spores of heterocaryons involving different formae of *F. oxysporum* severely restricts the possibilities offered by the parasexual cycle in studies of the origin and nature of formae. Experiments now in progress have been designed to determine the pathogenicity and host-specificity of "prototrophic" colonies from the heterocaryons.

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# STUDIES IN THE QUERCUS UNDULATA COMPLEX. II. THE CONTRIBUTION OF QUERCUS TURBINELLA[1]

JOHN M. TUCKER, WALTER P. COTTAM, AND RUDY DROBNICK

ABSTRACT

TUCKER, J. M. (U. California, Davis), W. P. COTTAM, and R. DROBNICK. Studies in the Quercus undulata complex. II. The contribution of Quercus turbinella. Amer. Jour. Bot. 48(4): 329–339. Illus. 1961.—*Quercus undulata* has been interpreted as a hybrid complex involving *Q. gambelii* and several other species, including *Q. turbinella* (Tucker, 1961). In the present paper, the total distribution of the hybrids between *Q. gambelii* and *Q. turbinella* is given. Lacking direct genetic evidence, proof of hybridity is sought in a demonstration of the morphological intermediacy of these putative hybrids. Population samples of both parental species, other samples containing hybrids, and numerous individual hybrids, are analyzed on the basis of 6 differences between the parental species. The data obtained, presented in the form of pictorialized scatter diagrams, clearly show the general intermediacy of the hybrids. Of the various binomials that have been applied to forms in the *Q. undulata* complex, *Quercus pauciloba* Rydb. applies to this hybrid. The appropriate change in status (*Quercus* × *pauciloba* Rydb.) is made.

IN A RECENT paper (Tucker, 1961) *Quercus undulata* was discussed as a highly variable complex of the Southwest, putatively of hybrid origin between *Q. gambelii* and a number of other species. *Quercus turbinella* was indicated as being one contributor to this complex. It was stated, in fact, that specimens from northwestern Arizona and southwestern Utah that have been identified as "*Quercus undulata*" are quite consistently hybrids between *Q. gambelii* and *Q. turbinella.*

In an earlier paper concerned with such hybrids in Utah (Cottam et al., 1959), the present authors were concerned with the implications for postpluvial climatology of the distribution of the hybrids, but no cognizance was taken of the part this hybrid plays in the *Q. undulata* complex. The objectives of the present paper are (1) to indicate the total distri-

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bution of these putative field hybrids as presently known; (2) to provide detailed documentation of their morphological intermediacy (as evidence of their hybrid nature); and (3) to indicate which of the various names applied to different forms in the *Q. undulata* complex applies to this hybrid combination.

DISTRIBUTION.—The ecology of *Q. gambelii* and *Q. turbinella* was discussed briefly in the study cited above (Cottam et al., 1959) and many of the known

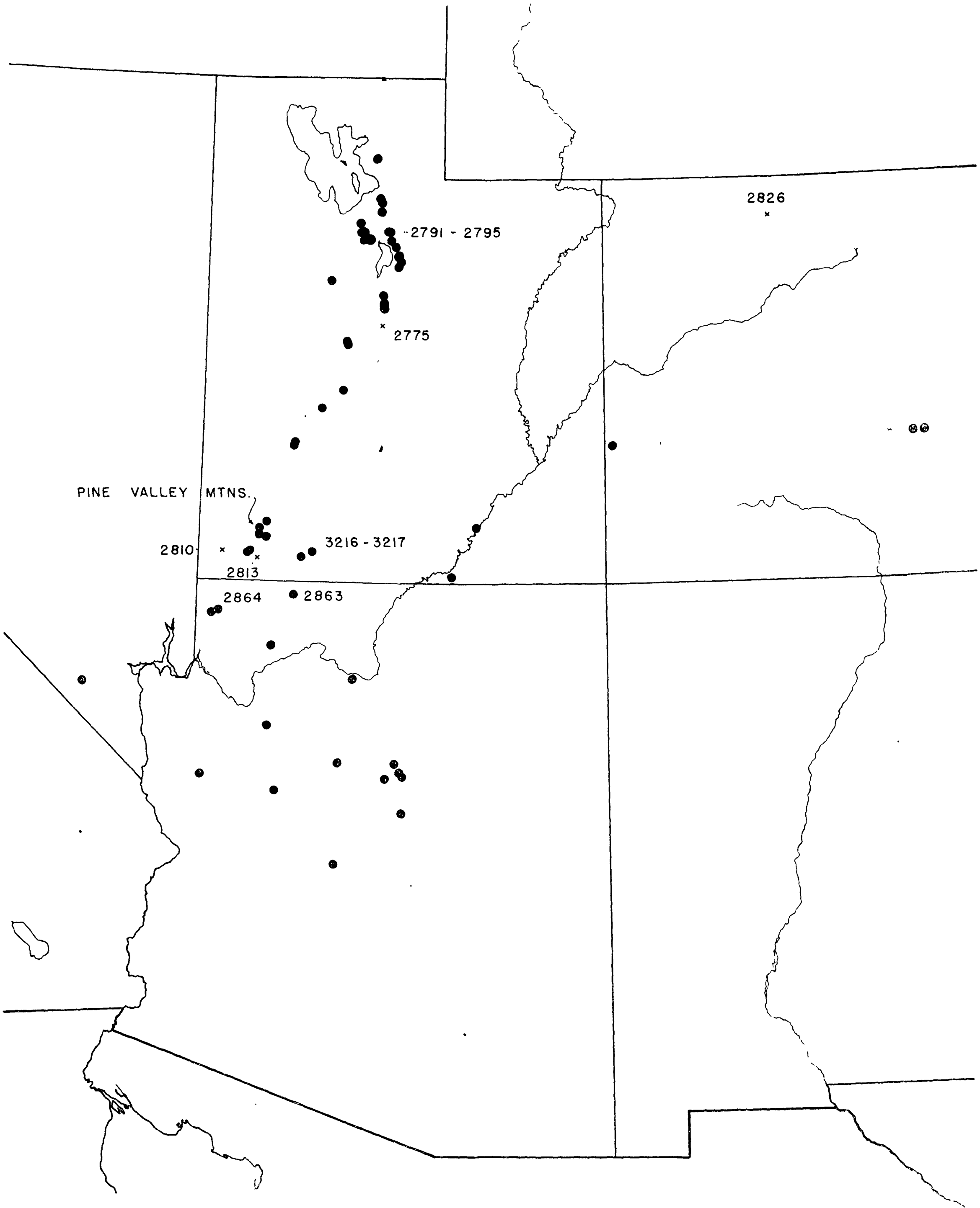



Fig. 1. Distribution of the hybrid between *Quercus gambelii* and *Q. turbinella* (hybrid locations indicated by dots; population samples of the parental species indicated by ×).

hybrid occurrences were shown (op. cit., fig. 2). Since only Utah and northwestern Arizona locations were shown, however, it seems worthwhile to record its complete distribution here (fig. 1). (Specimens and their locations are listed in the Appendix.)

