

Wood and bark anatomy of Muntingiaceae: A phylogenetic comparison within Malvales s. l.

SHERWIN CARLQUIST

Carlquist, S. (Santa Barbara Botanic Garden, 1212 Mission Canyon Road, Santa Barbara, California 93105, U.S.A.; e-mail: s.carlquist@verizon.net). Wood and bark anatomy of Muntingiaceae: A phylogenetic comparison within Malvales s. l. *Brittonia* 57: 59–67. 2005.—Quantitative and qualitative data on wood and bark anatomy are given for *Muntingia calabura* L. and *Dicraspidia donnell-smithii* Standley. These data are compared with phylogenetic schemes, based on DNA analysis, in which Muntingiaceae belong to the “dipterocarp clade” within Malvales. The data are consistent with this hypothesis, although Muntingiaceae lack pit vestures in vessels, which are seen in the other malvacean families (Cistaceae, Dipterocarpaceae, Neuradaceae, Sarcolaenaceae, Thymeleaceae), and this may represent a loss of pit vestures. All families of the dipterocarp clade agree with both genera of Muntingiaceae in having tracheids as the imperforate tracheary element type (at least ancestrally), although fiber-tracheids also occur in some Dipterocarpaceae and Thymeleaceae. The large size of some malvacean families (with attendant greater diversity in character states) and a paucity of wood studies in those families make for difficulty in comparison of features such as axial parenchyma and ray types with those of Muntingiaceae; character states of these features are consistent with placement of Muntingiaceae in the dipterocarp clade of Malvales. Banded phloem fibers in bark of Muntingiaceae are much like those of other Malvales. Wood of Muntingiaceae is highly mesomorphic according to quantitative vessel features.

Key words: bark anatomy, Cistaceae, Dipterocarpaceae, Elaeocarpaceae, Malvales, Thymeleaceae, tracheids, vessel grouping, vested pits.

Introduction

Muntingiaceae consist of two monotypic genera, *Muntingia* (Mexico to West Indies, but now weedy in tropical America) and *Dicraspidia* (Central America). These two genera had frequently been placed in Elaeocarpaceae, although evidence from wood anatomy (Metcalf and Chalk, 1950; Gasson, 1996) indicated they were discordant elements in that family. This contention was confirmed by molecular work (Alverson et al., 1998), who placed them in a “dipterocarp clade” of Malvales. The family Muntingiaceae was formally proposed by Bayer et al. (1998), who present reasons for its recognition. *Neoressmannia* has been tentatively referred to Muntingiaceae (Bayer et al., 1998) but is not included in the

present study. The dipterocarp clade of Malvales includes Neuradaceae, Muntingiaceae, Cistaceae, Sarcolaenaceae, and Dipterocarpaceae according to Alverson et al. (1998). A similar result was reached by Soltis et al. (2000), who excluded Neuradaceae (but placed it as an outgroup to the clade) and placed Thymeleaceae as an outgroup to the remainder of the dipterocarp clade. This placement of Muntingiaceae was accepted by Jansen et al. (2001) in a study of vested pits in Malvales. The Angiosperm Phylogeny Group (APGII, 2003) included Muntingiaceae within Malvales but did not offer an explicit phylogenetic placement within that order.

One purpose of the present study is to offer as complete as possible a description

of wood anatomy of Muntingiaceae based on the materials available, and to describe bark anatomy, the latter not previously recorded. The second purpose of this study is to compare the wood of Muntingiaceae, primarily to the wood of other members in the dipterocarp ("dipterocarpean") clade of Malvales (tentatively defined here as including Thymeleaceae, Muntingiaceae, Cistaceae, Sarcocaulaceae, Dipterocarpaceae), and to give a preliminary analysis of the differences and similarities among the families of that clade with respect to wood character states. Comparisons of features of Muntingiaceae to the other clade of Malvales (Bixaceae-Malvaceae) are also appropriate. The Bixaceae-Malvaceae clade includes Bixaceae, Bombacaceae, Malvaceae, Sterculiaceae, and Tiliaceae, according to Soltis et al. (2000). The treatments of Soltis et al. (2000) and APGII (2003) group the latter four families as Malvaceae. For convenience, the four families are recognized here.

There is rather extensive information on the wood of Dipterocarpaceae (Gottwald and Parneswaran, 1966) and on the wood of Sarcocaulaceae (Den Outer and Schütz, 1981). There have been no family-level monographs on woods of the remaining families, although many good generic descriptions have been published (see Gregory, 1994). Comparison of Muntingiaceae to Thymeleaceae is particularly troubling because wood anatomy of Thymeleaceae is remarkably diverse, and much of the diversity has not been recorded. I have attempted to supply citation of key wood character states of Thymeleaceae from my slides of the family, which have been accumulated for the purpose of a familial monograph that I hope to publish soon. However, detailed presentation of information on Thymeleaceae is inappropriate for this paper. The summaries of Metcalfe and Chalk (1950) prove helpful because of their coverage of all families concerned. These are the references used for comparisons with Muntingiaceae unless otherwise stated below.

