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WOOD ANATOMY OF *TASMANNIA*; SUMMARY OF WOOD
ANATOMY OF WINTERACEAE

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ABSTRACT

Quantitative and qualitative data are presented for 11 collections of eight taxa. Diameter and length of tracheids are related to plant size, but populations in cooler locations have narrower and shorter tracheids than one would expect on the basis of plant size and age, and smaller tracheids are believed to be of selective value in these environments because of their resistance to embolisms. Vesturing is absent from tracheids in taxa from warmer localities but pronounced in colder places; this, too, is a probable mechanism for resistance to embolism formation. Helical thickenings are reported for one collection of *T. insipida*; these thickenings, otherwise known in the family only from *Pseudowintera*, may play a role similar to vesturing. Scalariform pitting on end walls of tracheids occurs during the first three years of secondary xylem formation, and may also occur after cambial trauma. Axial parenchyma is scarce to absent, and diffuse when present. Rays in *Tasmannia* wood have relatively few procumbent cells. A summary wood description for the family is presented, and a key to the eight genera is given. Although wood anatomy does contain some features of generic value, data from floral morphology, pollen structure, and leaf anatomy more strongly support the recognition of eight genera. Some species have very distinctive features, but genera are difficult to define; pending acquisition of chemical data, eight genera may be provisionally recognized. The only feature considered as a possible phylogenetic trend in wood within the family is an increased tendency for alternate pits to supplant scalariform pits on end walls of tracheids. Tracheids of Winteraceae demonstrate that scalariform pitting is pervasive and preserved in a flexible way; alternate pits are hypothesized to have been evolved in the family for increased wall strength. Ecological correlations, presented for the entirety of the family, are much like those shown within *Tasmannia*.

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

INTRODUCTION

With the completion of the present study, comparative studies of all of the genera of Winteraceae except for *Takhtajania* are at hand. No wood sample of *Takhtajania* is available; the limited material of the original collection would not yield a sufficient amount of secondary xylem to be informative. Generic monographs of wood anatomy of the family include those for *Pseudowintera* (Patel 1974; Meylan and Butterfield 1978), *Zygogynum* (Carlquist 1981), *Exospermum* (Carlquist 1982a), *Belliolum* (Carlquist 1983a), *Bubbia* (Carlquist 1983b), and *Drimys* s. str. (Carlquist 1988a). Prior to the completion of these monographs, data for the family had been presented in terms of a small number of species (Thompson 1918, Gupta 1934, Bailey 1944, Takahashi 1985).

Tasmannia is recognized as a genus separate from *Drimys* by recent authors (Ehrendorfer, Krendl, Habeler, and Sauer 1968; Smith 1969; Takahashi 1985), although Vink (1970) demurred. Ehrendorfer et al. (1968) say, "clearly, *Drimys* sect. *Tasmannia* (R. Br.) F. v. Muell. has to be accorded at least generic rank as *Tasmannia* R. Br. There are drastic differences in morphology (dioecious flowers,

narrow filaments, carpels not utriculate with short unifacial basal zone etc.), palynology and anatomy . . . as well as chemistry which separate *Tasmannia* not only from *Drimys* s. str. but from all other Winteraceae. It is significant that *Tasmannia* on a lower ploidy level is morphologically and chemically more advanced than the rest of the family on a much higher level." As Smith (1969) notes, the claim that the *Tasmannia* carpel is more specialized runs counter to the tenets of many morphologists (Bailey and Swamy 1951).

Tasmannia ranges from Tasmania and eastern Australia (Victoria to Queensland) to the Philippines, Celebes, Borneo, New Guinea, and the Solomon Islands (Smith 1943b, Vink 1970). The delimitation of species within *Tasmannia* has proved difficult, with either a few or many species recognized. The source of difficulty is undoubtedly the occurrence of apomixis, as Vink (1970) acknowledges in his treatment of the "entities" (the taxa placed in quotation marks in the present paper) under *T. piperita* (Hook.) Miers. The entities grouped within *T. piperita* do have a remarkable ecological and morphological range, however. They extend from the cool alpine conditions of southeastern Australia (*T. piperita* "xerophila") to wet tropical montane forest (*T. piperita* "heteromera" of New Guinea, *T. piperita* subsp. *piperita* of Mt. Kinabalu, Sabah) to wet subtropical forest (*T. piperita* "membranea"). This ecological range is greater than the range of all other species: *T. lanceolata* (Poir.) A. C. Smith (Tasmania, Victoria) occupies sites about as extreme as those of *T. piperita* "xerophila"; *T. purpurascens* (Vickery) A. C. Smith, endemic to the Barrington Tops area of northern New South Wales, comes from a somewhat less extreme montane area; *T. stipitata* (Vickery) A. C. Smith occurs in cool forests, Victoria to northern New South Wales; *T. insipida* R. Br. occurs in coastal and inland forests from southern New South Wales to southern Queensland.

As in the study of wood of *Drimys* (Carlquist 1988a), one of the objects of the present study is to see if presence of vesturing (warts) on the inner surfaces of tracheids is related to coolness of habitat. In *Drimys*, this correlation was quite clear. The great ecological range within *Tasmannia* offers an ideal basis for demonstrating if this trend is valid if indeed duplicated within *Tasmannia*.

In *Drimys*, study of wood representing a wide range of plant sizes as well as climatic sites demonstrated a probable correlation that tracheid diameter and length relate to plant size and age, but also to coolness of habitats. Because a similar ecological range exists in *Tasmannia*, a second genus suitable for demonstrating factors controlling tracheid dimensions exists.

Scalariform and transitional pitting are present in some tracheids of *Tasmannia* wood. The present study attempts to discover the distribution of this pitting to see if patterns like those in *Bubbia* and *Zygogynum* (scalariform pitting in later-formed secondary xylem) or like those in *Drimys* (scalariform pitting in earlier-formed wood and after cambial injury) are present.

The completion of this series of monographs on wood anatomy of Winteraceae offers an opportunity for a retrospective look at patterns of characters in wood throughout the family. The ecological dimensions cited above can be examined over a broader base of comparison. In addition, whether wood character states parallel generic lines can now be analyzed, and the fact that generic characters do exist in terms of wood features is demonstrated below in the form of a key.

Designation of species characters with respect to wood is provisional in view of the limited quantities of material available for study.

MATERIALS AND METHODS

Wood samples were available in dried condition. Samples are of more than twig size except for the herbarium specimen portions studied for three Australian species (*T. insipida*, *T. purpurascens*, and *T. stipitata*). Xylarium specimens of the former two species were available, and comparison between these two kinds of specimens allows examination of the relationship between tracheid dimensions and stem size, as well as the nature of juvenilism in earlier-formed secondary xylem. For donation of the two xylarium specimens cited, I am grateful to J. Ilic of the Dadswell Wood Collection (FPAw), CSIRO Division of Chemical and Wood Technology, Highett, Victoria. A sample of *T. piperita* "*xerophila*" was also taken from an herbarium specimen, but the stem of this plant (an alpine shrub) was 11 years old (as shown by well-demarcated growth rings, Fig. 11). Wood samples of larger diameter were available for the remainder of the taxa studied here (for stem diameter, see Table 1, column 1).

