



Hydraulics of *Psilophyton* and evolutionary trends in plant water transport after terrestrialization



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ABSTRACT

Mathematical models of fluid flow through and embolism resistance of extinct plant xylem provide insight into the ecology and physiology of individual fossil plants. Disparate lineages of vascular plants exhibit a variety of ecophysiological strategies: extreme adaptations for maximum flow and maximum safety have both been documented in living and extinct plants. Analysis of early-diverging vascular plants and early-diverging seed plants shows that a variety of hydraulic strategies were pursued early in the evolution of terrestrial plants, especially during the Devonian and Carboniferous Periods. Analysis of five species of the Lower and Middle Devonian trimerophyte genus *Psilophyton* indicates that some species possess low-resistance metaxylem tracheids with numerous, highly porous pits and relatively low embolism resistance, whereas other species contain xylem with higher embolism resistance and lower hydraulic conductivity. Despite a simple vegetative morphology, physiological analysis of several *Psilophyton* fossils suggests that species possessed distinct ecophysiological strategies and there may be cryptic functional diversity within other trimerophyte genera. When integrated with previous hydraulic analyses of extinct and extant plants, including the Lower Devonian stem group lycophyte *Asteroxylon mackiei*; a series of Carboniferous stem group seed plants, including *Medullosa*, *Callistophyton*, and *Lyginopteris*; eleven genera of extant conifers and cycads; two species of ginkgophytes, and others, the occupation of tracheid-based hydraulic ecospace can be mapped. Soon after the evolution of vascular tissue in land plants, the high-conductivity/low-safety-margin space was occupied; particularly by plants that grew in the tropical lowland swamps during the Carboniferous Period. Upon the disappearance of the coal swamp floras during the Permian Period, that portion of the ecospace may have remained unoccupied until the evolution of angiosperms with vessels in the Cretaceous Period. Taken as a whole, the evolution of vascular tissue during (and after) the terrestrialization process records several physiological adaptive radiations, occurring early in plant evolution, which likely had major effects on global environmental and biogeochemical processes.

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1. Introduction

The evolution of a terrestrial flora required, and was facilitated by, a series of anatomical adaptations to enable oxygenic photosynthesis in an aerobic environment. Among the most important vegetative adaptations are the components of an integrated gas exchange system to which water is supplied through a vascular system. Exposing the hydrated interior of plant tissues to the atmosphere results in a loss of water, along with the capacity to absorb carbon dioxide as a substrate for photosynthesis, but evaporation of too great magnitude can cause embolism, wilting, dehydration, and, ultimately, death. Land plants, therefore, must balance the supply of water to sites of evaporation with demands imposed by the external environment with individual ecological strategies. Investigating the physiological ecology of extinct plants by analysis of their vascular system enables insight into broader

trends within land plant evolution, and the physiology of early vascular plants and seed plants serves as initial data points for long-term trends in plant evolution (Baas et al., 2004).

The land plant fossil record contains an extensive record of hydraulic structures (Fig. 1): unambiguous conducting cells are preserved within well-studied deposits, including the Rhynie Chert (Emsian: 405 Ma (Mark et al., 2011)) but banded tubes with morphological resemblance to early conducting cells can be found in Silurian deposits (Fig. 2) (Edwards and Wellman, 2001; Graham and Gray, 2001; Edwards, 2003). Within the Rhynie Chert, nonvascular plants such as *Aglaophyton major* (Fig. 3.1) can be distinguished from true vascular plants, such as *Asteroxylon mackiei* (Fig. 3.2) by examining cell wall differentiation within preserved axes. Multiple origins of secondary growth during the Devonian and Carboniferous Periods facilitated more complex anatomical structures, including dense wood (Fig. 3.3) in *Calamites* and unifacial cambial growth in *Sphenophyllum* (Fig. 3.4; Cichan, 1985; Eggert and Gaunt, 1973). However, nearly all xylem found within Paleozoic Era plants contains tracheids – with the exception of the

