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QUERCUS (FAGACEAE) IN THE UTAH FLORA

Stanley L. Welsh¹

ABSTRACT.—Reviewed are the oak taxa as they are presently understood in Utah. Keys and descriptions are included, occurrences are cited, and problems of hybridization are discussed. Named as new varieties from Utah are *Quercus gambelii* Nutt. var. *bonina* Welsh and *Quercus havardii* Rydb. var. *tuckeri* Welsh. Both varieties occur in southeastern Utah. *Quercus eastwoodiae* Rydb. is proposed as a hybrid.

The native oaks have been a source of confusion almost from the beginning of botanical exploration, and a huge bibliography has accumulated dealing with the oaks of Utah and the West (Harper et al. 1985). Collection of the materials serving in typification of the earliest known portion of the complex of species existing in Utah confounded interpretation from the beginning. The first epithet in our baks and a name that has long plagued Utah plant taxonomy, Quercus undulata Torr., was published in 1828 and is based on material taken by Dr. James on the Long Expedition in the summer of 1820 (Tucker 1971). The exact nature of the type material has remained obscure for reasons reviewed by Tucker (1971), but the material was evidently taken in Harding County, New Mexico, a place where Q. gambelii Nutt. and Q. grisea Liebm. coexist. Although indicating that "the type shows scant evidence of the influence of Q. gambelii (aside from characters of foliar trichomes)," Tucker (1971) concludes that the locality from which the type was taken contains a mixture of intermediates between the parental taxa and that the "species'—Quercus undulata—is in fact a variable complex derived from hybridization." The observations made by Tucker suggest, however, quite a different application of the name, i.e., that it should replace Q. grisea, a later synonym. Interpretation of the type specimen, not the population that it came from, is crucial in typification. The cloud still remains, but fortunately it is beyond the bounds of Utah.

The Utah oaks belong to three main population complexes: *Q. gambelii* Nutt., *Q. turbin*-

ella Greene, and *Q. havardii* Rydb. Within those complexes the species concepts are mostly clear and unarguable, but they have no really apparent barriers to hybridization, and intermediates are known between nearly all of them.

The following taxonomic treatment is based on the examination of more than 300 specimens in Utah herbaria and more than three decades of experience with oaks in the field.

Numbers following the descriptions of the taxa and hybrids indicate the number examined (in Arabic numerals) and the number collected by me (in Roman numerals).

Quercus L.

Trees or shrubs; wood hard, ring-porous, with prominent rays; leaves alternate, lobed, toothed, or entire; staminate flowers in usually pendulous, naked catkins; bracts caducous; calyx with 2–8 lobes; stamens 3–12; pistillate flowers with a subtrilocular, 6-ovuled ovary; stigma 3-lobed, enclosed by a scaly involucre, this hard-ened and cuplike, surrounding the base of the nut or acorn.

- 2(1). Leaf lobes typically 1–2 times longer than the width of the leaf axis, rounded to obtuse or less commonly acute and often bilobed apically; plants broadly distributed Q. gambelii

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- Leaf lobes seldom, if ever, as long as the width of the leaf axis, acute to acuminate apically 3

Quercus gambelii Nutt. Q. stellata var. utahensis A. DC., type from west of Salt Lake City (?); Q. utahensis (A. DC.) Rydb.]. Clonal, deciduous shrubs or small trees, or less commonly trees to 10 m tall and with a trunk diameter to 6 dm or more thick, spreading by rhizomes; leaves densely grayish or yellowish stellate hairy on both surfaces when young, in age stellate hairy and paler beneath but glabrate and green and subglossy above, 2.4–17 cm long, 1–11 cm wide, obovate to elliptic in outline, the sinuses obliquely descending about 1/4-3/4 to the midrib, the lateral lobes (0) 2–10, oblong to lance-oblong, entire or notched apically and sometimes again laterally; staminate catkins 3.5-5 cm long; involucral cup 3–10 mm long, 10–17 mm wide, short-pedunculate to subsessile, ca 1/4-1/2 the length of the acorn, clothed with imbricate, densely hairy scales; acorns 8–18 mm long, 7–15 mm thick. Mountain brush, sagebrush, pinyon-juniper, ponderosa pine, and aspen communities at 1,125 to 2,745 m in all Utah counties except Daggett and Rich (?); Wyoming, Colorado, New Mexico, Arizona, Nevada, Texas, and Mexico; 206 (xxi).

