

Some Thoughts on Evolutionary and Phylogenetic Perspectives in the Oaks - *Quercus* and *Lithocarpus*

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Introduction - the family *Fagaceae*

An important justification for carrying out experimental taxonomic studies on a large group such as the oaks is the belief that these can help to resolve difficulties and ambiguities which the classical taxonomic approaches cannot. The oaks are a widely distributed and species-rich group with a complex evolutionary history, and it is therefore helpful to view our present perceptions of the oaks particularly in the broader context of the family to which they belong.

The *Fagaceae* is not a large family; there are ten recognised genera (Nixon, 1989). *Fagus* - the beeches, *Nothofagus* - the southern beeches, *Castanea* - the chestnuts, *Castanopsis* and *Chrysolepis* - the chinkapins and two genera of oaks, *Lithocarpus* and *Quercus*. In terms of species richness, the oak genera are by far the largest. Camus (1936-1954), in her monumental work *Les Chenes*, recognises 279 species of *Lithocarpus* and 430 of *Quercus*. In addition, there are 3 very small genera containing rare and possibly relict species, namely *Trigonobalanus*, *Colombobalanus* and *Formanodendron*. The number of species she recognised in the other genera is 8 in *Fagus*, 12 in *Nothofagus*, 7 in *Castanea* and 27 in *Castanopsis*. Although the actual number of species recognised by different authorities varies, these figures indicate relative species richness. On this basis, oaks constitute the bulk of the family, the majority of which belong to the genus *Quercus*.

The characteristic feature of the family is that seed (or seeds) are borne in a cupule; in some genera (*Castanea*, *Fagus* and *Nothofagus*), seeds are enclosed; in *Castanopsis*, *Chrysolepis*, *Lithocarpus*, and *Quercus*, they are not. The form of the cupule in the latter two genera is a well-marked feature of the oaks, as a whole, and can be considered to be the most important single diagnostic feature of the group. A very basic definition of an oak might well be a tree or shrub which produces acorns. Other variable characters within the family have been used as diagnostics, not always with entirely satisfactory results. This can be illustrated by reference to a simple phylogenetic tree of the family.

The basic and most primitive form is best represented by the genera *Castanopsis* and *Chrysolepis*. The salient features are:

1. They include both evergreen trees and shrubs
2. The fruit is a burr which is open at the apex; 1-3 seeds per fruit may be produced
3. The fruit mature in their second season
4. Distribution is tropical Asia and California (*Chrysolepis*)
5. Rigid male inflorescence occur.

The chestnuts, *Castanea*:

1. Deciduous trees and shrubs
2. The fruit is a burr which may contain up to 3 seeds and which are fully enclosed
3. The fruit mature in a single season
4. Distribution is north-temperate
5. Rigid male inflorescence

The southern beeches, *Nothofagus*:

1. Evergreen or deciduous shrubs and trees
2. The fruit is a burr enclosing up to 3 seeds, commonly 2, which are fully enclosed and relatively small in size
3. Fruit may mature in one or two seasons
4. Distribution is in the southern hemisphere

The beeches, *Fagus*:

1. Deciduous trees
2. The fruit is a burr enclosing up to 3 seeds, commonly 2 which are fully enclosed and relatively small in size (cf *Nothofagus*)
3. Fruit mature in a single season
4. Distribution is in the northern hemisphere.

The oaks, *Lithocarpus*:

1. Evergreen trees
2. Fruit an acorn, single seeds are borne in an open cupule
3. Fruits mature in second season
4. Male inflorescence is rigid as in *Castanopsis*
5. Distribution more or less subtropical-tropical, Asia and California

The oaks, *Quercus*:

1. Evergreen or deciduous trees and shrubs (some scrubby)
2. Fruit an acorn
3. Fruits may mature in first or second season
4. Male inflorescence lax
5. Distribution, northern hemisphere (Old and New Worlds)

From the salient points listed it is possible to identify the evolutionary lineages from the basic *Castanopsis* type, which might be called oak, chestnut and beech lines. The major evolutionary imperative seems to have been the expansion of range from the tropical Asian centre of the family. Ancestral forms appear to have been components of rainforest at middle elevations. For such taxa, one means of increasing geographic range is to colonise lower elevations at higher latitudes. This has been a very successful strategy in all three evolutionary lineages, certainly as far as temperate latitudes are concerned. Oak, beech, and chestnut are all to be found as significant and even dominant elements of temperate woodland climax vegetation in the northern hemisphere, and in the case of the beech line, in parts of the southern hemisphere, also. This migration has been accompanied by a number of common evolutionary tendencies, most notably the adoption of the deciduous

habit and the shortening of the period taken by fruits to mature from two seasons to a single season.

