VEGETATIVE REMAINS OF THE ROSACEAE FROM THE PRINCETON CHERT (MIDDLE EOCENE) OF BRITISH COLUMBIA

by

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Summary
Several anatomically preserved twigs, a branching specimen and the wood of a large axis with affinities to Rosaceae are described from the Princeton chert (Middle Eocene) of British Columbia, Canada. Specimens are characterised by a heterocellular pith with a peri-medullary zone of thick-walled oval cells and semi-ring-porous secondary xylem with vertical traumatic ducts, fibres with circular bordered pits, and mostly scanty paratracheal and occasionally apotracheal parenchyma. Ray to vessel pitting is similar to the alternate intervacular pitting. Secondary phloem is composed of tangentially oriented discontinuous bands of alternating fibres and thin-walled cells. Secondary cortical tissues are represented by a phelloderm characterised by rectangular cells and phellem with rectangular concave cells. Anatomical variation between specimens can be related to age of the woody axes. Juvenile and mature wood of this species differ in vessel arrangement and presence of scanty paratracheal parenchyma in mature wood. Vessel elements are arranged in radial multiples, occasional clusters as well as solitary vessels. Tyloses and dark cellular contents are present mainly in mature wood. Some twigs have a heterocellular pith with a few scattered cells with dark contents or, occasionally, short irregular rows of these cells. In the branching specimen cells of this type also are organised in longer rows. Together, these anatomical features suggest that all specimens belong to the same taxon, Prunus allenbyensis Cevallos-Ferriz & Stockey n. sp. Anatomy of this plant reinforces the interpretation of a subtropical to temperate climate during the time of deposition.

Key words: Rosaceae, Prunoideae, Maloideae, Prunus, fossil wood, Middle Eocene.

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 Basiinger 1976 (Rosaceae), Prinetonia allenbyensis Stockey 1987 (incertae sedis), and a sapindaceous flower (Erwin & Stockey 1990). Fruits and seeds include Decodon allenbyensis Cevallos-Ferriz & Stockey 1988 (Lythraceae), Allenbya collinsonae Cevallos-Ferriz & Stockey 1989 (Nymphaeaceae), and Ampelocissus similkameenensis Cevallos-Ferriz & 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 the 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 repre-

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sented 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 & Person 1973). Recently, Cevallos-Ferriz & Stockey (1990b) described *Liriodendroxylon allenbyensis*, of the family 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 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 Rosaceae underwent an important adaptive 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 from Princeton and Joseph Creek, British Columbia, and Republic, Washington (Wolfe & Wehr 1988). From these localities about 40 taxa have been identified based on leaf remains (Wolfe & Wehr 1988). Among these leaves are members of the subfamilies Spiraeoideae, Maloideae, Rosoideae, and Prunoideae. Rosaceous flowers from the Princeton chert, *Paleorosa similkaemenensis* Basinger (1976), has now been shown to be a member of the subfamily Spiraeoideae, tribe Sorbarieae (Cevallos-Ferriz et al. 1990).

In the present study a new species, *Prunus allenbyensis* Cevallos-Ferriz & 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 'T' (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 & Srivastava 1970), mammals and fishes (Russell 1935; Gazin 1953; Wilson 1977, 1982), and potassium-argon dating (Hills & 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 & Rothwell 1977). Peel sections were mounted in Eukitt or Coverbond xyylene 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 SI 1827), and *Prunus pennsylvanica* L. (ALTA 72159, UAPC-ALTA SI 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 & Wheeler 1987). All averages represent a series of 25 separate measurements (Carquist 1988).

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

Class: Magnoliopsida  
Order: Rosales  
Family: Rosaceae  
Subfamily: Prunoideae  
Genus: Prunus L.  
Species: Prunus allenbyensis  
Cevallos-Ferriz 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 (Figs. 14, 24, 26), B (Figs. 17, 19, 22), P1095 C (Figs. 2, 4, 9, 11, 13, 15, 16, 23, 25), D (Fig. 8); Paratypes — P1184 B (Figs. 1, 7); P1235 A (Figs. 3, 6, 10, 21), D (Figs. 12, 18, 20); P1720 C (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 vertical 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. Uniserate rays homocellular and heterocellular, up to 18 cells high. Multiserate rays heterocellular with one or two rows of marginal cells of upright cells, up to 8-seriate. Vessel to ray pits similar to intervascular pits. Aporotracheal 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 a thin cuticle. 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. Phellogen up to three cells thick of rectangular cells. Phellem of concave cells up to five cells thick.

