STUDIES IN THE QUERCUS UNDULATA COMPLEX
I. A PRELIMINARY STATEMENT[1]

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ABSTRACT

TUCKER, JOHN M. (U. California, Davis.) Studies in the Quercus undulata complex. I. A preliminary statement. Amer. Jour. Bot. 48(3): 202–208. Illus. 1961.—The taxonomic history of *Quercus undulata*, a highly variable, problematic complex of the Southwest, is discussed. Conservatively treated as a single species, it comprises a wide range of forms which at one extreme approach *Q. gambelii* morphologically, and, at the other, *Q. grisea*, *Q. turbinella*, and other species. The postulate was made that *Q. undulata* had arisen through hybridization between these very different oaks. Field observations and preliminary study of numerous population samples confirm this postulate. (Detailed morphological analyses are in progress.) Seven species have apparently been involved—*Q. gambelii* (the "common denominator" of the complex) has hybridized in different parts of its range with one or another of the following: *Q. arizonica*, *Q. turbinella*, *Q. havardii*, *Q. muehlenbergii*, *Q. mohriana*, and *Q. grisea*. The latter 6 species are discussed individually, and the extent to which each contributes to the complex, and the area in which this occurs, are indicated.

DURING the century and more that has passed since its naming, *Quercus undulata* Torr. has been one of the most problematic oaks, taxonomically, in the western United States. On the one hand, it has been treated as a single polymorphic species; on the other, as an aggregate of many species, but rarely—until recent years—in a fashion satisfactory to the field taxonomist. Briefly, its taxonomic history is as follows. The name is based on a collection by Edwin P. James, naturalist with an expedition to the Rocky Mountains in 1819–1820, under the command of Major S. H. Long, U. S. Topographic Engineers. The type locality given by Torrey was: "sources of the Canadian [River], and the Rocky Mountains" (1828, p. 248).

Nearly 50 years after its naming, and after a number of other species had been described from the Southwest, George Engelmann published a memoir on the oaks of the United States (1876). Engelmann's observations on the interrelationships of several white oaks of the Southwest, including *Q. undulata*, went directly to the crux of the problem, but his conclusions laid the groundwork for subsequent taxonomic confusion. Citing an area on the Arkansas River near Cañon City, Colorado, as the "classical locality" of "the common Rocky Mountain scrub oak" (*Q. gambelii* Nutt.), he observed how, within a small localized area, the latter occurred with a number of other well-marked forms, each different from the rest. Several of these (*Q. undulata*, among others) had long been known as distinct species. The presence of numerous intermediate forms, however, clearly united them all, in Engelmann's view, "as forms of one single extremely polymorphous species" but, Engelmann continued in perplexity, "If one oak behaves thus, why not others? Thrown into a sea of doubt, what can guide us to a correct knowledge?" *Quercus undulata* was the name he applied to the complex as a whole (since this was the earliest name to be applied to any of the oaks involved), the other forms being treated as varieties of it. However, in addition to the various forms actually present in the vicinity of Cañon City, Engelmann also included under *Q. undulata*, at least tentatively, other oaks of the Southwest which do not occur in Colorado and which are not closely connected with *Q. gambelii* or the *undulata* complex as it is now known, namely, *Q. drummondii* Liebm., of central Texas, and *Q. oblongifolia* Torr. of southern Arizona (Engelmann, 1876, p. 382). Later, he added *Q. sinuata* var. *breviloba* (Torr.) C. H. Mull. (as var. *breviloba* of *Q. undulata*), another oak of central Texas, but excluded Q. *oblongifolia* (1877, pp. 392–393).

Engelmann's unduly conservative classification of these white oaks was paralleled, in large part, by the treatment of Sargent (1895), which differed mainly in maintaining *Q. gambelii* and *Q. undulata* as distinct species. In retrospect, Sargent's treatment of the latter complex is clearly unsatisfactory, although it must be acknowledged that we have vastly more knowledge about the oaks of the Southwest today than he had in the early 1890's. It was probably inevitable that a reaction should come about before long, and come about it did! In 1901

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Field work for this study was carried out during 1955–56, the Dept. of Biology, University of New Mexico, Albuquerque, serving as a base of operations. Thanks are due Prof. E. F. Castetter, then Chairman of the Department, for assistance and provision of facilities.

