CONIFER TRACHEIDS RESOLVE CONFLICTING STRUCTURAL REQUIREMENTS: DATA, HYPOTHESES, QUESTIONS

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ABSTRACT

The nature of conduction involves movement of a liquid (under tension or pressure) through a solid (cell walls necessary to direct the liquid and provide mechanical strength). The numerous consequences of the liquid/solid nature of the conductive interface in plants can be viewed as a series of conflicting requirements that are resolved by various mechanisms. For example, the types of mechanical strength conferred by thicker cell walls (latewood) run counter to optimal conduction (earlywood). Conflict resolution situations are examined with light microscopy and SEM to show in detail not merely conflicting requirements but the various types of resolution in various conifers. *Abies* is presented as exemplary of a cool temperate conifer with numerous aspects to earlywood/latewood structure. Tropical conifers (*Araucaria*) present different compromises; the riparian conifer *Dacrydium guillauminii* has only earlywood; the parasitic conifer *Parasitaxus* has only latewood. Particular conifers have only some of the features by which latewood differs from earlywood. Cell dimorphism is only one aspect of resolution of conflicting requirements; others include modifications in pit size, shape, and density; the nature of the pit membrane; the nature of the pit cavity, pit border and pit aperture; and surface relief (warty layer) of the tracheid wall. The invention of coniferous bordered pits involves a circular shape, so that tension on the margo strands is equal, and thus the pit can be closed. These factors and margo pore maximization necessitate expending a large amount of space to pits in earlywood, the strength of which is thereby lessened and must be compensated by greater wall strength in latewood. The paper concludes with a series of twenty features which represent resolutions of conflicting requirements in terms of anatomical structure. Wood physiological literature is integrated with the anatomical observations.

Key Words: growth rings, margo, torus, wood anatomy, wood physiology

RESUMEN

La naturaleza de la conducción implica el movimiento de un líquido (bajo tensión o presión) a través de un sólido (paredes celulares necesarias para dirigir el líquido y dar fuerza mecánica). Las numerosas consecuencias de la naturaleza líquido/sólido de la interfaz conductiva en plantas puede verse como una serie de requerimientos conflictivos que se resuelven por varios mecanismos. Por ejemplo, los tipos de fuerza mecánica conferida por las paredes celulares más gruesas (leño tardío) va en contra de la conducción óptima (leño temprano). Se examinan mediante microscopio lumínico y SEM situaciones con conflicto de resolución para mostrar en detalle no solo requerimientos en conflicto sino los varios tipos of resolución en varias coníferas. *Abies* se presenta para ejemplarizar una conífera del templado frío con numerosos aspectos de la estructura leño temprano/leño tardío. Las coníferas tropicales (*Araucaria*) presentan diferentes compromisos; la conífera riparia *Dacrydium guillauminii* solo tiene leño temprano; la conífera parásita *Parasitaxus* solo tiene leño tardío. Hay coníferas particulares que solo tienen algunas de las características por las que el leño tardío difiere del leño temprano. El dimorfismo celular es solo un aspecto de resolución de requerimientos en conflicto; otros incluyen modificaciones en el tamaño de las punteaduras, forma, y densidad; la naturaleza de la membrana de la punteadura; la naturaleza de la cavidad de la punteadura, borde de la punteadura y su apertura; y relieve superficial (capa verrugosa) de la pared de la traqueida. La invención de las punteaduras bordeadas de coníferas implican una forma circular, para que la tensión el margen de las punteaduras con toro sea igual, y así el poro pueda cerrarse. Estos factores y la maximalización del margen del toro necesitan gastar una gran cantidad de espacio para las punteaduras en el leño temprano, la fuerza que es disminuida por ello debe ser compensada por una fuerza mayor en la pared del leño tardío. El artículo concluye con una serie de veinte características que representan resoluciones de requerimientos conflictivos en términos de estructura anatómica. La bibliografía de la fisiología del leño se integra con las observaciones anatómicas.

INTRODUCTION

Study of physiology of conduction in conifer woods has yielded some outstanding contributions in recent years (Hacke et al. 2015). A number of workers, cited below, have recently clarified many aspects of conduction in conifers. The advances in anatomy of conifer woods, especially at mid-levels of magnification, such as are represented by scanning electron microscopy (SEM), have been relatively few in comparison. There is an implicit message that conifer wood anatomy is well known, but at a comparative level and at levels above those of light microscopy, the literature is relatively sparser. When new anatomical information is combined with new find-

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ings in wood physiology, some fascinating new insights emerge. What are the evolutionary strategies of conductive cells in conifers with only one type of conductive cell, the tracheid, and how can we understand them in broader terms?

Many of these insights can be described in terms of resolutions between conflicting requirements. This concept is not equivalent to "trade-offs." We might use the concept of "trade-off" to connote that increase in leaf surface can produce more photosynthates, but at a cost of greater heating and greater loss of water than for a smaller leaf of the same thickness. The concept of conflict resolution in plant structure goes one step further. For example, by compacting more numerous and, more densely designed chlorenchyma cells into a leaf, more light can be absorbed and less water lost, but the gas exchange (e.g., carbon dioxide intake) is lowered by the imperviousness of the epidermis. By the production and location of stomata, this conflict is resolved. The palisade chlorenchyma of a leaf can capture more light, but compactness of palisade cells lessens gas exchange. The opposite problem applies to spongy parenchyma, which has large air spaces with close access to stomata and thus greater gas exchange possibility, but fewer chloroplasts per cell and therefore less photosynthesis than palisade chlorenchyma. The resolution of this conflict is formation of both palisade and spongy chlorenchyma in a given "typical" leaf, the spongy tissue positioned on the lower (abaxial) surface, the palisade on the adaxial. Thus a pairing of two different versions of chlorenchyma, a dimorphism, achieves the goal. These leaf examples can be elaborated to show that a complex train of functions requires dimorphisms, compromises, and ways to satisfy conflicting requirements (e.g., evaporation to achieve leaf cooling and to produce tension in the conductive system that draws water to the leaves). These resolutions of conflicting physiological requirements are well understood for leaves, but have been less well explored for wood. We can agree with Raven (1976) that primary cell walls are insufficient to counter tension in a conductive system, yet tension is required for conveying water to aerial parts of a plant; the resolution is production of tracheary tissue with secondary walls capable of withstanding tension in water columns. This resolution has been basic to the development and diversification of land plants. However, the resolution is not a simple one. The open system of growth of plants is a necessity for competing for light, a competition that requires stiffness of stems for positioning of leaves. To what degree do xylem cells have secondary walls to resist tension and to what degree do they provide mechanical strength for positioning light-acquisition surfaces and countering weight of plant parts, wind pressure, etc.?

Conifer wood, less complex than angiosperm wood, provides a convenient introduction to resolution of conflicting requirements by anatomical means. Conifer wood consists of one type of conducting cell (tracheary element), the tracheid. Understanding of angiosperm wood, best analyzed separately, involves a different series of considerations, because most angiosperm woods have two parallel systems of tracheary elements: vessel elements and imperforate tracheary elements, both of which offer evolutionary possibilities.

Relevant papers on wood physiology of conifers include the following. An excellent review of water conduction in conifers and its relationship to tracheid structure has been offered by Hacke et al. (2015). Earlywood was compared with latewood by Domec and Gartner (2002). The effect of length and diameter on conductive characteristics of tracheids has been studied by Sperry et al. (2006), while the effect of microfibril angles on tracheid wall stiffness was considered by Evans and Ilic (2001). The relationship between tracheid diameter and recovery from freezing of water in tracheids was discussed by Pittermann and Sperry (2003). Xylem design limitations are claimed to govern the distribution of conifers (Brodribb & Hill 1999). Mechanical reinforcement of tracheids compromises hydraulic efficiency according to Pittermann et al. (2006a, 2006b). Conifer tracheids can be better understood if we compare them to fern tracheids, most of which provide less mechanical strength than do conifer tracheids (Pittermann et al. 2011).

Sperry et al. (2006) view conifers [plus *Ginkgo*] as having hydraulic systems that angiosperms lack. One can take this view, but certainly the two groups early went in divergent directions that have proved highly effective. The order Gnetales, a conifer offshoot, has essentially all of the hydraulic mechanisms that angiosperms have, but has been less successful than angiosperms, apparently mostly because of the lengthy gymnosperm life cycle (Carlquist 2012).

The design of the coniferous bordered pit is considered central to understanding of the hydraulics of coniferous wood. Hacke and Jansen (2009) considered how bordered pits function in embolism resistance. Long ago, Liese and Bauch (1967) demonstrated how coniferous pits aspirate (close) to isolate tracheids from embolisms. The decrease in pit aperture diameter with tree height was explored by Domec et al. (2008). Porousness of the pit torus and its consequences was noted by Jansen et al. (2012). Cavitation resistance was related to pit aperture diameter according to Pittermann et al. (2010). Conduction through bordered pits is related to pit membrane resistance, as was shown by Lancaster and Ennos (2002). Bordered pits were found to be sites of air seeding during embolism formation (Delzon et al. 2010).

