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WOOD ANATOMY OF STILBACEAE AND RETZIACEAE:
ECOLOGICAL AND SYSTEMATIC IMPLICATIONS

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ABSTRACT

Wood anatomy of ten species in five genera of the Cape Province (South Africa) family Stilbaceae is reported in quantitative and qualitative terms. Wood anatomy for stem, root, and lignotuber is reported for the monotypic Cape genus *Retzia*. Stilbaceae and Retziaceae are alike in wood anatomy but differ from Verbenaceae by having scalariform perforation plates with few and wide-bordered bars (simple plates and modified scalariform plates are also present); vessel elements clearly fibriform in shape; very scarce axial parenchyma; and long uniseriate wings on multiseriate rays. When added to endosperm presence and ericoid habit, these features may serve to segregate Stilbaceae from Verbenaceae. The wood of Stilbaceae is xeromorphic in having very narrow vessels, numerous vessels per mm², and pores grouped into radial multiples. The least xeromorphic wood within Stilbaceae is found in species from relatively moist montane localities; these species also have scalariform perforation plates in vessels. The most xeromorphic wood occurs in those Stilbaceae restricted to lowlands or lowlands plus dry montane sites. Scalariform perforation plates are interpreted as an indicator of primitiveness in Stilbaceae and Retziaceae, an interpretation reinforced by presence of borders on pits of imperforate tracheary elements in *Eurylobium serrulatum* (all other Stilbaceae have libriform fibers with simple pits). The rock-crevice species *Stilbe rupestris* has caudex wood specialized for storage, stem wood adapted for mechanical strength. Species characters appear to be related to ecology, but sampling is inadequate for establishment of many features as systematic indicators. Wood anatomy confirms close relationship between Stilbaceae and Retziaceae, and union of the families is endorsed.

Key words: ecological wood anatomy, Retziaceae, Stilbaceae, Verbenaceae, wood anatomy.

INTRODUCTION

Stilbaceae have been recognized as a family by some authors (e.g., Riley 1963; Hutchinson 1973; Dahlgren et al. 1979), but they are more often recognized as a tribe (Stilbeae) or subfamily (Stilboideae) of Verbenaceae. This group has been defined on the basis of a small number of constant differences. Seeds of Stilbaceae possess endosperm. The habit of the stilboids is shrubby to subshrubby; leaves are ericoid. The familial name is used here not merely to call attention to these few features, but to highly distinctive features of wood anatomy as well, features not characteristic of other Verbenaceae. In addition, Stilbaceae are characteristic of the Table Mountain Sandstones of Cape Province, South Africa, a distinctive edaphic and geological setting that hosts other endemic groups such as the families Geissolomataceae, Grubbiaceae, Roridulaceae, and most of Bruniaceae, as well as many Ericaceae and Proteaceae.

Stilbaceae consist of five genera: *Campylostachys*, *Eurylobium*, *Euthystachys*, *Stilbe*, and *Xeroplana*. All of these are currently monotypic except for *Stilbe*, in which six species are usually recognized. Pearson (1912) provides taxonomic, ecological, and geographical data for the group. *Euthystachys* and *Xeroplana* are known from very limited material.

Retzia capensis Thunb., sole species of Retziaceae, is also limited to Cape Province, where it grows on sandstone areas. Although Leeuwenberg (1964, 1980) claimed that *Retzia* belongs in Loganiaceae, a review of numerous features by Dahlgren et al. (1979) made a persuasive case for relationship to Stilbaceae. Although wood anatomy of *Retzia* was studied by Mennega (in Leeuwenberg 1980), material I collected in Cape Province in 1973 included root and lignotuber portions not available in the material studied by Mennega. In addition, the opportunity to see if *Retzia* has affinity to Stilbaceae by side-by-side comparisons offered a reason for including that genus in the present study.

Herbarium specimens have been used as the source of material for study of the woods of Stilbaceae. This is not considered a disadvantage, for the shrubs are often so small that field-collected material would yield stems only a little larger than those on herbarium specimens. Very likely the small size of stems is the reason why wood anatomy has been studied so little in the group. Briquet (1894) reports scalariform perforation plates, along with simple ones, in vessels of *Campylostachys* and *Stilbe*. Solereder (1908) confirms this, citing *S. pinastra* L. (now *S. vestita* Berg.). Solereder also reports septate fibers for *Euthystachys* and *Stilbe*.

Wood anatomy of Stilbaceae is worthy of attention with respect to ecology. Stilbaceae occupy exposed sites, some of which are dry much of the year although others, in higher montane areas, may feature prolonged water availability by virtue of seeps and south-facing slope exposure. The ericoid leaves of Stilbaceae suggest periods of restricted water availability, as does the small size of shrubs. The ecological range is appreciable (Pearson 1912), and, despite the modifying influence of microphylls, does bear comparison to data from wood anatomy.

Stilbe rupestris Compton is a distinctive rock-crevice shrub, and its wood is worthy of investigation not merely with respect to adaptation to such a dry habitat but also with regard to differentiation into a woody caudex from which several wiry stems of various durations arise. For this species, wood of both these portions has been described and illustrated separately.

Retzia also occupies sunny sites on sandstone in Cape Province, and therefore wood anatomy with relation to ecology is also of interest. *Retzia* tends to grow among sandstone boulders or rubble, and may therefore occur in sites with somewhat greater water availability than an exposed area would seem to offer.

The present study of Stilbaceae and Retziaceae is part of a survey of wood anatomy of families of tubiflorous dicotyledons. An attempt will be made to see which ordinal concepts correspond not only to data from wood anatomy, but to the totality of data for these families. Although detailed coverage of wood anatomy of Verbenaceae is not contemplated at the present time, a detailed examination of Stilbaceae is attempted because they, like Chloanthaceae (Carlquist 1981a) and Avicenniaceae, appear to merit segregation from Verbenaceae on the basis of wood anatomy.

MATERIALS AND METHODS

Most of the material of Stilbaceae studied was derived from herbarium specimens in the Bolus Herbarium, University of Cape Town, kindly supplied by Dr. Daryl Koutnik. Material of *Campylostachys cernua* Kunth and *Stilbe phyllicoides* A. DC. was supplied by the U.S. National Herbarium, courtesy of Dr. Richard Eyde. The Rancho Santa Ana Botanic Garden Herbarium provided material of

S. ericoides L. and *S. rupestris*. Dr. John Rourke of the Compton Herbarium, Kirstenbosch Botanic Gardens, kindly provided the wood samples of *Euthystachys abbreviata* A. DC. and *Xeroplana zeyheri* Briq. All stems were relatively small, ranging from 1.5 to 5 mm in diameter.

Material of *Retzia capensis* was collected at two localities; wood samples were dried; herbarium specimens were prepared and given to the Rancho Santa Ana Botanic Garden. The specimen *Carlquist 4514*, from upper Fernkloof, near Hermanus, provided better material of stems. The collection *Carlquist 4693*, from Mt. Bredasdorp, had smaller stems (which were, however, also sectioned), but provided good root and lignotuber material.

Stems were boiled in water, stored in 50% ethyl alcohol, and sectioned on a sliding microtome. Sections were stained with safranin and counterstained with fast green. Macerations were prepared with Jeffrey's Fluid and stained in safranin. Means are based upon 20 measurements per feature (fewer where structures are scarce, as in rays of some species). Imperforate tracheary element diameter, imperforate tracheary element wall thickness, and vessel wall thickness are based upon typical conditions rather than repeated measurements. Measurements of vessel diameter include the wall, as is typically done, although for ecological considerations one might prefer diameter of lumen (which can be calculated by subtracting the vessel wall thickness, given in the descriptions). Width of multiseriate rays is measured in terms of number of cells seen at the widest point in each multiseriate ray.

