# A REVISION OF THE EOCENE FLORA OF SOUTHEASTERN NORTH AMERICA*

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## ABSTRACT

The Lower Eocene floras of southeastern North America were first published as a comprehensive flora by E. W. Berry in 1916 and later revised by him in 1930. This flora is one of the largest and most completely studied Eocene floras in North America. However, reinvestigation, presently in progress, has resulted in several revisions. Improved methods of research, more detailed and inclusive study expanding into new areas of research, and the increased understanding that has resulted from continued study in previously established areas of research, as well as the recent remapping of important deposits and the continued collection of fossil material, have provided the tools and information necessary for this revision. The age of these deposits has been revised from Wilcox group (Lower Eocene) to Claiborne group (Middle Eocene) and the nature of the deposits may now best be considered to be leaf-bearing clays laid down in ancient oxbow lakes. Recent studies of the cuticular remains of some leaves and pollen indicate that the clay pits are not isochronous but span the range of time of the Middle Eocene.

Work which has been completed indicates that at least 60% of the taxonomic relationships of fossil forms to modern families and genera published by Berry are incorrect.

When the fine venation and cuticular remains of the leaves are examined the presence of several extant taxa which Berry reported can not be substantiated. Some taxonomic revisions are proposed; some of the fossil leaves studied could not be assigned to any known taxa and may represent extinct forms. The evolution of the angiosperms in the early Tertiary is often misunderstood because of the excessive number of extant generic and family names that are applied to fossil leaves with little or no detailed analysis of the fine venation or cuticular features of either modern or fossil angiosperms.

The use of taxonomic affinities, community structure, and foliar physiognomy in making palaeoecological interpretations of early Tertiary floras is mentioned and the climate during Middle Eocene time in western Kentucky and Tennessee is reevaluated. The climate appears to have been dryer and somewhat cooler than previous investigators indicated.

## INTRODUCTION

THE record of the Eocene floras of southeastern North America published by E. W. Berry (1916, 1924, 1930, 1941) has remained an outstanding contribution to paleobotany for nearly half a century. Except for the work of R. W. Brown (1944, 1946, 1960), no previous attempt has been made to reinvestigate the megafossils of these floras and palaeobotanists and systematic botanists have accepted and used the record as published by Berry. A few years ago, the author began a reinvestigation of the exceptionally large and well-preserved flora published as Wilcox age by E. W. Berry (1916, 1930, 1941) applying new techniques of investigation. At the same time a U.S.G.S. mapping project was in progress in western Kentucky and several clay companies were actively searching for new deposits of clay. Because of the continued clay-mining operations in western Kentucky and Tennessee large collections of fossil plant remains could be collected from several localities.

Berry published records from nearly 200 plant-bearing localities which he designated as Wilcox (Lower Eocene), Claiborne (Middle Eocene) or Jackson (Upper Eocene). These localities are plotted in figure 1 using the age and location published by Berry (1924, 1930). This reinvestigation is based upon material collected from 19 clay pits in western Kentucky and Tennessee as shown in figure 2 and the revisions suggested here can be applied only to fossil plant material of that area. The majority of Berry's plant material for his Wilcox flora was collected in western Kentucky and Tennessee, so in spite of the relatively small area sampled for this study, numerous specimens of most of the forms described by Berry have been collected.

## AGE

The fossil deposits in this investigation are either the same localities or very near localities described by Berry (1930) as Wilcox age (Lower Eocene) (Figs. 1 & 2). They are all isolated lenses of clay usually underlain by sands and overlain by unsorted

