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VEGETATIVE GROWTH OF *DECODON ALLENBYENSIS* (LYTHRACEAE) FROM THE MIDDLE EOCENE PRINCETON CHERT WITH ANATOMICAL COMPARISONS TO *DECODON VERTICILLATUS*

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Large numbers of roots and stems of aquatic Lythraceae have been found in association with fruits and seeds of *Decodon allenbyensis* Cevallos-Ferriz et Stockey in the Princeton chert, British Columbia, Canada. The permineralized fossils come from layer 43 in the chert, part of the Middle Eocene, Allenby Formation. Vegetative remains were studied using the cellulose acetate peel technique in an attempt to reconstruct the whole plant of *D. allenbyensis*. Reconstruction is based on close anatomical comparisons of tissues in the fossil organs to those of extant *Decodon verticillatus* (L.) Ell. and on attachment of organs and tissue systems. A detailed description of both root and stem wood anatomy is provided for the fossil species. Stem anatomy is revised for extant *D. verticillatus*, and detailed root anatomy is described for the first time using paraffin sectioning techniques and scanning electron microscopy. Fossil roots and stems show diffuse porous wood with vessels that are solitary or in radial multiples of two to five with numerous tyloses. Heterocellular rays vary from one to at least five cells wide. Secondary phloem with clusters of thick-walled fibers is preserved in some axes. Most roots and some stems show distinctive concentric layers of thin-walled lacunate phellem, characteristic of submerged aquatics. This tissue has been described in extant *Decodon* J.F. Gmelin and other Lythraceae. Anatomy of *D. allenbyensis* indicates that these plants were growing under submerged conditions with stable water levels at the edge of a quiet body of fresh water.

Keywords: aquatic plants, *Decodon*, Eocene, Lythraceae, Onagraceae, Myrtaceae, Myrtales, phellem.

Introduction

Lythraceae is a large tropical to subtropical angiosperm family of 31 genera and 600 species that includes some temperate species (Graham 1964). Plants are generally terrestrial, but many are semiaquatic to aquatic (Schrenk 1889; Graham 1964; Sculthorpe 1967; Graham et al. 1993). North American genera include *Ammannia* L., *Cuphea* P. Browne, *Decodon* J.F. Gmelin, *Didiplis* Raf., *Heimia* Link et Otto, *Lythrum* L., *Nesaea* Comm., *Peplis* L., and *Rotala* L. (Conti et al. 1996, 1997; Graham 1999; Judd et al. 1999). Many of these taxa show a tolerance to flooding (Lempe et al. 2001), and one, *Lythrum salicaria* L., is a noxious weed that competitively excludes even hardy species such as *Typha angustifolia* L. in North American wetlands (Mal et al. 1997; Stevens et al. 1997).

The fossil record of Lythraceae is based mainly on dispersed fruits, seeds, and pollen (Graham and Graham 1971; Tiffney 1981). The oldest records of seeds are from the Paleocene of southern England (Reid and Chandler 1933; Chandler 1961). Vegetative remains of Lythraceae include compression/impression leaves that have been assigned to the genus *Decodon* (Wolfe and Tanai 1980; Wehr and Hopkins 1994; Stockey and Wehr 1996). Many myrtalean leaves have similar structure; therefore, it has been suggested that it is not always advisable

to assign Tertiary foliage to modern genera in the absence of fruit and flower data (Manchester et al. 1998).

In recent years there have been a number of reports of well-preserved *Decodon* in the fossil record (Cevallos-Ferriz and Stockey 1988; Matsumoto et al. 1997; Bertram 1998; Kvaček and Sakala 1999). To date, the only *Decodon* plant that has been partially reconstructed is *Decodon gibbosus* (E.M. Reid) E.M. Reid ex Nikitin emend. Kvaček et Sakala (1999), based on attached stems, leaves, and fruits from compression fossils found in the Lower Miocene, Bilina Mine, northern Bohemia. Permineralized material from the Miocene of Japan so far has revealed only *Decodon* seeds (Matsumoto et al. 1997), and the Miocene fossil plants, which may include a *Decodon* sp., from the Virgin Valley Formation in Nevada are yet to be described (Bertram and Pigg 1997; Bertram 1998).

The presence of aquatic Lythraceae in the Princeton chert was first recognized by Cevallos-Ferriz and Stockey (1988), who described the permineralized fruits and seeds of *Decodon allenbyensis*. Recently, large numbers of roots, stems, and leaves have been found in the chert in association with fruits and seeds of *D. allenbyensis*. In this study we reconstruct stems and roots of *D. allenbyensis* from the Princeton chert using anatomical comparisons to the only extant *Decodon* species, *Decodon verticillatus* (L.) Ell., and through attachments of plant organs. One of the ultimate goals of this whole plant reconstruction will be to use *D. allenbyensis* in morphological cladistic analyses, using information from both extant and fossil Lythraceae. These well-preserved lythraceous vegetative remains from the Princeton chert, many found in growth posi-

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tion, also add to our knowledge of growth habit and habitat reconstruction for this fossil *Decodon* species.

Material and Methods

The permineralized specimens studied here come from the Princeton chert locality situated on the east bank of the Similkameen River, ca. 8.4 km southwest of the town of Princeton, British Columbia (UTM 783724; lat. 49°22.7'N, long. 120°32.7'W). This chert outcrop has been called locality "I" (Boneham 1968) and is part of the Allenby Formation in the Princeton Group. There are at least 49 interbedded layers of chert and coal, with an occasional ash bed replacing a chert layer (Stockey 1983; Cevallos-Ferriz et al. 1991), and differing plant associations are found in each chert layer (Pigg and Stockey 1996). The locality is dated as Middle Eocene, based on data from pollen (Rouse and Srivastava 1970), fossil mammals (Russell 1935; Gazin 1953), fish (Wilson 1977, 1982), and potassium-argon dating (Hills and Baadsgaard 1967; H. Baadsgaard, personal communication, 1999).

Chert slabs were peeled with the cellulose acetate peel technique (Joy et al. 1956) modified for hydrofluoric acid (Basinger and Rothwell 1977; Basinger 1981). Several hundred chert blocks from layer 43 were examined for putative *Decodon allenbyensis* Cevallos-Ferriz and Stockey (1988) vegetative material in the University of Alberta Paleobotanical Collection, and the best were chosen for further peeling. Peel sections were mounted with Eukitt rapid mounting medium (O. Kindler, Freiburg, Germany) for microscopic examination.

Extant *Decodon verticillatus* material was obtained from three sources: the margin of Wingfoot Lake, just west of Route 43 between Kent and Hartville, Ohio; Queen's University greenhouses, Kingston, Ontario; and University of Guelph greenhouses, Ontario. This material was embedded and sectioned using standard paraffin techniques (Johansen 1940). Slides were stained with safranin-fast green (Johansen 1940); potassium iodide was used on unstained sections to test for starch. Sections were mounted with standard DPX mounting medium (Electron Microscopy Sciences, Ft. Washington, Pa.).

Extant plant samples were prepared for scanning electron microscopy (SEM) after washes in absolute EtOH and dehydration. Critical-point drying used a Polaron apparatus (Waterford, England) for SEM. Roots and leaves were examined by cryo-SEM, using an EMJTECK (K1250) cryosystem.

Wood anatomy utilized several axes for both fossil and extant *Decodon*. Because *D. verticillatus* stem wood was described by Baas and Zweypfenning (1979) based on only one 6-mm stem, and root wood was not described, we sectioned living material to provide these descriptions. Measurements of the following specimens were described based on axes of these diameters: *D. verticillatus* stems, 5, 6, and 16 mm; *D. verticillatus* roots, 4, 7, and 16 mm; *D. allenbyensis* stems, 6 and 10 mm; *D. allenbyensis* roots, 5, 7, and 10 mm. Because of the limitations of techniques using fossils, vessel and fiber lengths are probably conservative, as macerated cells cannot be observed. Observations of *D. verticillatus* wood were performed on sections only to allow for comparable observations; therefore, fiber and vessel lengths are also conservative and probably lack the upper range of these cell lengths. Vesturing classification follows Van Vliet (1978).

Samples for SEM were coated with 150 Å gold with a Nanotek sputter-coater and viewed with a JEOL scanning electron microscope (JSM 6301) at 5 kV. Images were taken with a Microlumina (Leaf Systems) digital scanning camera and a Phase One digital studio camera (Phase One A/S, Frederiksberg, Denmark) using a Leitz Aristophot and processed using Adobe Photoshop 5.5 and 6.0.

Results

Roots

***Decodon allenbyensis*.** Large numbers of branching roots with lacunate phellem have been identified in the chert (fig. 1a, 1b, 1d; fig. 2a, 2c, 2d). Some specimens show extensive interconnected branching systems with roots of several sizes all surrounded by thin walled phellem (fig. 1a, 1b). Others are attached to and arising from stems (figs. 1c, 2a). Roots also are observed arising from submerged stems in extant *Decodon verticillatus* (fig. 2b). In small roots with very little secondary vascular tissue, diameters including phellem tissues range from 0.5 to 15 mm or more, due to the extensive lacunate phellem. Roots in the chert are woody (fig. 1a, 1d; fig. 2a, 2c, 2d), and large numbers of small attached roots that lack secondary tissues have also been identified (figs. 2e–2g, 3a).

Primary xylem in young roots is pentarch to hexarch (fig. 2e, 2f) to septarch. Primary phloem is not well preserved (figs. 2e, 3a). The endodermis and several inner cortical layers are often filled with dark contents in young roots (fig. 2e, 2g; fig. 3a). In addition, the cortex of young roots is aerenchymatous and the cells often are poorly preserved (fig. 2e, 2g). Epidermal cells are small and rectangular in outline in transverse section (fig. 2e). A distinctive hypodermis consisting of a single layer of radially elongate cells is present (figs. 2e, 3a).

