

WOOD ANATOMY OF MYROTHAMNUS FLABELLIFOLIA  
(MYROTHAMNACEAE) AND THE PROBLEM OF  
MULTIPERFORATE PERFORATION PLATES

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THE WOOD ANATOMY of *Myrothamnus flabellifolia* Welw. has been briefly described by Tippe (1938). The purpose of the present study is to expand Tippe's description, to present illustrations of the wood anatomy of this species for the first time, to interpret ecologically the peculiarities of this wood, and to offer some preliminary comments on possible relationships of Myrothamnaceae. The family consists of two species: *M. moschatus* Baillon, of Madagascar, and *M. flabellifolia*, which ranges from Angola and Southwest Africa to the Transvaal (Niedenzu & Engler, 1930; Zemke, 1939). *Myrothamnus moschatus* has never been studied anatomically, and unfortunately material of this species was not available. *Myrothamnus flabellifolia* has been studied for its vegetative anatomy (Grundell, 1933; Zemke, 1939) because of its notable leaves, which expand and contract markedly with water availability. The xeromorphic habit of *M. flabellifolia* may be somewhat deceptive. Although it does grow in winter-dry areas, it tends to occur in crevices of rocky outcrops. Where I observed and collected this shrub in the Magaliesberg just north of Pretoria, Republic of South Africa, the sites it occupied were rock crevices that also proved to be seeps, suggesting attenuated availability of water. Thus *Myrothamnus* can be considered to have both xeric and mesic aspects in its niche preferences, a fact of significance with respect to wood anatomy.

Other features of *Myrothamnus* wood needing explanation include such peculiarities as the type of multiperforate perforation plates, the absence of axial parenchyma, and the nature of the ray histology. Some of these peculiarities may be related to limited accumulation of secondary xylem. Although *M. flabellifolia* is a shrub, stems never become large without splitting into several segments, a habit typical of desert shrubs from various parts of the world. Because secondary xylem accumulation is limited, and because wood anatomy by itself yields restricted data with respect to systematics, the sum of the wood characteristics may not provide much information of use in phylogenetic comparisons. Often the chief dividend of studies in wood anatomy may be an understanding of the ecological and habital characteristics of a species (Carlquist, 1975). Phylogenists can be said to agree generally on the phyletic placement of the Myrothamnaceae, but they differ to various degrees concerning the family's placement in particular orders or its sequence in phylogenies.

