MORPHOLOGY AND RELATIONSHIPS
OF LACTORIDACEAE

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INTRODUCTION

Lactoris fernandeziana Phil. has been construed as the sole species of a family, Lactoridaceae. This species has an assemblage of features which mark it as ranalian but which preclude its inclusion in any other family. Phylogenetic understanding of *Lactoris* has been hindered by the fact that it combines highly specialized and reduced characteristics with primitive ones, a combination in part related to its isolation as a relict, endemic on Masatierra of the Juan Fernandez Islands.

Features such as the apocarpus gynoecium, abundant endosperm with small undifferentiated embryo, undifferentiated perianth, and presence of ethereal oil cells serve to insure inclusion of Lactoridaceae in Ranales, but its alignment with particular families within this broad and heterogeneous order has been subject to controversy. Workers who have emphasized the specialized or reduced characteristics, such as Bentham and Hooker (1880), Hallier (1903), or McLaughlin (1933) have proposed relationship with Piperaceae or Saururaceae. Closeness of Lactoridaceae to Magnoliaceae, Himantandraceae, etc., has been suggested by those who prefer to stress the primitive characteristics. Among those botanists are Engler (1886; 1891), Metcalfe and Chalk (1950), and Hutchinson (1959). Although similarities with *Drimys,* now of Winteraceae, were noted by Engler (1886), the pollen tetrads of Winteraceae suggested to Eames (1961) that Lactoridaceae are phylogenetically close to Winteraceae. Many authors have mentioned anatomical chracteristics in discussions of affinities of *Lactoris.* A careful reconsideration of anatomy appears desirable, however, because, as with other groups of specialized and isolated plants, anatomical data seem to offer the best hope for systematic placement of this species.

MATERIALS AND METHODS

Lactoris fernandeziana was reported by Skottsberg (1953) to be scarce in the Masatierra cloud forest where it grows. According to letters written by Skottsberg (personal communication) after his 1955 expedition to the Juan Fernandez Islands, the recent devastation of the native vegetation may have resulted in the extinction of *Lactoris.* Material for the present study was obtained from a dried specimen, Skottsberg 230, in the U. S. National Herbarium. This collection provided a very good, though small, wood sample, as well as leaves, flowers, etc. These fragments were treated with 2.5% aqueous NaOH to clear and expand them. Treated fragments were then used either for whole mounts or for embedding in paraffin and sectioning according to the usual techniques. Sectioned material was stained with a safranin-fast green combination in a staining series incorporating tannic acid and ferric chloride. Whole mounts, including pollen grains, were stained with safranin. Wood

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sections were prepared by means of a sliding microtome and stained with safranin. Pollen-grain structure was studied both in whole mounts of tetrads and in sectioned preparations. Pollen terminology follows that of Erdtman (1952).

ACKNOWLEDGMENTS

ANATOMICAL DESCRIPTIONS

LEAF HISTOLOGY

The leaf of *Lactoris* (fig. 1) contains about six or seven mesophyll layers. The uppermost of these is more or less differentiated into a palisade. Ethereal oil cells (fig. 1, 3) are present in the mesophyll, as reported by Solereder (1908) and Metcalfe and Chalk (1950). These cells are bordered by radiating arms of spongy parenchyma cells (fig. 3). Veins do not have bundle-sheath extensions, nor are fibers present except in the midvein (fig. 1) or other major veins, where they are infrequent. No fibers or other mechanical tissue are present in the leaf margins (fig. 2).

Cells of the upper epidermis are large, polygonal in outline as seen in paradermal section. Cells of the lower epidermis are papillate (fig. 1–3), as reported by Solereder (1908). These papillate cells are restricted to the lower surface, but do not extend to the leaf margins (fig. 2). Stomata are characterized by thin-walled guard cells (fig. 3) and are ranunculaceous in mode of occurrence, for no subsidiary cells can be distinguished by virtue of planes of cell division. The anatomy of the leaf reflects the ecology of the habitat of *Lactoris:* relative lack of palisade, thinness of the leaf, papillate epidermal cells, and lack of foliar sclerenchyma are features one would expect in a plant from shady moist cloud-forest environments.

The base of the leaf and the petiole contain relatively compact, isodiametric parenchyma cells (fig. 4).

NODE, PETIOLE AND LEAF VENATION

Depending on diameter of the stem, six to 14 bundles were observed in stems. In internodal regions, these bundles are close together (fig. 7); in nodal regions, they are separated by a wide pith (fig. 5, 6). At nodes, a pair of bundles, one from either side of the leaf gap, diverge into the leaf base (fig. 5). This dual nature of the leaf trace is also evident in the petiole (fig. 4). This two-trace unilacunar node was reported for Lactoridaceae by Bailey and Swamy (1949) and in other subsequent papers by Bailey and his co-workers. The pair of traces may be distinguished in the leaf base (fig. 23, 24), and join to form a single bundle only within the lamina. This dual-trace nature of the midvein within the lamina has been reported in *Austrobaileya* (Bailey and Swamy, 1949), Monimiaceae (Money, Bailey and Swamy, 1950) and Chloranthaceae (Swamy, 1953). The emphasis placed by these authors on this nodal type and the duality of the midvein even into the

