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Wood Anatomy of Gesneriaceae

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WOOD ANATOMY OF GESNERIACEAE

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ABSTRACT

Qualitative and quantitative data are presented for woods of 37 species representing 11 genera; most species included represent a maximal degree of woodiness for the family, and herbaceous groups are mostly omitted. Growth rings are absent or nearly so. Vessel elements have simple perforation plates (except for *Kohleria elegans*) and alternate circular or oval pits of various sizes on vessel-vessel walls (often laterally elongate, often with gaping apertures, on vessel-parenchyma and vessel-septate fiber interfaces). Grooves interconnect pit apertures in vessels of four genera. Vessels are grouped, usually in radial chains, to a moderate extent. Tyloses are present. Imperforate tracheary elements are libriform fibers or (*Coronanthera*) fiber tracheids with vestigial borders on pits. Septa are present in imperforate tracheary elements of most species, but in most species of *Cyrtandra*, septate fibers occur only near vessels. Uniseriate rays are present in some species, but in most species rays are multiseriate only or are absent altogether. Vascular and vasicentric tracheids are absent. In *Cyrtandra*, wood with multiseriate rays can be demonstrated to be rayless earlier in ontogeny. Crystals are present in rays and in septate fibers of a few species. Storying is present in a few species. All features of wood reflect the mesic habitats characteristic of Gesneriaceae, but moderate degrees of xeromorphy are illustrated by species in which narrow vessels, grouped vessels, and grooves in vessel walls occur. The wood anatomy of *Drymonia* reflects its vining habit. Raylessness may indicate secondary woodiness in *Besleria* and *Cyrtandra*. Wood anatomy of Gesneriaceae is consonant with a hypothesis that the family is closely related to Acanthaceae, Scrophulariaceae, and other families of Scrophulariales.

Key words: Gesneriaceae, raylessness, Scrophulariales, wood anatomy.

INTRODUCTION

Gesneriaceae is a large pantropical family generally referred to the order Scroph-ulariales. Heywood (1978) estimates that the family contains 125 genera and 2000 species. Despite its large size, Gesneriaceae contains only a small proportion of woody species. Most of these belong to the genus *Cyrtandra*. The species studied here represent woodier taxa of the family (e.g., *Cyrtandra*) except for *Chirita*, which was studied to see what wood characteristics may be found in relatively herbaceous gesneriads.

Wood anatomy can offer information concerning relationships, and thus is studied for Gesneriaceae here despite the fact that the affinities of the family are not controversial. The order Scrophulariales (Bignoniales of Thorne 1976) is generally construed as containing Acanthaceae, Bignoniaceae, Lentibulariaceae, Martyniaceae, Myoporaceae, Orobanchaceae, Pedaliaceae, Plantaginaceae,

Scrophulariaceae, and a few smaller families according to Cronquist (1981), Dahlgren (1980), Takhtajan (1980), and Thorne (1976). The families most often placed next to Gesneriaceae in the phylogenetic sequences of these authors are Acanthaceae, Myoporaceae, and Scrophulariaceae, although the sequences given differ considerably. The present study is part of a review of wood anatomy of tubiflorous families of dicotyledons in an attempt to define orders and assign families to logical positions within these orders.

Monographic studies on wood anatomy often offer opportunities for comparisons between wood anatomy and ecology. However, Gesneriaceae as a family have typically mesic preferences, and thus ecological comparisons can cover only a limited range. In addition, the family is typically tropical. *Rhabdothamnus*, which extends a little south of 40°S (Allan 1961), represents the furthest entry by the family into the temperate zone, although the coastal habitats *Rhabdothamnus* occupies have minimal extremes for that latitude. Given the relatively mesic preferences of taxa in the family, one may see if wood anatomy is correspondingly mesomorphic.

Relatively little work has been done on wood anatomy of Gesneriaceae. The summary of Metcalfe and Chalk (1950) cites references in which data are quite limited in detail. Thus most of the observations by Metcalfe and Chalk are original rather than derived from other authors; even Solereder (1908) offers little information on the family.

Gesneriaceae are unusual in having a large number of species in which wood is rayless, at least earlier in ontogeny. The significance of this phenomenon is interesting in its implication for evolution of habit. Raylessness appears to indicate secondary woodiness in Gesneriaceae as it does in *Plantago* (Carlquist 1970). Because raylessness is pervasive in Gesneriaceae, the family is an excellent one for study of the phenomenon. The fact that *Drymonia* is exceptional for Gesneriaceae in its vining habit makes it an interesting subject for study of how wood anatomy of vines differs from that of shrubby or arboreal dicotyledons.

MATERIALS AND METHODS

With few exceptions, wood samples were available in dried form. Stems of *Chirita lavandulacea* were removed from plants cultivated at the Rancho Santa Ana Botanic Garden by Mr. Walter Wisura and preserved in formalin-acetic-alcohol. The stems of *Chirita* have only a thin cylinder of secondary xylem. Information is doubtless lost by use of dried material; for example, nuclei in septate fibers and starch (observed for *Kohleria elegans*) could have been demonstrated had liquid-preserved material been available. The majority of the samples, as indicated in Table 1, were obtained from the Samuel J. Record Collection of the U.S. Forest Products Laboratory. The courtesy of Dr. Regis B. Miller in making those materials available to me is gratefully acknowledged.

Geographical sources for the Gesneriaceae studied are as follows: *Besleria* sp., Panama; *B. pauciflora* var. *uniflora*, Panama; *Chirita lavandulacea*, native to Indonesia; *Columnea purpurata*, Panama; *C. rubra*, Panama; *Coronanthera pulchra*, New Caledonia; *Cyrtandra anthropophagarum*, Fiji; *C. ciliata*, Fiji; *C. cordifolia*, Oahu, Hawaii; *C. filibracteata*, Bougainville, Solomon Is.; *C. gayana*, Kauai, Hawaii; *C. grayana* var. *lanaiensis*, Lanai, Hawaii; *C. harveyi*, Viti Levu, Fiji; *C. hornei*, Viti Levu, Fiji; *C. kandavuensis*, Fiji; *C. lysiosepala*, W. Maui,

Hawaii; *C. marthae,* Raivavae, Austral Is.; *C. platyphylla,* Hilo, Hawaii; *C. prattii,* Viti Levu, Fiji; *C. propinqua,* Oahu, Hawaii; *C. rarotongensis,* Rarotonga, Cook Is.; *C. spathacea,* Fiji; *C. urvillei,* Ponape, Micronesia; *C. victoriae,* Viti Levu, Fiji; *C. yaeyamae,* Iriomiote, Ryukyu Is.; *Drymonia spectabilis,* Panama; *Gesneria calycosa,* Jamaica; *G. duchartreoides,* Cuba; *G. ventricosa,* Dominica; *Kohleria elegans,* native to Guatemala (cultivated at the University of California Botanic Garden, Berkeley); *Rechsteineria reitzii,* Santa Catarina, Brazil; *Rhabdothamnus solandri,* N. Island, New Zealand; *Rhytidophyllum auriculatum,* Haiti; *R. crenulatum,* Cuba; *R. tomentosum,* Cuba.

Dried wood samples were boiled prior to sectioning. For both boiled and liquid-preserved specimens, sectioning on a sliding microtome without further treatment proved to be the most effective procedure. No woods of Gesneriaceae are so hard that any softening prior to sliding-microtome sectioning is necessary. On the contrary, some taxa have woods so soft that sectioning on a sliding microtome produces poor results, usually excessive tearing of vessel walls. These species (notably *Chirita lavandulacea, Drymonia spectabilis,* and some species of *Cyrtandra*) yielded good sections when samples were softened with ethylene diamine, embedded in paraffin, and sectioned on a rotary microtome (Carlquist 1982).

Sections were stained with safranin; most sections were also counterstained with fast green. This counterstaining method proved useful for demonstrating such details as pit membranes and septa in libriform fibers. Macerations were prepared with Jeffrey's Fluid and stained with safranin.

