Fagaceous Flowers, Fruits, and Cupules from the Campanian (Late Cretaceous) of Central Georgia, USA

Author(s): Patrick S. Herendeen, Peter R. Crane and Andrew N. Drinnan

Source: *International Journal of Plant Sciences*, Jan., 1995, Vol. 156, No. 1 (Jan., 1995), pp. 93-116

Published by: The University of Chicago Press

Stable URL: http://www.jstor.com/stable/2474901

Int. J. Plant Sci. 156(1):93–116. 1995.

1058-5893/95/5601-0010$02.00

FAGACEOUS FLOWERS, FRUITS, AND CUPULES FROM THE CAMPANIAN (LATE CRETACEOUS) OF CENTRAL GEORGIA, USA

PATRICK S. HERENDEEN,[1,*] PETER R. CRANE,* AND ANDREW N. DRINNAN†

*Department of Geology, The Field Museum, Roosevelt Road at Lake Shore Drive, Chicago, Illinois 60605; and †School of Botany, University of Melbourne, Parkville, Victoria 3052, Australia

A new genus of fossil angiosperms (*Protofagacea allonensis* gen. et sp. nov.) is established for staminate flowers with associated fruits and cupules from the Campanian (Late Cretaceous) Buffalo Creek Member of the Gaillard Formation in central Georgia, U.S.A. Staminate flowers are typically borne in seven-flowered dichasia (more rarely three- or five-flowered) subtended by three series of bracts. Flowers have six small imbricate tepals in two cycles of three, 12 stamens in two cycles of six, and a vestigial gynoecium with three styles surrounded by a mass of simple trichomes. Pollen is very small, prolate, tricolporate, and reticulate to microfoveolate. Associated fruits are triangular or lenticular in cross section and the triangular fruits bear six short tepals at the apex. Fossil pollen identical to that produced by the staminate flowers is attached to the apex of the fruits. Associated cupules are pedunculate and four-lobed and bear three or more fruits. The cupule lobes bear three series of bracts similar to those subtending the staminate dichasia. Scars on the internal surface indicate that each cupule contained a central fruit that was elliptical in cross section and two lateral fruits that were triangular in cross section. Comparisons of *P. allonensis* with extant taxa clearly indicate a relationship to extant Fagaceae *sensu lato,* based particularly on the presence of the cupule, the form of the fruits, and the morphology of staminate inflorescences and flowers. However, pollen morphology (probably plesiomorphic) differs from that of extant taxa, and detailed resolution of the affinities of *Protofagacea* will require a clearer understanding of relationships among extant Fagaceae *sensu stricto* and Nothofagaceae.

Introduction

The paleobotanical record documents the initial major radiation of flowering plants between the Aptian and Cenomanian, and during this interval angiosperms rapidly became the most diverse component of most terrestrial floras (Brenner 1963; Doyle 1969; Muller 1970; Doyle and Hickey 1976; Friis et al. 1987; Lidgard and Crane 1988, 1990; Crane 1989; Crane and Lidgard 1989). By the early Cenomanian, fossil taxa related to extant monocots (Herendeen and Crane, in press), eudicots, and various taxa at the magnoliid grade were already represented. Mid-Cretaceous magnoliids included taxa closely related to Magnoliaceae (Dilcher and Crane 1985), Winteraceae (Walker et al. 1983), Lauraceae (Drinnan et al. 1990), Calycanthaceae (Friis et al. 1994), and possibly Chloranthaceae (Friis et al. 1986; Crane et al. 1989; Pedersen et al. 1991). Mid-Cretaceous eudicots included Platanaceae (Friis et al. 1988; Crane 1989; Crane et al. 1993; Pedersen et al. 1994) and possibly Buxaceae (Drinnan et al. 1991), Myrothamnaceae (Doyle 1969; Ward and Doyle 1988, p. 179), Trochodendrales (Hickey and Doyle 1977), and perhaps also Circaeasteraceae (Crane et al. 1994). By the Turonian to Campanian a still greater diversity of angiosperms is known, including numerous taxa referable to Chloranthaceae (Friis et al. 1986; Crane et al. 1989; Herendeen et al. 1993), Lauraceae (Herendeen et al. 1994), Hamamelidales (Endress and Friis 1991; Crepet et al. 1992), Saxifragales (Friis and Skarby 1982; Friis 1990), Ericales (Friis 1985; Nixon and Crepet 1993), and monocots such as Arecaceae (Christopher 1979) and Zingiberales (Friis 1988). One of the most conspicuous components of Turonian to Campanian floras are pollen grains referable to the Normapolles complex, many of which were undoubtedly produced by plants related to extant "higher" Hamamelididae, e.g., Juglandaceae, Betulaceae, and perhaps Myricaceae and Casuarinaceae. Several of these pollen types are known in situ within flowers of juglandalean/myricalean affinity (Friis 1983; Friis and Crane 1989). A key family of "higher" Hamamelididae that is believed to be closely related to the Normapolles complex is the Fagaceae *sensu lato* (Crane 1989), but despite the Late Cretaceous fossil history of putative *Nothofagus* and castaneoid pollen (Chmura 1973; Dettmann et al. 1990), unequivocal fagaceous megafossils have not been recovered from Late Cretaceous rocks.

In this article we document fossil staminate flowers, fruits, and cupules of Fagaceae from the Campanian Buffalo Creek Member of the Gaillard Formation in central Georgia, U.S.A. This material substantially extends the megafossil record of the Fagaceae, which previously has been known only from early Eocene and younger strata (Crepet 1989; Crepet and Nixon 1989*a,* 1989*b;* Nixon and Crepet 1989). The Campanian fossils provide important data on pollen structure in early Fagaceae, which exhibits plesiomorphic features similar to the pollen of some extant rosids. The fossils also document the presence of

---

[1] Author for correspondence and reprints.

Manuscript received June 1994; revised manuscript received August 1994.

fagaceous cupules in early members of the family. Structural similarities between staminate and pistillate inflorescences provide evidence of homology between the cupule and inflorescence axes and bracts.

Material and methods

Floras of Campanian age are widely scattered in North America (Crabtree 1987; Crane 1987), and along the Atlantic Coastal Plain they are known from Martha's Vineyard to central Georgia (Crane 1987). The fossil material described here is from a new Campanian locality in Crawford County, Georgia, approximately 9.5 km southeast of Roberta. The fossil material was isolated from a carbonaceous clay lens that is exposed on the south face of the south pit ("Allon" quarry) of the Atlanta Sand and Supply Company at Gaillard, Georgia (Knoxville Quadrangle, lat. 32°37'47"N, long. 83°59'10"W). The sediments have been assigned to the Buffalo Creek Member of the Gaillard Formation (Huddlestun and Hetrick 1991). Based on palynological analyses, the Gaillard Formation is thought to be of earliest Campanian age (Christopher 1979; Huddlestun and Hetrick 1991).

Bulk samples of clay were dissolved in water and then washed through a series of sieves (finest mesh 125 μm). The isolated plant material was cleaned using HCl, followed by HF, and then thoroughly washed in water. The fossil material was dried in air and examined using a binocular stereomicroscope. In addition to the fagaceous remains, the fossil assemblage also includes conifers as well as diverse angiosperm inflorescences, flowers, fruits, and seeds, preserved as lignitic and fusainized fragments. Flowers of extant *Nothofagus* and *Trigonobalanus* were removed from herbarium specimens (F). Specimen details are given in the figure captions. Specimens were mounted on stubs, coated with gold, and examined with an Amray 1810 SEM. After scanning, selected staminate flower specimens were partially dissected to reveal androecial organization and then recoated and scanned. All fossil specimens are deposited in the paleobotanical collection of the Department of Geology, The Field Museum, Chicago (PP).

Systematics

FAMILY—FAGACEAE SENSU LATO

GENUS—PROTOFAGACEA HERENDEEN, CRANE ET DRINNAN, GEN. NOV.

TYPE SPECIES—PROTOFAGACEA ALLONENSIS HERENDEEN, CRANE ET DRINNAN, SP. NOV.

GENERIC DIAGNOSIS. Pedunculate dichasia bearing seven, less frequently five or three, staminate flowers (one central primary flower, two lateral secondary flowers, and four lateral tertiary flowers). Flowers of dichasium subtended by three series of bracts. Each of the four tertiary flowers is subtended by two very small bracteoles; these are subtended by a pair of larger bracteoles. Outermost in the dichasium are two pairs of bracts; the distal bract of each pair (i.e., the bract farthest from the laterally inserted peduncle) is usually larger than the proximal bract. Flowers composed of six small, imbricate tepals in two cycles of three. Androecium of 12 stamens in two cycles of six; the cycle alternate to the tepals develops first, followed by the cycle opposite the tepals. Anthers dorsifixed, composed almost entirely of two thecae with little development of connective tissue. Pollen grains small and tricolporate. Gynoecium vestigial, consisting of three styles. Center of the flower consisting of a dense mass of simple trichomes.

SPECIES—PROTOFAGACEA ALLONENSIS HERENDEEN, CRANE ET DRINNAN, SP. NOV. (FIGS. 1–41, 64*A*)

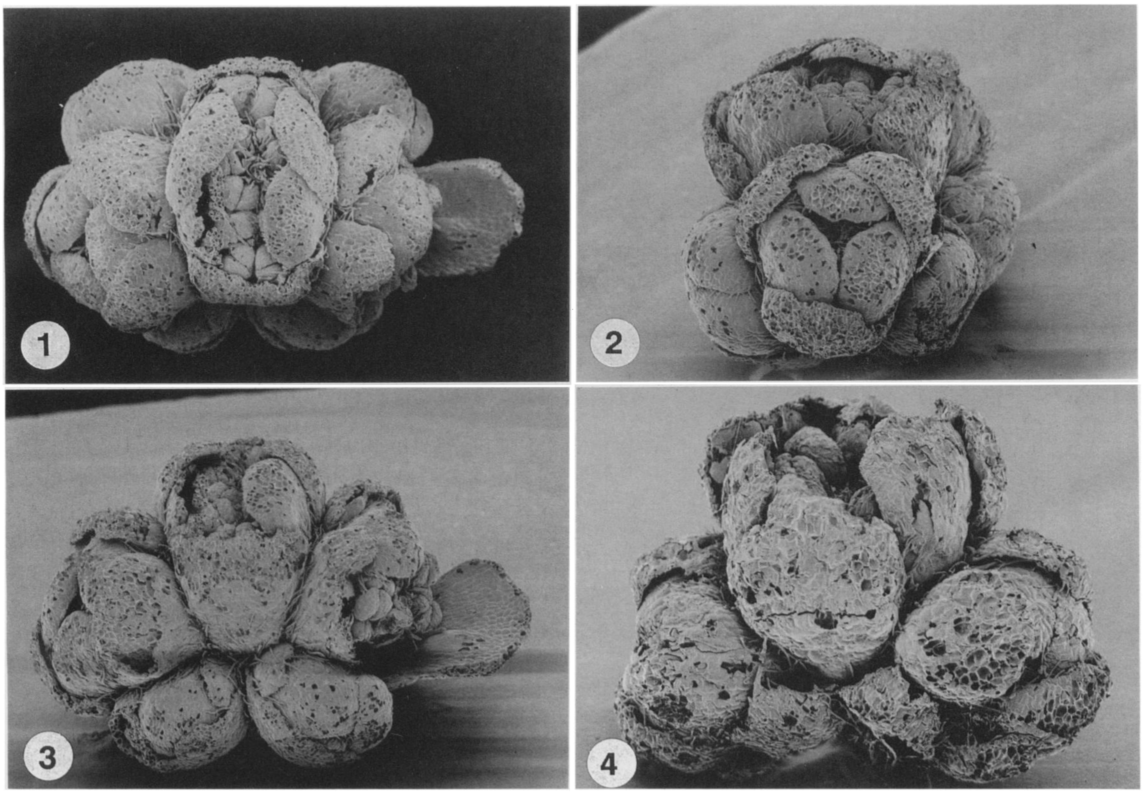
SPECIFIC DIAGNOSIS. As for the genus, with the following additions: highest order bracteoles of the dichasium usually bilobed; flowers actinomorphic, ca. 0.7–1.3 mm long, 0.6–1.1 mm wide; outer tepals usually broader and shorter than inner tepals; tricolporate pollen grains very small (polar axis ca. 5.6–7.6 μm long, diameter ca. 4.2–5.4 μm), exine reticulate to microfoveolate.

HOLOTYPE. PP43913 (figs. 1–3).

PARATYPES. PP43838, PP43843, PP43849, PP43850, PP43861, PP43879, PP43889, PP-43912, PP43915, PP44457, PP44480, PP44483, PP44486, PP44489, PP44493, PP44502, PP-44504, PP44516, PP44523, PP44540, PP44545, PP44570.

OTHER MATERIAL. PP43831–43837, 43839–43842, 43844–43848, 43851–43860, 43862–43878, 43880–43888, 43890–43911, 43913, 43914, 43816, 44458–44479, 44481, 44482, 44484, 44485, 44487, 44488, 44490–44492, 44494–44501, 44503, 44505–44515, 44517–44522, 44524–44539, 44541–44544, 44546–44569, and several hundred uncataloged specimens.

TYPE LOCALITY. Approximately 9.5 km southeast of Roberta, Georgia, at the south pit of the Atlanta Sand and Supply Company at Gaillard, Crawford County, Georgia (Knoxville Quadrangle, lat. 32°37'47"N, long. 83°59'10"W).



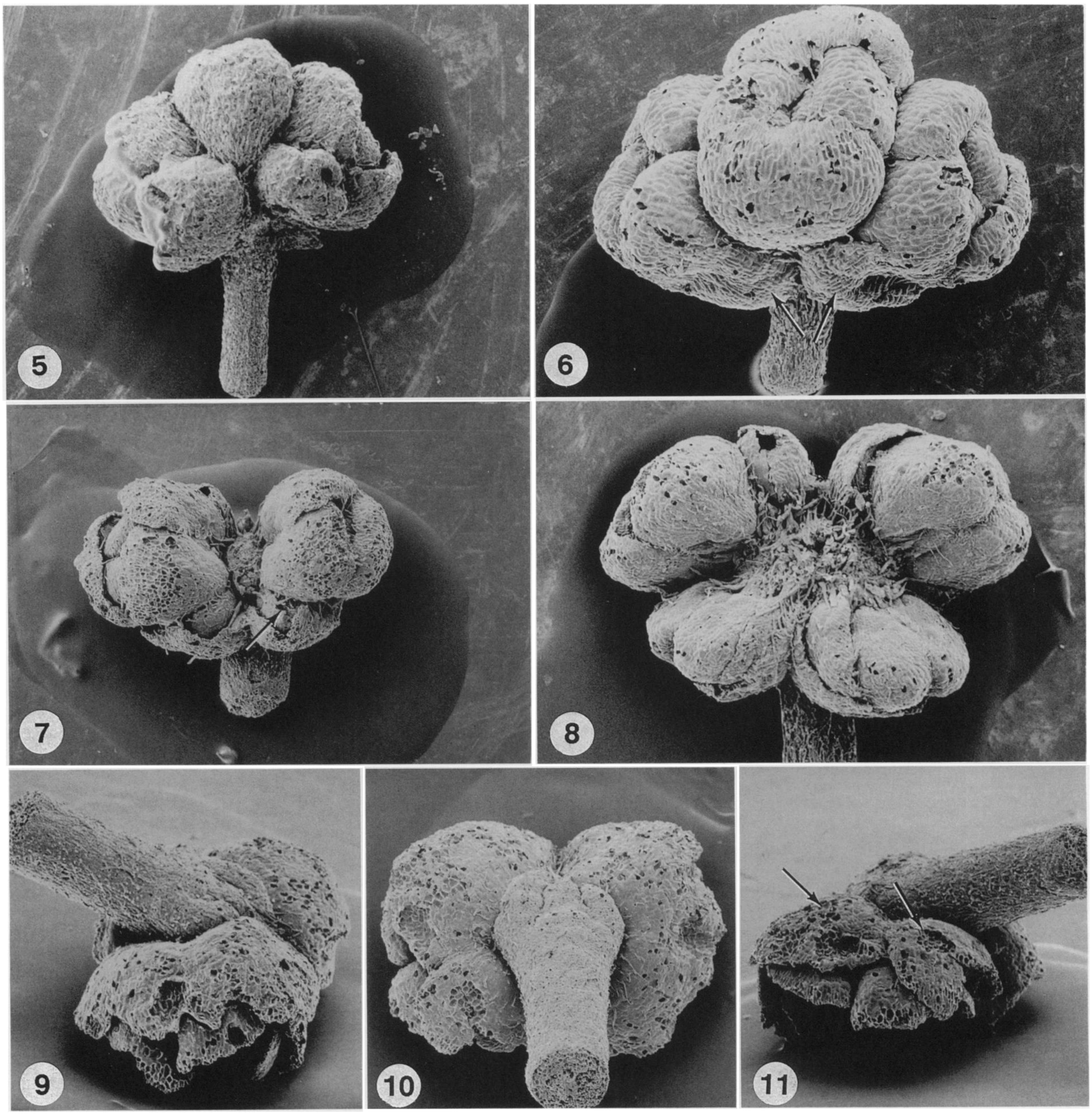
Figs. 1–4 Staminate dichasia of *Protofagacea allonensis*. Figs. 1–3, Dichasium composed of seven flower buds with the central (primary) flower closest to anthesis (PP43913, holotype; all × 50), viewed from above (fig. 1), laterally to illustrate one of the two secondary flowers (fig. 2), and from one side with two of the four tertiary flowers emerging below (lateral to) the secondary flowers (fig. 3; also evident in fig. 2). Fig. 4, A seven-flowered dichasium (PP44457; × 75).