Materials and Methods

Stems of the two genera were collected by Dr. Scott Zona in the Montgomery Bo-

tanical Center and preserved in 50% aqueous ethanol. The collection data are: *Dicraspidia donnell-smithii* [Montgomery Botanic Garden 941105c; Zona 935 (FTG)]; *Muntingia calabura* [Montgomery Botanic Garden 982204; Zona 933 (FTG)]. The stem of the *Muntingia* (4.9 cm including bark; bark thickness 3 mm) was appreciably wider than that of the *Dicraspidia* (1.4 cm including bark), a fact that is of significance in the descriptions below.

Wood of both genera was only moderately hard, and thus was successfully sectioned without treatment on a sliding microtome. Presence of secondary phloem fibers in the bark, which is otherwise soft in texture, necessitated use of a different method (Carlquist, 1982). Sections to be made into permanent slides were stained with safranin and counterstained with fast green. Sections to be studied with scanning electron microscopy (SEM) were dried between clean slides, mounted on aluminum stubs, sputter coated, and studied with a Hitachi S-2600N scanning electron microscope. SEM studies of vessel pits were attempted only with *Muntingia* because the pervasive deposits of resinlike compounds in *Dicraspidia* obscured fine cellular details. Macerations were prepared with Jeffrey's Fluid and stained with safranin.

Vessel diameter is measured as vessel lumen diameter, because the lumen volume is hydrologically significant, whereas the outside vessel dimension is not (vessel wall thickness is, however, also given in the descriptions). Diameter of vessels, oval in transection, is measured as an average of long and short chords. Mean number of vessels per group is based on a solitary vessel = 1, a pair of vessels in contact = 2, etc. Means are based on 25 measurements. Terms are used in accordance with the IAWA Committee on Nomenclature (1964) and Carlquist (2001). The term "tracheid" for imperforate tracheary elements of Muntingiaceae is advisable because Muntingiaceae are one of the families that validate the concept that in dicotyledons, tracheids are conductive cells and thereby forestall the evolution of grouping of vessels (Carlquist, 1984). Wood of *Muntingia* is described before that of *Dicraspidia* because

the wood pattern was more mature and more information was obtained because more sections were examined.

Wood Anatomy

Muntingia calabura (Figs. 1–2). Inconspicuous growth rings present, not easily discerned at low power, but evident from diminished radial diameter of latewood tracheids and axial parenchyma cells at higher power (Fig. 1C); latewood vessels are narrower than earlywood vessels, but not more numerous (Fig. 1A). Latewood tracheids with walls not appreciably thicker than those of earlywood tracheids (Fig. 1C). Vessels almost entirely solitary (Fig. 1A); the mean number of vessels per group, 1.04. Vessels circular to somewhat oval in transection (Fig. 1A). Mean vessel lumen diameter, 104 μm . Mean number of vessels per mm^2 , 14. Mean vessel element length, 205 μm . Most vessels noncaudate. Mean vessel wall thickness, 2–2.6 μm (wider vessels with slightly thicker walls). Perforation plates simple. Perforation plates non-bordered or minimally bordered. Lateral wall pits of vessels (both intervascular and vessel-to-ray pits) alternate with slitlike apertures (Fig. 2A) and wide borders (Fig. 2B). Pits nonvestured, accretions of a secondary compound visible as deposits (which are not to be confused with vestures) sometimes present on the pit membrane (Fig. 2B, bottom center). Mean axial diameter of pit cavities about 3 μm . Imperforate tracheary elements all tracheids. Central portions of tracheids often wider, matching the storied strands of axial parenchyma but tapered above and below this central portion. Mean tracheid length, 1004 μm . Mean tracheid wall thickness 2.1 μm . Pits about 3 μm , bordered (Figs. 1D, 2C), relatively densely placed. Axial parenchyma diffuse, scanty vasicentric, diffuse-in-aggregates, and in bands typically two cells thick (Figs. 1A, 1C). Axial parenchyma typically in strands of two cells, but unsubdivided axial parenchyma cells and strands up to five cells long also present. Rays mostly multiseriate, but a few uniseriate rays present (Fig. 1B). As seen in radial sections, cells mostly procumbent; some

square cells at growth ring margins and a few square or upright sheath cells present. Mean multiseriate ray height, 258 μm . Mean width of multiseriate rays, 4.54 cells. Mean height of uniseriate rays, 110 μm . Mean ray cell wall thickness about 1.4 μm . Storying prominent in axial parenchyma (Fig. 1B); the storied pattern also evident in some vessel elements adjacent to axial parenchyma. Yellowish deposits common in vessels, often forming a thick cylinder at the peripheries of vessel lumina. Dark-staining deposits in small droplets in rays and in pit cavities (Fig. 1D). Rhomboidal crystals present in a few ray cells, crystals encapsulated in thin secondary wall material (Fig. 2D). A very small number of crystals seen in axial parenchyma in the form of chambered solitary crystals in axial parenchyma subdivided into strands of four cells.

