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THE GENUS *QUERCUS* (FAGACEAE) IN INDIANA: PHYTOGEOGRAPHY AND A KEY TO THE SPECIES

Alicia Biagi and Richard J. Jensen
Department of Biological Sciences
University of Notre Dame
Notre Dame, Indiana 46556

ABSTRACT: A comprehensive survey of herbarium collections and our own field work provided updated information on the distributions of oak species and hybrids in Indiana. The nineteen species of oaks native to Indiana illustrate three basic types of distribution (widespread, northern, and southern) and are shown to have different floristic affinities. The number of hybrids reported for Indiana is increased from twelve to eighteen. A key to the species is provided.

KEYWORDS: Floristics, hybrids, oak, plant geography, *Quercus*.

INTRODUCTION

Oaks (*Quercus*; Fagaceae) are among the most abundant and ecologically important trees in Indiana. They occur throughout the State in virtually every type of habitat. The oaks native to Indiana vary from species that are widespread (e.g., *Quercus alba* L.) to those that have very limited distributions (e.g., *Q. pagoda* Raf.). Despite their abundance and importance, little effort has been spent in recent years to update the status and distribution of the species and their putative hybrids.

Deam (1940) provided fairly complete distribution maps for eighteen oak species native to Indiana. His maps were based on specimens deposited in both private and institutional herbaria, and these maps became the standard upon which other authors based their accounts of oak distributions in Indiana. For example, Little (1971, 1977) relied almost exclusively on Deam's maps, when preparing his own maps. Other authors followed suit (e.g., Preston, 1976; Elias, 1980), and a consensus of opinion with respect to oak distributions in Indiana seemed to appear. But as noted by Jensen (1985), this consensus developed because these authors all adopted the same set of reference maps and not because of any change in our knowledge of oak distributions.

The distributions of certain oaks were examined carefully in the early 1980s. Jensen (1985) provided updated maps for the ten species of *Quercus* subgenus *Erythrobalanus* (the red and black oaks) known to occur in Indiana. Jensen (1985) found that although Deam's (1940) maps were fairly complete for some species (e.g., *Q. shumardii* Buckl.), there were others (e.g., *Q. ellipsoidalis* Hill) for which Deam's maps were quite incomplete. After visiting a number of herbaria, Jensen (1985) reached two important conclusions relative to the distributions reported by Deam: 1) voucher specimens for numerous new county records had been deposited in these herbaria in the 40+ years following Deam's (1940) last treatment; and 2) a number of Deam's county reports could not be verified by specimens in the herbaria he cited. While some of the latter instances reflected the misidentification of specimens, others were the result of the apparent loss of specimens and/or collections.

Hybridization is a common phenomenon among oaks (e.g., Palmer, 1948; Knops and Jensen, 1980), and a number of oak hybrids have been reported from Indiana. Deam (1940) reported nine nominal hybrid combinations from Indiana, but one of these (*Q.* x *schuettei* Trel.) was later shown to be synonymous with *Q.* x *hillii* Trel. (Palmer, 1948). In his comprehensive review of the hybrid oaks of North America, Palmer (1948) reported three additional hybrids from Indiana, bringing the total to eleven. Jensen (1985) added two more to the list, but noted that the occurrence of one hybrid, reported by both Deam (1940) and Palmer (1948), was based on a misidentified specimen. Thus, the number of hybrids in Indiana stood at twelve. In addition, Jensen (1985) indicated that evidence existed for at least three other hybrids in Indiana.

Natural hybridization among oaks is known to occur only between species in the same subgenus. Based on ten species of subgenus *Erythrobalanus* and nine species of subgenus *Quercus* (the white and chestnut oaks) reported from Indiana, the maximum number of hybrid combinations that could occur in the State is 81. Even when allowance is made for the fact that some species pairs are allopatric within the State (e.g., the range of *Q. ellipsoidalis* does not overlap with those of *Q. falcata* Michx., *Q. marilandica* Muenchh., or *Q. pagoda*), the number of possible hybrid combinations is still approximately 75. However, not all possible hybrid combinations have been documented in North America, much less in Indiana. For example, despite the fact that *Q. palustris* Muenchh. occurs in sympatry with each of the nine other species of subgenus *Erythrobalanus* native to Indiana, it reportedly only hybridizes with six (Palmer, 1948; Jensen, 1985). The same circumstance exists, to a greater or lesser degree, for most other species. Thus, careful examination of both the distributions of and variation within each species may reveal evidence of unrecorded hybrids and, possibly, new hybrid combinations.

