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MORPHOGENESIS OF THE SPECIALIZED PERIDERMAL TISSUES IN *DECODON ALLENBYENSIS* FROM THE MIDDLE EOCENE PRINCETON CHERT

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SUMMARY

Aquatic tissues in the submerged axes of *Decodon allenbyensis* Cevallos-Ferriz *et* Stockey are investigated and described in detail. Numerous well-preserved roots have primary aerenchymatous cortex and no secondary vascular tissues while other axes show transitions to secondary xylem and phloem, as well as periderm composed of thin-walled lacunate phellem. Phellem appears similar to the primary aerenchyma seen in aquatic roots of species of *Ludwigia* L.; however, similar lacunate tissue in extant *Decodon verticillatus* (L.) Ell. is secondary (phellem) and this study shows this tissue to be homologous to that seen in the fossil *Decodon* J.F. Gmel. A complex rhytidome is described in the largest fossil axes. It is composed of alternating bands of 'phelloids' and bands of non-active phloem with lacunae. This complex aquatic rhytidome is currently unknown in other living or fossil taxa.

Key words: Fossil stems, phellem, phelloids, rhytidome, Lythraceae.

INTRODUCTION

The term 'aerenchyma' was originally coined by Schenck (1889) to describe lacunate tissue derived from a phellogen (Ellmore 1981). Such tissues, also called lacunate phellem (Lempe *et al*. 2001), are found in numerous aquatic and semi-aquatic plants (Schenck 1889; Sculthorpe 1967). Lacunate phellem occurs in several semi-aquatic taxa in Lythraceae, Melastomataceae, Onagraceae, Euphorbiaceae (Schenck 1889), Myrtaceae (Cook *et al*. 1980), and Fabaceae (Schenck 1889; Shimamura *et al*. 2002, 2003). Recent work by Stevens *et al*. (2002) on *Lythrum salicaria* L. (Lythraceae) has established the first direct evidence for gaseous connection between shoots and submerged roots via lacunate phellem.

Lythraceae, an angiosperm family of 31 genera and 600 species (Graham 1964; Graham *et al*. 1993; Judd *et al*. 1999) has several taxa with lacunate phellem. *Decodon verticillatus* (L.) Ell. is known to produce abundant lacunate phellem in submerged conditions (Schrenk 1889; Graham 1964; Lempe *et al*. 2001). Recently the anatomically preserved aquatic roots and stems of the fossil plant *Decodon allenbyensis* Cevallos-Ferriz *et* Stockey 1988, were described, and well-preserved aerenchymatous tissues were shown (Little & Stockey 2003). This study describes, in detail, the development of aquatic tissues in submerged axes of *Decodon allenbyensis*. Transitions from primary

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tissue organization to the development of secondary tissues are illustrated and a novel rhytidome system is described.

MATERIALS AND METHODS

Permineralized *Decodon* axes come from the Princeton Chert (Allenby Formation), located on the east bank of the Similkameen River approximately 8.4 km southwest of the town of Princeton, British Columbia (UTM 783724; 49° 22.7' N, 120° 32.7' W). The locality is dated as Middle Eocene, based on data from pollen (Rouse & Srivastava 1970), fossil mammals (Russell 1935; Gazin 1953), fish (Wilson 1977, 1982), and potassium-argon dating (Hills & Baadsgaard 1967; H. Baadsgaard, pers. commun. 1999).

Chert slabs were prepared using the cellulose acetate peel technique (Joy *et al.* 1956) modified for hydrofluoric acid (Basinger & Rothwell 1977; Basinger 1981). Specimens (SL12708–SL123104) are housed in the University of Alberta Paleobotanical Collection (UAPC-ALTA). Peel sections were mounted with Eukitt rapid mounting medium (O. Kindler GmbH & Co., Freiburg, Germany) for microscopic examination. Images were taken with a Microlumina (Leaf Systems, Inc.) 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.

RESULTS

Numerous interconnected branching roots of *Decodon allenbyensis* were described by Little and Stockey (2003). Roots arise adventitiously from stems, and many of these have tissues typical of aquatic plants. Stems and roots without aerenchymatous tissues also occur in the chert, but most of the remains have either an aerenchymatous primary cortex or lacunate phellem. Further observations on the development of the tissues in aquatic axes are described below.

Primary growth

Abundant small roots lacking secondary tissues are found both isolated in the chert matrix and attached to larger woody axes (Fig. 1a–d). Exarch actinosteles are surrounded by an endodermis that is composed of dark, rectangular cells (Fig. 1a–d). In many

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Fig. 1. Roots of *Decodon allenbyensis* prior to, and shortly after secondary tissue production. – a: Transverse section of young branching root with early vascular cambium activity; arrow at epidermis with enlarged hypodermal cells beneath; double arrow at early branching young root with unexpanded cortex. P6427 L bot #6. – b: Transverse section of young root with pentarch primary xylem surrounded by dark endodermis, aerenchymatous cortex, and a prominent hypodermis (at arrow). P6427 L bot #6. – c: Transverse section of young root with hexarch primary xylem and aerenchyma surrounding the central cylinder. P6019 B #4. – d: Oblique transverse section of young root with septarch primary xylem. P1303 C_2 side #2. – e: Young root with aerenchymatous primary cortex with some secondary xylem and early lacunate phellem; inset left: close-up of the specimen at epidermal layer; inset right: close-up of the specimen showing edge of the secondary xylem, secondary phloem (arrow at phloem fiber bundle), and early lacunate phellem. P6019 B #6. — Scale bar = 200 μm.