Means for data (Table 1) are based upon 25 measurements per feature except for vessel wall thickness, libriform fiber diameter, and libriform fiber wall thickness. In these, typical conditions were selected for measurement. Fewer than 25 measurements were used for libriform fiber diameter and for some of the other features if the structure was scarce (e.g., uniseriate rays are never common in Gesneriaceae). Number of vessels per mm² is based, as in earlier papers, on counting all vessels in a field (grouped vessels are not counted as a single vessel). Vessel diameter measurements are based on lumen diameter rather than external diameter. Although the latter has been more commonly used, the former is now considered preferable because the lumen diameter has more physiological significance. Number of vessels per group is determined by averaging counts when a solitary vessel = 1.0, a pair of vessels in contact = 2.0, etc. The figure termed Conductivity has been included in Table 1, since some current authors consider it potentially a good way of expressing conductive capacity of the xylem; it does not, however, seem as predictive of ecological features and their numerical range as the Mesomorphy figure utilized in Table 1.

Data in Table 1 represent the work of the junior author, who also prepared the majority of the sections and macerations. The remainder of the paper is the work of the senior author.

ANATOMICAL FEATURES

Growth Rings

The Gesneriaceae studied are entirely diffuse porous with the exception of *Rhabdothamnus solandri,* in which there is a slight change in accordance with season in the diameter of vessels and of other cells (Fig. 21). Thicker-walled libriform fibers occur in latewood of that species.

Table 1. Wood features of Gesneriaceae.

Species	Collection	VD	V/MM	VL	V/G	VWT	TD	TL	TWT	MRH	MRW	URH	URW	SEP	MESO	COND
Besleria sp.	*Oxford 3696*	41.3	34.2	372	2.0	2.1	33.6	411	2.4	—	—	—	—	+	449	8.5
B. pauciflora Rusby var. *uniflora* Rusby	*SJRw 54884*	42.6	62.7	547	1.8	2.4	25.0	640	2.9	—	—	—	—	+	372	5.3
Chirita lavandulacea Stapf.	RSABG	56.9	54.0	309	2.1	1.8	29.7	334	2.3	—	—	—	—	0	326	19.4
Columnea purpurata Hanst.	*SJRw 54640*	57.3	35.7	386	1.6	2.3	27.9	559	2.4	462	57.2	304	23.5	+	620	30.2
C. rubra Morton	*Skog 4146* (Pom)	37.8	54.0	362	1.5	2.0	25.6	548	2.3	389	52.8	256	21.2	−	253	3.8
Coronanthera pulchra Clarke	*Baumann-Bodenh. 15714* (RSAw)	32.1	112.0	387	2.4	2.5	31.7	529	3.5	496	62.3	83	14.2	+	111	0.9
Crytandra sp. (Tahiti)	*SJRw 25480*	62.5	22.2	396	1.3	2.3	30.7	519	2.5	—	—	—	—	−	1110	68.7
C. sp. (Waikane, Hawaii)	*Carlquist 1837* (RSAw)	53.5	17.3	343	1.7	2.9	30.8	448	3.4	400	62.7	—	—	−	1060	47.4
C. sp. (Kona, Hawaii)	*Carlquist 2076* (RSAw)	82.6	8.0	434	1.7	3.4	42.3	642	2.5	760	115.0	—	—	−	4460	580.0
C. anthropophagarum Seem.	*SJRw 25630*	71.1	20.7	422	1.5	2.4	32.0	577	2.5	2211	640.0	—	—	−	1450	123.0
C. ciliata Seem.	*SJRw 25993*	43.0	35.2	401	1.3	2.8	27.5	500	2.4	—	—	—	—	−	490	9.7
C. cordifolia Gaud.	*SJRw 26334*	71.6	15.7	361	1.4	2.4	40.0	478	2.6	—	—	—	—	−	1650	167.0
C. filibracteata B. C. Burtt	*SJRw 22845*	66.3	28.4	451	1.6	2.9	28.2	563	2.8	—	—	—	—	−	1050	68.0
C. gayana Heller	*Carlquist 519* (RSAw)	67.3	24.6	394	1.2	2.9	27.6	512	3.2	808	147.0	—	—	−	1080	83.4
C. gayana	*Carlquist 1997* (RSAw)	61.4	16.4	387	1.6	2.8	32.2	460	3.6	2250	495.0	—	—	−	1450	86.7
C. grayana Hbd. var. *lanaiensis* Hbd.	*Carlquist 2016* (RSAw)	42.0	15.7	310	1.5	2.2	31.9	400	3.8	830	173.0	—	—	−	829	19.8
C. harveyi Seem.	*SJRw 25395*	62.5	31.8	389	2.3	2.5	35.8	520	2.3	766	153.0	—	—	−	765	48.0
C. hornei Clarke	*SJRw 25885*	60.5	51.1	381	1.4	2.9	24.6	522	2.2	—	—	—	—	−	451	26.2
C. kandavuensis A. C. Smith	*SJRw 27728*	71.5	21.7	302	1.9	3.0	39.7	412	2.6	1300	194.0	—	—	−	995	120.0
C. lysiosepala (Gray) Hbd.	*Carlquist 1853* (RSAw)	67.9	21.3	426	1.3	2.9	32.2	559	3.2	1730	240.0	—	—	0	1360	99.8
C. lysiosepala	*Carlquist 2147* (RSAw)	60.4	25.5	423	1.5	2.5	27.7	576	2.5	730	100.0	—	—	−	1000	52.2
C. marthae St. John	*SJRw 37389*	74.1	31.7	332	1.6	2.6	36.2	406	2.3	1500	152.0	—	—	−	776	95.1
C. platyphylla Gray	*Carlquist 2036* (RSAw)	75.2	20.7	353	1.5	3.1	33.8	397	3.4	2630	285.0	—	—	−	1280	154.0
C. prattii Gillespie	*SJRw 25865*	59.9	18.9	329	2.5	2.3	46.1	413	2.1	—	—	—	—	−	1040	68.1

Table 1. Continued.

