

The Anatomy of Arborescent Plant Life Through Time

Mike Viney

Collectors of petrified wood focus on permineralized plant material related to arborescent (tree-like) plant life. Evidence for the first fossil forest occurs in the Devonian. Fossil forest composition changes through geologic time, reflecting variety in evolutionary strategies for constructing a tree form. It is helpful and informative to study the anatomy of various trunk designs. Permineralized plant material is often cut and polished in the cross-sectional or transverse plane to reveal the anatomy perpendicular to a trunk, stem, or root axis. Evolutionary adaptations for trunk structure can be recognized by the arrangement of tissues. Familiarity with the anatomy may even allow one to identify the taxon to which a specimen belongs; however, for many specimens radial and tangential sections of the stem must also be studied. In this article, we will focus only on stems in cross-section.

Lycopods

The extinct clubmoss trees or arborescent lycopods dominated the canopy of Carboniferous forests and went extinct during the Permian. In cross-section the lycopod trunk anatomy consists of a small central pith surrounded by a xylem ring with medullary rays. The core of water conducting woody tissue (xylem ring) is encased in a wide area of living parenchyma tissue. The cambium produced a hard, lignified outer layer. This non-water conducting outer layer provided the structural support for the tree (Kenrick & Davis, 2004, p. 70). Although not hollow, the lycopsid trunk acted as a tube-like structure. The hard outer layer along with the soft inner tissue is referred to as the bark and accounts for 98% of the cross-section, making the term "bark stem" appropriate for these trees (Selmeier, 1996, p. 139). The best cross-sections of lycopsid stems and trunks come from coal ball cellulose acetate peels. Paleozoic tree clubmosses could reach heights of 40 m and attain diameters of 2 m.

Horsetails

Arboreal horsetails contributed to the canopy of Paleozoic forests. The trunk of *Calamites* grew in a telescoping fashion from one node to another (Selmeier, 1996, p. 139). In cross-section the stem consists of pith and or a medullary cavity surrounded by primary and secondary xylem; bark tissue covered the exterior. The stem of the *Calamites* specimen to the right was compressed during the fossilization process. The stem is made mostly of secondary xylem. Medullary rays can be seen radiating from the center to the periphery. There is no bark on this Permian aged





specimen from Brazil. The periphery of the inner bark of *Calamites* possessed air spaces called valescular canals. As the tree grew, secondary xylem added to the girth of the trunk, while the central pith area formed hollow interior chambers (see image to the left). In fact, the pith cast of *Calamites* is the most common plant steinkern. As a *Calamites* tree matured the center of the stem (pith) became hollow, developing into a tube-shaped air cavity. In many instances this hollowed out area became filled with sediment forming an internal cast or steinkern. The pith cast preserves an impression of the pith cavities outside surface, which

represents the inside vascular and cortex tissue (Taylor, Taylor & Kring, 2009, p. 23).

The xylem or wood of these trees was made primarily of tracheid cells that are very similar to modern gymnosperms. Xylem tissue consists of an interconnected system of tube-like cells (tracheids) that conduct water throughout the plant. The tracheids that make up the xylem of arboreal horsetails have cell walls strengthened with lignin. To the right, a close-up of the central pith of *Calamites* reveals tubular structures called carinal canals, which are surrounded by primary xylem. Secondary xylem can be seen radiating away from the carinal canals. In this specimen, medullary rays can be seen between the carinal canals and secondary xylem. With this close-up we can make sense of the exterior ribs found on



Calamites pith casts (image to the left). The ribs correspond to the rays. The depressed areas between the ribs are where the carinal canals extended into the pith cavity. The hollow trunk of *Calamites* formed a kind of reinforced tube. These trees were fast growing, but sensitive to local buckling (Kenrick &

Davis, 2004, p. 70). Paleozoic horsetail trees reached heights of 30 m, attained diameters of 1 m, and were anchored to the ground with prostrate rhizomes. The tube-like trunk of the lycopsid and horsetail tree supported small, sparsely branched crowns.



