THE QUERCUS UNDULATA TORREY COMPLEX IN OKLAHOMA

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Abstract: A reexamination of voucher specimens used for the Flora of Oklahoma project revealed those of *Quercus gambelii* Nuttall, are hybrids likely between it and four other species, *Q. grisea, Q. macrocarpa, Q. muehlenbergii, and Q. turbinella*. The specimens are from or near Tesequite Canyon in Cimarron County, Oklahoma, however, none of parent species occur in the region. Evidence from morphological analysis and prior studies supports their hybrid origin, with a proposed case for their presence based on historical events.

Introduction

My preliminary study of disjunct populations of *Quercus muehlenbergii* Engelmann, in the Four Canyon Nature Preserve, of Ellis County, Oklahoma, (2024), suggested they were of hybrid origin but, at that point, of uncertain parentage. While examining herbarium specimens for the potential source, I found a putative hybrid of *Q. gambelii* × *muehlenbergii* on deposit in the Oklahoma State University herbarium (OKLA) from Woodward County, about 60km northeast of the study site,

In examining the specimen, I found two distinct types of trichomes occurring on the abaxial leaf surface: fasciculate with 1-4 rays and stellate appressed with 6-12 rays. A study of foliar trichomes of species of White Oaks, Thomson and Mohlenbrock (1979) showed this combination to be indicative of *Q. gambelii* × *muehlenbergii.*

This hybridization was first proposed by John Tucker in his seminal work on western white oak hybridization between *Q. gambelii* and six other white oaks, *Q. arizonica* Sargent, *Q. grisea* Liebmann, *Q. havardii* Rydberg, *Q. mohriana* Buckley, *Q. muehlenbergii* Engelmann and *Q. turbinella* Greene, he titled *The Quercus Undulata Complex* (1961). In subsequent studies (1961a,b,1963, 1970, 1971) he provided evidence that *Q. undulata* Torrey was not a species but the hybrid intermediates of species of the Complex where they are or have been sympatric. His preliminary report (1961) contained range maps of the Complex in which its eastern-most extent reached into northeast New Mexico and southeast Colorado. He cited no evidence of the Complex reaching Oklahoma

While Tucker did not provide evidence of the cross in any of his following studies, adding trichome types to the evidence, I was able to report putative populations of *Q. muehlenbergii* introgressed by *Q. gambelii* in the Capitan Mountains of New Mexico, Thomson (2022). Finding the same evidence on the Woodward County specimen was the first indication to me that the Complex may have made its way into the State. Consequently, I decided to conduct a SEINet search (2023) for other records of *Q. gambelii* in Oklahoma. The search returned 17 specimens on deposit in four herbaria. All were collected in or near a place known as Tesequite Canyon about 241 km west of the Preserve in the Panhandle

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County of Cimarron.

Two of the specimens from the search were on deposit in the herbariums of the University of Oklahoma (OKL) and Oklahoma State University (OKLA). I examined them on site and determined them to be *Q. gambelii* × *muehlenbergii* and Q. *mohriana* respectively. Both are members of the Complex.

The Woodward specimen, collected by E. J. Little, Jr (36016: OKLA), is a reference specimen for the Flora of Oklahoma project. With this finding I decided to examine the other specimens and obtained loans for their study. After an initial review, I found five to be duplicates, or erroneously reported for Oklahoma. The 12 specimens in the initial study are listed by herbarium in Table 1.

Members of The Complex, except for *Q. arizonica*, *Q. grisea* and *Q. turbinella*, are included in the Flora of Oklahoma (2023), but the Complex, as such, has not been reported for the State. Because of my previous work with the members of the Complex (2022) I decided to suspend my search for the source of the Preserve hybrids and look further into the oaks of the Tesequite Canyon area. This study purports to show the *Quercus Undulata Complex* in Oklahoma and its influence on the white oak flora.

Methods

As noted above, the specimens of this study were located in the herbaria of the University of Oklahoma and the Oklahoma State University and by searching on-line for records of *Q. gambelii* in Oklahoma on deposit in the herbaria of the Southwest Biodiversity Organization, SEINet (2023), and The Texas and Oklahoma Consortium of Herbaria, TORCH (2023).

Since the specimens all had the determination of *Q. gambelii*, I examined them for three features known to be characteristic for the species: contour of the leaf margin (lobed), twig markings (transverse fissures) and trichome types (fasciculate with 1-4 rays). The features are described further below and pictured in Figs. 1, 2, and 3.