This study was initiated for two reasons. First, the study was expanded to include all the oaks in Indiana; Jensen (1985) dealt only with the red and black oaks. Second, during two weeks of field work in a five county area, one of the authors (AB) was able to document ten new county records, indicating the need for a more thorough survey. As a consequence, the authors decided to document the distributions of all Indiana oak species and hybrids. This goal was reached primarily through the examination of herbarium collections supplemented by some field work.

MATERIALS AND METHODS

The majority of the distributional records for this update were based on Indiana specimens on loan from or observed during visits to fifteen herbaria (Table 1). Additional records are based on the authors' personal collections (RJJ's at Saint Mary's College; AB's at Notre Dame). Herbarium specimens were determined to species, and the collector, collection number, date of acquisition, county, herbarium, and accession number were recorded from the label. A single collection sheet was chosen, based on chronological priority, as the official record of that taxon in each county for two reasons. First, this approach provides the most accurate account of the original distribution of the

Table 1. The 15 herbaria holding collections used in this study (herbarium abbreviations according to Holmgren, *et al.* (1990)).

New York Botanical Garden (NY)	Indiana University (IND)
Eastern Illinois University (EIU)	Purdue University (PUL)
Field Museum of Natural HIstory (F)	Butler University (BUT)
University of Kentucky (KY)	Earlham College (EAR)
University of Michigan (MICH)	Indiana University Southeast (JEF)
University of Illinois (ILL)	Ball State University (BSUH)
Miami University (MU)	University of Notre Dame (ND, NDG)
University of Evansville	

taxon. Second, it gives priority to the first collector of that taxon in that area. By acknowledging the earliest collectors, the distribution records will also serve as a historical record for the State and its respective botanists. Label data for all specimens used to document county records have been stored in a microcomputer database and are available on request (contact RJJ for information).

Distribution information was also obtained from literature sources. The issues of the *Proceedings of the Indiana Academy of Science* published since 1891 were reviewed for citations of oak occurrences which were supplemental to those documented by herbarium specimens. The majority of these references were obtained from reports in the Plant Taxonomy, Botany, Ecology, Biological Survey, and Fungi Sections of the *Proceedings.* Although these identifications could not be verified, they do provide valuable historical information.

Several records of oaks were omitted from this update. These citations were first reported in Deam (1918) but were discarded in all of his later works. Deam (1918) described these records in his introduction using the following statement:

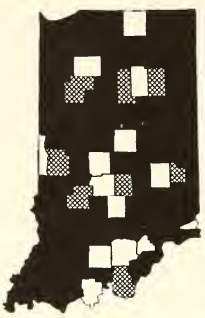
> In considering some of the older publications it should be borne in mind that scientific accuracy was not as rigorously demanded as at present, and that some of the authors were not trained botanists.

For example, as Jensen (1985) discovered, early reports of the presence of *Q. nigra* L. and *Q. phellos* L. in Indiana were based on erroneous identifications.

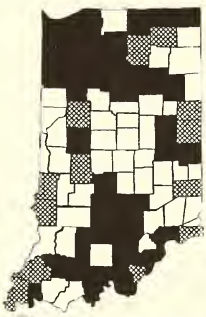
Universal agreement does not exist on the status of the species of oaks in eastern North America or their distributions. Our species' identifications follow Elias (1980) with one exception: *Q. pagoda* is recognized as a species distinct from *Q. falcata* (Jensen, 1989). In addition, the authors maintain the distinction between *Q. ellipsoidalis* and *Q. coccinea* Muenchh., following Deam (1940) and Jensen (1986); and *Q. prinoides* Willd. is recognized as a widespread (e.g., Hardin, 1975) species distinct from *Q. muehlenbergii* Engelm.