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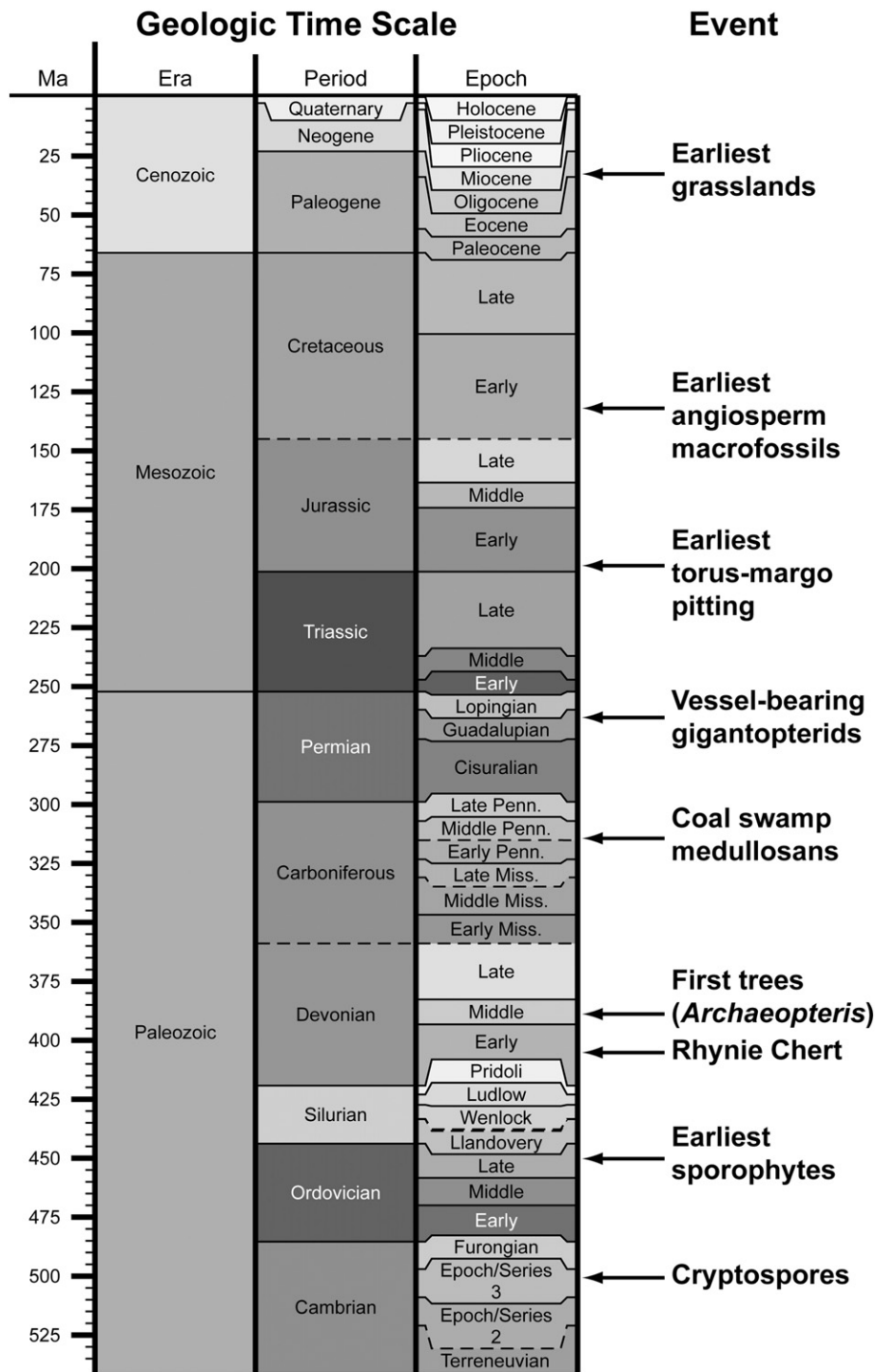


Fig. 1. Geologic time scale with plant evolutionary events in a chronostratigraphic context. Early events: cryptospores possibly related to stem group embryophytes are found in the Late Cambrian; early sporophytes appear no later than the Late Ordovician (Katian; Wellman et al., 2003); the Rhynie Chert lagerstätten is ~405 Ma (Early Devonian); first true trees (i.e. *Archaeopteris*) appear by the Middle Devonian. Middle events: coal swamp medullosans are widespread in Laurentia during the Pennsylvanian, and vessel-bearing gigantopterids appear in the Late Permian. Late events: the earliest torus-margo pits appear in the Early Jurassic (Hettangian); the first angiosperm macrofossils are approximately ~130 Ma (Early Cretaceous); grasslands appear and radiate in the last ~30 Ma. Geologic time scale produced using TimeScale Creator© 2015, Geologic TimeScale Foundation.

gigantopterids (Li et al., 1996; Li and Taylor, 1999) – which are dead and lignified water transport cells that are closed at the ends, and can therefore be compared between phylogenetic groups.

During the Devonian and Carboniferous Periods, fossilized xylem captures increasingly elaborate structures on the lateral walls of conducting cells (Kenrick and Crane, 1997; Edwards, 2003). Nonvascular plants, including *Aglaophyton major*, contain putative conducting cells which occasionally contain ambiguous features resembling lateral

bars, perhaps indicating deposition of secondary cell wall material (Fig. 4.1), in contrast with true vascular plants, such as *Asteroxylon mackiei*, which contain xylem with helical-annular thickenings and differentiated porous zones in between (Fig. 4.2) (Edwards, 1998; Wilson and Fischer, 2011a). Analysis of trimerophyte xylem, particularly *Psilophyton*, shows the presence of a diverse suite of xylem cell wall features, including secondary wall deposits (Fig. 4.3), scalariform-shaped pit apertures (Fig. 4.4), bars across the aperture (Fig. 4.5), and hints of

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