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WOOD AND BARK ANATOMY OF *DEGENERIA*

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ABSTRACT

Wood anatomy of the recently described *Degeneria roseiflora* differs from that of *D. vitiensis* by possessing narrower vessels, much thicker-walled vessels and fiber-tracheids, abundant uniseriate rays, and greater numbers of ethereal oil cells in rays. Because both large and smaller wood samples of *D. vitiensis* were studied, ontogenetic changes in the wood are presented and separated from those features that probably vary with the species. Tyloses and perforated ray cells are newly reported for *Degeneria*. Anatomy of mature bark of *D. roseiflora* is described. Wood anatomy of *Degeneria* is moderately primitive. Although *Degeneria* is often compared to Himantandraceae and Magnoliaceae, Eupomatiaceae also seem very close, if not closer.

Key words: bark anatomy, *Degeneria*, Degeneriaceae, Eupomatiaceae, wood anatomy.

INTRODUCTION

Wood anatomy of *Degeneria vitiensis* I. W. Bailey & A. C. Smith was described by Bailey and Smith (1942), Swamy (1949), and Takahashi (1985). Certain aspects of wood anatomy have also been covered by Lemesle and Duchaigne (1955*a*, *b*), whose application of certain new terms (e.g., "pseudotracheids") invites review here. Metcalfe and Chalk (1987) offered a review of vegetative anatomy of Degeneriaceae.

The discovery of a new species, *Degeneria roseiflora* J. M. Miller (Miller 1988) and the availability of wood and bark material of this species have provided an opportunity for study of bark of *Degeneria*, hitherto little known, and for comparison of wood of the two species. John M. Miller kindly placed liquid-preserved material of wood and bark of *D. roseiflora* (*Miller 1200*) at my disposal. The wood sample, collected in 1987, was 66 mm in diameter; the bark was 6 mm thick.

The wood of *D. vitiensis* studied here comes from a mature wood sample (*R 1193-1*) provided by the Forestry Commission of New South Wales. The rays of this wood block are parallel, indicating that the sample was obtained from a large trunk. In contrast, a wood sample 33 mm in diameter (*Carlquist 695*) representing a basal shoot from an uninjured tree, provided a relatively small accumulation of secondary xylem. The latter wood sample was collected in Fiji in 1962, thanks to the aid of John W. Parham. These two wood samples offer contrast in age and offer a way to determine which wood features alter with ontogeny in *Degeneria* wood. Miller (1988) suggests that *D. roseiflora* may have neotenic features in its floral structures. One would not necessarily expect juvenilistic features in the sense of paedomorphosis in wood of this species, however, because typically woody dicotyledons do not show paedomorphosis in wood features as do dicotyledons with special growth forms (e.g., rosette trees, stem succulents; for a review, see Carlquist 1988). In any case, the wood available of *D. vitiensis* permits study of

change in wood features from pith to the outside of a large stem; the wood sample of *D. roseiflora* is intermediate in size between the two *D. vitiensis* samples studied, and thus differences among the samples that are related to ontogeny can be differentiated from those that may be related to species limits.

MATERIALS AND METHODS

The wood sample *Miller 1200* of *D. roseiflora* was preserved in formalin-acetic-alcohol in the field, whereas wood samples of *D. vitiensis* were dried. The latter wood samples were boiled in water and stored in 50% aqueous ethyl alcohol.

Woods were sectioned on a sliding microtome. Sectioning by means of a sliding microtome proved unsuccessful for sample *R 1193-1* of *D. vitiensis* because of the thin-walled nature of wood cells. For that sample, therefore, an alternative technique that involves softening in ethylene diamine followed by sectioning in paraffin (Carlquist 1982) was employed. This technique provided the sections illustrated in Figures 10–14. This method was also used for the bark sections of *D. roseiflora* illustrated in Figures 15–18. Wood sections were stained in safranin or in a safranin-fast green combination. Macerations were prepared with Jeffrey's solution and stained with safranin.

Some sections of *D. roseiflora* wood cut with a sliding microtome were placed between glass slides and allowed to dry. These sections were observed with an ISI WB-6 scanning electron microscope (Fig. 5–7).