Conifer woods differ, so that there is no single pattern for resolution of conflicting structural requirements. In Figure 7, earlywood features and latewood features are compared, but these are summaries of differences, and particular conifers may represent only some of these features. *Abies concolor* was chosen for SEM analysis because it is a boreal tree conifer with a large suite of features differentiating earlywood from latewood. Araucariaceae have earlywood and latewood but are tropical and subtropical, and have distinctive earlywood/latewood differences that need to be understood if we are to understand the nature of their growth rings. By contrast, stems of a riparian New Caledonian conifer (*Dacrydium guillauminii*) and pneumatophores of *Taxodium distichum*, the "bald cypress," consist wholly of earlywood. Finally, data are presented for the wood of the New Caledonian parasitic conifer *Parasitaxus usta,* the wood of which consists, rather surprisingly, only of latewood. Conifers such as *Dacrydium guillauminii* and *Parasitaxus usta* show that formation of latewood together with earlywood is not the only resolution to conflicting seasonal structural requirements and capabilities of conifer wood.

The central and final element of this essay is a tabulation of structural/physiological requirements that are conflicting, together with, in a corresponding second column, the resolutions to these conflicts one finds in conifer woods. The nature of adaptation requires us not to consider adaptations in terms of unilateral change. All too often, we have "ancestral" (plesiomorphic) conditions co-existing with "derived" (apomorphic) expressions. For example, vessel elements are not necessarily more advantageous than tracheids. Rather, particular groups of plants utilize these cells in combination with other features to achieve optimal conductive systems for particular growth forms and ecological situations.

MATERIALS AND METHODS

Sources of materials and authors of binomials are given in the captions for figures. Light microscope illustrations of wood of *Parasitaxus usta* (formerly *P. ustus*) were presented earlier (Carlquist 1982) because they served as the object on which a new microtechnical method was employed. In order to make new preparations from this wood, a different method was used: sections of material stored in 50% ethanol were made by hand using a single-edged razor blade. This method was also used for wood of *Dacrydium guillauminii*. For the remaining species, standard sliding microtome sections were used. Woods of Araucariaceae and Podocarpaceae were studied with light microscopy. "Permanent" slides of *Abies concolor* and *Thuja plicata* prepared with standard sliding microtome techniques by Ripon Microslides (Triarch) were soaked in xylene to remove the cover slips, and further changes of xylene at 60°C removed all of the Canada balsam. These sections were then dried under light pressure between clean glass slides on a warming table. Warm xylene is judged to have removed not merely the Canada balsam but also natural resin deposits from these conifer woods. Only the tracheids of conifers are studied in the present essay, and only tracheid-to-tracheid pits are considered; cross-field (tracheid to ray) pits are not included here.

Transmission electron microscopy (TEM) of conifer woods (Pittermann et al. 2010; Jansen et al. 2012) is particularly good at showing wall layers. SEM reveals a wider range of features and can be applied with ease to reveal certain features very well because of depth of focus (Figs. 1–6).

RESULTS

***Abies concolor* (Fig. 1A–F; Fig. 2 A–F; Fig. 3A–C) and other Boreal/North Temperate Conifers.**—*Abies concolor* has well-marked growth rings (Fig. 1A) and is representative of Boreal/North Temperate conifers, judging by the data from Kennedy (1961), Bannan (1967), Zobel and Van Buitenen (1989), and Le Bourgeois (2000).

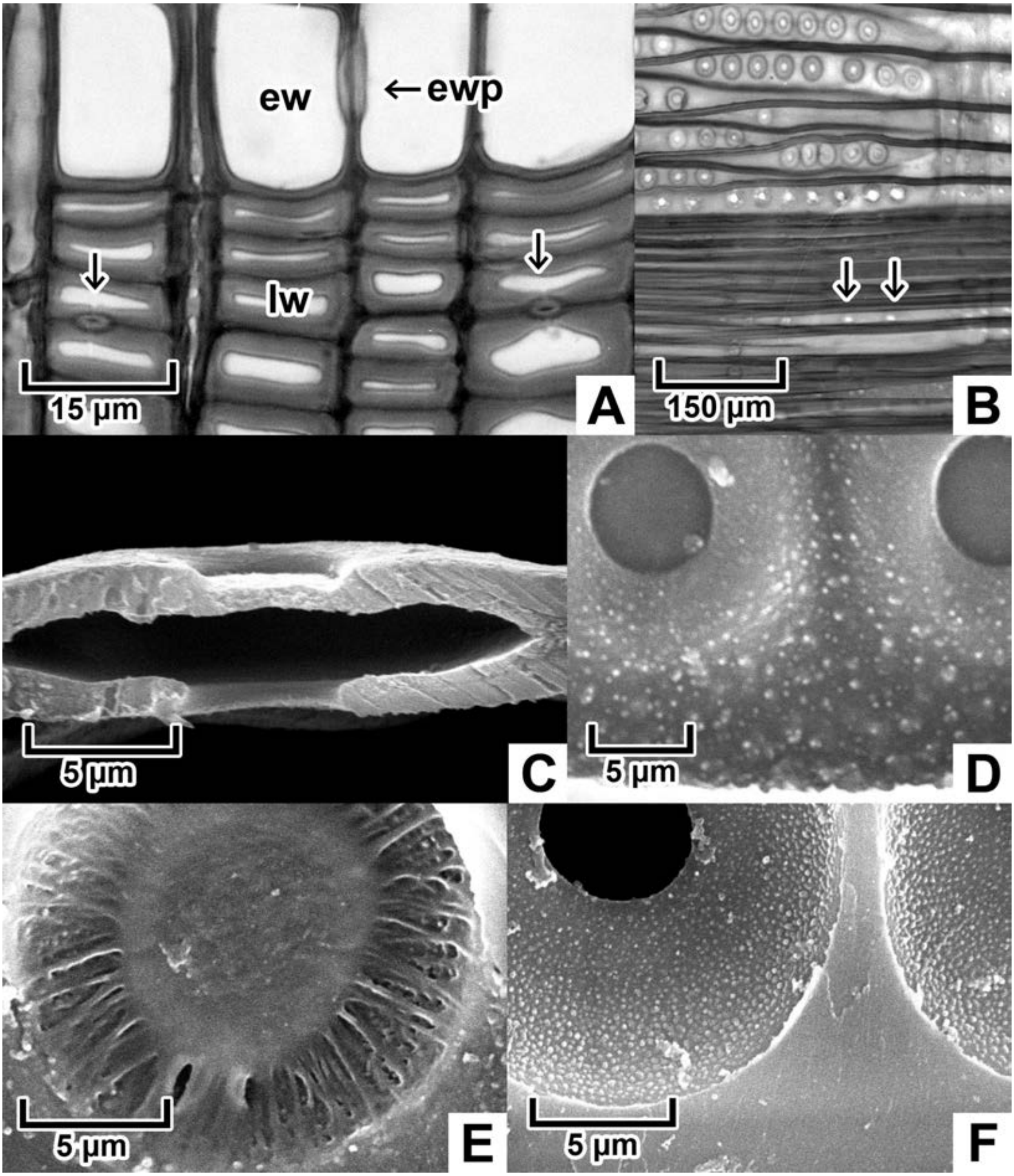

Fig. 1. *Abies concolor* (Ripon W-2w), light microscope (A–B) and SEM (C–F) views of wood sections. **A.** Transverse section of latewood (lw) and adjacent earlywood (ew) to show earlywood pit (ewp) and latewood pits (arrows). **B.** Radial section; end walls of earlywood tracheids above, sparsely pitted (arrows) latewood below. **C.** Pit pair from a tangential section of earlywood; torus is adherent to the upper pit cavity; margo is so thin it cannot be distinguished from the pit border. D–F. Radial sections. **D.** Earlywood pit portions seen from the lumen side of a tracheid; warted (vestured) surface evident. **E.** Earlywood pit membrane with central torus and peripheral margo; margo threads coarsened by accretion of some material. **F.** Surfaces of pit cavities (pit aperture above left), pit borders vestured.

