



## The taxonomic status of the Mexican oak *Quercus undata* (Fagaceae, *Quercus*, Section *Quercus*)

### El estatus taxonómico del encino mexicano *Quercus undata* (Fagaceae, *Quercus*, Sección *Quercus*)

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**Abstract.** *Quercus undata* Trel. (Fagaceae, *Quercus*, Section *Quercus*) has a complex taxonomic and nomenclatural history. Intensive sampling of oaks at the type locality of *Q. undata* Trel. in Durango, Mexico and evaluation of herbarium specimens and plants in the field indicate that *Q. undata* represents variation in *Quercus chihuahuensis* Trel. in white oak communities where introgressive hybridization among *Q. chihuahuensis*, *Q. grisea* Liebm., and a third white oak, *Q. arizonica* Sarg. made species identification difficult. Endlich's type specimen of *Q. undata*, as designated by Trelease, was apparently destroyed in bombing raids on Berlin during World War II, and we propose herein as lectotype the Trelease illustration of the type. An epitype is also designated in support of the lectotype, given that some features cannot be critically observed on the illustration. The long peduncles of the specimen illustrated by Trelease indicate a close relation to *Q. chihuahuensis*.

Key words: Sierra Madre Occidental, Mexico, epitype, lectotype, introgressive hybridization.

**Resumen.** *Quercus undata* Trel. (Fagaceae, *Quercus*, Section *Quercus*) tiene una compleja historia taxonómica y de nomenclatura. Un muestreo intensivo de los encinos en la localidad tipo de *Q. undata* en Durango, México y análisis de ejemplares en herbario y en el campo indican que *Q. undata* representa variación en *Q. chihuahuensis* Trel. en los sitios donde la hibridación introgresiva entre *Q. chihuahuensis*, *Q. grisea* Liebm., y un tercer encino blanco, *Q. arizonica* Sarg., dificultan la identificación de especies. El ejemplar tipo designado por Trelease aparentemente fue destruido en el bombardeo de Berlín durante la Segunda Guerra Mundial, por lo que se propone como lectotipo a la ilustración del tipo en la obra de Trelease. Se designa también un epitipo dado que algunos rasgos no pueden ser críticamente observados en la ilustración. Los largos pedúnculos del espécimen ilustrado por Trelease indican la relación cercana a *Q. chihuahuensis*.

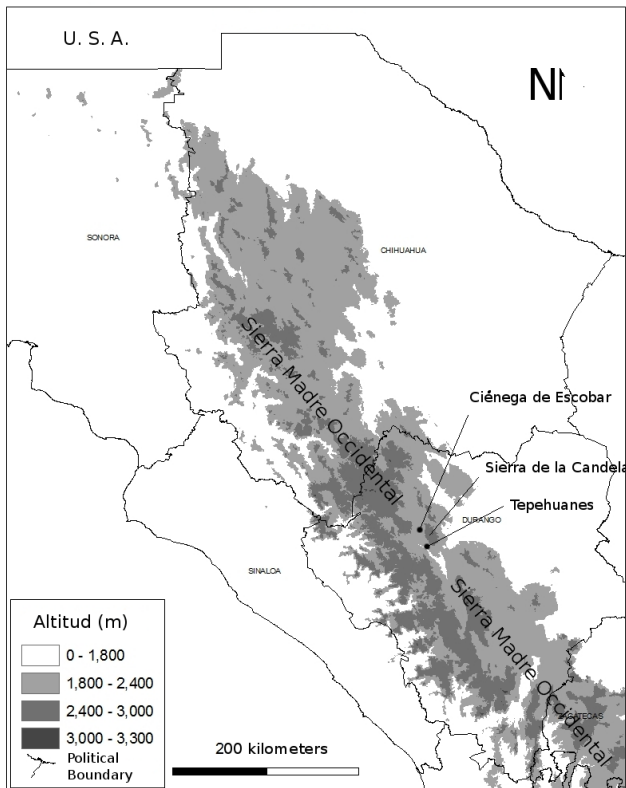
Palabras clave: sierra Madre Occidental, México, epitipo, lectotipo, hibridación introgresiva.

## Introduction

The genus *Quercus* in Mexico includes about 161 species (Valencia Avalos, 2004), and past estimates have placed more than 253 scientific names in the Mexican portion of the genus (Trelease, 1924). White oaks (Fagaceae, Section *Quercus*) in the Mexican flora remain taxonomically perplexing, due to poor morphological differentiation among many species, abundant hybridization, inadequate documentation of subgeneric

epithets, and poor representation of fertile structures in herbaria. Herbarium specimens of Mexican white oaks are commonly misidentified. Therefore revision and adequate typification of taxa in this group are important to understanding and clarifying the species.

Trelease (1924) described *Quercus undata* Trel. based on 3 herbarium specimens collected on the low elevation slopes of the interior of the Sierra Madre Occidental, in Durango, Mexico (Fig. 1). He considered *Q. undata* a close relative of *Q. chihuahuensis* Trel., a small tree from northern Mexico, common at low elevations in the Sierra Madre Occidental, having classified them in the same group (series): *Chihuahuenses* Trel. Martínez (1957) considered



**Figure 1.** The Sierra Madre Occidental of Mexico, with locations of Tepehuanes and Ciénega de Escobar, Durango, Mexico.

