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# Permineralized fruits and seeds from the Middle Eocene Princeton chert locality, British Columbia, Canada

by

Sergio Rafael Silvestre Cevallos Ferriz

A THESIS

SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH

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Ruth A. Stockey

Supervisor

David D. Cass

Date November 17, 1986

**To Veronica, Andres, and Maria Jose**

# Abstract

The Princeton chert (Middle Eocene, Allenby Fm.) has yielded several fruits with seeds and numerous dispersed seeds. Internal anatomy of these remains is described from permineralizations. Several hundred seeds with a palisade-like integument of macrosclereids, sinuous outlines of radial walls (both longitudinally and in face view), a conspicuous perisperm and operculum, are related to the Cabombaceae. One seed with three integumentary layers, the outer bearing hair-like projections, two vascular bundles in the middle integumentary layer, polyhedral to isodiametric cells, and a coiled, peripheral, dicotyledonous embryo probably belongs to the Caryophyllales. Anatropous seeds with four integumentary layers, one palisade of rectangular cells that form a valve, is identified as a member of the Malvales, closely related to the Malvaceae and Sterculiaceae. Aggregate fruits with rosaceous affinities have achenes enclosed by receptacular tissue. Achene anatomy is close to that of *Fragaria* (Rosaceae). A unilocular single-seeded fruit with intermediate anatomy between a berry and a drupe belongs to Amygdaleae (Rosaceae). Anatropous, pyramidal seeds with three distinct integumentary layers, germination valve, hypostase and linear, dicotyledonous embryos in a capsular fruit are referred to *Decodon* Gmel. (Lythraceae). Other lythraceous seeds are larger than those of *Decodon* with an outer mucilage-like integumentary layer that in surface view shows polygonal cells. Three types of ruminate seeds, with five distinct integumentary layers, and a "W" shape in transverse section, belong to the Vitaceae. Anatropous reniform, spiny seeds with two integumentary layers and linear, monocotyledonous embryos are closely related to *Cyrtosperma* Schott (Araceae). A bilocular fruit and a ruminate seed with similar seed and fruit anatomy are described as *Incertae sedis*; however, some evidence suggests their relationship to the Ebenaceae. The anatomy and morphology of fruit and seed remains as well as those of previously reported macrofossils from Princeton indicate a tropical-subtropical climate around a marsh. Vegetation of the basin is reconstructed with five strata: aquatic plants (Cabombaceae, *Eorhiza arnoldii* Robison and Person, *Cyrtosperma*-like plants), climbers (Vitaceae), underbrush (*Paleorosa similkameenensis* Basinger, aggregate fruits, ferns), small angiospermous trees (*Decodon*, Amygdaleae, Malvales) and tall coniferous trees (*Pinus*, *Metasequoia*).

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# I. Introduction

The study of fossil fruits and seeds is not a new area of investigation, but its development has been gradual. Formal work on fossil seeds and fruits was first carried out by Reid and Chandler in the early 1920's (Reid and Reid, 1915; Reid, 1920a, 1920b, 1924; Reid and Chandler 1926, 1933; Chandler, 1925, 1926). Leaves had always attracted more attention, preceding Reid and Chandler's work there were only a few sporadic reports, especially by Russian and German scientists, on fossil fruits and seeds (Kirchheimer, 1936, 1957; Mai, 1960, 1976; Dorofeev, 1951; Nikitin, 1929, 1935). Since that time a large body of information has been accumulated and deposits containing fossil fruit and seed floras are being actively studied around the world.

Paleobotanical work often needs reference collections of extant taxa for comparative purposes. Most herbarium specimens, however, lack fruit and seed data. The best representation of these organs is in a few herbaria with special organ collections. The apparent lack of special organ collections is now being remedied by the development of museums for fruits, seeds or wood. Gregor *et al.* (1979) recently cited some of the more complete fruit and seed collections as well the names of specialists, according to family, who study this type of material. It is obvious, however, that despite our growing knowledge of fruits and seeds based on these collections, there is still an enormous lack of information on these plant organs. Most of the material studied so far has dealt with species that are economically important. Furthermore, descriptions of extant fruits and seeds are almost always restricted to external morphological characters, restricting their use in paleobotanical studies to impression and compression fossils. Most reports on fossil fruits and seeds have dealt with this type of preservation. Some authors, however, have been fortunate enough to find structurally preserved tissues, thus enabling them to describe at least some anatomical characters of their material (e.g., Eyde and Barghoorn, 1963; Tiffney, 1981; Friis, 1985).

Detailed descriptions of anatomical characters of extant seeds and fruits have been done on only a few angiosperm families. Perhaps, some of the most complete works are those of Netolitzky (1926b), Ulbrich (1928), Corner (1976a, 1976b), and Roth (1977). Nevertheless, while these works are very useful for identification, they are far from being complete and their illustrations are sometimes difficult to interpret.

The present study describes the anatomy and morphology of a group of permineralized seeds, some contained in fruits or with remains of fruit wall. Many of the seeds contain endosperm and embryo tissues, rare in fossil plants. Anatomical and morphological studies have allowed detailed descriptions of cell and tissue types in these Middle Eocene angiosperms. Identification of these fossils will help in the reconstruction of whole plants from the Princeton chert and will allow the linkage of the numerous vegetative organs to their reproductive structures. Well preserved seed and embryo tissues have further made discussion of the reproductive biology of these plants possible. Comparisons have been made with several extant seeds and fruits reinforcing the determination of affinities and allowing a meaningful discussion of the paleoecology of the Princeton Basin and the environment of deposition of the Princeton chert.

## A. Fruit and Seed Concepts

In understanding fruits and seeds and what they represent phylogenetically it is important to understand their ontogeny. In short, a seed may be defined as a fertilized ovule. To clarify this definition it is necessary to say that an ovule is an unfertilized integumented, indehiscent, megasporangium (nucellus). The fruit may be defined as the mature ovary,(Gaertner, 1788); however, since a fruit may also be formed by other floral parts, it seems more appropriate to define it as a flower in a state of seed maturation (Knoll, 1939). In the case of inflorescences developing into infructescences, Knoll (1939) suggested the use of terms like "fruit-umbel", "fruit-capitulum" and "fruit-raceme". Eames and MacDaniels (1947) and Esau (1967) also included infructescences within the term "fruit".

### Fruit terminology

A single definite classification systen of fruits used by all botanists is not available at present time. Recently, Roth (1977) reviewed this problem. In Roth's anatomical classification of fruits there are five large groups: dehiscent fruits (the capsule *sensu lato*), indehiscent fruits (the nut *sensu stricto*), the fleshy-stoney indehiscent fruit or sarcosclerocarpium (the drupe), fleshy indehiscent fruit or sarcocarpium (the berry), aggregate fruits from apocarpous multiple fruits.

The dehiscent fruits are divided into two subgroups, dry capsules (mostly Papaveraceae) and fleshy fruits. The latter are represented by the capsule (Caryophyllaceae), legume (Leguminosae), loment (Rutaceae), and follicle (Papilionaceae). A capsule *sensu stricta* is regarded as a pluricarpellated, multi-seeded, dry fruit. Dry capsules are divided into several categories: winged (*Dioscorea* [Dioscoreaceae]), xerochastic (*Aspidosperma* [Apocynaceae]), porate (*Trematobella* [Lobeliaceae]), loculisidal (*Decodon* [Lythraceae]), septicidal (*Veronica* [Scrophulariceae]), and silicle and silique (*Capsella, Mathiola* [Cruciferae]).

The legume, the characteristic but not only type of fruit of the Leguminosae, dehisces explosively along the ventral and dorsal sutures; while the follicle, that looks similar to a legume, dehisces slowly along the ventral suture. The presence of a false transverse partition or wall in a legume defines a "loment".

The schizocarp is a fruit that may be included under the group of dehiscent or indehiscent fruits. It splits into a number of one-seeded parts termed mericarps (e.g. Umbelliferae = 2 mericarps, Boraginaceae = 4 mericarps) (Roth, 1977).

Within indehiscent fruits several different types can also be distinguished: nut, drupe, berry, and aggregate fruits. The nut can be described as a dry, indehiscent fruit that usually contains a single ovule (e. g., *Quercus, Tilia, Chenopodium*).

The achene is also an indehiscent fruit characteristic of the family Compositae. In it, the integument and fruit wall are tightly attached to each other, but frequently do not coalesce completely (Roth, 1977). Roth (1977) suggested that the term "achene" should be restricted to the family Compositae. However, and as she herself noted, the term achene was introduced by Richard in 1808, (see Roth (1977) to include the nut-like follicles of the Ranales and Rosaceae, as well as the special fruit types of the Umbelliferae, Labiatae, and Compositae. Beck in 1891, (see Roth 1977), on the other hand, considered only dry indehiscent fruits developed from apocarpous gynoecia as "achenia", and introduced the term "cypsela" for the fruit of the Compositae. The cypsela can, therefore, be defined as an achene-like structure derived from an inferior ovary.

The caryopsis, another indehiscent fruit arises from a superior ovary in which the pericarp and the integument grow tightly together (e.g. Poaceae).

Another related nut-like fruit is the samara. It is a dry indehiscent fruit producing one or two seeds bearing one to several wings.

The fleshy, stony, indehiscent fruit (sarcosclerocarpium of Roth, 1977) more commonly called the drupe represents a very specialized fruit. It is composed of exocarp (epidermis), mesocarp (parenchyma and edible parts), and endocarp (sclereids or fibers), usually developed from a single carpel. However, drupes can be developed from coenocarpic-paracarpic ovaries with several seeds or even from coenocarpic-syncarpic gynoecia subdivided into pyrenes (Roth, 1977).

A fleshy indehiscent fruit (sarcocarpium of Roth, 1977) the berry is defined as a indehiscent mono- or multicarpellary fleshy fruit, mainly composed of parenchyma and containing from a few to many seeds. A special type of more or less "hard-shelled" berry typical of the family Cucurbitaceae is called a "pepo". It originates from a three to five carpellate inferior ovary usually with parietal placentation (Roth, 1977). Judson (1929) reported that the outer fruit tissue of the pepo is receptacular in origin. The fruit of *Carica papaya* L. (Caricaceae) is sometimes considered a pepo-like fruit (Roth and Clausnitzer, 1972); however, it develops from a superior ovary with marginal placentation. Another special type of berry is the "hesperidium", typical of the genus *Citrus* (Rutaceae), having a leathery rind arising from exo-and mesocarp, a juicy pulp that proliferates from the endocarp, and is developed from a multicarpellary superior ovary with two rows of ovules per locule on marginal placentae.

In the aggregate fruit, monocarpellary ovaries, usually of the follicle type, are united into a single flower and remain united at fruit maturity either by coherence or postgenital connation with one another or by adnation to the floral axis (Roth, 1977). This fruit arises from apocarpous, multipistillate gynoecia, with the Rosaceae, Annonaceae, Nymphaeaceae, etc., being examples of this type. The pericarp of the follicle may represent either a nut-like fruit as in *Fragaria* (Rosaceae), a drupe-like fruit as in *Rubus* (Rosaceae), a berry-like fruit as in *Annona* (Annonaceae) or even a follicle *sensu stricto* as in *Malus* or *Pyrus* (Rosaceae) (Roth, 1977).

The final fruit category, the infructescence is developed from dispersal units composed of a few to many flowers, originating from an inflorescence. The inflorescence axis may be elongated as in the pineapple (*Annanas*), more or less disc-shaped as in certain Moraceae (e.g. *Morus*) or, cup-shaped as in the fig (*Ficus*). Individual fruits may be regarded as berries in *Annanas*, nuts in *Morus* or drupes in *Ficus*.

## Seed Terminology

In angiosperms ovules reach the seed stage in two ways. One is through fertilization of the ovule, the second is due to parthenogenesis (Roth, 1977). Ovules develop in the ovary from the placenta. By division of placental tissue the nucellus arises in which the megaspore mother cell differentiates. If there is a large amount of nucellar tissue located between megaspore mother cell and the nearest epidermis, the ovule is termed crassinucellate, but if there is a small amount, the ovule is termed tenuinucellate.

Near the basal region of the nucellus, one or two rim-like outgrowths arise. They represent the inner and outer integuments. The integuments are formed by a varying number of cell layers. Most angiosperm ovules have two integuments, in others only the inner or the outer integument are present. One modification of the nucellus is the hypostase, composed of lignified cells that may contain tracheary elements, and located in the chalazal end of the ovule. The growing together of the integuments forms a narrow, more or less tubular opening, the micropyle. As the integuments develop, a stalk-like projection, the funiculus, to which the ovule is attached develops from the placenta. The base of the nucellus that may fuse to the integuments represents the chalaza. Netolitzky (1926a, b) defined "chalaza" as the region of the seed or its primordium where the integuments originate. The scar left at the place where the funiculus joins the ovule is the hilum. The funiculus-like tissue that separates funiculus from hilum is the raphe (Singh, 1964).

Other structures that may be present in the ovule are the obturator, jaculator or retinaculum, caruncle, aril and a third middle integument. An obturator is an outgrowth from the placenta or the lining of the stylar canal that enters or covers the micropyle (Singh, 1964). A jaculator or retinaculum represents an outgrowth of the funiculus that facilitates dispersal (Singh, 1964). The caruncle is a fleshy, reflexed outgrowth of variable size developed from the outer integument. An aril is a fleshy outgrowth that envelops the ovule, usually arising at its base. The origin of the aril has been widely discussed (de Lanesson, 1876; Van der Pijl, 1952, 1955, 1957, 1966; Corner, 1976a). Planchon (see Corner, 1976a) defines the true aril as an out-growth of the funiculus, and an arilloide as an outgrowth of the exostome. Van der Pijil (1966) coined the term "arilloi" for outgrowths developed from other parts of the seed. Furthermore, the term "exarilloid" (previously exarillate) is used for naked seeds (Corner, 1976a).

The vascular supply of an ovule is, in general, a single vascular strand that joins the funiculus to the chalaza in the raphe. Sometimes two bundles are present, and vascular elements may be also found in the nucellus of certain seeds (Maheshwari, 1950; Taylor, 1965). Cuticle is an important component of the ovule. It usually forms a uniform layer from the funiculus to the micropyle.

Due to even or uneven growth the ovule may take various forms. Bocquet (1959) reviewed this problem stating that three types of ovules represent the basic developmental sequence. If growth is even, hilum and micropyle are situated in a straight line; that is, the long axis of the nucellus is an extension of that of the funiculus. In this case, the ovule is orthotropous or atropous. If the funiculus bends in such a way that hilum and micropyle are close to each other, the ovule is anatropous. In a campylotropous ovule, chalaza and micropyle lie in one line parallel to the long body of the ovule and more or less perpendicular to the orthotropous condition. Bocquet (1959) also recognized the presence of intermediate forms. Considering the mode of ovule development and organization of its vascular supply, he proposed what he called the "orthotropous-anatropous" series with the following intermediate stages: ortho-campylotropous, ortho-amphytropous, ana-campylotropous and ana-amphytropous. This scheme rejects terms like hemi-anatropous and hemi-campylotropous of Warming (1913) and hemitropous of Goebel (1933) that Bocquet (1959) believes poorly reflect any systematic or phylogenetic relationships.

Chalazal development may also change post-fertilization. Corner (1949) introduced the term "perichalaza" to distinguish seeds with chalazal areas that undergo unidirectional extension. This implies that the ovule loses its initial radial symmetry, becoming bilaterally symetrical. If the chalaza in the mature seed does not show an appreciable size alteration, it is referred to as a normal chalaza. Periasmay (1962a) reported a third type of chalaza, the pachychalaza, that shows an over all post-fertilization increase in size, so that the greater part of the mature seed is occupied by the chalaza.

The endosperm may also undergo changes with time. The term ruminate endosperm, first used by Gray (1879) to describe the endosperm of the nutmeg (*Myristica*) that looked as if it had been chewed, was reviewed and redefined by Periasmay (1962a). He defined a ruminate endosperm as an endosperm with any degree of irregularity and unevenness in its surface contour within the mature seed; such contour being caused by the irregular inner surface of the integument.

## B. Area of Study

The Princeton chert locality is located on the east bank of the Similkameen River, aproximately five miles SSW of the town of the Princeton, British Columbia and almost directly across the river from the abandonned mining camp of Ashnola (Basinger, 1976a). The first published description of the Princeton Basin sediments was that of Dawson (1879). Earlier Bauerman recognized the presence of Tertiary deposits in British Columbia, but his work was not published until 1884. Cansell (1907) determined the extent of these sediments and pointed out some of the geomorphological features of the area. Other studies in the area were carried out by Rice (1947), who described the Princeton lavas and Shaw (1952) who recognized three formations in the Princeton Basin (Lower Volcanic Fm., Allenby Fm., and Upper Volcanic Fm.).

An age of Lower Middle Eocene was suggested for the Allenby Fm., based on the presence of *Pistillipollenites macgregorii* (Rouse and Srivastavava, 1970). Such grains have been reported in the Allenby Fm. a number of times in the past by Rouse (1962), Mathews and Rouse (1963); Hills (1965), Hills and Baadsgaard (1967), and Boneham (1968). However, *P. macgregorii* has also been found in Maestrichtian sediments and is very common during the Paleocene (Crepet, 1984). An Eocene age was also proposed by Russell (1935) and Gazin (1953) due to the presence of tillodontid mammals. Finally, Wilson (1977a, 1977b, 1978, 1980, 1982) established a Middle Eocene age by comparing insect and fish faunas of Princeton and other equivalent basins.

The Princeton chert locality, Allenby Formation of British Columbia has yielded some of the most diverse and best preserved remains of Tertiary fossil plants. This locality, also referred to as the "Ashnola locality" by some authors (Basinger 1976a), was studied palynologically by Boneham (1968). Since that time several other studies have been made on fossil plants from the chert based on large collections most of which are housed in the University of Alberta Paleobotanical Collection (UAPC-ALTA).

Early work includes a study by Miller (1973) who described the seed cone *Pinus arnoldii* and associated foliage *P. similkameenensis*. Robison and Person (1973) added to the knowledge of the flora by describing a semi-aquatic dicotyledonous rhizome, *Eorhiza arnoldii*. The affinities of this plant remain uncertain at the present time.

Studies of the Princeton chert began at the University of Alberta in the mid-1970's and have continued to the present time. Basinger (1976a, 1976b) described a rosaceous flower *Paleorosa similkameenensis*. In 1977, Basinger and Rothwell provided the first account of the diversity of the plants preserved in the chert, and indicated the presence of numerous angiosperm fruits and seeds as well as fertile and vegetative organs of angiosperms, conifers, ferns and fungi. At the same time they commented on the "superb" anatomical preservation that includes developmental stages of various plant organs. The wide diversity of plants present makes this flora "the most diverse Eocene permineralization flora ever discovered" (Basinger and Rothwell, 1977).

Since 1977, some of the diverse plant organs have been described in more detail. The conifers *Metasequoia milleri* (Rothwell and Basinger, 1979; Basinger, 1981, 1984), *Pinus princetonensis*, and *P. andersonii* (Stockey, 1984) have attracted most of the attention in recent years.

With the exception of *Paleorosa* and *Eorhiza* most of the other angiosperm remains have not been studied. Potential for angiosperm studies at this locality is great with several types of permineralized remains available including flower buds currently under investigation (Stockey, submitted); stems, wood, and roots; as well as several fruits and seeds, of both monocots and dicots some of which are treated in the present study.

Other sedimentary basins in British Columbia have been studied paleontologically and correlated to the Middle Eocene Princeton Group. There has been some disagreement about these correlations; however, Wilson (1977) using fossil fish remains showed the relationships of these sediments and volcanic rocks to the Allenby Formation. It is now accepted that the Allenby Formation is syncronic with the Tulameen Basin of the Tulameen area, the Quilchena Beds of the Quilchena-Merritt Basins, the Tranquille Beds from the Tranquille-Red Point Basin, the upper section of the Kamloops Group in the Split Rock-McAbee area, the Horsefly River beds of the Horsefly area and the Driftwood Creek Beds of the Francois Lake-Smithers area. Thus, it is important to point out that the Princeton chert locality is only a part of what may be a fairly large depositional basin within British Columbia. In addition, these basin in British Columbia must also be viewed as part of a large and more or less continuous belt of western North American Eocene outcrops.

## C. Materials and Methods

The Princeton fossil plant remains presented in this study are preserved in chert collected from a section on the Similkameen River consisting of an interbedded sequence of chert and coal with an occasional thin ash bed (Stockey pers. comm.). Forty-nine exposed layers of chert have been recorded and systematically sampled (Stockey, pers. comm.). According to Basinger (1976a) the color of the chert is a good indicator of the amount original organic residue in the rock, and indirectly shows how efficient the peel technique will be on the samples. In this respect, black cherts will give better peels than the lighter ones. Fractures in the chert are filled with blue-white siliceous bands.

For the purpose of this project the cross-index card file from the Paleobotanical Collection of the University of Alberta was examined (about 4200 samples of chert from the collection have already been reference peeled). All the peels with seeds and fruits from the cross index card file were examined with the help of a dissecting microscope and those with well-preserved seeds and fruits, especially those with cellular contents, were chosen for study. The original rock samples of peels containing good seeds or fruits were studied by consecutive peels. The peel technique used was the same as that used by Basinger (1976a, 1981), a modification of the cellulose-acetate peel technique of Joy *et al*. (1956). Large rocks were trimmed to a workable size before further peeling. Consecutive peels were numbered and those showing good contrast and cell detail were mounted as permanent slides with Coverbond xylene soluble mounting medium. For comparision with extant material modern seeds and fruits were fixed, dehydratated, infiltrated, embedded, sectioned, and stained (Johansen, 1940; O'Brian and McCully, 1981). For fixation, formalin acetic acid (FAA) and a mixture of glutaraldehyde and acrolein were used. Dehydration began in 10%, 30% and 50% ETOH and proceeded in a tert-butyl alcohol series (TBA). For infiltration and embedding Paraplast Plus medium was used. Sections 10 um to 13 um thick were cut on a rotary microtome and stained with safranin-fast green or hematoxylin-orange G. *Fragaria* and *Vitis* were purchased locally. Araceae seeds were borrowed from Dr. D. Nicolson, Smithsonian Institution, Vitaceous and ebenaceous seeds were borrowed from Herbario Nacional Instituto de Biologia Mexico, and a lythraceous fruit was borowed from the herbarium of the Botany Department, University of Alberta (Table 1). *Rosa* was collected by the author along Saskatchewan Drive, in front of the Biological Sciences Building of the University in Alberta, Edmonton. In the main entrance of this same building *Prunus, Sorbus*, and *Malus* were also collected in January 24 and February 10, 1986.

All specimens are deposited in the University of Alberta Paleobotanical Collection (UAPC-ALTA).