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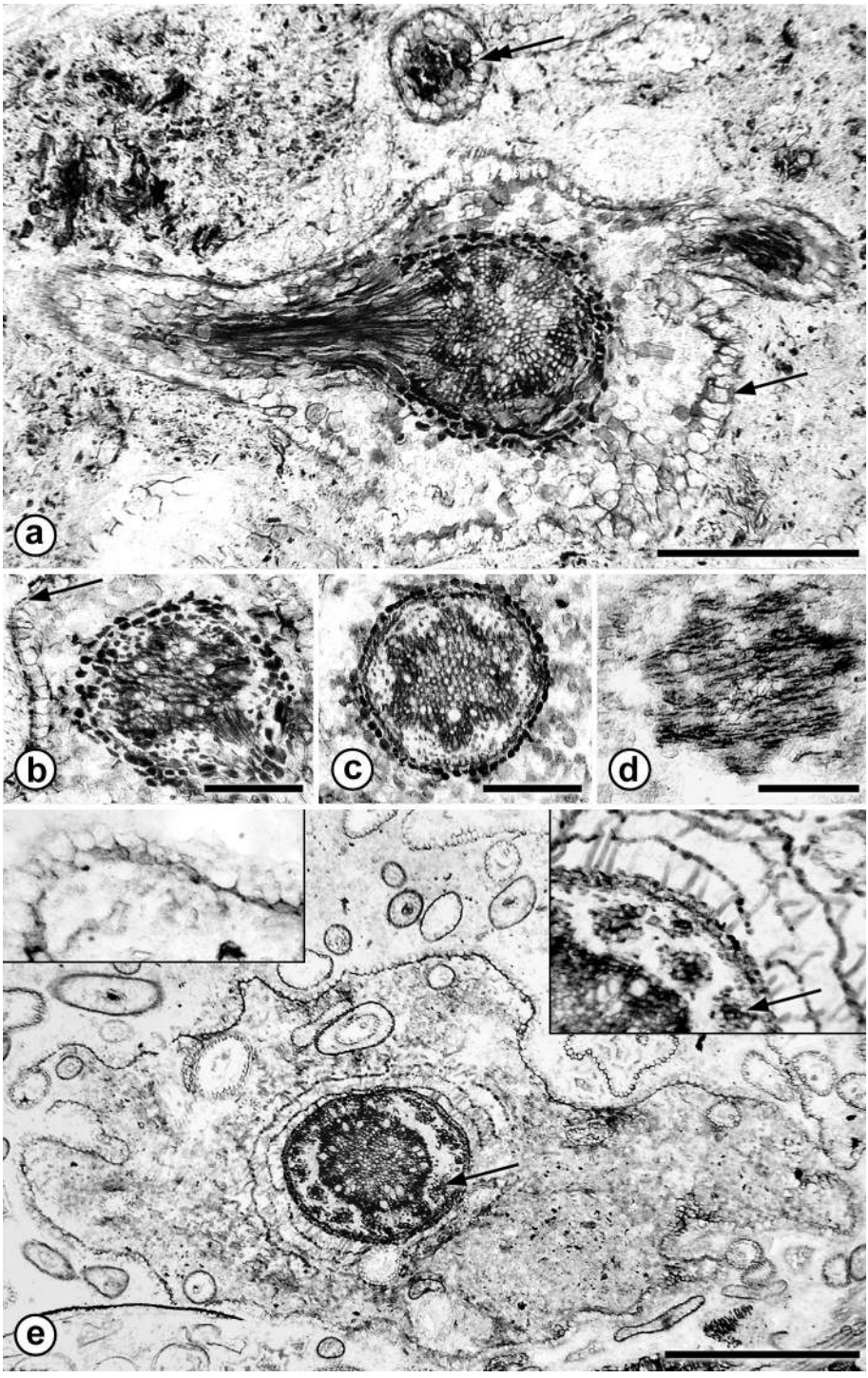

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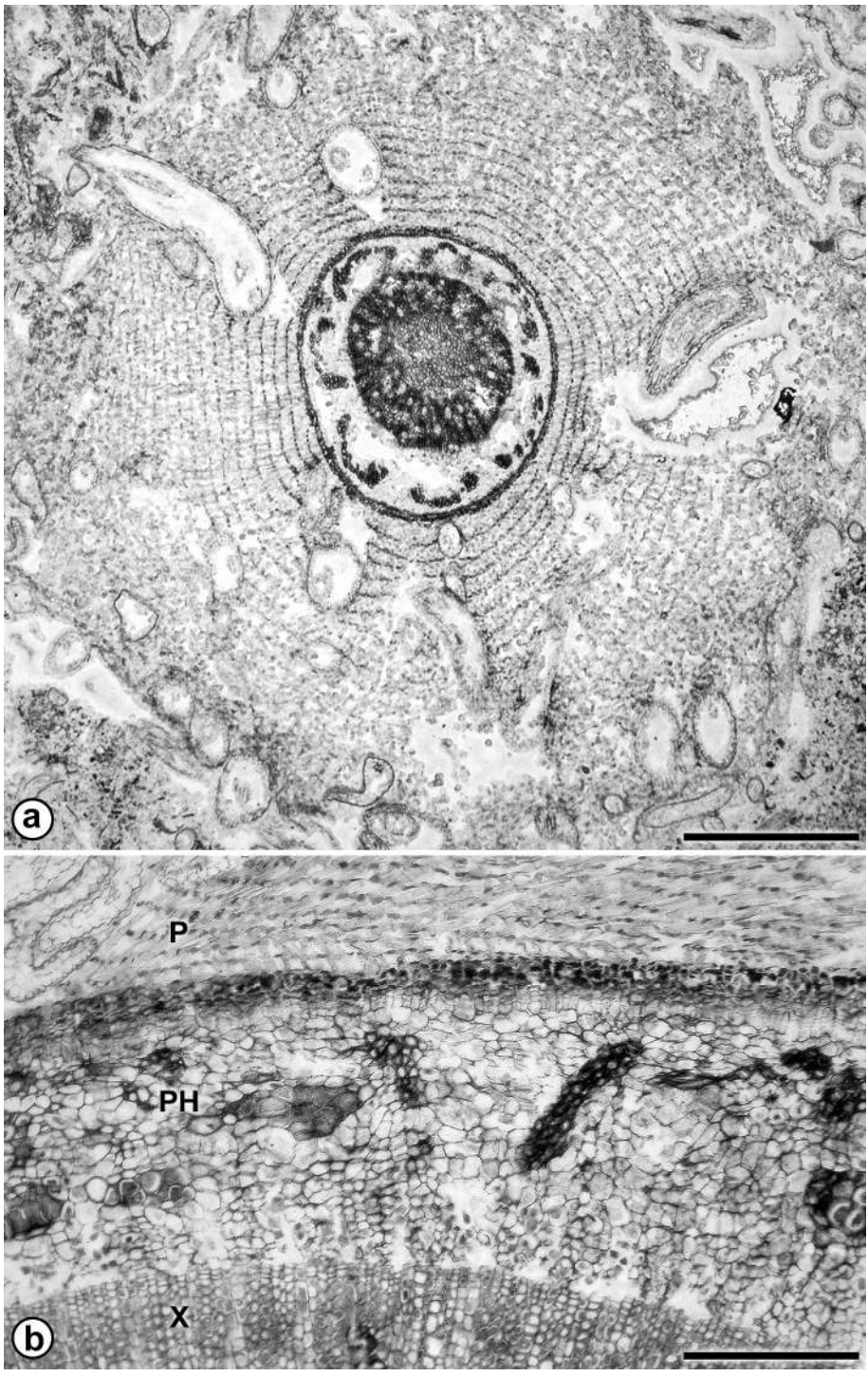

