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BRIEF COMMENTS ON THE NOMENCLATURE OF SOFTWOOD AXIAL RESIN CANALS AND THEIR ASSOCIATED CELLS

by

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SUMMARY

The terminology related to axial resin canals in conifers is briefly reviewed, standard terms are clarified and a new term is proposed. The definitions proposed are intended primarily for light microscopic observations. All the cells and spaces of an axial resin canal as differentiated from the axial tracheids are collectively referred to as the resin canal complex. The resin canal is the intercellular space itself, and the epithelium is the uniseriate layer of cells lining the canal. We propose the term subsidiary cells to include all cells exterior to the epithelium, which may be subsidiary parenchyma and/or strand tracheids.

Key words: Wood anatomy, resin canal, epithelium, subsidiary cells.

INTRODUCTION

In the course of research into the utility of resin canal diameters for pine species identification, we discovered a lack of consensus in the nomenclature for resin canals and their associated cells. Most texts covering the anatomy of resin canals stop their analyses at the level of thick- and thin-walled epithelial cells (Jane 1970; Esau 1977; Grosser 1977; Schweingruber 1978; Core et al. 1979; Hoadley 1990; Dickison 2000). The IAWA multilingual glossary of terms (IAWA 1964) defines an epithelial cell as "a cell of the epithelium" and the epithelial layer as synonymous with epithelium. The epithelium itself is defined as "the layer of secretory parenchymatous cells that surrounds an intercellular canal or cavity." We understand "layer" to mean a single layer of cells. The resin canal is defined as "an intercellular canal containing resin." (IAWA 1964). Thus resin canal is the term for the intercellular space, but the secretory definition for the cells that surround it is unclear and difficult to apply when more than one layer of cells is present.

Authors of plant anatomy, wood anatomy, and wood identification texts do not agree upon the specific names to be used for the various parenchymatous elements associated with an axial resin canal (Bosshard 1974; Panshin & De Zeeuw 1980; Wilson & White 1986) or they do not explicitly mention them (IAWA 1964; Jane 1970; Esau 1977; Grosser 1977; Schweingruber 1978; Core et al. 1979; Hoadley 1990; Dickison 2000). Most authors address only the resin canal itself and the epithelium, a variously-defined term.

In research papers, the term resin canal complex was used to define the resin canal and all associated cells (Kibblewhite & Thompson 1973; Sato & Ishida 1982). For most authors, the innermost layer of cells immediately adjacent to the resin canal is termed the epithelium. Subsequent layers of parenchymatous cells have been given different names by authors studying different taxa. Kibblewhite and Thompson (1973) recognize intermediate and outer cells when examining *Pinus elliotii*. Ickert-Bond (2001) refers to associated axial parenchyma in *Pinus krempfii*. LaPasha and Wheeler (1990) recognized longitudinal parenchyma in *Pinus taeda*, and Howard and Manwiller (1969) use the same name for cells exterior to the epithelium in ten species of yellow pine grown in the southern United States. Takahara et al. (1982) refer to all parenchyma exterior to the epithelium as accompanying cells in *Picea abies*. Sato and Ishida (1982) recognize two types of parenchyma exterior to the epithelium in *Larix leptolepis*: parenchymatous cells type I and type II, depending on the cell shape. Fahn (1979) examining *Pinus densiflora* labels parenchyma exterior to the epithelium as sheath cells. Obviously there is a lack of consensus in the literature regarding the name of these cells.

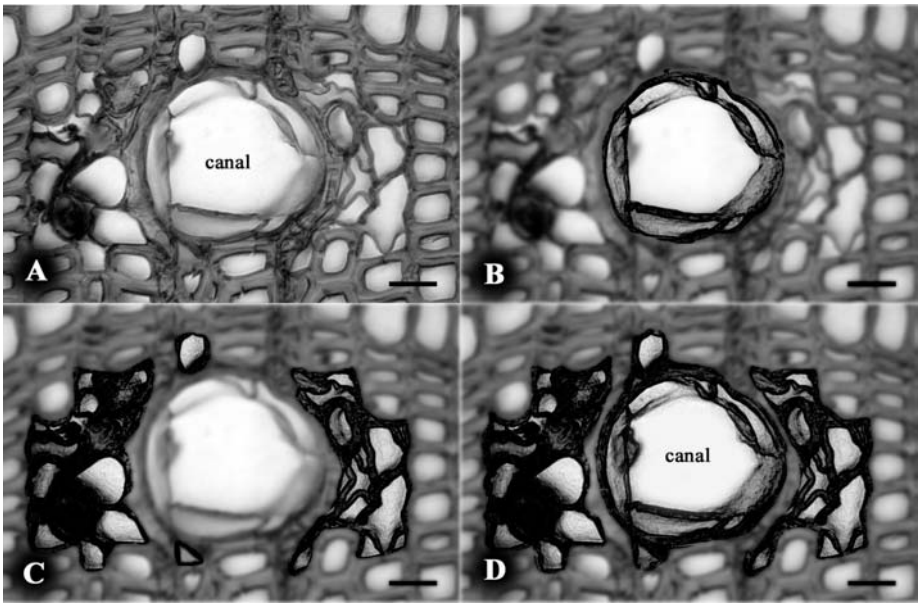

Fig. 1. Transverse section of *Pinus contorta*. – A: Resin canal labeled. – B: Epithelial cells with dark contrast, background blurred. – C: Subsidiary cells with dark contrast, background blurred. Note that four disjunct areas are differentiated from the axial tracheids. – D: Resin canal complex with dark contrast, background blurred. Note that ray cells are not included. — Scale bars = 25 μm.