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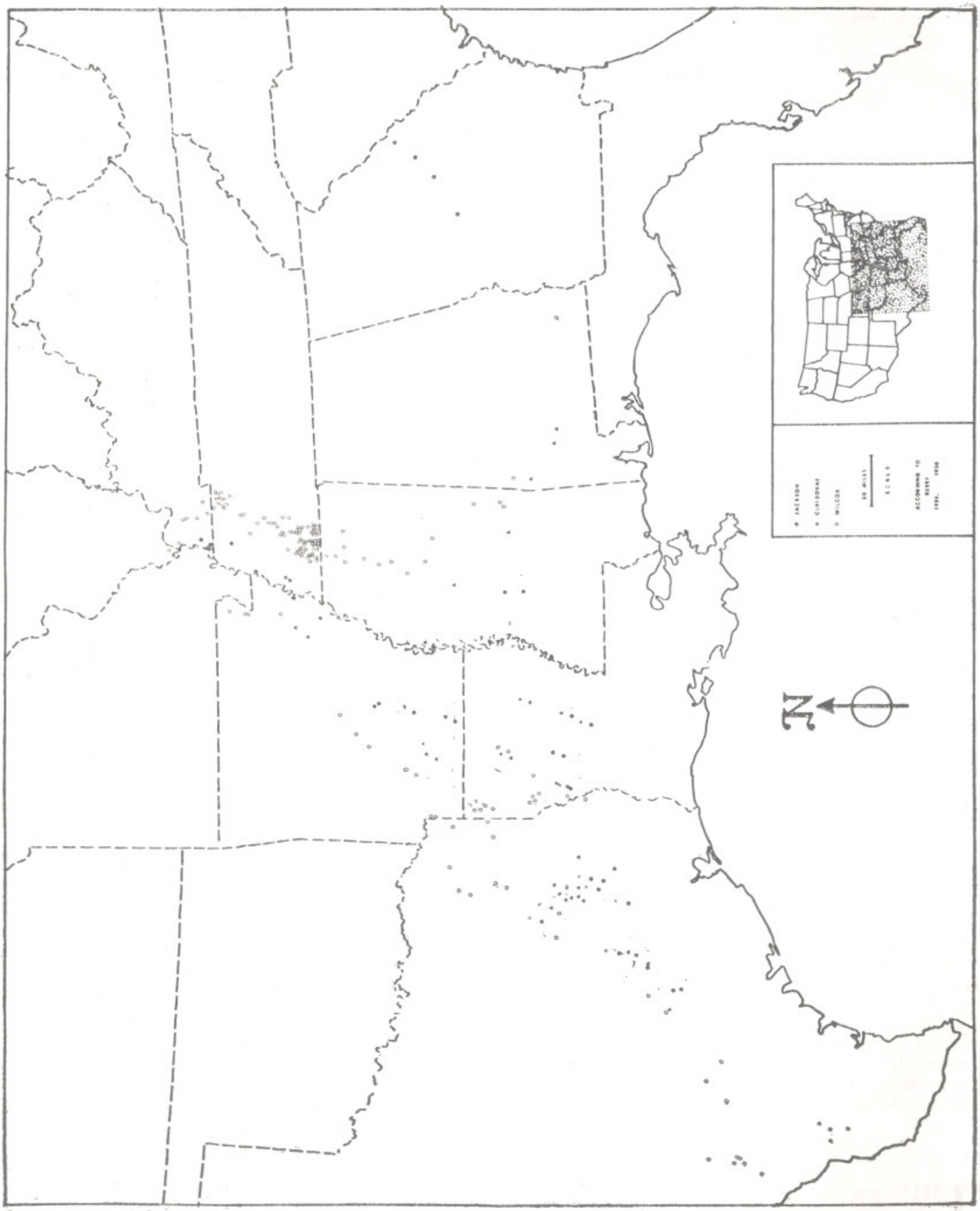
● JACKSON
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50 MILES
SCALE
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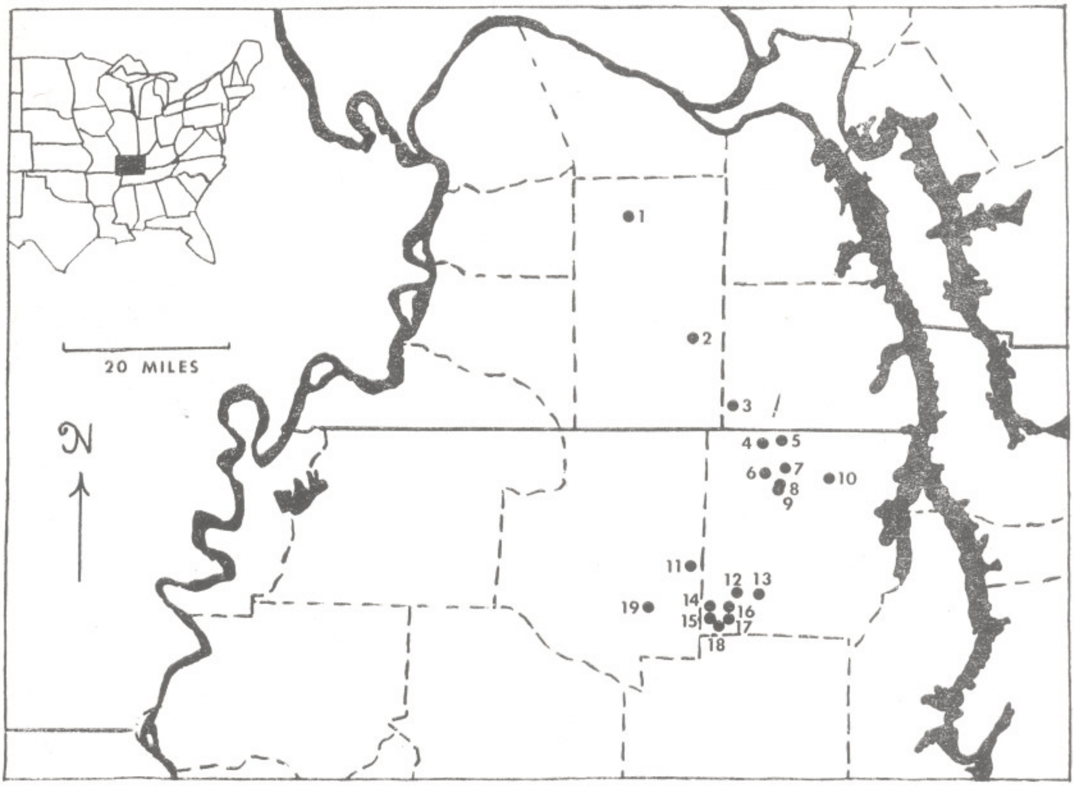
TEXT FIG. 1



TEXT-FIG. 2 — Map of the localities used in this investigation in western Kentucky and Tennessee. The age of these localities is Claiborne (Middle Eocene).

1. Lamkin Clay Pit. 2. South Forty Clay Pit. *3. Bell City Clay Pit. 4. New Puryear Clay Pit. 5. Old Whitlock Clay Pit. 6. Martin Clay Pit. *7. Puryear Clay Pit. 8. Spink's Puryear Clay Pit. 9. K. & T. Puryear Clay Pit. 10. Buchanan Clay Pit. 11. Warman Clay Pit. 12. Richie's Black Clay Pit. 13. Haynes Clay Pit. 14. Lawrence Clay Pit. 15. New Lawrence Clay Pit. 16. Tan Clay Pit. 17. Miller Clay Pit. 18. Rancho Clay Pit. 19. Gleason Clay Pits.

