Notes on the Genus *Quercus* in Mexico

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Introduction

The genus *Quercus* is one of the most important groups of woody plants of the Northern Hemisphere (Nixon 1997, 2002). With approximately 500 species in the world and more than 200 in the Americas, it is the most diverse of the members of the Beech family. It is assumed that there are two areas with the greatest specific diversity in this genus: the first and most diverse is Mexico, with an estimated 140-160 species (Nixon 2002; Valenica, 2004); the second is Southeast Asia, with approximately 125 species (Govaerts and Frodin, 1998).

In the context of this meeting on the genus *Quercus* in the world, the present work aims to present some aspects of Mexican oaks, such as their importance, taxonomy, diversity, distribution, and ecology, as well as the current areas of study of this genus, together with a discussion of some selected groups of species.

Historical importance

Mankind has conferred a special importance on the oaks, considering them a symbol of strength and power. In ancient history, the Greeks regarded oaks as the temple of Zeus. In France, it was common knowledge that their King was only capable of governing and making wise decisions when he did it in the shade of a mighty oak which he had near his palace. Soothsayers could only divine the future through the sounds of the leaves moved by the wind. On the other hand, the hardness of oak wood gave popular sayings such as "as strong as an oak" or "he has the head of an alcornoque", the common name of the European native *Quercus suber* L. In Mexico there are stories of the worship of fragments of oak wood or of temples raised for the worship of oaks. Indeed, on the national seal of Mexico, one of the two tree branches which are crossed at the base is that of an oak.

Economic importance

Oaks constitute one of the most economically important groups in the whole world. They are esteemed for the beauty and durability of their wood; in Mexico, however, despite the fact that it is the greatest center of diversity of the genus, they are utilized principally for wood and charcoal, or in some cases as a source for pulp for paper or for the manufacture of tannins.

In some rural communities acorns are used for human consumption or for animal feed. Nevertheless, they may contain a high concentration of tannins

or other toxic substances considered to be poisonous such as those of *Quercus chrysolepis* Liebm.; it is therefore necessary to use them with care or to remove the toxic substances through certain preparatory processes in order for them to be consumed.

For the aging of alcoholic beverages it is traditional to use barrels of white oak. At the present time, however, various species of Mexican oak are under consideration as replacements for the barrels, whereby wood chips alone are added to the containers where the beverage is aged.

The economic potential of Mexican oaks highlights the importance of studies of wood anatomy in order to be able to suggest better ways to utilize this resource in Mexico. Recent studies have linked the anatomy of the wood of some oak species with their environment, providing solid bases for adequate management of this resource.

Ecology

The importance of oaks is well known as the dominant element among many types of vegetation and for playing a fundamental role in the equilibrium of ecosystems. Thier habitat ranges from tropical and subtropical regions to temperate and cold climates. Thus it is possible to find oaks in most vegetation types of Mexico, except aquatic and semiaquatic, often dominating the communities in which they appear, an example of which is the oak forest.

The oak forests of Mexico occupy approximately 4.29% of the surface of the country (Challenger 1998). They can grow in climates with scant precipitation, where species of the section *Quercus* (white oaks) dominate because of their greater tolerance of drought stress, for example *Q. magnoliifolia* Née, *Q.glaucoides* M. Martens & Galeotti, and *Q. liebmannii* Oerst., which form oak thickets growing in the center and south of the country, often mixed with deciduous tropical forest or with xerophyllic underbrush. Oak copses can be found in dry situations at elevations of 400-1000 m. Oak groves in these zones are deciduous and generally do not exceed six meters in height.

Other oak groves somewhat less dry than the foregoing can grow at altitudes of 800 to approximately 1500 m. In the mountains of the north of the country, *Quercus laceyi* Small., *Q. gravesii* Sudw., *Q. arizonica* Sarg., and *Q. jonesii* Trel. are well represented, while towards the center of the country they are replaced by *Q. crassipes* Bonpl., *Q. castanea* Née, *Q. furfuracea* Liebm., *Q. conspersa* Benth. and *Q. laeta* Liebm. Trees of these species can be between ten and fifteen meters tall.

Moist oak groves grow for the most part between 1500 and 2500 meters in altitude. In the mountains of eastern Mexico the dominant elements are *Q. acherdophylla* Trel., *Q. corrugata* Hook., *Q. sartorii* Liebm. and *Q. affinis* Scheidw. In the Sierra Madre Occidental can be found representatives of *Q. crassifolia* Bonpl, *Q. rugosa* Née and *Q. candicans* Née among others. In the center and south of Mexico are *Q. rubramenta* Trel., *Q. martinezii* C.H. Mull., *Q. laurina* Bonpl. and *Q. macdougallii* Martínez. These groves are very rich in diversity; the mature trees surpass 18 m in height, even reaching 35 m and are associated with deep soils rich in nutrients. This forest is often mixed with cloud forest, making it difficult to separate the two.

Cloud forest, though a community restricted to less than 1% of southern Mexico, presents a high diversity of oak species; some of these, indicative of and endemic in this type of vegetation are *Q. cortesii* Liebm., *Q. germana* Schltdl. & Cham., *Q. hirtifolia* M.L. Vazquez *et al*., *Q. insignis* M. Martens & Galeotti, *Q. pinnativenulosa* C.H. Mull. and *Q. uxoris* McVaugh among others.

Oaks can be present in pine forests, forming mixed forests with conifers. In the north of the country in the state of Coahuila grow *Q. mexicana* Bonpl., *Q. saltillensis* Trel., *Q. convallata* Trel. and *Q. laeta* Liebm., forming mixed stands of pines and oaks. In the case of *Q. greggii* (A. DC.) Trel. and *Q. hintoniorium* Nixon & C.H. Mull., they can form thickets which are mixed with trees of sacred fir (*Abies religiosa* (Kunth) Schltdl. & Cham.). Toward the center and south of Mexico mixed forest is frequent in which grow *Q. crassifolia* Bonpl., *Q. candicans* Née, *Q. laurina* Bonpl, *Q. urbanii* Trel. and *Q. rugosa* Née. It is interesting that in the communities occurring above 3000 m in the center and east of the country, in the zone at the limit of arboreal vegetation, oaks form thickets of *Q. depressa* Bonpl, and *Q. repanda* Bonpl. mixed with pines.

Q. pringlei Seemen ex Loes., *Q. intricata* Trel., *Q. striatula* Trel., *Q. invaginata* Trel., Q. *sebifera* Trel. and *Q. fusiformis* Small are well represented in some scrublands.

The dominance of oaks in different communities, in addition to the fact that the majority of the individuals of this genus are habitat specific for numerous species of epiphytic plants such as orchids, bromeliads, ferns and mosses, and for animals such as rodents, birds, reptiles, insects and arachnids, as well as a source of direct or indirect nutrition for these organisms, guarantees that cutting or completely removing oaks will have a considerable impact on the communities where they grow.