Some characteristics of the rainforest ancestry are still retained. The relatively large seed size is still to be found in the oaks and chestnuts, although significant reduction has occurred in beeches. Seed dormancy is a common feature of temperate plants, coupled with some measure of seed longevity. These features are conspicuously lacking in most groups in the family. An interesting divergence is to be found in the oaks, in North American and European species; the white oaks have no seed dormancy and can germinate soon after being shed. This exposes the seedlings to winter conditions which they may be able to survive when and if they are protected by fallen leaves from the canopy. The black oaks have a short-term dormancy which ensures that seed germinates in the spring, thus avoiding adverse winter conditions. This probably increases seed longevity to a small degree and has probable survival value.

The evergreen habit, characteristic of tropical rainforest, has been retained within both the oaks and southern beeches. Evergreen oaks and southern beeches survive well in the northern latitudes of the British Isles; they are adversely affected in very severe winters in less oceanic climates, however.

The distribution of groups within the family is both interesting and intriguing. Relatively few arborescent families are as strongly represented in both hemispheres as the Fagaceae, and the presence in the southern hemisphere of *Nothofagus* and that of *Fagus* in the northern hemisphere suggests that the family is very ancient and occurred in Pangaea before this land mass broke up. While all three lineages within the family were represented in Laurasia, which gave rise to North America and Eurasia, the progenitors of *Nothofagus* beeches were present in Gondwanaland, which gave rise to South America and Australasia where it is well represented. No ancient lineages of the Fagaceae persisted in the proto-African land mass, it seems; modern Fagaceae in Africa bordering the Mediterranean are obviously recent immigrants.

The evolutionary strategies successfully followed in the chestnut, beech and oak lines are closely similar and merit further consideration because the differences generated are often used diagnostically in the generation of systems of classification. Their actual diagnostic value may well be more limited than generally appreciated. What may appear to be a clear cut distinction may, on examination, appear to be much less so. Discussion can most usefully be based on the situation in the oaks generally and more particularly on those included in *Quercus*. The broad position in the family at large can most conveniently be summarised in diagrammatic form in the scheme presented in Figure 1.

Biosystematics and Taxonomy of the Oaks

In the Fagaceae as a whole, there is a repetitive pattern of change from evergreen to the deciduous habit, and a reduction of time of fruit maturation from two to a single season. The feature which distinguishes the oak lineage from the other two is the production of the very distinctive acorn fruit. In this, a single seed is borne in a cupule in which no evidence of the basic primitive valved structure is apparent. This circumstance justifies the concept that any tree, shrub, or scrubby plant which produces an acorn is an oak.

If we review the perception of the oaks held by botanists over the past three

centuries, Linnaeus had no difficulty in recognising the genus *Quercus* as embracing the oak species known to him. Bentham and Hooker (1880) followed Linnaeus. Engler and Prantl (1894) however divided the oaks into two genera, *Quercus* and *Pasania*, which included the more highly evolved and more primitive forms respectively. Further collections and the study of these resulted in recognition of two oak genera, *Quercus* and *Lithocarpus* (of which *Pasania* became a synonym). It was considered that the more primitive genus had features shared with the chestnut lineage. However, in subsequent taxonomic revisions the section *Chlamydoalanus*, as defined by Engler and Prantl, has been transferred to *Castanopsis*. This section is truly intermediate between the chinkapins and the oaks; it has consistent reduction of the number of seeds to one per cupule, and the morphology of the latter strongly tends to an acorn-like form.

Both genera are large, and this has generally militated against production of monographs, however, Camus (1936-1958) did produce her monograph *Les Chenes*, the most comprehensive treatment available. This was produced without the benefit of the modern aids to taxonomy such as population genetics, cytogenetics, serological and chemical approaches, and the more recently developed statistical techniques of multivariate analysis, to name only a sample of those available. Camus recognises 279 species of *Lithocarpus* and 430 of *Quercus*. A curious feature of her system is that she recognizes only two subgenera in the more species rich *Quercus*, but 14 in *Lithocarpus*, one of which is the chinkapin-like *Pseudocastanopsis*. It is possible that the problems of classifying oaks have been exacerbated by the decision to erect two genera in the first place; perhaps Bentham and Hooker's view was the soundest. An alternative, and possibly a more productive approach, might be a cladistic one. Bentham and Hooker recognized *Cyclobalanus* as a section of *Quercus*. This is characterized by the presence of annular, concentric scales on the cupule and appears to be well defined on this character. Engler and Prantl divide this section into two; *Cyclobalanopsis* in *Quercus*, and *Cyclobalanus* in *Pasania* (*Lithocarpus*). Camus' approach is similar, but the sections are raised to sub-generic rank. Recognition at this level implies a high degree of distinctness from other members of the two genera. (Figure 2)