Ferns

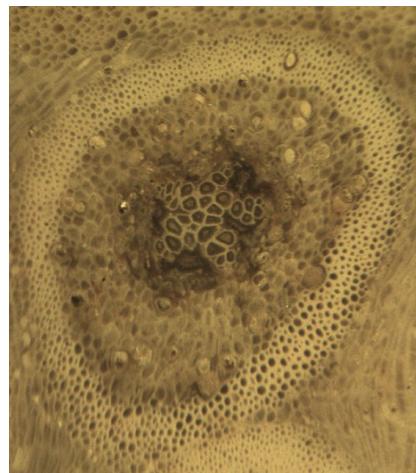
Ferns occupied many habitats in the Carboniferous. Fern species grew as epiphytes, ground cover, understory and canopy in these ancient forests. Isolated, but intertwined roots and leaf petioles formed an important part of the stems of ferns with tree and shrub-like forms.

Tree Ferns



Arborescent ferns possess a kind of buttressed or braced trunk and evolved during the Carboniferous and Lower Permian. *Psaronius* was the largest arborescent fern found in the coal measure swamps (Willis & McElvain, 2002, p. 108). *Psaronius* was up to 10 m tall and occupied the drier areas of the swamps. The trunk had no secondary wood for strength. In cross section, tree fern stems consisted of a narrow cylinder composed of vascular tissue. Enclosing this cylinder was a mantle of petioles and aerial roots, which created a fibrous, tough, lightweight structure (Kenrick & Davis, 2004, p. 71).

The central vascular cylinder of the tree fern pictured above is composed of a complex arrangement of banded-shaped xylem strands. At the periphery of the central vascular cylinder c-shaped vascular strands of petioles can be seen. Surrounding the vascular cylinder is a mantle of roots. The specimen above is a Permian aged tree fern (*Psaronius brasiliensis*) from Brazil. The root mantle was thickest towards the base of the trunk. The adventitious roots making up this mantle became narrower towards the top of the tree, while the stem diameter actually increased. Thus, the stem was an inverted cone supported by a thick mantle of roots, which acted as guy ropes, tethering the tree to the ground (Willis & McElwain, 2002, p. 89). The fibrous nature of the tree fern trunk allowed it to absorb and retain rainwater; however, the intertwined strengthening elements were isolated, making the structure prone to bending from perpendicular forces such as wind (Kenrick & Davis, 2004, p. 71). Tree ferns were generally small and did not support much branching. Pictured to the right is a cross-section of an aerial root, found in the mantle of a tree fern, which reveals a central, star-shaped xylem strand. As the aerial root developed, primary xylem grew from five different points. Metaxylem was then produced towards the center forming a star shape. Phloem tissue developed between the arms of the star. The aerial rootlet pictured to the right comes from a permian aged Brazilian tree fern (*Titea singularis*). The picture was taken at 40x.



Ground Cover

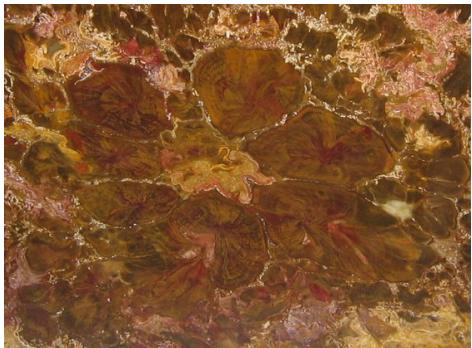
Osmundaceae, the Royal Fern family, makes its appearance in the Permian. Sixteen living species are recognized along with nearly a hundred fossil forms (Miller, 1971). Osmundaceae is the best-represented family of ferns in the fossil record and is known from foliage, stems, roots and reproductive structures. The family diversified and was

widespread during the Mesozoic era, but decreased in numbers and geographic range during the Tertiary (Tidwell, 2002, p. 135). The ferns in this family have rhizomes that grow upright and produce closely spaced fronds (leaves). Not unlike *Psaronius*, the fossil osmundales also possessed leaf-root-trunk stems. The stem is composed of persistent leaf bases and rootlets (Tidwell, 1998). The image to the left reveals that the central stele consists of pith, xylem and

phloem. Surrounding the small stem is a thick mantle of persistent leaf bases and roots. When alive, the stem and mantle would have formed an inverted cone-shaped structure that was topped with a cluster of closely spaced fronds (Tidwell, 1998, p. 187). The specimen pictured is Jurassic aged *Osmunda* from Australia. It is the wonderful pattern of leaf traces, petiole cross-sections and rootlets surrounding a central stele (pith, xylem and phloem) in the permineralized stem, which attracts the interest of the fossil wood collector. The typical anatomy of the osmundaceous stem in cross-section starts with a centralized pith surrounded by a circle of horseshoe-shaped xylem strands. Phloem tissue is just outside the central xylem and may be just inside as well in some species. A mantle of material surrounds this central stele that is composed of leaf shoots that contain C-shaped xylem strands. As one moves outwards from the center, the C-shaped xylem strands become enclosed in a ring of supportive tissue, denoting cross-sections of frond petioles. Some of these petioles are outlined with stipular wings. The C-shaped xylem strand can be clearly seen in the petiole cross-section pictured to the right. A sclerotic ring of fibers encloses the xylem. Smaller root structures can be seen interspersed between the petiole cross-sections. The specimen is a 20x close-up of the stem pictured above.



