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FRUITS AND SEEDS OF THE BRANDON LIGNITE, V. RUTACEAE

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THE BRANDON LIGNITE (lat. 43°50' N., long. 73°03' W.) is a small deposit of Early Oligocene brown coal located in the town of Forestdale, Vermont, 27 km. north of Rutland, Vermont, and 230 km. northwest of Boston, Massachusetts. This locality is of particular value both because of the care with which it has been studied, and because it is the only known plant-megafossil-bearing terrestrial deposit of Tertiary age north of New Jersey in eastern North America. Fossil fruits and seeds were first described from the locality by Hitchcock (1853) and by Lesquereux (1861; and in Hitchcock *et al.*, 1861) and were subsequently redescribed by Perkins (1904a, 1904b, 1905, 1906a, 1906b). Barghoorn and his students initiated a modern evaluation of the deposit in the late 1940's, leading to a series of papers on the wood, pollen, and some of the fruits (Spackman, 1949; Barghoorn & Spackman, 1949; Barghoorn, 1950; Traverse & Barghoorn, 1953; Traverse, 1955; Eyde & Barghoorn, 1963; Eyde, Bartlett, & Barghoorn, 1969). The author is presently investigating the remaining fruits and seeds of the deposit (Tiffney & Barghoorn, 1976, 1979; Tiffney, 1977, 1979).

GEOLOGY

The lignite and its associated clays, sands, and gravels unconformably overlie the contact of the Lower Cambrian Cheshire Quartzite and Dunham Dolomite, and are in turn unconformably overlain by Quaternary drift (Burt, 1928, 1930; Cady, 1945; Spackman, 1949). Most of the fossiliferous sediment is subsurface, but an area of roughly 82 square meters was exposed at the northern end of the deposit in 1974. The fossiliferous sediment is divisible into two separate units: a fine- to coarse-grained lignite, rich in fruits, seeds, and wood; and a fine-grained, purple-brown silt containing widely scattered fruits, seeds, wood, flowers, broken leaves, and particulate organic matter.

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These two fossiliferous units are associated with a complex of sediments that appear to be a remnant of an extensive river system that flowed through west-central Vermont in mid Tertiary time. The silt, which is rich in anemophilous pollen, is interpreted to represent an open body of still water, perhaps an oxbow lake, within this river system. By contrast, the lignite is seen to represent a sluggish to stagnant fluvial environment, closely overhung by vegetated banks and subject to a considerable influx of organic material. The stratigraphic relationship of the silt and lignite has been rendered indefinite by the deformation associated with the passage of the Quaternary ice sheet. However, the present-day proximity of the two sediments, together with the extreme similarity of their contained flora, suggests that the two were deposited within a short period of time. Thus, while the two sediments represent slightly different ecological circumstances, they are here treated as coeval, and their flora considered as a single unit.

MATERIALS AND METHODS

The Brandon fruits and seeds are preserved as compactions—original organic matter retaining three dimensions and full morphological and anatomical detail. Larger specimens were recovered by manually breaking the matrix and then picking the fossils off of the freshly exposed face. The resulting matrix fragments were subsequently disaggregated in a solution of either sodium carbonate or hydrogen peroxide and were passed through sieves to recover smaller organic fragments. This material was viewed under a dissecting microscope, and the smaller specimens of interest were removed with a small brush. Adherent mineral matter was removed from the specimens with a toothbrush, and they were treated with 52 percent hydrofluoric acid to remove embedded mineral matter. All specimens were stored in a 1:1 solution of glycerine and 50 percent ethyl alcohol. Photomicrographs were made by means of a Wild M-20 compound microscope with camera attachment; whole specimens were photographed in air by using a Leicaflex camera with extension tubes and a Zeiss Planar or Tessar lens. Scanning electron micrographs were made with a model 1000a AMR microscope.

Comparative modern material was obtained from herbarium specimens held by the Arnold Arboretum (A) and Gray Herbarium (GH) of Harvard University. Although many of these sheets had recently been annotated by specialists working in the Rutaceae, several others had only original label data, occasionally over 100 years old. This situation raises the problem of the serious, and often underestimated, potential for utilizing misidentified modern comparative material in the identification of angiosperm fossils. Although the paleobotanist can avoid specimens of particularly dubious provenance, he cannot hope to fulfill his paleontological goals if all modern identifications must also be checked. For this reason, the herbarium sheets examined have been annotated, indicating that they were used in a study of the Brandon flora. Thus, if any of the modern comparative specimens used are subsequently assigned to a different taxon by a neobotanist, it becomes that individual's responsibility to notify the paleobotanical community of the changes, particularly if the specimen is of significance. In addition, fruits and seeds of all

the modern comparative specimens, together with all appropriate label data, have been placed in the fruit and seed collection of the Harvard University Herbaria. All modern material was cleaned and prepared by boiling in 10 percent potassium hydroxide for five to fifteen minutes, then washed, scrubbed with a stiff toothbrush, and dried, thus partially simulating the fossil condition.

FOSSIL RUTACEAE

Fossil seeds of the Rutaceae are known from Lower Eocene through Holocene sediments and comprise over sixty species in eleven genera, including one extinct genus, *Caxtonia* (Chandler, 1961b). The other genera reported are *Acronychia*, *Euodia*, *Fagara*, *Orixa*, *Phellodendron*, *Ruta*, *Ptelea*, *Spathelia*, *Toddalia*, and *Zanthoxylum*. The form genus *Rutaspermum* primarily includes seeds assignable to *Zanthoxylum*, although some members are rutaceous seeds of uncertain generic affinity. The use of this form genus is discussed further in the description of the *Zanthoxylum* seeds from Brandon.

No extensive summary of the living or fossil seeds of the group is available, although Kirchheimer (1957) discussed the then-known remains of *Phellodendron*, and Gallet (1913) has summarized the development and anatomical structure of the seeds of several genera within the family. Because of this dearth of information, the process of identifying the Brandon fossils commenced with a survey of the modern fruits and seeds of the family. Approximately 151 species in 55 genera were examined, with emphasis on genera and species presently found in the New World and in the tropical and temperate areas of eastern Asia, although representatives from other areas were included. The number of species examined per genus will be presented in the systematic descriptions.

The family Rutaceae is characterized by one, two, or up to a large number of anatropous seeds per carpel, the seeds often being marked by a distinctively elongate hilar scar along their ventral margin. At maturity the carpels can be variously united into berries (*Citrus*) or drupes (*Phellodendron*), or can develop into samaras (*Ptelea*, *Skimmia*). They may also form papery to woody capsules (*Euodia*, *Zanthoxylum*). To summarize the seed structure of the family as a whole is not necessary or possible in the present context. In view of the range of variation in fruit and seed morphology of the group, and of the diversity of forms present in the Brandon Lignite flora, this paper will diverge from the pattern set in the earlier portions of the Brandon Lignite investigation (Tiffney, 1977, 1979; Tiffney & Barghoorn, 1976, 1979) and consider the morphology and fossil history of the seeds of each genus independently. In all cases the important morphological characters of the seeds of each genus are summarized in a table and in an illustration accompanying the description of that genus.

SYSTEMATIC DESCRIPTIONS

Rutaceae A. L. de Jussieu, Gen. Pl. 296. 1789.

Lesquereux (1861; and in Hitchcock *et al.*, 1861) described *Drupa rhabdosperma* (later illustrated in Perkins, 1904b, 1905, 1906b) without assigning

it to a family. This seed is here recognized as belonging to the genus *Zanthoxylum*.

Traverse (1955) reported one species of pollen from the Brandon Lignite, which was provisionally assigned to the tribe Toddalieae, fruiting remains of which are represented at Brandon by seeds of the genus *Phellodendron*.

Euodia J. R. & G. Forster, Char. Gen. Pl. 13. 1776.

The genus *Euodia* consists of some forty-five (Li, 1963; Willis, 1973) to over one hundred (Mai, 1970a) species of trees and shrubs of temperate to tropical forests in the Old World. These range from northern China south to Australia and east to eastern Africa. The majority of these species are evergreen, although many from northern and central China are deciduous (Wang, 1961). Chinese species of *Euodia* are particularly concentrated in the mixed mesophytic forests of the Yangtze Valley (Wang, 1961).

The fruit is a sometimes rather thinly woody, loculicidal capsule, usually four to five lobed (occasionally unilobed), each lobe separating into two valves to reveal one or two seeds loosely enclosed in a bipartite, parchmentlike endocarp. This endocarp may provide a mechanical means of seed dispersal (see section on ecology). In many specimens, the shiny to iridescent seeds are attached to the open carpel or dangle from it on a short funicle.

The present investigation is based on a survey of the seeds of 26 species of *Euodia*, 13 from China, India, and Japan, and 13 from Malaysia, Indonesia, and the Philippines. The recognition of this geographic separation is suggested by a dichotomy in the morphology of the seeds from the two areas. The seeds of the southern species are rugose and conspicuously irregular in shape, while those of the Indian, Japanese, and northern and central Chinese species are smooth to faintly reticulate and vary from nearly spherical to ellipsoid. These characters are all obtained following the removal of the smooth, shiny outer coat that is common to all seeds of the genus. Since the seeds of *Euodia* from the Brandon locality are comparable to those of the Chinese and Japanese species of the genus, the following discussion of the modern seeds will be limited to this northerly group of species.

The seeds of the northern species of *Euodia* (see FIGURE 2 for a generalized example) are small (2.2–5.3 mm. long by 2.0–3.9 mm. in diameter) and vary from nearly spheroidal to ellipsoid. In those species bearing two seeds per carpel the seeds are superimposed, the points of mutual contact appearing as flattened faces on the mature seeds (see PLATE 1, F). The shiny to iridescent, black or dark brown seed surface is broken only by a light tan ventral hilar scar. This shiny outer surface is formed by a thin, crustaceous layer that is easily removed to reveal the inner layer of the outer integument, thus simulating the fossil condition. The surface of this second, hard layer may be smooth (*Euodia daniellii* Hemsley ex Forbes & Hemsley, *E. hupehensis* Dode) or may be marked by gentle longitudinal ridges that are systematically broken by fainter transverse ridges to form a weak but distinct reticulum (*E. bodinieri* Dode, *E. colorata* Dunn, *E. glauca* Miq., *E. hirsutifolia* Hayata, *E. meliifolia* Benthham, *E. officinalis* Dode, and the fossil reported here; see PLATE 1, A, D). The distinct hilar scar traverses the ventral face of

the seed from the apex to the base; occasionally it develops a wide, distinctive lip or margin on either side of the hilum. The basal end of the hilum leads to a short raphe canal, which bends around to the large basal chalaza. The apical micropyle is small and inconspicuous. The apex in some species bears a more or less developed knob, which, according to Mai (1970a), results from the adherence of an abortive seed to the apex of the remaining seed. If this is correct, then it is always the upper of the two seeds that aborts in a biovular carpel.

The anatomy of the seeds of *Euodia* was briefly summarized by Gallet (1913). The outer integument consists of a thin external unit and a sclerified internal unit. The outer two or three layers of cells are spongy and have a thicker external face that forms the shiny layer. It is this unit that is removed to reveal the inner layer of spirally thickened, radially elongate sclereids that form the sclerotesta. The inner integument is also bipartite, with an outermost single layer of small, longitudinally elongate cells having punctate or spirally thickened walls and an underlying layer, one or two cells thick, of large thin-walled cells.

Fossil seeds of the genus have been reported on two previous occasions. Miki and Kokawa (1962) cited seeds of *Euodia glauca* from Recent deposits of Kyushu, Japan, and Mai (1970a, 1970b) has suggested that a previously unidentified seed of the Oligocene and Miocene of Europe is allied to the genus. This latter report is based on over one hundred specimens of consistent morphology from localities in Germany and western Siberia. Nötzold (1963) identified this seed as *Aldrovanda praevesiculosa* Kirchheimer, which Mai (1970a) correctly argues on morphological grounds it cannot be. Nikitin (1965; and in Dorofeev, 1963) cited it as *Carpolithus nitidus* Nikitin and tentatively allied it with the Rutaceae.

As described by Mai (1970a, 1970b), the seed in question is 1.5–1.8 mm. long and about 1.2–1.3 mm. in diameter, pear shaped in ventral (hilar) view and elliptic in lateral view. Its shiny external surface is marked by a broad, light-colored hilum that passes from a terminal perforation identified as the micropyle, to a point approximately halfway down the ventral face of the seed. From the terminus of the hilum, an angular raphe passes over the remainder of the ventral side to the subbasal chalaza (see FIGURE 1, A, a schematic drawing). Nikitin (1965) has interpreted the seed differently, placing the micropyle at the end of the hilum near the center of the ventral face of the seed, and the chalaza at the terminus now occupied by the perforation (see FIGURE 1, B).