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young roots there are several layers of inner cortical cells adjacent to the endodermis that also have dark contents (Fig. 1a–d). Primary phloem and pericycle are present but are not usually well preserved. Primary xylem is pentarch to hexarch (Fig. 1b, c) and rarely septarch (Fig. 1d). Primary phloem lacks sclereids or phloem fiber bundles at this stage of development (Fig. 1a–d).

Primary cortex of young roots is typically aerenchymatous (Fig. 1a, b) but does not always appear so in the youngest roots (Fig. 1a, double arrow). Beneath the epidermis is a distinctive hypodermis one cell layer thick, composed of radially elongate cells with internally thickened walls (Fig. 1a, b; e left inset). Epidermal cells are rectangular in transverse section and are much smaller than the hypodermal cells (Fig. 1a, b).

Transition to secondary growth

Early stages of development (shortly after initiation of secondary growth) are preserved in the Princeton Chert specimens and provide information on the timing and synchronization of wood and periderm production in this fossil plant. Initiation of the vascular cambium, and subsequent secondary xylem and phloem production, precedes the initiation of phellogen activity. Evidence for this timing of cambial activity is shown by roots that possess small amounts of wood and secondary phloem but no periderm (Fig. 1a). These roots still have intact epidermis with an aerenchymatous primary cortex surrounding a partially woody stele (Fig. 1a).

Phellogen initiation occurs in the pericycle. In aquatic roots the phellogen produces a lacunate phellem. This is in contrast to non-aquatic roots that produce radially aligned compact rectangular phellem. At the time of phellogen formation the secondary phloem begins to produce clusters of fiber bundles (Fig. 1e, at arrows), while in both the primary and early secondary phloem there are no phloem fiber bundles (Fig. 1b, c). The primary cortex is sloughed off by the early lacunate phellem and in relatively young specimens the delicate aerenchymatous primary cortex is still associated with the root (Fig. 1e).

Secondary growth

Xylem – Wood with distinct growth increments (Fig. 3) and secondary phloem are produced in older axes (Fig. 2, 3). These larger roots are easily distinguished from other root types in the matrix by their diffuse and wide vessels, large parenchymatous ray cells and lacunate phellem. Wood anatomy of the fossil roots and stems have been described in detail by Little and Stockey (2003).

Phloem – Secondary phloem is composed of thin-walled cells and clusters of phloem fiber bundles (Fig. 1e, 2, 3, 5a). Even when phloem cells are largely missing due to poor preservation, the thick-walled fibers are prominent (Fig. 1e, 2a, 3). Fiber bundles typically range 156–700 μm in diameter. Individual fibers are round to polygonal in transverse section, 39–147 μm in diameter.

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Fig. 2. Roots of *Decodon allenbyensis*. – a: Young root with limited secondary xylem and extensive thin-walled phellem and several secondary roots. P5956 E bot #3b. – b: Transverse section of xylem, phloem and periderm. Note phloem fiber bundles. P6427 K bot #34. – P = phellem; PH = phloem; X = secondary xylem. — Scale bar = 500 μm.