Species	Collection	VD	V/MM	VL	V/G	VWT	TD	TL	TWT	MRH	MRW	URH	URW	SEP	MESO	COND
C. propinqua Forbes	*Carlquist 1836* (RSAw)	59.4	15.9	364	1.7	2.4	30.2	504	3.0	834	162.0	—	—	—	1360	78.3
C. rarotongensis Cheesman	*SJRw 24786*	66.8	17.4	296	1.5	2.9	42.7	342	2.4	2020	352.0	—	—	—	1140	114.0
C. spathacea A. C. Smith	*SJRw 27745*	67.4	18.3	319	1.4	2.6	34.8	414	2.1	1350	134.0	—	—	—	1170	113.0
C. urvillei Clarke	*SJRw 26775*	67.5	21.2	356	2.0	2.6	30.6	520	2.5	2570	156.0	—	—	—	1130	97.9
C. urvillei	*Carlquist 15767* (RSAw)	78.8	31.3	351	1.5	2.6	27.0	470	2.4	—	—	—	—	—	884	123.0
C. victoriae Gillespie	*SJRw 25863*	68.4	24.6	360	1.6	4.0	30.7	508	3.6	—	—	—	—	—	1000	89.0
C. yaeyamae Ohwi	*Carlquist 15676* (RSAw)	62.6	39.5	344	2.0	3.0	17.6	462	2.7	1800	700.0	—	—	0	545	38.9
Drymonia spectabilis (HBK) Mart.	*SJRw 12090*	141.0	22.9	338	1.4	2.6	25.3	541	2.3	8000	92.0	—	—	+	2080	1730.0
D. spectabilis	*SJRw 54706*	72.7	54.9	373	1.6	2.8	21.9	431	2.7	1670	28.8	160	13.1	+	494	50.9
Gesneria calycosa (Hook) Kuntze	*MADw 20810*	49.1	43.9	534	2.0	2.5	27.0	727	3.5	472	27.1	245	16.6	+	597	13.2
G. duchartreoides (C. Wr.) Urb.	*SJRw 16824*	43.1	41.9	470	1.7	2.5	24.5	689	3.5	622	31.5	131	18.7	+	483	8.2
G. ventricosa Swartz	*MADw 24124*	34.9	69.4	440	1.6	2.4	18.6	670	3.2	572	32.3	193	18.2	+	221	2.1
Kohleria elegans Loes.	*Carlquist 15668* (RSAw)	40.8	54.9	279	2.3	2.2	30.9	355	3.0	630	49.0	301	19.0	—	207	5.1
Rechsteineria reitzii Hoehne	*Reitz & Klein 4068* (UC)	47.2	26.0	350	1.4	2.3	29.0	425	3.3	942	98.1	—	—	+	635	19.1
Rhabdothamnus solandri A. Cunn.	*PRFw 3826*	25.0	136.0	314	2.1	2.6	20.8	513	3.5	431	30.5	115	17.3	+	58	0.3
Rhytidophyllum auriculatum Urb.	*SJRw 4843*	42.0	76.2	398	2.2	3.4	21.4	537	3.5	705	48.4	165	18.4	+	219	4.1
R. crenulatum DC.	*SJRw 16233*	59.9	65.5	428	2.3	3.6	26.0	605	3.2	1520	46.5	—	—	+	391	19.7
R. tomentosum (L.) DC.	*SJRw 16296*	36.8	85.8	405	2.1	2.8	22.9	553	3.0	476	30.9	258	17.0	+	174	2.1
Family means		59.2	38.7	379	1.7	2.7	29.9	505	2.9	1350	160.0	201	17.9		887	107.0

Key to columns: VD = mean diameter of vessels (lumen diameter), μm; V/MM = mean number of vessels per mm^2 of transection; VL = mean vessel element length, μm; V/G = mean number of vessels per group; VWT = vessel wall thickness, μm; TD = diameter of imperforate tracheary elements at widest point, μm; TL = mean length of imperforate tracheary elements, μm; TWT = wall thickness of imperforate tracheary elements, μm; MRH = mean height of multiseriate rays, μm; MRW = mean width of multiseriate rays at widest point, μm; URH = mean height of uniseriate rays, μm; URW = mean width of uniseriate rays at widest point, μm; SEP = presence of septate imperforate tracheary elements (+ = abundant; − = present only around vessels; 0 = absent); MESO = Mesomorphy ratio (vessel diameter times vessel element length divided by vessels per mm^2); COND = Conductivity (vessel diameter^4 times 0.0001 divided by number of vessels per mm^2). Further explanation in Materials and Methods.

Vessel Elements

In Gesneriaceae as a whole, vessel elements are relatively wide and long (Table 1) as compared to those of certain nonarboreal dicotyledon groups, such as those in the woody flora of southern California (Carlquist and Hoekman 1985). The widest vessels in the family were observed in the vining genus *Drymonia* (Fig. 10). Relatively wide vessels also occur in various species of *Cyrtandra* (Fig. 6). The vessels of *Kohleria elegans* (Fig. 14) are slightly below the family mean; those of *Rhabdothamnus solandri* (Fig. 21) are the narrowest observed in Gesneriaceae. *Rhabdothamnus solandri* also has notably short vessel elements (Fig. 22), although the shortest in the study belong to *Kohleria elegans* (Fig. 15). Notably long vessel elements occur in the species of *Gesneria* (Table 1).

Vessels tend to be grouped into radial chains or multiples in Gesneriaceae as shown in Fig. 1, 6, 14, and 21. The number of vessels per group (Table 1) shows a moderate range within the family. Figures above 2.25 can be observed in *Coronanthera pulchra, Cyrtandra harveyi, C. pratii,* and *Rhytidophyllum crenulatum* (Table 1). Figures below 1.40 were found in *Cyrtandra* sp. (Tahiti), *C. gayana, Drymonia spectabilis* (Fig. 10), and *Rechsteineria reitzii.*

The number of vessels per mm^2 does show an appreciable range in the family as a whole (Table 1), although the range is not nearly as large as in such families as Asteraceae or Ericaceae. The greatest density of vessels is shown by *Rhabdothamnus solandri* (Fig. 21), followed by *Coronanthera pulchra.* The values in these species are about double the vessel density for the family as a whole. Notably low vessel density is shown by a number of *Cyrtandra* species. The genera other than *Cyrtandra* exceed *Cyrtandra* in vessel density except for *Drymonia,* in which high vessel density would not be expected because of the great vessel diameter in that genus.

Vessel wall thickness is moderate, with most species close to 2.5 μm.

Perforation plates are simple throughout the family. An exception to this is seen in *Kohleria elegans* (Fig. 16–20). Metaxylem perforation plates in this species (Fig. 19, right) are scalariform. Although simple perforation plates are predominant in secondary xylem in *K. elegans,* various types of perforation plates that may be regarded as modifications of a scalariform condition occur in at least 5% of the end plates of vessel elements. As shown in Figure 18–20, three or more perforations, separated by bordered bars, are characteristic. Some perforation plates in *K. elegans* are simple except for presence of a strand of wall material (Fig. 16, 17).

Lateral walls of vessels in Gesneriaceae show an interesting range. Intervascular pits are basically circular to slightly oval, as shown for *Drymonia spectabilis* (Fig. 12) or *Rechsteineria reitzii* (Fig. 4). Where pits are crowded, pit cavities take on a polygonal outline. Such polygonal pits were observed in vessels of *Cyrtandra filibracteata, C. harveyi, C. kandavuensis, C. platyphylla, C. propinqua, C. spathacea,* and *C. yaeyamae.* Most pits bear rather markedly elliptical apertures. Exceptions to this, in which pit apertures are circular to oval in outline, were observed in *Cyrtandra gayana, C. hornei, C. yaeyamae, Drymonia spectabilis* (Fig. 12), and *Rechsteineria reitzii* (Fig. 4).