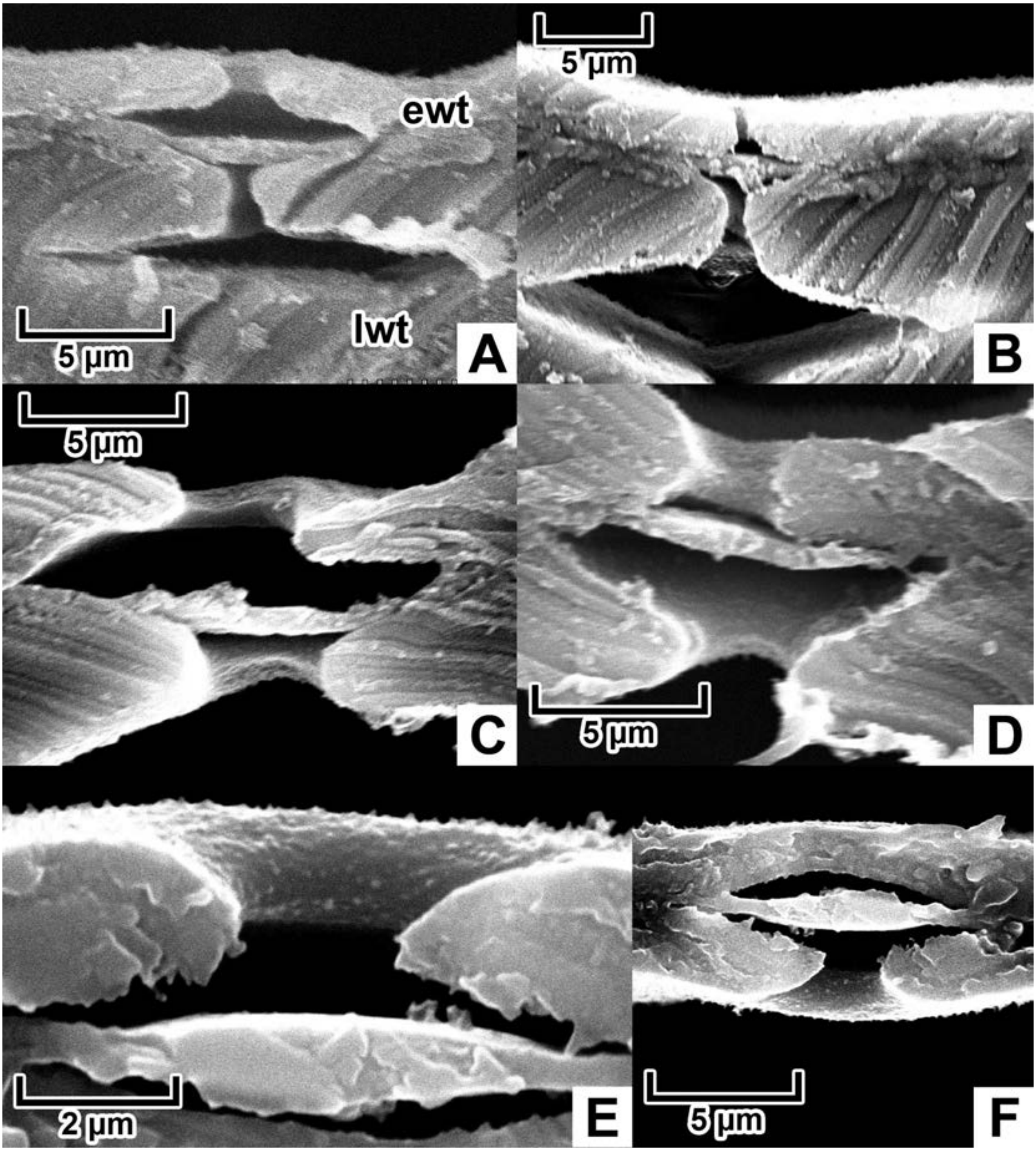

Fig. 2. SEM micrographs of pits on tangential walls of latewood, seen in transverse section (A–D) of *Abies concolor* (Ripon W-2w). Pit membranes are all thick and have no porous peripheral (margo) region. A–B. Pit pairs interconnecting last-formed latewood tracheids (lwt), below with first-formed earlywood tracheids (ewt), above. **A.** Pit pair with wider pit cavity. **B.** Pit pair with narrower pit cavity. C–D. Pit pairs linking adjacent latewood tracheids, on tangential walls. **C.** Thinner latewood walls. **D.** Thicker latewood walls. E–F. An unusually small pit pair from a radial wall, but not from the end wall of the tracheid. **E.** Pit aperture surface warted, pit membrane (below) thick and without perceptible porousness. **F.** Lower magnification of a pit pair, showing lack of adherence between the pit membrane and the pit cavity.

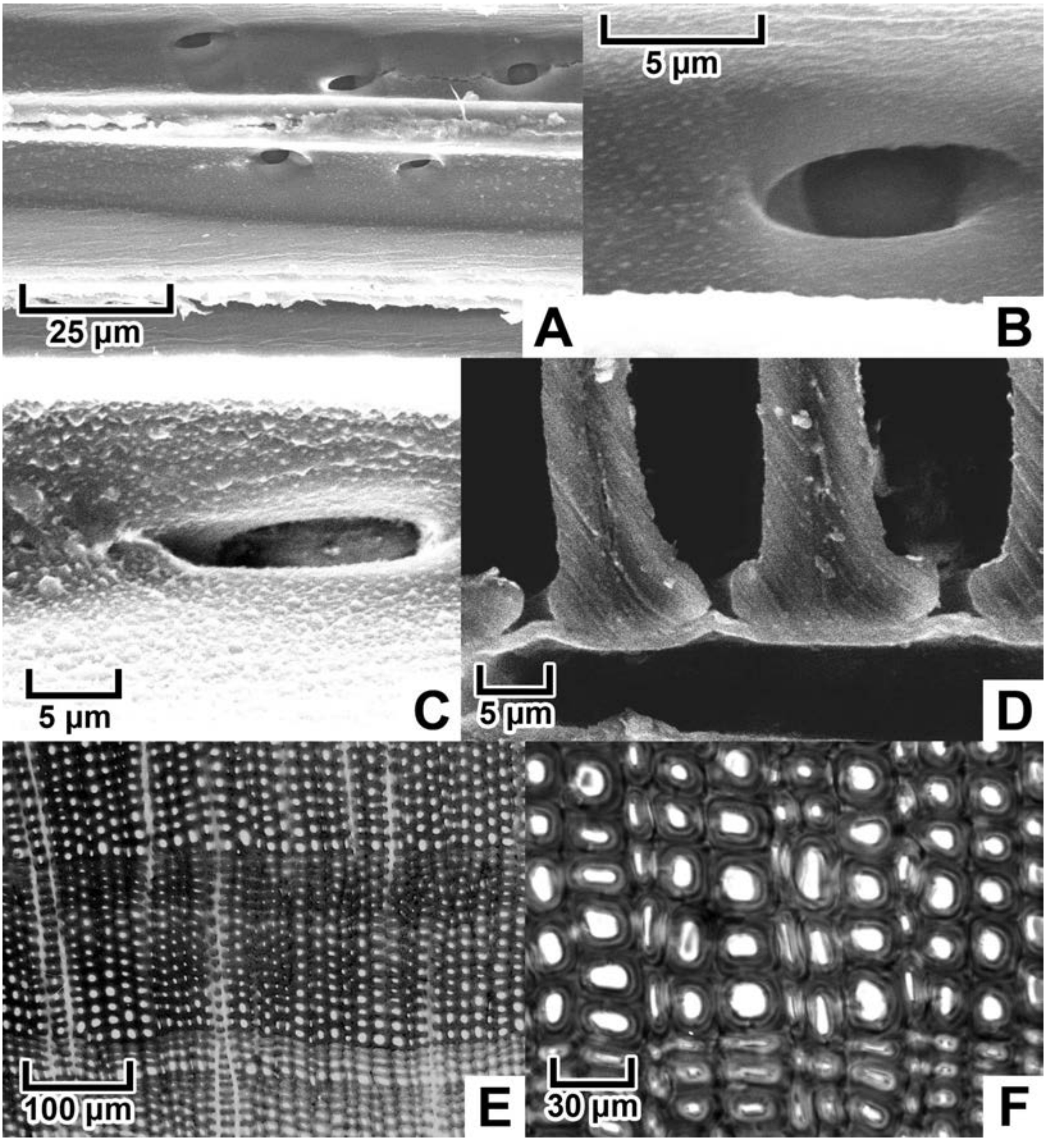

Fig. 3. Latewood tracheids. A–C. SEM micrographs of radial sections of latewood tracheids of *Abies concolor* (Ripon W-2w). A. Several pits with elliptical pit apertures on wider latewood tracheids. B. Enlarged pit aperture; faint vesturing is present. C. Pit from narrower latewood tracheid; vestures are more prominent. D. *Thuja plicata* Donn (Ripon W-63w), SEM micrograph of transverse section of latewood, contact between three tracheids (above) and ray cell (below). Note thick pit membrane in tracheid-to-ray pits. E–F. *Pherosphaera hookeriana* W. Archer (Podocarpaceae) (*C.T. White 8262*, Aw), light micrographs of transverse sections. E. Lowerpower, growth rings variable. F. Higher power, earlywood, above, has wall to lumen ratio typical of most coniferous latewood.

As cold weather approaches, there is a moderately rapid change in the radial diameter of tracheids (decreases) and tracheid wall thickness. With the advent of a new growing season, the reversal in these conditions is abrupt (Fig. 1A, top). As tracheids narrow with onset of latewood, there is a tendency for pits to occur more on tangential walls (Fig. 1A vertical arrows) whereas in earlywood, pits are on radial walls almost exclusively (Fig. 1A, horizontal arrow). There is a difference in pit size and density between earlywood and latewood (Fig. 1B).

Our ideas on conifer pits are, at this point in time, based largely pits on radial walls of earlywood (Fig. 1C–F). The torus (Fig. 1C, E) is wider than the pit aperture in any given earlywood pit (Fig 1D, F). The pit margo is very thin in the pit shown in Figure 1C; it is, in fact, not evident in that sectional view. Very thin margos are figured for North Temperate conifers by Jansen et al. (2012) and Pittermann et al. (2010). The pit margo in Figure 1E appears to have coarse threads, but that coarseness may relate to ageing of tracheids that are no longer actively conducting. The pit apertures in earlywood pits appear circular with very little deviation (Fig. 1D, F).

