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STUDIES IN THE QUERCUS UNDULATA COMPLEX. III. THE CONTRIBUTION OF Q. ARIZONICA[1]

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ABSTRACT

Tucker, J. M. (U. California, Davis.) Studies in the Quercus undulata complex. III. The contribution of Q. arizonica. Amer. Jour. Bot. 50(7): 699–708. Illus. 1963.—Of the 7 oak species involved in the Quercus undulata complex, Q. arizonica contributes the least of all. The latter has hybridized with Q. gambelii at a few widely separated localities (listed in Table 1) in central Arizona, and northern Sonora and Chihuahua, Mexico. The putative hybrids (identifiable as Quercus undulata) occur as isolated individuals with the parental species. The parents, although regionally sympatric, are usually ecologically isolated. They differ in a number of morphological characters, 6 of which were analyzed in detail. The resulting data, presented as pictorialized scatter diagrams, demonstrate that the putative hybrids are intermediate, in general. This is taken as evidence of their hybrid nature. Factors limiting hybridization in oaks are discussed. It is speculated that hybridization between Q. arizonica and Q. gambelii has occurred since the postglacial hypsithermal interval.

In an earlier paper (Tucker, 1961) Quercus undulata Torr. was discussed as a highly variable complex, widespread in the Southwest. In broad outline, the complex has evidently resulted from hybridization between Q. gambelii Nutt. and, in one part of its range or another, 6 other species (op. cit., Fig. 1). In the resulting assemblage, some hybrid combinations (e.g., the one considered in this paper—Q. gambelii × Q. arizonica) are represented by isolated, individual hybrids; other combinations by highly variable populations frequently intergrading with the parental species; and still others, by moderately stable populations. The whole assemblage is variably intermediate between Q. gambelii and one or another of the other 6 species.

Of the species involved in the complex, as it is presently understood, Q. arizonica Sarg. contributes the least of all. In fact, this contribution con-

TABLE 1. *Collections of the hybrid between Q. gambelii and Q. arizonica*

Collection	Elevation (feet)	Associated species	Location
J. M. Tucker 2490[a]		Q. gambelii, Q. arizonica, Q. fulva, Q. omissa	Sierra Madre Occidental, 47.4 miles (by road) w. of Casas Grandes, Chihuahua, Mex.
J. M. T. and H. S. Haskell 2904	6400	Q. gambelii, Q. arizonica, Q. turbinella, Pinus ponderosa, Pseudotsuga menziesii, Juniperus deppeana	19 miles (by road) n. of Young, Gila Co., Ariz.
J. M. T. and H. S. H. 2905	6400	Same as for 2904	Same as for 2904
J. M. T. and H. S. H. 2927	7300	Q. gambelii, Q. arizonica, Pinus ponderosa	Senator Highway, 12 miles s. of Prescott, Yavapai Co., Ariz.
J. M. T. and H. S. H. 2930	7300	Q. gambelii, Q. arizonica, Pinus ponderosa	Senator Highway, 12.7 miles s. of Prescott.
J. M. T. 3483	6900	Q. gambelii, Q. arizonica, Q. hypoleucoides	Sierra San José, ne. side; ca. 5 miles s. of Naco, Sonora, Mex.

[a]All collections cited in this paper are on file in the Botany Department Herbarium, University of California, Davis.

sists of only a few known hybrids at widely separated localities in central Arizona and northern Chihuahua and Sonora, Mexico (op. cit., Fig. 3). These have usually been single individuals occurring with the 2 putative parents. These circumstances, plus the morphological intermediacy of the trees in question, are precisely the criteria long used for diagnosing natural hybrids in the field. Inasmuch as these individuals would "key down" to *Quercus undulata* in Kearney and Peebles' "Arizona Flora" (1960), however, this hybrid is considered an element of the complex. I know of no mention of this hybrid combination in the literature prior to this study, nor have I seen specimens, other than my own, in herbaria. Furthermore, none of the numerous binomials that have been applied to forms in the *Q. undulata* complex seem to apply to this hybrid.

The main objectives of this paper, then, are to indicate the distribution of these hybrids more precisely, and to show their morphological intermediacy between the putative parents as evidence of their hybrid nature.

DISTRIBUTION AND HABITAT—The locations of these putative hybrids have been previously indicated in a very general way (Fig. 3, Tucker, 1961). (In this figure, however, the hybrid location on Sierra San José, Sonora, Mexico, is not shown. At that time, this collection [J. M. Tucker 3483] had not yet been analyzed in detail, and the author considered its identification as a hybrid to be highly tentative.) Their locations (together with other data) are given more exactly in Table 1 of this paper.

