

AMERICAN JOURNAL OF Botany

Castaneoid Inflorescences from the Middle Eocene of Tennessee and the Diagnostic Value of Pollen (at the Subfamily Level) in the Fagaceae

Author(s): William L. Crepet and Charles P. Daghljan

Source: *American Journal of Botany*, Vol. 67, No. 5 (May - Jun., 1980), pp. 739-757

Published by: Botanical Society of America, Inc.

Stable URL: <http://www.jstor.org/stable/2442667>

Accessed: 04-08-2016 19:04 UTC

Your use of the JSTOR archive indicates your acceptance of the Terms & Conditions of Use, available at

<http://about.jstor.org/terms>

JSTOR is a not-for-profit service that helps scholars, researchers, and students discover, use, and build upon a wide range of content in a trusted digital archive. We use information technology and tools to increase productivity and facilitate new forms of scholarship. For more information about JSTOR, please contact support@jstor.org.



Botanical Society of America, Inc. is collaborating with JSTOR to digitize, preserve and extend access to *American Journal of Botany*

CASTANEOID INFLORESCENCES FROM THE MIDDLE EOCENE OF TENNESSEE AND THE DIAGNOSTIC VALUE OF POLLEN (AT THE SUBFAMILY LEVEL) IN THE FAGACEAE¹

WILLIAM L. CREPET AND CHARLES P. DAGHLIAN

Biological Sciences Group, U-42, University of Connecticut,
Storrs, Connecticut 06268

ABSTRACT

In order to help evaluate the actual affinities of four types of inflorescences that shared gross pollen and inflorescence morphology with the extant Fagaceae, the pollen of the extant Fagaceae was analyzed with light, scanning, and in some cases transmission electron microscopy. The survey illustrates the range in pollen structure in the Fagaceae and confirms that exine ornamentation is a good diagnostic character for determining subfamilies within the modern Fagaceae. Careful comparison of the pollen and floral morphology of the fossils with similar features of the extant Fagaceae revealed only one of these fossil inflorescences was actually fagoid (the other inflorescences will be considered in a subsequent manuscript). The fagaceous inflorescences are catkins conforming in all aspects of pollen, inflorescence, and floret morphology with catkins of the modern subfamily Castaneoideae. The fossil catkins also share the relatively robust inflorescence axis with modern castaneoid inflorescences suggesting that they, too, may have been upright and insect pollinated. The nature of these fossils is consistent with observations that several other families of the "Amentiferae" evolved rapidly during the Upper Cretaceous-Middle Eocene and this trend suggests that conditions favoring wind pollinated arborescent angiosperm species were optimal during that interval.

FOUR DISTINCT TYPES OF CATKINS OR heads of simple florets are now known from the Middle Eocene Claiborne Formation of western Tennessee that are similar to those of the extant Fagaceae in gross floral and palynological features. In order to assess the possibility that they represent relatives of the Fagaceae, morphological and palynological features of these fossils have been investigated in detail and compared with similar features of a variety of modern families. Such comparisons were necessary for a definitive identification, since several modern families share gross inflorescence morphology with the Fagaceae (e.g., Betulaceae, Juglandaceae), or gross inflorescence and gross pollen morphology with the Fagaceae (e.g., Hamamelidaceae, Salicaceae, and even in certain instances, the Euphorbiaceae). In order that the features available from the fossils (i.e., inflorescence, basic floret, and pollen morphology) be used with maximum effectiveness in determining their possible af-

finities, it was necessary to have a better idea of certain palynological features of several modern families than was available in the literature. As a consequence, surveys of the pollens of certain extant families (i.e., those that share *gross* pollen and inflorescence morphology with the fossils) were conducted as preludes to the evaluation of the affinities of the fossil inflorescences. The intensity of these surveys varied from family to family depending on how much information was available for the pollen of each family in the contemporary literature. The most extensive survey was conducted for the Fagaceae (61 species), but pollen of the Hamamelidaceae, Tetracentraceae, Euphorbiaceae, and Salicaceae was also examined. After compiling this information and considering it along with fossil and modern floral morphological features, it became obvious that only one of these inflorescences was clearly related to the extant Fagaceae. The survey of the pollen of the extant Fagaceae and the morphology and significance of this fossil inflorescence will be considered here while the other inflorescences will be the subjects of subsequent publications.

Inflorescences of the Fagaceae are cymes or simple or branched spikes. Florets are pedicellate or sessile, bract or bracteole subtended, and occur singly or in dichasia of from 2-30 florets. Inflorescences are staminate, pistillate, androgenous or mixed. Florets are unisexual or functionally so (for exceptional hermaph-

¹ Received for publication 3 August 1979; revision accepted 8 February 1980.

Research supported by NSF grant DEB 78-11120 to W.L.C. The authors gratefully acknowledge Professor John M. Tucker, Botany Department, University of California, Davis, for valuable discussions which prompted the extensive survey of the pollen of the Fagaceae. We also wish to thank Professor Allen W. Wachtel, Biological Sciences Group, University of Connecticut, Storrs, Ct., for his valuable and generous assistance in scanning and transmission electron microscopy.

TABLE 1. *Geographic range of species examined; aperture type and measurements of pollen in the Fagaceae*

	No. species examined	Geographic range sampled	Aperture type	Polar diameter (P) × equatorial diameter (E) (averages—in μm)	P/E (average)	Colpus length/P (average)	Size range of species P × E—P × E
QUERCOIDEAE							
<i>Trigonobalanus</i>	1	Malay Peninsula	Tricolporate	28.2 × 21.9	1.29	1.00	— ^a
<i>Quercus</i>	28	Borneo, China, Hong Kong, India, Japan, North America (Europe?)	Tricolporate, Tricolporoidate	27.5 × 25.4	1.08	0.95	21 × 21–23 × 35
FAGOIDEAE							
<i>Fagus</i>	10	England, China, Japan, Korea, North America	Tricolporate	37.6 × 36.3	1.04	0.74 ^b	29 × 28–44 × 43
<i>Nothofagus</i>	1	Argentina	5-colpoid	20.0 × 30.7	0.65	~0.49 ^c	—
CASTANEOIDEAE							
<i>Castanea</i>	5	North America	Tricolporate	16.2 × 10.0	1.62	0.94	15 × 9–17 × 10
<i>Castaneoidea</i> (Fossil)	1	North America (Middle Eocene)	Tricolporate	15.0 × 9.0	1.67	1.00	—
<i>Castanopsis</i>	6	China, Taiwan	Tricolporate	19 × 13.5	1.42	1.00	16 × 10–20 × 15
<i>Chrysolepis</i>	1	California	Tricolporate	17 × 11	1.54	1.00	—
<i>Lithocarpus</i>	7	China, Japan, Malay Peninsula, North America, Taiwan	Tricolporate	18.0 × 10.7	1.68	1.00	16 × 10–20 × 11

^a Since size range is for the range of average sizes among the species, no range is given in instances where only 1 species has been examined (i.e. no within-species ranges—since they are not comparable with among species ranges).

^b *Fagus* exhibits great variation in colpus length; one standard deviation = .21.

^c Because of the peroblate nature of *Nothofagus*, accurate polar diam. measurements are difficult, making this a somewhat approximate figure.

roditic flowers see Tucker, 1972), with a campanulate or tubular 4–9 lobed floral envelope (frequently six). Staminate florets have between four and 90 stamens (six and 12 are common) and anthers are exserted and vary in size and morphology. The three subfamilies of the Fagaceae have staminate inflorescences with different combinations of the above features (Hjelmqvist, 1948; Soepadmo, 1972; Abbe, 1974).

The Fagaceae are predominantly a Northern Hemisphere family, although *Castanopsis*, *Trigonobalanus*, *Lithocarpus* and *Quercus* occur in subequatorial Malesia and *Nothofagus*, an exclusively Southern Hemisphere genus, is found in Australia, Malesia, Tasmania, New Zealand and South America (Soepadmo, 1972). The fossil distribution of the Fagaceae is also predominantly Northern Hemisphere (Wolfe, 1973; Raven and Axelrod, 1974), again with the exception of *Nothofagus*, and it has been suggested that the family may have originated prior to the Maestrichtian (Wolfe, 1973) in the

Aquilapollenites province (western North America and Asia).

There has been relatively little fossil evidence about the early diversification of the Fagaceae or relating to its often hypothesized origin from more primitive families of the Hamamelididae (e.g., Cronquist, 1968; Hutchinson, 1967; Takhtajan, 1969). There are presently no valid reports of leaves of the Fagaceae from Cretaceous sediments. Fagaceous leaves do appear in the fossil record of the Lower Paleocene; fagoid leaves of uncertain affinity have been reported from the Eocene; and leaves of the extant genera *Castanopsis* and *Quercus* have been reported from Eocene sediments (Wolfe, 1973). Acorns of *Quercus* are known from the Middle Eocene Clarno Formation (Manchester, pers. comm.) and remains of *Fagus* fruits are present in the London Clays (Chandler, 1964). Finally, fagoid leaves of apparently extinct genera persist to the Oligocene (e.g., *Fagopsis*, MacGinitie, 1953).

TABLE 2. Measurements of the exine of pollen of the Fagaceae based on transmission electron micrographs

	Overall exine thickness (μm)	Ektexine thickness (μm)	Tectum thickness (μm)	Columellae thickness (μm)	Foot layer thickness (μm)	Exdexine thickness (μm)	Foot layer/tectum ratio
QUERCOIDEAE							
<i>Trigonobalanus verticillata</i>	1.48	1.28	0.37	0.23	0.68	0.20	1.84
<i>Quercus nigra</i>	0.83	0.73	0.43	0.20	0.10	0.10	0.23
<i>Quercus palustris</i>	0.70	0.60	0.30	0.24	0.06	~0.10 ^a	0.20
<i>Quercus spinosa</i>	1.30	1.14	0.49	0.23	0.42	0.16	0.85
FAGOIDEAE							
<i>Fagus crenata</i>	1.12	1.00	0.55	0.31	0.14	0.12	0.25
<i>Nothofagus pumila</i>	0.59	0.59	0.15	0.20	0.24	—	1.60
CASTANEOIDEAE ^d							
<i>Castanoidea puryearensis</i> (Fossil)	~0.53 ^b	0.43	0.19	0.11	0.13	~0.10 ^c	0.68
<i>Chrysolepis sempervirens</i>	0.85	0.72	0.38	0.11	0.23	0.13	0.61
<i>Lithocarpus henryi</i>	0.65	0.55	0.24	0.15	0.16	0.10	0.67

^a Endexine of this species did not survive acetolysis well and measurement an approximation.

^b Due to uniform exine staining a foot layer could not be discerned.

^c The exine thickness listed for *Castanoidea* includes an estimated 0.10 μm thick endexine. This was necessary due to the nonuniform preservation of the endexine in the fossil pollen.

^d The size range and average size of pollen of the Castanoideae given in the text are averages for the subfamily excluding the fossil.

The dispersed pollen record of the Fagaceae has contributed even less to the understanding of the evolutionary history of the family than the megafossil record. This has been due to the fact that the pollen, with the exception of *Nothofagus*, is of a general type common to a multitude of angiosperm families and it has been difficult to identify dispersed fagoid pollen against a background of similar, but unrelated, types (e.g., Erdtman, 1966; Wolfe, 1973). Pollen of *Nothofagus* is distinctive and has been reported as early as the Maestrichtian (e.g., Muller, 1970; Wolfe, 1973; Jarzen, 1979). The infrequency of careful studies of the pollen of the extant family has minimized the value of studies of dispersed pollen in attempting to understand the family's evolutionary history. Studies of pollen of the extant Fagaceae have set the stage for an improved understanding of the palynological record of the family and studies of fossil inflorescences provide additional information about the level of diversity and adaptation of the family by the Middle Eocene.

