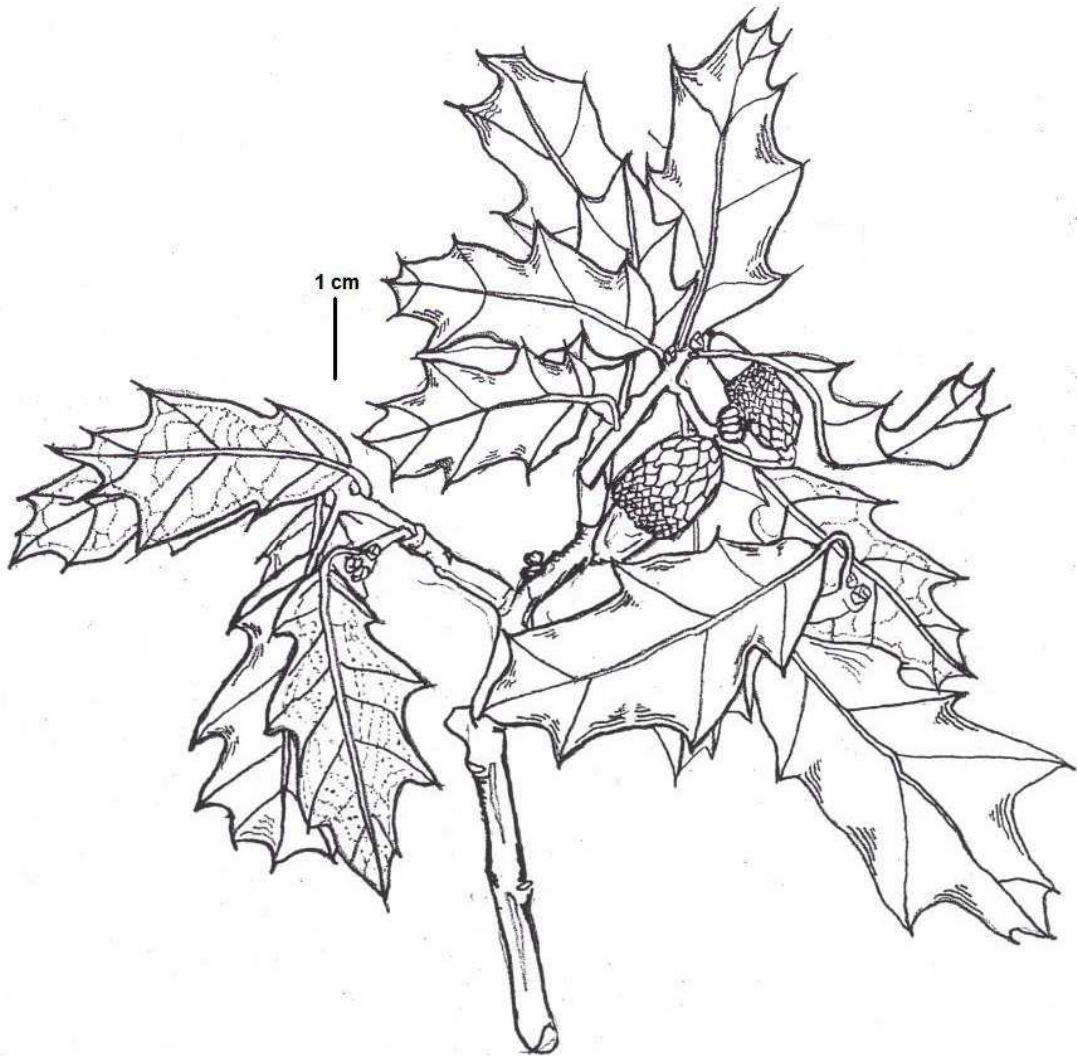


Figure 50. Foliage and acorns of *Quercus turbinella* specimen collected in Tesequite Canyon, Cimarron County, Oklahoma.