Pit apertures are mostly much smaller than pit cavities. In a few Gesneriaceae, however, the pit apertures are "gaping," i.e., nearly as wide as the pit cavity. This condition is illustrated clearly in the case of intervascular pits for *Rechsteineria*
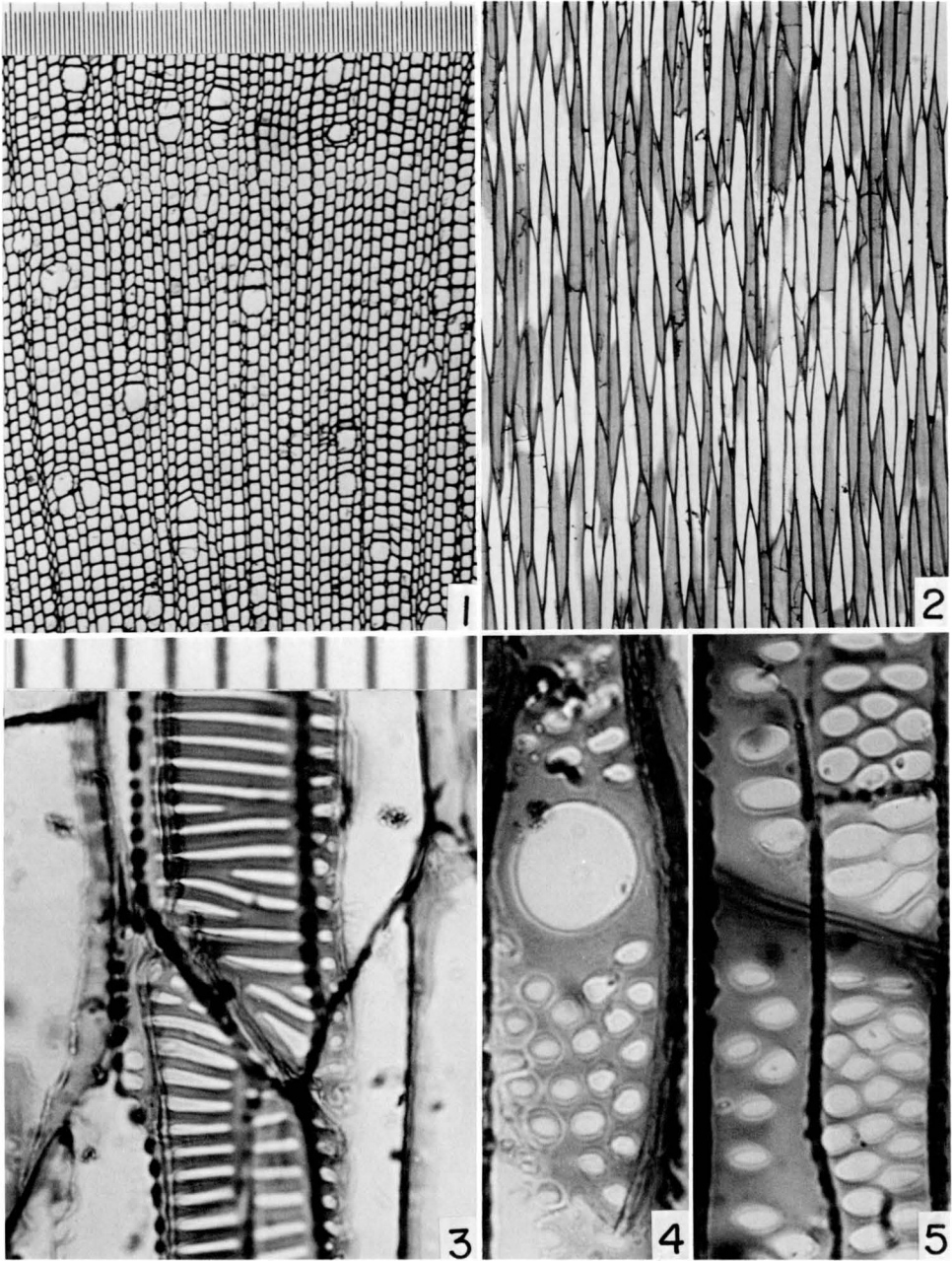
Fig. 1–5. Wood sections of Gesneriaceae.—1–2. *Besleria* sp. (*Oxford FPRI 3696*).—1. Transection. Pores are sparse.—2. Tangential section. The wood is rayless.—3. *Chirita lavandulacea* (*cult*. RSABG), portion of tangential section, showing vessel wall facing parenchyma. Scalariform and pseudoscalariform pitting evident.—4–5. *Rechsteineria reitzii* (*Reitz & Klein 4068*, UC), vessel walls from radial section, showing relatively wide pit apertures.—4. Intervascular pitting, perforation plate.—5. Vessel-parenchyma pitting. (Fig. 1, 2, magnification scale above Fig. 1 [finest divisions = 10 μm]; Fig. 3–5, scale above Fig. 2 [divisions = 10 μm].)