*Q. undata* to be a synonym of *Q. chihuahuensis*. Later, McVaugh (1974) suggested that *Q. undata* was probably a name that has been applied to hybrids between *Q. grisea* Liebm. and *Q. chihuahuensis*. Despite the placement of *Q. undata* into synonymy by Martínez and McVaugh's implication that the taxon probably represents a hybrid, the taxon has since been reported in species lists of different floristic and taxonomic revisions (González-Elizondo et al., 1991 and Valencia-Avalos, 2004) and appears as a name accepted for the species in the *Royal Botanic Garden's Kew World Checklist of Seed Plants* (Govaerts and Frodin, 1998) and sources citing this reference. In regional herbaria with numerous good collections there are few specimens identified as *Quercus undata*.

Fruits visible in the published photograph of the type specimen (*Endlich 1*) in Trelease (1924: 235) have peduncles that are much longer than those of the other cited specimens (*Palmer 408* and *828*). The latter were described as “[p]ossibly to be referred here also . . .,” suggesting that Trelease may have been unsure of the range of morphological variation and character states defining this taxon; his brief description of the taxon, based on vegetative structures, lacks characters that clearly distinguish it from other taxa of low elevation white oaks

(Fagaceae, *Quercus*, Section *Quercus*) in the region: *Q. arizonica* Sarg., *Q. chihuahuensis*, and *Q. grisea*.

The type specimen of *Q. undata*, as designated by Trelease (1924): Mexico, Durango, Municipio Tepehuanes, Sierra de la Candela, 2500 m, 27 Aug 1903, *Endlich 1* (B), was apparently destroyed in bombing raids on Berlin during World War II. In this paper we select the illustration of the type of *Q. undata* as a lectotype and designate an epitype to support it. This work aims to clarify the taxonomic nature of *Q. undata* as a means of rectifying the following:

1. the absence of an extant type,
2. uncertain and unclear description of the taxon: citation, in the original description (Trelease, 1924) and, subsequently by Camus (1938 – 1939) of specimens with fruits clearly belonging to 2 distinct morphological species,
3. disagreements among taxonomists about the taxonomic nature of *Q. undata* (Trelease, 1924; Martínez, 1957; McVaugh, 1974; Valencia-Ávalos, 2004),
4. literature citations that use the name incorrectly (Govaerts and Frodin, 1998), and
5. taxonomic confusion among the species of white oaks in the region.

## Materials and methods

*Examination of herbarium specimens:* specimens of *Q. arizonica*, *Q. chihuahuensis*, *Q. grisea*, *Q. undata*, and the other white oaks from the Sierra Madre Occidental region were examined at herbaria containing ample collections from the region: CIIDIR, F, IZTA, MEXU, NMC, P, and others. Remaining specimens cited in Trelease's description (*Palmer 408* and *828*) and deposited at A were also examined.

*Field sites:* principal and secondary routes of the Sierra Madre Occidental were extensively searched, including transects described by Spellenberg (2001) and Spellenberg et al. (1998). The Sierra de la Candela area, where Endlich reported have collected the type specimen, was intensively searched and systematically surveyed throughout its altitudinal range, combinations of slope directions, and various vegetation types. Samples of all white oak species encountered were collected, pressed, dried, and identified in each of the habitat types where they occurred.

The area of the type locality was determined (see “The Type Locality,” below) to be in the zone where the 3 species of white oaks, *Q. arizonica*, *Q. chihuahuensis*, and *Q. grisea* were abundant and sympatric (15.4 km north of Tepehuanes, en route to Ciénega de Escobar, and centered on 25°03'38"N, 105°20'57"W). A 1 000 m × 30 m belt transect crossing a gradient from low to high elevation

was sampled there, collecting material from all white oak individuals encountered.

Samples of foliage of each tree sampled were collected 2 m above ground level, on the south side of each tree. From each sample, morphological characters from the abaxial surface of 7 leaves and their trichomes were evaluated as shown in Fig. 2, and veins reaching the leaf margin and exceeding 0.5 mm in diameter were counted. Mean values of leaf and trichome variables were calculated for each variable and used for multivariate analyses.

Plants from the site and other sites where each species was found in allopatry were evaluated based on vegetative characters (Fig. 2), with both principal coordinates analysis and principal components analysis, to evaluate morphological variation in *Q. undata* and related taxa. Data from all variables had relatively normal distributions and similar variance among taxa, making data transformation unnecessary.

**Results**

Review of herbarium and field specimens of white oaks from much of the Sierra Madre Occidental revealed that those identified as *Quercus undata* appeared to fall within the variation observed in *Q. chihuahuensis* in hybrid swarms from this region. Trelease’s plate of the type (pl.

