PHLOEM ARCS/WEDGES

By Marcelo R. Pace

This cambial variant (also known as furrowed xylem or interrupted xylem) is formed by differential production of vascular tissue by the cambium during secondary growth. While most of the cambium maintains a regular secondary growth, in localized areas there is an increment in the production of phloem at the expense of xylem production. The net result is that phloem wedges or arcs are formed as progressive invaginations within the periphery of the xylem. Phloem arcs and wedges occur in lianas or scandent plants within several families in the Neotropics, most notably Apocynaceae, Asteraceae, Bignoniaceae, Celastraceae, Combretaceae, Convolvulaceae, Euphorbiaceae, Fabaceae, Malpighiaceae, Passifloraceae, Sapindaceae, and Trigoniaceae.

Within this cambial variant two main groups are distinguished based on the structure of the vascular cambium. One group is distinguished by the presence of **discontinuous cambium**, resulting in the inclusion of fragments of the original (concentric) cambium within the phloem wedges. These phloem wedges are radially lined by wide rays which sharply demarcate the phloem from the surrounding xylem. This feature was referred to as limiting rays by Scheck (1893). Phloem wedges of this type are characteristic of Bignoniaceae, Celastraceae (Hippocrateoideae), Fabaceae (Mimosoidae), and Icacinaceae. Within this category, **Bignoniaceae** is the easiest family to distinguish, as the phloem wedges are always **four** (or multiples of four) and **equidistant**. These occur in alternation with the decussate leaf orthostichies. Some of the patterns observed in Bignoniaceae are exclusive of genera or groups of genera, and therefore useful in their characterization as follows:

- a. <u>Four phloem arcs</u>: *Perianthomega* (Fig. 1) and in non-climbing species of *Adenocalymma*,
 Cuspidaria, and *Fridericia* that occupy dry habitats.
- <u>Four phloem wedges in mature stems</u>: most *Adenocalymma*, and all *Cuspidaria*,
 Fridericia (including most of the former *Arrabidaea*), *Manaosella*, *Martinella*, *Pachyptera*,
 Pleonotoma, *Stizophyllum*, *Tanaecium*, *Tynanthus*, and *Xylophragma*.
 - i. Within this group, *Manaosella* (Fig. 2A) is the only genus that has sclereids instead of fibers in the regular phloem (between phloem wedges).
 - ii. *Tanaecium* (Fig. 2B) is the only genus in which the phloem wedges do not form lateral steps.
 - iii. Cuspidaria and Tynanthus (Fig.3C) are the only genera that produce perfectly

symmetrical phloem wedges, with an almost equal number of steps on each side of the phloem wedges.

- iv. *Stizophyllum* (Fig. 2D) is the only genus in this group with a hollow medulla.
- c. <u>Multiple of four phloem wedges in mature stems</u>: some *Adenocalymma*, *Lundia*, *Anemopaegma*, *Bignonia*, *Mansoa*, and *Pyrostegia*.
- d. <u>Included phloem wedges in mature stems</u>: The cambium resumes its regular activity after the initial period where phloem wedges are produced, resulting in the inclusion of the wedges into the xylem. This process characterizes the genus *Amphilophium* (Pace et al., 2009).
- e. <u>Multiple dissected phloem wedges</u>: the non-lignified parenchyma within the xylem multiplies, breaking up the lignified cells and engulfing the phloem wedges. This pattern characterizes the genus *Dolichandra*.

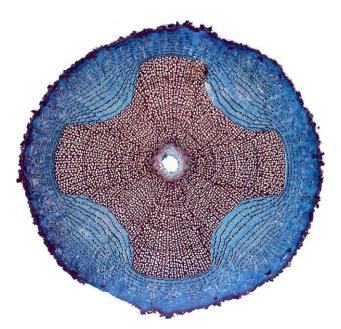


Fig. 1. Cross-section of stem in Perianthomega vellozoi showing four phloem arcs.