Perhaps the most sensible solution to this problem is to reunite these sections/subgenera in the taxon *Cyclobalanus*, recognising that the characters used in generic diagnosis are perhaps relatively trivial. Further study of the two genera as defined at the present time might well reveal further clades which could be studied profitably. The value of some of the features used diagnostically, such as the nature of the male inflorescence whether rigid or lax, could have quite a simple genetic basis.

Informal classification approaches

The difficulty over the past half century of producing a revised and up-dated monograph of the oaks has led to the development of informal schemes of classification which are both interesting and useful. This development has taken place in North America, which has a richer and more diverse oak flora than Europe. It is unfortunate that while highly significant studies have been carried out, these are all too frequently somewhat parochial in nature, delimited by political rather than sensible geographical boundaries. Fortunately, in the case of American studies the species covered include all those native to the United States and Canada, as well as those whose range extends into Mexico. Excluded commonly are Mexican endemics.

In Asia, a similar situation exists where oak species are treated in national floras rather than on a sensible geographical or biosystematic basis.

For the North American oaks, Sargent (1949) presents a very simple scheme based on two sub-genera; Erythrobalanus and Lepidobalanus. Within each group he recognises two sub-groups. His scheme can be summarised as follows:

1. Erythrobalanus- characterized by the dark color of the bark and the maturation of acorns in their second season
 - a) Black oaks - leaves lobed, with bristle tips on lobes; examples *Quercus rubra*, *Q. palustris*, *Q. nigra*
 - b) Willow oaks - leaf margins entire; examples *Q. phellos*, *Q. laurifolia*, *Q. agrifolia*
2. Lepidobalanus- characterised by the light grey bark color, with acorns maturing in a single season
 - a) White oaks- margins deeply sinuate, leaves lobed, e.g. *Q. alba*, *Q. stellata*
 - b) Chestnut oaks- margins shallowly sinuate, leaves lobed or toothed, e.g. *Q. montana*, *Q. bicolor*, *Q. muehlenbergii*

Sargent includes the live oak, *Q. virginiana*, in this group because its acorns mature in a single season; live oaks such as *Q. agrifolia*, with 2-season acorns, he includes under the willow oaks. Preston (1961) recognizes three sub-genera, with sub-divisions:

1. Erythrobalanus - Red oaks; a name based on autumn leaf colour
 - a) True red oaks (=Sargent's black oaks, except for *Q. nigra*)
 - b) Willow oaks (= Sargent's willow oaks with *Q. nigra*, but excluding *Q. agrifolia*)
2. Lepidobalanus - White oaks (bark colour)
 - a) True white oaks (= Sargent's white oaks, except *Q. virginiana*)
 - b) Chestnut oaks (= Sargent's chestnut oaks)
3. Sclerophyllodrys - Live Oaks (evergreen); includes forms maturing acorns in both first and second seasons; e.g. *Q. virginiana*, *Q. agrifolia*, *Q. wizlizenii*

The Flora Europaea recognizes four sub-genera:

1. Erythrobalanus (introduced Black oaks) -e.g. *Q. rubra*, *Q. palustris* (commonly planted)
2. Sclerophyllodrys - e.g. *Q. ilex*
3. Cerris - e.g. *Q. suber*, *Q. cerris*
4. Quercus - e.g. *Q. robur*, *Q. petraea*

Rehder (1954), reviewing cultivated trees and shrubs, considers oak species in three sub-genera:

1. Cyclobalanopsis - e.g. *Q. myrsinaefolia*
2. Erythrobalanus - e.g. *Q. phellos*, *Q. nigra*, *Q. laurifolia*, *Q. marilandica*, *Q. rubra*
3. Lepidobalanus - e.g. *Q. cerris*, *Q. suber*, *Q. ilex*, *Q. virginiana*, *Q. robur*, *Q. petraea*, *Q. alba*, *Q. stellata*, *Q. lyrata*, *Q. montana*

This brief and by no means comprehensive summary of perceptions of the structure of the genus shows that there is no overall consensus on what species should be included in the various sub-generic taxa. The species groups which are most useful practically are the informal classes developed and used by North American botanists and dendrologists. These work very well on the whole for the deciduous species, but the evergreen live oaks do create some difficulties. Problems also are likely to arise if this informal system is extended to include the Eurasian species.

