INVESTIGATIONS OF ANGIOSPERMS FROM THE EOCENE OF NORTH AMERICA: RHAMNUS MARGINATUS (RHAMNACEAE) REEXAMINED[1]

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ABSTRACT

Leaf compressions, previously assigned to *Rhamnus marginatus* Lesquereux, were collected from the Middle Eocene Claiborne Formation of western Kentucky and Tennessee. The leaf architecture and cuticular features of over 40 compressions were carefully examined and compared to those of many extant species of Rhamnaceae and related families as well as fossil specimens previously assigned to this taxon. This leaf type appears to belong to the Rhamnaceae. however, it conforms more closely to species of several genera in the tribe Zizypheae than to those of *Rhamnus* or other genera in the tribe Rhamneae. Confident assignment to any specific genus within this complex of genera cannot be made on the basis of leaf characteristics alone and would require discovery and analysis of additional vegetative and reproductive organs. Because this fossil leaf form cannot be confidently assigned to any modern genus and earlier classifications appear to be improper, this leaf type has been reassigned to the taxon *Berhamniphyllum claibornense* gen. et sp. nov. The transfer of this leaf form at the tribe level reaffirms the need for close examination of taxonomic determinations made by early workers.

The characteristics and stratigraphic position of this leaf type support the hypothesis that modern tribes and possibly genera of Rhamnaceae had evolved by the Middle Eocene.

TWO MAJOR PROBLEMS confront paleobotanists when working with most taxa described in early paleobotanical literature. One problem arises from taxonomic diagnoses which are incomplete, vague (see Lesquereux, 1860) or in some cases entirely absent (see Forbes, 1851). This results in taxa which accommodate large numbers of leaf forms and cross natural taxonomic boundaries. A second problem is the result of assignments made on the basis of superficial similarities between fossil and extant leaf forms with little or no attention given to cuticular features or venation beyond the third rank. Such incomplete analyses lead to frequent and unavoidable errors. These errors abound in Berry's (1916, 1930) work on the "Wilcox" flora. Of those taxa which have been reexamined, over half required revision at the generic level and some required transfer to other families (Dilcher, 1971).

A leaf type which Berry assigned to the species *Rhamnus marginatus* Lesquereux is the subject of this report. Our objectives were to test the validity of Berry's taxonomic treatment of this leaf type, revise it if necessary and, finally, determine the evolutionary significance of this material.

MATERIALS AND METHODS—Forty-two leaf compressions of *Rhamnus marginatus* which correspond to fig. 1 in plate 72 of Berry (1916) were collected from among three clay pits in western Kentucky and Tennessee. The Puryear clay pit, Puryear County, Tennessee provided the largest number of specimens (22) with fewer coming from Lawrence clay pit, Henry County, Tennessee (4), and Lamkin clay pit, Graves County, Kentucky (16). Precise descriptions of the localities can be found in Potter (1976). Specimens used in this study are in the Paleontological Collection, Department of Geology, Indiana University.

The gross morphology, leaf architecture and, when possible, cuticular morphology of each fossil specimen were studied using methods described by Dilcher (1974), Hickey (1973), and Hickey and Wolfe (1975). An extensive and detailed investigation of the same features of similar extant leaves also was conducted, using herbarium materials from Indiana University, the Missouri Botanical Garden and the Field Museum of Natural History. Leaves from over 150 species representing 45 of the 58 genera in the Rhamnaceae, as well as leaves from several species of related families, were thoroughly examined. Stace's solution (Stace, 1965) was found to be the most

effective reagent for preparing cuticles from herbarium specimens. All preparations of extant materials are in the modern reference collection of the Indiana University Paleobotany Laboratory.