Description

Five twig fragments, averaging $1.0 \times 0.7 \times 4.0$ cm (Fig. 1), a larger branch, $2.3 \times 2.0 \times 9.3$ cm (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 vertical traumatic ducts in the secondary xylem. Most pith cells are thin-walled and polyhedral or irregular in transverse section (Fig. 3). In longitudinal section they are rectangular or irregular, averaging $107 \times 73 \times 88$ μm (Fig. 4). A few polyhedral, thick-walled cells with dark contents and smaller dimensions, averaging $46 \times 34 \times 63$ μm, are scattered in the pith, sometimes forming irregular rows (Figs. 1, 3). The periphery of the pith is characterised by four to five layers of larger, thick-walled, oval to polyhedral cells filled with dark contents, the peri-medullary region (Fig. 5). In longitudinal section these cells are rectangular to quadrangular, averaging $44 \times 22 \times 72$ μm. Almost all pith cells are elongated parallel to the long axis of the twig (Fig. 4).

In transverse section axes have about 19 protoxylem points composed of oval cells with a mean diameter of c. 14 μm (Fig. 5); in longitudinal section these cells have helical secondary walls (Fig. 6). Metaxylem cells in transverse section are also oval with a diameter of c. 18 μm (Fig. 5). In longitudinal section they can be distinguished from the protoxylem elements by the presence of scalariform thickenings (Fig. 6). Associated with
Figs. 1–4. *Prunus allenbyensis* n. sp. — Fig. 1. Transverse section of twig showing pith and complete extraxylary tissues. Note prominent banded appearance of secondary phloem, and vertical traumatic ducts in wood. P1184 B top No. 0, × 10. — Fig. 2. Transverse section of larger branch with banded secondary phloem. P1095 C bot No. 0, × 10. — Fig. 3. Transverse section of pith showing irregular rows of cells with dark contents. P1235 A No. 0, × 150. — Fig. 4. Longitudinal section of pith showing chains of cells with dark contents (arrows). P1095 C side No. 1, × 125.
Figs. 5–8. *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, × 110. — Fig. 6. Longitudinal section of primary xylem. Note vessel element of the first growing season. P1235 A side No. 1, × 35. — Fig. 7. Oblique transverse section of cortex and radially aligned cells of the periderm. P1184 B top No. 1, × 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, × 250. — C = cortex, MX = metaxylem, P = pith, PE = phelloderm, PL = phellem, PM = peri-medullary region, PX = protoxylem, VE = vessel element.
the primary xylem are a few thin-walled parenchymatous cells with dark contents.

The cortex is up to 15 cell layers thick (Figs. 7, 8). Cells in the cortex are thin-walled, oval in transverse section, and average 57 × 16 × 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 (Fig. 26). At the inner margin of the cortex, primary phloem is represented by fibres (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.

Secondary tissues — In the first five growth rings of the secondary xylem, vessel elements are solitary (c. 5%), in radial and oblique multiples of two to four cells (c. 73%) and occasionally in clusters (c. 21%; Fig. 9). Vessel elements are oval to weakly angular with a small diameter (c. 28 μm tang. × 29 μm rad.) in wood produced during the first growing season. Vessel diameter increases to c. 30 μm in the second growth year, and the wood becomes semi-ring-porous. 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 c. 33 μm (tang.) × 34 μm (rad.), while in latewood it is c. 26 μm (tang.) × 31 μm (rad.). In these first four growth increments vessel element density is about 283/mm². 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 × 18 × 294 μm (Fig. 18). Vertical traumatic ducts are present at the beginning of some growing seasons in most twigs (Figs. 1, 13). These ducts are either tangen-

Legends to Figures 9–26:

Figs. 9–14. Prunus allenbyensis n. sp. — Fig. 9. Transverse section of secondary xylem of large branch. P1095 C bot No. 0, × 120. — Fig. 10. Transverse section of xylem of the larger piece of wood. P 1235 A No. 2, × 120. — Fig. 11. Radial section showing vessel elements with tyloses. P1095 C side No. 1, × 195. — Fig. 12. Vessel elements with alternate intervacular pitting. P1235 D side No. 4, × 250. — Fig. 13. Transverse section of vertical traumatic canals. P1095 C bot No. 0, × 110. — Fig. 14. Vessel element with simple perforation plates and thin helical thickenings (arrows). P1095 A side No. 1, × 290.

Figs. 15–20. Prunus allenbyensis n. sp. — Fig. 15. Oval, alternate intervacular pitting with coalescent pit apertures (arrow). P1095 C side No. 1, × 1750. — Fig. 16. Circular to oval, alternate intervacular pitting with coalescent pit apertures (arrow). P1095 C side No. 1, × 1500. — Fig. 17. Ray to vessel pits. P1095 B side No. 0 × 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, × 130. — Fig. 19. Tangential section of large branch at level close to the pith showing uniseriate and multiseriate rays. P1095 B side No. 0, × 125. — Fig. 20. Tangential section of larger piece of wood. Note large amount of dark contents. P1235 D side No. 4, × 125.