Table 1. Specimens of the study by herbarium
*reference specimen for the Flora of Oklahoma Project

Herbarium	Barcode Number	Collector	Collector Number
BRIT	568108	D. Demaree	13389
BRIT	567802	J & C Taylor	25159
BRIT	567803	P. Nighswonger	1518
BRIT	567804	J & C Taylor	14179-A
BRIT	567805	J & C Taylor	14179-D
BRIT	567806	U.T. Waterfall	7951*
BRIT	567807	U.T. Waterfall	7950
BRIT	745842	P. Nighswonger	1624
MOR	0061510	P. Nighswonger	1669
MOR	0061511	J. Taylor	25197
OKL	52095	E. Little Jr	36016*
OKLA	00573	J & C Taylor	6895

Figure 1. Specimen of *Quercus gambelii* on deposit at the Baylor University Herbarium (BAYLU) depicting lobed contour margins. The specimen was collected and determined by John Tucker. Image from SEINet.

Leaf margin contour. The distinctly lobed leaf margins of *Q. gambelii* are depicted in Fig. 1. Lobes vary from 4-8 with sinuses often extending to the midpoint of the leaf or deeper, Nixon and Mueller (1997).

Twig markings. Transverse fissures are openings in the periderm developing at right angles to the long axis of twigs. This feature was used by Tucker and Mueller (1958) to distinguish *Q. gambelii* from *Q. margaretta* in a reexamination of the origin of *Q. margaretta* and *Q. drummondii*. A photo of a specimen collected by John Tucker (2775-6: DAV) with transverse fissures is shown in Fig. 2.

Figure 2. Twig of *Q. gambelii* showing transverse fissures. Photo by Dan Potter, University of California, Davis. Used with permission.

Trichome type(s). As cited above, fasciculate trichomes with 1-4 rays, are definitive for Gambel's Oak, Fig. 3, plate 20.

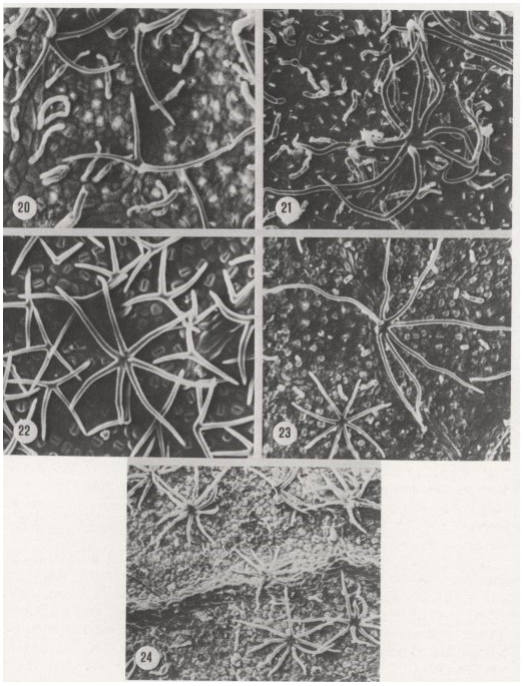

Figure 3. SEMs of *Q. gambelii* trichomes, plate 20, 220x, *Q. grisea* trichomes plate 21, 130x, *Q. gambelii* × *muehlenbergii* plate 22, 220x and *Q. muehlenbergii* plate 24, 130x. Thomson and Mohlenbrock 1979. Used with permission.

Each of the specimens was examined for the definitive characteristics. Margin contour was determined and recorded, twigs were examined for transverse fissures and recorded on a presence/absence basis and the abaxial leaf surface was examined for trichome types. The types were observed using a compound light microscope at 120x and recorded with nomenclature following Hardin (1979).

Study Site

The specimens of this study were collected in an area of Cimarron County, Oklahoma known as Tesequite Canyon (36.9050N -102.8890W) situated at an elevation of 1281ft (930.4m). The Canyon, under private ownership, is near the Black Mesa region about 6 miles (9.7 km) south of Kenton, Oklahoma (36. 5411N -102.5748W). The Mesa, featuring the highest point in Oklahoma at an elevation of 4973 ft. (1516 m), is part of the Western High Plains, a geological feature that begins in Colorado, extends southeasterly into New Mexico and ends in the Oklahoma Panhandle County of Cimarron. To the east the physiography grades into prairie grassland, Johnson and Luza (2008). The climate is semiarid with annual precipitation averaging 17.26 in. (43.84 cm) Oklahoma Climatological Survey (2010).

