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Permineralized dicotyledonous remains from the Middle Eocene Princeton chert locality, British Columbia, Canada: Magnoliaceae and Rosaceae.

BY

Sergio Rafael Silvestre Cevallos-Ferriz

A THESIS SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH IN PARTIAL FULFILLMENT OF THE REQUIREMENTS FOR THE DEGREE OF
Doctor of Philosophy
IN
Paleobotany

DEPARTMENT OF BOTANY

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Permineralized dicotyledonous remains from the Middle Eocene Princeton chert locality, British Columbia, Canada: Magnoliaceae and Rosaceae.

SUBMITTED BY: Sergio Rafael Silvestre Cevallos-Ferriz

IN PARTIAL FULFILLMENT OF THE REQUIREMENTS FOR THE DEGREE OF
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To Verónica, Andrés, and María José

Abstract

The Middle Eocene Princeton chert from southern British Columbia represents a rich assemblage of permineralized plants that were growing during a time of important angiosperm radiation. Vegetative and/or reproductive organs of at least three plants in two families, Magnoliaceae and Rosaceae, are described. Twigs and wood of the Magnoliaceae represent the oldest known vegetative axes related to *Liriodendron*. A new species of *Liriodendroxylon* Prakash et al. is based on a unique combination of three characters in mature wood: opposite intervascular pitting, homocellular rays, and secondary phloem structure. Vegetative axes of a rosaceous plant exhibit characters in primary and secondary tissues of Subfamily Prunoideae of the Rosaceae. Vertical traumatic ducts and vessels in multiple radials in secondary xylem support their identification as *Prunus* L. In addition to *Prunus* vegetative axes, three ovoid, unicarpellate drupes have been placed in this taxon. Fruits are characterized by having sclerotic endocarps with distinct ventral sutures. Seeds are anatropous, bitegmic, ventrally attached to the carpel, with a ventral raphe and dorsal vascular plexus. Re-examination of the rosaceous flower, *Paleorosa* Basinger, shows new evidence for follicular fruits, seeds with embryos, a hypostase, and prolate, semitectate, columellate, tricolporate pollen. The intermediate characters of *Paleorosa* add strength to the hypothesis that subfamily Spiraeoideae may be ancestral to subfamily Maloideae. This study shows that several of the putative specialized characters in Rosaceae are present by the Middle Eocene. Affinities with modern groups, relative number of plant organs of the same type, *in situ* rooting, association with fresh water fauna, and anatomical/morphological adaptations indicate the presence of both aquatic and terrestrial plants at the chert locality.

Acknowledgments

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Special thanks are extended to my wife, Verónica, and children, Andrés and María José, for their constant support and encouragement throughout the years. Thank you also to the many friends that made our stay in Canada easier and more enjoyable. The support and advice from Dr. R. A. Stockey were very valuable and greatly appreciated.

Table of Contents

List of Tables

List of Plates

Introduction

The Princeton chert locality is located on the east bank of the Similkameen River, approximately 8.4 km SSW of the town of Princeton, British Columbia, and almost directly across the river from the abandoned mining camp of Ashnola (Basinger, 1976a). The first published description of the Princeton Basin sediments was that of Dawson (1879). The presence of Tertiary deposits in British Columbia was recognized earlier by Bauerman; however, 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 3 formations in the Princeton Basin (Lower Volcanic Formation, Allenby Formation, and Upper Volcanic Formation).

Biostratigraphic analysis has suggested an age of Lower Middle Eocene for the Allenby Formation based on the presence of *Pistillipollenites macgregorii* Rouse (Rouse and Srivastava 1970). Such grains have been reported in the Allenby Formation a number of times in the past (Rouse, 1962; Mathews and Rouse, 1963; Hills, 1965; Hills and Baadsgaard, 1967; Boneham,1968). However, *P. macgregorii* has also been found in Maestrichtian sediments and also now appears to be common in Paleocene sediments (Crepet, 1984). An Eocene age for the Allenby Formation was also proposed by Russell (1935) and Gazin (1953) due to the presence of *Trogosus* Marsh, a tillodontid mammal which is unknown from sediments younger than Middle Eocene. Finally, Wilson (1977a, 1977b, 1982) established a Middle Eocene age by comparing insect and fish faunas of Princeton and other equivalent basins. Plant micro- and megafossils also support the correlation of some of these Eocene basins (Rouse and Mathews, 1961). It is now accepted that the Allenby Formation in the Princeton-Tulameen area is synchronic with the Quilchena Beds of the Quilchena-Merritt area, the Tranquille Beds from the Tranquille-Red Point area, the upper section of the Kamloops Group in the Split Rock-McAbee area, the Horsefly River Beds in the Horsefly area and the Driftwood Creek Beds in the Francois

Lake-Smithers area. Potassium-argon dates from the Princeton ash (48 m.y.), near the Princeton-Black coal zone, and the Collins Gulch (47 m.y.), near the coal bearing strata of the Tulameen area also support a Middle Eocene age for the Princeton chert (Hills and Baadsgaard, 1967).

In his studies, Wilson (1980, 1988) also reconstructed Middle Eocene lacustrine environments of British Columbia. Three environments were recognized based on the presence and relative abundance of articulated fish remains, insects, coprolites, and plants: off-shore/deep water deposits, near-shore/shallow water deposits, and intermediate deposits. Taphonomic data suggest that the plants at the Princeton chert locality were deposited in a shallow, swampy, near-shore environment (e. g., Basinger, 1976a; Cevallos-Ferriz and Stockey, 1988a, 1988b, 1989; Erwin and Stockey, 1989; Wilson, 1982).

Fossil plant remains contain different types and amounts of information depending on how they are preserved. Early silicification protects plants or their remains from destruction due to compaction, biological degradation and transport (Knoll, 1985). The excellent preservation of plant material from the Princeton chert suggests that biological decomposition and lithological compaction in the chert layers from this locality were minimal. In fact, the Princeton chert locality contains one of the best preserved and probably most diverse silicified Tertiary floras (Basinger and Rothwell, 1977).

Permineralized plant material offers the unique opportunity to study the internal anatomy of vegetative and reproductive organs. Information retrieved through the study of this material broadens our understanding of the plants that bore these organs. While during the last 16 years extensive work has produced important insights on the anatomy, taxonomy, ecology, and biology of some Middle Eocene plants of this locality (e. g., Miller, 1973; Robison and Person, 1973; Basinger, 1976a 1976b, 1981, 1984; Basinger and Rothwell, 1977; Stockey, 1984, 1987; Cevallos-Ferriz and Stockey, 1988a, 1988b, 1989, 1990; Erwin and Stockey, 1989), there is still much to be learned from these plant remains.

Comparisons of the Princeton chert material with fossil plants of other localities are not always possible. Most Tertiary fossil localities have plants preserved as impression/compression fossils, and only a few localities have permineralized remains. However, the anatomy of most of these permineralized remains has been only partially described. In North America, the Eocene Clarno Formation has a diverse flora. Some of these remains are preserved as silica permineralizations and have been described in detail (e. g., Arnold, 1952; Arnold and Daugherty, 1963, 1964; Brown, 1975; Dennis, 1974). The morphology of fruits and seeds of the Clarno nuts was described by Scott (1954). Recently, it has been noted that many of these carpological remains have preserved internal cell structure (Manchester, 1987).

In Europe, the Eocene London Clay flora contains many different types of fruits and seeds (e. g., Reid and Chandler, 1933; Chandler, 1958, 1964, 1978; Collinson, 1983). Several remains of this fossil flora have been pyritized and allow anatomical study (e. g., Scott and Klerk, 1974; Collinson and Ribbins, 1977; Ribbins and Collinson, 1978; Wilkinson, 1981). Complete anatomical description of the London Clay reproductive organs is not always possible and their description is based mainly on morphological characters. Many of the plant organs so far studied from Princeton have been characterized on anatomical features. Thus, comparison of fruits and seeds of the Princeton chert and London Clay awaits more complete anatomical description of the fossils of the London Clay flora.

Permineralized plant remains of the Cretaceous-Eocene Deccan Intertrappean Series of India also have been subject to extensive investigation (e. g., Blanford, 1867; Sahni, 1931, 1941, 1943, 1947; Trivedi and Chandra, 1933; Rao, 1936; Shukla, 1944; Chitaley, 1955, 1964; Lakhanpal, 1970; Sahni, Rana, and Prasad, 1984). While some fossils from Princeton and India have been compared to the same extant taxon, differences occur. For example, in the Lythraceae, *Decodon allenbyensis* Cevallos-Ferriz and Stockey differs from *Enigmocarpon* Sahni in several characters including the smaller size, general shape, and integumentary anatomy (Cevallos-Ferriz and Stockey, 1988a). Palm remains are also known from these two localities and are currently under investigation by Erwin (1990, pers. commun.).

The present study began as a continuation of the preliminary survey on fruits and seeds of the Princeton chert made by Cevallos-Ferriz (1987). It has been noted that potential for angiosperm studies at the Princeton chert locality is excellent with several types of permineralized remains available, including flower buds, mature flowers, fruits, seeds, stems, wood, etc. (Basinger and Rothwell, 1977). Different developmental stages of many plant organs also allow for a more complete understanding of the particular plant organ. In addition, the well preserved anatomy here has allowed the reconstruction of whole plants (Rothwell and Basinger, 1979; Basinger 1981, 1984; Erwin and Stockey, 1987)

The present investigation increases our knowledge of the Middle Eocene Magnoliaceae and Rosaceae by describing vegetative and reproductive organs assignable to these families. Similarities and differences in plant characters have been used to assess closeness of relationship between genera in Magnoliaceae and Rosaceae. These two families have a scanty and dubious fossil record in pre-Eocene sediments, while their post-Eocene record is more complete. Documentation of these Princeton chert vegetative and reproductive remains is important since the source of some extant lineages, including members of Magnoliaceae and Rosaceae, may be found among these Eocene fossil remains. Detailed systematic treatment and the data base constructed may be used in future phylogenetic studies (Wolfe and Wehr, 1988).

In this new project, besides the examination of other fruits and seeds, vegetative axes were also investigated. The initial observations on vegetative axes showed that two of the several types observed have characters that can be correlated with the families

Magnoliaceae and Rosaceae. Fruit and seed observations also suggested that, among other reproductive structures, 3 endocarps each with an enclosed seed were related to Rosaceae. New specimens of a previously described rosaceous flower, *Paleorosa similkameenensis* Basinger, have been also discovered. I decided to study these Princeton chert fossil remains in order to document the occurrence of plant organs with similar organization to that of extant plants, and the amount of anatomical change in the vegetative and reproductive organs of these plants since the Middle Eocene.

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Magnoliaceae: vegetative axes*

Introduction

Vegetative and reproductive fossil remains from the Princeton chert locality, Allenby Formation, British Columbia, represent one of the best preserved and most diverse Tertiary floras. Detailed description and comparison of coniferous (Miller 1973, Rothwell and Basinger 1979, Basinger 1981, 1984, Stockey 1984), dicotyledonous (Robison and Person 1973, Basinger 1976a, Stockey 1987, Cevallos-Ferriz and Stockey 1988a, 1988b, 1989a, 1989b) and monocotyledonous (Erwin 1987, Erwin and Stockey 1989) remains have added to our knowledge of plant biology during the Middle Eocene. The well preserved plant remains from the Princeton chert promise to broaden our understanding of the whole plant biology of Tertiary angiosperms, gymnosperms, and ferns.

Among the dicotyledonous remains are several specimens of wood and twigs assignable to the Magnoliaceae. The family Magnoliaceae has a long fossil record with widespread occurrences, although not all reports are now accepted as valid (Wheeler et al. 1977, Baghai 1988). Leaves, fruits, probable perianth parts, and bud scales from the mid-Cretaceous (Crane and Dilcher 1985, Dilcher and Crane 1985, Ohana and Kimura 1987, Nishida and Nishida 1988) may be related to the Magnoliaceae. Vegetative and reproductive remains with undoubted affinity to the Magnoliaceae are known from Upper Cretaceous to Pleistocene sediments (e.g. Page 1970, Tiffney 1977, Muller 1981, Scott and Wheeler 1982, and Baghai 1988). Most authors follow the classification of the family by Dandy (1927). After 1927; however, several new genera were described, and recently modifications to this classification were proposed by Nooteboom (1985), who synonymized several of these genera. In the present study we describe a new species,

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* A version of this chapter has been accepted for publication: Cevallos-Ferriz, S. R. S. and Stockey, R. A. 1990. Can. J. Bot. 68:

Liriodendroxylon princetonensis sp. nov., based on magnoliaceous vegetative axes, with well preserved primary and secondary tissues, and compare them to extant and fossil axes assigned to this family.

Material and methods

One wood fragment and several magnoliaceous twigs have been found in the Princeton chert (Allenby Formation) 8 km south of Princeton, British Columbia. The Allenby Formation of the Princeton Group has been dated as Middle Eocene based on palynology (Rouse and Srivastava 1970), mammals and fishes (Russell 1935, Gazin 1953, Wilson 1977, 1982), and potassium-argon dating (Hills and Baadsgaard 1967). Specimens come from the east side of the Similkameen River, from a section consisting of an alternating sequence of chert and coal with an occasional thin ash bed replacing a chert layer. Forty-nine exposed layers of chert have been recorded and systematically sampled (Stockey 1987). The locality has been referred to as locality "I" (Boneham 1968) and the Princeton chert locality (Basinger 1976a, Stockey 1984, 1987).

Fossils are preserved as silica permineralizations. All chert blocks were cut into slabs and studied using the cellulose acetate peel technique modified for hydrofluoric acid (Joy et al. 1956, Basinger and Rothwell 1977). Peel sections were mounted in Coverbond xylene-soluble mounting medium for microscopic examination.

Extant woods of *Magnolia fraseri* Walt. (ALTA 57648, UAPC-ALTA Sl 1827), *M. tripetala* L. (UAPC-ALTA Sl 1828), *M. acuminata* L. (ALTA 26541) and *Liriodendron tulipifera* L. (ALTA 81863, UAPC-ALTA Sl 8117) were compared anatomically to the fossil wood. Dehydration began in 10%, 30%, and 50% EtOH and proceeded in tert-butyl alcohol series (TBA) (Johansen 1940). Paraplast Plus medium was used for infiltration and embedding. Sections 10-13 μm thick were cut on a rotary microtome and stained with safranin-fast green.

The identification of fossil material was aided by the computer-assisted identification system Guess v 1.1 and NCSU wood database (Wheeler et al. 1986;

LaPasha and Wheeler 1987). All averages represent a series of 25 separate measurements (Carlquist 1988).

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

Systematic description

Class: Magnoliopsida

Subclass: Magnoliidae

Order: Magnoliales

Family: Magnoliaceae

Genus: *Liriodendroxylon* Prakash et al.

Species: *Liriodendroxylon princetonensis* Cevallos-Ferriz et Stockey sp. nov.

Holotype: P1209 K.

Paratypes: P1235 C, P1728 B, P1786 A, P1728 A, P1720 E.

Diagnosis - Twigs and branches containing chambered pith. Pith with thin-walled parenchyma cells rectangular to polyhedral in cross section, containing septa of thick-walled parenchyma cells and sclereids, secretory cells polyhedral to oval in cross section. Protoxylem thickenings helical, metaxylem thickenings scalariform. Primary phloem with prominent fibrous bundle cap. Rectangular thin-walled cells of inner cortex with dark contents, outer cortex of smaller cells with fewer contents. Rectangular epidermal cells with thick cuticle. Diffuse porous secondary xylem; transverse outline of vessel elements angular, vessel elements solitary or in, radial multiples, and clusters, with oblique, scalariform perforation plates; scalariform, transitional and opposite intervascular pitting; thin-walled tyloses. Imperforate tracheary elements with circular bordered pits on radial walls. Multiseriate rays heterocellular and homocellular, two to four cells wide; uniseriate rays up to 10 cells high with upright cells; ray to vessel pits similar to or slightly smaller than intervascular pits. Marginal parenchyma present. Secondary phloem with dilated rays, irregular alternating bands of fibers and thin-walled cells, some ray and axial cells sclerified. Up to four rows of rectangular thick-walled periderm cells present.

DESCRIPTION

PRIMARY TISSUES

Twig fragments 0.6 cm to 1.3 cm in diameter with a chambered pith are easy to recognize in the chert (Pl. II, 1 Fig. 1). The largest fragments are about 4 cm long (Pl. II, 1 Fig. 2). A fragment of a larger branch, 3.2 x 6.1 cm, in which pith cannot be observed, is also known.

The pith is composed mainly of axially oriented thin-walled parenchyma cells, rectangular to polyhedral in shape, ranging from 26 to 48 µm in transverse section, 37 to 50 µm in tangential section, and 35 to 70 µm in radial section (Pl. II, 1 Fig. 3). Strands of rectangular to polyhedral thick-walled parenchyma cells and sclereids traverse the pith (Pl. II, 1 Figs. 1-3). Secretory cells occur at the pith boundary near the primary xylem bundles (Pl. II, 1 Figs. 4, 5). These cells are polyhedral to circular in outline, averaging 60 x 48 x 50 µm, and can be easily distinguished by their red to brown contents (Pl. II, 1 Figs. 4, 5).

Protoxylem cells are polyhedral in transverse section, averaging 14 µm in diameter, and have spiral secondary wall thickenings (Pl. II, 1 Fig. 6). Metaxylem cells, averaging 21 µm in diameter, are polyhedral to oval and have helical to scalariform secondary wall thickenings (Pl. II, 1 Figs. 4, 6, 7). Metaxylem cells near the secondary xylem have anastomosing scalariform thickenings (Pl. II, 1 Fig. 8). Primary phloem in these twigs is represented by phloem fibers, polyhedral to oval in transverse section, and averaging 24 µm in diameter (Pl. II, 1 Fig. 9). Sieve tube elements are not preserved, and are represented by a gap in tissue preservation.

The inner cortex is several cells thick and composed of rectangular to polyhedral cells, averaging 72 x 60 x 60 µm, with thin walls (Pl. II, 1 Fig. 9). The outer cortex is composed of fewer cell layers, has smaller cells with fewer dark contents, and clusters of stone cells (Pl. II, 1 Figs. 1, 10).

Epidermal cells are not well preserved on most twigs, but small, rectangular cells covered with a thick cuticie can be seen in some specimens (Pl. II, 1 Fig. 10). Periderm is composed of up to four layers of rectangular thick-walled cells averaging 12 x 36 x 24 µm (Pl. II, 1 Fig. 10).

SECONDARY TISSUES

Twigs - During the first year of secondary growth, vessel elements in transverse section are small, solitary and in radial multiples, averaging 27 µm (range 18-30 µm) in tangential x 33 µm (range 24-39 µm) in radial diameter (Pl. II, 2 Fig. 11). In the second growth increment vessel elements are larger, averaging 36 µm (range 21-39 µm) in tangential x 42 µm (range 30-51 µm) in radial diameter. Vessel arrangement also changes during the second increment. Solitary vessels are not as frequent as in the previous growing season, clusters of vessel elements are common, and radial multiples of vessels are typical (Pl. II, 2 Fig. 12). In the third growth season, in the most complete transverse section, vessels are mainly arranged in radial multiples and some clusters, averaging 46 µm in tangential x 62 µm in radial diameter (Pl. II, 2 Fig. 12). Vessel shape in transverse section is mostly angular with ca. 80 vessels per square millimeter (Pl. II, 2 Figs. 11, 12). The boundary between two growing seasons is marked by the presence of rectangular cells, averaging 30 x 24 x 108 µm, representing marginal parenchyma four to six cells wide (Pl. II, 2 Fig. 13). Imperforate tracheary elements, polyhedral in transverse section, show moderately thick walls. Most of the radial system in twigs consists of medullary rays.

In longitudinal section vessel elements average 670 µm in length and have oblique [illegible], with scalariform perforation plates (Pl. II, 2 Figs. 16, 17). The number of bars per perforation plate is variable, ranging from 8 to 18 (Pl. II, 2 Figs. 16, 17). Intervascular pitting is mainly scalariform; however, transitional and opposite intervascular pits are present in many vessel elements (Pl. II, 2 Fig. 19). Pits are oval and bordered when scalariform, but their shape is almost rectangular when they are opposite. Thin-walled tyloses are frequently found in vessels. Imperforate tracheary elements have circular bordered pits on radial walls. Parenchyma cells of the marginal bands are thin-walled with simple pits on tangential walls (Pl. II, 2 Fig. 13). Rays are heterocellular with one or two rows of upright cells at the margins (Pl. II, 2 Fig. 18). Multiseriate rays, two to four cells wide, are most common and are 8 to 40 cells high, averaging 713 µm (range 67-990 µm). A few uniseriate rays, two to 10 cells high, are also present. Ray to vessel pits are similar or slightly smaller than intervascular pits, oval in outline, and arranged in a scalariform or opposite pattern, but other irregular patterns can be seen (Pl. II, 2 Figs. 14, 15).

Between secondary phloem and secondary xylem a zone of thin-walled cells probably represents the vascular cambium (Pl. II, 3 Fig. 20). In transverse section the secondary phloem is composed of dilated rays and irregular alternating bands of fibers and large thin-walled cells (Pl. II, 3 Figs. 21, 25). The identification of sieve tube members is difficult; however, cells with large diameters and oblique end walls probably represent sieve tube members. Some oblique end walls have perforations suggesting the presence of a sieve plate, but in most cells it is difficult to see this feature. Sieve tube members tend to be oval in transverse section, and measure ca. 78 x 30 x 168 µm. Companion cells have not been identified. Phloem fibers are polyhedral in transverse section (Pl. II, 3 Fig. 25), and moderately thick-walled. Rays are composed of procumbent cells except at the top and bottom margins where one or two rows of upright cells are present (Pl. II, 3 Figs. 22, 23). In longitudinal section near the cambial zone, multiseriate phloem rays are two to three cells wide and up to 19 cells high (Pl. II, 3 Fig. 23). Uniseriate rays are rare in the phloem and up to four cells high. Some phloem ray cells have yellow contents, suggesting that they may have had a secretory function like those in the genus *Talauma* Juss. and some species of *Magnolia* L.

Wood fragment - In addition to these twigs a piece of wood of the same type with more than 10 growth increments has been found (Pl. II, 4 Fig. 26). Qualitatively this wood fragment is very similar to the twigs; however, rays in the wood fragment are homocellular, one to four cells wide and up to 28 cells or averaging 663 µm (range 424-915µm) high (Pl. II, 4 Figs. 27, 28). Rays in twigs are heterocellular and taller. Opposite intervascular pitting is more common than scalariform (Pl. II, 4 Figs. 27, 29), and imperforate tracheary elements with bordered pits are better preserved than in twigs (Pl. II, 4 Fig. 30). All other characters differ only quantitatively. For example, vessel elements are larger than in twigs, averaging 90 µm (range 49-106) in tangential diameter by 110 µm (range 84-119µm) in radial diameter. The number of bars per perforation plate ranges from 9 to 27 (8 to 18 in twigs). Small amounts of secondary phloem with anatomical organization similar to that of twigs are present in the wood fragment. The main difference between these remains is the frequent occurrence of sclerotized ray parenchyma cells and heavy deposition of secondary wall in the phloem fibers (Pl. II, 3 Fig. 24). Thus, the wood and twigs probably represent the same taxon.

DISCUSSION

Comparison with extant plants - Quantitative and qualitative variation in wood within the same taxon is well documented (e.g. Bailey and Tupper 1918; Baas 1976; Fahn et al. 1986; Carlquist 1975, 1977, 1980, 1988). Like most woods of the Princeton chert the specimens described here are represented mainly by small twigs where some difficulties in identification are encountered due to the presence of juvenile wood. Structural differences between juvenile and mature wood may include amount and type of axial parenchyma, ray structure, and dimensions and frequency of tracheary elements (Carlquist 1975, 1988). Little is known about the factors causing these differences, or their duration (Page 1979). The importance of comparing material produced by the same-aged cambium was emphasized by Carlquist (1961). In recent years it has been suggested that some characters remain constant at any topographic level in the above ground parts of woody plants (Schweingruber 1978). In studies of the Betulaceae, Fagaceae, Platanaceae, and Salicaceae, basic vessel distribution, perforation plate type, and type of ray to vessel pitting are constant characters (Schweingruber 1978). Our studies of magnoliaceous twigs also suggest this constancy and support the assignment of the fossil twigs and larger branch to the same taxon based on the following characters: (1) scalariform perforation plates, (2) diffuse pore distribution with vessels arranged solitarily, in radial multiples and clusters, (3) ray to vessel pits that are similar or slightly smaller than intervascular pits, (4) vessels with thin-walled tyloses, (5) marginal parenchyma, and (6) imperforate tracheary elements with circular bordered pits. Differences between the two include presence of opposite intervascular pitting and homocellular rays in the branch in contrast to mainly scalariform and transitional intervascular pitting and heterocellular rays in the twig. Other minor quantitative differences include the number of bars per perforation plate, diameter of vessel elements, and number of vessel elements per square mm.

Fifteen genera in 6 families of angiosperms show the combination of characters in the wood described here, using the computer-aided wood identification program of Wheeler et al. (1986). The characters used were: solitary vessels and radial multiples (characters 1-4, absent), scalariform perforation plate (character 6 absent, 7 present), opposite or scalariform intervascular pitting (character 11 present), presence of marginal parenchyma (character 57 present), and wood diffuse porous (characters 85, 86, absent). They include: Betulaceae, Cercidiphyllaceae, Eucryphiaceae, Eupteleaceae, Magnoliaceae, and Myristicaceae. Several anatomical differences are found between the genera in these families and *Liriodendroxylon princetonensis* (Wheeler et al. 1986, LaPasha and Wheeler 1987, Metcalfe and Chalk 1950a, 1950b). Rays with two distinct widths (character 33) are present in *Alnus* (Tourn.) L. (Betulaceae) and *Euptelea* Sieb. & Zucc. (Eupteleaceae). Vessel elements with helical thickenings (character 9) are characteristic of *Cercidiphyllum* Sieb. & Zucc. (Cercidiphyllaceae). Axial parenchyma is predominantly diffuse and in uniseriate bands (characters 46, 52) in *Eucryphia* Cav. (Eucryphiaceae), and it is paratracheal (characters 47, 48) in *Compsoneura* Warb., *Gymnacranthera* Warb., *Iryanthera* Warb. and *Knema* Lour. (Myristicaceae).

Anatomical comparison of the wood of nine of the ten extant genera of the Magnoliaceae (Dandy 1927) to *Liriodendroxylon princetonensis* is given in Table II, 1. Data for *Pachylarnax* Dandy is lacking. Mature wood of the Magnoliaceae has been described by McLaughlin (1933), Metcalfe and Chalk (1950a), Canright (1955), Gottwald (1972), Nooteboom (1985), and Metcalfe (1987). Magnoliaceous genera can be divided into two groups based on the type of intervascular pitting (Table II, 1). Presence of opposite intervascular pitting in mature wood of *L. princetonensis* suggests a potential relation to *Liriodendron* L. Other extant taxa have scalariform to transitional pits, except for *Magnolia fraseri* and *M. tripetala* which also have opposite intervascular pitting (Scott and Wheeler 1982), and *Alcimandra* Dandy which has some opposite pitting in older wood (Canright 1955). However, *Liriodendron* usually has vessel distribution of the solitary and radial multiple type as in *Alcimandra, Elmerrillia* L., *Kmeria* Pierre, *Manglietia* Blume, *Michelia* L., and *Talauma* Juss. Vessel clusters, as in *Liriodendroxylon princetonensis*, have been observed in extant *Liriodendron* (Wheeler 1989, pers. comm.), and the vessel outline in transverse section of the fossil looks no more angular than the samples of extant *Liriodendron, Alcimandra* and *Magnolia* (Table II, 1). *Aromadendron* Blume differs from the fossil wood in having distinct solitary vessel distribution and helical thickenings in vessels (Table II, 1). The presence of oil cells on ray margins in *Aromadendron, Elmerrillia, Michelia*, and some species of *Magnolia* and *Talauma* distinguishes them from the Princeton wood, since the latter lacks oil cells in this tissue (Table II, 1). In *Elmerrillia* and *Kmeria* vessel distribution is mainly of the solitary type with a few radial multiples and intervascular pitting is only scalariform and, therefore, different from the Princeton wood (Table II, 1).

The phloem of *Liriodendroxylon princetonensis* also contains important characters that clearly relate it to the Magnoliaceae. These include the orderly radial series of thin-walled cells and fibers, slightly dilated rays, and the presence of sclerotized ray parenchyma and axial cells (Cheadle and Esau 1964; Pl. II, 4 Figs. 31, 33).

The best studied phloem of modern Magnoliaceae is that of *Liriodendron tulipifera* (Cheadle and Esau 1964, Zahur 1959). In this species the sieve tube members are the cells with the widest diameter, as in the fossil axes. When functional they have a distinct crenulate nacreous wall that is absent in sieve areas. This character is less distinct in nonfunctional phloem. Sieve plates are mostly oblique in *L. tulipifera*, but some are transverse and have five sieve areas per plate. Sieve plates have not been observed in *Liriodendroxylon princetonensis*; however, cells that may represent sieve tube members have oblique end walls as in extant phloem. Companion cells are short and narrow in *Liriodendron tulipifera*, with four per sieve tube member. They are as wide as sieve tube members in tangential section, but narrower in radial diameter. In *Liriodendroxylon princetonensis* companion cells have not been observed. In both extant and fossil plants some phloem parenchyma cells have lignified secondary walls. Phloem fibers in tangential section are as wide as the sieve tube elements, but are narrower in radial diameter. In addition to fibers and sclerified parenchyma, sclereids are present occasionally in the phloem of *Liriodendron tulipifera* (Cheadle and Esau 1964, Zahur 1959). Rays in both fossil and extant taxa are heterocellular with square marginal cells, variable in height, up to four cells wide, and may develop lignified secondary walls. Oil cells also occur in some rays of *L. tulipifera*. Some cells with yellow contents in the Princeton twigs are associated with the ray tissue and may represent oil cells or other types of secretory cells. In contrast to the banded arrangement of the sieve tube elements and fibers typical of *L. tulipifera*, some species of *Magnolia* such as *M. acuminata* and *M. tripetala* have an irregular scattered distribution of sieve tube members, as in *Liriodendroxylon princetonensis* (Canright 1955, Zahur 1959). Thus, phloem anatomy suggests a potential relation of *L. princetonensis* to *Magnolia* rather than to *Liriodendron*.

