

EARLIEST MEGAFOSSIL EVIDENCE OF FAGACEAE: PHYLOGENETIC AND BIOGEOGRAPHIC IMPLICATIONS¹

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ABSTRACT

Fossil evidence of Fagaceae from the Paleocene/Eocene boundary of western Tennessee is described and discussed. These fossils include a newly discovered pistillate inflorescence and dispersed fruits of subfamily Castaneoideae as well as a taxon that resembles modern trigonobalanoids (pistillate inflorescences and dispersed mature fruits). Fossil staminate catkins with fagaceous pollen, which we suggest may be conspecific with the trigonobalanoid infructescences, are also found at the locality. Two distinct types of fagaceous leaves are present at the locality. The reproductive structures are the oldest megafossils unequivocally assignable to Fagaceae and represent the oldest remains of subfamily Fagoideae and the oldest megafossil remains of Castaneoideae. In addition, the fossils provide insights into the chronology of diversification, biogeography, and phylogeny of Fagaceae. The trigonobalanoid remains may also provide insights into the timing and circumstances of the evolution of wind pollination in Fagaceae.

THE OAK FAMILY (Fagaceae) includes nine genera and approximately 700–800 species, which we place in two subfamilies, Fagoideae and Castaneoideae. This classification is based on phylogenetic analyses and differs somewhat from previous subfamilial and generic classifications of the family. We include the following genera in subfamily Fagoideae: *Trigonobalanus* Forman, *Colombobalanus* Nixon & Crepet, *Formanodendron* Nixon & Crepet, *Fagus* L. (the beeches), and *Quercus* L. (the oaks). In subfamily Castaneoideae we place *Castanea* Miller (the chestnuts), *Castanopsis*, *Chrysolepis* Helmquist (western chinkapin), and *Lithocarpus* Blume. *Nothofagus* is excluded from Fagaceae on the basis of phylogenetic analyses of numerous characters (Nixon, 1982; Nixon and Crepet, 1985).

Fagaceae *sensu stricto* are predominantly Northern Hemisphere in distribution (e.g., Trelease, 1924; Soepadmo, 1972). Within Fagaceae, members of subfamily Castaneoideae retain several plesiomorphic characters and, of the modern Fagaceae, probably most closely approximate the ancestral fagaceous stock (Nixon and Crepet, 1985). Castaneoids are apparently all entomophilous, while, with the exception of *Trigonobalanus*, all Fagoideae are

anemophilous. Modern castaneoids are most diverse in eastern Asia and Malaysia.

Based on phylogenetic analyses, we have segregated 2 genera, *Colombobalanus* and *Formanodendron*, from *Trigonobalanus* (Nixon and Crepet, 1989). These three monotypic genera are clearly paraphyletic and do not share any derived characters by which they can be united into a monophyletic group. In our discussions below, we will refer to these three modern genera as “trigonobalanoid” when discussing character states shared by the three species. The three modern trigonobalanoids are probably relics of a larger extinct group that is transitional between the insect-pollinated castaneoids and the wind-pollinated oaks and beeches and, therefore, is basal within subfamily Fagoideae (Nixon and Crepet, 1989). The trigonobalanoids have a distinct distribution within Fagaceae. *Trigonobalanus* is found in Borneo, Sumatra, Celebes, and on the Malay peninsula, while *Formanodendron* is restricted to Thailand and nearby China (Forman, 1964; Soepadmo, 1972). The most recently discovered trigonobalanoid, *Colombobalanus*, is restricted to Colombia, South America (Lozano-C, Hernandez-Camacho, and Henao-S, 1979). In addition to lacking any clear synapomorphies, the paraphyletic nature of the trigonobalanoids is supported by the fact that *Trigonobalanus* has been described as probably entomophilous (Soepadmo, 1972), as are the castaneoids, while *Colombobalanus* and *Formanodendron* have floral and inflorescence morphology indicative of anemophily (Forman, 1964; Lozano-C et al., 1979).