Fig. 1–5. *Lactoris fernandeziana.*—Fig. 1. Transection of leaf, showing midvein at right, papillate abaxial epidermis below; two ethereal oil cells may be seen in mesophyll. × 100.—Fig. 2. Margin of leaf; papillate cells begin at right, below. × 100.—Fig. 3. Paradermal section of leaf; ethereal oil cell in spongy mesophyll at left; papillate epidermal cells and stomata at right. × 230.—Fig. 4. Leaf base in transection; stipule below; pedicel is enclosed, center; note double vascular bundle in leaf midrib. × 90.—Fig. 5. Nodal region; double leaf trace, above; wings, below, are extensions of stipules. × 80.
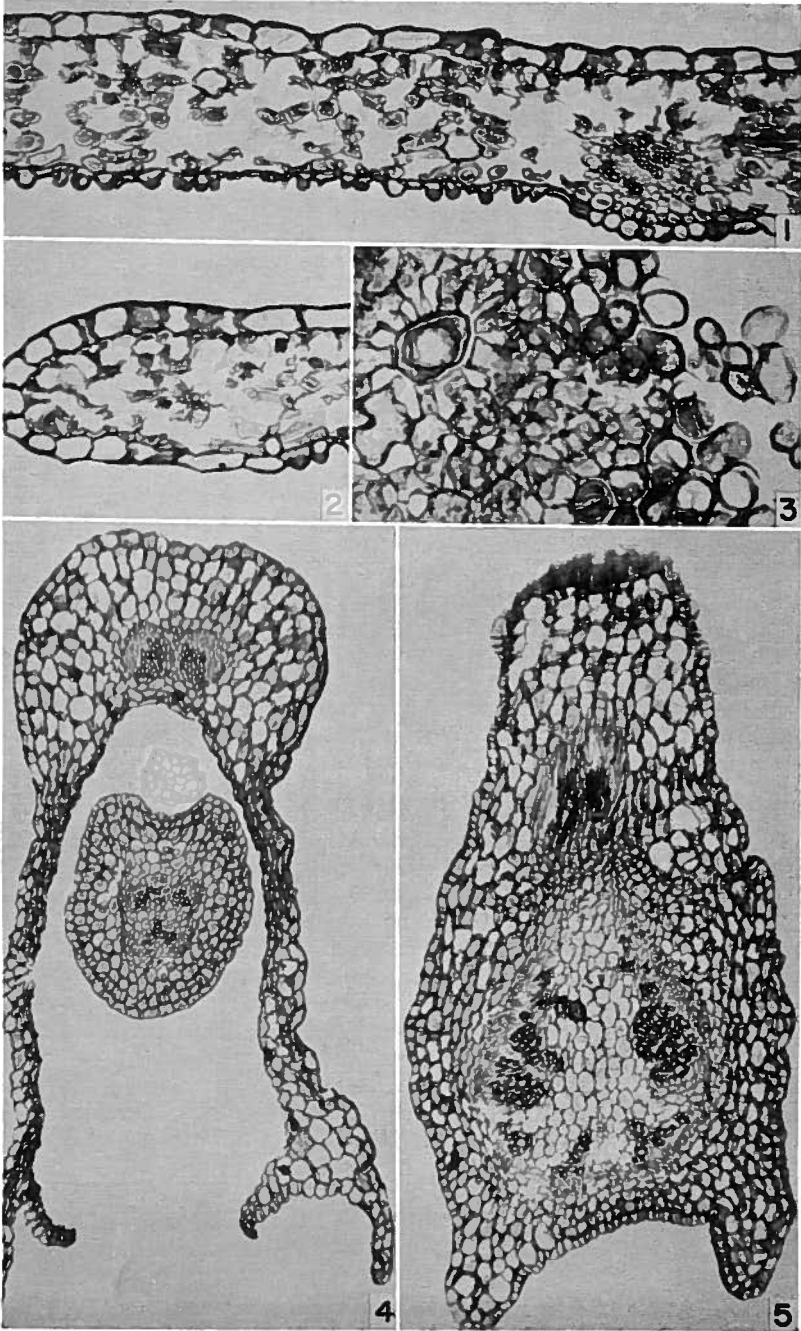
lamina is based upon the concept that this may be considered a very primitive characteristic in angiosperms. With respect to venation of the lamina itself, the drawings of fig. 23 and 24 are self-explanatory. Attention should be called to the tendency of the marginal veins to be connected to the submarginal veins by means of a parallel series of transverse veins in the distal half of the lamina. Also, a small protuberance, at the apex of the leaf, contains the terminal portion of the midvein, an extension beyond the point at which the marginal veins join the midvein. This apical protuberance is a feature which may be found in various angiosperms, such as *Liriodendron*. Smaller leaves (fig. 24) of *Lactoris* have much the same venation as large leaves (fig. 23).

STEM HISTOLOGY

As suggested above, stem anatomy varies with diameter. This variation is related, in part, to nodal versus internodal areas. Nodal areas often appear swollen in *Lactoris*. This is expressed anatomically by greater abundance of pith and cortex in nodal areas, as shown in fig. 6. This pattern contrasts with internodal areas (fig. 7). This internodal pattern features a narrow pith, the cells of which develop thicker secondary walls during secondary growth of the stem. In this internodal portion of the stem, bundle caps composed of sclerenchyma are prominent, and inner cells of the cortex between the bundle caps develop into sclereids in places. In the wider stem, representing a nodal area (fig. 6), the broad pith, consisting of thin-walled cells, is evident. The bundles are widely spaced, and in the arms of the pith between the bundles, nests of sclereids are formed. These may also be seen in fig. 10, left. Sclereid nests may serve a mechanical function in this portion of the stem, which is otherwise poor in sclerenchyma. No fibrous bundle caps are present, and few cortical sclereids were observed. In all stem sections, ethereal oil cells were observed. They are especially prominent in cortical regions (fig. 7, above). Cortical parenchyma otherwise consists of cells isodiametric in transection, elongate in longitudinal section, which are accompanied by relatively small intercellular spaces. Collenchyma is absent. Resin-like deposits are present in some cortical and pith cells.

WOOD ANATOMY

Wood anatomy of *Lactoris* has been described by McLaughlin (1933) and Record and Hess (1943). Unfortunately, neither of these accounts is based upon more than a single season's accumulation of xylem (e.g., as shown in fig. 7 here). The sections shown in fig. 8–10 represent at least three seasons' growth, and possess some anatomical features not previously mentioned for *Lactoris*. In addition, these sections were prepared from a nodal region, which provides wood patterns different from those of internodal regions. An important distinction between these is shown with respect to the rays. Internodal regions, such as that shown in fig. 7, have narrow pith regions with narrow pith rays. With the commencement of secondary growth, a rayless condition is quickly achieved in inter-fascicular areas (fig. 7), a fact mentioned by Record and Hess (1943). Where pith rays are wide, as in the nodal region (fig. 6), the rayless condition cannot properly be said to exist, because conversion to fusiform elements is incomplete. Rays of wood in such a