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Rydberg published a study of the oaks of the Rockies and the Southwest, outspokenly critical of Sargent's treatment of *Q. gambelii* and the *Q. undulata* complex. *Quercus gambelii*, as treated by Sargent, was regarded by Rydberg as comprising no less than 9 species.[2] The various forms included under *Q. undulata* by Sargent were regarded by Rydberg as comprising 7 species[2]. *Quercus pauciloba*, a "new species" described by Rydberg in this study, is also referable to the *Q. undulata* complex, and subsequently five additional binomials have been applied to various forms in the complex by other authors.

Thus, until recent years, the botanist casually concerned with identifying white oaks of the southern Rocky Mountains has floundered in a morass of taxonomic confusion. Confronted on the one hand with Sargent's ultraconservative treatment, and on the other with the finely "split" entities of Rydberg and others (some of which have been perpetuated in all but the more recent manuals of the Rockies and the Southwest), he not infrequently has given up in complete frustration. Today, however, taxonomic treatments which steer a middle course between these 2 extremes are not lacking in regional floras (Muller, 1951a,b), although until fairly recent years such treatments had appeared only in less readily accessible research papers (Muller, 1944, p. 446). It is in this latter sense that *Q. undulata* is considered here. If one follows such a middle course and sets aside those taxa now generally treated as distinct species (but which Engelmann linked to *Q. undulata* as varieties: *Q. gambelii, Q. grisea, Q. oblongifolia, Q. turbinella,* and *Q. drummondii), Q. undulata* is still a highly polymorphic, far-flung complex.

[2] *Quercus gambelii,* as treated by Sargent (1895), was regarded by Rydberg (1901) as comprising the following species: *Q. eastwoodiae* Rydb., Bull. N.Y. Bot. Gard. 2:210. pl. 28, fig. 2. 1901. *Q. gambelii* Nutt., Jour. Acad. Phila. n.s. 1:179. 1848. *Q. gunnisonii* (Torr.) Rydb., Bull. N.Y. Bot. Gard. 2:206. 1901. *Q. leptophylla* Rydb., Bull. N.Y. Bot. Gard. 2:205. pl. 26, fig. 1, 2. 1901. *Q. nitescens* Rydb., Bull. N.Y. Bot. Gard. 2:207. pl. 27, fig. 1. 1901. *Q. novomexicana* (A.DC.) Rydb., Bull. N.Y. Bot. Gard. 2:208. 1901. *Q. submollis* Rydb., Bull. N.Y. Bot. Gard. 2:202. pl. 25, fig. 1. 1901. *Q. utahensis* (A.DC.) Rydb., Bull. N.Y. Bot. Gard. 2:202. 1901. and *Q. vreelandii* Rydb., Bull. N.Y. Bot. Gard. 2:204. pl. 25, fig. 3. 1901.

Quercus undulata, as treated by Sargent, was regarded by Rydberg as comprising the following species: *Q. fendleri* Liebm., Overs. Danske Vidensk. Selsk., Forhandl. 1854:170. *Q. grisea* Liebm., Overs. Danske Vidensk. Selsk., Forhandl. 1854: 171. *Q. obtusifolia* (A.DC.) Rydb., Bull. N.Y. Bot. Gard. 2:213. 1901. *Q. pungens* Liebm., Overs. Danske Vidensk. Selsk., Forhandl. 1854:171. *Q. turbinella* Greene, Ill. West. Amer. Oaks 37. 1889. *Q. undulata* Torr., Ann. Lyceum N.Y. 2:248. pl. 4. 1828. *Q. venustula* Greene, Ill.. West. Amer. Oaks 2:69. pl. 32. 1890. Also referable to the *Q. undulata* complex are: *Q. pauciloba* Rydb., Bull. N.Y. Bot. Gard. 2:215. pl. 30, fig. 2. 1901. *Q. rydbergiana* Cockerell, Torreya 3:7. 1903. *Q. confusa* Woot. and Standl., Contrib. U.S. Nat. Herb. 16: 116. 1913. *Q. media* Woot. and Standl., Contrib. U.S. Nat. Herb. 16:116. 1913. *Q. subobtusifolia* A. Camus, Bull. Soc. Bot. France 81:816. 1934. and *Q. carmenensis* C. H. Mull., Amer. Midl. Nat. 18:847. 1937.