After reviewing herbarium specimens and the literature, distribution information was entered into a computer database using SYSTAT, version 4.0. These data were used to generate maps illustrating the county by county distribution of each species. The database information was also used as input for a numerical taxonomic analysis of the distributional relationships among the species. For this analysis, the species were treated as operational taxonomic units (OTUs) and the county presences were treated as characters. Because one species (*Quercus prinoides* Willd.) is known from only two localities in the State, it was not included in this analysis. Thus, the data matrix consisted of 18 OTUs (oak

1. Quercus alba



2. Quercus bicolor



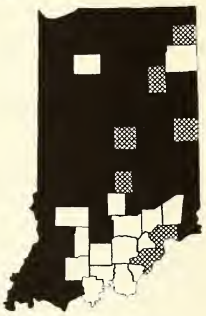
3. Quercus coccinea

4. Quercus ellipsoidalis

5. Quercus falcata

6. Quercus imbricaria

7. Quercus lyrata



8. Quercus macrocarpa

9. Quercus marilandica

10. Quercus michauxii

11. Quercus muehlenbergii

12. Quercus pagoda

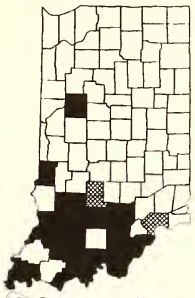
13. Quercus palustris

14. Quercus prinoides

15. Quercus prinus

16. Quercus rubra

17. Quercus shumardii



18. Quercus stellata

19. Quercus velutina

Figures 1-19. The distributions of 19 oak species in Indiana (filled = county record verified by an herbarium specimen; crosshatched = county record based solely on a literature citation; open = no record for this species in the county).

species) and 92 characters (Indiana counties). Each character was scored 0/1 based on the occurrence (either documented by a specimen or a literature citation) of each species. The raw data were converted to an 18 x 18 similarity matrix based on Jaccard's coefficient. This matrix was used to create a phenogram by means of UPGMA cluster analysis and an ordination by means of principal coordinates analysis (Sneath and Sokal, 1973). All computations were performed using a test copy of NTSYS-pc, version 1.8, provided by F.J. Rohlf.

RESULTS

Table 2 provides an alphabetical list of the species documented for Indiana, and distribution maps for each species are presented in Figures 1-19. Counties for which a species' occurrence has been verified by an herbarium specimen are completely darkened while cross-hatching indicates a literature citation that could not be confirmed by reference to a specimen.

The phenogram in Figure 20 depicts relationships among the 18 OTUs based on both specimen and literature county occurrences. The OTUs are identified by the first 3-5 letters of their respective species epithet. There are two primary clusters reflecting: 1) species found throughout the State (the cluster ALB - ELL); and 2) species with limited distributions within the State (the cluster FAL - PRINU). One OTU with limited distribution (ELL; Figure 4) occurs in the first cluster, but joins those OTUs at a very low level of similarity. Figure 21, a plot of the first two dimensions of the principal coordinates analysis, reveals that ELL is located near the middle of coordinate 1 and is distinctly separated from all other OTUs on coordinate 2. The minimum spanning tree superimposed on this plot indicates that the distribution of ELL has more in common with COC than with that of any other OTU, but ELL is an outlier with respect to the overall pattern.

Table 3 and Figure 22 summarize the information on the oak hybrids known to occur in Indiana. While most hybrids are encountered infrequently, two appear to be rather common in Indiana: *Quercus* x *leana* Nutt. has been reported from 19 counties, and *Q.* x *runcinata* Engelm. has been reported from 10 counties.

Table 2. Oak species native to Indiana. Except for *Quercus pagoda* (Jensen, 1989), the nomenclature follows Elias (1980).

Quercus alba L.	*Q. muehlenbergii* Engelm.
Q. bicolor Willd.	*Q. pagoda* Raf.
Q coccinea Muenchh.	*Q. palustris* Muenchh.
Q. ellipsoidalis Hill	*Q. prinoides* Willd.
Q. falcata Michx.	*Q. prinus* L.
Q. imbricaria Michx.	*Q. rubra* L.
Q. lyrata Walt.	*Q. shumardii* Buckl.
Q. macrocarpa Michx.	*Q. stellata* Wang.
Q. marilandica Michx.	*Q. velutina* Lam.
Q. michauxii Nutt.	