Illustrations represent wood of upright stems (Fig. 1-7, 8-9) except for the two illustrations (Fig. 10-11) in which the woody caudex is shown. The divergence in wood structure between the stem (Fig. 8-9) and caudex (Fig. 10-11) of *Stilbe rupestris* shows that minor differences in wood anatomy between species may relate more to age, ecology, and habit than to any deep-seated taxonomic differences. Therefore, quantitative data on such features as ray height and width should not be interpreted as representing characters of taxonomic significance.

ANATOMICAL DESCRIPTIONS

Stilbaceae

CAMPYLOSTACHYS CERNUA (*Galpin 12834*).—Growth rings very weakly demarcated: vessels slightly more numerous in earlywood. Vessels mostly in short to long radial multiples, few solitary. Mean number of vessels per mm², 639. Mean vessel diameter, 21.0 μm . Mean vessel element length, 395 μm . Mean vessel wall thickness, 2.3 μm . Perforation plates simple. A small number of vasicentric tracheids present. All other imperforate tracheary elements are libriform fibers with apparently simple pits. Mean diameter of libriform fibers at widest point, 17 μm . Mean length of libriform fibers, 570 μm . Mean wall thickness libriform fibers, 4.1 μm . No septa observed in libriform fibers. No axial parenchyma observed. Uniseriate rays more abundant than multiseriate rays. Long uniseriate wings present on multiseriate rays. Uniseriate rays and the wings of multiseriate rays composed of upright cells. Multiseriate rays also composed of erect cells except for a very few square to procumbent cells in the central portions of multiseriate rays. Mean width of multiseriate rays at widest point, 2.0 cells. Mean height of multiseriate rays, 482 μm . Mean height of uniseriate rays, 405 μm .

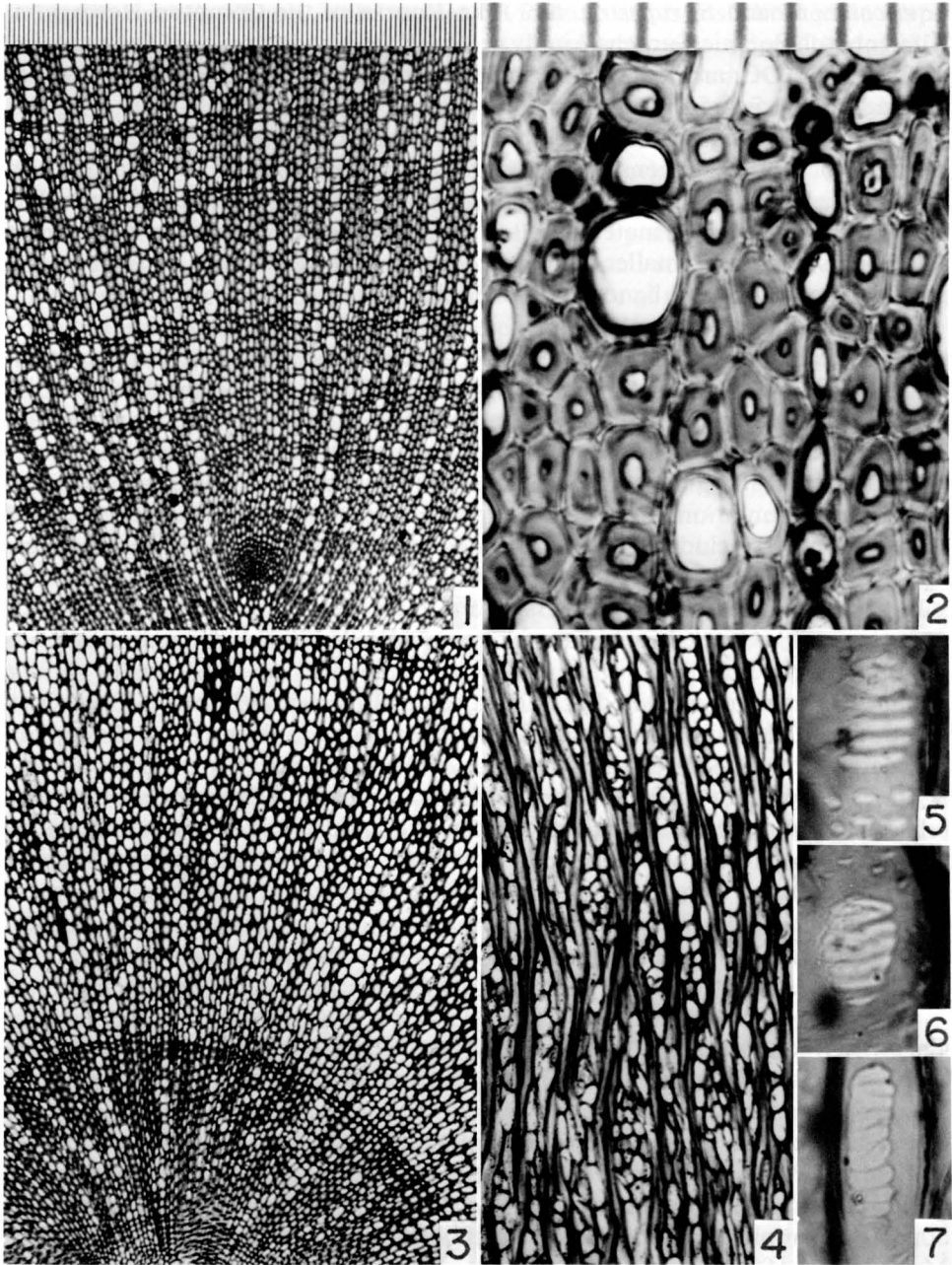


Fig. 1-7. Wood sections of Stilbaceae.—1. *Stilbe mucronata* (Stokoe VII-1932). Transsection; seven weakly demarcated growth rings are present.—2. *Stilbe ericoides*. Portion of transsection; libriform fibers are notably thick walled.—3-6. *Eurylobium serrulatum* (Stokoe 1059).—3. Transsection; a growth ring is demarcated by thick-walled fibers, below.—4. Tangential section; numerous multiserial rays are present.—5-6. Scalariform perforation plates from radial section.—5. A nearly perfect scalariform plate.—6. A scalariform plated with fused and incomplete bars.—7. *Stilbe mucronata* (Stokoe VII-1932). Scalariform perforation plate with thin nonbordered bars. (Fig. 1, 3, 4, magnification scale above Fig. 1; Fig. 2, 5-7, magnification scale above Fig. 2 [divisions = 10 μ m].)

EURYLOBIUM SERRULATUM Hochst. (*Stokoe 1059*) (Fig. 3–6).—One growth ring noted in the specimen studied (Fig. 3) earlywood vessels wider, earlywood imperforate tracheary elements wider and thinner walled than those in latewood. Vessels mostly in short radial multiples. Mean number of vessels per mm², 119. Mean vessel diameter, 38.8 μm. Mean vessel element length, 439 μm. Mean vessel wall thickness, 4.14 μm. Perforation plates exclusively scalariform in material studied (Fig. 5, 6), the bars always bordered. Perforation plates mostly deviate from an ideal scalariform configuration at least to some degree (Fig. 6), by fusion or incompleteness of bars. Lateral wall pitting of vessels circular, alternate; the pits about 2.4 μm in diameter. No vasicentric tracheids observed. All imperforate tracheary elements can be called fiber-tracheids, because a small circular border about 1 μm in diameter occurs on the otherwise slitlike pits. Mean fiber-tracheid diameter at widest point, 34.5 μm. Mean fiber-tracheid length, 589 μm. Mean fiber-tracheid wall thickness, 4.14 μm. No septa observed in fiber-tracheids. Axial parenchyma cells scarce; all seen are adjacent to vessels. Axial parenchyma occurs as strands of two cells. Multiseriate rays much more abundant than uniseriate rays (Fig. 8). Uniseriate rays and multiseriate rays are composed predominantly of upright cells, but square and procumbent cells are moderately common in multiseriate portions of multiseriate rays. Mean width of multiseriate rays at widest point, 3.3 cells. Mean height of multiseriate rays, 800 μm. Mean height of uniseriate rays, 68 μm.