MATERIALS AND METHODS—Examples of species representing all genera of the Fagaceae and reflecting their worldwide distribution were obtained from the University of Connecticut Herbarium (CONN), The Gray Herbarium of Harvard University (G), The Plant Resource Center of the University of Texas (TEX), and the U.S. National Herbarium (U.S.). Genera, species, and localities of all specimens studied are listed in the appendix

(Table 3). Pollen of all species was acetolyzed and examined with light and scanning electron microscopy (SEM). Average measurements were determined from 10 random grains for each species mounted in Piccolyte.[®] Scanning electron microscopy was done with a Coates and Welter Field Emission Microscope and pollen and floral parts were mounted on stubs with Epiezon W-100[®] wax for viewing. In addition, pollen of representative species was sectioned for transmission electron microscopy (TEM) and examined with a Phillips EM-300. Pollen of the fossil inflorescences, although processed with HF, was not acetolyzed, but was otherwise handled in the same manner as pollen of the extant species.

Fossil inflorescences were investigated by a combination of techniques that have become standard in studies of Claiborne floral compressions including dégageant, maceration, cuticular clearing and preparation, modified transfer technique, and TEM and SEM of the pollen (e.g., Crepet and Dilcher, 1977; Daghljan, Crepet and Delevoryas, 1980). There were seven examples of this type of fossil inflorescence available for investigation; all from the Laird Brick Company Pit in Puryear, Tennessee. So far this type of inflorescence has not been discovered at any other Claiborne locality. Specimens are compressions with copious amounts of well preserved pollen in the anthers and well preserved features of inflorescence and floret morphology. The quality of cuticular preservation varies considerably, depending primarily on the degree of oxidation. In some

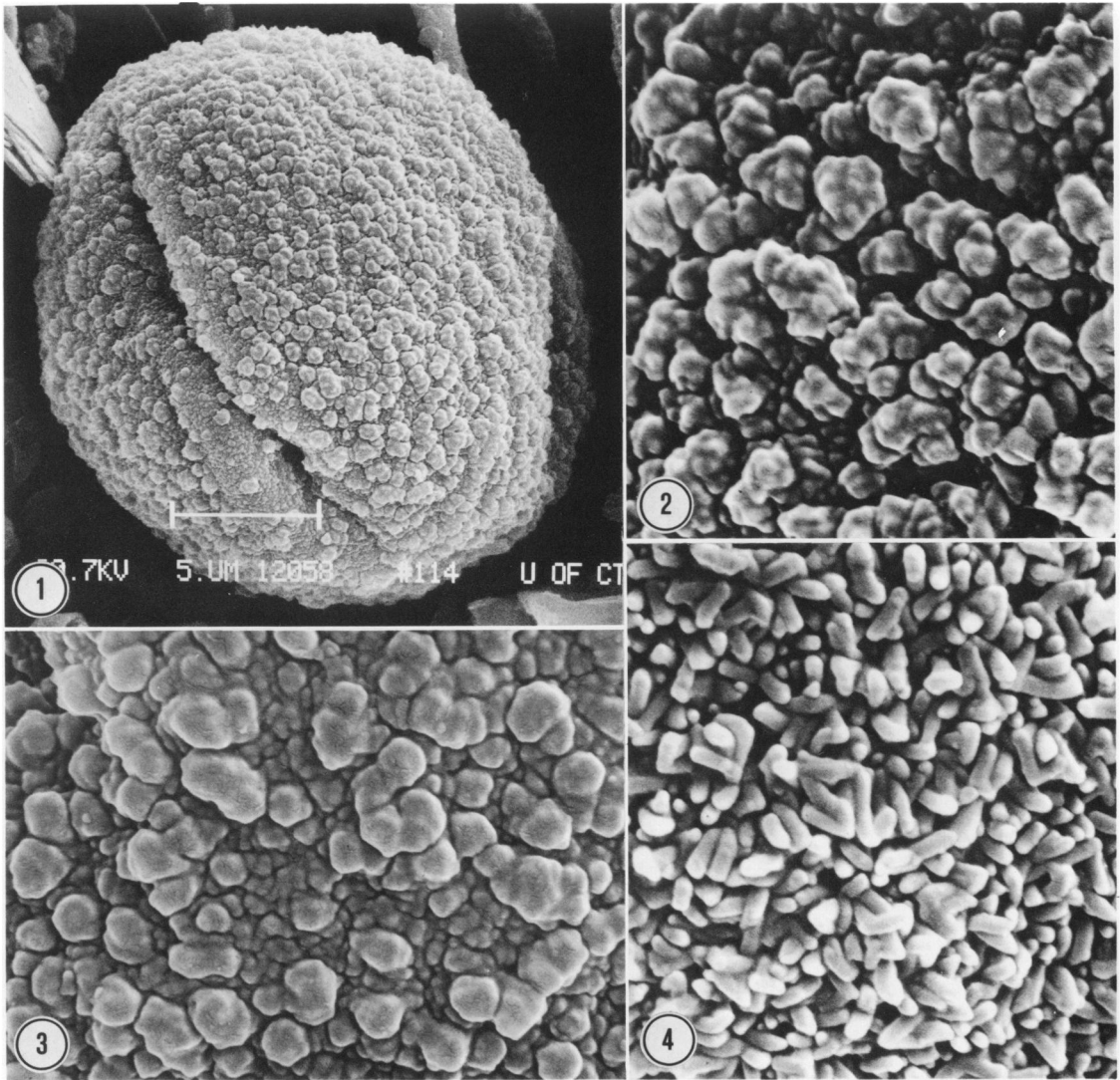


Fig. 1-4. Pollen of the Quercoideae. 1. *Quercus velutina*, Eames 1892 (CONN). The coarse scabrate pollen type with typical large verrucose processes. $\times 4,000$. 2. *Q. mongolica*, Togashi 2276731 (US). Coarse scabrate pollen with more uniformly distributed large processes. $\times 14,900$. 3. *Q. dentata* Smith 1756896 (US). Coarse scabrate pollen with unevenly distributed large processes. Note the small papillar on the larger verrucose processes. $\times 12,110$. 4. *Q. spinosa*, Wilson 596815 (US). Detail of exine of the fine(r) scabrate type apparently composed of small vertical closely spaced variously entwined rods. $\times 15,100$.

cases one half of the fossil inflorescence lacks cuticular preservation completely while the other, less oxidized half has well preserved cuticle.

RESULTS—Pollen of Fagaceae—The details of pollen structure and size of the Fagaceae are summarized in Table 1, 2. Perhaps the most interesting aspect of the survey of the pollen is the confirmation that exine ornamentation alone is a good diagnostic feature allowing discrimination among the three subfamilies of the Fagaceae. Size also allows some discrimina-

tion among subfamilies, but is not as precise as exine sculpturing because of overlapping ranges. Exine stratification and pollen shape may also be useful diagnostic characters, but only in certain instances.

Exine ornamentation allows the subfamily of any of the species of pollen examined in this survey to be identified. This was recognized by Soepadmo (1972), but his delineation of groups based on similar exine ornamentation differs from ours because of the limitations of light microscopy. Soepadmo suggested that there was a *Quercus-Fagus-Trigonobalanus*

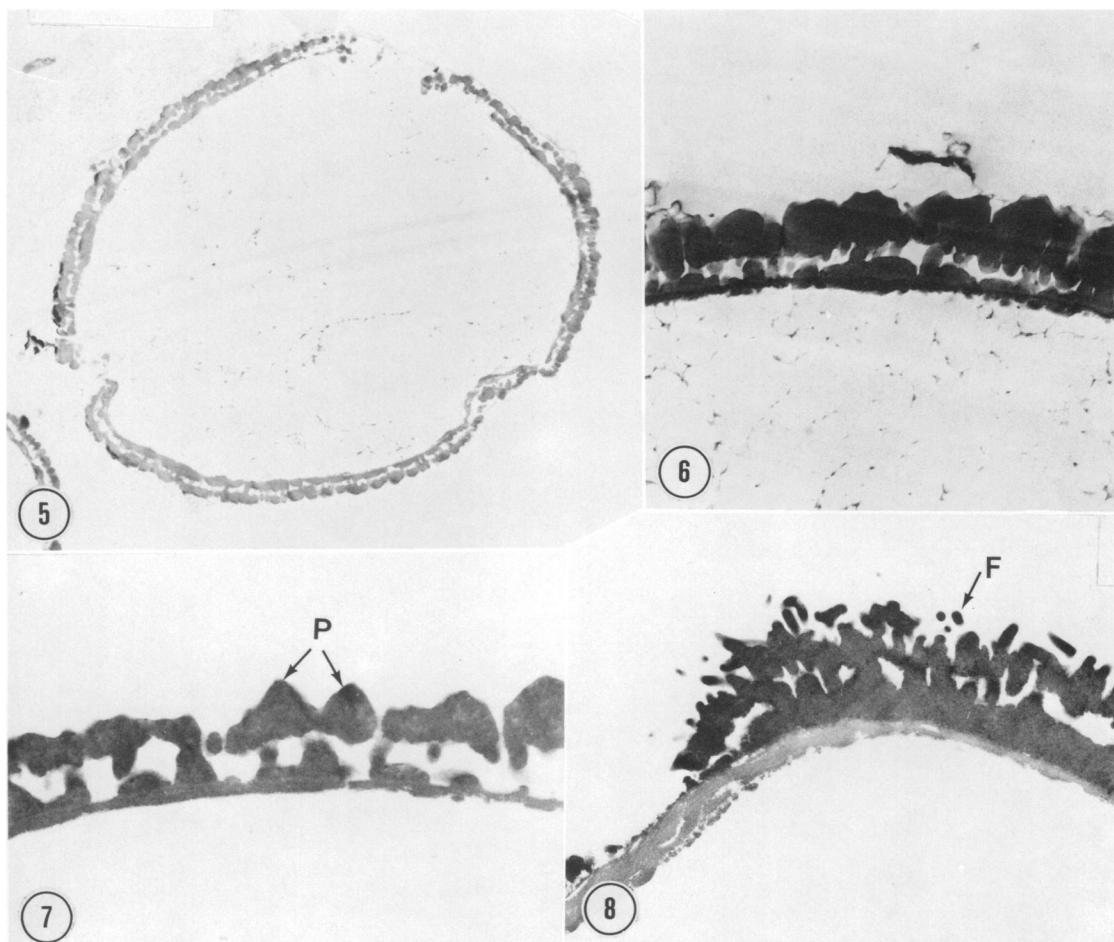


Fig. 5–8. Pollen of the Quercoideae. 5, 6. *Quercus nigra*, Thomas 1971 (CONN). 5. Thin section through a single grain and parallel to the equatorial plane. Note occasional perforations. $\times 3500$. 6. Higher magnification view of the thin section showing the relatively uniformly thick tectum, columellae, and uneven foot layer. $\times 15,125$. 7. *Q. palustris*, Jansson 1927 (CONN). Thin section of exine showing uneven tectum thickness caused by the wide spacing of the larger verrucose processes (P). $\times 16,500$. 8. *Q. spinosa*, Wilson 596815 (US). Thin section of exine showing the thick foot layer, “floating” ends of vertical processes (F), and the thickening of the endexine in the colpus. $\times 13,250$.

group, a *Castanea* group, and a *Nothofagus* group. In fact, SEM reveals that the divisions can be more precise. The Quercoideae have two types of exine. By far the most common in the species surveyed were those with a coarse scabrate exine. The basic pattern in these species was having large verrucate processes and smaller papillate processes on the same grain (Fig. 1, 3). The relative proportions of the two types of protuberances varies and sometimes the surface is almost uniformly covered with the large processes (e.g., *Quercus mongolica*, Fig. 2). The large verrucate processes are themselves often covered with smaller papillate protuberances (Fig. 3). The other type of exine ornamentation in the Quercoideae has been noted only in three species and with light microscopy appears to be fine(r)

scabrate. At higher magnifications the exine appears as if it is composed of small vertical closely spaced variously entwined rods (e.g., *Q. spinosa*, Fig. 4). The length of the vertical processes varies among these species and they may be considerably shorter than those of *Q. spinosa* (e.g., Fig. 26). This represents more variation than has been noted in any other subfamily of the Fagaceae and the possibility that exine ornamentation might have diagnostic value within the Quercoideae is now under investigation.