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CLADOGRAM

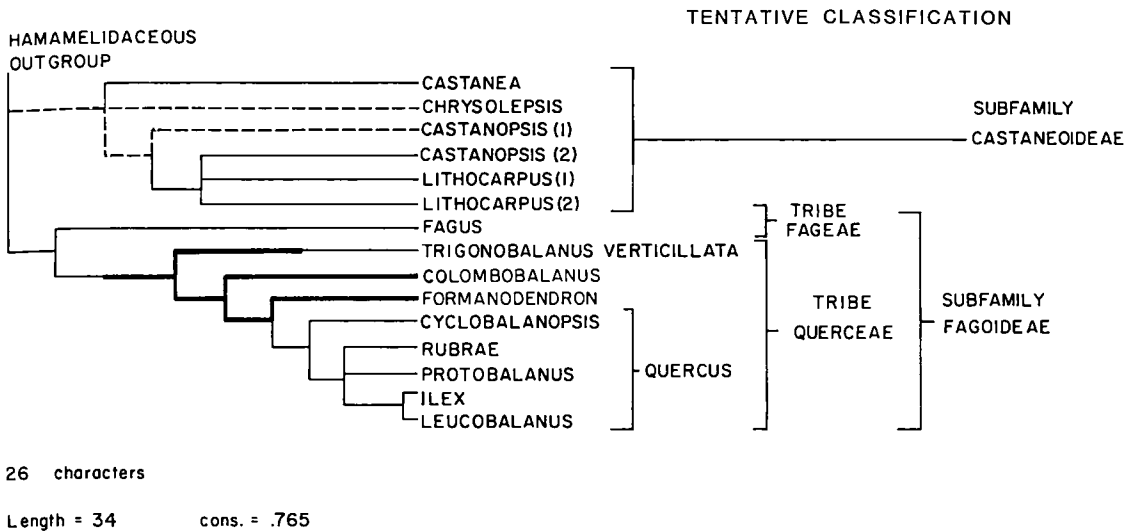


FIGURE 1

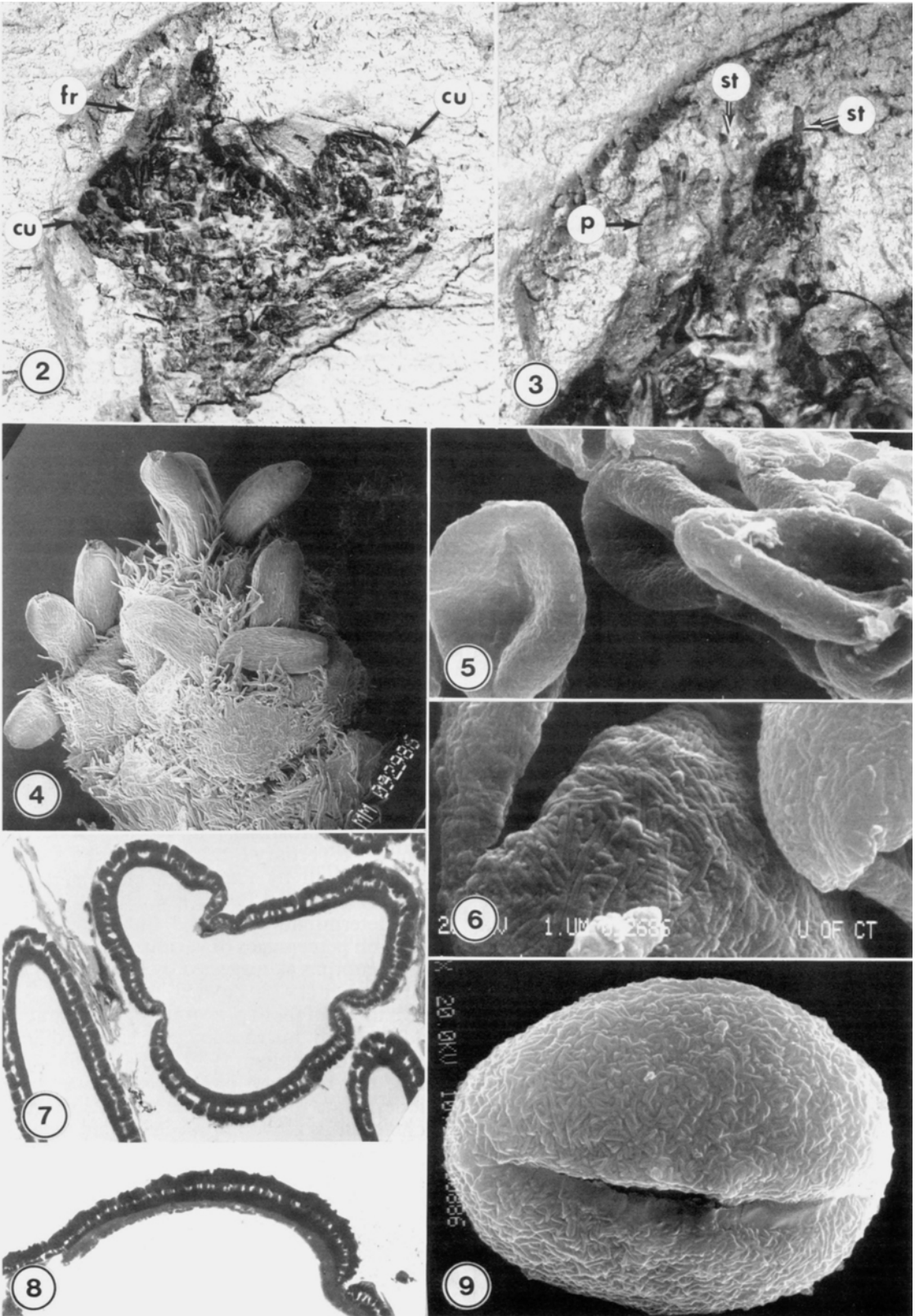
Fig. 1. Strict consensus cladogram of Fagaceae sensu stricto. The tree presented was derived from the two shortest cladograms of a parsimony analysis of 25 characters, each with a length of 33 steps (consistency = 0.81); regions of the cladogram with which each of the pistillate fossils matches (patristic distance of 0 for all available characters) are shown. The region of the cladogram matching *Castanopsoidea* is shown in broken lines; the region matching *Trigonobalanoidea* is shown by heavy lines. The classification presented is tentative.

The analysis of contemporary biogeographical patterns, understanding character state polarities through transitional extinct types, and establishment of minimal times of divergence between clades are all valuable applications of fossil data. Within Fagaceae, questions regarding the origin of wind pollination, the origins of major taxonomic groups, and biogeography of genera are of particular interest. The newly discovered fossils described and evaluated below in a phylogenetic context contribute to understanding these questions.

MATERIALS AND METHODS—The fagaceous fossils described here are from a Paleocene/Eocene plant fossil locality near Buchanan, in western Tennessee. This locality, like the other Tertiary western Tennessee localities, was associated with a deltaic system. Microfossil data suggest that the locality represents a depositional environment with brackish water and thus, that it was relatively close to the Gulf of Mexico (Zavada, in progress). The flora associated with the fagaceous fossils considered here included diverse legumes of the subfamilies Mimosoideae and Papilionoideae (Crepet and

Taylor, 1985, 1986); at least two tribes of Euphorbiaceae (in progress); Juglandaceae; Palmae (Feldman, in progress); and Philadelphaceae (in progress). The geology of western Tennessee Tertiary localities has been considered in detail by Parks (1971), Russell and Parks (1975), and Potter and Dilcher (1980). Age determination for the Buchanan site is based on percentages of various juglandaceous palynomorphs as suggested by Frederiksen and Christopher (1978; Zavada, in progress).

Methods of fossil preparation, photography, and electron microscopy are standard (e.g., Crepet and Daghljan, 1980). Less standard perhaps, has been the integration of fossil and modern data in the cladistic analysis of a particular family. Two approaches were taken in analyzing the phylogenetic significance of the fossils. First, a cladogram was constructed for extant genera of Fagaceae using parsimony (PAUP) and polarizing characters on the basis of outgroup comparison with Hamamelidaceae. The available character states of each fossil were compared with the character state combinations of terminal taxa and nodes (hypothetical ancestors) of the cladogram (Fig. 1).



Second, fossils were included as terminal taxa in a parsimony analysis with the modern taxa.

RESULTS—The new fossils include dispersed pollen, fruits, pistillate inflorescences, infructescences, and staminate catkins. Only leaves of Fagaceae from Buchanan have been previously mentioned (Jones, 1984, 1986). Dispersed pollen and leaves are common in the sediments, but one of the two leaf types is relatively uncommon. Heretofore undescribed dispersed pollen was studied by the preparation of mounts for SEM and light slides from macerated sediment. Ten examples of young infructescences of a trigonobalanoid and one partial pistillate inflorescence of a castaneoid have been collected. Collections also include several examples of apparently mature cupules of the castaneoid taxon and about one dozen dispersed trigonobalanoid fruits. Most trigonobalanoid fruits are preserved without cupules, but several examples of fruits preserved within their cupules have also been discovered. Castaneoid staminate catkins have not been collected from the locality although unequivocal castaneoid pollen is common in the dispersed pollen flora and is known from the staminodes of the castaneoid pistillate inflorescence. Three examples of one type of fagaceous staminate catkin have been collected from the locality and these are considered representative of a trigonobalanoid taxon for reasons discussed below.

In summary, there are two types of pistillate inflorescences, two types of dispersed mature fruits, two types of pollen (dispersed and in various inflorescences), one type of staminate catkin and two types of putatively fagaceous leaves known from the Buchanan locality. We are interpreting the aggregate pistillate and fruit remains as representing two discrete fagaceous taxa, one castaneoid and one trigonobalanoid,

that existed in the immediate vicinity of the depositional environment. We place the staminate catkin in a separate genus and species, but suggest that it is conspecific with the trigonobalanoid pistillate remains. Such an interpretation is consistent with all available data.

Castaneoid remains—The fossil immature pistillate partial infructescence (inflorescence) of the castaneoid has a key synapomorphic character syndrome of Fagaceae, the cupule-fruit complex. It is apparently a dichasium, part of a larger infructescence, of scaly cupules each bearing three young fruits with stylopodium-perianth complexes at the apices (Fig. 2). Each immature fruit bears three styles (Fig. 3). Styles are linear, ca. 2 mm in length, and without a clearly expanded stigmatic area. Darkened areas at the tips of some styles are suggestive of punctate stigmatic surfaces (Fig. 3). Reduced stamens are represented by amorphous masses of pollen (presumed staminodia) preserved within the perianth. The pollen grains are castaneoid in size, shape, micromorphology and ultrastructure as illustrated by SEM and TEM (Fig. 5–9).

