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| Kc Nixon. Infrageneric classification of *Quercus* (Fagaceae) and typification of sectional names. *Annales des sciences forestières*, INRA/EDP Sciences, 1993, 50 (Suppl1), pp.25s-34s. hal-00882872

HAL Id: hal-00882872

<https://hal.archives-ouvertes.fr/hal-00882872>

Submitted on 1 Jan 1993

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Review article

Infrageneric classification of *Quercus* (Fagaceae) and typification of sectional names

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Summary — The genus *Quercus* L (the true oaks) is widespread in the Northern hemisphere, in habitats ranging from temperate and tropical forests to dry thorn scrub and semi-desert. As far as is known, all species are anemophilous. The genus is most closely related to *Trigonobalanus* Forman, *Colombobalanus* Nixon and Crepet, and *Formanodendron* Nixon and Crepet, 3 extant tropical monotypic genera. The oldest unequivocal oak fossils are Oligocene in age, although fossilized catkins and stellate trichomes that may represent earlier *Quercus* are preserved in Baltic amber, of uncertain Early Tertiary age. Trigonobalanoid fossils are known from the Oligocene and Paleocene of North America, and later deposits in Europe. A subgeneric and sectional classification of *Quercus* that is slightly modified from that proposed by Camus is most consistent with recent phylogenetic analyses within *Quercus*. Such a classification recognizes 2 subgenera, *Quercus* and *Cyclobalanopsis* (Oersted) Schneider. The latter is restricted to eastern Asia and Malesia. Subgenus *Quercus* is divided into sections *Lobatae* Loudon (red oaks: North and South America), *Protobalanus* (Trelease) Schwarz (intermediate oaks: western North America), and *Quercus* (white oaks: E and W hemispheres). Two groups of white oaks that are sometimes recognized as sections, *Ilex* (Eurasia), and *Cerris* (Eurasia) are considered part of section *Quercus*, but merit subsectional or higher rank following more complete analyses.

***Quercus* / taxonomy / phylogeny / subgenera / sections**

Résumé — Classification à l'intérieur du genre *Quercus* et caractérisation des noms de sections. Le genre *Quercus* (les vrais chênes) couvre l'ensemble de l'hémisphère nord et colonise des habitats allant des forêts tempérées et tropicales aux formations arbustives et semi désertiques. D'après les connaissances acquises à ce jour, toutes les espèces sont anémophiles. Le genre est proche de 3 genres tropicaux monotypiques vivants : *Trigonobalanus* Forman, *Colombobalanus* Nixon et Crepet et *Formanodendron* Nixon et Crepet. Les restes fossiles les plus âgés datent de l'oligocène, bien que des chatons et des trichomes étoilés susceptibles de représenter le genre *Quercus* et datés de manière imprécise du début du tertiaire aient été préservés dans de l'ambre de la mer Baltique. Des fossiles trigobalanoides datant de l'oligocène et du paléogène en Amérique du Nord et des dépôts postérieurs en Europe ont été reconnus. La classification en sous-genres et en sections, tenant compte des analyses phylogénétiques récentes, est proche de celle proposée par Camus. Cette classification comprend 2 sous-genres, *Quercus* et *Cyclobalanopsis* (Oersted). Le dernier n'est représenté qu'en Asie. Le sous-genre *Quercus* est divisé en 3 sections : *Lobatae* Loudon (chênes rouges : Amérique du Nord et du Sud), *Protobalanus* (Trelease) Schwarz (chênes intermédiaires : Amérique du Nord occidentale) et *Quercus* (chênes blancs : hémisphères est et ouest). Deux groupes de chênes blancs souvent classés dans les chênes blancs comme sections, *Ilex* (Eu-

rasie) et *Cerris* (Eurasie) sont considérés comme appartenant à la section *Quercus*; ils mériteraient cependant d'être classés en sous-sections ou à un niveau supérieur après analyses complémentaires.