DISCUSSION

Distributions. The distribution maps (Figures 1-19) reveal that some species (*Q. alba, Q. bicolor, Q. coccinea, Q. imbricaria, Q. macrocarpa, Q. muehlenbergii, Q. palustris, Q. rubra,* and *Q. velutina*) are, or could be expected to be, found in almost every county. Other species have regional distributions in Indiana (*Q. ellipsoidalis, Q. falcata, Q. lyrata, Q. marilandica, Q. michauxii, Q. pagoda, Q. prinus, Q. shumardii,* and *Q. stellata*), while one (*Q. prinoides*) appears to be quite rare.

Two species illustrate complementary distributions. If the maps for *Q. ellipsoidalis* (Figure 4) and *Q. shumardii* (Figure 17) are superimposed, then the entire State is covered. The ranges overlap somewhat, but it is of interest to note that the area where they overlap corresponds roughly to the southern boundary of the Kankakee Outwash and Morainal Plain to the west and the Steuben Morainal Lake Area to the east (Schneider, 1966). The distributional limits of these two species reflect environmental constraints, not incomplete sampling.

There are some anomalies in these distributions. For example, *Q. muehlenbergii* (Figure 11) is undocumented for many counties, primarily in the north. Because this species has a range that extends to both the north and west

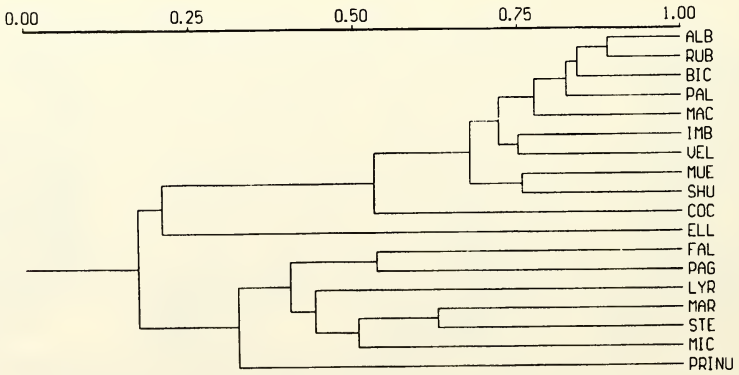


Figure 20. Phenogram produced by UPGMA cluster analysis of the presence/absence of each species in each county. Abbreviations are the first 3-5 letters of the specific epithets.

Table 3. Hybrid oaks reported to occur in Indiana. The nomenclature follows Little (1979).

Quercus x *anceps* Palmer (*falcata* x *imbricaria*)
Q. x *beadlei* Trel. (*alba* x *michauxii*)
Q. x *bebbiana* Schneid. (*alba* x *macrocarpa*)
Q. x *bushii* Sarg. (*marilandica* x *imbricaria*)
Q. x *deamii* Trel. (*macrocarpa* x *muehlenbergii*)
Q. x *fernowii* Trel. (*alba* x *stellata*)
Q. x *fontana* Laughlin (*coccinea* x *velutina*)
Q. x *hawkinsii* Sudw. (*rubra* x *velutina*)
Q. x *hillii* Trel. (*bicolor* x *macrocarpa*)
Q. x *jackiana* Schneid. (*alba* x *bicolor*)
Q. x *leana* Nutt. (*imbricaria* x *velutina*)
Q. x *mutabilis* Palmer & Steyerm. (*palustris* x *shumardii*)
Q. x *paleolithicola* Trel. (*ellipsoidalis* x *velutina*)
Q. x *riparia* Laughlin (*rubra* x *shumardii*)
Q. x *runcinata* (A. DC.) Engelm. (*imbricaria* x *rubra*)
Q. x *saulii* Schneid. (*alba* x *prinus*)
Q. x *tridentata* (A. DC.) Engelm. (*imbricaria* x *marilandica*)
Q. x *vaga* Palmer & Steyerm. (*palustris* x *velutina*)

of Indiana, its absence from many northern counties is likely the result of oversight by collectors, although we cannot discount the possibility that this reflects a lack of suitable habitat in northern Indiana. Similarly, incomplete sampling probably explains why a number of other species (Figures 2, 3, 6, 8, 13, 16, and 19) have a large number of undocumented counties.

