

INTERXYLARY PHLOEM (included phloem)

By Marcelo R. Pace

Interxylary phloem is the presence of phloem strands embedded within the secondary xylem (wood), and produced by the activity of a single cambium (Carlquist 2013). Stems with this cambial variant are also referred to as foraminate, due to the conspicuous interxylary phloem strands in the shape of dots scattered within the wood. (Fig. 1A). However, the presence of interxylary phloem is sometimes less evident and can only be confirmed by microscopy.

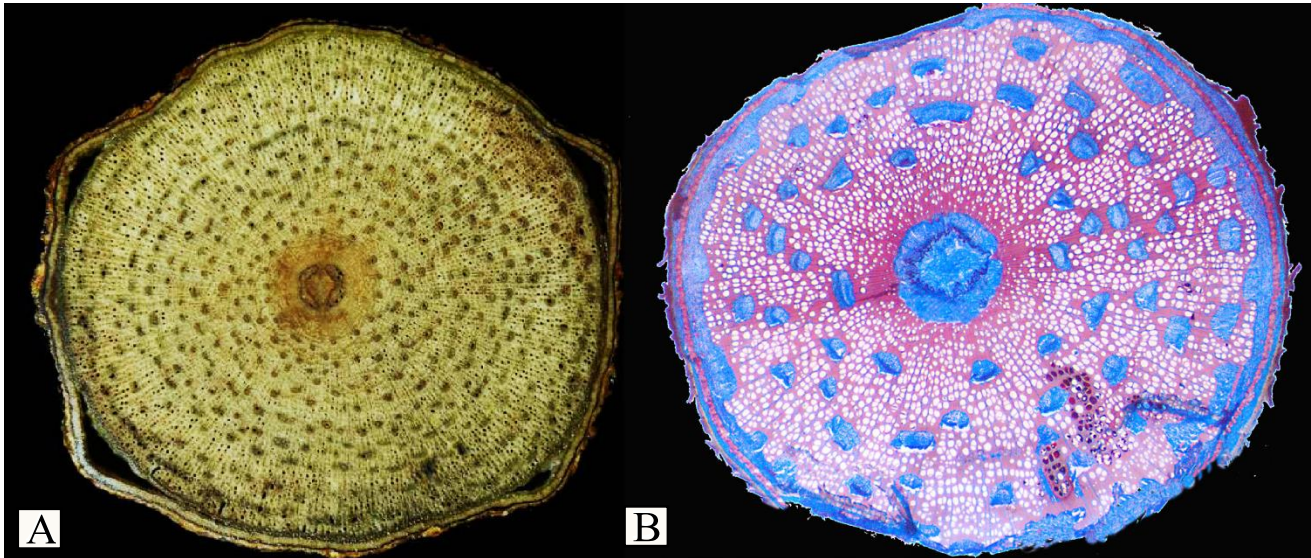


Fig. 1. Stem cross-section of *Strychnos* (Loganiaceae). A. *S. guianensis*, macroscopic view. B. *S. millepunctata*, microscopic view.

Interxylary phloem can have four different ontogenetic origins. The first one is where the cambium produces phloem in both directions (inside and outside), followed by the formation of xylem only towards the inside, and as a result, enclosing the phloem in the wood. Examples of this origin are present in *Thunbergia* (Acanthaceae; Fig. 2A) and *Dicella* (Malpighiaceae; Fig. 2B). However, in *Thunbergia* the interxylary phloem is derived from the interfascicular cambium resulting in radial patches that alternate with regions of the xylem that originate from the fascicular cambium (Fig. 2A).

A second origin of the interxylary phloem is through the formation of small phloem arcs. These later become embedded in the wood through the production of xylem by the cambium on their flanks. The resulting phloem islands will contain a fragment of cambium at the bottom. This type is present in *Strychnos* (Loganiaceae; Fig. 1), the African species of *Combretum* (Combretaceae; Van Vliet, 1979), and in at least one neotropical species of *Combretum* (Acevedo-Rodríguez, pers. com.). This type is possibly also present in Nyctaginaceae, such as *Neea* and *Pisonia*. Nevertheless, it is unclear whether the phloem islands in Nyctaginaceae indeed represent interxylary phloem or perhaps successive cambia in which the conjunctive parenchyma get lignified and resemble xylem fibers. This issue is currently under study by Israel Cunha-Neto (University of São Paulo).

