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WOOD ANATOMY OF ARGOPHYLLACEAE (ASTERALES): ADAPTATION IN A SMALL CLADE

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ABSTRACT

Argophyllaceae (Argophyllum, 14 spp.; Corokia, 6 spp.; Lautea, 1 sp.), are shrubs that occur in the southwestern Pacific and eastern Australia. They occur in habitats where moisture is relatively common but dry days and mild frost may occur. The woods of these genera show enough distinctive features to justify their grouping in a single family: perforation plates with 10–20 bars, vessel elements narrow and numerous per mm2, imperforate tracheary elements about 50% longer than the vessel elements, axial parenchyma scarce, diffuse, multiseriate rays narrow and heterocellular (upright cells common in uniseriate rays), crystals absent, gum deposits common. These features group the genera of Argophyllaceae more closely with each other than with the nearest families in Asterales (Alseuosmiaceae, Phellinaceae). Probable apomorphies of the genera include helical thickenings in vessels and tracheids, together with abundant tracheids and rare septate fiber-tracheids (Corokia); almost total absence of axial parenchyma and tracheids combined with maximal abundance of septate fiber-tracheids and no helical thickenings (Argophyllum, Lautea). Lautea, formerly included within Corokia, has floral and foliar distinctions and is endemic to a single island, Rapa Iti. Woods of Argophyllaceae are alike in their ecological adaptations (perforation plates, vessel diameter and density) but the presence of tracheids and helical thickenings in Corokia suggest adaptations to frost and mild drought. As expected, vessels group more prominently in the tracheid-free species (Argophyllum, Lautea) but very little in the tracheid-rich genus Corokia.

Key words: Corokia, ecological wood anatomy, Lautea, septate fiber-tracheids, Zealandia.

INTRODUCTION

Wood can reflect rapid evolution of characters or it can indicate stasis in a relatively unchanged land area that has habitats with mesic features that fluctuate very little. Argophyllaceae (Asterales) are an interesting example because some features of the wood are plesiomorphic (e.g., scalariform perforation plates). Other features, however, suggest an overlay of characters that are adaptations to some moderate degrees of frost and drought. The shrubby habit is indicative of this ecological positioning as well.

If we look at Araucariaceae (Araucariales), we see an essentially Gondwanic distribution (southwestern Pacific and the southern half of South America) plus fossil species elsewhere (Florin 1963). Agathis Salisb., Araucaria Juss., and Wollemia W.G. Jones, K.D. Hill & J.M. Allen have a complex of features in wood and other parts of the plant that seem slow-evolving and thus related to limited dispersal, long life cycles, and adaptation to mesic habitats. Atherospermataceae (Laurales) also illustrate wood features thought to be primitive with respect to most angiosperms (Carlquist 2018), and are an angiosperm family with an essentially Gondwanic distribution and a clearly mesic ecology (Renner 1999; Renner et al. 2000). The mesic ecology adaptation of Atherospermataceae seems related to the persistence of areas of cool wet conditions as the extent and climate of Gondwana changed. By contrast, the two centers of radiation in the Southern Hemisphere Proteaceae (Proteales) are Australia (especially Western Australia) and South Africa (especially Cape Province). In these two localities, Proteaceae have specialized extensively on sandstone/acid sand areas. Proteaceae have a different water conduction system as compared to Atherospermataceae: with simple perforation plates, marked fluctuation in conductive rates is possible in Proteaceae. Axial parenchyma and prominent rays may aid in embolism prevention by osmotic means, and clearly foliar modifications also favor lowered transpiration in Proteaceae.

