

WOOD ANATOMY AND RELATIONSHIPS OF LACTORIDACEAE¹

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Mature wood of *Lactoris*, not previously available for study, reveals ten distinctive characters: vessels with simple perforation plates; vessels in pore multiples; vessel-to-axial parenchyma pits scalariform or transitional, vessel-to-vessel pits alternate; fiber-tracheids with vestigial pits; fiber-tracheids, vessels, and axial parenchyma storied; axial parenchyma vasicentric scanty; axial parenchyma either not subdivided or, if subdivided, with thin nonlignified walls between the cells (like the septa in septate fibers); rays wide and tall, little altered during ontogeny; ray cells upright; and ray cells taller adjacent to fascicular areas. All of these features occur in woods of *Piper* and other Piperaceae. The systematic position of *Lactoris* is therefore reassessed. Evidence available to date is consonant with placement of Lactoridaceae in Piperales, in which it would be more primitive than Piperaceae or Saururaceae. Features cited as evidence for alternative placements of Lactoridaceae are reviewed.

Earlier studies of anatomy of *Lactoris fernandeziana* Phil., sole species of Lactoridaceae, were based on limited material (Carlquist, 1964). The stems used in that study were only twigs, so that the mature wood pattern of that plant could not be determined. However, recently a stem of near-maximal size (1 cm in diameter) for the species was made available to me by Dr. Delbert Wiens. This stem was collected by Dr. Wiens and Dr. Tod F. Stuessy during field work on the island Masatierra, to which *Lactoris* is endemic, in the Juan Fernandez Islands. This stem provides adequate material for an accurate description of the mature wood pattern of this species.

The results of study on this wood sample are of great significance with respect to understanding the relationships of *Lactoris*. *Lactoris* has relatively few gross morphology characters that lend themselves to decisive establishment of relationships. The mature wood of *Lactoris*, however, proves to have a series of distinctive features of systematic significance, and wood anatomy is therefore of special significance in assessing relationship. The position of *Lactoris* has been uncertain. All workers agree that the genus belongs in a grouping that corresponds to the superorder Annonanae of Dahlgren (1983), a superorder termed Annoniflorae by Thorne (1976) and Magnolianae by Takhtajan (1980). This is not unlike the older concept Ranales, and includes all families in which ethereal oil cells are present. *Lactoris* has been

variously referred to each of the orders in the superorder Annonanae (for a detailed history, see Lammers, Stuessy, and Silva O., 1986); Magnoliales (Hutchinson, 1964; Cronquist, 1981; Lammers, Stuessy, and Silva O., 1986); Laurales (Smith, 1971; Takhtajan, 1980; Thorne, 1983); and Piperales (Melchior, 1964; Walker, 1976). Others who wish to stress the isolation of the genus have placed it in the monofamilial order Lactoridales (Dahlgren, 1983; Walker and Walker, 1984). Suggested affinities of Lactoridaceae with particular families within the three orders cited above are reviewed by Lammers, Stuessy, and Silva O. (1986). The component families of the superorder Annonanae offer considerable diversity in wood structure, and therefore wood anatomy ought to provide an excellent opportunity for developing better ideas about placement of Lactoridaceae.

A detailed description of wood of *Lactoris fernandeziana* is given below. This description is based on both light microscopy and scanning electron microscopy (SEM). Species with which *Lactoris* is compared are represented in the Rancho Santa Ana Botanic Garden wood slide collection. In addition, descriptions of woods, as compiled by authors such as Metcalfe and Chalk (1950), Patel and Bowles (1980), and Metcalfe (1987), have been consulted.

MATERIALS AND METHODS

The stem of *Lactoris fernandeziana* studied here is vouchered by the specimen *Stuessy 11178* (OSU). This wood sample was available in dried condition. It was boiled in water and stored in 50% aqueous ethyl alcohol. Sections were prepared from near the base of this stem,

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with care to select portions with relatively straight grain. Sections were prepared on a sliding microtome. Some sections were stained with safranin and counterstained with fast green. Other sections were dried between clean glass slides and examined with SEM after sputter-coating with gold. Macerations were prepared with Jeffrey's fluid and stained with safranin.

