

1988

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Carlquist, Sherwin (1988) "Wood Anatomy of Drimys S.S. (Winteraceae)," *Aliso: A Journal of Systematic and Floristic Botany*. Vol. 12: Iss. 1, Article 10.

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WOOD ANATOMY OF *DRIMYS* S.S. (WINTERACEAE)

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ABSTRACT

Qualitative and quantitative data are reported for seven specimens representing six varieties of the four species of *Drimys* generally recognized. Tracheid length and diameter are correlated both with plant size and with severity of climate: wide, long tracheids, not fluctuating in diameter seasonally, occur in *Drimys* of moderate elevations in subtropical latitude; narrower, shorter tracheids, becoming radially narrower briefly in latewood, occur in *Drimys* from higher altitudes and latitudes. Vesturing (wart layer) on the inside surface of tracheids occurs in *Drimys* from latitudes and altitudes where appreciable freezing is to be expected, but vesturing is absent at lower elevations and latitudes. Vesturing may bond water to tracheid walls better so that water columns do not break under high tensions produced by such conditions as transpiration when soil remains frozen. Scleriform pitting on end walls of *Drimys* tracheids occurs during the first year (metaxylem), but is replaced by alternate circular pits later; injury to the cambium, even of a mild kind, results in reversion to scleriform end wall pitting. Tracheid wall thickness is not correlated with tracheid diameter. Tracheid-ray pits are 75% the diameter of tracheid-tracheid pits. Axial parenchyma is sparse and diffuse (occasionally cells in tangential or radial pairs). Rays are Heterogeneous Type I; ray cells commonly have bordered pits on tangential walls. Silica bodies are reported (first report for Winteraceae) in rays of three collections of *Drimys*.

Key words: *Drimys*, ecological wood anatomy, silica bodies, vesturing, Winteraceae, wood anatomy.

INTRODUCTION

Drimys s.s. has been treated as containing four species (Smith 1943), all of which are represented in the present study. *Drimys* as recognized here excludes *Tasmannia*, a treatment recommended by Smith (1966) and Ehrendorfer, Silberbauer-Gottsberger, and Gottsberger (1979), although Vink (1970) recognized the more inclusive concept. *Drimys* s.s. has carpels with restricted stigmatic areas unlike the often-figured stigmatic crests of *Tasmannia* carpels, and the ontogeny is likewise different (Tucker and Gifford 1966). *Tasmannia* has not merely flavonoids, as does *Drimys*, but flavones as well (Kubitzki and Reznik 1966). The chromosome number in *Tasmannia*, $X = 13$, differs from the base number of all other Winteraceae (including *Drimys*) known cytologically, $X = 43$ (Ehrendorfer, Krendl, Habeler, and Sauer 1968). Foliar differences between *Drimys* and *Tasmannia* are evident (Bailey and Nast 1944; Bongers 1973). Palynological studies have revealed minor but constant differences regarding size of tetrads and aperture margins (Pragowski 1979). *Tasmannia* is the only dioecious genus of Winteraceae (Smith 1943). These differences, in combination with the occurrence of *Drimys* only in the New World and *Tasmannia* only in the Old World, do seem to merit recognition at the generic level. Although wood anatomy does tend to be more conservative than other anatomical features, the present study, together with one in progress on *Tasmannia*, will examine whether any wood details differentiate *Drimys* from *Tasmannia*. Studies of the wood anatomy of other genera of Win-

teraceae are now at hand for the genera *Pseudowintera* (Patel 1974), *Zygogynum* (Carlquist 1981), *Exospermum* (Carlquist 1982a), *Belliolum* (Carlquist 1983a), and *Bubbia* (Carlquist 1983b).

The paper by Bailey (1944) on wood anatomy of Winteraceae is essentially a survey at the family level, with little attention to generic or specific features. The relative paucity of materials at that time necessitated that approach. A few others have offered information on wood anatomy of *Drimys*, but they provide a few details for *D. winteri* only (Bailey and Tupper 1918; Gupta 1934; Takahashi 1985). Although the present study does not incorporate materials of all of the infraspecific taxa recognized by Smith (1943) or all of the Brazilian taxa proposed by Ehrendorfer et al. (1979), it does include material of all of Smith's species, and it attempts to include in sampling all of the extremes of habit, geographical range, and ecology. Material of *Drimys* wood is scarce in xylaria, perhaps because most species do not occur in well-traveled areas, and because wood of shrubs is less often collected than that of trees.

The ecological range in *Drimys* is of interest with respect to wood anatomy. All *Drimys* populations occur in areas where soil moisture is readily available throughout the year; the variable is one of temperature. The habitat of *D. brasiliensis* (Irwin 12678) (Veadeiros, Goias, Brazil, 1000 m) is very close to the equator, and is surely frost-free. Also likely to be free from frost is the locality of *D. brasiliensis* (Occhioni 985), the Itatiaia District of Rio de Janeiro Province. Likewise, the maritime nature of the climate of the Juan Fernandez Islands makes it unlikely that *D. confertifolia* plants experience any appreciable frost. Occasional frost, but with very little freezing of soil moisture, is experienced by the population of *D. winteri* var. *chilensis* represented by the collection Carlquist 7172, which is from about 500 m in Parque Nacional Campaña de la Dormida, about 100 km north of Santiago, Chile. The remainder of the collections studied are from areas that not only experience frost, but very likely have freezing of soil moisture because of lower temperatures than those experienced in the above localities. The collection of *D. granadensis* var. *mexicana* (Thorne 40117) is from Zontehuitz, Chiapas, Mexico, 3300 m. The collection *D. winteri* var. *winteri* (Goodall 841) comes from Upper Harberton Park, Tierra del Fuego, Argentina. The collection of *D. winteri* var. *andina* is from at least as cold a locality, Antillanca, about 1100 m, Parque Nacional Puyehue, Chile (about 900 km south of Santiago). At Antillanca, for which climatic data are available, temperatures fall below 0 C many nights of the year (Schick 1980).