The distribution of *Q. velutina* (Figure 19) illustrates a strange gap in the center of the State which is present in at least two other species expected to occur statewide as well: *Q. imbricaria* (Figure 6) and *Q. coccinea* (Figure 3). The gap, extending from Carroll County in the north to Jennings County in the south, cuts

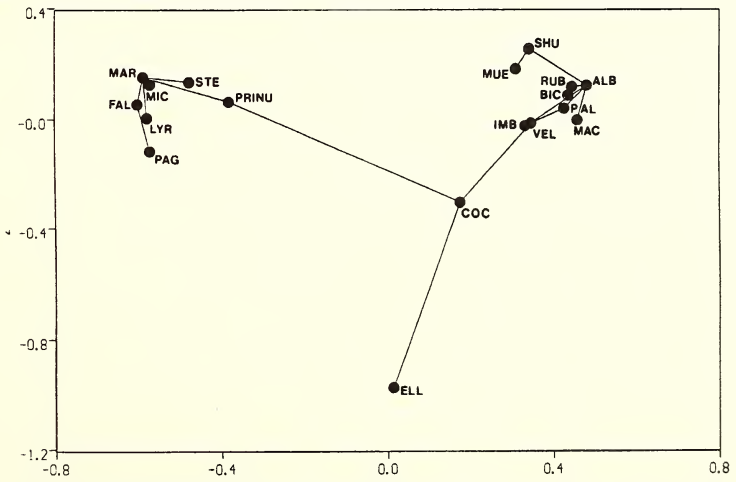


Figure 21. A plot of species relationships on the first two dimensions of a principal coordinates analysis of the matrix of similarities used to produce Figure 20. Coordinate 1 accounts for 33% of the variation; coordinate 2 accounts for 12% of the variation.

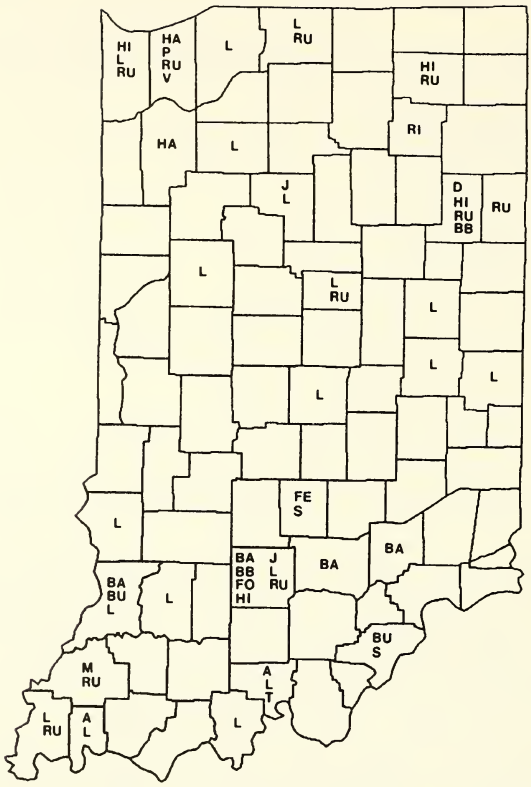


Figure 22. County distributions for the hybrids listed in Table 3. Abbreviations are the first one or two letters of the hybrid epithets (except for BA and BB, which represent *Q.* x *beadlei* and *Q.* x *bebbiana,* respectively).

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across both the Tipton Till Plain and the Muscatatuck Regional Slope (Schneider, 1966). When maps for the three species are superimposed, a span of eleven counties remains undocumented. These three species belong to subgenus *Erythrobalanus* and often occur in similar habitats. Their mutual absence from these counties might reflect a lack of suitable habitats. However, *Q. alba* (Figure 1) also occurs in the same types of habitats as these three, and it is present in this eleven county area. Because the topography of the undocumented and surrounding documented counties is similar, elevational differences are not responsible for these three species being absent from these eleven counties. Other maps (Schall, 1966; Ulrich, 1966) indicate that this gap does not coincide with climatic patterns or general soil types. Thus, the joint absence of these three species from these counties appears to represent an artifact of collecting. This is supported by the presence of the hybrid, *Q.* x *leana* Nutt., a cross between *Q. imbricaria* and *Q. velutina*, in Marion County, which lies in the center of the gap.