***Quercus velutina* Lam. Black Oak**

Plants trees; 5-28 m tall; deciduous. **Bark of Trunks** dark brown to black; coarsely ridged to blocky; pink inner bark occasionally exposed by fissures or furrows. **Primary Branches** ascending to horizontal. **Twigs** 3-8 mm in diameter; reddish brown to sulphurous yellow; glabrate to densely stellate; hairs silvery or sulphurous yellow to rusty red. **Terminal Buds** 5-angled in cross-section; ovoid to ellipsoidal or subconical; 5-13 mm long; silvery to yellow or reddish brown; densely silvery to sulphurous yellow and/or red pubescent, sometimes with a glabrous band parallel to margin. **Leaves** orbicular to obovate or ovate; 6-21.4 cm wide; 7.1-31 cm long; thick; chartaceous to coriaceous; apices broadly acute to attenuate; margins 5- to 9-lobed; lobes deltoid to lanceolate or oblong to spatulate, apically 1- to 5- toothed and constricted or rarely expanded; sinuses extending equal to or greater than 3/4 distance to midribs; 15-50 awns, present along margins and/or along lobe apices; bases truncate to cuneate or obtuse to sparingly acute; adaxial surfaces dark green, glossy, densely pubescent or glabrate except for inconspicuous hairs along midribs or becoming glabrous; abaxial surfaces light green to golden, glossy, densely pubescent or densely pubescent along midribs or glabrate except for minute tufts of silvery to rust colored pubescence in vein axils; petioles 25-75 mm long, sparsely to densely pubescent; hairs like those of leaf surfaces. **Hairs of Adaxial Surfaces** stellate; silvery to golden tinged; scattered; inconspicuously stalked; 4- to 12-rayed; rays firmly attached to base or stalk, 0.1-0.4 mm long; appressed to erect; curling to straight. **Hairs of Abaxial Surfaces** stellate; silvery to golden tinged covering surfaces, silvery to reddish tinged in vein axils; scattered covering surfaces, crowded in vein axils; sessile to minutely stalked covering

surfaces, conspicuously stalked in vein axils; 4- to 8-rayed covering surfaces, 4- to 12-rayed in vein axils; rays loosely attached to base, firmly attached to stalk, 0.2-1.5 mm long, approaching longer 1/3 of range in vein axils, appressed to erect, approaching erect in vein axils, curling to sparingly straight; bulbous-filiform-scurfy; golden or intermittently golden and silvery; crowded along vasculature or absent; 0.1-0.5 mm long; appearing adnate to leaf surface; filiform. **Hairs of Abaxial Midribs** glabrate or hairs like those of abaxial surfaces; golden to silvery setaceous, crowded to scattered or absent, 0.1-1.5 mm long, antrorsely appressed; straight. **Catkins** 5-8 cm long. **Mature Acorns** turbinate to ovoid; 10-21 mm long; solitary or in clusters of 2 or 3; sessile or pedunculate, peduncles to 8 mm long. **Cupules** bowl-shaped; 11.5-22 mm in diameter; 8-16.5 mm deep; enclosing 1/2 of nuts; reddish brown to orange-brown; scales loosely appressed, recurved towards rim, oblong to ovate to oval, densely to sparsely silvery or reddish tomentose, margins red to dark orange colored, glabrous or obscured by tomentum, bases thickened. **Nuts** globose to ovoid; 9-18 mm in diameter; 9-20 mm long; light brown to brown; tomentose. Foliage and acorns of *Q. velutina* are illustrated in Figures 51, 52, and 53.

The specific epithet of *Quercus velutina* reflects the dense pubescence of the abaxial surfaces of the leaves, i.e., a velvety feeling. The species is found throughout the eastern half of the United States, with its western most limits in Oklahoma (Little, 1971; Jensen 1997). In Oklahoma, trees are encountered primarily in the eastern half of the state. Disjunct populations occur in the the Wichita Mountains and Caddo Canyons (Hoagland, 2000; Tyrl et al., 2002). Soils occupied by this species range from deep sandy loams of stream terraces and bottomlands to stony loams of upper slopes and

ridges. It is a dominant taxon in parts of the Cross Timbers and in the oak- hickory association of the eastern deciduous forest.