Pollen morphology and style and stigma characters are among the most important features used to delimit groups within Fagaceae (e.g., Crepet and Daghljan, 1980; Solomon, 1983a, b; Nixon and Crepet, 1985). On the basis of these characters this fossil is clearly castaneoid in its affinities. Of modern castaneoid genera, the fossil is most similar to Asian species of *Castanopsis* with three fruits/cupule (Fig. 4). The fossil differs from *Lithocarpus* species; these always have a single fruit in each cupule. The fossil is also different from *Castanea* and *Chrysolepis* which have relatively long styles and fruits that are almost completely enclosed by the cupules. In addition, *Castanea* differs in having six styles per pistil as opposed to three in the fossil. Staminodia are

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Fig. 2–9. 2. Overall view of young pistillate infructescence of *Castanopsoidea* showing at least two cupules (cu) and the distal ends of the three fruits and their stylopodia enclosed by one of the cupules (fr) UCPC B627a. $\times 5$. 3. A higher magnification view of the immature fruits showing the stylopodium perianth complex of one young fruit with a perianth (p) and three protruding styles. Styles (st) and other parts of the stylopodium-perianth complexes of the other two fruits enclosed by the cupule may also be observed. UCPC B627a. $\times 12$. 4. Three pistillate florets and a subtending cupule of *Castanopsis microphylla*. Note the three styles/floret and their similarity in shape to those of the fossil (Fig. 3). $\times 52$. Fig. 5–7. Pollen isolated from staminodea of UCPC B627b. 5. SEM of pollen illustrating its prolate nature and size. $\times 3,400$. 6. SEM closeup of the surface illustrating the fused-vermiform exine micromorphology. $\times 11,500$. 7. TEM illustrating the triaperturate nature of the pollen and the thick footlayer relative to tectum. Note the well preserved tapetal membranes between adjacent grains and the sparsely preserved endexine. $\times 6,500$. Fig. 8, 9. Pollen of extant *Castanopsis stipitata* (Bogle & Bogle 620, GH) for comparison with the fossil pollen. 8. TEM showing wall structure and footlayer/tectum ratio similar to the pollen of *Castanopsoidea*. $\times 5,300$. 9. Overall SEM of a single grain illustrating its shape and the fused vermiform exine micromorphology. $\times 4,550$.

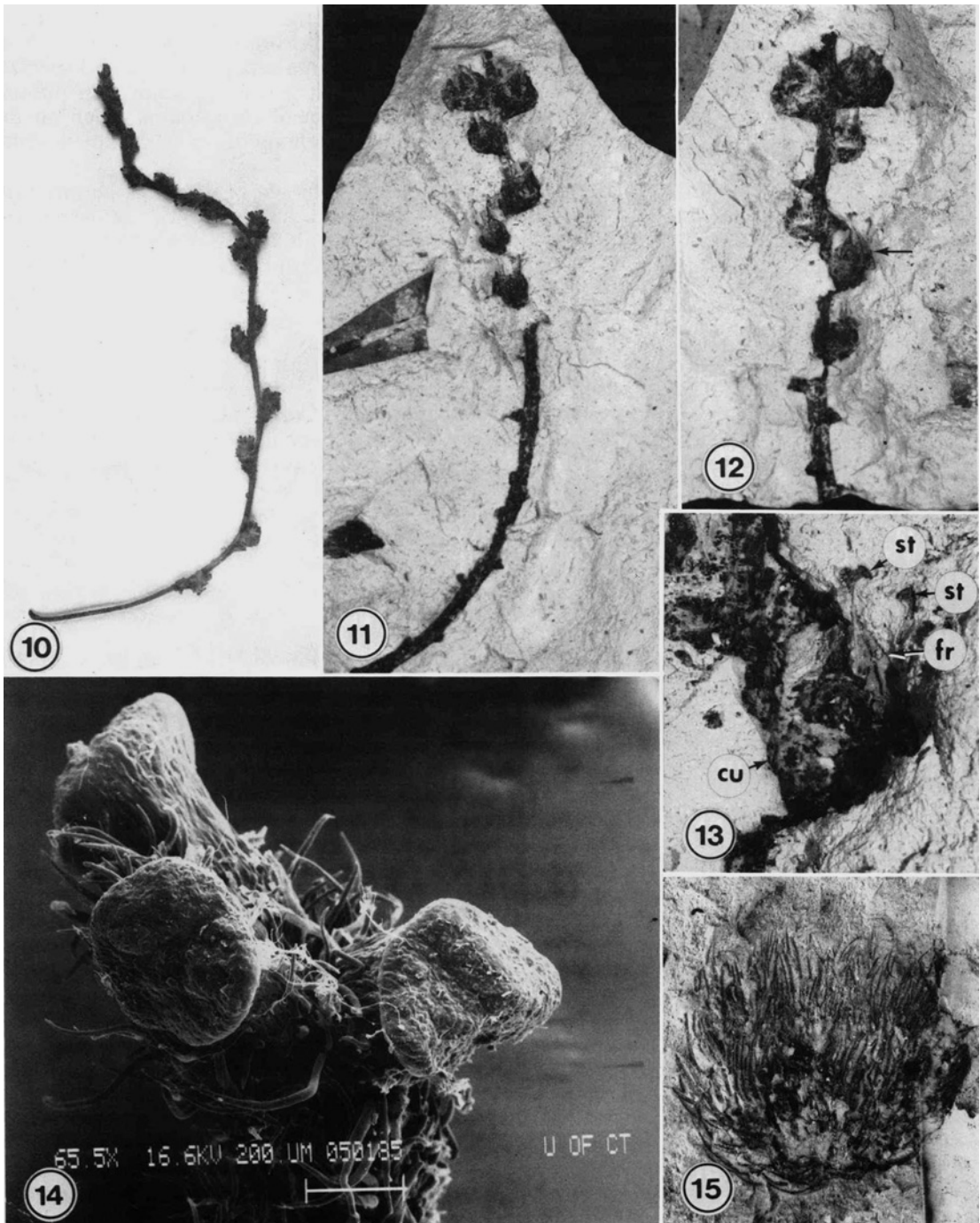


Fig. 10–15. 10. Pistillate inflorescence of *Formanodendron doichangensis* (J. F. Rock 1030274, MO) showing the alternately arranged cupules with protruding stigmas. $\times 1.2$. Fig. 11–13. Pistillate inflorescence/inflorescence of *Trigonobalanoidea*. 11. Overall view of the inflorescence showing the alternately arranged cupules and undeveloped (unfertilized?) proximal florets. UCPC B672a. $\times 1.66$. 12. Slightly higher magnification view of the counterpart (UCPC B672b) showing one cupule (arrow) with protruding young fruits that retain their styles and stigmas. $\times 2.1$. 13. A higher magnification view of the cupule (cu) illustrated in Fig. 12 showing one fruit (fr) compressed with an elongate depression in the center indicative of its triangular cross-sectional configuration in life. Note the styles and the capitate/discoid stigmas (st) of the same fruit. One style and stigma of another fruit enclosed by the same cupule is also evident in the figure (st). $\times 6.5$. 14. SEM view of the styles and capitate/discoid stigmas of a pistillate floret of modern *Trigonobalanus verticillata* (M. D. Poole 1106337, US). Note that the three styles converge proximally as is apparently the case in the fossil fruit illustrated in Fig. 13. $\times 65.5$. 15. Presumably ripe cupule of *Castanopsioidea* showing the external cupule spines. UCPC B849. $\times 2$.

typical of pistillate flowers of all modern genera of Castaneoideae and therefore are not diagnostic at the generic level.