The numerous occurrences of the hybrid discovered by Drobnick in central and northern Utah are of special interest because of their relictual nature. *Quercus turbinella* is completely absent from this region at present (as discussed in our previous study). The most northerly of these relictual hybrids is about 260 mi. north of the present northern limits of *Q. turbinella.* The hybrids indicated in central Colorado (fig. 1) are noteworthy also. Here, however, they occur with both parents, for *Q. turbinella* is still to be found in the area as a rare relict, hitherto unrecognized (*Brandegee 547,* canyon of the Arkansas, UC; *Engelmann s.n.,* September 25, 1874, canyon of the Arkansas, MO; *Tucker 2856–7, –23,* Phantom Canyon, beside road from Florence to Victor, DAV). It may be noted that although Harrington (1954) records *Q. turbinella* for Colorado, the one collection on which his citation is based (*E. P. Walker 181,* Paradox, Montrose Co., CS, MO, US) is, rather, our hybrid, as is another collection (*E. P. Walker 208,* US) from the same location (indicated in extreme western Colorado in fig. 1).

In areas where the parental species occur sympatrically, hybrids have usually been found at sites where one species is infrequent or rare and the other quite abundant. At locations where the parental species are equally abundant, a search for hybrids has usually been quite unproductive. They have been found commonly as single isolated individuals, but in the occasional instances where several occur together, the group will usually include apparent back-crosses to the more abundant parent. The following are 2 examples: (1) 1.2 mi. north, northeast of Alpine, Utah County, Utah, and (2) near the mouth of Willow Creek Canyon, southeast of Mona, Juab County, Utah. At both locations, hybrids (probably $F_1$'s) were found in the immediate vicinity of a number of *gambelii*-like intermediates, in all probability back-crosses to *Q. gambelii,* which was common at both localities.

DIFFERENCES BETWEEN QUERCUS GAMBELII AND Q. TURBINELLA.—*Quercus turbinella* is perhaps more strikingly different from *Q. gambelii* morphologically than is any other species involved in the *Q. undulata* complex (Tucker, 1961, fig. 1). Their principal morphological differences are summarized in table 1, the most conspicuous of these being leaf differences. The medium-sized to moderately large, lobed, green (and often glossy) leaves of *Q. gambelii* contrast sharply with the very small, spinose-dentate, pale grayish-green leaves of *Q. turbinella. Quercus gambelii* is deciduous, losing its leaves in late fall, whereas the leaves of *Q. turbinella* are persistent through the winter. These species tend to differ in a number of other characters. In *Q. turbinella* the lower leaf surface bears, in addition to stellate pubescence, yellow glandular puberulence, usually in abundance. In *Q. gambelii* such puberulence is often lacking, and, when present, lacks the yellow color of *Q. turbinella.* The acorns are typically smaller in *Q. turbinella.* The cups, for example, seldom exceed 12 or 13 mm. in diameter, whereas in *Q. gambelii* they are commonly 12–16 (infrequently to 20) mm. in diameter. The cup scales tend to be more conspicuously thickened basally in *Q. gambelii* than in *Q. turbinella.* Both species are usually shrubby in growth habit, *Q. turbinella* fairly consistently so; only infrequently does it become a small tree. *Quercus gambelii,* however, often differs in either of 2 ways. On the one hand it is often distinctly arborescent. In some parts of its range (notably in the mountains of west central New Mexico, the Abajo Mountains of southeastern Utah, and on Mt. Trumbull in northern Arizona) it is sometimes a tree of quite respectable dimensions (40–50 ft. in height, with trunk diameters up to 2 ft.). On the other hand, although often shrubby, single individuals commonly form rather extensive thickets through clonal proliferation, a mode of development rarely encountered in *Q. turbinella.*

EVIDENCE OF HYBRIDITY.—The best proof of the actual hybrid nature of putative field hybrids is obtained by the synthesis of closely similar hybrids by experimentally crossing the species presumed to be the parents. In the present study no experimental crossing has thus far been attempted. Direct genetic evidence can also be obtained if seedling

TABLE 1. *Principal morphological differences between Quercus gambelii and Q. turbinella*

| | *Q. gambelii* | *Q. turbinella* |
|---|---|---|
| Leaves | | |
| size | moderately large—55–120 (or more) mm. long. | small—15–35 (or more) mm. long. |
| margin | moderately to deeply lobed; lobes rounded to obtusely pointed at apex. | leaves not lobed, but dentate; teeth spinose. |
| color | upper leaf surface dark to bright green, and (commonly) glossy. | upper leaf surface gray-green and dull (often more or less glaucous—rarely if ever glossy). |
| foliar trichomes | stellate hairs of lower leaf surface with 4 or fewer rays. | stellate hairs with 8 or more rays. |
| Branchlets | moderately to sparsely pubescent or glabrate. | usually densely tomentulose. |
| Buds | moderate in size and ovoid. | small, globose or sub-globose. |

progenies of such putative hybrids show a segregation of parental characteristics. We have several such progeny tests in progress, but none have as yet been completed. In the absence of such direct genetic evidence, hybridity is best established by demonstrating the putative hybrids to be morphologically intermediate between the presumed parents.

Intermediacy in a single conspicuous character can be merely a coincidence, of course, rather than an expression of hybridity. It is hazardous, furthermore, for the casual student to assume the occasional aberrant form to be a hybrid merely on the basis of a general impression, and in the absence of an analysis of characters. Such assumptions of hybridity have been decried—and properly so—by students of difficult groups (e.g., Wiegand, 1935; Muller, 1941, 1951, p. 22) in which unusual variation may result from a number of causes. When analysis of the aberrant form does, however, reveal intermediacy in many characters—indeed, in virtually any character in which the presumed parents differ—any other explanation becomes highly improbable.

In order to have a basis for judging our putative hybrids, analyses were made of several population samples of both parental species, using 6 of the most constant differences between them. Population samples containing hybrids, as well as numerous individual hybrids, were analyzed in turn, in exactly the same way. Data from all these analyses are presented in the form of pictorialized scatter diagrams (cf. Anderson, 1949). The symbols used are explained in table 2; locations and other data for the population samples are included in table 3; and similar data for the numerous individual collections analyzed for fig. 9–11 are listed in the appendix.

In the pictorialized scatter diagrams the values for leaf length (horizontal axis) and vein:lobe ratio (vertical axis) are plotted on a logarithmic scale rather than a simple arithmetical scale. In quantitative characters such as these, a comparison of *relative* variation in different species is better shown in this fashion (cf. Smith, 1937). In leaf length, for example, *Q. gambelii* has a far greater range in absolute values (ca. 60–130 mm.) than *Q. turbinella* (ca. 15–35). Thus, when plotted on an arithmetical scale, a population sample of *Q. gambelii* appears to be much more variable in this character than one of *Q. turbinella*. The relative variation, however, or percentage increase from smallest to largest value, is actually not very different in the 2. This fact is well portrayed when a logarithmic scale is used, and doubtless gives a more faithful picture of the relative genetic variability of the 2 species.

The 6 characters, and our methods of analysis, were as follows:

*Leaf length.*—A single respresentative leaf (blade + petiole) of each specimen was measured with a millimeter scale.