Wood terminology follows that of the IAWA Committee on Nomenclature (1964). Vessel diameter is measured as lumen diameter at widest point. All quantitative data are based upon 25 measurements per feature except for vessel wall thickness, fiber-tracheid wall thickness, and fiber-tracheid diameter at widest point; for these three features, figures for typical conditions rather than means were obtained (e.g., nonobliquely sectioned cells selected; cell wall thickness measured not at cell corners). Number of vessels per group is calculated as: a solitary vessel = 1, a pair of vessels in contact = 2, etc. In addition to observations made on outer stems, observations were made on wood of twigs of *D. vitiensis* in order to find the most juvenile expressions of ray types and ray histology, although no quantitative data were computed from these. Specimens documenting the Carlquist and the Miller collections are located in the herbarium of the Rancho Santa Ana Botanic Garden.

ANATOMICAL RESULTS

Wood

DEGENERIA ROSEIFLORA, *Miller 1200* (Fig. 1–9).—Growth rings absent, vessels fluctuating only a little in diameter with respect to season. Vessels mostly solitary (Fig. 1); mean number of vessels per group, 1.2. Mean vessel diameter, 79 μm. Mean number of vessels per mm^2, 27. Mean vessel element length, 984 μm. Perforation plates scalariform; bars slender (Fig. 8), or, in narrower vessels, a little wider (Fig. 7), vestigially bordered and with microfibrillar webs present to a limited extent in the perforations (Fig. 7). Mean number of bars per perforation plate, 20.4. Vessel-to-vessel pitting, vessel-axial parenchyma pitting (Fig. 9), and vessel-ray pitting (Fig. 6) scalariform. Vessel-to-fiber-tracheid pitting sparse. Mean vessel wall thickness, 3.1 μm. Imperforate tracheary elements all fiber-tracheids, the pits