*Clay pits from which Berry also collected fossil plant material.

gravels of the Lafayette formation in Kentucky or top soils in Tennessee. The plant remains found are essentially the same as those described by Berry (1916, 1930). The use of pollen studies to relate the age of these isolated lenses of clay to assemblages of microfossils of known age has shown that these localities are not Wilcox but Claiborne age (Middle Eocene). Pollen analysis of several clay pits has been completed by Dr. William Elsik and Dr. Robert Tschudy. The pollen assemblage is typically Claiborne (Elsik & Dilcher, in preparation; Tschudy, personal communication).

The question of relative ages of the numerous clay pits shown in figure 2 has also been considered. The leaf assemblages vary slightly from one clay pit to another but many leaf forms occur commonly in all of the pits examined. However, there is some variation of the cuticle of leaves identical in gross morphology from one pit to another and this variation led us to suspect that these clay pits are of different ages. This was recently confirmed by pollen

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TEXT-FIG. 1 — Map of southeastern North America showing the position of each of the Eocene localities of the fossil material analyzed by E. W. Berry. The ages given (Wilcox, Claiborne, Jackson) are according to Berry (1924, 1930). The age of some of them has since been revised (see text).

analysis (Tschudy, personal communication). The age of the pits varies from lower Caliborne to upper Claiborne, spanning a time of about 7 million years. However, we have not been able to ascertain a change in age within a single clay lens even though the clay may be 40 feet thick. We are continuing detailed pollen sampling within various thick clay lenses along with an analysis of the megafossils and microfossils at each level in order to establish whether any floristic changes occurred during the deposition of such a lens that might indicate a change in age within a single deposit.

## DEPOSITIONAL HISTORY

Berry (1916, 1924, 1930, 1941) described plant remains from 199 localities of Eocene age extending from Georgia to Kentucky to Texas as shown in figure 1. He interpreted these plant-bearing clays to be fine-grain deposits laid down in lagoons or seashore lakes at the time of a major transgression of the Mississippi embayment sea which caused the drowning of barrier beaches. According to Berry this transgression impounded water behind barrier beaches and because of the low gradient of the coastal plain during the Eocene " caused these impounded lagoon waters to be often rather distant from the open sea of the embayment " (Berry, 1930, p. 2). This interpretation directly relates the deposition of these Eocene plant-bearing sediments to the level of the sea.

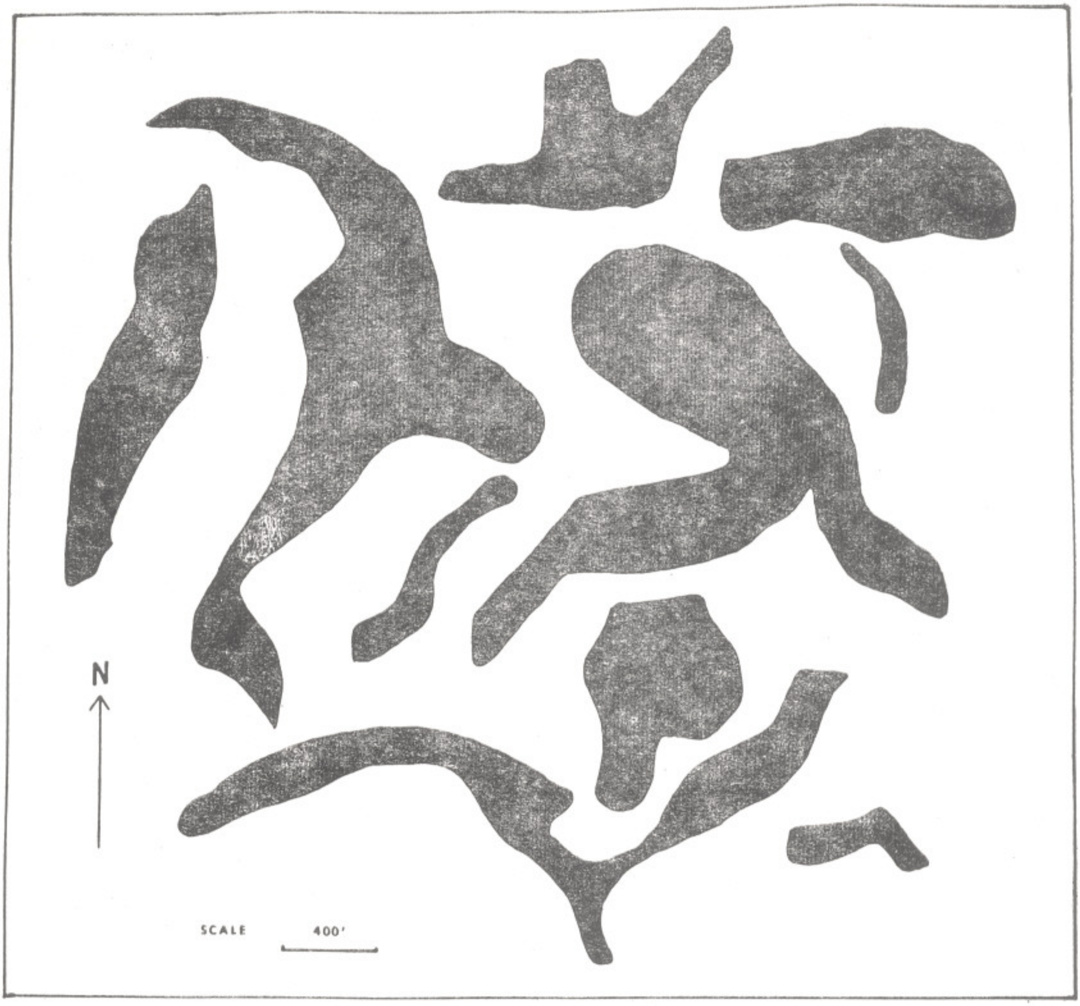
The plant-bearing clay deposits in western Kentucky and Tennessee occur as isolated clays generally underlain by sands and overlain by Pliocene-Pleistocene age conglomerate gravels to the north and Pleistocene soils to the south. In cross section the clay deposits are more or less flat-topped, thin on the edges and thick in the center. In long section most of the deposits that have been mined or are mapped (see Fig. 3) are elongate and bend in an arc. The clays are generally dark gray near the base of the deposit and grade into a red, pink, or brown clay in which the plant remains are badly oxidized near the top. Thin lignite deposits are frequently associated with these clay deposits. The underlying cross-bedded sands and the cross-section and long-section shapes of the deposits (Fig. 3) strongly suggest that the Eocene clays in western Kentucky and Tennessee are predominantly channel fills or ancient oxbow lakes associated with low gradient streams. The Warman and Lawrence clay pits (No. 11 & 14, Fig. 2) are only 5 miles apart but Warman is lower upper Claiborne while the Lawrence is lower Claiborne (Tschudy, personal communication). Thus the area of Henry County, Tennessee, was probably the site of meandering streams and oxbow lakes throughout much of middle Eocene time. The nearest marine deposits of Eocene age are approximately 120 miles south in Mississippi (Berry, 1930). The large oxbow lakes associated with the flood plain of the Mississippi River today are about 50 to 300 miles from the Gulf of Mexico. The sea has no influence on the impounding of water in these modern oxbow lakes and it is unlikely that the sea of the Mississippi embayment influenced the impounding of water in the oxbow lakes of Eocene times.