Chambered pith is often found in Magnoliaceae (Metcalfe and Chalk 1950a, Metcalfe 1987). We observed it during this study in *Magnolia fraseri, M. tripetala, Liriodendron tulipifera,* and *Talauma mexicana* Don. In both extant Magnoliaceae and *Liriodendroxylon princetonensis* septa traverse the entire pith. Secretory cells in parenchymatous tissue are also widespread in magnoliaceous taxa; however, as with the chambered pith, they do not serve as diagnostic features for lower taxonomic categories.

The cortex of *Magnolia* and *Manglietia* contains stone cells and/or branched sclerenchymatous idioblasts (Metcalfe and Chalk 1950a). Holm (1909) reported these types of cells in *Liriodendron*. Young stems and twigs of *Magnolia tripetala* and *Liriodendron tulipifera*, examined during this study, have some irregularly distributed thick-walled cells in the cortex (Pl. II, 4 Fig. 31). The cortex of *Liriodendroxylon princetonensis* is homogeneous, composed of thin-walled parenchyma cells. Isolated thick-walled idioblasts have not been observed. However, sclerotic nests do occur in the outer cortex.

Presence of the primary phloem fibers at the boundary of the secondary phloem and cortex is a feature shared by extant magnoliaceous taxa and twigs from Princeton. Periderm in *M. tripetala* and *Liriodendron tulipifera* is very similar to that of *Liriodendroxylon princetonensis* and adds little to distinguish these genera.

Comparison with fossil Magnoliaceae - Fossil remains with affinities to Magnoliaceae are recognized in the Cretaceous (e.g. Heer 1870, Page 1970, Tiffney 1977, Baghai 1988). However, these plant remains have not been related to a particular taxon in the family due to many overlapping characters found in both fossil and extant members of Magnoliaceae. Some of these reports need to be reinvestigated (Baghai 1988). It is not until the Eocene that *Magnolia, Talauma,* and *Michelia* are recognized based on seeds (e.g. Reid and Chandler 1933, Chandler 1964, Palamarev 1973, Tiffney 1977). *Manglietia* has been recognized in Oligocene sediments based on seed remains (Mai 1971) and was probably present during the Eocene (Tiffney 1977). *Magnolia* is also identifiable by this time based on wood fragments (Scott and Wheeler 1982), whereas wood of *Michelia* is known from the Oligocene (Suzuki 1976). During the Eocene a number of woods show magnoliaceous characteristics (*Magnoliaceoxylon* Wheeler et al., *Magnolioxylon* Hofmann, and *Liriodendroxylon* Prakash et al.), but cannot be related with confidence to any extant genus (Wheeler et al. 1977, Scott and Wheeler 1982, the present study). Taxa related to extant species are known only from late Tertiary deposits.

Wheeler et al. (1977) proposed the genus *Magnoliaceoxylon* for magnoliaceous wood which cannot be allied to any extant genus. *Magnoliaceoxylon panochensis* (Page) Wheeler, Scott & Barghoorn from the Upper Cretaceous of California is distinct from the Princeton wood in having mostly solitary vessels (few clusters), diffuse and paratracheal axial parenchyma, and rays with uniseriate margins two to three cells high (Table II, 2). *Magnoliaceoxylon wetmorei* Wheeler, Scott & Barghoorn from the Eocene sediments of Yellowstone National Park, Wyoming, differs from the Princeton wood in having larger ray to vessel pits compared to intervascular pits, and rays with uniseriate margins composed of one to five rows of upright and square cells (Table II, 2, Wheeler et al. 1977).

Scott and Wheeler (1982) described two fossil species of *Magnolia* from the Eocene Clarno Formation of Oregon, *M. longiradiata* and *M. angulata*. Both plants have wood with scalariform and opposite intervascular pitting, as does the large wood block from Princeton. However, the fossil *Magnolia* taxa have heterocellular rays, while the mature wood of *L. princetonensis* has homocellular rays. *Magnolia longiradiata* differs further from *L. princetonensis* by the presence of a single inflated marginal ray cell (Table II, 2).

Magnoliaceous woods have also been reported from Europe; however, some of these may be misidentified and a reinvestigation is needed (Kramer 1974, Wheeler et al. 1977). Among those classified by Kramer (1974) as Magnoliaceae is *Magnolioxylon parenchymatosum* from the Oligocene brown coal localities of the Maria Theresia pit at Herzogenrath, Zukunft West pit at Eschweiler, Victor pit at Zuplich, and the Fischer clay pit at Adendorf, all in The Netherlands (van der Burgh 1973). These differ from the Princeton material in having only scalariform intervascular pitting, vessel elements with helical thickenings, apotracheal parenchyma bands up to three cells wide and rays that are up to triseriate (Table II, 2). *Magnolioxylon krauselii* (Greguss) van der Burgh from the Sarmientan of Nogradszakah, Hungary, has solitary vessel elements or multiples of two, perforation plates that are scalariform and simple, and rays that are uni- or biseriate (Table II, 2, Greguss 1969). *Magnolioxylon scandens* Schönfeld differs from the Princeton wood in the presence of simple and scalariform perforation plates, the latter with as many as 33 bars (Table II, 2, Schönfeld 1958). *Magnolia* sp. from the Lower Pleistocene of Tegelen, The Netherlands, differs from *Liriodendroxylon princetonensis* in having vessel elements with spiral thickenings, paratracheal parenchyma, and only scalariform intervascular pits (Table II, 2, van der Burgh 1974).

Michelia oleifera was described from the Oligocene of the Tsuyasuki Formation, Fukuoka, Japan (Suzuki 1976). The wood of this plant differs from that of Princeton in having fewer (7-15) bars per perforation plate, helical thickenings in vessel elements, marginal parenchyma bands two to 14 cells wide, and large oil cells in both axial parenchyma and multiseriate rays (Table II, 2).

Among the magnoliaceous fossil remains those of *Liriodendroxylon* are most similar to the Princeton fossils. *Liriodendroxylon tulipiferum* Prakash et al. (1971) from Tertiary sediments of Bohemia is very similar to *L. princetonensis*, but differs in having heterocellular rays five or more cells wide, and lacks clusters of vessel elements. *Liriodendroxylon multiporosum* Scott and Wheeler (1982) from the Eocene Clarno Formation of Oregon shares many features with *L. princetonensis*, but differs in lacking scalariform intervascular pitting, and having less angular vessel elements in transverse section, and occasional clusters of vessel elements. Further minor differences between the three species of *Liriodendroxylon* are quantitative (Table II, 2). Variation between the species of *Liriodendroxylon* and the Princeton wood probably reflects differences in the age of the plant part, or differences due to environmental factors. We prefer to name a new species since primary tissues and secondary extraxylary tissues of the Princeton material are important in the diagnosis. These tissues are unknown in the other fossil woods making comparisons very difficult. The discovery of extraxylary tissues in material from Oregon and Europe would enable closer comparisons with the Princeton material.

Environmental inferences - Aquatic affinities of some plants of the Princeton chert locality can be suggested based on plant anatomy, the systematic relationships of fossil taxa to extant forms, and plant habit. For example, presence of aerenchyma in the cortex and leaves of *Eorhiza* Robison and Person (1973) and in some palm roots (Basinger 1976b) can be correlated with an aquatic environment. Monocots (Alismataceae) from this locality have cells with suberized inner walls that surround the protoxylem lacunae characteristic of many aquatics (Tomlinson 1982, Erwin and Stockey 1989). Plants with systematic affinities to aquatic or semi-aquatic plants include *Keratosperma* (Araceae) Cevallos-Ferriz and Stockey (1988b), *Allenbya* (Nymphaeaceae) Cevallos-Ferriz and Stockey (1989a), *Heleophyton* (Alismataceae) Erwin and Stockey (1989), and *Decodon* (Lythraceae) Cevallos-Ferriz and Stockey (1988a).

There is, however, another group of plants at this locality that apparently do not have aquatic or semi-aquatic affinities. This group is represented by seeds, twigs, and other disarticulated organs that are found less commonly and probably indicate that these plants grew in an adjacent community. Among these remains are seeds of *Ampelocissus* Planch. (Vitaceae), two other vitaceous seeds Cevallos-Ferriz and Stockey (1989b), seeds and wood of *Prunus* L., flowers of *Paleorosa* Basinger (Rosaceae) (Basinger 1976a, Cevallos-Ferriz 1989c) and the vegetative remains of *Liriodendroxylon*. Remains of *Pinus* and *Metasequoia* are very abundant in the chert and certainly form part of the surrounding vegetation.

Anatomical characters of the Princeton chert plants provide information on the general ecology of this area during the time of deposition. While growth rings in the woods of the Princeton chert indicate some type of seasonality, the presence of diffuse porous woods (e. g. *Liriodendroxylon* and *Eorhiza*) suggest it was not pronounced. In accordance with the evidence so far available, *Liriodendroxylon* grew in a wet, warm to temperate seasonal environment. Carlquist (1987, pers. comm.) suggested that the anatomical characteristics of the angiosperm twigs from the Princeton chert are similar to plants that form rain forest vegetation, but that more detailed studies of all the wood types present in the chert would be necessary to confirm this.

Liriodendroxylon princetonensis represents the oldest known plant with affinities to *Liriodendron* and the first example of anatomically preserved magnoliaceous phloem. Anatomy of the vegetative axes of this fossil plant clearly shows the difficulty in distinguishing (based on anatomical characters) species of *Magnolia* and *Liriodendron*. The overlapping of anatomical characters, not only in wood and phloem structure, but in leaf and seed anatomy within Magnoliaceae, suggests the need for a revision of fossil magnoliaceous material in accordance with the new arrangement of the family proposed by Nooteboom (1985). *Liriodendron*, however, was not discussed in the revision of the family by Nooteboom (1985) and much is unknown about its relationship to other taxa within the Magnoliaceae. It is hoped that eventually knowledge of root, leaf, flower, and seed remains associated with this wood in the Princeton chert will enable a greater understanding of these isolated remains in terms of whole plants and a closer comparison with extant taxa.

Plate II, 1

Liriodendroxylon princetonensis gen. et sp. nov., twigs.

Fig. 1. Transverse section. P1235 C top No. 0. x 8.

Fig. 2. Oblique longitudinal section. P1728 B top No. 3. x 1.2.

Fig. 3. Longitudinal section of pith with septa. P1728 A side No. 2. x 26.

Fig. 4. Transverse section of pith-primary xylem boundary with secretory cells (arrows). P1728 A1 side No. 1. x 29.

Fig. 5. Longitudinal section of primary xylem with secretory cells (arrows) in medullary rays. P1728 A side No. 2. x 25.

Fig. 6. Longitudinal section of primary xylem with helical and scalariform thickenings. P1786 A side No. 2. x 164.

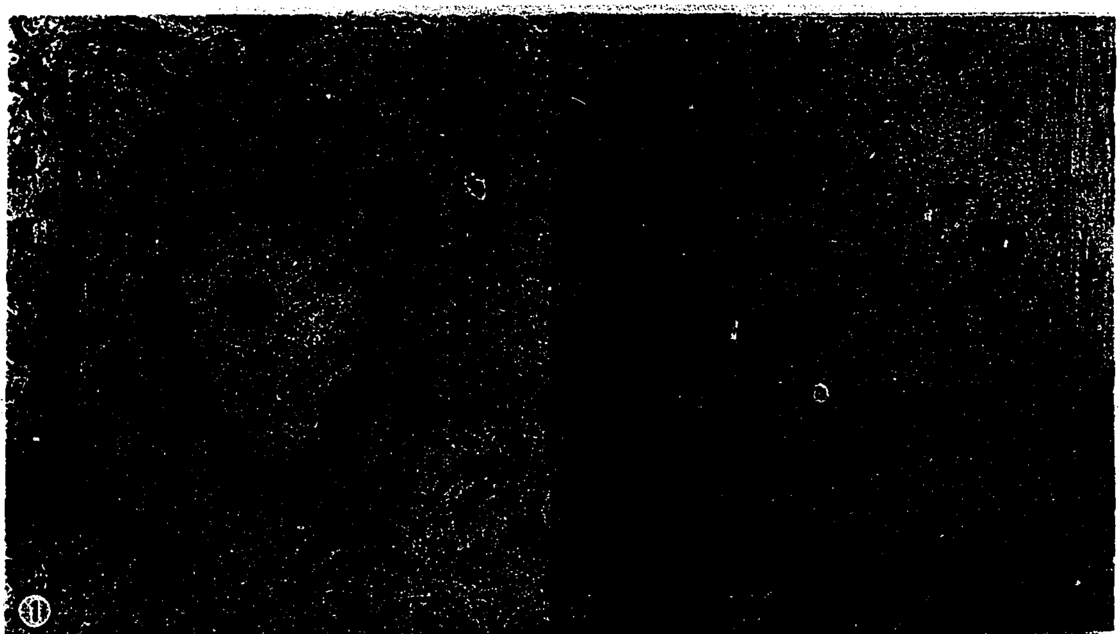
Fig. 7. Longitudinal section of metaxylem with scalariform and helical thickenings. P1786 A side No. 2. x 174.

Fig. 8. Longitudinal section of metaxylem with sinuous thickenings. P 1728 B top No. 1. x 447.

Fig. 9. Transverse section of primary and secondary phloem. Arrows indicate primary phloem fiber bundle cap. P1728 A side No. 1. x 17.

Fig.10. Transverse section of cortex, periderm and epidermis cells. P1209 K2 top side No. 2. x 62.

c=cortex, e=epidermis, p=pith, ph=secondary phloem, x=secondary xylem.



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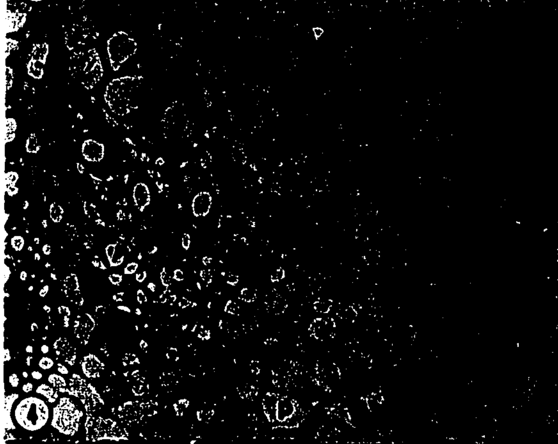

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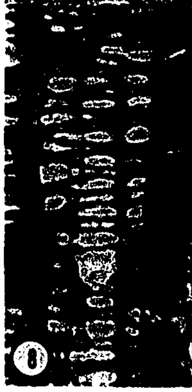

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Plate II, 2

Liriodendroxylon princetonensis gen. ct sp. nov., twigs.

Fig. 11. Transverse section of first growth increment. P1728 A1 side No. 1 x 21.

Fig. 12. Transverse section of portions of second and third growth increments. P1728 A1 side No. 1. x 30.

Fig 13. Longitudinal section of apotracheal parenchyma. P1209 K top No. 6. x 68.

Fig. 14. Scalariform vessel to ray pitting. P1209 K top No. 3. x 429.

Fig. 15. Irregularly distributed vessel to ray pitting. P1209 K top No. 5. x 429.

Fig 16. Scalariform perforation plate. P1209 K top No. 15. x 437.

Fig. 17. Radial section showing scalariform perforation plates and opposite vessel to ray pitting (arrow). P1209 K top No. 3. x 342.

Fig. 18. Radial section with heterocellular rays. P1786 A side No. 2. x 191.

Fig. 19. Tangential section at the beginning of the first growth increment showing vessel element with scalariform intervascular pitting. P1209 K top No. 6. x 380.

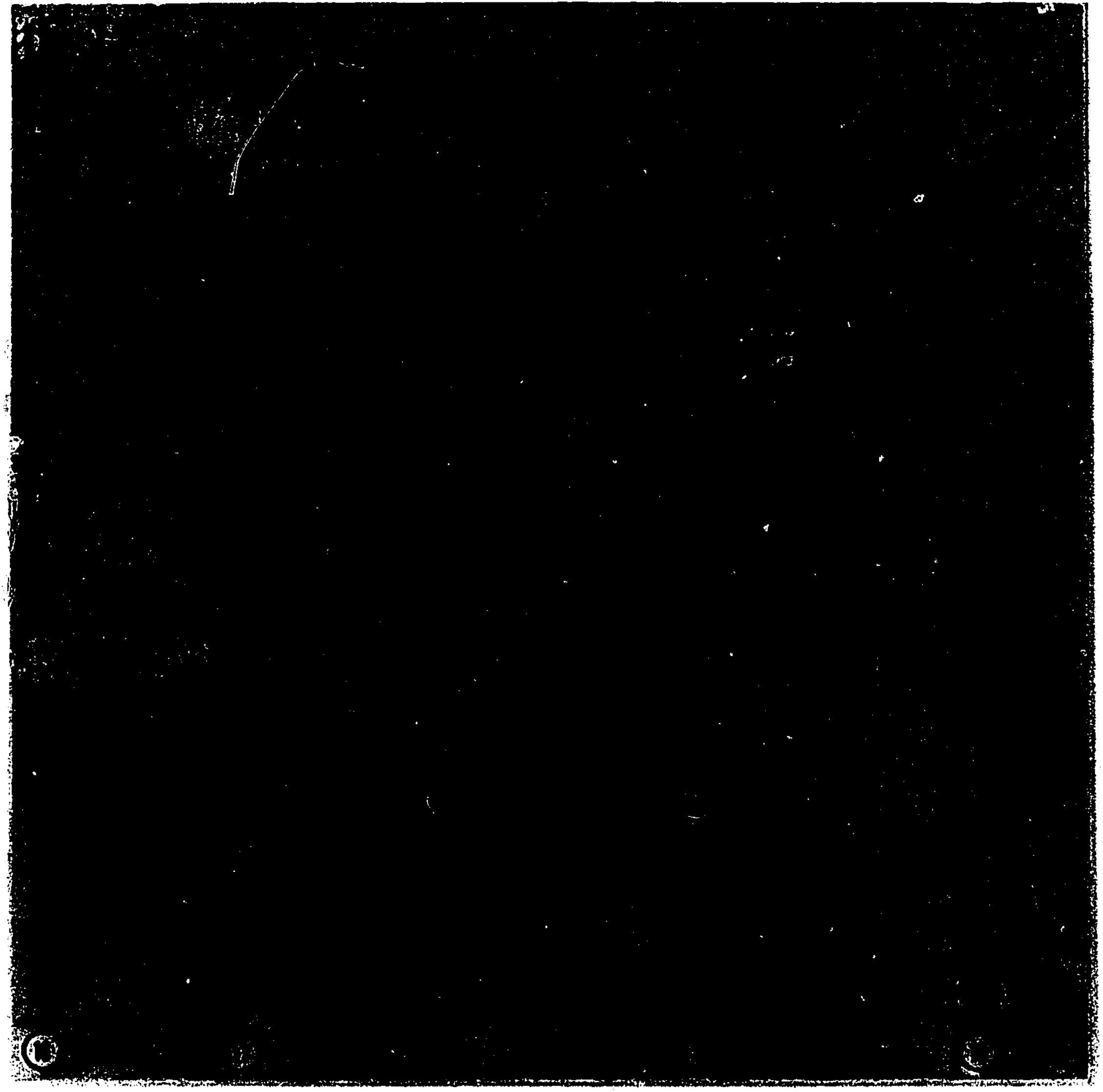

Plate II, 3

Liriodendroxylon princetonensis gen. et sp. nov., phloem.

Fig. 20. Transverse section showing cambial zone. P1209 K2 top side No. 1. x 29.

Fig. 21. Transverse section of secondary phloem. P1209 K2 side No. 2. x 31.

Fig. 22. Radial section of secondary phloem and cortex. P1728 A2 side No. 1. x 17.

Fig. 23. Tangential section of secondary phloem. P1209 K2 top side No. 2. x 17.

Fig. 24. Radial section of phloem with sclerified ray cells. P1720 E2 side No. 6. x 319.

Fig. 25. Transverse section of secondary phloem with alternating fibers (arrows) and thin walled cells. P1209 K top side No. 1. x 228.

c=cortex, ca=vascular cambium, f=primary phloem fibers, ph=secondary phloem, s=sclerified ray cells, x=secondary xylem.

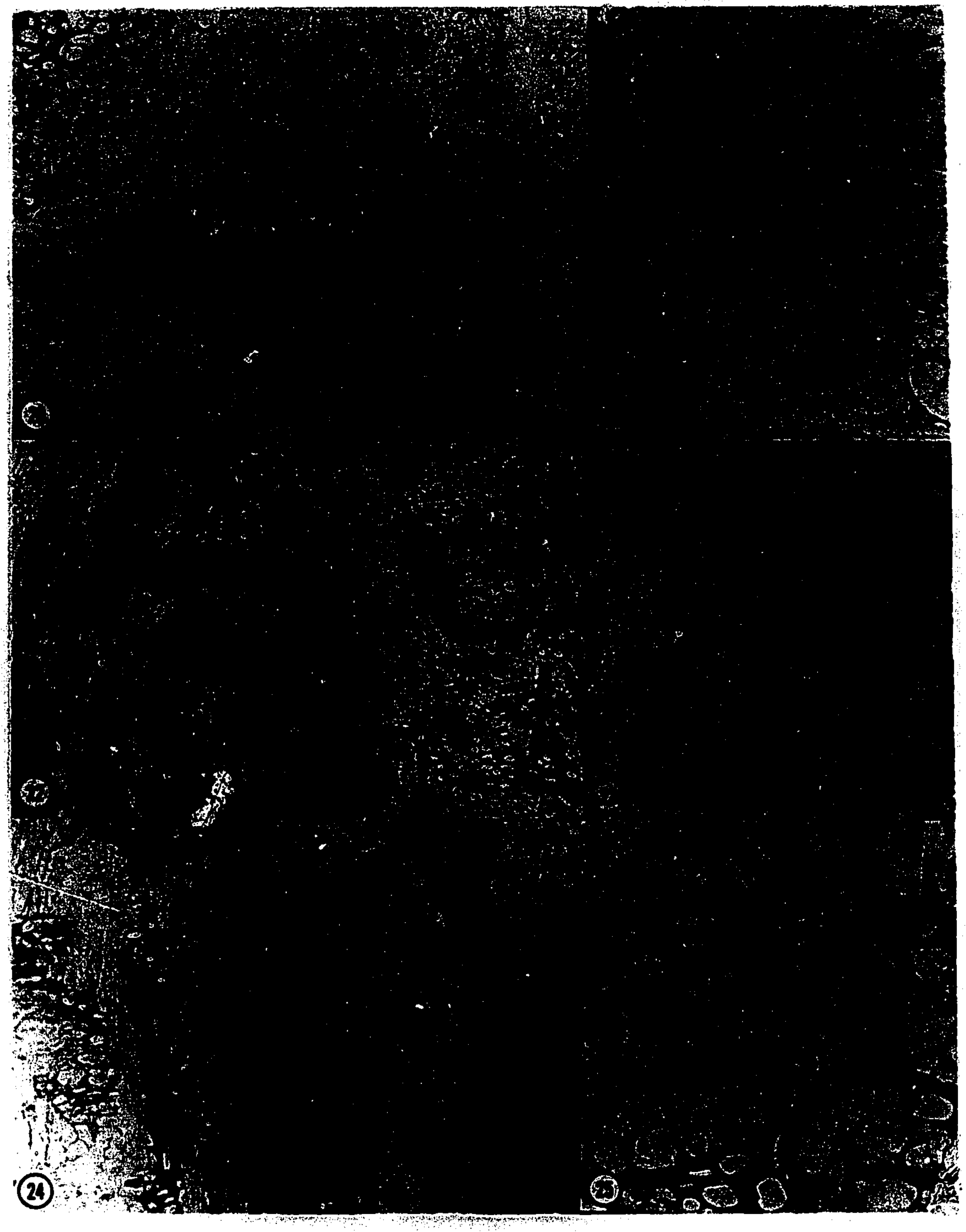

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Plate II, 4

Liriodendroxylon princetonensis gen. et sp. nov. mature wood.

Fig. 26. Transverse section with several marginal parenchyma bands (arrows). P1720 E No. 2. x 10.

Fig. 27. Radial section with tyloses and homocellular rays. P1720 E2 side No. 9. x 260.

Fig. 28. Tangential section with tyloses in one vessel. P1720 E side No. 1. x 114.

Fig. 29. Vessel element with opposite intervascular pitting. P1720 E2 side No. 5. x 272.

Fig. 30. Imperforate tracheary element with bordered pits on radial walls (left) and scalariform ray to vessel pitting (top). P1720 E2 side No. 6. x 553.

Fig. 31. *Liriodendron tulipifera*. Transverse section of twig. Sl 8117. x 44.

Fig. 32. *Magnolia tripetala*. Transverse section of young stem. Sl 1828. x 44.

Fig. 33. *Liriodendron tulipifera*. Transverse section of young stem. Sl 8117. x 44.

c=cortex, ph=secondary phloem, sc=secretory cells, x=secondary xylem.

Table II, 1. Anatomical characteristics of some extant magnoliaceous genera. Data from McLaughlin (1933), Canright (1955), Gottwald (1972), and Wheeler et al. (1977).

		Alcimandra	*Aromadendron*	*Elmerrillia*	*Kmeria*	*Liriodendron*	*Magnolia*	*Manglietia*	*Michelia*	*Talauma*	*Liriodendroxylon*
Growth rings	Distinct		■		■	■	■				■
	Indistinct	■		■			■	■		■	
Pore arrangement	Diffuse	■	■	■	■	■	■				■
	Solitary	■	■	■	■	■	■	■	■	■	■
	Radial multiples	■		■	■	■	■	■	■	■	■
	Clusters					■	■		■		■
Pore shape	Angular	■				■	■				■
	Round								■	■	
	Oval		■	■					■	■	
Perforation plate	Simple						■				
	Scalariform	■	■	■	■	■	■	■	■	■	■
Vessel	Spiral thickenings		■				■			■	
Intervascular pitting	Scalariform	■	■	■	■		■	■	■	■	■
	Transitional						■	■		■	■
	Opposite	■				■	■				■
Axial parenchyma	Marginal		■	■	■	■	■	■	■		■
	Apotracheal	■							■	■	
	Paratracheal								■		
Rays	Heterocellular	■	■	■	?		■	■	■	■	
	Homocellular					■	■				■
	Oil cells		■	■			■			■	
	Tyloses	■	■	■	■	■	■	■	■	■	■

Table II, 2. Anatomical characteristics of some fossil magnoliaceous genera. Data from [1]Schönfeld (1958), [2]Greguss (1969), [3]Page (1970), [4]Prakash et al. (1971), van der Burgh (1973[5], 1974[6]), [7]Suzuki (1976), [8]Wheeler et al. (1977), [9]Scott and Wheeler (1982). ?=not determinable, S=and simple perforation plate.

		Michelia oleifera[7]	*Magnolioxylon parenchymatosum*[3]	*Magnolioxylon scandens*[1]	*Magnolioxylon krauselii*[2]	*Magnoliaceoxylon panochensis*[3]	*Magnoliaceoxylon wetmorei*[8]	*Magnolia* sp.[5,6]	*Magnolia longiradiata*[9]	*Magnolia angulata*[9]	*Liriodendroxylon tulipiferum*[4]	*Liriodendroxylon multiporosum*[9]	*Liriodendroxylon princetonensis*
Pores	oval	■		■		■			■		■		
	angular	■	■		■					■			■
	solitary	■		■	■	■	■	■	■	■	■	■	■
	multiple	■		■	■		■	■	■	■	■	■	■
	clusters	■				■						■	■
Vessels with spiral thickenings		■	■		■			■					
Intervascular pitting	scalariform	■	■	■	■		■		■	■			■
	opposite	■			■	■	■		■	■	■	■	■
	transitional	■				■							■
Scalariform ray-vessel pits			■		■	■	■	■	?	?			■
Scalariform perforation plate		■	■	S	S	■	■	S	■	■	■	■	■
Axial parenchyma	paratracheal					■		■					
	apotracheal						?	■					
	marginal	■	■					■	■	■	■	■	■
Rays	homocellualr					■		■					■
	heterocellular	■	■	■	■	■	■	■	■	■	■	■	■
Growth rings		■	■		■		■	■	■	■	■	■	■
Tyloses		■			■	■		■					■
Oil cells							■		?				

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Rosaceae (Spiraeoideae): *Paleorosa similkameenensis* Basinger*

The Middle Eocene Princeton chert locality in southern British Columbia, Canada has yielded the most diverse assemblage of permineralized flowers recovered from Tertiary sediments of western North America. To date, three different dicotyledonous flowers have been studied in detail: *Paleorosa* (Basinger, 1976), *Princetonia* (Stockey, 1987), and *Wehrwolfea* (Erwin and Stockey, 1988, 1990). Among these, *Paleorosa similkameenensis* Basinger was the first flower reported. At the present time it not only remains the most abundant and completely known flower in the chert, but continues to represent the oldest known rosaceous fossil flower (Basinger, 1976).

Basinger (1976) established *Paleorosa* as a primitive member of the Rosaceae and discussed its possible affinities with genera in the Spiraeoideae, Maloideae, and Rosoideae, but was unable to definitively assign *Paleorosa* to a subfamily or tribe. Reinvestigation of the type material, in conjunction with newly discovered specimens, for the first time has allowed the opportunity to describe embryo structure, pollen morphology and ultrastructure. This material provides a more detailed account of seed, fruit, and floral anatomy, important characters not included in the original generic description. This new information not only reconfirms the assignment of *Paleorosa* to the Rosaceae, but further supports its placement in Spiraeoideae within the tribe Sorbarieae. Furthermore, *Paleorosa* pollen represents the earliest record of pollen of Rosaceae, thus extending the family's palynological record from the Oligocene (Muller, 1981) back to the Middle Eocene.