Results

My initial review revealed forms of the characteristics inconsistent with those of *Q. gambelii.* Some had one or two of the characters but then in combination with characters of other species e.g., lobed leaf margins of *Q. gambelii* with stellate trichomes typical of *Q.muehlenbergii*. Several had none of the *Q. gambelii* features and none displayed all three diagnostic characters. Table 2 shows the characters observed and the species associated with them. The species except for *Q. macrocarpa* are members of the Complex.

Leaf contours were of various forms; entire, undulate, dentate, spiny toothed, lobed and deeply lobed. I found trichomes of the *Q. gambelii* type on five of the specimens, but no fissures on any of them. One specimen, had markings on twigs where one would expect fissures. Whether these are undeveloped fissures or something else I did not pursue. The following are descriptions of the findings by herbarium barcode below and summarized in Table 3.

On five of the specimens I found no features of *Q.gambelii.* Their features were, however, consistent with those of known species. BRIT 568108 and 567802, OKLA 00573 with entire margins and stellate erect trichomes with 6-10 wavy rays that, I believe, are typical of *Q. mohriana.* Leaves of BRIT 567803 and 567804 have undulate and dentate margins respectively and bear stellate erect trichomes with 8-10 straight

Table 2. Trichomes types, Leaf Margin Contour and Presence/Absence of Transverse Fissures displayed by of Species in this study.

Trichome type (s)	Fasciculate with 1-4 rays	Stellate With 8-10 straight rays	Fasciculate erect; stellate appressed; bulbous	Stellate with 6-8 whitish rays	Stellate appressed with 6-12 (16) rays	Minute stellate; Reddish or yellowish glandular	Fasciculate with 6-8 wavy rays
Leaf Margin Contour	Lobed with 4-6 sinuses reaching up to ½ distance to midrib	Undulate with 2-3 rounded teeth per side	Lobed, deepest sinuses below mid-leaf	Entire or 1-3 teeth per side	Dentate, 6-14 mucronate teeth per side	Undulate with 3-5 spinose teeth per side	Entire or Dentate with mucronate teeth
Transverse Fissures	Present	Absent	Absent	Absent	Absent	Absent	Absent

Table 3. Specimen features with annotation. *Presence of transverse markings.

Specimen	Original Determination	Trichome Type(s)	Leaf Contour	Presence/Absence Of Transverse Fissures	Annotation
BRIT 568108	Q. gambelii	Stellate, erect with 6-10 wavy rays	Entire	Absent	Q. mohriana
BRIT 567802	Q. gambelii	Stellate, erect with 6-10 wavy rays	Entire	Absent	Q. mohriana
BRIT 567803	Q. gambelii	Stellate, Stipitate with 6-8 straight rays	Undulate	Absent	Q. havardii
BRIT 567804	Q. gambelii	Stellate, Stipitate with 6-8 straight rays	Five Shallow Lobes	Absent	Q. havardii
BRIT 567805	Q. gambelii	Fasciculate with 6-10 wavy rays; Reddish, Simple	Four Spinose Teeth	Absent	Q. turbinella × grisea
BRIT 567806	Q. gambelii	Fasciculate; rays 1- 4 and stellate-appressed; rays 6-12	Dentate	Transverse Markings*	Q. gambelii × muehlenbergii
BRIT 567807	Q. gambelii	Stellate erect; Fasciculate; 6-8 rays; bulbous; Uniserrate; pigmented	Lobed	Absent	Q. gambelii × macrocarpa
BRIT 745842	Q. gambelii	Fasciculate, rays 1-4; minute; stellate	Six Spinose Teeth	Absent	Q. gambelii × turbinella
MOR 00061510	Q. gambelii	Fasciculate, rays 1-4; Stellate-appressed; rays 6-12	Dentate	Absent	Q. gambelii × muehlenbergii
MOR 00061511	Q. gambelii	Fasciculate, rays 1-4; minute stellate	Five Spinose Teeth	Absent	Q. gambelii × turbinella
OKL 52095	Q. gambelii	Fasciculate; 1-4 rays; Stellate-appressed; 6-12 rays	Dentate	Absent	Q. gambelii × muehlenbergii
OKLA 00573	Q. gambelii	Stellate, non-appressed with 6-10 wavy rays	Entire	Absent	Q. mohriana

rays associated with *Q. havardii*.

