

COMPARATIVE ANALYSIS OF WIDE-BAND TRACHEIDS AND *EQUISETUM* SPORANGIAL LINING CELLS—SIMILAR ONLY IN FUNCTION AND NOT BY EVOLUTIONARY ORIGINS

ABSTRACT

Wide-band tracheids are unique to several related succulent families (Aizoaceae, Cactaceae, and Portulacaceae) and serve as either the primary water conducting cells (as in stems of most cacti and in the genus *Anacampseros* [Portulacaceae] and in leaves in species of both Aizoaceae and Portulacaceae). Wide-band tracheids are characterized by their wide secondary walls that resist hydrogen-bonding collapses under water stress events. In the horsetail genus *Equisetum*, similar cells line the sporangia in the cone-like reproductive structure but are not found anywhere else in the xylem.

The question examined here was that of function—do these cells in *Equisetum* sporangia function in a similar manner (i.e., not collapsing under stress), or is this a question of completely different functions resulting in a physical similarity? In other words, is this similarity a simple tweaking of existing cells, or two independent evolutionary events that result in a similar cell type? Analysis of the dimensions, cell wall characteristics, and locations argue for an independent evolutionary origin of wide-band tracheids in comparison to the cells that line the sporangia of *Equisetum*.

Keywords: tracheid, wide-band, horsetail, evolutionary origin

1. INTRODUCTION

Wide-band tracheids (WBTs) are water-conducting cells characterized by their wide secondary walls, usually in annular or helical patterns (see Mauseth & Landrum, 1997; Landrum, 2006; Landrum, 2008; and Landrum, 2001). The width of the secondary walls are hypothesized to prevent these cells from collapsing under water-stress, as opposed to common tracheids that, under water-stress, will have their primary cell walls collapse and hydrogen-bond, preventing any future conductive ability.

Wide-band tracheids as defined above occur in the stems of almost all cacti (Cactaceae, although in periphery to common tracheids in the vascular bundles), in stems of *Anacampseros* (Portulacaceae; nearly replacing all other tracheids), and in leaf xylem of species in Aizoaceae (Ruschioideae) and Portulacaceae (*Anacampseros*, but not *Portulacaria*).

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In a past conversation with Dr. Sherwin Carlquist, noted plant anatomist (pers. comm.), we had discussed similar cell types in horsetails (Plate 4 in Newcombe, 1888; Figures 91 & 168 in Orpen, 1884) and possibly in some fern groups; however, neither of us had explored this topic any further, and upon his death in 2021, I resolved to explore this topic as a dedication to his honored career. The results published here are a conclusion to the question posed by Dr. Carlquist: are wide-band tracheids similar to those horsetail cells only in appearance, or is this an example of nature 'tweaking' pre-existing cells due to a common functionality?

2. MATERIALS AND METHODS

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Cells of the sporangial structures of *Equisetum arvense* were prepared using safranin staining, mounted on standard slides, and examined under brightfield microscopy. Secondary cell walls were measured for over 100 cells from different individuals for overall width, band width, and overall length. These were compared to previous measurements of wide-band tracheids from prepared slides, with both stem and leaf sections cut at 15µm from many species of cacti and *Anacampseros* (Portulacaceae) and Aizoaceae (leaves of species in Ruschioideae), all prepared as in Mauseth & Landrum (1995).

3. RESULTS AND DISCUSSION

Wide-band tracheids (WBTs) and horsetail sporangial lining cells (SLCs) do appear similar in construction; SLCs with similar traits were not found in any other major fern or Lower Vascular Plant clades examined.

Wide-band tracheids (Fig. 1) are characterized by their secondary wall traits but can have different size groupings based on their location, being larger in stems and smaller in leaves, but having the same constructional patterns regardless of size or location.

