WOOD ANATOMY OF HORSFIELDIA (MYRISTICACEAE)

by

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Summary
The wood of Horsfieldia is, on the whole, very homogeneous. The greatest differences observed are related to the relative age of the specimens. In contrast to the wood of Knema the mature wood of Horsfieldia lacks oil cells in the rays and has a predominance of simple perforation plates as well as shorter, wider vessel elements and wider rays. The homogeneity of the secondary xylem of Horsfieldia makes it of little taxonomic value on a specific level. Based on wood anatomy, Horsfieldia can be distinguished from the other three Asiatic genera of the Myristicaceae.

Introduction
Horsfieldia is the second largest genus of the nutmeg family with 70–80 species. Warburg (1897) recognized 52 species of Horsfieldia which he placed into 3 sections based upon characteristics of the staminate flowers. In his revision of the Malayan Myristicaceae, Sinclair (1958) felt that these sections were largely artificial and declined to place the Malayan species into sections. However, Sinclair did use the perianth structure to tentatively divide the genus into two sections depending upon whether the perianth was bivalved or trivalved. The only survey of myristaceous wood (Garratt, 1933) was based on a small number of specimens and the descriptions were rather general. Siddiqi and Wilson (1974) have provided a comprehensive study of the genus Knema. Siddiqi and Wilson were unable to weigh intra-family relationships due to the lack of information on the other genera. From available information they judged Knema to be more similar to Myristica than Gymnacranthera and supported Garratt’s conclusion that Horsfieldia stands apart from the other three southeast Asia genera. Hopefully this study will help clarify the position and relationships of Horsfieldia within the Myristicaceae, as well as determine whether there is any anatomical support for the division of the genus into sections.

Methods and Materials
Fifty specimens representing 31 species of Horsfieldia were examined. Collections are cited according to the recommendations by Stern and Chambers (1960). This sample included 23 of Warburg’s (1897) original 52 species and represented all three sections of the genus (Table 1). Sections Pyrrhosa and Irya are each subdivided on the basis of perianth lobing, bivalved or trivalved.

<table>
<thead>
<tr>
<th>Section</th>
<th>Species</th>
</tr>
</thead>
<tbody>
<tr>
<td>Pyrrhosa</td>
<td>H. ardisifolia, H. novae-lauenburgiae, H. polyantha, H. subtilis, H. tuberculata</td>
</tr>
<tr>
<td>Eupyrhosa</td>
<td>H. amygdalina, H. glabra, H. macrocoma, H. motleyi, H. superba, H. tomentosa</td>
</tr>
<tr>
<td>Irya</td>
<td>H. irya, H. crassifolia, H. sucosa</td>
</tr>
<tr>
<td>Euiya</td>
<td>H. brachiata, H. lemanniana, H. subglobosa</td>
</tr>
<tr>
<td>Trivalve</td>
<td>H. iryaghedhi, H. sylvestris</td>
</tr>
</tbody>
</table>

Table 1. Sections of the genus Horsfieldia after Warburg (1897)

Species examined
The wood blocks were prepared and sectioned using standard techniques. The sections were stained with modified Heidenhain's hematoxylin (Wilson & Shutt, 1957) and iron-alum safranin (Gray & Pickle, 1956). Small samples were macerated with Jeffrey's fluid (Johansen, 1940). The macerated wood was stained with iron-alum safranin and dehydrated with an acetone series to prevent excessive destaining. While mounting the tissue a binocular dissection microscope was used to help isolate large numbers of vessel elements from the numerous surrounding fibres. The isolated vessel elements were mounted on a single slide. The additional preparation time was more than adequately compensated for when 25–75 vessel elements could be easily observed without a lengthy search of numerous slides. This is especially useful in a wood with relatively few vessel elements.

The measurement data for each anatomical parameter were accumulated from a randomly selected sample of 30 per specimen. The angle of the end wall of vessel elements was measured from the vertical with a transverse end wall having an angle of 90°. Descriptive terminology follows the recommendations of the Committee of Nomenclature, International Association of Wood Anatomists (1964). Size classifications conform to the recommendations of Chattaway (1932) and the Committee on the Standardization of Terms of Cell Size, International Association of Wood Anatomists (1937, 1939).