Seed Ferns



Seed ferns (Pteridospermatophyta) flourished from the Carboniferous to the Lower Permian. Pteridosperms had fern-like foliage, but reproduced with seeds (Selmeier, 1996, p. 142). Seed ferns exhibited both vine-like and arborescent forms. The stems and trunks of many seed ferns consisted of separate vascular segments in the form of wedges (polystele). Multiple wedges of xylem surround the pith of the Jurassic-aged seed fern from Australia pictured to the left. Beyond these central wedges

xylem formed rings of wave-like patterns. In some species wedges produced secondary xylem (wood) only to the inside, others produced wood towards the inside and outside, and still others produced wood all the way around the wedge. There is a distinct evolutionary trend in the number of vascular bundles embedded in the pith along with the position of peripheral vascular bundles. Over time, a single, deeply divided vascular bundle evolved into three or more. Outer vascular bundles became fused, forming rings of secondary wood by the Lower Permian (Jung, 1996, p. 158).

Glossopteris is a seed fern with a eustele vascular bundle (concentric vascular bundles with enclosed pith), which is characteristic of conifers and angiosperms (see picture to the right). The Permian aged *Glossopteris* stem to the right is from Australia. Both the polystele and eustele wood of seed fern stems was composed of conifer-like wood. The solid xylem making up the trunks of seed ferns made them strong and resistant to buckling. The adaptation of a woody cylinder stem would also develop in arborescent gymnosperms and later angiosperm dicots. Solid, woody trunks can support profuse branching and large crowns.



Paleozoic flora was dominated by ferns and clubmosses (Paleophytic flora). Paleophytic flora would give way to a new Mesophytic flora during the Triassic period. Woody seed-bearing plants and their relatives would come to dominate the Mesophytic flora. Thus, the change from Paleophytic to Mesophytic represented a change in reproductive strategy; from spore producers to seed producers. Conifers, cycads, and ginkgoes diversified during this time and dominated the landscape (Kenrick & Davis, 2004, p. 143).

Gymnosperms

Gymnosperms ("naked-seeds") include plants that usually bear their seeds in cone-like structures as opposed to the angiosperms (flowering plants) that have seeds enclosed in an ovary. Gymnosperms range from the Carboniferous to recent times. Gymnosperms include the following extant divisions: Pinophyta, Ginkgophyta, Cycadophyta, and Gnetales. Conifers (Division Pinophyta) are by far the most abundant and widespread of the living gymnosperms.

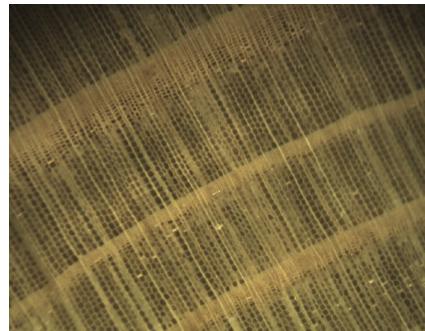


In most modern trees, trunks are woody cylinders. In modern day gymnosperms secondary growth begins early. The vascular cambium produces secondary xylem to the inside and secondary phloem to the outside. Phloem is the living tissue in plants that transports sugars made from photosynthesis to the rest of the plant. All of the tissues produced outside the vascular cambium comprise the bark. Thus, the typical gymnosperm stem is a eustele with central pith surrounded by substantial amounts of secondary

xylem, which in turn is enclosed by bark (Raven, Evert, & Curtis, 1981, pp. 340-343). The permineralized *Sequoia* trunk from Sunnyside Washington, pictured above, is typical of conifer wood. A small pith is surrounded by rings of secondary woody growth composed mostly of xylem tissue (tracheids). Like most petrified wood the bark tissue has not been preserved. Xylem tissue is composed of tracheids that function as an

interconnected system of tubes for conducting water throughout the plant. The tracheids making up this fossil *Sequoia* specimen, pictured to the right, are typical of a conifer. The cells are fairly uniform in appearance and arranged in radial rows. Notice the difference in the tracheid diameter as one moves from earlywood to latewood in the growth ring. The micrograph was originally taken at 40x. Tracheid cell walls are reinforced with the polymer lignin.