Table 1. List of reviewed extant seeds.

| Family | Specific name | Collector | Herbarium |
|---|---|---|---|
| Araceae<br>Tribe Lasioideae | *Cyrtosperma chamissonis* (Schott) Merr. | Canfield & Byochel 450 | US |
|  | *C. merkusii* (Hassk.) Schott | Nicolson 1352 | US |
|  | *C. merkusii* (Hassk.) Schott | Nicholson 1217 | US |
|  | *C. merkusii* Hassk.) Schott | Bartlett 6442 | US |
|  | *C. merkusii* (Hassk.) Schott | King 4357 | US |
|  | *Urospatha friedrichsthalii* Schott | Steves & Montiel 24318 | CR |
| Tribe Monsteroideae | *Epipremnum pinnatum* (L.) Engl. | Smith 4836 | US |
|  | *E. pinnatum* (L.) Engl. | Lohes 2461 | US |
|  | *E. pinnatum* (L.) Engl. | Nicolson 1405 | US |
|  | *E. amplissimum* Schott | Nicolson 1500 | US |
|  | *Rhodospatha latifolia* Poepp. | Harley 17919 | US |
|  | *R. venosa* Gleason | Garcia Barroja 1434 | US |
|  | *R. wendlandii* Schott | Styerman & Rabe 96161 | US |
| Vitaceae | *Cissus* sp. L. | Ibarra 1121 | MEXU |
|  | *C. gossypiifolia* Standl. | Ibarra 1170 | MEXU |
| Lythraceae<br>Tribe Nesaeae | *Decodon verticillatus* (L.) Ell. | McCalla 228 | ALTA |
| Ebenaceae | *Diospyros* sp. L. | Ibarra 1012 | MEXU |
|  | *D. digina* Jacq. | Ibarra 1121 | MEXU |

## II. Class Magnoliopsida

### A. Subclass Magnoliidae

Order Nymphaeales

Family Cabombaceae

#### Description

Hundreds of subspherical to ovoid seeds about 7 mm long 3.5 mm wide are among the commonest remains present in some chert layers (Figs. 1, 5). One specimen shows a row of three seeds with a strand of tissue on either side (Fig. 1). This tissue 2.5 cm long probably represents part of the fruit, however, preservation and tissue continuity do not allow a complete description. The counterpart of this slab shows a fourth seed from the same fruit (Fig. 2). This seed is also enclosed by fruit tissue, but also shows an axis 3.6 mm long and 0.3 mm in diameter at the base that may represent a pedicel (Fig. 2). Actual attachment is not observable, since a fracture line containing silica runs through the tissues at this level. However, it seems obvious that the pedicel and the fruit were once attached to each other.

The small ovoid seeds have an operculum located at one end (Figs. 10, 12). When the operculum is removed in the micropylar area a large gap occurs (Fig. 11). The operculum is composed of a single layer of radially elongated cells about 250 um x 61 um with dark contents and straight radial walls (Fig 12). Seeds have two integumentary layers (Fig. 3, 13). In longitudinal section the outer shows a single palisade of sinuous, thick-walled cells, (Fig. 13). Transverse sections of these cells are oval to polyhedral in outline. Surface views of these cells are sinuous with between 4 and 20 undulations of the wall (Fig. 9). Some cells are almost cruciate in surface view (Fig. 9). At the base of the inner integumentary layer near the nucellus is one vascular bundle that traverses the seed for almost half of its length (Figs. 4, 5, 6). In the region of the vascular strand the seed shows a protuberance in section view, that is actually a ridge in longitudinal section (Figs. 4, 5, 7). Nucellus is usually a single cell layer thick in most seeds (Fig. 4); however, a perisperm has been seen in one seed (Figs. 7, 8). Cell walls in this region are invaded by fungal hyphae (Fig. 8).

## Discussion

Longitudinal sections of these seeds show a close similarity to those of *Ondinea purpurea* den Harfog (Schneider and Ford, 1978) or *Barclaya longifolia* Wall. (Schneider, 1978) of the Nymphaeales. Furthermore, Corner (1976a) describes the seeds of this order as having an outer palisade-like integument of cuboid or short, columnar cells, with thickened more or less lignified cells, varying from stellate to undulate in surface view. In several genera the integument thins toward the micropyle to form an operculum. The inner integument is not multicellular, and is unspecialized and crushed at maturity. Other characteristics are the presence of an aril, operculum and perisperm.

The order Nymphaeales is divided into 5 families by Cronquist (1981), Nelumbonaceae, Nymphaeaceae, Barclayaceae, Cabombaceae and Ceratophyllaceae. Hutchinson (1959) and Walker (1976a, 1976b) treat these families as subfamilies of the family Nymphaeaceae. Seeds of the family Ceratophyllaceae lack both perisperm and endosperm and are, therefore, unlike the fossil seed. The pachychalazal or multivascularized seeds of the family Nelumbonaceae are much more complex than the fossil seeds. Four genera of the family Nymphaeaceae are arillate unlike the fossil seeds, *Nymphaea*, *Euryale*, *Victoria* and *Ondinea*. The fifth genus of this family, *Nuphar*, has surface integumentary cells with hexagonal facets unlike the undulating cells in the fossil seed. The presence of brittle epidermal hairs in the family Barclayaceae is unlike the fossils. The family Cabombaceae with two genera is most similar to the fossil seed. *Cabomba* Aubl. in the outer integumentary layer has one conical thick-walled papilla per cell.

Using surface views of the outer integumentary layer to distinguish between the genera of the Nymphaeales, Collinson (1980) reported that *Euryale*, *Nelumbo* and *Nuphar* have polyhedral walls, and thus, cannot be related to the fossil seed that has sinuous walls. *Victoria*, *Nymphaea*, and *Ondinea* have an operculum with two holes, one representing the hilum and the other the micropyle, while the fossil seed has only one. *Barclaya* and *Cabomba* have conspicuous hair-like projections unlike the fossil. *Brasenia* has an operculum similar to that of the fossil seed, and the cells of the outer integument in surface view are also sinuous like the fossil seed. However, Collinson (1980) reported the presence of a solid rounded tubercle up to 50 um in high and occupying one third of the cell diameter for *Brasenia*, and stated that the inner integumentary layer is 2-5 cell layers thick. Therefore, *Brasenia* is the closest extant genus to the fossil seed. The operculate and exarillate seeds of *Brasenia* have an outer integumentary layer with cells in surface view showing very thick walls, somewhat stellate to undulate outlines (Collinson, 1980)., The Princeton seeds have fewer undulations and do not have tubercles as *Brasenia*; therefore, some differences are evident between these seeds.

The fossil record of the Nymphaeales is extensive. Collinson (1980) reviewed the fruit and seed record, and pointed out the presence of seeds related to this group from the early Tertiary (Chandler, 1961) to the Quaternary (Katz, et al., 1965). In her review, she also illustrated the surface view of cells of the outer integumentary layer. This character allowed the separation of some genera of fossil seeds into different groups based on the rectangular or polyhedral shape of their cells. *Tadvenia* Dorof., *Nikitinella* Dorof., *Tomskiella*, *Eoeuryale* Miki, *Irtyshenia* Dorof., *Pseudoeuryale* Dorof. and *Palaeoeuryale* Dorof. all have cells of this type. Four other genera have stellate to undulate cells (Collinson, 1980). *Palaeonymphaea* Chandler has few and very weak undulations, and *Dusemloaya* Dorof. has more than 10 undulations per cell. However, both have an operculum with two holes, representing the hilum and the micropyle, unlike the fossils. Collinson (1980) described *Braseniella* Dorof. that has stellate cells and a singleholed operculum, making it very similar to the fossil seeds.

The living *Brasenia* differs from the Princeton fossil seeds, in that its outer integumentary layer when seen in longitudinal section has very sinuous walls, and the radial walls of the outer integument are straight. *Saberina chandlerae* Coll., another fossil cabombaceous seed differs from the fossil seed in having two holes in the operculum (micropyle and hilum), and straight radial walls of the outer integumentary layer. At the present time it seems reasonable to refer to the Princeton fossil seed as a probable new member of the Cabombaceae.

## B. Subclass Caryophyllidae

### Order Caryophyllales

### Description

A single oval seed has been found with maximum dimensions of 1.2 mm x 0.8 mm (Fig. 14). Its appearance changes according to the level of the section (Figs. 15, 17). At mid-levels a central circular seed body with two lateral wing-like extensions are seen (Figs. 14, 15). The integument is composed of three layers. The outermost contains rectangular cells, about 50 um x 23 um, each with a clavate hair-like protuberance about 112 um long and 40 um in diameter (Figs. 16, 18, 19). The second integumentary layer is composed of polyhedral cells that are 40 um to 25 um in diameter, nine cells thick in the lateral expanded areas thinning to three or four cells around the central seed cavity (Figs. 14, 15). In the central part of each expanded area a vascular bundle is present for most of the seed length (Figs. 14 - 16). The third and innermost integumentary layer is composed of a single row of tangentially elongated cells about 55 um x 15 um (Fig. 16). Nucellar tissue has not been identified. Endosperm is represented in each section by a dark circle, sometimes with an irregular outline, and contains rectangular cells with dark contents (Figs. 20, 22). A well-preserved dicotyledonous embryo is present toward one side of the seed cavity (Figs. 20 - 25). The embryo is curved with two rather long cotyledons. Around the region of the shoot apex the embryo shows rectangular cells near the notch (Figs. 21, 22). This area (Fig. 22) probably corresponds to the coyledonary node. Cotyledons are almost circular in outline throughout their length, but become flattened near the tips (Fig. 25).

### Discussion

The peripheral position of the embryo is a characteristic feature of the Subclass Caryophyllidae. According to Martin (1946) no other angiosperm subclass has this arrangement. A somewhat similarly oriented embryo is present in the Graminae. However, the fossil embryo is dicotyledonous. Three orders form this Subclass: Caryophyllales, Polygonales, and Plumbaginales (Cronquist, 1981). The later have straight, large, spatulate dicotyledonous embryos. In the other two orders, the embryo is a large, nearly always dicotyledonous, peripheral, straight or most often curved or annular. In the

Caryophyllales this embryo is surrounded by a more or less abundant, starchy perisperm. However, in the order Polygonales perisperm is essentially lacking and the seed is sometimes ruminate. The integumentary structure of this order does not match the fossil seed since P[illegible]gonales seeds show a smooth outer integumentary layer that may have reticulate thickenings and a hypostase (Corner, 1976a). Comparisions of the integument structure within these orders are restricted since only a few genera have been described. What's more, most of the descriptions are based on young ovules. A rough estimate in the number of genera per order is 370 for Caryophyllales and 30 for the Plumbaginales (Cronquist, 1981). Of these, only about 40 genera have been described for both orders, thus making comparisions difficult. Only the family Nyctaginaceae has two postchalazal branches of vascular tissue, as in the fossil. However, hairs or hair-like structures have not been described for this family and its second integumentary layer, if present, is aerenchymatous. On the other hand, families with hairs or hair-like structures in the first integumentary layer show other differences when compared to the fossil seed. The Caryophyllaceae have sinuous cells, as seen in surface view unlike the rectangular cell outlines in the Princeton seed. A second layer of cells associated with the first integumentary layer is present in the Phytolacaceae. Families Aizoaceae and Molluginaceae (Corner, 1976a) have a smooth surface or the outer tangential wall becomes wavy and thick. The first integumentary layer is crushed at maturity in the Didiercaceae, and is thick-walled in the Cactaceae; therefore, it is difficult to relate any of these families to the fossil seed. According to Corner (1976a) the families Chenopodiaceae, Amaranthaceae and Basellaceae have a very similar integumentary anatomy. In these groups the first integumentary layer is composed of cuboidal or short, radially elongated cells. In some genera, the cells have a papilla or hair, generally containing tannins. This group also has at least four integumentary layers, making it difficult to indicate a relationship to the fossil seed. Finally, seeds of the Portulacaceae have three integumentary layers and hairs or hair-like structures in the first integumentary layer. Corner (1976a) however, reports that the third integumentary layer has slight bar-like thickenings, not seen in the fossil seed.

The fossil record does little to aid in the identification of this seed. Pollen grains of the families Amaranthaceae/Chenopodiaceae are known from the Cretaceous; the

Polygonaceae from the Paleocene, the Nyctaginaceae and Caryophyllaceae from the Oligocene, and the Portulacaceae from the Upper Miocene (Muller, 1981). Tertiary fruit and seed remains of the family Polygonaceae are common; however, since they are mainly fruit compressions, it is not possible to compare them to the permineralized seed described here (Kirchheimer, 1942; Dorofeev, 1963; Mai, 1964; Friis, 1985). Fossil fruit and seed remains of the Caryophyllales are known only from the quaternary (Schweger, pers. comm.).

and pollen record is known from the Upper Cretaceous. While it is possible to say that the fossil seed fits very well in the order Caryophyllales, further taxonomic determination awaits more detailed descriptions of the extant seeds and the discovery of more fossil material. The seed shows many similarities with the Portulacaceae, however, it is premature to assign the single fossil seed to this family.

## C. Subclass Dilleniidae

### Order Malvales

### Family Sterculiaceae / Malvaceae

### Description

Two oval, anatropous and multilayered seeds have been found with a maximum length of 1.8 mm and width of 1.2 mm (Figs. 26, 28). A valve 0.9 mm x 0.3 mm composed of a palisade of rectangular cells one layer thick is present on these seeds (Fig. 31). Four easily distinguishable integumentary layers form the seed integument (Figs. 26, 27). The outer integument, about 9 cells thick is composed of tangentially elongated cells about 28 um x 10 um (Fig. 27). Gland-like cells about 30 um in diameter occur in this layer and extend into the second integumentary layer (Fig. 29). The second integumentary layer is multicellular and composed of isodiametric cells about 23 um in diameter (Figs. 27, 30). The raphe runs through this integumentary layer from an area just below the micropyle deep in the second integumentary layer, then into the chalaza at the opposite end (Fig. 30). The third integumentary layer contains a single layer of radially elongated cells with 25 um x 7 um, that form a palisade (Figs. 27, 32). This layer projects from the seed surface to form a valve. Valve cells are also full of dark contents (Fig. 31). The inner-most and fourth integumentary layer is three to four cells thick, and composed of tangentially elongated cells 25 um x 5 um. Nucellus, endosperm or embryo have not been observed in these seeds.

### Discussion

The presence of a palisade in the third integumentary layer in these seeds is very characteristic and easy to identify with the exotegmic group of seeds described by Corner (1976a). He divided this group into two subgroups, exotegmic seeds with a palisade and exotegmic seeds with fibers. Corner (1976a) further divided the group with a palisade into two smaller groups, those with more or less prismatic cells with angular, isodiametric or shortly oblong facets and those with tubular or radially elongated cells with stellate to undulate or lobate facets. The fossil seeds belong to the former group. Only a few angiosperm families have similar characteristics to the fossil seed; however, as Corner (1976a) pointed out, it is very difficult to distinguish between them. The presence of a complicated chalazal region distinguishes families Bixaceae and Cistaceae from the fossil seed. Aerenchymatous tissue is present at some levels of the integument in families Tiliaceae, Passifloraceae and Bombacaceae, unlike the fossil seed. Since the second integumentary layer is multicellular in the fossil seed and families Piperaceae and Thymelaeaceae do not have multicellular integuments at all, a relationship to them cannot be supported. Seeds with a large and conspicuous vascular system like those of the families Gonystylaceae and Dipterocarpaceae cannot be compared to the fossil seeds with a single vascular bundle. The palisade layer of family Turneraceae is oriented obliquely, making it quite different from that of the fossils. Within the family Celastraceae one genus (*Perrotetia* HBK) has a palisade like that of the fossil seed; however, its integuments are only three to five cells thick (Corner, 1976a), making it different from the fossil seed discussed here. Another family with a palisade layer in a similar position to that of the fossil seed is the Euphorbiaceae (Crotonoideae). However, seeds differ from the fossils in having the first integumentary layer and generally the second integumentary layer composed of a short palisade. Crotonoideae seeds may also have aspetate hairs not seen in the fossil. Seeds of the family Sterculiaceae look very similar to the fossils, but their first integumentary layer is a short palisade and integuments sometimes contain mucilage sacs. Finally, integuments in the family Malvaceae are also very similar to the fossil; however, a hypostase occurs. No evidence of a hypostase has been seen in the fossil seeds. It appears, therefore, that the Sterculiaceae and Malvaceae have seeds most similar to the fossils. Perhaps the outer palisade as in sterculiaceous seeds was not developed at the time of fossilization. Different developmental stages were shown to occur in *Gossypium* (Malvaceae) by Balls (1915). Perhaps this layer was abraded prior to fossilization. The hypostase in malvaceous seeds, does not always persist in the mature seed, therefore these fossil seeds may have had a hypostase at one time.

At the present time it is not possible to positively relate the fossil seeds to any of these families. Thus, more data are needed in order to give a more precise taxonomic interpretation of these Princeton seeds. The fossil record of both families goes back to at least the Eocene (Dorofeev, 1963; Möller, 1981). Cronquist (1981) notes that the Sterculiaceae may even be present by the latest Cretaceous.

## D. Subcl[illegible]sidae

Order Rosales

Family Rosaceae

Subfamily Amygdaloideae

Drupe/Berry (*Prunus*-like fruit)

### Description

Five fruits of this type, three of which are well preserved, have been found in the chert. Fruits are ovoidal with a maximum diameter of 1.8 mm and contain one seed (Fig. 33). At the basal end of two fruits an attached narrow pedicel 4 mm in diameter is observable (Figs. 34, 39). Opposite the pedicel a short persistent style about 0.1 mm in diameter and 0.1 mm high can be seen in some sections (Figs. 33, 34, 35, 42). The pericarp can be divided into three layers. An exocarp is present around the whole fruit and composed of a single layer of isodiametric to slightly rectangular cells 40 um in diameter (Figs. 36-38), that have slightly thicker tangential walls. The multilayered mesocarp thins as it approaches the stylar region and is not present beneath this area (Figs. 34, 35). Cells of the mesocarp are polyhedral to isodiametric with a maximum diameter of about 40 um. The multilayered endocarp is not well preserved, however, the cells seem to be similar in shape to those of the mesocarp but with much thinner walls (Figs. 36, 37).

The fruit has three vascular strands situated between endocarp and mesocarp (Figs. 38, 41, 42). The three strands depart at the fruit base, from the vascular tissue of the pedicel. The fruit pedicel has a well-developed vascular tissue surrounded by large parenchymatous cells with dark contents (Fig. 40). Tracheids of both fruit and pedicel have well-developed helical thickenings (Figs. 40, 41).

The seed itself is circular to ovoid with a maximum diameter of 0.9 mm (Figs. 33 - 37, 39). Two integumentary layers have been distinguished even though they are crushed and not well preserved (Fig. 44). The outer is a single layer of isodiametric to polyhedral cells, 30 um in diameter. The inner integumentary layer contains crushed quadrangular to rectangular cells with dark contents one or two cells thick (Fig. 44). In one seed, some rectangular to slightly polyhedral cells 83 um x 46 um in diameter are preserved with dark contents (Figs. 43, 45). These may be remains of the nucellus or possible endosperm tissue.

### Subfamily Rosoideae

### Tribe Fragarieae

### Aggregate fruit

### Description

Two well-preserved fruits known from longitudinal section and one from transverse section have been found in the slabs of one chert block. Six other fruits with smashed tissues are difficult to interpret.

The aggregate fruit is pear-shaped with a length of 6.5 mm (Fig. 46). A mid-fruit cross section appears oval, with a maximum width of 7.2 mm and a minimum width of 2.3 mm (Fig. 47), but these fruit tissues may have been slightly compressed prior to fossilization. Two persistent sepals are present at the base of the aggregate fruit (Figs. 46, 48). The tissue that forms the aggregate fruit and enclosing the actual fruits (achenes) may be divided into two zones. The central basal portion of the fruit is occupied by a pith-like region of parenchymatous cells with rectangular outlines 147 um x 95 um in diameter (Fig. 50).

This region is surrounded by vascular tissue containing tracheids with helical thickenings (Fig. 49). The second zone of fruit tissue envelops the actual fruits, producing a floral cup structure. At least two layers can be distinguished in this zone. The outer is represented by a single layered epidermis, of tangentially elongated cells about 35 um x 20 um in diameter (Figs. 51). Beneath the epidermis are more or less tangentially elongated cells with dark contents about the same size as epidermal cells (Fig. 51). These same types of cells are loosely distributed between the fruits, and serve as a supportive matrix.

The actual fruit is an achene or a follicle. In it, five differnt layers can be distinguished, three corresponding to the fruit and two corresponding to the seed. (Figs. 51, 52). The exocarp is single-layered with tangentially elongated cells about 40 um x 20 um in diameter (Fig. 52). Sometimes it is possible to distinguish one or two additional layers of smaller cells with similar cell characteristics to those of the exocarp. The next conspicuous layer is composed of isodiametric thick-walled cells about five cells thick (Figs. 51, 52). Individual cells are about 16 um in diameter with a wall thickness of about

13 um.

The endocarp is represented by a single layer of rectangular thin-walled cells 25 um x 11 um in diameter (Fig. 51).

The outer seed integument is composed of two to three layers of rectangular thin-walled cells, 30 um x 13 um in diameter, full of dark contents (Fig. 52). The inner integumentary larger is composed of polyhedral cells about 60 um in diameter with helical secondary wall thickenings (Fig. 54). The general outline of the seed is pear-shaped with one concave side (Fig. 53). A cross section toward the tip of the seed shows an elongated micropylar end (Fig. 55).

The endosperm, three to four cells thick, is composed of polyhedral thin-walled cells 23 um x 9 um in diameter (Figs. 56, 57). Embryo tissue is preserved in a few seeds and in some sections two large cotyledons with cellular preservation can be seen (Figs. 56, 58).

## Discussion

Seed anatomy of these two fruits is not distinctive in any way. It is the apparent lack of diagnostic characters that actually relates them to the family Rosaceae. Corner (1976a) states that seeds of this family offer no striking microscopic structure. However, he adds, most appear to have non-multicellular seed-coats and to be variously reduced and simplified with little differentiation of cell layers, in accordance with the prevailing indehiscense of the fruit. The concept of seed integument reduction in indehiscent fruits of this family is discussed by Roth (1977).

The Rosaceae is a very large family with more than 110 extant genera and over 3,000 species. The family has been studied for a long time; however, fruit and seed anatomy still need more detailed study. Tschierske (1886), Farmer (1889), Malfatti (1896), Pechoutre (1902), Hillmann (1910), Kraus (1913, 1916), Juel (1918), Netolitzky (1926b), Bonne (1928), Kuhn (1927), Tukey (1934), MacDaniels (1940), Rauh and Reznik (1951), Reeve (1954a, 1954b), Hjelmquist (1962), Sterling (1964a, 1964b, 1964c, 1965a, 1965b, 1965c, 1966a, 1966b, 1966c, 1969), Vaughan (1970), Corner (1976a, 1976b), Roth (1977) and Olson and Steeves (1982, 1983) have all examined fruit and/or seed anatomy to some degree.

Fruit morphology and anatomy are of great taxonomic value in subdividing the family Rosaceae into subfamilies and tribes. Among other characters, Robertson (1974) states that the fruit of Subfamily Spiraeoideae is a follicle. In Subfamily Rosoideae the fruit is indehiscent, a solitary achene or aggregate or accessory fruit with several druplets or achenes (Robertson, 1974). In Subfamily Maloideae he lists the pome as the typical fruit and the drupe as fruit of the Subfamily Amygdaloideae. Using this scheme, the fruit from Princeton probably represents a member of the Subfamily Amygdaloideae.

The Princeton fruit resembles a typical drupe in having three distinct pericarp layers (exocarp, mesocarp and endocarp). However, Roth (1977) noted that in a drupe the mesocarp is generally composed of parenchymatous cells and the endocarp is formed either by sclereids, fibers or a mixture of both. The Princeton fruit has a mesocarp of thick-walled cells and an endocarp of thin-walled cells. Thus, the cell layers are reversed from the situation seen in the typical drupe. Integuments and probable endosperm as well as mesocarp and exocarp are well preserved; however, the endocarp is badly preserved in all fruits so far studied. It is important to point out that fruits of peach (*Prunus persica*) can be divided into two groups, melting and non-melting types due to the presence or absence of watering areas (Appleman and Conrad, 1926). A watering area is formed by the breakdown of cell walls of the mesocarp and the accumulation of cell contents in the intercellular spaces. It is possible that a situation similar to this is responsible for the absence of the endocarp in the Princeton fruit. Thus, its absence may not be due to preservation but to a natural phenomenon known in at least one species of the genus *Prunus*.

Another indehiscent fleshy fruit is the berry. By definition, a berry contains several to many seeds and is monocarpellary or multicarpellary (Roth, 1977). It also can be divided into exocarp, mesocarp and endocarp. Here, the mesocarp can be differentiated into several specialized parenchymatous layers while the endocarp is usually single-layered. However, sometimes these parenchyma layers are at least partially replaced by thick-walled cells. This situation sometimes makes it extremely difficult to draw a line between a berry and a drupe, and many transition forms exist (Roth, 1977). In fact, drupes may be present in one species and berries in other species of the same genus (e.g. *Vaccinium, Ribes*) (Roth, 1977).