Materials and Methods - In addition to the more than 50 flowers reported by Basinger (1976), four new mature flowers including one with well-preserved *in situ* pollen have been recovered from the Princeton chert locality. The chert crops out on the east side of the Similkameen River 8 km south of Princeton, British Columbia. The section consists

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of an interbedded sequence of chert and coal with an occasional thin ash bed replacing a chert layer (Stockey, 1987). Forty-nine exposed layers of chert have been recorded and systematically sampled (Stockey, 1987). This locality has been referred to as locality "I" (Boneham, 1968) and the "Princeton chert locality" (Basinger, 1976; Stockey, 1984, 1987). The Allenby Formation of the Princeton Group is regarded as Middle Eocene based on palynology (Rouse and Srivastava, 1970), mammals and freshwater fishes (Russell, 1935; Gazin, 1953; Wilson, 1977, 1982), and potassium-argon dating (Hills and Baadsgaard, 1967).

The specimens are preserved as silica permineralizations. All chert blocks were cut into slabs and studied in serial sections using a modified cellulose acetate peel technique and hydrofluoric acid (Joy et al., 1956; Basinger and Rothwell, 1977). Peel sections were mounted in Eukitt or Coverbond xylene-soluble mounting medium for microscopic examination.

Scanning electron microscopy of the fossil pollen was done using the back side of deeply etched peels, while pollen was recovered directly from the anthers of extant *Gillenia trifoliata* Moench (=*Porteranthus trifoliatus* (L.) Britton; Alta 59143), *Spiraeanthus schrenckianus* Maxim. (Alta 89488), *Pyracantha crenato-serrata* Rehd. (ASU 42788), *P. crenulata* (Roxb.) Roem. (ASU 54561), *P. coccinea* Roem. (ASU 63101), *P. kordzumii* Rehd. (ASU 44385), and *P. fortuneana* (Maxim.) Li (ASU 54562). Peel sections and extant pollen were mounted on stubs with double-sided tape, covered with 150 Å Au on a Nanotek Sputter Coater, and viewed at 20 kV with a Cambridge Stereoscan 250. Peel sections were prepared for transmission electron microscopy first by demineralizing in concentrated hydrofluoric acid followed by several washes in distilled water. The acetate matrix was then dissolved in two changes of acetone. Pollen was fixed in OsO4 for 2 hrs., dehydrated in acetone, embedded in Spurr's (1969) resin, and sections 90 - 100 nm thick were cut using a Reichert Ultracut E microtome. Sections were then collected on formvarcoated grids, double stained with uranyl acetate and lead citrate, and viewed with a Phillips EM 200 at 60 kV.

A comparison of fossil flower, fruit, and seed morphology with that of extant families was made using the data set of Hansen and Rahn (1969, 1972) with the MEKA 1.3 program provided by T. Duncan and C. A. Meacham (1987), University Herbarium, University of California, Berkeley.

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

Systematic description

Class: Magnoliopsida
  Subclass: Rosidae
    Order: Rosales
      Family: Rosaceae
        Subfamily: Spiraeoideae
          Tribe: Sorbarieae
            Genus: *Paleorosa* Basinger
              Species:*Paleorosa similkameenensis* Basinger

Holotype: P1122 I (Pl. III, 1 Fig. 5 ; Basinger, 1976).

Paratypes: P1118 Ebot, (Pl. III, 3 Figs. 14-16); P1119 J; P1123 Btop; 1143 Ebot, (Pl. III, 2 Figs. 7-9, 11-13; Basinger, 1976).

Topotypes: P1122 D (Pl. III, 1 Fig. 6); P1197 A, (Pl. III, 1 Figs. 4, 10); P1256 Dtop, (Pl. III, 3 Figs. 17-20); P1349 Ebot, (pl. III, 1 Figs. 1-3).

Amplified diagnosis - Generic diagnosis: Flowers anatomically preserved, bisexual, perigynous, actinomorphic. Calyx of five sepals, corolla of five petals inserted alternately, androecium polystamenous, gynoecium apocarpus, pentacarpellate. Hypanthium surrounding apocarpous gynoecium. Ovules two per carpel, collateral, erect, anatropous, placentation basal. Fruit a two seeds follicle. Seed bitegmic, with hypostase; embryo straight. Pollen prolate, tricolporate, striate with microperforations.

Specific diagnosis: Flowers as described in generic diagnosis. Pedicel 1.2-2.1 mm long, 0.4-0.5 mm in diameter, bract single 1.0-1.6 mm long. Hypanthium 0.5-1.8 mm in diameter, 0.5-2.0 mm deep from point of insertion of petals to base of cup, with five histological zones; sepals 0.5-0.8 mm long; petal size unknown; stamens 13-19; filaments 0.3-0.4 mm long, 0.1 mm in diameter; anthers bilocular, dorsifixed, 0.5-0.6 mm long, 0.2-0.4 mm wide. Pollen semi-tectate, sexine thicker than nexine. Carpels pubescent, inserted opposite sepals, borne at base of hypanthium, fused to wall of cup up to level of ovular insertion, free at ventral margins, with three histological zones. Carpels at stages of early seed development, 0.7-1.3 mm high, 0.4-0.6 mm deep; style terminal, 1.1-2.1 mm long, 0.2 mm in diameter, with hollow center; dorsal vascular bundle of carpel extending into style. Ovules/seeds 0.5-0.9 mm long, 0.3 mm in diameter, placentation basal, erect on funiculus 0.1 mm long, anatropous; integuments fused throughout length of ovules.

Description - The four new *Palæorosa similkameenensis* flowers reported here conform to Basinger's (1976) original description. These specimens represent mature flowers that are actinomorphic with five, free, pubescent carpels surrounded by a U-shaped hypanthium in longitudinal section with associated remnants of the perianth and anthers (Pl. III, 1 Figs. 1, 2). Each carpel contains two collateral, basally attached, anatropous ovules, several of which represent seeds with embryonic tissue inside (Pl. III, 2 Fig. 7). Anthers of most specimens have dehisced, but in one flower they are well-preserved and contain abundant *in situ* tricolporate, striate pollen (Pl. III, 3 Fig. 14).

The hypanthium is composed of five different zones (Pl. III, 1 Fig. 3). The outer-most zone represents a single-layered epidermis with cuboidal thin-walled cells, averaging 17 x 13 x 13 µm. The second zone is composed of two to three cell layers of rectangular thin-walled cells, averaging 27 x 23 x 23 µm, while the third has over 10 layers composed of rectangular cells, averaging 36 x 10 x 23 µm and includes the vascular tissue. A fourth zone is composed of about five layers of rectangular cells with rounded corners, averaging 13 x 17 x 17 µm, whereas the fifth layer or inner epidermis is single layered and composed of almost cuboidal cells, averaging 10 x 10 x 7 µm.

Carpels are fused partially to the hypanthium at the base and remain adnate along their dorsal margins up to the level of the hilum (i.e. the level of ovular insertion; Pl. III,1 Figs. 1, 4). They are ovoid in longitudinal section (Pl. III, 1 Figs. 1, 4) and subtriangular in transverse section (Pl. III, 1 Fig. 5, 6). At all levels of the gynoecium, the ventral margins of adjacent carpels are free (Pl. III, 1 Figs. 1, 4-6); however, the two lateral walls of individual carpels are closed in the area of the ventral suture (Pl. III, 1 Figs. 5-6). In distal cross sections the inner portion of the ventral suture forms a "V"-shaped invagination (Pl. III, 1 Fig. 6), but the ventral carpel margins are never completely open.

Three distinct pericarp layers can be distinguished. The exocarp is composed of a single layer of rectangular, radially elongated cells, averaging 13 x 13 x 17 µm (Pl. III, 2 Fig. 8). Unicellular hairs with their bases sunken in the epidermal cells are characteristic of the gynoecium (Pl. III, 2 Fig. 9). The mesocarp is ca. 10 cell layers thick, composed of two different cell types, and includes the vascular tissue (Pl. III, 2 Fig. 7). Most mesocarp cells are thin-walled, rectangular to polyhedral, and average 17 x 17 x 27 µm (Pl. III, 2 Fig. 8). Scattered among the thin-walled cells are oval thick-walled cells with dark contents (Pl. III, 1 Fig. 4, Pl. III,2 Fig. 9). Tracheary elements comprising the dorsal, ventral, and vegetative bundles show scalariform secondary wall thickenings. The endocarp is a single layer of thin-walled, tangentially elongated cells, that average 17 x 7 x 33 µm (Pl. III, 2 Fig. 8).

The seed integument is composed of two zones. In longitudinal section, the inner integumentary zone is a single layer of rectangular, thin-walled cells, averaging 10 x 10 x 17 µm (Pl. III, 2 Fig. 7). In surface view these cells are arranged in longitudinal rows (Pl. III, 2 Fig. 10). The outer integumentary zone is composed of several layers of rectangular, radially elongate, thin-walled cells (Pl. III, 2 Fig. 7). Fungal hyphae are present throughout the tissue of the gynoecium and probably responsible, at least partially, for the quality of preservation. In those specimens where the outer integumentary zone is poorly preserved, the two integuments appear to be separate (Pl. III, 1 Fig. 6); however, this is probably due to fungal activity. In better preserved ovules with out fungi the integumentary zones are fused throughout the length of the ovules (Pl. III, 2 Fig. 7). The raphe composed of a single strand of tracheary elements with scalariform wall thickenings is located in the outer integumentary zone and extends to the chalaza (Pl. III, 2 Fig. 10, 12). At least two small branches of the raphe are present in the chalaza (Pl. III, 2 Fig. 13).

Embryonic tissue is present in the paratype P1143 E and topotype P1197 A. The most complete specimen, P1143 E, shows a distinct heart-shaped structure, 143 μm long x 102 μm wide, more or less centrally located in the seed cavity, that probably represents an immature embryo (Pl. III, 2 Figs. 7, 11). Cellular detail is not well preserved; however, the end of the structure opposite the chalaza is the widest point and appears weakly bi-lobed. Each lobe, therefore, is interpreted as an undeveloped cotyledon (Pl. III, 2 Fig. 11). At the apex of the hypocotyl in the area of the root cap, there is a group of dark colored cells (Pl. III, 2 Fig. 11). The space between the embryo and the integuments lacks cellularization. This may be due either to bad preservation or to the fact that the seed did not have endosperm.

Attached to the chalazal end and protruding into the seed cavity is a dome shaped mass of polyhedral cells, averaging 13 μm in diameter, some of which have thickened cell walls (Pl. III, 2 Figs. 7, 10, 11). The location of these cells near the ends of the seed vascular strand suggest that they may represent a hypostase derived from nucellar tissue (Pl. III, 2 Figs. 10, 11). Seeds with a hypostase have been reported in some Rosaceae (Corner, 1976).

Pollen grains recovered from two different flowers, paratype P1118 Ebot and topotype P1256 Dtop, show differences in exine sculpturing (Pl. III, 3 Figs. 14, 17). Paratype P1118 Ebot represents a flower bud (Basinger, 1976). Grains from this specimen show a rugose exine with numerous microperforations averaging 0.4 µm in diameter (Pl. III, 3 Figs. 15, 16). Topotype P1256 Dtop, on the other hand, appears to be a more mature flower and pollen from this flower is striate (Pl. III, 3 Fig. 17). Striate grains are prolate, 22 x 14 µm, and tricolporate with long, fairly wide colpi that have a granular colpus surface (Pl. III, 3 Figs. 14-17). Striae vary in width, averaging 0.2 µm, are dichotomously branched and anastomose. Minute perforations are found occasionally between striae. Scanning and transmission electron microscopy show a semi-tectate columellate exine with a thick foot layer (Pl. III, 3 Figs. 18-20). The nexine (dark layer) is very thin relative to the sexine (lighter layer); however, the sexine thins in the area of the colpus, while the underlying nexine becomes thicker (Pl. III, 3 Fig. 19).

Discussion - Taxonomic affinity of *Paleorosa similkameenensis* with the Rosaceae was initially suggested by Basinger (1976), and has been reconfirmed in this investigation based on additional structural data and using the computer aided key MEKA 1.3 (Hansen and Rahn, 1969, 1972; Duncan and Meacham, 1987). The following eleven characters were used: "flowers bisexual (50), receptacle enlarged, totally or partially free from the ovary (56), sepals five (75), petals five (86), anthers more than 10, fertile (109), styles more than one, free (carpels connate) (130), carpels five (free or united) (137), ovules two in each locule (146), ovules attached to the base of the ovary (153), fruit a capsule (incl. pod, follicle etc.) (154), and fruit with two seeds (158)". Only one family, Rosaceae, matches this combination of characters exactly, while 7 families miss by one character. The Dilleniaceae, Clusiaceae, and Rutaceae differ with respect to character 56. Flacourtiaceae and Rhizophoraceae differ from *Paleorosa* in having ovules with axile or parietal placentation (Cronquist, 1981). Melastomataceae, unlike *Paleorosa*, have only one style and Ficoidaceae differ with respect to petal number (Cronquist, 1981). Pollen morphology and integumentary anatomy of the 7 families above also differ from *Paleorosa*. Exine sculpturing is mainly reticulate or the pollen of these families has a pattern other than striate (Erdtman, 1952). The integuments are either sclerotic, multilayered or include a palisade (Corner, 1976), and therefore are distinct from *Paleorosa.*

Within Rosaceae four subfamilies are recognized based on fruit type (Robertson, 1974). Drupes are found in Prunoideae, achenes and drupes in Rosoideae, pomes in Maloideae, and follicles in Spiraeoideae (Robertson, 1974). Fruits of *Paleorosa similkameenensis* most likely represent an aggregation of follicles (Basinger, 1976). We accept this interpretation based on histological and morphological similarities to this fruit type, which include the presence of two seeds per fruit, and the predominance of thin-walled parenchyma cells in the mesocarp (Roth, 1977). Apparently, as the fruit of *Paleorosa* developed and matured, the thin-walled cells of the mesocarp became thick-walled and full of dark contents (Pl. III, 1 Fig. 4, Pl. III,2 Fig. 9). Follicles of Rosaceae are frequently described as having "bony" pericarps (Robertson, 1974) and therefore, the presence of thick-walled cells in the mesocarp of some *Paleorosa* specimens suggests that these fruits were also eventually stony. If *Paleorosa* fruits dehisced, this probably occurred at the ventral suture.

As pointed out by Basinger (1976) difficulty arises when attempting to assign *Paleorosa* to one tribe based on fruit type since certain features of *Paleorosa* fruits are unknown. However, a combination of other characteristics such as carpel and ovule structure and orientation, plus pollen morphology make it possible to eliminate most tribes that have genera with five carpels and two ovules per carpel from further consideration. The monogeneric tribe Osmaronieae (Subfamily Prunoideae; *Oemleria* RCHB.), unlike *Paleorosa,* has unisexual flowers, carpels that open in the area of the ventral suture, pendant, epitropic, campylotropous ovules, and free integuments (Sterling, 1964b). Tribe Ulmarieae (Subfamily Rosoideae) which includes the single genus *Filipendula* Miller, differs from *Paleorosa* in having pendant, epitropic, campylotropous, and unitegmic ovules (Sterling, 1966b; Robertson, 1974). Pollen grains of *Filipendula* differ from those of *Paleorosa* in having scabrate or microechinate to echinate ornamentation (Reitsma, 1966; Eide, 1981).

Flowers closely resembling *Paleorosa* belong to the genus *Pyracantha* Roem. (Subfamily Maloideae; Tribe Crataegeae); however, *Pyracantha* has several features not present in *Paleorosa*. These include: presence of a fleshy nectary ring around the edge of the hypanthium (Robertson, 1974), open ventral sutures, and a pome-like fruit (Sterling, 1965). However, *Pyracantha* does share the following characters with *Paleorosa*: little fusion of carpel to hypanthium, stamens arranged in one cycle, fused ventral sutures, fused integuments, tricolporate pollen with a similar striate exine pattern, and an indistinct pore (Pl. III, 3 Figs. 16, 17, Pl. III,4 Figs. 26, 27). Likewise the striate pattern of *Paleorosa* pollen is similar to that of *Prunus* L. (Prunoideae) and *Rubus* L. (Rosoideae), but in *Prunus* the pore is conspicuous in each colpus, whereas pores are indistinct in *Paleorosa*. Indistinct pores also characterize certain species of *Rubus* (Hebda, 1989 pers. comm.); however, floral and fruit morphology of both *Prunus* and *Rubus* are very different from *Paleorosa*. Since very little is known about pollen morphology and seed anatomy of Rosaceae the taxonomic significance of these characters at the generic level is obscure. It is important to note that in the present study, the five *Pyracantha* species viewed with SEM are nearly identical.

Post-chalazal branches of the raphe as seen in *Paleorosa* have been reported in Maloideae and Prunoideae (Corner, 1976). More detailed studies are needed however, in order to determine whether this character is present in other subfamilies and its taxonomic significance. Endosperm is lacking in Rosoideae, Prunoideae, Maloideae, and in some Spiraeoideae, but is abundant in certain genera of Spiraeoideae, e.g.. *Physocarpus* (Camb.) Maxim. and *Gillenia* (Robertson, 1974). The lack of endosperm in *Paleorosa* may be due to poor preservation or fungal decay, so this character is of limited use. Although *Paleorosa* shares similarities with several genera among the four subfamilies, the follicular nature of *Paleorosa* fruits suggests close affinities with the Spiraeoideae.

Within the Spiraeoideae, *Holodiscus* (Koch.) Maxim. (Tribe Holodisceae) unlike *Paleorosa* has pendant, campylotropous, epitropic, unitegmic ovules (Sterling, 1966b). *Vauquelina* Corrêa ex HBK. (Tribe Quillajeae) is in many respects similar to *Paleorosa*, but the fruit is pomoid, and the ventral carpellary margins are fused up to the locular base (Sterling, 1966c). Carpels in *Spiraea* L. (Tribe Spiraeeae) are antepetalous and ovules are pendant, whereas carpels are antesepalous and ovules erect in *Paleorosa* (Basinger, 1976). Flowers of *Spiraeanthus* Maxim. (Tribe Sorbarieae) are also similar to the fossil, but have unitegmic ovules (Sterling, 1966c), and the pollen has a unique swirled striate pattern distinct from that of *Paleorosa* (Pl. III, 4 Figs. 24-25, 28).

Gillenia Moench (Tribe Sorbarieae) is perhaps the most similar taxon; however, it differs in having carpels fused ventrally up to the level of ovular insertion, carpels non-adnate to the hypanthium, stamens arranged in two cycles, and open ventral sutures (Sterling, 1966c). Follicles in *Gillenia* dehisce along the ventral margin and partially on the dorsal side, while those of *Paleorosa*, if they actually opened, probably split along the ventral margin. With respect to pollen morphology, the exine is very thin in *Gillenia* (Pl. III, 4 Fig. 21) as compared to a much thicker exine in *Paleorosa* (Figs. 18-20). *Gillenia* pollen is tricolporate and the exine is weakly striate to reticulate with minute perforations between the striae (Pl. III, 4 Figs. 22, 23, 29). In contrast, pores in *Paleorosa* are indistinct while the exine shows wider anastomosing striations (Pl. III, 3 Figs. 14-17). Therefore, the unique set of rosaceous characters present in *Paleorosa* strongly supports its recognition as a distinct taxon.

At the subfamily level, texture (fleshy vs. dry) of the hypanthium and its role in fruit development are considered important taxonomic characters. The presence of a non-fleshy hypanthium and follicles in *Paleorosa* support its placement in Spiraeoideae. Within Spiraeoideae, tribes are divided into two groups based on carpel position relative to the perianth (Schulze-Menz, 1964). Flowers bearing carpels opposite the sepals are included in Quillajeae, Exchordeae, and Sorbarieae (Schulze-Menz, 1964; Robertson, 1974).

Among these three tribes apotropic ovules are present in Quillajeae and Sorbarieae (Schulze-Menz, 1964; Robertson, 1974). *Vauquelinia* (Quillajeae) has apotropic ovules, but important differences to *Paleorosa* are mentioned above. Therefore, the closest affinity of *Paleorosa* is with the Sorbarieae.

Paleorosa is not the first taxon that is difficult to classify within the Rosaceae based on fruit type. For the most part, fruits in this family are well characterized; however, some are difficult to categorize because they show intermediate or transitional morphologies (Maximowicz, 1879; Sterling, 1966b, 1966c). For example, a taxon with intermediate fruit characteristics is *Filipendula* (Tribe Ulmarieae). Based on the presence of one whorl of free carpels on a flat receptacle and fruits resembling one-seeded follicles (although these do not dehisce), some authors consider it a member of Spiraeoideae (Rydberg, 1908; Sterling, 1966b). Others regard it as Rosoideae based on compound leaves and the interpretation that the fruits are achenes (Maximowicz, 1879; Focke, 1894; Robertson, 1974). Additional plants with intermediate fruit characteristics include *Lindleya* HKB. (Spiraeoideae), which Bonne (1928) compared to a pome with free carpels. The maloid genus *Dichotomanthes* Kurtz. also has been compared to members of Spiraeoideae due to absence of carpel to hypanthium fusion (Juel, 1927; Sterling, 1965). *Lindleya* differs from *Paleorosa* in having carpels fused to each other up to the level of ovular insertion, epitropic ovules, and separate integuments. *Dichotomanthes* has a single carpel and free integuments, thus, it is also different from *Paleorosa*.

Rosaceae have a long geologic history with all four subfamilies well represented in the fossil record by the Eocene (Wolfe and Wehr, 1988). Although there have been reports of Cretaceous *Prunus* L. leaves and fruits, these fossils need to be reinvestigated (Dilcher, 1974). Remains of *Rosa* L. (Rosoideae) from Paleocene or Eocene sediments, on the other hand, seem to constitute a reliable fossil record (Becker, 1963; Cronquist, 1981). Megafossils related to Maloideae and Spiraeoideae are abundant in Eocene deposits of the Pacific northwestern United States and southwestern Canada (Wolfe and Wehr, 1988).

Several leaves have been referred to Maloideae (Wolfe and Wehr, 1988), but none of these fossils can be related to the five-carpellate, bi-ovulate plants of extant Maloideae. Fossil leaves of Spiraeoideae include *Spiraea* and *Holodiscus* (Wolfe and Wehr, 1988). Also, from this same geographic area several leaves representing extinct taxa are known (Wolfe and Wehr, 1988). Although *Paleorosa* flowers differ from extant taxa the possibility that *Paleorosa* leaves correspond morphologically to *Spiraea* or *Holodiscus* exists. This is especially true, if, as Wolfe and Wehr (1988) suggest, Rosaceae had a major generic diversification during the Middle Eocene. Apart from the compressed rosaceous material, other permineralized remains include three prunoid seeds and wood fragments related to *Prunus* from the Middle Eocene Princeton chert (Cevallos-Ferriz, 1989).

According to Muller (1981), dispersed pollen related to Rosaceae, including Chrysobalanaceae, is recognized from Oligocene and younger sediments. *Parastemon*-type (Chrysobalanaceae) pollen is known from the Oligocene and upper Miocene. Pollen referred to *Filipendula*-type (Subfamily Rosoideae) and to extant *Sanguisorba officinalis* L. have been reported from the Pliocene. Although pollen from Cretaceous deposits have been reported these are rejected by Muller (1981).

In a series of papers on the comparative morphology of the carpel in extant Rosaceae, Sterling (e.g. 1964a, 1964b, 1965, 1966a, 1966b, 1966c) suggested several phylogenetic trends based on certain developmental characters of carpels and seeds. He considered open carpels, unfused integuments, and the presence of two ovules per carpel to be unspecialized, and fused carpels and integuments and multi-ovulate carpels specialized. It is significant that *Paleorosa*, the oldest rosaceous flower known to date, shows the specialized characters of fused carpels and integuments and the unspecialized condition of two ovules per carpel. It is becoming evident, therefore, that verification of these putative evolutionary trends in rosaceous floral structure may come from the fossil record. Thus, the discovery of additional fossil rosaceous flowers and fruits is necessary in order to accurately polarize these characters. As Wolfe and Wehr (1988) suggest, a cladistic analysis using information from extant and fossil taxa is greatly needed. Studies of these permineralized floral remains, combined with data from wood, seeds, and leaves from the Princeton chert will add anatomical information about this family that can be used in a cladistic analysis, in conjunction with data from the compression fossils of the Middle Eocene basins of northwestern U. S. A. and southwestern Canada.

Pollen of *Paleorosa* extends the palynological record of this family to the Middle Eocene, and underscores the need for the investigation of the morphology and variability of rosaceous pollen in extant Rosaceae. These flowers remain the oldest anatomically preserved rosaceous flowers and show transitional characters between the subfamilies Maloideae and Spiraeoideae. These data indicate that the Spiraeoideae, as Stebbins (1950) suggests, probably were involved in the evolution of Maloideae (which perhaps arose as amphiploid hybrids of Spiraeoideae and Prunoideae). Further investigations of the remains of Prunoideae in the chert may help to clarify phylogenetic relationships within this family.

Plate III, 1

Paleorosa similkameenensis Basinger.

Fig. 1. Longitudinal section of a mature flower showing three carpels basally attached to hypanthium (arrows) and extension of the style (S) above hypanthium. P1349 Ebot No. 18. X 39.

Fig. 2. Detail of style showing extension above hypanthium. P1349 Ebot No. 23. X 41.

Fig. 3. Transverse section of hypanthium showing five histological zones. P1349 Ebot No. 16. X 190.

Fig. 4. Longitudinal section of carpel showing basal placentation of one ovule (arrow), hairs, free ventral margins, fusion of carpel to hypanthium up to level of ovular insertion, and thick-walled cells with dark contents in mesocarp. P1197 A No. 14. X 58.

Fig. 5. Proximal transverse section of carpels showing two ovules per carpel with fused integuments, fused ventral margins, and free intercarpellary margins. Holotype, P1122 I No. 3a. X 53.

Fig. 6. Distal transverse section of carpels showing closed ventral sutures and "V"-shaped invagination (arrow). P1121 Dtop No. 9. X 84.

A=anther, FC=hypanthium, S=style, 1=abaxial epidermis of hypanthium, 2=second cell zone of hypanthium, 3=third cell zone of hypanthium, 4=fourth cell zone of hypanthium, 5=adaxial epidermis of hypanthium.

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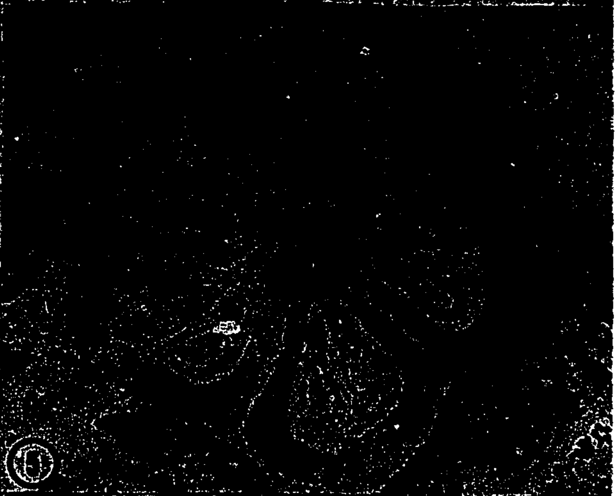

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Plate III, 2

Paleorosa similkameenensis Basinger.

Fig. 7. Longitudinal section of carpel with two seeds showing seeds with fused integuments, embryo and hypostase. P1143 Ebot No. 25. X 71.

Fig. 8. Longitudinal section of carpel showing three carpellary layers and hair bases (arrow). P 1143 Ebot No. 25. X 150.

Fig. 9. Longitudinal section of exocarp with unicellular hairs. Note thick-walled cells with dark contents. P1143 Ebot No. 25. X 155.

Fig. 10. Longitudinal section of seed showing raphe, hypostase, and radial files of cells of the inner integument. P1197 A No. 14. X 109.

Fig. 11. Longitudinal section of hypostase and straight, immature, heart-shaped embryo with possible remains of suspensor (dark region). P 1143 Ebot No. 25. X 378.

Fig. 12. Oblique longitudinal section of raphe showing helical thickenings. Note presence of two vascular strands. P1143 Ebot No. 25. X 378.

Fig. 13. Oblique longitudinal section of raphe showing post chalazal branches (arrows). P1143 Ebot No. 24. X 233.

E=embryo, H=hypostase, R=raphe.

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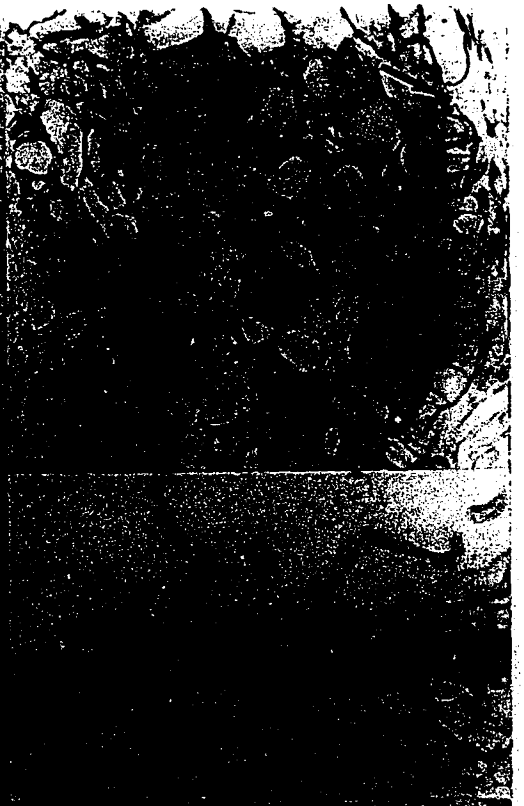

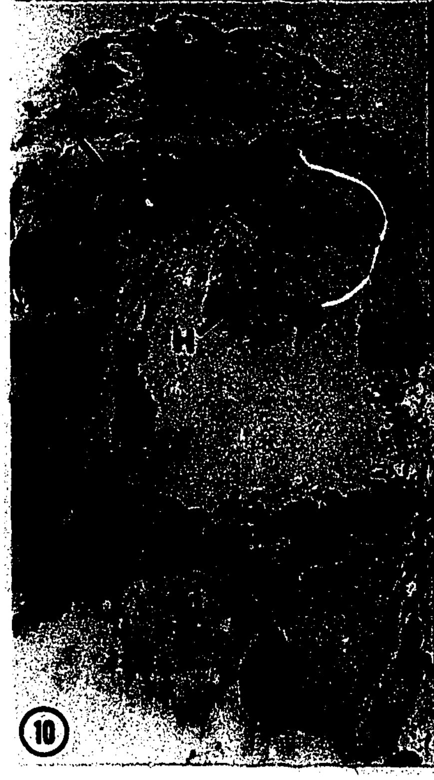

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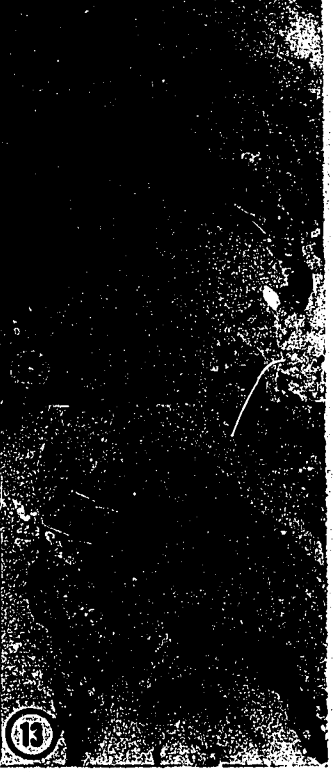

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Plate III, 3

Pollen of *Paleorosa similkameenensis* Basinger (Figs. 14-20) and *Gillenia* Moench (Fig. 21).