Dicraspidia donnell-smithii (Fig. 3A). Growth rings not pronounced; latewood characterized by narrower vessels and by thicker-walled tracheids. Appearance of the transection much like that of *Muntingia* (Fig. 1A). Vessels mostly solitary, circular to somewhat oval in transection; mean number of vessels per group, 1.02 (excluding metaxylem, in which grouped vessels are to be expected in many dicotyledons that have solitary vessels in secondary xylem). Mean vessel diameter, 81 μm . Mean number of vessels per mm^2 , 14. Mean vessel element length, 444 μm , many vessels caudate. Mean vessel wall thickness, 4.1 μm . Perforation plates simple, with narrow borders. Lateral wall pits of vessels mostly circular to somewhat oval, alternate, non-vestured, with slitlike apertures. Pit cavity axial diameter about 4.5 μm . Imperforate tracheary elements all fusiform tracheids. Mean length of tracheids, 696 μm . Mean wall thickness of tracheids, 4.1 μm . Pits circular, rather densely placed, mean pit cavity diameter about 4.5 μm . Axial parenchyma diffuse, scanty vasicentric, and diffuse-in-aggregates. Axial parenchyma commonly in strands of two or three cells, occasionally more. Rays all multiseriate (Fig. 3A), ray cells upright to square as seen in radial section, procumbent cells present closer to the cambium. Mean multiseriate ray height,