Exine of the Fagoideae is distinct from that of the Quercoideae. In all species of *Fagus* the exine ornamentation pattern is similar to that of the species of *Quercus* with the fine scabrate exine (i.e., the *Q. spinosa* type), but still distinct from that type. In *Fagus* also, the exine

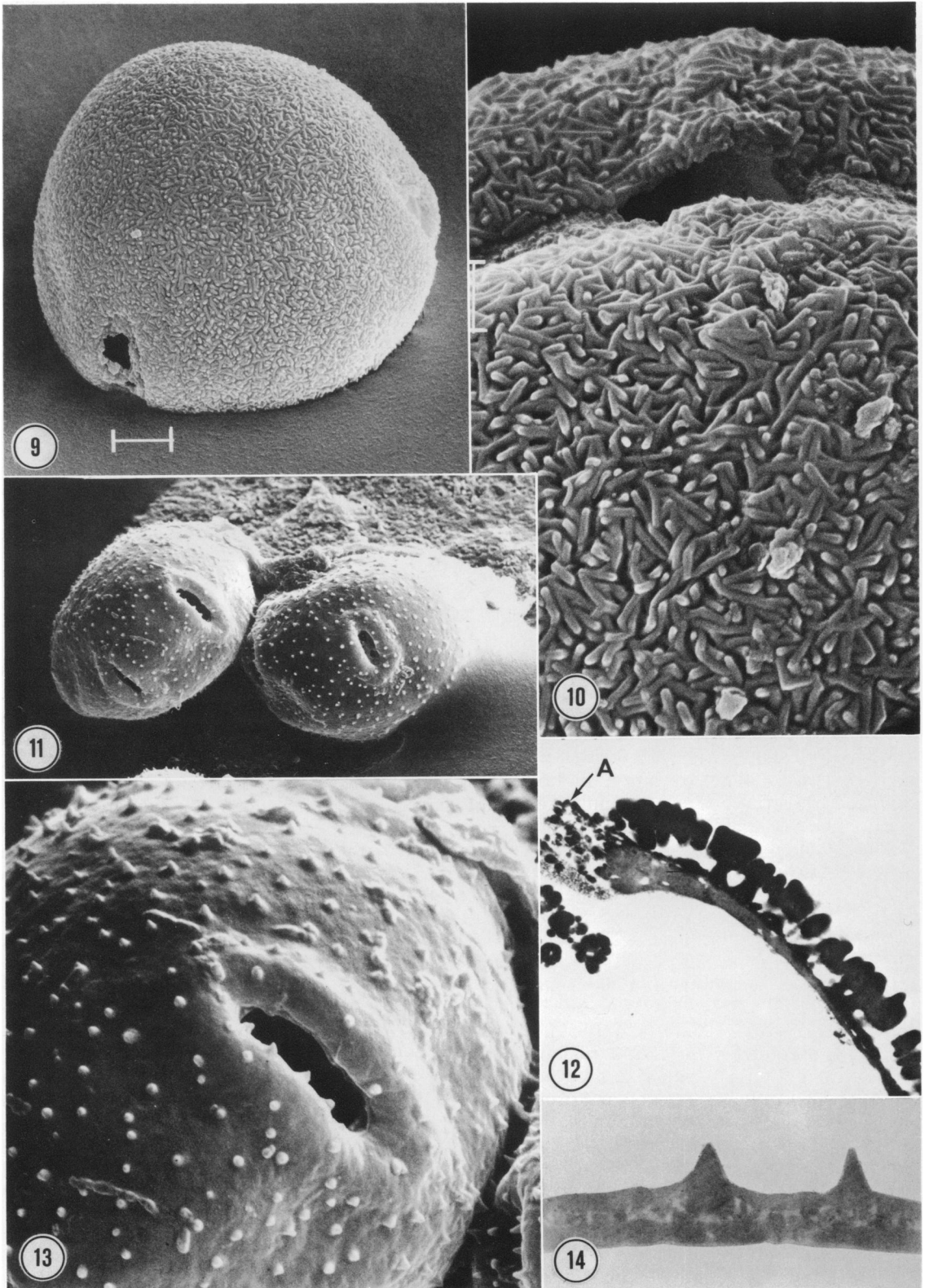


Fig. 9–14. Fagoideae pollen. 9. *Fagus crenata*, Togashi 1963 (Gray). $\times 1,730$. 10. *F. grandifolia*, Leavitt 1899 (TEX). Typical fagoid exine sculpturing apparently consisting of fused small rods, primarily horizontally disposed. Note the short vertical ends of the rods. $\times 5,310$. 11. *Nothofagus pumila*, Goodall 1967 (CONN). Equatorial views

appears to be composed of fused small rods, but they are primarily horizontally disposed, somewhat anastomosing, and have one free vertical end (Fig. 9, 10). The length and angle of the “vertical” part of the rod varies. Species having rougher exine have a greater proportion of the rods free from the surface and they extend at greater angles from the surface (Fig. 10). Exine sculpturing was used with limited success by Hanks and Fairbrothers (1976) to distinguish among the species of *Fagus*. The results of the present study also suggest that it is difficult if not impossible to differentiate among *Fagus* species using exine ornamentation alone. The pollen of *Nothofagus* is different from that of the rest of the Fagoideae and Fagaceae in having 3–10 equatorial, meridionally elongate apertures with swollen margins (e.g., Fig. 11, 13). Pollen of *Nothofagus* is also unique in exine ornamentation. The exine is smooth with small, widely spaced, conical projections up to $0.44\ \mu\text{m}$ high (Fig. 11, 13, 14). Variation in distribution of these projections has been used in conjunction with other features to identify three groups of species within the genus *Nothofagus* (Hanks and Fairbrothers, 1976).

Pollen of the Castaneoideae is also readily distinguished from the other subfamilies on the basis of exine sculpturing and has the most uniform pattern of ornamentation. Exine sculpturing consists of a smooth surface of striate, anastomosing rounded ridges and the surface appears as if it were formed by fused rods. There is some variation in how pronounced the striations are, ranging from quite well defined (Fig. 15) to having an exine that is almost smooth (Fig. 16).

The mean sizes of pollen in the three subfamilies are different, but the size ranges overlap. Pollen shape also varies, but again, each subfamily has an overall distinctive shape. The Quercoideae are distinguished by predominantly round pollen (mean P/E = 1.08 with a size range of 24×21 – $34 \times 35\ \mu\text{m}$ and a mean pollen size of $27.5 \times 25.4\ \mu\text{m}$ [Table 1]). *Fagus* also has predominantly round pollen (mean P/E = 1.04) with a pollen size range of 29×28 – $44 \times 43\ \mu\text{m}$ and a mean pollen size of $37.6 \times 36.3\ \mu\text{m}$ (Table 1; see also Hanks and Fairbrothers 1976, for similar results). The Castaneoideae stand out as the most prolate (P/E = 1.57) and the smallest (mean size $17.5 \times$

$11.2\ \mu\text{m}$ and range 15×9 – $20 \times 15\ \mu\text{m}$) of the three subfamilies (Table 1).

Exine stratification was examined by sampling species with what appeared to be typical exine ornamentation for each subfamily and preparing them for transmission electron microscopy. Only one or two examples of each subfamily, *Trigonobalanus* and *Nothofagus* were examined in this way. So while there is no reason to suspect that the stratification patterns described are not typical, there may be undetected exceptions.

The Fagaceae all (with the exception of *Nothofagus*) have tectate columellate pollen and a perforate tectum. Perforation size varies in the subfamilies and even within species, but the perforations are always very small. In the Quercoideae, two examples of the “course scabrate exine” type were examined; *Q. nigra* and *Q. palustris*. In *Q. nigra* exine ornamentation consists of fairly contiguous large verrucate processes. Sections of the exine reflect this, revealing a uniformly thick tectum ($0.43\ \mu\text{m}$) with occasional minute openings (Fig. 5, 6). Columellae are $0.20\ \mu\text{m}$ in height and account for about one-fourth of the thickness of the exine (Fig. 6). The foot layer is thin ($0.10\ \mu\text{m}$ average thickness), uneven, and occasionally disappears altogether (Fig. 6). The endexine is also about $0.10\ \mu\text{m}$ in thickness, but does not survive acetolysis uniformly well (Fig. 6). As in all species examined the endexine does not persist in the pore areas but does persist in the colpi without obvious modifications (Fig. 5), and the ektexine thins out along the colpar margin and does not extend over the wider areas of the colpi (Fig. 5). *Q. palustris* has an exine with more widely spaced large verrucate processes. In thin sections the tectum appears uneven in thickness, the thicker parts presumably corresponding to the large verrucate processes (Fig. 7). Otherwise exine stratification of the two species is similar.

The species of *Quercus* with finer scabrate exines (the “*Q. spinosa*” type) are notably different in exine structure. The most conspicuous difference is the thick foot layer (Fig. 8). Coarse scabrate species (i.e., as *Q. nigra*) have a foot layer/tectum ratio of 0.20–0.23 (Table 2). The ratio in the fine scabrate species (i.e., the *Q. spinosa* type) is 0.85. The exine of the finer scabrate species is thicker overall than that of the coarse scabrate species (1.30

←

of two grains showing elongate apertures. Grain to left is relatively undistorted demonstrating the prolate shape. $\times 1,490$. 12. *F. crenata*, Togashi 1963 (Gray). Thin section of pollen near aperture (A). Note relatively thick perforate tectum and thin foot layer. $\times 10,500$. 13. *Nothofagus pumila*, Goodall 1967 (CONN). Detail of aperture showing thickened margins. Note evenly distributed spines. $\times 5,500$. 14. *N. pumila*. Thin section of pollen wall showing weakly developed, granular layer rather than distinct columellae as in other Fagaceae. $\times 10,500$.