A preliminary study was made of a large series of herbarium specimens which had been identified as *Q. undulata* or one or another of the numerous binomials applied to various forms in the complex. It was found that these specimens comprised a wide range of variable forms which, at one extreme, approached *Q. gambelii,* and, at the other, approached certain of the small-leaved, more-or-less evergreen oaks of the Southwest (notably *Q. grisea* and *Q. turbinella*). Furthermore, such specimens were, in general, intermediate between *Q. gambelii* and these other very different species of the Southwest. These features, of course, are commonly the attributes of segregating hybrid populations. As a working hypothesis, therefore, the postulate was made that *Quercus undulata* had arisen through hybridization between *Q. gambelii* on the one hand, and 2, or perhaps more, small-leaved species on the other.

Field observations and collections (mainly population samples) were made during 1955–56 throughout much of the range of the complex, and also into the ranges of those species that appeared to be involved in the complex, but in areas where they were relatively pure. A few sets of acorns from putative hybrids were collected for progeny tests.

It should be emphasized that this is a preliminary report. Conclusions to be presented here are based on field observations and general study of the collections; detailed morphological analyses are being made but are far from completion. Detailed documentation—citation of specimens, etc.—will appear later. Nevertheless, certain generalities seem to be warranted. For one thing, the evidence indicates that *Quercus undulata* is, indeed, a complex derived from hybridization. Furthermore, not just 2 or 3 species, but a total of 7 taxa generally recognized as species have apparently been involved, hybridizing in different combinations in one part or another of the southern Rocky Mountain region and the Southwest (fig. 1).

Quercus gambelii seems to be the "common denominator" of the complex. This species is a deciduous shrub or small tree with medium-sized leaves that are moderately-to-deeply lobed and commonly glossy green above. This is the common oak of the ponderosa pine zone, and is widely distributed in the central and southern Rockies and the higher mountain ranges of the Southwest. Its range extends from southern Wyoming and northern Utah southward into northern Mexico, and from southern Nevada eastward to western Texas (fig. 2).

In various parts of its range *Q. gambelii* has hybridized with 6 other species, none of them closely related to it but all in the same subgenus (*Lepidobalanus*, the white oaks): *Q. arizonica* Sarg., *Q. turbinella* Greene, *Q. havardii* Rydb., *Q. muehlenbergii* Engelm., *Q. mohriana* Buckl. ex Rydb., and *Q. grisea* Liebm. The resulting intermediate forms usually show the influence of *Q.*