Quantitative data are derived from outer portions of the stem studied. Vessel element length, vessel diameter, vessel density, and number of vessels per group are given as means based on 25 measurements. Other quantitative data represent measurements of conditions judged to be typical. Rays of *Lactoris* are so wide and tall, and therefore few in number, that meaningful quantitative data cannot be readily obtained. Terminology follows that of the IAWA Committee on Nomenclature (1964).

ANATOMICAL DESCRIPTIONS

Growth rings absent (Fig. 1). Vessels solitary or in radial multiples or radial chains (Fig. 1). Mean number of vessels per group, 1.6. Number of vessels per mm² (ray areas not excluded), 22.5. Vessels angular to rounded in outline (Fig. 1). Perforation plates simple; a few plates partly or completely traversed by a single wide bar are located in vessels near the pith. Mean vessel lumen diameter at widest point, 41 μm . Mean vessel element length, 173 μm . Mean vessel wall thickness, 2.4 μm . Vessel-to-vessel and vessel-to-fiber-tracheid pits alternate, circular in outline or slightly elliptical, about 5 μm in diameter (Fig. 3); pit apertures narrowly elliptical. Vessel-to-axial parenchyma pits alternate, transitional, or scalariform (Fig. 4; Fig. 8, left). All imperforate tracheary elements are fiber-tracheids according to the terminology of the IAWA Committee on Nomenclature (1964), because vestigial borders are present, as revealed by SEM (Figs. 5–7). Mean fiber-tracheid diameter at widest point, 28 μm . Mean fiber-tracheid length, 371 μm . Mean fiber-tracheid wall thickness, 3.2 μm . Pits on fiber-tracheids narrow, oriented obliquely (Figs. 9–11). Fiber-tracheids storied, conforming to the storied pattern shared by vessels and axial parenchyma. Axial parenchyma cells scanty vasicentric, usually a sheath one cell thick around vessels or vessel groups. Axial parenchyma not subdivided into strands or, more commonly, subdivided once or twice by means of thin walls that are mostly not lignified (Fig. 4), and are therefore like the walls subdividing septate fibers rather than axial parenchyma strands. Rays wide and tall (Fig. 1, left; Fig. 2, right),