Large numbers of fungal hyphae and circular chlamydo-spore-like structures occur in the cortical tissues of some of the youngest roots (fig. 3a, 3b). The fungi, all well preserved, may represent mycorrhizae or saprophytes and should provide the basis for several further investigations.

Secondary tissues in the fossil roots are well preserved, and there are several distinct growth increments (figs. 1d, 2c). Roots that have begun to form secondary xylem have thick-walled fiber bundles in well-preserved secondary phloem (fig. 1d; fig. 2c, 2d; fig. 3c). These phloem bundles typically range from 156 to 700 μm diameter, and individual fibers are round to polygonal in cross section, with diameters ranging from 39 to 147 μm .

Fossil root wood description. Growth rings distinct. Wood diffuse to semi-ring-porous (fig. 3d). Vessels number ca. (27–)46(–66) mm^2 , 6%–55% solitary or in radial multiples of 2–5(–7) or rarely in clusters of 3–4, round to oval or tending to angular, tangential diameter (30–)88(–156) μm , radial diameter up to 160 μm ; walls 2–4 μm thick. Vessel member length (160–)234(–459) μm . Perforations are simple in oblique end walls (fig. 3i). Intervessel pits 4–10(–20) μm , crowded, alternate or opposite to reticulate (fig. 3j), often with reduced borders or with more pronounced border and slitlike apertures (fig. 4a); intervessel pits are vestured (type B1-2) (fig. 4b), round to polygonal to elongate (figs. 3j, 4d). Vessel-ray and vessel-parenchyma pits similar to intervessel pitting, half-

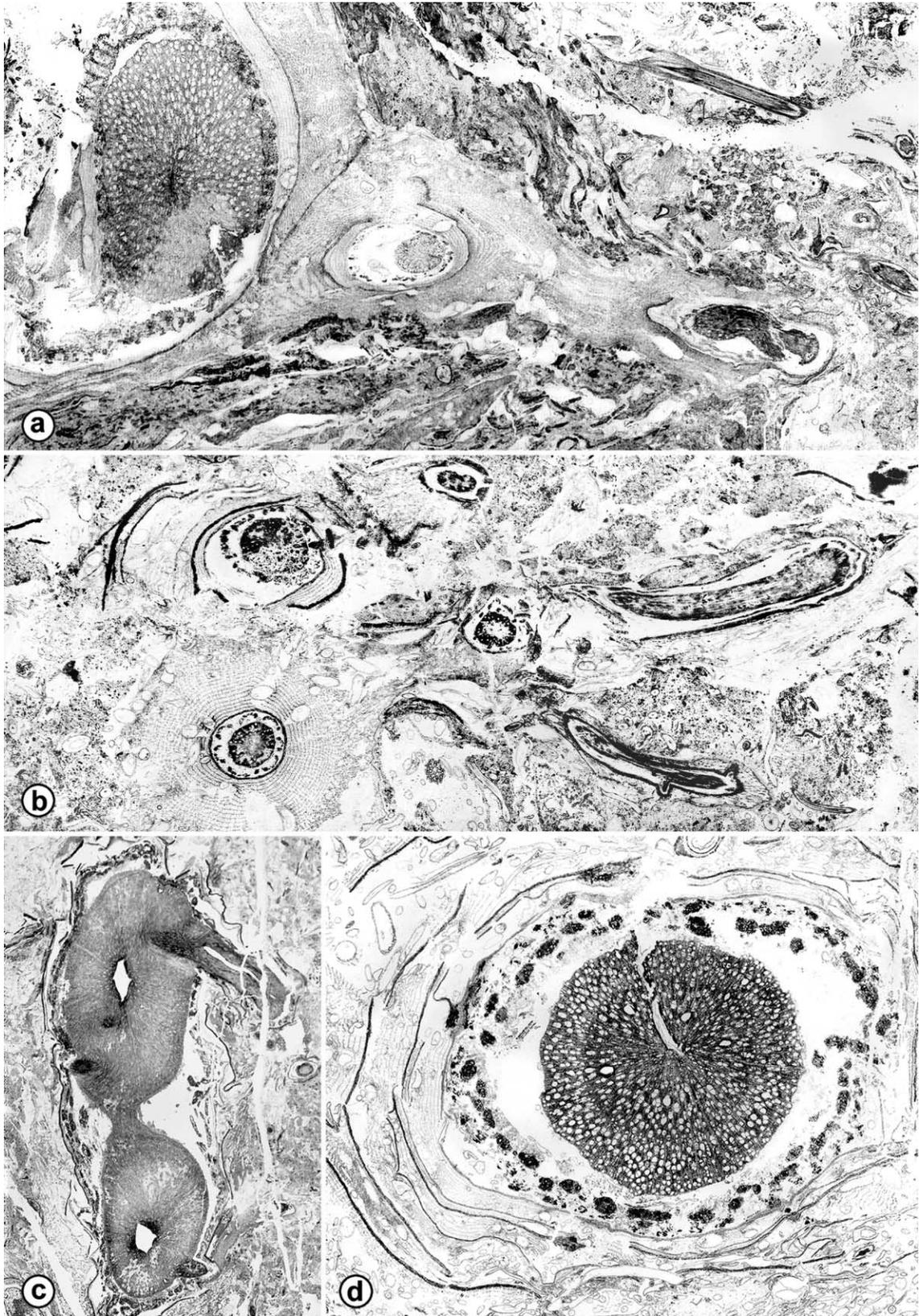


Fig. 1 *Decodon allenbyensis* rooting systems. *a*, Peel with transverse and oblique sections of branching roots producing thin-walled lacunate phellem. P5105 D bot #1a, $\times 6.6$. *b*, Transverse and longitudinal section of branching roots surrounded by thin-walled lacunate phellem. P5956 E bot #1b, $\times 8.6$. *c*, Transverse section of a submerged bent stem giving rise to adventitious roots. P6427 L top #1, $\times 2.4$. *d*, Transverse section of root showing phloem fiber bundles and positions of numerous dark bands of small rectangular cells in the lacunate phellem. P6019B #6, $\times 7.6$.

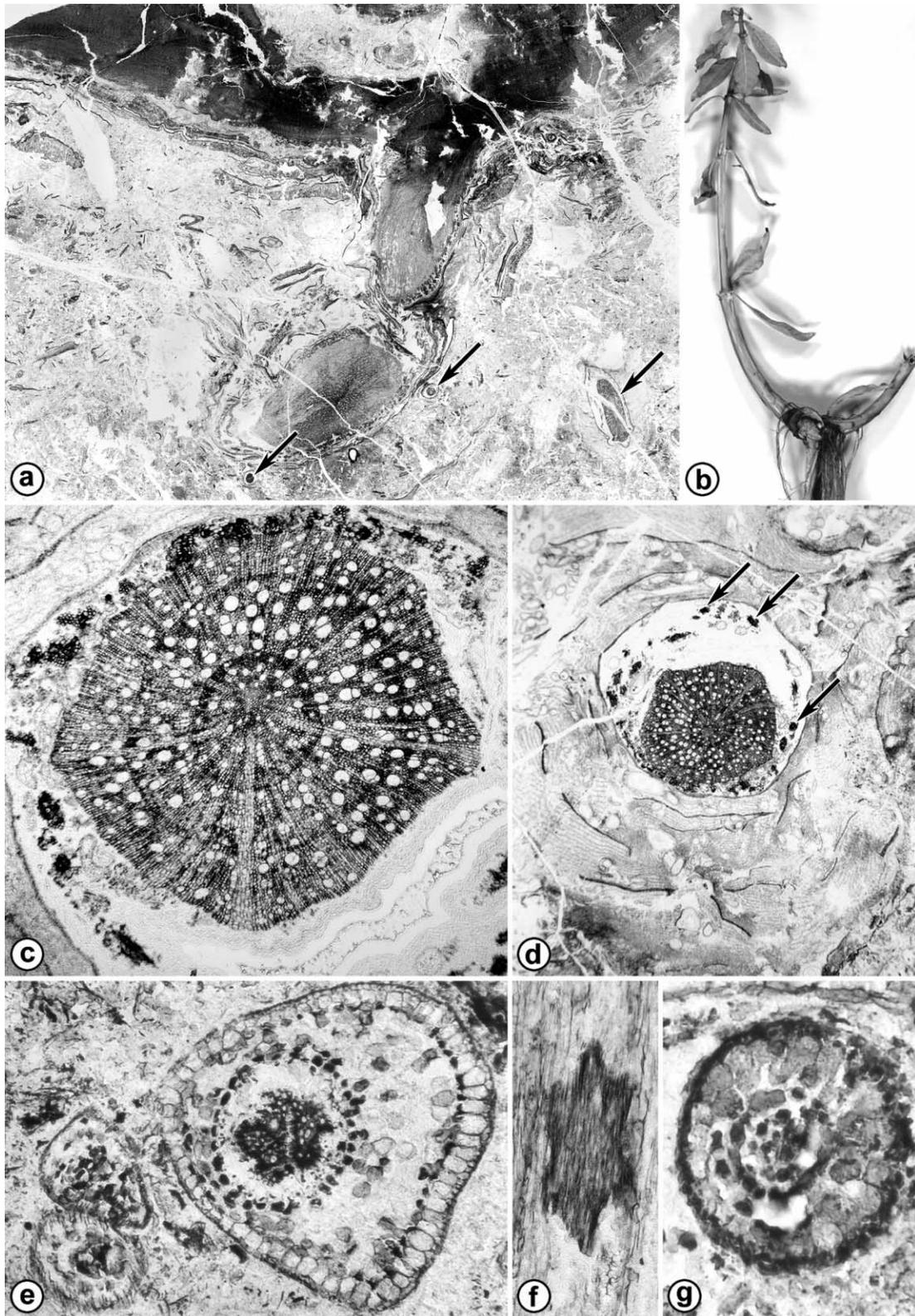


Fig. 2 *Decodon allenbyensis* and *Decodon verticillatus* stems and roots. *a*, Longitudinal section of a large degraded *D. allenbyensis* stem (at top) with branching adventitious roots. Arrows indicate young roots. P6427 L bot #6, $\times 1.4$. *b*, *D. verticillatus* stem with adventitious roots. $\times 1.8$. *c*, *D. allenbyensis* root, transverse section showing numerous bands of phellem. P5912 H top #1, $\times 28$. *d*, *D. allenbyensis* root stele showing diffuse porous wood with large-celled rays. Arrows indicate phloem fiber bundles. P5912 H top #1, $\times 9.2$. *e*, *D. allenbyensis* young roots in transverse section showing elongate hypodermal cells, aerenchymatous cortex, and pentarch stele at right. P6427 K bot #34, $\times 143$. *f*, *D. allenbyensis* hexarch root stele. P6427 K bot #56, $\times 74$. *g*, *D. allenbyensis* very small young root. P5956 E bot #1b, $\times 244$.