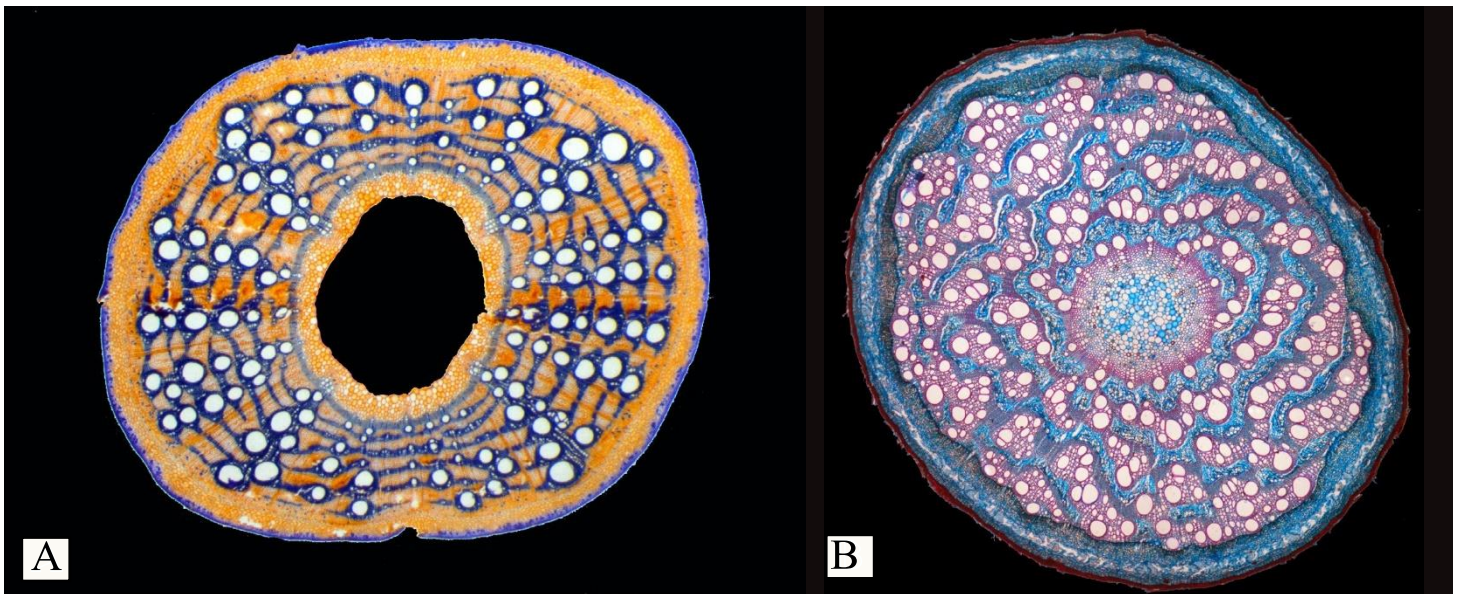


Fig. 2. Interxylary phloem derived from inward production of the cambium. A. *Thunbergia alata* (Acanthaceae), where patches of phloem coincide with interfascicular tissue. B. *Dicella nucifera* (Malpighiaceae), the interxylary phloem forms confluent patches of interxylary phloem.