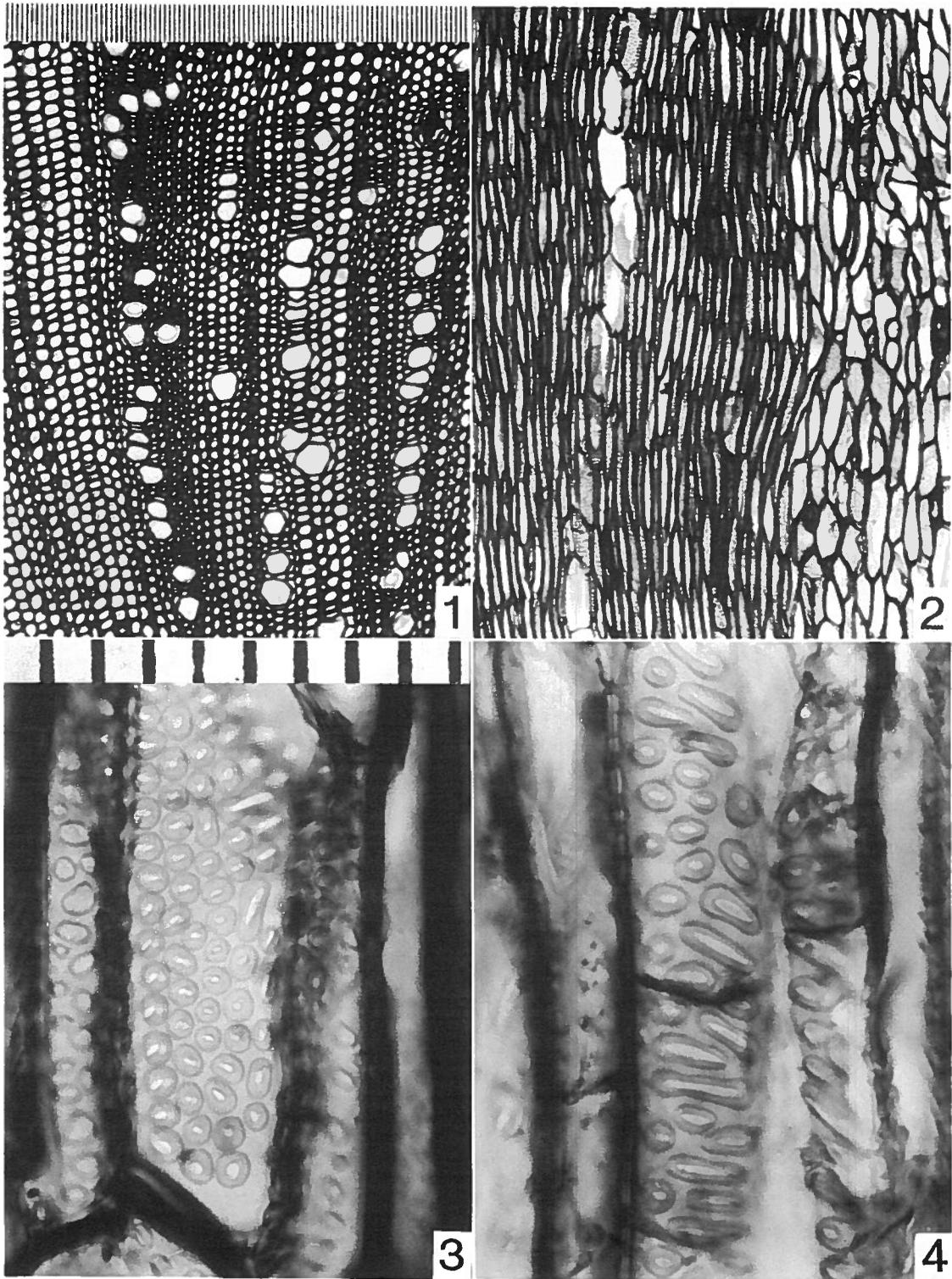
tending to extend unbroken from pith to cambium but widening during growth of the stem. Ray cells mostly upright, a few square or procumbent cells present (Fig. 2, right). Ray cells adjacent to fascicular areas tend to be taller and more like fiber-tracheids than cells in the center of the rays (Fig. 2). Ray cell walls about 2.2 μm thick. Some pits among ray cells bordered, others apparently simple. Ray cells adjacent to fascicular areas storied, indicating that increase in ray width occurs by means of radial longitudinal divisions in ray initials near the ray margins (or else by conversion of ray cell initials into fusiform initials). Small crystals present in fiber-tracheids (Figs. 8–11). Rhomboidal crystals present, mostly near tips of fiber-tracheids (Figs. 10, 11) as solitary crystals (Figs. 8, 9), or in small groups (Figs. 10, 11). Resinlike deposits yellow in color in unstained material present in ray cells as well as in some vessels (Fig. 2). The occurrence of crystals and resinlike deposits in *Lactoris* wood was not reported earlier (Carlquist, 1964).

Patches of sclereids were observed in the secondary phloem. The sclereids are not abundant, and most of the bark consists of sieve tube elements, phloem parenchyma, and ray parenchyma. The resinlike deposits seen in wood are also present in bark, and their carbonized or semicarbonized nature gives the bark a dark brown color.