Age and stratigraphy. Buffalo Creek Member of the Gaillard Formation (Upper Cretaceous, Campanian).

Description and remarks. Staminate inflorescence unit is a dichasium, typically bearing seven flowers, less frequently three or five (figs. 1–5). The dichasium is borne on a peduncle, ca. 0.5–1.0 mm long, 0.15–0.2 mm wide, which is usually laterally inserted (figs. 5–11) and bears numerous simple, sometimes twisted trichomes (figs. 38, 39). In a few dichasia the stalk is centrally inserted (fig. 13), indicating that these were terminal dichasia in a compound inflorescence composed primarily of numerous lateral dichasia. Seven-flowered dichasia consist of a central primary flower, flanked by two cymes, each with a central secondary flower and two lateral tertiary flowers. The primary flower develops first, followed by the two secondary flowers and finally the four tertiary flowers. This sometimes makes it difficult to distinguish three- or five-flowered dichasia from seven-flowered immature forms in which the tertiary flowers are still enclosed within the inflorescence bracts.

Staminate flowers are sessile, closely aggregated, and subtended by two pairs of outer bracts (figs. 11 [arrow], 15–18). The distal bract of each pair, relative to the asymmetric peduncle attachment, is usually broader than the proximal bract. Internal to these bracts are usually eight smaller bracts, four on each side of the dichasium, two of which are associated with each tertiary flower (fig. 64*A*). Internal to these are eight small bracts that are usually shallowly to deeply bilobed, less frequently entire, and are also associated with the tertiary flowers (figs. 14, 17). The four outer bracts are completely separate in young dichasia with flower buds (figs. 5, 7, 8, arrows) but enlarge through intercalary growth as the dichasium matures and are laterally connate at the time of anthesis of the tertiary flowers (figs. 9, 10). The number and arrangement of these bracts is consistent with their interpretation as prophylls.

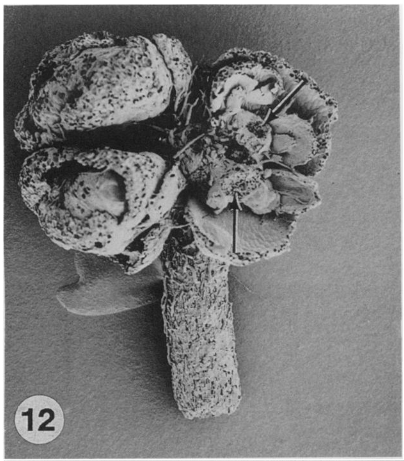
Staminate flowers (figs. 19–31) are actinomorphic, ca. 0.7–1.3 mm long, 0.6–1.1 mm wide. Tepals are free, usually six, imbricate in bud in two cycles of three, broadly obovate, ca. 0.5–0.8 mm long, 0.3–0.5 mm wide; outer tepals are usually broader and shorter than inner tepals (figs. 26–29). Tepals bear an indumentum of simple trichomes on the margins and also near the apex on the abaxial surface (fig. 39). Stamens are free, usually 12, in two cycles of six, but tertiary flowers

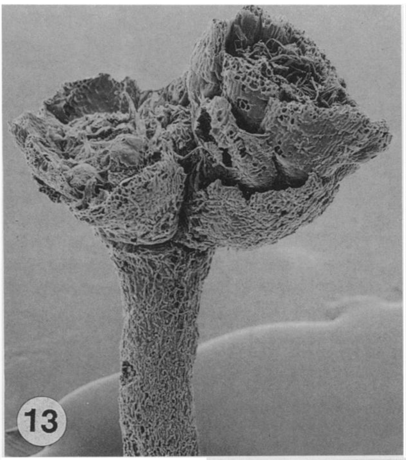


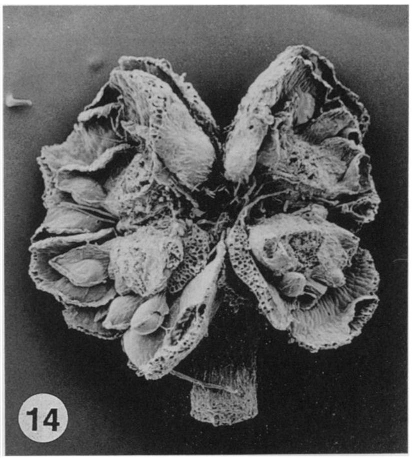
Figs. 5–11 Staminate dichasia of *Protofagacea allonensis*. All × 50. Figs. 5–8, Developmental series for staminate dichasia. Fig. 5, Young dichasium with only the primary and two secondary flower buds evident (PP44486). Fig. 6, Older dichasium with primary and secondary flower buds near anthesis. Arrows indicate two of the outer bracts (PP44483). Fig. 7, Older dichasium in which the primary flower has been shed and the secondary flower buds are expanding. Arrow indicates tertiary flower bud (PP44489). Fig. 8, Dichasium in which the primary and secondary flowers have been shed and the four tertiary flowers are expanding (PP44493). Figs. 9–11, Dichasium after all flowers have been shed illustrating lateral peduncle attachment and the outer bracts of the dichasium. Fig. 9, View from the side. Fig. 10, View from below. Fig. 11, View from other side. Arrows indicate two of the four outer bracts.

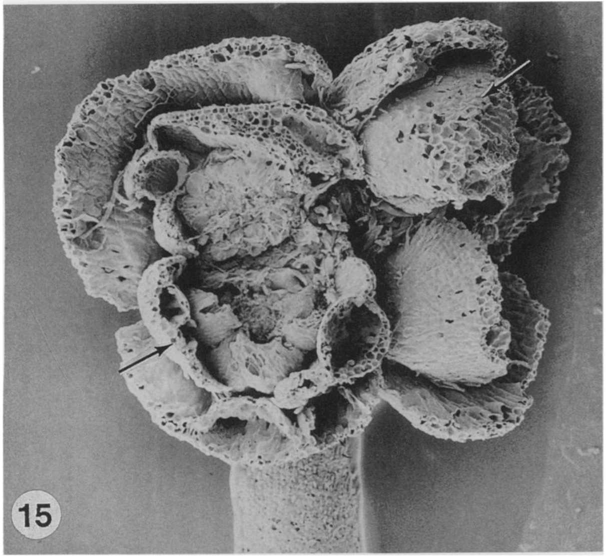
⟶

Figs. 12–18 Staminate dichasia of *Protofagacea allonensis* to illustrate bract structure. Fig. 12, Dichasium with two tertiary flower buds on left side and lacking flower buds on right side. Arrows indicate attachment points for two tertiary flowers. Note several series of bracts subtending the tertiary flower scars (PP43843). × 50. Fig. 13, Abraded dichasium with a terminal centrally attached peduncle and remains of two secondary flowers (PP44570). × 50. Fig. 14, Dichasium composed of at least three series of bracts, which subtend the four tertiary flower scars (PP44504). × 50. Fig. 15, Dichasium in which several secondary bracts are indicated (arrows). Note that several of the bracts are distorted due to charcoalification. (PP44500). × 75. Fig. 16, Dichasium with one tertiary flower (PP44502). × 40. Fig. 17, Enlargement of fig. 14 to illustrate bract structure in one side of a dichasium. Primary (1°), secondary (2°), and tertiary (3°) bracts are indicated by arrows. Note that the tertiary bracts are lobed and that one of the secondary bracts is missing on the lower side. × 100. Fig. 18, One side of a dichasium in which an extra series of bracts (quaternary) appears to be present (PP44545). × 150.

