WOOD ANATOMY AND FAMILIAL STATUS OF *VIVIANIA*

Sherwin Carlquist

*Rancho Santa Ana Botanic Garden
and
Department of Biology, Pomona College
Claremont, California 91711*

ABSTRACT

Wood of three species of *Viviania* from Chile was studied. The wood has growth rings, moderately grouped vessels, helical sculpture in vessels, fiber-tracheids with small pits, and various degrees of storying. Axial parenchyma and rays are absent, regardless of age of stem. These facts are in accord with close relationship to other genera of Geraniaceae s.l. *Viviania* differs from other Geraniaceae in presence of borders on imperforate tracheary elements and presence of endosperm; other differences (polyporate pollen; loculicidal capsules) are shared with some other genera which have familial status according to some authors, subfamilial status according to others. *Viviania* is probably the most distinctive element within Geraniaceae s.l., but other genera are close behind in this regard. Wood features of *Viviania* are in accord with the dry habitats occupied by this genus.

Key words: comparative plant anatomy, ecological wood anatomy, Geraniaceae, Ledocarpaceae, *Viviania*, wood anatomy.

INTRODUCTION

The genus *Viviania* consists of 28 species native mostly to Chile, but a few species occur in Uruguay and southern Brazil (Knuth 1912). *Viviania* constitutes either a subfamily of Geraniaceae or an independent family according to recent authors. Advocates of familial status include Dahlgren (1980) and Thorne (1983). Those who retain *Viviania* within Geraniaceae as a tribe or subfamily include Cronquist (1981), Hoffmann (1978), Knuth (1912), Muñoz (1959), and Takhtajan (1980). The features by which *Viviania* differs from Geraniaceae other than *Viviania* include (data from Knuth 1912) polyporate nature of pollen (tricolpate in Geranieae, polyporate or nonaperturate in Wendtieae); loculicidal nature of capsule (present also in *Balbisia* and *Wendtia,* carpels ventrally dehiscent in *Dirachma,* otherwise mericarps which separate from the floral axis); presence of endosperm (scanty or absent in Geraniaceae); and nature of leaves (opposite and simple in *Viviania,* mostly not opposite and often palmatifid in the Geraniaceae). Segregation of *Viviania* from Geraniaceae requires decisions on whether Ledocarpaceae (Wendtieae as a tribe: *Balbisia, Rhyncotheca,* and *Wendtia*), Biebersteiniaceae (*Biebersteinia*) and Dirachmaceae (*Dirachma*) should also be segregated.

During my travel in Chile in 1982, I collected material of *Viviania crenata* (Hook.) G. Don. This has been supplemented by material available from herbarium specimens of *V. laxa* Phil. and *V. spinescens* Presl. *Viviania* can be described as a subshrub bearing branches attached to a woody caudex. Branches persist variously; the bases of some may become woody for several years. The wood of branches may differ somewhat from that of the caudex, so one should not regard a wood description based upon one part as applying to the other.

In addition to availability of material, study of *Viviania* wood is prompted by the desirability of understanding woods other than those of arboreal species.

Geraniaceae are a nonwoody group typically; the fact that Geraniaceae have rayless woods (Barghoorn 1941; Carlquist 1986) suggests that they, like other groups with rayless woods, may represent phylesis toward woodiness from an essentially herbaceous ancestry (Carlquist 1970). The present study examines whether or not all Geraniaceae s.l. follow this pattern.

The study of only three species of *Viviania* may seem to represent an inadequate sampling of the genus. In fact, most species provide insufficient wood for convenient study, and those represented here are among the woodiest. The ecological range represented here is probably nearly maximal for the genus, since *V. spinescens* represents a xeric area, whereas *V. cuneata* comes from an only moderately dry area (all *Viviania* localities could be described as relatively dry; although weather data for the localities are not available, the vegetation, compared to that of localities in California where rainfall records are available, suggests precipitation of between 25 and 50 cm per year). About half of the species in the genus belong to what could be termed the "*V. rosea* Hook. complex" and were segregated from *V. rosea* by Knuth (1912) and others; these species do not represent any marked differentiation from each other in growth form, ecology, or other factors that would tend to be reflected by differences in wood anatomy.

MATERIALS AND METHODS

Wood samples were available in dried form. The material of *V. crenata* represents aboveground stems about 7 mm in diameter, collected in scree areas in the Parque National "La Campaña," along the Cuesta de la Dormida road west of Tiltil, north of Santiago, Chile. The material of *V. laxa* represents aboveground stems 8 mm in diameter; it comes from the "Cuesta del Espino" between Combarbala and Illapel, Coquimbo Prov., Chile. The wood of *V. spinescens* is from a woody caudex, 1.5 cm in diameter, at ground level; that specimen was collected on the Llano de Junalillo, 2600–2700 m, Aconcagua Prov., Chile.