The section/sub-genus *Erythrobalanus* includes forms variously called Black oaks, Red oaks, and Willow oaks. It is somewhat unfortunate that the name *Erythrobalanus* literally means red oaks since the name "Black Oaks" applies equally well to Red Oaks and Willow Oaks which both have dark coloured or "black" bark. A useful informal hierarchy would be to apply the term "Black Oak" to all the deciduous members of the section, the term "Red Oak" to those with strongly lobed leaves and "Willow Oak" to those with entire leaves e.g. (*Q.phellos*, *Q.laurifolia*) or only slightly lobed leaves (*Q.nigra*). Some species such as *Q.marilandica* might be problematic in their assignment but on the basis of leaf size would probably be best assigned to the Red Oaks.

A parallel breakdown can be applied to American species of *Lepidobalanus*. The whole group share one feature in common - they all have relatively light-coloured bark, hence the term "White Oak". A distinction is made between constituent groups on leaf shape, those with a sinuous margin with shallow indentations, or toothed, are called "Chestnut Oaks", while those with more deeply cut leaves are called "True White Oaks" by Preston (1961). There are, however, some species with only slight or irregular lobing, and these are somewhat arbitrarily assigned to the "True White Oaks"; the blue oak *Q. douglasii*, for example.

In addition to the bark character difference, Red Oaks can be distinguished from the White Oaks (*sens.lat.*) in that the lobes have angular extremities which have bristle-like tips. In species such as *Q. nigra*, only leaves with the most developed lobing actually develop bristle tips. Such bristle tips are absent from the white oaks. A second difference is in the time taken by fruits to mature. In most Black Oaks, this takes two seasons; the White Oak acorns mature in the first.

The live oaks are, as mentioned, evergreens and have been grouped together by Preston on this basis. Sargent, however, separates them into those with single-season acorns and those which require two seasons for fruit maturation. The first group are assigned to the White Oaks, the latter to the Black Oaks. Leaf size is relatively small, and no obvious patterns of leaf shape have evolved; all are relatively simple and some may be toothed. Clarification of the true relationships between live oak species and the white and black oaks has come from the study of wood anatomy in these groups. This has shown that the relatively primitive type found in the black oaks (with respect to the white oaks) is also found in the live oaks, regardless of the differences in maturation period of their acorns. This raises the possibility of assigning all live oaks to *Erythrobalanus*, and suggests that the significance of difference in the acorn maturation period be re-evaluated, as well as the true nature of the difference between the evergreen and deciduous habits. In *Lepidobalanus*, wood anatomy is the more advanced type.

Evaluation of diagnostic features

Taking the question of maturation period first, a study of the interspecific hybrids

noted by Sargent (1949) shows that all are within Erythrobalanus or Lepidobalanus. This has led to the conclusion being drawn that a formidable isolating mechanism exists between the two groups.

The difference between the evergreen and deciduous habits is frequently regarded as a discontinuity. However, if one considers this in terms of leaf longevity it actually becomes a continuum. The life span of individual oak leaves ranges from six months (or less) to upwards of four years. In mild environments, leaf longevity in deciduous species may be such that young leaves have emerged before the old leaves have fully senesced and been shed; *Q. canariensis* shows this trait in southern England.

It is a moot point whether this could be considered an evergreen, as most would recognize that the persistent leaves are obviously senescent. A similar situation occurs in American live oaks such as *Q. virginiana*, where leaves persist until the new ones appear but are less obviously senescent at the time they fall, and it is considered to be evergreen.

Variation in leaf morphology also has implications in the oaks. If we take the leaf form of the tanbark oak, *Lithocarpus densiflorus*, as representing primitive leaf morphology, we can consider the changes which have come about in the course of oak dispersion in the Northern Hemisphere. Relative reduction of leaf size is more apparent in the advanced evergreen species, however with development of the deciduous habit, there has been a reversal of this trend. Leaves of *Lithocarpus densiflorus* are characteristically robust with a very firm texture, midrib and lateral leaf veins robust and prominent. The margin is very slightly toothed. Leaf size is relatively large for a simple-leaved form. Leaf texture is generally softer in *Quercus* than in *Lithocarpus*.