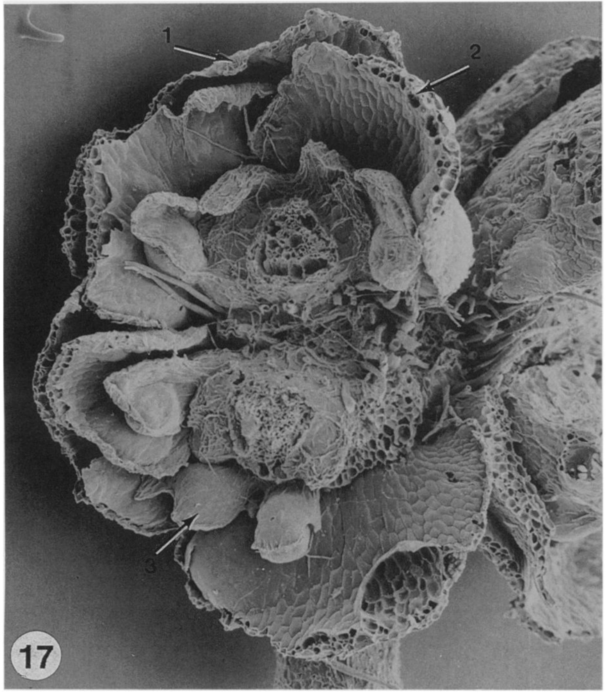

12

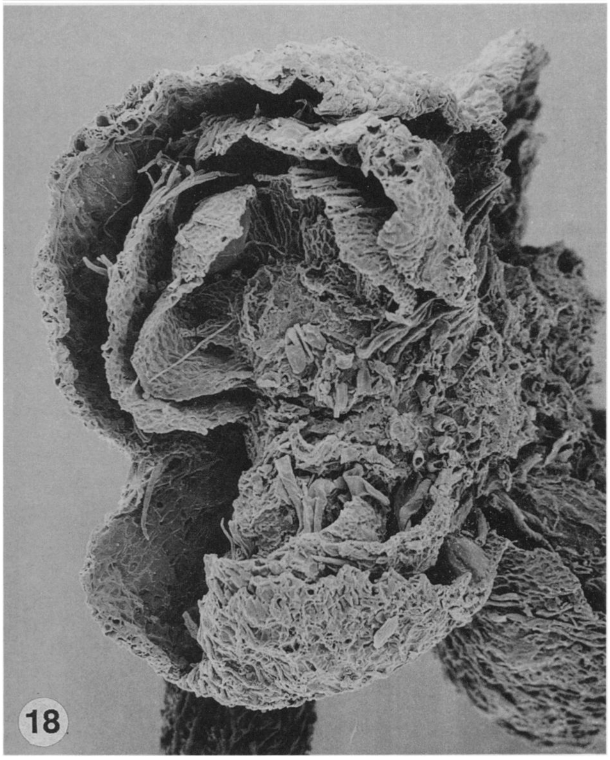

13

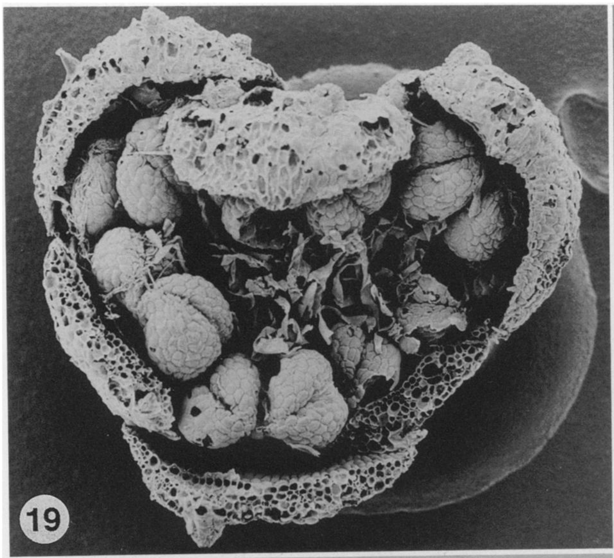

14

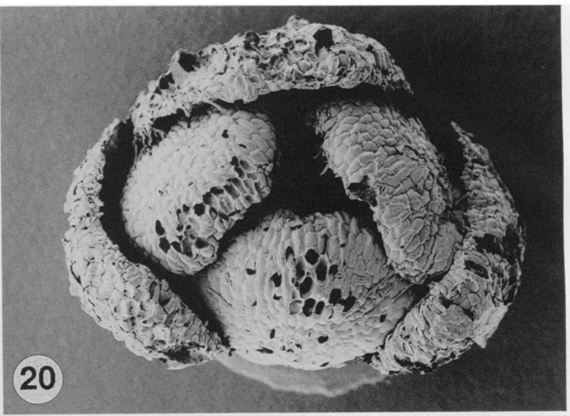

15

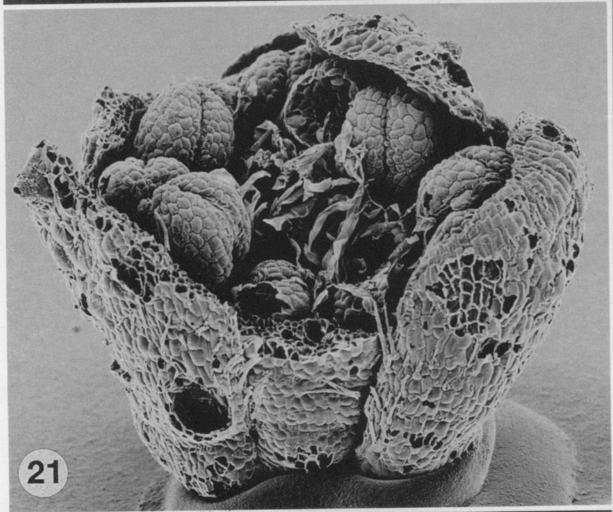

16

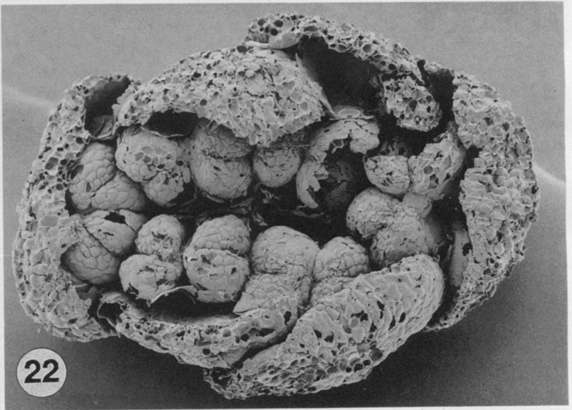

1
2
3
17

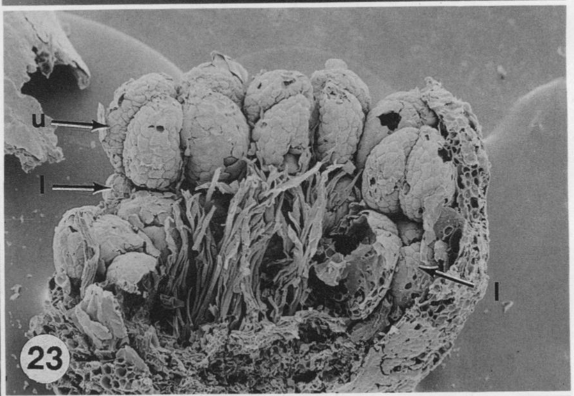

18

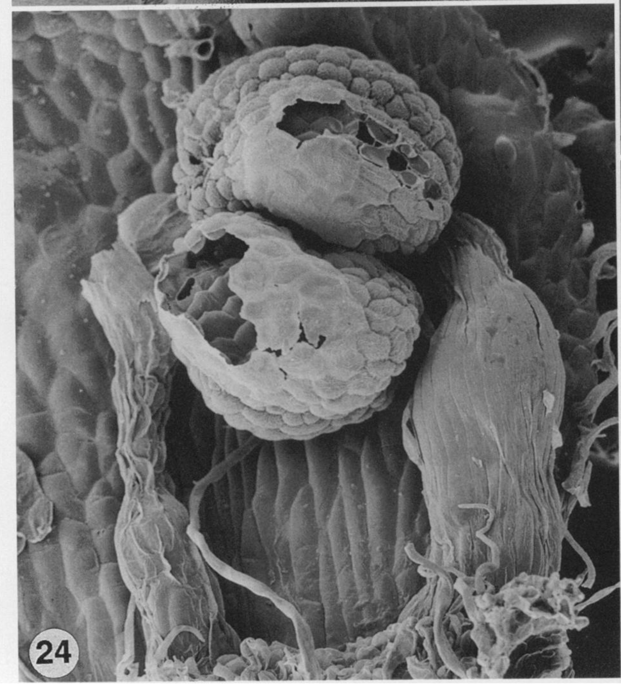

19

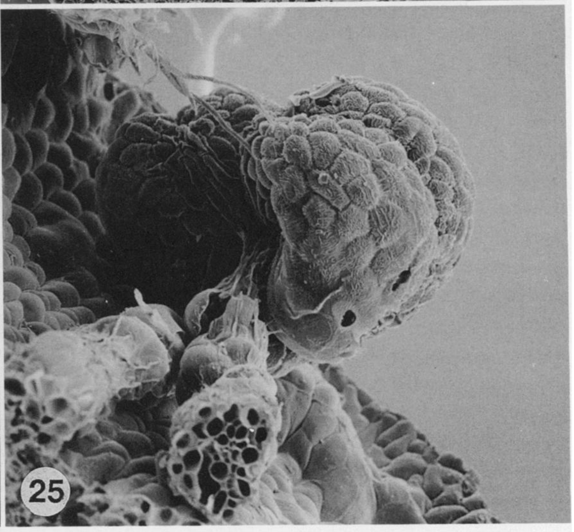

20


21


22


23


24


25

are sometimes smaller than the others in the dichasium and occasionally have reduced numbers of stamens (10–8) and tepals (5–4). In dissected buds and young flowers it is clear that two cycles of stamens are present; the outer cycle is alternate to the tepals, and the inner cycle is opposite the tepals. The cycle of stamens alternate to the tepals emerges first and has thicker filaments (figs. 29, 30, arrows) than the cycle of stamens opposite the tepals. Anthers of the alternate cycle are positioned higher in the bud than are the anthers of the opposite cycle (figs. 23, 27, arrows). Stamens are composed of filaments and dorsifixed anthers (figs. 24, 25) that dehisce by two simple longitudinal slits. Filaments are ca. 1–1.5 mm long, with simple trichomes, and anthers are ca. 0.15 mm long and 0.2 mm wide. There is no extensive development of connective tissue either between the thecae or as an apical extension. The center of the flower is occupied by a mass of simple trichomes; there is no ovary. A vestigial gynoecium of three separate styles is usually present among the trichomes; a stigmatic surface is not apparent (figs. 29, 31). Pollen grains are very small, prolate, tricolporate, tectate, reticulate to microfoveolate; polar axis ca. 5.6–7.6 μm long, diameter ca. 4.2–5.4 μm (figs. 32–35).

Associated fruits (figs. 42–48)

The isolated fruits that occur in the same samples as the staminate flowers and dichasia of *Protofagacea allonensis* are either triangular or lenticular in cross section. Approximately 15 specimens have been recovered, of which four are lenticular. The edges of the fruits are sometimes slightly winged (figs. 42, 44). One side of the trigonous fruits is consistently wider than the other two sides (1.4–2.0 mm vs. 1.1–1.7 mm; fig. 44), and the bilateral symmetry of these specimens may indicate that several fruits were grouped together in a cupule (see below). The fruits are 1.7–2.6 mm long and bear short tepals at the apex (figs. 44, 45, 47), showing that they were derived from an inferior ovary. Trigonous fruits bear six tepals, which are shorter than those of the staminate flowers (ca. 0.3 mm) but are similar in width (ca. 0.3–0.4 mm). The perianth has been abraded in most specimens, including all of the lenticular fruits, and details are not clear. Several specimens indicate that the triangular fruits had three separate styles, and the lenticular fruits had two separate styles (figs. 42, 43, 47). However, stigma structure is unknown because all styles are broken below the stigma. Several specimens also demonstrate that stamens or staminodes were present in the pistillate flowers (figs. 44, 47). Numerous simple trichomes are borne on the inner surface of the fruit wall (fig. 48). Fossil pollen identical to that produced by the staminate flowers occurs on the distal portions of several fruit specimens (figs. 36, 37).

Associated cupules (figs. 49–63, 64*B*)

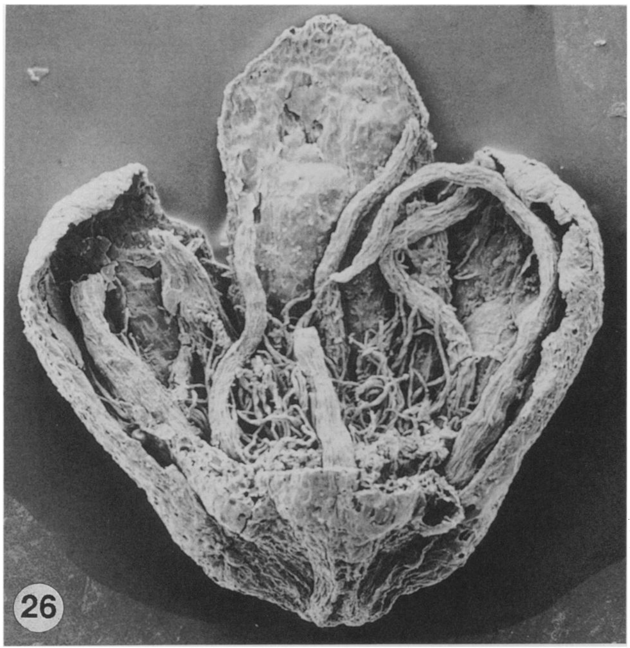
Both mature and immature cupules are present, and five specimens are known from the same samples that yield the staminate flowers, dichasia, and fruits. Three specimens are interpreted to be immature cupules (figs. 49–57), and two appear to have been relatively mature (figs. 58–63). The presumed immature specimens are substantially smaller than the other cupules, particularly in diameter (1.5–2.0 mm vs. 3.0 mm, respectively) and size of the cupule lobes (length 0.5–1.1 mm vs. 1.8 mm, respectively). In addition, the abaxial lamellae on the cupule lobes are better developed on the presumed mature specimens where they form broad horizontal structures (figs. 61, 63). The fruit scars in the center of the presumed immature cupules are suggestive of breakage rather than abscission of mature fruits (figs. 51, 52, 54, 56, 57). The assertion that specimens PP44563 and PP44582 represent mature cupules is based on their being approximately three times larger than the other specimens. In addition, the fruit scar outlines are subtly defined (fig. 58), indicating abscission rather than breakage.

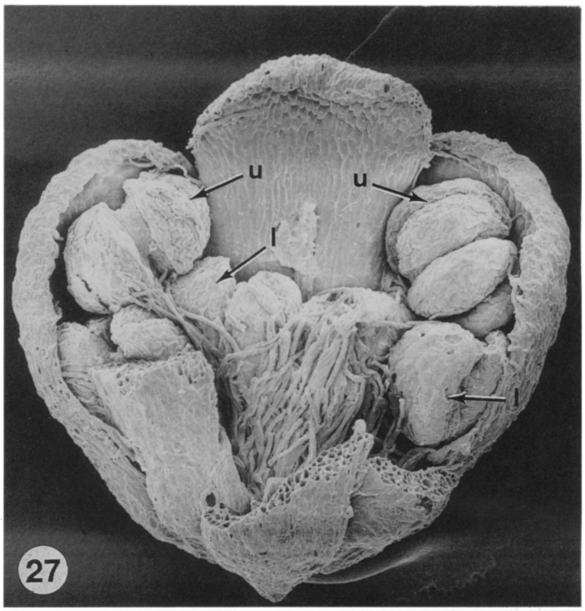
The cupules are pedunculate and four-lobed, and scars on the internal surface show that each cupule bore at least three fruits. The central fruit was lenticular in cross section and lateral fruits were triangular (figs. 51, 52, 54, 56). The peduncle is 0.8–1.4 mm long and 0.6–0.8 mm wide. The cupules are 1.2–4 mm in maximum diameter, which may reflect different stages of maturity, and the cupule lobes are at least 1.8 mm long and 1.7 mm wide at the base in the presumed mature specimens. The outermost structures in the cupule are a series of small bracts that are ca. 0.75 mm long in the more mature specimens. Internal (adaxial) to these small bracts are four larger structures, one of which subtends each of the four primary lobes of the cupule. Adaxial to each of these are two smaller, narrower bracts. Inside these

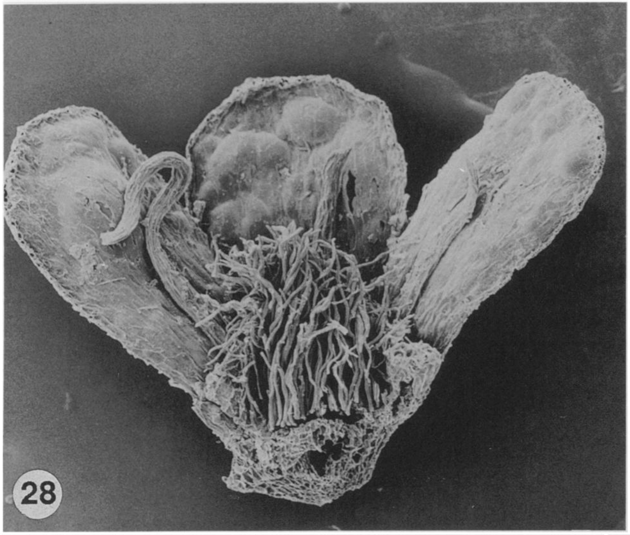
---

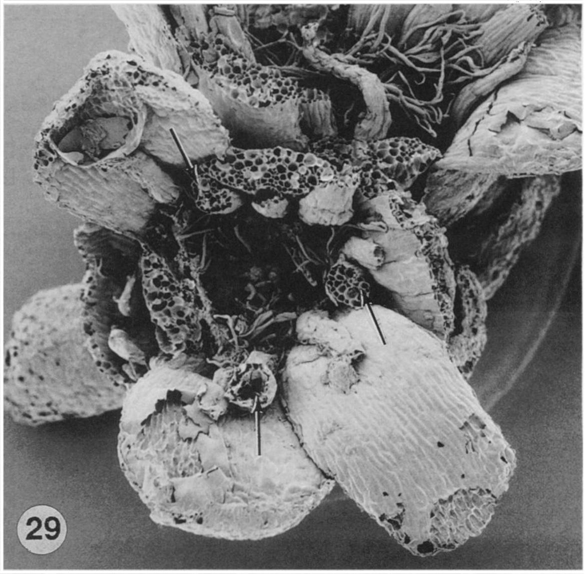
←

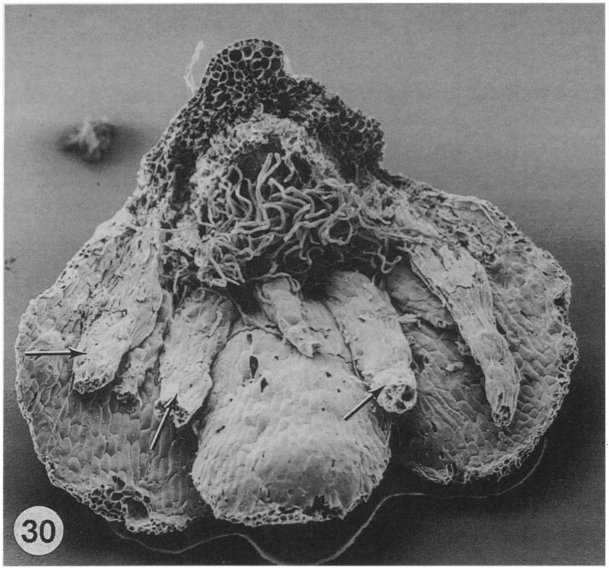
Figs. 19–25 Staminate flower structure in *Protofagacea allonensis*. Fig. 19, Flower bud with six tepals showing several anthers (PP43838). × 100. Fig. 20, Flower bud with two series of three tepals (PP43850). × 100. Fig. 21, Oblique view of flower in fig. 19. × 100. Fig. 22, Flower bud showing anthers of the first cycle of stamens (PP44480). × 100. Fig. 23, Same flower as in fig. 22 after dissection to reveal the anthers of second series of stamens below anthers of the first series. Arrows designated *u* indicate anthers of the first (upper) series; arrows designated *l* indicate anthers of the second (lower) series. × 100. Fig. 24, Dorsifixed anther (PP44523). × 250. Fig. 25, Dorsifixed anther viewed from below (PP44523). × 250.