The 2 putative parental species are regionally sympatric from central Arizona southeastward into northern Mexico. It will be noted that 4 of our 6 hybrids were found in Yavapai and Gila counties in central Arizona (Table 1). It may be that *Q. gambelii* and *Q. arizonica* are more frequently in contact in this area than elsewhere, and

more intensive botanizing here may well bring additional hybrids to light. Even though the ranges of the parental species overlap broadly, they are ordinarily separated altitudinally and ecologically, and represent components of very different floristic assemblages. *Quercus gambelii* is widely distributed in the central and southern Rockies, and in the higher mountains of the Southwest, and through this region is the common (oftentimes the only) oak of the ponderosa pine zone. Toward the southern end of its range, this oak occurs only in the upper, more mesic parts of high isolated ranges. *Quercus arizonica* is a more southerly species whose floristic affinities are Mexican. It is a common component of the more xeric *encinal* (evergreen oak woodland) or of pine-oak woodland (Marshall, 1957) of lower mountain slopes, being found in a broad zone below the limit of ponderosa pine. The hybrids have been found at or near the upper limits of *Q. arizonica*, usually in ponderosa pine woods (Table 1).

Over most of the region of geographic overlap of these 2 oaks, their respective plant communities commonly lie adjacent to one another (Nichol, 1952, map between pp. 208 and 209; Marshall, 1957, Fig. 20). However, in most of the small ranges of southeastern Arizona, extreme southwestern New Mexico, and adjacent Mexico, *Q. gambelii* is often less abundant and more restricted in distribution than in central Arizona. Ordinarily it occurs at higher elevations than *Q. arizonica*, or, where they overlap altitudinally, the former is commonly restricted to more mesic situations—north-facing slopes or canyon bottoms—whereas the latter occurs on open, more xeric exposures. Due to variations in slope exposure and other factors, however, complex intermixing of plant communities is not rare in these southerly ranges (Wallmo, 1955; Marshall, 1957). As a result, opportunities for hybridization between these 2 oaks may occasionally be at hand—witness our

TABLE 2. *Principal morphological differences between Quercus gambelii and Q. arizonica*

	Q. *gambelii*	Q. *arizonica*
Leaves		
size	moderately large: 55–130 (or more) mm long × 30–70 (or more) mm wide.	relatively small: 35–65 (or more) mm long × 14–25 (or more) mm wide.
margin	moderately to deeply lobed, the lobes commonly rounded, to subacute.	entire to low-dentate, the teeth mucronate.
base	variable: cuneate to rounded or truncate.	cordate to rounded.
venation	major secondary veins commonly 3–5 on each side, not impressed on upper surface; reticulum of veinlets not prominently raised on lower surface.	major secondary veins 6–10 on each side, commonly slightly impressed on upper surface; these and the reticulum of veinlets prominently raised on lower surface.
foliar trichomes	stellate hairs of under side of leaf with 4 or fewer rays, not contorted or kinky—at most, slightly curved or undulate, the rays up to 0.40 mm long.	stellate hairs of underside of leaf with 4–8 rays, conspicuously kinky, to 0.75 (or more) mm long.
Branchlets	first year's growth commonly brown or reddish-brown, moderately to sparsely pubescent or glabrate.	first year's growth commonly buff-colored or tawny with dense tomentum.

collection on the Sierra San José in northern Sonora and in the Sierra Madre Occidental in northern Chihuahua (Table 1).

MORPHOLOGICAL DIFFERENCES BETWEEN QUERCUS GAMBELII AND Q. ARIZONICA—The principal morphological differences between these very different oaks are summarized in Table 2. The most conspicuous of these are leaf differences. The medium-sized to moderately large, lobed, green, and often glossy leaves of Q. *gambelii* stand in marked contrast to the smaller low-dentate to entire leaves of Q. *arizonica* (Fig. 1). In Q. *arizonica* both the secondary veins and the intercostal reticulum of smaller veinlets are prominently raised on the undersurface of the leaf, giving this surface a "veiny" or reticulate appearance. In Q. *gambelii*, on the other hand, the secondaries may be fairly prominent on the undersurface, but the intercostal reticulum is usually inconspicuous and scarcely, if at all, raised.

Each of the putative hybrids, when encountered in the field, was noticeably intermediate. Indeed, this was the principal reason for diagnosing them as hybrids. However, in order to go beyond the characters mainly responsible for this impression—leaf size, and degree of marginal identation—an analysis was also made of other characters in which the putative parents differ. Data on 6 characters were used in the construction of the pictorialized scatter diagrams (cf. Anderson, 1949) shown in Fig. 5, 6. The characters used and procedures of analysis were as follows:

Leaf width—A single representative leaf of each specimen was measured to the nearest millimeter.

Relative depth of marginal indentation—Probably the most conspicuous of all the differences between Q. *gambelii* and Q. *arizonica* is that the leaves of the former are strongly lobed, whereas those of the latter are usually entire to low-dentate, or at most coarsely and rather sharply toothed—but

never lobed (Fig. 1). However, since Q. *gambelii* has larger leaves than Q. *arizonica*, and since there is probably a positive correlation between absolute values for leaf size and depth of indentation, an index was devised to express *relative* depth of indentation as a character independent of leaf size. The longest lobe or tooth of one leaf was chosen and the total length of its secondary vein was measured (value A, Fig. 4). The length of the lobe proper (value B) was then subtracted from the vein length. The ratio of A to A-B was taken as the "indentation index." Thus, a leaf with an entire margin (which is sometimes the case in Q. *arizonica*) would have an index value of 1, whereas the more deeply indented the leaf, the higher the index value.