Quercus / taxonomie / phylogénie / sous-genres / sections

INTRODUCTION

Recent studies of the phylogeny of *Quercus* (Nixon, 1984, 1989) (Manos *et al*, KC Nixon, P Manos, manuscripts in preparation) have provided the basis for a revised infrageneric classification of the genus. *Quercus* is most closely related to the recently discovered tropical genera *Trigonobalanus* Forman, *Formanodendron* Nixon and Crepet, and *Colombobalanus* Nixon and Crepet (Nixon, 1989; Nixon and Crepet, 1989). Cladistic analysis of 17 morphological characters (Nixon, 1984) (KC Nixon, P Manos, manuscript in preparation) has been undertaken in combination with chloroplast (cp) DNA restriction site analyses of 92 informative sites among 33

species of *Quercus*, *Trigonobalanus* and *Colombobalanus* (Manos *et al*, manuscript in preparation). The relationships of various groups within *Quercus* are summarized in figure 1, based on a combination of the morphological and molecular data analyses that will be presented elsewhere (KC Nixon, P Manos, manuscript in preparation). The morphological data set allowed greater resolution of among-section relationships, while the molecular data set added synapomorphies for sectional groups. In general, the results of these analyses support recognition of 4 monophyletic groups of oaks, the *Cyclobalanopsis*, the *Lobatae* (the red oaks, subg *Erythrobalanus* of recent literature), the *Protobalanus* (the intermediate oaks) and the white oaks in the

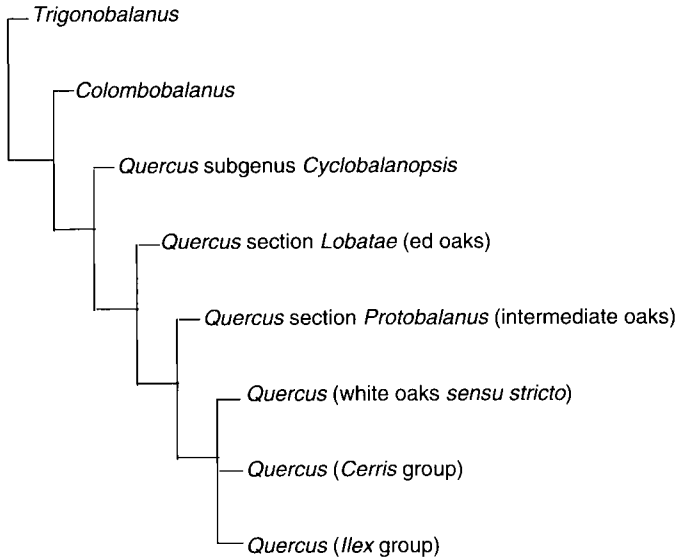


Fig 1. Proposed phylogenetic relationships of major infrageneric groups of *Quercus*.

broad sense (variously referred to as *Lepidobalanus*, *Euquercus*, or *Leucobalanus* in recent literature). Note that the "Cerris" and "Ilex" groups are not recognized here as sections, and may merit recognition as subsections within section *Quercus* but the limits of these groups in terms of both species and characters is not clear at this time, particularly when the Asian species of *Quercus* are considered. Because of this uncertainty, I have chosen to defer a subsectional treatment within the white oaks until more data are available.

Because of the general similarity of the results of recent phylogenetic analyses to the previous classification proposed by Camus (1938), and in order to maintain the greatest level of taxonomic stability, I have followed her classification as closely as possible. However, Camus did not always adequately search for the earliest names at the sectional level in *Quercus*, and some of the names which she used must be replaced by earlier names. In particular, the sectional name of the red oak group must be changed to the oldest available name, *Lobatae* Loudon. In addition to the names accepted below, lectotypification of the sectional names proposed by Loudon (1830, 1835–1838) and others, even though they are treated as synonyms here, is important in order to stabilize the infrageneric nomenclature of *Quercus*. In all cases of lectotypification below, an attempt has been made, where possible, to lectotypify these names so that names currently and widely in use are not replaced. This has not been possible in all cases.