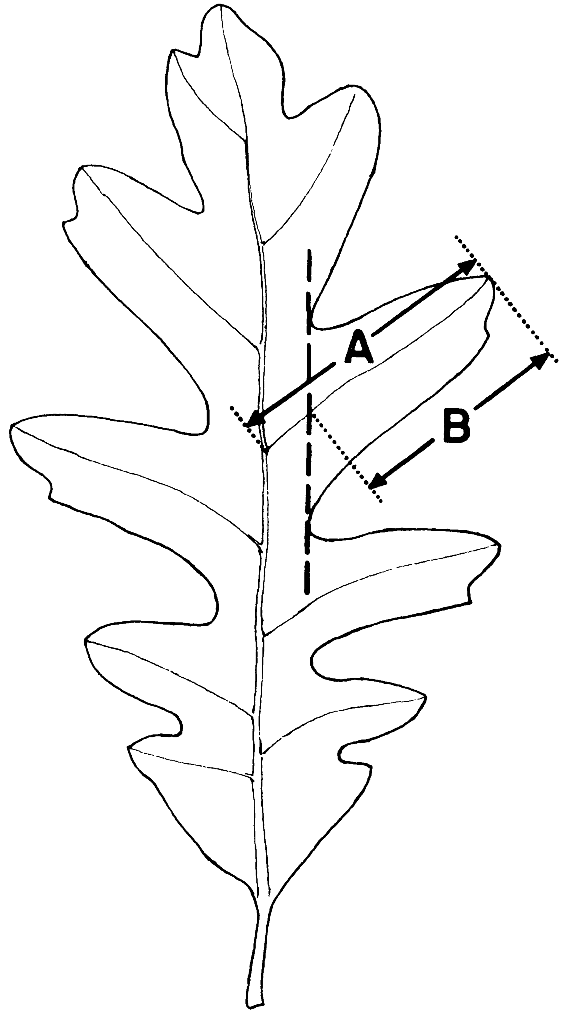



Fig. 2. Measurements taken for vein length (A) and lobe length (B). The ratio, A:B, is used as an index of the degree of lobing (vertical axis, figs. 3–11).

TABLE 2. *Explanation of symbols used in pictorialized scatter diagrams*

| Character | *Q. gambelii* (●) | Intermediate (ꝺ) | *Q. turbinella* (ꝺ) |
|---|---|---|---|
| leaf color | ● | ⊙ | ○ |
| lobe apex | ○ | ό | ό |
| twig pubescence | ○ | ɓ | ɓ |
| stellate hairs | ○ | ꝺ | ꝺ |

Whenever possible, the same leaf was used in analyzing the 2 following characters, also.

*Relative depth of lobing or indentation.*—The longest lobe (or tooth) of the leaf was measured with a millimeter scale as shown in fig. 2. In measuring small teeth (e.g., those of most specimens of *Q. turbinella*), an ocular micrometer in a dissecting microscope was used, the values obtained then being converted to millimeters. *Quercus turbinella* and *Q. gambelii* differ in absolute depth of indentation as well as in relative depth. The latter difference, it was felt, would be more nearly independent of leaf size than absolute depth of indentation. Therefore, it was used in our analysis, and expressed as a ratio of the total length of the secondary vein of the lobe (value A, fig. 2), to the length of the lobe proper (value B, fig. 2).

*Stellate hairs.*—Using a compound microscope (at ca. 100×) and reflected light, an area on the underside near the middle of the leaf was examined, and 10 stellate hairs (5 each from 2 different fields) were chosen at random, and the ray number of each was counted and recorded. Whenever all 10 counts were typical of *Q. gambelii*—4 or fewer (as was nearly always the case with pure *gambelii*), or of *Q. turbinella*—8 or more (as was nearly always the case with pure *turbinella*), only the 1 leaf was checked. Whenever 2 or more of the counts were in the intermediate range (5–7), however, an additional leaf was checked. If results from the 2 differed markedly, still others were checked—the total being as high as 5 leaves in some cases. Finally, the mean of all counts for each specimen was computed, a figure of 4.0 or less being rated as *Q. gambelii*, 4.1–7.9 as intermediate, and 8.0 or more as *Q. turbinella*.

*Leaf color, lobe apex, twig pubescence.*—On each of these characters, 3 grades were recognized, *gambelii*, intermediate, and *turbinella*, determinations being made by comparison with a series of graded specimens used as standards. The latter are on file with the voucher specimens of this study, in the Botany Department Herbarium, University of California, Davis.

In the several population samples of the parental species analyzed, no very great differences were apparent between those of each species. Data for 2 of each, presented as pictorialized scatter diagrams (fig. 3, 4), will serve to show their patterns of variation. Comparing *Q. gambelii* with *Q. turbinella*, the obviously very distinct patterns are a reflection of the fact that these are extremely different species morphologically. In fig. 5–11 several different situations are illustrated, all of them involving putative hybrids. These will be discussed briefly.

*No. 2864* (fig. 5).—This represents a sampling across an area about 200 yd. in extent, where *Q. turbinella* was abundant and *Q. gambelii* much less so. The xeric association included *Juniperus osteosperma*, *Pinus edulis*, *Artemisia tridentata*, and *Amelanchier utahensis*. The infrequent hybrids were sought out over the area, and a number of individuals of the parental species collected along with them, but not necessarily in numbers that would give an accurate picture of the number of hybrids relative to parental species, nor even of the relative numbers of the 2 parents. Hence, this is clearly not a random sample.

It was evident that the shrubs of *Q. turbinella* were occasionally aberrant, and several such forms were collected along with others more representative of the species. Judging by our analysis (fig. 5), occasional back-crossing of the hybrids is probably the source of this variability. Such *selective* sampling thus brings out an important point that could well have been missed altogether in a sample of comparable size taken in a truly random fashion.

*Nos. 2791–2795* (fig. 6).—This series of collections was made at one of the numerous relictual hybrid localities in Utah, far north of the present

TABLE 3. *Population samples illustrated in fig. 3–8*

| Taxon | Collection and date | Figure | Location |
|---|---|---|---|
| *Q. gambelii* | J. M. Tucker 2775<br>6 August, 1955 | 3 | Chicken Creek Canyon, 2 mi. east of Levan, Juab Co., Utah |
| *Q. gambelii* and hybrids | J.M.T. 2791–2795<br>11 August, 1955 | 6 | 1.2 mi. north, northeast of Alpine, Utah Co., Utah |
| *Q. turbinella* | J.M.T. 2810<br>15 August, 1955 | 3 | Ca. 2½ mi. north of Gunlock, beside road from Veyo, Washington Co., Utah |
| *Q. turbinella* | J.M.T. 2813<br>16 August, 1955 | 4 | Ca. 1 mi. northeast of Leeds, Washington Co., Utah |
| *Q. gambelii* | J.M.T. 2826<br>31 August, 1955 | 4 | Ca. 16 mi. north of Steamboat Springs, Routt Co., Colo. |
| hybrids | J.M.T. and<br>H.S. Haskell 2863 | 8 | Ca. 10 mi. west of Pipe Springs, Mohave Co., Ariz. |
| *Q. gambelii*, *Q. turbinella*, and hybrids | J.M.T. and H.S.H.<br>2864 | 5 | Black Rock Mountain, ca. 19 mi. west of Wolfhole, Mohave Co., Ariz. |
| *Q. gambelii*, *Q. turbinella*, and hybrids | J.M.T. 3216–3217 | 7 | Hills on east edge of Glendale, Kane Co., Utah |

northern limits of *Q. turbinella*. Here, 2 extensive hybrid clones (indicated by "H" in fig. 6)—clearly different individuals—grew side by side. In August, 1955 (when visited by Cottam and Tucker) one was bearing acorns in some abundance, a noteworthy fact in view of the usual sterility of such hybrids. *Quercus gambelii* was common in the vicinity (individuals indicated by "G" in fig. 6). On the slope immediately below the 2 hybrids was a cluster of 10 much smaller shrubs (the 10 remaining symbols in fig. 6) from 4 to 7 ft. in height, distinctly more *gambelii*-like than the hybrids. At one extreme morphologically they were perceptibly intermediate, but at the other extreme they graded into, and seemed scarcely distinguishable from *Q. gambelii*. Most, if not all, are probably back-crosses to that species.