Do Argophyllaceae constitute a group with adaptations that represent conservative water economy features, like Atherospermataceae, but with some wood modifications that favor lowered transpiration? Araucariaceae and Atherospermataceae retain Gondwanic distributions, but Argophyllaceae follow a more restricted pattern. Recently, the continent of Zealandia—mostly now submerged but still a continent—has been recognized as a significant Gondwanic fragment (Luyendyk 1995; Mortimer 2004). It includes New Zealand and New Caledonia, but also some small continental islands (Lord Howe Island, Chatham Islands). Although Australia was not part of Zealandia, it was close enough so that interchange of floric characters of life was probably possible. Separation of Zealandia from Gondwana began about 90 million years ago (Mortimer 2004; Neall and Trewick 2008). Sea floor spreading began 52 million years ago (Schollart et al. 2006). The Chatham Islands, east of New Zealand, probably emerged only 4 million years ago on the eastern margins of Zealandia. The narrow straits between Australia and Zealandia remained possible dispersal avenues until the separation of Australia and Zealandia.
Mild frost, generally cool temperatures, drying winds, and rainfall between 34 and 289 cm per year prevail in New Zealand (Allan 1961). Similar conditions can be expected in upland localities of New Caledonia where Argophyllum J.R. Forst & G. Forst grows (World Climate Guide 2019) and Lord Howe Island (Pickard 1983), although frost is unknown on Lord Howe Island. Both Argophyllum and Corokia A. Cunn. are represented on limited areas of eastern Australia, and thus one might expect more fluctuation of temperature and rainfall to be reflected in wood structure of those species. Argophyllaceae have one non-continental outlier, Lautea F. Br. on Rapa Iti, which has a cool, humid subtropical climate like the New Caledonian uplands (Wikipedia 2019). Wood anatomy and climate should be compared where a genus or family (at least a smaller one) extends across a variety of different ecological regimens.

Argophyllum occurs in New Caledonia (14 species) and portions of Australia (9 species) according to listing in the International Plant Names Index (2019). This assemblage may represent dispersal between Australia and Zealandia as the two continents were separating. The colorful fleshy fruits of Argophyllaceae are best characterized as shrubs of various sizes, some (C. macrocarpa) approaching treehood. The evolution of Argophyllaceae appears centered in New Zealand may have evolved during colder, glaciated times, and we should consider the possibility that features of Corokia wood may retain some features from that era. In addition, images from scanning electron microscopy (SEM) permit inclusion of some hitherto unreported features, such as presence of pit membrane remnants in perforations of perforation plates. Liquid-preserved wood material proves important to our studies. We can now consider wood of Argophyllaceae in a more accurate context, in Asterales of Campanulidae (euasterid II), as proposed by Kårehed (2002), Lundberg (2001), and Tank and Donoghue (2010). Earlier, Argophyllum and Corokia were placed in Escalloniales or Cornales (Patel 1973; Cutler and Donaldson 1998) is essentially systems-based, following the traditions of Solereder (1908) and Metcalfe and Chalk (1950). These workers did not have access to ecological and habit data, and molecular systematics was more fragmentary than it is today. Our new account adds Lautea collenetti and two species of Argophyllum (A. cryptophlebum and A. vernicosum). We now have some guidelines for interpreting wood data in the light of ecology and habit. Argophyllaceae are best characterized as shrubs of various sizes, some (C. macrocarpa) approaching treehood.

Our picture of wood of Argophyllaceae thus far (Gornall et al. 1998) is essentially systems-based, following the traditions of Solereder (1908) and Metcalfe and Chalk (1950). These workers did not have access to ecological and habit data, and molecular systematics was more fragmentary than it is today. Our new account adds Lautea collenetti and two species of Argophyllum (A. cryptophlebum and A. vernicosum). We now have some guidelines for interpreting wood data in the light of ecology and habit. Argophyllaceae are best characterized as shrubs of various sizes, some (C. macrocarpa) approaching treehood.

In this study, wood anatomy and wood chemistry, especially histology and anatomy of vessels, tracheids, and thin-walled elements, are compared where a genus or family (at least a smaller one) occurs. We can now consider wood of Argophyllaceae in a more accurate context, in Asterales of Campanulidae (euasterid II), as proposed by Kårehed (2002), Lundberg (2001), and Tank and Donoghue (2010). Earlier, Argophyllum and Corokia were placed in Escalloniales or Cornales (Patel 1973; Cutler and Gregory 1998), and their wood features were compared to families and genera that are not closely related to Argophyllaceae; more closely related families according to molecular data (Phellinaeae) were placed elsewhere. Although we do not have as much relevant information as we would like from a range of fields, we favor a more comprehensive way of viewing wood anatomy and attempt to represent that to the extent materials are available to us.