Is it beyond the scope of this paper to exhaustively review the history of subgeneric and sectional names in *Quercus*, but the synonymy presented below includes all names which have been used extensively. I present here an infrageneric classification of the genus *Quercus* which broadly follows that of Camus, but utilizes Loudon's sectional names which have priority for

some of the taxa Camus recognized. It is important to synonymize some of Loudon's sectional names which were published simultaneously.

FOSSIL HISTORY

The oldest unequivocal oak fossils are acorns, staminate catkins/pollen and compressed leaves from Oligocene deposits of North America (Daghlian and Crepet, 1983; Crepet, 1989; Crepet and Nixon, 1989a, b; Nixon and Crepet, 1989). Staminate catkins and stellate trichomes that resemble those of modern oaks are preserved in Baltic amber of northern Europe (Conwentz, 1986), but need further investigation, because they occur with fruits which appear to be trigonobalanoid.

Prior to the Oligocene, the oak lineage is represented by trigonobalanoid fossils consisting of well-preserved fruits and infructescences, pistillate and staminate inflorescences with *in situ* pollen, and associated '*Dryophyllum*' type leaf compressions (Crepet and Nixon, 1989a, 1989b). While these fossils are not identical with modern trigonobalanoids, they share plesiomorphic features, such as several free triangular fruits in a valved cupule, capitate stigmas and cupules arranged along an elongate axis.

Throughout mid- and late-Tertiary deposits of the northern hemisphere, oak leaf compressions and impressions are abundant, and many of these, particularly from North America, have been identified as close relatives of modern species. Whether or not the Miocene and Pliocene species are as close to modern species as some authors have presumed, it is clear that by this time the oak flora had become prominent and diverse, and at least superficially resembled the assemblages seen in modern subtropical and temperate forests.

Further work is necessary to resolve the phylogenetic affinities of these abundant Tertiary oak leaf fossils.

KEY TO THE SUBGENERA AND SECTIONS OF *QUERCUS*

A. Stigmas capitate to subcapitate or discoid, styles generally terete without adaxial stigmatic groove; staminate catkins usually with prominent bracteoles, these subpersistent to caducous; scales of cupule in concentric or spiral rings, usually obviously connate laterally to form lamellae; east Asian. Subgenus *Cyclobalanopsis*.

AA. Stigmas usually linear ampliate or broadly ampliate, styles grooved, or with a short stigmatic groove extending from the stigma; staminate catkins with inconspicuous, caducous bracteoles, or these sometimes lacking; scales of cupule various, imbricately arranged and free; widespread in the northern hemisphere. Subgenus *Quercus*.

B. Base of pistillate perianth (perigon) free, forming a skirt or flange; styles usually elongate, linear-ampliate; endocarp always tomentose; cup scales typically flat, unkeeled; teeth of leaves if present usually aristate or spinose, rarely mucronate. Section *Lobatae*.

BB. Base of pistillate perianth (perigon) adnate to ovary/style bases, not forming a flange or skirt; styles elongate and linear-ampliate or short and broadly ampliate or cuneate; endocarp tomentose or glabrescent; cup scales typically keeled or tuberculate or both; teeth of leaves if present aristate, pungent, or mucronate.

C. Abortive ovules apical to lateral, rarely appearing basal; leaves persistent

2–3 years; acorn maturation biennial. Section *Protobalanus*.

CC. Abortive ovules always basal; leaves deciduous to subpersistent, rarely persistent for more than 1 year; acorn maturation biennial or annual. Section *Quercus*.