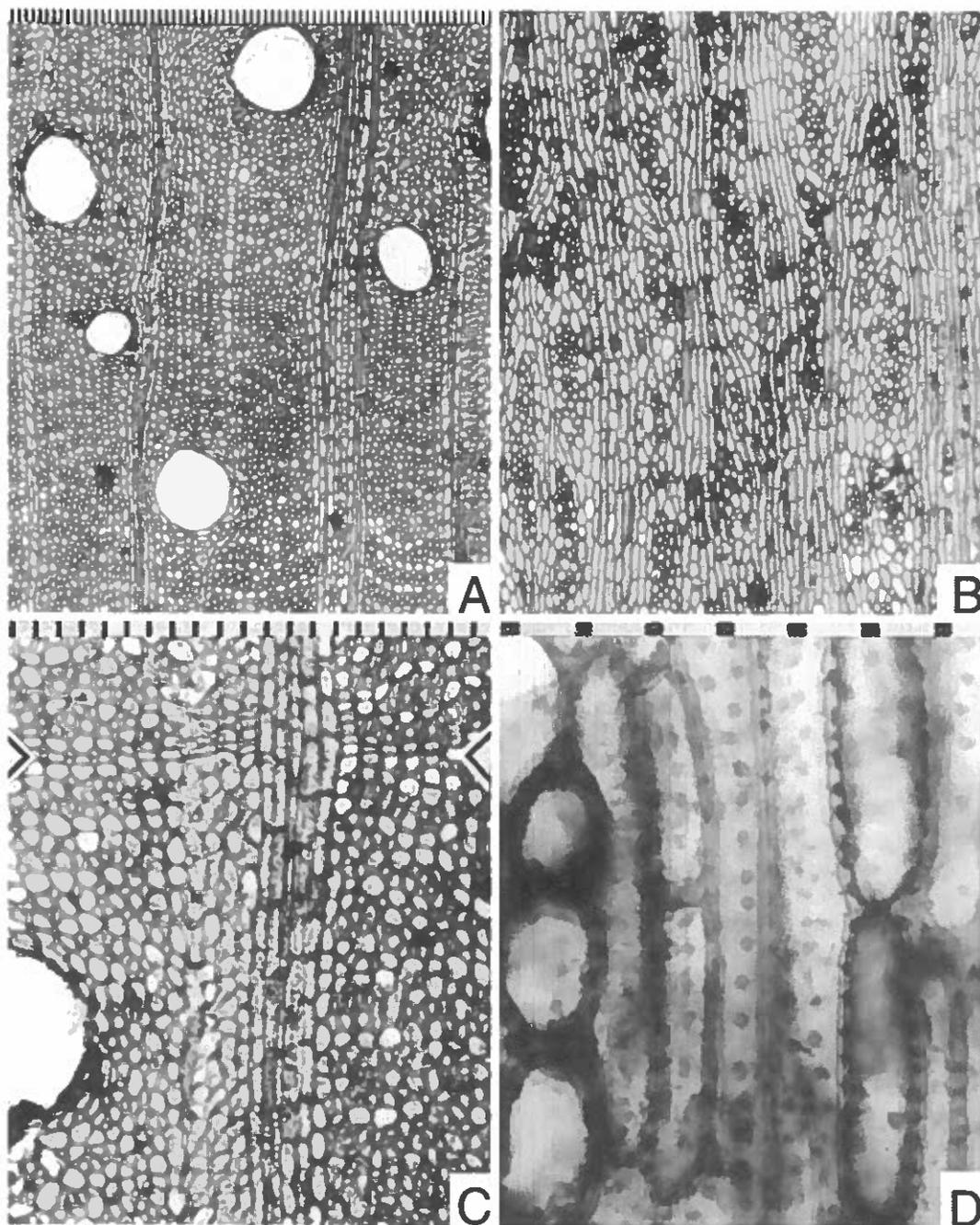


FIG. 1. Wood section of *Muntingia calabura*. A. Transection; narrow vessel and thicker-walled tracheids near center denote latewood. B. Tangential section; the numerous storied cells are axial parenchyma strands. C. Transection portion to show indistinct margin of growth ring (pointers at left and right) and axial parenchyma configurations. D. Tangential section portion to show deposits that color ray cells (left) axial parenchyma (right), and make the bordered pits of tracheids (center) more easily visible. Figure 1A, 1B, scale above Figure 1A (divisions = 10 μ m). Figure 1C, scale above Figure 1C (divisions = 10 μ m). Figure 1D, scale above Figure 1D (divisions = 10 μ m).