The above ecological gamut is potentially related to wood features. Patel (1974) and Meylan and Butterfield (1978) reported vesturing ("warts": see Ohtani, Meylan, and Butterfield 1984 concerning the terminological question) in *Pseudowintera*. Such vesturing is absent in tracheids of *Bubbia* (Carlquist 1983b). The presence of vesturing has been hypothesized to be of physiological significance with respect to cold (Carlquist 1982b, 1983b). By increasing the wall surface considerably, vesturing potentially increases bonding of water to wall, and thereby higher tensions could be sustained without breaking of water columns. If transpiration occurs on a sunny day while the ground is still frozen, high tensions can develop in tracheids (Lutz 1952). One might therefore expect presence of vesturing on *Drimys* tracheids from colder localities, and absence of vesturing on tracheids of collections from warmer localities, if my hypothesis is correct.

Tracheid size is thought to be related to plant size in vesselless dicotyledons (Carlquist 1975); however, plant size and plant ecology are also closely related because cold habitats such as the subalpine localities where shrubby *Drimys* specimens grow tend to contain plants of reduced stature, whereas treelike specimens occur in areas with less-marked temperature fluctuations. Narrow tracheids embolize less readily than wide tracheids in conifers (Lewis and Tyree 1985), so that narrowness of tracheids may have a physiological explanation, and shortness of tracheids appears related to narrowness (Bannan 1965). The wood samples of *Drimys* in the present study were selected in order to see if plant habit, climate, or both are related to tracheid length and diameter.

A feature of considerable physiological and evolutionary interest in Winteraceae is the occurrence of scalariform pitting on end walls of tracheids together with alternate circular pits on lateral walls in some species, as in *Zygogynum* (Bailey 1944, Carlquist 1981), *Belliolum* (Carlquist 1983a), and *Bubbia* (Carlquist 1983b). In other Winteraceae, such as *Drimys*, only circular alternate pits on overlap areas have been reported. However, scalariform end-wall pitting does occur in tracheids of *Drimys* under some circumstances, and the present study examines the nature of these occurrences.

The results of the present study include some other noteworthy wood features, such as presence of borders on ray cells and occurrence of silica bodies in ray cells (the latter hitherto unreported in Winteraceae).

MATERIALS AND METHODS

Wood samples of *Drimys* were all available in dried form. Those samples for which woody cylinder diameter was less than 15 mm (Table 1) were obtained from herbarium specimens in the collection of the Rancho Santa Ana Botanic Garden. The specimen of *D. brasiliensis* (Occhioni 985) was provided by the Xiloteca de Seção de Anatomia Vegetal, Jardim Botânico do Rio de Janeiro (RBw) through the courtesy of Dr. Armando de Mattos Filho. The specimens of *D. winteri* var. *andina* and *D. winteri* var. *chilensis* were collected by the writer under the auspices of a National Science Foundation Grant, BSR 8419469.

Wood sample portions were boiled in water and then stored in aqueous 50% ethyl alcohol. All woods proved amenable to sectioning on a sliding microtome without further treatment except for *D. brasiliensis* (Occhioni 985), in which an alternative method (Carlquist 1982c) was attempted because the large, thin-walled tracheids proved difficult to section. Sections were stained with safranin and lightly counterstained with fast green. Some longitudinal sections were left unstained and observed with an ISI WB-6 scanning electron microscope (SEM). Macerations of samples were prepared with Jeffrey's Fluid and stained with safranin.

Quantitative data are reported in Table 1. In the case of tracheid length and ray dimensions, means are based on 25 measurements each. Calculations show that in general, increasing the number of measurements per wood feature beyond 20 does not lower the standard deviation for the mean appreciably. For other features, means are based only on a few measurements judged to be typical for the specimen because random measurements are not likely to reveal representative conditions for these features. Field-collected materials represent basal stems, whereas samples from herbarium specimens are branch segments.

Table 1. Wood characteristics of *Drimys*.

Taxon	Collection	Diameter of wood cylinder, cm	1	2	3	4	5	6	7	8
<i>D. brasiliensis</i> Miers	Irwin 12678 (RSAw)									
<i>D. brasiliensis</i>	Occhioni 985 (RBw)	1.1	44	3453	4.1	7	3367	2294	4.7	3.9
<i>D. confertifolia</i> Phil.	USw-33841	≈10	69	3974	3.7	10	1512	4806	5.0	2.1
<i>D. granadensis</i> L.f. var. <i>mexicana</i> (DC.) A. C. Smith	Thorne 40117 (RSA)	≈9	46	3172	4.4	10	610	4208	4.9	4.1
		0.7	32	1477	4.1	9	524	3364	4.2	3.5
<i>D. winteri</i> J. R. & G. Forst. var. <i>andina</i> Reiche	Carlquist 7386 (RSAw)	1.8	30	1316	4.1	7	513	2805	3.9	3.5
<i>D. winteri</i> var. <i>chilensis</i> (DC.) A. Gray	Carlquist 7172 (RSAw)	8.5	55	2418	3.5	9	318	1249	4.8	2.8
<i>D. winteri</i> var. <i>winteri</i>	Goodall 841 (RSA)	0.6	25	863	2.3	7	419	1581	3.8	3.0

Legends for columns: 1, mean tangential diameter of tracheids at widest point, μm ; 2, mean tracheid length, μm ; 3, mean thickness of tracheid walls, μm ; 4, mean diameter of tracheid-tracheid pits (circular), μm ; 5, mean height of uniseriate rays, μm ; 6, mean height of multiseriate rays, μm ; 7, mean width of multiseriate rays at widest point, cells; 8, mean wall thickness of ray cells, μm .