bordered and sometimes opposite to scalariform; some rays and axial parenchyma cells with perforations, not easily observed in fossils. Possible tyloses present in some axes (fig. 3*k*). Fibers up to 520 μm long, thin walled (2 μm thick) with simple pits, minute and not easily observed, occasionally septate (fig. 3*f*, 3*g*). Parenchyma scanty paratracheal and very scanty apotracheally diffuse, with fusiform strands of (1–)2–4(–5) cells. Rays ca. 10 per mm, 1–4(–5)-seriate, heterocellular with upright marginal cells and procumbent to square central cells (fig. 3*e*), with occasional sheath cells. Uniseriate rays often completely composed of upright cells with occasional procumbent to square central cells in some rays. Crystals not observable in fossil tissues.

***Decodon verticillatus*.** Young adventitious, aquatic roots of *D. verticillatus* (fig. 2*b*) commonly have pentarch or hexarch (fig. 4*e*) protosteles, occasionally septarch (fig. 4*c*). The endodermis is surrounded by an aerenchymatous cortex (fig. 4*b*), a prominent zone of elongate hypodermal cells, and very small epidermal cells (fig. 4*c*) as in *D. allenbyensis*. In all respects these roots are similar to those in the fossil material.

Roots of extant *D. verticillatus* with secondary tissues produce bundle fibers in the secondary phloem. Size ranges of both the bundles and individual cells are similar to those in the fossil material. Parenchyma cells of the secondary phloem contain abundant druses.

Extant *D. verticillatus* root wood description. Growth rings distinct. Wood is diffuse to semi-ring-porous (fig. 5*a*). Vessels number ca. (12–)22(–37) mm^2 , 35%–55% solitary or in radial multiples of 2–5(–6) or rarely in clusters of 3–6, round to oval or tending to angular, tangential diameter (30–)49(–62) μm , radial diameter up to 68 μm , the walls 2–4 μm thick. Vessel member length (132–)245(–430) μm . Perforations are simple in oblique end walls, with rare scalariform perforations found mainly at or near growth increments (fig. 4*f*, 4*g*). Intervessel pits 4–10(–20) μm , crowded, alternate or opposite to reticulate, often with reduced borders or with more pronounced border and slitlike apertures; intervessel pits vested (type B1-2), round to polygonal to elongate. Vessel-ray and vessel-parenchyma pits similar, half-bordered, sometimes opposite to scalariform, some ray and most axial parenchyma cells with perforations. Tyloses and vessel contents absent. Fibers up to 612 μm long, thin walled (2 μm thick) with simple minute pits, confined mainly to the radial walls, occasionally septate. Many fiber cells show nuclei and contain abundant oval starch grains. Parenchyma scanty paratracheal and very scanty apotracheally diffuse, with fusiform strands of (1–)2–4 cells. Rays ca. 10 per mm, 1–4(–6)-seriate, heterocellular with upright marginal cells and procumbent to square central cells (fig. 5*b*); rays with occasional sheath cells (fig. 5*c*). Uniseriate rays completely composed of upright cells with occasional procumbent to square central cells in some rays. Ray parenchyma cells may contain abundant oval starch grains. Crystals prismatic in ray parenchyma, more commonly in irregular clusters.

Phellem

***Decodon allenbyensis*.** Thin-walled, aerenchymatous, lacunate phellem surrounding woody axes was observed in many of the fossil root specimens (fig. 1*a*, 1*c*, 1*d*; fig. 2*d*; fig. 6*a*–6*d*). Nearly all fossil roots observed, excluding the youngest aeren-

chymatous roots, possess this lacunate phellem. Phellem is often extensive, up to 4 mm thick, even around small axes (fig. 1*a*, 1*b*). Concentric layers of several small rectangular, usually dark-colored, cells interrupt the regular pattern of lacunate phellem (fig. 2*d*; fig. 6*a*, 6*c*, 6*d*). These bands occur often, and at least 12 such bands of unelongated cells are present around some axes (fig. 6*d*). The regular lacunate phellem is composed of radially elongate cells that are T-shaped (fig. 6*c*). Small rectangular phellem cells separate the elongate cells, giving the aerenchymatous phellem a crosshatched appearance (fig. 6*a*–6*d*).

***Decodon verticillatus*.** Lacunate phellem closely resembles that in fossil roots (fig. 6*e*, 6*f*). This secondary growth is very delicate and spongy and does not maintain its integrity well even in paraffin histology. Cell types are the same as described for the fossil, with radially elongate T-shaped cells. Small rectangular cells separate the elongate cells (fig. 6*f*). Consecutive layers of compressed cells are also produced in *D. verticillatus*.

Stems

***Decodon allenbyensis*.** Many stem axes (fig. 1*c*; fig. 7*a*, 7*d*) were observed in close association with the fossil roots with thin-walled phellem. Some of these stems do not show sufficient anatomical characters for identification because of their age and often because of fungal degradation. Without organic connection of these young stems to other organs, it is not known if they represent inflorescence axes or twigs of other taxa. However, some isolated stems show sufficient anatomical characters to link them to the roots, and some are found in attachment.

Pith cells in *D. allenbyensis* are homocellular and are made up of isodiametric, or somewhat axially elongated, cells 20–70 μm in diameter (fig. 7*d*). Associated with the outer pith cells is a zone of what appears to be phloem tissue just internal to the wood. Many young stems are decorticated (fig. 7*d*); however, some show well-preserved extraxylary primary tissues (fig. 7*a*). These young stems have an undulating and angular, often square, outline in transverse section. The cortical cells often have prominent irregular air spaces between them (fig. 7*a*). A band of sclerotic cells is found to the outside of the phloem.

In addition to stems with lacunate phellem and adventitious roots, several woody stems were peeled because of their abundance and close association with *D. allenbyensis* roots. In stems with substantial secondary xylem, secondary phloem can also be well preserved (fig. 7*i*). Secondary phloem has phloem fiber bundles, similar in size and appearance to those seen in secondary phloem of fossil and extant roots.

Fossil stem wood description. Growth rings distinct (fig. 7*e*). Wood is diffuse to semi-ring-porous (fig. 7*d*, 7*e*). Vessels number ca. (25–)46(–86) mm^2 ; 4%–12% are solitary or in radial multiples 2–5(–7) or in clusters of 3–8, round to oval or tending to angular, tangential diameter (28–)70(–130) μm ; radial diameter up to 109 μm , walls 2–4 μm thick. Vessel member length (170–)275(–430) μm . Perforations are simple in oblique end walls. Intervessel pits 4–10(–20) μm , crowded, alternate or opposite to reticulate; intervessel pits with reduced borders, vested (type B1-2) and round to polygonal to elongate. Vessel-ray and vessel-parenchyma pits similar, half-

