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Evolution of Tracheary Elements and the Gnetophyta

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Abstract

Extensive comparative studies of the Tracheophyta demonstrate that vessels originated independently in the Selaginellales, Salviniales, Filicales, the Angiospermae and the Gnetophyta. These investigations reveal that the first vessels to appear in these groups developed as modifications of tracheids with bordered pits. In the Angiospermae, vessel perforations evolved through the dissolution of pit membranes in scalariform bordered pitting. In the Gnetophyta, perforations developed through the modification of circular bordered pits. The possession of vessels by these groups has raised questions about their phylogenetic relationships. The mode of vessel development, their origin and specialization are quite distinct, illustrating independent evolution.

Key Words: Tracheids, Vessels, Tracheophyta, Gnetophyta, Angiospermae, Evolution

Introduction

Few people have chosen to study the Gnetales, composed of three diverse and unique extant genera: Welwitschia, Gnetum and Ephedra, however those who have had the opportunity, experience a profound sense of extraordinary beauty and complexity in examining the evolutionary process of this most intriguing of plant lineages [1]. During the transition of plants from an aquatic to a terrestrial environment, significant morphological and physiological changes occurred. Water loss by transpiration with carbon dioxide uptake through stomata, the accelerated transport of water and solutes over greater distances with increased mechanical strength in the plant necessitated the development of a cell capable of enhancing conduction and imparting rigidity and support to its tissues. Thus, the Tracheophyta arose characterized by the formation of tracheary elements [2].

Xylem

Xylem is a complex plant tissue composed of several types of cells. The most characteristic components of this tissue are the tracheary elements, which are non-living cells with a supporting function principally concerned with the transport of water, minerals and food storage. The xylem produced by the meristematic procambium is called primary xylem, and secondary xylem is derived from the vascular cambium [3].

There are two types of tracheary elements: tracheids and vessel members. They both have secondary walls with pits, and lack protoplasts at maturity, which is the protoplasm of an individual plant cell. Protoplasm is the living substance of plant cells within the cell wall [3]. Tracheids are considered more primitive than vessels. Vessel members are perforated on their end or lateral walls, where they are in contact with other vessel members. They are fused into long continuous tubes, where sap flows through them, passing freely from vessel element to vessel element through these perforation plates [4]. Scalariform perforations are ladder-like and are arranged in a parallel series. Foraminate perforations are arranged as a group of circular or elliptical holes.

In the Ophioglossales, Coniferales, Ginkgoales and the Gnetophyta, scalariform pitted tracheary elements are not present [5]. Secondary walls of tracheary elements are lignified and often develop as a series of annular rings, spiral bands, helical thickening or pits. Tracheids are typically more elongated than vessel elements and their diameter is generally smaller. The xylem of most of the Angiospermae is composed of both vessel elements and tracheids. Vessel members are considered more efficient water conductors than tracheids as water flows through their perforation plates, however they are less safe for the plant body than tracheids. Water flowing from tracheid to tracheid passes through their pit pair membranes and this can block air bubbles. Air bubbles that may form in a tracheid are confined to that tracheid. If an embolism is formed in a vessel element, this can impede the water flow through the entire length of the vessel. Shorter vessels are safer than longer ones yet wider vessels are more efficient water conductors [3,6].

Tracheids of the gymnospermous Gnetophyta and Coniferales have a torus, which is a thickened central part of the pit membrane [3]. The function of the torus, which is suspended by slender, flexible strand-like margo threads is closure of the aperture of the pit during aspiration, when a tracheid that has filled with air is sealed off, by displacement of tori thus closing the pit apertures, from functioning tracheary elements [6].

Phylogenetic Considerations

Xylem anatomy plays an important role in the study of phylogeny. Extensive comparative studies have evaluated variation in the morphology of tracheary elements and have explained their significance [4]. The tracheid is considered a more primitive element than the vessel member as it is found in the Pteridospermae, fossil seed plants, seedless vascular plants and the Gymnospermae. All gymnosperms are vesselless except for the three genera of the Gnetales – Ephedra, Gnetum and Welwitschia (Carlquist 1975:83). Vessel elements evolved from tracheids and are present in the Gnetophyta, Angiospermae, Pteridium, Marsilea, Equisetum and the Selaginellales. Vessels arose independently by parallel evolution in these groups [4,5]. Gnetalean vessels appear to have originated from a vesselless gymnosperm group [6]. The Gnetales may have originated in the Permian and radiated in the Mesozoic probably predating angiosperms and coexisting and competing with them since the lower Cretaceous, however inferential molecular timing for Gnetum places its origin in the Eocene [7].

In the Gnetophyta, vessel members evolved from tracheids that had circular bordered pits. Intercalated bordered pits are not present in the primary xylem of the Angiospermae. The circular bordered pits on the lateral walls of Welwitschia, Gnetum and Ephedra vessels are markedly unlike those on the lateral walls of Angiospermae vessels. Tracheids of the Gnetales from which gnetalean vessels are to be derived, bear little resemblance to Angiospermae vessels [6]. The possession of vessels by the Angiospermae and the Gnetotyphta is a remarkable illustration of vessel development by different plants of a similar highly specialized structure [8]. Gnetalean vessels were derived independently from those of the Angiospermae. The likely sister group of the Gnetales is a vesselless gymnosperm [6].