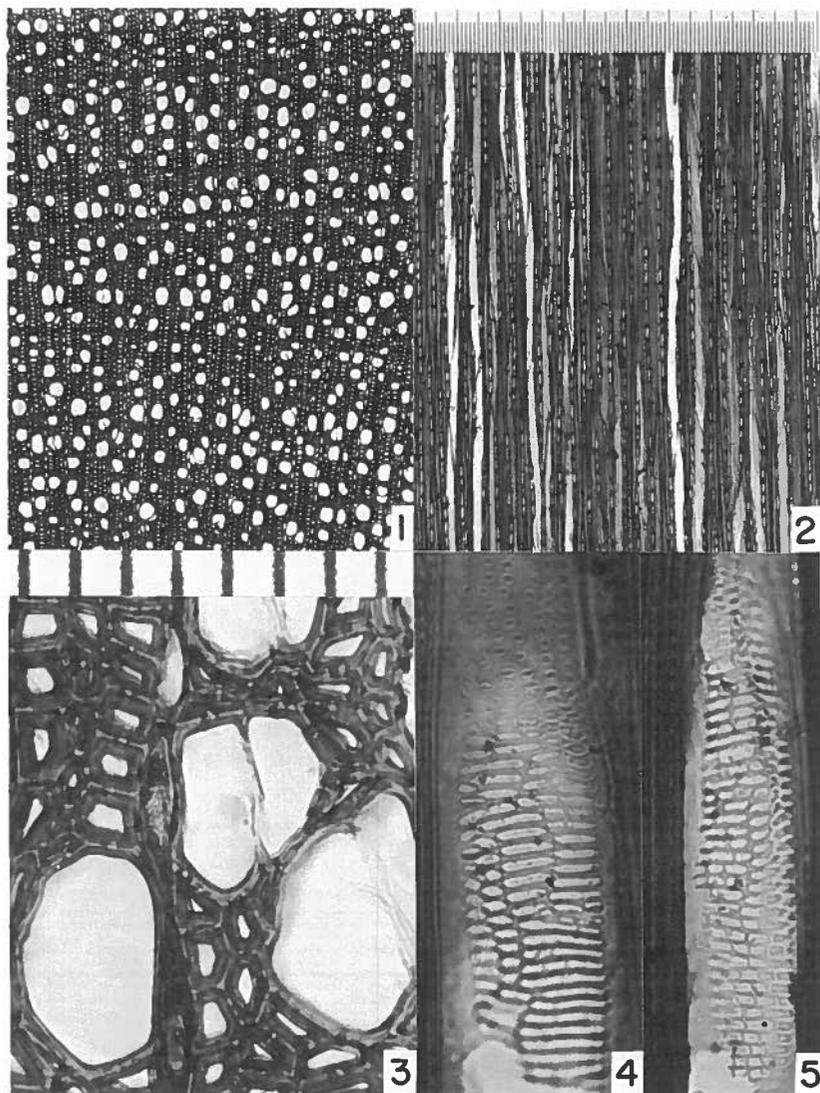
## MATERIALS AND METHODS

Wood samples of *Myrothamnus flabellifolia* were collected in the field and dried; the specimen *Carlquist 5133* (RSA, A, and other herbaria) documents this Magaliesberg population. Wood of the largest stem available (ca. 3 cm. in diameter) was sectioned, and the sections were stained with safranin. Macerations were also prepared from this stem, as well as from a large root and a twig, by means of Jeffrey's fluid; a safranin stain was used. Unfortunately, circumstances did not permit liquid preservation of wood samples, a procedure desirable in view of the possible nucleated nature of tracheids. For quantitative data, 50 measurements per feature were obtained.

## ANATOMICAL OBSERVATIONS

**Description.** The following description is based on stem material, with data from the root and twig samples added where noted.

Woody cylinder furrowed at periphery. Growth rings inconspicuous (FIGURE 1) but definitely present. Vessels mostly solitary (FIGURE 1), the average number of vessels per group 1.05. Mean vessel diameter 36  $\mu\text{m}$ . Mean vessel-element length 534  $\mu\text{m}$ . in stem, 621  $\mu\text{m}$ . in twig, 613  $\mu\text{m}$ . in root. Vessels angular in transectional outline (FIGURE 3). Perforation plates of a modified scalariform type (FIGURES 4 & 5), somewhat reminiscent of radially very much widened pits and thus networklike, sometimes with thin strands of wall material interconnecting the bars (FIGURE 5). Range and average number of bars not determinable because of the networklike pattern. Bars at least sometimes with inconspicuous vestigial borders. Lateral wall pits of vessels circular in outline (FIGURE 4, above), sometimes opposite but elsewhere so sparse that the pattern cannot be termed alternate or opposite. All imperforate elements tracheids, with pits fully bordered and apertures circular to elliptical, the longest axis still shorter than the diameter of the pit cavity. Apertures sometimes appearing to lengthen by the fracturing of the apparently gelatinous inner secondary wall. Marked shrinkage patterns indicative of gelatinous nature of tracheids not evident, but staining reactions (FIGURE 3) of inner secondary wall layers different from those of outer layers. Tracheids often rectangular in transectional outline (FIGURE 1; FIGURE 3, upper left), tangentially up to twice as wide as radially (often 16  $\mu\text{m}$ .  $\times$  9  $\mu\text{m}$ . or 16  $\mu\text{m}$ .  $\times$  8  $\mu\text{m}$ .). Pits in more than a single series on the walls that are tangentially widened. Mean tracheid length in stem 533  $\mu\text{m}$ .; in twig 633  $\mu\text{m}$ .; in root 655  $\mu\text{m}$ . Mean tracheid-wall thickness 2.3  $\mu\text{m}$ . Axial parenchyma absent. Rays exclusively uniseriate (FIGURE 2), composed mostly of erect cells, with a few square cells and virtually no procumbent cells (if present, only slightly wider radially than vertically). Mean ray height 427  $\mu\text{m}$ . Crystals absent. Amorphous deposits (tending to appear threadlike or webby) present in ray cells and tracheids; presence of such deposits uniform in both ray cells and tracheids,