Floristic Relationships. The distributions documented in Figures 1-19 can be placed in context by applying Cain's (1944) suggestion of classifying each species as an intraneous or extraneous element of the flora. The intraneous

species, those for which Indiana lies well within the broader distribution, are *Q. alba, Q. bicolor, Q. imbricaria, Q. macrocarpa, Q. muehlenbergii, Q. palustris, Q. prinoides, Q. rubra,* and *Q. velutina.* The remaining ten species are extraneous; i.e., Indiana is at or near the limits of their broader distribution.

The extraneous species can be further characterized by reference to the direction from Indiana to which their range extends. For example, *Q. ellipsoidalis* is a north-northwest extraneous element, while *Q. prinus* is a southern-eastern extraneous element. Several species are southern extraneous elements, representing the northern limits of distributions that follow the Atlantic Coastal Plain and the Mississippi River Valley: *Q. falcata, Q. lyrata, Q. michauxii,* and *Q. pagoda.* The four remaining extraneous species (*Q. coccinea, Q. marilandica, Q. shumardii,* and *Q. stellata*) are harder to characterize. In each case, Indiana lies at the northern limits of a range that extends both to the west and to the east or northeast.

These geographic relationships can be seen in Figure 20. First, the lower cluster (FAL - PRINU) consists entirely of extraneous species. *Quercus prinus,* the only one of these species that does not have a Coastal Plain distribution, is depicted here as distinct from the other six. Second, the upper cluster (ALB - ELL) has both intraneous and extraneous species. *Quercus ellipsoidalis* and *Q. coccinea,* both extraneous elements, are separated from the other species. At the next level, seven species (all intraneous elements) are separated from a cluster consisting of *Q. muehlenbergii* and *Q. shumardii.* While the latter two species represent intraneous and extraneous elements, respectively, the reason they cluster together is apparent from Figures 11 and 17. Both species are found throughout much of the State but have not been documented for many counties in the northwest and north-central areas. For *Q. shumardii,* this represents the northwest limit of its range. On the other hand, *Q. muehlenbergii* occurs both to the north and west of Indiana; its absence in these counties may reflect nothing more than oversight by collectors. Similarly, the pattern in Figure 21 is one in which the first coordinate emphasizes differences between intraneous (upper right) and southern extraneous (upper left) species, while the second coordinate separates the one northern extraneous species (*Q. ellipsoidalis*) from the others.

Six species, all southern extraneous species (Figures 5, 7, 9, 10, 12, and 18), have quite similar distributions in Indiana. A comparison of these distributions to climatological maps (Schaal, 1966) suggests that winter temperatures may be the critical factor limiting the distributions of these species. With the exception of *Q. stellata,* which has two more northern county records, the northern limits for each species coincide roughly with isotherms representing a January mean daily minimum temperature of 24° F and a January mean daily maximum temperature of 42° F. Interestingly, these six species consist of three that typically are found in upland xeric habitats (*Q. falcata, Q. marilandica,* and *Q. stellata*) and three that typically are found in lowland mesic and/or riparian habitats (*Q. lyrata, Q. michauxii,* and *Q. pagoda*). Topographically, the degree of dissection of the Indiana landscape decreases as one moves north into the Tipton Till Plain (Schneider, 1966) and these distributions may be influenced by a lack of suitable habitat in the central portion of the State.

Hybrids. As a result of examining several thousand herbarium specimens, the number of nominal hybrid oaks found in Indiana has increased from 12 to 18

(Table 3; Figure 22). The two most frequently encountered hybrids are *Q.* x *leana* and *Q.* x *runcinata,* both hybrids between an entire-leaved species (*Q. imbricaria* in both cases) and a lobed-leaved species (*Q. velutina* and *Q. rubra,* respectively). Such hybrids are well-known and frequently reported, probably because the leaves, which are typically asymmetrically lobed (see Wagner and Schoen, 1976), are quite distinctive and easily noticed by collectors.