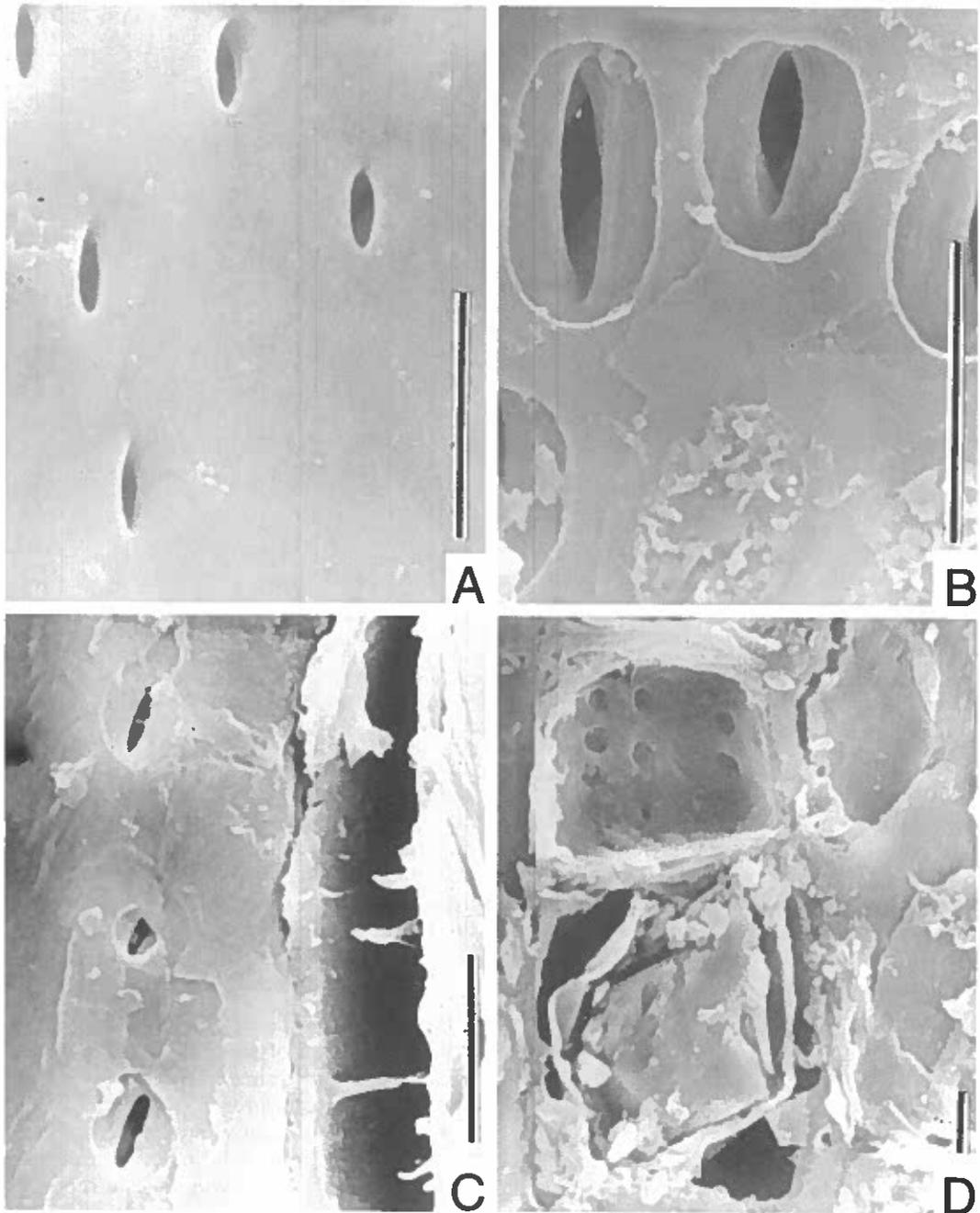


FIG. 2. SEM photographs from tangential section of *Muntingia calabura* wood. A. Elliptical pit apertures on lumen face of vessel; axis of vessel is oriented horizontally. B. Pits (two below, still with membranes, encrusted with deposits) from outside of vessel; axis of vessel oriented horizontally. C. Portion of tracheid (left) to show three bordered pits. D. Empty ray cell (above) and ray cell containing encapsulated crystal that has been cut during sectioning (below). Figure 2A, 2B, bars = 5 μm ; Figure 2C, bar = 10 μm ; Figure 2D, bar = 10 μm .

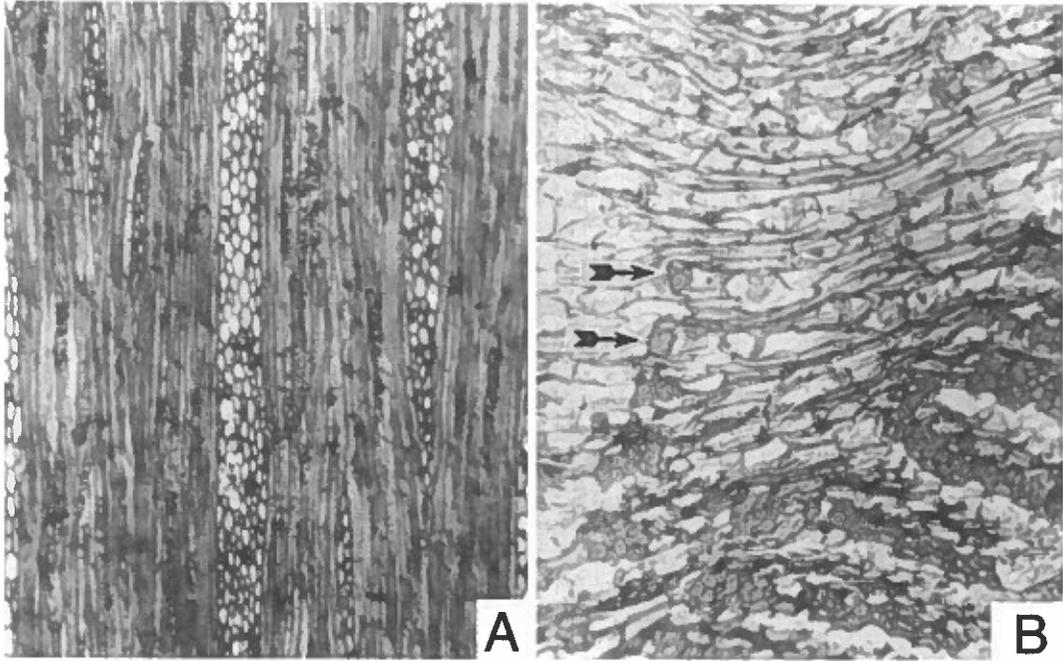


FIG. 3. Sections of wood (left) and bark (right) of Muntingiaceae. **A.** *Dicraspidia donnell-smithii*. Tangential section, showing wide, tall, rays and lack of storying. **B.** *Muntingia calabura*. Transection of bark, phellem (which would be above) not shown. Plates of phloem fibers are shown in the secondary phloem at lower right; arrows indicate druses in parenchyma cells of dilated phloem ray. Figure 3A, scale above Figure 1A. Figure 3B, scale above Figure 1C.

1242 μm , mean multiseriate ray width, 6.0 cells. Axial parenchyma, vessel elements, tracheids, and rays are nonstoried (Fig. 3A). Storying vaguely present in tracheids, but identifiable in sieve-tube elements and in axial parenchyma when compared with adjacent vessels. Droplets of dark-staining compounds present in axial parenchyma, ray cells, tracheids, and vessels, especially in pit cavities. No crystals observed in ray cells or axial parenchyma.