Localities of the collections represented in this study are as follows: *T. insipida*, *Boorman IX-1900* (POM), Port Jackson District (= Sydney), N.S.W., Australia; *T. insipida*, *FPAw-12789*, N.S.W., Australia; *T. lanceolata*, *Carlquist 1115* (RSA, RSAw), Mt. Dobson, Tasmania, Australia; *T. piperita* subsp. *piperita*, *Davidson 1073* (LAM, RSAw), Mt. Kinabalu, Sabah, Malaysia; *T. piperita* "*heteromera*," *Henty & Carlquist 16564* (RSA, RSAw), Mt. Piora, New Guinea; *T. piperita* "*membranea*," *Carlquist 5212* (RSA, RSAw), Atherton District, Queensland, Australia; *T. piperita* "*membranea*," *Carlquist 15549* (RSA, RSAw), Atherton District, Queensland, Australia; *T. piperita* "*xerophila*," *Hartley 14193* (RSA), Mt. Kosciusko, N.S.W., Australia; *T. purpurascens*, *Briggs & Johnson B2459* (RSA), Gloucester Tops, 1300 m, N.S.W., Australia; *T. purpurascens*, *FPAw-12884*, Barrington Tops, N.S.W., Australia; *T. stipitata*, *Hotchkiss 195* (RSA), Rocky Creek Gully, Dorriggo, N.S.W., Australia. Unfortunately, stations that record climatic data are not near any of the localities cited, and the conclusions about relationship between ecology and wood anatomy in *Tasmannia* would benefit from measurements of climate in the localities where these plants grow.

Wood samples were boiled in water and stored in 50% aqueous ethyl alcohol. Sections were prepared on a sliding microtome. Sections were stained in safranin, with varying amounts of counterstaining with fast green in order to reveal pit membranes. Some sections were kept unstained and dried between clean slides and examined by means of a ISI WB-6 scanning electron microscope (SEM). Sections from already-prepared slides were also readied for study by SEM by soaking off coverslips and removing resin from sections with xylene. Wood macerations (used for measuring tracheid lengths) were prepared from the wood stored in 50% ethyl alcohol by means of Jeffrey's Fluid and stained with safranin.

Quantitative data (Table 1) are based on 25 measurements for each feature except for tracheid diameter, tracheid wall thickness, pit diameter, and ray cell wall thickness, in which typical conditions were selected for measurement because 25 truly comparable measurements cannot be obtained in these features. Tracheid

diameter includes wall thickness, and is a tangential diameter because radial diameter fluctuates with position in a growth ring. Tracheid wall thickness was estimated on the basis of a few measurements per collection. This feature is of interest only where marked differences occur among species; in a single tracheid, wall thickness varies (wall is thicker in angles) and statistically significant measurements are probably not possible unless two species differ markedly in this respect. Diameter of woody cylinder (Table 1, column 1) is a rough indicator of age. In species of colder habitats, more numerous growth rings per radial mm of wood occur. The sample of *T. lanceolata* had 28 growth rings, that of *T. piperita* "xerophila" 11 growth rings. Diameters of the xylarium samples of *T. insipida* and *T. purpurascens* were estimated based on the curvature of the cambial surface and on the divergence angle of rays (rays are more nearly parallel at the outside of large stems than near the pith). Although the microscopical methods used are not recommended for understanding of ultrastructure, they are the ones that have been widely used as reliable for studies in comparative wood anatomy.

ANATOMICAL RESULTS

Growth Rings

Growth rings are almost absent in *T. piperita* "membranea" (Fig. 1), clearly absent in *T. piperita* "heteromera" (Fig. 6). In the collections from higher latitudes and altitudes, growth rings are more marked; for example, in *T. piperita* "xerophila" (Fig. 11). One should note, however, that normal growth rings are evident only at lower right in Fig. 11; in the remainder of Fig. 11, growth rings are more strongly marked because of cambial damage during winter cold followed by irregularity in radial files of earlywood as wood production is resumed (enlarged in Fig. 12). Some cambial damage of this sort, as revealed by presence of traumatic parenchyma and irregularity in radial files of tracheids, was observed in all of the taxa with more marked growth rings. Growth rings occur in strongly marked form in *T. lanceolata* and *T. purpurascens*, but are less strongly marked in *T. insipida* and *T. stipitata*, and are least evident in the collections of *T. piperita* other than *T. piperita* "xerophila." The degree of climatic severity correlates with the proportion of the growth ring in which latewood is present: in *T. lanceolata* and *T. piperita* "xerophila," narrower latewood tracheids are present in the last third or even half of the growth ring; in taxa with less-marked growth rings, latewood is limited to the last quarter or less of a growth ring.

Tracheid Dimensions

The range in tangential diameter of tracheids in *Tasmannia* (Table 1, column 2) ranges from 46 μm in *T. piperita* "heteromera" (Fig. 6) to 16 μm in *T. piperita* "xerophila" (Fig. 11, 12). *Tasmannia piperita* "membranea" (Fig. 1) is intermediate in tracheid diameter. Radial tracheid diameter varies with position of a tracheid in a growth ring. Earlywood tracheids sometimes have radial diameters greater than their tangential diameters (Fig. 1, bottom).

Tracheid length (Table 1, column 3) ranges from a maximum of 3528 μm in *T. piperita* "heteromera" to a minimum of 1076 μm in *T. piperita* "xerophila." This is the same pair of taxa cited for extremes in tracheid diameter. Comparison of columns 2 and 3 in Table 1 shows that tracheid diameter and length run in

Table 1. Wood characteristics of *Tasmania*.

Name	Collection	1	2	3	4	5	6	7	8	9	10
<i>T. insipida</i>	Boorman IX-1904 (POM) FPAw-12789	5 14	30 28	2107 2502	4.0 2.8	8.0 8.0	5.3 5.5	1700 1109	2887 1055	3.1 3.5	5.3 5.5
<i>T. lanceolata</i>	Carlquist 1115 (RSA)	28	25	1444	3.2	7.0	5.6	775	1578	4.4	2.4
<i>T. piperita</i> subsp. <i>piperita</i>	Davidson 1073 (LAM)	16	34	3106	3.2	8.3	7.0	1609	2920	3.3	3.0
<i>T. piperita</i> "heteromera"	Henty & Carlquist 16564 (RSA)	34	46	3528	4.0	8.8	7.1	1816	5148	4.3	4.5
<i>T. piperita</i> "membranea"	Carlquist 5212 (RSA)	18	37	2122	3.5	9.2	7.2	642	2375	3.5	3.9
	Carlquist 15549 (RSA)	22	38	2585	3.7	9.1	7.1	1006	3147	3.9	2.3
<i>T. piperita</i> "xerophila"	Hartley 14193 (RSA)	7	16	1076	3.9	6.0	5.5	286	2055	4.9	2.2
<i>T. purpurascens</i>	Briggs & Johnson B2459 (RSA)	6	26	1519	2.2	7.1	5.4	480	1509	4.1	1.6
	FPAw-12884	12	28	1930	3.0	7.0	5.3	607	1609	4.0	2.5
<i>T. stipitata</i>	Hotchkiss 195 (RSA)	4	23	1502	2.2	6.7	5.1	375	1093	3.6	2.4