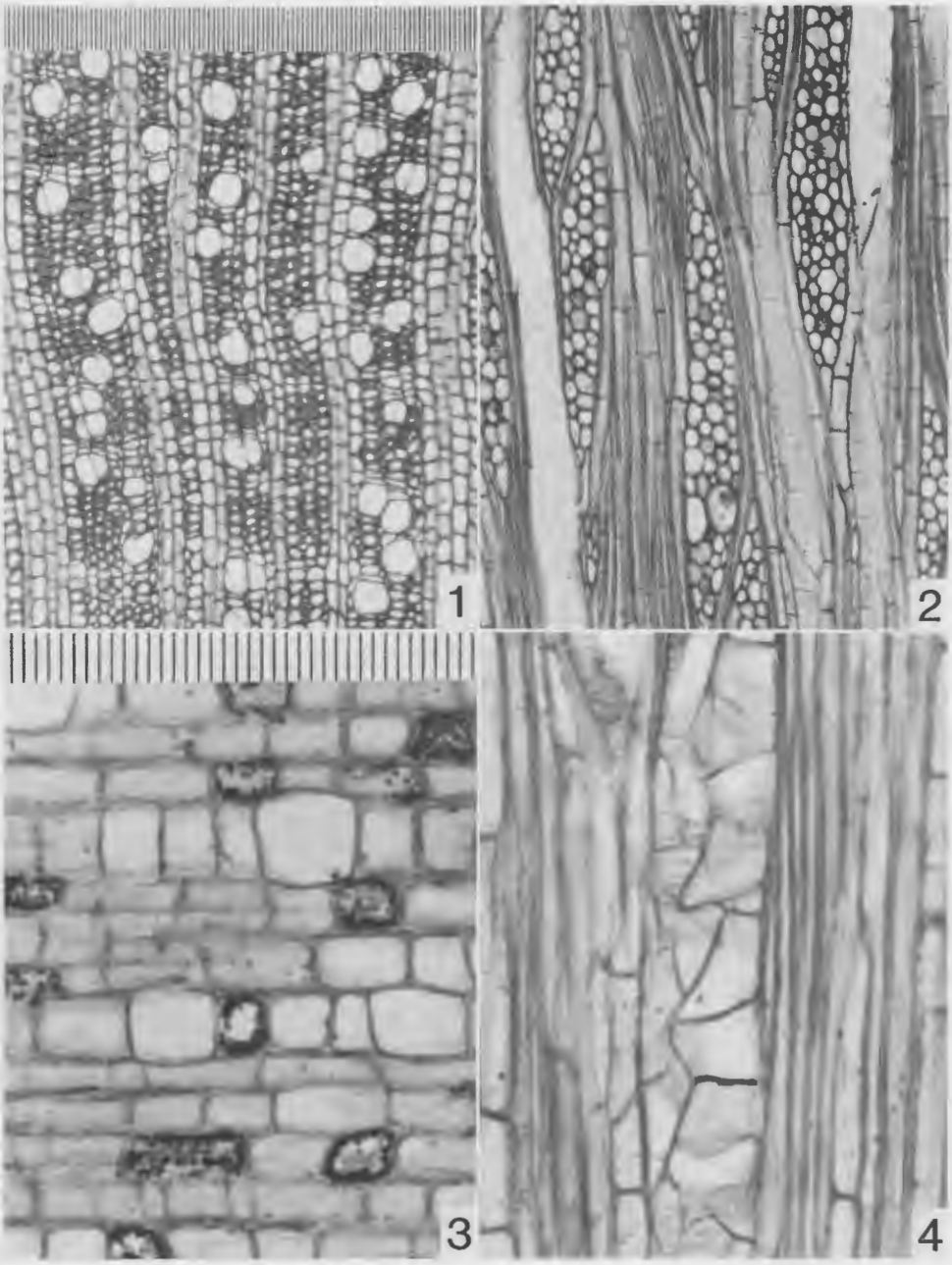

Fig. 1–4. Wood sections of *Degeneria roseiflora* (*Miller 1200*).—1. Transection; vessels are relatively narrow, fiber-tracheids thick walled.—2. Tangential section; two ethereal oil cells in ray, bottom center; two uniseriate rays near lower left corner.—3. Radial section; enlarged cells are ethereal oil cells; dark-staining droplets restricted to certain other cells.—4. Radial section; tyloses in vessel, center. (Fig. 1–2, magnification scale above Fig. 1 [finest divisions = 10 μm]; Fig. 3, 4, scale above Fig. 3 [divisions = 10 μm].)