TAXONOMIC TREATMENT OF *QUERCUS*

Quercus (*oak, encino, chêne*)

Quercus L, *Syst Pl* ed 2, II, 994. 1753. [for complete synonymy at the generic level, see Camus (1938)]. - Type: *Quercus robur* L (*vide* ING)

Trees or shrubs, flowers monoecious; wood ring-porous or diffuse-porous; terminal buds prominent, quadrangular to pentangular or rounded in cross-section; bud scales imbricate, bud stipules sometimes persistent; axillary buds often closely associated with and subtending terminal bud; leaves spirally arranged, craspedodromous, mixed craspedodromous or campylodromous, rarely bronchidodromous, often with parallel secondary veins, marginal teeth (if present) simple, aristate, mucronate or oblique, 1 associated with each secondary vein, or in some species the secondary vein branching and terminating in several teeth; staminate inflorescences lax-spicate (catkins), clustered at the base of new growth or occurring singly in the axils of some of the lower leaves, emerging at vernalization; staminate flowers single or in groups of 1–3 along rachis, subtending bracteole prominent and often exceeding perianth and persistent past anthesis, or inconspicuous and caducous; stamens 6 (2–12), usually exerted at anthesis, surrounding a tuft of simple trichomes inter-

preted as representative of a rudimentary pistillode: pollen tricolporate (-tricolpate), spheroidal to subprolate or suboblate, exine sculpture generally rugulate or scabrate, often microscabrate; pistillate inflorescence borne in the axils of leaves of young branches, usually stiff, with 1-several partial inflorescences, each subtended by a cupule, only the single central flower of each inflorescence developing; pistillate perianth cupped to campanulate or rotate, shallowly to deeply 5–6 lobed, or the lobes obscure, basally adnate to the ovary or free; ovary 3 (–6+) carpellate, inferior; styles 3 (–6+), linear or sessile, stigmas capitate to linear-ampliate and extending along adaxial styler suture; fruit an acorn, a single rounded indehiscent nut subtended by a cupule that lacks suture zones and does not separate into valves, cupule with external imbricate or concentric scales, the 2 lateral abortive flowers of the partial inflorescence within the cupule; fruit maturation biennial or annual, or occasionally 'pseudoannual' as in some species of section *Protobalanus*; endocarp sericeo-tomentose to glabrescent, columella and remnants of the septa of the carpels often impressed on the seed, forming irregular longitudinal grooves; seed coats usually brownish, adhering tightly to the seed at maturity or adhering to the endocarp wall; cotyledons free or sometimes fused completely: abortive ovules apical, lateral or basal; cupule scales arranged in concentric rows and partially or wholly connate laterally, to form concentric lamellae, or imbricate and free, sometimes reflexed and spinose. $n = 12$.

Distribution: north temperate and subtropical, tropical montane, and particularly in Asia sometimes lowland tropical (subgenus *Cyclobalanopsis*); the greatest concentrations of species are in eastern North America (ca 60), highland Mexico and central America (150–200), and montane subtropical Eurasia from the Middle East to

China and southeast Asia (150?); fewer species are found in the western United States (ca 25) and temperate Europe and North Africa (8–12?); 1 species is found in northern South America (Colombia).

Subgenus *Cyclobalanopsis* — (cycle-cup oaks)

Quercus subgenus Cyclobalanopsis (Oersted) Schneider, *Handb Laubh*, 1, 210. 1906.

– *Cyclobalanopsis* Oersted (as genus), *Bidrat til Kundskab om Egefamilien*, 69. 1871. – *Quercus* section *Cyclobalanopsis* Bentham and Hooker, *Gen Pl III*, 1 p 408. 1880. –Type: *Quercus velutina* Lindley ex Wallich, non Lamarck. (*vide* ING)

Trees or shrubs; bark usually smooth or furrowed, hard, gray or black, rarely light-colored; leaves persistent or subpersistent, entire or serrate-toothed, teeth if present mucronate or rarely setate; foliar trichomes thin-walled and glandular, uniseriate, fasciculate, multiradiate or rosulate, rarely if ever thick-walled and/or stellate; staminate flowers usually distributed in groups of 1–3 along rachis, subtending bracteole usually prominent and often exceeding perianth and persistent, staminate perianth often regularly 6-lobed; anthers apiculate or retuse; pollen exine sculpture typically rugulate, often microscabrate; pistillate perianth 5–6 lobed, base adnate to ovary; styles 3 (–6+), usually linear with an expanded flat or subcapitate stigma, the stigmatic surface extending only partially along styler suture or sometimes not extending along suture at all, in any case not forming a prominent stigmatic groove; stylopodial umbo often annulate with 1–3 (–5) distinct rings; fruit maturing the 2 season or in the 1 year, but at least sometimes 'pseudoannual' as in some species of section *Protobalanus*; endocarp sericeo-tomentose, remnants of the septa of the carpels often