### MATERIALS AND METHODS

The materials of Argophyllum, Corokia and Lautea were available in the form of dried specimens except for A. cryptophlebum, A. vernicosum and C. cotoneaster. Specimens of these three species were preserved in 50% aqueous ethanol. Dried specimens were boiled in water and then stored in 50% aqueous ethanol. Sections were prepared by means of standard sliding microtome techniques. Some sections of each species were used to provide a more comprehensive view of wood anatomy.
were stained by means of Northen’s modification of Foster’s tannic acid-ferric chloride method (Johansen 1940) and made into permanent slides. Other sections of each collection were rinsed with three changes of distilled water and dried between glass slides under pressure (to assure flatness) on a warming table. These dried sections were sputter-coated with gold and examined with a Hitachi S2600N scanning electron microscope (SEM). Portions of wood samples were macerated by means of Jeffrey’s Fluid (Johansen 1940) and stained with safranin in an ethyl alcohol series and made into permanent slides.

Specimens were judged to have a mature wood pattern, except for twigs about three years old, from C. buddleoides A. Cunn., C. macrocarpa Kirk, C. cv. Greenty’s Green, and C. cv. Renegade. These were provided by the nursery Greenmachine in Tuatapere, New Zealand. The sources for the other collections were A. cryptophlebus Zemann, M. E. Olson 1964 (UNAM) A. vernicosum Däniker, M. E. Olson 1337 (UNAM); C. cotonaster Raoul, cultivated by San Marcos Growers, Santa Barbara, CA; Lautea colletetti (L. Riley) F. Br., BISHw:433. The specimen of L. colletetti unfortunately shows some fungal infection. The descriptions and illustrations of this species offered here are based as much as possible on intact portions of the specimen. This underlines one more limitation of xylarium specimens, along with absence of starch, nuclei, and other features that are reliably present in liquid-preserved wood samples and thus indicate function unambiguously (see Carlquist 2014).

Conventions used here include use of averages rather than ranges in quantitative features. Function in woods is reflected more by means rather than by the extremes. Lengths and diameters depend more on specimen diameter than on phylogenetic position. Vessel diameter is measured as lumen diameter, which is more important physiologically than outside diameter. Vessels that are not circular in transection are measured as an average between radial and tangential dimensions. Terminology is based on Carlquist (1988). Scanty parastrachal is not separable from sparse diffuse where both are present in a wood: with random distribution of a few axial parenchyma cells, some will contact vessels, some will not, and two patterns cannot be clearly differentiated and nominated. Vessels per group is based on a solitary vessel = 1, a pair of vessels in contact = 2, etc, and an average obtained from 25 data points. The term “gum” is used in a vague way by wood anatomists, as in Metcalfe and Chalk (1950).

The ray terminology of Patel (1973) was based on Brazier and Franklin (1961), a scheme that has not won acceptance, so it is not used here. The system of Kribs (1935) has been followed by many authors, but while it purports to represent evolutionary levels (see Olson 2012), one wishes for a nomenclature that reflects actual ecology and physiology. Failing that, we can use distributions of upright, square, and procumbent cells (as seen in radial sections) in multiserial and uniseriate rays. The situation is complicated, however, by the fact that closer to the pith rays are composed of a higher proportion of upright cells (sometimes exclusively upright cells, or even rayless secondary xylem), whereas in the same stem, procumbent cells are produced as the stem expands in diameter. This is not true in stems of “woody herbs” of various kinds, where upright ray cells often comprise the totality of ray tissue for the life of a stem (Carlquist 1962). This has been considered an attribute of protracted juvenilism. Another complication is that before Carlquist (2007), ray cell pits were assumed to be simple, whereas they are quite often bordered (Fig. 6F, G in the present study).

RESULTS

Quantitative data and certain types of qualitative data (ray histology) are given in Table 1. Inclusion of the Rapa Iti species, Lautea colletetti, shifts our knowledge of Argophyllaceae appreciably, although it obviously belongs to Argophyllaceae. Two data sets are given for C. macrocarpa, because my observations were based on a three-year-old sample whereas Patel’s (1973) data for this species were based on two trees; C. macrocarpa is the most arborecent species in the family.

Growth Rings

Growth rings can be deemed present in Argophyllaceae (Gornall et al. 1998) to various degrees, but are not readily evident in most transverse sections (Fig. 1A, 3A, 5A). They are least evident in Lautea colletetti (Fig. 4A). The most pronounced growth rings are present in C. buddleoides. Latewood of C. buddleoides consists of thick-walled tracheids plus small-diameter vessels. Latewood is very brief in growth rings of most Argophyllaceae, which is noteworthy because it suggests that growing conditions are favorable throughout most of the year.