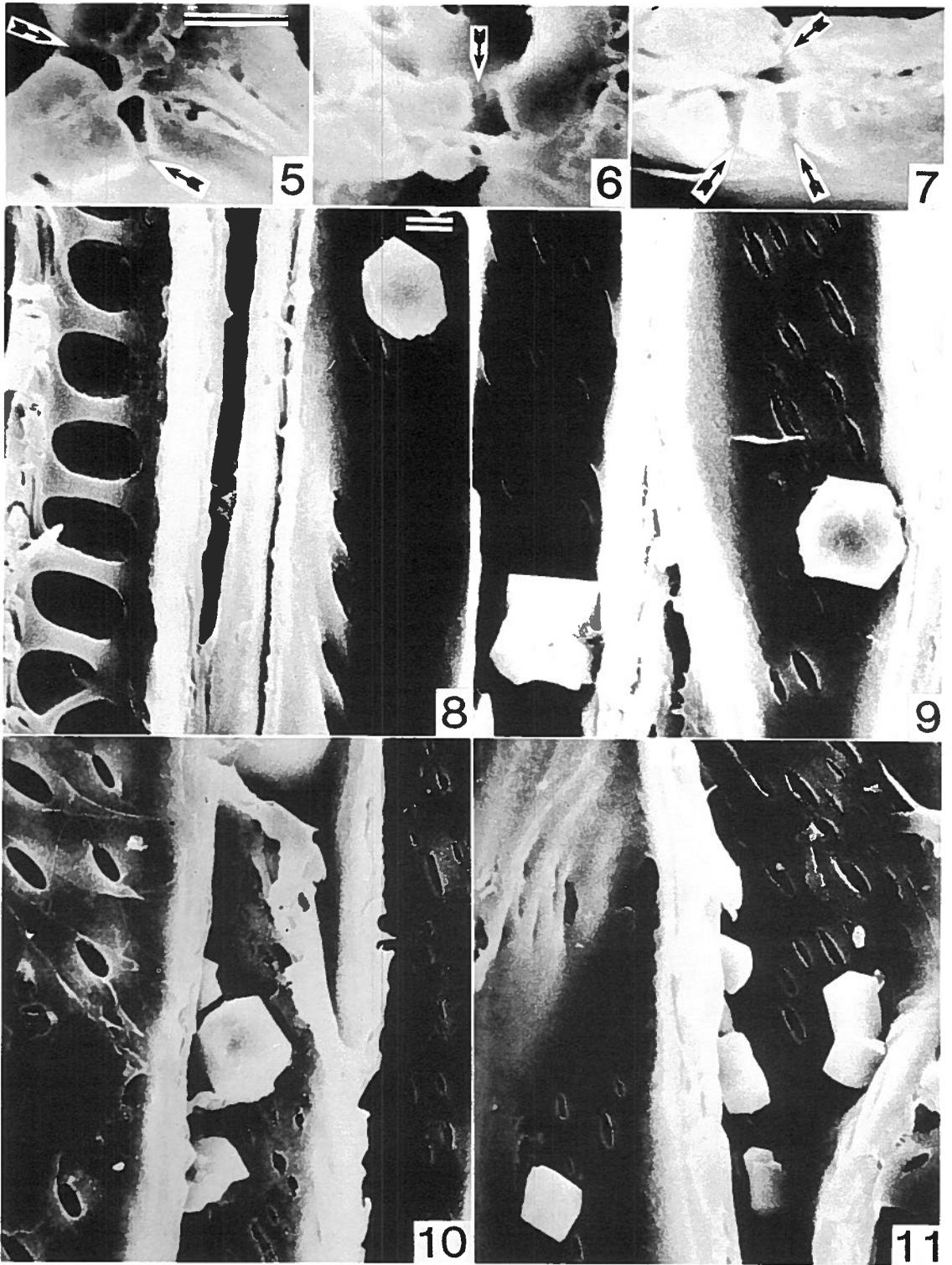
DISCUSSION

Wood of *Lactoris* has a number of very distinctive features, features not commonly found in the superorder Annonanae, the group to which *Lactoris* must be referred regardless of its affinities within that superorder. These features include: vessels with simple perforation plates; vessels in radial chains or pore multiples; vessel to axial parenchyma pitting scalariform to alternate, vessel-to-vessel pitting alternate; fiber-tracheids with vestigially bordered pits; fiber tracheids storied, conforming to storied pattern of vessels and axial parenchyma; axial parenchyma vasicentric scanty; axial parenchyma not subdivided or, if in strands, cells separated by thin nonlignified walls; rays wide and tall, little subdivided; ray cells mostly upright; ray cells taller adjacent to fascicular areas.