*Nos. 3216–3217* (fig. 7).—This was a hybrid swarm occurring along the top of a ridge, intermingled with shrubs of both parental species. *Quercus turbinella* was largely confined to the south-facing slope, *Q. gambelii* to the north-facing slope.

*No. 2863* (fig. 8).—This population sample was from a very large hybrid swarm of low shrubby clones up to 5 or 6 ft. in height, some of them very extensive. It occupied an area of sandy washes and

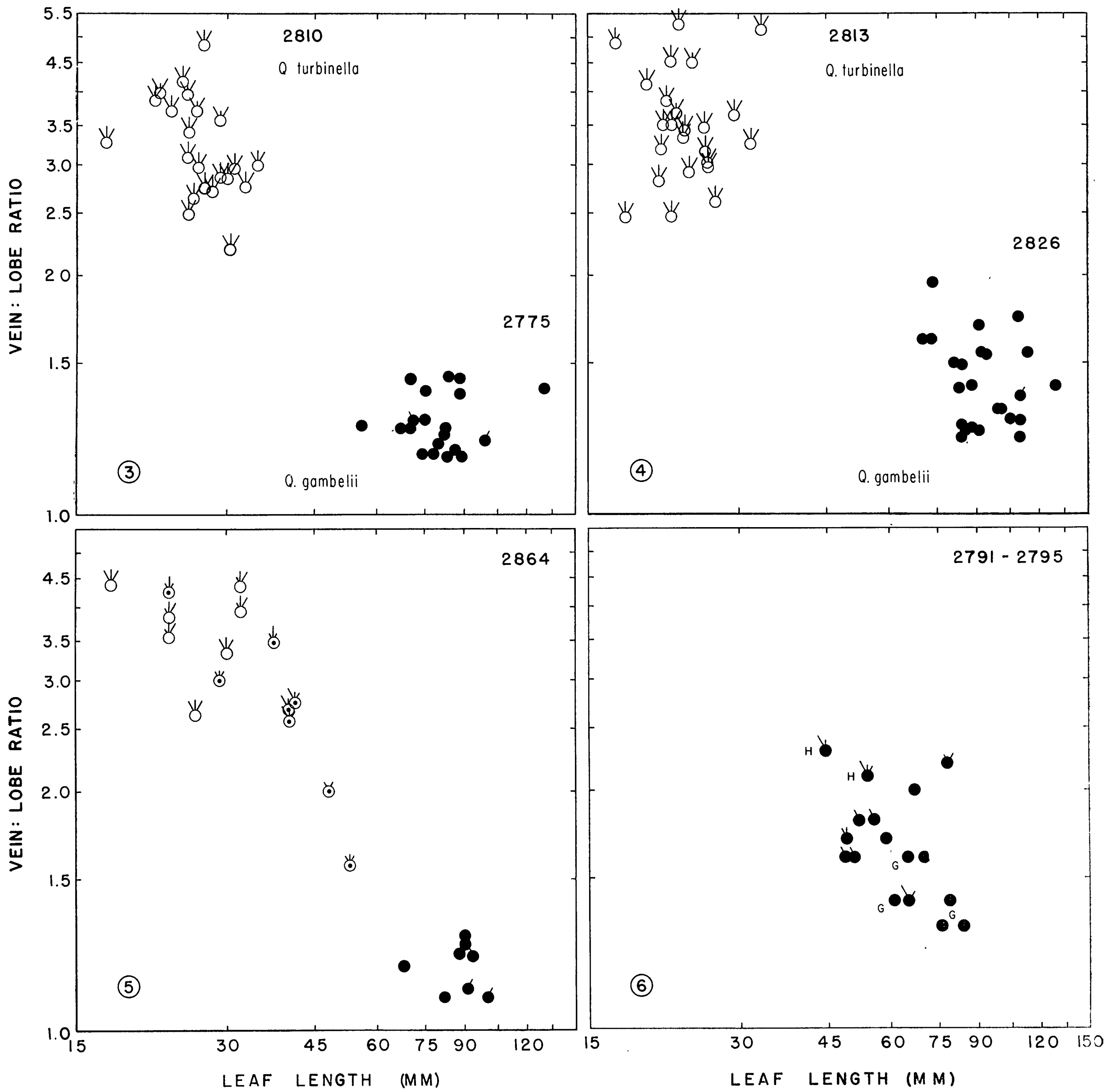
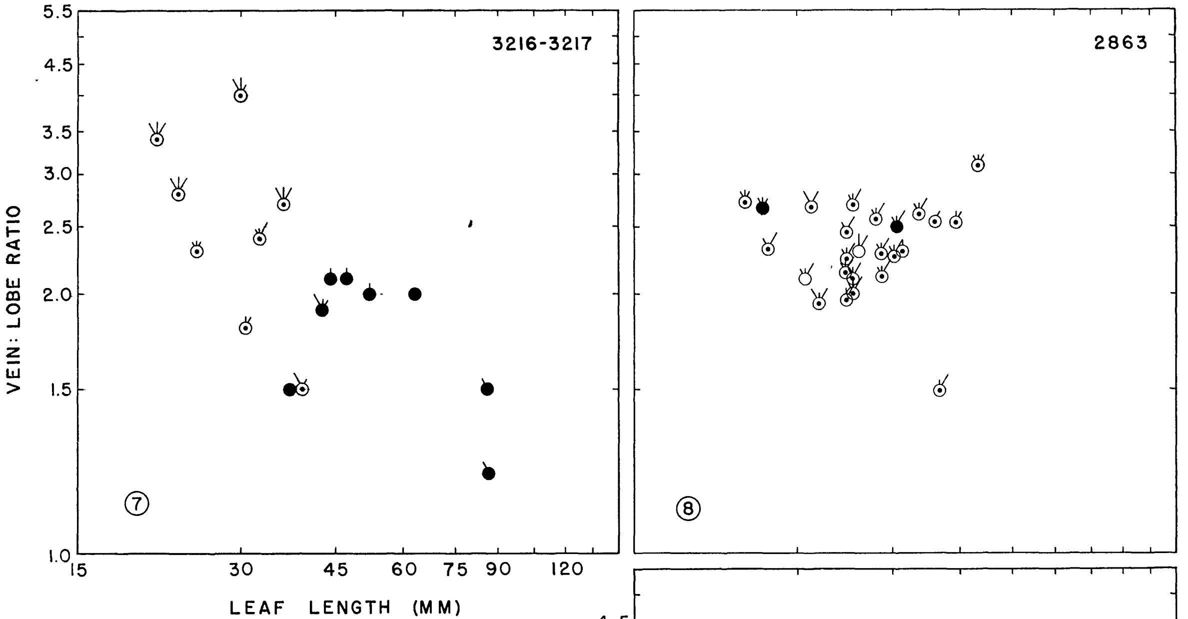