Fig. 6–9.   Wood sections of *Cyrtandra.*—6–7. *C. yaeyamae* (*Carlquist 15676,* RSA).—6. Transection; fibers thin walled, pores in short radial chains.—7. Tangential section; multiseriate rays scarce (one at left), uniseriate rays absent.—8. *C. lysiosepala* (*Carlquist 2147,* RSA). Tangential section, showing rayless condition.—9. *C. lysiosepala* (*Carlquist 1853,* RSA), radial section, showing two rhomboidal crystals. (Fig. 6–8, magnification scale above Fig. 1; Fig. 9, scale above Fig. 3).
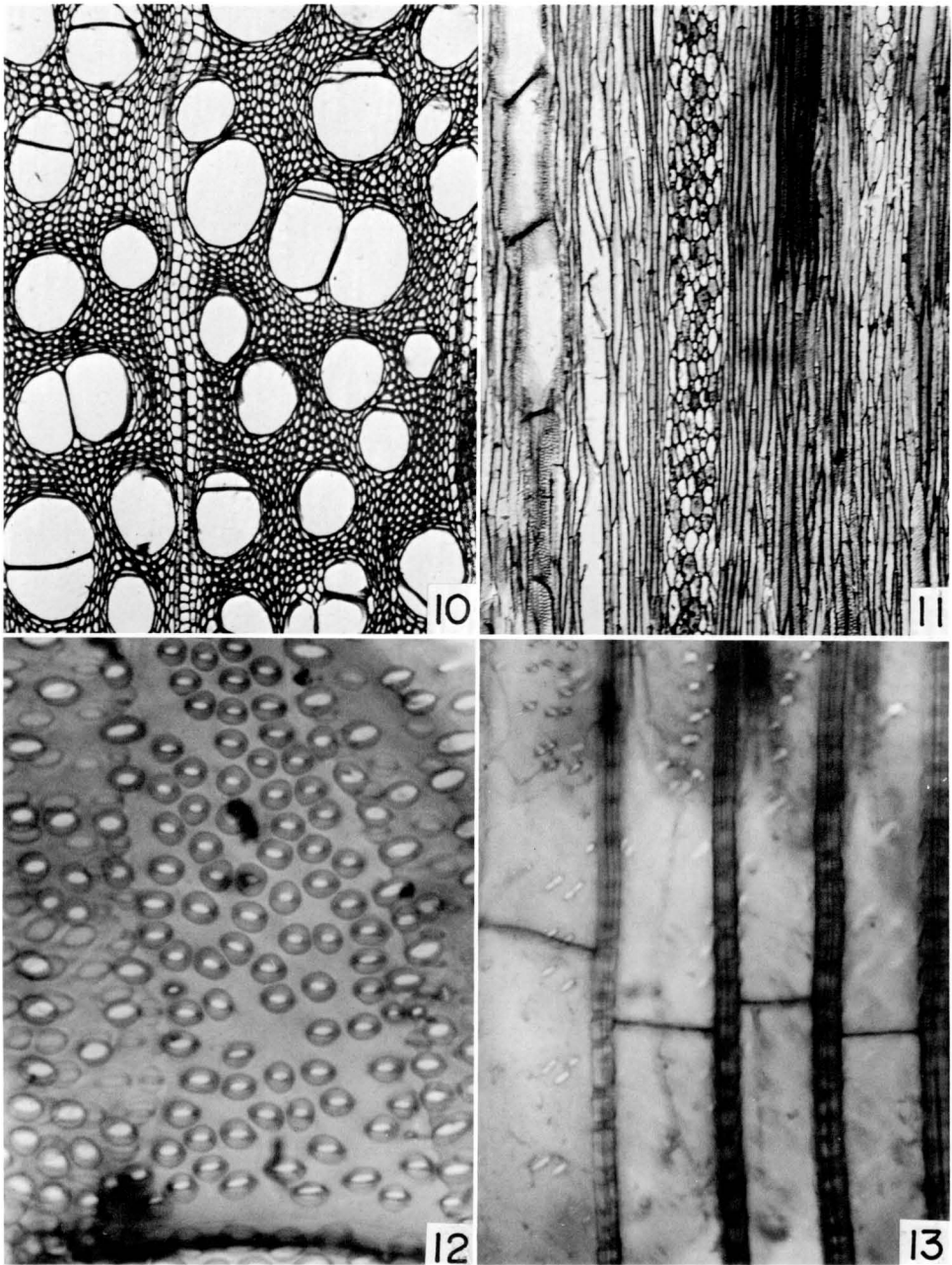
Fig. 10–13. Wood sections of *Drymonia spectabilis* (*SJRw 12090*).—10. Transection. Pores are notably wide.—11. Tangential section. To right of ray, near center, libriform fibers are storied.—12. Portion of vessel wall from tangential section.—13. Septate fibers from radial section. (Fig. 10–22, magnification scale above Fig. 1; Fig. 12–13, scale above Fig. 3.)
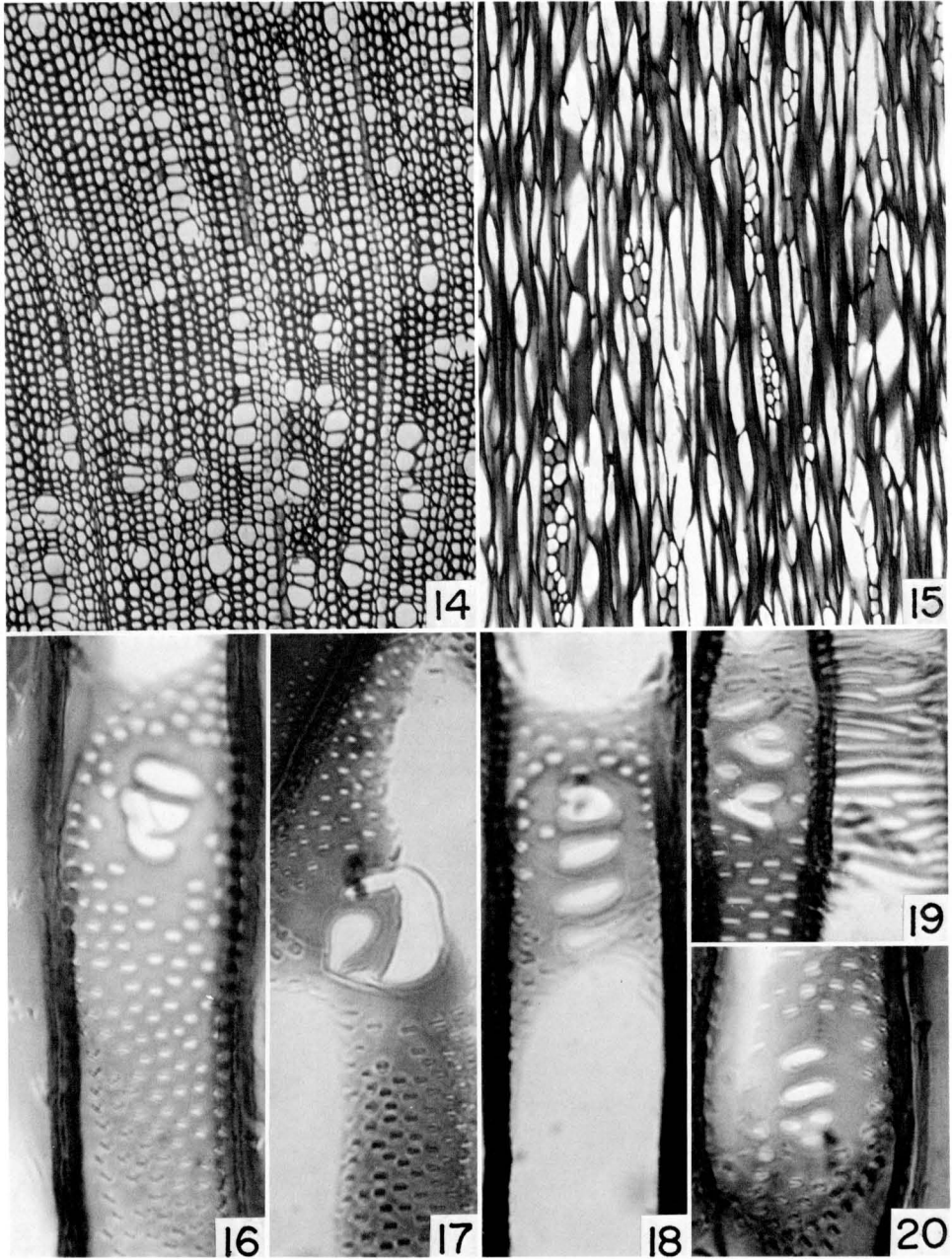
Fig. 14–20. Wood sections of *Kohleria elegans* (*Carlquist 15668*, RSA).—14. Transection. Pores are in radial chains.—15. Tangential sections. All rays shown are multiseriate.—16–20. Perforation plates from radial sections.—16. Plate traversed by one bar, portion of a second.—17. Arc of wall material across plate.—18. Plate bearing three bordered bars.—19. Aberrant plate at left; scalariform perforation from metaxylem at right.—20. Plate bearing pitlike perforations. (Fig. 14–15, magnification scale above Fig. 1; Fig. 16–20, scale above Fig. 3.)
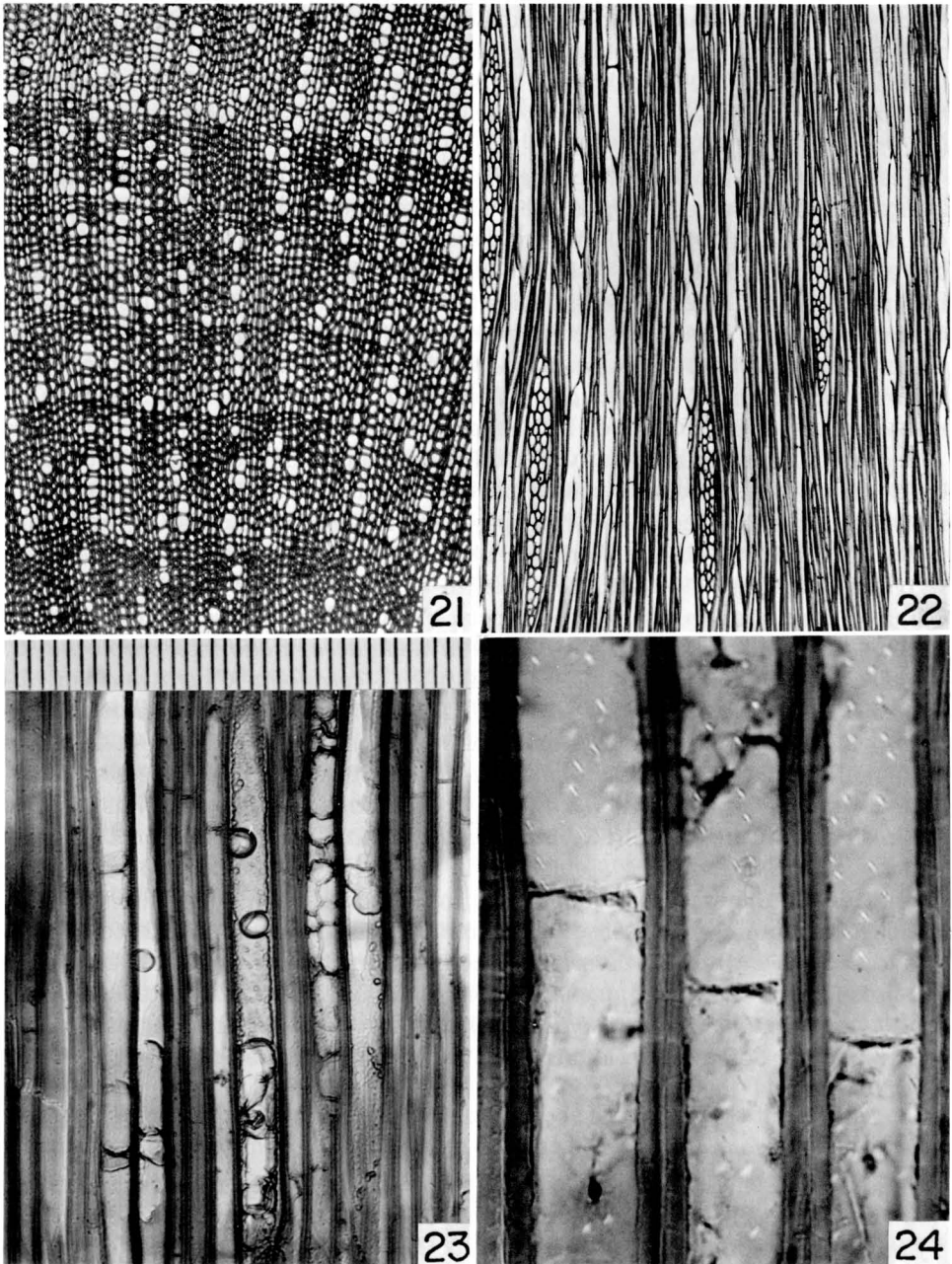
Fig. 21–24.   Wood sections of *Rhabdothamnus solandri* (*FPRIw 6830*).—21. Transection. Pores are especially narrow.—22. Tangential section. Multiseriate rays are present.—23. Radial section, showing tyloses, some of which are outlined by deposits of gummy material.—24. Septate fibers with simple pits from radial section. (Fig. 21–22, magnification scale above Fig. 1; Fig. 23, scale above Fig. 23 [divisions = 10 μm]; Fig. 24, scale above Fig. 3.)