EUTHYSTACHYS ABBREVIATA (*Rycroft 2128a*).—Growth rings indistinct. Vessels commonly in radial multiples of various extent, some solitary. Mean number of vessels per mm², 403. Mean vessel diameter, 22.2 μm. Mean vessel element length, 495 μm. Mean vessel wall thickness, 2.3 μm. Perforation plates simple. A few double perforation plates (two circular plates interconnecting a pair of vessel elements) seen. Lateral wall pitting of vessels alternate, pits about 2.5 μm in diameter. Most vessel elements fibriform. A few vasicentric tracheids present. All other imperforate tracheary elements are libriform fibers by virtue of apparently simple pits. Mean diameter of libriform fibers at widest point, 16 μm. Mean length of libriform fibers, 557 μm. Mean wall thickness of libriform fibers, 9.2 μm. A few septa observed in libriform fibers. Axial parenchyma cells occasional, but still relatively infrequent, all axial parenchyma cells vasicentric. Uniseriate rays more frequent than multiseriate rays. Uniseriate rays and rings of multiseriate rays composed of erect cells. Multiseriate portions of multiseriate rays composed of erect cells with very few square or procumbent cells. Mean width of multiseriate rays at widest point, 2.0 cells (no rays wider than two cells observed). Mean height of multiseriate rays, 651 μm. Mean height of uniseriate rays, 208 μm.

STILBE ALBIFLORA E. Meyer (*Schlechter 9835*).—Growth rings not observed. Vessels in short to long radial multiples, but some solitary. Mean number of vessels per mm², 199. Mean vessel diameter, 14.8 μm. Mean vessel element length, 372 μm. Mean vessel wall thickness, 4.6 μm. Perforation plates all scalariform, no simple plates seen. Bars of perforation plates fully bordered. Plates that represent a modification of the scalariform pattern (bars fused, incomplete) more common than truly scalariform plates. Lateral walls of vessels with circular alternate pits about 2.5 μm in diameter. All vessel elements fibriform in shape. No vasicentric tracheids observed. All imperforate tracheary elements must be termed libriform

fibers because their pits are apparently simple. Mean diameter of libriform fibers at widest point, 23 μm . Mean length of libriform fibers, 528 μm . Mean wall thickness of libriform fibers, 2.1 μm . Septa not observed in libriform fibers. Axial parenchyma very scarce; all seen is in contact with vessels. Axial parenchyma in strands of two cells. Uniseriate rays about equal to multiseriate rays in frequency. Multiseriate rays composed of erect to square cells; procumbent cells rare and in the central portions of multiseriate rays. Uniseriate rays and the uniseriate wings of multiseriate rays composed of erect cells. Mean width of multiseriate rays at widest point, 2.5 cells. Mean height of multiseriate rays, 998 μm . Mean height of uniseriate rays, 339 μm .

STILBE ERICOIDES (*Martin 722*) (*Fig. 2*).—No growth rings observed. Vessels in moderate to long radial multiples (*Fig. 6*). Mean number of vessels per mm^2 , 474. Mean vessel diameter, 24.8 μm . Mean vessel element length, 382 μm . Mean vessel wall thickness, 2.8 μm . Perforation plates mostly simple, some vestigial scalariform (one or more bars partially traversing the plate, bars slender and nonbordered). Lateral walls of vessels with alternate circular pits about 2.4 μm in diameter. All vessel elements fibriform. A very small number of vasicentric tracheids present. All other imperforate tracheary elements are libriform fibers by virtue of having apparently simple pits. Mean libriform fiber diameter at widest point, 21 μm . Mean libriform fiber length, 514 μm . Mean libriform fiber wall thickness, 5.4 μm . Septa not observed in libriform fibers. No axial parenchyma observed. Multiseriate rays about as frequent as uniseriate rays. Uniseriate wings present on multiseriate rays, composed of erect cells. Multiseriate portions of multiseriate rays composed chiefly of square to procumbent cells. Uniseriate rays composed of erect cells. Mean width of multiseriate rays at widest point, 3.1 cells. Mean height of multiseriate rays, 565 μm . Mean height of uniseriate rays, 408 μm . Ray cells notably thick walled, some pits interconnecting ray cells minutely bordered.

STILBE MUCRONATA *N. E. Br.* (*Stokoe VII-1932*) (*Fig. 1, 7*).—Numerous growth rings present (*Fig. 1*), weakly demarcated by formation of narrower libriform fibers in latewood. Vessel elements solitary or in radial multiples of various length. Mean number of vessels per mm^2 , 312. Mean diameter of vessel elements, 31.0 μm . Mean length of vessel elements, 543 μm . Mean wall thickness of vessel elements, 1.8 μm . Perforation plates simple or with a few vestigial bars (*Fig. 7*), sometimes simple but with a ragged outline (suggesting bar vestiges) or double (two circular perforations interconnecting a pair of vessel elements). Lateral walls of vessels with circular alternate pits about 2.7 μm in diameter. All vessel elements fibriform. No vasicentric tracheids observed. All imperforate tracheary elements are libriform fibers by virtue of having apparently simple pits. Mean libriform fiber diameter at widest point, 21 μm . Mean libriform fiber length, 862 μm . Mean wall thickness of libriform fibers, 4.4 μm . Axial parenchyma very rare, vasicentric and composed of strands of two cells. Procumbent cells rare, present only in central portions of multiseriate rays; uniseriate rays and uniseriate wings of multiseriate rays composed of erect to square cells. Mean width of multiseriate rays at widest point, 2.3 cells. Mean height of multiseriate rays, 1160 μm . Mean height of uniseriate rays, 424 μm .

STILBE PHYLICOIDES (*Schlechter 13-IV-1892*).—No growth rings observed (only a

small-diameter stem studied, however). Vessels in radial multiples of various lengths. Mean number of vessels per mm^2 , 632. Mean vessel diameter, $27.1 \mu\text{m}$. Mean vessel element length, $420 \mu\text{m}$. Mean vessel wall thickness, $3.9 \mu\text{m}$. Perforation plates simple, a few with irregular margins suggesting vestiges of bars. Lateral wall pitting circular, alternate, about $2.5 \mu\text{m}$ in diameter. All vessel elements fibriform. No vasicentric tracheids observed. All imperforate tracheary elements can be termed libriform fibers because pits are apparently simple (pit apertures are lengthened by splitting in prepared slides). Mean diameter of libriform fibers at widest point, $18 \mu\text{m}$. Mean length of libriform fibers, $648 \mu\text{m}$. Mean wall thickness of libriform fibers, $3.9 \mu\text{m}$. Septa observed in a few libriform fibers. No axial parenchyma cells observed. Multiseriate rays about as frequent as uniseriate rays. Procumbent cells infrequent, found only in multiseriate portions of multiseriate rays; uniseriate rays and uniseriate portions of multiseriate rays composed of erect to square cells. Mean width of multiseriate rays at widest part, 2.8 cells. Mean height of multiseriate rays, $832 \mu\text{m}$. Mean height of uniseriate rays, $400 \mu\text{m}$.

STILBE RUPESTRIS (Esterhuysen 35658) (Upper stem. Fig. 8, 9).—No growth rings apparent (Fig. 8). Vessels commonly in radial multiples of various length (Fig. 8), some solitary. Mean number of vessels per mm^2 , 294. Mean vessel diameter, $28.4 \mu\text{m}$. Mean vessel element length, $349 \mu\text{m}$. Mean vessel wall thickness, $2.1 \mu\text{m}$. Perforation plates predominantly simple. A few double perforation plates (two circular plates interconnecting a pair of vessel elements) and perforation plates with ragged edges (indicative of vestigial bars) seen. Lateral wall pitting of vessels circular, alternate, pits about $2.3 \mu\text{m}$ in diameter. All vessel elements fibriform. No vasicentric tracheids observed. All imperforate tracheary elements are libriform fibers with apparently simple pits. Mean diameter of libriform fibers at widest point, $23 \mu\text{m}$. Mean libriform fiber length, $534 \mu\text{m}$. Mean wall thickness of libriform fibers, $2.8 \mu\text{m}$. Septate fibers abundant. Axial parenchyma very scarce, thick walled, vasicentric, in strands of two cells. Uniseriate rays much more frequent than multiseriate rays (Fig. 9), multiseriate rays present only at periphery of stem. Rays composed of upright and square cells except for central portions of multiseriate rays, where a few procumbent cells are present. Multiseriate rays too few to provide dimension data. Mean height of uniseriate rays, $728 \mu\text{m}$.