Figs. 21–26. Prunus allenbyensis n. sp. — Fig. 21. Radial section of uniseriate ray with upright cells. P 1235 A side No. 1, × 235. — Fig. 22. Tangential section showing aprotachae parenchyma. P 1095 B side No. 0, × 280. — Fig. 23. Tangential section showing scanty paratracheal parenchyma. P1095 C side No. 1, × 280. — Fig. 24. Radial section of multiseriate ray with upright and square to procumbent cells. P1095 A side No. 1, × 190. — Fig. 25. Transverse section of secondary phloem. P 1095 C bot No. 0, × 180. — Fig. 26. Oblique radial section of secondary phloem and cortex. P 1095 A side No. 1, × 180. — C = cortex, F = fibres, PH = secondary phloem, R = ray.
tially arranged along the whole ring (Fig. 1), or located in only a part of it. Vertical traumatic ducts are short (c. 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 vertical traumatic ducts in the second growth ring. Traumatic ducts lack an epithelial lining (Fig. 13) and are apparently, therefore, lysigenous in origin (Panshin & De Zeeuw 1980). The brownish contents present in some of these vertical ducts may represent former cell contents, gum, or perhaps mucilage.

Vessel elements have slightly oblique end walls with simple perforation plates (Figs. 6, 14, 18), and alternate intervacular pits (c. 6 × 4 μm) on lateral walls (Figs. 12, 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 (Figs. 15, 16). Vessel elements have thin helical thickening, especially those of the latewood (Figs. 14, 18). These helical thickening are more common in smaller vessel elements. Some vessels have dark contents. Fibres have circular to oval bordered pits, c. 4 μm in diameter in tangential and radial walls (Fig. 18).

Rays are one- to five-seriate and five to 28 cells high (Figs. 19, 20), averaging 370 μm (range 150–630 μm), and have simple pits on radial and tangential walls. There are c. 10 rays per millimetre. Multiseriate rays are composed mainly of procumbent cells with one or two upright cells in the margins (Fig. 24). Uniseriate rays 2 to 12 (up to 18) cells high near the pith (range 36–115 μm). Some rays are composed of upright cells near the pith (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 c. 500 μm high, but as the branch grew, rays became shorter. Ray to vessel pits are similar or slightly smaller, but less crowded, than intervacular pits (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 5 cells tall (Fig. 22).

Secondary phloem is composed of discontinuous, tangentially oriented, alternating bands of thin-walled cells and fibre clusters (Figs. 1, 2, 8, 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 (Figs. 1, 2). Periderm is present in all twigs examined (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 (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 (Fig. 3). The large wood fragment has vessel grouping similar to twigs; however, most vessels are solitary (c. 46%), fewer occur in radial and oblique multiples (c. 42%) and clusters (c. 12%). Vessel distribution is semiring-porous (Fig. 10); however, there are fewer (100) and larger vessel elements per square millimetre. Vessel elements almost double in size in older wood. 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 (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 composed of procumbent, square, and upright cells. Parenchyma cells form apotracheal strands as in the twig (Fig. 22), but in a few cases scanty paratracheal cells not found in twigs are also present (Fig. 23). Vessels and parenchyma cells in these more mature woods have more dark contents than in the twigs.

Discussion

Comparison with extant Rosaceae — Anatomical similarities between 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 intervacular pitting, simple perforation plates, fibres with circular bordered pits in tangential and radial walls, and ray to vessel pits that are similar to intervacular 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 & 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, i.e., semi-ring-porous wood, simple perforation plates, alternate intervacular pitting, and ray to vessel pits similar to intervacular pits that characterise P. allenbyensis are found in combination in over 50 families of dicotyledonous plants (Wheeler et al. 1986; LaPasha & 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 & 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 vertical traumatic ducts. The most definitive of these characters is the presence of vertical 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. comm.). Although pith with a peri-medullary zone has been reported in Meliaceae and Rosaceae (Metcalfe & 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., Megaphylla Hemsl. and Sandoricum Cav.; Metcalfe & Chalk 1950). Neither are present in the pith of Prunus 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 & 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 vertical 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 & 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 vertical 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 & Chalk 1950; Zhang Shuyin 1989, pers. comm.)