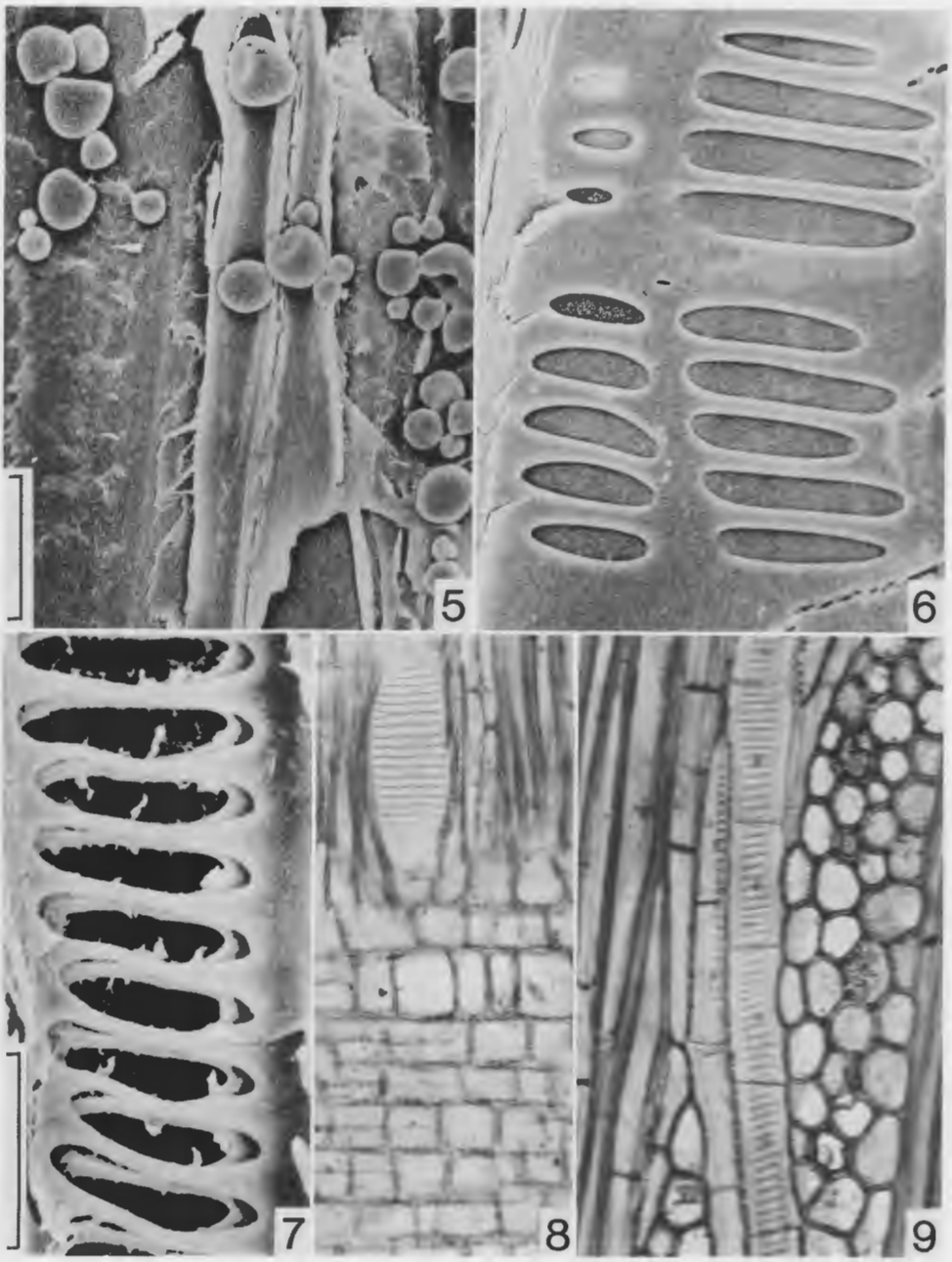

Fig. 5–9. Wood sections of *Degeneria roseiflora* (*Miller 1200*).—5. SEM photomicrograph of starch grains dislodged from axial parenchyma cells, from radial section.—6. SEM photomicrograph of vessel-ray pitting from radial section.—7. SEM photomicrograph of scalariform perforation plate from radial section, showing fragments of primary walls that remain in the perforations.—8. Light photomicrograph of radial section; perforation plate (above, left); ray cells (below) are square to upright in shape.—9. Light photomicrograph of tangential section, to show scalariform vessel-axial parenchyma pitting, multiseriate rays. (Fig. 5, 6, magnification bracket at left in Fig. 5 [bracket = 10 μm]; Fig. 7, bracket at left [bracket = 10 μm]; Fig. 8, 9, scale above Fig. 3.)

fully bordered but sparse and with pit cavity diameter 1–2 μm in diameter. Mean fiber-tracheid length, 1637 μm. Mean fiber-tracheid diameter at widest point, 35 μm. Mean fiber-tracheid wall thickness, 7.0 μm (Fig. 1). Axial parenchyma present as diffuse cells but more commonly in groupings: diffuse-in-aggregates, abaxial, and narrow bands two to three cells wide (Fig. 1). Axial parenchyma cells with simple or, less commonly, inconspicuously bordered pits. Axial parenchyma in strands of 3–8, mostly 5 cells. Rays both multiseriate and uniseriate; uniseriate rays much less common than multiseriates, but definitely present (Fig. 2). Ray cells of multiseriate portion of multiseriate rays mostly square to procumbent, occasional upright cells present (Fig. 3). Wings of multiseriate rays of one or two cells, composed of upright cells. Occasional upright cells present on sides of multiseriate rays as sheathing cells (Fig. 2). Uniseriate rays composed of upright cells. Mean multiseriate ray height, 678 μm. Mean multiseriate ray width at widest point, 4.2 cells. Mean uniseriate ray height, 290 μm. Mean ray cell wall thickness, 2.0 μm. Pits on ray cells simple or slightly bordered. Ethereal oil cells commonly present in multiseriate rays (Fig. 1, 3). Starch abundant in axial parenchyma (Fig. 5), also present in ray cells. Dark-staining compounds present as droplets in some ray cells (Fig. 3). Tyloses present in a few vessels (Fig. 4). Wood nonstoried (Fig. 2).

