

WOOD ANATOMY OF BELLIOLUM (WINTERACEAE) AND A NOTE ON FLOWERING

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THE GENUS *Belliolum* Van Tieghem occurs in the Solomon Islands and in New Caledonia (Smith, 1943). Of the Solomon Islands species, three were described by Smith (1942); a fourth, *B. haplopus* (Burr) A. C. Sm., was transferred from *Bubbia* Van Tieghem. Although four New Caledonian species of *Belliolum* were recognized by Van Tieghem (1900), all except *B. pancheri* (Baillon) Van Tieghem are known from inadequate material or are otherwise of uncertain status. This situation will doubtless be remedied by the studies of W. Vink, who has kindly determined my New Caledonian material as *B. pancheri*.

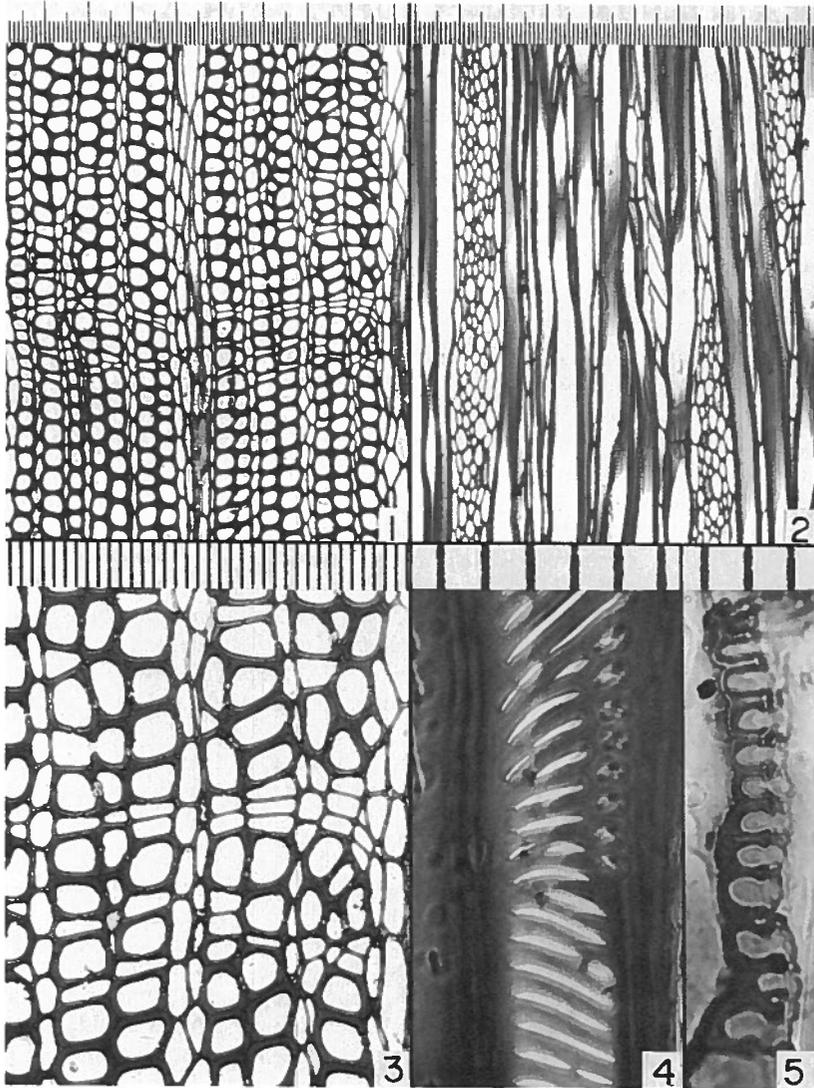
The present study gives comparative data on the wood of *Belliolum*, which has previously been known only from an illustration in Bailey (1944); his article contained a description of the wood of Winteraceae as a whole but no characterization of genera and species. The paucity of material available at that time rendered comparative studies within the family impossible. However, more abundant material now at hand renders comparative studies of winteraceous woods feasible. Patel (1974) produced an admirable monograph of the woods of the genus *Pseudowintera* Dandy, and a study of woods of *Zygodynum* Baillon (Carlquist, 1981) has been published. Comparative study of woods yields not merely taxonomic dividends, but a better understanding of wood in relation to ecology as well.

A few illustrations of flowers of *Belliolum pancheri* and brief descriptions of details of anthesis are appended to supplement the account of pollination of the Winteraceae given by Thien (1980).