Fig. 6–7. *Lactoris fernandeziana.*—Fig. 6. Transection of primary stem in nodal region of a wider stem. Note nests of sclereids between bundles, wide pith, lack of bundle-cap fibers; a few cortical sclereids are present; other dark cells in cortex contain resin-like compounds. Gaps in cortex are artifacts. × 60.—Fig. 7. Transection of narrower stem in internodal region, showing a year's accumulation of secondary xylem. Pith cells have secondary walls; bundle cap fibers and cortical sclereids are present. Lobes, above, represent decurrent extensions of stipule base (cf. fig. 5). × 60.
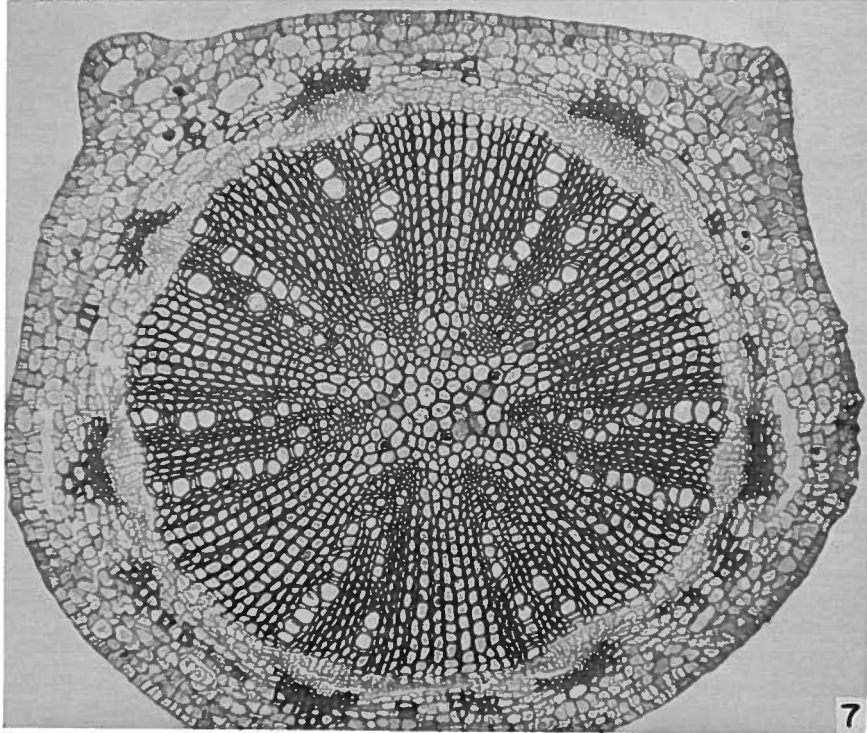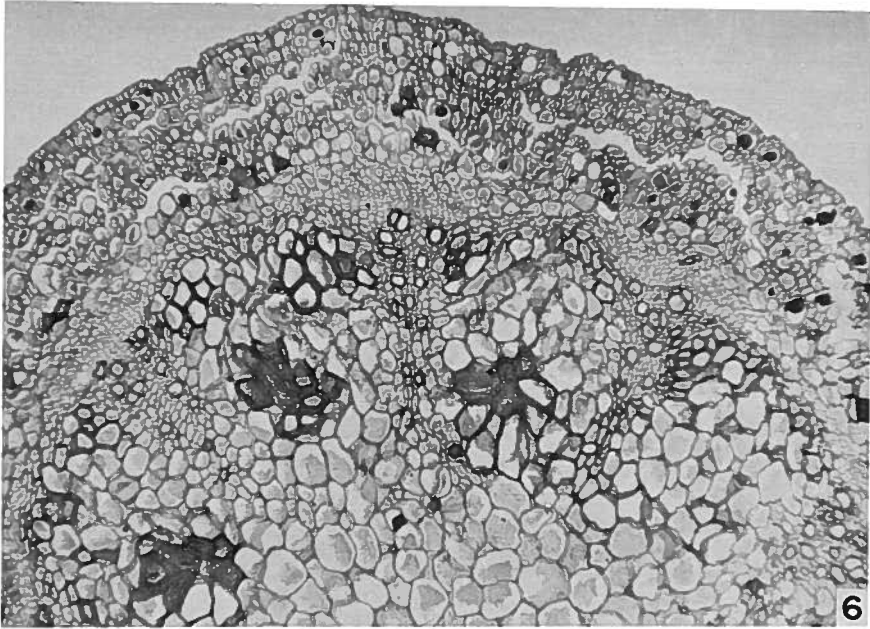
FIGURES 6-7

portion (fig. 9, right and left; fig. 10, right; not shown in fig. 8, because only a fascicular area is presented) are composed of cells square to erect (fig. 10), with erect cells predominant. These cells, however, often have tapered ends (fig. 9) and thick secondary walls with slit-like pits. Such elongate ray cells resemble libriform fibers in these respects. They are transitional between ray cells and libriform fibers, indicating an only partial conversion of the cambium from ray initials to fusiform initials in interfascicular areas. New rays were not observed to have been formed in fascicular areas.

The section shown in fig. 8 demonstrates that elements gradually become wider in diameter. As growth progresses, wider libriform fibers are formed, approaching the diameter of vessels. Axial parenchyma is, at first, diffuse, as noted by Record and Hess (1943) and McLaughlin (1933) and shown here by cells with contents, fig. 8, left. Later, axial parenchyma occurs mostly as paratracheal scanty, and may not have contents. Another feature not previously mentioned for wood of *Lactoris* is the tendency for storied wood structure, which may be seen in fig. 9 as well as, for a few elements, fig. 11. Some breakup of the large rays may be seen, and perforated ray cells are associated with this phenomenon.