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 & Chalk 1950; Zhang Shuyin 1989, pers. comm.). 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 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 & Chalk 1950). However, some extant Prunus species and other taxa in Maloideae have pits with clearly distinct borders (Zhang Shuyin 1989, personal comm.), as in P. allenbyensis.

In Rosaceae, ray to vessel pits have been described as similar to intervascular pits (Tippo 1938; Fabbri-Tarchi 1960). In Prunus, however, vessel to ray pits are usually much smaller than the intervesSEL pits (Zhang Shuyin 1989, pers. comm.). Yet in some Prunus species (e.g., Prunus serotina Ehrh., Wheeler 1990, pers. comm.) the vessel to ray pits are similar in size to the intervascular pits, as in P. allenbyensis.

Most rosaceous taxa have unicellular rays composed of upright and square cells (Metcalfe & Chalk 1950). Rays in Maloideae are characterised by their tendency to be homocellular (Fabbri-Tarchi 1960), while uniseriate rays in extant Prunoideae are heterocellular composed of square and upright cells (Metcalfe & Chalk 1950; Zhang Shuyin 1989, pers. comm.). Through ontogeny ray structure is highly variable. Near the pits the fossil twigs and branch have some uniseriate homocellular rays composed of upright cells. However, further away from the pit, 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. palaeosippeliana 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 vertical traumatic ducts and vessels that occur in oblique and radial multiples, occasionally in clusters, as well as solitary.

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., France 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 *P. padus* L., *P. avium* L., and *P. spinosa* Walt. (Schweingruber 1978) as well as in other rosaceous genera such as *Neillia* 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 & 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 1). They have been included in Maloideae (Grambast-Fessard 1966; Wheeler & 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 & Müller-Stoll 1980, 1982; Suzuki 1984; Takahashi & Suzuki 1988). In the family Chrysobalanaceae one species has been described (Pfeiffer & Van Heuren 1928).

*Prunus allenbyensis* differs from other fossilised rosaceous stem woods, excluding Prunoideae, by the presence of vertical traumatic ducts (Table 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 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 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 1; Grambast-Fessard 1966; Wheeler & Matten 1977). *Rosaceoxylon* Shilkina from Russia is distinct in having septate fibres and scalariform intervacular pitting (Table 1; Shilkina 1958; Süss & Müller-Stoll 1982). *Parinaroxylon* is characterised by the presence of uniseriate rays and lacks helical thickenings (Pfeiffer & Van Heuren 1928).

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

Stem woods described as Prunoideae are most similar to the fossil Princeton remains (Table 1). However, vessel distribution in
Table 1. Comparison of Prunus allenbyensis to other fossil Rosaceae.

From Hofmann (19441, 19522), Page (19642), Grambast-Fessard (19663), Van der Burgh (19744, 19785), Dupéron (19766), Wheeler and Matten (19776), Wheeler et al. (19787), Süss and Müller-Stoll (19808, 19829), Suzuki (198410), and Takahashi and Suzuki (198811). -- PA = parenchyma; H = halfbordered pits, S = and scalariform; v.e. = vessel element, i.v.p. = intervessel pitting.

<table>
<thead>
<tr>
<th>VESSEL ELEMENTS</th>
<th>RAYS</th>
<th>PA</th>
</tr>
</thead>
<tbody>
<tr>
<td>Growth rings present</td>
<td>Semi-ring-porous</td>
<td>Diffuse-porous</td>
</tr>
<tr>
<td>Prunus allenbyensis</td>
<td>x</td>
<td>x</td>
</tr>
<tr>
<td>Pruninium kraeseltii10</td>
<td>x</td>
<td>x</td>
</tr>
<tr>
<td>Prunus sp.4,7</td>
<td>x</td>
<td>x</td>
</tr>
<tr>
<td>Prunus gummosa8</td>
<td>x</td>
<td>x</td>
</tr>
<tr>
<td>Prunus iwatense12</td>
<td>x</td>
<td>x</td>
</tr>
<tr>
<td>Prunus palaeozippeliana11</td>
<td>x</td>
<td>x</td>
</tr>
<tr>
<td>Prunus ascendentiporulosa11</td>
<td>x</td>
<td>x</td>
</tr>
<tr>
<td>Prunus uviporulosa11</td>
<td>x</td>
<td>x</td>
</tr>
<tr>
<td>Prunus polyborulosa11</td>
<td>x</td>
<td>x</td>
</tr>
<tr>
<td>Prunoidoxylon</td>
<td>x</td>
<td>x</td>
</tr>
<tr>
<td>multiporosum5</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Lyonomaphnoxyzon</td>
<td>nevadensis2</td>
<td>x</td>
</tr>
<tr>
<td>Rosaceoxylon</td>
<td>spiraeoides3,9</td>
<td>x</td>
</tr>
<tr>
<td>Sorbus4</td>
<td>x</td>
<td>x</td>
</tr>
<tr>
<td>Crataegus4</td>
<td>x</td>
<td>x</td>
</tr>
<tr>
<td>Pomoxylon1,7</td>
<td>x</td>
<td>x</td>
</tr>
<tr>
<td>Maloidoxylon galbreathii6</td>
<td>x</td>
<td>x</td>
</tr>
<tr>
<td>Maloidoxylon coloradoense6</td>
<td>x</td>
<td>x</td>
</tr>
<tr>
<td>Maloidoxylon castellane53</td>
<td>x</td>
<td>x</td>
</tr>
</tbody>
</table>