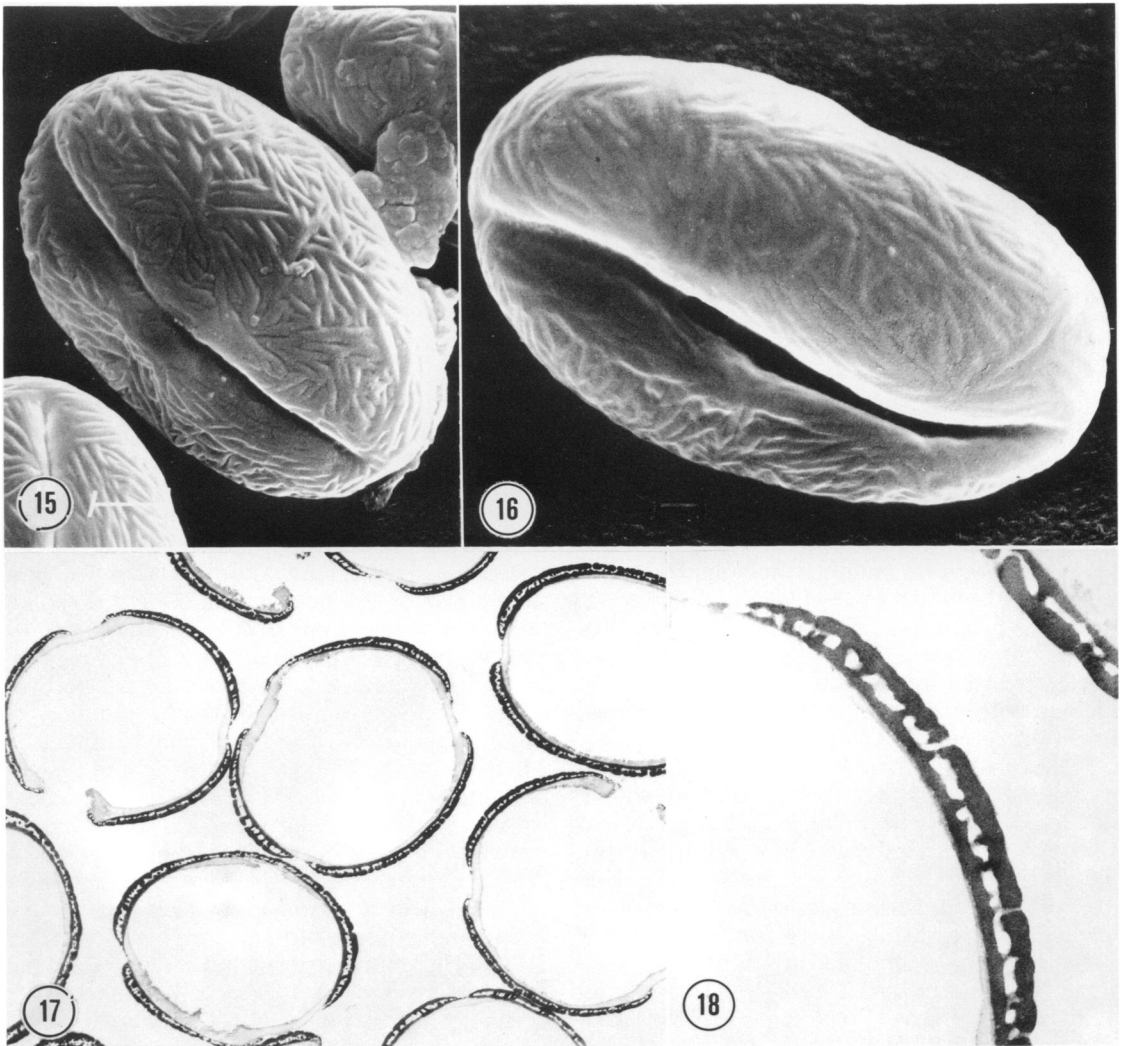


Fig. 15–18. Castaneoideae pollen. 15. *Lithocarpus edulis*, Sagani 1176257 (US). An example of well defined striate exine sculpturing. $\times 4,680$. 16. *Lithocarpus brevicaudata*, Sasaki 2063528 (US). An example of nearly smooth sculpturing, although striations are still obvious. $\times 5,830$. 17, 18. *Lithocarpus henryi*, Wilson 596968 (US). 17. Thin sections of several grains showing tectate-perforate exine. $\times 2,700$. 18. *L. henryi*. Detail of exine section, slightly oblique, showing perforate tectum and relatively thick foot layer. $\times 13,250$.

μm vs. $0.73 \mu\text{m}$) and most of the difference can be accounted for by the thicker foot layer (Table 2). The tectum of *Q. spinosa* is perforate and about the same thickness as that of the coarse scabrate species (0.49 vs. $0.43 \mu\text{m}$; Table 2) and in *Q. spinosa* it has a distinctive appearance in section due to the “floating” ends of the vertical processes included in the plane of section (Fig. 8). The endexine persists in the colpi of *Q. spinosa* pollen, but is thicker in this region than in the colpar area of the coarse scabrate species (Fig. 5, 8).

Exine stratification of pollen of the Fagoideae is similar to that of *Quercus* species with coarse scabrate exines (Fig. 12). The ektexine

in *Fagus* is $1.12 \mu\text{m}$ in thickness and consists of a uniformly thick perforate tectum ($0.55 \mu\text{m}$), $0.31 \mu\text{m}$ thick columellae and a foot layer (Table 2). The latter is about $0.14 \mu\text{m}$ thick, but as in *Q. nigra* and *Q. palustris* is somewhat uneven. The foot layer/tectum ratio is about the same as in coarse scabrate species of *Quercus* (0.25). The endexine is thin (about $0.12 \mu\text{m}$ thick) and differs from that of *Quercus* in becoming thicker and more vesicular in the colpar region (Fig. 12). As in *Quercus*, ektexine is not present as a uniform layer in the wide colpus area (Fig. 12). Measurements of exine layers made by Hanks and Fairbrothers (1976) generally coincide with our measurements, but

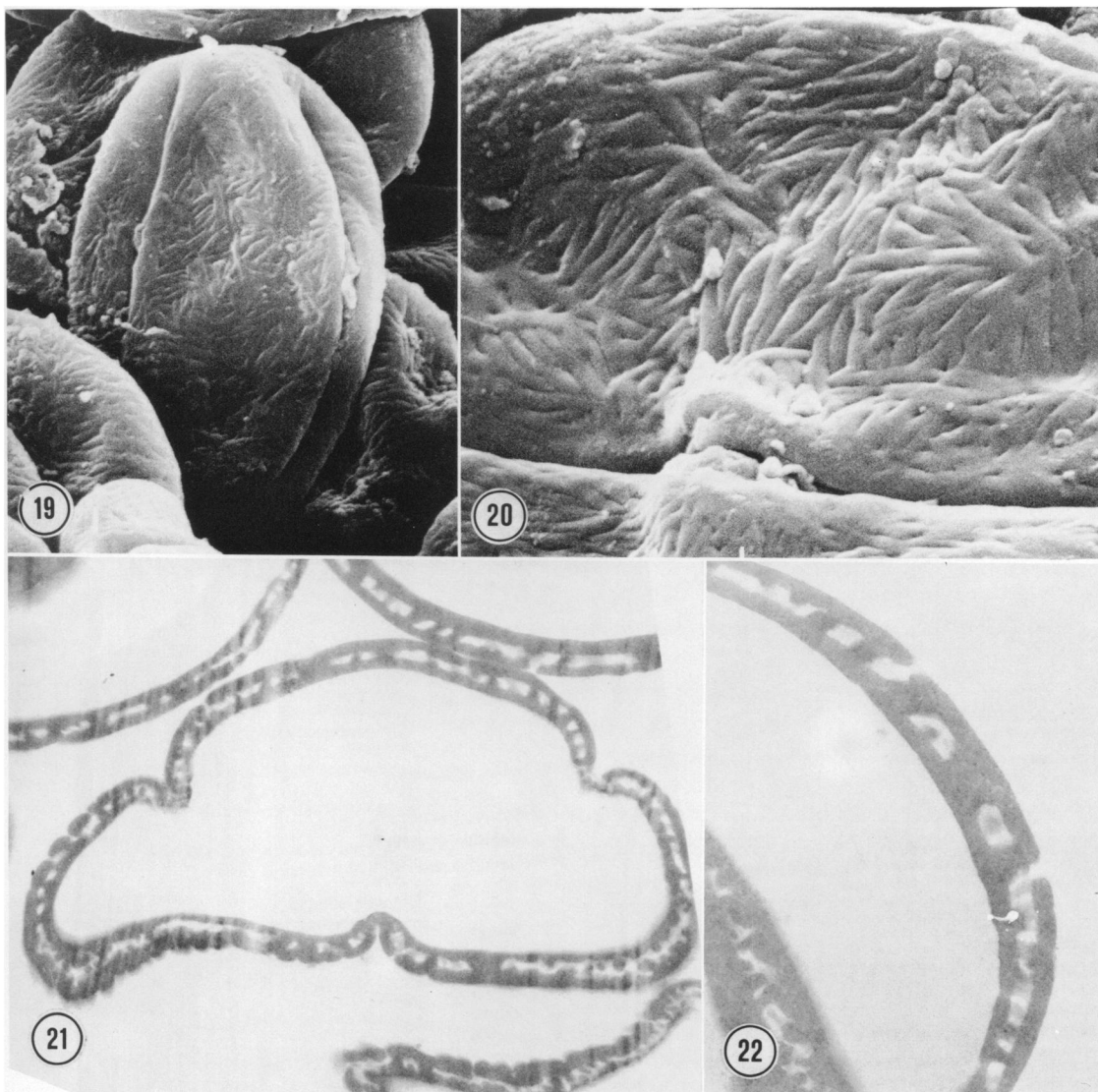


Fig. 19–22. *Castaneoidea puryearensis* (UCPC 36) pollen. 19. Flattened pollen grain with two colpi exposed. From a mass of *in situ* pollen. $\times 5,080$. 20. Detail of exine sculpturing. Compare these striations with those in Figs. 15, 16. $\times 11,410$. 21. Thin section of isolated grain, slightly flattened, showing three colpi. $\times 13,000$. 22. Detail of slightly oblique section through pollen wall showing perforate tectum, short columellae, and relatively thick foot layer. Compare with Fig. 18. $\times 16,500$.

there is uncertainty as to how they were able to determine endexine thickness without TEM, since endexine is visible only through differential staining. In *Nothofagus pumila* exine stratification is unique with respect to the rest of the Fagaceae. Stratification is less well defined and the most conspicuous difference is the nature of the columellar layer. Instead of being a typical layer of columellae, the “columellar” layer is more granular than truly columellar (Fig. 14). This layer is $0.20\ \mu\text{m}$ in thickness and bounded by a $0.15\ \mu\text{m}$ thick tectum and a $0.24\ \mu\text{m}$ thick foot layer (Table 2). There

was no differential staining between the endexine and ectexine with the techniques employed (see Daghljan, Crepet, and Delevoryas, 1980).

Although columellate exine has been reported by Hanks and Fairbrothers (1976) for *Nothofagus*, their only evidence is a single SEM micrograph of a fractured grain (Plate 36, Fig. K) and this figure illustrates a granular, not a columellate exine. Although the possibility of a range of types of exine structure within the genus *Nothofagus* cannot be ruled out without further evidence (even though it

seems unlikely), the two species examined so far (one by Hanks and Fairbrothers, 1976; one in the present investigation) clearly have granular infrastructure.

The exine stratification of pollen in the Castaneoideae is as different from that of the other two subfamilies as the exine ornamentation (Table 2). The ektexine is the thinnest of the subfamilies (e.g., about $0.65\ \mu\text{m}$ thick in *Lithocarpus*; $0.85\ \mu\text{m}$ thick in *Chrysolepis*) with short columellae (about 0.15 and $0.11\ \mu\text{m}$, respectively) (Fig. 18). The tectum is perforate and uniform in thickness (about $0.24\ \mu\text{m}$ and $0.38\ \mu\text{m}$ thick), as is the foot layer (about 0.16 and $0.23\ \mu\text{m}$ thick). The foot layer/tectum ratio in the Castaneoideae is larger than that in the Fagoideae and the scabrate oaks (0.67 and 0.61). The endexine is thin and thickens in the area of the colpus (Fig. 17). As in the other subfamilies the ektexine is not persistent in the wider colpus regions (Fig. 18).