In *Abies concolor*, surfaces of earlywood tracheids (Fig. 1D) and the pit cavity surfaces (Fig. 1F) are prominently vestured (warted). Warts on pit cavity surfaces were well-illustrated for certain New Zealand conifers by Meylan and Butterfield (1978).

Sections of several pits in *Abies concolor* latewood as seen with SEM are shown here (Fig. 2). The reason for this coverage is that earlywood pits traditionally have been illustrated almost exclusively for conifers, presumably because their structure related to the more active conductive status of earlywood. The study of Domec and Gartner (2002a) on *Pseudotsuga* tracheids found that latewood is involved with "water storage" rather than conduction and has only about 10% of the flow of earlywood.

The latewood pits in Figure 2 may surprise those who have seen only illustrations of earlywood coniferous bordered pits. In fact, latewood pits (Fig. 2A–D), as well as the occasional small pits on tangential surfaces of earlywood tracheids (Fig. 2E–F) have thick margos with no apparent pores. The pit margos in these pits are too inflexible to be deflected to the extent that earlywood pit margos are, and do not adhere to the pit cavity surfaces (as do earlywood pit margos if deflected: Fig. 1C).

The latewood-to-earlywood pits on tangential walls dividing latewood from earlywood (Fig. 2A, B) in *Abies concolor* conform to the pits interconnecting latewood tracheids in size and morphology. The narrow pit cavities facing earlywood tracheids are notable in this regard. Similar pits have been figured for *Cryptomeria* by Kitin et al. (2009).

Latewood tracheid-to-tracheid pits in *Abies* (Fig. 2C–D) on tangential walls show little torus-margo differentiation and have rather thick pit membranes. The earlywood pits on tangential walls, which resemble latewood pits (Fig. 2E–F), have vestures (warts) that extend into the pit cavities (Fig. 2E).

Warts are variously conspicuous on the latewood tracheids of *A. concolor* (Fig. 3A–C). Warts are notably prominent in the tracheid of Figure 3C. Although pit apertures of some latewood tracheids in *A. concolo*r are circular, oblique elliptical pit apertures (Fig. 3A–C) are common on latewood.

Latewood tracheid-to-ray pits of *Thuja plicata* have thicker pit membranes (Fig. 3D). The nature of pit membranes in conifer latewood has been rarely mentioned, but in my experience, pit membranes in latewood tend to be thicker than those in earlywood.

A conifer from cold South Temperate habitats.—The wood of *Pherosphaera hookeriana* of the Podocarpaceae (Fig. 3E–F) exemplifies an unusual growth ring mode. At low power (Fig. 3E), there is obvious fluctuation in tracheid wall thickness, suggesting "false" growth rings; thicker-walled tracheids predominate, however. At higher power (Fig. 3F), one can see that the earlywood tracheids have thick secondary walls that would, on a wall-thickness-to-lumen-diameter basis, be classified as latewood in some conifers, such as *Araucaria* (Fig. 4A–B). This would accord with the idea that a higher proportion of latewood is triggered by drought stress, as claimed for various conifers by Zobel and Van Buijtenen (1989). *Pherosphaera hookeriana* grows in an area that is not notably dry, but is subject to prolonged freezing—physiologically equivalent to drought. Pit sizes are smaller than for most Podocarpaceae on tracheids of *Pherosphaera*, a latewood characteristic. Novak et al. (2016) and Bräunning et al. (2016) have offered explanations for how drought affects irregular ring formation.

Araucariaceae, a subtropical conifer family.—One could characterize Araucariaceae as having growth rings less well-differentiated into earlywood and latewood than in the North Temperate conifers, but in fact, latewood does occur (Fig. 4). The fact that tracheids of Araucariaceae are relatively wide in diameter (especially in radial dimensions) and that thick walls are not so noticeable because of cell diameter makes growth rings less

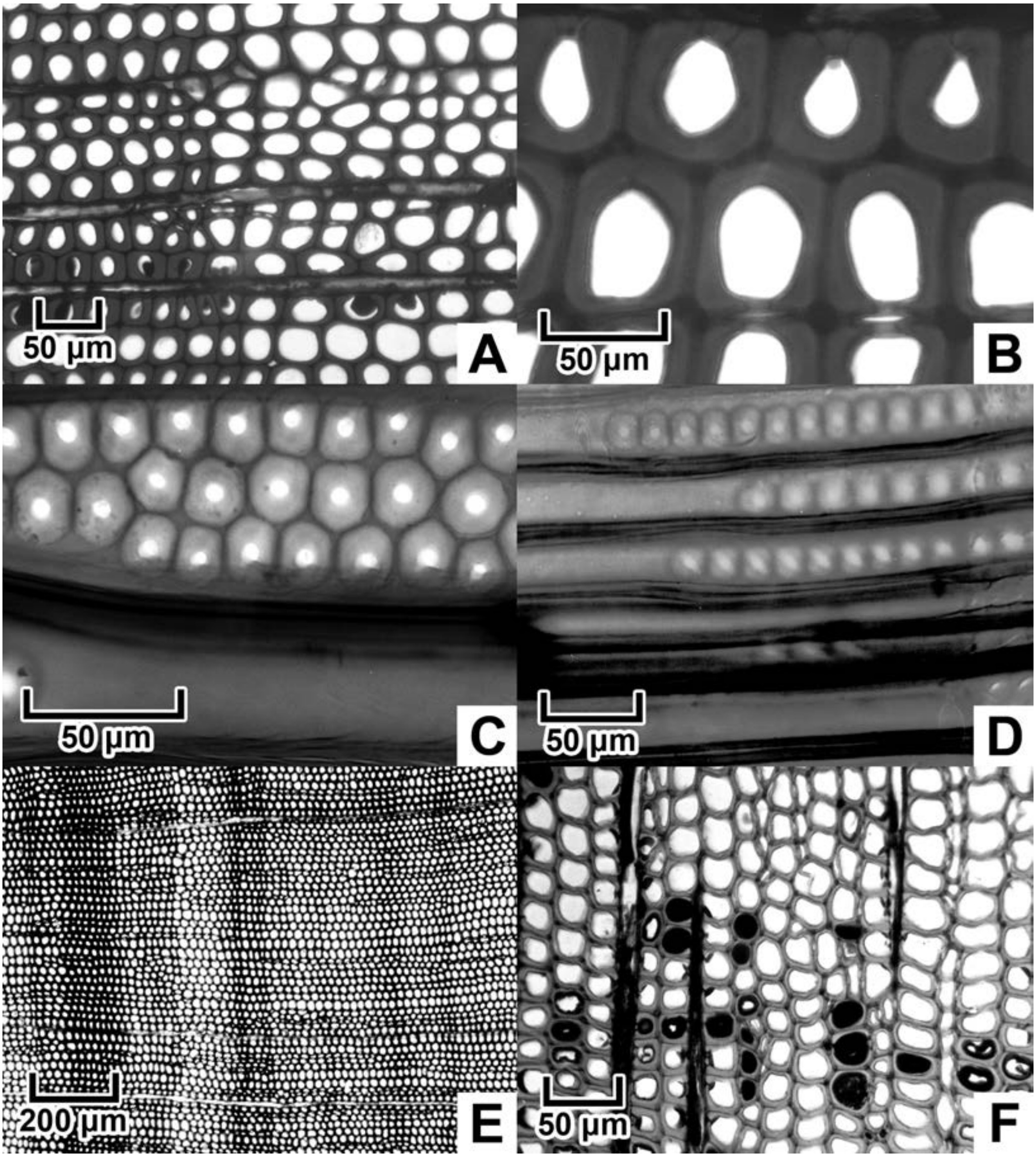

Fig. 4. Light micrographs of woods of *Araucaria*. A–C. *Araucaria angustifolia* (Bertol.) Kuntze (Ripon F-2ew). A. Transverse section to compare latewood (at left) with earlywood. B. Transverse section of latewood; latewood tracheids have notably thick walls but lumina are not compressed as in *Abies* (c.f. Fig. 1A). C. Radial section, end wall of earlywood tracheid with crowded pits on end wall above. D–F. *Araucaria cunninghamii* Mudie (cult., Huntington Botanical Garden, San Marino, CA). D. Radial section, earlywood tracheids above; end walls have single files of bordered pits. E. Transverse section, lower power; wall thickness fluctuates and growth rings are uncertain. F. Transverse section, higher power; thicker-walled tracheids below.

conspicuous. The wall thickness in *Araucaria* tracheids (Fig. 4B) leads Pittermann et al. (2006a, 2006b) to characterize the tracheids in *Araucaria* and *Podocarpus* as "overbuilt for their embolism protection" and "hydraulically inefficient, having greater density thickness:span ratio [a ratio of wall thickness to lumen diameter] and R_{ca} [resistivity based on cross-sectional area]." The transverse sectional area of walls in latewood of *Araucaria angustifolia* (Fig. 4B) shows us that latewood does occur in Araucariaceae, but other considerations may be taken into account. The tracheids of Araucariaceae are the longest in conifers (Carlquist 1975:141) and may approach 10,000 µm. In fact, these tracheids are very difficult to measure accurately because in macerations, broken tracheids are frequent, and intact tracheids are probably the shorter ones. Because of great length, tracheids of Araucariaceae provide only about half the resistance per unit length of stem than tracheids of typical conifers (which average around 5000 µm in length). Allometry considerations alone would dictate that Araucariaceae should have tracheids about twice as long as those of most conifers with correspondingly greater wall thickness. Also, a wider, longer tracheid provides more mechanical strength because of greater surface area adherent to neighboring tracheids (Wellwood 1962).