Bark Anatomy

Bark of *Muntingia* has a thick accumulation of phellem, not shown in Figure 3B. Stretched and subdivided cortical cells are present inside the periderm, and dilated phloem rays are present (Fig. 3D); all cells of these two parenchyma zones have non-lignified walls. In both phloem rays and in cortex, occasional druses (arrows in Fig. 3D) may be observed; some of these consist of only three or four united crystals. Fascicular secondary phloem (Fig. 3D, lower

right) consists of tangential bands of fibers, alternating with crushed phloem parenchyma and crushed sieve-tube elements. The fiber bands are typically two cells in thickness. The bark of *Dicraspidia* agrees with the above description in all respects.

Discussion and Conclusions

The descriptions of Metcalfe and Chalk (1950) for wood of *Muntingia* and *Discraspidia* agree with mine in most respects, although they are briefer. My material of *Dicraspidia* did not show storying, probably because it was relatively juvenile compared to the material of *Muntingia*. The report of septate fibers in *Dicraspidia* given by Metcalfe and Chalk (1950) is not confirmed by my observations, nor by those of Gasson (1996). The report of fibers with simple pits in *Dicraspidia* by Metcalfe and Chalk (1950) is not confirmed here; lack of staining or refractiveness frequently makes pit cavities difficult to see, but when the pit cavities are filled with secondary com-

pounds, as they are in my material, presence of borders on pits can be readily confirmed. The description of wood of *Muntingia* by Gasson (1996), although briefer than mine, agrees in all respects. My studies confirm the report by Jansen et al. (2000) that vessel pits are nonvestured in *Dicraspidia* and *Muntingia*. The absence of vestures applies not only to the pit cavity, but to the pit aperture facing the lumen; instances elsewhere in Malvales show vestures in both locations (e.g., Baas and Werker, 1981).

Let us, for the purposes of discussion of relationships of Muntingiaceae in relation to wood anatomy, assume that the dipterocarp clade can be defined as including, in addition to Muntingiaceae, the families Cistaceae, Dipterocarpaceae, Sarcolaenaceae, and Thymeleaceae (in accordance with Soltis et al., 2000). The absence in this clade of Elaeocarpaceae is notable, and in agreement with the exclusion of Muntingiaceae from Elaeocarpaceae on the basis of wood anatomy by Metcalfe and Chalk (1950) and Gasson (1996).

Using this as the definition of the dipterocarp clade, one notes the distinction offered by the absence of vested pits only in Muntingiaceae is in agreement with the findings of Jansen et al. (2000). Jansen et al. (2001) consider the absence of vested pits in Malvales to be a symplesiomorphy. This interpretation is interesting in that Muntingiaceae is then the only family of the dipterocarp clade not to have acquired vested pits (Jansen et al., 2000), unless one considers Neuradaceae (which lack vested pits: Jansen et al., 2000) to be part of the dipterocarp clade (cf. Alverson et al., 2001). Jansen et al. (2000) consider that "monophyly of the core Malvales... is supported by this lack of vested pits," but they note occurrence of vested pits in several malvalean clades, of which the assemblage termed the dipterocarp clade here is one. Although Jansen et al. (2000) seem to favor acquisition of vesturing in pits rather than loss as more parsimonious in dicotyledons as a whole, one can imagine that both acquisition and loss of vesturing in pits may have occurred (Jansen et al., 2001). The lack of vested pits in vessels of two

genera of Onagraceae (Carlquist, 1975) and Rubiaceae (Jansen et al., 1998) may be examples of loss.

The presence of tracheids in the dipterocarp clade is notable: they are present in Cistaceae, Dipterocarpaceae (vasicentric tracheids plus fiber-tracheids in some genera), Sarcolaenaceae, and some Thymeleaceae. Metcalfe and Chalk (1950) offer a minimal coverage of imperforate tracheary elements in Thymeleaceae. In this family, tracheids occur in *Lagetta* and *Phaleria*; vasicentric tracheids plus fiber-tracheids in *Dirca* and *Pimelea*; tracheids in latewood plus fiber-tracheids in latewood in *Wikstroemia* (data original, but do not represent an extensive survey for the family). The tracheids of Malvaceae fall within my definition of tracheids (Carlquist, 2001) in that they have fully bordered pits; malvalean tracheids often have pits that are not large (3–4.5 μm in Muntingiaceae) but are rather densely placed. Moreover, the very low figure for vessel grouping in Muntingiaceae and most other members of the dipterocarp clade families (except, for example, Thymeleaceae with fiber-tracheids or libriform fibers) is indicative of tracheid presence, as postulated in my study linking occurrence of minimal grouping of vessels with presence of tracheids as the predominant or sole imperforate tracheary element type in secondary xylem (Carlquist, 1984). The five genera of Dipterocarpaceae in which tracheids ("Fasern mit Hoftüpfeln") are reported are the same genera as those in which solitary vessels are reported (Gottwald and Parameswaran, 1966). Tracheids seem to be a symplesiomorphy in the dipterocarp clade. Tracheids may also be a symplesiomorphy in the Bixaceae-Malvaceae clade, because tracheids and vasicentric tracheids occur in most Malvaceae; tracheids occur in many Bombaceae; fiber-tracheids in Bixaceae and some Bombacaceae; and libriform fibers are common in Sterculiaceae and Tiliaceae. Thus, tracheids appear to be a symplesiomorphy for Malvales as a whole, with reduction in pit borders leading to fiber-tracheids or even libriform fibers. The Malvales are a good example of how phylads that had tracheids or fiber-tracheids have probably added libri-