Vessel Grouping

Two species, A. cryptophlebus (Fig. 1A) and L. colletetti (Fig. 4A), have vessel grouping higher than 1.50. Vessel grouping may also be high in A. nullumense R.T. Baker (Gornall et al. 1998). The other species reported have 1.22 or fewer vessels per group except for A. vernicosum (Fig. 3A) and C. cotonaster (Fig. 5A). Both species have 1.40 vessels per group. The numerical levels are important here because species of woody angiosperms with low degrees of vessel grouping have tracheids instead of fibers (or else are in notably mesic situations) (Carlquist 1984). Septate fiber-tracheids instead of tracheids predominate in Argophyllum and Lautea.

Vessel Diameter and Density

The range of mean vessel diameters in the species studied (Table 1) suggests narrower vessels in those with greater density (vessels per mm²). The inverse relationship of figures for vessel density and vessel diameter in a species and the correlation of these figures with ecology has been noted earlier (Carlquist 1975). Departures from this relationship are more notable in woody lianas and in stem succulents. In woody groups without such habits, however, departures from a straight-line relationship are smaller, and are more closely related to packing considerations. The data in Argophyllaceae depart from a straight-line relationship somewhat because of specimen size: smaller-diameter stems have narrower vessels at the beginning of secondary growth.

Vessel Element Length

Length of vessel elements (Table 1) is relatively short. The range of 560–1020 µm given by Patel (1973) for the family is...
Fig. 1. *Argophyllum cryptophlebium*.—A. Transverse section; numerous vessels grouped.—B. Tangential section; septate fiber-tracheids present.—C, D. Tangential section, starch in cells of multiseriate ray.—C. Procumbent cells (below) and a sheathing cell (above).—D. Cells of wing of multiseriate ray, plus a septate fiber-tracheid (bottom).—E, F. Radial sections.—E. Upright cells of multiseriate ray. F. Portion of band of axial parenchyma, small starch grains present. A, B: light microscope photomicrographs; C–F: scanning electron microscope images.
based on wood of mature shrubs (and small trees). In younger stems, vessel elements are shorter (shrub clippings of \textit{Corokia} \textit{cv. G. Green} and \textit{Corokia} \textit{cv. Renegade}). The shrub cutting from \textit{C. macrocarpa} is compared with figures from a mature specimen given by Patel (1973) in Table 1. Comparisons of this sort follow the Bailey and Tupper (1918) finding that fusiform cambial initial length increases with stem diameter increase (in truly woody angiosperms).

The vessel element lengths of the two \textit{Argophyllum} species are appreciably longer than those found in \textit{Corokia}. The specimen of \textit{L. collenettei} has a vessel element length longer than those found in \textit{Argophyllum} or \textit{Corokia}.

\textbf{F/V Ratio}

The ratio between length of imperforate tracheary element (F) and vessel element length (V) is indicative of the degree of intrusive growth of cells destined to be imperforate tracheary elements. This, in turn, reflects some parameters of the mechanical strength of the stem. The F/V ratio in Argophyllaceae (Table 1) is relatively uniform and, for woody angiosperms as a whole, moderately low. The F/V ratio in “primitive” woody angiosperms is often thought to be low, but one can find exceptions to this.

\textbf{Bars Per Perforation Plate}

The number of bars per perforation plate appears to be relatively uniform throughout Argophyllaceae (Table 1). This uniformity is not expected in most angiosperm groups that show marked diversity in habitat type, and indicates that Argophyllaceae are all operating on a conductive system that features slow rates, correlated with predominantly cool air temperatures and low transpiration rates. Such woods, like those of Atherospermataceae (Carlquist 2018) and others with scalariform perforation plates can use high resistance features (narrow vessel diameter, the bars of the plate) as ways of spatially confining embolisms, rather than osmotic effects produced by axial parenchyma (which is virtually absent in Argophyllaceae). One should note that bars are relatively uniform in width as measured axially (Fig. 2C–F, 3C–D, and 5C–F). There is some variation in the thickness of bars (compare Fig. 5E, 5F with the slender bars in Fig. 5D). There are a few double perforation plates (Fig. 3D). The bars of perforation plates are narrowly bordered (Fig. 5E; note cut-away portions of bars in Fig. 5D compared with intact bars).