The described and illustrated characters, particularly in view of the slight amount of variation in the abundant material (Mai, 1970a, 1970b), make it difficult to accept this as a seed of the genus *Euodia*. The pearlike shape of the fossil, with its narrowed “micropylar” end (*sensu* Mai), is distinct from the elliptic to ovoid shape of most modern *Euodia* seeds, and the absence of flattened surfaces on any of the fossils suggests that they were consistently borne singly in the carpel. The short hilum that extends about halfway down the ventral face of the fossil contrasts with those of the extant seeds, which run the entire length of the ventral face. The fossils are

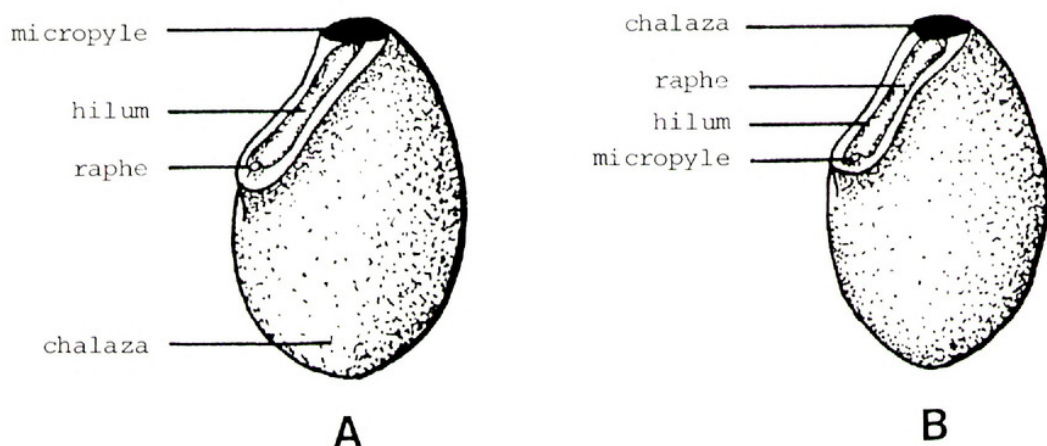


FIGURE 1. Two interpretations of *Carpolithus nitidus*: A, by Mai (1970a, 1970b); B, by Nikitin (1965).

characterized by a shiny exterior surface similar to that of *Euodia*; however, in *Euodia* this coat is easily abraded away to reveal the dull sclerotesta. The fact that the shiny surface of the fossil is consistently whole and is formed by a layer of radially elongate sclereids (Nötzold, 1963; Mai, 1970a) suggests that its structure is quite distinct from that of the membranaceous outer layer of *Euodia*. No modern species of *Euodia* exhibit the large "micropylar" perforation of the fossil, although its consistent presence and location suggest that it is a true morphological character of the seed and not a chance degradational feature. Since these fossils are thus not really comparable with the seeds of *Euodia*, perhaps it is best to return them to the form genus *Carpolithus* in the hope that their correct affinities might be elucidated in the future.

This reevaluation of *Carpolithus* (*Euodia*) *nitidus* does not signal the demise of the genus from the European Tertiary, however, since seeds originally identified as *Phellodendron costatum* Chandler from the Eocene of England show a close resemblance to the seeds of modern species of *Euodia*. The seeds of *P. costatum* (Chandler, 1925-26, p. 28, pl. 4, figs. 6a-c; 1961a, p. 125; 1961b, p. 75, pl. 7, figs. 10, 11; 1962, p. 73, pl. 10, fig. 1; 1963b, p. 92, pl. 14, figs. 24-28) are 3.0-3.5 mm. long, 2.0-2.25 mm. in diameter, and ellipsoid, often with a protruding knob on the micropylar terminus. The hilum and its broad margins extend the length of the ventral face of the seed (see particularly Chandler, 1963b, pl. 14, fig. 28), with the short raphal canal commencing at the basal end of the hilum and leading to the large basal chalaza. The micropyle is situated on the knob at the apical terminus of the hilum. The sclerotesta is marked by a series of strong longitudinal ribs connected by weaker transverse ridges, the whole forming a reticulum. The sclerotesta is approximately 300 μ m. thick and is formed of radial rows of equiaxial cells 20-25 μ m. in diameter (Chandler, 1961a). While modern seeds of both *Phellodendron* and *Euodia* have an elongate hilum and a reticulate sclerotestal surface, those of *Phellodendron* are longer, have a narrower hilum without margins, and are flattened laterally from the mutual pressure of

the five seeds in the drupe. Since the other reported fossil species of *Phellodendron* conform to these characters (Kirchheimer, 1957), it is best to consider *P. costatum* not as an aberrant *Phellodendron*, but as a distinct species of *Euodia*. Chandler (1925–26) assumed that the morphology of *P. costatum* was linked to that of the modern species through the Pliocene *P. elegans* C. & E. M. Reid, but Kirchheimer (1957) and Tralau (1963) both expressed doubt as to the assignment of this seed to *Phellodendron*, and Kirchheimer (1957) suggested its possible affinity with the Toddalieae. However, the rounded shape suggesting derivation from a one-seeded carpel, the elongate hilum with wide margins, the apical knob, and the small size suggest placement of this seed in the genus *Euodia*. A formal reassignment of this taxon will be proposed and discussed in detail in a pending publication.

***Euodia lignita* Tiffney, sp. nov.**

PLATE 1, A–G.

MATERIALS. Six seeds have been recovered from the lignite at Brandon. The type specimen (PLATE 1, A, D) is assigned number 51378 of the Paleobotanical Collections of the Botanical Museum, Harvard University. The paratypes are assigned number 51379 in the same collection.

DESCRIPTION. The seeds average 4.5 mm. long (range 3.4–4.9 mm.) and 2.8 mm. in diameter (range 2.7–2.9 mm.). With one exception, each is the product of a carpel containing one seed and is ellipsoid. The exception (PLATE 1, F) is more rounded and has one face flattened from the pressure of a second seed in the mature carpel. One of the seeds bears a very distinct apical knob (PLATE 1, G), and two others display it to a lesser degree. All are marked by a hilar scar that extends from the apex to the base of the seed and is bordered by a wide margin (see FIGURE 2 and PLATE 1, A, E). At the base of the hilum a short raphe leads to the large, pitlike basal chalaza. The micropyle is at the apex of the seed, just beyond the terminus of the hilum. The dull black external surface of the sclerotesta is marked by many faint longitudinal ridges that are crossed at intervals by weak, short transverse ridges, the whole yielding a very faint reticulum of spaces ranging from 175 to 250 μm . on a side. At higher resolution the surface is marked by a faint pattern of pits 20–30 μm . in diameter in the outermost layer of sclerotestal cells. Two seeds exhibit only the latter pattern and show distinct signs of abrasion. None shows any evidence of the external layer of the outer integument that forms the shiny surface of the modern seeds. The inner layer of the outer integument (sclerotesta) is 150–250 μm . thick and is formed of many layers of isodiametric sclereids. The inner integument is thin and hyaline, with an outermost layer of small, longitudinally elongate cells with spiral thickenings, underlain by two (three?) layers of larger isodiametric cells (PLATE 1, B, C).

AFFINITIES. No single modern species is completely similar to the fossil, and only one that has been examined, *Euodia colorata*, is as large. Although *E. colorata* has a reticulate sclerotestal pattern, it lacks hilar margins, any suggestion of an apical knob, and any evidence that more than one seed was ever borne in a carpel. Both *E. glauca* and *E. hirsutifolia*, although

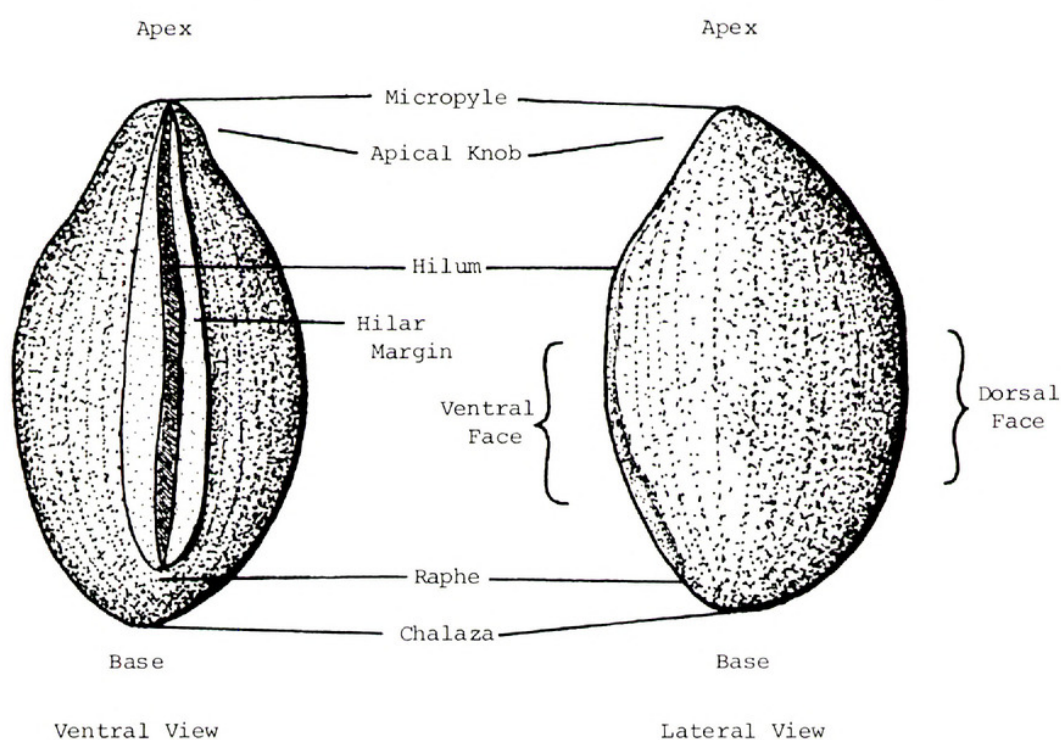


FIGURE 2. Descriptive characters of *Euodia* seeds.

small, have wide hilar margins and a reticulate sclerotestal pattern. *Euodia glauca* has occasional biseminal carpels yielding seeds with flattened sides, and *E. hirsutifolia* has an apical knob and surficial pitting not unlike that of the fossil. Thus, although the fossil is similar to certain modern species, it is not completely comparable to any one, and it is best to regard it as belonging to an extinct species. Two of the three modern species discussed (*E. colorata* and *E. hirsutifolia*) are members of the evergreen oak communities of China, while the third (*E. glauca*) is a member of the mixed mesophytic forests of central China (Wang, 1961).

"*Phellodendron*" *costatum* is smaller and has both a more pronounced sclerotestal reticulation and (in many cases) a more prominent apical knob than *E. lignita*. Thus, while the two fossil species are similar in their wide hilar margins and their sclerotestal pitting, they definitely represent two distinct entities.

The specific epithet *lignita* commemorates the source of this fossil.

ECOLOGY. Although the members of the northerly *Euodia* group (as distinguished by their seeds) range from deciduous species of northern China (*E. daniellii*) to evergreen taxa of the southern Chinese rainforests (*E. meliifolia*) (MAP 1), the strongest concentration of extant species is in the upper Yangtze River valley, where ten occur in the intermixed deciduous and evergreen mesophytic forests of the hills and valleys (Wang, 1961). Both *E. colorata* and *E. hirsutifolia* are probably evergreen since they occur in the evergreen oak forests of Yunnan and the mountains of Taiwan, respectively. *Euodia*

TABLE 1. Descriptive characters of *Euodia* seeds.

Size	Hilum
Length	Percent length of ventral face
Diameter	Hilar margin
Shape	Present/absent
Spherical	Micropylar knob
Ellipsoid	Present/absent
Number of seeds/carpel	Seed surface
One	Smooth
Two	Predominantly low reticulation
	Predominantly low parallel ridges

glauca is a canopy tree of the mixed mesophytic forests, found from 800 to 1400 meters elevation along the Yangtze River. Of interest is its association with species of *Alangium*, *Ilex*, *Illicium*, *Magnolia*, *Nyssa*, and *Quercus* (Lee, 1935; Wang, 1961), all of which are genera found at Brandon. The habitats of the modern species suggest that *E. lignita* was perhaps a denizen of a mixed mesophytic or evergreen broad-leaved sclerophyllous type of forest. Although possibly deciduous, it could equally well have been evergreen, particularly in light of the presence at Brandon of a species of *Magnolia* comparable to the extant evergreen *M. grandiflora* L.

The small number of *Euodia* seeds in the deposit and their abraded condition (two more noticeably so than the others) suggest transport from a distant source. Ridley (1930) has suggested that the dispersal of *Euodia* seeds is similar to that of *Dictamnus*, where the seeds are mechanically tossed from the carpel by tensions created within the drying endocarp. The writer has not seen any evidence of mechanical dispersal in *Euodia*; indeed, the glistening, black seeds hanging free of the carpel on a short funicle seem perfectly adapted for avian dispersal. It is uncertain whether the abrasion of the fossils could have been produced by passage through a bird's digestive tract, or whether it represents aquatic transport from a distant source. In view of the diversity of *Euodia* species in the hills of western China, it is tempting to conceive of *E. lignita* as having grown on the slopes of the Oligocene Green Mountains of Vermont, and then having been transported down to the Brandon deposit. The limited ecological data on the genus (Lee, 1935; Wang, 1961) suggest that it prefers drier, forested slopes, rather than moist riverbottom land, and thus favor a somewhat distant source for the seeds. It is unlikely that the genus was a dominant element in the forests surrounding Brandon in the Oligocene.