Results

There is a great deal of similarity among the various specimens of Horsfieldia that were examined. The greatest differences were directly related to the relative ages of the wood specimens. The wood specimens obtained from various sources represent either young stems or twigs, which are easily identified, or blocks of wood, which because of their parallel, non-converging rays must have come from peripheral portions of larger stems or branches. While the maturity of the latter specimens is still open to question, the obvious homogeneity of these wood specimens is sufficient rational for presenting the observations for twig specimens and the mature specimens separately. In addition, anatomists are often confronted with the task of attempting an identification or comparison with little more than a twig from an herbarium specimen. Descriptions of mature wood are of little use in comparisons with such specimens. The age determination of the specimens is indicated in the list of specimens examined.

Wood from Twig Specimens

There were 15 specimens of Horsfieldia wood from young twigs examined. These specimens represent the first 1–1.5 cm of secondary xylem formed.

Vessels – The vessels are usually very numerous, and diffusely distributed in pairs (58%), solitarily (31%), or in short radial chains (11%) (Table 2, Fig. 1). Vessel element size is moderately small to medium in diameter, and medium to moderately long, with a length to width.
Table 2. Summary of anatomical features of the wood of *Horsfieldia*

<table>
<thead>
<tr>
<th>Anatomical features</th>
<th>Young</th>
<th>Mature</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Mean ± 1 standard deviation</td>
<td>Mean ± 1 standard deviation</td>
</tr>
<tr>
<td>Vessels</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Number/mm²</td>
<td>18.9 ± 1.41</td>
<td>4.1 ± 2.0</td>
</tr>
<tr>
<td>Distribution</td>
<td>Diffuse</td>
<td>Diffuse</td>
</tr>
<tr>
<td>% Solitary</td>
<td>58.1 ± 12.5</td>
<td>51.1 ± 12.2</td>
</tr>
<tr>
<td>% Pairs</td>
<td>30.6 ± 9.2</td>
<td>37.6 ± 11.5</td>
</tr>
<tr>
<td>% Chains</td>
<td>11.3 ± 4.7</td>
<td>11.3 ± 4.1</td>
</tr>
<tr>
<td>Diameter</td>
<td>0.08 ± 0.02 mm</td>
<td>0.149 ± 0.003 mm</td>
</tr>
<tr>
<td>Length</td>
<td>0.84 ± 0.22 mm</td>
<td>1.02 ± 0.20 mm</td>
</tr>
<tr>
<td>Length/diameter ratio</td>
<td>10.4 ± 2.0</td>
<td>6.8 ± 1.3</td>
</tr>
<tr>
<td>% Simple perforation plates</td>
<td>58.1 ± 23.1</td>
<td>87.3 ± 9.7</td>
</tr>
<tr>
<td>End wall angle (degrees)</td>
<td>34.1 ± 3.6</td>
<td>53.6 ± 14.5</td>
</tr>
<tr>
<td>Intervascular pitting</td>
<td>Opposite-Alternate</td>
<td>Opposite-Alternate</td>
</tr>
<tr>
<td>Libriform fibres</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Length</td>
<td>1.14 ± 0.18 mm</td>
<td>1.61 ± 0.26 mm</td>
</tr>
<tr>
<td>Axial parenchyma</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Apotracheal</td>
<td>Banded</td>
<td>Banded</td>
</tr>
<tr>
<td>Paratracheal</td>
<td>Scanty</td>
<td>Scanty</td>
</tr>
<tr>
<td>Radial parenchyma</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Rays/linear mm</td>
<td>11.3 ± 1.6</td>
<td>8.1 ± 1.5</td>
</tr>
<tr>
<td>Kribs’ ray type</td>
<td>Heterogeneous I–IIA</td>
<td>Heterogeneous IIB</td>
</tr>
<tr>
<td>Ray width</td>
<td>0.025 ± 0.008 mm</td>
<td>0.040 ± 0.013 mm</td>
</tr>
<tr>
<td>Uniseriate ray height</td>
<td>0.47 ± 0.25 mm</td>
<td>0.29 ± 0.14 mm</td>
</tr>
<tr>
<td>Biseriate ray height</td>
<td>0.72 ± 0.41 mm</td>
<td>0.89 ± 0.39 mm</td>
</tr>
</tbody>
</table>