FIGURES 1-5. Wood sections of *Myrothamnus flabellifolia*: 1, transection, showing numerous but inconspicuous growth rings; 2, tangential section — note numerous uniseriate rays; 3, portion of transection, the walls of tracheids showing darker-staining inner wall layer; 4 & 5, portions of perforation plates from radial sections: 4, sparse lateral-wall pitting visible above perforation plate; 5, perforation plate with tenuous interconnections of strands between bars. Magnifications indicated by photographs of stage micrometer enlarged at same scale as applicable figures: 1 & 2, scale above FIGURE 2 (finest divisions = 10  $\mu\text{m}$ .); 3-5, scale above FIGURE 3 (divisions = 10  $\mu\text{m}$ .).

suggesting that tracheids may have a longevity like that of ray cells and may therefore be nucleated.

**Element length.** Tippo (1938) found the mean vessel-element length in his material to be 905  $\mu\text{m}$ ., which is appreciably longer than the mean in my material. The provenance of Tippo's specimen is not reported, but different populations and different portions of a plant can easily yield differences in element length of this magnitude.

The ratio of mean tracheid length to mean vessel-element length for any given wood sample is of interest, for ratios only a little greater than 1.00 indicate the primitiveness of a wood (a sort of measure of minimal differentiation between mechanical and conductive systems in wood), while ratios may range as high as 8.00 in specialized woods (Carlquist, 1975). In my data above, the ratio would be 0.99 in the stem, 1.07 in the root, and 1.02 in the twig. That vessel elements should on the average be shorter than tracheids in a given wood sample is an anomaly seemingly contrary to the commonly held notion that imperforate elements are at least a little longer than the vessel elements they accompany. I have noted (1975) an exception to the low ratio as indicator of primitiveness in *Leitneria floridana*, which has specialized wood with libriform fibers only slightly longer than vessel elements. This I ascribed to the limited stem size in *Leitneria*, in that mechanical elements, which tend to be stronger when longer (for a discussion, see Carlquist, 1975), would be of lessened selective value for length. Cumbie (1967) has, in fact, reported circumstantial evidence of limited intrusiveness of libriform fibers during maturation in *Leitneria*. Except in the stem of *M. flabellifolia*, the only other instance I know in which the tracheid-to-vessel element length ratio falls below 1.00 is in the stem of *Grubbia rosmarinifolia* (unpublished data); this species is also a small shrub of finite size. While one might say that in these two instances a ratio below 1.00 is an anomaly due to insufficient number of measurements and that a ratio of 1.00 or more would be obtained had more cells been measured, there is another possibility. In these two species, as well as in *Leitneria floridana*, finite stem size may well be related to lack of intrusiveness of imperforate elements, for reasons cited above. At the same time, the enlargement of vessel elements in diameter during their maturation might have, as an inevitable component, a tendency toward intrusiveness in length also. One must remember that our knowledge of wood anatomy in shrubby and herbaceous species is still rudimentary compared with the data on hand concerning the wood of tree species. However, I would interpret the low ratios in *M. flabellifolia* to be indicative of primitiveness, because they are associated with morphological primitiveness of both tracheids and vessel elements.

