



Comparative Analysis of Wide-band Tracheids and *Equisetum* Sporangial Lining Cells: Similar Only in Function and Not by Evolutionary Origins

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Author's contribution

The sole author designed, analyzed, interpreted and prepared the manuscript.

Article Information

DOI: <https://doi.org/10.9734/ijpss/2024/v36i115152>

Open Peer Review History:

This journal follows the Advanced Open Peer Review policy. Identity of the Reviewers, Editor(s) and additional Reviewers, peer review comments, different versions of the manuscript, comments of the editors, etc are available here: <https://www.sdiarticle5.com/review-history/126059>

Original Research Article

Received: 08/09/2024

Accepted: 10/11/2024

Published: 21/11/2024

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 (sporangial lining cells or SLCs) 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

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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; sporangia; lining cells; 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; Landrum, 2002; 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; see Melo-de-Pinna et al. 2006; Terrazas et al. 2016; Maceda 2024), in stems of desert rose (*Anacampseros* spp. (Portulacaceae; nearly replacing all other tracheids), and in leaf xylem of species in Aizoaceae (Ruschioideae) and Portulacaceae (*Anacampseros*, but not in species of *Portulacaria* or *Ceraria*).

In a past conversation with Dr. Sherwin Carlquist, a renowned plant anatomist, this author had discussed similar cell types in horsetails (genus *Equisetum*; Equisetaceae) (Plate 4 in Newcombe 1888; Figures 91 & 168 in Orpen 1884) and possibly in some fern groups; however, the topic was not explored any further. With Professor Carlquist's death in 2021, the author resolved to resolve the apparent similarity between these two types of cells as a memorial to Professor Carlquist's 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 in appearance only

(i.e., is this an example of nature 'tweaking' pre-existing cells due to a common functionality) or is this an indication of common evolutionary origin?

2. MATERIALS AND METHODS

Cells of the sporangial structures of horsetail strobili were prepared by smearing onto a glass slide and stained using dilute safranin stain; a cover slip was then applied, and the slides were examined under brightfield microscopy at both low and high magnifications. Photographs were taken with a digital camera attached to the eyepiece at a resolution of eight megapixels. Secondary cell walls of the SLCs were measured for over 100 cells from three different individuals for overall width, band width, and overall length.

These were then compared to previous measurements of wide-band tracheids from prepared slides, with both stem and leaf sections cut into 15µm sections from many species of cacti, Portulacaceae, and Aizoaceae (leaves of species in Ruschioideae), all prepared as described 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.

Table 1. Comparative measurements of wide-Band Tracheids (WBTs) versus Sporangial Lining Cells (SLCs)

| Taxon | Number of cells measured | Average Secondary Wall Width (µm) | Average Cell Length(µm) |
|--|--------------------------|-----------------------------------|-------------------------|
| SLCs in strobili of <i>Equisetum arvense</i> | 112 | 23.8 (±0.6) | 181 (±1.8) |
| Stem WBTs (<i>Anacampseros</i> spp.) | 341 | 33.6 (±3.4) | 212 (±5.1) |
| Leaf WBTs (<i>Anacampseros</i> spp.) | 163 | 29.1 (±0.6) | 186 (±4.7) |