Conspicuousness of intercosial reticulum—This character was analyzed and scored as follows. Two leaves were selected as standards—one of Q. *gambelii* to establish the maximum of "veininess" for that species, and one of Q. *arizonica* to establish the minimum for that species. Any leaf whose intercostal veinlets were no more prominent than those of the first standard was classed as Q. *gambelii* and given a score of 0. Any whose veinlets were at least as prominent as the second standard was classed as Q. *arizonica* and given a score of 2. Any intermediate condition was given a score of 1. Ten representative leaves per specimen were thus scored, and the mean value tabulated for each specimen.

Since the difference to be judged between the 2 parental species was in the intercostal reticulum, it was necessary to conceal the secondaries so that their appearance could not bias the judgments in this analysis. For this purpose small rectangular holes, each ca. 3 × 8 mm, were cut—3 in a row—in a piece of paper. The holes were spaced about 15 mm apart. The standard leaf of Q. *gambelii* was taped under one of the end holes in such a way
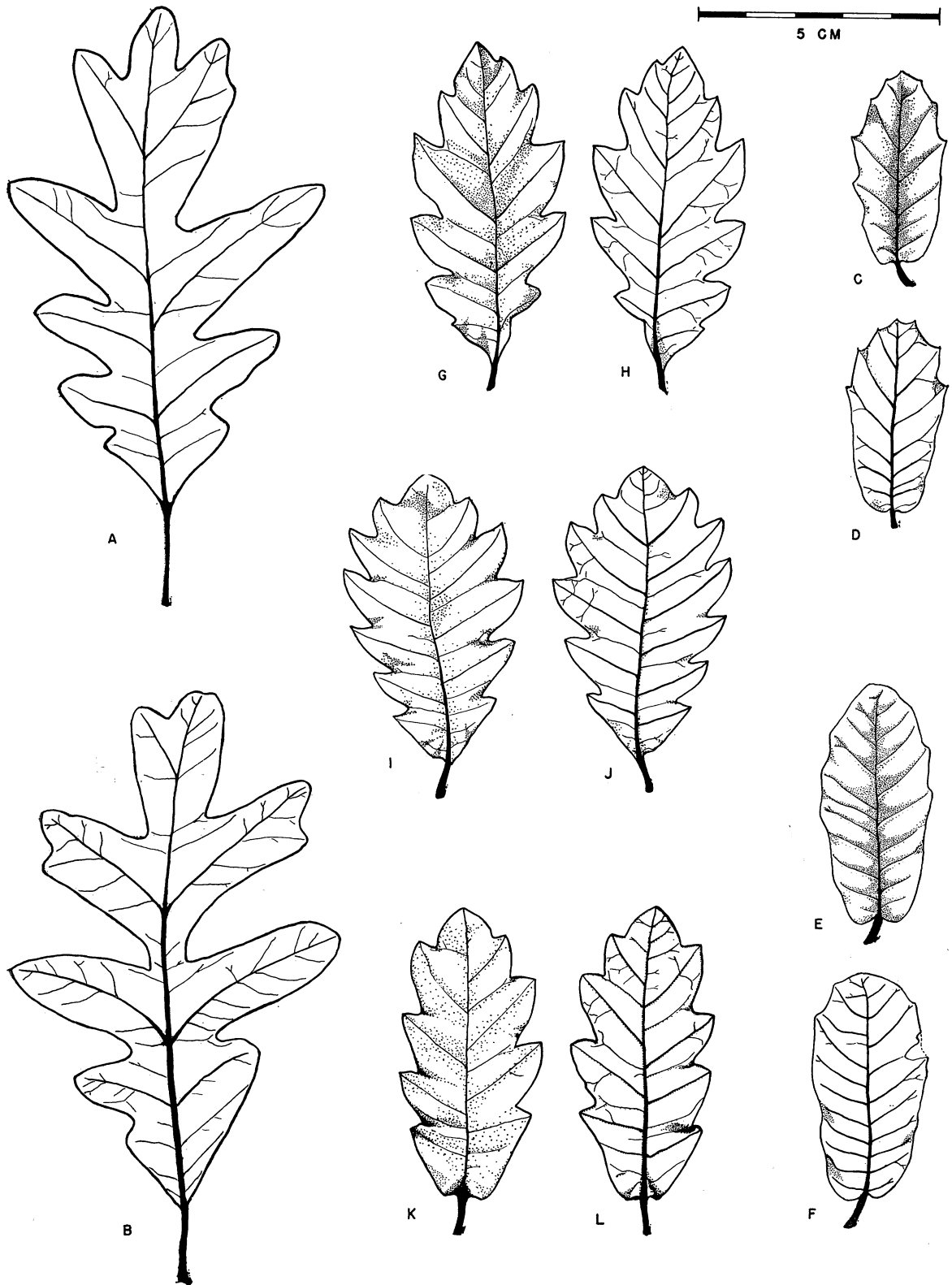
Fig. 1. Representative leaves of *Quercus gambelii* (A–B), *Q. arizonica* (C–F), and hybrids (G–L). A, C, E, G, I, K: upper side of leaves; B, D, F, H, J, L: lower side of leaves. (Drawings by Miss Maris Chirone.)