Fig. 3–6. Pictorialized scatter diagrams.—Fig. 3, 4. In each figure a population sample of *Q. gambelii* is included in the same diagram, for ready comparison, with one of *Q. turbinella*.—Fig. 5. Population sample including *Q. gambelii*, *Q. turbinella*, and hybrids.—Fig. 6. Population sample including *Q. gambelii* (G), hybrids (H), and putative back-crosses.

hummocks several hundred yd. across, at an elevation of about 4900–5000 ft. Associated species included *Juniperus osteosperma,* scattered pinyon pines (*Pinus edulis*), *Amelanchier utahensis,* and *Yucca* sp. The great majority of these oaks were distinctly intermediate in the sum of their characters, but exhibited remarkable variation from clone to clone. Indeed, close inspection of fig. 8 reveals such unusual character combinations as the stellate hairs typical of *Q. turbinella* combined with relatively large and deeply lobed leaves, and the presence of *gambelii* leaf color in one of the smallest-leaved individuals in the collection.

*Hybrids from the vicinity of Oak Grove, Pine Valley Mountains* (fig. 9).—This series of collections does not represent a single population sample, but an aggregation of scattered hybrids plus several small hybrid swarms from a limited area perhaps 2–3 square mi. in extent, including and surrounding Oak Grove Forest Camp. This location is on the southeast side of the Pine Valley Mountains, Washington County, Utah, at an elevation of 6200 ft., approximately 9 mi. northwest of the small community of Leeds. The area sampled lies between 5000 and 7000 ft. The terrain is extremely rugged, the rocky, exposed, and frequently precipitous slopes occupied by xeric shrubby species, including *Q. turbinella,* with *Q. gambelii* occurring mainly in sheltered draws and on north-facing slopes.

The frequency of hybrids is remarkable here. *Quercus turbinella,* moreover, is quite evidently "absorbing" *Q. gambelii* genes in this area. For example, a number of individuals of *Q. turbinella*



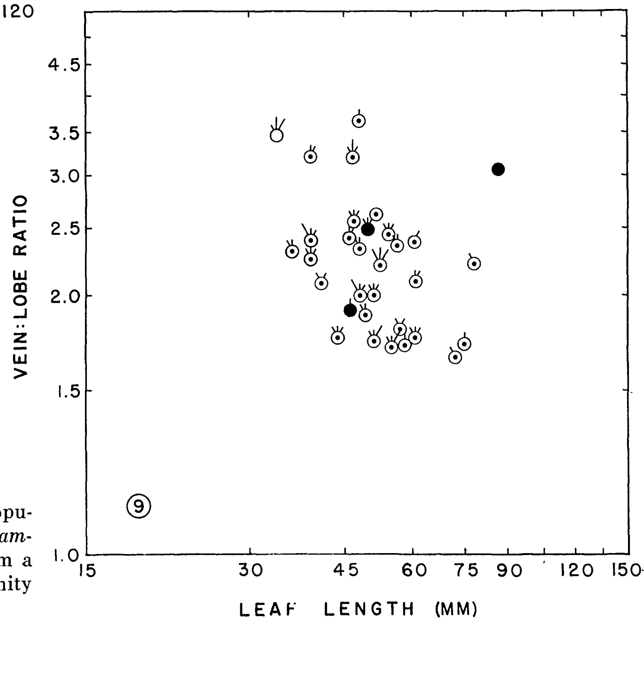




Fig. 7–9. Pictorialized scatter diagrams.—Fig. 7. Population sample from a hybrid swarm together with *Q. gambelii* and *Q. turbinella.*—Fig. 8. Population sample from a large hybrid swarm.—Fig. 9. Hybrids from the vicinity of Oak Grove, Pine Valley Mountains.

and *Q. gambelii* were collected along with the hybrids (shown in fig. 9) by Cottam in 1956. Several of the collections of *Q. turbinella* appeared to show slight hybrid influence, and 2 that were obviously "aberrant" are included in fig. 9 (*Cottam 14443*—the symbol nearest the upper left corner, and *14605*).

In some instances, the hybrids here show rather unusual and extreme character recombinations, as in the hybrid swarm discussed above (2863). Such individuals may well represent $F_2$ or later generations, rather than simply $F_1$'s or back-crosses, which our hybrids usually seem to be.

*Other hybrids of the Pine Valley Mountain area* (fig. 10).—The collections from this area, analyzed and depicted in fig. 10, are an extensive series of hybrids and back-crosses, mostly to *Q. turbinella,* from a relatively limited area in Iron and Washington counties, Utah. Although they do not constitute a single hybrid swarm, their abundance does, however, indicate the freedom with which *Q. turbinella* and *Q. gambelii* have hybridized here.

The marked prevalence of hybrids in this general area, as indicated by these reconnaissance surveys, certainly marks the Pine Valley Mountain area as one of unusual interest. The area would appear to be an ideal one for studies of establishment, competition, or comparative ecology in general, of these 2 very dissimilar oaks and their hybrids.

*Relictual hybrids in Utah* (fig. 11).—These are hybrids from the various localities in central and northern Utah discovered by Rudy Drobnick. Since a number of hybrids were found at some locations, there are many more symbols in fig. 11 than there