STILBE RUPESTRIS (Esterhuysen 35658) (Caudex. Fig. 10, 11).—No growth rings evident. Vessels grouped into radial multiples, many of these of indefinite radial extent (identification of vessels in Fig. 10 is difficult because vessels are so similar in diameter and wall thickness to libriform fibers). Mean number of vessels per mm^2 , 641. Mean vessel diameter, $21.2 \mu\text{m}$. Mean vessel element length, $399 \mu\text{m}$. Mean vessel wall thickness, $1.6 \mu\text{m}$. Perforation plates in vessels predominantly simple. A few double perforation plates (both perforations interconnecting a pair of vessel elements) seen. A few perforation plates with vestigial bars (bars slender, few, partly to wholly traversing the plate) or vestiges of bars (simple plates with ragged lateral margins) seen. Lateral wall pitting of vessels circular, alternate, about $2.4 \mu\text{m}$ in diameter. Vessel elements all at least somewhat fibriform in shape. A few vasicentric tracheids present. All other imperforate tracheary elements are libriform fibers by virtue of having apparently simple pits. Mean diameter of libriform fibers at widest point, $16 \mu\text{m}$. Mean length of libriform fibers,

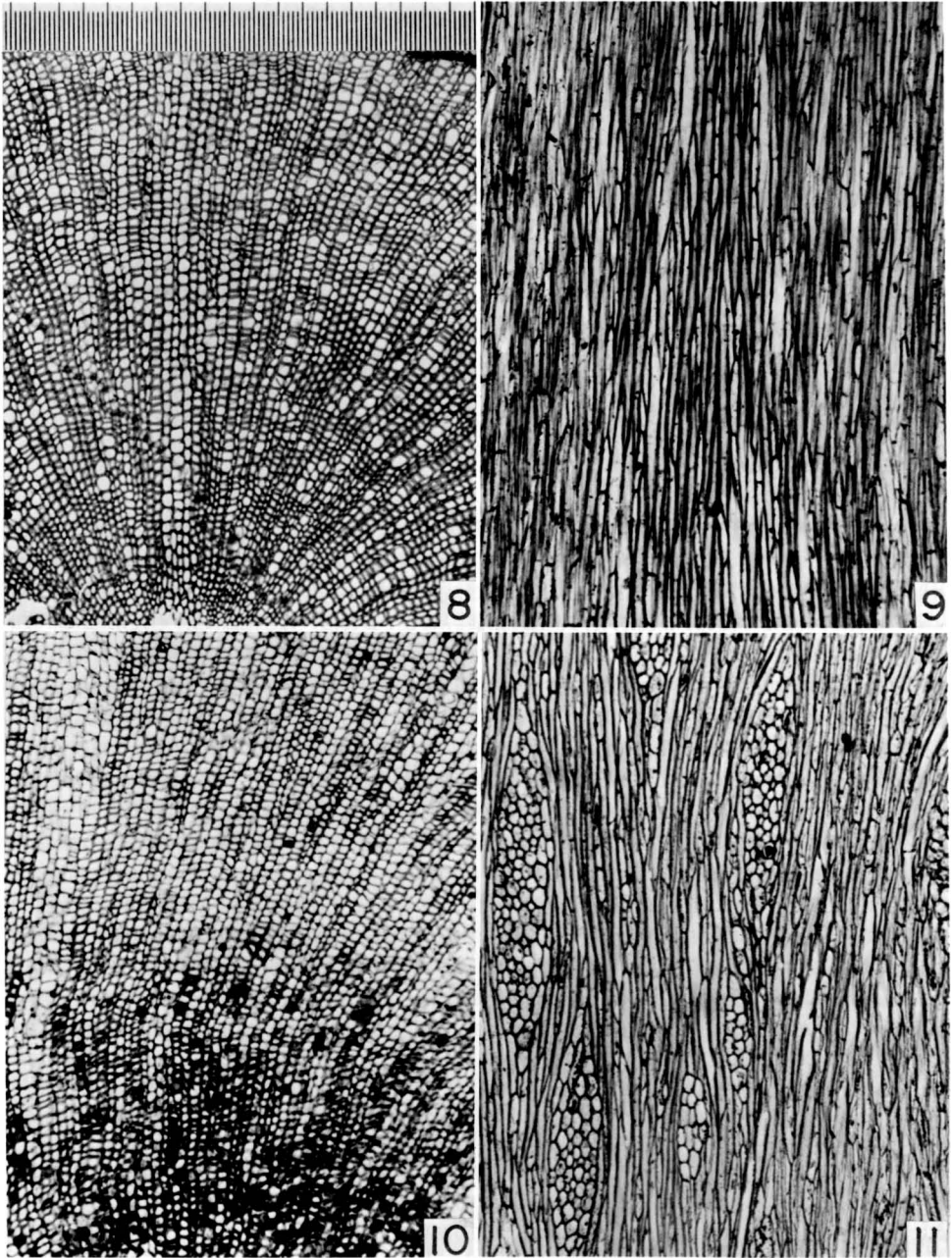


Fig. 8-11. Wood sections of *Stilbe rupestris* (Esterhuysen 35658).—8-9. wood from upper stem.—8. Transsection; libriform fibers are relatively thick walled.—9. Tangential section; rays are uniseriate only, ray cells are upright.—10-11. Wood from caudex.—10. Transsection. Libriform fibers are very nearly the same diameter as vessels; dark-staining compounds occlude many cells near bottom of photograph.—11. Tangential section. Wide multiseriate rays are present. (Fig. 8-11, magnification scale above Fig. 8 [finest divisions = 10 μ m].)

740 μm . Mean wall thickness of libriform fibers, 2.8 μm . Few libriform fibers septate. Axial parenchyma scarce, vasicentric, thin walled, in strands of two cells. Multiseriate rays more conspicuous than uniseriate rays (Fig. 11), but about equally frequent. Uniseriate rays and uniseriate wings of multiseriate rays composed of upright cells; square to procumbent cells abundant in the multiseriate portions of multiseriate rays (Fig. 11). Mean width of multiseriate rays at widest point, 5.0 cells. Mean height of multiseriate rays, 998 μm . Mean height of uniseriate rays, 190 μm .

STILBE VESTITA Berg. (*MacOwen 926*).—Growth rings not readily perceptible. Vessels grouped in moderate to long radial multiples. Mean number of vessels per mm^2 , 306. Mean vessel element diameter, 25.7 μm . Mean vessel element length, 491 μm . Mean vessel wall thickness, 2.1 μm . Perforation plates mostly simple; a few perforation plates within ragged lateral margins (indicative of presence of vestigial bars) observed. Lateral wall pitting of vessels composed of alternate circular pits about 2.5 μm in diameter. Vessel elements all fibriform. Vasicentric tracheids not observed. All imperforate tracheary elements are libriform fibers by virtue of having apparently simple pits. Mean diameter of libriform fibers at widest point, 23 μm . Mean length of libriform fibers, 728 μm . Mean wall thickness of libriform fibers, 4.6 μm . No septa observed in libriform fibers. No axial parenchyma observed. Multiseriate rays about as frequent as uniseriate rays. Uniseriate rays and uniseriate wings on multiseriate rays composed of erect to square cells. Multiseriate portions of multiseriate rays composed mostly of erect cells with a few procumbent cells. Mean width of multiseriate rays, 2.3 cells. Mean height of multiseriate rays, 1561 μm . Mean height of uniseriate rays, 548 μm .