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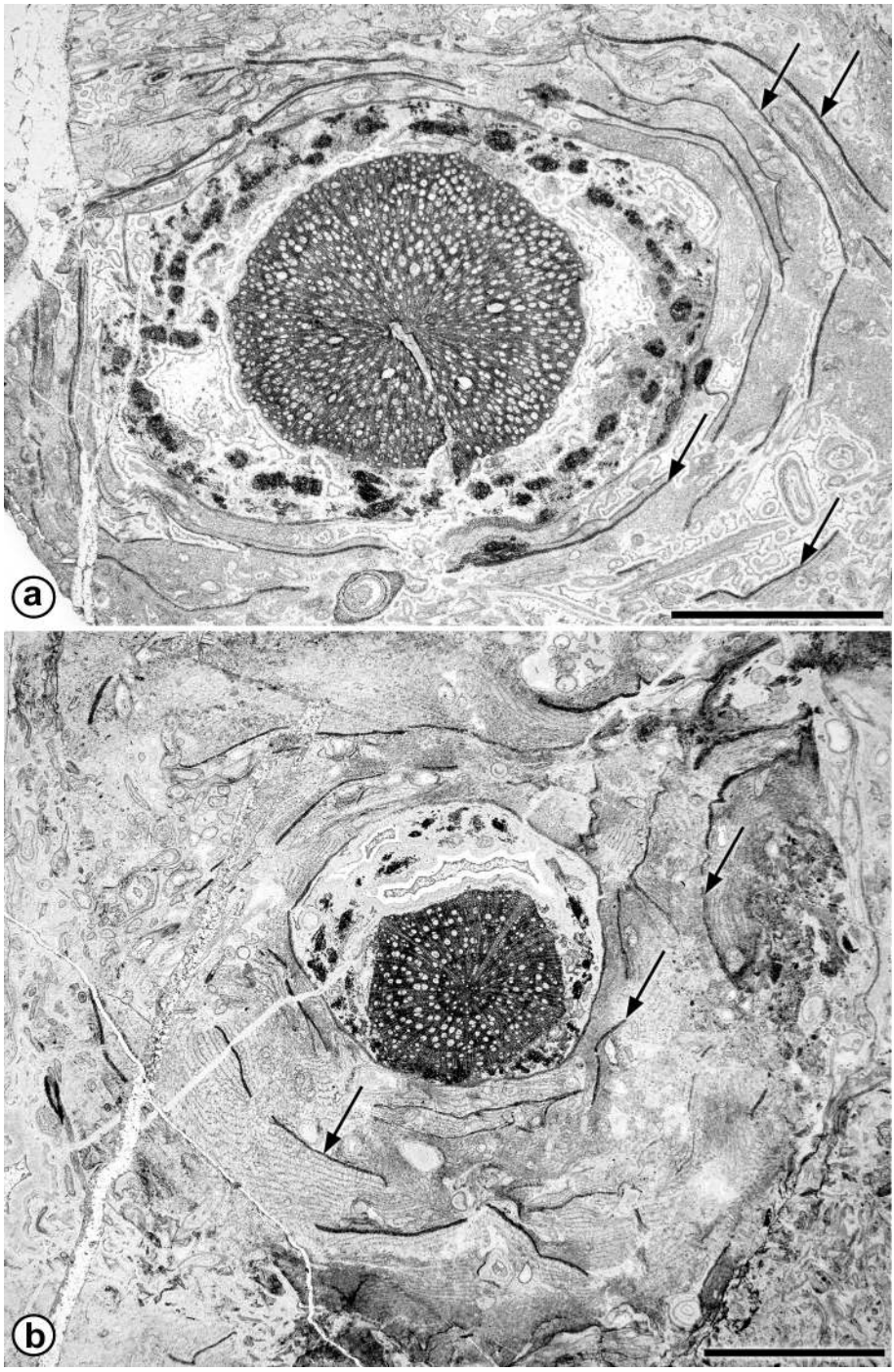

Fig. 3; for legends, see page 80.

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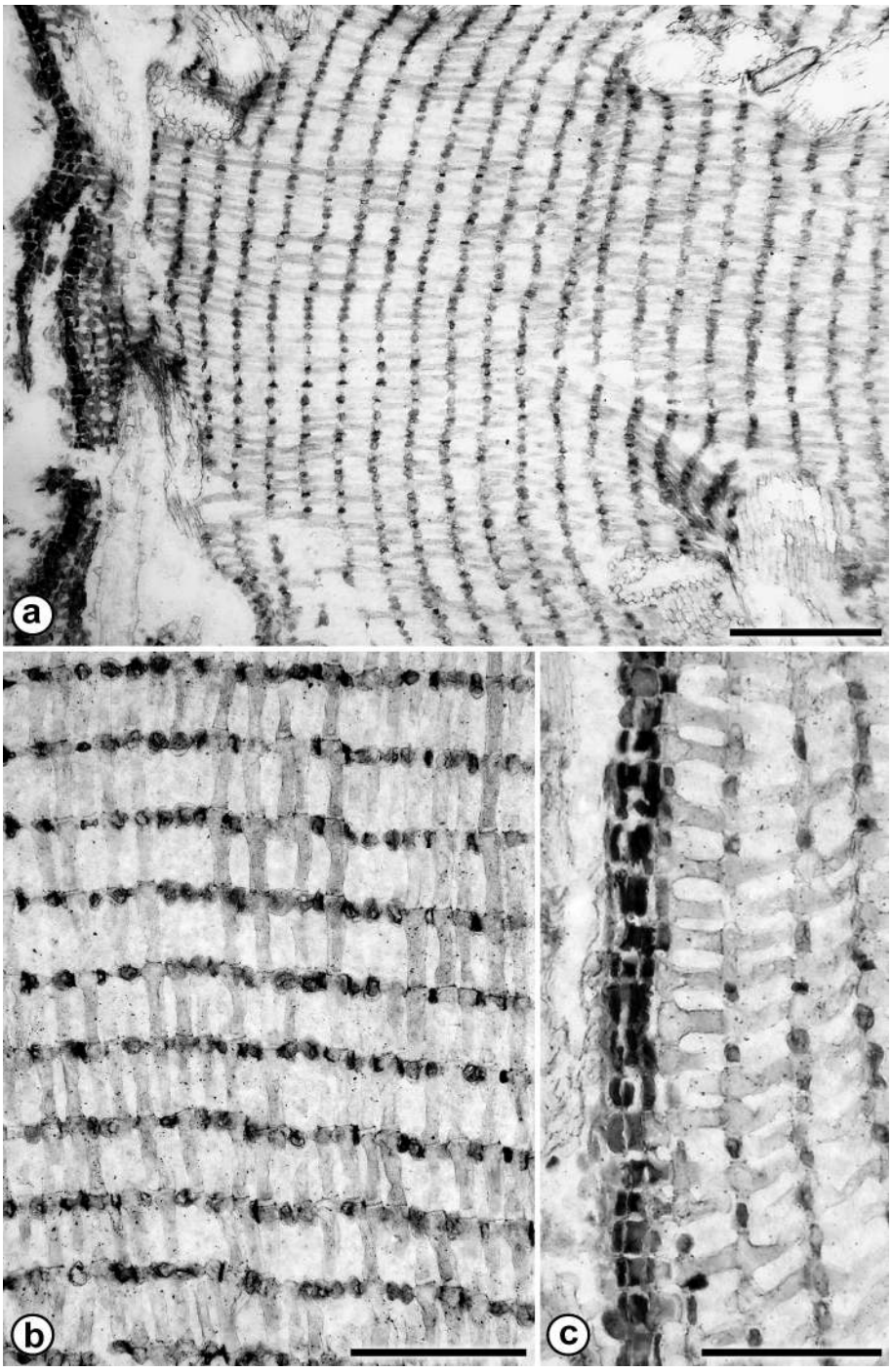