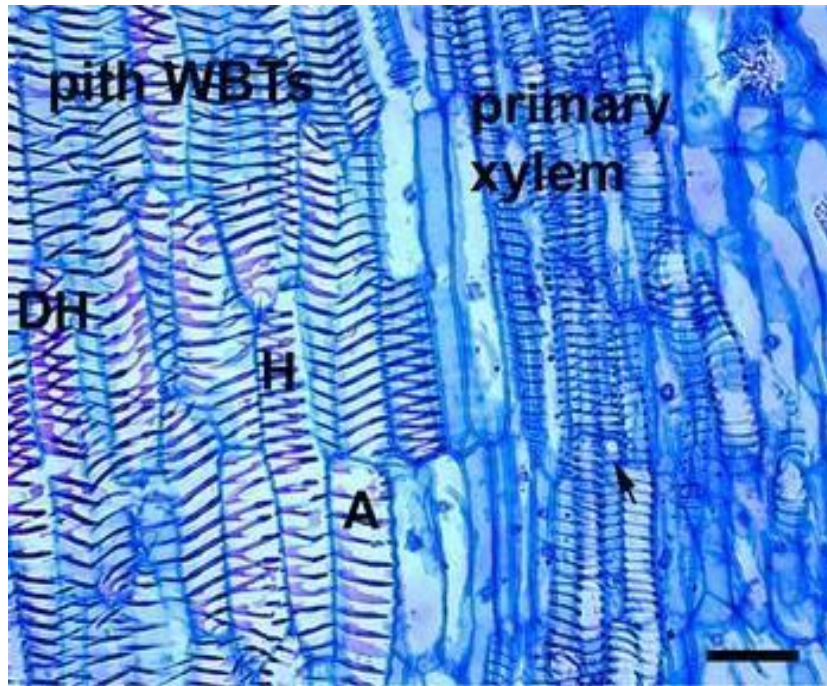


Fig. 1. Side view of Wide-Band Tracheids (WBTs) found in stems of *Anacampseros ustulata* (Portulacaceae)

DH = double-helical; H = helical; A = annual. Fig. 4 from Landrum (2006). Bar = 100 μ m

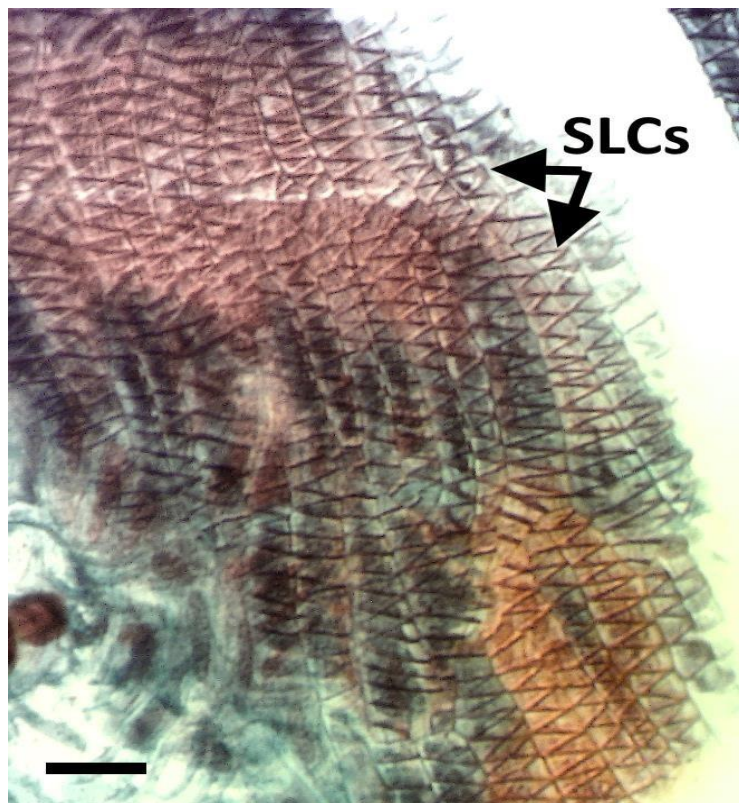


Fig. 2. Side view of sporangial lining cells (SLCs) found in the strobilus of horsetail (*Equisetum arvense*; Equisetaceae). Bar = 100 μ m

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 (Table 1). 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), whereas WBTs have been noted to have annular, helical, and double-helical constructions (Landrum 2006, 2008).

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 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.

DISCLAIMER (ARTIFICIAL INTELLIGENCE)

Author(s) hereby declare that NO generative AI technologies such as Large Language Models (ChatGPT, COPILOT, etc) and text-to-image generators have been used during writing or editing of this manuscript.

COMPETING INTERESTS

Author has declared that no competing interests exist.

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