MATERIALS AND METHODS

The wood samples of *Belliolum pancheri* analyzed were collected in mid-elevation forests of the Plateau de Dogny, New Caledonia, where the species grows as an understory tree on humid, shady slopes. Wood samples were prepared by removing the bark to facilitate drying. Samples could not be completely dried prior to shipping, so they were enclosed in plastic bags in which paraformaldehyde sufficient to retard fungal growth had been added. Upon receipt in Claremont, these wood samples were extracted, washed, and air dried. This method prevented the mold that would otherwise have grown. The wood sample of *B. pancheri* was 10 cm in diameter.

Wood samples of the Solomon Islands species were provided through the



FIGURES 1-5. *Belliolum haplopus* (MADw-22694), wood sections: 1, transverse section, illustrating long and short tangential parenchyma bands; 2, tangential section, showing thin-walled rays; 3, transverse section, tracheids wide and thin walled; 4, radial section, scalariform and transitional pitting on overlap areas of tracheid; 5, radial section, borders of pits on ray-cell walls. Scale: 1, 2, finest divisions = 10 μm ; 3-5, divisions = 10 μm .

TABLE 1. Features of the wood of *Belliolum*.

SPECIES AND COLLECTION	TRACHEID			RAY WIDTH†
	DIAMETER (μm)*	WALL THICKNESS (μm)	LENGTH (μm)	
<i>B. gracile</i> , MADw-29483	60	1.4	6290	6.2
<i>B. haplopus</i> , MADw-22694	56	4.8	4902	6.7
<i>B. haplopus</i> , MADw-29285	54	5.4	4570	6.3
<i>B. kajewskii</i> , MADw-29294	50	5.0	3958	6.2
<i>B. pancheri</i> , <i>Carlquist 15564</i>	42	7.7	4260	4.4

*Mean diameter at widest point.

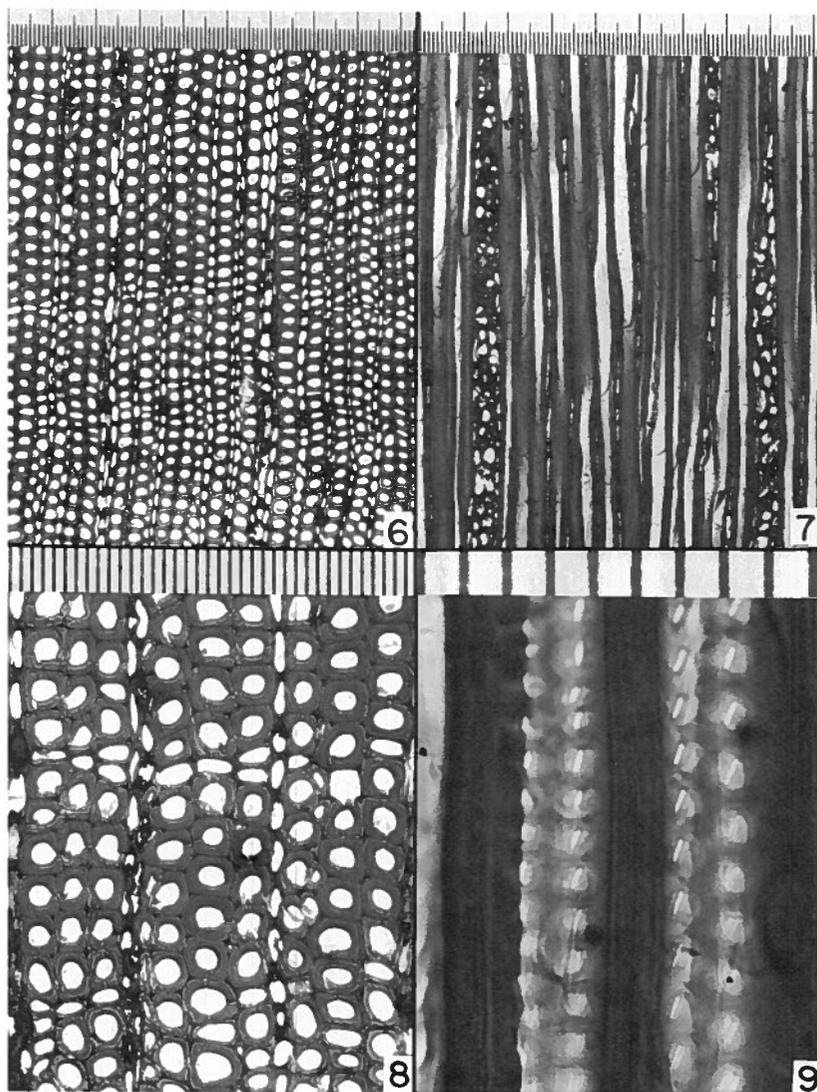
†Number of cells of multiseriate rays at widest point.