Key to columns: 1, diameter of woody cylinder, mm; 2, mean tangential diameter of tracheid at widest point, μm ; 3, mean tracheid length, μm ; 4, mean tracheid wall thickness, μm ; 5, mean diameter of circular tracheid-tracheid pits, μm ; 6, mean diameter of circular tracheid-ray pits, μm ; 7, mean height of uniseriate rays, μm ; 8, mean height of multiseriate rays at widest point, cells; 9, mean width of multiseriate rays at widest point, cells; 10, mean wall thickness of ray cells, μm .

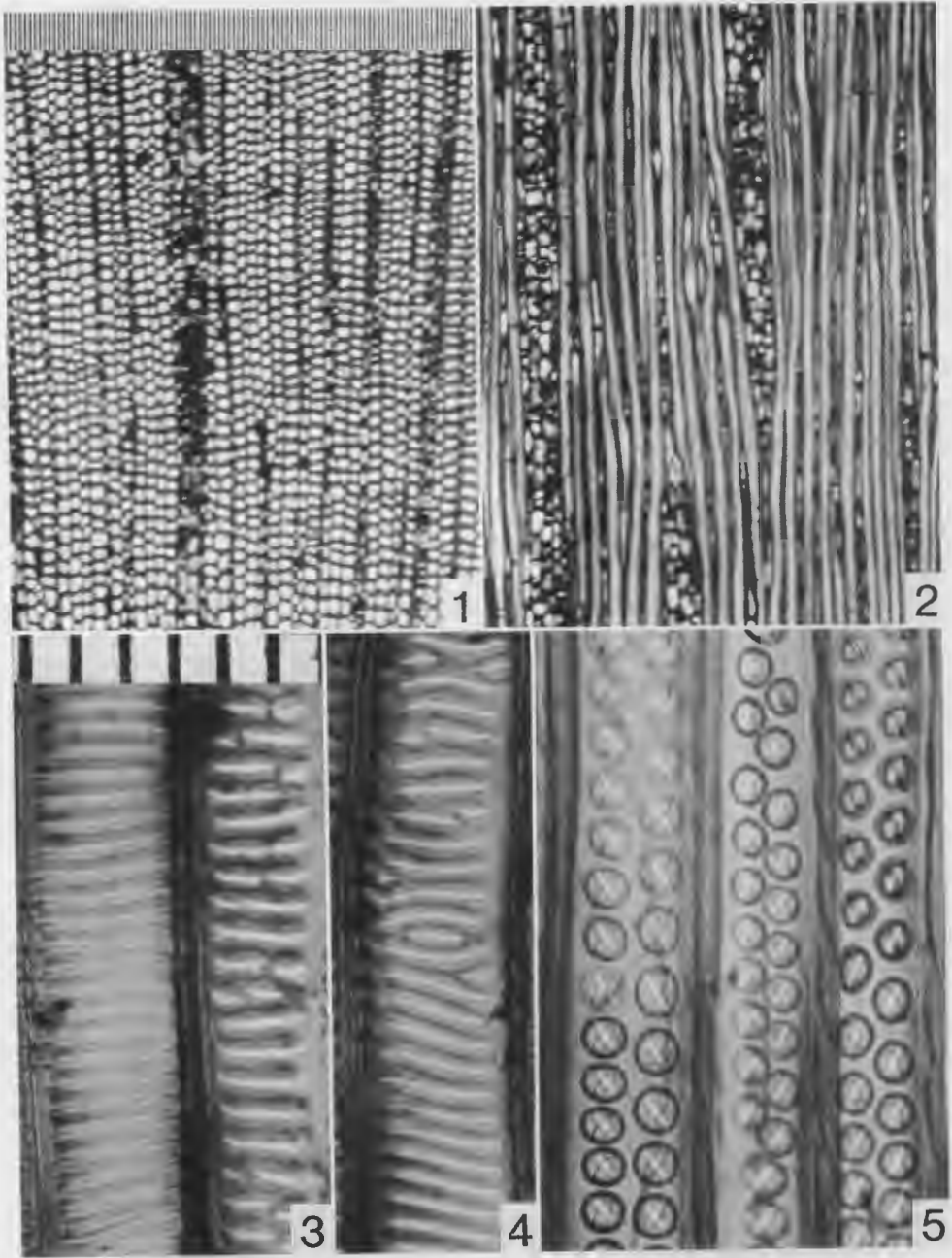


Fig. 1-5. Wood sections of *Tasmania piperita* "membranea" (Carlquist 5212).—1. Transection; growth rings are absent.—2. Tangential section; multiseriate rays more numerous than uniseriate rays.—3. Overlap areas of tracheids from radial section, near pith (metaxylem tracheid at left).—4. Overlap area of tracheids from radial section, wood more than three years from pith; pit cavities circular in outline. (Fig. 1, 2, magnification scale above Fig. 1 [divisions = 10 μm]; Fig. 3-5, magnification scale above Fig. 3 [divisions = 10 μm].)



Fig. 6-10. Wood sections of *Tasmannia piperita* "heteromera" (Henty & Carlquist 16564).—6. Transection; tracheids are of maximal diameter for *Tasmannia*.—7. Tangential section; dark-staining amorphous deposits occur in ray cells.—8. Overlap areas of tracheids from radial section near pith, showing scalariform and transitional pitting.—9. Overlap areas of tracheids from radial section in third year of wood.—10. Tangential walls of ray cells (oriented horizontally), from radial section, showing bordered nature of pits. (Fig. 6, 7, magnification scale above Fig. 1; Fig. 8, scale above Fig. 3.)