XEROPLANA ZEYHERI (*Rourke 1557*).—Growth rings indistinct. A portion of the vessels solitary; others grouped in clusters or radial multiples. Mean number of vessels per mm^2 , 653. Mean vessel diameter, 22.2 μm . Mean vessel element length, 370 μm . Mean vessel wall thickness, 2.6 μm . Perforation plates either simple, or traversed by a single bar, or with ragged outlines indicative of bar vestiges, or with an irregular fusion of a few bar portions: each of these four types is about equally frequent. Lateral wall pitting of vessels composed of circular alternate pits about 2.5 μm in diameter. Vessel elements commonly fibriform. A few vasicentric tracheids present. All other imperforate tracheary elements are libriform fibers by virtue of apparently simple pits. Mean diameter of libriform fibers at widest point, 18 μm . Mean length of libriform fibers, 370 μm . Mean wall thickness of libriform fibers, 4.6 μm . No septa observed in libriform fibers. No axial parenchyma observed. Multiseriate rays about as common as uniseriate rays. Uniseriate rays and uniseriate wings of multiseriate rays composed of erect cells. Multiseriate portions of multiseriate rays composed mostly of erect cells and a few square and procumbent cells. Mean width of multiseriate rays, 2.4 cells. Mean height of multiseriate rays, 490 μm . Mean height of uniseriate rays, 424 μm .

Retziaceae

RETZIA CAPENSIS (*Carlquist 4514*) (*Stem. Fig. 12–14, 19–22*).—Growth rings absent (Fig. 12). Vessels in radial multiples; mean number of vessels per group, 1.93. Mean number of vessels per mm^2 , 215. Mean diameter of vessels at widest point,

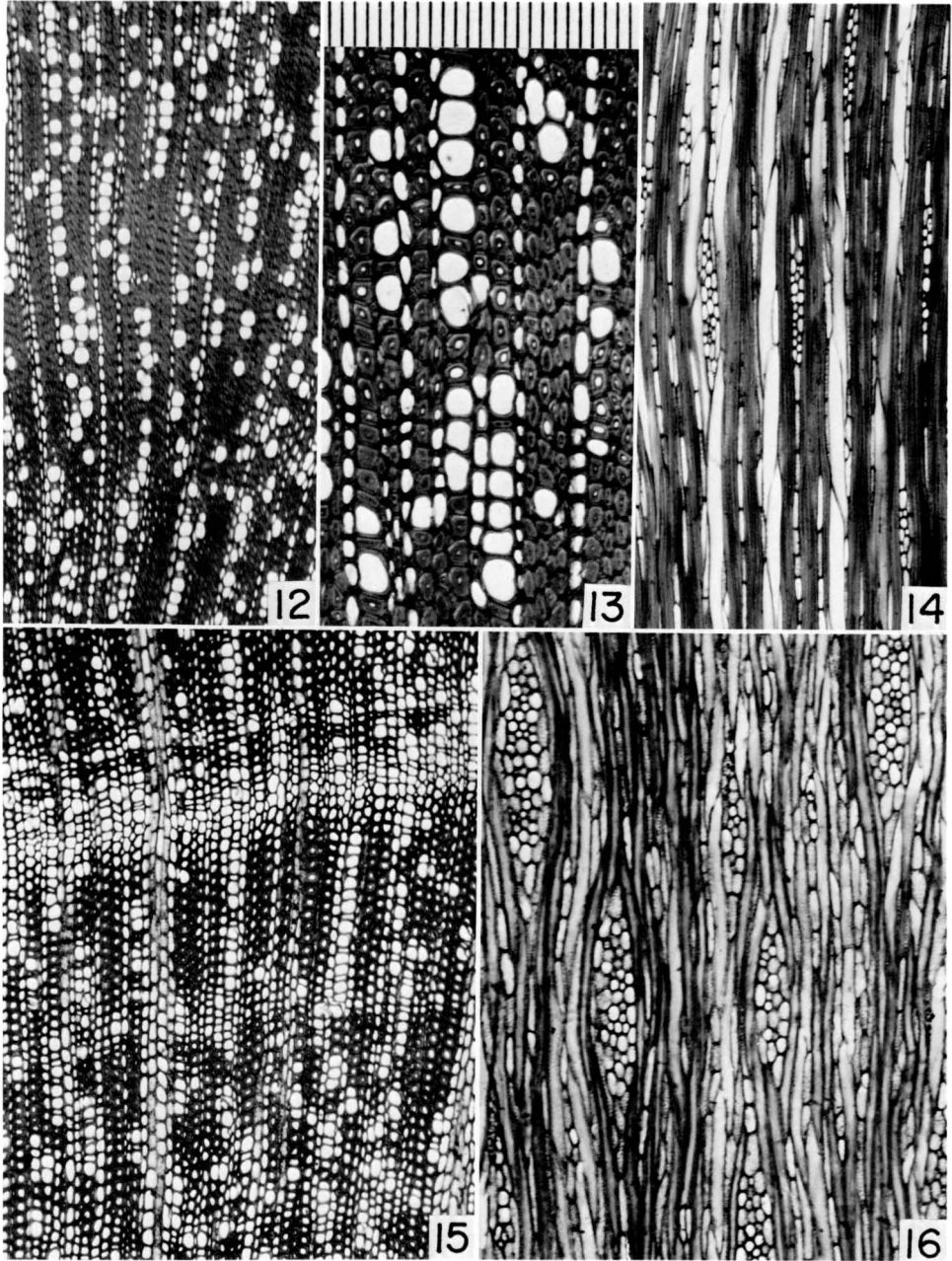


Fig. 12-16. Wood sections of *Retzia capensis*.—12-14. Sections from stem of *Carlquist 4514*.—12. Transection, showing lack of growth rings.—13. Transection, illustrating pore radial multiples and thick walled imperforate tracheary elements.—14. Tangential section; multiseriate rays are narrow.—15-16. Sections from root of *Carlquist 4693*.—15. Transection, showing band of parenchyma, near top, derived from fiber dimorphism.—16. Tangential section, showing rays much wider than those of stem. (Fig. 12, 14, 15, 16, magnification scale above Fig. 1; Fig. 13, scale above Fig. 13 [divisions = 10 μ m].)

31.3 μm . Mean vessel element length, 556 μm . Vessels mostly with prominently caudate tips, many vessels fibriform or nearly so. Mean vessel wall thickness, 2.4 μm . Perforation plates mostly simple (Fig. 19, 21). Only a few scalariform perforation plates present, bars in these few, unbordered, tenuous, and sometimes faint or incomplete (Fig. 20, 22). Perforation plates often vertically elongate (Fig. 21, 22). Occasional double perforation plates (a pair of perforations between a pair of vessel elements, not indicating a vessel bifurcation) present (Fig. 19). A few simple perforation plates are surrounded by malformed pits (Fig. 21, right). Lateral wall pitting of vessels typically alternate in vessel-vessel contacts, about 2.3 μm in diameter. Vessel-ray pitting alternate to scalariform, the former consisting of elliptical pits about $2.5 \times 3 \mu\text{m}$. Vasicentric tracheids absent. All imperforate tracheary elements can be termed fiber-tracheids or libriform fibers because only the most vestigial borders can be observed. Mean diameter of fiber-tracheids, 27.5 μm . Mean length of fiber-tracheids, 887 μm . Mean wall thickness of fiber-tracheids, 6.9 μm (Fig. 13), walls somewhat gelatinous as indicated by shrinkage patterns. Septa not seen in stem fiber-tracheids. Axial parenchyma vasicentric, scarce (a single cell adjacent to a few vessels), in strands of two cells. Uniseriate and multiseriate rays present, about equally abundant (Fig. 14). Uniseriate rays and uniseriate wings of multiseriate rays composed wholly of erect cells (Fig. 14). Central portions of multiseriate rays composed of erect, square, and procumbent cells. Mean width of multiseriate rays at widest point, 2.08 cells. Mean height of multiseriate rays, 1000 μm . Mean height of uniseriate rays, 421 μm . Wood nonstoried. No crystals observed.