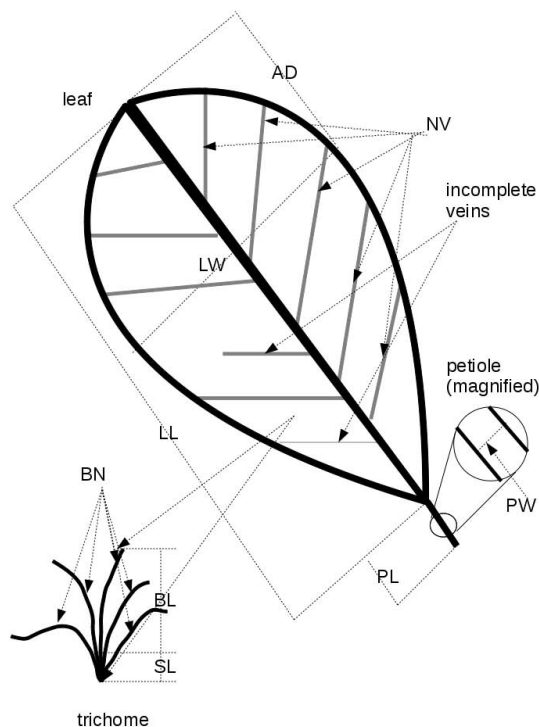
135) illustrates a specimen with densely pubescent leaves and long peduncles, characteristics of *Q. chihuahuensis*, that distinguish it from *Q. arizonica*, based on both characters, and *Q. grisea* based on the latter. *Quercus chihuahuensis* is the only low-elevation white oak with long (1.5- 3.0 [- 6.0] cm) peduncles and tomentose leaves in the Sierra de la Candela region.

According to the label data reported by Trelease (1924), Endlich collected the type specimen in the Sierra de la Candela at 2 500 m above sea level. *Quercus arizonica*, *Q. chihuahuensis*, and *Q. grisea* are common near this elevation in the Sierra de la Candela.

Communities of low elevation white oak species discussed here, with morphological variation like that described in hybrid swarms of other species pairs (Bacon and Spellenberg, 1996; Howard et al., 1997; Scareli-Santos et al., 2007; Albarran-Lara et al., 2010; and documents cited in those papers) were present on the slopes of the Sierra de la Candela and much of the interior slopes of the Sierra Madre Occidental wherever these white oak species were found in sympatry.

Descriptive statistics (Table 1) show little differentiation among vegetative characters of the taxa. Likewise, analysis of vegetative morphology from specimens at the type locality and sites where parental species were allopatric, using both principal components analysis (Fig. 3 and Table 2) and principal coordinates analysis (not shown, due to similarity in graphed point distributions) shows strongly overlapping, poorly defined groups when the first 2 components are graphed.

*Taxonomic comments.* The long, dense pubescence on leaf laminas and the long peduncles depicted in plate 135 (Trelease, 1924), suggest that the plate shows a specimen of *Q. chihuahuensis*. Lack of a scale on the photos and uncertainty as to whether the plate depicts one long



**Figure 2.** Variables measured on leaf blades and trichomes.

**Table 1.** Factor Loadings for principal components analysis based on a correlation matrix show that variables are weakly correlated among poorly delineated taxa evaluated in this study

Character	Factor Loadings	
	1	2
Mean leaf width	0.46752	-0.02932
Mean petiole diameter	0.37100	-0.02308
Apical distance	0.42487	-0.15407
Mean lamina length	0.46642	-0.17806
Mean petiole length	0.21573	-0.35396
Mean trichome branch length	0.17219	0.54998
Mean No. trichome branches	-0.26212	-0.22647
Mean trichome stipe length	0.27472	0.56200
Mean vein number	0.15923	-0.38506