The juvenile twigs of *Q. velutina* are green to yellow, whereas the young leaves are abaxially dark red to whitish or sulphurous yellow due to the dense pubescence present. The hairs covering the surfaces of the juvenile leaves are stellate, whereas those above the veins are setaceous. During expansion and maturation of the leaves, the surface hairs leaves exposed to full sunlight are typically shed completely or sparsely persistent in the vein axils during expansion, whereas shaded leaves retain them (Figures 47 and 48). As might be expected, trees growing in dense shade may produce primarily shade leaves which unfortunately can lead to misidentification of the species (Trelease, 1924; Sargent, 1926; Philips et al., 1953). These shade leaves are generally obovate to orbicular and bear numerous silver to reddish stalked hairs that are persistent, but easily rubbed off when the surfaces are touched. In contrast, the sun leaves are ovate to elliptic and glabrate. The twigs from which shade leaves arise produce red to orange apical buds with sparse pubescent in contrast to the densely pubescent, silver apical buds of the twigs giving rise to sun leaves.

Profuse acorn production occurs at 2- or 3-year intervals (Bonner, 2008). The acorns are shed in the fall and are quickly consumed by birds, animals, and insects. Mature twigs are consumed to some degree by mule and white-tail deer (Tyrl et al., 2002). Individuals have been observed to have root systems 10 to 20 years older than the shoot portion plant due to repeated mechanical damage followed by vegetative regeneration (Sander and Clark, 1971; Sander, 1990b).

Palmer (1948), Little (1979), and Jensen (1997) reported hybrids of *Q. velutina* with other members of Section *Lobatae* in Oklahoma including: *Q. incana* (= *Q. x podophylla* Trelease), *Q. falcata* [= *Q. x willdenowiana* (Dippel) Zamble], *Q. marilandica* (= *Q. x bushii* Sarg.), *Q. nigra* (= *Q. x demareii* Ashe), *Q. palustris* (= *Q. x vaga* E. J. Palmer & Steyermark), *Q. phellos* (= *Q. x filialis* Little), *Q. rubra* (= *Q. x hawkinsii* Sudworth; Figure 54), and *Q. shumardii* (= *Q. x discreta* Laughlin). Individuals of *Q. velutina* exhibiting aberrant leaf lobe shapes were treated as forms by Trelease (1924). These forms are probably due to hybridization with these other species and not deserving of formal taxonomic recognition. Extensive hybridization with *Q. marilandica* is observed at the summits of Rich and Winding Stair Mountains in the Ouachita Mountain National Forest in LeFlore County. These hybrids are morphologically quite different from other hybrid plants between the two species; presumably because of the droughty, harsh conditions that occur on the tops of these two mountains.



Figure 51. Foliage and acorn of *Quercus velutina* specimen collected in Siloam Springs State Park, Delaware County, Oklahoma.



Figure 52. Foliage and acorn of *Quercus velutina* specimens collected along the Spring River, Ottawa County, Oklahoma.