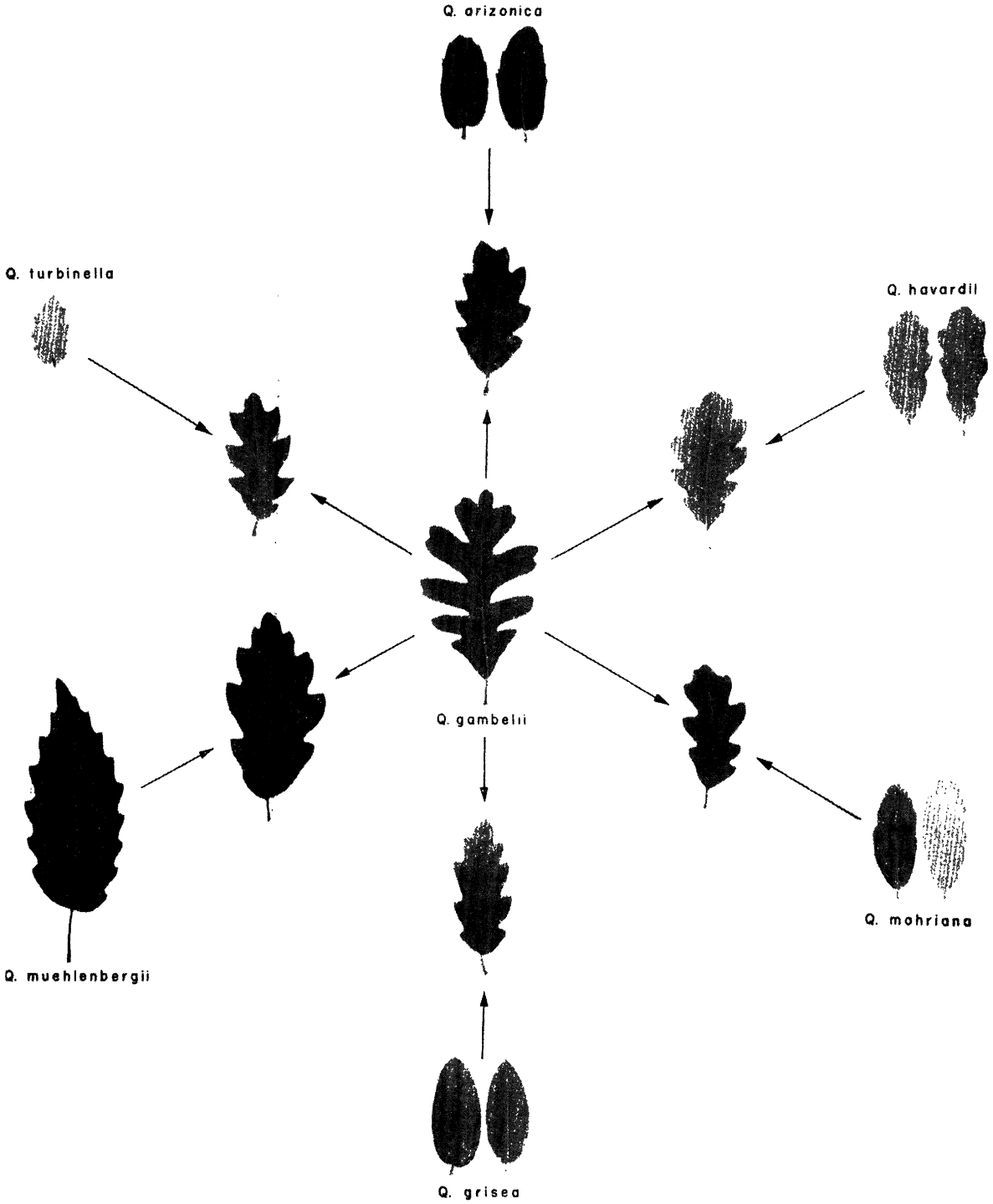

Fig. 1. Taxa involved in the *Quercus undulata* complex. (See table 1 for locations and collections from which these leaves were taken.)

TABLE I. *Specimens illustrated in fig. 1*

Taxon	Collection	Location
Q. gambelii	J. M. Tucker 2821–2	2 mi. w. of Monticello, San Juan Co., Utah
Q. arizonica	J. M. T. and H. S. Haskell 2897-14	1.8 mi. n. of Parker Creek, Gila Co., Ariz.
Q. grisea	J. M. T. 3002–9	8.8 mi. n. e. of Ft. Davis, Jeff Davis Co., Tex.
Q. havardii	J. M. T. 2971–5	Road 1053, 5 mi. s. of junction with Highway 80, Crane Co., Tex.
Q. mohriana	J. M. T. 3265–11	Palo Duro Canyon, 3 mi. e. of Wayside, Armstrong Co., Tex.
Q. muehlenbergii	J. M. T. 3115	Dark Canyon, Guadalupe Mtns., Eddy Co., N. Mex.
Q. turbinella	J. M. T. and H. S. Haskell 2897–7	1.8 mi. n. of Parker Creek, Gila Co., Ariz.
Q. gambelii × *Q. arizonica*	J. M. T. and H. S. H. 2927	12 mi. s. of Prescott, Yavapai Co., Ariz.
Q. gambelii × *Q. grisea*	J. M. T. 2838–2	1 mi. s. of Trinidad, Las Animas Co., Colo.
Q. gambelii × *Q. havardii*	J. M. T. 2820–3	0.9 mi. n. of Bluff, San Juan Co., Utah
Q. gambelii × *Q. mohriana*	J. M. T. 3260–7	East Fork Tramperos Creek, Pasamonte Ranch, Union Co., N. Mex.
Q. gambelii × *Q. muehlenbergii*	J. M. T. 3204	Bonito Creek, White Mtns., Lincoln Co., N. Mex.
Q. gambelii × *Q. turbinella*	J. M. T. 3222–7	¼ mi. s. s. e. of New Harmony, Washington Co., Utah