In addition to conserving their habitat and providing nourishment for other organisms, oaks can form, improve, and retain soil wherever they grow. They can provide edaphic conditions adequate for the establishment of other species of plants in their vicinity. Adding the former to the great diversity of species and the tolerance and plasticity of some of these gives them the potential to be utilized for reforestation wherever soil has been lost through erosion. Little has been done in this field in our country, but research is underway on the propagation and establishment of some species, as well as projects in propagation in nurseries and greenhouses (as for example the one developed at the University of Puebla by Doctor Maricela Rodriguez), including also some species managed commercially by some nurserymen. All of this establishes a foundation for the development of this area which will permit reforestation with native species of wide expanses of our territory.

Taxonomic Position

The genus *Quercus* is in the family *Fagaceae,* in the order Fagales, and in the Fabid group of the Eudicots (APG 2009). In addition, the family includes the genera *Fagus* (situated as the basal clade in the phylogenetic scheme of the family, Manos *et al*., 2001), *Lithocarpus, Notholithocarpus* (recently segregated from *Lithocarpus*, by Manos *et al*. 2008), *Colombobalanus, Trigonobalanus,*

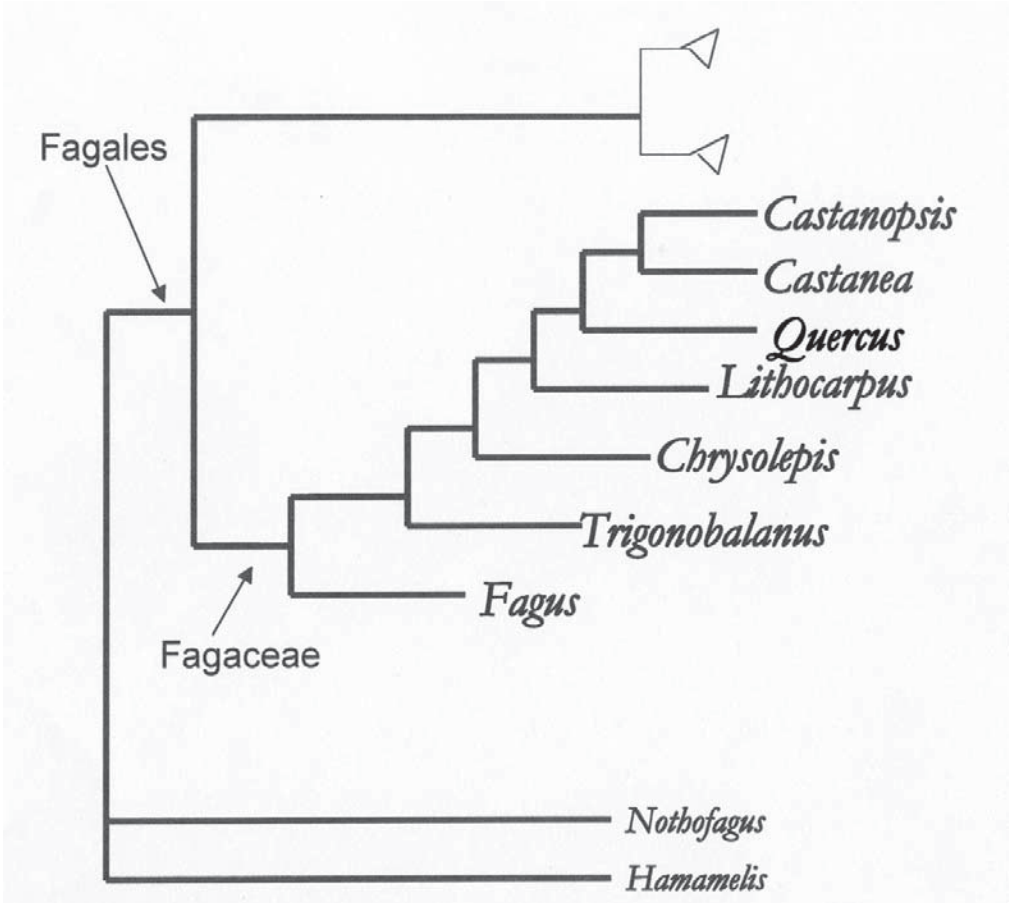

Figure 1. Relationships of *Quercus* and the other genera in Fagaceae (based on Manos *et al*., 2001).

Formanodendron, Chrysolepis, Castanea and *Castanopsis*, the latter two proposed as the most derivative of the family (Manos *et al*.,. 2001) (Figure 1). The family has approximately 900 species in the world (Sang-Hun and Manos 2008).

The genus *Quercus* has been traditionally divided into two subgenera: *Cyclobalanopsis* (distributed in south east Asia) and *Quercus*, with four sections: *Lobatae* (red oaks, America), *Quercus* (white oaks, America, Europe, Asia), *Cerris* (white oaks of the old world) and *Protobalanus* (oaks with a golden cup, western America) (Nixon 1993 and Manos *et al*. 1999). (Figure 2).

In 1924 Trelease proposed the grouping of the species of each section in series. Subsequently Camus (1936-1952) treated them as subsections, but Muller (1942a) showed that these groups lack substance, with the exception of the subsections Virentes, Glaucoideae and Acutifoliae. Subsequent studies (Valencia 1995, 2005) support what Muller demonstrated by showing that the series or subsections reflect neither monophyletic groups nor ancestral relationships among the species which they include, almost all of the groups are artificial and at the present time many no longer exist, since the species from which they were constituted have become synonyms of other species placed in other groups.

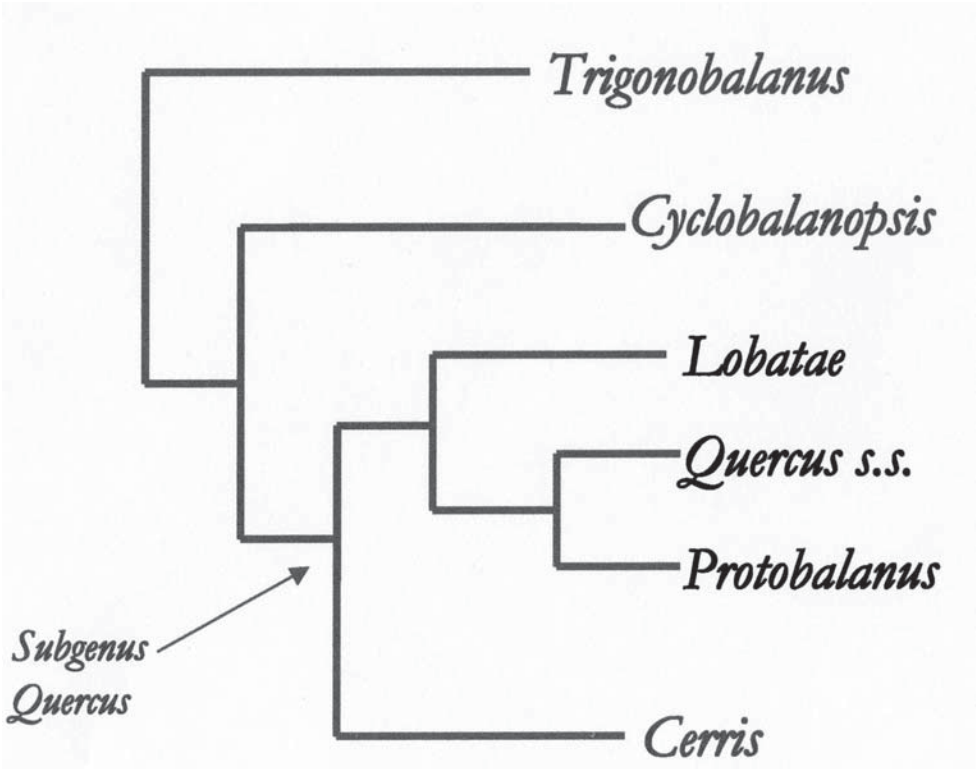

Figure 2. Relationships of subgenera and sections in genus *Quercus* (based on Manos *et al.*, 1999).