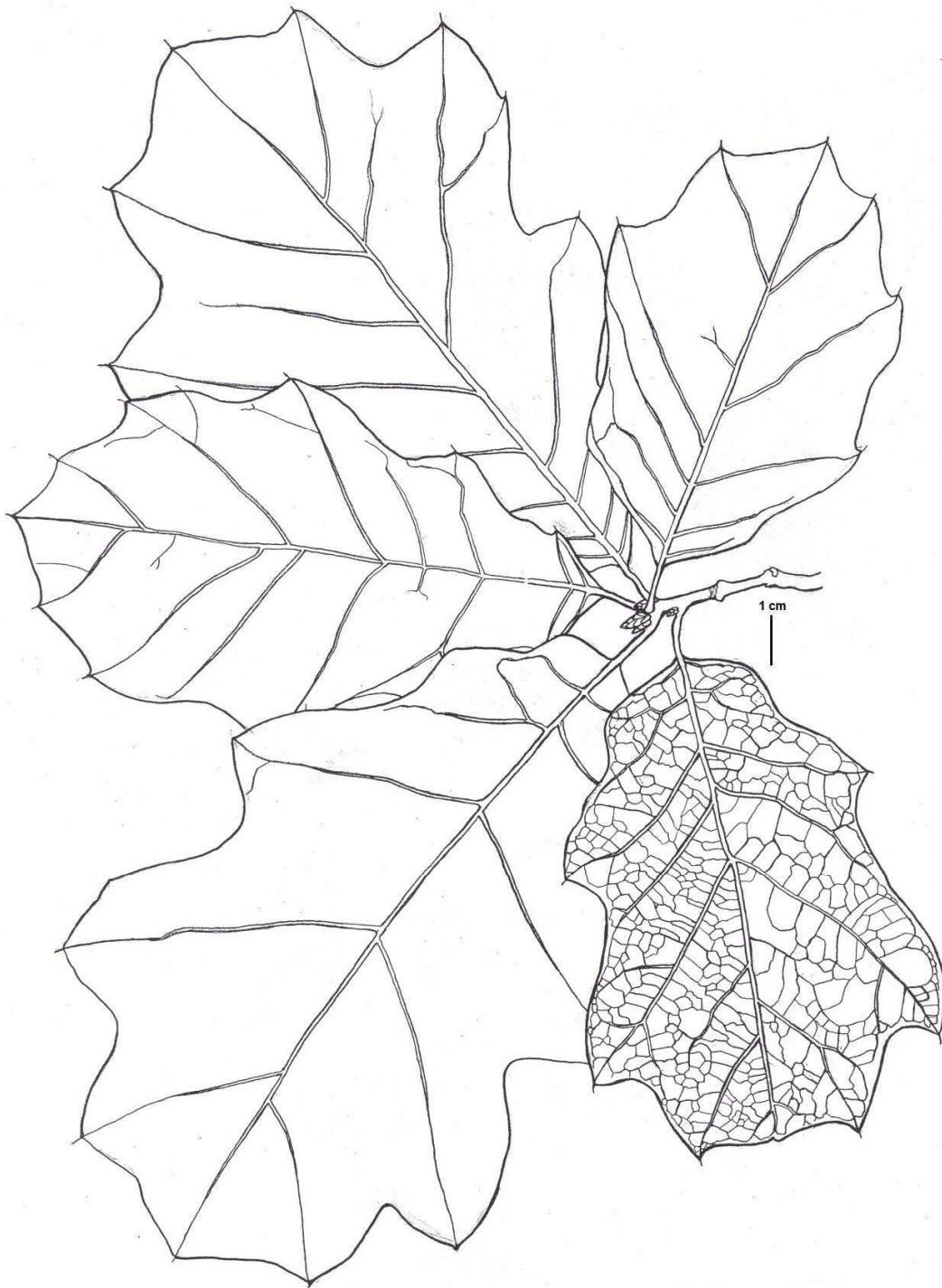


Figure 53. Foliage (shade leaves) of *Q. velutina* specimen collected in Oologah Wildlife Management Area, Rogers County, Oklahoma.



Figure 54. Foliage and acorn of putative hybrid between *Quercus velutina* and *Quercus marilandica* (= *Q. x bushii*) collected near Horsethief Creek, Payne County, Oklahoma.