The tube-like cells only become functional after they die and lose their protoplasm. New wood produced by the vascular cambium towards the inside of the trunk is termed sapwood. The older wood in the center of the stem is termed heartwood. The transition from sapwood to heartwood marks the area where tracheids shut down and die. In some species, tracheids making up the heartwood act to store waste products called extractives as they age and no longer conduct water. Rays are ribbon-like tissues that cross the growth rings at right angles. Medullary rays connect the central pith to the cambium. Rays are made primarily of living parenchyma cells and function to carry sap radially through the plant. The rays of conifers are usually very thin, being one to two cells wide. Overall, the rays of softwoods (conifers) account for 8% of the wood's volume (Raven, Evert, & Curtis, 1981, p. 492). Trunks formed from solid xylem tissue are very strong and resistant to buckling (Kenrick & Davis, 2004, pp. 69-70).

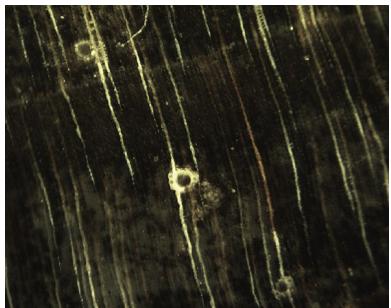




As long as the tree is alive, vascular cambium, just beneath the bark, continues to produce xylem, increasing the girth of the stem. Trees growing in temperate regions experience life cycles that include seasons of growth and dormancy. Seasonal growth results in growth rings or annual rings. The tracheids making up the earlywood of this *Sequoia*, pictured to the left, are visible at 20x. The latewood tracheid diameter is not as visible. In general, a 20x loupe is needed to view the tracheids of gymnosperms.

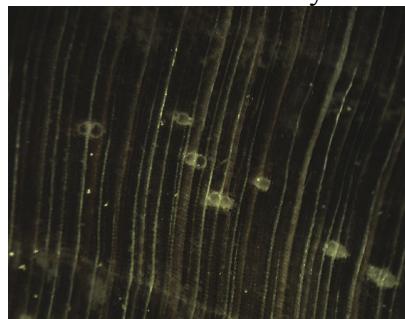
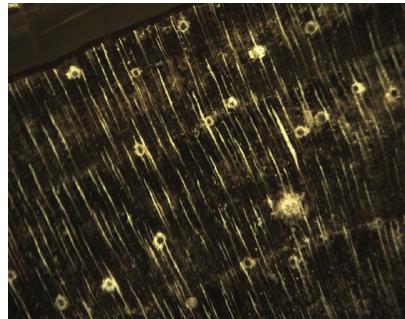
Tracheid diameters in gymnosperms range from 20 to 80 micrometers depending on the species. Earlywood consists of tracheids that have a wide diameter; whereas latewood consists of tracheids with smaller diameters. In tropical climates, growth may be consistent year around, resulting in wood that does not have growth rings (Hoadley, 1990, p. 10).

Some conifers possess tubular passages in their wood called resin canals. Resin canals are intercellular spaces lined with epithelial cells (see picture to the right). The epithelial cells exude pitch or resin, which functions to seal wounds caused by mechanical damage or boring insects. Resin canals can be found in four genera of the family Pinaceae (*Pinus*, *Picea*, *Larix*, and *Pseudotsuga*). The presence of resin canals helps to separate species within these genera from all other conifers (Hoadley,



1990, p. 20). Pines have relatively large resin canals. The resin canals in pines can be found distributed somewhat evenly throughout the growth ring. Resin canals in pines are usually found singly. The epithelial cells surrounding the resin canals in pines are thin-walled (see picture to the left). In spruces, larches, and Douglas fir resin canals are distributed unevenly. The resin canals are relatively small and often occur in tangential groups of two

to several (see image to the right). Some growth rings may lack resin canals. The epithelial cells surrounding the resin canals are thick-walled. Traumatic resin canals may also form as a result of environmental stress in both species that have resin canals as well as species that do not normally have them. Traumatic resin canals appear in cross-section as a single continuous line extending for some distance along a growth ring. Traumatic resin canals are usually only slightly larger than tracheids (Hoadley, 1990, pp. 20-21).