Voucher specimens for all collections are located at RSA. The monograph of Knuth (1912) was used for identification of specimens.

Wood samples were boiled and stored in 50% ethyl alcohol. All samples proved suitable for sectioning without prior softening; they were sectioned on a sliding microtome. Presence of starch was established in *V. spinescens* sections by means of staining with IKI. Permanent slides were made of wood sections of all three species by means of staining with a safranin-fast green combination and mounting in Coverbond (Piccolyte). Macerations were prepared with Jeffrey's Fluid and stained with safranin. Quantitative feature means were obtained from average of 25 measurements except in vessel wall thickness, fiber-tracheid wall thickness, and fiber-tracheid diameter, where a typical condition was selected.

ANATOMICAL RESULTS

VIVIANIA CRENATA, *Carlquist 7433* (Fig. 1–4). Growth rings present, vessels wider in earlywood (Fig. 1). Vessels round or oval (radially widened) in transection. Mean vessel diameter, 28 μm. Mean number of vessels per mm^2, 322 μm. Mean number of vessels per group, 1.91; many vessels in radial multiples. Mean vessel wall thickness, 2.5 μm. Mean vessel element length, 135 μm. Perforation plates predominantly simple; a small number of perforation plates crossed by a single bar seen. Lateral walls of vessels with pits circular to elliptical in outline, 2–4 mm in diameter (Fig. 4). Pit apertures interconnected by grooves but raised sculpture
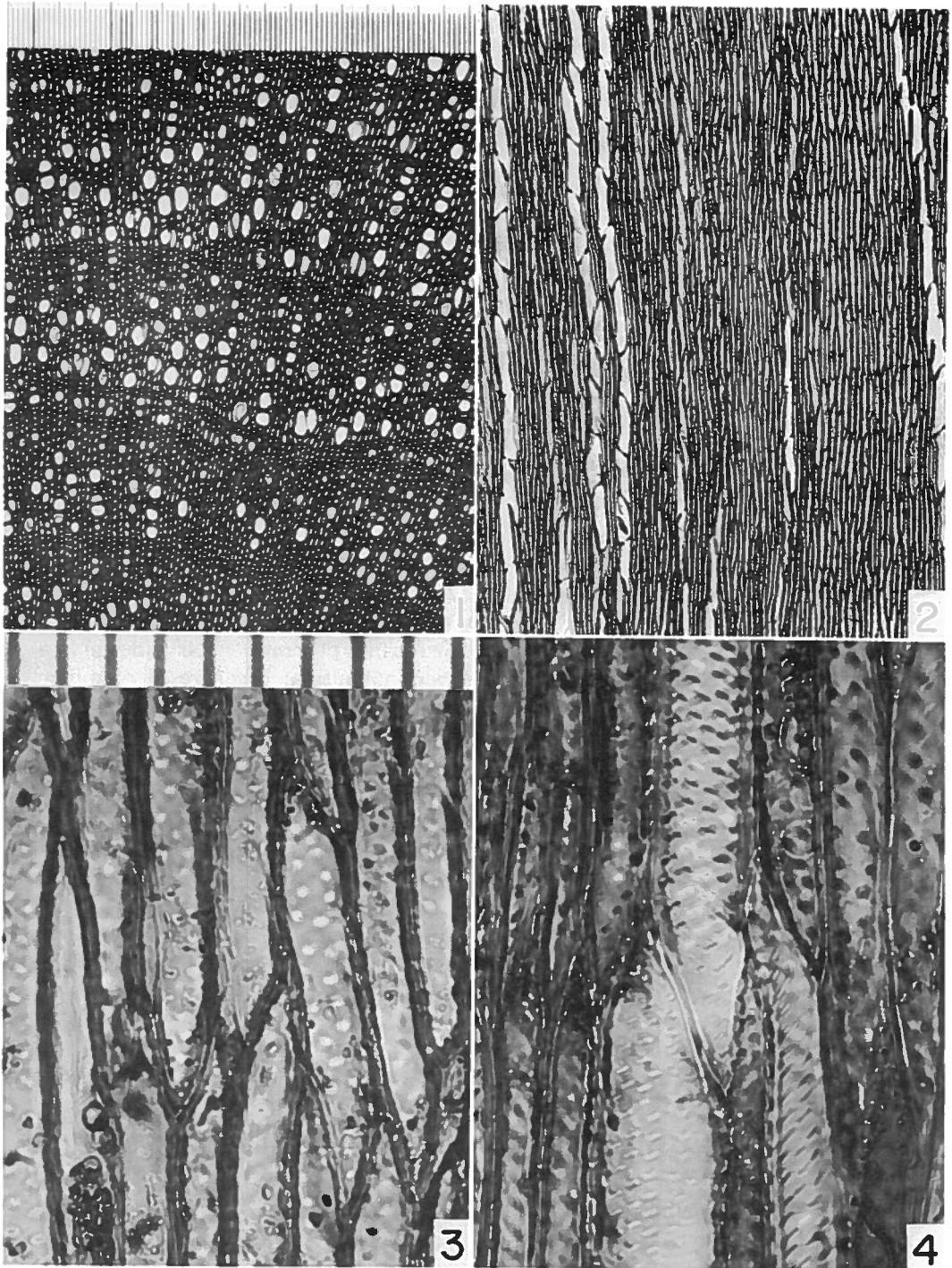
Fig. 1–4.   Wood sections of *Viviania crenata* (*Carlquist 7322*).—1. Transection; growth rings are evident; rays are absent.—2. Tangential section; storying is evident, especially in fiber-tracheids at right.—3. Portion of tangential section; small bordered pits are evident in the fiber-tracheids.—4. Portions of tangential section; vessels, center, have small pits; grooves interconnecting pit apertures are inconspicuous. (Fig. 1, 2, magnification scale above Fig. 1 [finest divisions = 10 μm]. Fig. 3, 4, magnification scale above Fig. 3 [divisions = 10 μm].).