In view of the fact that the Fagoideae can be distinguished from the Quercoideae on the basis of exine ornamentation, it was interesting to examine the exine of *Trigonobalanus*.

Trigonobalanus was originally assigned to the Quercoideae because of the capitate stigmas and male florets with six stamens and no pistillode (Forman, 1962). Hutchinson (1967) concurred with Forman, but Melchior (1964) considered *Trigonobalanus* best placed with the Fagoideae because of the trigonous fruits and valvate cupules. Abbe (1974) and Soepadmo (1968) suggested that more information was necessary regarding the genus before it could be reliably assigned to a subfamily, but Soepadmo later (1972) included *Trigonobalanus* with the Quercoideae. The study of pollen of *Trigonobalanus verticillata* expands our understanding of the genus and tends to support Soepadmo's recent (1972) assignment of the genus to the Quercoideae.

The exine ornamentation of *Trigonobalanus verticillata* is fine scabrate with a superficial pattern of uniform, small, rounded protuberances which sometimes extend slightly in a vertical direction (Fig. 23, 24). This is similar to, although not identical with, the exine sculpturing seen in the fine scabrate species of *Quercus* (i.e., the *Q. spinosa* type), especially *Q. championi* (Fig. 26), and is quite distinct from the ornamentation pattern of all species of *Fagus*. Interestingly, the exine stratification is also more similar to that of the *Q. spinosa* type oaks than to that of *Fagus* spp. The most notable similarity is in the thick foot layer (Fig. 25). In *Fagus* the foot layer is relatively thin (Fig. 11) with a foot layer/tectum ratio of 0.25. In *Q. spinosa* the foot layer/tectum ratio is 0.85 and in *Trigonobalanus verticillata* the foot lay-

er is extremely thick with a foot layer/tectum ratio of 1.84 (compare Figs. 8 and 25).

Fossil Inflorescences of the Fagaceae—Fossil inflorescences are elongate catkins (up to 90 mm in length) with an average axis diameter of 1.3 mm (Fig. 27, 28). Dichasia composed of three florets are subtended by bracts up to 1 mm in length (Fig. 29) and are helically arranged on the catkin axis. The helical arrangement is best observed by comparing the part and counterpart of the specimen that most clearly demonstrates floret arrangement—UCPC P36 (Fig. 27, 28). The first two dichasia (D_1 and D_2 , Fig. 27, 28, 38, 39) are laterally compressed with all of the florets compressed together. The next two dichasia (D_3 and D_4 , Fig. 27, 28, 38, 39) are compressed in face view so that individual florets of the same dichasium can be observed on either side of the axis (Fig. 29). In D_3 the florets are on the matrix side of the axis indicating that the dichasium was compressed on the back side of the axis (Fig. 29). Note that in D_3 the lateral florets are partially covered by the axis that has been compressed over them (Fig. 29). In D_4 the florets are on the near side of the axis partially overlying the axis and on the opposite side of the axis from the florets of the preceding dichasium. Immediately following D_4 is part of an inflorescence of a second catkin (C_2 , Fig. 27, 28, 38, 39) the axis of which lies in a different plane from the catkin under consideration. Then dichasia D_5 – D_{10} appear alternately before the florets become disturbed and confused with yet another catkin (Fig. 27, 28). Thus, the helical pattern of dichasium arrangement on the catkin axis is evident.

By comparing occasional isolated florets with whole laterally compressed dichasia or even by closely examining a single laterally compressed dichasium, it becomes evident that the dichasia are indeed composed of several florets. In some instances it is easy to observe that the dichasia are composed of three florets. The best example is a dichasium compressed in face view with one floret on either side of the axis at the same level and a third floret radially compressed in the center of the axis between the two lateral florets (Fig. 30, 40). **This pattern is repeated frequently and suggests that three florets per dichasium is the usual number.**

Florets have never been found open with exerted anthers suggesting that the catkins abscised prior to anthesis. Individual compressed florets are $0.8\ \text{mm} \times 1.0\ \text{mm}$. Cuticular preservation is not exceptional and it has not been possible to isolate entire floral envelopes from the matrix. Nearly complete flo-

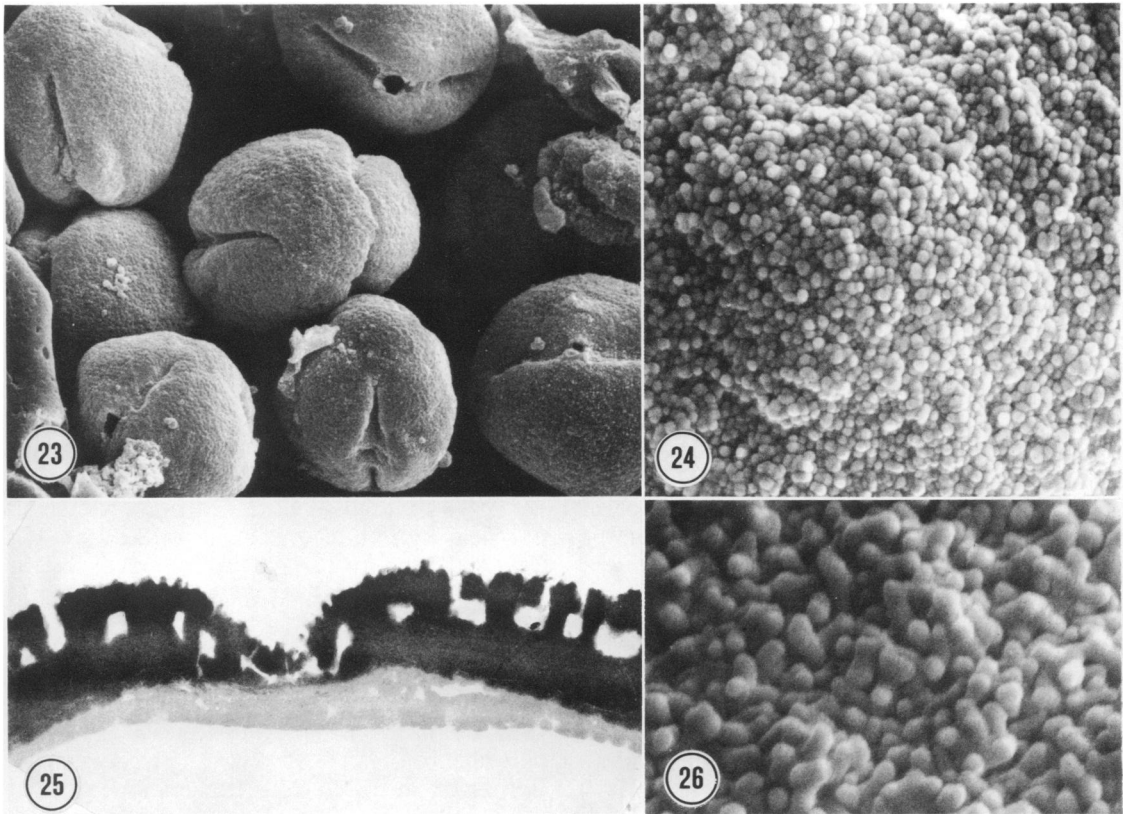


Fig. 23–26. Quercoidae pollen. 23. *Trigonobalanus verticillata*, Poore 06337 (U.S.). $\times 1,434$. 24. *T. verticillata*. Detail of exine showing the numerous small, rounded protuberances making up the fine scabrate surface. $\times 10,850$. 25. *T. verticillata*. Thin section of pollen wall. Note the perforate tectum and very thick foot layer. Compare with Fig. 8. $\times 13,250$. 26. *Quercus championi*, Faber 156293 (U.S.). Detail of exine sculpturing. $\times 18,500$.

ral envelopes have been observed during the course of preparation and these are connate with up to five lobes, suggesting that six lobes were likely in complete florets. These larger floret fragments do not survive the physical stresses of dehydration during preparation for mounting for light microscopy or the preparations necessary for critical point drying and SEM. Fragments of florets illustrating part of the perigon with two ovate lobes, however, have been successfully mounted for SEM (Fig. 31) and light microscopy (Fig. 32, 33).

Cuticle of the floral envelope reflects an epidermis with rectangular epidermal cells sometimes arranged in rows and conspicuous round trichome bases (Fig. 32, 33). Trichome bases may also be contiguous or one round trichome base may be divided in two by an anticlinal wall suggesting trichomes were sometimes attached in fascicles of two (Fig. 32, 33). Trichomes are rarely attached and not well preserved, but in instances where they can be observed, they appear to be short, probably unicellular hairs (Fig. 34).

Stamens have small (av. length 0.24 mm), more or less elliptical (Fig. 35) anthers. The number of anthers can best be estimated by viewing radially compressed florets and up to ten anthers have been observed in some florets. Pollen is well preserved in the anthers, is tricolporate, and the colpi extend almost 100% of the length of the grains (Fig. 19, 20, 35). The pollen is prolate with average polar diameter of $15.0 \mu\text{m}$ and average equatorial diameter of $9.0 \mu\text{m}$ ($P/E = 1.67$) (Table 1). Exine sculpturing is identical with that of pollen of the modern Castaneoideae and consists of striate, variously anastomosing ridges suggesting a surface composed of fused rods (Fig. 19, 20). Pollen is tectate and the tectum is minutely perforate (Fig. 21, 22). The ectexine is relatively thin ($0.43 \mu\text{m}$ av.) and consists of a $0.19 \mu\text{m}$ (av.) thick tectum, $0.11 \mu\text{m}$ (av.) thick columellae, and a 0.13 (av.) thick foot layer (Table 2). The foot layer is thick relative to the tectum and the foot layer/tectum ratio is 0.68 (Table 2). The endexine is not well preserved and if represented at all appears as a