Earlywood tracheids of *Araucaria* (Fig. 4C) have end walls with numerous, large, crowded pits, often in three series. However, if we look at radial sections, latewood pitting, based on pit sparseness, size, and sometimes elliptical nature of pit apertures, also is evident (Fig. 4D, bottom). The differences from latewood of *Abies* (Fig. 1B) are less conspicuous than the similarities. Some Araucariaceae have woods with "false" growth rings that could be termed as various degrees of latewood in anatomical terms (Fig. 4E). Wall thicknesses in such rings are less perceptible than in North Temperate conifers, but can be seen at higher power (Fig. 4F, lower left). De Micco et al. (2016) have reported on and explained such "false" growth rings in conifers.

Conifer woods consisting of earlywood exclusively or nearly so.—There are several instances of conifer wood lacking in latewood or nearly so. One of these is the New Caledonian conifer *Dacrydium guillauminii* (Fig. 5). This species occurs along the banks of streams which fluctuate rather little in flow rate or level. Not evident in Fig. 5A is the finite height (no more than about 2–2.5 m) and the tapered stem structure, widest at the base. Likewise, temperatures do not change much seasonally in this habitat, and no appreciable growth ring activity is evident (Fig. 5B). The tracheids have all of the features of earlywood with typical torus-margo structure of the pit membranes (Fig. 5B–D), as cited above for *Abies*. The wood of *Dacrydium guillauminii* contains evenly-spaced air passages (a portion shown in Fig. 5C, center), parallel to tracheids and about the diameter of tracheids (Carlquist & Nazaire 2016). These air passages presumptively convey air from stems into the roots.

The pneumatophores of *Taxodium distichum* (known as "cypress knees") have been shown to function in aeration of root wood (Martin & Franke 2015). These pneumatophores do not have an appreciable structural support function because they grow upward from submersed roots, forming conical structures of finite height (rarely attaining 1 m). Perhaps because water is available in the swamp habitats of *T. distichum*, tracheid diameter is relatively uniform (Fig. 5E). Tracheid walls are uniformly thin (Fig. 5F), and some air spaces among the tracheids can be found (Fig. 5F, is), a possible aeration mechanism. All of the features of *T. distichum* pneumatophore tracheids correspond to those of earlywood, such as the earlywood of *Abies*.

***Parasitaxus* (Podocarpaceae): A parasitic conifer with latewood exclusively.—**At an opposite extreme from the riparian and lacustrine conifers is *Parasitaxus*, the only conifer known to be parasitic. The plant reaches 1–1.3 m in height (Laubenfels 1972), with a cluster of branches at the ends of virgate stems (Fig. 6A). The leaves are amphistomatic (Stockey et al. 1995). The parasitism is distinctive, with two aspects: a carbon pathway from the host (*Falcatifolium taxoides* (Brogn.) Gris), to which it is not closely related (Kelch 1998; Sinclair et al. 2002) like those of mycoheterotrophic angiosperms such as the monotropoid Ericaceae; and a direct water transfer like that of mistletoes (Feild & Brodribb 2005). Appreciable negative pressures have been recorded in *Parasitaxus* (Feild & Brodribb 2005), so the uniformly thick walls of the secondary xylem tracheids (Fig. 6B–E) may serve for countering hydraulic tension, but they may also reflect the tensile strength of the virgate stem. The wood anatomy was illustrated earlier (Carlquist 1982).

The uniformly thick-walled tracheids (Fig. 6C–D) may reflect the constantly humid cloud forest location in which *Parasitaxus* has been found. The report of both fibers and tracheids in wood of *Parasitaxus* by Kopke et al. (1981) is in error, as are their statement that tracheids of *Parasitaxus* wood have helical thickenings and that rays contain tracheids as well as parenchyma. The pits, on radial walls of the tracheids (Fig. 6E), are circular, relatively small in diameter and uniform in distribution. The pits have lenticular pit apertures, characteristic of latewood in many conifers (Greguss 1955). The pit membranes lack torus-margo differentiation (Fig. 6B), like latewood pits in many other conifers (Fig. 2). Lack of pit-margo differentiation would correlate with steady

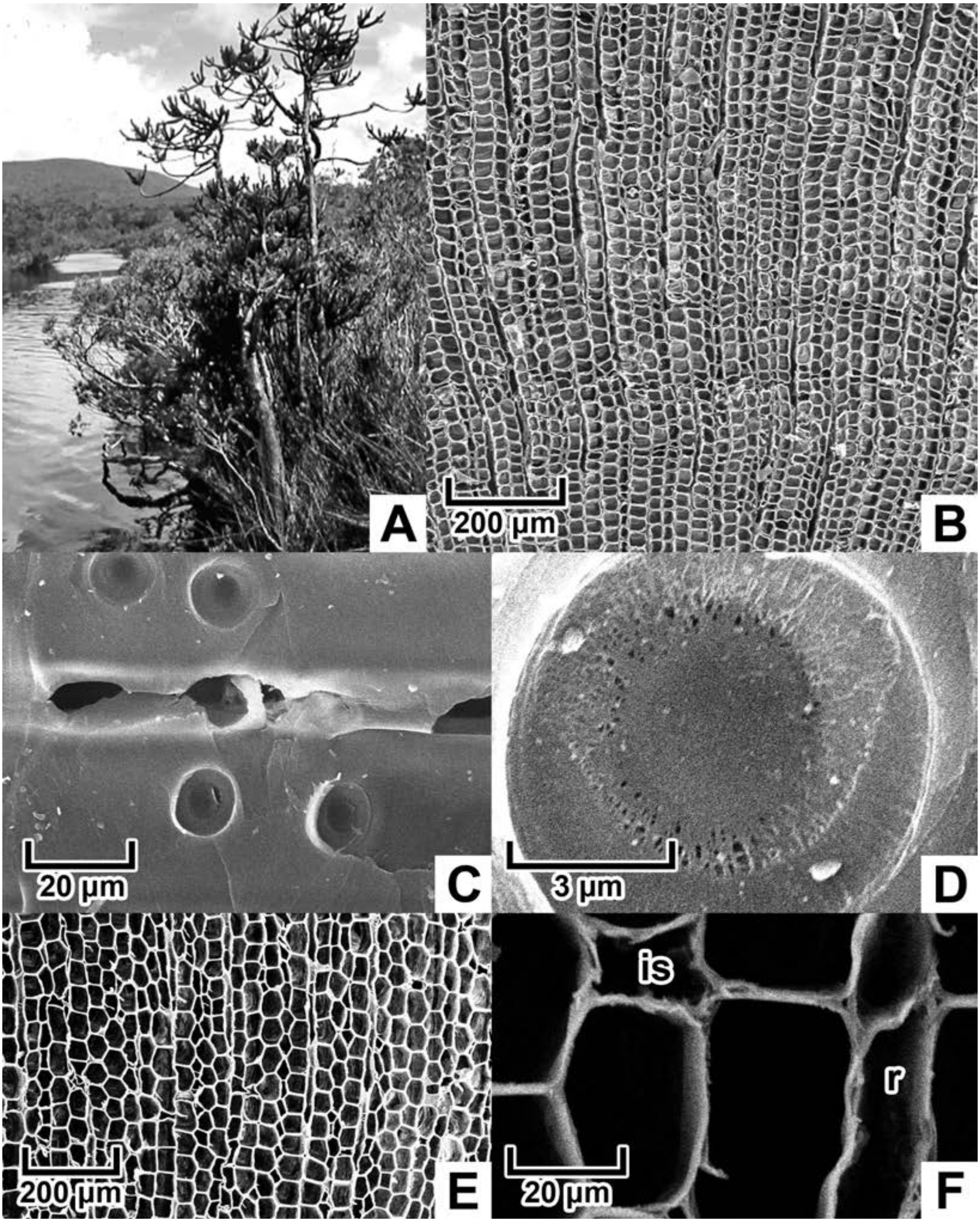

Fig. 5. Conifer woods which consist of earlywood only. A–D. *Dacrydium guillauminii* J. Buchholz, (*Carlquist 4319*, RSAw). **A.** Habit of plant (ca. 2 m tall; note tapered stems) on streambank, New Caledonia. B–D. SEM micrographs of wood. **B.** Transverse section of wood; no fluctuation in tracheid wall thickness, little fluctuation in diameter. C–D. Radial sections portions. **C.** Pits are typical earlywood pits. **D.** Pit membrane, enlarged; margo pores are present (more would be evident, but some adherence to pit border has occurred). E–F. *Taxodium distichum* (L.) Rich. (*Mulledge s.n.* Sep 2015, Monticello, AR), transverse sections of pneumatophore. **E.** lower power; very thin tracheid walls. **F.** Higher power (is = intercellular spaces; r = ray cell).