Fig. 4; for legends, see page 80.

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Phellem – Aquatic lacunate phellem, a very delicate tissue that is difficult to study in living plants (Lempe *et al*. 2001; Stevens *et al*. 1997, 2002; Little & Stockey 2003), is usually well preserved and intact in the Princeton fossils (Fig. 1e, 2a, 3, 4). The expanded aerenchymatous lacunate phellem appreciably widens the diameter of young roots that have very little secondary vascular tissue. Such young roots typically measure 0.5 mm to 15 mm in diameter (Fig. 2a, 3b).

At low magnifications phellem appears highly organized with ordered concentric layers of cells surrounding the vascular cylinder (Fig. 2a, 3). At regular intervals bands c. 3 to 5 cells thick, of dark-colored rectangular 'phelloids' ('phellem-like cells' *sensu* Esau 1965) (Fig. 4a, c), occur among the light colored thin-walled lacunate phellem (Fig. 3). Up to 12 such rings of phelloids are present in some roots. The light colored, thin-walled lacunate phellem is composed of T-shaped cells, with radial extensions and air spaces between cells (Fig. 4).

Rhytidome – The largest axes of *Decodon allenbyensis*, some with up to 18 growth increments of wood, have a complex rhytidome with tissue organization that is distinct from that of the lacunate phellem system described above (Fig. 5c). The rhytidome is composed of alternating bands of non-aquatic periderm and aerenchymatous secondary phloem (Fig. 5c, 7). Phloem bands have typical phloem fiber bundles (Fig. 5b, c). The periderm bands vary in thickness, from 5–25 cells thick per band, or rarely up to ~50 cells thick per band.

Parenchymatous cells in the phloem have tangentially aligned extensions with air spaces between cells. Rectangular cells, lacking extensions, are arranged in radial rows between the elongate cells with lacunae (Fig. 5b, d). Rhytidome with up to five bands of 'lacunate phloem' have been observed around an axis. However, this aerenchymatous phloem is also commonly found as isolated fragments that have been sloughed off the plants and preserved in the chert matrix.

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Fig. 5. Phloem and rhytidome of *Decodon allenbyensis* – a: Radial longitudinal section of secondary xylem and phloem. P6427 K bot #24. – b: Tranverse section of large, crushed stem (at right) with a rhytidome to the left, composed of zones of old secondary phloem alternating with zones of phelloids (arrows). P6427 L bot #7. – c: Transverse section of lacunate secondary phloem with tangentially elongated cells and clusters of phloem fibers. P6427 L bot #6. – d: Higher magnification of Fig. 5c showing tangentially elongated cells alternating with radial rows of small rectangular cells interrupted by phloem fiber bundles. P6427 L bot #6. – P = phellem; PH = phloem; X = secondary xylem. — Scale bar = 500 μm.

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Fig. 3. Roots of *Decodon allenbyensis*. – a: Transverse section of root with two growth increments, diffuse-porous wood, phloem fiber bundles and abundant thin-walled phellem with layers of dark colored phelloids (arrows). P6019 B #7. – b: Transverse section of a root with three growth increments, and extensive thin-walled phellem with several layers of dark colored phelloids (arrows). P5912 H top #3. — Scale bar = 2.5 mm.

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Fig. 4. Phellem in roots of *Decodon allenbyensis*. – a: Rows of lacunate thin-walled phellem. P6288 A #1. – b: Alternating isodiametric and radially elongate cells of the phellem separated by rectangular lacunae. P6288 A #1. – c: Phellem with elongated cells in contact with dark non-aerenchymatous cells representing former location of phellogen. P6288 A #1. — Scale bar = 100 μm.