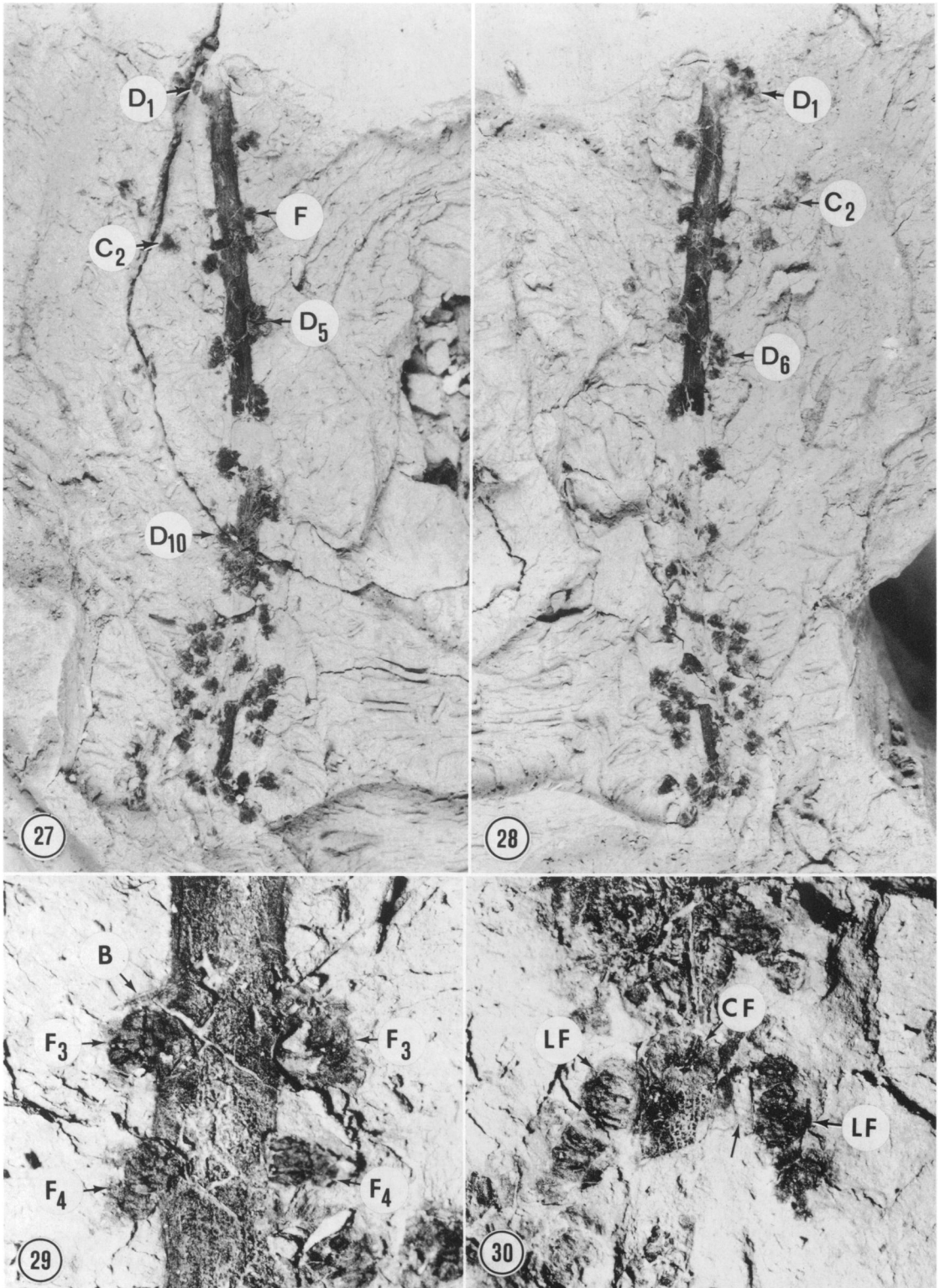


Fig. 27–30. *Castaneoidea puryearensis* UCPC P36a, b, all illustrations are oriented so that the apex of the inflorescence is toward the base of the figure. 27,28. Part and counterpart of the inflorescence axis showing the spiral arrangement of dichasia. Compare these Figs. with Figs. 38 and 39 which are line drawings of the same specimens. Note that 10 of the dichasia are labelled on Figs. 38 and 39, but only a few key dichasia are indicated on 27 and 28—enough for correlation with Figs. 38 and 39. Note the small size of a single lateral floret (F, part of D₃—see Fig. 38)

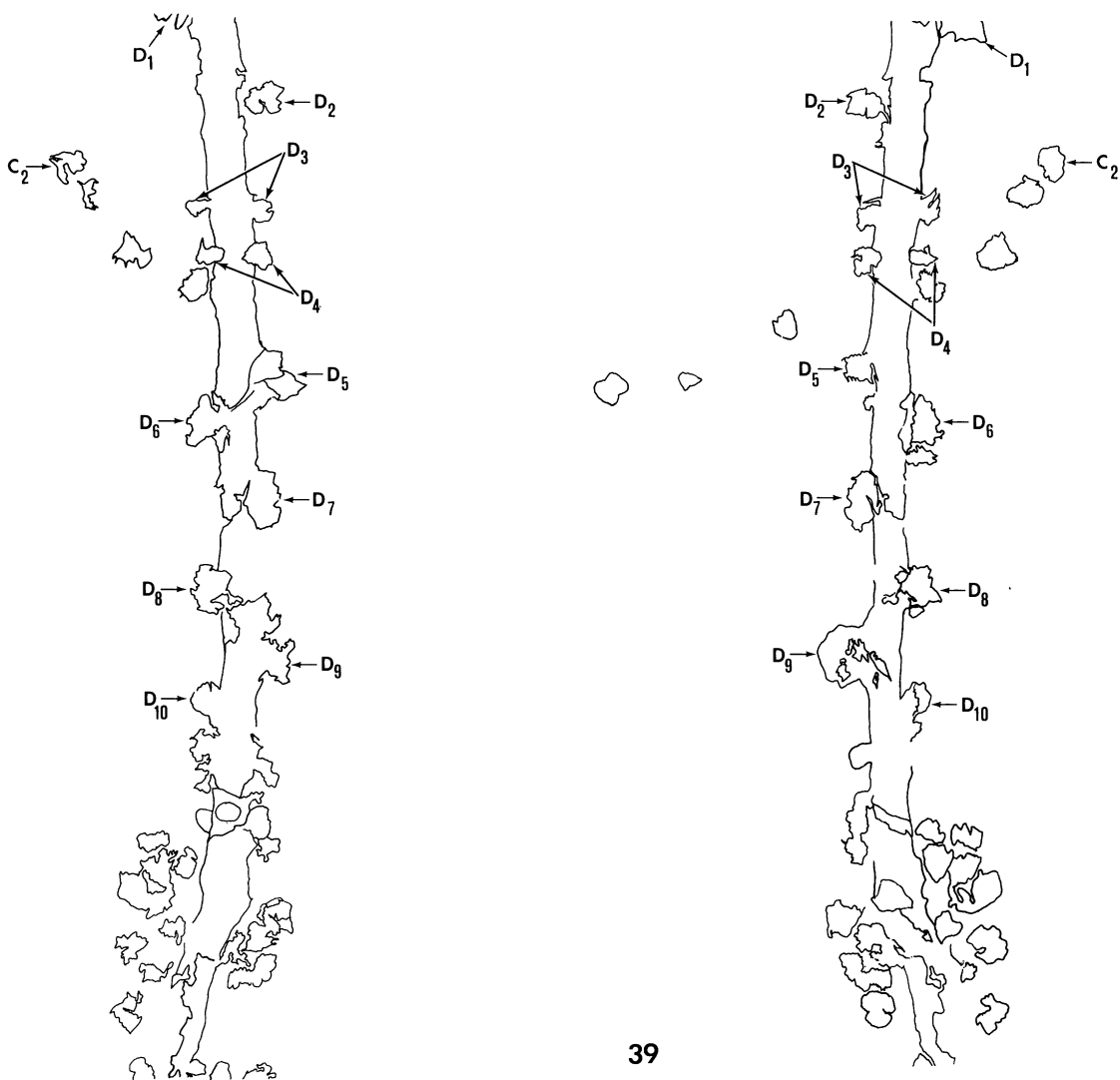


Fig. 38-39. Line drawings of P36a, b (see Figs. 27, 28) showing the spiral arrangement of dichasia (D₁-D₁₀). Dichasia D₃ and D₄ are compressed so that in each dichasium one floret appears on either side of the axis. Note also catkin C₂. ×6.

sporadic thin granular layer. The ektexine thins out rather abruptly at the margins of the colpi leaving only the poorly preserved endexine in the colpi (Fig. 21).

Affinities—These fossil catkins are most closely related to the subfamily Castaneoideae of the Fagaceae. They have general inflorescence morphology, flowers borne in bract sub-

tended dichasia, connate lobed floral envelopes with at least five lobes, stamen number and trichomes in common with the Fagaceae (Hjelmqvist, 1948; Soepadmo, 1972; Abbe 1974). The affinities of the fossils may be further traced to the subfamily Castaneoideae. The diagnostic value of pollen exine ornamentation, size and shape within the Fagaceae has

← relative to an entire laterally compressed dichasium (e.g., D₃). Note also catkin C₂. ×3. 29. A closeup of D₃ and D₄. Note that the lateral florets of D₃ (F₃'s) are partially covered by the axis, suggesting they were on the far side and note that the florets of the other dichasium (F₄'s) overlie the compressed axis suggesting that it was on the near side. Note also a subtending bract (B). ×15. 30. A single dichasium with one floret compressed on each side of the axis (LF's) and a central floret (CF) compressed in face view on the axis. The arrow indicates where part of one lateral floret has flaked from the matrix leaving only an impression. ×15. Note also the line drawing of this dichasium (Fig. 40).

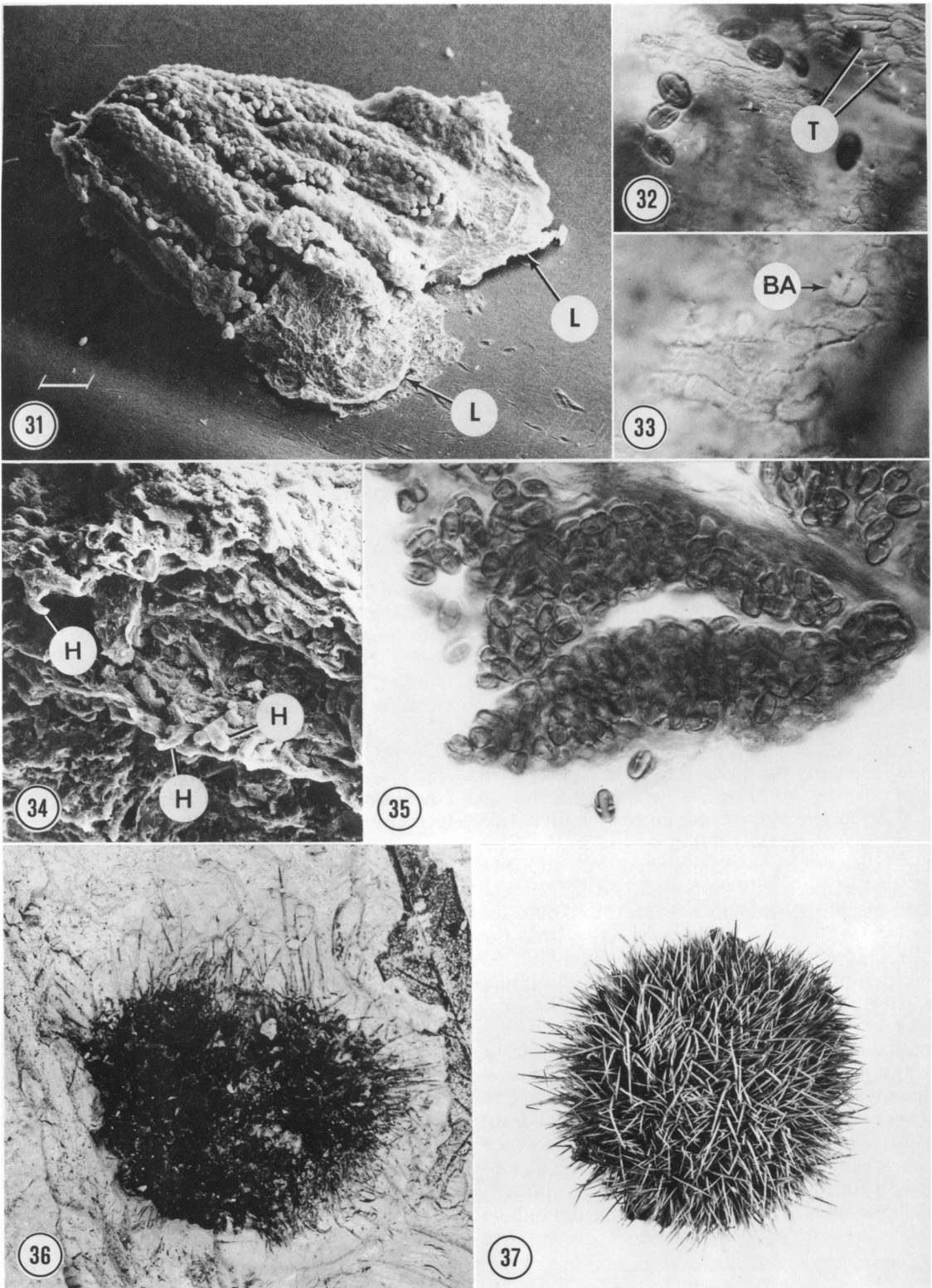
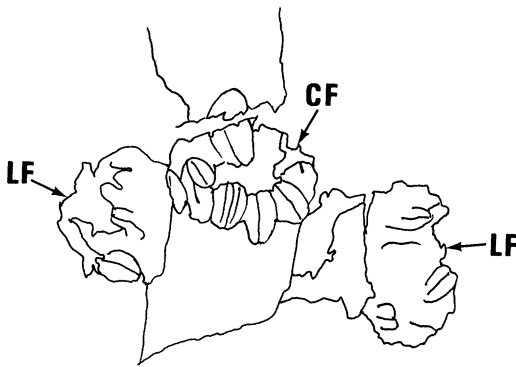