As we have worked only with plant-bearing clay deposits in western Kentucky and Tennessee, this interpretation is directed toward those deposits and should not be interpreted as relating to the plant-bearing clay deposits elsewhere in the embayment.

## BERRY'S APPROACH TO THIS FLORA

The study of angiosperm floras was first developed about the middle of the 19th century by paleobotanists such as von Ettingshausen and Saporta. During the latter 19th and early 20th centuries American paleobotanists continued to modify and further develop the techniques of studying angiosperm floras. E. W. Berry was one of the most proficient and prolific angiosperm floristic paleobotanists who developed from this background. He used the experience and observations of earlier angiosperm floristic paleobotanists from the United States and Europe while maintaining an open and independent mind and relying on his own keen observations. At the same time Berry was working with fossil floras, new and important modern plant collections were being made. He compared his fossil material with modern forms, first with the flora near the fossil locality and then progressively looking for satisfactory matches with more distant modern floras.

Berry was not timid in his approach to the classification of fossil plants. He generally tried to work with relationships of



TEXT-FIG. 3 — Map of the clay deposits determined by drilling on 100′ centers. These clay deposits are in or near Henry County, Tennessee. The orientation of one clay deposit to another has been altered however the north arrow and scale indicate the correct north-south orientation and extent of each deposit. In cross section these deposits resemble channel fills.

fossil to modern forms at the generic and only occasionally at the less precise family level. Relating fossil angiosperm remains to modern or near modern genera or families had been the rule in angiosperm floristic studies and Berry continued to follow it. He listed 180 genera in his Wilcox flora (Berry, 1930) of which 158 were assigned angiosperm affinities. Of these forms, 102 were assigned extant generic names, 46 were assigned modern generic names with a prefix or suffix (e.g. pseudo-, para-, or -ites, -phyllum, -oides) to indicate they were fossil genera rather than modern genera. Only 10 forms out of 158 were assigned generic names not suggestive of modern relationships; 5 of these were placed in specific families and 5 classified as " position uncertain ".

Berry used a comparison of leaf form and gross features of the margin and venation of fossil and modern leaves to establish his relationships. He rarely failed to find some modern leaf which could be matched with the fossil leaves. Thus his work was mainly directed towards phytogeography and minor shifts of evolution at the species level. In retrospect Berry seems overly positive concerning the modern relations he proposed for the plant remains he studied; however, in terms of the tools and techniques then available to him the results of his work must be viewed with respect. A more refined analysis of these Eocene plant remains using tools and techniques unavailable to Berry has yielded new evidence which must now be considered, and which demonstrates that at least 60 per cent of the generic and/or family identifications proposed by Berry (1930) are incorrect.

## A NEW APPROACH TO THIS FLORA

The techniques used to study fossil plant remains depend primarily upon the nature of the material and the type of data desired. In the major floristic studies published by Berry the leaf remains are treated as impressions and thus the data used is limited to the gross morphology of the fossil leaves. Although Berry's work serves as a preliminary assessment of the taxonomy of the flora, we hope to arrive at a closer approximation of the relationships of the units within this flora by using observations of cuticular features and fine venation as well as gross morphology.

The Eocene leaf remains from Kentucky and Tennessee lend themselves well to a critical morphological and anatomical approach. The leaf compressions frequently have well-preserved cuticle and fine venation. Berry found fossil leaf compressions with the cuticle still intact and in 1933 published a short paper in which he described the cuticle of one such specimen, a *Combretum petraflumensis* leaf. Berry wrote, " I have not compared these fossil preparations with those from existing leaves as the subject is so vast in its details and so little is known in a systematic way of Angiosperm cuticular structures."

