

Comparative in situ analysis reveals the dynamic nature of sclerenchyma cell walls of the fern *Asplenium rutifolium*

Abstract

- **Background and Aims** A key structural adaptation of vascular plants was the evolution of specialized vascular and mechanical tissues, innovations likely to have generated novel cell wall architectures. While collenchyma is a strengthening tissue typically found in growing organs of angiosperms, a similar tissue occurs in the petiole of the fern *Asplenium rutifolium*.

- **Methods** The in situ cell wall (ultra)structure and composition of this tissue was investigated and characterized mechanically as well as structurally through nano-indentation and wide-angle X-ray diffraction, respectively.

- **Key Results** Structurally the mechanical tissue resembles sclerenchyma, while its biomechanical properties and molecular composition both share more characteristics with angiosperm collenchyma. Cell wall thickening only occurs late during cell expansion or after cell expansion has ceased.

- **Conclusions** If the term collenchyma is reserved for walls that thicken during expansive growth, the mechanical tissue in *A. rutifolium* represents sclerenchyma that mimics the properties of collenchyma and has the ability to modify its mechanical properties through sclerification. These results support the view that collenchyma does not occur in ferns and most probably evolved in angiosperms.

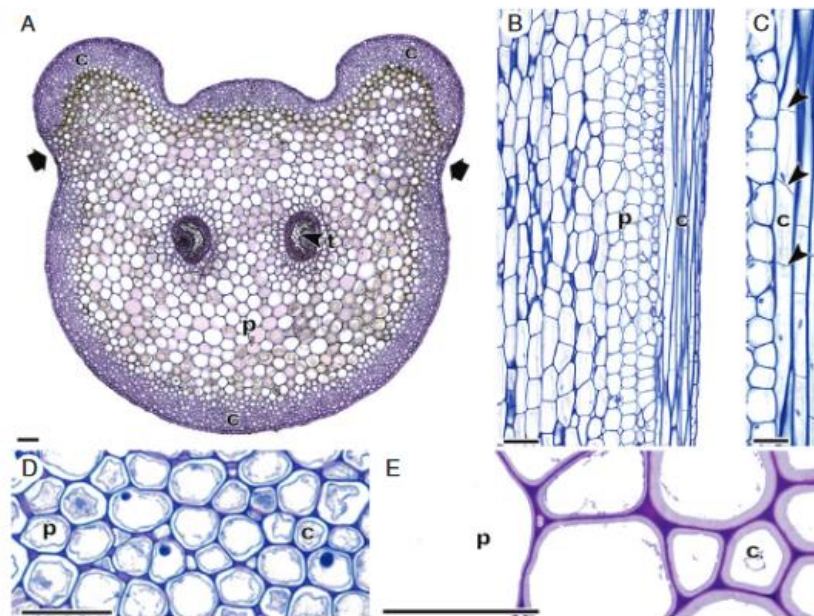


FIG. 2. Transverse (A, D, E) and longitudinal (B, C) sections through the petiole of *A. rutifolium* stained with Delafield's haematoxylin (A) and toluidine blue O (B–E). (A) The sub-epidermal collenchymatous tissue (c) is interrupted by parenchyma at the lateral respiration lines (arrows). The parenchyma tissue (p) consists of cortex parenchyma, enclosing two vascular bundles. (B) The collenchymatous cells have tapering ends and are narrow and elongated; the cortical parenchyma tissue (p) is isodiametric to moderately elongated. (C) A higher magnification showing collenchymatous cells divided by several thin-walled septae (arrowheads). (D) Section through a young petiole base showing undifferentiated (non-thickened) collenchymatous tissue (c) and parenchymatous tissue (p). (E) Section through a mature petiole base showing thickened collenchymatous (c) and parenchyma tissue (p). t: tracheids. Scale bars = (A) 250 μm ; (B) 100 μm ; (C–E) 50 μm .