kindness of the Forest Products Laboratory of the U. S. Forest Service (MADw). The provenance of these samples is Bougainville Island, as follows: *Belliolum gracile* A. C. Sm., MADw-29483, R. Schodde & L. Craven 3718 (CANB), primary montane rain forest, 2700 ft (tree 15 m, DBH ca. 20 cm), S foothill slopes of Lake Loloru crater, ca. 17 mi N of Buin; *B. haplopus* (Burt) A. C. Sm., MADw-22694, no further locality, and MADw-29285, R. Schodde 261 (CANB), primary rain forest, ca. 2300 ft (small bushy tree ca. 7 m tall, DBH 6 cm), lower S slopes of Lake Loloru crater, ca. 14 mi N of Buin; *B. kajewskii* A. C. Sm., MADw-29294, L. A. Craven & R. Schodde 307 (CANB), primary montane rain forest with a number of small watercourses, ca. 2200 ft (tree 9 m tall, DBH 12 cm), lower S slopes of Lake Loloru crater, ca. 15 mi N of Buin. The identity of the specimen supplied as *B. gracile* is questionable because that species is not reported by Smith (1942) to occur on Bougainville Island, the provenance of the sample.

The wood sample of *Belliolum pancheri* was boiled and softened with ethylene diamine before being sectioned on a sliding microtome, according to the technique of Kukachka (1977). The wood of *B. pancheri* is moderately hard for a winteraceous wood. Woods of the Solomon Islands species, however, proved too soft for sectioning on a sliding microtome after being boiled (but without any treatment with ethylene diamine). Consequently, an alternative method was used for these species. They were treated with ethylene diamine according to Kukachka's method—but for one month. The woods were then washed, put through a tertiary butyl alcohol series (Johansen, 1940), embedded in paraffin, and sectioned at 15 μm . This novel use of ethylene diamine as a softening agent prior to paraffin sectioning yielded excellent results (see FIGURES 1-5) and is strongly recommended for woods that are extremely soft. All wood sections of *Belliolum* were stained with safranin, while macerations were prepared with Jeffrey's fluid and also stained with safranin.

ANATOMICAL DESCRIPTIONS

As shown in TABLE 1, quantitative data for the *Belliolum* collections were obtained on a limited number of wood features. The figures show that the



FIGURES 6-9. *Bellium pancheri* (Carlquist 15564, RSA), wood sections: 6, transverse section, showing bands of axial parenchyma; 7, tangential section, illustrating narrowness of rays and accumulation of resinlike materials; 8, transverse section, showing thickness of tracheid walls and bands of axial parenchyma; 9, radial section, showing biserial pits of overlap areas of tracheids. Scale: 6, 7, finest divisions = 10 μm ; 8, 9, divisions = 10 μm .

tracheids of *B. gracile* are thinner walled than those of other species. Compared to *B. pancheri* (FIGURE 8), the Solomon Islands species as a whole (e.g., *B. haplopus*, FIGURE 3) have much wider tracheids with thinner walls.

Overlap areas (end walls) of tracheids in some Winteraceae show patterns markedly different from those on lateral walls. Pitting is generally denser on end walls than on lateral walls, and in *Belliolum* can frequently be biseriate (as shown for *B. pancheri* in FIGURE 9) or triseriate. In addition, overlap areas of tracheids in all *Belliolum* species except *B. kajewskii* (which has only the biseriate and triseriate end-wall pitting mentioned above) also bear scalariform, scalariform transitional to opposite, and opposite pitting. The scalariform and scalariform transitional to opposite end-wall pitting types are shown here for *B. haplopus* (FIGURE 4).

Pits on lateral walls of tracheids of *Belliolum* are circular, about 7 μm in diameter, and with elliptic apertures like those of the pits shown in FIGURE 9. Patel (1974) has reported similar pits on *Pseudowintera* tracheids.

The helical thickenings and trabeculae reported by Patel (1974) for tracheids of *Pseudowintera* are not present in *Belliolum*. In groups with characteristics that reflect mesic environmental conditions, helical thickenings may relate to adaptation to areas where frost occurs. This tendency can be traced in such families as Illiciaceae, where such thickenings occur in vessel elements.