gambelii in the shallowly lobed, or at least coarsely toothed, leaf margins. Also, they are sufficiently similar among themselves to have been considered, in the aggregate, a single, although highly variable, taxonomic species. In some parts of the range of the complex, especially in certain parts of New Mexico, fairly stabilized populations are to be found over sizeable areas. However, the complex includes not just a series of hybrids (or populations) neatly intermediate between the parental species, but also populations which intergrade completely with the parents in many areas. Thus, the picture has been perplexing to the taxonomist from Engelmann's day down to the present. The following discussion, which reduces the complex to its simplest terms in order to stress broad generalities, is concerned primarily with indicating the species that are involved, the extent to which each contributes to the complex, and the area in which this occurs. The maps illustrating this latter point do not show the total distributions of the species (other than *Q. gambelii*), but only the areas in which they contribute to the *Q. undulata* complex.

QUERCUS ARIZONICA Sarg. (fig. 3).—Of the 7 species involved in the complex, *Quercus arizonica* has evidently contributed the least of all. Its range extends from central Arizona eastward across southern New Mexico into western Texas, and southward into northern Mexico from Sonora to Coahuila. Field study has revealed only a relatively few occurrences of putative hybrids between this species and *Q. gambelii*. Except for one instance, these were single, isolated trees growing with both presumed parents, and in macroscopic morphological characters were approximately of median intermediacy between them. These circumstances would indicate that they were probably F_1's. At 1 such hybrid site, a tree (J. M. Tucker and H. S. Haskell 2905) that may have been a back-cross to *Q. gambelii* was noted. All these putative hybrids and the back-cross "key" readily to *Q. undulata* in Muller's treatment of the genus in Kearney and Peebles, "Arizona Flora" (1951a).

It seems likely that more intensive field study will, in time, bring to light other instances of this hybrid. Although the 2 parents commonly are separated ecologically, the respective associations in which they occur do interdigitate rather frequently in the mountains of southern Arizona and northern Sonora and Chihuahua.

QUERCUS TURBINELLA Greene (fig. 4).—This species is an evergreen shrub having small, grayish-green leaves with spinose-dentate margins. Its total distribution extends from western Texas across New Mexico, Arizona, southwestern Utah, southern Nevada, and southern California. It commonly occurs in pinyon-juniper woodland, or as a dominant shrub in semi-arid chaparral and is ordinarily well-separated ecologically from *Q. gambelii*, which occurs in more mesic situations, commonly at higher elevations. Their ranges are broadly sympatric, however, in central to northwestern Arizona, southwestern Utah, and southern Nevada, and in areas where pinyon–juniper woodland and ponderosa pine forest interdigitate, the 2 oaks may hybridize sporadically.

Two areas of hybrid occurrence indicated in fig. 4, however, require explanation. First, and most intriguing of all, are numerous hybrids well to the north (by, at most, some 260 miles) of the present northern limits of *Q. turbinella* in southwestern Utah. These living hybrids, in all probability relictual, must date back to a period in post-glacial time when the climate was sufficiently warmer than at present to have permitted the existence of *Q. turbinella* at the latitude of Salt Lake City (Cottam, et al., 1959). Secondly, both *Q. gambelii* and *Q. turbinella* are known from several localities in southern Nevada (e.g., the Charleston Mountains), although, to the best of my knowledge, the hybrid

(or "*Q. undulata*") has not yet been reported from this area. The 2 parental species are apparently abundant in the Charleston Range, and I suspect that they must occasionally occur in close proximity to one another (although Clokey, 1951, p. 67, indicates both altitudinal separation and a difference in time of flowering). With more intensive botanical exploration, however, it is to be expected (cf. Muller, 1940, p. 4) that hybrids will eventually be discovered. Indeed, at least 1 specimen I have seen from this range (*Clokey 8314* #2, University of Nevada 8701; identified as *Q. turbinella*) shows slight, but evident, hybrid influence.

The hybrids usually occur as isolated individuals with the parental species. Occasionally, several may occur together, among them, not uncommonly, apparent back-crosses to the more abundant parent. Hybrid swarms have been observed in a few localities, notably: (1) in the Pine Valley Mountains, Washington County, Utah (by W. P. Cottam and R. Drobnick); and (2) approximately 10 mi. west of Pipe Springs, Mohave County, Arizona. (I was originally informed of this latter occurrence by Dr. Lyman Benson.)