Gambel oak is central to a series of problematical taxa, belonging in a broad sense to the *Q. undulata* Torr. complex, in which every degree of consanguinity is recognized. All our indigenous oaks are portions of the complex, and all form intermediates wherever contact is or has been made. Viewed broadly, all could be regarded as phases of *Q. undulata*, sensu latissimo. Problems related to such an approach involve similar circumstances of hybridization with species belonging to other oak groups away from the *Q*.

undulatum centrum. Ultimate consolidation of all intergrading groups would lead to absurdity. There is one variant within Q. gambelii, however, that is so different as to require taxonomic recognition, as follows: Var. bonina Welsh var. nov. Persimilis Querco gambelii var. gambelii in foliis et habitu sed in glandibus (27–33 mm longis nec 8–18) et cupulis (20–25 mm latis nec 10–17) majoribus differt. Type: USA: Utah. San Juan County, T36S, R13E, S28, GCNRA, Lake Powell, Goodhope Bay springs, Cottonwood, oak, willow community, sandy alluvium over Chinle Formation, 21 Sept. 1983, S. L. Welsh & E. Neese 22575 (Holotype BRY; 6 isotypes | the distributed previously as Quercus). The Goodhope oak clusters about several springs Into on the east side of Goodhope Bay in the Glen Canyon National Recreation area. One of the stands has been burned by negligent recreationists, but all bear the large acorns atypical lum of Q. gambelii from other sites. Seeds taken at the time of the original collection were grown in the greenhouse at Brigham Young University by Mr. Tom Black, who planted them limit simultaneously with others of Q. gambelii Ima from Utah County. By May of the year following, the seedlings of the Goodhope oak were twice as large as those from Utah County. The plants at Goodhope Bay tend to average larger I me than those from other localities along Glen luker Canyon, but they do not appear to differ otherwise. The size might be a function of the land continuous water supply available in the late spring and seep areas. The spring area seems to be associated with joint systems in the Wingate Formation to the east, these allowing | Mail water to penetrate to the impervious Chinle Man Formation, where the water surfaces.

Quercus havardii Rydberg. Shinnery Oak.

[Q. undulata authors, not Torr.]. Clonal, deciduous, sand-binding shrubs, or, less commonly, small trees to 2 m or more; leaves densely grayish to yellowish stellate-hairy on both sides when young, less densely so in age, but only slightly, if at all, paler beneath than above, even in age, 1.5–5.5 cm long, 0.9–3.3 cm wide, oblanceolate to elliptic in outline, with usually 6–10 toothlike lateral lobes, these typically apiculate-acuminate and sometimes further notched or toothed apically; catkins 1–2.5 cm long; involucral cups 7–10 mm long, 14–18 mm wide, subsessile, ca

4-1/3 the length of the acorn, clothed with abricate, densely hairy scales; acorns 15–23 m long, 14–18 mm thick. Blackbrush, ephera, vanclevea, purple sage, and pinyon-juper communities, usually in sand, at 1,125 2,135 m in Emery, Garfield, Grand, Kane, an Juan, and Wayne counties; Arizona, New lexico, Oklahoma, and Texas; 54 (x). The innery oak, as it occurs in Utah and adjacent rizona, is more or less influenced by inrgradation with the partially sympatric Q. imbelii and Q. turbinella (Tucker 1970). Inrmediates between both of those parental pes and Q. havardii are known. However, the sandy footslope of the San Rafael Swell Emery and Wayne counties and adjacent ortions of the Navajo Basin of Utah and Ariona, the species is more or less stable and nds to be habitat specific.