The remaining specimens displayed characters of two species. Leaves of MOR 0061510, OKL 52095 and BRIT 56806 have dentate margins and trichomes of two types, 1-4 rayed fasciculate and stellate appressed with 6-12 rays suggesting the combination of *Q. gambelii* × *muehlenbergii*. Leaves of BRIT 745842 and MOR 005111 have margins with spinose teeth and trichomes that are fasciculate with 1-4 rays as well as minute, stellate appressed which I believe are of indicitive of *Q. gambelii* × *turbinella*. The combination is also referred to as Quercus × pauciloba Rydb. (pro sp.), (Bull. N.Y. Bot. Gard. 2:215.1901.).

The leaves of BRIT 57807 produced a combination of trichomes typical of Bur Oak; stellate, fasciculate with 6-8 rays and bulbous, Thomson and Mohlenbrock (1979). The specimen has distinctly lobed leaves with sinuses extending more than half way to the midrib. It is also the specimen bearing the transverse markings noted above. Trichomes typical of *Q. gambelii* were not found. The trichome combination together with features of leaf and twig suggested *Q. gambelii* × *macrocarpa*.

Eleven of the twelve Tesequite Canyon specimens of Table 3 have characteristics of the Undulata Complex: five are species, three of *Q. mohriana* and two of *Q. havardii;* six are putative hybrids, three of *Q. gambelii* × *Q. muehlengbergii,* two of *Q. gambelii* × *Q. turbinella* and one of *Q. turbinella* × *grisea.* The 12th specimen, a suspected hybrid between *Q. gambelii* and *Q. macrocarpa,* is not a member of the Undulate Complex per Tucker. I found no suspected hybrids involving *Q. mohriana* or *Q. havardii.*

I initially annotated BRIT 567805 as *Q. turbinella* but based on further review believe it to be a hybrid of *Q. turbinella* and *Q. grisea* as it bears spinose teeth and fasciculate trichomes of the type produced by *Q. grisea* leaves as shown in Fig. 3, plate 21 and Fig. 4. Present also are reddish pigmented, simple hairs found on *Q. turbinella* which may become yellowish or amber upon drying. Leaves of *Q. turbinella* typically produce minute stellate hairs as well, but these were not present on the specimen.

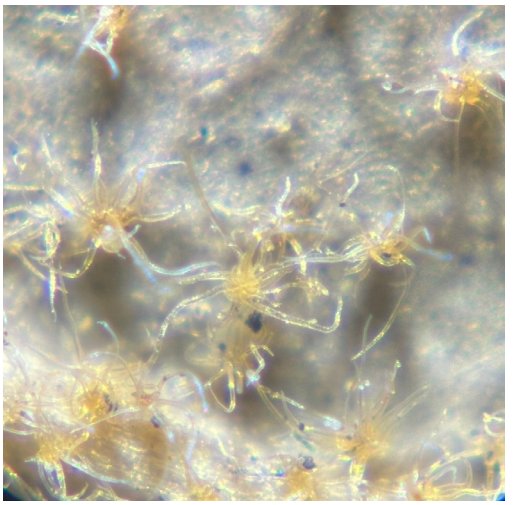

Figure 4. Photo through a compound light microscope of Q. grisea trichomes from a Tesequite Canyon Specimen at 120x

Because seven of the twelve Tesequite Canyon records were putative hybrids, I made a further search for records of the presumed parental species in Oklahoma. For *Q. turbinella* and *Q. grisea,* the search returned three records of *Q. turbinella*, J&C Taylor (14179D: BRIT), and Lowry (4000, 4001: OKLA) and two of *Q. grisea,* Demaree (13395: NYBG) and McGrath (10317: OKLA) all from Tesequite Canyon. All but the Demaree specimen were on site or on loan and were examined. The *Q. turbinella* records I believe are *Q. turbinella* × *grisea.* The specimens bear spinose teeth typical of *Q. turbinella* but trichomes of *Q. grisea*. Fig. 3 plate 21 shows *Q. grisea* trichomes from the 1979 paper. Fig. 4 is a photo of trichomes of *Q. turbinella* × *grisea* from Lowry (4001: OKLA). In both figures the trichomes are fasciculate with 6-10 wavy rays. Trichomes of *Q. turbinella* are of two types, minute stellate, and simple, Nixon and Mueller in the Flora of North America (1997). The stellate type of *Q. turbinella* were not observed in these specimens but the simple hairs were.