Based on the characters used in the cladistic analyses, the fossil has affinities with the genera *Castanopsis* and *Chrysolepis* or the common ancestor of these genera (Fig. 1). The addition of phenetic characters (i.e., style and valve length) not used in the cladistic analyses suggest that the fossil is actually more similar to modern *Castanopsis* than to modern species of *Chrysolepis*.

Several apparently mature castaneoid cupules are known from the Buchanan locality. These are obscurely lobed, consistent with their representing mature cupules of the same taxon as the younger pistillate infructescence (Fig. 15). The ripe cupules have elongate spines externally suggesting that if these fruits indeed represent the same taxon as the younger infructescence, the spines on the cupule developed late and elongated considerably during maturation, as in modern *Castanea*, *Castanopsis*, and *Chrysolepis* (Fey and Endress, 1983).

Trigonobalanoid remains—A second fagaceous taxon from Buchanan is represented by various fossilized organs. As mentioned above, with the exception of staminate catkins, two sets of fagaceous fossils occur at the locality—one set considered castaneoid (discussed above) and one that is clearly trigonobalanoid. Furthermore, two and only two types of fagaceous pollen occur in the dispersed pollen flora. The locality has been intensively collected for over eight years and dispersed pollen samples have been extensively (10 hr \times 10 preparations) examined with scanning electron microscopy. We propose to include the aggregate remains in the description of three genera and species, which we place in subfamilies Castaneoideae and Fagoideae. However, we favor the interpretation that the staminate catkin described here is conspecific with the trigonobalanoid infructescences and fruits.

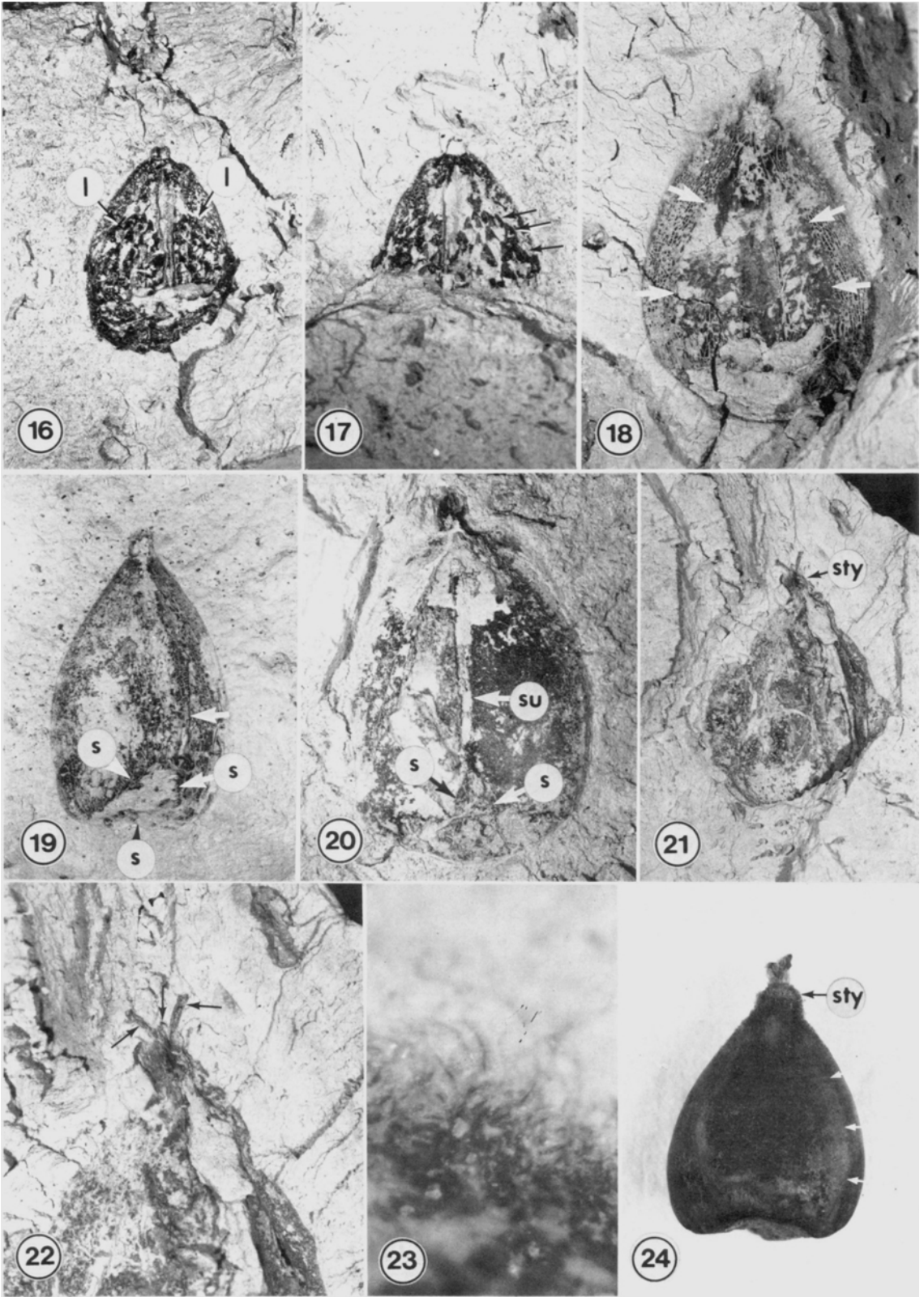
Infructescences—Approximately 10 fossils of trigonobalanoid infructescences consist of a straight to slightly curved main axis with several lateral, alternately arranged, scaly cupules each with three trigonous fruits (Fig. 11, 12). Scales are indistinct but appear to be oriented in transverse rows. Styles and stigmas are well-preserved and stigmas are capitate-discoid (Fig. 13). The suite of characters embodied in these fossils unequivocally indicates affinities with subfamily Fagoideae and, in particular (trigonous fruits + capitate/discoid stigmas), members of the modern trigonobalanoid genera (Fig.

10–14). Other fagoidean genera have character combinations that are not found in the fossil. *Fagus* differs from the fossil by lacking 3-fruit-ed, open cupules and its cupules are solitary and terminal on short stalks in the leaf axils. *Fagus* also differs in having elongate styles with decurrent stigmatic surfaces. *Quercus* is distinguished from the fossil by the single rounded fruit in each evalvate cupule. These fossils are most similar to *Formanodendron doichangensis* (Fig. 10) and *Colombobalanus excelsa* on the basis of the alternate cupule arrangement. They are also similar to these two modern species in having winged fruits. In contrast, *Trigonobalanus verticillata* typically has oppositely arranged cupules and wingless fruits.