Nomenclature follows Smith (1943) except that names of varieties that include the type of the species have been altered so as to repeat the species name, in conformity with current nomenclatural requirements. The study of Brazilian species of *Drimys* by Ehrendorfer et al. (1979) is very thorough, but unfortunately was not suitable for the present study because those authors do not cover non-Brazilian populations. Therefore, Smith (1943), although his study is earlier and based on much less material, was followed here in the interests of consistency. Also, the plant of *D. brasiliensis* represented by the specimen *Irwin 12678* is well out of range of *Drimys* populations treated by Ehrendorfer et al. (1979), so it probably should not be assigned to an infraspecific taxon in *D. brasiliensis* at this time. The collection *Occhioni 985* of *D. brasiliensis* would fall under subsp. *sylvatica* in the treatment of Ehrendorfer et al. (1979).

ANATOMICAL RESULTS

Growth Rings

In discussing growth rings in *Drimys*, we should first take into account the occurrence of interruptions in cambial activity in which callus is not formed, but production of tracheids continues (Fig. 1). The wider tracheids produced after the interruption are probably earlywood tracheids in virtually all instances of this sort, because cambial injury is likely to occur as a result of cold at the end of a growing season. Tracheids that follow traumatic interruption of cambial activity tend to be slightly irregular in outline and to represent, as do rays, nonconformity with the radial sequences in latewood preceding the interruption (Fig. 1).

True growth rings in *Drimys*, when present, are demarcated by earlywood tracheids wider than the latewood tracheids that precede them, but the difference is not strongly marked. Growth rings are present in all the taxa studied except *D. brasiliensis* (*Occhioni 985*): Fig. 5, 9, 13. Growth rings very weakly demarcated are present in *D. brasiliensis* (*Irwin 12678*). Growth rings in *D. winteri* var. *andina* (Fig. 13) and *D. winteri* var. *winteri* are more strongly demarcated, with latewood tracheids appreciably narrower than earlywood tracheids; growth rings are also radially narrow in these two specimens.

Tracheid Dimensions

Tracheid diameters are shown in Table 1, column 1. These are measured tangentially, and thus are not affected by the fluctuation in radial diameter as latewood is succeeded by earlywood. Mean tracheid diameter at widest point of tracheid ranges from 69 μm in *D. brasiliensis* (*Occhioni 985*) to less than half of that in the two taxa from the coldest areas, *D. winteri* var. *andina* (30 μm : Fig. 13) and *D. winteri* var. *winteri* (25 μm). In comparing tracheid diameter in the transections shown here, the reader should take into account that Fig. 1 is at a different magnification from that of Figs. 5, 9, and 13.

Tracheid length in the samples studied here (Table 1, column 2) ranges from 3974 μm in *D. brasiliensis* (*Occhioni 985*) to 863 μm in *D. winteri* var. *winteri*. There were, incidentally, nine growth rings in the latter sample, so that more than juvenile wood is represented.

Bailey and Tupper (1918) reported mean tracheid length of 4300 μm in mature wood of *D. winteri* (very likely var. *chilensis*) and 1600 μm in the first growth ring of that sample.