The Gnetophyta

The Gnetophyta is comprised of three diverse extant genera: Welwitschia, Gnetum and Ephedra. The tracheids of Welwitschia are not unlike the tracheids of angiosperms as the pit membranes depend on minute pores and their relative stiffness prevents cavitation. Welwitschia, the extraordinary African desert wash shrub is often regarded as ecologically, morphologically and physiologically unique. The presence of vessels in Welwitschia provides conductive efficiency rather than having an all-tracheid system. The tracheids and vessels of the Namib desert wash endemic, Welwitschia are quite narrow with simple perforation plates [7]. The vessels in the Gnetophyta are believed to have evolved independently and differently from Angiospermae vessels [9].

The universal cladistic placement of Ephedra is considered basal to Welwitschia and Gnetum [6]. The tracheids of Ephedra are pitted with large circular fully bordered pits and the vessels are larger in diameter. Numerous transitional stages between tracheids and vessels may be observed in the xylem of Ephedra [10]. Perforations in the end walls of the tracheids, which give rise to the vessels originated from circular bordered pits [5]. Ephedra is noted for its foraminate perforation plates however helical thickenings are prevalent in the tracheids and vessels of some species of Ephedra [10]. The helical thickenings on vessels and tracheids of numerous Ephedra species are probably a function in embolism prevention and reversal [7]. The tracheids of Ephedra, with their large torus-bearing circular bordered pits are unlike those of the Angiospermae, whose metaxylem possesses the prevalent scalariform pitting that is absent in Ephedra. The primary xylem of Ephedra and the conifers have tracheids, which bear bordered pits intercalated into helical bordered bands. Perforation plates of Ephedra appear to be derived from tracheids like those of conifers rather than those of angiosperms, which supports Thompson's interpretation of independent origin of Gnetales and the Angiospermae [8,10].

Helical thickenings are prominent in the tracheids and vessels of Ephedra. They are believed to serve as a means for increasing wall surface area in conducting cells and deterring embolisms or possibly aiding in the repair of embolisms. Helical thickenings in the vessels and tracheids of Ephedra are present in almost all North American species however no South American species of Ephedra with helical thickenings has been reported [7].

Most of the characteristics by which species of Ephedra differ from one another are best interpreted in terms of rapid and sensitive adaptation to habitat and ecology. Ephedra rupestris, which is a high alpine shrub, is nearly vesselless. Ephedra reveals a strong conductive safety presence with virtually no vessels in alpine desert species. Narrow vessels, which are characteristic of species of Ephedra embolize less readily than wider vessels and characterize quite arid and desert habitats [7]. Lianoid species of Ephedra have more numerous and wider vessels in the stem latewood than do other species of Ephedra. Thus, with increased transpiration, wider and more numerous vessels represent an adaptation to conduction of larger volumes of water in Ephedra species that have greater water availability and therefore diminution in conductive safety has little or no negative effect [10].

Carlquist observed that vessel element and tracheid length increased with the enlargement of stem diameter in Ephedra, and vessel diameter tends to increase with age. Narrower vessels are less likely to embolize than wider vessels. A decrease in vessel diameter correlates with lower water availability. Larger shrubs, small trees and lianas have wider vessels. Carlquist suggested that this may be a mechanism for coping with greater demands for the conductive volume in plants. There are no Ephedra habitats that qualify as mesic. They range from dry to very dry [10].

All Gnetum species have tracheids with torus-margo pit membrane structure, which is indicative of conductive efficiency and safety as observed in non-gnetalean conifers. The torus-margo system occurs in tracheid-tracheid pits as well as tracheid-vessel pits [7].

In Gnetum, the vessel elements are characterized by having large circular or elliptical simple perforations [9]. Gnetum is the only genus of the Gnetales in which vestured pits have been noted mostly in vessels however there is some vesturing in the pits of tracheids [7]. The vessels of Gnetum resemble the vessels of some angiosperms however the similarity is not an indication of close relationship but provides a significant illustration of convergent evolution in plants [2].

The circular bordered pits on the lateral walls of Welwitschia, Gnetum and Ephedra are markedly unlike those on the lateral walls of Angiospermae vessels reported tori of tracheary elements in three lianoid Indomalesian and Asiatic species of Gnetum [6,11]. Tori were observed on pit membranes of vessel to tracheid and tracheid to tracheid contact in two African species of Gnetum. The tori are quite thick with fibrillar margo strands surrounding them. The circular torus serves as a closure valve to maximize conduction and permit closure of the pit upon cell aspiration [12].