(thickenings) not present. Thin-walled spherical tyloses present in some vessels. All imperforate tracheary elements are fiber-tracheids. Mean fiber-tracheid diameter, 18 μm. Mean fiber-tracheid wall thickness, 2.1 μm. Mean length of fiber-tracheids, 173 μm. Fiber-tracheids occasionally septate. Fiber-tracheid pits bordered, 2–3 μm in diameter (Fig. 2, 3). Axial parenchyma absent. Rays absent (Fig. 2). Storying variously evident (Fig. 2).

VIVIANIA LAXA, *Simon 117* (Fig. 5–8). Growth rings present, strongly demarcated (Fig. 5), vessels wider in earlywood and relatively narrow, often about the same diameter as fiber-tracheids, in latewood (Fig. 7). Vessels round or oval in transection. Mean vessel diameter, 17.5 μm. Mean number of vessels per mm², 1001. Mean number of vessels per group, 2.0, many vessels grouped in radial clusters. Mean vessel wall thickness, 1.4 μm. Mean vessel element length, 162 μm. Perforation plates simple. Lateral walls of vessels with pits 2–4 μm in diameter. Helical sculpture on vessel walls consisting of grooves interconnecting pit apertures; on either side of grooves, thickening bands occur (Fig. 8). Some vessel elements are fibriform. A few thin-walled spherical tyloses are present in vessels. All imperforate tracheary elements are fiber-tracheids that are very tracheidlike. Fiber-tracheids bear pits that are 2 μm in diameter, densely placed, and fully bordered. Only in size of pits do the elements fall short of qualifying as true tracheids. Mean fiber-tracheid diameter, 16.5 μm. Mean fiber-tracheid wall thickness, 2.2 μm. Mean fiber-tracheid length, 204 μm. Axial parenchyma absent. Rays absent (Fig. 6). Storying present, but not strongly marked (Fig. 6).

VIVIANIA SPINESCENS, *Ricordi 2912*. Growth rings present, vessels wider in earlywood. Vessels circular to oblong in transectional outline. Mean vessel diameter, 36 μm. Mean number of vessels per mm², 223. Mean number of vessels per group, 1.76; some vessels in radial multiples. Mean vessel wall thickness, 2.6 μm. Mean vessel element length, 144 μm. Perforation plates simple. Lateral walls of vessels with pits 2–4 μm in diameter. Pit apertures interconnected by grooves; additionally, pairs of faint thickenings are present beside grooves in some vessels. Numerous thin-walled spherical tyloses present in vessels. All imperforate tracheary elements are fiber-tracheids. Mean fiber-tracheid diameter, 28 μm. Mean fiber-tracheid wall thickness, 2.3 μm. Mean fiber-tracheid length, 193 μm. Fiber-tracheid pits about 2 μm in diameter, borders present but less conspicuously present than in the other species. Starch abundantly present in some of the fiber-tracheids. Axial parenchyma absent. Rays absent. Storying variously evident but not strongly marked.