**Rays.** Tippo (1938) described rays of his material of *Myrothamnus flabellifolia* as corresponding to Kribs's "Heterogeneous Type 3," that is, uniseriate rays present exclusively and these composed of procumbent,

square, and erect ray cells. If procumbent cells were lacking or nearly so, as I found in my material, these rays would not fall into any of the categories of Kribs (1935). In fact, rays composed solely of square and erect cells, or of erect cells only, can be found in a number of dicotyledons with limited secondary xylem accumulation. A hypothesis for the possible functional significance of such rays has been given elsewhere (Carlquist, 1962, 1975, 1976b) and is mentioned below in relation to axial parenchyma.

**Axial parenchyma.** The absence of axial parenchyma in *Myrothamnus flabellifolia* might be explained in two ways. First, the abundance of uniseriate rays (FIGURE 1), with ray cells predominantly erect, may represent a tissue that functions both in vertical and radial horizontal conduction and in storage of photosynthates. This condition would be expected more in stems with small size, and therefore little radial conduction, than in large stems, where procumbent cells would improve radial conduction (Carlquist, 1975). A second possible explanation might be that tracheids in *M. flabellifolia* may have greater than normal longevity and, as nucleated cells, function like axial parenchyma in conduction and storage (see Wolkinger, 1969 & 1970, and Carlquist, 1975, for data and discussions). A number (but by no means all) of the dicotyledons that lack axial parenchyma have limited secondary xylem accumulation. However, the correlation between the absence of axial parenchyma and the nucleated nature of imperforate elements is nearly perfect.

**Perforation plates.** In *Myrothamnus flabellifolia*, Tippe (1938) claimed that "all the perforation plates are scalariform. There are many bars (about 45) and the perforations are narrow." My data differ somewhat, for I found perforation plates to be relatively wide and easily distinguished (FIGURES 4 & 5), with fewer than 45 bars, if bars can be distinguished where plates are rather networklike. Some perforation plates in my material were superficially scalariform, but even in these plates strands of secondary wall material interconnecting the bars could be seen. More commonly, the perforation plates appeared to consist of two or three series of perforations (FIGURE 4), as though alternate pits without membranes were widened radially into perforations. Such perforation plates have been figured by Jane (1956) for *Vaccinium leschenaultii* and by Wilson (1960) for *Warburgia ugandensis*, *Cinnamosma madagascariensis*, and *Canella alba*. The type of perforation plate with strands irregularly interconnecting the bars has been figured by Carlquist (1961b) for *Carpenteria californica*, by Solereder (1908) for *Epacris heteronema*, and by Wilson (1960) for *Warburgia stuhlmanii*. Multiperforate perforation plates with variously random arrangement of bars and openings, unlike those of *Myrothamnus*, have been figured by a number of authors, such as Butterfield and Meylan (1975), Carlquist (1956a, 1961a, 1976a), Chalk (1933), Gottwald and Parameswaran (1964), MacDuffie (1921), and Parameswaran and Liese (1973). Such perforation plates may, in a few cases, be simplifications of the perforation plate related to the vin-

ing habit, as in the Bignoniaceae or in *Tetracera* (Dickison, 1967), or they may be based on metaxylem perforation plate patterns, as figured for the metaxylem of various dicotyledons by Bierhorst and Zamora (1965). Irregular presence of multiperforate plates in secondary xylem may characterize some families of a predominantly herbaceous nature, such as the Asteraceae, in which the secondary xylem may contain more metaxylem characteristics than in exclusively arborescent families.