RESULTS AND DISCUSSION—*Description of fossil leaves*—The leaves are elliptical to narrowly elliptical with a length of 4.5 to 11.0 cm and a width of 1.3 to 3.0 cm (Fig. 1–5). They are symmetrical with an acute to nearly attenuate apex. The base is acute and normal (sensu Dilcher, 1974) to cuneate in shape. These specimens possess entire margins although some show a mild tendency toward crenation. They appear to have been fairly sturdy and were probably chartaceous to coriaceous. The petioles are normal (sensu Dilcher, 1974) in shape and range from 0.6 to 1.0 cm in length (Fig. 1–4). One of the most distinctive features is the eucamptodromous venation, with a conspicuous absence of looping even at higher orders (Fig. 6, 7). The midrib is straight to slightly curved, and moderately thick to stout. Secondary veins are moderately thick and emerge from the midrib at acute angles ranging from 25° to 40°. The angle of divergence is slightly more acute in secondaries near the leaf apex than those near the base. The secondary veins are uniformly curved, very rarely split and represent the highest order of venation showing excurrent branching (Fig. 6, 7). Intersecondary and intramarginal veins are absent. Tertiary veins are conspicuous and form acute angles exmedially at the lower sides and obtuse angles at the upper sides of secondary veins. The tertiary veins are closely spaced, percurrent, predominately opposite, straight, and form approximate right angles with respect to the midrib (Fig. 6, 7). Tertiary veins comprise the highest order of venation detectable in most carbonized compressions (Fig. 6). However, some specimens from the Lamkin clay pit show well-developed quarternary venation, which appears to be the highest order present in this fossil leaf type. In these specimens the quaternary veins are thick and randomly oriented (Fig. 7). This leaf type possesses poorly developed aerolation and fimbriate ultimate venation.

