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WOOD ANATOMY AND RELATIONSHIPS OF *MONTINIA*

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ABSTRACT

Quantitative and qualitative data are presented on wood anatomy of root, basal stem, and upper stem of *Montinia caryophyllacea*. Anatomy of twig wood of *Kaliphora madagascariensis* is compared with these results, as is the data of Ramamonjariisoa (1980) on wood of the genus *Grevea*. Features common to the three genera in wood as well as other portions of the plant are reviewed; these are consistent with the interpretation that *Montinia* and *Kaliphora* are very close to each other, despite previous positions of the two genera in Saxifragaceae and Cornaceae, respectively. *Grevea*, although more distant from *Montinia* than is *Kaliphora*, can be included in a trigenic family, Montiniaceae. The ordinal position of *Montinia* is reviewed in terms of Rosales (Saxifragales) and Myrtales. Resemblances between Montiniaceae and rosalean families are fewer than resemblances between Montiniaceae and myrtalean families. Montiniaceae have (in part) storied wood structure, a feature not found in Rosales or Myrtales sensu stricto. However, storied structure does occur in Thymeleaceae, which have sometimes been placed in or near Myrtales. Both Montiniaceae and Thymeleaceae might be regarded as outliers of Myrtales, closer to that order than to others. The presence of iridoid compounds in *Montinia* complicates the task of placement.

Key words: *Grevea*, *Kaliphora*, *Montinia*, Montiniaceae, Myrtales, Rosales, Saxifragales, Thymeleaceae, wood anatomy.

INTRODUCTION

The genus *Montinia* consists of a single species, *M. caryophyllacea* Thunb., native to southern Africa and Angola (Mendes 1978). *Montinia* has most frequently been included within Cunoniales, Hydrangeales, Rosales, or Saxifragales (concepts much alike, differing mostly in the ordinal name employed) under the families Saxifragaceae (Engler 1928, Thorne 1983), Grossulariaceae (Cronquist 1968, 1981), or Escalloniaceae (Hutchinson 1973). Dahlgren's (1980) placement of *Montinia* as a separate family, Montiniaceae, under Cornales is much like these concepts, because Dahlgren's Cornales contains Columelliaceae, Escalloniaceae, and Hydrangeaceae. A departure from this concept was originated by Milne Redhead (1955), who first segregated Montiniaceae but claimed the family should be located in Myrtales between Onagraceae and Oliniaceae. In a study of African and Malagasy Saxifragaceae (sensu lato), Ramamonjariisoa (1980) came to a similar conclusion. The present study is concerned with reviewing the ordinal placement of *Montinia* on the basis of excellent material of wood collected by the author in 1973.

If Montiniaceae are recognized as a segregate family, the problem of its generic composition is also a matter worthy of review on the basis of wood anatomy. *Grevea*, which consists of three species from Madagascar and West Africa (Létozey 1977), was included by Milne Redhead (1955) in Montiniaceae, although it had been assigned to Saxifragaceae by Baillon (1884) and had been similarly

treated by subsequent authors. Hutchinson's (1973) inclusion of *Grevea* in Escalloniaceae is typical; Takhtajan (1987) includes *Grevea* as the only genus of Montiniaceae other than *Montinia*, in accord with the Milne Redhead treatment.

Kaliphora, a monotypic genus from Madagascar, was described by Hooker (1867) under Cornaceae. This treatment was followed by such authors as Cronquist (1968) and Hutchinson (1973). Capuron (1969a) stressed similarity between *Grevea* and *Kaliphora* with respect to embryological and seed features. Nevertheless, Takhtajan (1987) placed *Montinia* and *Grevea* in Montiniaceae, but relegated *Kaliphora* to a neighboring family, Melanophyllaceae, under the suborder Escalloniinae of Hydrangeales.