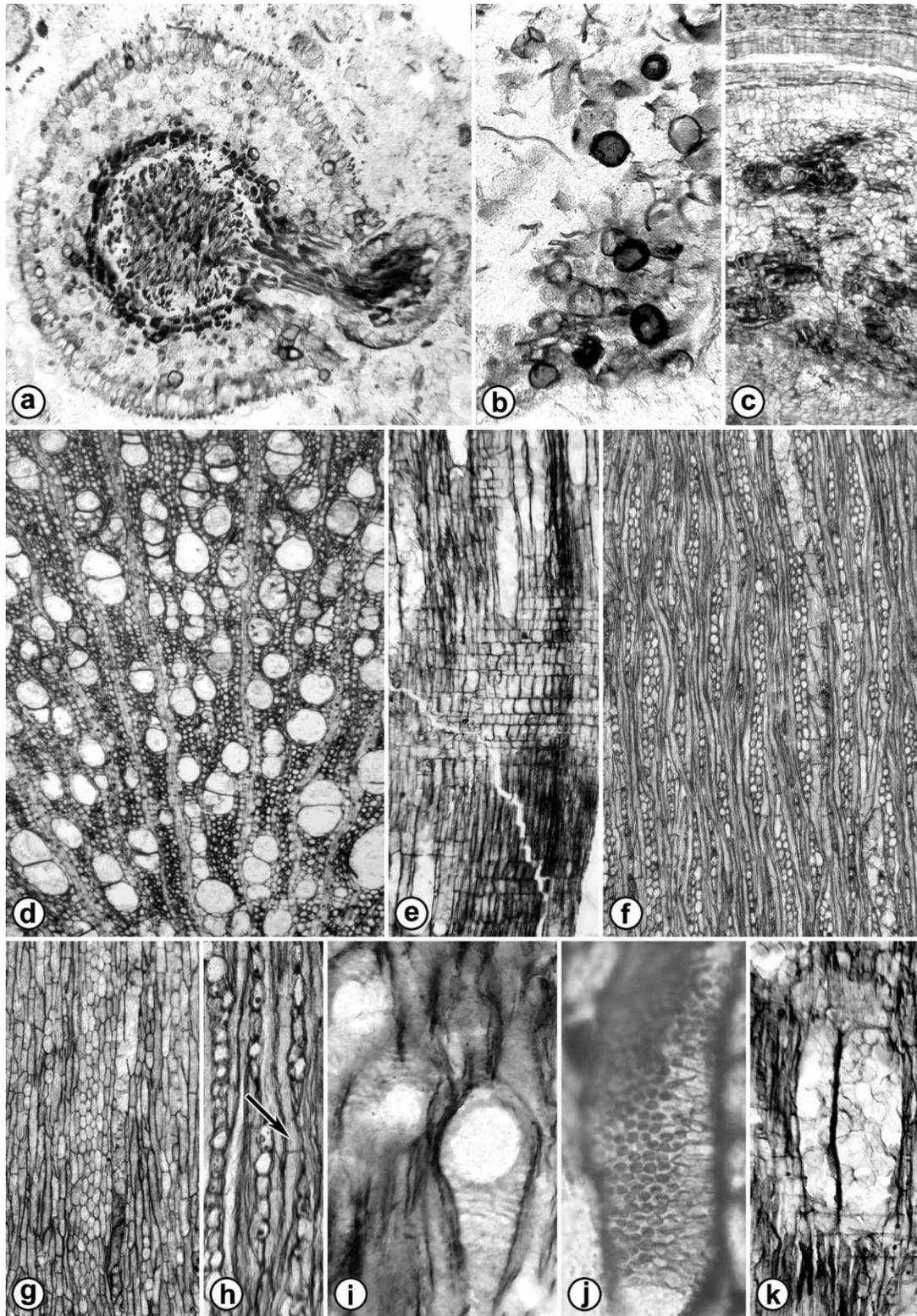


Fig. 3 Fossil *Decodon allenbyensis* roots. *a*, Transverse section of young branching root showing cortex with fungal chlamydospore-like structures and radially elongate hypodermal cells. P5956E bot #1b, $\times 95$. *b*, Transverse section of young root cortex showing numerous fungal hyphae and possible chlamydospores. P5956 E bot #1b, $\times 216$. *c*, Transverse section of phloem showing fiber bundles and periderm, at top. P6427 L bot #6, $\times 41$. *d*, Root wood, transverse section showing solitary vessels in radial multiples and rays with large cells. P6019 B #6, $\times 45$.

bordered, and sometimes opposite to scalariform, not easily observed in fossils. Possible tyloses present in some axes. Fibers up to 571 μm long, thin walled (2 μm thick) with simple fiber pits minute and not easily observed, occasionally septate. Parenchyma scanty paratracheal and very scanty apotracheally diffuse, with fusiform strands of (1–)2–4 cells. Rays ca. 10 per mm, 1–4(–5)–seriate (fig. 7g), heterocellular with upright marginal cells and procumbent to square central cells (fig. 7b); rays with occasional sheath cells. Uniseriate rays completely composed of upright cells with occasional procumbent to square central cells in some rays. Crystals not observable in fossils.

***Decodon verticillatus*.** Younger stems are nearly square or polygonal in cross section (fig. 7c). *Decodon verticillatus* has mainly opposite but also subopposite to verticillate branching, and leaves are also opposite to verticillate. Pith cells are homocellular and isodiametric or somewhat axially elongate and range from 12 to 92 μm in diameter (figs. 7c, 8a). Many of the parenchymatous cells in stems contain druses (fig. 8a, at arrow). There are irregular, aerenchymatous air spaces between the outer cortical cells in stems of *D. verticillatus* (fig. 7c), contributing to the shape of the undulating stem margin. A band of sclerotic cells is found to the outside of the phloem and is part of the primary cortex. These primary sclerotic cells are eventually sloughed off along with the cortex, because of phellem production.

Secondary phloem fibers that are produced by woody stems are similar in appearance and size range to those of extant roots and to those of fossil axes (fig. 7b). Abundant druses are observed in parenchyma cells of the secondary phloem (fig. 7b).

Stem wood of *D. verticillatus* was described by Baas and Zweypfenning (1979), and additional observations and measurements are reported here. This description adds new observations and extends the ranges of some quantitative measurements.

Extant stem wood description. Growth rings distinct. Wood is diffuse to semi-ring-porous (fig. 8c). Vessels number ca. (39–)60(–84) mm^2 , 6%–35% solitary or radial multiples of 2–5(–6) (fig. 8c, 8e) or rarely in clusters of 3–6, round to oval or tending to angular, tangential diameter (30–)49(–78) μm , radial diameter up to 80 μm , walls 2–4 μm thick. Vessel member length (109–)240(–490) μm . Perforations are simple in oblique end walls (fig. 7k; fig. 8b, 8d). Intervessel pits 4–10(–20) μm , crowded, alternate or opposite to reticulate, often with reduced borders or with more pronounced border and slitlike apertures; intervessel pits are vested (type B1-2) (fig. 8d, 8f), round to polygonal to elongate. Vessel-ray and vessel-parenchyma pits similar, half-bordered, and sometimes opposite to scalariform, ray and axial parenchyma cells rarely with perforations (observed only once out of several sections). Tyloses and vessel contents absent. Fibers up to 632(–700) μm (Baas and Zweypfenning 1979) long, thin walled (2 μm thick),

with simple, minute pits, confined mainly to radial walls, occasionally septate. Many fiber cells show nuclei and contain abundant oval starch grains. Parenchyma scanty paratracheal and very scanty apotracheally diffuse, with fusiform strands of (1–)2–4(–6) cells. Rays ca. 10 per mm, 1–4(–6)–seriate (fig. 7j), heterocellular with upright marginal cells and procumbent to square central cells (fig. 7f), with occasional sheath cells. Uniseriate rays often completely composed of upright cells with occasional procumbent to square central cells in some rays. Ray parenchyma cells may contain abundant oval starch grains. Crystals prismatic in ray parenchyma, often found as irregular clusters.

Habit

***Decodon allenbyensis*.** Large, sometimes partially crushed, axes exist with as many as 18 growth increments. They were at least 5–10 cm in diameter in life. Axes tend to be found in a horizontal orientation, near or dipping away from the coal at the top of the chert layer. The longest such axis known extends obliquely and completely through a 28.5-cm chert block. Typical branching root systems that produce delicate lacunate phellem are observed arising and extending downward from these large prostrate axes.

Discussion

Woody dicot roots with lacunate phellem are among the most common remains in layer 43 of the Princeton chert. Other vascular plants in this layer include two types of monocot seeds and several monocot vegetative organs. Dicot remains include seeds or crushed axes of *Eorhiza arnoldii* Robison and Person (1973) and seeds of *Allenbya collinsonae* Cevallos-Ferriz and Stockey (1989), Nymphaeaceae. Both of these taxa are rare in layer 43, and their vegetative remains are either known or unlikely to be similar to the vegetative material described here. Among the most common dicot remains are two myrtalean taxa based on fruits and seeds: *Decodon allenbyensis* Cevallos-Ferriz and Stockey (1988), Lythraceae, and *Paleomyrtinaea princetonensis* Pigg et al. (1993), Myrtaceae. The stems and roots described here, like many plants at Princeton, are *in situ* aquatics preserved in growth position (Cevallos-Ferriz et al. 1991). Therefore, we would expect all of the organs of this plant to be present in the layer.

Spongy, aerenchymatous tissues like those found in the fossil are also produced by several semiaquatic Lythraceae, Melastomataceae, Onagraceae, Fabaceae, and Euphorbiaceae (Schenck 1889). However, general wood features of the fossil, such as vested pits and intraxylary phloem, exclude Fabaceae and Euphorbiaceae and may indicate that the roots and stems investigated in this study are those of a member of Myrtales (Van Vliet and Baas 1984). Broad wood anatomical patterns

e, Root wood, radial longitudinal section showing heterogeneous rays with both upright and procumbent cells. P6288A #3, $\times 68$. f, Root wood, tangential section showing tall rays. P6427 L bot #11, $\times 63$. g, Root wood, tangential section showing five-seriate ray, center. P1303 C₁ side #2, $\times 45$. h, Root wood, tangential section showing septate fiber (arrow). P6427 L bot #11, $\times 144$. i, Vessel elements with simple perforations. P4947 A #12, $\times 500$. j, Vessel element showing crowded alternate pitting. P6427 L bot #11, $\times 441$. k, Root wood, radial section showing vessel elements with possible tyloses. P6288 A #3, $\times 104$.