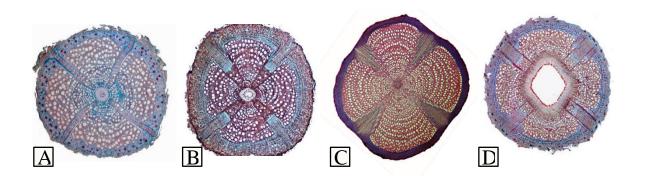


Fig. 2. Stems of Bignoniaceae with four phloem wedges. A. Pleonotoma tetraquetra, regular phloem (between

phloem wedges) has sclereid clusters instead of fibers. B. *Tanaecium pyramidatum*, straight phloem wedges that don't form lateral steps. C. *Tynanthus cognatus*, phloem wedges with symmetrical lateral steps. D. *Stizophyllum riparium*, with a hollow medulla.

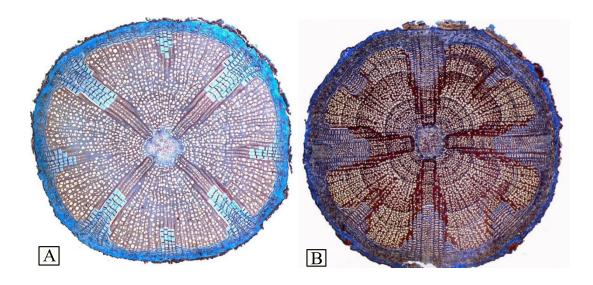


Fig. 3. Stems of Bignoniaceae with phloem wedges in multiples of four. A. *Mansoa difficilis*, showing stratified phloem with alternating bands of regularly spaced fibers. B. *Adenocalymma divaricatum*, with abundant fibers, throughout the ground tissue in the phloem.

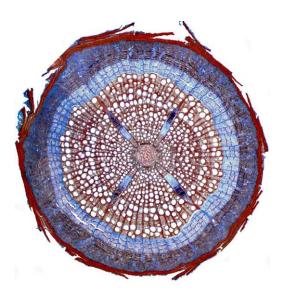


Fig. 4. Included phloem wedges in mature stems of Amphilophium crucigerum.



Fig. 5. Multiple-dissected phloem wedges in stems of Dolichandra unguis-cati.

A second group is characterized by the presence of a **continuous cambium**, which is characteristic of many Malpighiaceae (*Banisteriopsis, Heteropterys, Mascagnia s.s., Niedenzuella, Peixotoa* and some *Stigmaphyllon*), Euphorbiaceae (e.g., *Dalechampia*), Passifloraceae, Apocynaceae, Convolvulaceae, and Polemoniaceae. Within these, Malpighiaceae is distinguished by the production of secondary phloem that contains abundant **tanniniferous cells** and **druse crystals**. In *Niedenzuella, Heteropterys* (Fig. 6b), and *Stigmaphyllon*, the sclerenchyma is composed of large **sclereid clusters**, while in *Banisteriopsis* and *Peixotoa* it is composed of **bands of fiber-sclereids** that form a **stratified phloem** (Fig. 6a).

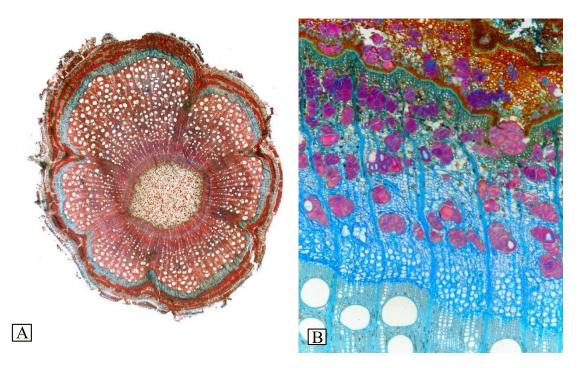


Fig. 6. Malpighiaceae with phloem wedges in cross-section. A. *Peixotoa sericea*, stem showing continuous phloem wedges with bands of fiber-sclereids forming a stratified phloem. B. *Heteropterys* stem showing large sclereid clusters.