Fig. 14. Light photomicrograph of *in situ* pollen grains. P1118 Ebot No. 4. X 340.

Fig. 15. SEM of *in situ* pollen grains from a flower bud. P1118 Ebot No. 3. X 873.

Fig. 16. Equatorial view of grain from a flower bud showing one colpus, and rugose exine. P1118 Ebot No. 3. X 3395.

Fig. 17. Polar view of grain from a mature flower showing three colpi, and granular surface of colpus. P1256 Dtop No. 0. X 4365.

Fig. 18. SEM of the exine showing thick columellae. P1256 Dtop No. 0. X 12610.

Fig. 19. TEM showing thin nexine becoming thicker in region of colpus. P1256 Dtop No. 3. X 6082.

Fig. 20. TEM showing thick foot layer, columellae, and tectum. P1256 Dtop No. 3. X 26481.

Fig. 21. TEM of *Gillenia* showing semi-tectate exine. ALTA 59143. X 26481.

C=colpus.


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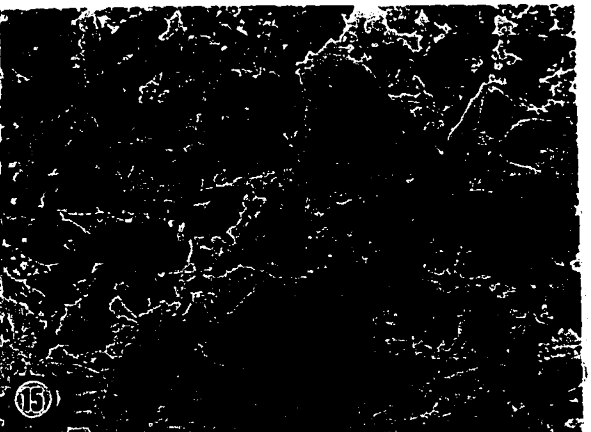
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Plate III, 4

Pollen of extant Rosaceae.

Fig. 22. *Gillenia trifoliata* equatorial view.ALTA 59143. X 2668.

Fig. 23. *G. trifoliata* polar view. ALTA 59143. X 2425.

Fig. 24. *Spiraeanthus schrenckianus* equatorial view. ALTA 89488. X 3395.

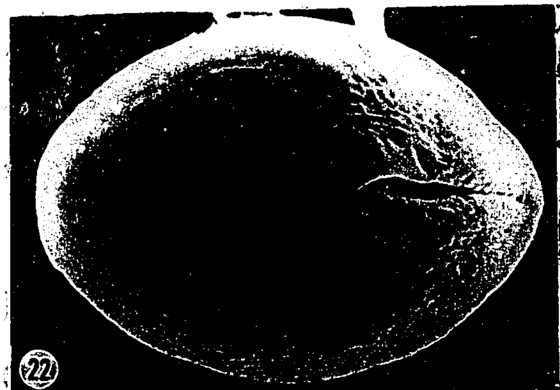
Fig. 25. *S. schrenckianus* polar view. ALTA 89488.X 2546.

Fig. 26. *Pyracantha fortuneana* equatorial view. ASU 54562. X 1261.

Fig. 27. *P. coccinea* polar view. ASU 63101. X 2037.

Fig. 28. *S. schrenckianus* detail of striae. ALTA 89488. X 19400.

Fig. 29. *G. trifoliata* detail of striae and minute perforations. ALTA 59143. X 10913.



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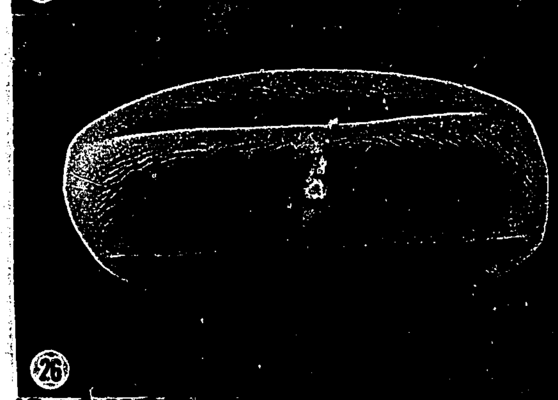

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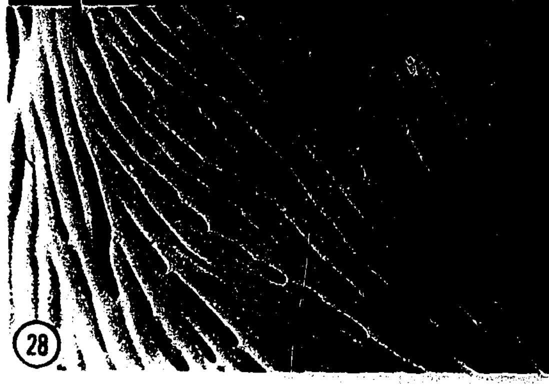

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Rosaceae (Prunoideae): vegetative axes*

Introduction

The Middle Eocene Princeton chert locality of British Columbia has a diverse permineralised flora that includes vegetative and reproductive organs of ferns, conifers, monocotyledons and dicotyledons. Among dicotyledonous plant reproductive organs are flowers represented by *Paleorosa similkameenensis* Basinger 1976 (Rosaceae), *Princetonia allenbyensis* Stockey 1987 (*incertae sedis*), and a sapindaceous flower (Erwin and Stockey 1990). Fruits and seeds include *Decodon allenbyensis* Cevallos-Ferriz and Stockey 1988 (Lythraceae), *Allenbya collinsonae* Cevallos-Ferriz and Stockey 1989 (Nymphaeaceae), and *Ampelocissus similkameenensis* Cevallos-Ferriz and Stockey 1990a (Vitaceae). Additional flowers, fruits and seeds currently under investigation continue to demonstrate that a diverse angiosperm flora occurred here during the Middle Eocene.

Although studies of angiosperms at this locality have concentrated on reproductive structures, vegetative remains including stems, roots, and leaves are also well preserved in the chert. Their identification and attachment to reproductive structures is essential to the reconstruction of whole plants and the understanding of their biology. Vegetative axes from the Princeton chert are represented by a diverse array of twigs, branches and roots. The first angiosperm vegetative stem described from Princeton was *Eorhiza arnoldii*, a dicotyledonous rhizome of uncertain affinities (Robison and Person 1973). Recently, Cevallos-Ferriz and Stockey (1990b) described *Liriodendroxylon allenbyensis* (Magnoliaceae) based on several twigs and one branching specimen. They noted that many of the vegetative axes in the chert have well preserved phloem, cortex, epidermis and/or periderm. These authors stressed the importance of extraxylary tissues in the identification of the Princeton fossil twigs, especially phloem and primary cortical tissues, since some

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* A version of this chapter has been accepted for publication: Cevallos-Ferriz, S. R. S., and Stockey, R. A. 1990. IAWA Bull. n. s. 11(3):

characteristics of juvenile wood differ in mature wood (Page 1979).

Rosaceous leaf remains have been reported from Cretaceous sediments (Hughes 1976), but it is not until the early Tertiary that flowers and fruits are found (Dorofeev 1963, Basinger 1976). During the early Tertiary the Rosaceae underwent an important adaptative radiation forming a characteristic component of the broad-leaved deciduous vegetation (Wolfe 1987). Rosaceous remains of Middle Eocene age from the northwestern United States and southwestern Canada occur at several localities near Princeton and Joseph Creek, British Columbia, and Republic, Washington (Wolfe and Wehr 1988). From these localities about 40 taxa have been identified based on leaf remains (Wolfe and Wehr 1988). Among these leaves are members of the subfamilies Spiraeoideae, Maloideae, Rosoideae, and Prunoideae. The rosaceous flowers from the Princeton chert, *Paleorosa similkameenensis* Basinger (1976), have closest affinities with Subfamily Spiraeoideae, Tribe Sorbarieae (Cevallos-Ferriz *et al.* 1990).

In the present study a new species, *Prunus allenbyensis* Cevallos-Ferriz and Stockey n. sp. (Rosaceae) is described based on vegetative stem and wood remains. Anatomical differences in axes of several ages are compared to similar types of variation seen in extant trees. This provides the basis for understanding some differences between the anatomy of young stems, twigs and more mature wood of this fossil plant.

Material and Methods

Seven rosaceous axes have been found in the Princeton chert (Allenby Formation). The locality is 8.4 km south of Princeton, British Columbia, on the east side of the Similkameen River. Fossils occur in a section consisting of an interbedded sequence of chert and coal with an occasional thin ash bed replacing a chert layer. Forty-nine exposed layers of chert have been recorded and systematically sampled (Stockey 1987). The locality has been referred to as locality "I" (Boneham 1968) and the "Princeton chert locality" (Basinger 1976, Stockey 1984, 1987). The Allenby Formation of the Princeton Group has been dated as Middle Eocene based on palynology (Rouse and Srivastava 1970), mammals and fishes (Russell 1935, Gazin 1953, Wilson 1977, 1982), and potassium-argon dating (Hills and Baadsgaard 1967).

Fossils are preserved as silica permineralisations. All chert blocks were cut into slabs and studied in serial sections using a modified cellulose acetate peel technique and hydrofluoric acid (Joy *et al.* 1956, Basinger and Rothwell 1977). Peel sections were mounted in Eukitt or Coverbond xylene soluble mounting medium for microscopic examination.

In addition to taxa described in the published literature, twigs of extant *Crataegus punctata* Jacq. (ALTA 10621, UAPC-ALTA S1 1827), and *Prunus pennsylvanica* L. (ALTA 72159, UAPC-ALTA S1 1828) were compared anatomically to the fossil wood. Wood was dehydrated in 10%, 30%, and 50% EtOH followed by a tert-butyl alcohol series (Johansen 1940). Paraplast Plus medium was used for infiltration and embedding. Sections 10-13 μm thick were cut on a rotary microtome and stained with safranin-fast green.

The wood identification process was aided by the computer-assisted identification system Guess v 1.1 and NCSU wood database (Wheeler *et al.* 1986; LaPasha and Wheeler 1987). All averages represent a series of 25 separate measurements (Carlquist 1988).

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

Systematic Description

Class: Magnoliopsida

Subclass: Rosidae

Order: Rosales

Family: Rosaceae

Subfamily: Prunoideae

Genus: *Prunus* L.

Species: *Prunus allenbyensis* CevallosFerriz et Stockey n. sp.

Etymology: The specific epithet *allenbyensis* refers to the abandoned mining town of Allenby near which the Princeton chert locality is found.

Holotype: P1095 A (Pl. IV, 3 Fig. 14; Pl. IV, 5 Figs. 24, 26), B (Pl. IV, 4 Figs. 17, 19; Pl. IV, 5 Fig. 22), P1095 C (Pl. IV, 1 Figs. 2, 4; Pl. IV, 3 Figs. 9, 11, 13; Pl. IV, 4 Figs 15, 16; Pl. IV, 5 Figs. 23, 25), D (Pl. IV, 2 Fig. 8).

Paratypes: P1184 B (Pl. IV, 1 Fig. 1; Pl. IV, 2 Fig. 7); P1235 A (Pl. IV, 1 Fig. 3; Pl. IV, 2 Fig. 6; Pl. IV, 3 Fig. 10; Pl. IV, 5 Fig. 21), D (Pl. IV, 3 Fig. 12; Pl. IV, 4 Figs 18, 20); P1720 C (Pl. IV, 2 Fig. 5).

Diagnosis - Pith composed of thin-walled polyhedral cells and smaller polyhedral thick-walled cells with dark contents either organised in rows or scattered at centre, and a peri-medullary zone of thick-walled oval cells. Primary xylem containing protoxylem elements with helical secondary walls, metaxylem tracheary elements with scalariform wall thickenings and occasional parenchyma cells with dark contents. Secondary xylem semi-ring-porous, with axial traumatic ducts, vessel elements oval to weakly angular in transverse section, solitary, in radial and oblique multiples and occasionally in clusters; vessel elements with oblique end walls and simple perforation plates, alternate intervascular pitting, and helical thickenings, some with dark contents and/or tyloses. Fibres with circular to oval bordered pits (4 μm in diam.), and dark deposits in older wood. Uniseriate rays homocellular and heterocellular, up to 18 cells high. Multiseriate rays heterocellular with one or two marginal rows of upright cells, up to 8-seriate. Vessel to ray pits similar to intervascular pits. Apotracheal diffuse parenchyma, and scanty paratracheal cells in mature wood. Primary phloem fibre bundles present. Cortical cells oval with dark contents; scattered fibre clusters in cortex, fibres sometimes irregularly shaped. Epidermis of rectangular cells with thin cuticle layer. Secondary phloem with alternating discontinuous bands of tangentially oriented fibres and thin-walled cells. Dilated phloem rays, one to several cells wide, with dark contents. Phelloderm up to three cells thick of rectangular cells. Phellem of concave cells up to five cells thick.

Description

Five twig fragments, averaging 1.0 x 0.7 x 4.0 cm (Pl. IV, 1 Fig. 1), a larger branch, 2.3 x 2.0 x 9.3 cm (Pl. IV, 1 Fig. 2), and one wood fragment, more than 9.4 cm in diameter (Fig. 10; >16 years) have been found in the chert. Anatomical similarities in primary and secondary tissues of all of these vegetative remains enable us to interpret them as belonging to a single taxon.

Anatomy of the first five growth increments

Primary tissues - The twigs and the branching specimen are characterised by the presence of a heterocellular pith and tangentially arranged axial traumatic ducts in the secondary xylem. Most pith cells are thin-walled and polyhedral or irregular in transverse section (Pl. IV, 1 Fig. 3). In longitudinal section they are rectangular or irregular, averaging 107 x 73 x 88 µm (Pl. IV, 1 Fig. 4). A few polyhedral, thick-walled cells with dark contents and smaller dimensions, averaging 46 x 34 x 63 µm, are scattered in the pith, sometimes forming irregular rows (Pl. IV, 1 Figs. 1, 3). The periphery of the pith is characterised by four to five layers of smaller, thick-walled, oval to polyhedral cells filled with dark contents, the peri-medullary region (Pl. IV, 2 Fig. 5). In longitudinal section these cells are rectangular to quadrangular, averaging 44 x 22 x 72 µm. Almost all pith cells are elongated parallel to the long axis of the twig (Pl. IV, 1 Fig. 4).

In transverse section axes have about 19 protoxylem points composed of oval cells with a mean diameter of ca. 14 µm (Pl. IV, 2 Fig. 5); in longitudinal section these cells have helical secondary walls (Pl. IV, 2 Fig. 6). Metaxylem cells in transverse section are also oval with a diameter of ca. 18 µm (Pl. IV, 2 Fig. 5). In longitudinal section they can be distinguished from the protoxylem elements by the presence of scalariform thickenings (Pl. IV, 2 Fig. 6). Associated with the primary xylem are a few thin-walled parenchymatous cells with dark contents.

The cortex is up to 15 cell layers thick (Pl. IV, 2 Figs. 7, 8). Cells in the cortex are thin-walled, oval in transverse section, and average 57 x 16 x 44 µm, with dark contents. The abundance of cell contents increases towards the middle cortex. The cortex is also characterised by clusters of fibres up to 6 cells in diameter (Pl. IV, 5 Fig. 26). At the inner margin of the cortex, primary phloem is represented by fibres (Pl. IV, 2 Fig. 8). Sieve elements and parenchyma cells are not preserved. Epidermal cells usually are not well preserved; however, in some twigs a few crushed cells can be observed covered by cuticle.

<u>Secondary tissues</u> - In the first five growth rings of the secondary xylem, vessel elements are rarely solitary (ca. 5 %), often in radial and oblique multiples of two to four cells (ca. 73%) and occasionally in clusters (ca. 21%; Pl. IV, 3 Fig. 9). Vessel elements are oval to weakly angular with a small diameter (ca. 28 µm tang. x 29 µm rad.) in wood produced during the first growing season. Vessel diameter increases to ca. 30 µm in the second growth year, and the wood becomes semi-ring-porous from a diffuse porous condition in the first year. Vessel elements continue to increase in diameter in successive years. In the last growth ring of the older twig (four years old) vessel element diameter in earlywood is ca. 33 µm (tang.) x 34 µm (rad.), while in latewood it is ca. 26 µm (tang.) x 31 µm (rad.). In these first four growth increments vessel element density is about 283/mm^2. A large proportion of the wood in twigs is composed of thin-walled (*sensu* Wheeler *et al.* 1986) fibres, rectangular to polyhedral in transverse section, averaging 12 x 18 x 294 µm (Pl. IV, 4 Fig. 18). Vertical traumatic ducts are present at the beginning of

some growing seasons in most twigs (Pl. IV, 1 Fig. 1, Pl. IV, 3 Fig. 13). These ducts are either tangentially arranged along the whole ring (Pl. IV, 1 Fig. 1), or located in only a part of it. Vertical traumatic ducts are short (ca. 1.5 mm long), and distributed in such a way that while an axis may have them at one level, they may disappear completely at another. Most of the twigs have axial traumatic ducts in the second growth ring. Traumatic ducts lack an epithelial lining (Pl. IV, 3 Fig. 13) and are apparently, therefore, lysigenous in origin (Panshin and de Zeeuw 1980). The brownish contents present in some of these vertical ducts may represent former cell contents.

Vessel elements have slightly oblique end walls with simple perforation plates (Pl. IV, 2 Fig. 6, Pl. IV, 3 Fig. 14, Pl. IV, 4 Fig.18), and alternate intervascular pits (ca. 6 x 4 µm) on lateral walls (Pl. IV, 3 Fig. 12, Pl. IV, 4 Figs. 15, 16). Intervascular pitting in some areas is crowded, oval, mostly alternate, rarely opposite, and in very few cases scalariform because of the coalescence of pit apertures (Pl. IV, 4 Figs. 15, 16). Vessel elements have thin helical thickenings, especially those of the latewood (Pl. IV, 3 Fig. 14, Pl. IV, 4 Fig. 18). These helical thickenings are more common in smaller vessel elements. Some vessels have dark contents. Fibres have circular to oval bordered pits, ca. 4 µm in diameter in tangential and radial walls (Pl. IV, 4 Fig. 18).

Rays are one to five-seriate and five to 28 cells high (Pl. IV, 4 Figs. 19, 20), averaging 370 µm (range 150-630 µm), and have simple pits on radial and tangential walls. There are about 10 rays per millimetre. Multiseriate rays are composed mainly of procumbent cells with one or two upright cells in the margins (Pl. IV, 5 Fig. 24). Uniseriate rays are two to 12 (up to 18) cells high near the pith (range 36-115 µm). Rays are composed of upright cells near the pith (Pl. IV, 5 Fig. 21), but in later wood they have procumbent, square, and upright cells. In the branching specimen, some multiseriate rays near the margin of the pith are over 1 mm high. In later wood of the same specimen rays are ca. 500 µm high, but as the branch grew, rays became shorter. Ray to vessel pits are similar or slightly smaller, but less crowded, than intervascular pits (Pl. IV, 4 Fig. 17).

Parenchyma cells with dark contents are also present in the wood and usually form apotracheal strands up to 7 cells wide and about five cells tall (Pl. IV, 5 Fig. 22).

Secondary phloem is composed of discontinuous, tangentially oriented, alternating bands of thin-walled cells and fibre clusters (Pl. IV, 1 Figs. 1, 2, Pl. IV, 2 Fig. 8, Pl. IV, 5 Fig. 25). Thin-walled cells tend to be ovoid and may represent sieve tube members. Adjacent to the vascular cambium, phloem rays are thin (two or three cells wide). They dilate toward the cortex where they may be up to 8 cells wide. A few uniseriate rays may also be present. In some twigs rays appear straight in transverse section, but in other specimens they have an undulating outline. However, these rays are not always well preserved and often appear as large spaces (Pl. IV, 1 Figs. 1, 2). Periderm is present in all twigs examined (Pl. IV, 2 Fig. 7). The phellem is typically around five cells thick, but may be more extensive in larger twigs. It is composed of rectangular cells with a concave surface facing towards the pith. Three cell layers of rectangular cells form the phelloderm in most twigs (Pl. IV, 2 Fig. 7).

Anatomy of the older growth increments

The last growth ring of the branching stem and wood of the large wood fragment have anatomy similar to twigs, but differ quantitatively in several aspects. As in the twigs, the pith is heterocellular. However, while small cells with dark contents are found both scattered and in short rows in the central part of the pith in twigs, in the larger branch cells of this type are organised into irregular rows (Pl. IV, 1 Fig. 3). The large wood fragment has vessel grouping similar to twigs; however, most vessels are solitary (ca. 46%), with fewer in radial and oblique multiples (ca. 42%) and clusters (ca. 12%). Vessel distribution is semi-ring-porous (Pl. IV, 3 Fig. 10); however, there are fewer (100) and larger vessel elements per square millimetre. Vessel elements almost double in size in older wood compared to the first five growth rings. In earlywood they have a tangential diameter of 55 µm (range 47-65 µm) and a radial diameter of 70 µm (range 40-83 µm). In latewood vessels have an average tangential diameter of 32 µm (range 28-45 µm), and average radial diameter of 35 μm (range 22-40 μm). Tyloses are frequently found in these larger axes (Pl. IV, 3 Fig. 11), while they are rare or absent in the twigs. Vertical traumatic ducts are also present, and as in twigs they apparently have a lysigenous origin. In contrast to smaller axes in which traumatic ducts are typically empty, ducts in the branch and large wood fragment frequently have contents. Multiseriate rays are heterocellular, with one or two rows of marginal upright cells, up to 8-seriate and are almost 40 cells high (average 360 μm). A few homocellular uniseriate rays up to 12 cells high are present; however, most unicellular rays are heterocellular and are composed of procumbent, square, and upright cells. Parenchyma cells form apotracheal strands as in the twig (Pl. IV, 5 Fig. 22), but in a few cases scanty paratracheal cells not found in twigs are also present (Pl. IV, 5 Fig. 23). Vessels and parenchyma cells in these more mature woods have darker contents than in the twigs.

Discussion

Comparison with extant Rosaceae - Anatomical similarities among all of the vegetative axes under study support their interpretation as specimens belonging to the same taxon. These include: heterocellular pith with a peri-medullary zone, semi-ring-porosity, alternate intervascular pitting, simple perforation plates, fibres with circular bordered pits in tangential and radial walls, and ray to vessel pits that are similar to intervascular pits. The observed variation in vessel element density, height of rays, amount of dark cellular contents and presence of scanty paratracheal parenchyma, and tyloses, is consistent with what one would expect in wood of different parts of the same tree or different individuals of the same species (Schweingruber 1978). General vessel distribution (which may vary slightly in the first few growing seasons), type of perforation plate, and type of ray to vessel pitting are characters that typically remain constant in the above-ground parts of selected taxa in Betulaceae, Fagaceae, Platanaceae and Salicaceae (Schweingruber 1978), while ray structure, for example, can vary depending on cambial age (Barghoorn 1940, 1941a, 1941b). Our previous study of twigs of *Magnolia* L. and *Liriodendron* L. further supports the constancy of Schweingruber's anatomical characters (Cevallos-Ferriz and Stockey, 1990b). Observations of extant *Prunus pennsylvanica* and *Crataegus punctata* made during this study confirm the constancy of these characters for these two taxa.

Comparison of wood characters - Four of the characters, (semi-ring-porosity, simple perforation plates, alternate intervascular pitting, and ray to vessel pits similar to intervascular pits) found in *P. allenbyensis* are found in combination in over 50 families of dicotyledonous plants (Wheeler *et al.* 1986, LaPasha and Wheeler 1987). However, the combination of these and an additional five characters are found together only in two families, Rosaceae and Meliaceae (Wheeler *et al.* 1986, LaPasha and Wheeler 1987). These additional characters include: vessel elements with helical thickenings, fibres with distinctly bordered pits, gum in vessels, rays commonly 4-10-seriate, and axial traumatic ducts. The most definitive of these characters is the presence of axial traumatic ducts.

Although *Prunus allenbyensis* has many characters in common with Meliaceae, the two differ with respect to features of the fibres, distribution of parenchyma, and histology of the ground tissue. Fibres with distinctly bordered pits, the high number of vessels per square millimetre and scanty paratracheal and occasional apotracheal parenchyma are more reminiscent of Rosaceae than of the Meliaceae (Wheeler 1989 pers. commun.). Although pith with a peri-medullary zone has been reported in Meliaceae and Rosaceae (Metcalfe and Chalk 1950) members of Meliaceae also commonly have either secretory cells (*Entandrophragma* DC. and *Melia* L.), or stone cells (*Cabralea* Juss., *Chisocheton* Blume, *Hearnia* Muell., *Megaphyllaea* Hemsl. and *Sandoricum* Cav.; Metcalfe and Chalk 1950). Neither are present in the pith of *P. allenbyensis*. Secretory cells also characterise the cortex and secondary phloem of Meliaceae (Roth 1971, 1981) while these cells are absent in *P. allenbyensis*.

The fossil vegetative axes exhibit a large number of characters that typify wood of Rosaceae. These include: small (but in some genera large) and numerous vessels, a tendency to ring-porosity, vessel elements often with helical thickenings, perforation plates that are typically simple (but occasionally with scalariform or irregular perforation plates), mainly alternate or occasionally opposite intervascular pitting; axial parenchyma that is apotracheal diffuse, diffuse in aggregates, or sometimes scanty paratracheal; heterocellular to homocellular rays that are two-to five-seriate, or sometimes wider, occasionally with two distinct widths; ray to vessel pits often similar to intervascular pits, and fibres with distinct bordered pits on radial and tangential walls in most genera (Metcalfe and Chalk 1950, Fabbri-Tarchi 1960).

Prunus allenbyensis has some characters that can be found in the subfamilies Prunoideae and/or Maloideae. These include presence of axial traumatic ducts, vessel distribution, distribution and distinctiveness of bordered pits in fibres, type of ray to vessel pitting, and type of uniseriate ray. Vertical traumatic ducts within Rosaceae were thought to be almost unique to the subfamily Prunoideae (Record 1925, Metcalfe and Chalk 1950). Recently these ducts have been reported in species of Rosaceae other than those included in Prunoideae (Fahn *et al.* 1986). The combination, however, of axial traumatic ducts and vessel elements in radial and oblique multiples, occasional clusters and solitary vessels, as in *P. allenbyensis* is more common in the subfamily Prunoideae. Nevertheless, the higher number of solitary vessels in more mature wood is reminiscent of Maloideae (Metcalfe and Chalk 1950, Zhang Shuying 1989 pers. commun.).

Presence of distinct bordered pits in tangential and radial walls of fibres of the Princeton wood is a character shared with most Rosaceae. Metcalfe and Chalk (1950) noted that in most Maloideae and some species of *Spiraea* L. (Spiraeoideae) pits are less common in tangential than in radial walls of the fibres. This same character is thought to be of importance in identifying Prunoideae (Metcalfe and Chalk 1950, Zhang Shuying 1989 pers. commun.). The quality of preservation of *Prunus allenbyensis* does not allow a comparison of the abundance of pits in tangential and radial walls of the fibres. Difficulty in observing the pit borders in most *Prunus* species was also noted by Metcalfe and Chalk (1950). Fibres with pit borders that are difficult to observe are not restricted to Prunoideae, but can be found for example in some species of *Spiraea* (Spiraeoideae; Metcalfe and Chalk 1950). However, some extant *Prunus* species and other taxa in Maloideae have pits with clearly distinct borders (Zhang Shuying 1989 pers commun.), as in *P. allenbyensis*.

In Rosaceae, ray to vessel pits have been described as similar to intervascular pits (Tippo 1938, Fabbri-Tarchi 1960). However, reinvestigation of some rosaceous species, in the four subfamilies, has revealed that in at least some taxa the ray to vessel pits are half bordered (Fahn et al. 1986). In *Prunus*, this character has been found in most species (Zhang Shuying 1989 pers commun.); however, there are some species that have ray to vessel pits similar to intervascular pits (e. g., *Prunus serotina* Ehrh., Wheeler 1990 pers. commun.), as in *P. allenbyensis*.

Most rosaceous taxa have unicellular rays composed of upright and square cells (Metcalfe and Chalk 1950). Rays in Maloideae are characterized by their tendency to be homocellular (Fabbri-Tarchi 1960), while uniseriate rays in extant Prunoideae are heterocellular, composed of square and upright cells (Metcalfe and Chalk 1950; Zhang Shuying per. commun. 1989). Ray structure varies with developmental stage. Near the pith the fossil twigs and branch have uniseriate homocellular rays composed of procumbent cells. However, farther away from the pith, uniseriate rays become slightly heterocellular, composed of procumbent, square, and upright cells. Structure of uniseriate rays in fossil *Prunus* varies from those composed of exclusively upright cells (*P. palaeozippeliana* Suzuki, *P. polyporulosa* Suzuki) to those with upright and square cells (*P. ascendentiporulosa* Suzuki) or with procumbent and upright cells (*P. iwatense* (Watari) Takahashi & Suzuki), to those with at least some rays composed of upright, square, and procumbent cells (*P. gummosa* Wheeler *et al.*).