Axial parenchyma expressions vary within *Belliolum*. In *B. pancheri* short bands, usually a single cell thick, can be seen in addition to isolated diffuse cells (FIGURE 8). In *B. haplopus* bands are one to three cells thick, but diffuse cells are also present (FIGURE 3). In *B. gracile* and *B. kajewskii*, however, only diffuse cells, occasionally grouped two or three together, were observed. Although the range of axial parenchyma types is somewhat greater in *Zygogynum* (axial parenchyma is scarce in some collections of *Zygogynum*), the two genera are very similar. *Pseudowintera* also has the same range of axial parenchyma types as is found in *Belliolum* (Patel, 1974). Axial parenchyma strands are long in *Belliolum*, commonly ranging from 17 to 24 cells.

Rays vary relatively little in width in *Belliolum* (TABLE 1) but are appreciably narrower in *B. pancheri* (FIGURE 7) than in the Solomon Islands species such as *B. haplopus* (FIGURE 2). This cannot be related to stem size, for the stems of *B. pancheri* are comparable in size to those of *B. gracile* and *B. haplopus*. As judged from Patel's (1974) data, the rays are much narrower in *Belliolum* than in *Pseudowintera*, but are about the same as those in *Zygogynum*.

Ray cells have thicker walls in *Belliolum pancheri* than in the Solomon Islands species. In no species of *Belliolum* did rays contain the ethereal oil idioblasts or sclereids found in some species of *Zygogynum* (Carlquist, 1981). Ray cells, as in *Zygogynum* and *Pseudowintera* (Patel, 1974), often have borders (FIGURE 5). In none of the *Belliolum* species, however, are borders present in all ray cells. Resinlike deposits (FIGURE 5) could be observed in ray cells in all *Belliolum* species but are much more conspicuous in *B. pancheri* (FIGURES 6-8). As in other species of Winteraceae, ray histology corresponds to Kribs's (1935) Heterogeneous Type I.

Growth rings are absent in *Belliolum* but present in *Pseudowintera* (Patel, 1974) and other species of Winteraceae from markedly temperate climates.