The epidermis of berries is composed of one layer of small, thick-walled, isodiametric cells. This same type of epidermis is found in the Princeton fruit. It is important to point out that the epidermis in a drupe usually is accompanied by two or three hypodermal layers; thus the fossil fruit is different in lacking these hypodermal layers.

Using pericarp anatomy, the fruit can be identified as a berry with a two-layered mesocarp. However, a single-layered endocarp usually characteristic of berries is not present in the fossil fruit. Therefore, it is more accurate perhaps to interpret this part of the pericarp as similar to that in a drupe. The fruit then may represent a transitional form between a drupe and a berry. Another characteristic of the fossil fruit that makes it more drupe-like is the presence of a single seed. Berries usually have two or more seeds per fruit; however, some palm fruits are single seeded berries (Corner, 1966). Seed anatomy shows little in the way of diagnostic features; nevertheless, its reduced structure corresponds to the typical situation in a drupe. In this kind of fruit the endocarp takes over the protective function of the integuments, forming a unit (seed + endocarp) comparable to the single seed surrounded by hard integuments (Roth, 1977). In the Princeton carpological remains this unit includes the whole pericarp plus the seed.

Drupes are well known in the Rosaceae (*Prunus, Ceresus, Rubus*); however, they are also found in other families like *Cornaceae*, (*Cornus*), Caprifoliaceae (*Sambucus*), Araliaceae (*Hedera*), Rubiaceae (*Coffea*), Ranunculaceae (*Laurus*), Rhamnaceae, (*Rhamnus*), Myristicaceae (*Myristica*), Oleaceae (*Olea*), Rutaceae (*Casimiroa*), Anacardiaceae (*Mangifera*), *Saxifragaceae* (*Ribes*), Ericaceae (*Vaccinium*), and Juglandaceae (*Carya*) among others (Roth, 1977). Netolitzky (1926b) and Corner (1976a) described the seed anatomy of these families, and they do not resemble the Princeton fossils. Some of them, like Caprifoliaceae, Araliaceae, Menispermaceae, and Rubiaceae have ruminate or subruminate seeds, for example. Multicellular integuments are reported in families such as Ranunculaceae, Rhamnaceae, Myristicaceae, Lauraceae, Linaceae, Simaroubaceae, Meliaceae, Rutaceae, Polygalaceae, Elaeocarpaceae, Trapaceae, Theophrastaceae, Myrsinaceae and Celastraceae. Furthermore, a palisade or palisade-like layer is present in integuments of Chloranthaceae, Phytolaccaceae, Schizandraceae, Acanthaceae, Oleaceae, Saxifragaceae and Juglandaceae. A hypostase is well-developed in Myricaceae, Ulmaceae, Moraceae, Urticaceae, Thymelaeaceae and Alangiaceae. Thickenings (spiral, reticulate, bar-like) in some integumentary cells are present in Monimiaceae, Anacardiaceae and Verbenaceae. Finally, the presence of sinuous cells in the outer integumentary layers in Cornaceae, a rather large funiculus in Anacardiaceae, absence of an outer integument in Santalaceae, presence of an aerenchyma-like integumentary layer in Malpighiaceae, an outer integumentary layer formed of cuboidal cells in Proteaceae, a crushed outer integumentary layer in Piperaceae and presence of an aril in Amaranthaceae negate a relationship of the fossil seeds to these families.

Fruit anatomy of these families also shows some differences compared to the fossil fruits (Roth, 1977). For example, Cornaceae and Rhamnaceae are characterized by the presence of a crystal layer in the endocarp. A palisade or palisade-like structure in the mesocarp is diagnostic of the Caprifoliaceae, Araliaceae and Rubiaceae, unlike the fossil fruit. Two or more carpels are present in Rutaceae and Saxifragaceae while only one is present in the fossil fruit. Extensive vascularization of the pericarp is found in Oleaceae, Anacardiaceae, and Juglandaceae, while the fossil fruit has only three vascular strands. Sinuous cell outlines are found in the endocarp of the Ranunculaceae, unlike the fossil described here. Stomata are present in the endocarp of Ericaceae, and large intercellular spaces are found in the inner epidermis of Myristicaceae, these structures are not found in the Princeton fossil fruit.

The family with the most similar fruit and seed characteristics to the Princeton fruit is the Rosaceae. As mentioned above, the Subfamily Amygdaloideae typically have drupes. Subfamily Rosoideae may have drupes; however, when this type of fruit is present in the Rosoideae it invariably forms part of an aggregate fruit. Since the drupe/berry of Princeton shows no indication that it is part of an aggregate fruit, any relationship with the Rosoideae is weakened.

The presence of a well-developed pedicel in the Princeton drupe/berry supports its interpretation as a single and isolated fruit, indicating a relationship to the subfamily Amygdaloideae. Seed or fruit anatomy of the subfamily is known only from *Prunus*; however, *Prunus* shows a typical drupe (Roth, 1977). The Princeton fruit compares closely in seed anatomy to the description of *Prunus* by Corner (1976a). It has an outer integumentary layer composed of rounded cells while other integumentary layers are crushed. However, three to 10 post-chalazal branches of vascular tissue occur in *Prunus* (Corner, 1976a), while in the fossil no vascular tissue has been identified although the fruit is well preserved. Vaughan's (1970) descriptions and illustrations of the seeds of some species of *Prunus* show great similarity to the fruit discussed here; however, the inner part of the outer integumentary layer in the fossil seed is not as distinct as in *Prunus*. Fossil carpological remains of the subfamily Amygdaloideae referred to as *Prunus* have been reported from several localities (Dorofeev, 1963; Gregor, 1978, 1982; Friis, 1985). Unfortunately, the internal anatomy of these remains is not known, making comparison with the Princeton material impossible. The small size of the Princeton drupe/berry differs from those of *Prunus* that range from two to 12 cm in diameter.

At the present time, this fruit appears to be related to the one-seeded drupaceous fruits of the Amygdaloideae, however, the lack of seed and fruit information on other genera of the Subfamily, precludes further comparisions.

Aggregate fruits are found in families like Magnoliaceae (*Magnolia*) Ranunculaceae (*Ranunculus*), Annonaceae (*Annona*), Rubiaceae (*Morinda*), Convolvulaceae (*Cuscuta*), Dispacaceae (*Dispacus*), Nymphaeaceae (*Nelumbo*) and Rosaceae (*Fragaria, Rubus, Rosa, Malus, Pyrus*) among others (Roth, 1977). Comparing fruits and seeds of the Princeton aggregate fruit with these families, the Rosaceae show the greatest number of similarities. Seeds of the Princeton aggregate fruit differ from those of the family Magnoliaceae in being extremely small. Magnoliaceous seeds have a multicellular outer integumentary layer, fleshy sarcotesta and a small or microscopic embryo.

Fruits of the Ranunculaceae differ from the fossils in having three to five vascular bundles (Roth, 1977) while the fossils do not show vascular bundles in the actual fruits, only in the receptacle. Ranunculaceous fruits also may be completely parenchymatous, or possess a sclerenchymatous endocarp. In this last case, the endocarp cells are thick-walled with wavy outlines or at fruit maturity the cells are partially separated due to growth in circumference (Roth, 1977). Ranunculaceous seeds differ from those at Princeton by having a hypostase, minute embryos, and integumentary layers that may develop in a palisade-like fashion.

Fruits of the Annonaceae differ from those of the Princeton aggregate fruit in having an extensive vascular system, and a parenchymatous mesocarp (Roth, 1977). Furthermore, at fruit maturity, cells of the endocarp tend to separate from one other in a similar way to those of the Ranunculaceae. Annonaceous seeds are clearly different from the fossil under discussion since their integuments are multicellular; they sometimes possess a third integument, and are often ruminate.

Seeds of the Rubiaceae differ from seeds of the Princeton aggregate fruit since they are pachychalazal, and ruminate, (Corner, 1976a). They also have multicellular integumentary layers, some with at least one palisade layer and curved ~~or~~ coiled embryos with intricately folded cotyledons, unlike those in the Princeton aggregate fruit.

Seeds of the Dispacaceae have crushed integuments at maturity, and the outer integumentary layer is 10-15 cells thick (Corner, 1976a), contrasted to the two integumentary layers in seeds of the Princeton fruits. Finally, the seeds of the Nymphaeaceae have perisperm, a well-developed palisade and are arillate, unlike those of the fossil aggregate fruit.

The Princeton fruits shows a receptacular tissue with pith, vascular tissue and two outer cell layers surrounding the achenes. Fruits of the Rosoideae are interpreted as being appendicular and/or receptacular in origin (Roth, 1977), thus, a central pith surrounded by vascular tissue, a cortex-like tissue and epidermis can be identified in most Rosoideae fruits. This simplistic pattern is often complicated further (Bonne, 1928; Roth, 1977).

Since the achenes of the Princeton aggregate fruit are enclosed in tissue that may be interpretated as a fleshy floral cup, these fossil fruits appear to be related to the Rosaceae, Subfamily Rosoideae. The origin of the fleshy tissue enclosing the actual fruits and seeds is difficult to assess, since no developmental sequence is known. The fossil aggregate fruit cannot be regarded as a pome, since the sepals participate actively in the formation of the floral cup in pomes (e. g. *Malus*; Roth, 1977), and the sepals of the Princeton aggregate fruit are free from the fleshy tissue enclosing the actual fruits and seeds. A pome fruit as seen in cross section, has fruits and seeds located in the central region surrounded by at least two distinct parenchyma zones separated from one another by a ring of discrete vascular bundles. In the Princeton aggregate fruits, one cylinder of vascular tissue is present surrounding the pith, and sepals do not participate in the construction of the floral cup.

The origin of the hypanthium in *Rosa* is still not clear. Bonne (1928) postulated that the lower part of the aggregate fruit was receptacular, while the upper part was appendicular in origin. Later, Douglas (1944, 1957) concluded that the hypanthium in *Rosa* was the result of receptacular invagination. Whatever the origin of this floral cup, its vascular tissue is represented by recurrent bundles, making the hypanthium a heavily vascularized structure. Another characteristic of the *Rosa* hypanthium is the presence of sepals that crown the structure. In the Princeton aggregate fruits sepals are located at the base and are free for their total length from the fleshy tissue enclosing the fruits and seeds. No vascular strands are present in the receptacle tissue surrounding fruit and seed. In transverse section the hypanthium of *Rosa* is a thick, multilayered structure with at least five distinct layers and an extensive vasculature. In the Princeton aggregate fruit only three distinct cell layers are observable. Furthermore, the pith region of the fossil aggregate fruit is not present in the *Rosa* hypanthium.

The organization of the fruits of *Rubus* and *Fragaria* (Tschierske, 1886) are very similar to the organization of the Princeton aggregate fruits. The three fruits have a pith surrounded by vascular tissue, parenchymatous cortex, two to three hypodermal layers, and a single-celled epidermis. The hypodermal layers are not extensive in the fossil aggregate fruit, however, in some areas cells with smaller diameters are seen beneath the epidermis suggesting the presence of a hypodermis. The cortical tissue arrangement in the receptacle is very spongy in appearance. The arrangement of pith, vascular tissue, cortex and epidermis surrounding the fruits and seeds in the Princeton aggregate fruits are very close in organization to that of *Rubus* and *Fragaria*; therefore, its receptacular origin is certainly plausible.

In comparing the anatomy of the actual fruits and seeds of the fossil aggregate fruits with those of the two extant genera, the fossils are more similar to *Fragaria* than to *Rubus* that has a deeply wrinkled pubescent endocarp (Tschierske, 1886; Winton, 1902). Neither *Fragaria* nor the fossil fruit have a wrinkled exocarp or hairs. In the inner integumentary layer the seeds of the fossil aggregate fruits have reticulate cells as in the outer integumentary layer of *Fragaria* (Tschierske, 1886; Winton, 1902). These characteristic thickenings are not present in *Rubus* (Tschierske, 1886; Winton, 1902).

It is clear that similarities in fruit and seed morphology and anatomy of the fossil aggregate fruit to *Fragaria* indicate affinities to the tribe Fragarieae. Fruit epidermis is very similar between the two, and, although hypodermal layers are difficult to discern in the fossil, they can be seen in some sections. The next two fruit layers, represented by the vascular tissue and a crystal layer in *Fragaria*, have not been observed at all in the fossil aggregate fruit. The stony endocarp of *Fragaria* is also seen in the fossil, while the transverse fibers of the inner endocarp of *Fragaria* are represented by tangentially elongated thin-walled cells in the fossil. The seed of *Fragaria* has an outer integumentary layer characterized by the presence of cylindrical cells with reticulate thickenings and an inner integumentary layer characterized by rectangular cells with brown contents. In contrast, the seed of the fossil aggregate fruit has an outer integumentary layer of cells with dark contents and an inner integumentary layer with secondary thickenings. From this comparison it is evident that fruit and seed of both, *Fragaria* and the fossil aggregate fruit, have almost identical cell layers. However, seed integumentary layers are reversed. This difference combined with those of fruit anatomy indicate that these two fruits and seeds are probably different taxa. Another great difference between *Fragaria* and the fossil aggregate fruit is the fact that actual fruits in *Fragaria* are sitting on the receptacular tissue in small depressions, while fruits of the fossil aggregate fruit are enclosed by the receptacular tissue at maturity.

Compaŕisions with the fossil record are difficult since the only report of *Fragaria* or *Fragaria*-like fruits or seeds are those of Dorofeev (1963, 1977) from the Pliocene and Pleistocene in the USSR. These fruits are fairly large when compared to the fruits from Princeton. Another closely related genus, *Potentilla* L., has known fossil remains from the Eocene (Friis, 1985; Dorofeev, 1963, 1977). However, seed anatomy of the fossils has not been described. Extant *Potentilla* is known to retain only the outer integumentary layer at maturity (Corner, 1976a). Thus, the Princeton fossils probably represent a new taxon of the family Rosaceae, tribe Rosoideae most closely related to *Fragaria*.

### Order Myrtales

#### Family Lythraceae

#### Tribe Nesaeae

#### Subtribe Nesaeineae

#### Genus *Decodon* sp. Gmel.

#### Description

Seven fruits with enclosed seeds have been recovered from the chert. In addition to fruits, hundreds of dispersed seeds are present in the chert. Morphological variation in fruits and seeds is restricted to shape and size, and is probably related to maturity and degree of locular compression.

In transverse section the fruits are oval to globose, 5 mm tall, 4 mm wide, and 3 mm thick (Fig. 59). Four to six locules, are divided by complete septa connected to the central fruit axis (Figs. 59, 61). Each locule has between 12 and 18 seeds arranged in three to four rows with axial placentation. One fruit shows one locule full of aborted ovules (Fig. 62). However, sometimes locules with well-developed seeds have a few aborted ovules. Sepals persist at fruit maturity (Figs. 60, 62). Both sepals and fruit wall have swollen areas about 150 um in diameter (Figs. 62, 70). These areas are composed of several rows of cells 19 um in diameter (Fig. 70). In some longitudinal sections these cells are seen to be fungal hyphae forming cleistothecium-like structures. Cells of the sepals are not well-preserved; however, they appear to be thin-walled, rectangular in outline, and some of them have a few dark contents (Fig. 62). From the pedicel, at least one vascular strand goes into each sepal. The pedicel, 0.9 mm in diameter in longitudinal section, shows a central parenchymatous pith surrounded by vascular tissue, cortex with rectangular thin-walled cells (Fig. 60). Sometimes, cleistothecia similar to those of the fruit and sepals are present on the fruit axis. The fruit axis extends into the fruit for almost one half of its length (Figs. 60, 64). The fruit axis also contains a central pith with thin-walled cells (3 um thick) 26 um in diameter. It is surrounded by a ring of vascular bundles (Fig. 65). The endocarp is represented by a palisade layer of radially elongated cells, each cell of the palisade with one dark cellular inclusion (Fig. 63). The exocarp is composed of tangentially elongated cells full of dark contents. One vascular strand with helically thickened tracheids has been seen in the exocarp (Fig. 63).

Seeds, in general, have a roughly pyramidal shape with rounded corners (Figs. 59, 60, 68). Some seeds are more rounded in outline depending on the arrangement in the fruit (Fig. 71). The integument can be divided into three layers according to cell characteristics (Figs. 63, 67). The outer integumentary cells are rectangular and tangentially elongated, 22 um long x 6 um wide, and full of dark contents (Fig. 67). The middle integument is multilayered, with finely pitted, isodiametric cells averaging 25 um (Fig. 67). In some areas it is possible to distinguish in this middle layer internal and external zones, based on the amount of dark contents in cells; cells of the internal zone have more dark contents (Fig. 67). In a few cases, the raphe marks the limit between these two zones; however, it is usually not possible to make this distinction. The inner integumentary layer three to four cells thick is composed of thick-walled fibers (5 um wall thickness) with helical thickenings (Fig. 72). Rectangular thin-walled cells similar to those of the outer integumentary layer, but with fewer dark contents form a ventral germination valve (Figs. 69, 71), like that described in seeds of extant *Decodon* Gmel. (Tiffney, 1981).

The three integumentary layers are also present at the micropyle (Fig. 73). The mycropylar end of the seed is slightly elongated and narrow. Near the micropyle, and toward the dorsal side of the seed, is the hilum (Fig. 73). The raphe can be seen deep in the middle integumentary layer running from the hilum to the chalazal end of the seed (Fig. 68). This area is composed of tracheids with helical thickenings and few parenchyma cells. The chalazal end of the seed is rounded and broader than the micropylar end (Figs. 66, 68). Nucellus and endosperm cells have not been identified; however, these seeds have a small area of dark tissue at the chalazal end that may represent a hypostase (Fig. 75). In one seed this hypostase-like tissue is associated with a dicotyledonous embryo (Figs. 74,76). In one section it is even possible to distinguish a thin-walled tissue connected to the embryo proper that probably represents a suspensor (Fig. 75).

### Tribe Naseeae

### Description

One broken fruit with some associated seeds and several dispersed seeds have been found (Fig. 77). The exocarp is composed of three layers of thin-walled cells with scattered dark contents. Cell size increases towards the outside of the exocarp. The fruit endocarp is composed of two layers of thin-walled rectangular cells with dark contents and vascular tissue with helical thickenings. Cells of the inner layer tend to be smaller than those of the outer layer.

The seeds have a roughly pyramidal outline with rounded corners (Figs. 77 - 80). The integument can be divided into three layers. The outer is composed of a single cell layer of rectangular tangentially elongated, 0.12 mm long 0.30 mm wide, full of dark contents. Cell consistency appears to have been mucilage-like (Figs. 78, 81). The middle integument is multilayered with finely pitted cells, 0.45 um in diameter, that tend to be isodiametric, (Figs. 78, 81). The inner integumentary layer is very inconspicuous with only a single layer of rectangular, tangentially elongated cells. The three integumentary layers can all be seen at the slightly elongated and narrow micropylar end. The hilum is located near the micropyle and toward the dorsal side (Tiffney, 1981) of the seed, cells near the hilum are represented by dark tissue in some seed sections (Fig. 79). The raphe runs from the hilum deep into the middle integumentary layer to the chalazal end (Figs. 78, 80). This area contains tracheary elements with helical thickenings and few parenchyma cells (Fig. 80). The chalazal end of the seed is rounded and wider than the micropylar end. Nucellus and endosperm have not been identified.

## Discussion

The presence of three well-developed integumentary layers in these seeds, with the inner composed of helically thickened fibers is similar to seeds in the families Combretaceae, Lythraceae, Onagraceae, Punicaceae, Sonneratiaceae, and Trapaceae. However, these remains can be distinguished from Combretaceae since the latter has a middle integumentary layer composed of thin-walled cells, with scattered sclerotic cells, in some cases spiral or annular thickenings (Corner, 1976a). Seeds of the Onagraceae according to Corner (1976a) have no essential differences from seeds of the Lythraceae. Nevertheless, the middle integumentary layer in the Onagraceae is aerenchymatous, crushed at maturity or with some sclerotic cells (e. g. *Oenothera* Spach) (Corner, 1976a), unlike the isodiametric cells reported in the Princeton seeds. The presence of a watery translucent sarcotesta in the family Punicaceae precludes any relationship with the fossil seed. The integument in the Sonneratiaceae is very similar to at least some genera of the families Punicaceae and Lythraceae. The seed of *Sonneratia* L. is close to that of *Pemphis* Lythraceae (Tribe Lythreae) (Corner, 1976a), and it has been compared to two fossil seeds of the Lythraceae, *Enigmocarpon* Sahni and *Sahnianthus* Shukla (Mahabale and Deshpande, 1957). The larger size and general outline of the seeds as well as the presence of a large, curved embryo with short contorted cotyledons in this family negates a relationship to the Princeton fossil seeds. The other sonneratiaceous genus, *Daubanga* Buch. *et* Ham., has a minute and straight embryo with flat cotyledons, and its inner integumentary layer is composed of pitted, lignified fibers (Corner 1976a), unlike the larger embryo and helically thickened fibers in the fossil seeds. The monotypic family Trapaceae shows a multilayered outer integumentary layer, unlike the fossil seed, thus, leaving the Lythraceae as the most likely affinity for the fossil seeds.

According to Koehne (1903) the study of the family Lythraceae began as early as the middle 1700's; however, fruit and seed anatomy were first described late in the 1800's (Koehne, 1877, 1880). Since that time different biological aspects of the family have been reported. In addition to Koehne (1885), Graham (1964) studied the Lythraceae of the United States, Mauritzon (1934, 1939) described embryological aspects of the family, Joshi and Venkateswarlu (1935a, 1935b, 1936) and Joshi (1939) added embryological studies, and Graham and Graham (1971) and Eyde (1972) reviewed the geologic history of the family. Anatomical description of seeds was first carried out by Netolitzky (1926b) and later Corner (1976a) added the descriptions of a few more genera. Recently Tiffney (1981) described the seed of extant *Decodon verticillatus* (L.) Ell. in detail and compared it with fossil *Decodon* and closely related genera like *Microdiptera* Chandler, *Mneme* Eyde and *Alatospermum* Chandler.

Tiffney (1981) discussed the fossil seed and fruit record of the family and put the remains into three groups. The first group fits within the tribe Lythreae; its representatives are *Ammonia lakensis* Chandler (Chandler) (Lower Eocene), *Palaeolythrum bournense* Chandler (Middle Eocene), *P. gailense* Chandler (Pliocene), and *Lythrum* L. (Pliocene). The second group includes members of the tribe Nesaeeae, including *Alatospermum lakense* Chandler (Early Eocene), *Ministerocarpum alatum* Reid and Chandler (Middle Eocene), *Lagerstroemia indica* L. (Pliocene), and *Decodon* Gmel. (Late Eocene), *Microdiptera* Chandler (Late Eocene) and *Mneme* Eyde (Late Eocene) that together with *Alatospermum* Chandler (Early Eocene) form a morphological complex. Tiffney's third group included those carpological remains not assignable to either section. This group includes, *Crammeria trilocularis* Reid and Chandler, *Pachysperma quinqueloculare* Reid and Chandler, and *Tamesicarpum polyspermum* Reid and Chandler all from the latest Paleocene and Early Eocene, and *Enigmocarpon parijai* Sahni from the Paleogene.

The fossil pollen record of the family goes back to the Upper Eocene (Müller, 1981); however, it is not as diverse as the seed and fruit record. Only three types of pollen grains have been referred to genera already reported either by seeds or fruits, *Lythrum*, *Lagerstroemia* and possibly *Decodon* (Muller, 1981).