The procedure used in working on the revision of this flora has been to make large collections from the same clay pits visited by Berry (e.g. Bell City & Puryear, Nos. 3 & 7 on Fig. 2) and to collect at new pits which have been opened in the same areas in Kentucky and Tennessee from which Berry described material (Fig. 1). In these large collections numerous specimens of each taxonomic unit as defined by Berry (1916, 1924, 1930) are available in various states of preservation. The method of study has been to choose a taxonomic unit, generally at the generic or family level, and select from the fossil-leaf collection specimens which are the same as, or similar to, those illustrated and described by Berry (1916, 1924, 1930). The collection is repeatedly searched during the progress of the study as the investigator becomes more familiar with the limits and variations of the leaf material being investigated. The gross features of the fossil leaves selected and fine features of the venation are noted. Then modern leaves of the genus and family suggested by Berry, as well as those leaves in other groups with similar gross features, are examined and added to the reference collection of modern leaf types which we have established in Indiana. Cuticular preparations of the modern leaves are made and they are cleared for a study of their fine venation. The nature of the cuticle and the fine venation as well as the gross features of the leaves are studied for each modern taxonomic group until the general patterns and variations of these characters are determined. Then cuticular preparations of the fossil leaves are made and studied to see how variable the cuticle is in fossil leaves with like gross morphology and fine venation.

Finally, using as large an assemblage of fossil leaf material as possible, the gross morphology, fine venation, and cuticular characters and their variability are critically compared to the same features of the modern leaves studied. Then an evaluation is made of the relationship of the fossil leaf material to modern forms. Large numbers of modern forms are studied for each fossil type considered and this often involves a wide sampling of families and genera with similar leaf form throughout the world as well as a careful analysis of each genus or species suggested by Berry.

## TAXONOMIC REVISIONS

The following are the forms within this Eocene flora which have been reinvestigated. For some the research has been completed and published and for others the research is completed or in progress but has not yet been published. As previously explained, this "floristic" revision is being approached by intensive studies of individual taxonomic units within the flora and is not a complete revision of the total work published by Berry (1916, 1924, 1930) at this time.

*Podocarpus* sp.— Leafy shoots and isolated leaves of gymnosperms were found in three of the clay pits from which collections have been made. An analysis of the cuticular features of the leaves of this material (Dilcher, 1969) indicated that these leaves belong to the genus *Podocarpus*.

Berry (1916, 1924) described and illustrated leafy shoots of gymnosperm material from Eocene deposits in Tennessee which he assigned to *Taxodium*. Berry's material was examined and it is very similar to the fossil shoots which we have identified as *Podocarpus*; unfortunately his material yielded no cuticle for a cuticular comparison.

*Proteaceae — Fagaceae* — Berry (1916, 1930) identified four genera of Proteaceae, *Knightiophyllum*, *Proteoides*, *Paleodendron*, and *Banksia*. A reinvestigation of each of these forms has led to the conclusion that none of them are related to any modern members of the Proteaceae (Dilcher & Mehrotra, 1969a). A detailed study has been published of one of the genera, *Knightiophyllum* (Dilcher & Mehrotra, 1969b), in which it is clearly shown that the fossil material has no relationship to the modern genus *Knightia* or to any other genus of the Proteaceae. Upon examining the fine venation and cuticular characters of *Proteoides* and *Paleodendron* it was found that they were also not similar to any modern genus in the Proteaceae. However, no modern genera have been found to which *Knightiophyllum*, *Proteoides* or *Paleodendron* could be assigned.

The fossil leaf material identified by Berry as *Banksia* is similar to leaves identified by him as *Dryophyllum*, a form genus of leaves thought to have affinities with the Fagaceae. There is a range in forms, recognized as species by Berry (1916, 1924, 1930), in *Banksia* and *Dryophyllum*. However, the leaves of one species of *Banksia*, *B. saffordi*, can not be differentiated by cuticular analysis from *Dryophyllum puryearensis* and appear to be variations of it (Dilcher and Mehrotra, 1969a). *Dryophyllum* is the only genus present in the flora that has been related to the Fagaceae. Leaf material of this genus is generally abundant at all of the localities sampled in this study. These leaves are variable in their venation, size and shape and were separated into various species and even genera (such as *Banksia*) by Berry. A study of the cuticular characters and the fine venation of two species, *D. tennesseensis* and *D. puryearensis*, established that these should indeed be recognized as separate species (Anderson & Dilcher, 1968). However, some of the other species recognized by Berry appear to be variations in leaf form of a single type.

One particularly interesting aspect of the investigation of this genus is that leaf forms which have identical venation and gross morphological features from one pit to another may have very different types of trichomes (work in progress). Just as the leaves of modern oaks can often be identified by the nature of their trichomes we find such a variation present during the Middle Eocene in leaves of *Dryophyllum*. Preliminary pollen studies (Robert Tschudy, personal communication) have indicated that the clay pits yielding such cuticular variations are in fact separated in time by 5-7 million years (lower Middle Eocene to upper Middle Eocene). Thus we have an opportunity to study the variation of leaf form, fine venation and cuticular characters in one geographical area through a measured unit of time.

Based upon work in progress the genus *Dryophyllum* is best regarded as a fossil form genus having affinities with the Fagaceae. Its relationships appear to be most closely allied with the modern genera *Castanea*, *Castanopsis* and *Lithocarpus*.