reitzii (Fig. 4) and was also observed in *Cyrtandra urvillei*. Vessel-parenchyma and vessel-septate fiber pits are gaping rather more often, as was noted in *Chirita lavandulacea* (Fig. 3), *Cyrtandra kandavuensis, C. platyphylla, C. propinqua, C. rarotongensis, C. spathacea, C. victoriae, C. yaeyamae,* and *Rechsteineria reitzii* (Fig. 5).

Vessel-parenchyma and vessel-septate fiber pits are often much more laterally elongate than intervascular pits. This phenomenon is shown conspicuously by *Chirita lavandulacea* (Fig. 3), in which scalariform or pseudoscalariform pitting characteristically occurs on vessel walls. In this species, almost all vessel walls face parenchyma. Markedly elliptical pits, the alternate arrangement of which is evident but which sometimes verges on a scalariform pattern, were seen on lateral vessel walls of *Besleria* sp., *B. pauciflora* var. *uniflora, Columnea rubra, Cyrtandra anthropophagarum, C. cordifolia, C. filibracteata, C. harveyi, C. kandavuensis, C. rarotongensis, C. spathacea, C. urvillei,* and *Drymonia spectabilis.*

Because pit cavities are relatively isodiametric in intervascular pits but not on other vessel faces, measurement of pit cavity diameter was attempted only on intervascular pits. Species in which pit diameter falls in the 2.5–3.0 μm range include *Besleria* sp., *B. pauciflora* var. *uniflora, Cyrtandra ciliata, C. kandavuensis, Gesneria calycosa, G. duchartreoides, G. ventricosa, Kohleria elegans* (Fig. 16–20), and *Rhabdothamnus solandri.* Species in which intervascular pits average about 4 μm in diameter include *Chirita lavandulacea, Columnea purpurata, C. rubra, Cyrtandra* sp. (Kona), *C.* sp. (Tahiti), *C. cordifolia, C. grayana* var. *lanaiensis, C. harveyi, C. hornei, C. marthae, C. prattii, Rhytidophyllum auriculatum, R. crenulatum,* and *R. tomentosum.* Intervascular pits about 5 μm in diameter were recorded in *Cyrtandra anthropophagarum, C. filibracteata, C. gayana, C. lysiosepala, C. rarotongensis, C. spathacea,* and *C. urvillei.* Pits about 6 μm in diameter were found in *Cyrtandra platyphylla, C. propinqua,* and *Drymonia spectabilis.* The largest intervascular pits in the family were those of *Rechsteineria reitzii* (Fig. 4); they measure about 7 μm in diameter.

Helical sculpture in the sense of helical thickenings was not observed in Gesneriaceae. However, grooves interconnecting numerous pit apertures in a helix were seen in *Coronanthera pulchra, Gesneria calycosa, G. duchartreoides, G. ventricosa,* and *Rhabdothamnus solandri.* Short grooves interconnecting pairs of pit apertures were observed on lateral walls of vessels of *Kohleria elegans.*

Tyloses

Vessels of Gesneriaceae often contain tyloses. Where present, these are small, numerous, and very thin walled, as shown for *Rhabdothamnus solandri* (Fig. 23). Tyloses of this sort were also observed in *Columnea purpurata, C. rubra, Cyrtandra anthropophagarum, C. gayana, C. harveyi, C. hornei, C. marthae, C. urvillei, C. yaeyamae, Rhytidophyllum crenulatum,* and *R. tomentosum.*

Imperforate Tracheary Elements

In most Gesneriaceae, the imperforate tracheary elements can be termed libriform fibers because they bear simple pits (Fig. 24). In *Coronanthera pulchra,* however, vestigial borders characteristically occur on pits, so fiber-tracheids must be claimed for that species.

Septate fibers are cited for the family by Metcalfe and Chalk (1950). This was confirmed on the basis of the present study for all species except *Chirita lavandulacea, Cyrtandra yaeyamae,* and *Rechsteineria reitzii.* There is a possibility that septa in libriform fibers of these species might have been destroyed by treatment with ethylene diamine. This possibility is cited because septa were not observed in a portion of wood of *Kohleria elegans* treated with ethylene diamine, whereas they were seen in a portion from the same collection sectioned without ethylene diamine treatment. The fiber-tracheids of *Coronanthera pulchra* are septate.

Septate fibers in Gesneriaceae may be abundant, occurring throughout the wood of a species, or they may be present only immediately around vessels, with nonseptate fibers present farther away. Abundant septate fibers were observed in *Besleria* sp., *B. pauciflora* var. *uniflora* (Fig. 2), *Columnea purpurata, Coronanthera pulchra, Drymonia spectabilis* (Fig. 13), *Gesneria calycosa, G. duchartreoides, G. ventricosa, Kohleria elegans, Rhabdothamnus solandri* (Fig. 24), *Rhytidophyllum auriculatum, R. crenulatum,* and *R. tomentosum.*

Septate fibers only around vessels were observed in all species of *Cyrtandra* (Fig. 7, 8). Septate fibers are very few in number in some species of *Cyrtandra.*

Starch in septate fibers was observed in *Kohleria elegans.* Starch may have been present in wood samples of other Gesneriaceae but lost during treatment prior to sectioning.

Dimensions of imperforate tracheary elements are given in Table 1. Imperforate tracheary elements in most dicotyledons have a diameter of between 20 and 30 μm, walls included, at their widest point. Imperforate tracheary elements in this size range can be found in Gesneriaceae, as in *Drymonia spectabilis* (Fig. 10, 11, 13) and *Rhabdothamnus solandri* (Fig. 21, 22, 24). However, many Gesneriaceae have imperforate tracheary elements in excess of 30 μm in diameter, a few in excess of 40 μm. The genus *Cyrtandra* is especially noteworthy in this regard (Fig. 6, 7, 8). Relatively wide fibers are also illustrated here for *Besleria* (Fig. 1, 2) and *Kohleria* (Fig. 14, 15).

Imperforate tracheary elements mostly range between 1.2 and 1.5 times as long as vessel elements in the various species of Gesneriaceae. Notably long libriform fibers for the family were observed in *Besleria pauciflora* var. *uniflora, Cyrtandra* sp. (Kona), and the three species of *Gesneria.* Notably short libriform fibers for the family are reported for *Cyrtandra rarotongensis* and *Kohleria elegans* (Fig. 15).

Imperforate tracheary elements in Gesneriaceae are relatively thin-walled compared with those of many dicotyledons. In no species of Gesneriaceae was wall thickness of imperforate tracheary elements more than 4 μm. Relatively thick-walled imperforate tracheary elements (for the family) characterize the species of *Coronanthera* and *Gesneria.* There is a range in wall thickness of libriform fibers in *Cyrtandra,* but thin walls predominate (Fig. 6, 7). Notably thin walls on imperforate tracheary elements characterize *Besleria* sp. (Fig. 1, 2) and *Drymonia spectabilis* (Fig. 10, 11, 13).