ratio of 10.4:1 (Table 2). In transverse section the shapes are broadly oval to slightly oblong, often with slightly flattened radial sides (Fig. 1, 10). Perforation plates are a mixture of simple pores (58%) (Fig. 2) and scalariform plates with few bars (1–10) (Fig. 3), often with only 1 or 2 vestigial bars (Fig. 4). End wall inclination is variable from almost vertical, 5°, to a more common 20–50° (Table 2). The intervascular pits are full-bordered, slightly elongate and arranged in opposite (Fig. 5) to almost alternate, rarely transitional patterns.

*Rays* — There is a mixture of uniseriate and biseriate rays, very numerous and very fine in width (Table 2, Fig. 6, 7). Uniseriate ray height is extremely low and biseriate ray height is very low. The biseriate rays often have long uniseriate wings and intermittent uniseriate portions in the middle (Fig. 6, 7). All the specimens have heterogeneous rays. The biseriate rays show distinct vertically elongate marginal cells and radially elongate or square cells in the biseriate portion (Fig. 8). The uniseriate rays are composed of either all vertically elongate cells with some squarish cells (Fig. 9), or rarely mixed with rows of radially elongate cells. The rays were classified as Kribs’ types heterogeneous I and IIA (Kribs, 1935). All specimens have tanniferous tubules in their rays. These are recognized by their lack of end walls and their darkly-coloured contents.

*Axial parenchyma* — Apotracheal parenchyma when present is usually in tangential bands, often forming concentric lines or bands 1–5 cells wide, but is absent in 2 specimens (Fig. 1). Little or no differences in fibre cell size and wall thickness are on either side of the bands. The spacing of the bands is irregular, varying from immediately adjacent to widely spaced. Paratracheal parenchyma is very scanty, often consisting of a single cell or two found on either or both tangential sides of a vessel element or a vessel pair (Fig. 10).

*Fibres* — These are exclusively libriform fibres which are medium-sized in length with thin walls (Fig. 10). The minute pits are located primarily on radial walls, and are simple or have minute borders and a slit-like aperture. In transverse section the fibres form straight radial files (Fig. 1, 10).

*Wood from Mature Specimens* — The 35 specimens examined here represent mature portions of branches or stems. While a few of the mature specimens display some
Generally within the young and mature specimens, the majority of the specimens form a very homogeneous aggregation (Table 2).

**Vessels** – Generally the few vessels are diffusely distributed, solitary (51%), in pairs (38%), or in short radial chains (11%) (Table 2, Fig. 11). Their size is medium to moderately large in diameter and they are moderately long with an average length to width ratio 7:1 with the exception of one specimen (*H. confertiflora* CLPw-22551), which due to relatively narrow vessels has a ratio of 11:1. In transverse section the shapes are oval to broadly oval and often with flattened tangential sides (Fig. 11, 20). Perforation plates have a mixture of simple pores (82%) (Fig. 12) and scalariform plates with few bars (1–10), most often with only 1 or 2 vestigial bars at the upper or lower edge of the pore (Fig. 13). End wall inclinations vary from 10–90° (Table 2). Intervascular pits are elongate and full bordered, sometimes arranged in an opposite pattern, but most approach an alternate pattern (Fig. 15).

**Rays** – The moderately numerous to numerous rays are moderately fine to medium in width (Table 2, Fig. 16, 17). The uniseriate ray height is extremely low and the biseriate ray height is very low to low (Table 2). Uniseriate rays are few in number usually less than 4% of the sample (Fig. 16). The wider biseriate rays are often multiseral in the middle portions (Fig. 14, 16, 17), to a true multiseral condition noted in *H. subtilis* WIBw-10153 which has rays 4–5 cells wide. Both biseriate and multiseral rays usually have 1 or 2 rows of uniseriate wing cells which are square or vertically elongate (Fig. 17, 18, 19). Uniseriate rays have mixed rows of radially and vertically elongated or square cells. The rays of all specimens are classified as Kribs’ type heterogeneous IIB (Kribs, 1935). All specimens contain tanniferous tubules in the rays, where they are easily recognized in both tangential (Fig. 14) and radial (Fig. 18) sections by their darkly-coloured contents.