form fibers by a kind of tracheid dimorphism (or fiber-tracheid dimorphism), a process hypothesized earlier (Carlquist, 1988). Introduction of libriform fibers into woods with tracheids results in presence of vasicentric tracheids (because conducting imperforate tracheary elements always cluster around vessels in woods with vasicentric tracheids). The use of the term tracheid in woods earlier in this sequence and vasicentric tracheid in woods later in the sequence seems entirely justified, since the tracheids are morphologically the same, whether with or without concomitant occurrence of libriform fibers. Recent terminologies retain the term vasicentric tracheids where libriform fibers co-occur in a wood, but use the term fiber-tracheid for morphologically identical cells in woods where libriform fibers are absent.

Axial parenchyma is mostly diffuse-in-aggregates in Sarcolaenaceae; diffuse or absent in Cistaceae; diffuse, abaxial, ray-adjacent (*Monotes*), aliform, terminal, apotracheal banded and paratracheal banded in Dipterocarpaceae; abaxial (*Wikstroemia*), aliform, scanty vasicentric, apotracheal banded and paratracheal banded in Thymeleaceae. These distributions, together with the great diversity of axial parenchyma types in Malvales as a whole (e.g., Malvaceae: Metcalfe & Chalk, 1950) provide difficulties in establishing phyletic sequences in axial parenchyma in families of Malvales.

Likewise, the diversity of rays in Malvales discourages one from attempting to construct phylogenetic sequences within Malvales. The rays of *Muntingia* are Heterogenous Type IIB, transitional to Homogeneous Type I. Rays of *Dicraspidia* are Heterogeneous Type IIA (probably cambial change with age would result in Type IIB rays). Heterogeneous Type IIA and IIB rays have been reported for Dipterocarpaceae and Homogeneous Type III rays have been reported for Sarcolaenaceae and Thymeleaceae; Heterogeneous Type IIB and Heterogeneous Type III rays are cited for Cistaceae. Thus, a diverse picture emerges with respect to rays. This picture becomes even more diverse if one takes into account the Bixaceae-Malvaceae clade, in which tile

cells, which represent a kind of division of labor within ray cells, occur; tile cells are not known to occur outside of families in this clade (Carlquist, 2001).

Storying, conspicuous in the axial parenchyma of *Muntingia*, can be found in a number of Thymeleaceae, such as *Craterosiphon*, *Daphne*, *Daphnopsis*, *Diplocarpha*, and *Lasiosiphon* (Carlquist, unpubl. data), and has been reported for all portions of the wood of *Balanocarpus* (Dipterocarpaceae), including rays, by Gottwald and Parameswaran (1966). Storying is, however, widely present in the Bixaceae-Malvaceae clade, and is widely reported in Bixaceae, Bombacaceae, Malvaceae, Sterculiaceae, and Tiliaceae (Carlquist, 2001). There may have been a phyletic loss of storying, therefore, within the members of the dipterocarp clade, in species with long imperforate tracheary elements (as compared to the fusiform cambial initials from which they were derived). The explanation for why storying in the material studied of *Dicraspidia* is less prominent than in that of *Muntingia* probably lies with the relatively old stem of *Muntingia* studied compared to that of *Dicraspidia*. Storying tends to develop with age, because the longitudinal divisions that lead to a storied pattern are fewer in a smaller stem.

With respect to bark anatomy, banded phloem fibers are a conspicuous feature. Metcalfe and Chalk (1950) figure this feature for *Hopea* of the Dipterocarpaceae and *Lagetta* of the Thymeleaceae in the case of the dipterocarp clade. In the Bixaceae-Malvaceae clade, those authors figure such fibers for *Bixa* (Bixaceae), *Durio* (Bombacaceae), *Hibiscus* (Malvaceae), *Theobroma* (Sterculiaceae), and *Tilia* (Tiliaceae). Undoubtedly such fibers are quite widespread within Malvales.