Phellodendron Ruprecht, Bull. Acad. Imp. St.-Petersb. **15**: 353. 1857.

This genus comprises between nine and thirteen species (Kirchheimer, 1957; Tralau, 1963; Willis, 1973) of small and large dioecious trees. In the absence of a monographic study, the disposition of species is uncertain, and revision may result in a reduction of the total number (Tralau, 1963). Owhi (1965)

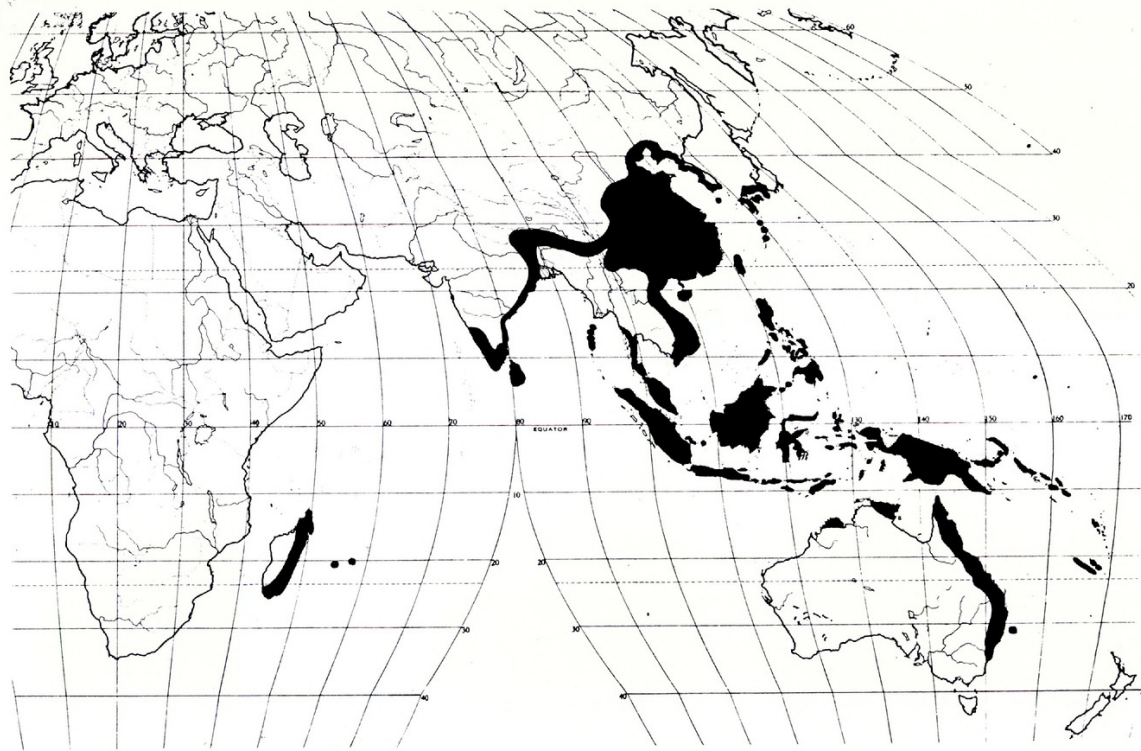
recognizes three of the species considered here (*Phellodendron japonicum* Maxim., *P. lavalleyi* Dode, and *P. sachalinense* Sarg.) as varieties of *P. amurense* Rupr. *Phellodendron* is restricted to the temperate and subtropical regions of eastern Asia. The species with the northernmost distribution is *P. amurense*, a tree of the coniferous and northern hardwood forests of Siberia, northeastern China, Korea, Japan, and Sakhalin. The southern distribution of the genus centers about the mixed mesophytic forests of the Yangtze Valley, where up to five deciduous species occur as low trees in the understory (Wang, 1961).

The fruit of *Phellodendron* is a resinous, black, five-loculed drupe (Lee, 1935), although it may rarely develop four to six locules (Kirchheimer, 1957). Each locule is lined with a two-valved, thin, membranaceous endocarp that splits on a median plane to release the enclosed seed. The mature carpel usually bears only one seed, but two-seeded carpels are known, with the resulting seeds being small and highly deformed (Kirchheimer, 1957).

Dorofeev (1970) noted the absence of herbarium specimens for comparative work, a seemingly not uncommon problem with the genus. The present study is based on seeds from six species (*Phellodendron amurense*, *P. chinense* Schneider, *P. japonicum*, *P. lavalleyi*, *P. molle* Nakai, *P. sachalinense*), the total number available in the herbaria (A and GH) at Harvard University.

Seed morphology is rather consistent throughout the species of the genus. Excluding abnormal ones, the seeds range from approximately 4 to 6 mm. in length, 2.5 to 3.5 mm. in height (from the ventral to the dorsal margin), and 1.8 to 2.3 mm. in width (perpendicular to the dorsal-ventral plane). The overall shape is that of a laterally compressed hemisphere, the convex dorsal face bending at either end to meet the essentially linear, sharp, raphe-bearing ventral face formed by the junction of the two shallowly arched lateral faces (see FIGURE 3 and PLATE 2, A-E). The flattened lateral faces are shaped by the mutual pressure of the five seeds within the drupe. Occasionally the dorsal face is marked by large, uneven depressions of unknown origin. These may be seen in the present fossil, *Phellodendron sachalinense*, and in some specimens of *P. amurense*.

The linear hilum extends from one half to the whole length of the ventral face, depending on the species. The raphal canal begins at the basal end of the hilum and leads to the basal chalaza of the seed. The micropyle is situated at the apical end of the hilum, occasionally on a small protrusion or micropylar beak (FIGURE 4). The two lateral faces are marked by a reticulate pattern of varying intensity and organization. In some species (e.g., *Phellodendron lavalleyi*) this consists of a faint pattern of small depressions, while in others more distinct longitudinal ridges parallel the dorsal margin of the seed and are crossed by transverse ridges to form a reticulum. This latter pattern may be strong (*P. japonicum*) or weak (*P. amurense*, *P. chinense*, *P. molle*, and *P. sachalinense*), depending on the species. Germination results in the seed splitting into two equal halves, commencing on the ventral face and passing around to the opposite dorsal face. The outer integument is formed of two layers, an exterior layer of large, open cells, often abraded away in the fossils, underlain by a sclerotesta of many layers of isodiametric



MAP 1. Present distribution of *Euodia* (after Engler (1896), Chiarugi (1933), Lee (1935), and herbarium specimens at A and GH).

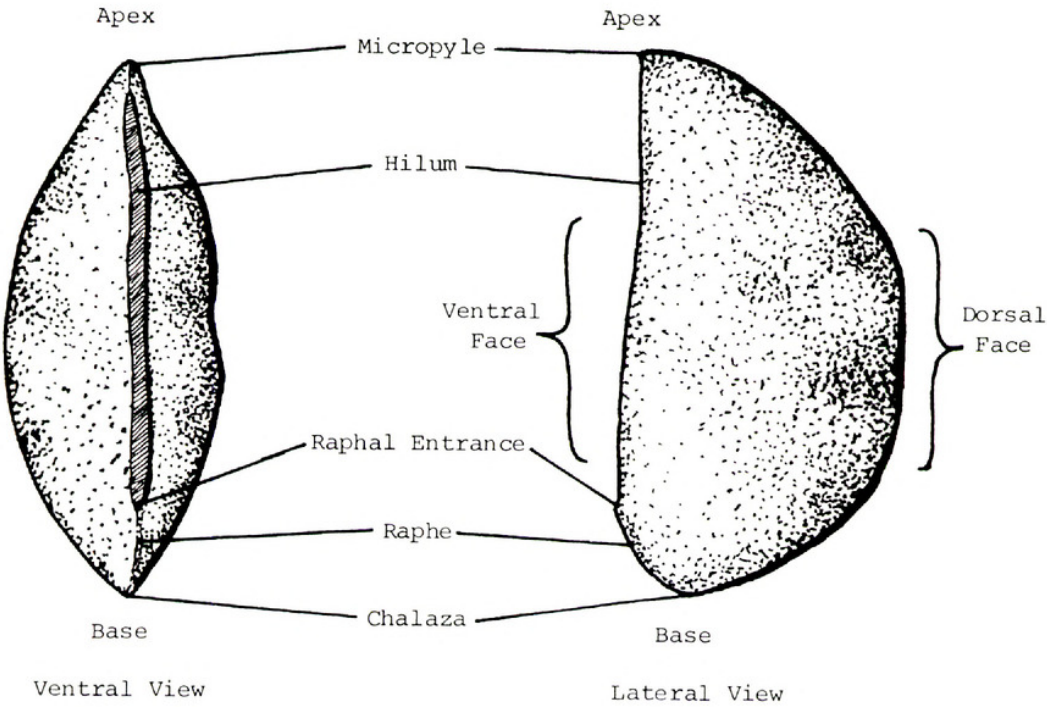


FIGURE 3. Descriptive characters of *Phellodendron* seeds.

sclereids. The exterior of these two layers frequently appears to be striate, a pattern impressed upon it by the inner wall of the fibrous endocarp, likewise striate. The inner integument is formed of three cell layers, the central of which consists of flattened, tangentially elongate cells and is bounded by

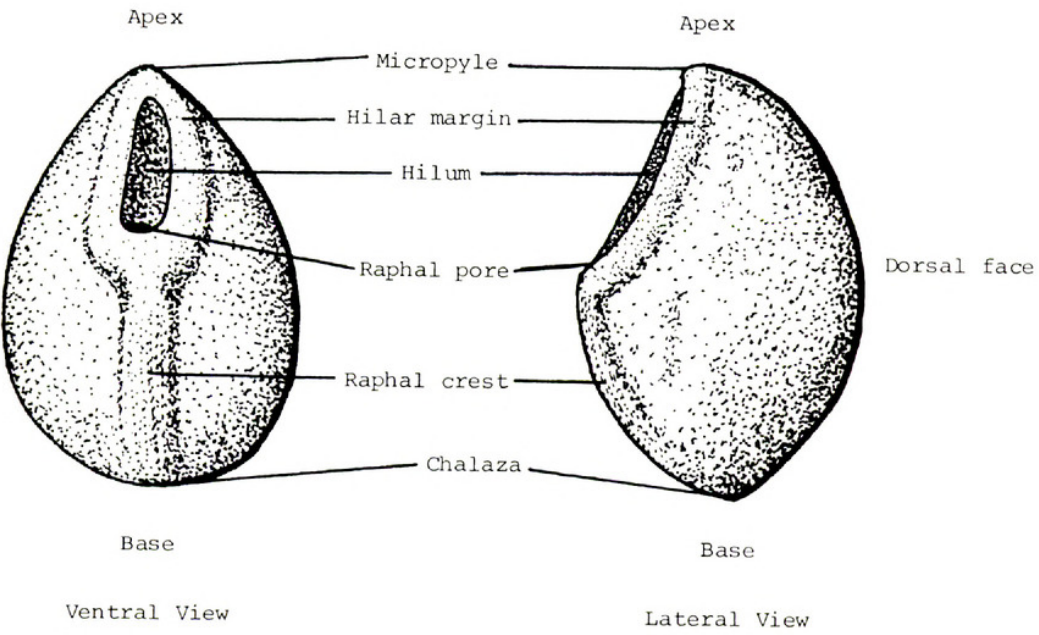


FIGURE 4. Descriptive characters of *Zanthoxylum* seeds.

a layer of large, isodiametric, thin-walled cells on either side. The cell walls of these two enclosing layers have cellulosic spiral thickenings (Gallet, 1913). The foregoing suite of characters is presented in TABLE 2.

Unfortunately, even with the aforementioned characters, it is often difficult or impossible to distinguish between the seeds of the modern species, an observation already made by Tralau (1963) and Dorofeev (1970). This might support the view (Tralau, 1963; Owhi, 1965) that a revision of the genus would reduce the number of species. The seeds of *Phellodendron japonicum* seem to have a stronger sclerotestal pattern than do those of other species, and the seeds of *P. chinense* are marked by a distinctively angled face (as seen in lateral view), but the stability of these characters in a large sample is not established. Certainly the variation in the length of the hilum in three samples of *P. amurense* is sufficiently great as to exclude it as a specific character. Reid (1923) presented a table of characters of modern and fossil *Phellodendron* seeds, but many seeds of the same species examined in the present study do not conform to her descriptions. This suggests that the seed characters cited are not particularly constant. Although some fossil seeds have been determined to an extant species of the genus, the practice is not defensible.

In approximately 20 reports, the fossil seeds of the genus have been placed in three extinct and two extant species. This total excludes "*Phellodendron*" *costatum* and *P. europaeum* Menzel (1913), a five-locular drupe that Kirchheimer (1957) concluded could not be proven to belong to the genus. The remaining species can be divided into those displaying strong sclerotestal sculpturing and those showing the weaker sculpturing equivalent to that of today's species.

The former group includes three species that range from the mid-Oligocene to the Pliocene of Europe. *Phellodendron lusaticum* Kirchheimer, of the German Oligocene, is represented by a small, thick-walled, strongly sculptured seed first reported by Kirchheimer (1940). More recent fossils from the Miocene of Germany are of fragments (Mai, 1964), and in one case (Nötzold, 1963) may be incorrectly assigned in view of their divergent morphology. *Phellodendron elegans* C. Reid (Reid & Reid, 1915), of the Miocene and Pliocene

TABLE 2. Descriptive characters of *Phellodendron* seeds.