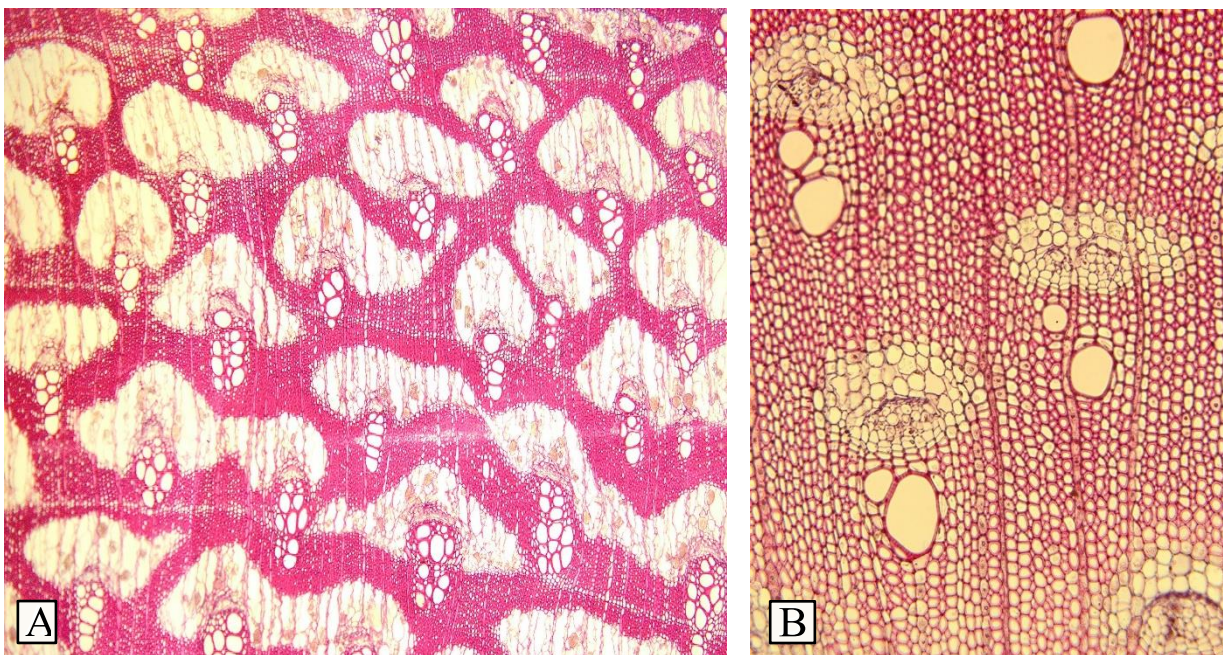


Fig. 3. Stem cross-section of Nyctaginaceae showing interxylary phloem. A. *Pisonia obtusa*. B. *Pisonia aculeata*.

A third type of interxylary phloem origin is present in *Amphilophium* (Bignoniaceae), where the interxylary phloem is the result of the inclusion of phloem wedges within the xylem (Fig. 4; Pace et al., 2009). This feature is a synapomorphic character of *Amphilophium*, which in the most recent taxonomic revision (Lohmann & Taylor 2014), reunites the former genera *Distictella*, *Distictis*, *Haplolophium*, and *Pithecoctenium*, most of which were included in the subtribe Pithecocteniinae of Melchior (1927).

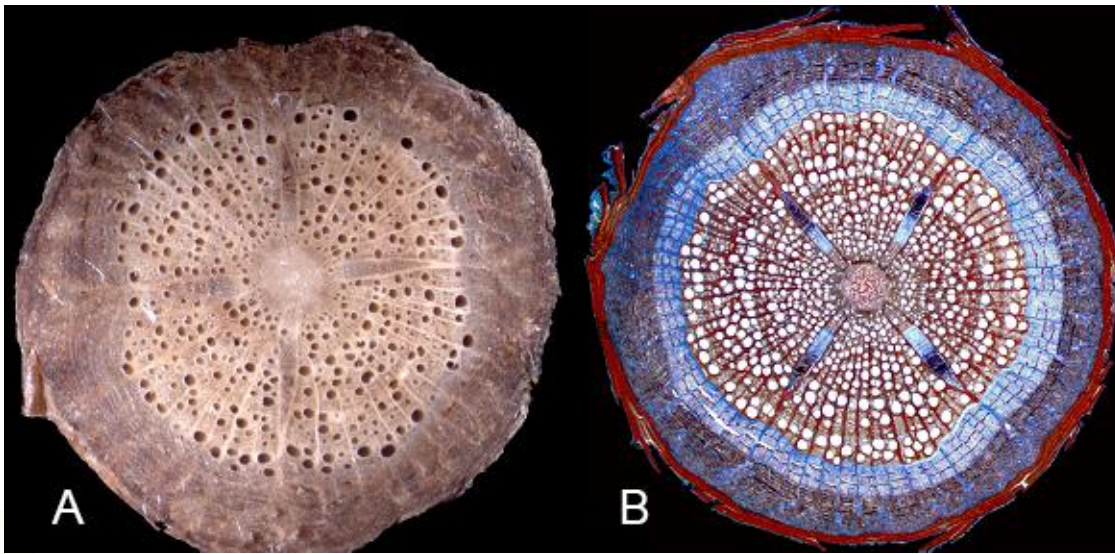


Fig. 4. Stem cross-section of *Amphilophium crucigerum* showing interxylary phloem by the inclusion of phloem wedges. A. Macroscopy. B. Microscopy.