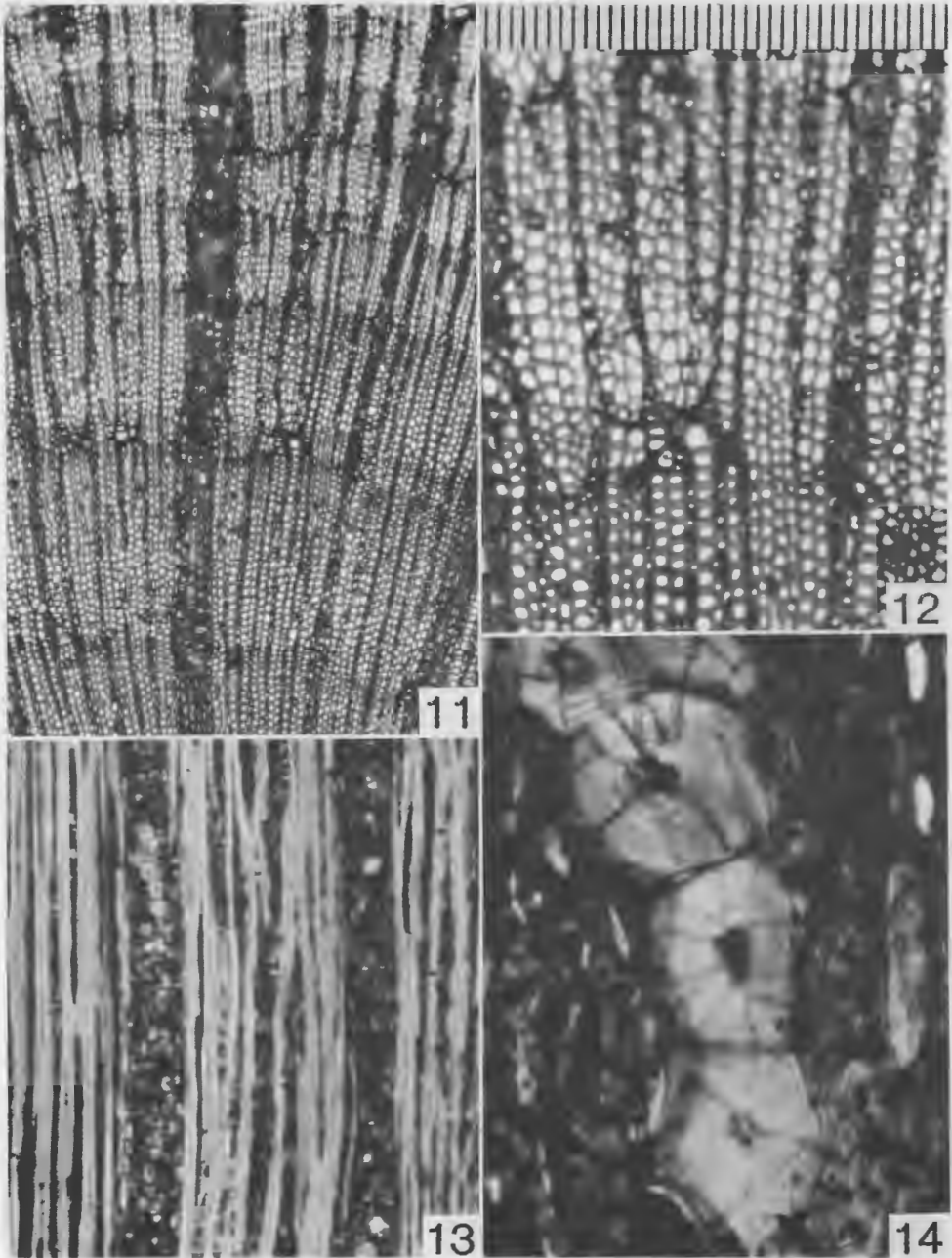


Fig. 11–14. Wood sections of *Tasmania piperita* “*xerophila*” (Hartley 14193).—11. Transection; seven growth rings are present.—12. Portion of transection, showing irregularity in tracheid files due to cambial injury.—13. Tangential section; multiseriate rays are relatively wide.—14. Sclereids from ray, tangential section. (Fig. 11, 13, magnification scale above Fig. 1; Fig. 12, scale above Fig. 12 [divisions = 10 μ m]; Fig. 14, scale above Fig. 3.)

close parallel. Smaller stems (fewer years old) have narrower and shorter tracheids, but so do the relatively old stems of *T. lanceolata* and *T. piperita* "xerophila."

Mean tracheid wall thickness (Table 1, column 4) ranges from 22 μm in *T. purpurascens* and *T. stipitata* (herbarium specimens) to 4.0 μm in *T. piperita* "heteromera" (Fig. 6). However, mean wall thickness is misleading because wall thickness can fluctuate so much with respect to position of a tracheid in a growth ring. For example, in *T. piperita* "xerophila" (Fig. 12), earlywood tracheids average 2 μm in mean wall thickness, whereas latewood tracheids average 5 μm . The range is less marked in *T. purpurascens* (FPAw-12884): 2.5 μm in earlywood, 3.5 μm in latewood.

Tracheid Wall Pitting

Pits of both overlap and lateral walls of tracheids tend to be circular in outline (Fig. 5), with exceptions as noted below. Pits are much more abundant on radial walls than on tangential walls, and so pits on radial walls are discussed below. Tracheid-to-tracheid pits (Table 1, column 5) were measured separately from tracheid-to-ray pits (Table 1, column 6). The largest tracheid-to-tracheid pits were observed in *T. piperita* "membranea" (Fig. 5), although those of *T. piperita* "heteromera" (Fig. 9) were found to be only a little smaller. The smallest tracheid-to-tracheid pits were observed in the taxon with the smallest tracheids, *T. piperita* "xerophila." Tracheid-to-ray pits have a similar size range, but are about 25% smaller than tracheid-to-tracheid pits (compare Table 1, columns 5 and 6).

Scalariform pitting occurs on metaxylem tracheids of *Tasmannia*, but persist on end walls of tracheids for one to three years in *T. insipida*, *T. lanceolata*, *T. piperita* "heteromera" (Fig. 8), *T. piperita* "membranea," *T. purpurascens*, and *T. stipitata*. Some wood samples provided pith as well as five or more years of wood accumulation, whereas for other species (*T. insipida*, *T. purpurascens*) both twigs and portions from older stems but not including the pith were available. Both kinds of samples can be used to demonstrate the change during the first several years from scalariform to circular pits on end walls of tracheids. The scalariformly pitted tracheid in Figure 3 is best considered late metaxylem, the tracheid at right secondary xylem. In Figure 4, an overlap area from an earlywood tracheid of the first year's secondary xylem illustrates the persistence of the scalariform pattern. In *T. piperita* "membranea," transitional pitting but not true scalariform pitting was observed on overlap areas of tracheids in wood five or more years from the pith. Otherwise circular bordered pits characterize overlap areas of tracheids more than three years from the pith in all taxa (e.g., Fig. 5, 9) except *T. piperita* "xerophila." In *T. piperita* "xerophila," scalariform pitting on end walls was observed on end walls of earlywood tracheids throughout the stem studied (Fig. 15). The reader will note that the stem studied exhibited a high degree of cambial damage during winter (Fig. 11, 12).