**Axial parenchyma** – The apotracheal parenchyma is usually present in moderate to abundant amounts in tangential bands forming concentric lines 1–10 cells wide or intermittent lines 1–4 cells wide (Fig. 11). *H. confertiflora* CLPw-22551 lacks apotracheal parenchyma. The banded parenchyma is widely spaced or immediately adjacent separated by only a few rows of fibres. Generally there are no differences in fibre cell size and wall thickness on either side of the parenchyma bands. Paratracheal parenchyma is very scanty, usually consisting of only a few cells often on the tangential sides of the vessels (Fig. 20). Occasionally there is an almost complete vessel sheath, but this is associated with the proliferation of cells from adjacent rays and parenchyma bands.

**Fibres** – These are exclusively libriform fibres which are of medium to moderate length with thin walls (Fig. 20). The minute pits less than 3 μm diameter with simple or minute borders and slit-like apertures, are located primarily on the radial walls. In transverse section the libriform fibres form straight radial files (Fig. 11, 20).

**Discussion**

The most outstanding feature of the secondary xylem of *Horsfieldia* is the extraordinary degree of similarity the wood specimens exhibit, even though the collection represents specimens of various species and different geographic locations. Those specimens which are

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Fig. 1–10. Wood from twigs of *Horsfieldia*. — 1: *H. subglobosa* USw-29280. Diffuse vessel elements arranged solitarily, in pairs, or in short radial chains. Note the almost complete absence of axial parenchyma and the straight radial files of fibres; x 16. — 2: *H. polyspernula* USw-29412. A vessel element showing a simple perforation on a long-slanted end wall. Note the long tail. Maceration; x 110. — 3: *H. subglobosa* USw-29280. A scalariform perforation plate located on a steeply inclined end wall. Some fungal hyphae are present; x 250. — 4: *H. brachiatna* USw-28587. A vessel element showing 2 scalariform perforation plates, with 1 and 2 vestigial bars respectively. Maceration; x 80. — 5–7: *H. tomentosa* USw-27588. 5: Intervascular pitting arranged in an opposite to alternate pattern; x 380. 6: Tangential section showing taller and shorter uniseriate rays and a few biseriate rays with long uniseriate wings and often with intermittent uniseriate portions (arrow); x 40. 7: Tangential section showing uniseriate rays and biseriate rays with long uniseriate wings and often with intermittent uniseriate portions (arrow); x 100. — 8: *H. brachiatna* USw-28587. A biseriate ray showing 2–3 rows of uniseriate, vertically elongate cells on either side; x 70. — 9: *H. tomentosa* USw-27588. A uniseriate ray showing all vertically elongate cells; x 80. — 10: *H. polyspernula* USw-29412. Transverse section showing oval to oblong vessels with scanty paratracheal parenchyma (arrows). Note the straight files of fibres; x 65.
known to be from twigs varied considerably from those specimens which represent the more mature wood (Table 2). This is not surprising since some of the inherent anatomical variation of wood relates to the relative maturity of the specimens (Rendle & Clarke, 1934). It is hoped that reporting the wood structure of twigs separately may be of use to anyone attempting a comparison with a juvenile vegetative specimen. Further, it should be noted, that the general description of the wood of *Horsfieldia* would be somewhat altered by including the numerical data from twig specimens.

The mature wood of *Horsfieldia* appears to be of moderate specialization. The only characters which can be considered primitive are the diffuse-porous vessels, with uniformly thin walls and full-bordered, slightly elongate pits (Tippo, 1946). The majority of the characters of *Horsfieldia* wood appear to be of moderate specialization: medium to moderately long vessel members with a medium to moderately large diameter, oval to broad oval in shape; pitting primarily opposite to alternate, predominantly simple perforation plates, and moderately to slightly inclined end walls; short to medium-sized libriform fibres; Kribs' type heterogeneous IIB rays with few extremely low uniseriate rays; narrow tangential bands of apotracheal parenchyma and scanty paratracheal parenchyma (Kribs, 1937; Tippo, 1946).