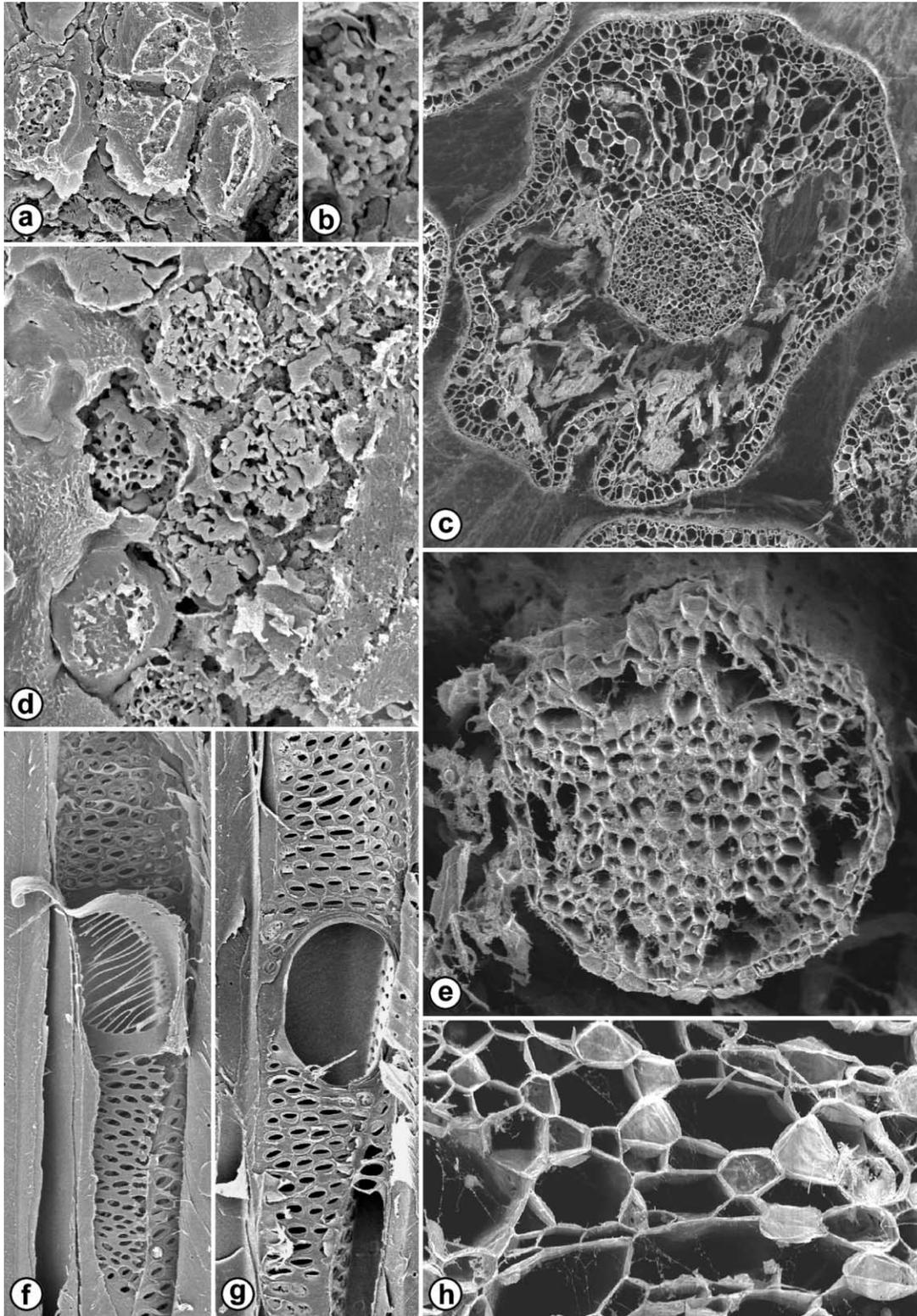


Fig. 4 *Decodon allenbyensis* (fossil) and *Decodon verticillatus* (extant) roots under SEM. *a*, *D. allenbyensis*, showing elongate-bordered pits with slitlike apertures and vestures. P1303 C₁ side #8, ×4212. *b*, *D. allenbyensis* enlarged vessel element pit cavity showing type B vesturing. P1303C₁ side #8, ×8712. *c*, *D. verticillatus* transverse section of young root showing stele, aerenchymatous cortex, and radially elongate

in Myrtales are discussed in depth by Van Vliet and Baas (1984), and this study helped us to exclude many families and subfamilies for the fossil wood.

The fossil wood described here has vessels in radial multiples and lacks fiber tracheids. Within Myrtales, Penaeaceae; Melastomataceae, subfamily Memecyloideae and Combretaceae, subfamily Strephonematoideae have wood with exclusively solitary vessels, or nearly so, that co-occur with fiber tracheids (Van Vliet and Baas 1984). Vessels in radial multiples occur in Melastomataceae, subfamily Crypteronioideae, but these taxa also have fiber tracheids (Van Vliet and Baas 1984). Combretaceae, subfamily Combretaceae, while they can have vessels in radial multiples and scanty paratracheal parenchyma, like the fossils, also have aliform, banded, or confluent and infrequently marginal parenchyma, mostly uniseriate rays composed of mainly procumbent cells, and large idioblasts in ray and axial parenchyma (Van Vliet 1978; Van Vliet and Baas 1984). These axial parenchyma patterns, rays, and idioblasts are absent from the fossil wood.

Vegetative remains of Myrtaceae are likely to occur in layer 43 because of the presence of fruits and seeds of *P. princetoniensis*. Myrtaceous wood typically has solitary vessels, often forming oblique patterns. *Xanthomyrtus* Diels (subfamily Myrtoideae), *Eucalyptopsis* C.T. White, and *Eucalyptus* L'Herit. (subfamily Leptospermoideae), however, have vessels in radial multiples and lack fiber tracheids (Van Vliet and Baas 1984), like the fossil wood. These genera have aliform to confluent wood parenchyma (Van Vliet and Baas 1984), in contrast to the fossil wood with scanty paratracheal parenchyma. Thus, it is unlikely that these axes represent the vegetative remains of *P. princetoniensis* or other Myrtaceae.

Heteropyxis Harv. and *Psiloxylon* Thou. ex Tul. historically have been placed in various orders and families, including Myrtaceae, based on detailed morphological characters (Schmid 1980). Based on *rbcL* sequence data, these two genera have been included in a clade that contains Myrtaceae and Vochysiaceae (Conti et al. 1997). *Heteropyxis* is reported to lack axial parenchyma, and both *Heteropyxis* and *Psiloxylon* have fibers with distinctly bordered pits (Schmid 1980), differing from the fossil wood with scanty paratracheal parenchyma and libriform fibers. However, *Psiloxylon* is also reported to have fibers with minute pits (Van Vliet and Baas 1984). In Vochysiaceae, axial parenchyma is vasicentric or commonly in paratracheal bands (Cronquist 1981), whereas the fossil wood has scanty paratracheal parenchyma. These taxa are unlikely to be related to the fossil plant since they are not aquatics nor are they reported to produce spongy lacunate phellem.

In the Conti et al. (1997) *rbcL* gene tree, the genera *Rhynchochalyx* Oliver, *Alzatea* Ruiz & Pav., *Olinia* Thunb., and *Penaea* L. form a clade sister to the Melastomataceae, and

Rhynchochalyx and *Alzatea* appear as sister groups, based on the morphological analysis of Johnson and Briggs (1984). *Rhynchochalyx*, *Alzatea* and *Olinia*, each in a monogeneric family, have wood anatomy similar to Lythraceae, and wood descriptions for *Rhynchochalyx* and *Alzatea* were included in Lythraceae (Van Vliet and Baas 1984). However, these African and Central to South American taxa are trees or shrubs and are not reported to be aquatics (Cronquist 1981; Graham 1984; Johnson and Briggs 1984). In addition, *Rhynchochalyx* has thin-walled fibers surrounding the vessels; *Alzatea* has coarse, elongated, simple vessel-ray pits (Baas 1979; Baas and Zweypfenning 1979). Therefore, these genera are unlikely to be closely related to the fossil plant.

Some Melastomataceae have been reported to produce aerenchyma from a phellogen (Schenk 1889). *Rhynchanthera dichotoma* DC and *Acisanthera variabilis* Triana have phellem similar to that produced by extant *Decodon* and the fossil plant. The fossil wood has already been excluded from subfamilies Memecyloideae and Crypteronioideae (see discussion toward the beginning of this section). Subfamily Melastomatoideae has alternate, plus elongate and curved or scalariform intervessel pitting. Fibers in this subfamily also tend to be dimorphic, where some fibers appear parenchyma-like and are distributed in narrow tangential arcs or in confluent and banded patterns (Van Vliet and Baas 1984). This plant is unlikely to be a member of Melastomataceae, since this type of intervessel pitting and fiber type are absent in the wood.

Onagraceae and Lythraceae are sister groups in the Conti et al. (1997) *rbcL* phylogenetic study and have very similar basic wood anatomy (Van Vliet and Baas 1984). Many Onagraceae are herbaceous or only produce small amounts of secondary xylem (Carlquist 1975); however, some taxa may be shrubs and small trees, e.g., *Ludwigia anastomosans* (DC) Hara (Carlquist 1987). The Onagraceae also has aquatic taxa that produce lacunate phellem. Some species of Onagraceae have included phloem, and some also have elongate and curved intervessel pitting, but this is not common to all taxa in the family (Carlquist 1975, 1977, 1982, 1987). Some species of *Ludwigia* L. lack both of these wood characters, having wood similar to Lythraceae. Therefore, the presence of lacunate phellem and similarity of wood characters in both Lythraceae and Onagraceae make identification of the fossil to one or the other of the families difficult, even though certain characters, such as included phloem and irregular curved intervessel pitting, exclude many Onagraceae.

Most Onagraceae that do produce aerenchyma do not show the same cellular organization in this tissue as in the fossil; however, some species of *Ludwigia* (= *Jussiaea*) are reported to have spongy lacunate phellem produced on submerged axes (Schenk 1889). Ellmore (1981) states that *Ludwigia peploides* (Kunth) P.H. Raven only produces true lacunate phellem on

hypodermal cells; freeze fractured in cryo-SEM. Decrt00, $\times 45$. *d*, Fossil vessel element wall showing mold-casts of alternate pits with type B vestures. P1303 C₁ side #8, $\times 5940$. *e*, Transverse section of young extant *Decodon* root with hexarch stele and endodermis; freeze fractured in cryo-SEM. Decrt06, $\times 293$. *f*, Longitudinal section of extant *Decodon* root wood, showing vessel element with scalariform perforation plate and alternate pitting. Decrt101 stub#2, $\times 540$. *g*, Longitudinal section of root wood, showing vessel element with simple perforation plate and alternate pitting. Decrt105 stub#3, $\times 1251$. *h*, Transverse section of aerenchymatous primary cortex in young root of extant *Decodon*; freeze fractured in cryo-SEM. Decrt02, $\times 329$.