DEGENERIA VITIENSIS, a sample from a large tree, *SFCw-R 1193-1* (Fig. 10–14).—Growth rings indistinct, fluctuations in vessel diameter rather minor (Fig. 10, center) with respect to season. Vessels mostly solitary; mean number of vessels per group, 1.4. Mean vessel diameter, 131 μm. Mean number of vessels per mm^2, 10.8. Mean vessel element length, 1204 μm. Perforation plates scalariform, with slender but vestigially bordered bars; mean number of bars per perforation, 28.7. Vessel-to-vessel, vessel-axial parenchyma (Fig. 12), and vessel-ray pitting scalariform; vessel-to-fiber-tracheid pits sparse. Mean vessel wall thickness, 2.5 μm. Imperforate tracheary elements all fiber-tracheids because pits are small and sparse; pit cavity diameter about 1 μm in diameter, pit apertures slitlike, 2–4 μm long. Mean fiber-tracheid length, 1970 μm. Mean fiber-tracheid diameter at widest point, 36 μm. Mean fiber-tracheid wall thickness, 2.5 μm. Axial parenchyma diffuse, but more commonly in groupings: diffuse-in-aggregates, abaxial, and bands 2–4 (commonly 3) cells thick (Fig. 10). Axial parenchyma in strands of 3–11, mostly 7, cells. Pitting on axial parenchyma cells mostly simple, some pits inconspicuously bordered. Rays multiseriate, uniseriate rays so infrequent as to be effectively absent. Multiseriate portions of rays composed wholly of procumbent cells (Fig. 14). Upper and lower tips of rays composed of a single row of cells, these cells square to upright (Fig. 11). Mean multiseriate ray height, 867 μm. Mean width of multiseriate rays at widest point, 3.8 cells. Perforated ray cells occasional (Fig. 13). Mean ray cell wall thickness, 1.6 μm. Pits on ray cells simple or slightly bordered. A few ethereal oil cells present in rays, but not common. Dark-staining deposits common in ray cells (Fig. 14). Starch present in axial parenchyma and ray cells. Wood nonstoried.