that an intercostal area—with no secondary veins showing—was exposed to view through the hole. The standard leaf of *Q. arizonica* was taped under the other end hole in the same way, and the middle hole was left open. To score a leaf, an intercostal area of its underside was positioned under the middle hole. Thus, a ready comparison could be made with the standards, one on either side.
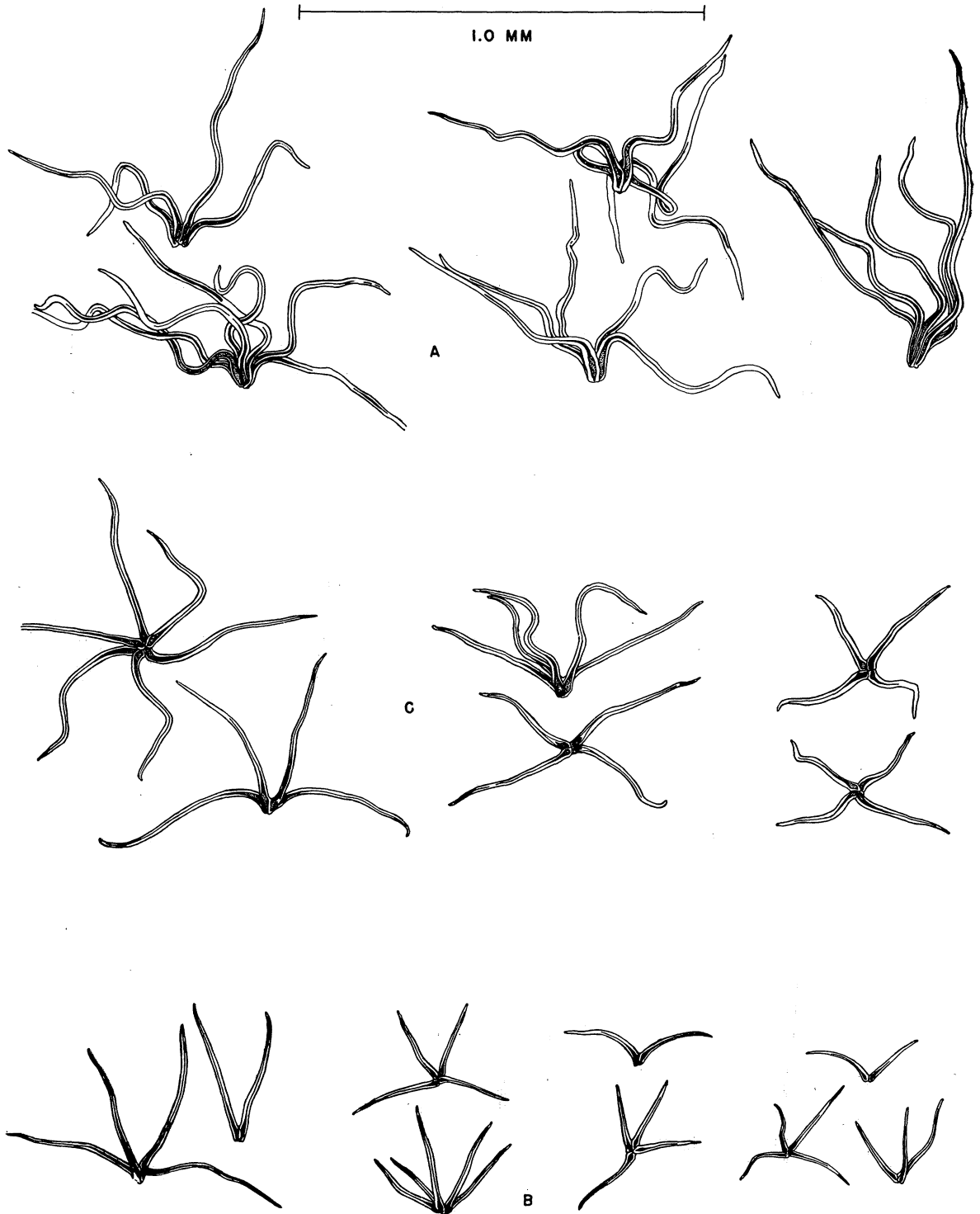
Fig. 2. Stellate hairs of *Quercus arizonica* (A), *Q. gambelii* (B), and hybrids (C). (Drawings by Miss Jean Addicott.)

Number of major secondary veins—The major secondary veins, as seen on the lower surface of the leaf, were counted for 5 representative leaves from each specimen, and the mean value recorded. Values of 8.9 or less were scored as *Q. gambelii*; 12.0 or more, as *Q. arizonica*; and 9.0–11.9, as intermediate.

Although *Q. gambelii* and *Q. arizonica* ordinarily differ markedly in this character, it was a difficult one to analyze. In *Q. gambelii* the secondary vein running the length of each lobe is well-developed. Such veins would qualify as "major" veins in all but the smallest apical or basal lobes. The complete gradation in prominence, however, from the most strongly developed to the weakest secondaries of a leaf, made a certain degree of arbitrariness inevitable in making these counts.