Most Frequent Problems in the Recognition of Species of the Genus *Quercus*

Any kind of study (biogeographic, evolutionary, phylogenetic, ecological, of diversity or use, among others) regarding the recognition of any group is based on its taxonomy. Nevertheless, the genus *Quercus* is considered a difficult taxonomic group and although there have been substantial advances in the recognition of the Mexican species of the genus, there are still severe problems, above all in certain complexes of species which hybridize and form gradients. Among the most common aspects which lead to taxonomic problems for the species of the genus *Quercus* in Mexico are the following:

High intraspecific morphological variation, even in a single individual, which on occasion can lead to the extreme case of mistakenly identifying a specimen from a tree as one species and another specimen from the same tree as a different species. This obviously reflects the imprecision of specific diversity in the species of this group.

Deficient original descriptions produced in the 19th and first half of the 20th century offer limited information on the variation of the species, with the result that they are insufficient for differentiation of very similar species. The paucity of material for describing new species, the great morphological variation, and the poor understanding of the groups, have led to the interpretation of any variation as indicating a new species, resulting in over description. Subsequent reviews of type specimens, original descriptions, herbarium specimens, and field work, have permitted the recognition and understanding of specific variation and the reduction of many names to the status of synonymy. Thus, for *Q. castanea,* 16

synonyms have been proposed, while for *Q. laurina*, 13 can be cited. Among the most problematic species in this connection are those described by Liebmann (1854) and by Trelease (1924, 1934).

Hybridization between some oak species of the same section is common; this has been observed in the field and amply documented in different bibliographic sources, for different places and between different species. Greater frequency of hybridization has been observed among some species of the section *Quercus* of wide distribution than in the red oaks of narrow distribution. Figures 3 and 4 show some of the most frequent syngameons; some of these are so large and complex that they must be studied intensively in order to understand the comportment of their participants. Hybridization does not only occur between phylogenetically related species; it is sufficient that the species which hybridize be sympatric and have weak barriers to cross breeding.

The resulting hybrids in most cases appear in the field in a sporadic and isolated way among the parents, without forming large masses of hybrid individuals. The hybrids may present a mosaic of intermediate characters, or they may resemble one of the parents more than the other; if introgression is involved, the variation will increase. In these cases the morphological and genetic limits are diluted and taxonomic identification becomes a difficult problem, requiring great care in the observation of the variation in order to adequately identify the species or possible hybrids.

Limited access to the original material. It is estimated that around 160 species of oaks occur in Mexico, but around 800 names and descriptions are associated with them, many times of doubtful form. The cleansing of the

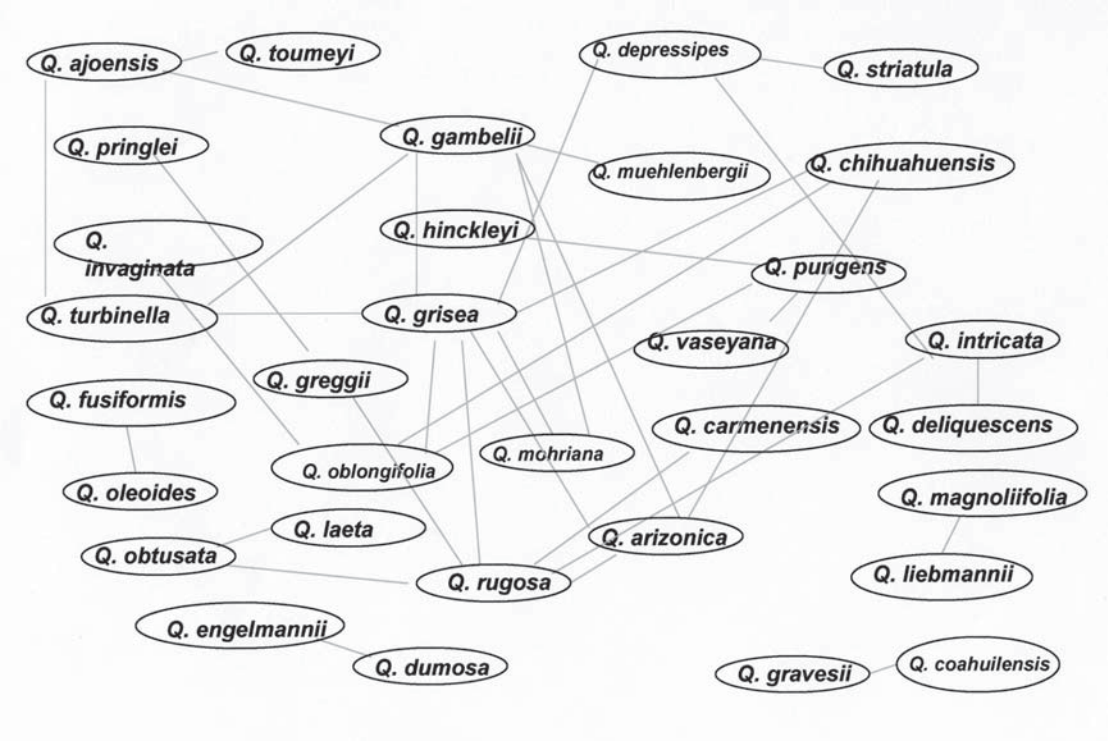

Figure 3. Hybridization documented or observed between some white oak species in Mexico.