\textbf{Pit Membrane Remnants}

Although not conspicuously present, pit membrane remnants may be found at lateral ends of perforations (Fig. 3F, 5F). Sometimes pit membrane remnants appear as irregular fragments or strands (Fig. 2D–F, 3C, 5E). Pit membrane remnants are probably indicative of slow conductive rates, and thus correlated with the presence of bars on perforation plates as ways of creating higher impedance in some woods (Carlquist 2018) with lower transpiration (due to smaller size or habitat).

\textbf{Lateral Wall Pitting of Vessels}

Pits between vessels and tracheids or fiber-tracheids are mainly in the form of alternate circular bordered pits, with borders 3–4 \( \mu \text{m} \) in diameter (Fig. 2A, center). Vessel-to-vessel pits may be scalariform or transitional on tangential vessel walls where vessels are in contact with each other (Fig. 3E).

\textbf{Helical Thickenings}

Helical thickenings of vessel walls can be seen in Fig. 6C, D. They were observed to various extents on walls of vessels in \textit{Corokia}, but were not detected in \textit{L. collenettei}. Sometimes helical grooves with little or no ridging at the edge of the grooves extend away from pits, fading away at various distances from the pit aperture (Fig. 2B). In \textit{C. cotoneaster}, thick ridges may extend around the circumference of the inside of a vessel (Fig. 6D). The dots on these ridges probably represent “gum” droplets and are not integral portions of the wall. Helical ridges of intermediate thickness were figured by Patel (1973) for vessels of \textit{C. macrocarpa}. Helical thickenings may also be found in the tracheids of \textit{Corokia}, a confirmation that the tracheids in \textit{Corokia} are conductive rather than merely of mechanical importance.

\textbf{Imperforate Tracheary Elements}

Imperforate tracheary elements are all septate fiber-tracheids in the two \textit{Argophyllum} species studied (Fig. 2A) as well as in \textit{L. collenettei} (Fig. 4C–F). In the species of \textit{Corokia} studied, septate fiber-tracheids are sparse, only two or three per section observed. The remainder of the axial tissue in \textit{Corokia} consists of tracheids (Fig. 6B) and sparse axial parenchyma. The tracheids of \textit{Corokia} vary somewhat in size, but the pits shown in Fig. 6A, B, about 3 \( \mu \text{m} \) in diameter, are typical. The pits are densely placed (Fig. 6A) as seen in longitudinal sections. The dark-staining material which outlines the pits in Fig. 5A is what Gornall et al. (1998) call “gum.” Borders are prominent on tracheid pits. The pits of septate fiber-tracheids (Fig. 2A, 4F) are small, about 2 \( \mu \text{m} \) or less in diameter, irregularly scattered, and with vestigial borders. Starch is present in septate fiber-tracheids (Fig. 2A) in liquid-preserved material. Imperforate tracheary element diameter is 12.5–30 \( \mu \text{m} \). The diameter and wall thickness shown for \textit{A. cryptophlebium} (Fig. 1A) are about average for the family. Imperforate tracheary element length, diameter, and wall thickness are given for the species studied in Table 1. Note that number of vessels per group is higher in species with fiber-tracheids (\textit{Argophyllum}, Fig. 1A, 3A; \textit{L. Lautea}, Fig. 4A), but much smaller (\textit{Corokia}, Fig. 5A) in species with tracheids. Vessel grouping in species with non-conductive imperforate elements, and solitary vessels in those with true tracheids, is a pattern observed throughout woody flowering plants (Carlquist 1984).