Dispersed fruits—Fruits were typically dispersed without cupules (Fig. 18–22). They are rounded-triangular in lateral aspect and triangular in cross section (Fig. 18–21). At the angles, fruits have prominent wings up to 3 mm in width (Fig. 18). Dispersed fruits are frequently preserved as though the suture at the angle had opened (Fig. 16, 17, 20, 21). This phenomenon can also be observed in dried fruits of modern trigonobalanoids (Fig. 25). The ovary is inferior with a perigon terminating the apex (Fig. 16–22) and styles are occasionally preserved. There are three styles per ovary that expand into terminal, capitate, presumably stigmatic areas (Fig. 21, 22). A final notable feature of fruits dispersed without their cupules is the pronounced triangular attachment scar (Fig. 19, 20), also seen in modern trigonobalanoids and *Fagus*.

Several dispersed fruits have been preserved within the cupules. One has a single fruit enclosed by the cupule (Fig. 16, 17), but specimens with up to three fruits/cupule have also been collected (Fig. 26). Such variation is typical of modern trigonobalanoids that commonly have from 1 to 7 fruits per cupule in different parts of the same infructescence of a single individual. The cupule is lobed and extends ca. $\frac{2}{3}$ of the height of the fruit (Fig. 16). Cupule scales are flattened, tongue-shaped, and arranged in transverse rows (Fig. 17). Both the fruit and the cupule scales have an indument of elongate hairs (Fig. 23). The scaly cupule subtending 1–3 triangular fruits, inferior ovaries of three carpels, and capitate stigmas is a combination of characters restricted to Fagaceae and, more specifically, to the three trigonobalanoid genera within the family (Fig. 24, 25).

Based solely on characters used for the cladistic analysis, the fossil pistillate trigonobalanoid is consistent with all three modern trigonobalanoid species. However, the alternate



arrangement of cupules and the presence of wings on the margins of the fruits in the fossil suggest a closer affinity to *Formanodendron* and *Colombobalanus* than to *Trigonobalanus*.

Staminate catkins—Dispersed staminate catkins are interpreted as probably conspecific with pistillate inflorescences and dispersed fruits described above, but no specimens are known that have both staminate and pistillate parts attached. Because the combination of characters limits the affinities of these fossils to Fagaceae and there are no other staminate remains or dispersed pollen at the locality that might represent catkins of the trigonobalanoid taxon, this interpretation is probably correct. However, we take a conservative approach and, therefore, name the staminate catkin as a separate genus and species of subfamily Fagoideae.

The catkins have delicate axes, ca. 1 mm in diameter and are sinuously preserved, and thus, they were probably lax in life. Catkins are found in a mature expanded condition with discrete clusters (probable dichasia), of about three florets each (Fig. 28), or are preserved with the florets crowded together suggesting that they were unexpanded and not fully mature at the time of deposition (Fig. 27). The florets are tiny (1 mm in diam), and not especially well preserved, but certain significant characters can be observed. The florets have a lobed perigon (Fig. 30) and an indument of simple hairs. There are ca. six stamens per floret. The radially compressed floret in Fig. 29 is not well preserved, but the perigon margin is obvious, and the bilocular anthers are preserved as contiguous elongate masses of pollen. The pollen of three complete anthers is preserved in addition to fragments of two other locules (Fig. 29). The

size of the complete anthers vs. the floral envelope circumference and the arrangement of anthers within the perigon suggest that these florets had no more than six stamens. Anthers are less than 0.5 mm in length and have rounded locules (Fig. 30, a1), and thus, they are similar in size and shape to the anthers of the Castaneoideae (Hjelmqvist, 1948). The stamens have short filaments and a broad cuneiform anther connective similar to dorsifixed anthers of modern castaneoids (Fig. 30, a1).

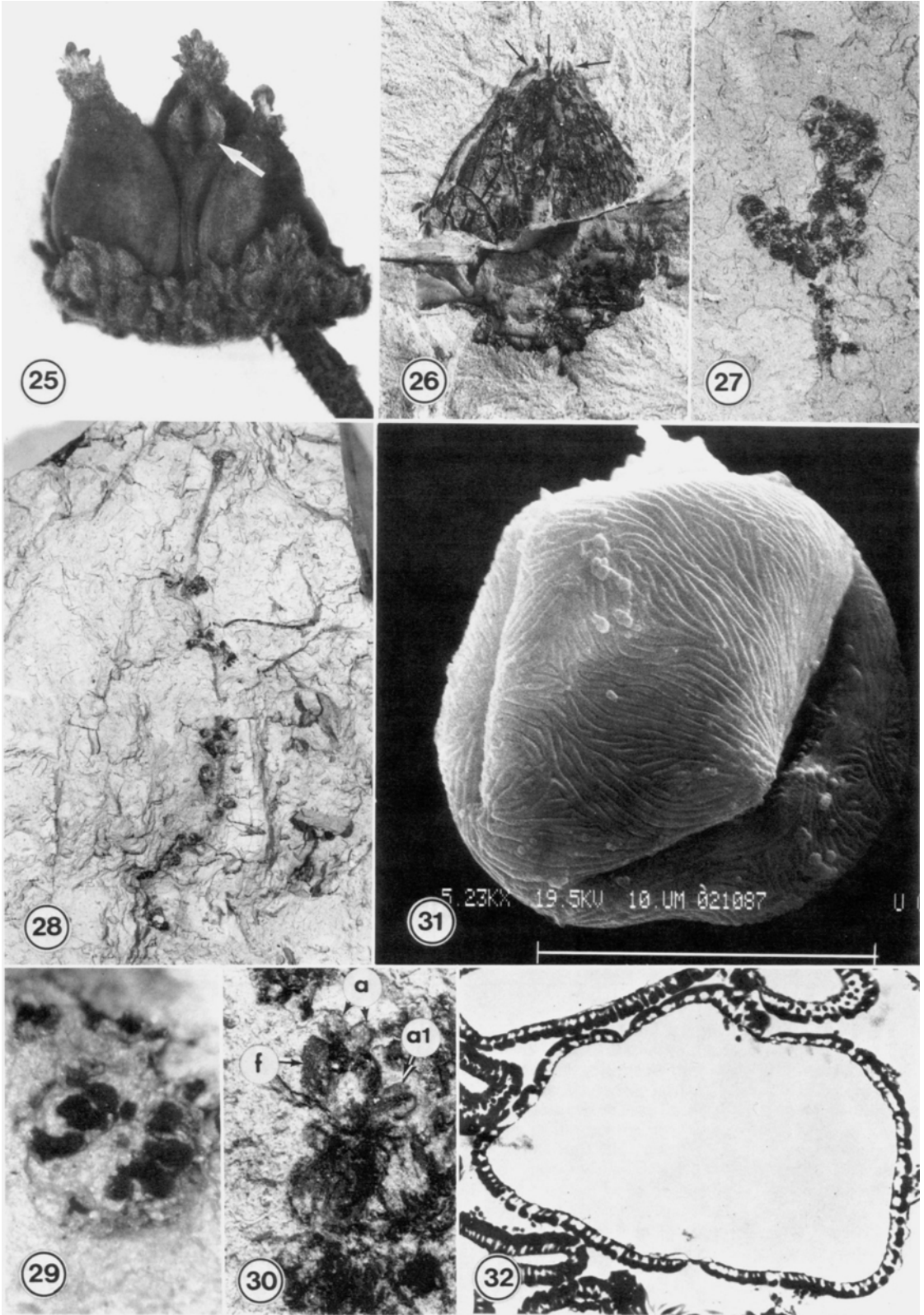
Pollen from the fossil catkins displays an interesting mixture of characters found in no single subfamily of Fagaceae today. Pollen is tricolporate, small (less than 15 μm in polar diam) and oblate/spheroidal ($P/E = 1$; Fig. 31). Wall structure is tectate columellate with a very thin footlayer (f/T ratio = 0.21; Fig. 32) and exine micromorphology is fused-vermiform (Fig. 31), somewhat like modern castaneoids. The exine is 0.87 μm in thickness.