***Quercus virginiana* P. Mill.**

Live Oak

Plants trees or colony forming shrubs; to 10 m in height; evergreen. **Bark of Trunks** brown to black; smooth to scaly to coarsely ridged; inner bark not exposed. **Primary Branches** horizontal to descending. **Twigs** 1-3 mm diameter; gray; densely to sparsely stellate; hairs silvery or inconspicuously sulpherous yellow. **Terminal buds** terete in cross-section; ovoid; 1-3 mm long; reddish to dark brown; sparsely pubescent to glabrate, sometimes merely ciliate along scale margins. **Leaves** elliptic to oblong or obovate to ovate; 1.2-5.3 mm wide; 2.2-9.7 cm long; thin or thick; coriaceous; apices rounded to obtuse to acute to mucronate; margins revolute and entire to revolute and denticulate; awns absent or as many as 13, present at apex and/or margins; bases rounded to cuneate or acute; adaxial surfaces dark green, glossy, sparsely pubescent to glabrate; abaxial surfaces white or whitish green, dull, densely pubescent but inconspicuously so; petioles 1-12.5 mm long; densely pubescent, hairs like those of abaxial surfaces; stipules caducous. **Hairs of Adaxial Surfaces** like those of abaxial surfaces; but sparse. **Hairs of Abaxial Surfaces** persistent; stellate; silvery; sessile; 8- to 16-rayed; rays equal to or less than 0.2 mm long, appressed, straight to slightly curving. **Catkins** 2-4 cm long. **Mature Acorns** ellipsoidal to ellipsoidal-fusiform to broadly fusiform; 18-32 mm long; solitary or in clusters of 2 or 3; sessile or pedunculate, peduncles to 30 mm long. **Cupules** deeply bowl- to cone-shaped; 9-13 mm in diameter; 10-13 mm deep; enclosing 1/7-1/4 of nuts; silvery white; scales tightly appressed, those at cupule rims lanceolate, those at cupule bases deltoid to oval, silvery tomentose, margins red to reddish brown in distal 1/2-1/4, glabrous or tomentulose, bases slightly

tuberculate to keeled or thickened, callus black at maturity. **Nuts** ellipsoidal to fusiform; 8-15 mm in diameter; 17-30 mm long; dark brown with blackened stripes; glabrous.

The foliage and acorns of *Q. virginiana* are illustrated in Figure 55.

The specific epithet of *Quercus virginiana* refers to the state of Virginia where it has been cultivated since early colonial times (Olsen, 1974). It is a climax forest species along the Atlantic and Gulf Coastal Plain of the southeastern United States (Little 1971; Nixon and Muller, 1997). In the southern Great Plains it is a dominant woodland species of xeric uplands and mountain canyons (Carey, 1992). In Oklahoma it is present only in the Wichita and Quartz Mountains (Little, 1981), where is associated with *Q. stellata*, *Q. marilandica* var. *asheii*, *Q. sinuata* var. *breviloba*, *Celtis reticulata*, and *Juniperus virginiana* (Hoagland, 2000). Muller (1952) described it as associating with *Q. mohriana* and *Q. vaseyana* in dry uplands in Texas. In Oklahoma, it occupies soils that are clay to sandy loams, especially influenced by granite parent material (Lamar, 1979). In the Southern Plains, establishment of clones of *Q. virginiana* via rhizomes appears to predominate because the consumption of the nuts by herbivores hinders establishment via seed (Russel and Fowler, 1999). Acorns are a preferred forage item for wild turkey, deer, bears, song birds, and feral hogs (Carey, 1992).

This species of oak was prized by the early federal government as prime ship building material for the naval fleet (Austin, 2004). Pioneers of the Southeast would harvest the young tuberous roots of seedling to make “French fries” (Nixon and Muller, 1997). The Seminole used the bark as an analgesic, antirheumatic, dermatological, and orthopedic aid (Moerman, 1998).

Little (1979) and Nixon and Muller (1997) reported hybridization of *Quercus virginiana* with *Q. stellata* (= *Q. x harbisonii* Sargent), *Q. macrocarpa* (= *Q. x burnetensis* Little), and *Q. lyrata* (= *Q. x comptonae* Sargent), albeit the last hybrid occurs in Texas not Oklahoma. Harms (1990) reported a hybrid with *Q. sinuate*; however, stands of *Q. sinuata* var. *breviloba* and *Q. virginiana* in the Quartz Mountains exhibit no hybridization (Muller, 1952). Based on my observations of these oaks, I concur with Muller's conclusion; hybridization of *Q. virginiana* apparently only involves *Q. stellata* in the mountains.