Ecological diversification

As has already been noted, extension of the distribution range of oaks has occurred through an ecological adaptive radiation process. From an original tropical sub-montane rainforest, centre migration to higher latitudes has necessitated adaptation to more variable environments with greater ranges of both temperature and relative humidity. Initially, to marked wet and dry seasons, subsequently to summer and winter temperature regimes. Much can be done to accommodate such changes by migration to lower elevations. The American live oak, *Q. virginiana*, provides a good illustration of this strategy. In Mexico, it occurs in the mountains, while in the northern part of its range it is found on the coastal plain of the Atlantic seaboard, as far north as Virginia. This distribution suggests it is not tolerant of continental temperature extremes. In size, the leaves are slightly smaller than those of *Lithocarpus* (3-13 cm in length, as against 8-13).

The live oaks of western North America tend to have smaller leaves, in the range of 2-5cm. They are often to be found in dry conditions, and presumably the reduced leaf size is adaptive. A common feature of many western oaks such as the scrub oak is for leaf fall to occur at or about the time of the emergence of new leaves. Some of these oaks are known as "live" oaks, even though the life span of the individual leaves is rarely over twelve months. This is probably due to the leaf texture; coriaceous leaves do not show their age as obviously as those of a softer texture. For this reason, *Q. canariensis* might lack credibility as an evergreen while a western live oak such as *Q. agrifolia* is acceptable as such.

It is interesting to note that retention of the primitive coriaceous leaf texture

coupled with reduction in leaf size is adaptive to the harsher ecology of desert fringe and seasonally arid areas. The next major expansion of range into temperature regions depended on a further reduction of leaf longevity and the generation of the deciduous habit. In the case of the oaks this enabled the colonization of temperate continental areas to occur, where loss of leaves in autumn proved an effective strategy to avoid the stress of extremely low temperatures. Coupled with the often very short days and low light intensities at high latitudes the deciduous habit reduced the drain of resources entailed by periods when respiration outstripped photosynthesis in the energy balance.

Migration to northern temperate latitudes also brought about a reversal in the evolutionary strategy of leaf size reduction and change in leaf shape. However, increased leaf size brings about enhanced interception of both light and heat energy. The resulting increase in temperature could be deleterious in both its direct effect on living tissues, producing death, and also in wastefully increasing rates of respiration and transpiration. Development of lobing increases the rate at which the leaves can radiate excessive heat energy. Temperate species with the largest leaves tend to be the more strongly lobed; *Q. rubra* and *Q. frainetto* are good examples.

Leaf shape evolution is well illustrated in the American black oaks, the deciduous members of which fall into two reasonably well-defined groups; the willow oaks and the red oaks. The former, typified by *Q. phellos* and *Q. laurifolia*, have elongated but relatively narrow leaves with a length/breadth ratio in excess of 2.5; this shape provides reasonably effective radiation capacity, provided that length is not excessive. The red oaks with the largest leaves such as *Q. rubra* and *Q. velutina* have deeply incised leaves and the lobes so produced are markedly toothed. In species such as *Q. georgiana*, the degree of lobing is much less while leaf size is appreciably smaller. The situation in the white oaks follows a similar trend with much less contrast in the range of leaf shape. It is interesting to note that the most widely distributed oaks in North America, the red oak *Q. velutina* and the white oak *Q. alba* both have strongly lobed leaves. Among white oaks, the chestnut oaks tend to have more restricted distributions.

A characteristic difference between white oaks and black oaks is in the palatability of the kernels; those of white oaks (sens.lat.) are sweet while in the black oaks they are bitter. This may be correlated with the tannin content of the bark, which is less in the white oaks. The North American species within *Lepidobalanus* differ from those in Europe, regarding the darker bark colour of the latter, and in their low acorn palatability. The acorns of the native British oaks are eaten avidly by swine but are toxic to cattle and horses, hence the practice of herding pigs in woodland of the New Forest in England (pannage) to reduce the hazard to cattle and ponies. In the live oak group, there are some species with palatable kernels and some in which they are bitter. It may be that this divergence predates the divergence of the deciduous black and white oak lineages.