Size	Seed surface
Length	Smooth
Width	Rough
Thickness	Pattern type, if distinctive
Hilum	Pattern scale
Length	Micropylar beak
Percent length of ventral face	Present/absent
Dorsal face	Ventral face
Smooth or marked by small depressions	Notable breaks in straight line of face

deposits of Europe and western Russia, is a larger seed with sculpturing intermediate between that of *P. lusaticum* and that of the extant species. *Phellodendron ornatum* E. M. Reid, of the Pliocene of France (Reid, 1923), is intermediate in size (4.5 mm. long) but very strongly sculptured. The remaining group includes seeds assigned to *P. amurense* (Miki, 1937, 1938; Szafer, 1946, 1954; Kolakovskii, 1958; Miki & Kokawa, 1962; Kokawa, 1966), *P. japonicum* (Szafer, 1946, 1954), and *Phellodendron* sp. (Dorofeev, 1963, 1970), which collectively range from the Miocene through the Recent. Although these assignments are not defensible in view of the variability of the modern seeds, they do correctly imply a greater resemblance to seeds of the present than to the more deeply sculptured and patterned ones of the past.

The chronological transition from the older forms with stronger and more orderly sclerotestal patterns, through the increasing dominance of forms having less pronounced patterns, to the present seeds with faint and only marginally ordered patterns, suggests a directional trend. This could conceivably be paralleled by a trend from the thick sclerotestal walls of *Phellodendron lusaticum* (400 μ m., Kirchheimer, 1940) to the thinner walls (average 200 μ m.) of the present-day species, a tendency not dissimilar to that previously noted for the Vitaceae (Tiffney & Barghoorn, 1976) and the Magnoliaceae (Tiffney, 1977). However, the true significance of these trends in seeds of *Phellodendron* can only be established in light of an understanding of the whole organism.

Phellodendron novae-angliae Tiffney, sp. nov.

PLATES 1, H; 2, A-E.

MATERIAL. Two seeds have been recovered from the lignite at Brandon. Each is broken but is held together by its internal contents. The type specimen (PLATE 2, A, C, E) is assigned number 51380 of the Paleobotanical Collections, Botanical Museum, Harvard University; the paratype is assigned number 51381 in the same collection.

DESCRIPTION. One seed is 5.3 mm. long, 2.9 mm. high (from the dorsal to the ventral margin), and 2.1 mm. wide (perpendicular to the dorsal-ventral plane); the other is 4.8 mm. long, 2.7 mm. high, and 2.0 mm. wide. Their shape is similar to that of the modern seeds: the two gently convex lateral faces join on one margin to form the elliptically curved dorsal surface, which bends upward at either end to join the straight, linelike ventral surface formed by the juncture of the opposite margins of the lateral faces. The narrow hilum extends from the apical end, three quarters of the way toward the base of the seed, where it terminates at the entrance to the raphe, which continues over the remaining portion of the ventral face and leads to the basal chalaza. The micropyle is situated on a beak that protrudes above the ventral margin at the extreme terminus of the hilum (PLATE 2, A). A small depression occurs in the ventral margin just below this apical beak. The dorsal and dorsal-lateral surfaces of both seeds appear broadly scalloped (PLATE 2, E) and bear approximately three large indentations of indefinite origin on each side. The external layer of sclerotestal wall cells provides a faint pitting to the vaguely vitreous surface of the fossil seed. On the

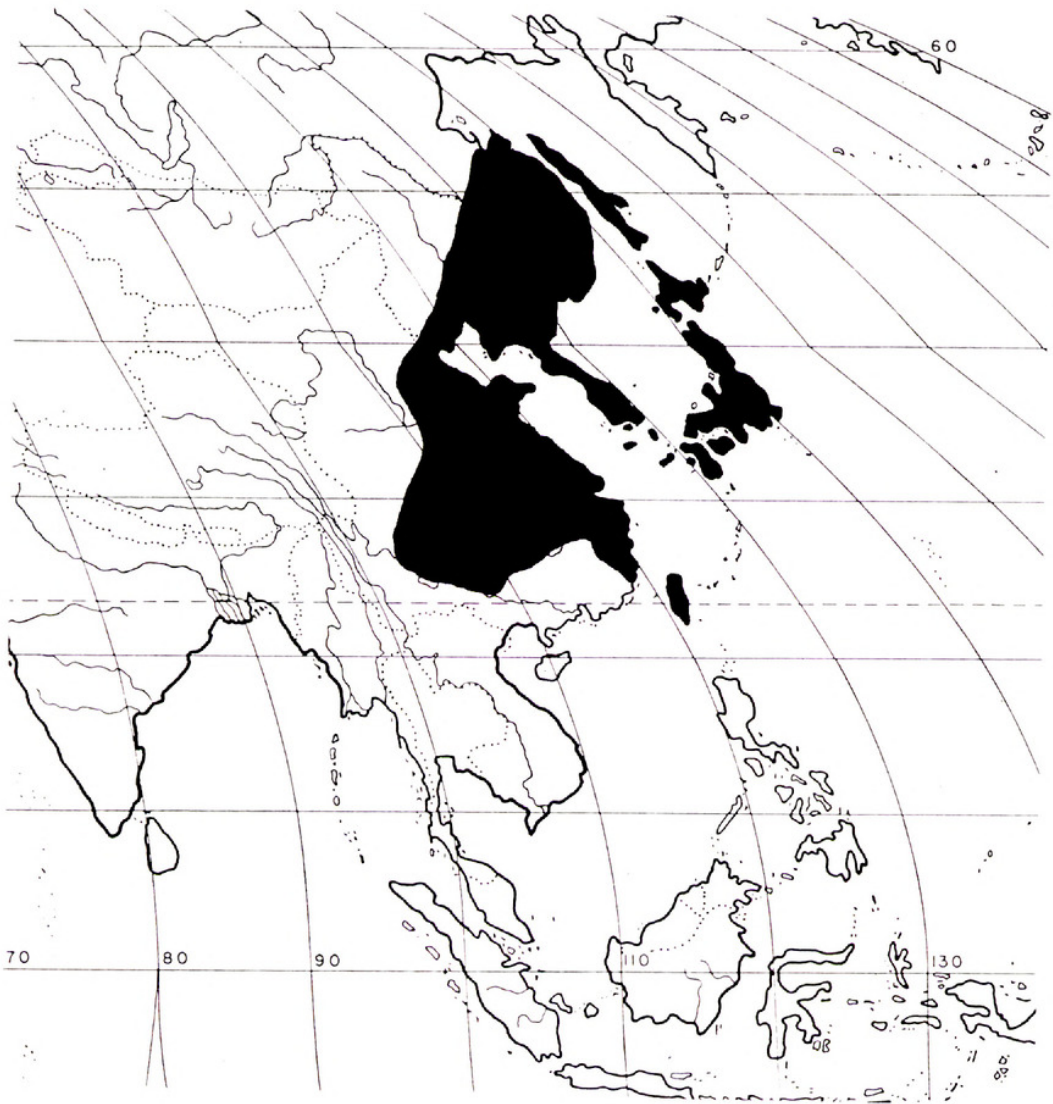
lateral faces this pitting is dominated by a larger pattern of randomly organized weak ridges and depressions (PLATE 2, A).

The outermost layer of the outer integument is missing. The internal portion of the outer integument ranges from 110 to 140 μm . in thickness and is composed of eight to ten layers of isodiametric sclereids. The inner integument is rather badly distorted and its cellular arrangement obscured, but its outermost layer consists of irregular cells, 60–75 μm . long by 20–35 μm . wide. These have spiral thickenings that are 1–2 μm . wide spaced at intervals of 6–8 μm . The remaining portion of the inner integument includes a thick mass of small (25–45 μm . diameter) isodiametric cells with collapsed contents, which could be interpreted as albuminous cells.

AFFINITIES. The laterally compressed shape and long, linear hilum, in conjunction with the spirally thickened cells of the inner integument, mark this as a species of *Phellodendron*. The somewhat similar seeds of *Euodia* and, to a lesser degree, *Zanthoxylum*, can be excluded from comparison on the basis of their round shape, which stems from an absence of interocular pressure. Similarities can be found with seeds of many of the modern species of *Phellodendron*. The seeds of an unvouchered specimen of *P. amurense* in the seed collection at Harvard (A and GH) are particularly similar to those of *P. novae-angliae*. No evolutionary link is to be inferred from this similarity, however, since other collections of *P. amurense* seeds differ distinctly from the fossil, as well as from each other. Thus, the identification can be pursued no further than to the generic level. *Phellodendron novae-angliae* shares the distinction with *P. lusaticum* of being the earliest reported seed of the genus, but is not similar to this, or any other, fossil seed. *Phellodendron novae-angliae* is primarily distinguished by its distinctively subdued sclerotestal pattern, the chronological appearance of which casts doubt on the possible evolutionary trend toward the reduction of the strength of sclerotestal sculpturing suggested earlier. Similarly, its sclerotestal thickness is far less than that expected in view of the aforementioned trend from thicker Paleogene forms toward thinner Neogene ones.

The specific epithet *novae-angliae* commemorates the geographic source of this paleofloristically important fossil seed.

ECOLOGY. The modern genus *Phellodendron* is restricted to temperate east Asia and is of deciduous habit. Although *P. amurense* is a northerly species of the *Picea-Abies* and northern hardwood forests, the majority of species are low trees of the mixed mesophytic forests of the Yangtze River valley (Wang, 1961) growing in conjunction with other species found at Brandon, including *Euodia* (MAP 2). Since no one modern species is particularly similar to the fossil, the assumption that *P. novae-angliae* is a temperate form rests primarily upon the concentration of modern species in temperate forests, and on its association with other temperate forms, such as *Magnolia*, *Illicium*, and *Euodia*, found at Brandon. Perhaps the greatest significance of *Phellodendron* as an element of the Brandon flora is as a paleobotanical reinforcement of the classic eastern North America–eastern Asia distribution pattern of species, since the genus is restricted today to eastern Asia.



MAP 2. Present distribution of *Phellodendron* (after Engler (1896), Wang (1961), Tralau (1963), and herbarium specimens at A and GH).

No mention is made in the literature of how the seeds of *Phellodendron* are dispersed, although it is to be hoped that Starshova's continuing study (1972, 1973) of the genus will ultimately answer the question. One might logically assume that a fleshy drupe would be dispersed by an animal, most likely a bird; however, the drupes of *Phellodendron* are particularly resinous, even after fifty years on a herbarium sheet. Since strong resins are normally considered repellent to animals, the seeds may be dispersed in another manner. Because only two seeds of *Phellodendron* were found in the deposit, their source may have been relatively distant.

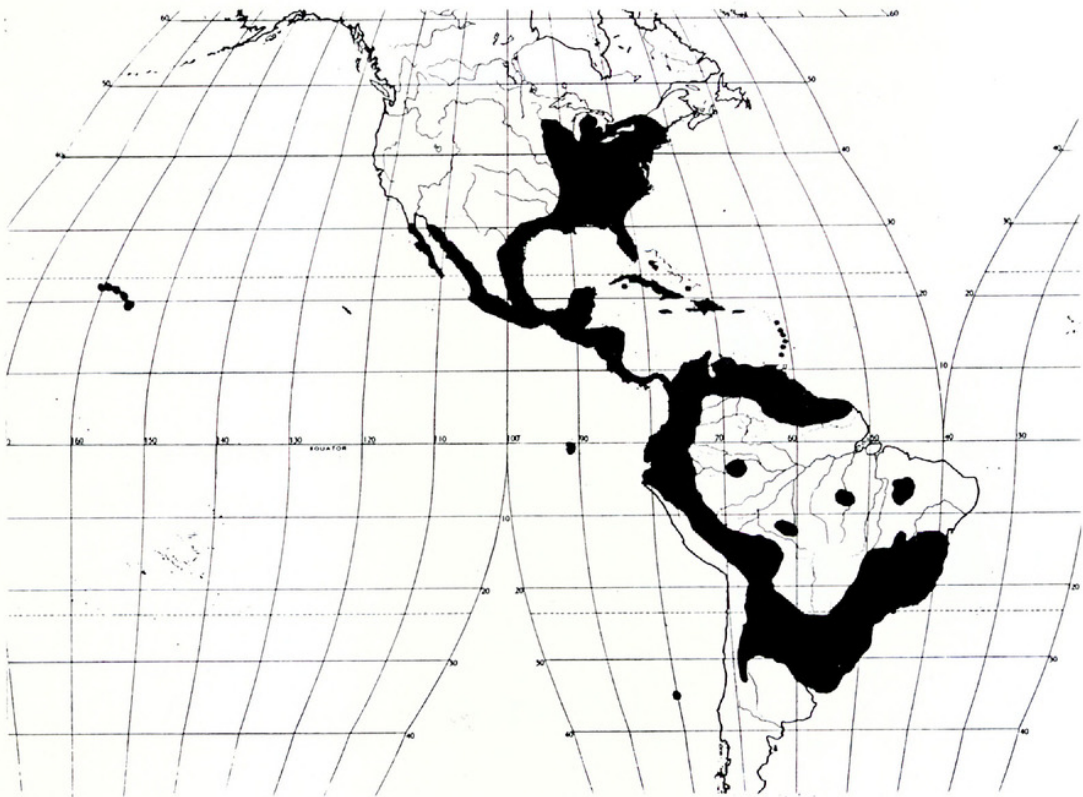
Zanthoxylum L. Sp. Pl. 1: 270. 1753; Gen. Pl. ed. 5. 130. 1754.