Possibly because of the contribution of both . gambelii and Q. turbinella, even the more niform portions of the species differ from the ody of the taxon lying far to the east in New exico, Texas, and Oklahoma. The Navajo asin material differs from the parental type smaller and more densely hairy leaves that nd to be sharply toothed. Because of the fferences noted and because of the isolation the Navajo Basin material from its eastern ounterpart, our material is regarded as Var. ckeri Welsh var. nov. Planta inter Querco ımbelii Nutt. et Q. turbinella Greene et Q. wardii Rydb. var. havardii sed in pro max arte Q. harvardii Rydb. var. harvardii axime affini, sed in foliis minoribus et pilis us dense, et dentibus acutis differt. TYPE: SA: Utah. San Juan Co., Low Pass, ca 8 mi E of Moab, T27S, R23E, S.5, mixed desert rub community, Entrada Sandstone Foration, at 1,635 m, 10 July 1985, S.L. Welsh nd L. C. Higgins 23630 (Holotype BRY; Isopes to be distributed). Additional speciens: Utah, San Juan County, Elephant Hill cinity, in pinyon-juniper community, anyonlands National Park, 6 May 1969, S. L. elsh, D. Atwood, & L. Higgins 8878 (stamiate, BRY); Garfield Co., Henry Mts., 5 May 977, E. Neese & S. White 2784. Grand Co., loab, 8 June 1927, W. P. Cottam, 2139; ourthouse Towers, 25 Apr 1947, B. F. Harson 11124; Arches National Park, 2 May 963, L. B. Barnett et al. 56, 66; 13 July 1972, S. Allan 128; 19 July 1972, J. S. Alan 133; 5

mi NW of Moab, 21 May 1984, D. Atwood et al. 9699. Kane Co., 28 mi e of Kanab, 11 May 1953, B. F. Harrison 12049; 60 mi SE of Escalante, 7 Aug. 1957, B. F. Harrison 12723; Dance Hall Rock, 2 May 1962, J. R. Murdock 381; Hole-in-the-Rock, 4 May 1962, D. A. White 125, 27 Apr 1977, R. Foster 3602; Escalante Arm of Lake Powell, 5 June 1927, S. L. Welsh & G. Moore 11825, 11826. San Juan Co., Bluff, 2 July 1927, W. P. Cottam 2529, 2532; Monument Valley, 4 July 1927, W. P. Cottam & S. Hutchings 2585; Cow Canyon, 29 Apr 1961, C. A. Hansen 97; Squaw Flat, 15 May 1965, G. Moore 375. All are deposited at BRY.

Quercus pauciloba Rydb. (hybrid) Clonal, semievergreen shrubs or small trees mainly 2-4 m tall and with trunks 4-15 cm in diameter; leaves stellate-hairy on both surfaces when young, becoming sparingly so to glabrate on one or both sides in age, bicolored (more or less), typically green to dark green above and paler beneath, 2–10 cm long, 1–7 cm wide, usually with (0) 4–8 toothlike lateral lobes, these typically apiculate and sometimes apiculate-acuminate, rarely some of them again notched or toothed; staminate catkins 3-4 cm long; pistillate catkins, mature involucral cups, and mature acorns not present in specimens examined. Sagebrush, mountain brush, pinyon-juniper, and ponderosa pine communities at 1,220 to 2,045 m in Beaver, Iron, Juab, Kane, Millard, Salt Lake, Tooele, Utah, Washington, and Weber counties; Colorado, Arizona, and Nevada; 11 (0). Specimens designated as Q. pauciloba consist of an aggregation of hybrids and presumed introgressants involving Q. gambelii and Q. turbinella as parental types. They occur relatively commonly in areas where the two parental species coexist in Washington and Kane counties, but they occur also along the western margin of the plateaus and mountains north to Weber County, far removed from the body of Q. turbinella in Washington, Kane, and San Juan counties. The hybrids and introgressants are about on a line marking the edge of the major overthrust fault that bisects Utah. Cottam et al. (1959) and Tucker (1961a, 1961b, 1970) have postulated an interglacial advance of Q. turbinella into the Great Basin, followed by a retreat during return of harsh conditions. The hybrids were presumed to

represent first generation only, were postulated to have resulted during the incursion, and were judged to have persisted following the retreat of the one parental type. Ruled out are other possibilities such as long-distance pollination, suggested as a probability by Harper et al. (1985) and concurred in by me, because of lack of coincidence of flowering times, primarily.