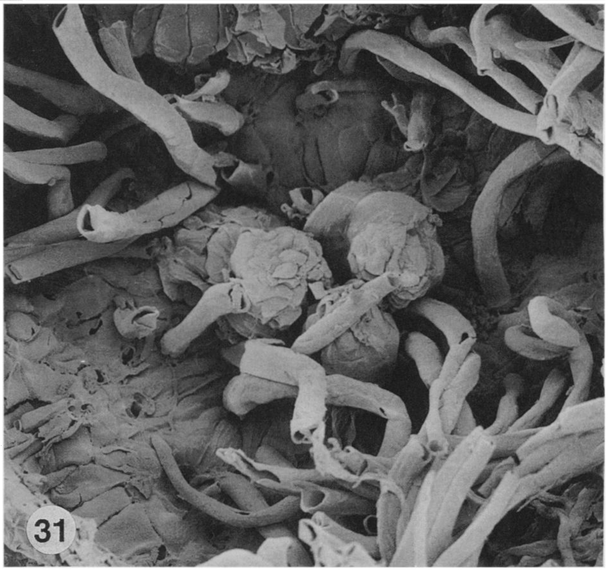

26

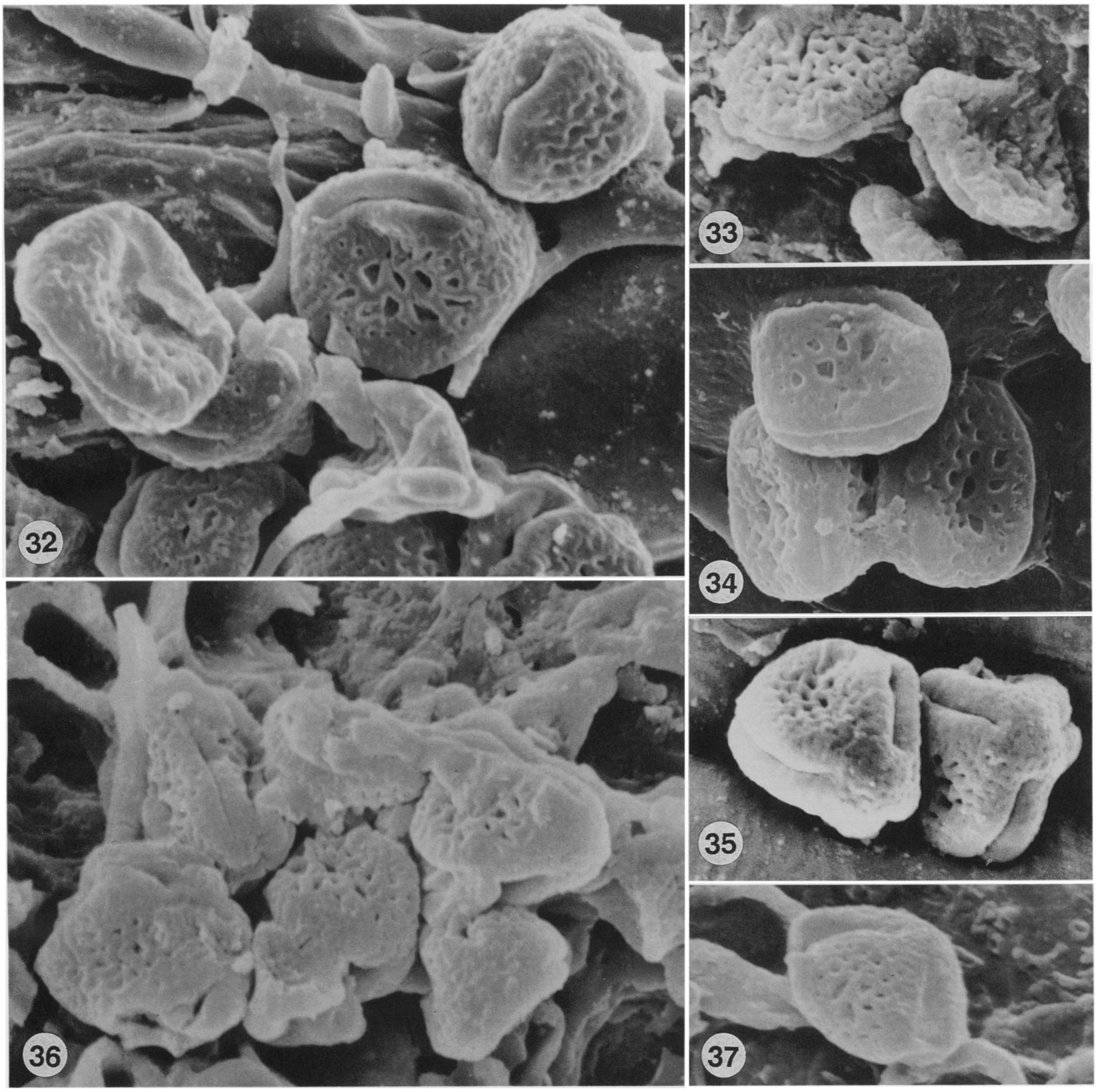

u
u
l
l
27


28


29


30


31

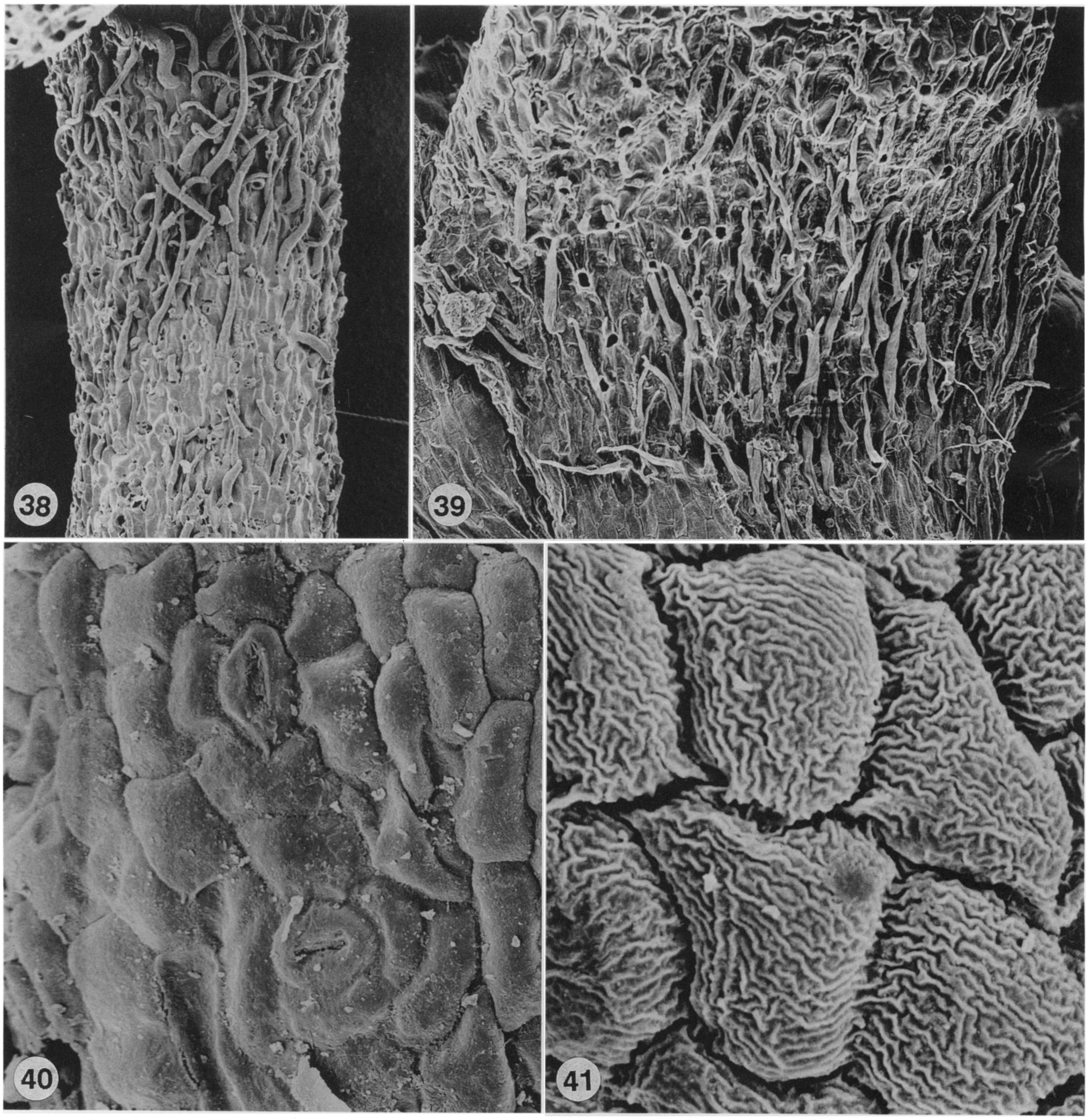


Figs. 32–37 Pollen of *Protofagacea allonensis.* Figs. 32–35, Pollen from staminate flowers showing variation in exine sculpture of the tricolporate grains from microfoveolate (figs. 32 [center], 34) to reticulate (figs. 32, 33, 35). Fig. 32, PP43879. Fig. 33, PP43889. Fig. 34, PP43861. Fig. 35, PP43849. Figs. 36, 37, Pollen from fruits. Fig. 36, PP44557. Fig. 37, PP44558. All × 5,000.

are several higher order bracts that subtend the secondary flowers of the cupule and that are similar in morphology to the bracts of the staminate dichasia (figs. 54–56). Additional series of bracts are present on cupule lobes where additional pistillate flowers appear to have been initiated (figs. 51, 52). Although the fruits are missing from the immature cupules, the outline of the scars reflects

←

Figs. 26–31 Staminate flowers of *Protofagacea allonensis.* Fig. 26, Flower with three tepals removed. Note long filaments alternate and opposite to the tepals (PP44516). × 75. Fig. 27, Flower with three tepals removed. Note inner tepal is longer and narrower than the two outer tepals. Note anthers in two cycles, one above the other. Arrows designated *u* indicate anthers of the first (upper) series; arrows designated *l* indicate anthers of the second (lower) series (PP43912). × 100. Fig. 28, Flower with three tepals removed. Note mass of trichomes in center of flower (PP44514). × 75. Fig. 29, Flower from above showing broken filaments. Note filaments alternate to tepals (arrows) are thicker than filaments opposite the tepals (PP43915). × 75. Fig. 30, Oblique view of flower. Note two size classes of filaments. Arrows indicate filaments alternate to the tepals (PP44472). × 75. Fig. 31, Enlargement of fig. 29 illustrating small pistillode in the center of the flower. × 500.



Figs. 38–41 Epidermal details from staminate dichasia of *Protofagacea allonensis*. Fig. 38, Trichomes on peduncle of staminate dichasium (PP43846). × 250. Fig. 39, Abaxial epidermis of a tepal (PP43834). × 250. Fig. 40, Epidermis with anomocytic stomata (PP44487). × 1,000. Fig. 41, Sculpture pattern on epidermal cells of the anther (PP43838). × 2,300.

the shape of the fruits. The central scar is consistently oblong (0.2–0.3 × 0.5 mm), and the lateral scars are always triangular (0.3–0.4 × 0.3–0.4 × 0.5 mm). The fossil cupules are similar to the staminate inflorescence units in their dichasial organization.

Several cupule specimens show evidence of more than three fruit scars. Two of the immature cupules have two additional, small triangular scars, one flanking each lateral (secondary) fruit scar in the cupule (figs. 51, 52, 56, 57). In both specimens the two additional scars occur on the same side of the secondary fruit scars (figs. 51, 52). The third immature specimen shows no sign of additional scars. One of the presumed mature cupules also appears to have additional scars (figs. 58, 59) along with the abscission scars of the primary and secondary fruits, but all are difficult to distinguish clearly and the total number of scars in this cupule is difficult to determine because the specimen is incomplete. The additional scars measure ca. 0.15 × 0.15 × 0.25 mm (approximately one-half the size of other fruit scars) and appear to occur at two levels on the better preserved of the two cupule lobes (figs. 58, 59). We interpret these scars as either aborted pistillate flowers or very small fruits that were initiated at several levels on the cupule lobes.

A similar situation has been observed in cupules of extant genera such as *Chrysolepis* and *Nothofagus* (Langdon 1947; Hjelmqvist 1948; Brett 1964). Cupules of *Nothofagus dombeyi* frequently contain one or several tertiary fruits (figs. 65–69) that may be much smaller (figs. 66, 68) to nearly the same size (fig. 69) as the primary and secondary fruits. Note that the fruit scars in figure 69, a *Nothofagus* cupule in which three mature fruits have been removed, are subtly defined, similar to the situation in the presumed mature fossil cupule.

ASSOCIATION OF FLOWERS, CUPULES, AND FRUITS

We interpret the fossil staminate flowers, cupules, and fruits described here as dispersed parts of the same plant species for the following reasons: (i) pollen identical to that produced by the staminate flowers occurs on the apical portions of several fruit specimens, (ii) the lenticular fruits are the same size and have the same structural organization as the trigonous fruits, except that they are bicarpellate rather than tricarpellate, (iii) the cupules have triangular and oblong scars that correspond in size to the base of the trigonous and lenticular fruits, and (iv) the staminate dichasia and cupules have the same dichasial inflorescence organization and are very similar in general aspect (cf. figs. 13 and 52, 53; also figs. 14–16 and 64).

Discussion

SYSTEMATICS OF FAGACEAE

Traditional classifications of the family Fagaceae generally recognize approximately 400–800 species, divided among eight to nine genera in two or three subfamilies (Hutchinson 1967; Abbe 1974; Nixon 1989; table 1). In these classifications the Fagaceae *sensu lato* (i.e., including *Nothofagus*) are united by the presence of a cupule (fig. 72*A*). However, the recent treatment by Nixon (1989) differs from traditional systems in several respects, particularly in recognizing the genus *Nothofagus* as a family separate from Fagaceae *sensu stricto,* based on differences in flower, fruit, and pollen structure (table 2). Other innovations in the Nixon classification, such as dividing *Trigonobalanus* into three monotypic genera and grouping *Quercus, Trigonobalanus,* and *Fagus* in the subfamily Fagoideae, are less relevant to the systematic relationships of *Protofagacea.* Resolution of the relationship between Fagaceae and Nothofagaceae is complicated by several apparent similarities between *Nothofagus* and the "higher" hamamelid families Betulaceae, Juglandaceae, Myricaceae, and Casuarinaceae, which are placed together as sister to *Nothofagus* by Nixon (1989) (fig. 72*B*). For example, like Juglandaceae, Myricaceae, and Betulaceae (excluding *Carpinus* [Cronquist 1981]), *Nothofagus* is reported to have unitegmic ovules, whereas the ovules of Fagaceae *sensu stricto* and Casuarinaceae are bitegmic. Similarly, the pollen grains of *Nothofagus,* Betulaceae, Juglandaceae, and Myricaceae have a granular exine, as compared with a columellate exine in Fagaceae *sensu stricto* (Nixon 1989). Three recent cladistic analyses utilizing data from chloroplast DNA have yielded phylogenetic hypotheses that differ somewhat from Nixon (1989), although they also fail to support the monophyly of the Fagaceae *sensu lato.* Manos et al. (1993) group the "higher" hamamelids as sister to Fagaceae *sensu stricto,* with *Nothofagus* sister to this larger clade (fig. 72*C*), whereas Chase et al. (1993) and Martin and Dowd (1993) recognize Fagaceae *sensu stricto* as paraphyletic to the "higher" hamamelids with *Nothofagus* basal to this group (fig. 72*D*).

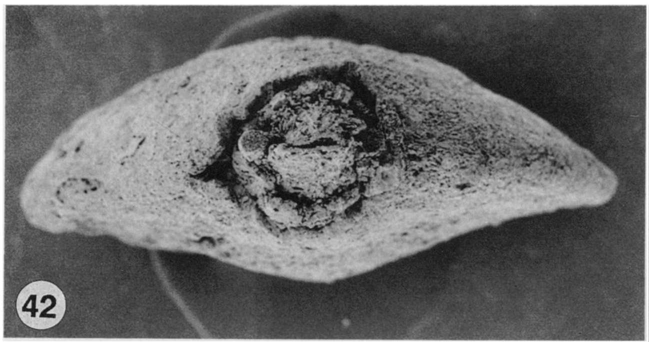
SYSTEMATIC RELATIONSHIPS OF PROTOFAGACEA

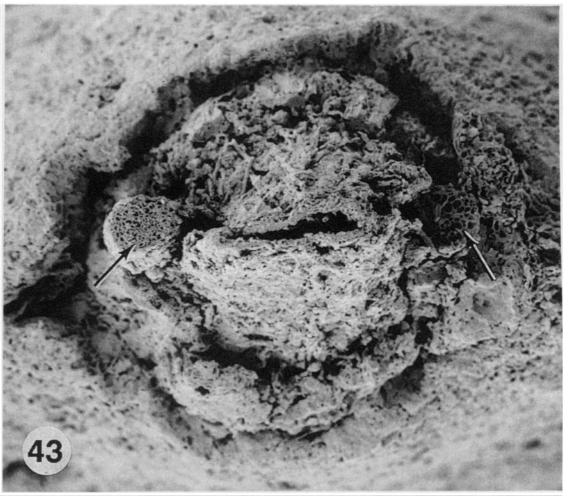
Information on cupules, fruits, and staminate inflorescences and flowers provides numerous

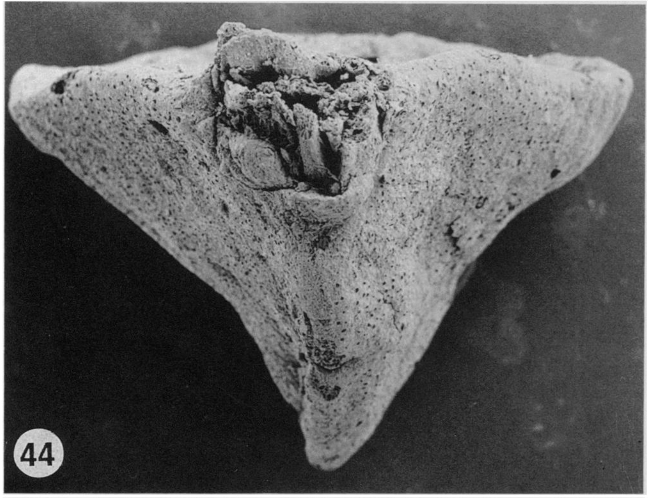
⟶

Figs. 42–48 Fruits associated with *Protofagacea allonensis.* Figs. 42, 43, Lenticular bicarpellate fruit (PP44561). Fig. 42, × 40. Fig. 43, Enlargement of apex to illustrate bases of two styles (arrows). × 100. Figs. 44–46, Triangular tricarpellate fruit. Note tepals in two cycles of three at apex of fruit (PP44557). Figs. 44, 46, × 40; fig. 45, × 75. Fig. 47, Tricarpellate fruit with tepals and three styles evident (PP44577). × 40. Fig. 48, Inner surface of fruit valve bearing numerous trichomes (PP44572). × 250.