Several of the hybrids are crosses between morphologically similar species. These hybrids characteristically have the general appearance of one or the other of the parental species, and as a consequence, these trees are often viewed by collectors as nothing more than aberrant forms of one of the parents. In most cases, if the specimen includes leaves, twigs, and fruits, its hybrid status is apparent.

In addition to the hybrids listed in Table 3, specimens were found that suggested *Q. exacta* Trel. (*Q. imbricaria* x *Q. palustris*; Deam 29116, IND 18560) and two unnamed combinations: *Q. coccinea* x *Q. rubra* (Friesner 25367, BUT 96529) and *Q. alba* x *Q. muehlenbergii* (Deam & Williamson 10544; NY *s.n.*). The first putative hybrid was reported by Deam (1940) and Palmer (1948), but Jensen (1985) concluded that the tree in question belonged in *Q.* x *runcinata.* The second putative hybrid is a combination referred to as *Q.* x *benderi* Baenitz, a name that has been rejected (Palmer, 1948; the type specimen of this taxon was apparently from a tree of *Q. ellipsoidalis*). The third putative hybrid is a combination that has not been formally named, despite the fact that a number of authors (e.g., Hardin, 1975; Little, 1979) have reported instances of this hybrid. For the sake of clarity, remember that *Q.* x *deamii* Trel. was originally described as a cross of *Q. alba* x *Q. muehlenbergii.* Deam (1940) and Palmer (1948) both discuss this hybrid and, despite reservations, ascribe it that parentage. However, as discussed by Hardin (1975), the type tree of *Q.* x *deamii* and its progeny appear to represent a cross of *Q. macrocarpa* x *Q. muehlenbergii.*

Reports of several hybrids indicate the presence in a county of a species that has not otherwise been documented. *Quercus michauxii, Q. stellata,* and *Q. velutina* have not been documented for Brown, Lawrence, or Marion Counties, respectively (Figures 10, 18, and 19). In each case, there is a hybrid report (Figure 22), indicating that these species do occur in these counties.

Seven different hybrids have been found in Lawrence County (Figure 22). Their occurrence could be the result of the high diversity of oaks in Lawrence County; of the 19 species native to Indiana, 14 are known or are suspected to occur in the County. The diversity of species might increase the likelihood of hybridization. However, if that were the case, then there should be more reports of hybrids from Gibson, Posey, and Spencer Counties, each of which has 16 species of oaks documented.

The number of hybrids reported from a particular county is most likely a reflection of the time collectors interested in oaks have spent in that county. For example, four hybrids have been reported from Wells County, and a total of six have been reported from Lake and Porter Counties. C.C. Deam lived in Wells County, and he, along with R.C. Friesner, R. Kriebel, and others, spent considerable time in the field in Lake and Porter Counties. Seven hybrids have been reported from Lawrence County, and the aforementioned collectors seem to have spent considerable time hiking the hills near Bedford and other parts of

the county. If other counties were as thoroughly explored, additional species and hybrid reports might arise.

A KEY TO THE OAKS OF INDIANA

The following key can be used to identify trees that are more or less typical of each species found in Indiana. Given the high degree of variability in some species and the existence of various hybrid combinations, some individual specimens (either in the herbarium or in the field) will be difficult to key. It is always best to examine all leaves and fruits present on the herbarium specimen. In the field, it is always best to view the general phenotype of the entire tree, not just that of a few leaves and fruits.

