

AXIAL VASCULARELEMENTS IN RADIAL SEGMENTS

By Marcelo R. Pace

This cambial variant is marked by the presence of very wide vascular rays that separate the axial elements of xylem and phloem into seemingly discrete portions.

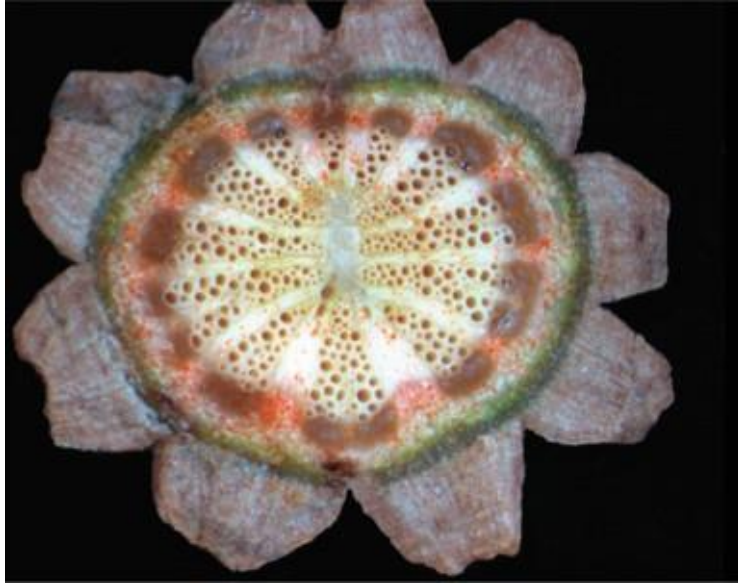


Fig. 1. Stem cross-section of *Aristolochia gigantea* (Aristolochiaceae). Note axial xylem and phloem elements separated by wide rays.

Although this cambial variant is not exclusive of lianas, it has been suggested that its presence may favor the evolution of the lianoid habit within the lineages where it occurs (Trueba et al. 2015). It is regarded as some sort of preadaptation (exaptation sensu Gould & Vrba 1982) to the climbing habit, since wide and tall rays are known to make stems more flexible.

This cambial variant is present in many members of **order Piperales** (Isnard et al. 2012, Trueba et al. 2015), which include the species-rich families Piperaceae and Aristolochiaceae. These include noteworthy lianas such as the black pepper (*Piper nigrum*) and the ornamental aristolochias (Aristolochiaceae). In some *Piper*, the ray has the height of an entire internode, reaching several centimeters (Pace, 2015).

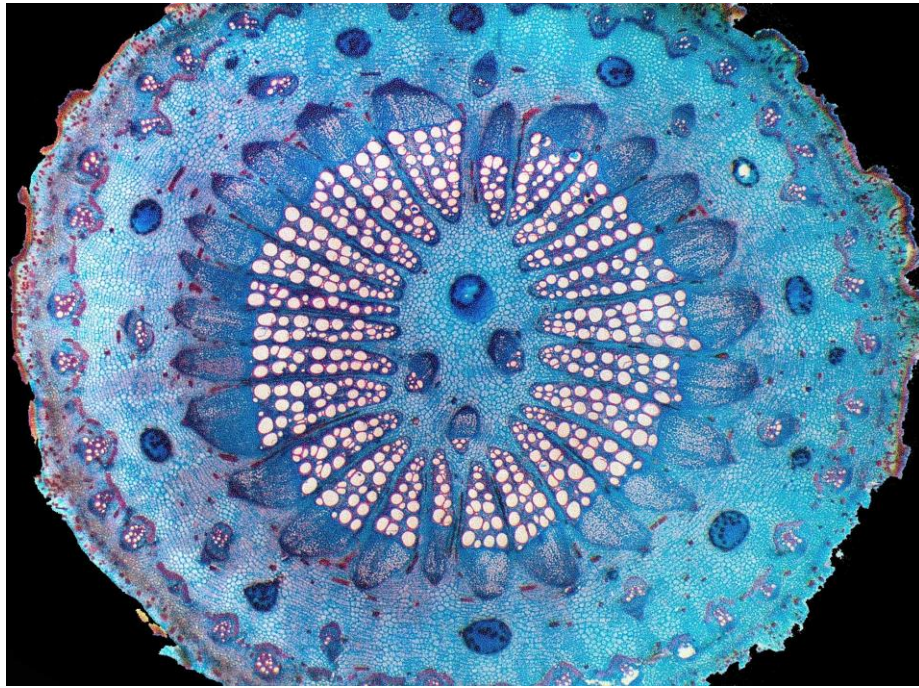


Fig. 2. Stem cross-section of *Manekia obtusa* (Piperaceae). Notice the additional formation of vascular bundles in the pith and cortex.