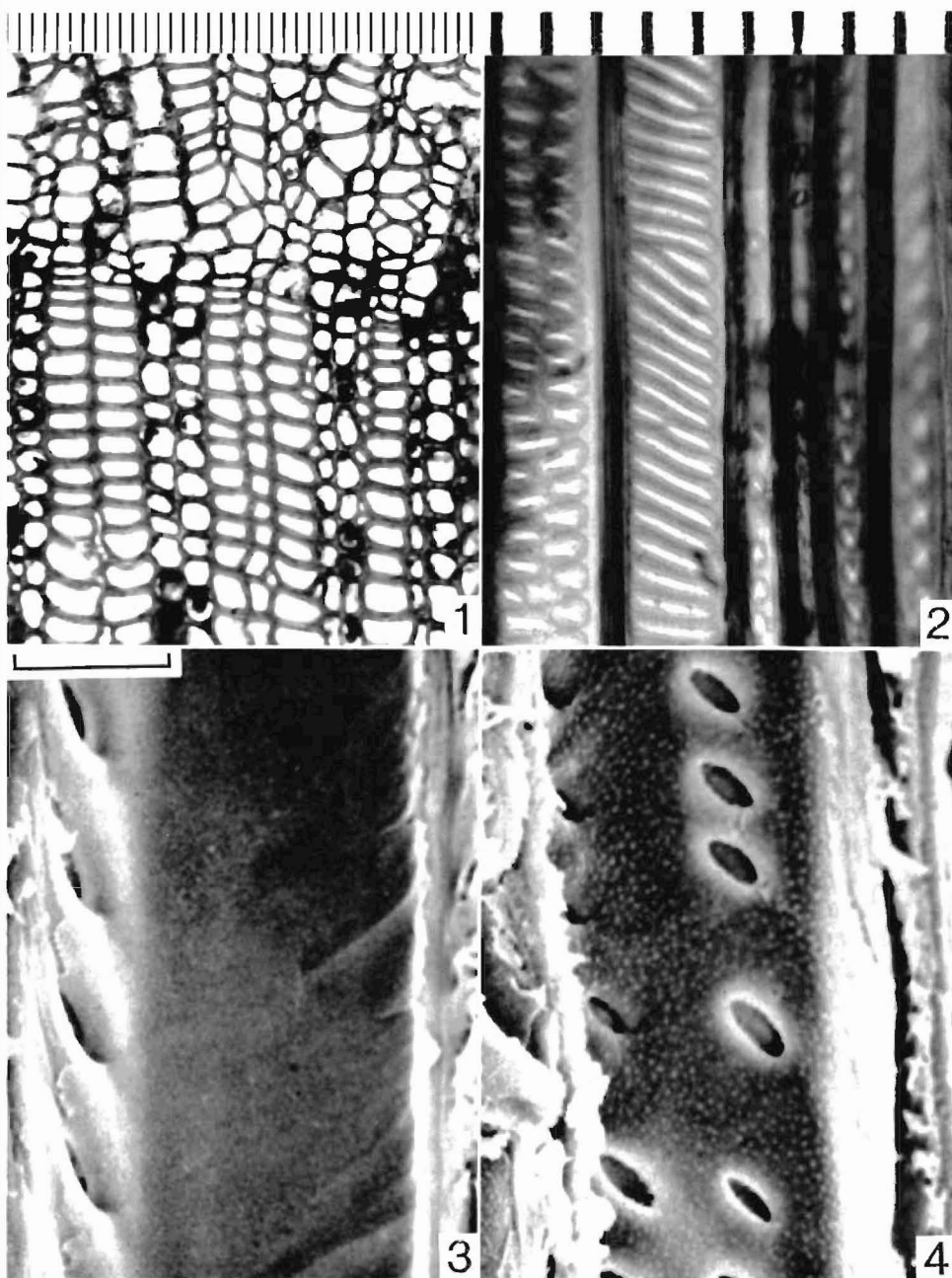


Fig. 1-4. Wood sections of *Drimys*.—1-3. *D. brasiliensis* (Irwin 12678).—1. Transection; cambial injury has resulted in nonconformity between latewood and earlywood, one third the distance from top of photograph.—2. Radial section. Scalariform pitting in earlywood tracheid formed just after the cambial injury shown in Fig. 1.—3. SEM photograph of tracheid inner surface from tangential section, showing absence of vesturing.—4. *D. granadensis* var. *mexicana* (Thorne 40117). SEM photograph of inner surface of tracheid from radial section; vesturing is present. (Fig. 1, magnification scale above Fig. 1 [divisions = 10 μ m]; Fig. 2, scale above Fig. 2 [divisions = 10 μ m]; Fig. 3, 4, scale above Fig. 3 [bracket = 5 μ m].)

Tracheid Wall Thickness

Tracheid wall thickness fluctuates relatively little in *Drimys* (Table 1, column 3; Fig. 1, 5, 9, 13). Noteworthy in these figures is a lack of correlation between tracheid diameter and tracheid wall thickness: wall thickness is, in fact, below average for the genus in *D. brasiliensis* (Occhioni 1985), which has the widest and longest tracheids of the samples studied here. The uniformity in wall thickness of tracheids in the genus can be seen by comparing Fig. 1, 5, 9, and 13.

Tracheid Pitting

Pitting is much denser on radial walls than on tangential walls of tracheids of *Drimys* (compare Fig. 3 and 4). Long overlap areas occur on radial walls of *Drimys* tracheids. These overlap areas typically bear circular bordered pits (Fig. 11), as do nonoverlap radial walls. Mean diameters of circular tracheid-tracheid pits are given in Table 1, column 4. The diameter of tracheid-ray pits averages about 75% of that of tracheid-tracheid pits.

Scalariform pitting as well as some transitional pitting were observed on overlap areas of tracheids in *D. brasiliensis* (Irwin 12678) (Fig. 2), *D. granadensis* var. *mexicana*, *D. winteri* var. *chilensis*, and *D. winteri* var. *winteri*. The samples of *D. granadensis* var. *mexicana* and *D. winteri* var. *winteri* had scalariform pitting on overlap areas of tracheids only in the first growth ring. In *D. brasiliensis* (Irwin 12678) and *D. winteri* var. *chilensis*, scalariform pitting was observed in the first one or two growth rings, where it could be termed juvenile pitting (pitting like that of metaxylem, but persisting a little longer); scalariform end-wall pitting in these two collections was also observed in bands intercalated later in the wood. In both of these, one can relate the scalariform pitting to the occurrence of an interruption in cambial activity, as shown in Fig. 1. The scalariform pitting of Fig. 2 shows, in a radial section, the same incident of cambium interruption and recovery. Scalariform pitting does not occur on latewood tracheids (Fig. 2, right) for spatial reasons: only circular pits can be accommodated on the narrow radial walls of latewood tracheids. The tracheids formed after a cambial interruption are, with few exceptions, earlywood tracheids (cambial injury chiefly occurs in a cold season), and the wider radial walls of earlywood tracheids do permit scalariform pits to be formed. Attention is called to the fact that interruption of cambial activity in *Drimys*, as in other Winteraceae, is not of the drastic sort that results in formation of callus tissue (pith flecks); recovery is evidently rapid and perhaps only a portion of the cells is damaged. The size and shape of tracheids after the interruption show abnormalities, and there are irregularities in the sequence of tracheid and ray files from the preceding latewood into the earlywood after the interruption (Fig. 1).

Vesturing on Inner Surfaces of Tracheids

SEM studies permit one to demonstrate the occurrence of vesturing (warts) on inner surfaces of tracheids; vesturing of this kind is not readily evident with light microscopy. Vesturing was absent in tracheids of both collections of *D. brasiliensis* (Fig. 3) and in tracheids of *D. confertifolia* (Fig. 7). Very small and sparse warts were evident in tracheids of *D. winteri* var. *chilensis* (Fig. 8). Warts maximal for the genus (and the family) were found in *D. granadensis* var. *mexicana* (Fig. 4),

