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Permian Vessel Elements

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Anatomically preserved stems from the Late Permian (250 to 270 million years ago) of China have been discovered that contain vessels. The stems possess several features commonly found in vines, including tendril-like appendages, and are associated with large leaves assignable to the Gigantopteridales, an enigmatic group of Permian plants. The individual vessel elements contain foraminate perforation plates in their end walls and are anatomically similar to the conducting elements of modern gnetophytes and of some extant flowering plants.

Tracheids and vessels are the two principal types of water-conducting cells in vascular plants. Tracheids are generally elongate cells with imperforate end walls, whereas vessels consist of a series of individual members joined by perforate end walls. As water moves through a vertical series of tracheids, it must move through primary wall material at the end of each cell. Because of their perforated end walls, however, vessels allow barrier-free water movement and thus result in a considerably more efficient water conduction system. Although vessels have been reported in a few vascular cryptogams (*1*), for the most part they are characteristic of angiosperms. Vessels have been documented in fossil angiosperms as early as the Lower Cretaceous (Albian) (*2*) but had not been found in other groups of fossil plants. Here we describe vessel-bearing plants from the Upper Permian of western Guizhou Province, China. They are preserved as calcium carbonate permineralizations and were studied by means of cellulose acetate peels for light microscopy or as fractured stem sections for scanning electron microscopy.

The stems are slender, typically less than 1 cm in diameter, and are characterized by elongate tendril-like appendages extending from the epidermis. Surrounding the central pith are five to nine fan-shaped, mesarch, primary xylem segments, each bordered by a zone of secondary xylem to the outside (Fig. 1). Protoxylem tracheids possess annular to helical secondary wall thickenings, whereas the metaxylem elements range from reticulate-scalariform pitting to circular bordered pits. Secondary xylem elements consist of a small number of vessels on the inside of the stem and several rows of tracheids toward the periphery. Extending through the secondary xylem are vascular rays that are 1 to 2 cells wide and up to 60 cells high.

Within the secondary xylem, tracheids are triangular-rectangular in cross section and from 50 to 90 µm in diameter; side walls possess circular bordered pits, each approximately 9 µm in diameter. Vessels vary from 150 to 300 µm in diameter; a few near the stem center are nearly 500 µm in diameter (Fig. 2). Vessel elements are 5 to 7 mm long, with end walls that are generally oblique (Fig. 3). A few are shorter and possess end walls that are nearly perpendicular. Each end wall consists of a multiperforate perforation plate with approximately 14 rows of circular perforations (Fig. 4), each approximately 14 to 16 µm in diameter. Perforations near the margin of the perforation plate are slightly smaller, and typically the primary cell wall material is incompletely dissolved within the perforation (Fig. 5). The side walls of these Permian vessels exhibit multiple rows of circular-to-oval bordered pits, and these are generally less than 10 µm in diameter.

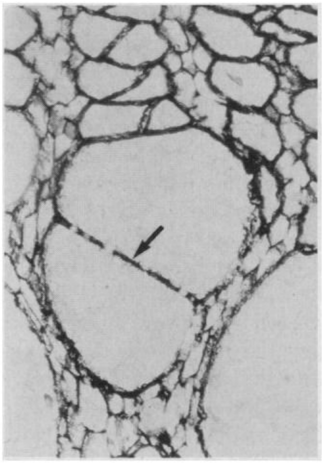

Fig. 2. Transverse section showing two vessel elements with perforation plate (arrow) between them. Width of photograph, 66 mm.

In the same blocks as the permineralized stems are numerous leaves assignable to *Gigantopteris* and *Gigantonoclea*, two leaf morphotypes included in the Gigantopteridales (*3*). Although the gigantop-

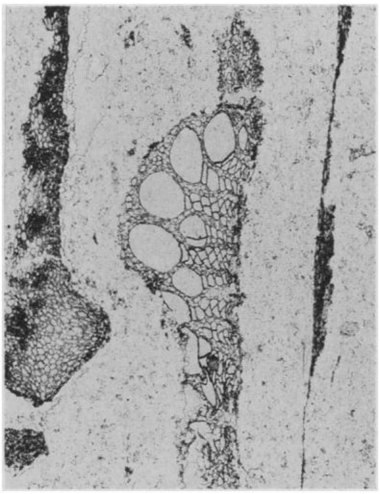

Fig. 1. Transverse section of a wedge of secondary xylem showing tracheids and large vessels. Width of photograph, 70 mm.

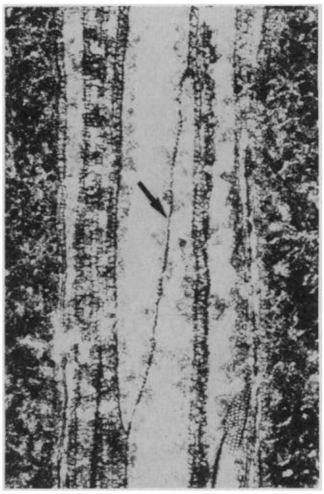

Fig. 3. Longitudinal section of vessel showing oblique end wall (arrow). Width of photograph, 66 mm.