DEGENERIA VITIENSIS, a small basal shoot, *Carlquist 695*.—Qualitative features like those of the above collection unless otherwise stated. Mean number of vessels per group, 1.2. Mean vessel diameter, 91 μm. Mean number of vessels per mm^2, 14.5. Mean vessel element length, 798 μm. Mean number of bars per perforation

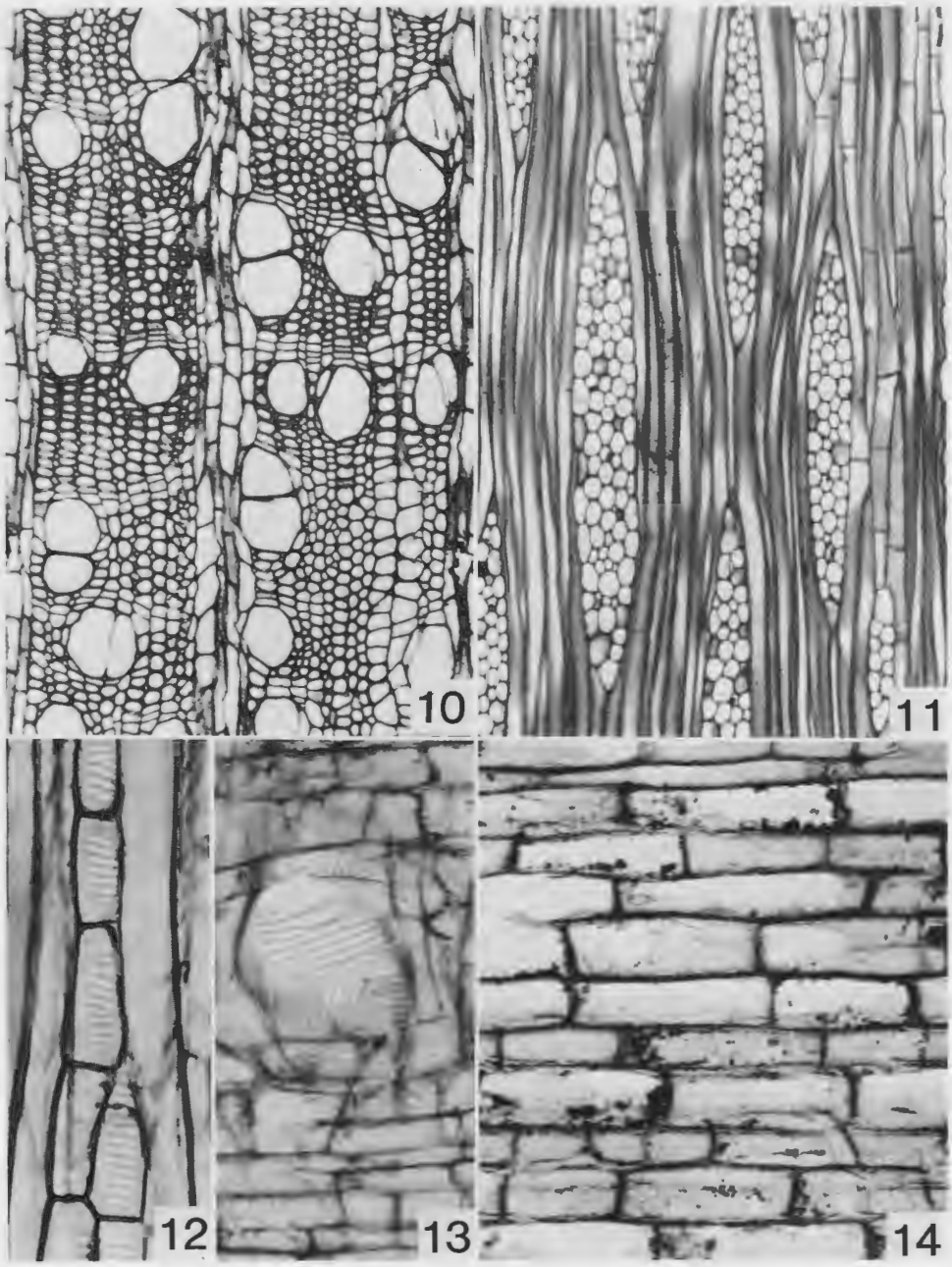

Fig. 10–14. Wood sections of *Degeneria vitiensis* (*SFCw-R 1193-1*).—10. Transection; vessels are relatively wide, fiber-tracheids thin walled.—11. Tangential section; rays are all multiseriate.—12. Radial section; scalariform vessel-axial parenchyma pitting.—13. Radial section; perforated ray cell with scalariform perforation plate.—14. Radial section; ray cells are all markedly procumbent; some contain dark-staining droplets. (Fig. 10, 11, magnification scale above Fig. 1; Fig. 12–14, scale above Fig. 3.)

plate, 21.9. Mean vessel wall thickness, 1.8 μm. Pits on fiber-tracheids moderately sparse, pit cavities about 2 μm in diameter. Mean fiber-tracheid diameter at widest point, 46 μm. Mean fiber-tracheid length, 1223 μm. Mean fiber-tracheid wall thickness, 1.8 μm. Rays both multiseriate and uniseriate, the latter rather rare. Multiseriate portion of multiseriate rays composed of square to procumbent cells, the cell row that forms the upper and lower tips of rays composed of upright cells. Mean height of multiseriate rays, 988 μm. Mean width of multiseriate rays at widest point, 5.1 cells. Mean height of uniseriate rays, 224 μm. Mean wall thickness of ray cells, 1.6 μm.

Bark

The bark of *D. roseiflora* is illustrated in Figures 15–18. Outer bark (Fig. 15) shows disruptions because of formation of successive periderms; bark tends to form breaks at the phellogen in sectioning. Periderm formation occurs only in outer bark; Figure 16 shows periderm only at top. Periderm typically consists of four or five layers of phellem, and, internal to the phellogen, a single layer of phelloderm.

Axial portions of secondary phloem consist of a succession of plates of fibers, alternating with thin-walled cells (Fig. 16). The fibers are thick walled (Fig. 18, top). The thin-walled cells consist of sieve tube elements, companion cells, and phloem parenchyma. The phloem parenchyma may accumulate massive deposits of dark-staining compounds (Fig. 18), and some of the phloem parenchyma cells acquire lignified walls (Fig. 18: near bottom, lower right).

Phloem rays consist of thin-walled cells that tend to be stretched tangentially as stem diameter increases (Fig. 16). A few of these cells acquire lignified walls (Fig. 17, upper left). Druses are common in phloem ray cells (Fig. 17).

DISCUSSION

The three collections of *Degeneria* studied represent ontogenetic stages in the sequence *D. vitiensis* (*Carlquist 695*), *D. roseiflora* (*Miller 1200*), and *D. vitiensis* (*SFCw-R 1193-1*). Quantitative data when arranged in this order can be used to demonstrate changes during ontogeny of particular wood features. In addition, a few sections from the center of stems of *D. vitiensis* and *D. roseiflora* were used to determine the earliest point in ontogenetic sequences of these characters. Features subject to ontogenetic change are discussed first, so that a residue of features by which the two species might differ then can be considered.

Quantitative features that show change include (least juvenile expression given): longer vessel elements, longer fiber-tracheids, taller multiseriate rays, and wider multiseriate rays. The changes in ray dimensions are apparently minimal, however. Ray histology shifts to a high proportion of procumbent cells (upright cells may be found in the multiseriate portions of multiseriate rays in younger stems of *D. vitiensis*). In rays of the largest stem studied, cells are exclusively procumbent except for a few sheathing cells and tip cells (cells at the upper and lower tips of rays), and the procumbent cells are markedly elongate radially. Uniseriate rays are uncommon in *D. vitiensis*, but grow even less common (essentially they are absent) as ontogeny proceeds. All of these tendencies are in accord with Barghoorn's (1941) findings on ray ontogeny. The quantitative data offered by Taka-