Taxonomists differ in their opinions as to whether the live oaks of southwestern Oklahoma and central Texas are one or two species. Small (1901) classified the trees in this region that exhibited turbinate-shaped cupules and fusiform-shaped nuts as *Q. fusiformis*. Waterfall (1969) and Little (1971, 1981) disagreed and treated these oaks as a variety of *Q. virginiana*. Nixon and Muller (1997) in their treatment of the Section for the *Flora of North America* agreed with Small and recognized the western *Q. fusiformis* as distinct from the southeastern *Q. virginiana*. They contended that they are different because individuals in Oklahoma and Texas reproduce clonally, occur on stony outcrops or gravelly-sands, and produce "acute acorns". In an earlier work, Nixon (1961) reported that shrub forms of *Q. virginiana* are frequently dispersed between the taller individuals throughout the Gulf Coastal forests. In contrast, the tallest individuals in Oklahoma grow in the moist and shaded areas of the Quartz Mountains. Also, some of these individuals produce acorns that prematurely germinate upon storage demonstrating viability. Most individuals produce broadly ovoid to oblong shaped acorns

in addition to fusiform ones, albeit it is possible that these characters may be related to hybridization with *Q. stellata*.

When comparing herbarium sheets of collections made along the Gulf Coast to those made in Oklahoma and Texas, morphological differences of the leaves and fruits are not always apparent. Unfortunately, the original description of *Q. virginiana* offered by Miller (1768) says only that the acorns are "...smaller than those of the common oak". Nevertheless, populations in Oklahoma and Texas should be considered races of the species. Cavender-Bares (2007) showed that the differences in cold tolerance between two populations of *Q. virginiana* from North Carolina and central Florida is inherited and reflects adaptations of populations following migration. Diseases have been shown to alter regional diversity in this species rather abruptly. Selective pressures exerted by fungal blight, *Ceratocystis fagacearum*, altered allozyme frequencies in a Texas population 20 years post infection (McDonald et al., 1998).



Figure 50. Foliage and acorn of *Quercus virginiana* specimen collected in Quartz Mountain State Park, Kiowa county, Oklahoma.

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VITA

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Thesis: FLORISTIC INVESTIGATIONS OF THE OZARK PLATEAU NATIONAL WILDLIFE REFUGE AND THE GENUS *QUERCUS* IN OKLAHOMA

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Scope of Study and Results:

The work presented in this thesis comprises two parts. The first part is a floristic survey of three tracts of the Ozark Plateau National Wildlife Refuge located in the Boston Mountains ecoregion in Adair County. The second part is a taxonomic treatment of the genus *Quercus* in Oklahoma which is to be incorporated in the forthcoming *Flora of Oklahoma*. Results of these studies are summarized in the following paragraphs.

In a three-year (2007–2009) inventory of the Gittin Down Mountain, Liver and Varmint tracts of the Ozark Plateau National Wildlife Refuge in Adair County, Oklahoma, 392 species in 275 genera and 85 families were encountered. Three hundred sixty (91.8%) of the species were native to North America. Constituting 23.6% of the flora, the Asteraceae and Poaceae were the largest families. *Quercus*, *Carex*, *Desmodium*, and *Dichanthelium* were the largest genera present. Eighty-two species were new records for Adair County. Species designated threatened or endangered by The Endangered Species Program of the United States Fish & Wildlife Service were not discovered. Thirteen species designated rare (S1 or S2) by the Oklahoma Natural Heritage Inventory were documented as present.

Herbarium and field studies conducted from 2006 to 2009 revealed that the oak (*Quercus*) flora of Oklahoma comprises 24 species, 3 varieties, 4 named hybrids and numerous putative hybrid individuals. Sixty-five morphological characters were examined and scored in order to generate taxon descriptions. The range of variation for each character exhibited by Oklahoma individuals was determined and incorporated in the species descriptions. Nomenclatural, taxonomic, and ecological notes were added as appropriate to complement the morphological descriptions. A dichotomous key for the identification of the 24 species and 4 named hybrids was constructed.

Adviser's Approval: Ronald J. Tyrl _____