*Monocotyledons* — A revision of the monocotyledons is in progress and work has been completed on the sabaloid palms (Daghlian & Dilcher, in press b) and a large-leafed *Philodendron* (Daghlian & Dilcher, in press a). Work is in progress on the chamaedoriod palms and some sedge-like material. This is the diversity of the monocotyledonous material we have identified in our collections. However, using our collections we have not been able to substantiate the following monocotyledons which Berry (1930) included in his Wilcox flora: *Poacites*, *Cyperacites* (3 species), *Potamogeton* (3 species), *Araceaeites*, *Acornus*, *Pistia*, *Sparganium* and *Nipadites* (2 species). Most of these genera are represented in Berry's collections by specimens which are rare and not well preserved.

*Sabaloid palms* — Remains of sabaloid palms have been found at 9 localities of the 19 from which collections have been made. All of the 9 localities are those deposits from which larger samples of fossil leaves were collected. Both nearly entire leaves and isolated fragmentary rays have been studied. Attachment of the leaflets, number of veins in the rays at particular distances from their origin and the nature of the petiole were carefully studied when preserved for over 60 specimens. In addition to this the cuticular characters were carefully studied and all of these leaf characters were compared to similar observations of nearly 100 modern palms used as reference material.

Berry (1916, 1924, 1930) referred the sabaloid palms he frequently found in his "Wilcox" material to *Sabalites grayanus* and those he found in his "Claiborne" material to *Thrinax eocenica* and *Sabalites vicksburgensis*. We have found specimens which are costa palmate with about 80 veins per leaflet and sunken occluded stomata. These characters, as well as the accessory cell arrangement, are indicative of the genus *Sabal* and we feel there is strong evidence for the identification of this modern genus in the middle Eocene (Daghlian & Dilcher, in press b). On the basis of the characters outlined above, two other forms of sabaloid palms can be identified in the flora. These are both palmately compound palms, one having 4-10 veins per ray and the other having 16-20 veins per ray, which do not resemble modern *Sabal* but rather genera such as *Serenoa* or *Thrinax*. The material Berry described and illustrated as *Sabalites grayanus* (Plate XIV, 1916) has both cellular and venation characters similar to those of these two forms.

In an attempt to establish the affinities of the isolated fragments of rays which are commonly found we first worked with a carefully chosen group of fossils which were well preserved and included the attachment of the rays to the petiole. Once the nature of the venation and cuticular features were established for rather complete and well preserved specimens, it was possible to analyse the fragments of palm rays and relate them with some certainty to more completely preserved material.

Chamaedoroid palm fragments can be easily distinguished from sabaloid-type by the nature of the epidermal cells (Dilcher, 1968). However, the chamaedoroid palms have not yet been studied in detail. Preliminary work indicates that one or perhaps two forms will be recognized.

*Philodendron*—Large elephant-ear shaped leaves 30″ wide have been found in two clay pits in Tennessee. Numerous fragments of this leaf type in which the cuticle and fine venation are well preserved have been collected. This leaf appears to have had a rather fleshy midrib and thick secondary veins. The fine venation suggests affinities with the section Meconostigma in the genus *Philodendron*. This is the first fossil record of this genus in North America (Daghlian & Dilcher, in press a).

Cuticular studies of modern members of the Araceae were made and found to be of little help taxonomically in assigning this leaf to more than the family. However, fine venation studies were very helpful in assigning the leaf to a modern genus and further, to a particular subsection of the genus which is presently restricted to the subtropical areas of South America.

*Dendropanax eocenensis* — Over 70 fossil specimens of a particular lobed leaf which Berry (1916) identified as *Aralia dakotana* were collected from one clay pit. As Dilcher and Dolph (1970) noted, " The genus *Aralia* has often been used rather loosely by palaeobotanists for fossil leaves which seem to have some affinities with the Araliaceae. As a result of this use, the genus, as it exists in the fossil record, is no more than a convenient catchall genus . . .generally indicating no more than a possible familiar relationship." A great deal of variability in the gross morphology of the fossil leaves was found. However, the cuticular features were constant througn all of the leaves examined. After examining the venation and cuticle of many modern lobed leaves, the immature foliage of the genus *Dendropanax* in the Araliaceae was found to be the closest modern form. However, in the minds of the authors, this identification is not entirely satisfactory at the generic level and only represents an attempt to relate the fossil to a living form which is more similar to the fossil leaves than other living forms investigated. Whether or not this relationship should in fact be at the generic level is still open to question.

*Sapindus* — One of the most common, most widely distributed and best preserved fossil forms in this flora was identified by Berry (1916, 1930) as leaflets of *Sapindus*. He identified many species including 6 species from the clay pit at Puryear. The gross morphology, cuticle and fine venation of over 400 specimens from the Lawrence clay pit were studied and found to be similar. These specimens encompass the entire range of Berry's 6 species from Puryear and probably represent natural variations of a single species (Dilcher, 1965). The venation and cuticular characters of all the modern species of *Sapindus* and of numerous other genera with similar leaflet or leaf form in the Sapindaceae and many other modern angiosperm families have been studied and no modern form has yet been found which can be related to this fossil material.

Leaflets of *Sapindus* have frequently been reported in floristic studies of early Tertiary deposits in North America. However, I expect that a careful study of the fine venation and/or cuticle of these forms will show that the majority are incorrectly placed taxonomically.