The upper cuticle of the fossil leaf is moderately thick with more or less isodiametric cells, averaging 26 μm (range 17–39 μm), over nonvenous areas (Fig. 13). The leaf is hypostomatous with stomata arranged randomly over nonvenous areas (Fig. 14). The anticlinal walls are fairly straight and lack ornamentation. Lower epidermal cells in nonvenous areas are isodiametric and 3–6 sided (avg. 29 μm, range 17–55 μm). The stomatal complexes are anomocytic with 3–5 adjacent epidermal cells (Fig. 15, 16). Stomata average 28 μm (range 17–33 μm) in length and 25 μm in width. The guard cells are slightly sunken below the epidermal surface (Fig. 17) and possess stomatal ledges which lack ornamentation. Trichome bases are extremely rare having been observed on only one specimen (Fig. 18). They are unicellular and surrounded by slightly modified epidermal cells. No trichomes have been found.
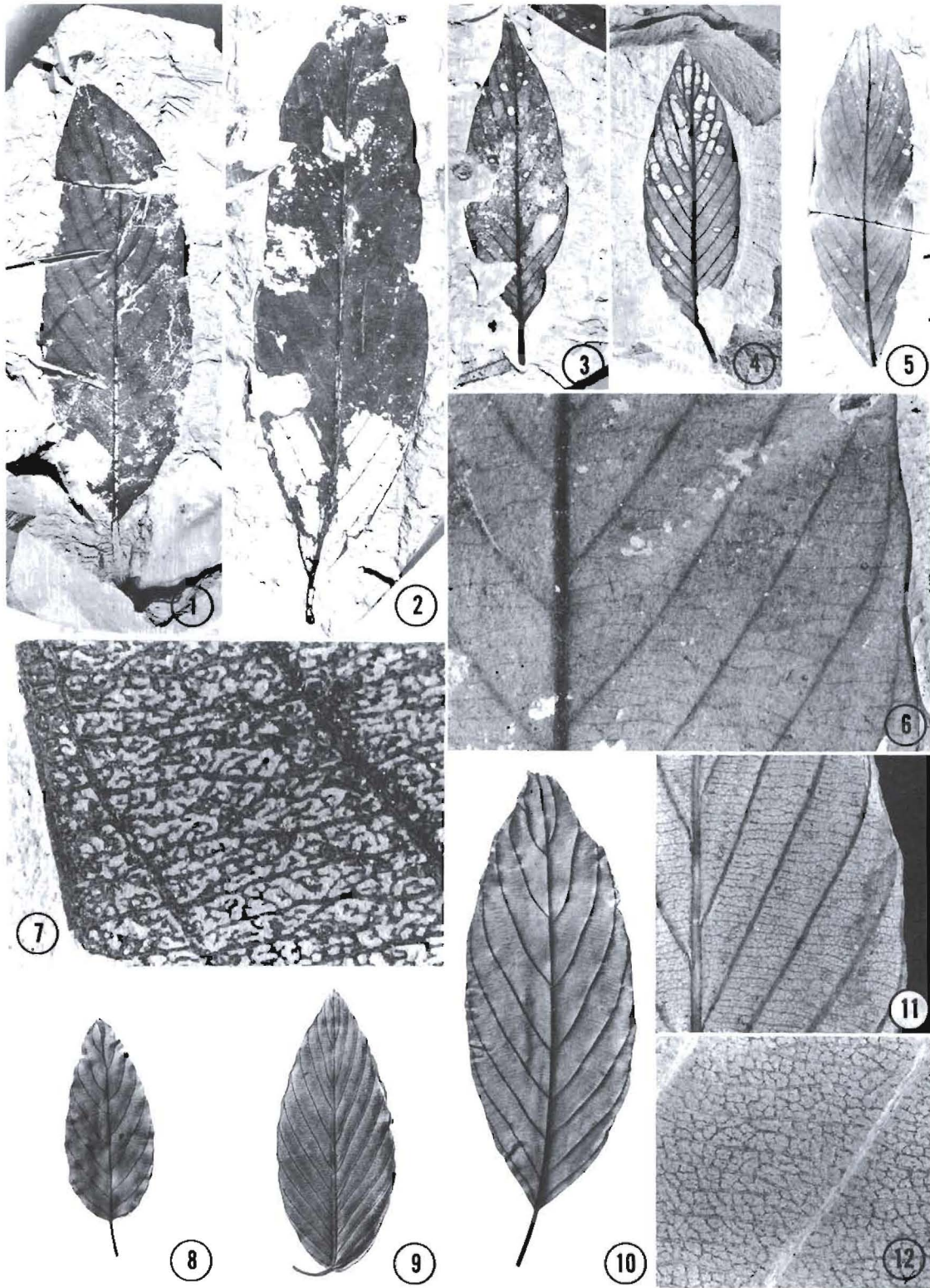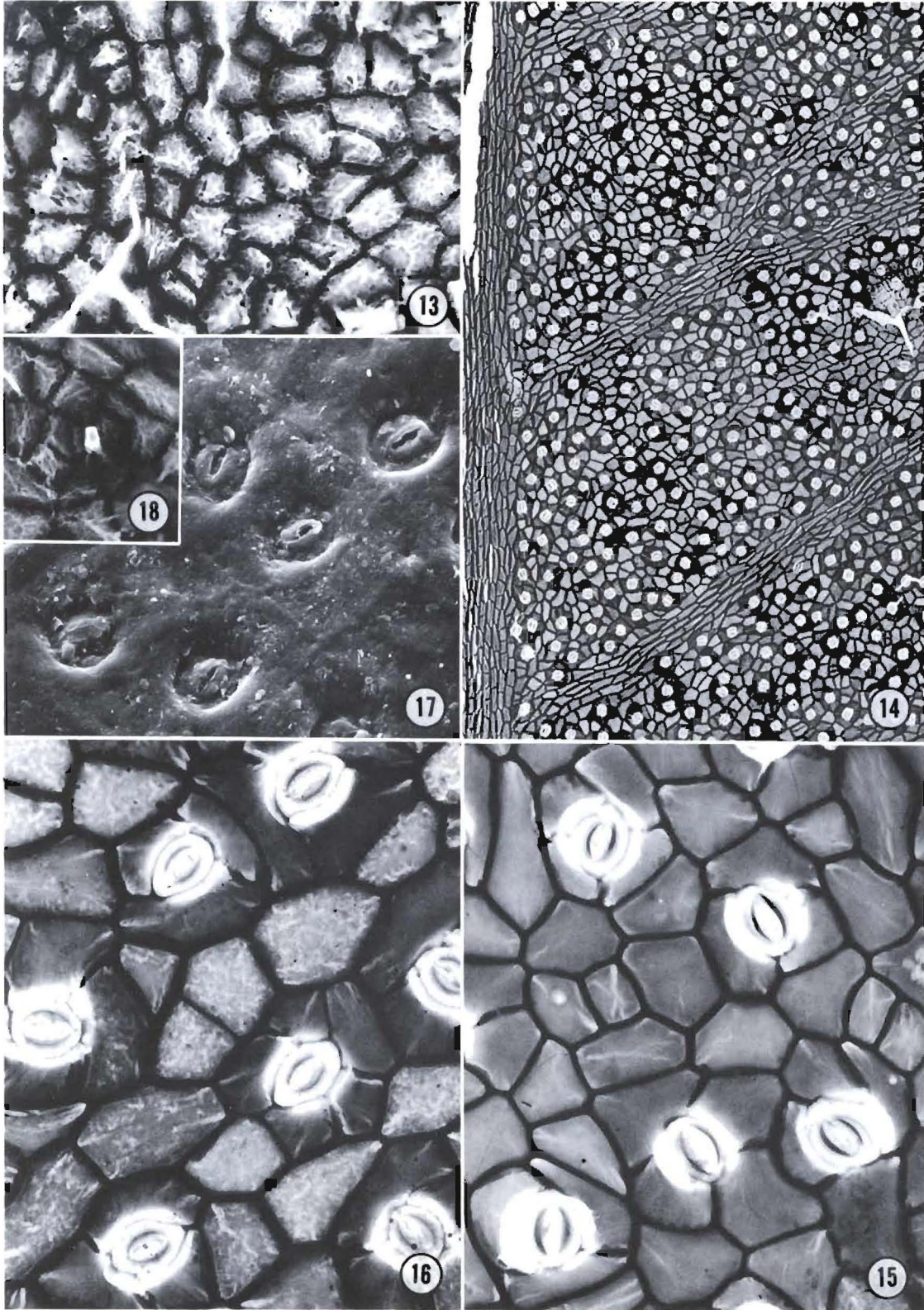
Some diversity exists among specimens of