Fig. 31-37. 31. A portion of a floret consisting of a corolla fragment terminating in two ovate lobes (L's) and several anthers. P 116. $\times 136$. 32. Very thin floral envelope cuticle with some adhering pollen. Note the rows of more or less rectangular cells interrupted occasionally by round trichome bases (T). P 116. $\times 400$. 33. Floral envelope cuticle



40

Fig. 40. A line drawing of the dichasium illustrated in Fig. 30 compressed with one floret on either side of the axis (LF's) and a central floret compressed in face view on the axis (CF). The arrow indicates where part of a floret has flaked away from the compression. $\times 21$.

already been demonstrated. The pollen of the fossil is indistinguishable in every respect from the pollen of the modern Castaneoideae (Table 1, Fig. 15–22) and on this basis alone the fossils could be reliably assigned to that subfamily. However, there are additional diagnostic features that also indicate the castaneoid nature of these fossils. Anther size is a good diagnostic feature in the Fagaceae (Hjelmqvist, 1948; Soepadmo, 1972) and the anthers of the Castaneoideae are the smallest in the family. In *Quercus* the length varies between 0.5 and 1.0 mm, in *Fagus* the average anther length is 1.55 mm, in *Nothofagus* 4.0 mm, and in the Castaneoideae the range is between 0.2 and 0.35 mm (Hjelmqvist, 1948; Soepadmo, 1972). The average anther length of the fossil inflorescences is 0.24 mm and fits clearly within the range of anther sizes of the Castaneoideae. Stamen number is another diagnostic feature separating the catkin-bearing fagoids (i.e., the Quercoideae vs. the Castaneoideae) and suggesting the fossils have castaneoid affinities. There are usually six stamens in the Quercoideae with the Castaneoideae having a range of from 10–15 (90) stamens (e.g., Soepadmo, 1972). Finally, the fossils' robust inflorescence axis, relative to floret size, is a feature shared by the upright inflorescences of the modern Castaneoideae, but lacking in the pendulous

inflorescences of the Quercoideae (Soepadmo, 1972).

The fossil inflorescences are extremely modern in aspect, but the staminate inflorescences of the modern Castaneoideae are not the best of diagnostic features for distinguishing among the four genera in the subfamily (Soepadmo, 1972). The pollen of the four genera does demonstrate some difference in mean size (Table 1) and the pollen of the fossils is closest in size to the pollen of the modern genus *Castanea*. Size ranges overlap, however, and it would be unreasonable to suggest affinities with a particular genus on the basis of pollen size alone. Since suggesting affinities with a particular genus is not feasible, especially without knowledge of other plant organs, the inflorescences are placed in a form genus.

SYSTEMATICS—*Family*: Fagaceae; *Subfamily*: Castaneoideae; *Genus*: **Castaneoidea** Crepet & Daghljan gen. n.; *Diagnosis*: Staminate catkins up to at least 90 mm in length having helically arranged, bract subtended, dichasia of three florets each. Florets have minute floral envelopes (0.8 mm \times 1.0 mm) terminating in at least five ovate lobes. Floral envelope cuticle with rectangular epidermal cells, sometimes in rows, and with round trichome bases. Trichomes short hairs attached singly or in fascicles of at least two. Florets with up to ten stamens; anthers elliptical and small (length 0.24 mm). Pollen tricolporate; 15.6 μm \times 9 μm ; exine ornamentation striate. *Species*: **Castaneoidea puryearensis** Crepet & Daghljan sp. n.; *Diagnosis*: same as for genus.

Stratigraphic occurrence—Claiborne Formation, Middle Eocene.

Holotype—University of Connecticut Paleobotanical Collection P36 (Fig. 27, 28).

DISCUSSION AND CONCLUSIONS—The survey of the pollen of the extant Fagaceae has verified the possibility that subfamily can be determined on the basis of certain palynological features, especially exine ornamentation, and has refined concepts previously held regarding the division of the family on the basis of palynological features (Erdtman, 1966; Soepadmo, 1972). This information should permit improved understanding of the dispersed pol-

reflecting some distorted rectangular epidermal cells and what appear to be the basal cells of a fascicle of two trichomes (BA). P 116. $\times 800$. 34. A SEM micrograph of the edge of an inflorescence axis showing some twisted and apparently broken off hairs (H). $\times 298$. 35. An isolated anther. P 116. $\times 400$. 36. Compressed castaneoid cupule from Puryear, Tenn. P 119. $\times 1.5$. 37. Ripe cupule of *Castanea dentata*, Tidestrom 1914 (CONN). $\times 1.5$.

len record of the Fagaceae. If dispersed single grains are isolated for SEM (something presently technically feasible), then it should be possible to assess their affinities with the extant Fagaceae.

The survey of the pollen of the extant Fagaceae has also helped place the pollen structure of *Trigonobalanus* and *Nothofagus* in clearer perspective with regard to the rest of the family. The pollen of *Trigonobalanus* is more like the pollen of the Quercoideae than the pollen of the Fagoideae. This tends to support Forman (1962) and Soepadmo (1972) in their assignments of *Trigonobalanus* to the Quercoideae, but it should be kept in mind that pollen of *Trigonobalanus* remains unique in certain respects (e.g., the foot layer notably thicker than the tectum and the exine ornamentation similar to, but not identical with that of certain of the Quercoideae). The pollen of *Nothofagus* is well known to be different from that of all other genera of the Fagaceae (e.g., Erdtman, 1966; Soepadmo, 1972, and especially Hanks and Fairbrothers, 1976). The survey of fagoid pollen and the additional studies of the pollen of *Nothofagus* have pointed out these differences. The number of apertures, nature of exine ornamentation, and perhaps most interesting, the exine stratification are unique in the Fagaceae. One wonders whether this is the result of long term geographic isolation from the rest of the family over most of its range (as suggested by the fossil record) coupled with different selective pressures or whether the degree of relationship to the rest of the Fagaceae is less than has been supposed in the past. Differences of this magnitude are usually, but certainly not always, associated with different families rather than different genera (Erdtman, 1966).

The discovery of an inflorescence of the Castaneoideae in Middle Eocene deposits is interesting from a variety of viewpoints. This fossil verifies the presence of the Castaneoideae by that time. Although leaves of the Castaneoideae have been reported from the Eocene, there remains some question as to whether leaves are good diagnostic features for separating the subfamilies of the Fagaceae, but studies now underway on fossil and extant leaves of the Fagaceae will probably resolve this question (J. Jones and D. L. Dilcher, Indiana University, work in progress). In addition, the fossil inflorescences illustrate that essentially modern floral and pollen morphology has evolved in the Castaneoideae by the Middle Eocene. This is especially noteworthy because many species of the modern Castaneoideae are thought to be insect-pollinated

(Faegri and Van der Pijl, 1971; Soepadmo, 1972). All of the modern castaneoids have a relatively robust upright inflorescence axis thought to be adaptive for insect pollination. The fossil inflorescence has the same relatively robust inflorescence axis as the modern castaneoids, suggesting that it too had an upright habit and may have been insect-pollinated. If insect pollination is secondarily derived from wind pollination in the modern Fagaceae (Castaneoideae), it is apparent that by the Middle Eocene, not only had each of the subfamilies of the Fagaceae differentiated, but also that the morphological features characteristic of the insect-pollinated Fagaceae today had already evolved from presumably wind-pollinated ancestors. This, and the fossil record of the Fagaceae as presently understood, suggest a relatively rapid diversification of the Fagaceae between the Upper Cretaceous and the Middle Eocene.

In considering pollination mechanisms of the extant Fagaceae against the background of the survey of pollen of extant Fagaceae, it becomes obvious that there appear to be certain discrepancies between pollination mechanisms and pollen morphology. Those species that are exclusively wind-pollinated, the Quercoideae and the Fagoideae, have the roughest and largest pollen in the family (although usually well within the size limits suggested for wind-pollinated species [e.g., Whitehead, 1969]), while the Castaneoideae, most often insect-pollinated, have the smallest and smoothest grains in the family appearing superficially, at least, best suited for wind dispersal. Certainly, the pollen of the Fagoideae and Quercoideae is adequately adapted for wind dispersal but it is curious that the Castaneoideae should have such small, smooth pollen. Perhaps further studies of pollination mechanisms in the living Fagaceae would clarify the situation. It seems probable though, that modern castaneoids might have some supracteal substances to promote clumping as occurs in several insect-pollinated species (e.g., *Tilia*, Stanley and Kirby, 1973).

The identification of a castaneoid inflorescence from the Puryear, Tennessee locality may help clarify the affinities of certain fossils found in the same sediments. These are ovoid compressions, apparently representing a woody plant organ judging by the thickness of the residual carbon, and profusely covered with robust and often branched spines (Fig. 36). They are very like the ripe cupules of the modern Castaneoideae (e.g., *Castanea dentata*, Fig. 37) in morphology and size (about 3.5×4 mm; see Soepadmo, 1972) and the presence of inflorescences of the Castaneoideae in the same

sediments suggests that the morphological similarities reflect an actual relationship with the modern Fagaceae.

The identification of these fossil inflorescences also has ramifications with regard to another fossil common in many Claiborne localities; leaves assigned to the genus *Dryophyllum*. *Dryophyllum* is a form genus for leaves thought to have fagoid affinities and E. W. Berry identified seven species from the Claiborne Formation (Berry, 1916, 1924, 1930). *Dryophyllum* leaves are very similar in gross morphology and venation features to leaves of certain species of the Castaneoideae and the discovery of castaneoid inflorescences in the same sediments indicates that some species of *Dryophyllum* are undoubtedly castaneoid. Whether all species of *Dryophyllum* represent the Castaneoideae will presumably be determined when more is known about the diagnostic value of leaves in the Fagaceae and about the Claiborne *Dryophyllum* species (work in progress, J. Jones and D. L. Dilcher, Indiana University).

Although inflorescences of the Castaneoideae have so far only been found at the Puryear, Tennessee locality, *Dryophyllum* and what now appear to be castaneoid fruits are common in many of the Claiborne localities of western Tennessee and Kentucky, **suggesting that populations of Middle Eocene castaneoids were large and may have been continuous over reasonably large areas.**

It is becoming evident that the pattern demonstrated by the Fagaceae (i.e., an apparently rapid radiation from the Upper Cretaceous to the Middle Eocene resulting in considerable diversity, and floral morphology as well adapted to pollen dispersal as inflorescences of modern members of the family), is common to many families of the Amentiferae. It is well known that the Juglandaceae were as well adapted to wind pollination during the Middle Eocene as at the present time (Crepet, Dilcher and Potter, 1975; Crepet, Daghljan and Zavada, 1980) and that they were even more diverse (Dilcher, Potter and Crepet, 1976; Wolfe, 1973). In addition, flowers or inflorescences of *Casuarina*, the Myricaceae, and the Ulmaceae are known from Middle Eocene sediments (Lange, 1970; authors, work in progress). Although the possibility bears further investigation this pattern suggests the possibility of optimization of conditions favoring wind pollination in arborescent species during the Upper Cretaceous–Middle Eocene and concomitant rapid diversification of the Hamamelididae to take advantage of these conditions.