Garratt's (1933) survey of myristicaceous wood and Siddiqi and Wilson's (1974) study of the wood of *Knema* are the only bases for comparison within the family. Contrary to Garratt's generalized description of the wood of *Horsfieldia*, the specimens that we examined have only medium to moderately long vessel members, and while uniseriate rays are always present, they usually comprise less than 4% of the random samples measured. Garratt also described growth rings in several specimens of *Horsfieldia*. Only occasionally are there differences in libriform fibre size and wall thickness associated with the banded parenchyma and while this may be due to periodic growth, well-defined growth rings do not exist in *Horsfieldia*. The wood of *Knema* was reported by Siddiqi and Wilson (1974) as frequently having patterns of banded parenchyma and fibres that were indicative of periodic growth.

While oil cells have been reported in the rays of *Knema*, *Myristica* and *Virola* (Garratt, 1933; Siddiqi & Wilson, 1974), no oil cells were found in *Horsfieldia*. Oil cells, however, were not found in all species of *Knema* (Siddiqi & Wilson, 1974) and may not be a universal feature in the rays of either *Myristica* or *Virola*. One specimen examined during this study, *H. brachiate* (USW-30850) was found to have prominent oil cells in its rays and all the perforation plates were scalariform. This specimen also had longer, narrower vessel elements (length to width ratio of 9.7) than *Horsfieldia* (6.8 average, Table 2). In contrast to the intervascular pitting of *Horsfieldia* which mostly approached an alternate pattern, this specimen had pitting patterns that were sometimes scalariform, mostly transitional, and sometimes opposite. The specimen was similar to reference specimens of *Knema* with regard to vessel element size, pitting patterns, scalariform perforation plates, and oil cells, and was probably incorrectly identified as *Horsfieldia*. While the gross appearance of the wood of the four Asian genera is quite similar and no

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Fig. 11-20. Mature wood of *Horsfieldia*. — 11: *H. polysphera* USW-30853. Diffuse vessels arranged solitarily and in pairs, with banded apotracheal parenchyma. Note the straight files of fibres and the lack of any differences in cell size and wall thickness indicative of periodic growth; x 28.—12–13: *H. polyantha* WIBw-9064. 12: A vessel element showing a simple perforation and a small, short tail. Maceration; x 150. 13: A vessel element showing a scalariform perforation plate with only 1 vestigial bar (arrow). End wall inclination is approx. 60°. Maceration; x 150. — 14: *H. acuminata* CLPw-29176. A triseriate ray showing centrally and laterally located tanniniferous tubules; x 240. — 15–16: *H. polyantha* WIBw-9064. 15: Intervascular pitting arranged in a pattern approaching alternate; x 380. 16: Tall and short biseriate rays showing occasional triseriate portions. A few low uniseriate rays are present (arrows); x 40. — 17: *H. sylvestris* BZFw-29884. Biseriate rays showing 1 or 2 rows of uniseriate, vertically elongate wing cells. Note the single low uniseriate ray and the uniseriate portion of the biseriate ray (arrow); x 100. — 18: *H. polyantha* WIBw-9064. A biseriate ray showing 2 tanniniferous tubules (arrows); x 40. — 19: *H. confertiflora* CLPw-22551. A biseriate ray showing 2 rows of uniseriate wing cells, the outermost composed of vertically elongated cells, and the innermost composed of square or radially elongated cells. Maceration; x 100. — 20: *H. polysphera* USW-30853. A vessel showing association with ray parenchyma and 2 paratracheal parenchyma cells located on the tangential sides (arrows); x 130.
single feature can be used to distinguish *Horsfeldia* from the others, the combination of characteristics described above is sufficient to separate the mature wood of *Horsfeldia* from that of *Knema*, *Myristica* and *Gymnacranthera*. In that regard we support Garratt's (1933) conclusion that *Horsfeldia* is rather distinctly set off from the other three Asian genera.

Garratt (1933) also concluded that the wood of all four Asian genera was more similar to each other than to any other genera in the family. This analysis is questionable since Garratt (1933) also found predominantly simple perforation plates in *Brochoneura*, *Cephalosphaera*, *Osteophloeum*, and *Pycnanthus* and some specimens with rays wider than biseriate rays, 3 to 6 cells wide in *Compsoneura*, *Knema*, *Pycnanthus*, and *Staudtia*.