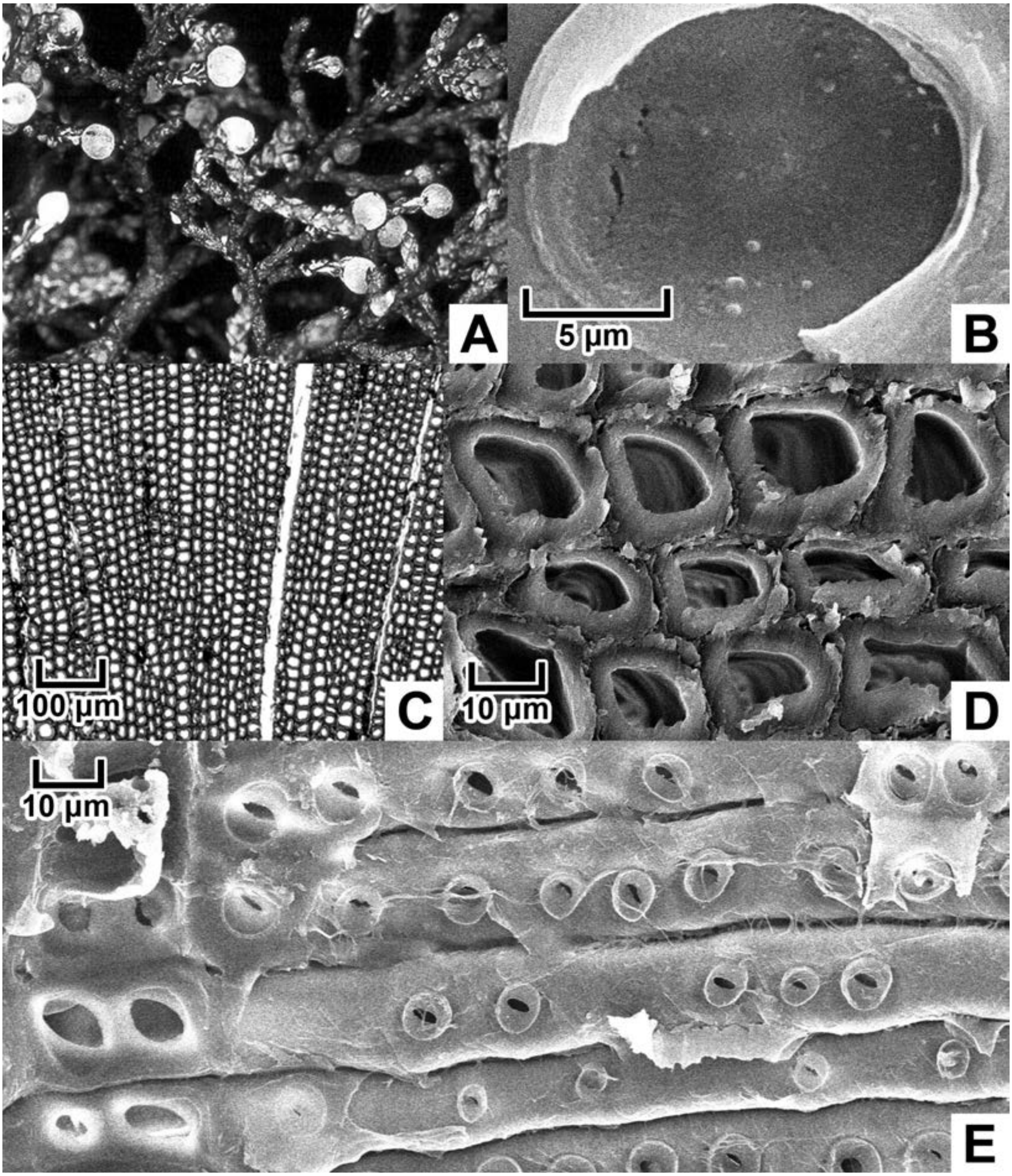

Fig. 6. *Parasitaxus usta* (Vieill.) de Laub. (Podocarpaceae), a parasitic conifer from New Caledonia, in which only latewood is present. **A.** Habit of some branchlets (photograph by Tim Motley, courtesy of Tatyana Lobova). B–E. Portions of dried specimen (*Vieillon 645* (ORSTOM), sample from branch collection donated by Nouméa Museum). B, D, E. SEM micrographs. **B.** Pit membrane from radial section; pit membrane is homogeneous and non-porous (a small fracture in membrane at left due to handling). **C.** Transverse section portion with light micrography; tracheids are uniform. **D.** Transverse section, higher power; walls have thickness typical of conifer latewood. **E.** Radial section, showing cross-field (tracheid to ray) pitting at left, but tracheid to tracheid pitting in most of micrograph; pit apertures are mostly small and elliptical.

but slow conductive rates. The pit membranes are also thicker than those of earlywood conifer pit membranes. Long elliptical pit apertures would fail to cover margo pores during aspiration if margo pores were present, and thus the co-occurrence of lenticular pit apertures and absence of margo-torus differentiation is understandable. The thickness of latewood pit membranes is also indicative of the unlikelihood that aspiration occurs.

COMPARISONS OF EARLYWOOD AND LATEWOOD IN CONIFERS

Although the phenomenon of growth rings in conifers is familiar, a comparison of earlywood and latewood features is in order. The differences between earlywood and latewood constitute perhaps the most familiar of the resolutions of conflicting requirements: the requirements for conduction and for mechanical strength. Figure 7 represents a compilation of most features by which coniferous latewood differs from earlywood. The circular pits of earlywood are much larger than those of latewood, and the two are not shown accurately to scale with each other in Figure 7. Earlywood pit membranes have clear differentiation into margo and torus, consistent with the optimal design of earlywood for conduction. Latewood pits are much smaller than earlywood pits, a decrease in diameter as one follows the progression from earlywood into latewood. The decrease in pit size probably correlates with decrease in conductive capability, because other features change during the progression into latewood: pit membrane thickness increases, and pit density wanes markedly. There is a shift from circular pit apertures to lenticular apertures in latewood of many conifers, as noted by Greguss (1955). As noted above, a lenticular pit aperture cannot close over margo pores, and pits with lenticular pit apertures apparently lack appreciable differentiation into margo and torus. Thus, latewood pitting of conifers shifts into relatively diminished conductive capabilities in a number of features, and the capability for pit aspiration is also lost in latewood of many species (probably not in the case of Araucariaceae). Thicker pit membranes found in latewood of many conifers cannot deflect and seal readily in case of pressure drop on one side of a tracheid interface compared to the other.

Conduction can occur in conifer latewood, but it amounts to a fraction of what can be observed in earlywood (Domec & Gartner 2002). Earlywood tracheids can enlarge somewhat in a radial direction, so that one can often observe earlywood tracheids with lumina wider in a radial direction than in a tangential direction. Latewood tracheids show various degrees of narrowing in radial walls, so that lumina become much smaller during the progression into latewood. Why do conifer tracheids maintain such uniform tangential diameter while shifting radial dimension so much? The reasons for this are not well understood. One can, however, cite the fact that with origin of vessels in Gnetales, vessels become appreciably larger than tracheids. This is certainly true with angiosperms also, and workers in wood anatomy look for differences in diameter to decide whether a cell is a vessel element or an imperforate tracheary element. There are a few instances in angiosperms in which vessels are so narrow that they are likely to be mistaken for imperforate tracheary elements (Convolvulaceae, Grubbiaceae, and others). The maintenance of tangential tracheid uniformity in confers does facilitate great flexibility to latewood formation, which can be initiated at any time of the year should conditions for earlywood production become unfavorable—a fact well known to those who study tree rings and the dating of woods in the Southwestern U.S. A growth ring can contain only a single layer of earlywood tracheids, or even none at all in an extreme year. The gradient from earlywood into latewood can be gradual or abrupt. The uniformity in tangential diameter of tracheids within conifers does prevent tracheid diameter from exceeding the maximum diameter for tracheid recovery after freezing—43 µm according to Pittermann and Sperry (2003).

The number of rows of bordered pits on end walls of earlywood tracheids (Fig. 7, bottom) varies, although the size of pits within such a grouping of pits varies relatively little. End walls of earlywood tracheids of Araucariaceae can bear as many as five series of pits, although three or four are more common (Greguss 1955). In conifers with very narrow tracheids, such as the Tasmanian Podocarpaceae or some Cupressaceae, earlywood tracheids may bear only a single series of pits.