Corner (1976a) described the lythraceous seed as minute to small and subcylindrical to trigonous or pyramidal with a convex base (outer end), or of medium size and winged or by extension of the chalazal end of the raphe, exalbuminous, and exarillate. The integument is more or less multicellular in the larger seeds. The outer layer of the seed is a palisade of rather wide cells, is composed of cuboid and often somewhat compressed cells, or cuboid cells with an invaginated musilagenous hair. The middle integument often has two layers, an outer composed of large cells that are thin-walled, pitted and lignified and an inner densely sclerotic region. Furthermore, the middle integumentary layer may be wholely sclerotic or the sclerotic layer may be situated in the outer part. Sometimes, the inner cells of the middle integumentary layer have thickened, pitted and lignified radial walls and often contain crystals. The inner integumentary layer is a continuous hard palisade of narrow, longitudinally elongated tracheids with spiral, annular, scalariform or sub-reticulate thickenings, or it may be very narrow containing thick-walled fibers without visible pitting. Integumment of the fossil seeds with a single celled outer integument, sclerotic middle integument, and fibers with helical thickenings in the inner integument, follow the lythraceous integumentary pattern.

Detailed fruit anatomy in the Lythraceae has not yet been described. However, the presence of complete or incomplete septa is used to distinguish the two tribes. In Tribe Lythreae (e.g., *Ammania*, *Palaeolythrum*), septation is not complete to the apex, while in the tribe Nesaeeae (e.g. *Decodon*) it is complete to the apex. Since the fossil fruit has complete septa, it belongs to the tribe Nesaeae that has been divided into two subtribes based mainly on the presence or absence of winged seeds: Nesaeineae and Lagerstroemiinae (Koehne, 1903). Eight living non-winged genera are included in the subtribe, Nesaeineae, *Crenea* Aubla., *Nesaea* Comm., *Heimia* Link et Otto, *Decodon* Gmel., *Grisela* L., *Adenasia* H.B.K., *Tetrataxis* Hook., and *Glonoria* Jacq., and two winged genera are included in the subtribe Lagerstroemiinae, *Lagerostroemia* L., and *Lawsonia* L. *Lagerostroemia* is distinguished from the fossil seed by its folded cotyledons; and *Lawsonia* differs by having an inner integumentary layer composed of narrow longitudinal fibers with rather coarse pitting (Corner, 1976a).

*Grisela* has a two-locular fruit, unlike the four to six locules in the fossil fruit. The fruit of *Nesaea* has an operculum, and the fruits of *Crenea* and *Ademaria* are indehiscent, unlike the fossil (Koenhe, 1903). Koehne (1903) and Sahni (1943) characterized *Tetrataxis* and *Glonoria* as having septifragal capsules leaving the septa attached as wings on the placenta, unlike the fossil fruit. *Crenea* has a large elongated seed with a sub apendicular apex.

*Decodon* and *Heimia* are the two genera with more similarities to the fossil remains. *Decodon verticillatus* fruits and seeds were sectioned during this study and compared to the fossils. The fruit is quite similar, and composed of an endocarp of quadrangular to slightly radially elongated cells. The exocarp has tangentially elongated cells with dark contents, as in the fossil fruit. Seeds of extant *Decodon* are very similar to those of the fossil fruits. Three integumentary layers can be easily recognized, the raphe passes through the middle integumentary layer as in the fossil, and the seed has a germination valve. (For a detailed description of the seed of extant *Decodon*, see Tiffney, 1981.) However, if a layer by layer comparison is made between extant and fossil seeds it is evident that the outer integumentary layer of *Decodon verticillatus* is more radially elongate while in the fossil seed cells of this layer are mainly tangentially elongated. In addition, the inner integumentary layer is very conspicuous in *Decodon verticillatus* and not so in the fossil seed. Size is also a difference between these two seeds, *Decodon verticillatus* is almost three times larger than the fossil seed. The presence of mature embryos and well developed integuments precludes differences due to developmental stage.

The last genus to which the fossil may be related is *Heimia*. Unfortunately neither its fruit nor seeds have been described in detail. From Koehne's (1903) description and illustrations this genus seems to be closely related. Furthermore, Sahni (1943) describe the fruit as thin and subcoriaceous, resembling that of the fossil.

Similarities of the fossil seed with those of *Decodon verticillatus* clearly indicate that it is closely related. Relating the fossil to *Heimia* must wait until more information about the fruit and seeds of this extant genus is available.

Among the fossil lythraceous carpological remains, a close relationship of the Princeton chert fossils with *Decodon, Alatospermum, Mneme,* and *Microdiptera* is evident. From this group only *Decodon* lacks wings, thus, making it more similar to the fossil under discussion. Unfortunately, there is not a detailed anatomical description of a fossil *Decodon* with which to compare the Princeton seeds. Friis (1985) showed some scanning electron micrographs of *Decodon gibbosus* (Reid) Reid from which it is possible to suggest differences like the presence of crystals and smooth inner integumentary layer, unlike the fossils from the Princeton chert.

These new fossil remains probably represent the tribe Nesaeeae, and are closely related to *Decodon*. From a biostratigraphic point of view, this *Decodon* fruit is the oldest described unwinged seed of the *Alatospermum-Decodon-Mneme-Microdiptera* alliance (Tiffney, 1981). Lythraceous carpological remains have been thought to be restricted to Europe and Asia. In North America Tiffney (1981) reported the presence of *Microdiptera donata* (Holy) Tiffney from the Oligocene Brandon Lignite, Vermont. Other North American megafossil remains are *Decodon* leaves from the Miocene Kenai Group, Alaska (Wolfe and Tanai, 1980). Wolfe and Tanai (1980) noted the probability that *Myrtus oregonensis* Lesq. from the Miocene of California may represent a species of *Decodon*, and pointed out the occurence of the same or closely allied species in the Miocene Collawash flora of Oregon. Wolfe (pers. comm.) reports that a *Decodon*-type leaf has been collected from the Tulameen Road locality (Allenby Fm.) near Princeton, B.C. The pollen record of the family is not very common in North America. Graham and Graham (1971) mention the presence of *Cuphea* from the Middle Miocene of Alabama and Mexico. Thus, lythraceous remains in North America are more widespread than previously expected; however, as the Princeton fossils illustrate, relationships to the extant Lythraceae require further detailed study of extant genera.

Comparing the environmental conditions of extant *Decodon* and those where fossil assemblages have been reported by Reid (1920a, 1927) Chandler (1960) and Dorofeev (1963) among others, the presence of *Decodon* plants in tropical to subtropical environments like that represented at the Princeton chert locality, is well supported.

In the large lythraceous seed the presence of three integumentary layers, raphe in the middle integumentary layer and micropyle area with the three integumentary layers, fits very well with characteristics of the family Lythraceae, described above.

The fossil *Decodon* sp. is about one third of the size of this seed and differs in having an outer integumentary layer composed of polyhedral, tangentially elongated cells, a more sclerotic middle integumentary layer and an inner integumentary layer composed of small, tangentially elongated thick-walled cells. The absence of mucilaginous hairs in the outer integumentary layer precludes any relationship with *Ammania, Cuphea, Lythrum,* and *Pemphis* in the Lythraceae (Corner, 1976a).

Corner (1976a) reports the presence of a palisade of rather wide cells in *Lafoensia, Lagerstroemia,* and *Pemphis,* thus, making these genera different from the large lythraceous fossil seed from Princeton. According to Corner (1976a) *Lafoensia, Lagerstroemia, Pemphis,* and *Lawsonia* have an inner integumentary layer composed of tracheids with spiral, annular, scalariform or subreticulate thickenings. *Lythrum* has thick-walled fibers with pits, and *Ammania* has thick-walled cuboidal cells unlike the large lythraceous fossil seeds.

For some seeds of this family no detailed description is available. However, Koehne's (1903) general description of genera can be used. Small seeds, about the same size as *Decodon* or smaller, are reported for *Rotala* L., *Woodarfia* Salisb., *Pleurophora* D. Don, *Nesaea* Comm., *Heimia* Link et Otto, and *Tetrataxis* Hook. f. *Pleurophora* can further be distinguished from the large lythraceous fossil seeds, by the presence of dense secretory hairs on the outer integument, and *Tetrataxis* by its large size and oblong shape. The presence of wings in the seeds of *Diplusodon* Pohl, *Physocalymma* Pohl, and *Crenea* Aubl. eliminates these genera from consideration. Seeds with an outline ranging from circular to ovoid or subglobose are known for *Ginoria* Jacq., *Adenaria* H. B. K. and *Grislea* L., and cannot be compared to the pyramidal fossil seed. Unfortunately, a description of the seed of *Galpinia* N. E. Br. is not available, thus, comparisons with the fossil seed await work on the extant genus.

In size and shape the large lythraceous fossil seeds resemble *Lawsonia*. The outer integumentary layer of both, *Lawsonia* and the large lythraceous fossil seed, in surface view display polygonal to irregularly faceted cells. The main difference between these two is in the structure of the inner integumentary layer. Since this layer has been difficult to observe in the fossil seeds, a final comparison is needed when more fossils are found in the chert. However, it appears that if the large lythraceous fossil seeds do not represent a fossil taxon related to *Lawsonia*, they are not far from one another evolutionarily.

## Order Rhamnales

### Family Vitaceae

### Vitaceae # 1

### Description

Two seeds, 2.5 mm x 2.6 mm in transverse section with well-developed ruminations are known from the chert. Ruminations display a "W"-shape in cross section, with the central arm of the "W" being taller than the two lateral arms (Fig. 82). The chalaza is located opposite the central arm of the seed. (Fig. 82).

The integument is composed of five integumentary layers, except at the chalazal end. The first and outermost integumentary layer is composed of tangentially elongated cells 120 um x 26 um with dark contents (Fig. 83). The second integumentary layer is composed of thick-walled radially elongated cells. Poor preservation of the seed makes this layer appear multicellular; however, closer observation shows that it composed of a single cell layer with unevenly distributed dark contents (Fig. 85). The cells of this second integumentary layer vary in size according to their position; near the chalaza, cells reach 450 um x 45 um, while in the innermost part of the rumination, they are only 180 um x 18 um. A third integumentary layer is composed of fibers with helical thickenings. In the specimen described here, it is not well-preserved and when present it is difficult to distinguish. The fourth integumentary layer is not preserved. Its presence is suggested by the space left between integumentary layers three and five. At the chalazal end, between layers three and five a space is also present (Fig. 84). The innermost and fifth integumentary layer is composed of a single layer of tangentially elongated cells, 90 um x 34 um, also with dark contents (Figs. 84, 85). No identifiable endosperm or embryo tissues are preserved.

The chalazal area, develops as a perichalaza. It has a completely different histological arrangement compared to the rest of the integument and is composed of about 12 rectangular to oval thick-walled cells 10-15 um in diameter full of dark contents. At the chalazal end, cells form a slight protuberance (Fig. 84). The central part of the chalazal area is not well preserved, but was probably occupied by vascular tissue (Fig. 84). The inner integumentary layer is composed of circular to polyhedral cells, 15 um to 20 um in diameter with walls almost 8 um thick.

Vitaceae # 2

### Description

One ruminate seed, 3.4 um x 3.6 um in diameter, with a well-developed "W"-shape has been found. The central arm of the "W" is slightly longer than the two lateral arms. (Fig. 86). The chalaza is located as in other vitaceous seeds opposite to the central and larger arm of the "W" (Fig. 86). The integument is composed of five layers, except at the chalazal end where it show three layers. The first and outermost integumentary layer is composed of rectangular to polyhedral cells 10 ~~um~~- 32 um in diameter, with walls 3 um thick (Fig. 89). The second integumentary layer is composed of thick-walled polyhedral to isodiametric cells. Poor preservation makes it difficult to determine the exact number of cell layers in this layer; however, it appears to be 30 cells thick at the tips of the "W" arms to 13 cells thick in the deepest area of the rumination (Figs. 88, 90). A third integumentary layer is well-preserved in some areas and contains a single layer of fibers with helical thickenings (Fig. 87). The fourth integumentary layer is not preserved, but its presence is indicated by the space left between integumentary layers three and five. The innermost integument of this seed is a single layer of tangentially elongated cells with dark contents 20 um x 30 um in diameter (Figs. 87, 88). No endosperm or embryo tissues have been preserved.

The chalazal area, that develops as a perichalaza, has a different histological arrangement compared to the rest of the seed. Poor preservation will not allow a detailed description, however, it is possible to say that it is divided into at least three layers (Fig. 86). The first layer has cells similar to those of the second integumentary layer in the rest of the seed. The area lacking tissue (represented by a space) represents position of the raphe (Fig. 86). Next to this raphe, a band of dark tissue with different histological organization from the previous two layers is present.

Vitaceae # 3

### Description

One seed, 4.5 mm x 2 mm, with a slight "W" shape in transverse section is known from the chert. Ruminations cannot be seen in a single section, due to the oblique orientation of the sections (Fig. 91). The seed is broken on the chalazal side and along one of the lateral arms. The two lateral arms of the "W" are somewhat larger than the central arm, that is very wide. A wide chalazal area is located opposite to the central arm of the "W" (Fig. 91).

The integument is composed of five layers, except at the chalazal end where it has fewer. The first integumentary layer has rectangular to polyhedral thin-walled cells. The second integumentary layer is composed of four to six more or less rectangular thick-walled cells 35 um in diameter with large lumens (Fig. 93). A third integumentary layer contains fibers with helical thickenings. Since sections are oblique it is difficult to estimate the actual number of cell layers in this part of the integument, but it is certainly multilayered (Fig. 92). In cross section, these fibers appear to be two or three cells wide, thick-walled (5 um), and tend to be circular in outline (Fig. 93). The fourth integumentary layer is not preserved. Its presence is suggested by the space left between layers three and five. The inner-most and fifth integumentary layer of this seed is composed of radially elongated sclereids 150 um x 70 um in diameter (Fig. 94). In the seed cavity, fragments of irregularly-shaped cells containing tracheids with helical thickenings are preserved (Fig. 95).

The chalaza end of the seeds is slightly broader than the rest of the seed but does not form an extensive perichalaza as in the other two vitaceous seeds. Three different parts can be distinguished. The outermost layer contains cells (eight cells thick) similar to those of the second integumentary layer. The second part of in the chalaza is occupied by a space, representing the raphe area. This part is surrounded by cells similar to those of the second integumentary layer. Finally, the third part of the chalaza has small, oval to polyhedral cells, arranged in two to three rows. These are followed by cells of the third integumentary layer.

## Discussion

Studies of seeds with ruminations (ingrowths of the integument) were first carried out by Gray (1879) and later by Periasmay (1959, 1961, 1962a, 1962b, 1966). Since then this integument type has been reported in 30 families of dicotyledons, three families of monocotyledons and one gymnosperm (Periasmay, 1959). Since the three seeds described here show definite ingrowths or infoldings of the integument, the integumentary tissue is more than one layer thick and the integuments are not vascularized in the area of ingrowths, these seeds can be said to have the "*Annona*" type of rumination (Periasmay, 1962b). Within this group, Periasmay (1962b) lists eight families: Annonaceae, Aristolochiaceae, Degeneriaceae, Dipterocarpaceae, Ebenaceae, Menispermaceae, Vitaceae, and Palmae. Since the seeds have two ruminations, one at each side and in front of the raphe, and they are perichalazal, they are similar to seeds of the Vitaceae. Their integumentary structure strengthens this relationship.

Annonaceous seeds are bitegmic or tritegmic (Corner, 1949). In these seeds, the area corresponding to the second integumentary layer is composed of cuboidal, radially elongated or shortly elongated thin-walled cells (Corner, 1976a). Furthermore, the area occupied by integumentary layers three to five is multicellular in the Annonaceae (Corner, 1976a). In published descriptions of annonaceous seeds by Netolitzky (1926b), Corner (1949, 1976a, 1976b), and Periasmay and Swamy (1961), the number and orientation the ruminations in the Annonaceae differ from those in the fossil seeds.

Corner (1976a) described the area occupied by integumentary layer two in seeds of the Aristolochiaceae with cuboidal to radially elongated cells, that have thin or variously thickened, pitted and lignified walls, even as a compact palisade. He also indicated that aristolochiaceous seeds are not perichalazal, unlike the fossil seeds described here. Degeneriaceous seeds are composed of a palisade of radially elongated cells and clusters of two to 10 resin cells opposite the ruminations, in the area occupied by integumentary layers one and two of the fossil seeds (Corner, 1976a).

In the family Dipterocarpaceae the presence of extensive vascularization either in the chalaza, in the topographic area occupied by layers one and two in the fossil seeds, or in both areas, suggests the presence of pachychalazal seeds (Corner, 1976a), while the three fossil seeds are perichalazal seeds.

Corner (1976a) reported that seeds of the family Ebenaceae have three integumentary layers and are not perichalazal, making them different from the fossil seeds. The Menispermaceae generally have curved seeds with unspecialized and crushed integuments. Sometimes only the area occupied by integumentary layers one and two of the fossil seeds are found in the menispermaceous seed. If persistent at maturity, this area is composed of a layer of tabular cells with thin, lignified walls, thus, the fossil seeds have a different anatomical arrangement.

Vaughan (1970) described two integumentary layers in palms, the outer one composed of spindle-shaped cells and the inner one composed of isodiametric to slightly elongated thin-walled cells containing pigments (yellow-brown contents), unlike the three fossil seeds.

Finally, seeds of the family Vitaceae are perichalazal, have five integumentary layers and one to three ruminations infolding opposite and lateral to the chalaza (Berlese 1892a, Periasmay 1962a, Corner 1976a). The first integumentary layer (sometimes called sarcotesta), is composed of thin-walled cells that may collapse at maturity. The second integumentary layer (sometimes referred to as endotesta) is woody, and two to six cells thick or more near the base of the raphe. The third integumentary layer referred to by Corner (1976a) as "outer epidermal tegmen" consists of a compact layer of short, tangentially elongated, lignified tracheids with spiral thickenings. Periasmay (1962a) states that integumentary layer number four contains "cells that during early development undergo slight radial elongation and become rich in contents, but become completely crushed in the mature seed and eventually disappear". He also mentions the presence of abundant tannins in integumentary layer number five. Thus, anatomically the three fossil seeds appear to be typical vitaceous seeds.

Anatomical studies of vitaceous seeds go back to at least the 1880's (Portes and Ruyseen, 1886). However, it was not until 1892, when Berlese (1892a, b) reviewed of some genera and species that an accurate description of the internal features of these seeds was made. Later, Netolitzky (1926b) also added to the knowledge of vitaceous seed anatomy. More recently, Periasmay (1962a) contributed to the understanding of these seeds through a developmental study of various genera. Nair and Bajaj (1966) described seed anatomy and development of *Cyphostemma* (Planch.) Alston (placed in synonymy with *Cissus* L. by Sussenguth, 1953). Finally, Vaughan (1970) discussed *Vitis* L. seed anatomy and Corner (1976a, 1976b) summarized the structure of the genera *Ampelocissus* Planch., *Ampelopsis* L.C. Rich, *Cayratia* Juss., *Cissus* L., *Cyphostemma* (Planch.) Alston, *Leea* L., *Parthenocissus* Planch., *Tetrastigma* Planch., and *Vitis* L. The following comparison is based on these works, however, since information is not available on the genera *Pterisanthus*, *Clematicissus*, *Landuteia*, *Quinaria*, and *Roicissus*, it must be clear that any conclusions must be preliminary, and final results need the compilation of information on these genera.

According to Periasmay (1962a) the extent of perichalazal growth and related change in the position and shape of rumination ingrowths as well as the distribution of raphides in the integument and the number of layers in the mechanical tissue serve as characters of taxonomic value. It is clear that by looking at the final shape and position of ingrowths that the seed described as Vitaceae # 3 is different from the remaining two seeds. In addition, integumentary layer two that forms the mechanical layer of the integumentary tissue of Vitaceae # 3 and Vitaceae # 2, is composed of similar kinds of cells in both seeds, even though they have markedly different numbers of cell layers. Differences between Vitaceae # 3 and Vitaceae # 1 seeds are the number of cell layers as well as cell shape of integumentary layer two.

Comparing Vitaceae # 1 and Vitaceae # 2 seeds it becomes evident that some differences are present in shape and position of the ingrowths. However, these differences are not as notable as between seeds types one and three. The second integumentary layer in both seeds is different in number of cell layers and cell shape. Therefore, these three seeds probably represent different taxa.

The Vitaceae # 1 seed has an outline in transverse section similar to that shown for *Vitis* and *Cissus* by Periasmay (1962a). However, drawings of *Parthenocissus* by Berlese (1892b) more closely resemble this fossil seed. They are even similar in the length the central arm of the "W" compared to the lateral arms. Even arm shape in Berlese's (1892b) figure 46 looks identical to those in the fossil seed. Tiffney and Barghoorn (1976), however, noted the degree of morphological variability within the seeds of modern Vitaceae and stated that shape and morphology of seeds from the same source plant can be influenced to a remarkable degree by the number of seeds per fruit.

The integument that most closely resembles that of Vitaceae # 1 is that of *Tetrastigma* Planch. that has three or four slightly radially elongated cell layers, and *Ampelocissus* Planch. with one or two layers of slightly radially elongated cells. Further information is needed, however, on extant vitaceous seeds to make closer comparisions.

The Vitaceae # 2 seed also has an outline in transverse section similar to *Vitis* and *Cissus*. In addition, the length of the three arms of the "W" closely match that reported in Periasmay's (1962) figure 25 of *Cissus*, but the general outline looks more like *Vitis* (Periasmay 1962b, fig. 22). Integument histology is very similar to *Cissus* L. and *Leea* L., especially the second integumentary layer. This layer in the fossil seed contains slightly rounded to rectangular cells in a palisade with the cells abutting integumentary layer number one being slightly larger. *Cissus* and *Leea* have this same feature; however, the number of cell layers in this integumentary zone in the fossil seed (13-30) and those of *Cissus* (3-5) and *Leea* (4-5) is markedly different.

The Vitaceae # 3 seed has an outline in transverse section similar to *Cayratia* Juss. as illustrated by Periasmay (1962a) and some resemblance to *Ampelocissus* Planch. as illustrated by Berlese (1892b). Unfortunately, the sections of this seed are oblique, making comparisions difficult. Comparing the second integumentary layer in these three seeds, the fossil seed is seen to have four to six layers while *Cayratia* has two cell layers and *Ampelocissus* has one or two cell layers. In the fossil seed, integumentary layer number three is conspicuous, and multicellular while in the extant genera it is only one cell layer thick.

Tiffney and Barghoorn (1976) noted that vitaceous seeds are well represented in the fossil record. They list more than 116 published reports of seeds ranging in age from lower Eocene to Pleistocene. The most frequent genus reported is *Vitis* (56%) and the remainder include: *Ampelopsis*, *Ampelocissus*, *Cayratia*, *Parthenocissus*, and *Tetrastigma*. Recognition of a large number of fossil vitaceous species from a single assemblage by Chandler (1961, 1962) who described 21 species from the London Clay and 18 from the Pipe Clay of southern England, is partly believed to represent ontogenetic, phenetic and preservational variation (Tiffney and Barghoorn, 1976). It is important to mention as Kirchheimer (1938, 1939, 1957) pointed out that it is not always possible to assign fossil seeds to modern species, though they may be related. The large number of described species probably reflects a more diverse vitaceous assemblage in the past. Because of this diversity and the inability to distinguish between modern species, Kirchheimer (1938, 1939, 1957) established two form-species: *Vitis teutonia* A. Braun that includes all vitaceous seeds with a smooth surface (*Cissus*, *Parthenocissus*, *Vitis* subgenus *Vitis*, and some *Ampelopsis*), and *Vitis ludwigii* A. Braun that includes vitaceous seeds with a furrowed or rugose dorsal face (*Tetrastigma*, *Ampelocissus*, *Vitis* subgenus *Muscadinia* and some *Ampelopsis* (Tiffney and Barghoorn, 1976). Comparing the three fossil seeds to Kirchheimer's (1938, 1939, 1957) form-species, it seems that Vitaceae # 1 and Vitaceae # 2 seeds would be referred as *Vitis teutonica* while Vitaceae # 3 seed would be referred as *Vitis ludwigii*.