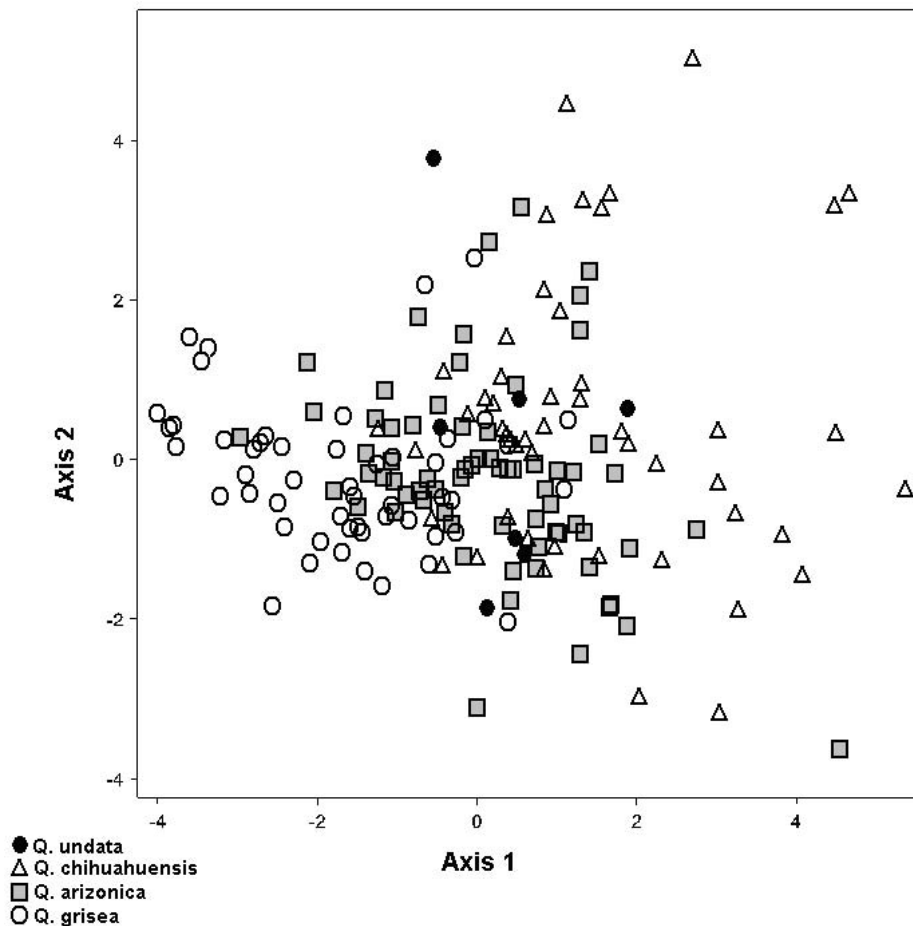


Figure 3. Principal Components Analysis.

peduncle partially covered by a leaf or 2 peduncles prevents precise determination of the peduncle length on the type. However, Trelease reported that the leaves of *Q. undata* vary from 5 to 7 cm in length, and the longest peduncle in the image measures 0.87 to 1.1 times (6 to 8 cm) the length of the longest leaf visible in the same photo. Hence the peduncle length of *Q. undata* is well beyond the maximum length of *Q. grisea* (0 to 30 mm) or *Q. arizonica* peduncles (0 to 15 mm) (Nixon and Muller, 1997).

*Type locality:* surveillance of the Sierra de la Candela at the altitudes near 2 500 m above sea level, where Trelease (1924) reported that Endlich collected the type specimen of *Q. undata*, revealed that *Q. arizonica*, *Q. chihuahuensis*, and *Q. grisea* were the only common low elevation white oaks that fitted the type description. Endlich likely traveled from Tepehuanes, the largest, and most well-connected old village in the range. Two travel routes lead upward into oak habitat from Tepehuanes. One route, following a ridge that leads up and over the Sierra de la Candela, to Boleras has only *Q. arizonica*

populations and a single sapling of *Q. grisea*. That sapling was growing in a highly disturbed stream area at the lowest portion of the ridge, very much below any other white oaks, at a site long used nowadays as a garbage dump. The oak sapling may have been established as a result of recent dumping activities.

The second route, leading from Tepehuanes to Ciénega de Escobar, has been a major travel route for more than a century. This route climbs steadily through elevations where one may find several other oak species. The type specimen, according to Trelease's list of Endlich's cited specimens (page 235), was the first of a series collected in the Sierra de la Candela, beginning on 27 August of 1903 (Endlich 1). Following in the series were *Q. eduardii* Trel. (Endlich 2a), *Q. striatula* Trel., *Q. depressipes* Trel. (both from the mixed collection Endlich 3), *Q. eduardii* (Endlich 4), *Q. fulva* Liebm. (Endlich 5), and *Q. jonesi* Trel. (Endlich 6) (Trelease, 1924: 235). Climbing up along the highway from Tepehuanes to Ciénega de Escobar, one finds the same species sequence observed in Endlich's

**Table 2.** Descriptive statistics for characters used for principal components analysis and principal coordinates analysis

Taxon	Leaf Width (mm)		Taxon	Petiole Length (mm)	
	Mean	S		Mean	S
a	21.5	4.370	a	3.91	1.131
c	25.6	6.2	c	4.23	1.39
g	17.5	5.35	g	3.58	1.016
u	21.2	1.9	u	3.75	0.986
	Peciole Diameter (mm)			Trichome Branch Length (mm*)	
a	0.91	0.225	a	2.24	0.9745
c	1.25	0.326	c	2.42	1.2699
g	0.81	0.186	g	1.84	0.7441
u	0.91	0.121	u	2.83	1.6549
	Apical Distance (mm)			Branches per Trichome	
a	26.5	6.64	a	5.8	1.16
c	28.1	6.16	c	5.1	1.08
g	21.9	5.69	g	6.8	0.95
u	30.2	5.36	u	6.3	1.17
	Lamina Length (mm)			Trichome Stipe Length (mm*)	
a	53	9.1	a	0.3	0.1706
c	52.2	10.04	c	0.48	0.248
g	39.3	10.48	g	0.23	0.0911
u	54.7	7.62	u	0.32	0.1562

sequential collections from 27 August 1903, hence the type locality is on this route.

*Role of introgression:* communities of the 3 white oak species found on the lower slopes of the Sierra de la Candela, as in other parts of the Sierra Madre Occidental, were characterized by plants with morphological variation similar to that described in hybrid swarms from the region (Bacon and Spellenberg, 1996; Howard et al. 1997; and documents cited in both papers). Sympatry occurred over extensive areas, suggesting that introgressive hybridization is probably very common in this region.