The McGrath specimen was examined and found to possess features typical of *Q. mohri-*

ana, however, the Demaree specimen was not examined on site, but from its observable features, via SEINet, I believe them to be of *Q. mohriana* also.

I widened the search for *Q. grisea,* and *Q. turbinella* to the counties of Colorado, New Mexico and Texas bordering Cimarron County. For *Q. grisea,* six records were returned from Union County New Mexico, two of Q. *gambelii* × *grisea*, Tucker (3249-9, 3254-4: UTEP) and four of *Q. grisea,* Demarcee (13396: NYBG), Zimmerman, Jr (1987-09-17: NMC), Castetter (1940-09-26: UNM) and Schiebot (2005-06-09: GREE: GREE). Twelve of *Q. grisea* were recorded in Baca County, Colorado, including one nearest Oklahoma by Tucker (2848-10: BYU). All Colorado records are about 19 km north of the study site. None was found in Dallam County, Texas.

Tucker (1961b) did not indicate the presence of *Q. turbinella* in Oklahoma. His records show occurrence as far east as central Colorado and New Mexico, but none in eastern New Mexico or Oklahoma. However, as noted above, its *Q. gambelii* hybrid, *Q.* × pauciloba, Tucker (2847-18: FLD), was collected in Baca County, CO and Union County, NM, Stevens (17310: KANU). The specimens from BRIT (745842) and MOR (0061511) from the study area bear characters of *Q.* × *pauciloba.* Together with the two specimens of Lowry (4000, 4001: OKLA), *Q. turbinella* × *Q. grisea,* these add further to the evidence of past influence of *Q. turbinella* near and in the State. Although the Flora of Oklahoma includes *Q. gambelii*, I could not confirm it in species form

Table 4. The species and putative hybrids of the Undulata Complex, in Oklahoma. Proposed in this study*.

Specimen	Original Determination	Trichome Type(s)	Leaf Contour	Presence/Absence Of Transverse Fissures	Annotation
BRIT 568108	Q. gambelii	Stellate, erect with 6-10 wavy rays	Entire	Absent	Q. mohriana
BRIT 567802	Q. gambelii	Stellate, erect with 6-10 wavy rays	Entire	Absent	Q. mohriana
BRIT 567803	Q. gambelii	Stellate, Stipitate with 6-8 straight rays	Undulate	Absent	Q. havardii
BRIT 567804	Q. gambelii	Stellate, Stipitate with 6-8 straight rays	Five Shallow Lobes	Absent	Q. havardii
BRIT 567805	Q. gambelii	Fasciculate with 6-10 wavy rays; Reddish, Simple	Four Spinose Teeth	Absent	Q. turbinella × grisea
BRIT 567806	Q. gambelii	Fasciculate; rays 1- 4 and stellate-appressed; rays 6-12	Dentate	Transverse Markings*	Q. gambelii × muehlenbergii
BRIT 567807	Q. gambelii	Stellate erect; Fasciculate; 6-8 rays; bulbous; Uniserrate; pigmented	Lobed	Absent	Q. gambelii × macrocarpa

from the specimens examined in this study.

Characteristics of two species of the Complex not included in the Flora, *Q. grisea* and *Q. turbinella*, were found on two of the specimens; BRIT 567805 (*Q. turbinella* × *grisea)* and BRIT 745842 (*Q. turbinella* × *gambelii)* have leaves with spinose teeth typical of *Q. turbinella* and BRIT 567805 the fasciculate trichomes of *Q. grisea. Quercus macrocarpa* appears to have contributed to the Complex as *Q. gambelii* × *macrocarpa.* No evidence of the seventh member of the Complex per Tucker, *Q. arizonica,* was found. The Oklahoma species and putative hybrids of the Complex with their Oklahoma locations are listed in Table 4. Except for *Q. gambelii* × *macrocarpa* the presumed hybrids are intermediates of the Complex.

Discussion

None of the potential parents of the hybrids occur in Cimarron County. *Quercus macrocarpa* and *Q. muehlenbergii* do occur in Oklahoma, but their nearest records, (Ertreeb 1570 and 1557: OKLA respectively), are in Ellis County 241 km east of the study site. *Quercus gambelii* is noted as occurring in Cimarron County in The Flora of Oklahoma (2024) and by Little in Forest Trees of Oklahoma (2010), but as evidenced above, believed to be in hybrid form only. The search for *Q. turbinella* returned no records from Baca County, or Dallam County, but a record was found (Stevens 17310: KANU) in Union County near the town of Moses, located about 5 km west of the Oklahoma border. While no records of either species were recorded from Cimarron County, their presence in putative hybrid form, *Q. turbinella* × *Q. grisea* and *Q. turbinella* × *gambelii* and the proximity of present day records, suggests their occurrence at some time.