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Fig. 1–12. 1–7. *Berhamniphyllum claibornense* gen. et sp. nov. 8–12. Extant members of the complex of genera within the tribe Zizypheae to which the fossil leaf type appears to belong. 1. Holotype. spec. P419 ×.94. 2. Paratype. P2023. ×.94. 3. Paratype. LK2966. ×.94. 4. Paratype. LK2967 ×.94. 5. Paratype. P2531. ×.94. 6. Portion of specimen L1968 showing the regularity of secondary and tertiary venation. ×5.6. 7. Portion of LK2952 showing higher order venation. ×11. 8. *Karwinskia calderoni* Standley. Note the similarity between this leaf, those of the fossil (Fig. 9, 10). spec. 2379. × 94. 9. *Berchemia scandens* (Hill) K. Koch. 2503. ×.94. 10. *Rhamnidium glabrum* Reissek. 3027. ×.94. 11. Portion of a *Berchemia formosana* C. K Schneider leaf showing fine venation and margin for comparison with Fig. 6. 2502. ×4.0. 12. Portion of a *Berchemia scandens* leaf showing fine venation for comparison with that shown in Fig. 7. 2370. ×6.6.

Fig. 13–18. *Berhamniphyllum claibornense* gen. et sp. nov. 13. Upper cuticle. P2536. ×470 14. Lower cuticle showing random arrangement of stomata over non-venous areas. The course of an underlying secondary vein and those of tertiary veins can be seen. P2530 ×61. 15. Lower cuticle showing stomatal complexes with normal staining characteristics P2542. ×470. 16. Lower cuticle showing stomatal complexes with darkly staining adjacent epidermal cells. P2530. ×470. 17. SEM micrograph of the outer surface of the lower cuticle. Note the slightly sunken stomata. P2530 ×470. 18. A trichome base on the upper cuticle. P2536. × 520.
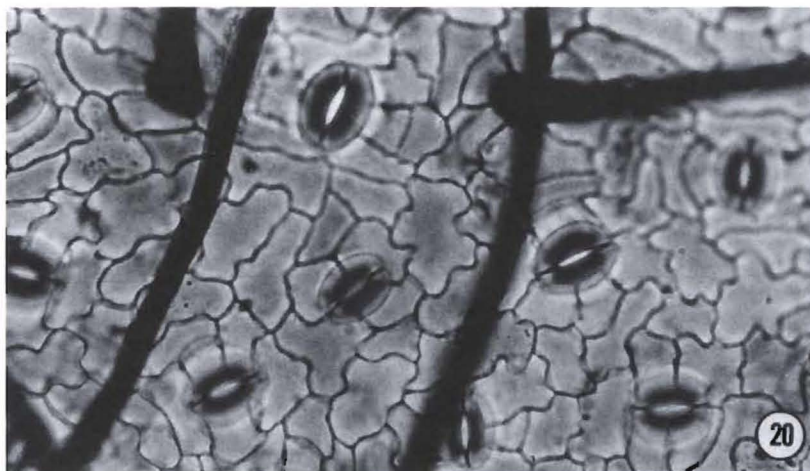
Fig. 19–24. 19. *Rhamnus californica* Eschsch. leaf showing prominent looping of secondary veins. 2387. ×.94 20. Lower cuticle of *Rhamnus carolinianus* Walt. 2365 ×470. 21. Lower cuticle of *Berchemia discolor* Hemsl. This cuticle as well as those in Fig. 22, 23 are from species of the complex to which the fossil belongs. 2369. ×470 22. Lower cuticle of *Berchemia floribunda* Brongn. 2963. ×470. 23. Lower cuticle of *Rhamnidium glabrum* 3027. ×470. 24. *Rhamnus carolinianus*. Note the presence of sporadic intersecondary veins, minute serations, marginal looping and tertiary veins with less regularity than those shown in Fig. 6–12. 3255. × 94.
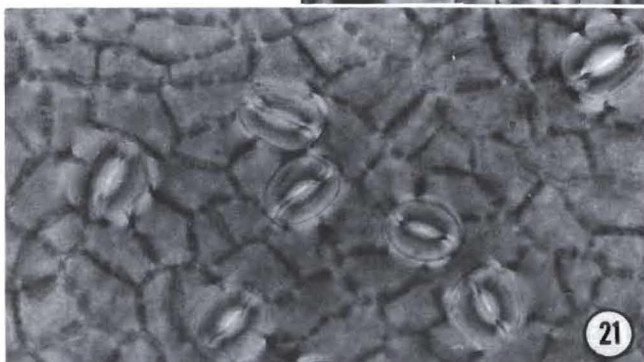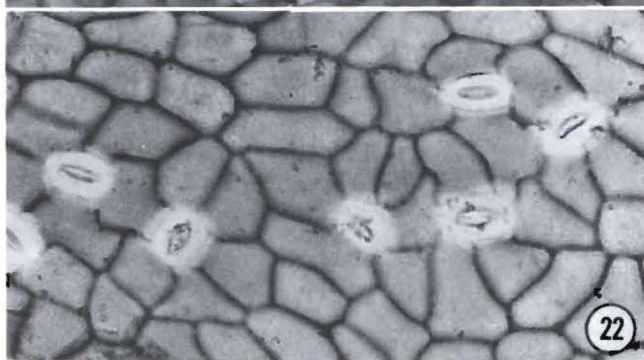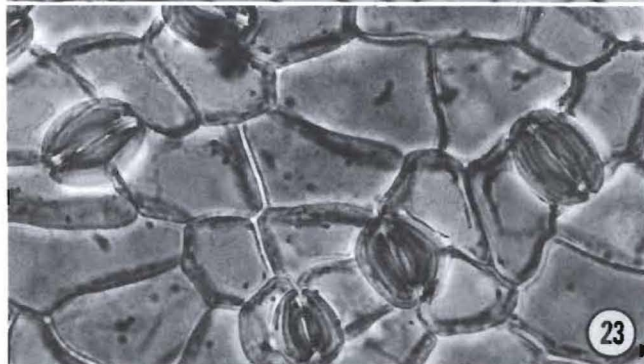
this leaf type. For example, the form of the leaf apex may vary from slightly mucronate (Fig. 3) to evenly tapered (Fig. 1). There may also be considerable variation in the relative size and shape of petioles (Fig. 2, 4). In addition, leaves from Lamkin clay pit tend to be smaller (avg. length 6.4 cm) and possess stronger tertiary and quaternary venation than those from other clay pits (avg. length 8.3 cm). Yet, intermediate forms exist which bridge all of these variants and thus distinct forms cannot be recognized. The cuticle of one well preserved specimen from Puryear clay pit has darkly staining "subsidiary cells" (Fig. 16) unlike those of other specimens (Fig. 15). No other cuticular or leaf architectural differences were apparent. This difference does not appear to be very important and may well be a function of preparation or preservation. Even though this fossil leaf type may represent more than one biological species or even genus it seems unwise to create separate taxa until various forms can be shown to be truly distinct.