Trelease's (1924) inclusion of specimens of *Q. chihuahuensis* and *Q. grisea*, with very distinctive fruits, in his description of *Q. undata* may seem surprising. However, the leaves of the low elevation white oaks in this region (*Q. arizonica*, *Q. chihuahuensis*, and *Q. grisea*) look similar, and the species identification is difficult at many sites where introgressive hybridization has played a role in populations of white oaks. Principal components analysis and principal coordinates analysis, as well as descriptive statistics measured on vegetative characters, confirmed that morphology of vegetative characters overlaps and that taxa are distinguished with difficulty based upon vegetative characters. Also evident is the fact that plants identified as

*Q. undata*, based on foliage, do not group closely with any of the 3 taxa observed or with each other. As such, any of the hybrid combinations, hybrids subsequently crossing among themselves, selfing, or backcrossing to the parental types, could generate individuals with leaves fitting the description of Trelease's *Q. undata*. Fruits were not evaluated because they were not available the year plants were sampled, nor for two years thereafter, but results from these analyses coincide with observations that these white oak species are very difficult to distinguish based on the vegetative characters that Trelease used to describe *Q. undata*, which could explain the inclusion of 2 distinct taxa within the leaf variation that Trelease considered to encompass *Q. undata*.

*Typification of Quercus undata:* the name of *Q. undata* was published (Trelease, 1924) with (1), a type specimen (*Endlich 1*) deposited at the Botanic Garden and Botanic Museum-Berlin Dahlem, of the Free University of Berlin (B); (2), a brief descriptive text, and (3), a plate with 2 photographs documenting it (Trelease, 1924, page 235 + pl. 135, *Endlich 1*). Manfred Baessler at B, reported that the specimen does not exist in the collections (pers. comm., 1999). That herbarium lost many type specimens during a fire in a bombing raid on the night of

March 1-2 in 1943 (Hiepko, 1987), and the type specimen of *Q. undata* (Endlich 1) most likely destroyed in that event. Other herbaria that might be expected to have an Endlich duplicate (including A, CIIDIR, F, ECON, FH, GH, MEXU, NEBC, and US) reported no duplicates of the collection. Remaining specimens cited in Trelease's description (Palmer 408 and 828) deposited at Arnold Arboretum (A) at Harvard University were available for examination (see Appendix A for a list of "Selected Specimens Examined" including herbaria consulted), but they do not correspond to *Q. undata* (see discussion below).

Given that Endlich's specimen was apparently destroyed in bombing raids on Berlin during World War II and no duplicates are known to exist we propose here as a lectotype the Trelease illustration of the type depicted in plate 135 of Trelease's treatment (1924).

*Selection of Quercus undata epitype*: because some features cannot be critically identified from the lectotype (plate 135 in Trelease (1924) for purposes of the precise application of the name *Quercus undata*, an epitype is designated here in support of the lectotype (see McNeill et al., 2006, Article 9.7): Mexico, Durango, Municipality Tepehuanes, along the highway from Tepehuanes to Ciénega de Escobar, 25°26'55"N, 105°47'27"W, 2 020 m, 19 Oct 2006, Bacon et Bustamante-Longoria 2006-XI-19-2 (CIIDIR).

This specimen is from a site at, or very near, the type locality of *Q. undata* in the Sierra de la Candela, Durango. It was collected from the lower edge of a hybrid swarm containing all 3 of the low elevation white oak species mentioned by Trelease (1924). Its morphology resembles that of *Q. chihuahuensis*, but varies in the nuances that Trelease noted when examining the Endlich specimen and, similarly, Palmer's *Q. grisea* specimens. It also has abundant vegetative and fertile material. Duplicates of the same collection, although not representing epitypes (McNeill et al., 2006, Article 9.19) will be distributed to other herbaria.

Originally, we considered that 1 of the other 2 specimens (Palmer 408 and 828) listed by Trelease (1924) in his description of *Q. undata*, and in Camus (1938 – 1939), could serve as a suitable type. However, neither of those specimens belongs to the same taxon. Both have very short peduncles and thick, leathery stellate-pubescent leaves with interlocking hairs typical of that described for *Q. grisea* (Nixon and Muller, 1997). The lectotype depicts variation of *Q. chihuahuensis* derived from genetic introgression, corresponding to the morphological characters described by Trelease for the published name *Q. undata*. Such variation and the presence of alleles introgressed from other species is common in white oaks

(Bacon and Spellenberg, 1996; Howard et al., 1997; and documents cited in both papers).

*The identity of Quercus undata*: *Quercus undata* grows in hybrid swarms. Although we strongly considered the use of a hybrid name, *Q. × undata*, Trelease's type specimen is not intermediate between any species pair among the low elevation white oaks from this region. The presence of crisped leaf margins mentioned by Trelease and evident in the lectotype, is very common on leaves of trees at many sites where introgressive hybridization occurs between any 2 oak species. However, we cannot consider it a sure sign of hybridization. In addition, the specimen shown in Plate 135 (the lectotype) has much stronger affinity to *Q. chihuahuensis* than *Q. grisea* (or *Q. arizonica*) and, genetically, it probably coheres much more strongly to *Q. chihuahuensis*. We suggest that the name *Q. undata* applies to a population *Q. chihuahuensis* influenced by past hybridization.