Number of rays per stellate hair (Fig. 2)—This was determined with a compound microscope (at 100 ×). With all specimens of *Q. gambelii*, and with some of the others, also, it was possible to count the rays by direct inspection of the underside of the leaf, using reflected light. With many specimens of *Q. arizonica*, however, the rays were so tortuous and interlaced that it was extremely difficult to obtain satisfactory counts in this manner. For this species, therefore, counts were usually made from temporary mounts of pubescence scraped from the leaf with a razor blade. Wetting the area to be scraped with a drop of a ·wetting agent ("Kwik Wet") facilitated this operation. The pubescence thus detached was mounted in a drop or 2 of the same material on a slide, carefully teased apart, and covered with a cover glass. As the rays are fused together at the base in *Q. arizonica*, it was possible by close inspection to

distinguish intact trichomes from those that had had rays detached, the latter being avoided in making counts. Three leaves were examined for most specimens of *Q. arizonica*, and 10 counts obtained for each leaf to give a mean of 30 counts. With many specimens of *Q. gambelii*, however, only a single leaf was examined.

In *Q. gambelii* the ray number is 4 or less; in *Q. arizonica*, generally from 4 to 8. Numbers outside these ranges are quite rare. The relatively high frequency of 4-rayed trichomes in both species would appear to make their separation difficult or impossible on this character. In *Q. arizonica*, however, because of the rarity of numbers lower than 4, and the general abundance of numbers higher than 4, the *mean* was never lower than 5.0 (Fig. 3).

For purposes of scoring, therefore, a mean value of 4.0 or less was rated as *Q. gambelii*, 5.0 or more as *Q. arizonica*, and values between 4.0 and 5.0 as intermediate.

Curliness of hairs—For this character, 3 classes were recognized—*gambelii* (least curly), intermediate, and *arizonica* (most curly). Grading was done by comparison with standard specimens. One to several leaves were examined. If the degree of curliness was obviously well within the range established for *Q. gambelii* or *Q. arizonica*, only 1 leaf was examined. In the hybrids, and borderline cases in the parental species, 2 or more leaves were examined. The standard specimens are on file, with the voucher specimens of this study, in the Botany Department Herbarium, University of California, Davis.

For purposes of comparison in the pictorialized scatter diagrams, specimens of the parental species are included along with the hybrids. In Fig. 5, the
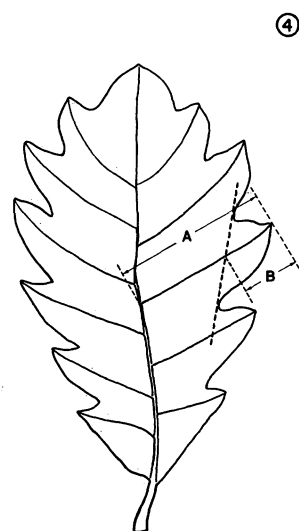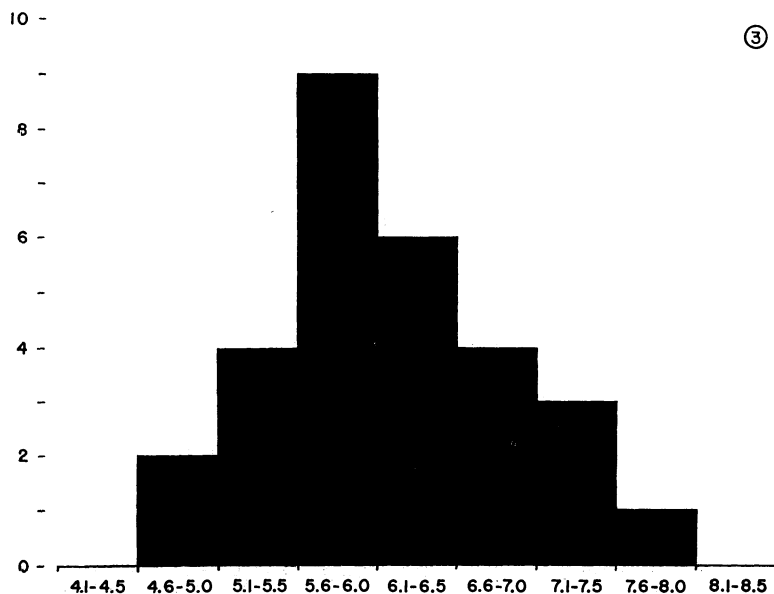

Fig. 3–4—Fig. 3. Frequency of mean ray numbers in 29 representative specimens of *Quercus arizonica*. (The 2 in the class 4.6–5.0 both had mean values of 5.0.) Vertical scale: number of specimens.—Fig. 4. Measurements taken for vein length (A) and lobe length (B). The ratio, A to A–B, is used as an indentation index.

hybrids are compared with a number of individual parental specimens which were collected at all the hybrid sites except one, at the same time as the hybrids. In Fig. 6, the hybrids are compared with a population sample of each parental species. That of *Q. arizonica* (*Tucker 2497*) was collected in the Sierra Madre Occidental, 57 miles (by road) west of Vieja Casas Grandes, Chihuahua, Mexico; that of *Q. gambelii* (*Tucker and Haskell 2931*) was collected in the vicinity of the Apache Maid Ranger Station, Coconino County, Arizona. Thus, in both Fig. 5, 6, elements from widely separated localities have been aggregated together, for the purpose of ready comparison, to form *composite* scatter diagrams. The symbols used are explained in Table 3; locations of the hybrids are given in Table 1.