Tracheid Wall Sculpture

Inner surfaces of *Tasmannia* tracheids range from smooth to warty as seen with SEM. The warts may be termed "vestures" in accordance with the terminology of Ohtani et al. (1984), although there is disagreement on this terminology. Schmid and Machado (1964) and Schmid (1965) showed, for several tropical Fabaceae,

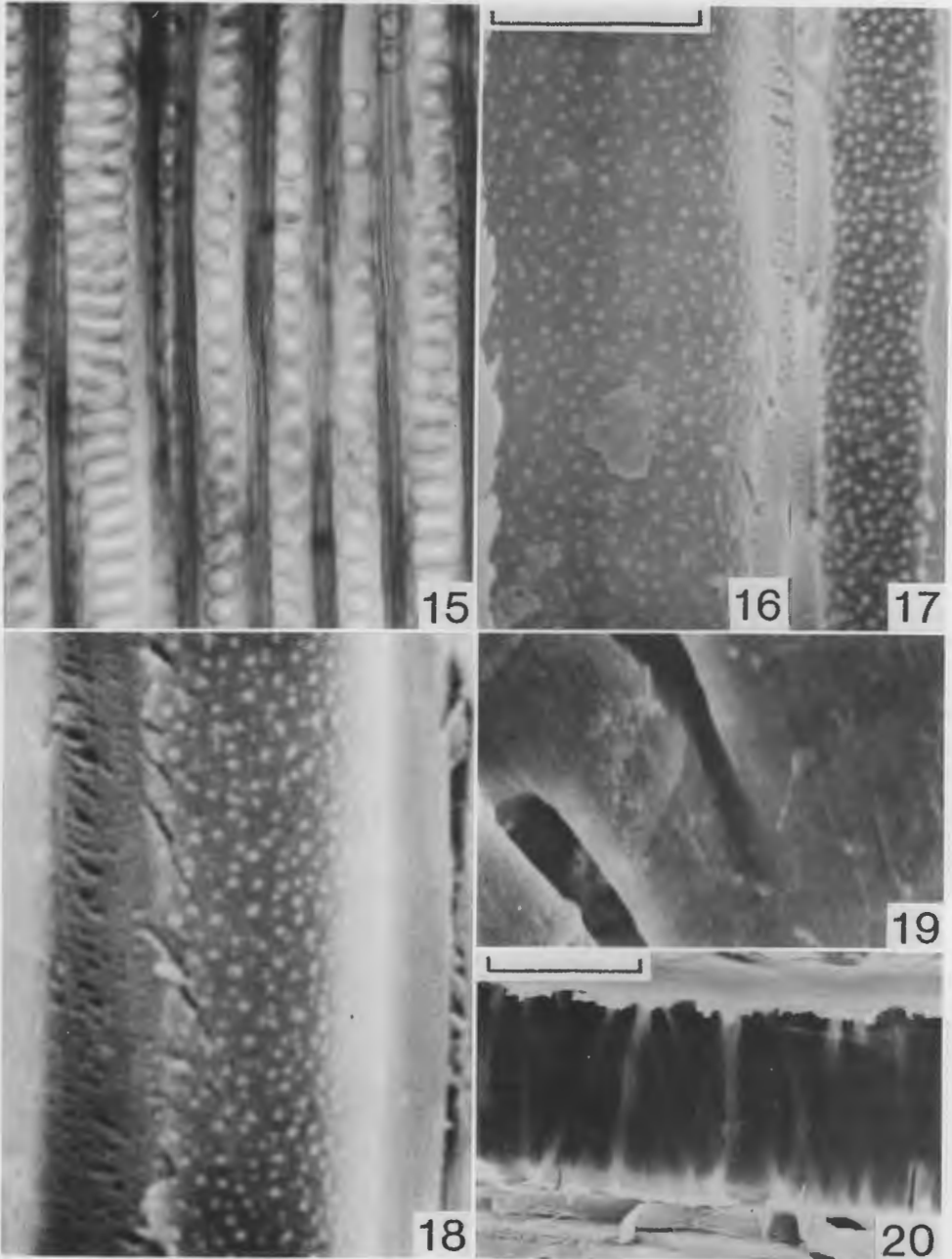


Fig. 15–20. Details of tracheids from wood of *Tasmannia*.—15–17. *T. piperita* “*xerophila*” (Harley 14193).—15. Light microscope photograph of radial section, showing scalariform and transitional pitting on overlap areas of wider tracheids, circular pitting on narrow tracheids.—16–17. SEM photographs of vesturing on walls of tracheids from tangential sections.—16. Wide tracheid from earlywood.—17. Narrow tracheid from latewood.—18. *T. lanceolata* (Carlquist 1115). Vesturing on latewood tracheid.—19. *T. piperita* “*heteromera*” (Henty & Carlquist 16564). Smooth wall of tracheid (portions of two pits present).—20. *T. insipida* (FPAw-12789). Helical thickenings on wall of tracheid. (Fig. 15, magnification scale above Fig. 3; Fig. 16–19, scale above Fig. 16 [bracket = 10 μ m]; Fig. 20, scale above Fig. 20 [bracket = 10 μ m].)

that vessel elements at first develop a membrane system that settles at the pits' borders or at the secondary wall and produces the vestures, whereas subsequently another membrane system that occurs atop the vestures finally produces the warty layer. Those studies may contradict the concept of Côté and Day (1962) and Ohtani et al. (1984) that vestures and warts are alternative expressions of the same phenomenon, but more studies are needed. Because many authors today are working with SEM rather than TEM results, the term vesturing as an all-inclusive, vague term may be used, with the caveat that vesturing within pits and wartiness on a vessel wall surface may, even within a single species, have different origins. Vesturing is well known in *T. piperita* "*xerophila*" (Fig. 16, 17). Vesturing is often less dense on wider tracheids (Fig. 16), denser on narrower tracheids (Fig. 17). The protuberances may be slightly larger on narrower tracheids. Dense vesturing also is characteristic of inner tracheid surfaces in *T. lanceolata* (Fig. 18) and *T. purpurascens*. Sparsely placed very low vestures were observed on tracheids of *T. insipida* and *T. stipitata*. Smooth walls apparently free from vesturing were observed on tracheids of *T. piperita* "*heteromera*" (Fig. 19), *T. piperita* "*membranea*," and *T. piperita* subsp. *piperita*.

In wood of *T. insipida* (FPAw-12789), about 20% of tracheids bear helical thickenings on walls (Fig. 20). The tracheid thickenings are visible under the light microscope. Thickenings are present throughout the wood, and no correlation with position of tracheid in a growth ring could be established.

Axial Parenchyma

Axial parenchyma is not common in wood of *Tasmannia*. In *T. piperita* "*membranea*" (Carlquist 5212), diffuse parenchyma is present, and occasional tangentially or radially oriented pairs of parenchyma strands could be observed. Diffuse axial parenchyma moderately common in latewood but uncommon in earlywood was observed in *T. lanceolata*. Moderately scarce axial parenchyma was observed in *T. stipitata*. Very scarce axial parenchyma (e.g., only a single strand seen on a transection) was observed in *T. piperita* subsp. *piperita*, *T. piperita* and *T. purpurascens*. No axial parenchyma was observed in *T. insipida* and *T. piperita* "*heteromera*." Identification of axial parenchyma was not based on presence of resinlike compounds (Fig. 1, 6) but rather on presence of thin vertical walls and on presence of cross-walls, indicating strand cells. Longitudinal sections showing strands were used to confirm presence of axial parenchyma.