Convolvulaceae and Apocynaceae are distinguished from other families that have phloem wedges by the presence of **intraxylary phloem** (also known as internal phloem or perimedullar phloem) and **laticifers**. In Convolvulaceae, in addition to phloem wedges, many taxa have successive cambia.

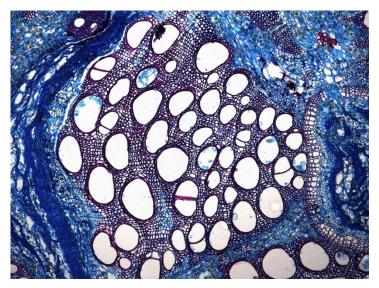


Fig. 7. Stem cross-section of *Ipomoea saopaulista* (Convolvulaceae), with intraxylary phloem in the area between the medulla and the primary xylem. The large cells in the secondary phloem and medulla are laticifers.

Fabaceae with phloem wedges are distinguished from other families by the presence of **nondispersive P-protein** within the sieve tube elements and a tendency to show aliform to aliform-confluent parenchyma, but not nearly as conspicuous as in the arboreal genera.

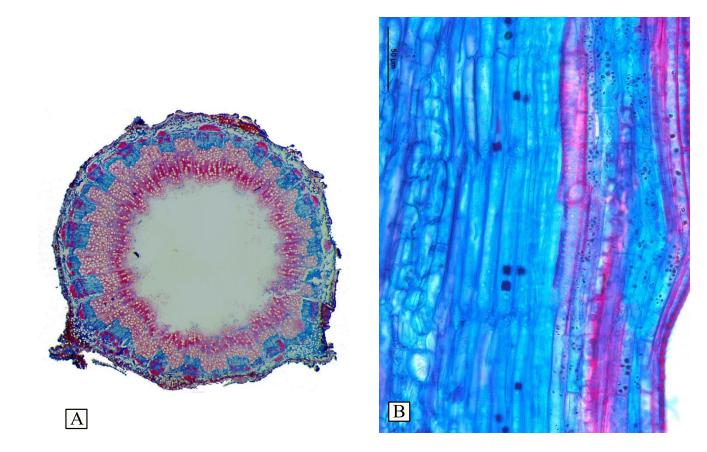


Fig. 8. A. Phloem wedges in *Mimosa velloziana* (Fabaceae). B. Nondispersive protein (seen as dark bodies) within the sieve tube elements.

Old World Icacinaceae are anatomically very similar to Bignoniaceae, except that the phloem wedges are not in multiples of four. Lens *et al.* (2008) mention that the rays in genera of Icacinaceae with phloem wedges are partly non-lignified and that the crystals in the phloem are **druses**. In Bignoniaceae, the rays are typically lignified (except in the phloem portion of the limiting rays of the phloem wedge) and the crystals are never druses, being either **acicular** or **prismatic**. In Icacinaceae, the presence of phloem wedges combined with successive cambia is not unusual (Lens et al. 2008).

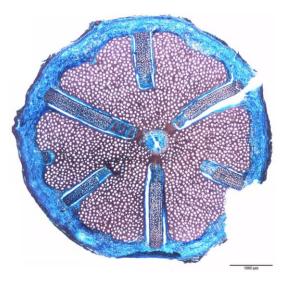


Fig. 9. Stem of *Pyrenacantha lebrunii* (Icacinaceae) with equidistant phloem wedges produced in multiples of three. Reproduced with permission from F. Lens.

For further discussions on the ontogeny of phloem wedges and arcs refer to Schenck (1893), Carlquist (2001), Dobbins (1969, 1971, 1981), Pace *et al.* (2009, 2011, 2015), and Angyalossy *et al.* (2012, 2015).

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