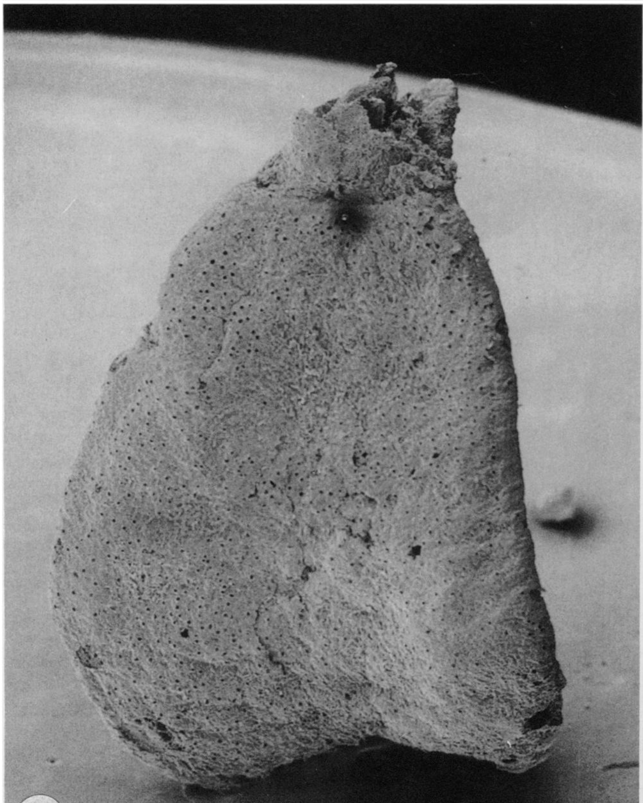
Figs. 49–57 Immature cupules associated with *Protofagacea allonensis.* Figs. 49–52, Cupule viewed from the side and above (PP44567). Figs. 49, 50, Lateral views from both sides illustrating four primary lobes and bracts of the cupule. Note that the cupule is somewhat abraded. Fig. 51, Cupule from above illustrating three scars in the center of the cupule, one oblong scar flanked by two triangular scars. Note that the upper two cupule lobes each bear additional series of bracts subtending what may be an additional pistillate flower, but due to abrasion the details are not clear. Fig. 52, Oblique view of cupule illustrating cupule lobes and central scars. Figs. 53, 54, Cupule with three fruit scars and cupule lobes, showing several series of bracts (PP44564). Fig. 53, Oblique view to illustrate cupule lobes and bracts. Fig. 54, View from above. Note two series of bracts in lower left cupule lobe. Figs. 55–57, Cupule with one tertiary flower/fruit scar in addition to central oblong and two secondary triangular scars (PP44565). Note that the scars on this and the other specimens on this plate resemble breakage scars (cf. scars on specimen of the following plate). Fig. 55, Oblique view of cupule. Fig. 56, View from above illustrating fruit scars and four cupule lobes with several series of bracts. Fig. 57, Enlargement of center of cupule. Note smaller triangular scar (arrow) flanking larger triangular scar, which is lateral to the central oblong scar. Figs. 49–56, × 30; fig. 57, × 75.

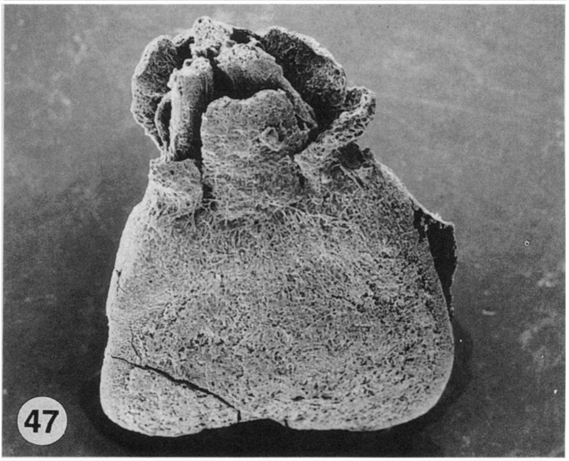

42


43

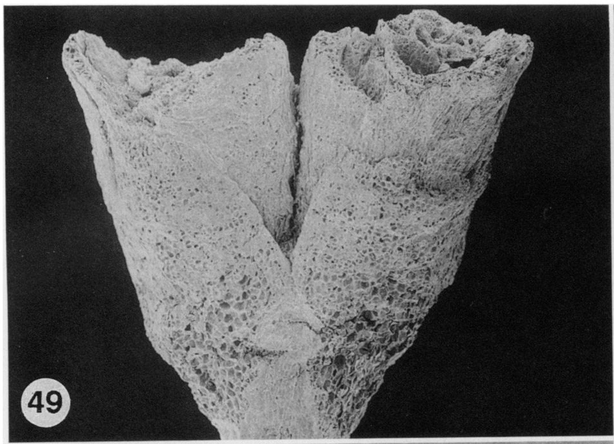

44

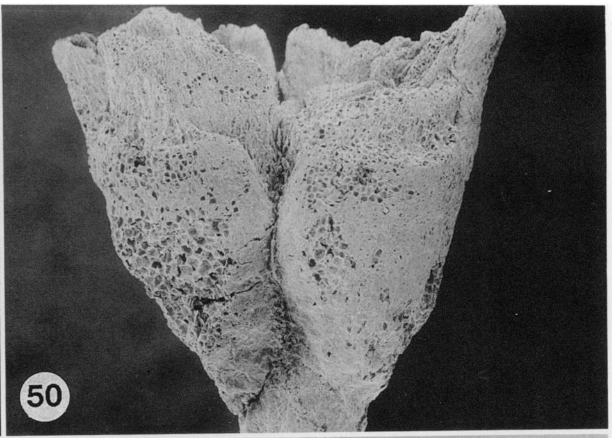

45


46

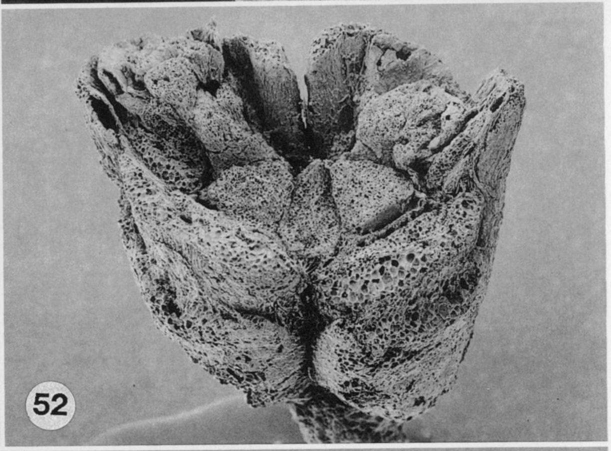

47

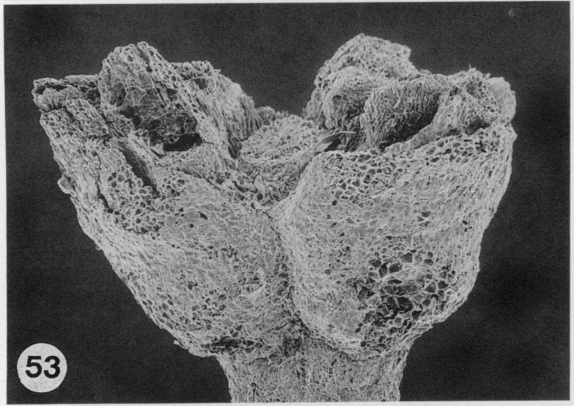

48

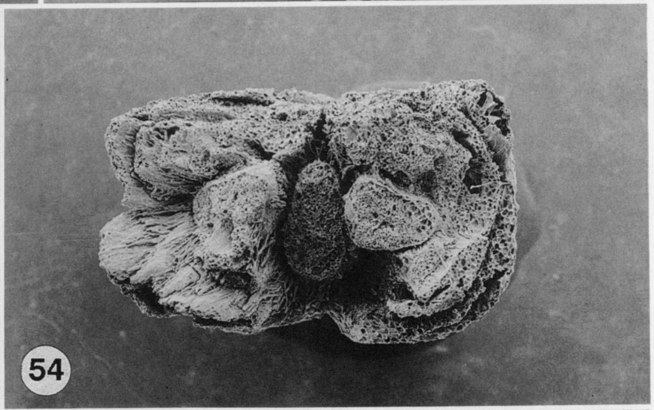

49

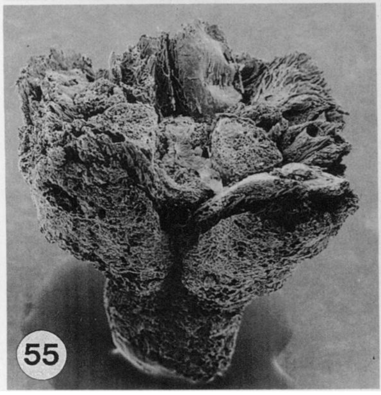

50

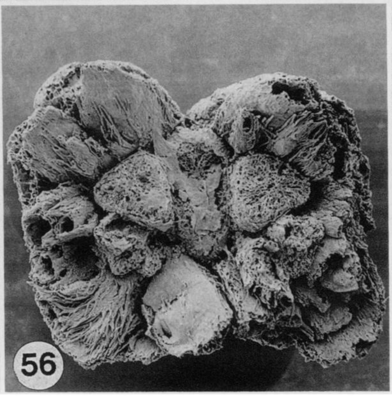

51

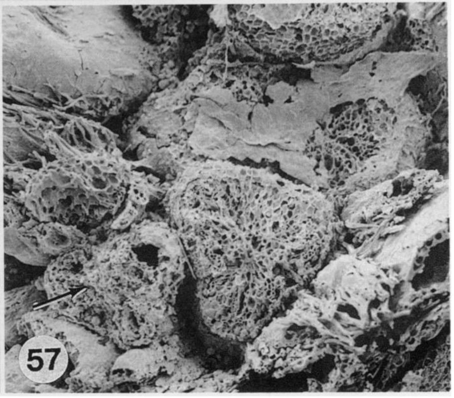

52

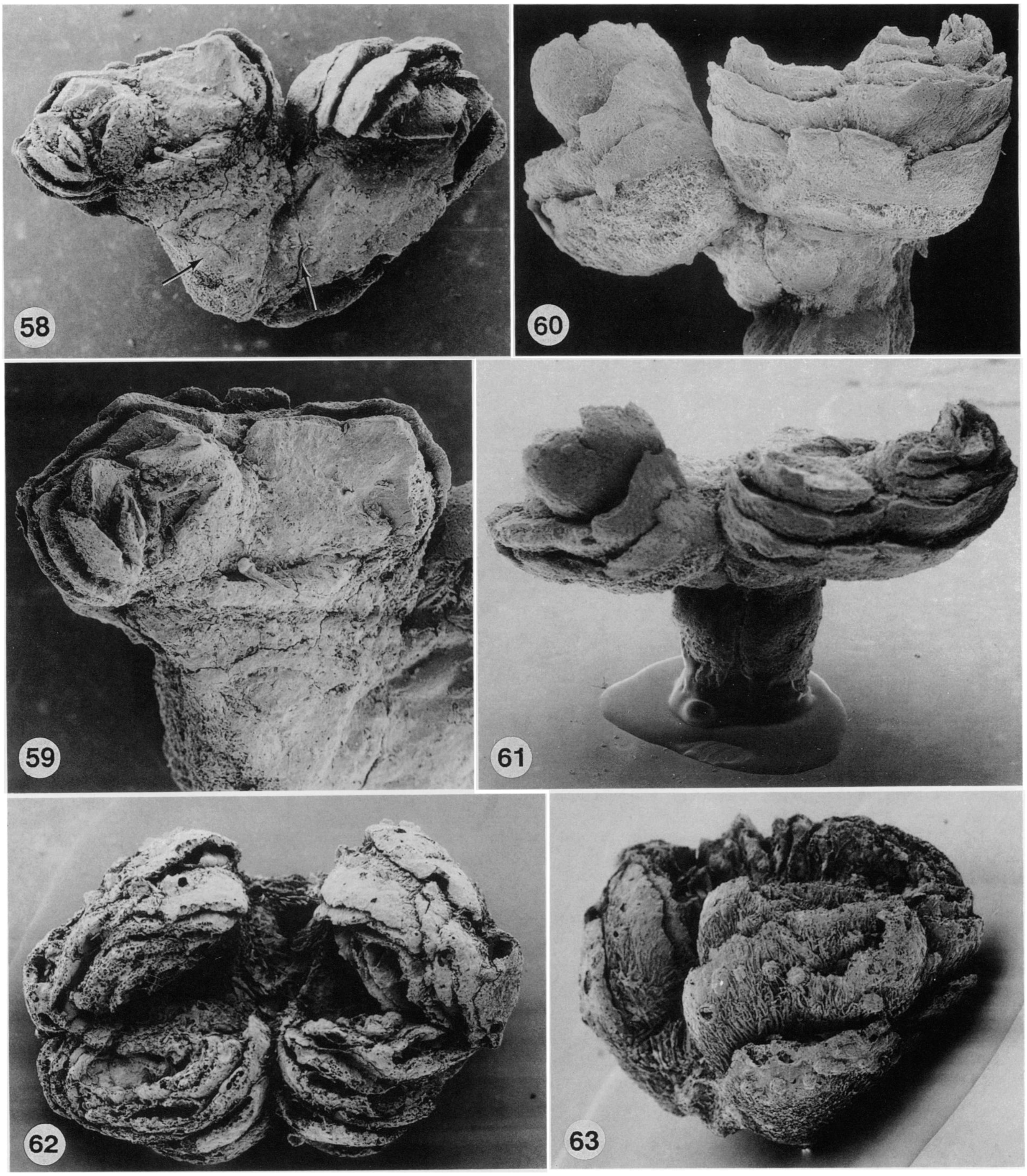

53


54


55


56


57



Figs. 58–63 Mature cupules associated with *Protofagacea allonensis.* Figs. 58–61, PP44563. Fig. 58, View from above to illustrate two primary cupule lobes. Arrows indicate poorly defined fruit abscission scars. Note additional triangular marks on the left lobe. × 25. Fig. 59, Enlargement of left lobe in fig. 58 to illustrate scars, which are subtended by additional series of bracts. × 40. Fig. 60, Lateral view of cupule illustrating horizontal lamellae. Note that many of the lamellae are bilobed. Two of the four outermost bracts are present below the lamellae. × 30. Fig. 61, Oblique view of cupule. Note that the cupule lobe on the right is somewhat bilobed (same lobe as in fig. 59). × 25. Figs. 62, 63, PP44582. Fig. 62, View of cupule from above illustrating four cupule lobes and well-developed abaxial lamellae. × 40. Fig. 63, Lateral view of cupule to illustrate lamellae. × 40.

characters for evaluating the systematic relationships and phylogenetic significance of *Protofagacea.* The presence of a cupule is a potential defining character (i.e., synapomorphy) for the Fagaceae and Nothofagaceae (see below). Numerous other characters of the fossils are also consistent with a relationship to Fagaceae *sensu lato,* including trimerous unisexual flowers, sta-

Table 1

Comparison of classification schemes for Fagaceae sensu lato

Traditional[a]	Nixon (1989)
Fagaceae	Nothofagaceae
Fagoideae	*Nothofagus*
Fagus	Fagaceae
Nothofagus	Fagoideae
Castaneoideae	*Fagus*
Chrysolepis	*Quercus*
Castanea	*Trigonobalanus*
Castanopsis	*Colombobalanus*
Lithocarpus	*Formanodendron*
Quercoideae	Castaneoideae
Quercus	*Chrysolepis*
Trigonobalanus[b]	*Castanea*
	Castanopsis
	Lithocarpus

[a] For example, Forman (1964), Hutchinson (1967), Abbe (1974).