impressed on the seed, forming irregular longitudinal grooves, or subglabrous; seed coats usually brownish, adhering tightly to the seed at maturity or adhering to the endocarp wall; cotyledons free; abortive ovules apical; cupule scales arranged in concentric or spiral rows and partially or wholly connate laterally, to form concentric lamellae, often densely vestitured.

Distribution: subtropical, montane tropical and lowland tropical east Asia and Malaysia.

I recognize the possible utility of generic rank for *Cyclobalanopsis* as proposed by Schwarz (1936). Until careful studies produce stronger evidence that *Quercus* as broadly defined is polyphyletic, the conservative stance of recognizing a single genus is appropriate.

Subgenus *Quercus*: (scale-cup oaks)

***Quercus* subgenus *Euquercus* (Hickel and Camus) A Camus, Les Chênes. *Monographie du genre Quercus*. Vol I. 373. 1938**

Large trees, shrubs or sometimes low rhizomatous shrubs; bark variable, from smooth to scally or furrowed; leaves persistent, subpersistent or deciduous, entire, serrate-toothed or lobed, teeth if present setate, aristate, pungent or mucronate; foliar trichomes thin-walled and glandular, uniseriate, fasciculate, multiradiate or rosulate, and/or thick-walled and/or stellate; staminate flowers distributed singly along rachis, the single subtending bracteole caducous or sometimes lacking, staminate perianth irregularly or regularly 2–6 lobed; anthers retuse, or with an apiculate or attenuate connective; pollen exine sculpture typically scabrate with obscure or obvious perforations; styles 3 (–6+), with expanded stigmatic surface, capitate to linear ampliate with an adaxial stigmatic groove; stylo-

podial umbo often annulate with 1–3 (–5) distinct rings; fruit solitary in each cupule, rounded in cross-section, maturing the 1 or 2 season; abortive ovules apical, or in some species variable in position or basal; cupule hemispheric, cup-shaped to flat; cupule scales variable, spirally or concentrically arranged; laterally connate or free.

I follow Camus in her broad interpretation of subgenus *Quercus*, to include all oak species except the *Cyclobalanopsis* group, although American workers usually recognize 3 subgenera in North America. Camus' classification is compatible with results of phylogenetic analyses. Certain Eurasian oaks (eg *Q. coccifera*) as well as *Protobalanus* are morphologically 'intermediate' in certain characters between red oaks and white oaks *sensu stricto*, and this further supports the closer relationship of these oaks to each other than to *Cyclobalanopsis*. If *Cyclobalanopsis* is included in *Quercus* as a subgenus, prudence recommends that the remainder of *Quercus* be accommodated in a single subgenus. The 3 major groups of oaks in North America may then be recognized as sections (see below).

Quercus subgenus *Quercus* section *Lobatae* (red oaks)

Quercus section *Lobatae* Loudon, Hort Brit 385. 1830. Lectotype (here chosen): *Quercus aquatica* Walt (= *Q. nigra* L). The 4 species which Loudon included in this section are red oaks. This eliminates any possibility of lectotypifying the section so that it is a synonym of the 'type' section, the white oaks. Thus, this name must stand as the earliest name for the red oaks if they are recognized at the level of section.

Quercus section *Integrifoliae* Loudon, Hort Brit 384. 1830. Lectotype (here chosen): *Quercus phellos* L.

Quercus section *Mucronatae* Loudon, *Hort Brit* 385. 1830. Lectotype (here chosen): *Quercus rubra* L.