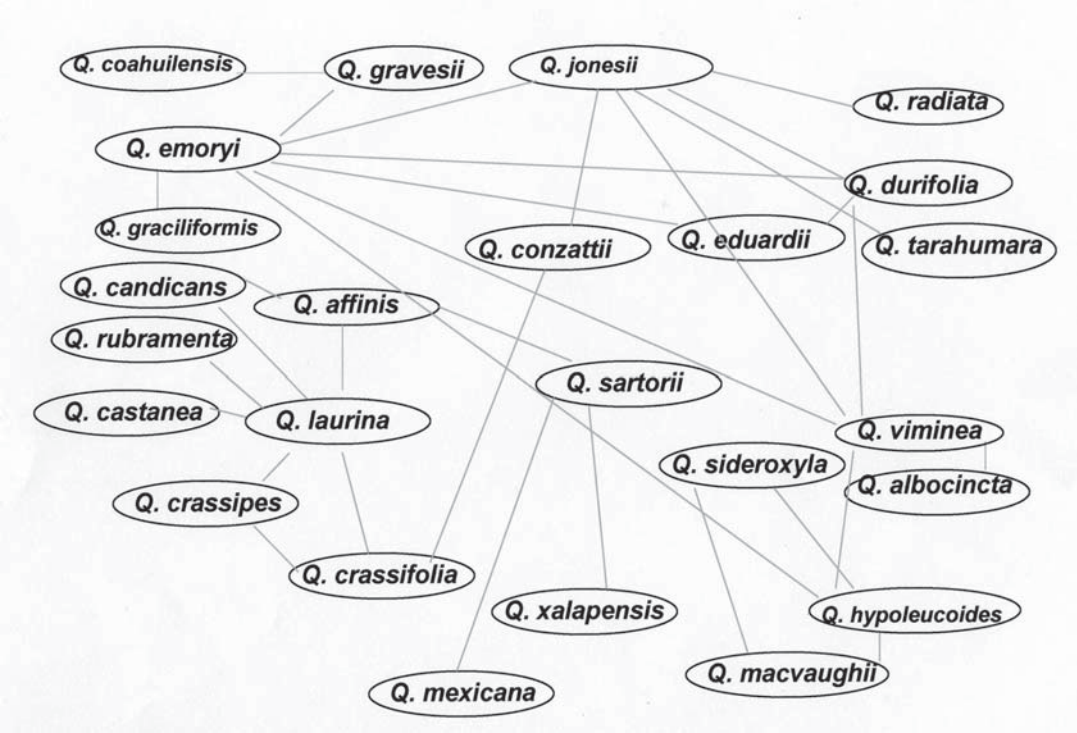

Figure 4. Hybridization documented or observed between some red oak species in Mexico.

nomenclature requires revision of the types and of the associated original descriptions. Unfortunately, much of the literature and the majority of the oak type specimens are outside the country. Only about 6.8% of the type specimens of the genus *Quercus* are in Mexican herbaria. Modern communications permit more easy access to this information, but there are still problems such as that of observing the details of the trichomes, which are often indispensible for identifying oaks at the species level and which cannot be seen in photographs of herbarium specimens; they can only be observed directly on the material, access to which can be expensive and often unaffordable.

Field Work. Most solutions to specific taxonomic problems require field work, because it is in so doing that the taxonomic variation of the species can be recognized. When collecting it is necessary to exercise caution to not label samples coming from different individuals with a single collection number, since it is only with accurate records that the recognition of intraspecific variation is possible. The information obtained by field work is invaluable, for which reason it is necessary to take maximum advantage of it, even though it is expensive and often highly dangerous in some regions of the country.

Characters of taxonomic value in the identification of species

In the genus *Quercus*, the mature leaves provide the most useful information for identification. The size, general form of the blade, of the apex, of the base, the number of veins, the type of margin, the consistency, and the color are very important; but by these alone it is possible to misidentify the material, for which reason it is necessary to consider everything all together and to include also the

characters of the twigs, buds, stipules and fruit, which together permit a better identification of the species.

Despite the great value of the characters offered by the leaves for species recognition, it is necessary to take into account characters which converge because of the habitat type, such as is the case with consistency. For example, sclerophyllous leaves predominate in the species from high tablelands (the Central Altiplano in Mexico) and areas of semidesert, while in more humid and temperate zones, leaves tend to be more delicate.

Of all leaf characters, trichomes are the most useful: their type, size, the number of radii and the extent of fusion analyzed with the aid of a microscope; they provide, in most cases, the most constant characters which permit species identification in the most precise manner. This character has been explored in detail, resulting in important contributions, beginning with the pioneer work of Hardin (1979), the ample and detailed work of Jones (1986), up to the most recent and specific contributions of Manos (1993), Valencia and Delgado (2003) and Vázquez (2006). All of these trichomes analyzed by scanning electron microscope have furnished very valuable data for recognizing species.

In some taxonomic treatments (e.g. McVaugh 1974 and González Villarreal 1986) juvenile leaves have been described as elements characteristic of the species. But these do not provide stable characters because the size, consistency and certain types of trichomes are modified during their development. For this reason they are not useful for the recognition of species.

The male and female flowers of oaks have traditionally been considered as having little or no taxonomic value. Although there may be some differences in type of pubescence, in the length of pedicels and in the size and form of the tepals of the male flowers, all of these vary within species and converge between species. The scant specialization of the flowers, due possibly to wind pollination, may be the cause of this slight variation. Additional research on the characters of the flowers may yield information for characterizing some groups of species. For this are required more collections of flowers which are not well represented in herbaria.

The Diversity of Oaks in Mexico

Due to the great wealth of species, the oaks of Mexico have been the subject of almost constant taxonomic study, which begins with the description of 16 new species published by the Spaniard Luis Née (1801). Shortly afterwards Humboldt and Bonpland (1809) described another 20 species of Mexican oaks. Prominent subsequently are the descriptions of Liebmann (1854), the monographic work of Trelease on American oaks (1924), and the extensive study by Maximino Martínez of the oaks of Mexico (1953). Also important in this context are the contributions of Muller (1936, 1942a, 1942b), Nixon and Muller (1992, 1993) and Spellenberg (1992, 2001) on different regions in the north of our country, for which they describe various new species.

Later begin the formal taxonomic treatments of various regions of Mexico: Nueva Galicia (McVaugh 1974), Jalisco (González-Villarreal 1986), Michoacán (Bello & Labat, 1987), the Valley of Mexico (Espinosa-G 2002), Guerrero

(Valencia 1995 and Valencia *et al*. 2002), Puebla (Vázquez 1992), Mexico (Romero *et al*., 2002), and Aguascalientes (De la Cerda 1989).

These studies are not finished and at the present time the elaboration of taxonomic studies of the oaks of the Bajío (Central Plateau), Oaxaca, Hidalgo, San Luis Potosí, Veracruz, Coahuila and Tlaxcala is underway. Important also are works which furnish tools for the recognition of Mexican oak species such as the compilation of keys by Zavala-Chávez (2003) and the work of Soto-Arellano (2007), which offers a universal key (polykey) for Mexican oaks.

The number of species for the genus *Quercus* is as yet imprecise. The most recent data estimate that there exists in Mexico some 160 species, of which 109 are endemic (Valencia 2004), which means that Mexico possesses 32.2-40.2 % of the world total and approximately 75% of American species. Of the world total, estimated at between 400 and 500 species, a quarter is endemic in our national territory.

The numerous studies of different oak characters, of their distribution, of hybridization, of the progress in regional taxonomic treatments and the analyses of some complexes of Mexican species have permitted better recognition and understanding of the species. This has resulted in modification of the specific diversity of the genus in some regions and for Mexico in general, due not to the description of new species (during the last five years there have been none) or to modification of the total number of species (which basically remains the same), but to the reconsideration of the status of some of them or to the reconsideration of herbarium material, as can be seen in the following examples.