Tiffney and Barghoorn (1976), however, did not accept this scheme, stating that, indeed, it was possible to determine extant material to genus and sometimes to species levels. So they followed other authors like Krausel (1920), Miki (1956) and Lancucka-Srodoniowa (1966) in identification to the most similar modern genus, and where possible species.

The Princeton vitaceous seeds show that by the Middle Eocene at least some vitaceous seeds were different in internal anatomical characteristics when compared to their extant relatives. Tiffney and Barghoorn (1976, figures 16 and 12) illustrated integuments that they refer to the genus *Vitis*. However, if these illustrations are compared with the description and illustrations of extant genera by Berlese (1892b), Netolitzky (1962b), Periasmay (1962a) or Corner (1976a, 1976b) it is not possible to accept these two seeds as members of the extant *Vitis* complex. On the other hand, Kirchheimer (1938) shows two photographs of fossil vitaceous integuments with a more similar organization to that seen in the extant genus. Nevertheless, fossil seeds seem to have to many cell layers when compared to extant material. The following questions still remain: 1) To what extent does integumentary anatomy reflect taxonomic variability? 2) Is seed external morphology more suitable than internal anatomy for taxonomic purposes?, and 3) Were vitaceous seeds actually more diverse during the Eocene? Or 4) are the differences cited merely preservational biases?

Netolitzky (1926b) and Corner (1976a) discussed the advantages of using integument anatomy as a taxonomical tool. Both agree that it is in general a very useful tool in taxonomy. However, they pointed out that the use of integument anatomy will vary with the family in question. For example, the taxonomy of the family Nymphaeaceae is based mainly in integument anatomy, but the families in the order Malvales are almost impossible to distinguish using only integument anatomy. With respect to the family Vitaceae, both agree in that integument anatomy is a very useful taxonomic tool. This is re-enforced by the developmental study of vitaceous seeds done by Periasmay (1962a). Tiffney and Barghoorn (1976) noted, as stated above, that shape and morphology of seeds from the same source plant can be influenced to a remarkable degree by the number of seeds per fruit. Thus, seeds with similar external morphology need internal anatomical investigation for a correct determination. The presence of three new seed types at Princeton adds to the diversity of the Vitaceae during the Eocene, thus supporting Tiffney and Barghoorn's (1976) suggestion that this family was much more diverse in the past.

## III. Class Liliopsida

**A. Subclass Arecidae**

Order Arales

Family Araceae

Tribe Lasioideae/Monsteroideae

Description

The seed described here is the most conspicuous type in the Princeton chert. Hundreds of dispersed seeds occur. Unfortunately, no clear evidence of a fruit was found. Seeds are occasionally arranged in clusters with some surrounding tissues suggesting fruit wall, but this structure could not be confirmed.

Seeds are spiny and reniform in longitudinal section (Fig.97). The micropylar region in longitudinal section is elongated and narrower than the rest of the seed (Figs. 96, 97). The chalazal area is also narrower when compared to the central part of the seed cavity; but is rounded at its base (Figs. 97, 106). The raphe is located between the micropylar and chalazal areas in the concave side of the seed, the hilum is next to the micropyle. Vascular tissue in the raphe is represented by tracheids with helical thickenings (Fig. 111). In most seeds the raphe is represented by a lighter colored area or it is not preserved at all (Figs. 97, 100). In transverse section the seed shows spines and ridges, and either one, two or three circular to oval internal cavities depending on the plane of section. If the seed section is cut above the raphe area a single more or less oval cavity is seen. (Fig. 98). As the sections near the raphe area the cavity changes in outline from oval to a figure eight (Fig. 99). Finally, if the section crosses the raphe, three individual circular to oval areas will appear. The central one represents the raphe. It is larger and more oval than the two lateral ones, that tend to be circular (Fig. 100). One of the circular areas represents the micropylar area, the other the chalazal area. Seeds are reflexed almost 140°, and measure 2 mm high, 3.5 mm wide, and 1 mm thick. The length of the spines varies; the larger ones are about 0.8 mm long while the smaller ones look like small protuberances about 0.1 mm long (Fig. 96, 97, 99). Morphological variation is very common in the spine morphology of these seeds. These can vary seed by seed or with the plane of section. In three dimensions seeds are symmetrically to slightly asymmetrically reniform, the surface has spines and ridges that tend to be in parallel rows on the convex side of the seed.

All integumentary sclereids are morphologically similar in appearance; however, they are divided into inner and outer layers according to cell characteristics. The inner layer has thick-walled cells, 15 um in a diameter, and is less conspicuous than the outer layer that is composed of thin-walled cells with a diameter of 23 um. Cells in the raphe area have even thinner cell walls (1.5 um) and larger diameters (27 um) (Fig. 109). Cells of both, the inner and outer integument are finely pitted, and tend to be arranged in radial rows (Figs. 99, 100).

The outer layer of integument has scattered circular to oval lysigenous spaces covered by a cuticle (Fig. 101) that may represent raphide sacs like those described in *Pistia* L. (Araceae) (Friis, 1985). They are situated near the periphery of the seed, mostly between spines and ridges. The micropylar apex is delimited by a single layer of thin-walled integumentary cells, that form a convex pyramid-like structure (Figs. 102, 104). The micropyle proper is a small aperture at the tip of the pyramid-like structure (Fig. 104).

Nucellus is present inside the integument and is fused almost all the way to its apex. Nucellar cells are rectangular, 98 um x 67 um (Figs. 103, 107). At the chalazal end, the nucellus in most seeds is three to four layers thick (Fig. 106); it thins toward the raphe (Fig. 103). At the micropylar end it is free from the integument (Fig. 107). In most seeds nucellar cells appear without contents with a well defined outline; however, at the micropylar end, they are sometimes crushed and appear to have dark contents (Figs. 104, 105).

The endosperm is represented by nearly cuboidal cells (averaging 17 um x 17 um x 12 um), that are full of dark contents (Figs. 105, 108). The central part of the seed cavity is occupied by a monocotyledonous embryo. Most embryos are represented by cells with brown contents (Fig. 108), others are invaded by fungal hyphae (Fig. 98). Few of them show a clear cellular pattern (Fig. 110). In a seed transverse section the embryo shows a single cotyledon, shoot apex and root apex regions (Fig. 110). The shoot apex is located in a notch at the level of the cotyledonary node (Figs. 112, 113). The cells of the notch at the cotyledonary node are rectangular in outline (Fig. 113). The hypocotyl shows protoderm, ground tissue, and vascular tissue. Vascular tissue in the hypocotyl contains tracheids with helical thickenings (Fig. 115). The root apex is surrounded by rectangular cells of the root cap (Fig. 114). Where cells of the cotyledon are preserved they appear rectangular (Fig. 115).

## Discussion

This fossil campylotropous, reniform seed, bearing spines and ridges, with an integument composed of thick and thin walled sclereids in parallel rows, lysigenous spaces that may represent raphide sacs, and a monocotyledonous embryo, clearly belongs to the family Araceae.

Studies of the family Araceae began during the middle 1700's (Engler, 1920a). Since then, a great amount of literature has accumulated; however, new information is still adding important knowledge to the biology of the family. In recent years anatomical contributions by French (1985a, 1985b, 1986) on patterns of the endothecial wall thickenings, French and Tomlinson (1980, 1981a, 1981b, 1981c, 1981d, 1983, 1984) on stem vasculature, and Grayum (1984) on palynology, have been important in reevaluating the classification scheme of the family. Other important recent works that create a more complete concept of the family are those of Hotta (1971) who discussed the general features of the family, Blanc (1977a, 1977b, 1978, 1980) who discussed the patterns of branching stems of the family, Madison (1977) who reviewed the North American genera and Madison and Tiffney (1978) who discussed the tribe Monsterae. Based on this new information, Grayum (1984) and Bogner and Nicholson (1986) have proposed some changes to the classification.

All of the works mentioned above were based mainly on observations of extant plants. The araceous fossil record is a large one; nevertheless, not all reports are now accepted as valid ones (Crepet, 1978, Müller, 1981). The pollen record of the family (Tribe Monsterae) goes back to the Upper Miocene, (Müller, 1981). On the other hand, the megafossil record of the family shows that seeds of the tribes Monsterae, Lasieae and Pothoideae, and subfamily Pistoideae were present by the Oligocene (Reid & Reid, 1915; Nikitin, 1944; Dorofeev, 1958, 1963; Rasky, 1964) and that leaves of the tribe Philodendreae and spadices of the tribe Acoreae were present by the Middle Eocene (Dilcher and Daghlian, 1977; Crepet, 1978).

Studies on seed anatomy and morphology began in the middle 1800's, but they focused more on embryological aspects. Engler (1905, 1911, 1915, 1920a, 1920b), Engler and Krause (1908, 1912, 1913, 1920), and Krause (1908, 1913) gave a general description of the seed at family and subfamily levels, with specific comments, at the level of genus and species. They also used the absence or presence of endosperm as a generic character. Since then, no comprehensive work has been published on seed anatomy and morphology, but some isolated descriptions are available. Buell (1935) described the seed of *Acorus* and Madison and Tiffney (1976) reviewed the morphology and fossil record of the seeds of the tribe Monsterae. More recently, Friis (1985) characterized the fruit of extant Araceae as in general a berry with one to many locules. Seeds, are anatropous, campylotropous or orthotropous, with one to many in each locule (Friis, 1985). Seeds are bitegmic, usually with well developed outer integument, and many genera have raphide sacs. The integument may be smooth, rugose or spinose, and most cells of the integument tend to be isodiametric to polyhedral; however, some are elongated, with finely pitted walls. The number of integumentary layers varies from two to three in different genera.

At the subfamily level, the presence of spines and ridges on seeds, allow inclusion in either in the Monsteroideae or in the Lasioideae. By using only external characters to distinguish seeds with the above characteristics Kirchheimer (1957) and Dorofeev (1963, 1970) had great difficulties due to similarities with some seeds of the Leguminosae and Malvaceae. Madison and Tiffney (1976) discussed this problem in relation to the climatic affinities of the floras associated with the fossils.

Madison and Tiffney (1976) noted that from the twelve Tertiary species attributed to the Monstereae based on seeds, only four were actually assignable to this subfamily (*Epipremnum crassum* Reid & Reid, *E. ornatum* Reid & Chandler, *E. uralense* Dorofeev, and *Epipremnum* sp. Reid & Reid). From the remaining species, three were assigned to the subfamily Lasioideae (*E. cristatum* Nikitin, *E. rugosum* Dorofeev, and *E. visimense* Dorofeev), one to the subfamily Pothoideae (*Araceites hungaricus* Rasky), and the remaining taxa were referred to as of uncertain affinity (*A. parisiensis* Fritel, *A. fritelli* Berry, *Acoropsis minor* Conwentz, *Cytospermites hirdwellensis* (Chandler) Bogner, *E. reniculum* (Ludwing) Kirchheimer, *Epipremnum* sp. 3 Nikitin, and

*Aracispermum* Nikitin. This division of the fossil Monstereae (*sensu lato*) makes it clear that since spiny seeds belong to the subfamily Lasioideae, the fossil seed described here would be placed in this same subfamily.

The seed surfaces of extant species of *Epipremnum* and other Monstereae genera are generally smooth or slightly rugose or cristate (Madison and Tiffney, 1976). In *Rhodospatha* the seed is verrucose or cristate; however, its small size, the uniformity of the verrucae and amount of curvature of the seed, differ from the fossil seed described here.

From the seed descriptions of extant species of the subfamily Lasioideae by Engler (1911) it is clear that *Cytosperma* and *Dracontioides* are the only other genera with spiny seeds. Gregor and Bogner (1984) illustrated a seed of *Urospatha saggittifalia* (Rudge) Schott with spines. Among the species of *Cyrtosperma* some have well developed spines and ridges, *(e.g. C. senegalense* (Schott) Engl., *C. lasioides* Griff), others have a very irregular seed surface (*C. americanum* Engl.), and still others are almost smooth (*C. edule* Schott). The monotypic genus *Dracontioides* (*D. desciscens* (Schott) Engl.) shows well-developed spines and ridges; however, its current geographic distribution, restricted to the southern part of Brazil, and scarce fossil record, weakens, but does not exclude, any possible relationship with the fossil seed. A similar situation is present with *Urospatha*, that is found from Mexico to Brazil.

The fossil seed most likely represents a member of the subfamily Lasioideae, and can be classified in the tribe Lasieae. In order to confirm this taxonomic determination, sections about 10 um thick were prepared of seeds of several species of *Epipremnum, Cyrtosperma* and *Rhodospatha*. Unfortunately no seeds of *Dracontioides* and *Urospatha* were available for comparisions (Table 1). In *Epipremnum* and *Cyrtosperma* the central part of the seeds is occupied by a monocotyledonous embryo that is surrounded by endosperm with dark contents. These tissues are surrounded by nucellar tissue that is composed of rectangular cells, and attached to the integument for most of its length. The integument is composed of isodiametric to polyhedral sclereids. Two types of sclereids can be distinguished. Sclereids with thick walls and small lumens occupy the inner part of the integument while thin-walled cells with larger lumens occupy the outer part of the integument. Isodiametric raphide sacs are scattered in the outer integumentary layers. Some areas of the inner integument are composed of elongated sclereids. The raphe area is composed of large, polyhedral, thin-walled cells, and conspicuous vascular tissue. The position of hilum in relation to the micropyle and the curvature of the nucellus makes these seeds campylotropous.

The seed of *Rhodospatha* is composed of two integumentary layers with raphide sacs in the outer integumentary layer. However, the inner integumentary layer is composed of a single layer of thick-walled cells and the outer integument contains about 6 cell layers. The individual cells are rectangular to quadrangular in shape, and the raphide sacs are not circular, but rectangular in outline. Raphe cells are thin-walled, and rectangular to oval in outline. Thus, *Rhodospatha* is very different from the fossil seed. Nucellus, endosperm and embryo are similar to *Epipremnum and Cyrtosperma*.

The integuments of the three genera are very similar, fitting within the family diagnosis; however, when compared to the fossil seeds from Princeton, *Rhodospatha* is quite different. On the other hand, the *Epipremnum* integument has a single outer layer that can be differentiated easily from the rest of the isodiametric to polyhedral cells of the integument. This integumentary layer is not so conspicuous in *Cyrtosperma*. Another difference between these two genera is the fact that *Cyrtosperma* has a higher degree of reflexion than *Epipremnum*. The absence of a conspicuous single outer layer in the fossil seeds points toward a relationship with the Lasioideae, but the curvature of the seed looks similar to *Epipremnum* (Monstereae). The presence of elongated sclereids in the integument of the two living genera and their absence in the fossil seeds is a significant difference.

Thus, the fossil seed probably represents a new araceous genus with an integument similar to both subfamilies, Monstereae and Lasioideae. It is more closely related to the tribe Lasieae, but cannot be included in any living genus. Gregor and Bogner (1984) reviewed identification problems of fossil Monstereae-Lasioideae seeds. They recognized three groups. Their "ornatum" and "crassum" groups are similar to the *Epipremnum* assigned to the subfamily Monstereae by Madison and Tiffney (1976), while their "cristatum" group reflects the *Epipremnum* species that have been assigned to the subfamily Lasioideae. In their "ornatum" group they made a new combination, *Epipremnites ornatus* (Reid & Chandler) Gregor & Bogner. In their "crassum" group they also made a new combination, *Scindapsites crassus* (Reid & Reid) Gregor & Bogner. Finally they related the "cristatum" group not only to *Cyrtosperma* but also to *Dracontioides* and *Urospatha*. They also added two fossil seeds to this group: *E. avimontanum* Gregor and *Urospathites dalgasii* (Hartz) Gregor & Bogner. The relationship of the fossil seed discussed here and *Urospatha* or *Dracontioides* is not strengthened by its actual geographic distribution, in tropical America, from Mexico to Brazil.

The study of araceous seed compressions has reached an acceptable status; however, there still much to be done. As Madison and Tiffney (1976) point out, there is great possibility to find similar seed morphologies in groups unrelated to the Araceae. Kirchheimer (1957) noted the similarity of seeds of *Epipremnun* to those of some species of the Leguminosae and Malvaceae. Regarding this problem, Tiffney (1985, pers. comm.) disagrees with some araceous identifications from the Late Miocene and Pliocene of Europe and Western Russia. By that time these areas were too cool for tropical to warm temperate *Epipremnum* seeds. Thus, Tiffney believes that what we call "*Epipremnum*" in the fossil record, really includes two quite different taxa and that the cool climate fossils perhaps belong to other families. Since the fossil seeds discussed here come from a fossil locality interpreted as tropical-subtropical, their classification within the Araceae is reasonable. Seed anatomy confirms it.

Unfortunately, until now only seeds preserved as compressions, except for the report of Bown *et al.* (1982), for which anatomy has not yet been described, have been reported. Seed anatomy is an important taxonomic tool that can help in understanding relationships between different seeds and the plants that bore them. The seed described here can be traced taxonomically to the tribe Lasieae, but little can be said about its position when compared with other fossil reniform, spiny seeds, except that it may be related to *Epipremnum cristatum* Nikitin due to the presence in the dorsal and lateral faces of parallel ridges capped with strongly protuberant spines. However, it is essential to know the anatomy of *E. cristatum* seeds in order to assess any relationship.

The problem of the relationships between the Monstereae and Lasioideae is not restricted to seed anatomy. French (1985a, 1985b) found that the most common pattern of endothecial wall thickenings in both subfamilies are the helical thickenings.

Furthermore, he found that the pattern of endothecial thickenings in the tribe Lasieae most closely resembles that in *Monstera* (Monsteroideae) and *Heteropsis* (Pothoeae). French (1986) also found that stamen vasculature in virtually all Monsteroideae as well as in the Lasioideae (tribe Lasieae) consists of a single unbranched vascular bundle. Grayum (1984), based on palynological analysis, strongly supported the separation of the tribe Lasieae as a separate subfamily. This suggestion is supported by French (1986) on the basis of the large differences between the dioecious Lasieae and the rest of the Lasioideae that are monoecious. The acceptance of this change, depends on the belief that previously used taxonomic characters, such as, similarities in leaf and stem morphology and venation are superficial ones.

To date, the genus *Epipremnum* (either Monsteroideae or Lasioideae) has never been reported from Eocene deposits. The oldest known specimens, thus far, are from the Oligocene of the U.S.S.R. and England. Moreover, its fossil record is restricted to Europe and Asia. Some authors have suggested that some types of seeds have been overlooked in North America (Eyde, 1972; Madison and Tiffney, 1976). Thus, the presence of this seed in the Middle Eocene Allenby Formation changes the biostratigraphic and biogeographic concepts of the group, at least of those seeds referred to the tribe Lasieae. With this information it is not surprising to find by the Middle Eocene a seed that can be referred to the Lasieae at the same time has Monsteroideae affinities. Its presence in these sediments supports Crepet's (1978) suggestion that the family Araceae radiated in the Late Cretaceous or Paleocene, and that by the Eocene some tribes were well differentiated, including one modern genus, *Philodendron*.

## IV. Incertae sedis

Fruit with one ruminate seed

### Description

One single-seeded fruit has been found with one convex and one flattened side, 2.7 mm long and 1.2 mm wide. The pericarp is thin and homogeneous, composed of tangentially elongated, rectangular to polyhedral cells 2 um x 9 um in diameter (Figs. 116 - 119). In the basal part of the fruit a receptacular-like structure with crown shape is observable (Fig. 122). From this area, at least three vascular strands depart and surround the fruit (Fig. 121). Tracheids of these strands have a diameter of about 6 um and helical thickenings. This specimen may, in fact, represent a pyrene of a larger fruit.

The seed is the same shape as the fruit and has well-developed ruminations of the integument (Fig. 116, 117). Three integumentary layers occur in the seed (Fig. 120). The outermost as seen in longitudinal section is composed of a single layer of isodiametric thin-walled cells with a maximum diameter of 9 um (Fig. 120). The middle integumentary layer about 8 cell layers thick, is composed of isodiametric to polyhedral cells, some with dark contents, with a maximum diameter of about 12 um (Fig. 120). The inner layer is composed of short tangentially elongated cells with dark contents (Fig. 120). This inner layer is difficult to discern and might have been under reabsorption at the time of fossilization. Between this inner layer and the nucellus, a space surrounds the integumentary cavity (Fig. 119), suggesting that the nucellus is free from the integument for most of its length. The nucellus represented by a single layer of tangentially elongated cells full of dark contents about 33 um x 18 um in diameter (Figs. 120, 125). An endosperm is preserved and composed of irregularly shaped cells with what appear to be a few scattered almost isodiametric sclereids, (Figs. 125, 126). Primary pit fields 2.3 um in diameter are observable in the walls. A fragment of probable embryo tissue is present at one end of the seed (Figs. 123, 124). It is composed of polyhedral to irregular-shaped cells, and contains some vascular tissue (Fig. 124). Tracheids have helical thickenings.

Bilocular Fruit

### Description

Large numbers of bilocular fruits occur in the chert and range in shape from almost spherical to oval with a maximum diameter of about 1.8 mm (Figs. 131, 137, 138, 141). Each locule has one seed (Fig. 131). In some fruits, there appears to be a tendency for the fruit to split into two pyrenes (Fig. 141). However, individual dispersed seeds have not yet been found. One fruit shows some gland-like areas on its outer surface (Fig. 143). Three persistant sepals, 0.8 mm long, with acuminate tips are distinguishable (Figs. 127, 128). Their cellular structure is not well-preserved, however, most of the cells appear rectangular in shape, and some of them have dark contents. In one sepal a cluster of sclereids is seen near the sepal base (Figs. 128, 144). Sepals are inserted at the base of fruit (Figs. 128, 129), where the receptacle is located. Fruit tissue is very homogeneous, thick and formed by five or six tangentially elongated cell layers (Figs. 129, 130). In this tissue several vascular strands can be followed. Individual fruit cells are rectangular, 90 um x 30 um. Fruit structure is consistent with that described for a berry (Roth, 1977)

Seeds are oval, 1.6 mm long and 0.6 mm wide, with a slight flattened side, corresponding to the area where the two seeds face each other in the fruit. The integument has three distinct layers (Fig. 132). The outer integumentary layer is composed of circular to polyhedral cells, 12 um in diameter and can be seen just inside the fruit tissue (Fig. 132). The middle integumentary layer has thick-walled rectangular to quadrangular, sinuous cells full of dark contents (Fig. 132). Cells tend to be arranged in a palisade. In tangential section of the seed surface, cells of this integumentary layer are polyhedral to sinuous in outline (Fig. 142). In this same tangential section, cells of the outer integumentary layer appear circular to polyhedral. Cells of the inner integumentary layer are rectangular in shape in tangential section. In a longitudinal section these cells are rectangular to quadrangular, 18 um x 12 um, and full of dark contents. Small projections of this integumentary layer toward the seed cavity have been seen in a few seeds.

A space between the inner integumentary layer and the nucellus suggests that the nucellus was free from the integument (Figs. 132, 139). The nucellus is single layered except at the micropylar end where it appears multicellular (Figs. 131, 133). Individual cells are about 18 um x 6 um, and full of dark contents. Endosperm is composed of irregularly shaped cells full of dark contents and scattered sclereids (Figs. 135, 136, 138). One embryo has been found (Fig. 139), and possibly a second one is present (Fig. 130). Its cells, however, are replaced by fungi (Fig. 134).

As mentioned above, vasculature in the fruit is extensive, at least two vascular strands can be followed from the receptacle area to the upper part of the fruit (Fig. 137). Seed vasculature was not seen; however, it is very characteristic for this seed type that one vascular strand apparently coming directly from the receptacle intrudes the seed cavity (Fig. 140). This intrusion occurs very near and in the same zone as the micropylar area.