Vascular tracheids were reported by Metcalfe and Chalk (1950) for Gesneriaceae, no genera specified. No such cells were found in the present study of Gesneriaceae, despite attention paid to these cells during a recent survey of vasicentric tracheids (Carlquist 1985), which includes reports of cells termed vascular tracheids by various authors. Possible reasons for the contradiction in report of this cell type in Gesneriaceae are given below.

Axial Parenchyma

Axial parenchyma is not common in any species of Gesneriaceae studied. Where present, it takes the form of one to several cells (as seen in transection, which in longisection consist of vertical strands of two or three cells each), adjacent to vessels. Vasicentric scanty parenchyma of this type was observed in all Gesneriaceae studied with the exception of *Columnea purpurata, Cyrtandra kandavuensis, C. prattii,* and *C. spathacea.* Axial parenchyma cells facing a vessel wall are illustrated for *Rechsteineria reitzii* in Figure 5. The species with axial parenchyma cells most abundant are *C. yaeyamae* and *Kohleria elegans,* but even in these species axial parenchyma cells are so scarce that they do not appear in the tangential section shown in Figure 7.

Vascular Rays

Ray presence in Gesneriaceae can be described under three categories: (1), both multiseriate and uniseriate rays present; (2), multiseriate rays only present; (3), rayless. These three categories are evident from Table 1, in which figures are shown for multiseriate and uniseriate rays where they are present in appreciable numbers (uniseriate rays are not common in any species of Gesneriaceae, however).

Both multiseriate and uniseriate rays characterize the genera *Columnea, Coronanthera, Gesneria, Kohleria* (Fig. 15), and *Rhabdothamnus* (Fig. 22). Uniseriate rays are moderately abundant only in *Columnea, Coronanthera,* and *Kohleria;* in other genera data on uniseriate rays are based on 15 or fewer measurements.

Multiseriate rays exclusively were observed in the older stems of *Drymonia spectabilis* (Fig. 11), *Rechsteineria reitzii, Rhytidophyllum crenulatum,* and the majority of species of *Cyrtandra,* such as *C. yaeyamae* (Fig. 7).

Rayless wood is characteristic of *Besleria* (Fig. 1, 2), *Chirita,* and a scattering of species of *Cyrtandra,* such as *C. lysiosepala* (Fig. 8). To characterize particular species as rayless or with multiseriate rays only would be misleading, however. Study of large stems of *Cyrtandra* in which a sequence from pith to cambium was complete invariably revealed that woods of *Cyrtandra* begin rayless. Multiseriate rays are innovated soon; one cannot say how soon because growth rings are lacking in *Cyrtandra.* The multiseriate rays become wider and taller with age. Thus the species of *Cyrtandra* with notably tall rays (Table 1) also have wide rays, and these species are represented by older wood samples than are those species with smaller rays.

Ray height is not in proportion to ray width in *Drymonia spectabilis.* In this species, which is a vine, rays are extremely tall (Fig. 11). The figure specified in Table 1 is essentially based on the size of sections, and represents a minimal size; few rays were represented completely within the confines of a single tangential section.

Rays, where present in Gesneriaceae, typically consist of upright cells. A few procumbent cells were observed in rays of *Cyrtandra* sp. (Tahiti), *C. gayana, C. kandavuensis, C. rarotongensis, C. spathacea, C. yaeyamae* (Fig. 7), *Drymonia spectabilis* (Fig. 11), *Rhabdothamnus solandri* (Fig. 22), and *Rhytidophyllum crenulatum.* In no species are procumbent cells more abundant than erect cells. Procumbent cells do tend to be restricted to central portions of multiseriate rays.

Erect cells are not merely at the margins of rays, but throughout rays. Ray cells have relatively thin but lignified walls (Fig. 7, 9, 11, 15, 22).

Crystals and Other Substances

Small rhomboidal crystals in ray cells were observed in *Cyrtandra lysiosepala* (Fig. 9), *C. rarotongensis,* and *Rhytidophyllum crenulatum.*

Small and inconspicuous crystals, several per cell, were observed in septate fibers in *Besleria* sp., *Coronanthera pulchra,* and *Columnea purpurata.*

Deposits of gummy substances could be observed in some wood sections. These are illustrated in the radial section of *Rhabdothamnus solandri* (Fig. 23).

Storied Structure

If one views tangential sections of Gesneriaceae, one sees weak storying in a few instances (e.g., Fig. 8, right). In *Drymonia spectabilis* storying is clearly present in some places in older stems (Fig. 11, to right of ray).

<div align="center">CONCLUSIONS</div>

Raylessness and Habit

The genera in which uniseriate rays are relatively common (*Columnea, Coronanthera,* and *Kohleria*) do not show any indications of any but a woody ancestry. These genera do show abundance of erect cells in rays, suggesting a degree of paedomorphosis, but procumbent cells are also present.

In *Besleria, Chirita, Cyrtandra, Drymonia, Rechsteineria,* and *Rhytidophyllum,* woods are rayless or with multiseriate rays exclusively. As noted above for *Cyrtandra,* species in which wood of stems begins rayless acquire multiseriate rays soon during secondary growth; the proportion of procumbent cells also increases over time, beginning with no procumbent cells. Production of rays in woods that begin rayless was signalled by Barghoorn (1941). Rayless woods typically occur in taxa that seem to be secondarily woody (Carlquist 1970). An exception to this is provided only by annual species of *Phacelia* (Carlquist and Eckhart 1984). These species, however, have tall upright stems and raylessness may be related to an evolutionarily rapid acquisition of greater mechanical strength in this phylad.

The fact that imperforate tracheary elements (libriform fibers except for *Coronanthera*) are relatively wide and thin walled compared with those of other dicotyledons may relate to the limited woodiness of the family: selection for mechanically strong wood by production of thick-walled fibers evidently is not pronounced.

The vining habit of *Drymonia* is reflected in its wide mean vessel diameter, which is not coupled with a correspondingly low number of vessels per mm^2, so that the conductive area per mm^2 is greater than in nonvining species. This is in accordance with earlier findings about wood anatomy of vines (Carlquist 1975). The prominence of the multiseriate rays in *Drymonia*—they are by far the tallest in the family—is also characteristic of vines.

Histological Features

Septate fibers characterize nearly all Gesneriaceae, in accordance with the report by Metcalfe and Chalk (1950). However, the mode of occurrence of septate fibers

in *Cyrtandra*—adjacent to vessels only—is distinctive. Noteworthy in this regard is the absence of axial parenchyma from three species of *Cyrtandra*; axial parenchyma is scarce in the other species. Septate fibers, which can be assumed to have prolonged longevity compared to nonseptate fibers (Wolkinger 1969), may represent a kind of substitute for axial parenchyma. Axial parenchyma is scarce or absent in the other families listed by Wolkinger (1970) as having septate fibers. Wolkinger (1970) reports living fibers for Gesneriaceae.

The scalariform and pseudoscalariform pitting of certain Gesneriaceae, notably *Chirita lavandulacea,* may relate to paedomorphosis (Carlquist 1962). Wide, "gaping" pit apertures on lateral wall pits of vessels can also be cited in this regard. Both features seem indicative of probable low mechanical strength of the woods in which they occur.