For *Q. pinnativenulosa* C.H. Mull. only the type specimen from Nuevo León was known, but recently it has been collected in Hidalgo, Querétaro, Tamaulipas, Veracruz and San Luis Potosí. In a similar position is *Q. furfuracea* Liebm., which was also known only from the type specimen, but which has now been collected in the states of Hidalgo, San Luis Potosí, and Puebla. *Q. ariifolia* Trel. has also been reconsidered as a species distinct from *Q. rugosa* Née (Valencia in prep.), and *Q. trinitatis* Trel. as different from *Q. laurina* Bonpl.

A different case is that of *Q. salicifolia* Née, previously treated as a species of broad distribution from Jalisco to Central America; but a review of herbarium material, including the type specimen, and field work, demonstrated that it has a very restricted distribution, only on the Pacific slope of the Sierra Madre del Sur and apparently only in Guerrrero. The treatment of *Q. salicifolia* as a species of broad distribution was due to the scant knowledge of this species and to the fact that all specimens which have narrow, lanceolate, glabrous leaves were erroneously identified as *Q. salicifolia*: *Q. eugeniifolia* Liebm. (from Central America); *Q. nixoniana* S. Valencia & Lozada-Pérez and *Q. laurina* Bonpl. from Oaxaca and Guerrero, *Q. benthamii* A. DC. from Chiapas, *Q. pinnativenulosa* C.H. Mull. and *Q. sapotifolia* Liebm. from the Gulf slope.

When speaking of the richness and diversity of species in Mexico it is necessary to refer to this by regions and by states. From the physiographic point of view, Mexican oak species are concentrated in the Sierra Madre Occidental, Sierra Madre Oriental, and Sierra Madre del Sur, but there are also important elements in the isolated mountains of Baja California, in the mountains of Chihuahua and Sonora, in the desert portion of the Central Altiplano, and in the

	SMOr	SOax	SMOcc	SMS	FVT	AC	BC	SChis
Totals	55	23	44	31	31	46	15	24
Lobatae	33	11	24	20	17	13	3	13
Lobatae endemic	14	0	8	8	2	2	2	1
Quercus	23	12	20	11	14	32	9	11
Quercus endemic	5	1	5	1	2	10	1	0
Protobalanus	0	0	0	0	0	1	4	0
Protobalanus endem	0	0	0	0	0	0	1	0

Table 1. Estimated wealth of species for the principal physiographic regions of Mexico.

SMOr = Sierra Madre Oriental
SOax = Sierra Norte de Oaxaca
SMOcc = Sierra Madre Occidental
SMS = Sierra Madre del Sur
FVT = Transmexican Volanic Belt
AC = Central Plateau (Altiplano)
BC = Baja California
SChis = Sierra de Chiapas

mountainous regions of Chiapas. Based on preliminary data we present next the estimated wealth of species for the principal physiographic regions of Mexico; these data are summarized in **Table 1**.

The Sierra Madre Oriental remains the most diverse region in Mexico; it contains around 55 species. 33 % belong to Section *Lobatae*, of which 14 are endemic, and 23 in Section *Quercus*, of which 5 are endemic. Prominent in this region is the highest number of endemics among red oaks stands, although this fact needs to be taken with caution, since some of these are known only from the type specimen.

Endemic species for this zone are the following: *Quercus cortesii* Liebm., *Q. cupreata* Trel., *Q. flocculenta* C.H. Mull., *Q. furfuracea* Liebm., *Q. galeanensis* C.H. Mull., *Q. graciliramis* C.H. Mull., *Q. hirtifolia* M.L. Vazquez et al., *Q. hypoxantha* Trel., *Q. miquihuanensis* Nixon & C.H. Mull., *Q. pinnativenulosa* C.H. Mull, *Q. rysophylla* Weath., *Q. tenuiloba* C.H. Mull., *Q. xalapensis* Bonpl., *Q. runcinatifolia* Trel., *Q. ariifolia* Trel., *Q. clivicola* Trel., *Q. edwardsiae* C.H. Mull., *Q. germana* Schltdl. & Cham., *Q. verde* C.H. Mull.

The Sierra Norte de Oaxaca. Some consider this a continuation of the Sierra Madre Oriental, but although it is evident that this region receives some influence from that mountain range, there is a certain physiographic discontinuity and for this reason it is treated here as a different region. In this zone there grow around 23 species, 11 are from Section *Lobatae* and 12 from Section *Quercus* with a single endemic species: *Q. macdougalli* Martínez.

The Sierra Madre Occidental. With an estimated 44 oak species, this physiographic region is in third place in oak diversity; 24 species are from Section *Lobatae*, of which 8 are endemic and 20 belong to Section *Quercus* with 5 endemic. The species endemic to this region are *Q. albocincta* Trel., *Q. aristata* Hook & Arn., *Q. durifolia* Seemen ex Loes., *Q. fulva* Liebm., *Q. macvaughii* Spellenb., *Q. coffeicolor* Trel., *Q. radiata* Trel., *Q. tarahumara* Spellenb., *Q. convallata* Trel., *Q. praeco* Trel., *Q. subspathulata* Trel., Q. ×*basaseachicensis* C.H. Mull. (*Q. depressipes* Trel. × *Q. rugosa* Née), and *Q. ignaciensis* C.H. Mull.

The Sierra Madre del Sur. The diversity of this range is relatively low; 31 species have been identified, 20 in Section *Lobatae,* 8 being endemic and 11 in Section *Quercus* with a single endemic species. The endemic species of this zone are *Q. cualensis* L.M. González, *Q. iltisii* L.M. González, *Q. mulleri* Martínez, *Q. nixoniana* S. Valencia & Lozada-Pérez, *Q. rubramenta* Trel., *Q. salicifolia* Née, *Q. tuitensis* L.M. González, *Q. uxoris* McVaugh and *Q. martinezii* C.H. Mull.

The Transmexican Volcanic Belt. Both the diversity and the endemism of this region are relatively low for the genus *Quercus*; revisions show that there are 31 species, of which 17 belong to Section *Lobatae* with two endemics and 14 are placed in Section *Quercus* with two endemics. The endemic species in this region are *Q. ×dysophylla* Benth. (*Q. crassipes* Bonpl. × *Q. crassifolia* Bonpl.), *Q. hintonii* E.F. Warb., *Q. frutex* Trel. and *Q. microphylla* Née.

The Central Plateau (Altiplano). This is the second most diverse region, it harbors around 46 species of oak, 13 belong to Section *Lobatae* with two endemics and 32 are from Section *Quercus* with ten endemics; *Q. chrysolepis* Liebm., which belongs to Section *Protobalanus*, also grows in this region. It is interesting to stress the high endemism of Section *Quercus* in the Altiplano. The endemic species are the following: *Q. gravesii* Sudw., *Q. tardifolia* C.H. Mull. (*Q. gravesii* × *Q. coahuilensis*), *Q. carmenensis* C.H. Mull., *Q. deliquescens* C.H. Mull., *Q. filiformis* C.H. Mull., *Q. hinckleyi* C.H. Mull., *Q. invaginata* Trel., *Q. potosina* Trel., *Q. pungens* Liebm., *Q. striatula* Trel., *Q. tinkhamii* C.H. Mull., and *Q. undata* Trel.