## Discussion

The two types of fruits and seeds included as *Incertae sedis* have many similarities to each other. However, ruminations are present in seeds of the one-seeded fruit but are absent in the bilocular fruit. In the fruit with the ruminated seed no persistant sepals were found. It is important to point out, that sepals in the bilocular fruit are present, or at least clearly distinguishable, in only one specimen. The integumentary tissues are anatomically and topographically almost identical. Both have an outer single integumentary layer composed of nearly isodiametric cells. A second integumentary layer is composed of five or six sclereid layers. In the fruit with the ruminate seed, individual cells of this second integumentary layer are almost isodiametric with a tendency to form polyhedral to slightly irregularly shaped cells. In the bilocular fruit, the individual cells of the second integumentary layer are mostly polyhedral to irregularly shaped. One specimen shows these cells as being large and rectangular with sinuous walls and arranged in a palisade-like fashion (Fig. 132). A third integumentary layer in both seeds is represented by tangentially elongated cells with dark contents. It is also important to note that nucellus is free from the integuments in both, the ruminate seed and the bilocular fruit. Nucellus in both seeds is one cell layer thick and with tangentially elongated cells. The endosperm of both seeds shows sclereids. Both fruits have a thin pericarp about 10 cell layers thick with tangentially elongated cells, some with dark contents. One vascular strand runs through the pericarp. Thus, it appears that both fruits may be from related taxa.

Using the ruminations as an important taxonomic character it is possible to treat the fruit with ruminate seeds in the *Annona* group of Periasmay (1962a). Mature seeds of this type have definite ingrowths or infoldings of the integument, mature integument is composed of more than one layer, and the ingrowths are not supplied by vascular tissue. About eight different families have been found with this type of ruminate seed (Netolitzky, 1926b; Corner, 1949, 1966, 1976a; and Periasmay, 1926b, 1966). Seeds of the family Annonaceae have multicellular inner or middle integuments, and fibers are well-developed in the middle integumentary layer (Corner, 1976a), unlike the multicellular integument of the fossil seed. Sometimes seeds of this family have a third integument, unlike those of the fossil ruminate seed described here. The family Aristolochiaceae has flattened or winged seeds, that usually contain five integumentary layers. The inner integument of seeds of this family has two palisade layers unlike the probable single palisade layer of the fossil seed. The presence of a waxy sarcotesta and clusters of oil cells opposite the ruminations in the Degeneriaceae is unlike that of the fossil seed. The family Dipterocarpaceae has multicellular integuments and the outer integumentary layer has a variable number of vascular bundles (*Vatica* L.=20 approx.) (Corner, 1976a) making any relationship with the Princeton seed difficult to support. The curved seeds with unspecialized and crushed integuments at maturity of the family Menispermaceae are not comparable to those of the fossil. Even if the outer integumentary layer is persistent in menispermaceous seeds, it is represented by a layer of tabular cells with thin lignified walls unlike the isodiametric cells of the fossil seeds. Seeds of the family Vitaceae display a typical "W"-shape in transverse section and five distinct integumentary layers, and the Palmae seeds consist mainly of hard and soft endosperm surrounded by a thin dry brownish integumentary layer, making them different from the fossil seed. Finally, the Ebenaceae has three distinct integumentary layers. The outermost is more or less multicellular, formed by a palisade of enlarged cuboidal or radially elongated cells, with hexagonal or gyrose facets; or it is composed of all fibriform cells, with more or less lignified walls, often sparcely and finely pitted in radial and tangential walls. The middle integumentary layer is composed of thin-walled cells or has scattered brown sclereids with the inner layers often obliterated. The inner integumentary layer has mucilaginous cells that eventually break down when the seed is mature.

Similarities of the seed to the Ebenaceae as described by Corner (1976b) are notable however, coil types do not match 100%. At this point, the fruit with one ruminate seed can probably be said to have ebenaceous affinities. Corner (1976a) pointed out that Periasmay (1962a, 1966) described ebenaceous ruminations as the *Annona*-type, and noted that this was true in as far as they are "infoldings of the testa", but the seeds are not perichalazal and the ruminations are always basal and longitudinal, and do not correspond to the transverse ruminations of the annonaceous seed. Thus, the arrangement of ruminations in the fossil supports its inclusion within the family Ebenaceae.

The bilocular fruit on the other hand, does not have ruminations, however, integument and fruit anatomy are quite similar to the fruit with ruminate seeds. Furthermore, it is known that in this large family with about five genera and more than 400 species, some species are fairly ruminate (e.g. *Diospyros oblonga* Wall), others are not ruminate (e.g. *D. mollis* Wall) and still others are subruminate (e.g. *Euclea divinorum* Hiern) (Corner, 1976a). One bilocular fruit specimen, however shows persistant sepals and a calyx that is not gamosepalous, a characteristic of the Ebenaceae. Therefore, inclusion of these fossils in the Ebenaceae seems unlikely.

The Ebenaceae is probably related to the families Styracaceae and Sapotaceae (Cronquist, 1981). Seed integuments of the family Sapotaceae are multicellular in all layers and in the Styracaceae the outer integument is thick at first, but becomes crushed at maturity (Corner, 1976a). The calyx in these two families is not gamosepalous, however, their seeds are not reported to be ruminate. Corner (1976a) suggested, based on the ebenaceous integumentary anatomy, affinities of this family to the families Theaceae, Symplocaceae or Sapotaceae. The integument in Symplocaceae is very thin and apparently unspecialized and crushed at maturity, while two post-chalazal branches of vascular tissue subdivide the seed. Since the symplocaceous flower is epigynous, any relationship with the bilocular fruit is difficult to support. The fossil seeds from Princeton show some similarities to integuments within the family Theaceae. However, since the theaceous seed is winged and possesses a hypostase, a possible relationship is weakened. Another difference is the presence of a capsular fruit in the Theaceae and a berry-like fruit in the Princeton remains.

It is evident that integuments of the fruit with a ruminate seed and the bilocular fruit have ebenaceous characteristics. However, important differences prevent their identification as typical ebenaceous carpological remains. Seed similarities between the fossil remains and the family Theaceae seem important, but fruit differences are great. However, Corner's (1976a) proposal relating the Ebenaceae and Theaceae seed based on integuments suggest a possibility of intermediate forms such as the two fruits described here.

At the present time more information is needed in order to make a more accurate determination. For example, it is important to clarify why a vascular bundle intrudes the seed cavity. Perhaps this vascular tissue is an indication of a vascularized nucellus, as suggested for other families by Maheshwari (1950) and Corner (1976a). The presence of sclereids in the endosperm is also unusual. Furthermore, it is important to find more ruminate seeds of this type to determine if the fruit is really single seeded or if the single fruit found is a pyrene or schizocarp of a larger fruit. Irrefutable Ebenaceous fruits are known by the Eocene from Anjou, France (Vaudois-Mejia, 1980, 1982) and flowers from southern Australia (Basinger and Christophel, 1985). Based on the available information the Princeton remains are probably related to the family Ebenaceae, but more information is needed to justify this conclusion. Therefore, they are referred as *Incertae sedis*.

## V. General Discussion

The present study represents the first more or less extensive attempt to identify fossil fruits and seeds using internal anatomical characteristics. As noted earlier by Netolitzky (1926b) and Corner (1976a) integument characteristics represent a important information for taxonomic purposes. Furthermore, embryonic tissues as well as type of embryo are important supplementary characteristics (Martin, 1946). Interpreting fossil fruits and seeds using these characteristics is more complicated than studing living representatives, since it is difficult to establish complete developmental sequences. It is well known that there is variability in the number of integumentary layers depending on the developmental stage of the ovule. Also, each integumentary layer may have different cell layers throughout development. Furthermore, at maturity, a complete integumentary layer may be reabsorbed (Berlese, 1892a; Pechoutre, 1902; Netolitzky, 1926b; Ulbrich, 1928; Periasmay, 1962b; Corner, 1976a). Thus, seeds must have completed their development in order to compare them. In the present study most seeds are considered mature because they show embryo tissues (e.g. Caryophyllales, rosaceous aggregate fruit and drupe, Vitaceae # 3, *Decodon*, Araceae, *Incertae sedis*) or because their integument arrangement closely resembles previous reports of mature seeds (e. g. Cabombaceae, Sterculiaceae/Malvaceae, Vitaceae # 1 and # 2).

Unfortunately, fruit and seed knowledge has not reached the point in which anatomical characteristics can be use for enviromental interpretations. However, it can be said that capsular fruits can be used for floatation enhancing seed dispersal, thus, the seeds of the Nymphaeaceae and *Decodon* seem to be adapted for this type of transport. On the other hand, the rosaceous drupe/berry fruit can be interpreted as equipped with edible pericarp suggesting the intervention of animals for their dispersal (Van der Pijl, 1955; Roth 1977). The rosaceous aggregate fruit also has an edible pericarp, suggesting some relationship with an animal for dispersal of its seeds. Vitaceous seeds have a sarcotesta (integumentary layer 1) and their fruit usually is a berry, thus they are also dispersed by animals (Van der Pijl, 1955; Tiffney and Barghoorn, 1976). The berry of the *Incertae sedis* remains is difficult to interpret because the pericarp has little in the way of edible parts. Fruits of the other remains described here are not yet known.

From seed structure, it can be suggested that the palisade in the Cabombaceae seed prevented water penetration in to the seed cavity, enhancing floatation capability and potential for dispersal. The palisade in the Sterculiaceae/Malvaceae seed may play a similar function, however, since extant plants of these families do not have aquatic dispersal, the palisade in this case may be related to the delay of germination by preventing water permeability. Both functions have been suggested for seed palisade tissues, especially in Leguminosae (Spunry, 1971, Roth, 1977). Mucilage-like cells in the large Lythraceae seed may also prevent water uptake, but their presence may be related more to a delay of germination than to a floating function. Wind dispersal is not well represented by seeds found in the Princeton chert; however, the presence of multicellular tissues composed of thin-walled cells (e. g. *Decodon*, Caryophyllales) may be interpreted as a trend to increase the surface/volume (mass) ratio. This situation will facilitate floatation in both, air or water. Animal dispersal, on the other hand, might be inferred for the Caryophyllales seed. The presence of hair-like structures may help the seed stick to an animal.

Using plant remains as indicators of environment, two clearly different environments can be recognized within the paleoflora at Princeton. As Basinger (1976a) pointed out, a temperate flora is indicated by the conifers and rosaceous remains. A tropical-subtropical flora is indicated by ferns, cabombaceous, araceous, and the sterculiaceous/malvaceous remains, as well as the presence of sabaloid palms (Basinger, 1976a). Lythraceous, vitaceous, and caryophyllaceous plants may be found in either environment, but tend to be more succesful in tropical-subtropical environments. Thus, the environment that can be inferred from the plant assemblage at Princeton tends to be tropical to subtropical. The association of temperate and tropical-subtropical forms in this assemblage, therefore, needs to be explained.

The possibility that the temperate forms represent allochthonous material is insupportable. Conifer remains are very abundant and the quality of preservation is superb. Conifer stumps have been seen in growth position in the chert outcrop (Stockey, pers. comm.). Cones are preserved intact with seeds in place, and fascicle sheaths are still present. Furthermore, the presence of numerous roots in the deposit supports the idea of autochthonous deposition of the conifer remains. From a more dynamic point of view, it is difficult if not impossible to explain, how organs of the same plant with different potentials for transportation reached the same area of deposition if they were not preserved very close to their growth habitat. The rosaceous remains are more difficult to assess. This group is represented by only one flower and two fruits with seeds. None of these are as abundant as one would expect if they were autochthonous remains. However, since most of their tissues are delicate ones and they are very well-preserved, they were not transported extensively prior to preservation. It may be possible to explain their scanty representation by their topographic position in the community.

In order to more accurately determine the climate present at the time the Princeton chert locality was deposited, a physiognomic analysis of the leaf remains would be useful. However, at the present time this has not been done and does not form part of this thesis. Wolfe and Barghoorn (1960) noted that leaves of woody plants with entire margins tend to predominate in tropical, alpine, and arctic regions and in physiologically arid environments. Taxa with a high percentage of leaves with entire margins present in the Princeton chert locality are Cabombaceae, Caryophyllales, Lythraceae, Malvaceae/Sterculiaceae and Araceae. Wolfe and Barghoorn (1960) added that leaves with non-entire margins like Rosaceae and Vitaceae are very numerous in temperate regions. Thus, it is possible to extrapolate a tropical-subtropical climate from the angiosperm families represented in the assemblage.

Basinger (1976a) postulated that the Princeton chert locality represents part of an ecotone in which subtropical and warm temperate forms were deposited. This idea in many ways follows Chaney's (1949) views on Tertiary climatology. However, by examining only the megafossil record of the locality that must be considered to be autochthonous, the flora represents a tropical-subtropical assemblage. Boneham's (1968) study on the palynology of Tertiary coal basins in south-central British Columbia indicate 29 different taxa of pollen grains and spores, 68% of the taxa were spores of fungi, algae and bryophytes. Other remains of these organisms have not been described in detail; however, different kinds of hyphae are known to be present in the Princeton chert. *Pistillipollenites mcgregorii* Rouse is the only angiosperm pollen grain he found represented in significant quantity. *Pistillipollenites* however, can not be related to a single family. Pollen-grains of this type may indicate relationships to the Gentianaceae or Euphorbiaceae (Crepet, 1984; Stockey and Manchester, 1986). From Boneham's (1968) study it is not possible to assess what percentage of the flora was composed of angiosperms, and what percentage was composed of gymnosperms. Sometimes it is also difficult to relate a pollen grain to a group of extant plants. However, Boneham (1968) was able to identify subtropical elements like the Cycadaceae and Taxodiaceae and temperate elements like Ginkgoaceae and Fagaceae. From these families, only Taxodiaceae is represented in the megafossils known so far from the Princeton chert locality. Nevertheless, it is difficult to assess if pollen grains represent autocthonous or allocthonous plants. Therefore, the following discussion is based on megafossils interpreted as autocthonous.

Periodicity may be also inferred for the Princeton chert locality. Analysis of wood from this locality is not part of this thesis, however, wood samples with well developed growth rings are abundant in the chert. Basinger (1976a) illustrated the presence of well-developed annual rings in woods of *Pinus similkameenensis* and *Metasequoia milleri* Basinger (1981). He interpreted these plants to be indicative of a temperate climate. However, he concluded that the climate "could be termed subtropical to warm temperate", and that it "would be quite warm and moist, with winter frost rare or absent". Thus, in his interpretation annual rings are not related to a marked seasonality. Some years ago it was thought that growth-rings were indicators of temperate conditions. Metcalfe and Chalk (1983), however, pointed out that the physiology of growth-ring formation is far from being fully understood. It may be related to fluctuations in water supply, temperature, intensity of illumination, variations in day-length and in auxin gradients. Tomlinson and Craighead (1972) studied the formation of growth rings in trees of subtropical Florida. They noted that growth rings in this subtropical assemblage were not necessarily annual and not always correlated with deciduous taxa. However, Metcalfe and Chalk (1985) pointed out that the formation of a new crown, whether complete or partial, demands an increase in the water conducting tissues, thus, producing early and late wood. Bass and Van der Graff (1974) noted that species from temperate to subtropical climates are characterized by conspicuous growth rings while in species of tropical lowlands and montane regions, growth rings are absent or less marked. The presence of growth rings at the Princeton chert locality indicates some sort of periodicity, and suggests a subtropical environment over a tropical one. However, more detailed studies of wood anatomy are needed to confirm this.

During the middle Eocene time, there was not a sharp division between tropical, subtropical or temperate floras (Tiffney, 1985; Wolfe, 1975). At Princeton these elements coexisted in the same depositional basin. Vegetation by that time is characterized by a mixture of elements now restricted to different climates. Thus, it has been noted that after the Middle Eocene, as an effect of climatic deterioration as well as the establishment of modern physiography, the vegetation became differentiated according to changing climatic characters.

The organization of the vegetation here seems to follow a tropical rainforest pattern. As suggested by Basinger (1976a), the locality at that time could be influenced by the 49° tropical-subtropical marine climate postulated by Durham (1950). Thus, this oceanic influence, that may be weakened due to the distance of the locality from the coast, could be of great importance in the establishment of a tropical-subtropical rainforest. Five strata can be recognized in the vegetation present at Princeton based on megafossils. The highest stratum is represented by the conifers, *Pinus* and *Metasequoia*. A second stratum is represented by forms of intermediate size like *Prunus*, *Decodon*, and perhaps the Malvaceae/Sterculiaceae and Caryophyllales plants. A third stratum is represented by vine-like plants like *Vitis* and the araceous (*Cyrtosperma*-like) plant. A fourth stratum contains small plants like *Paleorosa*, ferns and probably the plant that produced the aggregate fruit. The lowest stratum is represented by aquatic plants like the Cabombaceae.

In a horizontal transect, the plant assemblages can be visualized as organized around a water body. Since preservation at the locality is very good and thin-walled cells and delicate flower structures are preserved, it can be inferred that energy transport was low; thus, a very quiet lake or marsh is an ideal environment. Turtle bones, in fact, have been identified in the chert (R. C. Fox, per. comm.). Since biological degradation is minimal, an environment with reductive characteristics like a marsh seems highly possible. In this marsh the nymphaeaceous plants, were well established. The araceous

(*Cyrtosperma*-like) plant was also a marsh dweller or perhaps occupied a more peripheral distribution while the Cabombaceae had a more central distribution. Also, along the marsh shoreline *Decodon* (the swamp willow), would be present. *Eorhiza* grew in close association with both, the araceous (*Cyrtosperma*-like) plant and the Cabombaceae. Surrounding this aquatic system, a mixture of *Pinus*, *Metasequoia*, *Prunus*, Malvaceae/Sterculiaceae, Caryophyllales and palms formed the two highest strata. The three vitaceous taxa utilized the other trees and shrubs for support. On the forest floor, herbs like *Paleorosa*, perhaps the aggregate fruit, and the ferns filled this ecological niche.

It is now accepted that by the end of the Cretaceous climatic deterioration was a general phenomenon in the northern hemisphere (Tiffney, 1985; Wolfe, 1975). During the Late Paleocene the northern hemisphere had a temperate climate, but it began to warm and reached a maximum by the Middle Eocene. During Late Eocene cooling began again and extended through the Oligocene. During Miocene time there was another warming trend, but it did not reach the Middle Eocene maximum. The late Miocene and Pliocene suffer a cooling trend that finished with the glaciations of the Pleistocene (Tiffney, 1985; Wolfe, 1975, 1980). These climatic changes appear to be responsible for the segregation of tropical, subtropical, and temperate floras as they are understood today (Collinson, *et al*. 1981; Wolfe, 1978). The fact that the climate of the Princeton chert locality is tropical to subtropical reinforces the Middle Eocene age for this fossil flora.

From a biostratigraphic point of view it is also important to note that the araceous (*Cyrtosperma*-like) forms adds the tribe Monstereae to the araceous tribes known by the Middle Eocene. Tiffney (pers. comm.) argues that "*Epipremnum*" fossil seeds described from the Late Miocene and Pliocene of Europe and western Russia occupied areas too cool for *Epipremnum* as it grows today. In his opinion there are three possibilities to explain this situation: 1) All of what we call *Epipremnum* really belongs to some other more cold-adapted taxon, 2) What we call *Epipremnum* really includes two quite different taxa, and 3) *Epipremnum* has changed its climatic affinities during the Tertiary. Since there are very few (if indeed any) cases where it can be demonstrated that the climatic tolerance of a taxon shifted substantially during the

Tertiary and, if *Epipremnum* did shift its climatic tolerances through the Tertiary, one would expect to find some species growing in cool temperate floras in the present day (none reported yet), possibility three can be discarded. Furthermore, the Oligocene material reported by Bown, *et al.* (1982) in which they show "*Epipremnum*" seeds associated with a fruit that is clearly *Epipremnum*. Tiffney (pers. comm) believes that the *Epipremnum*-like seeds from the fossil record can be divided into two groups. One that is distributed in cool climates and a second that is distributed in warm-temperate floras. In his opinion the later group represents real araceous seeds while the former may represent other taxa. The presence of the monocotyledonous embryo and endosperm in this seed, represents the first report of these structures as fossils from the Liliopsida. The linear embryo and scanty endosperm correspond to Martin's (1946) description for araceous embryos, reinforcing in the identification.

The peripheral dicotyledonous embryo of the Caryophyllales seed represents the first fossil embryo known for the Magnoliopsida. Some cells have been identified as endosperm, however, since in this order perisperm may be abundant, more seeds are needed to clarify the nature of this tissue.

The fossil *Decodon* described here also represents the oldest *Decodon* reported and belongs to the *Alatosperma-Decodon-Mneme-Microdiptera* alliance of Tiffney (1981). The hypostase and suspensor described for the fossil *Decodon* may be present in mature seeds of the Lythraceae, however, the embryo is difficult to evaluate since it may be linear or spatulate with slightly expanded cotyledons. Martin (1946) reports spatulate embryos in *Cuphea, Didiplis, Lythrum* and *Decodon*, investing embryos in *Rotala*, and he suspects that others in the family leaned toward the Dwarf type. Tiffney (1981) recognizes that the *Alatosperma-Decodon-Mneme-Microdiptera* complex of nearly related genera needs to be reviewed to correctly interpret the *Microdiptera* from the Brandon Lignite, Vermont. *Decodon* described here also shows need for a review, however, the phylogeny proposed by Tiffney (1981) for this group is reinforced by the present study. It was proposed that seeds of the *Alatosperma*-type (Early Eocene), gave rise to *Decodon* (Middle Eocene) by reduction of the wings and to *Mneme* (Late Eocene) through complete detachment of the germination valve. *Mneme*-like plants in turn gave rise to *Microdiptera* (Late Eocene) through a small reduction and flattening of the seed wings and the development of shallow dorsal grooves. The presence of *Decodon* in a marshy environment such as the Princeton chert, is supported by the habitat of extant *D. verticillatus* that lives along lakes, marshes or rivers in SE North America.

In the Rosaceae, the presence of forms with a mixture of tribe characters, like *Paleorosa* with affinities to Maleae, Quillajeae and Sorbarieae (Basinger, 1976b) and the aggregate fruit with affinities to Fragarieae and Roseae, suggest that by the Middle Eocene this family was undergoing active evolution. The spatulate embryo with rather broad cotyledons of the Rosaceae, corresponds closely to the cotyledons found in one seed of the Princeton chert aggregate fruit. Furthermore, the scanty endosperm of this seed, also corresponds, to the thin endosperm of *Fragaria* and *Rosa*. Further discussion on these reproductive structures awaits the recovery of more seeds with embryonic tissues.

Other groups like the Vitaceae appear to be much more diverse by the Middle Eocene than was previously suspected. Tiffney and Barghoorn (1976) recognized that seed anatomy in the Vitaceae underwent significant evolution during the Tertiary. Differences in integument anatomy in the seeds described here cannot be explained by the effect of the number of seeds per fruit, the amount of seed compression per locule or age of the seeds. More likely, each of these three types of seeds represents a different taxon. This is supported by the reports of distinct vitaceous integuments by Kirchheimer (1938) and Tiffney and Barghoorn (1974) that cannot be related to extant species as reported by Periasmay (1962b). The integuments, have been discussed by Netolizky (1926b) and Corner (1976a). Furthermore, identification of seeds based on external morphology may lead to misidentifications as has been shown for some Araceae seeds that are very similar to Leguminosae or Malvaceae seeds (Kirchheimer, 1957). Therefore, understanding of vitaceous integuments will promote a better taxonomic understanding of the family. Thus, carpological remains of this family need to be reviewed.