\textbf{Axial Parenchyma}

Axial parenchyma is scarce in all of the species studied. It was not observed at all in \textit{A. vernicosum}. Axial parenchyma is said to be diffuse or paratracheal in \textit{Corokia} by Patel (1973), but because it is sparse and randomly distributed, some axial parenchyma strands contact vessels whereas others contact only imperforate tracheary elements. We need ecological and
Fig. 2. *Argophyllum cryptophlebum*. Scanning electron microscope images of radial sections.—A. Vessel element flanked by septate fiber-tracheids containing starch grains.—B. Inner surface of vessel, showing grooved nature of pitting.—C–F. Perforation plates.—C. Perforation plate lacking pit membrane remnants.—D–F. End of perforation plate, showing subdivision of perforations.—E. Perforation plate with clot-like pit membrane remnants.—F. Perforation plate with thread-like pit membrane remnants.
Fig. 3. *Argophyllum vernicosum*.—A. Transverse section; vessels narrow, mostly solitary. B. Tangential section, multiseriate rays with short wings.—C–F. SEM images of radial section.—C. Perforation plate with clot-like pit membrane remnants.—D. Double perforation plate.—E. Inside of vessel, showing pitting to upright ray cells.—F. Two perforation plates; pit membranes are absent, bars are very narrowly bordered. A, B: light microscope photomicrographs; C–F: scanning electron microscope images.
Fig. 4. *Lautea collenettei*. Light microscope photomicrographs.—A. Transverse section; gums in ray cells.—B. Tangential section; multiserial and uniserial rays about equal in number.—C–F. Radial sections.—C. Section showing numerous procumbent and square cells in multiserial ray.—D. Portion of upright ray cells (left), multiserial ray (right) and some septate fiber-tracheids (center below).—E. Perforation plate in vessel and some septate fiber-tracheids.—F. Septate fiber-tracheids containing small pits filled with dark-staining gum, and ray cells (upper right).
Fig. 5. Corokia cotoneaster. —A. Transverse section; vessels are mostly solitary.—B. Tangential section. Uniseriate rays are more abundant than multiseriate rays.—C–F. SEM images of radial section.—C. Entire perforation plate (tracheids above).—D. End of vessel element (bordered pit of tracheid above; bars of perforation plate cut away in places, revealing narrow bordering).—E. Perforations of perforation plate, showing varied pit membrane remnants.—F. Perforations with pit membrane remnants at lateral ends of perforations. A, B: light microscope photomicrographs; C–F: scanning electron microscope images.
Fig. 6. *Corokia cotoneaster*. Radial sections of wood.—A. Dark-staining gum deposits outline bordered pits in tracheids (perforation plate at top).—B. Tracheid portion showing bordered pits and pit apertures.—C, D. Inner surfaces of vessel.—C. Helical thickenings minimal (bottom) to moderate (top), in pairs flanking pit apertures.—D. Helical thickenings pronounced (warty appearance probably due to gum deposits).—E. Portion of multiseries ray, showing gum deposit and upright, square, and procumbent cell shapes.—F. Small bordered pits as seen from outer surface of ray cell.—G. Tangential wall of upright ray cell in sectional view; a large dark-staining gum deposit is present. A, E, G: light microscope photomicrographs; B–D, F: scanning electron microscope images.
physiological studies on conduction in woods that have very little axial parenchyma (Carlquist 2015). Axial parenchyma is difficult to identify with certainty in transverse sections in Argophyllaceae, so radial sections should be used for an assessment in this family. A pair of adjacent strands of axial parenchyma, containing minute starch grains, was seen in A. cryptophlebun (Fig. 1F).

Rays in Argophyllaceae are multisierate plus uniseriate, in about equal numbers. The uniseriate rays are composed mostly of upright cell (Fig. 4D, left), although procumbent cells are present in some uniseriate rays (Fig. 1B, 3B, 4B, 5B). The multisierate rays are composed, as a stem expands (Fig. 4C, 6E), of increasing numbers of procumbent cells (in addition to the upright cells of wings (and a few sheath cells). The histological differences found in multisierate rays reported here (Table 1; Fig. 4C; Fig. 4D, right) should be considered related to ray ontogeny rather than systematics in the context of plant size and ecological strategy. Sections close to the pith of argophyllaceous woods reveal that at first, all rays are uniseriate (compare Fig. 3B with Fig. 5B). Multisierate portions of multisierate rays are composed mostly of procumbent cells (Fig. 1D) when a mature wood structure is attained, but some upright cells may also be present (Fig. 1D). The upright rays sheathe some parts of the wider portions of multisierate rays. The multisierate rays terminate in uniseriate wings from one to five cells in length (Fig. 6E).