One should note that as evidenced in the preceding generalizations, conifers exhibit a gamut of latewood expressions. The diversity among conifers with respect to latewood is less pronounced. The right column in

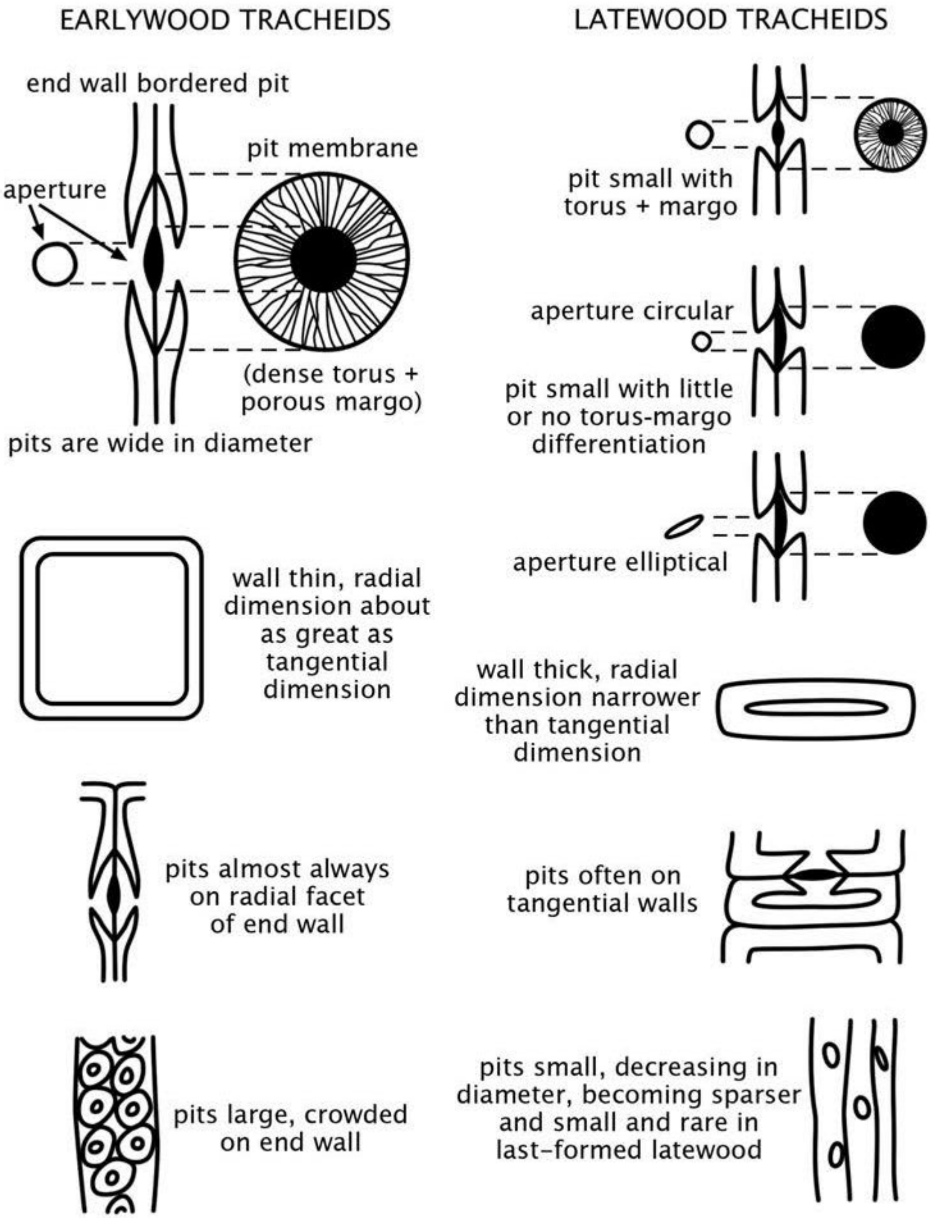

Fig. 7. Comparison of earlywood and latewood features of conifer tracheids. **Top comparison:** pits as seen in tangential section, with pit membranes and pit apertures also in face view. Central comparisons: walls and pits as seen in transverse section. **Bottom comparison:** pits of end walls as seen in radial sections. Although earlywood features are typical for most conifers, particular conifers have only some of the latewood features.

Figure 7, therefore, can be considered a kind of menu from which any of several features may occur in latewood of a particular species. With this in mind, one can ask why any particular conifer wood has the assemblage of features that it does.

RESOLUTION OF CONFLICTING FACTORS IN CONIFER TRACHEID CONSTRUCTION: AN ENUMERATION

Table 1 is composed of hypotheses about how conflicting structural situations in conifer wood have been resolved. "Conflict" often corresponds to a gamut of conditions called "trade-offs" by some workers: the opposing conditions are mutually exclusive. For example greater deposition of cellulose per unit transection of wood enhances various kinds of strength, but diminishes the area devoted to conduction. The present essay attempts to find instances like these in which opposing conditions are resolved so that opposing expressions are optimally satisfied. "Trade-offs" represent points along a spectrum of expressions and are not, therefore, equivalent to "resolutions."

Growth rings are the most familiar form of resolution of opposing functions in conifers: this resolution takes the form of production of two kinds of cells each year. Not generally realized is the train of adaptations and compromises that flow from the invention of the coniferous bordered pit. The coniferous bordered pit has three interconnected features in the pit membrane. (1) The shape must be circular, so that tension on all of the margo strands is equal. Some angiosperms have a torus, but do not have a functional margo in the sense that conifers do. (2) The margo strands must be separated by pores sufficient to meet conductive demands. (3) The center of the pit is devoted to the torus, which permits closure (aspiration) of the pit, but lessens the area (margo pores) devoted to conduction. The net effect of this structural design is that the tracheid wall is weakened by the large amount of space devoted to the pit membrane, and there is no way to compensate for this in earlywood. The production of latewood, thus, is a necessity for producing compensatory wall strength by minimal devotion of space to pit membranes.

Given that earlywood and latewood meet different and opposite demands, the proportion of earlywood to latewood can be altered within a species in order to meet the balance between conductive and mechanical strength demands. Latewood is, as seen above, a tissue that achieves greater mechanical strength characteristics, but it also does conduct water, albeit a small proportion of the flow compared to earlywood (Domec & Gartner 2002). This is not the only possible balance adjustment: greater conductive capacity can be achieved by maintenance of conduction in more than one growth ring. This was shown for *Pseudotsuga* by Braun (1970), who injected fluorescent dyes into the conductive stream. As yet we have little knowledge of how many growth rings can stay active in conduction, but we should avoid the assumption that only a single year's growth is functional. Study of the longevity of ray cells in particular conifers might be a good proxy for determining the duration of conductive activity in any particular growth ring.

The fact that conifers in the narrow sense (excluding Gnetales) have not developed vessels and yet have excellent conductive characteristics is noteworthy. Gnetales (and presumably the occurrence of vessels in Gnetales) predate angiosperms, but have not proved a great advantage in diversification of Gnetales in numbers or ecological coverage. Despite having similar ranges of xylem features, Gnetales have not competed well, presumably because of their long life cycle (Carlquist 2012). Is there an advantage of an all-tracheid system, or is this plan in conifer wood simply a maximization of conductive tissue? Tracheids are wider in roots than in stems for a selection of conifer species, and wall thickness is less for the root tracheids (Pittermann et al. 2006). These authors find that there is a kind of "release" in root tracheids for better conduction, whereas in stem tracheids, narrower tracheid diameter and greater wall thickness represent a requirement for greater strength. The all-tracheid condition has other reasons for existence, such as greater safety. One should ideally compare the all-tracheid system to an all-vessel system; a few examples of the latter exist, but one common close approach is found in angiosperm earlywood, in which the space allocation for vessels far outweighs the transactional area devoted to imperforate tracheary elements. Narrowness of tracheids also prevents embolisms from forming in tracheids. Tracheids narrower than 43 µm recover from freezing without embolism formation (Pittermann & Sperry 2002).

Table 1. Conflicting Restraints of Conifer Tracheids and their Resolutions.