This study points out the importance of seed and fruit anatomy in taxonomy. Continued studies of these fossil remains are important in order to clarify evolutionary lines within the angiosperms. In Cabombaceae, e.g. the presence of sinuous radial walls in the integument of the Princeton Eocene material do not indicate an exact relationship between this fossil and other extant or fossil forms. Perisperm tissue of these seeds represents the first report of this tissue in the fossil record. However, since it is replaced by fungal hyphae, better preserved seeds are needed.

Further studies of fruits and seeds in the Princeton chert promise to add much to our knowledge of these evolutionary lineages. In addition, the investigation of whole plants in these deposits will allow a greater understanding of these Eocene taxa and their reproductive biology.

## VI. Photographic Plates

Plate 1

Figs. 1 - 5. Nymphaeaceous fruit and seeds.

Fig. 1. Longitudinal section of fruit showing three seeds. P 3678 E top #2 x 5.

Fig. 2. Counterpart of fruit in Fig. 1 showing longitudinal section of fruit with one seed and possible pedicel. P 3678 E top #0 x 15.

Fig. 3. Oblique section of seed showing inner and middle integumentary layers. P 3674 G bot #0 x 200.

Fig. 4. Oblique transverse section of a seed showing one vascular bundle and the remains of the nucellus. P 3674 G bot #0 x 24.

Fig. 5. Transverse section of a seed in face view. Note sinuous cells around the vascular bundle. P 3674 H top #0 x 35.

F = fruit, I = inner integumentary layer, N = nucellus, O = outer integumentary layer, PE = pedicel, S = seed, V = vascular bundle.


F
①
④

## Plate 2

Figs. 6 - 8. Nymphaeaceous seeds.

Fig. 6. Transverse section of seed showing the vascular bundle and surrounding cells with thin wavey cell outlines. P 3674 H top #0 x 80.

Fig. 7. Transverse section of seed with perisperm replaced by fungi. P 2581 E bot #3 x 38.

Fig. 8. Perisperm with cell-walls invaded by fungi. P 2581 E bot #3 x 230.

Fig. 9. Cells of the outer integumentary layer in face view. P 3678 E bot #25 x 270.

N = nucellus, PR = perisperm, V = vascular bundle.

## Plate 3

Fig. 10 - 13. Nymphaeaceous seeds.

Fig. 10. Longitudinal section of seed with operculum *in situ*. P 3773 A #26 x 38.

Fig. 11. Longitudinal section of a seed without operculum. P 3773 A # 26 x 35.

Fig. 12. Isolated operculum. P 2581 E bot # 3 x 98.

Fig. 13. Longitudinal section of outer integumentary layer showing cells with sinuous outlines. P 3773 A # 26 x 155.

I = inner integumentary layer, OP = operculum, O = outer integumentary layer.

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Plate 4

Figs. 14 - 19. Caryophyllales seed.

Fig. 14. Cross section of seed showing two vascular bundles and two cotyledons. P 3771 C top #14 x 70.

Fig. 15. Cross section of seed, after 11 consecutive sections, showing a more irregular surface and decrease in diameter of the internal seed cavity. P 3771 C top #25 x 70.

Fig. 16. Cross section of integument showing inner, middle, and outer integumentary layers. P 3771 C top # 17 x 200.

Fig. 17. Tangential section of seed near chalaza. P 3771 C top #35 x 115.

Fig. 18. Cross section of middle and outer integumentary layers showing clavate hair-like projections. P 3771 C top #27 x 760.

Fig. 19. Paradermal section of integument. P 3771 C top #39 x 200.

C = cotyledon, I = inner integumentary layer, M = middle integumentary layer, O = outer integumentary layer, V = vascular bundle.


C
V
I
M

Plate 5

Figs. 20 - 25. Sequential series of peripheral embryo tissue in a Caryophyllales seed.

Fig. 20. Oblique section of cotyledon. P 3771 C top #1 x 90.

Fig. 21. Cross and oblique sections of two cotyledons with preservation of the shoot apex region. P 3771 C top #2 x 90.

Fig. 22. Cross and oblique sections of two cotyledons with cells near shoot apex area. P 3771 C top # 3 x 90.

Fig. 23. Cross and oblique sections of two cotyledons. P 3771 C top #19 x 90.

Fig. 24. Cross section of two cotyledons. P 3771 C top #21 x 130.

Fig. 25. Cross section of two cotyledons. P 3771 C top #35 x 200.

C = cotyledon, E = endosperm, SA = shoot apex.


NO
C
C
24

## Plate 6

Figs. 26 - 32. Malvales seeds.

Fig. 26. Near transverse section of seed. P 3988 C bot #0 x 70.

Fig. 27. Four integumentary layers. P 3988 C bot #0 x 420.

Fig. 28. Oblique section of seed showing micropyle. P 1631 B bot #34 x 70.

Fig. 29. Cross section of gland-like structures located in two outermost integumentary layers. P 1631 B bot #28 x 416.

Fig. 30. Oblique section of seed showing raphe and well-developed palisade. P1631 B bot #46 x 50.

Fig. 31. Oblique section of seed with possible valve composed of palisade cells. P1631 B bot #29 x 70.

Fig. 32. Cells of palisade layer. P 1631 B bot #40 x 195.

G = gland-like structure, I = inner integumentary layer, IP = inner palisade, M = middle integumentary layer, MI = micropyle, O = outer integumentary layer, R = raphe.

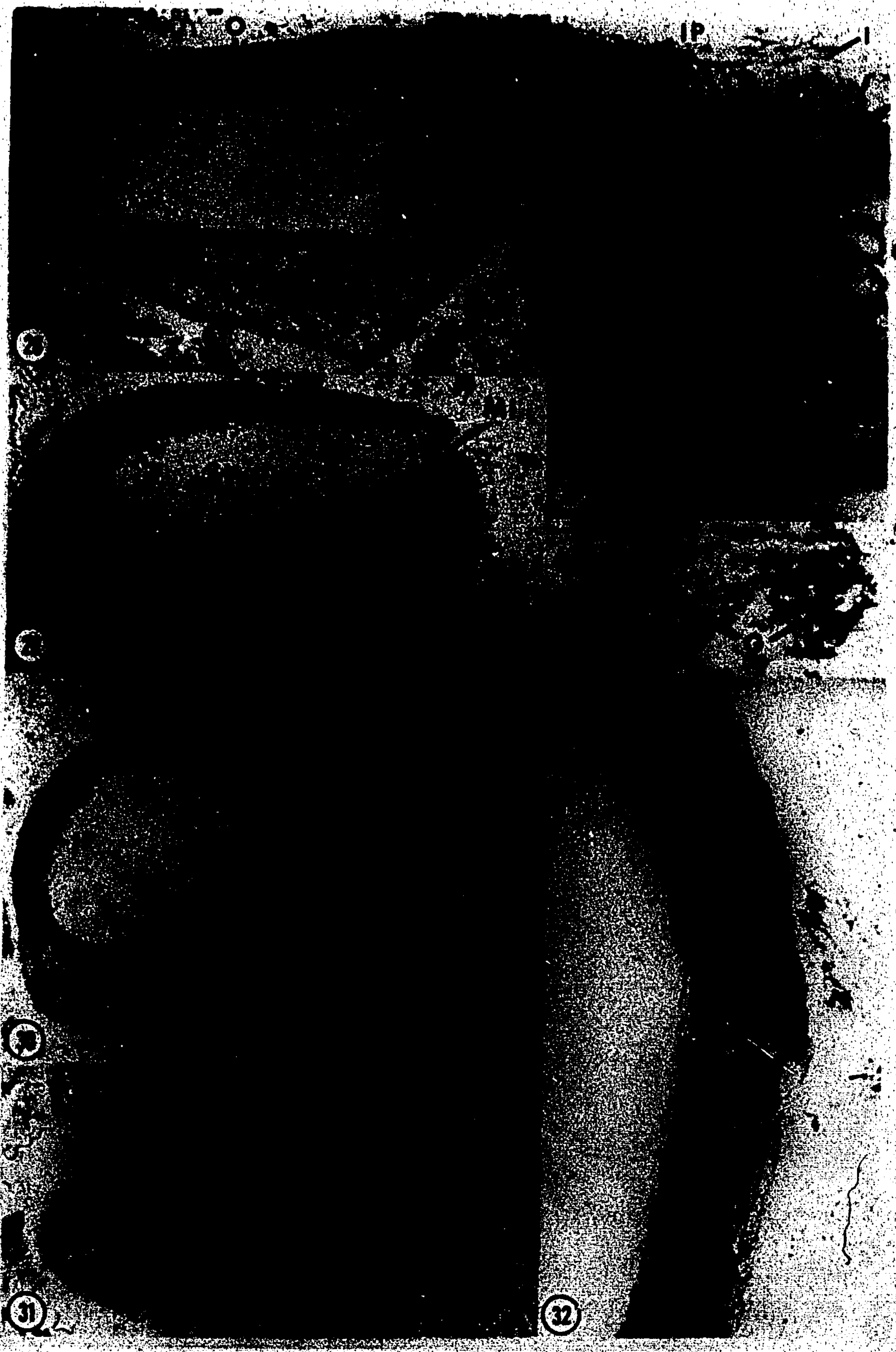

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Plate 7

Figs. 33 - 38. Serial longitudinal sections of a rosaceous drupe.

Fig. 33. Longitudinal section of fruit showing mesocarp, vascular strand, style, and one seed. P 1631 C bot #24 x 50.

Fig. 34. Longitudinal section showing mesocarp, endocarp, style, pedicel and one seed. P 1631 C bot #20 x 40.

Fig. 35. Longitudinal section showing mesocarp, endocarp, style, integument and pedicel. P 1631 C bot #22 x 44.

Fig. 36. Longitudinal section showing exocarp, mesocarp, endocarp, and seed. P 1631 C bot #16 x 42.

Fig. 37. Tangential longitudinal section showing exocarp, mesocarp, endocarp, and seed. P 1631 C bot #14 x 42.

Fig. 38. Tangential longitudinal section showing a vascular strand between exocarp and endocarp. P 1631 C top #12 x 53.

EC = endocarp, EX = exocarp, MC = mesocarp, PE = pedicel, S = seed, ST = style.


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Plate 8

Fig. 39 - 45. Fruit and seed of rosaseous drupe.

Fig. 39. Oblique longitudinal section showing pedicel, mesocarp, endocarp and seed. P 2613 F top #10 x 70.

Fig. 40. Longitudinal section of pedicel showing parenchyma cells with dark contents and vascular tissue with helical thickenings. P 2613 F top #10 x 410.

Fig. 41. Longitudinal section of fruit showing vascular strand running along contact area of mesocarp and endocarp. P 2613 F top #10 x 420.

Fig. 42. Longitudinal section of fruit showing style remnants and vascular strand running between mesocarp and endocarp. P 2613 G top #14 x 140.

Fig. 43. Possible nucellar cells. P 2613 G top #14 x 340.

Fig. 44. Integument with outer sclereid layer and cell inner layer with dark contents. P 2613 F top #10 x 410.

Fig. 45. Oblique longitudinal section showing fruit and seed structure with possible nucellar tissue. P 2613 G top #15 x 98.

EC = endocarp, MC = mesocarp, N = nucellus, PE = pedicel, S = seed, ST = style.

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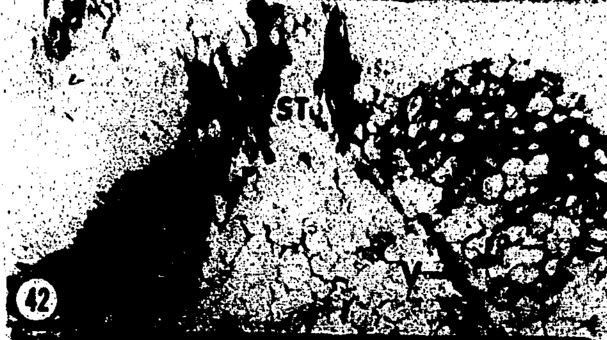

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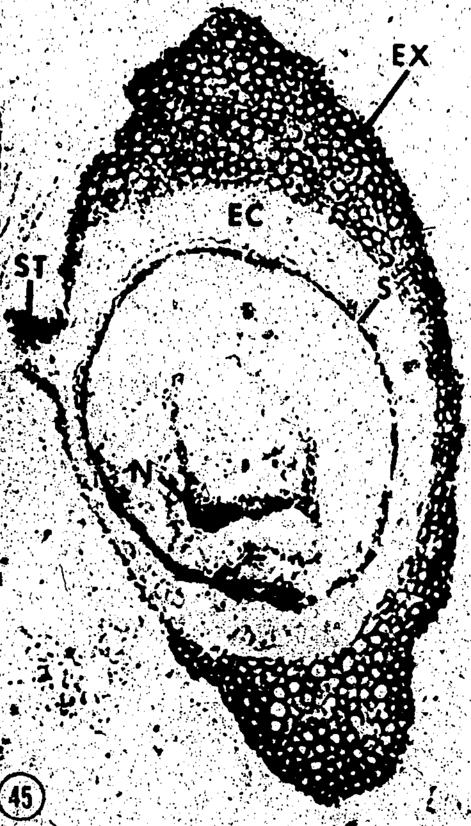

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## Plate 9

Figs. 46 - 51. Rosaceous aggregate fruit with achenes.

Fig. 46. Longitudinal section of aggregate fruit showing two sepals, and several achenes. P 1631 B bot #1 x 15.

Fig. 47. Cross section of aggregate fruit with achenes in receptacular tissue. P 1631 B top #12 x 15.

Fig. 48. Longitudinal section of aggregate fruit showing several achenes in receptacular tissue, and one sepal. P 1631 B top #2 x 37.

Fig. 49. Tracheid with helical thickenings from vascular cylinder of the aggregate fruit. P 1631 B top #21 x 510.

Fig. 50. Longitudinal section of aggregate fruit showing pith surrounded by vascular tissue. P 1631 B top #37 x 28.

Fig. 51. Cross section of achene in receptacular tissue; showing endocarp, mesocarp, exocarp, inner integumentary layer, endosperm, and embryo tissue. P 1631 B top #6 x 130.

A = achene, E = endosperm, EC = endocarp, EM = embryo tissue, EP = epicarp, EX = exocarp, F = fruit, MC = mesocarp, PI = pith, RE = receptacle, S = seed, SE = sepal, V = vascular bundle.

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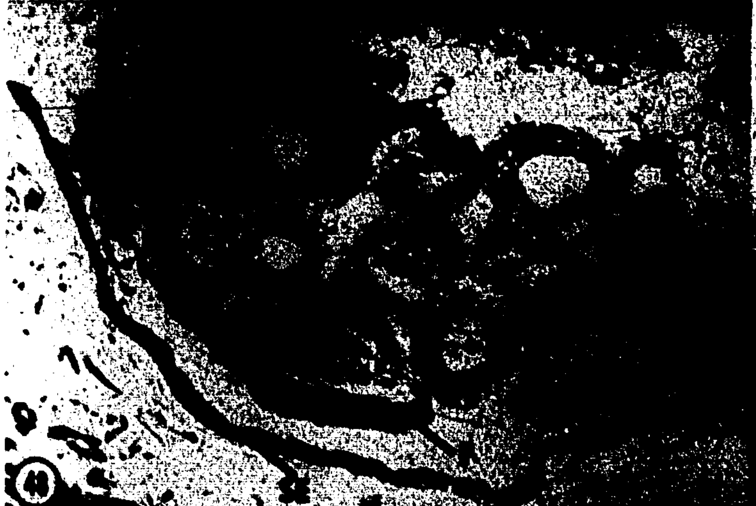

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Plate 10

Figs. 52 - 58. Rosaceous achene and aggregate fruit.

Fig. 52. Oblique cross section of achene showing exocarp, mesocarp, endocarp, outer and inner integumentary layers. P1631 B top #8 x 100.

Fig. 53. Oblique longitudinal section of seed showing general shape. P 1631 B top #8 x 100.

Fig. 54. Longitudinal section of inner integumentary layer showing helical thickenings. P 1631 B top #8 x 170.

Fig. 55. Oblique cross section of seed showing micropylar area and inner integumentary layer. P 1631 B top #13 x 130.

Fig. 56. Cross section of achene showing fruit tissue, outer integumentary layer, endosperm and two cotyledons. P 1631 B top #12 x 130.

Fig. 57. Cross section of achene showing endosperm, and embryo tissue. P 1631 B top #8 x 130.

Fig. 58. Cross section of embryo cotyledons with cellular preservation. P 1631 B top #12 x 370.

C = cotyledon, E = endosperm, EC = endocarp, EM = embryo tisue, EX = exocarp, I = inner integumentary layer, MC = mesocarp, MI = micropyle, O = outer integumentary layer, RE = receptacle.

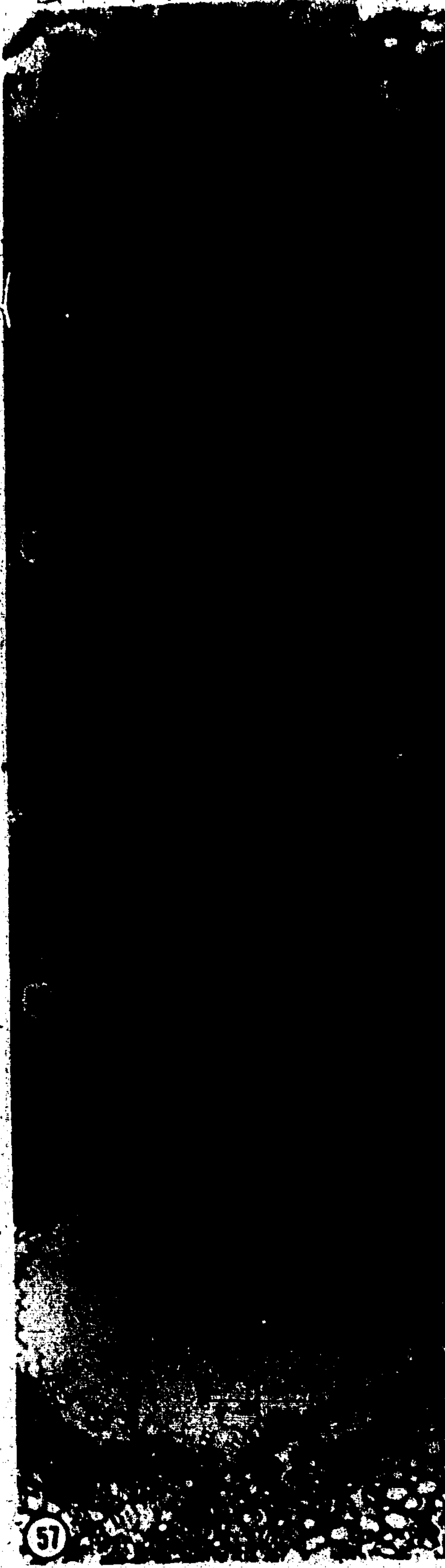

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Plate 11

Fig. 59 - 65. *Decodon* sp. (Lythraceae).

Fig. 59. Cross section showing septa (arrows), fruit axis, and several seeds. P 1142 D bot #2 x 25.

Fig. 60. Longitudinal section showing persistent sepals, fungal cleistothecia in sepals, a pedicel, and remains of two seeds. P 4019 D top #0 x 17.

Fig. 61. Longitudinal section of fruit attached to an axis. P 4019 D top #0 x 5.

Fig. 62. Oblique longitudinal section showing four locules, one with several aborted ovules, one possible gland near fruit apex and persistant sepal. P 3794 C top #36 x 25.

Fig 63. Longitudinal section of fruit showing endocarp with inner palisade layer and tangentially elongated cells of exocarp with helically thickened tracheids. P 1294 A #15 x 40.

Fig. 64. Longitudinal section showing pedicel and bases of sepals (arrows). P1294 A #11 x 15.

Fig. 65. Oblique cross section of fruit axis showing central pith surrounded by several vascular bundles. P 3794 C top #27 x 98.

EN = endocarp, EX = exocarp, FA = fruit axis, = gland-like structures, PI = pith, S = seed, SE = sepals, SP = septa, V = vascular bundle.

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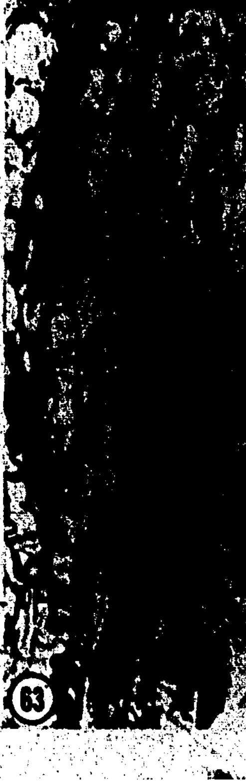

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Plate #12

Fig. 66 - 73. *Decodon* sp. (Lythraceae).

Fig. 66. Oblique longitudinal section of seed showing micropylar and chalazal areas. P 1142 D bot #34 x 104.

Fig. 67. Longitudinal section of integument showing rectangular cells with dark contents of outer integumentary layer and polyhedral to isodiametric cells of middle integumentary layer. P 1294 A #15 x 308.

Fig. 68. Longitudinal section showing raphe in central part of middle integumentary layer. P 1142 D bot #18 x 98.

Fig. 69. Cross section of germination valve showing rectangular cells. P 1294 A #27 x 314.

Fig. 70. Fungal cleistothecia in sepal. P 4019 D top #0 x 233.

Fig. 71. Longitudinal section of seed showing germination valve with thin rectangular cells. P 1294 A #25 x 200.

Fig.. 72. Inner integumentary layer with helical thickenings. P 1294 A #15 x 781.

Fig. 73. Micropylar area and hilum. P 1142 D bot #2 x234.

H = hilum, I = inner integumentary layer, M = middle integumentary layer, MI = micropyle, O = outer integumentary layer, R = raphe, V = valve.

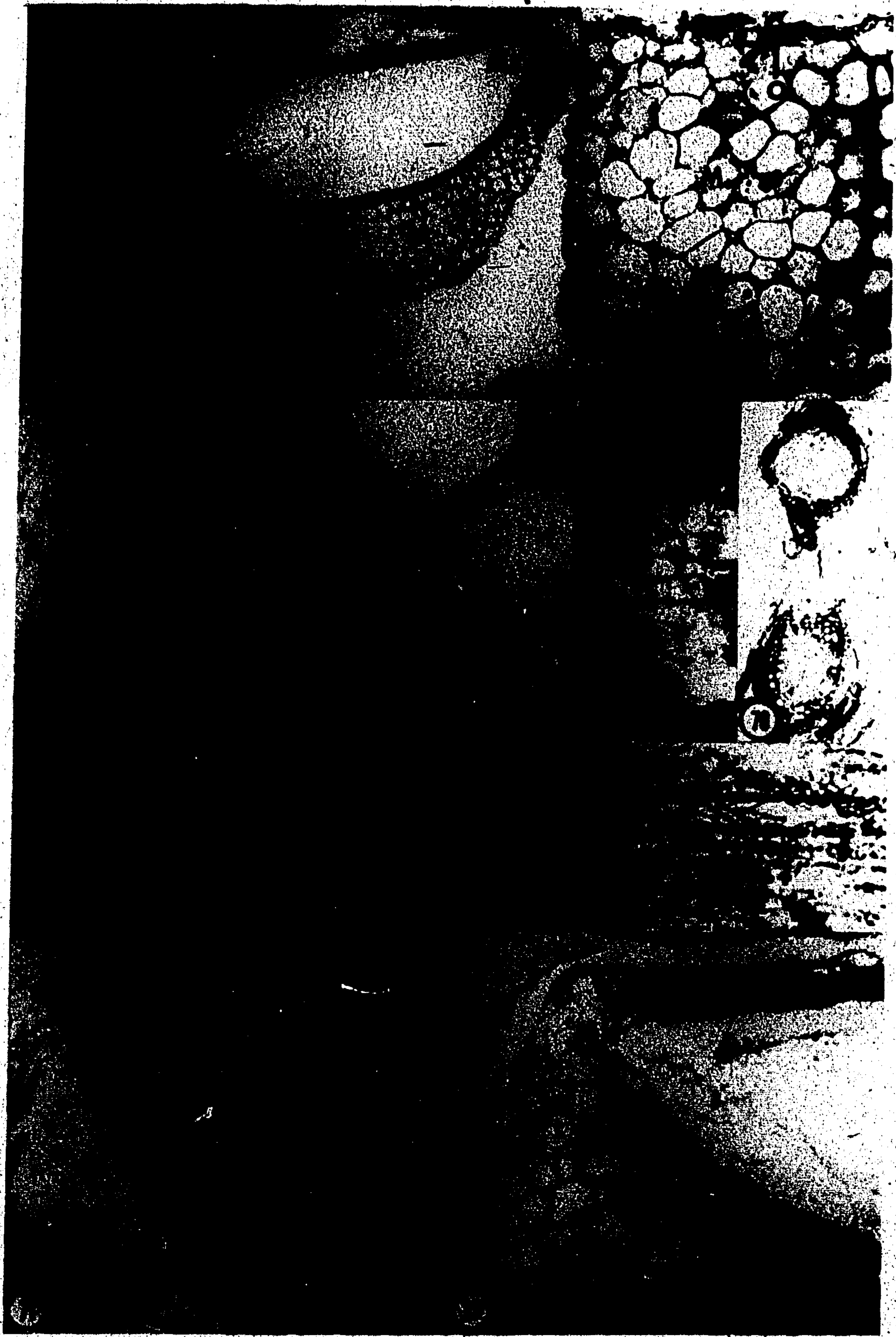

Plate 13.