These hybrids would ordinarily "key down" to *Quercus undulata* in both Muller's (1951a) treatment of *Quercus* in Kearney and Peebles' "Arizona Flora" and Tidestrom's "Flora of Utah and Nevada" (1925). In fact, specimens in herbaria which have been identified as *Q. undulata* from this general area (but not from north*eastern* Arizona or south*eastern* Utah) appear quite consistently to be this hybrid combination.

QUERCUS HAVARDII Rydb. (fig. 5).—*Q. havardii* is a low, rhizomatous sub-shrub, oftentimes no more than a foot in height, which forms extensive clones by lateral vegetative growth. This is the "shinnery oak" of the sandy, semi-arid plains of southeastern New Mexico, the southern panhandle of Texas, and western Oklahoma.

Four hundred miles to the northwest, in the sandy, semidesert country of southeastern Utah and northeastern Arizona, occurs a series of populations which, in general, are very similar to shinnery oak both morphologically and ecologically. Their low stature, spreading, rhizomatous habit resulting in extensive clones, and slender, erect shoots, are all highly suggestive of shinnery. The ecological setting—flat semi-desert plains of hummocky, shifting sand—is exactly the habitat of *Q. havardii* in the Staked Plains country in the Texas panhandle. Nearly all the herbarium specimens that I have seen from this part of Utah and Arizona have been identified as *Q. undulata.*

These Utah and Arizona populations are at times quite variable. At one extreme, one finds clones in which the characters of *Q. havardii* predominate; at the other are individuals showing unmistakable influence of *Q. gambelii*, i.e., larger, darker green leaves, sometimes slightly glossy above, distinctly lobed, with occasionally an arborescent growth habit. In one instance, along a desert wash 15 mi. north of Kayenta, Navajo County, Arizona, a small population was noted which was mainly arborescent, and although intermediate in leaf characters, had a strong *Q. gambelii* cast. Another small, but highly variable, population near Bluff, San Juan County, Utah, included *Q. gambelii* growing with a series of variable intermediates, the most extreme being a low, rhizomatous clone 2–3 ft. in height.

In even the most shinnery-like populations, however, I have seen no individuals that would be readily identified as *Q. havardii.* The series is evidently a hybrid complex, probably *Q. havardii* strongly introgressed by *Q. gambelii.* A few rare, disjunct occurrences of *Q. turbinella* are known from the region, and, to a very limited extent, the latter seems to be involved locally as a third component.

The most intriguing aspect of this segment of the *Q. undulata* complex is its geographic distribution as compared with that of present-day *Q. havardii.* The gap of approximately 400 mi. between the 2 regions, to the best of my knowledge containing no *Q. havardii* at all, plus the relative stability of at least some of the Utah and Arizona populations, suggests a separation of very long duration.

QUERCUS MUEHLENBERGII Engelm. (fig. 5).—*Q. muehlenbergii* is a tall, erect, deciduous tree of calcareous soil, commonly occurring on dry, rocky uplands. It extends from western New England and the Atlantic states to central Oklahoma and Texas, with disjunct populations in western Texas, New Mexico, Coahuila, and Nuevo Leon (Muller, 1951b).

This species has contributed to the *Q. undulata* complex in several areas in New Mexico: in the Guadalupe, Capitan, and White mountains in the south-central part of the state, and locally in several scattered places in the northeastern part. It appears to have contributed to the complex primarily through introgression of populations of *Q. grisea* or *grisea*-like "*undulata*" (i.e., populations probably derived from original hybridization between *Q. grisea* and *Q. gambelii*, followed by repeated back-crossing to *Q. grisea*). Putative hybrids between *Q. muehlenbergii* and *Q. gambelii* have been noted at only a few localities (all in New Mexico: *Eddy Co.:* Dark Canyon, Guadalupe Mountains; *Harding Co.:* Rd. 57, Ute Creek crossing; *Lincoln Co.:* Bonito Canyon, White Mountains).

QUERCUS MOHRIANA Buckl. ex Rydb. (fig. 4).—*Q. mohriana* is a shrub or small tree with relatively small, oblong or elliptic leaves which characteristically have dark glossy green upper surfaces and whitish tomentose lower surfaces. This species occurs on dry limestone hills of the Edwards Plateau in west-central Texas, extending westward into trans-Pecos Texas, northward into the Panhandle, and southward into Coahuila.