Possible approaches to taxonomic revision

Broad studies of the oaks indicate that a more serviceable system of taxonomy could be developed by judicious use of a range of approaches. The morphological approach is not only the classical method but the easiest to use, and the most cost effective. A problem does arise when diagnostic characters used are ambivalent, if not ambiguous. Difficulties arise most often when these are used at an inappropriate level or when the probable phylogeny is not appreciated and the extent of parallel

evolution is not realised. Homologous mutants can arise independently in different evolutionary lineages. There are several examples; lax inflorescences have arisen in both the beech and oak lineages, and the deciduous habit has evolved in all lineages as has the development of fruit which mature in a single season. The extent of the adaptive radiation, which has occurred in the oak lineage, greatly exceeds that of the other two. While all three groups have evolved deciduous forms which flourish in mesic environments, only the live oak line has colonized additionally arid and semi desert habitats. Even in mesic environments, where all three lines are sympatric, the oaks exceed the number of species which have evolved in the other two lines.

Because they are less numerous in terms of species number, the taxonomy of beeches, chestnuts, and chinkapins presents no very great difficulty. The phenomenal biodiversity within the oak lineage does create difficulties and problems. Some clarification might be achieved by seeking diagnostic characters which identify clades. A number of these have been suggested; the cyclobalanoids form just such a group. Anatomical differences in wood structure appears to have identified clades, already. The situation in the live oaks is particularly interesting, when considered in conjunction with the chemical differences in the bark and the acorns, observable in the white and black oak groups. It may be possible to identify a point in evolution where the two groups diverged.

The diagnostic value of the difference between species maturing fruit in a single season and those in which it takes two would certainly repay exploration. Since this difference is also to be found in species-poor lineages, it is perfectly feasible that it has arisen more than once and possibly several times independently, in the very numerous oak species. Ostensibly this difference could have considerable physiological implications in reproduction, with disruption of fertilization processes. This difference has been considered important as an isolating mechanism between groups of North American oaks.

Isolation between black and white oaks may be determined by a great deal more than what could possibly be a relatively simple genetic difference affecting success of pollination.

Exploration of the genera for additional diagnostic characters could be valuable. The morphology of the cupule itself could be helpful in the indication of clades. The majority of oaks produce cupules with imbricate scales, apart from the Cyclobalanoids already noted. In *Q. ithaburensis* subsp. *macrolepis* (syn. *Q. vallonina*), the scales are elongated and extend at right angles to the cupule surface.

Arguably the most remarkable feature of the oaks among the members of the Fagaceae is that in the course of their evolution they have colonized a much wider range of habitats. The western North American and Mexican oaks include species which are to be found in semi-arid environments on the fringes of deserts. They have adapted to this morphologically by the adoption of a scrubby growth habit and production of small coriaceous leaves, a xeromorphic feature. Leaf longevity is often reduced to little more than twelve months, but a continuous leaf canopy is effectively maintained. It is difficult to easily assess the considerable adaptive changes which must also have occurred and probably been extensive.

The use of chemical and other data (Manos et al, 2001)

It is very salutary to review progress in developing understanding of the phylogeny and evolution of the oaks in the past century. From the recent studies on Systematics of the Fagaceae (Manos et al, 2001), the only conclusion that can be

drawn is that these are inconclusive. Manos et al categorize taxonomic approaches as traditional, and what might loosely be called modern. Traditional approaches based on very detailed morphological studies of *all* material classified in bio-systematic schemes or taxonomies depend on what might well be considered judgements, which though possibly largely intuitive, are actually founded on a very sophisticated and highly educated intuition. Modern taxonomic approaches can be regarded as broadly numerical and experimental. These approaches have been considered to be more objective than the traditional intuitive approaches which have been regarded as, if not dismissed as, overly subjective. It has been asserted by those who developed numerical approaches (principally Sokal and Sneath in the sixties) that use of unselected characters in large numbers would produce more objective schemes of classification. Experience has tended to show that many, if not most, of these characters generate noise. The argument was also put forward that classification schemes could be produced by operatives with little experience.

The alternative experimental approaches had much to commend them. "Experimental taxonomy" based on hybridization studies as well as cyto- and sero-taxonomy yielded very interesting information. The value of this frequently was in the resolution of particular problems where morphological studies gave equivocal results. These two approaches were particularly useful in resolving difficulties in distinguishing and characterising close relatives. Cyto-taxonomy was useful in some instances in resolving problems up to the family level. Sero-taxonomy was limited by the extent to which antigen-antibody reactions could be detected.