Fig. 74 - 81. *Decodon* sp. seed and large lythraceous seed.

Fig. 74. Longitudinal section of seed showing embryo tissue. P 3794 C top #26 x 156.

Fig. 75. Chalazal end showing possible hypotase, suspensor and embryo. The three tissues are invaded by fungal hyphae. P 3794 C #27 x 235.

Fig. 76. Dicotyledoneous embryo. P 3794 C top #26 x 193.

Fig. 77. Large lythraceous fruit with several seeds. P 1906 B bot #23 x 10.

Fig. 78. Lythraceous seed showing outer integumentary layer with dark contents, middle integumentary layer with isodiametric cells and raphe. P 3771 C top #33 x 33.

Fig. 79. Lythraceous seeds showing hilum (arrow) and raphe. P 1906 B bot #23 x 30.

Fig. 80. Lythraceous seed showing raphe [illegible] middle layer of integument. P 1906 B bot #19 x 33.

Fig. 81. Iintegument showing outer and middle layers. P 3771 C top #33 x 300.

C = cotyledon, EM = embryo tissue, F = fruit, HY = hypostase, M = middle integumentary layer, N = nucellus, O = outer integumentary layer, R = raphe, SU = suspensor.

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Plate 14

Fig. 82 - 87. Vitaceous seeds (Vitaceae # 1 = 82 - 85; Vitaceae # 2 = 86, 87).

Fig. 82. Transverse section of seed (Vitaceae # 1) showing "W" shape due to two ruminations located opposite the chalaza. P 1912 D top #17 x 28.

Fig. 83. Transverse section of integument at rumination showing the possition of integumentary layers one, two, four and five. P 1789 G bot #7 x 39.

Fig. 84. Transverse section of chalazal end of seed. P 1789 G bot #11 x 101.

Fig. 85. Integument composed of tangentially elongated cells of layer five, a space representing layer four, radially elongated cells layer two, and tangentially elongated cells of layer one. P 1789 G bot #11 x 288.

Fig. 86. Transverse section of seed (Vitaceae # 2) showing "W" shape due to presence of two ruminations located opposite the chalaza. P 3984 F bot #3 x 22.

Fig. 87. Transverse section of integument showing tangentially elongated cells of layer five, cells with helical thickenings of layer three, and badly preserved cells of layer two. P 3984 F bot #3 x 260.

CH = chalazal end, 1 = integumentary layer one, 2 = integumentary layer two, 3 = integumentary layer three, 4 = integumentary layer four, 5 = integumentary layer five, RU = rumination.

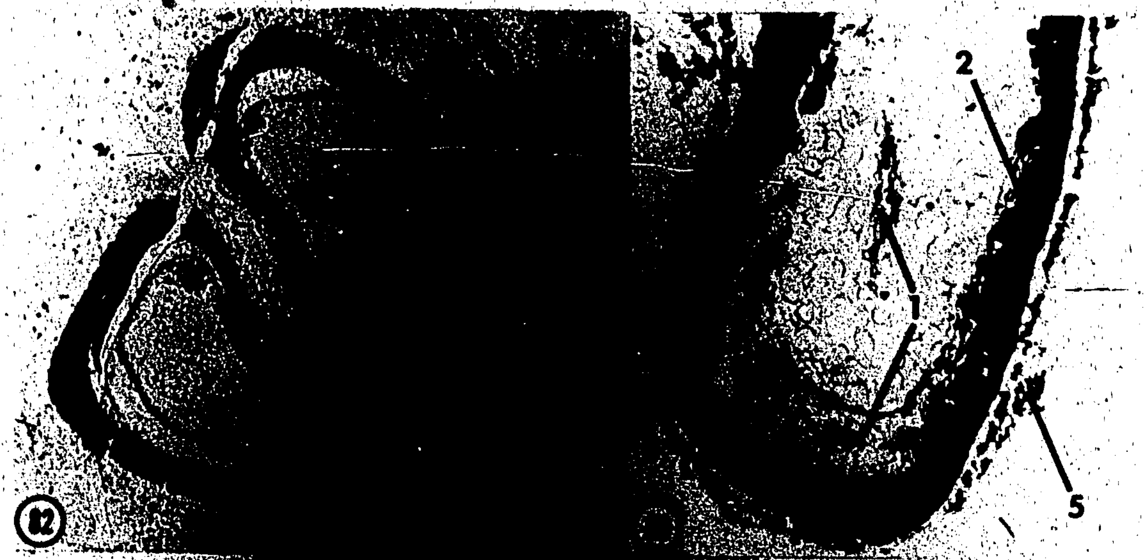

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Plate 15

Fig. 88 - 95. Vitaceous seeds (Vitaceae # 2 = 88 - 90; Vitaceae # 3 = 91 - 95).

Fig. 88. Transverse section of integument with tangentially elongated cells of layer five, and polyhedral cells of layer two. P 3984 bot #3 x 200.

Fig. 89. Transverse section of layer one with quadrangular to rectangular thin-walled cells. P 3989 F bot #3 x 280.

Fig. 90. Transverse section of layer two with polyhedral cells. P 3984 F bot #2 x 170.

Fig. 91. Transverse section of seed Vitaceae # 3 with a slight "W" shape. P 1912 D top #19 x 20.

Fig. 92. Transverse section of integument showing sclereids of layer five, a space representing layer four, tangentially elongated cells with helical thickenings of layer three, and irregular-shaped cells of layer two. P 1912 D top #3 x 200.

Fig. 93. Transverse section of integument showing isodiametric cells of layer three and rectangular to irregular-shaped cells of layer two. P 3984 F bot #0 x 384.

Fig. 94. Oblique section of sclereids of layer five. P 1912 D top #7 x 321.

Fig. 95. Embryonic tissue showing tracheids with helical thickenings. P 1912 d top # 7 x 200.

CH = chalazal end, 1 = integumentary layer one, 2 = integumentary layer two, 3 = integumentary layer three, 4 = integumentary layer four, 5 = integumentary layer five, RU = rumination.


(89)


(90)


(91)


(92)


(93)


(94)


(95)

## Plate 16

Fig. 96 - 101. Araceaous seeds.

Fig. 96. Oblique longitudinal section showing micropylar area, spines and ridges of integument. P 2592 B bot #4 x 32.

Fig. 97. Longitudinal section showing micropylar, chalazal, and raphe areas. P 2613 B bot #7 x 39.

Fig. 98. Cross section of seed showing spines and lysigenous spaces (arrow), endosperm and embryo. P 2541 D #1 x 36.

Fig. 99. Cross section of seed showing spines and lysigenous spaces. P2613 D bot #20 x 33.

Fig. 100. Cross section of seed showing spines and lysigenous spaces (arrows). Central space represents raphe, the lateral ones represent chalazal and micropylar areas. P 2613 E bot #30 x 39.

Fig. 101. Integument with lysigenous spaces. P 2613 D bot #14 x 67.

E = endosperm, EM = embryo tissue, F = possible fruit tissue, MI = micropylar area, N = nucellus, R = raphe.


MI
MI
EN
E
R

## Plate 17

Fig. 102 - 108. Araceous seeds.

Fig. 102. Oblique longitudinal section of micropyle area . P 2592 B bot #4 x 102.

Fig. 103. Cross section of seed showing showing rectangular nucellar cells. P 2613 D bot #35 x 156.

Fig. 104. Oblique cross section.showing micropylar opening. P 2613 B bot #4 x 128.

Fig. 105. Oblique longitudinal section of micropylar area with nucellus, endosperm and possible embryo cells. P 2613 G top #18 x 250.

Fig. 106. Longitudinal section at chalazal end, showing rectangular to polygonal nucellar cells. P 2613 B bot #10 x 78.

Fig. 107. Oblique longitudinal section of micropylar area showing rectangular nucellar cells. P 2613 G bot #35 x 350.

Fig. 108. Cross section showing nucellus, endosperm and embryo. P 2613 D bot #34 x 300.

E = endosperm, EM = embryo tissue, F = possible fruit tissue, MI = micropyle, N = nucellus.


N
E
E

Plate 18

Fig. 109 - 115, Araceous seeds.

Fig. 109. Longitudinal section of raphe showing polyhedral thin-walled cells. P 2613 E bot #33 x 350.

Fig. 110. Longitudinal section of seed showing embryo with one cotyledon, area of shoot apex, root apex and root cap. P 2613 E bot #24 x 120.

Fig. 111. Longitudinal section of raphe showing tracheids with helical thickenings. P 2613 B bot #10 x 339.

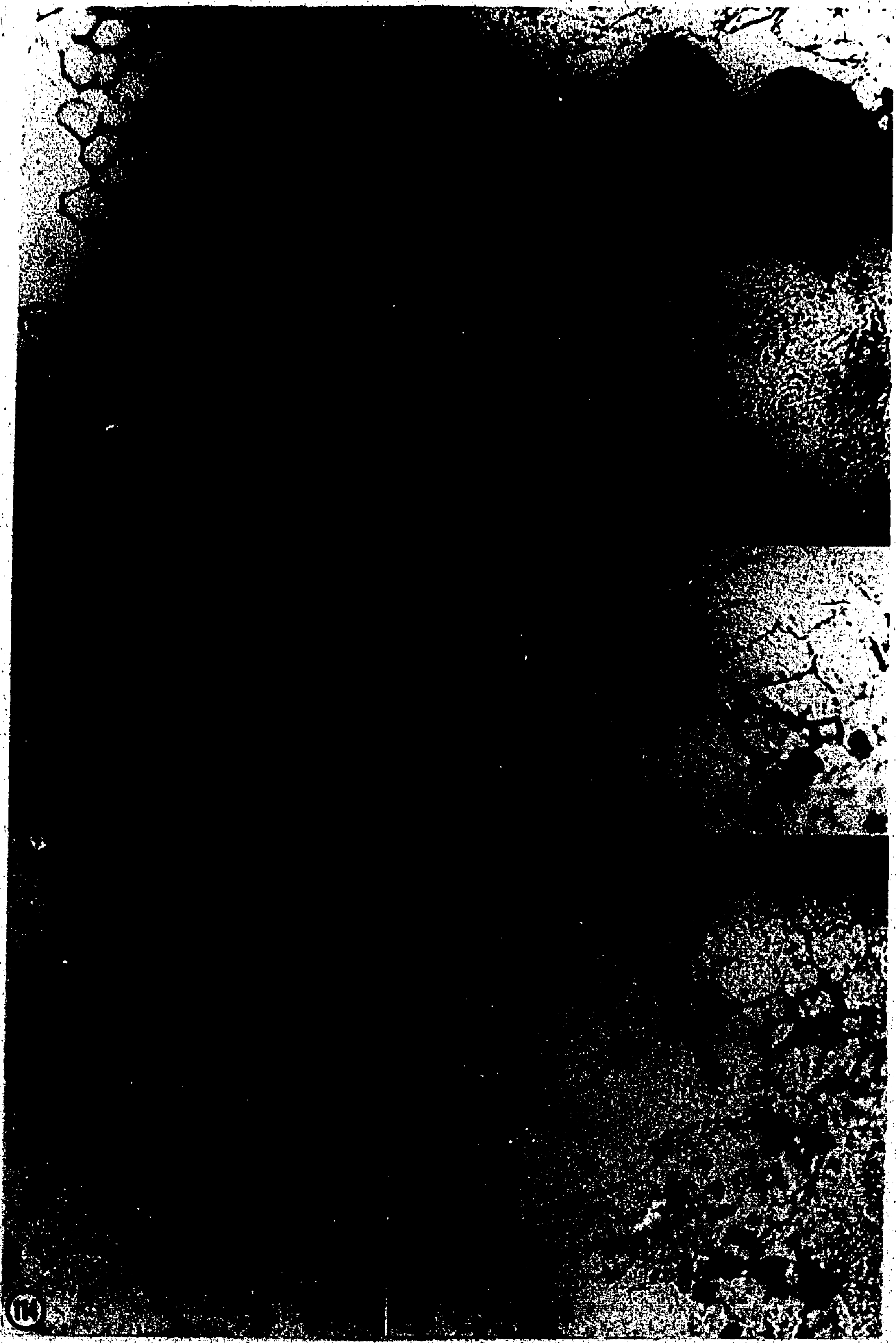
Fig. 112. Shoot apex area. P 2613 E bot #25 x 500.

Fig. 113. Shoot apex area with elongated cells of notch. P 2613 E bot #26 x 625.

Fig. 114. Root apex area with cells of root cap. P 2613 E bot #23 x 232.

Fig. 115. Shoot apex area showing tracheids with helical thickenings in hypocotyl. P 2613 E bot #26 x 312.

C = cotyledon, CN = cotyledonary node, RA = root apex, RC = root cap, SA = shoot apex, V = vascular bundle.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## Plate 19

Figs. 116 - 122. *Incertae sedis* fruit with one ruminate seed.

Fig. 116. Longitudinal section of seed with well developed ruminations and embryo tissue filling part of seed cavity. P 2077 F bot #1 x 30.

Fig. 117. Longitudinal section of seed with rumination. P 2077 F bot #8 x 30.

Fig. 118. Longitudinal section of seed with small rumination. P 2077 F bot #5 x 30.

Fig. 119. Longitudinal section of seed without rumination showing well developed nucellus and endosperm. P 2077 F #26 x 60.

Fig. 120. Integument showing three cell layers and nucellus. P 2077 F bot #27 x 234.

Fig. 121. Fruit and seed tissues near receptacular area showing a vascular bundle. P 2077 F bot #11 x 210.

Fig. 122. Fruit and seed tissues near receptacular area. P 2077 F bot #13 x 210.

E = endosperm, EM = embryo tissue, F = fruit, I = inner integumentary layer, M = middle integumentary layer, O = outer integumentary layer, RU = rumination, S = seed.


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Plate 20

Figs. 123 - 126. *Insertae sedis* ruminate seed.

Fig. 123. Seed with rumination and possible embryo tissue. P 2077 F bot #1 x 160.

Fig. 124. Seed with rumination and possible embryo tissue. P 2077 F bot #5 x 161.

Fig. 125. Nucellus and endosperm. P 2077 F bot #27 x 210.

Fig. 126. Endosperm with possible sclereid. P 2077 F bot #25 x 560.

E = endosperm, EM = embryo tissue, F = fruit, N = nucellus, RU = rumination, S = seed,
SC = sclereid, VB = vascular bundle.

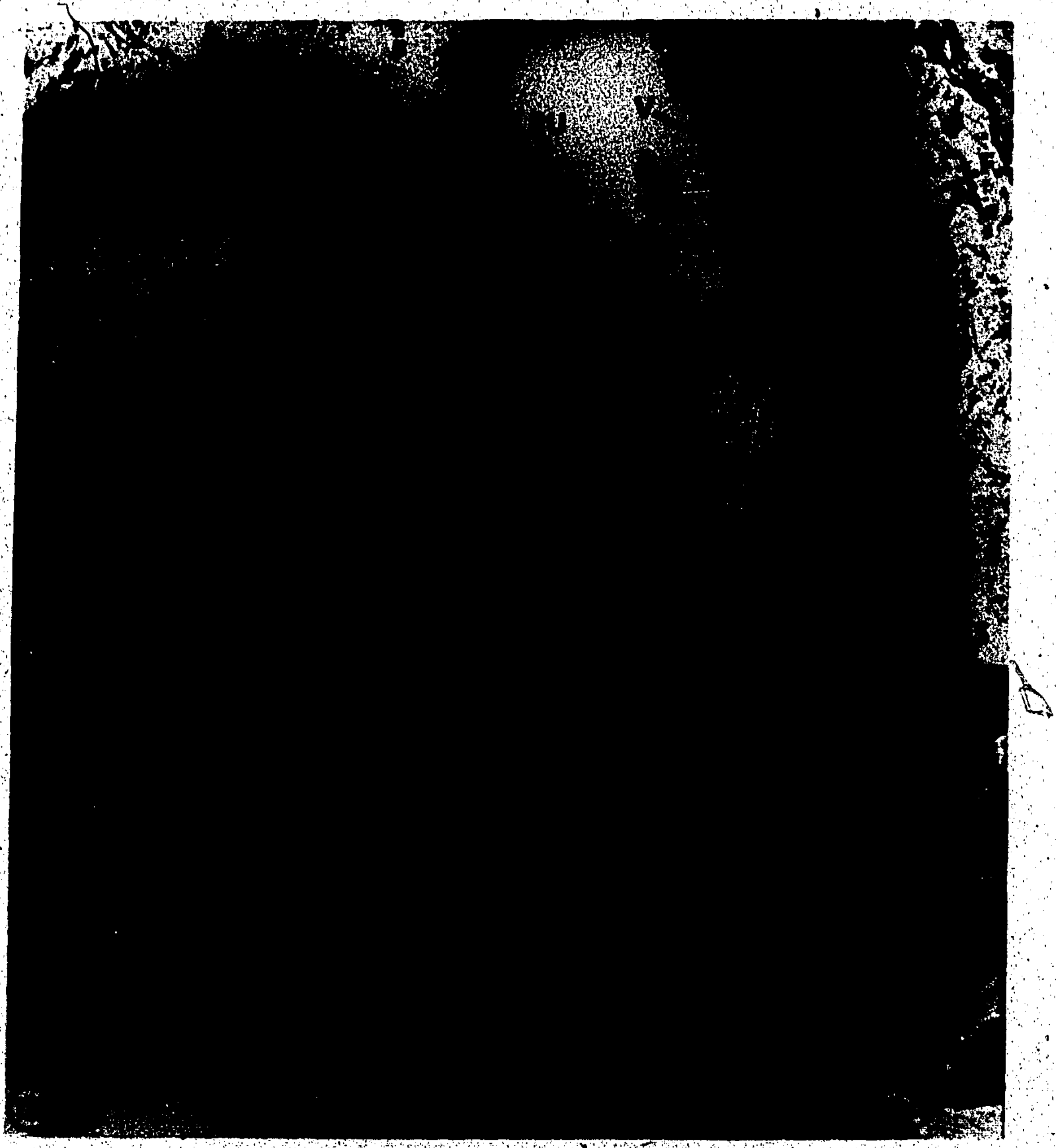

Plate 21

Figs. 127 - 136. *Insertae sedis* bilocular fruit.

Fig. 127. Tangential section of fruit showing three sepals (arrows). P 3773 B bot #19 x 80.

Fig. 128. Tangential section of fruit showing integument, pericarp and two sepals (arrows). Note presence of sclereids in sepal at right. P 3773 B bot #17 x 62.

Fig. 129. Longitudinal section of fruit showing seed, pericarp, and vascular bundle intruding seed cavity. Note elongated cells of the receptacle below the vascular bundle. P 3773 B bot #13 x 52.

Fig. 130. Longitudinal section of fruit showing pericarp and possible embryo tissue. P 3773 B bot #11 x 42

Fig. 131. Longitudinal section of fruit showing two locules with one seed with nucellusin the micropylar region and possible embryo tissue. P 3773 B bot #7 x 60.

Fig. 132. Integument showing inner palisade of sinuous cells, and quadrangular to rectangular cells, and outer layer of polyhedral to isodiametric cells beneath fruit wall tissue. P 3771 C top #29 x 160.

Fig. 133. Micropylar area showing nucellus. P 3771 C bot #33 x 160.

Fig. 134. Embryo tissues invaded by fungal hyphae. P 3771 A #9 x 430.

Fig. 135. Endosperm and nucellus. P 2077 F #25 x 480.

Fig. 136. Endoperm with sclereids. P 3771 C top #33 x 260.

E = endosperm, EM = embryo tissue, F = fruit, G = gland-like structure, N = nucellus, RE = receptacle, S = seed, V = vascular bundle.

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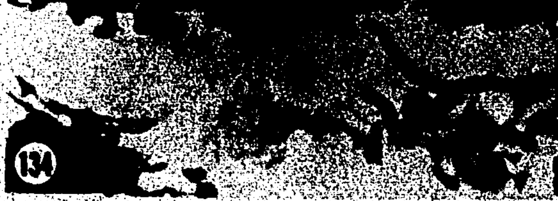

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## Plate 22

Figs. 137 - 14[illegible] *Insertae sedis* bilocular fruit.

Fig. 137. Cross section of fruit showing two vascular strands. P 3772 J top #18 x 60.

Fig. 138. Longitudinal section of fruit showing seeds with endosperm. P 3771 C top #33 x 60.

Fig. 139. Longitudinal section of one fruit locule with possible embryo tissue. P 3771 A #3 x 60.

Fig. 140. Receptacle cells and vascular tissue intruding seed cavity. P 3773 B bot #13 x 260.

Fig. 141. Longitudinal section of bilocular fruit showing tendency to split into two pyrenes. P 3771 A #7 x 70.

Fig. 142. Tangential view of surface of fruit showing irregularly shaped cells. (Outer side of fruit toward right.) P 3771 C top #19 x 130.

Fig. 143. Gland-like structure in fruit tissue. P 3772 J top #12.

Fig. 144. Group of sclereids in sepal. P 3773 B bot #17 x 260.

E = endosperm, EM = embryo tissue, F = fruit, I = inner integumentary layer, M = middle integumentary layer, N = nucellus, O = outer integumentary layer, RU = rumination, S = seed.

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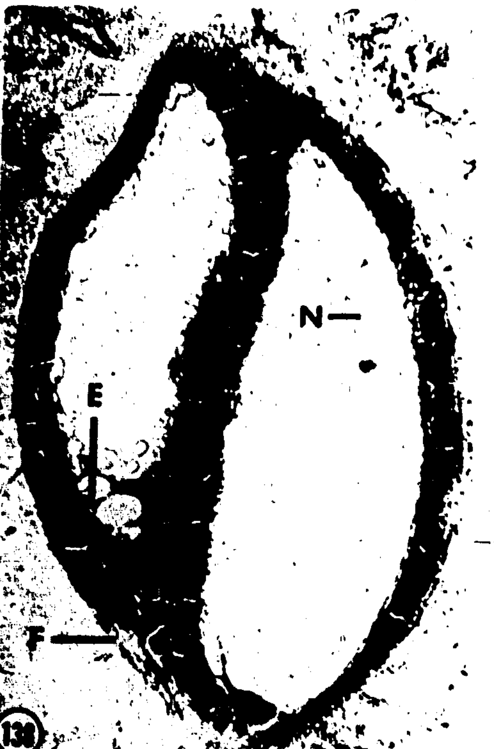

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