Comparison with modern taxa—The fossil leaf possesses morphological and anatomical characteristics consistent with those found in extant Rhamnaceae. For instance, the Rhamnaceae bear only simple leaves, many of which possess entire margins (previously noted by Suessenguth, 1953), eucamptodromous venation, and percurrent tertiaries which are approximately perpendicular to the midrib. Like the fossil, most members of this family possess anomocytic stomatal complexes (previously noted by Metcalfe and Chalk, 1950). Leaves of several species of Rhamnaceae are glabrous and trichomes, when present, are commonly unicellular and almost invariably uniseriate, thus leaving trichome bases similar to those observed in the fossil material. In addition to these similarities the fossil leaves did not have any characteristic which would contraindicate assignment to the Rhamnaceae.

The fossil leaf type is not similar to those of any extant species in families closely related to the Rhamnaceae. A survey of the leaves of the Vitaceae and Celastraceae revealed no eucamptodromous leaves with the closely spaced percurrent tertiary veins characteristic of the fossil. These features are present in one genus of the distantly related Cornaceae. Many species of *Cornus* superficially resemble the fossil leaf in general form and venation. Species of *Cornus* and *Rhamnus* have often been confused in the fossil record (LaMotte, 1952). Closer examination, however, reveals important differences. Leaves of *Cornus* species tend to be broader and many have minutely erose margins. They possess vena-

tion which is more complex (some have 6° venation) and which exhibits considerable looping above the secondary level. The secondary veins are more broadly sweeping and usually arise only in the proximal two-thirds of the leaf. This leaves a very thin unbranching midrib in the distal third of the leaf. The tertiary veins are not quite as close and regular as those of the fossil. In addition to other cuticular differences, all nine species of *Cornus* examined have characteristic two-celled trichome "tufts" which leave bicellular bases that are not found in the fossil material. It is evident, then, that this fossil leaf is not a species of *Cornus* or other Cornaceae. These comparisons allow us to assign this fossil leaf type to the Rhamnaceae with reasonable confidence.

Although this leaf type can be assigned to the Rhamnaceae it is difficult to support assignment to the genus *Rhamnus* L. In contrast to the fossil material, some extant species of *Rhamnus* have brochidodromous venation and most species which have eucamptodromous venation exhibit considerable looping (Fig. 19). Few *Rhamnus* species have closely spaced tertiary veins and when present they lack the regularity characteristic of the fossil. The venation is also more complex in members of this genus. Most possess sixth order venation or higher. The leaves of nearly all species of *Rhamnus* including *Rhamnus carolinianus* Walt., a species which Lesquereux (1860, 1869) maintained was closely related if not identical to the fossil, have teeth (Fig. 24). This species also differs from the fossil in leaf shape and the presence of numerous uniseriate trichomes, stomatal complexes with 4–7 adjacent epidermal cells and considerable variability in stomatal size (Fig. 20).

The fossil seems to be more closely allied to a group of genera in the tribe Zizypheae. In fact, it is almost identical to certain species in the genera *Aurodendron* Urban, *Berchemia* Necker, *Chaydaia* Pitard, *Karwinskia* Zuccarini and *Rhamnidium* Reissek. Species such as *Aurodendron jamaicense* Urban, *Berchemia scandens* (Hill) K. Koch, *Chaydaia bercheiniaefolia* Makino, *Karwinskia calderonii* Standley and *Rhamnidium glabrum* Reissek possess the "pure" eucamptodromous character and closely spaced tertiaries found in the fossil (Fig. 8–10). Most species of *Aurodendron, Chaydaia* and *Karwinskia* differ from the fossil in that their quaternary venation is well developed and in the case of *Chaydaia* may even possess fifth order venation. In addition, species of *Karwinskia* and *Aurodendron* as well as a few species of *Berchemia* have papillate lower cuticles. The most similar extant species were found in the genera *Rhamnidium*

and *Berchemia*. Even these species exhibit cuticular differences and thus no identical modern counterpart was found (Fig. 21–23). These differences are minor and well within the limits of interspecific variation observed in various genera of this complex. Therefore it is quite possible that the fossil represents a species of *Berchemia, Rhamnidium* or some other extant or extinct genus in this complex. Yet, it is impossible to assign this fossil to any specific genus on the basis of leaf characteristics alone. Additional vegetative information, such as leaf arrangement and reproductive materials, would be required before such an assignment could be made.