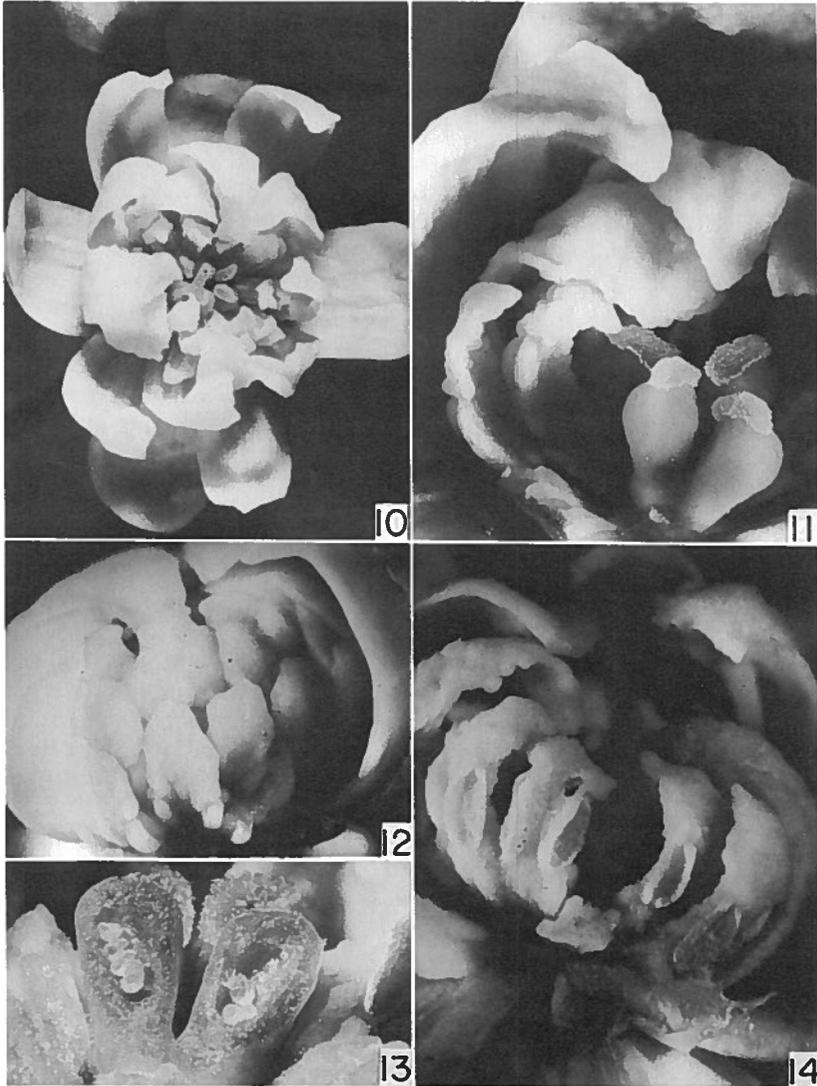
CONCLUSIONS

The species differ in tracheid length, probably in relation to size of plant. Bailey and Faull (1934) showed that tracheid length increases steadily with age in *Sequoia*, a pattern confirmed for other gymnosperms and for vesselless dicotyledons by Carlquist (1975). Tree (or shrub) size and trunk diameter appear to correlate with tracheid length. Tracheid diameter also appears to correlate with tracheid length in vesselless woods (Bannan, 1965). Compared to those of the other species studied here, the tracheids of *Belliolum gracile* are the longest (and widest); they were obtained from what is probably the largest tree (DBH = 20 cm) of the group. The longest tracheids (5580 μm) hitherto reported for vesselless angiosperms were from a sample of *Bubbia semecarpoides* that was 12 cm in diameter (Carlquist, 1975). Although trunk diameter and tracheid length are generally correlated (as they are in gymnosperms), the relation is not at all precise, as proved true in *Zygogynum* (Carlquist, 1981). Tracheids of *Agathis* are slightly longer than trunk diameter and plant height might suggest, but not greatly so (Carlquist, 1975). Stüss (1980), who attempts to use tracheid length as a phylogenetic indicator in plants with vesselless wood, seems unaware of correlations between plant height and size and tracheid length (and diameter).

The differentiation of overlap areas in the tracheids of Winteraceae was noted by Bailey (1944) and has been illustrated for *Bubbia semecarpoides* and *Zygogynum bicolor* (as "*Z. cf. pomiferum*") (Carlquist, 1975), as well as for three other species of *Zygogynum* (Carlquist, 1981). As in *Belliolum*, scalariform end-wall pitting is clearly present in some collections of *Zygogynum* but absent in others. In *Pseudowintera* it is present only on enlarged traumatic tracheids (Patel, 1974). The presence of these scalariform pits on end walls in winteraceous tracheids has been claimed to be a kind of prevessel specialization of the tracheid for maximizing conductive ability (Carlquist, 1975, 1981). The presence on the end wall of scalariform pits rather than merely crowded circular pits may also be seen as a remnant of the capability—present in primitive vesselless woods—to produce scalariform pitting.

The range of axial parenchyma of *Belliolum* (diffuse and diffuse-in-aggregates, plus bands up to three cells wide in some collections) resembles that in *Zygogynum*, as does the typical ray width. The ray cells, however, do not show the division of labor (ethereal oil cells, sclereids) in *Belliolum* that they do in *Zygogynum*. The wood of *Belliolum* is less similar to that of *Pseudowintera*, as described by Patel, and most closely resembles those of *Bubbia* and *Zygogynum*, two genera phyto-geographically closer to *Belliolum* than *Pseudowintera*. Some distinctive features of *Pseudowintera* (growth rings, helices in tracheids) are doubtless related to the strongly temperate climate of New Zealand, and thus the woods of *Bubbia*, *Belliolum*, and *Zygogynum* (which lack these features) reflect a mild and relatively seasonless climate.

On the basis of a limited number of samples, the Solomon Islands species of *Belliolum* differ from *B. pancheri* from New Caledonia. *Belliolum pancheri* has thicker-walled, narrower tracheids and narrower rays with thicker-walled cells than do the Solomon Islands species. Smith (1943) mentioned possible



FIGURES 10-14. *Belliolum pancheri*: 10, flower with stigmas receptive, $\times 2$; 11, portion of flower at anthesis, $\times 6$, dissected to show stamens (left) and carpels; 12, bud, dissected, $\times 4$, showing stamens just prior to anthesis; 13, two carpels in longitudinal section, $\times 7.5$, ovules in carpel at right displaced by sectioning; 14, dissection of flower at late anthesis, $\times 6$, showing anthers open.

sectional differences between the Solomon Islands and New Caledonian groups of species on the basis of carpel morphology; xylary characters might be taken into account in this connection. Bongers (1973) mentioned that stomata are much more deeply sunken in leaves of *B. crassifolium* (Baillon) Van Tieghem,

a New Caledonian species, than they are in leaves of *B. haplopus*, from the Solomon Islands.