Surprisingly, all ten of these features occur in woods of Piperaceae. The wood of *Lactoris* is virtually identical to that of Piperaceae (observations based on *Piper sancti-felicis* Trelease, Davidson 5266, two species of *Piper* from Fiji—Carlquist 15626 and Carlquist 15630—and several collections of *Macropiper*



Figs. 1-4. Wood sections from near periphery of mature stem of *Lactoris fernandeziana*, *Stuessy 11178*. 1. Transverse section, ray at left. 2. Tangential section, ray at right. Note storied condition. 3. Vessel-to-vessel pitting from tangential section. 4. Vessel-to-axial parenchyma pitting; horizontal cell walls subdividing cells of axial parenchyma strand; from tangential section. (Figs. 1, 2, magnification scale above Fig. 1 [divisions = 10 μ m]; Figs. 3, 4, scale above Fig. 3 [divisions = 10 μ m].)



Figs. 5-11. SEM photographs of wood sections from near periphery of mature stem of *Lactoris fernandeziana*, *Stuessy 11178*. 5-7. Portions of fiber-tracheid walls from transection, showing bordered nature of pits (pits indicated by arrows). 8-11. Rhomboidal crystals in fiber-tracheids, from tangential section. 8. Fiber-tracheid with axial parenchyma cell (scalariform pitting) at left. 9. Adjacent fiber-tracheids, showing nature of pitting in face view. 10. Tip of fiber-tracheid, showing three crystals; portion of vessel wall at left. 11. Adjacent fiber-tracheids, showing smaller crystals, pitting in face view. (Figs. 5-7, bar in Fig. 5 = 1 μ m; Figs. 8-11, bar in Fig. 8 = 1 μ m.)

excelsum Miq.). The only feature in which *Piper* differs to any degree from *Lactoris* in these features is that vessels of Piperaceae typically bear scalariform pits on vessel-to-vessel and vessel-to-libriform fiber contacts. However, the vessel-to-vessel pitting of *Piper sancti-felicis* is alternate, as in *Lactoris*. Although simple pits have been reported in imperforate tracheary elements of *Piper* (Metcalf and Chalk, 1950), I was able to observe vestigially bordered pits, like those in *Lactoris*, in what must therefore be called fiber-tracheids of *Piper* sp. (Carlquist 15630) and, less commonly, *P.* sp. (Carlquist 15626). The former species clearly showed the tendency for marginal cells of rays to be taller, similar to those of adjacent imperforate tracheary elements.

Wood of *Lactoris* was previously reported to be rayless (Carlquist, 1964). Technically it can be called rayless in young stems because cells of the potential ray areas are about the same length as fiber-tracheids, although they are somewhat wider. Study of the larger stem shows that differentiation between fiber-tracheids and ray cells increases with time, so that in the mature stem, rays are clearly present. Examination of tangential and transverse sections of the mature *Lactoris* stem in gross aspect leaves no doubt that rays exist. Incidentally, minute borders do occur on both ray cells and fiber-tracheids, so that the resemblance in young stems between ray cells and fiber-tracheids is close, except for width. The seemingly rayless nature of young stems of *Lactoris* prevented me from seeing in my earlier study the resemblances in wood anatomy between *Lactoris* and Piperaceae. This resemblance is quite pronounced, on the basis of the present study. Many of these features are of limited distribution in dicotyledons; for example, no families of superorder Annonaceae other than Lactoridaceae and Piperaceae have storied woods.