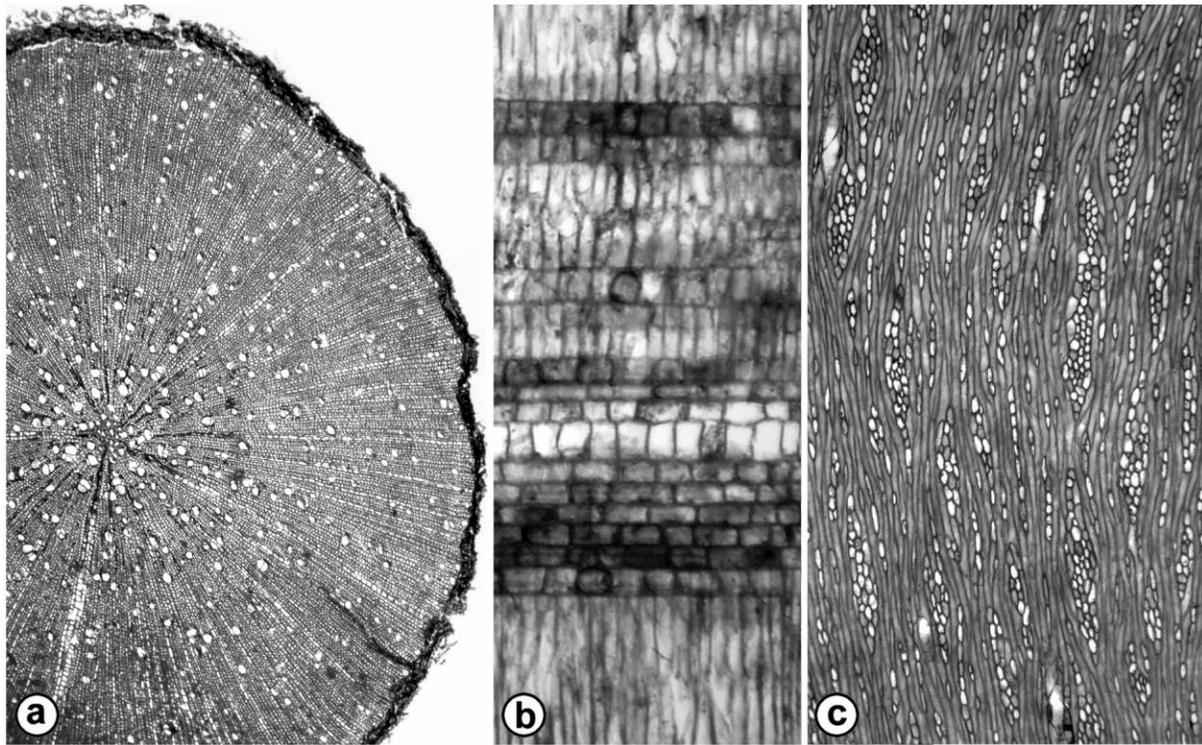


Fig. 5 *Decodon verticillatus* root wood anatomy. *a*, Transverse section showing diffuse porous wood and rays with large cells. SL12720, $\times 25$. *b*, Radial longitudinal section showing heterocellular rays with upright and procumbent cells. SL12721, $\times 112$. *c*, Tangential longitudinal section showing unicellular and multicellular rays. SL12722 $\times 55$.

lateral submerged stems that grow out across the water. The downward-growing adventitious roots arising from lateral submerged stems do not produce aerenchymatous tissues (Ellmore 1981). A tissue similar to lacunate phellem, presumed to improve aeration to the submerged organs, is produced by the upward-growing adventitious roots (Ellmore 1981). The aerenchyma of these upward-growing roots was observed by Ellmore (1981) to be derived from the regular radial elongation of primary cortical cells, emulating the organized pattern of lacunae seen in aerenchyma derived from a phellogen. Schenck (1889) also reports that aerenchyma is produced from the *primäre Rindenparenchym* (primary cortex) in the submerged adventitious roots of *Ludwigia* spp. Upward-growing roots do not produce true phellem or secondary xylem (Ellmore 1981; Schenck 1889). All our fossil roots appear to have been downward growing, and all lacunate tissues are produced by a phellogen on roots with secondary xylem. Schenck (1889) reports that downward-growing roots of other *Ludwigia* species, however, do produce lacunate phellem.

Downward-growing roots in Onagraceae that become aerenchymatous begin by producing lacunate, phellem-like tissue derived from primary cortex in the same way as upward-growing roots. However, these roots will eventually begin producing true lacunate phellem from a phellogen arising in the pericycle (Schenck 1889; Ellmore 1981). It is clear from our observations of the fossil roots and those of *Decodon verticillatus* that the primary cortex produces a network of air spaces within the bounds of the epidermis, and a true phel-

logen-producing lacunate phellem is the only source of the organized crosshatched aerenchyma. The fossil roots probably produced a phellogen in the pericycle, as in extant *D. verticillatus*, that co-occurs with secondary vascular tissue production. This developmental pattern in downward-growing roots is not known in Onagraceae.

Within Lythraceae aerenchymatous tissue produced by a phellogen on submerged axes has been reported for *Lythrum* L., *Peplis* L., *Ammannia* L., *Cuphea* P. Browne, *Heimia* Link et Otto, *Pleurophora* D. Don, and *Decodon* J.F. Gmelin (Schrenk 1889; Graham 1964; Sculthorpe 1967; Stevens et al. 1997; Lempe et al. 2001). *Peplis* is an herbaceous genus (Graham 1964) and is therefore unlike the woody fossil. *Ammannia* is generally thought of as herbaceous but produces small amounts of wood (Baas and Zwegpfenning 1979). *Ammannia* has nonseptate fibers and uniseriate rays, differing from the fossil that has septate fibers and multiseriate rays. *Cuphea* usually also has uniseriate rays, except for *Cuphea speciosa* (Anders.) Kuntze that has 1–4-seriate rays (Baas and Zwegpfenning 1979). However, in *Cuphea* the axial parenchyma is in strands of one or two cells, unlike the fossil that has axial parenchyma in strands of two to four cells. *Heimia* and *Pleurophora* produce lacunate phellem with cells elongating in an irregular pattern (Schrenk 1889; Lempe et al. 2001), differing from the regular appearance of the fossil phellem. *Pleurophora* and *Heimia* have vascular tracheids, and *Heimia* also has well-marked spiral thickenings on the tracheary elements (Baas and Zwegpfenning 1979; Baas 1986). Vascular tracheids and spiral

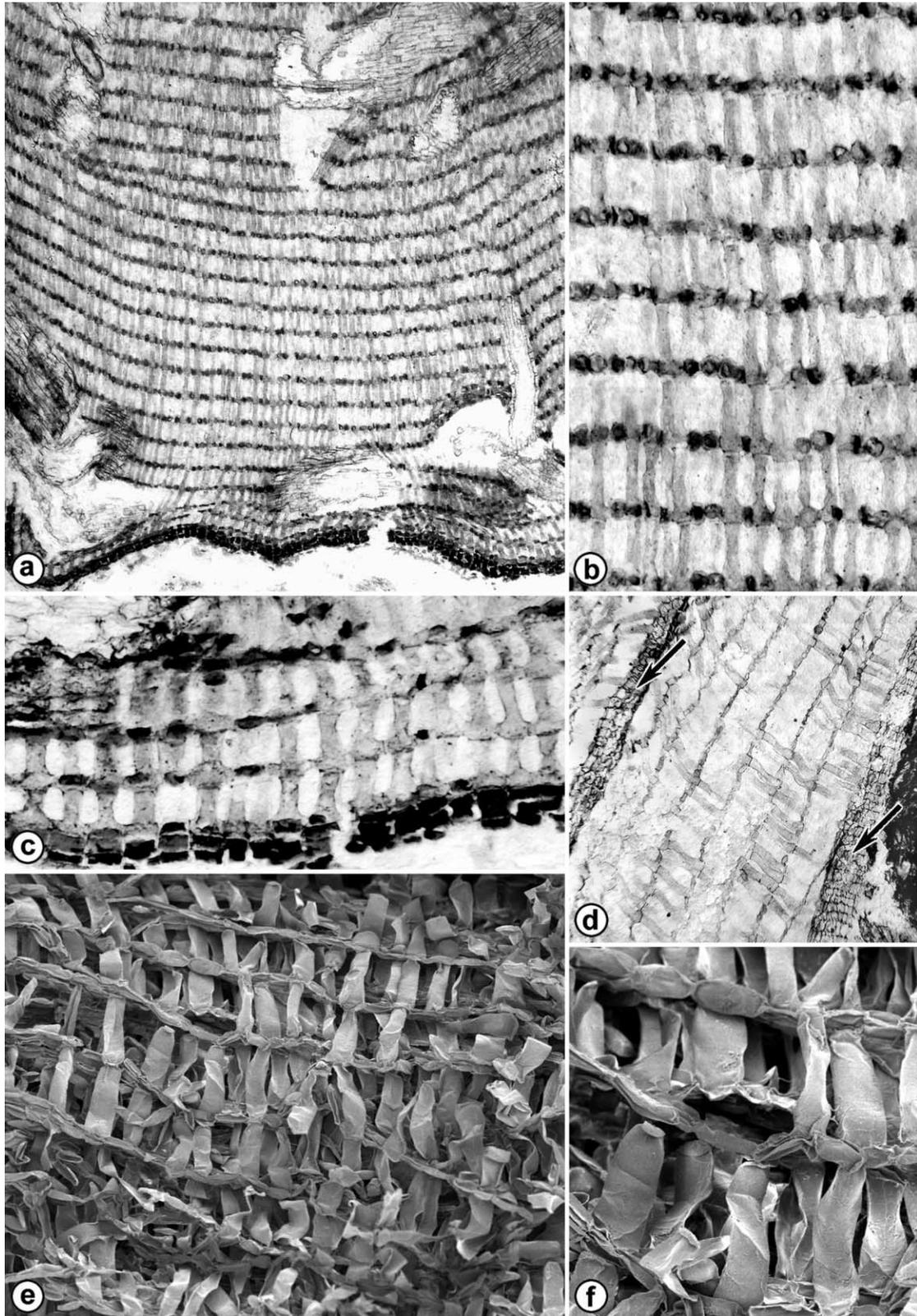


Fig. 6 Phellem of fossil and extant *Decodon*. *a*, *Decodon allenbyensis* thin-walled lacunate phellem. P6288 A #3, $\times 51$. *b*, Transverse section of *D. allenbyensis* phellem showing regular pattern of lacunae. P6288 A #3, $\times 149$. *c*, Phellem of *D. allenbyensis* showing radially elongated T-shaped cells and unelongated cells with dark contents (bottom). P6288 A #3, $\times 214$. *d*, Lacunate phellem of *D. allenbyensis* showing unelongated rectangular cells (arrows). P5105 D bot #2, $\times 79$. *e*, *Decodon verticillatus* lacunate phellem under critical-point drying and SEM. Decphl01 stub#6, $\times 97$. *f*, *D. verticillatus* phellem showing branched, T-shaped cells and lacunae under critical-point drying and SEM. Decphl02 stub#6, $\times 125$.