The traumatic parenchyma produced after cambial injury (Fig. 11, 12) may be present as large lenses of tissue (not shown here). Traumatic parenchyma is not included here under the category of axial parenchyma. In addition to traumatic parenchyma, a very few strands of axial parenchyma were observed in the wood of *T. piperita* "*xerophila*."

Ray Types and Dimensions

Rays in wood of *Tasmannia* correspond to the Heterogeneous Type I of Kribs (1935), but procumbent cells in rays, a requisite of Heterogeneous Type I, were not observed in all specimens. Cells in uniseriate rays are exclusively upright throughout the genus. Upright cells likewise compose the uniseriate wings on multiseriate rays. Multiseriate portions of multiseriate rays are composed of up-

right cells predominantly, but with a few files of procumbent cells, in the specimens studied of *T. insipida* (FPAw-12789), *T. lanceolata*, *T. piperita* "membranea," *T. piperita* "xerophila," and *T. purpurascens* (FPAw-12884). The presence of procumbent cells may be expected nearer the cambium in larger wood samples of *Tasmannia*, based on the ontogenetic considerations of Barghoorn (1941). Thus, absence of procumbent cells in some wood samples of *Tasmannia* must be considered in terms of the small size of these wood samples. Ray cells isodiametric in outline in tangential sections (Fig. 2, 7, 13) are not necessarily procumbent cells; most of these are square in radial sections. Multiseriate rays are more common than uniseriate rays throughout the genus (biseriate rays are counted as multiseriate here).

Uniseriate rays range from 286 μm in 1816 μm in mean height (Table 1, column 7). Multiseriate rays range from 1093 μm to 5148 μm in mean height (Table 1, column 8), a span not unlike that of tracheid lengths in the genus.

Mean ray width of rays at widest point is shown for the collections studied in Table 1, column 9. Most of the collections range narrowly in mean width at the widest point (3.1 to 4.1 cells). Multiseriate rays of this range are shown in Fig. 2 and Fig. 7. The two collections with rays wider than this range are *T. lanceolata* and *T. piperita* "xerophila" (Fig. 13).

Ray Histology

Ray cell wall thickness varies appreciably within the genus (Table 1, column 10). Ray cell walls are lignified, and tend to be thicker on tangential than on radial walls. Tangentially oriented walls typically bear bordered pits, as shown for *T. piperita* "heteromera" (Fig. 10).

Sclereids (possibly of traumatic origin) were observed in several rays in sections of *T. piperita* "xerophila" (Fig. 14). The sclereids are thick walled, and there are no cells transitional between ordinary ray cells and the sclereids. A few sclereids were observed in rays of *T. piperita* "membranea" (Carlquist 15549) and *T. purpurascens* (FPAw-12884).

No ethereal oil cells were observed in rays of *Tasmannia* wood. Bark sections of the genus do commonly show ethereal oil cells in phloem rays, however.

Droplets of densely staining amorphous accumulations are common in ray cells of *Tasmannia* (Fig. 2, 7, 11, 12, 13, 14). These compounds occasionally are found in tracheids (Fig. 1, 6), especially in tracheid tips, as well as in traumatic parenchyma (Fig. 11, 12).

CONCLUSIONS

Growth rings in *Tasmannia* occur in proportion to probable degree and duration of coldness. All *Tasmannia* localities can be characterized as moist, so degrees of coldness must be responsible for growth-ring phenomena. The extent of latewood in comparison to earlywood within a growth ring correlates with extremeness of cold: latewood is prominent and occupies a third to a half of a growth ring in *T. piperita* "xerophila" and *T. lanceolata*, native to Mt. Kosciusko, N.S.W., and Mt. Field National Park, Tasmania, respectively. Narrower tracheids of the latewood can be assumed to embolize (cavitate) less readily than the earlywood tracheids, in accordance with the findings of Lewis and Tyree (1985) on conifer tracheids.

One also notes that the tracheids of *T. lanceolata* and especially *T. piperita* “*xerophila*”—even earlywood tracheids—are small and short compared to tracheids of other populations of *Tasmannia*. Therefore, resistance to embolism formation in these two taxa ought to be high at any time of year; in fact, in these localities, frost may occur during spring and autumn, not just during the winter.

Do tracheid dimensions relate to size of plant only, or do they also represent adaptations to cold? One might expect shorter tracheids also to be narrower, judging from the close correlations between these two dimensions demonstrated in conifer tracheids by Bannan (1965). The age-on-length curves published by Bailey and Tupper (1918) show a rapid increase in tracheid length with the onset of secondary growth, and a gradual plateau effect in length as secondary growth continues. This suggests a relationship between stem size and tracheid length. A survey comparing tracheid lengths to known stem size and plant height in a large assemblage of conifer woods also showed a clear relationship (Carlquist 1975). If one uses the tracheid dimensions and diameter of wood samples of *Tasmannia* to look for correlation, one finds that the tracheids of *T. lanceolata* and *T. piperita* “*xerophila*” fall well short of the expected correlation. This also proved true in the case of taxa of *Drimys* from cold localities (Carlquist 1988a). One can therefore conclude that while tracheid dimensions in general relate to stem size, extremely cold localities may provide a selective advantage for reduction of tracheid dimensions beyond what would correspond to a length-on-age curve based on species from more moderate habitats.

The occurrence of vesturing on tracheid walls in *Tasmannia* parallels very closely the degree of prominence of growth rings within the genus. Those taxa with growth rings absent or very weakly marked also lack vesturing on inner surfaces of tracheids. Vesturing (wartiness) is most prominent in the tracheids of *Tasmannia* populations from cold areas: *T. lanceolata*, *T. piperita* “*xerophila*,” and *T. purpurascens*. Degree of vesturing is related to ecology, not to any taxonomic distinctions per se. This validates the hypothesis originated earlier for the family (Carlquist 1983b), as does the distribution of vesturing within the genus *Drimys* (Carlquist 1988a). According to a discussion on the functional significance of vesturing in vessels and tracheids (Carlquist 1982b), increase in surface of a conducting cell by means of sculptural relief might have the effect of bonding the water column more strongly to the wall surface. Therefore, breakage of the water column under conditions of high tension induced by freezing might be lessened. This freezing need not be envisioned as occurring within the tracheid itself. Rather, extraordinarily high tensions, capable of causing implosive collapse of wood, can occur when ground water is frozen but transpiration occurs on a sunny day (Lutz 1952). Alternatively, increased wall surface might aid in recovery of a water column as tracheids that contain frozen water thaw. The ecological distribution of vesturing within not only Winteraceae but also other groups provides an interesting line of circumstantial evidence (Carlquist 1982b). As yet, no experimental testing of potential functions of vesturing has been attempted.