In the absence of co-occurrence, how then to account for the combination of characters possessed by the putative hybrids of Table 4?

Tucker found this situation in his study of The *Quercus Undulata* Complex. To explain, he postulated that migrations occurring during pluvial periods of the Pleistocene allowed for range expansion and sympatry. He further posited that during this time of co-occurrence hybridization and introgression occurred between Gambel's Oak, the six other members of the Complex, and to a more limited extent, some of them with one another where they co-occurred. As the climate became cooler and dryer, traits obtained through the interactions allowed for some to adapt. Today, he believed, we find descendants of those ancient plants bearing signs of their hybrid ancestry and often in areas where the parent species no longer grow.

Similarly, in a study of introgressed populations of *Q. macrocarpa* by *Q. gambelii* in South Dakota, Wyoming and Union County New Mexico, Tucker and Maze (1966) concluded that at one time Bur Oak grew considerably west of its present-day range. To account for hybrids where parent species are not extant, Maze (1968) also posited that the migration occurred during pluvial periods of the Pleistocene. This, he believed, allowed for sympatry and hybridization. Subsequently, as the climate became cooler and drier, conditions favored the hybrids but not the parents.

Finding a putative cross of *Q. macrocarpa* with *Q. gambelii,* in Tesequite Canyon where Bur Oak is not extant, adds to Maze's assertion of an ancient migration. Furthermore, the soils of the Tesequite Canyon area date to the Pleistocene, Johnson and Luza (2008); a supporting element if *Q. macrocarpa* were to occur in the study area during its westward expansion as Tucker and Maze proposed. Because this is a second documented occurrence of *Q. macrocarpa* interacting with a member of the Complex, I believe it should be considered part of it albeit one of local influence. As cited above, Thomson (2022) introgressed populations of *Q. muehlenbergii* by *Q. gambelii* and *Q. muehlenbergii* by *Q. grisea* in disjunct populations of the Capitan Mountains of New Mexico also suggest an ancient range expansion for the Complex.

Tucker found *Q. mohriana* third most active in hybridization, after *Q. gambelii* and *Q. grisea*. As reported above I found three records of the species among the study specimens but with no evidence of hybridization. A SEINet search

(2023) returned 32 records of *Q. mohriana* from Cimarron County, all near to or in Tesequite Canyon. I have examined 20 of those on deposit at OKL and OKLA and again found no indication of hybridization. With a member of the Complex as active in hybridization as Tucker found, I think it surprising. I have not pursued any cause for the absence of interaction in this study, but Tucker reported this situation also with *Q. mohriana* in the Colorado and New Mexico populations (1961).

Quercus havardii is well known in western Oklahoma as a shinnery oak. In a study of shinnery in Oklahoma, Wiedeman and Penfound (1960) mapped the species by county. Their records do not cite any occurrences of *Q. havardii* from Cimarron County, however, a SEIN search for the species (2024) returned eight occurrences from the county including the two from BRIT cited above. None of the other six specimens displayed observable features to suggest they are hybrids of the Complex.

The obvious outlier among the 12 records is *Q. gambelii* × *macrocarpa.* While not a component of the Complex as described by Tucker, finding the putative hybrid in Cimarron County suggests *Q. macrocarpa* once occurred here and appears to have contributed locally to the Complex via *Q. gambelii* as Maze posited it had with *Q. gambelii* in Union County, New Mexico and South Dakota.

From the specimens of this study, I was not able to determine *Q. gambelii* as the source for the aberrant features of the Preserve Oaks, Thomson (2024). Neither was I able to confirm its occurrence in typical species form in Oklahoma. However, it and other members of the Complex in their introgressed forms can be confirmed as occurring in Oklahoma and have left their indelible mark. Lacking extant parental species to account for the hybrids, I am left to assume that these hybrids occurring in Oklahoma today, are also descendants of an ancient time of sympatry. Today they stand as a testiment to resilence in a time of climate change.

What began as a search for features of a putative parent of the Preserve hybrids resulted in evidence for the presence of the Undulata Complex in Oklahoma. The findings not only build upon Tucker's work but change our understanding of the composition of the White Oak Flora in western Oklahoma.

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