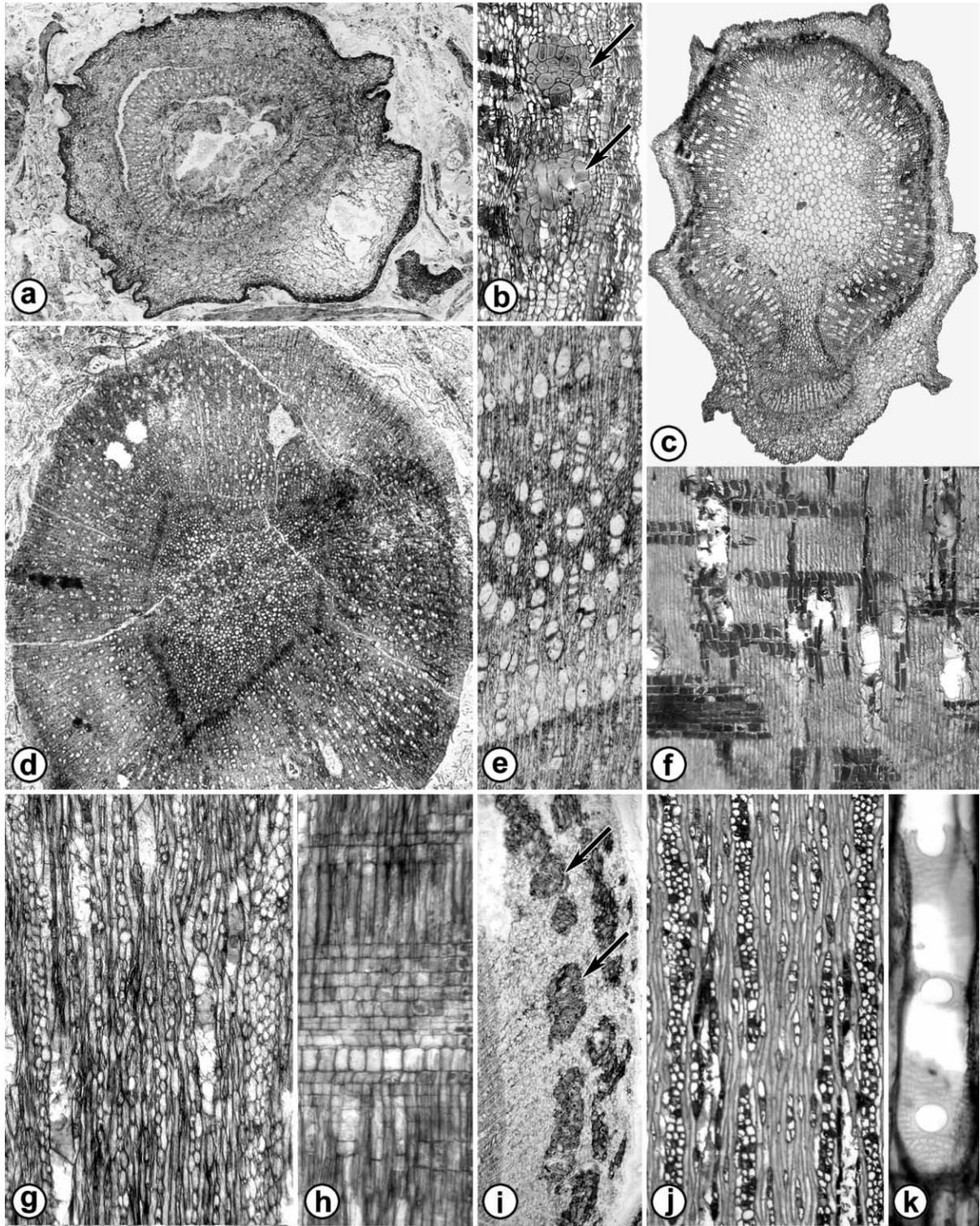


Fig. 7 Extant and fossil *Decodon* stems. *a*, Transverse section of young *Decodon allenbyensis* stem with well-preserved cortical tissues. P6394 G bot #0, $\times 12$. *b*, Transverse section through *Decodon verticillatus* secondary phloem and periderm, showing phloem fiber bundles (arrows). SL12725, $\times 65$. *c*, Transverse section of *D. verticillatus* young branching stem. SL12726, $\times 30$. *d*, Transverse section of decorticated stem of *D. allenbyensis* showing pith and diffuse porous wood. P5949 B bot #1a, $\times 15$. *e*, Transverse section of *D. allenbyensis* wood with three growth

thickenings on tracheary elements are not observed in the fossil wood.

The only other taxa of Lythraceae known to produce similar spongy tissue to the fossil are *Lythrum* and *Decodon*. There are no known qualitative differences reported by Lempe et al. (2001) in the structure of the lacunate phellem produced by *Lythrum* spp. and *D. verticillatus*, both with phellem similar to the fossil. However, Schrenck (1889) observed occasional concentric layers of compact suberized cells in the phellem of *D. verticillatus*. He suggested that these suberized layers prevent aeration of submerged axes since the suberized cell layers would seal off the stem from both the environment and the inner axis. He suggested, therefore, that the lacunate phellem was important for flotation. We have also seen these suberized layers in both living *Decodon* and the fossil plants and interpret them to be evidence of consecutive phellogens. This sort of occasional compact cell layer is not reported in *Lythrum* (Schrenck 1889). The production of consecutive phellogens may contribute to the ability of the *Decodon* to produce large amounts of lacunate phellem.

The wood anatomy in *Lythrum* spp. is very similar to *Decodon*, but *Lythrum* differs in having exclusively uniseriate rays and occasionally unilaterally compound vessel-ray and vessel-parenchyma pitting (Baas and Zweypfenning 1979). The fossil and *D. verticillatus* often have bi- to triseriate or wider rays and lack unilaterally compound vessel-ray and vessel-parenchyma pitting.

When we compare fossil axes with those of extant *D. verticillatus*, similarities are obvious. Both plants possess young adventitious roots that have pectate to septate primary xylem, with an aerenchymatous cortex and a radially elongate hypodermal layer. The fossil and extant plants possess large fiber bundles in secondary phloem and multiple phellogens that produce lacunate phellem on submerged roots and stems. Pith cells are of similar size and shape, and primary cortical tissues are similar in both taxa.

Fungi are particularly abundant within these fossil plant remains and within the chert in general (Currah and Stockey 1991; LePage et al. 1994, 1997; Hill-Rackette et al. 1995; Currah et al. 1998). We did not observe similar structures in young extant roots. There is a possibility that the large number of hyphae and chlamydospore-like structures found in the youngest roots in the chert represent mycorrhizal fungi, as have been reported in other Lythraceae (K. J. Stevens, personal communication, 1999).

Secondary xylem in *D. verticillatus* and the fossil have similar qualitative characters including distinct growth rings, diffuse to semi-ring-porous wood, vessels with simple perforations, vessels in radial multiples of two to five, similar intercellular pitting patterns, type B1-2 vesturing on intervessel pits, septate fibers, scanty paratracheal axial parenchyma in

strands of two to four, and number of rays per square millimeter. Both taxa have root wood with some intervessel pits that have slitlike apertures. Perforated axial parenchyma and rare perforated ray parenchyma in the root wood of extant *D. verticillatus* are also present in the fossil root wood although they are difficult to observe. Perforated axial parenchyma is a new character within Lythraceae and appears unique to the fossil and extant *Decodon*.

The fossil wood and the wood of *D. verticillatus* differ in some qualitative characters. Fossil axes possess tyloses, whereas extant *D. verticillatus* lacks tyloses. Extant *Decodon* root wood has occasional scalariform perforations, while scalariform perforations were not seen in vessel elements of the fossil root wood.

There are quantitative differences between the root wood and the stem wood of *D. verticillatus* in vessel widths, vessel density, and percentage of grouped vessels. *Decodon verticillatus* has more solitary vessels and fewer per square millimeter in its roots than in its stems. It is important to note that *D. verticillatus* stem material studied in depth for wood anatomy came from a wild population growing on the margin of Wingfoot Lake (near Kent, Ohio), in contrast to the root material that came from greenhouse-grown plants. Greenhouse plants grew in soil and had regular watering, whereas wild-grown plants were subjected to fluctuation in water levels as they grew on the margin of the lake. Increasing vessel grouping and vessel density in wood during times of increased water stress may prevent embolisms in woods that lack tracheids associated with vessels (Carlquist 1988). In greenhouse-grown plants, root wood vessel width is narrower than that in stems from plants growing near the lake. Greenhouse conditions would not have given the plants access to a large volume of water at any one time; therefore, they would have been unable to produce vessels as wide as a submerged plant. Wood with narrower vessels is less efficient in water conduction, but plants are less likely to develop embolisms (Ewers 1985).