*Description of Q. undata*: to clarify the nature of *Q. undata* we present, based on Trelease's (1924) original description, a modified and expanded description:

Small trees or shrubs, evergreen, to 4 m tall. Bark gray to brown, fissured, becoming brittle with age. Twigs round, occasionally laterally striated, often fluted in immature twigs, 3 (-4) mm in diam., densely tawny-yellow tomentose and variably hoary in mature. Buds brown or beige, densely hoary to glabrous, round to broadly obovate. Petioles 2 - 6 cm long, 1 mm in diam., tomentose with stellate trichomes. Leaf lamina base obtuse, rounded, or cordate; the lamina elliptical, entire or shallowly toothed apically, margins crisped, revolute or weakly revolute, horny to densely tomentose, (2.5-) 3 - 6 (-7) cm long, 1 - 4 cm wide, thick and leathery, abaxial surface glaucous green gray to blue green, densely to moderately tomentose, with variable stellate trichomes, occasionally weakly rugose, the midrib yellow tomentose, secondary veins 10 - 12 on each side, visible to slightly obscured, impressed, adaxial surface green to green gray, densely to moderately tomentose, with variable stellate trichomes, the midrib and secondary veins readily visible, raised and reticulate, colored like the lamina epidermis to yellowish; apex acute to broadly acute, rarely obtuse or rounded, generally mucronate. Fruits poorly known, the peduncles 6 - 8 (-10) cm long, with 2 - 3 elliptical acorns, ca. 1 cm in diam. Catkins (according to Trelease [1924]) 30 mm long, fleecy, rather loosely flowered, anthers glabrous and rounded, long-exserted.

*Distribution and ecology of Q. undata*: distributed on low elevation slopes (2 000 - 2 800 m) of the interior Sierra Madre Occidental, in Durango and Chihuahua, in low oak woodlands, where *Q. arizonica*, *Q. chihuahuensis*, and *Q. grisea* form hybrid swarms. Occasionally associated with

the black oaks *Q. conzattii* Trel., *Q. eduardi*, or *Q. emoryi* Torr. *Taxonomic summary*. Specimens indicated as hybrids are more or less intermediate between the 2 putative parental species.

*Quercus undata* Trel. Mem. Natl. Acad. Sci. 20: 86. 1924. Lectotype, here designated: plate 135 in Trelease (1924), depicting Mexico, Durango, Municipio Tepehuanes, Sierra de la Candela, 2 500 m, 27 Aug 1903, *Endlich 1* (B); epitype, here designated: along the highway from Tepehuanes to Ciénega de Escobar, 25°26'55"N, 105°47'27"W, 2 020 m, 19 Oct 2006, *Bacon et Bustamante-Longoria 2006-XI-19-2* (MEXU, CIIDIR).

*Collections that seem to represent Q. undata*: Mexico. Chihuahua. W of Cuauhtemoc, 2 000 m, 10 Feb 1985, *Spellenberg et al. 7965-B* (DAV, INIF, MEXU, NMC); Durango, Municipio Tepehuanes, N of Tepehuanes, along the highway to Ciénega de Escobar, 25°03'38"N, 105°20'57"W, 2 259 m, 16 Aug 1996, *Bacon et al. 3079* (CIIDIR, MEXU, NMC); Municipio Durango, S of Ferreria, 7 Jul 1992, *Spellenberg and Bacon 1114-A, C, D and E* (CAS, CIIDIR, MEXU, NMC); Presa Santiago Bayacora, 23°54'N, 104°42'W, 15 Dec 1992, *González and González 5374* (CIIDIR); Municipio Durango, collection date unknown, *Rosales 2* (CIIDIR); *Rosales 3* (CIIDIR); Municipio Suchil, Cerro Blanco, Reserva La Michilia, 2 600 m, 23 Jul 1990, *González and Spellenberg 4652* (CIIDIR).

*Other taxa: Quercus arizonica* Sarg., U.S.A., Texas, Hidalgo Co., Peloncillo Mts., 17 Sep 1998, *Spellenberg 9734* (NMC, BH, NY, TEX, UNM, CIIDIR); Arizona, Cochise Co., Chiricahua Mts., Cave Creek Canyon, 17 Sep 1988, *Spellenberg 9731* (NMC, BH, CIIDIR); Mt. Huachuca, 23 March 1894, *C. S. Sargent s/n* (A! accession numbers, 00034034 and 00034033, the holotype). Mexico, Sonora, Municipio Los Alamos, Sierra de los Alamos, 18 Aug 1991, *Schwabe 36-B* (CIIDIR); Chihuahua, Municipio I. Zaragoza, SW of Buenaventura, Sierra Catarina, 29°46'N, 107°38'W, 1 975 m, 16 Nov 1986, *Spellenberg and Zimmerman 8957* (NMC, CIIDIR); Municipio Madera, La Tinaja, Ejido El Largo, 1 840 m, 29 Aug 1990, *Bravo-Bolaños 1340* (CIIDIR); Madera, 29°11'41.3"N, 108°14'55.0"W, 2 200 m, 5 Aug 1998, *Bacon et al. 5333* (CIIDIR). Municipio Saucillo, 28°24'10.2"N, 107°35'40.2"W, 2 390 m, 3 Aug 1998, *Bacon et al. 5281* (BH, CIIDIR, NMC, F, IBUG, MEXU, IEB). Municipio Ocampo, Pinos Altos, W of Basaseachic, 28°17'54"N, 108°17'02"W, 1 700 – 2 000 m, 9-12 Oct 1977, *Tejero-Diaz and Muñoz-Viveros 3962* (CIIDIR); Municipio Maguarichi, between Creel and San Rafael, 27°37'10.1"N, 107°49'06.8"W, 2 320 m,