Ramamonjariisoa (1980) contributed evidence that *Grevea*, *Kaliphora*, and *Montinia* should be grouped as Montiniaceae. For example, all three genera have tripartite unilacunar nodes (Ramamonjariisoa 1980). The three genera are also alike by being dioecious and epigynous and by having ascending ovules and capsular fruits (Capuron 1969a, 1969b). Tetramery characterizes *Kaliphora* and *Montinia*, whereas *Grevea* is trimerous. The three genera lack tannins. Stems of *Grevea* have pith bundles, both phloic and collateral, whereas the other two genera lack them (Ramamonjariisoa 1980). Vessels of *Kaliphora* and *Montinia* are reported to have vestured pits, whereas those of *Grevea* are claimed to have vestured walls (Ramamonjariisoa 1980). Details of pollen structure can be cited as suggestive of affinity between the three genera (Erdtman 1952; Hideux 1972; Hideux and Ferguson 1976). Pollen structure suggests that grouping the three genera as Montiniaceae is defensible; the data also suggest that the case for inclusion of Montiniaceae in a rosalean order is weaker than had been thought earlier. The ordinal position of Montiniaceae is therefore subjected to a review in the present paper.

This material on Montiniaceae is offered at this time so that data may be used in a forthcoming volume of the second edition of Metcalfe and Chalk's "Anatomy of the Dicotyledons."

MATERIALS AND METHODS

Wood samples were available in dried form. Portions were boiled, stored in aqueous 50% aqueous ethyl alcohol, and sectioned on a sliding microtome. Sections were stained with safranin and counterstained with haematoxylin or fast green. Some sections were examined with an ISI WB-6 scanning electron microscope to demonstrate nature of crystals and presence of vestured pits in vessels. Macerations were prepared with Jeffrey's fluid and stained with safranin.

Cellular dimensions in the descriptions below are based on 25 measurements each, except for wall thickness of vessels and of libriform fibers, and diameter of libriform fibers; for these three features, typical expressions were selected for measurement. Vessel diameter is the diameter of the lumen at the widest point. Number of vessels per mm² is based on vessel number, not number of vessel groups per unit area. Vessels per group is calculated on the basis that a solitary vessel = 1.0, a pair of vessels in contact = 2.0, etc. Terminology for wood features follows the recommendations of the IAWA Committee on Nomenclature (1964).

Specimens documenting the woods studied are located in the herbarium of the Rancho Santa Ana Botanic Garden. The wood samples of *Montinia* were taken from a mature plant, in which the basal stem was 14 mm in diameter.

ANATOMICAL RESULTS

Descriptions rather than tabular summaries are offered here to achieve an economical presentation. The wood of *Montinia caryophyllacea* is described completely for the root; wood data for basal stem and upper stem wood may be assumed to be the same except for the features (mostly quantitative) given under these latter headings. The wood of *Kaliphora madagascariensis* Hook. was taken from an herbarium specimen.

MONTINIA CARYOPHYLLACEA, root (near juncture with stem), *Carlquist 4536* (Fig. 1, 2, 6).—Growth rings present, weakly demarcated (semi-ring porous) by means of vessel diameter; vessels may be wider a little after the beginning of the growth ring, as indicated in Fig. 1. Mean number of vessels per group, 3.48. Vessels grouped mostly in the form of radial multiples (Fig. 1). Mean vessel diameter, 42 μm . Mean number of vessels per mm^2 , 87. Mean vessel element length, 262 μm . Mean vessel wall thickness, 3.5 μm . Perforation plates simple. Lateral wall pitting of vessels composed of alternate circular pits, both on vessel-vessel and on vessel-parenchyma contacts; pits about 4 μm in diameter. Vesturing present inconspicuously in pits of vessels. Imperforate tracheary elements all libriform fibers (careful examination of well-stained material reveals only simple pits). Mean libriform fiber diameter at widest point, 23 μm . Mean libriform fiber length, 493 μm . Mean libriform fiber wall thickness, 3.7 μm . Libriform fibers nonseptate. Tracheids (presumably vascentric tracheids) effectively absent, only a single tracheid seen in macerations. Axial parenchyma vascentric scanty, forming incomplete sheaths near vessels; often only a single parenchyma cell adjacent to a vessel. Axial parenchyma in strands of two cells. Rays both multiseriate and uniseriate, the former more abundant (Fig. 2). Ray cells larger than those of stem (compare Fig. 2, 3). Mean multiseriate ray height, 440 μm . Mean width of multiseriate rays at widest point, 2.7 cells. Mean uniseriate ray height, 120 μm . Ray cells as seen in radial section mostly square; upright and procumbent cells about equal in number, but fewer than square cells. Ray cell wall thickness about 2 μm . Pits among ray cells simple or bordered, the latter often on tangentially oriented walls. Starch abundantly present in ray cells (Fig. 6) and libriform fibers. Small rhomboidal or prismatic crystals (Fig. 6, arrows) present in ray cells, often more than one per cell. Storied structure evident in wider libriform fibers (a mild form of fiber dimorphism is present), vessel elements, and axial parenchyma (Fig. 2).