Quercus section *Rubrae* Loudon, *Arbor Frut Brit* 3, 1877. [1835–]1838. – Type: *Quercus rubra* L. Loudon's concept of *Q rubra* was that of the northern red oak, not of the southern red oak (= *Q falcata*), as the name *Q rubra* was applied by some later authors (eg Sargent, 1922).

Quercus section *Nigrae* Loudon, *Arbor Frut Brit* 3, 1980. [1835–]1838. – Type: *Q nigra* L. Loudon followed Michaux in his concept of *Q nigra* as the blackjack oak (= *Q marilandica*), but included the real *Q nigra* in this section as *Q aquatica*.

Quercus section *Phellos* Loudon, *Arbor Frut Brit* 3, 1894. [1835–]1838. – Type: *Quercus phellos* L.

Quercus section *Erythrobalanus* Spach, *Hist veg Phan* 11, 160. 1842. – *Quercus* subgenus *Erythrobalanus* (Spach) Endlicher, *Gen Plant* suppl 4, 24. 1847. – *Quercus* subsection *Erythrobalanus* (Spach) Post and Kuntze, *Lexicon generum Phaner* 474. 1904. – Genus *Erythrobalanus* (Spach) Schwarz, *Notizbl Bot Gard Berlin* 13, 8. 1936. Lectotype (here chosen): *Quercus rubra* L.

Quercus subgenus *Melanobalanus* Engelman, *Trans St Louis Acad Sci* 3, 388. 1877.

Large trees, shrubs or sometimes low rhizomatous shrubs; bark usually smooth or furrowed, hard, gray or black, rarely light-colored; leaves persistent, subpersistent, or deciduous, entire, serrate-toothed or lobed, teeth if present usually aristate or setate, a terminal seta often present even on untoothed leaves; foliar trichomes thin-walled and glandular, uniseriate, fascicu-

late, multiradiate or rosulate, rarely if even thick-walled and/or stellate; staminate flowers usually distributed singly along rachis, subtending bracteole caducous or lacking, staminate perianth irregularly, often deeply 2–6 lobed; anthers usually somewhat apiculate, occasionally retuse; pollen exine sculpture typically rugulate and microscabrate to scabrate; pistillate perianth 5–6 lobed, the base not adnate to the ovary, therefore forming a minute free skirt or flange, the inner cupule scales often inserted beneath this flange; styles 3(–6+), linear-spatulate, the stigmatic surface extending proximally along stylar suture, forming a darkened stigmatic groove; stylopodial umbo often annulate with 1–3 (–5) distinct rings; fruit maturing the 2 season, or in several species in the 1 year; endocarp sericeo-tomentose, remnants of the septa of the carpels often impressed on the seed, forming irregular longitudinal grooves; seed coats reddish or brownish, adhering tightly to the seed at maturity; cotyledons free or rarely partially connate; abortive ovules apical, or rarely in some species variable in position or subbasal; cupule scales thin, flat, only rarely keeled or tuberculate, imbricate, never spinescent.

Distribution: restricted to temperate, subtropical and montane tropical parts of the new world, from Colombia, South America (1 sp) through central America to forests of southeastern Canada, and westward to southern Oregon; largely absent from the Rocky Mountain area, except for Arizona and New Mexico.

***Quercus* subgenus *Quercus* section Protobalanus (intermediate oaks, golden cup oaks)**

Subgenus *Protobalanus* Trelease, in Standley, *Contr U S Natl Herb* 23, 176. 1922. – *Quercus* section *Protobalanus* (Trelease)