SYSTEMATIC CONCLUSIONS

Knuth (1912) recognizes five tribes of Geraniaceae: Geranieae (all genera except those listed following); Biebersteinieae (*Biebersteinia*); Wendtieae (*Balbisia, Rhynchotheca, Wendtia*); Vivianieae (*Viviania*); and Dirachmeae (*Dirachma*). Dahlgren (1980) raised all of these to the level of family (Ledocarpaceae applies to Wendtieae when recognized as a family). Thorne (1983) gives familial status to two of these (Vivianiaceae and Ledocarpaceae) but retains Dirachmoideae and Biebersteinioideae as subfamilies. Vivianiaceae may be the most distinctive of these on the basis of wood because of presence of borders on pits of imperforate tracheary elements and absence of axial parenchyma (*Balbisia* has axial parenchyma: original observation based on *B. peduncularis* [Lindl.] D. Don, *Ricardi 4347*, RSA). Presence of pits on imperforate tracheary elements of *Viviania* was
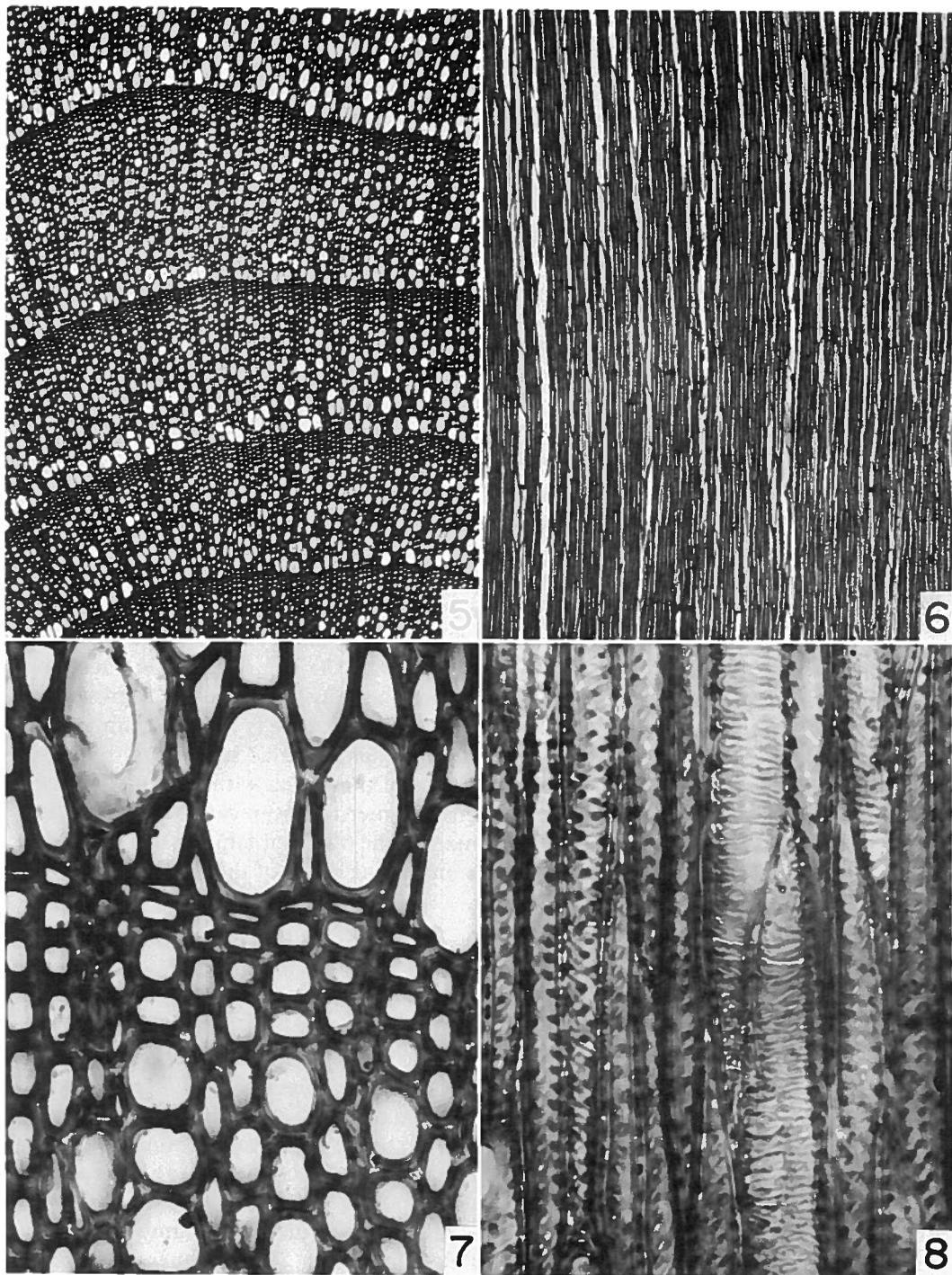
Fig. 5–8.   Wood sections of *Viviania laxa* (*Simon 117*). — 5. Transection; sharply demarcated growth rings are evident. — 6. Tangential section, showing absence of rays; fiber-tracheids are weakly storied. — 7. Transection showing margin of growth ring; vessels are nearly as narrow as fiber-tracheids in latewood. — 8. Portion of tangential section; small bordered pits evident in fiber-tracheids; grooves accompanied by pairs of thickening bands evident on vessel walls. (Fig. 5, 6, magnification scale above Fig. 1; Fig. 7, 8, scale above Fig. 3.)