Although still successful today, gymnosperms dominated the world's Mesophytic flora from the Triassic to the Early Cretaceous. Flowering plants first emerge during the Early Cretaceous and undergo a great adaptive radiation during the Middle Cretaceous. Flowering plants quickly became a major constituent of species diversity and the world entered the third great age of plant life known as the Cenophytic by the Late Cretaceous (Kenrick & Davis, 2004, p. 143). The transition from Mesophytic to Cenophytic represents a change in reproductive strategy. Gymnosperms and their relatives relied mostly on wind pollination and bore naked seeds clustered in cones or on the end of stocks. Flowering plants coevolved with animal pollinators, underwent double fertilization, and encased seeds in a fleshy ovary that encouraged seed dispersal. Our modern plant world is a continuation of the Cenophytic age of plants.

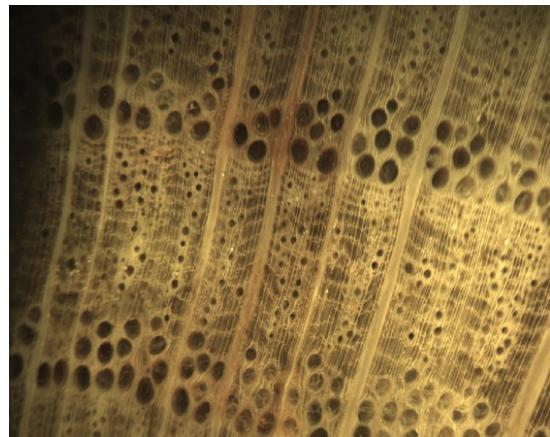
Angiosperms

Dicots

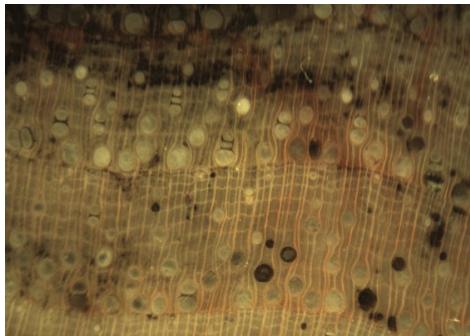


Flowering plants or angiosperms (phylum Magnoliophyta) range from the Cretaceous to recent times. Traditionally angiosperms are divided into the monocotyledons and dicotyledons. Today angiosperms are divided into the monocots, eudicots, and magnoliids. Monocots and eudicots are monophyletic groups. Eudicots contain most of the dicots. It is useful to know the major differences in stem structure between monocots and dicots (eudicots & magnoliids) when studying both extinct and extant plants.

Woody dicots possess eustele stems. A eustele stem is composed of a central pith surrounded by secondary wood and bark (see picture above). The woody stems of arborescent dicots are strong and resistant to buckling. Vascular cambium produces secondary xylem to the inside and secondary phloem to the outside. Most angiosperms have cell types that are distinctly different in size making up their xylem tissue (wood). Vessels are larger diameter water conducting cells. Smaller, less numerous, water conducting cells called tracheids along with abundant fibers can also be viewed in cross-section. In the image of this fossil oak from Oregon (genus *Quercus*), pictured to the right, one can see the large vessels making up the earlywood and the smaller diameter vessels arranged in flamelike patches making up the latewood. Wide, multiseriate rays cut across the growth rings. Very fine uniseriate

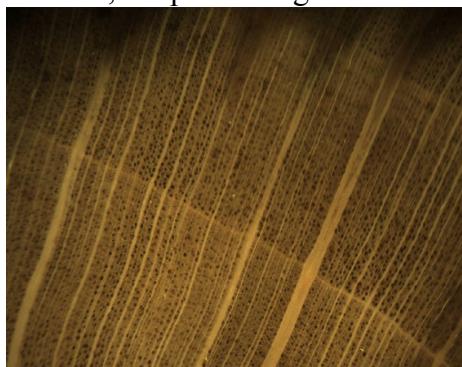
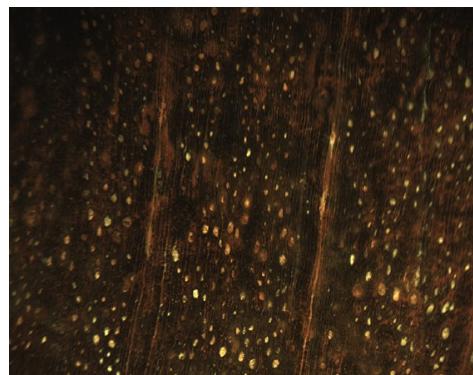


rays can be seen in the wood between the more visible thicker rays. Vessels in angiosperms range in size from 50 to 300 micrometers in diameter depending upon the species. The rays making up the hardwood of dicots can be from one to 30 cells wide depending upon the species. Oak rays can be 30 cells wide and hundreds of cells high, making them visible to the naked eye. Rays make up, on average, 17% of the volume of wood in hardwoods (Raven, Evert, & Curtis, 1981, p. 492). The wood of angiosperm dicots is more complex than that of the conifers. This complexity can actually make identification easier in some instances.