We have assigned the Princeton vegetative axes to *Prunus* based on the combined presence of axial traumatic ducts and vessels that are solitary, and in oblique and radial multiples, or occasionally in clusters. Furthermore, uniseriate rays that become heterocellular as the plant grew, as well as presence of uniseriate rays that are similar to those found in other fossil *Prunus* species serve to further support this identification.

Comparison of secondary phloem and pith characters - Of the several patterns that characterise secondary phloem of rosaceous species, ***Prunus allenbyensis*** is most similar to that reported for extant *Rubus* L. (Rosoideae; Zahur 1959, Roth 1973). In both taxa, the mechanical tissue is well developed and is represented by discontinuous tangential bands of fibres. Although other species of extant Rosaceae also have mechanical tissue, the arrangement of the bands seen in the fossil has not been reported. For example, mechanical tissue in the Maloideae species investigated by Zahur (1959) is composed of tangentially arranged, continuous bands of sclereids. In Spiraeoideae, *Exochorda grandiflora* Lindl. is the only species in which phloem has been studied in some detail, and lacks sclereids. The most complete description of rosaceous phloem is that of *Prunus*. Phloem of the fossil vegetative axes shares the following features with extant *Prunus*: large number of fibres, and moderate dilation of rays. The presence of U-shaped cells in the phellem, and lack of a secretory system are also shared characters with Rosaceae (Bastin 1895, Schneider 1945, Roth 1973). In the Chrysobalanaceae, a family thought by some to be closely related (e. g., Prance 1972, Hutchinson 1973, Cronquist 1988), an arrangement similar to that found in the Princeton material has been noted in two species of *Licania* Aubl. (Roth 1973, 1981). Since the phloem of about only 13 out of about 3000 species of Rosaceae and only 7 out of 430 species of *Prunus* has been described to date and the anatomy of this tissue seems to be quite variable within the family, it would not be surprising to find phloem with organisation like *P. allenbyensis* in *Prunus* or taxa of other subfamilies.

Pith like that of *Prunus allenbyensis* with a differentiated peri-medullary region has been reported in *Prunus padus* L., *P. avium* L., and *P. spinosa* Walt. (Schweingruber 1978) as well as in other rosaceous genera such as *Neillia* D. Don (Spiraeoideae), and *Rubus* and *Kerria* DC. (Rosoideae; Metcalfe and Chalk 1950). As in *P. allenbyensis*, the presence of scattered smaller cells with dark contents in the pith is a frequent character of

Prunus (Schweingruber 1978) and other rosaceous taxa (Metcalfe and Chalk 1950). The presence of small rows of cells between larger cells is an arrangement found in some twigs and in the branching specimen of *P. allenbyensis* and has been noted in *Rosa* L. (Rosoideae; Schweingruber 1978).

Comparison with fossil Rosaceae - At least 18 rosaceous woods are known from the fossil record (Table IV, 1). They have been included in Maloideae (Grambast-Fessard 1966, Wheeler and Matten 1977, Hofmann 1944, 1952, van der Burgh 1974, 1978), Rosoideae (Shilkina 1958), Spiraeoideae (Page 1964), and Prunoideae (van der Burgh 1974, Dupéron 1976, Wheeler *et al.* 1978, Süss and Müller-Stoll 1980, 1982, Suzuki 1984, Takahashi and Suzuki 1988). One species has been described in the Chrysobalanaceae (Pfeiffer and van Heuren 1928).

Prunus allenbyensis differs from other fossilised rosaceous stem woods, excluding Prunoideae, by the presence of axial traumatic ducts (Table IV, 1). Species of *Pomoxylon* (Hofmann 1944, 1952, van der Burgh 1978) differ further from *P. allenbyensis* in having only solitary vessel elements, rather than radial multiples and clusters of vessels (Table IV, 1). *Crataegus* and *Sorbus* L. from the Pleistocene of Tegelen, The Netherlands, have homocellular rays, and mainly solitary vessels (van der Burgh 1974), in contrast to the heterocellular rays, and vessels that are solitary, in radial and oblique multiples and clusters of *P. allenbyensis* (Table IV, 1). *Maloidoxylon coloradoense* and *M. galbreathii* from Colorado, U.S.A., and *M. castellanense* from Castellane, France, differ in lacking helical thickenings, and gum or gum-like deposits (Table IV, 1; Grambast-Fessard 1966, Wheeler and Matten 1977). *Rosaceoxylon* Shilkina from Russia is distinct in having septate fibres and scalariform intervascular pitting (Table IV, 1; Shilkina 1958, Süss and Müller-Stoll 1982). *Parinarioxylon* is characterised by the presence of uniseriate rays and lacks helical thickenings (Pfeiffer and van Heuren 1928).

The root wood described as *Pruninium kraeuselii* (Schönfeld) Süss and Müller-Stoll (1982) is difficult to compare to *P. allenbyensis* since variation in roots is even greater than variation in the above-ground axes. However, the root wood of this taxon lacks axial traumatic ducts and has rays with more marginal cells (Süss and Müller-Stoll 1982).

Stem woods described as Prunoideae are most similar to the fossil Princeton remains (Table IV, 1). However, vessel distribution in the Princeton plant is unlike almost all other fossil Prunoideae. Semi-ring-porosity, as in the wood of *Prunus allenbyensis*, is only reported in one other fossil form, *Prunoideoxylon multisporosum* from Agenais, France (Dupéron 1976). However, this taxon has a dendritic vessel arrangement, lacks gum or gum-like deposits and axial traumatic ducts, and some vessels have scalariform perforation plates with a few bars.

Suzuki (1984) described four species of *Prunus* from Kyushu, Japan, as diffuse porous, but in his description he noted that latewood vessel elements have a smaller diameter. This pattern may suggest that the woods are semi-ring-porous rather than diffuse-porous. His photographs (Suzuki 1984, figs. 1, 3, 6, 7, 11, and 14) also support this interpretation, especially for *P. palaeozippeliana*, *P. ascendentiporulosa* and *P. uviporulosa*. The Japanese material commonly has characters absent from the Princeton plant, including ray structure, and the large number of vessel elements in clusters and radial multiples (Table IV, 1; Suzuki 1984). The Lower Miocene species, *P. iwatense*, from Nesori, Japan, is distinct from *P. allenbyensis* in having circular thick-walled vessel elements in transverse section with a diffuse-porous pattern, little or no axial parenchyma, and lacking axial traumatic ducts (Table IV, 1; Takahashi and Suzuki 1988). *Prunus* sp. from the Pleistocene of Tegelen, The Netherlands (van der Burgh 1974), differs from *P. allenbyensis* in lacking gum deposits, and axial traumatic ducts, and having only solitary vessels and half bordered pits in fibres; however, as in *P. allenbyensis* it has scanty paratracheal parenchyma.

Prunus allenbyensis appears to be most closely related to the Eocene *P. gummosa* from Amethyst Mountain, Yellowstone National Park, Wyoming (Wheeler *et al.* 1978).

Differences between the woods from these two localities are mostly quantitative, and fall within the range of variation expected among populations (Table IV, 2; Panshin and de Zeeuw 1980, Carlquist 1988). This variation could reflect either environmental differences, or the level in the tree from which the material was derived. There are differences in distribution of vessels, ray and axial parenchyma, and size of individual cells. While the Princeton wood is semi-ring-porous, wood from Yellowstone is diffuse porous. Generally, and within Rosaceae, this type of variation correlates well with environmental differences (Tomlinson and Craighead 1972, Baas 1973, Bissing 1982, Fahn *et al.* 1986, Carlquist 1988). Secondly, rosaceous wood from both localities is typified by multiseriate rays with one or two rows of marginal cells in mature wood (Table IV, 2), although the wood from Yellowstone may have up to 6 rows of marginal cells (Wheeler *et al.* 1978). Thirdly, scanty paratracheal parenchyma is present in the Princeton wood but absent in wood from Yellowstone. A final difference between *P. allenbyensis* and the Yellowstone wood is vessel element diameter (Table IV, 2). This difference may reflect variation in altitude, latitude, or other ecological parameters (Baas 1973, Carlquist 1988). Another possible explanation for these differences is that the Yellowstone wood was definitely trunk wood (Wheeler 1989 pers. commun.).

Primary tissues, secondary phloem, and periderm are unknown in *P. gummosa*. Because primary tissues, secondary phloem, and periderm are known for *P. allenbyensis* and are of taxonomic value and important to its diagnosis, we prefer to describe it as a new species. Further taxonomic comparison between *P. allenbyensis* and *P. gummosa* awaits the discovery of more completely preserved stems of the Yellowstone material and/or larger specimens from Princeton.

Several other rosaceous remains are known from these localities. In the Princeton chert, the rosaceous flower *Paleorosa similkameenensis* Basinger (1976) has been identified as a member of the Subfamily Spiraeoideae, Tribe Sorbarieae (Cevallos-Ferriz *et al.*, 1990). Three types of *Prunus* fruits, including endocarp and seed, from the Princeton chert are currently under investigation. However, at the present time the relationship of these organs to the wood is unclear. From compression localities in the Allenby Formation three different types of *Prunus* leaves have been recognised (Wolfe and Wehr 1988 pers. commun.). Connection of these isolated organs promises to broaden our understanding of these isolated organs as whole plants.

Paleoclimatic implications - Ecological studies based on wood anatomy have shown potential in drawing paleoclimatic conclusions (Carlquist 1988, Fahn *et al.* 1986). While many ideas involved in this procedure are still speculative, it is important to discuss some of the probable functional-ecological significance of *Prunus allenbyensis.*

The presence of distinct growth rings with narrow vessel elements in latewood may indicate that the fossil plants grew in a seasonal environment. Growth rings have been interpreted as indicators of some sort of seasonality over a long period of time. The relationship between growth rings and environment is not always straightforward. Although some taxa develop the same type of growth ring under different environmental conditions, others are sensitive indicators of environmental changes (de Paolis 1948, Bissing 1982, Carlquist 1988). Since most wood fragments so far recovered from the Princeton chert locality have distinct growth rings, it is most likely that they reflect seasonality. Secondly, *P. allenbyensis* is semi-ring-porous also showing seasonality.

Presence of helical thickenings in small vessel elements of latewood may indicate a decrease in water availability toward the end of the growing season. In today's vegetation helical thickenings in vessel elements are widespread in dry areas (Webber 1936, Carlquist 1966); however, they can also be found in areas subject to freezing (Carlquist 1982, 1984). In addition, helical thickenings have been suggested to enhance water movement in vessel elements (Jeje and Zimmerman 1979; Carlquist 1988). On the other hand, the helical thickening has been correlated with latitude in geographically widespread genera like *Ilex* and *Symplocos* (Baas 1973, van der Oever *et al.* 1981, Baas and Carlquist 1985, Baas and Schweingruber 1987).

The wood anatomy of *Prunus allenbyensis* and the inferred information provided by other plants from the chert (Erwin and Stockey 1989), suggest that these plants grew in a mesic environment. Sedimentologic and taphonomic observations of the laminated couplets of Eocene lakes in British Columbia suggest the presence of a seasonal climate with wet summers and dry winters (Wilson 1988). This interpretation correlates with paleobotanical data about the Eocene climate (Hopkins *et al.* 1972). A short winter with rare frost periods has been postulated by Basinger (1976). Warm temperatures during the Princeton chert deposition are inferred from fossil plants with extant relatives living under these conditions (e. g., Arecaceae, Araceae).

The plant assemblage so far known from the Princeton chert suggests the presence of two distinct, but nearby, environments in the sedimentary basin. Aquatic and semi-aquatic plants like *Keratosperma* (Araceae), *Heleophyton* (Alismataceae), *Allenbya* (Nymphaeaceae), *Eorhiza* (incertae sedis), and *Decodon* (Lythraceae) are most common. A second group of plants not closely related to the aquatic system includes *Ampelocissus* (Vitaceae), and *Liriodendroxylon* (Magnoliaceae). *Prunus allenbyensis* should be added to this second group. This terrestrial component of the Princeton chert may include important angiospermous plants of the coniferous forest that surrounded the lakes of the area (Wolfe 1987, Wolfe and Wehr 1988).

Plate IV, 1

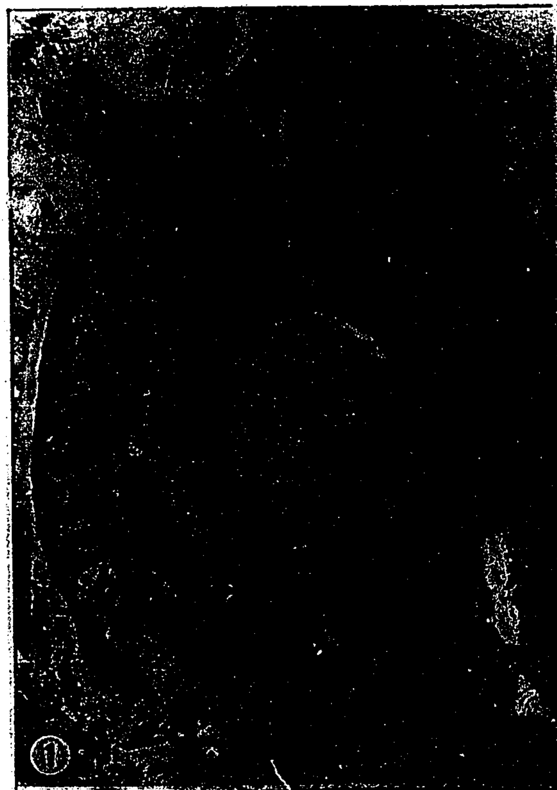
Prunus allenbyensis n. sp.

Fig. 1. Transverse section of twig showing pith and complete extraxylary tissues. Note prominent banded appearance of secondary phloem, and axial traumatic ducts in wood. P1184 B top No. 0, x 10.

Fig. 2. Transverse section of larger branch with banded secondary phloem. P1095 C bot No. 0, x 10.

Fig. 3. Transverse section of pith showing irregular rows of cells with dark contents. P1235 A No. 0, x 150.

Fig. 4. Longitudinal section of pith showing chains of cells with dark contents (arrows). P1095 C side No. 1, x 125.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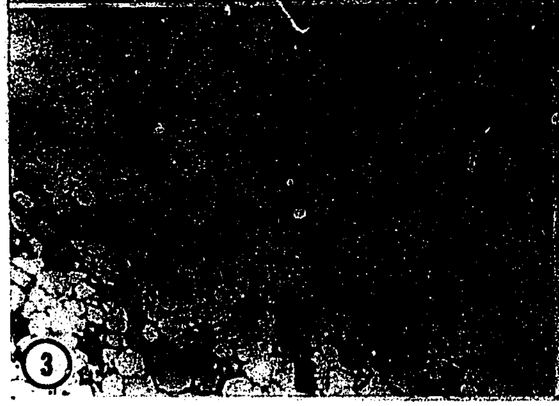
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Plate IV, 2

Prunus allenbyensis n. sp.

Fig. 5. Transverse section of large primary xylem bundle. Note thick-walled cells of peri-medullary region. P1720 C bot No. 4, x 110.

Fig. 6. Longitudinal section of primary xylem. Note vessel element of the first growing season. P1235 A side No. 1, x 35.

Fig. 7. Oblique transverse section of cortex and radially aligned cells of the periderm. P1184 B top No. 1, x 600.

Fig. 8. Transverse section of secondary phloem with fibre caps of the primary phloem at margin of the cortex (arrows). P1095 D top No. 0, x 250.

C=cortex, MX=metaxylem, P=pith, PE=phelloderm, PL=phellem, PM=peri-medullary region, PX=protoxylem, VE=vessel element.

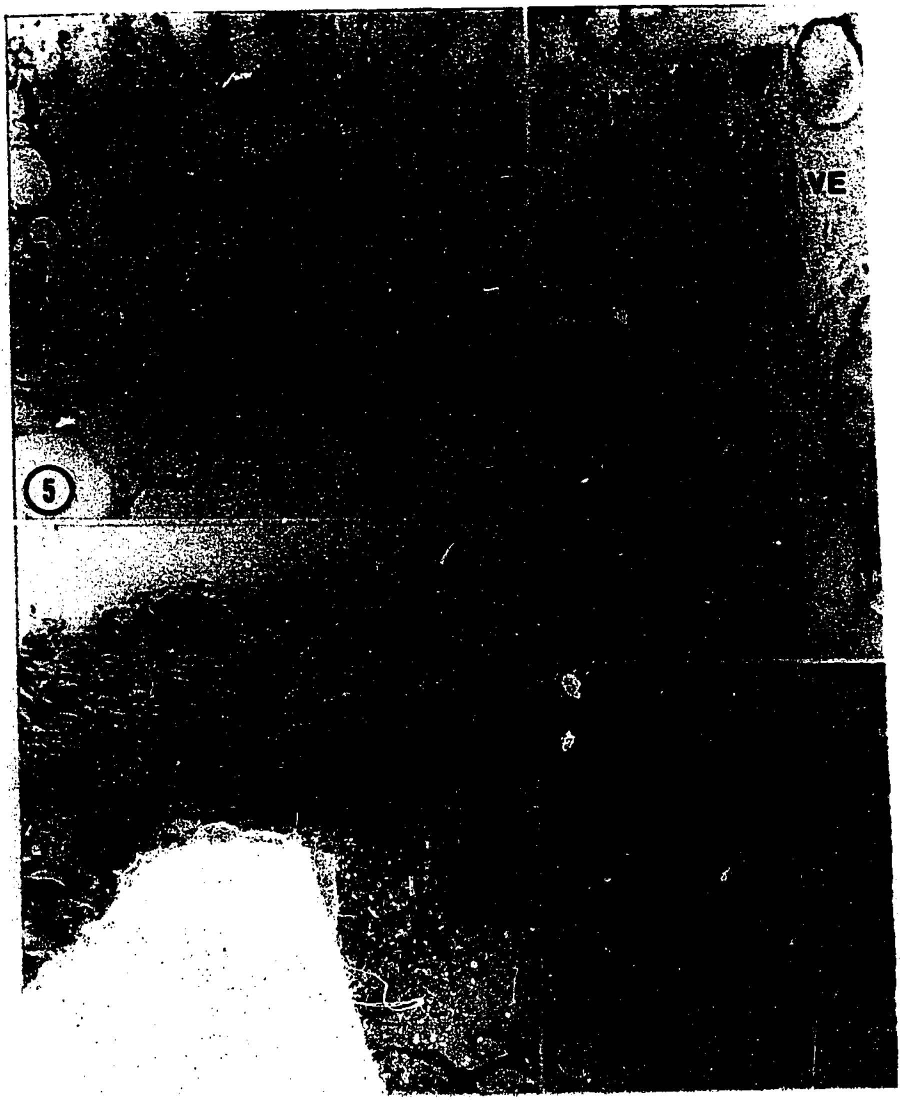
VE
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Plate IV, 3

Prunus allenbyensis n. sp.

Fig. 9. Transverse section of secondary xylem of large branch. P1095 C bot No. 0, x 120.

Fig. 10. Transverse section of xylem of the larger piece of wood. P 1235 A No. 2, x 120.

Fig. 11. Radial section showing vessel elements with tyloses (arrows). P1095 C side No. 1, x 195.

Fig. 12. Vessel elements with alternate intervascular pitting. P1235 D side No. 4, x 250.

Fig. 13. Transverse section of axial traumatic canals. P1095 C bot No. 0, x 110.

Fig. 14. Vessel element with simple perforation plates and thin helical thickenings (arrows). P1095 A side No. 1, x 290.

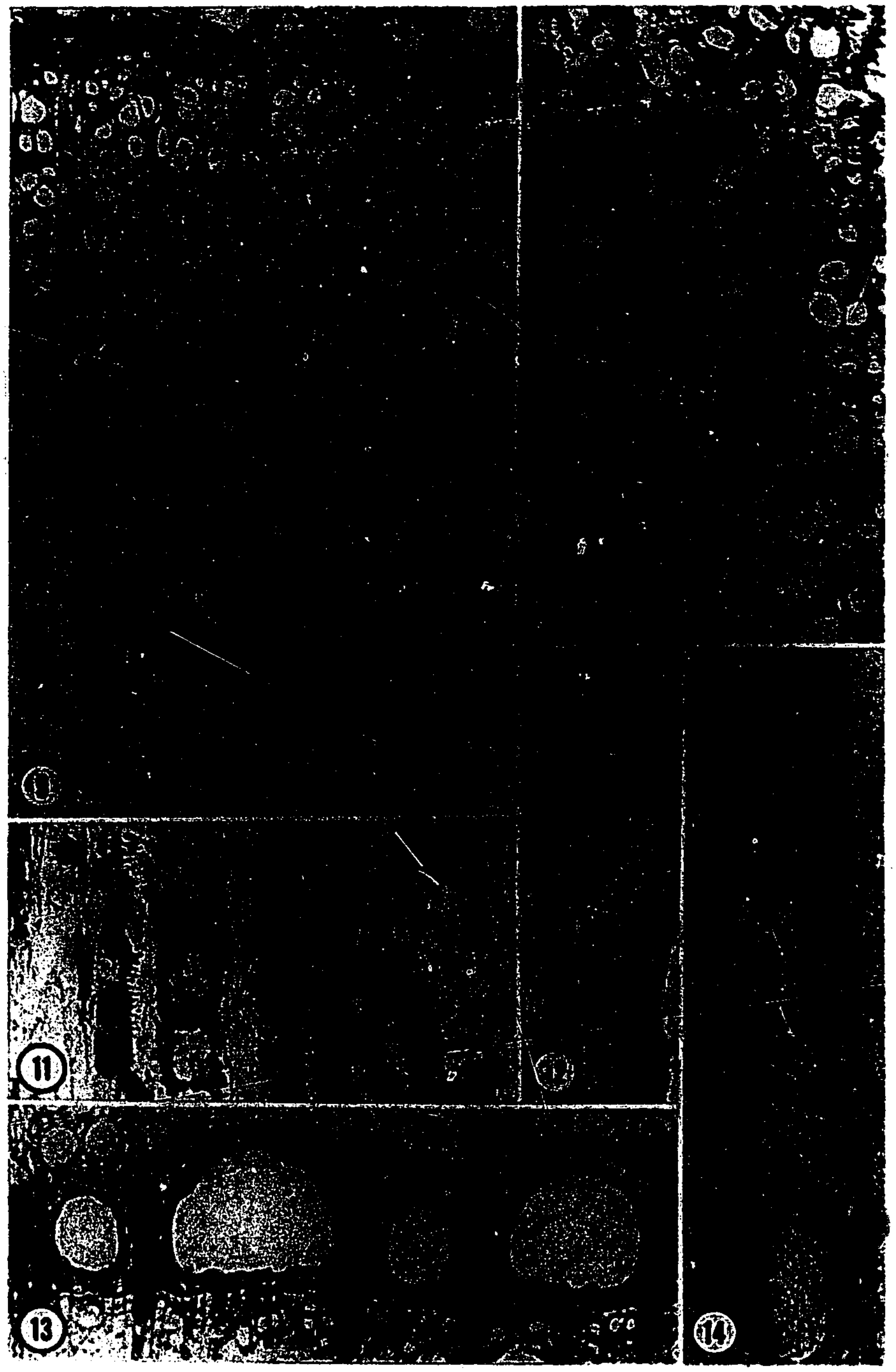
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Plate IV, 4

Prunus allenbyensis n. sp.

Fig. 15. Oval, alternate intervascular pitting with coalescent pit apertures (arrow). P1095 C side No. 1, x 1750.

Fig. 16. Circular to oval, alternate intervascular pitting with coalescent pit apertures (arrow). P1095 C side No. 1, x 1500.

Fig. 17. Ray to vessel pits. P1095 B side No. 0 x, 900.

Fig. 18. Small vessel element of latewood with helical sculpturing surrounded by imperforate tracheary elements with distinctly bordered pits. P1235 D side No. 4, x 130.

Fig. 19. Tangential section of large branch at level close to the pith showing uni- and multiseriate rays . P1095 B side No. 0, x 125.

Fig. 20. Tangential section of larger piece of wood. Note large amount of dark contents. P1235 D side No. 4, x 125.

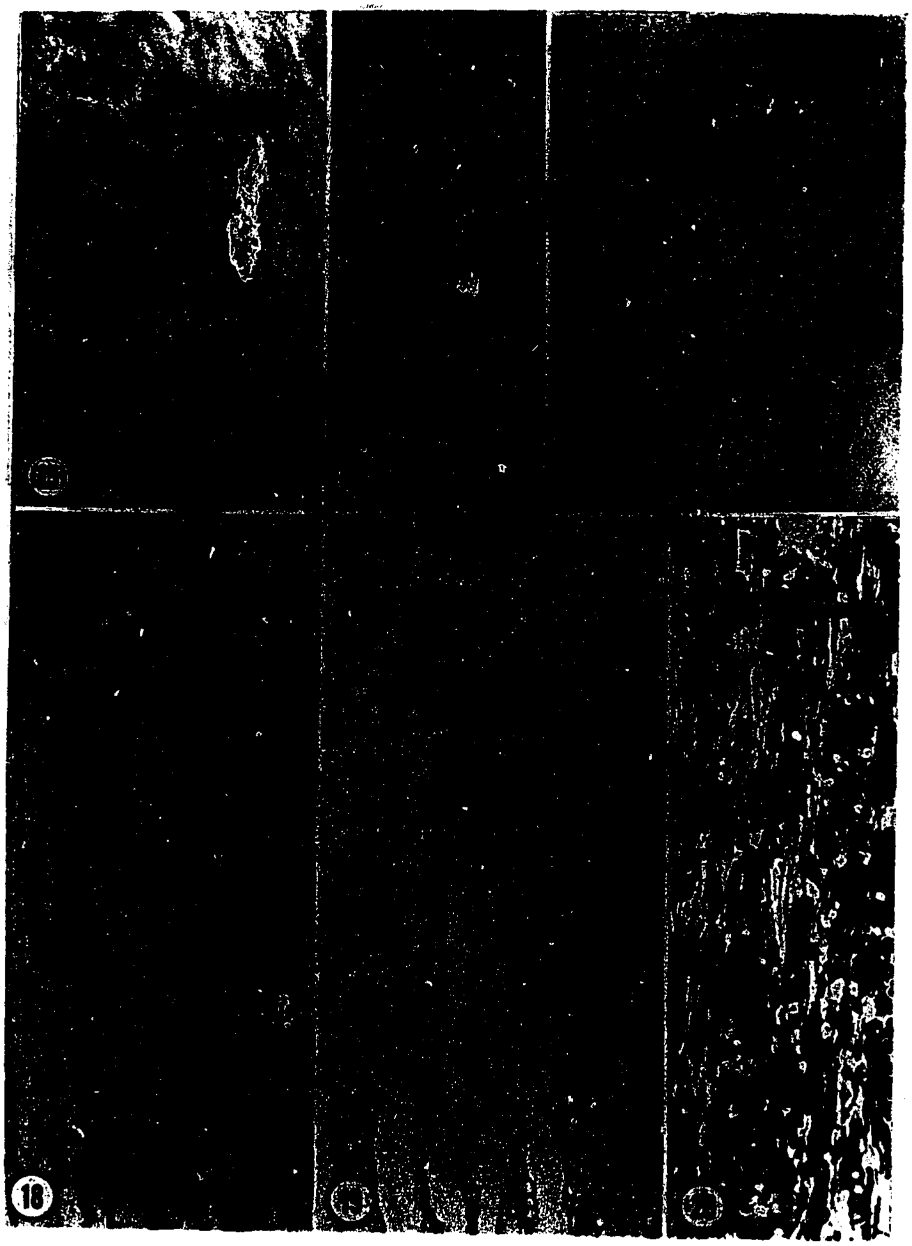
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Plate IV, 5

Prunus allenbyensis n. sp.

Fig. 21. Radial section of uniseriate ray with upright cells. P 1235 A side No. 1, x 235.

Fig. 22. Tangential section showing apotracheal parenchyma. P 1095 B side No. 0, x 280.

Fig. 23. Tangential section showing scanty paratracheal parenchyma. P1095 C side No. 1, x 280.

Fig. 24. Radial section of multiseriate ray with upright and square to procumbent cells. P1095 A side No. 1, x 190.

Fig. 25. Transverse section of secondary phloem. P 1095 C bot No. 0, x 180.

Fig. 26. Oblique radial section of secondary phloem and cortex. P 1095 A side No. 1, x 180.

C=cortex, F=fibres, PH=secondary phloem, R=ray, V=vessel member.


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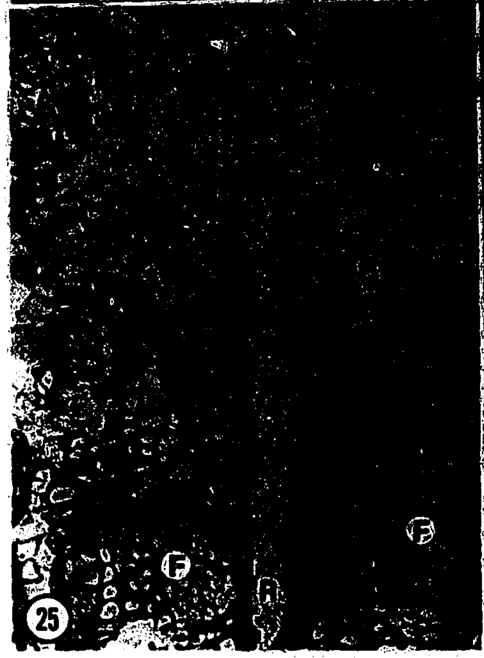
V
23


24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25


F
26

Table IV, 1. Comparison of *Prunus allenbyensis* to other fossil Rosaceae. From Hofmann (1944[1], 19521), Page (1964[2]), Grambast-Fessard (1966[3]), van der Burgh (1974[4], 1978[7]), Dupéron (1976[5]), Wheeler and Matten (1977[6]), Wheeler et al. (1978[8]), Süss and Müller-Stoll (1980[9], 1982[10]), Suzuki (1984[11]), and Takahashi and Suzuki (1988[12]). H=half-bordered pits, S=and scalariform, v. e.=vessel element, i. v. p.=intervascular pitting.