Zanthoxylum is a large, pantropical genus with outlying species in the Temperate Zone of eastern Asia and North America (Brizicky, 1962a; MAPS

3, 4). *Zanthoxylum*, in the broad sense (including *Fagara*; Brizicky, 1962b), consists of approximately 215 species. The genus is varied in habit and encompasses deciduous and evergreen trees and shrubs of both wet and dry habitats. The seeds of 79 species, including 26 species of eastern Asia and 53 of the New World, and representing the available fruiting material in the herbaria of Harvard University (A and GH), were examined in the present study.

The bivalved carpels occur in clusters, each carpel dehiscing along its dorsal margin to expose shiny seeds, which dangle from the carpel by a short funicle. The membranaceous to woody follicular valves are pitted with oil cells and lined by a free or adherent, cartilaginous, bipartite endocarp. Although two ovules are present in each locule, one normally aborts. Thus only one seed is usually found in the mature carpel.

Modern seeds of *Zanthoxylum* range from 2.5 to 6.2 mm. (average 4.1 mm.) in their maximum dimension and have a variety of shapes, reflecting the nature of the hilar scar and raphe. The majority of the seeds are spherical or roundly ellipsoid, but a few are elongate-ellipsoid and some are laterally compressed hemispheres, with one straight (ventral) and one arched (dorsal) margin. This variation in shape often makes it difficult to define an obvious dorsal and ventral face as was done for the seeds of *Euodia* and *Phellodendron*. In many of the spherical *Zanthoxylum* seeds, the funicle attaches only at

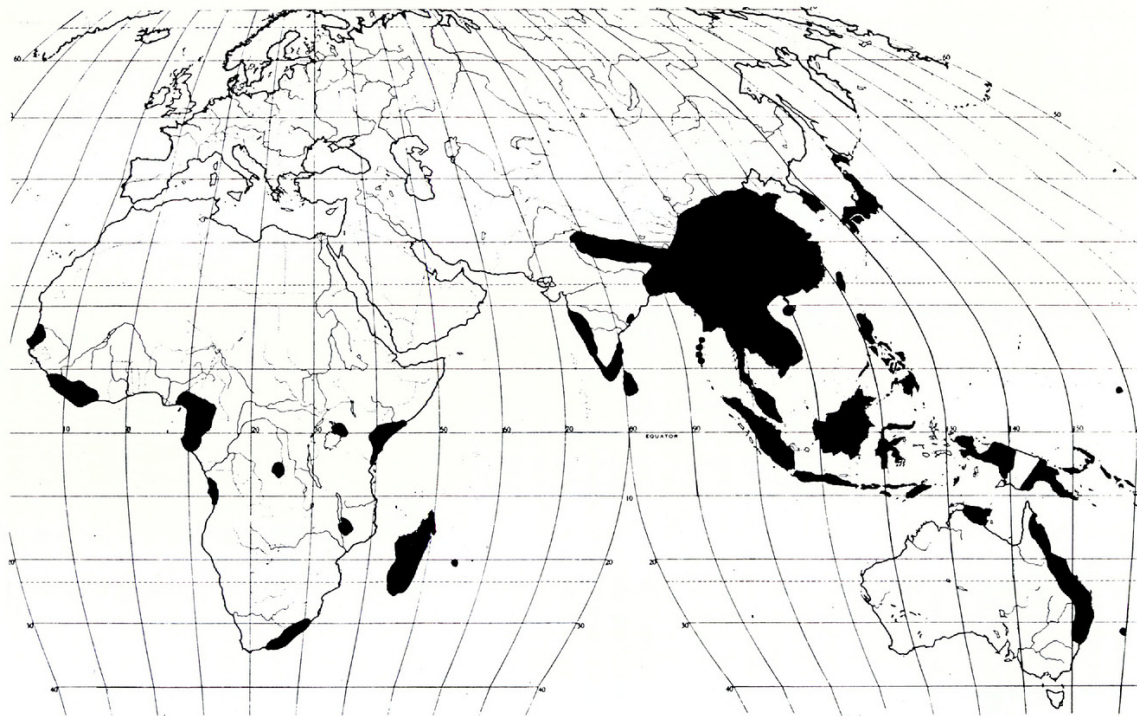


MAP 3. Present New World distribution of *Zanthoxylum* (after Engler (1896) and herbarium specimens at A and GH).

one point; thus, the ventral face is more properly termed a ventral hemisphere. In the more elongate forms, the long axis of the ellipsoid is parallel to that of the follicle, with the micropyle at the apex and the chalaza at the base of the ellipsoid, thus isolating the ventral face as the one located between these two points and facing into the locule. If an elongate hilum passes along the entire length of this face, the extent of the ventral margin is made clear; if the hilum is shorter and occupies only a portion of the inwardly directed face (FIGURE 4), the ventral margin becomes less obvious—in isolated seeds it is best defined by the position of the chalaza and micropyle. This interpretation differs from that of Chandler (1925–26, 1960, 1961a, 1961b, 1962, 1963a, 1963b, 1964), who uses the point of funicle attachment (the hilum) to define the extent of the ventral face. In a few seeds (*Z. limonella* (Dennst.) Alston of the extant flora, and the fossil species *Z. bognorensense* Chandler (Chandler, 1961a)) the very long raphe and the hilum oriented perpendicular to the long axis of the seed combine to make Chandler's interpretation more serviceable, but these cases are rare.

The hilum can vary from a circular to an elongate-linear scar, but it is most commonly an elongate triangle with the point directed toward the apex of the seed, and with the flat end, bearing the raphal entrance, toward the base. In those cases where the hilum occupies a portion of the ventral face, it often follows the slope of the ellipsoid, thus falling at an angle relative to a line passing from the apex to the base of the seed. Although the presence or absence (in which case the hilum parallels the long axis of the seed) of this angle seems to be a specific character, the magnitude of the angle does not, since it varies widely on seeds of a single species. The area around the hilum is occasionally differentiated from the rest of the sclerotesta by its inflation (see *Zanthoxylum rhabdospermum* below, and PLATE 3, C) or by the absence of sculpture. The raphe commences at the base of the hilum and passes as a canal around to the hollowed-out basal chalaza. The path of the raphe is often traced externally by a ridge or raphal crest that may occasionally be quite prominent (*Z. rhabdospermum*, PLATE 3, A) and that is frequently more faintly sculptured than is the rest of the seed surface. The micropyle is at the opposite end of the seed, at or just beyond the apical terminus of the hilum (see FIGURE 4).

The seed surface may be completely smooth (*Zanthoxylum americanum* Miller, *Z. dissitum* Hemsley ex Forbes & Hemsley, *Z. scandens* Blume) or may bear a gross pattern of varying intensity and organization. Many species have a rugose surface of small bumps that in some cases (*Z. procerum* Donn. Sm., *Z. piperitum* DC., *Z. pimpinelloides* DC.) are organized into rows paralleling the dorsal margin. In a few species (e.g., *Z. microcarpum* Griseb.) the bumps coalesce into flanges and ridges that approach spines, while in others (*Z. micranthum* Hemsley, *Z. schinifolium* Sieb. & Zucc.) the ridges all join together and form a strong and distinctive reticulum. Occasionally there is a smaller version of this reticulum, which parallels the dorsal margin of the seeds in a series of lunate rows (*Z. myriacanthum* Wall., *Z. panamense* P. Wilson). In many species this large-magnitude sculpture is underlain by a finer pattern of very small pits that vary from 10 μm .



MAP 4. Present Old World distribution of *Zanthoxylum* (after Engler (1896), Hartley (1966), and herbarium specimens at A and GH).

to approximately 70 μm . in diameter, depending on the species, and occur over the entire seed. They do not seem to be derived from the cells of the sclerotesta and may, as implied by Corner (1976), represent imprints of cells of the external layer of the outer integument upon the surface of the internal layer of the outer integument.

The anatomy of these seeds is similar to that of the other rutaceous genera discussed. The outer integument is subdivided into an easily removed papery exterior layer and an underlying thick sclerotesta having the described sculpture. The exterior layer is thin and invariably shiny, while the inner sclerotesta is dull black and averages 300–400 μm . in thickness, ranging up to 1 mm. in extreme cases (*Zanthoxylum dissitoides* Huang, *Z. nitidum* DC.). Within a single seed the wall is often 100–200 μm . thicker beneath the raphe than on the lateral walls. The multi-layered inner integument is formed of large, spirally thickened, isodiametric cells, which are compressed into a membranaceous layer in the mature seed (Gallet, 1913; see also PLATE 4, A, B).

The majority of the modern seeds seen are rounded or slightly elliptic and have a randomly organized, rough external sculpture. With the exception of certain particularly distinctive seeds (*Zanthoxylum melanostictum* Schlecht. & Cham., for example), it is often difficult to discern clear specific differences between seeds of separate species. In the species examined, smooth-walled forms occurred with equal frequency in both the Old and the New World (four species in each), but seeds with an organized sculptural pattern paralleling the dorsal margin were more common in the New World. Circular hila, representing the attachment of the funicle at a single point, are restricted to New World seeds in the sample examined, while seeds of the Old World species most commonly have hila that extend one-quarter to one-half the length of the ventral face. A summary of these characters is presented in TABLE 3.

Twenty-three species of fossil seeds ostensibly related to *Zanthoxylum* have been reported in the literature. The majority of these are either Eocene (Chandler, 1925–26, 1957, 1960, 1961a, 1961b, 1962, 1963a, 1963b, 1964; Palamarev, 1973; Mai, 1976) or Plio-Pleistocene in age (Miki, 1937, 1938; Miki & Kokawa, 1962; Kokawa, 1966), although a few Miocene species have been reported (Palamarev, 1968; Gregor, 1975, 1978a, 1978b). All of the Plio-Pleistocene reports are from Japan and are of modern species.

Although Berry (1929) did cite an Eocene *Zanthoxylum* seed (as *Fagara*) from western Peru, the majority of the Paleogene reports are from Europe and include seeds of the form genus *Rutaspermum*. This latter genus was erected by Chandler (1957) for rutaceous seeds of uncertain affinity, although many of the seeds included are quite similar to those of *Zanthoxylum*. Chandler (1961a), in transferring *Zanthoxylum ornatum* Chandler to *Rutaspermum*, stated that "it is now clear that no living representative of *Zanthoxylum* has such clearly defined regular superficial ornamentation." However, Palamarev (1973) transferred two species of *Rutaspermum* (*R. bognorense* Chandler and *R. rugosum* Chandler) to *Zanthoxylum*. Since seeds of *Rutaspermum excavatum* Chandler (Chandler, 1962, 1963b), *R. glabrum* Chandler (Chandler,

TABLE 3. Descriptive characters of *Zanthoxylum* seeds.

Size	Raphal crest
Length	Present/absent
Diameter	Prominent/faint
Testal thickness	Smooth/rough
	Percent length of seed
Shape	Surface
Spherical	Smooth
Ellipsoid	Rough
Compressed-hemispheric	Random pattern
Hilum	Spines
Shape	Bumps
Circular	Ridges
Triangular	Reticulation
Slitlike	Organized pattern
Hilar angle in degrees	Pattern strength
Percent length of seed	Pattern scale
Hilar margin	Small pits
Present/absent	Present/absent
Smooth/rough	Diameter
Inflated	

1962), *R. magnificum* Chandler (Chandler, 1962), and *R. striatum* Chandler (Chandler, 1962) are likewise all similar to those of *Zanthoxylum*, they too are perhaps best considered to be representatives of this modern genus. A formal proposal of this transfer must await examination of all the fossils involved. However, it would seem wise to avoid placing a specimen in a form genus when its characters, although not entirely comparable to those of any single modern species, conform closely to those of only one modern genus. *Rutaspermum* sp. (Chandler, 1960, p. 225) is rather similar to the previously reported *R. ornatum* (Chandler) Chandler (Chandler, 1925-26, 1961a), while *R. bognoense* (Chandler, 1961b; Palamarev, 1973) may be conspecific with *Zanthoxylum compressum* Chandler (Chandler, 1925-26, 1961a) on the basis of morphological similarity. Of the remaining *Rutaspermum* seeds, *R. minimum* Chandler (Chandler, 1961b), *Rutaspermum* sp. (Chandler, 1960, p. 226) and *Rutaspermum* sp. (Chandler, 1964) are distinctly different from *Zanthoxylum* and are appropriately assigned to *Rutaspermum* in its function as a form genus. Mai (1976) proposed the transferral of seeds identified as *R. ornatum* to the extant genus *Acronychia*. The differing seed morphologies of these two forms argue against this proposal.