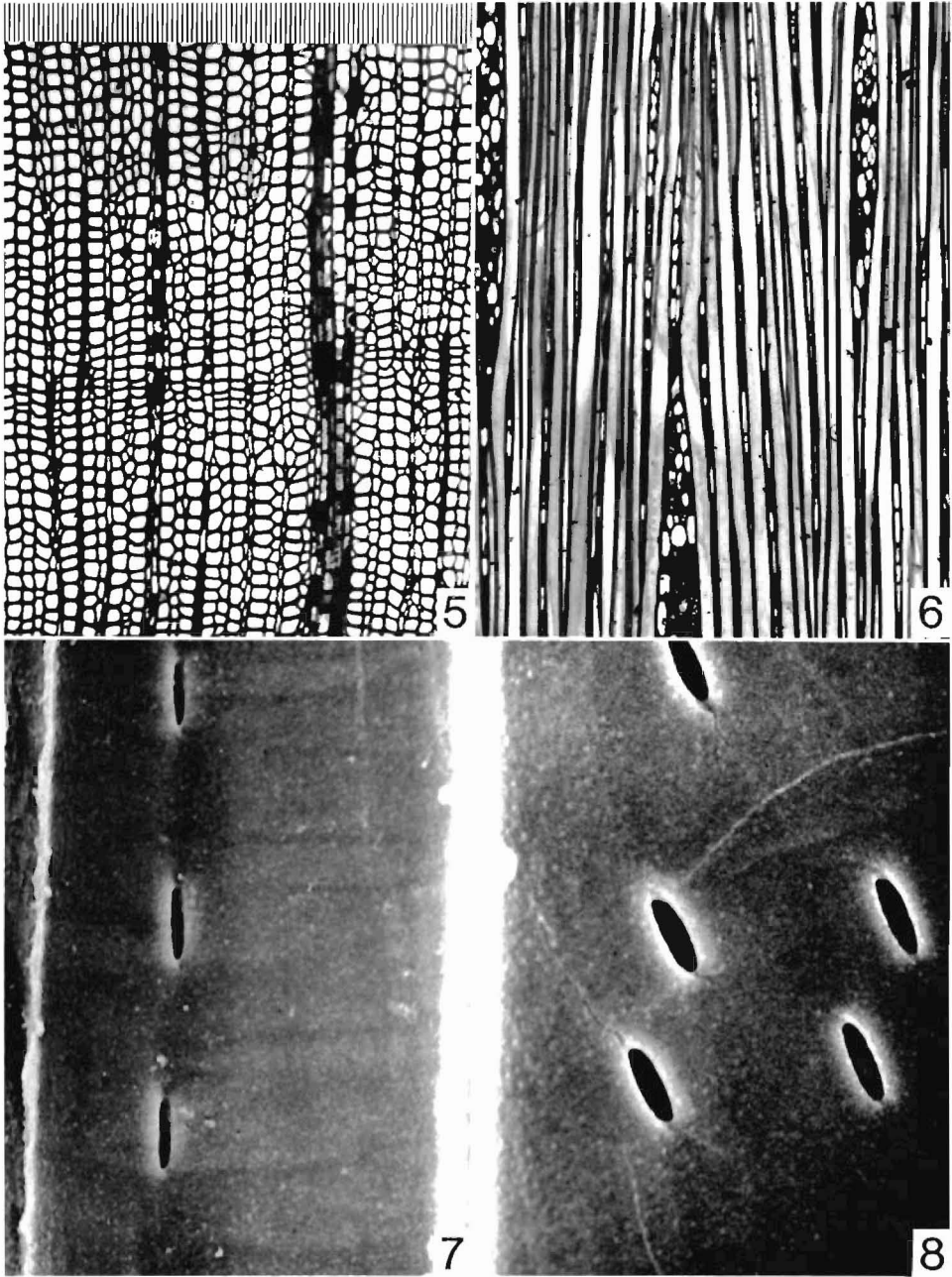


Fig. 5–8. Wood sections of *Drimys*.—5–7. *D. confertifolia* (USw-33841).—5. Transection. Growth ring begins at center of photograph.—6. Tangential section. Biseriate ray near top, left of center.—7. SEM photograph of inner surface of tracheid from tangential section, showing absence of vesturing.—8. *D. winteri* var. *chilensis* (Carlquist 7172). SEM photograph of inner surface of tracheid from tangential section; vesturing is low, sparse. (Fig. 5, 6, magnification scale above Fig. 5 [divisions = 10 μ m]; Fig. 7, 8, scale above Fig. 3.)