Wide, tall rays infrequently subdivided with growth of the stem and composed mostly of upright cells can be seen in the chloranthaceous genera *Ascarina*, *Hedyosmum*, and *Sarcandra* (Carlquist, 1987, 1990; Metcalfe, 1987). The imperforate tracheary elements of *Ascarina* and *Hedyosmum* are fiber-tracheids (Metcalf, 1987; Carlquist, 1990). Thus, they resemble imperforate tracheary elements of Lactoridaceae and Piperaceae. There is definitely a contrast between Chloranthaceae on the one hand and Lactoridaceae and Piperaceae on the other with respect to evolutionary status of vessel elements. The scalariform perforation plates of *Ascarina*, *Hedyosmum*, and *Sarcandra* retain strands of primary wall material in per-

forations (Carlquist, 1987, 1988, 1990), and are thus quite primitive by comparison to perforation plates of Lactoridaceae and Piperaceae. The few perforation plates of *Lactoris* subdivided by a single bar are located in vessels near the pith (where they ought to be retained if ontogenetically earlier features are modified less readily). These plates represent the last vestige in Lactoridaceae of scalariform perforation plates. Chloranthaceae do not have storied woods. There are, other than the features mentioned above, no major differences in wood anatomy between Chloranthaceae and Lactoridaceae or Piperaceae. Although Chloranthaceae are less commonly included in Piperales by current authors than was done formerly (see Lammers, Stuessy, and Silva O., 1986), that placement seems supported on the basis of wood anatomy: the notably wide tall rays of Chloranthaceae are a significant feature in this regard.

If wood of Lactoridaceae is remarkably similar to that of Piperaceae, one must account for why Lammers, Stuessy, and Silva O. (1986) conclude that Lactoridaceae cannot be placed in either Piperales or Chloranthales, but must instead be included in Magnoliales. They ally Lactoridaceae most closely with Annonaceae and Myristicaceae. One must note that Lammers, Stuessy, and Silva O. (1986) employ only a single wood feature: perforation plate morphology. Simple perforation plates characterize not merely Lactoridaceae, but the vast majority of dicotyledon families (Carlquist, 1988), so this feature is not a likely indicator of relationship. The systematic distribution of simple perforation plates shows that this feature is a specialization that has occurred in many phylads independently. If one examines the cladogram of Lammers, Stuessy, and Silva O. (1986), that includes Lactoridaceae, one finds the following synapomorphies leading to the node from which branch the trio of families Annonaceae-Lactoridaceae-Myristicaceae: simplification of the perforation plates; reduction in perianth segment number (to 1-9), and differentiation of stamens into filaments and anthers (as opposed to laminar stamens). These are all specializations that have developed in numerous angiosperms; the specialized character state in these characters, represented by Lactoridaceae, also occurs in the majority of dicotyledon families (over 90% of dicotyledons likely have the specialized character state for these features). These synapomorphies are, therefore, not high in significance as indicators of relationship. In nodes further down in the Lammers, Stuessy, and Silva O. cladogram are symplesiomorphies of a similar nature: ves-

selless woods (Winteraceae) yield to vessel-bearing woods (all others); partially sealed carpels yield to closed carpels; styleless carpels give rise to those differentiated into a stylar region; and carpel number is reduced to 1–4. Again, the specialized character states of these features characterize the vast majority of dicotyledons. Features that occur in Lactoridaceae that would be more indicative of relationship are of limited distribution in angiosperms and with distributions in related groups of families, such as stomatal type, ovule type, embryological details, pollen exine stratification, seed coat anatomy, and the occurrence of particular secondary plant products.

The presence of stipules in Lactoridaceae is a very distinctive character. Stipules are also present in Piperaceae, Saururaceae (Weberling, 1970), and Chloranthaceae (Lammers, Stuessy, and Silva O., 1986), but are absent from remaining families of Magnoliales other than Magnoliaceae, which has rather different stipules (Lammers, Stuessy, and Silva O., 1986). In the Lammers, Stuessy, and Silva O. cladogram, however, stipules figure not as a character indicative of relationship, but as a homoplasy evolved four different times (Chloranthaceae, Lactoridaceae, Piperales, and Magnoliaceae).

The trimery of flowers of Lactoridaceae, if not conspicuously expressed in Saururaceae, is certainly reflected in the three (or six) stamens and three carpels found in the majority of Saururaceae (Tucker, 1979, 1985; Han-Xing and Tucker, 1990). In Piperaceae, *Piper* is tricarpellate, although *Peperomia* is not apparently so (Tucker, 1980, 1982a,b). Some Chloranthaceae also show floral trimery: three-toothed calyces (Endress, 1987); the three stamens of *Chloranthus* may or may not represent true trimery (Swamy, 1953; Endress, 1987). This trimery may be more indicative of relationship than the trimery of Annonaceae, which is limited to the perianth. In this regard, one notes that Lammers, Stuessy, and Silva O. (1986) do not code perianth trimery as a character state, but code the range of 0–9 parts as a character state instead.