A formal description of the wood is as follows. Growth rings absent, although small variations in wall thickness present as indicators of seasonal variation. Vessels solitary or in small groups, either multiples or radial chains. Vessels from 40 to 70 μ in diameter; average: 53 μ. Vessel elements from 44 μ to 198 μ in length; average: 108 μ. Perforations simple. Lateral-wall pitting consists mostly of alternate pits; pit cavities sometimes angular in shape where crowded; pit apertures often wide; scalariform or opposite pitting scarce. Libriform fibers present exclusively (borders not observed on pits), varying in diameter, up to 500 μ in length; shorter fibers intergrade with ray cells in size and morphology; walls about 3 μ in thickness (2 μ thick in later-formed increments) ; a few libriform fibers septate. Axial parenchyma diffuse, or diffuse and paratracheal scanty in later-formed increments; axial parenchyma cells not subdivided into strands. Rays absent (in internodal regions) or present (in nodal regions), wide; no uniseriate rays present. Ray cells square to erect (mostly erect), with secondary walls; some ray cells intergrading to libriform fibers in morphology and size and wall characteristics; perforated ray cells present. Some libriform fibers storied and some ray cells (which intergrade to fibers) storied. Crystals absent. Resin-like deposits in parenchyma cells of rays and axial parenchyma, although also in some tracheary elements.

FLORAL VENATION

Flowers of *Lactoris* (fig. 17) consist of a short pedicel, a single whorl of three perianth members, two whorls of three stamens each, and carpels. This situation may be altered somewhat in expression by the varied sexual conditions in *Lactoris*. As stated by Skottsberg (1953), flowers may be bisexual, female, or even male. The flowers studied here appear to be functionally bisexual, although the inner whorl of stamens (fig. 12, 21) is reduced to staminodia.

The pedicel (fig. 4, center; fig. 18) contains three bundles. Curiously, the entire vascularization of the flower is formed simply by branching of these three traces, without anastomoses, regardless of the alternation of the whorls. Thus, as shown in fig. 18, one of

Fig. 8–11. *Lactoris fernandeziana*. Wood sections.—Fig. 8. Transection. Most recently formed elements at right; portions of at least three seasons' growth are visible. × 100.—Fig. 9. Tangential section, taken from a nodal region, where wide rays are characteristic. Portions of rays, intergrading into fascicular elements, may be seen at left and right. Storied condition can be observed in places. × 60.—Fig. 10. Radial section. Nests of pith sclereids at left; ray tissue of secondary xylem at right. × 60.—Fig. 11. Portion of tangential section, showing vessel and storied libriform fibers. × 170.
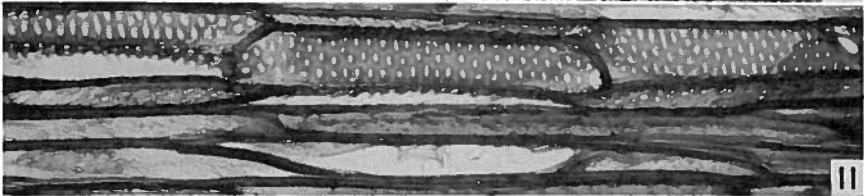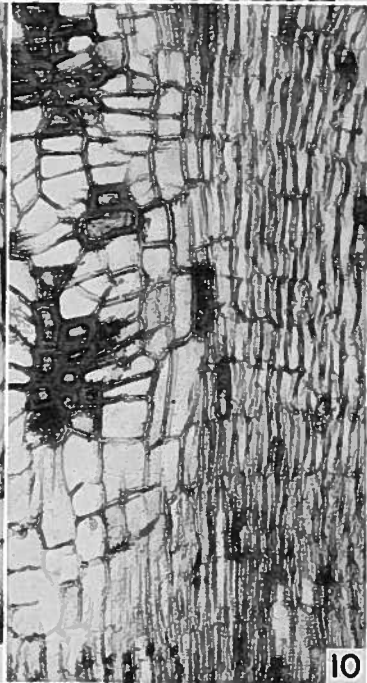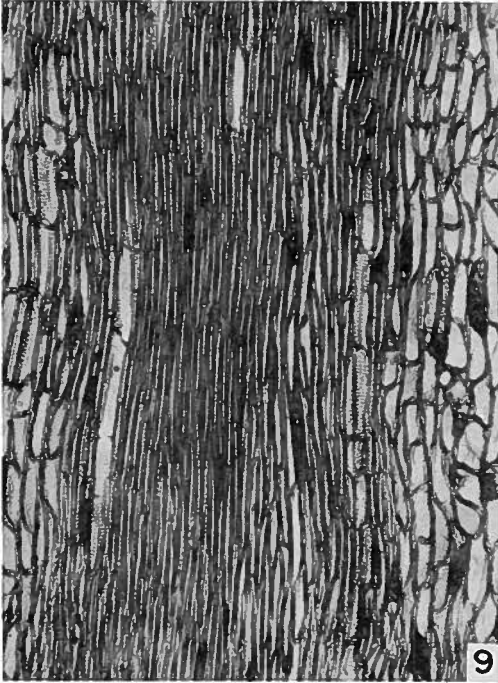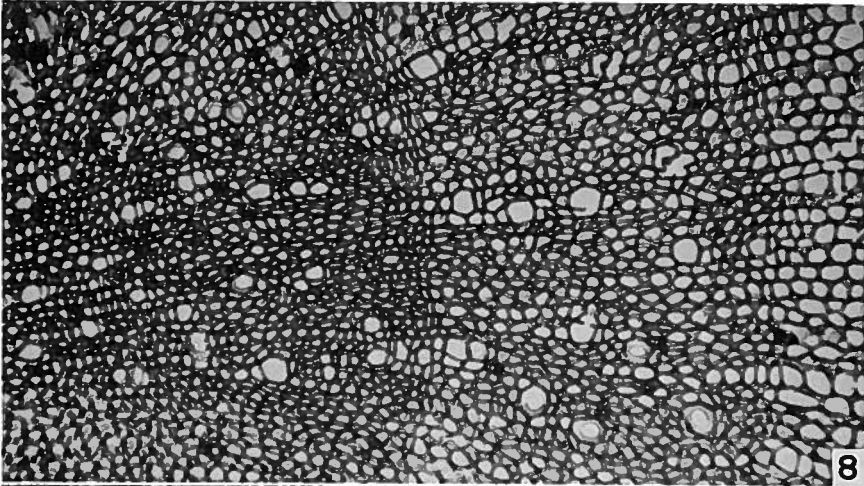
FIGURES 8-11