The combination of characters found in the staminate catkins is transitional between the castaneoids and fagoids (*Fagus*, *Quercus*, *Colombobalanus*, and *Formanodendron*; see discussion below), but the combination of a lax elongate catkin axis and oblate/spheroidal pollen is presently restricted to Quercoideae within Fagoideae (i.e., *Colombobalanus*, *Formanodendron*, and *Quercus*).

Dispersed leaves—Jones (1984) has recently investigated fossil fagaceous leaves from the Tertiary of western Tennessee. He recognized two species groups, one of which more closely resembles extant castaneoid leaves in leaf architecture and cuticular morphology. Jones considered the other species group to have more features in common with the tribe Quercoideae (his Quercoideae) and stated that this latter group is the only one he found at the Paleocene

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Fig. 16–24. 16–23. Dispersed mature fruits of *Trigonobalanoidea*. 16. A single fruit enclosed by a cupule with two lobes (1). Note the perianth at the apex of the enclosed fruit. UCPC B788a. $\times 4$. 17. Counterpart of the previously illustrated fruit (UCPC B788b) illustrating the flat, tongue-shaped cupule scales. The arrows point out three transverse rows of scales. $\times 4.5$. 18. A fruit preserved without a cupule. Note the faintly preserved style protruding from the perianth and the extent of the wings. The white arrows indicate the juncture of the fruit margin-wing attachment. UCPC 798b. $\times 5.8$. 19. A dispersed fruit showing its compressed third angle (arrow) and the triangular attachment scar—an “s” points to each side of the scar. The fruit is preserved as a somewhat three dimensional compression leaving no doubts as to its shape or to the triangular nature of the attachment scar. UCPC B799b. $\times 6$. 20. A fruit showing a rupture of the suture at an angle (su) and a carbonized attachment scar. Two sides of the scar are indicated by arrows (s). UCPC B800. $\times 7$. 21. A fruit with a well preserved stylopodium-perianth complex (sty). UCPC B822. $\times 4.2$. 22. A higher magnification view of stylopodium-perianth complex of UCPC B822. Note two capitate styles projecting from the perianth (arrows) and the base of a third style (central arrow) that extends into the matrix. $\times 8.5$. 23. High magnification view of the distal wing margin of UCPC B798b showing elongate hairs. $\times 200$. 24. Dispersed mature fruit of *Colombobalanus excelsa* (Gentry, Juncosa & Ladrach 40903, Mo, ex Tex). Note the stylopodium perianth complex (sty) and the juncture of the wing and fruit margin (white arrows). Note the styles and stigmas protruding from the perianth. $\times 4.3$.



Buchanan locality. However, our ongoing studies of Buchanan fossils have also revealed leaves with cuticular morphology similar to that of the castaneoid type. Two questions concerning the leaves from Buchanan suggest further investigations: 1) Which of the leaf types represents castaneoids vs. trigonobalanoids, and 2) Are the characteristics of these ancient fagaceous leaves congruent with our assessment of ancestry of the Fagaceae? Studies of leaves aimed at clarifying these questions are now in progress and the results will be the subject of a separate manuscript (Steele and Crepet, in progress).

TAXONOMIC TREATMENT

SUBFAMILY CASTANEOIDEAE—Subfamily Castaneae Oersted, Vidensk. Selsk. Skr. 5: 372. 1871.

Orthographically corrected to Castaneoideae.

1. *Castanopsoidea* gen. nov. Crepet & Nixon

Partial pistillate inflorescences of scaly cupules enclosing three fruits. Fruits with an apical stylopodium-perianth complex. Styles three/fruit, linear, short (ca. 2 mm), and without an expanded stigmatic area. Stam-inodia (stamens?) enclosed by perianth and bearing tricolporate prolate pollen with fused-vermiform exine micromorphology. Wall structure tectate columellate and footlayer/tectum ratio ca. 1.

1a. *Castanopsoidea columbiana* sp. nov. Crepet & Nixon

Description as for the genus.

Holotype: UCPC B627. Paratypes: UCPC B849, UCPC B851.

SUBFAMILY FAGOIDEAE—Subfamily Fagineae Oersted, Vidensk. Selsk. Skr. 5: 351. 1871.

Orthographically corrected to Fagoideae.

Subfamily Quercineae Oersted, Vidensk. Selsk. Skr. 5: 355. 1871.

Orthographically corrected to Quercoidae.

Subfamily Trigonobalanoideae, Lozano-C., Hernandez-Camacho & Henao, *Caldasia* 12: 517–537. 1979.

2. *Trigonobalanoidea* gen. nov. Crepet & Nixon

Immature pistillate inflorescences and dispersed fruits. Inflorescences elongate, unbranched, with a straight to slightly curved axis bearing alternately arranged cupules. Cupules scaly, obscurely lobed, partially enclosing up to three trigonous fruits. Styles 3 per fruit, divergent, ca. 2 mm long. Stigmas terminal, capitate or discoid. Mature dispersed fruits: Fruits with valvate cupules enclosing about $\frac{2}{3}$ of the fruit. Cupule scales tongue-shaped, arranged in (sometimes obscure) transverse rows. Fruits 1–3 in each cupule, trigonous, winged, with an indument of elongate simple trichomes particularly along wings and apices. Perianth often persistent at fruit apex, with 3 styles that expand distally to the capitate stigmatic region. Triangular attachment scar visible basally on some solitary dispersed fruits.

2a. *Trigonobalanoidea americana* sp. nov. Crepet & Nixon

Description as for genus.

Holotype: pistillate inflorescence UCPC B672; Paratypes: (mature fruit) B788. Paratypes UCPC B797–800, UCPC B822, UCPC B847.