6 Aug 1998, *Bacon et al. 5362* (BH, CIIDIR, NMC); Municipio Guerrero, WSW of La Junta, 2 290 m, 21 Sep. 1991, *Spellenberg et al. 10893* (NMC, CAS, MEXU, BH, IBUG, CIIDIR). Durango. Municipio Tepehuanes, N of Tepehuanes, along the highway to Ciénega de Escobar, 25°03'38"N, 105°20'57"W, 2 259 m, 16 Aug 1996, *Bacon et al. 3076* (CIIDIR, MEXU, NMC); Municipio Santiago Papasquiario, along the highway from Santiago Papasquiario to Altares, 2 140 m, 30 Sep 1990, *Benitez-P. and Famos-M. 2497* (CIIDIR); Municipio Nuevo Ideal, SSE of Los Molinos, 24°44'36"N, 105°0'29"W, 2 200 m, 15 Nov 1998, *M. González and Torres 3007* (CIIDIR); Municipio Canatlan, Sierra del Epazote, La Cieneguita, 24°34'47"N, 104°57'58"W, 2 370 m, *M. González et al. 3367* (CIIDIR).

*Quercus arizonica* Sarg. × *grisea* Liebm., Mexico. Chihuahua. Municipio Chihuahua, S of Arco Iris, 106°18'W, 29°17'N, 6 Oct 1986, *Spellenberg et al. 8896* (NMC, MEXU, NY, CIIDIR, IBUG, IEB, UC, BYU, BRIT, TEX, MT, RSA); Durango. Municipio Tepehuanes, N of Tepehuanes, along the highway to Ciénega de Escobar, 25°03'38"N, 105°20'57"W, 2 259 m, 16 Aug 1996, *Bacon et al. 3076* (CIIDIR, MEXU, NMC).

*Quercus chihuahuensis* Trel., Mexico, Chihuahua, Municipio Chihuahua, N of Chihuahua, 5 500 ft., 12 Jul 1986, *Spellenberg and Zimmerman 8566* (CIIDIR); Municipio Cuauhtemoc, E of Cuauhtemoc, 28°22'40.4"N, 106°39'48.1"W, 1 950 m, 3 Aug 1998, *Bacon et al. 5276* (BH, CIIDIR, MEXU, NMC); Chihuahua, October 1885, *C. G. Pringle 2401* (F!, the syntype); Municipio Matamoros, S. of Villa Matamoros, 5 300 ft., 14 Jul 1986, *Spellenberg and Zimmerman 8,565* (CIIDIR, MEXU, NMC); Municipio Balleza, W of Chihuahua, 1 525 m, 3 Aug 1991, *Spellenberg et al. 10,846* (CIIDIR, NMC); Durango, Municipio Ocampo, S of Las Nieves, 1 650 m, *Spellenberg et al. 10,848* (CIIDIR, MEXU, NMC, NY); Municipio Tepehuanes, N of Tepehuanes, along the highway to Ciénega de Escobar, 25°03'38"N, 105°20'57"W, 2 259 m, 16 Aug 1996, *Bacon et al. 3078* (CIIDIR, MEXU, NMC); Municipio Santiago Papasquiario, between Santiago Papasquiario and Topia, 1 770 m, 1 Jul 1992, *Spellenberg and Bacon 11,097* (CIIDIR, MEXU, NMC); Municipio Tepehuanes, Rancho El Purgatorio, 1 580 m, 20 Oct 1990, *González 2524* (CIIDIR); Municipio Villa Hidalgo, Casa Blanca, 1 700 m, 27 Jun 1992, *Spellenberg and Bacon 11,006* (CAS, CIIDIR, MEXU, NMC); Municipio Rodeo, Boquilla de Gerardo, 21 Feb. 1987, *Spellenberg et al. 9032* (CAS, CIIDIR, INIF, MEXU, NMC, NY); Municipio Nuevo Ideal, Guatimape, 24°55'49"N, 104°46'4"W, 2 140 m, 18 Sep 2001, *González et al. 6369* (CIIDIR);

Municipio Canatlan, W. of Santa Teresa de los Pinos, 24°34'30"N, 104°54'9"W, 2 054 m, 25 Jan 2000, *M. González et al.* 3358 (CIIDIR); Municipio Durango, Cd. Durango, 23°59.208'N, 104°44.897'W, 2 070 m, 28 Oct 1996, *Bacon et al.* 3226 (BRIT, CIIDIR, F, BH, IBUG, MOBOT, IEB, TEX, NMC); SW of Ferreria, 23°56'N, 104°42'W, 1 920 m, 6 Jan 1993, *Spellenberg and Bacon 11691* (CIIDIR, NMC).