*Engelhardia* — Berry (1916, 1924, 1930) identified both leaves and fruits of *Engelhardia*. Winged fruits similar to fruits of the extant American forms have been collected and Juglandaceous pollen is common in the clays in which the fruits occur. The leaflets of both Asiatic and American modern forms were studied in detail and were found to have distinct morphological and cuticular characters. Examination of the leaflet cuticle indicates that American and Asiatic forms can be differentiated by the variation in cuticular characters. After searching through several thousand fossil specimens and sampling the cuticle of several hundred, no leaflets were found which are similar to either the extant Asiatic or American forms. However, some leaf forms have been found with glands which are similar to those found in *Engelhardia* and work is in progress on this material. The only fossil material in this flora upon which to establish a good relationship to the modern American forms (now placed in *Oreomunnea*) are the fruits (Potter & Dilcher, in press). On the basis of the fruits, the fossil *Engelhardia puryearensis* appears to be closely allied to extant Central American forms such as *Oreomunnea mexicana*. Berry's report (1924) of an *Engelhardia* fruit found only as a single poorly-preserved specimen is the only record in this flora of a fruit which is similar to the extant Asiatic forms. This record should be questioned until further evidence is found to substantiate the report.

One other winged fruit which is more abundant than *Engelhardia* was called *Paraengelhardtia* by Berry (1916, 1930). The wings of the fruit are much less developed and it probably represents, as Berry indicates, an extinct form closely allied to *Engelhardia puyrearensis*.

*Apocynaceae* — A review of the fossil forms of the Apocynaceae is in progress by G. Dolph. He has already investigated several of the leaf types identified by Berry (1916, 1930) as various species of *Apocynophyllum, Myrcia* and *Ficus*. Upon examination of the fine venation and cuticular features of these forms several revisions will be forthcoming (Dolph, in press). Work is also in progress by Gary Dolph on the relationships of these fossil forms to extant taxa.

*Myrica* — Berry (1916, 1924, 1930) recognized 6 species of *Myrica* from these Eocene deposits. A detailed study of the leaf form, fine venation and cuticular characteristics of modern species of this genus has been completed by Mary Sheffy. Using this information a search was undertaken to find out if any of the leaves in the palaeobotanical collection at Indiana University were similar to the extant species of *Myrica*. After a detailed study of over 180 fossil leaves similar to *Myrica* in gross morphology none of them exactly matched any extant form of the genus (M. Sheffy, work in progress). Although several characters of a few of the fossils were similar to the genus, they lacked one or two important characters found throughout the extant genus. Thus the identification of the fossil forms which Berry refers to the genus *Myrica* can not be substantiated at the generic level as this genus is understood today when fine venation and cuticular features are considered.

*Nyssa and Palaeoweatherellia* — Numerous fruits and seeds which commonly occur in the leaf-bearing clays have been collected. Berry (1916, 1924, 1950) published records of many fruits and seeds. Impressions of the endocarps of *Nyssa* were reported by Berry (1916, 1930) and several unaltered endocarps were studied by Dilcher and McQuade (1967) and found to be good evidence to support this Eocene occurrence of the genus. Berry (1930) also reported a leaf, *Nyssa tennesseensis*; however, we have not yet attempted to confiim this report from our collection of leaf material.

Several well-preserved fruits which Berry (1922) designated as *Monocarpellites* have been studied and found to be very similar to *Palaeowetherellia*, a genus established by Chandler (1954) for some Eocene fruits from Egypt. These fruits are unaltered remains allowing detailed observations of the surface features and the cellular nature of the fruit from sectioned material (Lambert & Dilcher, 1970). Modern affinities of this fruit are uncertain but it may have some affinities with the Euphorbiaceae as suggested by Chandler (1954).

*Lauraceae* — The family Lauraceae was recognized by Berry (1916, 1930) as one of the most common, diverse and widespread families in the flora. Both leaf material and fruits have been collected which certainly have affinities with this family. One form which has been studied, *Ocotea obtusifolia*, could not be matched to any modern species, but the nature of the venation and cuticular features leave no doubt about its relation to the Lauraceae. Therefore the generic designation given by Berry (1916) was not revised even though, after examining nearly 300 modern species in several genera of the Lauraceae, no modern genus or species was found with which the fossil matched in more than a general manner (Dilcher, 1963). Certainly the family can be recognized but more work must be completed before we can be certain of generic relationships.

*Leguminosae* — The legume family is represented by numerous leaflets and several seed pods in our collection. Berry (1916) recognized it as a common family in his "Wilcox" flora and assigned the leaflets to a large number of genera. We have not yet made a detailed study of this family but certainly accept its presence at the family level.

*Moraceae* — Berry (1916, 1924, 1930) assigned fossil material from his collection to a large number of genera and species in this family, although he indicated that several forms were placed in the family, especially in the genus *Ficus*, for lack of a better place to put them. Work has not yet been initiated on the numerous leaf fossils which in our collection appear to have affinities with this family. Several fruits in our collection do appear to be similar to modern fruits in this family. Based upon preliminary observations of these fruits, the family does appear to be represented in the flora, although some of the forms placed in it by Berry may be questioned.