One should note that because Muntingiaceae consists merely of two species, comparisons to other families involve a hidden difficulty. Much greater diversity within any particular anatomical feature is to be expected in a large family such as Dipterocarpaceae or Malvaceae, and this must be considered in making phylogenetic comparisons.

In sum, the segregation of Muntingiaceae

from Elaeocarpaceae or any other family is justified on the basis of wood anatomy. Wood anatomy is, however, consistent with the placement of Muntingiaceae in Malvales s.l. in general and the dipterocarp clade in particular.

The relatively wide, long vessel elements of Muntingiaceae and their low density in the wood mark the wood as mesomorphic, like that of rain forest or cloud forest trees.

Acknowledgment

Appreciation is expressed to Dr. Scott Zona of the Fairchild Tropical Garden, who collected fresh wood samples of the two genera in the Montgomery Botanical Center and also made voucher specimens from these plants.

Literature Cited

- Alverson, W. S., K. G. Karol, D. A. Baum, M. W. Chase, S. M. Swensen, R. McCourt & K. J. Sytsma. 1998. Circumscription of the Malvales and relationships to other Rosidae: evidence from rbcL sequence data. *Amer. J. Bot.* 85: 876–887.
- APGII (Angiosperm Phylogeny Group II). 2003. An update of the Angiosperm Phylogeny Group classification for the orders and families of flowering plants: APG II. *J. Linn. Soc. Bot.* 141: 300–436.
- Baas, P. & E. Werker. 1981. A new record of vested pits in Cistaceae. *IAWA Bull. n. s.* 2: 41–42.
- Bayer, C., M. W. Chase & M. F. Fay. 1998. Muntingiaceae, a new family of dicotyledons with malvalean affinities. *Taxon* 47: 37–42.
- Carlquist, S. 1975. Wood anatomy of Onagraceae, with notes on alternative modes of photosynthate movement in dicotyledon woods. *Ann. Missouri Bot. Gard.* 62: 386–424.
- . 1982. The use of ethylenediamine in softening hard plant structures for paraffin sectioning. *Stain Technol.* 57: 311–317.
- . 1984. Vessel grouping in dicotyledon woods: significance and relationship to imperforate tracheary elements. *Aliso* 10: 505–525.
- . 1988. Tracheid dimorphism: a new pathway in evolution of imperforate tracheary elements. *Aliso* 12: 102–118.
- . 2001. *Comparative wood anatomy*. 2nd ed. Springer Verlag, Heidelberg, Berlin, New York.
- Den Outer R. W. & P. R. Schütz. 1981. Wood anatomy of some Sarcolaenaceae and Rhopalocarpaceae and their systematic position. *Meded. Landbouwhoges. Wageningen* 81(8): 1–25.
- Gasson, P. 1996. Wood anatomy of the Elaeocarpaceae. Pages 47–71. *In*: L. Donaldson, A. P. Singh, B. G. Butterfield, L. J. Whitehouse, editors, *Recent advances in wood anatomy*. Rotorua.
- Gottwald H. & N. Parameswaran. 1966. Das sekundäre Xylem de Familie Dipterocarpaceae, anatomische Untersuchungen zur Taxonomie und Phylogenie. *Bot. Jahrb.* 85: 410–508.
- Gregory, M. 1994. Bibliography of systematic wood anatomy of dicotyledons. *IAWA J.*, suppl. 1: 1–265.
- IAWA Committee on Nomenclature. 1964. Multilingual glossary of terms used in wood anatomy. *Verlagsbuchanstalt Buchdruckerei Konkordia*. Winterthur.
- , ——— & ———. 2000. Vested pits in Malvales s. l.: a character with taxonomic significance hidden in the secondary xylem. *Taxon* 49: 169–182.
- , ——— & ———. 2001. Vested pits: their occurrence and systematic importance in eudicots. *Taxon* 50: 135–167.
- , E. Smets & P. Baas. 1998. Vestures in woody plants: a review. *IAWA J.* 19: 347–382.
- Metcalfe, C. R. & L. Chalk. 1950. *Anatomy of the dicotyledons*. Clarendon Press, Oxford.
- Soltis, D. E., P. S. Soltis, M. W. Chase, M. E. Mort, D. C. Albach, M. Zanis, V. Savolainen, W. H. Hahn, S. B. Hoot, M. F. Fay, M. Axtell, S. M. Swensen, L. M. Prince, W. J. Kress, K. C. Nixon & J. S. Farris. 2000. Angiosperm phylogeny inferred from 18S rDNA, rbcL, and atpB sequences. *J. Linn. Soc. Bot.* 133: 381–461.