EVIDENCE OF HYBRIDITY—No direct genetic proof of hybridity is available, however desirable it might be. A progeny test was attempted with a sparse crop of acorns (collected Oct. 5, 1955) from one putative hybrid (*Tucker and Haskell 2927*). Although the hybrid is thus partially fertile, none of the acorns germinated. To what extent this was due to inviability, if at all, is not clear, however, for they proved to be badly infested with weevils. No experimental crosses have thus far been attempted.

Under the circumstances, therefore, the best evidence of hybridity is a demonstration of morphological intermediacy, as in the preceding paper in this series (Tucker, Cottam, and Drobnick, 1961). That the putative hybrids are, indeed, intermediate in some degree is readily apparent in leaf size and marginal indentation (Fig. 1). Furthermore, even such minute details as characters

TABLE 3. *Explanation of symbols used in pictorialized scatter diagrams*

Character	Q. gambelii	Inter-mediate	Q. arizonica
	●	⊎	⅄
intercostal reticulum	●	⊙	○
number of secondary veins	○	○	○
number of rays per hair	○	⊃	⊃
curliness of hairs	○	⊂	⊂

of the foliar trichomes are also intermediate (Fig. 2), as has been the case in other oak hybrids (Tucker, 1952; Tucker et al., 1961). The pictorialized scatter diagrams indicate that the hybrids are, in general, intermediate in the 6 characters analyzed. This is especially clear in Fig. 5, in which the hybrids are compared with individuals of the parental species with which they were actually growing.

It may be noted that one of the putative hybrids—indicated by "B" in Fig. 5, 6 (*Tucker 3483*, Table 1)—was quite *gambelii*-like. In the field it was diagnosed as either aberrant *Q. gambelii*, or possibly a hybrid; it was growing with *Q. gambelii* and *Q. arizonica*. After detailed study, it was considered to be of hybrid derivation, perhaps a backcross to *Q. gambelii*. Although it was scored as *Q. gambelii* on 4 of the 6 characters, it was more or less intermediate in leaf size and degree of indentation, as well as in certain other characters not used in the scatter diagrams, viz: the leaf
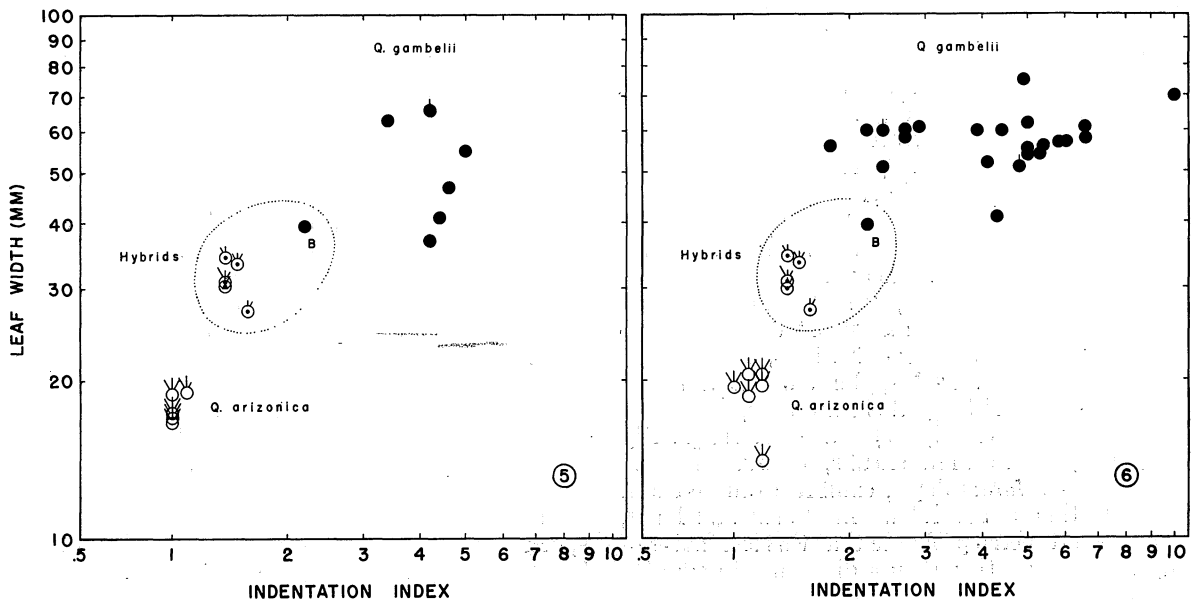

Fig. 5–6. Pictorialized scatter diagrams comparing the putative hybrids with *Quercus arizonica* and *Q. gambelii.*—Fig. 5. *Q. arizonica* and *Q. gambelii* are individual collections from the several hybrid sites.—Fig. 6. *Q. arizonica* and *Q. gambelii* are population samples collected at a considerable distance from any of the hybrid sites (see text for locations).

base, and the pigmentation of the stellate trichomes. (In *Q. arizonica* the leaf base is cordate to rounded; in *Q. gambelii*, usually more or less cuneate. Number *3483* was intermediate. The stellate hairs of *Q. arizonica* commonly contain a conspicuous deposition of orange-red pigment in the lumen at the base of each ray; this is quite lacking in *Q. gambelii*. In No. *3483* the stellate hairs frequently contained a perceptible deposition of orange pigment.)