In the radial walls of ray cells, SEM study of outer surfaces reveals that the pits are sparse; if pit membranes are removed by handling (Fig. 6F, right), we see these pits are often demonstrably bordered. The tangential walls of upright ray cells (Fig. 6G) are often densely pitted, and the pits are mostly bordered. Ray cells, either the upright ones (Fig. 1C, E) or the procumbent ones (Fig. 1D), have moderately thick lignified walls and contain starch grains.

Vessel to ray cell pitting may be scalariform, transitional, opposite, or alternate. These types may all be present on a single cell surface.

Gum Deposits and Crystals

Gum deposits are present in all species examined. These deposits are seen in rays (Fig. 1A) and in septate fibers (Fig. 4D, E). They can also be seen in septate fiber-tracheids (Fig. 4D, E). Gum deposits are especially abundant in the sample of C. cotoneaster studied (Fig. 6E, G, black areas). Deposits are present in older, inactive cells rather than in more recently formed cells (Fig. 6A). These gum deposits are not soluble in water or ethyl alcohol or commonly used reagents such as xylene. The gums become darker with age, and account for the dark brown color of bark of Argophyllaceae.

Crystals were not observed in the woods of Argophyllaceae studied here. They were not reported in the Corokia collections studied by Patel (1973).

CONCLUSIONS

1. Growth rings are minimal to virtually non-existent. The presence of smaller-diameter vessels in the brief lateward of growth rings (as in C. Buddhleioites, Patel 1973) suggests that lateward is controlled by cold rather than drought. The localities given by Allan (1961) for Corokia are for-
The number of bars per perforation plate in species of Argophyllaceae is relatively uniform (Table 1). If a scalariform perforation plate serves to trap air embolisms within individual vessel elements, it also provides impedance to the conductive flow. This is adaptive only if conductive rates are slow (Carlquist 2018). This can happen in cool climates and under other conditions where peak transpiration is moderate. The number of bars per perforation plate in Argophyllaceae (Table 1) is consistently intermediate, without the extremes of many or very few bars. One can conclude that the wood anatomical pattern or other features of Argophyllaceae and their ecology are not adapted to extremes of transpiration and that the family has not entered very xeromorphic woods, and are more prominent in latewood than in earlywood, in angiosperms at large (Carlquist 1988). They may resist embolism formation, as has been claimed for various forms of sculpture on tracheary element walls (Carlquist 1966; Kohonen and Helland 2009; Lens et al. 2011), as indicated by their greater abundance in colder or drier localities in any given family or genus.

Axial parenchyma is absent from Argophyllum and Lautea, with the exception of a single instance seen in A. cryptophlebium. The living septate fibers of Argophyllum and Lautea can be considered an analogue for axial parenchyma, although with less direct contact with vessels. Therefore the living septate fibers are more likely functional in starch storage rather than conduction control. Corokia has no septate fibers (with very rare exceptions). Woods without axial parenchyma or living fibers tend to have more frequent rays per linear mm measured transversely on a tangential section; they also tend to have more uniseriate rays (Carlquist 2015). These features are conceivable analogs to axial parenchyma and septate fiber-tracheids provided that conduction is steady and slow and that growth and flowering events are not massive. Corokia appears to meet these criteria.

Although adult stems have both narrow multiseriate and uniseriate rays, the rays are all uniseriate and composed of upright cells at their point of origin close to the pith. This stage corresponds to Paedomorphic Type III rays (Carlquist 1988). The adult stems have Heterogeneous Type II rays as defined by Kribs (1935) and Patel (1973), with procumbent cells and square cells. This progression requires more than one year, as reported for “truly woody” plants in the curves given by Bailey and Tupper (1918). Intermediate multiseriate rays with square cells outnumbering procumbent cells are common.

Upright ray cells of Argophyllaceae have pits, commonly bordered and densely placed, on the tangential walls. This suggests mechanical strength (all ray cells have secondary walls) combined with conductive capabilities (Carlquist 2007). Upright cells predominate in uniseriate rays.

Despite the brief period (early secondary growth) in which rays of Argophyllaceae correspond to Paedomorphic Type III, horizontal ray cell initials subdivide horizontally relatively rapidly, as do fusiform cambial initials. Both of these are indicative of a truly woody condition rather than an herbaceous or woody herb wood as seen in woods that have prolonged juvenilism (Carlquist 1962). Prolonged
juvenile involves fewer horizontal subdivisions in the ray initials and in the fusiform cambial initials.