These Paleogene seeds range from 2.0 mm. (*Rutaspermum excavatum*) to 8.0 mm. (*Rutaspermum* sp., Chandler, 1960, p. 226) in length, the latter fossil exceeding the size of the seeds of all of the modern species of *Zanthoxylum* examined. A few seeds show patches of the external papery layer of the outer integument, but most exhibit only the inner sclerotestal layer. In three cases (assuming *R. bognoense* and *Z. compressum* Chandler

to be conspecific) this is smooth, while in nine others the sclerotesta is marked by an organized coarse sculpture of ridges paralleling the dorsal margin of the seed. Excluding *R. minimum* (not included here in *Zanthoxylum*), all of the Paleogene seeds have an elongate-triangular hilar scar, which varies from 0° to 30° inclination relative to the micropyle-chalazal axis. The sclerotestal thickness of these fossils ranges from approximately 100 to 200 μm . up to 1000 μm . (*Zanthoxylum* cf. *planispinum* Sieb. & Zucc.; Palamarev, 1968) but may vary within a single seed. The Miocene species described by Gregor (1978a, 1978b) include *Z. ailanthiforme* Gregor, *Z. tiffneyi* Gregor, and *Z. giganteum* Gregor. The last-named is particularly distinctive for its large size (5.0–8.0 mm. long), which approaches that of *Z. hawaiiense* (Hillebr.) Engler and *Z. kauaiense* A. Gray. The seeds all appear to be the products of one-seeded carpels.

These various European *Zanthoxylum* and *Zanthoxylum*-like *Rutaspermum* seeds indicate the distinctive nature of the genus *Zanthoxylum* by Eocene time, while the contemporaneous existence of a Peruvian species suggests its widespread distribution. Although the earliest forms are comparable in size, general morphology, and sclerotestal thickness to today's species, the sclerotestal patterning of the Eocene seeds tends to be stronger and more organized than that of modern ones, an observation also made by Chandler (1961a, 1962, 1963b). The constancy of this distinction between Eocene and modern seed sculpture mirrors a decrease in the randomness of its organization through time. This may represent an evolutionary trend, in view of its predominance, although some modern seeds do have weak but regular sclerotestal patterns and a few Eocene seeds are smooth surfaced.

***Zanthoxylum rhabdospermum* (Lesquereux) Tiffney, comb. nov.**

PLATES 3, A–I; 4, A, B.

Unnamed seed, E. Hitchcock, Am. Jour. Sci. II. **15**: 100. fig. 19. 1853; Geol. Vermont **1**: 231. fig. 150. 1861.

Drupa rhabdosperma Lesquereux, Am. Jour. Sci. II. **32**: 360. 1861, in Hitchcock *et al.*, Geol. Vermont **2**: 716. 1861; Perkins, Rep. Vermont State Geol. **4**: 210. pl. 81, figs. 168–170. 1904, Bull. Geol. Soc. Am. **16**: 514. pl. 87, fig. 25. 1905, Rep. Vermont State Geol. **5**: pl. 53, fig. 25. 1906.

MATERIAL. Approximately 370 seeds have been recovered from the lignite at Brandon. The type specimen described by Lesquereux is in the collection of the Division of Paleobotany of the U. S. National Museum and bears the number USNM 222845. Ten selected specimens in the Paleobotanical Collections of the Botanical Museum, Harvard University, have been assigned number 51382 and are stored there with the remainder of the material.

DESCRIPTION. The seeds average 4.9 mm. long (range 4.0 mm.–5.7 mm., standard deviation 0.64 mm.) and 3.3 mm. in diameter (range 2.9 mm.–4.4 mm., standard deviation 0.29 mm.). They range from ovoid to ellipsoid and have a rounded basal terminus and a somewhat pointed apical terminus, the latter formed by the intersection of the curving dorsal face and the flattened ventral hilar

scar. In some cases this point is a ventrally directed beak or hook. Although the laterally compressed shape of one specimen (PLATE 3, E) indicates the presence of two seeds in one carpel, the remaining seeds lack flattened surfaces and are probably from single-seeded carpels. The elongate-triangular to rectangular hilar scar is inclined at an angle of 20–25° relative to the long axis of the seed; in side view it appears as an inclined plane cutting off the apical one third to one half of the ventral face of the seed (PLATE 3, B, H). This hilum averages 2 mm. in length (range 1.5 mm.–2.6 mm.) by 0.7 mm. in width (range 0.6 mm.–0.9 mm.) and is surrounded by a smooth, inflated margin. Occasionally the remains of a vascular strand are seen within this scar, leading to the raphal entrance at the basal end of the hilum. The path of the raphe is marked by a slight ridge or crest with reduced external sculpture, which passes from the base of the hilum over the remainder of the gently curved ventral face to the large basal chalaza (PLATE 3, G). The micropyle is located at the extreme apex of the hilar scar.

The vitreous black surface of the seed is marked by 30 to 32 regular longitudinal ridges that occasionally anastomose and that parallel the curved dorsal margin. These range from 60 to 120 μm . in width and are spaced 180–320 μm . apart. They are absent from the hilar margin and are considerably reduced on the raphal crest. Underlying this pattern is an all-pervasive one of small pits in the seed surface (PLATE 3, D). These pits average 50 μm . in diameter (30 μm . on the hilar margin and portions of the raphal crest). Occasionally they are absent from the crests of some of the longitudinal ridges of the seed coat due to abrasion.

In no case were any remains of the external layer of the outer integument seen. The thickness of the inner sclerotestal portion of the outer integument is 200–300 μm . (to a maximum of 400 μm .) on the lateral and dorsal walls, ranging up to 600 μm . underlying the ventral raphal canal. The inner integument consists of three to five layers of rectangular cells ranging from 40 to 170 μm . in length and from 30 to 45 μm . in width. All the inner integumental cells have spiral thickenings 1–2 μm . wide that are spaced every 3–4 μm . along the cell wall (PLATE 4, A, B).

AFFINITIES. Although the elongate hilar scar, rounded shape, surficial sculpture, and spirally thickened cells of the inner integument clearly identify this as a member of the genus *Zanthoxylum*, no single modern species is comparable. As with the seeds described by Chandler, this is particularly true of the regular sclerotestal structure of the fossil, which is much more pronounced than that of any modern seed of the genus examined in this study. However, other characters of *Z. rhabdospermum* may be found in modern species, and although they do not occur in the same combinations as those of the fossil seed, they confirm the placement of the fossil in the genus *Zanthoxylum*.

Of the modern seeds examined, the most similar were those from Central America and the Caribbean, including *Zanthoxylum acuminatum* Sw., *Z. caribaeum* Lam., *Z. pimpinelloides*, and *Z. pringlei* S. Watson. All are decidedly smaller and more spherical than the fossil, but each has a few characters in common with *Z. rhabdospermum*. *Zanthoxylum acuminatum* has an inflated

hilar margin, *Z. caribaeum* a surficial pitting and sclerotestal sculpture similar to that of the fossil, *Z. pimpinelloides* an inflated hilar margin, and *Z. pringlei* a similar surficial pitting.

Zanthoxylum rhabdospermum is most similar to previously reported fossil species in its strong and regular sculptural pattern, which is held in common with a number of English Eocene forms including *Rutaspermum magnificum*, *R. striatum*, and *R. ornatum*. Of these, *R. striatum* has the pattern most similar to that of the Brandon form, although more weakly displayed. In size, shape, hilar length and angle, fine sclerotestal pitting, and general appearance *R. magnificum* is the most similar to *Z. rhabdospermum*, but it lacks the inflated hilar margin and the parallel sclerotestal ridges of the Brandon species. Although *R. ornatum* is of the correct size and has a similar sclerotestal pattern, the hilum is too long, and while the hilar margin is free of sculpture, it is not inflated. With reference to previously reported fossils, perhaps the most significant factor is that *Z. rhabdospermum* conforms to the previously noted tendency for Paleogene *Zanthoxylum* seeds to have a stronger and more regular sclerotestal pattern than the modern seeds of the genus.

Two other fossil seeds have been ascribed to *Drupa rhabdosperma* since Lesquereux's publication of the species. That figured by Hartz (1909, pp. 18, 19, 275, *pl. 2, fig. 5*) as *D. rhabdospermus* exhibits a similar pattern of sclerotestal ridges, but the greatly elongate "beak" and the clear hilumlike area on one face are quite unlike the Brandon form. The seed illustrated exhibits little relation to *Zanthoxylum* and may not belong to the Rutaceae. On the other hand, the specimen of *D. rhabdosperma* described by Hofmann from the Eocene of Gaumnitz (1930, pp. 49, 50, *pl. 5, figs. 28, 29*) is definitely a seed of *Zanthoxylum*. Although these seeds are quite similar to those of *Z. rhabdospermum* from Brandon, particularly with respect to their size and to the strength of seed coat sculpturing, some distinct differences do separate the two. The German form has strong longitudinal ridges joined by short transverse walls; its long, narrow hilum extends for most of the length of the ventral face and is parallel to the long axis of the seed. This is in contrast to the Brandon form, which lacks conspicuous transverse sculptural elements and has a short hilum inclined at an angle of 20–25° relative to the long axis of the seed. For these reasons, Hofmann's material cannot be considered conspecific with that of *Z. rhabdospermum* from Brandon. The characters of Hofmann's specimens are quite similar to those of *Rutaspermum ornatum*, and Mai (1976) has united the two under *Acronychia ornata* (Chandler) Mai in his study of the Eocene Geiseltal flora.

ECOLOGY. The wide ecological range of the species of *Zanthoxylum* (MAPS 3, 4), coupled with the lack of a single modern species comparable to the fossil, forestalls any worthwhile ecological conjectures. Even among the four most similar modern species, habitat preferences range from wet (*Z. caribaeum*, Little *et al.*, 1974; *Z. acuminatum*, Fawcett & Rendle, 1920) to quite dry (*Z. pringlei*, Standley, 1923). The presence of a shiny, slightly fleshy, exterior layer around the seeds, and the manner in which they dangle from the carpel

by a short funicle suggests that they are bird dispersed (van der Pijl, 1969). They have been observed to be eaten by a species of thrush in Java (Ridley, 1930) and occasionally by white-winged doves (*Zenaisa asiatica*) and American pipits (*Anthus spinoletta*) in the southern United States (Martin *et al.*, 1961).

Although some *Zanthoxylum* seeds may have arrived at Brandon through bird dispersal, the large number of seeds in the lignite indicates that the plants, either trees or shrubs, grew quite close to the site of deposition and thus presumably preferred wet ground. The slightly abraded nature of a few of the seeds suggests that they were transported to the site of deposition from a distant upstream source, and thus that *Z. rhabdospermum* was a widespread plant—at least along the river margins of the area—in Brandon time.

Also of ecological note is the presence of a circular hole, 1.0–1.2 mm. in diameter, in the sclerotesta of two of the seeds examined (see PLATE 3, I). These closely resemble insect holes observed in some modern species (*Zanthoxylum foetidum* Rose of Mexico, *Z. limoncello* Planchon & Oersted ex Triana & Planchon of Costa Rica, and *Z. microcarpum* of Mexico) and in one other fossil (Chandler, 1925–26). This similarity between modern and fossil holes suggests that perhaps an herbivore-host relationship was established in early Tertiary time and has since persisted. According to Prof. Horace Burke of Texas A & M University (pers. comm.), the holes in the modern seeds of the genus are most likely made by weevils when they mature and emerge from within the seed.

The Rutaceae are well known for their distinctive plant chemistry, an example of which may be evident in these fossils. A single seed of *Zanthoxylum rhabdospermum*, removed from the glycerine-alcohol preservative mixture (to which phenol was finally added), washed, and placed in water, developed a mass of fungal hyphae in four days. This distinction is seemingly specific, since the seeds of other Brandon species were not similarly afflicted; it may provide the basis for future investigation.

***Zanthoxylum echinospermum* Tiffney, sp. nov.**

PLATE 4, E–G.

MATERIAL. One whole seed and several fragments were recovered from the silt at Brandon in 1949; the whole seed was carefully photographed but was subsequently broken. Of necessity, the type now consists of a photograph and a number of fragments, which are collectively assigned number 51384 of the Paleobotanical Collections of the Botanical Museum, Harvard University.

DESCRIPTION. The whole seed is 6.0 mm. long, 3.8 mm. high (from the dorsal to the ventral margin), and 3.4 mm. wide (from lateral face to lateral face). It is essentially ellipsoid (PLATE 4, F, G), with the apical half of the ventral margin appearing flat in lateral view due to the hilum, which, in ventral view, protrudes to form an apical beak. The elongate-triangular hilum, 4.0 mm. long by 0.9 mm. wide, is inclined at an angle of 25° relative to the long axis of the seed and is surrounded by a smooth, inflated margin. The raphe commences at the widened base of the hilum and passes along the

remainder of the ventral margin to the basal chalaza. The external path of the raphe is marked by a low raphal crest, which bears a surficial pattern similar to that of the rest of the seed. The micropyle is located at the apical terminus of the hilum.