LITERATURE CITED

- ABBE, E. C. 1974. Flowers and inflorescences of the "Amentiferae." *Bot. Rev.* 40: 159–261.
- BERRY, E. W. 1916. The Lower Eocene floras of southeastern North America. U.S. Geol. Surv. Prof. Pap. 91: 1–481.
- . 1924. The Middle and Upper Eocene floras of southeastern North America. U.S. Geol. Surv. Prof. Pap. 92: 1–206.
- . 1930. Revision of the Lower Eocene Wilcox flora of the southeastern states. U.S. Geol. Surv. Prof. Pap. 156: 1–196.
- CHANDLER, M. E. J. 1964. The lower Tertiary floras of southern England, IV. London: Br. Mus. Nat. Hist. 1–151.
- CREPET, W. L., AND D. L. DILCHER. 1977. Investigations of angiosperms from the Eocene of North America: a mimosoid inflorescence. *Amer. J. Bot.* 64: 714–725.
- , C. P. DAGHLIAN, AND M. ZAVADA. 1980. Investigations of angiosperms from the Eocene of North America: a new juglandaceous catkin. *Rev. Palaeobot. and Palynol.* (In press).
- , D. L. DILCHER, AND F. W. POTTER. 1975. Investigations of angiosperms from the Eocene of North America: a catkin with juglandaceous affinities. *Amer. J. Bot.* 62: 813–823.
- CRONQUIST, A. 1968. The evolution and classification of flowering plants. Houghton Mifflin Co., Boston.
- DAGHLIAN, C. P., W. L. CREPET, AND T. DELEVORYAS. 1980. Investigations of Tertiary angiosperms: *Eomimosoidea plumosa* from the Lower Oligocene of eastern Texas. *Amer. J. Bot.* (In press.)
- DILCHER, D. L., F. W. POTTER, AND W. L. CREPET. 1976. Investigations of angiosperms from the Eocene of North America: juglandaceous winged fruits. *Amer. J. Bot.* 63: 532–544.
- ERDTMAN, G. 1966. An introduction to Palynology. I. Pollen morphology and plant taxonomy. Angiosperms. Hafner, New York.
- FAEGRI, K., AND L. VAN DER PIJL. 1971. The principles of pollination ecology. Pergamon, Oxford.
- FORMAN, L. I. 1962. A new genus in the Fagaceae. *Taxon* 11: 139.
- HANKS, S., AND D. E. FAIRBROTHERS. 1976. Palynotaxonomic investigations of *Fagus* L. and *Nothofagus* Bl.: light microscopy, scanning electron microscopy and computer analysis. *In* V. H. Heywood [Ed.] *Bot. Syst.* 1: 1–141.
- HJELMQVIST, H. 1948. Studies on the floral morphology and phylogeny of the Amentiferae. *Bot. Not. Suppl.* 2(1): 1–171.
- HUTCHINSON, J. 1967. The genera of flowering plants. Dicotyledons. Vol. 11. Oxford.
- JARZEN, D. M. 1979. The terrestrial palynoflora from the Cretaceous–Tertiary transition, Alabama, U.S.A. *Pollen Spores* 20: 535–553.
- LANGHE, R. T. 1970. The Maslin Bay flora, South Australia. 2. The assemblage of fossils. *Neues Jahrb. Geol. Paläontol. Monatsh.* 486–490.
- MACGINITIE, H. D. 1953. Fossil plants of the Florissant Beds, Colorado. *Publ. Carnegie Inst. Wash.* 543: 1–178.
- MELCHIOR, H. 1964. Juglandales, Leitneriales, Salicales, Fagales. *In* Engler's *Syllabus der Pflanzenfamilien*. (12th ed.) Vol. 2. Berlin.
- MULLER, J. 1970. Palynological evidence on early differentiation of the angiosperms. *Biol. Rev.* 45: 417–450.

- RAVEN, P. H., AND D. I. AXELROD. 1974. Angiosperm biogeography and past continental movements. *Ann. M. Bot. Gard.* 61: 539–673.
- SOEPADMO, E. 1968. A revision of the genus *Quercus* L. Subgen. *Cyclobalanopsis* (Oersted) Schneider in Malesia. *Gardens' Bull., Singapore* 22: 355–427.
- . 1972. Fagaceae. *In* *Flora Malesiana*. Ser. 1, Vol. 7, Pt. 2: 265–403.
- STANLEY, R. G., AND E. G. KIRBY. 1973. Shedding of pollen and seeds. *In* T. T. Kozlowski, [ed.] *Shedding of plant parts*. 295–340. Academic Press, New York.
- TAKHTAJAN, A. 1969. Flowering plants—origin and dispersal. Oliver and Boyd Ltd., Edinburgh.
- TUCKER, J. M. 1972. Hermaphroditic flowers in Californian oaks. *Madroño*. 21: 482–486.
- WHITEHEAD, D. R. 1969. Wind pollination in the angiosperms: evolutionary and environmental considerations. *Evolution* 23: 28–35.
- WOLFE, J. A. 1973. Fossil forms of the Amentiferae. *Brittonia* 25: 334–355.

TABLE 3. Appendix—voucher specimens of the Fagaceae used for pollen analysis

Species	Locality	Collector	Herbarium	Date
CASTANEOIDEAE				
<i>Castanea ashei</i>	U.S.A., Tex.	Lundell s.n.	TEX 10531	
<i>Castanea crenata</i>	Japan	Gillis s.n.	TEX 4693	
<i>Castanea dentata</i>	U.S.A., Conn.	Torrey s.n.	UCONN	1936
<i>Castanea ozarkensis</i>	U.S.A., Ia.	Warrock s.n.	TEX 20513	
<i>Castanea pumila</i>	U.S.A., La.	Thomas s.n.	UCONN	1972
<i>Castanopsis borneensis</i>	Borneo	Elmer s.n.	US 265605	
<i>Castanopsis carlesii</i>	Taiwan	Wilson s.n., <i>fide</i> Hui-Lui Li	US 1053024	
<i>Castanopsis formosana</i>	China	Liang s.n.	US 1671201	
<i>Castanopsis hainanensis</i>	China	How and Chun s.n.	US 1675586	
<i>Castanopsis indica</i>	China	Henry s.n.	US 459317	
<i>Castanopsis platycantha</i>	China	Wilson s.n.	US 778949	
<i>Castanopsis tribuloides</i>	China	Forrest s.n.	US 137702	
<i>Chrysolepis sempervirens</i>	U.S.A., Calif.	Traverse s.n.	TEX 504	
<i>Lithocarpus brevicaudata</i>	Taiwan	Sasaki s.n.	US 2063528	
<i>Lithocarpus cantleyanus</i>	Malay Peninsula	King s.n., <i>fide</i> Soepadmo	US 149922	
<i>Lithocarpus densiflorus</i>	U.S.A., Calif.	Traverse s.n.	TEX 509	
<i>Lithocarpus edulis</i>	Japan	Sagani s.n.	US 1176257	
<i>Lithocarpus glabrus</i>	Japan	Lynch s.n.	TEX 2092	
<i>Lithocarpus havilandii</i>	Sabah	Chew and Corner s.n.	US 25176781	
QUERCOIDEAE				
<i>Trigonobalanus verticillata</i>	Malay Peninsula	Poore s.n., <i>fide</i> Soepadmo	US 6337	
<i>Quercus alba</i>	U.S.A, Conn.	Smith s.n.	CONN	1934
<i>Quercus bicolor</i>	U.S.A., Conn.	Smith s.n.	CONN	1930
<i>Quercus championi</i>	Hong Kong	Faber s.n.	US 156293	
<i>Quercus chapmani</i>	U.S.A., Fla.	Curtiss s.n.	CONN	1897
<i>Quercus coccinea</i>	U.S.A., Conn.	Jansson s.n.	CONN	1929
<i>Quercus dentata</i>	Korea	Smith s.n.	US 1756896	
<i>Quercus ellipsoidalis</i>	U.S.A., Ill.	Hill s.n.	CONN	1899
<i>Quercus falcata</i>	U.S.A., La.	Thomas s.n.	CONN	1971
<i>Quercus ilicifolia</i>	U.S.A., Conn.	Torrey s.n.	CONN	1911
<i>Quercus imbricaria</i>	U.S.A., Ill.	Umbach s.n.	CONN 1092966	
<i>Quercus incana</i>	U.S.A., Fla.	Curtiss s.n.	CONN	1896
<i>Quercus laevis</i>	U.S.A., Fla.	Curtiss s.n.	CONN	1894
<i>Quercus macrocarpa</i>	U.S.A., Conn.	Dodge s.n.	CONN	1895
<i>Quercus marilandica</i>	U.S.A., Md.	Tidestrom s.n.	CONN	1911
<i>Quercus mongolica</i>	Japan	Togashi s.n.	US 2276731	
<i>Quercus muhlenbergii</i>	U.S.A., Conn.	Eames s.n.	CONN	1931
<i>Quercus nigra</i>	U.S.A., La.	Thomas s.n.	CONN	1971
<i>Quercus oglethorpensis</i>	U.S.A., Ga.	Duncan s.n.	CONN	1942
<i>Quercus palustris</i>	U.S.A., Conn.	Jansson s.n.	CONN	1927
<i>Quercus phellos</i>	U.S.A., Fla.	Curtiss s.n.	CONN	1896
<i>Quercus prinoides</i>	U.S.A., Conn.	Diggs s.n.	CONN	1914
<i>Quercus prinus</i>	U.S.A., Conn.	Eames s.n.	CONN	1903
<i>Quercus pumila</i>	U.S.A., Fla.	Curtiss s.n.	CONN	1898
<i>Quercus rubra</i>	U.S.A., Conn.	Eames s.n.	CONN	1895
<i>Quercus spathulata</i>	China	Wilson s.n.	US 777641	
<i>Quercus spinosa</i>	China	Wilson s.n.	US 596815	
<i>Quercus variabilis</i>	China	Purdom s.n.	US 1092966	
<i>Quercus velutina</i>	U.S.A., Conn.	Eames s.n.	CONN	1892
FAGOIDEAE				
<i>Fagus crenata</i>	Japan	Togashi 7138	G	1963
<i>Fagus engleriana</i>	China	Sierren s.n.	G	1942
<i>Fagus grandifolia</i>	England	Leavitt s.n.	TEX	1899
<i>Fagus japonica</i>	Japan	Mizashima 1885	G	1950
<i>Fagus longipetiolata</i>	China	Wang-Te-Hin s.n.	US 1271109	
<i>Fagus maximowicziana</i>	China	Camp and Gilly s.n.	G 6733	
<i>Fagus multinervis</i>	Korea	Wilson 8497	G	1917
<i>Fagus orientalis</i>	USSR (Caucacus)	Marcowicz s.n.	G	1898
<i>Fagus sieboldii</i>	Japan	Wilson 6728	G	1914
<i>Fagus sylvatica</i>	U.S.A., Wash., DC	Canby s.n.	CONN	—
<i>Nothofagus pumila</i>	Argentina	Goodall s.n.	CONN	1967