MONTINIA CARYOPHYLLACEA, basal stem, *Carlquist 4631*.—Growth rings present (semi-ring porous), with thicker-walled libriform fibers as well as narrower vessels in latewood. Mean number of vessels per group, 1.92. Mean vessel diameter, 42 μm . Mean number of vessels per mm^2 , 83. Mean vessel element length, 250 μm . Mean vessel wall thickness, 3.2 μm . Mean libriform fiber diameter at widest point, 25 μm . Mean libriform fiber length, 476 μm . Mean libriform fiber wall thickness, 4.0 μm . Mean multiseriate ray height, 443 μm . Mean width of multiseriate rays at widest point, 3.0 cells. Mean uniseriate ray height, 175 μm . Ray cells as seen in radial section mostly procumbent; upright cells mostly in uniseriate rays or in uniseriate tips of multiseriate rays. Crystals present in ray cells, but relatively infrequent.

MONTINIA CARYOPHYLLACEA, upper stem, *Carlquist 4536* (Fig. 3, 5–7).—Growth rings as in basal stem. Mean number of vessels per group, 2.16. Mean vessel

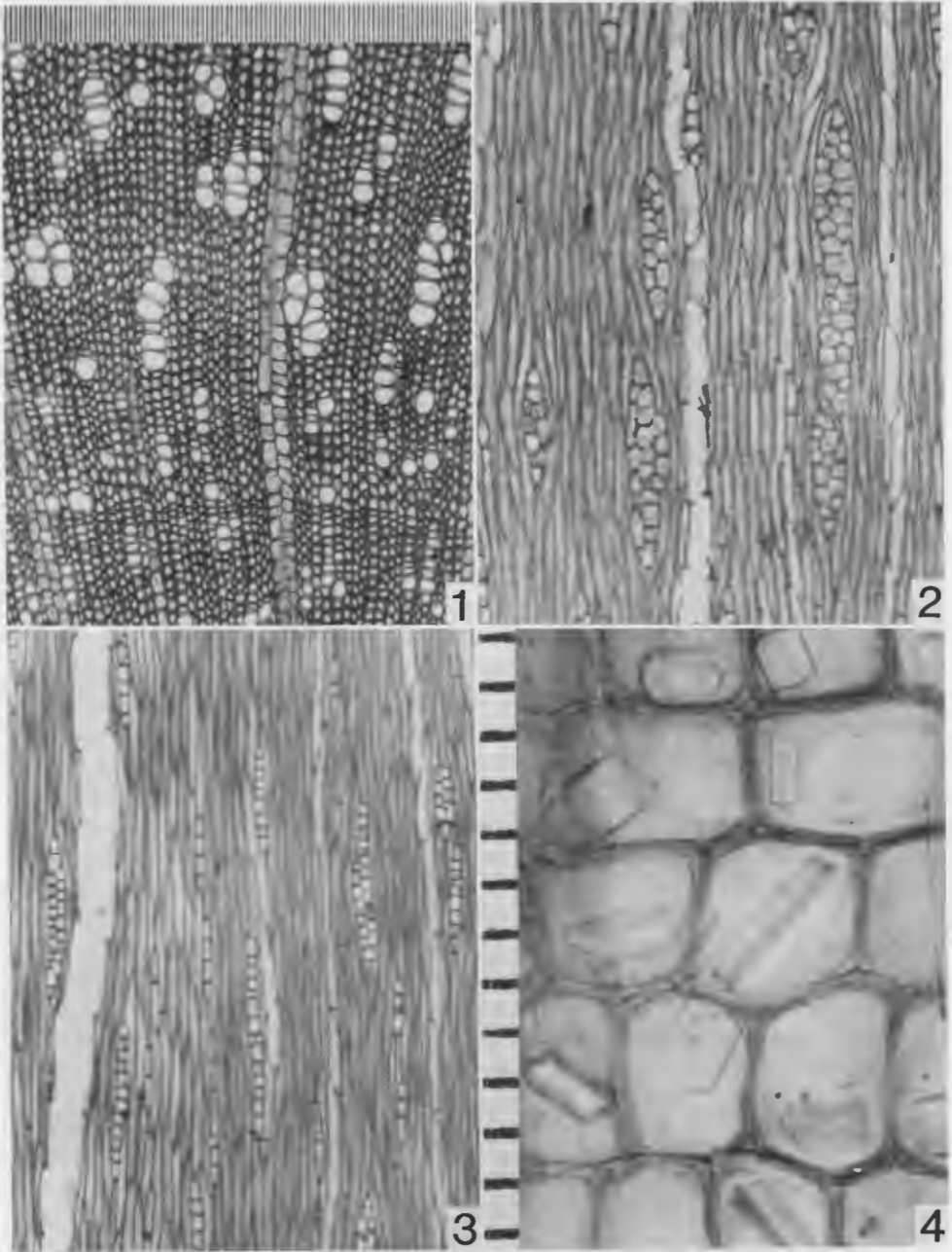


Fig. 1-4. Wood sections of *Montinia caryophyllacea* (Carlquist 4536).—1-2. Sections of upper root.—1. Transection; vessels in radial multiples.—2. Tangential section; most libriform fibers are storied.—3-4. Sections of upper stem.—3. Tangential section; libriform fibers are storied, below left.—4. Radial section, showing prismatic crystals in ray cells. (Magnification scale for Fig. 1-3 above Fig. 1 [divisions = 10 μm]; scale for Fig. 4 to left of Fig. 4 [divisions = 10 μm].)

diameter, 26 μm . Mean number of vessels per mm^2 , 83. Mean vessel element length, 269 μm . Mean vessel wall thickness, 4.1 μm . Vesturing in lateral wall pits of vessels composed of a small number of warts (Fig. 7). Mean libriform fiber diameter at widest point, 29 μm . Mean libriform fiber length, 520 μm . Mean libriform fiber wall thickness, 4.8 μm . Mean multiseriate ray height, 511 μm . Mean width of multiseriate rays at widest point, 2.4 cells. Mean uniseriate ray height, 172 μm . Ray cell size (Fig. 3) smaller than in roots (Fig. 2). Ray cells as seen in radial section about equally commonly upright, square, or procumbent. Crystals common in ray cells, often one per cell (Fig. 3). Crystals range from large and rectangular, about half the cell diameter in length, to smaller or more slender, more than four times as long as wide (Fig. 4, 5). Many crystals obviously dual, with the two halves forming mirror images of each other (Fig. 5). Storied structure more evident in wider libriform fibers (Fig. 3, lower left) than in narrower ones (remainder of Fig. 3).

KALIPHORA MADAGASCARIENSIS, upper stem, *Fosberg 52604* (Fig. 8, 9).—Growth rings not evident on sample studied, although more than one year's secondary xylem present. Mean number of vessels per group, 1.55. Vessels solitary or in radial multiples (Fig. 8). Mean vessel diameter, 37 μm . Mean number of vessels per mm^2 , 133. Mean vessel element length, 310 μm . Mean vessel wall thickness, 2.5 μm . Perforation plates simple. Lateral wall pitting of vessels composed of alternate circular pits about 2.5 μm in diameter, both on vessel-vessel and vessel-parenchyma interfaces. Grooves interconnecting pit apertures inconspicuously present. Vesturing present in vessel pits. Thin-walled tyloses present in a few vessels. Imperforate tracheary elements all libriform fibers, pits apparently simple; splits extending from pits apertures in fiber walls. Mean libriform fiber diameter at widest point, 22 μm . Mean libriform fiber length, 486 μm . Mean libriform fiber wall thickness, 3.0 μm . Axial parenchyma scarce, vasicentric, in strands of two cells. Rays both multiseriate and uniseriate (Fig. 9), about equal in frequency. Mean multiseriate ray height, 443 μm . Mean width of multiseriate rays at widest point, 2.1 cells. Mean uniseriate ray height, 196 μm . Ray cells as seen in radial section mostly square or upright; procumbent cells present in central portions of multiseriate rays. Starch present in ray cells. Crystals absent in rays. Storying vaguely apparent in some areas of libriform fibers.