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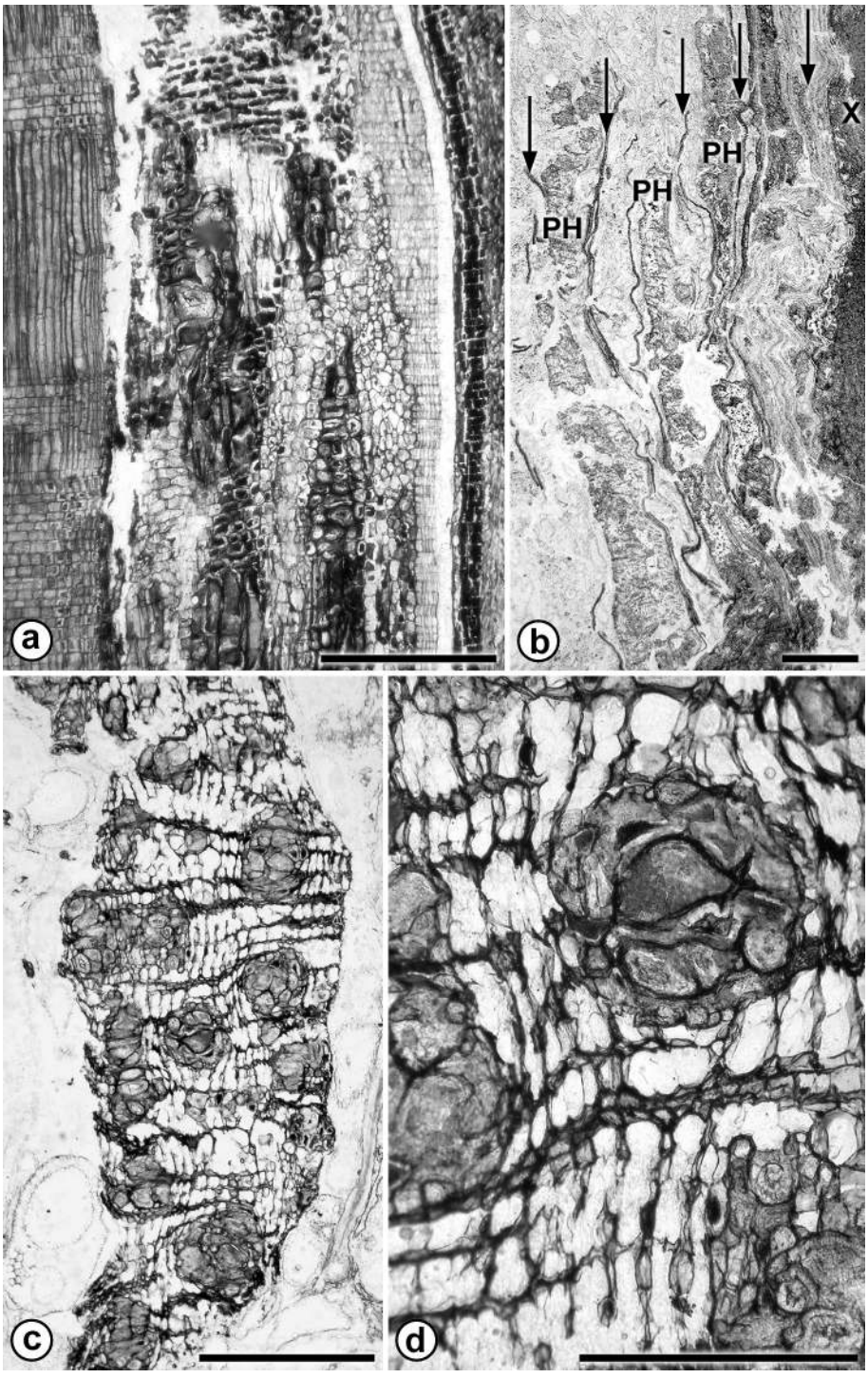

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While most roots have lacunae in the non-active secondary phloem there is rare non-lacunate phloem with transitions from non-lacunate phloem to lacunate phloem also observed. Throughout the rhytidome the zones of periderm are composed of radially aligned compact phelloids. These periderm bands maintain their organization and structure and do not radially elongate to produce lacunae.

DISCUSSION

The present investigation provides additional developmental data on aquatic tissues in the submerged axes of the fossil aquatic dicot, *Decodon allenbyensis*, originally known only from isolated fruits and seeds (Cevallos-Ferriz & Stockey 1988). Recent studies on this species from the Princeton Chert have produced data on the growth habit, anatomy of roots and stems (Little & Stockey 2003), and anatomy of the leaves of this plant (Little & Stockey 2002; Little *et al*. 2004). The present study adds to our knowledge of the growth and morphogenesis of peridermal tissues in this plant, making *D. allenbyensis* the best known fossil *Decodon* species.

In the fossilized roots of *Decodon allenbyensis*, the morphogenesis of aquatic tissues follows a consistent sequence. Primary cortex in roots forms lacunae beneath intact dermal layers prior to secondary vascular cambium initiation. The vascular cambium is the first to produce secondary tissues. Shortly after vascular cambial activity is initiated, fiber bundles develop in the secondary phloem and are present in all later produced secondary phloem. Phellogen activity is then initiated in the pericycle. Lacunate phellem is produced by the phellogen in submerged conditions. Lacunae in the phellem were most likely formed by the radial elongation of phellem cells as in extant *D. verticillatus* (Schrenk 1889; Lempe *et al*. 2001).

The anatomy of primary and secondary aquatic tissues in the fossil roots is comparable with those of living *Decodon verticillatus* roots (Little & Stockey 2003). The coordination of the timing of secondary tissue initiation in roots of extant *D. verticillatus* is also identical to that in the fossil roots. Primary cortex forms lacunae beneath intact dermal layers, followed by secondary vascular cambium growth with phloem fiber bundles (Little & Stockey 2003). In the pericycle, phellogen activity is initiated as is typical in Lythraceae (Graham 1964; Lempe *et al*. 2001), and in aquatic conditions phellem undergoes radial elongation to produce T-shaped cells with air spaces between (Schrenk 1889; Lempe *et al*. 2001). These early stages in the development of primary and secondary aquatic modifications in roots of living *D. verticillatus* are similar in all respects to those in the fossil roots.