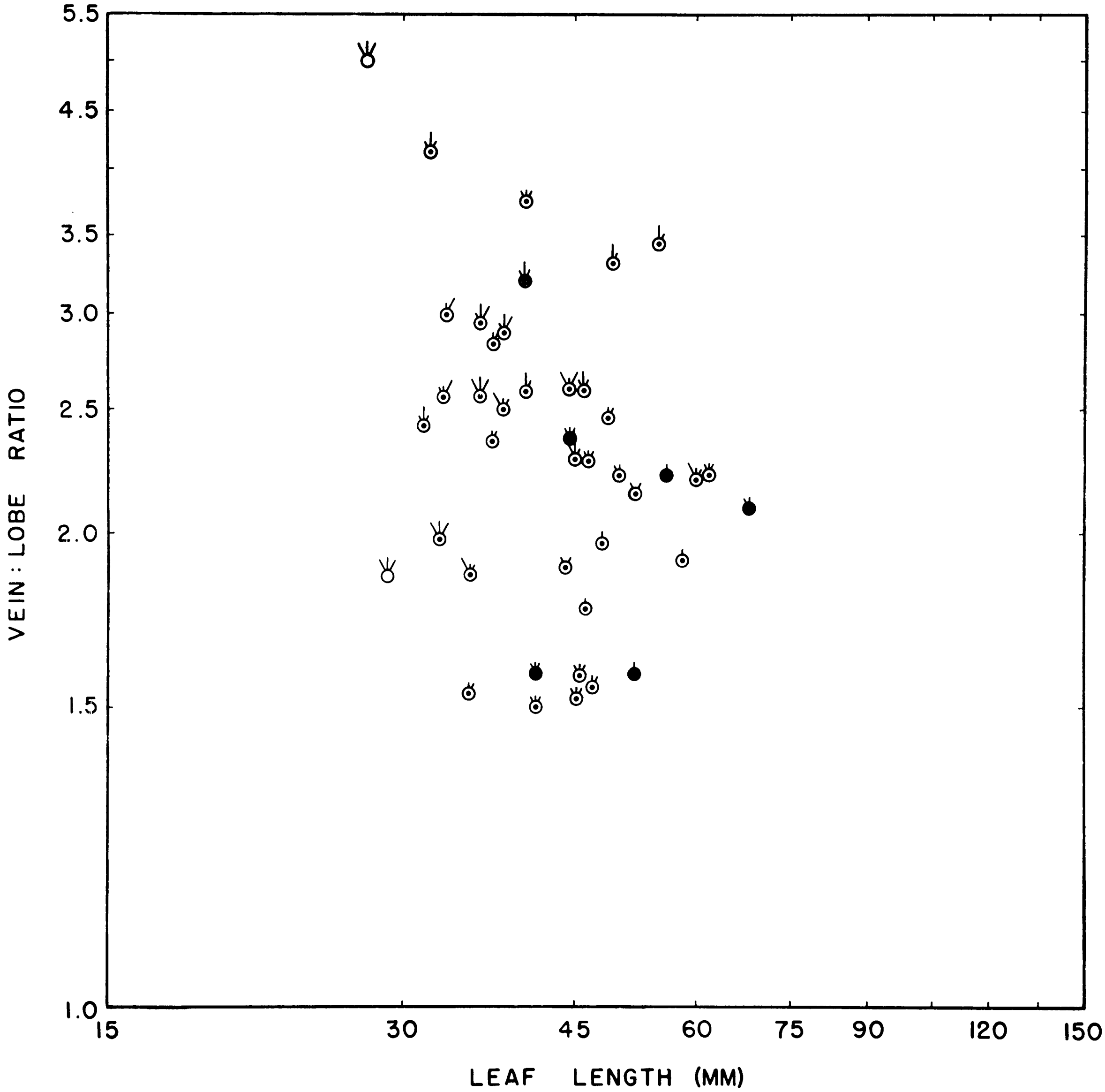



Fig. 10. Pictorialized scatter diagram of hybrids from the Pine Valley Mountain area, Utah.

are locations indicated in central and northern Utah in fig. 1. The general intermediacy of these oaks is readily apparent in fig. 11, for the great mass of the symbols occupies a central position in the diagram. On closer inspection it is apparent that the characters other than leaf length and vein: lobe ratio are in general intermediate, also. This is shown in systematized form in table 4. Thus, the best evidence one can adduce on morphological grounds for the fact of hybridity is shown here.

Another inference can be drawn from fig. 11 and table 4, which probably has more relevance, however, to the study previously reported (Cottam, et al., 1959). It will be noted that characters of the hybrids not actually scored as "intermediate" were scored as "*gambelii*" far more often than as "*turbinella.*" This indicates that genes of *Q. gambelii* occur in these hybrids with much higher frequency than genes of *turbinella.* From these data, plus the fact that putative back-crosses to *Q. turbinella* are distinctly rare (although a few examples have been found: George's Hollow, 5650 ft., Wasatch Mountains, Salt Lake County, Utah, *Drobnick 62, Tucker 2787,* DAV; Harker's Canyon, 5640 ft., Oquirrh Mountains, Salt Lake County, Utah, *Cottam and Drobnick 14094, Drobnick 3, Tucker 2779,* DAV), it would seem that the climatic change that has come about since the post-pluvial Altithermal Period (Antevs, 1955) has eliminated not only *Q. turbinella* but also most hybrids having a preponderance of *Q. turbinella* genes. Any recent reproduction on the part of the hybrids would usually have been through backcrossing to *Q. gambelii,* since *Q. turbinella* no longer exists in the area, and selfing probably oc-

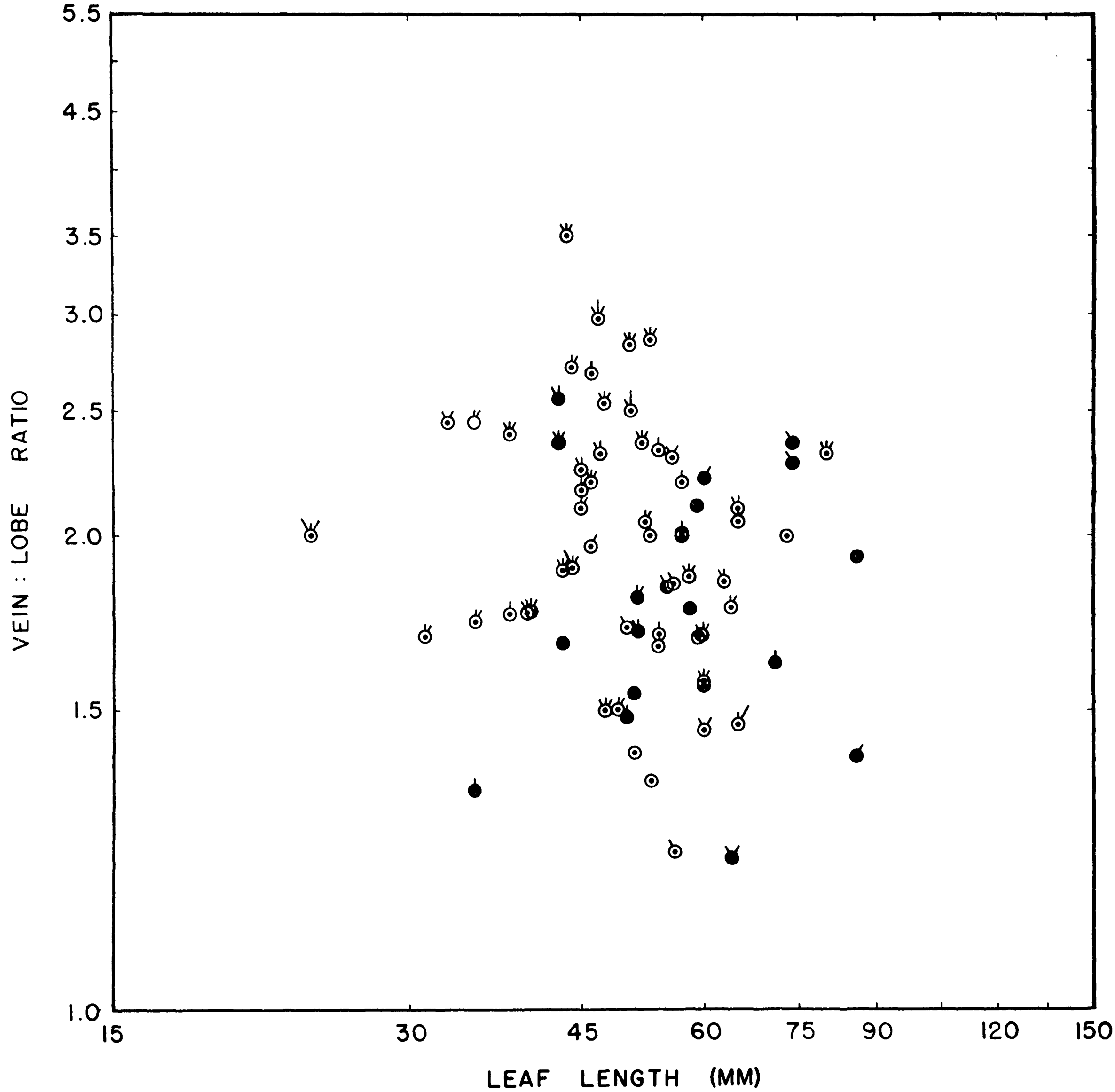



Fig. 11. Pictorialized scatter diagram of relictual hybrids from Utah.