Quercus mohriana has contributed to the *Q. undulata* complex in 2 general areas: in the Guadalupe Mountains and in northeastern New Mexico.

In the former area the species occurs in fairly representative form in McKittrick Canyon, and perhaps elsewhere. Its influence is evident in many "*undulata*" populations of this range. In northeastern New Mexico, its influence is noticeable in the populations of shrubby oaks on rocky mesa and canyon slopes, notably on the watershed of the Canadian River. Through this area, however, no representative *Q. mohriana* is to be found, the nearest being in the Palo Duro Canyon in the Texas Panhandle, to the eastward. The extent of the influence of this species in northeastern New Mexico is rather difficult to assess. More specifically, it is sometimes difficult to differentiate between the influence of this species and that of *Q. grisea*, for these 2 oaks are quite similar in some respects, and

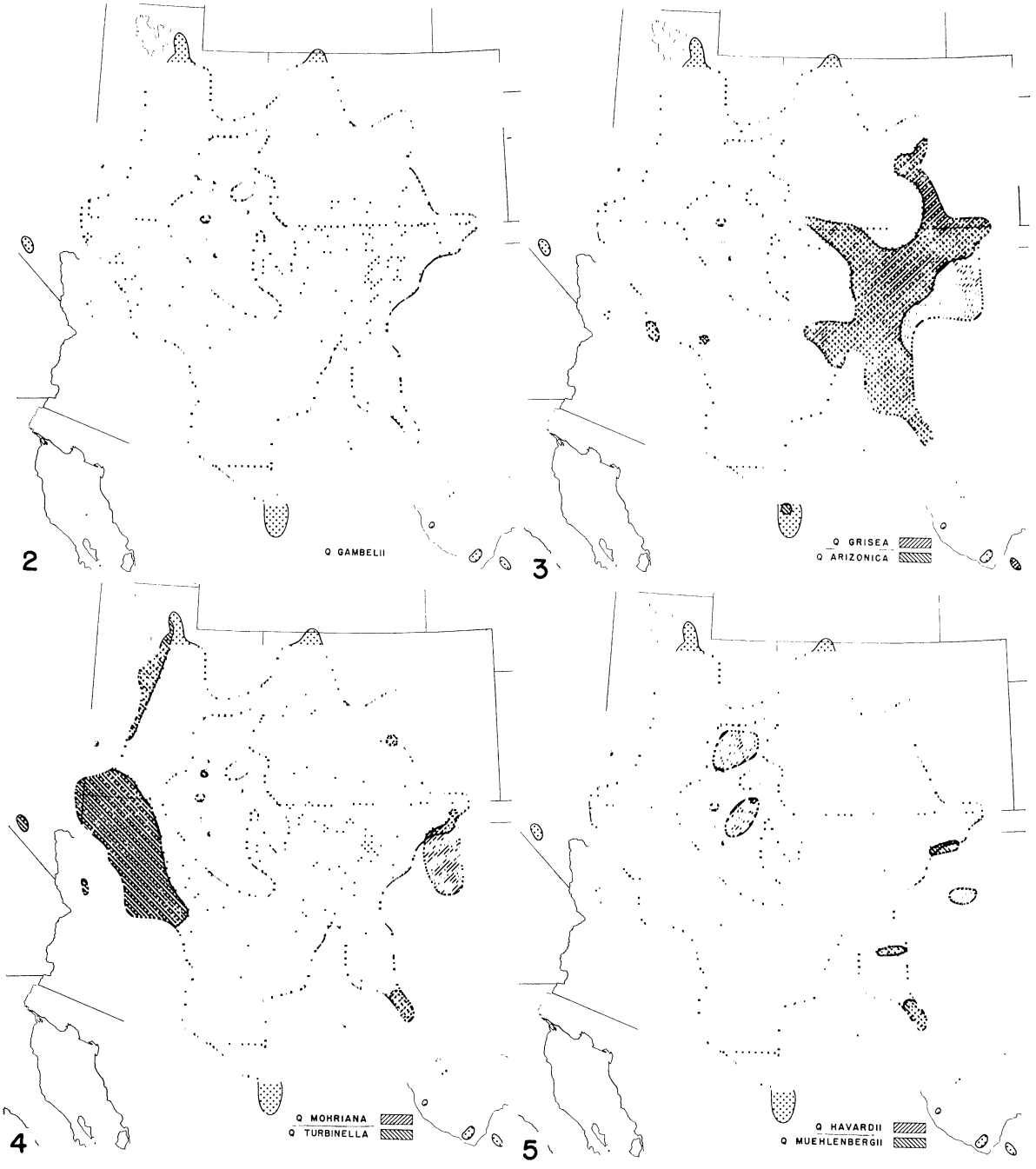

Fig. 2–5.—Fig. 2. Geographic distribution of *Q. gambelii*.—Fig. 3–5. Areas in which the other taxa contribute to the *Q. undulata* complex (total distributions of these taxa are not shown).

they themselves hybridize in some areas.

QUERCUS GRISEA Liebm. (fig. 3).—This species is commonly a small to moderate-sized tree, although sometimes shrubby, with small, grayish-pubescent, deciduous or subevergreen leaves. Most typically developed at moderate elevations in the region of the Davis Mountains in western Texas, its range extends northward into New Mexico (with rare, widely disjunct occurrences in Colorado), westward into Arizona, and southward into Coahuila and Durango.

Of all the 6 species other than *Q. gambelii*, *Q. grisea* has contributed most to the *Quercus undulata* complex. The latter is most extensively developed in an area extending from south-central through northeastern New Mexico and south-central Colorado. The most nearly stabilized populations of *Q. undulata* occur in this area, especially the northeastern quarter of New Mexico. Through most of this general area the complex appears to have been basically derived from hybridization between *Q. gambelii* and *Q. grisea*. Isolated individuals referable to *Q. grisea* have been found in highly variable "*undulata*" populations at widely separated localities through northern New Mexico and southern Colorado as far north as Phantom Canyon, Fremont County (ca. 8 mi. northeast of Cañon City) in central Colorado. The influence of *Q. grisea* (specifically, the presence of "griseoid *undulata*" forms in populations of *Q. gambelii*) has been noted as far north as Colorado Springs. Interestingly enough, however, where *Q. gambelii* and *Q. grisea* come in contact at present in western New Mexico, they hybridize only infrequently or not at all (e.g., in the Pinos Altos, Mimbres, Black, and San Mateo mountains).