Examination of specimens of the hybrid complex demonstrates several problems. First, the variation among the intermediates is greater than would be expected from first generation hybrids, suggesting introgression as well as hybridity. Indeed, a specimen from the mouth of American Fork Canyon (Lindquist s.n. 20 Jan 1981 BRY) is strictly evergreen, has staminate catkins and abortive acorns, and, if placed within specimens of Q. turbinella from Washington County, would be identified as that species. Second, although mature acorns and caps were not noted on the specimens examined, staminate catkins were present in some, suggesting the possibility of introgression occurring far north of the primary pollen source. And, the following questions are unanswered by the flow and ebb hypothesis: (1) Did a migration route occur during the time of the thermal maximum that is not now in evidence? (2) Was not a simpler and as equally accessible a route available along the canyons of the Colorado (where Q. turbinella exists in some small part, even now) and, if so, where is the matching set of hybrids in the Colorado Basin? (3) Could not long-distance pollination, even though the juxtaposition of flowering time occurs only irregularly, be sufficient to account for some, if not all, of the occurrences of the hybridization northward? And does not the pattern of distribution of hybrids along the windward side of the Wasatch frontal ranges suggest long-distance pollination? Additional studies are indicated.

Quercus eastwoodiae Rydb. (hybrid) In the Navajo Basin of Utah, along the Colorado River and its canyons, another set of hybrids and presumed introgressants are known. In general aspect and leaf morphology they resemble Q. pauciloba, but their origin seems to be different. Gambel oak grows at even the lowermost elevations in mesic canyons, on stream terraces, and around seeps, springs,

and hanging gardens. Although *Q. turbinella* is present also, the extent and total numbers appear to be limited now, and there does not seem to be evidence of a much greater incidence in the past. The turbinella live-oak is present at the confluence of Glen Canyon and the San Juan River, and also occurs as a narrow tongue along the Cockscomb in central Kane County, where it is confluent southward into the Houserock Valley area of Arizona. Intermediates between turbinella live-oak and Gambel oak are also known from this latter region.

In the remainder of the Navajo Basin the picture is complicated by still another Quercus species, i.e., the shinnery oak, Q. havardii. That species occurs as a moderately stable entity on the sandy plateaus and slopes away from the canyons proper but reaches to their margins, where the stream courses are deeply entrenched. They, too, hybridize with Gambel oak, and the hybrids and presumed introgressants survive in usually sheltered positions adjacent to or intermixed with Gambel Oak. Such intermediates are known also from the islandlike mountains that protrude from the floor of the Navajo Basin. Intermediate specimens appear superficially like those of Q. pauciloba, but they tend to be more densely hairy, to have hairs persistent on the upper surface, even in age, and to be less distinctly green, even if bicolored. These intermediates are here designated as Q. x eastwoodiae Rydb. (Bull. New York Bot. Gard. 2 210. 1901; based on, Eastwood 141, from Butler Wash, San Juan County, Utah in 1895). although the description of the type specimen indicates it to be a portion of the variation nearer to Q. gambelii. The plants are present in blackbrush, other warm-desert shrub, mountain brush, pinyon-juniper, and Douglas-fir communities at 1,130 to 1,830 m in Garfield, Grand, Kane, and San Juan counties: Arizona; 13 (ii).

Quercus turbinella Greene Turbinella Live-oak. Clump-forming (clonal?) evergreen shrubs or, less commonly, small trees, mainly 1–4 dm tall and with stem diameters to 2 dm; leaves yellowish stellate-hairy on both surfaces when young, finally glabrate and glaucous above, not especially bicolored, typically 1.3–4 cm long, 0.7–2.4 cm wide, lanceolate to oblong or suborbicular in outline, with 2–6

pairs of lateral, spine-tipped teeth or entire; staminate catkins 1–3 cm long; involucral cup 6–8 mm long, 10–14 mm wide, ca 1/4 as long as the acorn; acorns 12–24 mm long, 7–10 mm thick. Chaparral (oak, manzanita, ceanothus), pinyon-juniper, and riparian communities at 820 to 1,710 m in Kane, San Juan, and Washington counties; Nevada and Arizona; 39 (iv).