TABLE 4. *Character analysis of 74 relictual hybrids*

| Character | Scored as *gambelii* No. | % | Scored as intermediate No. | % | Scored as *turbinella* No. | % |
|---|---|---|---|---|---|---|
| | (over 63 mm.) | | (37–63 mm. incl.) | | (under 37 mm.) | |
| leaf length | 12 | 16.2 | 56 | 75.7 | 6 | 8.1 |
| | (under 1.75) | | (1.75–2.4) | | (over 2.4) | |
| vein:lobe ratio | 25 | 33.8 | 38 | 51.3 | 11 | 14.9 |
| leaf color | 20 | 27.0 | 53 | 71.6 | 1 | 1.4 |
| lobe apex | 23 | 31.1 | 49 | 66.2 | 2 | 2.7 |
| twig pubescence | 38 | 51.3 | 33 | 44.6 | 3 | 4.1 |
| stellate trichomes | 34 | 46.0 | 38 | 51.3 | 2 | 2.7 |

curs only infrequently. Thus it may be inferred that a fair proportion of our hybrids are probably back-crosses to *Q. gambelii.*

NOMENCLATURE.—Of the various binomials that have been applied to forms in the *Quercus undulata* complex, 1—*Quercus pauciloba* Rydberg—clearly applies to the hybrid between *Q. gambelii* and *Q. turbinella.* The following change in status is therefore necessitated:

*Quercus* × *pauciloba* Rydb. (pro sp.) (Bull. N. Y. Bot. Gard. 2:215,1901).

Rydberg's type (*D. T. MacDougal, s.n.,* 1891, Beaver Creek, Arizona; U. S. National Herbarium no. 243708) is quite similar, in a general way, to a number of the hybrids we have seen. It can be matched fairly closely by one of our specimens in particular: *Drobnick 84,* north of mouth of Long Canyon, 5350 ft., Wasatch Mountains, Juab Co., Utah.

The type was analyzed on the same 6 characters used in our other analyses. On leaf color and twig pubescence it was scored as *gambelii;* on leaf size and depth of lobing, as an aberrant *gambelii,* or a *gambelii*-like intermediate; and on lobe apex and stellate hairs it was scored as intermediate. Thus it may possibly represent a back-cross to *Q. gambelii,* an impression created also by even a casual inspection of the type (see Plate 160-b, Trelease, 1924).

The locality given by MacDougal ("Beaver Creek") is somewhat indefinite since it does not specify whether it was Wet Beaver Creek or Dry Beaver Creek (much less specify *where* on "Beaver Creek"). It does at least indicate a general area, however, from which we have seen one other collection of our hybrid: *H. kuhne, s.n.,* Nov. 11, 1959, Bar-D Ranch, Apache Maid Ranger Station, Coconino Co., Arizona (DAV 28118). This location, on the upper Wet Beaver watershed in an area forested by *Pinus ponderosa* and *Q. gambelii,* lies slightly above the altitudinal range of *Q. turbinella.* The latter does not occur in this immediate area. It may be noted, incidentally, that several other hybrids are known from the Flagstaff area 20–30 mi. farther north (Mt. Eldon, 7500 ft.; Lake Mary, 7200 ft.). These locations are still higher and probably even farther removed from the range of *Q. turbinella.* Long-range pollination could possibly account for these hybrids of course, but to us a more likely explanation would be to regard them as relicts of the altithermal period of postglacial time. During this period, the increased temperature and dryness of which has been well established by evidence from a number of fields, *Q. turbinella* may well have extended its range altitudinally above its present limits in this area, just as it evidently extended its range latitudinally into northern Utah, some 260 mi. beyond its present northern limits (Cottam, Tucker, and Drobnick, 1959).

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## APPENDIX

Hybrids included in fig. 1, 10, 11.

A. Hybrids of the Pine Valley Mountain area, Utah, included in figures 1 and 10 (all collections are by Cottam and Drobnick).—*IRON COUNTY:* 3–4 mi. NW of Kanarraville, *14759;* 4 mi. NW of Kanarraville, 6000 ft., *14760;* ditto, 6500 ft., *14761, 14762, 14763, 14764. WASHINGTON COUNTY:* ¼ mi. N of Oak Grove, Pine Valley Mountains, *14708;* E of Oak Grove, 6500 ft., Pine Valley Mountains, *14709;* road 1–3 mi. N of New Harmony, 6000 ft., *14710;* near road 1 mi. N of New Harmony, 5500–6000 ft., *14711;* along road 1–3 mi. N of New Harmony, 5500 ft., *14712;* canyon road 1–3 mi. N of New Harmony, 5500 ft., *14713, 14715, 14717, 14718, 14719, 14720, 14721, 14722, 14723, 14724, 14726, 14727, 14728, 14729;* Pinto road, 1–3 mi. N of New Harmony, 5500 ft., *14730, 14732;* 1 mi. W of New Harmony, 5500 ft., *14733;* ditto, 6000 ft., *14734;* canyon 1½ mi. W of New Harmony, 6500 ft., *14735, 14738, 14740, 14741, 14742; ridge* 1½ mi. W of New Harmony, 6500 ft., *14743, 14736; ridge* 1 mi. W. of New Harmony, 6500 ft., *14748;* 1 mi. W of New Harmony, 6000 ft., *14752, 14753, 14754, 14755;* ¼ mi. SE of New Harmony, 5300 ft., *14756;* ditto, 5200 ft., *14757.*