3. *Paleojulacea* genus nov. Crepet & Nixon

Catkins lax, florets (diam 1 mm) in dichasia of 3 or more, perigon lobed, with an indument of elongate simple hairs. Stamens small (less than 0.5 mm in length), bilocular and dorsifixed with rounded locules, ca. 6 per floret. Pollen tricolporate, less than 15 μm in polar diameter, exine ornamentation fused-vermiform. Pollen wall tectate colu-

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Fig. 25–32. 25. A lobed cupule of *Colombobalanus excelsa* (Gentry, Juncosa & Ladrach 40903, Mo, ex Tex) showing three enclosed fruits. Note the ruptured suture of one (arrow). $\times 4.3$. 26. *Trigonobalanoidea*. Three fruits within a cupule. Note the floral envelope or parts of the floral envelopes of each of the fruits (arrows). UCPC B847b. $\times 3.5$. Fig. 27–32. *Paleojulacea*. 27. Unexpanded staminate catkin. UCPC B820a. $\times 5$. 28. Mature staminate catkin. Note the clusters of tiny florets and the delicate, sinuous nature of the catkin axis. UCPC B555a. $\times 2.34$. 29. High magnification view of a radially compressed floret of UCPC B555a. Anthers are represented by dark masses of pollen. There are three complete bilocular anthers preserved and parts of two others. $\times 28$. 30. A high magnification view of several florets of an unexpanded catkin (UCPC B820b). Note several floral envelope lobes (f) and two slightly exerted anthers (a) in one laterally compressed floret. Note also the bilocular anther associated with another floret that has short rounded locules and a broad cuneiform connective (a1) that suggests the anthers were dorsifixed. $\times 13$. 31. SEM of pollen isolated from an anther of UCPC B820a. Note the pronounced geniculi over the endoapertures and the fused-vermiform exine micromorphology. $\times 5,230$. 32. TEM of pollen from another anther. Note the tectate columellate wall structure and thin footlayer. $\times 4,150$.

mellate, 0.87 μm thick, foot layer/tectum ratio = 0.21.

3a. *Paleojulacea laxa* sp. nov. Crepet & Nixon

Description as for the genus.

Holotype: UCPC B555. Paratypes: UCPC B820, UCPC B821.

Results of cladistic analyses—Two equally parsimonious cladograms for Fagaceae were previously constructed, differing only in the placement of two subgroups of *Quercus*; however, these cladograms had identical topologies at the generic level. The strict consensus of these two cladograms is presented in Fig. 1. Character congruence between the two pistillate fossils and hypothetical ancestors on the cladogram is indicated by deeper shading or broken lines in the regions of all nodes and terminal taxa that match fossil character states. The relationship of *Paleojulacea* with taxa in the cladogram is not shown but is discussed below.

Additional parsimony analyses were performed using the two pistillate fossils as terminal taxa. Because the fossils lacked several characters used in the analysis, multiple trees were found that were equally parsimonious, but the topological relationship among the modern taxa within these trees was the same as in the two trees found with modern taxa alone. The inclusion of the fossils in the analysis did not introduce homoplasy into the original cladogram, providing independent support for that topology. We therefore have not presented the multiple solutions possible with the inclusion of fossils with no additional homoplasy, but missing character data. A consensus tree of the various possible placements of the pistillate fossils relative to modern taxa is presented in Fig. 1.

Paleojulacea, if included in the cladistic analysis as a terminal taxon, introduces additional homoplasy because of the combination of a lax catkin (a derived feature) with some pollen features that must be considered ancestral and castaneoid. There are many possible solutions due, again, to the missing characters, and the consensus tree of these multiple trees provides less resolution than the two trees derived without the fossil. For reasons discussed below, we did not include the results of the cladistic analyses using *Paleojulacea* as a terminal taxon, but for now, prefer to discuss the implications of this fossil and its relationships to modern taxa.

DISCUSSION—Paleoclimate—Paleoclimate at the Buchanan locality during the late Paleocene is generally considered to have been warm tem-

perate to tropical with seasonal drought (e.g., Dilcher, 1971; Frederiksen, 1980). Such a paleoclimate is consistent with the assemblage of taxa that is already known from the locality. The proposed subtropical environment is also consistent with the modern distribution of many species of Castaneoideae, including the genus *Castanopsis* in Asia. Modern trigonobalanoid species, however, are restricted to relatively wet montane tropical habitats.

Phylogenetic implications—The two pistillate fossils are consistent with our previous phylogenetic studies based solely on extant fagaceous taxa. The inclusion of these fossil taxa in cladistic analyses did not introduce additional homoplasy into the resulting cladograms, increasing our confidence in the analyses.

Although providing information about minimum times of divergence and paleobiogeography, fossil *Castanopsoidea* does not provide additional insight into phylogenetic patterns within Fagaceae or subfamily Castaneoideae. The characters available suggest a general affinity with *Castanopsis* and *Chrysolepis*, but no novel combinations or unique character states are available in the fossil material.

The staminate catkin assigned to *Paleojulacea* is lax, with pollen that is somewhat castaneoid in overall size and exine sculpturing, but trigonobalanoid/quercooid in shape and footlayer thickness. This combination of characters is not found in modern trigonobalanoids, and therefore, if the staminate and pistillate catkins were assigned to the same species (*Trigonobalanoidea americana*), suggests that *Paleojulacea* may have been intermediate morphologically between the entomophilous castaneoids and anemophilous fagoid line. Because we cannot be sure of the association between *Paleojulacea* and *Trigonobalanoidea*, we are also uncertain of the exact affinities of *Paleojulacea*, and thus, there are only characters available for the staminate catkin and pollen. Consequently, we have not yet included this fossil directly in our cladistic analyses, as we have done with the pistillate materials, which provide more diagnostic characters. If the two form taxa represent the same species, then the topology of our cladogram (Fig. 1) would be altered in the region of the trigonobalanoids in a way that might suggest 1) the possibility of an independent origin of the lax catkin and anemophily in the higher trigonobalanoids, *Fagus*, and *Quercus*, or 2) that the erect catkin has been rederived in *Trigonobalanus verticillata*. Whether anemophily was derived independently in more than one clade within Fagoideae needs to be investigated further in light

of the interesting character mosaic of *Paleojulacea*.

Age of Fagaceae and subfamilies—*Castanopsioidea* represents the earliest unequivocal evidence of the subfamily Castaneoideae. Reports of late Cretaceous castaneoids are based solely on palynological evidence (e.g., Chmura, 1973) that needs review. The results of our cladistic analyses suggest that the castaneoids are similar to ancestral Fagaceae, particularly in floral features. The timing of the appearance of the castaneoids is consistent with our hypothesis of phylogeny (Fig. 1), although the simultaneous appearance of *Trigonobalanoidea* suggests an earlier origin for the family.

Trigonobalanoidea is the first and oldest evidence of a trigonobalanoid taxon from North America. The appearance of this trigonobalanoid in the Paleocene/Eocene prior to other known fossil Fagoideae (*Pseudofagus*, *Fagus* and *Quercus*; Chaney, 1927; Tanai, 1972, 1974; Smiley and Huggins, 1981; Daghljan and Crepet, 1983), also provides evidence consistent with the phylogeny based on modern taxa and supports the hypothesis that trigonobalanoids, in the broad sense, are ancestral to extant wind-pollinated Fagaceae.