Schwarz, *Notizbl Bot Gart Berlin* 13, 21. 1936. – *Quercus* section *Protobalanus* (Trelease) Camus, *Les Chênes*, vol 1, 157. 1938. – Type: *Quercus chrysolepis* Liebm. Both Camus and Schwarz interpreted Trellease's *Protobalanus* as a section, and attributed this rank to Trellease. Confusion regarding the original rank of this name apparently arose from ambiguity in Trellease's presentation of the name in his 1924 monograph. Trellease used several infrageneric names that had been proposed by earlier authors, eg, *Leucobalanus* Engelmann, without reference to the original authority, publication, or rank at which the names were published. *Protobalanus* was presented in the 1924 monograph in a similar 'naked' manner, leading later authors to believe that this was the original publication of the name. However, the first use by Trellease of the name *Protobalanus* dates to 1916 in *Proc Natl Acad Sci* 2, 627, where he clearly referred to it as a subgenus, as well as referring to the type of *Protobalanus* as *Q chrysolepis* (*loc cit*, p 629). *Protobalanus* was again used by Trellease in 1918 (*Brooklyn Bot Gard Mem* 1, 497), and again in Standley's *Trees and Shrubs of Mexico*, 1922. No description appeared in the earlier publications, but in the latter, Trellease included the name in a key to the species of Mexico, with clear diagnostic characters. The 1922 publication therefore must be considered the first valid publication of the name, and there is no ambiguity in the earlier publications as to the rank (subgenus) at which the name was intended.

Evergreen shrubs or trees, bark usually scaly and rough (as in various white oaks) on older branches; twigs tomentose to glabrous; leaves persistent 2 or more years coriaceous, glaucous and waxy on the abaxial surface, entire or toothed, often spinose, never lobed as in *Q robur*; foliar trichomes thin-walled, semi-glandular, simple or with 2–several fasciculate single-

celled rays emerging from the epidermis together, or multicellular glandular uniseriate; staminate flowers with 4–12 stamens, the anthers apiculate; pollen exine sculpture rugulate to scabrate, with nanno-striae on rugulae; (*fide* Solomon, 1983a, 1983b); pistillate flowers 1–3, usually sessile, peduncule sometimes developed; styles short and ampliate to long with ampliate stigma (*Q palmeri*); fruit maturing in 2nd year, but often the fertile branches do not grow in 2nd year, so that the fruit may appear annual (pseudoannual maturation); endocarp tomentose to appearing glabrous, the seed coats usually attached to the seed but sometimes attached to the endocarp; cotyledons furrowed, subequal.

Distribution: western North America from southern Oregon, south to northern Baja California, Mexico, eastward to central Arizona, and barely into adjacent Chihuahua; also present on the channel islands of southern California, and the only group of oaks present on the islands of Guadalupe and Cedros off the coast of Baja California.

Protobalanus is a distinctive group of about 5 species, 1 of which (*Q chrysolepis* Liebm) is widely distributed and highly variable. The distribution of this group, which is restricted to western North America, suggests a possible common biogeographical history with *Lithocarpus densiflora* and *Chrysolepis sempervirens* and *C chrysophylla* of the California region. The latter 3 species are apparently relicts of a previously richer Asian element in western North America that is no longer prevalent. *Protobalanus* is undoubtedly the most interesting group of oaks in North America from the standpoint of phylogeny and biogeography. The phylogenetic affinities of this distinctive and unique group are uncertain, although for the present, *Protobalanus* must be considered a part of the nominal subgenus. They appear to be closely related to but intermediate between the red oaks and the white oaks. In this respect,

Protobalanus closely parallels the somewhat intermediate groups of Eurasian oaks that center around *Q cerris*, *Q suber*, and *Q coccifera*. *Protobalanus* species appear to be strongly reproductively isolated from the other groups of North American oaks, as no verified natural or artificial hybrids are known.

***Quercus* subgenus *Quercus*
section *Quercus* (white oaks)**

Quercus section *Dentatae* Loudon, *Hort Brit* 384. 1830. Lectotype (here chosen): *Quercus prinus* L. Loudon included a broad array of white oaks, including both American and Eurasian species, in this section.

Quercus section *Ilex* Loudon, *Arbor Frut Brit* 3, 1899. [1835–]1838. Type: *Quercus ilex* L.

Quercus section *Cerris* Loudon, *Arbor Frut Brit* 3, 1730. [1835–]1838. – Type: *Quercus cerris* L.