these three bundles would form branches to provide the traces for a perianth segment, a stamen, a second stamen or staminode (trace not shown), and finally, a carpel. The perianth segment (fig. 19) is provided with a single unbranched trace. Likewise, the stamen (fig. 20) and staminode (fig. 21) have a single unbranched trace each. The vascular bundle supplying each carpel (fig. 22) branches at the base. The midvein of the carpel curves outward and up, and a pair of adaxial (ventral) traces diverge from the base. These may be seen in sectional view (fig. 12, 13). The two adaxial traces each branch (fig. 18; fig. 13, upper right carpel), thus forming marginal and submarginal veins. All five veins unite in a plexus at the tip of the carpel (fig. 18). Although most ovules are each supplied with a vein below the point at which adaxial veins fork into marginal and submarginal veins, a few ovule traces may depart above this juncture. In this case, they are connected with the marginal, not the submarginal vein. In studying flowers in various stages from bud through fruit, one sees that the midvein of each carpel is the first to mature, followed by the adaxial traces (basal portion first). Thus, in the carpels shown in fig. 12, some of the adaxial veins (marginal and submarginal) are still procambial, and are not easily identified. The carpel in fruit shows the same venation as the carpel shown in fig. 18.

The venation of the flower is thus simple, although the carpel shows venation characteristic of various primitive and somewhat advanced angiosperms. The presence of submarginal veins is less reminiscent of Winteraceae (Bailcy and Nast, 1943b) than of such specialized genera as *Sedum* and *Physocarpus* (cf. Eames, 1961). There is no evidence that submarginal, rather than marginal bundles are the point of attachment for ovules.

FLOWER AND FRUIT HISTOLOGY

The perianth segments (fig. 12, 13) are composed of several layers of sphaeroidal parenchyma cells. Epidermal cells are bulging or papillate. Stamens might be described as flat and sporophyll-like, as in other primitive angiosperms, but their size is so small that no prominent form of this nature is achieved. In transection, the anther sacs face toward the outside, but cannot truly be said to be embedded in the surface, as in *Liriodendron*. The connective region contains cells which have slightly thickened, lignified walls (fig. 12, 13). Ethereal oil cells are also present. On the external surface of the connective, epidermal cells are papillate. Anthers open by a longitudinal slit. Staminodia (fig. 12) are similar, but smaller, and the anther sacs are vestigial, one on either side of the anther. Anther sacs contain collapsed degenerate cells. Carpels are not free at their bases, for the adaxial edges of each carpel are composed of parenchyma continuous with that of the other carpels along the lower third of the carpel (fig. 13). The carpel walls are composed of isodiametric parenchyma cells, distinctive in the large number of ethereal oil cells present (fig. 13). The presence of nectary areas cannot be established unequivocally from dried material, but small cells with staining reactions suggestive of nectary cells were observed at the base of stamens and perianth segments.

As the carpels mature into fruit, distinctive wall characteristics develop in cells. The inner epidermis of the carpel matures into fiber-like cells, their long axes oriented transversely to spirally in the carpel (fig. 14; fig. 15, above). These cells may function in dehiscence of