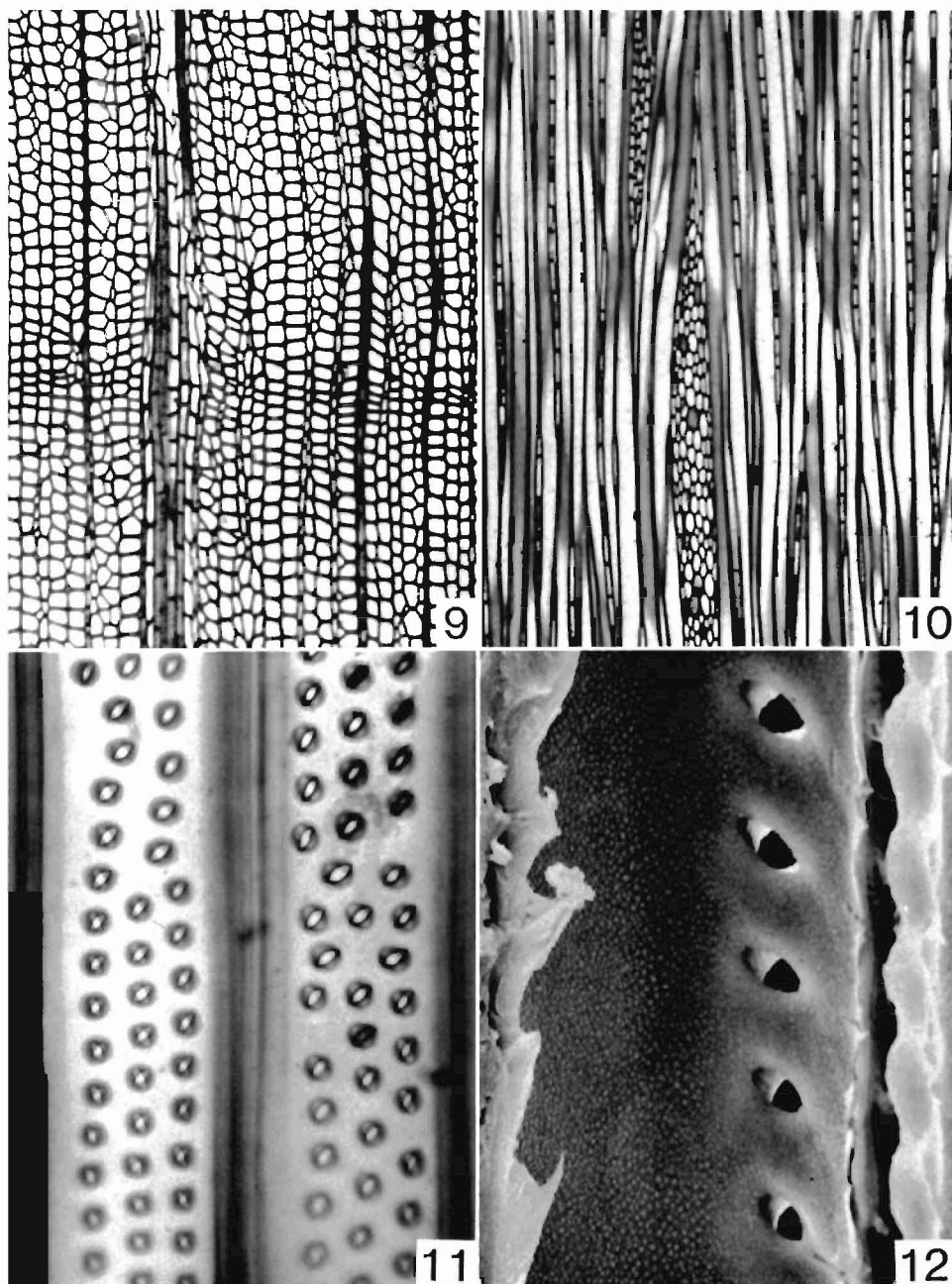


Fig. 9–12. Wood sections of *Drimys*.—9–11. *D. winteri* var. *chilensis* (Carlquist 7172).—9. Trans-section. Growth ring begins just below center (latewood below).—10. Tangential section. Uniseriate rays more numerous than multiseriate rays.—11. Pitting on overlap areas of tracheids from radial section.—12. *D. winteri* var. *winteri* (Goodall 841). SEM photograph of inner surface of tracheid from radial section, showing vesturing. (Fig. 9, 10, magnification scale above Fig. 5; Fig. 11, scale above Fig. 2; Fig. 4, scale above Fig. 3).

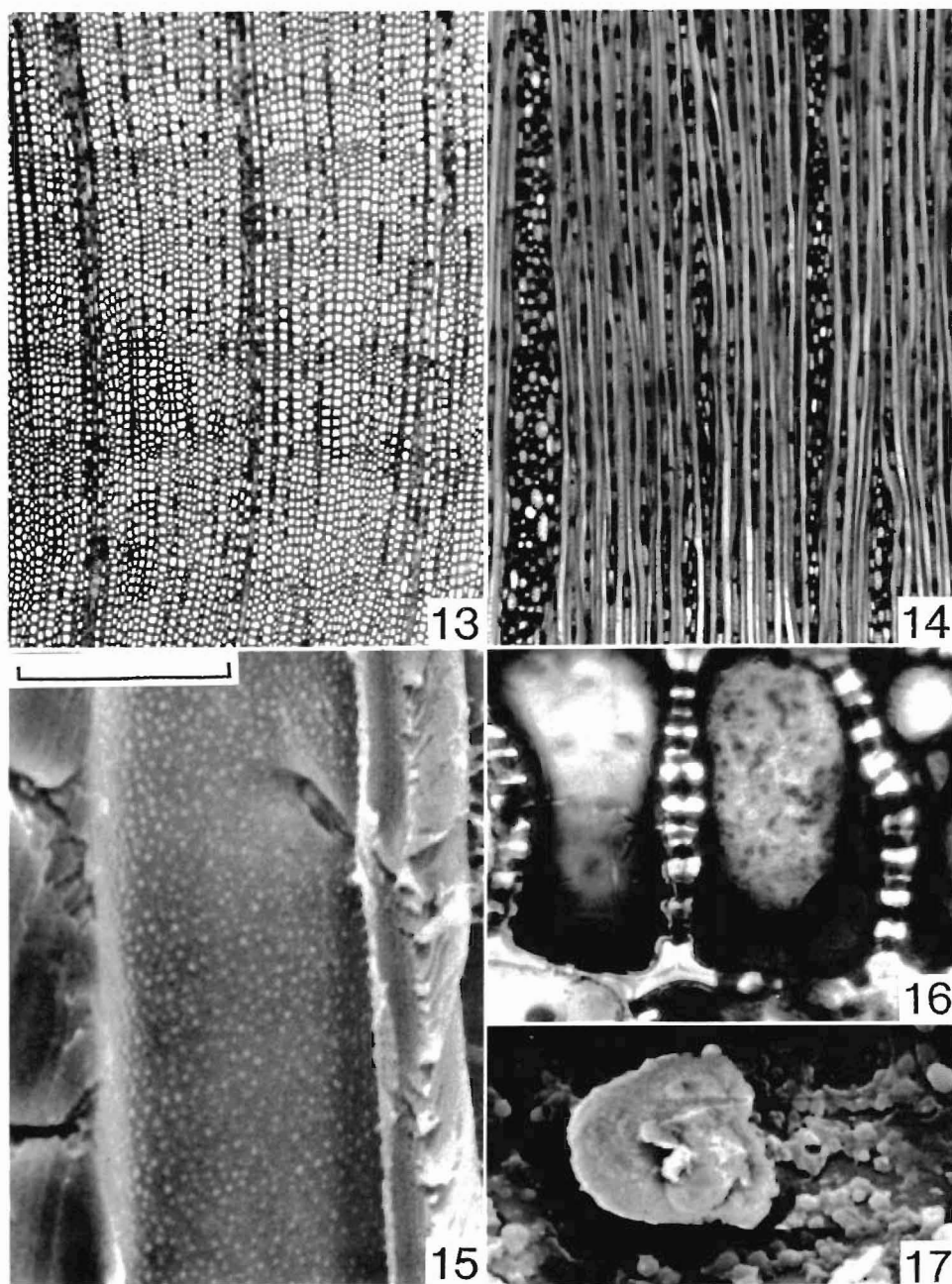


Fig. 13–17. Wood sections of *Drimys winteri* var. *andina* (Carlquist 7286).—13. Transection; six growth rings are present; tracheids are notably narrow.—14. Tangential section; dark-staining compounds are abundant in ray cells.—15. SEM photograph of inner surface of tracheid from radial section, showing prominent vesturing.—16. Ray cells from radial section; sectional view of bordered pits is shown; amorphous deposits are abundant.—17. SEM photograph of a silica body in a ray cell from a radial section. Smaller sphaeroidal objects in photograph are droplets of dark-staining compounds. (Fig. 13, 14, magnification scale above Fig. 5; Fig. 15, 17, scale above Fig. 15 [bracket = 5 μ m]; Fig. 16, scale above Fig. 2.)