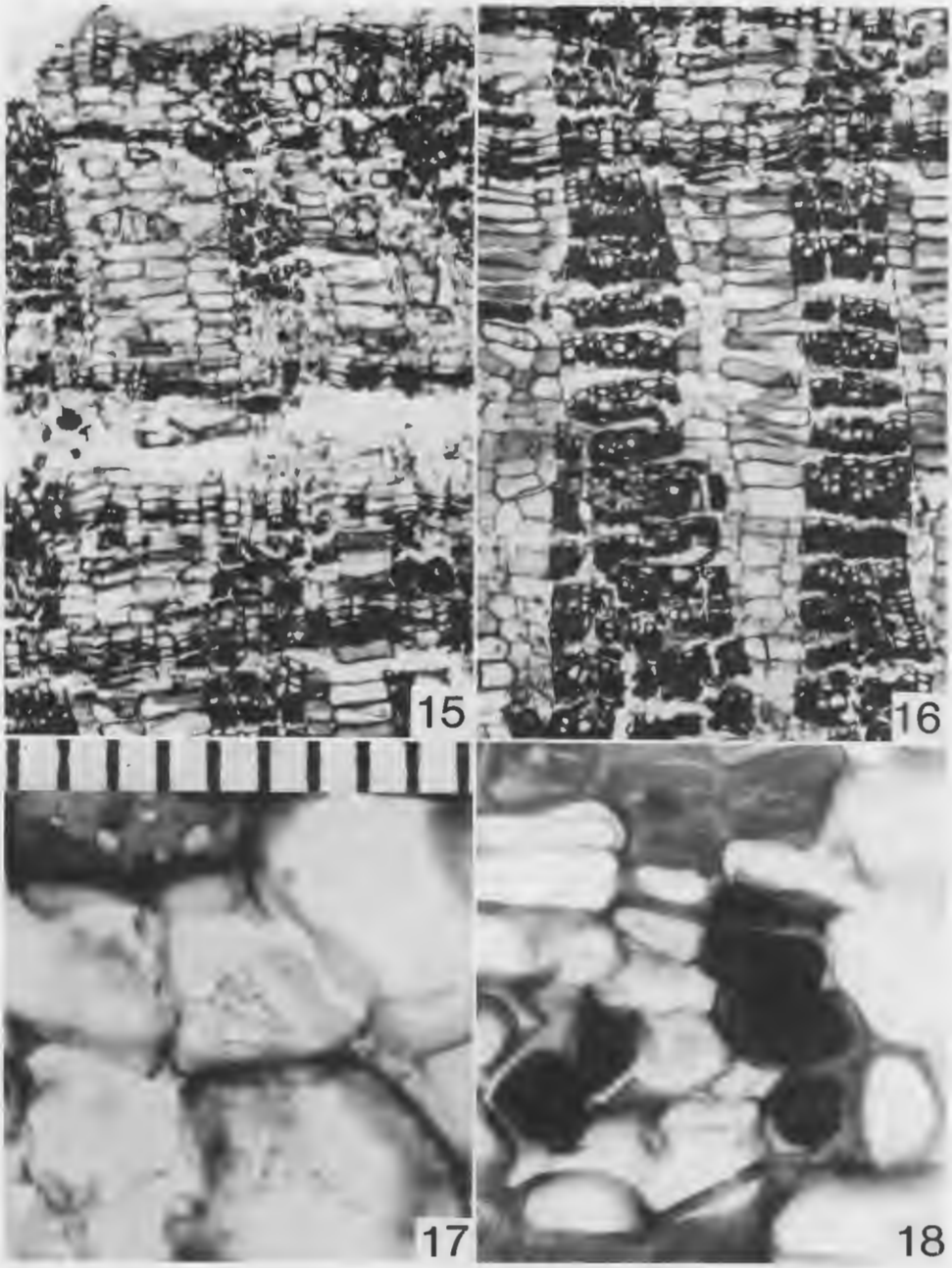

Fig. 15–18. Transections of bark of *Degeneria roseiflora* (*Miller 1200*).—15. Outer portion of bark (surface above); break is present in a periderm, center.—16. Inner portion of bark (innermost periderm above), showing plates of fibers in secondary phloem.—17. Ray cells from secondary phloem, showing lignified cell (above) and druses (center, below).—18. Portion of axial secondary phloem; fibers, above; dark-staining deposits in phloem parenchyma cells, center; phloem parenchyma with lignified cell walls, near bottom. (Fig. 15, 16, magnification scale above Fig. 1; Fig. 17, 18, scale above Fig. 17 [divisions = 10 μm].)

hashi (1985) suggest that he was studying relatively small stems; he reports mean vessel element length shorter than that of the sample *Carlquist 695,* and he found square as well as procument cells in the multiseriate portions of multiseriate rays.