## RELATIONSHIP TO MODERN FORMS

The development of angiosperm diversity has generally been misunderstood because fossil material from the early Tertiary has been assigned modern generic or family names based upon superficial similarities between the modern and fossil leaves. As mentioned earlier in this paper, Berry (1930) either assigned fossil forms to modern genera directly, or implied modern generic relationships by using a suffix or prefix to make a fossil form name, to 148 of the 158 angiosperm genera identified in his "Wilcox" flora. Only a few modern genera, *Sabal*, *Philodendron*, *Nyssa*, *Podocarpus* and *Engelhardia* (*Oreomunnea*) can confidently be accepted as being represented in this fossil flora at this time. The genera *Ocotea* and *Dendropanax* have been proposed as the best modern match available for certain fossil forms in our collection but not with complete confidence in their designation at the generic level. Several fossil leaves studied appear not to have the generic affinities, and in many cases family affinities, designated by Berry; however, no satisfactory modern generic designation has been found. The pressure often felt by the palaeobotanist working in early Tertiary floras to assign to fossil material the name of the most similar modern form has probably resulted in an incorrect view of the fossil record of early Tertiary angiosperms. Many early Tertiary, and certainly many Cretaceous, fossil angiosperm leaves should not be expected to have characters which relate them at the generic level with modern forms. As this revision progresses we should begin to develop a better understanding of the levels (generic and family) of relationships to which these fossils can be assigned and the degree of the relationships.

Levels of confidence based on the degree of the relationship should be determined for fossil material when modern relationships are established. The more characters which are used to compare modern and fossil material and the greater the similarities of these characters the more confidently the relationship could be expressed and used in establishing distribution patterns or ecological implications of specific taxa. Often relationships, once established, are used to draw extensive conclusions without considering how close the relationship is, i.e. how much confidence may be placed in it. If a level of confidence of the relationship could be assigned, we could then use the designated relationships accordingly.

## EVOLUTIONARY IMPLICATIONS OF THE FLORA

Because of the approach used in this revision, data are being gathered which tell us a great deal more than whether particular forms are present or absent in the flora. The levels of similarity or difference between modern and fossil forms and between one fossil form and another can be measured with great accuracy because of the number and nature of the characters being used.

There is evidence that evolution in cuticular features occurred during the Middle Eocene. Leaves of *Dryophyllum tennesseensis* are good examples of this evolution. *D. tennesseensis* is a common leaf found in several clay pits in Kentucky and Tennessee. The trichomes, from leaves otherwise identical, vary from long loose tufts of 4-5 hairs to short compacted tufts to star-shaped clusters of hairs. Each trichome type is specific to a particular clay pit. Each of these pits has been dated by pollen analysis; the pits vary in age from lower Middle Eocene to upper Middle Eocene (Tschudy, personal communication). Thus the gross morphology of this fossil leaf has remained constant while the nature of the trichomes has changed through Middle Eocene time. Variations in the cuticular features of other forms is also becoming evident as work with other fossil leaves progresses.

Evolution of the various organs of plants through time has been little understood. In this flora several forms are represented by leaves, fruits and pollen providing an excellent opportunity to study the relationships of these organs to those of modern genera and families. Fruits, leaves and pollen have been reported for *Nyssa* and *Engelhardia* (*Oreomunnea*). However, leaves of these genera have not been recognized in our collection. Leaves and fruits of fossil forms in the Moraceae, Lauraceae and Leguminosae are common and should provide an inxcellent basis for understanding the evolution of these families.

A detailed study undertaken by Frank Potter of the various organs of *Engelhardia* (*Oreomunnea*) has resulted in the rather certain identification of fruits of the American forms (*Oreomunnea*) and in the discovery that the pollen can not satisfactorily be used to designate generic affinities for this and related forms (also by personal communication, Douglas Nichols). Just as the fruits of the American and Asiatic forms differ, the cuticular features of their leaves were also found to differ (also by personal communication, Donald Stone). However, after a careful search through our entire collection no fossil leaflets have been found which match those of the modern forms. If the winged fruits of these forms are preserved we should also expect to find leaflets preserved. The fact that we have not yet been able to discover fossil leaflets of the genus suggests that the Middle Eocene leaflets were different from the modern forms; thus the rate of evolution of each of these organs, fruits, leaflets, and pollen may have progressed independently through time.

## ECOLOGY OF THE FLORA

Recently I have completed a manuscript (Dilcher, in press) dealing with the paleoclimatic interpretations of this flora. In that paper I mention some of the revisions which are discussed in more detail in this paper. However, because these two papers have been written within a few months of each other I have no new data to present concerning the paleoecology of the fossil flora. Thus I will summarize the paper in press here and refer the reader interested in the details of the analysis to the paper in press.

The climate was interpreted by using three approaches: 1) identifying individual fossils to their nearest living similar forms and basing paleoclimatic interpretations on the climatic range of these modern forms, 2) identifying fossils to similar living forms and analysing the climate of the communities in which these living similar forms are found today, and 3) using the form of the fossil vegetation, its foliar physiognomy, and relating this to modern climates where vegetation with a similar foliar physiognomy is found. An attempt was made to evaluate the methods of drawing paleoclimatic conclusions from fossil plant floras as well as to establish a reasonable climatic interpretation from the flora under consideration. It was found that any one index of paleoclimate could easily lead to incorrect interpretations and that the examination of several variables which are dependent upon climate is necessary in order to propose a paleoclimate with any degree of reliability. As I wrote (Dilcher, in press), "The approximate paleoclimate of this flora is concluded to be seasonally dry to slightly moist, moisture regime and an equable warm temperate to cool subtropical temperature regime. The paleoclimatic conclusions drawn are based on all the available data. However, they are only approximations, since our present knowledge of the evolution of plants and plant communities and of the relationship of foliar physiognomy and climate is not refined enough to allow a precise statement of early Tertiary climates."

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