D. winteri var. *winteri* (Fig. 12), and *D. winteri* var. *andina* (Fig. 15). Differences in vesturing between earlywood and latewood are not evident; vesturing is apparently about equally well developed in all portions of a wood sample.

Axial Parenchyma

Axial parenchyma in *Drimys* is diffuse, and in no species common. The collections can be arranged in the following order of parenchyma abundance, from moderately common to very scarce: *D. confertifolia*, *D. brasiliensis* (Irwin 12678), *D. granadensis* var. *mexicana*, *D. winteri* var. *chilensis*, *D. winteri* var. *winteri*, *D. brasiliensis* (Occhioni 985), *D. winteri* var. *andina*. Radially arranged pairs of parenchyma cells were observed in a few places in wood of *D. confertifolia*, *D. granadensis* var. *mexicana*, and *D. winteri* var. *winteri*; tangential pairs of parenchyma cells were seen in a few places in wood of *D. confertifolia* and *D. brasiliensis* (Occhioni 985).

Ray Types and Dimension

Rays in *Drimys* can be referred to Heterogeneous Type I of Kribs (1935). Uniseriate rays are present in all species, and are more common than multiseriate rays (Fig. 6, 10, 14). Biseriate rays are present in all species, but are less common than uniseriate rays (a biseriate ray may be seen in Fig. 6, top, left of center). Uniseriate rays were observed to be scarcer in larger wood samples. Procumbent cells are more common in *D. winteri* var. *andina* than in *D. confertifolia* (Fig. 6) or *D. winteri* var. *chilensis* (Fig. 10), although this is difficult to quantify because wider multiseriate rays contain a higher proportion of procumbent cells than do narrower multiseriate rays in the genus.

Height of uniseriate rays (Table 1, column 5) tends to parallel tracheid length except in *D. brasiliensis*, in which the unusually tall uniseriate rays may represent a characteristic of that species. The height of multiseriate rays (Table 1, column 6) does appear to parallel tracheid length. The width of multiseriate rays (Table 1, column 7) appears relatively constant throughout the genus.

Ray Cell Walls

Ray cell walls vary appreciably within *Drimys* (Table 1, column 8). They are notably thick in *D. confertifolia* (Fig. 6), *D. granadensis* var. *mexicana*, and *D. winteri* var. *andina* (Fig. 14, 16); they are relatively thin in *D. brasiliensis* (Occhioni 985).

Bordered pits characteristically occur on tangentially oriented walls of ray cells in *Drimys* (Fig. 16). This is true regardless of species. Borders on ray cell pits were also observed on horizontally oriented ray cell walls of *D. confertifolia*. Borders are conspicuous on *Drimys* ray cells that have thicker walls. Note should be taken that border presence is established on the basis of pits seen in sectional view (Fig. 16), not face view. Presence of dark-staining compounds outlining the pit cavity aids observation of pit border presence.

Ray Cell Contents

Silica bodies were observed in ray cells of *D. winteri* var. *andina* (Fig. 17), *D. winteri* var. *winteri*, and *D. confertifolia*. In *D. winteri* var. *andina*, about one third

to one half of the ray cells contain one (rarely two) silica bodies each. Silica bodies are less common in *D. confertifolia* and *D. winteri* var. *winteri*. Identification of silica bodies was based upon both light microscope and SEM characteristics. Under the light microscope, silica bodies were observed to have a slight degree of refractiveness (but no birefringence under polarized light), a round but irregular contour, and a light lavender coloration when slightly out of focus. Under SEM, the silica bodies of Winteraceae (Fig. 17) are relatively smooth but contain minute irregularities and depressions. This is the first report of silica bodies in wood of Winteraceae (for a list of families with silica bodies in wood, see Carlquist 1988).

Dark-staining compounds as amorphous masses or droplets can be observed in many ray cells of *Drimys* (Fig. 6, 14, 16; see also the droplets peripheral to the silica body in Fig. 17). Dark-staining deposits may occasionally be seen in tracheids adjacent to ray cells. Although common in ray cells of all species of *Drimys*, dark-staining deposits were observed to be most abundant in *D. confertifolia* (Fig. 5) and *D. winteri* var. *andina* (Fig. 14). The presence of small amounts of the dark-staining compounds accounts for the prominence with which the pit cavities are rendered in Fig. 11.

Oil cells, although present in phloem rays of *Drimys*, do not occur in xylem rays of any of the collections of *Drimys* examined.

Reaction Wood

Reaction wood has been observed in *Drimys* (Kučera and Philipson 1977) and other Winteraceae (Meylan 1981). It was not observed in my materials, perhaps because my samples were either from main trunks and upright branches rather than from horizontally or diagonally oriented branches.

CONCLUSIONS

Growth rings in *Drimys* show little difference between latewood (which is relatively brief) and earlywood. These growth rings are best interpreted as an accommodation for slightly greater transpirational rates during warmer months in the more seasonal climates in which *Drimys* grows. The habitats where *Drimys* occurs can be regarded as perpetually moist, but seasonally warmer temperatures would provide a selective value for wider earlywood tracheids suited to greater flow rates.