Features by which the two species differ that seem unrelated to ontogenetic change include (expressions in *D. roseiflora* given): narrow vessels, thicker-walled vessels, thicker-walled fiber-tracheids, greater abundance of pits on fiber-tracheids, and greater abundance of ethereal oil cells in rays. Uniseriate rays are appreciably more common in the *D. roseiflora* sample, despite the fact that its size is greater than that of *Carlquist 695* (which has fewer uniseriate rays; *R 1193-1* has essentially no uniseriate rays); as noted above, uniseriate rays decrease in number with age. None of the features by which the two species differ offer a true presence-versus-absence kind of contrast, and all are differences of degree. The differences between the two species do not seem related to differences in ecology; from the observations of Smith (1981) and Miller (1988), the ecology of the two species is similar.

Lemesle and Duchaigne (1955*a, b*) use terms that suggest new or uncommon phenomena, but I believe their observations can be explained more simply. The "parenchymatous cells" with bordered pits they cite could be either axial parenchyma cells or ray cells. Both kinds of parenchyma cells in wood have borders much more commonly than is indicated in wood literature at present, although the pits in axial parenchyma and ray cells of *Degeneria,* where bordered, are much less conspicuously bordered than those of many dicotyledons. Bordered pits in parenchyma cells of wood are best observed in sectional view; the borders are very poorly seen if the pits are studied in face view, and that accounts for lack of mention of bordered pits on those cells in the literature (see Carlquist 1988). The "pseudotracheids" these authors claim may be axial parenchyma cells with bordered pits.

Takahashi's (1985) claim that pits of fiber-tracheids of *D. vitiensis* could be either bordered or simple could not be confirmed. The possibility remains that borders, always quite inconspicuous on fiber-tracheids of *Degeneria,* may be present but not easily seen and therefore overlooked.

The low degree of grouping of vessels in *Degeneria* accords with the mesomorphic ecology in which this genus occurs; grouping is only a little more than random adjacence (if one calculates for the given density and vessel diameter what random placement of vessels would be produced: David A. Hoekman, unpublished). Woods with tracheids tend to have minimal grouping of vessels, and in woods with fiber-tracheids rather than tracheids, vessel grouping is a little more than random distribution would dictate even in woods from very mesomorphic areas (Carlquist 1984).

The wood of *Degeneria* is less primitive than that of some other dicotyledons, such as *Euptelea* or *Illicium. Degeneria* wood is specialized in ray histology, corresponding to Heterogeneous Type IIB, tending toward Homogeneous Type II. Other relatively specialized features include presence of fiber-tracheids rather than tracheids, presence of various types of parenchyma aggregation (e.g., banded) and the only moderately long perforation plates (fewer than 25 bars). The comparisons offered by Bailey, Nast and Smith (1943) and by Canright (1955) between Degeneriaceae and Magnoliaceae or Himantandraceae are based in part on similar

degrees of specialization of woods in these three families. To be sure, the three families share monosulcate pollen grains (Walker and Doyle 1975). However, monosulcate pollen occurs in other families thought to be closely related (Canellaceae), and the zonicolpate pollen grains of Eupomatiaceae and the various apertural configurations of annonaceous pollen grains represent only small modifications of the monosulcate condition. Perhaps more significantly, Annonaceae, Degeneriaceae, Eupomatiaceae, Himantandraceae, and Magnoliaceae share atectate (primitively columellaless) pollen (Walker and Doyle 1975). Sclerenchyma plates in pith, present in Degeneriaceae, are shared by Annonaceae, Canellaceae, Eupomatiaceae, and Myristicaceae (Ehrendorfer, Krendl, Habeler, and Sauer 1968). Wood anatomy of *Eupomatia* and the curious staminodes of that genus may be closer to comparable conditions in *Degeneria* than hitherto appreciated. Endress (1977), in reviewing information on Eupomatiaceae and Himantandraceae, believes that Magnoliaceae, Degeneriaceae, Himantandraceae, and Eupomatiaceae form a close group, but he also believes that the group comprised of Annonaceae, Canellaceae, and Myristicaceae should be placed in close proximity to the former group of families so that both groups of families unite into a single assemblage.

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