Helical thickenings on walls of conductive cells have been regarded as forms of relief that might have much the same effect as vesturing (Carlquist 1982b). Some *T. insipida* tracheids have helical thickenings. Growth rings of *T. insipida* are well marked, suggesting that other phenomena representing adaptations to cold are to be expected. Helical thickenings in tracheids of *T. insipida* and *Pseu-*

dowintera may increase bonding of water to the tracheid wall, conferring the same potential benefits as cited in the account of vesturing above. Genetic information leading to the formation of vesturing may not occur in all the groups where vesturing might be valuable, but helical thickenings may evolve instead, or both vesturing and helical thickenings may occur simultaneously, as in *Persoonia toru* A. Cunn. (Meylan and Butterfield 1978).

Scalariform pitting on end walls of tracheids characterizes not just metaxylem of *Tasmannia*, but tracheids of the first one to three years as well. There are reasons therefore to believe this is a juvenile phenomenon (juvenile not in the sense of being characteristic of primary xylem, but of being characteristic of early formed secondary xylem as well). Vestiges of the scalariform pattern, as in the transitional pitting on some overlap areas of tracheids after the first three years in *T. piperita* "*membranea*," suggest incomplete extinction of the scalariform pattern as secondary growth proceeds. The presence of scalariform pitting on tracheids of later years in *T. piperita* "*xerophila*" represents renewal of juvenile pattern after injury; cambial injury in this plant appears to take place annually, suggesting that it is at the margin of its range, receiving sufficient water but experiencing enough frost to cause moderate injury. Occurrence of scalariform pitting after cambial trauma was observed in *Drimys* (Carlquist 1988a) and *Pseudowintera* (Jeffrey and Cole 1916; Patel 1974); although Patel does not comment on the explanation for this, temporary reversion to a juvenile pattern seems a logical reason in all instances observed.

Ray heights in *Tasmannia* parallel tracheid lengths, as one might expect. Perfect correlations are not to be expected for various reasons, notably sampling (in a particular section, a few large rays representing relatively intact extensions of primary rays may increase the mean ray height figure appreciably).

Bordered pits are common on tangential walls of ray cells, suggesting an adaptation to radial conduction of photosynthates. This phenomenon is by no means restricted to Winteraceae, but is common (despite rarity of mention in the literature) in woody dicotyledons (Carlquist 1988b).

Procumbent ray cells do occur in larger stems of *Tasmannia*, but they appear somewhat less common than in rays of *Drimys*, where they were observed in all except the smallest stems (Carlquist 1988a). Degree of ray cell wall thickness may be a characteristic of a particular population of *Tasmannia* rather than of particular species.

In features cited above as relating to ecology, the degree of presence of a particular feature should not be regarded as an expression of an essentially taxonomic distinction. In this connection, one notes that the *Tasmannia piperita* complex may well represent a single species, diverse though some populations are; the ecological (and therefore anatomical) range of features in *T. piperita*, however, is greater than in the remainder of the genus. This should not be surprising. Vink's (1970) union of various populations formerly regarded as species as "entities" under *T. piperita* does not imply that the complex is uniform, but that the apparently apomictic (perhaps to various degrees) populations are not separated by discontinuities as are the remaining (presumably sexual) species in *Tasmannia*, and that shared flower and fruit features can be used to link all of the *T. piperita* entities into a single species. Sampling in the present study is insufficient to allow one to designate anatomical features as of specific or infraspecific significance with

any degree of assurance. However, features that appear more probable in this respect are the helical thickenings in tracheids of *T. insipida* and the wide rays (and possibly ray sclereids) of *T. piperita* "*xerophila*."

WOOD ANATOMY OF WINTERACEAE: A SUMMARY

The following comments are based on monographs on wood anatomy of the genera *Pseudowintera* (Patel 1974; Meylan and Butterfield 1978), *Zygogynum* (Carlquist 1981), *Exospermum* (Carlquist 1982a), *Belliolum* (Carlquist 1983a), *Bubbia* (Carlquist 1983b), and *Drimys* s. str. (Carlquist 1988a), in addition to information on *Tasmannia* above.

Familial Description

Growth rings are absent in subtropical and tropical species but present to varying degrees in temperate species: latewood tracheids are tangentially narrower and thicker walled; the proportion of latewood to earlywood increases with severity of climate. Vessels are absent. Tracheids have pits more abundant on radial walls than on tangential walls. Pits are commonly circular in outline. Pits are scalariform on overlap areas of tracheids in juvenile wood (years one to three), and characteristically scalariform thereafter in some genera and species (apparently in relation to enhanced transpiration), but also occasional in other species after cambial injury. Lateral wall tracheid-to-tracheid pits are circular, 7–10 μm in diameter, and about 25% larger than tracheid-to-ray pits. Internal surfaces of tracheids are smooth, vested, or with helical thickenings. Axial parenchyma is present in most species, occasionally very rare or absent; when present, it is diffuse, in radial or tangential pairs, diffuse-in-aggregates, in narrow bands, or marginal. Rays are Heterogeneous Type I; uniseriate rays are somewhat more abundant than multiseriate rays. Uniseriate rays are composed of upright cells, as are uniseriate wings on multiseriate rays. Multiseriate portions of multiseriate rays contain upright cells, and various quantities of upright cells (often upright cells exclusively in juvenile wood). Ray cell pits are commonly bordered on tangential walls. Ray cells (and occasionally other cells) contain droplets or massive amorphous deposits of dark-staining compounds. Ray cells occasionally contain starch; silica bodies reported in a few species of *Drimys*. Wood is nonstoried.

Generic Characteristics

Although there is diversity within genera, the characters of the genera can be summarized in the form of a key. Noncontrasting information has been added in parentheses so that comparable information can be presented. The woods of *Pseudowintera* studied by Patel (1974) are from relatively mature trees. In my studies, relatively mature stems were studied for the majority of taxa, but small stems were used in a few instances.

1. Axial parenchyma present at termini of growth rings; multiseriate rays 7–21 cells wide, mostly composed of procumbent cells. (Axial parenchyma present also in other forms: diffuse, diffuse-in-aggregates, and bands one to three cells in thickness. Pits on end walls of tracheids circular and multiseriate) *Pseudowintera*
1. No marginal axial parenchyma present. Mean width of multiseriate rays at widest point less than 7 cells; upright cells as abundant as procumbent cells or more abundant.