Quercus section *Albae* Loudon, *Arbor Frut Brit* 3, 1730, 1863. [1835–]1838. Type: *Quercus alba* L.

Quercus section *Robur* Loudon, *Arbor Frut Brit* 3, 1730, 1731. [1835–]1838. Type: *Quercus robur* L.

Quercus section *Prinus* Loudon, *Arbor Frut Brit* 3, 1730, 1872. [1835–]1838. Type: *Quercus prinus* L.

Quercus section *Lanatae* Loudon, *Arbor Frut Brit* 3, 1730, 1920. [1835–]1838. Type: *Quercus lanata* Smith.

Quercus section *Virentes* Loudon, *Arbor Frut Brit* 3, 1730, 1918. [1835–]1838. Type: *Quercus virens* Aiton.

Quercus section *Lepidobalanus* Endlicher, *Gen Plant*, suppl 4, part 2, p 24. 1847, *pro parte*. Lectotype (here chosen): *Quercus robur* L.

Quercus section *Leucobalanus* Engelm., *Trans Acad Sci St Louis* 3, 381. 1876.

Quercus section *Mesobalanus* Camus, *Monographe Genre Quercus*, Atlas I, p 49. 1936.

Quercus section *Euquercus* Hickel and Camus, *Ann Sci Nat Bot*, 9^e ser. III, p 379. 1921. – Type: *Quercus robur* L.

Quercus subgenus *Heterobalanus* Oersted, *Bidr til Kundskab Om Engefamilien*. 1871

Trees or shrubs: bark smooth, rough, scaly or flaky, relatively soft, occasionally hard and furrowed; leaves persistent, subsistent, or deciduous, entire, serrate-toothed or lobed, teeth if present mucronate, pungent, or sometimes on juvenile growth aristate, or rarely (*Cerris* and *Ilex* groups) consistently aristate; foliar trichomes thin-walled and glandular, uniseriate, fasciculate, multiradiate or rosulate, and often thick-walled and/or stellate; staminate flowers usually distributed singly along rachis, subtending bracteole caducous or lacking, staminate perianth regularly to irregularly, often deeply 2–6 lobed; anthers usually retuse, rarely apiculate; pollen exine sculpture scabrate or rugulate–scabrate; pistillate perianth 5–6 lobed, the base adnate to the ovary; styles 3(–6+), usually abruptly ampliate or dilated, sometimes more gradually ampliate or subulate, stigmatic surface extending proximally along styler suture, the stigmatic surface often cuneate in shape; stylopodial umbo usually not annulate; fruit maturing in the 1st year, occasionally (*Ilex* and *Cer-*

ris) maturing in the 2nd year; endocarp glabrate or with minute tomentose vestiture near apex and base, but obscured by the adhering seed coats, or occasionally (*Ilex* and *Cerris*) tomentose-sericeous; colleumellar scar typically not present on lateral part of seed or endocarp; seed coats at maturity adhering to endocarp, or (*Ilex* and *Cerris*) to seed; cotyledons equal or unequal, free, or connate (*Virentes* and *Glaucoideae*); abortive ovules basal; cupule scales keeled or tuberculate, imbricate, usually with thickened corky base, sometimes reflexed and spinescent.

Distribution: the most widespread section of *Quercus*, occurring throughout favorable habitats in temperate, subtropical and tropical montane parts of North and Central America, Europe and (extratropical) Asia.

It is clear, based on morphological and molecular data, that the *Cerris* and *Ilex* groups of oaks are part of the broader white oak group, sharing the synapomorphy of basal abortive ovules. Because the exact relationships of these groups are uncertain (*Ilex* may be paraphyletic to one or more other groups within the white oaks), it seems best at this time to recognize only one section for the white oaks *sensu lato*. As more data within the white oaks become available, a subsectional classification will be proposed, and the variation encompassed by the *Ilex*, *Cerris*, *Virentes*, *Glaucoideae* and other groups of white oaks can be formally recognized based on phylogenetic pattern.

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