*Quercus chihuahuensis* Trel. × *grisea* Liebm., Mexico. Durango. Municipio Tepehuanes, N of Tepehuanes, along the highway to Ciénega de Escobar, 25°03'38"N, 105°20'57"W, 2 259 m, 16 Aug 1996, *Bacon et al.* 3078 (CIIDIR, MEXU, NMC); Municipio Durango, Presa Santiago Bayacora, 23°54'N, 104°42'W, 15 Dec 1992, *González and González 5377* (CIIDIR).

*Quercus grisea* Liebm., U.S.A., New Mexico. San Miguel Co., Montezuma, 7 200 ft., 18 Oct 1995, *Tucker 2937-19* (CIIDIR); Texas, Jeff Davis Co., S. of Fort Davis, 103°49.14'W, 30°31.65'N, 1 420 m, 31 Aug 1997, *Spellenberg and Zucker 12450* (NMC, CIIDIR); western Texas, May – October 1849, *C. Wright 665*, GH! accession numbers 00034059, 00034060, the type); Mexico. Chihuahua, Municipio Manuel Benavides, Sierra Azul, 29°00'06"N, 103°56'47"W, 1 200 m, 18 Aug 2000, *Carrera s/n* (CIIDIR); Municipio Madera, Highway 16, 28°22'52.2"N, 107°47'17.1"W, 2 200 m, 3 Aug 1998, *Bacon et al.* 5288 (BH, CIIDIR, NMC, MEXU, IBUG, F, BRIT); Madera – Las Varas, 2 240 m, 5 Aug 1998, *Bacon et al.* 5310 (CIIDIR, NMC, MEXU); Municipio Chihuahua, N of Chihuahua, 1 570 m, 27 Sep 1997, *Yen and Estrada 8820* (CIIDIR); Municipio Guadalupe y Calvo, América, 25°15'N, 105°0'W, 1 890 m, 27 Jun 1992, *Bacon and Spellenberg 1214* (CIIDIR); Coahuila, Sierra Madera del Carmen, Rancho el Secadero, Cañon Polano, 102°20'W, 29°00'N, 2 100-2 800 m, 20 Aug 1994, *Carranza et al.* 111 (CIIDIR); Municipio General Cepeda, Sierra de la Concordia, Ejido La Casital, Santa Victoria, 25°13'45", 101°25'50"W, 2 345 m, 5 Oct 1998, *Carranza and Zamora-M.* C-3218 (CIIDIR); Durango, Municipio Durango, City of Durango, 17 May 1940, *Palmer 828* (A); Las Nieves, 21 Feb. 1 1987, *Spellenberg et al.* 9033 (NMC, CIIDIR, CAS, MEXU); Municipio Hidalgo, W of La Zarca, 1 920 m, 27 Jun 1992, *Spellenberg and Bacon 11,004* (NMC, CIIDIR, MEXU, CAS); Municipio Santiago Papasquiaro, Santiago Papasquiaro, Apr and Aug 1986, *Palmer 408* (US); Municipio Tepehuanes, N of Tepehuanes, along the highway to Ciénega de Escobar, 25°03'38"N, 105°20'57"W, 2 259 m, 16 Aug 1996, *Bacon et al.* 3077 (CIIDIR, MEXU, NMC); Municipio Nuevo Ideal, Poblado America, 1 890 m, 27 Jun 1992, *Spellenberg*

*et Bacon 11,009* (NMC, CIIDIR); Municipio Cantatlan, San Diego de Alcalá, 24°28'10"N, 105°9'58"W, 2 110 m, 27 Jan 2000, *González et al.* 3415 (CIIDIR); Municipio Panuco de Coronado, Ejido F. J. Mina, NW of Francisco I. Madero, 2 150 m, 7 Oct 1989, *González et al.* 4198 (CIIDIR); Municipio Durango, S. of Puerta de la Cantera, Cerro Chicuiquitillo, 24°54'N, 104°35'W, *Bacon and Spellenberg 1289* (CIIDIR, NMC); Municipio Nombre de Dios, San Jose de la Parrilla, 23° N, 104° W, *Sanchez 1595* (CIIDIR); Municipio Suchil, SW of Vicente Guerrero, 23°30'N, 104°10'W, 1 860 m, 6 Jul 1992, *Bacon et al.* 1316 (CIIDIR, NMC, F, MO); Arroyo El Aleman, between El Aleman and La Quebrada, 23°18'49"N, 104°10'45"W, 2 250 m, 26 Jun 1999, *González et al.* 6173 (CIIDIR); Zacatecas, Municipio Sombrerete, Parque Nacional Sierra de Organos, 23°46'45"N, 103°47'26"W, 2 300 m, 22 Sep 2001, *Enriquez et al. s/n* (CIIDIR).

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