B. Relictual hybrids of the Great Basin in Utah, included in fig. 1 and 11 (all collections are by Drobnick).—*BEAVER COUNTY, Mineral Mountains:* ½ mi. N. of Adamsville to Milford Mt. Pass road, *86;* E of Milford, *88. JUAB COUNTY:* 4.6 mi. N of Nephi, Wasatch Mountains, *63, 64, 65, 66, 83, 84. MILLARD COUNTY, Canyon Mountains:* first draw N from mouth of Oak Creek Canyon, *72, 73, 74, 75, 76. Pahvant Mountains:* ½ mi. N. from mouth of Pioneer Creek Canyon, 6100 ft., *69;* Baker Canyon, 5800 ft., 13.5 mi. by highway, S of Kanosh, *70. SALT LAKE COUNTY, Oquirrh Mountains:* Harkers Canyon, 5760 ft., *1, 2;* 5640 ft., *3;* 6000 ft., *4;* 1½ mi. W of Orr's Ranch, 5700 ft., *5, 6, 7, 8;* Coon Canyon, 5300 ft., *10, 11;* ditto, 5600 ft., *12, 13, 14;* Keystone Gulch, 6360 ft., 1.3 mi. W of Lark, *15. Wasatch Mountains:* George's Hollow, E of Fort Douglas, 5650 ft., *61, 62;* mouth of Dry Canyon, 5250 ft., *67;* mouth of Big Cottonwood Canyon, 5000 ft., *68. Traverse Mountains:* 2 mi. S of Herriman, 5400 ft., *16, 17, 18, 19, 20, 80. TOOELE COUNTY, Oquirrh Mountains:* 0.8 mi. N from mouth of Flood Canyon, 5600 ft., *47, 48;* small draw between Flood and Pass canyons, 5650 ft., *49, 50;* small canyon between Flood and Pass canyons, 5900 ft., *51;* ditto, 6950 ft., *52;* 0.2 mi. N from mouth of Pass Canyon, 5600 ft., *53, 54;* ditto, 5500 ft., *55, 57;* 0.2 mi. NW from mouth of Pass Canyon, *56, 58, 59;* 0.3 mi. up Pass Canyon from mouth, 5850 ft., *60;* between Flood and Pass Canyons, 5060 ft., *89. Sheeprock Mountains:* rocky draw N from mouth of East Government Canyon, 6400 ft., *85. UTAH COUNTY, Wasatch Mountains:* 1.9 mi. NNE of Alpine, 5700 ft., *21, 22;* 1.2 mi. NNE of Alpine, 5250 ft., *23, 24, 25, 26, 28, 29, 30, 31, 32, 33, 34, 35;* ditto, 5500 ft., *81, 82;* 2.5 mi. S from mouth of American Fork Canyon, 5460 ft., *36;* near mouth of Sumac Hollow, 5020 ft., *37, 38, 39, 41, 42;* 1.5 mi. N from mouth of Hobble Creek Canyon, 5650 ft., *44, 45, 46. WASHINGTON COUNTY:* 1 mi. W of New Harmony, Pine Valley Mountains, 6000 ft., 77.

C. Additional hybrid locations included in fig. 1 (where a single dot, however, may represent a location from which numerous collections have been seen).—*ARIZONA, Coconino County:* Oak Creek Canyon, *Deaver 1869* (DAV); Mt. Elden, 7500 ft., *Deaver 1241* (DAV); vicinity of Flagstaff, *Deaver s.n.*, 1935 (ARIZ); near El Tovar, Grand Canyon, *Eastwood 3780* (ARIZ); Oak Creek, *Fernow 1896* (US); Mt. Elden, 7000 ft., *Goldman 2137* (US); Grand Canyon (El Tovar) 6866 ft., *Goldman 2216* (US); Aubrey Valley, 10 mi. N of Pica, 5600 ft., *Goldman 2276* (US); Mount Elden, E slope, 7500 ft., *Haskell & Butchart 2110, 2111* (DAV); Bar-D Ranch, Apache Maid Ranger Station, *Kuhne s.n.*, 11 Nov., 1959 (DAV); Trash tank and dam, South Rim, Grand Canyon National Park, *Lehnert s.n.*, 12 Nov., 1955 (DAV); Beaver Creek, central Arizona [Coconino County?], *MacDougal s.n.*, 7 Aug., 1891 (US) [Type of *Q. pauciloba* Rydb.]; Observatory Mesa, Flagstaff, *Rehder 81* (US); Turkey Hill, E of Flagstaff, 6800 ft., *Rehder 566* (US); ½ mi. NE of Lake Mary, 7200 ft., *Tucker & Haskell 2908* (DAV); ¼ mi. above Lake Mary, beside road to Lake Marshall, 7150 ft., *Tucker & Haskell 2910, 2912* (DAV); 10 mi. E of Ashfork, 6700 ft., *Tucker & Haskell 2914* (DAV). *Mohave County:* 1 mi. NE of Maple Canyon, Black Rock Mountain, 4500 ft., *Cottam 14223, 14226, 14227* (DAV); top of Maple Canyon, Black Rock Mountain, *Cottam 14235, 14236, 14237* (DAV); Mt. Trumbull-Uinkaret Plateau, 7500 ft., *Cottam 14258* (DAV); 2 mi. S of Cougar Springs, Bunkerville Mountains, *Cottam 14247* (DAV); S slope Mt. Trumbull, 5600 ft., *Cottam 14289, 14290* (DAV); Mt. Trumbull Plateau, 7500 ft., *Cottam 14628, 14629, 14630, 14631, 14632* (DAV); Hualpai Mts., 6500 ft., *Goldman 2990* (US). *Yavapai County:* Greene Cattle Corporation Ranch, 2 mi. E of Mt. Hope, *Tucker & Haskell 2920* (DAV); Crown King, 6000 ft., *Collector Unknown*, 25 August, 1916 (ARIZ).

*COLORADO, Fremont County:* canyon of the Arkansas, *Brandegee 547* (UC); ditto, *Engelmann s.n.*, 25 September, 1874 (MO); Phantom Canyon, beside road from Florence to Victor, *Tucker 2856–7, —23* (DAV). *Montrose County:* Paradox, 5500 ft., *Walker 181* (MO, US); Paradox, 5600 ft., *Walker 208* (US).

*NEVADA, Clark County:* Wilson's Ranch, 1180 m., *Clokey 8314 #2* (RENO).

*UTAH* (Unless cited otherwise, the following collections are in the Botany Dept. Herbarium, Univ. Calif., Davis), *Garfield County:* Little Eden, Colorado River, ca. 20 mi. SW of Hite, *Cottam 14792. Kane County:* Zion Canyon, summit of Mt. Carmel Highway, 3 mi. E of tunnel, *Cottam 14291;* S side Highway 15, 4.6 mi. E of eastern boundary of Zion National Park, *Tucker 3218–3 to 7, incl. San Juan County:* Oak Canyon, Rainbow Bridge National Monument, *Lehnert s.n.*, October, 1959. *Utah County:* 830 East 1430 North St., Provo, *Christensen s.n.*, 31 August, 1955. *Washington County:* Highway 91, 1 mi. S of New Harmony Junction, *Cottam 14282;* Highway 91, 2 mi. S of New Harmony Junction, *Cottam 14430;* road to Oak Grove, Pine Valley Mountains, 5000 ft., *Cottam 14431;* ditto, 5200 ft., *Cottam 14432;* ditto, 5300 ft., *Cottam 14433;* ditto, 5400 ft., *Cottam 14440, 14441;* ditto, 6100 ft., *Cottam 14445;* ditto 5900 ft., *Cottam 14446;* Oak Grove, East entrance, 6200 ft., *Cottam 14447;* N of Oak Grove, 6700 ft., *Cottam 14448, 14450;* ¼ mi. N of Oak Grove, 6700 ft., *Cottam 14592, 14593, 14595;* 300 yards E of Oak Grove fence, 6500 ft., *Cottam 14597, 14598, 14599, 14600;* 500 yards NE of Oak Grove, 6600 ft., *Cottam 14601;* ½ mi. NE of Oak Grove, 7000 ft., *Cottam 14608, 14609, 14610, 14611;* ¼ mi. E. of Oak Grove, 6500 ft., *Cottam 14613, 14614;* 1 mi E of Oak Grove, 6500 ft., *Cottam 14615, 14617, 14618, 14619, 14621, 14623;* Highway 91, 1.5 mi. S of New Harmony Junction, *Tucker 3221;* ¼ mi. SSE of New Harmony, *Tucker 3222–1–9 incl. Weber County:* between Bens and Birch canyons, Wasatch Mountains, 5880 ft., *Drobnick 101.*