Fig. 12–16. *Lactoris fernandeziana.*—Fig. 12. Transection of flower; perianth segment, above right; base of gynoecium, lower left; between this and the two stamens, a staminode may be seen. × 75.—Fig. 13. Transection of flower; perianth segment at lower left. Carpels at this level are united; ovules may be seen. × 75.—Fig. 14. Fibrous epidermis of inner face of carpel, from paradermal section of fruit. × 175.—Fig. 15. Transection of carpel wall in fruit, internal face above. × 155.—Fig. 16. Portion of transection, endosperm at upper left. × 155.
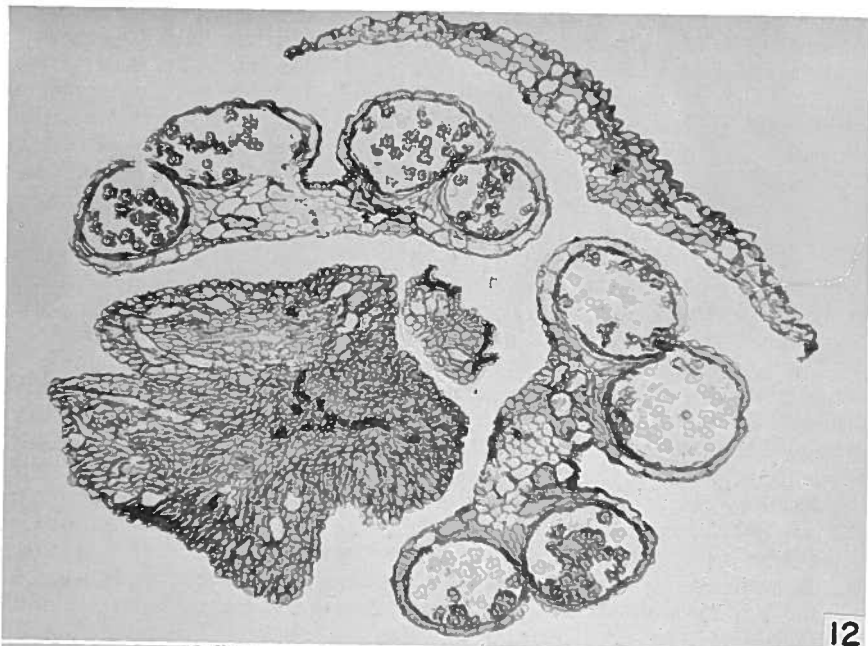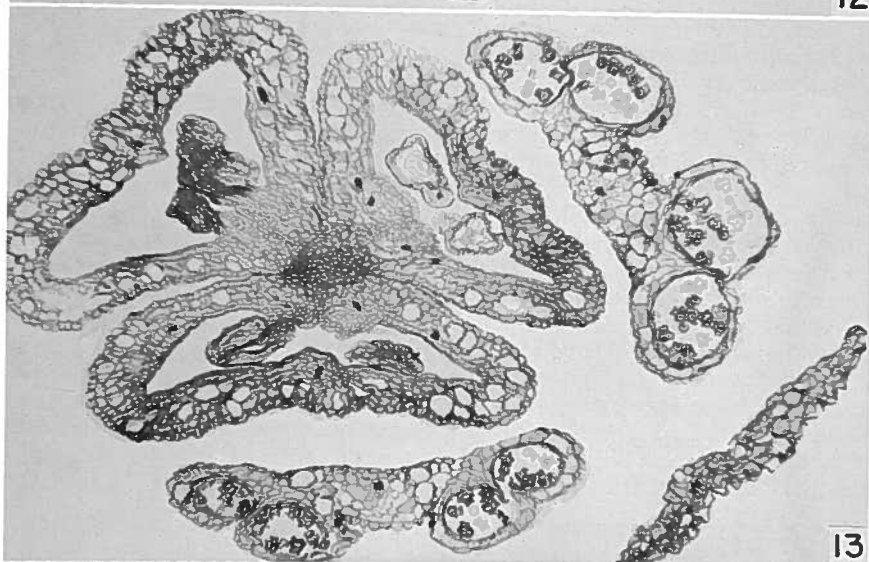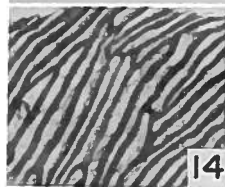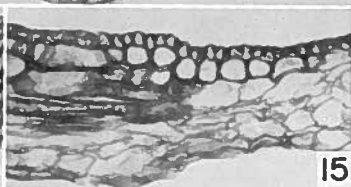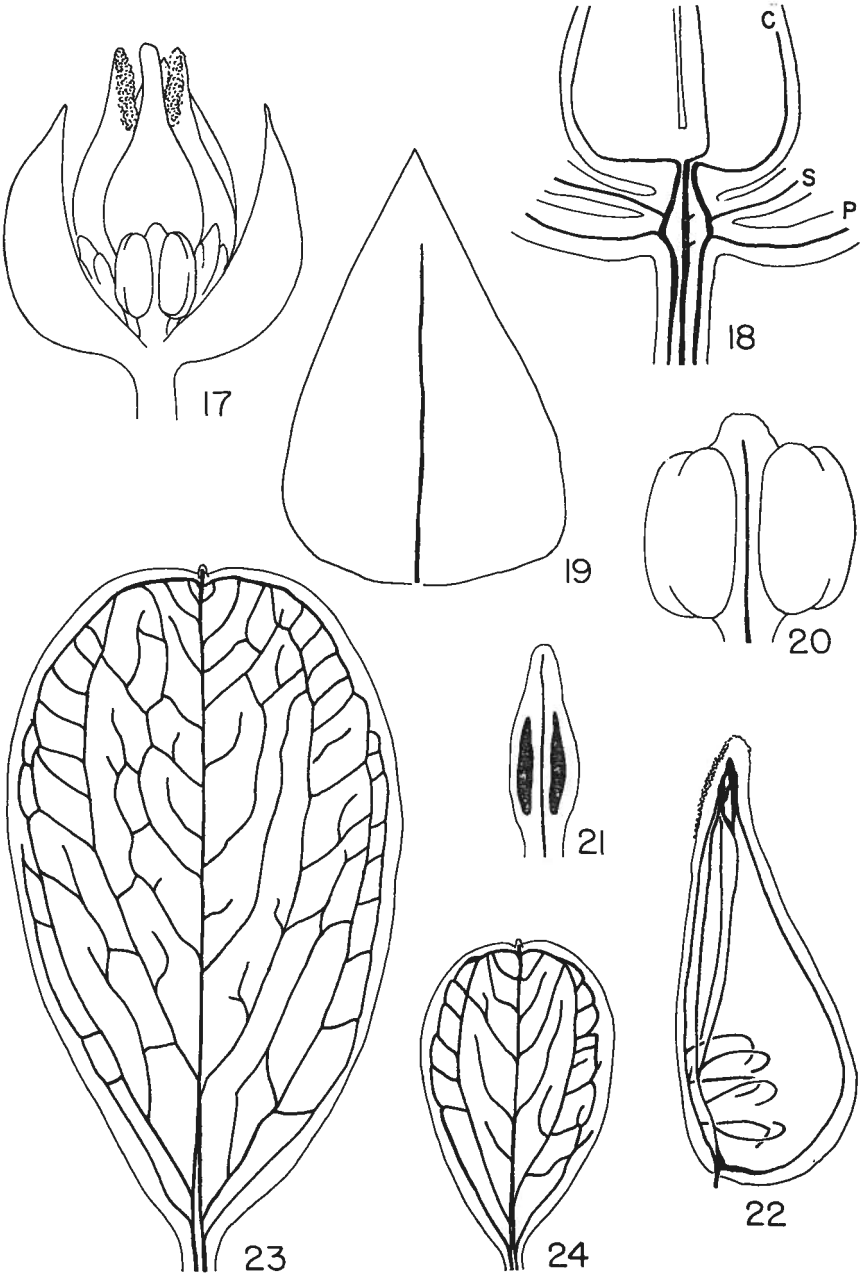
FIGURES 12-16

the mature carpel. The adjacent subepidermal layer, or layers, may also develop into sclerenchyma, especially near veins, as shown in fig. 15. The seed (fig. 16) possesses an epidermis in which the inner wall is somewhat thickened. Other cell layers of the ovule collapse at maturity. The endosperm (fig. 16, above) is composed of thin-walled cells. Suitably mature seeds for study of the embryo were not available. Hutchinson (1959) has figured a longisection of the mature seed which shows a small, undifferentiated embryo embedded in abundant endosperm.

POLLEN GRAINS

Pollen grains of *Lactoris* are united into tetrads (fig. 25, 26). The peculiar external appearance of the tetrads, which has been described and figured by Erdtman (1952), is caused by a phenomenon which has not previously been mentioned in connection with *Lactoris*. The peculiar flaring stump-like shape of each of the component grains is caused by a saccate condition. Sections were necessary to demonstrate this, emphasizing that study of permanently-united tetrads must include sectioned material. The sexine is in contact with the nexine adjacent to the juncture of grains on the external surface of the tetrad. Also, it comes close to the nexine in the concave distal face of each grain. Elsewhere, the sexine is markedly saccate, forming irregular wavy shapes, as shown in fig. 25–27. The sexine is thus not nearly as thick as its external contours would suggest. There are many folds in the sexine, the outer surface of which is not otherwise textured. Erdtman (1952), however, describes the surface as "not quite smooth." The internal surface, however, is irregular and textured, and it is this sculpture which is probably responsible for the patterning of sexine shown in face view in fig. 28. This pattern, which is a minute O-L pattern, does contain thicker spots, indicated by denser stippling, and thus might be regarded as formed from the union of pila, although such basic units are certainly not clearly differentiated, and would be quite minute in any case.