RETZIA CAPENSIS (Carlquist 4693) (Root. Fig. 15, 16, 23, 24).—Growth rings not evident (parenchyma bands not clearly annual in nature). Vessels grouped in radial multiples to a moderate extent (most vessels solitary); mean number of vessels per group, 1.19. Mean number of vessels per mm^2 , 159. Mean vessel diameter at widest point, 31.9 μm . Mean vessel element length, 378 μm . Vessel elements often caudate, some fibriform in nature. Mean vessel wall thickness, 2.3 μm . Perforation plates mostly simple; a few scalariform with thin and often incomplete bars (Fig. 23). Some simple plates vertically elongate, a few with ragged margins indicating minimal vestiges of bars. Vessel-vessel lateral wall pitting alternate; pits oval, about $2.3 \times 5 \mu\text{m}$. Vessel-ray pitting of oval pits, alternate to scalariform (Fig. 24). Vasicentric tracheids absent. All imperforate elements may be termed fiber-tracheids, because very small vestigial borders could be observed (Fig. 24, left). Mean fiber-tracheid diameter at widest point, 27.5 μm . Mean length of fiber-tracheids, 656 μm . Mean wall thickness fiber-tracheids, 4.6 μm . Walls of fiber-tracheids somewhat gelatinous, as revealed by presence of occasional shrinkage patterns. Septa occasional in fiber-tracheids (Fig. 24, upper right). Axial parenchyma scarce, consisting of only a single cell adjacent to a few vessels; parenchyma in strands of two cells. Additionally, bands of axial parenchyma are present as a result of fiber dimorphism (Fig. 15, above), a few of these parenchyma cells in strands of two cells but most undivided. Both multiseriate and uniseriate rays present, the former more abundant (Fig. 16). Uniseriate rays and uniseriate wings of multiseriate rays composed of upright cells. Multiseriate portions of multiseriate rays composed of square and procumbent cells with some sheathing erect cells. Mean width of multiseriate rays at widest point, 3.92 cells (Fig. 16). Mean height

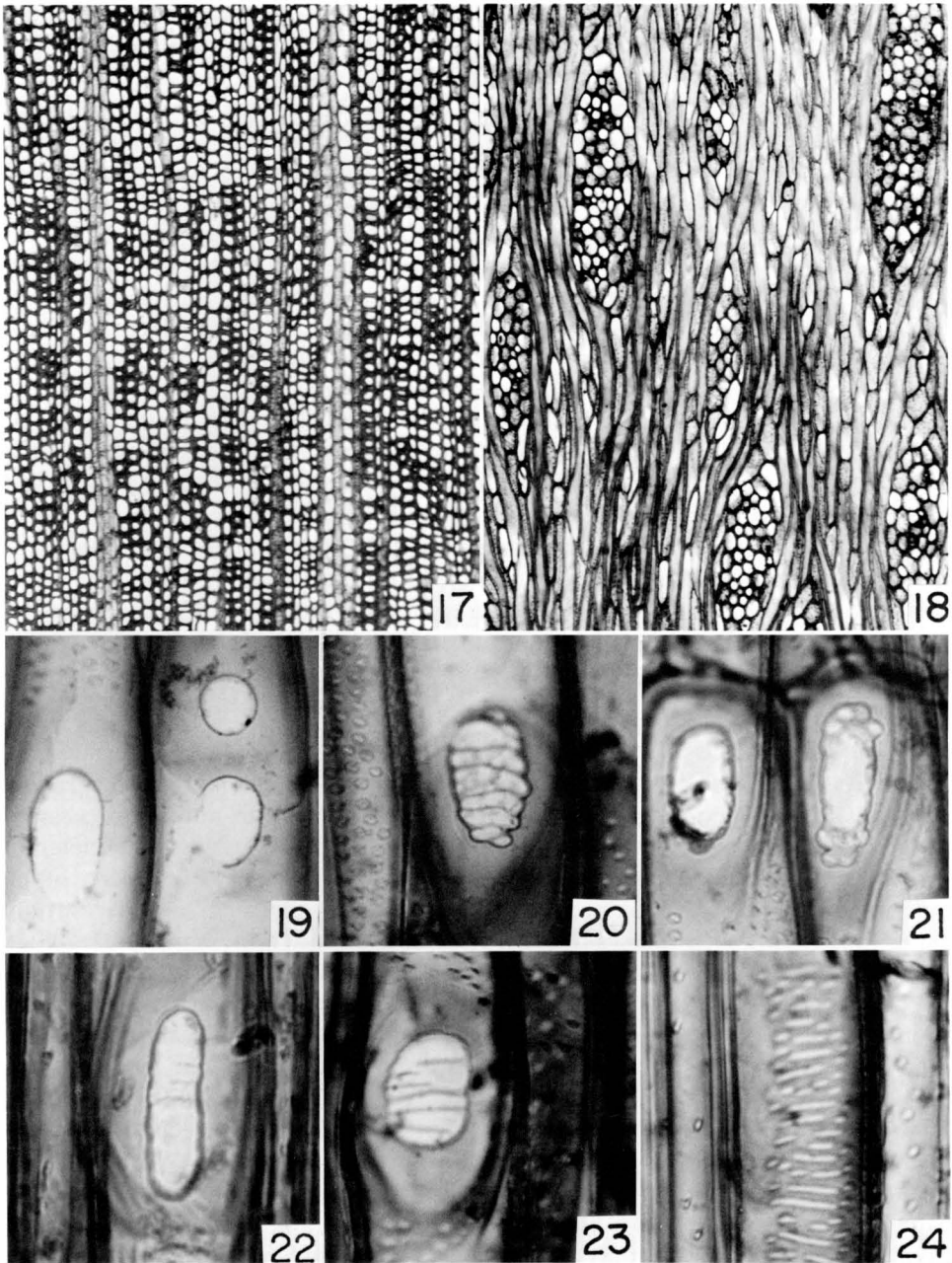


Fig. 17-24. Wood sections of *Retzia capensis*.—17-18. Sections of lignotuber from *Carlquist 4693*.—17. Transverse section, showing vessels the same diameter as imperforate tracheary elements.—18. Tangential section, showing notably wide multiseriate rays.—19-22. Perforation plates from radial section of stem, *Carlquist 4514*.—19. Single and double perforation plates.—20. Scalariform perforation plate with several bars.—21. Two simple perforation plates, the one at right surrounded by pits that merge into the perforation plate margin.—22. Scalariform perforation plate with a few tenuous bars.—23. Perforation plate from radial section of root of *Carlquist 4693*.—24. Vessel-ray lateral wall pitting, much of it scalariform, from radial section of root of *Carlquist 4693*. (Fig. 17-18, magnification scale above Fig. 1; Fig. 19-24, scale above Fig. 2.)

of multiseriate rays, 735 μm . Mean height of uniseriate rays, 222 μm . Wood nonstoried. Crystals absent.