The occurrence of *Paleojulacea*, a taxon morphologically well adapted for wind dispersal of pollen at a time previous to the climatic decay of the late Eocene-Oligocene (Wolfe, 1978), is consistent with the hypothesis that wind pollination in Fagaceae or Fagoideae evolved in response to seasonal dry periods or overall dryness in subtropical climates (Upchurch and Wolfe, 1987). This possibility may be further evaluated when more is known about the fossil record of trigonobalanoids (i.e., the sequence of appearance within trigonobalanoids and better knowledge of their paleobiogeography).

The occurrence of fossils that are assignable to each of the two modern subfamilies of Fagaceae in the early Tertiary sets a minimum time of divergence for these two clades. This timing is consistent with the appearance of putative castaneoid pollen in Upper Cretaceous sediments (Chmura, 1973), and indicates an origin of subfamily Fagoideae as certainly no later than Paleocene. The Fagaceae probably originated in the Late Cretaceous, but unequivocal megafossils of the family or ancestral forms of that age are unknown (Wolfe, 1974; Crepet and Daghljan, 1980).

Biogeographical implications—Numerous reports of castaneoid fossils from mid-Late Tertiary deposits in North America (Crepet and Daghljan, 1980) suggest that during the

Tertiary in North America, Castaneoideae were more diverse than at the present. The 5 or 6 extant species in temperate North America include *Castanea* (2–3 spp.), *Lithocarpus* (1 sp.) and *Chrysolepis* (2 spp.). Additionally, the tropics of North and Central America have no extant castaneoids, in marked contrast to the great diversity of castaneoids in montane tropical and subtropical areas of Asia and Malaysia (*Castanopsis* and *Lithocarpus*; see Soepadmo, 1972). On the basis of modern and extinct fossil taxa, all modern genera of Castaneoideae were present in North America in the Tertiary. Thus, the diversity of modern species of castaneoids in southeast Asia and their absence in tropical North America today most likely reflects differential rates of diversification and extinction that were the result of different paleoecological conditions in the two regions.

The distribution of modern trigonobalanoids is disjunct and has engendered at least two opposing biogeographical hypotheses. Hernandez-C., Lozano-C., and Henao-S. (1980) and Van der Hammen and Cleff (1983) proposed that the Colombian *T. excelsa* (*Colombobalanus*) was a north temperate element that arrived in South America in the Pleistocene. In contrast, Melville (1982) suggested that the distribution of the three trigonobalanoid species represents a vicariance pattern which is the result of the breakup of a Pacific continent and movement of land masses carrying trigonobalanoids to their current sites. Both these biogeographical hypotheses were performed without the benefit of fossil data and were based on the assumption that the modern trigonobalanoids are a single, closely related genus. However, biogeographical analysis of the modern trigonobalanoids is complicated because they are a paraphyletic group (Nixon and Crepet, 1989; Patterson, 1981), and fossil trigonobalanoids are found on two continents which have no modern species.

Biogeographical hypotheses must be based on an interpretation of the status of a particular clade (preexistent, monophyletic, paraphyletic, extinct) in relation to geologic and climatic events. Thus, "chronoclares" are monophyletic or paraphyletic only in relation to the span of time in which they are evaluated. Groups that are monophyletic become paraphyletic through the origin of new derivative clades, and paraphyletic groups may become monophyletic through the extinction of derivative clades. For modern taxa, monophyly is generally simpler to determine because one can assume with reasonable certainty that all relevant extant taxa have been discovered.

Based on our understanding of the fossil history of Fagaceae, we assume that the trigo-

nobalanoid clade was monophyletic in the Paleocene/Eocene, prior to the evolution of the genus *Quercus*. A more broadly defined group, including the modern trigonobalanoids plus modern *Quercus*, is monophyletic at the present time, and the distribution of this group may thus be considered in the context of a formal biogeographic analysis using modern and fossil distributions. We have been able to approach the biogeography of the trigonobalanoids in a two-tiered fashion largely because of the availability of fossils, and our conclusions might be different if they were based solely on modern distributions and relationships.

In addition to the fossils reported here, unequivocal fossil trigonobalanoids are found in the Eocene of Europe (Conwentz, 1886) and the Oligocene of North America (Crepet and Nixon, 1989), suggesting that the trigonobalanoid clade had a Euro-American distribution in the early Tertiary. Mai (1970) has reported *Trigonobalanus* from the upper Eocene of Europe, but his fossil fruits do not have preserved stigmas and so cannot be conclusively placed with that genus, although they probably have affinities with the trigonobalanoids and/or *Fagus*. Mai reported and illustrated two fruits per cupule for these fossils, a condition found in *Fagus* but not the modern trigonobalanoids. The earliest trigonobalanoid fossils on either continent are the Paleocene fossils (from Tennessee) described here. Evidence is strong for an Eocene land bridge between Europe and North America (Tiffney, 1985), but without a more complete and compelling fossil record, placing the origins of trigonobalanoids on either continent would be premature.

Quercus has a Holarctic distribution with the exception of one species that occurs in Colombia. The available fossil evidence suggests that the Colombian species of *Quercus* is not a vicariant element of a distribution that predates the separation of North and South America. Instead, *Quercus* may be considered as having a northern hemisphere track in the Tertiary which extended into South America during favorable conditions after land connections and/or island proximity allowed dispersal between the continents. Independent evidence suggests that such connections were not available until early Pleistocene (Webb, 1976). In support of this hypothesis, pollen of *Quercus* appears in the fossil record suddenly and in quantity in Colombia in the Pleistocene (Van der Hammen, Werner, and Van Dommelen, 1973; Van der Hammen and Cleef, 1983). A similar pattern is seen in other North temperate elements such as *Alnus* and *Juglans*. As far as we know, no efforts have been made to identify trigo-

nobalanoid fossil pollen in these deposits. No other fossils of Fagaceae sensu stricto are known from South America.

The hypothesis that *Quercus* and *Colombobalanus* both arrived in South America in the Pleistocene, as suggested by Lozano et al. (1979) and Van der Hammen and Cleef (1983), is consistent with 1) the available data on the timing of the appearance of *Quercus* in the fossil record, 2) the fossil evidence that is available on distribution of *Quercus* and trigonobalanoids in the past, and 3) the plate tectonics of Central America during the Late Tertiary. The presence of one species of modern trigonobalanoid in South America and the two remaining species in Southeast Asia is therefore best *not* interpreted as the result of strict vicariance involving a Pacific continent, Southeast Asia and South America. Instead, the modern distributions are part of a more complex pattern that includes now extinct trigonobalanoids in Europe and North America. Thus, the Asian and South American distribution of modern trigonobalanoids probably reflects a combination of relictual populations from a more widespread and diverse northern hemisphere distribution and a relatively recent incursion into South America from a North or Central American source. The absence of modern trigonobalanoids in North and Central America is an independent extinction event that does not shed doubt on a North American or Central American source for the South American species. The fossil record and modern distributions of both castaneoids and trigonobalanoids clearly indicate that Tertiary extinction in Fagaceae was more significant in the Americas than in the Old World, and that this extinction probably accelerated in the late Tertiary.

From any perspective, the modern distribution of trigonobalanoids now has to be analyzed in the context of the distribution of *Quercus* with which the 3 extant species of trigonobalanoids form a monophyletic group. This will require a more complete understanding of the major monophyletic groups within the genus *Quercus*.

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