Sections of pollen grains demonstrate the nature of the aperture quite clearly. The bulging germ pore, covered by a thin nexine layer, is within the concave portion of the sexine. The sexine is much thinner over the concave distal surface of each grain, forming a tenuitas, as Erdtman suggests, although occasionally the appearance is that of an ulceroid aperture, as figured (fig. 25, center). The distinction between an extremely thin zone of sexine (fig. 27) and an actual absence of sexine over this germinal area seems unimportant, and probably both conditions exist. In any case, *Lactoris* clearly seems to have monosulcate pollen grains. The primitive dicotyledonous families having this type of pollen, or some closely related derivative type, have been listed by Swamy (1953) and other authors. The list includes various families supposedly related to Lactoridaceae. Because of the peculiar morphology of lactoridaceous tetrads, one cannot easily find homologs in pollen structure. For example, saccate structure is suggested by grains of *Cananga odorata* (Annonaceae) in the writer's pollen-slide collection, for a wrinkled (and perhaps thus somewhat saccate) sexine surface surrounds the aperture in this species. However, the aperture in *Cananga odorata* is proximal, not distal, a fact demonstrated by Periasamy and Swamy (1960). The descriptions

Fig. 17–24. *Lactoris fernandeziana.*—Fig. 17. Flower. × 25.—Fig. 18. Semi-diagrammatic longisection of flower, to show vascular pattern; P = perianth segment; S = stamen; C = carpel; traces to inner whorl of stamens not shown. × 30.—Fig. 19. Perianth segment, showing vascularization. × 30.—Fig. 20. Fertile stamen, to show vascularization. × 40.—Fig. 21. Sterile stamen, to show vascularization. Anther sacs (black) are formed, but contain only obliterated cells. × 40.—Fig. 22. Carpel beginning to mature into fruit, to show vascularization; abaxial trace at right; ovule traces below. × 30.—Fig. 23, 24. Leaves, showing vascularization; fig. 23 represents large leaf; fig. 24, a small (but mature) leaf. × 6.6.

FIGURES 17-24

and figures for pollen grains of *Hortonia floribunda* (Monimiaceae) given by Money, Bailey, and Swamy (1950) suggest that the ridges in the exine of these pollen grains may be saccate folds. *Hortonia,* however, has nonaperturate single grains.

Likewise, the occurrence of pollen-grain tetrads in families with monosulcate (or some closely related aperture form, such as nonaperturate, etc.) does not, by itself, imply relationship. Permanently united tetrads of *Hedycarya* (Monimiaceae; Money, Bailey and Swamy, 1950) and eleven genera of Annonaceae (Canright, 1963) are undoubtedly parallelisms. The tendency toward a poorly-defined aperture in Monimiaceae, Annonaceae, etc., is interesting, for certainly the aperture in *Lactoris* does not have precise limits. The permanently-united tetrads of Winteraceae (Bailey and Nast, 1943a), which seem to have persuaded Eames (1961) that *Lactoris* is allied to Winteraceae, are actually quite different. Winteraceae have clearly-defined apertures with bulging germ pores not covered by sexine, are not saccate, have prominent sexine sculpture composed of thick resistant elements; all of these features contrast with characteristics of *Lactoris* pollen.

CONCLUSIONS

The diminutive size and simple appearance of plants of *Lactoris* are matched by the relatively uncomplicated anatomy. This simplicity, and the paucity of characters either in gross morphology or anatomy, provide problems in phylogenetic interpretation. One may list, however, the features which are probably specializations peculiar to *Lactoris* and which therefore should not be stressed in attempts to demonstrate the relationships of *Lactoris:*

(1) *Leaves.*—The thin, mesic leaves of *Lactoris* show anatomical adjustment to the moist habitats it occupies. The ochrea-like stipules of *Lactoris* are probably not indicative of relationship with other stipulate plants because stipules in *Lactoris* are small non-vascularized structures which may well not be vestiges. Stipules in dicotyledons occur in various families and are not reliable indicators of relationship among these families anyway.

(2) *Wood.*—*Lactoris* has extremely specialized wood compared with that of most dicotyledons. To be sure, the high degree of specialization is related to the habit of *Lactoris* as a small shrub, for wood of small shrubs or woody herbs is usually highly advanced. The rayless condition is to be expected in some plants of this habit (Barghoorn, 1941; Carlquist, 1961). Nevertheless, the extremely short vessel elements, the lack of tracheids in axial xylem, and the simple perforation plates of vessels are all features which suggest that *Lactoris* was derived from a stock with relatively specialized wood. If *Lactoris* had been derived from ancestors with primitive wood characteristics, at least one of these primitive features should be retained to some degree, but this is not true. The immediate ancestors of *Lactoris,* therefore, probably had specialized wood, and thus relationship with Winteraceae is relatively unlikely. On the contrary, other ranalian families, such as Lauraceae (Stern, 1954), Annonaceae (Vander Wyk and Canright, 1956) and Monimiaceae (Garratt, 1935) have a wide gamut of wood specialization, and thus would offer better starting-points for the type of wood found in *Lactoris.*

(3) *Pollen.*—As mentioned above, the tetrads of *Lactoris* are unique, and no true similarity with those of Winteraceae exists. The tetrad habit is a specialization which has occurred many times independently among dicotyledons, and one should probably not look primarily to tetrad-bearing species in seeking the relatives of *Lactoris.*

On the other hand, we should consider the following characteristics of a relatively unspecialized nature, for they are probably better indicators of the nature of the ancestral stock of *Lactoris.*