Examination of radial sections which extend to pith in all four of the above categories demonstrates that primary xylem tracheary elements, as far as can be determined, all have simple perforation plates.

SYSTEMATIC CONCLUSIONS

For systematic conclusions to be valid, the roster of features presented must be accurate. There are a few disagreements between the features reported by Ramamonjariisoa (1980) and those in the account above. Despite having excellent preparations with sensitive haematoxylin staining of primary walls, I was unable to find bordered pits in imperforate tracheary elements, which must therefore be termed libriform fibers rather than fiber-tracheids as reported by Ramamonjariisoa (1980). Ramamonjariisoa also reports tracheids in *Montinia* and *Kaliphora*. Although I observed a single tracheid (presumably vasicentric) in a maceration of *Montinia* wood, tracheids are so scarce as to be effectively absent in my

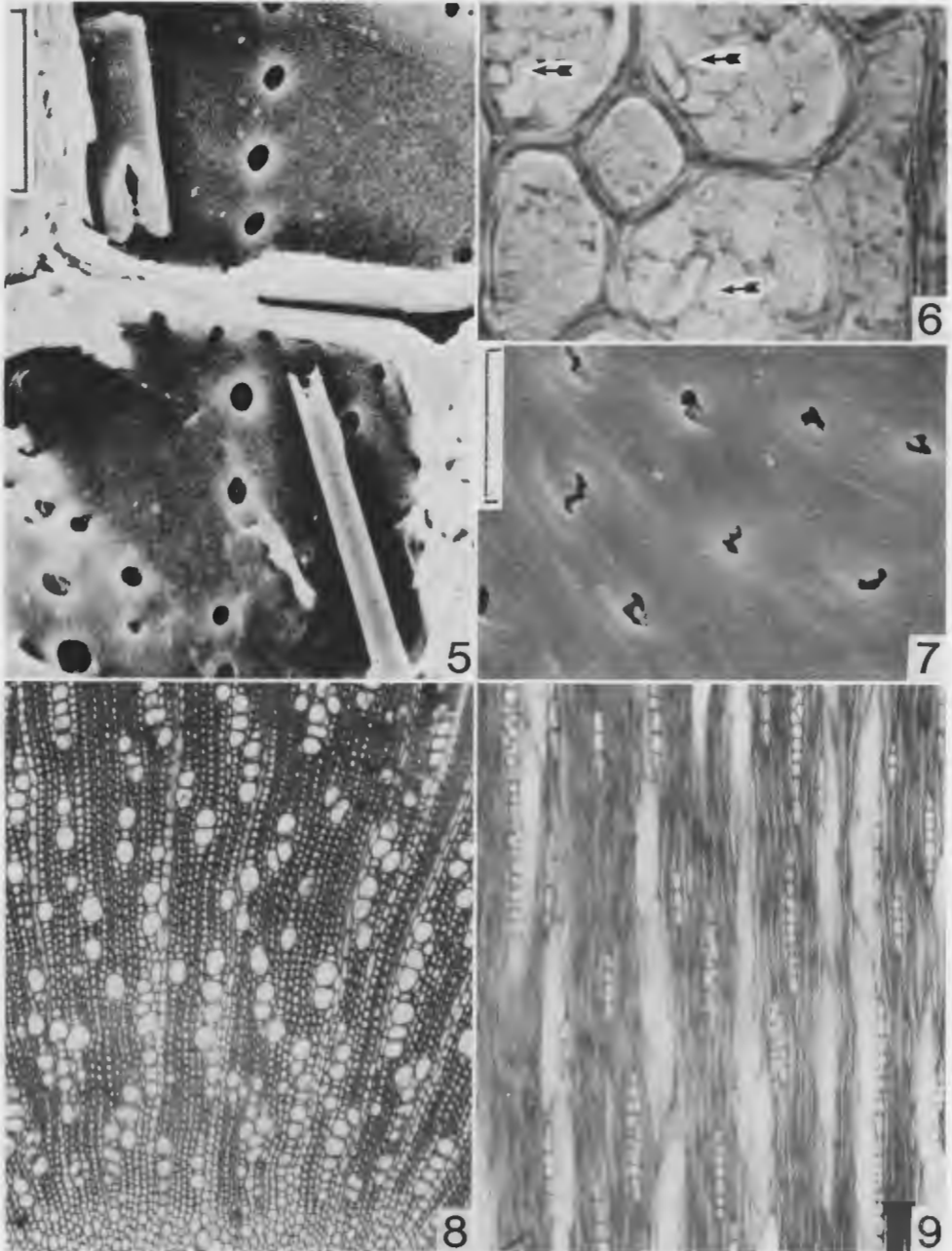


Fig. 5-9. Wood sections of *Montinia* and *Kaliphora*.—5-7. *Montinia caryophyllacea* (Carlquist 4536).—5. Upper stem; SEM micrograph of crystals from radial section of ray, showing duality in form of each crystal.—6. Root, light micrograph of tangential section showing small rhomboidal crystals in ray cells (arrows) plus starch (indistinct outlines within cells).—7. Upper stem, SEM micrograph of vessel wall, showing vestures lining the pit apertures, which therefore have irregular outlines.—8-9. *Kaliphora madagascariensis* (Fosberg 52604).—8. Transection; growth rings absent.—9. Tangential section; all rays are uniseriate or biseriate. (Magnification scales for Fig. 5, 7, at upper left [bracket = 5 μ m]; scale for Fig. 6, to left of Fig. 4; scale for Fig. 8-9, above Fig. 1.)

material. In sections of various woods, one can occasionally obtain the appearance of tracheid presence (and tracheids have been reported in the literature accordingly) where a libriform fiber faces a vessel, and thus the lateral wall pitting of the vessel is seen within the fibriform outlines of the libriform fiber, but that is an interface between two different cell types rather than a tracheid. Ramamonjjarisoa's report of tracheid presence in *Montinia* and *Kaliphora* may be valid, but if so, tracheids are so