A much broader field was opened when differences in proteins and secondary metabolites were studied in a taxonomic context. The ultimate chemo-taxonomic approach involves the comparative study of the DNA in defined taxa. This is an enormously complicated and complex field, but useful taxonomic information can be generated. The studies of Manos et al (2001) have generated significant and important data on the relationships within the Fagaceae. The most interesting feature of this work is that it supports the conclusions of traditional taxonomists, rather than those of investigators using more arcane and esoteric characters (Nixon, 1989), who reach strongly anti-intuitive conclusions that do not produce a credible phylogeny.

In species-rich genera such as *Quercus* (± 450 species) and *Lithocarpus* (± 300 species), both the numerical-multivariate analytical approach and the experimental taxonomic approach pose enormous logistical problems in the generation of databases that truly represent the variability within genera such as these. In the work of Nixon and collaborators, questions can be raised as to how representative the sampling of species actually is, and what is the discriminative power of the character differences explored. The genetic basis of such discriminants is not considered, for example, a great deal is made of the difference between epigeal and hypogeal germination; this could be due to a simple allelic difference.

Perhaps the most telling criticism of much modern chemical information is that when used taxonomically, inconsistent results are produced (when, for example, different secondary metabolites are used). Such incongruences lead to the conclusion that the data is just taxonomic noise. They may be virtually plucked out of the air with little or nothing in the way of justification for their taxonomic use.

It is to be hoped that in the foreseeable future that an improved taxonomic conspectus of the oaks can be produced. The accumulation of knowledge of oaks in the field and their geographic range, and the range of experimental studies coupled

with the sophistication of numerical taxonomic and statistical procedures which have been developed in recent times, should make this feasible. The wealth of information collected by Camus and the application of new procedures to it, such as cladistics, could well serve to reduce the present state of uncertainty.

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References

- Baranski, M. (1975) An analysis of variation within white oak (*Quercus alba* L.). North Carolina Agriculture Experimental Station Technical Bulletin No 236, Raleigh N.C.
- Benson, L. (1962) Plant Taxonomy. Ronald Press, New York.
- Bentham, G. and Hooker, J.D. (1880) Genera Plantarum. A. Black, London
- Camus, A. (1936-1954) Les Chenes. Monographie de genre *Quercus* (3 volumes). Paul Lechevalier, Paris.
- Engler, H.G.A. and Prantl, K.A.E. (1897-1915) Die natürlichen Pflanzenfamilien. Leipzig.
- Hardin, J.W. (1975) Hybridization and introgression in *Quercus alba*. Journal of the Arnold Arboretum, 56 : 336-363.
- Kelleher, C.T., Hodkinson, T.R. and Kelly, D.R. (2004) Species status, hybridisation and distribution of Irish populations of *Quercus petraea* (Mall.) Liebl. and *Q. robur* L. *Watsonia*, 25 : 83-97.
- Manos, P.S., Zhou, Z.K. and Cannon, C.H. (2001) Systematics of Fagaceae: phylogenetic tests of reproductive trait evolution. *International Journal of Plant Science*, 162: 1361-1379.
- Nixon, K.C. (1989) Origins of Fagaceae, pp 23-44 in P.R. Crane and S. Blackmore (eds), *Evolution systematics and fossil history of the Hamamelidae*, vol.2, "Higher" Hamamelidae, Clarendon Press, Oxford.
- Preston, R.J. (Jr.) (1961) North American Tree The Iowa State University Press, Ames, Iowa.
- Rehder, A. (1954) Manual of cultivated trees and shrubs. (2nd.ed.) Macmillan, New York.
- Stebbins, G.L. (1950) Variation and evolution in plants. Columbia University Press, New York.
- Tutin, T.G., Heywood, V.H., Burgess, N.A., Valentine, D.H., Walters, S.M. and Webb, D.A. (1964) *Flora Europaea*. Cambridge University Press, Cambridge.

Figure 1 Generic inter-relationships in the Fagaceae:

Castanopsis and Chrysolepis:

1. Distribution- Northern Hemisphere, Tropical and sub-tropical Asia and California (Chrysolepis)
2. Evergreen
3. Fruit an incompletely sealed burr, dehiscent, 1-3 seeded, maturing in second season
4. Male inflorescence rigid



Oak Lineages

Beech and Chestnut Lineages

1. Distribution- Northern Hemisphere, Tropical and sub-tropical Asia, Europe, North and Central America
2. Evergreen and deciduous
3. Fruit an open cupule, valvate structure lost; typical acorn single-seeded, maturing in 1 or 2 seasons
4. Rigid or lax inflorescences

Lithocarpus (Pasania):