The type of multiperforate plate in which irregular interconnections between bars occur (and this may be construed to include the *Myrothamnus* type) may have a functional significance. As I (1975) hypothesized in the case of "Langsbälchkenstrukturen" crossing pits in scalariformly pitted tracheids of *Sigillaria* (figured by Henes, 1959), a form of strengthening, representing a phylogenetic innovation and not a relictual phenomenon, may have been evolved. One can hypothesize that in dicotyledons with primitive wood structure most have adapted to seasonal water availability through simplification of the perforation plate to fewer bars (Carlquist, 1975). However, in other cases, strengthening of the scalariform perforation plate by innovation of strands that interconnect the bars may have evolved as a mechanism for accommodation of high tensions in the xylem during dry seasons. This would be understandable if slow rates of conduction also occurred, for narrowing of the total perforation area would be selectively tolerable only with slow conductive rates. Such slow rates can be achieved by means such as heavy cuticularization of leaves (as in *Carpenteria californica*), reduction in leaf size (as in *Myrothamnus*), or both reduction in leaf size and alteration in leaf surfaces to reduce transpiration (as in *Roridula dentata*, Carlquist, 1976a). Thus, a few plants with scalariform perforation plates of an altered type may persist in areas of seasonal dryness. This hypothesis was also employed to explain the fact that multiperforate perforation plates are present in vessels of *Ephedra*, while *Gnetum* (with large leaves and presumptively occasionally rapid rates of transpiration) almost always has simple perforation plates (Carlquist, 1975).

#### SYSTEMATIC RELATIONSHIPS

Wood anatomy alone can offer only a limited amount of relevant information. Tippo (1938) claimed that *Myrothamnus* resembles Hamamelidaceae very closely with respect to wood anatomy. This is in a sense true, although Hamamelidaceae differ in their heterogeneous multi-seriate rays and in their possession of axial parenchyma. The family Myrothamnaceae has been placed in the Hamamelidales by a number of authors (e.g., Cronquist, 1968; Hutchinson, 1959), a position not very different from its placement in the Rosales in other systems (e.g., Wettstein, 1935). Thorne (1968) included Myrothamnaceae in his order Pittosporales, the composition of which represents one of Thorne's bolder innovations. Thus *Myrothamnus* can be considered generally "rosoid" according to all the authors cited. *Myrothamnus* could be compared

closely in wood anatomy to families other than the Hamamelidaceae. For example, the wood of Roridulaceae differs only in the presence of axial parenchyma and a few very minor details (Carlquist, 1976a). Therefore, although wood anatomy confirms a "rosoid" position for *Myrothamnus*, other lines of evidence are required for formulation of a more precise statement of familial relationships. Wood anatomy does clearly mark *Myrothamnus* as one of the few relictual groups that have retained primitive xylem in pockets of mesic habitat within southern Africa. Other such families include the Bruniaceae, Canellaceae, Cornaceae (*Curtisia*), Geissolomataceae, Grubbiaceae, and Roridulaceae. The compensatory mechanisms by which such groups, even in mesic microclimates, have proved adaptive despite primitive types of conducting tissue form an interesting topic in ecological anatomy, which I have sketched in an earlier book (Carlquist, 1975, pp. 149-150).

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#### LITERATURE CITED

- BIERHORST, D. W., & P. M. ZAMORA. 1965. Primary xylem elements and element association of angiosperms. *Am. Jour. Bot.* 52: 657-710.
- BUTTERFIELD, B. G., & B. A. MEYLAN. 1975. Simple to scalariform combination perforation plates in *Vitex lucens* Kirk (Verbenaceae) and *Brachyglottis repanda* J. R. et G. Forst. (Compositae). *IAWA Bull.* 1975(3): 39-42.
- CARLQUIST, S. 1959. Wood anatomy of Helenieae (Compositae). *Trop. Woods* 111: 19-39.
- . 1961a. Wood anatomy of Cichorieae (Compositae). *Ibid.* 112: 65-91.
- . 1961b. Comparative plant anatomy. ix + 146 pp. Holt, Rinehart, & Winston, New York.
- . 1962. A theory of pedomorphosis in dicotyledonous woods. *Phytomorphology* 12: 30-45.
- . 1975. Ecological strategies of xylem evolution. xi + 259 pp. Univ. Calif. Press, Berkeley, Los Angeles, & London.
- . 1976a. Wood anatomy of Roridulaceae. *Am. Jour. Bot.* (in press).
- . 1976b. Wood anatomy of Byblidaceae. *Bot. Gaz.* (in press).
- CHALK, L. 1933. Multiperforate plates in vessels, with special reference to the Bignoniaceae. *Forestry* 7: 16-22.
- CRONQUIST, A. 1968. The evolution and classification of flowering plants. x + 396 pp. Houghton Mifflin, Boston.
- CUMBLE, B. G. 1967. Developmental changes in the vascular cambium in *Leitneria floridana*. *Am. Jour. Bot.* 54: 414-424.
- DICKISON, W. C. 1967. Comparative morphological studies in Dilleniaceae. I. Wood anatomy. *Jour. Arnold Arb.* 48: 1-23.