RETZIA CAPENSIS (Carlquist 4692), (*Lignotuber*. Fig. 17–18).—Growth rings absent. Vessels mostly solitary; mean numbers of vessels per group, 1.26. Mean number of vessels per mm^2 , 64. Mean diameter of vessels at widest point, 34.0 μm . Mean vessel element length, 359 μm . A few vessel elements markedly caudate. Mean vessel wall thickness, 2.2 μm . Perforation plates mostly simple, but some double circular plates and some scalariform variants present. Scalariform plate variants have few and thin, often incomplete and always unbordered bars. Vertically elongate simple plates are common. Lateral wall pitting of vessels alternate to scalariform, either in vessel-vessel or vessel-ray contacts; alternate pits oval, about $2.5 \times 5 \mu\text{m}$. Vasicentric tracheids absent. All imperforate tracheary elements are fiber-tracheids or libriform fibers, the borders vestigial or absent. Mean diameter of fiber-tracheids at widest point, 33.2 μm , the fiber-tracheids thus about as wide as vessels and therefore difficult to distinguish from them (Fig. 17), especially because thin-walled fibers are present by virtue of fiber dimorphism. Mean fiber-tracheid length, 589 μm . Mean fiber-tracheid wall thickness ranging from 5.0 μm to 1.5 μm , the latter in the case of parenchymalike fiber-tracheids. Walls of fiber-tracheids (libriform fibers) gelatinous by virtue of shrinkage patterns. Septate fiber-tracheids (or libriform fibers) common. Axial parenchyma scarce, present as single cells adjacent to a few vessel elements, in strands of two cells. In addition, bands of parenchyma resulting from fiber dimorphism (Fig. 18, upper right) also present, some of these cells subdivided into strands of two cells. Both multiseriate and uniseriate rays are present, the former much more common (Fig. 18). Uniseriate rays and uniseriate wings of multiseriate rays composed of upright cells. Multiseriate portions of multiseriate rays composed of square and procumbent cells, with a few upright sheathing cells also present. Mean width of multiseriate rays at widest point, 5.05 cells (Fig. 18). Mean height of multiseriate rays, 763 μm . Mean height of uniseriate rays, 183 μm . Wood nonstoried. Crystals absent. Some portions of the lignotuber have markedly wavy grain and greater parenchymatous intrusions (presumably highly distorted rays) than the areas selected for illustration; those areas were selected precisely because they illustrate representative lignotuber wood but without the much contorted grain common in some portions of lignotubers.

DISCUSSION AND CONCLUSIONS

Habit

Within Stilbaceae, the only marked divergence in habit is represented by *Stilbe rupestris*; the remainder of the species can be regarded as stiff, sparsely branched subshrubs or small shrubs with normally woody bases. *Stilbe rupestris* is distinctive more in degree than in kind, because it is a rock-crevice shrub. South African rock-crevice shrubs (often better called subshrubs) tend to have small woody caudices from which relatively short-lived branches arise. Apparently the extreme heat and lack of water experienced by rock-crevice shrubs are related to dieback to a caudex which can, upon renewal of favorable conditions, innovate new shoots. This habit may be expected to result in production of two modalities of wood, as does happen in *S. rupestris* (compare Fig. 8 & 9 with Fig. 10 & 11). The upper

stem (Fig. 8, 9) illustrates a mechanically strong pattern: thicker-walled libriform fibers, smaller proportion of wood occupied by rays, and rays narrower. In contrast, the caudex (Fig. 10, 11) shows libriform fibers which are wider (and therefore fewer in number per unit area), thinner walled, and which therefore simulate vessels in diameter. The wide, multiseriate rays connote a storage capability (perhaps storage of both water and photosynthates). These tendencies can also be found in rock-crevice species of other families from Cape Province, notably *Liconia cuspidata* Swartz of the Bruniaceae (Carlquist 1978) and *Brachysiphon rupestris* Sonder of the Penaeaceae (Carlquist and DeBuhr 1977).

The wiry, slender but tough stems of Stilbaceae may owe their strength to presence of thick-walled fibers primarily, but lack of parenchymatization can also be cited. Axial parenchyma is nearly absent throughout the family, and ray tissue is minimal in young stems (uniseriate rays predominate). Mechanical strength is presumably enhanced by addition of libriform fibers, and formation of multiseriate rays at the periphery of a stem may indicate that this enhancement is not of great significance in peripheral stem portions, although storage and conduction functions of ray parenchyma may be more vital as a stem increases in diameter. Conceivably, the fibriform vessels so characteristic of Stilbaceae may represent a vessel configuration which is, by virtue of its resemblance to fiber structure, maximally strong mechanically. The narrow vessel diameter characteristic of fibriform vessels would be disadvantageous in dicotyledons where large volumes of water are conducted per unit time, but that surely does not apply to a family of ericoid shrubs such as Stilbaceae.

Retzia has wandlike unbranched stems emerging from the lignotuber, usually only one or less frequently several per plant. The strength of these slender stems is doubtless related to the thick-walled imperforate tracheary elements. In turn, the fibriform vessel elements and lack of axial parenchyma may contribute to the toughness of stem wood, as mentioned above for Stilbaceae. Both lignotuber and root have imperforate tracheary elements with thinner walls, which may relate to lower strength requirements in these organs. The shorter lengths of imperforate tracheary elements and vessel elements in roots and lignotubers may also relate to lessened strength requirements. Greater width of multiseriate rays in lignotubers and roots as compared to those in stems doubtless also relates to storage of water or photosynthates or both in those organs as compared to the stem, where minimal width of multiseriate rays would be expected because rays would tend to diminish the strength of the stem. Also related to storage functions of the root and lignotuber may be the innovation of parenchyma by means of fiber dimorphism, a process described earlier (Carlquist 1961). One may also note that septate fibers are absent in the stem, relatively uncommon in the root, but rather common in the lignotuber of *Retzia*; these degrees of abundance relate to probable storage function. Differentiation among stem, lignotuber, and root in wood anatomy has been found in other Cape Province genera, notably those of Bruniaceae (Carlquist 1978).

Ecology

Growth rings are not strongly marked in woods of most of the Stilbaceae. This may seem counterintuitive when one thinks of the highly seasonal climate of a Mediterranean-type region such as the Cape Province. However, one must note that the wood of Stilbaceae as a whole qualifies as xeromorphic, so that modifi-

cations for increased safety in latewood are of minimal value. Modifications for enhanced conduction in earlywood are also of minimal value, because during the maximal times of transpiration very likely only a little more water is lost than during times of minimal transpiration, if one may judge from the constant but small leaf area characteristic of these evergreen ericoid-leaved plants.

One can quantify xeromorphy of woods of Stilbaceae by using the Mesomorphy ratio (vessel diameter times vessel element length divided by number of vessels per mm²): see Carlquist and DeBuhr (1977). If one averages the Mesomorphy ratio for species of Stilbaceae collectively, one obtains the figure 43, which is comparable to the Mesomorphy figure for dryland (but not most) Bruniaceae (Carlquist 1978), dryland Pittosporaceae (Carlquist 1981*b*), and chaparral plants of southern California (Carlquist and Hoekman 1985).

Do characteristics of particular species correlate with their respective ecology? Using the Mesomorphy ratio for the respective species of Stilbaceae, one finds that they do. One can divide the Stilbaceae of this study into three categories, based upon data from Pearson (1912) and from original observations. The figures for Mesomorphy in these comparisons are placed in parentheses following species names.

Lowland species include *Campylostachys cernua* (13), which ranges from the Cape Town area to nearby dry mountain slopes; *Stilbe ericoides* (20), from the Cape flats to lower montane sites; and *S. rupestris* (stem 33, caudex 13) which ranges from lowland valleys (as at Vogelgat) to Sir Lowry's Pass, a dry locality.

Dry montane species could be said to include *Euthystachys abbreviata* (27) in the Drakenstein Mts. (Worcester Div.); *Stilbe phylicoides* (21), which ranges from Swellendam to Garcias Pass; and *S. vestita* (41), native to Table Mountain and Constantiaberg. Wet montane species include *S. albiflora* (46), *S. mucronata* (54), and *Eurylobium serrulatum* (143). All three of these species can be found in the moist complex of mountains that include the Palmiet River, Baviaanskloof, and the mountains north of Genadendal.