This cambial variant is also typical of all members of the family Dilleniaceae, which contains large lianescent genera such as *Davilla* and *Doliocarpus*, all members of Proteaceae, and several almost entirely lianescent families such as Convolvulaceae, Cucurbitaceae, Gnetaceae, Menispermaceae, Passifloraceae, and Vitaceae. In Asteraceae, it seemsto have evolved in concert with the lianescent habit in *Mikania*.

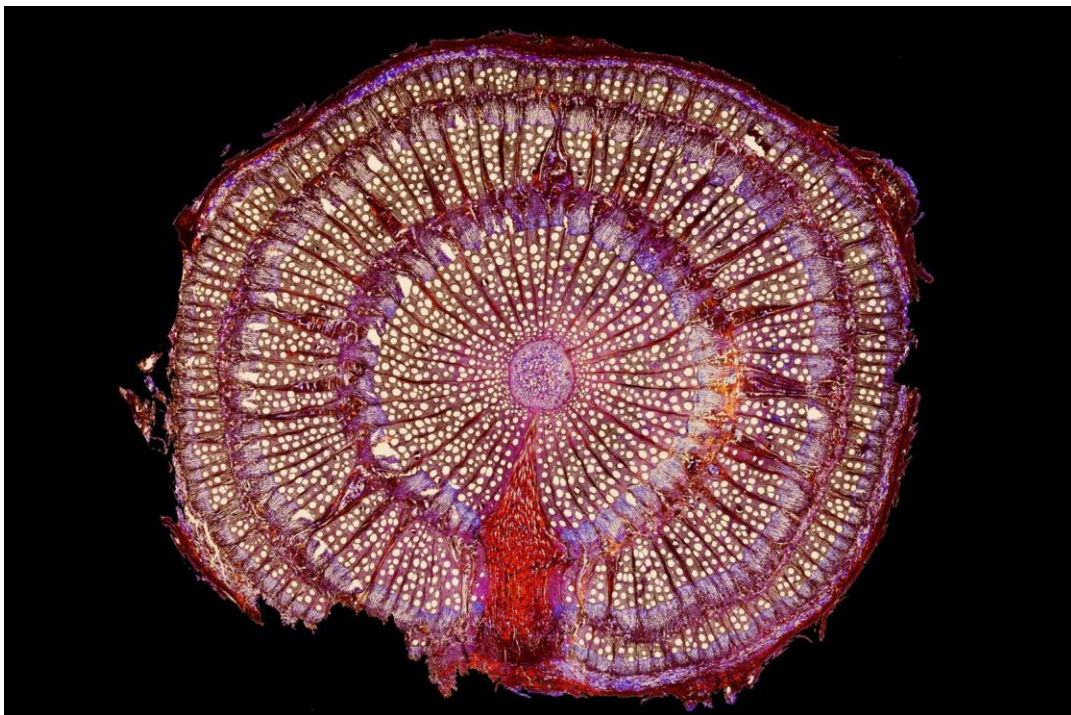


Fig. 3. Stem cross-section of *Doliocarpus dentatus* (Dilleniaceae). Note axial xylem and phloem elements separated by wide rays, and the presence of successive cambia.

Ontogenetically, this cambial variant derives from a differential activity between the fascicular and interfascicular cambium, with the fascicular cambium producing exclusively the axial elements of xylem and phloem and the interfascicular cambium producing exclusively xylem and phloem rays.

There are many misnomers involving this cambial variant, especially the use of terms such as vascular bundles for the discrete portions of secondary axial elements or referring to this variant as ‘xylem in plates’. In both cases, these terms convey the idea that the rays are not part of the xylem, phloem or the vascular cylinder. Therefore, a better, more accurate term is “axial elements in plates”, clarifying that the axial elements are separated by the extremely wide rays, but that the vascular cylinder is still a complete, cohesive structure including the rays.

Some families and genera that have this cambial variant, display additional informative anatomical characters that can set them apart. For instance, *Aristolochia* usually has a very thick outer bark (rhytidome – see Fig. 1). Many species of Menispermaceae, Gnetaceae and *Doliocarpus* (Dilleniaceae) have successive cambia. In Piperaceae there will be additional vascular bundles either in the cortex, the pith or both, depending on the genus (Fig. 2; Trueba et al. 2015).

References

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- Trueba S., N.P. Rowe, C. Neinhuis, S. Wanke, S.T. Wagner, and S. Isnard. 2015. Stem anatomy and the evolution of woodiness in Piperales. *International Journal of Plant Sciences* 176: 468-485.