Scalariform pitting on end walls of tracheids is characteristically not present in *Drimys*, although it is present in the winteraceous genera *Zygogynum* (Carlquist 1981), *Belliolum* (Carlquist 1983a) and *Bubbia* (Carlquist 1983b). End walls of tracheids of *Drimys* typically bear several series of alternate circular pits. Scalariform end wall (and lateral wall) pitting occurs on metaxylem tracheids of all Winteraceae, and could thus be considered a feature of juvenile wood. In *Drimys*, this juvenile condition is evidently reinstated when the cambium is subjected to trauma, because all instances of scalariform pitting on tracheids observed here are associated with interruption in cambial activity. These interruptions are mostly not sufficient to produce callus (pith flecks) but they do produce irregularities in tracheid outline and radial files of tracheids and rays (as seen in transection). *Drimys* appears quite subject to the occurrence of these mild cambial interruptions. Because cambial interruption tends to occur at the end of a growing season, the tracheids that are produced after the interruption are likely to be earlywood

tracheids which, by virtue of their wideness, can accomodate scalariform pitting on radial walls whereas only circular pits can be accomodated on latewood tracheids.

The significance of tracheid length in vesselless dicotyledons is illuminated by *Drimys*. The concept that tracheid length is related to plant size in vesselless dicotyledons was advanced earlier (Carlquist 1975). Larger plant size tends to be correlated with ecologically more favorable areas (warmer areas in the case of *Drimys*), so separating ecology and plant size as factors influencing tracheid length is not easy. The samples selected for this study of *Drimys* wood do permit a distinction to be drawn, however. The sample *D. brasiliensis* (Irwin 12678) is from a small upper stem of a tree, whereas the sample *D. brasiliensis* (Occhioni 985) is very likely a basal stem of a tree. Shorter tracheids are evident in the smaller stem. A similar situation is reported by Bailey and Tupper (1918) for *D. winteri*, in which the first year's tracheids are about a third as long as those from the outside of a large stem. However, the tracheids of a basal stem of *D. winteri* var. *andina*, about 20 years old, are longer than those of the small stem of *D. brasiliensis*, but shorter than the tracheids of the small stem of *D. brasiliensis*. This is also true of the stem of the plant of *D. winteri* var. *winteri* from Tierra del Fuego. This suggests that cold conditions in the habitats of *D. winteri* var. *andina* and *D. winteri* var. *winteri* may also influence production of short tracheids. Thus, both plant (or plant portion) size and habitat influence tracheid length in *Drimys* (and very likely in other vesselless dicotyledons).

In speaking of short tracheids, we are inevitably speaking of narrow tracheids, if the relationship claimed by Bannan (1965) for conifer tracheids obtains (the data in Table 1 do show a linear relationship between tracheid diameter and length). Thus, tracheid diameter is also related not merely to plant size but to ecology as well. Transpiration is likely to stay low in high altitudes and high latitudes, so narrow tracheids may be sufficient to handle peak conductive capacity. Narrow tracheids, which are more numerous per unit transectional area than wide tracheids, offer potentially more safety in the freezing conditions under which the high altitude and high latitude *Drimys* plants exist. Night temperatures are below freezing many nights of the year in the habitat of *D. winteri* var. *andina* (Schick 1980), and very likely the same is true for *D. winteri* var. *winteri*. Under conditions of water stress, narrow tracheids embolize less readily than wider ones in conifers (Lewis and Tyree 1985), and very likely the same is true in vesselless dicotyledons. Water stress may occur when the ground is frozen but when transpiration occurs on a sunny day, as reported for conifers by Lutz (1952), and this very likely applies to vesselless dicotyledons as well as the conifers in which Lutz reported tensions so high under these conditions that woods imploded.

The presence of vesturing on inside surfaces of tracheids in *Drimys* may also serve to sustain high tensions during times when transpiration increases but ground water is unavailable due to freezing. By bonding water more strongly to the wall because of increasing the surface, high tensions in water columns could theoretically be sustained without breakage in the water column (Carlquist 1982b, 1983b). If this or similar hypotheses are operable, one would expect vesturing only in tracheids of *Drimys* woods from areas where freezing of soil is likely to occur. The hypothesis appears to be validated on the basis of distribution of vesturing, for appreciable vesturing was observed only in *D. granadensis* var. *mexicana*, *D.*

winteri var. *andina*, and *D. winteri* var. *winteri*, all of which are in areas subject to low temperatures.

Although the nature of wood anatomy in *Drimys* does reveal structural modes distributed with respect to ecology in ways that invite interpretation, one should not forget the role of other features in water economy of this genus. For example, the fact that stomata in *Drimys* characteristically have alveolar plugs (Bongers 1973) is commonly interpreted as a mechanism for reducing transpiration in the mature leaves. Leaf size doubtless also plays a role in this respect; leaves of *D. winteri* var. *andina* are smaller than those of *D. winteri* var. *chilensis*, for example.

Ray cell walls are nearly as thick as tracheid walls in *Drimys*, suggesting that they contribute to wood strength to an appreciable degree. Mechanical strength of walls is maximized by the development of borders on pits in wood cells in which conduction is active (accounting for large pit membrane areas that maximize conduction but for which borders represent a compensatory restoration of strength to the wall). Many instances of bordered ray cell pits can be found in dicotyledons, far more than the literature would suggest. If borders are indeed common on ray cell pits, one can theorize both mechanical strength of these cells (which one would have assumed on account of the presence of relatively thick secondary walls) and their function in active transport of photosynthates in solution (Carlquist 1988).

Silica bodies are reported here for rays of *D. confertifolia*, *D. winteri* var. *andina*, and *D. winteri* var. *winteri*. This is a first report for the family Winteraceae. Although only a minority of families of dicotyledons has been reported to have silica deposits in wood (see Carlquist 1988 for a list), the systematic distribution of silica bodies in woods forces one to conclude that ability to accumulate silica in wood has been evolved repeatedly in dicotyledons. Therefore silica presence is not an important criterion for relationship of a group.

The number of samples studied of *Drimys* is too few to permit one to say that species characters can be found in wood in this genus. Certainly differences do exist among the collections, but most of these can be interpreted with relation to ecology, a circumstance that would lead one to conclude that discontinuities in variation patterns of wood features would not relate to variety or species limits so much as they would relate to discontinuities in distribution of ecological conditions. Comments will be offered on whether generic characters exist in wood anatomy in Winteraceae in a concluding paper in this series, dealing with the wood anatomy of *Tasmannia*.

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