DISCUSSION—The apparent scarcity of hybrids between *Q. gambelii* and *Q. arizonica* suggests either the existence of effective barriers to interbreeding or only a limited period of contact, or both.

Aside from geographic isolation, the principal factors which limit hybridization in *Quercus* are evidently these: (1) ecological isolation; (2) absence of suitable site conditions for the establishment of hybrids; (3) seasonal isolation; (4) incompatibility of foreign pollen; (5) hybrid inviability; and (6) reduced viability in the F_2 or backcross generations. This enumeration is based largely on Riley's (1952) classification of isolating mechanisms. Examples could be cited in which each of these is probably of some importance in limiting hybridization between various oaks. However, only those which appear to be involved in our present case will be considered here. Certain of these are probably much more important than others, as will be noted below. As Riley (1952) has emphasized, in many genera several barriers may act together and perhaps in a definite sequence. In our present case, it seems likely that several may well be operative.

As indicated previously, *Q. gambelii* and *Q. arizonica* are commonly well separated ecologically. Such differences in ecological preference are common among otherwise reproductively compatible oaks (cf. Heiberg, 1951; Muller, 1952, for a number of examples; Forde and Faris, 1962; Salisbury, 1940; Tucker, 1953a; Tucker and Haskell, 1960). Indeed, ecological isolation may well be one of the most important mechanisms by which hybridization between related oaks is prevented or minimized.

Seasonal isolation in oaks has been thought by some authors to be of little or no importance as a barrier to hybridization, "since related species usually shed their pollen at about the same time in the spring,..." (Stebbins, Matzke, and Epling, 1947). Although this may be true as a broad generality, undoubtedly there are exceptions. For example, the 2 closely related (and frequently sympatric) Californian shrubs, *Quercus dumosa* Nutt. and *Q. durata* Jeps., exhibit a difference in flowering time of several weeks (Forde and Faris, 1962), and it seems probable that this is a factor of importance (together with a difference in edaphic preference) in limiting hybridization between them. The same may be true in the case of *Q. arizonica* and *Q. gambelii*, for Sargent (1895) gave different flowering times for these species: April

for *Q. arizonica* (p. 89), and May and June for *Q. gambelii* (p. 34). Although this may be a function of their altitudinal difference (and, of course, these simple generalizations should be accepted with caution), one cannot dismiss the possibility of at least partial seasonal isolation in areas where the 2 are sympatric.

Incompatibility of foreign pollen may well be of some importance in the present case, although I have no evidence on this point. It may be noted that attempts at experimental hybridization of other combinations of species have frequently been unsuccessful (J. W. Duffield, unpubl. data; Tucker, unpubl. data). Incompatibility of the foreign pollen would be a possible explanation in such cases. So, also, would hybrid inviability (either zygotic or embryonic), of course. Although these 2 factors are difficult to demonstrate, one or both could be operative in areas where *Q. gambelii* and *Q. arizonica* are sympatric.

Reduced viability in the F_2 or backcross generations may be a factor of importance in restricting interbreeding between *Q. gambelii* and *Q. arizonica*. As noted earlier, however, the available evidence, derived from one limited progeny test, is not clear. Considering oak hybrids in general, this factor evidently varies widely. Oftentimes it seems to be relatively unimportant as a mechanism restricting interbreeding between species (although for most hybrids really critical data are probably lacking). In other words, the progeny of natural oak hybrids frequently show a high degree of viability. This has long been recognized. Indeed, many years ago Engelmann (1877) expressed the view that in *Quercus* "all the supposed hybrids are abundantly fertile, and those of their acorns which have been tested have well germinated; in fact, as far as I know, no difference in fertility or germinating power between them and the acknowledged species has been discovered." (Engelmann enumerated only 10 forms which he considered to be "real hybrids"—many times this number are known today.) Although viable progeny may, indeed, be produced in abundance by many oak hybrids (MacDougal, 1907; Allard, 1932; Wolf, 1938, 1944; Deam, 1940), in any individual case fertility should not be merely assumed a priori, for the degree of taxonomic relationship between the parental species unquestionably has a bearing on the matter. Thus, it has long been recognized (Engelmann, 1877) that oaks of different subgenera do not even hybridize in nature (although Piatnitsky [1946] has reported the experimental production of such hybrids). Studies in recent years, moreover, have indicated that even within a subgenus, hybrids between distantly related species may show marked reduction in fertility. Thus, sterility in the F_1 (Tucker, 1953b; Tucker et al., 1961: 334) or reduced viability in F_2 or backcross progenies (cf. Wolf, 1938; Coker and Totten, 1945) can be at least partially effective as isolating mechanisms in some cases.

The available evidence suggests that hybridization between *Q. gambelii* and *Q. arizonica* is a phenomenon of the present and the very recent past. The hybrids are small to medium-sized trees, apparently of no great age; they appear to be F_1's in most cases; and no evidence of extensive backcrossing or introgression has thus far come to light.