Fiber-tracheids, which are non-conductive and supportive were reported in the lianoid species of Gnetum and Ephedra. Fiber-tracheids are not present in Welwitschia. Perforation plates of Gnetum are simple or foraminate. The broad leaves of Gnetum favor simple perforation plates to accommodate peak flows in vessels. The presence of tori and foraminate perforation plates are features that are more reminiscent of Ephedra and other Gymnospermae rather than of the Angiospermae. The classical perspective that the vessels of Gnetum are unlike those of the Angiospermae is supported [6,13,14]. Fine helical thickenings of vessels are present in some species of Gnetum. As observed through Scanning Electron Microscopy, most vessel surfaces of Gnetum are smooth [7].

When considering the anatomy and morphology of the three notably diverse gnetalean genera, Welwitschia, the African desert endemic has departed from a hypothetical common ancestor. Welwitschia vessels are significantly different from those in Ephedra and Gnetum. Welwitschia possesses simple perforation plates and fiber tracheids are absent [7].

Quantitative tracheid and vessel data have not been presented for the secondary xylem of Welwitschia, whose xeromorphic wood is not comparable to a desert shrub, succulent or other xerophytic plant. Welwitschia root tracheids are quite conduction-effective and are three times as numerous as vessel elements in the secondary xylem. Welwitschia, as many species of Ephedra possess the xeromorphic helical sculpturing on the inner surfaces of tracheids and vessels. Helical sculpturing occurs in some species of the Coniferales [6].

In Welwitschia and Ephedra, the tracheids are slightly longer than vessel elements. The lengths of vessel elements in xeromorphic Welwitschia and Ephedra are quite similar. Observations of secondary growth in Welwitschia roots were reported by Carlquist and Gowans in 1995. The walls of tracheary elements in Welwitschia are somewhat gelatinous, which may be related to water economy to a minor extent. The abundance of cells with gelatinous secondary walls in Welwitschia may be for short-term storage of small amounts of water [15]. The presence of minute calcium oxalate crystals lining intercellular spaces in the xylem and phloem rays were documented. This extraordinary feature is also present in Ephedra and has not been observed in other vascular plants [6].

Conclusion

The most important element of vegetative anatomy when attempting to decipher the phylogenetic relationship of the Gnetales is the gnetalean vessel, which has originated separately from those of angiosperms. The nature of the perforation plates represents an extension of, or a modification of lateral wall pitting. The foraminate perforation plate of Ephedra is regarded as derived from an assemblage of circular bordered pits. This condition in Ephedra is considered as little modified from primitive Gnetales vessels in accordance with the universal cladistic placement of Ephedra as basal to Welwitschia and Gnetum [6].

Habitat and ecology are significant considerations in analyzing quantitative vessel characteristics [12]. Structural similarities may not be indicative of close phylogenetic relationships. Parallel specializations of vessel elements have taken place independently in diverse groups [2]. To attain a clean understanding of phylogenies, we must analyze the evidence from all plant tissues, organs and parts carefully and extensively. The tracheary elements of Gnetum are not fundamentally different from those of Ephedra, which can be considered evidence for the monophyly of the Gnetales. Ephedra and Gnetum both possess fiber tracheids, tracheids and foraminate perforation plates [6].

The careful and extensive investigations of Carlquist and Robinson reveal the presence of tori and foraminate perforation plates in Gnetum that exhibit resemblance to Ephedra as well as other gymnosperms rather than angiosperms [12]. These clear findings illustrate potential phylogenetic significance. In addition, a special feature of the helical bands of secondary wall material in the metaxylem tracheids of the Gnetales, conifers and Ginkgo, which has been observed for many years, is that circular bordered pits are intercalated into these bands. This is not present in the primary xylem of the Angiospermae [6].

In the Gnetophyta, vessels developed from tracheids with circular bordered pits. In the Coniferales, Ginkgoales and Gnetales, true scalariform bordered pitting does not exist and circular bordered pits develop in the earlier stages of the ontogenetic sequence. In the Angiospermae and in Pteridium, vessels originated by the modification of tracheids with scalariform bordered pits. These are significant fundamental anatomical differences. Thus, vessel development in these groups reveal independent evolution [2]. There is no phyletic connection between the Gnetales and primitive dicotyledonous angiosperms (Carlquist 1975:83). The Gnetales appear to have originated from a vesselless gymnosperm group [6]. Extensive studies have laid the groundwork for confirming the concept that the Gnetales are coniferalean ("gnetifers", gnepines"). Although Ephedra, Gnetum and Welwitschia do have vessels, they are different from those of the Angiospermae [7].

The Gnetales have a relatively long fossil history and Ephedra, Gnetum and Welwitschia had an already distinct presence in the lower Cretaceous [12]. As the interrelationships of the three gnetalean genera continue to be researched with great interest, we will be able to develop a more accurate assessment of their phylogeny. In addition, we will come to better understand how the Gnetophyta are related to other vascular plant groups [15].

Bailey wrote, "As one who is approaching the terminal stages of his career, to offer a word of friendly advice to the younger generation of taxonomists, paleobotanists and morphologists who may become interested in the origin of angiosperms: Look West…toward the remnants of Gondwana Land [16,17]

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