Conflict	Resolution
1. Wider tracheids provide greater volume of flow per unit time, but too small an amount of wall material in a wider tracheid can weaken it excessively (Raven 1987).	**1.** Production of both earlywood and latewood annually, with earlywood lumina suited for conduction and latewood suited for strength; amount of latewood and earlywood and lumen diameter can be adjusted to suit requirements.
2. Conifer tracheids must have lumina less than 43 μm in diameter to avoid embolism from freezing, but narrow diameter offers greater hydraulic resistance (Pittermann & Sperry 2001).	**2.** A number of tropical conifers exceed this diameter; narrow-tracheid conifers are able to live in desert, alpine and boreal conditions. Larger tracheids have greater surface, providing greater inter-tracheid adherence and strength characteristics.
3. Vesturing ("wartiness") on conifer tracheid lumen surfaces enhances wettability (Kohonen 2006; Kohonen & Helland 2009) but adds friction to the conductive pathway.	**3.** Vesturing increases conductive safety (embolism resistance); vesturing is less in earlywood, where conduction is greater, but more prominent in latewood.
4. An all-tracheid wood structure offers more resistivity (Hagen-Poiseuille equation) in diameter as well as in the numerous end walls (compared to vessel elements of Gnetales or angiosperms).	**4.** Tracheids have greater conductive safety (resistance to embolisms) than vessels; an all-tracheid wood has more numerous conductive conduits, compensation for narrowness. Conifer tracheids can be much longer (3500 μm mean) compared to gnetalean or angiosperm vessel elements and tracheids, thereby having fewer end walls per unit stem length.
5. Conifers do not have the rapid embolism repair that permits angiosperms to occupy a wide range of habitats, and are restricted to habitats with deep water availability or mycorrhizae that provide a long season of water availability.	**5.** Conifers have greater "hydraulic safety margins" (Johnson et al. 2012) as a substitute for rapid embolism repair, and diversify in habitats where embolism repair by axial parenchyma carbohydrates (rarer in conifers than in angiosperms) is possible.
6. Conifers require a long season for pollination and maturation of seeds because they lack the double fertilization that shortens the angiosperm life cycle. Conifers must, however, provide photosynthates year round for the long duration required for cone and seed maturation year except for the few deciduous conifer species.	**6.** Conifers excel in habitats with deep water availability (or a mycorrhiza that provides a greater water-absorptive surface) and most conifer species are temperate or boreal in distribution, with narrow evergreen leaves that provide photosynthates over a longer period of the year in sunny locations. At least some wood remains functional during the coldest parts of the year to maintain this foliage. Long duration of needles often compensates for their smaller surface, mostly not suited to short seasons.
7. Earlywood tracheids provide lightness to conifer woods ("softwoods") and represent minimal investment in wall material, but conifers do not typically have large canopies that benefit from greater mechanical support.	**7.** An all-tracheid wood has large outer tracheid surfaces that, by bonding to each other, provide an increase in strength (Wellwood 1962). Latewood provides some compensatory strength without exceeding the advantages of lightness of wood. The lightness of conifer woods is suited to the decurrent habit (longer branches lower on the trunk), and so conifers compete well and can become tall in areas where canopy-type architecture of trees is not paramount.
8. Stem tracheids are narrower than root tracheids in any given conifer tree, which maximizes conduction but lowers strength.	**8.** Gravitational loading is highest in stems, which must be self-supporting. The narrowness of tracheids in stems can be adjusted to suit their gravitational loading and the amount of latewood can be adjusted also to improve strength characteristics.
9. Conifers are less good at embolism repair than angiosperms, which have mechanisms for restoring and enhancing conductive flow during the growing season, Conifer woods are not well adapted to high peak demands as in flushing of new foliage, production of large masses of reproductive structures, etc.	**9.** Conifer woods are less good than angiosperm wood at providing for peak flows involved in flushing, flowering, and fruiting, but they have exceptionally high safety margins (Johnson et al. 2012) that serve well for the long reproductive cycle of conifers and for the longevity of evergreen foliage.
10. Pits are a way of permitting cell-to-cell movement of water and solutes; the permeability of the pit membrane is utilized, but the secondary wall strength is lessened and wall strength therefore is sacrificed.	**10.** A bordered pit can, by the overarching of the secondary wall, minimize the loss of wall strength while maximizing the area of the pit border. The pit aperture of a given pit can be narrowed to the point where its water transmission equals the collective water transmission of the pores of the pit membrane of that pit. The pores of a pit membrane are designed not to pass bubbles under conditions of normal transport (Carlquist 2001:112). The coniferous bordered pit, found only in conifers (including Gnetales) and *Ginkgo* is specialized to permit pit closure by membrane deflection, a mostly impermeable torus, and a margo porose enough to maximize water flow.

Table 1. *continued*

Conflict	Resolution
11. The pit membrane of a coniferous bordered pit is circular; this shape is necessitated by the fact that tension on the margo strands must be even in order for the pit membrane to be deflected owing to unequal pressure on the two sides of the pit membrane, closing the pit. An oval pit based on the coniferous pit type could not function because tension on the margo strands would be unequal. The torus must be at least as large as the pit aperture and centrally placed for pit closure to be effective.	**11.** Coniferous tracheid-to-tracheid bordered pits must always be circular (not including the aperture). Wider areas of tracheids are covered by more than one series of pits.
12. In order to be effective in transmitting water optimally, the margo portion of a pit membrane of a coniferous pit must be relatively large, and the central torus proportioned accordingly. A large pit membrane, however, constitutes a serious interruption in the secondary wall, weakening the tracheid proportionately.	**12.** The only compensation for the diminished strength of a tracheid wall by large coniferous bordered pits is tracheid dimorphism: formation of earlywood tracheids with strength sufficient to counter water column tensions but not optimal for other mechanical considerations (tensile strength). The other products of this dimorphism, latewood tracheids, have small bordered pits with significantly less conductive capability, but thick walls promoting various types of strength. Wide pit apertures are formed in situations where water stress is low, but narrower where water stress is higher (Pittermann et al. 2010).
13. The pit aperture in earlywood must be circular and appreciably narrower than the torus to seal a pit during aspiration (pit deflection); by being wider, with the margo proportionately narrower, conduction is lessened.	**13.** The number of earlywood pits on an earlywood tracheid can be greater to meet the need for conduction. Increase in number of pits may weaken the earlywood tracheid wall, but the compensation of latewood, in which little conduction occurs, is available to produce mechanical strength commensurate with weakness of walls in earlywood.
14. Pit apertures diminish and may approach zero conductivity at upper levels of tall conifers (Domec et al. 2008; Lazzarin et al. 2016).	**14.** Conifer height does not exceed conductive ability as limited by the pit aperture diameter.
15. Pits on conifer tracheids are predominantly on radial walls, but radial walls are too narrow for pits that conduct effectively on radial walls of latewood.	**15.** Bordered pits on latewood conifer tracheids are commonly on tangential walls. This assures conduction between latewood tracheids and between the last-formed latewood tracheid and the first-formed earlywood tracheid of the following year.
16. The microfibrils of tracheid walls are parallel and are oriented in various diagonal directions, but earlywood pits must interrupt wide circular areas of the wall; microfibrils curving around pits have lesser strength than do straight, parallel microfibrils that can adhere to each other laterally.	**16.** In later-formed latewood (and in cross-field pitting), pits can be elliptical, and can parallel the predominant oblique direction of the microfibrils, thus interrupting the tensile strength of the tracheid wall minimally. Latewood tracheids have pits that are few, small in diameter, and sparse, all features that result in less weakening of the wall.
17. Pits in coniferous latewood are conductive, although to a much lesser degree than those of earlywood; they lack torus-margo differentiation by not having margo pores that can conduct water. Pit membranes cannot deflect well and often lack the ability to close pits by aspiration.	**17.** Ability to close pits by aspiration is not significant in conifer latewood, just as latewood tracheids in angiosperms with tracheids (*Rosa, Hamamelis*) cannot aspirate. In both cases, latewood tracheids (with little torus-margo differentiation in conifer latewood) have thick pit membranes and do not aspirate because their pit membranes are non-porous and air-seeding is unlikely to occur through them.
18. Compared to gnetalean (and angiosperm) perforation plates, end walls of conifer tracheids offer more resistance to the conductive process because the margo pores are relatively small.	**18.** Conifers partially compensate for end-wall resistance in tracheids by the large numbers of tracheids in a homoxylous wood and the greater length of conifer tracheids, providing fewer end walls per unit length, and the crowding of pits on end walls. The resistance of the conifer tracheid end wall is offset by the safety of the pit's ability to close by aspiration, limiting conductive stream failure to individual tracheid.
19. The torus-margo system of coniferous bordered pits is successful in vascular plants that have primary xylem tracheary elements with annular, helical, or reticulate thickenings, but is therefore not compatible with the spaces between thickenings, especially those that are extensible and elongate during growth.	**19.** Conifers (including Gnetales) and *Ginkgo* have circular bordered pits interpolated into annular and helical protoxylem tracheids with extensible walls. There is then an abrupt change to non-extensible walls that have circular bordered pits in them, as do all subsequent secondary xylem tracheids (reticulate and scalariform wall patterns are absent in conifer primary xylem).

Table 1. *continued*

Conflict	Resolution
20. The design of wood of conifers (including Gnetales) and *Ginkgo* is limited in diversification because all of its characteristics stem from the margo-torus design of the circular bordered pit, a defining structure underlying the coniferophyte line.	**20.** Wood of conifers, if not adapted to as wide a range of situations as that of angiosperms and other vascular plants, represents a quite distinctive adaptive optimum compatible with the long life cycle (gametophyte formation followed by embryo formation) that conifers (including Gnetales) plus *Ginkgo* have. Coniferophyte wood is also advantaged by enhanced embolism resistance because of the torus-margo structure of pits and because of the all-tracheid design.

Some conifer wood consists of tracheids wider than 43 µm. In *Agathis palmerstonii* F.M. Bailey, tracheid diameter ranges between 50 and 80 µm in mature wood (Greguss 1955). *Agathis palmerstonii* occupies zones where freezing is unlikely. This species also has the longest tracheids measured in conifers (about 8000 µm; Carlquist 1975:141). Long tracheids are a way of taking advantage of long end walls devoted to pitting to maximize conduction, and the end wall resistance is potentially less (per unit length of stems) if tracheids are longer. Detailed information on how diameter and wall thickness of conifer tracheids influence conductive characteristics is offered by Pittermann et al. (2006) and Sperry et al. (2006).

The "Conflicts" and "Resolutions" of Table 1 are presented as hypotheses. There is observational evidence, as cited, for these from wood anatomy. Some of them follow from work on wood physiology, cited in the present essay. As with all hypotheses, questions remain to be answered, and examples need to be identified and studied. The potential value of Table 1 and the material covered in the present essay is to further an appreciation of how anatomical features interact or are interrelated, directly or indirectly, to maximize the functional conditions observed.

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