The Peninsula of Baja California. This is the least diverse of the regions analyzed. Found there are 16 species of oaks, with three from Section *Lobatae,* two endemic; nine belong to Section *Quercus* with one endemic, and four are in Section *Protobalanus* with one endemic. The endemic species in this region are *Q. devia* Goldman, *Q. peninsularis* Trel., *Q. brandegeei* Goldman, and *Q. cedrosensis* C.H. Mull. (the latter on Cedros Island).

Sierras de Chiapas. This region has continuity with the mountain ranges of Guatemala; it is thought to harbor 24 species with 13 in Section *Lobatae* and one endemic, while 11 are in Section *Quercus* without any endemics. The diversity of this zone could change with study, since it has received little attention and its relations with Central America are problematic. The only endemic species is *Q. duratifolia* C.H. Mull., which should also be reviewed.

Analysis of the Distribution of the Genus *Quercus* by Physiographic Region

The previously mentioned regions were analyzed in order to recognize the relationship which is evident among them, based on the distribution of oaks in

Mexico. The programs WinClada (Nixon 1999) and Nona (Goloboff 1977) for personal computers were utilized for this. A matrix was constructed with the eight physiographic regions indicated above with an additional hypothetical group which was considered a root (a total of 9 rows functioning as terminals) and 145 columns of the oak species (72 *Lobatae*, 69 *Quercus*, and four *Protobalanus*) which were considered as characters. Three kinds of analysis were done. The first used all included species; the second only those from Section *Lobatae* and the third, the white oaks. Data on *Protobalanus* were not utilized to do a separate analysis since there are only four species in this section.

Tree A in Figure 5 shows the results of the inclusion of the 145 species. In this one can appreciate the relationship which the Sierra Madre del Sur has with the Transmexican Volcanic Belt and the Peninsula of Baja California as a sister group of the clade which unites the Sierra Madre Occidental and the Central Altiplano. For their part, the Sierra Madre Oriental, the Sierra Norte of Oaxaca and the Ranges of Chiapas form a basal grade.

Tree B in Figure 5 shows the results when only red oaks are included. The same basal grade is found in this one. Subsequently The Central Plateau (Altiplano) and the Peninsula of Lower California form a clade which behaves as a sister group of the one formed by the Sierra Madre del Sur, the Sierra Madre Occidental and the Transmexican Volcanic Belt.

Tree C in Figure 5 was obtained by considering only the white oaks; in this one a grade is formed with the Central Altiplano in the base, followed by the Sierra Madre Occidental and this as a sister group of the clade formed by the Sierra Madre del Sur and the Transmexican Volcanic Belt on the one hand and

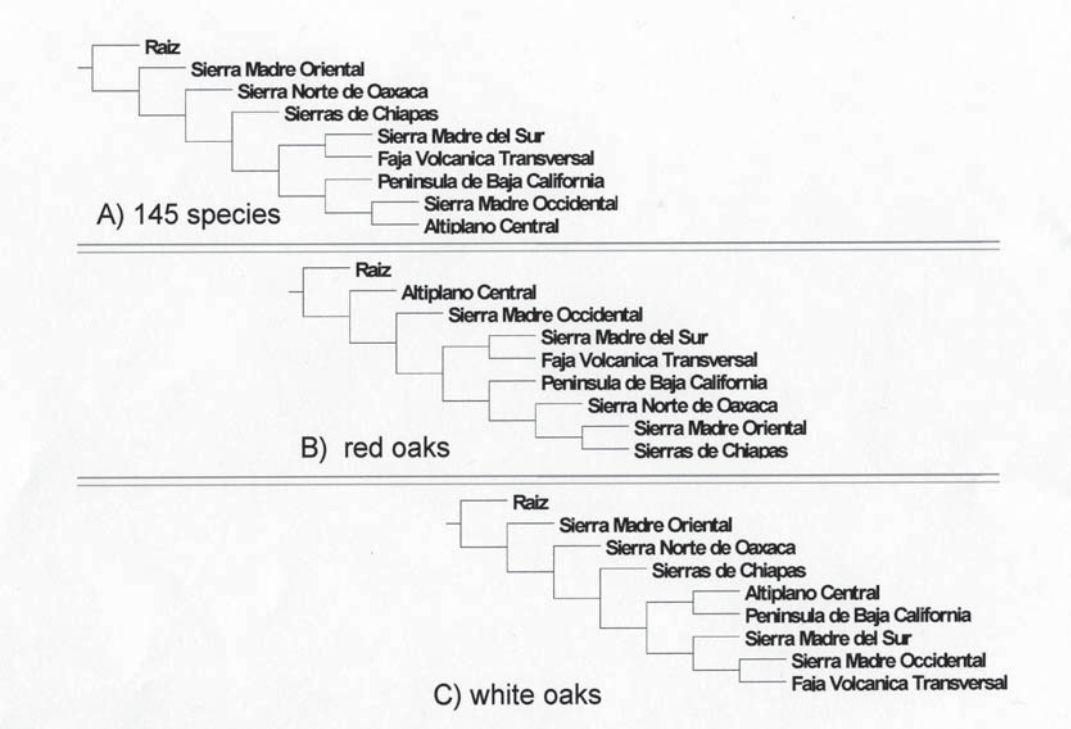

Figure 5. Analysis of the distribution of the genus *Quercus* by physiographic region. A) Tree with the inclusion of the 145 species. B) Tree with the inclusion of only red oaks. C) Tree with the inclusion of only white oaks.

on the other a grade with the Peninsula of Baja California and the Sierra Madre Oriental, while the Sierra Norte of Oaxaca and the Ranges of Chiapas form a more derived group.

The relationships shown in the cladograms indicate that the Sierra Madre Oriental, Sierra Madre Occidental and the ranges of the Central Altiplano have played an important role in the diversity and radiation of oaks, the first preferentially for the red oaks and the latter two for the white oaks.

On the other hand, in the context of the states, the numbers for specific diversity have been modified and in accordance with these, the state with the greatest richness of species is San Luis Potosí with 54, followed by Oaxaca with 50, following this is Nuevo León with 47, Jalisco with 45, Hidalgo with 42, Chihuahua with 40 and Veracruz with 39. The richness known for the rest of the states is equal or inferior to the last number.

The Sections of *Quercus* in Mexico. In Mexico there are three sections in the genus *Quercus: Protobalanus, Lobatae* and *Quercus*. Below is a brief summary of different important aspects of each of the sections of the subgenus *Quercus* in Mexico.

Golden cupped oaks (Section *Protobalanus*). Restricted to the American continent, this is the smallest section of the genus *Quercus*, with only five species. It is localized in the northwest of Mexico and the western-most states of the United States. In accordance with the phylogenetic analyses of Nixon (1993) and of Manos *et al*., (1999), this section is related to Section *Quercus* (or American white oaks) (Figure 2).