On a specific level the characters of the secondary xylem of *Horsfeldia* are of little taxonomic value. This is not completely unexpected since comparative studies of wood on taxa smaller than families have rarely produced characters of significance on a species level, e.g., Heimsch (1940), Heimsch and Wetmore (1939), Siddiqi and Wilson (1974). Siddiqi and Wilson found no support for Sinclair's (1961) subdivision of *Knema* into seven sections, and likewise this study lends no support to either Warburg's (1897) division of the genus (Table 1) or Sinclair's (1958) tentative subdivision of *Horsfeldia* into two sections on the basis of perianth lobing.

The intra- and inter-family relationships of the Myristicaceae are still somewhat in doubt. Although the Myristicaceae has been regarded as a distinct and somewhat isolated family (Smith & Wodehouse, 1937; Cronquist, 1968) it has usually been associated with the ranalean complex. At various times the Myristicaceae has been allied to 10–12 families of the Ranales and Laurales. Many studies have provided information that supports the position of the Myristicaceae in the woody Ranales and supports its relationship to the Annonaceae and Canellaceae (Armstrong & Wilson, 1978; Behnke, 1971; Ehrendorfer et al., 1968; Vander Wyk & Canright, 1956; Walker, 1971, 1972; and Wilson & Maculans, 1967). This study is in basic agreement with the determinations of Vander Wyk and Canright (1956) which indicated similarities between the wood of the Annonaceae and the Myristicaceae especially as represented by *Horsfeldia*. A more comprehensive study of Myristicaceae should be undertaken to better determine the relationships of the genera and the family.

References


ASSOCIATION AFFAIRS

(see also pages 86 & 143)

Report from the IAWA Business Meeting in Oxford

During the IUFRO Division V Meeting in Oxford from April 8–16, 1980, an IAWA Business Meeting was held in the Commonwealth Forestry Institute on Monday evening April 14. On the agenda were current Association affairs such as the IAWA Bulletin, finances, future of the Executive Office and future IAWA meetings. During discussions on these topics no changes in current policy of the IAWA Council were advocated.

The main part of the evening was devoted to the subject of computerized wood identification. A progress report on the work of the IAWA Committee on the Standardization of Characters suitable for Computerized Hardwood Identification by P. Baas and R.B. Miller was followed by lively discussions. Roughly the opinions expressed can be classified into three groups: 1. opposed to computerized wood identification for various reasons (mainly in view of high cost in terms of money and labour to complete a comprehensive data matrix); 2. in favour of developing computerized identification and data storage, directly using available information from marginally perforated card keys; 3. in favour of computerized identification and making full use of the potential of the computer by adopting a comprehensive coding system for dichotomous, multistate and quantitative characters, as developed in Madison by R.B. Miller. No votes were cast or final decisions taken, but the Committee can deduce a valuable compromise from the Oxford discussions by presenting a standard list of wood characters independently of cross references to different possible coding systems (see also below).

IAWA is indebted to the IUFRO Conference organizers for offering facilities to IAWA during this well-attended and successful meeting.

Pieter Baas

IAWA Committee for the Standardization of Characters used in Computerized Hardwood Identification

Following the discussions on computerized wood identification initiated by Dr. R.B. Miller at the Amsterdam Wood Anatomy Congress in 1979, the IAWA Council has installed a Committee which works towards a standard list of characters suitable for computerized hardwood identification. The Committee is co-ordinated by R.B. Miller (Madison) and P. Baas (Leiden). Members are J.D. Brazier (UK), H. Gottwald (FRG), W.E. Hillis (Australia), J. Koek-Noorman (The Netherlands), C. Manieri (Brazil), A. Mariaux (France) and C.H. de Zeeuw (USA). A first draft by R.B. Miller has been a starting point for the Committee to work on; a second, amended draft is nearly finished and will be available on request by IAWA Members for comment or criticism before a final version will be officially published. The next IAWA Bulletin will contain an explanatory paper on computerized identification by Dr. R.B. Miller. See also report on the Oxford meeting.