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107
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- 4(3). Plants deciduous, colonial in sandy sites, typically with branch ends protruding above tlie substrate 1-5 dm; acorns mostly over 15 mm long and about as broad; hybridizing with the former along canyons Q. luivardii
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ivardii Rydb. var. havardii sed in pro max

irte Q. harvardii Rydb. var. harvardii axime affini, sed in foliis minoribus et pilis us dense, et dentibus acutis diflfert. Type: SA: Utah. San Juan Co., Low Pass, ca 8 mi E of Moab, T27S, R23E, S.5, mixed desert irub community, Entrada Sandstone Foration, at 1,635 m, 10 July 1985, S.L. Welsh id L. C. Higgins 23630 (Holotype BRY; Isopes to be distributed). Additional speciens: Utah, San Juan County, Elephant Hill cinity, in pinyon-juniper community, anyonlands National Park, 6 May 1969, S. L. ^elsh, D. Atwood, & L. Higgins 8878 (stamiite, BRY); Garfield Co., Henry Mts., 5 May)77, E. Neese & S. White 2784. Grand Co.', [oab, 8 June 1927, W. P. Cottam, 2139; ourthouse Towers, 25 Apr 1947, B. F. Harson 11124; Arches National Park, 2, May ^63, L. B. Barnett et al. 56, 66; 13 July 1972,

S. Allan 128; 19 July 1972, J. S. Alan 133; 5

mi NW of Moab, 21 May 1984, D. Atwood et al. 9699. Kane Co., 28 mi e of Kanab, 11 May 1953, B. F. Harrison 12049; 60 mi SE of Escalante, 7 Aug. 1957, B. F. Harrison 12723; Dance Hall Rock, 2 May 1962, J. R. Murdock 381; Hole-in-the-Rock, 4 May 1962, D. A. White 125, 27 Apr 1977, R. Foster 3602; Es-

calante Arm of Lake Powell, 5 June 1927, S.
L. Welsh &G. Moore 11825, 11826. San Juan
Co., BluflF, 2 July 1927, W. P. Cottam 2529,
2532; Monument Valley, 4 July 1927, W. P.
Cottam & S. Hutchings 2585; Cow Canyon,
29 Apr 1961, C. A. Hansen 97; Squaw Flat, 15
May 1965, G. Moore 375. All are deposited at
BRY.

Quercus pauciloba Rydb. (hybrid) Clonal, semievergreen shrubs or small trees mainly 2-4 m tall and with trunks 4-15 cm in diameter; leaves stellate-hairy on both surfaces when young, becoming sparingly so to glabrate on one or both sides in age, bicolored (more or less), typically green to dark green above and paler beneath, 2-10 cm long, 1-7 cm wide, usually with (0) 4-8 toothlike lateral lobes, these typically apiculate and sometimes apiculate-acuminate, rarely some of them again notched or toothed; staminate catkins 3-4 cm long; pistillate catkins, mature involucral cups, and mature acorns not present in specimens examined. Sagebrush, mountain brush, pinyon-juniper, and ponderosa pine communities at 1,220 to 2,045 m in Beaver, Iron, Juab, Kane, Millard, Salt Lake, Tooele, Utah, Washington, and Weber

counties; Colorado, Arizona, and Nevada; 11 (0). Specimens designated as Q. pauciloba consist of an aggregation of hybrids and presumed introgressants involving Q. gambelii and Q. turbineUa as parental types. They occur relatively commonly in areas where the two parental species coexist in Washington and Kane counties, but they occur also along the western margin of the plateaus and mountains north to Weber County, far removed from the body of Q. turbiiiella in Washington, Kane, and San Juan counties. The hybrids and introgressants are about on a line marking the edge of the major overthrust fault that bisects Utah. Cottam et al. (1959) and Tucker (1961a, 1961b, 1970) have postulated an interglacial advance oiQ. turbineUa into the Great Basin, followed by a retreat during return of harsh conditions. The hybrids were presumed to

[Begin Page: Page 110]

110

Great Basin Naturalist

Vol. 46, No. 1

represent first generation only, were postulated to have resulted during the ineursion, and were judged to have persisted following the retreat of the one parental type. Ruled out are other possibilities such as long-distance pollination, suggested as a probability by Harper et al. (1985) and concurred in by me, because of lack of coincidence of flowering times, primarily.