Of the five species recognized for Section *Protobalanus*, four, *Q. palmeri* Engelm., *Q. tomentella* Engelm., *Q. cedrosensis* C.H. Mull., and *Q. chrysolepis* Liebm. are present in Mexico, constituting 3% of Mexican oaks. The last is the species of greatest distribution and morphological variation of the four (Manos 1997).

All the oaks of this section are biennial fruiting, although due to their character of possessing perennial leaves, in which the leaves can last more than one year, they give a false appearance of being annual.

Red Oaks (Section *Lobatae*). This section is also endemic to the American continent; it has approximately 120 species distributed from North America to Colombia. In Mexico there are around 76, which constitute 48% of Mexican oaks (Valencia 2004).

In Mexico the red oaks dominate in regions of greater altitude and the more humid forests; they are less diverse in dry regions, although in some regions there may be exceptions in which some red oaks such as *Q. castanea* Née and *Q. urbanii* Trel. are more tolerant than the white oaks.

Section *Lobatae* is found towards the base of the phylogenetic tree of the sections of the Subgenus *Quercus*, implying that sections *Quercus* and *Protobalanus* are derived and are more closely related than they are to the red oaks (Nixon 1993, Manos *et al*., 1999) (Figure 2).

The maturation of the acorns of the red oaks may require two years in the species of greatest altitude and latitude, or one year in the more southern species or those growing in warmer and more humid zones, as for example *Q. salicifolia* Née, *Q. crispifolia* Trel. and *Q. nixoniana* S. Valencia & Lozada-Pérez.

There is a clear distinction among the sections of the genus *Quercus*. The red oaks display leaves with a margin that is either entire, lobed or dentate-aristate, the scales of the acorn cups are striped, the internal surface of the endocarp is tomentose, the abortive ovules are in apical position and the free perianth of the female flowers forms a rim. The anatomy and color of the wood also show differences and this latter gives a name to the two largest sections of oaks in America: *Lobatae* (red oaks) and *Quercus* (white oaks).

The majority of red oaks have wood with a light red tint and with vascular elements having a greater diameter, a round form, and thicker walls in comparison with those of the white oaks. In the same way, they have fewer tyloses in the vascular elements and therefore the wood is more porous than that of the white oaks, and it has little resistance to damage by fungus or insects. Several studies have been done on the anatomy of the wood of Mexican oaks. Among these, those of De la Paz (1976, 1982, 1985) and Valencia and Barajas-Morales (1995) stand out.

Mexican red oaks have received more attention than the white oaks. Various works have approached them in different ways, such as that headed by Dr. Ken Oyama in Morelia who, based on molecular data, carried out investigations on the phylogenetic relations of the red oaks, as well as diverse problems of hybridization.

Other teams, also experienced, are those of Dr. Antonio González Rodríguez, that of Dr. Efrain Tovar and of Dr Ana Mendoza, who study oak hybridization, while the first (González Rodríguez) treats, in addition, the relationship of the species and their morphology with the environmental conditions in which they grow. The section has also been approached in the biogeographical context by Torres (2009). Vázquez (2001), Valencia (2005), and Romero (2006), studied different complexes of red oaks from the taxonomic point of view, thus contributing to the taxonomic knowledge of this group.

The most problematic taxonomic groups in Section *Lobatae*. Described below are some groups of species which present frequent taxonomic problems or which are important because of their broad geographic spread. The groupings do not aim to include species which are related phylogenetically, since in the majority of cases there are no data for this, but they do seek to illustrate frequent taxonomic problems by including together the species which are confused with great frequency. It is sufficient to note that in the case of some species they could be counted in two or more groups.

The *Quercus laurina* group. This group is found in cold, humid zones in cloud forests, moist oak forests and forests of conifers and *Quercus*. Most of the species of this group have lanceolate leaves, with a pointed, bristled apex, dorsal and ventral surface glabrous or retaining only some clustered trichomes in the axils of the secondary veins. Included here are *Q. acherdophylla*, *Q. affinis*, *Q. laurina*, *Q. crassipes*, *Q. mexicana*, *Q. crispipilis*, *Q. depressa*, *Q. gentryi* C.H. Mull., *Q. benthamii*, *Q. rubramenta*, *Q. mulleri*, *Q. trinitatis*, *Q. pinnativenulosa*, *Q. viminea* Trel., *Q. emoryi* Torr., *Q. saltillensis* and *Q. salicifolia*. These species could in turn be segregated into subgroups which present particular problems, for example, *Q. crassipes*, *Q. mexicana*, and *Q. crispipilis*. This group is treated as based on the species of greatest distribution and apparently greatest promiscuity,

Q. laurina, since the latter has been observed as hybridizing with *Q. affinis*, *Q. crassipes*, *Q. mexicana*, and *Q. rubramenta* of this group, as well as with *Q. crassifolia* and occasionally with *Q. candicans*.

The specimens of these species in herbaria are frequently confused, especially if they lack acorns, since the maturation time of one or two years permits differentiation of some of them, e.g. *Q. acherdophylla* is of annual maturation while *Q. laurina* is biennial. Requiring mention here is *Q. depressa* which, in contrast to the other species, is a shrub oak impossible to confuse in the field, but whose herbarium specimens show great similarity to *Q. affinis* and *Q. laurina*.

This group has been treated by Valencia (1994, 2005) through an analysis of different morphological characters and with phylogenetic analysis by González et al. (2004) using molecular data.

The *Quercus acutifolia* group. *Quercus acutifolia* Née is the best known species of this group and in fact many species included here have been erroneously identified as this. Its distribution is restricted to the Sierra Madre del Sur, the Transmexican Volcanic Belt and Sierra Madre Oriental. This group of species is characterized by lanceolate to elliptical leaves, glabrous on both surfaces, with some clustered trichomes in the axils of the veins and with a dentate-aristate margin. Apparently there is less hybridization among the species of this group than in the previous one and the majority of the species have a more restricted distribution. Included here are the species *Q. acutifolia*, *Q. albocincta*, *Q. canbyi* Trel., *Q. conspersa*, *Q. cortesii*, *Q. brenesii* Trel., *Q. furfuracea*, *Q. skinneri* Benth., *Q. paxtalensis* C.H. Mull., *Q. sartorii*, *Q. xalapensis*, and *Q. uxoris*.

The *Quercus castanea* group. This group is so named because *Q. castanea* is the species of broadest distribution and most abundant in herbarium collections. The species included are *Q. eduardii* Trel., *Q. castanea*, *Q. sideroxyla* Bonpl., *Q. scytophylla* Liebm. and *Q. hypoleucoides* A. Camus. The lower surface of leaves of *Q. castanea* can be completely covered by trichomes and then it gets confused with *Q. sideroxyla*, while more glabrous specimens can be confused with *Q. eduardii*. This group is being studied by the team of Dr. Ken Oyama in order to learn the relationships and possible degrees of hybridization among them using molecular data.