The few multiperforate perforation plates observable in wood of *Kohleria elegans* require explanation. Are they merely an aberrant occurrence, or are they the vestige of an ancestrally scalariform condition? The latter explanation appears likely if we view the compilation on primary xylem of dicotyledons by Bierhorst and Zamora (1965). They list 22 genera of Gesneriaceae in which vessels with scalariform perforation plates occur in primary xylem. In all of these examples, tracheids as well as vessel elements with simple perforation plates occur intermixed with the vessel elements with scalariform perforation plates. The interpretation that appeals as the most likely is that the primary xylem is, as Bailey (1944) regarded it, a refuge of primitive features. Vessels with scalariform perforation plates are, in Gesneriaceae, restricted to primary xylem, and even there vessels with simple perforation plates may be said to have supplanted some of them. This distribution is also reported for Scrophulariaceae by Bierhorst and Zamora (1965). The scalariform perforation plates of *Kohleria elegans* may be regarded as an extension into the primary xylem of the scalariform pattern—perhaps a minor instance of paedomorphosis. Note should be taken that Bierhorst and Zamora confused Bailey's refugium concept (specialized characters originating in secondary xylem, so that the primary xylem becomes a refugium for primitive features) with my paedomorphosis concept (in particular groups, notably those with an herbaceous ancestry, the primitive primary xylem characteristics are secondarily introduced into secondary xylem, a process permitted by altered ontogeny). Paedomorphosis is also reflected in Gesneriaceae in the abundance of erect ray cells in various genera and in the relatively long vessel elements and libriform fibers of *Chirita lavandulacea.*

Although tracheids occur in primary xylem of 21 genera of Gesneriaceae according to Bierhorst and Zamora (1965), there are no tracheids in secondary xylem of Gesneriaceae. The occurrence of fiber-tracheids in *Coronanthera pulchra* may be regarded as a relictual feature of minor degree. Evolution of septate fibers in a phylad of dicotyledons is apparently accompanied by rapid loss of borders from pits of imperforate tracheary elements (Carlquist 1984). Presence of uniseriate rays along with multiseriate rays in *Coronanthera* should also be regarded as a primitive expression, based on the considerations of Kribs (1935). Thus, the rayless species of Gesneriaceae can be cited as more specialized; some of them remain rayless indefinitely, some of them develop multiseriate rays as the cambium continues to function, but none of them develop uniseriate rays (or, if uniseriate rays can be found, they are of such infrequence as to be lacking in interpretative significance).

Vascular tracheids, reported for Gesneriaceae by Metcalfe and Chalk (1950), are absent according to the present study. Possibly what those authors observed were interfaces between lateral vessel walls and libriform fibers. Such interfaces, in longitudinal sections, appear as a zone of densely placed bordered pits within the confines of a fusiform cell, but examination reveals that portions of adjacent cells are, in fact, involved. Macerations of wood of Gesneriaceae reveal no instances of imperforate tracheary elements with pits characteristic of tracheids. Moreover, vascular and vasicentric tracheids are quite unlikely to be associated with such mesic ecology as Gesneriaceae typify (Carlquist 1985).

Ecology

Mesic habitats can experience brief dry periods; cold can occur in the habitat of at least one genus of Gesneriaceae (*Rhabdothamnus*). Therefore, the occurrence of a few very mild indicators of xeromorphy in the family would not be unexpected. Helical sculpture shows association with both drought and cold (Carlquist 1983); cold can be regarded as producing the physiological equivalent of drought. In Gesneriaceae, helical sculpture (grooves interconnecting pit apertures on vessel walls) occurs in *Coronanthera pulchra, Gesneria calycosa, G. duchartreoides, G. ventricosa, Rhabdothamnus solandri,* and *Rhytidophyllum crenulatum.* The last of these occurs in areas of New Zealand where frost can occur to a limited extent (Allan 1961). The others occur in cloud forest scrub that can experience brief seasonal drought. Conforming the interpretation of helical sculpture as indicative of mild xeromorphy is the low Mesomorphy ratio figure for these species (Table 1). However, one should stress that even these figures are not low by standards of dicotyledon groups in dry habitats (e.g., see Carlquist and Hoekman 1985). The lowest figure for the family is that for *Rhabdothamnus solandri.* The narrow vessels and high number of vessels per mm^2 in this species correlate with its habitat, which represents the furthest entry into a temperate zone for a woody representative of the family. The figures for Mesomorphy are more predictive of ecology than are the figures for Conductivity. Conductivity, based on the Hagen-Poiseuille equation, essentially predicts conductive ability of cylindrical structures. Thus Conductivity would be numerically applicable to situations such as the vascular system of animals, or the pipe system of a building. In these situations, there is no redundancy. However, vessel size and abundance in wood represent not merely conductive efficiency, but conductive efficiency compromised by various degrees of safety. Woods with narrow vessels have great safety at the expense of some conductive efficiency, for example. They would have a low figure for Conductivity, but that low figure would be misleading if one failed to realize that the wood was not poor at conduction (which it would not be) but rather high in safety. The Hagen-Poiseuille equation is also not applicable to woods without other modifications. Vessels are not indefinite in extent, as are blood vessels which form a circular conductive pattern. Rather, vessels are of various lengths in vessel-bearing plants; in some plants they extend nearly the length of the plant, in others they are only a few vessel elements long. The terminations of the vessels form obstacles to passage of water. Other factors, such as the degree to which vessels in a wood do or do not form interconnecting networks (compensating for the blockages imposed by the terminations of vessels) would be relevant. If Conductivity were to be a predictive measure either in terms of conductive ability or

ecology where vessels of plants are concerned, the equation would have to be modified by means of regressions in order to weight the modifying factors cited above. The figure Mesomorphy is based on data similar to that for Conductivity, and can be criticized as limited in applicability. It has the merit of being based on figures readily available to plant anatomists, and the numerical range of Mesomorphy values for wood of various taxa of dicotyledons is very much like the range for ecological factors such as rainfall for those taxa, respectively.

Relationships

Wood of Gesneriaceae is characterized by the following features. Vessels are circular in transectional outline, grouped to a limited extent, often in radial chains. Perforation plates are simple. Lateral wall pitting consists of alternate circular or polygonal elliptic bordered pits 2.5–7 μm in diameter. Helical sculpturing is present in the form of grooves interconnecting two or more pit apertures in a helix. Thin-walled tyloses are often present. Imperforate tracheary elements are libriform fibers, or exceptionally, fiber-tracheids with vestigial pit borders. Imperforate tracheary elements are all septate (often with two septa) or septate only near vessels with nonseptate fibers more distal to vessels. Vascular tracheids and vasicentric tracheids are absent. Axial parenchyma is vasicentric scanty, quite infrequent or absent in some taxa; strands are typically two to three cells. Rays are multiseriate plus uniseriate, multiseriate only, or rays are absent. Ray cells are mostly erect; procumbent cells are confined to the central portions of multiseriate rays. Rays have thin lignified walls bearing simple pits. Crystals are present to a limited extent in rays and in septate imperforate tracheary elements. Amorphous deposits are often present. Storying occurs in a few taxa.

If one compares the above description to features listed for Acanthaceae and Scrophulariaceae (e.g., Metcalfe and Chalk 1950), one finds near-identity with features or ranges of features in Gesneriaceae. Acanthaceae has pits simple only on imperforate tracheary elements, and no helical sculpture is reported in vessel elements, but these features occur in a minority of Gesneriaceae. In Scrophulariaceae, some taxa do have fiber-tracheids, the remainder have libriform fibers; helical sculpture is present in vessels. Because some Scrophulariaceae occur in habitats much drier than those occupied by Acanthaceae and Gesneriaceae, a higher degree of xeromorphy in woods of the former family is to be expected. In this connection, one notes that vascular tracheids occur in woods of some Scrophulariaceae (Michener 1981). Raylessness occurs in a few genera of Scrophulariaceae, such as *Calceolaria* (Michener, unpublished), and in some Acanthaceae, such as *Jacobinia* (Carlquist 1970) and *Beloperone* (Carlquist and Hoekman 1985). Septate fibers are found in a scattering of genera in both Acanthaceae and Scrophulariaceae. The three families do not really differ at all in qualitative features present, they merely differ in the proportion of species that have particular xeromorphic or mesomorphic expressions of those features.

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