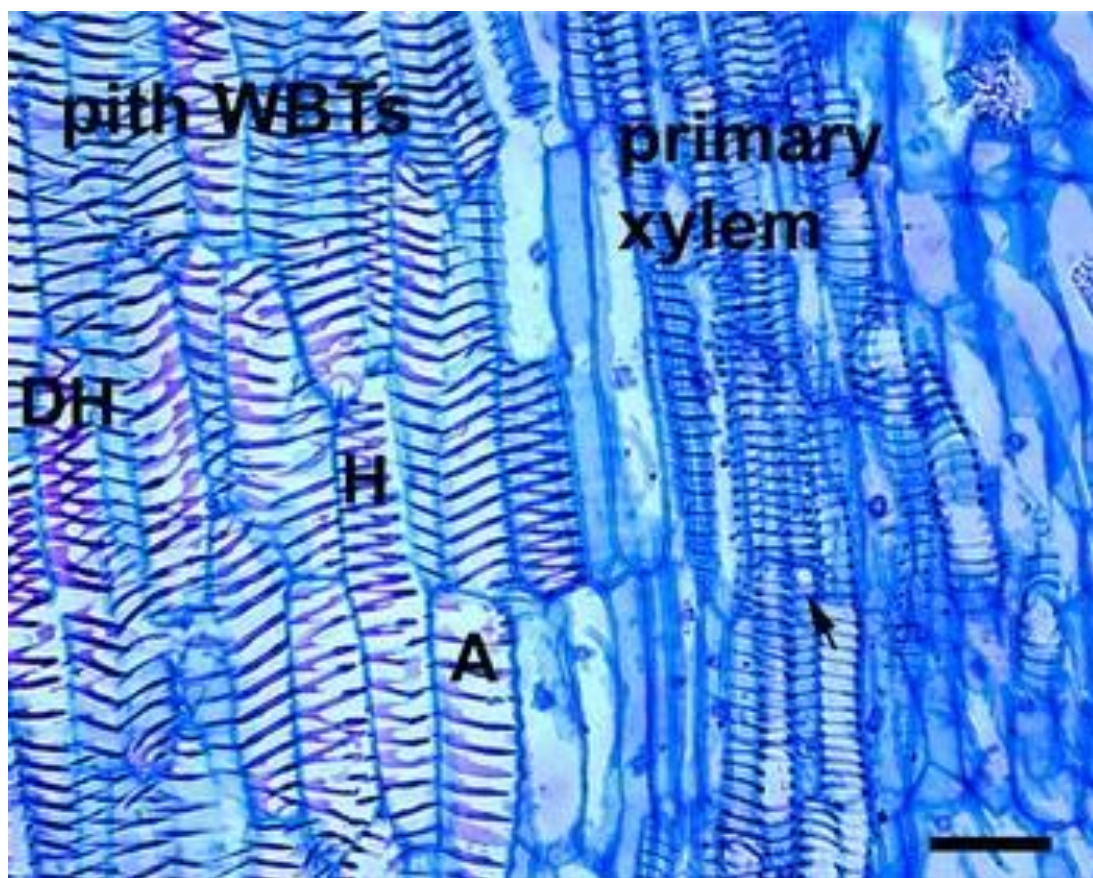


Figure 1. Side view of wide-band tracheids found in stems of *Anacampseros ustulata* (Portulacaceae). Figure 4 from Landrum (2006). Bar = 100 μ m.

In contrast, the horsetail sporangial lining cells (SLCs) appear to be remarkably consistent in their wall patterns and sizes, regardless of the position of the sporangium in which they were found. Additionally, the pattern of the secondary wall was primarily helical and without much variation in the sizes of both the widths and lengths (Fig. 2).