The slightly vitreous black surface is traversed by rows of conical to faintly laminar spines that parallel the curved dorsal margin of the seed. These spines project approximately 230 μm . from the surface of the seed and are about 200 μm . in diameter. The laminar forms are usually 200 μm . wide and up to 400 μm . long, with the long axis always parallel to the long axis of the seed. The spines may be from 130 to 250 μm . apart. This pattern of spines is absent from the hilar margin and is slightly suppressed on the top of the raphal crest, but otherwise covers the seed. A pattern of finer pits, 35–50 μm . in diameter, covers the entire surface of the seed including the faces of the spines. This pattern may be derived in a manner similar to that of *Zanthoxylum rhabdospermum*.

Presumably a crustaceous or fleshy external portion of the outer integument was present in life, but no evidence of it is found in the fossil. The patterned sclerotesta, assumedly the inner portion of the outer integument, ranges in thickness from 175 μm . on the lateral walls to 300 μm . beneath the ventral raphe. The inner integument is composed of three or four layers of oblong cells ranging from 60 to 80 μm . in length and from 40 to 60 μm . in width. All of these inner integumental cells have anastomosing spiral thickenings on their walls, the bands being 1–2 μm . wide and occurring at intervals of up to 4 μm . (PLATE 4, E).

AFFINITIES. The rounded shape, indicative of development in a one-seeded carpel, the elongate-triangular hilum, the nature of the sclerotestal pattern, and the presence of spiral thickenings in the walls of the cells of the inner integument all conform with the seeds of *Zanthoxylum*. However, no modern species of *Zanthoxylum* seen has such simultaneously large and regularly placed spines, or combines a strongly patterned sclerotesta with such a large and distinctive hilum. *Zanthoxylum melanostictum* Schlecht. & Cham., of Central America, bears rows of small spines 300 μm . in diameter and 60–80 μm . high; however, the size and shape of the seed and its hilum, the absence of a hilar margin, and the lack of surficial pitting clearly separate it from *Z. echinospermum*. Other modern species (e.g., *Z. coco* Engler, *Z. monophyllum* P. Wilson, and *Z. tomentellum* Hooker f.) have spines, but theirs are really elongate flanges and are not regularly spaced. From the present evidence it may be concluded that *Zanthoxylum echinospermum* represents a highly distinctive and extinct species of the genus; its characters do not match those of any one modern species but do fall well within the range of variation of species of *Zanthoxylum*.

Among the previously reported *Zanthoxylum* fossil seeds, much the same situation obtains. *Rutaspermum excavatum* (Chandler, 1962, 1963b) has an organized surficial pattern of protrusions intermediate between bumps and spines, but its small size, different shape, flat hilum, and lack of a hilar margin disqualify it from comparison with *Z. echinospermum*. *Rutaspermum*

magnificum (Chandler, 1962) is similar in size and shape to *Z. echinospermum*, but lacks the spinose exterior and the inflated hilar margin. Although the overall configuration of *R. striatum* (Chandler, 1962) is also similar, this species may be dismissed for the same reasons; it is also too small. The common denominator between *Z. echinospermum* and the previously reported Paleogene forms is in the strength and regularity of their collective sclerotestal patterns. Although *Z. echinospermum* is represented by only a single specimen, it is rather unlikely that it is a morphological variant of the previously described *Z. rhabdospermum*. In addition to the distinctly different sclerotestal patterns, *Z. echinospermum* has a stronger pattern on the raphe crest and a less vitreous sclerotesta that is decidedly more brittle than that of *Z. rhabdospermum*. Additionally, the large sample of *Z. rhabdospermum* seeds has presented a fairly clear knowledge of the range of variation within that species.

The specific epithet *echinospermum* is in recognition of the echinate nature of the testa of this form.

ECOLOGY. The restriction of this form to the Brandon silt, coupled with its limited representation, suggests that the parent plant was a minor component of the surrounding vegetation. Alternatively, in view of the avian dispersal of at least some modern species (as discussed under *Zanthoxylum rhabdospermum*), these seeds may have been carried from a distant source by birds.

Zanthoxylum* cf. *tiffneyi Gregor, Acta Paleobot. 19: 33. 1978. PLATE 2, F-I.

MATERIAL. One whole seed and four fragments have been recovered from the lignite of the deposit. The entire seed is assigned number 51385 in the Paleobotanical Collections of the Botanical Museum, Harvard University. The fragments are collectively assigned number 51386 in the same collection.

DESCRIPTION. The whole seed is 6.25 mm. long, 3.9 mm. high (from the dorsal to the ventral margin), and 3.7 mm. wide (from lateral face to lateral face). It is essentially ellipsoid, the dorsal portion being well rounded, while the ventral part is slightly compressed laterally to form a ridgelike ventral margin. The hilum is 4.4 mm. long; it lacks a true hilar margin but is surrounded by a raised lip. It follows a slightly curved path along most of the ventral face, widening from 0.5 mm. at the apical end to 1.0 mm. at the basal end (PLATE 2, F). The short raphe passes from the hilar terminus around to the large basal chalaza and is marked by a very faint raphe crest. The vitreous black surface of the seed is completely covered with small depressions that range from isodiametric pits 40–50 μ m. in diameter, to elongate pits 40 μ m. wide by 70–90 μ m. long, which parallel the long axis of the seed. This pattern is overlain by a very faint reticulation formed by weak transverse and cross ridges; this occurs over the entire surface of the seed, including the raphe crest.

No evidence of the external portion of the outer integument was seen. The hard inner portion of the outer integument (the sclerotesta) is 130–150 μ m. thick, except beneath the raphe, where it may exceed 280 μ m. The inner integument consists of two or three layers of isodiametric to rectangular cells that average 35 by 80 μ m. in size, all of which have spiral thickenings

on their walls. These thickenings, which range from 1 to 3 μm . in width and are separated by 4–10 μm ; often anastomose and create a particularly spidery pattern (PLATE 2, H).

AFFINITIES. Although this seed is superficially similar to those of *Euodia* (notably with respect to the faintly reticulate sclerotesta and the length of the hilum), its large size, broad but marginless hilum, and, in particular, its inner integument of entirely spirally thickened cells, place it in the genus *Zanthoxylum*. However, no single modern seed has all the characteristics of the fossil. The seeds of many species of *Zanthoxylum* have a long, straplike hilum, but often in conjunction with a rough sclerotestal surface. Only *Z. williamsii* Standley, of Honduras, has a large, smooth seed with an elongate hilum comparable to that of the fossil, but it lacks the appropriate faint surficial pitting and reticulation and is more ovoid than ellipsoid. Among other modern species, a surficial pattern similar to that of the fossil can be found in *Z. jamaicense* P. Wilson (Jamaica) and *Z. obtriangulare* (Urban) Jiménez (Dominican Republic), but neither has the fine pitting of the fossil form. Thus, although parallels can be drawn with a number of modern seeds, the fossil is distinct and has no modern counterparts among the species examined.

The fossil is very similar in several respects to *Zanthoxylum tiffneyi*, described by Gregor (1978a, 1978b) on the basis of three fossils from Middle Miocene (floral zone 6) sediments near Wackersdorf, West Germany. The parallels include large size, thick sclerotestal walls, and, in particular, an elongate hilum and a smooth sclerotestal surface marked by faint pitting. Certain of the reported Paleogene forms (*Rutaspermum bognoense* (Chandler, 1961b); *Z. compressum* Chandler (Chandler, 1925–26, 1961a)—here considered probably conspecific with *R. bognoense*) do resemble the Brandon fossil in overall shape but deviate from it in significant respects (hilar shape, testal surface).

While the Brandon form resembles *Zanthoxylum tiffneyi* more closely than any other known fossil, the limited amount of fossil material presently available, together with the absence of completely distinctive seed characters below the generic level in modern *Zanthoxylum*, renders the present identification somewhat tentative. In addition, certain fragments, which are assumed on the basis of sclerotestal characters to be of the same species, suggest that the morphology of the Brandon form varies beyond that seen in the single whole seed. For these reasons, the identification is cited as “conforming to” *Z. tiffneyi* pending the collection of further material.

ECOLOGY. The limited material is not sufficient to permit any ecological inferences. The rarity of this form may reflect its importation from a distant source, either by birds, or—less likely in view of its unabraded condition—by flowing water.

DISCUSSION

Wolfe (1975) has proposed that a rather homogeneous flora existed in the Northern Hemisphere in early Tertiary time. This view is based on

considerable evidence, which includes the similarity of the Paleogene fruit and seed floras of Clarno, Oregon (Scott, 1954; Manchester, 1976), and the London Clay (Reid & Chandler, 1933; Chandler, 1961b, 1962, 1963b, 1964) of southern England. The presence of *Euodia* and *Phellodendron* in the Paleogene of eastern North America tends to support this hypothesis; both genera are known from the European Tertiary and are presently restricted to eastern Asia. On the other hand, *Zanthoxylum* does not fit this pattern quite as clearly. While it follows a boreotropical distribution in the Tertiary of Europe and eastern North America, the modern distribution of the genus is much larger and includes the Southern Hemisphere (MAPS 3, 4). It is possible that the genus could have attained its present range by post-early Tertiary dispersal, particularly if it was primarily bird dispersed. However, the presence of an apparently correctly identified seed of *Zanthoxylum* (*Fagara*) from the Eocene of Peru (Berry, 1929) indicates that, at least in the New World, the genus had spread beyond the Northern Hemisphere boundary of the boreotropical forest by Eocene time.

Raven and Axelrod (1974) consider the Rutaceae to have a pre-Tertiary, presumably Late Cretaceous, origin and to have been widely dispersed throughout both hemispheres by the early Tertiary. Since floral exchange between North and South America is assumed to have been minimal prior to the Early Miocene (Raven & Axelrod, 1974), the Paleogene *Zanthoxylum* species of Europe and North America were probably more closely related to each other than either was to the group of South American species represented by *Z. piurianum* Berry (Berry, 1929). This possibility is supported by the strong differences in morphology between *Z. piurianum* and the other known Paleogene rutaceous seeds, particularly with respect to the strong rectilinear pattern of the square pits on the testa of the Peruvian specimen.

The postulated early Tertiary division of the range of *Zanthoxylum* would explain the dominance of strong, regular sclerotestal patterns among the Paleogene species of the Northern Hemisphere, since they would all presumably belong to one lineage or a group of related lineages. This postulate does not explain why, of the modern forms examined, all of those most similar to the Paleogene *Z. rhabdospermum* are restricted to the New World. Based on the strong similarity of the European Tertiary flora to the extant flora of southeastern Asia, together with the close affinities of the North American and European Paleogene seeds of *Zanthoxylum*, it is logical to expect to find the modern relatives of the Brandon form in southeastern Asia. A complete resolution of the relationships and distributions of the various lineages of *Zanthoxylum* can result only from the collection of fossil material of the Rutaceae from the Southern Hemisphere.

The taxonomic similarity of the Early Eocene London Clay flora and the Mid Eocene Clarno flora occasionally extends to the specific level. However, those known elements of the presumably Oligocene Brandon flora that are also common to contemporaneous European floras are similar only at the generic level (e.g., *Phellodendron*, *Euodia*, *Illicium*, *Turpinia*). This also holds in the cases of *Magnolia waltonii* Tiffney (Tiffney, 1977) and *Zanthoxylum* cf. *tiffneyi* (described here), which, although similar to previously described

European species, are not sufficiently so to warrant being considered conspecific. This taxonomic distinctiveness of the Brandon flora relative to contemporary European floras may be explained in one of two ways. The Brandon flora may represent the initial stages in the evolutionary divergence between the Old and New World elements of the boreotropical flora. Such a divergence would presumably be a direct result of the disappearance of the Early Eocene land bridge postulated to have linked eastern North America and Europe (Lehmann, 1973; McKenna, 1975), thus cutting off biotic exchange between the two areas. On the other hand, it is also possible that the boreotropical flora was not a completely homogeneous unit, but contained distinct geographic and ecological subunits. Indeed, the proposed geographic extent of the boreotropical flora (Wolfe, 1975) is such that one would expect some degree of local differentiation. In this light, the London Clay and Clarno floras might represent an ecologically specialized facies within the larger flora that occurred together with other facies restricted to different habitats. The western European floras of the late Paleogene could then be descendents of one such facies, while the Brandon flora could be derived from a different one.

Of these two possibilities, the former is presently felt to be the more acceptable. The concept of the boreotropical forest provides an adequate explanation of the patterns seen in both the past and present flora and vegetation of the Northern Hemisphere. Additionally, it does so within a framework that acknowledges the individualistic nature of the geographic migration of plant species through time.

The presence in the Brandon flora of several genera restricted in modern time to eastern Asia demonstrates that the classic floristic affinities between eastern Asia and eastern North America, which are established on modern distributions, become stronger with increasing age through the Tertiary. The question remains, however, whether both areas commenced in the early Tertiary with an entirely similar flora. Certainly the extant flora of eastern Asia is considerably more diverse than that of eastern North America, even if one includes related Central American floras in the latter category. Wolfe (1977) has suggested four historical factors that could account for this modern disparity in diversity, one of which is "isolation." Such isolation could be enforced from the west by the development of continental climates following the retreat of the Late Cretaceous Mid-Continental Seaway, together with the development of topographic barriers. To the east, isolation might have been a direct result of the opening of the North Atlantic Ocean. Some intracontinental communication between eastern and western North America was undoubtedly possible; there are many instances in which the closest living relatives of western North American fossil species are in the eastern part of the continent. However, the possibility exists that a significant portion of the boreotropical forest of eastern North America was derived from European floras during the early Tertiary via the North Atlantic land bridge. The tenuous temporal and geographic nature of this link might have led to the establishment of a less diverse sample of the boreotropical flora in Paleogene eastern North America. Since the Brandon flora is presumed to

predate the Paleogene climatic deterioration (Wolfe, 1978), it might provide the best sample of this eastern North American boreotropical forest to date, but one that had undergone some 20 million years of evolution since its last exchange with the boreotropical forest at large.