1. Distribution- Northern Hemisphere, Tropical and sub-tropical Asia and California
2. Evergreen
3. Fruit maturing in second season
4. Rigid male inflorescence

Quercus:

1. Distribution- Northern Hemisphere, Eurasia, North and Central America
2. Evergreen and deciduous
3. Fruit maturing in first or second season
4. Lax male inflorescence

Castanea:

1. Distribution- Temperate Northern Hemisphere, Eurasia, North America
2. Deciduous- leaves relatively large
3. Fruit a sealed burr, relatively large, maturing in a single season
4. Rigid male inflorescence



Chestnut Lineage

1. Deciduous and evergreen
2. Enclosure of burr valved, dehiscent, with 1-3 seeds maturing in 1-2 seasons
3. Male inflorescence rigid or lax



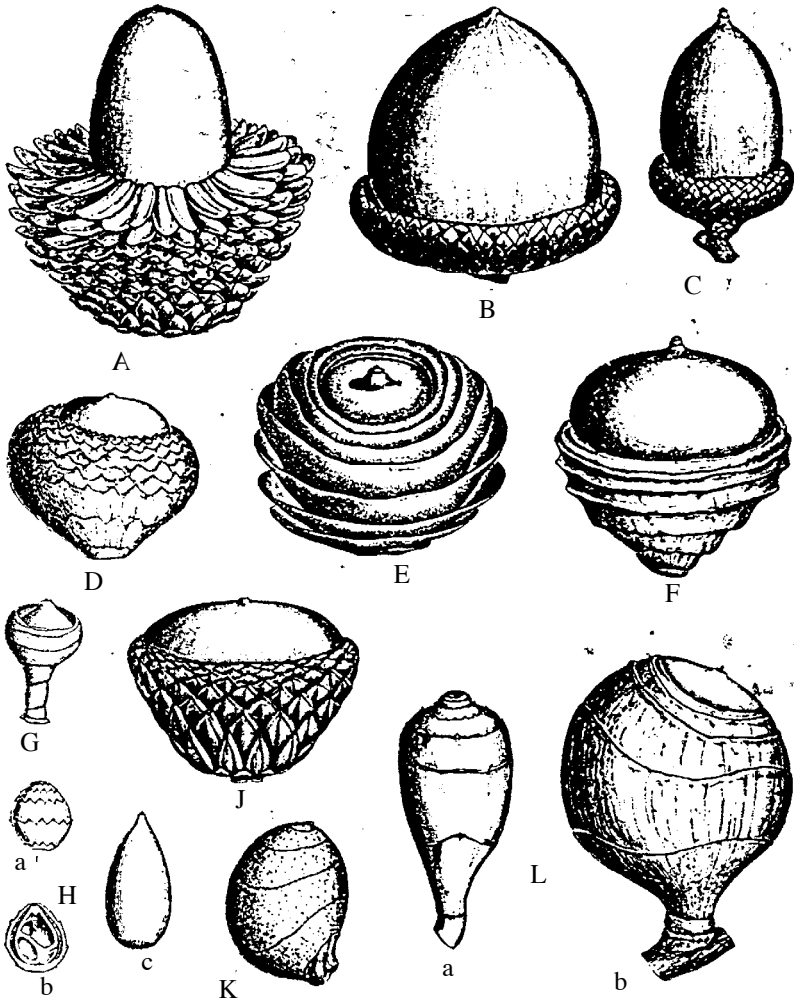
Beech Lineage

Southern beeches (Nothofagus):

1. Distribution- Southern Hemisphere, S. America, Australasia
1. Deciduous and evergreen, leaf size small
2. Fruit size relatively small, maturing in 1 or 2 seasons
3. Lax male inflorescence

Northern beeches (Fagus):

1. Distribution - Northern Hemisphere, Eurasia, N. America
2. Deciduous leaf, size relatively small
3. Fruit maturing in a single season
4. Lax male inflorescence



Cupule scale types

1. Elongate (A)
2. Imbricate (B,C,D, and J)
3. Concentric (E,F,G,H,K and L)



Flowers of *Castanea mollissima* (© Guy Sternberg)



Flowers of *Lithocarpus henryi* (© Guy Sternberg)



Fruit of *Castanopsis orthacantha* (© Guy Sternberg)



Fruit of *Fagus sylvatica* (© Guy Sternberg)



Flowers of a white oak, *Quercus prinoides* (© Guy Sternberg)



Flowers of a red oak, *Quercus ilicifolia* (© Guy Sternberg)