vessels are relatively large, while the latewood pores are much smaller in diameter. The image was taken at 20x. Semi-ring-porous wood possesses relatively large early wood pores. Pores in the growth ring gradually reduce in size from early to late wood. Live oak, tanoak, and walnut are typical semi-ring-porous woods. The fossil live oak specimen (genus *Quercus*) from Oregon exhibits semi-ring porous pore distribution (see image to the right). The growth rings are not distinct; however, the pore size grades from larger to

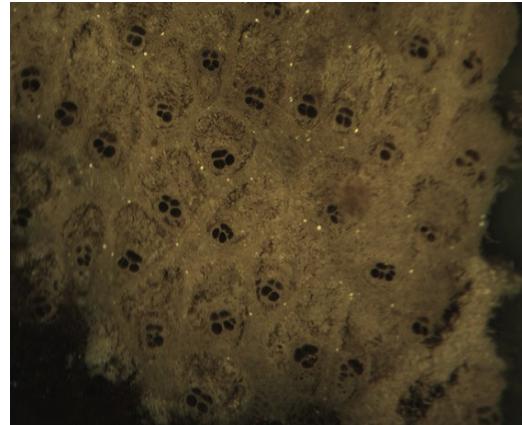
The distribution of vessels in cross-section aids in hardwood identification. Three types of vessel distribution are recognized. Ring-porous woods are characterized by a row or rows of relatively large earlywood vessel or pores. Vessels throughout the rest of the growth ring are much smaller in size. Oak, elm, and hickory are typical ring-porous woods. The fossil hickory specimen (genus *Carya*) from Oregon exhibits a ring-porous pore distribution (see image to the left). The earlywood



smaller across a growth ring. This image was taken at 20x. Diffuse porous woods possess vessels of equal size from early to latewood. Beech, sycamore, maple, and cherry are diffuse-porous woods (Hoadley, 1990, pp. 99-100). The fossil beech specimen (genus *Fagus*) from Oregon exhibits diffuse porous pore distribution (see image to the left). The pores are pretty much the same diameter across the entire growth ring. This image was taken at 20x.

Monocots

Monocots usually show no woody growth. However, some species, like the palms, produce fibrous, wood-like stems. In cross-section monocot fiber is fairly uniform yielding little specific taxonomic information. In cross-section fibrous monocots possess scattered vascular bundles embedded in a ground mass of parenchyma tissue (see picture to the right). In the center of the stem vascular bundles are spaced far apart. Towards the periphery of the stem the vascular bundles become more numerous and crowded. The individual vascular bundles can be seen in this Eocene aged fossil palm (genus *Palmoxylon*) specimen from Wyoming (see image to the right). Each vascular bundle is surrounded by numerous fibers, which thicken into a cap shape on one end. The fibers provide structural support. The empty spaces represent vessel for water conduction and sometimes air spaces. The phloem tissue would be found between the vessels and the bundle cap. This image was taken at 40x. The scattered vascular bundles making up the palm trunk form a fibrous composite, a design strategy that evolved earlier in the tree ferns.