15. Pit membrane remnants occur in some perforations in vessel perforation plates of several Argophyllaceae. This indicates an angiosperm wood with moderate and steady conductive streams, which would sweep away such membrane remnants in most angiosperm vessels. They are one more line of evidence of the “safer” conductive formula of Argophyllaceae, which also includes narrow vessels, scalariform perforation plates, and lack of parenchyma associated with vessels. This combination of features is held to be adaptive in cool climates where steady transpiration rates, matched with evergreen foliage and flowering over prolonged periods, are characteristic. These features were similarly related to a very comparable syndrome of anatomical features in an unrelated family of Laurales, Atherospermataceae (Carlquist 2018). Abundant presence of septate fiber-tracheids in Argophyllum and Lautea and near-absence of septate fiber-tracheids in Corokia correlate with slow rates of conduction and gradual formation of leaves and flowers rather than flushing events.

16. Foliage shows parallels to wood anatomy in degrees of xeromorphy. Although the study of both twigs and larger wood samples for the family does not provide a clear picture of degrees of xeromorphy (Table 1), some instances can be cited. The smallest leaves are those of C. cotoneaster, which extends more widely in New Zealand and into more seasonal habitats than C. buddleoides (Allan 1961). The cultivars with smaller leaves in Corokia have been referred either to C. cotoneaster or to hybrids involving C. cotoneaster. The hybrid swarms on North Island, New Zealand, suggest that there has been post-glacial radiation. The wide ranges of leaf forms, venature, texture, color, and size in the hybrids are indicative of genetic diversity related to degree of xeromorphy or mesomorphy. Detailed comparisons of leaf anatomy in the family would be rewarding.

17. Gums occur in living cells but not in actively conducting ones. Gornall et al. (1998) have reported the occurrence of dark-staining gums in Corokia; these are present in the other genera of Argophyllaceae also. Whether for protection against pathogens or foraging, gums are present chiefly in older portions of wood. These gums occur primarily in ray cells, but may extend into conductive cells as well where gum secretion is abundant.

18. Liquid-preserved material of Argophyllum demonstrates, as in many other groups of angiosperms, the value of this preservation method. Bacteria degrade or digest starch in xylarium material of woods, even after a day or two of drying. The material of Argophyllum, which was liquid preserved, permitted the demonstration of starch grains in ray cells, septate fiber-tracheids, and axial parenchyma.

If the drying process is prolonged, fungi invade wood samples and can result in loss of information about pitting. Loss of information about presence of starch and other components has delayed our understanding of parenchyma function.

19. Argophyllaceae form one of numerous examples of families in the Asterales clade (Donoghue and Tank 2012). The families closest to Argophyllaceae include Phellinaceae and Alseuosmiaceae (Platysperma is tentatively included in Alseuosmiaceae). These two families have wood with rays of two distinct sizes (Baas 1975; Dickison 1986) or have rayless representatives (Alseuosmia). Determining relationships with the use of wood anatomy is now subordinated to the evidence from molecular systematics. More importantly, in families with more numerous plesiomorphic conditions, such as Argophyllaceae, there tend to be fewer synapomorphies. Argophyllaceae have typically been included in rosids (asterids I) along with Cornales, Escalloniales, Hydrangeales, and Saxifragales, but they prove to be members of campanulids (asterids II) as a sister group of Aquifoliaceae (Soltis et al. 2000; Lundberg 2001; Bremer et al. 2002; Soltis et al. 2011).

20. Asteraceae have traditionally been one of the few families of Asterales, but newer phylogenetic constructions (Tank and Donoghue 2010) have expanded the order so as to include ten families in addition to Asteraceae. Now that the order Asterales is more inclusive and can be defined with the aid of molecular data, we are faced with the question of evolution of woodiness. Were Asterales ancestrally woody or herbaceous? Because a large percentage of northern hemisphere Asteraceae are herbaceous, botanists have traditionally regarded the family as stemming from a non-woody ancestry, but we now consider the family as having a barnadesioid ancestry (Funk et al. 2009). Barnadesioids are woody, although most are not arboreal. Argophyllaceae, Rousseaeaceae and some other Asterales do not have characters usually regarded as herbaceous, although our concepts of woodiness are not clear and the anatomical characters that define these modes are more diverse than we have imagined them (Carlquist 2013).

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