[b] Also placed in Fagoideae (Melchior 1964) or unassigned (Abbe 1974).

minate and pistillate flowers in separate dichasial inflorescence units, and trigonous and lenticular fruits derived from inferior ovaries. Taken together, these features provide strong support for assigning *Protofagacea* to the Fagaceae.

Within the extant Fagaceae *sensu stricto* and Nothofagaceae, *Protofagacea* shares some features with *Nothofagus* and other features with Fagaceae *sensu stricto,* primarily the castaneoids (table 3). In general aspect the fossil cupule is most similar to cupules of several species of *Nothofagus,* especially those species with horizontal lamellae on the outer surface of the cupule valves (e.g., *Nothofagus antarctica, Nothofagus dombeyi*). In addition, the cupules in both *Protofagacea* and *Nothofagus* have a lenticular, bicarpellate central fruit and trigonous, tricarpellate lateral fruits. Among extant taxa this character generally occurs only in *Nothofagus,* although it has been reported occasionally in extant *Fagus* (P. S. Manos, personal communication). In most respects *Protofagacea* is more similar to genera of Fagaceae *sensu stricto.* For example, the fruits of *Protofagacea* are similar to Fagaceae *sensu stricto* in bearing numerous trichomes on the inner surface of the fruit walls (fig. 48), whereas the fruits of *Nothofagus* lack trichomes in the locules. The fossil fruits of *Protofagacea* bear two cycles of tepals (two cycles of three tepals in the trigonous fruits; figs. 44, 45, 47) like Fagaceae *sensu stricto,* whereas only one cycle of tepals is present in the mature fruit of *Nothofagus* (figs. 65, 66, 68). Similarly, the fruits assigned to *Protofagacea* bear stamens or staminodes and the staminate flowers bear pistillodes: neither of these features occurs in *Nothofagus,* but they are shared with certain other Fagaceae, particularly the castaneoids, where they are interpreted to be plesiomorphic features (Nixon 1989). Other characters of *Protofagacea* shared with the castaneoids include staminate flowers composed of six tepals and 12 stamens with very small dorsifixed anthers and staminate dichasia primarily composed of seven flowers. The fossil staminate dichasia are particularly similar to the castaneoid genus *Chrysolepis* in bearing several orders of bracteoles in the dichasium (Hjelmqvist 1948), but because staminate inflorescence structure has not been closely studied among extant genera this character may occur more widely. In contrast, the

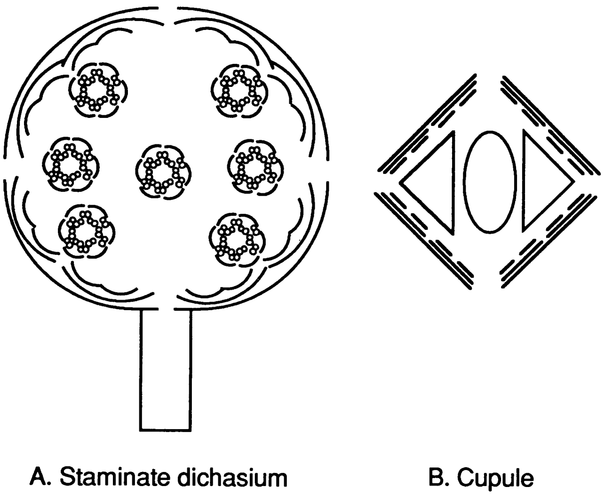
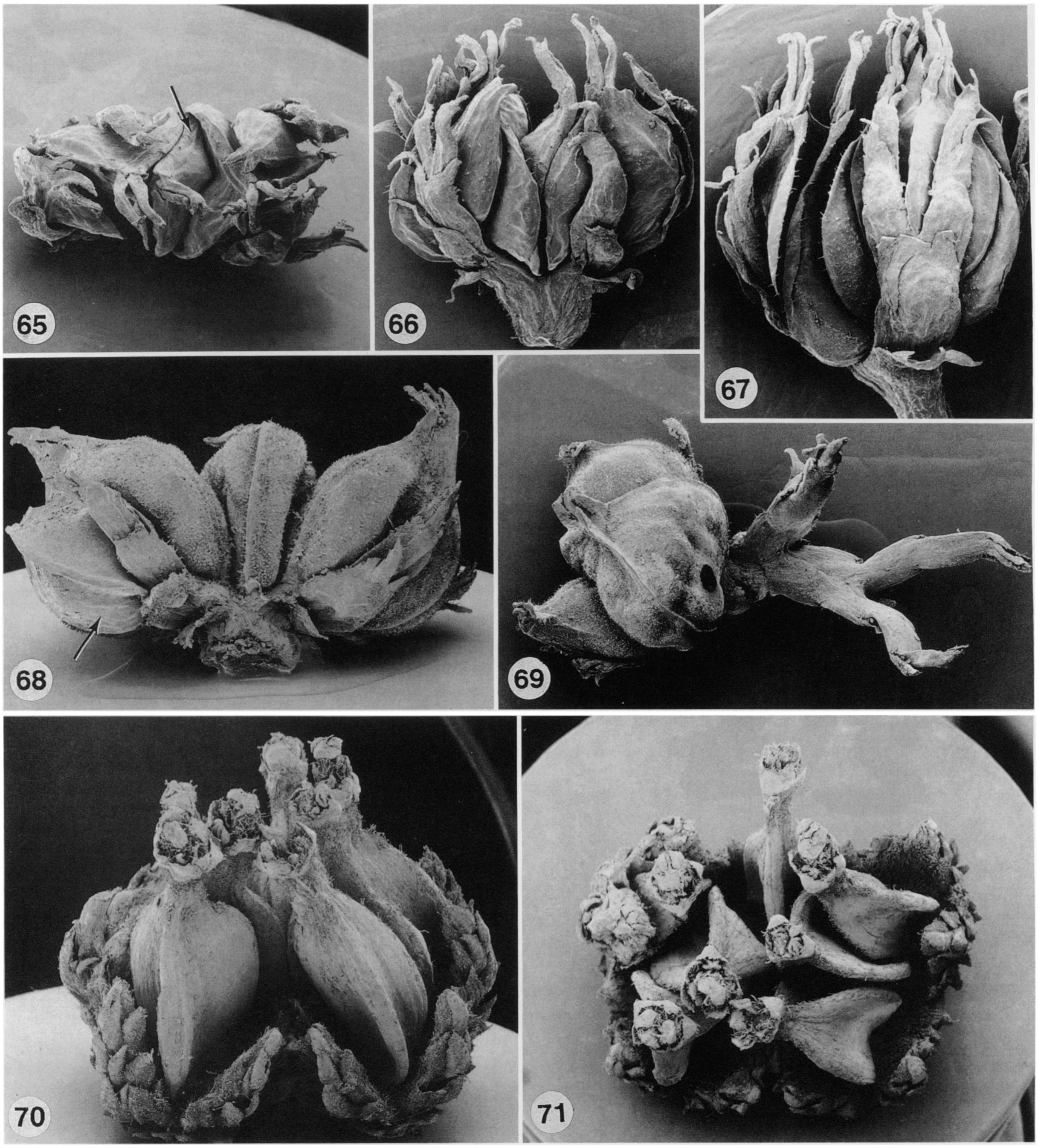


Fig. 64 Schematic diagrams of fossil staminate dichasium (*A*) and cupule (*B*) showing structural organization.

Table 2

Differences between Nothofagus and Fagaceae sensu stricto

	Nothofagus	Fagaceae *sensu stricto*
Ovules	Unitegmic	Bitegmic
Anthers	Basifixed	Dorsifixed
Connective extension	Pronounced	Lacking
Pollen exine	Granular	Columellate
Peltate foliar glands	Present	None
No. of cycles of tepals borne by fruits	1	2
Fruit locule	Glabrous	With trichomes



Figs. 65–71 Cupules and fruits of *Nothofagus* and *Trigonobalanus* (all from F). Figs. 65–67, Cupules of *Nothofagus dombeyi* showing primary, secondary, and tertiary fruits (A. L. Cabrera 5973). Note only one cycle of tepals is present at the apex of the fruits. Fig. 65, View from above. Note central fruit (arrow) is lenticular and bears two styles. Fig. 66, Lateral view of cupule. Note cupule lobe on the left is bifid and subtends a small tertiary fruit. Fig. 67, A different cupule from the same specimen showing a deeply bilobed cupule lobe subtending a well-developed tertiary fruit. Figs. 68, 69, Cupules of *N. dombeyi* showing variation in cupule structure (Schlegel 758). Fig. 68, Cupule bearing one primary, two secondary, and one small tertiary fruit (arrow). Note cupule lobe bearing tertiary fruit is not branched. Fig. 69, Cupule bearing one secondary and two tertiary fruits on the left side. The primary, secondary, and tertiary fruits have been removed from the right side of the cupule. Note the divided cupule lobe that bore the tertiary fruit. Figs. 70, 71, Cupule and fruits of *Trigonobalanus verticillata* (W. L. Chew & E. J. H. Corner, RSNB no. 7021). Fig. 70, Oblique lateral view of cupule. Note two cycles of three tepals at the apex of the fruits. Fig. 71, View of cupule from above. Note all of the cupule fruits are trigonous. All figures × 10.

Table 3

COMPARISON OF REPRODUCTIVE FEATURES IN FAGACEAE, NOTHOFAGACEAE, AND PROTOFAGACEA

Taxa	Staminate inflorescence	Staminate flowers per dichasium	Peduncle of dichasium	Staminate flowers	Number of stamens	Anther size shape, and attachment
Castanea	Compound	3–7(–20)	Sessile	Sessile	(6–)12(–18)	Small, square, dorsifixed, versatile
Castanopsis	Compound	1–7	Sessile	Sessile	(10–)12(–15)	Small, square, dorsifixed, versatile
Chrysolepis	Compound	3–7	Sessile	Sessile	12	Small, square, dorsifixed, versatile
Quercus	Compound	1(–4)	Sessile	Sessile	(4–)5–6(–9)	Moderate, subbasifixed, apex sometimes apiculate
Trigonobalanus	Compound	(1–)3–7(–12)	Sessile	Sessile	6	Moderate, dorsifixed, apex apiculate
Fagus	Simple, axillary	2–20	Filiform, centrally inserted	Sessile to pedicellate	8–16	Moderate, oblong, basifixed, base cordate
Nothofagus	Simple, axillary	1–3	Stout to filiform, centrally inserted	Pedicellate	8–40	Large, linear, apical connective extension, basifixed
Protofagacea	Compound?	(3–)7	Stout, laterally inserted	Sessile	(8–)12	Small, dorsifixed

(*Table continues*)

staminate inflorescences of *Nothofagus* are single axillary dichasia composed of one to three flowers, and the anthers of *Nothofagus* are much larger, elongate, and basifixed and bear an apical connective extension.

Although *Protofagacea* resembles Fagaceae-Nothofagaceae in many respects, several characters of the fossils do not occur among any of the extant genera. In particular the very small pollen grains of *Protofagacea* (5.6–7.6 × 4.2–5.4 μm, polar × equator; table 3) with a reticulate to microfoveolate exine ornamentation are unlike pollen of any extant Fagaceae *sensu lato.* Pollen of the castaneoids, which have the smallest pollen grains of any extant Fagaceae, are 15 × 9 to 20 × 15 μm, tricolporate with a smoothly anastomosing striate exine sculpture. Quercoid pollen is larger (27 × 21 to 29 × 25 μm) and tricolporate, with a scabrate verrucate sculpture pattern. *Fagus* has still larger grains (29 × 28 to 44 × 43 μm), which are also tricolporate with a fine scabrate sculpture pattern. Pollen of *Nothofagus,* which measures ca. 20 × 30 μm, is quite different in being 4-9-colporate with long to very short colpi, a tectate granular exine, and a psilate surface with scattered microspinules (Crepet and Daghlian 1980; Wang 1991). The pollen of *Protofagacea* resembles more closely that found in several potential sister groups to Fagaceae such as Cunoniaceae (Hideux and Ferguson 1976, pl. 3, figs. 1, 2, pl. 6, fig. 8) and Hydrangeaceae (Hideux and Ferguson 1976, pl. 3, fig. 13, pl. 6, fig. 6), in which pollen is frequently less than 10μm in polar length. Pollen size and exine ornamentation in *Protofagacea* are possibly retained plesiomorphies in early Fagaceae.

Protofagacea also apparently differs from Fagaceae-Nothofagaceae in inflorescence structure. Because most of the fossil dichasia bear a laterally attached peduncle and very few specimens have the peduncle centrally attached, we envisage that the inflorescence of *Protofagacea* was probably a spikate axis composed of numerous, pedunculate dichasia. Thus the inflorescence of *Protofagacea* differs from all extant Fagaceae with a compound staminate inflorescence by bearing pedunculate rather than sessile dichasia. The inflorescence of *Protofagacea* also differs from *Nothofagus* and *Fagus,* in which a single dichasium composed of one to numerous, pedicellate to sessile flowers is borne in the axil of a leaf.

In summary, the available characters in *Protofagacea* demonstrate a unique combination that does not occur in any extant taxa. The fossil staminate flowers and dichasia are most comparable to the castaneoids, whereas the fossil cupules, which bear lateral tricarpellate fruits and a central bicarpellate fruit, are almost identical to those of *Nothofagus.* Although the gross morphology and organization of the cupules and fruits are comparable with *Nothofagus,* the locular trichomes are a feature of the Fagaceae *sensu stricto.* Were it not for the unique pollen structure of *Protofagacea* compared with extant Fagaceae-Nothofagaceae, it is conceivable that the staminate and pistillate organs, if only known independently,

Table 3 (*Extended*)

Taxa	Pollen size (μm)	Pollen exine sculpture	Pollen aperture type and number	Pistillode in staminate flower	Staminodes in pistillate flower
Castanea	15 × 9 to 17 × 10	Smooth, anastomosing striate	Tricolporate	Sometimes present	Present
Castanopsis	16 × 10 to 20 × 15	Smooth, anastomosing striate	Tricolporate	Villous rudimentary cushion present	Present
Chrysolepis	17 × 11	Smooth, anastomosing striate	Tricolporate	Present, tomentose	Present
Quercus	21 × 21 to 23 × 35	Scabrate, verrucate, rugulate	Tricolporate	Absent, tuft of trichomes sometimes present	Present or absent
Trigonobalanus	18 × 20 to 28 × 22	Scabrate, verrucate, rugulate	Tricolporate	Absent, tuft of trichomes present	Present
Fagus	29 × 28 to 44 × 43	Fine scabrate, fused small horizontal rods	Tricolporate	Absent	Absent
Nothofagus	20 × 30	Psilate with microspinules	4–9-colporate, colpi long to very short	Absent	Absent
Protofagacea	6 × 4 to 8 × 6	Microfoveolate	Tricolporate	Three styles present, surrounded by trichomes	Present

could be assigned to the Castaneoideae and Nothofagaceae, respectively. *Protofagacea* clearly belongs in the Fagaceae-Nothofagaceae clade(s), but an understanding of its precise relationships must await more information on the fossils as well as a detailed resolution of phylogenetic relationships among Fagaceae, Nothofagaceae, and relevant "higher" hamamelids and rosids. The primary character of *Protofagacea* that remains to be clarified in better preserved material is the nature of the style and stigma, which have been used to group *Quercus* and the trigonobalanoids (flattened styles with terminal capitate or swollen stigmas) relative to other Fagaceae (slender, round styles with a stigma that is medially decurrent—*Fagus,* or terminal and punctate—castaneoids).