2. Axial parenchyma scarce, diffuse, and never in bands; cells of multiseriate rays predominantly upright. Mean ray width 2.1–4.1 cells wide at widest point. (Scalariform pitting on end walls of tracheids in years one to three, otherwise scalariform pitting present only after injury).
 3. Procumbent cells in rays absent during first three years, relatively uncommon later *Tasmannia*
 3. Procumbent cells in rays present in some rays during first three years, commoner later *Drimys*
2. Axial parenchyma diffuse, relatively common, sometimes also diffuse-in-aggregates and banded. Multiseriate rays wider at widest point. Scalariform pitting commonly present on overlap areas of tracheids of mature wood in some species.
 3. Scalariform pitting commonly present on overlap areas of tracheids in mature wood.
 4. Ethereal oil cells absent in rays *Belliolum*, *Bubbia* except *B. balansae*.
 4. Ethereal oil cells present in rays *Zygogynum*, *Bubbia balansae*
 3. Scalariform pitting not present in mature wood (ethereal oil cells present in rays) *Exospermum*

Details of wood anatomy do not enhance generic definitions very greatly compared to data from other disciplines, such as gross morphology of flowers. This is not unexpected, for wood anatomy modally tends to be somewhat more conservative than the characters commonly used for generic definition in dicotyledons at large. I believe that Ehrendorfer et al. (1968) and Smith (1969) are justified in recognizing *Tasmannia* as separate from *Drimys*, although Vink (1970) demurs (see Introduction). Praglowski (1979) has found minor but constant differences between the two genera with respect to pollen, and Bongers (1973) regards *Tasmannia* (as well as *Takhtajania*) as isolated in the family with respect to foliar characters.

Vink (1985) has made a case for grouping *Bubbia*, *Exospermum*, and *Zygogynum* (as *Zygogynum sensu lato*); he accepts Burt's (1936) union of *Belliolum* with *Bubbia*, and therefore Vink unites all four genera. On the basis of pollen, one could make a case for uniting *Pseudowintera* with these four genera, because it differs only in having slight endonexinous thickening near apertures. I mention this situation because *Pseudowintera* has not been discussed when proposals for union of genera have been made, but it is not as highly distinctive as this lack of mention might lead one to suppose.

Praglowski (1979) demonstrates many generic and specific characters within the family based on pollen, but in his key, *Tasmannia* and *Bubbia* key out together. This seems of interest because pollen is obviously rich in taxonomic criteria, but in this case, union of *Tasmannia* with *Drimys* on the one hand and union of *Belliolum*, *Bubbia*, *Exospermum*, and *Zygogynum* on the other is not supported. If degree of distinctiveness is stressed sufficiently, one could advocate a single polymorphic genus (perhaps not even excepting *Takhtajania*). However, I think that by using data from macromorphology (Smith 1943*a, b*; Vink 1970, 1977, 1983, 1985), pollen (Bailey and Nast 1943; Praglowski 1979), and leaf anatomy (Baranova 1972; Bongers 1973) in concert, the eight genera can be recognized. Even *Exospermum* can be recognized by a series of features (gynoecia not truly syncarpous; carpels with distinctive epidermis; flowers tetramerous [at least some parts, such as outer petals]; carpels with elongate stigmas; carpellary epidermis not smooth; pollen grains of tetrad not bulging but conforming to the sphaeroidal form of the entire tetrad; wood lacking scalariform perforation plates on end walls of tracheids when mature). Several authors have noted that distinctive species or

species groups can be recognized on the basis of one or more features, perhaps more readily than genera. Winteraceae may be a family in which genera are not separated by the degrees of discontinuity one could wish, but which are still worthy of recognition. Chemical data are likely to supply more criteria, and when we have such data, a better expression of the generic constitution of the family may be possible.

Phylogeny Within Winteraceae

Relatively few wood characters show phyletic trends within Winteraceae. One that seems worthy of consideration is the occurrence of scalariform pitting on end walls of tracheids. One can hypothesize that the ability to form scalariform pitting is primitive in dicotyledons, and that this ability has been translated into the scalariform perforation plates and scalariform lateral wall pitting of vessel elements; one need not hypothesize that a wood wholly composed of scalariformly pitted tracheids is primitive in dicotyledons, because such a wood would be excessively weak (Carlquist 1975). If these considerations are valid, then the degree to which scalariform pitting in tracheids has been modified in Winteraceae might be considered an indicator of phyletic specialization. In that case, the genera that form scalariform end-wall pitting on tracheids later in ontogeny (*Belliolum*, *Bubbia*, and *Zygogynum*) should be regarded as more primitive than those that do not have protracted ability to form scalariform pitting (*Drimys*, *Exospermum*, *Pseudowintera*, *Tasmannia*) except after cambial injury.

Ecological Aspects of Wood Anatomy

Woods of Winteraceae show adaptations to ecology well. Within the Old World genera other than *Exospermum*, *Pseudowintera*, and *Tasmannia*, canopy status of trees has been shown to correlate with production of scalariform end walls on tracheids. Another feature that relates to greater conductive capacity in the tree Winteraceae and is probably of greater significance than the scalariform pitting is the large diameter of tracheids (mostly more than 45 μm in tangential diameter) in *Belliolum*, *Bubbia*, *Exospermum*, and *Zygogynum*—genera that probably transpire more water because of greater warmth in their habitats. Tracheids relatively short and narrow (less than 45 μm in tangential diameter) correlate with colder habitats in species of *Drimys* (Carlquist 1988a), *Pseudowintera* (Patel 1974) and *Tasmannia*. One would not expect the *Pseudowintera* tracheids to be so narrow and short on the basis of wood sample size, for Patel studied unusually old stems; the relatively small size of tracheids in *Pseudowintera* probably relates to ecology as it does in the species of *Drimys* (*D. winteri* J. R. & G. Forst. var. *andina* Reiche, *D. winteri* var. *winteri*) and *Tasmannia* (*T. lanceolata*, *T. piperita* “*xerophila*”) from colder localities. Lewis and Tyree (1985) have found that in conifers, narrower tracheids embolize less readily than wider ones, which would be of value when tensions mount at times when ground is frozen but transpiration occurs on a sunny day. Resistance to embolism formation inherent in narrower tracheids doubtless also relates to growth ring formation in Winteraceae: not only is presence of growth rings proportional to cold in Winteraceae, but those Winteraceae from extreme localities have a greater proportion of each growth ring devoted to narrower latewood tracheids.

The distribution of vesturing (warts) on inner surfaces of tracheids in Winteraceae also shows perfect correlation with ecology. Warts were reported in tracheids of *Pseudowintera* (Meylan and Butterfield 1978) but vesturing is absent in tracheids of *Bubbia* (Carlquist 1983b) and other New Caledonian Winteraceae. I hypothesized (Carlquist 1983b) that the warts in *Pseudowintera* tracheids were related to resistance to cold, in that by increasing of water bonding to the tracheid surface, higher tensions (as in the abovementioned circumstance of transpiration while ground remains frozen) could be sustained without breakage of water columns. The distribution of vesturing in tracheids of *Drimys* and of *Tasmannia* correlates perfectly with this hypothesis.

The presence of helical thickenings in tracheids (*Pseudowintera*, all species; *Tasmannia insipida*) represents another feature with similar ecological significance (Carlquist 1982b). Helical thickenings and vesturing may represent independent responses to similar ecological conditions, judging from the distribution of these features in tracheids of Winteraceae as well as in vessels and tracheids of vessel-bearing dicotyledons. Helical thickenings characterize taxa in areas subject to drought, but also taxa in areas subject to appreciable cold—a physiological form of drought similar in the problems involved in maintenance of water columns in conductive cells (Carlquist 1982b).

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