DEFINITIONS

To avoid confusion and provide nomenclature that can be applied to the resin canals and associated cells of any taxon viewed with a light microscope, we propose the following definitions of terms.

Axial resin canal complex — the resin canal and its associated cells as differentiable from the surrounding axial tracheids or ray tissue (Kibblewhite & Thompson 1973; Sato & Ishida 1982). Figure 1D.

Resin canal — an intercellular canal containing resin (IAWA 1964). Figure 1A.

Epithelium (syn. *epithelial layer*) — the uniseriate layer of cells delimiting the resin canal (sensu Wilson & White 1986). Figure 1B.

Subsidiary cells — all cells associated with the resin canal complex that are not part of the epithelium. There are two types of subsidiary cells, defined below. Figure 1C

Subsidiary parenchyma — the parenchymatous elements of the resin canal complex exterior to the epithelium.

Strand tracheid — a tracheid of an axial series (strand) of tracheids (or of mixed tracheids and parenchyma cells), each series originating from a single cambial initial (IAWA 1964).

DISCUSSION

For *Larix*, *Pseudotsuga* and *Picea* the resin canal complex is generally composed only of the resin canal and the epithelium. For *Larix leptolepis* (Sato & Ishida 1982) and *Picea abies* (Takahara et al. 1982) there are known additional parenchymatous components, but often only a single layer of cells is visible with the light microscope. *Pinus* typically has more than one layer of cells (Fig. 1).

The terms resin canal complex and subsidiary cells are introduced in parallel with the terminology in leaf anatomy for the stomatal complex. A stoma is the intercellular space delimited by two specialized cells: the guard cells. The guard cells in turn may or may not be adjacent to subsidiary cells which, when present, are a part of the stomatal complex. All the cells of a mesogenous stomatal complex are ontogenetically more closely related to one another than to the adjacent epidermal cells not associated with the stomatal complex (Esau 1977). In a resin canal complex, the epithelium and subsidiary cells (subsidiary parenchyma and strand tracheids, if present) are derived from one or more fusiform initials that underwent mitotic divisions (Kibblewhite & Thompson 1973; Esau 1977; Panshin & De Zeeuw 1980) and thus are ontogenetically closely related.

We intend our definitions to be practical and applicable to light microscopic observation, particularly from the transverse section. It is often impossible to determine the exact cell type from the transverse section. For example, in *Pinus contorta* there are

thick-walled subsidiary parenchyma cells that can be easily differentiated from strand tracheids in a longitudinal section (personal observation). Seen from the transverse section, however, these thick-walled cells appear much like those of strand tracheids. In cases like this, where correct determination of the specific cell type is dubious or impossible, the general term subsidiary cell is useful.

It is important to note that our definition of the resin canal complex does not include ray cells that may pass through in a given plane of section. In Figure 1, ray cells pass to either side of the epithelium but are not considered a part of the resin canal complex. For normal rays this pattern is clear, but at the point of anastomosis between an axial resin canal complex and a radial resin canal in a fusiform ray, it may be difficult to determine whether cells are derived from fusiform or ray initials. An author describing such a situation should exercise judgment in assigning names to such cells.

We prefer the term subsidiary cells over accompanying cell (Takahara et al. 1982) because the latter recalls companion cell–albuminous cell nomenclature in phloem, but an analogous role for these cells is not indicated. Intermediate and outer cells (Kibblewhite & Thompson 1973) and parenchyma types I and II (Sato & Ishida 1982) would be considered specific types of subsidiary parenchyma. Sheath cells (Fahn 1979) cannot be accepted, as that term is already widely accepted in hardwood anatomy (IAWA 1989). The rationale for the definitions we propose is developmental, but we recognize that in most taxa developmental evidence will be lacking. For this reason we have also included spatial components in each of the definitions. We prefer to avoid physiological requirements in the definitions, while acknowledging the importance of structure to function.

The proposed terminology for axial resin canals can be applied to radial resin canals as well. Radial canals occur in fusiform rays, which are each composed of a radial resin canal complex typically bordered axially by normal ray cells. As with axial canals, the resin canal of a fusiform ray is easily identified. Similarly, epithelial cells are easily identified and can be defined in parallel with axial resin canals. The radial resin canal complex, while perhaps impossible to delineate practically, should retain a parallel definition from the axial terminology, including in the definition the concept of excluding the normal ray cells. The distinction between a subsidiary cell and a normal ray cell can be difficult or impossible to make, particularly from a tangential section. Consequently, the terminology for subsidiary parenchyma should be applied in parallel to axial terminology only in those cases when an author can demonstrate that a given cell is unquestionably a non-epithelial part of the resin canal complex rather than a normal ray cell. We suggest that authors exercise care and judgment when examining and referring to the non-epithelial cells of fusiform rays.

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