Examination of specimens of the hybrid complex demonstrates several problems. First, the variation among the intermediates is greater than would be expected from first generation hybrids, suggesting introgression as well as hybridity. Indeed, a specimen from the mouth of American Fork Canyon (Lindquist s.n. 20 Jan 1981 BRY) is strictly evergreen, has staminate catkins and abortive acorns, and, if placed within specimens of Q. turbinella from Washington County, would be identified as that species. Second, although mature acorns and caps were not noted on the specimens examined, staminate catkins were present in some, suggesting the possibility of introgression occurring far north of the primary pollen source. And, the following questions are unanswered by the flow and ebb hypothesis: (1) Did a migration route occur during the time of the thermal maximum that is not now in evidence? (2) Was not a simpler and as equally accessible a route available along the canyons of the Colorado (where Q. turbiriella exists in some small part, even now) and, if so, where is the matching set of hybrids in the Colorado Basin? (3) Could not long-distance pollination, even though the juxtaposition of flowering time occurs only irregularly, be sufficient to account for some, if not all, of the occurrences of the hybridization northward? And does not the pattern of distribution of hybrids along the windward side of the Wasatch frontal ranges suggest long-distance pollination? Additional studies are indicated.

Quercus eastwoodiae Rydb. (hybrid) In the Navajo Basin of Utah, along the Colorado River and its canyons, another set of hybrids and presumed introgressants are known. In general aspect and leaf morphology they resemble Q. pauciloba, but their origin seems to be different. Gambel oak grows at even the lowermost elevations in mesic canyons, on stream terraces, and around seeps, springs.

and hanging gardens. Although Q. turbinella is present also, the extent and total numbers appear to be limited now, and there does not seem to be evidence of a much greater incidence in the past. The turbinella live-oak is present at the confluence of Glen Canyon and the San Juan River, and also occurs as a narrow tongue along the Cockscomb in central Kane County, where it is confluent southward into the Houserock Valley area of Arizona. Intermediates between turbinella live-oak and Gambel oak are also known from this latter region.

In the remainder of the Navajo Basin the picture is complicated by still another Quercus species, i.e., the shinnery oak, Q. havardii. That species occurs as a moderately stable entity on the sandy plateaus and slopes away from the canyons proper but reaches to their margins, where the stream courses are deeply entrenched. They, too, hybridize with Gambel oak, and the hybrids and presumed introgressants survive in usually sheltered positions adjacent to or intermixed with Gambel Oak. Such intermediates are known also from the islandlike mountains that protrude from the floor of the Navajo Basin. Intermediate specimens appear superficially like those oi

Q. pauciloba, but they tend to be more densely hairy, to have hairs persistent on the upper surface, even in age, and to be les* distinctly green, even if bicolored. These intermediates are here designated as Q. x eastwoodiae Rydb. (Bull. New York Bot. Card. 2 210. 1901; based on, Eastwood 141, from But ler Wash, San Juan County, Utah in 1895), although the description of the type specimer indicates it to be a portion of the variatior nearer to Q. g,ambeUi. The plants are present in blackbrush, other warm-desert shrub, mountain brush, pinyon-juniper, and Douglas-fir communities at 1, 130 to 1,830 m in Garfield, Grand, Kane, and San Juan counties Arizona; 13 (ii).

Quercus turbinella Greene Turbinelk
Live-oak. Clump-forming (clonal?) evergreen
shrubs or, less commonly, small trees, mainly
1-4 dm tall and with stem diameters to 2 dm:i
leaves yellowish stellate-hairy on both surfaces when young, finally glabrate and glaucous above, not especially bicolored, typicallyj
1.3-4 cm long, 0.7-2.4 cm wide, lanceolate to
oblong or suborbicular in outline, with 2-6

[Begin Page: Page 111]

January 1986

WELSH: Utah Flora, Quercus

111

pairs of lateral, spine-tipped teeth or entire; staminate catkins 1-3 cm long; involucral cup 6-8 mm long, 10-14 mm wide, ca 1/4 as long as the acorn; acorns 12-24 mm long, 7-10 mm thick. Chaparral (oak, manzanita, ceanothus), pinyon-juniper, and riparian communities at 820 to 1,710 m in Kane, San Juan, and Washington counties; Nevada and Arizona; 39 (iv).

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