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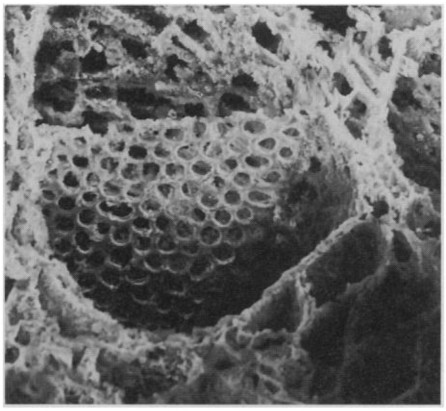

Fig. 4. Two vessel elements showing foraminate perforation plates in face view. Width of photograph, 73 mm.

terids were widely distributed throughout China, Japan, Korea, and southeast Asia during much of the Permian, their taxonomic affinities remain poorly understood because of a lack of well-preserved reproductive organs. Leaves believed to represent this group have also been reported from the Lower Permian of the southwestern United States (*4*). Gigantopterid leaves are unusual because of their large size (typically greater than 400 cm^2) and multiple orders of venation, which compare in complexity with the venation patterns of certain angiosperms (*3*).

Among living plants, vessel elements are found principally in angiosperms (*5*). Vessels also are found in several vascular cryptogams, such as *Selaginella* (*6*), *Equisetum* (*7*), and some filicalean ferns (*8*), as well as in modern gnetophytes (*9*). Vessel elements may be highly variable in diameter, length, end-wall orientation, and type of perforation plate (*10*). Narrow vessels are typically found in more arid sites (*11*), although lianas typically have vessels larger in diameter (157 μm on average, and up to 500 μm in diameter) than those of woody dicots (*11*, *12*). Modern lianas typically have large leaves relative to their stem diameter, and vessels in these narrow stems are the largest for any category based on habit or habitat (*13*). Large vessels in climbing stems probably represent an adaptation to more efficient water conduction, especially where evapotranspiration is high in sunny canopy tops. In addition, because these plants are not self-supporting, their xylem tissue can be used principally for water conduction instead of compromising between support and conduction, as is the case in other woody plants. These same anatomical characters that are typical of a liane habit (narrow stems, large vessel diameters, and massive leaves) also appear in the gigantopterid plants and probably represent similar physiological adaptations. Thus, because it appears that both the environment and the liane habit demand high water efficiency, it is perhaps not surprising that vessels are found in these Permian plants. The presence of elongate tendril-like epidermal appendages on the stems and the fragmented nature of the vascular tissue provide additional support for the reconstruction of these plants as lianes.

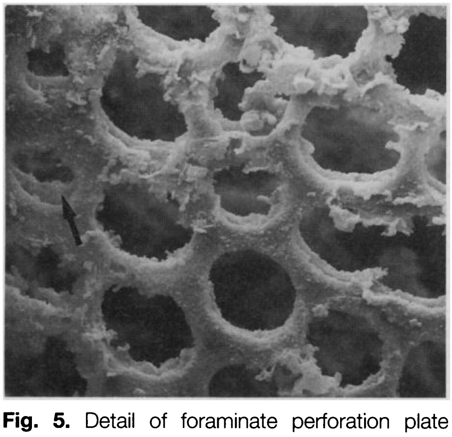

Fig. 5. Detail of foraminate perforation plate showing remnants of primary cell wall at arrow. Width of photograph, 94 mm.

There are currently at least two theories regarding the origin of vessels in seed plants, but in both, vessels are thought to have originated by dissolution of the primary cell wall in certain areas of the end walls, thus forming perforations. If seed plant vessels are polyphyletic, then they arose separately in gnetophytes and angiosperms (*9*, *14*), and gnetophyte vessels are fundamentally different from those in angiosperms. Because foraminate perforations are found only in gnetophytes, gnetophyte vessels are believed to have developed from tracheids with circular bordered pits on their end walls. Angiosperm vessels, on the other hand, evolved from tracheids with scalariform end-wall pitting. Muhammad and Sattler (*15*) have suggested that *Gnetum* contains both foraminate and scalariform perforation plates, thus implying that gnetalean and angiosperm vessels may be homologous (*5*). Although neither type is designated as primitive, these authors suggest that the scalariform type could have resulted from lateral fusion of foraminate perforations (*15*). Carlquist examined a number of species in the gnetalean genera *Ephedra* (*16*) and *Gnetum* (*9*) and concluded that gnetalean vessels are fundamentally more similar to conifer tracheids (perforation plates developed from circular bordered pits) than to angiosperm vessels. The presence of typical foraminate perforation plates and gymnospermous circular bordered pits in these fossil gigantopterids, which predate the first appearance of angiosperms by many millions of years, would seem to support this hypothesis.

Thus the presence of vessels in a group of Permian vascular plants provides a dilemma as to the importance of this character in tracing the origin of angiosperms. On the basis of the presence of vessels and leaves with a complex venation pattern, the Asian gigantopterids most closely resemble both the extant gymnosperm *Gnetum* and the angiosperms, two groups that are included in the anthophyte clade in cladistic analyses (*17*). Despite these vegetative similarities, the absence of well-documented gigantopterid reproductive structures makes assignment to any group premature at this time. Although some chloroplast DNA data have placed angiosperm diversification as early as the Permian (*18*), the earliest fossil evidence continues to position the origin of the group during the Early Cretaceous (*19*). A more realistic hypothesis is that the vessels in these Permian plants demonstrate an example of structure-function relations that became coupled during the evolution of a liane habit, rather than evidence of the origin of a particular group of plants. The gigantopterid vessels do, however, provide anatomical evidence for an ancient origin of foraminate perforation plates similar to those seen in modern gnetophytes.

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