infrequent as to be negligible, as they are in a scattering of other dicotyledons. Ramamonjjarisoa (1980) mentions occasional septate fibers in *Montinia*, although not in *Kaliphora*. I was unable to find septate fibers in either genus; Ramamonjjarisoa's claim of septate fibers in *Montinia* may refer to axial parenchyma (which she did not find in *Montinia*), which is subdivided into strands of two cells in that genus, causing a resemblance to septate fibers. Ramamonjjarisoa (1980) does not mention storying in wood of *Montinia* or *Kaliphora*; my material clearly showed it, at least in some places within the secondary xylem. Storying may be expected to increase with age, so that my relatively large stems of *Montinia* may have been more favorable for demonstration of storying. In all other respects, our accounts on wood of the two genera agree.

Because wood of *Montinia* resembles that of *Kaliphora* and *Grevea*, one can construct a description of features common to all three genera, with exceptions as noted in parentheses. Such a description follows. Wood diffuse porous to semiring porous. Vessels solitary or grouped into radial multiples. Perforation plates simple, even in primary xylem. Lateral wall pitting of vessels composed of alternate circular bordered pits. Pits vested (*Kaliphora*, *Montinia*) or vessel walls vested (*Grevea*). Imperforate tracheary elements are libriform fibers, with simple pits commoner on radial than on tangential walls. Vasicentric tracheids present in very small numbers or absent. Axial parenchyma vasicentric scanty, not common, composed of strands of two cells. Multiseriate rays as common as uniseriate rays, more common, or (some species of *Grevea*) uniseriate rays absent. Procumbent cells present to various degrees; rays Heterogeneous Type IIB of Kribs (1935) in *Kaliphora* and *Montinia* or Homogeneous Type I or II (*Grevea*). Multiseriate rays chiefly biseriate, but wider in some species of *Grevea*. Rhomboidal crystals, some with mirror-image duality, present in ray cells of *Montinia* (not reported in *Grevea* or *Kaliphora*). Wood storied (*Montinia*) or vaguely so (*Kaliphora*), or storying apparently absent (*Grevea*). Intraxylary phloem absent, but pith bundles, either phloic or collateral, present in *Grevea*.