			Maloidoxylon castellanense 3	*Maloidoxylon coloradoense* 6	*Maloidoxylon galbreathii* 6	*Pomoxylon* 1,7	*Crataegus* 4	*Sorbus* 4	*Rosaceoxylon spiraeoides* 3,9	*Lyonothamnoxylon nevadensis* 2	*Prunoidoxylon multiporosum* 5	*Prunus polyporulosa* 11	*Prunus uviporulosa* 11	*Prunus ascendeliporulosa* 11	*Prunus palaeozippeliana* 11	*Prunus iwatense* 12	*Prunus gummosa* 8	*Prunus* sp.4,7	*Pruninium kraeuselii* 10	*Prunus allenbyensis*
Growth rings present			x			x	x	x		x	x	x	x	x	x		x	x		x
VESSEL ELEMENT	Porousity	Semi-ring porous								x	x								x	x
		Diffuse porous	x	x	x		x			x		x	x	x	x	x	x		x	
		Solitary	x	x	x	x	x	x	x	x		x	x	x	x	x	x	x	x	x
		Multiple radial		x								x	x	x	x	x	x		x	x
		Clusters										x	x		x		x			x
	Perforation plates	Simple	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
		Scalariform	x								x									
	Alternate intervascular pitting		?	x	x				S	x		x	x	x	x	x	x	x	x	x
	Spiral thickenings						x	x	x	x	x	x	x	x	x	x	x	x	x	x
RAYS	Heterocellular		x	x	x	x	x			x	x	x	x	x	x	x	x	x	x	x
	Homocellular					x	x	x												
	Pits to v. e. similar to i. v. p.			x	x					x		x	x	x	x		x			x
PARENCHYMA	Apotracheal		x	x	x	x	x			x	?	x	x	x	x		x	x	x	x
	Paratracheal			x		x	x		x		?							x	x	x
Fibres with bordered pits				x	x	x	x	x		x	x	?		?			x	H	x	x
Dark contents										x		x	x	x	x				x	x
Tyloses			x										x	x	x		x		x	x
Vertical traumatic canals												x	x	x	x		x			x

Table IV, 2. Comparison of some features of *Prunus gummosa* (Wheeler *et al.* 1989) from Amethyst Mountain, Yellowstone National Park, Wyoming, and *P. allenbyensis* from Princeton chert locality, British Columbia.

	Prunus gummosa	***Prunus allenbyensis***
VESSEL ELEMENTS		
POROSITY	Diffuse	Semi-ring
	Solitary, Radial multiples,	Clusters Solitary, Radial multiples,Clusters
RADIAL DIAMETER	90 µm	55 µm
TANGENTIAL DIAMETER	47 µm	70 µm
INTERVASCULAR PITTING	Alternate	Alternate
SPIRAL THICKENINGS	Present	Present
PERFORATION PLATES	Simple	Simple
RAY PITTING	Similar to intervascular	Similar to intervascular
TYLOSES	Present	Present
DARK CONTENTS	Present	Present
RAYS		
PER MILLIMETRE	8 - 17	10
UNISERIATE:		
CELLS TALL	10	12
µm TALL	46 - 185 µm	37 -124 µm
MULTISERIATE:		
CELLS TALL	5 - 44	8 - 40
µm TALL	105 - 763 µm	150 - 630 µm
n-SERIATE	2 - 4	2 - 5 (8)
MARGINAL CELL ROWS	1 - 2 (6)	1- 2
IMPERFORATE TRACHEARY ELEMENTS		
THIN-WALLED	Present	Present
CIRCULAR BORDERED PITS	In radialandtangentialwalls	In radial and tangential walls
DIAMETER	5 µm	4 µm
AXIAL PARENCHYMA	Apotracheal	Apotracheal and scanty paratracheal

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Rosaceae (Prunoideae): fruits and seeds*

Introduction

In the last 16 years permineralized plant remains from the Princeton chert locality, British Columbia, have added to our knowledge of the anatomy of reproductive and vegetative plant organs from the Middle Eocene. From this locality reproductive and vegetative organs of *Metasequoia milleri* (ROTHWELL and BASINGER 1979; BASINGER 1981, 1984) have been found and the plant has been reconstructed in detail. Vegetative organs of a sabaloid palm and other monocotyledonous plants also have been found in organic connection (ERWIN and STOCKEY 1987, 1990). Comparisons of vegetative remains from the Princeton chert with extant plants have yielded information on the variability and diversity of several Middle Eocene plants. These include two species of *Pinus* based on foliage, wood and twigs (MILLER 1973; STOCKEY 1984), an alismataceous petiole, *Heleophyton*, (ERWIN and STOCKEY 1989), and, *Eorhiza*, a semi-aquatic dicotyledonous rhizome of uncertain affinities (ROBISON and PERSON 1973). Observations on primary and secondary growth of twigs and branches have provided insight into the developmental changes in magnoliaceous and rosaceous plants found at this site (CEVALLOS-FERRIZ and STOCKEY 1990a, 1990b). Reproductive structures including the flowers of *Paleorosa similkameenensis* (Rosaceae; BASINGER 1976; CEVALLOS-FERRIZ et al. 1990), *Wehrwolfea* (Sapindaceae; ERWIN and STOCKEY 1990), and *Princetonia* (a plant of uncertain affinities; STOCKEY 1987; STOCKEY and PIGG 1990) have been shown to have a variety of characters not present in a single extant taxon. Fruits and seeds of monocotyledonous and dicotyledonous plants have also provided information about the diversity and habitat of the Eocene plants from Princeton (CEVALLOS-FERRIZ and STOCKEY 1988a, 1988b, 1989, 1990c).

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There are only a few North American reports of rosaceous fruits comparable to *Prunus* (e. g., LESQUEREUX 1861; PERKINS 1904, 1906; BERRY 1916a, 1916b, 1924, 1930; BROWN 1962). Their ages range from Paleocene (BROWN 1962) to Pleistocene (BERRY 1924). Although the North American specimens seem to be well identified (TIFFNEY 1989 pers. commun.), a review all of these reports is in order. Rosaceous remains from the Princeton chert and approximately correlative localities include 40 taxa based on leaf impressions and compressions (WOLFE and WEHR 1988), one taxon on twigs, branches and mature wood (CEVALLOS-FERRIZ and STOCKEY 1990b), and the flowers of *Paleorosa* (BASINGER 1976; CEVALLOS-FERRIZ et al. 1990). Worldwide there is a large carpological fossil record of Rosaceae. In Europe, Tertiary fruits and seeds preserved principally as molds and casts are an important component of the fossil floras, and rosaceous remains have been frequently described (e. g., REID and REID 1910, 1915; KIRCHHEIMER 1942; SZAFER 1961; DOROFEEV 1963, 1977; MAI 1984; GREGOR 1975, 1978).

The Rosaceae are a very large family with more than 100 extant genera and over 3000 species (CRONQUIST 1981). It is an important element of the extant vegetation, especially in temperate and subtropical areas. WOLFE (1987) pointed out that the Rosaceae underwent a tremendous diversification during the Eocene, once the climatic conditions for the development of broad-leafed deciduous forests were established. The family has attracted the attention of researchers in a variety of areas for over a century. Numerous authors have examined fruit and/or seed anatomy (e.g., TSCHIERSKE 1886; PÉCHOUTRE 1902; Juel 1918; NETOLITZKY 1926; TUKEY 1935; STERLING 1964a, 1964b; VAUGHAN 1970; CORNER 1976; ROTH 1977), but detailed descriptions of extant taxa are far from complete and more inclusive studies are needed.

In the present study we describe three fossil permineralized rosaceous endocarps enclosing seeds from the Princeton chert of British Columbia. These forms are referable to the subfamily Prunoideae, and document significant anatomical diversity for Rosaceae during the Eocene.

Material and methods

Three rosaceous endocarps, each enclosing one seed, have been found in the Princeton chert (Allenby Formation). The locality occurs approximately 8.4 km south of Princeton, British Columbia. The chert outcrops on the east side of the Similkameen River, in a section consisting of an interbedded sequence of chert and coal with an occasional thin ash bed replacing a chert layer. Forty-nine exposed layers of chert have been recorded and systematically sampled (STOCKEY 1987). The locality has been referred to as locality "I" (BONEHAM 1968) and the "Princeton chert locality" (BASINGER 1976, 1981; STOCKEY 1984, 1987). The Allenby Formation of the Princeton Group has been dated as Middle Eocene based on palynology (ROUSE and SRIVASTAVA 1970), mammals and fishes (RUSSELL 1935; GAZIN 1953; WILSON 1977, 1982), and potassium-argon dating (HILLS and BAADSGAARD 1967).

Fossils are preserved as silica permineralizations. All chert blocks were cut into slabs and studied in serial sections using a modified cellulose acetate peel technique and hydrofluoric acid (JOY et al. 1956; BASINGER and ROTHWELL 1977). Peel sections were mounted in Eukitt or Coverbond xylene-soluble mounting medium for microscopic examination.

Extant fruits and seeds of *Prunus virginiana* (UAPC-ALTA S1 8827) were compared anatomically to the fossil material. The fruits and seeds were dehydrated in 10%, 30%, and 50% EtOH and proceeded in tert-butyl alcohol series (JOHANSEN 1940). Paraplast Plus medium was used for infiltration and embedding. Sections 15-25 μm thick were cut on a rotary microtome and stained with safranin-fast green.

A comparison of fruit morphology with that of extant families was made using the data set of HANSEN and RAHN (1969, 1972) with the MEKA 1.3 program provided by

T. DUNCAN and C. A. MEACHAM, University Herbarium, University of California, Berkeley.

All specimens are housed in the University of Alberta Paleobotanical Collection (UAPC-ALTA). All cell dimensions given in the description correspond to cell sizes measured in fruit and seed transverse sections.

Results

SYSTEMATIC DESCRIPTION

Class: Magnoliopsida
Subclass: Rosidae
Order: Rosales
Family: Rosaceae
Subfamily: Prunoideae
Genus: *Prunus* L. (type 1)

Specimen: P1099 D bot.

Description

The description of *Prunus* (Pl. V, 1 type 1) is based on a single specimen consisting of approximately 3/4 of an ovoid, unilocular and unicarpellate fruit, 1.2 x 0.5 cm, showing a ventral suture (Pl. V, 1 fig. 1). The dorsal surface has a small ridge. The distal portion of the fruit was lost in the saw cut.

A sclerotic endocarp composed of two distinct zones is the only preserved fruit tissue (Pl. V, 1 fig. 2). The endocarp is more or less uniform in thickness. However, the outer fruit surface is irregular probably due to abrasion (Pl. V, 1 fig. 2). The outer zone of the endocarp is up to 22 cell layers thick, and composed of sclereids that are polyhedral in transverse section, and average 69 x 50 µm in diameter (Pl. V, 1 fig. 2). Scattered throughout this zone are small thin-walled idioblasts ca. 36 x 30 µm, containing crystals (Pl. V, 1 fig. 2). Crystals are cuboidal or rhomboidal and frequently organized into short chains (Pl. V, 1 fig. 2). The inner zone of the endocarp is up to 10 cell layers thick (Pl. V, 1 fig. 2). Sclereids in this zone are ca. 171 x 13 µm and have sinuous longitudinal walls. Very few crystalliferous cells are found in the inner endocarp zone. The dorsal zone of the endocarp is disrupted by a quartz vein and tissues are broken (Pl. V, 1 fig. 1). However, a small ridge is visible in some sections of the endocarp. The ventral suture is very prominent in transverse sections. The distinction between inner and outer endocarp along the suture area is not sharp (Pl. V, 1 fig. 3). Cells of the ventral suture are characterized by their parallel orientation to the suture, secondary walls that are thinner than other endocarp cells, and the presence of dark contents. Cells of the suture area form a small multilayered zone of rectangular thin-walled cells, that probably represent an obturator (Pl. V, 1 fig. 3). The obturator occupies an opening that almost equals one fourth of the total width of the endocarp and (Pl. V, 1 figs. 1, 3). Along the remaining length of the fruit the ventral suture is more difficult to detect, but cells with dark contents that are oriented perpendicular to the endocarp surface mark its presence.

A single seed, 4.0 x 2.5 mm, with two integumentary zones is found in the fruit (Pl. V, 1 figs. 1, 2, 4). The outer integumentary zone contains a single layer of oval, thick-walled, pitted cells, filled with dark contents and averaging 178 x 89 µm (Pl. V, 1 figs. 2, 4, 5). The inner integumentary zone is composed of thin-walled rectangular cells, filled with dark contents, and averaging 165 x 11 µm, that are difficult to distinguish in most sections (Pl. V, 1 figs. 2, 4). At the level of the obturator, the seed has two important structural features. First, in some sections tracheary elements are oriented perpendicular to the integument, suggesting that the point of entrance of the ovular vascular strand is at this level (Pl. V, 1 fig. 7). The hilar scar has not been observed and vascular tissue has not been seen either in the space between the integument and the endocarp, or in the endocarp. Second, in this same area, the inner integumentary zone is up to 6 cell layers thick (Pl. V, 1 fig. 7).

The vascular tissue in the seed has a complex pattern. The raphe that runs from the micropylar area to the chalaza, forms a single strand. At the chalaza several vascular strands develop, forming a plexus in the inner integumentary zone (Pl. V, 1 figs. 5, 6). This vascular plexus develops in the dorsal side of the seed and is opposite to the raphe. It has two large strands that almost reach the level of the micropyle. From these postchalazal vascular strands one or two shorter branches develop (Pl. V, 1 fig. 6). The ground tissue of the vascular plexus is up to 6 cell layers thick and composed of thin-walled polyhedral cells (Pl. V, 1 fig. 5). The nucellus is composed of a single layer of thin-walled rectangular cells which is not well preserved in most sections (Pl. V, 1 fig. 5). Endosperm and embryo are not preserved.

Genus: *Prunus* L. (type 2)

Specimen: P 1212 A.

Description

Description of *Prunus* (Pl. V, 2 type 2) is based on a single specimen consisting of approximately 3/4 of one ovoid, unilocular and unicarpellate fruit, ca. 0.9 x 0.6 cm, showing a ventral suture (Pl. V, 2 fig. 8). The dorsal surface is grooved (Pl. V, 2 figs. 8, 11). The distal portion of the fruit was lost in the saw cut.

A sclerotic endocarp composed of two zones is the only fruit tissue preserved (Pl. V, 2 fig. 9). The endocarp is more or less uniform in thickness. The outer surface of the fruit, however, is irregular probably due to abrasion (Pl. V, 2 fig. 11). The outer zone of the endocarp is up to 40 cell layers thick and composed of sclereids that are polyhedral in transverse section, and average 36 x 26 µm in diameter (Pl. V, 2 fig. 9). The inner zone of the endocarp is up to 8 or 9 cell layers thick (Pl. V, 2 fig. 9). These cells are elongated, measuring ca. 160 x 17 µm with straight longitudinal walls. The distinction between inner and outer endocarp along the suture area is not sharp. Cells of the ventral suture are characterized by a parallel orientation to the suture, secondary walls that are thinner than other cells of the endocarp, and presence of dark contents (Pl. V, 2 fig. 15). A group of cells in the partially open area of the suture form a small multilayered structure of thin-walled cells, ca. 12 x 16 µm, which we interpret as an obturator (Pl. V, 2 fig. 10). The obturator occupies an opening that extends almost the total width of the endocarp. Along the remaining length of the fruit the ventral suture lacks this tissue; however, a small opening lined by cells with dark contents persists through the remaining length of the fruit (Pl. V, 2 fig. 15).

A single seed, 0.6 x 0.3 mm, with two integumentary zones is found in the fruit (Pl. V, 2 figs. 8, 9, 12). The outer integumentary zone contains a single layer of pear-shaped, thick-walled, pitted cells, usually filled with dark contents, and averaging 50 x 33 µm (Pl. V, 2 fig. 12), alternating with thin-walled-cells averaging 26 x 13 µm. The inner integumentary zone is composed of thin-walled rectangular cells, filled with dark contents, averaging 160 x 17 µm that are usually difficult to distinguish in most sections. At the same level as the rectangular thin-walled cells of the obturator, the seed integument has two important structural features. In the inner integumentary zone a gap in tissue preservation is seen close to the micropylar area. This gap is interpreted as representing the area that once contained vascular tissue of the raphe, similar to the seed in fruit type 1 (Pl. V, 1 fig. 7). At the chalaza several vascular strands are seen, forming a vascular plexus in the inner integumentary zone (Pl. V, 2 figs. 11, 13, 14). This vascular plexus develops in the dorsal surface of the seed, is opposite to the raphe, and resembles a partial pachychalaza (PERIASAMY, 1962), as in *Prunus javanica* MIQ. (CORNER 1976). The vascular plexus forms an extensive tissue from which several branches of vascular tissue arise almost perpendicularly from a central strand that is oriented parallel to the long axis of the seed (Pl. V, 2 figs. 13, 14). The ground tissue around the vascular plexus is up to 8 cell layers thick and composed of thin-walled polyhedral cells filled with dark contents. Nucellus, endosperm and embryo are not preserved.

Genus: *Prunus* L. (type 3)

Specimen: P 1720 C bot.

Description

Description of *Prunus* (Pl. V, 3 type 3) is based on a single specimen consisting of approximately 3/5 of one ovoid, unilocular and unicarpellate fruit, ca. 0.7 x 0.4 cm, showing a ventral suture. The dorsal surface has two or three distinct small ridges (Pl. V, 3 figs. 16, 22, 23). The distal end of the fruit was lost in the saw cut.

A sclerotic endocarp composed of two zones of sclereids is the only fruit tissue preserved (Pl. V, 3 figs. 18, 20). The endocarp is more or less uniform in thickness except on the ventral side where it is noticeably thicker (Pl. V, 3 fig. 16). However, the outer surface, as in the other two fruits described here, is irregular probably due to abrasion (Pl. V, 3 fig. 24). The outer zone of the endocarp is up to 8 cell layers thick, except at the ridges, and is composed of sclereids that are polyhedral in transverse section, and average 47 x 33 µm in diameter (Pl. V, 3 fig. 18). The outermost layer of this endocarp zone has sclereids mainly oriented parallel to the fruit surface (Pl. V, 3 fig. 18). The inner zone of the endocarp is up to 11 cell layers thick (Pl. V, 3 fig. 18, 20). Sclereids of this layer on the sides of the fruit are oriented at right angles with respect to those of the outer zone (Pl. V, 3 fig. 18). Toward the dorsal and ventral sides they have the same orientation as cells in the outer endocarp (Pl. V, 3 fig. 20). The diameter of sclereids of the inner endocarp increases from the outside toward the inside. It is possible to divide it into two zones according to cell diameter (Pl. V, 3 fig. 20). There is no sharp distinction between inner and outer endocarp along the suture (Pl. V, 3 fig. 17). Cells lining the ventral suture are characterized by their parallel orientation to the suture.

A single seed, 5.0 x 3.0 mm, with two integumentary zones is found in the fruit (Pl. V, 3 figs. 16, 19). The outer zone contains a single layer of more or less bell-shaped, thick-walled cells, filled with dark contents, and averaging 23 x 30 µm, alternating with thin-walled rectangular cells averaging 13 x 11 µm (Pl. V, 3 fig. 19). The inner integumentary zone is composed of a single layer of thin-walled rectangular cells, averaging 43 x 17 μm (Pl. V, 3 fig. 19). On the ventral side of the seed, toward the micropylar end, the inner integumentary zone is up to 6 cell layers thick (Pl. V, 3 fig. 19). On the dorsal side this zone is up to 8 cells and includes a vascular plexus. This dorsal plexus resembles a partial pachychalaza composed of a central vascular strand from which many closely arranged lateral branches arise (Pl. V, 3 fig. 21). Similar pachychalazal seeds are known in members of Prunoideae (e. g., *Prunus javanica*, *P. juliana* DC.; CORNER 1976). The nucellus, composed of a single layer of thin-walled rectangular cells is not well preserved in most sections. Endosperm and embryo are not preserved.

Discussion

The fossil fruits from Princeton clearly represent a mature developmental stage since the endocarp layers and seed integuments are fully sclerotized. Based on the fact that the Princeton seeds are found within a closed endocarp, the fossil fruits are interpreted as indehiscent. These fruits are interpreted as representing fleshy-stony indehiscent fruits (drupes) based on features of the endocarp, pericarp histology, and the relationship between pericarp and seed integuments. Endocarps of drupes are typically multilayered, composed of several zones of sclereids, usually have only one seed of which the integuments are reduced to a few layers (Roth 1977), as in the Princeton material. In contrast, fleshy indehiscent fruits (e. g., Berry, pepo, hesperidium) are typically parenchymatous although they may contain occasional areas of stone cells, and generally have more than one seed. The Princeton chert fruits, on the other hand, have an endocarp with two distinct zones of sclereids. In indehiscent sclerocarpia (e. g., nut, achene, caryopsis, nutlet) very specific types of cells are present in the pericarp. They may have wavy cell walls, U-shaped cell wall thickenings, form a palisade, or sometimes have crossing superimposed cells (ROTH 1977). None of these cell types are present in the fruits from Princeton.

The distal ends of the endocarps and proximal seed surfaces described here are not completely preserved. The actual attachment of the seed to the fruit, the position of the hilar scar, and the micropyle are therefore unknown. In the ventral suture of the endocarp, in two of the fossil seeds, is a group of thin-walled cells that we interpret as an obturator. A similar structure has been reported in extant Prunoideae by JUEL (1918) and STERLING (1964b). Interpretations of the origin of this structure have varied. Although JUEL (1918) interpreted the obturator as an outgrowth of the funiculus, STERLING (1964a) demonstrated that it was an outgrowth of the carpellary margin, and further interpreted it as placental continuation of the stigmatic surface that is in close proximity to the micropyle. Since the obturator in extant forms occurs close to the micropylar area, this structure in the fossil seeds was used to distinguish micropylar from chalazal end. The inner integumentary zone becomes multilayered at nearly the same level where the obturator appears in the fossil seeds from Princeton. A similar thickening occurs in the inner integument near the micropylar area in seeds of many extant plants (MAHESHWARI 1950). In *Prunus* (type 1) a group of tracheary elements, or a gap in tissue preservation (e. g., *Prunus* type 2), in the ventral side of the seed located at the level of the obturator suggests that the ovular strand entered the seed approximately at this level. Based on the relative position of the obturator, vascular strands, and changes of integumentary thickness, it can be inferred that the fossil fruits had ventrally pendant, epitropic, anatropous ovules.

Comparison to extant Rosaceae.- Drupes develop in a very large number of families (CRONQUIST 1981; HANSEN and RAHN 1969, 1972). However, the combination of unicarpellate, unilocular, one-seeded fruits, with ventrally attached seeds, are found together in fewer than 40 families (HANSEN and RAHN 1969, 1972). Additional comparisons of fruits (ROTH 1977) and seeds (NETOLITZKY 1926; CORNER 1976) underscore similarities of the Princeton fossils to Rosaceae, subfamily Prunoideae, rather than to other possible families suggested by the computer search. The pericarp is fleshy or fleshy with a few scattered sclereids in Monimiaceae, Flacourtiaceae, Clusiaceae, and Elaeagnaceae (CRONQUIST 1981; ROTH 1977), compared to the sclerotic endocarp of the Princeton fruits. Thin-walled cells in the outer integumentary zone are typical of Leitneriaceae, Moraceae, Urticaceae, and Opiliaceae (CORNER 1976), while in the Princeton material thick-walled cells are always present. At least one palisade layer is found in seeds of Caesalpinaceae, Euphorbiaceae, Fabaceae, Lauraceae, Magnoliaceae, Malvaceae, Nandinaceae, Podophyllaceae, Rhamnaceae, Rutaceae, Sterculiaceae, and Winteraceae (CORNER 1976), whereas in the Princeton *Prunus* seeds a palisade is absent. Multilayered (three or more cell layers thick) integuments are known in Anacardiaceae (CORNER 1976), while the seeds described here are reduced to 2 more or less single layered integumentary zones. Seed vasculature restricted to the raphe is characteristic of Convolvulaceae, Proteaceae, Simaroubaceae, Thymelaeaceae, and most Ranunculaceae (CORNER 1976), while in the fossil *Prunus* seeds from Princeton post-chalazal branches of the raphe form a vascular plexus. Dilleniaceae, Combretaceae, and Scyphostegiaceae have arillate seeds (CORNER 1976), whereas the Princeton seeds described here are exarillate. Curved ruminate seeds are common in Menispermaceae (CORNER 1976), while the *Prunus* fossil material has a straight nucellar axis.

The fossil remains, therefore, are most likely related to Rosaceae. The three endocarps and their enclosed seeds have characters that strongly support referring them to this family (VAUGHAN 1970; CORNER 1976; ROTH 1977). These features include: (1) unicarpellated drupes, (2) endocarp composed of two zones of sclereids, (3) presence of a suture along the ventral surface, which is lined by thin-walled cells that are parallel to it, (4) fruit with a single pendant, anatropous seed attached ventrally to the carpel, (5) seed with two integumentary zones, an outer zone with thick-walled cells and inner zone of thin-walled cells, (6) seed vascularized by a raphe and post-chalazal branches.

Within the Rosaceae drupes are typical of the subfamily Prunoideae (CRONQUIST 1981; ROBERTSON 1974). Some authors treat the Prunoideae as a subfamily, others classify it as a separate family or divide it into at least two families, and still others only recognize tribes (e.g., STERLING 1964a, 1964b; ROBERTSON 1974; DALGHREN 1980; MAI 1984; KALKMAN 1988). Studies of extant and fossil fruits of Prunoideae have suggested recognition of two or three subgroups (STERLING 1964b; MAI 1984). Most often *Prunus* L., *Maddenia* HOOK. f. et THOMS., *Pygeum* GAERTN., *Oemleria* RCHB. (=*Osmaronia* GREENE), and *Prinsepia* ROYLE (=*Plagiospermum* OLIV.) are recognized as valid members of this subfamily; however, occasionally at least some of these genera are synonymized with *Prunus* (STERLING 1964b, MAI 1984).

Seeds of *Oemleria* differ from the seeds from Princeton in having completely unfused integuments (STERLING 1964b). Unlike the apical placentation of the *Prunus* seeds from Princeton, *Prinsepia* ovules are characterized by sub-basal placentation (MAI 1984). Carpellary margins in *Maddenia* and *Pygeum* are completely fused, although a commisural suture is sometimes seen externally (STERLING 1964b). The carpellary margins of *Prunus* (type 1) and *Prunus* (type 2) show clear evidence of a suture that has at least one small opening, while in *Prunus* (type 3) an opening has not been observed. Absence of an opening in *Prunus* (type 3) may suggest affinities to *Maddenia* and *Pygeum*, however, these genera have unitegmic ovules (STERLING 1964b). Based on histological characteristics (STERLING 1953) the three Princeton fruits are most similar to the genus *Prunus*. In extant *Prunus*, the closure of the carpellary margins varies widely such that at the level of ovular insertion the margins of the carpels may be completely separated, or show varying degrees of fusion (STERLING 1964a).

A correlation between presence of a sutural opening and number of integuments was found in *Prunus* by STERLING (1964a). In two *Prunus* fruits (type 1 and type 2) from Princeton a slight sulcus is evident in the ventral zone, and according to STERLING's (1964a) observation seeds have two integumentary zones. *Prunus* drupes with this type of anatomical organization are regarded as relatively specialized within the taxon (STERLING 1964a, 1964b). In *Prunus* (type 3) a sulcus in the ventral suture has not been observed suggesting that there should be only one integumentary layer. However, as in the other two *Prunus* fruits from Princeton the seed of *Prunus* (type 3) has two distinct integumentary zones, thus, showing both unspecialized and specialized characters (STERLING 1964a, 1964b).

The relative simplicity of the seed of the Princeton material reinforces its putative relationship to the Prunoideae. CORNER (1976) states that seeds of Rosaceae offer no striking microscopic structure. They typically have non-multilayered integuments and are variously reduced with relatively undifferentiated cell layers (CORNER 1976). Seeds of most Prunoideae are characterized by the presence of two integumentary zones (Pl. V, 3 fig. 27). The outer zone is composed of rounded, enlarged, thick-walled, cutinized, pitted cells which sometimes alternate with thin-walled cells (Pl. V, 3 fig. 27). The inner integumentary zone is crushed, but some layers may persist in some species (Pl. V, 3 fig. 27; CORNER 1976; VAUGHAN 1970). The vascular tissue in the seeds of Prunoideae is represented by the raphe and around three to 10 post-chalazal branches, some of them almost reaching the micropyle (fig. 26; CORNER 1976; VAUGHAN 1970). All of these characters are present in the three specimens of *Prunus* from Princeton.

Little is known about intraspecific variation but interspecific variation between extant species of *Prunus* seems to be similar to that seen in the fossil material (VAUGHAN 1970; CORNER 1976). For example, the thick-walled cells of the outer integumentary layer vary in size from 40-50 µm x 70 µm in *P. armeniaca* L. (apricot) to 80-160 µm x 90 µm in *P. persica* BATSCH. (peach). In *P. cerasus* L. (cherry) the cell walls of the outer integumentary layer are not pitted throughout their width, while in *P. domestica* L. (plum) they are pitted completely. The number of post-chalazal branches of the raphe varies from three to ten, or the seeds can be pachychalazal as in *P. spinosa* L. and *P. juliana*. The surface of the endocarp ranges from grooved as in *P. munsoniana* WIGHT and HEDRIK (plum) to smooth as in *P. cerasus* (WIGHT 1915). Endocarp shape can also vary from globose as in *P. besseyi* BAILEY (dwarf cherry) to round as in *P. mexicana* WATS. (plum) to oval as in *P. emarginata* (DOUGL.) WALP. (cherry; WIGHT 1915).

Based on their similarities, the three Princeton fruits are assigned to the same genus. However, based on substantial qualitative and quantitative differences in endocarp and seed anatomy we cannot regard them as the same species of *Prunus* until intraspecific and interspecific variation is fully understood in this taxon (Table V, 1). Fruits differ in size and shape (Table V, 1). While the outer surface of the three endocarps is relatively uniform, distinct grooves occur in the dorsal surface of the three specimens, although they may have been abraded (Table V, 1). The number of cell layers and cell size in the outer and inner endocarp zones also varies, again possibly due to abrasion (Table V, 1). Only *Prunus* (type 1) lacks thin walled cells between the thick-walled cells of the outer integumentary zone (Table V, 1). The number and extent of post-chalazal branches of the raphe also varies in the three seeds (Table V, 1).