The hybrid sites are all at or near the upper altitudinal limits of *Q. arizonica*. The Arizona occurrences are, in addition, near the northern limits of this species. It seems virtually certain that *Q. arizonica* did not occupy these sites at the height of the last glacio-pluvial maximum in late Pleistocene time. During this period the encinal species were no doubt largely, if not completely, eliminated from the mountains they now occupy in central and southern Arizona. Evidence from several sources indicates that biotic zones were considerably displaced downward during this period (Martin, 1958). Martin has estimated this to have been on the order of 4000–4500 ft in the Southwest. Martin (1961) has evidently assumed the complete elimination of encinal species from Arizona during the last glacial maximum, and has postulated a northward advance of this biota and entry in the mountains it now occupies in post-glacial time.

The necessity of postulating complete elimination of these species from the *region* might be questioned, for it may be supposed that they could have found refuge at lower elevations. For example, the country around Wickenberg, Arizona, is not more than 35 miles, airline, to the southwest of 2 of our hybrid localities, but it is fully 5200 ft lower, lying at slightly over 2000 ft elevation. Similarly, the valley of the Santa Cruz River, a few miles southwest of the Santa Catalina Mountains in which our encinal species are common, lies at 2300–2400 ft. Thus, even though the encinal had been displaced downward by 4000 ft or more, it might be supposed that *Q. arizonica* could have survived there, nevertheless.

On the basis of meteorological information discussed by Martin (1961), however, there may be grounds for questioning this supposition. *Quercus arizonica* and other species of the encinal are adapted to a biseasonal distribution of rainfall, much of it coming in the summer as thunder showers. Martin has postulated that the summer monsoon would have been largely eliminated in the Southwest during full glacial time. The absence of summer rainfall, in turn, would probably have eliminated the encinal oaks. By the same token, it may be noted that, whereas the Tertiary equivalent of *Q. arizonica* (*Q. turneri* Knowlton) was a dominant element in the Lower Pliocene Esmeralda Flora of western Nevada (Axelrod, 1940), the woodland of which it was a member was subsequently eliminated from the area by the disappearance of summer rainfall, as well as the development of colder winter climate (Axelrod,

1958). The problem of whether or not the encinal species were completely eliminated from Arizona during the last glacial maximum, however, is not really relevant to our main question. It seems certain that the present upper and northern limits of encinal species such as *Q. arizonica* have been attained in post-glacial time. And it will be recalled that it is at or near these limits that *Q. arizonica* has hybridized with *Q. gambelii*.

The maximum spread northward and upward of *Q. arizonica* was most likely attained during the post-glacial "Altithermal" (Antevs, 1955) or "Hypsithermal Interval" (Deevey and Flint, 1957). Inasmuch as this was a period warmer than the present, it may well be that these northern and upper limits were somewhat in excess of the present limits of the species. With lowering temperatures since the hypsithermal, it would seem likely that *Q. arizonica* is being restricted southward and downward once again. Under these circumstances, where hardy stragglers persist along its receding northern and upper limits in Yavapai and southern Coconino counties, it has been brought into ever more frequent contact with *Q. gambelii* as the more mesophytic ponderosa pine forest has expanded. It is under circumstances such as these that oak hybrids have commonly been observed (Palmer, 1948; Cottam, Tucker, and Drobnick, 1959) where one species, infrequent or rare, grows in association with an abundant species. At flowering time the rare species receives an abundance of pollen of the other. What little pollen of its own species it receives is via self-pollination. Inasmuch as oaks appear to be cross-pollinated in general, and at least partially self-sterile (J. W. Duffield, unpubl. data; data of Piatnitsky, 1934; Wright, 1953 [Table 9]), if such isolated individuals reproduce at all, some of their offspring will often be hybrids. That this pattern is of general occurrence in other groups is suggested by the cases cited by Baker (1951).

An interesting parallel may be found in the genus *Juniperus* in very nearly this same region. *Juniperus deppeana* Steud., the common alligator juniper of the pine-oak woodland of central and southeastern Arizona (Marshall, 1957, Table 1) is often an associate of *Q. arizonica*. Its range extends slightly north of the latter, however, at least to the Flagstaff area (Kearney and Peebles, 1960). Through this northern end of its distribution it comes in contact with a more mesophytic juniper, *J. scopulorum* Sarg., which, like *Q. gambelii*, is a characteristic element of the ponderosa pine forest. Interestingly enough, intermediate individuals presumably of hybrid origin between these 2 junipers have been noted in this area (Whiting, 1942).

In conclusion, then, only a few hybrids between *Q. arizonica* and *Q. gambelii* have been discovered to date, and in most cases these appear to be F_1's. There would appear to be several reasons for

this scarcity, the most important being the fact that the parental species are ordinarily well-separated ecologically. Where they do occur together, however, the frequency of hybridization may be held to a low level by a partial difference in flowering time. It is conceivable, also, that pollen incompatibility and/or hybrid inviability may be effective in this regard. When the few hybrids that have become established do produce acorns, as sometimes happens, it would appear that reduced viability in the progeny may well impose still further restrictions on interbreeding, and largely prevent gene exchange between the parental species.

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