The above summation shows that *Kaliphora* and *Montinia* are closely related. Certain embryological data also connect *Kaliphora* to *Montinia* (Capuron 1969a), and the two genera should be grouped as Montiniaceae despite Takhtajan's (1987) inclusion of *Kaliphora* in a neighboring family, Melanophyllaceae. Wood data place *Grevea* further from *Montinia* than *Kaliphora* is from *Montinia*, but *Grevea* is includable in Montiniaceae on the basis of wood data, as suggested by Takhtajan (1987). The three genera are linked by having tripartite unilacunar nodes (Ramamonjjarisoa 1980) and, as mentioned earlier, epigyny, dioecy, and lack of tannins. The three genera can also be said to share pollen features of phyletic significance, such as sphaeroidal grain shape, isopolar nature, and presence of three colpae provided with transverse furrows with "nexinous thickenings" (Erdtman 1952; Hideux and Ferguson 1976). Recognition of Montiniaceae as a trigeneric family seems a defensible taxonomic concept on the basis of present

information. In this regard, one notes that phytogeography is suggestive, since the three genera are limited to Africa and Madagascar.

With respect to ordinal position of Montiniaceae, the view of various authors that it should be placed near Saxifragaceae can be critically examined in terms of anatomy and other features. Epigyny, characteristic of Montiniaceae, occurs in such rosalean genera as *Ribes*. Dioecy, another feature of Montiniaceae, is much rarer in the order. However, relative frequency of features is not as important as the constellation of features that are likely indicators of relationship. Wood of Rosales shows many primitive characteristics, but simple perforation plates occur in a number of genera—very likely an evolutionary adaptation to seasonal availability of water. However, even in those genera of Rosales with simple perforation plates in secondary xylem, scalariform perforation plates may be found in primary xylem, because primary xylem tends to be a refuge for primitive features (Bierhorst and Zamora 1965). Montiniaceae, on the contrary, have simple perforation plates in primary xylem. Vestured pits have not been reported in vessels of Rosales (note: Fabaceae is considered here as sapindalean, in agreement with recent views). The photograph of wartiness in vessels of *Ixerba* of the Escalloniaceae (Meylan and Butterfield 1978) may represent merely a chance deposition of a secondary plant product, for those authors characterize vessel walls as smooth in *Ixerba*, and also figure that condition. Imperforate tracheary elements of Rosales are mostly tracheids; fiber-tracheids occur in a few genera, whereas Montiniaceae have libriform fibers (Metcalf and Chalk 1950; terminology in accordance with IAWA Committee on Nomenclature 1964). Axial parenchyma of Rosales is mostly apotracheal (diffuse); scanty vasicentric axial parenchyma, the type found in Montiniaceae, occurs in only a few genera of Hydrangeaceae, such as *Philadelphus* (Metcalf and Chalk 1950). The strands of axial parenchyma are two cells long in Montiniaceae, but mostly longer in Rosales. Rays of Rosales are mostly taller than those of Montiniaceae, and conform to more primitive types. Storied wood structure, reported here in Montiniaceae, is absent in Rosales unless Greyiaceae are regarded as rosalean. Intraxylary phloem has not been reported in rosalean genera (Metcalf and Chalk 1950). However, iridoid compounds have been reported in *Montinia* (Dahlgren, Jensen, and Nielsen 1977). Iridoid compounds are characteristic of some cornalean (rosalean, saxifragalean) families such as Alseuosmiaceae, Escalloniaceae, and Hydrangeaceae (Jensen, Nielsen, and Dahlgren 1975), but have not been reported in Myrtales.