The *Quercus crassifolia* group. In this group are included *Q. fulva, Q. crassifolia, Q. conzattii* Trel., *Q. macvaughii, Q. tarahumara, Q. urbanii, Q. hypoleucoides*, *Q. hintonii*, and *Q. dysophylla*. Characterized by very leathery leaves completely tomentose on the lower surface; the upper surface has sunken veins giving it a rugose appearance. Some of the species of this group were treated by Vázquez in his doctoral dissertation (2001).

The case of *Q. dysophylla* must be emphasized; it was described as a new species by Bentham in 1840, but a hybrid nature was suspected due to the fact that only rare isolated individuals were observed in the field, and when only *Q. crassifolia* and *Q. crassipes* were present in sympatry. Tovar and Oyama (2004) studied this taxon both morphologically and from the molecular point of view, confirming that it is a hybrid formed by the crossing of these two species in sympatric surroundings. Unfortunately there are other problems, since hybridization between *Q. mexicana* and *Q. crassifolia* can produce morphology

similar to that of *Q. dysophylla*, for which reason it is necessary to be careful when collecting.

White Oaks (Section *Quercus* sensu stricto). Section *Quercus* has a broad distribution in the Northern Hemisphere. In Mexico there are around 80 species which is equivalent to 49% of the total for the country.

White oaks are more tolerant of conditions of moisture stress, and for this reason they have a wider range of habitats than the red oaks; they can therefore be more common in dry regions than in moist surroundings, as indicated by their greater diversity and endemism in the region of the Central Plateau (Altiplano). Some exceptions may exist such as *Q. germana*, *Q. martinezii*, and *Q. macdougalli,* which are dominant and characteristic of humid oak populations and of cloud forests.

Section *Quercus* is a sister group to Section *Protobalanus*, both derived with respect to the *Lobatae* (Nixon 1993; Manos *et al*., 1999) (Figure 2). Maturity of the acorns of white oaks is always annual and this is considered to be a derived characteristic in the maturation of the fruit of oaks.

White oaks have leaves with a lobed, toothed, or entire margin, but without bristles, present is only a mucron which can be sharp and give the false impression of a bristle; the scales of the cups of the acorns are frequently keeled, the internal surface of the endocarp is smooth and the abortive ovules are in a basal position. The vascular elements in the wood are smaller, having a somewhat angular form in a transverse cut and their walls are more delicate than those of the red oaks. They have tyloses which block the vascular elements in the heartwood and for this reason they are less liable to attack by fungus and insects; this property has been an advantage in the manufacture of barrels for aging alcoholic beverages.

In this section are placed the subsections Virentes and Glaucoideae, studied by Nixon (1984), who contributed important data on their taxonomy and ecology. Nixon holds that these subsections are characterized by the presence of fused cotyledons and at the time of germination, the hypocotyl-epicotylic axis is placed more deeply into the soil, giving protection to the young seedling. Nixon (2002) postulates that these are characteristics adaptive for desiccation and fire, since the species which constitute these groups are broadly tolerant of conditions of dryness.

The white oak group presents greater taxonomic difficulty and has received less attention. Only some species such as *Q. magnoliifolia* and *Q. resinosa* are undergoing study in order to understand their variation and hybridization. *Q. rugosa* has also received a great deal of attention because of its broad geographic and ecological distribution.

The most problematic taxonomic groups of Section *Quercus.* Below are described some groups of species which present frequent taxonomic problems or are important because of their broad geographic distribution. As mentioned earlier, the groups do not aim to include phylogenetically related species, but rather to demonstrate taxonomic problems.

The *Quercus rugosa* group. This may be one of the largest complexes because of the wide distribution of *Q. rugosa*. In this group are included, in addition to *Q. rugosa*, *Q. greggii*, *Q. ariifolia*, *Q. obtusata* Bonpl., *Q. laeta*, *Q. potosina*, and *Q. peduncularis* Née, characterized by obovate, occasionally

broadly obovate or oblanceolate leaves, with the upper surface strongly rugose and the lower with clustered trichomes.

In this same group the problem is exacerbated between *Q. laeta* and *Q. obtusata*, including their consideration as a single species. *Q. laeta* is a problem because of the wide morphological variation that it shows, making its delimitation and identity more difficult.

The *Quercus magnoliifolia* group. This group is characterized by species with large obovate glabrous or tomentose leaves, with parallel secondary veins and dentate margins. Included here are *Q. magnoliifolia* Née, *Q. resinosa* Liebm., *Q. liebmannii* Oerst., *Q. muehlenbergii* Engelm., *Q. obtusata*. All of these can be easily confused if one is not careful to use a microscope to observe in detail the type of trichomes present. Hybridization among them is likely in areas of sympatry, which accentuates the problem. This complex is under investigation in the laboratory of Dr. Ken Oyama.

The complex of *Q. insignis* and *Q. oocarpa*. These two species of oaks from beautiful Mexican cloud forests are characterized by oblanceolate to obovate leaves with a dentate margin and parallel veins, the shoots and the lower surface of leaves with fasciculate trichomes having erect, golden radii and acorns the largest among American oaks, reaching 9 cm in diameter when fresh in *Q. insignis*. Unfortunately the differences between these two species are not very clear, as is their distribution. Small populations have been found in Veracruz, Oaxaca, and Chiapas which undoubtedly belong to *Q. insignis*; but rarer specimens, with smaller fruits and leaves, coming from Jalisco, Nayarit, and Guerrero raise doubts about the identity of these two species. These species are under study by the working group of Dr. Antonio González.

The group of shrub White Oaks. Included in this group are *Q. frutex* Trel., *Q. repanda*, *Q. intricata* Trel., *Q. microphylla*, *Q. grisea* Liebm., *Q. sebifera*, *Q. tinkhamii*, *Q. striatula*, *Q. pringlei*, *Q. depressipes*. All are shrubby, either growing very close to the ground or reaching a height of around a meter, sometimes, as *Q. grisea*, a small tree. Most of these species are poorly known and seldom collected with acorns. With the exception of *Q. sebifera*, *Q. pringlei*, and *Q. depressipes*, they have trichomes which cover the lower surface of the leaf. Herbarium specimens of these species possess similarities which cause many problems for their identification.

Conclusion. Mexico possesses the greatest wealth of species of the genus *Quercus*, brought about by diverse factors among which the physical geography of the country is prominent. Some of its mountains, strategically situated or isolated, have functioned as islands which allowed speciation and great endemism in Mexico. The continuity of the great mountain chains have functioned as corridors permitting the wide distribution of many other species such as *Q. laurina*, *Q. candicans*, *Q. crassifolia*, *Q. rugosa*, and *Q. polymorpha* Schltdl. & Cham.

The extraordinary diversity of the genus as well as its ecological and economic potential, give high priority to an increase in studies to learn more about this important genus. Although knowledge of oaks has increased considerably in recent years, there are still serious problems to resolve. Individually these problems are not exclusive to the oaks, but together, they make the taxonomic study of the genus difficult.

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