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EXPLANATION OF PLATES

PLATE I

FIGURES A–G. Seeds of *Euodia lignita*. A, #51378, SEM of ventral face, apex directed forward, $\times 12$. B–G, #51379: B, SEM of cross section of sclerotestal wall (outer integument of small rounded cells at bottom of picture is succeeded in a vertical direction by one layer of spirally thickened cells of exterior coat of inner integument, followed by a layer of large, isodiametric parenchymatous cells of interior coat of inner integument), $\times 211$; C, SEM of spirally thickened cells of exterior layer of inner integument, $\times 291$; D, dorsal view, apex directed downward, $\times 8.5$; E, ventral view, apex directed downward, $\times 8.5$; F, ventral view of product of two-seeded carpel (note flattened area to lower left), $\times 8.5$; G, dorsal view (note apical knob on lower end of seed), $\times 8.5$.

FIGURE H. Seed of *Phellodendron novae-angliae* (#51381): spirally thickened cells of outer portion of inner integument, $\times 339$.

PLATE II

FIGURES A–E. Seeds of *Phellodendron*: A, *P. novae-angliae* (#51380), lateral view, ventral margin on right; B, *P. amurense* (C. S. Sargent, August 23, 1903 (A)), lateral view, ventral margin on right; C, *P. novae-angliae* (#51380), ventral view, break in seed disrupting path of hilum; D, *P. amurense* (C. S. Sargent, August 23, 1903 (A)), ventral view; E, *P. novae-angliae* (#51380), dorsal view (note scalloped nature of dorsal face); all $\times 10$.

FIGURES F–I. Seeds of *Zanthoxylum* cf. *tiffneyi*: F, #51385, ventral view, $\times 6.5$; G, #51385, dorsal view, $\times 6.5$; H, #51386, spirally thickened cells of inner integument, $\times 166$; I, #51385, lateral view, ventral margin (hilum) facing upward, $\times 6.5$.

PLATE III

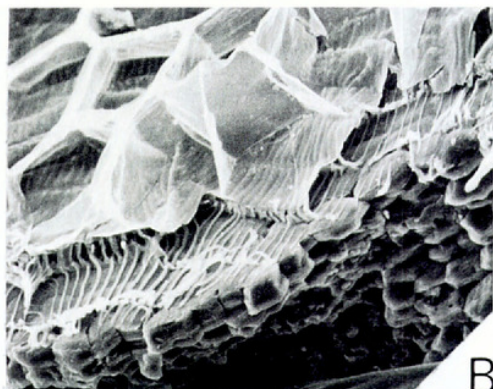
FIGURES A–I. Seeds of *Zanthoxylum rhabdospermum* (#51383): A, SEM of ventral face, apex to left (note central raphal crest), $\times 9.5$; B, SEM of lateral face, apex and hilar area to right, $\times 9.5$; C, SEM of apex, looking basally past hilum and inflated hilar margin, $\times 11$; D, SEM of surficial pits of sclerotesta, $\times 436$; E, ventral view of seed from two-seeded carpel (note flattened face to right), $\times 11$; F, dorsal view, $\times 8.25$; G, interior view of basal chalaza, $\times 8.25$; H, lateral view with apex to left, ventral surface up, $\times 8.25$; I, lateral view with apex to right, ventral surface up (note insect hole in lateral-rear quadrant), $\times 8.25$.

PLATE IV

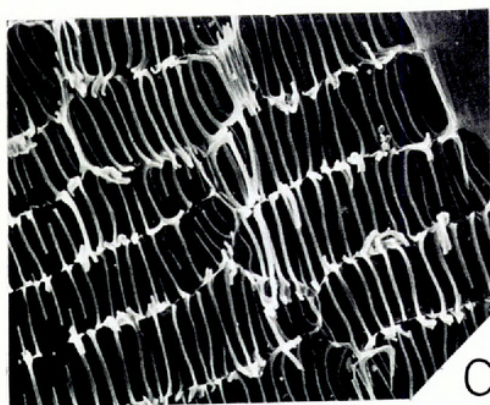
FIGURES A–G. Seeds of *Zanthoxylum*: A, B, *Z. rhabdospermum* (#51383), spirally thickened cells of inner integument: A, $\times 166$; B, $\times 339$. C, D, *Z. caribaeum* (O'Neill 8784 (A)): C, lateral view, apex to right, ventral face up, $\times 7$; D, ventral view, apex uppermost, $\times 7$. E–G, *Z. echinospermum* (#51384): E, remnant spiral thickenings of cells of inner integument, $\times 339$; F, ventral view, apex to left (note small spines), $\times 7$; G, lateral view, apex to left, ventral face up, hilum on upper left margin, $\times 7$.



A



B



C



D



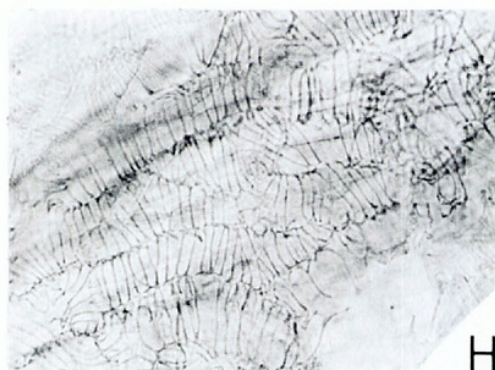
E



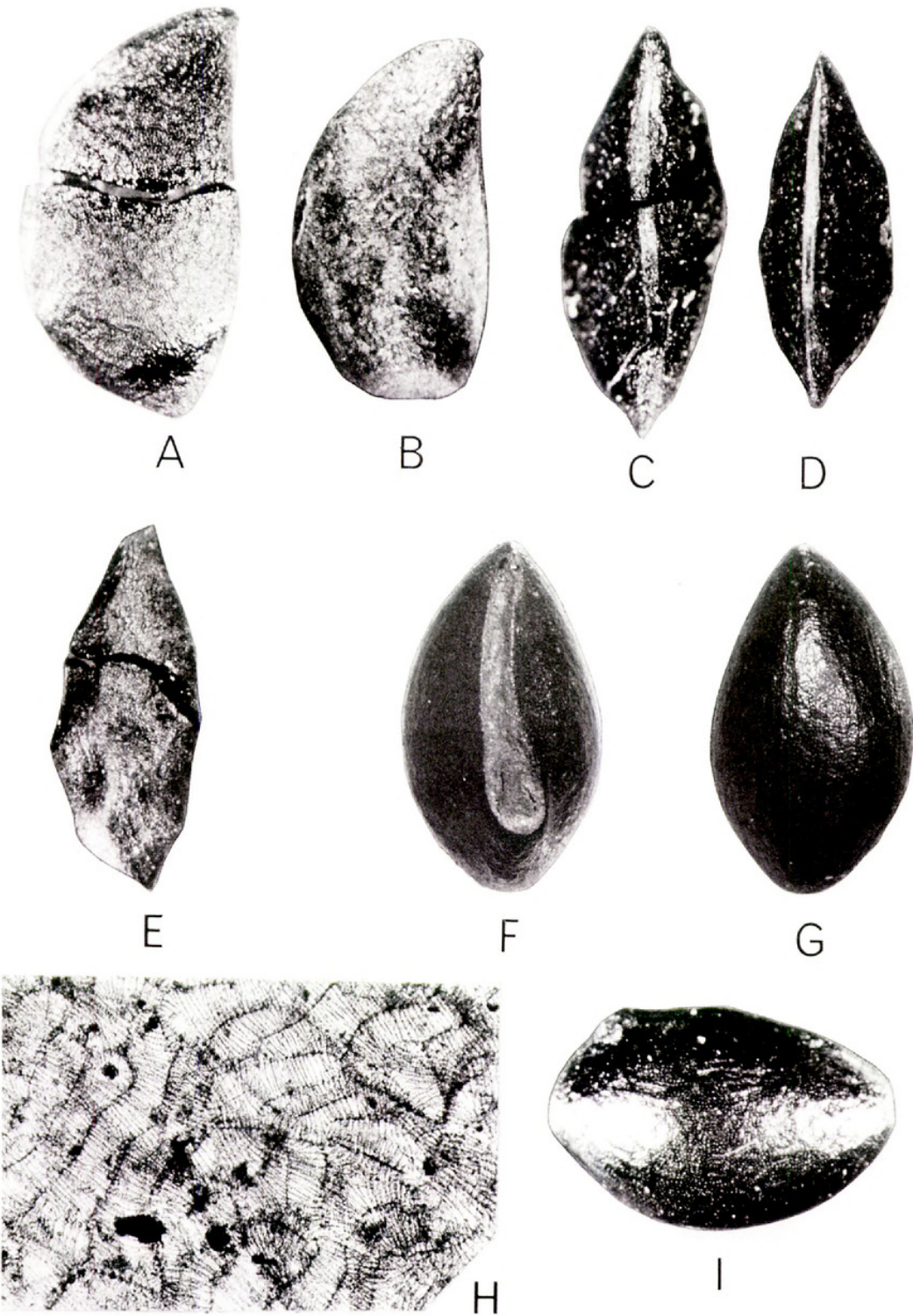
F



G



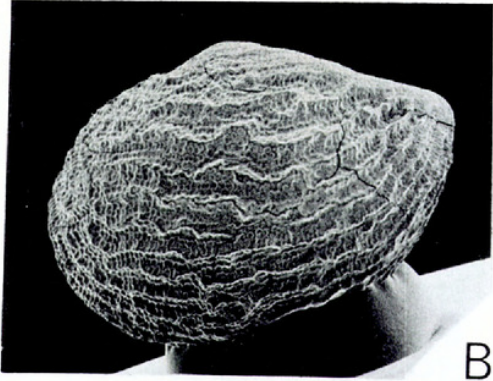
H



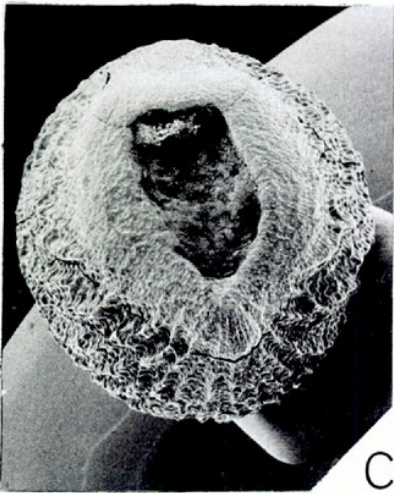
TIFFNEY, BRANDON LIGNITE, V



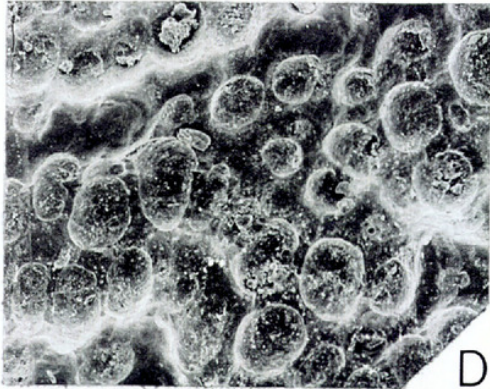
A



B



C



D



E



F



G



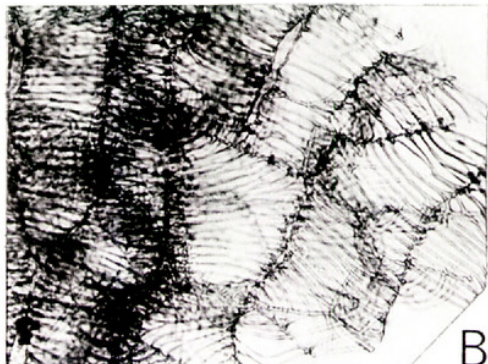
H



I



A



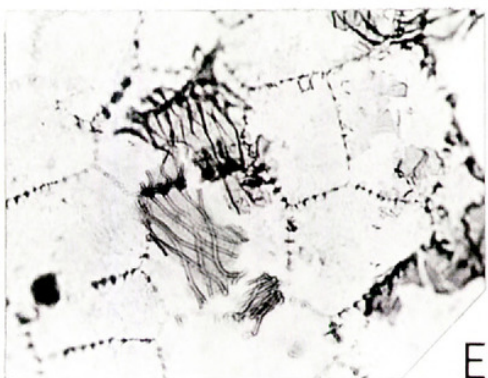
B



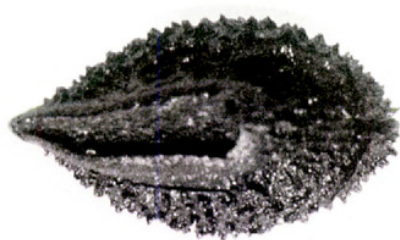
C



D



E



F



G



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