The idea of Milne Redhead (1955) that Montiniaceae are closer to Onagraceae than to rosalean families is worthy of consideration in view of the lack of congruence between Montiniaceae and rosalean families with respect to wood anatomy. Montiniaceae should be compared not merely with Onagraceae, but with other Myrtales as well. Vliet and Baas (1984), who offer a valuable summary of wood of Myrtales, unfortunately did not consider Montiniaceae in their survey, nor did Dahlgren and Thorne (1984) take Montiniaceae into account in their attempt to circumscribe the order Myrtales. Tetramery and epigyny, characteristic of *Kaliphora* and *Montinia*, typifies Onagraceae and some other myrtalean families (Dahlgren and Thorne 1984). Perforation plates in secondary xylem of Myrtales are predominantly simple (Vliet and Baas 1984), as they are in Montiniaceae. Of greater significance, however, is that myrtalean families such as Combretaceae, Lythraceae, and Melastomataceae have simple perforation plates in primary xylem as well (Bierhorst and Zamora 1965:701), as in Montiniaceae; such specialized

xylem characterizes only a small number of dicotyledon families. Vestured pits, a noteworthy feature of *Kaliphora* and *Montinia*, are cited as one of the ordinal features of Myrtales (Vliet and Baas 1984), but they occur in only a scattering of other dicotyledonous orders. Although tracheids occur in some myrtalean families, such as Penaeaceae (Carlquist and DeBuhr 1977), libriform fibers occur in others, such as Onagraceae (Carlquist 1975). Mirror-image double crystals, a peculiar feature of *Montinia*, have been reported in Onagraceae and Melastomataceae but very few other families (Carlquist 1988). Storied wood structure, present in Montiniaceae, has not been reported in the families of Myrtales in the narrow sense utilized by Dahlgren and Thorne (1984), but a special case discussed below is worthy of consideration. Intraxylary phloem is absent in *Kaliphora* and *Montinia*, but pith bundles are present in *Grevea*. Pith bundles of this sort have been reported in numerous genera of Melastomataceae (see Metcalfe and Chalk 1983:209).

The fact that storied wood structure is absent in Myrtales (Vliet and Baas 1984) but present in Montiniaceae is worthy of further consideration because storied wood structure has been reported from only a limited number of orders of dicotyledons, such as Malvales and Sapindales. However, storied wood structure does occur in two families that have been referred to Myrtales by some authors, Eleagnaceae and Thymeleaceae (Metcalfe and Chalk 1950, 1983). Thymeleaceae are regarded as myrtalean by Cronquist (1984), although Dahlgren and Thorne (1984) demur. Vliet and Baas (1984) do find xylary grounds for regarding Thymeleaceae as myrtalean: Thymeleaceae have vestured pits and intraxylary phloem, two features regarded as diagnostic of Myrtales. Perhaps Thymeleaceae should be regarded as an outlier of Myrtales, closer to Myrtales than to other orders; Vliet and Baas (1984) do not find evidence from wood anatomy to support the idea offered by Dahlgren and Thorne (1984) that Thymeleaceae is closer to Euphorbiales than to Myrtales. If Thymeleaceae is an outlier of Myrtales, perhaps Montiniaceae is another such outlier, which may not fit within the tight grouping of the families in the narrow sense of Myrtales, but which may be includable in a Myrtales defined more loosely. This concept is the one to which Milne Redhead (1955) and Ramamonjiarisoa (1980) subscribe. The presence or iridoid compounds (absent in Myrtales and in Thymeleaceae) in *Montinia*, however is troubling. The chromosome number of *Montinia*, $n = 34$ (Goldblatt 1976) does not appear helpful: it is an unusual number not found (or if so, very rarely) in the families and orders most prominently mentioned as possibly containing Montiniaceae. One might expect that even if one can define a particular order well, there may be families that are peripheral to such orders, and one is tempted to exclude them so that the order can be defined with more numerous features and thus circumscribed more clearly. However, ultimately such families must be placed. Such families as Barbeyaceae, Daphniphyllaceae, and Sabiaceae come to mind: no matter what orders, respectively, ultimately receive these families, the definitions of those orders will have to be widened (unless one opts for monofamilial orders, in which case the problem is merely transferred to a superordinal level).

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