Comparison to fossil *Prunus*.- The fossil record of *Prunus* is extensive. Leaves assigned to this genus are known from the Upper Cretaceous, but the reliability of some reports is uncertain (KIRCHHEIMER 1942; HUGHES 1976; MAI 1984). Wood related to this genus is known from Middle Eocene and younger strata (CEVALLOS-FERRIZ and STOCKEY 1990b). Fruits and seeds are particularly valuable to the systematic delimitation of *Prunus* and are also known from Eocene sediments. In the fossil record, based on fruit morphology, MAI (1984) has been able to recognize the five subgenera of this taxon.

Endocarps of the Princeton *Prunus* plants are most similar to the endocarps of the subgenus *Prunus* Koehne which is characterized by mostly smooth, but sometimes slightly grooved endocarps. However, since the Princeton endocarps may be abraded, recovery of further material is needed to confirm this taxonomic determination. This subgenus was previously known from Oligocene and younger strata (MAI 1984). However, if the irregular endocarp surface is similar to that seen in *Prunus virginiana* (Pl. V, 3 fig. 25), the three species of *Prunus* from Princeton might be closer to section *Euprunus* KOEHNE.

The presence of small grooves on the dorsal side of the fruit as in the three Princeton fruits are also characteristic of section *Euprunus*.

WOLFE and WEHR (1990 pers. commun.) have identified, as impressions and compressions, three different species of *Prunus* from the Princeton basin based on leaves. Wood of a *Prunus* plant is also known from the Princeton chert (CEVALLOS-FERRIZ and STOCKEY 1990b). Unfortunately it is not possible to say at this time what organs belong together. However, leaf, fruit and seed information strongly suggest the presence of at least three types of *Prunus* in the Princeton chert.

Plate V,1

Prunus type 1.

Fig. 1, Transverse section of endocarp and seed near distal zone of fruit. P 1099 Dbot No. 0, x 13.

Fig. 2, Transverse section of seed and endocarp with idioblasts containing crystals. P 1099 Dbot No. 10, x 94.

Fig. 3, Transverse section of endocarp ventral zone close to the area of the obturator. Note that cells in the ventral suture have a different orientation. P 1099 Dbot No. 3, x 99.

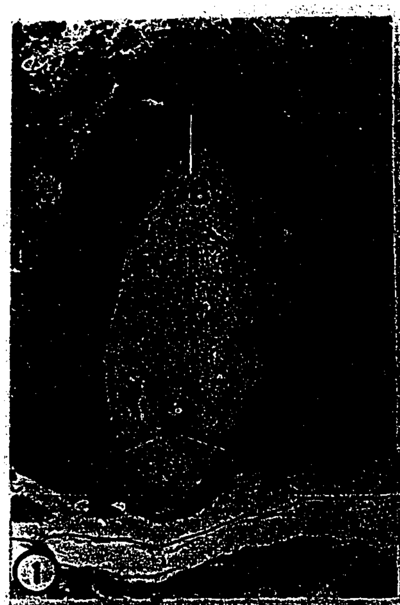
Fig. 4, Transverse section of seed and inner endocarp zone. Note presence of a single inner integumentary layer. P 1099 Dbot No. 0, x 129.

Fig. 5, Transverse section of vascular plexus in dorsal area. Note multilayered inner integumentary zone (arrow). P 1099 Dbot No. 0, x 68.

Fig. 6, Transverse section of vascular plexus in dorsal area. Note presence of vascular tissue (arrows). P 1099 Dbot No. 18, x 81.

Fig. 7, Transverse section of seed close to the area of the obturator with vascular tissue (arrow) in inner integument. P 1099 Dbot No. 3, x 144.

E=endocarp, N= nucellus, OB=obturator, S=seed.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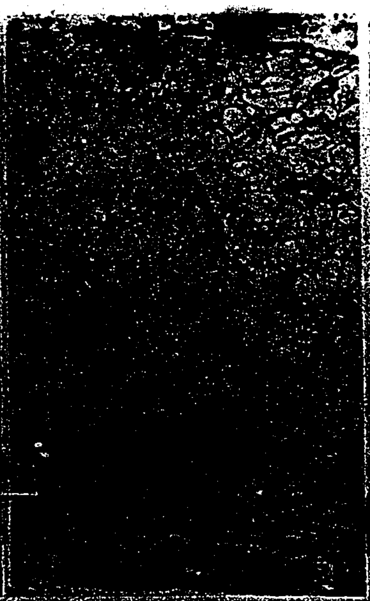


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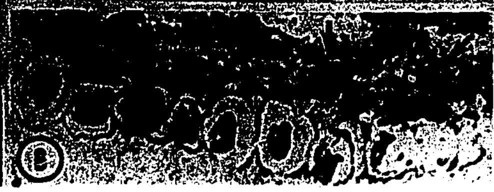
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Plate V, 2

Prunus type 2.

Fig. 8, Transverse section of endocarp and seed near distal zone of the fruit. P 1212 A No. 3, x 11.

Fig. 9, Transverse section of endocarp. Note different orientation of sclereids in inner and outer endocarp zones. P 1212 A No. 0, x 46.

Fig. 10, Transverse section of endocarp ventral zone with obturator. P 1212 A No. 0, x 96.

Fig. 11, Transverse section of endocarp dorsal zone with a middle furrow and vascular plexus (arrow). P 1212 A No. 0, x 18.

Fig. 12, Transverse section of seed. P 1212 A No. 4, x 288.

Fig. 13, Transverse section of vascular plexus in dorsal area with vascular tissue. P 1212 A No. 18, x 192.

Fig. 14, Transverse section of vascular plexus in dorsal area with vascular tissue. P 1212 A No. 4, x 269.

Fig. 15, Transverse section of endocarp with ventral suture almost closed (arrow). P 1212 A No. 18, x 37.

E=endocarp, S=seed.


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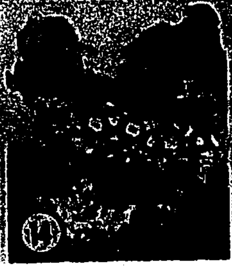
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Plate V, 3

Figs. 16-24 *Prunus* type 3, Figs. 25-27 *Prunus virginiana.*

Fig. 16, Transverse section of endocarp and seed near distal zone of fruit. P 1720 Cbot No. 21, x 12.

Fig. 17, Transverse section of endocarp with closed ventral suture (arrow). P 1720 Cbot No. 28, x 72.

Fig. 18, Transverse section of endocarp in lateral zone. Note different orientation of sclereids in inner and outer zone of endocarp. P 1720 Cbot No. 2, x 188.

Fig. 19, Transverse section of seed in ventral zone. Note multilayered inner integumentary zone. P 1720 Cbot No. 2, x 329.

Fig. 20 Transverse section of endocarp in dorsal zone. Note that sclereids in inner and outer endocarp have the same orientation P 1720 Cbot No. 2, x 188.

Fig. 21, Tracheids of vascular plexus in dorsal area. P 1720 Cbot No. 1, x 282.

Fig 22, Transverse section of endocarp with central ridge in dorsal side. P 1720 Cbot No. 37, x 38.

Fig. 23, Transverse section of endocarp with a lateral ridge in dorsal side. P 1720 Cbot No. 9, x 37.

Fig. 24, Transverse section of endocarp with a ridge in the center of the dorsal zone showing probable abrasion. P 1720 Cbot No. 21, x 113.

Fig. 25, Oblique transverse section of endocarp and mesocarp. Note irregular outer surface of endocarp. Sl 8827, x 56.

Fig. 26, Transverse section of vascular plexus. Sl 8827, x 38.

Fig. 27, Transverse section of seed. Sl 8827, x 75.

E=endocarp, I=inner integumentary zone, M=mesocarp, O=outer integumentary zone, S=seed.


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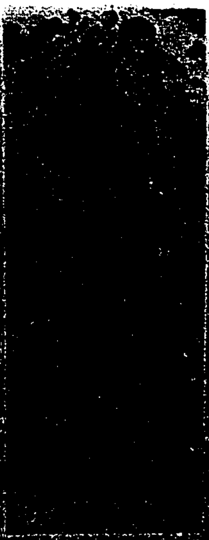


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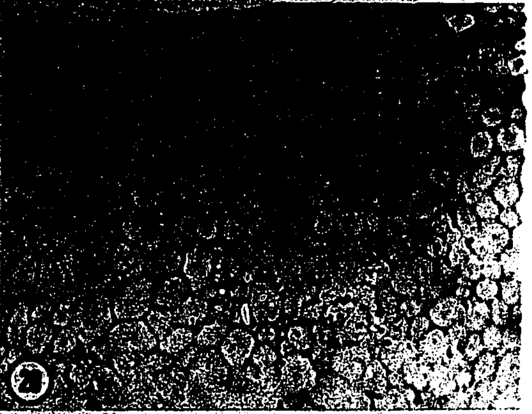
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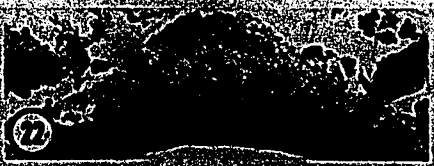
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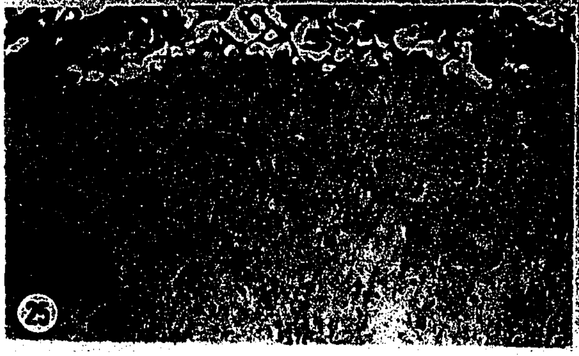
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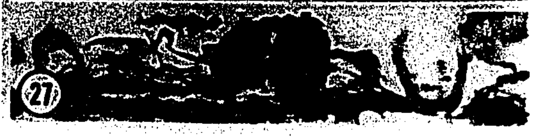
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Table V, 1. Comparison of the three types of *Prunus* remains from the Princeton chert.

	type 1	type 2	type 3
ENDOCARP			
Size (cm)	1.2 x 0.5	0.9 x 0.6	0.7 x 0.4
Outer zone			
Thickness (mm)	0.7	1.4	0.2
Idioblasts	present	absent	absent
No. of cell layers	22	40	8
Cell diameter (µm)	50	26	33
Suture	open	open	close
Inner zone			
Width (mm)	1.8	7.2	1.8
Idioblasts	present	absent	absent
No. of cell layers	10	9	11
Cell length (µm)	171	160	112
Cell width (µm)	13	17	11
SEED			
Size (mm)	4.0 x 2.5	6.0 x 3.0	5.0 x 3.0
Outer integumentary layer			
THICK-WALLED CELLS			
Shape	oval	pear-shaped	bell-shaped
Size (µm)	178 x 89	50 x 33	23 x 30
THIN-WALLED CELLS	absent	present	present
Size (µm)	------	26 x 17	13 x 11
Inner integumentary layer			
Cell size (µm)	165 x 11	50 x 7	47 x 17
Post-chalazal branches	2	pachychalaza	pachychalaza

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In situ aquatic plants*

INTRODUCTION

The study of plants preserved as chert permineralizations from the Allenby Formation began with the description of reproductive and vegetative remains of *Pinus* L. (Miller, 1973) and a semi-aquatic dicotyledonous rhizome of uncertain affinities, *Eorhiza* Robison and Person (1973). Later, another conifer, *Metasequoia milleri* Rothwell and Basinger, and flowers of a rosaceous plant, *Paleorosa similkameenensis* Basinger, were described (Basinger, 1976a, 1976b, 1981, 1984; Rothwell and Basinger, 1979). Other aquatic or semi-aquatic angiosperms were documented through a study of some of the preserved seeds (Cevallos-Ferriz and Stockey, 1988a, 1988b, 1989), vegetative remains of monocots including a coryphoid palm (Erwin and Stockey, 1987) and an alismataceous petiole, *Heleophyton* Erwin and Stockey 1989. Other remains of plants that may not have been growing in or at the margins of the lake are also known. These include woods (Cevallos-Ferriz and Stockey, 1990b, 1990c), seeds (Cevallos-Ferriz and Stockey, 1990a), and fruits (Cevallos-Ferriz and Stockey, previous chapter).

Evidence for the *in situ* aquatic habitat of some of the plant remains from Princeton comes from several sources: (1) association with fresh water fauna, (2) anatomical/morphological adaptations, (3) affinities with modern groups, (4) evidence of *in situ* rooting, (5) number of plant organs of the same type, and (6) preservation of delicate tissues.

MATERIALS AND METHODS

Evidence presented in this paper is based on the interpretation of information gathered by many researchers regarding the permineralized plants of the Princeton chert.

* A version of this chapter has been submitted (1990) for publication: Cevallos-Ferriz, S. R. S., and Stockey, R. A. Rev. Palaeobot. Palynol.

The plants discussed have been collected in the Princeton chert (Allenby Formation) approximately 8.4 km south of Princeton, British Columbia. The Allenby Formation of the Princeton Group has been dated as Middle Eocene based on palynology (Rouse and Srivastava, 1970), mammals and fishes (Russell, 1935; Gazin, 1953; Wilson, 1977, 1982), and potassium-argon dating (Hills and BAADSGAARD, 1967). Specimens come from the east side of the Similkameen River, from a section consisting of an interbedded sequence of chert and coal with an occasional thin ash bed replacing a chert layer. Forty-nine exposed layers of chert have been recorded and systematically sampled (Stockey, 1987). The locality has been referred to as locality "I" (Boneham, 1968) and the Princeton chert locality (Basinger, 1976a; Stockey, 1984, 1987).

Fossils are preserved as silica permineralizations. All chert blocks were cut into slabs and studied using a modified cellulose acetate peel technique and hydrofluoric acid (JOY et al., 1956; Basinger and Rothwell, 1977, Basinger, 1981). Peel sections were mounted in Coverbond xylene-soluble mounting medium for microscopic examination.

All plant specimens are housed in the University of Alberta Paleobotanical Collection (UAPC-ALTA). Animal specimens are housed in the University of Alberta Laboratory for Vertebrate Paleontology (UALVP).

RESULTS

Ecology

Sediments of the Allenby Formation are black to dark grey thick-bedded siliceous shales alternating with coal seams. At the Princeton chert locality the siliceous shales are replaced by plant-rich chert layers (Wilson, 1980). Sediments of the Allenby Formation and correlated localities in British Columbia (e. g., Quilchena Beds, Tranquille Beds, Horsefly River Beds, and Driftwood Creek Beds) represent soft-bottom lake deposits with no indication of fluviatile sedimentation (Wilson, 1988). Correlation of the Princeton Group with other Tertiary sedimentary and volcanic sequences in south-central [illegible]

Columbia is based on fish, insect, and plant material (Rouse and Mathews, 1961; Wilson, 1977).

Seasonal variation in some of these ancient lakes has been demonstrated. Varved lacustrine sediments composed of couplets of laminae of different composition are taken as indicators of seasonality (Olsen et al., 1978; Wilson, 1988). For the lacustrine sediments of Horsefly, British Columbia, summer sediments are characterized by large numbers of leaves and coprolite material, while winter sediments have abundant fish material (Wilson, 1988). For the Allenby Formation detailed studies of this kind are missing. However, taphonomic data strongly suggest a similar sedimentological pattern. Laminated, possibly varved sediments occur at Whipsaw Creek, Princeton-Tulameen Road, and China Creek (Wilson, 1990 pers. commun.).

Three distinct lateral biofacies have been distinguished in the Middle Eocene lakes of British Columbia (Wilson, 1980, 1988): (1) off-shore/deep water association, (2) shallow/near-shore association, and (3) intermediate to near-shore association. In studies of the Horsefly varves (Wilson, 1980) and other Eocene lake deposits in British Columbia, Wilson (1988) characterized the shallow/near-shore environment. These deposits typically have abundant disarticulated fish, *Amia* L. and *Libotonius* Wilson, abundant and incomplete insects (Bibionidae), abundant pinaceous needles or taxodiaceous leaves, and high diversity in all fossil groups (Wilson, 1980, 1988). Evidence for a shallow/near-shore environment in the Princeton chert has been gathered by several researchers over the past 17 years. A partially articulated skeleton and several disarticulated bones of *Amia* as well as disarticulated remains of *Amyzon* Cope and *Libotonius* from the shale that overlies the chert-coal sequence were reported by Wilson (1982). Further evidence for a shallow/near-shore environment include the remains of a soft-shelled turtle (Pl. VI, Fig. 1) in the shale above the chert (Wilson, 1982), and fragments of turtle bones in the chert itself (Fox, 1989 pers. commun.). Plant remains in the shale above the chert include stems, twigs, dicotyledonous leaves, seeds, taxodiaceous leafy shoots, ferns, and amber (Wilson, 1980, 1982).

Aerenchyma

A widespread effect of an aquatic system upon the plants that grow there is the development of aerenchyma (Sculthorpe, 1967). For example, some organs that grow near and just below the water level develop large amounts of lacunate tissue (Sculthorpe, 1967). Several plant organs described from the Princeton chert have well developed aerenchyma tissues. Both schizogenous (Pl. VI, 1 Figs. 2, 5, 7) and lysigenous (Pl. VI, 2 Fig. 4; Esau, 1965) air spaces occur. Mesophyll of immature leaves of *Eorhiza* lacks air spaces (Pl. VI, 1 Fig. 3), but as leaves mature the aerenchyma becomes conspicuous (Pl. VI, 1 Figs. 2, 4). In this plant, aerenchyma in the cortical tissue (Pl. VI, 1 Fig. 2) is well developed further supporting its aquatic nature. Air spaces in the leaves are more or less rectangular and larger than those in the rhizome where they are angular to slightly oval (Robison and Person, 1973). One should note that the relatively large amounts of vascular tissue present in *Eorhiza* are uncommon for an aquatic plant (Robison and Person, 1973). However, like many other extant aquatic plants (Sculthorpe, 1967) *Eorhiza* is also heteroblastic. Aquatic, heteroblastic plants may have submerged stems, roots, and at least one type of leaf, while the second type of leaf may float or be emergent (Sculthorpe, 1967). Both types of leaves of *Eorhiza* have aerenchyma; the scale-like leaves that surround the rhizome were probably submerged, while the second leaf type was either floating or emergent.

Depending on the plant habit, petioles may show special adaptations to their environment (Sculthorpe, 1967). Presence of large air spaces in the cortex of *Heleophyton* Erwin and Stockey 1989 (Pl. VI, 1 Fig. 5) is similar to the anatomy of petioles of emergent and submerged plants, as well as to the peduncle of nymphaeaceous taxa (Sculthorpe, 1967; Tomlinson, 1982). This arrangement is thought to maximize resistance to bending and pulling strains, and to enhance aeration in submerged organs (Sculthorpe, 1967).

All vegetative parts of the Princeton coryphoid palm have well developed aerenchyma, except for the leaf laminae (Basinger, 1976a; Erwin and Stockey, 1987). However, the area occupied by these air spaces varies in each organ. Roots have a larger zone of aerenchyma when compared to stems and petioles, suggesting that the latter organs were probably not submerged. In roots, parenchyma cells of the cortex alternate with smaller, polyhedral cells with dark contents, and the lacunae tend to be radially elongate (Pl. VI, 1 Fig. 7). In the stem and petiole lacunae are less regularly arranged and scattered throughout the cortex (Pl. VI, 1 Fig. 6).

Several types of fern rhizomes and petioles from the chert are presently being investigated (Nishida, pers. commun., 1987), and like *Dennstaedtiopsis* Arnold and Daugherty they do not represent true aquatic ferns, though at least part of their vegetative body has aerenchyma (Basinger, 1976a) unlike the living *Dennstaedtia* (Arnold and Daugherty, 1964). As in the palm, rhizomes and petioles of *Dennstaedtiopsis aerenchymata* have well preserved aerenchyma (Pl. VI, 2 Fig. 1, 6; Basinger, 1976a). A similar distribution of aerenchyma is found in a polypodiaceous fern referred to as fern B by Basinger (1976a; Pl. VI, 2 Fig. 2).

Another organ with large numbers of lacunae is the fruit originally described by Cevallos-Ferriz (1987) whose affinities remain uncertain (Pl. VI, 2 Fig. 3). It represents a mericarp of an apocarpous four carpellate flower. Presence of air spaces in extant fruit or seed tissues has been shown to enhance buoyancy (Ridley, 1930). The most frequent modifications are the formation of subepidermal lacunate tissue or the development of rather large intercellular spaces (Sculthorpe, 1967). The endocarp of this Princeton fruit at maturity is represented by a large lacuna (Pl. VI, 2 Fig. 3), and the mesocarp has obvious lysigenous intercellular spaces (Pl. VI, 2 Fig. 4; Cevallos-Ferriz, 1987). These two features could enhance flotation capabilities of the mericarps. Small amounts of endosperm have been found in the seeds (Cevallos-Ferriz, 1987). Most probably these small amounts of food reserve restricted germination to shallow water conditions (Frankland et al., 1987).

Xylem

Reduced vascular systems and little mechanical tissue are common in aquatic plants. Vascular tissue of the petiole of *Heleophyton* has four features that clearly indicate an aquatic environment: (1) presence of protoxylem lacunae, (2) thick, inner tangential walls of cells that lie adjacent to the lacuna (3) little lignification of tracheary elements, and (4) a relatively large amount of phloem compared to xylem (Pl. VI, 2 Fig. 5; Sculthorpe, 1967; Tomlinson, 1982; Erwin and Stockey, 1989). All the above features have been described in aquatic plants, especially hydrophytes with a submerged or floating habit (e. g., Arber, 1920; Sculthorpe, 1967; Tomlinson, 1982).

Affinities to extant aquatics

Seeds of *Allenbya* Cevallos-Ferriz and Stockey are ovoid in shape, have adjacent hilum and micropyle, longitudinal raphal ridge, apical operculum, outer columnar sclerotesta that is one cell thick, and composed of pitted cells with digitate surface cell shapes, inner thin-walled integument one to two cells thick, and perisperm (Pl. VI, 3 Fig. 3; Cevallos-Ferriz and Stockey, 1989). These anatomical characters have allowed its inclusion in the Nymphaeales, family Nymphaeaceae, a group known to inhabit still waters (Cronquist, 1981). *Allenbya* seeds do not have an aril as in some extant Nymphaeaceae which can trap air allowing the seed to float for a short period (e. g., *Nymphaea caerulea* Andr.; Sculthorpe, 1967). Therefore, *Allenbya* seeds most likely sank after they were released. The presence of abundant perisperm in the seeds of this plant might suggest that the seedling was established in a light poor environment (Frankland et al., 1987).

The presence of *Heleophyton*, a member of the Alismataceae, can also be used to infer an aquatic environment. Extant members of this family are aquatic or semi-aquatic herbs (Cronquist, 1981; Tomlinson, 1982). As indicated above, anatomy of the petiole of this plant not only supports its assignment to this family, but clearly shows its hydrophytic nature (Erwin and Stockey, 1989; Pl. VI, 1 Fig. 5).

It is not unusual to find some hydrophytes in otherwise terrestrial families of angiosperms (Sculthorpe, 1967). For example, in the family Lythraceae some species of *Ammannia* L., *Lythrum* L., *Rotala* L. and *Decodon* Gmel., represent aquatic plants. Extant *Decodon verticillatus* (L.) Ell. is known to grow along riverbanks and lake shores. However, its stems bend toward the aquatic system forming a floating rhizome-like structure that produces new roots and vertical shoots. Anatomical adaptation to an aquatic environment in extant *Decodon* can be seen in the stems that bend and come in contact with water (Graham and Graham, 1964; Sculthorpe, 1967). Only the seeds and fruits of *Decodon* have been found in the Princeton chert (Pl. VI, 2 Fig. 7); however, these are anatomically very similar to extant *D. verticillatus* (Cevallos-Ferriz and Stockey, 1988a). The capsules may have been able to float for a short time, but as soon as the seeds were released they would most likely sink. Endosperm has not been observed in these seeds or in extant *Decodon* (Graham and Graham, 1964). The establishment of the seedling could have been along the shore where light requirements for photosynthesis would be easy to obtain and copious endosperm would not be necessary (Salisbury, 1942; Levin, 1974; Frankland et al., 1987).

In contrast, the large lythraceous seed (Cevallos-Ferriz and Stockey, 1988a), shows, like *Lythrum* L., an outer mucilaginous integumentary layer (Pl. VI, 3 Fig. 1) that may enhance buoyancy or adhesion to animals for dispersal. A similar floating mechanism has been noticed in some aquatic plants (Sculthorpe, 1967).

Keratosperma Cevallos-Ferriz and Stockey (Araceae) is represented by seeds (Pl. VI, 3 Fig. 2) and fruits in the Princeton chert. Seed characters including the presence of a spiny integument composed of isodiametric sclereids that increase in diameter toward the periphery of the seed, three rows of dorsal spines, idioblasts between spines and ridges, an expanded and conical micropylar region, scanty endosperm, and monocotyledonous embryo support their assignment to the Araceae (Cevallos-Ferriz and Stockey, 1988b). Based on the small amount of endosperm, this seed also may have germinated in shallow/near-shore environments (Frankland et al., 1987). This type of habitat can be compared to that of some extant araceous plants (Muenscher, 1944; Braun, 1967). The closest extant genus to which *Keratosperma* can be compared is *Cyrtosperma* Griff. (Cevallos-Ferriz and Stockey, 1988b). This is an Indonesian genus that lives along the shoreline of lakes, suggesting that the fossil plant may have inhabited a similar habitat.

Evidence for in situ *growth*

Several types of plants in the chert show evidence of *in situ* growth. Rhizomes of *Eorhiza* are one of the most abundant organs in the chert. Roots growing from these rhizomes clearly indicate that the plant was rooted in plant debris accumulated in the aquatic basin (Pl. VI, 3 Fig. 5). Stems of the coryphoid palm, and several other small monocot axes, also show *in situ* rooting (Erwin, pers. commun. 1990). The fossil material, like some extant coryphoid palms (Uhl and Dransfield, 1987), most likely inhabited areas close to the shore of the aquatic system. In addition to remains of these herbaceous plants a small stump of *Metasequoia* has also been found rooted in the lower layers of the chert (Pl. VI, 3 Fig. 6). Evidence from extant and fossil *Metasequoia* indicates that plants of this taxon may grow in swampy environments (Mitchell, 1985).

Plant organs may be transported for different distances according to their physical characteristics. The presence of all, or most, organs of a single plant in the Princeton chert suggests that the plant may have been growing *in situ*. Whole plant reconstruction so far from the Princeton chert is limited to *Metasequoia milleri* (Rothwell and Basinger, 1979; Basinger, 1981, 1984), and the remains of several monocots (Erwin and Stockey, 1987, pers. commun. 1990).

The number of organs of a particular plant present in the chert may also give some indication on how far away plants were growing from the site of deposition. Seeds of fossil plants related to known extant aquatics like *Decodon* occur in the chert in the thousands. Using these numbers it becomes evident that some plants were growing at the site of deposition (e. g., *Eorhiza, Decodon, Allenbya, Keratosperma*), while remains of other plants may have been transported by animals (e. g., *Prunus* L. fruits, *Ampelocissus* Planch. seeds), or dropped into the basin from nearby terrestrial environments. *Pinus similkameenensis* (leaves and twigs) and *P. arnoldii* (cones) are also found in thousands suggesting that like extant *Pinus* (e. g., *P sylvestris* L. and *P. contorta* Dougl.) these plants may also have been growing in the swamp (Mirov, 1967).

The idea that at least some plants whose organs were transported to the Princeton chert basin were growing in or close to the system is suggested by the preservation of organs with delicate tissues (Pl. VI, 3 Fig. 6). Flowers like those of *Paleorosa* Basinger (1976b), *Princetonia* Stockey (1987) and *Wehrwolfea* Erwin and Stockey (1990) show organic connection of their parts. Furthermore, almost every delicate detail of tissues of sepals, petals, carpel, and stamens with *in situ* pollen have been preserved. Other tissues whose preservation also suggests little transportation are phloem and cortex. In the rosaceous and magnoliaceous vegetative axes sieve plates are present in the phloem (Cevallos-Ferriz and Stockey, 1990b, 1990c). In these taxa, as well as in twigs and roots of *Pinus* and *Metasequoia* sieve areas are also preserved (Basinger 1976a, 1981).

CONCLUSIONS

Anatomical characteristics, abundance of plant organs, relationship to extant taxa, preservation of delicate tissues, and *in situ* rooting support the *in situ* growth in an aquatic system of some plants from the Princeton chert locality. Relative abundance of seeds of aquatic plants, like *Keratosperma* and *Decodon*, with small seeds containing little or no endosperm supports the idea of the Princeton chert locality representing a shallow lake, or as Wilson's (1980, 1988) sedimentologic and taphonomic studies suggest a shallow/near-shore environment such as a pond, swamp, or bay. Presence of plants with aerenchymatous cortex and whose extant relatives neither have aerenchyma nor live in an aquatic system (e. g., *Dennstaedtiopsis*) suggest that the lake was surrounded by swampy terrain. Seeds of other plants such as *Princetonia* and *Allenbya* suggest that this aquatic system may have had suspended material preventing light from reaching deep in the system. Animal remains from this locality, such as *Amia* and the turtle, further support the presence of shallow, swampy conditions at the Princeton chert locality during deposition.

Plate VI, 1

Soft-shelled turtle and plant organs with aquatic adaptations.

Fig. 1. Carapace and part of the skeleton of a soft-shelled turtle from the shale above the chert. UALVP 13392, x 0.69.

Fig. 2. Transverse section of a rhizome of *Eorhiza* with air spaces in leaf mesophyll (above) and rhizome cortex (below). P2733 $\mathrm{H}_{\mathrm{bot}}$ No.10, x 30.