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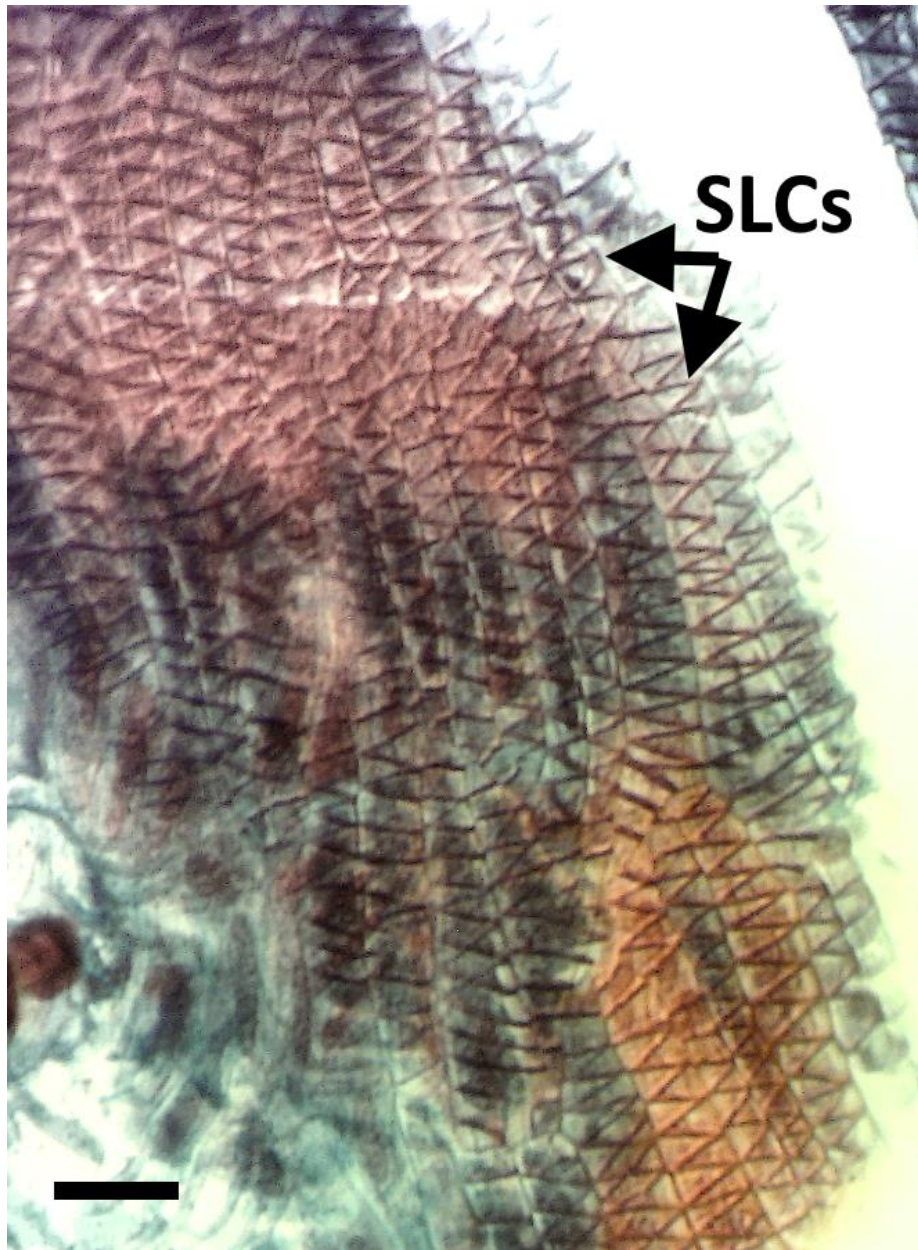


Figure 2. Side view of sporangial lining cells (SLCs) found in the strobilus of *Equisetum arvense* (Equisetaceae). Bar = 100 μ m.

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4. CONCLUSION

Wide-band tracheids are similar in construction to the cells lining the sporangia of horsetails, but with a different function and cell walls with narrower widths than WBTs. In species of Aizoaceae, Cactaceae, and Portulacaceae in which wide-band tracheids occur, they are

hypothesized to function as an alternative water conduction pathway in time where normal tracheids may experience hydrogen-bonding of the primary cell walls under water stress; such contact of the primary walls will result in the permanent collapse of the tracheids. Wide-band tracheids can shrink under water stress and rebound to normal size when water returns, thus the wide-bands of the secondary walls prevent hydrogen-bonding contact problem of the primary walls.

The sporangial lining cells (SLCs) of the horsetail (*Equisetum arvense*) strobilus are similar in design, but function in nearly the opposite way from wide-band tracheids. In the strobilus, these cells will dehydrate and shrink in size, thus allowing the sporangium to tear and release the spores within to the outside environment.

Both cell types, WBTs and SLCs, have secondary cell walls that are similar in construction that allow shrinkage of the cell; however, in WBTs, that shrinkage only lasts until water returns the cells to their original shapes; in SLCs, the shrinkage of the cells results in the tearing of the sporangium, and these cells are no longer functional after that event.

It is therefore logical to conclude that the similar construction of these cells is an evolutionary coincidence, due to the requirement that both cell types shrink during water removal. Beyond that construction constraint, there is no other evidence to suggest a common origin, and thus these two cell types reflect independent origins.

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