DISCUSSION.—Not only is the *Q. undulata* complex most extensively developed through New Mexico, particularly the northeastern quarter of the state, but here, also, are the greatest complexities. Some populations seem to exhibit characters of 3 (or possibly more) species. Preliminary study indicates that the following species are most commonly involved: *Q. gambelii*, *Q. grisea*, and/or *Q. mohriana*. However, in some populations *Q. muehlenbergii* or *Q. havardii* appear to be involved, also. In any given population very careful study is required to determine the taxa that are actually involved.

Another problem is the determination of the eastern limits of the complex. The influence of *Q. gambelii* in the complex is usually obvious along the eastern foot-slopes of the southern Rockies and on mesas and canyon slopes immediately to the east. As one proceeds eastward, however, it becomes less and less apparent. On rocky slopes of canyons and high mesas far out on the plains of eastern New Mexico, the *Q. undulata* complex passes imperceptibly into shrubby populations which appear to be a mongrelized amalgam of *Q. mohriana* (possibly with some *grisea* influence) and *Q. havardii*.

The possible ramifications of this study are many, with numerous fascinating problems awaiting investigation. What have been the distributions of the species involved, going back into Pleistocene and Tertiary time? At what period in past time did *Q. gambelii* first come in contact and hybridize with these various other species? Why has it hybridized freely with a certain species (e.g., *Q. grisea*) in one region, and only rarely or not at all in others?

Completion of this study will be largely a matter of making detailed morphological analyses of the population samples collected to date, taking the segments of the complex one by one. In addition, progeny tests of putative field hybrids will be made when circumstances permit. Finally, over and beyond the problem of determining as accurately as possible the taxa involved in any area or segment of the complex, an attempt to unravel its history will necessitate collating data from biogeography, paleontology, geology, or any other scientific discipline which gives promise of providing information pertinent to the problems involved.

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