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, Prunoidoxylon multiporosum from Agenais, France (Dupéron 1976). However, this taxon has a dendritic vessel arrangement, lacks gum or gum-like deposits and vertical 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 those of P. palaeozippeliana, P. ascendentiporulosa and P. uvi-
Table 2. Comparison of some features of *Prunus gummosa* (Wheeler *et al.* 1989) from Amethyst Mountain, Yellowstone National Park, and *P. allenbyensis* from Princeton chert locality, British Columbia.

<table>
<thead>
<tr>
<th>Vessel elements</th>
<th><em>Prunus gummosa</em></th>
<th><em>Prunus allenbyensis</em></th>
</tr>
</thead>
<tbody>
<tr>
<td>porosity</td>
<td>diffuse</td>
<td>semi-ring</td>
</tr>
<tr>
<td>radial diameter</td>
<td>90 μm</td>
<td>70 μm</td>
</tr>
<tr>
<td>tangential diameter</td>
<td>47 μm</td>
<td>55 μm</td>
</tr>
<tr>
<td>intervascular pitting</td>
<td>alternate</td>
<td>alternate</td>
</tr>
<tr>
<td>spiral thickenings</td>
<td>present</td>
<td>present</td>
</tr>
<tr>
<td>perforation plates</td>
<td>simple</td>
<td>simple</td>
</tr>
<tr>
<td>ray pitting</td>
<td>similar to intervascular</td>
<td>similar to intervascular</td>
</tr>
<tr>
<td>tyloses</td>
<td>present</td>
<td>present</td>
</tr>
<tr>
<td>dark contents</td>
<td>present</td>
<td>present</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Rays</th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>per millimetre</td>
<td>8–17</td>
<td>10</td>
</tr>
<tr>
<td>uniseriate:</td>
<td></td>
<td></td>
</tr>
<tr>
<td>cells tall</td>
<td>10</td>
<td>12</td>
</tr>
<tr>
<td>μm tall</td>
<td>46–185 μm</td>
<td>37–124 μm</td>
</tr>
<tr>
<td>multiseriate:</td>
<td></td>
<td></td>
</tr>
<tr>
<td>cells tall</td>
<td>5–44</td>
<td>8–40</td>
</tr>
<tr>
<td>μm tall</td>
<td>105–763 μm</td>
<td>150–630 μm</td>
</tr>
<tr>
<td>n-seriate</td>
<td>2–4</td>
<td>2–5 (8)</td>
</tr>
<tr>
<td>marginal cell rows</td>
<td>1–2 (6)</td>
<td>1–2</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Imperforate tracheary elements</th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>thin-walled</td>
<td>present</td>
<td>present</td>
</tr>
<tr>
<td>circular bordered</td>
<td>in radial and tangential walls</td>
<td>in radial and tangential walls</td>
</tr>
<tr>
<td>pits</td>
<td></td>
<td></td>
</tr>
<tr>
<td>diameter</td>
<td>5 μm</td>
<td>4 μm</td>
</tr>
</tbody>
</table>

**Axial parenchyma**

- *Prunus gummosa* has abundant gum deposits and vertical 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 (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 2; Panshin & 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 with environmental differences (Tomlinson & 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 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 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. comm.).

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 simikameensensis* Basinger (1976) has been identified as a member of Subfamily Spiraeoideae, Tribe Sorbariaeae (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 & Wehr 1988, pers. comm.). Connection of these isolated organs promise 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 & 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 & Carlquist 1985; Baas & Schweingruber 1987).

The wood anatomy of *Prunus allenbyensis* and the inferred information provided by
other plants from the chert (Erwin & 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), Heliophyton (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.

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References


Barghoorn, E.S. 1940. The ontogenetic development and phylogenetic specialization of rays in the xylem of dicotyledons. I. Primitive ray structure. Amer. J. Bot. 27: 918–928.