ORIGIN AND HOMOLOGY OF THE FAGACEOUS CUPULE

There has been considerable debate concerning the origin of the cupule in Fagaceae (Berridge 1914; Hjelmqvist 1948; Brett 1964; Forman 1966; Abbe 1974; Endress 1977; Macdonald 1979; Fey 1981; Fey and Endress 1983; Kaul and Abbe 1984; Nixon 1989). This structure has been interpreted morphologically as fused inflorescence bracts, a de novo intercalary structure of the inflorescence axis, or a cladode-like structure formed from the outer (ultimate order) sterile axes of the dichasial inflorescence. Most morphologists now accept the latter view, and interpret the cupule as formed from the sterile compact outer (ultimate) axes that flank the highest order flowers in the pistillate dichasium. Fey and Endress (1983) have further elaborated this model by demonstrating that each cupule lobe represents an entire sterile cymose branching system of several orders rather than just one sterile branch of the pistillate inflorescence. Under this interpretation the cupule appendages (scales, thorns) in extant Fagaceae may be interpreted as the pherophylls (= bracts) of the lateral sterile branches that constitute the cupule lobes.

The fossil material described here is consistent with the interpretation of Fey and Endress (1983) that the pistillate inflorescence is dichasial in construction and that the cupule lobes are sterile complex parts of the dichasium. The fossil cupules bear at least three pistillate flowers in a cymose arrangement, and each of the two secondary flowers is subtended by several series of bracts that are inserted on two lateral axes to yield a four-lobed cupule. The fossil staminate dichasia normally bear one more order of flowers than the cupules (i.e., seven vs. three flowers) but otherwise have an identical organization and arrangement of bracts, which supports the morphological interpretation of the fossil cupules.

Although the cupules of *Nothofagus* and Fagaceae *sensu stricto* are morphologically similar and have a comparable structural organization and developmental pattern, there have been sug-

Table 3 (*Extended*)

Number of carpels	Style and stigma shape	Number of tepal cycles on mature fruit	Fruit cross section	Trichomes in fruit locule	Ovules	Cupule appendages
6–9	Slender with terminal pore	2	Rounded irregular	Present	Bitegmic	Spines
3(–5)	Slender with terminal pore	2	Rounded irregular	Present	Bitegmic	Spines and lamellae
3	Slender with terminal pore	2	Triangular	Present	Bitegmic	Spines
3(4–6)	Stout with capitate or decurrent stigma	2	Round	Present	Bitegmic	Scales and lamellae (subgenus *Cyclobalanopsis*)
3	Stout with capitate stigma	2	Triangular	Present	Bitegmic	Scales
3	Slender with decurrent stigma	2	Triangular	Present	Bitegmic	Scales
2 (central), 2 or 3 (lateral)	Slender, stigmatic distally	1	Lenticular and triangular	Absent	Unitegmic	Lamellae
2 (central), 3 (lateral)	Unknown	2	Lenticular and triangular	Present	Unknown	Lamellae

gestions that the cupules of these two groups are not homologous. Following the phylogenetic interpretations of Nixon (1989) or Manos et al. (1993) it is equally parsimonious to hypothesize independent origins of the cupule in Fagaceae *sensu stricto* and Nothofagaceae or a single origin of the cupule followed by its loss in the Betulaceae-"higher" Hamamelididae clade (fig. 72*B, C*). Nixon (1989) notes that in *Nothofagus alessandri* there is a variable number of flowers in the cupule (three to seven), yet the cupule is consistently four-valved. He also notes that the cupules of *Nothofagus* species of the *brassii* group are always two-valved at maturity regardless of whether there are one or three flowers or fruits. Both of these observations conflict with the situation in the cupules of Fagaceae *sensu stricto,* in which the number of valves equals the number of flowers plus one (N + 1) and were interpreted as possible evidence of nonhomology by Nixon (1989). However, other species of *Nothofagus* do follow the N + 1 rule, even when the number of flowers exceeds three. Cupules of *N. dombeyi* bear three to seven fruits, and the number of cupule lobes is usually equal to N + 1 (figs. 65–67, 69). Where four-lobed cupules bearing four fruits do occur (fig. 68), the extra fruit is generally much smaller than the other fruits. Similarly, Brett (1964) notes that, in cupules with extra flowers that are either male or pistillate and poorly developed, the cupule lobe will be slightly cleft (fig. 66), but if the extra flower forms a well-developed fruit, then the lobe will be deeply divided (figs. 67, 69). In our view, notwithstanding the recent analysis of relationships within *Nothofagus* by Hill and Jordan (1993), currently there are insufficient data to evaluate the evolution of the cupule in *Nothofagus.* Therefore it is impossible to determine whether the apparent anomalies noted by Nixon (1989) are derived or general within the genus.

EVOLUTIONARY HISTORY OF THE FAGACEAE

The early fossil history of the families Fagaceae and Nothofagaceae, and their constituent genera, has received considerable attention (e.g., Manchester and Crane 1983; Romero 1986, 1993; Jones and Dilcher 1988; Crepet 1989; Kvacek and Walther 1989; Dettmann et al. 1990; Hill 1991, 1994; table 4). The earliest evidence of the Fagaceae *sensu lato* is provided by dispersed pollen grains of *Nothofagidites senectus* from early Campanian and younger strata of southern Gondwana (Dettmann et al. 1990). Subsequently, *Nothofagus*-like pollen becomes diverse through the Late Cretaceous in high latitude areas of the Southern Hemisphere. The earliest report of fossil *Nothofagus* cupules is from the early Oligocene of Tasmania (Hill 1994). By the late Oligocene megafossils of *Nothofagus* are relatively abundant in Tasmania, Antarctica, and South America (Hill 1983, 1984, 1991, 1994; Romero 1986, 1993).

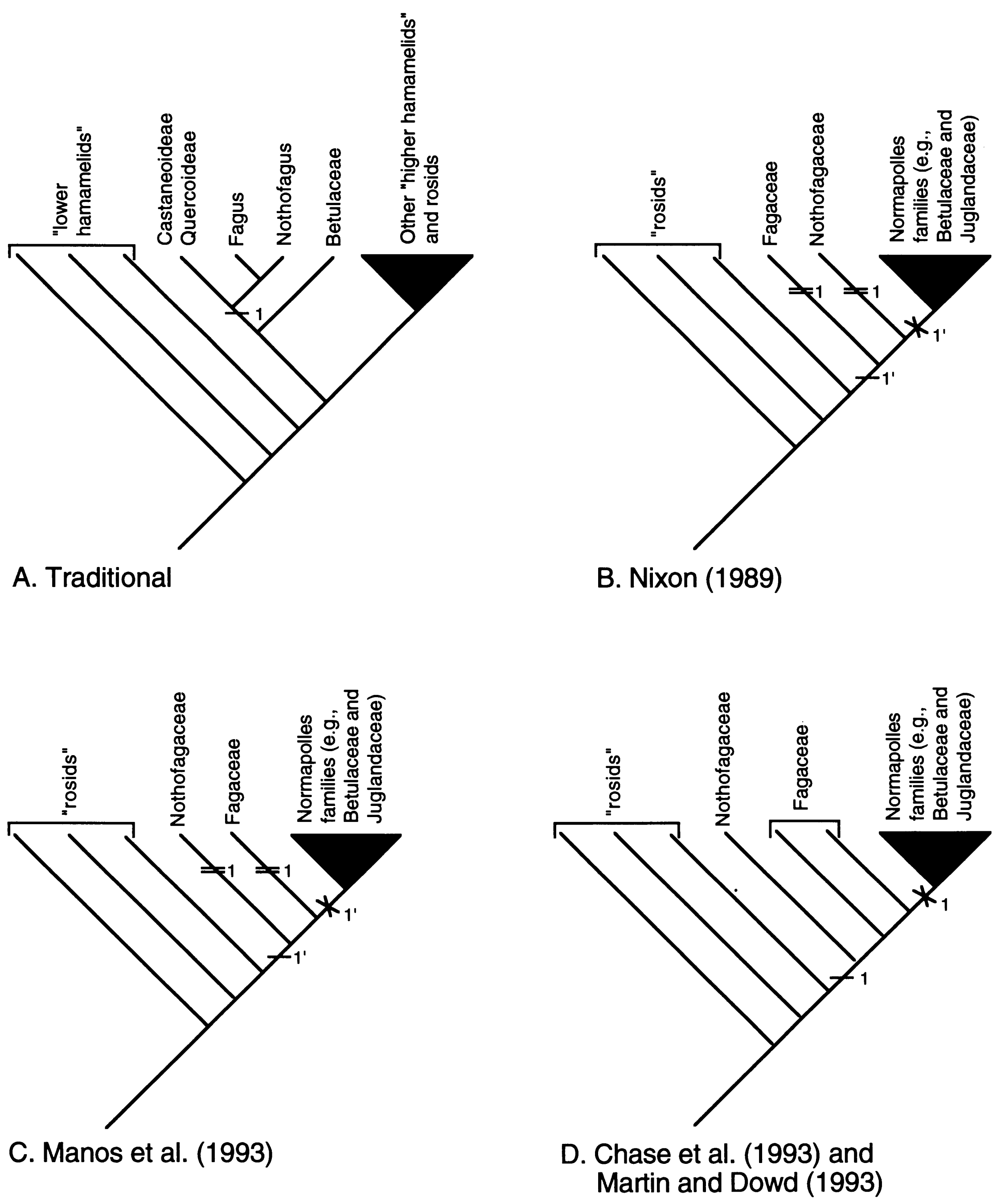


Fig. 72 Cladograms illustrating three contrasting hypotheses of relationships among Fagaceae, Nothofagaceae, and Normapolles families (e.g., Betulaceae and Juglandaceae). *A*, Traditional scheme with Fagaceae monophyletic including *Nothofagus* sister to *Fagus*. The family is united by the presence of the cupule (1). *B*, Hypothesis of Nixon (1989) in which *Nothofagus* is recognized as a separate family sister to the Normapolles families. In this topology either the cupule has originated independently in Fagaceae and Nothofagaceae or it arose once and was subsequently lost in the lineage leading to the Normapolles group. *C*, Hypothesis of Manos et al. (1993) based on data from chloroplast DNA with Fagaceae *sensu stricto* sister to the Normapolles families. Consequences for evolution of the cupule as in the Nixon hypothesis (fig. 72*B*). *D*, Hypothesis of Chase et al. (1993) and Martin and Dowd (1993) based on data from chloroplast DNA with Fagaceae paraphyletic to the Normapolles families. For this topology it is more parsimonious to hypothesize a single origin and loss for the cupule.

In the Northern Hemisphere the earliest plausible evidence of the Fagaceae *sensu stricto* is based on dispersed castaneoid pollen (Chmura 1973) from the Maastrichtian of California, but the affinities of this material require reconfirmation by detailed scanning and transmission electron microscopy (Crepet 1989). The earliest megafossil evidence of Fagaceae *sensu stricto*, prior to this article is from early Eocene and younger strata. Castaneoid staminate inflorescences, fruits and

Table 4

Summary of selected megafossils of the Fagaceae and Nothofagaceae

Taxa	Locality and age	Structure	Relationship	Primary reference
Nothofagus spp.	Five localities in Tasmania and Antarctica; Oligocene to Pleistocene	Leaves and cupules	*Nothofagus*	Hill (1991)
Pseudofagus	Clarkia, Idaho; Miocene	Cupule with fruit	Close to *Fagus*	Smiley and Huggins (1981)
Castanopsis	Europe; Oligocene-Miocene	Fruits	*Castanopsis*	Mai (1989*a*)
Nothofagus cethanica	Tasmania; early Eocene to uppermost Oligocene, precise age uncertain	Leaves	*Nothofagus*	Hill (1984)
Nothofagus johnstonii	Tasmania; Oligocene	Leaves	*Nothofagus*	Hill (1983)
Fagopsis	Florissant, Colo.; Oligocene	Leaves, staminate and pistillate inflorescences and infructescences	? Fagaceae	Manchester and Crane (1983)
"Contracuparius"	Huntsville, Tex.; Oligocene	Infructescence with cupules and fruits	"Pre-trigonobalanoid"	Crepet and Nixon (1989*b*)
"Amentogerdiopollenites" and "Amentoplexipollenites"	Huntsville, Tex.; Oligocene	Staminate catkins	"Pre-trigonobalanoid"	Crepet and Nixon (1989*b*)
"Parvobalanus" and "Amplobalanus"	Huntsville, Tex.; Oligocene	Staminate catkins	"Pre-trigonobalanoid"	Crepet and Nixon (1989*b*)
Quercus oligocenensis	Huntsville, Tex.; Oligocene	Staminate catkins; also cupule and leaves of *Quercus* present	*Quercus* subgenus *Erythrobalanus*	Daghlian and Crepet (1983)
Nothofagus smithtonensis	Little Rapid River, Tasmania; Early Oligocene	Cupule with fruits	*Nothofagus* subgenus *Brassospora*	Hill (1994)
Quercus, Castanea and *Fagus* spp.	Baltic Amber; Eocene	Flowers	Castaneoideae *Quercus* and *Fagus*	Conwentz (1886)
Trigonobalanus andreanszkyi	Europe; Upper Eocene/Lower Oligocene	Cupules with fruits	Trigonobalanoid?	Mai (1970)
Quercus paleocarpa	Clarno, Oreg.; Middle Eocene	Cupule with fruit	*Quercus*	Manchester (1994)
Castanopsis	Clarno, Oreg.; Middle Eocene	Cupule with fruits	*Castanopsis*	Manchester (1994)
Castaneoidea	Puryear, Tenn.; Claiborne Formation, Middle Eocene	Staminate inflorescence	Castaneoideae	Crepet and Daghlian (1980)
Berryophyllum	Kentucky and Tennessee; Claiborne Formation, Early and Middle Eocene	Leaves	Fagaceae	Jones and Dilcher (1988)
Castanophyllum	Kentucky and Tennessee; Claiborne Formation, Early and Middle Eocene	Leaves	Castaneoideae	Jones and Dilcher (1988)
Castanopsoidea	Buchanan, Tenn.; Claiborne Formation, Early Eocene	Cupules with fruits	Castaneoideae	Crepet and Nixon (1989*a*)
Trigonobalanoidea	Buchanan, Tenn.; Claiborne Formation, Early Eocene	Infructescence with cupules and fruits	Trigonobalanoid	Crepet and Nixon (1989*a*)
Paleojulacea	Buchanan, Tenn.; Claiborne Formation; Early Eocene	Staminate catkins	Trigonobalanoid or possibly Castaneoideae?	Crepet and Nixon (1989*a*)
Protofagacea	Allon, Ga.; Campanian, Late Cretaceous	Staminate dichasia, fruits, and cupules	Early Fagaceae *sensu lato*	This article

cupules, and leaves are known from the early Eocene of Tennessee (Crepet and Daghlian 1980; Jones and Dilcher 1988; Crepet and Nixon 1989*a*). Trigonobalanoid staminate inflorescences, cupules, and fruits have also been documented from the same deposits (Crepet and Nixon 1989*a*), as well as the Oligocene of Texas (Crepet and Nixon 1989*b*). Mai (1970) has reported trigonobalanoid fruits and cupules from upper Eocene/lower Oligocene and younger strata. Although these structures are not precisely like *Trigonobalanus,* they are unequivocally fagaceous (Manchester and Crane 1983). A fossil *Quercus*-like fruit and cupule is known from the Eocene of Oregon (Manchester 1981, 1994), *Quercus*-like staminate flowers and pollen are known from the upper Eocene Baltic Amber (Conwentz 1886; Crepet 1989), and staminate catkins of *Quercus* are known from the Oligocene of Texas (Daghlian and Crepet 1983).