Members of Onagraceae produce a tissue in young roots that is strikingly similar in appearance to lacunate phellem, but it is a primary tissue (Schenck 1889; Ellmore 1981; Fig. 6A). As cortical parenchyma radially elongates to form regular and rectangular lacunae, the outer cortical parenchyma is disrupted and the epidermis is torn (Schenck 1889; Ellmore 1981). Ellmore (1981) corroborated Schenck's (1889) original developmental interpretation of this tissue in species of *Ludwigia* and clearly showed that the phellem-like aerenchyma, in aerial roots of *Ludwigia peploides* (Onagraceae), is a primary tissue (Fig. 6A).

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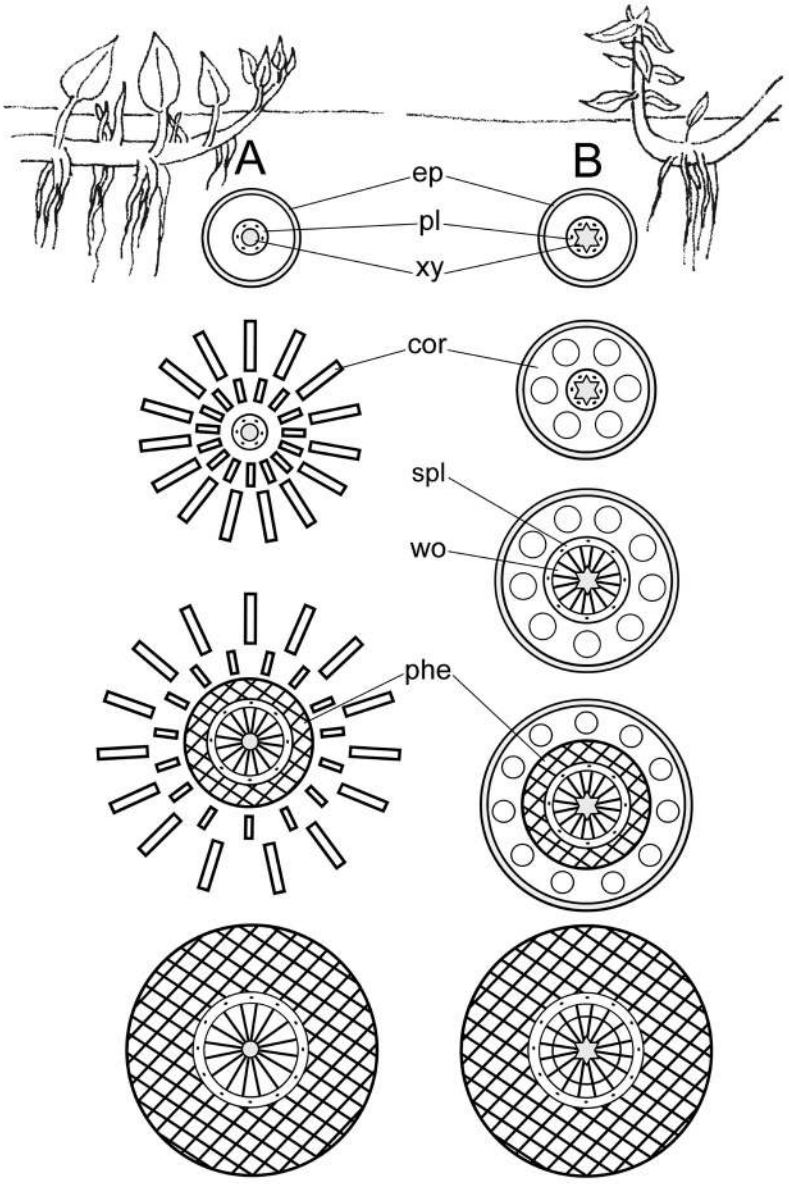

Fig. 6. Diagram representing *Ludwigia*-type and *Decodon*-type morphogenetic stages in aquatic roots. – A column: *Ludwigia*-type morphogenesis: cells of primary cortex radially elongate, shedding dermal layers to make a tiered aerenchyma. True lacunate phellem is produced by phellogen in association with secondary vascular tissues; phellogen is formed in the pericycle. – B column: *Decodon*-type morphogenesis: cells of primary cortex form lacunae to make an aerenchyma that is contained by the dermal layers. Secondary vascular tissues are produced prior to phellogen initiation. Lacunate phellem is then produced by the phellogen that is formed in the pericycle. — ep = epidermis with hypodermis, pl = phloem, xy = primary xylem, cor = primary cortex, spl = secondary phloem, wo = wood, phe = phellem.

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In contrast to this '*Ludwigia*-type' of primary cortical aerenchyma development, roots of extant *Decodon* and of the fossil described here have '*Decodon*-type' development with more circular lacunae that form beneath intact dermal layers (Fig. 6B). Although lacunate phellem and *Ludwigia*-type primary aerenchyma have different developmental origins, their superficial resemblance has lead to misidentification (Metcalfe & Chalk 1950, 1983; Sculthorpe 1967). Without the observation of the early stages of morphogenesis in the fossil roots with lacunate phellem it would be difficult to distinguish which type of aerenchyma development is present. However, the excellent *in situ* preservation and the wide range of morphogenetic stages of these plants provide the information necessary to illustrate the *Decodon*-type primary aerenchyma development in the fossil roots of *D. allenbyensis* and to demonstrate morphogenetic similarities to extant *D. verticillatus* (Little & Stockey 2003).