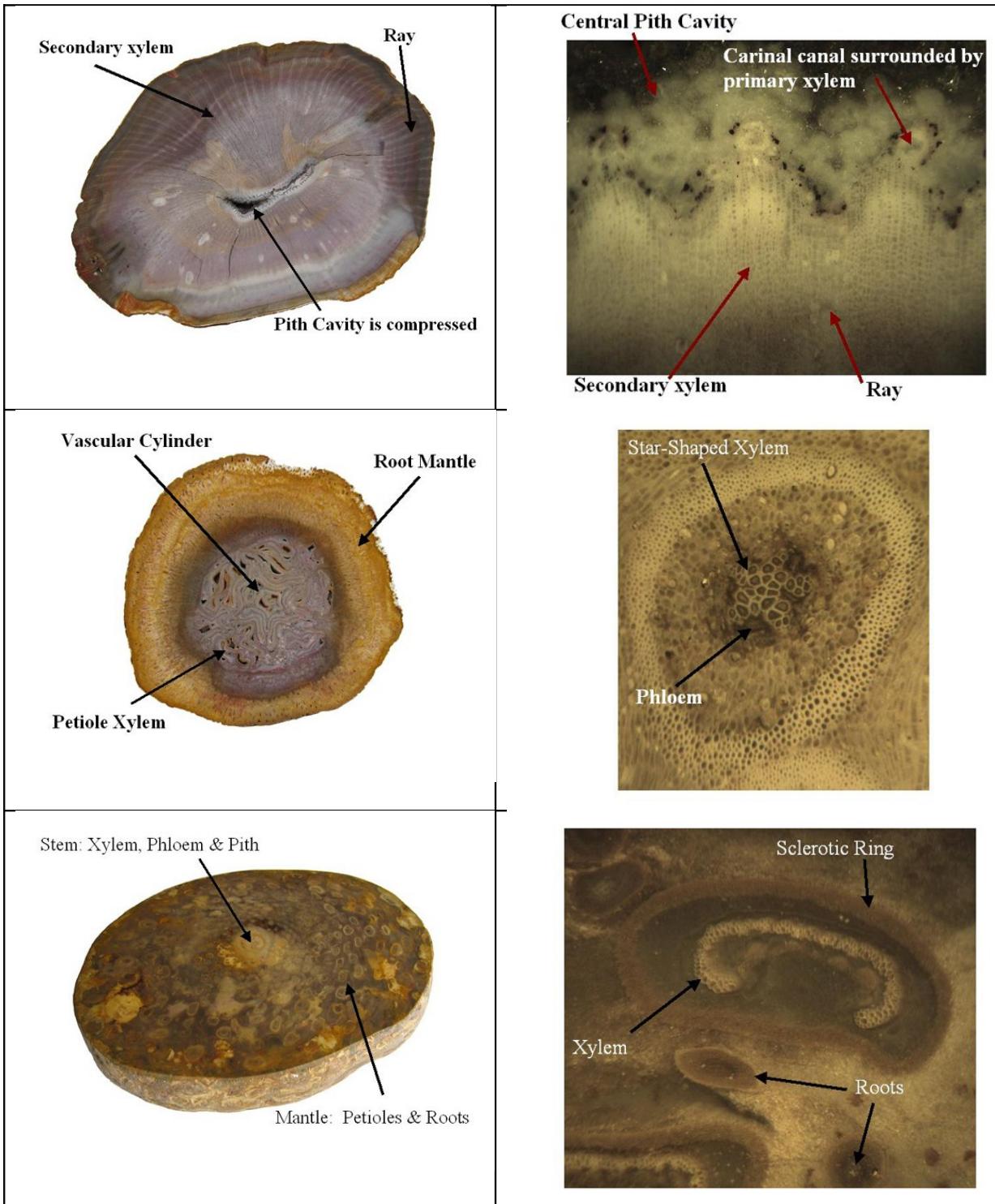


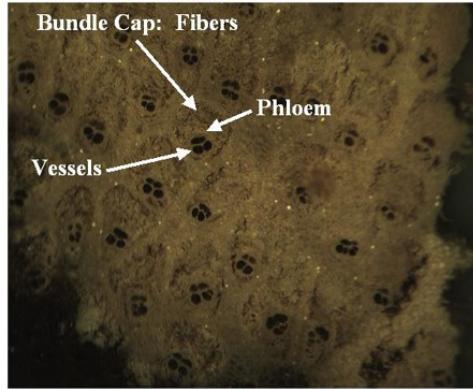
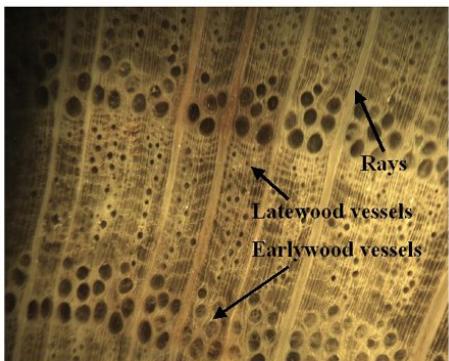
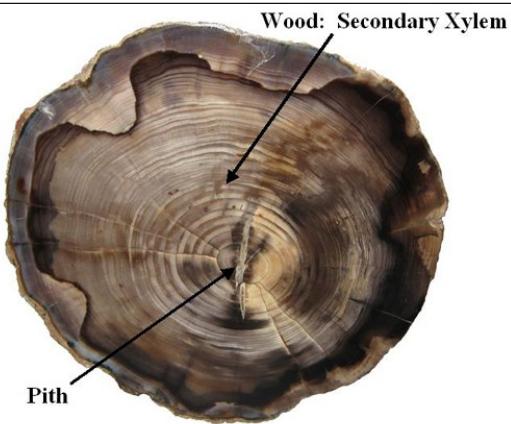
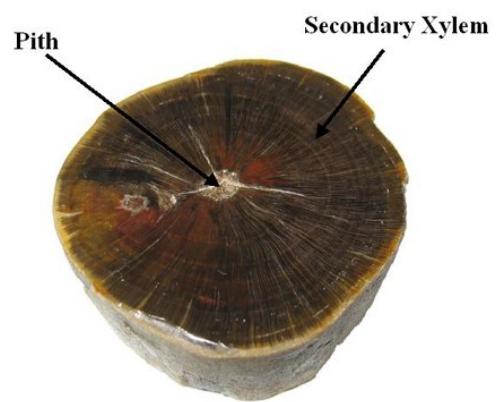
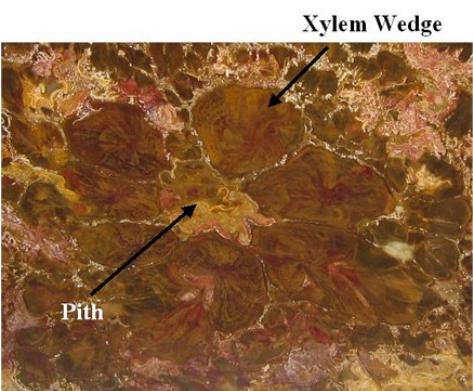
Convergent Evolution

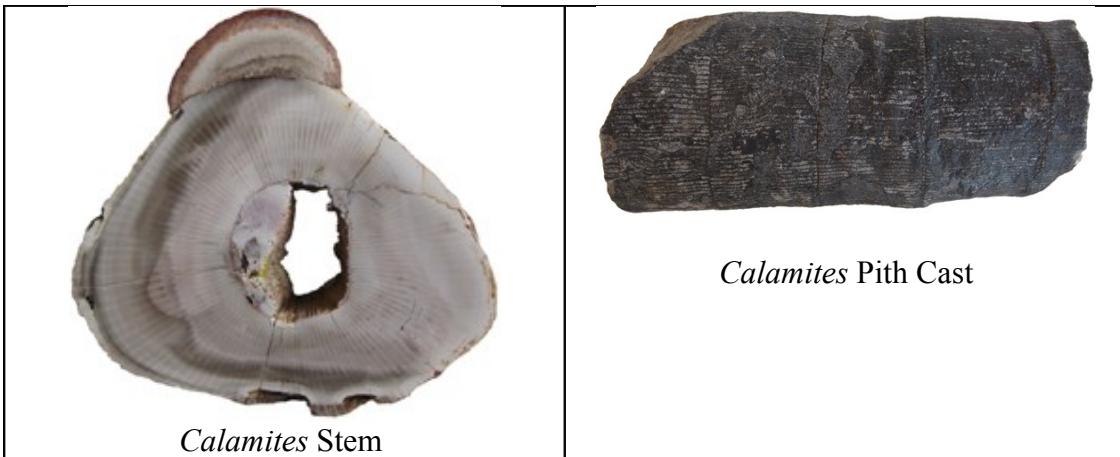
Growing taller than surrounding plants can be of real value when competing for sunlight; the tree form affords the adaptive advantage of height. The value of the arborescent form is reflected in the convergent evolution represented by the various tree forms we have examined. Several strategies for trunk designs have evolved multiple times. Arborescent lycopsids and horsetails utilized tube-like structures for their trunks. Arborescent ferns and latter monocots (palms) employed individual elements to form a fibrous composite trunk. Finally, arborescent seed ferns, gymnosperms, and angiosperm dicots constructed trunks of solid xylem cylinders. These different trunk designs co-opted a variety of plant tissues as strengthening elements. The student of permineralized tree forms can learn to identify these different evolutionary strategies and enjoy their unique structures. To view this article online, visit:

<http://petrifiedwoodmuseum.org>

Labeled Pictures







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