(1) *Nodal Anatomy.*—The two-trace unilacunar node is clearly demonstrated in *Lactoris.* Moreover, the tendency for the two traces to remain distinct even in the lower portion

of the lamina before merging into a single midvein confirms that this is an unspecialized condition. Families with the two-trace unilacunar node include Austrobaileyaceae, Chloranthaceae, Trimeniaceae, Amborellaceae, Monimiaceae, Lauraceae, Gomortegaceae, Hernandiaceae, Gyrocarpaceae and Calycanthaceae. The tendency for the pair of traces to remain distinct even in the lamina is found in *Austrobaileya,* Chloranthaceae and Monimiaceae.
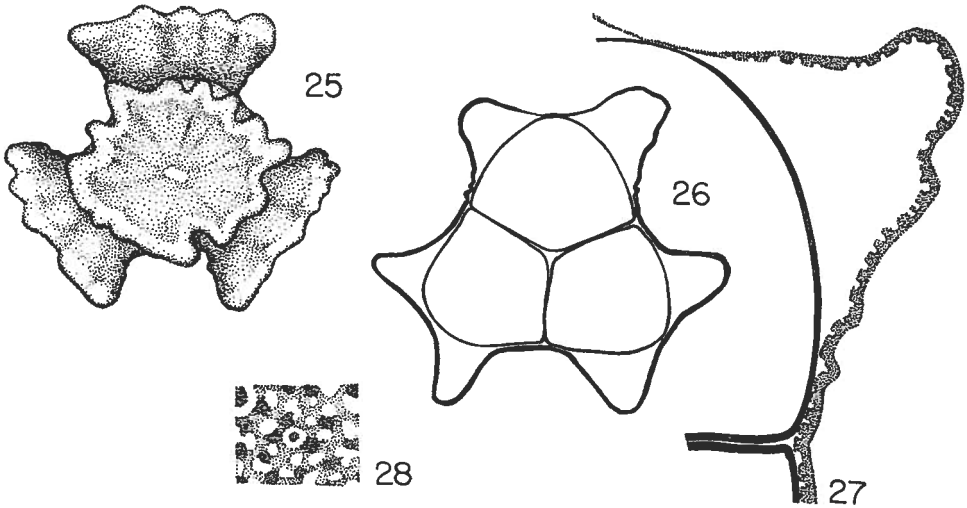

Fig. 25–28. *Lactoris fernandeziana. Pollen.*—Fig. 25. Entire pollen tetrad; in center, polar view of one of the four grains. × 1530.—Fig. 26. Pollen tetrad in sectional view; upper grain in median section; note saccate condition. × 1530.—Fig. 27. Portion of sectional view, corresponding to fig. 26, upper right; apertural area ("tenuitas") above, saccate portion at right, juncture of grains below. × 4590.— Fig. 28. Optical section of surface, showing the "O-L" pattern. × 4590.

(2) *Ethereal oil cells.*—These idioblasts are a clear indicator of the ranalian nature of *Lactoris.* This characteristic has often been used to define this order, and is cited by Robert F. Thorne as an important criterion for his Annonales. The Annonales of Thorne include Winteraceae, Illiciaceae, Schisandraceae, Degeneriaceae, Magnoliaceae, Himantandraceae, Annonaceae, Eupomatiaceae, Calycanthaceae, Myristicaceae, Canellaceae, Aristolochiaceae, Austrobaileyaceae, Chloranthaceae, Amborellaceae, Trimeniaceae, Monimiaceae, Gomortegaceae, Lauraceae, Hernandiaceae, Gyrocarpaceae, Piperaceae and Saururaceae in addition to Lactoridaceae (Thorne, personal communication).

(3) *Floral anatomy.*—Floral morphology of *Lactoris* certainly suggests an unspecialized condition, although small size of the flowers is accompanied by a rather simple venation pattern. The carpels possess a rather primitive venation type, although such carpels occur in families other than those of the Annonales above. The fruit type of *Lactoris,* a follicle, is not exactly matched by other annonalian families, although one may cite Monimiaceae as having some degree of resemblance in this respect. The baccate fruits of Winteraceae and the drupes of Lauraceae are quite different, although fruit type is usually not one of the more conservative features of evolution in dicotyledons, and therefore should not be strongly stressed in assessing the precise relationships of *Lactoris.*

(4) *Seeds.*—The abundant endosperm, coupled with a small undifferentiated embryo, is a typical annonalian feature, and, interestingly, has been retained in *Lactoris* despite the diminutive seed size.

(5) *Pollen grains.*—Despite the tetrad habit, the monosulcate grains with poorly-defined apertures are characteristic of most annonalian families, such as Austrobaileyaceae, Trimeniaceae, Monimiaceae, Amborellaceae, and Annonaceae. Lauraceae, Gomortegaceae and Hernandiaceae have nonaperturate grains, a form considered close to monosulcate, although in at least one genus of these three families (*Umbellularia* of the Lauraceae: Kasapligil, 1951) monosulcate grains occur.

Lactoris is unquestionably annonalian, but worthy of recognition as a distinct family. In attempting to select those families in which the important basic features of *Lactoris* are most closely matched, one may emphasize families which have unilacunar two-trace nodes and a monosulcate pollen-grain type. Of these, Chloranthaceae has rather primitive wood combined with highly specialized floral anatomy and morphology. Curiously, the swollen nodes of Chloranthaceae are reminiscent of those of *Lactoris,* although this is probably a parallelism. Floral morphology in *Austrobaileya, Trimenia,* Calycanthaceae and Monimiaceae is characterized by an indefinite number of floral parts, and thus dissuades one from allying *Lactoris* very closely in these respects. On the other hand, the clear floral trimery in Lauraceae, Gomortegaceae and Hernandiaceae, as well as in a family with another nodal type, Annonaceae, is reminiscent of the condition in *Lactoris.*

Despite the fact that none of the families mentioned in the preceding paragraph provides a close match, they are probably more closely allied to *Lactoris* than are the Magnoliaceae or its allies, or Piperaceae and Saururaceae, or Winteraceae. One cannot narrow the list of families close to *Lactoris* to a single family, but the list should probably include Monimiaceae, Chloranthaceae, Lauraceae and Gomortegaceae. These families, despite their distinctive characteristics, seem to have the greatest constellation of morphological and anatomical features like those of *Lactoris.* Interestingly, those four families are represented in the land mass nearest the Juan Fernandez Islands, South America.

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