The peculiar pollen tetrads of *Lactoris* (Erdtman, 1952; Carlquist, 1964) are unique within angiosperms in having a saccate exine (Carlquist, 1964; Zavada and Taylor, 1986). The occurrence of tetrads tends not to be a good indicator of relationship, because this feature evidently has evolved independently in various families not regarded as closely related: Fabaceae, Myrothamnaceae, Nepenthaceae, Sarcolaenaceae, and Typhaceae, for example. The pollen tetrads found in Annonaceae may

not be indicative of relationship to Lactoridaceae. Tetrads with a catasulcate orientation of the aperture occur in Annonaceae, whereas the lactoridaceous tetrads have an anasulcate condition. Zavada and Taylor (1986) found that saccate grains much like those of *Lactoris* may be found in early Cretaceous deposits. Exine stratification of *Lactoris* pollen grains is not of decisive significance in relating this genus to just one or a few families, but is of a type found in a number of families with numerous primitive features (Zavada and Taylor, 1986).

In view of the near-identity of the distinctive wood of *Lactoris* with wood of Piperaceae, a reappraisal is in order. These data would change to a marked extent the topology of the cladogram offered by Lammers, Stuessy, and Silva O. (1986). Lammers (personal communication) points out that the assignment of Lactoridaceae to Magnoliales was made on the basis of phenetic analysis, and that cladistic analysis was not undertaken for several reasons: 1) good "polarizable" characters with clear homology were difficult to find; 2) cladistic analysis should be performed only on holophyletic groups, but without such orders as Illiciales a holophyletic group was not at hand; and 3) taxa used in an analysis should be relatively coherent in their morphology, anatomy, chemistry, etc., for cladistic analysis to be feasible. Lammers (personal communication) still believes that Lactoridaceae could be assigned to Magnoliales, because he believes that Piperales take their origin from Magnoliales, and that Lactoridaceae may occupy an intermediate position between the two orders. In the interests of overall phenetic homogeneity, he believes that the transitional family is best placed in the ancestral order rather than the derivative. However, I find that if Magnoliales are to incorporate Lactoridaceae, then Piperales and Chloranthales should be included in the concept Magnoliales. I prefer that for the present, Piperales and Chloranthales be recognized as distinct orders, and that Lactoridaceae be included within Piperales. In this regard, a more recent cladogram that includes Lactoridaceae (Donoghue and Doyle, 1989) pairs Lactoridaceae with Aristolochiaceae as an offshoot of a branch from which, further up, depart Piperaceae and Saururaceae as a pair and then Liliaceae, Cabombaceae, and Nymphaeaceae. The Donoghue and Doyle (1989) cladogram does indicate relationship between Lactoridaceae and Piperales, but between these two groups and the magnolialean families lie Hamamelidales, Ranunculaceae, and Nelumbonaceae. Therefore, in the Donoghue and

Doyle (1989) cladogram, Chloranthaceae (located among such families as Amborellaceae and Trimeniaceae) are clearly separated from Chloranthaceae.

Other issues are affected by the present study. Burger's (1977) idea that Lactoridaceae are of significance in the origin of monocotyledons seems not to be supported by the present data, because *Lactoris* wood is quite specialized. Primitive monocotyledons have vessel features at a much lower level of specialization than does the xylem of *Lactoris* or of Piperales. At best, Piperales offer a parallel to origin of monocotyledons in the origin of the herbaceous habit in Saururaceae. There are many interesting phylogenetic issues regarding Piperales, Chloranthales, and Magnoliales that need clarification. However, additional data that will yield features likely to be indicative of relationship are needed. While data from anatomy and ultrastructure may yet yield some data, information from molecular studies will doubtless prove most valuable.

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