The fossil roots and stems have a less pronounced difference in the vessel densities; however, the fossil wood shows a marked increase in the proportion of vessels in groups for the stems versus roots. Vessel diameter tends to be wider in the roots compared with diameters in stems. Vessels are expected to be longer and wider in the roots than in the stems of a given species (Carlquist 1978). Since the roots observed were submerged in water, it would be expected that these axes would be under little water stress; however, the stems are farther away from the water source, and therefore we would expect them to have anatomical adaptations to mitigate the effects of water stress. Increasing the percentage of grouped vessels allows for adjacent vessels to maintain the water column in case of an embolism (Carlquist 1988). The similarity of vessel density in

increments showing vessels solitary and in radial multiples. P1982 D bot #1b, $\times 100$. *f*, Radial longitudinal section of *D. verticillatus* wood, showing upright and procumbent cells of heterocellular ray. SL12729, $\times 50$. *g*, Tangential longitudinal section of *D. allenbyensis* wood showing both narrow and wide, often tall, rays. P6427 K bot #56, $\times 45$. *h*, Radial longitudinal section of *D. allenbyensis* wood showing upright, weakly procumbent, and procumbent cells of heterocellular ray. P6427 K bot #24, $\times 80$. *i*, Transverse section of *D. allenbyensis* phloem. Arrows indicate fiber bundles. P6427 K bot #57, $\times 60$. *j*, Tangential longitudinal section of *D. verticillatus* wood showing narrow and wide, often tall, rays. SL12732, $\times 60$. *k*, *D. verticillatus* vessel elements with simple perforations. SL12733, $\times 300$.

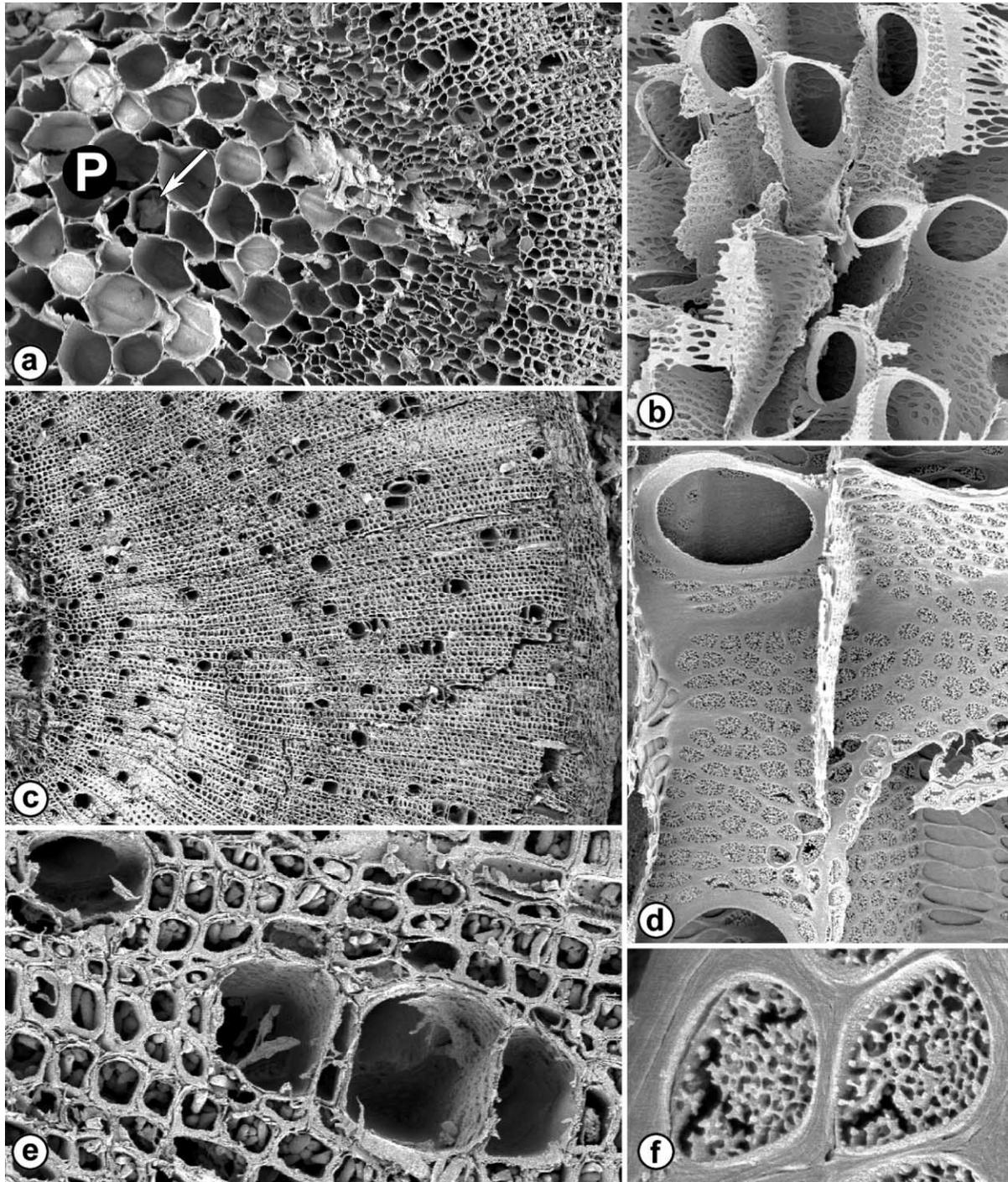


Fig. 8 *Decodon verticillatus* stem wood under SEM. *a*, Transverse section showing pith (*P*) and wood. Arrow indicates druse. Decxs04 stub#1, $\times 90$. *b*, Tangential longitudinal section showing vessel elements with simple perforations. Decod22 stub#10, $\times 420$. *c*, Transverse section with vessels solitary and in radial multiples. Decxs01 stub#1, $\times 70$. *d*, Tangential longitudinal section showing vessel elements with alternate vestured pitting and simple perforations. Decod21 stub#11, $\times 860$. *e*, Transverse section showing oval starch grains in fibers, a single vessel element (upper left), and radial multiple of four. Decxs02 stub#1, $\times 540$. *f*, Tangential longitudinal section of wood showing type B vestured pits. Decod17 stub#11, $\times 7250$.

the fossil roots and stems may indicate that water levels were steady over the growing season.

There are differences between extant and fossil plants in percent vessel grouping, vessel density, and vessel width; however, the ranges of these values overlap between the fossil and extant woods. Therefore, we treat these differences in wood anatomy as evidence of minor environmental variations. These data indicate that, compared with the extant plants sectioned for comparison, the fossil plants were subject to stable water levels.

We consider the fossil axes described here to be those of *Decodon* because of the anatomical and developmental characters shared with living *D. verticillatus*. In addition, Baas and Zweypfenning (1979, p. 122) note that within Lythraceae, *D. verticillatus* has relatively large ray cells, "creating a characteristic histology as seen in transverse and tangential sections." Although this is a somewhat subjective character, we note that the ray cells in the fossil wood also appear large, causing the rays to look quite large in transverse and tangential sections. In particular, these fossil *Decodon* axes are considered to be the vegetative organs belonging to *D. allenbyensis* because of the abundance and close association of these *in situ* preserved axes with the fruits and seeds of *D. allenbyensis*.

The growth habit of the fossil appears to have been similar in all respects to that of living *D. verticillatus*. This plant probably grew near the water's edge, forming procumbent stems over the water, spongy buoyant phellem, and adventitious roots growing down into the water, as is seen in the only extant species of *Decodon* (Graham 1964; Sculthorpe 1967). These plants also probably formed similar thickets in and around the water margin.

Decodon allenbyensis has axes with up to 18 growth increments that are at least 5–10 cm in diameter. In contrast, the "typical" stems of extant *D. verticillatus* (S. A. Graham, personal communication, 2002) range from 2 to 4 cm in diameter, including several branching roots. In more established populations or populations growing in warmer climates, stems may get significantly wider (C. Eckert, personal communication, 2002). However, upper ranges of diameters for *D. verticillatus* have not been recorded or published. Therefore, we can only conclude that the fossil *D. allenbyensis* may have been a larger plant than *D. verticillatus*, but at the very least, the fossil was a well established plant, producing substantial wood.

Morphological cladistic analyses of Lythraceae (Graham et

al. 1993) and molecular cladistic analysis using *cpDNA* (Conti et al. 1999) show that relationships are not clear within this family. Even with the addition of *nrDNA* ITS and *psaA-ycf3* spacer sequence data, some of the relationships in Lythraceae are still not well supported (Shi et al. 2000; Huang and Shi 2002). Therefore, *D. allenbyensis* may provide invaluable data for future analyses and phylogenetic understanding of Lythraceae.

Leaves have not yet been found attached to *D. allenbyensis* stems, but large numbers of dicot leaves have been found in close association with stems and roots (Little and Stockey 2002) and are currently under study. As the reconstruction of *D. allenbyensis* is completed, it will become increasingly valuable for cladistic analyses based on morphological characters. These will be the subject of further investigations.

Decodon allenbyensis adds to the detailed and rich data set already known for the Princeton chert. The characteristic aquatic anatomy of the plant provides additional evidence that this locality preserves a wetland community of the Middle Eocene. Cevallos-Ferriz et al. (1991) discussed the aquatic nature of the Princeton chert and summarized the numerous plants that were growing in place and preserved *in situ*. The excellent preservation of abundant delicate lacunate phellem of *D. allenbyensis* supports the argument that this species was preserved *in situ*. *Decodon allenbyensis* probably displayed a similar life history pattern to extant *Decodon*, rooting at the margin of a quiet body of fresh water and growing out over the surface.

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