reported by Metcalfe and Chalk (1950). The borders are most prominent, among the species studied here, on fiber-tracheids of *V. laxa*. Endosperm presence, like pit border presence in fiber-tracheid in *Viviania,* can be considered a primitive feature. Most workers, however, would consider the polyporate pollen condition, as well as the absence of axial parenchyma, to be specialized conditions in *Viviania*. Wendtieae (Ledocarpaceae) have simple pits on imperforate tracheary elements and do have axial parenchyma (original observation, *Balbisia peduncularis*), but they have polyporate or nonaperture pollen (Erdtman 1952). The capsular fruit types of the subfamilies or tribes other than Geranieae were mentioned in the Introduction; these fruit types may be considered less specialized than the mericarps of Geranieae and Biebersteinieae.

One can conclude that of the five tribes of Geraniaceae recognized by Knuth (1912), also cited as five families by Dahlgren (1980), Vivianiaceae is the most distinctive one. Wendtieae (Ledocarpaceae) is close morphologically to Vivianiaceae, since both groups are native to southern South America. *Dirachma* (endemic to Socotra Island) is isolated geographically and may be nearly as distinctive as *Viviania,* but nothing has been reported on its anatomy to date.

The presence of rayless wood, reported here for *Viviania,* has also been found in *Balbisia* and *Wendtia* (Metcalfe and Chalk 1950). Rayless wood has been reported in Geraniaceae s.s. (Barghoorn 1941, Metcalfe and Chalk 1950, Carlquist 1986). The fact that this feature, unusual in dicotyledons at large, is present in all of the geranioid groups, suggests the closeness of these entities. There seems little doubt that *Viviania* is related to Geraniaceae; the only remaining question is how to demonstrate the degree of taxonomic affinity that *Viviania* represents. The problem in segregating Vivianiaceae from Geraniaceae is that Dirachmaceae and Ledocarpaceae would be only slightly less justifiable as segregants, Biebersteiniaceae even less defensible. The presence of these taxa with varying degrees of difference from Geraniaceae s.s. lessens the merit of segregation of *Viviania,* which very likely would readily be recognized if the other subfamilies (or families) did not represent smaller discontinuities, involving some of the same characters as those that distinguish *Viviania*.

ECOLOGICAL CONCLUSIONS

If one calculates the ratio "Mesomorphy" (Carlquist 1977) for the *Viviania* collections studied here, one finds the values: *V. crenata,* 11.7; *V. laxa,* 2.8; *V. spinescens,* 23.2. These are all of the same order of magnitude and reflect the dry habitats occupied by *Viviania*. The somewhat higher value for *V. spinescens* may be related to the fact that an underground caudex was studied in that species, whereas aboveground branches were studied in the others. Underground portions of dicotyledons tend to have more mesomorphic wood structure than aboveground portions. Xeromorphy is shown in *Viviania* about equally by all three of the features represented by the Mesomorphy ratio—vessel diameter, number of vessels per mm^2 of transection, and vessel element length. The number of vessels per mm^2 in *V. laxa,* 1001, is exceptionally high, and indicates a high degree of xeromorphy.

The number of vessels per group in *Viviania* is not exceptional, but it probably does represent a degree of adaptation to xeromorphy. The occurrence of helical

sculpture in vessels is an even clearer indication. The conspicuous sculpturing in vessels of *V. laxa* correlates with the low Mesomorphy figure for that species.

Because starch was observed in the fiber-tracheids of two of the species and septate fiber-tracheids of one species, one can suspect that the fiber-tracheids are nucleated and do not function in water conduction. The abundant starch storage in *V. spinescens* relates to the caudex studied in that species.

As in groups studied by Barghoorn (1941) and Carlquist (1970), raylessness appears to indicate secondary woodiness in *Viviania*. One can hypothesize that in the relatively moderate conditions of central Chile, the subshrub habit arose from more nearly herbaceous ancestors.

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