The bands of compact phelloids with suberized walls that occur in the phellem of extant *Decodon verticillatus* (Schrenk 1889) and in the fossil *Decodon allenbyensis* were hypothesized to be evidence of consecutive phelloderm production (Little & Stockey 2003). Similar bands of compact suberized cells are also seen in the lacunate phellem of submerged axes in extant species of *Leptospermum* J.R. Forst. & G. Forst., and these bands have also been interpreted as evidence for consecutive phellogen production (Cook *et al*. 1980). Schrenk (1889) states that the suberized bands are tightly sealed, preventing gas exchange between the inner part of an axis and the majority of the aerenchyma to the outside of this layer. Since lacunate phellem is produced more abundantly below the axes than above in a horizontal axis, and because the bands of phelloids are sealed by suberin, Schrenk (1889) concluded that in *Decodon verticillatus* lacunate phellem must only serve to aid in buoyancy. However, lacunate phellem in living and fossil *Decodon* species probably does aid aeration, an idea supported by recent work on *Lythrum salicaria* by Stevens *et al*. (2002), which demonstrates a gaseous connection between submerged and non-submerged axes. In addition to gaseous

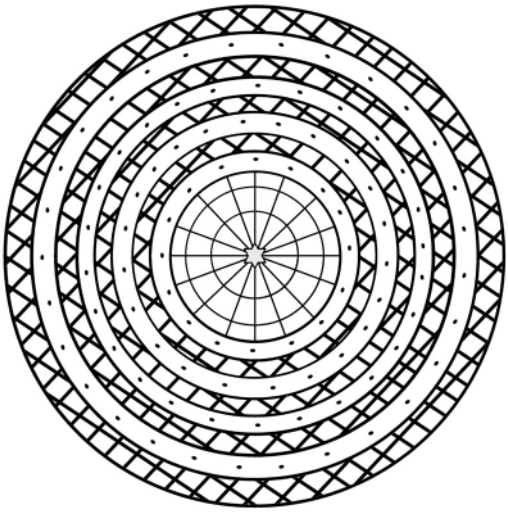

Fig. 7. Diagram representing complex aquatic rhytidome described in this study; this aquatic rhytidome is known only in the fossil *Decodon allenbyensis*. Tissues are as in Fig. 6, but the cross-hatch zones represent non-aquatic phelloids, and the secondary phloem zones represent aquatic lacunate phloem.

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exchange the phellem probably also serves in flotation since it is produced in such large amounts in both the living and fossil taxa.

Lacunate phellem is the most prevalent form of periderm in the fossil axes. In living *D. verticillatus* the radially elongate cells of the lacunate phellem have cellulose walls and the bands of compact phelloids have suberized walls (Schrenk 1889). The fossil lacunate phellem probably also had walls with similar components to those of living *Decodon*. However, trying to draw additional parallels between the fossil periderm and the periderm of other extant taxa may not be advisable since aquatic phellem develops differently in members of Lythraceae (Lempe *et al*. 2001), and aquatic phellem is also found in various unrelated groups (Schenck 1889; Cook *et al*. 1980; Shimamura *et al*. 2002, 2003). Further studies on lacunate phellem in Lythraceae and other families are needed in order to assess variation in details of anatomy and composition, as well as the various potential developmental syndromes in these plants.

The largest fossil axes observed, with several woody growth increments, have a rhytidome with more complex tissue organization than that seen in the smaller axes with lacunate phellem (Fig. 7). Consecutive phellogens are formed as in lacunate phellem discussed above, but bands of non-elongate phelloids are produced and the number of cells per layer is larger than three per band typically found in the lacunate phellem. These thick bands of phelloids were probably suberized and waterproof, similar to suberized bands in lacunate phellem of extant *Decodon*. The bands of phloem with lacunae and fiber bundles are found between the compact phelloid bands and were presumably non-active. This 'lacunate phloem' probably replaced the lacunate phellem in the function of aeration and/or flotation. Tangential elongation of cells in the non-active phloem contrasts with the radial elongation of cells in lacunate phellem of smaller axes. Parenchyma is the most likely cell type to be tangentially elongated in the non-active phloem. This lacuna production probably would have occurred just prior to, or just after the phloem was cut off by a new phellogen. Tangential elongation in lacunate phloem of the rhytidome would better accommodate increases in girth of the large woody axes than the radially elongate cells of lacunate phellem. The alternating rings of phelloids, several cells thick, would have provided more protection from mechanical damage and microbial attack than thin-walled lacunate phellem. However, this rhytidome system was probably shed regularly because it is commonly found isolated in the chert suggesting that its main function was to accommodate increases in girth due to woody growth of the axes.

Little and Stockey (2003) hypothesized that the fossil, *Decodon allenbyensis*, was larger than the extant species *Decodon verticillatus*. The representative size of stems from lake populations in Ohio ranges from 2–4 cm in diameter including some roots (Shirley A. Graham, pers. commun. 2002). Plants in the southernmost populations, such as those in Florida, may get as wide as the largest fossil axes (~20 cm in diameter) (Christopher G. Eckert, pers. commun. 2001), but no girth measurements have yet been documented. Further investigations are required to determine whether extant *Decodon* can reach the size of the fossil species. Such investigations may determine whether the complex aquatic rhytidome, seen here in the fossil, is also produced by large axes of extant *Decodon*. However, such delicate aerenchymatous tissue may prove harder

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to observe in life than in the permineralized tissues of the fossils without special techniques such as critical point drying or freeze fracturing (Lempe *et al*. 2001; Little & Stockey 2003).

The remains from the Princeton Chert have provided crucial comparative anatomy that is of systematic importance and highlight the aquatic habitat at the time of preservation. Such detailed understanding of the anatomical structure and sequence of the various stages of primary and secondary aquatic anatomical adaptations for a fossil plant is rare. As a result of this study the anatomical and developmental data now known for *Decodon allenbyensis* is more complete than that of most extant Lythraceae. Currently, the aquatic rhytidome made up of alternating bands of compact phelloids and non-active secondary lacunate phloem is considered unique and has not been previously described in living or fossil plants.

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