Interestingly, the two species which have scalariform perforation plates characteristically, *Eurylobium serrulatum* (Fig. 3, 4) and *S. albiflora*, have higher Mesomorphy figures. The third wet-montane species, *S. mucronata*, has at least some scalariform perforation plates (Fig. 7). A correlation between scalariform perforation plates and mesic ecology was stressed earlier (Carlquist 1975:182-183). In that reference, note is made of sites, as in montane South Africa, in which seeps or shady slope exposure maximizes water availability in areas that otherwise might be thought to be rather dry. These factors certainly apply to the Stilbaceae cited here as from wet areas. Because the figure for Mesomorphy includes vessel element length, the relatively great length of vessels in Stilbaceae makes this ratio greater in Stilbaceae than one might perhaps expect by virtue of the dryness of habitats and xeromorphic appearance of the plants. The fibriform nature of vessel elements in Stilbaceae should be mentioned in this connection, because narrow fibriform vessels in dicotyledonous woods tend to be longer than are vessel elements with oblique to transverse end walls bearing terminal perforation plates (perforation plates are often lateral in fibriform vessel elements).

Vasicentric tracheids were reported for *Stilbe ericoides* (Carlquist 1985). They are quite scarce in that species, but are only moderately scarce in *Campylostachys cernua* and *S. rupestris* (caudex only). All three species are lowland or dry-montane

species, and thus can be cited as supporting the correlation claimed between Mediterranean-type ecology and presence of vasicentric tracheids (Carlquist 1985).

Wood of *Retzia* could be regarded as mesomorphic in its retention of scalariform perforation plates. However, in this regard one should note that simple perforation plates were much more common than scalariform plates in both of my collections of *Retzia capensis*. Evidently, scalariform plates were somewhat more common in the material studied by Mennega (in Leeuwenberg 1980), although even there simple plates were reported. The habitats of *Retzia*, although not especially mesic, are not as dry as those characteristic of many montane sandstone areas in Cape Province. Xeromorphic characteristics of *Retzia* wood include narrowness of vessels and the tendency of vessels (in the stem; much less so in root and lignotuber) to be grouped. Grouping of vessels as seen in transection is a reliable indication of xeromorphy (Carlquist and Hoekman 1985). The acicular leaves of *Retzia* have quite limited surface area, and this doubtless correlates with a xeromorphic wood, especially in the stems, in which conduction of water volume per unit time is probably small.

Systematics

Some features distinctive of Stilbaceae can also be found in a number of Verbenaceae (sensu stricto): for example, the presence of relatively minute pits on lateral walls of vessels. Other features of wood of Stilbaceae are technically present in Verbenaceae but not in the same form: for example, vasicentric parenchyma is present in Verbenaceae, but not in the extremely sparse quantity characteristic of Stilbaceae. Vessels in short radial multiples occur in Verbenaceae, but medium to long radial clusters occur in Stilbaceae. The scalariform perforation plates found in a few species of *Vitex* (Metcalf and Chalk 1950; Meylan and Butterfield 1978) are the only ones reported from Verbenaceae (sensu stricto). However, the scalariform plates in *Vitex* are scattered throughout woods in which simple plates predominate; the *Vitex* plates have numerous nonbordered bars. This situation is essentially unlike that seen in *Eurylobium serrulatum* and *Stilbe albiflora*, in which scalariform perforation plates are found exclusively, and in which the plates have bars that are few, wide, and bordered. In the remaining Stilbaceae, vestigially scalariform perforation plates are not uncommon. Therefore, the perforation plates of Stilbaceae appear to be a persistence of a primitive feature. The occasional scalariform plates of *Vitex* might be a carryover from primary xylem due to ontogenetic anomalies; in this connection, one notes that primary xylem of some Verbenaceae can have scalariform perforation plates in species in which only simple plates occur in secondary xylem. This combination is listed for *Callicarpa* and *Stachytarpheta* of the Verbenaceae by Bierhorst and Zamora (1965). The interpretation of scalariform perforation plates as relictual is reinforced by presence of fiber-tracheids rather than libriform fibers in *Eurylobium*. Fiber-tracheids have been reported in Verbenaceae (sensu stricto) only in *Petrea arborea* HBK. (Metcalf and Chalk 1950), although they occur in a family closely allied to Verbenaceae, Chloanthaceae (Carlquist 1981a).

There are other wood features that can be considered characteristic of Stilbaceae. Among the most conspicuous of these is the presence of fibriform vessel elements. This feature is common in Convolvulaceae and Hydrophyllaceae (Carlquist and

Eckhart 1984), but has not been reported thus far in Verbenaceae (sensu stricto), Chloanthaceae, or Avicenniaceae.

Thus, wood anatomy of Stilbaceae marks it as a distinctive group that may represent an offshoot of the stock leading to Verbenaceae (sensu stricto). The presence of endosperm in seeds of Stilbaceae, like the presence of scalariform perforation plates, underlines its less specialized position with relation to Verbenaceae (sensu stricto).

Distinctive anatomical characters at generic and specific levels may exist in Stilbaceae, but ontogenetic variation within woods is so great that the limited sampling of the present study cannot supply reliable taxonomic criteria. Features that do appear of specific value may relate primarily to ecology, and are cited above in that connection. Markedly thick-walled libriform fibers and ray cells of *Stilbe ericoides* might be of specific significance.

The wood of *Retzia capensis* is of considerable significance with regard to the possibility that Retziaceae may be closely related to Stilbaceae. This possibility was raised by Dahlgren et al. (1979), who did not have any appreciable data on wood available to them. Data on wood of *Retzia* (stems only) was contributed by Mennega (in Leeuwenberg 1980), but that account does not take into account the possibility that *Retzia* may have relationships other than to Loganiaceae, the affinity designated by Leeuwenberg (1964) on the basis of a much more limited roster of characters than those cited by Dahlgren et al. (1979) as indicating relationship between Stilbaceae and Retziaceae. The wood anatomy of *Retzia* proves astonishingly like that of Stilbaceae. The slender, often caudate and fibriform vessel elements, uncommon in dicotyledon families other than vining ones, are similar in the two families. If one cites perforation plates as similar between Stilbaceae and Retziaceae, one must stress not merely that scalariform perforation plates occur in both families, but that unusual peculiarities of these plates unite the two families. The scalariform perforation plates in both families have few bars; the bars are nonbordered and often delicate, frequently not traversing the width of the perforation plate. Perforation plates with "ragged" margins indicative of vestiges of bars along the edges of the plates may be encountered frequently in woods of both families. Double circular perforation plates (two perforations connecting a pair of vessel elements, not indicating a branching of a vessel) may be encountered in both families with a degree of frequency. In both Stilbaceae and Retziaceae, vertically elongate simple perforation plates are common, perhaps related to the fibriform nature of vessel elements; such simple perforation plates are uncommon in dicotyledons at large. Lateral wall pitting in vessels of both families consists of rather small alternate pits. Imperforate tracheary elements of both families are thick walled and have much reduced (perhaps absent) borders. Axial parenchyma (disregarding fiber dimorphism in roots and lignotubers of *Retzia*) is identical in being very scarce, limited to single cells adjacent to a few vessels; these parenchyma cells are, when viewed in longitudinal sections, in strands of two cells. Rays are both multiseriate and uniseriate, but multiseriate rays in stems of both Retziaceae and Stilbaceae have relatively narrow multiseriate portions; uniseriate rays and uniseriate wings on multiseriate rays are composed of upright cells exclusively in both families. So striking is the constellation of features by which Stilbaceae and Retziaceae are alike in wood features that a wood anatomist, if shown slides of both families, would find no evidence for

recognition of two families instead of one. The additional pair of ovules in the gynoeceum of *Retzia* as compared to the biovulate condition in Stilbaceae is the only difference that seems worthy of citation as separating the two families, and one such difference could only be considered of subfamilial importance. Although Dahlgren et al. (1979) do not review evidence from pollen, one can see by comparing the monograph on pollen of Stilbaceae by Raj (1983) with Erdtman's (1952) description of pollen of *Retzia* that *Retzia* pollen is like that of those species of Stilbaceae that have no pronounced differentiation of a pore region in each furrow. *Retzia* thus appears to be an ornithophilous offshoot of a line that also produced the entomophilous Stilbaceae. If the stilboid genera are segregated from Verbenaceae, I see little choice but to include *Retzia* in that family also, although the two groups probably deserve subfamilial status.

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