- GOTTWALD, H., & N. PARAMESWARAN. 1964. Vielfache Gefässdurchbrechungen in der Familie Dipterocarpaceae. *Zeit. Bot.* 52: 321-334.
- GRUNDELL, R. 1933. Zur Anatomie von *Myrothamnus flabellifolia* Welw. *Symb. Bot. Upsal.* 2: 1-17.
- HENES, E. 1959. Fossile Wandstruktur. *Handbuch der Pflanzenanatomie* III(5): 1-108. Gebrüder Borntraeger, Berlin-Nikolassee.
- HUTCHINSON, J. 1935. The families of flowering plants. ed. 2. Vol. 1. Dicotyledons. x + 510 pp. Clarendon Press, Oxford.
- JANE, F. W. 1956. The structure of wood. vii + 427 pp. Macmillan Co., New York.
- KRIBS, D. A. 1935. Salient lines of structural specialization in the wood rays of dicotyledons. *Bot. Gaz.* 96: 547-557.
- MACDUFFIE, R. C. 1921. Vessels of the gnetalean type in angiosperms. *Bot. Gaz.* 71: 438-445.
- NIEDENZU, F., & A. ENGLER. 1930. Myrothamnaceae. *In*: A. ENGLER & K. PRANTL, Die natürlichen Pflanzenfamilien. ed. 2. 18A. Engelmann, Leipzig.
- PARAMESWARAN, N., & W. LIESE. 1973. Scanning electron microscopy of multiperforate perforation plates. *Holzforschung* 27: 181-186.
- SOLEREDER, H. 1908. Systematic anatomy of the dicotyledons. (Translated by L. A. BOODLE & F. E. FRITSCH; revised by D. H. SCOTT.) Vol. 1. xii + 644 pp. Clarendon Press, Oxford.
- THORNE, R. F. 1968. Synopsis of a putatively phylogenetic classification of the flowering plants. *Aliso* 6(4): 57-66.
- TIPPO, O. 1938. Comparative anatomy of the Moraceae and their presumed allies. *Bot. Gaz.* 100: 1-99.
- WETTSTEIN, R. 1935. *Handbuch der systematischen Botanik.* ed. 3. x + 1152 pp. Franz Deuticke, Leipzig & Wien.
- WILSON, T. K. 1960. The comparative morphology of the Canellaceae. I. Synopsis of genera and wood anatomy. *Trop. Woods* 112: 1-27.
- WOLKINGER, F. 1969. Morphologie und systematische Verbreitung der lebenden Holzfasern bei Sträuchern und Bäumen. I. Zur Morphologie und Zytologie. *Holzforschung* 23: 135-144.
- . 1970. Morphologie und systematische Verbreitung der lebenden Holzfasern bei Sträuchern und Bäumen. II. Zur Histologie. *Ibid.* 24: 141-151.
- ZEMKE, E. 1939. Anatomische Untersuchungen an Pflanzen der Namibwüste. *Flora* 33: 365-416.

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