A NOTE ON FLOWERING

Thien (1980) has described the stages of anthesis in various Winteraceae, including *Belliolum*. FIGURES 10–14, photographs of *B. pancheri* taken in New Caledonia, illustrate additional aspects.

The opening mechanism of the flower of *Belliolum* is hygrochastic, or dependent upon swelling of the flower rather than drying for opening to occur. Dissection of a bud (FIGURE 12) reveals petals and stamens to be relatively thin and smooth before anthesis. By the time when anthesis occurs, however, the petals and stamens have enlarged appreciably and have developed ridges and warts (FIGURES 10, 11, 14). The deltoid stamen tips may thus play a role in the opening of the flower. During early anthesis the deltoid tips of the innermost stamens often appear to fit between the stigmas, so that the stigmas are exposed with certainty. The stamens soon reflex away from the carpels, however. The anther sacs are more nearly lateral than adaxial, but may be described as extrorse-latorse (FIGURES 12, 14). Damage to anther tips by a chewing insect was noted (FIGURE 14). Sectioning the carpels (FIGURE 13) revealed that ovules are clearly positioned on the adaxial side of the locule, although the stigma extends down very little from the apex onto the adaxial face of the carpel. The stigmas would not be exposed at anthesis, because of carpel number and carpel crowding, if they were on adaxial faces; thus, one should expect the stigmas to be mostly apical in orientation in this genus. In the Solomon Islands species of *Belliolum* (Smith, 1942, 1943), the stigmas are even more clearly apical in nature than in *B. pancheri*, although the ovule position may be the same (Bailey & Nast, 1943).

LITERATURE CITED

- BAILEY, I. W. 1944. The comparative morphology of the Winteraceae. III. Wood. Jour. Arnold Arb. 25: 97–103.
- & A. F. FAULL. 1934. The cambium and its derivative tissues. IX. Structural variability in the redwood, *Sequoia sempervirens*, and its significance in the identification of fossil woods. Jour. Arnold Arb. 15: 233–254.
- & C. G. NAST. 1943. The comparative morphology of the Winteraceae. II. Carpels. Jour. Arnold Arb. 24: 472–481.
- BANNAN, M. W. 1965. The length, tangential diameter and length/width ratio of conifer tracheids. Canad. Jour. Bot. 43: 967–984.
- BONGERS, J. M. 1973. Epidermal leaf characters of the Winteraceae. Blumea 21: 381–411.
- CARLQUIST, S. 1975. Ecological strategies of xylem evolution. Univ. California Press, Berkeley and London.
- . 1981. Wood anatomy of *Zygogynum* (Winteraceae); field observations. Bull. Mus. Hist. Nat. Paris. Sect. B. Adansonia IV. 3: 281–292.
- JOHANSEN, D. A. 1940. Plant microtechnique. McGraw-Hill Book Co., New York.
- KRIBS, D. A. 1935. Salient lines of specialization in the wood rays of dicotyledons. Bot. Gaz. 96: 547–557.

- KUKACHKA, B. F. 1977. Sectioning refractory woods for anatomical studies. U. S. Forest Service Res. Note **FPL-0235**: 1-9.
- PATEL, R. N. 1974. Wood anatomy of the dicotyledons indigenous to New Zealand. 4. Winteraceae. *New Zealand Jour. Bot.* **12**: 19-32.
- SMITH, A. C. 1942. Studies of Papuasian plants. V. *Jour. Arnold Arb.* **23**: 417-443.
- . 1943. Taxonomic notes on the Old World species of Winteraceae. *Ibid.* **24**: 119-164.
- SÜSS, H. 1980. Über einiger holzanatomische Entwicklungsrichtungen bei Laubholzen. Pp. 19-27 in W. VENT, ed., *Beiträge zu Prinzipien und Problemen der Systematik und Evolutionsforschung aus dem Museum für Naturkunde. Humboldt University, Berlin.*
- THIEN, L. B. 1980. Patterns of pollination in the primitive angiosperms. *Biotropica* **12**: 1-13.
- TIEGHEM, P. VAN. 1900. Sur les dicotylédones du groupe des Homoxylées. *Jour. Bot. Morot* **14**: 259-297, 330-361.

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