Systematics—Although the fossil material under investigation certainly fits Lesquereux's (1860, 1869) vague description of *Rhamnus marginatus*, its leaf architecture and cuticular anatomy clearly show that it does not belong in the genus *Rhamnus* and therefore must be removed from this taxon. Because Lesquereux's description of *Rhamnus marginatus* is broad and surely encompasses many true *Rhamnus* leaf forms, we suggest that this taxon be retained for those leaf forms which possess leaf architectural and cuticular anatomies consistent with those found in modern members of this genus. Those assigning leaf forms to *Rhamnus marginatus* should emend the diagnosis of this species to reflect the foliar characteristics found in modern *Rhamnus*. A new type specimen also must be designated because the original figured specimen (plate 6; figure 2; Lesquereux, 1860) has been lost.

Since the leaf material under investigation could not be placed in the genus *Rhamnus*, it was necessary to transfer it to a more appropriate genus. Three alternatives were considered. The first was to assign the leaf type to an extant genus in the aforementioned complex of genera in the tribe Zizypheae. As mentioned above, these genera contain representatives with extremely similar leaf morphologies thus making assignments on the basis of leaf characters alone impossible. Therefore, any assignment of this leaf type to one of these modern genera would be tenuous at best. A second option was to assign this leaf type to a previously established fossil genus. The genus *Rhamnites* Forbes seemed to be a likely alternative because Bell (1949) had tacitly transferred the species *Rhamnus marginatus* to this genus, a judgement which LaMotte (1952) accepted. However, the genus was not validly published by Forbes (1851), as suggested by LaMotte (1952) and Andrews (1970), because neither a description nor analysis of figures was presented. The figures (Forbes, 1851) also re-

vealed differences in tertiary venation and other important characteristics when compared to the material under investigation. It is apparent, from more recent literature (Ball, 1931; Bell, 1949; Berry, 1916) that *Rhamnites* has been used as a catchall for those leaf forms which are thought to have rhamnaceous affinities but cannot be associated with any extant genus. This is in spite of the fact that the generic description is tied to that of the type species, apparently *Rhamnites concinnus* Newberry (1868), until a separate emended generic diagnosis is published. A similar problem exists with the genus *Rhamnophyllum* Weyland (1943). Weyland was apparently the first to use the generic name *Rhamnophyllum* (cf. Andrews, 1970) when he transferred the species *Pomaderris lanuginosa* Weber to this genus. Because no separate generic description was included, this genus too is defined by the description of the type species, *Rhamnophyllum lanuginosum* (Weber) Weyland. This generitype is characterized by acrodromous venation similar to that encountered in *Ceanothus*, thus preventing the inclusion of our material in the genus *Rhamnophyllum* without emending the generic description. Emending the diagnoses of either *Rhamnites* or *Rhamnophyllum* would effect the disposition of a large number of leaf forms and present many nomenclatural and taxonomic problems. The third alternative is to establish a new fossil genus to contain this and similar leaf forms. We therefore propose the genus *Berhamniphyllum* for leaf types with foliar morphologies similar to the closely related forms found among the aforementioned complex of extant genera in the tribe Zizypheae. The description of the genus is intended to be broad enough to accomodate related leaf forms yet narrow enough to restrict assignment to members of this complex.

Family: Rhamnaceae
  Tribe: Zizypheae
    Genus: **Berhamniphyllum** Jones and Dilcher gen. nov.

Generic diagnosis: Leaves, simple, symmetrical or slightly asymmetrical; margin, entire or slightly crenate; petiole shape, normal (sensu Dilcher, 1974); venation, eucamptodrome without significant marginal looping; midrib moderately thick to stout, straight or slightly curved; secondary veins, moderately thick, sweeping to the margins, branched or unbranched; tertiary veins, at approximate right angles to the midrib, closely spaced, straight, occasionally branched; highest order of venation, fourth rarely fifth; trichomes, ab-

sent or when present, always uniseriate and usually unicellular; stomatal complex, anomocytic with 3–7 adjacent epidermal cells, restricted to ahaxial surfaces.

Type species: *Berhamniphyllum* **claibornense** Jones and Dilcher sp. nov. Fig. 1–11.

Species diagnosis: Leaves, symmetrical, elliptical or narrowly elliptical; apex and base, acute; venation, eucamptodrome, without any visible marginal looping; midrib, moderately thick; secondary veins, unbranched or very rarely branched; highest order of venation, fourth; areolation, poor; ultimate marginal venation, fimbriate; stomatal complex, anomocytic with 3–5 adjacent epidermal cells; trichomes absent or rare with unicellular bases surrounded hy slightly smaller and somewhat radially modified epidermal cells.