A fourth and less common origin for this cambial variation is from the differentiation of xylem parenchyma into sieve tubes, as seen in the non-climbing taxa *Ixanthus* (Gentianaceae) and *Stylidium glandulosum* (Stylidiaceae).

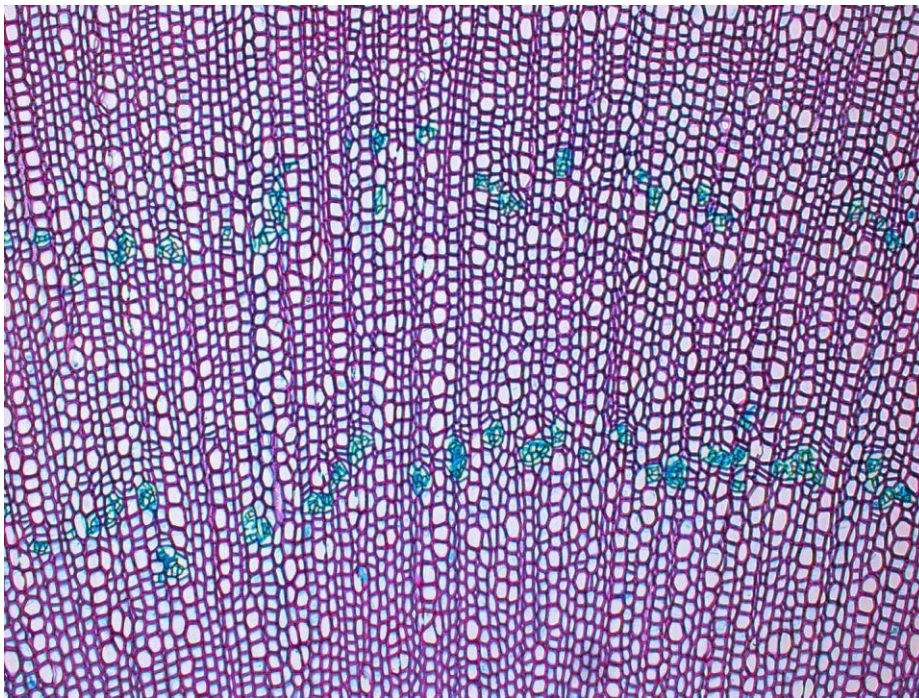


Fig. 5. *Ixanthus viscosus* (Gentianaceae) showing scattered sieve tubes and companion cells embedded in the secondary xylem. Photo courtesy of Frederic Lens.

The distribution of interxylary phloem islands generate patterns that are useful in the identification of species. For example, *Strychnos* (Loganiaceae; Fig. 1) and various genera of Nyctaginaceae (Fig.3) have evenly distributed, round islands of interxylary phloem. The Nyctaginaceae, however, differs by the presence of medullary bundles, which are lacking in *Strychnos*.

References

- Carlquist, S. 2013. Interxylary phloem: diversity and functions. *Brittonia* 65: 447-495.
- Melchior, H. 1927. Der natürliche Formenkreis der Pithecocteniinae innerhalb der Familie der Bignoniaceae. *Repert. Spec. Nov. Regni Veg. Beih.* 46: 71–82.
- Lohmann, L.G. and C.M. Taylor. 2014. A new generic classification of tribe Bignonieae (Bignoniaceae). *Annals Missouri Bot. Gard.* 99: 348-489.
- Pace, M.R., L.G. Lohmann, and V. Angyalossy. 2009. The rise and evolution of the cambial variant in Bignonieae (Bignoniaceae). *Evolution & Development* 11: 465-479.
- Van Vliet GJCM. 1979. Wood anatomy of the Combretaceae. *Blumea* 25: 141-223.