1. Leaves with bristle tips; mature acorns found on twigs of the previous year (red and black oaks; subgenus *Erythrobalanus*)
   2. Leaves entire to 3-lobed; if lobed, leaves widest above the middle
      3. Leaves shallowly to deeply lobed; widest near the apex
         4. Lower surface of leaves uniformly pubescent/tomentose; leaf bases u-shaped to rounded; petioles 2-7 cm long . . . . . *Quercus falcata*
         4. Lower surface of leaves glabrous or only sparsely pubescent; leaf bases rounded to cordate; petioles 1-2 cm long. . . . . *Quercus marilandica*
      3. Leaves entire, widest near the middle. . . . . *Quercus imbricaria*
   2. Leaves 5-11 lobed; if lobes fewer than 5, then leaves widest at or below the middle
      5. Lower surface of leaves uniformly pubescent/tomentose
         6. Leaf bases distinctly u-shaped; terminal leaf lobe often falcate and decidedly longer than lateral lobes . . . . . *Quercus falcata*
         6. Leaf bases broadly acute to truncate; terminal leaf lobe rarely falcate, not exceeding the lateral lobes in length. . . . . *Quercus pagoda*
      5. Lower surface of leaves glabrous (except for axillary tufts of tomentum) or only sparsely pubescent
         7. Lower surface of leaves glabrous except for prominent axillary tufts along the midrib
            8. Twigs and buds gray to gray-brown; buds glabrous; nuts large (15-30 mm long), ovate to oblong . . . . . *Quercus shumardii*

8. Twigs and buds reddish-brown; buds often with a tuft of hairs at the apex; nuts small (10-15 mm long), globose to ovate... ..... *Quercus palustris*

7. Lower surface of leaves glabrous or sparsely pubescent, axillary tufts along midrib minute or absent

9. Leaves typically 5-7 lobed, the lobes usually becoming wider toward their apices; acorn cups rounded and deep, covering 1/3 to 1/2 of the nut

10. Terminal buds 3-6 mm long, reddish-brown and glabrous or silvery pubescent above the middle; inner surface of acorn cups essentially glabrous

11. Nuts ovoid to sub-globose, with one or more concentric rings of pits at the apex; cup scales with broad, glossy bases, the scale margins often strongly concave .... *Quercus coccinea*

11. Nuts ellipsoid to ovoid, lacking rings of pits at the apex; cup scales pubescent with straight to slightly concave margins..... *Quercus ellipsoidalis*

10. Terminal buds 6-12 mm long, tawny tomentose; inner surface of acorn cups distinctly tomentose .... *Quercus velutina*

9. Leaves typically 7-11 lobed, the lobes usually tapering toward their apices; acorn cups shallow, covering 1/4 to 1/3 of the nut ..... *Quercus rubra*

1. Leaves lacking bristle tips; mature acorns found on twigs of the current year (white and chestnut oaks; subgenus *Quercus*)

12. Leaves with 5-20 pairs of teeth or shallow lobes; secondary teeth/lobes usually absent

13. Leaves with 5-8 lateral veins on each side

14. Shrub; each lateral vein ending in a tooth; acorns sessile or nearly so..... *Quercus prinoides*

14. Tree; several lateral veins not ending in teeth or lobes; acorns on peduncles 2-7 cm long ..... *Quercus bicolor*

13. Leaves with 9-20 lateral veins on each side

15. Teeth of leaves blunt, not or only slightly curved towards the leaf apex; leaves mostly ovate to obovate in outline; nuts 20-35 mm long

16. Bark dark and deeply furrowed; acorn cup scales fused; trees of dry habitats ..... *Quercus prinus*

16. Bark gray and scaly; acorn cup scales distinct; trees of moist habitats ..... *Quercus michauxii*

15. Teeth of leaves sharp, curved towards the leaf apex; leaves mostly lanceolate-elliptic in outline; nuts 15-20 mm long..... ..... *Quercus muehlenbergii*

12. Leaves with 1-5 pairs of lobes; secondary teeth/lobes common

17. Twigs essentially glabrous

18. Lower surface of leaves densely pubescent/tomentose

19. Sinuses of lower half of leaf blade much deeper than those of the upper half; upper portion of blade broad, obtuse in outline; scales at margins of acorn cups noticeably awned, cups covering about 1/2 of the nut.... *Quercus macrocarpa*

19. Sinuses of the lower and upper halves of the leaf blade about equal in depth; upper half of blade narrow, generally acute in outline; scales at margins of acorn cups not awned, cups covering 2/3 to all of the nut ..... *Quercus lyrata*

18. Lower surface of leaves glabrous ..... *Quercus alba*

17. Twigs densely pubescent ..... *Quercus stellata*

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