Fig. 3. Transverse section of a bud of *Eorhiza*, note absence of aerenchyma in young leaves. P2674 $\mathrm{E}_{\mathrm{bot}}$ No. 2, x 15.

Fig. 4. Transverse section of mature leaf of *Eorhiza*. P4268 $\mathrm{B}_{\mathrm{top}}$ No. 0, x 10.

Fig. 5. Transverse section of *Heleophyton* petiole. P2313 $\mathrm{B}_{\mathrm{top}}$ No. 0, x 175.

Fig. 6. Transverse section of a coryphoid palm petiole. P1274 A_2 No. 12, x 35.

Fig. 7. Transverse section of a coryphoid palm root with radially elongate lacunae. P1124 $\mathrm{E}_{\mathrm{bot}}$ No. 0, x 32.

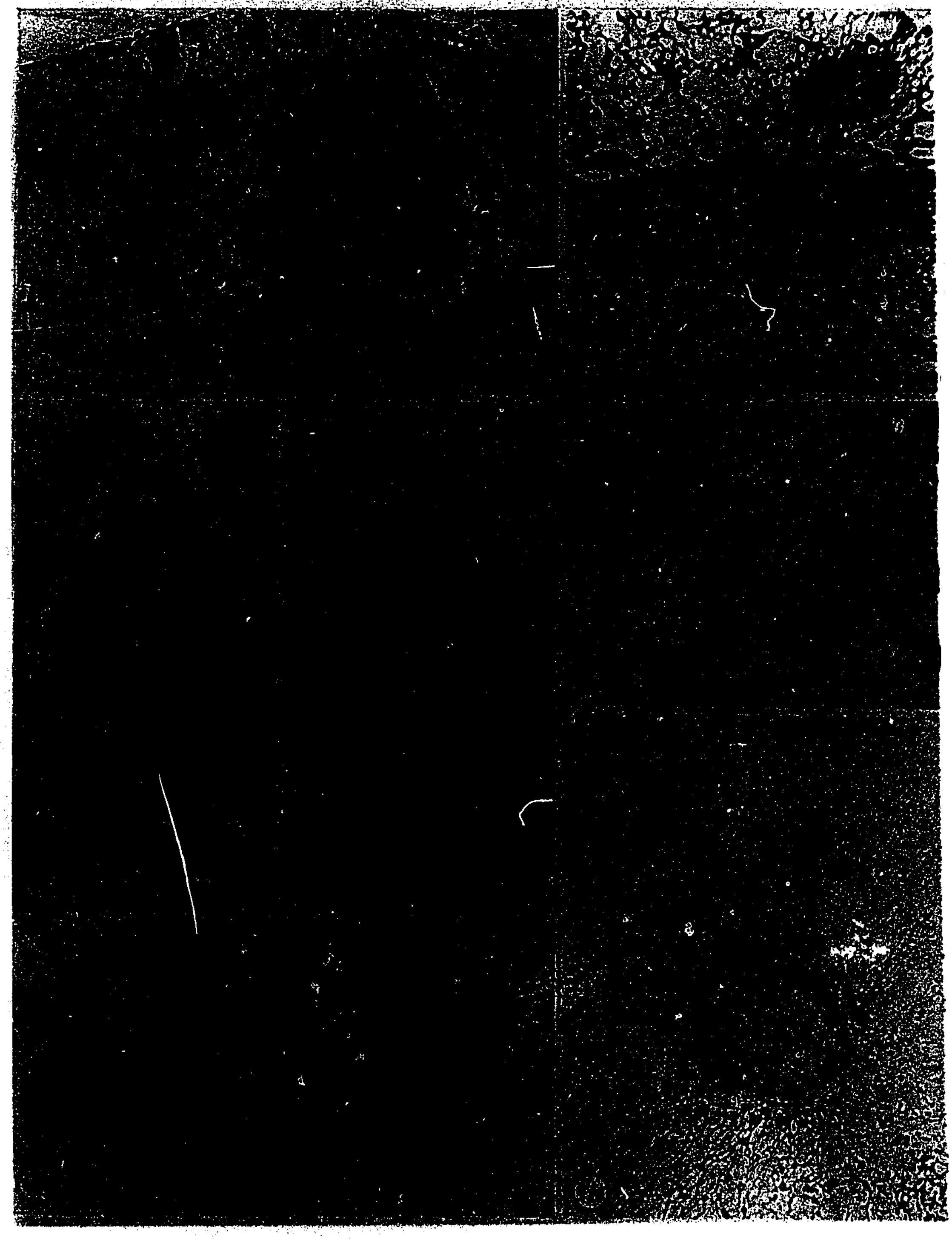

Plate VI, 2

Plant organs with aquatic adaptations.

Fig. 1. Transverse section of *Dennstaedtiopsis* petiole. P1194 B_{bot} No. 0, x 133.

Fig. 2. Transverse section of the petiole of Fern B. P1247 C_{bot} No. 0, x 13.

Fig. 3. Longitudinal section of a fruit with a lacuna in the area of the endocarp. P1631 C_{bot} No. 20_b, x 60.

Fig. 4. Longitudinal section of fruit mesocarp showing lysigenous air spaces. P2613 G_{top} No. 21, x 190.

Fig. 5. Transverse section of *Heleophyton* petiole with vascular bundles showing protoxylem lacunae (arrows). P2313 B_{top} No. 4, x 145.

Fig. 6. Transverse section of *Dennstaedtiopsis* rhizome with aerenchyma in middle cortex and sclerenchyma in inner cortex. P1223 A No. 21, x 13.

Fig. 7. Transverse section of *Decodon* fruit. P1142 $D2_{bot}$ No.1, x 22.


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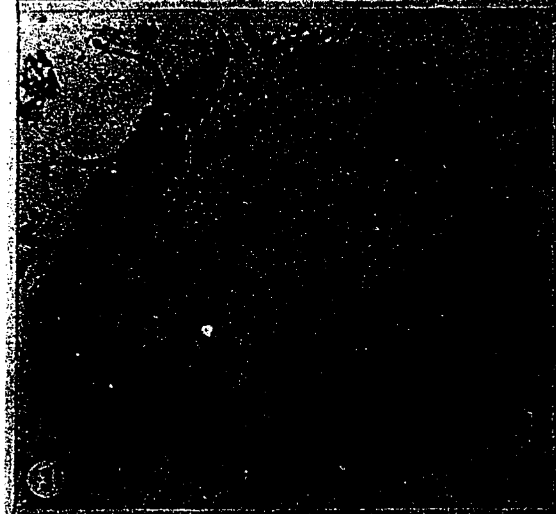
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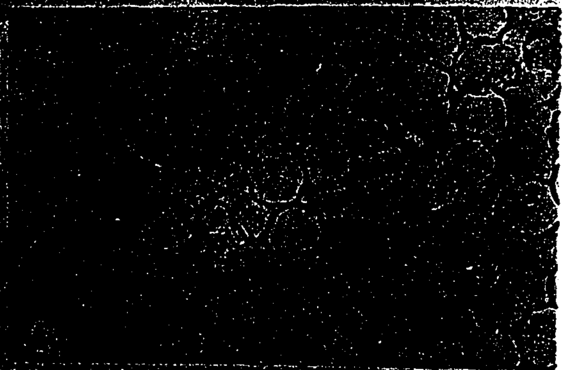

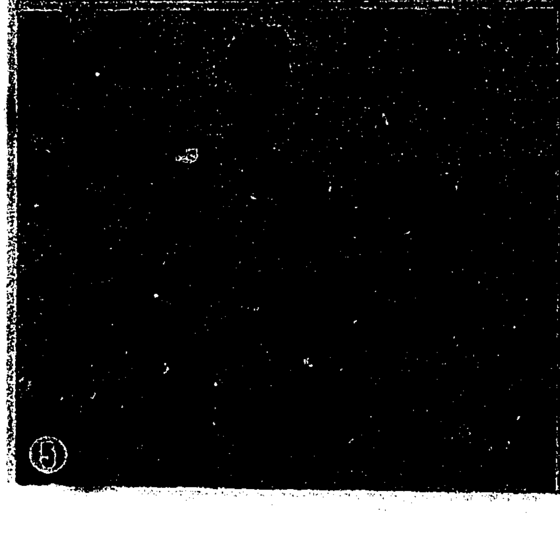
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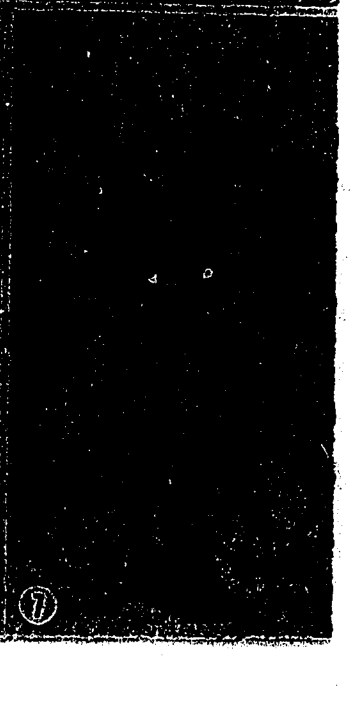
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Plate VI, 3

Seeds of aquatic plants, delicate tissue preservation, and *in situ* rooting.

Fig. 1. Oblique transverse section of large lythraceous seed showing mucilage layer (arrows). P2470 D_{bot} No. 0, x 43.

Fig. 2. Longitudinal section of the seed of *Keratosperma*. P2613 B_{1bot} No. 12, x 31.

Fig. 3. Longitudinal section of *Allenbya* with operculum (arrows) showing hilum and micropyle. P2328 C_{bot} No. 33, x 29.

Fig. 4. Transverse section of an *incertae sedis* flower with *in situ* perianth, anthers, and gynoecium. P1390 E_{1bot} No. 2, x 104.

Fig. 5. Transverse section of an *Eorhiza* rhizome with attached roots growing into plant debris. P1777 B_{bot} No. 1, x 3.

Fig. 6. Oblique longitudinal section of a *Metasequoia* stump rooted *in situ*, note presence of roots (arrows). x 0.15.

E=endosperm, M=micropylar area.

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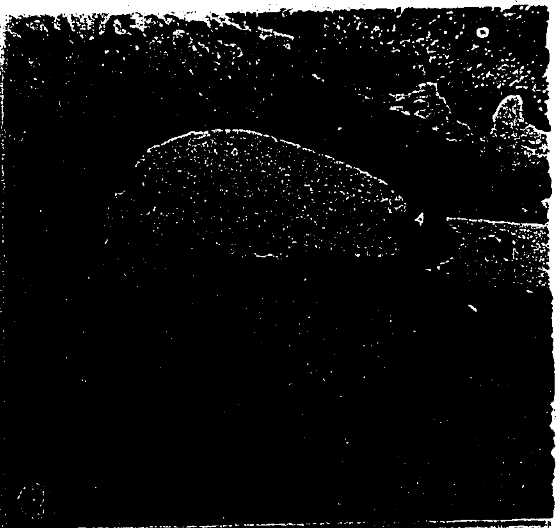

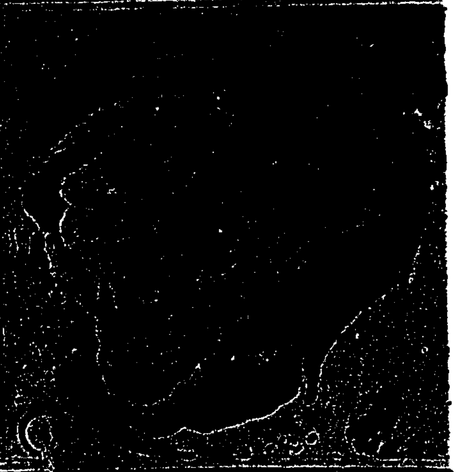

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General Discussion

Permineralized plant remains of the Princeton chert have preserved anatomical characters not always present in fossils from other localities. This adds important information to our understanding of botany during the Middle Eocene. The detailed preservation of even delicate tissues permits close comparisons with extant taxa (e. g., Cevallos-Ferriz and Stockey, 1988, 1989; Erwin and Stockey, 1989). Furthermore, since many of the plants preserved in the chert were growing *in situ*, or transported for only short distances to the basin of deposition, potential for whole plant reconstruction is great at this locality. It has been suggested that the Princeton chert locality has one of the most, if not the most, diverse permineralized Tertiary floras (Basinger and Rothwell, 1977; Cevallos-Ferriz and Stockey, 1988, 1989;). The Princeton chert locality, therefore, is important not only from a paleobotanical point of view, but the detailed anatomical data it provides is significant in the study of systematics and phylogeny of extant plants and fungi.

The vegetative and reproductive organs described in this study possess important characters that may be important in future phylogenetic analysis. The present study of vegetative organs of Magnoliaceae and Rosaceae, as well as reproductive organs of Rosaceae, suggest that these organs had a similar organization to that of their extant relatives. However, this study also shows that while the anatomical organization in extant and fossil organs is similar, a single fossil organ possesses characters found in different extant taxa within a family. Documenting this variability is important because the organs may be morphologically very similar, but anatomically they may have important differences.

Anatomical characters in extant plants have not been widely used in plant systematics; however, in some instances they have shown great potential. Seed anatomy has undergone an extensive revision and has been used for taxonomic purposes (Corner, 1976). The taxonomic conclusions presented by Corner (1976), however, have not been widely accepted because he based his ideas on the Durian theory (Corner, 1949, 1953a, 1953b, 1954) which has not been generally accepted. The Nymphaeales, can be divided into families based on seed anatomy that closely parallel a scheme based on flower characters (Collinson, 1980). Wood anatomy has also been used successfully in solving taxonomic problems. For example, the presence of intraxylary phloem and vestured pits has been successfully used to classify the families in the order Myrtales (van Vliet and Baas, 1984; Carlquist, 1988); and the taxonomic scheme proposed for this order based on wood anatomy differs little from the treatment given to this order by Thorne (1976) or Cronquist (1981) based mainly on floral characters.

The present study has shown that anatomical characters should be evaluated cautiously in interpreting relationships between taxa. Although ontogenetic variation in plant organs is well documented (e. g., Bailey, 1923; Barghoorn, 1940, 1941a, 1941b; Corner, 1976; Roth, 1977), its interpretation may become complicated when environmental variation is considered (Canright, 1955; Carlquist, 1975, 1988). Vegetative and reproductive organs from the Princeton chert have shown that anatomical characters may have some functional significance, but they also have systematic significance. For example, axial traumatic ducts are present in several dicotyledonous families, but within Rosaceae they can be associated with *Prunus* L. if used in conjunction with pore distribution. Similarly, while opposite intervascular pits are infrequent in dicotyledonous plants, they are not restricted to a single family. They are restricted to *Liriodendron* L., two species of *Magnolia* L., and older wood of *Alcimandra* Dandy within extant Magnoliaceae.

There are some families, such as Nymphaeaceae or Vitaceae, with very distinct integumentary patterns while others are almost impossible to distinguish based on integumentary anatomy (e. g., Malvaceae and Sterculiaceae; Corner, 1976). Although seeds of the different taxa in Rosaceae do not have a uniform type of construction (Corner, 1976), the seeds of *Prunus* and *Paleorosa* Basinger from Princeton have been shown to have characters that are associated with the seeds of extant *Prunus* and members of the Spiraeoideae respectively.

Evolution in different plant groups has proceeded at different rates in different organs (Cronquist, 1988). Evaluating evolution using isolated plant organs is difficult and comparisons of fossil plant organs with extant plant organs must be undertaken with caution in order to avoid over generalization. However, as Crane (1981) has shown, fossil floras may include more than one organ that on the basis of constant association may be regarded as representing a single fossil taxon. For example, *Palaeocarpinus* Crane, a Paleocene plant from England, has nutlets that are similar to nutlets of extant *Carpinus* L. and *Ostrya* Scop. The bract associated with the nutlets of *Palaeocarpinus* is similar to the bract of *Corylus* L., but the leaves associated with the reproductive organs are not even necessarily diagnostic of the family Betulaceae. The extinct plant *Macginitea* Manchester from the Eocene Clarno Formation has wood and fruits resembling extant *Platanus* L. but are associated with leaves that are unlike modern species of *Platanus* (Manchester, 1981). Further differences in rates of evolution are illustrated by the *Cercidiphyllum*-like complex from the Paleocene of Canada, England and Russia. Leaves of *Joffrea* (Crane and Stockey, 1985; Stockey and Crane, 1983), *Trochodendrocarpus* (Krassilov, 1973, 1976, 1977), *Nyssidium* (Crane 1984) and extant *Cercidiphyllum* (Crane and Stockey, 1986) are very similar to each other; however, these plants differ from *Cercidiphyllum* in shoot morphology, phyllotaxy, growth habit, and infructescence position (Crane and Stockey, 1986).

Isolated organs of fossil taxa may be very similar to those of extant plants, but unless whole plant reconstructions are made, phylogenetic inferences based on this evidence may give a distorted impression of the evolution of plant groups. The systematic interpretation of fossil angiosperms must be approached with great care to evaluate the diagnostic characters and avoid erroneous interpretations and conclusions (Dilcher, 1974; Roth and Dilcher, 1979; Jones and Dilcher, 1980). With this careful approach the systematic significance of fossil plants has become more valuable. There are plant groups that can only be recognized to the family level by the Eocene, while in other flowering plant groups genera or even species are differentiated by this time. For example, Tribe Betuleae (Betulaceae) is differentiated by the Late Cretaceous; however, the extant genera *Alnus* Mill. and *Betula* L. in this tribe are not recognizable until the Middle Eocene (Crane and Stockey, 1987). Tribe Coryleae (Betulaceae), on the other hand, may also be present in Cretaceous floras, but unequivocal extinct Coryleae are only known from the Paleocene and extant genera are not differentiated until the Late Eocene and Early Oligocene (Crane and Stockey, 1987). The fossil record of Ceratophyllaceae has been also analyzed based on the association of vegetative and reproductive organs (Herendeen et al., 1990). *Ceratophyllum* L. is differentiated by the Paleocene, and extant species and subspecies of this taxon are known from the Middle Eocene (Herendeen et al., 1990). In Salicaceae, *Populus* L. probably occurs in the Paleocene, and *Populus* and *Salix* L. are distinct by the Middle Eocene (Manchester et al., 1986). However, the time of appearance of extant species is still to be determined. The presence of few extant genera, and even fewer extant species, in Eocene floras contrasts with the many taxa found in sediments of this age that cannot be correlated with extant plants (Manchester et al. 1986).

Plant characters have been polarized as plesiomorphic (unspecialized) and apomorphic (specialized) based on neontological studies. Evidence retrieved from the fossil record has confirmed some of these interpretations. Several of the trends suggested by Bailey and his co-workers (e. g., Bailey and Tupper, 1918; Frost, 1930, 1931) in wood evolution have been confirmed using fossil material. For example, fusiform cambial initials have shortened over geologic time (Manchester, 1979). The unspecialized type of axial and radial parenchyma is more common in fossil woods than in extant plants (Bande and Prakash, 1984), and scalariform perforation plates are more common in plants recovered in older sediments (Scott and Wheeler, 1982).

Liriodendroxylon princetonensis Cevallos-Ferriz and Stockey has opposite intervascular pitting interpreted as an apomorphic character within the family Magnoliaceae (Canright, 1955), but has many bars per perforation plate and longer tracheary elements compared to extant *Liriodendron*. Therefore, while in terms of plesiomorphic and apomorphic characters *Liriodendroxylon* has specialized type of wood within the family Magnoliaceae (Scott and Wheeler, 1982), it also has some relatively plesiomorphic characters when compared to extant *Liriodendron*.

Polarization of the characters of the secondary phloem has been proposed by Roth (1981). Her assumptions of plesiomorphic and apomorphic characters are based on observations of extant plants and are very similar to those proposed for wood. *Liriodendroxylon princetonensis* and *Prunus allenbyensis* Cevallos-Ferriz and Stockey have, according to her concepts, a specialized status due to the presence of dilatation growth, heterocellular rays, and stratified arrangement of sclerenchyma. However, the phloem is unspecialized in having multi- and uniseriate rays, individual dilated rays, and sclerenchyma.

While *Liriodendroxylon princetonensis* has a putatively unspecialized organization, *Prunus allenbyensis* clearly have more specialized characters. The *Prunus* wood from Princeton has apomorphic characters when compared both within the family Rosaceae as well as to extant *Prunus*. These include the presence of only simple perforation plates, heterocellular rays, and scanty vasicentric parenchyma (Bailey and Tupper, 1918; Frost, 1930, 1931). In comparing the wood of *L. princetonensis* and *P. allenbyensis*, the former has more plesiomorphic characters (e. g., marginal parenchyma, scalariform perforation plates, opposite intervascular pitting) while in *Prunus* more apomorphic characters are found (e. g. paratracheal and apotracheal parenchyma, simple perforation plates, alternate intervascular pitting).

Plesiomorphic and apomorphic character states have been postulated for fruits and seeds (Roth, 1977) and these have been correlated with the fossil record (Friis and Crepet, 1987). For example, the fleshy fruit as in *Prunus*, is thought to represent an apomorphic character that is related to animal dispersal, while the dry fruit such as the follicle-like fruit of *Paleorosa*, is unspecialized (Friis and Crepet, 1987). Reduction of integuments and protection of the embryo by sclerotized fruit tissues as in *Prunus* is interpreted as an apomorphic character when compared to plants in which only the integument is responsible for protecting the embryonic tissues (Roth, 1977).

There is a general agreement among botanists that *Liriodendron* stands apart from the other members of the family based on anatomy, morphology, and chemical constituents (e. g., Nooteboom, 1985; Metcalfe, 1987). My study supports this interpretation based on the anatomy of vegetative axes of *Liriodendroxylon*. It further suggests that the relationship of *Liriodendron* to temperate species of *Magnolia*, such as *M. tripetala* L. and *M. acuminata* L. should be investigated based on the presence of many shared characters. Recently a phylogenetic analysis of Rosaceae showed that the traditionally recognized four subfamilies are not natural groups (Kalkman, 1988). The same problem has been noticed by Wolfe and Wehr (1988) based on their studies of fossil and extant rosaceous leaves. My study shows that while *Prunus* was differentiated by the Middle Eocene, *Paleorosa* has at least some characters found in extant Rosaceae that were not differentiated by this time. Therefore, my study also suggests that the classification of the Rosaceae should be reviewed.

Most Tertiary floras have plants preserved as impression/compression fossils. This situation makes comparisons to the permineralized material of Princeton difficult. For example, the shape of leaf laminae and venation patterns are important characters in identifying impression/compression fossils. These characters are difficult to determine from permineralized material. In contrast, anatomical information, which is important in identifying vegetative axes and reproductive organs in permineralized material, is unavailable in impression/compression fossils. However, there have been some attempts at comparison. Miller (1973) compared *Pinus similkameenensis* Miller to *P. latahensis* Berry and *P. tulameenensis* Penhallow, with respect to leaf size and number of needles per fascicle. *Metasequoia milleri* Rothwell and Basinger has also been compared in detail to *Metasequoia* fossils as well as other members of the family, allowing its recognition as a distinct species based on anatomical and morphological characters (Rothwell and Basinger, 1979; Basinger, 1981, 1984).

Comparisons of permineralized specimens from other known floras; however, are more easily made. Fern rhizomes and petioles from the Princeton chert described as *Dennstaedtiopsis aerenchymata* Arnold and Daugherty, originally described from the Clarno chert of Oregon, are thought to be conspecific (Basinger, 1976). *Liriodendroxylon princetonensis* Cevallos-Ferriz and Stockey and *Prunus allenbyensis* Cevallos-Ferriz and Stockey have been compared to other North American woods and show closest similarity to those also described from the Clarno Formation, Oregon, and those of Amethyst Mountain of Montana respectively. However, the specimens from Princeton were characterized, not only by wood characters, but also by many features of the primary tissues and secondary phloem that are unknown from the axes of other North American localities, making further comparisons difficult. Unfortunately, reproductive organs in fossil plants, similar to those of *Paleorosa* and *Prunus*, with anatomical descriptions, are unknown and they were compared only to extant material.

Twigs of *Liriodendroxylon princetonensis* Cevallos-Ferriz and Stockey represent the oldest known vegetative axes with anatomy similar to *Liriodendron* and contain the oldest known anatomically preserved magnoliaceous phloem. However, phloem anatomy of these vegetative axes is closer to that of temperate species of *Magnolia* L. (e. g., *M. acuminata* and *M. tripetala*). My study shows that characters found in extant *Liriodendron* and some species of *Magnolia*, especially temperate species, overlapped during the Middle Eocene. Extant species of *Magnolia* and *Liriodendron* have many characters in common, not only in wood and phloem structure, but in leaf and seed anatomy. The overlap of characters in the fossil material and shared characters between them and extant plants suggest that these taxa are closely related. In a recent study based on overall character comparison (phenetic analysis), a rearrangement of some magnoliaceous genera was proposed (Nooteboom, 1985); however, neither the fossil record of the Magnoliaceae nor *Liriodendron* were included in the analysis. The present study suggests the need for a reinvestigation of the family based on information provided from both extant and fossil plants. This would enable a greater understanding of the evolutionary relationships among fossil and extant members of the family Magnoliaceae.

A re-examination of the holotype and paratypes, as well as four new flowers of *Paleorosa similkameenensis* Basinger confirms its placement in Rosaceae. New anatomical information includes the presence of a follicular fruit composed, at least in part, of thick walled cells; seeds with immature embryos and hypostase; and the description of pollen morphology and ultrastructure. The fruit is a follicle enclosed by a non-fleshy hypanthium. Based on fruit and seed types *Paleorosa* is accepted as a member of Spiraeoideae, Tribe Sorbarieae. While fruit morphology strongly supports inclusion of *Paleorosa* in Spiraeoideae, morphological and anatomical features suggest similarities with Maloideae. The prolate, semi-tectate, columellate, tricolporate grains of *Paleorosa* are most similar to pollen grains of *Pyracantha* Roem. (Maloideae). Important pollen characters include striate exine pattern, thickness of the nexine relative to the sexine, and the presence of an indistinct pore. Short post-chalazal branching of the raphe, as in seeds of *Paleorosa*, is also characteristic of Maloideae and Prunoideae. The intermediate characters of *Paleorosa* add strength to the hypothesis that Spiraeoideae may be ancestral to Maloideae. In addition, these intermediate characters support the idea of an important radiation of Rosaceae during the Eocene. *Paleorosa similkameenensis* represents the oldest anatomically preserved rosaceous flower, and extends the palynological record of the family to the Middle Eocene.

Prunus allenbyensis, like *Paleorosa similkameenensis*, has some characters that may be found in the subfamilies Prunoideae and Maloideae. The combination, however, of axial traumatic ducts and vessel elements in radial and oblique multiples, occasional clusters, and solitary vessels is more common in the subfamily Prunoideae. The primary tissues and secondary phloem of *P. allenbyensis* represent the oldest anatomically preserved rosaceous tissues and along with the wood they show that by the Middle Eocene these plants had characters like those of extant *Prunus*.

The three endocarps of *Prunus*, each with one enclosed seed, represent the oldest anatomically preserved *Prunus* fruits and seeds known to date. These three reproductive organs have an anatomy very similar to each other and to fruits and seeds of extant *Prunus*. Variation in number of cell layers, and cell size and shape in each fruit and seed zone is similar to those seen in extant species of *Prunus*. However, the fruits and seeds of only 7 out of about 430 extant species of *Prunus* have been studied in detail. The description of these rosaceous (*Prunus* and *Paleorosa*) reproductive organs shows that by the Middle Eocene several of the postulated apomorphic characters in Rosaceae (e. g., Sterling, 1964a, 1964b, 1965, 1966a, 1966b, 1966c) were already present.

In a series of studies on the development of carpel and seed in the Rosaceae, Sterling (e. g., 1964a, 1964b, 1965, 1966a, 1966b, 1966c) proposed that fused parts are apomorphic and that multi-ovulate carpels represent a plesiomorphic character within the family. Recently, in a cladistic analysis based on 14 morphological characters, Kalkman (1988) showed that multi-ovulate carpels are unlikely to be unspecialized since some reversals would have to be postulated, making the phylogenetic analysis less parsimonious. However, from my study connation of tissues and organs seems to be apomorphic. The presence by the Middle Eocene of putatively apomorphic characters suggests that, for a better understanding of relationships in the family, evidence from reproductive and vegetative anatomy, fossil record, biosynthetic pathways, etc. have to be incorporated in the analysis (Kalkman, 1988; Wolfe and Wehr, 1988).

The Middle Eocene Princeton chert from southern British Columbia represents a rich assemblage of permineralized plants that were growing during a time of important angiosperm radiation. Among these are a number of plants with affinities to modern aquatic groups. These include representatives of the Nymphaeaceae (*Allenbya* Cevallos-Ferriz and Stockey), Araceae (*Keratosperma* Cevallos-Ferriz and Stockey), Alismataceae (*Heleophyton* Erwin and Stockey), and Lythraceae (*Decodon* Gmel.). Anatomical features suggesting an aquatic environment, include aerenchyma in rhizomes of *Eorhiza* Robison and Person and *Dennstaedtiopsis* Arnold and Daugherty, petioles of *Heleophyton*, several ferns, a coryphoid palm, and in isolated leaf laminae. Tracheary elements in several aquatic plants are reduced in number with little or no secondary wall thickening. In addition, some taxa show protoxylem lacunae surrounded by a ring of cells with thickened inner walls. Seed features including a palisade layer, presence of an operculum, external mucilage, small amounts of endosperm, and abundant perisperm, are concordant with features in known extant aquatics. The association of these plants with turtle bones in the matrix and the presence of fresh water fish at the top of the section also indicate an aquatic environment. Evidence that several of these plants were growing *in situ* includes the presence of rooted axes, a large number of plant organs of the same type, and the preservation of complete flowers, delicate tissues and whole plants.

The combination of anatomical characters found in the magnoliaceous and rosaceous plants from Princeton suggests that the Middle Eocene was a time where important angiosperm radiation occurred, leading to the diversity seen in the modern flora. The anatomical information retrieved from this study contributes to the understanding of the time of appearance and combination of characters through time, some of which may be of value in phylogenetic studies. Continued studies of these and other remains of the Princeton chert may help to unravel phylogenetic relationships within the angiosperms.

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