Based on existing knowledge of fagaceous fossils *Protofagacea* significantly extends the megafossil record of the Fagaceae-Nothofagaceae back to the Campanian. These fossils demonstrate the presence of a cupule in early Fagaceae *sensu lato* and document that other major structural features of the group were already differentiated by the Late Cretaceous. Significantly, however, *Protofagacea* indicates that at least some early taxa produced pollen that differs from that of all extant genera, and this underlines the difficulty of inferring the early fossil history of Fagaceae and Nothofagaceae from the dispersed palynological record alone.

Acknowledgments

We thank Peter K. Endress, Kevin C. Nixon, and Paul Manos for critical discussions on the morphology and affinities of the fossil material and Ruth A. Stockey for constructive criticisms during review. We are also indebted to the late Jurgen Reinhardt for first directing us to the Allon locality and the Atlanta Sand and Supply Company for permission to collect. This work was supported in part by NSF grants BSR 90-20237 and INT 90-15123 to P. R. Crane and Australian Research Council Grant A19031108 and DITAC Bilateral Science and Technology Collaboration Program 91/3627 to A. N. Drinnan.

Literature cited

Abbe EC 1974 Flowers and inflorescences of the "Amentiferae." Bot Rev 40:159–261.

Berridge EM 1914 The structure of the flower of Fagaceae, and its bearing on the affinities of the group. Ann Bot 28: 509–526.

Brenner GJ 1963 The spores and pollen of the Potomac Group of Maryland. Md Dep Geol Mines Water Res Bull 27:1–215.

Brett DW 1964 The inflorescence of *Fagus* and *Castanea,* and the evolution of the cupules of the Fagaceae. New Phytol 63:96–118.

Chase MW, DE Soltis, RG Olmstead, D Morgan, DH Les, BD Mishler, MR Duvall, et al 1993 Phylogenetics of seed plants: an analysis of nucleotide sequences from the plastid gene *rbc*L. Ann Mo Bot Gard 80:528–580.

Chmura CA 1973 Upper Cretaceous (Campanian-Maastrichtian) angiosperm pollen from the western San Joaquin valley, California, U.S.A. Palaeontographica Abt B 141: 89–171.

Christopher RA 1979 *Normapolles* and triporate pollen assemblages from the Raritan and Magothy Formations (Upper Cretaceous) of New Jersey. Palynology 3:73–122.

Conwentz H 1886 Die Flora des Bernsteins, Zweiter Band: Die Angiospermen des Bernsteins. Engelmann, Leipzig.

Crabtree DR 1987 Angiosperms of the northern Rocky Mountains: Albian to Campanian (Cretaceous) megafossil floras. Ann Mo Bot Gard 74:707–747.

Crane PR 1987 Vegetational consequences of angiosperm diversification. Pages 107–144 *in* EM Friis, WG Chaloner, PR Crane, eds. The origins of angiosperms and their biological consequences. Cambridge University Press, Cambridge.

——— 1989 Paleobotanical evidence on the early radiation of nonmagnoliid dicotyledons. Plant Syst Evol 162:165–191.

Crane PR, EM Friis, KR Pedersen 1989 Reproductive structure and function in Cretaceous Chloranthaceae. Plant Syst Evol 165:211–226.

——— 1994 Paleobotanical evidence on the early radiation of magnoliid angiosperms. Plant Syst Evol. (in press).

Crane PR, S Lidgard 1989 Angiosperm diversification and paleolatitudinal gradients in Cretaceous floristic diversity. Science 246:675–678.

Crane PR, KR Pedersen, EM Friis, AN Drinnan 1993 Early Cretaceous (Early to Middle Albian) platanoid inflorescences associated with *Sapindopsis* leaves from the Potomac Group of eastern North America. Syst Bot 18:328–344.

Crepet WL 1989 History and implications of the early North American fossil record of Fagaceae. Pages 45–66 *in* PR Crane, S Blackmore, eds. Evolution, systematics and fossil history of the Hamamilidae. Vol 2. "Higher" Hamemilidae. Oxford University Press, Oxford.

Crepet WL, Daghlian, CP 1980 Castaneoid inflorescences from the middle Eocene of Tennessee and the diagnostic value of pollen (at the subfamily level) in the Fagaceae. Am J Bot 67:739–757.

Crepet WL, KC Nixon 1989*a* Earliest megafossil evidence of Fagaceae: phylogenetic and biogeographic implications. Am J Bot 76:842–855.

——— 1989*b* Extinct transitional Fagaceae from the Oligocene and their phylogenetic implications. Am J Bot 76: 1493–1505.

Crepet WL, KC Nixon, EM Friis, JV Freudenstein 1992 Oldest fossil flowers of hamamelidaceous affinity, from the Late Cretaceous of New Jersey. Proc Nat Acad Sci USA 89:8986–8989.

Cronquist A 1981 An integrated system of classification of flowering plants. Columbia University Press, New York.

Daghlian CP, WL Crepet 1983 Oak catkins, leaves and fruits from the Oligocene Catahoula Formation and their evolutionary significance. Am J Bot 70:639–649.

Dettmann ME, DT Pocknall, EJ Romero, M Del C Zamaloa 1990 *Nothofagidites* Erdtman ex Potonié 1960: a catalogue of species with notes on the palaeogeographic distribution of *Nothofagus* Bl. (Southern Beech). NZ Geol Surv Paleontol Bull 60. 79 pp.

Dilcher DL, PR Crane 1985 *Archaeanthus:* an early angiosperm from the Cenomanian of the western interior of North America. Ann Mo Bot Gard 71:351–383.

Doyle JA 1969 Cretaceous angiosperm pollen of the Atlantic Coastal Plain and its evolutionary significance. J Arnold Arbor Harv Univ 50:1–35.

Doyle JA, LJ Hickey 1976 Pollen and leaves from the mid-Cretaceous Potomac Group and their bearing on early angiosperm evolution. Pages 139–206 *in* CB Beck, ed. Origin and early evolution of angiosperms. Columbia University Press, New York.

Drinnan AN, PR Crane, EM Friis, KR Pedersen 1990 Lauraceous flowers from the Potomac Group (mid-Cretaceous) of eastern North America. Bot Gaz 151:370–384.

——— 1991 Angiosperm flowers and tricolpate pollen of buxaceous affinity from the Potomac Group (mid-Cretaceous) of eastern North America. Am J Bot 78:153–176.

Endress PK 1977 Evolutionary trends in the Hamamelidales-Fagales group. Plant Syst Evol Suppl 1:321–347.

Endress PK, EM Friis 1991 *Archamamelis,* hamamelidalean flowers from the Upper Cretaceous of Sweden. Plant Syst Evol 175:101–114.

Fey BS 1981 Untersuchungen über Bau und Ontogenese der Cupula, Infloreszenzen und Blüten sowie zur Embryologie bei Vertretern der Fagaceae und ihre Bedeutung für die Systematik. Diss. University of Zürich. 185 pp.

Fey BS, PK Endress 1983 Development and morphological interpretation of the cupule in Fagaceae. Flora 173:451–468.

Forman LL 1964 *Trigonobalanus,* a new genus of Fagaceae, with notes on the classification of the family. Kew Bull 17: 381–396.

——— 1966 On the evolution of cupules in the Fagaceae. Kew Bull 18:385–419.

Friis EM 1983 Upper Cretaceous (Senonian) floral structures of juglandalean affinity containing Normapolles pollen. Rev Palaeobot Palynol 39:161–188.

——— 1985 *Actinocalyx* gen. nov., sympetalous angiosperm flowers from the Upper Cretaceous of southern Sweden. Rev Palaeobot Palynol 45:171–183.

——— 1988 *Spirematospermum chandlerae* sp. nov., an extinct Zingiberaceae from the North American Cretaceous. Tertiary Res 9:7–12.

——— 1990 *Silvianthemum suecicum* gen. et. sp. nov., a new saxifragalean flower from the Late Cretaceous of Sweden. Biol Skr Dan Vid Selsk 36:1–35

Friis EM, WG Chaloner, PR Crane, eds 1987 The origins of angiosperms and their biological consequences. Cambridge University Press, Cambridge. 358 pp.

Friis EM, PR Crane 1989 Reproductive structures of Cretaceous Hamamelidae. Pages 155–174 *in* PR Crane, S Blackmore, eds. Evolution, systematics and fossil history of the Hamamelidae. Oxford University Press, Oxford.

Friis EM, PR Crane, KR Pedersen 1986 Floral evidence for Cretaceous chloranthoid angiosperms. Nature 320:163–164.

——— 1988 Reproductive structures of Cretaceous Platanaceae. Biol Skr Dan Vid Selsk 31:1–56.

Friis EM, H Eklund, KR Pedersen, PR Crane 1994 *Virginianthus calycanthoides* gen. et sp. nov.—a calycanthaceous flower from the Potomac Group (Early Cretaceous) of eastern North America. Int J Plant Sci 155:766–779.

Friis EM, A Skarby 1982 *Scandianthus* gen. nov., angiosperm flowers of saxifragalean affinity from the Upper Cretaceous of southern Sweden. Ann Bot 50:569–583.

Herendeen PS, PR Crane In press The fossil history of monocotyledons. *In* PJ Rudall, P Cribb, DF Cutler, CJ Humphries. Monocotyledons: systematics and evolution. Kew, Royal Botanic Gardens.

Herendeen PS, WL Crepet, KC Nixon 1993 *Chloranthus*-like stamens from the Upper Cretaceous of New Jersey. Am J Bot 80:865–871.

——— 1994 Fossil flowers and pollen of Lauraceae from the Upper Cretaceous of New Jersey. Plant Syst Evol 189: 29–40.

Hickey LJ, JA Doyle 1977 Early Cretaceous fossil evidence for angiosperm evolution. Bot Rev 43:3–104.

Hideux MJ, IK Ferguson 1976 The stereostructure of the exine and its evolutionary significance in Saxifragaceae sensu lato. Pages 327–377 *in* IK Ferguson, J Muller, eds. The evolutionary significance of the exine. Academic Press, London.

Hill RS 1983 *Nothofagus* macrofossils from the Tertiary of Tasmania. Alcheringa 7:169–183.

——— 1984 Tertiary *Nothofagus* macrofossils from Cethana, Tasmania. Alcheringa 8:81–86.

——— 1991 Tertiary *Nothofagus* (Fagaceae) macrofossils from Tasmania and Antarctica and their bearing on the evolution of the genus. Bot J Linn Soc 105:73–112.

——— 1994 *Nothofagus smithtonensis* (Nothofagaceae), a new macrofossil species from Oligocene sediments in northwest Tasmania, Australia, and its phylogenetic significance. Rev Palaeobot Palynol 80:115–121.

Hill RS, GJ Jordan 1993 The evolutionary history of *Nothofagus* (Nothofagaceae). Aust J Bot 6:111–126.

Hjelmqvist H 1948 Studies on the floral morphology and phylogeny of the Amentiferae. Bot Not 2(suppl):1–171.

Huddlestun PF, JH Hetrick 1991 The stratigraphic framework of the Fort Valley Plateau and the Central Georgia Kaolin District. Georgia Geological Society Guidebooks, vol 11, no 1. Georgia Geological Society.

Hutchinson J 1967 The genera of flowering plants. Vol 2. Dicotyledons. Oxford University Press, London.

Jones JH, DL Dilcher 1988 A study of the "*Dryophyllum*" leaf forms from the Paleogene of southeastern North America. Paleontographica Abt B, 208:53–80.

Kaul RB, EC Abbe 1984 Inflorescence architecture and evolution in the Fagaceae. J Arnold Arbor Harv Univ 65:375–401.

Kvacek Z, H Walther 1989 Paleobotanical studies in Fagaceae of the European Tertiary. Plant Syst Evol 162:213–229.

Langdon LM 1947 The comparative morphology of the Fagaceae. I. The genus *Nothofagus.* Bot Gaz 108:350–371.

Lidgard S, PR Crane 1988 Quantitative analyses of the early angiosperm radiation. Nature 331:344–346.

——— 1990 Angiosperm diversification and Cretaceous floristic trends: a comparison of palynofloras and leaf macrofloras. Paleobiology 16:77–93.

Macdonald AD 1979 Inception of the cupule of *Quercus macrocarpa* and *Fagus grandifolia.* Can J Bot 57:1777–1782.

Mai DH 1970 Die tertiären Arten von *Trigonobalanus* Forman (Fagaceae) in Europa. Jahrb Geol (Berlin) 3:381–409.

——— 1989 Fossile Funde von *Castanopsis* (D. Don) Spach (Fagaceae) und ihre Bedeutung für die europäischen Lorbeerwälder. Flora 182:269–286.

Manchester SR 1981 Fossil plants of the Eocene Clarno Nut Beds. Oreg Geol 43:75–81.

——— 1994 Fruits and seeds of the middle Eocene Nut Beds Flora, Clarno Formation, Oregon. Palaeontographica Americana no. 58. Pp. 1–205.

Manchester SR, PR Crane 1983 Attached leaves, inflorescences, and fruits of *Fagopsis,* an extinct genus of Fagaceous affinity from the Oligocene Florissant flora of Colorado, U.S.A. Am J Bot 70:1147–1164.

Manos PS, KC Nixon, JJ Doyle 1993 Cladistic analysis of restriction site variation within the chloroplast DNA inverted repeat region of selected Hamamelididae. Syst Bot 18:551–562.

Martin PG, JM Dowd 1993 Using sequences of *rbc*L to study phylogeny and biogeography of *Nothofagus* species. Aust Syst Bot 6:441–447.

Melchior H 1964 Juglandales, Leitneriales, Salicales, Fagales. *In* Engler's Syllabus der Pflanzenfamilien. 12th ed. Vol 2. Borntraeger, Berlin.

Muller J 1970 Palynological evidence on early differentiation of angiosperms. Biol Rev 45:417–450.

Nixon KC 1989 Origins of Fagaceae. Pages 23–43 *in* PR Crane, S Blackmore, eds. Evolution, systematics and fossil history of the Hamamilidae. Vol 2. "Higher" Hamemilidae. Oxford University Press, Oxford.

Nixon KC, WL Crepet 1989 *Trigonobalanus* (Fagaceae): taxonomic status and phylogenetic relationships. Am J Bot 76:828–841.

——— 1993 Late Cretaceous fossil flowers of ericalean affinity. Am J Bot 80:616–623.

Pedersen KR, PR Crane, AN Drinnan, EM Friis 1991 Fruits from the mid-Cretaceous of North America with pollen grains of the *Clavatipollenites* type. Grana 30:577–590.

Pedersen KR, EM Friis, PR Crane, AN Drinnan 1994 Reproductive structures of an extinct platanoid from the Early Cretaceous (latest Albian) of eastern North America. Rev Palaeobot Palynol 80:291–303.

Romero EJ 1986 Fossil evidence regarding the evolution of *Nothofagus* Blume. Ann Mo Bot Gard 73:276–283.

——— 1993 South American paleofloras. Pages 62–85 *in* P Goldblatt, ed. Biological relationships between Africa and South America. Yale University Press, New Haven, Conn.

Smiley CJ, LM Huggins 1981 *Pseudofagus idahoensis,* n. gen. et sp. (Fagaceae) from the Miocene Clarkia flora of Idaho. Am J Bot 68:741–761.

Walker JW, GJ Brenner, AG Walker 1983 Winteraceous pollen in the Lower Cretaceous of Israel: early evidence of a magnolialean angiosperm family. Science 220:1273–1275.

Wang Ping-Li 1991 The pollen morphology in relation to the taxonomy and phylogeny of Fagaceae. Acta Phytotaxon Sin 29:60–66.

Ward JV, JA Doyle 1988 Possible affinities of two triporoidate tetrads from the mid-Cretaceous of Laurasia. 7th International Palynological Congress, Brisbane. Abstracts.