Holotype: Specimen and cuticle slides labeled P419 in the Paleontological Collection, Department of Geology, Indiana University.

Paratypes: Specimens and cuticle slides labeled P2024, P2530, P2531, LK2965, LK2966 and LK2967 in the above collection.

Etymology: The generic name *Berhamniphyllum* was chosen to indicate the similarity between the fossil and members of the genera *Berchemia* and *Rhamnidium*. The specific epithet *claibornense* was derived from the formation from which the leaf type was collected.

Synonymy and exclusions: Most specimens previously assigned to *Rhamnus marginatus* do not conform to the diagnosis of *Berhamniphyllum claibornense* and thus are excluded from this taxon. The only available specimen of *Rhamnus marginatus* identified by Lesquereux (1860; pl. 22, fig. 4; U.S.N.M. 36489) cannot be placed in this taxon. This specimen lacks both tertiary venation and cuticle, yet the presence of a very stout midrib and a broader leaf form clearly differentiates this leaf from those of the new species. The specimen (U.S.N.M. 35834) illustrated in pl. 71, fig. 4 of Berry (1916) is larger, has more broadly spaced secondaries which do not sweep uniformly to the margin and bears tertiary veins which are not as closely spaced and regular as those of the new species. Therefore, this specimen also must be excluded from this taxon. Specimens of *Rhamnites marginatus* (Lesquereux) Bell (1949) and *Cornus rhamnifolia* Penhallow (1902), two species considered synonymous with *Rhamnus marginatus* (LaMotte, 1952) also differ from those of the new species. These

specimens exhibit considerable looping near the margin, irregular tertiary veins and weak secondary veins. A brochidodromous leaf form assigned to *Rhamnus marginatus* (Hollick, 1936) obviously does not belong in *Berhamniphyllum claibornense*. Wolfe (1977) recently transferred this leaf type to the genus *Knema* Loure of the Myristicaceae. Further work is necessary for the precise and accurate disposition of the remaining excluded materials.

A few specimens appear, from all information available, to belong to the new genus. Berry's (1916; pl. 72, fig. 1) specimen of *Rhamnus marginatus* (U.S.N.M. 35832) from the Eocene of Mississippi lacks cuticle and is preserved in an ironstone matrix which seems to have provided more three-dimensionality than the Claiborne clays. Yet, the fine venation and all other features of this specimen lead us to believe that it belongs in *Berhamniphyllum claibornense*. Specimens assigned to *Rhamnus marginatus* by Ball (1931) and Sandborn (1935) also appear to belong to the new species. Ball's (1931) figured specimen (pl. 16, fig. 4) of *Rhamnus eolignicious* Berry closely resembles those of *Berhamniphyllum claibornense* as well and certainly does not represent the former species. In addition, some leaf types previously assigned to morphologically similar taxa, such as the obviously composite species *Berchemia multinervis* Heer, probably fit the diagnosis of *Berhamniphyllum*. Thorough examination of these leaf types is beyond the scope of this investigation.

CONCLUSION—Detailed leaf architectural and cuticular analyses have shown Berry's (1916) taxonomic treatment of this leaf type to be in error. The fossil belongs to the tribe Zizypheae rather than to the genus *Rhamnus* or other Rhamneae. The leaf type most closely resembles species of *Berchemia* and *Rhamnidium* but can be restricted only to a complex of genera within the Zizypheae. Even though the Rhamnaceae is noted for the taxonomic utility of its foliar characteristics (Weberbauer, 1896; Wolf, 1938), limitations iuvolved when working with leaf material alone prevent assignment to any specific genus within this complex. Because the leaf type cannot be placed in any extant genus and no suitable "fossil" genus could be found we have established the genus *Berhamniphyllum* and species *Berhamniphyllum claibornense* to accommodate this material.

The presence of *Berhamniphyllum claibornense* in the Claiborne Formation confirms earlier indications (Suessenguth, 1953) that the tribe Zizypheae and, perhaps, extant genera within this tribe had evolved by the Middle

Eocene. Apparently valid reports of species of *Zizyphus* Miller and *Paliurus* Miller (Berry, 1916; Suessenguth, 1953) from the early Tertiary further indicate that evolution of acrodromous and camptodromous veined leaves had occurred within the Zizypheae by this time.

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